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THE EFFECTS OF AGE ON THE BREEDING BIOLOGY AND RECRUITMENT OF THE HERRING GULL

(*LARUS ARGENTATUS*)

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ABSTRACT

Previous extensive ringing and the cull of Herring Gulls between 1972 and 1974 on the Isle of May by the Nature Conservancy Council facilitated an investigation of the effects of age on the breeding and recruitment of this gull species. Median laying date increased with increasing female age, four year old birds laid 11 days later than the colony median laying date, five year old gulls advanced their laying by six to nine days and laying dates progressively advanced up to the seventh year of life. Clutch size increased with the age of females. For four, five, six and seven year old birds mean clutch sizes were 1.71, 2.18, 2.43 and 2.74 eggs per female. Although clutch size decreased as the season progressed, in any time period the largest clutches were laid by the oldest birds. For all eggs laid regardless of clutch size, egg breadth and volume increased with age of the laying female. The seasonal decline in egg volume was not solely attributable to recruits laying later since four and five year old gulls laid smaller eggs than older birds regardless of the time of laying. Hatching and breeding success both increased with parental age. A large proportion of chicks raised by inexperienced breeders died within the first 10 days after hatching. This component of chick mortality was attributable to inadequate reproductive behaviour by inexperienced birds. Most four and five year old gulls nested at low densities and there was some evidence to suggest that breeding success may decrease at the highest nesting densities.

The colony of Herring Gulls on the Isle of May has been increasing at about 13-14% per annum since 1950. This rate of increase is similar to other Herring Gull colonies elsewhere in Britain. Using the survival of gulls ringed as adults prior to the cull, the average annual survival rate is estimated as 0.935 ± 0.100 and the survival rate in the first year of life

was calculated as 0.83, 0.83 and 0.67 in three successive year classes. Prior to culling, the Isle of May was a dense colony and although some three year old gulls held territory, none bred. Some four year old gulls held territories and bred, although the proportion was low. It is estimated that the mean age of recruitment was 5.00 years and that the mean age of first breeding was 5.25 years, with 55% of birds breeding for the first time when five years old. Some individuals probably do not breed until they are seven years old. There was no evidence of differences in the age of recruitment of male and female Herring Gulls. Calculations based on the life-table of the Herring Gull and the number of marked recruits recovered during the cull lead to the conclusion that approximately 70% of the surviving young did not return to breed at their natal colony. Young reared on the Isle of May have been found nesting up to 250km away. Of these recruits which returned to nest on the Isle of May, 66% nested close to their place of birth. Males showed a greater tendency to return to their natal area than females, and this was evident both amongst those birds nesting on the island and through a higher proportion of females emigrating into other colonies. Clearing experiments suggested that recruitment was influenced by the density of breeding birds. Recruits were attracted to dense, undisturbed areas but they had much greater difficulty in establishing a territory there. A comparison of pre- and post-cull age structure on the island indicated large increases in recruitment pressure from gulls in their third, fourth and fifth years of life as a result of culling.

From culled samples of known aged birds it was evident that body weight increased with age in both males and females. Body weight differences were correlated with increasing weights of *Pectoralis major* flight muscle, but not with overt visceral fat storage. Thus the breeding performance of recruits may have had both a physiological as well as a behavioural component.

In mid-May recruit gulls had smaller brood patches and males had undeveloped testes in comparison to established breeders. On previously culled areas, recruits had significantly larger brood patches, a result of the greater ease of establishing territories by these birds on partially cleared breeding areas.

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SECTION ONE INTRODUCTION

The dynamics of colonially nesting seabird populations have been the subject of study by many ecologists. It has become evident, as a result of these studies, that one of the distinctive characteristics of many seabird species is that there may be a relatively long interval between fledging and breeding for the first time, which may be regarded as a period of deferred maturity. Although deferred maturity also occurs in some land birds, for example in Spanish Imperial Eagles* (Valverde 1960), it is particularly marked in seabirds. Most sulids do not breed until five years old (Nelson 1970); Puffins and Short-tailed Shearwaters breed in their fifth or sixth years of life (Petersen 1977, Serventy 1967); Adélie Penguins breed for the first time between the ages of three and eight years (Ainley 1975); and in Sooty Terns, the period of deferred maturity may extend for nine years (Harrington 1974).

Wynne-Edwards (1962) noted that deferred maturity in seabirds is often associated with relatively low rates of reproduction and mortality once adult life is reached. He suggested that these factors were interrelated and that ..... "they (deferred maturity and low reproductive rates) had evolved in unison, through the process of group selection, in order to enhance the homeostatic control of recruitment and loss, in populations of long lived species" (1962, p. 565).

Wynne-Edwards argued that populations were able to control recruitment rates by holding back a reserve of full grown adolescents and virgin adults which were only admitted to breeding status when the circumstances allowed. Central to this argument is the suggestion that there exists a surplus of non-breeders which, although they may be physiologically capable of breeding, have been excluded from the breeding

* Scientific names of species are listed in Appendix 1.

population due to their inability to compete successfully for nesting sites. This pool of potential recruits, Wynne-Edwards believed, consists mainly of young birds which have never bred before.

An alternative explanation of deferred maturity has been advanced by Lack (1954, 1966) and Ashmole (1963). Both authors suggested that the individual birds in a population are adapted to rear the greatest possible number of young under prevailing conditions. Lack (1954, 1966) argued that breeding imposes a strain on the parents. In slowly maturing species, this may prove to be an excessive demand upon the resources of younger individuals whose survival chances diminish if breeding is attempted too soon. In Lack's view, natural selection consequently retards the onset of maturity in order that sufficient bodily reserves or "stamina" (1954, p. 63) are developed to cope with it.

Ashmole (1963) suggested that the stress imposed on younger breeders was mediated by competition pressure for food during the breeding season. Younger birds could not obtain sufficient food to raise a brood to independence. Lack (1954, 1966) had also argued that food was the limiting factor in many bird populations, although his general contention was that food availability outside the breeding season was critical.

Despite their divergent views regarding the ultimate causes of deferred maturity, both Wynne-Edwards (1962) and Ashmole (1963) recognised the importance of the length of the period of deferred maturity in determining recruitment rates and hence the rates of population growth or decline. If all other population parameters are constant, then increases in the period of deferred maturity would be expected to decrease the rate of recruitment. Variations in the length of time over which maturity is deferred might be interpreted as adaptive strategies in response to a changing food supply (Lack's view) or to numerical and behavioural changes in the resident breeders at a colony (Wynne-Edwards' view).

There is to date relatively little conclusive evidence to support the ideas of either Wynne-Edwards or Lack; indeed there is little information regarding the factors important in producing variations in the extent of deferred maturity for seabird species. Similarly, there is little information concerning other factors which may be important determinants of the rates at which seabirds recruit into breeding colonies.

Harrington (1974) studied a breeding colony of Sooty Terns in which the youngest breeding birds were four years old; most Sooty Terns did not breed until they were at least five years old. He observed regular colony visitations by two and three year old birds, but these "adolescents" were prevented from landing at the colony and establishing nesting sites by the aggressive behaviour of the resident breeding adults. Although these results lend support to the idea of socially determined recruitment rates advanced by Wynne-Edwards, Harrington presented no evidence to suggest homeostatic variations in recruitment rates.

Brown (1969), in reviewing the evidence for the regulation of population size by territorial behaviour in birds with Type A territories (species in which the same territory is used for feeding, mating and nesting Nice 1941, 1943), concluded that experiments, in which all or a proportion of the breeding population were removed, were necessary to demonstrate the presence of a non-breeding surplus of potential recruits. Such experiments have demonstrated the existence of a recruitment pool in Red Grouse (Jenkins, Watson and Miller 1963); Rock Ptarmigan (Watson 1965) and Dunlin (Holmes 1966). Less information exists for birds with Type C territories (where the foraging area is separate from the territory), which is the situation for most seabirds. Manuwal (1974) performed removal experiments of the type advocated by Brown on a population of Cassin's Auklets. On removal of known breeders, he found that burrows were rapidly taken over by mature birds, the majority (80%) of which did not have any previous breeding experience. Between 38% and 70% of these birds laid eggs on occupation of cleared burrows. A slightly different situation exists in the Shag. Removal of breeding adults (in this case due to the production of a neurotoxin by an outbreak of Protozoa of the genus *Gonyulax)* resulted in young birds (first breeders) occupying better quality nesting sites than they might otherwise have done. First breeding Shags at good quality nesting sites had a higher breeding success than first breeding birds at poor sites (Coulson 1971). The results of removing breeding adult Cassins's Auklets and Shags are not readily explained by the Lack-Ashmole interpretation of deferred maturity since recruits to cleared sites were capable of breeding or of improving their breeding performance. However, seabirds as a group differ widely in their ecology, and removal experiments on a wider variety of species with Type C territories may yield evidence to support the ideas of Lack and Ashmole.

There is some evidence to support the Lack-Ashmole hypothesis that young birds may not be able to acquire sufficient body reserves in order to attempt breeding. In some seabird species the efficiency of feeding behaviour in general and foraging skills in particular are known to increase with age and experience. An increase in feeding success with age has been reported for Sandwich Terns (Dunn 1972). In this species a significantly smaller proportion of plunge dives made by first winter birds (seven to nine months old) yielded prey than was the case for older birds. For Herring Gulls feeding on a rubbish tip, the number of food items eaten per bird per unit time was lowest in one year old birds and highest in birds older than three years. The feeding efficiency of Herring Gulls steadily increased between the ages of one and three years (Verbeek 1977). However, there is as yet no clearly established link between recruitment, age and feeding ability.

Another interpretation of deferred maturity has been advanced by Ainley (1975) who studied the reproductive capability of Adélie Penguins of known age. He found that non-breeding birds or birds breeding for the first time exhibited varying degrees of physiological immaturity (under-developed gonads, incompletely defeathered brood patches). Ainley advanced this as the most important proximate cause of deferred maturity and suggested that as Adélie Penguins mature the hypothalmic-hypophyseal endocrine system becomes more in phase with triggering environmental cues. Although Ainley discussed possible interactive mechanisms between pair formation, territorial behaviour and gonadal maturity (a measure of the ability to breed), he did not think such interactions were of importance in determining the age of first breeding.

The need to understand the population dynamics of seabirds has become evident from the results of the national census of seabirds breeding in Britain and Ireland undertaken by "Operation Seafarer" (Cramp, Bourne and Saunders 1974). The breeding populations of species such as Roseate and Sandwich Terns at some British colonies are in rapid decline. On the other hand, the populations of large gulls, Herring Gulls in particular, have shown explosive increases, so much so that these species have been, or soon will be, designated pest status. Excluding catastrophic events, long term changes in the size of breeding populations can only take place by changes in recruitment rate and pattern. An understanding of the recruitment process is thus an important step in establishing the causes of reported increases and declines in seabird numbers.

The research carried out in this study was concerned with a population of Herring Gulls breeding at an island colony (the Isle of May) off the south-east coast of Scotland. Herring Gulls in Britain are predominantly coastal breeders, the present large scale increases reported for British coastal colonies, particularly those on the east coast (Monaghan and Coulson 1977), point to an increase in environmental carrying capacity. The Herring Gull is catholic in its feeding habits and to a large extent is a scavenger of fishing, agricultural and urban organic waste materials. It has been variously suggested (Spaans 1971, Hunt 1972) that the present European and North American Herring Gull increase can be attributed to an increasing reliance upon artificially created food sources such as those made available by refuse tips and at fish docks.

Since the populations breeding at the majority of British colonies are increasing, it follows that the recruitment rate into these populations must also be increasing at a similar rate. Inherent in the arguments advanced by Lack (1954, 1966) and Wynne-Edwards (1962) is the possibility that as the carrying capacity increases, the period of deferred maturity might decrease. However, there are other determinants of recruitment rate that might have changed, apart from the period of deferred maturity. These include the productivity of the breeding pairs and an increase in post-fledging survival rates.

On the Isle of May there had been an extensive colour-ringing programme of pre-fledging Herring Gulls (see Parsons 1971a) and many of these ringed birds were breeding on the island over the 1972-74 period of this study. It was possible from sight records to investigate the age at which Herring Gulls breed for the first time. However, the age at which birds breed successfully for the first time, and the age at which they recruit into the population (i.e. establish a territory), need not necessarily be equivalent. There is a growing body of evidence to suggest that in some long-lived seabird species the breeding success of first time breeders is lower than that of established breeding adults at the colony. For example, studies on the Kittiwake (Coulson 1966), Arctic Tern (Coulson and Horobin 1976), Gannet (Nelson 1978) and Red-billed Gull (Mills 1973) indicate a close correlation between parental age and breeding success.

In terms of future population growth it is important to measure the age at which adults can contribute a significant number of fledged young to enter the potential pool of recruits. Little information exists regarding variations in breeding success with parental age in the Herring Gull. If breeding success in this species were to show a gradual increase as parental age increased, then the period of deferred maturity may be longer than previously suspected. In order to assess the period of deferred maturity a study was made of the breeding success of the colour-ringed nestlings that returned to breed as adults on the Isle of May (Section Three). It was also possible to monitor the overall productivity of the colony and compare this with previous estimates for the same and for different colonies. Thus the possibility that the increase in Herring Gulls recorded at British colonies might be due to an increase in breeding production could be assessed (Section Three).

By 1972 the breeding population of Herring Gulls on the Isle of May had increased so dramatically (Section Four) that the Nature Conservancy Council (N.C.C.) who administer this island as a National Nature Reserve felt it necessary to introduce extensive control measures against this species. From 1972 to 1977 yearly culls of Herring Gulls were carried out. The methods of culling are briefly described in Section Two, and the overall effectiveness of this series of culls has been recently described by Duncan (1978). The research carried out in this study spanned the three year period from 1972 to 1974 and thus coincided with the first three in the series of gull culls carried out on the Isle of May.

Since many of the birds culled had previously been ringed on known areas of the island as nestlings (Parsons 1971a), it was possible to evaluate some of the components of the recruitment process for Herring Gulls breeding on the Isle of May. From the cull recoveries of ringed birds it was possible to assess:

(i) the average age of recruitment and the variability in the age of recruitment (Section Four);

(ii) whether or not Herring Gulls returned to breed at the colony in which they were born (Section Four)and, once returned to the natal colony, whether or not they attempted to breed in the areas in which they were born (Section Five);

(iii) whether there were differences between different areas on the island in terms of their attractiveness to recruits (Section Five);

(iv) from the analysis of culled corpses whether there were any gross morphological or physiological differences between recruits and established adult breeders (Section Six).

In addition, since the culls removed many established territory-holding gulls, it was possible to test the Wynne-Edwards (1962) hypothesis that there is a pool of surplus non-breeders which are potentially capable of breeding as soon as there is a decrease in competition for nesting sites (Section Five).

In summary, the research carried out as part of this study attempted to quantify or at least indicate some of the important determinants of Herring Gull recruitment. Specifically it attempted to find out how recruitment takes place, and by comparisons with other studies whether there had been any noticeable changes in recruitment parameters within recent years. Such changes might account for the generally recorded increasing populations of this species.

SECTION TWO GENERAL METHODS

2.1 The Study Area

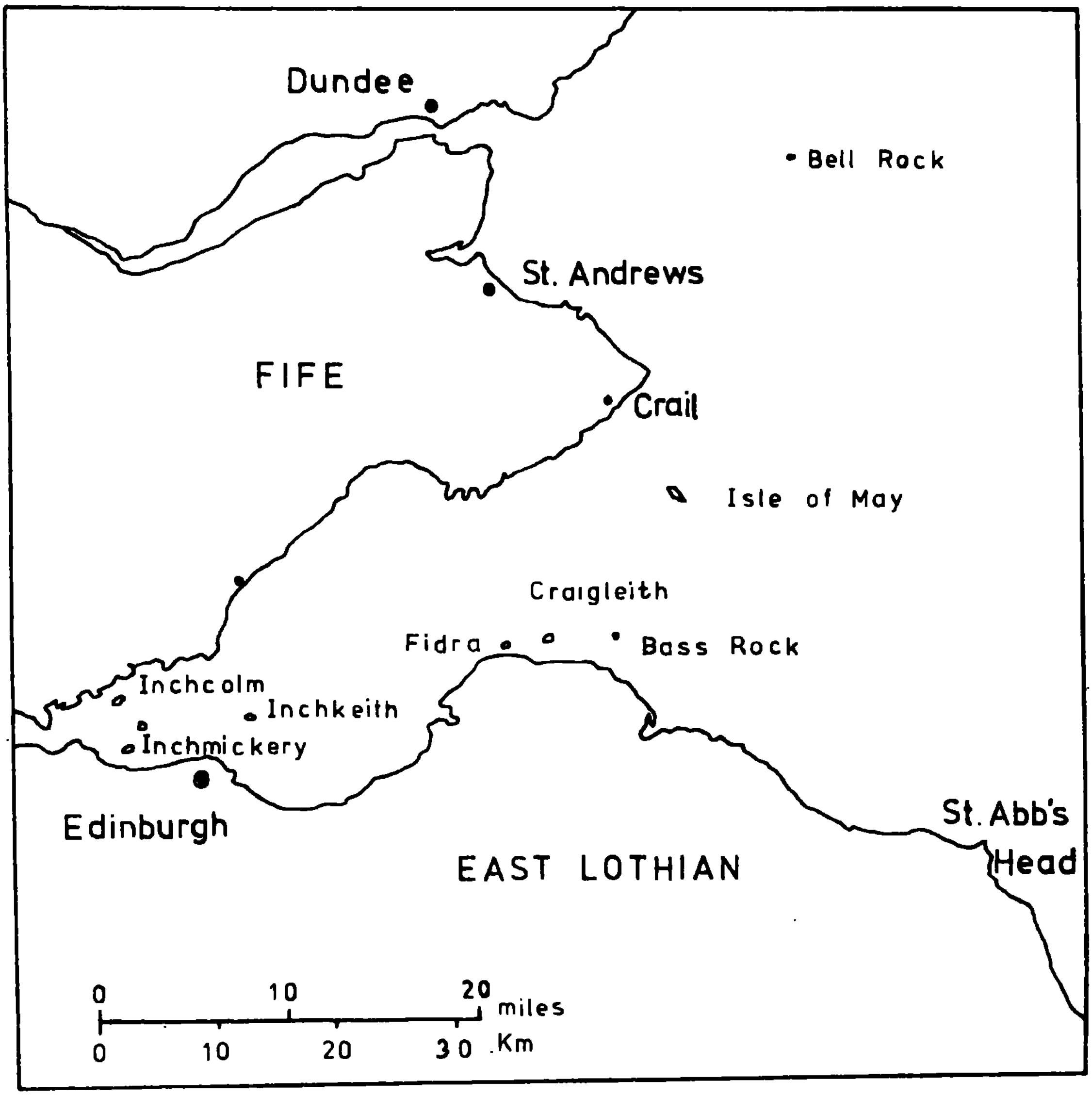
The Isle of May lies at the mouth of the Firth of Forth and is the first in a series of small islands that occur along the length of the firth (Figure 1). It is situated 10km south-east of the Fife coast and 18km north-east of the East Lothian coast (National Grid Reference : 655955) and is approximately 57 hectares in area (2km long and 0.5km at its widest point).

The island is composed of olivine-dolerite, a hard volcanic rock, outcrops of which are visible on much of the island surface. On its western side it is bounded by cliffs which at their highest reach 45m and the whole island slopes irregularly eastward to sea level. The soil cover on the Isle of May is thin, except in hollows and where soil has been artificially accumulated. There is an artificial loch, two usable wells and a number of semi-permanent pools, but no running water and no natural tree cover.

Both Lesser Black-backed Gulls and Herring Gulls breed over much of the island area although the highest densities of nesting Herring Gulls occurred on the shelving rock of the eastern coast and on the exposed rocks at the most northern and southern extremes of the island (North and South Ness, Figure 2). The number of breeding Herring Gulls on the Isle of May had steadily increased over a period of 65 years (Section 4.1) until in 1972 the Nature Conservancy (now the Nature Conservancy Council, N.C.C.) estimated the population to be approximately 17,000 breeding pairs (Anon. 1972). At the beginning of this study in 1972 Herring Gulls outnumbered Lesser Black-backed Gulls by about 10 to 1. On the whole, the distribution of breeding Lesser Black-backed Gulls was restricted to the more vegetated areas on the raised western (North and South Plateaus, Figure 2) and central regions of

Figure 1.

South-east coast of Scotland showing location of the Isle of May (National Grid Reference:655995).


Dundee
Bell Rock
St. Andrews
FIFE
Crail
Isle of May
Craigleith
Fidra
Bass Rock
Inchcolm
Inchkeith
Inchmickery
Edinburgh
EAST LOTHIAN
St. Abb's Head
0
10
20
miles
0
10
20
30
Km

the island, although the distribution of these two species overlapped considerably and Herring Gulls nesting on the western plateaus were by no means uncommon, whilst some Lesser Black-backed Gulls nested on the sea level rock of the eastern coast.

In addition to breeding populations of Herring and Lesser Black-backed Gulls, the Isle of May also supports large breeding populations of Kittiwakes, Fulmars, Shags, Guillemots, Razorbills, Puffins and Eider (see Appendix 2). The island's interest to ornithologists lies partly in this high diversity of nesting seabirds, but mostly is due to its reputation as a ringing station for passage migrants, the island having long supported a bird observatory and three Heligoland traps. Days of poor visibility and strong to moderate easterly or south-easterly winds in spring and autumn often result in displacement of many birds migrating to or from northern Europe from the normal north-south migration routes; some of these birds land and may become grounded on the Isle of May. Migrant species such as Wryneck and Great Grey Shrike are often caught and ringed under poor weather conditions. This, together with other aspects of the island's natural history, has been described by Eggeling (1960).

The Midlothian Ornithological Club established a bird observatory on the Isle of May in 1934. The island is owned by the Northern Lighthouse Board, although the bird observatory is maintained by the Isle of May Committee, on which the Scottish universities, ornithological clubs, the N.C.C. and Lighthouse Board are represented. The island was recommended as a Nature Reserve in 1949 and was subsequently declared a National Nature Reserve (N.N.R.) in 1956. Since that time nature conservation policies have largely been administered by the N.C.C.

Eggeling (1960) noted that the increasing number of breeding gulls (both Herring and Lesser Black-backed gulls) on the island have had serious adverse effects on some of the other bird species nesting on the N.N.R.

In particular he has documented the gradual decline of breeding terns as the gull population has increased. Common, Arctic, Sandwich and Roseate Terns were first recorded breeding on the Isle of May in the early nineteenth century. Sizeable colonies became established in the 1930s, and the tern population reached a peak in 1946 and 1947 with about 8,000 pairs breeding on the island (see Appendix 2). Since that time the numbers of breeding gulls have increased rapidly and gradually encroached upon and took over the terns' nesting areas. The principal reasons for the decline in numbers of nesting terns Eggeling attributed to the fact that the gulls establish territories one to two months before the terns arrive at the island and to increasing gull predation of tern eggs and chicks. The combined effect of competition for nest sites and of predation was to gradually push the terns to smaller and less suitable parts of the island. As a result, the numbers of breeding terns and their breeding success rapidly declined until 1958 when no terns nested on the island.

The vegetation of the Isle of May has most recently been described by Sobey (1976). The variety and interest of the vegetation was maintained, with little change, until the mid-1950s. Until 1956, when the N.N.R. was declared, the vegetation of the island was dominated by an extensive *Armeria maritima/Silene maritima* sward which grew on the island's thin peaty soil and formed a zone encircling the island. On the rockier ground between this belt and the western cliff edge the same species occurred in open communities of clumps and cushions which were associated with *Sedum anglicum* and *Cochlearia* spp. Towards the central parts of the island this sward merged with a grassy turf in which *Festuca rubra* and *Agrostis* spp. were important constituents.

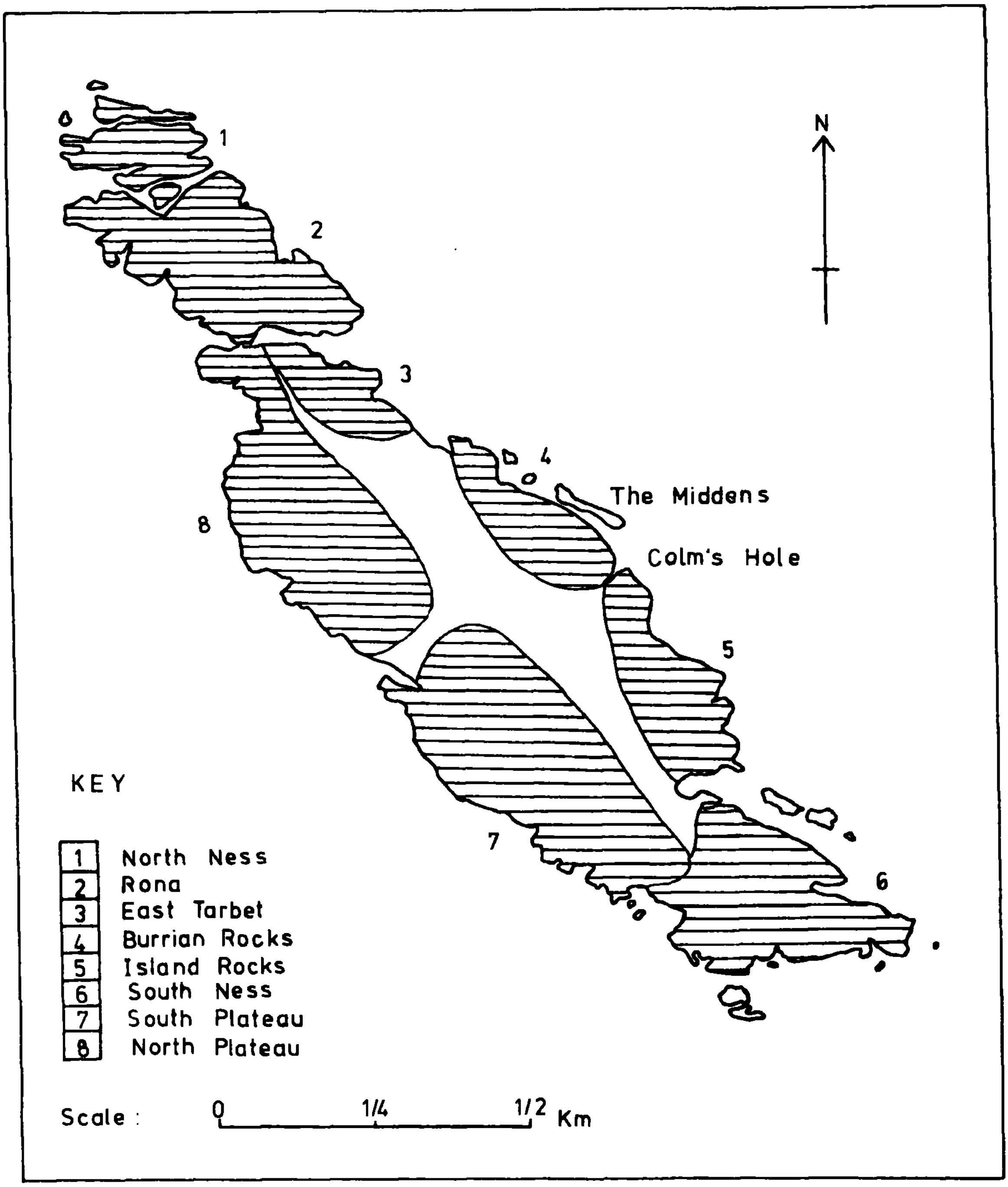
Since the 1960s the floristic character of the Isle of May has changed drastically, a change which has been largely attributed to the increasing numbers of breeding and roosting gulls (Anon. 1972, Sobey 1976).

As the numbers of breeding gulls increased there was an associated expansion of nesting range into the *Armeria/Silene* swards. Sobey noted that many of these swards had been eliminated by 1972 and that the *Sedum, Armeria* and *Festuca* communities had been largely replaced by communities dominated by *Holcus lanatus, Rumex acetosa, Rumex crispus, Stellaria media* and *Atriplex* spp. He suggested that the vegetational changes on the N.N.R. were directly attributable to the ever increasing amounts of vegetation uprooted by gulls in nest building and territorial behaviours (for example, Tinbergen 1953 described "grass-pulling" as a common displacement behaviour associated with territorial encounters).

The island may be divided into eight areas or 'sub-colonies' (Figure 2) on topographical characteristics. This sub-colony division of the Isle of May was made partly on the grounds that these eight areas formed convenient units of study and partly because two previous studies made by Parsons (1966-1969) and Emmerson (1970-1971) had distinguished between these areas in the ringing of chicks and adults. A deep east-west fault isolates an area of nearly nine hectares to the north of the island. This northern part is reached by bridge and contains two sub-colonies, North Ness, a low lying rocky outcrop, which is separated at high tide from Rona. A third sub-colony, East Tarbet, lies on the south eastern edge of this fault line. A further east-west fault separates the two high vegetated North and South Plateaus on the western side of the island and two predominantly rock areas on the east coast (Burrian Rocks and Island Rocks). The eighth sub-colony (South Ness) is situated on the southern tip of the island. South Ness, like its northern counterpart, is a shelving rock outcrop which at its southernmost tip is separated by high tide from the rest of the island.

Figure 2.

Sub-colonies on the Isle of May


1
2
3
4
5
6
7
8
N
The Middens
Colm's Hole
KEY
1 North Ness
2 Rona
3 East Tarbet
4 Burrian Rocks
5 Island Rocks
6 South Ness
7 South Plateau
8 North Plateau
Scale : 0 1/4 1/2 Km

2.2 Culling of Herring Gulls

In an attempt to arrest the gull-induced floristic changes occurring on the Isle of May, and also as a long-term strategy to re-introduce terns as a nesting species on the island in 1972, the N.C.C. implemented measures to control the rapidly increasing number of gulls on the island. These measures were principally directed at the Herring Gull population, although large numbers of Lesser Black-backed Gulls were also killed. The methods used have been described in detail by the N.C.C. (Anon. 1972). Essentially adult gulls were culled using the narcotic alpha-chloralose which had been mixed with soft margarine. The alpha-chloralose margarine mixture was spread on approximately 3 x 3cm squares of bread such that each contained a lethal dose of 200mg alpha-chloralose per Kg body weight of gull. From 1973 onwards, a barbiturate, quinalbarbitone (seconal), was added to the alpha-chloralose (35mg per bait) as this combination of narcotics had been found by the N.C.C. to have greater stupefying effects.

Narcotic baits were distributed over the cull areas, one bait being placed in each occupied territory. Most nests contained eggs at the time of culling, although nests without eggs were also baited. Territory holders disturbed by the baiting operation returned soon afterwards and the majority of baits were eaten by territorial gulls. Such birds would begin to succumb to the narcotic, or narcotic mixture, within 20 minutes. After initial baiting an area was left for at least three hours (sometimes overnight) before dead or drugged gulls were removed. All areas culled by the N.C.C. were baited at least twice in any one year. N.C.C. trials indicated that this form of control was most effective in mid- to late-May when the majority of egg laying had taken place and when gulls showed relatively high attachment to nest sites. Over the 1972-74 period, culling was carried out between 18-29 May 1972, 22-31 May 1973, 23-31 May 1974. A total of 45,916 baits were distributed on the Isle of May in these three years, which resulted in the recovery of 28,837 Herring and Lesser Black-backed Gulls from the island (figures supplied by Miss N. Gordon, N.C.C., Edinburgh). The great majority (approximately 90%) of these dead birds were Herring Gulls.

In 1972 all areas on the Isle of May except North and South Ness, Colm's Hole (Figure 2) and most of East Tarbet were culled by the N.C.C. In the following year the East Tarbet study area and the south-east edge of Rona (an area which had been culled in 1972) were the only areas in which a cull was not undertaken. In 1974 all areas, including the East Tarbet study area, were culled.

The numbers of Herring Gulls present on the entire island were counted before and after the 1972 cull and after the 1973 cull (pre-cull counts were made in April and early-May, and post-cull counting was in July, Table 40, Section 4.1 and Appendix 3). It was difficult to make precise counts on culled areas in July as few birds on these areas bred successfully (in June the N.C.C. removed eggs and chicks produced by birds which had escaped culling) and consequently attachment to nest site in territorial gulls was low. In addition, culled areas contained large numbers of prospecting recruits and these birds, like the resident territory holders, were easily disturbed. The numbers of gulls on each of the eight sub-colonies were counted between 16.00 hours and 20.00 hours at least four times, or until consistent counts for a sub-colony were obtained. Unlike the unculled study area (see Section 4.1), it was not possible to distinguish accurately between territorial or prospecting gulls using this method. In May 1972 there were an estimated 12,950 pairs of Herring Gulls on the island (Table 40, Section 4.1) and this total was reduced to 13,832 birds by July of that year. In July 1973 after a further cull, 8,870 gulls were counted (Appendix 3), so that two years' culling had reduced the numbers of Herring Gulls present on the island by 66%.

A more accurate measure of the effectiveness of the cull in reducing the breeding population is given by changes in nest density on the culled areas. Nesting densities on the various sub-colonies were compared directly by taking 50m line transects through nesting areas and determining the mean numbers of either occupied or partially built nests occurring within a 3m band along the transects. The eight sub-colonies varied in overall area (Figure 2, Table 55, Section 5.3) and the 50m transect was chosen as a convenient, albeit arbitrary, distance which provided a quick comparison between areas and caused the minimum of disturbance to gulls either breeding or attempting to establish territories. Transects were taken through the central and most densely occupied areas of each sub-colony. Five transects were taken in each culled sub-colony and the mean number of nests occurring per transect in July are given in Table 1.

Table 1. Densities of nesting Herring Gulls on five sub-colonies of the Isle of May before and after culling in 1972 and 1973

	Mean number of nests per 50m transect (± S.E.)*			
Sub-colony	Pre-cull May 1972	Post-cull July 1972	Pre-cull May 1973	Post-cull July 1973
Rona	17.8 ± 0.9	9.8 ± 1.1	11.4 ± 1.4	8.2 ± 0.6
North Plateau	14.0 ± 0.7	8.8 ± 0.9	10.2 ± 0.9	7.4 ± 1.0
South Plateau	9.6 ± 1.0	6.6 ± 0.5	7.0 ± 0.5	5.2 ± 0.9
Burrian Rocks	16.4 ± 0.8	9.4 ± 1.0	10.6 ± 0.9	7.8 ± 1.5
Island Rocks	15.4 ± 0.9	8.8 ± 0.7	9.6 ± 1.0	7.0 ± 0.8
Mean for culled sub-colonies	14.6 ± 0.7	8.7 ± 0.4	9.8 ± 0.5	7.1 ± 0.5

*S.E. = standard error

For the five sub-colonies persistently culled in 1972 and 1973 there were reductions in July nesting densities. In 1972 these ranged from 45% (Rona) to 31% (South Plateau), and in 1973 from 28% (Rona) to 26% (South Plateau and Burrian Rocks). For all five sub-colonies the cull resulted in a 40% reduction in nesting density in 1972 and a 28% reduction in 1973. This decrease in the effectiveness of culling was in part due to high post-cull recruitment rates to persistent cull areas (see Section 5.5). Also many gulls on these areas at the time of culling in 1973 were less advanced in the breeding cycle and showed noticeably lower attachment to territory than did birds on unculled areas. Gulls which had established territories but not laid eggs were easily disturbed by the culling operation and may have returned to resume breeding long after the period of culling.

The best estimate of the effectiveness of culling in reducing the number of breeding gulls on the Isle of May is given from a comparison of mean nesting densities before and after culls had taken place and from these figures (Table 1) it is evident that for the areas culled in 1972 and 1973 culling had reduced the number of breeding Herring Gulls by 50%.

2.3 Monitoring the Breeding Success

Various aspects of the breeding ecology of Herring Gulls were studied in the first two years of this study. In 1972 research was concentrated on gulls breeding on three study areas, Colm's Hole, East Tarbet and North Ness. Colm's Hole is a small area of approximately 4,000m^2 situated on the east coast of the island at the junction of the Burrian and Island Rocks sub-colonies (Figure 2). In 1973 studies were confined to the gulls breeding on East Tarbet, the only remaining unculled area on the island in that year.

Nests in the areas studied were marked with 25.4 x 2.5 x 0.6cm wooden stakes. Individual records for study nests were kept by numbering the marker stakes with waterproof felt pens. Nests were visited at two to three day intervals during May, when almost all egg laying took place, and eggs were marked with black felt pens according to laying sequence. The lengths and breadths of eggs were measured to 0.01mm using vernier calipers and the fate of clutches was followed until eggs hatched in June and July.

Upon hatching, chicks were marked as a, b, or c, according to whether they were first, second or third in the brood to hatch, by the use of different combinations of rings made from flexible coloured plastic insulation tubing, as described by Parsons (1971a). Pulli (pre-fledging young) were ringed with an individually numbered British Trust for Ornithology (B.T.O.) monel ring (11mm diameter, size G) as soon as the tarsus had grown sufficiently large to retain the ring without loss (usually one week after hatching). In addition, most pulli were colour-ringed with rings that were cut from 0.8mm thick sheets of I.C.I. Darvic plastic, as described by Coulson (1963). White and pale green Darvic rings denoted chicks hatched in 1972 and in the following year chicks were ringed with brown Darvic. The combinations of colour and B.T.O. metal rings used in one year denoted the age of parents (if known) and the area of birth.

In the course of this study it was necessary to catch and ring breeding adults. Adult birds were captured using the anaesthetic drug Avertin (tribromoethanol). Gelatin capsules containing 10g of Avertin were concealed in bread pellets. These pellets were placed at individual nests, and most site holders, on eating a drugged pellet, would become anaesthetised within 20-40 minutes. Recovery time varied, but most gulls recovered within one to two hours after drugging. Captured adults were ringed with a B.T.O. monel ring and an individual combination of three colour-rings.

Extensive colour-ringing of Herring Gull pulli and adults had been carried out in 1966, 1967, 1968 and, to a lesser extent in 1969 and 1970. Many of these birds bred on the Isle of May in 1972 and 1973. Study areas were regularly observed from the end of April to the end of July in both years, and territories established by pairs in which at least one member was colour-ringed (and therefore of known age) were marked with numbered stakes. In 1972, 141 territories belonging to known aged breeding gulls were staked together with a control group of 320 nests belonging to unringed birds in adult plumage (187 nests on East Tarbet and 133 nests on Colm's Hole). The distribution of territories established by colour-ringed gulls is given in Table 2.

The age of breeding gulls which had previously been ringed as adults was not known precisely, but most adults ringed by Emmerson in 1970, and many of the birds ringed by Parsons between 1966-1968, had been caught with the use of Avertin baits. This method was used for the capture of territorial gulls and since the evidence presented by this study suggests that most gulls do not breed before they are four years old, it was assumed that gulls were at least four years old on capture. Thus an adult ringed in 1970 and breeding in 1972 was at least six years old.

Table 2. The distribution of territories established by colour-ringed Herring Gulls on study areas in 1972

Study area	Year in which ringed as chicks 1966	1967	1968	Adults ringed 1966-70	Total
North Ness	29	19	6	6	60
East Tarbet	19	20	5	5	49
Colm's Hole	5	23	0	4	32
Total	53	62	11	15	141

In 1973, 61 territories belonging to colour-ringed birds and a control group of 264 nests were marked on the East Tarbet study area. Culling in both years resulted in many ringed gulls succumbing to the narcotic on or close to their nests. In 1973, wherever possible, the clutches of these culled birds were measured. These data were analysed together with those obtained from unculled ringed gulls. Laying sequence and date were determined from the extent of embryonic development. Usually two days after laying a network of blood vessels begins to develop around the embryo. This vascular development is clearly visible on the yolk surface as a disc of small radiating blood vessels (the area vasculosa) which gradually increases in diameter as incubation proceeds. At one week after laying the area vasculosa completely covers the yolk. In cases where the exact laying date was uncertain, the diameter of the area vasculosa was measured and the laying date was deduced from the area vasculosa growth curves given by Parsons (1971a). The difference between clutch sizes of culled and unculled birds is not significant ($\chi^2_{(2)} = 4.16$, $p > 0.05$), therefore the assumption that full clutches had been laid by the time of culling introduces only small error into subsequent calculations. The numbers of study nests belonging to culled and unculled Herring Gulls of known age are given in Table 3. Not all birds that established territories laid eggs, this being most marked in four and five year old gulls (Table 4).

Table 3. The numbers of territories established by colour-ringed Herring Gulls studied in 1973

	Year in which ringed as chicks					
	1966	1967	1968	1969	Adult-ringed	Total
Unculled (East Tarbet)	13	30	8	1	9	61
Culled (all areas except East Tarbet)	37	40	21	0	9	107
Total	50	70	29	1	18	168

Table 4. The number of Herring Gulls of known age that established territories* but did not lay eggs

Year in which ringed as chicks	1972			1973		
	Number of pairs in which one member was colour-ringed	Age of colour-ringed member of pair (years)	Number of territories in which no eggs were laid	Number of pairs in which one member was colour-ringed	Age of colour-ringed member of pair	Number of territories in which no eggs were laid
1969	0	-	0	1	4	1 (100%)
1968	11	4	4 (36%)	29	5	4 (14%)
1967	62	5	11 (18%)	70	6	5 (7%)
1966	53	6	3 (6%)	50	7	2 (4%)
Ringed as adults	15	> 6	0	18	> 7	2 (11%)

* (For territories established on study areas in 1972 and on study and cull areas in 1973)

It was the exception rather than the rule to find pairs in which both birds were colour-ringed. In all, nine pairs in which both the male and female were ringed were located; six of these pairs contained birds of the same age (three six year, and three five year old pairs). The remaining three pairs contained the following combinations of birds: six year old male and five year old female; five year old male and six year old female; adult-ringed female and six year old male. Throughout this study, in the absence of further information, it has been assumed that pair formation takes place between birds of the same age. Although this is evidently not always the case, there is evidence from birds aged on plumage characters that this was usually so. In eight out of the 11 pairs formed by ringed four year old birds, the mate of the ringed gull was four years old.

Plate 1. Marked study nest on East Tarbet

Plate 2. The East Tarbet study area in 1972

SECTION THREE BREEDING BIOLOGY IN RELATION TO AGE

3.1 Egg Laying

Egg laying in control groups

The patterns of egg laying for unringed control groups of adult Herring Gulls breeding on the East Tarbet study area in 1972 and 1973 are shown in Figures 3 and 4. In both years, the first egg was laid in the third week of April (25 April 1972 and 27 April 1973) and the last in the first week of June (4 June for both years). Thus in both years the range of dates over which clutches were started was very similar and the egg laying period of the breeding cycle spanned 38-40 days. There was no difference between median laying dates for gulls breeding on the East Tarbet and Colm's Hole areas in 1972, nor between gulls on East Tarbet in 1972 and 1973. In all these cases, 50% of clutches had been started by 16 May. This date was the same as the median date recorded for the Isle of May colony in 1969 (Parsons 1971a) and 1970 (Emmerson, unpublished). There has been little variation in the laying dates recorded for this colony since 1967, the range in medians being only two days from 16-18 May (Table 5).

Laying dates at other European colonies are given in Table 5. For some studies only the mean laying dates are known and to facilitate an easier comparison with these colonies the mean laying dates for East Tarbet are calculated to be 14 May 1972 and 17 May 1973 (Table 6). In general, the median date is more representative of majority egg laying than is the mean, since it is less influenced by late laying birds. For colonies where both mean and median laying dates are known it is notable that the median was usually earlier than the mean (Table 5).

Relative constancy of laying dates, from one year to the next, is also apparent for other colonies, with the exception of Kristiansand in Norway (where small samples were involved, Barth 1967a) and there was not

Table 5. A comparison of the dates on which clutches were initiated at various European Herring Gull colonies

Location of study	Latitude	Year of study	Number of nests	Mean laying date	Median laying date	Authority
Troms, Norway	69°42'	1964	95	17 May	-	Barth (1967a)
		1965	90	15 May	-	
		1966	93	16 May	-	
Tarva, Norway	63°48'	1955	32	6 May	-	Barth (1967a)
		1956	30	3 May	-	
Kristiansand, Norway	58°08'	1948	7	2 May	-	Barth (1967a)
		1954	3	7 May	-	
Priest Island, Scotland	58°01'	1937	65	15 May	14 May	Darling (1938)
Isle of May, Scotland	56°12'	1967	1,101	-	18 May	Parsons (1971a)
		1968	903	-	17 May	
		1969	400	-	16 May	
		1970	200	18 May	16 May	Emmerson (unpublished data)
		1972	187	14 May	16 May	This study
		1973	264	17 May	16 May	
Graesholm Island, Denmark	55°19'	1943	90	24 April	23 April	Paludan (1951)
		1944	87	24 April	22 April	
Walney Island, England	54°05'	1969	729	-	5 May	MacRoberts and MacRoberts (1972)
Skomer Island, Wales	51°45'	1962	297	5 May	4 May	Harris (1964a)
Skokholm Island, Wales	51°42'	1969	293	-	ca.10 May	Davis (1975)
		1970	366	-	ca.10 May	
		1972	224	-	ca.10 May	

Table 6. The effect of parental age on the date of egg laying for Herring Gulls breeding on the Isle of May in 1972 and 1973

(All dates are in May)

1972

Year of hatching	Age (years)	Number of pairs	Mean laying date ± S.E.	Median laying date	S.D.*
1968	4	5	29.3 ± 2.3	27	6.9
1967	5	51	20.8 ± 1.0	19	7.3
1966	6	50	17.2 ± 1.0	17	7.0
Ringed as adults	≥ 6	15	13.7 ± 2.0	12	7.7
Unringed sample East Tarbet	-	187	14.1 ± 0.7	16	9.8

1973

Year of hatching	Age (years)	Number of pairs	Mean laying date ± S.E.	Median laying date	S.D.*
1968	5	25	20.6 ± 0.8	21	4.2
1967	6	65	19.7 ± 0.7	19	5.3
1966	7	48	19.1 ± 0.6	20	4.0
Ringed as adults	≥ 7	16	16.6 ± 0.8	16	3.3
Unringed sample East Tarbet	-	264	17.0 ± 0.4	16	7.1

* S.D. = standard deviation

more than three days difference between either means or medians recorded at the same colony in different years. Such constancy has also been noted by Paludan (1951) for Herring Gulls breeding on the Christiansø group of islands off the Danish coast. The situation in Herring Gulls is thus similar to that in Gannets where peak laying varies little from one year to the next in a given locality (Nelson 1978).

For Norwegian Herring Gulls, Barth (1967a) commented upon the tendency for eggs to be laid later at northern colonies than at southern ones. This is in keeping with traditional theory regarding photoperiod and the timing of breeding seasons which predicts that birds at higher latitudes breed later than those at lower latitudes (Lack 1954). This trend is not as clear when the Danish and British data are added to those from Norway (Table 5). Thus the range of means recorded for the Isle of May (14-18 May) overlaps with those for the more northerly Norwegian colonies (2-17 May) and with that for Priest Island (15 May). Indeed, gulls at the Tarva (overall mean = 5 May) and Kristiansand (overall mean = 4 May) colonies bred earlier than birds on the Isle of May. In keeping with expectation, gulls at colonies to the south of the Isle of May bred earlier than those on the Isle of May (median laying dates on the Isle of May = 16- 18 May, median laying dates for the islands of Graesholm, Walney, Skomer and Skokholm = 22 April - 10 May). However, the much earlier breeding of gulls on Graesholm Island and the disparity in laying dates for Skomer and Skokholm Islands do not point to a simple relationship between latitude and laying date.

Some of the factors that may have contributed to local variations in laying dates are evident from a consideration of laying on the Isle of May in 1972 and 1973. Although the median laying dates recorded for these two years were the same, the patterns of laying recorded differed appreciably (Figures 3 and 4). In both years, egg laying was spread over a similar

Figure 3

The dates on which clutches were started on East Tarbet in 1972

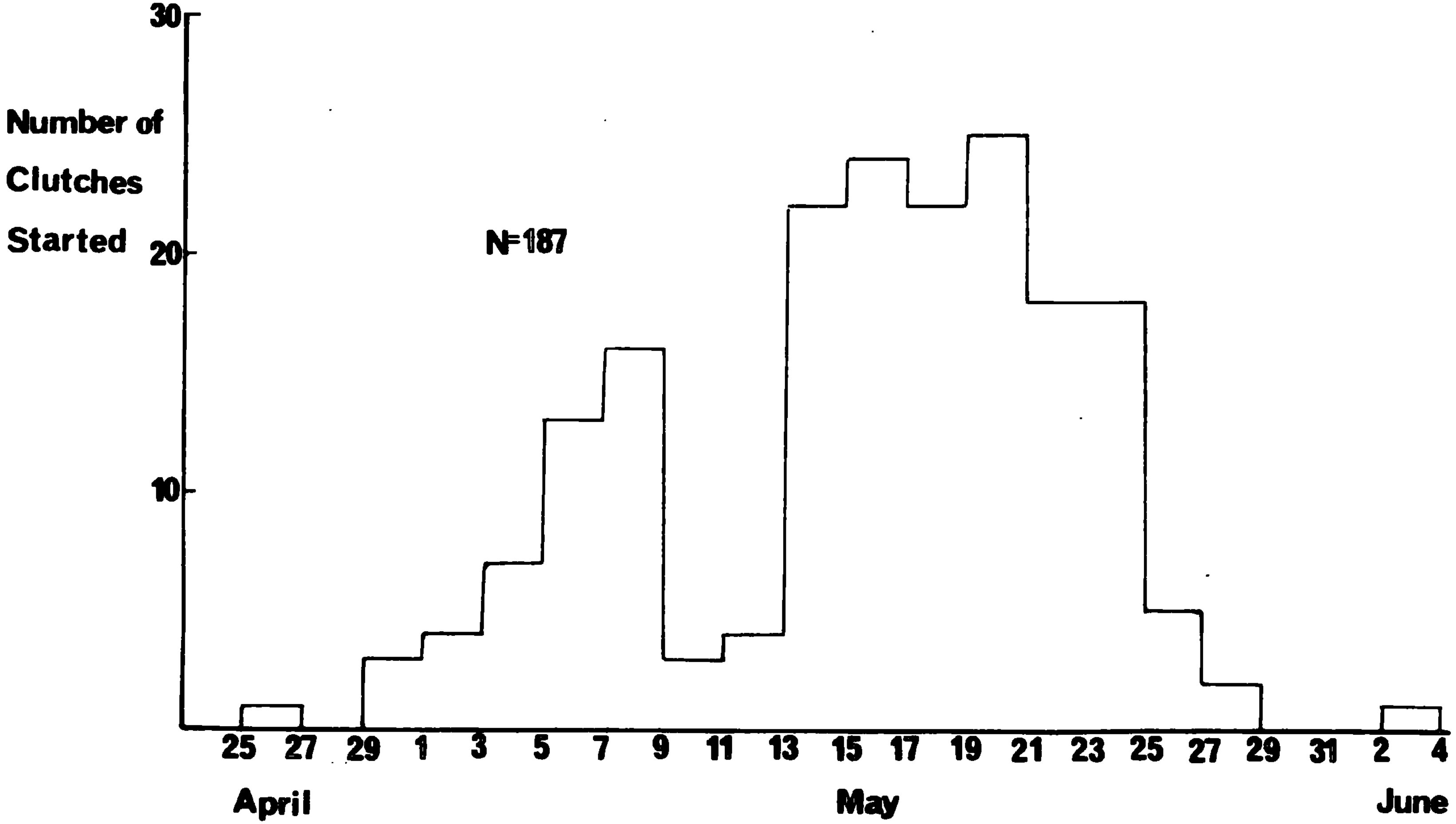
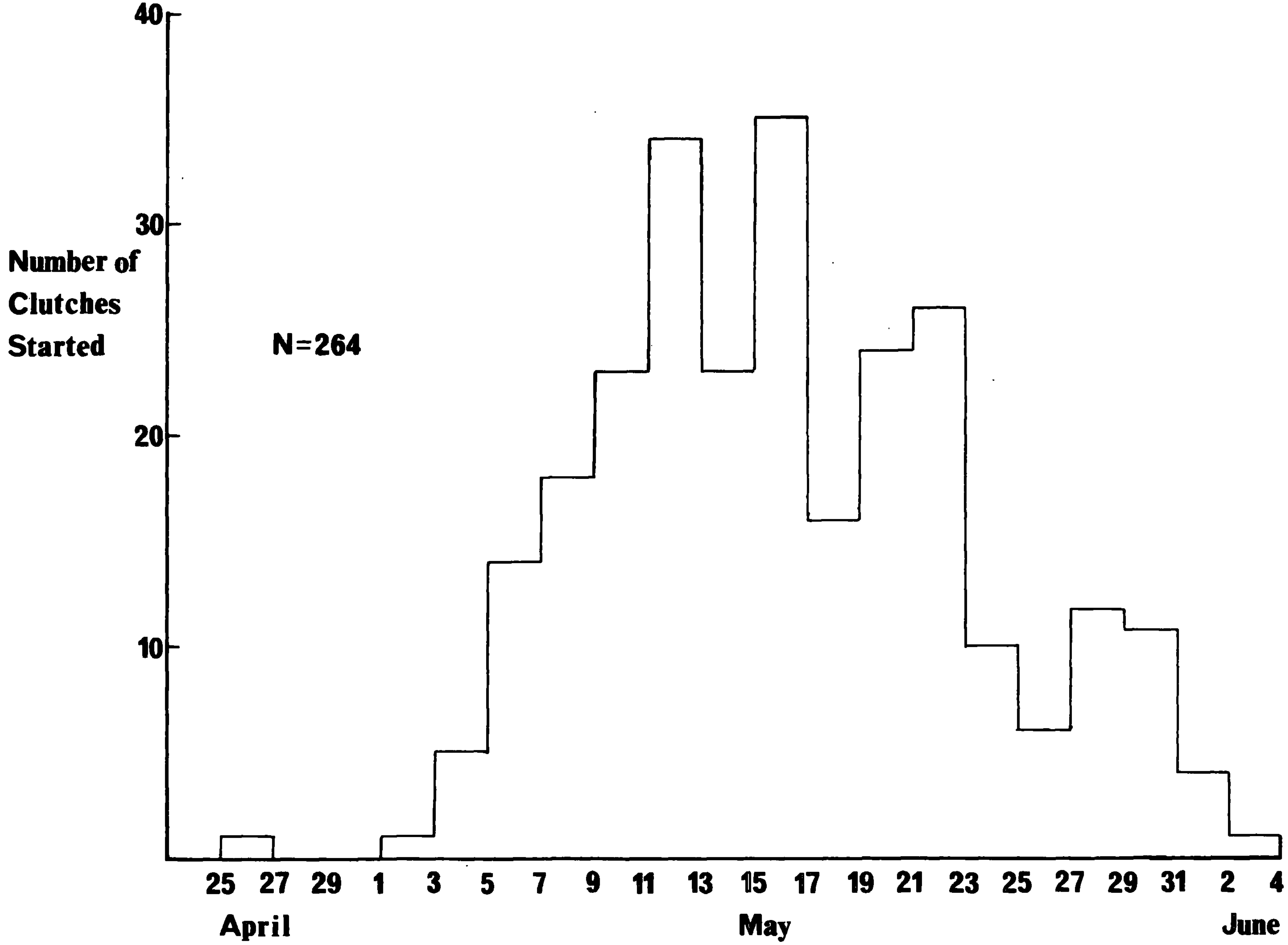

30
20
10
Number of
Clutches
Started
N=187
25
27
29
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
2
4
April
May
June

Figure 4

The dates on which clutches were started on East Tarbet

in 1973


40
30
20
10
Number of
Clutches
Started
N=264
25
27
29
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
2
4
April
May
June

period of time (40 days in 1972 and 38 days in 1973). However, in 1972 the build-up to peak egg laying was more gradual and less clearly defined than in the following year. This difference indicated greater variability in egg laying and was reflected in the large standard deviation of the 1972 laying frequency distribution. The standard deviation of laying in 1972 was significantly greater than that calculated for 1973 ($F = 1.905$, $p < 0.01$, Table 5). The large standard deviation in 1972 was largely due to a well defined peak of early layers. By comparison, the distribution of egg laying for 1973 showed little tendency towards bimodality and approached normality where the mean (17 May) equalled the median (16 May).

In 1972 there was a sharp decrease in the numbers of eggs laid between 9 and 13 May, a time period over which a rapid, continuous increase in numbers of clutches started was observed in 1973 in the same area. Moreover, a similar discontinuity in egg laying was evident for the Colm's Hole study area in 1972 (Appendix 4). For gulls breeding on Colm's Hole there was a lull in egg laying over the slightly longer period of 9-15 May. The fact that two groups of birds in topographically distinct areas showed a sharp decrease in egg laying on the same day suggests the action of some extrinsic factor such as bad weather or disturbance of the female at the nest site. Over this time period there was no evidence of excessive disturbance of nesting birds. However, the 6-12 May was a week of steadily increasing winds and heavy rainfall and it seems likely that these poor conditions contributed to the observed decrease in laying. It is clear that local weather conditions may be of importance in the initiation of egg laying.

