Aspects of the biology of the herring gull (larus atgentatus pont.)

Duncan, W. N. M.

How to cite:

Duncan, W. N. M. (1978) *Aspects of the biology of the herring gull (larus atgentatus pont.)*, Durham theses, Durham University. Available at Durham E-Theses Online: http://etheses.dur.ac.uk/8290/

ASPECTS OF THE BIOLOGY OF THE HERRING GULL

(*Larus argentatus* Pont.)

W.N.M. Duncan, B.Sc. (Aberdeen)

A thesis presented in candidature for the degree of
Doctor of Philosophy in the University of Durham, 1978

CONTENTS

page number

page number

page number

6. MOVEMENTS OF GULLS FROM THE NATAL COLONY

7. ASPECTS OF POPULATION DYNAMICS (II), AGE

8. BREEDING BIOLOGY

9. ASPECTS OF CHICK FLEDGING SUCCESS AND POPULATION DYNAMICS

10. EFFECTS OF DENSITY ON RECRUITMENT

Plate 1.

1. Nesting herring gulls on the Isle of May.

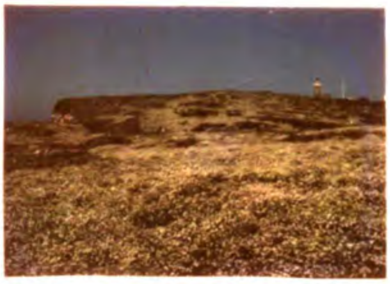
2. The South Plateau on the Isle of May. Note the extensive *Silene maritima* sward in the foreground.

3. The view into the gull colony from the top of Tarnbrook. The colony extends to the skyline.

4. The East Tarbet study areas on the Isle of May.

Plate 1

1



2

3

4

ABSTRACT

A study of the herring gull *Larus argentatus* emphasising inter-relationships of population ecology, social behaviour and breeding biology was undertaken on the Isle of May, Scotland, with some comparative work in a moorland gull colony on Mallowdale Fell in the Pennines.

A cull of the herring gull population, which had hitherto been increasing at 13% per annum, has been practised by the Nature Conservancy Council on the Isle of May yearly since 1972, and special attention was given in this study to the biological effects of culling. The population trends were followed in detail up to 1977, and it was shown that the annual recruitment rate has been very variable since 1972 and there has been a shortfall in the number of young gulls predicted to join the breeding population. These have presumably moved and some ringed gulls were located breeding in other colonies. The population has been held at about 20-25% of its 1972 level since 1975. With many of the older gulls having been culled, the average age of the population had been reduced, so that by 1977 about 50% of the population was breeding for the first time. Despite a strong correlation between parental age and percentage breeding success, the average number of chicks fledged per pair in control areas was 0.82, which was as high as that recorded in a previous study by Parsons (1971, unpublished Ph.D. thesis, Durham University) on the Isle of May in the late 1960s. In addition, it was found that the median date of laying was the same as that estimated by Parsons, and that egg size (positively correlated with chick survival) had increased significantly.

Experiments on recruitment by manipulating breeding density showed that at the highest densities recorded the annual recruitment rate was close to the average annual mortality rate. In areas where density had been greatly reduced, the recruitment rate was insufficient to replace annual adult mortality, and in some areas no recruitment was recorded. There was a broad, optimal breeding density of between 2 and 10 nests/100m^2 where highest recruitment rates took place. Much of the Isle of May was found to be at this density as a result of culling. Birds which spread their nests most uniformly were the most successful breeders, and the majority of nests were thus spaced. Aggression was found to increase with density. The rationale of gull culling has been discussed for the Isle of May, together with recommendations for future culls on the island and elsewhere.

ACKNOWLEDGEMENTS

It is a particular pleasure to thank my supervisor Dr J.C. Coulson for his unstinting help and wise guidance in the course of this study. I thank Professor D. Barker for granting facilities in the Department of Zoology at Durham, and also members of the technical and administrative staff who have willingly catered for my whims.

Much of the work would not have been possible without the help and cooperation of the staff of the N.C.C. - particularly A.W. Colling and Miss N.J. Gordon. Their enthusiasm and interest has always encouraged me. The Isle of May Bird Observatory were particularly helpful in providing accommodation on the Isle of May, and I should like to thank John Arnott and his colleagues for so much cooperation, allowing access to data on gulls ringed previously on the Isle of May, and also much stimulating discussion. The Psychology Department of the University of St Andrews also provided excellent accommodation and facilities in their field station (the "Mouse House") and I would like to thank Dr Robert Prescott for this privilege, and his colleagues for excellent company. Mr Jim Smith of Crail cheerfully sailed in all weathers and at all hours to take me to the island and provided many obligements, as did the hospitable lighthouse keepers of Northern Lights.

Mr Richard Challenor, estate agent with Davis and Bowring, gave most helpful information about the gull colony on Tarnbrook and Mallowdale Fell, and Mr Bowman, head keeper on the Abbeystead estate, and Mr Barlow, keeper on Brennand estate, freely gave of their knowledge and provided many kindnesses. I am particularly grateful to the agents of Abbeystead and the owners of Mallowdale and Brennand for permission to work in their impressive gullery.

Mr John MacNeill of Gigha was unfailingly ever at the ready to ferry me to Cara, and it is a pleasure to thank Captain J. MacDonald of Largie for permission to visit his island.

Many colleagues have willingly assisted in collecting data on the Isle of May, but I give special mention to Dr R. Wooller, Dr P. Monaghan, G. Chabrzyk, M. Tasker, S. Moon, R. Quick and G. Wiersema. Dr J. Parsons kindly allowed me to quote from his unpublished Ph.D. thesis, and without the legacy of so many ringed gulls this study would have been very much harder.

D. Hutchinson helped to prepare the plates and reproduced the figures, and Mrs R.L. Reed took on one of the hardest tasks of all - typing the final draft from my innumerable revised versions. Finally, but by no means least, Sarah Wanless has ever helped to foster the ideal, and a love of islands.

The study was supported by a N.E.R.C. Studentship held from October 1973 to September 1977.

1. INTRODUCTION

> "The two great motives which regulate the proceedings of the brute creation are love and hunger; the former incites animals to perpetuate their kind, the latter induces them to preserve individuals ......"
>
> Gilbert White, Selbourne, 8 Feb. 1772

This thesis reports on research where an attempt has been made to bring together aspects of population ecology, breeding biology and social behaviour with reference to the colonial herring gull *Larus argentatus*. The unification of the three subjects can be seen as a logical progression towards a fuller understanding of the animal's life history now that the biology of the herring gull has been extensively studied for over five decades on both sides of the North Atlantic.

In recent years an increasing interest in ecological problems has fostered a specific interest in the biology of large gulls. In part, this has been responsible for an already impressive literature, particularly with reference to the herring gull. In many respects the life history and habits of the herring gull are among the best documented of any bird. Furthermore, it is not entirely coincidental that research on herring gulls has been undertaken at a time when the population (in common with nearly all North Atlantic seabird species) has been characterised by a sustained increase in numbers which has been taking place from early in this century. This phenomenon has given added impetus and interest to the studies and has helped to ensure that even where work has been repetitive new interpretations are always possible on the comparative data.

The increase in herring gull numbers has been relatively well documented for the British Isles (Parslow 1967) and has been further considered by several authors on a regional basis e.g. Harris (1970), Cramp *et al.* (1974). From the data given by Cramp *et al.* *(loc. cit.)*, Chabrzyk and Coulson (1976) calculated that a 12-13% annual increase in numbers of breeding herring gulls has been a widespread and general phenomenon throughout the British Isles since the 1930s, and in some cases since near the beginning of the century. Nor has the population increase been restricted to the British Isles: it has been common to both the east and west coasts of the North Atlantic, and much of north-west Europe. Increases have been recorded in the Netherlands (Voous 1960), North Germany (Goethe 1964), Denmark (Salomonsen 1963) and Finland (Bergman and Koskimies 1958). In some eastern regions of the U.S.A., Kadlec and Drury (1968) recorded a rate of increase of 4-6% per annum which had been sustained from the early years of the twentieth century until the mid 1960s. Since that time there has been evidence of a levelling off of numbers with a possible decrease in some areas (Nisbet 1978).

In nature, a sustained increase in the number of animals over many generations is regarded as a very singular occurrence, the more so where the animal concerned is a long-lived vertebrate. Normally, it is to be assumed that a change in the fortunes of the animal has permitted an increase in the survival rate or birth rate. Rather less commonly, there can be an intrinsic change within the animal itself as it evolves towards new adaptive "peaks". As Williams (1966) suggested: "The central biological problem is not survival as such, but design for survival." New adaptability is often most manifest by a change in behaviour which permits new environmental conditions to be exploited. With this in mind, it is relevant to introduce another aspect of herring gull populations which is not necessarily related to the increase in numbers - namely changes which have taken place during this century in breeding distribution. It was only in 1925 that herring gulls colonised Iceland. Since 1940, there has been little further expansion of their range, and numbers now appear to be fairly stable (Ingolfsson 1978). The increase in numbers of gulls in the eastern United States was also accompanied by a progressive spread southwards of the breeding range, particularly during the 1920s and 1930s. The southern limit for the species is now 34°N (Nisbet 1978). It is perhaps significant that the major expansions in range coincided with the initial increase in numbers, and that it has not been a particularly notable feature of the population since. The phenomenal spread of the fulmar from the Arctic into the eastern sectors of the North Atlantic (Fisher 1952) may provide a comparative situation, the precise causes being no less clear.

Within the British Isles there has been a more recent tendency for herring gulls to extend their breeding range from the traditional rocky coasts and islands into marshes, moorlands and, oddly, towns (Parslow 1967; Cramp 1971; Greenhalgh 1974; Monaghan and Coulson 1977). It has been taken for granted that these changes in the traditional type of breeding habitat have been associated with the increase in the population, especially as a consequence of overflow from existing colonies which have reached saturation point, but there is no good evidence that this is so. Rather it seems a further indication of how an unspecialised species which has reached new adaptive peaks can successfully utilise new resources.

Inevitably, the herring gull has now become a pest. The claim has been made that large numbers of gulls in their wintering and breeding areas have had a deleterious effect on other wildlife (Eggeling 1960; Thomas 1972) and the possible hazards to human welfare from gulls which have become more associated with centres of human population have been speculated upon by Monaghan (1977 unpublished Ph.D. thesis). Gulls of all species common in Britain have never been immune to destruction by man despite various Bird Protection Acts which have passed through Parliament since the late nineteenth century, but recent opinions have favoured, as a means of control where it has been considered necessary, the large scale culling of the adult breeding population in the colony.

In Britain, organised and officially approved gull control by killing began in the 1960s when the seriousness of the "gull problem" became increasingly realised. In 1972 the then Nature Conservancy began what was at the time the largest programme of gull control yet undertaken in the British Isles on the National Nature Reserve of the Isle of May , Scotland. The undertaking was to reduce the breeding population of gulls (about 17,000 pairs) to some 200 pairs within 3 years (Anon. 1972). The programme is still continuing.

This study has relied heavily on data accruing from such control measures for two major reasons. Firstly, there has been opportunity to consider a cull as a "removal" experiment - an experimental approach which although very valuable in ecological studies can seldom be justified on moral and conservation grounds. The manipulation of breeding numbers has permitted detailed comparative observations on breeding biology with reference to age and year and also social behaviour. Secondly, it has been possible to study the effects of culling, especially the reactions of the population, and to assess the usefulness of this method of control. The results of culling have therefore been reported in some depth.

The increase in herring gull numbers *per se*, although not receiving detailed treatment in this thesis, nevertheless provides the ultimate argument and justification for much of the experimentation. Many previous population studies on birds have been based on a working hypothesis which incorporates a theory of population regulation (see, for example, studies on red grouse (Jenkins, Watson and Miller 1963, Jenkins *et al.* 1967, Miller and Watson 1978, Watson and Miller 1971) where social behaviour has been considered important or have *a priori* been cited as proof of one or other theory (such as the studies on the great tit (e.g. Lack 1964, 1966; Lack *et al.* 1957, Perrins 1965, 1970; Perrins and Moss 1974, 1975).

In this thesis the usefulness and applicability of a general theory of population regulation is left to the final section for discussion. Most of the experimental work has been approached without predilection or prejudice for any particular idea on the regulation of populations, although it is difficult to see how density independent effects, as visualised by Andrewartha and Birch (1954), can be meaningfully tested in the field since environmental conditions for seabirds would be very difficult to manipulate in the field. The importance of social behaviour has been emphasised however, and some experiments have been undertaken to demonstrate that social behaviour can influence numbers, albeit indirectly.

Whilst it is a relatively simple matter to record population trends of the herring gull, it is less easy to reveal the mechanisms whereby the population reaches its observed size, and similarly to forward reasons with real confidence of why population regulation does or does not operate for an unspecialised and highly adaptable bird such as the herring gull. Most of the work has been undertaken on the Isle of May, Scotland, which can now be considered to be one of the world's best known herring gull colonies. There, previous workers have established that the population has indeed increased at approximately 13% per annum since the early years of the century (Parsons 1971, Chabrzyk and Coulson 1976). Detailed studies have been conducted on reproductive biology (Parsons 1970, 1971, 1975, 1976; Parsons *et al.* 1976) and dispersion and winter movement have been examined (Parsons and Duncan 1978). Chabrzyk and Coulson (*loc. cit.*) have estimated a realistic average annual survival rate for adult herring gulls of 0.935, which gives an average adult life expectancy of 14.9 years. These studies have proved invaluable in providing a basis for the investigation of recruitment to the colony by mature gulls, and the work of Parsons has been especially useful in providing comparative information on breeding biology.

2. THE STUDY AREAS

2.1 THE CHOICE OF STUDY AREAS

The three colonies, the Isles of May, Cara and the Tarnbrook/Mallowdale colony, were chosen for comparative purposes, each colony presenting very contrasting ecological situations. The Isle of May was the main study area and most time and effort was afforded to fieldwork there.

To work in three widely spaced colonies during the restricted breeding season was, with hindsight, an over-ambitious approach. The logistical problems of working intensively in the field in the Tarnbrook/Mallowdale colony were in themselves sufficient to discourage the kind of detailed observations which could be made with ease on the Isle of May. As a consequence, this colony received little close attention after the breeding season of 1975, and then with most observations being restricted to the parts which lay inside the Mallowdale estate. On the Isle of May itself, seven study areas were chosen which were considered initially to be broadly representative of the island as a whole, but each with different breeding densities (see Figure 4).

The island of Cara was chosen as an example of a small colony where the rate of increase of the gull population was much slower than either the Isle of May or the Tarnbrook/Mallowdale colony. Here, it was felt that information on breeding biology and age composition could provide an interesting contrast to the Isle of May. Perhaps the most useful aspect of the work on Cara is that the existence of a herring gull colony has been established, and that its rate of increase is indeed low when compared with the national average.

Nonetheless, it has been felt that it is worthwhile to describe both Cara and the Tarnbrook/Mallowdale colonies, and to include at least the available data on the present status of the gulls found breeding there. Cara has probably never been visited by a zoologist, and the Tarnbrook/ Mallowdale colony seemingly on only a few occasions. If the current intentions of the landowners and shooting tenants, together with those of the North West Water Authority (much of the colony lies within one of their major catchment areas) prevail, then it can be expected that this huge moorland colony, which is one of the largest in the world, will be very much reduced in size in the years to come.

2.1.1 The Isle of May

The Isle of May ($56^{o}11'$N. $2^{o}33'$W) lies toward the entrance of the Firth of Forth, 9km from the coast of Fife and 14km from the nearest point on the East Lothian shore (Figure 1). The island is about 2km long, 0.5km wide and 57ha in area. It is formed of a hard igneous rock (olivine dolerite) with cliffs rising to 50m on the west coast. The east side of the island is entirely rocky, but with few cliffs. The soil cover is thin and mainly peaty. Much of the island is covered by a grassy turf in which *Festuca rubra* L. and *Agrostis* spp. are dominant, whilst close to the extensive rocky outcrops, and the more low lying northern and eastern sectors, patches of *Armeria maritima* (Mill.) and *Silene maritima* (With.) sward are prevalent. Areas which are colonised by gulls are characterised by dense summer growths of *Rumex* spp., *Atriplex* and *Cochlearia* (see Figure 3).

Prior to the first gull cull, the herring gull was the most numerous breeding bird. Although the reduction in numbers has continued since 1972 on a massive scale, the breeding population remains large (Figure 11, Section 3.4). There has been a considerable drop in numbers of the lesser black-backed gull as well, but the decrease has not paralleled that of the herring gull. With the exception of the complete loss of sizeable tern colonies which had reached their peak in the early 1950s, other seabird species have continued to prosper throughout this century. Kittiwakes were estimated at 3,550 pairs in 1976 (personal observations) and puffins have increased spectacularly with about 3,000 pairs in 1976 (Harris 1976). Of the cliff nesting auks, razorbills were about 500 pairs in 1973 and guillemots about 3,700 pairs in the same year (Eggeling 1974). These figures represent substantial increases throughout this century. Shags have likewise increased, reaching a peak in 1973 when the population was estimated at 1,130 pairs. By 1977 this figure had dropped to just over 600 pairs, however, the cause of which is not known.

In recent years the island has suffered from unacceptably high numbers of casual visitors. This trend has increased and must give cause for concern from the point of view of management by the N.C.C. and the Isle of May Bird Observatory Management Committee. Increased interference by the general public in the pursuit of recreation and even unsolicited biological research cannot be accommodated indefinitely by this small and biologically interesting National Nature Reserve.

2.1.2 History of the gull colony

The growth of the herring gull colony, since the first record of a pair of herring gulls which bred in 1907 (Baxter and Rintoul 1925), is now well documented (Eggeling 1960, 1974; Chabrzyk and Coulson 1976). To reiterate briefly: evidence from counts since the first records (deposited in the Isle of May Bird Observatory) indicate that the increase in the number of breeding pairs has been taking place at a near constant 13% per annum, up to 1972. In this year the breeding population was estimated at 16,700 pairs (Figure 5). This rate of increase in the numbers of herring gulls approximates closely to an overall average of 12.8% per annum calculated for the British Isles (Chabrzyk and Coulson 1976) and thus it would seem that the colony was in no way atypical in its remarkable and sustained rate of growth. Figure 2 indicates the extent of the colony in 1974.

Figure 1. The location of the Isle of May in the Firth of Forth. Neighbouring gull colonies are named.

Figure 1

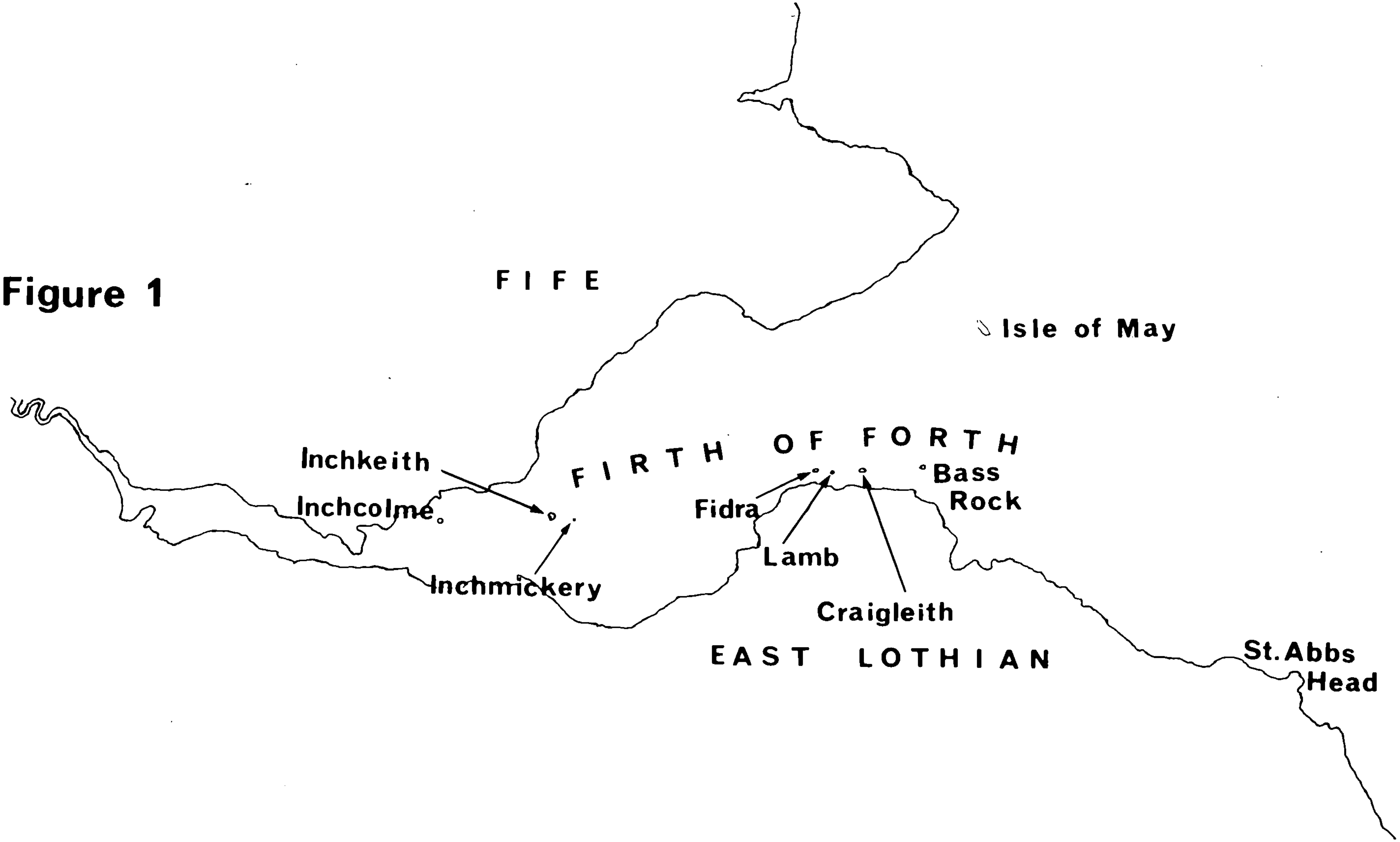

FIFE
Isle of May
Inchkeith
FIRTH OF FORTH
Bass Rock
Inchcolme
Fidra
Lamb
Inchmickery
Craigleith
St. Abbs Head
EAST LOTHIAN

Figure 2. The Isle of May, showing the areas colonised by gulls in 1974 (stippled areas).

Figure 2

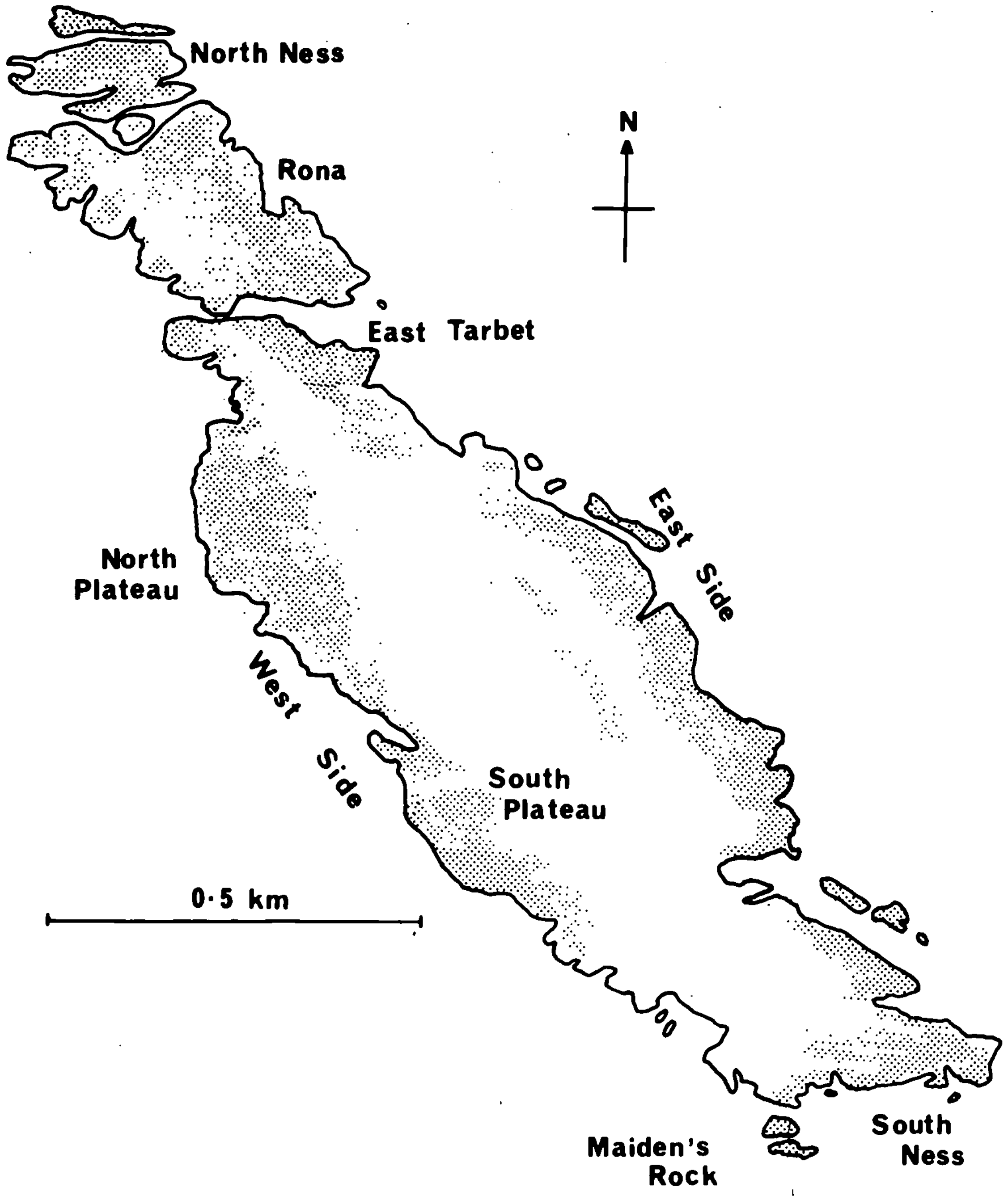

North Ness
Rona
N
East Tarbet
East Side
North Plateau
West Side
South Plateau
0·5 km
Maiden's Rock
South Ness

Figure 3. The Isle of May, showing the major vegetation types (from Sobey 1976)

Figure 3


bare rock
rock; Poa annua
mixed species
Stellaria
Holcus
Rumex
Armeria
Silene
transitional areas
fescue sward

Figure 4. The location of the study areas on the Isle of May.

Figure 4

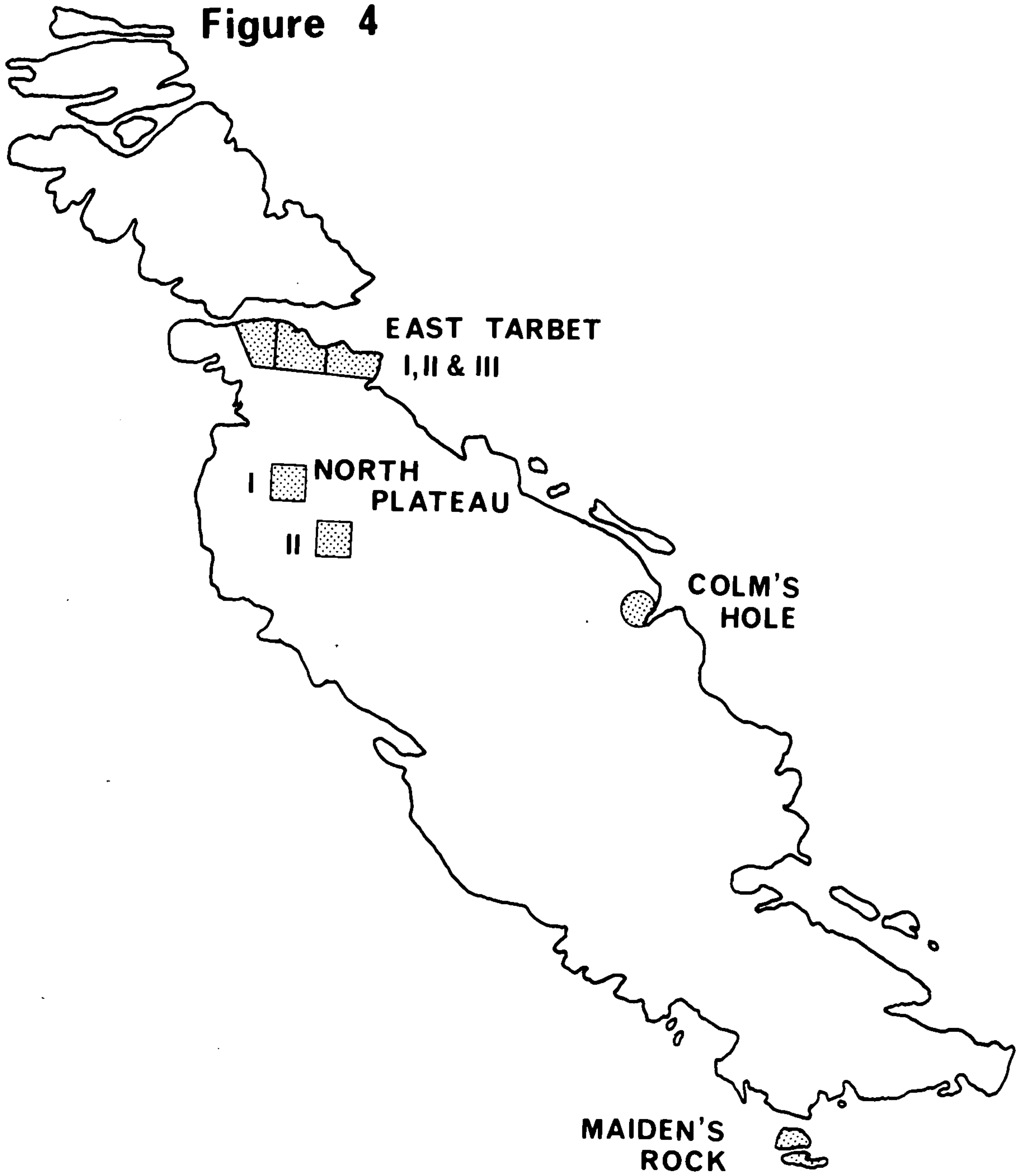

EAST TARBET
I, II & III
I
NORTH
PLATEAU
II
COLM'S
HOLE
MAIDEN'S
ROCK

Figure 5. The increase of the herring gull population on the Isle of May between 1907 and 1972. The log of the number of breeding pairs is plotted against year.

Figure 5

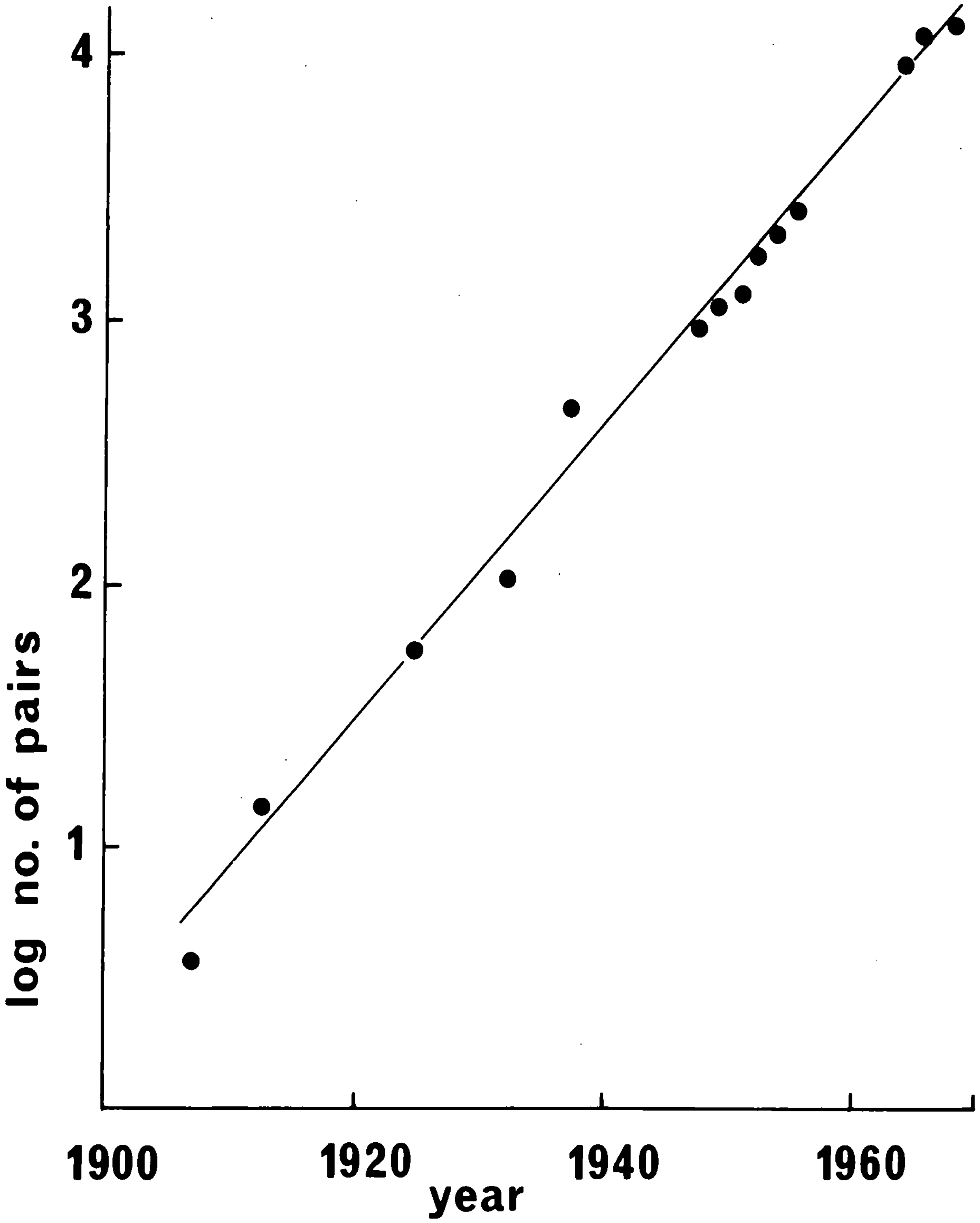
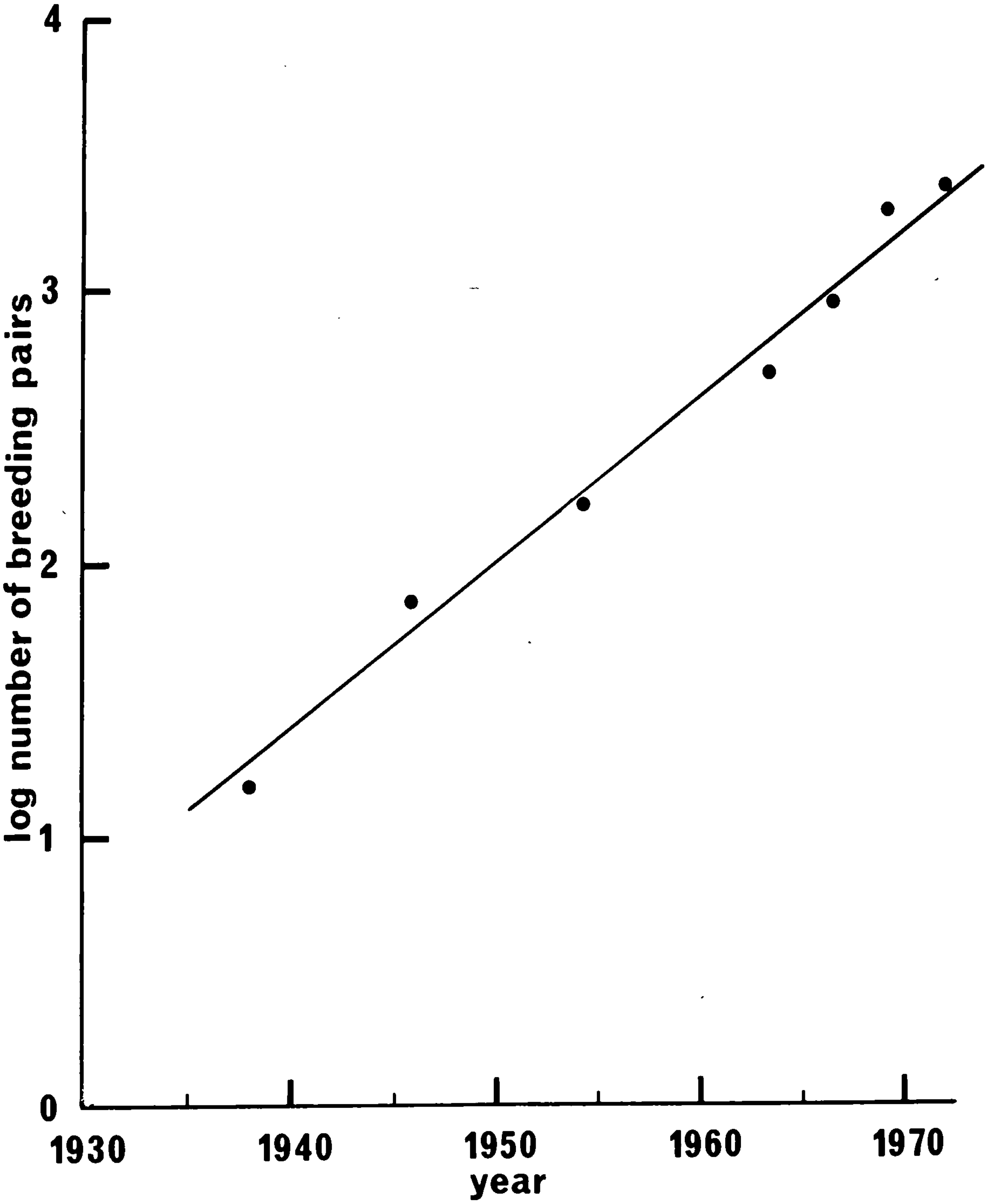


Figure 6. The increase of the lesser black-backed gull population on the Isle of May between 1930 and 1972. The log of the number of breeding pairs is plotted against year.

Figure 6


4
3
2
1
0
log number of breeding pairs
1930
1940
1950
1960
1970
year

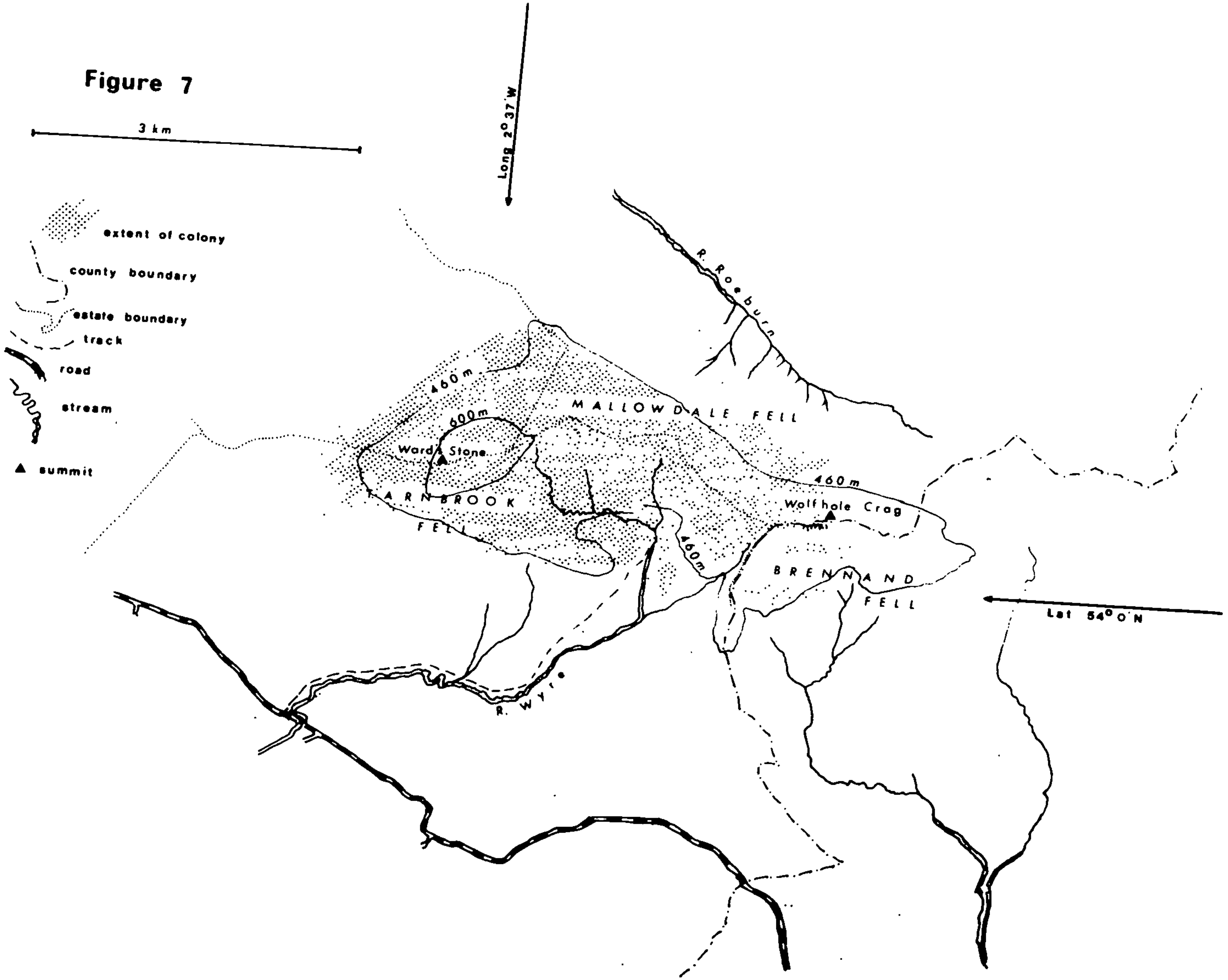
The lesser black-backed gull did not breed on the Isle of May until 1930, but according to data given by Eggeling (1974) it has increased at a rate of 14.3% per annum which is comparable to that of the herring gull (see Figure 6). . In the years immediately before 1974 it constituted about 10% of the *Larus* gull population, but the proportion has since increased.

2.2 THE TARNBROOK/MALLOWDALE COLONY

The Tarnbrook/Mallowdale colony lies on the western slopes of the Pennines within the area known as the Forest of Bowland. Access to the colony is best effected from Tarnbrook, following the headwaters of the River Wyre towards its watershed. At 54° 01'N 2° 35'W (Nat. Grid Ref. SD614.595) at an altitude of 450m, the southern edge of the colony is reached (Figure 7). On the western perimeter the colony extends as far as the longitude of Ward's Stone (Nat. Grid Ref. SD 595.578) and reaches 5.5km in an easterly direction onto Mallowdale Fell. Here, the edge of the colony virtually marches with the Lancashire/Yorkshire boundary. These easterly limits of the colony are not well defined however, being both an area of recent, patchy colonisation and active persecution by the landowners. In all, the colony covers an area of roughly 2000 hectares of typical west Pennine moorland lying between 450 and 515m. Pearsall (1950) describes the area in general as one of originally *Molinia-Sphagnum* bog which has been modified mostly throughout the twentieth century to a moorland where *Eriophorum* and *Calluna* predominate. Within the colony limits, *Eriophorum* spp. and heather *Calluna vulgaris* (L.) Hull. are common. *Vaccinium myrtillus* L. is presently disappearing from the more densely colonised areas. *Juncus* spp. are common in water-logged areas, and a variety of grasses, especially *Poa* and *Deschampsia* have recently been introduced, probably by the gulls. Since the colony reaches into three separate estates, where past and present management practices have had different emphases

Figure 7. Tarnbrook and Mallowdale. The extent of the colony is shown, with major features of relief and topography.

Figure 7


3 km
extent of colony
county boundary
estate boundary
track
road
stream
summit
Long 2°37'W
Lat 54°0'N
R. Roeburn
MALLOWDALE FELL
460m
600m
Ward's Stone
TARNBROOK FELL
460m
Wolfhole Crag
460m
BRENNAND FELL
R. Wyre

especially in relation to heather management for grouse and sheep grazing, it is only possible to generalise about the vegetation types. In addition, the areas which have had the longest association with gulls have become the most modified as a result of nutrient input from droppings. The peat cover, which is variable in depth, is deeply intersected by hags and watercourses (Plate1,3). The underlying rock is mostly millstone grit and frequently outcrops on the higher slopes.

2.2.1 History and growth of the gull colony

About 85% of the gulls breeding in the Tarnbrook/Mallowdale colony are lesser black-backed gulls, the first pair of which were reported to have bred in 1938 (J. Bowman and R. Challenor, pers. comm.). This was on Abbeystead estate, belonging to the late Lord Sefton. Prior to the outbreak of the Second World War, Abbeystead and Tarnbrook Fell could claim to be among the finest grouse moors in Britain. Surprisingly, there seems to have been no immediate attempt to eradicate the gulls in the early years of the founding of the colony. This might have been a more difficult task than it would seem today since much of the initial breeding population probably immigrated within a short space of time from other nearby colonies such as Foulshaw Moss in Westmorland which had been reclaimed for agricultural use during the 1920s and 1930s. It was also during this time that the nearby Walney colony was formed, which is now probably one of the largest lesser black-backed gull colonies in the world. However, during the 1940s the colony in Tarnbrook became well established, and by the 1950s the colony must have been increasing at a dramatic rate. Greenhalgh (1974) reported that there were 17,000 pairs of gulls breeding there in 1972, with about 3,500 pairs of herring gulls.

The history of the colony is rather enigmatic and incompletely documented. Access has always been restricted by the owners and there are very few published accounts to be found. Oakes (1953) makes reference to the origins and date of founding of the colony and Greenhalgh (*loc. cit.*) has indicated what the rate of growth might be. Figure 8 plots the increase of the lesser black-back breeding population and Figure 9 the herring gull population, based on figures published in Greenhalgh (*loc. cit.*) and given in the footnote below.[†] Clearly, the latter species has increased at a rate comparable to the lesser black-back, but it seems that the counts made since at least 1965 could be over-estimates.

Whatever the lesser black-back population might have been in the early 1970s, the rate of increase of this species has been remarkable, with an approximate doubling of numbers every three years, and an average rate of increase of close to 32% per annum. Herring gulls, on the other hand, have increased even faster at a rate which is certainly more than 35% per annum (38% excluding personal counts in 1974 and 1975). Such a high rate of increase for these two species can only be accountable to enormous immigration from other colonies (see Section 6).

For many years, gamekeepers and tenant farmers have attempted to reduce the breeding population and lower breeding success to a minimum under instructions from the owners. The main reason has been to reduce predation and pressure on grouse stocks. Up to 1977 this task has been

[†] Data from Greenhalgh (1974) is as follows:

For lesser black-backed gulls: 1938 - "a few pairs bred"; 1944, 600 birds; 1945 and 1947 - "over 1000 birds"; 1951, 2000 adults, 1961, 8000 pairs; 1965, 16,000 pairs; 1966, 15,000 pairs; 1967 and 1969, 15,000 pairs; 1970, 14,000 pairs; 1972, 17,000 pairs.

For herring gulls: 1949, 1 pair; 1956, 20 pairs; 1961, 80 pairs; 1965 and 1966, 160 pairs; 1967, 500 pairs; 1969, 1700 pairs; 1970, 1000 pairs; 1972, 3,500 pairs.

Figure 8. The [illegible] increase of the lesser black-backed gull population (1938-1975) on Tarnbrook and Mallowdale. The log number of breeding pairs is plotted against year.

