BREEDING BIOLOGY AND SURVIVAL OF GUILLEMOTS (*Uria aalge*)

by

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Frontispiece. Guillemot with chick.

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ABSTRACT

The aims of the study were to examine some population parameters of the Common Guillemot Uria aalge on Skomer Island, Wales, where a decline in numbers has occurred, and to examine a number of different aspects of the birds' breeding biology.

The Common Guillemot is one of the most numerous seabirds in the northern hemisphere and breeds at densities unparalleled by any other bird species. Chapter 2 describes some Guillemot population parameters on Skomer. Between 1934 and 1975 a 62% decrease in numbers took place. The population may have stabilized during the course of this study and the population in 1975 was estimated at about 2,200 pairs. Breeding success over three years averaged 70%, adult survival was 93% in 1974 and 88% in 1975. The age at which Common Guillemots start to breed is not known, but is assumed to be similar to other auks, i.e. about 5 years. Survival rates of birds up to five years derived from recoveries of ringed birds varied between 27-41% in different areas. High adult mortality, as in 1975, caused by chronic oil pollution may be limiting the Skomer population at present.

Chapter 3 investigates the adaptive nature of high density nesting. Breeding success was highest among those Guillemots nesting at high densities on broad ledges, and was lowest among those on broad ledges at low densities. Breeding success was related to the synchrony of laying; dense groups had a shorter spread of laying than sparse groups, and a short spread of laying minimized the number of birds at the beginning and end of the season whose

breeding was out of phase with the rest. Birds which were out of phase suffered higher losses of eggs and chicks, mainly through gull predation.

Photographs of Skomer Guillemot colonies taken in 1934 show that at that time most available ledge-space was occupied and birds bred on both broad and narrow ledges. In 1973-1975 relatively few birds nested on broad ledges, most were on narrow ledges at Medium densities. It is suggested that as the population declined the density of birds on broad ledges also decreased, resulting in increased predation and reduced breeding success. Because Medium density groups on narrow ledges are more productive than low density groups on broad ledges, Medium density groups have persisted. Guillemots apparently do not have the ability to coalesce into a few high density groups.

Chapter 4 describes how adult Guillemots provision their chick, and the development of the chick to fledging. Comparisons are made with other auk studies, and Guillemot chicks on Skomer show similar growth rates and fledge at similar weights to Guillemots in other areas.

Chapter 5 describes the social behaviour of the Common Guillemot, which generally nests in bodily contact with conspecifics, and comparisons are made with the Razorbill, which spaces itself away from conspecifics at the breeding colony. Behavioural adaptations to high density nesting in the Guillemot are pinpointed. Guillemots perform a large number of appeasement displays; active appeasement displays are performed in response to a threat or attack, and passive appeasement to avoid eliciting aggression. Razorbills possess a smaller repertoire of social signals than Common Guillemots.

In Chapter 6 I have drawn together information from previous chapters, and from Appendix II, on moult, and have tried to outline the inter-relationships between several different aspects of the Guillemot's biology, in terms of its overall adaptiveness.

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CHAPTER 1

INTRODUCTION

The Scope and Objects of the Study

The Common Guillemot Uria aalge (Pont.) (family: Alcidae) is one of the most numerous seabirds in the Northern Hemisphere (Tuck 1960), and breeds at densities unparalleled by any other avian species.

Recent studies of biology and behaviour, particularly those of birds, have explored adaptive themes in natural populations (Simmons 1970). Over the last 20 years or so there has been a great expansion of seabird studies (Ashmole 1971), and these have provided much new information for the study of adaptive themes. The major emphasis has been on selective pressures of predation (Cullen 1957, Kruuk 1964, Patterson 1965), feeding ecology (Simmons 1970, Lack 1968, Ashmole 1971) and social behaviour (Tinbergen 1959, Nelson 1970). Additionally, it has been recognised that many different aspects of a species' biology, including those listed above, are intimately linked; this is apparent from studies of insects (Wilson 1971), birds (Crook 1965, Lack 1968), carnivores (Kruuk 1972, Schaller 1972) and primates (Eisenberg et.al. 1972).

The aims of the present study were. to examine adaptions for breeding in the Common Guillemot in relation to high density nesting, and to consider the inter-relationships that exist between various features of the birds' breeding biology.

During the present century numbers of Common Guillemots in the southern part of their range in the north-east Atlantic have declined, for unknown reasons. This decline in numbers has occurred on Skomer Island (51°40'N 05°15'W); the location of this study, although sufficient numbers still remain for study purposes.

The study had a number of objectives:

1. To investigate the extent of the population decrease on Skomer, to measure the size of the present population, and to examine a number of population parameters in an effort to construct a life table for the Common Guillemot on Skomer.
2. To examine the adaptive nature of high density breeding, in other words to compare breeding success at different densities and to look at the factors responsible for the differences.
3. To examine behavioural adaptations to high density nesting. Since there have been no previous quantitative studies of social behaviour in the Common Guillemot, one of my objectives was to provide a detailed account of behaviour patterns and postures. The second, and more important objective, was to compare the social behaviour of the dense-nesting Common Guillemot with the closely related Razorbill, which breeds at much lower densities, in order to pinpoint specific behavioural adaptations in the Guillemot to dense nesting.
4. Since food is generally regarded as being a limiting factor (Lack 1954), I wanted to see if the reduction in population size was associated with a shortage of food during the breeding season.

Until recently there had been relatively few studies of alcid species, probably because of methodological problems associated with their study. The sort of problems which hampered previous Guillemot studies probably include; inaccessibility, difficulty of capture, the effect of disturbance and subsequent vulnerability of eggs and chicks to predation, and difficulties of observing birds away from breeding colonies.