Egg laying in Herring Gulls of known age

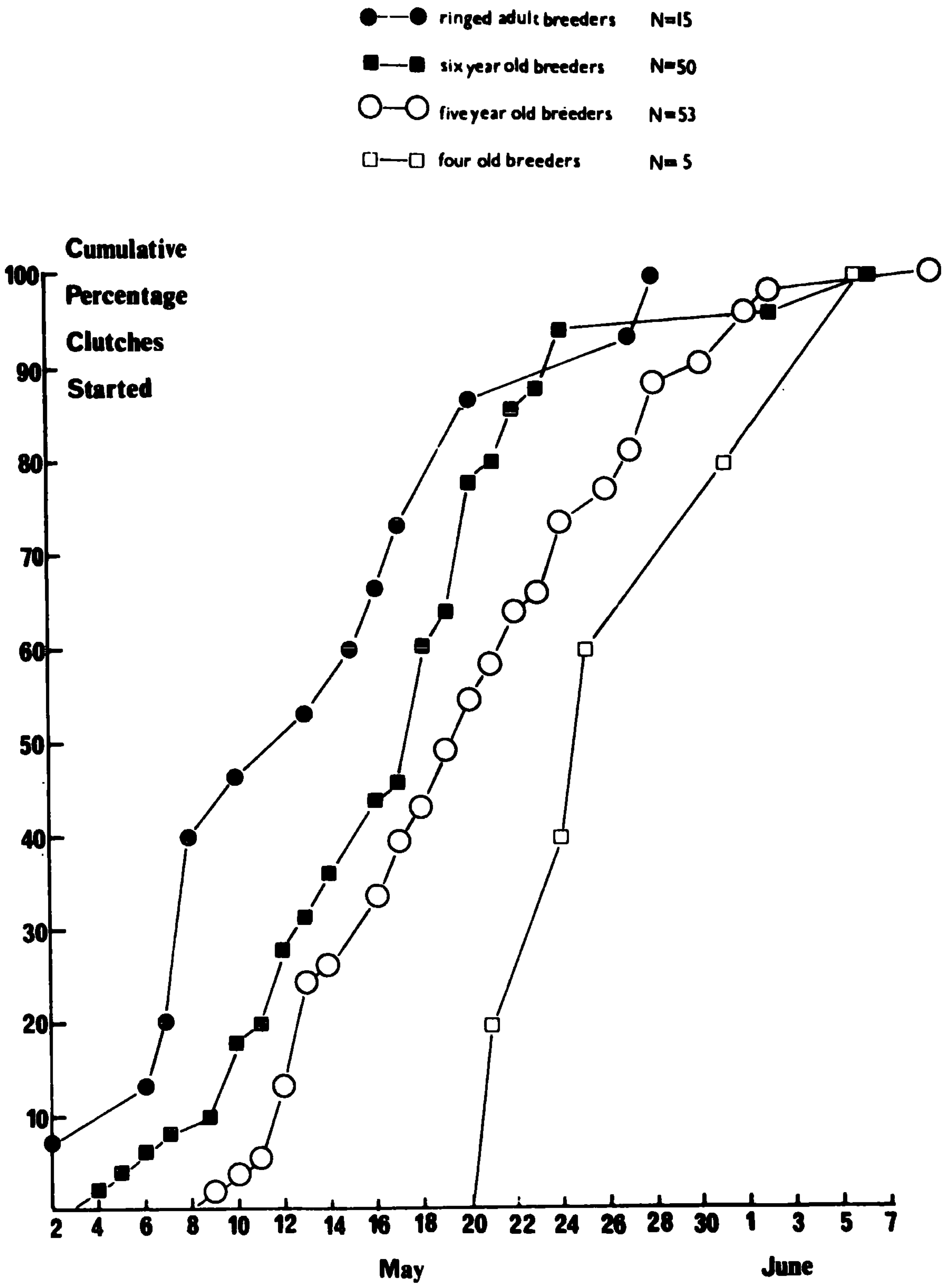
The effect of age on the date of egg laying is well documented in other seabird species and, in general, increasing age tends to advance the date of laying. This tendency has been recorded in the Kittiwake (Coulson 1966), the Gannet (Nelson 1978), the Yellow-eyed Penguin (Richdale 1957), the Storm Petrel (Davis 1957) and for the Red-billed Gull (Mills 1973). No comparable study has been made on the Herring Gull, although Drost, Focke and Freytag (1961) observed younger birds breeding later than established breeders and Davis (1975) noted that older breeding Herring Gulls tended not to lay eggs in the latest part of the season.

Both the mean and the median laying dates for Herring Gulls of known age are given in Table 6. The data presented in this table indicate a tendency for birds to lay progressively earlier as they get older. The cumulative percentage laying frequencies for birds of known age breeding in 1972 are presented in Figure 5. These distributions were compared for the 1966, 1967 and 1968 ringed cohorts (four, five and six year old birds in 1972) within each year and, in addition, each ringed class was compared from one year to the next. Differences in laying pattern could result either from differences in average laying date or from the number of days over which laying took place. Both facets of egg laying are compared using the Kolmogorov-Smirnov one-tailed test transformed to χ^2 for two degrees of freedom.

The tests outlined above involved 16 comparisons, six between age classes in each year and four between the two years. In making this number of comparisons approximately one comparison would be expected to give a significant difference by chance, at the 5% level of confidence. Of the 16 tests performed, six differed at the 5% level.

Figure 5

The cumulative increases in number of clutches started by Herring Gulls of known age on the East Tarbet, North Ness and Colm's Hole study areas in 1972


●—● ringed adult breeders N=15
■—■ six year old breeders N=50
○—○ five year old breeders N=53
□—□ four old breeders N= 5
Cumulative Percentage Clutches Started
100
90
80
70
60
50
40
30
20
10
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
1
3
5
7
May
June

In 1972, adult-ringed gulls laid significantly earlier than gulls that were either four or five years old, and the difference between four and five year old breeders was also significant. The difference between adult-ringed gulls in this year and the control group on East Tarbet was not significant. For the 1973 season the differences between adult-ringed gulls and all other age classes were significant, as was the difference between laying adult-ringed birds and the control group. Only the 1968 ringed cohort significantly advanced their laying when the 1972 and 1973 laying patterns are compared.

The laying dates of Herring Gulls breeding for the first time, that is all four and many five year old birds (Section 4.4), were later than those of established breeders (those ringed as adults and the majority of the control). The situation was clearest in four year old gulls. In the 1972 breeding season the difference between median laying dates for four and five year old birds was eight days, while the difference between median dates of the 1968 ringed cohort between the two years was six days (differences between mean dates were 8.5 and 8.7 days respectively). It therefore seems reasonable to conclude that gulls with one year's breeding experience, that returned to breed for a second time, advanced their laying date by six to nine days.

The majority of gulls breeding when five years old were also breeding for the first time and the differences in median dates between these birds and adult-ringed gulls were seven days in 1972 and five days in 1973. It is to be expected that the advancement shown in laying date by five year old breeders would be less than that for four year old birds since some birds in their fifth year of life had already bred before and the change was partly masked by these birds. On these grounds it would be expected that the 1967 cohort would breed earlier in 1973 (when six years old) than in the preceding year. In fact, there was no significant difference between the time of egg laying in these two years. However, the laying patterns in these two years were significantly different. The mean date for colour- ringed gulls being significantly later in 1973 than in 1972 ($p < 0.05$) such that the comparisons between the two seasons (unless the difference was large, as for the 1968 cohort) were masked by the generally later laying in 1973. For each year there was a trend for older birds to lay earlier, and this advancement of laying date took place at least until the seventh year of life.

In 1972 the laying distributions of the 1968 and 1967 ringed cohorts were positively skewed (Figure 5) which is a reflection of the presence of late-layers in these age classes. The extent to which a distribution is skewed is given by Pearson's second coefficient of skewness, K, which can be calculated from the formula:

$$K = \frac{3\ (\text{mean-median})}{\text{standard deviation}}$$

For the 1968 and 1967 cohorts K values in 1972 are calculated as +1.000 and +0.740 respectively. There was a marked decrease in the numbers of late layers in the following year and a consequent decrease in coefficients of skewness (in 1973, $K_{1968} = -0.286$ and $K_{1967} = +0.396$). In both years, for gulls six years and older, there was close agreement between the mean and the median, suggesting few late-breeders. For the control group, values of K were small (+0.582 and -0.393 for 1972 and 1973), suggesting that there were few late breeders within the samples.

3.2 Clutch Size

Introduction

For Herring Gulls breeding on the Isle of May the mean clutch sizes in 1972 and 1973 were 2.48 and 2.56 eggs per female, the overall colony mean for these two years being 2.52 eggs per female. Thus, clutch size on the Isle of May was comparable to that recorded for this species at other colonies (Table 7). The greatest variation in mean clutch size indicated by the studies listed in Table 7 is between 2.30 (Hunt 1972, for Flat Island, U.S.A.) and 2.95 (Paludan 1951, Graesholm Island, Denmark); a variation of 0.65 eggs per female. Completed clutches can vary from one to four eggs (Paludan 1951) but most females lay clutches of three eggs (Table 7).

For Herring Gulls breeding on the East Tarbet and Colm's Hole study areas in 1972 and 1973, 63% of completed clutches contained three eggs (c.3), 26% were two egg clutches (c.2) and 11% were one egg clutches (c.1). Only two clutches of four eggs (c.4) were found in the two years (in a total of 583 clutches: c.1 66; c.2 149; c.3 366; c.4 2). For most of the studies referred to in Table 7, mean clutch size approached three eggs per female and low mean clutch sizes appeared to be indicative of peculiar circumstances. For example, Flat Island was subject to a great deal of disturbance by picnickers (Hunt 1972), and Belopol'skii (1961) attributed the small clutches laid on the Seven Islands in 1939 to a decrease in the available food spectrum in that year. Predation of eggs is another factor which may result in an apparent decrease in clutch size. Erwin (1971) studied the breeding biology of Herring Gulls at Sandy Point on Rhode Island; a part of this study colony was particularly subject to predation by Greater Black-backed Gulls; the mean clutch size of gulls subject to predation (2.70) was lower than that for birds in the rest of the colony (2.90).

Lack (1968) pointed out that in many birds (both passerine and non-passerine) clutch size tends to increase with increasing latitude. He argued that this was so because the longer day lengths at higher latitudes allowed more time for food collection, as a consequence of which larger broods could be successfully raised. (It was Lack's view that clutch size has evolved to that size which results in the maximum number of young successfully fledged.) No such trend is evident for Herring Gulls; in this species clutch size at low latitudes can be as large as, or larger than, those at higher latitudes (Table 7). For clutch size, as with laying dates (Section 3.1), there is no clear ecogeographical relationship between breeding and latitude. Such a result is not surprising since Herring Gulls are scavengers of man-made wastes and there is little evidence to suggest that seasonal variations in food supply limit reproductive rates for this species in Europe and North America. The Seven Island colonies in the Baerents Sea may be exceptional in this respect. Belopol'skii (1961) recorded that Herring Gulls breeding at these colonies placed little reliance upon domestic refuse and other wastes (such materials constituted 1.3 - 2.3% of the stomach contents). In comparison Spaans (1971) found that up to 50% of the food fed to chicks by gulls breeding at colonies on the Dutch Frisian Islands was man-made in origin.

Parsons (1971a) and Keith (1966) have suggested that the variations in mean clutch sizes recorded at different colonies indicated different methods of study and varying degrees of disturbance caused by the investigator. In addition to disturbance, other factors such as predation pressure and, for some colonies, local food availability, may also contribute to clutch size variation.

Table 7. Mean clutch sizes recorded for Herring Gulls breeding at various colonies

Location of study	Latitude	Number of nests	Mean clutch size (eggs per female)	Number of* C.3 clutches	Year of study	Authority
Seven Islands, U.S.S.R.	68°48'	370	2.80	78	1937	Modestov in Belopol'skii (1961)
		51	2.63	63	1938	
		176	2.34	34	1939	
Isle of May, U.K.	56°12'	903	2.73	77	1968	Parsons (1975)
		200	2.59	65	1970	Emmerson (unpublished data)
		317	2.48	60	1972	This study
		264	2.56	66	1973	
Graesholm Island, Denmark	55°19'	88	2.95	95	1943	Paludan (1951)
		82	2.95	93	1944	
Walney Island, U.K.	54°05'	139	2.56	63	1962-1965	Brown (1967)
Skomer Island, U.K.	51°45'	220	2.76	82	1962	Harris (1964a)
Gull Island, Canada	47°15'	113	2.73	N.D.**	1971	Haycock and Threlfall (1975)
Flat Island, U.S.A.	44°19'	50	2.60	N.D.**	1968	Hunt (1972)
		94	2.30	N.D.**	1969	
		143	2.40	N.D.**	1970	

* As a percentage of the total number of clutches laid

** N.D. = no available data

Table continued overleaf.......

Table 7. Mean clutch sizes recorded for Herring Gulls breeding at various colonies (continued)

Location of study	Latitude	Number of nests	Mean clutch size (eggs per female)	Number of* C.3 clutches	Year of study	Authority
Nantucket Island, U.S.A.	$41^{o}17'$	44	2.77	77	1963	Kadlec and Drury (1968a)
Rhode Island, U.S.A.	$41^{o}13'$	370	2.85	85	1963	Kadlec and Drury (1968a)
Rhode Island, U.S.A.	$41^{o}13'$	96	2.69 - 2.90	N.D.**	1969	Erwin (1971)
Block Island, U.S.A.	$41^{o}11'$	275	2.41	55	1963	Kadlec and Drury (1968a)
		258	2.84	84	1965	
		266	2.88	88	1966	

* As a percentage of the total number of clutches laid

** N.D. = no available data

Clutch size in relation to parental age

The sizes of clutches laid by ringed females or by females paired with ringed males were recorded in 1972 and 1973. In 1972 clutch sizes were recorded for birds breeding on East Tarbet, North Ness and Colm's Hole. In the following year data were obtained from the East Tarbet study area and from the areas culled in that year (Rona, North and South Ness, North and South Plateaus, Burrian and Island Rocks). In the case of cull areas, nests were visited between 30 April and the start of the 1973 cull on 18 May. In both years nest visits were made at two to three day intervals which was close enough to the mean laying period of 48.9 hours and within the mean relaying period of 13.2 days (Parsons 1976b) to ensure that only completed clutches and few relayed clutches were included.

The sizes of clutches laid by gulls of known age are given in Table 8. The smallest clutches were laid by four year old birds, and in a comparison between the two years the largest change in clutch size attributable to parental age occurred in the 1968 cohort. For these birds clutch size increased by 0.57 eggs per female, from a mean of 1.71 in 1972 to 2.28 in the following year. Only 14% of the clutches laid by four year old gulls were c.3 clutches; five year old birds laid much higher proportions of c.3 clutches (39% in 1972 and 40% in 1973). Emmerson was able to observe birds ringed as pulli in 1966 breeding for the first time in 1970 (then four years old); she recorded a mean clutch size for this cohort of 1.91, only two of the 11 clutches laid were c.3 clutches (c.1 3, c.2 6, c.3 2). Herring Gulls breeding in their fourth year of life laid on average fewer eggs than older birds and unlike older gulls rarely laid c.3 clutches. A similar situation has been described in the Yellow-eyed Penguin by Richdale (1949). In this species females normally lay a c.2 clutch, but a large proportion (38%) of the youngest breeding penguins (two years old) laid c.1 clutches. Clutch size increased with age and only 1.5% of birds older than three years laid c.1 clutches.

Table 8. The size of clutches laid by Herring Gulls of known age and by control groups of adults

	1 9 7 2						1 9 7 3					
Year of ringing as chicks	Age of parent (years)	Number of pairs	Number of eggs laid			Mean clutch size ± S.E.	Age of parent (years)	Number of pairs	Number of eggs laid			Mean clutch size ± S.E.
			1	2	3				1	2	3	
1968	4	7	3 (43)	3 (43)	1 (14)	1.71±0.29	5	25	3 (12)	12 (48)	10 (40)	2.28±0.14
1967	5	51	13 (26)	18 (35)	20 (39)	2.14±0.14	6	65	11 (17)	23 (35)	31 (48)	2.31±0.09
1966	6	50	5 (10)	11 (22)	34 (68)	2.58±0.10	7	48	3 (6)	5 (10)	40 (83)	2.77±0.11
Ringed as adults	≥ 6	13	1 (8)	2 (15)	10 (77)	2.69±0.18	≥ 7	16	1 (6)	3 (19)	12 (75)	2.69±0.22
Unringed sample East Tarbet		184	23 (13)	59 (32)	102 (55)	2.43±0.05		264	28 (11)	61 (23)	175 (66)	2.56±0.04
Unringed sample Colm's Hole		133	15 (11)	29 (22)	89 (67)	2.56±0.06						

The figures in brackets are percentages of the total number of clutches laid

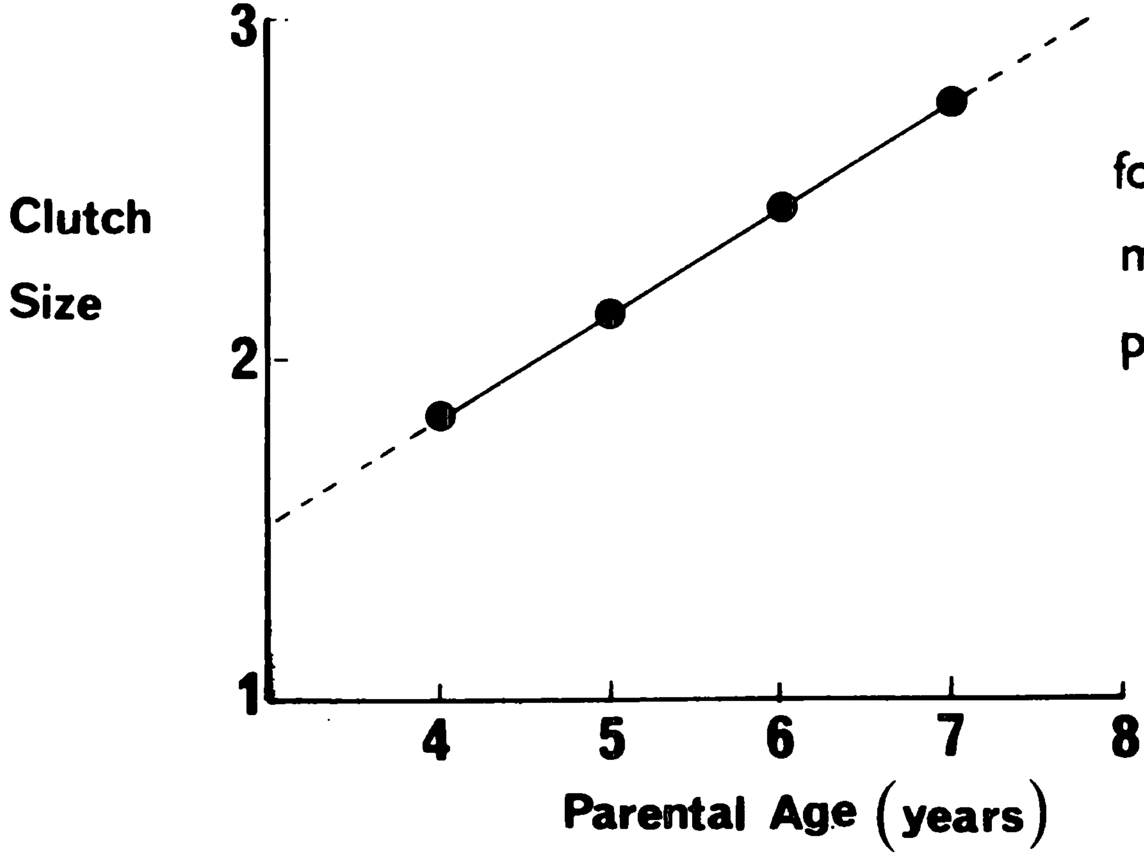
There were no significant differences between the sizes of clutches laid by equivalent age classes in the two years (i.e. for five and six year old gulls in each year). Similarly the differences between seven year old birds in 1973 and the adult-ringed birds in both years were not significant. Since this was the case, the data for overlapping age classes were combined to facilitate an easier comparison between age classes (Table 9); the relationship between age and clutch size is given in Figure 6 and is based on cumulative data.

Table 9. The number of eggs laid in 1972 and 1973 by Herring Gulls of known age

Age of one member of the pair (years)	Number of pairs	Number of eggs laid 1	2	3	Mean clutch size ± S.E.
4	7	3	3	1	1.71 ± 0.29
5	76	16	30	30	2.18 ± 0.09
6	115	16	34	65	2.43 ± 0.07
≥ 6	77	5	10	62	2.74 ± 0.07

For the age classes sampled there was a linear relationship between parental age and clutch size (Figure 6); mean clutch size increased as age increased. Extrapolation of the mean clutch size on age regression indicates that a mean clutch size of 3.00 eggs would be recorded for eight year old adults. Since c.4 clutches were rarely found and there was no evidence that such clutches were more frequently laid as birds got older, four years (i.e. between the ages of four and eight years) is the maximum period over which mean clutch size can be expected to increase with age. Mills (1973) studied the breeding success of Red-billed Gulls between the ages of two and ten years. As with Herring Gulls, the youngest Red-billed Gulls (two to four years old) laid the smallest clutches. There was no significant increase in mean clutch size after the fifth year of life.

Figure 6. The variation of mean clutch size with parental age



for the regression of
mean clutch size on
parental age :

$y = 0{\cdot}31\,x + 0{\cdot}60$

It is important to distinguish between the effects of parental age and of past breeding experience. The ability of older gulls to lay larger clutches may be interpreted in terms of maturation changes that occur up to seven years after fledging; for example, the endocrine control of ovarian function may become more closely coupled with environmental factors, such as changes in photoperiod, that limit reproduction. It may also be argued, as Lack (1954) has done, that older females are able to mobilise a greater proportion of body reserves into egg production. However, it is necessary to exercise caution in making such interpretations since the relationship between parental age and clutch size was not as straightforward as the data in Table 9 suggest. Thus, although a comparison of five and six year old gulls breeding in 1972 shows a significant increase of 0.44 in mean clutch size with age ($\chi^2_{(2)} = 8.88$ $p < 0.05$, Table 8), there was no significant increase in the size of clutches laid by birds of the 1967 cohort in 1973 ($\chi^2_{(2)} = 1.48$ $p > 0.05$), nor was there a significant difference between the mean clutch sizes of five and six year old gulls in 1973 ($\chi^2_{(2)} = 1.25$ $p > 0.05$).

In the Kittiwake (Coulson and White 1961, Wooller and Coulson 1977) and the Sandwich Tern (Veen 1977) past breeding experience has a marked effect on breeding performance. In both species recruit breeders (i.e. Kittiwakes less than four years old and two to four year old Sandwich Terns) were observed to lay smaller clutches than birds which had bred at least once before. From the analysis of recruitment age (Section 4.4) and observations of the proportion of recruits that bred (Table 4), it is clear that all four year old and most five year old Herring Gulls on the Isle of May were recruits. Breeding birds between the ages of five and seven years were a mixture of recruits and experienced (so-called 'recindivist', Veen 1977) birds. Unlike five year old gulls, the majority of gulls aged six years and older were breeding for at least the second time. Recruit Herring Gulls laid significantly smaller clutches than recindivists ($\chi^2_{(2)} = 19.94$ $p < 0.01$, Table 10). It is probable that recruits lay fewer eggs than recindivists regardless of age and that past breeding experience may be a more important factor than age per se. This may explain the overlap between mean clutch sizes of five and six year old birds observed in 1972 and 1973 for the 1967 cohort and for the 1968 and 1967 cohorts breeding in 1973.

Table 10. The effect of past breeding experience on clutch size for Herring Gulls breeding on the Isle of May in 1972 and 1973

Parental age (years)	Breeding status	Percentage that were breeding for at least the second time*	Mean clutch size ± S.E.
4	first time (recruits)	0	2.15 ± 0.08
5	first or second time (recruits and recindivists)	14	
≥ 6	predominantly second time or more (recindivists)	69	2.55 ± 0.05

* Based on a spread of recruitment age between four and seven years and a mean age of first breeding of 5.25 years (Section 4.4).

Only 14% (approximately 11 out of 76 pairs, Table 9) of five year old breeders were recindivists and most birds in this age class were recruits. Thus the large difference in clutch sizes between four and five year old breeding birds is unlikely to have been the result of past breeding experience. Whilst previous experience is likely to have been an important influence on clutch size in birds aged five years and older, four year old breeders may have had insufficient resources to lay larger clutches.

The difference between mean clutch sizes of young (≤ five years old) and old (≥ six years old) Herring Gulls was 0.40 eggs per female. This was of a similar order to the difference between recruit and recindivist Sandwich Terns (0.48 Veen 1977) and Kittiwakes (0.6 Coulson and White 1961); young (two to three years old) and old (five years old) Red-billed Gulls

(0.44 Mills 1973); although larger than that reported (0.29) for young and old Yellow-eyed Penguins (for a comparison of birds aged two years and those older than two years, Richdale 1959).

Clutch size in relation to laying date

Some birds are known to lay clutches of constant size throughout the egg laying period of the breeding season. Lapwings, for example, consistently lay a c.4 clutch (Klomp 1970) and Woodpigeons invariably lay c.2 clutches (Murton, Westwood and Isaacson 1974) regardless of time of laying. In some double or triple brooded species, such as the European Blackbird, clutch size initially increases as the breeding season progresses (Snow 1958). The Laridae belong to a large group of birds in which clutch size decreases as eggs are laid later. This phenomenon has been reported for the Kittiwake (Coulson and White 1961) and also for Glaucous-winged, Lesser Black-backed and Common Gulls (Vermeer 1963, Brown 1967, Boll 1931 and Bergman 1939). Late-laying Herring Gulls were observed to lay smaller clutches than early-laying gulls on Walney Island (Brown 1967), Gull Island (Haycock and Threlfall 1975) and on the Isle of May (Parsons 1975), although not on Kent Island (Paynter 1949).

Since the majority of recruit Herring Gulls were late-layers, it was difficult to separate the effects of parental age and the timing of egg laying on clutch size. Both factors were cited by Brown (1967) to account for smaller, late-laid clutches. The Herring Gull is a species in which lost clutches are frequently replaced. Parsons (1975) artificially lengthened the breeding season by constantly removing eggs from nests on several areas on the Isle of May. In this way he was able to measure clutch size in older Herring Gulls that were relaying at the same time as late-laying younger birds. Parsons found that delayed birds did not, on average, lay a larger number of eggs than young birds and concluded that the date of laying was of prime importance in determining clutch size.

The egg laying data for Herring Gulls breeding on East Tarbet in 1972 and 1973 have been grouped into seven day intervals (Table 11). In both years there were decreases in the numbers of c.3 clutches and increases in the numbers of c.1 and c.2 clutches laid as the breeding season progressed. For example in 1973, 76% of clutches laid before 19 May were c.3 clutches whereas only 52% of clutches laid after this date were c.3. The proportions of c.1 and c.2 clutches increased from 8% (c.1) and 16% (c.2) before 19 May 1973 to 15% (c.1) and 34% (c.2) after this date. The changes recorded during the 1972 and 1973 breeding seasons in mean clutch size are shown in Figure 7.

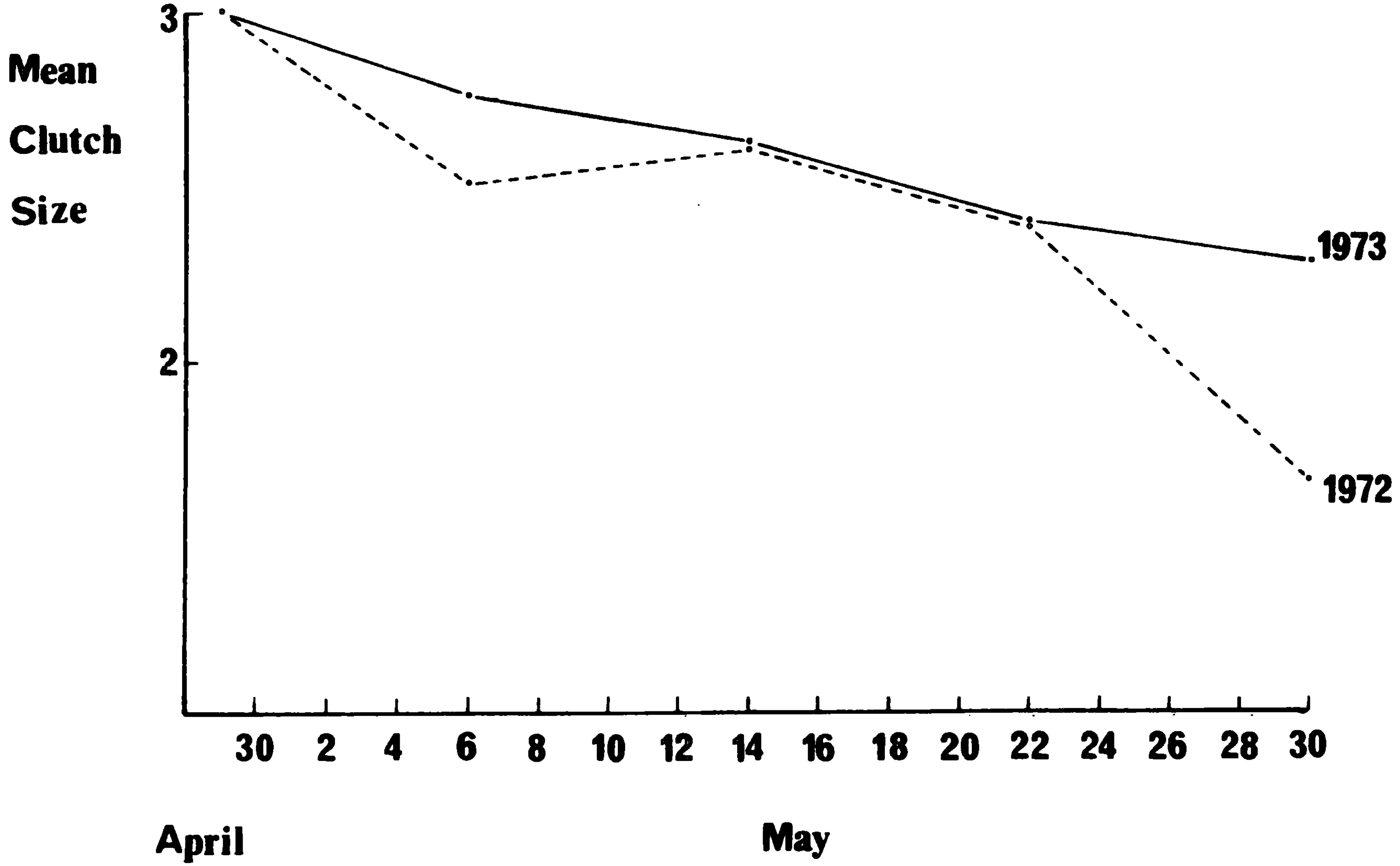
Table 11. The effect of laying date on mean clutch sizes in the Herring Gull

(For Herring Gulls breeding on the East Tarbet study area in 1972 and 1973)

	1972				1973			
Laying date of first egg	No. of clutches laid which were: c.1	c.2	c.3	Mean clutch size ± S.E.	No. of clutches laid which were: c.1	c.2	c.3	Mean clutch size ± S.E.
25 April - 2 May	0	0	6	3.00	0	0	1	3.00
3-10 May	7	4	26	2.51 ± 0.13	3	5	40	2.77 ± 0.05
11-18 May	2	24	45	2.61 ± 0.05	10	21	81	2.63 ± 0.06
19-26 May	10	21	36	2.39 ± 0.08	9	24	37	2.40 ± 0.08
27 May - 3 June	2	4	0	1.67	6	11	16	2.30 ± 0.11

Over the two years, the maximum difference in average size of clutches laid at the beginning and at the end of the egg laying period was 1.33 eggs per female (3.00 - 1.67, Table 11). However, few clutches were

Figure 7. The effect of laying date on the size of clutches laid by Herring Gulls on the East Tarbet study area in 1972 and 1973


Mean
Clutch
Size
3
2
30
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
April
May
1973
1972

laid between 25 April and 2 May in 1972 and 1973 or between 27 May and 3 June 1972. In addition, many birds appeared to postpone laying between 2 and 10 May 1972 because of adverse weather conditions (Section 2.1) which may have accounted for the mean clutch size recorded during this period being lower than that for the equivalent time period in 1973 and for that recorded between 11 and 18 May 1972 (Table 11). For Herring Gulls breeding on the Isle of May in 1967 there was a difference of 0.56 between the mean clutch size at the beginning of the season (mean clutch size of 2.92) and at the end of egg laying (mean of 2.36, Parsons 1971a). On Walney Island the difference between early-laid and late-laid clutches was 0.37 (2.77 - 2.40, Brown 1967). The most comparable measure of the extent to which seasonal influences affected clutch size in the present study is given by a comparison of the mean size of clutches laid between 3-10 May and between 27 May - 3 June 1973, i.e. a seasonal decrease of 0.47 in mean clutch size.

Clutches laid by birds of known age have been grouped according to laying date (Table 12) and the extent to which parental age and laying date interacted in determining clutch sizes is shown in Figure 8. A seasonal decrease in clutch size was apparent in birds of known age breeding in 1972 and 1973.

Few clutches were laid by birds of known age before 11 May in either year and most of these were c.3 clutches (Table 12). After this date there was some evidence to suggest that larger clutches were laid by older gulls in equivalent time periods. Most clutches were laid between 11-26 May. Between 11-18 May five year old birds laid significantly smaller clutches than six year old gulls ($p < 0.01$). Between 19-26 May significantly smaller clutches were laid by five year old birds than by birds over the age of six years ($p < 0.01$) although there was no significant difference between clutches laid between 19-26 May by five and six year old birds.

Figure 8. The effect of laying date on mean clutch size in Herring Gulls of known age breeding in 1972 and 1973

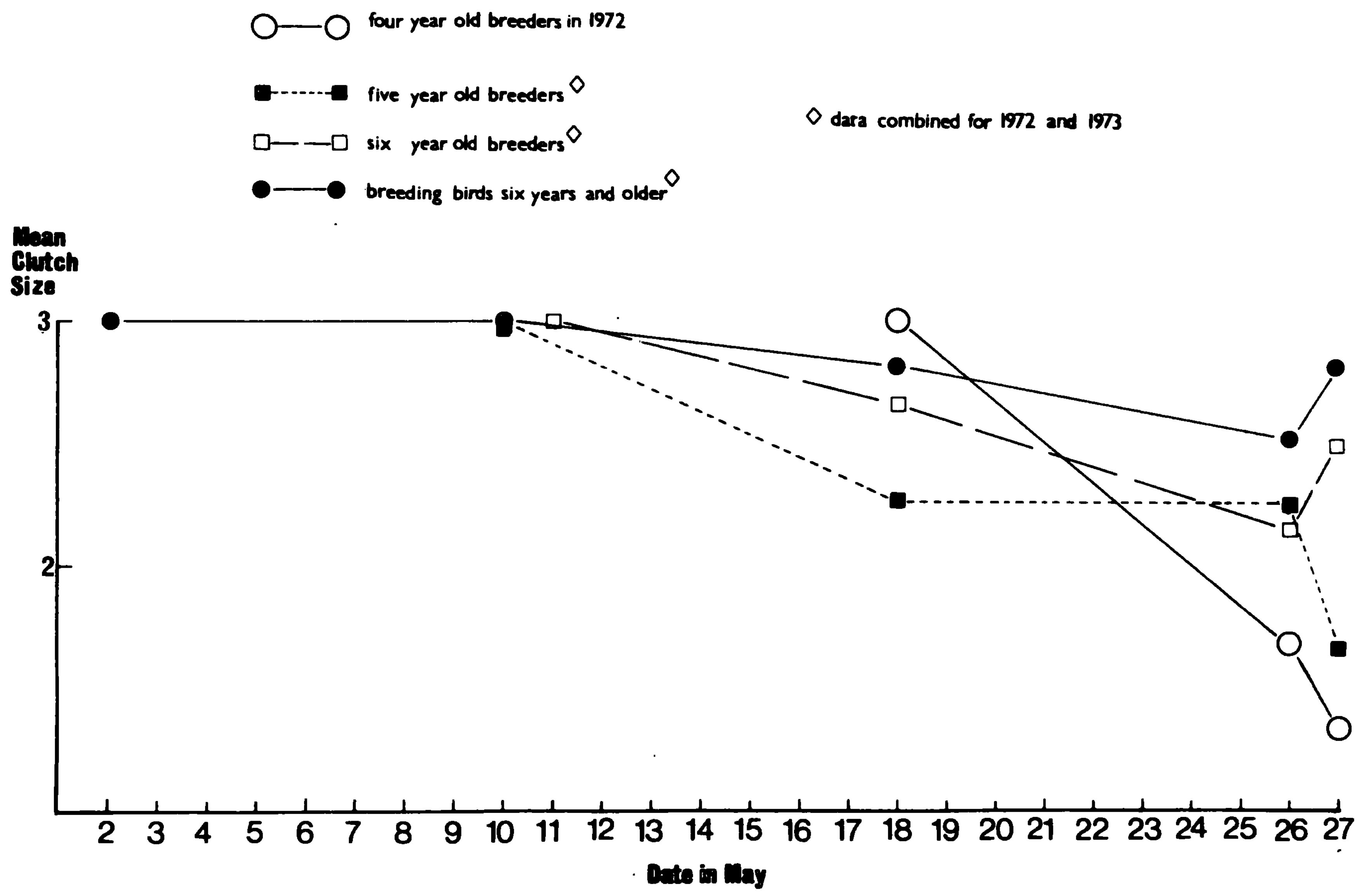
four year old breeders in 1972
five year old breeders ◇
six year old breeders ◇
breeding birds six years and older ◇
◇ dara combined for 1972 and 1973
Mean Clutch Size
3
2
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
Date in May

Table 12. The effect of laying date on clutch size in Herring Gulls of known age breeding on study and cull areas in 1972 and 1973

Age (years) of one member of the breeding pair	Date on which first egg laid				
	Up to 2 May	3-10 May	11-18 May	19-26 May	After 27 May
4	0, 0, 0	0, 0, 0	0, 0, 1	1, 2, 0	2, 1, 0
			(3.00)	(1.67)	(1.33)
5	0, 0, 0	0, 0, 2	5, 10, 12	7, 13, 16	4, 7, 0
		(3.00)	(2.26)	(2.25)	(1.64)
6	0, 0, 0	1, 2, 7*	3, 9, 32	11, 23, 19	1, 1, 4
		(2.80)	(2.66)	(2.15)	(2.50)
≥ 6	0, 0, 2	0, 0, 13	1, 3, 24	4, 6, 19	0, 1, 4
	(3.00)	(3.00)	(2.82)	(2.52)	(2.80)

* Clutch sizes are given as number of c.1, c.2 and c.3 clutches. For example, for the grouped data of six year old Herring Gulls laying clutches between 3 and 10 May, 1 c.1; 2 c.2; and 7 c.3 were laid. Mean clutch sizes for each laying interval are given in brackets.

Table 13. The effects of laying date on the number of eggs laid by Herring Gulls of known age breeding on the Isle of May in 1972 and 1973

	Laying date of first egg						Difference in mean clutch size due to timing of egg laying (eggs per female)
	Up to 18 May			19 May - 3 June			
	c.1	c.2	c.3	c.1	c.2	c.3	
Recruits*	5	10	15	14	23	16	- 0.67
		(2.33)***			(1.66)		
Recindivists **	5	14	78	16	31	46	- 0.43
		(2.75)			(2.32)		
Difference in mean clutch size due to parental age (eggs per female)		+ 0.42			+ 0.66		

* Breeding gulls aged five years and younger

** Breeding gulls aged six years and older

*** Mean clutch size

The effects of laying date on clutch size can be most clearly seen when the egg laying data are considered in terms of past breeding experience (Table 13). The largest difference in mean clutch size attributable to the effects of laying date occurred in recruit breeders (0.67 eggs per female, Table 13). This was of a similar magnitude to the maximum difference in clutch size due to parental age and past experience (0.66 eggs per female, Table 13). Thus both parental age and laying date affected clutch size to a similar extent. Whilst both recruits and recindivists laid smaller clutches at the end of the egg laying period than at its beginning, recruit breeders laid smaller clutches than recindivists regardless of the time of laying. Thus both parental age and the time of egg laying were important proximate determinants of clutch size. The lower mean clutch sizes recorded towards the end of the egg laying period resulted from the later laying of small clutches by recruits and seasonal influences which affected all breeding birds.

Parsons (1975) argued that the duration of egg laying in Herring Gulls was likely to be photoperiodically controlled and was largely independent of changing abundance in food supply. He showed that there was a minimum size that eggs must reach before they are laid, developing eggs below a certain threshold size being reabsorbed by the ovary. Parsons suggested that late-laying birds had insufficient time for the physiological development necessary for the formation of eggs which were large enough to exceed this threshold. As a result, fewer eggs (smaller clutches) were laid towards the end of the egg laying phase of the breeding season. Whatever environmental factors operated in limiting clutch size in Herring Gulls, it was clear that their action was most severe in recruit breeders (Table 13). This evidence supports the arguments advanced by Parsons, since it seems likely that intrinsic factors would act more acutely in recruit breeders than in experienced birds.

3.3 Egg Size

Egg size in relation to parental age

The size of eggs laid by female seabirds belonging to a wide range of species is known to be influenced by both the age and previous breeding experience of the pair. Thus first breeding Kittiwakes (Coulson 1963); young Shags (Coulson, Potts and Horobin 1969); Short-tailed Shearwaters (Serventy 1967); Yellow-eyed Penguins (Richdale 1957); Buller's Mollymawks (Richdale and Wareham 1973) and Gannets (Nelson 1978) lay smaller eggs than older established breeding birds.

In Herring Gulls age effects on egg size have been inferred by Anderson (1957) and Parsons (1971a). Anderson analysed egg measurements from two Danish colonies, one of which was suspected to have a breeding population of predominantly old birds, whilst the other had a "normal" age structure. He found that eggs laid by the suspected older gulls had significantly larger breadths than those laid by birds breeding at the "normal" colony. Parsons (1971a) found that eggs laid at the sub-colony periphery on the Isle of May were of smaller volume than eggs in the sub-colony centre; this difference he suggested was due to younger birds breeding at the edges of principal breeding areas.

More recently egg sizes in individually marked Herring Gulls breeding on Skokholm Island have been measured by Davis (1975). Davis found that the volumes of clutches laid by individual females in successive years tended to remain constant, although overall he found that clutch volumes increased with age up to seven or eight years of age, and thereafter showed a progressive decline.

On the Isle of May in 1972 and 1973 the sizes of eggs laid by birds of known age breeding on the study areas were measured. Also measured were the eggs laid by gulls of known age which had died during the cull whilst incubating full clutches. Egg volumes were calculated from the modified formula for the volume of an ellipsoid : egg volume = $K \times L \times B^2$, where L is the maximum length and B the maximum breadth of each egg. The constant K in the relationship modifies the formula for the imperfect ellipsoidal shape of the egg and has been determined volumetrically by Paludan (1951) as 0.519, Barth (1967a), 0.508 and Harris (1964a), 0.476. In keeping with the only British study, the value of K determined by Harris has been used throughout the present study. A measure of egg shape was given by a shape index (I) which was determined from the ratio of maximum egg length to maximum egg breadth as : $I = \frac{B}{L} \times 100$. Of the two measurements taken (length and breadth), the breadths of eggs laid in 417 clutches by samples of unringed gulls in the two years showed least variability. The variability of a series of measurements can be expressed as the coefficient of variation (C.V.) where $C.V. = \frac{\text{standard deviation}}{\text{sample size}} \times 100$. In comparison to length measurements, egg breadths always had the lowest values of C.V. (see Appendix 5) and thus were the most stable egg parameter.

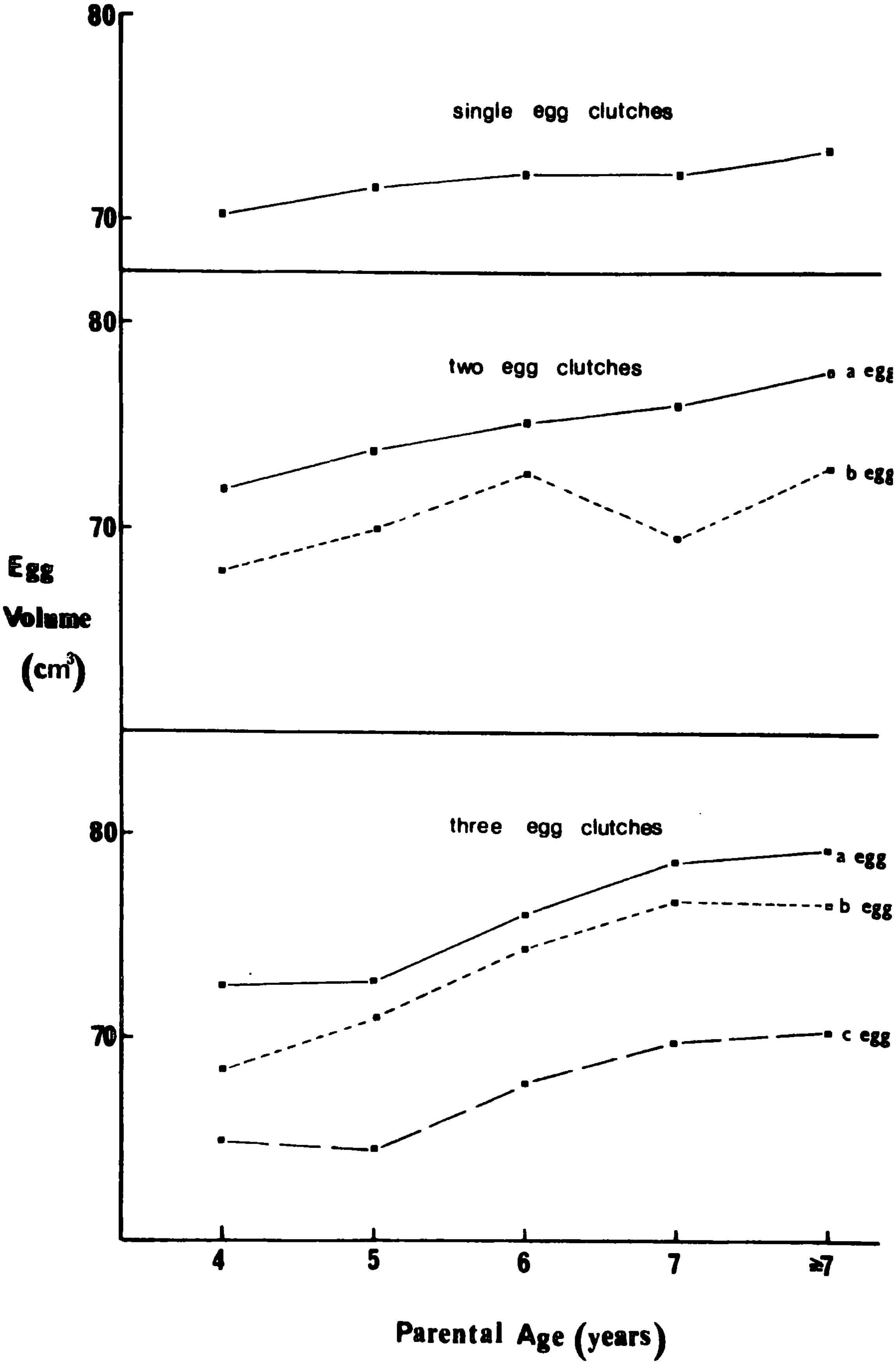
The measurements of eggs laid in 235 clutches by gulls of known age are presented in Table 14. In general, the largest eggs were laid by the oldest birds and egg volumes increased with parental age. Eggs laid by the oldest known gulls (adult-ringed) were between 8-9% larger in volume than those laid by five year old females. Considering equivalent eggs in the laying sequence (where the a-egg was the first egg to be laid, and the c-egg the last egg in a c.3 clutch), the percentage differences in volume were 8.7% (a-egg); 7.7% (b-egg) and 9.3% (c-egg). The smallest eggs were those laid by the single four year old female which laid a c.3 clutch; in this case eggs laid by adult-ringed gulls were 9.1%, 12.1% and 8.4% larger for a-, b-, and c-eggs respectively. The relationship between egg volume and parental age is shown in Figure 9. Egg volumes increased most markedly between the age range of five to seven years.

Table 14. The size of eggs laid by colour-ringed Herring Gulls on the Isle of May between 1972 and 1973

	Age (years)	Laying sequence	Mean length (mm)	Mean breadth (mm)	Volume (cm^3)	Shape index	Number of clutches
c.1 clutches	4		68.50	46.23	70.21	67.5	3
	5		68.45	46.93	71.90	68.6	13
	6		68.29	47.13	72.30	69.0	16
	7		67.46	47.43	72.25	70.3	3
	≥ 6		67.25	48.05	73.94	71.5	2
c.2 clutches	4	a	68.87	46.23	71.09	67.1	3
		b	64.90	46.73	67.95	72.0	
	5	a	68.88	47.41	73.79	68.8	26
		b	67.65	46.59	69.98	68.9	
	6	a	69.91	47.47	75.14	67.9	32
		b	68.60	47.15	72.68	68.73	
	7	a	70.22	47.70	76.0	67.9	5
		b	66.50	46.86	69.55	70.5	
	≥ 6	a	69.94	48.30	77.60	69.1	4
		b	66.73	47.91	72.99	71.8	
c.3 clutches	4	a	68.50	47.20	72.64	68.9	1
		b	65.5	46.8	68.29	71.5	
		c	67.7	44.9	64.97	66.3	
	5	a	67.89	47.47	72.93	69.9	31
		b	67.27	47.06	71.02	70.0	
		c	65.86	45.41	64.46	68.9	
	6	a	69.65	47.86	76.12	68.7	51
		b	68.37	47.73	74.42	69.8	
		c	66.56	46.19	67.80	69.4	
	7	a	70.88	48.3	78.68	68.1	28
		b	70.17	47.9	76.76	68.3	
		c	67.14	46.82	69.96	69.7	
	≥ 6	a	69.03	49.20	79.26	71.3	17
		b	68.43	48.43	76.52	70.8	
		c	66.21	47.17	70.44	71.2	

Figure 9

The variation of mean egg volume with parental age for eggs laid in 1972 and 1973


80
70
single egg clutches
80
70
two egg clutches
a egg
b egg
Egg
Volume
(cm³)
80
70
three egg clutches
a egg
b egg
c egg
4
5
6
7
≥7
Parental Age (years)

For c.3 clutches laid by Herring Gulls breeding on Skokholm Island, Davis (1975) found that birds older than seven years laid progressively smaller eggs. On the Isle of May, there was no evidence that gulls older than seven years laid smaller eggs. The evidence from adult-ringed birds suggests that much smaller volume changes occurred after the seventh year of life, although in comparison to seven year old birds there was a slight volume decrease in b-eggs in adult-ringed females, this difference was not significant ($p > 0.05$). The Isle of May data suggest that eggs laid by the oldest breeders showed little volume change and that egg volumes were relatively constant after the first two to three years of breeding. Similarly, Coulson (1963) found that in the Kittiwake there was an initial increase in egg volumes over the first four years of breeding, but thereafter egg volumes increased at a much lower rate. In neither the Herring Gull on the Isle of May nor in the Kittiwake was there evidence of the decrease in egg size that is known to take place in old domestic hens (Romanoff and Romanoff 1949). As was the case for the study made by Davis (1975), the increase in clutch volume for c.3 clutches was not attributable to any one egg in the clutch since all three eggs showed similar increases with parental age. In c.2 clutches there was a progressive increase in a-egg volume with female age (an overall increase of 9.2%) which paralleled the change in a-egg volume from c.3 clutches (9.1%). Although for b-eggs in c.2 clutches the volume increase at 7.4% was slightly lower than that for c.3 clutches (7.7%) and further for these eggs the increase was discontinuous (Figure 9). The mean volume of the b-eggs laid by seven year old gulls was smaller than that laid by six year old birds, although this difference was not significant ($t_{35} = 1.556$ $p > 0.05$).

Although the mean volume of eggs laid as c.1 clutches also increased in older gulls, the rate of volume increase (5.3%) was lower than that of any egg laid in c.2 and c.3 clutches. In addition, unlike these larger clutches, the percentage volume change between eggs laid by seven year old birds and by birds older than six years (2.4%) almost equalled that between eggs laid by gulls aged four and seven years (2.9%).

It seems likely that egg size will in part be determined by the available body reserves of lipids, carbohydrates and proteins. In birds, egg formation is a physiologically demanding process. It is known to deplete the mineral content, in particular calcium and phosphorus of medullary bone in Pigeons (Bloom, Bloom and McLean 1941) and the Domestic Fowl (Bloom, Domm, Nalbandov and Bloom 1958) and to deplete the protein reserves of skeletal muscles in Red-billed Queleas (Jones and Ward 1976). The physiological demands of egg laying in Herring Gulls have yet to be assessed, but it seems likely that the production of eggs, which are on average 10% of the female body weight, for an 85g egg, places demands upon the female skeleto-muscular system. It will be shown later (Section 6.2) that in comparison with old established breeding gulls recruits were of lower body weight and, in addition, had lower Pectoralis major muscle weights. In Red-billed Queleas at least, Jones and Ward (1976) have shown that this muscle contains a residual protein reserve which breeding females frequently call upon in egg formation. If similar processes operate in Herring Gulls, recruit breeders may lack sufficient body reserves to form large eggs. Within an age category, birds laying c.1 clutches may have been birds of poor quality (as defined by protein and fat reserves, (Wolfson 1954; Macdonald 1962; Jones and Ward 1976)) and of low reproductive drive. The evidence from Table 15 and Table 69 (Section 6.2) indicates that such birds improved their breeding condition slowly as age, body reserves, and presumably past experience, increased.

It is evident from Table 14 that the increasing egg volumes laid by older birds were largely the result of these birds laying broader eggs.

Egg length was variable and could decrease with age, for example in c.1 clutches there was an overall decrease in mean egg length with increasing age (Figure 10). A comparison of four year old breeders with adult-ringed gulls shows that the decrease in mean egg length of 1.25mm (1.8%) was more than compensated for by a 3.9% increase in mean egg breadth (46.23 - 48.05mm) and a resulting increase in volume.

The decrease in egg length was most marked in adult-ringed gulls laying c.3 clutches (Figure 10). For these eggs the mean length could be smaller than that of eggs laid by six year old gulls (a- and c-eggs). The initial length decrease between eggs laid in c.3 clutches by four and five year old birds may have been spurious since only one c.3 clutch laid by a four year old female was found; such an initial decrease in length did not occur for eggs laid in c.2 and c.1 clutches.