Figure 8

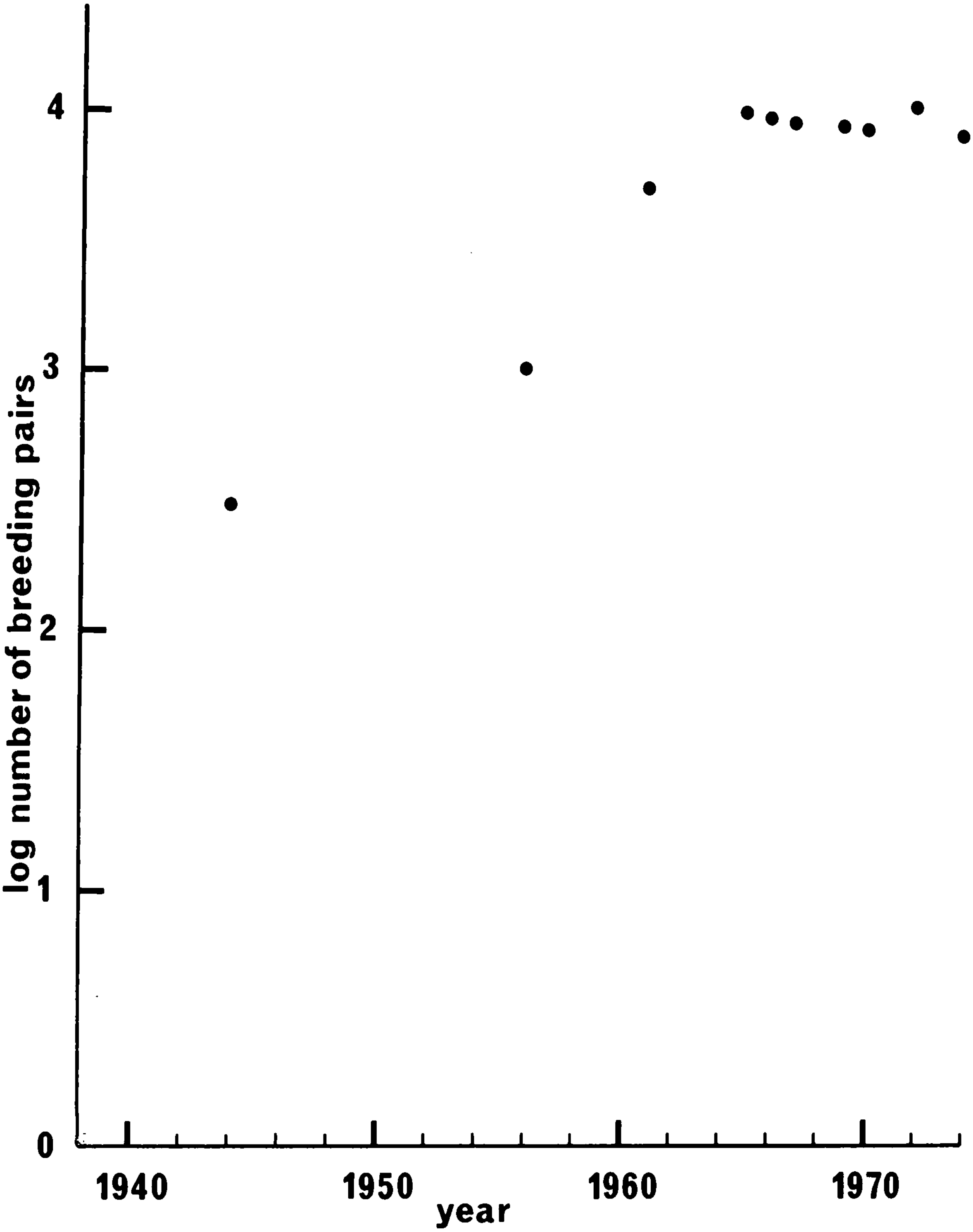
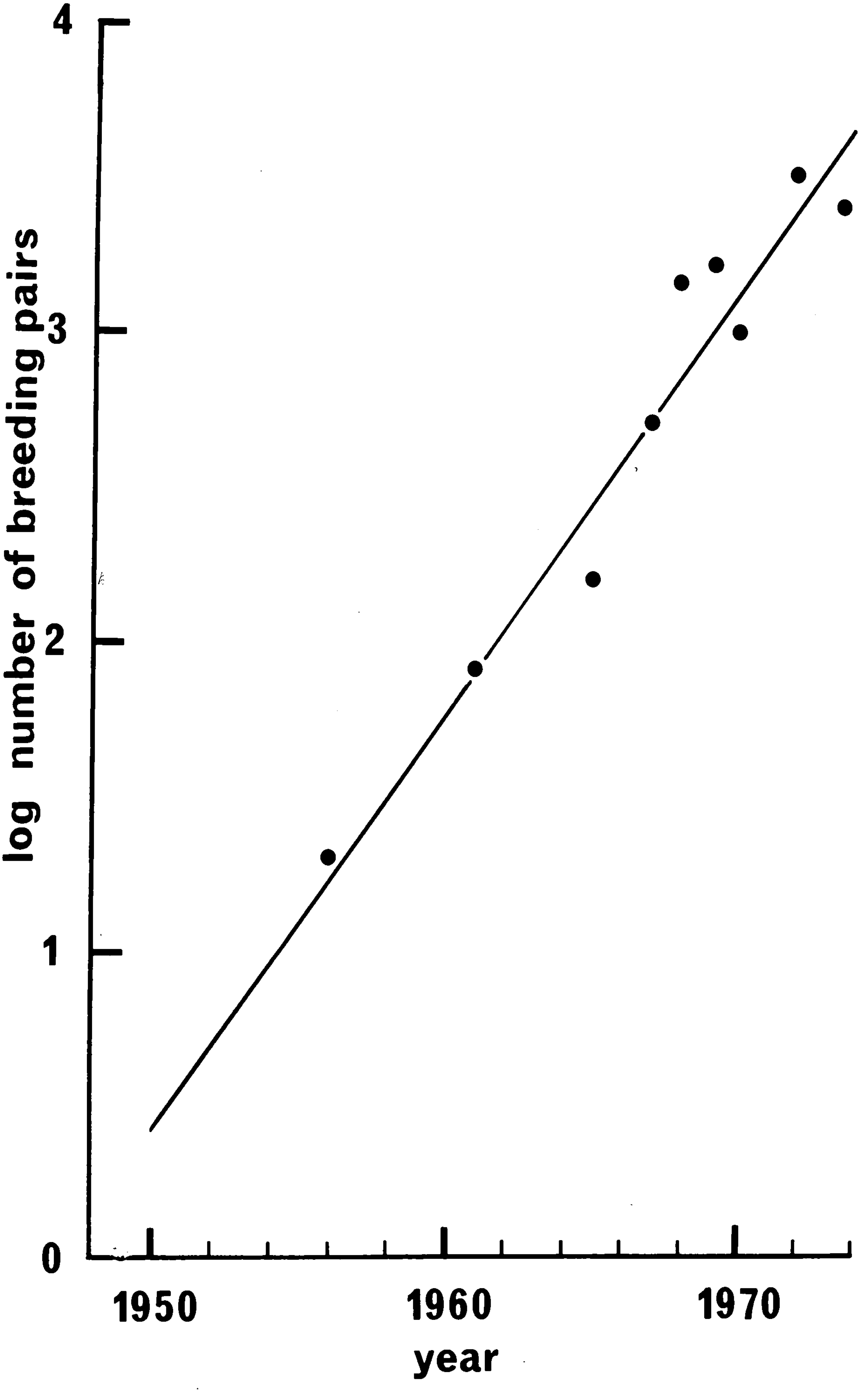


Figure 9. The rate of increase of the herring gull population (1949-1975) on Tarnbrook and Mallowdale. The log number of breeding pairs is plotted against year.

Figure 9



both difficult and unsuccessful since without M.A.F.F. approval, control by poisoning is illegal. However, since the mid-1960s M.A.F.F. have shown an interest in the colony, and in 1978 approved a licence for the North West Water Authority to cull up to 25,000 gulls. At the time of writing, the results of this exercise are not known.

2.3 THE ISLAND OF CARA

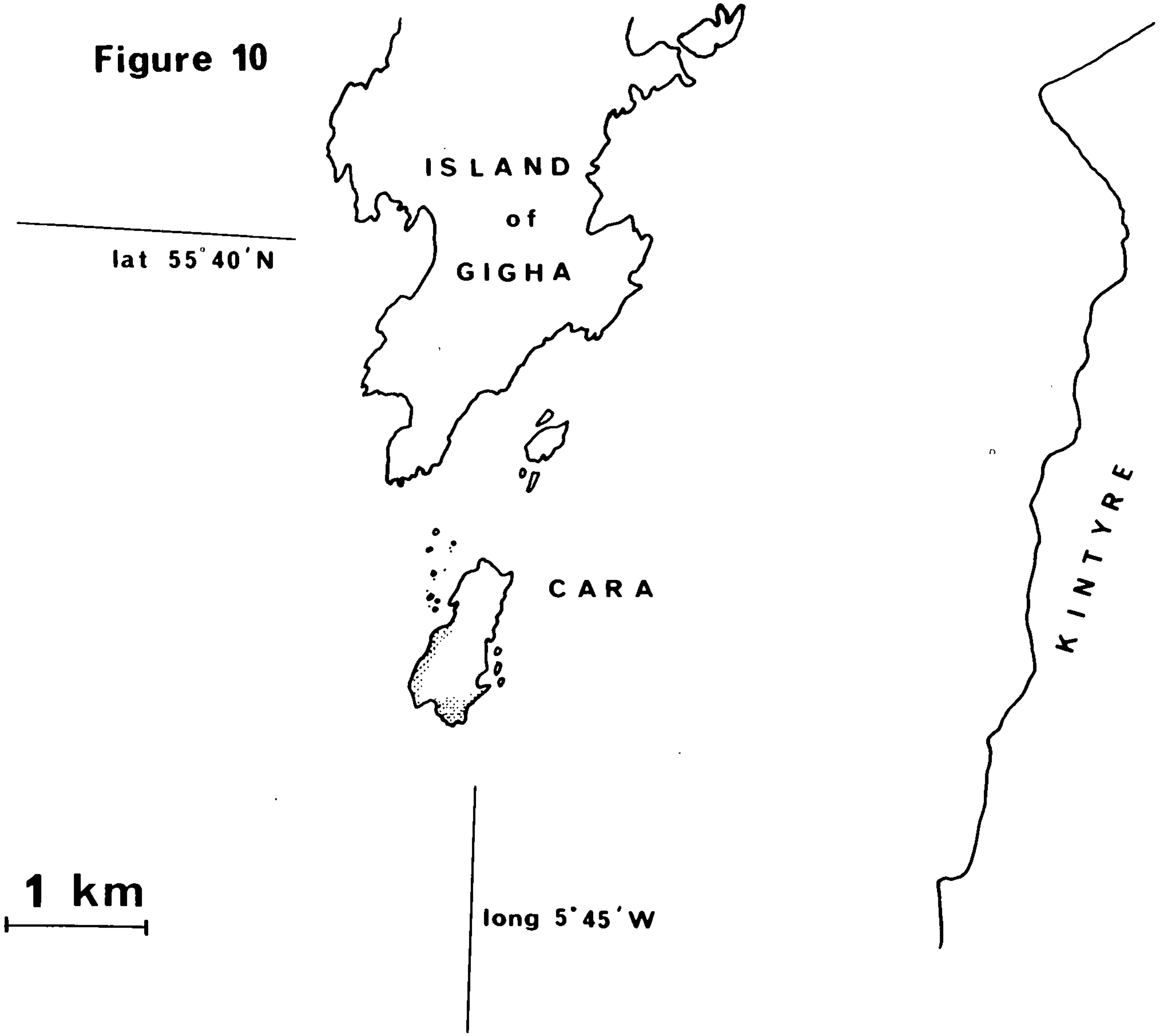
Cara is a small island 3.5km off the west coast of Kintyre (Argyll) and lies 1km from the southern extremity of the island of Gigha ($55^{o}38$'N. $5^{o}45$'W) (Figure 10). It is about 70ha in area and although uninhabited, it is grazed by sheep, rabbits and a herd of wild goats. The island is privately owned and very seldom visited.

The vegetation is varied, but has been modified by grazing and early attempts at crofting. *Erica cinerea* L. and *Culluna vulgaris* covers much of the better drained slopes. *Juncus* spp., *Eriophorum* spp. and *Iris pseudacorus* L. occupy much of the damper areas. *Pteridium aquilinum* (L.) Kuhn has now invaded much of the better grassland.

The Mull of Cara is an area of large boulders and cliffs which rise to 60m on the southern end of the island. Shags, fulmars, black guillemots, herring and great black-backed gulls nest in this area. On the west facing shore is where the majority of herring gulls are to be found. Other breeding seabirds include common gulls, eider duck, roseate, common, Arctic and little terns, oystercatchers and a variety of littoral and marshland waders. The histories of the gull colonies are not known.

Figure 10. The island of Cara. The extent of the herring gull colony is indicated, and also the extent of the greater black-backed gull colony.

Figure 10



3. GENERAL METHODS

3.1 RINGING

Since the beginning of detailed gull studies on the Isle of May in 1966, large numbers of young gulls have been ringed annually (Table 1), mostly by Dr Jasper Parsons. A proportion of gulls have returned to the natal colony to breed, and appreciable numbers of these have been recovered in each year of the cull programme. Each chick had been ringed with a BTO monel ring bearing a unique number. A coloured Darvic ring identified the year of birth and, in some instances, the natal area within the colony.

Ringing was continued by the late Margaret Emmerson in 1970. There were no chicks ringed in 1971, but G. Chabrzyk began studies in 1972 and chicks were once again ringed in quantity. In 1974, when this study began, the NCC culled all parts of the island in late May (except for Maiden's Rock) and followed up this operation in mid June by destroying eggs and newly hatched chicks of gulls which had survived the cull. These actions effectively precluded the ringing of many chicks. Since 1974 the main aim has been to mark a proportion of surviving chicks, mostly in the study areas, which could aid future study on the island. No ringing was done on Mallowdale Fell since it would have required a massive number of gulls to be marked to have any appreciable benefit for the study.

3.2 CULLING

3.2.1 Legal requirements

Offering a poison bait to gulls was the only effective method of killing birds on their territories in the required numbers. Poisoning however is illegal except under licence, and it was important that the law was strictly observed. The NCC are legally entitled to issue licences under Section 10(1)(a) of the Protection of Birds Act 1954 for the purpose of taking and killing gulls for biological research. Such licences were granted each year in advance of clearing experiments on the Isle of May and on Mallowdale Fell. The conditions of the licences were adhered to at all times.

A .22 rifle was used to shoot gulls in the study area, requiring a Firearms Certificate issued by the police, and also requiring compliance with the Firearms Act 1968. Permission was given by the NCC and the landowners of Tarnbrook and Mallowdale Fells to use a rifle for scientific purposes.

3.2.2 Specifications for a suitable narcotic

In drawing up the terms of the licence to kill gulls (wherein the type of narcotic to be used is stipulated) the NCC acknowledge the need to specify a narcotic which can fulfil the following requirements in the field:

(1) The narcotic must be acceptable to the gulls when offered in lethal doses.

(2) It must kill humanely and effectively with the minimum disturbance to other birds.

(3) It must be effective within a short time to prevent dispersion of moribund gulls.

(4) It must not be a danger to other animals or to the experimenter.

The narcotic which best satisfied these requirements was a-chloralose which was well tested in pest control both in the U.K. and abroad. Field trials on gulls had been conducted by DAFS and the NCC had used the narcotic with success in the culls of 1972 and 1973.

3.2.3 Techniques used in clearing experiments

The quantities of a-chloralose to be used per bait were stated in the terms of the licence i.e. 200mg of poison per bait. Administering the poison on a bread and margarine bait at this dosage gave generally satisfactory results, although gulls showed considerable variation in their reactions to it. It had been recommended that c. 35mg of Seconal should be added to each bait as well to reduce convulsions and to quieten the birds, but this produced no measurable improvement in the performance of the technique. When Seconal was added it appeared that the frequency of regurgitations increased and so greatly reduced the chances of taking the bird. After initial attempts to clear areas of gulls, its use was discontinued.

Baits were prepared by blending a weighed quantity of a-chloralose with margarine, which was then spread on sliced bread in the required quantities. One bait was then placed in a nest. The operation was completed quietly and with minimum disturbance. The baited area was then kept under constant observation from a portable hide. At least one member of a pair would return within an hour, and when sufficient time had lapsed for the poison to take effect, the narcotised gulls were collected and new baits distributed to take the other member of the pair. The amount of disturbance was minimal when less than 50 baits were used at a time. When repeated quickly, it was often possible to kill both members of the pair in the same day. When this was not achieved, especially when an individual gull refused to take a bait, it was usually a simple matter to shoot the gull from a range of about 50m or more, using a telescopic sight and high velocity ammunition. This was not a method that could be used frequently however, since gulls very soon became wary of shooting.

Killing large numbers of gulls is an unpleasant task by any standards, but the birds were killed efficiently, painlessly and without stress. Experience in the use of firearms helped to ensure that on nearly all occasions gulls were shot dead instantly.

3.3 MARKING NESTS AND EGGS

All nests in the study areas on the Isle of May were marked before the first eggs appeared. Twenty-five centimetre wooden stakes were used, each numbered with indelible ink for this purpose. On Mallowdale Fell it was necessary to mark nests using 1m garden canes since the height of vegetation and the topography precluded the use of shorter markers. Eggs were numbered in order of appearance, and throughout this thesis the convention c/3 is used to denote a clutch of three, c/2 a clutch of two, and c/1 a single egg clutch.

Table 1. The numbers of herring gulls ringed as chicks on the Isle of May since 1966

Year of ringing	No. ringed	Colour ring	Ringer
1966	4,325	Red	Parsons
1967	5,230	Yellow	Parsons
1968	4,812	Blue	Parsons
1969	400	Black	Parsons
1970	367	Green	Emmerson
1972	1,350	White/Light Green	Chabrzyk
1973	c.1,200	Brown	Chabrzyk
1974	350	Orange	Duncan
1975	250	Red	Duncan
1976	250	Red/Yellow	Duncan
1977	350	Light Green	Duncan

3.4 POPULATION COUNTS

3.4.1 Isle of May

The most satisfactory method of censusing the breeding population (and probably the only one with an acceptable measure of accuracy) was to count all the occupied nest sites in the sub-colonies. This was undertaken in mid May of each year when the majority of nests had eggs, and was repeated in mid June to ascertain the proportion of gulls which had survived the cull and had succeeded in breeding.

The entire island was divided into longitudinal transects 2-4m wide (depending on density) and each nest with its contents noted. Repeated counts indicated that the degree of accuracy was within 2% for the island as a whole. The few pairs of gulls which were nesting on inaccessible parts of the cliffs were counted through binoculars from either the sea or suitable vantage points. The distinction between the nests of herring and lesser black-backed gulls could not always be made with certainty, although the areas colonised by the two species are fairly well defined. Lesser black-backed gulls were in a minority and the best approach was to count the number of pairs of lesser black-backed gulls by direct observation and to subtract this total from the total number of nests counted.

3.4.2 Tarnbrook/Mallowdale Fell

The only satisfactory means of censusing the Tarnbrook/Mallowdale Fell colony was to count nests within representative transects, take the average count, and multiply up to obtain a figure for the entire colony. In 1974 and 1975 a complete census of the colony was undertaken using this method. In 1976 only the study area on Mallowdale Fell was counted, and in 1977 no counts were made. Each transect was 0.5ha in area (100m x 50m).

In 1974, 85 such transects were counted, and in 1975, 72 were counted. In order to establish a reliable and standard procedure over such large areas, the transects were plotted on an Ordnance Survey map using grid references. Each transect was further divided into five, each of 100m x 10m, and the number of nests in each $1000m^2$ area were counted.

3.4.3 Cara

The number of herring and greater black-backed gull nests were counted on Cara in all years 1974-1977. These counts were made in mid June, with the exception of the 1974 count, which took place in late July. Since the total breeding population was small compared to other colonies, and the colonies confined to the westward and southern parts of the island, it was possible to find all the gull nests without undue difficulty.

3.4.4 Age class counts: Isle of May

Whenever possible, regular counts of aged gulls were made on the six areas of Maiden's Rock, North Plateau I and II, Tarbet I, II and II, and Colm's Hole. These counts were undertaken daily and early in the breeding season in order to identify ringed birds which were breeding, and so that their success could be followed. Such counts were also continued throughout the season, however, so that young gulls which were prospecting territories could also be identified. The age of such birds was usually apparent from their sub-adult plumage, and in all cases these birds could be distinguished from other young birds which were already breeding in these areas.

3.4.5 Age class counts: Tarnbrook/Mallowdale Fell

There were no marked birds in this colony (bar a small minority which had been ringed mostly on Walney) so it was important to establish the ratio of gulls in sub-adult to those in adult plumage. From this, a rough estimate of the age of recruitment could be calculated, at least for the younger gulls. A more precise estimate of the age of first breeding could be calculated from the examination of culled gulls, both herring and lesser black-backed. Counts were therefore made in the more easily observed parts of the colony of gulls in sub-adult plumage. Second and third year lesser black-backed gulls could be distinguished with some certainty using binoculars, but older birds could not be so distinguished. Herring gulls up to their fourth year were easily recognisable (see Appendix I).

3.4.6 Age class counts: Cara

Although the numbers of breeding gulls in attendance at the colony were invariably low, the same procedure was followed as described in 3.4.4 above.

4. THE ISLE OF MAY CULL

4.1 INTRODUCTION

The biological consequences of the remarkable increase in the numbers of gulls has provoked comment from several authors (e.g. Tinbergen 1953, Wynne-Edwards 1962, Cramp *et al.* 1974). The increase has also been the cause of concern to others who have specifically associated the impact of large numbers of gulls in both their wintering and breeding areas with a deleterious effect on other wildlife (Eggeling 1960, Thomas 1972).

Various methods of gull control have been tried, some of which have been reviewed by Thomas (1972). Recent opinions have favoured the large-scale culling of the breeding population as the most effective means for reducing the number of herring gulls associated with nature reserves, roof-tops of inhabited buildings, the proximity of airfields and other localities which bring this ubiquitous gull into conflict with man. Since 1972, such a cull has been undertaken annually by the NCC on the Isle of May, the scale of which operation has been greater than any previously attempted. The rationale of artificial control is further considered in Section 12, but the background to the Isle of May cull is outlined below.

4.1.1 Reasons for culling on the Isle of May

The effects of large numbers of breeding and roosting gulls on the Isle of May throughout the 1950s and 1960s was viewed with increasing concern by the Isle of May Bird Observatory and the then Nature Conservancy alike. Serious and progressive damage was occurring to vegetation and soil cover. The continued expansion of the gulls from the rocky peripheries of the island into the vegetated regions caused much of the *Armeria maritima/Silene maritima* sward to give way to seasonal growths of *Holcus lanatus* and *Rumex* spp. (Anon. 1972). The accumulation of droppings and the innate habit of tearing up vegetation for nest material and during courtship displays has done much to promote the invasion of other species such as *Cerastium* spp., *Cochlearia* spp. and *Atriplex* spp.

The effects of the gull increase on the other breeding species are less clear and more subject to unconsidered opinion. Eggeling (1960) states: "The Herring Gull and the Lesser Black-back are, without any doubt at all, a menace to the other nesting species of the May, taking a heavy toll of the eggs and young of Kittiwakes, Fulmars, Eiders and Oystercatchers. The birds which have suffered most from their presence, however, are terns, of which great numbers formerly bred." That the herring gull was directly responsible for the movement of the tern colonies, there can be little doubt - even when the fickle attachment which terns have to their colonies is taken into account. That gulls on the Isle of May prey on the eggs and young of other species, to a large extent, is unsubstantiated. Whilst a degree of predation undoubtedly occurs, it can be attributed for the most part to a few individual gulls which have learned the habit.* All seabirds on the island, with the exception of terns, have shown a sustained increase since the late 1940s and some species (especially kittiwakes and guillemots) may be close to maximum numbers due to a shortage of suitable nest sites.

* In the summer of 1977, an adult herring gull was observed on several occasions patrolling the cliffs on the west of the island. On numerous instances the same bird was seen to roll guillemot eggs from exposed ledges and attempt to catch them. The nest site of this gull was found on the South Plateau where the shells of one razorbill and and three guillemot eggs were identified.

4.1.2 The effect of culling on gull research

The effects of culling gulls on the Isle of May have had a weighty influence on the surviving population, and any study on the biology of gulls cannot be undertaken without due consideration of the consequences of the cull. In particular, numbers, age composition and nesting density have been changed, but there have been other more subtle changes too in the breeding biology which may have arisen as responses to culling. The following sections emphasise their importance. The publication of technical details of the cull remain the responsibility of the NCC, but an outline of the techniques have been given since they constitute an important experimental approach which I have used extensively both on the Isle of May and on Mallowdale Fell. Further, an appraisal for the need to control gull populations is given in Section 12 wherein the success of the Isle of May cull is also discussed.

4.2 CENSUS OF BREEDING GULLS ON THE ISLE OF MAY

The numbers of breeding herring gulls on the Isle of May between 1974 and 1977 are given in Table 2 with the percentage change in the population from the previous year. Figure 11 illustrates these annual changes, with the log of the number of breeding pairs being plotted against year. In 1975 the breeding population was lower than the 1974 population by 35.5% and the 1976 population dropped a further 33.7% from the 1975 level. However, the 1977 population actually showed an appreciable increase (23.4%) over the 1976 level. In 1977 it was apparent that the areas of East Tarbert and Rona had greatly increased numbers of gulls breeding on them, and these two areas between them accounted for more than half (56%) the overall increase. The numbers on the North Ness remained relatively unchanged. (It is noteworthy that the North Ness was one of the easiest parts of the island to cull, in terms of locating nests and dead birds, which may in part explain this stability).

Table 3 gives the numbers of breeding pairs of lesser black-backed gulls during the same period. These data contrast with those for the herring gull on two main points. First, the numbers of lesser black-backed gulls are considerably less, but their proportion to herring gulls has steadily increased during the time when herring gulls were being severely reduced. Although the numbers in 1975 were 18.1% down on the 1974 totals, herring gull numbers dropped by nearly twice as much in the same year. In 1974, the lesser black-back constituted 10.3% of the gull population, 12.7% in 1975, 17.6% in 1976, and increasing to 18.6% in 1977. Second, there are three areas which are favoured by nesting lesser black-backed gulls (the west and east sides of the island and the area around the South Ness), and in 1976 and 1977 substantial increases were recorded in these localities. It will be remembered that these areas are generally much more vegetated than the northern parts of the island (Figure 3).

Table 2. The number of pairs of breeding herring gulls on the Isle of May 1974-1977

Area	1974	1975	% change	1976	% change	1977	% change
North Ness	640	265	-58.6	247	- 6.8	243	- 1.6
Rona	1,350	882	-34.7	564	-36.1	778	+37.9
East Tarbert	1,254	654	-47.8	420	-35.8	593	+41.2
West Side	1,741	1,156	-33.6	706	-38.9	823	+16.6
East Side	1,073	1,001	- 6.7	598	-40.3	658	+10.0
South Ness	897	527	-41.2	440	-16.5	575	+30.1
Totals	6,955	4,485	-35.5	2,975	-33.7	3,670	+23.4

Table 3. The number of pairs of breeding lesser black-backed gulls on the Isle of May 1974 - 1977

Area	1974	1975	% change	1976	% change	1977	% change
North Ness	22	4	-81.8	8	+100	6	-25.0
Rona	144	85	-41.0	106	+ 24.7	98	- 7.5
East Tarbert	19	12	-36.8	8	+ 33.3	11	+37.5
West Side	225	214	- 4.9	236	+ 10.3	285	+20.8
East Side	178	150	-15.7	164	+ 9.3	197	+20.1
South Ness	207	186	-10.1	220	+ 18.3	244	+10.9
Totals	795	651	-18.1	742	+ 14.0	841	+13.3

Elsewhere on the island the numbers of lesser black-backed gulls are relatively insignificant. Since the destruction of the island's vegetation was a major factor influencing the decision to cull the herring gull population, the importance of the lesser black-backed gull in relation to the natural history interest of the island warrants further investigation.

In general, lesser black-backed gulls lay later in the season than do herring gulls, and it is not unusual to find newly completed first clutches at the beginning of June. However, since counts were made just before culling began, it is unlikely that many pairs were missed.

4.3 EFFECT OF THE N.C.C. GULL CULL ON NUMBERS OF GULLS ON THE ISLE OF MAY

The breeding population of herring gulls on the island for the years between 1972 and 1977, together with the numbers of gulls killed and recovered, are given in Table 4. In order to calculate the effectiveness of culling, an estimate of those gulls which took baits and which died at sea unrecorded must be included. Reasonable precautions were taken on the island to minimise disturbance during the culling operations, thus ensuring a minimal number of partly narcotized and moribund gulls left their territories before succumbing to the drug. When baited nests were kept under observation (by myself) from a hide, it was noted that the proportion of gulls which took baits, but were not recovered on the island, was on average 10%. Although such monitoring was not undertaken during each cull, this proportion was probably constant from year to year.

The numbers of non-breeding gulls in 1972 and 1973 are based on counts by the NCC (N.J. Gordon, pers. comm.), whilst those between 1974 and 1977 are the figures quoted in Table 2. The overall total of gulls killed takes into account the numbers which have been narcotized or shot in the course of clearing experiments.

Table 4. The breeding population of herring gulls on the Isle of May (1972 - 1977) and the numbers killed through culling. The number dying at sea are estimated at being 10% of the number of gulls recovered on the island

Year	No. of breeding gulls	No. of non-breeding gulls	No. of gulls recovered dead on island	Estimated no. dying at sea	No. killed as result of clearing experiments	Totals killed	% of breeding population killed
1972	29,700	8,000	12,288	1,230	320*	13,838	46.59
1973	18,000	4,000	8,374	840	220*	9,434	52.41
1974	13,910	450	7,995	800	277	9,072	65.22
1975	8,970	300	2,745	270	224	3,239	36.11
1976	5,950	280	1,878	190	116	2,184	36.70
1977	7,340	100+	439	40	0	479	6.53
Totals			33,719	3,370	1,157	38,246	

* Data from G. Chabrzyk, pers. comm.

From Table 4 it can be seen that the large majority of herring gulls were killed in the culls of 1972-1974, with much reduced numbers in 1975 and 1976. In 1977 only 6.5% of the breeding population was killed (this doubling the average adult mortality from natural causes for the population as a whole). In all, more than 38,000 gulls have been killed between 1972 and 1977.

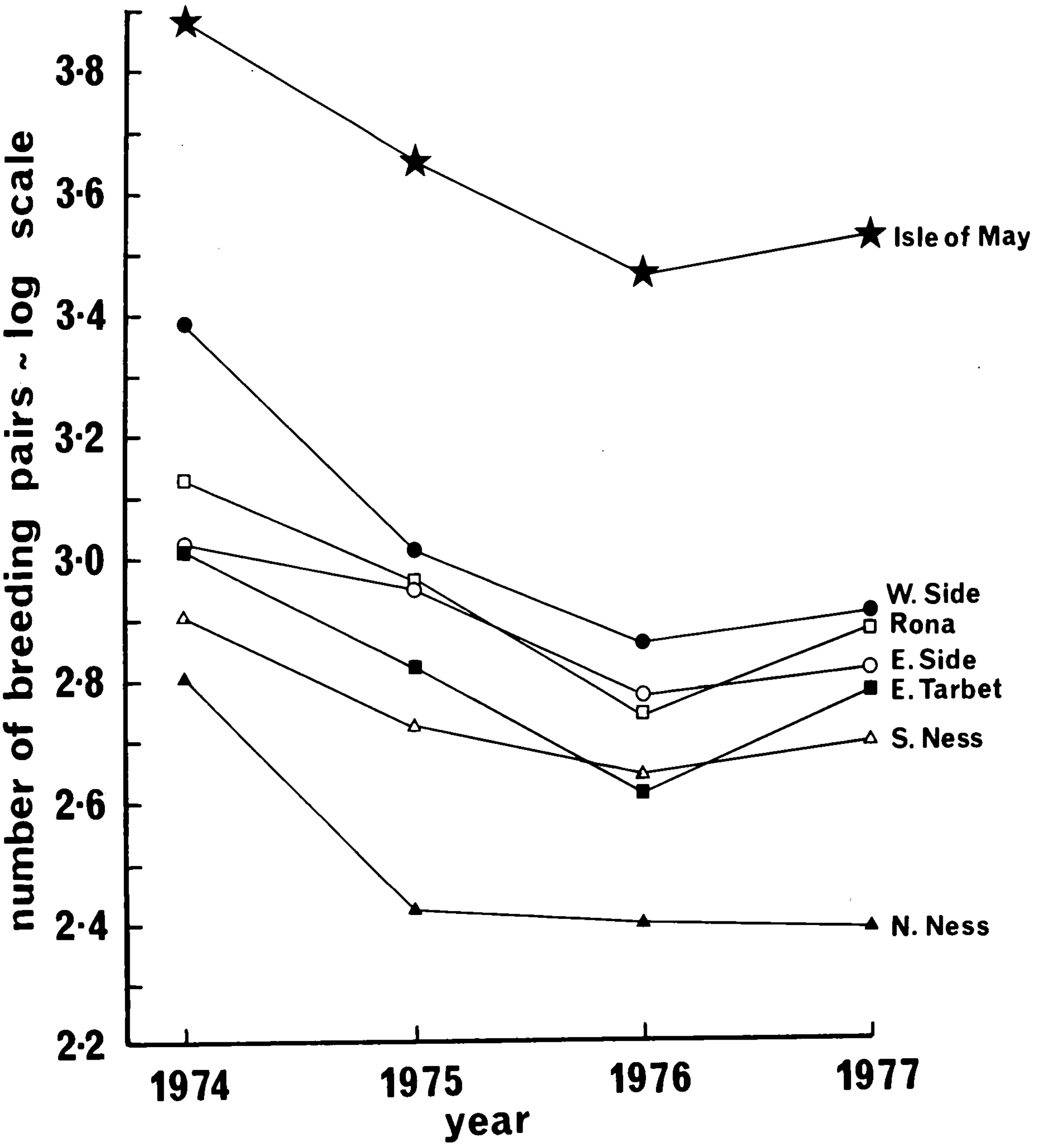
Table 5 summarises the effects of culling lesser black-backed gulls on the Isle of May since 1974. In the years previous, there are no reliable estimates for the numbers of pairs breeding, although in the cull of 1973 there were 694 corpses recovered on the island. Compared with the data given in Table 4 for herring gulls, it is clear that the control of lesser black-backed gulls has been much less effective.

Table 5. The breeding population of lesser black-backed gulls on the Isle of May (1974-1977) and the numbers killed through culling. The number dying at sea are estimated at being 10% of the number of gulls recovered on the island

Year	No. of breeding gulls	No. of non-breeding gulls	No. of gulls recovered dead on island	Estimated no. dying at sea	No. killed as result of clearing experiments	Totals killed	% breeding population killed
1974	1,590	< 100	503	50	28	581	36.5
1975	1,302	< 70	251	25	10	276	21.2
1976	1,484	< 50	304	30	15	349	23.5
1977	1,682	< 50	24	2	0	26	1.5
Totals			1028	107	54	1189	

Figure 11. Herring gull population trends in sub-colonies and sections of the Isle of May, 1974-1977.

Figure 11



number of breeding pairs ~ log scale
3·8
3·6
3·4
3·2
3·0
2·8
2·6
2·4
2·2
1974
1975
1976
1977
year
Isle of May
W. Side
Rona
E. Side
E. Tarbet
S. Ness
N. Ness

4.4 INFORMATION ON THE NUMBERS OF BREEDING GULLS IN OTHER STUDY COLONIES

4.4.1 Tarnbrook/Mallowdale Fell

Table 6 gives the results of population counts on Mallowdale Fell and Tarnbrook made in 1974 and 1975. Since most attention had been focussed on the parts of the colony which lay in the Mallowdale and Brennand estates (Figure 7), counts for these areas were made separately and with greater accuracy.

Table 6. The numbers of breeding pairs of lesser black-backed and herring gulls on Mallowdale and Brennand, the total numbers in the colony, and an estimate of the non-breeding population

Year	Mallowdale & Brennand (no. of breeding pairs)		entire colony (no. of breeding pairs)		Total no. of non-breeding birds	
	Lesser black-backed gull	Herring gull	Lesser black-backed gull	Herring gull	Lesser black-backed gull	Herring gull
1974	340	134	13,200	2,650	c. 1,000	c. 500
1975	310	140	13,700	2,600	c. 1,000	c. 600
1976	260	120	.... no counts made			

4.4.2 Cara

Table 7 gives the number of breeding pairs of herring and greater black-backed gulls on Cara between 1974 and 1977. No lesser black-backed gulls nest on this island. In 1974, counts were made in early August and although most nests were still obvious, especially where chicks were still being fed, the counts are certainly under-estimates.

It can be seen that between 1975 and 1977 the herring gull colony increased by only 3 pairs (0.7% p.a.) and over the same period, greater black-backed gulls increased by 4 pairs (2.4% p.a.).

There are no published records of gulls nesting on Cara, and the origins of the colony are enigmatic. Captain J. Macdonald who owns the island was unable to inform me on the numbers of gulls in recent years, but in the years before the Second World War great black-backed gulls were shot by gamekeepers on the mainland. The island is privately owned and access is restricted and difficult. Distribution maps of lesser and greater black-backed gulls given in Cramp *et al.* (1974) indicate that lesser black-backed gulls breed in the order of 11 - 100 pairs (which was not confirmed in this study), that great black-backed gulls breed in the same proportions (which was an under-estimate), and that herring gulls are absent.

Table 7. The number of pairs of breeding herring and great black-backed gulls on Cara, 1974 - 1977

Year	herring gull	great black-backed gull
1974	125*	110*
1975	217	148
1976	219	152
1977	220	155

* counts made on 2 August

5. ASPECTS OF POPULATION DYNAMICS (I)

5.1 SURVIVAL RATES

Survival underlies the entire process of evolution. How well an organism survives is relative, but at least it can usually be measured in time, with distinctions being made between stages of the life cycle. In recent years there has been a proliferation of model building and in theories which attempt to construct optimal strategies for survival by highlighting such arguments as to whether an organism should reproduce once or many times, and what the adaptive value of different reproductive rates might be. Some useful and unifying new concepts have been introduced (reviewed by Stearns 1976), but in general the multiplicity of models has outstripped their experimental confirmation in the field. Much of the content of this thesis is concerned with survival of gulls, and particular use is made of survival rates from which simple models for age composition can be constructed. These have been attempted in the hope that it is possible to find a correlation with breeding success, as indeed there should be, if all the variables involved can be identified and quantified.

The basic measure of survival is the rate at which a cohort declines, and an important distinction is usually made between juvenile and adult survival. (This is not always acknowledged by the model builders e.g. Cole (1954)). In general, it is a fair assumption that age specific survival must play a major role in determining reproductive rates in a stable environment (it is not clear that the herring gull does exist in a stable environment) but ultimately it is the survival rate which is the yardstick by which the success of the species may be judged.

It has taken many years to establish realistic survival rates for only a few species of birds. Reliable means of marking birds in quantity are prerequisites, and in long-lived species the results are often enigmatic. For example, an adult survival rate of 0.45 would eliminate a population of 1,000 individuals, all in their first year of adulthood, within nine years, whilst a survival rate of 0.90 would take at least 66 years to do the same. Dunnet and Ollason (1978) quote an adult survival rate of 0.98 for the fulmar whereby theoretically there would still be a number of individuals alive after 200 years. Clearly, there is a problem in defining the adult survival rates for long-lived seabirds, but this may be less of a problem if it can be confirmed that the high survival rate is really a trait of birds at optimal breeding age, and as senility progresses the older individuals quickly leave the breeding population and are overtaken by a much increased mortality.

5.2 HERRING GULL SURVIVAL RATES

There are several estimates for the survival rate of adult herring gulls in the literature. Some of these are given in Table 8. The figure quoted by Flegg and Morgan (1976) is certainly unacceptably low.

Table 8. Some estimates for adult survival in the herring gull

Authority	Location	Rate
Paludan (1951)	Graesholm (Baltic)	0.85
Olsson (1958)	Fenno-Scandinavia	0.70 - 0.80
Drost *et al.* (1961)	North Germany	0.90
Kadlec and Drury (1968)	U.S.A.	0.91 - 0.93
Harris (1970)	Skokholm	0.94
Parsons (1971)	Isle of May	0.90 ± 0.03
Chabrzyk and Coulson (1976)	Isle of May	0.935± 0.1
Flegg and Morgan (1976)	British Isles	0.75 (average over first six years of life)

It has been established that the rate of increase in the number of breeding herring gulls in the British Isles is close to 13% per annum. From this figure it follows that the average survival rate must be greater than 0.90 per annum (assuming that on average adult gulls produce not more than one chick per annum during their breeding life and that annual survival rate of immature gulls is not greater than that of adult gulls). The basis for this statement is shown in Section 9.2 following a formula devised by Capildeo and Haldane (1954). In Table 8 Parsons (1971) based his estimate on a sample of colour ringed adult herring gulls between 1966 and 1968, whilst Chabrzyk and Coulson (1976) used a number of herring gulls ringed as adults between 1966 and 1970 and subsequently killed in the culls of 1972 - 1974. Despite the large standard error, it seems that an annual adult survival rate of 0.935 is a realistic estimate and consistent with the 13% annual growth of the colony. Accordingly, this figure has been used in this study as a basis for calculating recruitment rates and age composition. Any attempt at confirmation of the figure by individually marking large numbers of adult gulls was precluded by the cull.

5.3 AGE OF RECRUITMENT IN THE BREEDING POPULATION

Chabrzyk and Coulson (1976) produced estimates for age of first breeding based on the numbers of gulls ringed as young on the Isle of May and which were recovered in the first three gull culls. They suggested that the respective ages at which first breeding took place was 34% at four years of age, 55% at five years, 23% at six years, and 8% at seven years, with the mean age of first breeding being 5.25 years.

Since the gull culls have coincided with the recruitment of the majority of gulls which have been marked as chicks in previous years (Table 1), it is possible to calculated the ratio of the more recent cohorts against a standard number (100) of the oldest colour ringed cohort, that of 1966. It is necessary to make the assumption that all the 1966 ringed gulls had recruited by 1972, their sixth year. Since gulls recruiting to the Isle of May are at risk through culling only when they have nested and laid eggs, the ratios of other cohorts to that of 1966 will be biased, since the more recent recruits have not been at risk for as long. Chabrzyk and Coulson (1976) attempted to correct this by applying a cull rate of 25% of the breeding population in each year (based on information supplied by NCC). More recent data supplied by the NCC, and personal observations (Table 3), indicate that this assumption in fact under-estimates the proportion of breeding birds killed. Consequently, the age of first breeding has been re-calculated, incorporating the numbers of ringed gulls recovered up to the cull of 1976, and including the 1970 and 1972 ringed cohorts (Table 9).

In Table 10 it has been calculated that the age of first breeding extends up to the eighth year, although in general more than 70% of gulls have recruited to the breeding population by their fifth year. The probability that recruitment in the 1966 cohort had not finished by 1972 is real, but unlikely to significantly bias the estimates. Thus, from the evidence presented in Table 10, the mean age of first breeding is 5.0 years.

Chabrzyk and Coulson (1976) found no gulls breeding in their third year on the Isle of May despite the large numbers of ringed birds available for observation. However, in the 1975, 1976 and 1977 culls, five, two and one ringed gulls respectively, which were in their third year, were recovered. Thus it would seem that at least a small proportion of third year gulls were recruiting to the breeding population. Reports of herring gulls breeding in their third year are infrequent. Drost *et al.* (1961) found eight male herring gulls breeding at this age, and Harris (1970) found two breeding on Skokholm. Since the culls which took place

Table 9. Numbers of herring gulls ringed as chicks and later recovered in the culls.

(No ringing was done in 1971).

	Year of ringing					
	1966	1967	1968	1969	1970	1972
Number ringed	4,325	5,230	4,812	400	367	1,350
Approximate % of available chicks	40	45	50	5	5	35
	Numbers recovered in culls					
1972	122	111	38	0		
1973	188	226	150	2	0	
1974	153	211	184	22	1	0
1975	40	121	70	11	11	5
1976	13	28	32	8	7	21

between 1975 and 1977 have produced only small numbers of the 1966-ringed cohort, and the numbers of ringed third year gulls are also small, a more precise assessment of the contribution to the breeding population by third year gulls comes from counts taken of both colour-ringed gulls and those in characteristic third year plumage on the Isle of May between 1974 and 1976 (Table 11).

Despite the number of third year gulls (counted in each year before the cull started) being in all years less than 1% of the total population, their appearance is nonetheless interesting, and presumably is a consequence of the lowered density of the breeding population. A comparable situation exists in the Tarnbrook and Mallowdale Moor colony which for the most part is a colony of very low density, ranging from 3 or 4 nests per hectare to not more than 55 nests per hectare. From a

Table 10. The age of recruitment in five cohorts of herring gulls ringed as young on the Isle of May, and later recovered in the culls

Year of birth	Age of recruitment	No. culled/ 100 "1966" gulls culled	Recruits equivalent to 100 gulls ringed in 1966, allowing for effect of culls	% Recruitment
1967	(4 (5	91	91	72
	6	120	16	13
	7	138	6	5
	8	302	14	11
	9	215	0	0
1968	4	31	31	41
	5	80	26	34
	6	120	10	13
	7	175	55	7
	8	246	4	5
1969	3	0	0	0
	4	1	1	14
	5	14	3	43
	6	28	1	14
	7+	6	2	29
1970	3	0	0	0
	4	1	0.25	9
	5	28	20.99	80
	6+	34	0.34	11
1972	3	5	11	38
	4+	38	18	62

sample of 640 herring gulls which have been culled under licences granted by the N.C.C., herring gull recruits in their third year were found to amount to 9.5% of the total, with 7% breeding at this age.

Contrary to the observations of Drost *et al.* (1961) and Harris (1970), who found that all third year breeding gulls were male, 45% of the total sample of 49 third year gulls which bred between 1975 and 1977 were female. Similarly, a sample of 29 non-breeding third year recruits which were collected in 1975 and 1976 and sexed by dissection contained 55% females.

It is interesting to note that apart from a number of third year gulls which have bred, there has been no evidence of an appreciable lowering of the average age of first breeding as the cull has progressed.

Table 11. The number of third year recruits which held territories, and the number which progressed as far as egg laying, on the Isle of May between 1974 and 1977

Year	No. of breeding third year gulls	% of population	Total no. of third year recruits holding territories	% of recruits *	% of population
1974	0	0	0	0	0
1975	18	0.2	37	0.8	0.4
1976	24	0.4	46	7.8	0.8
1977	7	0.1	31	0.8	0.4

* N.B. Expressed as the percentage of all the gulls recruited to the population that year.

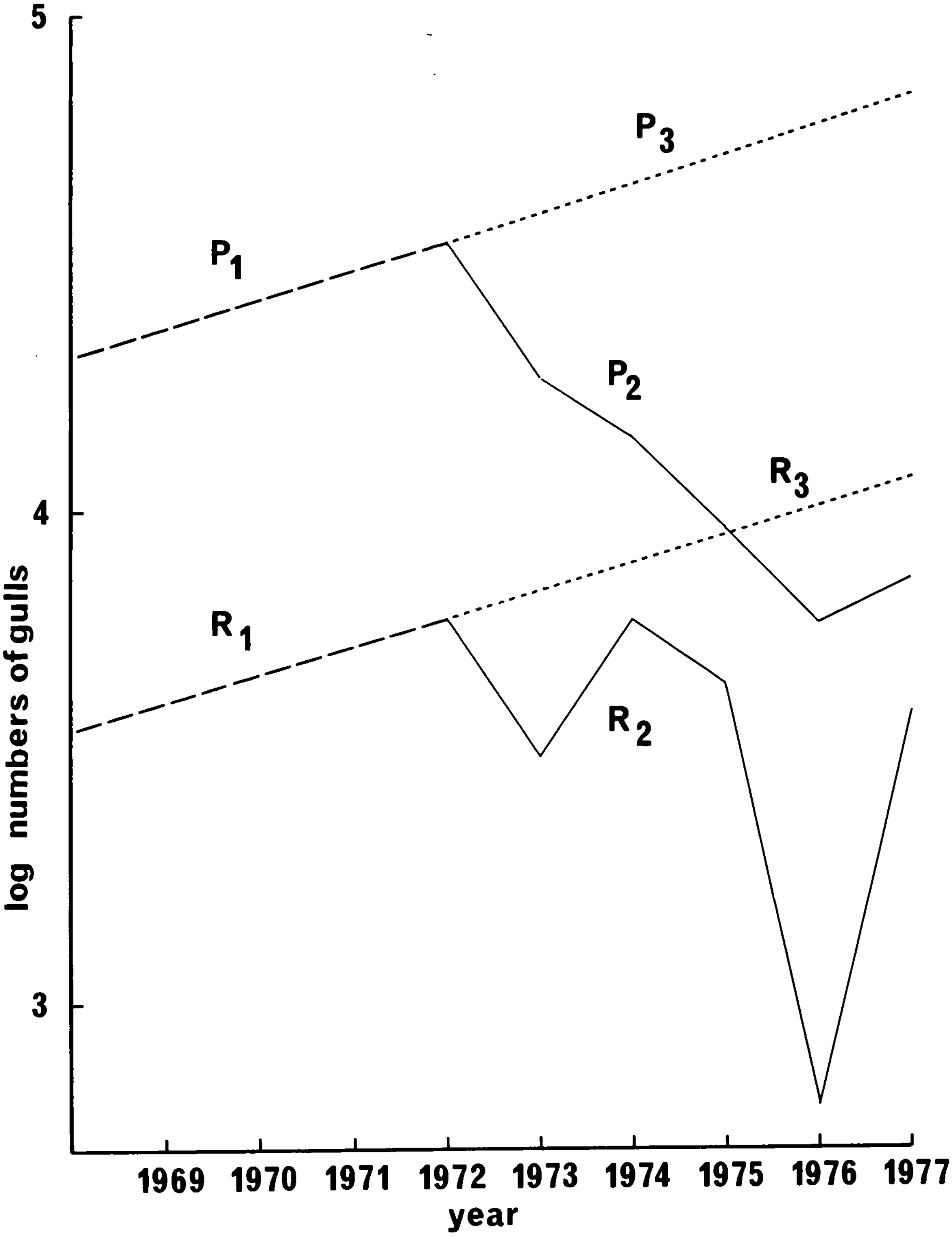
5.4 RECRUITMENT RATE

Recruitment is defined in this thesis as the numbers of mature gulls which annually enlist to the colony. Quantitatively, the recruitment rate can be expressed as the numbers of gulls which provide the yearly increase in the colony, plus the number required to replace the adult mortality of the previous year. Thus with an annual rate of increase of 13% per annum, 1,000 gulls will have increased to 1,130 by the following year, but with an annual mortality rate of 6.5%, 65 will have died in the same period. Consequently, the number of recruits required to sustain the increase is 130 + 65, and the recruitment rate, expressed in relation to the total population, is $\frac{195 \times 100}{1130} = 17.3\%$ per annum.

In common with almost all seabird species, the herring gull undergoes a period of adolescence referred to as deferred maturity. Thus, herring gulls are found to recruit to the breeding population between their third and eighth year on the Isle of May, and with the average age of first breeding being 5 years. As a consequence of deferred maturity, the expectation is that an annual cull would have no effect on the annual rise in numbers of gulls until at least four years from the onset, and no appreciable effect until the fifth year and thereafter (Figure 12). It is therefore possible to predict the numbers of gulls which should have been recruited to the Isle of May population up to 1977 - five years after the start of culling. In Figure 12, the dashed line (R) indicates this predicted recruitment rate. Since recruitment has two components - a proportion constituting gulls returning to their natal colony, and a proportion which are immigrants from other colonies, only the proportion which are native to the Isle of May are liable to suffer a lowering of numbers due to the disturbance of breeding success which had taken place in the colony five years previously. The proportion hatched in other colonies cannot be in any way affected, unless these colonies were also subjected to culling.