Almost without exception egg breadth increased progressively with increasing parental age (Figure 11). A similar trend exists in many other long-lived seabirds. It is notable that in species where egg volumes increase with the age of the laying female, for example in Shags (Coulson et al. 1969) and Short-tailed Shearwaters (Serventy 1967), volume increases are predominantly the result of increases in egg breadths. Such a result is not surprising, and in some measure is a facet of female reproductive anatomy. In birds, the oviduct is a highly convoluted muscular duct which is concerned with the transport of the ovum away from the ovary, with fertilization of the ovum and with the deposition of albumen, membranes and shell onto the ovum to form the finished egg. Thus the cross-sectional diameter and overall development of the oviduct will directly influence the size of the finished egg. Both these facets of oviductal morphology are under gonadotrophic control and it might be expected that in experienced breeding females extensive oviduct development takes place early in the breeding season. Such birds consequently are capable of producing broader eggs in comparison to recruit females where gonadotrophic

Figure 10

The variation of mean egg length with parental age

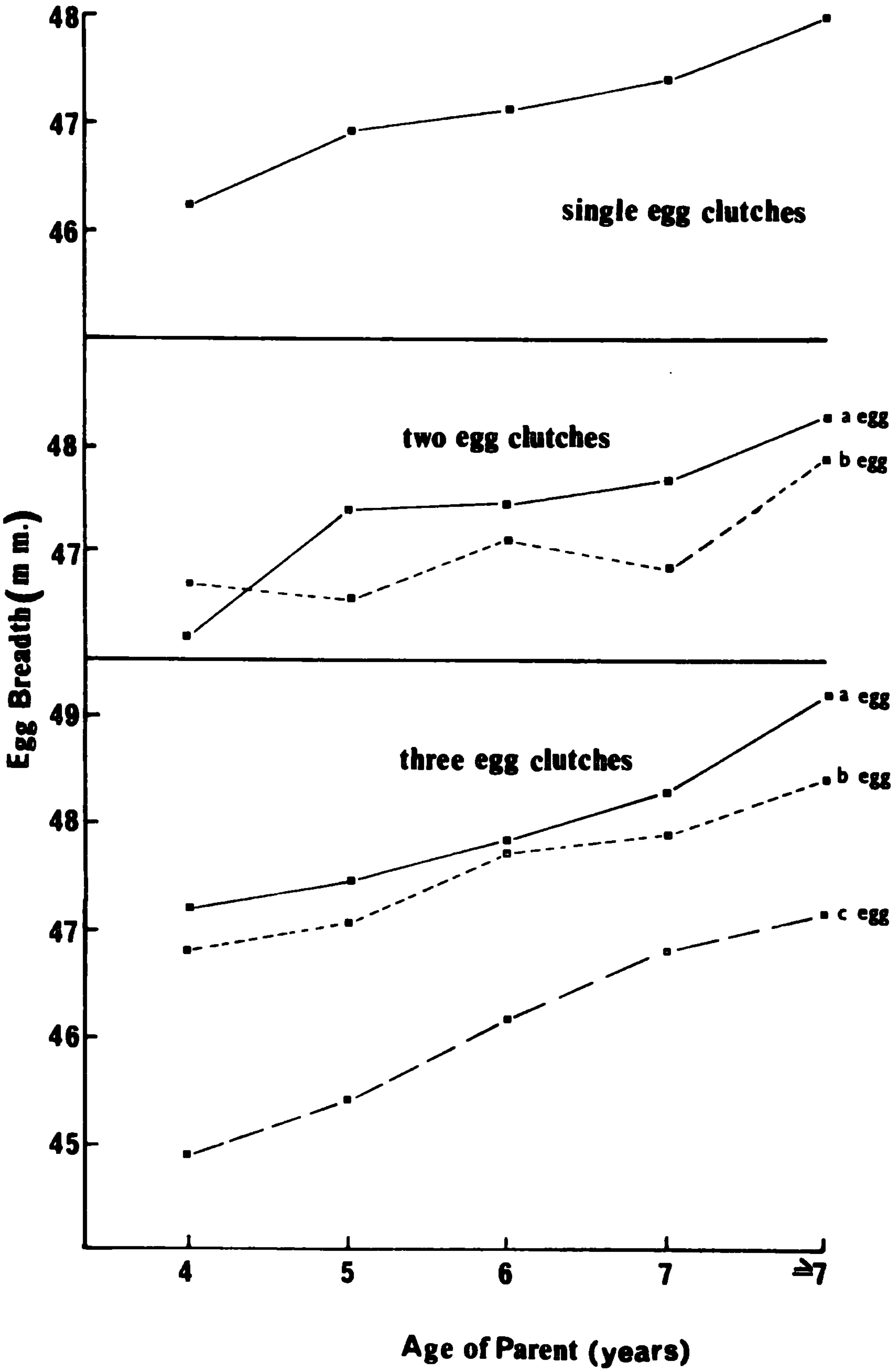
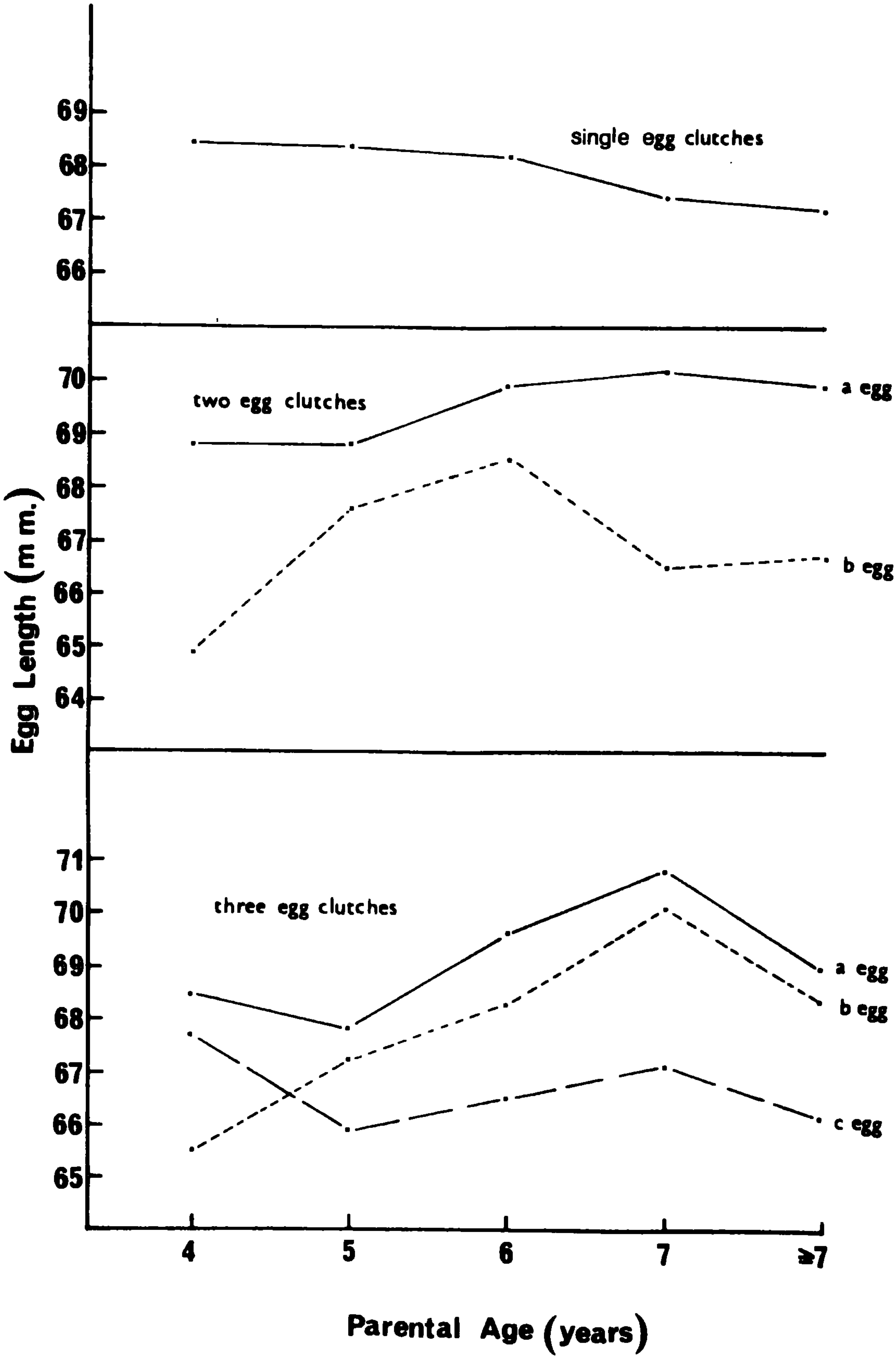

48
47
46
single egg clutches
two egg clutches
a egg
b egg
48
47
Egg Breadth (m m.)
49
three egg clutches
a egg
b egg
48
47
c egg
46
45
4
5
6
7
≥7
Age of Parent (years)

Figure 11

The variation of mean egg breadth with parental age



single egg clutches
two egg clutches
a egg
b egg
three egg clutches
a egg
b egg
c egg
Egg Length (m m.)
69
68
67
66
70
69
68
67
66
65
64
71
70
69
68
67
66
65
4
5
6
7
≥7
Parental Age (years)

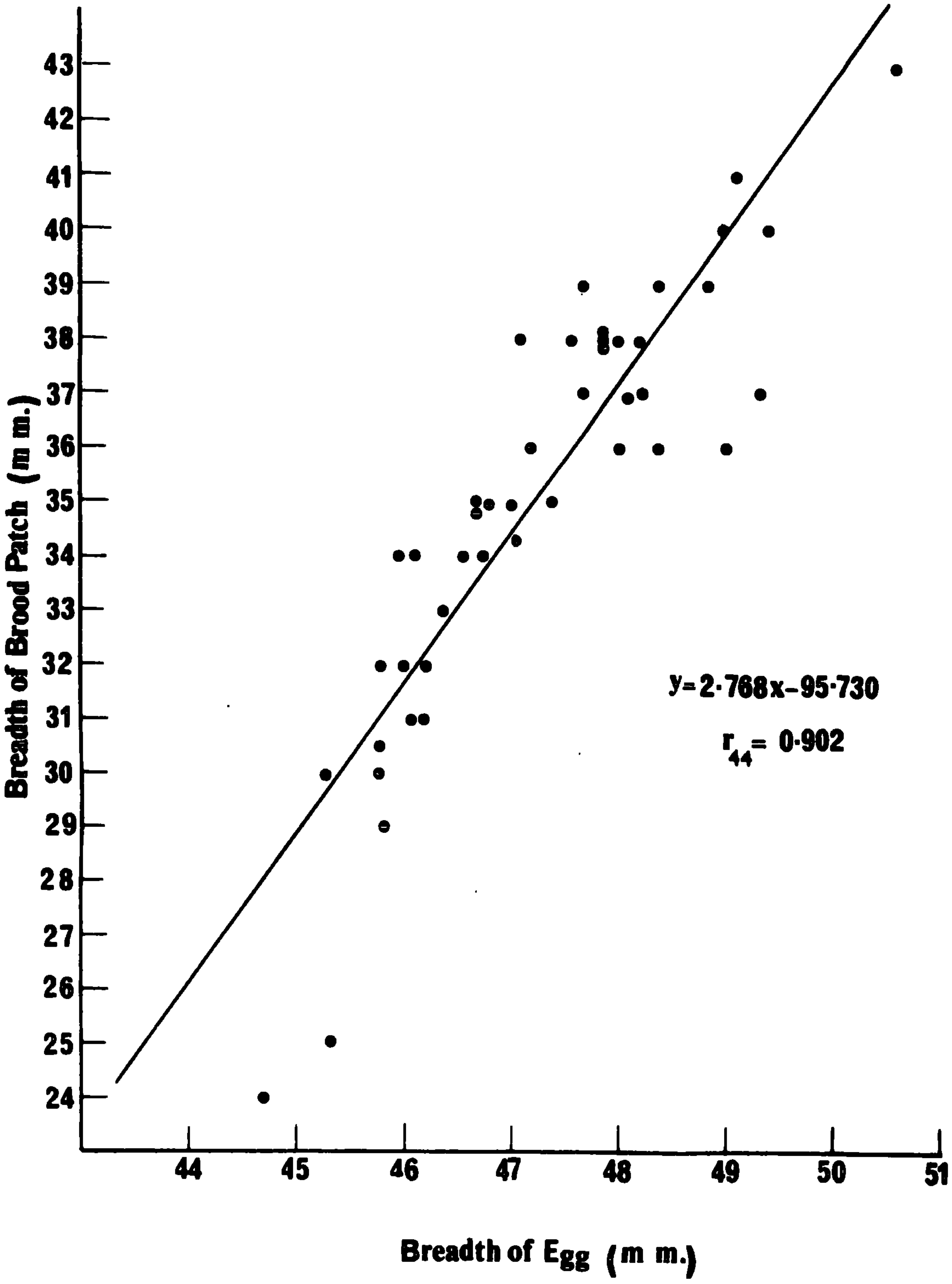
stimulation of the female reproductive tract probably takes longer to develop. It is doubtful whether egg length can be correlated with oviduct development.

Parsons (1975) demonstrated a close correlation between egg volume and subsequent chick survival; the highest pre-fledging survival rates being associated with the largest egg volumes. Increasing egg breadths result in proportionately greater egg volume increases than do length changes and may, in part, account for the higher pre-fledging survival of the progeny of experienced breeders (Table 35, Section 3.6). However, this can only be one of the factors involved in determining overall breeding success. Other factors, notably brood protection and feeding of chicks, are likely to be of greater importance.

In the 1973 cull a small number of Herring Gulls were found to have died while they were actually still on the nest. On the previously unculled areas of North Ness and South Ness many of these birds had succumbed to the narcotic whilst incubating one or more eggs. For these birds the sizes of eggs, together with the sizes of the corresponding brood patches, were measured, and since the orientation of the egg was always such that the long axis of the egg was aligned anterio-posteriorly, it was possible to investigate the relationship between brood patch size and egg size. For this sample there was a highly significant correlation between brood patch width and egg breadth ($r_{44} = 0.902$, $p < 0.001$; Figure 12); although there was no significant correlation between brood patch length and egg length ($r_{44} = 0.186$, $p > 0.05$). This result was surprising because in all cases brood patch size was smaller than egg size, and if contact between the egg and the developing brood patch was important in determining the extent of defeathering (as has been suggested for Canaries by Hutchison, Hinde and Steel 1967), it might be expected that both egg dimensions would have contributed to this process. Since this did not appear to be the case

Figure 12

The relationship between breadth of brood patch and breadth of corresponding egg


43
42
41
40
39
38
37
36
35
34
33
32
31
30
29
28
27
26
25
24
Breadth of Brood Patch (m m.)
44
45
46
47
48
49
50
51
Breadth of Egg (m m.)
y=2·768x−95·730
r44= 0·902

it suggested that axial differences in brood patch development and brood patch to egg contact existed. For Black-headed Gulls, Beer (1961) noted marked side-to-side movements in incubating birds; similar behaviour in Herring Gulls might have explained the close correlation observed between brood patch and egg breadth. In addition, the differences between brood patch length and the length of the corresponding egg were significantly larger than those between brood patch breadth and egg breadth (Table 15). In other words, long eggs may not have been covered by the vascularized brood patches to the same extent that shorter broader eggs would have been, and it might be expected that broader eggs would have been better incubated than longer, narrower eggs of equivalent volume. Another consequence of laying broader eggs is that such eggs would be better incubated, a fact which might account for the higher hatching success of eggs laid by experienced breeders (see Table 24, Section 3.4).

The trend for broader eggs to be laid by the most experienced birds was at its most pronounced in the clutches laid by adult-ringed breeding birds i.e. gulls which had bred at least once before, where a decrease in axial egg length occurred against a background of increasing egg breadth and volume.

Table 15. Brood patch size in relation to egg size in a sample of unringed adult Herring Gulls culled in May 1973

Number of gulls examined	Mean brood patch length (mm) ± S.E.	Mean egg length (mm) ± S.E.	Mean difference between brood patch and egg lengths (mm) ± S.E.	Mean brood patch breadth (mm) ± S.E.	Mean egg breadth (mm) ± S.E.	Mean difference between brood patch and egg breadths (mm) ± S.E.
46	48.50 ± 1.45	68.70 ± 0.43	20.34* ± 1.50	35.01 ± 0.57	47.23 ± 0.19	12.09* ± 0.41

* Means are significantly different from each other, $t_{90} = 5.305$, $p < 0.001$

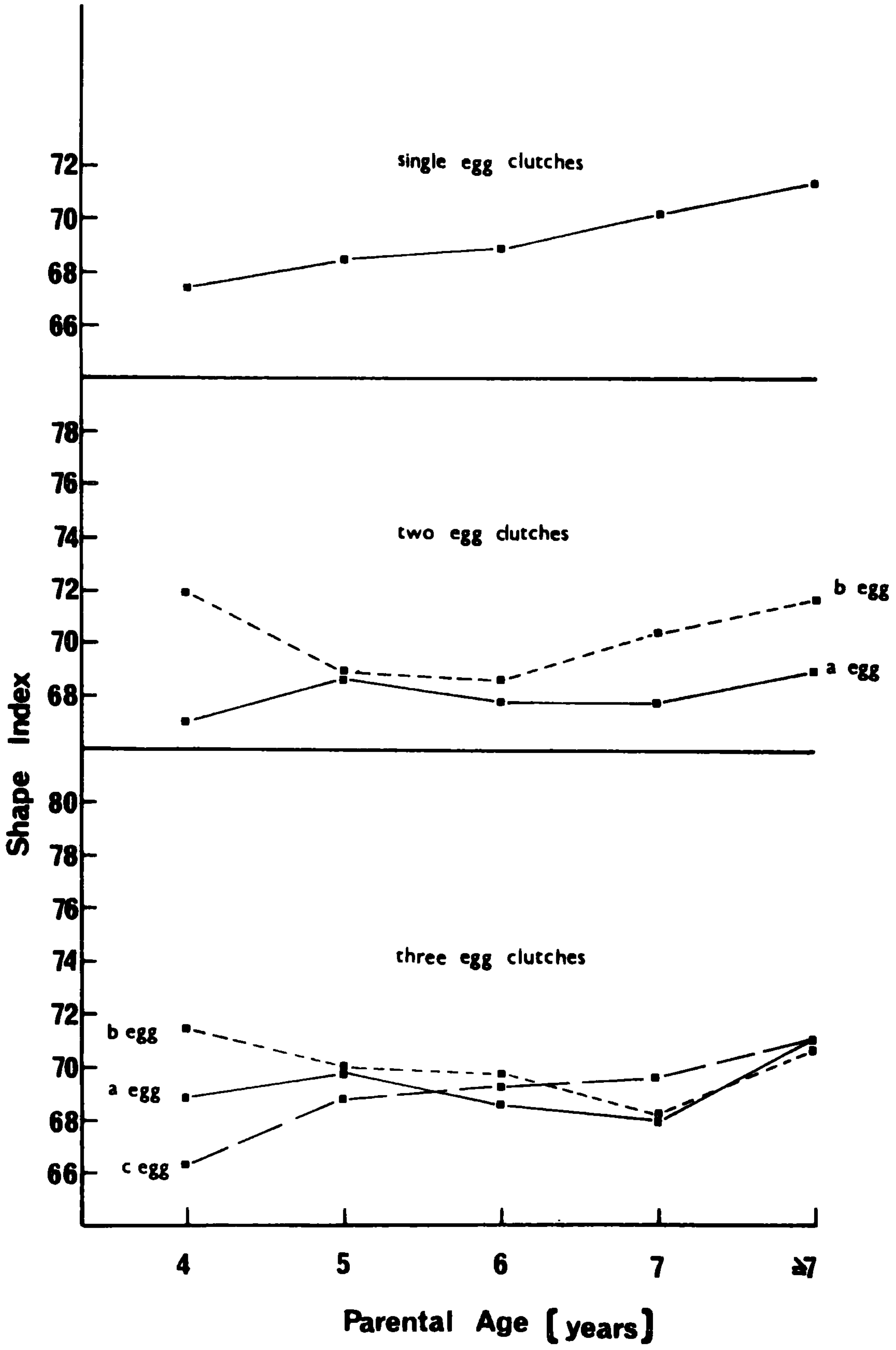
In the Kittiwake, the shape indices of eggs increase as the age of the breeding females increase (Coulson 1963). In Herring Gulls, shape indices varied considerably (Figure 13) and although they were highest for the shorter, broader eggs laid by the oldest birds, for recruit breeders there were virtually no changes and in some cases there were decreases in shape indices. For example, in the a-eggs of c.3 clutches, shape indices increased with parental age up to the fifth year of life, decreased from the fifth to the seventh year, and increased after the seventh year. Similarly, in c.2 clutches there were initial increases in a-egg shape indices up to the age of five years, followed by a gradual decline from five to seven years old, after which the indices increased. In c.2 and c.3 clutches there was no consistent pattern in the age variation of shape indices. In c.1 clutches, however, there were progressive increases in indices with age (Figure 13).

From the present study of the Herring Gull it seems that the best single parameter of use in determining age composition was egg breadth. Although, as Coulson (1963) points out, this is only of use when there is no clinal variation to account for, since birds at more northerly latitudes are larger (Bergman's Rule) and tend to lay larger eggs.

It will be suggested later (Section 5.3) that areas on the Isle of May which had been colonised by breeding Herring Gulls since 1966 were probably initially settled by predominantly young breeders (four and five year old gulls). It is known from N.C.C. records that part of the Colm's Hole study area is within the range of the recent, post-1966 expansion of breeding Herring Gulls on the Isle of May. In addition, census counts made of this area indicated a higher proportion of four and five year old breeding birds than occurred at East Tarbet (Table 58,Section 5.5). From what is known about the variation of egg size with age, any differences in age composition between the two study areas would be expected to be revealed

Figure 13

The variation of shape index and parental age


single egg clutches
72
70
68
66
two egg clutches
78
76
74
72
70
68
b egg
a egg
Shape Index
three egg clutches
80
78
76
74
72
70
68
66
b egg
a egg
c egg
4
5
6
7
≥7
Parental Age [years]

in the measurements of eggs laid by gulls breeding on the two areas. In fact, in comparison to East Tarbet, the 133 clutches measured on Colm's Hole showed that eggs laid on this area were of smaller volume (Table 16). The overall breadth of all eggs laid on Colm's Hole was 47.40 ± 0.10mm, which was significantly lower than 48.00 ± 0.10mm, the mean breadth of eggs laid on East Tarbet ($t_{668} = 4.194$; $p < 0.001$). On Colm's Hole the mean egg breadth was intermediate between the values for six and seven year old breeding gulls (Tables 14 & 16), whilst that for East Tarbet approached that of the adult-ringed gulls and suggests that breeding birds on the Colm's Hole area may have been on average younger than those on East Tarbet.

Table 16. The volumes of eggs laid on the Colm's Hole and East Tarbet study areas in 1972

		Colm's Hole		East Tarbet	
Clutch size	Laying sequence	Mean egg volume (cm^3) ± S.E.	Number of clutches	Mean egg volume (cm^3) ± S.E.	Number of clutches
1		73.69±1.59	12	76.71±1.20	20
2	a	73.49±1.16	31	75.57±0.78	52
	b	71.85±1.52		70.17±0.87	
3	a	76.08±0.70	90	78.56±0.69	97
	b	74.02±0.66		76.32±0.61	
	c	67.71±0.58		69.14±0.91	

From Table 17 it can be seen that between the ages of five and seven years there was an overall reduction in the variance of egg breadths. This reduction in variability was not necessarily a measure of increasing similarity of the eggs laid by older birds. The ranges in mean volumes of eggs laid by five,six, seven year old and adult-ringed breeders were as follows:

64.46 - 73.79 ($9.33cm^3$); 67.80 - 76.12 ($8.32cm^3$); 69.55 - 78.68 ($9.13cm^3$) and 70.44 - 79.26 ($8.82cm^3$) (Table 14). In all age classes, except five year old gulls, the largest eggs laid were the a-eggs, and the smallest the c-eggs in c.3 clutches (in five year old birds the largest eggs were the a-eggs of c.2 clutches). In five and six year old birds the decrease in the range of mean egg volumes was mainly attributable to the larger percentage increase in c-eggs (5.2%) than in a-eggs (3.2%) from one year to the next.

Table 17. The variation of egg breadth in relation to parental age

(For Isle of May Herring Gulls breeding in
1972 and 1973)

Parental age (years)	Number of eggs	Mean breadth of eggs laid ± S.E.	Variance of breadth	Value of Student's t
4	12	46.46 ± 0.18	0.389	
				N.S.*
5	168	46.80 ± 0.14	3.089	
				2.584, $p < 0.01$
6	233	47.26 ± 0.11	2.926	
				N.S.
7	97	47.63 ± 0.16	2.372	
				2.375, $p < 0.02$
≥ 6	61	48.22 ± 0.19	2.263	

* N.S. not significant at the 95% confidence level.

For the difference between mean breadths of eggs laid by four year old breeders and those laid by adult-ringed birds: $t_{71} = 6.725$, $p < 0.001$. However, there is no consistent pattern of relatively greater increases in c-volumes than in a-volumes, thus comparing six and seven year old birds the change in a-volumes (3.4%) was greater than that of c-eggs (2.3%); whilst between seven year old and adult-ringed birds the c-volume change (1.3%) was slightly larger than that for the a-eggs (0.74%).

Thus the greatest variability between eggs occurred in five year old birds and was due to small c-egg volumes. This egg also showed the greatest increase with parental age (a 5.2% increase between the ages of five and six years) and may have been the result of the demand placed on body reserves by young breeders in laying the first two eggs of a clutch. The volumes of eggs laid by four year old gulls were uniformly small and showed the least variability: 64.97 - 72.64cm^3 (7.67cm^3), there being little change in this range between the ages of four and five years; thus four and five year old breeders may have been at the limits of their physiological resources.

A similar analysis for egg breadths is given in Table 18 and indicates that a decrease in egg breadth range occurred as parental age increased up to the age of seven years. Up to this age, decreasing variability in breadth was mainly due to changes in the c-eggs in which increases were larger than in the a-eggs. The c-eggs in c.3 clutches gradually became more similar to the b- and a-eggs in the clutch. For adult-ringed gulls there was an increase in variability, but this was due to larger a-eggs rather than to changes in the c-egg.

Table 18. The components of variability in the breadth of eggs laid by Herring Gulls of known age breeding in 1972 and 1973

Parental age (years) sample size	4 (1)	5 (31)	6 (51)	7 (28)	≥ 6 (17)
Range in egg breadth (mm)	44.9 - 47.20 (2.3)	45.41 - 47.47 (2.06)	46.19 - 47.86 (1.67)	46.82 - 48.3 (1.48)	47.17 - 49.20 (2.03)
Percentage change in c-egg breadth	-	* 1.1	1.7	1.4	0.8
Percentage change in a-egg breadth	-	0.6	0.8	0.9	1.9

*Between the ages of four and five years the change in c-egg breadth was 44.9 to 45.41mm = 1.1%.

Coulson et al. (1969) have proposed that in Shags and Kittiwakes a useful ageing parameter is the within clutch variance of egg breadths which is a measure of the variability of egg breadths laid within individual clutches. In c.3 clutches laid by Kittiwakes, the mean within clutch variance increases with age; this increase has been attributed to the c-egg becoming increasingly dissimilar to the a- and b-eggs in older birds. In Herring Gulls the converse was true (Table 19), the mean within clutch variance of egg breadth for c.3 clutches decreased between the ages of five and seven years. As already suggested, this decrease in variability was due to the c-egg becoming more similar to the first laid eggs in the clutch.

The situation in the Herring Gull was thus analogous to that reported for the Shag by Coulson et al. (1969) in which the within clutch variance of egg breadths also decreases with increasing age.

Table 19. The variation of egg size within c.3 clutches as indicated by the within clutch variance, in relation to age

Parental age (years)	Mean within clutch variance ± S.E.	Number of clutches
4	(1.006)	1
5	1.2529 ± 0.0761	31
6	1.0751 ± 0.0532	51
7	0.7959 ± 0.0619	28
≥ 6	1.1082 ± 0.2309	17

The effects of age and laying date on egg size

An analysis of the effects of parental age upon egg size would be incomplete without some consideration of the effects of laying date. Previously for birds breeding on the Isle of May, Parsons (1975) had shown that egg volume in c.3 clutches decreased as egg laying progressed, with the smallest eggs being laid at the end of the laying period in late-May. Davis (1975) found a similar decrease in the volumes of eggs laid in c.3 clutches on Skokholm Island in 1969, although in the two subsequent breeding seasons of his study he found no changes attributable to date of laying.

It was pointed out in the discussion of clutch size that since recruits laid eggs later than older gulls, apparent differences in clutch size may have resulted from seasonal influence rather than from intrinsic differences between birds of different ages. Similar considerations apply to the effects of age upon egg size. It is also possible that smaller eggs laid at the end of the laying period may have been the result of recruit breeders which started to lay eggs at this time.

During the two years of the present study there were marked decreases in egg volumes as the breeding season progressed. This decline in volume was evident for eggs laid in c.1, c.2 and c.3 clutches (Table 20, Figures 14 and 15). There were some differences between the two years, in particular the volume decreases for the a-, b- and c-eggs of c.3 clutches laid in 1973 were larger than those for the preceding year. In part, this difference was due to the fact that no c.3 clutches were laid during the latest laying period in 1972. However, after 27 May of that year, eggs laid as c.1 and c.2 clutches continued to show volume decreases, and it seems likely that had c.3 clutches been laid after this date, the overall seasonal decrease would have been comparable to that observed in 1973. It should also be noted that in 1973 the time period up to 2 May was represented by a single, atypically large c.3 clutch (Table 20).

Figure 14

The seasonal decline in egg volume in 1972

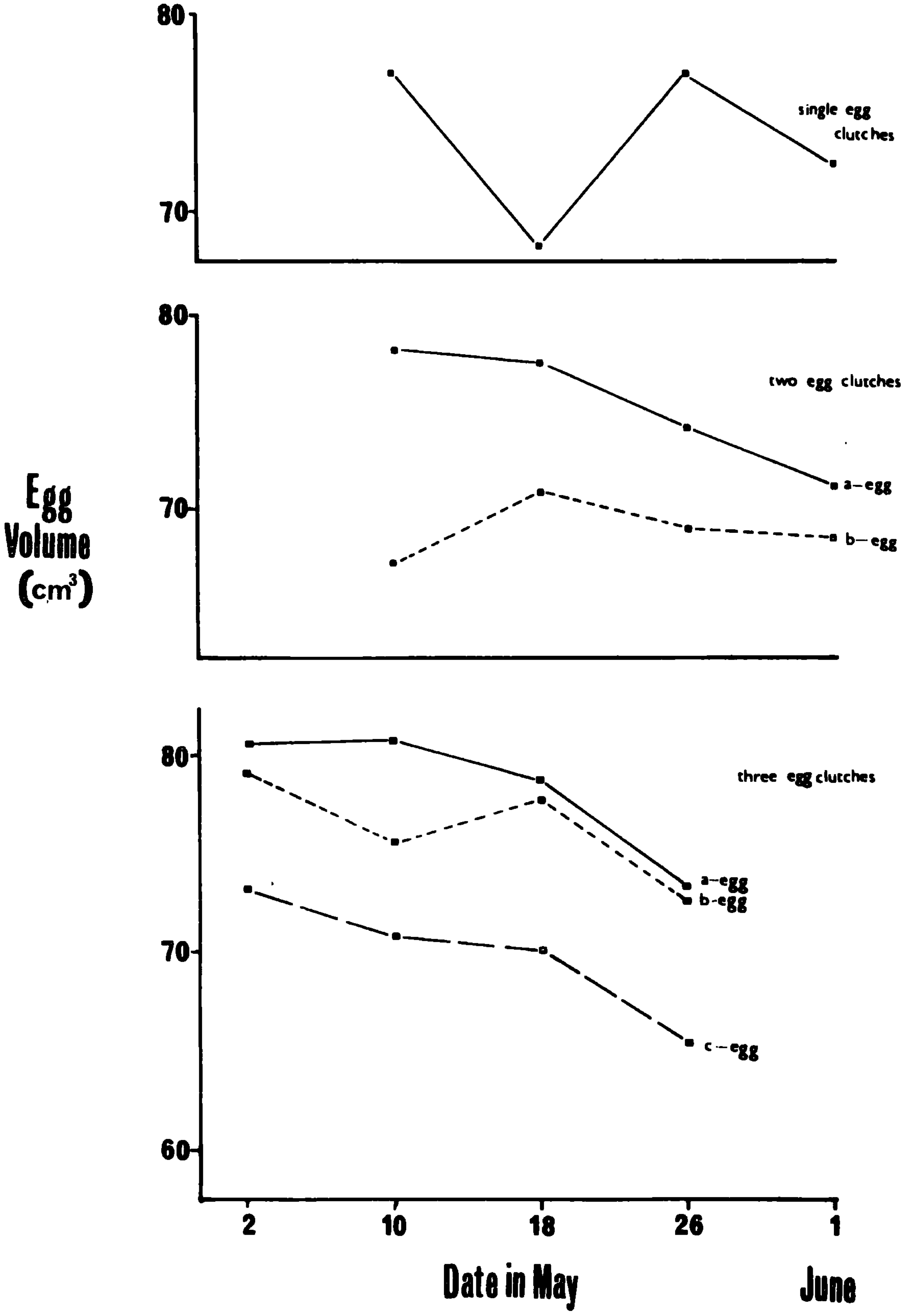

80
70
single egg clutches
80
70
two egg clutches
a–egg
b–egg
Egg Volume (cm³)
80
70
60
three egg clutches
a–egg
b–egg
c–egg
2
10
18
26
1
Date in May
June

Figure 15

The seasonal decline in egg volume in 1973

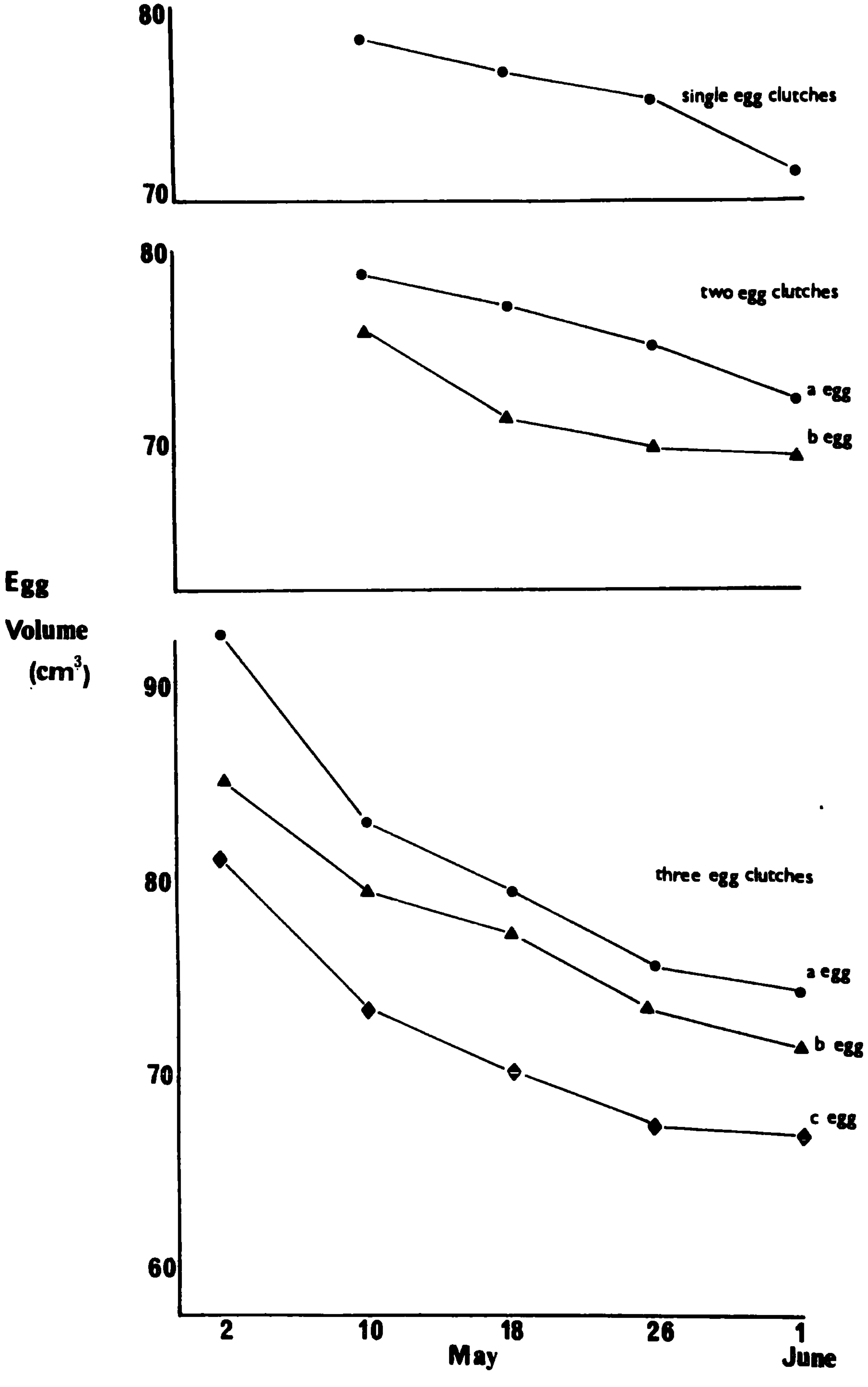

Egg
Volume
(cm^3)
80
70
single egg clutches
80
two egg clutches
a egg
b egg
70
90
80
three egg clutches
a egg
b egg
70
c egg
60
2
10
18
26
1
May
June

Table 20. The effect of laying date on mean egg volumes* for eggs laid by control groups of unringed Herring Gulls on East Tarbet in 1972 and 1973

	Clutch size	Laying sequence	Laying date					Percentage change in egg volumes
			up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May	
	1		N.L.**	77.20 ± 2.32 (7)***	68.4 (2)	77.06 ± 1.23 (9)	77.48 (2)	- 6.1
	2	a	N.L.	78.22 (4)	77.54 ± 0.95 (21)	74.39 ± 1.05 (24)	71.38 (4)	- 8.7
1972		b	N.L.	67.40 (4)	71.01 ± 1.50 (21)	69.26 ± 0.83 (24)	68.73 (4)	+ 2.0
	3	a	80.72 ± 2.04 (6)	81.27 ± 1.49 (28)	79.02 ± 0.95 (40)	73.60 ± 0.65 (22)	N.L.	- 8.8
		b	79.27 ± 1.99 (6)	75.75 ± 1.08 (28)	78.06 ± 0.99 (40)	72.93 ± 0.90 (22)	N.L.	- 8.0
		c	73.37 ± 2.03 (6)	71.02 ± 0.97 (28)	70.37 ± 0.92 (40)	65.56 ± 1.12 (22)	N.L.	- 10.6

* Egg volumes in cm^3, all means ± S.E. except where the sample size was less than 5.

** N.L. no eggs laid

*** Sample sizes are given in brackets

Continued overleaf

Table 20 (Continued)

	Clutch size	Laying sequence	Laying date					Percentage change in egg volumes
			up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May	
	1		N.L.	78.34 (3)	76.61 ± 0.89 (10)	72.25 ± 2.15 (5)	71.49 ± 0.64 (6)	- 8.7
	2	a	N.L.	78.77 (4)	77.20 ± 1.44 (21)	75.11 ± 1.38 (20)	72.48 ± 1.30 (6)	- 8.0
1973		b	N.L.	78.85 (4)	71.31 ± 1.35 (21)	69.83 ± 1.79 (20)	69.44 ± 1.57 (6)	- 8.5
	3	a	92.74 (1)	83.04 ± 0.84 (39)	79.47 ± 0.42 (68)	75.51 ± 0.89 (31)	74.28 ± 0.95 (16)	- 19.9
		b	85.16 (1)	79.40 ± 0.85 (39)	77.48 ± 0.50 (68)	73.19 ± 0.98 (31)	71.26 ± 1.04 (16)	- 16.3
		c	81.13 (1)	73.32 ± 0.90 (39)	70.13 ± 0.55 (68)	67.17 ± 0.83 (31)	66.90 ± 0.84 (16)	- 17.5

With the exception of b-eggs laid in c.2 clutches in 1972, the volume decreases in a- and b-eggs in c.2 clutches, and c.1 clutches in 1973 were similar (8.0 - 8.7%). The decrease for eggs laid as clutches in 1972 indicated lower volume decreases than other eggs, although final egg size for these eggs was based only on two clutches (Table 20), and more data than were available would be needed to establish whether the pattern of volume change in these eggs differed from those laid in other clutches.

In both years the most severe decrease attributable to laying date occurred in the volume of the c-eggs laid late in May and early June. In this respect the pattern of seasonal changes in 1972 and 1973 was similar to that recorded by Parsons (1975) on the Isle of May, and by Davis (1975) in the 1969 breeding season on Skokholm Island.

This finding accords with the suggestion made by Parsons (1975) to the effect that the smaller late-laid eggs in this species are a result of waning physiological capability rather than of seasonal food shortage. The c-egg results from the last developing follicle and might be expected to be most susceptible to reduced gonadotrophic secretion. Follicle growth and development in the avian ovary is known to be induced and sustained by follicle stimulating hormone (F.S.H.) secreted from the adenohypophysis (van Tienhoven 1961) whilst ovulation is probably stimulated by decreasing F.S.H. levels and rising blood titres of leutenising hormone (L.H.) (Farner 1967, van Tienhoven 1961). A seasonal decrease in F.S.H. production may result in the ovulation of a small poorly developed ovum giving rise to a small final egg.

The seasonal changes in the volumes of eggs laid by Herring Gulls of known age paralleled those occurring in the unringed control samples. In colour-ringed birds, egg volume also decreased as the breeding season progressed, with maximum changes taking place in the c-eggs of c.3 clutches.

The decline of egg volumes in relation to age, clutch size, laying sequence and laying date are given in Appendix 6, the combined data for all eggs being presented in Table 21 and Figure 15.

The largest volume decreases attributable to laying date occurred in eggs laid by the oldest breeders, and there was a gradual increase in the percentage volume change as the age of breeding females increased. This was due in large part to the larger eggs laid by older birds at the beginning of the laying period; four and five year old birds laid small eggs throughout the two seasons. Thus, early in the egg laying period (3-10 May) there were significant differences between the egg volumes laid by five and six year old gulls ($t_{28} = 2.356$, $p < 0.05$) and between those laid by five and seven year old birds ($t_{18} = 4.062$, $p < 0.001$); the difference between six and seven year old birds was not significant ($t_{39} = 1.995$, $p > 0.05$).

By the second half of the laying period (19 May onwards), the differences between the volumes of eggs laid by different age classes was greatly reduced. Eggs laid by six and seven year old birds and adult-ringed birds were similar, although eggs laid by five year old females were still significantly smaller than those of older birds (comparing the five and six year age classes: $t_{223} = 3.394$, $p < 0.001$). By the end of the season all eggs laid by colour-ringed birds were of similar size.

It therefore seems that for the Isle of May colony the smaller late-laid eggs were not simply the result of recruits laying later than old birds, since all eggs laid by this time were small. The uniformity of egg volumes in late-May suggests that whatever factors were responsible for diminished egg size, they operated upon recruit and experienced breeders alike. This means that four and five year old females, since they laid eggs later in the season than six and seven year old birds, effectively had a shorter laying period since for all birds the suppression of egg laying began in late-May. Similarly, Coulson _et al._ (1969) have noted that Shags, irrespective of age, lay larger eggs earlier in the season.

There were age differences between egg sizes earlier in the season, eggs laid by recruit breeders being smaller than those laid by older birds in equivalent time periods. Since this was the case, it seems that there were also intrinsic differences between age classes, and, as suggested before, the smaller eggs laid by four and five year old birds may have been the result of differences in the extent and in the mobilisation of energy reserves by these younger breeding females.

Table 21. The effect of laying date on the volumes* of all eggs laid in 1972 and 1973 by Herring Gulls of known age

	Laying date of first egg in clutch						
Parental age (years)	up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May	Number of clutches	Percentage change* in mean volume
4	N.L.**	N.L.	68.63±5.69 (3)***	70.25±0.89 (3)	69.31±1.80 (3)	7	+ 1.0
5	N.L.	73.18±1.10 (6)	71.83±1.19 (38)	68.97±0.80 (74)	69.35±1.40 (19)	70	- 5.2
6	N.L.	76.93±1.15 (20)	73.54±0.85 (82)	72.60±0.71 (113)	69.15±1.07 (12)	99	- 10.1
7	83.16±2.22 (6)	80.67±1.48 (15)	73.75±1.03 (30)	72.59±0.83 (35)	71.67±1.51 (9)	36	- 13.8
≥ 6	N.L.	78.47±2.37 (17)	75.32±1.04 (26)	73.00±1.25 (17)	69.14±1.28 (3)	23	- 11.9

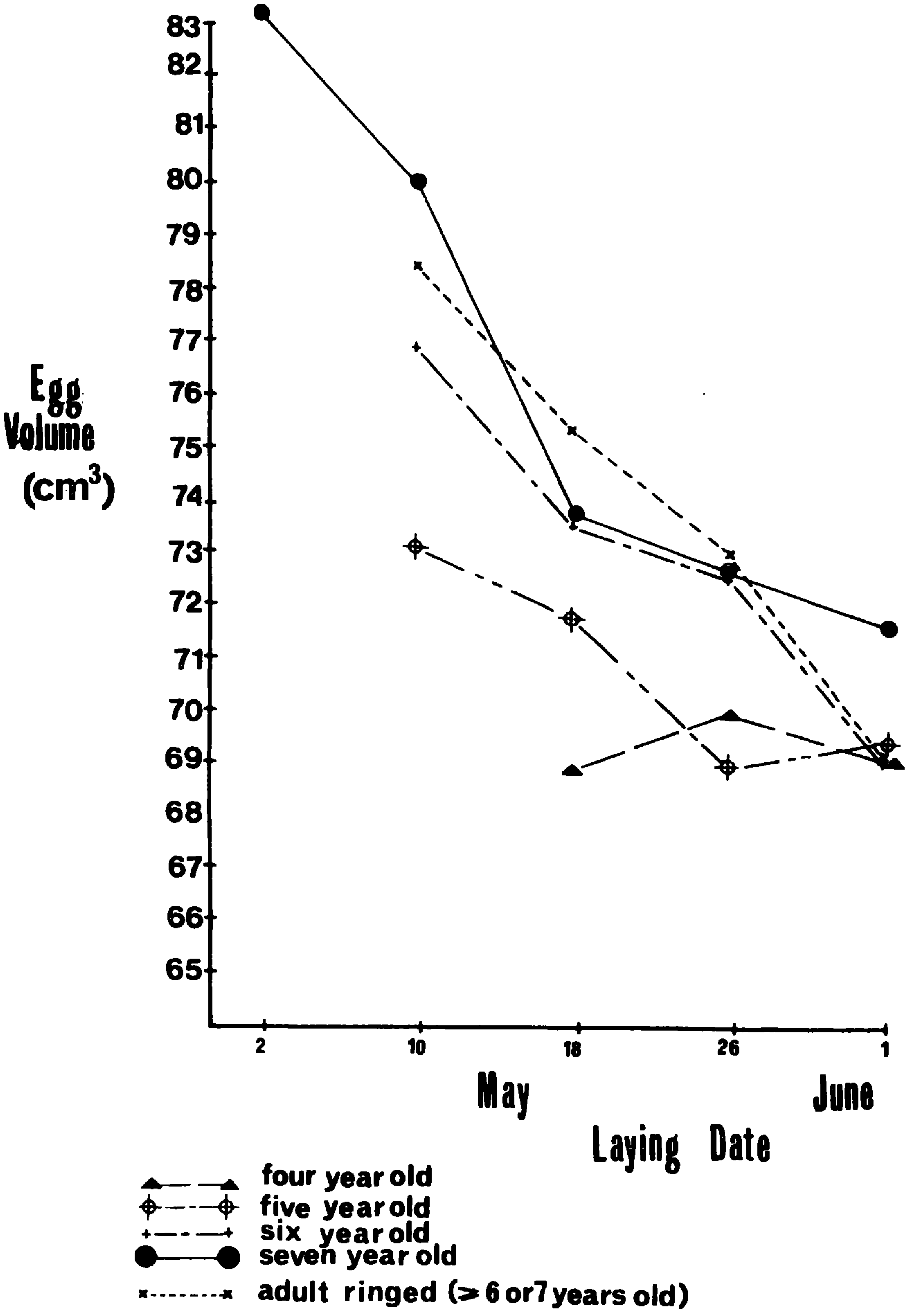
* Mean egg volume ± S.E.

** N.L. = none laid

*** Number of eggs measured in a given time period given in brackets

Figure 16

The effects of laying date and parental age on egg volume for clutches laid in 1972 and 1973


Egg Volume (cm³)
83
82
81
80
79
78
77
76
75
74
73
72
71
70
69
68
67
66
65
2
10
18
26
1
May
June
Laying Date
four year old
five year old
six year old
seven year old
adult ringed (> 6 or 7 years old)

3.4 Hatching Success

Introduction

Of the 447 eggs laid in study nests on East Tarbet in 1972, 295 (66.0%) hatched successfully. The hatching success for eggs laid on the Isle of May in this study was similar to that recorded previously for this colony by Parsons (1975) and falls within the range recorded by other workers at various British colonies, although for Herring Gulls breeding at northern European and American colonies the proportions of successfully hatched eggs may be much higher (for example the Danish colony studied by Paludan on Christianse Island, Table 22).

The data available from different studies of Herring Gull breeding biology indicate a wide variation in hatching success. The typical range of success for this species appears to be between 51 to 90%. The exceptionally low value of 19% obtained by Hunt (1972) for the Flat Island colony was the result of extensive human disturbance of nesting gulls rather than of high mortality rates.

Table 22. Hatching success recorded at various Herring Gull colonies

Study colony	Authority	Number of pairs studied	Percentage of eggs that hatched
Skomer Island, Pembrokeshire	Harris 1964a	220	64
Skokholm Island, Pembrokeshire	Davis 1975	ca. 92	51 - 79*
Walney Island, Cumbria	Brown 1967	139	66
Summer Isles, Ross and Cromarty	Darling 1938	ca. 50	88 - 96**
Isle of May, Fife	Parsons 1975	ca.1,000	64 - 70**
Island colonies, Penobscot Bay, USA	Hunt 1972	37 - 169	19 - 69***
Kent Island, Canada	Paynter 1949	100	71
Island colonies, New England, USA	Kadlec and Drury 1968a	ca.3,000	80
Christianse Island, Denmark	Paludan 1951	90	90
Sandy Point, Rhode Island, USA	Erwin 1971	48	67 - 82****

Ranges are given where * seasonal variation has been found, or ** annual variations existed, or where other factors have been cited as important determinants of hatching success, *** disturbance, **** predation.

Effects of clutch size

One of the factors that has been documented as contributing to variation in hatching success is clutch size. c.3 clutches have been reported to have a higher hatching success than c.1 clutches by Harris (1964a), Brown (1967) and Parsons 1971a); since birds breeding at the colonies listed in Table 22 were known to lay clutches of varying sizes, this factor may have accounted for the observed variability in hatching success.

On East Tarbet in 1972 eggs laid in c.1 clutches had a markedly lower hatching success than those laid in c.3 clutches (Table 23).

Table 23. The effect of clutch size on hatching success of eggs laid by unringed Herring Gulls breeding on East Tarbet in 1972

Clutch size	1	2	3	Total
Number of clutches laid	23	59	102	184
Number of eggs laid	23	118	306	447
Number of eggs that hatched	5	70	220	295
Hatching success † (%)	21.7*	59.3**	71.9	66.0

* For the difference between the hatching success of eggs laid in c.1 and c.2 clutches $\chi^2_{(1)} = 10.920$, $p < 0.01$ and similarly ** comparing c.2 with c.3 clutches $\chi^2_{(1)} = 6.228$, $p < 0.02$.

† The percentage of eggs laid that successfully hatched.

The differencesin hatching success for different clutch sizes were similar to those found by Harris (c.1, 0%; c.2, 50%; c.3, 67%); Paynter (29%, 56%, 80%), Brown (50% for c.1 and c.2; 72%, c.3) and

Parsons (18%, 54%, 73%). Each of these authors attributed clutch size differences in hatching success to the fact that small clutches were laid by "careless and inexperienced" breeders (see for example Harris 1964a). They implied that the low hatching success of c.1 clutches was due either to the deficiencies in incubation behaviour exhibited by inexperienced breeders (Harris 1964a, Brown 1967) or to intrinsic individual differences in reproductive drive (Parsons 1971a).

Hatching success was largest for eggs laid by the adult-ringed gulls breeding in 1972 (Table 23) and lowest in four year old birds, although the difference between the total hatching success of eggs laid by four and five year old females was not significantly different from that of eggs laid by females that were six years and older ($\chi^2_{(2)} = 4.191$, $p > 0.05$). Similarly, although the progressively increasing hatching success of eggs laid by older birds suggested an age effect, the differences between age classes were not significant for any clutch size (in all cases $p > 0.05$). Neither was there a statistically significant departure from predicted and observed numbers of eggs hatched (Table 24).

The most obvious cause of variations in hatching success was clutch size; the disparity between hatching success of eggs laid in c.1 and c.3 clutches, noted for the East Tarbet control sample, was maintained by birds of similar age. It was thus an oversimplification to equate low hatching success with the results of the inexperienced breeding of recruits, since clearly the hatching of eggs laid in c.1 clutches was markedly poorer than that for c.3 clutches, regardless of age.

It has been noted by Coulson <u>et</u> <u>al</u>. (1969) that individuals in a population of seabirds rarely reach the same state of reproductive drive and that in any given year individuals from a spectrum of stages in the reproductive cycle are present at the colony. These observations were clearly applicable to Herring Gulls on the Isle of May. Thus, in both years of this study, within one age class of gulls, some birds were observed not to acquire territory, others acquired territory but did not lay eggs, and others laid small clutches. It seems likely that differences in hatching success were a manifestation of individual variations of the extent to which reproductive tendency had developed. Although,on average, recruits appeared to have been of lower reproductive tendency than experienced birds, the variations within any given age class could be as large as those between age classes.

Causes of hatching failure

The causes of hatching failure for eggs laid in the 1972 season are summarized in Table 25. For colour-ringed birds, the largest single factor contributing to hatching failure was loss through predation. Egg predation took place by other gulls and was particularly high when there was any human disturbance of nesting birds. The disturbance caused by making visits to the study nests undoubtedly contributed to egg losses, although it was difficult to quantify the losses that resulted in this way.

In many cases eggs were eaten at the nest site by neighbouring gulls. The numbers of eggs lost in this way are given in Table 25 and relate specifically to cases where there was clear evidence of predator loss, either from direct observations or from the evidence of egg shell remains at the nest site. However, it was also common to see eggs being removed from nests and eaten some distance away from the robbed nest. Hence, estimates of egg losses based on shell remains and upon direct observations were probably too low. Many eggs simply disappeared without trace (11.4% of all eggs laid on East Tarbet), and the most likely cause of these losses would seem to have been predation. For the East Tarbet sample, 98 eggs out of a total of 447 eggs laid were probably lost as a result of predation (21.9%). Egg losses of a similar order had been reported to occur for Herring Gulls breeding on Skomer Island (24.9% of all eggs laid, Harris 1964a), Kent Island (28.7%, Paynter 1947), although for Herring Gulls nesting on Gull Island the figure was much lower (10.3%, Haycock and Threlfall 1975).

In 1972 there was evidence that the extent of egg loss due to predation was greater in six year old breeders than in younger breeding birds ($\chi^2_{(1)} = 9.004$, $p < 0.01$). As a general rule, four and five year old breeding birds were observed to be more prone to leave the nest during disturbance, and tended to leave the nest and eggs unattended for longer periods than did six year old breeders, and as a consequence might have been expected to have suffered high egg predation. However, four and five year old birds established territories on the sub-colony periphery, and on average were breeding at lower densities (Table 38, Section 3.6). The extent of egg robbing was greatest in areas of high nesting density and appeared to be the result of opportunist individuals rather than of selective egg predation. This is in contrast to some Herring Gulls which have been found to be persistent predators of chicks (Parsons 1971b).

It was evident that a high proportion of hatching failure in five year old gulls was due to the death of the chick at hatching (26.1% as compared with 7.0% and 8.6% of the total hatching failures in six year old and unringed gulls in the control sample). In comparison to the unringed sample on East Tarbet, the eggs laid by five year old gulls showed a three-fold proportionate increase in hatching failure due to this factor ($\chi^2_{(1)} = 9.841$, $p < 0.01$). Typically in this category of hatching failure chicks that had partially emerged from the egg shell were found to be flattened, and in some cases may have been trampled by the parents. In addition, this category included heavily pipped eggs which had been crushed by the parents. Mortality from this cause may have reflected the parents' inability to make the behavioural transition from incubation to brood care, as has been suggested by Brown (1967) and Kadlec, Drury and Onion (1969). The fact that the incidence of mortality from this agent decreased as the age of the breeding pair increased suggested behavioural changes which occurred with increasing breeding experience. Another index of changing behaviour was provided by the decreasing proportions of "addled" eggs in older birds. The term addled refers to eggs in which either no embryonic development had taken place, or in which development had ceased. The former case was due to the laying of unfertilised eggs, while the latter may have resulted from inadequate incubation of eggs where the temperature threshold fell below that necessary for embryonic development. There were indications that the incidence of both types of addled eggs decreased in gulls that were six years and older (Table 25). Increased numbers of unfertilised eggs implied low reproductive drive in males, whilst cessation of embryonic development may have been linked to the poorer nest site tenacity of inexperienced breeding birds where eggs were left unattended for long periods of time.

In some nests, eggs were found which were either rolled a short distance away from the nest or which had been covered by and incorporated into the nest material. All such eggs felt cold to the touch, and once rejected from the nest were never observed to be incubated. None of these eggs hatched. Similar instances were recorded by Parsons (1971a). The process by which these eggs came to be rejected was never observed, although it seemed likely that eggs became dislodged during boundary disputes which frequently occurred on the breeding areas. Certainly encounters that involved "wing pulling" (Tinbergen 1953) sometimes caused much disturbance to nests, and eggs may have become dislodged in the process. Frequently where this happened, replacement eggs were laid. These are not considered in Table 25. Where no replacements were laid, such rejection of eggs can legitimately be considered as a constituent of hatching failure. There

Table 24. Hatching success for eggs laid by Herring Gulls of known age in 1972 in relation to clutch size

	c.1 clutches			c.2 clutches			c.3 clutches					
Parental age (years)	Number of eggs laid	Number that hatched	Hatching success *	Number of eggs laid	Number that hatched	Hatching success *	Number of eggs laid	Number that hatched	Hatching success *	Total no. of eggs laid	Total no. that hatched	Overall hatching success *
4	3	1	33.3	6	2	33.3	3	2	66.7	12	5	41.7
	(expected**)	(1)			(2)			(2)				
5	13	3	23.1	36	19	52.8	60	41	68.3	109	63	57.8
	(expected)	(3)			(21)			(43)				
6	5	1	20.0	22	13	59.2	102	73	71.6	129	86	66.7
	(expected)	(1)			(13)			(73)				
≥ 6	1	0	0	4	3	75.0	30	22	73.3	35	25	71.4
	(expected)	(0)			(1)			(18)				

* $\frac{\text{number of eggs that hatched}}{\text{number of eggs laid}} \times 100$

** expected numbers hatched are calculated from the hatching successes for c.1, c.2 and c.3 clutches for the East Tarbet control sample (Table 23) and are given to the nearest whole egg.

Table 25. The causes of hatching failure in Herring Gulls of known age and for an unringed sample of birds breeding on the East Tarbet study area in 1972

	Number of eggs failing to hatch					
Parental age (years)	Predated	Addled + +	Died while hatching	Rejected	Unknown	Total
4	2 (28.6)†	3 (42.9)	1 (14.3)	0	1 (14.3)	7
5	15 (32.6)	11 * (23.9)	12 (26.1)	2 (4.4)	6 (13.0)	46
6	21 (48.8)	4 ** (9.3)	3 (7.0)	3	12 (27.9)	43
≥ 6	3 (30.0)	0	1 (1.0)	1 (1.0)	5 (50.0)	10
East Tarbet study area	47 (30.9)	34 *** (22.4)	13 (8.6)	7 (0.9)	51 (33.6)	152

† Percentages of the total hatching failures are given in brackets

* includes four eggs in which there were signs of embryonic development

** includes two eggs in which there were no signs of embryonic development

*** includes nine eggs in which there were no signs of embryonic development

\+ + addled eggs are those eggs in which either no embryonic development has taken place or in which embryonic development has ceased was a trend for the incidence of such eggs to increase with parental age. Rejection of eggs did not appear to imply behaviour inadequacy since when replaced into the nests the incubation of such eggs continued in most cases (for 12 eggs out of 15 replaced in nests of control breeders on East Tarbet) although these eggs never hatched.

Considering hatching failures due to suspected behavioural inadequacies (addled eggs and chicks dead at hatching) in four and five year old gulls, the number of eggs that failed to hatch as a result of these factors was 27 (50.9% of all hatching failures). The equivalent number in birds that were six years and older was eight (15.1%) and the proportion differs significantly from that of younger birds ($\chi^2_{(1)} = 15.399$, $p < 0.001$). However, considering total hatching failures, this difference between eggs was obscured by the greater egg losses due to predation of eggs laid by older breeding birds.

3.5 Post-hatching Survival

Introduction

For this study, in order to compare the breeding success of Herring Gulls of different ages, it was necessary to determine the post-hatching survival of the successfully hatched young. In 1972, the post-hatching survival of chicks was followed until 27 July on the three study areas: East Tarbet, North Ness and Colm's Hole. Territories belonging to colour-ringed breeding birds were mapped (Figure 19, and see Appendices 7 and 8) and visited at three to six day intervals.

Although attempts were made to keep disturbance on the study areas to a minimum by staggering visits and by keeping the time spent at any particular nest site to a minimum, some disturbance during the period of study was inevitable. In addition, more serious disturbance of nesting birds took place at irregular intervals as a result of visiting parties brought by boat from the Fife coast. At times, considerable disturbance did take place and was unavoidable, although it occurred relatively infrequently. One of the principal effects of human disturbance at breeding colonies is to increase chick mortality, and this has been noted by Harris (1964a), Parsons (1971a), Hunt (1972), Haycock and Threlfall (1975) as being an important factor in determining overall breeding success. Disturbance on the Isle of May undoubtedly contributed to chick mortality in the 1972 season. The extent of this contribution was difficult to quantify, although it is unlikely to have been as great as that observed by Hunt (1972) for the frequently visited colony at Flat Island in Penobscot Bay where, in comparison to other infrequently visited island colonies, human disturbance accounted for a two to threefold increase in chick mortalities.

The majority of eggs had hatched by early June (Table 26), although some eggs laid by four and five year old birds did not hatch until the end of this month. In order to compare the breeding success of as many birds of known age as possible, chick survival was followed up to 28 days after hatching.