Figure 12. Population trends of herring gulls on the Isle of May, 1970-1977. Until 1972, the population (P) was increasing at an average rate of 13% per annum. The average number of gulls recruited to the population (R) was 17.3% of the population. After 1972 the gull cull greatly increased mortality, with a consequent drop in the population. The dashed line on P indicates the previous 13% annual movement trend which should have been reached had there been no culling. The recruitment of gulls dropped dramatically after 1972, although because of the continued existence of cohorts of unculled juveniles it would have been expected to proceed for at least four or five further years at the same rate (indicated by the dashed line on R).

Figure 12



5
4
3
log numbers of gulls
P1
P2
P3
R1
R2
R3
1969
1970
1971
1972
1973
1974
1975
1976
1977
year

5.5 SURVIVAL AND RECRUITMENT OF GULLS SINCE CULLING BEGAN

The annual gull cull on the Isle of May has obviously become the greatest single factor affecting survival in the breeding population. Each year the numbers killed have been counted. Thus it is possible to calculate a different annual adult survival rate for the breeding population, incorporating the proportion that survive from year to year under normal circumstances (93.5%) and the proportion that survive the cull; the number belonging to the latter category varies from year to year according to the intensity of culling. These survival rates are given in Table 12, and from this information it is also possible to estimate the number of gulls recruited annually to the breeding population. The number of newcomers must equal the current breeding population less the number of breeders surviving from the previous year.

The effects of culling on recruitment are shown in Table 13 in which the number of new recruits to the island are compared with the numbers predicted from Figure 12. It can be seen that in all years the recruits fall well below the predicted figure. Very low recruitment in 1976 cannot be adequately explained from present knowledge. Generally, the numbers of recruits since 1972 are only about a third of the predicted level. From Table 13 the shortfall of recruits in the five year period since the cull began is approximately 31,000, whilst the total number of gulls killed on the island since 1972 is over 38,000. This means that for every ten gulls killed in the culls a further eight potential recruits have been deterred from entering the island's breeding population. Thus it would seem that apart from killing breeding gulls, the most potent effect of the cull has been in reducing recruitment. Presumably the birds that have been deterred from breeding on the Isle of May have moved to join other colonies (see Section 6).

Table 12. The effect of cullling on survival and recruitment rate. The survival rate is obtained by combining average adult survival (.935) with survival from culling. Thus, in 1973 the survival rate is 0.935 x (1-0.4659) = 0.4994

Year	No. of breeding gulls	% mortality due to culling	Survival rate	No. surviving from previous year	No. of gulls recruiting	% recruits
1972	29,700	46.59				
1973	18,000	52.41	0.4994	14,831	3,168	17.6
1974	13,910	65.22	0.4450	8,010	5,900	42.4
1975	8,970	36.11	0.3252	4,523	4,447	49.6
1976	5,950	36.71	0.5974	5,359	591	9.9
1977	7,340	6.53	0.5918	3,521	3,819	52.0
1978			0.8739	6,414		

Table 13. The number of recruits compared with number predicted from the pre-cull rate of increase of colony (13%) and adult survival rate (0.935)

Year	Predicted recruits	Actual recruits	Difference	% Difference
1973	7,716	3,168	4,548	59
1974	8,662	5,900	2,762	32
1975	9,516	4,447	5,069	53
1976	10,882	591	10,291	95
1977	12,130	3,819	8,311	69
Totals	48,906	17,925	30,981	63

6. MOVEMENTS OF GULLS FROM THE NATAL COLONY

6.1 INTRODUCTION

It has frequently been stated that the herring gull returns to the colony of birth to breed on reaching maturity (Gross 1940; Paynter 1949; Tinbergen 1953; Harris 1970; Davis 1975). Instances of herring gulls breeding at colonies other than those from which they were hatched have generally been held to be exceptional occurrences involving a minority of recruits (Spaans 1971). Drury and Nisbet (1972) on the other hand concluded from an analysis of ringing recoveries that as many as a third of adult herring gulls may be found during the breeding season more than 130km from the natal colony, whilst Ludwig (1963) and Chabrzyk and Coulson (1976) have calculated that recruitment of young gulls to other than the natal colony could be higher than 60%.

From the outset it was clear that a large proportion of herring gulls which had been ringed as chicks on the Isle of May had not returned there to breed, and the only way to trace their movements was to conduct extensive searches in other colonies. By examining ringing recoveries from the BTO it was also possible to speculate on inter-colony movements, but with certain reservations which are mentioned below.

6.2 METHODS

6.2.1 Searches in other colonies

These were undertaken in known colonies, mainly on the east coast of the British Isles, and particularly to the south of the Isle of May. Included were the Bass Rock, Craigleith and Fidra (in the Firth of Forth), St Abbs Head (Berwickshire), the Farne Islands and Coquet Island (Northumberland) and most of the Yorkshire coast as far south as

Bempton Cliffs. The town nesting gulls in Sunderland and South Shields (Tyne and Wear) had been subjected to particularly close scrutiny since these colonies were independently studied by Dr Patricia Monaghan and are small enough for almost all the birds to be examined individually for rings.

6.2.2 Ringed gulls killed by culling in other colonies

In recent years various organisations have been obliged to control gull numbers in the interests of conservation and pest control, as has been the case on the Isle of May. The gull colonies on the RSPB bird reserves of Inchmickery, Fidra and Inchkeith have been culled since 1973, and Coquet Island was culled in 1976. Some of the Farne Islands were also culled in 1976 by the National Trust. These culls have provided useful data since many Isle of May ringed gulls have been recovered while incubating eggs - the best proof of breeding.

Gulls ringed as chicks in other colonies and which have been recovered during the Isle of May cull are also considered. These immigrants to the Isle of May are few in number since ringing has unfortunately been minimal in other colonies throughout the 1960s and 70s. Comparative data from the Tarnbrook/Mallowdale colony (which relate almost solely to the lesser black-backed gull) are presented separately.

6.2.3 BTO Ringing Returns

Recoveries of gulls, ringed on the Isle of May and reported by the general public through the BTO ringing scheme, have been examined up to June 1977. Whenever the reported recovery coincided with the breeding season (taken as being between 20 April and 1 August), with the bird being of breeding age (at least in its fifth year), and with the recovery located in or near a known colony, the finder was asked for additional information as to whether the bird might have been breeding or not. The results were subjective, but the information suggested instances of gulls recruiting to colonies other than the Isle of May.

6.2.4 Recoveries from culling

The number of Isle of May ringed gulls recovered through organised culls is detailed in Table 14. Only those colonies where Isle of May ringed gulls have been recovered are given: where other culls have taken place, but no recoveries made, the result is inconclusive since culling efficiency is seldom greater than 50%, and often much less.

6.2.5 Searches in other colonies

Despite the considerable effort afforded to searching other colonies for colour-ringed gulls, it would seem that this method is ineffective as regards estimating the number of ringed gulls. Thus, by recording the numbers of ringed birds killed in culling activities in the same colony, the numbers sighted invariably prove to be underestimated. For example, searches on the Farne Islands in 1975 and 1976 resulted in the sighting of two and five Isle of May ringed herring gulls respectively, whilst in the cull of 1976 when 10 out of 16 islands were culled, a total of 31 Isle of May ringed herring gulls were recovered from the 1534 herring gulls killed (P. Hawkey, pers. comm.). Table 15 details the results of searches in these colonies between 1974 and 1976, as well as two incidental sightings reported by the public - one in Dundee and one on the Isle of Man.

6.2.6 Recoveries reported by the general public

It is probably permissible to assume that an adult gull reported as dying between mid April and the end of July, in or near a gull colony,

Table 14. Isle of May ringed gulls recovered in other colonies by culling

Date	Colony	Year of Ringing 1966	1967	1968	1969	1970	Totals	% Ringed herring gulls in cull	Distance and direction from Isle of May
5.73	Inchmickery		3				3	-	48km W.S.W.
5.73	Fidra	1					1	-	19km S.W.
22.5.74	Inchmickery	1	1	1			3	-	
	Fidra		1	1			2	-	
20.5.75	Copeland (Co. Down)			1			1	-	245km S.W.
30.4.75	South Shields			1			1	-	150km S.S.E.
20.5.75	Inchmickery		1			1	2	2	
21.5.75	Fidra	1	4	7		1	13	3.7	
25.5.75	Craigleith		1				1	-	16km S.W.
26.5.76	Fidra		3				3	3	
13.5.76	Coquet Island	2	4	3			9	2.1	115km S.E.
.5.76	<u>Farne Islands</u>								
	North Wamses	4	5	2	1	1	13	2.5	
	South Wamses	2	4	2			8	3.9	
	East Wideopen	1	6	1			8	2.0	82km S .E.
	West Wideopen			4			4	1.4	
	Skeeny Scar	1					1	2.6	
	TOTALS:	13	33	23	1	3	73		

Table 15. Isle of May colour-ringed gulls sighted breeding in other colonies

Breeding Season	Year of Ringing								
	1966	1967	1968	1969	1970	Totals	Location	Distance and Direction from Isle of May	% Ringed Gulls in Colony
1972			1			1	Breeding on roof-top in Dundee	41km N.N.W.	6.3
1975 + 1976	3	4	2			9	St Abbs Head (Berwickshire)	42km S.E.	0.9
1975 + 1976	1	7	5			13	Bass Rock	12km S.W.	
1975	1	7	2			10	Inchkeith	40km S.W.	
1975	2	8	3			13	Sunderland)	155km S.E.	3.4
1975		6	3		1	10	South Shields) (Breeding on) roof-tops))	150km S.E.	2.5
1976		2				2	Fidra (seen after cull)	19km S.W.	
1976			1			1	Port Erin (Isle of Man)	273km S.W.	
TOTALS:	7	34	17	0	1	59			

was one of the breeding population. The results given are best considered with some caution however as the date of recovery cannot always be taken as being accurate, nor any estimate of the actual date of death.

6.2.7 Gulls recruiting to the Isle of May from other colonies

Although over 38,000 herring gulls have been killed on the Isle of May between 1972 and 1977, with the vast majority having been examined for rings, only 11 have been found which have recruited to the Isle of May population, having been ringed as chicks in other colonies (Table 16, Figure 13). Although this is a very small number, it does no more than reflect a near absence of gull ringing during the last 15 years (except for the Isle of May) as well as the inadequate quality of gull rings prior to the adoption of monel alloy in the early 1960s.

The annual rate at which young gulls recruit to breeding colonies is regulated by several factors acting interdependently. The age of first breeding has been shown to be variable and recruitment to the breeding population by the proportion of young gulls which survive to breeding age is probably influenced by the rate of growth, attractiveness and density of the natal and adjacent colonies.

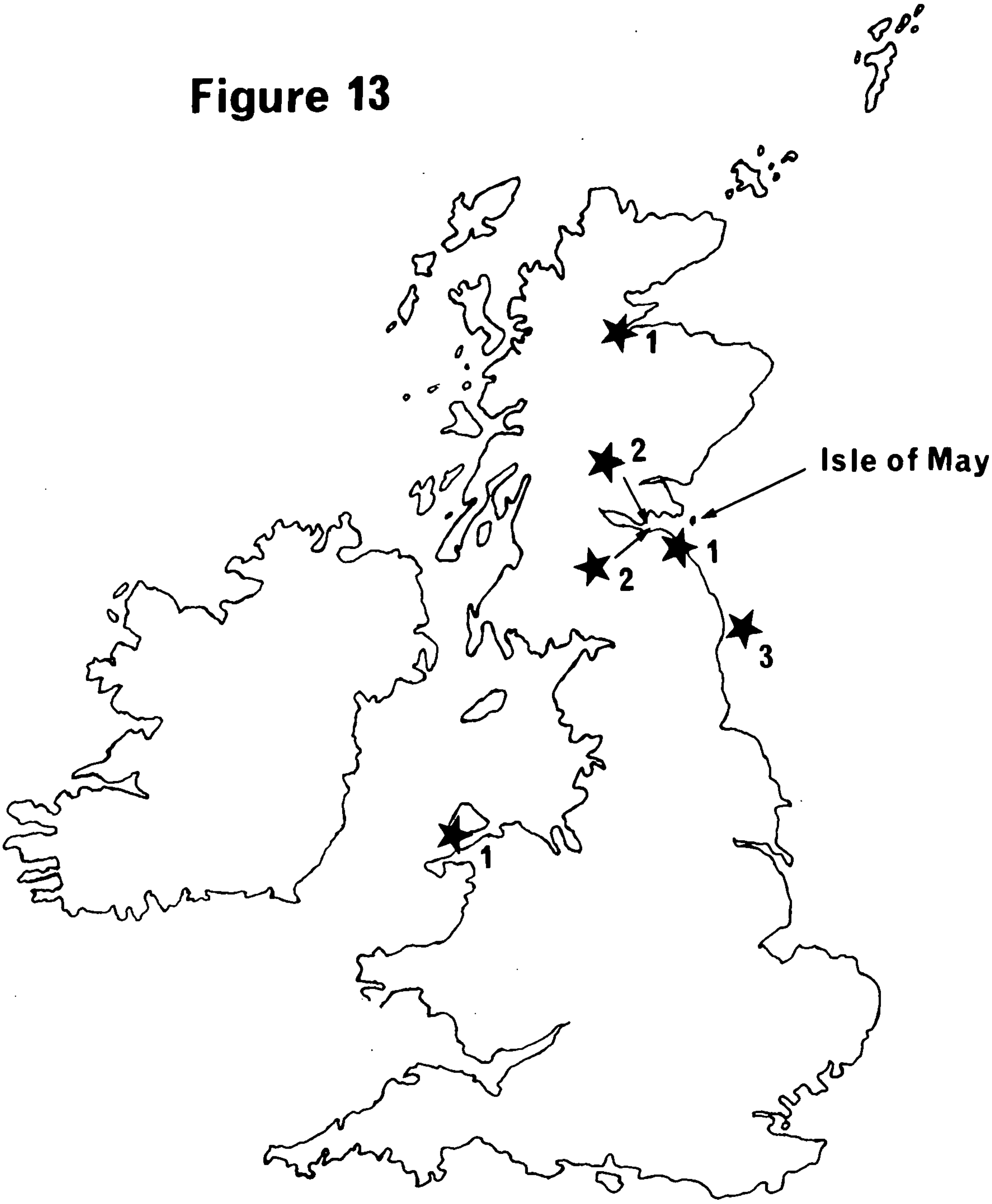
The numbers of gulls which have been ringed as chicks on the Isle of May, and have recruited to other colonies, cannot easily be calculated. The inference, however, from the detailed counts of colour-ringed gulls which still survive to breed on the Isle of May, and from totalling those ringed gulls which have been recovered during the culls of 1972-1977, is that several thousand marked gulls are breeding elsewhere, since they cannot be accounted for in their natal colony.

Table 16. Herring gulls ringed as chicks in other colonies and recovered in Isle of May gull culls

Ringing data	Finding data	Ring number	Ringing place	Distance and direction moved
22.7.65	22.5.73	GM27.344	Newborough Warren (Anglesey)	360km N.N.E.
25.7.65	22.5.72	AJ89.859	Bass Rock	12km N.N.E.
4.8.65	23.5.72	AJ79.115	Farne Islands	85km N.W.
27.8.64	22.5.73	AJ80.461	Farne Islands	85km N.W.
11.8.64	22.5.73	AJ74.245	Farne Islands	85km N.W.
26.6.62	22.5.73	AJ75.244	Nigg, Tain (Ross and Cromarty)	190km S.
12.7.68	21.5.74	GP08.255	Craigleith	16km N.E.
12.7.68	24.5.72	GP08.432	Craigleith	16km N.E.
12.7.68	30.5.74	GP08.404	Craigleith	16km N.E.
7.7.68	21.5.74	GP08.249	Inchkeith	40km E.N.E.
7.7.68	21.5.72	GP08.130	Inchkeith	40km E.N.E.

Figure 13. The origins of gulls which, after having been ringed as chicks, were later recovered in the culls on the Isle of May

Figure 13



The total number of gulls which have been identified breeding away from the Isle of May colony are summarised in Table 17, and illustrated in Figure 14.

Table 17.

	Year of ringing as chicks					
	1966	1967	1968	1969	1970	TOTALS
Total number found breeding away from Isle of May	29	78	51	1	3	162
% of total gulls ringed as chicks on Isle of May	0.67	1.49	1.06	0.25	0.82	1.07

6.3 DISCUSSION

The opinion has been widely held, though perhaps somewhat uncritically, that seabirds recruit to their natal colony to breed (Tinbergen 1953). Contrary findings have been remarked upon as exceptional and are not well documented in the literature. Harris (1966, 1972, 1976) described intercolony movements occurring on a small scale for the Manx shearwater and for the puffin. Further instances have been noted among the PROCELLARIIFORMES - in particular the British storm petrel (Spencer 1959). When, on occasions, herring gulls have been reported as recruiting to other than natal colonies, the movements have usually been attributed to disturbance (Tinbergen 1953; Spaans 1971). Ludwig (1963) on finding that only 40% of a surviving sample of herring gulls ringed in their natal colony returned to breed, considered that this low percentage was accounted for by environmental factors which prohibited return, rather than a tendency to recruit to new colonies.

On the other hand, Chabrzyk and Coulson (1976) also found that no more than 40% of young gulls returned to their natal colony on the

Isle of May, but inferred that large-scale dispersion was the normal course of events with female gulls showing a significantly greater tendency to nest away from the Isle of May than the males. Admittedly, considerable disturbance has occurred on the Isle of May as a result of culling, but the data indicate that for the majority of gulls in the 1966 and 1967 year classes at least, recruitment to other colonies had taken place before the onset of the cull of 1972. There are no records of any gulls moving to another colony, after having recruited to the Isle of May, although such an event is not improbable.

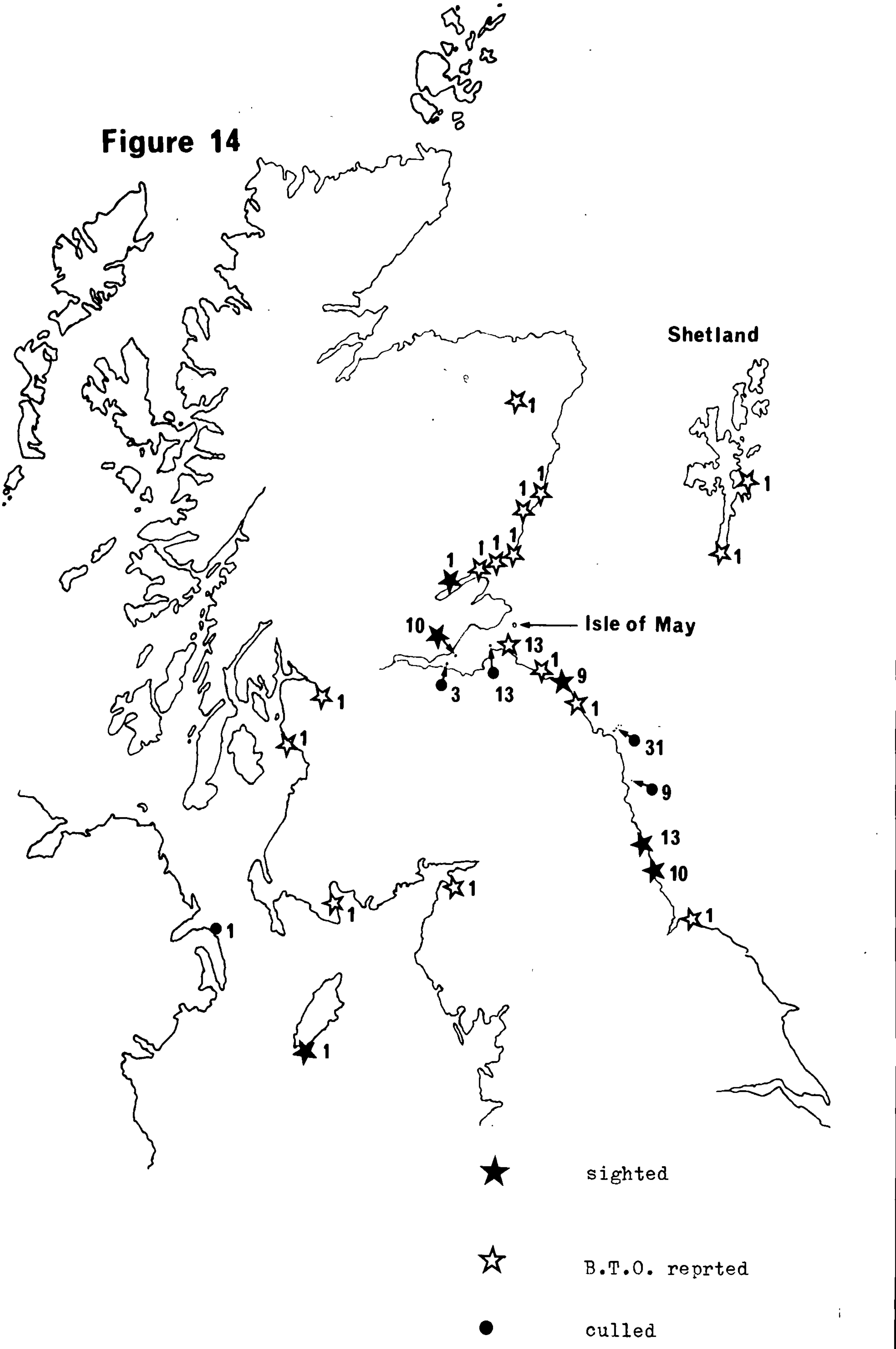
No more than a very small proportion of the marked gulls unaccounted for on the Isle of May have been located to date, but it should be remembered that the herring gull is one of our most numerous seabirds with a coastal breeding population estimated at about 334,000 pairs in 1969-70 (Cramp *et al.* 1974). It is clearly impractical, if not impossible, to search all the other colonies for the purpose of maximising the count of Isle of May ringed gulls.

The data indicate that movements are not only restricted to localised colonies, but exceptionally can be as great as 420km (Figure 14). It is interesting to note that several recoveries have been made on the west coast, e.g. Copeland (Co. Down) and Rockcliffe Marsh (Cumbria). The pattern of dispersion to other colonies agrees well with the general pattern of dispersion of recoveries of sub-adult gulls in the British Isles as a whole (Parsons and Duncan, 1978), indicating that sub-adult gulls may prospect new colonies whilst in their third and fourth year.

The habit of young gulls to disperse from the natal colony to breed has important implications for the evolutionary genetics of local gull populations as well as the control of the population by artificial means. For the former, it is necessary to consider herring gull

Figure 14. The location and numbers of herring gulls, ringed as chicks on the Isle of May, and recovered breeding in other colonies

Figure 14


Shetland
1
1
1
1
1
1
1
1
1
1
Isle of May
10
13
1
9
3
13
1
1
1
31
9
13
10
1
1
1
1
1
1
★ sighted
☆ B.T.O. reprted
● culled

colonies as being open populations with much gene flow. For the second consideration, since the herring gull is becoming a pest, any approach to control and management must take into account that herring gulls disperse over a wide area from any one colony.

6.4 COMPARATIVE INFORMATION ON THE MOVEMENTS OF LESSER BLACK-BACKED GULLS

6.4.1 The Isle of May

Between 1966 and 1968 Parsons (1971) ringed a total of 778 lesser black-backed gull chicks and 20 adult birds on the Isle of May. Some of these have been recovered in the culls between 1972 and 1976 (Table 18).

Table 18. The numbers of ringed lesser black-backed gulls recovered on the Isle of May in the culls 1972-1977

	Year of culling						
	1972	1973	1974	1975	1976	1977	Totals
Number ringed as:							
chicks	23	25	12	12	1	0	73
adults	7	1	1	0	0	0	9
Ringed as chicks elsewhere	9	2	2	3	0	0	16

In all, 9.4% of the lesser black-backed gulls ringed as chicks have been recovered on the Isle of May and a further 1.3% have been recovered breeding in other colonies, notably the Farne Islands (Table 19). Forty five percent of the gulls ringed as adults have been recovered on the Isle of May.

Sixteen lesser black-backed gulls ringed as chicks in other colonies have been recovered and, despite the much smaller number of lesser black-backed gulls culled on the island compared with herring gulls (600 as against over 38,000), this is a significantly higher total than has been recorded for the herring gull.

Table 19. The numbers of lesser black-backed gulls ringed as chicks on the Isle of May and recovered in other colonies

	Year of recovery			
	1974	1975	1976	Totals
Alford (Aberdeenshire)	1			
Mallowdale (Lancashire)		1		
Coquet Island			1	
Farne Islands			7	
Totals	1	1	8	10

6.4.2 The Tarnbrook/Mallowdale colony

Between 1958 and 1977 a recorded total of 40 ringed lesser black-backed gulls have been recovered in the colony during the breeding season. Only five of these were made in the years before 1972, and the remainder have been the result of control measures of one form or another by the land owners (nine recoveries since 1972) and MAFF (one recovery in 1972). In addition, a further four have been reported by the general public in the colony, most likely as a result of control by the owners. Since 1974, a further 21 recoveries have been made during the clearing experiments described in this study. Table 20 summarises the available data on these birds, most of which had been ringed as chicks. Twenty seven (67.5%) of the recoveries have been of chicks ringed in other colonies, mostly Walney. The notable exception was the recovery of an

Isle of May ringed female which had fledged in 1967. Thirteen lesser black-backed gulls ringed as chicks on Tarnbrook and Mallowdale, most of which were recovered on the Mallowdale side of the colony. It is not known what proportion this represents of the totals ringed in the past, but it seems that ringing was not extensive. In contrast, there have been many thousands of gulls ringed on Walney since the 1950s although, again, there are no precise figures.

The oldest gull recovered was 17 years (recovered on Mallowdale Fell) and it is also interesting to note that nine (22.5%) of the recoveries of gulls ringed as chicks in other colonies were aged five years or less, which indicates that the colony is still attracting a large proportion of young gulls from elsewhere. There has been one recovery of a Mallowdale ringed lesser black-backed gull ringed in 1966 and recovered "dead in colony" 55km N.E. on Sleightholm Moor (Yorkshire).

Table 20. The origins and age of ringed lesser black-backed gulls culled or otherwise recovered on Tarnbrook/Mallowdale Moors

Year ringed	Location	Year recovered	Age	Distance and direction moved
1958	nr. Lancaster	1962	4	c.8km E.
1958	Abbeystead	1975	17	nil
1960	Mallowdale	1970	10	nil
1962	Morecambe	1962	4+	nil
1962	Walney	1966	4	40km S.
1963	Walney	1970	7	40km S.
1963	Walney	1972	9	40km S. (2 recoveries)
1964	Walney	1972	8	40km S.
1964	Walney	1974	10	40km S.
1965	Walney	1975	10	40km S. (2 recoveries)
1966	Walney	1972	6	40km S.
1966	Walney	1974	8	40km S.
1967	Walney	1972	5	40km S.
1967	Walney	1975	8	40km S.
1967	Isle of May	1975	8	240km S.W.
1968	Walney	1972	4	40km S. (2 recoveries)
1968	Walney	1972	5	40km S. (2 recoveries)
1968	Walney	1974	6	40km S. (2 recoveries)
1968	Mallowdale	1977	9	nil
1969	Walney	1972	7	40km S. (2 recoveries)
1969	Walney	1974	5	40km S. (2 recoveries)
1969	Mallowdale	1972	3	nil
1969	Mallowdale	1974	5	nil (2 recoveries)
1969	Mallowdale	1975	6	nil (2 recoveries)
1969	Walney	1975	6	40km S.
1970	Walney	1974	4	40km S.
1970	Mallowdale	1974	4	nil (2 recoveries)
1970	Mallowdale	1975	5	nil (2 recoveries)
1970	Mallowdale	1976	6	nil (2 recoveries)

7. ASPECTS OF POPULATION DYNAMICS (II),

AGE

7.1 INTRODUCTION

The age composition of the population is fundamental to any consideration of an organism's life history. At its simplest, it can be considered as the configuration of age classes which results from the interrelationship between the survival of mature individuals and their reproductive effort. The relationship is cyclic, and variations which affect one trait will have some effect on the other two. For instance, total lack of breeding success in a season will influence the proportions of mature individuals available to breed in ensuing generations (especially when mortality is density dependent), and there will be concomitant changes in the age composition of the breeding population. This in turn could influence the relative success in future breeding seasons, the more so if reproductive success depends on age and experience of the parents.

Lotka (1907) established that a population will tend to a stable age composition when there is a stable sex-ratio, reproductive output and survival rate. Alternatively, where there is a steady rate of increase in a population, a stable age composition will result. The Isle of May population of herring gulls has been characterised by just such a steady rate of increase over many years (Figure 5) and with a known adult survival rate of 0.935 (Chabrzyk and Coulson 1976) it is possible to predict an age composition for the population.

7.2 AGE COMPOSITION OF THE ISLE OF MAY POPULATION

An important consequence of yearly culling has been to change the stable age composition of the breeding population of the Isle of May.

Assuming that all age classes are equally at risk to the method of culling (and there is good evidence that this is so), the elimination of a large proportion of older birds will lower the average age, with possible consequences for breeding success and the age of recruitment.

Since the age of first breeding is variable it is simpler to consider first the age composition in terms of "years since the start of breeding" rather than in actual years of age.

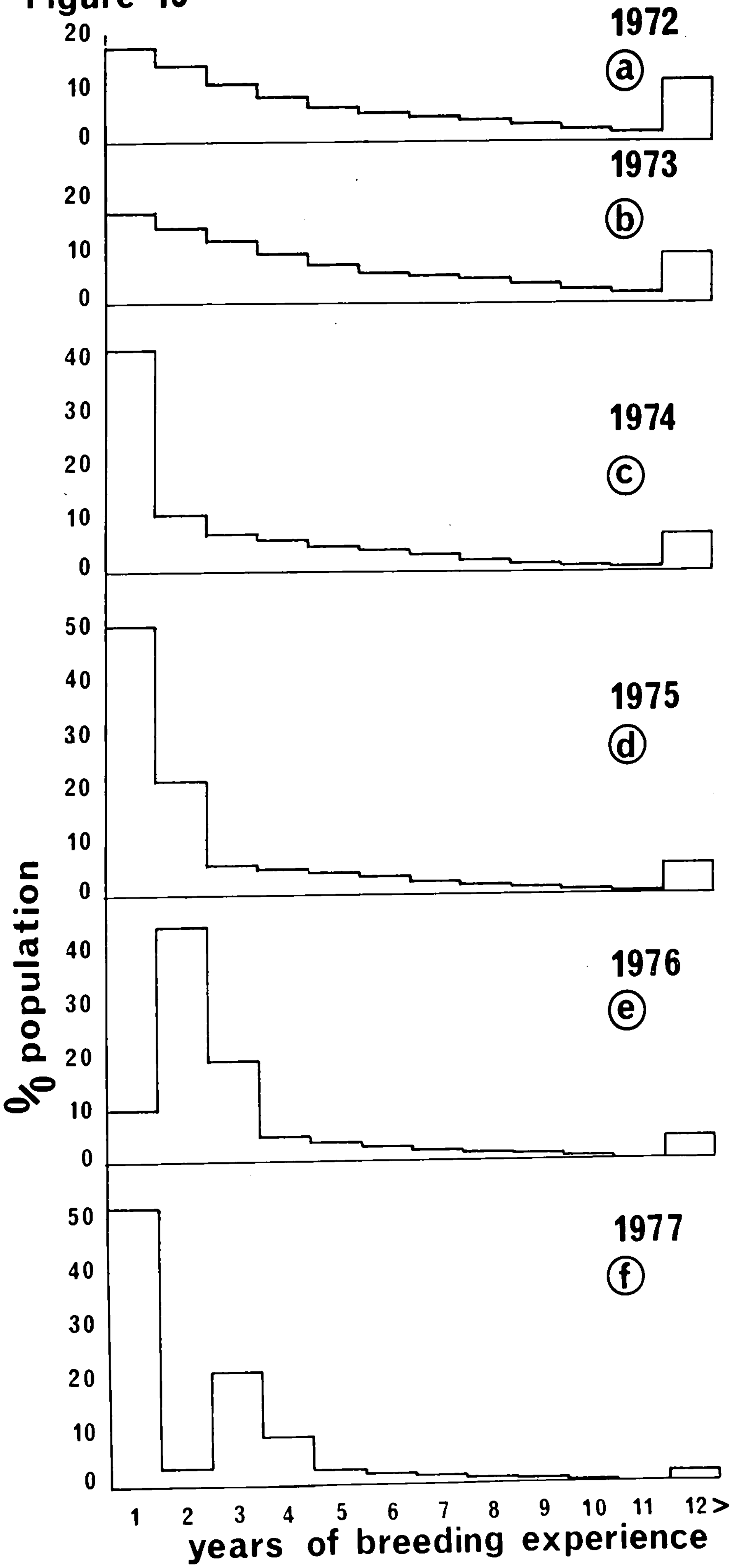
Once a constant annual rate of increase in the number of breeding gulls has been established, the age composition (but not numbers) becomes stabilised. Thus in each year 17.3% of the population (the new recruits) are breeding for the first time (see Section 5.3 for an explanation for the proportion of new recruits in each year). Birds breeding for the second time belong to the previous year's cohort of new recruits, which again numbered 17.3% of that year's population, but now less than 6.5% since they have been at risk for one year longer. Because the population has increased by 13% over the previous year, these birds which are breeding for the second time constitute 14.3% of the current year's population. Similarly, birds breeding for the third time will constitute 11.8% of the population, and so on. Figure 15(a) illustrates the distribution of "years since the start of breeding" for the population on the Isle of May in the breeding seasons prior to 1973.

The changes brought about in age composition by successive years of culling are illustrated in Figure 15 (b) - (f). While in the breeding season of 1972 the average breeding experience of the birds was 5.8 seasons, with 17.3% of the population breeding for the first time, by 1977 the average breeding experience had been reduced to 1.9 years, with just over 52% of the population breeding for the first time.

A consideration of the breeding experience of the population is useful when comparisons of breeding success (for example) are made between

Figure 15. The age composition of the herring gull population on the Isle of May, in each year between 1972 and 1977, expressed as "years of breeding experience" or "years since the start of breeding".

Figure 15



1972
a
1973
b
1974
c
1975
d
1976
e
1977
f
0
10
20
30
40
50
% population
1
2
3
4
5
6
7
8
9
10
11
12>
years of breeding experience

years. Notwithstanding, such an approach does not take into account such a potentially important factor as the age of first breeding. The relationship between age and fertility of breeding gulls is discussed in Section 9.2, but the importance of age composition, irrespective of breeding experience, is anticipated here by a careful consideration of how the age of first breeding influences the overall distribution of age classes within the population.

In Section 5.3 it was shown that on average 21% of herring gulls breed in their fourth year, 52% in their fifth, 13% in their sixth, 6% in their seventh, and 8% in their eighth year. We also know that in any one year 17.3% of the population are breeding for the first time when only natural adult mortality affects their numbers. Thus 21% of these gulls breeding for the first time are four, 52% are five. etc. If we take as an example a breeding population of 10,000 gulls, it is now possible to calculate the best estimate for the age composition. Table 21 shows how the calculation is made.

Let the current year be "Year A", then the population (P) is 10,000. The population in each previous year is calculated by the reduction of the present population by 13% for each year past. Thus the population three years previously (A-3) would have been

$$\frac{10{,}000}{1.13^3} = 6931$$

The number of gulls breeding for the first time (R) is 17.3% in each of these years. Thus in Year A this number is 1,730, and in Year A-1 the number would have been 1,531. It is now a straightforward matter to calculate the number of gulls in each age class from the fourth year onwards, but it is important to remember that there are two kinds of fifth year birds - those breeding for the first time, and those breeding for the second time. Similarly, there are three kinds of sixth year birds, and four kinds of seventh year birds etc.

Table 21. The calculation of age composition of a population of 10,000 gulls in year A. P is the population in years A back to A-11. R is the number of gulls breeding for the first time in each of these years. The numbers of gulls still alive in age groups 4-11 are calculated on the basis that 93.5% survive each year.

				age (years)											
year	P	R	s	4	5	6	7	8	9	10	11	12	13	14	15
A	10,000	1,730		363	900	225	104	138							
A-1	8,850	1,531	0.935		301	744	186	86	115						
A-2	7,832	1,355	0.874			249	616	154	71	95					
A-3	6,931	1,199	0.817				206	509	127	59	78				
A-4	6,133	1,061	0.764					170	422	105	48	64			
A-5	5,427	831	0.714						125	309	77	37	47		
A-6	4,805	735	0.668							103	255	64	29	39	
A-7	3,761	651	0.625								85	212	53	24	33
A-8	3,329	576	0.584									71	176	44	20
A-9	2,946	510	0.546										58	145	36
A-10	2,605	451	0.511											48	120
A-11	2,305	399	0.478												40
Totals				363	1,201	1,218	1,112	1,057	860	671	543	448	363	300	249
Percentages				3.6	12.0	12.2	11.1	10.6	8.6	6.7	5.4	4.5	3.6	3.0	2.5

In year A it is clear that 363 (21% of the new recruits) will be four years old, and similarly the number of five, six, seven and eight year old gulls will be 900, 225, 104 and 138 respectively. In order to calculate the numbers of fifth year gulls and older it is now necessary to consider the population in the years previous to A. In year A-1 there were 1,531 gulls breeding for the first time, 322 of them being four years old. This cohort which bred for the first time when in their fourth year now makes up the remainder of the fifth year birds in year A. Similarly, to calculate the number of sixth year gulls, we go back to year A-2, and so on.

When the numbers of gulls in each class are totalled it can be seen from Table 21 that 3.6% are four, 12.0% are five, 12.2% are six etc. There is little difference in the numbers of gulls in each age group between five and eight years, and nearly half the total population (49.5%) are aged between four and eight. Only 16.1% are more than 15 years old. This distribution of age should correspond to that on the Isle of May in 1972 before culling began, and is illustrated in Figure 16(a). The age composition of gulls from 1973 to 1977 is also given in Figure 16(b)-(f).

It can be seen that the distribution of ages in Figure 16 corresponds roughly to the distribution of "years of breeding experience". The similarities are most pronounced between the two histograms for 1972, but become less so after 1974. Since 1972, the proportion of birds in the population which bred for the first time at four years has steadily increased (except in 1976 when recruitment was low), whilst the proportion of fifth year gulls has also increased, but reaching a peak in 1975 of about 30%; since that time the proportion has remained fairly static at just under 30%. The proportion of old gulls (more than 15 years of age) has dropped from about 15% in 1972 to just over 3% in 1977. With reference to later sections on the effects of age of breeding, it is relevant to

Figure 16. The real age composition of the Isle of May herring gull population between 1972 and 1978.

Figure 16

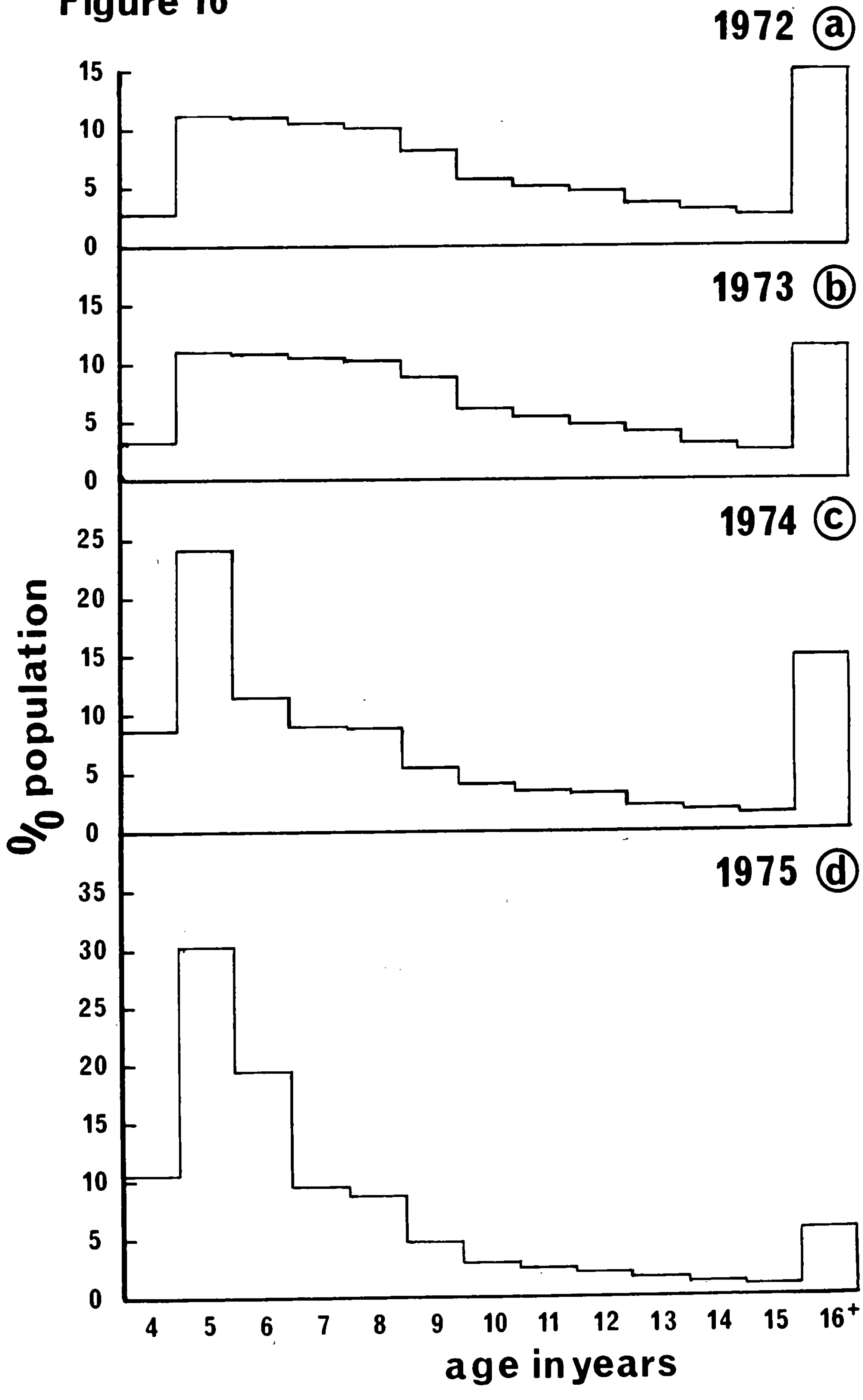
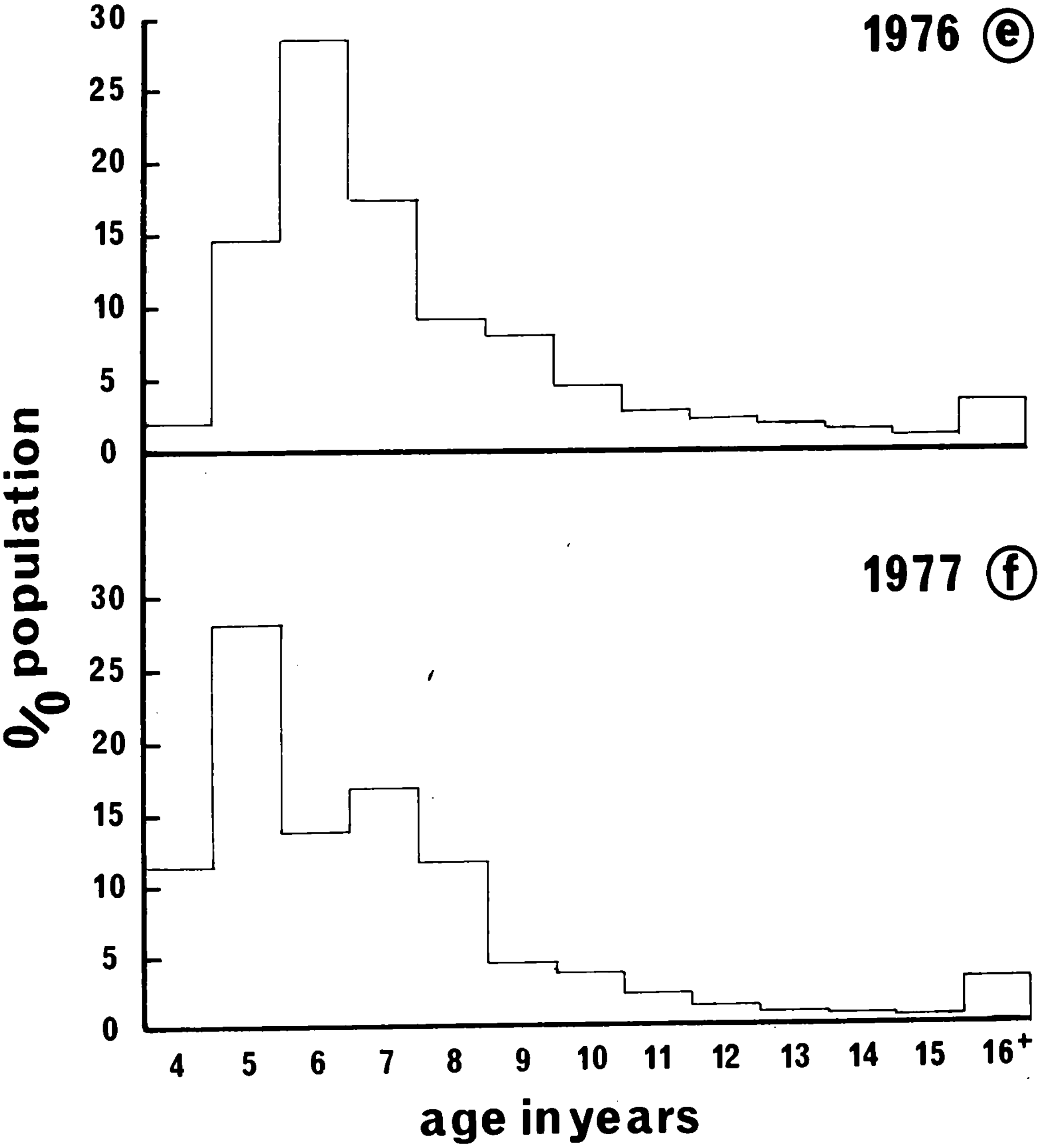

1972 ⓐ
15
10
5
0
1973 ⓑ
15
10
5
0
1974 ⓒ
25
20
15
10
5
0
1975 ⓓ
35
30
25
20
15
10
5
0
% population
4
5
6
7
8
9
10
11
12
13
14
15
16+
age in years

Figure 16 continued



point out that although 52% of the population bred for the first time in 1977, a very substantial proportion of the population (41%) had actually bred three or more times, and this may have been reflected by the above average breeding success for that year.

The basis for the calculation of age composition of course relies totally on realistic estimates for the age of first breeding and adult survival rates. It is important to emphasise that the histograms in Figures 15 and 16 are no more than best estimates for what we may intuitively understand to be one of the least reliably calculable properties of a population. For instance, no allowance has been made for intermittent breeding which may have been significantly increased since culling began, and it is not known how culling has affected the proportion of birds in each age class breeding for the first time. The assumption has been made that gulls recruit in the proportions shown above but, on the other hand, it has also been shown that a large proportion has moved elsewhere, and it is not known whether the cull has affected one particular age (or year) class more than another. The observation that a slightly higher proportion of gulls breed for the first time in their eighth year (8%) than in their seventh (6%) indicates that at least the cull may be dissuading birds at a younger age from joining the breeding population. There are two other variables which the calculation depends on: (1) an accurate count of the numbers of gulls killed each year so that the survival rate can be adjusted appropriately, and (2) an accurate count of the breeding population before the cull commences. Here, careful and precise observations can minimise the errors.

It is therefore worthwhile to make a simple check which can indicate the degree of accuracy of the age composition estimates. By calculating the complete range of ages (as indicated in Table 21) until the population disappears, the total number of gulls in each year class should equal the population count for that year. In 1973, the number of gulls was estimated at 18,000. Calculating backwards in time to find the complete age composition for all the gulls we find that the oldest bird would have been 48 years, and the number which are older than 40 is only 9 in all. The grand total of all age classes is 17,954 birds, and this figure for the population in 1973 is made independently of any population count actually made in that year. In fact, the population was estimated at 18,000 (N.J. Gordon, pers. comm.), so while this may be a fortuitous estimate, it is nevertheless an accurate one, and the error is only 0.3%. In other years the error is also acceptably small, so one can accept with some confidence that the calculation for survival rates and the counts of the breeding population made each year are realistic.

8. BREEDING BIOLOGY

INTRODUCTION

Many aspects of the breeding biology of the herring gull have received close attention from many workers in Europe and North America. Perhaps inevitably, many of the studies have been repeated several times and, whilst this is valuable for comparative purposes, interpretation is not always made the easier when reviewing the collective results. For example, Table 35 indicates but some of the estimates which have been confidently reported for chick fledging success, and similarly there are several published estimates for the numbers of chicks which a pair of gulls can be expected to raise when their broods are artificially increased (Table 22). Whilst most investigations of breeding success are interpreted as subjective reports based on careful observation, often there is little allowance made for such variables as human disturbance, and there are few attempts to relate the findings to the current trends in population dynamics. The experiments on multiple chick rearing seem of rather less value, other than to emphasise the fact that a herring gull (or any bird) can on occasion find enough food to feed a larger brood than has been evolved through natural selection. Such experiments are the hardest to set in an ecological context, and perhaps the hardest to justify. (An artificially increased brood can act possibly as an additional stimulus to the parent birds and there may be, as a consequence, an increased parental investment. However, there is no evidence that this can be sustained by parent birds in consecutive years and, moreover, the experiments are concerned with only one stage of the breeding cycle.)

Parsons (1971, and subsequent publications) undertook a thorough investigation of the breeding biology of the herring gull on the Isle of May whilst the colony was still in a state of expansion. This work has provided a basis for comparison with the findings of this study. There

Table 22. The size of some artificially enlarged broods in three closely related species of gulls, from which all the chicks were reported to fledge successfully

Authority	Species	Control or normal brood size	Enlarged brood size from which all chicks fledged	Location of study
Vermeer (1963)	glaucous gull	3	4 - 6	Mandarte, B.C., Canada
Harris and Plumb (1965)	lesser black-backed gull	2	4 - 5	Skokholm, Wales
Haynes and Morris (1976)	herring gull	3	5	Lake Erie, Canada

was little doubt that the cull has influenced breeding success on the island, but all indications are that where gulls remain undisturbed, as in the control areas, their ability to breed and raise chicks to fledging remains unimpaired. The cull has provided additional opportunities for new approaches and interpretations, especially where the effects of age and nesting density are involved. It is with these two important parameters that much of the investigation of breeding biology is concerned.

Comparative observations from the Mallowdale colony are scanty with respect to breeding biology, but a study of similar depth would have been impossible, with both time and resources being limited in the breeding season.

8.1 THE TIMING OF BREEDING

Perrins (1970) developed the argument that the date of laying of some species of birds (especially those of temperate regions) is influenced by the seasonal availability of food for the female. His conclusion was that the date at which the female lays is a resultant factor between the evolutionary advantages of laying early in the season (it is a widely observed fact that early hatching young tend to survive better), and the current physiological condition of the female. In general, the timing of laying may be delayed until food availability is such that eggs can be formed. Parsons (1975) has demonstrated, however, that the timing of breeding in the herring gull is in large measure independent of any stimulus mediated through food availability at the onset of breeding. In a like manner, it seems probable that the termination of laying is not directly influenced by food shortage since it coincides with the time when there is an abundance for both adults and young. The immediate relevance of Parsons' finding (*loc. cit.*) - that the timing of breeding was very similar over the four breeding seasons of 1966-1969 on the Isle of May - was that this gave an indication from the outset that information could be collected on aspects of breeding biology at the same time each year in the reasonably confident expectation that the onset of laying and the median date of laying (the date at which 50% of clutches were fully completed) would vary little between seasons. With all data standardised with respect to timing of breeding, interpretation of the other variables involved in breeding success would be made simpler. This was important since the gull cull was timed each year to take place towards the end of May, and it was necessary to collect data on fully completed clutches before culling commenced. Late breeding birds had to be excluded. As the breeding season progresses, there is a general decline in clutch size, egg size and fledging success in the herring gull (Parsons 1975). The same trend has been remarked upon (but with respect only to chick survival) by Painter (1949), Kadlec and Drury (1968) and Erwin (1971), although the opposite effect of an increase in chick survival as the breeding season progressed was reported by Harris (1969). Other species of gull show a similar seasonal decline in breeding success i.e. the lesser black-backed gull (Brown 1967) and the glaucous-winged gull (Vermeer 1963). Therefore, it would not be unexpected that estimates of breeding success from this study would be fairly high since most late breeding gulls have not been included in the analysis. As it proved, however, the proportion of gulls which had not started to lay by the time the cull had started was small (Table 23). Although clutch size and egg size is discussed in details for birds which had completed their laying by 23 May in each year, records were kept on the proportion of birds which had not completed their clutches by this date. With the exception of 1975, when the breeding season was particularly protracted, more than 90% of gulls had laid full clutches. Of the remainder, most were pairs which had lost nests and eggs earlier in the season and were in the process of replacing the clutch. Comparatively few pairs started laying after the median dates (Figure 17).

No truly comparative data could be collected from Mallowdale Fell on the timing of breeding since there was an initial difficulty of separating the nests and eggs of lesser black-backed and herring gulls, and in the time available this was not possible. Moreover, lesser black-backed gulls tend to breed later than do herring gulls, and in the course of nest counts at this colony the impression was that both species completed their clutches at a later date than on the Isle of May. Since the entire colony lies at over 450m a.s.l., the effects of temperature may have had some influence in determining laying date, but other factors, such as colony structure and density could have been involved as well.

8.1.1 Methods

Once laying commenced in each nest it was necessary to visit it only every second or third day in order to establish the ultimate clutch size and the date of completion. Since attendance at the Mallowdale Fell colony during the laying period was required for censusing, it was unavoidable that some of the laying period would be missed on the Isle of May. Accordingly, a timetable was arranged so that attendance was maintained on the Isle of May until more than 50% of clutches had been completed, or until at least one egg had appeared in all nests. In this way it was possible to estimate the ultimate date of clutch completion by extrapolation. Parsons (1971) had demonstrated that the average interval between a- and b-eggs, and between b- and c-eggs was 48.85 ± 0.44 hours (c.f. Drent (1967) who gave 48.72 ± 0.48 hours). Therefore, once the first egg had been recorded and marked, subsequent eggs could be checked several days later, and the date of completion calculated. The b- and c-eggs could be distinguished on size and colour differences, and also the amount of abrasion on the shell.

As a measure of the timing of laying, the median date was most appropriate. There was the possibility that younger gulls would tend to lay later in the season (as Coulson and White (1958) had demonstrated for the kittiwake). If the same tendency was true for the herring gull, it was anticipated that the clutch size might be under-recorded for the younger birds, since they would not have completed their clutch before the onset of culling. By collecting and analysing data on the timing of laying of a sample of aged gulls separately, with some estimate being made of the proportion of young gulls yet to lay, this possibility could in part be allowed for in the final analysis of breeding success of the population.

8.1.2 The median date of laying

In all years the median date of laying by the population was remarkably constant (Table 23) with the date falling on 17 May in the three years 1974, 1976 and 1977. In 1975, there was a protracted breeding season and enforced absences from the Isle of May made it difficult to judge accurately the date of clutch completion, but 21 May is a realistic estimate. Figure 17 emphasises the similarities in the distributions recorded for these years. Parsons (1971) reported that the median date of laying varied between 16 May and 18 May between 1966 and 1969.

Figure 18 illustrates the date of completion of clutches in a sample of aged birds. Despite small sample sizes for some age classes, there are still only small variations in the median date of laying. Thus for fourth year gulls (N=24) the median date of laying was 18 May,

Figure 17. The median date of laying on the Isle of May, 1974-77

Figure 17

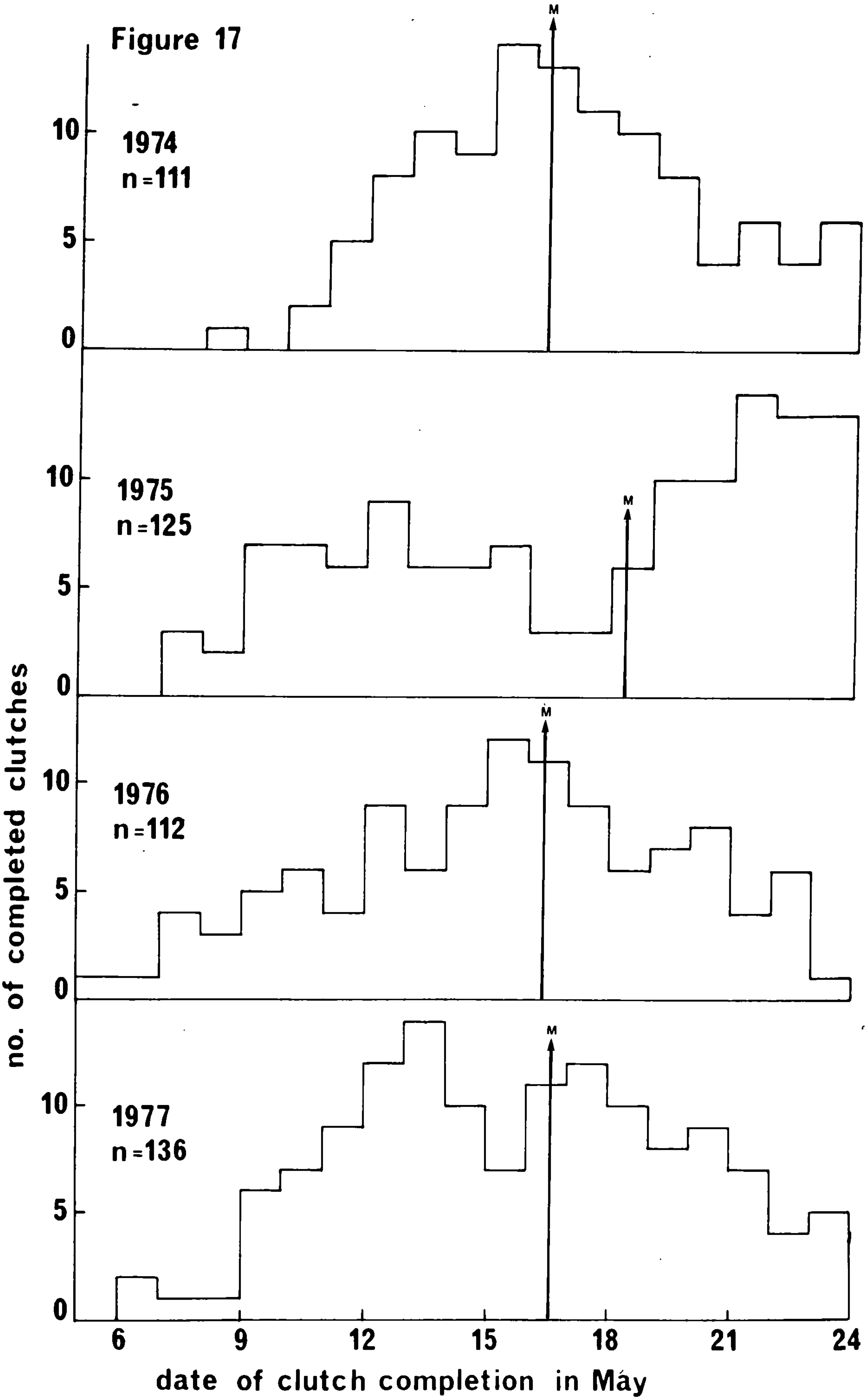
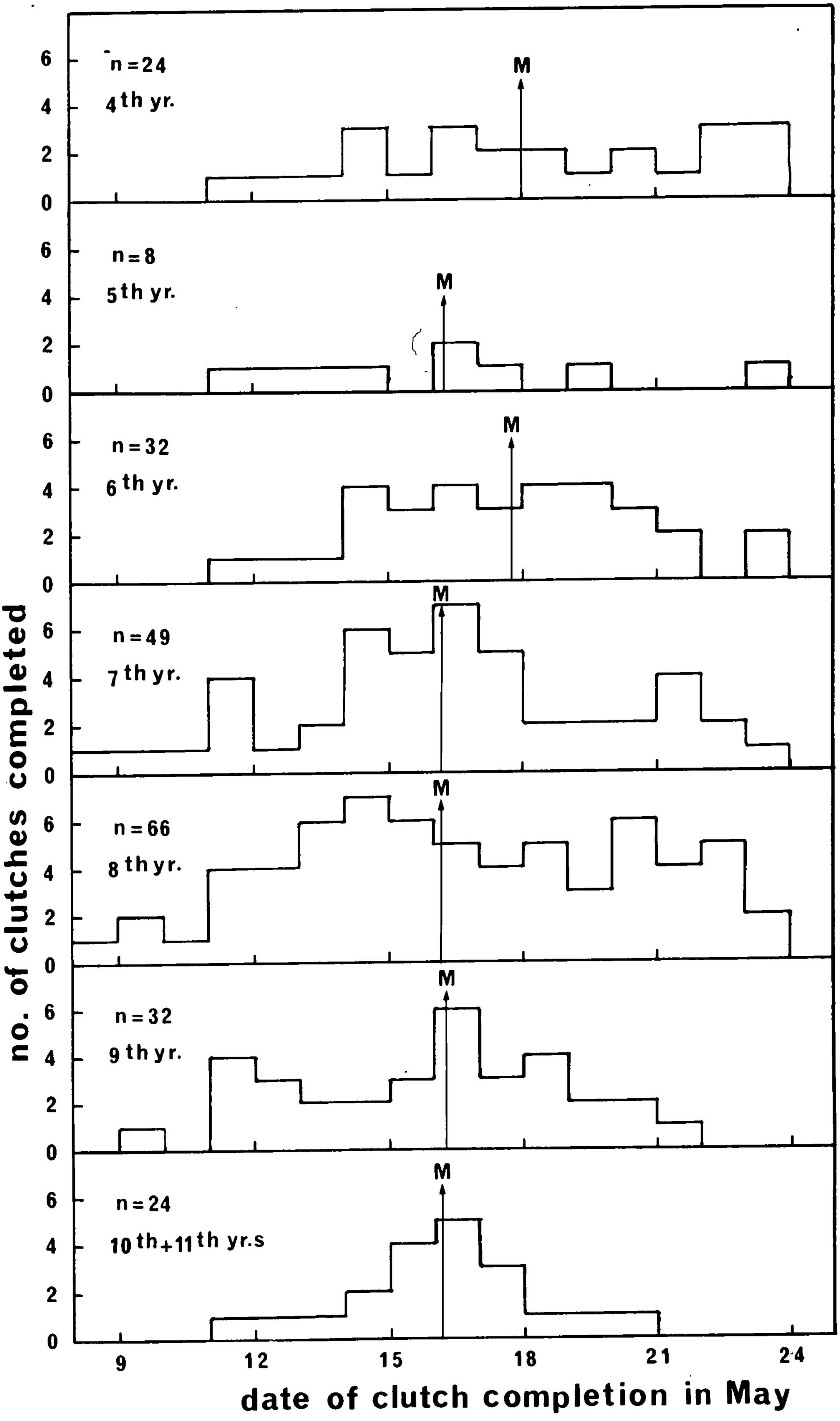

M
10
5
0
1974
n=111
M
10
5
0
1975
n=125
M
10
5
0
1976
n=112
M
10
5
0
1977
n=136
no. of completed clutches
6
9
12
15
18
21
24
date of clutch completion in May

Figure 18. The median date of laying in a sample of 235 pairs of gulls where the age of one parent bird was known. The sample of tenth and eleventh year birds has been combined.

Figure 18


n = 24
4th yr.
n = 8
5th yr.
n = 32
6th yr.
n = 49
7th yr.
n = 66
8th yr.
n = 32
9th yr.
n = 24
10th + 11th yr.s
M
0
2
4
6
no. of clutches completed
9
12
15
18
21
24
date of clutch completion in May

whilst for the combined ages of ten and eleven (N=24) there was a median laying date close to 16 May. In general, age differences in laying date are not extreme, and whilst younger birds may lay slightly later into the season, it was felt that such effects would have negligible consequences for reproductive success between different age groups.

Table 23. The proportion of completed clutches in three study areas 1974-1977. (These data refer only to those clutches which are again referred to in later sections on clutch size and egg dimensions.)

Year	Area	No. completed by 23 May	Max. no. of incomplete clutches on 23 May	% incomplete clutches on 23 May	Totals
1974	Tarbet III	111	9	7.5	120
1975	Tarbet III	63	39	38.6	102
	Maidens Rock	43	28	39.4	71
	North Plateau	19	31	62.0	50
	Total	125	98	43.9	223
1976	Tarbet III	72	8	10.0	80
	North Plateau	40	4	9.1	44
	Total	112	12	9.7	124
1977	Tarbet III	100	6	5.7	106
	North Plateau	35	5	12.5	40
	Total	135	11	7.5	146

8.2 CLUTCH SIZE

Introduction

Lack (1954, and many subsequent publications) repeatedly maintained that each species of bird has evolved those adaptations which permit it to reproduce as rapidly as possible in its natural habitat. In this respect, clutch size in nidicolous species has evolved to correspond to the maximum number of eggs which can give rise to fledged young. In a later publication (1968), Lack discussed clutch size with reference to seabirds, distinguishing between off-shore feeders which lay one egg, and in-shore feeders which lay two or three eggs. The distinction between the two categories is that off-shore feeding is a less predictable and reliable strategy than is in-shore feeding, and the single egg clutch has evolved as a consequence of the austere habitat.

Subsequent authors (e.g. Perrins 1970; Charnov and Krebs 1974) have supported the concept that clutch size is adapted to the largest number of young which parents can normally raise, and is regulated by food availability at the time of breeding. Wynne-Edwards (1962) on the other hand strongly contested this view and claimed that constraints are placed on levels of fecundity. Thus in those species where deferred breeding has evolved, such as in seabirds and raptors, the adaptation is in response to a need to prevent overpopulation.

In common with most other Larids, the usual clutch size of the herring gull is three eggs. Both sexes possess three brood patches and share incubation. The herring gull belongs to the category of in-shore feeders, and it is reasonable to suppose that the clutch size of three is not of recent evolutionary origins.

8.2.1 Methods

Throughout the four breeding seasons, clutch size was measured in samples of both aged and unaged gulls. Since the timing of the gull cull had been calculated to coincide with the maximum number of completed clutches in late May, measurement of clutch size was of necessity restricted to those birds which had completed laying on or before 23 May in each year. The nests were located in the six study areas previously mentioned, and as far as possible, clutch size was checked every 48 hours from the appearance of the first egg. Each egg was measured and marked in order of laying, and in this manner the sequence of laying could be followed, with replacement eggs or clutches easily identifiable. Similar investigations by Parsons (1971) had shown that the average interval between a- and b-eggs and between b- and c-eggs was about 49 hours. Clutches of two eggs were considered to be complete if a third egg did not appear after 72 hours. One-egg clutches were found on occasion, but they tended to occur more frequently as the late clutches of young birds, or as replacement clutches. One egg clutches were considered only when they belonged to birds which could be aged by plumage or rings. Only two single egg clutches were found between 1974 and 1977 among the unaged sample (there were very few birds with sub-adult plumage, and none which could be identified as less than four years old) and these clutches have been excluded from the results as it is by no means certain that they had not been deserted early in incubation.

8.3 ANNUAL VARIATIONS IN CLUTCH SIZE

The mean number of eggs recorded in clutches completed on or before 23 May from three study areas is given in Table 24. Replacement and incomplete clutches (as far as these could be identified) are not included. Clutch size was very constant from year to year, and although somewhat lower in 1975, paired Student's t-tests do not reveal any significant differences in the means between any two years.

Table 24. Mean clutch size in herring gulls on the Isle of May between 1974 and 1975

Year	N	$\bar{x}$	± s.e.
1974	120	2.76	0.045
1975	223	2.64	0.045
1976	124	2.72	0.040
1977	187	2.72	0.033

These figures are in close agreement with those of Parsons (1971) who found a mean clutch size of 2.73 ± 0.018 eggs in his control areas on the Isle of May in the years 1967 and 1968, and similar to that reported by Harris (1964) from Skomer (2.76 ± 0.037 eggs). However, they differ significantly from herring gull clutches on Walney where Brown (1967) found an average clutch size of 2.56 ± 0.53 eggs over a four year period ($p < 0.01$ in all years, except for 1975 where there was no significant difference).

8.4 VARIATION IN CLUTCH SIZE WITH AGE

Coulson (1966) drew attention to an increase in clutch size with age in the kittiwake, and the same trend has been shown for the Arctic tern (Coulson and Horrobin 1976). In other birds where the effect of age on clutch size has been investigated, such as the Shag (Potts 1966) and the white stork (Hornberger 1943), no such relationship has been demonstrated.

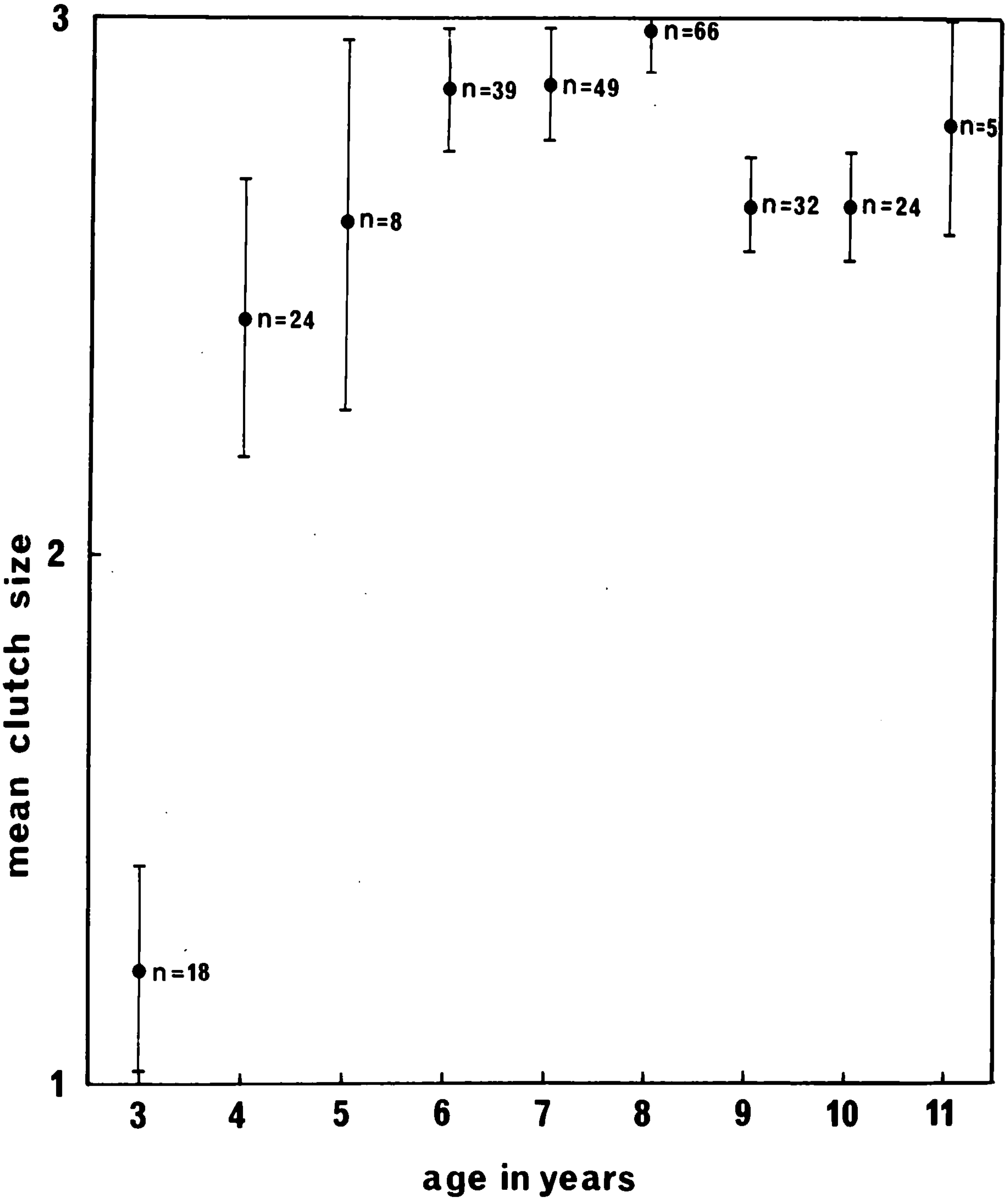
In the present study, clutch size in relation to age was investigated for a total of 265 clutches of eggs. At least one member of the pair was of known age, and data on the clutch size of each pair of gulls was collected for only one season (as far as was known). In the case of most third year gulls, ageing was based on plumage characters since few colour-ringed third year gulls were observed. Of the total of 265 aged birds, 127 were male and 125 were female, having been identified by behavioural characteristics or by dissection if they were later culled. In 13 pairs, the sex of the aged bird could not be determined.

Figure 19 portrays the results of this investigation, where mean clutch size (with 2 st. errors) is plotted against age. Since no significant differences could be found between years in average clutch size for the colony as a whole (Table 24), it is permissible to combine

Figure 19. Variations in clutch size with age

(with 2 standard errors)

Figure 19


3
2
1
mean clutch size
n=18
n=24
n=8
n=39
n=49
n=66
n=32
n=24
n=5
3
4
5
6
7
8
9
10
11
age in years

data on aged birds from all four breeding seasons. Table 25(a) summarises this data on clutch size for the age classes considered.

Table 25(a) Clutch size in aged herring gulls. with mean, standard deviation and standard error

clutch size	Age (in years)								
	3	4	5	6	7	8	9	10	11
c/1	14	2	0	0	0	0	0	0	0
c/2	4	10	3	7	8	8	12	9	1
c/3	0	12	5	32	41	58	20	15	4
N	18	24	8	39	49	66	32	24	5
$\bar{x}$	1.22	2.24	2.62	2.92	2.84	2.88	2.62	2.62	2.80
s.d.	0.43	0.65	0.52	0.39	0.37	0.33	0.49	0.49	0.45
± st. e.	0.10	0.13	0.18	0.06	0.05	0.04	0.09	0.10	0.20

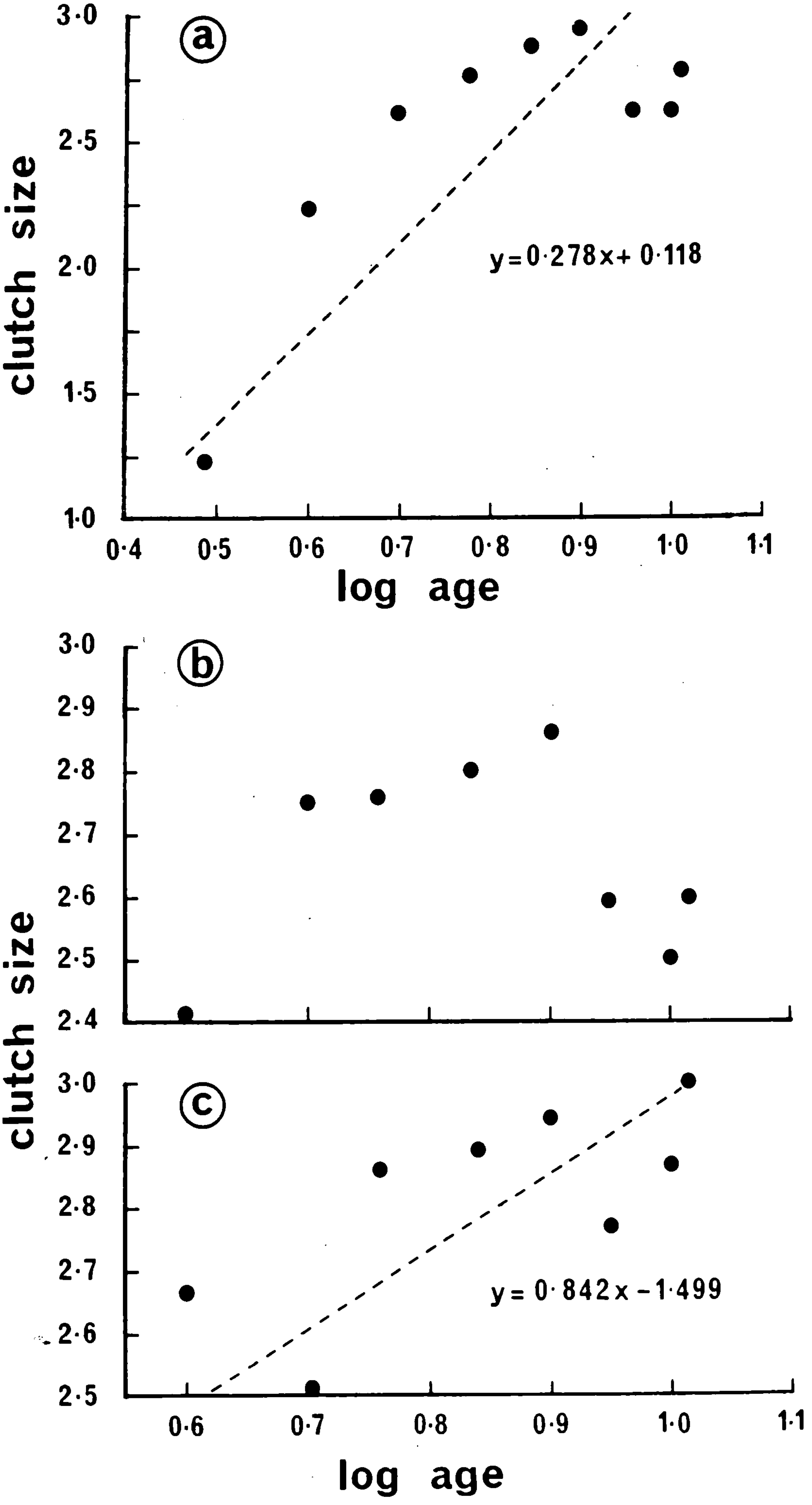
Sample sizes in gulls aged between 6 and 10 years are larger since these pertain to the recruits of the year classes ringed in quantity by Parsons between 1966 and 1968. In Figure 20 where mean clutch size is plotted against the log of age, it can be seen that mean clutch size increases with age in birds up to 8 years old, then becomes constant or declines. Clutch size in third year gulls is very low, the majority of birds laying only one egg. For herring gulls to breed in their third year is (in any case) unusual, and this age class has been omitted from Table 25(b), as has the two one-egg clutches of fourth year gulls which were probably atypical. From Table 25(b) it can be seen that the increase in clutch size in gulls between 4 and 8 years of age is significant ($p < 0.02$), and for gulls between 8 and 11 years of age the decline in clutch size is also significant ($p < 0.02$).

Figure 20. (a) Mean clutch size plotted against the log of age. The increase is significant ($r_7 = 0.771$, $p < 0.02$)

(b) The mean clutch size of pairs where only the male was of known age.

(c) The mean clutch size of pairs where only the female was of known age. The increase in clutch size is significant ($r_6 = 0.724$, $p < 0.05$)

Figure 20



ⓐ
3·0
2·5
2·0
1·5
1·0
clutch size
y=0·278x+ 0·118
0·4
0·5
0·6
0·7
0·8
0·9
1·0
1·1
log age
ⓑ
3·0
2·9
2·8
2·7
2·6
2·5
2·4
clutch size
ⓒ
3·0
2·9
2·8
2·7
2·6
2·5
y= 0· 842 x –1·499
0·6
0·7
0·8
0·9
1·0
1·1
log age

Table 25(b) Clutch size in aged herring gulls

Clutch size	Age (in years)							
	4	5	6	7	8	9	10	11
c/2	10	3	7	8	8	12	9	1
c/3	12	5	32	41	58	20	15	4

(For gulls aged between 4 and 8 years of age, the increase in clutch size is significant ($\chi^2 = 11.99$; d.f. = 4; $p < 0.02$). For gulls between 8 and 11 years of age, the decline in clutch size is also significant ($\chi^2 = 10.6$; d.f. = 3; $p < 0.02$)).

Coulson and Horrobin (1976) noticed a maximum clutch size in Arctic terns in birds which were between 6 and 8 years of age. Whilst increased clutch size with age has also been found in the kittiwake (Coulson 1966), there was no evidence of a decline in clutches laid by older birds, as was the case in this study.

8.4.1 The age of the female in the determination of clutch size

It has been assumed in this study that birds of a similar age will tend to pair together, as has been found for the Arctic tern (Coulson and Horrobin (loc. cit.) and for the kittiwake (Coulson loc. cit.). Unfortunately there were no instances in the above sample where both parents were of known age, but in five pairs of gulls where both members of the pair were found to be ringed, the evidence supported the assumption. (A four year-old male was paired with a five year-old female; three male seven year-old birds were paired with three females of the same age, and a nine year-old male was paired with an eight year old female). The breeding performance of these mated pairs could not be followed.

From the data presented in Table 26 (also illustrated in Figure 20) it can be seen that clutch size seems to be more associated with the age of the female than the male parent. In Table 26 the mean age of the male sample (7.59 ± 0.17 years) does not differ significantly from the mean age of the female sample (7.21 ± 0.15 years). However, the mean clutch size of pairs where only the age of the male parent is known (2.76 ± 0.04 eggs) does significantly differ from that where only the age of the female parent is known (2.85 ± 0.03 eggs) ($p < 0.001$). In Figure 20 where mean clutch size for each age class is plotted against the natural log of age in both sexes, there is no apparent relationship between clutch size and the age of the male parent, whilst for the female parent the linear correlation coefficient (r) is 0.729 ($p < 0.05$).

Table 26. The effects of age of each parent on clutch size

	age (male)							
clutch size	4	5	6	7	8	9	10	11
c/2	6	1	4	4	5	7	8	1
c/3	4	3	13	15	25	10	8	2
N	10	4	17	19	30	17	16	3
$\bar{X}$	2.40	2.75	2.76	2.79	2.83	2.59	2.50	2.67
	age (female)							
c/2	4	2	3	3	2	3	1	0
c/3	8	2	18	24	30	10	7	2
N	12	4	21	27	32	13	8	2
$\bar{X}$	2.67	2.50	2.86	2.89	2.94	2.77	2.87	3.00

These data indicate that the age of the female may be more important than the age of the male in determining clutch size. This may seem obvious from the outset, but it seems likely that clutch size is a better indication of age of the female than of the male parent.

8.5 EGG DIMENSIONS

8.5.1 Introduction

The physical dimensions of the egg are of fundamental functional significance when we consider both the physiological and ecological aspects of avian breeding biology. Generally, there is a broad correlation between egg volume and incubation period, which involves another intrinsically important parameter - the surface area. It is noticeable that the major correlations with which volume and surface area are associated (such as conductance of gases and heat, water loss and incubation period) have received increasing attention since the classic paper by Heinroth (1922) on egg weights and incubation periods, but rather less attention has been paid to ecological aspects of egg size. This is the more surprising since the dimensions of the egg can serve as indicators for subsequent breeding success and of parental age.

Two variables have been considered in this study - the axial length and breadth, from which the egg volume and an egg shape index can be calculated. Surface area was not considered (the calculation is complex (Besch *et al.* 1968; Hoyt 1976) and in any case was not of direct relevance). For egg volume and egg shape, a correlation has been shown to exist with age of the parent birds (see e.g. Richdale (1955) for the yellow-eyed penguin, Coulson (1963) for the kittiwake, and Coulson and Horrobin (1976) for the Arctic tern). Thus a change in age composition of the breeding population imposed by culling might be reflected by changes in egg size and shape. Moreover, a thorough investigation of egg size and shape is a prerequisite for further studies on hatching and fledging success of chicks. Eggs were not weighed as a measure of size since there is a progressive loss of weight as incubation advances.

It was felt that a more useful measure of size could be obtained from the volume. (Parsons (1971) checked the correlation between weight and calculated volume and found it to be extremely good (r was $+ 0.9854$, $p < 0.001$)).

8.5.2 Methods

The length and breadth of each egg in the 265 clutches of aged gulls and 537 clutches of unaged gulls (in all, 2,158 eggs) were measured to the nearest 0.1mm using Vernier callipers.

The volume was calculated from the expression

$$V = \frac{4\pi}{3} \cdot \left(\frac{B}{2}\right)^2 \cdot \frac{L}{2}$$ which is the volume of an ellipsoid,

and where V = volume, L = length and B = breadth.

Since the volume of a herring gull egg is less than that of an ellipsoid with the same length and breadth, a correction factor (k) has to be substituted. Several values of k have been calculated, based on the specific gravity of the egg. Parsons (1971) used the value 0.476 calculated by Harris (1964) and for the purposes of continuity the same value has been adopted in this study. The above expression can now be reduced to

$$V = 0.476.B^2.L$$

To calculate egg shape index, the expression $S = \frac{100.B}{L}$ was used (Coulson 1963) where S = shape index, B = breadth and L = length.

8.5.3 Variations in egg size

Parsons (1971) measured a total of 455 three-egg clutches in one breeding season (1968). The results of his investigation, taken from his unpublished Ph.D. thesis, are given in Table 27.

Table 27. Mean egg dimensions of 455 three-egg clutches laid in 1968 ± one standard error (from Parsons 1971)

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

The mean length, breadth and volume of the b-egg was significantly smaller than that of the a-egg and, similarly, the c-egg was significantly smaller than the b-egg. The volume differences between a- and b-eggs were however very much less than the differences between b- and c-eggs. Shape index tended to increase somewhat with decreasing volume (a relationship which was noticed by Barth (1967) as a feature of Larid eggs) although the legitimacy of calculating this correlation is questionable, since the two variables are not in any way independent.

The details of the mean egg dimensions in the present study are given in Table 28 and illustrated in Figures 21-23. These data refer to the 382 three-egg clutches which were laid in the consecutive breeding seasons 1974-77, and do not include data from aged gulls. It can be seen from Table 28 and Figures 21-23 that there is a considerable year-to-year variation in these data, and, most importantly, that there is a general trend of increasing egg size between 1968 and 1977. When the data in Table 28 are examined in detail two distinct features emerge which warrant discussion.

First, these differences are examined in Table 29. It can be seen that between 1968 and 1977 there was a significant and progressive increase in the length and breadth of a-, b- and c-eggs, with a

Table 28. Mean egg dimensions of three-egg clutches of breeding seasons 1974-77, with one standard error

Year	egg	N	length	breadth	volume	shape index
1974	a-	85	69.96 ± 0.19	49.31 ± 0.07	80.99 ± 0.34	70.52 ± 0.17
	b-	84	68.51 ± 0.16	48.45 ± 0.06	76.59 ± 0.30	70.72 ± 0.17
	c	84	67.34 ± 0.14	47.63 ± 0.08	72.75 ± 0.32	70.76 ± 0.17
1975	a-	90	69.95 ± 0.19	49.03 ± 0.10	79.73 ± 0.46	70.42 ± 0.19
	b-	90	68.51 ± 0.19	48.05 ± 0.09	75.30 ± 0.40	70.17 ± 0.20
	c-	90	67.24 ± 0.22	47.30 ± 0.12	71.66 ± 0.48	70.39 ± 0.24
1976	a-	72	70.28 ± 0.26	49.18 ± 0.10	80.94 ± 0.55	70.01 ± 0.23
	b-	72	68.80 ± 0.18	48.39 ± 0.13	76.73 ± 0.51	70.35 ± 0.20
	c-	72	67.20 ± 0.20	47.27 ± 0.12	71.55 ± 0.48	70.35 ± 0.23
1977	a-	135	70.33 ± 0.24	49.31 ± 0.10	81.48 ± 0.48	70.21 ± 0.24
	b-	135	69.64 ± 0.24	48.59 ± 0.11	78.38 ± 0.56	69.85 ± 0.25
	c-	135	68.01 ± 0.23	47.59 ± 0.11	73.42 ± 0.51	70.05 ± 0.26

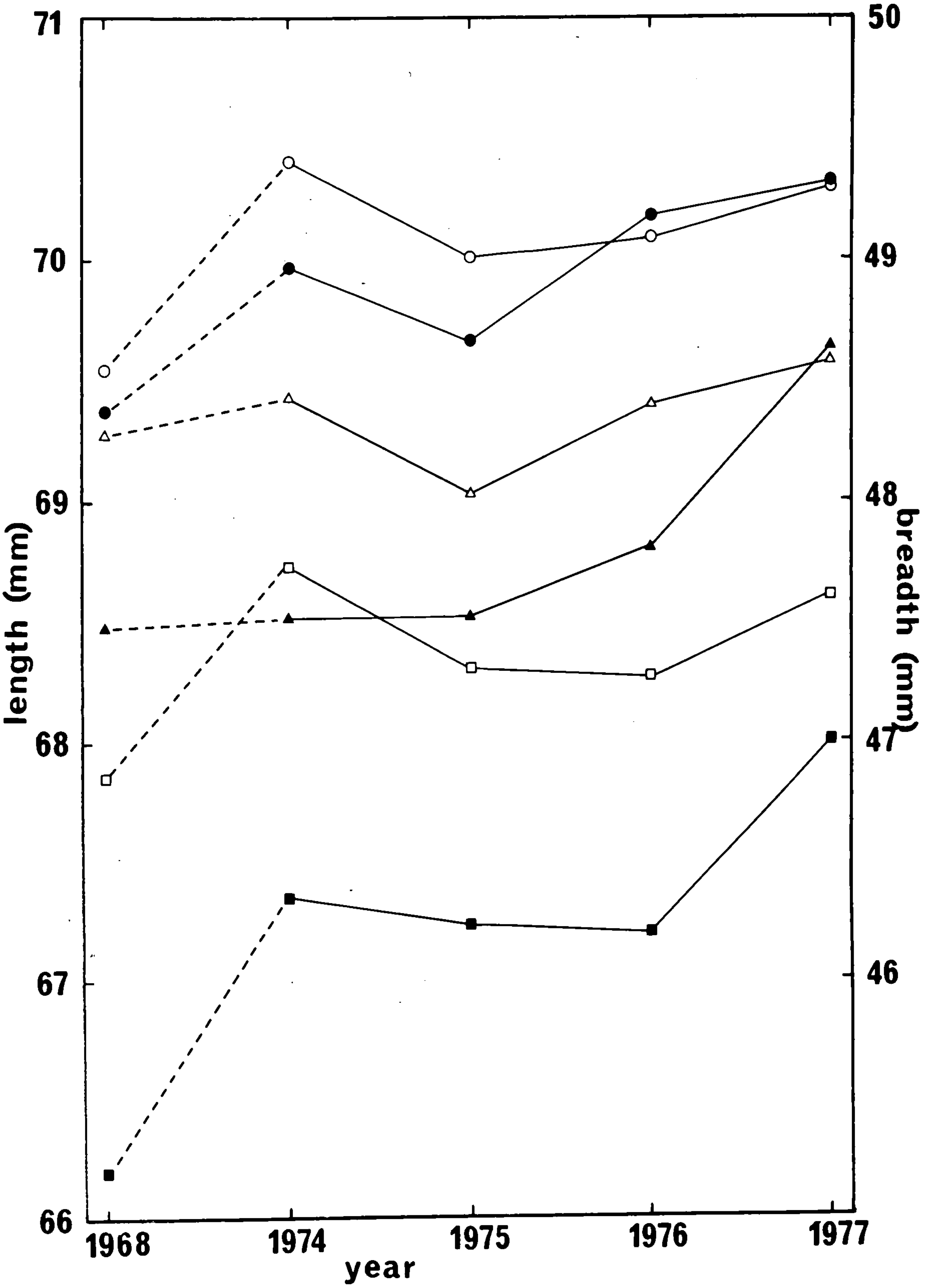
Table 29. Differences in egg dimensions between paired years (see Table 28). t is the value of Student's t and p is the level of significance. Only 3-egg clutches are considered. Data for 1968 is from Parsons (1971)

		a-egg		b-egg		c-egg	
Length	paired years	t	p	t	p	t	p
	1968 : 1977	$t_{588} = 3.42$	<0.001	$t_{588} = 4.25$	<0.001	$t_{588} = 7.83$	<0.001
	1974 : 1977	N.S.		$t_{217} = 5.44$	<0.001	$t_{217} = 2.49$	<0.02
Breadth	1968 : 1977	$t_{588} = 6.31$	<0.001	$t_{588} = 2.38$	<0.02	$t_{588} = 5.67$	<0.001
	1974 : 1977	N.S.		N.S.		N.S.	
Shape	1968 : 1977	N.S.		$t_{588} = 2.62$	<0.01	$t_{588} = 2.68$	<0.01
	1974 : 1977	N.S.		$t_{217} = 2.88$	<0.01	$t_{217} = 2.28$	<0.05
Volume	1968 : 1977	$t_{588} = 6.35$	<0.001	$t_{588} = 3.58$	<0.01	$t_{588} = 6.93$	<0.001
	1974 : 1977	N.S.		$t_{217} = 2.82$	<0.01	N.S.	

Figure 21. The mean lengths and breadths of herring gull eggs on the Isle of May in 1968 and 1974-77. The data for 1968 are from Parsons (1971).

●	a - egg length	○	a - egg breadth
▲	b - egg "	△	b - egg "
■	c - egg "	□	c - egg "

Figure 21



71
70
69
68
67
66
50
49
48
47
46
length (mm)
breadth (mm)
1968
1974
1975
1976
1977
year

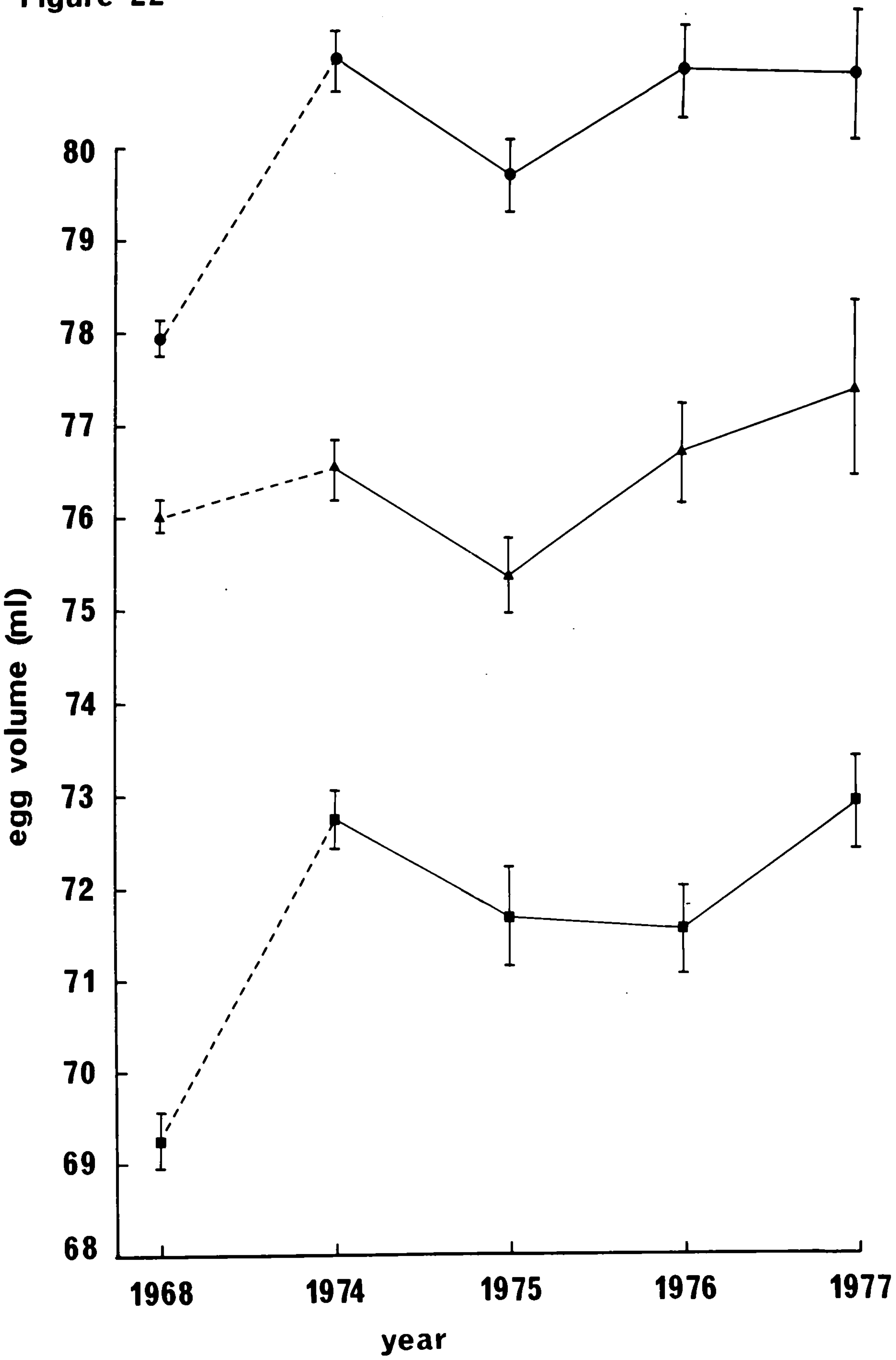
Figure 22. The mean volumes of herring gull eggs on the Isle of May in 1968 and 1974-77, with two standard errors. The data for 1968 are from Parsons (1971)

● a - egg volume

▲ b - egg "

■ c - egg "

Figure 22



egg volume (ml)
80
79
78
77
76
75
74
73
72
71
70
69
68
1968
1974
1975
1976
1977
year

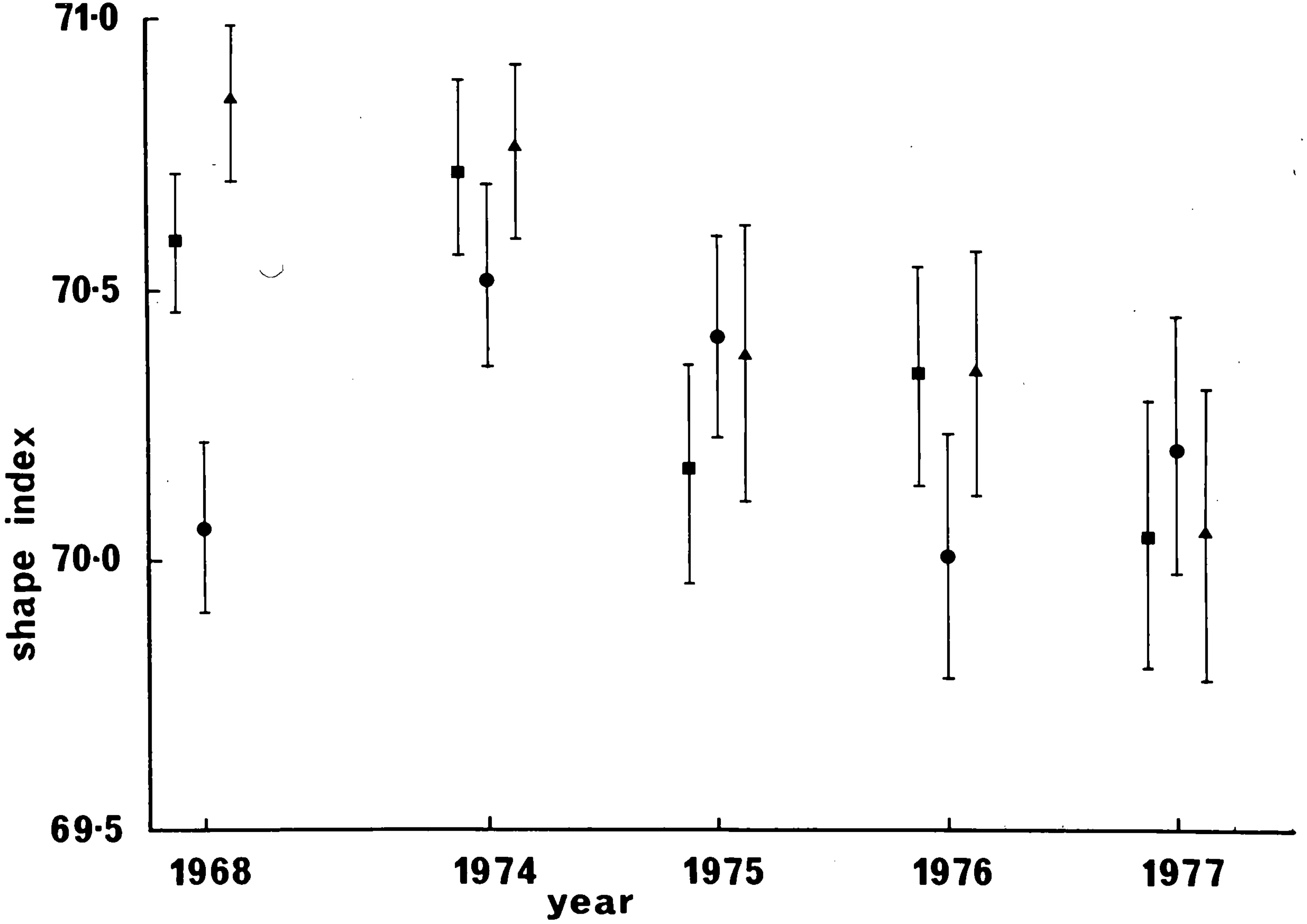
Figure 23. The mean egg shape index of herring gull eggs on the Isle of May in 1968 and 1974-77, with two standard errors. The data for 1968 are from Parsons (1971)

● a - egg shape index

▲ b - egg " "

■ c - egg " "

Figure 23



corresponding increase in egg volume. The shape index of a-eggs has not significantly changed in this period, but there has been a significant trend towards a smaller egg shape index in the b- and c-eggs. Between 1974 and 1977, these changes are not so pronounced. There is no significant change in egg breadth between 1974 and 1977 (which is the least variable factor in influencing the volume and the shape) and only the b- and c-eggs show a significant increase in breadth between 1968 and 1977. The volume of the b-egg however does show a significant increase between 1974 and 1977.