Table 26. Hatching dates for eggs laid by Herring Gulls of known age and by an unringed sample of birds on the East Tarbet study area in 1972

(for a-eggs in c.3 clutches*)

Age of one member of pair	Number of clutches laid	Mean date in May on which clutches started ± S.E.	Mean date in June of a-egg hatching ± S.E.	Mean incubation period of a-egg (days) ± S.E.
4	7	29.3 ± 3.3	21.7 ± 3.3 *	30.3 ± 1.2 *
5	51	20.8 ± 1.0	14.9 ± 1.2	28.6 ± 0.3
6	50	17.2 ± 1.0	13.3 ± 1.1	28.9 ± 0.7
≥ 6	13	13.7 ± 2.0	12.6 ± 1.9	28.8 ± 0.2
East Tarbet study area	184	14.1 ± 0.7	12.1 ± 0.5	29.4 ± 0.2

* three eggs successfully hatched.

Chick mortality in relation to brood size

On East Tarbet between 31 May and 27 July 1972, 295 eggs laid by unringed Herring Gulls were known to have hatched successfully; of these chicks, 107 (36.3%) had died by the end of the fourth week. For chicks born in 1972, it was possible to determine the relationship between brood size and chick survival. Previously, Brown (1967) had suggested that chicks belonging to broods of three (b.3) had a better chance of survival than chicks raised in smaller broods. This difference in survival was attributed by Brown to gulls of higher reproductive drive raising on average larger broods. In 1972 the percentage survival of chicks in b.3 was marginally higher than that for b.2 (65.2% as compared to 61.6%, Table 27). However, this difference was not statistically significant ($\chi^2_{(1)} = 0.392$, $p > 0.05$), neither was there a significant difference between the combined b.1 and b.2 chick survival when compared with b.3 survival ($\chi^2_{(1)} = 0.570$, $p > 0.05$).

From these data it appears that brood size did not influence chick survival. Similar conclusions were reached by Parsons (1971a), although it should be noted that, as with Brown's (1967) data, there was some suggestion of lower survival of chicks raised in single broods.

Table 27. The effect of brood size on post-hatching survival for chicks raised by a sample of unringed Herring Gulls breeding on East Tarbet in 1972

Brood size	1	2	3	Total
Number of broods	8	43	67	118
Number of chicks at risk	8	86	201	295
Number of chicks surviving to the fourth week after hatching	4	53	131	188
Percentage chick survival	50.0	61.6	65.2	63.7

The effect of parental age on post-hatching survival and causes of chick mortality

The survival of chicks raised by Herring Gulls of known age is summarised in Tables 28 and 30. All five of the chicks hatching in nests of four year old breeders died before the end of the third week (Table 30). For older parents, chick survival gradually increased as the age of the parent increased. There was no statistically significant difference between the proportions of chicks surviving according to parental age class ($\chi^2_{(2)} = 2.804$, $p > 0.05$), however, older parents successfully raised more offspring per pair than did four and five year old gulls. The major causes of chick mortality are summarised in Table 29.

In common with other studies of Herring Gull pre-fledging survival, many of the ringed chicks were difficult to trace. In all, 74 (16%) of ringed chicks disappeared from the marked nest sites, and although searches of the study areas were made, no trace of these chicks was found. Similarly, Brown (1967), Parsons (1971a), Harris (1964a) and Haycock and Threlfall (1975) found it impossible to follow the fate of all chicks after hatching. As with other studies, chicks which disappeared have been added to the numbers known to have died in the pre-fledging period. Since some of these chicks were probably not dead, the mortality rates given in Tables 27, 28 and 29 may be overestimates of the actual existent mortality.

In nests belonging to four and five year old gulls, chicks were found within the first week after hatching which had obviously been crushed on the nest site. These birds had no obvious wounds or injuries, and it seems probable that the difficulties in behavioural adjustment from incubation to brooding behaviour suggested by Kadlec et al. (1969) and noted previously as being evident in the poor hatching success of young breeders, may have contributed to this mortality.

Conversely, the numbers of dead chicks found to have wounding of the occipital region increased with parental age. Dead chicks in this category were found after the first week of life, when the young were generally more mobile. Observations from the hides showed that injuries of this sort were sustained when chicks strayed into neighbouring territories. Territory holding gulls were sometimes observed to give the "long call" (Tinbergen 1953) after an attack on a transgressing chick. It seems, therefore, that these injuries resulted from the defence of the territory and could be distinguished from active predation. Usually adults attacked the head region, although sometimes injuries were sustained on the back and beneath the wing base as chicks ran through a territory. As has been suggested for egg predation,the higher incidence of such injuries in the progeny of older gulls may be linked to the higher densities of nests belonging to older breeders. Not only was there subjective evidence that gulls at higher densities were more site tenacious and more vigorous in defending territories, but also territory sizes at high densities were smaller and, therefore, the chances of chicks straying into neighbouring territories were correspondingly higher.

In addition to mortality rates derived from ringed recoveries, it was possible to make direct observations on a limited number of nests from hides situated on the East Tarbet and North Ness areas. Dead chicks which had previously been ringed on the East Tarbet sub-colony were found at an unmarked nest site on the sub-colony periphery. Subsequent observations revealed the presence of three numbered metal rings within half a metre of this nest site. During the course of the breeding season, a further 11 ringed chicks were added to this total; all these chicks had been ringed on the East Tarbet sub-colony. The resident site holder was clearly a cannibal gull and on one occasion was observed to bring back a living, rather than an already dead, chick to the territory. Additional evidence of cannibalism was provided by the observation of the regurgitated stomach contents containing the remains of an approximately one week old chick (judged on tarsus size) by the single chick at the cannibal's nest site. There is thus little doubt that this particular bird was a cannibal and not simply a scavenger of already dead chicks. This bird was caught, using Avertin narcotised bait and individually marked; it was never observed taking chicks from other sub-colonies. Its activities were thus confined to the East Tarbet area where it accounted for 2.5% of the total chick mortality (Table 29). Although Parsons (1971a,b) found that several cannibalistic gulls could be supported on the North Ness area in 1968, in this study no other gulls of this sort were found on Colm's Hole, North Ness and elsewhere on East Tarbet.

The only other natural predator on the Isle of May, apart from the Herring Gull itself, is the Greater Black-backed Gull (G.B.b.). Harris (1964a) observed that much of the pre-fledging mortality of Herring Gulls breeding on Skomer Island could be accounted for by G.B.b. predation. On the Isle of May in 1972, however, only three pairs of G.B.bs were known to have bred; one of these pairs nested on the other end of the island from the study area (on the South Ness), whilst the other two pairs nested on the North Ness sub-colony. No active predation of Herring Gull chicks was ever observed and it seems unlikely that this species accounted for much of the mortality in this year.

In contrast to those chicks which simply disappeared without trace, 36 chicks (7.7%) of the East Tarbet control sample were found dead which had no obvious injuries. Although four of these were light in weight and had little development of the thoracic musculature, and may, therefore, have died of starvation, the others appeared not to be in abnormal condition. These dead chicks were examined pathologically (pers. comm. MacDonald, M.A.F.F. Laboratories), but showed no evident abnormalities.

Lastly, exceedingly heavy rain in early July flooded seven nests on East Tarbet, and 12 chicks which were found afterwards appeared to have died of exposure.

Table 28. The number of chicks surviving to 28 days after hatching in relation to parental age for Herring Gulls breeding on study areas in 1972

Parental age (years)	Number of pairs	Number of chicks at risk	Number of chicks surviving 28 days	Percentage chick survival	Number of chicks surviving per pair
4	7	5	0	0.0	0.00
5	51	63	25	39.7	0.45
6	50	86	41	47.7	0.82
≥ 6	13	25	13	52.0	1.00

Table 29. Causes of mortality for chicks raised by Herring Gulls of known age and by an unringed sample on East Tarbet in 1972

Parental age (years)	Number of chicks ringed	Numbers of chicks dying					
		Pre-dation	Terri-torial dispute	Crushed on nest	Weather con-ditions	Found dead with no visible injuries	Unknown
4	5	0	0	3	0	1	1
				(75.0)*		(25.0)	(25.0)
5	63	3	2	10	0	4	11
		(7.9)	(5.3)	(26.3)		(10.5)	(24.4)
6	86	0	10	2	0	13	20
			(11.6)	(2.3)		(15.1)	(23.3)
≥ 6	25	0	5	0	1	0	6
			(20.0		(4.0)		(24.0)
East Tarbet control	295	9	27	5	12	18	36
		(3.1)	(9.3)	(1.7)	(4.1)	(6.2)	(12.4)

* Figures in brackets represent the percentage mortalities attributable to any one mortality factor. Percentage mortalities are calculated as

$$\frac{\text{number of chicks dying x 100}}{\text{number of chicks ringed}}$$

Table 30. The number of Herring Gull chicks that died in relation to parental age and age of chicks (for study areas in 1972)

Parental age (years)	Number that hatched	Numbers dying			
		Age of chicks (days after hatching			
		0-7	8-14	15-21	22-28
4	5	4	1	-	-
		(80.0)	(20.0)		
5	63	23	8	3	4
		(36.5)	(12.7)	(4.8)	(6.3)
6	86	20	10	9	6
		(23.0)	(11.6)	(10.5)	(7.0)
≥ 6	25	5	2	3	2
		(20.0)	(8.0)	(12.0)	(8.0)
East Tarbet control	295	57	22	21	7
		(19.3)	(7.5)	(7.1)	(2.4)

Chick growth in relation to breeding success

In 1972 the greatest chick mortality occurred in the first week after hatching (Table 30). For the control sample of unringed breeding pairs, 19.3% of chicks died within this time period, the chick mortality rate decreased markedly after this time period, and was lowest in the fourth week after hatching (2.4%, Table 30).

It has been suggested by Kadlec et al. (1969) that a major cause of chick mortality in the first week or so after hatching is the inability of breeding adults to make a rapid and efficient behavioural change from incubation behaviour patterns to the behaviours associated with chick care, chiefly feeding behaviour and protection of the young against adverse environmental conditions. Differences in reproductive behaviour and therefore in the survival of chicks may show considerable individual variations from one breeding adult to another. Although Kadlec et al. (1969) had no information on the chick raising abilities of differently aged parents, they suggested that young breeding adults may exhibit the greatest behavioural deficiencies in brood care. This suggestion is supported by the 1972 breeding data. Mortality rates during the first week after hatching were considerably higher for chicks raised by four and five year old parents (80.0% and 36.5%) respectively than those for chicks raised by older parents (20.0 - 23.0%) (Table 30).

In the 1972 breeding season the rate of growth of selected broods belonging to parents of known age was monitored. On the assumption that the metabolic demands of growth and maintenance are similar for all chicks, differences in the growth rates of pre-fledging Herring Gulls reflect the ability of the parent to feed its offspring, which in itself is an expression of the parent-offspring bond.

The most obvious and most frequently cited parameter of chick growth is changing body weight. The weight changes in captive Herring Gull chicks have been measured by Goethe (1956), Peters and Müller (1951). Data for wild populations have been collected by Hunt (1972), Kadlec et al. (1969), Harris (1964a), Spaans (1971) and Haycock and Threlfall (1975). In general, weight can be an extremely variable measurement, depending on whether the chick has been recently fed and upon its metabolic state at the time of weighing. For these reasons, either several weighings are needed for a given sampling instance, or some allowance is necessary for recent feeding history. Hunt (1972), for example, forced chicks to empty the crop content before weighing. In addition, it is known that irrespective of recent feeding, nestling passerines exhibit circadian changes in body weight which may be linked to cycles of tissue growth (O'Connor 1975, 1976); similar processes may also operate in Herring Gulls.

In order to avoid the variations inherent in measuring weight, and to avoid unnecessary disturbance of breeding birds that would inevitably result from frequent visits to nest sites, an alternative measure of growth was used. Throughout the 1972 breeding season, growth rates were determined by measuring increments in wing length. Wing length was measured to within one millimetre, from the angle of hand flexure at the metacarpals to the wing tip, either at the termination of down (up to three weeks old) or to the primary tip (three weeks and older).

The growth of 88 chicks hatched by parents of known age was followed either from the time of hatching until the age of 28 days, or until the chick died or disappeared (Table 31). In all cases, hatching sequence followed the laying sequence. Out of 12 chicks that hatched last into broods of three, i.e. from the c-egg, five (42%) survived to the fourth week after hatching. The mortality of the c-chick was thus considerably higher than for a- and b-chicks, and even though the hatching success of

Table 31. The wing growth of Herring Gull chicks according to hatching sequence. (For broods raised by parents of known age on the East Tarbet, Colm's Hole and North Ness study areas in 1972)

	*a-chick		*b-chick		*c-chick	
Age of chick (days after hatching)	**N	Mean wing length ± S.E. (mm)	**N	Mean wing length ± S.E. (mm)	**N	Mean wing length ± S.E. (mm)
0	45	33.0 ± 0.3	32	33.3 ± 0.3	11	32.0 ± 0.4
2	45	35.8 ± 0.3	27	36.2 ± 0.9	11	35.1 ± 0.6
4	44	40.0 ± 0.4	30	39.5 ± 0.6	11	37.0 ± 0.7
6	41	45.2 ± 0.5	28	44.3 ± 0.8	11	39.6 ± 1.1
8	42	46.9 ± 0.7	26	49.8 ± 1.2	11	42.1 ± 1.6
10	40	58.6 ± 1.0	25	56.8 ± 3.3	10	46.6 ± 2.0
12	38	69.1 ± 1.4	22	66.7 ± 2.2	10	51.7 ± 2.7
14	37	82.2 ± 1.7	21	79.8 ± 3.2	10	58.2 ± 3.4
16	36	97.6 ± 2.1	20	91.0 ± 3.5	10	67.4 ± 4.3
18	32	115.2 ± 2.62	19	103.9 ± 3.8	10	79.3 ± 5.7
20	30	131.9 ± 2.9	17	120.9 ± 4.8	10	91.3 ± 5.5
22	23	151.2 ± 3.6	14	134.9 ± 4.9	9	102.3 ± 10.7
24	21	169.2 ± 3.7	13	153.6 ± 5.5	8	119.9 ± 7.9
26	19	187.7 ± 4.0	13	171.7 ± 5.6	7	128.0 ± 5.8
28	20	207.9 ± 3.8	7	191.6 ± 8.5	7	142.4 ± 5.5

* Hatching sequence denoted as follows: a-chick = first hatched
b-chick = second hatched
c-chick = third hatched

** The number of chicks that were measured in any particular age class.

this species is relatively high, the most common brood size is two rather than three. For the study population of 88 chicks, initially 36 chicks (41%) were in broods of three, 40 in broods of two, and 12 in single broods by the end of June (approximately two-three weeks after the hatching of most eggs). In the fourth week after hatching only 15 (24%) of the 62 surviving chicks were in broods of three. The growth pattern of c-chicks differed from that of a- and b-chicks (Figure 17) and tended to lag behind that of first hatched young.

Growth rates (r_g) were calculated from the expression:

$$r_g = \frac{\mathrm{Log}_{10}L_{t2} - \mathrm{Log}_{10}L_{t1}}{t2 - t1} \quad \text{(for the logarithmic transformation of growth curves)}$$

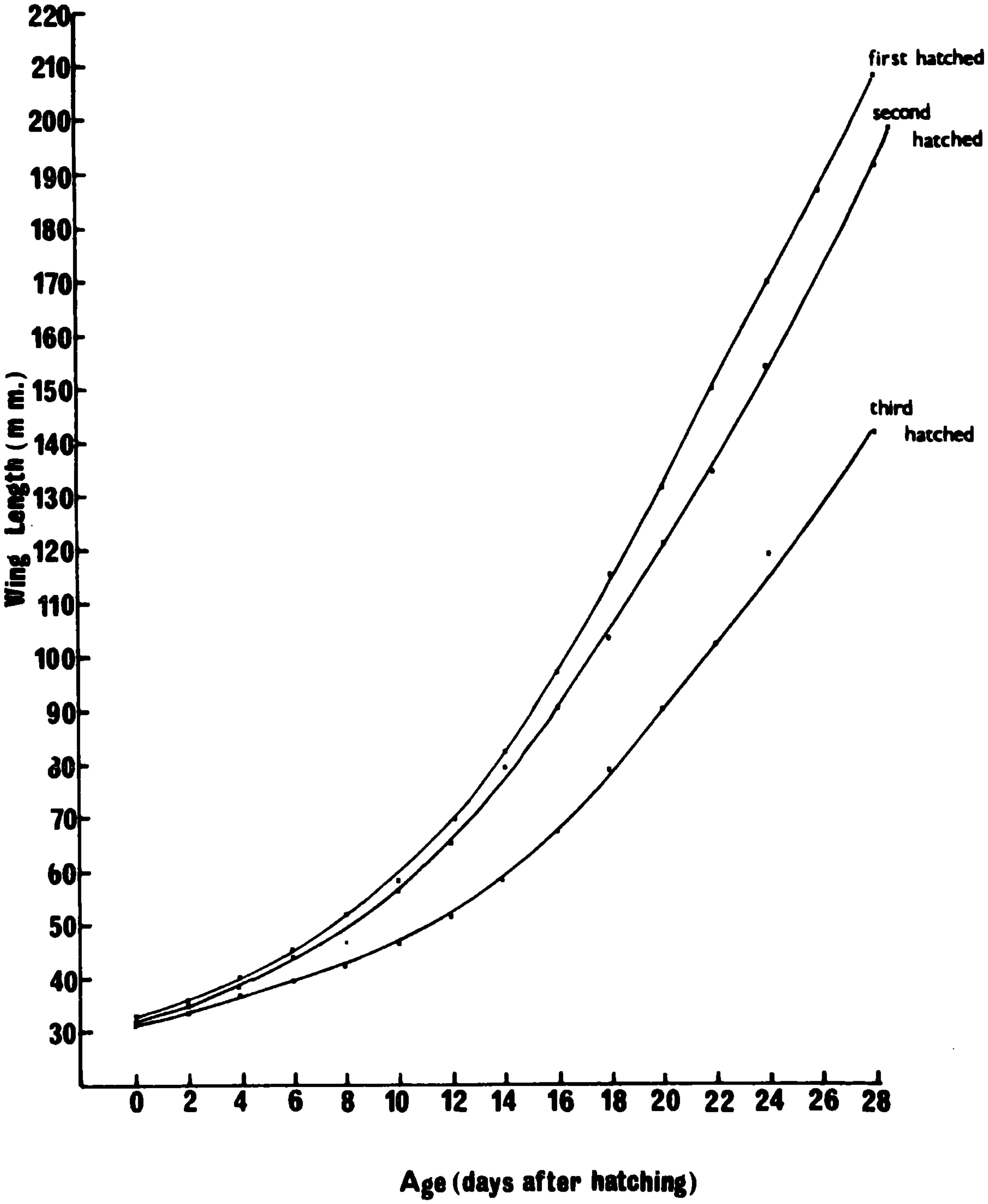
where L_{t1} was the wing length at time t1 and L_{t2} was the wing length at time t2 over a period of growth, t1 - t2.

For a-, b- and c-chicks measured in the first four weeks after hatching, the growth rates were calculated as 0.194 ± 0.002; 0.189 ± 0.004 and 0.168 ± 0.005mm day^{-1} respectively. The rate of growth in b-chicks did not differ significantly from that in first hatched chicks ($t_{29} = 1.636$, $p < 0.05$), although for c-chicks growth rates were significantly lower (differences between a- and c-growth rates $t_{25} = 7.814$, $p < 0.001$ and for b- and c-rates, $t = 5.553$, $p < 0.001$).

Although the growth of the c-chick was slowest, brood size did not affect the rate of growth in a- and b-chicks. It might be expected that the feeding of three offspring rather than two or one would have placed additional demands upon parents and reduced the amount of food received by a particular chick. This did not appear to be the case, and in fact a- and b-chicks in three chick broods had slightly higher growth rates (0.198 ± 0.005mm day^{-1}) than the equivalent chicks in smaller broods (0.192 ± 0.002mm day^{-1}), although this difference was not significant ($t_{31} = 1.563$, $p > 0.05$).

Figure 17

Growth of chicks in broods raised by Herring Gulls of known age in 1972 according to hatching sequence


Wing Length (m m.)
220
210
200
190
180
170
160
150
140
130
120
110
100
90
80
70
60
50
40
30
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Age (days after hatching)
first hatched
second hatched
third hatched

Spaans (1971) compared the growth of Herring Gull chicks in different sized broods and in broods of three where chicks had hatched either in the early- or mid-late part of the breeding season. He found evidence to suggest that chicks in broods of one grew faster than chicks in broods of three, although in six cases out of the eight he analysed (i.e. for chicks hatched mid-late 1966; early- and mid-early 1967; mid-early 1966, late-1967; mid-late 1968) there were no significant differences between brood sizes. Chicks hatched in the mid-late part of the season grew less fast than early hatchers. Spaans attributed this difference partly to differences in parental quality and partly to seasonally changing environmental factors such as water supply.

There was evidence from the present study that parental age may be an important factor in determining quality. Chicks raised by the most experienced parents (adult-ringed gulls) grew at a significantly faster rate than the chicks of either four and five or six year old parents, $p < 0.05$ (Table 32, Figure 19), although there was no significant difference between the combined data for four and five and six year old parents ($p > 0.05$). Spaans (1971) regarded food shortage as being unimportant in determining growth rates in pre-fledging Herring Gulls raised by young parents, since the differences he noted between early- and mid-late hatching chicks were maintained regardless of brood size. For Herring Gulls breeding on the Isle of May in 1972 neither chick survival nor chick growth rate was higher in smaller broods. This circumstantial evidence suggests that there was no shortage in food available to parents. However, the quantity, and perhaps quality, of food supplied to the young immediately after hatching may have been an important influence on subsequent chick survival. Growth rates of non-surviving chicks in the first nine days after hatching were significantly lower than those for chicks surviving past nine days (Table 33).

Table 32. The wing growth of chicks raised by Herring Gulls of known age in 1972

(data grouped regardless of brood size)

	Parental age (years)					
	≤ 5		6		≥ 6	
Age of chick (days after hatching)	*N	Mean wing length ± S.E. (mm)	*N	Mean wing length ± S.E. (mm)	*N	Mean wing length ± S.E. (mm)
0	32	(33)[†]	28	(34)	15	(34)
2	31	(36)	27	(36)	13	(37)
4	32	(39)	24	40 ± 1	13	40 ± 1
6	31	(45)	24	45 ± 1	12	46 ± 1
8	28	50 ± 1	25	51 ± 1	12	52 ± 1
10	29	57 ± 1	23	58 ± 2	12	60 ± 2
12	28	67 ± 1	20	70 ± 2	11	73 ± 2
14	26	80 ± 1	20	84 ± 3	11	86 ± 2
16	27	93 ± 1	17	97 ± 3	11	103 ± 3
18	24	108 ± 1	15	111 ± 3	11	118 ± 4
20	21	126 ± 1	14	124 ± 3	11	140 ± 3
22	18	145 ± 1	11	140 ± 3	6	161 ± 5
24	17	163 ± 1	10	159 ± 3	5	183 ± 5
26	15	181 ± 1	10	177 ± 3	5	202 ± 5
28	12	200 ± 1	11	199 ± 3	4	227 ± 3

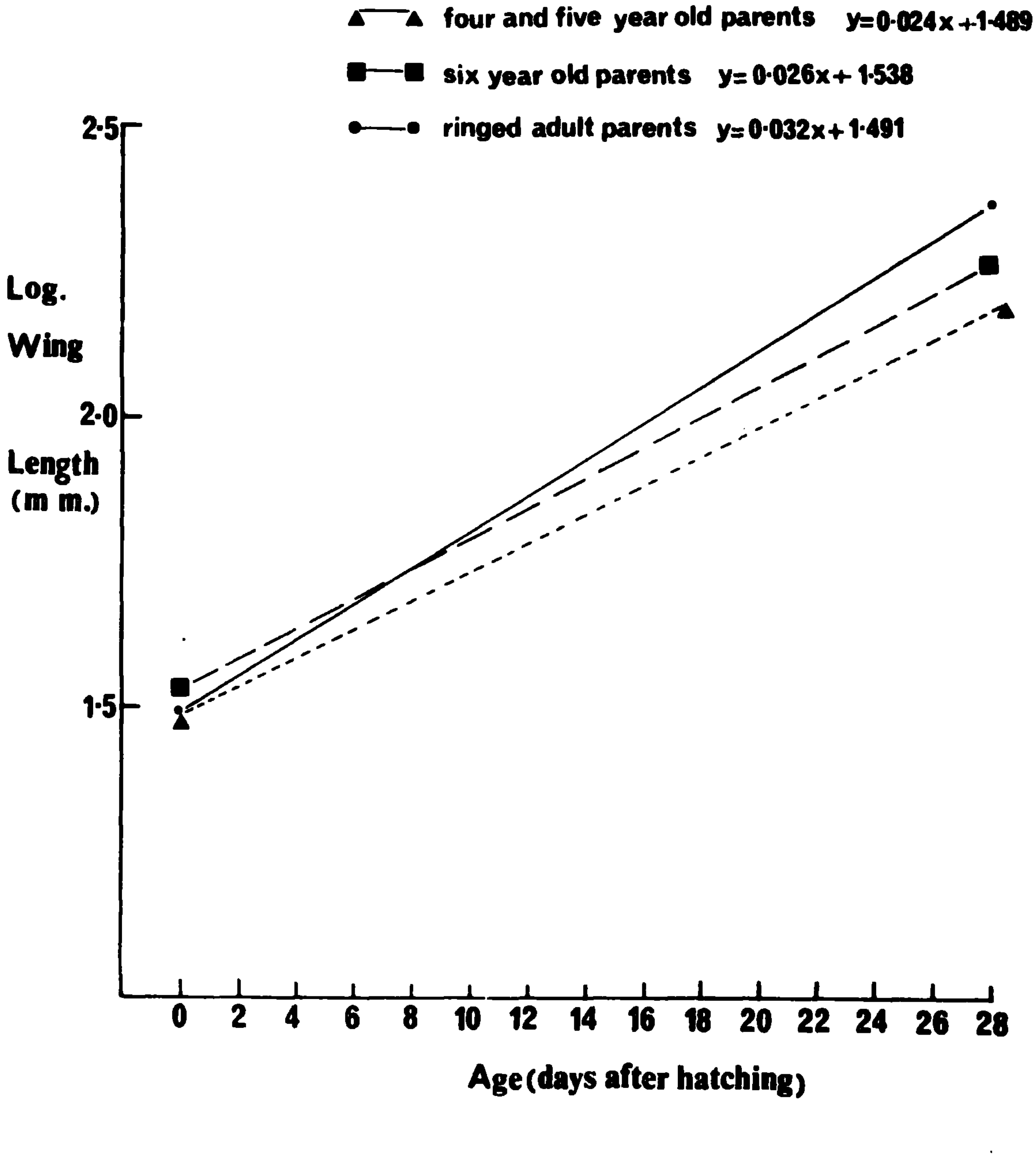
* The number of chicks that were measured in any particular age class

[†] Figures in brackets where S.E. < 0.5 mm.

Figure 18

Growth of chicks raised by Herring Gulls of known age

in 1972



▲—▲ four and five year old parents y=0·024x+1·489
■—■ six year old parents y=0·026x+1·538
●—● ringed adult parents y=0·032x+1·491
Log. Wing Length (m m.)
2·5
2·0
1·5
0
2
4
6
8
10
12
14
16
18
20
22
24
26
28
Age (days after hatching)

Although the existence of differences in chick quality cannot be discarded, it seems likely that chick survival in the period following hatching was a function of the parents' ability to feed their young adequately. This expression of the parent-chick bond (the behavioural transition referred to by Kadlec et al. 1969) takes a time to develop, and obviously the longer this development takes, the greater is the reliance upon vestigial yolk reserves. For recruit breeders laying small eggs, this may be critical since it is known that for this species yolk volume correlates significantly with egg volume (Parsons 1976b). Such an explanation may account for the high first week mortality rates of chicks raised by recruit breeders (Table 30).

Table 33. Growth rates of chicks which survived to 28 days after hatching compared with those that died before 28 days. For first, second and third chicks hatched on study areas in 1972

Age class (days after hatching)	Number that survived per age class	Mean growth rates ± S.E. (mm day^{-1})	Number that died before 28 days		Mean growth rates ± S.E. (mm day^{-1})
0 - 9	74	0.195 ± 0.024	14	*	0.134 ± 0.014
10 - 19	45	0.251 ± 0.017	21	**	0.327 ± 0.014
20 - 28	22	0.179 ± 0.006	16	**	0.174 ± 0.016

* For the difference between mean growth rates of surviving and non-surviving chicks: $t_{86} = 4.008$, $p < 0.001$.

** Not significant: $p > 0.05$.

There were no significant differences in the growth rates of surviving and non-surviving chicks after post-hatching day nine. This was a time when Herring Gull chicks became more mobile and when a major component of chick mortality resulted from territorial encounters with neighbouring site holders. This mortality agent was largely independent of the feeding relationship established in the parent-chick bond.

3.6 Breeding Success

Breeding success may be defined as the proportion of eggs laid per pair that will give rise to fully fledged offspring. Thus the important determinants of breeding success are the number of eggs laid; survival rates of eggs up to the time of hatching; the proportion of eggs that give rise to viable offspring and the survival rates of the offspring subsequent to hatching. Since these factors have been shown to vary with parental age it follows that breeding success will also be an age dependent variable.

A low breeding success for first time breeding birds has been reported in other species of larids, for example, two year old Red-billed Gulls have a lower success than five year old birds (Mills 1973) and first time breeding Sandwich Terns (Veen 1977) and Kittiwakes (Coulson and White 1966) have lower success than more experienced breeders. For the Herring Gull, Drost _et al_. (1961) suggested from the observation of two individually marked birds at the Wilhelmshaven study colony that there may be a tendency for young breeding pairs to raise fewer chicks to fledging than older breeding birds.

In the 1972 breeding season on the Isle of May the breeding success of pairs of Herring Gulls in which at least one member was of known age was monitored for birds breeding on the East Tarbet, North Ness and Colm's Hole study areas.

Herring Gulls have been reported to take between 45 to 56 days to fledge (Kadlec _et al_. 1969, Parsons 1971a). Since this is the case, calculations of breeding success based on chick survival up to the fourth week of life (Section 3.5) will be overestimates since they could not take into account the chick mortality which occurred during the latter part of the breeding season. A measure of this mortality was provided by the numbers of rings found on the island from late-July onwards. Visitors to the island observatory aided considerably in this process by collecting rings between the months of August and October. Inevitably some rings belonging to dead chicks were never found, and estimates of fledging success and therefore of breeding success for 1972 may have been overestimates. This error was in part compensated for by the fact that the direct observation methods used in measuring chick mortality probably underestimated chick survival.

A summary of the breeding success for pairs of birds of known age breeding on the three study areas and for the East Tarbet control group is presented in Table 35. Of the 474 chicks ringed on all areas in 1972, 38 (8%) were recovered dead on the island between June and October. Similarly, Parsons (1971a) in his study recovered between 8% and 9% of ringed chicks in the 1966 and 1967 seasons.

For all breeding pairs of Herring Gulls observed in 1972, 31% (229 chicks fledged from 732 eggs) of eggs laid gave rise to fledged young, and for parents aged six years and older between 0.76 and 0.92 chicks were successfully raised per pair. Similar figures are given by Paynter (1949), Drost _et al._ (1961), Harris (1964a), Brown (1967) and Parsons (1975). The breeding success of Herring Gulls at different colonies is compared in Table 34.

It is evident from Table 34 that breeding success varied between different colonies and for different years at the same colony. For example, Parsons (1975) reported that an epizootic of *Salmonella typhimurium* amongst pre-fledging young reduced the breeding success of Herring Gulls on the Isle of May in 1968. In that year only 24.7% of eggs gave rise to fledged young as compared to 32.6% in the previous year (Table 34).

Table 34. A comparison of breeding success recorded at various Herring Gull colonies

Location of study colony	Authority	Number of nests	Percentage of chicks surviving	Percentage breeding success	Number of chicks produced per pair
Summer Isle, U.K.	Darling (1938)				
1936		40	48.6	41.7	0.88
1937		65	42.0	40.2	1.16
Kent Island, Canada	Paynter (1949)	100	48.5	36.8	0.91
Christiansø Island, Denmark	Paludan (1951)	90	-	ca.5.0	0.50 (0.03 - 0.90)
Wilhelmshaven, Germany	Drost *et al.* (1961)	150	-	ca.25.0	0.70
Skomer Island, U.K.	Harris (1964a)	220	ca.30.0	ca.20.0	0.56
Walney Island, U.K.	Brown (1967)	139	35.5	ca.30.0	0.91
New England, coastal and island colonies	Kadlec *et al.* (1968a), (1969)	ca. 3,000	-	ca. 40.0-50.0	1.40
Gull Island, Canada	Haycock and Threlfall (1975)	23	-	-	0.96
Isle of May, U.K.	Parsons (1971a)				
1967		1,101	50.8	32.6	0.91
1968		903	35.4	24.7	0.67
Isle of May, U.K.	Emmerson (unpublished)	200	33.3	21.2	0.65
Isle of May, U.K.	This study				
1972		184	52.5	34.9	0.92

Table 35. The breeding success of a control group of Herring Gulls and Herring Gulls of known age in the 1972 season on the Isle of May

Age of parent (years)	Number of breeding pairs	Number of eggs laid	Number of eggs hatched	Number of chicks surviving to 28 days	Number of * rings recovered	Estimated number of chicks fledged	Breeding success (%)	Number of young produced per pair
4	7	12	5	0	0	0	0	0
5	51	109	63	25	2	23	21.1	0.45
6	50	129	86	41	3	38	29.5	0.76
≥ 6	13	35	25	13	1	12	34.3	0.92
East Tarbet control	184	447	295	188	32	156	34.9	0.85

* From 20 July onwards

Emmerson (unpublished data) reported that heavy rain in July and August resulted in high pre-fledging mortalities in 1970. Similar combinations of factors, both biotic and abiotic, no doubt contributed towards producing differences in breeding success between colonies. On Skomer Island, Harris (1964a) noted extensive predation of Herring Gull eggs and chicks by adult Greater Black-backed Gulls, a mortality factor of minimal importance on the Isle of May. Some of the Danish colonies studied by Paludan (1951) had a long history of egg collecting and therefore of human disturbance prior to Paludan's study.

With some exceptions, breeding success for this species ranges from 25.0 to 41.7%, and on average approximately one young is successfully raised per pair of adult Herring Gulls.

In the present study there was a marked increase in breeding success with parental age (Table 35). Low clutch size, poor hatching success and low pre-fledging survival for breeding four and five year old gulls combined and resulted in a markedly poorer breeding success in these breeding age classes. The combined breeding success of four and five year old birds (19.0% of eggs laid gave rise to fledged young, a reproductive rate of 0.4 young per pair) was significantly lower than that for breeding gulls aged six years and older (30.5%, 0.79 young per pair; $\chi^2_{(1)} = 4.816$, $p < 0.05$).

In the Herring Gull, as in Sandwich Terns and Kittiwakes, parental age was an important proximate factor in determining reproductive rates. In recruit breeding Herring Gulls poorly executed reproductive behaviour, especially in incubation and protection of the brood, largely contributed to the low breeding success of these birds. Presumably in Herring Gulls, as with Kittiwakes, breeding performance improves as more experience is acquired.

Breeding success in relation to nesting density

In addition to individual differences in parental age and experience, and to annual variations and differences between different breeding colonies, breeding success in the Herring Gull has been found to vary with nesting density (Parsons 1976a). Although no such variation exists in Black-headed Gulls (Patterson 1965) or Glaucous-winged Gulls (Vermeer 1963), Fordham (1964) found that egg losses due to predation in Southern Black-backed Gulls increased at high nesting densities.

The possibility that Herring Gulls breeding at different densities may have had different reproductive rates was investigated for birds breeding on the North Ness study area in 1972. By mid-May of that year it became evident that there was a wide variation of nest densities on the three study areas (Figure 19; and see Appendices 7 and 8). On North Ness, nests could be as close as 62cm apart at the sub-colony centre, or virtually isolated and 15m away from the nearest nest at the sub-colony periphery. Between 13 and 15 May, 500 nests were marked on North Ness with numbered wooden stakes, and 200 of these marked nests were selected from random number tables. For each nest the distance between it and its nearest neighbouring nest was measured (see Sections 5.3 and 5.4 for methods of measuring nesting density and nest distribution). For the North Ness, nests were subjectively grouped into three categories: high density nests (distance between nearest nests 0-2m); medium density nests (2 - 4m apart); and low density nests (where the distances between nests was 4m or greater). Since these nests had been marked after egg laying had started it was not possible to compare the size of clutches laid by birds breeding at different densities since it was likely that many eggs had been lost due to predation and other causes.

In these 200 nests, 365 chicks successfully hatched, i.e. 1.83 chicks per nest. The fate of these chicks was followed by nest site visits up to

Plate 3. High nesting density area on the North Ness sub-colony in 1972.

Figure 19

The distribution of areas of high, medium and low nesting density* on the North Ness sub-colony in 1972.

* Number of nests per 100 m^2 were as follows:

high density = 12·9
medium density = 5·7
low density = 2·6

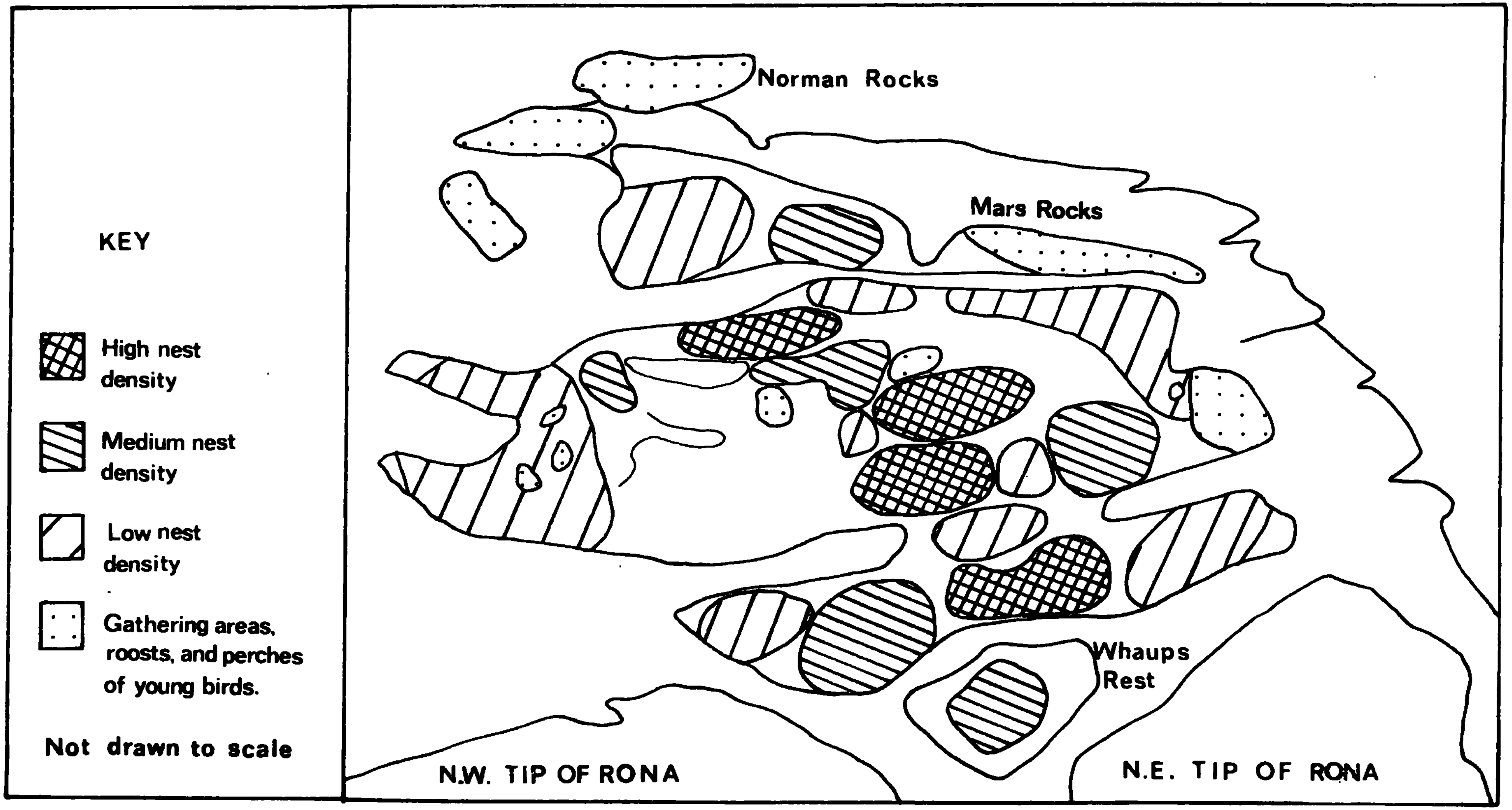

KEY
High nest density
Medium nest density
Low nest density
Gathering areas, roosts, and perches of young birds.
Not drawn to scale
Norman Rocks
Mars Rocks
Whaups Rest
N.W. TIP OF RONA
N.E. TIP OF RONA

Table 36 The survival of chicks in relation to density of nests on the North Ness study area in 1972

	Density zone ***		
	High	Medium	Low
Mean shortest inter-nest distance (metres) (± S.E.)	1.28 ±0.04	2.80 ±0.08	7.13 ±0.63
Number of nests	117	60	21
Number of chicks*	234	119	36
Number of chicks recovered or reported dead**	141	64	29
Number surviving	93	55	7
Percentage survival of chicks	40	46	19
Number of chicks fledged per nest	0.79	0.92	0.33

* Numbers found per nest at original time of nest marking

** Numbers recovered up to 27 July and subsequently reported by visitors and observers up to October 1972

*** Explained in text, p. 95.

Comparing the numbers of young surviving at low and medium densities, $\chi^2_{(1)} = 8.255$, $p < 0.005$. For chick survival at high and medium densities, $p > 0.05$ (N.S.).

ten days after hatching, and the surviving 292 chicks were ringed with both B.T.O. metal and Darvic plastic rings. The 20% mortality within the first ten days after hatching was similar to that recorded on East Tarbet (Table 30), and since the study nests on the North Ness were less frequently visited than those on East Tarbet, this suggests that human disturbance had little impact on chick mortality within the first ten days of life. On North Ness, chick survival up to the time of fledging was monitored largely on the recoveries of dead ringed chicks rather than on regular nest site visits.

The results from the North Ness study nests (Table 36) suggested that gulls nesting at the highest densities produced fewer surviving young than those at intermediate and low densities, although the majority (60%) of nests were located in the highest nest density zones. Of the 234 chicks known to have died, 26 (11%) were recovered after 27 July by members of the public, and for these chicks mortality causes were unknown. For the remaining 208 non-surviving chicks, a high proportion of chicks older than ten days from high density nests were found with severe occipital wounding; for high density nests this figure was 74 (53% of all chick deaths); for intermediate densities, 19 (30% of all chick deaths). This difference in proportion was significant ($\chi^2_{(1)} = 9.228$, $p < 0.01$) and suggested that a major cause of reduced reproductive rates of gulls breeding at high densities was due to territorial transgression by chicks. At low densities, 7 (24%) chicks were recovered with occipital wounding, and the reasons for the poor chick survival of young produced at these nests were not clear. Parsons (1971b) found that cannibal Herring Gulls on the Isle of May tended to select prey from low rather than high nest densities. It seems likely that predation may have resulted in some of the chick mortality at low densities. However, only one cannibal gull was located in 1972, so that predation was probably not the major factor of low pre-fledging survival rates at these peripheral sites.

The density of study nests on East Tarbet was measured towards the end of the season (10-15 July). The distribution of nests in relation to density differed from that on North Ness; on this area 59% of nests were at high densities; in contrast, only 27% of nests studied on East Tarbet were at high densities (Table 37). However, there were no significant differences between the two areas in mean nearest distances to neighbouring nests at the three different densities ($p > 0.05$). For birds breeding on East Tarbet the variation in breeding success between high and medium densities was less marked than on North Ness, and gulls nesting at both densities raised approximately one chick per pair. Although the hatching success of eggs laid at medium densities was lower than that at high densities, this difference was compensated for by the higher chick survival at medium densities.

At low densities, the effects of low clutch sizes, poor hatching success and low chick survival combined and resulted in a marked reduction in breeding success. Mean clutch size at low densities was significantly lower than that for higher densities ($\chi^2_{(2)} = 23.685$, $p < 0.05$), and suggested that these gulls were probably recruits (see Section 3.2). In fact, from the distribution of nests established by gulls of known age in 1972 (Table 38), it was clear that the great majority of recruits (all four year old and 97% of five year old birds) selected nest sites at low densities. For this species therefore, it was difficult to separate the effects of parental age from those of breeding density upon reproductive success. Only five out of the 15 adult-ringed breeders nested at low densities. These results suggested that there was local movement, mostly within a sub-colony (Section 5.4), to nest sites at higher densities as birds get older.

Table 37 Breeding success in relation to nest density on the East Tarbet study area in 1972

	Density zone*		
	High	Medium	Low
Mean nearest distance to neighbouring nest ± S.E. (m)	1.11 ± 0.55	2.72 ± 0.69	6.58 ± 0.35
Number of nests (percentage of nests per density zone)	50 (27.2)	77 (41.8)	57 (31.0)
Number of eggs laid	c.1. 2. c.2. 17. c.3. 31 (4)** (34) (62)	c.1. 6. c.2. 18 c.3. 53 (7.8) (23.3) (68.8)	c.1.15 c.2. 24 c.3. 18 (26.3) (42.1) (31.6)
Total eggs laid	129	201	117
Mean clutch size ± S.E.	2.58 ± 0.81	2.61 ± 0.72	2.05 ± 0.10
Number of chicks hatched	92	136	67
Hatching success (%)	71.3	67.7	57.3
Mean brood size ± S.E.	1.84 ± 0.05	1.77 ± 0.03	1.18 ± 0.07
Number of chicks at risk	92	136	67
Number of chicks surviving to fledging	47	81	28
Percentage chick survival to fledging	51.1	59.6	41.8
Breeding success (as % of total eggs laid	36.4	40.3	23.9
Number of young produced per nest	0.94	1.05	0.49

* See p. 95 for explanation of density zones

** Figures in brackets are percentages of c.1, c.2 and c.3 clutches laid by gulls nesting within a given density zone.

Table 38. The distribution of territory-holding Herring Gulls in relation to nesting density on East Tarbet, North Ness and Colm's Hole in 1972

Age of at least one member of pair (years)	Low density (nearest inter-nest distance over 4m)	High density (nearest inter-nest distance 0-4m)
4	11 (100)*	0 (0)
5	60 (96.8)	2 (3.2)
6	30 (56.6)	23 (43.4)
$\geq$ 6	5 (33.3)	10 (66.7)

* Figures in brackets are percentages of Herring Gulls of known age breeding at low or high densities.

SECTION FOUR POPULATION DYNAMICS

4.1 Population Increase

A recent census has estimated the breeding population of Herring Gulls in British and Irish coastal colonies at 334,000 pairs in 1969-70 (Cramp *et al.* 1974). If the number of Herring Gulls breeding in urban colonies, many of which are known to be increasing rapidly (Monaghan and Coulson 1977), is added to the total, it is clear that this species is one of the most common of British seabirds.

The status of the Herring Gull in the British Isles has altered considerably over the past two decades. This species has both widened its breeding distribution and increased rapidly in numbers. The expansion from relatively restricted coastal communities (see, for example, Baxter and Rintoul 1953) to habitats which include inland urban and agricultural ones, and its dramatic increase in numbers at many coastal colonies, are probably the result of catholic, opportunist feeding habits coupled with a decrease in persecution and a low annual adult mortality rate. The Herring Gull is a frequent scavenger on rubbish tips (Monaghan 1977, Verbeek 1977), agricultural land (Lloyd 1968, Davis 1973) and fishing trawlers (Watson 1978). In exploiting such a wide food spectrum, it seems unlikely that large seasonal variations in food supply are limiting for this species, and also man is taking Herring Gull eggs less and less frequently for food (Cramp *et al.* 1974).

Similar increases have been noted for the Herring Gull populations of northern Europe (Spaans 1971) and North America (Nettleship 1973), although the rate of population increase at colonies on the north-eastern seaboard of America appears to be gradually slowing down (Drury and Kadlec 1974). No such decrease is evident in the majority of British colonies (Cramp *et al.* 1974).

The rates of increase in the numbers of breeding Herring Gulls at some British and Irish colonies are compared in Table 39. Such a comparison indicates a range in rates of increase from 2.5 to 85.3% per annum. High rates of annual increase may be indicative of large scale immigration (Brown 1967) and it is probable that the colonies at Canna, Denny Island and Walney Island have increased in this way; for other colonies the range is 2.5 to 17.5% per annum.

On the Isle of May the Herring Gull was first noted as a breeding species in 1907 when one pair bred on the island (Baxter and Rintoul 1925). Since that time the increase has been dramatic and 14,000 pairs of Herring Gulls were estimated to have bred in 1970 (Emmerson, unpublished data).

Between the years of 1907 and 1967 Parsons (1971a) calculated the population to be increasing at a rate of 13% a year. In order to see whether this rate of increase had been maintained after 1967 the numbers of gulls breeding on the Isle of May in 1972 and 1973 were estimated both by direct counting and from photographs.

Parsons and Emmerson had estimated the breeding population from counts made in July and early August, that is, at a time when most nests contained chicks, and when breeding birds still exhibited a strong attachment to the nest site. The first year of this study coincided with the beginning of the N.C.C. control programme on 18 May 1972. It was, therefore, not possible to obtain equivalent census counts to those of previous workers who had counted breeding birds, in a relatively undisturbed colony in the middle of, or late, in the breeding season, when the majority of four and five year old gulls were recruiting or had recruited into the colony.

In both years counts were made before the cull (2 April - 16 May 1972, and 30 April - 16 May 1973), and unculled study areas were counted after the cull (20-25 July 1972 and 18 June - 20 July 1973).

Table 39. A comparison of the population increases recorded for expanding Herring Gull colonies in Britain and Ireland. Based on the "Operation Seafarer" census reported in Cramp et al. 1974

Breeding colony	Number of breeding pairs Census 1930-68	 Census 1969-70	Period of increase	Percentage annual rate of increase
Inchmarnock, Buteshire	300	1,250	1937-70	4.6
Caann a'Mhara, Tiree, Argyll	100 - 150	365	1955-70	6.1 - 9.0
Canna, W. Inverness	335	1,600	1963-70	25.0
Handa Island Sutherland	150	360	1959-70	8.3
Fair Isle, Shetland	140	315	1959-70	7.7
Orford Ness, Suffolk	2 - 3	150	1963-70	74.8 - 85.3
Steep Holm, Somerset	3,600	5,070	1956-70	2.5
Stert Island, Somerset	100	3,120	1946-70	15.4
Denhy Island Monmouthshire	8	95	1963-70	42.4
Flat Holm, Glamorgan	73	920	1954-70	17.2
Skokholm Island Pembrokeshire	570	1,350	1949-70	4.2
Skomer Island Pembrokeshire	700	2,200	1946-70	4.9
Newborough Warren, Anglesey	2,000-3,000	4,780	1960-70	4.8 - 9.1
Walney Island, Cumbria	120	15,500	1947-70	23.5

Continued overleaf

Table 39. (Continued)

Breeding colony	Number of breeding pairs Census 1930-68	Number of breeding pairs Census 1969-70	Period of increase	Percentage annual rate of increase
St Bees Head, Cumbria	1,670	3,000	1956-70	4.3
Ireland's Eye, Dublin	490	1,250	1961-70	11.0
Gt. Saltee, Wexford	2,000	3,600	1960-70	6.1
Irishmurray, Sligo	50	310	1955-70	12.9

The number of paired gulls on territories were counted separately and the total number of birds in a sub-colony was given as: 2 (census count - number of pairs counted). Census counts were made between 16.00 and 20.00 hours, whenever possible when between 80% and 90% of gulls were back at their nest sites. Total island counts were simply the result of combining the eight sub-colonies totals. The pre-cull population on the Isle of May in 1972 was estimated to be 12,950 pairs (Table 40).

However, counts of breeding Herring Gulls in April and May would be expected to underestimate the total breeding population (Kadlec and Drury 1968b) since they were made at a time when there was relatively low attachment of territorial birds to nest sites and because they did not include late breeding gulls. Many four and five year old breeders did not lay eggs on the study areas until late-May or early-June.

The number of Herring Gulls breeding on the East Tarbet study area increased by 17% from 479 to 560 pairs between early-May and late-July in 1972 (Table 40), whilst on North Ness the increase was 21%. The overall increase for the two areas was 20%; increasing the pre-cull island total by this amount would give the best estimate of what the Isle of May Herring Gull population would have been had the N.C.C. cull not taken place. This gave a predicted breeding population of 15,540 pairs on the island in 1972. By adding the population estimates for 1970 and 1972 to that made by Parsons in 1967, and to those made previously by various observers on the island (yearly counts are given in Appendix 9), the population increase can be plotted (Figure 20). The line of best fit is:

$$\log._{10} \text{ population size} = 0.058 \text{ year} + 0.587.$$

The rate of annual population increase (r) can be calculated from the expression:

$$\frac{\text{population size at time, t}}{\text{population size at time, O}} = (1+r)^n$$

where n is the time period over which the population has increased), using this regression equation, r is calculated to be 0.143 or 14.3% per annum.

This is a similar, although not equivalent rate of increase to that calculated by Parsons for the Isle of May breeding population up to 1967. Considering the assumptions made in calculating the 1972 total breeding population size, the agreement between these two calculations is close.

There are insufficient post-1967 data to warrant the conclusion that the population has continued to increase at 13% to 14% per annum since the study made by Parsons. However, it is clear that there has been an increase in population size since 1967 and that on an unculled area of the Isle of May that increase continued throughout the first two years of this study. For East Tarbet, considering late season counts, this increase was 16% between 1972 and 1973 (Table 40). Although this rate is higher than that calculated for the colony as a whole, different sub-colonies might be expected to increase at different rates since the eight sub-colonies on the island appear not to have been equally attractive to recruits (Section 5.3). The Isle of May was thus typical of the main expanding British and Irish coastal colonies in that its rate of annual population increase at the time of this study was in the 2% to 17% range (Table 39).

Figure 20

The increase in numbers of breeding Herring Gulls on the Isle of May between 1907 and 1972

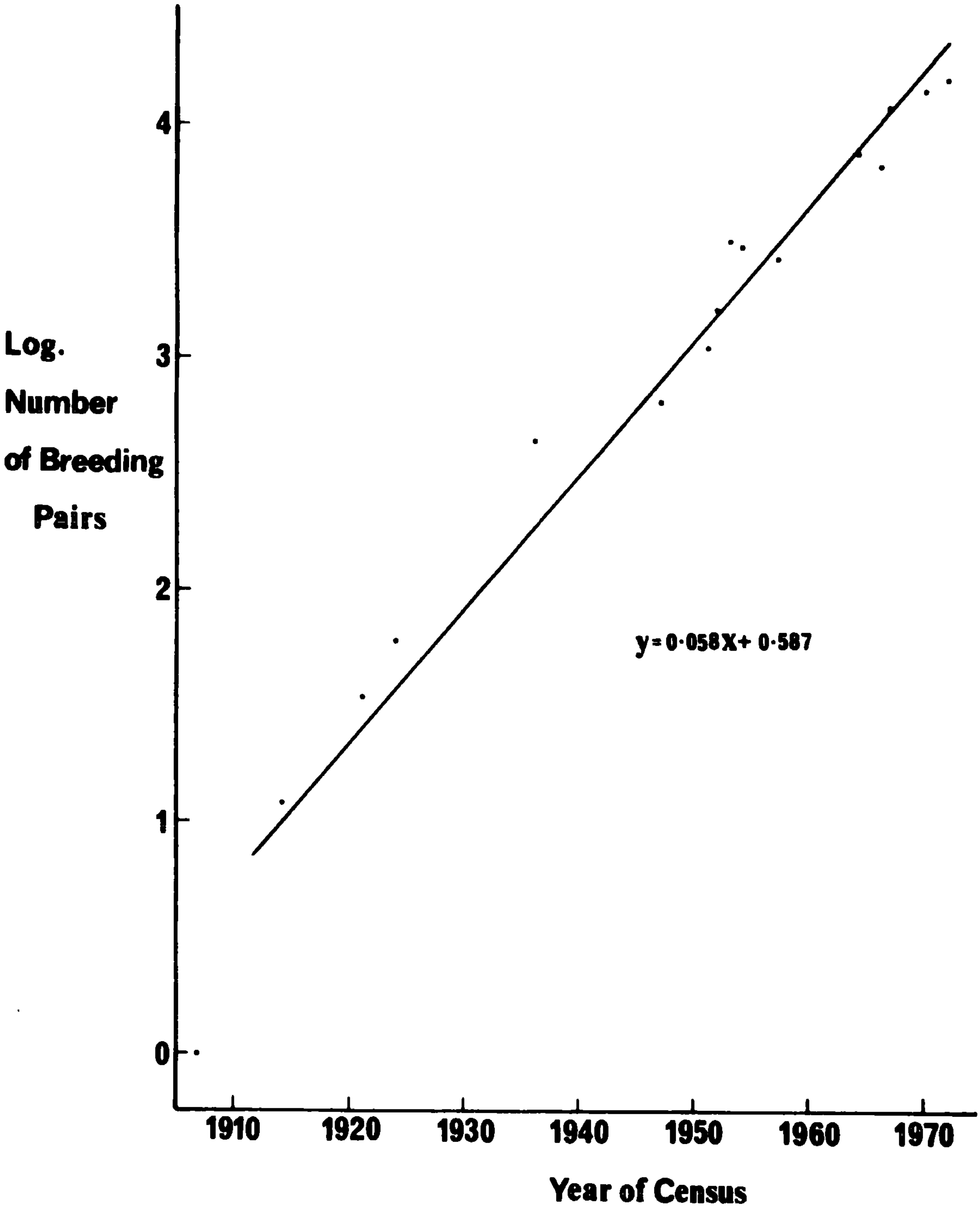

Log.
Number
of Breeding
Pairs
0
1
2
3
4
y = 0·058X + 0·587
1910
1920
1930
1940
1950
1960
1970
Year of Census

Table 40. The numbers of Herring Gulls counted on sub-colonies of the Isle of May before culling 1972-1973

	2 April - 16 May 1972	20 July - 25 July 1972	30 April - 16 May 1973	18 June - 20 July 1973
Sub-colony	Number of pairs counted			
North Ness	1,160	1,400	1,925	-
Rona	3,210	- ***	-	-
East Tarbet	659			
	(479) **	(560)	(600)	(650)
Burrian Rocks	1,016	-	-	-
Island Rocks	1,205	-	-	-
South Plateau	1,300	-	-	-
North Plateau	1,450	-	-	-
South Ness	2,300	2,600	-	-
Peripheral *	650	-	-	-
Island total	12,950	-	-	-

* Rocks lying off the south (Maiden's Hair (see Figure 22) and east (Middens, see Figure 22) coast of the Isle of May.