Second, Parsons'(1971) data showed that there was a volume difference of 1.8ml (2.3%) between a- and b-eggs, and a difference of 8.6ml (8.9%) between b- and c-eggs. The differences in volumes recorded in this study are given in Table 30.

Table 30. Differences in volumes between a- and b-eggs, and between b- and c-eggs in years from 1974 to 1977

	a- and b-egg		b- and c-egg	
Year	volume difference ml	% difference	volume difference ml	% difference
1974	4.40	5.43	3.84	5.01
1975	4.43	5.56	3.64	4.83
1976	4.21	5.20	5.18	6.75
1977	3.10	3.80	4.96	6.33

It can be seen, compared with the data for 1968, that the differences recorded between the volumes of the a- and b-eggs have become much more pronounced (about twice as great), whilst the volume difference between the b- and c-eggs has become somewhat reduced. Furthermore, in 1975, when eggs tended to be smaller than in the other years, the differences between the a- and b-eggs were greatest, and the difference between the b- and c-eggs the smallest.

8.5.4 Variations in egg size with age

As with a general trend of increasing clutch size with age, referred to in the previous section, there is a similar trend of increasing egg size with age. Table 31 presents data on mean dimensions of eggs which were measured in three- and two-egg clutches of gulls of known age in the breeding seasons of 1974, 1976 and 1977.

Any interpretation of the influence of age on egg size is complicated by the aforementioned observation that egg sizes of the unaged samples have tended to increase during the period of study. However, in 1975 when egg sizes were in general smaller than in other years, no data on aged birds were collected. In the seasons of 1974, 1976 and 1977 no significant differences could be found in the same age classes between years, and it seems reasonable to pool data from all years in order to summarize the trend of increasing egg size in a simplified form. Figure 24(a-c) illustrates the mean egg dimensions of a-, b- and c-eggs (dimensions from both three- and two-egg clutches have been combined).

It can be seen that for young gulls (i.e. in their fourth year) egg volume is, on average, 6.9% less than for older gulls (i.e. gulls in their tenth year). Egg breadth increases significantly between fourth and tenth year ($p < 0.001$) but egg length actually shows a slight (though not significant) decrease with age. There is no general inverse relationship between the small eggs of younger birds and increased shape index, but when a-, b- and c-eggs are examined separately (in Table 32) the a-egg invariably has a smaller shape index than the b-egg, which is likewise smaller than the c-egg. There is also some evidence that volume reached a plateau in the tenth and eleventh year (Table 32). Although clutch size showed a significant decline after the eighth year (Table 33) average clutch volume remained above 200ml thereafter.

Table 31. The mean length, breadth, volume and shape index of eggs laid by gulls of known age, with one standard error

			Age (years)								
			3	4	5	6	7	8	9	10	11
1974											
	No. of clutches		0	0	0	17	25	30	0	0	0
	No. of eggs		-	-	-	48	70	84	-	-	-
	Length	$\bar{X}$			68.77	68.58	68.56				
		± S.E.			0.27	0.38	0.22				
	Breadth	$\bar{X}$			47.14	47.55	48.17				
		± S.E.			0.11	0.12	0.12				
	Volume	$\bar{X}$			72.76	73.87	75.85				
		± S.E.			0.46	0.65	0.56				
	Shape	$\bar{X}$			68.97	69.49	70.28				
	index	± S.E.			0.28	0.32	0.19				
1976											
	No. of clutches		4	4	0	22	24	35	11	6	0
	No. of eggs		8	11	-	62	69	104	30	16	-
	Length	$\bar{X}$	65.69	68.59		68.47	68.19	68.85	68.51	68.35	
		± S.E.	0.45	0.49		0.24	0.28	0.23	0.35	0.35	
	Breadth	$\bar{X}$	46.30	46.93		47.01	47.35	48.18	48.55	48.56	
		± S.E.	0.51	0.35		0.10	0.13	0.13	0.18	0.19	
	Volume	$\bar{X}$	67.14	72.00		72.06	72.96	75.91	76.93	76.70	
		± S.E.	1.87	1.50		0.45	0.53	0.50	0.84	0.90	
	Shape	$\bar{X}$	70.48	68.42		68.38	69.69	69.91	71.87	71.12	
	Index	± S.E.	0.45	0.32		0.29	0.28	0.20	0.18	0.36	

Table 31 (continued)

			Age (years)							
		3	4	5	6	7	8	9	10	11
1977										
No. of clutches		0	18	8	0	0	0	21	18	5
No. of eggs		-	45	21	-	-	-	54	47	14
Length	$\bar{X}$		69.40	68.77				69.29	69.96	68.71
	± S.E.		0.31	0.29				0.42	0.32	0.36
Breadth	$\bar{X}$		46.74	46.46				48.17	48.64	48.86
	± S.E.		0.11	0.16				0.19	0.14	0.24
Volume	$\bar{X}$		72.21	71.26				76.60	77.72	78.14
	± S.E.		0.53	0.67				0.81	0.69	1.10
Shape	$\bar{X}$		67.45	67.92				69.37	70.58	71.11
index	± S.E.		0.29	0.23				0.27	0.28	0.23
Totals (all years)										
No. of clutches		4	22	8	39	49	65	32	24	5
No. of eggs		8	56	21	110	139	188	84	63	14
Length	$\bar{X}$	65.69	69.24	68.77	68.61	68.38	68.73	69.01	68.80	68.71
	± S.E.	0.45	0.27	0.29	0.18	0.23	0.16	0.23	0.26	0.36
Breadth	$\bar{X}$	46.30	46.78	46.46	47.07	47.47	48.11	48.31	48.78	48.86
	± S.E.	0.51	0.11	0.16	0.07	0.09	0.11	0.14	0.10	0.24
Volume	$\bar{X}$	67.14	72.17	71.26	72.38	73.43	75.89	76.72	77.51	78.14
	± S.E.	1.87	0.51	0.67	0.32	0.42	0.31	0.60	0.57	1.10
Shape	$\bar{X}$	70.48	67.64	67.92	68.48	69.52	70.07	70.03	70.72	71.11
index	± S.E.	0.45	0.25	0.23	0.21	0.23	0.21	0.23	0.23	0.23

Table 32. Variation in egg volume and egg shape index with age

Age (years)	N (Clutches)		c/3			N (Clutches)	c/2	
			a	b	c		a	b
3	0	Volume				4	65.82 1.4	62.50 0.54
		Shape index					71.3 0.42	69.57 0.49
4	12	volume	75.59±1.2	72.80±0.72	67.73±0.79	10	73.83±0.38	71.00±0.66
		Shape index	67.47±0.64	67.85±0.55	68.52±0.37		66.80±0.44	67.36±0.65
5	5	volume	74.53±1.00	71.13±1.2	68.22±0.77	3	71.14±1.5	72.25±1.7
		Shape index	67.59±0.49	68.17±0.47	68.55±0.57		67.58±0.21	67.27±0.25
6	32	volume	74.04±0.50	73.96±0.46	69.07±0.43	7	74.04±1.1	72.37±1.0
		Shape index	69.36±0.32	67.25±0.32	69.40±0.36		67.61±0.47	66.82±1.1
7	41	volume	76.22±0.40	73.86±0.45	68.43±0.52	8	79.82±2.2	75.98±2.5
		Shape index	69.18±0.44	69.36±0.39	69.55±0.23		69.27±1.5	69.28±1.3
8	58	volume	80.7 ±0.47	75.85±0.39	70.9 ±0.43	7	79.86±2.3	74.61±1.4
		Shape index	69.51±0.29	69.96±0.20	70.67±0.26		69.27±1.5	69.28±1.3
9	20	volume	81.65±0.81	77.03±0.81	70.12±0.65	12	80.5 ±0.74	75.20±1.3
		Shape index	70.45±0.49	70.59±0.35	69.83±0.56		69.54±0.59	69.25±0.52
10	15	volume	81.10±0.93	76.04±0.60	73.11±0.85	9	80.74±1.4	77.69±1.0
		Shape index	70.16±0.35	70.66±0.33	71.87±0.51		69.63±0.74	70.92±0.59
11	4	volume	80.79±0.93	79.01±1.0	72.99±1.4	1	84.07	78.67
		Shape index	71.14±0.36	71.43±0.40	71.35±0.46		69.51	70.32

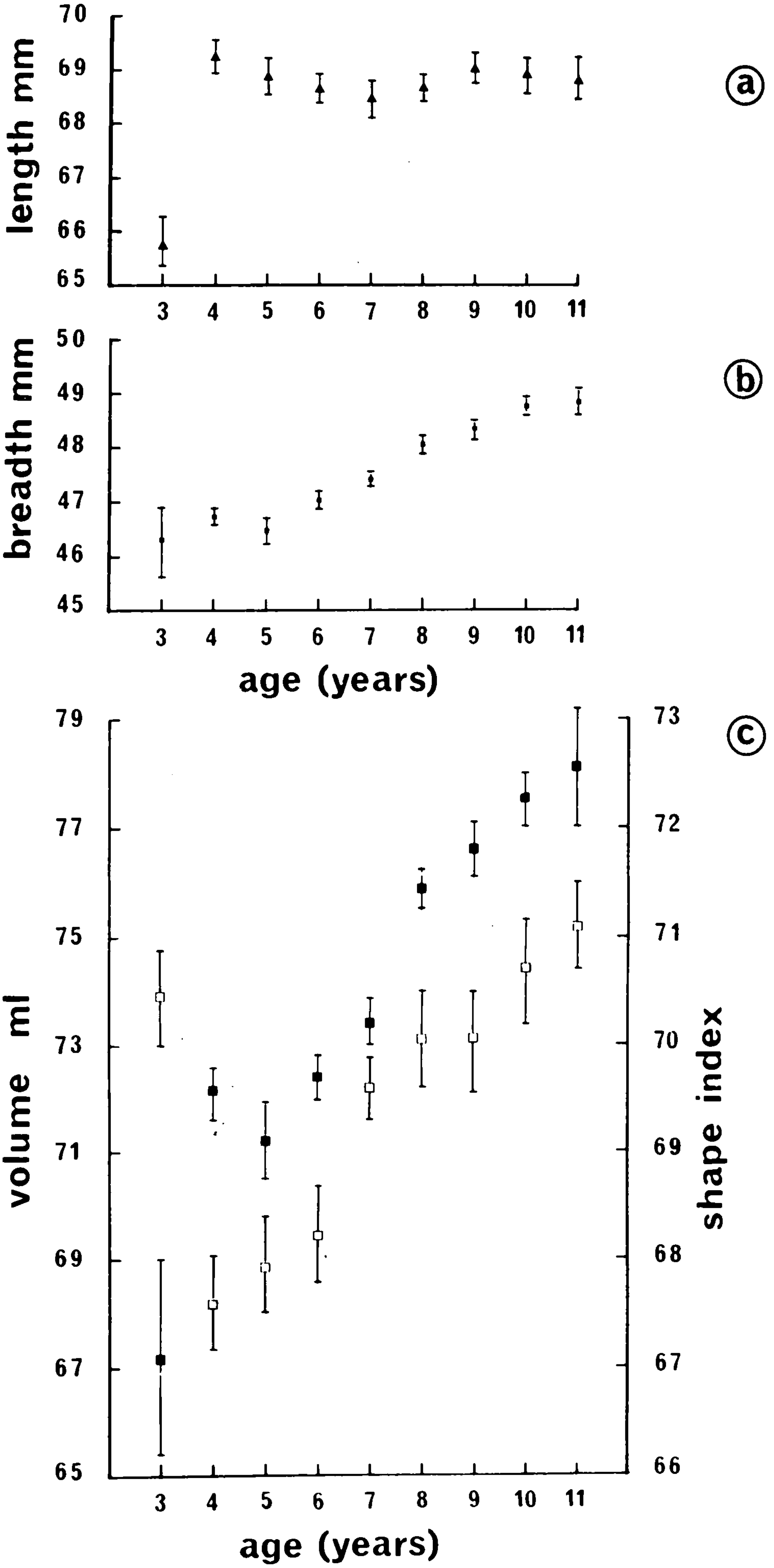
Figure 24. Changes in egg dimensions with age. All values are given with two standard errors.

(a) Variations in mean length

(b) Variations in mean breadth

(c) Variations in calculated mean volume (solid squares) and shape index (open squares)

Figure 24



ⓐ
length mm
70
69
68
67
66
65
3
4
5
6
7
8
9
10
11
ⓑ
breadth mm
50
49
48
47
46
45
3
4
5
6
7
8
9
10
11
age (years)
ⓒ
volume ml
79
77
75
73
71
69
67
65
shape index
73
72
71
70
69
68
67
66
3
4
5
6
7
8
9
10
11
age (years)

Table 33. Variations in mean clutch size and clutch volume with respect to age

	age (years)							
	4	5	6	7	8	9	10	11
mean no. of eggs/ clutch	2.24	2.62	2.82	2.84	2.88	2.62	2.62	2.80
average clutch volume (ml)	116.7	186.7	204.1	205.5	218.6	201.0	203.1	218.8

8.5.5 Discussion

When the likelihood of any laying date effects have been removed, a positive correlation between age and egg size clearly indicates that older female gulls are physiologically capable of allocating a greater quantity of material to their eggs than younger gulls. Reasons for this are not immediately clear, but it seems improbable that food availability is directly implicated., Gulls show individual differences in foraging behaviour, which may allow more experienced birds to gain advantages from exploiting more qualitative sources (personal observations). However, it is unlikely that age-related differences would persist beyond the first year.

Parsons (1970) has pointed to the positive correlation between the size of gull eggs and the lipid content of the yolk. Romanoff and Romanoff (1949) state that in large eggs of the domestic hen, yolk size is greater than that of smaller eggs, although there is proportionately more albumen than yolk. Parsons' (1970) samples related to unaged gulls, and since the sample was collected from only one season it remains to be established as to whether yolk weight and lipid content can show annual variations independent of egg size, or whether it remains a constant characteristic of a particular season or the age or condition of the female.

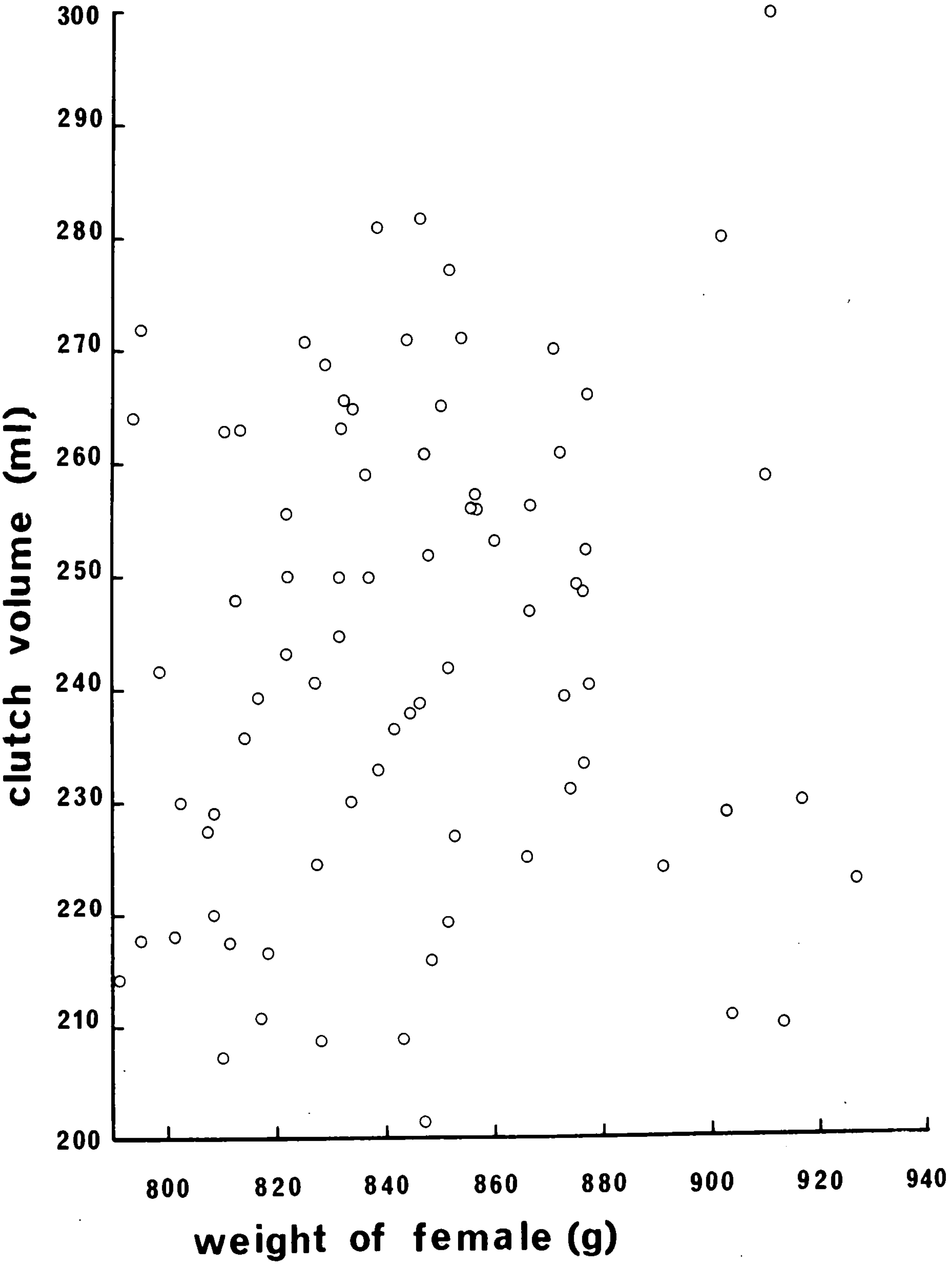
Most evidence would indicate that above average sized eggs contain proportionately more albumen, which will subsequently give rise to heavier than average chicks on hatching. Murton *et al.* (1974) suggest that for the wood pigeon, laying heavy eggs improved the chances of successful hatching rather than increasing the chances of chicks surviving better. Myrberget (1977) found a significant correlation between egg size and the weights of newly hatched chicks of willow grouse; in the domestic hen, chicks from the larger eggs have increased prospects of survival (Skoglund *et al.* 1952) - and presumably this relationship is a measure of their greater food reserves and their advanced development on hatching.

Whilst it is possible to explain individual differences in egg sizes in terms of an inherited component, a consequence of this would be that a particular female gull could be identified by her egg sizes in successive breeding seasons; this does not appear to be the case. It was not possible to measure the egg sizes of individual gulls in successive breeding seasons, but Coulson (1963) has emphasised that where data on kittiwake eggs laid by the same female are available from successive breeding seasons, individual variation is such that only in a small minority of cases could a particular female be recognised by her egg dimensions. The gull cull did however give an opportunity to seek further confirmation that egg dimensions are largely independent of the physical size of the female.

The practice of culling gulls on the nest made it possible to investigate the relationship between female weight and that of her total clutch volume (Figure 25). In 1977, a total of 78 dead or moribund female gulls which were found to be sitting on clutches of three eggs were weighed to the nearest gram, and their clutch volume was estimated. There was no significant correlation between female body weight and total clutch volume ($r_{76} = +0.08$).

Figure 25. Clutch volume plotted against the body weight of the female gull

Figure 25


clutch volume (ml)
300
290
280
270
260
250
240
230
220
210
200
800
820
840
860
880
900
920
940
weight of female (g)

In Table 28, where the mean volumes of a-, b- and c-eggs between 1974 and 1977 are given, there is considerable variation between years. From this data (the mean volumes of a-, b- and c-eggs between 1974 and 1977), the coefficient of variation can be calculated, where

$$C.V. = \frac{s.d. \times 100}{\bar{X}} .$$

These values are given in Table 34, and it can be seen that the amount of variability approximately doubled between 1974 and 1977, and that there was more variability in the c-eggs than in the a-eggs. If we discount for the meantime the possibility that changes in the age composition of the population might explain such marked annual variability in egg volume, two explanations can be offered at this juncture, which are essentially inter-related.

It is a fair assumption that egg size in general is adapted to promote maximum chick survival on hatching, and probably for some time thereafter until parent/chick responses can become fully developed. Some evidence for this in the herring gull comes from the observations of Parsons (1970,1975) that the chick which hatches from the smaller c-egg suffers an appreciably higher mortality than either of its siblings, and that the main value of the third egg is that it could give rise to a surviving chick should its siblings be lost without replacement. (All eggs have approximately equal hatching success). However, it seems possible that there is selection for variability in egg size as well, since this would be an adaptation which could accommodate variable environmental effects on hatching. On balance, a chick hatching from a large egg will have better chances of survival than a chick hatching from a smaller egg, but when benign environmental conditions prevail, all but chicks from the very smallest eggs will have good prospects for survival.

By allocating quantities of nutrient between first, second and third eggs as widely and as uniformly as possible, as can be deduced from the wide spacing of volumes between a-, b- and c-eggs which has been observed (Table 30), the chances of at least the largest chick surviving are even more enhanced.

Table 34. Coefficients of variation of the volumes of a-, b- and c-eggs between 1974 and 1977

	year			
	1974	1975	1976	1977
a-egg	3.87	5.47	5.76	6.84
b-egg	3.59	5.04	5.64	8.30
c-egg	4.03	6.35	5.69	8.07

Bad weather, during incubation and hatching, has frequently been recorded in this study, and at the Mallowdale colony where wet snow fell on 3 June 1974 an estimated 35-40% of recently hatched chicks died. Nelson (1966) has suggested that the wide seasonal spread of laying observed in the gannet is an adaptation to ensure that at least some eggs and chicks would survive the effects of a particularly catastrophic event such as an unseasonal snowfall.

A second factor which could influence an increase in egg volume (as well as the degree of variability from year to year) might be an effect of the cull, which takes place during egg laying and incubation. As shall be discussed, a notable effect of culling has been the lowering of breeding density. Section 11.3 is devoted to the effect of density on aspects of territorial behaviour of gulls, but one of the main conclusions is anticipated here by emphasising the strong positive correlation between the number of aggressive territory disputes, high levels of intense courtship behaviour and nesting density. These activities often require the prolonged attendance of both members of the pair on the territory, at the time when females also have to find enough food to form their eggs. There appear to be no published accounts which relate energy expenditure to intensity of fighting and courtship displays of breeding birds, but, intuitively at least, to witness a fierce fight between neighbouring gulls where often the victor appears as exhausted as the vanquished, leads one to the conclusion that the stresses involved must be considerable. Female gulls adopt a secondary role in fighting (although sometimes they are directly involved) but they are nonetheless very active in the defence of the territory. It is not inconceivable that a yearly increase in the spacing of nests has permitted female gulls to allocate a greater proportion of nutrients to their eggs through reduced levels of stress. In 1968, average clutch volume (three-egg clutches) was 223.4ml, whilst in 1977 average clutch volume was 233.3ml - an increase of 4.4%. This may seem a small increase (though proportionately quite large when female body weight is considered as a ratio of clutch volume) but there is also some support to be found in the observation that between 1972 and 1977 the mean weight of a sample of female gulls increased from 847 ± 7g to 860 ± 10g (see Appendix II). Bearing in mind the possibility of a slight increase in weight with age (the average age of the 1972 sample was 5.4 years, whilst the average age of the 1977 sample was 6.8 years), there is the further suggestion that an increase in body weight may be in some way influenced by changes in breeding density.

9. ASPECTS OF CHICK FLEDGING SUCCESS AND POPULATION DYNAMICS

9.1 INTRODUCTION

It has been mentioned in Section 5 that in order to sustain the 13% average annual increase in the number of gulls breeding on the Isle of May each pair of gulls require to fledge on average one chick per annum. This prior knowledge provided a basis for investigations of reproductive success by gulls which survived culling in control areas. Parsons (1975) quoted 0.91 and 0.67 as the number of chicks fledged per pair from this colony in the years 1967 and 1968 respectively, which indicates that there are likely to be variations in the productivity of the colony from year to year, and to underline this possibility there are wide ranging estimates in the literature as to the productivity of herring gull colonies in different parts of northern Europe and North America (Table 35).

Table 35. Some estimates of herring gull breeding success found in the literature

Authority	chicks/pair	Location
Darling (1938)	0.78 - 1.13	Priest Island (Scotland)
Paynter (1949)	0.91	Kent Island (Canada)
Paludan (1951)	0.50	Graesholm (Denmark)
Drost *et al.* (1961)	0.4 - 0.90	Wilhelmshaven (Germany)
Vermeer (1963)	1.0	Mandarte Island (Canada)
Harris (1964)	0.60	Skomer (Wales)
Brown (1967)	0.91	Walney Island (England)
Kadlec and Drury (1968)	0.80 - 1.40	Eastern U.S.A.
Parsons (1975)	0.91, 0.67	Isle of May (Scotland)
Spaans (1975)	1.20	Terschelling (Netherlands)
Monaghan (1977)	1.2 - 1.4	Rooftop colonies, Tyne and Wear, England

In this study, a measure of chick production could relate to the importance of nesting density and age in determining breeding success and what the effects of culling were (if any) on the productivity of the colony in areas which had remained as protected controls.

9.2 THE IMPORTANCE OF FLEDGING SUCCESS IN RELATION TO FUTURE RECRUITMENT

When predictions regarding the number of animals at a future point in their life cycle are made from measurements during juvenile or sub-adult stages it is profitable to be aware of the importance of small fluctuations in the survival of young which can influence the validity of such predictions. This is particularly the case in animals such as the herring gull where average survival rate is high after the first year of life. The reason for this can be illustrated by the following hypothetical situation:

If 1000 breeding pairs of gulls succeed in raising 1000 chicks to fledging, it would be expected that five years thereafter there would be $1000 \times 0.82 \times 0.935^4 = 627$ gulls alive, these being birds of breeding age (see Section 5). One thousand chicks from 1000 pairs of gulls is probably close to the average success rate (see Table 35), but if each pair of gulls produce 3 eggs, of which (say) 70% hatch successfully, then there will be 2100 chicks on hatching, and 1100 will die before fledging. This represents a chick survival rate of 0.476 during the pre-fledging period. If, on the other hand, chick survival dropped by 10% to 0.376, the numbers of chicks fledging would be 790. Applying the same survival rates as above, the numbers of chicks surviving to their fifth year would be 503, which represents a drop of 24.7%. Applying this reasoning to Parsons' (1975) data on chick survival, in 1967 1000 pairs of gulls would fledge 910 chicks, which would give rise to 570 surviving adults five years later, whilst in 1968, when only 670 chicks per 1000 pairs fledged, five years later there would be 420 surviving adults - a drop of 37.5%. It would be impossible to record a 13% annual increase in a colony where chick production was so low, unless there was immigration of recruits on a very large scale.

9.2.1 Methods

The control areas of Tarbert III, Maiden's Rock and North Plateau were used to measure chick fledging success. It has been stated in Section 2 that these areas were chosen for their diversity of nesting densities, but they also possessed discrete topographical boundaries and could be considered arbitrarily as sub-colonies which were separate from the rest of the island breeding population. Although data on clutch size and egg dimensions were taken for a representative sample in the Tarbert III area only, the number of breeding pairs in each sub-colony was accurately known and each nest was staked and numbered. Chicks were marked on hatching, or as soon as possible thereafter, except for the Maiden's Rock area which was left undisturbed until approximately the fourth week after hatching. Disturbance was a major factor influencing chick loss in this area. To mark chicks, Parsons (1971) had used strips of coloured insulating tubing. These were slipped over the leg and stapled in position. This method was likewise adopted in this study. For the youngest chicks they could easily be removed at a later date when the chicks had grown sufficiently to be marked with BTO monel rings (size G) and a single coloured Darvic ring 20mm in height. Moreover, should a chick survive to fledging but not be recaptured, the staple would rust within a few weeks and the ring fall away. An additional advantage was that these temporary rings avoided considerable wastage of expensive monel rings, since it was likely from the outset that more than half the chicks would die before they fledged.

Since most chick loss occurs in the first ten days after hatching (Parsons 1971) and with only a minority of chicks dying in the ensuing weeks up to fledging, if a chick survived for 35 days from the time of marking, it was considered that it would also fledge. In this way it was possible to assess fledging success with minimal disturbance to the colony, as it was necessary only to recapture chicks once.

9.2.2 Yearly variations in chick survival

In 1974 no data could be collected on chick survival. This was accountable to the NCC gull cull which did not allow provision for control areas to be left undisturbed. The best estimate for chick production in this year was that approximately 550 successfully fledged herring gull chicks and about 300 lesser black-backed gull chicks, from a total of about 950 pairs of gulls of both species which remained unaffected by the cull. This estimate is for the entire colony on the Isle of May. Data for the years 1975-1977 appear in Table 36. In general, these data are comparable to those of Parsons (1975), quoted in Table 35. The lowest fledging success was recorded in 1976 where, on average, 0.71 chicks per pair were fledged. This figure is somewhat biased by the apparently unusually poor survival of chicks on the North Plateau area, where only 0.50 chicks per pair survived beyond their fifth week. It was felt that at least one factor contributing to this poor survival may have been a summer of exceptionally low rainfall and high temperatures. There was severe dying back of protective vegetation cover for the chicks in the first week after hatching, and high mortality resulted.

Table 36. Yearly variations in the number of chicks surviving more than 35 days in control areas on the Isle of May

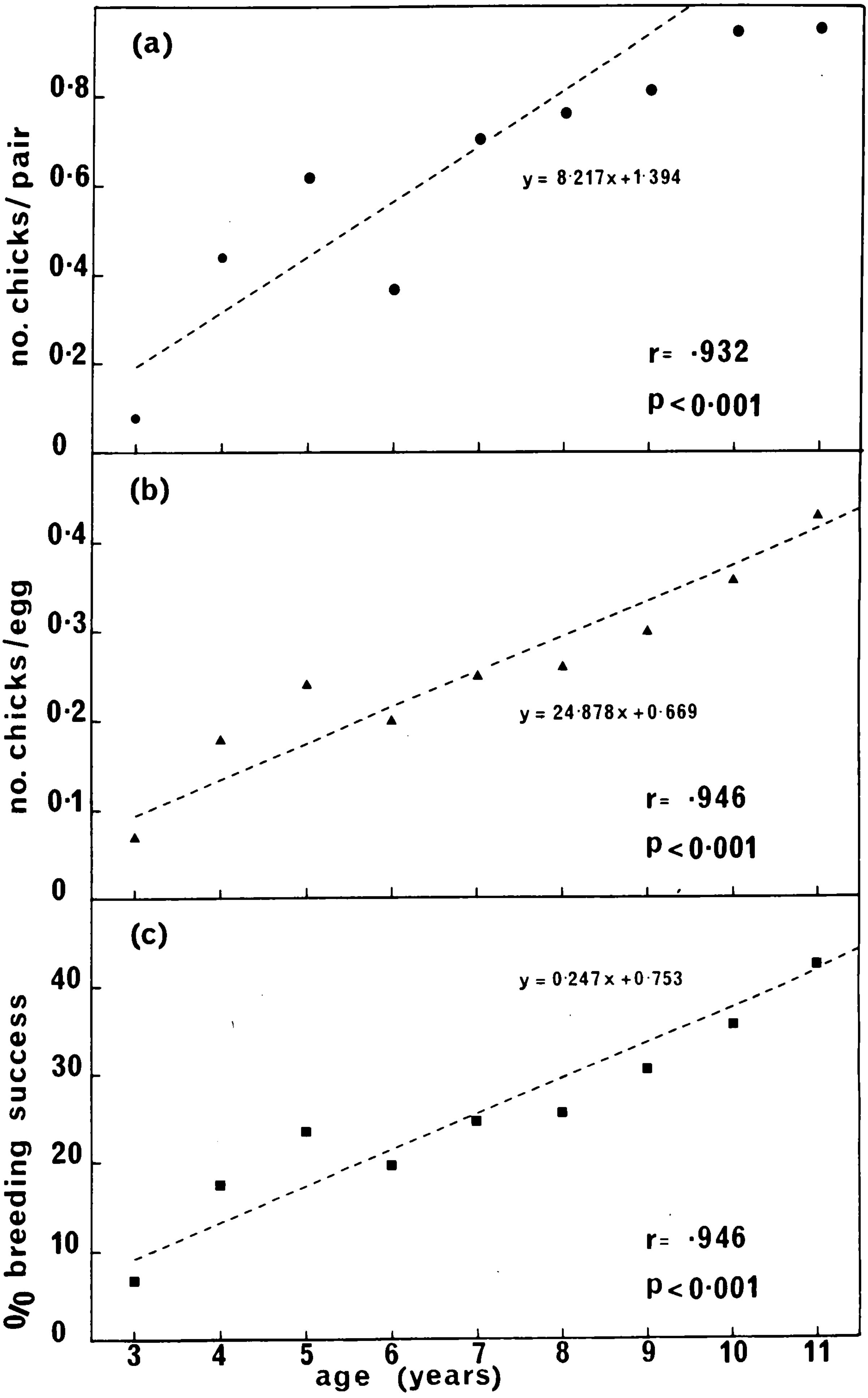
year	area	No. of pairs	No. of chicks	Chicks/pair
1974	no data			
1975	Maiden's Rock	145	95	0.65
	Tarbet III	234	206	0.88
	North Plateau	57	70	1.23
	Totals	436	371	0.85
1976	Maiden's Rock	165	117	0.71
	Tarbet III	98	85	0.87
	North Plateau	68	34	0.50
	Totals	331	236	0.71
1977	Maiden's Rock	100	88	0.88
	Tarbet III	59	60	1.02
	Totals	159	148	0.93
	Overall Totals	926	755	0.82

9.2.3 The influence of parental age on chick survival

Table 37 summarises the breeding success of 203 pairs of gulls where the age of one parent bird was known. (The sample had been reduced from 264 pairs of aged birds since some of the gulls were nesting outside the study area and had been culled before they hatched chicks.) There is a trend of increasing chick survival with increased age of parent birds, and with percentage breeding success ranging from 6.7% in third year gulls to 42.9% in eleventh year birds. Figure 26(a-c) illustrates these trends, and there is an extremely good correlation between the numbers of chicks which survive up to their 35th day, and parental age ($r_7 = 0.932$; $p < 0.001$). From Figure 26(c) it would seem that there are three stages in the general chick survival/parental age relationship.

Figure 26. The survival of herring gull chicks up to their 35th day, in relation to parental age.

Figure 26



(a)
0·8
0·6
0·4
0·2
0
no. chicks/pair
y = 8·217x + 1·394
r= ·932
p<0·001
(b)
0·4
0·3
0·2
0·1
0
no. chicks/egg
y = 24·878x + 0·669
r= ·946
p<0·001
(c)
40
30
20
10
0
% breeding success
y = 0·247x + 0·753
r= ·946
p<0·001
3
4
5
6
7
8
9
10
11
age (years)

Between the ages of three and five years there is a steep increase in the number of surviving chicks for each age class of parent. It can be stated with some certainty that most, if not all, gulls in this age group were breeding for the first time, and it would be expected that first-time breeding birds would be less successful on average than older birds. However, it is also possible that a third or fourth year gull might be more naïve as regards chick rearing than a fifth year bird. Between the fifth and eighth year there seems to be little difference in chick survival, but between the eighth and eleventh year there is another marked upward trend. It will be recalled that clutch size actually reached a maximum in eight year old birds, with a slight decline thereafter, so this reduction in the number of eggs by older females is more than compensated for by an increase in the number of chicks which survive to fledging. It is not known whether this age effect could continue in birds much older than eleven years of age.

There are two possible explanations for this trend of increased breeding success with age. One explanation may lie in the physiological ability of the female gull to produce better quality eggs the older she gets (i.e. larger eggs containing relatively greater quantities of albumen and yolk) whilst the other explanation could lie in the behaviour of the older birds whose breeding experience is such that they are more capable at raising chicks. In all, a combination of these two possibilities may be closest to the truth.

In almost all instances, it was not possible to identify which egg of a clutch had given rise to a surviving chick. Parsons (1971) established that egg volume and chick weight on hatching were positively correlated ($r_{74} = 0.91$; $p < 0.001$) and various studies on the domestic hen have also shown a chick weight dependent on egg weight (Wiley 1950, Skoglund *et al.* 1952). More importantly, Parsons (1971) established a marked

Table 37. The reproductive success of gulls of known age which have survived the gull cull to raise chicks. Percentage breeding success is calculated as the number of chicks which survive until at least 35 days of age after hatching x $\frac{100}{\text{no. of eggs}}$

	Age (years)									
	3	4	5	6	7	8	9	10	11	Totals
No. surviving clutches	12	16	8	30	35	51	26	20	5	203
No. eggs	15	39	21	86	101	149	69	53	14	547
No. chicks	1	7	5	17	25	38	21	19	6	148
No. chicks/pair	0.08	0.44	0.62	0.57	0.71	0.76	0.81	0.95	1.2	0.73
No. chicks/egg	0.07	0.18	0.24	0.20	0.25	0.26	0.30	0.36	0.43	0.27
% breeding success	6.7	17.9	23.8	19.8	24.7	25.5	30.4	35.8	42.9	27.1

Table 38. Comparison of the mean sizes of a- and b-eggs of gulls of known age, in clutches which gave rise to chicks, and clutches which did not

	Age (years)							
	4	5	6	7	8	9	10	11
Clutches with chicks								
No. clutches	7	5	15	24	33	19	16	5
Mean egg size (ml)	72.73	71.92	74.30	75.46	78.35	78.68	79.60	80.20
± s.e.	0.94	0.91	0.44	0.57	0.52	0.74	0.71	0.72
Clutches without chicks								
No. clutches	8	3	14	11	18	7	3	0
Mean egg size (ml)	74.51	72.62	73.90	74.51	78.53	79.99	78.96	-
± s.e.	0.95	1.22	0.57	0.52	0.59	1.11	1.30	-
Value of Student's t-test	1.32	0.45	0.55	1.23	0.23	0.98	0.45	-
significance	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	n.s.	-

correlation between egg size and chick survival ($p < 0.001$) and concluded that egg volume is a most important factor in determining post-hatching survival, with nearly all the chicks from eggs smaller than 65ml dying soon after hatching.

The problem in this study is therefore to try to separate the effects of an increase in egg with age (which influences chick survival) on one hand, from the possibility that age and experience *per se* can be responsible for increased chick survival on the other hand. It was not known which individual eggs gave rise to surviving chicks, but the mean volumes of the a- and b-eggs in clutches from which no chicks survived were close to the mean volumes of a- and b-eggs where at least one chick did survive. (The differences were not significant (Table 38)). (The c-eggs were not considered since in most cases it was definitely known that the c-egg did not give rise to a surviving chick). Parsons (1970) has emphasised the very poor survival of chicks hatching from small c-eggs and since the largest eggs did not always give rise to chicks which fledged, it is postulated that parental experience may be important in increasing the chick's prospects of survival.

Table 39 divides the aged sample of gulls into two groups - gulls less than 8 years of age, and gulls older than 8 years. The division is arbitrary, but by the eighth year all gulls in the sample should, bar a small minority, have bred at least once. The number of clutches from which at least one chick survived to the 35th day is compared with the number of clutches from which no chicks survived, in relation to egg volume. (Here egg volume is considered as the average of the two a- and b-eggs.) These data are also illustrated in Figure 27. For gulls in the age group 8-11, there was a total of 102 clutches, 73 (71.6%) of which gave rise to one or more surviving chicks. In the group aged 3-7 years, where there was a total of 87 clutches, 51 (58.6%)

gave rise to surviving chicks. As might be expected, the data illustrated in Figure 27 are not normally distributed because of the tendency for the larger eggs to give rise to chicks which survive better. In the 3-7 year old group the number of clutches where mean egg size was greater than 75ml totalled 27, of which 16 gave rise to surviving chicks. This represents a success rate for producing a chick of 59%. In the older age group there were 91 clutches where mean egg volume was greater than 75ml, and of these 65 (71%) gave rise to surviving chicks. In the egg size interval 75-80ml it can be seen that 56% of clutches gave rise to chicks in the 3-11 year old age group, whilst in the 8-11 year old age group 72% of clutches gave rise to successfully fledging chicks. However, despite this discrepancy in the breeding success between younger and older birds, this difference is not significant ($\chi^2 = 1.96$, 1 d.f.).

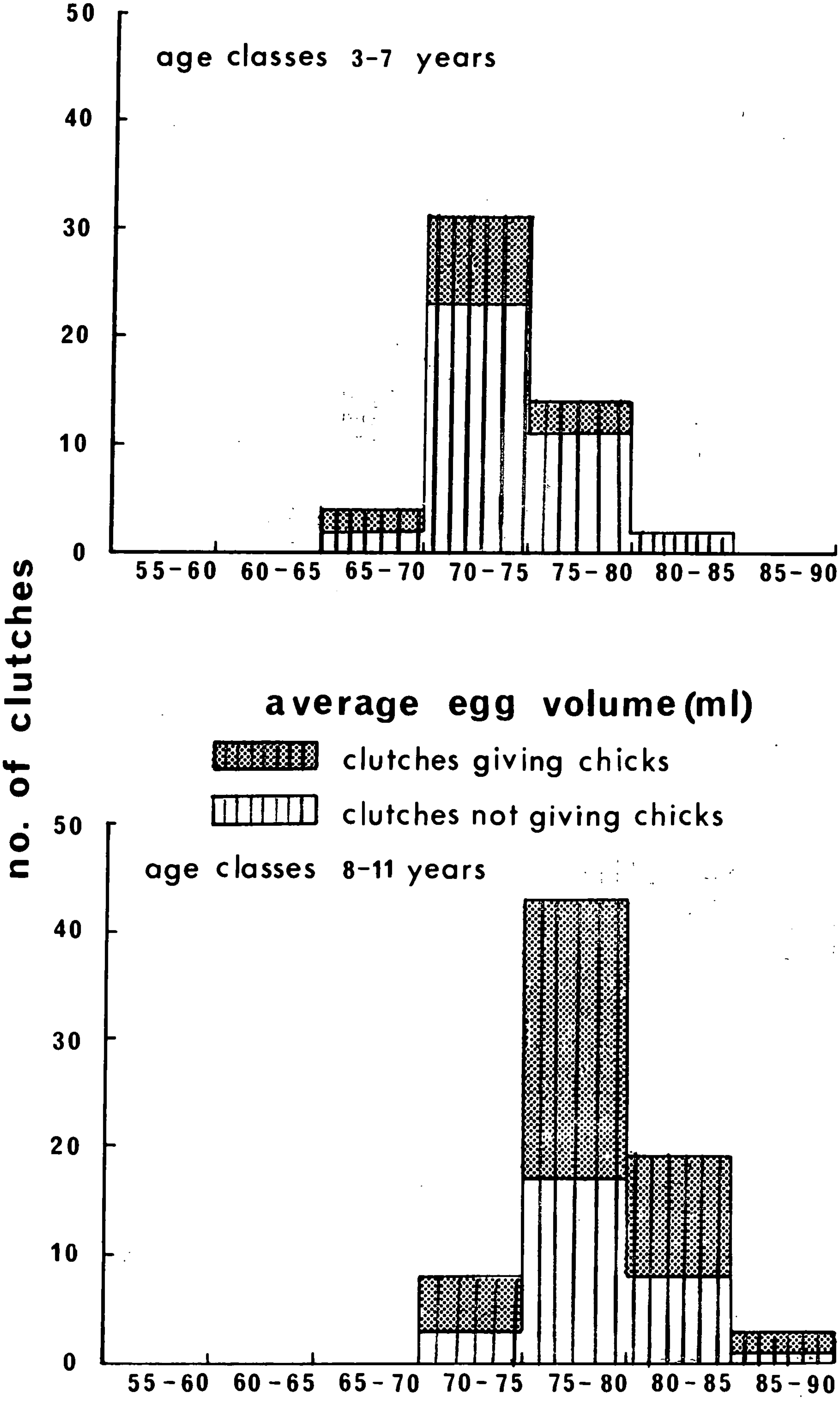
Although there is no clear-cut evidence for an age effect independent of egg size in the simple comparison of breeding success between younger and older gulls made above, there is some additional circumstantial evidence which tends to support the assumption that such an age effect may exist. For instance, it seems that older gulls are better able to raise two chicks than are younger birds. From a total of 87 clutches belonging to gulls less than 8 years of age, only from two of these was a second chick raised. In birds older than 8 years there were 11 clutches from a total of 102 from which a second chick survived ($\chi^2 = 5.28$, 1 d.f., $p < 0.05$). There were no clutches where three chicks were raised to fledging. Table 39 also indicates that for younger birds the mean size of the a- and b-egg which gave rise to successfully fledging chicks was actually smaller than the mean egg size in clutches which did not.

Table 39. The number of clutches which gave rise to chicks, and the number which did not, in relation to the mean volume of a- and b-eggs, in old and young gulls

	Mean egg size (ml)					
	60 -	65 -	70 -	75 -	80 -	85 -
Ages 3-7						
clutches with chicks	0	4	31	14	2	0
clutches without chicks	0	2	23	11	0	0
Ages 8-11						
clutches with chicks	0	0	8	43	19	3
clutches without chicks	0	0	3	17	8	1

Figure 27. The number of clutches of eggs from which at least one chick survived, compared against the number of clutches from which no chicks survived in two groups of gulls, aged less than 8 years and more than 8 years.

Figure 27


age classes 3-7 years

age classes 8-11 years

9.3 AGE COMPOSITION AND PRODUCTIVITY OF THE COLONY

It has been shown that between the breeding seasons of 1975-1977 the average number of chicks produced per pair was 0.82. From an estimate of fledging success, and a knowledge of the age of first breeding, first year and adult survival, it has been considered possible by Capildeo and Haldane(1954) to calculate the annual rate of increase or decrease of a population. The method involves the use of tables which inter-relate fertility rate (the number of young produced per pair which not only fledge, but survive for one year) with adult survival and the age of first breeding. The relationship is

$$f = \frac{c.k}{2s}$$

where f is the fertility, c the mean clutch size, k the fraction of eggs which hatch and give rise to young which survive for one year, and s is adult survival.

In this study, mean fledging success was 0.82 young per pair and first year survival rate was 0.82. Thus, with adult survival being 0.935

$$f = \frac{0.82 \times 0.82}{2 \times 0.935} = 0.3596$$

Table 1 (p. 218) of Capildeo and Haldane (*loc. cit.*) gives complex roots (x_1) for different values of f where the age of first breeding is variable. Since it has been found that the age of first breeding extends from the fourth year to the eighth, it is necessary to take the weighted average to calculate x_1 viz:

$$(0.21 \times 1.1795)+(0.52 \times 1.1617)+(0.13 \times 1.1479)+(0.06 \times 1.1367)+(0.08 \times 1.1273)$$
$$= 1.1594$$

(It will be remembered that 21% of gulls breed at four, 52% at five, 13% at six, 6% at seven and 8% at eight.) The value x_1 is such that when multiplied by the adult survival rate, the degree of population change is given i.e.

$$sx_1 = 0.935 \times 1.1594 = 1.08423$$

Thus the annual rate of increase would be 8.4%, which is only fractionally less than that calculated by Parsons (1971) who estimated an 8.6% annual increase, but without the detailed knowledge of the age of first breeding. Clearly, these estimates are at variance with the known 13% annual increase in this colony.

One of the postulates for the valid use of this method by Capildeo and Haldane (*loc. cit.*) is that breeding success must be independent of age. Reference to Table 37 indicates that this is clearly not the case. Percentage breeding success ranges from 17.9% in fourth year gulls to 42.9% in eleventh year birds. Previously, Parsons (*loc. cit.*) suggested that this discrepancy in the rate of increase of the colony estimated from two different methods might be caused by an under-estimation of first year survival rates. He calculated that a first year survival rate of 0.854 and an adult survival of 0.925 could result in a 13.3% annual rate of increase by the breeding population. However, it seems unlikely that first year survival could be sustained at such a high value (as it would be required to do) and Chabrzyk and Coulson (1976) have estimated a 33% first year mortality in the 1967 year class on the Isle of May. There seems in any case no adequate explanation as to why at least first year mortality should be under-estimated from the method used to calculate it.

Unfortunately, there are no data for the relative breeding success of gulls which start to breed for the first time between the ages of five and eight. If it was possible to state that all five year old birds (for example) had a breeding success of 23.8%, and all six year old birds had an average breeding success of 19.8% etc (see Table 40), then it would be possible to calculate the rate of increase or decrease of the colony using the above method of Capildeo and Haldane. However, it is not known whether a gull breeding for the first time in its sixth year (for example) is as successful as a sixth year gull which has already had experience of breeding in previous years. On balance, it is likely not to be the case. Since it is known that breeding success can increase with age, it seems probable that with some 50% of the gulls older than eight years (as would be the case in an unculled population, Table 21), the annual increase in numbers would truly be in excess of 8.4% per annum.

Using the age composition which has been calculated for the population prior to the onset of culling in Table 21, and assuming that gulls aged between four and eleven have an average breeding success the same as has been found in this study (Table 37), it is possible to estimate the annual rate of increase by an alternative method. The relative proportions of birds in each year class have been calculated (Table 21) where in a breeding population of 10,000 gulls, 70.25% of them will be aged between four and eleven. In Table 40, column 2 gives the relative numbers of each age. Column 3 gives the number of chicks which would be successfully fledged by each age class should they have a breeding success equal to that observed in this study (from Table 37). Column 4 gives the number of offspring which would still be alive one year later (with an average first year survival rate of 0.82), and column 5 gives the number of offspring which would be alive 8 years later (with an average adult survival rate of 0.935). Thus, 70.25% of the breeding population which stands at 10,000 birds can give rise to 2,499 surviving offspring eight years later - at a time when all of this number can be expected to have joined the breeding population. If the remaining 29.75% of the population can breed on average as well as the younger 70.25%, we would expect a total of 3,557 birds which are eight years old. (This may be an over-estimate since the oldest birds may not be able to breed so well.)

It can be calculated that when a 13% annual increase in the breeding population is sustained over eight years the original population of 10,000 birds will have increased to 23,527, and from Table 21 it can be calculated that with this rate of increase and with the same survival rates the proportion of eight year-old birds should be 10.57% of the population (i.e. 2,487). Here we have 3,557 eight year-old birds. The numbers of gulls in each age class must be in proportion to the rate of increase when survival rates and average ages of first breeding remain constant over a period long enough for the age composition to become stable. Therefore, the number of eight year-old gulls (2,487) can be considered proportional to a 13% annual rate of increase. With the average breeding success found in this study, the number of eight year-old birds would total 3,557, and for this number to be accommodated the rate of increase would have to change proportionately. Hence the new rate is 18.6%. Although this new rate of increase seems to be high, Monaghan (1977) has recorded an annual rate of increase of 17% in herring gulls nesting on town roof-tops since the 1950s, and her studies indicate that fledging success can be as high as 1.2 - 1.4 chicks per pair.

Table 40. The predicted relative proportions of gulls aged four to eleven in an unculled population of 10,000 with their relative breeding success, and the number of offspring predicted to be alive eight years later

age	Number of breeding pairs	number of chicks fledged	number surviving one year	number surviving eight years
4	363	160	131	77
5	1,201	745	611	357
6	1,218	730	599	350
7	1,112	790	648	379
8	1,057	803	658	384
9	860	697	572	334
10	671	637	522	305
11	543	652	535	313
Totals	7,025	5,214	4,276	2,499

10. EFFECTS OF DENSITY ON RECRUITMENT

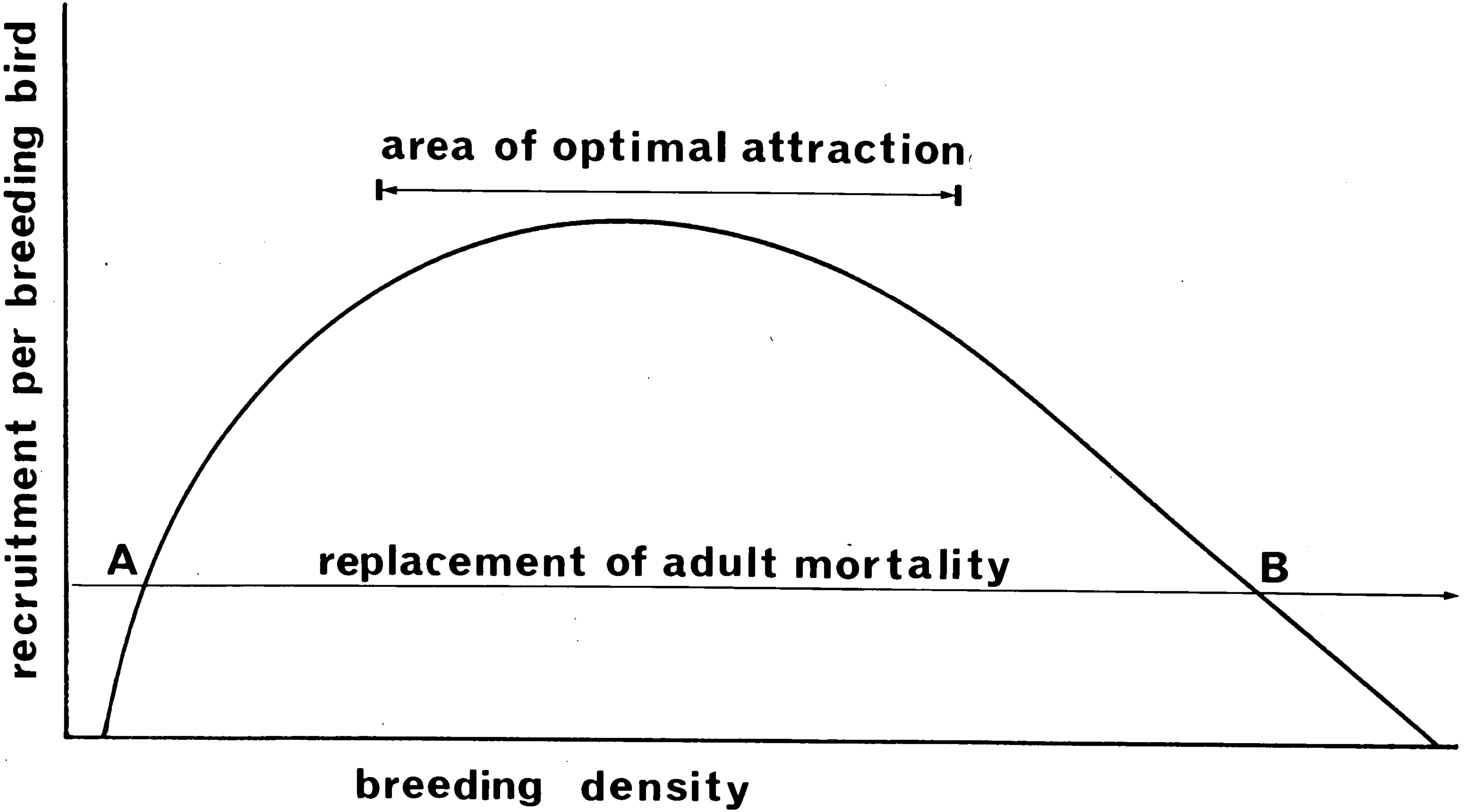
10.1 INTRODUCTION

One of the most noticeable results of culling gulls on the Isle of May has been the reduction of nesting density in the colonies. Nesting density throughout a colony tends to be variable, being determined by the constraints of competition for territories in what may be a limited area (being on an island) and also by the need to space nests to reduce both intra- and interspecific predation. Thus Patterson (1965) envisaged an optimal spacing of territories in the black-headed gull, dependent upon an equilibrium between a random scatter of nests to effect maximum protection for the eggs and chicks, and a clumping of nests to promote effective group protection. Parsons (1976) showed that herring gulls on the Isle of May began laying earliest in the season at an intermediate density, and that these subsequently were the most successful breeders. It would seem that there is a pronounced advantage for a colonially nesting gull in gaining a territory in an area of optimal density, and the inference is that higher density areas might be more attractive to recruits seeking a territory for the first time. Coulson (1968) has demonstrated the importance of position when drawing attention to differences of "bird quality" between male kittiwakes which hold a territory in the centre of the colony, and the edge (the two divisions being defined by the position and density of the nests). Birds which nest in the centre have a significantly higher survival rate, and breeding success in the centre is significantly higher than at the edge.

Chabrzyk and Coulson (1976) proposed a model which described recruitment in a herring gull colony, postulating that density of breeding gulls regulates the recruitment rate (Figure 28). At higher

Figure 28. A model depicting recruitment dynamics in a herring gull colony, from Chabrzyk and Coulson (1976). The horizontal line represents the adult mortality rate (0.065). The equilibrium points (A and B) indicate the minimum (A) densities between which the colony can exist, and the maximum (B). An area of optimal attraction lies between these two points, at which recruitment is maximal.

Figure 28


recruitment per breeding bird
area of optimal attraction
A
replacement of adult mortality
B
breeding density

densities the colony is more attractive to new recruits, but as density increases it becomes progressively more difficult to establish a territory. At the lowest densities the colony is one of minimal attractiveness, but it would be easy for a recruiting bird to gain a territory within it. Thus, in theory, maximum recruitment should occur at a density which is both attractive to recruiting birds and yet is low enough to permit them gaining a territory.

10.2 METHODS

Six representative areas of the island were marked out in the breeding season of 1974 and were culled in each year thereafter to give a range of breeding densities. The high density area known as Maiden's Rock was left unculled as a control area. As a standard procedure density has been expressed as the number of nests per $100m^2$ throughout.

New recruits in each area were identified from plumage characters (if there were signs of sub-adult plumage) or, if ringed, by the ring number. However, since only a minority were so easily aged and distinguished, the most practicable means of estimating numbers of recruits was, as described previously, to combine the average annual adult survival rate of 0.935 with the survival rate due to culling, from which the recruitment rate could be calculated.

10.2.1 Results

The results of the clearing experiments are shown in Table 41, listing the survival rates, the number of new recruits and the density of each area.

Table 41. Results of culling areas at different intensities. Density is expressed as nests/100m^2 and recruitment as a percentage of the breeding population

Colony	Year	No. of breeding birds	Adult survival rate	No. surviving from previous year	Nest density	No. of recruits	Recruits as percentage of area's population
Maiden's	1974	390	0.935				
Rock	1975	380	0.935	365	14.3	15	4.0
(control)	1976	396	0.935	365	14.9	40	10.1
	1977	410	0.935	370	16.2	40	9.8
Colm's	1974	84	0.786				
Hole	1975	82	0.821	66	10.0	16	19.5
(25%	1976	76	0.825	67	9.2	9	11.8
culled)	1977	80	0.935	63	9.5	17	21.3
North	1974	68	0.511				
Plateau I	1975	40	0.480	35	3.3	15	12.5
(50%	1976	20	0.420	20	1.3	0	0.0
culled)	1977	12	0.935	88	0.8	4	33.3
North	1974	29	0.065				
Plateau II	1975	2	0.234	4	0.1	0	0
(95%	1976	0	0.000	0	0.0	0	0
culled)	1977	2*	-	-	-	-	-
East	1974	1,644	0.264				
Tarbert I	1975	590	0.521	464	8.7	126	21.0
(culled)	1976	230	0.658	329	3.4	0	0
by N.C.C.)	1977	244	0.631	162	3.6	82	33.6
East	1974	864	0.264				
Tarbert II	1975**	438	0.935	217	8.1	224	50.4
(culled	1976**	610	0.935	410	11.7	200	32.8
by N.C.C.)	1977	668	0.531	570	11.9	98	14.7

* lesser black-backed gulls ** not culled

It can be seen that the relationship between density and recruitment is variable between years and between different areas. On the North Plateau II area (which had a low density and was on the edge of the colony - not having been colonised until the early 1970s, and hence having no tradition as a successful breeding area) no recruitment was recorded, although a few older gulls remained to breed successfully. The control area (Maiden's Rock), where there had been no culling in each year, remained at a high density throughout, and although the new recruits to this area increased slightly during the period of study, the annual average recruitment rate for the three years was only 8.0%, giving an average annual increase of 1.5%. It would seem that this area was close to the maximum density, so that recruitment approximated to mortality and the numbers remained constant.

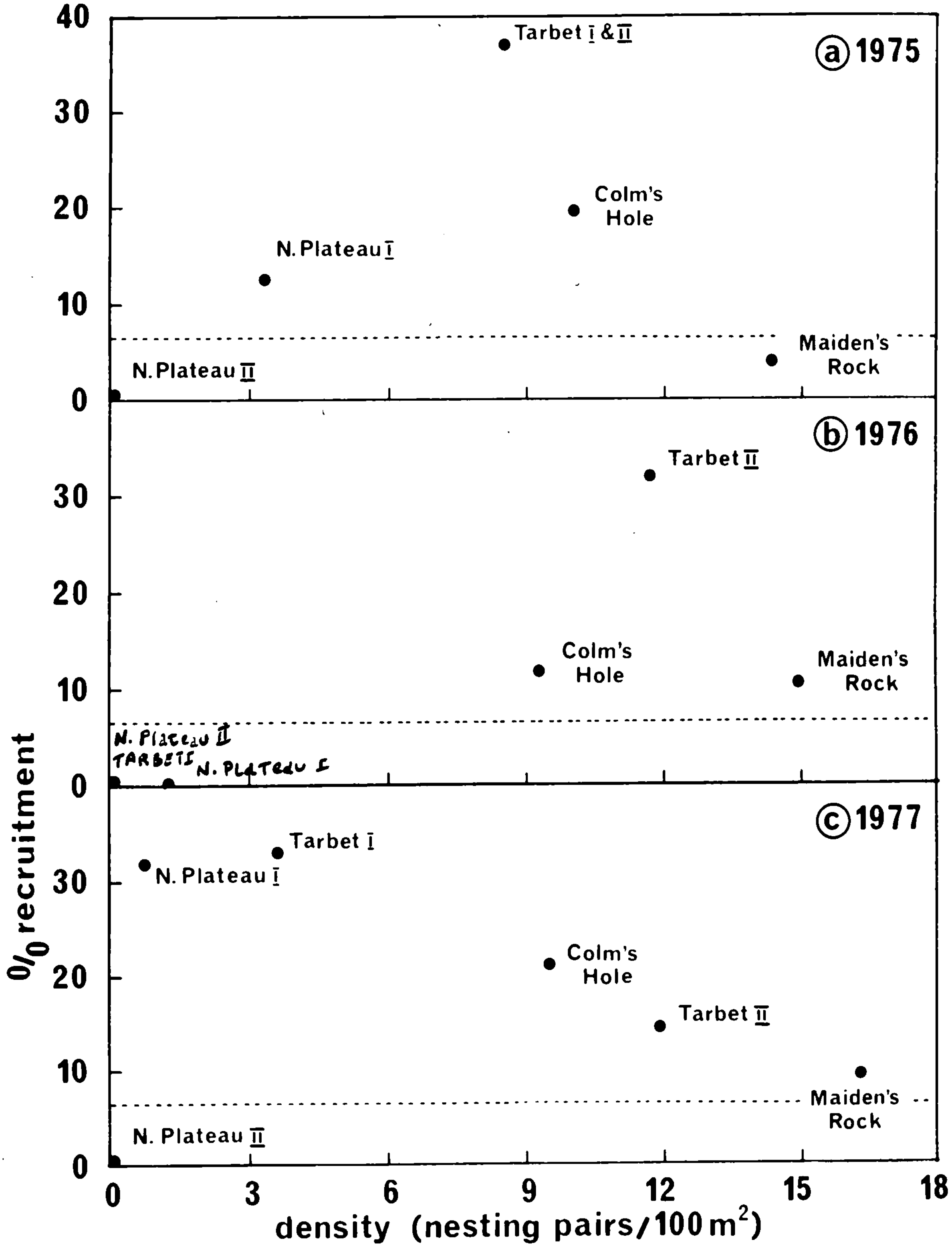
In Figure 29(a) the data for Tarbet I and Tarbet II have been pooled since the two areas belong to the same sub-colony and individual gulls have been observed on occasion to change nest sites between the two areas in consecutive years.

Figure 29 indicates that the relationship between recruitment and density differed in each year. It is probable that the variation can be accounted for only by a combination of factors which are difficult to separate, and much of the explanation may lie in the behavioural basis for recruitment which is not fully understood. Environmental factors which only directly influence reproductive state may be equally important, but further study is required to elucidate the mechanisms involved.

In 1976, when recruitment to the island as a whole was very low (Table 13), recruitment only occurred in the areas of highest density, whilst in 1977, a year in which 52% of the population were new recruits, recruitment was greatest in the study areas of lower density. The data

Figure 29. The relationship between rate of recruitment and density in six areas on the Isle of May between 1975 and 1977. Recruitment is expressed as the percentage of gulls in each area which are breeding for the first time, and density is expressed as the number of nests/100m^2

Figure 29



40
30
20
10
0
Tarbet I & II
Colm's Hole
N. Plateau I
Maiden's Rock
N. Plateau II
ⓐ 1975
ⓑ 1976
Tarbet II
Colm's Hole
Maiden's Rock
N. Plateau II
TARBET I
N. PLATEAU I
ⓒ 1977
Tarbet I
N. Plateau I
Colm's Hole
Tarbet II
Maiden's Rock
N. Plateau II
% recruitment
0
3
6
9
12
15
18
density (nesting pairs/100 m²)

for the 1975 breeding season indicate however that the most attractive density on the island was intermediate between that of 1976 and 1977. These data are not irreconcilable, for by pooling the data (Table 41) for all years, a curvilinear relationship results (Figure 30) which corresponds to the model proposed by Chabrzyk and Coulson (*loc. cit.*). Recruitment to the Tarbet II area was particularly high, but this was probably no more than a reflection of the tradition of high density nesting and attraction which this relatively undisturbed sub-colony held for recruits.

The results of these experiments indicate that there is a broad region of optimal attraction which corresponds to a density of between 2 and 10 nests/100m^2. Clearly, different colonies will have different recruitment rates regardless of density, since the topography of the colony must intervene to influence the distribution and number of nests. A more regular distribution can be achieved and a greater number of nests accommodated on flat ground, whilst on rocky slopes a less favourable clumping of territories tends to occur, particularly when competition for space becomes critical.

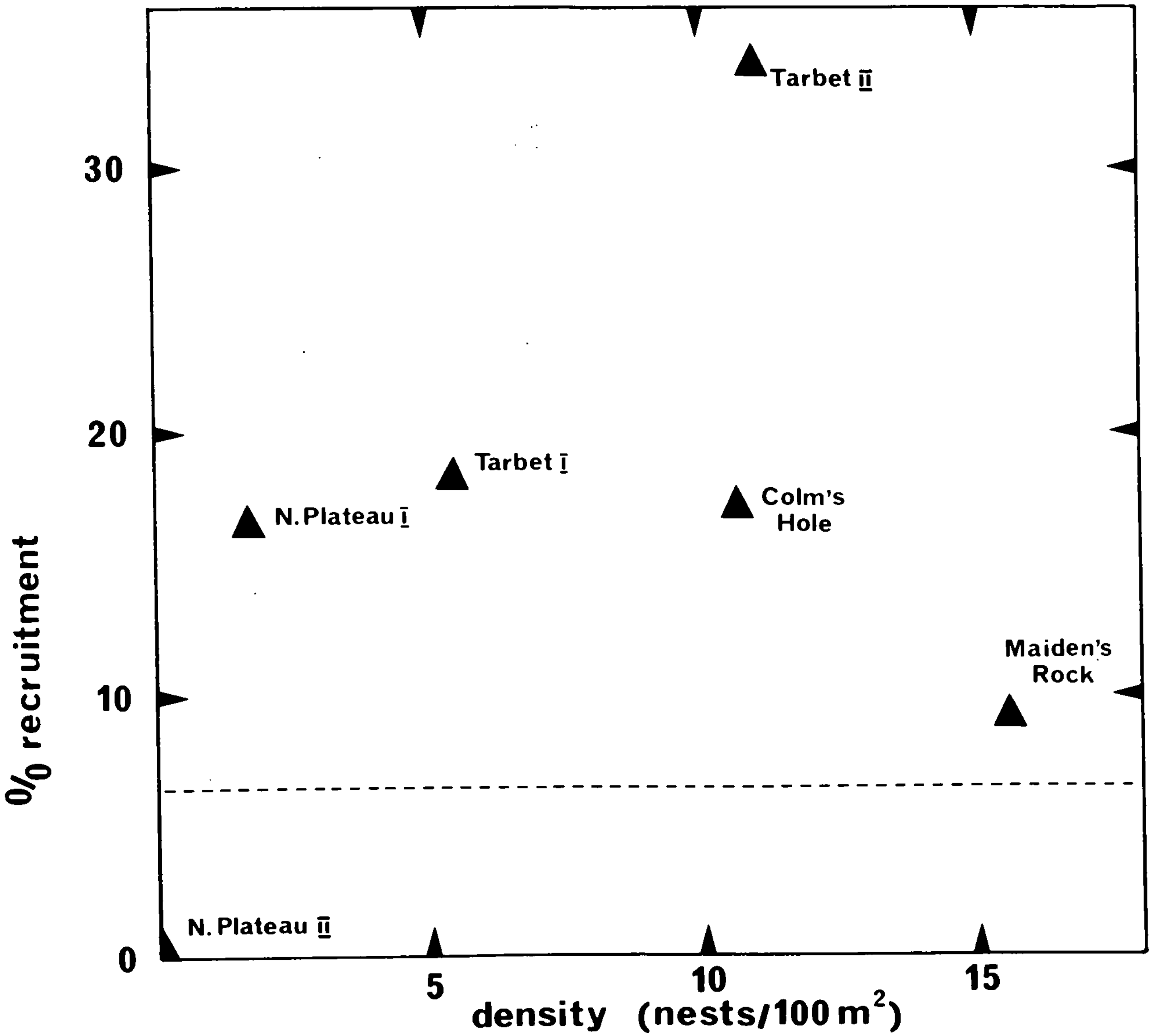
In areas of high density, the recruitment rate declines (as predicted by the model) and at the very highest densities, where nests tend to be most uniformly spaced, annual recruitment rate is of a level which is sufficient only to replace annual adult mortality and to sustain the population at a high density.

10.3 THE OVERALL EFFECTS OF CULLING ON THE BREEDING DENSITY OF THE ISLE OF MAY

In view of the relationship which has been found to exist between nesting density and recruitment, it is relevant to assess the effects of the cull with respect to the nesting density now to be found on the Isle of May as a whole.

Figure 30. The relationship between rate of recruitment and density, by pooling data for 1975-1977. The curve approximates to that proposed by Chabrzyk and Coulson (1976) for recruitment in a herring gull colony. The area Tarbet II is atypical in its exceptionally high rate of recruitment.

Figure 30



Tarbet ii
30
20
Tarbet i
N. Plateau i
Colm's Hole
% recruitment
10
Maiden's Rock
N. Plateau ii
0
5
10
15
density (nests/100 m²)

From the experiments described in the previous section it would seem that on the island, where nest density is comparatively high, the preferred density for recruitment is between 2 and 10 pairs/100m^2 and most probably towards the lower end of the scale. In 1972 when the breeding population was at a peak of 16,700 pairs, the gulls occupied an area of approximately 18.5 hectares (illustrated in Figure 31(a). By 1977, the population had been reduced to 3,670 pairs, not including lesser black-backed gulls, and still occupied an area of approximately 16ha, very nearly the same as before (Figure 31(b)). Only on the northwestern part of the island does the distribution differ significantly from that found in 1972; elsewhere it is relatively unchanged, but the density has been lowered from about 11.1 pairs to 2.3 pairs/100m^2 in the colonised regions. At this density future recruitment could continue in the region of 17% per annum or higher if the culling was to be relaxed.

Figure 31. The area colonised by gulls on the Isle of May in 1972 (a) and the area colonised by gulls in 1977 (b).

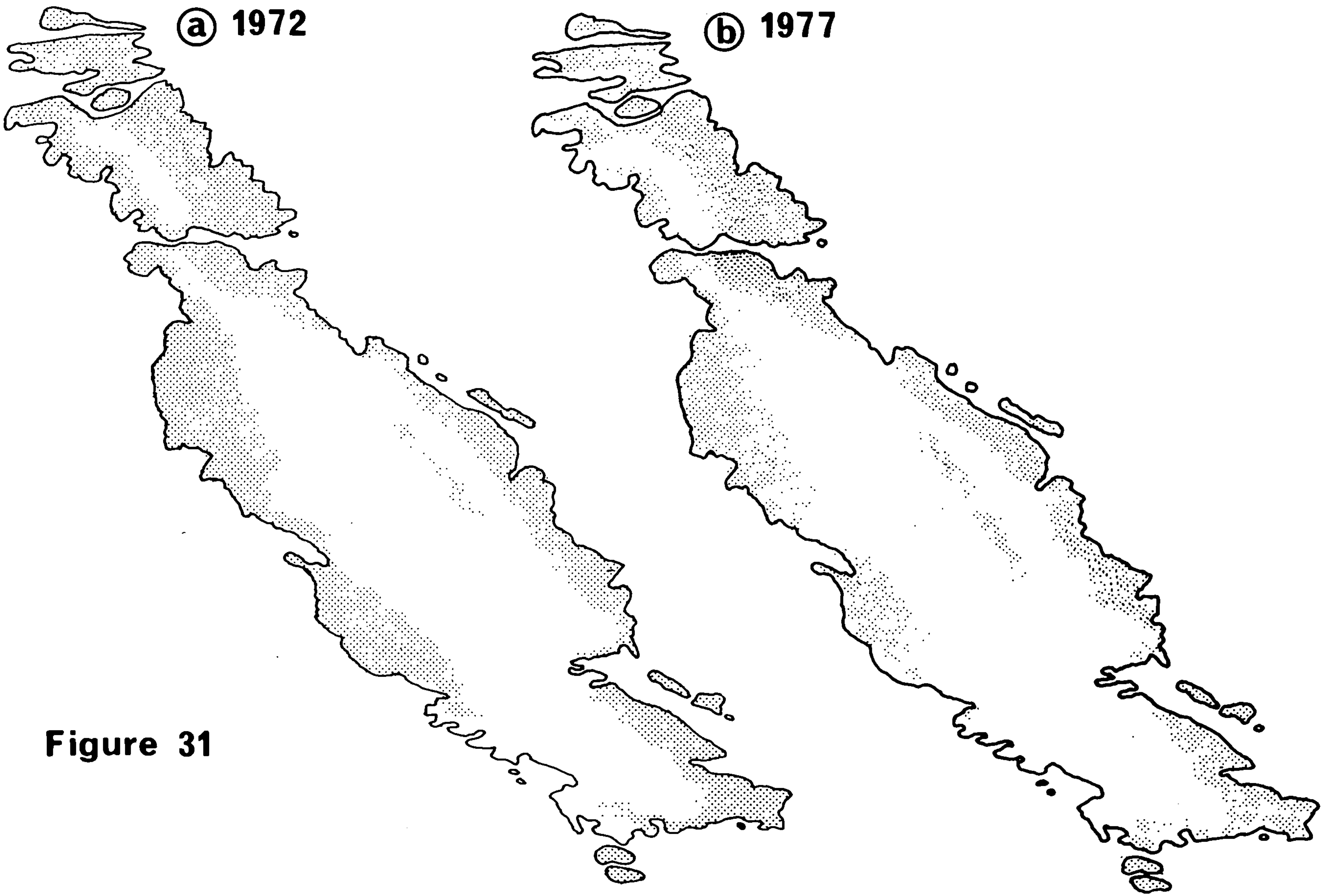


Figure 31

11. NEST DENSITY AND NEST DISPERSION

11.1 INTRODUCTION

Any intensive population study requires that the abundance of animals be in some way related to the space within which they are to be found. A measure of dispersion describes the configuration of positions which the animals take up in space, whilst a measure of density quantifies the numbers within the unit space. Unarguably, dispersion and density have the greatest fundamental significance for the population, and some consideration needs to be given to the practical difficulties encountered in their interpretation.

In this study the population has already been conveniently defined since it can be considered as synonymous with the colony. The size of the Isle of May delimits the physical extent of the colony, and with the vast majority of the population being of breeding status, the density of the breeding population is determined by the dispersion of the territories on the island. This dispersion tends to be uniform where numbers of breeding gulls are high and space is limited. The situation in the Tarnbrook/Mallowdale colony is somewhat different however. There, a physical boundary does not constrain the size of the colony so that it fluctuates in size annually, depending on the rate of increase in the population and the degree of disturbance suffered by the birds. In this colony the distribution of nests appears to be more random than on the Isle of May.

Within these two colonies, however, there is considerable variation in both dispersion and density of nests. At the simplest level there are three naturally occurring factors which influence the nest dispersion and density. These are:

(1) The type of nesting habitat: on flat, even ground a more regular spacing of nests can be achieved. When the topography is broken, nests in some areas cannot be safely accommodated.

(2) The territorial behaviour of the birds: the physical size and shape of a territory is influenced by (1), but more particularly by the degree of tolerance between neighbouring pairs.

(3) The timing of breeding: where synchrony in breeding is apparent, but with different proportions of the population breeding earlier or later than the norm, there will be variations throughout the season in both dispersion and density.

When colonial organisation is being investigated, the effects of these three criteria have considerable bearing on any interpretations to be made. Obviously it is best for the investigator to choose a colony or area where there is uniformity of nesting habitat type. For the second factor there are considerations of colony size, population size, recruitment rate, levels of aggression and site tenacity, all of which are important. The third factor is much influenced by the physiological state of the birds at the onset of the breeding season, and is in a large measure related to the age composition of the population as a whole. Patterson (1965) found that greater synchrony in nesting black-headed gulls tended to produce maximal aggregation. Parsons (1976) found that spacing of nests by herring gulls on the Isle of May tended to be uniform, but the nest density of gulls laying later in the season progressively approached a random distribution. As mentioned in Section 8.1.2, late breeding birds in this study were in only a very small minority, so the problem of seasonal variations in density and dispersion could be ignored.

There remains one other factor influencing dispersion and density - the effects of culling. Culling on the Isle of May has reduced density, but it is difficult to be certain whether dispersion has been significantly affected. On Mallowdale Fell it seems rather that density is unaffected by culling, but dispersion is. However, since it has been impossible to quantify the numbers of gulls killed there by gamekeepers working on their own initiative since 1974, or by the owners before that time, the interpretation of density measurements is not easy. Certainly it would seem that the gulls have become more scattered, and there has been an increasing tendency to form small outlying colonies of very low density some distance from the main body of the colony (Figure 7).

11.1.1 Methods

The nests on the study areas of East Tarbet I - III, Colme's Hole, North Plateau I and II, and Maiden's Rock were individually staked and numbered at the beginning of the breeding season (see p. 26). Tarbet III, Maiden's Rock and North Plateau I were not culled, so that breeding success could be measured. The remaining four areas were culled (Section 10). At the end of the breeding season the nest density of these areas was measured by two methods, called Density Measurement I and II respectively.

(1) Density Measurement I. A point was chosen at random within the area. Taking this point as the centre, a circle of radius 20m was described about it, using a tape measure. All the nests which then fell within this area ($1257m^2$) were then counted. This procedure was repeated until the entire area had been encompassed by a series of overlapping circles, and the average nest count was taken as the nest density and given as the number of nests/$100m^2$.

(2) Density Measurement II. The distance between nearest neighbours in each area was measured to the nearest 0.5m, which enabled the position of all nests to be plotted to scale on graph paper. The nest density was then

measured in a 3m unit. This was the number of nests which fell within a 3m radius of each nest. The maximum number of nests within each radius was variable according to the area, but could be as high as six in the densest parts of Maiden's Rock, or zero, which was the most frequent count on the low density North Plateau. The minimum distance recorded between any two nests was 1.25m.

11.1.2 Results

(a) Density Measurement I

Table 42 gives the density for each area expressed as the number of nests/100m^2. This measure of density was used in the investigation of recruitment rates (Section 10.1.1) since it could easily be related to the presence of birds on the ground irrespective of the actual position of their nests. This was based on the premise that the presence of gulls on the ground before nesting was fully under way (i.e. before the final density of nests has been decided) was the important factor in attracting new recruits, and that the final nesting density was a factor which was decided only later in the breeding season.

Table 42. Nest density on the Isle of May, 1975-1976, expressed as the number of nests/100m^2

Area	1975	1976	1977
		No. of nests/100m^2	
Tarbet I*	8.7	3.4	3.6
Tarbet II*	8.4	11.7	11.9
Tarbet III	9.9	12.4	15.6
North Plateau I †	3.3	1.3	0.8
North Plateau II*	0.1	0.0	0.0
Colme's Hole †	10.0	9.2	9.5
Maiden's Rock	14.3	14.9	16.2

* culled by NCC; † culled by the author at the end of each breeding season

(b) Density Measurement II

Table 43 gives the mean nest density (Measurement II) in each area between 1975 and 1977. Within each area, nests tended to be spaced uniformly. However, when the observed number of nests were compared with that expected by a Poisson distribution, there were only two instances where the departure from the expected was significant. In 1976, Tarbet II had a mean density of 2.1 nests/3m unit ($\chi^2 = 10.1$, 4 d.f., $p < 0.05$) and in 1977 Colme's Hole had a mean density of 0.75 nests/3m unit ($\chi^2 = 7.4$, 2 d.f., $p < 0.05$).

11.1.3 Nest dispersion

Table 44 gives the mean density with the standard deviation for each area. In most cases the standard deviation was large, and this variation can be expressed as the coefficient of dispersion (Southwood 1966). A coefficient of unity indicates a random distribution: uniform distributions are indicated by a coefficient less than unity, and clumped distributions are indicated by coefficients greater than unity. There were three areas where there was a degree of aggregation - Tarbet II in 1975, North Plateau I in 1976, and Colme's Hole in 1977. The significance of departure from a coefficient of unity can be calculated by using χ^2

$$\text{i.e. } \chi^2 = \frac{s^2(n - 1)}{\bar{x}}$$

where s^2 = variance, $\bar{x}$ = the arithmetic mean, and n = the sample size. When the sample size is large, it is assumed that $\sqrt{2\chi^2}$ is normally distributed about $\sqrt{2 \text{ d.f.} - 1}$ with a variance of unity. From this, $d = \sqrt{2\chi^2} - \sqrt{2 \text{ d.f.} - 1}$, where d = the unit standard deviation, d.f. = degrees of freedom = n - 1 (Southwood 1966). Values of d can be calculated from the normal distribution and are given in statistical tables.

Table 43. The density of nests on the Isle of May, 1975-1977, expressed as Density Measurement II, compared with that expected by a Poisson distribution. S is the variance

Area	1975					1976					1977				
	mean density	S^2	χ^2	d.f.	p	mean density	S^2	χ^2	d.f.	p	mean density	S^2	χ^2	d.f.	p
Maiden's Rock	2.78	1.63	9.4	6	n.s.	3.50	1.52	13.8	8	n.s.	2.08	1.69	6.9	6	n.s.
Tarbet I	1.33	0.87	5.7	4	n.s.	0.75	0.74	1.6	2	n.s.	0.60	0.62	5.7	2	n.s.
Tarbet II	3.21	1.05	6.1	7	n.s.	2.10	1.33	10.1	4	<0.05	2.04	1.5	8.1	5	n.s.
Tarbet III	2.79	1.5	7.3	6	n.s.	2.71	1.3	12.1	6	n.s.	3.25	1.4	9.4	7	n.s.
North Plateau I	0.48	0.81	5.2	2	n.s.	0.63	0.74	2.3	2	n.s.	0.82	0.85	3.4	2	n.s.
Colme's Hole	2.35	1.51	7.4	5	n.s.	1.89	1.25	1.4	5	n.s.	0.75	0.95	7.4	2	<0.05

Negative values of d indicate a uniform distribution and positive values a clumped distribution. Values of d and the corresponding levels of significance are given in Table 44. There are three categories of dispersion, of which two are represented in the table. Negative values of d which show a significantly uniform distribution - these were found in Tarbet III in all years, Tarbet II in 1975, Maiden's Rock in 1976 and North Plateau I in 1975. All other areas fall into the second category - either uniform or aggregated distributions, but which are not significantly so. Significantly aggregated distributions were not found in any of the study areas.

11.2 THE INFLUENCE OF DENSITY ON NUMBERS OF SUB-ADULT GULLS ON THE ISLE OF MAY

The effects of density on recruitment rate have been considered in Section 10.1.1 where recruitment rate was seen to be greatest at a density of between 2 and 10 nests/100m^2. The great majority of new recruits in each area had established a territory and had proceeded as far as laying by mid-May. However, there was always a proportion of young gulls which were associated with the breeding population, but did not succeed in laying eggs. These gulls were all in their third or fourth year, and were easily distinguished by their sub-adult plumage. Counts of these sub-adults were made at intervals from late April to mid-July and, as mentioned in Section 4, their numbers did not vary greatly throughout the breeding season. Some were shot to determine their sex ratio and their breeding condition, but this did not seem to affect their numbers greatly. It is likely that birds were being replaced continuously throughout the season.

Table 44. The coefficient of dispersion, sample size, the value of d and the probabilities of a deviation from a random distribution of nests on the Isle of May, 1975-1977

Area	1975				1976				1977			
	n	c.d.	d	p	n	c.d.	d	p	n	c.d.	d	p
Tarbet I	43	0.57	-2.31	<0.05	24	0.73	-1.06	n.s.	30	0.64	-1.58	n.s.
Tarbet II	74	1.07	+0.38	n.s.	50	0.84	-0.81	n.s.	76	0.73	-1.86	n.s.
Tarbet III	76	0.70	-2.04	<0.05	66	0.59	-2.64	<0.01	64	0.60	- 2.55	<0.02
Maiden's Rock	50	0.96	-0.27	n.s.	100	0.66	-2.70	<0.01	100	0.80	-1.56	n.s.
North Plateau I	57	0.67	-1.97	<0.05	42	1.14	+0.56	n.s.	22	0.88	-0.50	n.s.
Colme's Hole	37	0.97	-1.8	n.s.	38	0.83	-0.84	n.s.	32	1.20	+0.70	n.s.

Figure 32 indicates how the sub-adult gulls were distributed in relation to the nest density existing in the areas where they settled. Numbers are expressed as a percentage of the total numbers of gulls present at the time of the counts (not the total number of breeding pairs in each area). On each study area a minimum of 25 counts were made in each year, 1975-1977.

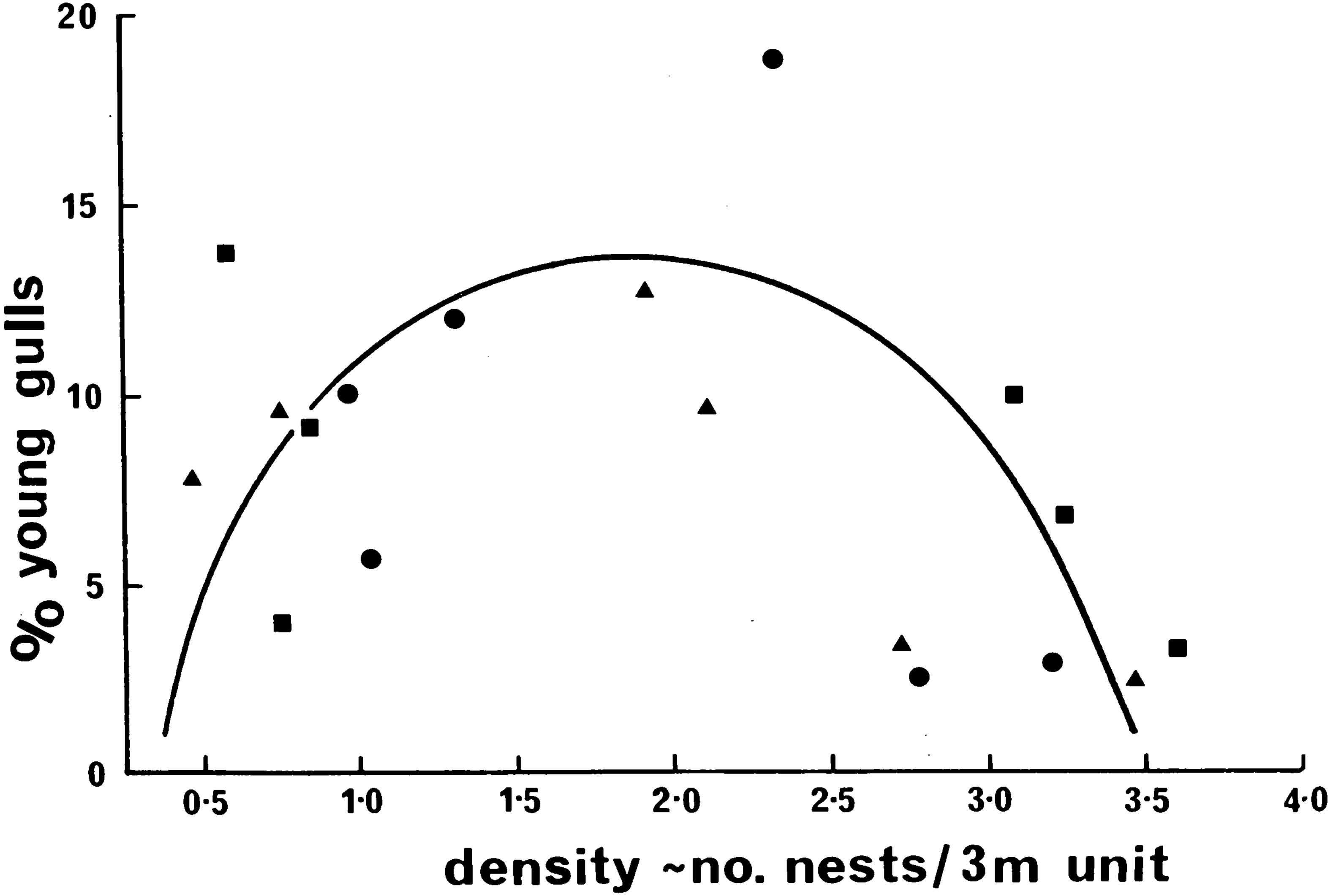
The results indicate that sub-adult gulls are fairly well distributed at all densities, although some areas are more favoured than others irrespective of density. However, at densities of less than one nest/3m unit, the percentage of young gulls present tends to be lower than the percentage present at intermediate densities of about 2 nests/unit. At densities higher than 2.5 nests/unit, the percentage present was lower still, usually less than 4%.

Interactions between sub-adult and adult gulls are often characterised by high levels of aggression. Female sub-adults assume a hunched,submissive posture in the presence of territory holding adult birds with little aggression shown towards them, but male sub-adults are attacked both on the ground and in the air above the colony, especially near the densest areas. Of 18 sub-adult gulls shot at the end of the breeding seasons of 1975 and 1976 in Tartbert II, 16 were females. It seems that males find it much harder to alight with impunity in these dense areas. In general, the data illustrated in Figure 32 conform to the model proposed by Chabrzyk and Coulson (1976) that describes the regulation of recruitment at various densities (Figure 28). These sub-adult gulls appear to be prospecting the colony, with a view to breeding the following year. From these observations it would seem that the densest areas are attractive to the young gulls, where they are treated as intruders by the resident territory holders. As a result, instead they tend to congregate in areas of intermediate density where there is a greater chance of remaining unmolested. They are seldom chased off low density areas, but these are not so attractive in any case.

Figure 32. The proportions of sub-adult gulls present in colonies of different densities on the Isle of May, 1975-1977

(● 1975, ▲ 1976, ■ 1977)

Figure 32


% young gulls
20
15
10
5
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
4·0
density ~no. nests/3m unit

It can be concluded that the highest recruitment rate should be recorded in areas of intermediate density - as has been shown to be the case in Section 10.1.1. A consequence would be that the density of birds breeding for the first time in a growing colony is in large part determined by their presence in the previous year. Thus there might be a tendency for these areas to be more attractive and more contested than areas where breeding density is already high, and where site ownership has been long established.

11.3 THE CORRELATION BETWEEN DENSITY AND AGGRESSION

Tinbergen (1953) has forwarded the hypothesis that the function of territory for the herring gull is the defence of the eggs and chicks against predators. This has been taken up by Patterson (1965) who suggested that the spacing of territories was compromised so as to effect maximum protection for the colony as well as for the contents of individual nests. This idea of the function of territory presupposes that the territory size must in some way be regulated by the birds themselves, and it seems likely that aggressive action is the best way of achieving both an optimal size and retaining ownership.

As Tinbergen (*loc. cit.*) acknowledged: "fighting in gulls, ... is a very complicated behaviour pattern. Not only are there various different ways of fighting, but fighting behaviour is often seen in an incomplete form, and it may also be combined with other activities, ..." This part of the study has been concerned however, not with causation, but rather the consequence of aggression. I have assumed that during the breeding season the main reason for a fight in the colony is to effect the withdrawal of an intruder from an occupied territory. At high densities, where nests are spaced only a few metres apart, there are numerous fights, some of them prolonged. At lower densities they occur less frequently.

Nevertheless, it is important to point out from the outset that at low densities much aggression may be discharged through other less overt forms of behaviour, such as displacement nest building and incipient aggressive movements where no contact is made. The argument then is that aggression plays a major role in determining territory size, and hence density in a colony where there are limits to continuous expansion. It is important to differentiate between a colony on a small island such as the Isle of May, and a colony without physical boundaries such as that on Mallowdale Fell. When the colony is numerically large, protection for the group against predators will be the more effective. However, when the physical limits of the colony have been reached, and if the population is to continue to grow, then there must be, perforce, an increase in density with a tendency towards smaller and uniformly distributed territories. If there is survival value for eggs and chicks in an optimal territory size compatible with the unhindered expansion of a colony, then it would seem logical that any reduction in territory size through crowding would be resisted by the resident territory holders, and this will be reflected in the levels of aggression for a particular density.

11.3.1 Methods

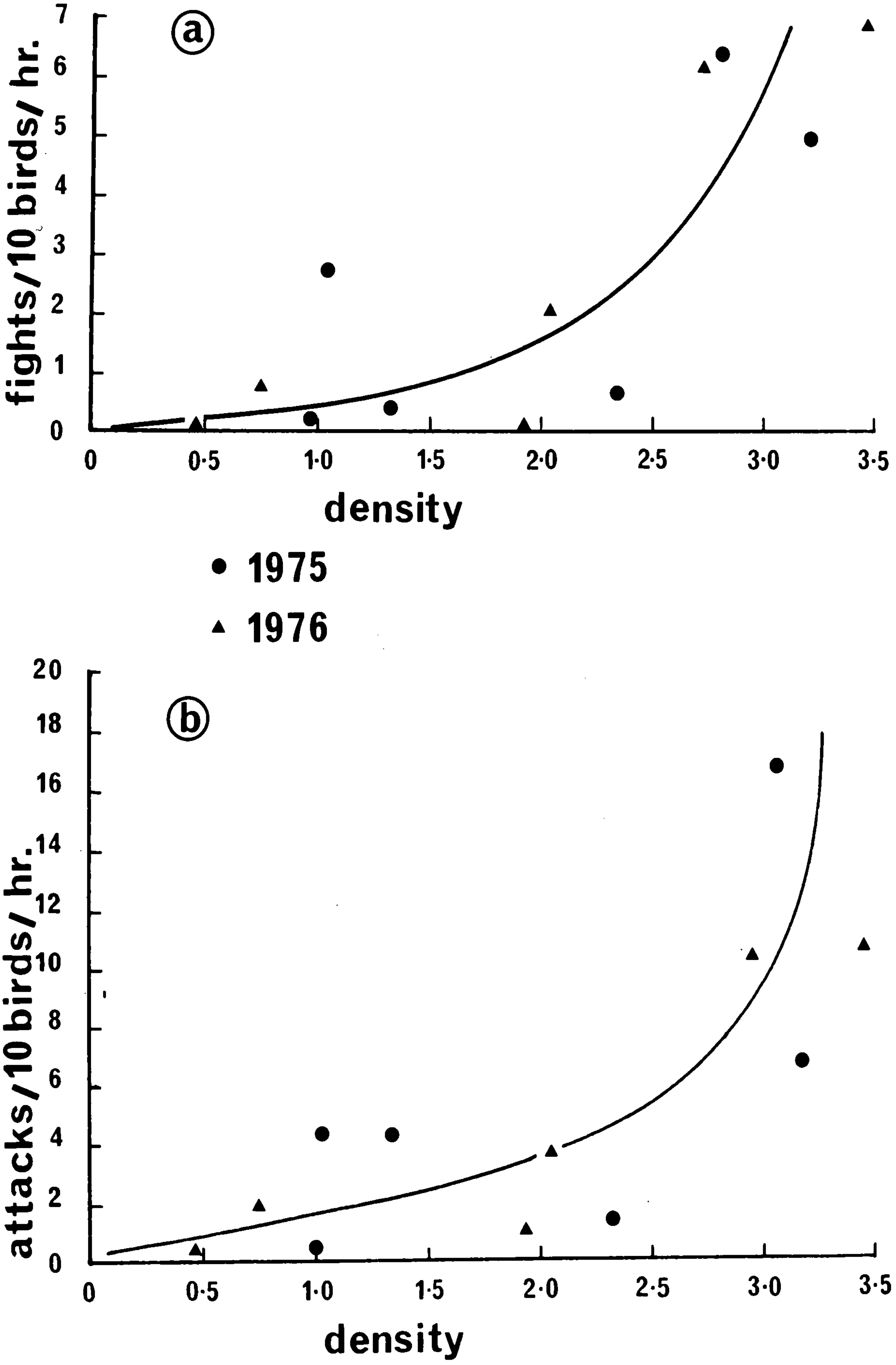
Aggressive behaviour was recorded in the six study areas throughout the peak of courtship behaviour and up to the appearance of the first eggs. Observations were restricted to the seasons of 1975 and 1976 only . Each area was observed for a one hour period on a rotational basis so that any daily or seasonal variations in activity were avoided for a particular area. Eight hours of observation were devoted to each area in 1975, and 12 hours to each area in 1976. At the beginning and end of each session the numbers of gulls visible were noted. Aggressive interactions were divided into 'fights' (where there was physical contact between two or more birds for not less than 3 seconds) and 'attacks' where contact was only momentary, as in a swoop from the air by one bird at another on its territory. Other aggressive behaviour was not considered since too many birds were being watched at a time for adequate recording. The frequency of aggressive interactions was then expressed as "the number of fights/10 gulls/hr" and the "number of attacks/10 gulls/hr".