** Part of the East Tarbet sub-colony was culled from 1972 onwards; the figure in brackets refers to the study area which was left unculled throughout 1972 and 1973.

*** Post-cull counts are given in Appendix 3.

4.2 Survival of Breeding Adults

Much variation exists in the published rates of adult Herring Gull survival (Table 41). Many of the earlier studies were based on the analysis of ringing recoveries and it seems likely that the considerable ring loss resulting from the wear and corrosion of aluminium rings tended to produce over-estimates of the adult mortality rate (Paynter 1966, Kadlec and Drury 1968a).

Table 41. A comparison of published adult survival rates for the Herring Gull

Authority	Methods and location of study	Annual adult survival rate
Paludan (1951)	Ringing recoveries, Denmark	0.85
Olsson (1958)	Ringing recoveries, Finland, Norway and Sweden	0.66
Hickey (1952)	Ringing recoveries, U.S.A.	0.70 - 0.80
Paynter (1966)	Ringing recoveries, Kent Island, Canada	0.66 - 0.84
Drost, Focke and Freytag (1961)	Sightings of colour-ringed adults, Wilhelmshaven, Germany	0.90
Brown (1967)	Ringing recoveries, Walney Island, U.K.	0.90
Kadlec and Drury 1968a)	Inferred from age class census, New England coastal colonies, U.S.A.	0.91 - 0.96
Harris (1970)	Sightings of colour-ringed adults, Skokholm Island, U.K.	0.94
Parsons (1971a)	Inferred from known productivity and rate of population increase, Isle of May, U.K.	0.93
Kadlec (1976)	Ringing recoveries, Milk Island, U.S.A.	0.75 - 0.80
Kadlec (1976)	Inferred from ratio of ringed to unringed adults, Milk Island, U.S.A.	0.80 - 0.85

Errors arising from ring losses were largely avoided by Drost et al. (1961) who estimated a 90% annual survival by observing the rate at which colour-ringed breeding birds disappeared from the colony. Similarly, Harris (1970) estimated an annual survival rate of 94% based on eight colour-ringed adults. In the U.S.A., Kadlec and Drury (1968a) deduced an adult survival rate of between 91% and 96% per annum from the observed age structure of their New England study colonies. The 93% estimate of adult survival made by Parsons (1971a) for birds breeding at the Isle of May colony also avoided any bias due to ring losses since it was inferred from the known rate of population increase at 13% per annum and a productivity of one chick fledged per pair. This last estimate, however, assumed that substantial immigration into the breeding population did not occur (see Section 4.5). 86 adult Herring Gulls were individually colour-ringed during the 1965 to 1969 period, mostly by Parsons (1971a). These birds, together with an additional 41 ringed by Emmerson (unpublished) gave a large enough sample for recapture analysis in 1972.

The numbers of individually colour-ringed adults alive in 1972 or later were obtained by adding the numbers of ringed birds recovered from the 1972, 1973 and 1974 N.C.C. culls to the number of ringed adult gulls that from sight records escaped the culls and were observed to be present on the island between 1972-1974. These data are presented in Table 42. Unlike the softer aluminium rings used by earlier workers, over the time period involved, that is the nine years between 1965 and 1974, the wear and subsequent loss of B.T.O. monel rings in Herring Gulls were negligible (Coulson 1976).

The annual adult mortality was calculated using Jackson's negative recapture technique modified for triple recapture (Bailey 1951). From the solution of equation 3.7 (Bailey 1951) the mean annual survival rate was calculated to be 0.935 ± 0.100 per annum.

Table 42. The number of Herring Gulls ringed as adults and killed in the cull (1972-74) or sighted (1972-74) and therefore known to be alive at the start of the 1972 breeding season

	Year of ringing			
	1965	1966	1968	1970
Number ringed	6	17	63	41
Number alive in 1972	2	7	34	24
Percentage surviving	33.3	41.2	54.0	58.5

These results are in agreement with the highest estimates of survival given by previous workers at British colonies, namely that observed by Harris (1970) and that deduced by Parsons (1971a). They also agree with the New England study made by Kadlec and Drury (1968a). However, Kadlec (1976) re-assessed survival rates at one island colony off the New England coast using a mixture of aluminium, titanium and incoloy (an alloy of nickel, chromium and iron) rings. His highest estimate of adult survival at 85% (based on ratios of ringed to unringed birds, and allowing for 20% non-breeding absentees from the colony) was considerably lower than that calculated as a result of this or other British studies. However, unlike the majority of British colonies, it appeared that the rate of population growth of Herring Gulls on the New England coast had either decreased, or ceased (Drury and Kadlec 1974). At British colonies the estimate made in this study and those of Parsons (1971a), Harris (1970) and Brown (1967) were arrived at either by extrapolation of known facts about the population dynamics of this species at a particular colony, or they were based on ringing that was not subject to considerable bias due to loss and wear of rings. This suggests that this was a realistic range of adult survival rate for this species at British colonies. The estimates of

Paludan (1951), Olssen (1958), Hickey (1952) and Paynter (1966) were clearly too low for adult Herring Gulls from the Isle of May breeding colony.

The average expectation of adult life (e) can be calculated from the expression

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

(Lack 1954), where m = the proportionate annual adult mortality rate and for the Isle of May was calculated to be 14.9 years.

4.3 Survival of immature* Herring Gulls

The published values of immature survival rates are as variable as those for adult survival (Table 43). There is general agreement that immature Herring Gulls have a lower survival rate than breeding adults. This finding is also true for other species of gulls, for example, the Southern Black-backed Gull, with first year and subsequent survival rates of 0.79 and 0.89 respectively (Fordham 1970), and the Kittiwake, where first year survival rate equals 0.79 and subsequent survival rates vary between 0.94 and 0.66 according to age (Coulson and White 1959; Coulson and Wooller 1976).

As with the estimates for adult survival rate, the lowest survival rates were recorded by earlier studies (Paludan 1951, Hickey 1952, Olsson 1958, Paynter 1966) where ring loss may have resulted in some underestimate of the numbers of birds that survive past the first two years after fledging.

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[*] In the present study some Isle of May Herring Gulls showed signs of immature plumage up to the fifth year of life (see Appendix 10). On this basis birds aged between one and five years may be regarded as "immatures", and are so defined in Section 5.5 (page 152) where the effects of culling on the recruitment process are discussed. However, the term "immature" is loosely defined in the literature, and in the context of studies on survival rates it is usual to regard these birds that have never bred before and that have not attempted to recruit into a breeding colony as "immatures". It is this definition of the term that is used in Section 4.3 i.e. immature gulls are those birds between the ages of one and two years.

Table 43. A comparison of published immature survival rates in Herring Gulls

Authority	Methods and location of study	Survival rate according to age (years)		
		0-1	1-2	>2
Paludan (1951)	Ringing recoveries, Denmark	0.38**	0.78	= adult
Hickey (1952)	Ringing recoveries, U.S.A.	0.40**	0.71	= adult
Olsson (1958)	Ringing recoveries, Finland, Norway and Sweden	0.43***	0.58	= adult
Paynter (1966)	Ringing recoveries, Kent Island, U.S.A.	0.55*	0.65	= adult
Brown (1967)	Ringing recoveries, Walney Island, U.K.	0.70***	= adult	
Kadlec and Drury (1968a)	Ringing recoveries and age class census, New England coast, U.S.A.	0.68*** 0.80	= adult	
Harris (1970)	Ringing recoveries, Skokholm Island, U.K.	0.82*	= adult	
Parsons (1971a)	Inferred from known reproductive rate and population growth, Isle of May, U.K.	0.86	= adult	

* Interval 0-1 is from fledging to the following 30 June; interval 1-2 is from 1 July to 30 June.

** Year begins 1 September.

*** Year begins 1 August.

More recent studies where more durable metal rings have been used (Brown 1967, Harris 1970), or some correction for ring loss has been made (Kadlec and Drury (1968a), or the survival rate has been deduced (Parsons 1971a), gave higher values for survival within the range 0.70 to 0.86 (Table 43).

Although Herring Gulls may be immature for up to five years after fledging, previous studies have indicated that the differential survival typical of gull species occurs either within the first two years after fledging (Paludan 1951, Hickey 1952, Olsson 1958, Paynter 1966), or within the first year of life (Brown 1967, Kadlec and Drury 1968a, Harris 1970, Parsons 1971a).

The numbers of Herring Gulls ringed before fledging on the Isle of May which were subsequently recovered through the B.T.O. ringing scheme are given in Table 44. This table presents recoveries according to age class; in keeping with the studies of Paludan (1951) and Hickey (1952), the age class 0-1 has been taken as the interval from fledging to the following 31 July.

Table 44. The number of recoveries of Herring Gulls ringed on the Isle of May, 1966-73, and recorded through the B.T.O. ringing scheme

Age class (years)	Year of ringing 1966	1967	1968	1969	1970	1972	1973
0-1	70	93	135	11	7	31	12
1-2	22	30	18	2	0	4	-
2-3	17	26	15	3	0	-	-
3-4	12	18	12	8	-	-	-
4-5	19	24	7	1	-	-	-
5-6	7	10	19	-	-	-	-
6-7	5	16	-	-	-	-	-
7-8	10	-	-	-	-	-	-

The recoveries of the 1966, 1967 and 1968 cohorts gave large enough sample sizes for the calculation of immature survival rates. For these three cohorts, the largest numbers of recoveries were of gulls in the 0-1 age class. In each case the numbers recovered in the four subsequent years did not differ significantly from what would be expected if a constant rate of mortality was in operation ($\chi^2_{(3)} = 3.158$ and 3.061 for 1966 and 1967 cohorts respectively, in both cases $p > 0.30$; $\chi^2_{(3)} = 5.077$, $p > 0.1$ for the 1968 cohort). On the assumption that the mortality rate is constant and equal to that of adult birds after the first year of life, the first year mortality rate (M_1) can be calculated from the expression:

$$\frac{M_1}{M_A} = \frac{R_1}{R_2}(1-M_1)$$

(Coulson and White 1959). Where M_A is the annual adult mortality rate, and the ratio of the mortalities is taken as being proportional to the ratio of the corresponding numbers recovered (R_1 and R_2 are the number of recoveries in the first and second year birds). For the three cohorts considered, the calculated survival rates ($1-M_1$) were 0.83, 0.83 and 0.67 in the year following the 1966, 1967 and 1968 breeding seasons respectively.

Applying the same procedure to the recoveries in the second and third year of life (i.e. assuming the third year survival rate to be the same as the adult, 0.935), the second year survival rates were 0.922, 0.930 and 0.928 for the 1966, 1967 and 1968 cohorts respectively. The calculated survival rates of second year Herring Gulls were sufficiently close to that of adult birds (at 0.935) to suggest that there are no serious errors in assuming a constant survival rate after the first year of life equal to that of adults.

The calculated first year mortality for the 1968 cohort was significantly higher than for the 1966 and 1967 cohorts. (Comparing the combined recoveries for 1966 and 1967 with 1968, $\chi^2_{(1)} = 10.313$, $p < 0.01$; whilst comparing 1966 with 1968, $\chi^2_{(1)} = 6.207$, $p < 0.02$, and 1967 compared to 1968, $\chi^2_{(1)} = 7.565$, $p < 0.01$).

The 1968 cohort was known to have suffered an exceptionally high pre-fledging mortality (Parsons 1975) and, as shown above, the first winter survival was much lower in that year than in the two preceding years (see also Parsons, Chabrzyk and Duncan 1976). For these reasons, and from a consideration of the population dynamics of the Isle of May colony (Section 4.5), it seems that the first year survival rate of 0.83 was more typical and that the 1968 value was exceptionally low.

On the basis of these survival rates, the average expectation of further life in the 1966, 1967 and 1968 ringed Herring Gulls in their first year after fledging was 5.38 years (1966 and 1967 cohorts) and 2.53 years (1968 cohort).

4.4 Age of Recruitment to the Breeding Population

The Herring Gull, in common with many other seabird species, has a period of deferred maturity. There is relatively little published information as to the length of this deferment. Paludan (1951) concluded that Danish Herring Gulls regularly bred in their third year, although this conclusion was based on a single observation of a gull in immature plumage at a breeding colony. Harris (1970) observed two three year old birds breeding on Skokholm, although Parsons (1971a) observed no breeding three year old gulls and only a minority breeding in their fourth year of life throughout his three year study on the Isle of May.

Drost *et al.* (1961) reported eight three year old male Herring Gulls breeding at Wilhelmshaven. Their study indicated that the age at which first breeding occurred was spread over a three year period with 20% breeding when three years old, 25% when four years old, and 55% when five years old. This gave a mean breeding age slightly in excess of four years. For Herring Gulls in the Dutch Wadden Sea area, Spaans (1971) also concluded that most gulls do not start breeding until they are four or five years old.

Although three year old Herring Gulls were observed throughout the 1972 and 1973 breeding seasons on both study and control areas (Section 5.5), no birds were found to be breeding at this age. In the 1972 breeding season, an intensive search for breeding birds of known age was undertaken on the three study areas. In a total of 141 nests located which belonged to gulls of known age, only 11 (7.8%) belonging to four year old gulls were found (Table 2, Section 2.3). Although this figure relates to the number of ringed birds breeding on the island in 1972, and did not necessarily indicate the numbers of birds in this age class present, it does agree with the observations made by Parsons that only a minority of birds breed in their fourth year.

The three major culls of gulls on the Isle of May by the N.C.C. coincided with the recruitment of many ringed birds. The numbers of ringed birds recovered in the 1972, 1973 and 1974 culls are presented in Table 45, whilst the proportional recruitment each year per ringed cohort is given in Table 46.

Table 45. The numbers of Isle of May Herring Gulls ringed as chicks that were recovered in the 1972-74 control programme

Year culled	Year of ringing as chicks			
	1966	1967	1968	1969
1972	122	111	38	0
1973	188	226	150	2
1974	153	211	184	22
Totals	463	548	372	24

For the analysis presented in Table 46 it has been assumed that all of the 1966 cohort had recruited in or before 1972 (that is, by or in their sixth year of life) and the numbers culled of each cohort are given for every hundred 1966 ringed gulls recovered in the same year. It was possible to estimate the age of recruitment by the change in ratio of more recent cohorts relative to this 1966 year class.

There are two advantages of considering proportional recruitment rather than simply comparing the numbers culled of each cohort in any given year. Firstly, some compensation for any annual variation in survival rates is inherent in this analysis. An exceptionally harsh winter, for example, will affect all cohorts adversely, although not necessarily equally. By using the 1966 cohort as a standard, the calculated recruitment rate in the following year is not lowered. Secondly, the number of birds recovered from the cull depended in part upon how many died on the island and how many died at sea; this in itself depended upon the level of disturbance of partially narcotised gulls. Disturbance varied from one year to the next, and was particularly high in 1973. This would tend to reduce the number of recoveries for 1973, but since disturbance affected all cohorts, a comparison using proportional recruitment was unaffected.

The analysis is complicated by the need to make some correction for the reduction in the numbers of the 1966 breeding birds which resulted from the colony being culled from one year to the next. The 1972 cull was estimated to have removed 40% of the existent breeding population (Section 2.2). The proportions culled in the two subsequent years were lower due to the large scale disturbance caused by the baiting and collecting operations involved in culling. In 1973 the proportion culled was estimated to be 28%. A constant reduction in breeding numbers of 25% has been assumed for the purposes of the analysis in Table 46, and the calculated cohort ratios for 1973 and 1974 have been altered by increasing the culled numbers of 1966 birds by 25% in each year. These figures are given in column 4 of Table 46.

Table 46. The age of recruitment of Herring Gulls on the Isle of May based on the ratios of birds culled of known age

Year of hatching	Age when culled (years)	Number culled per 100 1966-ringed birds culled	Number of recruits per 100 1966-ringed birds allowing for cull	Percentage of recruits culled
1967	4) 5)	91	91	74
	6	120	22	18
	7	138	10	8
	Total		123	
1968	4	31	31	34
	5	80	37	41
	6	120	23	25
	Total		91	
1969	3	0	0	0
	4	1	1	11
	5	14	8	89
	Total		9	

These results suggest that the great majority of recruitment took place between the fourth and sixth year of life. The cull recovery data for the 1967 and 1968 cohorts indicated a similar pattern of recruitment, with four and five year old gulls accounting for the largest proportion of the new recruits (74% and 75% of birds had recruited by their fifth year of life in these two years respectively). Although recruitment by six year old birds was lower, this age class still accounted for between 18% and 25% of the new recruits. The recoveries of the 1967 birds, at 18%, were a more realistic assessment of the extent of recruitment from this age class. The 1968 cohort had not fully recruited by 1974 and the 25% figure indicated by the return of these gulls did not take into account the much lower, but not insignificant, contribution of birds recruiting when they were seven years old. In the 1967 cohort, only 8% of birds had failed to recruit by the age of six years.

The recoveries of the 1969 hatched birds were significantly lower than those of the other three cohorts ($p < 0.001$). There are three probable reasons for this. First, this analysis stops at 1974 at a time when this cohort had incompletely recruited. Six year old recruits would not have appeared at the colony until 1975 and seven year old birds would have returned in 1976. Secondly, many fewer young were ringed in 1969 than in the preceding three years (400 as compared to the 4-5,000 ringed in each of the previous years (Table 47). This means that there were considerably fewer 1969 ringed gulls surviving to recruit into the population in 1973. Thirdly, evidence is presented (Section 5.4) to suggest that continuous culling may have reduced the attractiveness of some of the Isle of May sub-colonies to potential recruits.

However, the recoveries of 1969 ringed gulls showed that, in this cohort, no recruitment took place in the third year, and this strengthened the evidence from observations (Parsons 1971a, and this study) that very few Herring Gulls recruited this young into the Isle of May colony.

Recruitment to the breeding population is defined here as the age at which birds first held territories and not the age at which first breeding took place. This difference is important, since four and five year old birds sometimes established territories without breeding (Table 3, Section 2.3). This was rarely found in six and seven year old recruits. Census counts carried out throughout the 1972 and 1973 breeding seasons (Section 5.5) showed the presence of a much higher proportion of three year old Herring Gulls (assessed on plumage characters) at the colony than was indicated by cull recoveries, and moreover indicated a marked increase in the presence of this age class after the start of the control programme.

On the evidence presented in Tables 45 and 46 considering fully recruited cohorts, the best estimate of recruitment age (age at which territory is held) was four years old = 34%; five years old = 40%; six years old = 18%; seven years old = 8%. Taking into account territorial but non-breeding birds (Table 3, Section 2.3), the age of first breeding (producing eggs) was: four years old = 14%; five years old = 55%; six years old = 23%; seven years old = 8%. This gives a mean age of recruitment of 5.00 years and a mean age at first breeding of 5.25 years.

For Herring Gulls on the Isle of May, the age of first breeding was spread over at least a four year period, and three year old birds, although they may have been present in large numbers, did not normally breed. This suggests that there may be a pre-breeding year at the colony. The mean age of first breeding on the Isle of May between 1972-74 was almost a year later than that recorded by Drost et al. (1961) at Wilhelmshaven (mean age of first breeding = 4.35 years). This may have reflected the greater difficulty experienced by recruits of establishing territories in a larger, more densely populated colony. It also implies that the spread of age at first breeding may vary from colony to colony. There are errors involved in assuming (as do, for example, Paynter (1966) and Hickey (1952)) a published age of first breeding without close investigation of the population in question.

Table 47. The number of Herring Gulls ringed as chicks between 1966-70 and the number recovered during the culls on the Isle of May, 1972-74

Year ringed	Number of chicks ringed	Number recovered in the cull programme	Percentage recovered in culls
1966	4,340	463	10.7
1967	5,230	548	10.5
1968	4,825	372	7.7
1969	400	24	6.0
1970	367	2	0.5

Numbers of Herring Gulls ringed as chicks between 1966-8 from Parsons (1971a).

4.5 Relationship between the Rates of Survival, Productivity and Population Increase

Most authors have checked their survival estimates with known rates of productivity and population change to see if these estimates are reasonable. Paynter (1947, 1966), Kadlec and Drury (1968a) are examples of studies where survival estimates obtained from ringing returns were found to be inconsistent with the observed rates of population increase and measured breeding success. For both these studies, high rates of ring loss were thought to be responsible for the discrepancies.

Similarly, Parsons (1971a) found that his estimate of adult survival (0.88), based on sightings of colour-ringed adults, was too low to give a 13% annual increase in the Isle of May population, and he suggested that this increase was best accounted for by an annual adult survival of 0.93 and a first year survival equal to 0.86.

A similar approach is adopted here. For an initial population size of 1,000 pairs at a constant annual increase of 13% the population after five years will be 1,843 pairs (column 2 of Table 4).

Table 48. A simple model of recruitment into a population increasing at 13% per annum at two different first year survival rates (S1) and a constant post-first year survival of 0.935. (Assuming a closed population with no immigration or emigration)

Year	Number of pairs at a 13% p.a. increase	Number of surviving offspring at S1 = 0.83	Number of surviving offspring at S1 = 0.67
0	1,000	1,000	1,000
1	1,130	830	670
2	1,277	776	627
3	1,443	726	586
4	1,631	678	548
5	1,843	634	586

Between the fourth and fifth year, 212 breeding adults would die as a result of the operation of the 0.065 mortality rate (1,631 x 0.065). The number of recruits required to sustain a 13% population increase must be the difference between the population at year four and year five, plus the numbers dying, that is, 2(1,843 - 1,631) + 212 = 634 recruits would be needed. The initial population of 1,000 pairs produces 1,000 fledged young (horizontal arrow, time 0, Table 48), since the average production of breeding birds on the Isle of May is one young fledged per pair. The survival of these young at the first year survival rate of 0.83 and a subsequent annual survival of 0.935 (column 3 of Table 48) gives exactly 634 surviving gulls in year five available to recruit into the breeding population.

The agreement between young production and the number of recruits required suggests that the calculated survival rates are close to those operating in the natural population. Further, it shows that the Isle of May population could be self-sustaining and that unlike the Herring Gull population of Walney Island between 1950-57 (Brown 1967) there is no need to postulate large scale immigration to account for the observed rate of increase.

At a first year survival rate of 0.67 (calculated for the 1968 ringed cohort) there is a large discrepancy between the numbers available for recruitment (586) and the number of recruits required to maintain a 13% annual increase (634) (column 4 of Table 48).

Capildeo and Haldane (1954) have published tables which relate fecundity, adult survival and age of maturity to give a measure of the rate at which a closed population (with no immigration or emigration) would be expected to increase. The fecundity (f) of Herring Gulls can be calculated as:

$$f = \frac{\text{number of young surviving one year that are produced by each female}}{2\ (\text{annual adult survival rate})}$$

For a first year survival rate of 0.67, followed by a constant rate of survival equal to 0.935, and with one young fledged per female, then $f = \frac{0.670}{2\ (0.935)} = 0.36$. The steady rate of population increase is given by the product of the annual adult survival rate and x where the statistic x at the calculated value of f is 1.183 (Capildeo and Haldane 1954, 1954, Table 1, p. 218), with birds breeding in their fifth year. For a first year survival of 0.67, the calculated rate of population increase is 10.6%. (For a first year survival rate = 0.83, the population increase is 12.8%.)

The 1968 cohort clearly would not give rise to a population increase of about 13% when it recruits into the breeding population. In a closed population, four clear possibilities arise:

(1) A 13% annual increase is maintained by most of the 1968 cohort recruiting one year earlier than normal, that is, in 1972 rather than in 1973 when in their fourth year. With a four year deferment of maturity, x becomes 1.205 and the population increase is 12.7%. The evidence from cull recoveries shows that this did not take place; 41% of this cohort recruited in their fifth year (Table 46).

(2) The fecundity of Herring Gulls breeding in 1968 was greater than 0.36 for a 13% population increase f must be 0.4467 (Table 1, Capildeo and Haldane 1954) at a first year survival rate of 0.67. This implies that gulls breeding in 1968 fledged 1.25 chicks per female. In fact, fledging success was considerably lower in 1968 than in the previous two years as a result of bad weather and a possible epizootic of *Salmonella typhimurium* (Parsons 1975). In 1968, only 0.67 chicks were fledged per breeding female and this implies a population increase of 6.2%.

(3) The lower fledging success of 1968 breeding Herring Gulls and the lowest survival of birds born in this year could be compensated for by a higher post-first year survival rate. If the first year survival is 0.67, then the required 634 recruits needed to sustain a 13% population increase (Table 46) is the result of a constant survival after the first year of 0.986. This greatly exceeds the highest adult survival published for the Herring Gull (0.94, Harris 1970) and is clearly too high. Ringing recoveries of 1968 fledged gulls between 1969-74 showed no significant difference when compared to post-first year recoveries of 1966 and 1967 fledged gulls (Table 44).

(4) This cohort had a lower recruitment into the Isle of May breeding population between 1972-75. If 1968 ringed gulls are representative of birds fledged in this year, then it follows that the population in subsequent years, especially 1972 and 1973 when 74% of recruitment occurred, increased at a rate below 13% per annum.

In discarding the above alternatives it is apparent that the Isle of May colony was not a closed system and that some immigration must have taken place to maintain the observed population growth rate close to 13-14% per annum. There was evidence from the analysis of ringing recoveries to support this (Section 4.6).

4.6 Return to the Natal Colony

Several investigators have noted a strong tendency for Herring Gulls to return to breed at the colony of birth. Such a tendency has been reported for gulls breeding at Kent Island (Gross 1940 and Paynter 1947), the Dutch colonies of Wassenaar and Texel (Tinbergen 1953) and the Skokholm Island and Wilhelmshaven colonies (Harris 1970; Drost et al. 1961).

However, other studies have shown that whilst some Herring Gulls may return to the natal colony, many do not. Spaans (1971) analysed recoveries of gulls ringed as chicks on the Dutch Frisian Islands between 1950 and 1968. He found that out of 337 recoveries, 131 (39%) had returned to the island of birth, although he noted that in many cases birds had joined colonies near to the natal colony. Similarly, Ludwig's (1963) analysis of recoveries for Herring Gulls ringed at colonies in the North American great lakes showed that only 40% had returned to breed at their natal colony (based on 47 recoveries).

The numbers of young ringed on the Isle of May and subsequently recovered there in the culls are given in Table 47. These numbers considered by themselves, however, give an inadequate measure of the extent to which birds returned to the natal colony since no account is taken of the numbers that died due to natural mortality factors acting between ringing and culling. Table 49 gives the numbers of young birds ringed between 1966 and 1969 that were expected to have survived to breed. Cohort survival has been calculated on the basis of known rates of fledging (Parsons 1975), immature and adult survival ($0.67 \times 0.935^4 = 51\%$ of young fledged in 1968 are expected to survive to breed, the survival of other cohorts is 63%).

The numbers of ringed gulls recovered in the cull have been increased to account for the birds that died at sea (N.C.C. staff estimated that up to 10% died at sea). The total has been further increased by 30% to allow for those recruits which survived the cull. This value is excessive and probably lies between 10% and 30% since recruitment was taking place in most of these cohorts between 1972 and 1974, and all individuals were not at risk for the three years.

The percentage return calculated for the 1969 cohort (14%) is much lower than that for gulls ringed in the previous three years. This reflects the fact that data for this cohort are incomplete, and recruitment continued beyond 1974. Considering the three cohorts in which the majority of recruitment had taken place by the end of the 1974 cull, between 27% and 30% of the available Herring Gulls returned to breed at their colony of birth.

Since culling was carried out over the 1972-74 period, the estimated survival of potential recruits has been calculated up to 1973, the mid-point of the cull. There is a large discrepancy between the numbers expected to survive, based on life-table considerations and those that were recovered in the cull. Less than 30% of the young expected to be alive at the time of culling were recovered on the Isle of May, or were observed on the island after the 1974 cull.

Table 49. The number of Herring Gulls ringed as chicks which were estimated to be alive in 1973 compared with the numbers estimated to have returned to the Isle of May to breed

Year ringed as chicks	Number fledged (1)	Estimated number surviving to 1973 (2)	Total number culled or present on the Isle of May	Percentage of survivors found on the Isle of May
1966	3,943	2,187	662	30
1967	4,811	2,853	784	28
1968	3,896	1,995	532	27
1969	360 (3)	244	34	14

(1) Numbers fledged from Parsons (1975)

(2) Based on life-table data

(3) Based on a 10% recovery rate of ringed fledglings (Parsons and Emmerson, unpublished)

There are, however, good reasons to believe that the values used in the life-table are realistic. The differences between the expected numbers and the actual numbers of ringed birds culled are large. It seems unlikely that such large numbers of birds were culled but remained unlocated on the island. The alternative explanation is that approximately 70% of surviving young gulls reared on the Isle of May bred elsewhere. Herring Gulls originating from the Isle of May have been culled on the two Firth of Forth Islands of Fidra and Inchmickery (details supplied by the Royal Society for the Protection of Birds for gull control programmes carried out in 1973), and, in addition, have been observed to be breeding on Bass Rock, Craigleith, St Abbs (Berwickshire) and on the Farne Islands (Northumberland) (Duncan, in press). Further information on Herring Gull emigration from the Isle of May has been forthcoming from a recent study carried out by Monaghan (1977). Monaghan observed gulls nesting in urban areas of north-east England in 1974. Amongst the Herring Gulls she found breeding at these urban sites there were 21 birds originally ringed as chicks on the Isle of May during the 1966-68 period. These birds constituted 3% of urban colonies (21 gulls in 600). Although such observations do not give a quantitative measure of the extent to which emigration to other colonies took place, they show that some of the birds that failed to return to the Isle of May were breeding at other colonies.

It was difficult to assess the extent of immigration into the Isle of May breeding population. This difficulty is in large part due to a lack of extensive colour-ringing programmes on the surrounding islands in the Firth of Forth and nearby mainland colonies. Evidence for some immigration was provided by cull recoveries of Herring Gulls ringed on the Farne Islands, Bass Rock, Inchkeith, Inchmickery, Fidra, Inchgarvie, Craigleith and Inchcolm (for islands in the Firth of Forth small numbers of gulls had previously been ringed by Grant 1969). Since the number of young produced per pair in this species appears to be similar for most colonies studied (Section 3.6), and since the number of gulls at the majority of British colonies are increasing at similar rates (Section 4.1), it would seem reasonable to equate immigration rates with those for emigration. For the Isle of May colony, the emigration rate may be as high as 70% of all available recruits.

These results agree with those of Ludwig (1963) for Herring Gulls returning to breed at colonies in Lakes Huron, Michigan and Superior. Similarly, Ludwig (1974) has demonstrated a marked variation in the return of Ring-billed Gulls to the complex of island colonies within the North American Great lakes system. For this species, a range in faithfulness to natal colony of 0% to 54% was observed. Ludwig believed that for both Herring Gulls and Ring-billed Gulls this was a reflection of the relative physical instability of the colonies and of variations in nesting density. He suggested that gulls attempted to return to their natal colony, failed to recruit, and subsequently bred elsewhere.

This study provides little data in support of either this suggestion or for the random return theory proposed by Southern (1967). Certainly, on the Isle of May there were large numbers of three and four year old gulls on the edges of the main breeding areas late in the breeding season (late-June and throughout July, Section 5.5). Some of these birds may not have been able to establish territories at the natal colony and may have bred at other colonies in the following year. Such speculation may give a basis to the findings of Drury (1965) and Drury and Nisbet (1969) that recently founded and rapidly expanding Herring Gull colonies rely heavily upon immigration of young birds produced at established colonies.

SECTION FIVE THE RECRUITMENT PROCESS

5.1 Return to the Area of Birth

Several workers have noted that colonially breeding seabirds exhibit a strong attachment to their area of birth. The term "philopatry" has been widely used to describe such behaviour, and in its broadest sense philopatry may be taken to refer to recruitment to the natal colony (see Section 4.6). However, for some species there is evidence of a much more specific philopatric tendency, in that recruiting birds not only attempt to breed at their natal colony, but that they also attempt to establish breeding sites close to those in which they were born. For example, Serventy (1967) studied the breeding biology of Short-tailed Shearwaters on Fisher Island in the Bass Strait (Tasmania), an island which contained three discrete rookeries of shearwaters. Recruiting birds not only returned to the natal rookery but they also established burrows at distances of 0.6 to 18m from the burrow in which they had been born. (For males, the mean distance from the burrow of birth was 6.7m, and for females this distance was 7.6m.) Similarly, recruit Gannets on the Bass Rock in the Firth of Forth frequently attempted to breed in the vicinity of the parental nest site (Nelson 1978).

There is circumstantial evidence that an affinity to area of birth also exists in recruiting Herring Gulls. Both Tinbergen (1953) and Parsons (1971a) observed the presence of ringed adults within the approximate areas in which these birds had been ringed as chicks, although in both cases these were casual observations and gave no quantitative estimate of the extent of natal area faithfulness (i.e. "within colony" philopatry) in these species.

The existent ringing information for the Isle of May was insufficiently precise as to the locality of chick ringing to test the hypothesis that recruiting Herring Gulls returned to establish territories within the immediate vicinity of the natal nest site. It was however possible for many birds to ascertain the sub-colony into which recruitment had taken place. If gulls which had recruited over the 1970-74 period exhibited attachment to the natal area, then it was to be expected that the majority of birds ringed as pulli between 1968 and 1969 would have been culled on the sub-colony of birth.

There were eight possible sub-colonies on the island into which birds might have recruited. On the basis of a random selection of nesting area there would thus have been a one in eight chance of culling a bird on its sub-colony of birth, that is approximately 13% of the gulls which had recruited into the colony would have been expected to have been located on the sub-colony in which they were ringed as chicks. Analysis of the cull recoveries of ringed birds showed this not to be the case and there was a significant deviation from the random recruitment model ($\chi^2_{(3)} = 2.751$, $p < 0.01$). The majority (66%) of birds were culled on their natal sub-colony (Table 50).

Table 50 The extent of philopatry in the Herring Gull as indicated by the recovery of ringed birds culled between 1972-74 on the Isle of May

Year in which ringed as chicks	Number culled from known sub-colony	Number killed on sub-colony of ringing	Percentage in natal sub-colony
1966	414	278	67
1967	506	332	66
1968	342	212	62
1969	24	21	88
Total	1,287	843	66

There was clearly a marked tendency for many breeding gulls to return to the sub-colony from which they were hatched. A high percentage (88%) of philopatric birds belonging to the 1969 cohort were recovered, the majority of these birds being culled in 1974 (20 out of the 1972-74 total of 22 were culled in this year) when in their fifth year of life, and therefore at a time when most were recruiting into the breeding colony. This suggested that there was a strong tendency for recruiting gulls to return to their natal sub-colony. Similarly, the 1968 cohort exhibited a higher faithfulness to natal area (78%) in its main recruitment year of 1973 (when these birds were five years old) than did either the 1966 or the 1967 cohorts (both 67% in 1973).

These data were borne out by observations of colour-ringed birds at the edges of breeding areas throughout the 1972 and 1973 breeding seasons. For example, four gulls ringed as chicks by Emmerson on the Colm's Hole area in 1970 were persistently sighted at the seaward edge of this breeding area in 1973; these birds however never established territories. Similarly, in the previous year, birds of the 1969 cohort (then three years old) had been frequently sighted at the edges of East Tarbet and North Ness, areas where most of these birds had been ringed as chicks.

The evidence from sightings is circumstantial, but it lends support to the analysis of the cull data and suggests that birds recruiting when three to five years old were strongly attracted to their natal sub-colonies, although in the case of three year old gulls it seemed that these birds did not breed until a year or more later. Similar observations were made by Parsons (1971a) for the 1966 cohort in 1969.

If recruits were attracted to the area in which they had been hatched, it might be expected that those birds which, for various reasons, did not recruit into their natal sub-colony might breed in areas close to their natal sub-colony. A consideration of the recoveries of those birds that were not culled on the natal sub-colony indicated that over half had returned to areas immediately adjacent to that in which they were born (Table 51). This distribution again deviated significantly from what would have been expected from a random dispersal (in this case the probability of a bird recruiting into a sub-colony other than the natal one was one in seven, or approximately 14%: $\chi^2_{(3)} = 320$, $p < 0.01$).

Table 51 The distribution of Herring Gulls culled (1972-1974) on areas other than the natal sub-colony

Year in which ringed as chicks	Number of gulls not culled on natal sub-colony	Number of gulls on adjacent sub-colony	*Percentage on adjacent sub-colonies
1966	136	72	53
1967	174	90	52
1968	131	61	47
1969	2	2	100
Total	443	225	51

*Percentage on adjacent sub-colonies calculated as:

$$\frac{\text{number of gulls on adjacent sub-colony}}{\text{number of gulls not culled on natal sub-colony}} \times 100$$

Recruitment into the natal colony was evidently not a random process. Most Herring Gulls were attracted to and recruited into their natal sub-colony. The fact that over half of the gulls not found in their natal sub-colony recruited into adjacent sub-colonies was a measure of the strength of this tendency. There was also an indication that philopatry was strongly developed in four year old recruits. Although only two ringed four year old birds were not culled on their natal sub-colony in 1973, these birds, which had been ringed in 1969 on Rona, were both culled on the adjacent East Tarbet sub-colony.

Once recruited into the breeding population, Herring Gulls often returned to breed in the same area in subsequent years. Adult breeding birds had been colour-ringed on the Isle of May since 1965. Of the 55 recoveries of adult-ringed Herring Gulls, 46 (84%) were culled on the same sub-colony on which they had been ringed, and a further six (67% of those that had moved from the area of ringing) were found in adjacent sub-colonies. This indicated relatively little movement by experienced adults once they recruited into an area.

5.2 The Sex-ratio of Recruits

Ringed Herring Gulls which had been narcotised during the 1972-74 culls were routinely dissected and measured together with comparable samples of unringed adult and immature* birds. In a sample of 1,078 culled unringed adults examined over this period there were 552 males (51.2%), while in 80 culled gulls ringed originally as adults there were 39 males (48.9%). The sex-ratios of these samples were thus 1 : 0.95 and 1 : 1.05 (males to females) and in neither case was there a significant departure from an equal sex-ratio ($\chi^2_{(1)} = 0.267$ and 0.025 respectively, for both cases, $p > 0.05$). Accordingly, for Herring Gulls breeding on the Isle of May, there was no evidence of differential adult survival rates between the sexes. This contrasts with the available information for Kittiwakes where adult female survival is higher than that of males (Coulson and Wooller 1976).

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* These birds were identified on plumage characters; such birds were between the ages of three and five years (see Appendix 10).

The numbers of Herring Gulls ringed as chicks, and subsequently recovered on the Isle of May, are given in Table 52. For the 1967 and 1968 cohorts there was a slight decrease in the number of males killed as the cull progressed (60% to 56% for the 1967 cohort, and 62% to 59% for the 1968 cohort, Table 52). Since birds ringed in 1968 and 1967 were recruiting into the breeding colony in large numbers during 1972 and 1973, the possibility existed that these differences in sex-ratios were a result of males recruiting at a younger age than females. Such a difference in age of first breeding is known for Red-billed Gulls (Mills 1973), although in other species females breed younger than males, for example, Kittiwakes (Wooller and Coulson 1976), Gannets (Nelson 1978) and Short-tailed Shearwaters (Serventy 1967).

If a difference existed between the sexes in age of recruitment and first breeding, then a departure from equity would have been expected in the sex-ratio at the beginning of the cull in 1972 which would have gradually diminished as the cull progressed. In fact, for the three cohorts ringed in 1966, 1967 and 1968, the differences between sex-ratios in the 1972, 1973 and 1974 samples were not significant ($\chi^2_{(2)} = 0.015$, $p > 0.05$; $\chi^2_{(2)} = 0.741$, $p > 0.05$; and $\chi^2 = 0.143$, $p > 0.05$; for the 1966, 1967 and 1968 cohorts respectively), and for Herring Gulls breeding on the Isle of May there was no evident difference between males and females in age of recruitment.

The sample of birds ringed as chicks between 1966 and 1969 and recovered in the 1972-74 culls totalled 1,151, of which 660 (57%) were males. The sex-ratio of this sample (1 : 1.34 males to females) differed significantly from that of the unringed adult sample ($\chi^2_{(1)} = 8.201$, $p < 0.01$). Since there was no difference between males and females in the age of recruitment, and no evidence of differential survival, this suggested that more female than male gulls bred at colonies other than the natal one. Since overall 66% of surviving Herring Gulls were found not to return to the Isle of May, and the sex-ratio of recruited birds was 57% males to 43% females, then it would be expected that 70% of surviving females emigrated to other colonies.

There is some circumstantial evidence for a skewed sex-ratio of Isle of May immigrants to some colonies although there is little information for most colonies. Monaghan (1977) observed Isle of May ringed birds breeding on rooftops in Sunderland and South Shields. Of the ten gulls she observed, six were found to be females. Conversely, in 1972, nine out of the ten Herring Gulls culled on the Isle of May, which had been ringed at other colonies (on the Farne Islands and on the Bass Rock) were females, and four out of five immigrants culled in the following year (from the Farne Islands) were females. This suggests that female Herring Gulls on the Isle of May were not atypical in the tendency to select breeding colonies other than the natal one. Indeed, this must have been so, since the sex-ratio of breeding adults was equal.

The fact that female Herring Gulls were less likely than males to return to their natal colony suggested that there might have existed a difference between the sexes in the strength of the philopatric tendency. This was the case for Isle of May Herring Gulls. The sex-ratios of ringed Herring Gulls culled on the area of ringing (Table 53) showed that overall 77% of males and 54% of females were recovered on the natal sub-colony. This difference between the sexes was highly significant ($\chi^2_{(1)} = 59.34$, $p < 0.001$).

Table 52 The sex-ratios of Herring Gulls of known age culled on the Isle of May between 1972-74

	Year of hatching							
	1966		1967		1968		1969	
Year in which culled	Number culled of known sex	Number and percentage males *	Number culled of known sex	Number and percentage males *	Number culled of known sex	Number and percentage males *	Number culled of known sex	Number and percentage males *
1972	114	59 (52)	96	58 (60)	37	23 (62)	0	0
1973	128	80 (63)	177	98 (55)	106	64 (60)	0	0
1974	119	64 (54)	201	112 (56)	158	93 (59)	15	9 (60)
Total	361	203 (56)	474	268 (57)	301	180 (60)	15	9 (60)

* Percentages of male birds in the culled samples are given in brackets.

Table 53 The differences between male and female Herring Gulls in their faithfulness to their natal sub-colony on the Isle of May

Year in which culled	Number of males killed on known area	Number of males killed on natal area	Number of males on adjacent area	Number of females killed on known area	Number of females killed on natal area	Number of females killed on adjacent area
1972	130	94 (72)*	19	100	65 (65)	15
1973	227	190 (84)	17	154	87 (57)	26
1974	250	182 (73)	32	184	85 (46)	45
Total	607	466 (77)	68 (11)	438	237 (54)	86 (20)

* Percentages of birds killed are given in brackets.

5.3 Faithfulness to Natal Area in Relation to Sub-colony

The division of the Isle of May into eight sub-colonies does not imply that each sub-colony was similar in its pattern of recruitment. In other colonially nesting seabirds recruitment is known to be at least partially determined by age structure, nest density (Nelson 1970, 1978), or by the situation of a particular site within the colony (Coulson 1971). On the Isle of May the various sub-colonies are of different size, had different numbers of resident breeding birds, and have different physical characteristics (Section 2.1). It is probable, therefore, that the sub-colonies may have differed either quantitatively or qualitatively in the process by which birds recruited to them.

As the cull progressed it was observed that certain sub-colonies appeared to be particularly rich in the numbers of colour-ringed gulls recovered from them. This was also evident from census counts made throughout the 1972 and 1973 breeding seasons (Section 5.5). Given that some Herring Gulls exhibited a strong tendency to return to the sub-colony in which they were born, and that previous ringing of chicks tended to be more concentrated on the study areas than elsewhere (Parsons 1971a), then it follows that the various sub-colonies will have had different numbers of resident breeding colour-ringed birds.

However, despite this, some areas, for example, Rona and North Ness, had many more colour-ringed gulls than would have been expected if these birds had recruited at the same rate into all areas. The eight sub-colonies are compared in Table 54. It was evident from the recoveries of birds ringed on known areas that there were marked differences in the faithfulness to the natal sub-colony exhibited by gulls recruiting into the eight sub-colonies. Clearly, Herring Gulls born on North Ness, Rona and East Tarbet (71-75% return to the natal area) were more likely to return to breed at their natal sub-colonies than were birds ringed on Island Rocks, South Plateau and South Ness (43-50% return to natal area). This was so despite the fact that, with the exception of gulls ringed on South Plateau, the percentage recovery rates of ringed birds in the cull were very similar.

On the three northern sub-colonies many of the birds that were not culled in the area of birth were found breeding in an adjacent area (overall 65%) rather than elsewhere on the island. Since gulls not breeding in their natal area, but born on the northern half of the island, tended to be in an adjacent sub-colony, relatively few would have been expected on the east coast sub-colonies and on the North and South Plateaus. Of the 188 gulls ringed on the North Ness, East Tarbet and Rona, but not culled on their natal sub-colony, 44 (23%) were found on areas in the southern half of the island. This differed from a random dispersal where the expectation was that 63% should have been found at other sub-colonies (that is, there were five chances in eight of a bird going to other sub-colonies: $\chi^2_{(1)} = 34.89$, $p < 0.01$).

Conversely, the majority of birds ringed on the North and South Plateaus, South Ness and the east coast that were not culled on their natal areas were found to be breeding on the three northern sub-colonies (259 birds did not return to the natal area. Of these, 136 were culled on East Tarbet, North Ness and Rona, that is, 53% were culled, where 38% were expected on a random dispersal, this difference being significant, $\chi^2_{(1)} = 18.29$, $p < 0.01$). A possible explanation of these data is that the three northern sub-colonies were more attractive to gulls recruiting into the colony.

The spatial distribution of Herring Gull breeding areas on the Isle of May has altered considerably as the population has increased. In 1936, Southern (1938) noted that the majority of gulls were nesting in two main groups, one on the Middens, and the other on the Maiden's Hair, two rocky

Table 54 The differences in faithfulness to the natal area exhibited by Herring Gulls breeding on the different sub-colonies on the Isle of May in 1972-1974

Sub-colony	Number of chicks ringed on sub-colony 1966-68	Number of ringed gulls culled 1972-4 which had been ringed on sub-colony	Percentage recovery rate	Number culled on natal sub-colony	Percentage return to the natal sub-colony	Number of gulls culled on adjacent sub-colonies	Percentage * culled on adjacent sub-colonies
North Ness [2]	1,661	179	11	127	71	34	64
Rona [1]	4,417	443	10	330	75	73	65
East Tarbet [3]	881	86	10	63	73	15	65
Burrian Rocks [1]	2,539	245	10	146	60	50	51
Island Rocks [1]	906	88	10	44	50	15	34
North Plateau [1]	397	83	21	46	55	10	27
South Plateau [1]	280	56	20	28	50	12	52
South Ness [2]	1,077	89	8	38	43	10	20

[1] Areas culled in all three years

[2] Areas culled in 1973 and 1974 only

[3] Partially culled 1972 and 1973, mostly culled in 1974.

* Of the number of birds that did not return to the natal sub-colony.

prominences lying off the east coast and southerly tip of the island (Figure 21). As the population increased, the gulls which had first nested on rock ledges began to breed on the flatter parts of the island (Baxter and Rintoul 1953). By 1951, gulls were breeding around most of the island's periphery, and groups of breeding birds were well established on North Ness, East Tarbet and Rona by 1957. During the late fifties and sixties, as the population increased exponentially, the nesting density on established breeding areas increased, and new areas were colonised. The N.C.C's records indicate that approximately one third of the North Plateau, the majority of the South Plateau, and about one half of the Island Rocks sub-colonies have arisen since 1966 (Figure 21). In comparison, the spatial distribution of Herring Gulls breeding on North Ness, East Tarbet and South Ness has remained relatively constant since 1957. The number of gulls on these areas could not have increased by a change in distribution pattern as had obviously been the case for the South and North Plateaus, and must have increased as a result of changes in nesting densities.

Table 55. The relationship between nest density and the extent of faithfulness to the natal sub-colony

Sub-colony	* Area (m^2)	Estimated no. of pairs in mid-May 1972	Nesting density (nests per $100m^2$)	** Percentage return to the natal sub-colony
North Ness	10,661	1,160	10.9	71
Rona	45,562	3,210	7.1	75
East Tarbet	22,991	479	2.1	73
Burrian Rocks	28,791	1,016	3.5	60
Island Rocks	33,699	1,205	3.6	50
North Plateau	61,273	1,450	2.4	55
South Plateau	45,839	1,300	2.8	50
South Ness	39,194	2,300	5.9	43

* From a 33cm : 1km scale map

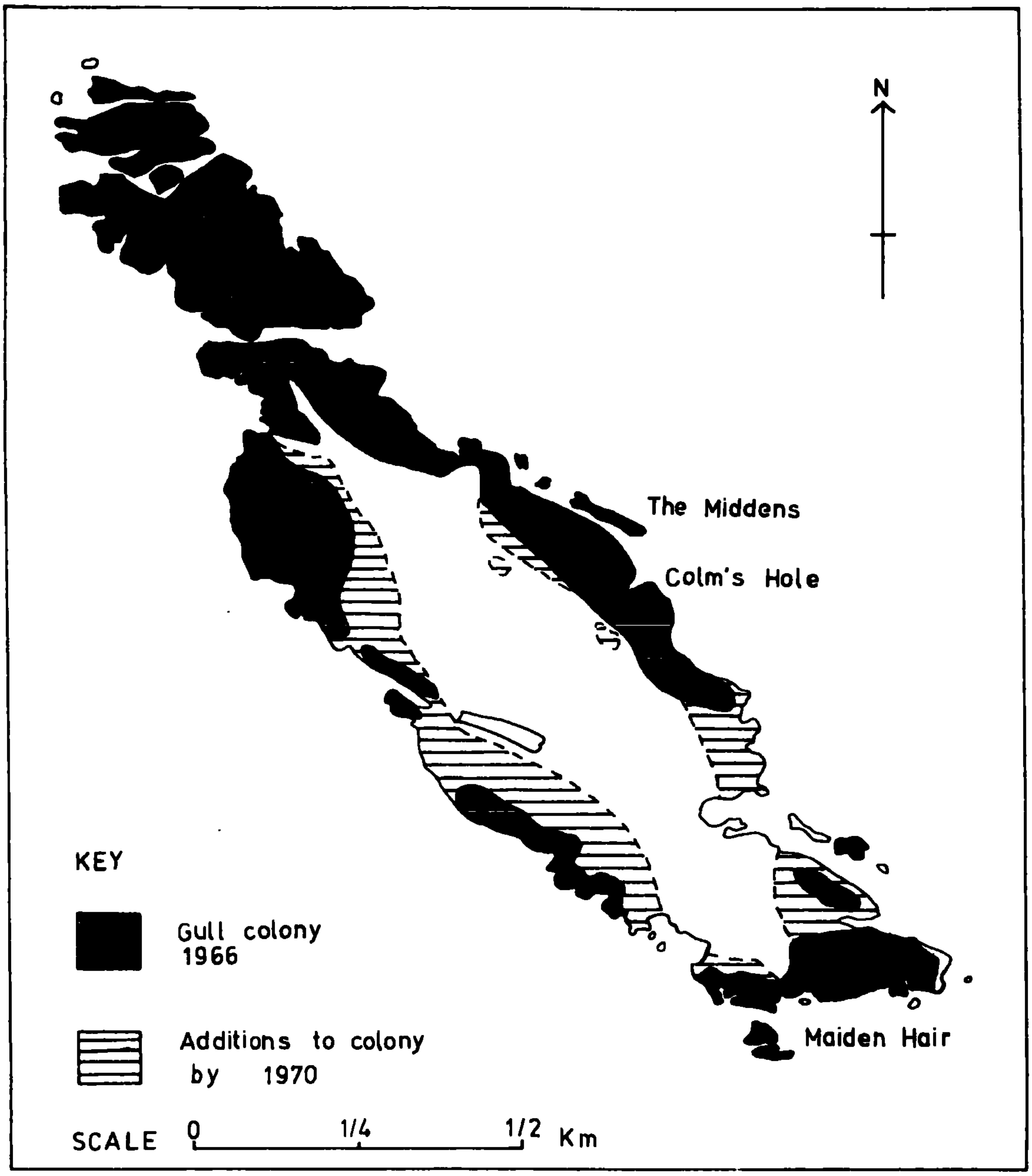
** The regression of percentage return to natal sub-colony (y) on nesting density (x) was not significant; $y = 1.436x + 52.75$; $r = 0.358$, N.S.

Figure 21

The boundaries of the gull colony in 1966 and 1970.

(Date and details for distribution map provided by

Miss N. Gordon of the N.C.C.).


N
The Middens
Colm's Hole
Maiden Hair
KEY
Gull colony 1966
Additions to colony by 1970
SCALE 0 1/4 1/2 Km

Herring Gulls breeding at low densities were known to have had lower breeding success than birds breeding at higher medium densities (Section 3.6). The attraction of recruits to high densities, therefore, had obvious selective advantage since by breeding at higher densities four and five year old birds could improve their breeding performance, thereby raising more young to fledging. However, the advantages of breeding at high densities may in part have been counterbalanced by the increased physiological stress encountered under these conditions (Wooller and Coulson 1977).

The suggestion that the recruitment into the breeding population of colonial seabirds is a function of nesting density is by no mean new, and has been proposed by various authors (for example, Ashmole 1963 and Wynne-Edwards 1962). In addition, there is evidence that recruits are attracted to sites where breeding success is high (good quality sites) in the Shag (Coulson 1971) and the Kittiwake (Wooller and Coulson 1977).

If a combination of high nesting density and established breeding tradition was attractive to Herring Gull recruits, then the high degree of philopatry of birds born on the East Tarbet, North Ness and Rona sub-colonies, and the large numbers of colour-ringed birds that were resident on these areas, may be seen to be expressions of this differential attractiveness of different sub-colonies.

This suggestion could be tested by comparing the densities of breeding Herring Gulls on the eight sub-colonies (Table 55). The absolute nesting densities of the sub-colonies were based on pre-cull census counts carried out in mid-May 1972 and the sub-colony areas taken from a scale map of the island. Although the density of nests on culled areas was known to have decreased between 1972-74, many ringed birds had recruited before 1972, on the basis of pre-cull rather than post-cull conditions on the sub-colonies. Although the data showed that for the two sub-colonies with the highest nesting densities, i.e. Rona and North Ness, there was a high degree of philopatry in recruiting Herring Gulls, generally there was no obvious trend of increasing philopatry with increasing density. Thus, birds recruiting into East Tarbet, which had the lowest absolute density in 1972, showed a high rate of return to the natal area (73%), whilst the lowest return to natal areas was evident for gulls born on the South Ness (43%), which had a comparatively high density of nests. The inadequacy of absolute density as a comparative measure was evident from a consideration of East Tarbet. At the highest density on this sub-colony, nests were often one metre or less apart although some of the available sub-colony area had no nests at all, or was occupied by breeding Lesser Black-backed Gulls. Similar deviations from a uniform distribution in the pattern of nesting have been found by Parsons (1976b) and obviously comparisons between areas required the use of a measure of nest distribution rather than a measure of nesting density.

If high densities were attractive to recruits, then South Ness was an obvious anomaly. Like the northern sub-colonies, South Ness had been a well-established breeding area since at least 1957. Its boundaries are fixed by three seaward edges and it would have been expected to have increased in density by as much as Rona, which is of comparable area (Table 55). A possible explanation of the relatively low philopatry of gulls born on the South Ness may be the fact that this area had been traditionally used by both visitors and lighthouse keepers as an egg-collecting area. This practice was well established on the Isle of May prior to the N.C.C. cull in 1972. Egg robbing has the effect of progressively delaying the breeding season with a resulting reduction in breeding success of gulls on collected areas. Parsons (1971a) continually robbed and disturbed a well-defined area on north-west Rona in order to observe the long-term effectiveness of this as a control method for Herring Gulls; Emmerson in 1970 continued this disturbance. Thus, the chicks fledged from this area between 1966-70 were from late-laid clutches. The cull recoveries of birds ringed on this area indicated a possible long term effect of such disturbance on future recruitment. Out of the 17 ringed birds culled that were known to have been born on this area, only five (29%) had returned to breed on the natal area; seven out of the 12 (58%) recoveries on areas other than the natal one were on the adjacent areas of North Ness and central Rona. A similar decrease in philopatry on South Ness suggested that prolonged egg-collecting on this sub-colony had made this area less attractive to potential recruits.

5.4 The Effects of Nesting Density on Recruitment

Comparisons between areas are sometimes difficult to interpret; often too many variables are involved, and generalisations made often have exceptions. The alternative approach is experimental and has the advantage of reducing the number or partially controlling some of the variables involved. Accordingly, in order to test the suggestion that high densities were attractive to recruits, two areas were experimentally cleared of territorial gulls. This experiment was carried out late in the 1972 breeding season between 10 and 28 July at a time when, from census counts, many recruiting gulls were known to be present at the colony. The areas cleared were both on the North Plateau sub-colony, this area being chosen principally because it was one of the few breeding areas that had a well defined edge beyond which no gulls nested. This edge thus represented the limit of expansion of the breeding population. Herring Gulls had only nested on this area since 1966 (shaded portion of southern part of the North Plateau, Figure 21). An area of $625m^2$ within this edge zone was cleared of gulls by using the same method of culling as the N.C.C. (see Section 2.2).