11.3.2 Results

Figure 33 illustrates the combined data for 1975 and 1976 with aggression plotted against colony density. Both (a) and (b) show the same sort of curve, where levels of aggression increase only slowly up to a density of about 2 nests/3m unit, whereupon there is a sharp rise in the frequency of fights and attacks for a further increase in density. These data show a difference in behaviour of gulls between extremes of nest density -- which might be reasonably expected - and the most likely reason for the shape of the curve is as follows: as suggested above, there can be sharp differences in the manner of how aggression is discharged. Above a particular threshold - which seems to be strongly influenced by density - aggression is discharged through fighting, whilst below the threshold density, fighting is less frequent but is replaced by other forms of aggressive behaviour. From Figure 33 this threshold density appears to be in the region of 2.5 nests/3m unit (or equivalent to about 11 nests/100m^2). From this, a step-wise increase in aggression with increasing density would result. Some individual birds showed a greater tendency to attack or sustain a fight than did others, but the incidence of aggressive encounters tended to be distributed throughout the entire area of the sub-colonies rather than be confined to the same group of territories.

Figure 33. The relationships between aggression and density in a herring gull colony. Aggression is measured as the "number of fights/10 birds/hr" and the "number of attacks/10 birds/hr". Density is expressed as the number of nests within a 3m unit around each individual nest.

Figure 33


ⓐ
fights/10 birds/ hr.
0
1
2
3
4
5
6
7
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
density
● 1975
▲ 1976
ⓑ
attacks/10 birds/ hr.
0
2
4
6
8
10
12
14
16
18
20
0
0·5
1·0
1·5
2·0
2·5
3·0
3·5
density

Male gulls in sub-adult plumage were rarely involved in fights, but very frequently were the object of attack by established, breeding gulls. There is a strong possibility that the very nature of sub-adult plumage elicits attack by a territorial gull on a young bird since the plumage is not dissimilar to that of a raptor or skua, especially if the distinctive black barred tail is retained into the third year (as it is in about 50% of male herring gulls). As shown in Table 11 a total of 114 third year gulls of either sex were found to be holding territories over the three year period 1975-1977, and without exception all of them were situated in areas of intermediate density, but close to the edge of the colony. The most favoured areas were Tarbet I, II and Colme's Hole, which had formerly been high density areas before being culled. No third year birds were found holding a territory in high density areas, and less than 6% of fourth year birds culled by the NCC came from areas which had a density higher than 1.75 nests/3m unit.

11.4 NEST DENSITY AND THE NUMBERS OF SUB-ADULT GULLS IN THE TARNBROOK/MALLOWDALE COLONY

In the study area on Mallowdale Fell, nest density ranged from 4 to 55 nests/ha (0.04 - 0.55 nests/100m^2). At this density nests become increasingly hard to find, especially in deep heather and on rough ground, but there were areas in the Tarnbrook watershed where density was higher. The coefficient of dispersion of the nests was not calculated since the distance of one nest to its nearest neighbour was frequently more than 20m and the procedure would have been very lengthy and time consuming.

11.4.1 The proportions of sub-adult gulls on Mallowdale Fell

The sub-colony on Mallowdale Fell was culled in successive years, 1974 - 1976 and a total of 640 herring gulls were recovered.

These were aged by plumage characters and sexed by dissection, and an assessment made of breeding condition from the state of the gonads. Table 45 gives the numbers culled, together with the age, sex and breeding status. A higher proportion of young males than females were in breeding condition, and more males than females overall were culled. It can be seen that, on average for the three years, 32% of the total male sample was aged three to four years, and with 19.5% of the female sample of this age. Although the average age of recruitment on Mallowdale Fell could not be calculated using the method given in Section 5.2, it would seem that the age at which herring gulls recruit in this low density is considerably less than has been found on the Isle of May colony; there it has been shown that the proportion of breeding gulls aged four years or less would probably be no more than 4% of the total population in the years prior to 1972.

11.5 CONCLUSIONS RELATING TO AGE OF RECRUITMENT AND COLONY DENSITY

Circumstantial evidence suggests that young gulls distinguished by sub-adult plumage find it harder to gain a territory within a dense colony. The function of sub-adult plumage in seabirds has been debated (e.g. Wynne-Edwards 1962) and although ideas have never acquired the substance of proven fact, it has generally been assumed that sub-adult plumage-types serve to distinguish the sexually immature. This is not entirely the case in the herring gull, as third and fourth year gulls have been found to breed successfully. However, it appears that if they are discriminated against by older gulls their presence is less likely to be recorded, especially in dense colonies. The lowering of average breeding density on the Isle of May has increased the chances of these birds to breed, and on Mallowdale Fell the naturally low density permits them to breed in unusually high numbers.

Table 45. The numbers, age, sex and breeding status of herring gulls culled on Mallowdale Fell, 1974-1976

	Year of culling									
	1974			1975			1976			totals
Age	3	4	5+	3	4	5+	3	4	5+	
No. of males	17	36	78	12	40	101	9	25	58	376
No. breeding	13	34	78	4	37	101	6	25	58	356
% breeding	76.5	94.4	100	25.0	92.5	100	66.6	100	100	94.7
No. of females	9	22	60	4	18	88	1	14	48	264
No. breeding	1	17	60	0	18	86	1	13	48	244
% breeding	11.1	77.3	100	0	100	97.7	100	92.9	100	92.4

11.6 DENSITY AND FLEDGING SUCCESS

Parsons (1976) showed that breeding success of herring gulls on the Isle of May was significantly better at the most common nesting density. (This corresponded to a density of 2 nests/2.3m unit.) At densities lower than this (i.e. density 0) or higher (density 3 and 4) clutch size, hatching success and fledging success tended to be reduced. There was also a significant decrease in fledging success as the spacing of nests approached a random distribution ($r_6 = -0.79$, $p < 0.02$).

In this study, fledging success measured in Tarbert III, North Plateau and Maiden's Rock in the years 1975-1977 was plotted against the coefficient of dispersion for these areas (Figure 34). Similar to the findings of Parsons (*loc. cit.*) there was a reduction in fledging success as the spacing of nests approached a random distribution. There was no good evidence, however, that the relationship is necessarily linear. Nevertheless, the conclusion remains the same with birds which spaced their nests most uniformly being the most successful breeders.

The relationship between nest density and chick fledging success cannot, unfortunately, be deduced on account of the inadequate range of breeding densities in the areas where chicks were allowed to survive (Figure 35).

Figure 34. The relationship between chick fledging success and the dispersion of nests within the colony

▲ indicates figures for 1975

● indicates figures for 1976

■ indicates figures for 1977

Figure 34

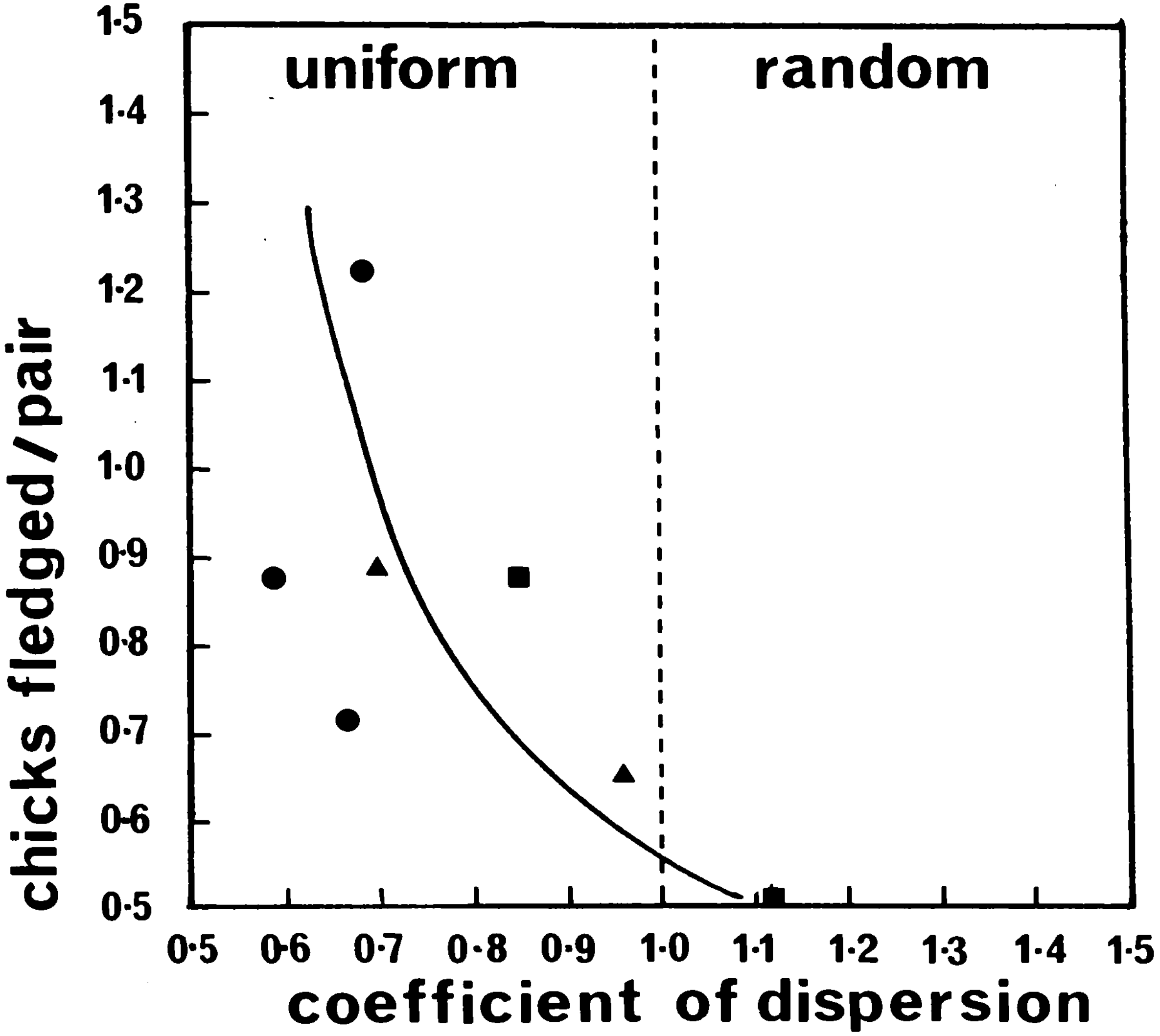

uniform
random
chicks fledged/pair
1·5
1·4
1·3
1·2
1·1
1·0
0·9
0·8
0·7
0·6
0·5
0·5
0·6
0·7
0·8
0·9
1·0
1·1
1·2
1·3
1·4
1·5
coefficient of dispersion

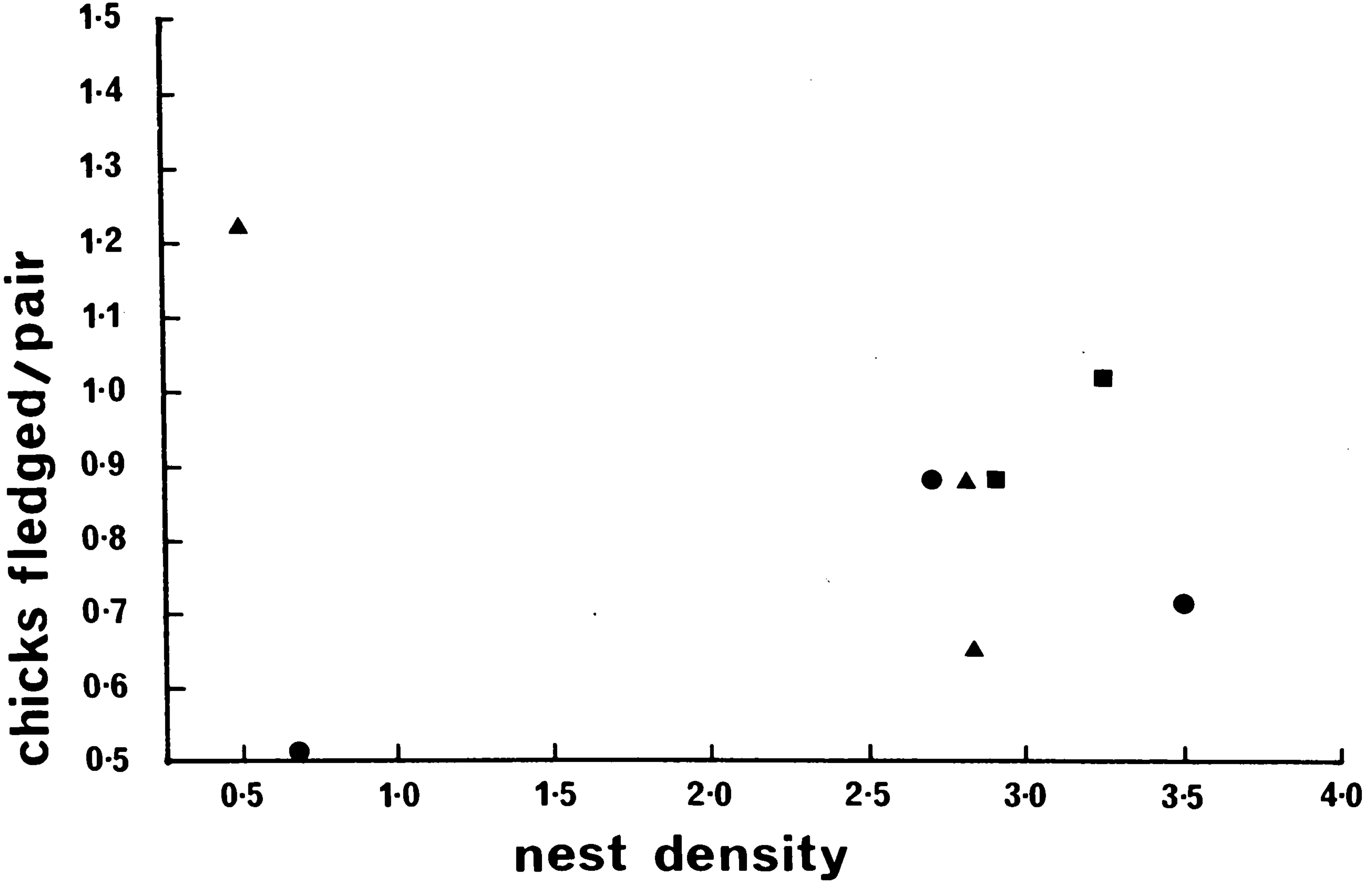
Figure 35. The relationship between chick fledging success and nest density of the colony

▲ indicates figures for 1975

● indicates figures for 1976

■ indicates figures for 1977

Figure 35



1·5
1·4
1·3
1·2
1·1
1·0
0·9
0·8
0·7
0·6
0·5
chicks fledged/pair
0·5
1·0
1·5
2·0
2·5
3·0
3·5
4·0
nest density

12. DISCUSSION

It is sometimes the case that numbers of bird species increase exponentially. This is never a commonly observed phenomenon, but within this century such occasions have been witnessed. In addition to the herring gull, the collared dove and the fulmar provide such examples. Murton (1971) draws attention to the spectacular increase in the number of collared doves in Britain which, having spread across Europe from central Asia, became established in this country in 1955, and now are important agricultural pests. Likewise, the spread of the fulmar has been characterised by a progressive colonisation of new ground (in this case southerly from the high Arctic) for at least the last 200 years (details are given in Fisher 1952). While the build-up in numbers of these two species has been remarkable, they differ from the herring gull situation in that there has been an accompanying major change in their distribution as well. It is reasonable to suppose that every successful species must possess some initiative for exploiting new opportunities when they arise, and for the herring gull, and to some extent the great black-backed, the lesser black-backed and the common gulls, this seems to be more manifest by a consolidation of their existing range. (The important colonisation of Iceland and the invasion of new southern areas in the eastern United States by the herring gull has already been mentioned.)

Fundamentally, either an increase in survival rate or the birth rate can cause an increase in the numbers of a species within its normally occupied range. The case of the herring gull suggests, however, that important changes in its life history have also taken place. In a stable population the adult mortality must balance the fertility rate (defined here as the number of progeny from one female which survive to reproduce) and it follows that this will be low in a species with a low reproductive output.

The average fertility rate of the herring gull is about 0.63 (the number of young surviving from each female to breed) and could be higher still if chick survival increased even fractionally. With an average annual adult mortality of only 0.065 and a sustained increase of 13% per annum, it is clear that the breeding population has been producing nearly three times the number of young necessary to hold the population stable.

The increase in herring gull numbers is to some extent correlated with the increase and spread of other gull species such as the greater black-backed and the black-headed gull, and it seems that there has been a genuine improvement in the environment for such species. While it can be generally argued that density dependent factors regulate the numbers of animals universally, there are certain difficulties in defining what those factors are for a species so versatile and opportunistic as the herring gull. There is no evidence that food shortage ever becomes critical (Pearson 1968; Monaghan 1977), predators are few, and until the recent attempts to control large numbers of herring gulls the influence of man's depredations on the population have been steadily diminishing throughout the century. In the absence of environmental checks, and confronted with the evidence of the doubling of the population every six years, it is arguable as to whether the herring gull population is regulated at all.

The argument can possibly find some solution in an appreciation of an almost complete lack of specialisation in the herring gull, for it possesses no strictly defined ecological niche. When one feeding habit chances to become untenable (for example a change in fisheries practice which results in the unavailability of fish offal), the bird is able to resort to catching its own fish, or seeks completely new feeding sites which could be terrestrial or littoral. In this manner of unspecialisation it is also possible for the species to invade new areas should they become available to it. The amelioration of the Icelandic climate during the first half of the present century may well have permitted immigration of not only herring gulls but also the black-headed, the lesser black-back and the common gulls into Iceland (Gudmundsson 1951). Strict specialisation in form and behaviour may bestow certain advantages on an animal seeking to invade novel niches (Mayr 1963) but the converse also holds true for an unspecialised animal such as the herring gull seeking to invade a series of niches where the "generalised" as opposed to the "specialised" habit is the more advantageous.

There is enormous scope and variation in the behavioural traits of the herring gull - in food, feeding sites and strategies (Harris 1965; Threlfall 1968; Lloyd 1968; Monaghan 1977), in nesting sites (Monaghan and Coulson 1977; this study), in breeding range (Voous 1960; Curry-Lindahl 1961; Vaurie 1965; Kadlec and Drury 1968), and even in movements (Parsons and Duncan 1978). A property of this non-specialist habit in the population as a whole is that there is in fact scope for the individual to develop and concentrate upon its own particular line of specialisation, and thus resources are more evenly allocated. Extreme examples are the habits of cannibalism in the breeding season by some individuals, or predation on other species, and the growing habit of roof-top nesting. Some individuals even lead a virtually solitary and predatory existence inland (Wynne-Edwards 1962, and personal observations). To optimise the total resources available in such a manner should surely be a most potent factor in assuring the success of a species.

This study has been closely associated with the effects of culling gulls, and it therefore seems a worthwhile exercise to review the rationale and comment on the prospects for the policy in the future, using the Isle of May gull cull as a specific example. The reasons for the cull on the Isle of May have been outlined in Section 4.1.1, where it was pointed out that damage was being caused to the nature reserve. The only facts which could be quantified were that the annual increase in the numbers of gulls was being sustained at 13%, and that the tern colonies had disappeared. Destruction to vegetation and soil cover had been observed, but not quantified, and the degree of pressure exerted on other species was arguable, but almost certainly insignificant. As with the British herring gull population as a whole, there seemed no immediate prospect of the numbers stabilising in the colony. To return the Isle of May to its previous status as a nature reserve with regards to species diversity and biological interest through the artificial control of the gulls was a worthy objective.

Earlier sections of this thesis have reported on the cull up to that of 1977, but since the time of writing the 1978 cull has taken place. Therefore the most up-to-date information after six consecutive culls is that about 38,000 gulls have been killed up to 1977, with a further 600 in 1978. The pre-cull breeding herring gull population in 1977 was 3,670 pairs which had increased to about 3,950 pairs in 1978. (With a lesser black-backed gull population of about 850 pairs, the total therefore stood at some 4,800 pairs of gulls before the 1978 cull). Breeding density has dropped since culling, although the areas occupied by nesting gulls in 1977 and 1978 were very similar to those in 1972. In addition, a large number of young gulls, estimated at 31,000 up to 1977, have been deterred from breeding on the island, presumably as a result of culling. From this information, and bearing in mind the essentially experimental nature of the cull, the following suggestions are made as to how the cull might progress in the future.

Clearly, it is not easy to eradicate a colony of gulls or to reduce numbers to a level where deleterious effects become insignificant. Since 1972, there has been a simple policy of culling a minimum quota of gulls annually. In the years up to 1974, this quota could be easily realised and, indeed, in these three years 32,344 gulls were culled, 84 % of the total up to 1978. Since 1974, however, it has been difficult to reduce the herring gull population below 3,000 breeding pairs. Consequently, it now seems important to consider what numbers of breeding gulls remaining on the island are compatible with enhancing the value and quality of the reserve. There are three alternatives here which can be discussed in detail. Firstly, an endeavour to hold the population at present levels, with its present spatial distribution, indefinitely. Secondly, to leave the island unculled for one or two years in the first instance and even abandon the cull altogether, and thirdly, to plan the cull as a series of experiments which would be compatible with the objectives. There is no evidence that this present level of culling will at some stage accelerate depopulation of the colony automatically, and there is every likelihood that if culling is stopped, the population will once again increase as dramatically as before. At present, there is no information as to when a gull colony becomes a problem, and at what point action should be taken to control numbers. While the problem can best be considered only subjectively, depending upon what the gulls might impinge, it seems that a prerequisite is to be able to state precisely what level the population should be reduced to. One way of quantifying the maximum number of gulls which can remain on the island would be to assess the impact of gulls on the vegetation and soil for different nesting densities and on different parts of the island. Sobey (1975, 1976) has recorded vegetation changes on the island between 1936 and 1972 and concluded that in 36 years the vegetation of much of the island changed from a typical *Armeria* and fescue sward to plant communities dominated by "coarse grass and weeds". His prognosis was that if the influence of the gulls could be removed from much of the island, then changes could be expected to occur in the vegetation with those species dependent on disturbance such as *Rumex acetosa* and *Holcus lanatus* eventually being replaced by perennials within a few years. However, in areas where erosion has followed the destruction of vegetation, it might take many years for species such as *Armeria* to regain their former position, if it could ever completely do so. No attempts have been made, however, to quantify the amount of damage for which gulls can be responsible in the breeding season. This is different from recording changes in vegetation on an annual basis by mapping, and could be conducted on the lines of investigating the four quantifiable activities which affect soil and vegetation - treading, which suppresses growth, defecation, which induces nutrient enrichment, the collection of nest material (usually outside of the colony boundaries), which can devastate certain slow-growing species such as *Armeria*, and the uprooting of vegetation during boundary disputes on territories at the time of breeding. The first of these is probably the least important, especially where the rocky areas of the island are colonised, and the effects of the other three are presumably to a large extent dependent upon nesting density.

In the absence of informative published accounts of vegetation changes on the island whilst the gull colony was growing, it is difficult to be clear as to what levels the population should be reduced to before a reversal in the trend towards the establishment of undesirable species which flourish through disturbance becomes evident. In 1957, when the herring gull population had just passed 3,000 pairs, Bell (1958) noted that "*Atriplex* species" were common on the periphery of the island, and covered much of Rona. Formerly, these areas had been predominantly *Armeria* sward, so it would seem that if this number of gulls could bring about the destruction of the original vegetation cover, it is improbable that a reduction to the same number of gulls at a much later date could reverse the trend. While it should be possible to predict the level to which the population should be reduced to improve the vegetation and lessen erosion, it is much more difficult to predict the point where the gull population would not interfere with the establishment of tern colonies. There has been no indication so far that terns might once again adopt the island as a breeding colony, but whether the present gull population acts as a deterrent (or even an attractant) is unknown.

With the present policy of culling an annual quota, which seems increasingly difficult to realise, and bearing in mind the attendant problems such as relating the quota to the objectives of the cull, my conclusions are that this policy cannot continue if the original objectives are to be adhered to with any prospect of success. One of the two remaining alternatives, which need not be permanent, would be to leave the island unculled for at least one year, possibly two, in order to quantify recruitment - which presumably would be mostly through immigration from elsewhere since the number of chicks fledging in recent years has been very low. This would have the advantage of giving new information on the effectiveness of culling (the danger of a huge influx of newly recruited gulls would be negligible). To discontinue the cull indefinitely, however, would not seem a practical alternative since a rapid return to the original population levels are indicated from the recruitment experiments already described, especially since much of the island is currently at an optimal density for high recruitment rates.

The third alternative, which could be profitably combined with the second, advocates a greater emphasis on experimentation and should, I feel, be adopted since it offers greater possibilities for acquiring new knowledge, is compatible with the original objectives, and does not ignore the problem of what should be done about the very appreciable proportion of young gulls which do not return to the natal colony, but which are recruited to colonies elsewhere.

A priority of this future policy would be that certain areas should be completely cleared of gulls, or if this proves impossible, the density lowered to a minimum level whereby there is no attraction for young gulls seeking a territory for the first time. The establishment of such areas (Rona and the North Ness would be convenient) could have the advantages of (a) immediately relieving the pressure on vegetation and soil cover, (b) offering a gull-free portion of the island to terns prospecting for a new colony, and (c) reducing the effort of culling large areas of the island each year since it is anticipated that without the presence of breeding gulls, recruitment of young gulls would virtually cease altogether. An area once densely colonised by gulls, but now cleared of their presence, would also provide a most useful area for recording changes in vegetation type - especially since no such area exists at present.

One important, practical aspect of clearing areas would be the allocation of the resources of time and man-power. It is much more difficult to clear large areas of gulls completely, but this study has shown that it is quite possible, although it would probably be a costly operation. In the first instance, it would be prudent to examine the feasibility of clearing from the economic point of view, but it seems likely that the alternatives could be costlier still.

A second priority would seem to be the establishment of a permanent control area on the island, where gulls are left unculled and undisturbed. Here it is anticipated that such an area would eventually reach a density whereby the numbers of gulls recruited annually would be no greater than those dying annually through natural causes. Providing this area was not too large (in case it encroached on gull-free areas) it would be possible to conduct further experiments on breeding success and, importantly, to permit the fledging of marked chicks so that their future movements might be followed, and particularly so that the colony to which they are ultimately recruited could be identified. (The present control area of Maiden's Rock would be unsuitable for experimental purposes since access is too restricted and disturbance to other breeding species too great to be countenanced).

With provision for the establishment of two experimental zones on the island, one free of breeding gulls, and the other of high breeding density, but neither contributing to increased numbers of gulls seeking to join the population, it is possible to rationalise about what should be done about the remainder of the island. It would seem the best policy to try to eradicate gulls completely from most areas, and this might be most easily achieved on the southern end and the entire western side of the island. Density in these areas is already moderately low and on the areas of the North and South Plateau the fescue sward is still well-established and large patches of *Silene maritima* are a particular feature of the South Plateau. To keep these areas clear of gulls would also do much to check the increasing number of lesser black-backed gulls, since they favour the more vegetated areas. Effectively, the areas left to be accounted for would then be restricted to the rocky east coast of the island. The most specific recommendation for this area would be to contain the gull population to within the rocky coastline, as serious erosion is already taking place on the east side of the island due to disturbance by puffins and rabbits. If restricted to the seaward perimeter, it is unlikely that this area could contain more than five or six hundred pairs of breeding gulls, and possibly much less, due to its uneven topography (unsuitable for nesting) and exposed aspect on the splash-zone.

The problem of dealing with the proportion of gulls which recruit to other colonies rather than return to the Isle of May is difficult to overcome. It has been shown that the discouragement of recruits has been almost as potent a factor in reducing the gulls as the killing of adults on the island. Between 1972 and 1977, over 38,000 gulls have been culled, but from the known rate of increase in the colony it is estimated that recruits to the colony would have numbered nearly 50,000 in this time. The fact that less than 18,000 could be accounted for suggests that about 31,000 recruits have enlisted to other colonies. While this may be satisfactory for one particular locality, since it temporarily achieves the depopulation of that colony, it can scarcely be viewed as an adequate long-term approach to control, as the problem is just being shifted elsewhere. Having deduced this fact, however, it seems to be possible to make progress in two directions. Firstly, by allowing marked chicks to fledge from a control area it should be possible ultimately to trace the colony to which they are recruited. Secondly, by completely clearing extensive areas, it should be possible to reduce the numbers of the two components of recruitment (those birds which are immigrants, and those which are returning to their natal colony) to a bare minimum. It is wasteful of effort to devote resources to controlling gulls which originate from elsewhere in any case, and if large areas are cleared of gulls, the numbers of chicks which survive to return to their natal colony will be small.

A future policy on controlling a population or a colony of herring gulls depends for its success on a consideration of two biological factors, quite apart from the mere destruction of a number of breeding adult gulls. Firstly, more attention needs to be focussed on the behavioural mechanisms underlying recruitment. We know very little about why some colonies may be more attractive than others to recruiting birds, and what the factors which control density might be. Secondly, the importance of inter-colony movements is not to be dismissed. Culling has the effect of deterring recruits and leads to the dispersion of the existing colony, possibly the formation of new ones, and certainly the movement of birds elsewhere, where they might be even less welcome. An additional factor is that in the artificial control of a herring gull population one must be cautious of claims of success whilst a scattered breeding population remain within the colony, providing attraction. The combined effects of killing adult gulls and the deterring of recruits may temporarily achieve depopulation, but this success will be short-lived if culling ceases permanently.

As a concluding thought, the artificial control of the herring gull population, however politically or economically expedient, should not be entirely divorced from the moral aspects, as they are unlikely to be in the eyes of the general public. This should not be overlooked by the authorities which are empowered to sanction and licence culls of "problem" species. While effective control may be possible, it is in large part a meaningless exercise unless there is some method of quantifying the benefits, both economically and in terms of enhanced aesthetic value. At present there is little attempt to do this, nor does there seem to be any defined national policy on gull control. There seems no danger of reducing the numbers of gulls to a state where their existence is threatened, but there is a great need to define what "acceptable" numbers might be, and to justify the reasons why the existence of one animal should be weighed against that of another.

APPENDIX I

AGEING

(1) PLUMAGE

a. Sub-adults

Using those gulls which had been ringed as chicks, and had later returned to the Isle of May before assuming full adult plumage (i.e. had not yet reached their fifth year), it was possible to draw up a scheme for ageing. Inevitably, there is considerable individual variation in the amount of brown plumage which is retained up to the fifth year, but Plate II illustrates some aspects of the general trend. Gulls in their second year were rare visitors to the island, and were never seen to venture into the breeding areas. However, as (1) indicates, the brown, speckled appearance of the wings is very much more extensive and characteristic than it is in third year gulls, and the two ages were unlikely to be confused. Once in their third year (2 - 8), there can be a very variable amount of brown marking. Usually the primary coverts and middle coverts are mottled with a light brown flecking, whilst the lesser coverts give way to the light, uniform and silvery grey of the fully mature adults. In the breeding season the orbital ring is sometimes more brown than yellow if the birds are not in full breeding condition. There is a slight complication in ageing third and fourth year gulls (2 - 12) since it appears that the female moult can start several weeks earlier than that of the males. The result is that female sub-adults can actually attain "adult" plumage in May or June of their fourth year, and these birds could be mistaken for adults in the field if they are not identifiable by rings. In 35 third and fourth year gulls (18 males, 17 females) which had their plumage examined in late May of 1975 and 1976, the primary moult in the female sample was, on average, more advanced than that of the males.

Furthermore, in fourth year gulls, the appearance of wing mirrors on the primaries tends to be more advanced in females than in males.

b. Adults

The vast majority of gulls have lost all their sub-adult plumage by their fifth year, although in about 4% of birds the bastard wing may still retain some brown by the fifth year and which may extend to the sixth or even seventh year. By the fifth year, most if not all herring gulls are sexually mature, and to all intents and purposes there seems no way of ageing these birds from plumage characters. Attempts were made to correlate the size of the wing mirrors on their primaries with age, using ringed gulls of known age killed in the culls, but although fifth year gulls tended to have a smaller area of wing mirror than older gulls (which was not statistically significant), there was no indication that the size of mirrors, or the amount of wear on the primaries, was in any way an indication of age. For birds older than five years, it was therefore necessary to base ageing on ringed birds only.

c. Lesser black-backed gulls

It was similarly difficult to age lesser black-backed gulls once they attained adult plumage, and there was some evidence that full adult plumage was reached in the fourth year. In Plate III (13, 14) where a second year male and female gull are shown, the amount of white on the head and the dark brown/black of the mantle is illustrated in these sexually immature birds. In sub-adults, the dark mantle and wings make it difficult to identify any flecking or mottling in the plumage in any case.

(2) RINGS

Those gulls which had been ringed as chicks with a BTO and Darvic colour ring obviously gave no problems in ageing, but they were in a minority. Table I indicates the proportions of ringed gulls in each year of the study as found in the culls. These proportions did not significantly differ from the marked to unmarked proportions of gulls sighted in the various parts of the Isle of May, except in East Tarbet in 1977, which was the only area culled in that year.

Table I The respective numbers of gulls killed in the culls which had been ringed as chicks on the Isle of May, and the numbers killed which were unmarked

year	numbers marked	numbers unmarked	% marked
1974	571	7424	7.14
1975	278	2467	10.13
1976	109	1769	5.80
1977*	84	355	23.66

* East Tarbet only

Since the study was largely dependent upon a reliably marked sample of birds, it was necessary to bear in mind that there might be some ring loss in the marked population which could be progressive with time. Coulson (1976) drew attention to the manner in which the variation in weight of monel (nickel-copper alloy) rings increased with time. The nature and degree of this loss of weight appeared to be very variable, but the conclusion was that the rings could cease to be effective in producing recoveries after about eight years. It might be reasoned that the coloured Darvic rings would deteriorate at an even faster rate, but this was not confirmed. Assuming that all gulls ringed as chicks and later recovered in the culls were ringed with both monel and Darvic rings, then there was only a slightly greater chance that the Darvic rings would drop off before the monel (Table II).

Table II The respective numbers of gulls which lost monel rings and Darvic rings separately

year	no. ringed gulls recovered	no. with monel rings only	no. with Darvic rings only
1974	571	12	6
1975	278	9	7
1976	109	7	7
1977	84	3	8

Kadlec (1975, 1976) has investigated the effectiveness of rings made of different metals (aluminium and titanium) and the alloy incoloy. He concluded that there would be some loss after seven years, but, more surprisingly, there was no difference between the three in their rate of loss from the legs of herring gulls. Quite contrary to this, experience in the British Isles has shown that a very high proportion of aluminium rings drop off, or are removed by, herring gulls within three or four years (Coulson and White 1955; personal observations). For most biological investigations, it is quite useless to use aluminium rings, and the more so when the species of bird concerned is long lived.

Plate 2.

Variations in wing colouration in second and third year herring gulls.

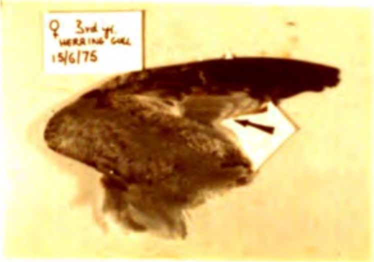
(a) 1. Second year male wing.

(b) 2, 4, 6, 7, 8. Third year female wings. In 2, 4 and 6 the arrows indicate newly moulted primaries. In 8, the arrow indicates that the brownish primary coverts are being replaced by grey adult plumage.

(c) 3, 5. Third year male wings.

Plate 2

1



2

3

4

5

6

7

8

Plate 3.

(a) 9, 11. Fourth year male herring gull plumage.

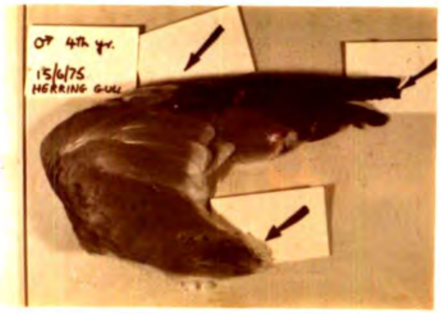
10, 12. Fourth year female herring gull plumage.

In general, the female attains full adult plumage a few weeks before the male. Note that small wing mirrors are present in both the females, and only one male (11).

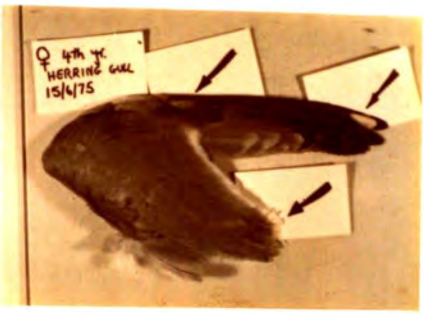
(b) 13, 14. Second year male and female lesser black-backed gulls

Note the mottled plumage on the wings, and the black tips on the tail feathers which are more extensive in the male than the female.

Plate 3



9



10

11

12

13

14

APPENDIX II

BIOMETRIC DATA

INTRODUCTION

Biometric information is often gathered as a standard procedure by ornithologists. Such data may be of use in taxonomic studies, and often is taken as a basis for distinguishing between local populations, subspecies or species, and even between sexes where outwardly sexual dimorphism is not immediately obvious. Seldom has there been opportunity, however, to gather biometric data from a large sample of birds of known age, and there are no instances in the literature where opportunities have apparently bettered the Isle of May gull cull in providing large numbers of aged individuals from a long-lived species.

Methods

As mentioned in earlier sections, an appreciable proportion of gulls ringed as chicks on the Isle of May have returned there to breed. Between 1972 and 1977 a total of 1,895 aged gulls have been recovered during the culls, and of this total 1,234 (695 males, 539 females) have individually been examined and the following measurements taken:

Wing length:	the maximum length of the right wing measured from carpel to wing tip.
Bill length:	the maximum length of the exposed culmen, from the tip of the curved upper mandible to where the rhinotheca (the horny covering of the upper mandible) overlaps with the feathered skin.
Bill depth:	the maximum vertical depth from the gonys.

Weight:	the weight of each bird was measured to the nearest g.
Size index:	as a measure of bird size, weight/wing length seemed appropriate. Wing length is one of the most consistent measurements, whilst weight is the most variable.

Wing length was measured to the nearest mm, and bill measurements were made to the nearest 0.1mm using Vernier calipers.

Results

Biometric measurements for the total sample of aged birds are presented in Table I. The data for each year of the gull cull on the Isle of May is presented separately, and that for 1972 and 1973 was collected mainly by G. Chabrzyk. The sample size for 1973 is comparatively small, but only for this number of birds was there complete data. Since the cull of 1974 a sample of unaged birds has been included for comparison (Table II). Table III gives all the available data on birds of known age, between the ages of three and eleven years. This table combines all data from the 1972-1977 culls inclusive. Figures I - VI illustrate these data. To illustrate annual differences, the data for each cull is plotted in Figures I - III (the mean age of each sample is given in parenthesis). Figures IV - VI illustrate how age *per se* may account for the variation in weights and measurements which have been recorded.

Discussion

There is considerable variation in the size of breeding male and female herring gulls between years and between different ages. This emphasises the importance of large sample sizes if any reasonable conclusions are to be made relating to this kind of data, especially when individual variation has to be taken into account as well. Clearly, it cannot be considered an easy matter to distinguish between geographical races of herring gulls on size differences alone unless such size differences prove to be very marked, and do not significantly overlap (see Monaghan 1977).

The data on aged birds given in Table III (illustrated in Figures IV - VI) indicate that there are small but progressive increases in weight, wing length and bill length with age. Bill depth remains fairly constant irrespective of the age represented. The most significant age differences to be found in the weight of breeding gulls is in weight, particularly of male birds (Figure IV). The weight of third year male gulls is rather heavier than might be expected when the general trend of an increase in weight is taken into account. All third year male gulls in the sample were breeding, and perhaps the explanation (should there be one) is to be found in the timing of the birds' arrival in the colony from the wintering areas and the timing of breeding. In general, younger birds do tend to be later, and may be in better physiological condition than the older gulls which have taken up territories earlier in the season.

The weight of female gulls at different ages (Figure V) is less variable between years than that of males, with no discernible increase with age. Figure II indicates, however, that with the exception of 1975 there has been a small overall increase in the mean weight of female gulls between 1972 and 1977.

The "size index" is the ratio of weight : wing length. Figure III shows the change in size index in each year between 1972 and 1977. This index of size provided both a crude measure of condition (lightest birds having the smallest index, assuming that wing length shows only small annual and age-related differences) and is also a method of sexing birds where the more usual practice (that of measuring bill depth) gives inconclusive results.

Van Balen (1967) made a study of the various factors contributing to variation in wing length and body weight of the great tit, according special attention to the reliability of age determination and the possible influences of habitat. The main conclusion was that environmental differences were important and could explain the sort of variation which could be found between years and between ages. Fjelsa (1977) in studies on variation in the wing length of the coot suggests that differences in ecological adaptation of the species are responsible for the observed variation. In the herring gull, it is unclear as to what could bring about both annual and age-related differences in weight and body measurements. Weight differences are possibly reflections of food availability and (in this study) the stresses of breeding. The weight of female gulls is less variable. As male gulls increase in age they may be progressively less affected by such stresses through behavioural adaptation, whereas female gulls with the additional burden of egg laying may be less likely to compensate through learning and experience. For other body measurements, such as bill dimension and wing length, allometric growth during juvenile development could be important. It should not go unmentioned, however, that where more than one observer has been taking measurements, there is the possibility of experimental error, the more so where small measurements are being taken. For weighing, however, the same electric balance was used in each year, and there was little opportunity to make a mistake in reading weights.

Table I. Biometric data on aged breeding herring gulls from the Isle of May population taken between 1972 and 1977

Weight is given in grams, and linear measurements in millimetres

	males					females				
	Weight	Wing length	Bill length	Bill depth	Size index	Weight	Wing length	Bill length	Bill depth	Size index
			(N = 124)	1972				(N = 101)		
$\bar{X}$	1004	414	53.2	19.9	2.426	847	399	48.9	17.8	2.125
S.D.	80.7	12.1	2.6	1.2	0.191	71.6	8.8	2.1	1.1	0.175
± S.E.	7.3	1.09	0.23	0.11	0.017	7.1	0.88	0.21	0.11	0.017
			(N = 32)	1973				(N = 31)		
$\bar{X}$	1026	428	53.5	19.4	2.392	855	402	48.5	17.4	2.130
S.D.	65.2	8.1	2.4	0.6	0.145	104.3	11.3	2.3	0.6	0.296
± S.E.	11.5	1.43	0.42	0.11	0.026	18.4	2.0	0.41	0.11	0.052
			(N = 254)	1974				(N = 190)		
$\bar{X}$	1029	429	53.4	19.6	2.388	856	409	48.4	17.6	2.094
S.D.	80.4	10.0	2.5	0.8	0.194	81.1	9.3	2.4	0.85	0.191
± S.E.	5.0	0.63	0.16	0.05	0.012	5.9	0.67	0.17	0.06	0.014
			(N = 139)	1975				(N = 110)		
$\bar{X}$	1049	428	53.4	19.8	2.450	846	411	48.5	17.7	2.055
S.D.	77.2	9.8	2.4	0.7	0.181	69.4	8.7	2.3	0.7	0.171
± S.E.	6.6	0.83	0.20	0.06	0.015	6.6	0.83	0.22	0.07	0.016

Continued overleaf.........