The cleared edge area was compared with an area of the same size centrally located within the sub-colony. Both areas were baited on four consecutive occasions, and narcotised birds were removed at between three to five hour intervals after baits had been placed. The area in the centre was observed before clearing to contain eight territories, whilst that at the edge of the sub-colony had seven resident pairs of Herring Gulls. The nesting densities of the two areas were therefore 2.56 nests per $100m^2$, and 2.24 per $100m^2$ for centre and edge respectively. However, these measures of nesting density did not accurately reflect the distribution of nests which in both areas was not uniform. Indeed, the central area had been chosen partly on the grounds that nests here were markedly aggregated. To overcome the inadequacy of absolute densities, a relative measure of nest density was used which involved measuring the shortest distance between one nest and its nearest neighbour. Nests were chosen at random, and 25 measurements were taken in each area. The mean distance between nearest nests in the central area was 1.42m ± 0.37, and that at the edge, 313m ± 0.55. The difference between nesting areas was significant ($t_{48} = 6.45, p < 0.001$).

The results of this clearing experiment are given in Table 56.

Table 56 The number of Herring Gulls recruited into two experimentally cleared areas on the North Plateau sub-colony in 1972

	Date of clearing (July)				Total number of Herring Gulls killed	Number originally present	Number of recruits into cleared areas
	10	12	21	28			
Centre	15	7	3	4	29	16	13 (45%)*
Edge	7	3	0	0	10	14	0

* The proportion of the total number killed that were recruits

In the central area, although only eight pairs were resident, a total of 29 Herring Gulls were narcotised, and birds were killed on each occasion that baits were laid. This suggests that at least 13 gulls were attracted into this area, although this number may have been greater as some birds were found dead at distances up to 75m outside the area (although sufficiently close to the centre to indicate that they had eaten baits on this area). Despite careful searches, some birds may have been hidden in the dense vegetation cover of the North Plateau.

The behaviour of gulls in July differed from that earlier in the breeding season. Observations made of the area after baiting indicated that whereas birds in mid-May often took only one bait per bird (Anon 1972), considerably more than one bait was eaten by individuals in late-July. One bird was found to have ten baits in the crop and had, therefore ingested ten times the lethal dosage of alpha-chloralose.

At the edge area, ten birds were culled in total and in contrast to the central area no birds were recovered on or in the vicinity of this area between 21 and 28 July (Table 56). On these two occasions few of the baits were missing, and almost the same number were recovered as had been originally placed. This suggested that these ten gulls were resident before clearing, and probably few, if any recruits entered the area. The difference between areas was further confirmed by the fact that at the edge the culled birds were all adults (six males to four females), whereas at the centre the resident birds had been unringed adults, although the birds culled included two colour-ringed five year old birds and a plumage identified three year old bird.

These results suggested that there was a difference in attractiveness to recruits between the two areas. The differences between them were in nesting density and position. Recruitment pressure at high density central areas was more intense than that at peripheral zones on a sub-colony.

In order to investigate the alternative possibility that recruiting birds were attracted to sparsely populated areas where (in contrast to central areas with a high density of nests) there was available space in which territories could be established, a comparison of two areas on the Rona sub-colony was made in 1973. Both areas were situated on the seaward edges of this sub-colony. The first area, 4,761m^2 on the N.W. tip of Rona, was culled by the N.C.C. in May 1973, and by the end of culling in 1973 there were 152 pairs left holding territories. This area was further culled on six occasions between 8 and 26 June. Clearance measures in June resulted in the death of 87 (29%) of the estimated 304 post-N.C.C. cull resident gulls. In addition, the few eggs laid on this area in June were either removed or broken. The second area on the S.E. edge of Rona (3,774m^2) was not culled by the N.C.C. and was left undisturbed throughout the 1973 breeding season. Consequently many nests in this area contained chicks, some of which fledged successfully. No young were produced by birds nesting on N.W. Rona.

The control area on S.E. Rona contained 163 resident pairs of Herring Gulls by the end of May and was observed at intervals throughout June and July. Clearance measures on the experimental area were stopped by the end of June and this area was also observed throughout July. Counts of plumage identified recruits (mainly three and four year old gulls) are given in Table 57. The numbers of recruits, and therefore the recruitment pressure, increased steadily throughout July on both areas (Figure 22), although the largest numbers of recruits were observed to enter the control area. The mean number of recruits on S.E. Rona was over twice as large as that for N.W. Rona. These two areas differed in their nest densities (considering resident breeders on S.E. Rona in June and N.W. Rona at the beginning of July the nesting densities were 4.45 nests per 100m^2 and 2.23 nests per 100m^2 respectively) and in the fact that the control area contained successful breeding pairs. These results suggested that undisturbed, high density areas were more attractive to recruiting birds than disturbed lower density areas. However, only six (19% of the mean number of recruits) of the recruits entering S.E. Rona were observed to establish territories, although none of these birds laid eggs. In contrast, ten (71%) of the mean 14 recruits observed on the culled area succeeded in maintaining territories. On the control area, competition for space was intense; potential recruits were observed to land continually amongst the resident breeders. Most of these birds were quickly driven away by territory holders and spent most of their time in the air flying from one "perch" to another. The three territories established on this area were on the extreme S.E. tip of the area where competition was less intense. On the culled area, recruits were less frequently chased off by resident breeders; they spent relatively longer periods on the ground than in the air. Only two of the territories established by these recruits were peripheral ones.

It therefore seemed that the greater attraction of undisturbed, high density areas was to some extent offset by the difficulties encountered by recruits in the establishment of territories.

Table 57 The numbers of recruiting Herring Gulls observed on an experimentally cleared area and on an uncleared control area within the same sub-colony in 1973

Date of count	Number of resident gulls	Number of recruits observed	Percentage recruitment *
Control area (S.E. Rona)			
2 June	326	16	4.9
8 June	326	27	8.3
22 June	326	25	7.7
4 July	326	34	10.4
10 July	326	32	9.8
15 July	326	44	13.5
20 July	326	49	15.0
	**Mean	32 ± 4	
Cleared area (N.W. Rona			
4 July	212	12	5.7
10 July	212	13	6.1
15 July	190	15	7.9
20 July	190	17	9.0
**Mean	201 ± 6	14 ± 1	

* For a given date percentage recruitment calculated as:

$$\frac{\text{number of observed recruits}}{\text{number of resident gulls}} \times 100$$

** Mean ± S.E.

Figure 22

The recruitment pressure on an experimentally cleared
and a control area on the Rona sub-colony in
1973

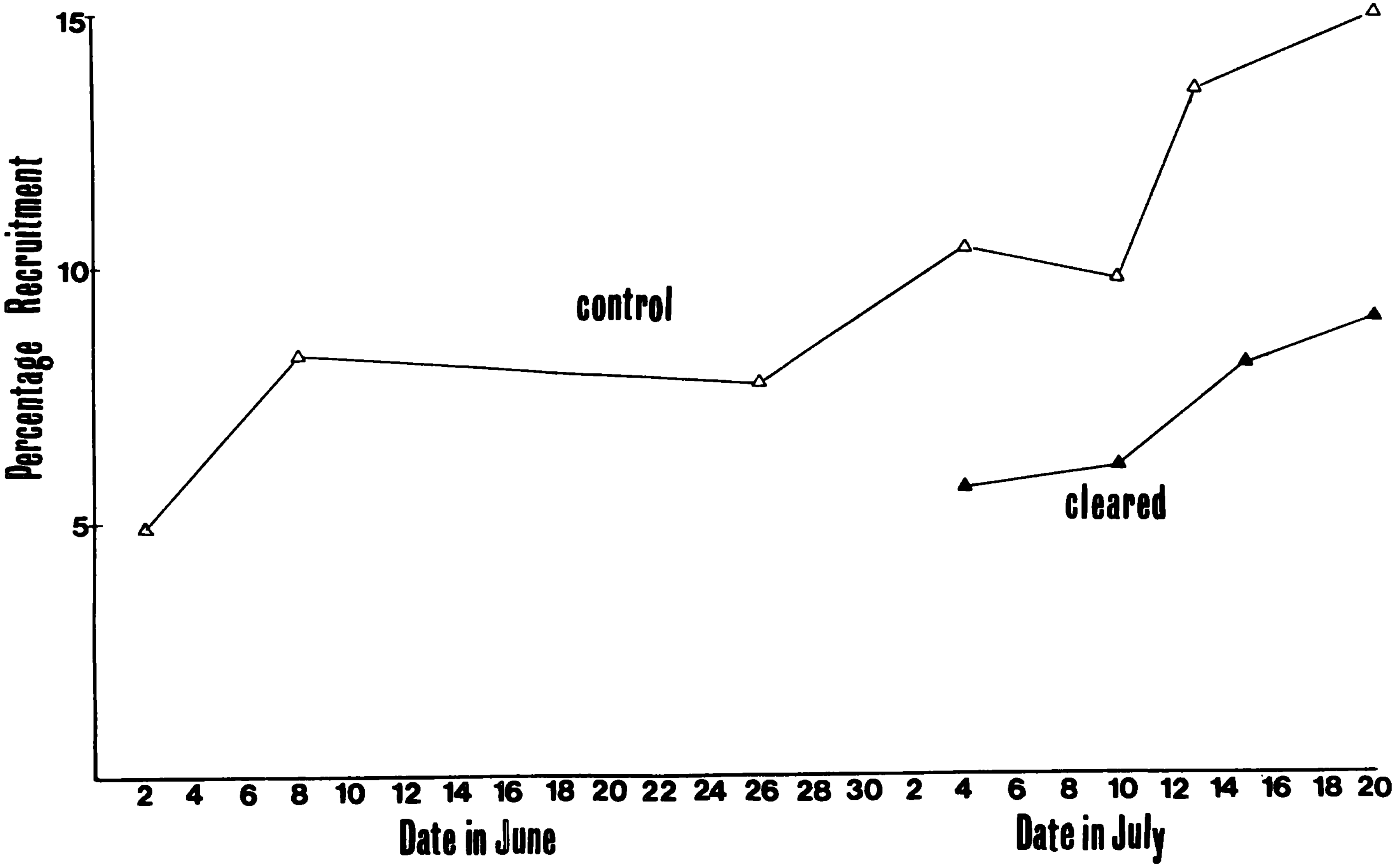

Percentage Recruitment
15
10
5
control
cleared
2
4
6
8
10
12
14
16
18
20
22
24
26
28
30
2
4
6
8
10
12
14
16
18
20
Date in June
Date in July

Plate 4. The North Plateau sub-colony after culling in 1972


115
ET

5.5 The effects of recruitment on the age composition of the colony

Introduction

In effect the N.C.C. culls on the Isle of May acted as large scale clearing experiments of the sort discussed in the previous section (Section 5.4). As recruitment proceeded, it was to be expected that changes in the age composition of the colony would take place as more recruits (principally four and five year old birds) became incorporated into the colony. Changes in age composition of the colony in 1972 and 1973 were followed in two ways; firstly by making counts of gulls of known age present on the island from April until July, and secondly from the evidence provided by the changing proportions of gulls of known age culled in these two years. From *a priori* considerations, it seemed likely that the culling programme, by its removal of many established pairs of breeding birds, would result in changes in recruitment rates to (and therefore age composition of) culled areas. However, it was not possible to ascribe changes in age composition to culling without some reference to control areas which were not culled. In 1972 and 1973 the study areas provided such a control.

Ringed gulls could be easily aged since both Parsons and Emmerson had used different colours of Darvic rings to denote the year in which a particular bird was hatched. However, only small numbers of chicks had been ringed on the Isle of May in 1969 and 1970, and none were ringed in 1971 (Table 59). It was therefore necessary to supplement sightings of ringed birds with counts of birds aged on plumage characters. This was especially true for three year old gulls in 1972, and for three and four year old gulls in 1973.

Virtually all three year old gulls, the majority of four year old and some five year old gulls, could be aged by the use of plumage characters.

It was not possible to age birds older than five years (see Appendix 10). In the age class counts that follow, whenever possible the numbers of plumage aged birds have been added to the counts of ringed birds. It must be noted, however, that ageing by plumage characters inevitably resulted in some underestimate of the number of four year old gulls and a larger underestimate of five year old birds. Counts made of birds older than five years were based solely on sightings of ringed birds.

In the discussion of results in this section the following nomenclature has been adopted: gulls between the ages of three and five years old (i.e. the major recruiting age classes) are termed 'immature'* adults, and the term adult refers to birds that were six years and older; these birds are simply referred to as 'adults'.

Age composition of gulls on the study areas

Counts of gulls of known age were carried out on the study areas from 17 April to 24 July 1972 and are presented in Table 58. With the exception of six year old gulls on North Ness, there were increases in all birds of known age as the 1972 breeding season progressed on the East Tarbet and North Ness study areas. The largest single increase occurred in the proportion of five year old birds on East Tarbet. On this area there was a six-fold proportional increase in five year old gulls which constituted 1.1% and 6.7% of the total gulls counted in April and July respectively. This situation was in marked contrast to the slight increase in five year old birds that occurred on North Ness (1.0% and 1.2% of the total counts in April and July). From this evidence it appeared that considerably more five year old gulls recruited to East Tarbet than to North Ness.

Due to the difficulties of ageing five year old gulls by plumage character the census of this age class as presented in Table 58 was heavily dependent upon the sightings of ringed birds. It was evident (Table 59)

* See also note on page 112.

Table 58 The numbers of Herring Gulls of known age observed on the study areas throughout the 1972 season

Area	Date of census	Age of Herring Gulls (years)				Total number birds counted	Adult to immature ratio*
		3	4	5	6		
East Tarbet	18 April	0	0	5 (1.1)*	4 (0.9)	460	1 : 1.25
	3 May	0	3 (0.4)	16 (2.0)	14 (1.8)	800	1 : 1.36
	20 June	1 (0.2)	2 (0.4)	14 (2.7)	7 (1.4)	515	1 : 2.43
	15 July	3 (0.6)	2 (0.4)	15 (2.9)	6 (1.2)	520	1 : 3.33
	22 July	8 (0.8)	8 (0.8)	68 (6.7)	24 (2.4)	1,012	1 : 3.50
North Ness	22 April	0	2 (0.4)	5 (1.0)	9 (1.7)	519	1 : 0.78
	27 May	0	3 (1.0)	5 (1.7)	6 (2.0)	300	1 : 1.33
	19 June	1 (0.1)	11 (1.4)	15 (1.9)	16 (2.0)	800	1 : 1.63
	24 July	10 (2.2)	14 (2.1)	25 (1.2)	26 (0.8)	1,200	1 : 1.89
	17 April	0	0	6 (4.6)	2 (1.5)	132	1 : 3.00
	10 May	0	1 (0.6)	8 (4.8)	4 (2.4)	166	1 : 2.25
	6 June	0	1 (0.4)	8 (3.2)	2 (0.8)	252	1 : 4.50
	24 July	0	1 (0.4)	13 (4.6)	5 (1.8)	280	1 : 2.80

* The percentage compositions that each age class contributed to the final counted samples are given in brackets.

** Adult to immature ratios are calculated as the numbers of birds younger than six years old to every six year old bird observed. The ratios thus calculated are indicators of the changing numbers of ringed gulls aged between three and six years observed on the study area throughout the season. They are similar, although not comparable to the adult to immature ratios calculated by Kadlec and Drury (1968a) which were based on the number of gulls in immature plumage to the total number of gulls counted.

Table 59 The number of Herring Gulls ringed as chicks on different sub-colonies throughout the 1966-1969 period (from Parsons and Emmerson, pers. comm.)

Sub-colony	Year of ringing 1966	1967	1968	1969	Total numbers ringed per sub-colony
Rona	1,369	1,355	1,693	400	4,817
North Ness	488	357	816	0	1,661
East Tarbet	257	513	111	0	881
Burrian Rocks	731	1,289	519	0	2,539
Island Rocks	841	65	0	0	906
(East Coast)*	1,572	1,354	519	0	3,445
North Plateau	106	185	106	0	397
South Plateau	0	150	130	0	280
South Ness	349	600	128	0	1,077

* The total number of chicks ringed on the Burrian and Island Rocks sub-colonies (see explanatory note to Table 60).

that different numbers of chicks were ringed on the same area in different years and that the numbers of chicks ringed in the same year varied from area to area.

In 1967 more chicks were ringed on East Tarbet (513 ringed) than on North Ness (357 ringed). Since there was evidence to suggest that recruits exhibited faithfulness to natal area, it follows that a census of a study area based on sightings of ringed birds may have reflected differences in ringing programmes as much as it reflected differences in recruitment to the study area. However, the differences between North Ness and East Tarbet in the numbers of chicks ringed were not large enough to adequately explain the much greater increase in five year old gulls which occurred on East Tarbet in 1972. It is suggested, therefore, that the larger increase of five year old birds on East Tarbet was due to an increase in the numbers of recruits on this sub-colony and may have been indicative of the relatively greater ease with which recruits established territories on the least densely occupied of the two study areas (see Sections 3.6 and 5.3). A similar explanation might be advanced for the smaller increase in six year old gulls which occurred on East Tarbet (a 1.5% increase from April to July); in comparison with East Tarbet there was a decrease in the proportion of six year old birds on North Ness (0.9% decrease). In this case, however, the birds involved were probably predominantly late breeders rather than prospecting recruits. Almost twice as many chicks were ringed on North Ness than on East Tarbet in 1966 (Table 59) and therefore it was expected that larger numbers of six year old gulls would have been sighted on North Ness rather than on East Tarbet.

There were also increases in the numbers of three and four year old gulls on the two study areas, and for these age classes the percentage increases on North Ness (2.2% and 1.7% increases in three and four year old birds between April and July) were greater than those on East Tarbet (0.8% increase for both age classes). In the case of four year old gulls the imbalance between the numbers of chicks ringed in 1968 on the two areas was not as critical as it was for older birds since plumage characters were a more reliable guide to age in four year old gulls. All three year old birds were aged on plumage characters.

It is important to distinguish between the behaviour of different age classes of immature birds observed on the study areas in 1972. Most three, many four, and some five year old gulls appeared to make little attempt to integrate with the resident breeding birds on the study areas and were often sighted as groups at the seaward edges of the study areas, usually on temporarily exposed tidal rocks or on the small rocky islands which lie off the seaward edges of North Ness and East Tarbet. In contrast, many five year old and some four year old birds were observed within the study areas proper (usually at the periphery of the main breeding areas) and some defended territories, although few four year old birds bred in 1972 (Table 3, Section 2.2). It was probable that birds which established territories, but did not breed in 1972, returned to the study areas in the following year to breed. A pre-breeding year in which territories are tentatively marked out has been noted in this species by Tinbergen (1953) and by Drost et al. (1961). The same tendency has been observed in other gull species, for example in the Lesser Black-backed Gull (Davis and Dunn 1976) and in the Ring-Billed Gull (Ryder 1976).

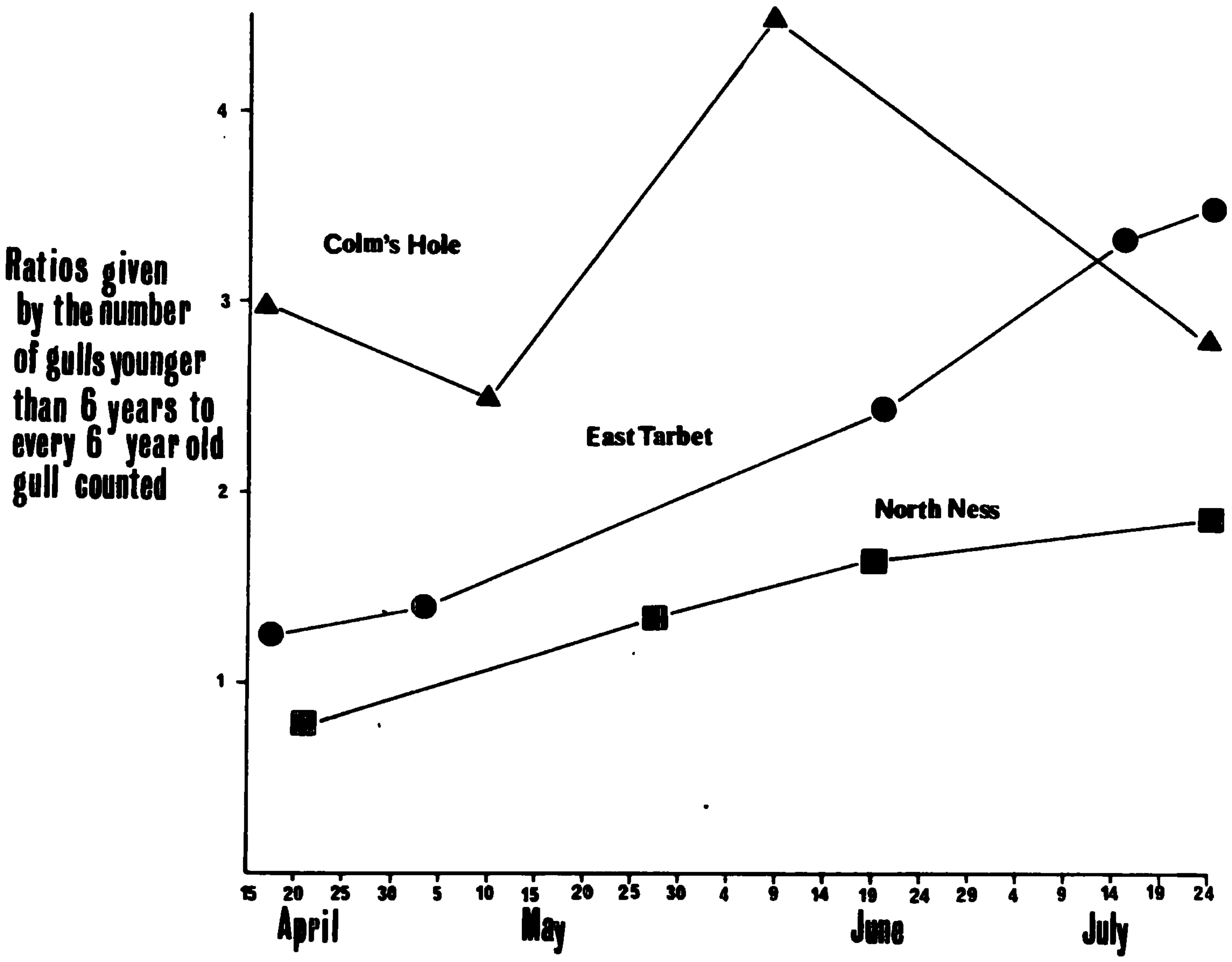
The observation of large increases in five year old gulls on East Tarbet and of large increases in three and four year old birds on North Ness thus paralleled the situation observed on experimentally cleared and control areas on Rona in 1973 (Section 5.3) where the greatest number of immature gulls was attracted to the undisturbed control area, which had a high density of nests, but most recruitment took place on the low density cleared area. Since the majority of gulls recruited in their fifth year of life, such birds would be expected to occur in larger numbers on East Tarbet rather than on North Ness.

A measure of the change in age composition of gulls on the study area was given by a comparison of the ratios of birds aged six years to birds younger than six years in April and July (the adult to immature ratio). On East Tarbet and North Ness there were progressive increases in adult to immature ratios as the breeding season progressed, and although these increases were of a similar order on the two study areas (a 2.8-fold increase on East Tarbet and a 2.4-fold increase on North Ness, Figure 23), the greatest number of gulls below the age of six years occurred on East Tarbet.

Figure 23

The numbers of immature* Herring Gulls present on the study areas in the 1972 breeding season

* Birds between the ages of three and five years.


Ratios given by the number of gulls younger than 6 years to every 6 year old gull counted
4
3
2
1
Colm's Hole
East Tarbet
North Ness
15
20
25
30
5
10
15
20
25
30
4
9
14
19
24
29
4
9
14
19
24
April
May
June
July

A similar pattern of age-dependent arrival data at breeding colonies has been reported for Gannets (Nelson 1978), Arctic Terns (Coulson and Horobin 1976) and Sooty Terns (Harrington 1974). For example, Harrington studied a breeding colony of Sooty Terns on Sand Island on the Johnston Atoll in the Pacific Ocean. In this species most eggs were laid between March and May, although two year old terns did not commonly appear at the colony until June, three year old terns appeared in May, four year old terns in late-April, and five year old birds in early-April.

The counts of gulls of known age on the Colm's Hole study area differed in two respects from those made at the other two study areas. Firstly, unlike the other study areas, a comparison of April and July adult to immature ratios indicated no increase in the numbers of immature gulls present. Further, for this area the adult to immature ratio reached a peak in June rather than in July, as was the case for East Tarbet and North Ness (Figure 23). Secondly, in comparison to East Tarbet and North Ness, the numbers of immature gulls in relation to adults for April to June were consistently higher on Colm's Hole. The Colm's Hole area is largely comprised of the southern edge of the Burrian Rocks sub-colony and the northern edge of the Island Rocks sub-colony (Figure 2, Section 2.1). Since this is the case, and since the majority of immature gulls recruited to areas of low nesting densities at the sub-colony edges (Section 3.6), it might be expected that Colm's Hole would have had a relatively large proportion of immature gulls. Corroboratory evidence was provided by the fact that a sample of eggs measured from this study area had a significantly smaller mean egg breadth than did a sample of eggs laid on East Tarbet over the equivalent time period (Section 3.3).

Age structure of areas culled in 1972 and the effects of the 1972 cull on recruitment

The numbers of year ringed birds (that is, Herring Gulls ringed before fledging in the 1966-1969 period) that were recovered in the 1972 cull are presented in Table 60. In addition to the 225 ringed birds recovered on known areas in that year a further 16 unringed adults aged on plumage characters were included in the data presented in Table 60.

Table 60 The numbers of Herring Gulls of known age recovered on different sub-colonies in the 1972 cull

	Age of culled birds (years)				Total numbers of Herring Gulls killed per sub-colony*
Sub-colony	3	4	5	6	
Rona	5 † (0.12)	23 (0.53)	31 (0.74)	44 (1.01)	4,354
East coast**	3 (0.08)	6 (0.16)	35 (0.94)	48 (1.28)	3,743
South Plateau	0	5 (0.70)	4 (0.56)	3 (0.42)	713
North Plateau	2 (0.07	7 (0.24)	18 (0.63)	7 (0.24)	2,881
Total for all areas	10 (0.09)	41 (0.35)	88 (0.75)	102 (0.87)	11,691

† The percentage that each age class contributed to the final total area kill is given in brackets.

* From N.C.C. records, made available by N.J. Gordon, N.C.C. Edinburgh.

** The N.C.C. records were compiled in such a way that the numbers culled on the Burrian and Island Rocks sub-colonies could only be presented as a combined total. Accordingly, recovery data for these two sub-colonies have also been combined.

Throughout the 1972 season no ringed three year old birds were ever observed to be breeding on the study areas nor were any recovered in the cull. However, ten birds in typically three year old plumage were culled in that year and evidently some birds of this age class recruited into the territory-holding population. From the evidence of the 1972 cull recoveries, the numbers of recruited three year old gulls appeared to be small.

It was apparent that there were proportionate differences in the numbers of gulls aged between three and five years culled on different areas. For example, the highest proportion of ringed four year old birds was found in the South Plateau sample. In comparison, the east coast sub-colonies contained considerably fewer birds of this age class (less than 25% in comparison to the South Plateau proportion). However, it would be an oversimplification to consider that these differences between areas represented differences in sub-colony age structure. It has already been pointed out that the numbers of chicks ringed on different areas varied considerably (Table 59). The majority of gulls culled in 1972 were recovered from their natal sub-colony (Table 61). On Rona, for example, 88% of birds were culled on the natal sub-colony (Table 61), and since chicks on this area were extensively ringed during the 1966-1969 period, this area would be expected to have a much larger number of ringed recruits recovered during culling.

Differences in the age composition of breeding populations on different areas have been compared by considering both the proportions of any age class recovered, together with the numbers originally ringed on the areas concerned. For example, proportionately over three times as many ringed four year old gulls were culled on Rona than on the combined east coast sub-colonies (Table 60). However, for every bird ringed on the east coast in 1968, 3.262 were ringed on Rona (Table 59). Increasing the observed number of four year old recoveries on the east coast by this factor (3.262) gives a calculated recovery of 20 birds (had equal numbers been ringed on all areas); 20 birds recovered on the east coast constituted a similar percentage of the total area cull (0.52%) as did the 23 birds recovered on Rona (0.53% of the total kill). However, this argument can only apply to ringed recoveries and not to birds aged on plumage. In Table 62 the observed number of recovered ringed birds has been adjusted to allow for area differences in ringing. The correction factor in each case is based on the area in any given year with the greatest numbers of ringed chicks.

This method of adjustment of recoveries according to the numbers ringed is at best only a general comparative method since it cannot take into account the differential attractiveness of different sub-colonies to recruits. This shortcoming is evident in Table 62 where no correction factor for the recoveries of six year old birds on the South Plateau is possible since no chicks were ringed on this area in 1966. However, given this limitation, since the 1972 cull recoveries indicated that the majority of gulls had returned to breed to the sub-colony of birth up to this year (Table 61), the adjusted recoveries can be used as a comparative measure of age composition.

For the four areas considered in this cull year it was possible to compare the age structure of culled Herring Gulls from the ratios of known aged gulls by considering the number of five and six year old birds to every four year old gull killed (Table 63).

In the case of the two newest formed and most recently expanding sub-colonies of the North and South Plateaus, the ratios of the recoveries of four to five to six year old birds indicated an age structure which is biased towards immature birds. Such a result was not surprising and suggested that just as new colonies may be founded largely by the immigration of

Table 61 The numbers of Herring Gulls culled between 1972-1974 per sub-colony and the numbers of Herring Gulls culled on their natal sub-colony

Area	Total number culled per sub-colony									Number and percentage* of birds culled on natal sub-colony								
Year of cull		1972			1973			1974			1972			1973			1974	
Year of ringing	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968
Rona	36	16	7	62	78	63	53	68	60	33 (91.7)	14 (87.5)	5 (71.4)	51 (82.3)	65 (89.0)	50 (79.4)	33 (62.3)	50 (73.5)	29 (48.3)
		59**			203			181			52(88.1) ***			166(81.8)			112(61.9)	
North Ness	4	2	2	30	27	16	27	34	37	0	0	0	22 (73.3)	17 (63.0)	16 (100)	20 (74.1)	28 (82.4)	23 (62.2)
		7			73			98			0			55(75.3)			71(72.5)	
East Tarbet	2	9	6	2	12	10	12	28	5	1 (50.0)	9 (100)	4 (66.7)	0	4 (33.3)	7 (70.0)	11 (91.7)	24 (85.7)	3 (60.0)
		17			24			45			14(82.4)			11(45.8)			38(84.4)	
North Plateau	3	19	4	1	11	17	0	10	18	1 (33.3)	10 (52.6)	4 (100)	1 (100)	5 (45.5)	14 (82.4)	0	2 (20.0)	9 (50.0)
		26			29			28			15(57.7)			20(29.7)			11(39.3)	

*Percentages culled per natal sub-colony are given in brackets.
**Total number of ringed gulls culled in any one year per sub-colony.
***The percentage of all ringed gulls that were culled in a given year per natal sub-colony.

Continued overleaf................

Table 61 (Continued)

Area	Total number culled per sub-colony									Number and percentage* of birds culled on natal sub-colony								
Year of cull	1972			1973			1974			1972			1973			1974		
Year of ringing	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968	1966	1967	1968
South Plateau	3	5	2	2	11	21	0	6	6	1 (33.3)	1 (20.0)	2 (100)	1 (50.0)	8 (72.7)	15 (71.4)	0	0	0
		10**			34						4(40.0)***			24(70.6)			0	
Burrian Rocks	23	35	8	31	61	13	16	34	24	18 (78.3)	21 (60.0)	3 (37.5)	21 (67.7)	41 (67.2)	10 (76.9)	8 (50.0)	16 (47.1)	8 (33.3)
		66			105			74			42(63.6)			72(68.6)			32(43.2)	
Island Rocks	28	7	0	28	3	2	15	0	5	24 (85.7)	4 (57.1)	0	11 (39.3)	0	0	3 (20.0)	0	2 (40.0)
		35			33			20			28(80.0)			11(33.3)			5(25.0)	
South Ness	3	2	1	17	22	5	16	13	10	1 (33.3)	1 (50.0)	0	10 (58.8)	10 (45.5)	2 (40.0)	6 (37.5)	4 (30.8)	4 (40.0)
		6			44			39			2(33.3)			22(50.0)			14(39.4)	

*Percentages culled per natal sub-colony are given in brackets)
**Total number of ringed gulls culled in any one year per sub-colony.
***The percentage of all ringed gulls that were culled in a given year per natal sub-colony.

Table 62 The adjustment of ringing recoveries to allow for different numbers of chicks ringed on different sub-colonies and in different years (Cull data for 1972)

	Age of recovered gulls (years)								
	4			5			6		
Sub-colony of recovery	correction factor	recorded recoveries	adjusted recoveries	correction factor	recorded recoveries	adjusted recoveries	correction factor	recorded recoveries	adjusted recoveries
Rona	1	13	13 (0.30)**	1	30	30 (0.69)	1.148	44	51 (1.17)
East Coast	3.262	4	13 (0.35)	1	34	34 (0.91)	1	48	48 (1.28)
South Plateau	13.023	3	39 (5.47)	9.033	4	36 (5.05)	-*	3	-*
North Plateau	15.970	6	96 (3.33)	7.324	17	125 (4.34)	14.830	7	104 (3.61)

* No chicks were ringed on the South Plateau in 1966; and the three recorded recoveries are therefore immigrants from another sub-colony.

** Figures in brackets are percentages of the total area kill (as given in Table 58)

Table 63 The observed ratios of Herring Gulls of known age recovered in the 1972 cull on the Isle of May

Sub-colony of recovery	Age (years) of recovered gulls 4	5	6
Rona	1	2.308	3.923
East Coast*	1	2.615	3.692
South Plateau	1	0.923	-
North Plateau	1	1.302	1.083

* Includes the Burrian and Island Rocks sub-colonies (see notes to Table 60).

immature birds (Drury and Nisbet 1969), this may also be the case with newly settled or recently expanded sections within established breeding colonies.

In contrast, the east coast and Rona sub-colonies indicated fewer immature gulls than on the other culled sub-colonies. However, the cull samples only indicated the age structure of the breeding population in mid-May. Census counts of the unculled study areas of East Tarbet and the North Ness clearly showed an increase in the numbers of four and five year old gulls as the breeding season progressed (Table 58, Figure 23). Thus, the numbers of immature gulls, and therefore the adult to immature ratios on Rona and the east coast sub-colonies, would have been expected to have increased by a similar amount as the season progressed.

Consideration has been given to the changes in age composition which occurred from May to June on the study areas. The percentage changes in the numbers of birds in their third, fourth and fifth years of life observed on East Tarbet were 0.19%, 0.01% and 0.72%, whilst the equivalent change on North Ness was 0.13%, 0.40% and 0.23%.

On Rona census counts were before and after the 1972 culling operation in order to establish the effects of culling on recruitment pressures. These data are presented in Table 64.

Table 64 The numbers of Herring Gulls of known age observed on the Rona sub-colony before and after culling in 1972

Date of observation		Age (years) of Herring Gulls				Total number birds counted	Adult to immature ratio ***
		3	4	5	6		
Pre-cull	7 May	8 (0.40)*	15 (0.75)	52 (2.60)	54 (2.70)	2,000**	1 : 1.39
Post-cull	3 June	27 (2.25)	20 (1.67)	30 (2.50)	43 (3.58)	1,200	1 : 1.79

* The percentage that each age class constitutes of the total number of Herring Gulls counted is given in brackets.

** Pre-cull figures were estimates since birds exhibited relatively low tenacity to nest sites and it was difficult to count birds accurately at this stage in the breeding cycle.

*** The combined numbers of three, four and five year old gulls to every six year old observed.

The much larger changes evident on Rona of three (1.85%) and four year old gulls (0.92%) indicated substantial recruitment from these age classes which exceeded that which might have been expected had no culling taken place. It was not possible to predict recruitment rates in the absence of culling. However, the increase in three year old gulls was substantial and it seems reasonable to attribute this at least in part to the effects of culling.

On Rona, the recruitment R_x of a given age class (x) which occurred between May and June must be given by the:

number of gulls aged x present in June	-	number of gulls aged x present in May	-	number of gulls aged x culled in May
N_j	-	N_m	-	N_c

Assuming that the census counts in May and June, and the culled sample in May (Table 58), are representative samples of the gulls of various age classes present at the sub-colony, the recruitment per age class on Rona for a sample of 100 birds is given as:

	x (years)			
	3	4	5	6
N_m	0.40	0.75	2.60	2.70
N_c	0.12	0.53	0.74	1.01
N_j	2.25	1.67	2.50	3.58
* R_x	1.97	1.45	0.64	1.89

* (On unculled areas the recruitment per age class is given simply as:

$$R_x = N_j - N_m$$

that is, the simple proportional difference between May and June census counts as given above in the text.)

The recruitment rates of three and four year old birds to Rona were considerably higher than those on the two study areas. For three year old birds (R_3 = 0.19 and 0.13 on East Tarbet and North Ness respectively). Recruitment on Rona was 15 times greater than on North Ness and 10 times greater than on East Tarbet, and for four year old gulls (R_4 = 0.01 and 0.40

on East Tarbet and North Ness), recruitment on Rona was over 100 times greater than that which occurred on East Tarbet and four times that on North Ness.

Apart from the fact that there may have been considerable differences between sub-colonies in the extent and timing of recruitment, it seems that the cull greatly accelerated the recruitment process on the Rona sub-colony. For five year old gulls (R_5 = 0.72 and 0.23 on East Tarbet and North Ness) the recruitment rate, whilst being almost three times that which occurred on North Ness, was not as great as that on East Tarbet.

These differences in the recruitment rates of three, four and five year old birds suggested that in June 1972 many three and four year old gulls which were present at the colony had not recruited into any of the sub-colony breeding populations. These birds were available to recruit into the partially cleared spaces created by the cull when this opportunity was presented. By contrast, five year old birds present at the colony had probably started to establish territories and did not form such a labile pool of recruits.

Counts made of six year old gulls on North Ness indicated no change in the presence of this age class between May and June, and on East Tarbet the numbers of this age class actually decreased in June (a decrease of 0.39%; Table 58). On Rona there was a large increase in six year old gulls (R_6 = 1.89). Unlike immature gulls, adult birds were not observed to form large, unattached flocks of non-breeding birds, and it seems unlikely that the increase in six year old gulls on Rona was due to recruitment from non-breeding adults already present at the colony. More likely is the possibility that the Rona increase may have been partly due to late breeding gulls which could have returned at this time and may have abandoned a former breeding area in favour of culled areas such as Rona.

For birds returning to unculled areas this would have the advantage of reduced competition from established breeding pairs. There was no evidence to suggest that breeding gulls established on unculled areas abandoned their former breeding grounds and established territories on culled areas. Certainly for all study nest sites on the study area there was no desertion of nests which contained eggs or chicks, although some territories in which no breeding had taken place were found unattended later on in the season, but whether these birds had established territories on culled areas or not was not known. The decrease in six year old gulls on the adjacent area of East Tarbet suggests that some adults which had not bred successfully on this area may have attempted to breed on Rona.

Age structure of areas in 1973 and the effects of culling on recruitment in that year

In 1973 an attempt was made to recover all culled birds which showed any traces of immature plumage. The numbers of birds of known age recovered in that year are given in Table 65. The recoveries of three and four year old gulls (with the exception of two ringed four year old birds on Rona) were based exclusively upon birds which were aged on plumage characters. Recoveries of over 50% the five year old gulls and of all the six and seven year old gulls were based on ringed recoveries.

Since the majority of immature gulls in 1973 were identified on plumage characters it was possible to compare the age structures of the different sub-colonies directly from the culled proportions of immature birds per area. If, as has been suggested for the previous year, culling greatly increased recruitment pressure, then in 1973 the expectation was that previously culled areas would have even greater numbers of immature gulls present on them. From Table 65 it was clear that the two previously unculled areas of North Ness and South Ness had the lowest numbers of immature gulls (combined percentage compositions of immature age classes of 1.97% and 1.63% respectively). In comparison, the previously culled areas of Rona (4.59% of the total number culled were immature birds), the east coast sub-colonies (5.77%); North Plateau (4.8%) and South Plateau (5.87%) had between two and almost four times as many immature gulls as did the non-culled areas. From this evidence alone it appeared that substantial recruitment of immature birds into previously culled areas had taken place by May 1973.

Table 65 The numbers of Herring Gulls of known age culled on the Isle of May in 1973

Sub-colony on which culled	Age (years) of culled birds					Total culled per sub-colony
	3	4	5	6	7	
Rona **	9 (0.36)	34 (1.37)	71 (2.86)	80 (3.22)	62 (2.50)	2,481
North Ness *	2 (0.14)	3 (0.20)	24 (1.63)	27 (1.84)	24 (1.63)	1,470
East coast	5 (0.40)	30 (2.41)	37 (2.97)	50 (4.01)	39 (3.13)	1,247
North Plateau	1 (0.10)	18 (1.84)	28 (2.86)	23 (2.35)	7 (0.72)	979
South Plateau	0	9 (1.55)	25 (4.32)	10 (1.73)	2 (0.35)	579
South Ness *	1 (0.07)	12 (0.89)	9 (0.67)	17 (1.26)	19 (1.41)	1,347

* Culled for the first time in 1973.

** Figures in brackets are the percentages that each age class constitutes of the total number of birds culled per area.

From previous arguments the two areas, North and South Plateaus, might be expected to have contained greater proportions of immature birds than did the older established sub-colonies of South Ness, North Ness and Rona. Thus the fact that the North and South Plateaus both contained higher proportions of immature gulls in 1973 was not necessarily indicative of cull induced recruitment. However, it was evident from Table 65 that the bulk of three year old gulls had recruited into the previously culled areas of Rona (where 0.36% of the total gulls culled were three years old) and the east coast (0.40% were three years old); rather than into the North and South Plateaus (0.10% and 0% aged three years respectively) or into the previously unculled areas of North Ness (0.14%) and South Ness (0.07%). The percentage recoveries of three year old gulls on areas other than those on the east coast and Rona in 1973 were similar and were roughly of the same order as the 1972 recoveries of three year olds on all areas (that is, around 0.1%) including the east coast and Rona (Table 60). Only Rona and the east coast sub-colonies showed substantial increases over and above the recruitment which had taken place in the previous year for this age class.

Although it should be noted that the 1972 recovery data (Table 60) may have underestimated the numbers of three year old gulls culled, since no systematic search for immature gulls was made in that year, there was no doubt that in general much larger numbers of three year old gulls were culled in 1973 than in 1972.

In 1973 the recruitment pattern of four year old gulls was similar to that which occurred in three year old birds, in that the lowest percentage recoveries of four year old birds were found for the first time culled areas of North and South Ness (0.20% and 0.89% respectively). The highest recovery rates were found for the east coast sub-colonies (2.41%). However, unlike the situation for three year old gulls, the North and South Plateaus each had higher percentage recovery rates of four year old birds (1.84% and 1.55% respectively) than did Rona (1.37%).

In comparing 1972 and 1973 recoveries of four year old gulls two complicating factors arise from the fact that the 1972 recoveries are largely based on ringing recoveries, whilst, in 1973, birds belonging to this age class were nearly all identified on plumage characters. Firstly, the 1973 recovery data underestimated the actual numbers of four year old gulls that were culled, since not all four year old birds could be distinguished on plumage characters alone (Appendix 10). Secondly, the inequalities between areas in numbers of chicks ringed in 1968 meant that the percentage recovery of four year old gulls may have been seriously underestimated on the two areas, North and South Plateaus, in comparison with the recovery data for 1972 presented in Table 60. It was evident that there were increases in 1973 of the percentage recoveries of four year old gulls on the east coast and Rona sub-colonies (1972 recoveries indicated that 0.35% and 0.30% of birds culled on these two areas were four years old, Table 60). Although the recoveries of four year old gulls on North and South Plateaus were not as great in 1972 as they were in 1973 (Tables 60 and 65), when adjustments were made for ringing inequalities (Table 62), it appeared that the previous year's culling did not result in large scale recruitment of this age class in 1973.

In both years the recoveries of five year old birds were based on an approximately equal mixture of ringing recoveries and plumage aged birds. In comparing the recruitment of this age class in 1973 with that which had occurred in 1972 there was the further complication that some of the 1968 ringed cohort (i.e. birds five years old in 1973) were culled in 1972 when four years old. Areas such as Rona and the east coast, where large numbers of chicks were ringed in 1968, contained breeding birds in which there were large numbers of ringed four year old gulls at risk to culling in 1972.

Therefore, the percentage composition that ringed five year old gulls constituted in 1973 was likely to underestimate the numbers of five year old gulls culled. This difficulty could be overcome by assuming that the numbers of plumage identifiable five year old birds constituted some fixed proportion of the total number of five year old gulls present at the colony at any given time. A consideration of plumage identified five year old gulls recovered in 1973 (Table 66) suggested that the highest recruitment pressure exerted by this age class was on the east coast sub-colonies, and on the North and South Plateaus.

Table 66. The numbers of plumage identified five year old Herring Gulls recovered in the 1973 cull

Sub-colony of recovery	North Plateau	South Plateau	East coast	Rona	North Ness	South Ness
Number recovered	12	8	20	16	5	4
Total number of gulls culled per sub-colony	979	579	1,247	2,481	1,470	1,347
Percentage of total gulls recovered per sub-colony which were five years old	1.23	1.38	1.60	0.65	0.34	0.30

The recruitment rate of five year old gulls to Rona in 1973 was approximately half of that which evidently occurred to the east coast sub-colonies and to the North and South Plateaus. Nevertheless, it was still approximately double that which occurred on the unculled areas of North Ness and South Ness (Table 66).

Assuming that the cull affected each age class equally, then a comparison of the ratios of six year old recoveries to five year old recoveries indicated any changes in the recruitment pattern of five year old birds in the two years. To make the data comparable between the two years firstly only recoveries of ringed five year old gulls were considered and, secondly, the 1973 ringing recovery data were adjusted to allow for biases due to unequal ringing on different areas. A high six year old to five year old ratio was interpreted as indicating a high rate of recruitment by this age class.

On the whole, the ratios given by the numbers of culled five year old to every six year old gull killed in 1973 (Table 67) were in agreement with the recruitment rates suggested by the recovery of gulls aged by plumage (Table 66). Thus the lowest ratios coincided with the lowest percentage recoveries of plumage aged birds. However, the agreement was not exact. The recovery data for South Ness indicated a deviation from this interpretation since the total number of gulls culled on this area had the lowest percentage recovery of identifiable five year old gulls (0.30%), but the second highest, six to five ratio (1 : 1.74). Similarly, the highest calculated ratio of 2.46 for South Plateau recoveries did not correspond with the highest percentage recovery of five year old birds which occurred on the east coast (1.60%).

The assumption of a strong philopatric tendency for birds recruiting to the South Ness sub-colony in 1973 was not a valid one (see Table 61). This assumption was implicit in the method used to adjust the ringing recoveries to compensate for area differences in ringing. Herring Gulls born on South Ness appeared to exhibit a relatively low attachment to the natal sub-colony (Section 5.3 and Table 61). Thus the adjusted numbers of recoveries of five year old birds may have considerably overestimated the numbers of ringed five year old birds that actually returned to this sub-colony to breed. The numbers of ringed six year old birds were also overestimated. However, since the correction factor for five year old gulls was considerably larger than that for six year old gulls, the major error in calculating six to five ratios came in overestimating the number of birds aged five years.

By contrast, birds ringed on the South Plateau exhibited a high faithfulness to the natal sub-colony (Section 5.3 and Table 61). In this case, either the percentage recovery of five year old gulls was low due to some culled five year olds being overlooked, or, more likely, the six year to five year ratio for east coast recoveries was artificially low. This was probably because there was a rapid decrease in the philopatry of recruiting five year old gulls to one of the constituent east coast sub-colonies in 1973, namely Island Rocks (Table 61).

A comparison of six to five ratios on areas culled in both years indicated that in 1973 there were increases in the recruitment from five year old gulls into the breeding populations of Rona (a 17% increase in ratio in 1973), the east coast sub-colonies (57.8% increase) and North Plateau (26.7% increase).

The largest increase in ratio, and therefore by inference the greatest recruitment of five year old gulls, took place at the east coast sub-colonies. The increased recruitment from this age class was smaller on the Rona and North Plateau sub-colonies; on both areas approximately equivalent changes in recruitment occurred.

The percentage recovery of five year old gulls on South Plateau in 1973 indicated large scale recruitment of this age class into the sub-colony (the percentage that the adjusted ringing recoveries of five year old birds constituted of the 1972 South Plateau cull total was 4.34% (Table 62). In 1973 the equivalent figure was 38.17%; calculated from Tables 64 and 67).

Table 67. The adjustment of 1973 cull ringing recoveries to correct for differences between sub-colonies in the numbers of Herring Gull chicks ringed between 1966 and 1969

	Age (years) on recovery							
	5			6				
Sub-colony culled	Correction factor *	Recorded recoveries	Adjusted recoveries	Correction factor	Recorded recoveries	Adjusted recoveries	Six year to five year ratio 1973	Six year ** to five year ratio 1972
North Ness	2.075	19	39	3.800	27	103	1 : 0.38	N.C. ***
Rona	1	55	55	1	80	80	1 : 0.69	1 : 0.59
East Coast	3.262	17	56	1	50	50	1 : 1.12	1 : 0.71
North Plateau	15.970	16	256	7.324	23	169	1 : 1.52	1 : 1.20
South Plateau	13.023	17	221	9.033	10	90	1 : 2.46	-
South Ness	13.227	5	66	2.258	17	38		N.C. ***

* Calculated as described in text, p. 159 and 160 and from data presented in Table 59.

** Calculated from data in Table 62.

*** N.C. = not culled.

Although it is not possible to compare six year to five year ratios in the two years for South Plateau (since no birds were ringed on this area in 1966), it was clear that the presence of this age class increased on the sub-colony by an amount similar to the increase on the east coast sub-colonies (percentage change on South Plateau was 33.85%).

The data discussed above indicate that considerable changes in recruitment took place in 1973 as a result of one previous year of culling, and that numbers of immature gulls present at the colony by mid-May 1973 were in excess of those predicted on the basis of the recovery data from the preceding year. It might therefore be expected that the 1973 cull had further increased the rate of recruitment into first and second time culled areas. In July 1973 a complete census of the island confirmed this expectation and indicated that large numbers of three and four year old Herring Gulls were present on all culled areas (Table 68).

Summarising, it was clear from the cull recovery data and from the census counts carried out during the two initial years of culling on the Isle of May that in 1973 there were increases in the numbers of immature Herring Gulls present on culled and control areas. This was most clearly seen by comparing census counts carried out throughout the 1972 and 1973 breeding seasons (Tables 58 and 68). On East Tarbet and North Ness there were substantial increases in three and four year old Herring Gulls recruiting into the sub-colonies.

The data provided by cull recoveries of gulls of known age were more difficult to interpret for two reasons: firstly, the recovery data in 1972 related only to ringed birds, whilst that in the following year included ringed birds and birds aged on plumage characteristics; secondly, some sub-colonies were more intensively culled than others. The numbers of ringed birds on Rona, for example, had been reduced in two successive culls by 1973, whilst on the North Ness only one cull had taken place over this period. Nevertheless, the increased adult (six year old gulls) to recruit (five year old gulls) ratios on these areas were indicative of increasing recruitment rates. It is suggested that increased recruitment to these sub-colonies was a direct result of the 1972-1973 culling programme.

Table 68. Census counts of Herring Gulls of known age present on the Isle of May in July 1973 (Census counts made 5-10 July 1973)

Sub-colony	Age (years) of birds 3	4	5*	6	7	Total number of birds counted
North Ness	1 (0.51)**	4 (2.03)	1 (0.51)	8 (4.06)	5 (2.53)	197
East Tarbet	9 (1.27)	52 (7.36)	21 (2.97)	54 (7.64)	19 (2.69)	707
Rona	7 (2.83)	15 (6.07)	4 (1.62)	15 (6.07)	9 (3.64)	247
North Plateau	6 (6.90)	4 (4.60)	4 (4.60)	3 (3.45)	0	87
South Plateau	13 (3.76)	13 (3.76)	1 (0.29)	1 (0.29)	0	346
South Ness	7 (0.77)	36 (3.95)	5 (0.55)	14 (1.54)	9 (0.99)	912
Island Rocks	12 (7.84)	30 (19.61)	1 (0.65)	3 (1.96)	3 (1.96)	153
Burrian Rocks	2 (1.24)	16 (9.88)	3 (1.85)	4 (2.47)	4 (2.47)	162
Island total count	57 (2.03)	170 (6.05)	40 (1.42)	102 (3.63)	49 (1.74)	2,811

* Numbers of five year old birds based on sightings of ringed gulls.

** The percentage that each age class constitutes of a total sub-colony count is given in brackets.

SECTION SIX MORPHOLOGICAL MEASUREMENTS OF RECRUITS AND SOME PHYSIOLOGICAL ASPECTS OF RECRUITMENT

6.1 Introduction and Methods

The proximate causes of deferred maturity are little understood. It has been suggested that recruitment of seabirds into breeding colonies may be delayed due to the stresses involved in site establishment (Nelson 1978), possibly as a direct result of physiological immaturity of the hypothalamus-pituitary-gonadal axis (Ainley 1975) or because younger birds do not have sufficient experience to exploit local food conditions, and consequently do not feed as well as established breeding adults. Under these circumstances such birds may not be able to acquire sufficient body reserves to breed successfully (Ashmole 1963, Carrick and Ingham 1967).

In either case, it is to be expected that recruiting birds might differ in gross morphology or in their physiological state. If such differences exist between recruits and established breeding Herring Gulls, they should be apparent from a comparison of the measurements of immature birds (up to and including the age of five years) and birds older than five years, the majority of which were probably breeding for at least the second time.

Much of the published literature concerning intraspecific variations in bird measurements has been concerned with the changes associated with pre-migratory adaptations such as lipid deposition and muscular hypertrophy (King and Farner 1959, 1965, King 1968, Odum and Connell 1956, Fry, Ferguson-Lees and Dowsett 1972), or with establishing the validity of certain ecogeographical rules (for example, Hamilton 1960, Barth 1967b and 1975). The information that exists concerning variations in body measurements within single, localised breeding populations of seabirds suggests that in comparison to established adults, immature birds tend to weigh less, have smaller fat deposits, less well developed brood patches and smaller and less active gonads (Marshall 1952, Johnston 1956, Carrick and Ingham 1967, Ainely 1975, Spurr 1975). In general, immature seabirds, whether they attempt to breed or not, are thought to be of poorer "quality" and lower motivational tendency than older birds. On this basis, the period of deferred maturity can be considered as one during which there is an increase in both quality and reproductive tendency with age and previous experience.

Samples of Herring Gulls of known age (both colour-ringed birds and those aged on plumage characters) were measured throughout the 1972-74 culls, although the majority of measurements for some factors relate to samples obtained in 1973. On the basis of existing published studies of seabird populations, the following measurements were made on the island as and when birds were culled, or in some cases shot after the main N.C.C. culling period; body weight, wing length, bill depth (at the gonys), bill length (the length of exposed culmen), extent of brood patch defeathering, and the extent of fat reserve. Not all ringed birds culled could be examined on the island and many were kept in store, from stored gulls samples of the principal flight muscle, *pectoralis major*, were removed and weighed. Gonadal development in male gulls was determined from the testes of birds examined on the island and from those subsequently stored.

Body weight were measured to 0.1g with a Mettler balance. Some birds were weighed after storage at $-20^{\circ}C$; the mean weight loss in a sample of 56 birds weighed before and after storage was 8.2g for males with an average weight of 1,004g (0.82%) and 8.4g for females (average weight 853g, weight loss 0.98%). Such losses in weight after storage at sub-zero temperatures occurred principally as the result of water loss from the tissues, and the weights of birds weighed after storage were adjusted to compensate for this loss.

Wing lengths were measured to 1mm with a metal wing rule, and in all cases the measurements were from wing base to primary tip, with the natural curvature of the wing straightened out.

Bill measurements were made to 0.1mm with vernier calipers, while brood patches were measured to 1mm at the chords of maximum width and breadth.

The total fat reserve was estimated by using a fat index which was the mean score on an 0 to 5 scale (where 0 = no fat and 5 = considerable fat, and 1 to 4 were graded scores between these extremes) for both visible fat overlying the ventral abdominal viscera and that visible subcutaneous fat underlying the ventral skin. Similar indices have been used for Chaffinches (Dolnik and Blyumental 1967) and Woodpigeons (Murton, Westwood and Isaacson 1974). The mean fat wet weights per fat index are given in Appendix 11.

In males, testes were weighed to 0.001g and upon removal were stored in 10% Bouin's solution. Sections for histological examination were taken from wax embedded testes at 8µm and stained with heamalum and eosin. In Isle of May Herring Gulls, five distinct stages in spermatogenesis were recognised.

Stage 1: At this stage there was a basal row of spermatogonia and Sertoli cells ringing the basement membrane. The seminiferous epithelium was dominated by primary spermatocytes and, in addition, secondary spermatocytes were present towards the tubule lumen.

Stage 2: Spermatids were present in the epithelium bordering the tubule lumen. A few spermatozoa were present on the inner epithelial margin but these occurred singly or at most in threes and fours. In stage 2 testes primary spermatocytes still dominated the epithelium.

Stage 3: Numerous bundles of spermatozoa, often present in rows, were found in the epithelium adjacent to the lumen. The interstitium, in contrast to stage 2, was uniformly well developed, with nuclei that were large and darkly staining. This was the most common spermatogenic stage of males culled in 1972 and 1973 and represented the breeding stage.

Stage 4: Very rarely were testes found at this stage which was characterised by the presence of spermatozoa and cellular debris in the tubule lumen.

Stage 5: Tubules were collapsed and the lumena were occluded by large amounts of cellular debris. This was the typical stage recorded for gulls shot in June and July and indicated testes regression.

The five spermatogenic stages found in Herring Gulls correspond closely with five of the eight spermatogenic stages recorded for the California Gull by Johnston (1956). Johnston found early spermatogenic stages in California Gulls where there were no secondary spermatocytes at all and only few primary spermatocytes. However, his study of migratory and non-migratory gulls involved taking samples of testes in February and March when such early stages in spermatogenesis were likely to be present. All male Herring Gulls, either shot in April or culled in May, had testes with secondary spermatocytes, although for some three and four year old birds the numbers of these cells could be quite low.

In addition to assessing spermatogenic stages, the tubule diameters of ten random tubules per testis were measured to 0.001mm and averaged to give a mean seminiferous tubule diameter per testis.

6.2 Variations in Adult Body Weight

Little information exists with regard to differences due to age in the body weights of adult Herring Gulls. Young sub-adult Adelie Penguins (Ainley 1975), Great Tits (van Balen 1967), Woodpigeons (Murton et al. 1974) and Oystercatchers (Dare 1977) are known to weigh less than breeding adults. There are age differences in weights of Kittiwakes recruiting into the centre of the breeding colony, although in this case young four year old males were heavier than five year old recruits (Wooller and Coulson 1976).

The weights of 1,298 known aged Herring Gulls culled between 1972-74 were determined, together with those of unringed adult samples over this time period (Table 69).

Table 69. The variation in adult body weight in relation to age, from samples of culled Herring Gulls on the Isle of May 1972-74

	MALES			FEMALES		
Age (years)	Sample size	Mean weight (g) ± S.D.**	C.V.*	Sample size	Mean weight (g) ± S.D.**	C.V.*
3	13	1017.7 ± 63.1	6.2	2	(859)	-
4	77	1003.8 ± 70.3	7.0	67	804.0 ± 266.9	33.2
5	102	1009.0 ± 77.7	7.7	63	846.6 ± 77.9	9.2
6	239	1017.0 ± 72.2	7.1	173	855.0 ± 36.1	8.9
7	175	1036.1 ± 75.6	7.3	148	847.1 ± 77.1	9.1
8	64	1029.2 ± 75.1	7.3	63	863.8 ± 111.4	12.9
Unringed adults	103	1027.9 81.2	7.9	138	859.7 74.8	8.7

* C.V. = coefficient of variation

** S.D. = standard deviation

Males in every age group culled over the 1972-74 period were significantly heavier than females and have been considered separately. The sexual dimorphism in body weight in the Herring Gull has also been noted by Barth (1967b) and similar differences are known in male and female Great Black-backed Gulls (Harris 1964b), Lesser Black-backed and Common Gulls (Barth 1967b). In Herring Gulls mean body weight increased with age in both sexes (Table 69);for the sample of males there was a significant increase in mean body weight of 33g between the fourth year to the seventh year of life ($p < 0.05$, multiple range test Snedecor and Cochran 1967). The increase in female weight was much larger, with eight year old gulls being on average 59g heavier than four year old birds, although this difference was not significant.

Females tended to have a wider range of body weight than males. For example, the range of body weights for four year old female gulls was 372g (coefficient of variation, c.v. = 33.2), compared with 318g in four year old males (c.v. = 7.0). This is in contrast to Norwegian Herring Gulls where males were more variable than females (coefficient of variation for males was 7.4 and 6.8 for females, Barth 1967b).

For samples weighed in 1972 and 1973, a relatively high proportion of females in some sohorts were found to have either fully formed or partially shelled eggs in the oviduct (for example 48% of the 1967 cohort in 1972). The mean weight of females without eggs in the oviduct ('non-laying' females) increased significantly in the 1968 and 1967 cohorts between 1972 and 1973 (Table 70).

For the females of the 1966 cohort there was no significant weight change from 1972 to 1973 (Table 71). It was also interesting to note that whilst the mean weights of males culled from the 1967 and 1968 cohorts increased significantly as culling progressed from 1972 to 1974, no significant body weight was detected in males of the 1966 cohort (Table 71).

Table 71. Variation in body size of colour-ringed Herring Gulls culled on the Isle of May, 1972-74

			MALES				FEMALES			
Year in which ringed as chicks	Age (years) when culled	Year culled	Mean body weight *(g)	Mean wing length * (mm)	Mean bill depth * (mm)	Mean bill length * (mm)	Mean body weight * (g)	Mean wing length * (mm)	Mean bill depth * (mm)	Mean bill length * (mm)
1968	4	1972	968.6±11.6 (21)**	415±2.0 (20)	19.34±0.34 (23)	52.01±0.60 (23)	831.1±22.7 (17)	400±2.4 (10)	17.51±0.16 (13)	48.56±0.83 (13)
	5	1973	1035.1±10.5 (45)	423±3.5 (13)	(18.97) (3)	(55.07) (3)	861.4±17.4 (26)	408±3 (10)	17.77±0.22 (7)	49.49±0.61 (7)
	6	1974	1017.3± 7.4 (105)	429±1.2 (82)	19.57±0.10 (96)	53.16±0.26 (96)	859.6± 9.1 (70)	410±1.9 (51)	17.59±0.10 (62)	48.23±0.30 (62)
1967	5	1972	988.5±10.2 (57)	415±1.9 (53)	19.95±0.17 (58)	52.55±0.98 (58)	836.2±11.3 (37)	399±1.5 (40)	17.88±0.22 (39)	49.19±0.37 (39)
	6	1973	1018.9±6.9 (79)	427±1.7 (23)	19.56±0.16 (14)	52.99±0.62 (14)	846.6± 9.3 (62)	403±2.8 (21)	17.29±0.12 (10)	48.02±0.65 (10)
	7	1974	1048.9± 6.6 (112)	429±1.2 (74)	19.69±0.09 (104)	53.54±0.24 (104)	851.5± 8.5 (97)	410±1.0 (62)	17.48±0.09 (88)	48.54±0.25 (88)
1966	6	1972	1013.9±10.8 (55)	414±1.81 (47)	19.81±0.16 (60)	53.21±0.36 (60)	853.5±10.8 (49)	398±1.37 (44)	17.78±0.16 (58)	48.56±0.33 (58)
	7	1973	1013.3±9.9 (63)	429±0.14 (16)	19.47±0.14 (13)	54.11±0.60 (13)	831.7±15.11 (29)	403±2.6 (13)	17.47±0.21 (10)	48.29±0.97 (10)
	8	1974	1029.2±11.0 (64)	429±1.6 (44)	19.57±0.09 (56)	53.74±0.30 (56)	863.8±11.1 (63)	411±1.3 (50)	17.56±0.13 (54)	48.24±0.32 (54)
1969	5	1974	1039.1±28.2 (10)	430±3.1 (8)	19.34±0.13 (13)	53.73±0.26 (13)	858.5±20.4 (8)	413±3.1 (7)	17.74±0.22 (13)	49.1±0.51 (13)

* All means are presented ± S.E.

** Sample sizes are given in brackets

Table 70 Mean body weights of female Herring Gulls of known age culled on the Isle of May, 1972-73

Year in which ringed	Year culled	Mean weight of non-laying** gulls (g) ± S.E.	Mean weight of laying gulls (g) ± S.E.
1968	1972	811.5 ± 19.8 (14)*	922.7 ± 62.2 (3)
	1973	842.2 ± 14.5 (22)	966.5 ± 51.9 (4)
1967	1972	817.2 ± 10.6 (25)	875.9 ± 22.2 (12)
	1973	834.6 ± 8.4 (48)	888.0 ± 26.1 (14)
1966	1972	821.1 ± 9.8 (25)	920.3 ± 51.9 (4)
	1973	817.6 ± 13.78 (23)	897.7 ± 48.1 (5)

* Sample sizes are given in brackets

** Refers to females with no eggs in the oviduct at the time of sampling in mid-May.

Body weight in adult Herring Gulls is known to vary with season and latitude (Barth 1967b). In general, body weight in birds is known to be a very variable parameter. Many factors are known to influence weight, apart from season and latitude. Diurnal and considerable individual variations are well known (Baldwin and Kendeigh 1938, MacDonald 1962, van Balen 1967) and have probably contributed to the variations in weight found for Isle of May Gulls. In particular, the time of sampling is important, although Barth (1967b) weighed breeding females these were probably not in the process of egg laying at the time of sampling, and hence the variations in weights of his Norwegian sample were considerably smaller than those recorded during the present study. In addition, it seems likely that for Isle of May ringed birds there may have been considerable cohort variation. The 1968 cohort, for example, was known to have had a poorer post-fledging and first year survival than either the 1966 or 1967 cohorts (Parsons, Chabrzyk and Duncan 1976). This poor survival may have been a reflection of poor quality, low weight birds.

For both sexes, body weight was lowest in four year old birds and appeared to increase up to the age of seven years. Such variation in weight may be explained on the grounds of increasing body size or individual variations in body size. The former possibility implies continued growth after the fourth year and seems unlikely, since for most bird species it is commonly believed that skeletal growth and tissue development cease after fledging, although the period over which gradual changes may take place is unknown. Barth (1967b) has suggested wing length as the best single parameter indicating body size in Herring Gulls. Similarly, van Balen (1967) found wing lengths of Great Tits breeding in different habitats to be a useful measure of body size.

For ringed Herring Gulls culled on the Isle of May, in every sample of killed birds examined during the three year there was a progressive and significant increase in wing length. The mean wing length increased on average by 4% in males and 3% in females (Table 71). However, wing lengths were remarkably constant in any given year for each cohort. It seemed unlikely that wing lengths of Herring Gulls in the breeding season were good indicators of size. Most wings measured had primaries which were abraded to different degrees which were consistent with a 3-4% decrease in wing length. Primary abrasion may therefore have been an indication of territorial encounters than general size.

Bill depth and bill length were the least variable parameters measured and of these bill depth varied by only a very small amount (0.61mm in males and 0.59mm in females), and had the lowest coefficients of variation (Appendix 13). Both parameters did not change with age, although they might have been expected to increase if general body size continued to increase with age. An overall measure of bill size is given by the bill index (bill length divided by bill depth; Dunnet and Anderson 1961); the regression of bill index on body weight is not significant ($r = 0.29$) in an unringed sample of full adults, and since, in general, body weight was found to increase with age, it seems unlikely that these weight increases were the result of marked increases in skeletal size from the third year of life onward.

Variation in fat storage

Although body weight must be a function of size, it is likely that this parameter also reflects recent feeding history and current physiological demand on body resources. It might be expected that in a species like the Herring Gull, in which feeding efficiency of immature birds is lower than that of adults (Verbeek 1977), that recruits into a breeding colony would be of lower weight. Such weight differences may be partly accounted for by differences in fat storage (particularly of triglyceride lipids) and fat mobilisation (Blem 1976).

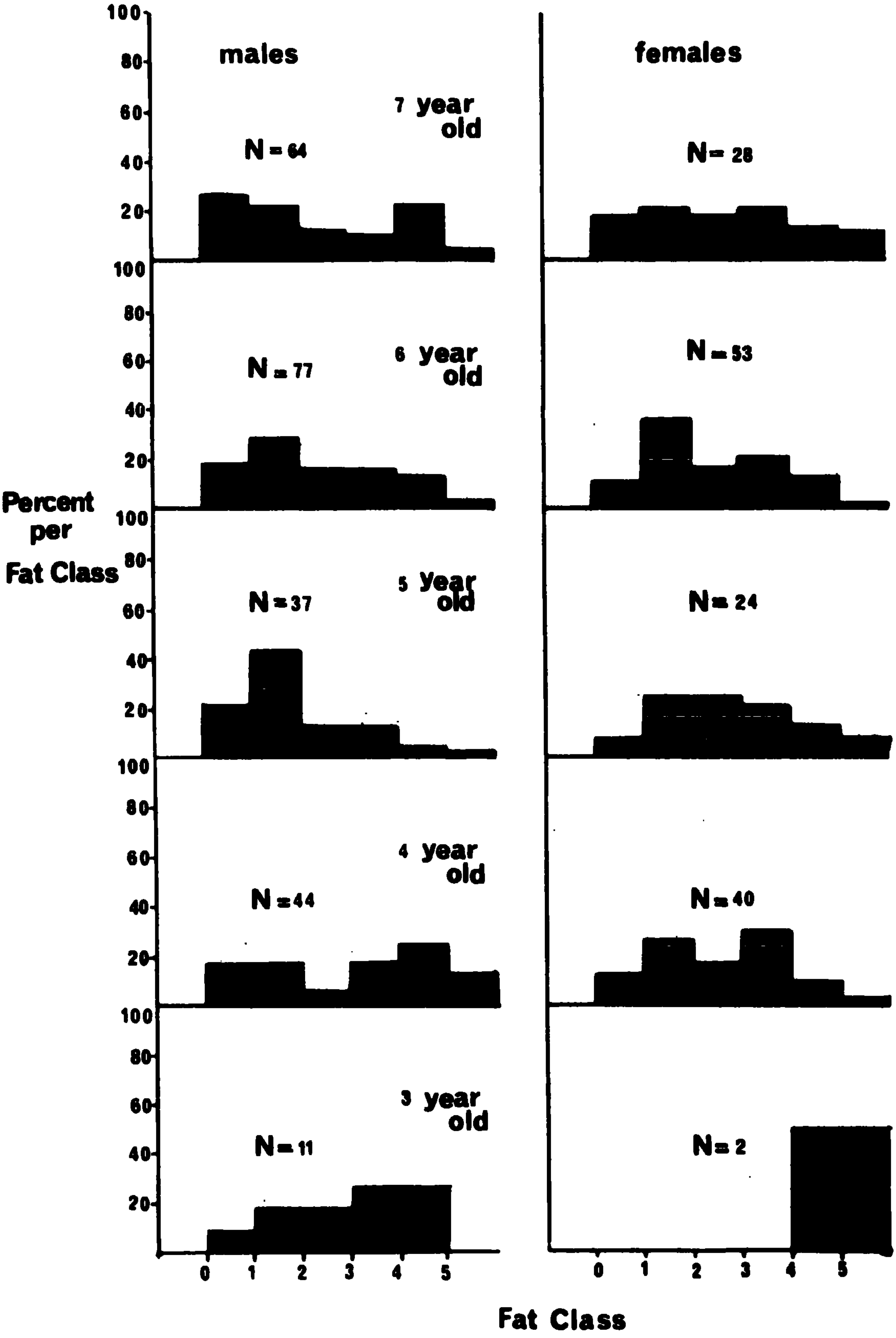
In penguins, old birds (birds with previous breeding experience) arriving to breed at the colony are heavier than recruits, principally as a result of increased fat reserves (Ainley 1975, Aedlie Penguin; Carrick and Ingham 1967, Royal Penguin). In these species, accumulated fat reserves are essential for successful breeding, providing an energy source for birds which may spend long periods at the rookery without feeding at all. The ecological significance of fat stores has been noted in breeding birds of other species; thus, in the Dunlin, Least Sandpiper and the Redpoll, fat stores decrease as the breeding season progresses, with a decline in measurable body fat in these species being correlated with increasing brood patch development and the onset of egg laying (Johnston 1964). Rogers and Odum (1964) have also shown that when fat stores in the body reach a certain critically low level in wood warblers, energy is derived by catabolic breakdown of non-fat body tissues, chiefly muscle proteins.

For Herring Gulls breeding on the Isle of May, feeding grounds on the Fife and Lothian coasts are near at hand, and there is no evidence of a seasonal shortage of food (Section 3.5 and Parsons 1971a). For these reasons it would seem unlikely that body weight differences between recruits and esyablished breeders could be accounted for by marked fat storage. Overt fat storage in Herring Gulls was found in visceral fat deposits, and sometimes a thin layer of subcutaneous adipose tissue. For Herring Gulls culled on the Isle of May in mid-May 1973 the combined subcutaneous and visceral fat deposits rarely exceeded 10g wet weight, although in some males they reached 15g, and thus constituted at most 1.5% of the body weight in males and 1.2% in females.

The mean fat index was found to vary according to age (Figure 24), although the differences between means were slight (Table 72). Three and four year old gulls culled in 1973 were more likely to belong to a higher fat class than older birds (Figure 24), although the variability in fat indices for any one age class was high and the differences in distribution of high and low fat indices were not significant ($\chi^2_{(2)} = 3.713$, $p > 0.05$). The lowest mean fat index occurred in five year old males (1.7) and may have reflected the high energy demands of establishing and maintaining territory for the first time. Territorial behaviour in Herring Gulls is known to wax and wane, being particularly high just after the eggs hatch (Tinbergen 1953). Since younger gulls lay eggs later than older gulls, it was expected that in mid-May three and four year old birds would not be placing such high demands

Figure 24

The variation in fat index in male and female Herring Gulls of known age in 1973


males
females
7 year old
N = 64
N = 28
6 year old
N = 77
N = 53
5 year old
N = 37
N = 24
4 year old
N = 44
N = 40
3 year old
N = 11
N = 2
Percent per Fat Class
100
80
60
40
20
0
1
2
3
4
5
Fat Class

for energy as older breeders, for which the majority of egg laying took place at this time. In addition, many three and four year old birds did not lay eggs although they acquired territories, so that the additional energy demands of egg formation in females (which may be considerable, Blem 1976), were not present.

However, both Tucker (1975) and Blem (1976) have pointed out that the mobilisation of avian fat stores can be very rapid. In passerines, total fat store depletion can occur over a 24 hour period. Moreover, in some species fat deposition occurs with a circadian periodicity and this inevitably complicates comparisons made between birds culled at different times of the day.

Variation in flight muscle weights

Considerably less variation was found in the weights of the major flight muscle, the *pectoralis major* (pectoral muscle). In both sexes the wet weight of pectoral muscle correlated significantly with body weights free of gut contents (Figure 25). Although the ranges of pectoral muscle weights for males and females overlapped, the overlap was small, and mean muscle weights were significantly different for the sexes (Table 73); $t_{49} = 9.10$; $t_{49} = 8.12$; $t_{64} = 6.00$ for four and five year old gulls and for birds older than six years, in each case $p < 0.001$).

The mean relative weight of pectoral muscle (g. muscle per g. body weight) increased with age in both males and females. The largest differences between muscle weights occurred between young and old females; four year old females had significantly smaller muscle weights than both five and six year old gulls ($t_{46} = 3.536$, $p < 0.01$, and $t_{58} = 6.128$, $p < 0.01$). In males, birds that were six years or older had significantly larger muscles than four year old birds ($t_{55} = 3.182$, $p < 0.01$).

Table 72. The variation in mean fat index[*] with age and sex of Herring Gulls, based on ringed birds killed in 1973

	MALES		FEMALES			**
Age (years)	Number of gulls examined	Mean fat index ± S.E.	Number of gulls examined	Mean fat index ± S.E.	Total number gulls examined	Total mean fat index ± S.E.
3	11	2.64 ± 0.37	2	(4.75)	13	2.96 ± 0.38
4	44	2.71 ± 0.26	40	2.28 ± 0.21	84	2.50 ± 0.17
5	37	1.70 ± 0.22	24	2.5 ± 0.38	61	2.02 ± 0.18
6	77	2.16 ± 0.16	53	2.03 ± 0.33	130	2.19 ± 0.12
7	64	2.22 ± 0.21	28	2.41 ± 0.27	92	2.28 ± 0.17

* Estimated as explained in text, p.181.

** Mean fat indices for combined male and female samples.

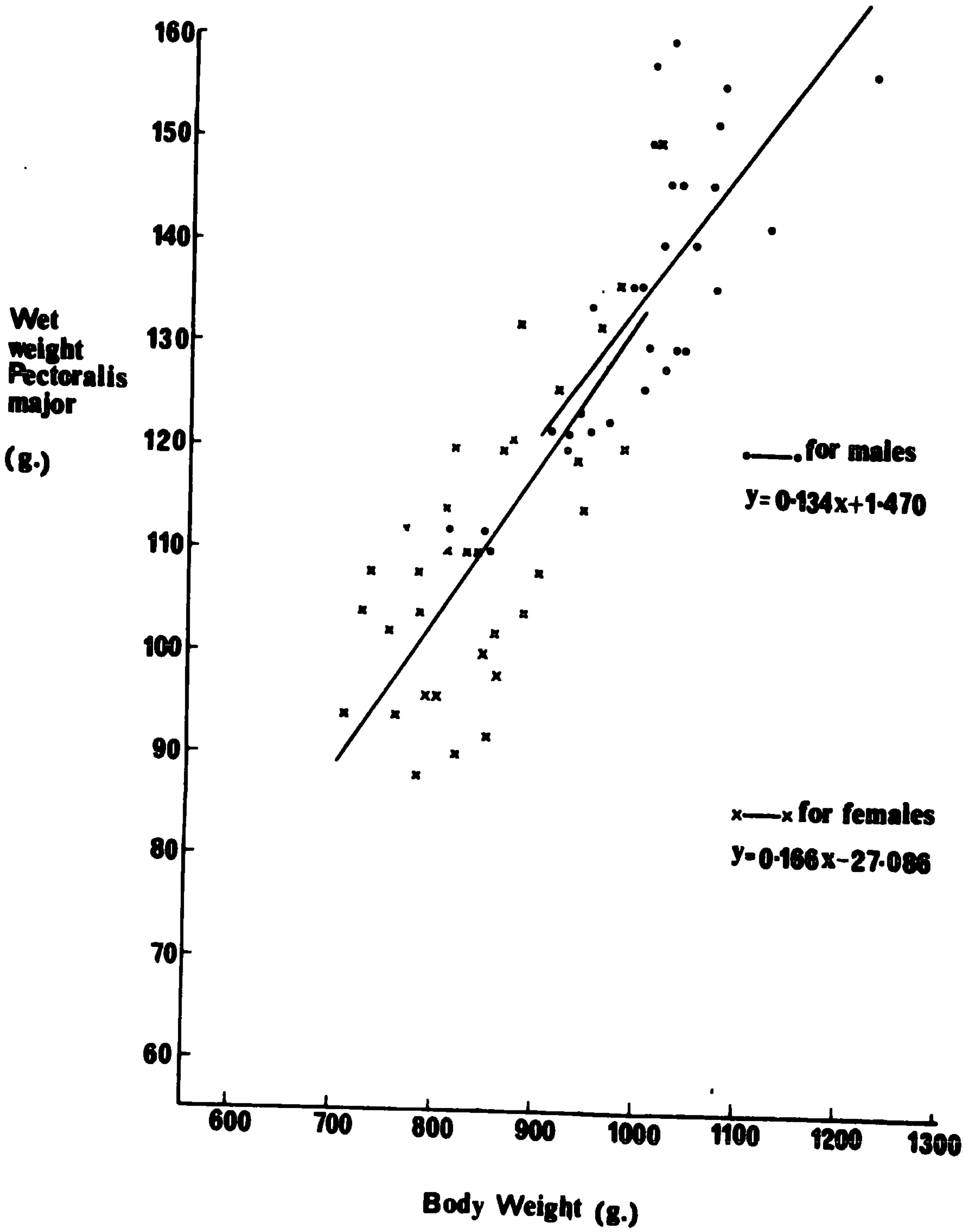
Table 73. The mean weight of pectoral muscle in relation to age of Herring Gulls

(for a sample of adult birds culled in May 1973)

	MALES			FEMALES		
Age (years)	Number of gulls examined	Mean wet weight of pectoral muscle (g) ± S.E.	Mean wet weight of pectoral muscle per g body weight g^{-2}/g ± S.E.	Number of gulls examined	Mean wet weight of pectoral muscle (g) ± S.E.	Mean wet weight of pectoral muscle per g body weight g^{-2}/g ± S.E.
4	25	128.08 ± 2.74	12.6 ± 0.2	26	89.73 ± 3.20	10.8 ± 0.3
5	29	132.34 ± 2.20	12.9 ± 0.2	22	102.90 ± 2.88	12.3 ± 0.3
> 5	32	140.01 ± 2.50	13.5 ± 0.2	34	110.52 ± 4.23	13.4 ± 0.3

Figure 25

The relationship between body weight and wet weight of *pectoralis major* flight muscle in a sample of adult Herring Gulls culled in May 1973


Wet weight Pectoralis major (g.)
160
150
140
130
120
110
100
90
80
70
60
600
700
800
900
1000
1100
1200
1300
Body Weight (g.)
•——• for males
y= 0·134x+1·470
x——x for females
y= 0·166x−27·086

The weight differences in pectoral muscle reflected the age and sex differences in body weights (Table 69) and suggested either component changes in the muscle or long-term growth and development of muscle.

In a variety of birds, pectoral muscles are known to be variable in weight as a result of changes in glycogen (King, Barker and Farner 1973); changes in water content (Newton 1968); and changes in protein (Kendall, Ward and Bacchus 1973).

Kendall _et_ _al_. (1973) have suggested that for Red-billed Queleas there is a labile protein reserve in the pectoral muscle which may act as a store to be drawn upon by protein demanding processes such as egg production and moult. In Red-billed Queleas, there is a net decrease in this protein fraction during egg laying. If a similar protein reserve exists in the pectoral musculature of Herring Gulls, this suggests that four and five year old females may have had fewer reserves to call upon at egg laying and may partially explain why these gulls laid smaller eggs.

6.3 Development of Brood Patches

Herring Gulls typically have three brood patches, two of which are situated ventro-laterally, whilst the third (the medial brood patch) is ventro-central and posterior in relation to the lateral patches. The factors affecting brood patch development have been recently reviewed by Jones (1972). The process by which the brood patches defeather and vascularize is known to be under endocrine control, chiefly by the anterior pituitary hormone prolactin (Farner 1967). Other hormones are also involved and it is probable that complete brood patch development is the result of a complex interaction between oestrogens, progesterone and prolactin (Hinde and Steel 1964, Hinde 1967, Hutchinson, Hinde and Steel 1967). In addition, behavioural factors such as the proximity of the nest, contact between the developing brood patches and eggs and the stimulatory action of the mate are known to be of importance for complete brood patch development (Hinde 1967, Lehrman 1964).

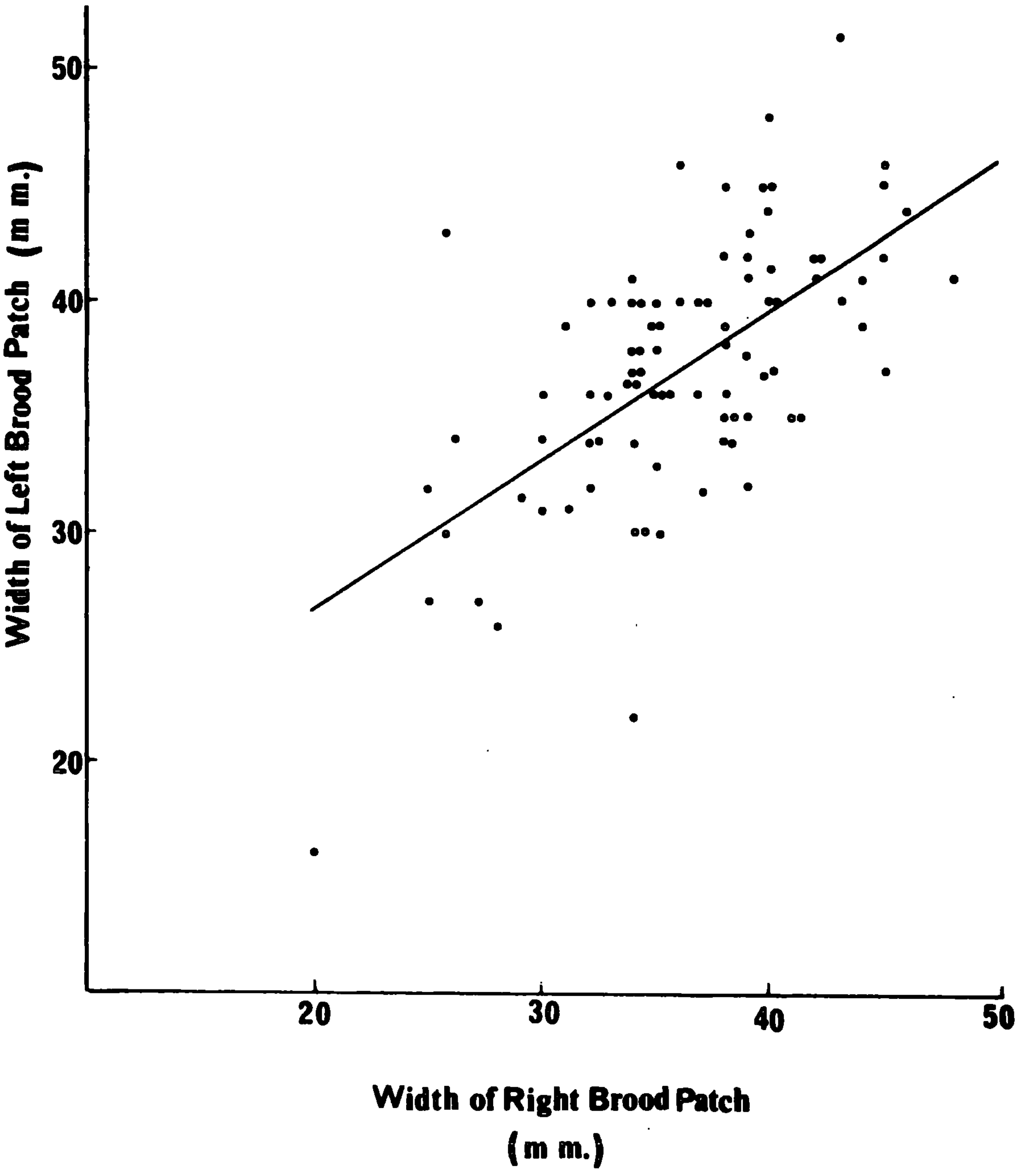
In assessing the extent of endocrine control of breeding in Canaries, Hinde (1967) considered that the extent of brood patch development was an accurate index of a bird's endocrine state. Similarly, Johnston (1956) concluded that the presence of brood patches was the best criterion to establish whether gulls were breeding or not. In California Gulls breeding typically takes place in the third and fourth years of life. Johnston found that no one and two year old gulls had brood patches, although these birds were present at the breeding colony; three year old gulls had smaller brood patches than older gulls. He concluded that no one and two year old, and only some of the three year gulls bred. The development of brood patches in two and three year old Adelie Penguins is also much slower than that of six and seven year old birds (Ainley 1975).

In Herring Gulls, the two lateral brood patches were found to be of similar size and development (Figure 26), whilst the median brood patch was very rarely as long, but could be as wide as the lateral ones. In 1973, brood patch development began in mid-April in most adults examined and brood patches had reached a maximum size by late-May and early-June. By July, refeathering had begun and the lateral brood patches were roughly two-thirds the size of those in the early-June sample (Table 74). The median brood patch was slower to develop and often it was the last to refeather in July.

A similar cycle of development takes place in California Gulls. In this species, defeathering of brood patches begins in April, although most brood patches had refeathered by mid-June (Johnston 1956) rather than late-July, indicating a more prolonged physiological decline from breeding condition in Herring Gulls on the Isle of May than was apparent for California Gulls breeding at Mono and Honey Lakes, California. This

Figure 26

The relationship between left brood patch width and right brood patch width for a sample of Herring Gulls culled in May 1973


Width of Left Brood Patch (m m.)
50
40
30
20
20
30
40
50
Width of Right Brood Patch
(m m.)

indicated that plasma prolactin levels decreased more slowly in Herring Gulls and may be the result of interspecific differences in photoperiodic response by the hypothalamo-hypophyseal endocrine system. In four and five year old Herring Gulls, egg laying in 1972 and 1973 took place at a later date than both the sub-colony and colony median laying dates. Although late breeding in recruiting seabirds has often been ascribed to inexperience, it is likely that the behavioural inadequacies displayed by recruits are the result of endocrinological phenomena. Herring Gulls in the first, second and third years of life have been found to have lower plasma levels of the pituitary gonadotrophic hormone L.H. (lutenising hormone) than older birds (four and five years old). In addition, the peak of L.H. secretion occurs later in the breeding season for young birds (Scanes, Cheeseman, Phillips and Follet 1974). No comparisons are available between four year old and older birds, but it is possible that gulls between the ages of four and five years bred later than birds six years and older as the result of a slowly increased gonadotrophic output from the pituitary. The secretions of gonadotrophins probably increase as recruits become integrated into the breeding colony over a number of years.

Young California Gulls and Adelie Penguins have been found to have smaller gonads and less well developed brood patches in relation to established breeding adults (Johnston 1956 and Ainley 1975). As yet, no comparable studies for the Herring Gull have been made. Brood patch development in Herring Gulls of known age culled in 1973 was determined by taking maximal length and breadth measurements of defeathered skin. In 1973, the cull began six days after the median laying date and thus spanned a period when most breeding adults could be expected to be in full breeding condition.

The brood patch areas of six and seven year old gulls were similar and, where differences in length or breadth occurred, the means

Table 74. Brood patch development during the breeding season in a sample of unringed adult Herring Gulls shot in 1973

Date	Number of gulls shot	Mean size of right brood patch (mm) ± S.E.		Mean size of left brood patch (mm) ± S.E.		Mean size of median brood patch (mm) ± S.E.	
		Length	Breadth	Length	Breadth	Length	Breadth
15-25 April	10	12 ± 3	8 ± 2	11 ± 2	9 ± 3	6 ± 1	5 ± 1
16-20 May	12	54 ± 2	39 ± 3	51 ± 3	37 ± 2	41 ± 3	36 ± 2
10-12 June	14	58 ± 3	38 ± 1	55 ± 3	37 ± 1	42 ± 2	32 ± 1
20-25 July	30	37 ± 3	24 ± 2	36 ± 3	25 ± 1	32 ± 3	25 ± 2

overlap at the 95% confidence level and were not significant. Younger birds had smaller brood patches (Table 75) although the differences between mean measurements were small and there was a gradual increase in brood patch area as age increased. Thus, while three year old birds had significantly smaller brood patches than all older birds, the differences between four and five and between five and six year old breeders were not significant. The differences, however, between four and six and between five and seven year old gulls were all significant (multiple range test, $p < 0.05$, Snedecor and Cochran 1967). Such slight changes between year classes were consistent with the suggestion that only small changes in circulating gonadotrophins occurred after the third year of life.

Five of the 15 three year old gulls examined in 1973 had no evidence of brood patch defeathering at all, and on Johnston's (1956) criteria these birds should have been classed as non-breeders. However, the fact that these birds were culled indicated that most were holding territory in May 1973. If subsequent defeathering did take place in such birds, then this age class was at least a month later in breeding than older birds (Table 74). Given the length of this delay in attaining reproductive condition, it seemed unlikely that these gulls would have laid many eggs. Many three year old gulls holding territory probably did not lay at all, and no birds of this age were observed to breed on the study areas in 1972 and 1973.

Table 75, The development of brood patches in Herring Gulls of known age culled in 1973

Year in which ringed as chicks	Age (years)	Number of gulls examined	Size of right lateral brood patch		Size of left lateral brood patch		Size of median brood patch		Number of gulls in which no brood patches de-feathered	Number of gulls in which only two brood patches de-feathered	Percentage of gulls in which three brood patches were present
			Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.			
1966	7	88	53±1	36±1	53±1	37±1	39±1	34±1	0	0	-
1967	6	130	52±1	36±1	50±1	37±1	38±1	34±1	5(4%)	4(3%)	93
1968	5	61	49±2	35±1	49±2	34±1	37±1	34±1	7(12%)	2(3%)	85
-	4*	90	47±1	33±1	47±1	35±1	35±1	31±1	4(4%)	4(4%)	92
-	3*	15	32±5	23±4	30±5	23±4	19±5	20±6	5(33%)	2(13%)	54

* Aged on plumage characters (see Appendix 10).

6.4 The Testis Cycle

The annual cycle in testicular growth and development has been described in a variety of bird species, for example, in the Eider (Gorman 1974), House Sparrow (Murton, Lofts and Orr 1970), Goosander (Erskine 1971), Teal (Lofts 1975) and California Gull (Johnston 1956). Typically for temperate species, testis size increases in the spring and declines in late-summer or early-autumn. The growth cycle is photoperiodically induced (Farner 1967) and is the result of secretions from the adenohypophysis. Early stages in spermatogenesis and seminiferous tubule growth are principally the result of the gonadotrophic hormone F.S.H. (follicle stimulating hormone) and L.H. (leutenising hormone) (Murton 1975). Androgens are also known to be important in the final stages of tubule development and in the production of spermatozoa (Lofts and Murton 1973).

In colonially breeding seabirds, the effects of age on gonad maturation have been demonstrated by Ainley (1975) for Adelie Penguins and Johnston (1956) in California Gulls. Both workers have shown that testis growth and development in young birds may be considerably retarded in comparison with older, more established members of the breeding colony.

For adult Herring Gulls, breeding on the Isle of May in 1973, testis weight reached a peak in mid-May, and by July testis regression was well marked (Table 76). The seasonal decline in testis weight was rapid and by the end of July the combined mean weight of both testes had decreased by 86.5% from the peak weight in May.

All testes examined from gulls shot in June and July were fully regressed (Stage 5) with involuted tubules and occluded tubule luminae. There was no evidence of the secondary late-season peak in spermatogenesis reported by Chan and Lofts (1974) in Tree Sparrows. A similar cycle in gonadal development is evident in Herring Gulls breeding on Skomer Island

(Harris 1964a), although for birds on Skomer, the peak mean weight was lower (combined weight of both testes, 1.45g) and occurred in April rather than in May. Herring Gulls on Skomer Island bred earlier during Harris's study than on the Isle of May in 1973, and it is therefore not surprising that gonadal maturation cycles of Skomer gulls were also earlier. On the Isle of May, the time at which maximum testis weight was attained preceded the period of peak egg laying. This was also true of Herring Gulls breeding on Skomer Island.

The left testis was always larger than the right, a situation which may have indicated either greater sensitivity or greater response to blood gonadotrophin levels by this testis (Marshall 1952, Johnston 1956). Both testes are approximately ellipsoidal in shape, and testis volume (V) was calculated from the formula for the volume of an ellipsoid:

$$V = \frac{4}{3}\pi ab^2$$

where: a was half the testis length, and b was half the breadth. For a sample of adult Herring Gulls culled in May 1973 there was a close linear correlation both between testis weight and volume (Figure 27, $r = 0.994$, $p < 0.01$), and also between the weights of the left and right testis, $r = 0.759$, $p < 0.01$). Thus weight was a good indicator of testis size, and although size comparisons have been made considering the left testis, these also indicated changes in the right testis.

In male Herring Gulls of known age culled between 22-31 May 1973 there was a significant increase in mean testis weight with age (Table 77). In comparison with the oldest males (seven years old), both mean testis weights and tubule diameters of three and four year old gulls are significantly smaller ($p < 0.01$). Only one of the three year old males was in breeding condition (Stage 3). This bird, culled on North Ness, had both well developed and fibroblastic Leydig cells in the interstitium.

Table 76. Changes in testis weight during the breeding season for adult Herring Gulls shot on the Isle of May in 1973

Date	Number of males shot	Mean wet weight of left testis (g) ± S.E.	Mean wet weight of right testis (g) ± S.E.	Total mean wet weight of testes (g) ± S.E.	Range in total wet weight (g)
15-25 April	19	1.086 ± 0.900	0.547 ± 0.041	1.646 ± 0.111	0.612 - 2.180
10-20 May	16	1.225 ± 0.145	0.569 ± 0.093	1.794 ± 0.222	0.501 - 3.489
6-22 June	13	0.919 ± 0.073	0.242 ± 0.033	0.661 ± 0.103	0.207 - 1.429
10-28 July	18	0.151 ± 0.036	0.086 ± 0.021	0.223 ± 0.043	0.069 - 0.418

Figure 27

The relationship between testis wet weight (y) and calculated testis volume (x)

$y = 0.913x - 0.018$

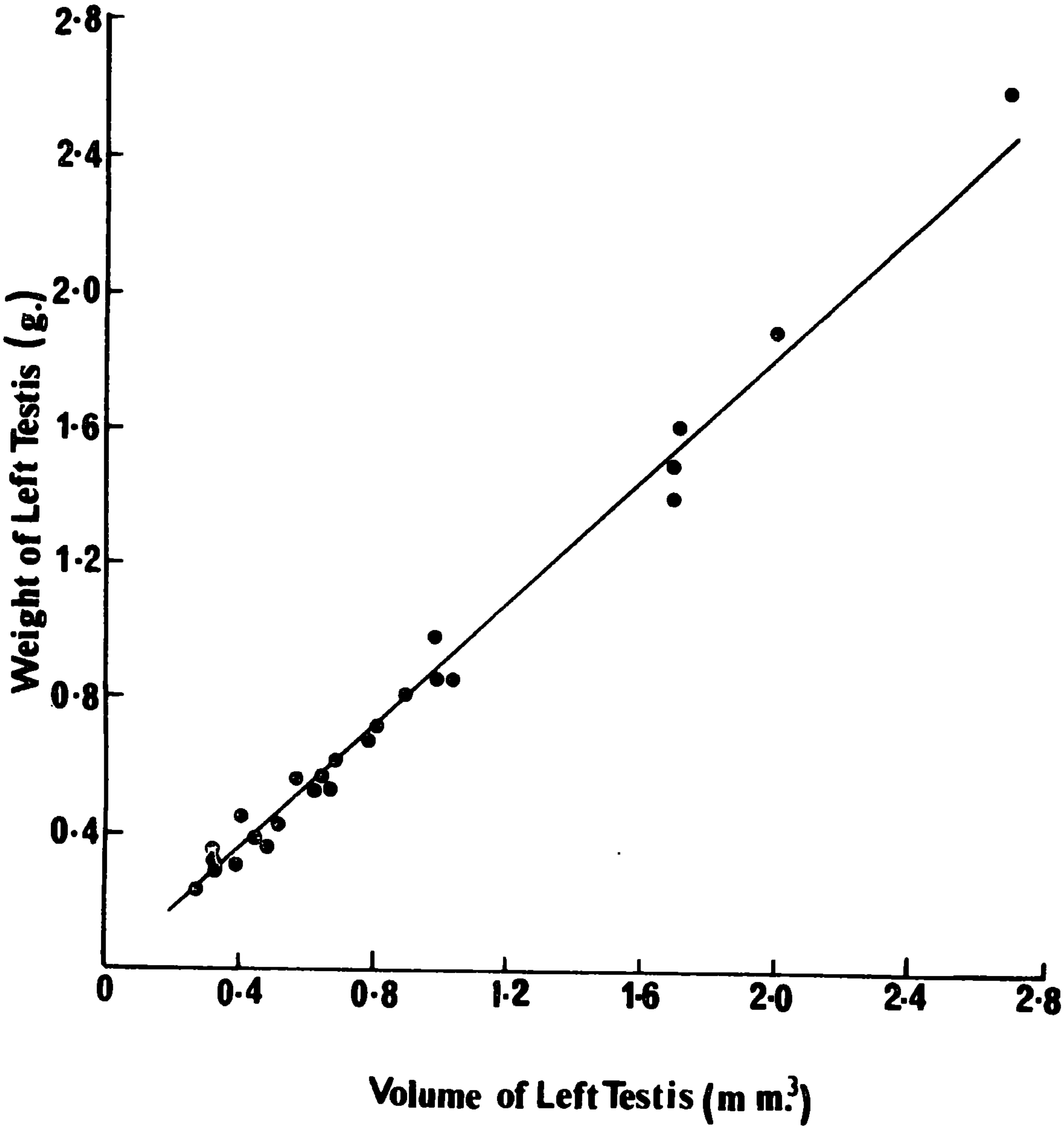

2·8
2·4
2·0
1·6
1·2
0·8
0·4
Weight of Left Testis (g.)
0
0·4
0·8
1·2
1·6
2·0
2·4
2·8
Volume of Left Testis (m m.³)

Table 77. Variation in testis size in Herring Gulls of known age culled in May 1973

Age (years)	Number of gulls	Mean wet weight of left testis (g) ± S.E.	Number of testes measured	Mean seminiferous tubule diameter (mm) ± S.E.
3	17	* 0.465 ± 0.066	10	0.223 ± 0.047 †
4	39	** 0.708 ± 0.052	26	0.267 ± 0.023 ††
5	37	0.816 ± 0.058	24	0.352 ± 0.031
		(N.S.)		(N.S.)
6	72	0.885 ± 0.046	39	0.371 ± 0.034
		(N.S.)		(N.S.)
7	63	0.960 ± 0.063	41	0.393 ± 0.050

For comparisons with seven year old males:

* $t_{78} = 5.468$ † $t_{49} = 2.477$

** $t_{100} = 3.084$ †† $t_{65} = 2.289$

For all cases $p < 0.01$. (N.S. = not significant)

It was difficult to quantify interstitial cell development. In general, interstitial cells of three year old males appeared to be poorly developed, with the majority of cells elongated and thin and clustered together in fibrous sheets forming a small triangle in the intertubular space at the tubule apex (the "fibroblastic" condition). In older birds, interstitial cells were observed to become progressively enlarged, and the nuclei were darkly stained, suggesting mitotic activity. Whereas inter-tubular distances were obvious in three year old gulls (mean inter-tubular distance in three year old testes, 0.085mm), in older birds the tubules were contiguous and there was rarely a gap between tubules. Decreasing intertubular distance with age was the result of a progressive increase in tubule diameter in older birds (Table 77). Tubule growth and development is known to be largely controlled by F.S.H. secretion from the anterior pituitary. Accordingly, it seemed reasonable to conclude that young gulls, three and four years old, had lower levels of plasma F.S.H. than those present in older breeding males. Similar conclusions were reached by Johnston (1956) and Ainley (1975) for young California Gulls and Adelie Penguins.

The progressively increased development of interstitial cells in older breeders suggests that the age differences found by Scanes et al. (1974) in L.H. secretion in Herring Gulls may also take place in natural populations. In Teal and in Tree Sparrows interstitial cell activity is correlated with androgen secretion (Lofts 1975). If similar processes occur in Herring Gull testes, three and four year old breeding birds might have been expected to have had lower testosterone levels than older birds. Such differences may have explained the poorer breeding success of Herring Gull recruits since testosterone is known to be important in the initiation and maintenance of reproductive behaviour (Farner 1967) which is where young breeders seemed to be inadequate.

6.5 The Effects of Culling

Brood patch development

The number of four year old late-breeders or non-breeders (as judged by lack of brood patch defeathering) was low in 1973, and only 4% had no evidence of brood patches. This represented a considerable decrease in such birds over the previous year (Table 78). In 1972, 43 four year old breeders were culled, of which 11 (26%) had no brood patch development.

Also, for those birds developing brood patches in this age class in 1972, the area of defeathered skin was markedly smaller than for birds of the same age in the following year. Although culling began earlier in 1972, the difference between the first dates of the cull was small (four days) and could not have accounted for the small brood patches of four year old gulls in 1972. In addition, Herring Gulls breeding on the Isle of May in 1973 laid later than in the preceding year, and consequently it was to be expected that birds culled in 1973 during equivalent time periods would have had smaller rather than larger brood patches.

The majority of three and four year old birds culled in 1973 were from previously culled areas (mostly from Rona and the east coast sub-colonies). 12 (80%) out of a total of 15 three year old, and 75 (83%) out of 90 four year old gulls were culled on former N.C.C. areas. By the end of May 1972 the cull had removed many central territory holders on five sub-colonies on the Isle of May. Partially cleared areas were observed to have large numbers of four and five year old gulls on them by July 1972 (Section 5.5). The possibility existed, therefore, that recruits attracted to cleared areas late in 1972 returned in the following year to breed on these same areas. Under normal circumstances recruits would be restricted in their choice of territory by competition from established breeders. Under cull conditions such competition, although it had not disappeared, was much reduced in 1973 and recruiting birds acquired territories relatively easily.

Although territorial behaviour is itself hormonally determined, it is known that in Canaries nest site acquisition and proximity of the nest can stimulate gonadotrophic hormone release from the pituitary (Hinde 1967). Similar processes may also operate in Herring Gulls. Circumstantial evidence for the advancement of breeding condition by territory acquisition was forthcoming from a comparison of brood patch

Table 78. Brood patch development in four year old Herring Gulls culled in May 1972

Number of gulls examined	Size of right lateral brood patch		Size of left lateral brood patch		Size of median brood patch		Number of gulls in which no brood patches were de-feathered	Number of gulls in which either one or two brood patches were de-feathered	Percentage of gulls in which three brood patches were present
	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.			
43*	26±3	19±2	29±4	19±2	29±4	22±3	11 (26%)	7 (16%)	58

* Includes 29 Herring Gulls ringed as chicks in 1968; the remainder were aged on plumage characters.

development in four year old gulls killed on areas previously culled in 1972 with those cleared for the first time in 1973 (Table 79). Brood patch width was the least variable measure of brood patch area and had the lowest coefficients of variation and was therefore the best single parameter to use in determining brood patch development. Mean lateral and median brood patch widths were significantly smaller in gulls culled on the North Ness and the South Ness ($t_{84} = 3.79$ for lateral brood patches; $t_{81} = 3.58$ for median brood patches; in both cases $p < 0.001$).

Table .79. Brood patch development in four year old Herring Gulls culled on known areas on the Isle of May in 1973

	Number of gulls examined	Mean lateral brood patch width (mm) ± S.E.	Mean median brood patch width (mm) ± S.E.	Number of birds in which brood patches were not defeathered
Previously culled areas	75	35±1	33±1	3 (4%)*
Unculled areas	15	23±3	25±2	2 (13%)

* As a percentage of the total number of gulls examined.

It might be expected that the energy demanding processes of territorial behaviour would have resulted in a relative depletion of fat stores in four and five year old Herring Gulls from cleared areas, whereas such birds that attempted to recruit into established areas did not easily acquire territory and may consequently have made fewer demands on body reserves. The fat indices of males on previously culled areas (Table 80) were lower than those for males on unculled areas. This conforms to expectation since initially much of the territorial establishment behaviour is performed by male Herring Gulls (Tinbergen 1953). However, the differences were small and, as has been argued earlier, may not have reflected accurately the energy demands made on body reserves.

By implication, it seemed that recruiting gulls were physiologically capable of breeding but did not always do so because of behavioural interactions (that is, competition at potential nest sites) rather than because a process of physiological maturation had not been completed) as Ainley (1975) has suggested for your Adelie Penguins). It is probable that complete physiological maturity is dependent upon behavioural interactions. The further implication was that continued culling would, by making clear areas available, decrease the age of first breeding. This prediction has, in part, been borne out by the progressively changing age structure of the Isle of May breeding population since 1974. Increasingly, larger proportions of three year old gulls have been culled by the N.C.C. (Duncan 1978).

Testes development

Although four year old gulls culled in 1973 showed greater brood patch development than birds of the same age in the previous year, there was, however, no significant difference between mean testes weights in birds of this age class in the two years. (In 1972 the mean weight of left testes for 23 four year old males was 0.790g, which did not differ significantly from the mean weight in the previous year (Table 77), $t_{60} = 1.219$, $p > 0.05$.) There was also a decrease in the number of testes in breeding condition for this age class. In 1972, 15 (65%) of the 23 testes examined were at Stage 3, although this difference is not significant ($\chi^2_{(1)} = 0.3$, $p > 0.05$).

In marked contrast to brood patch development, the weights of the testes of all males of known age were lower on previously culled areas than on areas culled for the first time in 1973 (Table 81). The testes weight

Table 80. The fat indices of Herring Gulls killed on previous cull areas compared with those of birds killed on areas culled for the first time in 1973

Age (years)	Number of gulls examined	MALES		FEMALES	
		Mean fat index of birds culled on new areas ± S.E.	Mean fat index of birds killed on previous cull areas ± S.E.	Mean fat index of birds culled on new areas ± S.E.	Mean fat index of birds culled on previous cull areas ± S.E.
3	13	3 (1)	2.60 ± 0.41 (10)	-	4.8 (2)
4	84	2.28 ± 0.46 (9)*	2.81 ± 0.30 (35)	2.67 ± 0.50 (6)	2.21 ± 0.23 (34)
5	61	1.43 ± 0.28 (14)	1.87 ± 0.30 (23)	3.08 ± 0.63 (6)	2.31 ± 0.29 (18)
6	130	1.74 ± 0.24 (23)	2.34 ± 0.20 (54)	2.70 ± 0.33 (15)	2.03 ± 0.21 (38)
7	92	2.38 ± 0.35 (24)	2.13 ± 0.26 (40)	2.21 ± 0.39 (12)	2.26 ± 0.38 (16)

* Sample sizes are given in brackets

Table 81. Mean weights of left testes in Herring Gulls of known age in relation to cull area

(from 1973 cull recoveries)

	Culled on previously cleared sub-colonies		Culled on sub-colonies cleared for the first time	
Age (years)	Number of males examined	Mean wet weight of left testis (g) ± S.E.	Number of males examined	Mean wet weight of left testis (g) ± S.E.
3	16	0.419 ± 0.051	1	(1.210)
4	30	0.640 ± 0.054	9	0.933 ± 0.102
5	25	0.715 ± 0.062	37	0.816 ± 0.058
6	53	0.792 ± 0.043	19	1.147 ± 0.107
7	38	0.778 ± 0.061	23	1.252 ± 0.112

differences between areas in four year old birds were significant ($t_{37} = 2.54$, $p < 0.02$), and for this age class may have reflected differences in spermatogenic activity in the testis. Of the 26 testes examined histologically for this age class (Table 82), 11 had not attained breeding condition, eight (73%) of these Stage 1 and Stage 2 testes were from males killed on previously culled areas. The differences between spermatogenic stages were not as marked for older gulls (57% for five year old, and 50% in seven year old birds) culled on previously cleared areas. Similarly, the single three year old male culled on North Ness was the only three year old male in breeding condition, and had a testis weight comparable to the overall mean for seven year old males (Table 77).

Table 82. Spermatogenesis in the testes of Herring Gulls of known age culled in May 1973

Age (years)	Number of testes examined	Spermatogenic stage* 1	2	3	4	Percentage in breeding condition
3	10	1	8	1	0	10
4	26	2	9	15	0	58
5	24	0	7	17	0	71
6	39	0	1	35	3	90
7	41	0	2	36	3	88

* A key to spermatogenic stages is given in Section 6.1.

Although testes development and brood patch defeathering are both hormonally controlled processes, the gonadotrophins concerned are different (FSH, LH for testes and prolactin for brood patches), and these different hormones may act independently to bring males into overall breeding condition. If these two hormonally induced processes were closely coupled, then large brood patches would indicate well developed testes, and vice-versa. In fact, it was quite common to find males with large brood patches but small testes, and conversely with small testes but large brood patches. These two processes were probably independent (there is no significant correlation between testes size and mean lateral brood patch width for all age classes: $r = 0.07$, $p > 0.05$).

Such a result was not surprising. The independent action of gonadotrophins has been noted by several workers (Murton 1975; Lofts, Murton and Thearle 1973; Lacy et al. 1969), and recently it has been suggested that there are separate endogenous circadian oscillators involved in the production and release of gonadotrophic hormones (Murton 1975).

Thus, while prolactin secretion may be enhanced by nest site acquisition, secretion of FSH and LH may involve other stimuli. For recruits to the breeding colony, the differences between cleared and uncleared areas were in nesting density (there was a decrease in nest density on cleared areas after the cull) and in the condition of existing breeding adults whose reproductive condition appeared to be retarded in relation to adults on uncleared areas (Table 81).

Stimulation of hypothalmic activity and FSH and LH secretion may in part have involved behavioural interactions between recruits and established breeders and may have reflected the importance of social stimuli in attainment of reproductive condition in male birds. The differences for testes development between cleared and uncleared areas in six and seven year old males were large (Table 81) and significant (for six year old birds, $t_{70} = 3.078$, $p < 0.001$; for seven year old birds, $t_{59} = 2.746$, $p < 0.01$). Males on unculled areas had much larger testes than those on previously culled areas. A variety of factors may have contributed to such differences. An important factor may have been that surviving adults returned later to breed on previously disturbed areas. In addition, some gulls probably abandoned their former nest sites as a result of disturbance in the previous year and may have experienced difficulties in establishing territories on different areas.

Whereas disturbance of older breeding adults may have been of importance, there was no evidence to suggest marked gonadotrophin deficiencies in gulls older than five years, since these birds had active interstitial cells and well advanced spermatogenesis in the testes. This was in marked contrast to the situation for recruiting birds.

SECTION SEVEN DISCUSSION

The evidence that emerges from the present study of Herring Gulls indicates that the large numerical increase recorded at the Isle of May is neither exceptional nor atypical. Over the duration of this study the majority of British colonies appear to have enjoyed periods of rapid numerical expansion, which for most colonies, including the Isle of May, have taken place since the early 1950s. There is no evidence to suggest that these increases can be attributed to increases in productivity. Experienced breeders on the Isle of May, on average, raised one offspring to fledging per pair each year. This is the typical reproductive rate for this species recorded even from the earliest studies (for example, Darling 1938, Paynter 1949).

An important factor determining recruitment rates is the length of the period of deferred maturity. It was pointed out in Section One that a decrease in this period could accelerate recruitment and thereby increase the rate at which a colony might increase. The converse situation has been observed for Manx Shearwaters breeding on Skokholm Island. Brooke (1973) found that the age at which Manx Shearwaters breed for the first time has apparently increased over a period of 10-15 years, an increase in the length of deferred maturity which was correlated with a slowing down of the rate at which shearwater numbers were increasing at the Skokholm colony.

It is difficult to assess the significance of changes in the length of deferred maturity in producing rapid rates of increase at established Herring Gull colonies. This difficulty is due to the paucity of long-term studies on birds of known age. Casual observations at various colonies have suggested that Herring Gulls frequently breed when three and four years old (see for example Paludan 1951, Tinbergen 1953, Drost *et al*. 1961, Harris 1970). However, the evidence from the present study has shown that the period of deferred maturity may be longer than these previous authors have suspected. On average, Herring Gulls entered the Isle of May breeding colony when five years old, although some delayed recruitment until they were seven years old.

It is clear that explanations of the Herring Gull increase on the Isle of May, and for that matter at most other established British colonies which invoke increased reproductive rates or decreased periods of deferred maturity, are unsatisfactory. The Herring Gull in western Europe and in North America is currently exploiting a large and aseasonal food supply. This, coupled with the fact that the species has few natural predators, has contributed towards high rates of adult survival and provides sufficient reason for the Herring Gull's recent historical and current biological success.

The basic question asked in Section One is whether population levels are controlled intrinsically by checks on recruitment imposed by the population itself (as suggested by Wynne-Edwards) or whether recruitment and population levels in Herring Gulls are controlled by mechanisms which maximise productivity (the neo-Darwinian view proposed by Lack and Ashmole). From the arguments already advanced it might be expected that the latter suggestion is the most applicable to Herring Gull populations. On this, the most widely held hypothesis, it is to be expected that clutch size would correspond to the maximum number of offspring that can be adequately fed and for breeding to occur as soon as possible.