Table I. (continued)

	males					females				
	Weight	Wing length	Bill length	Bill depth	Size index	Weight	Wing length	Bill length	Bill depth	Size index
			(N = 68)		1976			(N = 70)		
$\bar{X}$	1042	428	53.7	19.8	2.434	862	415	48.8	17.8	2.079
S.D.	68.7	9.9	2.2	0.8	0.124	61.6	8.9	2.1	0.7	0.181
± S.E.	8.3	1.20	0.27	0.10	0.015	7.4	1.06	0.25	0.08	0.022
			(N = 69)		1977			(N = 44)		
$\bar{X}$	1049	428	53.6	19.8	2.452	860	415	48.7	17.7	2.071
S.D.	69.9	10.1	2.1	0.7	0.199	65.1	8.8	2.1	0.7	0.176
± S.E.	8.4	1.22	0.25	0.08	0.024	9.9	1.33	0.32	0.11	0.027

Table II. Biometric data on unaged, breeding herring gulls from the Isle of May population between 1974 and 1977

Weight is given in grams, and linear measurements in millimetres

	males					females				
	Weight	Wing length	Bill length	Bill depth	Size index	Weight	Wing length	Bill length	Bill depth	Size index
			(N = 85)		1974			(N = 89)		
$\bar{X}$	1030	429	53.3	19.7	2.401	854	409	48.3	17.7	2.065
S.D.	77.8	11.1	2.6	0.7	0.188	70.6	8.1	2.5	0.8	0.192
± S.E.	8.5	1.20	0.28	0.08	0.020	7.5	0.86	0.27	0.09	0.020
			(N = 47)		1975			(N = 32)		
$\bar{X}$	1045	427	53.4	19.7	2.450	847	411	48.5	17.7	2.062
S.D.	83.4	10.4	2.1	0.8	0.127	80.3	8.9	2.1	0.7	0.188
± S.E.	12.1	1.51	0.30	0.12	0.018	143	1.59	0.37	0.12	0.034
			(N = 25)		1976			(N = 24)		
$\bar{X}$	1047	429	53.8	19.9	2.438	859	414	48.7	17.7	2.078
S.D.	78.9	10.1	2.0	0.6	0.143	70.1	7.0	1.1	0.2	0.167
± S.E.	15.8	2.02	0.40	0.12	0.029	14.3	1.43	0.22	0.04	0.204
			(N = 27)		1977			(N = 25)		
$\bar{X}$	1057	430	54.0	19.9	2.457	862	416	48.6	17.7	2.075
S.D.	60.0	7.4	1.7	0.5	0.162	47.8	9.1	2.2	0.6	0.201
± S.E.	11.5	1.42	0.33	0.10	0.031	9.6	1.82	0.44	0.12	0.040

Table III. The mean weight, wing length, bill length, bill depth and size index of male and female herring gulls, aged between three and eleven years. All measurements given ± one standard error

	Weight (g)	Wing length (mm)	Bill length (mm)	Bill depth (mm)	Size index
3rd year					
Male (N = 18)					
$\bar{X}$	1043	430	54.7	19.6	2.424
± S.E.	14.1	1.9	0.59	0.18	0.032
Female (N = 12)					
$\bar{X}$	833	419	46.7	18.05	1.988
± S.E.	13.9	1.8	2.12	0.10	0.014
4th year					
Male (N = 58)					
$\bar{X}$	999	415	52.6	19.4	2.311
± S.E.	9.6	0.9	0.36	0.12	0.016
Female (N = 40)					
$\bar{X}$	845	399	48.8	17.6	2.112
± S.E.	12.2	1.1	0.38	0.11	0.034
5th year					
Male (N = 77)					
$\bar{X}$	1000	416	53.1	19.8	2.417
± S.E.	7.3	1.7	0.29	0.14	0.019
Female (N = 64)					
$\bar{X}$	839	400	49.2	17.7	2.087
± S.E.	9.8	1.2	0.25	0.10	0.024
6th year					
Male (N = 170)					
$\bar{X}$	1017	425	53.3	19.6	2.341
± S.E.	5.9	1.0	0.19	0.07	0.0210
Female (N = 126)					
$\bar{X}$	861	403	48.36	17.65	2.136
± S.E.	6.8	1.0	0.20	0.08	0.017

Table III. (Continued)

	Weight (g)	Wing length (mm)	Bill length (mm)	Bill depth (mm)	Size index
7th year					
Male (N = 159)					
$\bar{X}$	1044	428	53.4	19.7	2.459
± S.E.	5.9	0.7	0.20	0.06	0.016
Female (N = 128)					
$\bar{X}$	841	408	48.4	17.5	2.056
± S.E.	6.8	0.8	0.22	0.08	0.016
8th year					
Male (N = 133)					
$\bar{X}$	1038	429	53.6	19.8	2.443
± S.E.	7.1	0.6	0.20	0.06	0.016
Female (N = 117)					
$\bar{X}$	863	411	48.7	17.7	2.098
± S.E.	6.9	0.8	0.22	0.08	0.016
9th year					
Male (N = 43)					
$\bar{X}$	1072	430	54.1	20.1	2.521
± S.E.	12.6	2.1	0.38	0.11	0.197
Female (N = 41)					
$\bar{X}$	867	411	48.6	17.7	2.075
± S.E.	11.5	1.8	0.22	0.13	0.031
10th year					
Male (N = 31)					
$\bar{X}$	1076	430	54.2	20.2	2.524
± S.E.	12.0	2.1	0.29	0.19	0.032
Female (N = 17)					
$\bar{X}$	838	414	49.8	17.9	2.031
± S.E.	13.0	2.0	0.36	0.29	0.059
11th year					
Male (N = 3)					
$\bar{X}$	1067	434	54.1	20.0	2.487
± S.E.	28.0	3.1	0.58	0.24	0.108
Female (N = 2)					
$\bar{X}$	866	410	48.8	17.7	2.112
± S.E.	50.6	2.0	0.09	0.20	0.033

Figure I

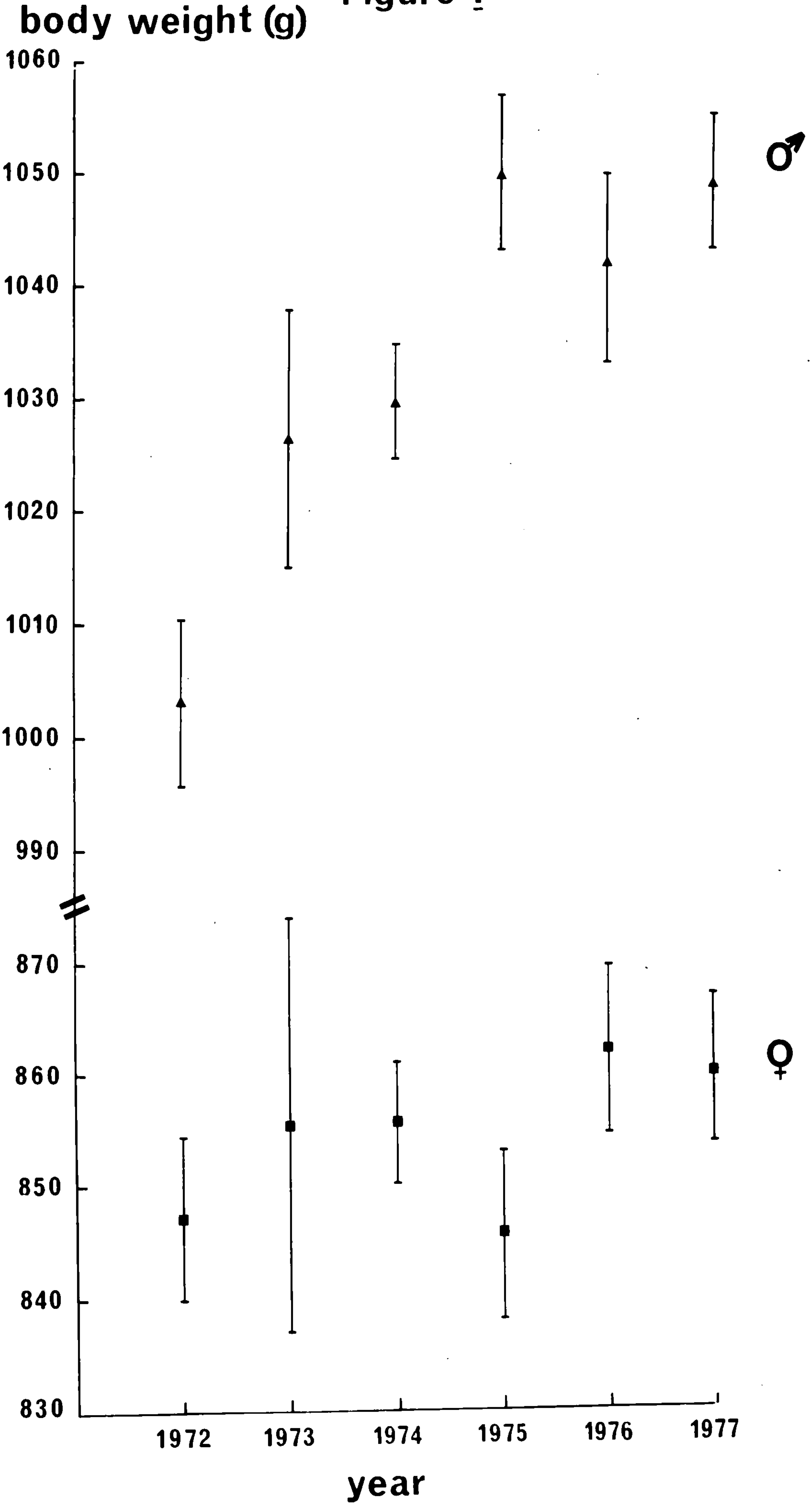

body weight (g)
1060
1050
1040
1030
1020
1010
1000
990
870
860
850
840
830
♂
♀
1972
1973
1974
1975
1976
1977
year

Figure II

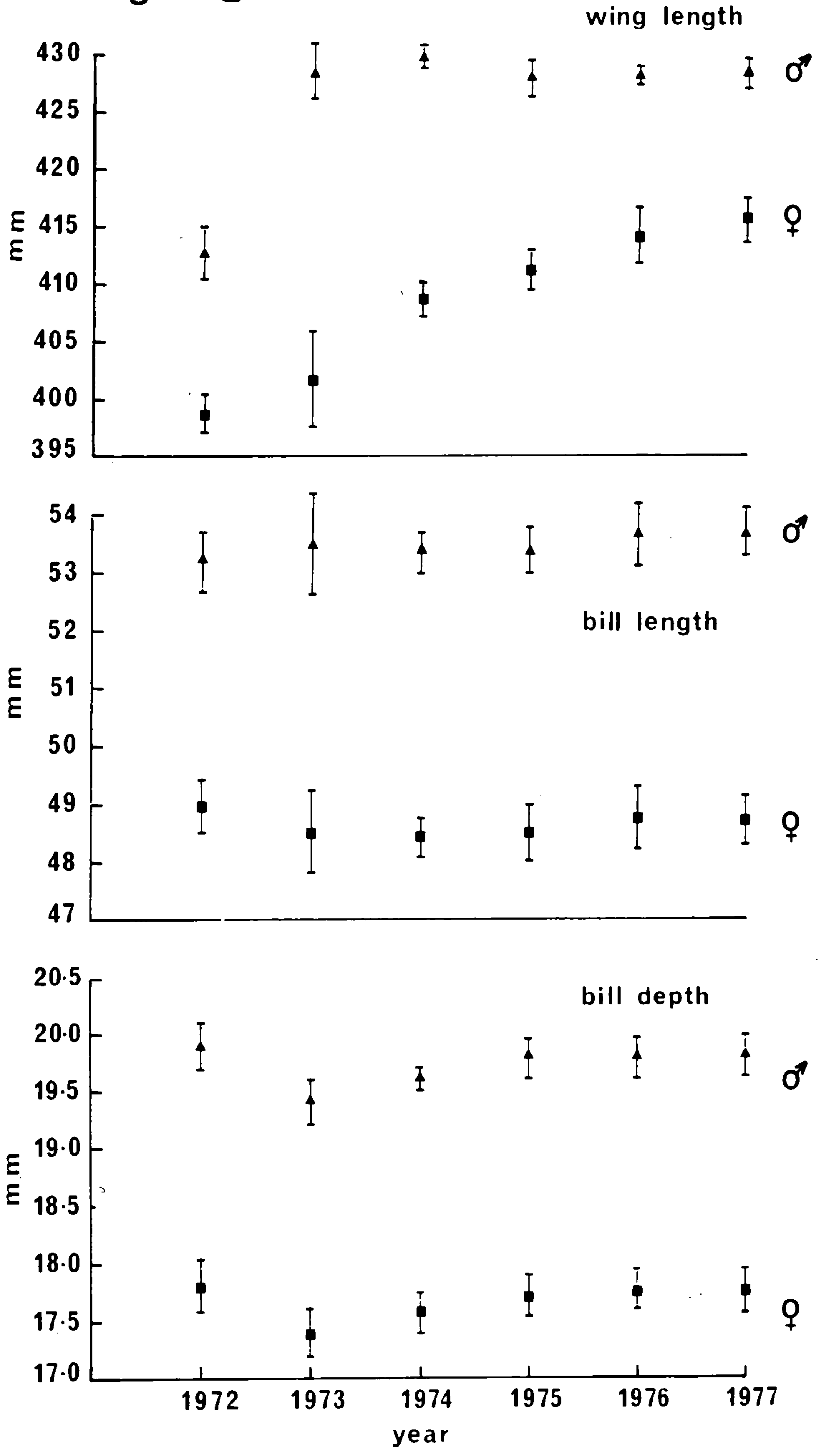

wing length
430
425
420
415
410
405
400
395
mm
♂
♀
54
53
52
51
50
49
48
47
bill length
mm
♂
♀
20·5
20·0
19·5
19·0
18·5
18·0
17·5
17·0
bill depth
mm
♂
♀
1972
1973
1974
1975
1976
1977
year

Figure III

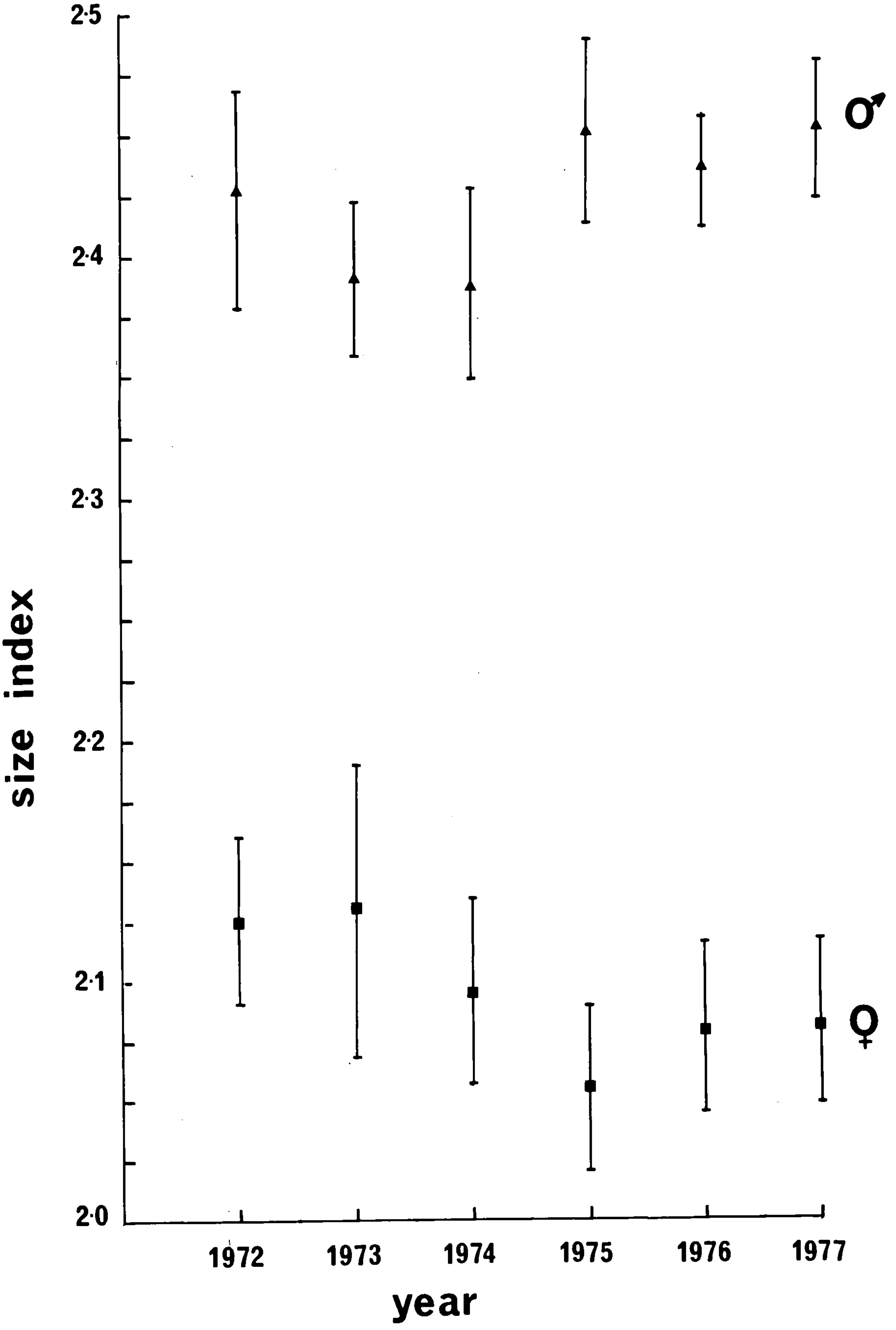
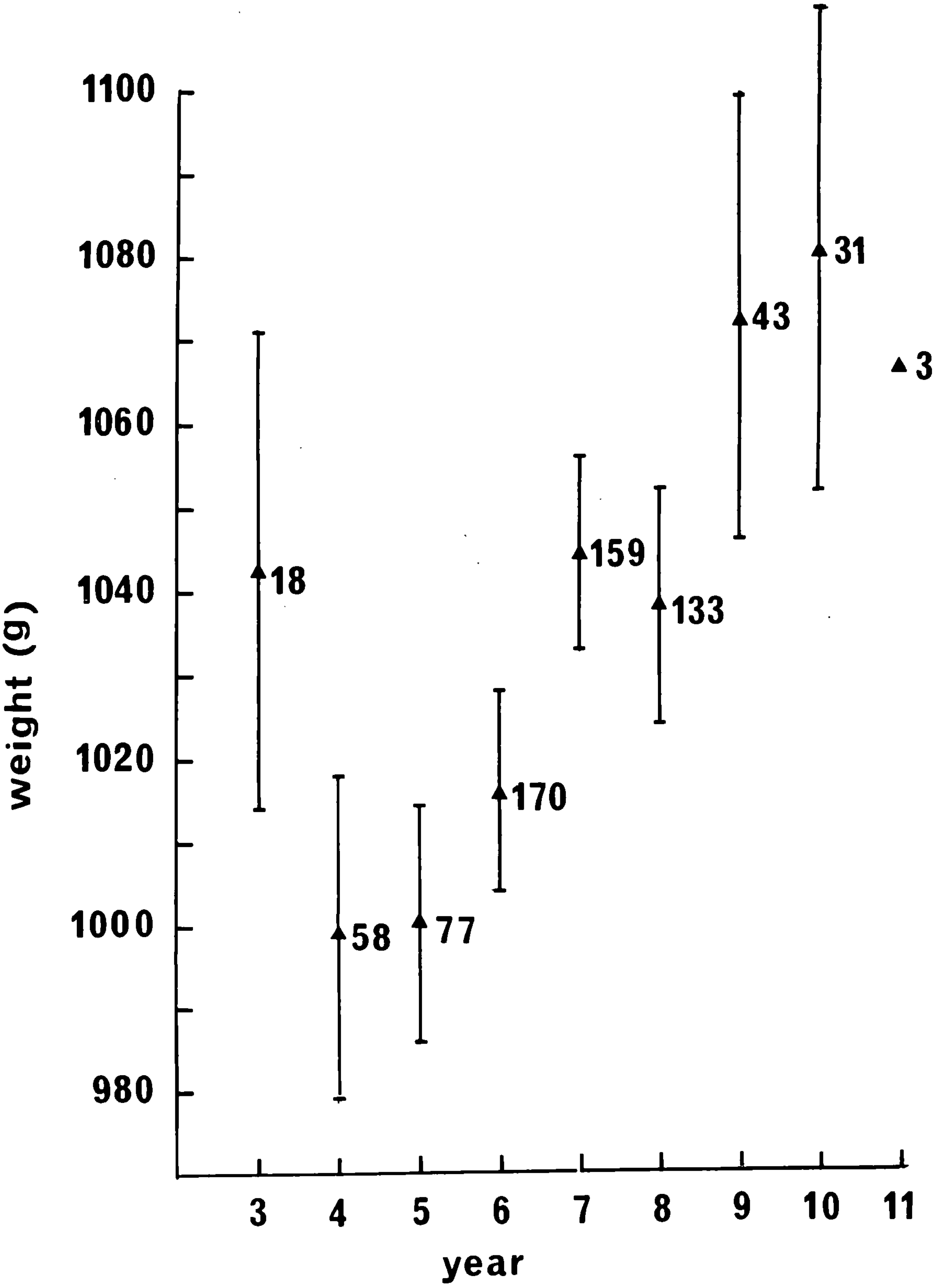
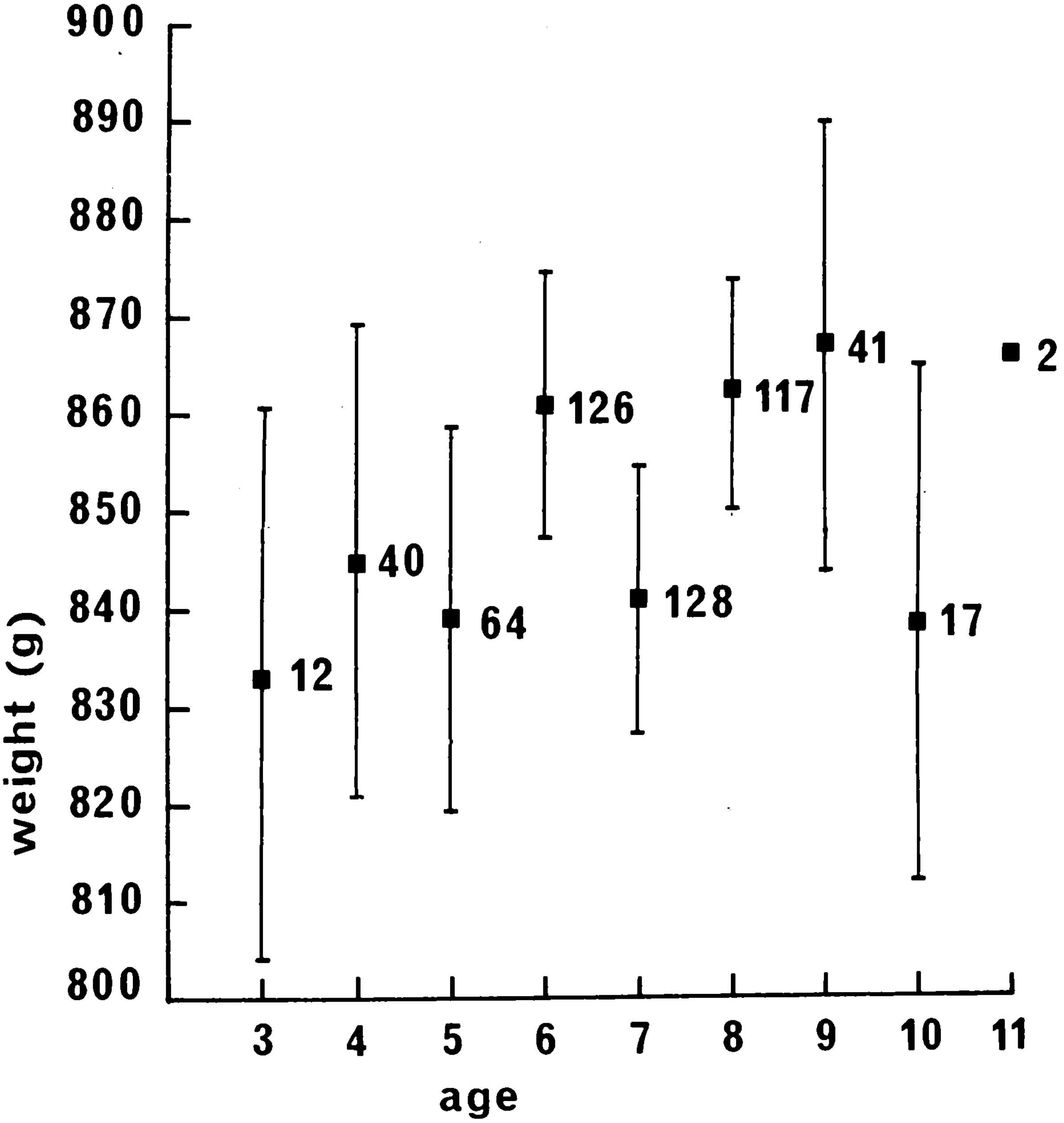


Figure IV



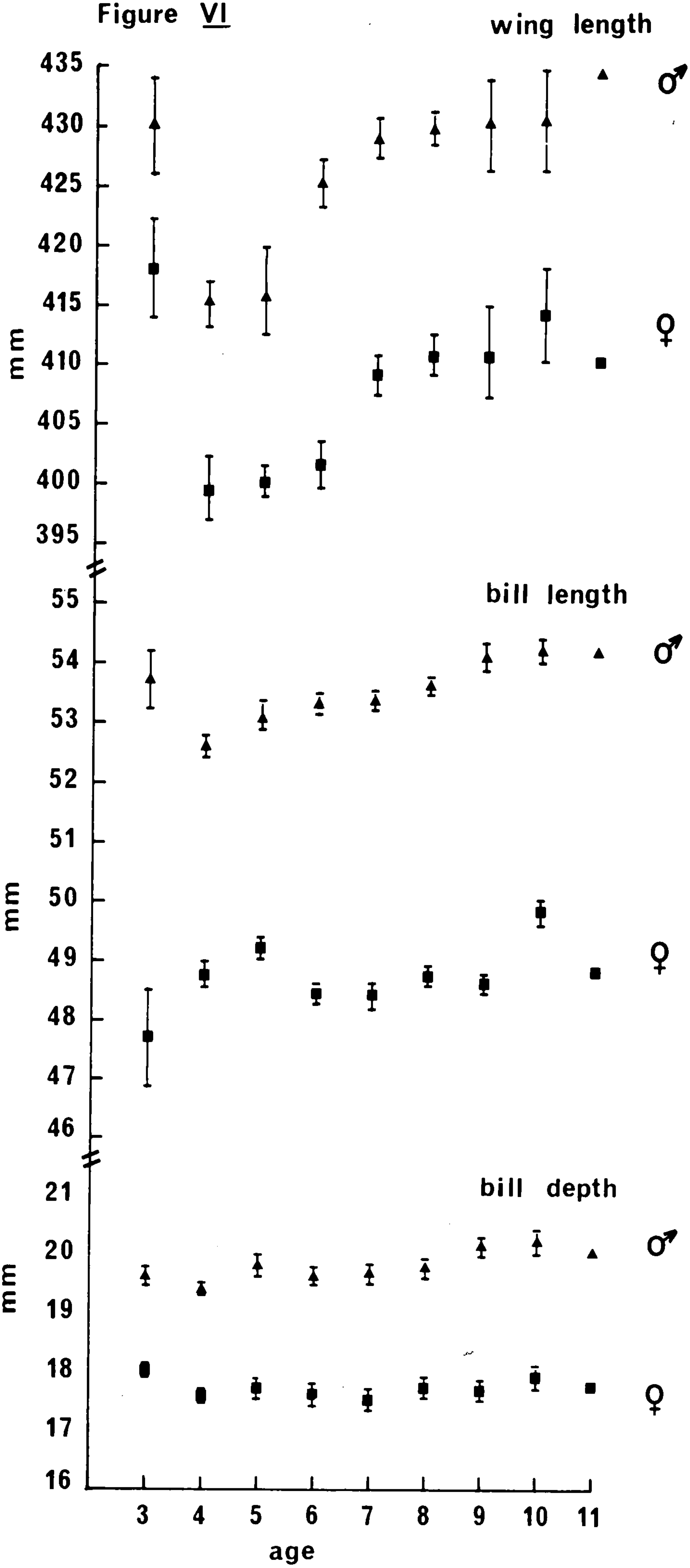
weight (g)
1100
1080
1060
1040
1020
1000
980
3
4
5
6
7
8
9
10
11
year
18
58
77
170
159
133
43
31
3

Figure V



900
890
880
870
860
850
840
830
820
810
800
weight (g)
3
4
5
6
7
8
9
10
11
age
12
40
64
126
128
117
41
17
2

Figure VI


wing length
bill length
bill depth
mm
435
430
425
420
415
410
405
400
395
55
54
53
52
51
50
49
48
47
46
21
20
19
18
17
16
♂
♀
3
4
5
6
7
8
9
10
11
age

APPENDIX III

SPECIES LIST OF ANIMALS REFERRED TO IN THE TEXT

BIRDS

herring gull	*Larus argentatus argenteus* Brehm
lesser black-backed gull	*Larus fuscus graellsii* Brehm
great black-backed gull	*Larus marinus* Linnaeus
common gull	*Larus canus canus* Linnaeus
black-headed gull	*Larus ridibundus ridibundus* Linnaeus
glaucous (winged) gull	*Larus hyperboreus* Gunnerus
kittiwake	*Rissa tridactyla tridactyla* (Linnaeus)
Arctic tern	*Sterna paradisaea* Pontoppidan (*Sterna macrura* Nauman (1819) *auctorum)*
common tern	*Sterna hirundo hirundo* Linnaeus
roseate tern	*Sterna dougallii dougallii* Montagu
little tern	*Sterna albifrons albifrons* Pallas (*Sterna minuta* of Linnaeus',*auctorum)*
shag	*Phalacrocorax aristotelis aristotelis* (Linnaeus)
fulmar	*Fulmarus glacialis glacialis* (Linnaeus)
yellow-eyed penguin	*Megadyptes antipodes* (Hombron and Jacquinot)
gannet	*Sula bassana* (Linnaeus)
British storm petrel	*Hydrobates pelagicus* (Linnaeus)
puffin	*Fraticula arctica grabae* (Brehm)
guillemot	*Uria aalge aalge* (Pontoppidan)
black guillemot	*Cepphus grylle atlantis* Salomonsen
razor bill	*Alca torda islandica* Brehm
oyster catcher	*Haematopus ostralegus occidentalis* Neumann
Manx shearwater	*Puffinus puffinus puffinus Brünnich*

white stork	*Ciconia ciconia ciconia* (Linnaeus)
eider duck	*Sommateria mollissima mollissima* (Linnaeus)
coot	*Fulica atra atra* Linnaeus
wood pigeon	*Columba palumbus palumbus* Linnaeus
collared dove	*Steptopelia decaocta decasito* (Frivaldsky)
willow grouse	*Lagopus lagopus lagopus* Linnaeus
red grouse	*Lagopus lagopus scoticus* (Latham)
domestic hen	*Gallus domesticus* Linnaeus
great tit	*Parus major newtoni* Prazak

MAMMALS

feral goat	*Capra* sp.*
sheep	*Ovis* sp.*
rabbit	*Oryctolagus cuniculus* Linnaeus

---

* The use of binomial names for domesticated species raises certain difficulties, and are best avoided.

REFERENCES

Andrewartha, H.G. and Birch, L.C. (1965) The Distribution and Abundance of Animals. University of Chicago Press, Chicago.

Anon. (1972) Gull control, Isle of May, Fife. Report, Nature Conservancy, Edinburgh.

Balen, J.H. van (1967) The significance of variations in body weight and wing length in the Great Tit, *Parus major*. Ardea, 55 : 1-59.

Barth, E.K. (1967) Standard body measurements in *Larus argentatus, L. fuscus, L. canus,* and *L. marinus*. Nytt Magasin for Zoologi, 14 : 7.83.

Baxter, E.V. and Rintoul, L.J. (1925) Fluctuations in breeding birds on the Isle of May. Scottish Naturalist, 175-179.

Bell, G.S. (1958) The vegetation of the Isle of May, Firth of Forth, in 1957, relative to exposure. Coturnix. (Annual Report of Bishop's Stortford Natural History Society).

Bergman, G. and Koskimies, J. (1958) Statement on the Herring Gull in Finland. VII Bulletin, ICBP : 111.

Besch, E.L., Sluka, S.J. and Smith, A.H. (1968) Determination of surface area using profile recordings. Poultry Science, 47 : 82-85.

Brown, R.G.B. (1967) Breeding success and population growth in a colony of Herring and Lesser Black-backed Gulls, *Larus argentatus* and *L. fuscus*. Ibis, 109 : 310-317.

Capildeo, R. and Haldane, J.B.S. (1954) The mathematics of bird population growth and decline. Journal of Animal Ecology, 23 : 215-223.

Chabrzyk, G. and Coulson, J.C. (1976) Survival and recruitment in the Herring Gull *Larus argentatus*. Journal of Animal Ecology, 45 : 187-203.

Charnov, E.L. and Krebs, J.R. (1974) On clutch size and fitness. Ibis, 116 : 217-219.

Cole, L.C. (1954) The population consequences of life history phenomena. The Quarterly Review of Biology, 29 : 103-137.

Coulson, J.C. (1963) The status of the Kittiwake in the British Isles. Bird Study, 10 : 147-179.

Coulson, J.C. (1966) The influence of the pair bond and age on the breeding biology of the kittiwake gull *Rissa tridactyla*. Journal of Animal Ecology, 35 : 269-279.

Coulson, J.C. (1968) Differences in the quality of birds nesting in the centre and on the edges of a colony. Nature, London, 217 : 478-479.

Coulson, J.C. (1976) An evaluation of the reliability of rings used on Herring and Lesser Black-backed gulls. Bird Study, 23 : 21-26.

Coulson, J.C. and Horrobin, J. (1976) The influence of age on the breeding biology and survival of the Arctic Tern. Journal of Zoology, London, 178 : 247-260.

Coulson, J.C. and White, E. (1955) Abrasion and loss of rings among seabirds. Bird Study, 2 : 41-44.

Coulson, J.C. and White, E. (1958) The effect of age on the breeding biology of the Kittiwake, *Rissa tridactyla*. Ibis, 100 : 40-51.

Cramp, S. (1971) Gulls nesting on buildings in Britain and Ireland. British Birds, 64 : 476-487.

Cramp, S., Bourne, W.R.P. and Saunders, D. (1974) The Seabirds of Britain and Ireland. Collins, London.

Curry-Lindahl, K. (1961) Vara Faglar i Norden. (Volume 3). Stockholm.

Darling, F.F. (1938) Bird Flocks and the Breeding Cycle. Cambridge University Press, Cambridge.

Davis, J.W.F. (1975) Age, egg size and breeding success in the Herring Gull *Larus argentatus*. Ibis, 117 : 460-473.

Drent, R.H. (1967) Functional Aspects of Incubation in the Herring Gull. Leiden.

Drost, R., Focke, E. and Freytag, G. (1961) Entwicklung und Aufbau einer Population der Silbermowe *Larus argentatus argentatus*. 102 : 404-429.

Drury, W.H. and Nisbet, I.C.T. (1972) The importance of movements in the biology of Herring Gulls in New England. In Population Ecology of Migratory Birds : A Symposium. U.S. Department of the Interior, Wildlife Research Report, 2 : 173-212.

Dunnet, G.M. and Ollason, J.C. (1978) The estimation of survival rate in the fulmar, *Fulmarus glacialis*. Journal of Animal Ecology, 47 : 507-520.

Eggeling, W.J. (1974) The birds of the Isle of May. Scottish Birds (Supplement), 8 : 93-148.

Eggeling, W.J. (1960) The Isle of May. Oliver and Boyd, Edinburgh.

Erwin, R.M. (1971) The breeding success of two sympatric gulls, the Herring Gull and the Great Black-backed Gull. Wilson Bulletin, 83 : 152-158.

Fisher, J. (1952) The Fulmar. Collins, London.

Fjelsa, J. (1977) Sex and age variation in wing-length in the Coot *Fulica atra*. Ardea, 65 : 115-125.

Flegg, J.J.M. and Morgan, R.A. (1976) Mortality in British Gulls. Ringing and Migration, 1 : 65-74.

Goethe, F. (1964) Lekung der Mowenbestande an der deutschen Nordsee. Int. Nat. Vogelschutz Deutche Sektion, 4 : 53-57.

Greenhalgh, M.E. (1974) The Pennine Gullery. Bird Study, 21 : 146-148.

Gross, A.O. (1940) The migration of Kent Island Herring gulls. Bird Banding, 11 : 129-155.

Gudmundsson, F. (1951) The effects of the recent climatic changes on the bird life of Iceland. Proceedings of the Tenth International Ornithology Conference. Uppsala : 502- 514.

Harris, M.P. (1964) Recoveries of ringed Herring Gulls. Bird Study, 11 : 183-191.

Harris, M.P. (1965) The food of some *Larus* gulls. Ibis, 107, 43-53.

Harris, M.P. (1966) Age of return to the colony, age of breeding and adult survival of Manx Shearwaters. Bird Study, 17 : 84-95.

Harris, M.P. (1969) Effect of laying date on chick production in Oystercatchers and Herring Gulls. British Birds, 62 : 70-75.

Harris, M.P. (1970) Rates and causes of increases of some British gull populations. Bird Study, 17 : 325-335.

Harris, M.P. (1972) Inter-island movements of Manx Shearwaters. Bird Study, 19 : 167-171.

Harris, M.P. (1976) Inter-colony movements of Farne Islands Puffins. Transactions of the Natural History Society of Northumberland, 42 : 115-118.

Harris, M.P. (1977) Puffins on the Isle of May. Scottish Birds, 9 : 285-290.

Harris, M.P. and Plumb, W.J. (1965) Experiments on the ability of Herring Gulls *Larus argentatus* and Lesser Black-backed gulls *L. fuscus* to raise larger than normal broods. Ibis, 107 : 256- 257.

Haymes, G.T. and Morris, R.D. (1977) Brood size manipulation in herring gulls. Canadian Journal of Zoology, 55 : 1762-1766.

Heinroth, O. (1922) Die Beziehungen zwischen Vogelgwicht, Eigewicht, Gelegegwicht und Brutdauer. Journal für Ornithologie, Leipzig, 70 : 172-285.

Hornberger, R. (1943) Einige Ergebrisse zehnjahriger Planarbeitim Storchforsschungskre is "Insterburgh" der Vogelwarte Rossitten. Journal für Ornithologie, 91 : 341-355½

Hoyt, D.F. (1976) The effect of shape on the surface-volume relationships of birds' eggs. Condor, 78 : 343-349.

Ingolfsson, A. (1978) Population phenomena associated with the colonisation of Iceland by Herring Gulls. Ibis, 120 : 126.

Jenkins, D., Watson, A., and Miller, G.R. (1963) Population studies on red grouse *Lagopus lagopus scoticus* (Lath.) in north-east Scotland. Journal of Animal Ecology, 32 : 317-376.

Jenkins, D., Watson, A. and Miller, G.R. (1967) Population fluctuations in the red grouse *Lagopus lagopus scoticus*. Journal of Animal Ecology, 36 : 97-122.

Kadlec, J.A. (1975) Recovery rates and loss of aluminium, titanium and incology bands on Herring Gulls. Bird-Banding, 46 : 230-235.

Kadlec, J.A. (1976) A re-evaluation of mortality rates in adult Herring Gulls. Bird-Banding, 47 : 8-12.

Kadlec, J.A. and Drury, W.H. (1968) Structure of the New England Herring Gull population. Ecology, 49 : 644-676.

Lack, D. (1954) The Natural Regulation of Animal Numbers. Clarendon Press, London.

Lack, D. (1964) A long-term study of the great tit (*Parus major*). Journal of Animal Ecology, 33, (Jubilee Supplement) : 159-173.

Lack, D. (1966) Population Studies of Birds. Clarendon Press, London.

Lack, D. (1968) Ecological Adaptations for Breeding in Birds. Methuen, London.

Lack, D., Gibb, J., and Owen, D.F. (1957) Survival in relation to brood size in tits. Proceedings of the Zoological Society of London, 128 : 313-326.

Lloyd, D.A.B. (1968) The Use of Inland Habitats by Gulls *Larus* spp. in the Ythan Valley, Aberdeenshire. Unpublished M.Sc. Thesis, University of Aberdeen.

Lotka, A.J. (1907) Studies on the mode of growth of material aggregates. American Journal of Science, 24 : 199-216; 375-376.

Ludwig, J.P. (1963) Return of Herring Gulls to natal colony. Bird-Banding, 34 : 68-72.

Mayr, E. (1963) Animal Species and Evolution. Harvard University Press, Cambridge, Massachusetts.

Monaghan, P. (1977) The Utilisation of Urban Resources by the Herring Gull *(Larus argentatus)*. Unpublished Ph.D. Thesis, University of Durham.

Monaghan, P. and Coulson, J.C. (1977) Status of large gulls nesting on buildings. Bird Study, 24 : 89-104.

Miller, G.R. and Watson, A. (1978) Territories and the food plants of individual red grouse. 1. Territory size, number of nests and brood size, compared with the abundance, production and diversity of heather. Journal of Animal Ecology, 47 : 293-305.

Murton, R. (1971) Man and Birds. Collins, London.

Murton, R.K., Westwood, N.J. and Isaacson, A.J. (1974) Factors affecting egg-weight, body-weight and moult in the Wood Pigeon *Columba palumbus*. Ibis, 116 : 52-73.

Myrberget, S. (1978) Size and shape of eggs of Willow Grouse, *Lagopus lagopus*. Ornis Scandinavica, 8 : 39-46.

Nelson, J.B. (1966) The breeding biology of the Gannet, *Sula bassana*, on the Bass Rock, Scotland. Ibis, 108 : 584-626.

Nisbet, I.C.T. (1978) Recent changes in gull population in the western North Atlantic. Ibis, 120 : 129-130.

Oakes, C. (1953) The Birds of Lancashire. Oliver and Boyd, Edinburgh and London.

Olsson, V. (1958) Dispersal, migration, longevity and death causes of *Strix aluco, Buteo buteo, Ardea cinerea* and *Larus argentatus*. Acta Vertebrata, 1 : 91-189.

Paludin, K. (1951) Contributions to the breeding biology of *Larus argentatus* and *Larus fuscus*. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening i Kjøbenhavn.

Parslow, J.L.F. (1967) Changes in status among breeding birds in Britain and Ireland. British Birds, 60 : 177-202.

Parsons, J. (1970) Relationship between egg size and post-hatching mortality in the Herring Gull (*Larus argentatus)*. Nature, London, 228 : 1221-1222.

Parsons, J. (1971) The breeding biology of the Herring Gull (*Larus argentatus)*. Unpublished Ph.D. Thesis. University of Durham.

Parsons, J. (1975) Seasonal variation in the breeding success of the herring gull: an experimental approach to pre-fledging success. Journal of Animal Ecology, 44 : 553-573.

Parsons, J. (1976) Nesting density and breeding success in the Herring Gull *Larus argentatus*. Ibis, 118 : 537-546.

Parsons, J., Chabrzyk, G. and Duncan, N. (1976) Effects of experimentally extended breeding season on post-fledging survival in herring gulls. Journal of Animal Ecology, 45 : 667-675.

Parsons, J. and Duncan, N. (1978) Dispersal of herring gulls from the Isle of May. Journal of Animal Ecology, 47 : In press.

Patterson, I.J. (1965) Timing and spacing of broods in the Black-headed Gull, *Larus ridibundus*. Ibis, 107 : 433-459.

Paynter, R.A., Jr. (1949) Clutch size and the egg and chick mortality of Kent Island Herring Gulls. Ecology, 30 : 146-166.

Pearsall, W.H. (1950) Mountains and Moorlands. Collins, London.

Pearson, T.H. (1968) The feeding biology of sea-bird species breeding on the Farne Islands, Northumberland. Journal of Animal Ecology, 37 : 531-552.

Perrins, C.M. (1965) Population fluctuations and clutch size in the Great Tit, *Parus major*. Journal of Animal Ecology, 34 : 601-647.

Perrins, C.M. (1970) The timing of birds' breeding seasons. Ibis, 112 : 242-255.

Perrins, C.M. and Moss, D. (1974) Survival of young great tits in relation to age of female parent. Ibis, 116, 220-224.

Perrins, C.M. and Moss, D. (1975) Reproductive rates in the great tit. Journal of Animal Ecology, 44 : 695-706.

Potts, G.R. (1966) Studies on a marked population of the Shag, *Phalacrocorax aristotelis*, with special reference to the breeding biology of birds of known age. Unpublished Ph.D. Thesis, University of Durham.

Richdale, L.E. (1955) Influence of age on size of eggs in Yellow-eyed Penguins. Ibis, 97 : 266-275.

Romanoff, A.L. and Romanoff, A.J. (1949) The Avian Egg. Wiley, New York; Chapman and Hall, London.

Salomonsen, F. (1963) Oversigt over Danmarks fugle. Munksgaard, København.

Skoglund, W.C., Seeger, K.C. and Ringrose, A.T. (1952) Growth of broiler chicks hatched from various sized eggs when reared in competition with each other. Poultry Science, 31 : 796-799.

Spaans, A.L. (1971) On the feeding ecology of the Herring Gull *Larus argentatus* Pont. in the northern part of the Netherlands. Ardea, 59 : 73-188.

Spaans, M.J. and Spaans, A.L. (1975) Some data on the breeding biology of the Herring Gull *Larus argentatus* on the Dutch Frisian Island of Terschelling. Limosa, 48 : 1-39.

Spencer, R. (1959) Report on bird ringing for 1958. British Birds, 52 : 441-492.

Sobey, D.G. (1975) The relationship between herring gulls and the vegetation of their nesting and roosting sites. Unpublished Ph.D. Thesis, University of Aberdeen.

Sobey, D. (1976) The effect of Herring Gulls on the vegetation of the Isle of May. Transactions of the Botanical Society of Edinburgh, 42 : 469-485.

Southwood, T.R.E. (1966) Ecological Methods. Methuen, London.

Stearns, S.C. (1976) Life-history tactics: a review of the ideas. The Quarterly Review of Biology, 51 : 3-47.

Thomas, G.J. (1972) A review of gull damage and management methods at nature reserves. Biological Conservation, 4 : 117-27.

Threlfall, W. (1968) The food of Herring Gulls in Anglesey and Caernarvonshire. Nature in Wales, 11 : 67-73.

Tinbergen, N. (1953) The Herring Gull's World. Collins, London.

Vaurie, C. (1965) The Birds of the Palearctic Fauna. Non-Passeriformes. Witherby, London.

Vermeer, K. (1963) The breeding ecology of the Glaucous-winged Gull *(Larus glaucescens)* on Mandarte Island, B.C. Occasional Papers of the B.C. Provincial Museum, 13 : 1-104.

Voous, K.H. (1960) Atlas of European Birds. Elsevier, Amsterdam and Brussels.

Watson, A. and Miller, G.R. (1971) Territory size and aggression in a fluctuating red grouse population. Journal of Animal Ecology, 40 : 367-383.

White, G. (1789) The Natural History of Selbourne. Undated edition by Warne, London and New York.

Wiley, W.H. (1950) The influence of egg weight in the pre-hatching growth rate in the fowl. 2. Egg-weight - chick-weight ratios. Poultry Science, 29 : 595-604.

Williams, G.C. (1966) Adaptation and Natural Selection. Princetown University Press, Princetown.

Wynne-Edwards, V.C. (1962) Animal Dispersion in Relation to Social Behaviour. Oliver and Boyd, Edinburgh.

SUMMARY

1. This study, undertaken between 1974 and 1977, has been largely concerned with the inter-relationships of population ecology, breeding biology and social behaviour with reference to the herring gull *Larus argentatus*.

2. Three study areas were originally chosen for their contrasting ecological situations for the herring gull. They were (i) the Isle of May, in the Firth of Forth, which was the main study colony (ii) the Tarnbrook/Mallowdale colony, situated in the western Pennines, and (iii) the island of Cara, off the west coast of Argyll. The Tarnbrook/Mallowdale colony and Cara were not intensively studied.

3. On the Isle of May the number of herring gulls has been increasing at a near constant rate of 13% since 1907 when the first pair were recorded breeding. The increase was considered to be incompatible with the proper management of the island as a National Nature Reserve and in 1972 the Nature Conservancy (now the Nature Conservancy Council) embarked on a policy of control to reduce the breeding population which had reached 16,700 breeding pairs to about 200 pairs within three years. The Tarnbrook/Mallowdale colony was founded in 1938 and has grown very rapidly since (on average, at more than 30% per annum). About 15% of its population are herring gulls (the remainder being lesser black-backed gulls). The origins of the colony on Cara are not known, but the population and the annual rate of increase is small.

4. A proportion of the breeding population on the Isle of May (which varied from about 10% in 1974 to 6% in 1977) were marked, as a result of past studies. Thus the age of birds could be determined by a coloured ring signifying their year of birth on the island. Each of these birds was also marked by a BTO metal ring bearing a unique number.

5. As a technique to remove breeding gulls on their territories the narcotic α-chloralose was used with a palatable bait. Birds which would not take the bait were shot.

6. In the three study areas the populations were censused by dividing the colonies into transects and counting all the nests within them. Transects varied in size with the nesting density of the area. Direct observational counts were also made. Age class counts of young gulls in sub-adult plumage were undertaken at regular intervals on the Isle of May as part of a study of recruitment.

7. By censusing the herring gull population of the Isle of May before the cull in each year it was shown that the population declined over that of the previous years in 1974, 1975 and 1976 by about one-third. In 1977 this trend was reversed, and the population showed an increase over that of 1976 of 23%. In the same period a smaller decline was recorded for the lesser black-back up to 1976 and 1977. In both these years an increase was recorded. Between 1974 and 1977 the lesser black-back increased from about 10% of the Larus gull population to about 19%.

8. Between 1972 and 1977, a total of 37,089 herring gulls were estimated to have been killed in the Isle of May culls. A further 1,157 were killed as a result of clearing experiments. The highest total of the breeding population killed in one year was 65.2% (1974) and the lowest was 6.5% (1977). Similarly, for the lesser black-back, between 1974 and 1977 a total of 1145 gulls were killed by the N.C.C. and 54 in the course of this study. In 1974, 36.5% of the current breeding population were killed, and in 1977 only 1.5%.

9. The last census of the Tarnbrook/Mallowdale colony (1975) showed that there were about 13,700 breeding pairs of lesser black-backs and about 1000 which were non-breeders. There were 2600 breeding pairs of herring gulls, with about 600 non-breeders.

10. On Cara, the herring gull population increased from 217 pairs in 1975 to 220 pairs in 1977. Great black-backs increased from 148 pairs to 155 pairs in the same period.

11. There are problems in calculating survival rates for long-lived species such as gulls. The best estimate for an average annual adult survival rate for the herring gull was accepted as being 0.935.

12. The mean age of recruitment (defined as the accession of sexually mature birds to the colony) was 5.0 years. Twenty one percent of gulls were recruited at four years, 52% at five years, 13% at six years, 6% at seven years, and 8% at eight years.

13. The annual recruitment rate was 17.3% per annum on the Isle of May before the cull began. It was thus possible to predict the number of herring gulls which should have been recruited to the Isle of May for each year since the onset of culling. By combining the average annual adult survival rate and the survival rate of the population which experienced the cull, the number of recruits in each year was calculated. This number fell below predicted levels with an overall shortfall of 31,000, 63% less than predicted.

14. The total number of gulls culled in the same period was over 38,000, so for every ten gulls killed, a further eight were deterred from colonizing the Isle of May by culling effects.

15. From about 15,000 gulls ringed as chicks on the Isle of May between 1966 and 1970, a total of 162 have been recovered or sighted breeding in other colonies between 1974 and 1977. Sixty-seven and a half percent of ringed lesser black-backs recovered in the Tarnbrook/ Mallowdale colony were ringed elsewhere, mostly at Walney (Cumbria).

16. Before culling started on the Isle of May, the population had a stable age composition. The average "breeding experience" of the population was 5.8 years, with 17.3% of the population breeding for the first time each year. By 1977, experience was reduced to 1.9 seasons, with 52% of the population breeding for the first time. The age composition in years was also calculated for the population between 1972 and 1977.

17. The median date of laying was calculated for a sample which bred in control areas between 1974 and 1977. Only in 1975 did the date differ from 17 May, when it was on 21 May. For aged gulls the date varied from 18 May (fourth year) to 16 May (tenth and eleventh year).

18. Mean clutch size in unaged birds varied between 2.76 eggs (1974), 2.64 eggs in 1975, and 2.72 eggs in 1976 and 1977.

19. Average clutch size increased significantly between the fourth and eighth year. Between the ninth and eleventh year there was a small decrease. The age of the female was more important than the age of the male in the determination of clutch size.

20. Egg volume and egg size index was calculated for 537 clutches from unaged gulls and 265 clutches from aged gulls. Incorporating data from Parsons (1971), a significant increase in egg size could be shown between 1968 and 1977. There was also a significant and progressive increase

in egg size with age. This may have been due to either a greater proportion of gulls laying earlier in the season, or selection for variability of egg size. A combination of the two might also be possible.

21. Chicks were marked on hatching in control areas of the Isle of May, using strips of coloured plastic. These were later replaced by BTO metal rings and a coloured Darvic ring. If a chick survived for 35 days, it was considered that it would fledge.

22. Average fledging success was 0.85 chicks/breeding pair in 1975, 0.71 chicks/breeding pair in 1976 and 0.93 chicks/breeding pair in 1977. The overall average was 0.82 chicks/breeding pair for the three years.

23. In aged gulls, average breeding success ranged from 6.7% in third year gulls to 42.9% in eleventh year gulls. Most of the youngest gulls were breeding for the first time, whilst the older cohorts were probably experienced. The latter may lay better quality eggs with more nutrients.

24. There were no significant differences between the size of a- (first laid) and b-eggs which gave rise to surviving chicks, and those that did not. It was postulated that parental experience was more important than egg size in chick survival. Older birds were better able to raise two chicks than were younger birds.

25. Using the average age of recruitment and the average breeding success which was found in this study, the calculated fertility and the adult survival rates, it is possible that the population could increase by as much as 18% per annum, once a stable age composition was re-established.

26. A notable effect of culling on the Isle of May has been to lower breeding density. It was suggested that breeding density could affect recruitment rate. Accordingly, experiments were set up in six areas of different density to record the number of gulls recruited to them over a three year period.

27. The relationship between density and recruitment was different in each year. At the highest densities, the average recruitment rate was 8%, at intermediate densities the rate varied between 12.5 and 50%, and at the lowest densities there was no recruitment.

28. For the entire colony on the Isle of May, an effect of the cull has been to reduce the nesting density from about 11.1 pairs/100m^2 in 1972 to 2.3 pairs/100m^2 in 1977. However, the population occupied in 1972 about 18.5ha whilst in 1977 the area still occupied was about 16ha.

29. Nest density was measured by two methods. Density Measurement I was the number of nests which fell within a unit area and expressed as nests/100m^2. Density Measurement II was the number of nests within a 3m radius around each nest.

30. The average number of nests/100m^2 varied between 0 and 16.2 for Density Measurement I. Density Measurement II gave a maximum mean density of 3.50 nests/3m unit, and a minimum of 0.48. When compared with a Poisson Distribution, this latter method indicated that most nests were spaced uniformly. Mean density at Tarnbrook/Mallowdale varied from only 0.04 nests to 0.55 nests/100m^2.

31. In testing the effects of density on new recruits and prospecting non-breeders, counts throughout the breeding season indicated that gulls in sub-adult plumage took up positions (not territories) in the colonies at most densities. Low and high density areas were less

favoured, but at intermediate densities the majority of young gulls could be found. Female sub-adult gulls were more common at high densities than males. It was concluded that highest recruitment would take place at intermediate densities.

32. The effects of density on territorial aggression were investigated. The incidence of fights and attacks on neighbouring territory holders and intruders increased as density increased. Male gulls in sub-adult plumage were frequently attacked by territory holders, but did not themselves attack.

33. A high proportion (32% males, 19.5% females) of herring gulls culled on Tarnbrook/Mallowdale were aged 3-4 years. It seemed that the age of recruitment at this colony was lower than on the Isle of May.

34. The relationship between nest dispersion and fledging success was measured. Birds which spaced their nests most uniformly were the most successful breeders. The relationship between density and fledging success could not be deduced through insufficient data.

35. The rationale of culling gulls is reviewed, and certain suggestions have been offered as to how the procedure might be improved upon.

36. Biometric data on aged and unaged herring gulls, and comments on ageing gulls, are given in an Appendix.