One way of testing the suggestion that productivity is maximal is to compare the growth rates of chicks in different brood sizes. On the Isle of May the growth rates of a- and b-chicks did not differ significantly in different brood sizes. This evidence, together with that which is forthcoming from experiments in which brood sizes have been manipulated, suggests that food is not a limiting factor for Herring Gulls, but whether or not more chicks could be raised to fledging is debatable. For example, Haymes and Morris (1977) altered brood sizes of Herring Gulls breeding at colonies on Lake Erie to give broods ranging from one to five chicks. The growth rates of chicks and chick weights at fledging were similar when control and experimental broods were compared, and chick survival was not reduced in the artificially enlarged broods. Haymes and Morris suggested that adults were supplementing their natural diet with a locally abundant source of fish refuse. They inferred that in this case, at least, productivity could be higher. In contrast to this study, Spaans (1971) found that chicks in supranormal broods had slower growth rates than those from modal broods. Only if he artificially introduced food (in the form of domestic refuse) to the experimentally enlarged broods did growth rates increase in these chicks. Spaans concluded that Herring Gulls breeding in the Dutch Wadden Sea area could not successfully raise more than three young per pair.

Both of these studies suggest that parents can only cope with raising broods which are larger than normal if food is either naturally very abundant and close to the nest site (as was the case at Lake Erie) or extra food (over and above what the parents collect themselves) is introduced to nests. Whilst these results indicate the adaptability of gulls in being able to exploit situations of food superabundance, they suggest that a brood size of three chicks may represent the normal and maximal brood for this species. The majority of studies on Herring Gull biology indicate that c.3 clutches are laid regardless of the local food situation. There is some evidence to indicate that small clutches may be laid in years of food shortage (Belopol'skii 1961); however, the converse situation has not been recorded. There is no evidence to suggest that larger clutches are being laid where food is especially abundant. Again the conclusion must be that reproductive rates at present are maximal. Even where food is very abundant it seems likely that an important factor in limiting reproductive rates is the quantity (and perhaps quality) of the food brought back to the nest rather than its general availability.

It is difficult to answer the question of whether breeding occurs as soon as possible. Wynne-Edwards theorised that the process by which maturity is deferred has evolved as a means of controlling recruitment rates. According to this argument the aggressive behaviour of resident breeders discourages recruits from establishing territories at the colony. Therefore, a reservoir of potential recruits is formed. For colonies where nesting densities are high there will be considerable competition for nest sites and the period of deferred maturity becomes long as recruits have to wait a long time to establish territories.

On the Isle of May the removal of established breeding gulls by culling greatly increased the recruitment rates of three, four and, in particular, five year old birds. It also resulted in a decrease in the age of recruitment with three year old birds being found on culled areas but not on unculled control areas. From this evidence it can be inferred that competition for nest sites had existed prior to culling and that some birds (three year old birds in particular) had been excluded from the territory-holding population. This conclusion suggests that breeding does not take place as soon as it is possible and that for Herring Gulls recruitment rates are some function of prevailing colony conditions (nesting density in particular). A similar conclusion was reached by Manuwal (1974) for Cassin's Auklets breeding at a colony in California. Manuwal removed established breeding birds from their burrows and found that many (between 38-70%) of the recruits which occupied these burrows were able to breed in the same year as they had recruited. This was not the case for Herring Gulls on the Isle of May; gulls that recruited to culled areas in 1972 did not breed in that year, but many had defeathering brood patches by May 1973 and would have bred in the year following recruitment. Non-breeding in territorial gulls was not confined to birds that recruited into culled areas. In 1972, 14% of the 141 territories occupied by birds of known age on unculled study areas did not contain breeding females. In the following year, 8% (in 167 study nests) did not breed. The highest proportions of non-breeders were in the youngest recruiting age classes (36% of four year old birds in 1972 and 14-18% of five year old birds in 1972 and 1973).

In the Herring gulls a pre-breeding year, where a territory is held but no eggs are laid, is not exceptional and may indeed be a comparatively normal occurrence. This is not inconsistent with the argument advanced by Wynne-Edwards; it simply means that if homeostatic control of population size does take place by means of socially determined recruitment rates, a time-lag of one year must be introduced into the feedback loop between population size and recruitment rate. Recruits had significantly lower breeding success than experienced and established birds (recindivists) so that in effect there is a two year gap between cause (removal of established site-holders) and effect (maintenance of productivity). In the light of the current numerical increase in Herring Gulls it seems unlikely that homeostatic regulation, as outlined above, plays an effective role in determining population size in this species.

The majority of recruits, at the time of culling, showed signs of physiological immaturity when compared with recindivists culled at the same time. Many of the differences between recruits and recindivists can be attributed to low rates of gonadotrophic secretion from the recruit pituitary gland. It appeared that in recruits either the stimulus which induces breeding (presumably photoperiod) took longer to detect than it did in experienced breeders, or that in recruits it took appreciably longer for that stimulus to have physiological effects. In comparison to recindivists, recruits took longer to come into breeding condition; in males the testes developed later; in females, eggs were laid later, and for both sexes brood patch defeathering occurred later. Most recruits were physiologically capable of breeding (in 1972, 64% of four year old and 82% of five year old females laid eggs) but were out of phase with the majority of birds breeding on the sub-colonies.

In both Black-headed Gulls (Patterson 1965) and Sandwich Terns (Veen 1977) it has been found that birds which laid eggs either before or after peak colony laying had low reproductive success. A similar situation exists in Herring Gulls (Parsons 1975). In these species, breeding behaviour within the colony is highly synchronised and birds that laid late in relation to the rest of the colony had poor breeding success. It seems that, as has been suggested by Ainley (1975), an important distinction between recruits and recindivists is that the latter have a closer coupling between environmental stimulatory cues and the initiation (and maintenance) of the sequence of endocrinological events that breeding depends upon. On this view the period of deferred maturity is not a device to lower productivity (as Wynne-Edwards suggests) but a necessary period during which maturation changes and learning processes take place, ensuring that individuals synchronise their breeding with the rest of the breeding colony. The period of deferment of maturity is not a fixed one and there may be considerable individual variations in the length of time that a bird needs to reach reproductive readiness (coupling with environmental cues and synchrony with its fellows). For a small minority (8%) of Herring Gulls on the Isle of May, this period extended over seven years.

A major attribute contributing to the success of the Herring Gull as a species is its ability to successfully establish new breeding colonies. This ability actively to colonise new areas within the breeding range is difficult to explain on traditional theories of colonial breeding in seabirds. Such theories hold that there is a strong tendency for seabirds to recruit to the colony of their birth. Such a tendency has been noted for a diverse list of species, for example in Southern Giant Petrels (Carrick and Ingham 1969), Red-billed Gulls (Mills 1973), Manx Shearwaters (Perrins, Harris and Britton 1973), Sooty Terns (Harrington 1974) and Royal Penguins (Warham 1975). A number of investigators have noted a similar tendency in Herring Gulls (Gross 1940, Paynter 1947, Paludan 1951, Tinbergen 1953, Olsson 1958, Drost *et al.* 1961).

Tinbergen (1953) discussed natal site tenacity in Herring Gulls and concluded "whereas in winter birds may wander over an area covering many breeding colonies, it seems unlikely that many Herring Gulls breed far from their home (i.e. natal) colony." (p. 84). He further suggested that the tendency of this species to return to the place in which it was born has important implications on the process of speciation, "because it means that a species may be composed of many populations, which, though they are mixing outside the breeding season, interbreed scarcely if at all. In other words, they may be reproductively isolated from each other ......" (p. 86).

The present study of Herring Gull recruitment to the Isle of May colony indicates that the majority (up to 70%) of surviving birds of recruitment age did not return to breed at their natal colony. Duncan and Monaghan (1977) observed the presence of Isle of May birds at other Firth of Forth island colonies; since these birds were observed in the breeding season (April - September) it is probable that many of these gulls had established breeding sites at these colonies. A similar situation was found by Spaans (1971) to exist for Herring Gulls breeding at colonies on the Dutch Frisian Islands. Spaans analysed recoveries of birds ringed at these Dutch colonies over the 1950-1968 period. This analysis revealed that in four colonies out of six the percentage recovery of natal birds was below 30%. In total he recaptured 337 ringed birds of which 131 (39%) were breeding on their natal colony.

Ludwig (1963) reported the results of a long-term ringing programme of Herring Gulls breeding at colonies in Lakes Huron, Michigan and Superior in North America. In this study, 60,000 chicks were ringed over a 32 year period of which 47 ringed breeding adults were recovered. He found that 40% were breeding at their natal colonies, 32% in the same general area to the natal colony (i.e. in adjacent colonies in the natal lake) and 28% were in a different area to the natal colony.

Both Spaans and Ludwig thought their results were exceptional and not typical of the species. Spaans attributed a low rate of return to the natal colony to the fact that his study colonies had been subject to a history of human disturbance (in the form of egg collecting). Ludwig pointed to the fact that many of his lake island colonies were physically unstable from one year to the next; this environmental instability was predominantly due to fluctuations in water levels. Over the time span of the present study the factors detailed by Spaans and by Ludwig were of little if any importance on the Isle of May colony. In common with the present study these workers did not make the assumption that all birds breed at their natal colony. When some attempt is made to account for recruiting age classes from life table considerations, or when searches are undertaken for ringed birds breeding outside the natal colony, it appears that the assumption of complete or high natal colony faithfulness in Herring Gulls is an unwarranted one.

Interestingly, where similar studies have been made of some other species, a similar conclusion emerges. Nelson (1978) has presented evidence for considerable colony interchanges made by Gannets in Britain. Southern (1967, 1977) and Ludwig (1974) have clearly established that the majority of Ring-billed Gulls breeding on island colonies in the North American great lakes do not breed at their colony of birth, although the majority breed at colonies in the natal lake (Ludwig 1974). In a recent study of the breeding ecology of Manx Shearwaters, Brooke (1978) presented evidence of regular interchanges of recruits between the two neighbouring island colonies of Skokholm and Skomer. He estimated that approximately 50% of female Shearwaters emigrated and did not breed at their natal colony. The finding that many Herring Gulls do not return to breed at the colony of their birth is not surprising in the light of the current status of this species; indeed this must be so in order that new colonies become established.

The advantage that birds gain by returning to breed at the colony of birth lies presumably in their knowledge of the local physiographic conditions that pertain to that colony and a knowledge of the location of food sources near to the colony. Such knowledge must be an important factor in increasing the chances of successful breeding. However, the majority of Herring Gulls born on the Isle of May bred at colonies other than the natal one and it seems that local colony knowledge is readily acquired by birds during the first few years of life. Parsons and Duncan (1978) analysed the recoveries of Herring Gulls ringed on the Isle of May and found a wide range of dispersal in the first two years of life. They noted that the majority of recoveries were found along a 240km stretch of the east coast from the Firth of Tay to Teesside and 120km westward from the Isle of May to the Firth of Clyde. In dispersing over such a wide area it seems likely that birds are able to assess conditions at a variety of colonies and that much of the knowledge pertaining to colony conditions is acquired during the first two years of life.

On the Isle of May, males were much likelier to return to the colony and sub-colony of birth than were females. This is also true of Red-billed Gulls (Mills 1973) and Manx Shearwaters (Brooke 1978) and may be a common phenomenon in species where the male plays a more important role than the female in securing a breeding territory. Greenwood and Harvey (1976) explained the high degree of philopatry in male Blackbirds in the

the following terms. The male maximises his chances of obtaining a territory by returning to the natal area where breeding territories already exist and where he is familiar with the spatial and temporal variations in resource availability. The female benefits from dispersal since she therefore avoids any deleterious effects (to her offspring) of inbreeding which would result if she was as faithful to the natal area as her male relatives. By dispersal she is also able to exercise a choice of breeding area and of mate when she does eventually settle to breed. Such an explanation is broadly acceptable for Herring Gulls breeding on the Isle of May.

The most usual biological definition of a population is in terms of a closed gene pool. For example, Mayr (1970, p. 82) "all members of a population share in a single gene pool ..... such a population may be defined as a group of individuals so situated that any two of them have an equal probability of mating with each other and producing offspring." If Mayr's definition is accepted, then clearly the research carried out as part of the present study was not concerned with an identifiable population of Herring Gulls. A more useful term than population is provided by the concept of a 'stock'. For the Grey Seal (*Halichoerus grypus* Fabricus) and the Common Seal (*Phoca vitulina* Linnaeus), Bonner (1976) has defined the term stock as a group breeding in one area whose members have a greater (rather than equal) chance of breeding with each other than with members of some other group. In this sense a colony is a local aggregation of stock members at a particular site for breeding.

This study has shown that recruits are attracted to situations where nesting densities are high and where resident gulls are breeding successfully. These are the conditions where severe competition takes place for available nest sites and where recruitment rates of three, four and five year old birds can be accelerated by the removal of resident site-holders. In the case of the Isle of May there is evidence that colony size is determined by socially induced recruitment rates (as Wynne-Edwards suggested). However there is no evidence for the homeostatic regulation of stock sizes in the collection of stocks that constitute the British Herring Gull population. In the case of the stock to which the Isle of May contributes it seems that clutch sizes correspond to the maximum number of young that can be successfully raised and that breeding occurs as soon as possible (i.e. as Lack suggested, that productivity is maximal).

SUMMARY

1. Aspects of the breeding biology of the Herring Gull were studied on the Isle of May between 1972 and 1974. Particular attention was paid to the effects of parental age on breeding and to the factors which might determine recruitment rate to the colony.

2. Breeding birds were culled between 1972 and 1974. Culling resulted in the recovery of many gulls which had been ringed as chicks on the Isle of May during the 1966-1969 period. In 1972 the cull reduced nesting densities on five sub-colonies by 40% and by a further 28% in 1973.

3. Eggs were laid over a 38 (in 1972) and a 40 (in 1973) day period and in both years the median laying date was 16 May. There has been little variation in median laying dates on the Isle of May since 1966. In 1972 some females delayed laying; it seems likely that this delay was a response to adverse weather conditions in the first half of May.

4. Median laying date advanced with increasing female age. Four year old gulls laid 11 days later than the overall colony median date and five year old birds advanced their laying by six to nine days.

5. In the present study, as in other studies of the Herring Gull, the most commonly recorded clutch size was three eggs per female (c.3). At other colonies, predation, food availability and disturbance have been noted as factors which can result in a decrease in recorded clutch size.

6. Four year old breeders rarely laid c.3s. Clutch size increased with age and past breeding experience of the female. Mean clutch sizes for four, five, six and seven year old birds were 1.71, 2.18, 2.43 and 2.74 eggs per female respectively. There was a close, linear relationship between

mean clutch size and age of female and there was probably little increase in clutch size after birds had reached their eighth summer. The mean clutch size of recruit females (2.15) was significantly smaller than that for females which had bred at least once before (2.55).

7. There was a decrease in the size of clutches laid as laying date progressed. Seasonal influences decreased mean clutch size by as much as 0.47 eggs per female. The size of clutches laid late in the breeding season by birds of known age also decreased and clutches laid by experienced breeders were larger than those laid by inexperienced breeders in equivalent time periods. The decrease in mean clutch size attributable to laying date was larger for recruits (0.67 eggs per female) than for experienced breeders (0.43 eggs per female). The effects of laying date, parental age and experience resulted in smaller clutches being laid later.

8. For all eggs laid, regardless of clutch size, egg volume increased with the age of the laying female. The smallest eggs were laid by four year old birds and the largest were laid by adult-ringed birds (with minimum ages in 1972 and 1973 of six and seven years). There was little evidence to suggest that egg volumes increased after birds had reached their seventh year, nor was there any evidence that older birds laid smaller eggs. For c.3 and c.2 clutches the increase in clutch volume with age was not attributable to any one egg, but rather to changes in all eggs laid. Eggs laid as c.1s showed the lowest increase in volume with age.

9. The increases in egg volume with age were due to older birds laying broader eggs. Egg lengths could decrease with age.

10. There was a significant correlation between egg breadth and the breadth of the corresponding brood patch, but no significant correlation between brood patch length and egg length. The observed relationship between

brood patch and egg breadths may result from the side-to-side movements performed by parents during incubation. The differences between brood patch length and egg length were significantly larger than those between brood patch breadth and egg breadth. Thus eggs which are short and broad will be better incubated than eggs of equivalent volume which are long and narrow.

11. For eggs laid as c.1 clutches, shape indices increased with increasing parental age. However, there was no consistent pattern of variation in shape indices with age for eggs laid in c.2 and c.3 clutches.

12. In 1972, eggs laid on East Tarbet were significantly broader than eggs laid on Colm's Hole. This suggests that the average age of breeding birds on Colm's Hole was lower than that for East Tarbet.

13. The volumes of eggs laid by four year old females showed little variation. In comparison to other age classes, eggs laid by four year old females were uniformly small. The greatest variability in egg volume was found in eggs laid by five year old females and was attributable to small c-egg volumes. Variability in egg volumes decreased up to the age of six years as the c-egg volumes approached those of the a- and b-eggs. For females older than six years there was an increase in the variability of egg volumes. This was attributable to larger a-eggs being laid by older birds. The changes in egg volume with parental age were paralleled by changes in the variability of egg breadths.

14. For females aged between five and seven years laying c.3 clutches there was a decrease in the within clutch variance of egg breadths.

15. In an unringed group of breeding adults there was a marked decrease in the volumes of eggs laid in c.1, c.2 and c.3 clutches as the breeding season progressed. The largest decrease in volume occurred in the c-eggs

of c.3 clutches. The volumes of eggs laid by birds of known age also decreased as the breeding season progressed. The largest seasonal decline was evident for the oldest birds. Over most of the egg laying period eggs laid by four and five year old females were smaller than those laid by birds that were over the age of five years. However, all eggs laid after 27 May were similar in size, regardless of parental age. Whatever factors resulted in diminished egg volumes by late-May, they operated in recruit and experienced breeders alike.

16. 66% of eggs laid on East Tarbet in 1972 hatched successfully. Hatching success varied with clutch size and was highest in c.3 clutches. Eggs laid by the oldest birds had the highest hatching success, but the hatching success of eggs laid as c.1 clutches was poor regardless of parental age. For breeding gulls older than four years, and for the control group of adults, the single largest known cause of hatching failure was egg loss through predation. The proportion of hatching failures attributable to predation was highest in gulls older than five years. 50.9% of hatching failures in four and five year old parents was attributable to behavioural inadequacies (addled eggs and chicks dead on hatching). In comparison only 15.1% of hatching failures in eggs laid by parents over the age of five years was due to poor incubation and brood care.

17. The mean hatching dates for eggs laid by four, five and six year old females were 21.67 ± 3.28, 14.90 ± 1.22 and 13.25 ± 1.11 in June. Chick survival was followed to 28 days after hatching; thereafter pre-fledging survival was inferred from ring recoveries. On East Tarbet a single cannibal Herring Gull accounted for 2.5% of the total chick mortality on this sub-colony. A further 4.1% of chicks died in heavy rains during July. A large proportion of chicks (16%) disappeared without trace.

18. There was no significant relationship between chick survival and brood size.

19. The percentage survival of chicks raised by experienced parents (older than five years) was higher than that of chicks raised by inexperienced younger parents (four and five years old), although this difference was not significant. For young parents a major cause of chick mortality was poorly executed reproductive behaviour. In older parents, territorial behaviour of surrounding adults was a more important mortality cause.

20. Within the first 28 days after hatching, the growth rates of chicks varied with hatching sequence. Regardless of parental age the last hatched chick in broods of three grew at a slower rate than first or second hatched young. Chicks raised by the most experienced parents (adult-ringed) had the highest growth rates. There was no relationship between chick growth rates and brood size.

21. Growth rates of non-surviving chicks in the first nine days after hatching were lower than those of chicks surviving past nine days. It is suggested that an important factor determining chick survival within this period was the ability of the parents to feed their young adequately.

22. 8% of chicks ringed were recovered dead before fledging. 31% of eggs laid gave rise to fledged young. Breeding success increased with age. The reproductive rate of parents aged four and five years was 0.40 young/pair. In comparison, parents over the age of five years raised 0.79 young/pair.

23. On the North Ness sub-colony most study nests were at high densities. Proportionately fewer chicks survived to fledging from nests at high densities than from nests at medium densities. This difference was

partly due to higher chick mortality resulting from territorial encounters between straying chicks and the surrounding adults (for chicks aged 10 days and older). On East Tarbet where most study nests were at medium densities, there was little difference in breeding success at high and medium nest densities. Birds breeding at low densities had the poorest breeding success. This was probably because the majority of birds at these densities were recruits. The majority of four and five year old gulls nested at low densities.

24. The numbers of Herring Gulls at the majority of British and Irish colonies are increasing. A typical rate of increase lies between 2.5 and 17.5% per annum. The pre-cull population on the island in May 1972 was 12,950 pairs. On the unculled study areas the number of gulls increased by 20% in late-July. Increasing the total pre-cull population by 20% gives a predicted population in 1972 of 15,540 pairs. The annual rate of increase for Isle of May Herring Gulls is calculated to be 14.3%. For the unculled study areas of East Tarbet the rate of increase was 16% between 1972 and 1973.

25. From the numbers of colour-ringed adults known to be alive in 1972 the annual adult survival rate was calculated to be 0.935 ± 0.100. The average expectation of further life is therefore 14.9 years.

26. For birds ringed as pre-fledging young in 1966, 1967 and 1968, the first year survival rates are 0.83, 0.83 and 0.67 p.a. The expectation of further life in each case is 5.4 and 2.5 years.

27. From cull recoveries of ringed birds it was evident that recruitment to the colony (establishing territory) could take place between the ages of four and seven years. However, most birds had recruited by their fifth year of life. Over the 1972-74 period, 34% of four year old, 40% of five year old, 18% of six year old, and 8% of seven year old gulls recruited to the

colony. The mean age of recruitment was 5.00 years. Not all birds that established territories laid eggs in the same year. The mean age of first breeding was 5.25 years.

28. For a closed population (no immigration or emigration) there is close agreement between the calculated rates of adult and immature survival (0.935 and 0.83), the observed rate of population increase and known reproductive rates. A first year survival rate of 0.67 implies a lower rate of population increase.

29. Between 27-30% of surviving gulls returned to breed at their natal colony. The majority of surviving Isle of May gulls breed at other colonies.

30. 66% of ringed birds culled were recovered on their natal sub-colony. This deviated markedly from a random return to areas within the colony and indicated a strong philopatric tendency. Philopatry was most marked in five year old recruits. 51% of gulls that did not recruit to the natal sub-colony were recovered from an adjacent area.

31. 84% of adults were found in the sub-colony of ringing. There appeared to be little interchange between sub-colonies once recruitment had taken place.

32. The sex ratio in a culled sample of adults did not differ significantly from equity. Neither was there a significant change in sex ratios for three ringed cohorts as recruitment proceeded. There was therefore no evidence to suggest either a difference between male and female survival rates nor a difference between the sexes in the age of recruitment.

33. The total sample of ringed birds recovered in the cull contained more females than males (1.00 males to 1.34 females). 77% of males and 54%

of females were recovered on the natal sub-colony. It seems that more females than males bred at colonies or sub-colonies other than the natal one.

34. Recruits were more attracted to sub-colonies in which numerical increases in breeding gulls had occurred as a result of increases in nesting density rather than changes in spatial distribution. However, there was no significant correlation between the numbers of gulls recruiting to the natal sub-colony and sub-colony nesting density. On South Ness, previous egg robbing may have decreased the attractiveness of the natal sub-colony to recruits.

35. More recruits were attracted to cleared areas in the centre of a sub-colony than to an equivalent area on the edge of the sub-colony. Nests at the centre were more aggregated than at the edge and it seems that nest spacing was important in determining recruitment rates. A comparison of an intensively culled area with one in which no culling had taken place indicated that more recruits were attracted to the unculled area where birds bred successfully and nest densities were high. However, only 19% of recruits to the unculled area established territories in comparison to 71% of the recruits to the culled area. Thus the greater attraction of undisturbed, high density areas may have been counterbalanced by the difficulties that recruits experienced in establishing territories.

36. In 1972, cull ring recoveries indicated differences in the age composition of gulls breeding on different sub-colonies. The recently expanding sub-colonies of North and South Plateaus contained proportionately higher numbers of four and five year old breeders than did the Rona and east coast sub-colonies, viz. sub-colonies on which the numbers of breeding gulls had probably increased by increases in nesting density.

37. A comparison of pre- and post-cull census counts on East Rona indicated much greater increases in the numbers of recruits to this area than was the case on the unculled study areas. This increase in recruitment was most evident for three and four year old birds and was probably a direct result of culling.

38. Sub-colonies culled for the second time in 1973 had between two and four times as many recruits as did those culled for the first time in 1973. Most of the recruitment from three and four year old birds was concentrated on Rona and the east coast.

39. Males were heavier than females, and in both sexes body weight increased with age. Females had the greatest variability in body weight and this was largely due to the heavier weights of birds about to lay eggs.

40. Wing lengths increased with age by 4% in males and 3% in females. However, considerable primary abrasion takes place as a result of territorial behaviour and wing length may not be the best indicator of body size.

41. Neither bill length nor bill depth changed with age and it seems unlikely that there was continued growth in body size from the third year of life onwards.

42. At maximum, overt fat storage reached 1.5% and 1.2% of the body weights of males and females. The variability in mean fat index was high. Three and four year old gulls were more likely to belong to a higher fat class than older birds. The lowest mean fat index occurred in five year old birds and coincided with the time when birds in this age class were actively establishing territories.

43. Females had significantly lower wet weights of pectoral muscle than males. There was a significant increase in mean relative weight of pectoral muscle with age in both sexes.

44. Brood patches began to develop in April, reached a maximum size in late-May and early-June and had begun to refeather in July. Four year old gulls had significantly smaller brood patches than six year old birds, and five year old gulls had smaller brood patches than those aged seven years. The increases in brood patch area between successive age classes were small and indicated slight changes in gonadotrophic secretion.

45. 33% of three year old birds had no brood patches when culled in May 1973 and it seems unlikely that these birds would have laid eggs in that year. Brood patch development was less well advanced in four year old birds culled in 1972 than for this age class culled in 1973. This difference in development may have been the result of the creation of partially cleared areas by previous culling into which young birds could recruit.

46. Testes reached their maximum weight in mid-May and had regressed by the end of July. Testes weight and development were greatest in the oldest males. In May, three and four year old males had the least developed tests.

47. There was no significant difference between mean testes weights in four year old males culled in 1972 and 1973. Testes weights in males of known age were lower on previously culled areas than on areas culled for the first time in 1973. In four year old males this difference reflected differences in spermatogenic activity. 73% of males that had not attained breeding condition were from previously culled areas. The interaction between male recruits and established breeders may have been an important factor in the attainment of reproductive condition.

48. Testes development and brood patch development were not correlated. This indicated the involvement of separate endocrine control mechanisms.

49. Six and seven year old males on unculled areas had larger testes than those on previously culled areas. However, there was no evidence to suggest gonadotrophin deficiencies in these age classes of males.

50. The factors which might determine recruitment rates and therefore population size are discussed. It is suggested that deferred maturity in Herring Gulls is a necessary period for maturation changes and learning processes to take place. Recruitment rates to the Isle of May colony were influenced by competition for nest sites between resident breeders and recruits (as Wynne-Edwards suggested). However, for the British population productivity appears to be maximal and there is no evidence for the homeostatic regulation of population size by means of socially determined recruitment rates.

Appendix 1 Scientific names of species referred to in text

Blackbird	*Turdus merula* (Linneaus)
Buller's Mollymawk	*Diomedea bulleri* (Rothschild)
Canary	*Serinus canaria* (Linnaeus)
Cassin's Auklet	*Ptychoramphus aleuticus (Pallas)*
Chaffinch	*Fringilla coelebs* (Linnaeus)
Domestic Hen* (Domestic Fowl)	*Gallus domesticus* (Bechstein)
Dunlin	*Calidris alpina* (Linnaeus)
Eagle, Spanish Imperial	*Aquila heliaca* (Savigny)
Fulmar	*Fulmarus glacialis* (Linnaeus)
Gannet	*Sula bassana* (Linnaeus)
Goosander	*Mergus merganser* (Linnaeus)
Grouse, Red	*Lagopus Lagopus scoticus* (Latham)
Gull, Black-headed	*Larus ridibundus* (Linnaeus)
California	*L. californicus* (Lawrence)
Common	*L. canus* (Linnaeus)
Glaucous-winged	*L. glaucescens* (Naumann)
Greater Black-backed	*L. marinus* (Linnaeus)
Herring	*L. argentatus* (Pontoppidan)
Lesser Black-backed	*L. fuscus* (Linnaeus)
Red-billed	*L. novaehollandiae* (Stephens)
Ring-billed	*L. delwarensis* (Ord)
Southern Black-backed	*L. dominicanus* (Lichtenstein)
Guillemot	*Uria aalge* (Pontoppidan)
Kittiwake	*Rissa tridactyla* (Linnaeus)

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* Not a distinct species, but a domesticated form of the Red Jungle Fowl, *Gallus gallus* (Linnaeus)

Appendix 1 (continued)

Lapwing	*Venellus vanellus* (Linnaeus)
Oystercatcher	*Haematopus ostralegus* (Linnaeus)
Penguin, Adelie	*Pygoscelia adeliae* (Hombron and Jacquinot)
Royal	*Eudyptes chrysolophus* (Brandt)
Yellow-eyed	*Megadyptes antipodes* (Hombron and Jaquinot)
Petrel, Storm	*Hydrobates pelagicus* (Linnaeus)
Pigeon (Feral or Rock Dove)	*Columba livia* (Gmelin)
Pigeon, Wood	*C. palumbus* (Linnaeus)
Ptarmigan, Rock	*Lagopus mutus* (Montin)
Puffin	*Fratercula arctica* (Linnaeus)
Quelea, Red-billed	*Quelea quelea* (Linnaeus)
Razorbill	*Alca torda* (Linnaeus)
Sandpiper, Least	*Calidris minutilla* (Vieillot)
Shag	*Phalacrocorax aristotelis* (Linnaeus)
Shearwater, Manx	*Puffinus puffinus* (Brunnich)
Short-tailed	*P. tenuirostris* (Temminck)
Shrike, Great Grey	*Lanius excubitor* (Linnaeus)
Sparrow, House,	*Passer domesticus* (Linnaeus)
Tree	*P. montanus* (Linnaeus)
Teal, Green-winged	*Anas crecca* (Linnaeus)
Tern, Arctic	*Sterna paradisaea* (Pontoppidan)
Common	*S. hirundo* (Linnaeus)
Roseate	*S. dougallii* (Montagu)
Royal	*S. maxima* (Boddaert)
Sandwich	*S. sandvicensis* (Latham)
Sooty	*S. fuscata* (Linnaeus)
Tit, Great	*Parus major* (Linnaeus)
Wryneck	*Jynx torquilla* (Linnaeus)

Appendix 2 The numbers of seabirds (numbers of pairs) breeding on the Isle of May from 1936 to 1970. (Mostly taken from Appendix 1. Anon, 1972)

	Year of census			
	1936	1946	1954	1970
Herring Gull	455	700	3,000	14,000
Greater Black-backed Gull	0	0	0	4
Lesser Black-backed Gull	7	75	200	2,000
Common Tern	3,400	5,000	150	0
Arctic Tern	800	500	150	0
Sandwich Tern	4	1,500	100	0
Roseate Tern	0	15	3	0
Guillemot	2,000	-	-	4,500
Razorbill	500	350	350	170
Puffin	50	20	7	2,000
Kittiwake	2,950	-	2,000	3,100
Shag	10	12	150	900
Fulmar	6	7	26	46
Eider	32	20	70	100

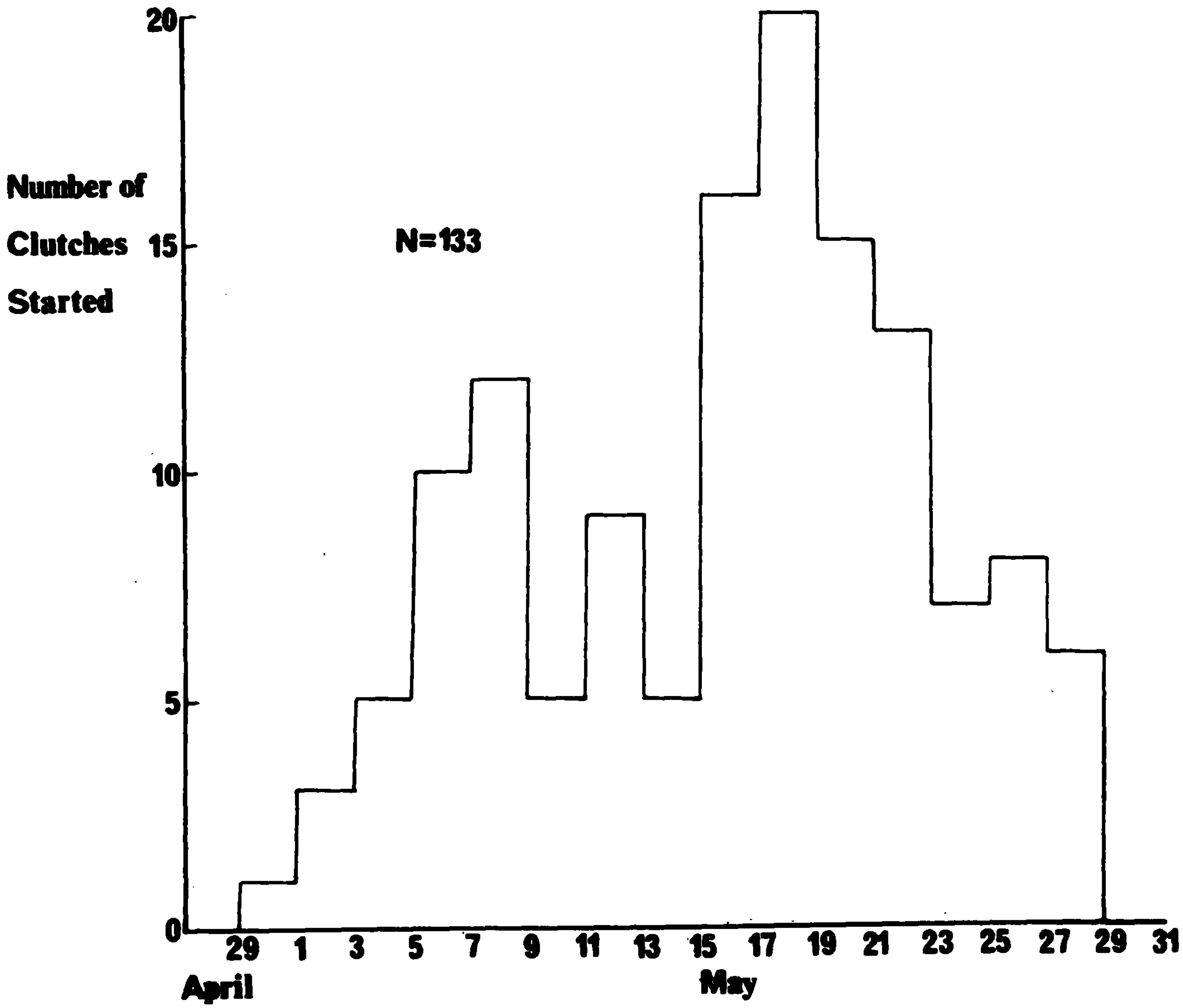
Appendix 3 The numbers of Herring Gulls counted on sub-colonies of the Isle of May

	20 July to 25 July 1972	10 July to 20 July 1973
	Number of gulls counted	
Sub-colony		
North Ness	2,800	1,779
Rona	2,010	1,448
East Tarbet	1,218	1,488
Burrian Rocks	322	157
Island Rocks	470	333
South Plateau	480	416
North Plateau	620	478
South Ness	5,200	2,165
Peripheral *	712	606
Island Total	13,832	8,870

* Rocks lying off the south (Maiden's Hair) and east (Middens and Clett) coast of the Isle of May

Appendix 4

The dates on which clutches were started on the Colm's Hole study area in 1972


Number of
Clutches
Started
N=133
0
5
10
15
20
29
1
3
5
7
9
11
13
15
17
19
21
23
25
27
29
31
April
May

Appendix 5 Egg measurements made for clutches laid on the East Tarbet study area in 1972 and 1973

		Laying (sequence)	Mean length (mm) ± S.E.	Mean breadth (mm) ± S.E.	Mean volume (cm^3) ± S.E.	Shape index (I)	Number of clutches
1972	c.1 clutches		69.53±0.62	48.12±0.26	76.71±1.20	69.2	20
	c.2 clutches	a	68.76±0.36	48.03±0.22	75.57±0.78	69.9	52
		b	66.58±0.36	47.01±0.27	70.17±0.87	70.6	
	c.3 clutches	a	69.31±0.29	48.75±0.16	78.56±0.69	70.4	97
		b	68.48±0.29	48.36±0.14	76.32±0.61	70.6	
		c	66.75±0.25	46.91±0.16	69.14±0.91	70.3	
1973	c.1 clutches		68.15±0.59	48.17±0.24	75.26±0.78	70.7	24
	c.2 clutches	a	68.98±0.38	47.96±0.23	75.70±0.89	69.5	54
		b	67.56±0.45	47.27±0.31	72.17±1.24	70.0	
	c.3 clutches	a	69.50±0.22	48.76±0.13	78.92±0.52	70.2	170
		b	68.89±0.21	48.56±0.11	77.00±0.51	70.5	
		c	66.59±0.18	47.19±0.12	70.87±0.46	70.9	

Appendix 6 The effects of laying date on mean volumes of eggs laid by Herring Gulls of known age in 1972 and 1973

Age (years)	Clutch size	Laying sequence	Date on which clutches started				
			up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May
4	1		N.L.	N.L.	N.L.	71.21 (1)	70.09 (2)
	2	a	N.L.	N.L.	N.L.	71.38 (2)	70.50 (1)
		b	N.L.	N.L.	N.L.	68.65 (2)	66.55 (1)
	3	a	N.L.	N.L.	72.64 (1)	N.L.	N.L.
		b	N.L.	N.L.	68.29 (1)	N.L.	N.L.
		c	N.L.	N.L.	64.97 (1)	N.L.	N.L.
5	1		N.L.	N.L.	72.92±2.57 (3)	70.96±0.20 (3)	67.79±2.80 (5)
	2	a	N.L.	N.L.	73.37±2.33 (10)	73.48±1.32 (10)	72.56±2.27 (7)
		b	N.L.	N.L.	68.69±1.28 (10)	68.52±1.39 (10)	67.26±1.70 (7)

Appendix 6 (continued)

Age (years)	Clutch size	Laying sequence	Date on which clutches started				
			up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May
	3	a	N.L.	75.09±0.13 (2)	74.46±2.55 (8)	71.58±1.53 (15)	N.L.
		b	N.L.	74.90±0.87 (2)	73.59±2.57 (8)	68.32±1.58 (15)	N.L.
		c	N.L.	69.55±0.55 (2)	67.79±2.53 (8)	61.72±1.40 (15)	N.L.
6	1		N.L.	78.6 (2)	71.27 (3)	71.63±1.36 (10)	69.05 (1)
	2	a	N.L.	75.58 (1)	77.15±2.59 (6)	74.40±1.31 (24)	70.82 (1)
		b	N.L.	75.36 (1)	76.21±3.43 (6)	71.85±1.50 (24)	68.49 (1)
	3	a	N.L.	81.50±1.21 (6)	77.07±1.21 (22)	75.55±1.74 (19)	71.81 (3)
		b	N.L.	76.18±1.89 (6)	74.52±1.40 (22)	74.07±1.78 (19)	69.83 (3)
		c	N.L.	72.39±1.60 (6)	68.14±2.05 (22)	67.66±1.60 (19)	65.50 (3)

Appendix 6 (continued)

Age (years)	Clutch size	Laying sequence	Date on which clutches started				
			up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May
7	1		N.L.	N.L.	N.L.	72.25 (3)	N.L.
	2	a	N.L.	N.L.	79.07 (1)	75.23 (4)	N.L.
		b	N.L.	N.L.	67.98 (1)	69.95 (4)	N.L.
	3	a	87.09 (2)	85.56±1.02 (5)	77.23±1.13 (10)	75.51±1.07 (8)	75.50 (3)
		b	82.11 (2)	82.00±1.67 (5)	75.22±1.47 (10)	74.55±1.00 (8)	74.12 (3)
≥ 6	1		N.L.	N.L.	79.51 (1)	76.92 (1)	N.L.
	2	a	N.L.	N.L.	78.10 (2)	77.09 (3)	N.L.
		b	N.L.	N.L.	74.94 (2)	71.09 (3)	N.L.

Appendix 6 (continued)

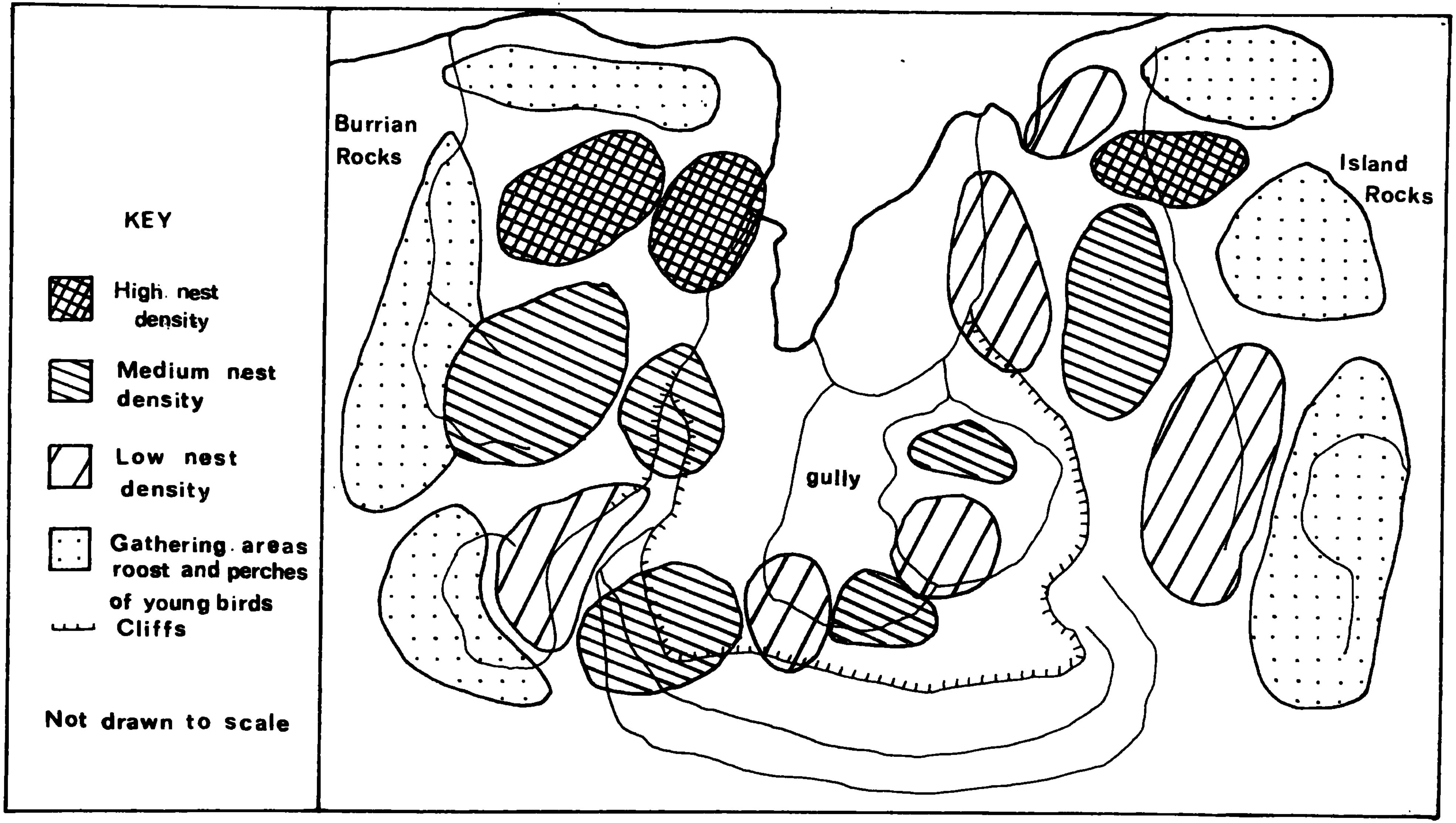
Age (years)	Clutch size	Laying sequence	up to 2 May	3-10 May	11-18 May	19-26 May	after 27 May
> 6	3	a	N.L.	87.62±2.15 (6)	76.54±2.04 (7)	75.07 (4)	70.69 (1)
		b	N.L.	76.15±3.73 (6)	76.83±1.22 (7)	74.42 (4)	70.33 (1)
		c	N.L.	71.92±3.20 (6)	70.03±1.55 (7)	67.45 (4)	66.41 (1)

N.L. No clutches laid. All mean egg volumes are in cm^3 and ± S.E. where the sample size is five or larger

Sample sizes are given in brackets.

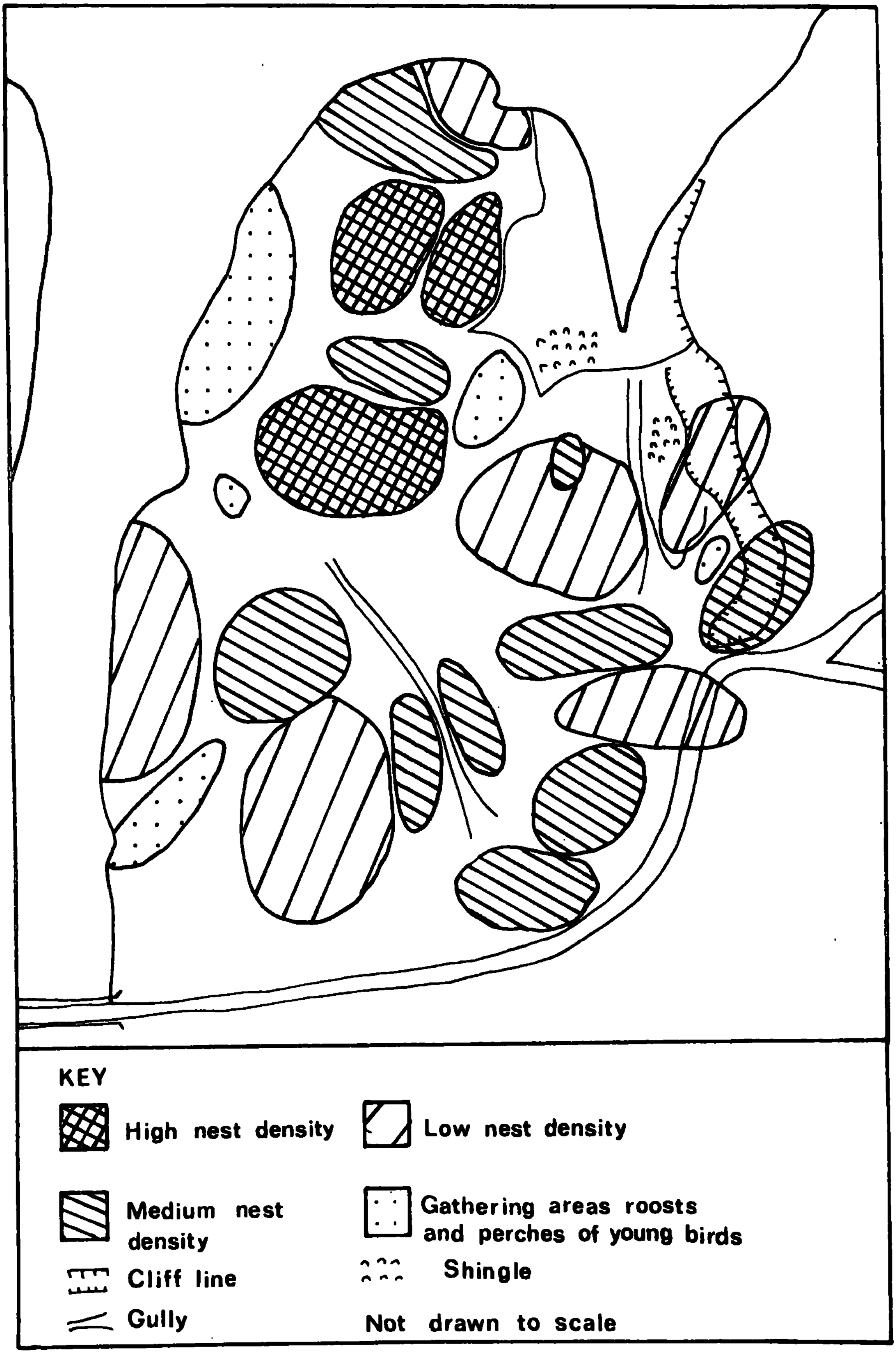
Appendix 7

The distribution of areas of high, medium and low nesting density on the Colm's Hole study area in 1972


Burrian Rocks
Island Rocks
gully
KEY
High nest density
Medium nest density
Low nest density
Gathering areas roost and perches of young birds
Cliffs
Not drawn to scale

Appendix 8

The distribution of areas of high, medium and low nesting density on the East Tarbet study area in 1972



KEY
High nest density
Low nest density
Medium nest density
Gathering areas roosts and perches of young birds
Cliff line
Shingle
Gully
Not drawn to scale

Appendix 9 The numbers of breeding Herring Gulls counted on the Isle of May between 1907 and 1972

Year of census	Number of breeding pairs	Authority
1907	1	Baxter and Rintoul (1925)
1914	12	Isle of May, special notes *
1921	35	" " " "
1924	58	" " " "
1936	455	" " " "
1947	760	" " " "
1951	1,125	" " " "
1952	1,750	" " " "
1953	3,300	" " " "
1954	3,000	" " " "
1957	2,700	Eggeling (1960)
1964	8,000	Isle of May, special notes
1966	7,000	" " " "
1967	12,000	Parsons (1971a)
1970	14,000	Coulson and Emmerson (unpublished data)
1972	15,540	This study

* The Isle of May special notes consist of a series of observations and census counts of breeding species made by visitors to the Isle of May bird observatory.

Appendix 10 Plumage descriptions of Herring Gulls of known age

Plumage of three year old gulls

Four ringed Herring Gulls in their third year of life were examined. Two (ringed as pulli in 1969) were shot in June 1972 and two (ringed in 1970) were shot in July of the following year. Although no ringed three year old birds were culled in either year, such birds were sighted on the edges of sub-colonies in 1972 and on culled areas in 1973. Three year old Herring Gulls were similar in plumage and could be readily distinguished from other age classes.

The characteristic slate-grey mantle, white breast and belly of adults were also present in three year old gulls, although the four birds examined had some brown markings in these areas. Tail coverts and retrices had prominent dark brown markings. Retrices were white proximally and became progressively darker distally, so that a brown band is formed running across the tip of the tail.

The most obvious plumage differences between three year old birds and adults were found in the wing coverts and remiges. Three year old gulls had obviously brown primaries, although the amount of brown present was variable. Primaries 1-6 (where 1 = bastard primary) were dark brown, while the remaining primaries (7-11) were white. The leading edges of all secondaries were prominently brown, whilst the trailing edges were grey with a brown tinge although the latter was not an obvious feature. Primary coverts were markedly brown with the amount of brown increasing towards the distal tip of the feathers. The feathers forming the greater coverts had brown leading edges and there was slight brown colouration on the median coverts and tertials.

In addition, three year old birds had dark brown markings on the upper and lower mandibles, although the amount of brown colouration and its distribution were variable.

Plumage of four year old gulls

22 four year old gulls were examined; all had been culled in May (20 birds ringed in 1968 culled in 1972, and two birds ringed in 1969 and culled in 1973). None of these birds had any brown markings on the mantle, breast or belly. The tail coverts were typically adult (grey) although in three (14%) cases these feathers had slight traces of brown on them. As with the three year old birds, the tips of the retrices in eight (36%) birds were brown, whilst the remaining 14 (65%) birds had all white tails. For those eight birds with brown tails there were also traces of brown on the primary coverts; other four year old gulls had grey primary coverts.

The remiges were not obviously brown as in three year old birds. The most obvious distinguishing plumage feature between four year old birds and adults was in the primary tips. In adults, primaries 2-7 were white proximately and black distally with white tips. Thus the tips of the primaries in a folded wing formed distinct white patches or "mirrors". Although two (9%) four year old gulls had distinctive wing mirrors, in 12 (55%) cases the tips of the primaries were totally black (i.e. no wing mirrors) and eight had very small indistinct mirrors. The absence of mirrors was the most distinctive feature in four year old gulls. Six (27%) birds had traces of brown on the leading edges of primaries 1, 6, 7 and 8, and prominent brown markings on the trailing edges of primaries 3-7.

Two of the four year old birds examined had slight brown markings on the upper mandible; the extent of brown was noticeably less than in three year old birds.

Plumage of five year old gulls

200 five year olds were examined (100 ringed in 1967, culled in 1972, and 100 ringed in 1968, culled in 1973). All these birds had a typically adult mantle (grey), breast and belly (white) with no trace of brown markings. Deviations from the adult condition were noted in the following characters: tail coverts (2, 1%, with brown colouration); retrices (23, 12%, with flecks of brown on the central feather); primary coverts (6, 3%, with brown markings); greater coverts (4, 2%, with brown markings); primaries 2-7 (17, 9%, with brown on the trailing edges); bastard primary (58, 29%, with brown on the leading edge).

The most obvious plumage characters distinguishing five year olds were the wing mirrors. Unlike four year old birds, all five year old gulls had mirrors, but in many cases these mirrors were evidently intermediate between the condition in fourth year birds and the condition in adults (84 birds, 42% of five year olds examined had obviously smaller mirrors than adults).

Adult plumage

Examination of six year old, seven year old and adult-ringed gulls revealed no single reliable plumage character which either distinguished between age classes or between these birds and samples of unringed adults examined. In the 252 ringed birds examined there were some cases where traces of immature wing plumage remained, sometimes on one wing only. Thus five birds (2%) had brown on primaries 2-6 and on the primary coverts, and 24 (10%) had brown on the bastard primary.

On plumage characters alone it was possible to distinguish all three and approximately 80% of four year old and 40% of five year old gulls. Ageing on these characters became increasingly more difficult as birds got older, especially since for characters such as wing mirrors there was overlap between four year old, five year old and adult-ringed gulls. All birds examined were dissected and sexed and there were no evident plumage differences between the sexes for any age class.

Appendix 11 The relationship between fat index and wet weight of visceral and subcutaneous fat deposits in a sample of adult Herring Gulls (culled in 1973)

Fat index	Number of gulls examined	Mean combined wet weight of fat deposits ± S.E. (g)
0	50	0.528 ± 0.053
1	57	1.304 ± 0.144
2	60	2.473 ± 0.248
3	60	3.513 ± 0.319
4	60	5.19 ± 0.413
5	44	8.241 ± 0.624

Appendix 12 The coefficients of variation of body weights and wing lengths for culled Herring Gulls of known age

Year in which ringed as chicks	Age when culled (years)	Year culled	MALES Body weight C.V.*	MALES Wing length C.V.	FEMALES Body weight C.V.	FEMALES Wing length C.V.
1968	4	1972	5.49	2.15	11.26	1.90
	5	1973	6.81	2.98	10.30	2.33
	6	1974	7.54	2.53	8.86	3.31
1967	5	1972	7.79	3.33	8.22	1.06
	6	1973	6.02	1.91	8.65	3.18
	7	1974	6.66	2.41	9.83	1.92
1966	6	1972	7.90	3.79	8.86	2.28
	7	1973	7.76	1.68	9.78	2.33
	8	1974	8.55	2.47	10.20	2.24
1969	5	1974	8.58	2.04	6.72	1.99

* where C.V. = coefficient of variation and is given by: $$\text{C.V.} = \frac{\text{standard deviation of measurements} \times 100}{\text{mean of measurements}}$$

Appendix 13 The coefficients of variation of bill size in Herring Gulls of known age, culled in May 1972-74

Year in which ringed as chicks	Age when culled (years)	Year culled	MALES		FEMALES	
			Bill depth C.V.*	Bill length C.V.	Bill depth C.V.	Bill length C.V.
1968	4	1972	8.43	5.53	3.30	6.16
	5	1973	-	-	-	-
	6	1974	5.00	4.79	3.28	3.26
1967	5	1972	6.49	14.20	4.48	4.90
	6	1973	3.06	4.38	7.68	4.70
	7	1974	4.66	4.57	2.20	4.28
1966	6	1972	6.26	5.24	6.85	4.83
	7	1973	2.59	4.0	3.80	6.35
	8	1974	3.44	4.18	5.44	4.87
1969	5	1974	2.42	1.75	4.47	3.74

* where C.V. is the coefficient of the variation and is given by: $\text{C.V.} = \dfrac{\text{standard deviation of measurements} \times 100}{\text{mean of measurements}}$

Appendix 14 Colour-ringing of Herring Gull pulli on the Isle of May, 1972-1973

W = white Darvic ring

BR = brown Darvic ring

LG = light green Darvic ring

M = B.T.O. monel ring

r = right leg

ℓ = left leg

Area of ringing	Year of ringing	Combinations of rings used	Number of pulli ringed
Colm's Hole	1972	$W/_{M}{}^{\ell}$	283
East Tarbet	1972	$W/_{M}{}^{r}$	390
North Ness	1972	$W/_{M}{}^{r}\ W^{\ell}$	389
General	1972	$W/_{M}{}^{\ell}\ W_{r}$	177
		$\frac{LG}{M}{}^{\ell}\ \ LG_{r}$	109
S.E. Rona	1973	$BR/_{M}{}^{\ell}$	119
East Tarbet	1973	$M_{r}BR_{l}$	666
General	1973	$\frac{BR}{M}{}^{r}$	238

These totals exclude chicks raised by parents of known age. Young reared by five year old parents were ringed $M_{r}W_{\ell}$ (1972) and $\frac{BR}{M}r.BR_{l}$(1973), and for six year old parents the ringing combinations were $M_{\ell}W_{r}$ (1972) and $M_{\ell}BR_{r}$ (1973).

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