However, the basic breeding biology of Guillemots is well known from extensive studies in northern USSR, where they constitute an important economic resource (Kaftanovski 1938, Uspenski 1956, Belopolski 1957). Important studies from other areas include those made in eastern north America by Johnson (1938a,b, 1940, 1941, 1944), in the Faeroes, by Norrevang (1958), in Britain by Southern (1938, 1939, 1951, 1962, 1966) and Southern *et.al.* (1965), in Alaska by Swartz (1966). In his monograph, Tuck (1960) has presented a good general outline of the seasonal pattern of activity and the breeding biology of both the Common Guillemot and Brunnich's Guillemot *U.lomvia* (Linn.) in Canada, and these will not be repeated here. Unless otherwise stated, 'Guillemot' in the text refers to the Common Guillemot *Uria aalge*, the species studied on Skomer.

The Study Area

Skomer Island lies approximately one mile (1.6km) from the Welsh mainland (Fig.1.1), and consists of a basalt tableland about 200' (61m) high. The island is 722 acres (292ha) in extent, and is 2 mi (3.2km) along its east-west axis, and 1.3 mi (2.1km) along its north-south axis. Skomer is bounded mainly by steeply sloping grassy cliffs on most sides. Details of the vegetation and other aspects of the island can be found in Buxton & Lockley's (1950) account.

Observations were made during June and July 1972, and between late March and late July 1973 - 1975. The climate of Skomer has been described as "mild, the rainfall (*c*36") lower than any other district of west Wales, the weather, changeable with frequent gales of short duration.... and

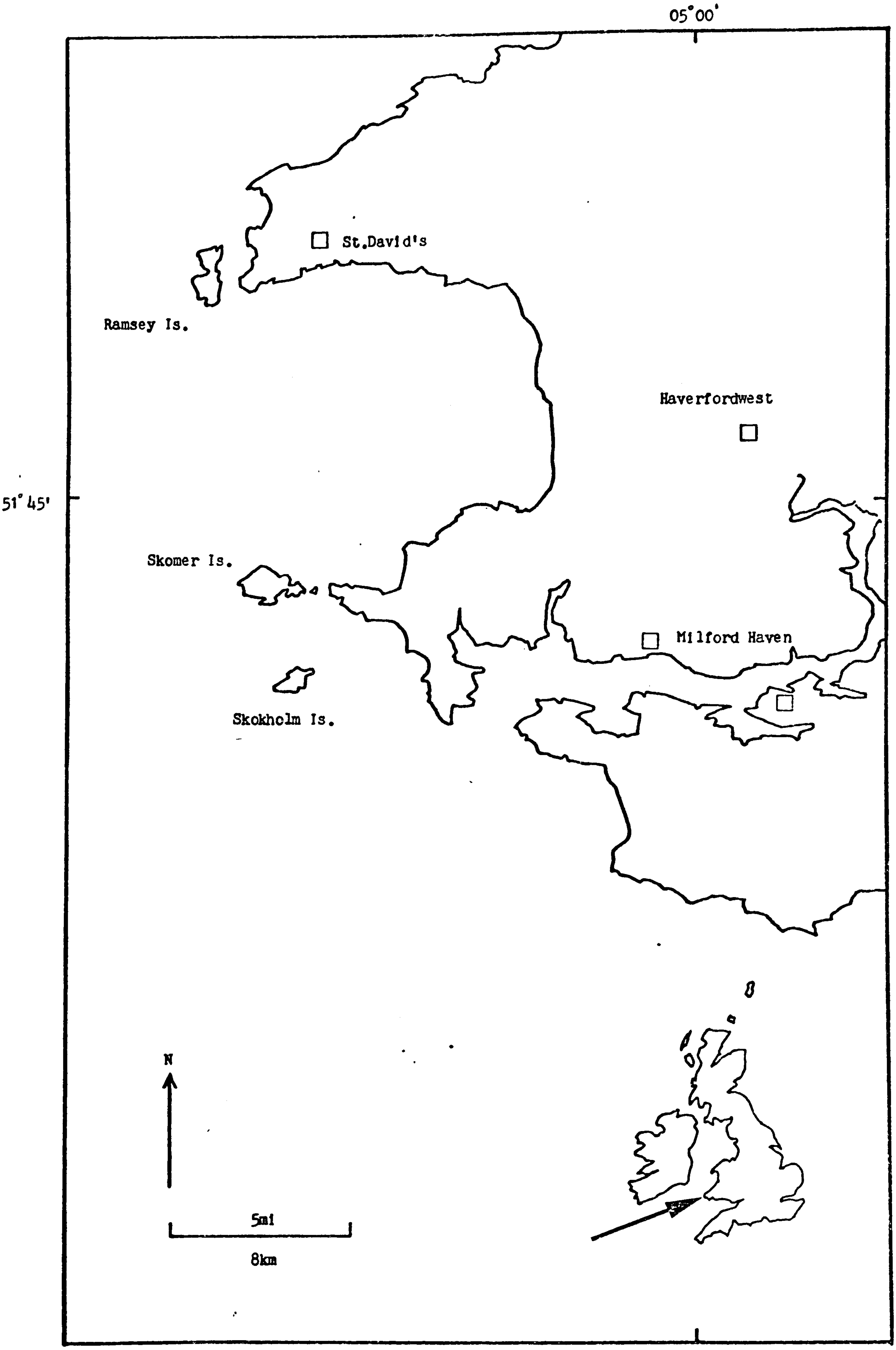


Fig.1.1. Map of south-west Wales showing location of Skomer Island.

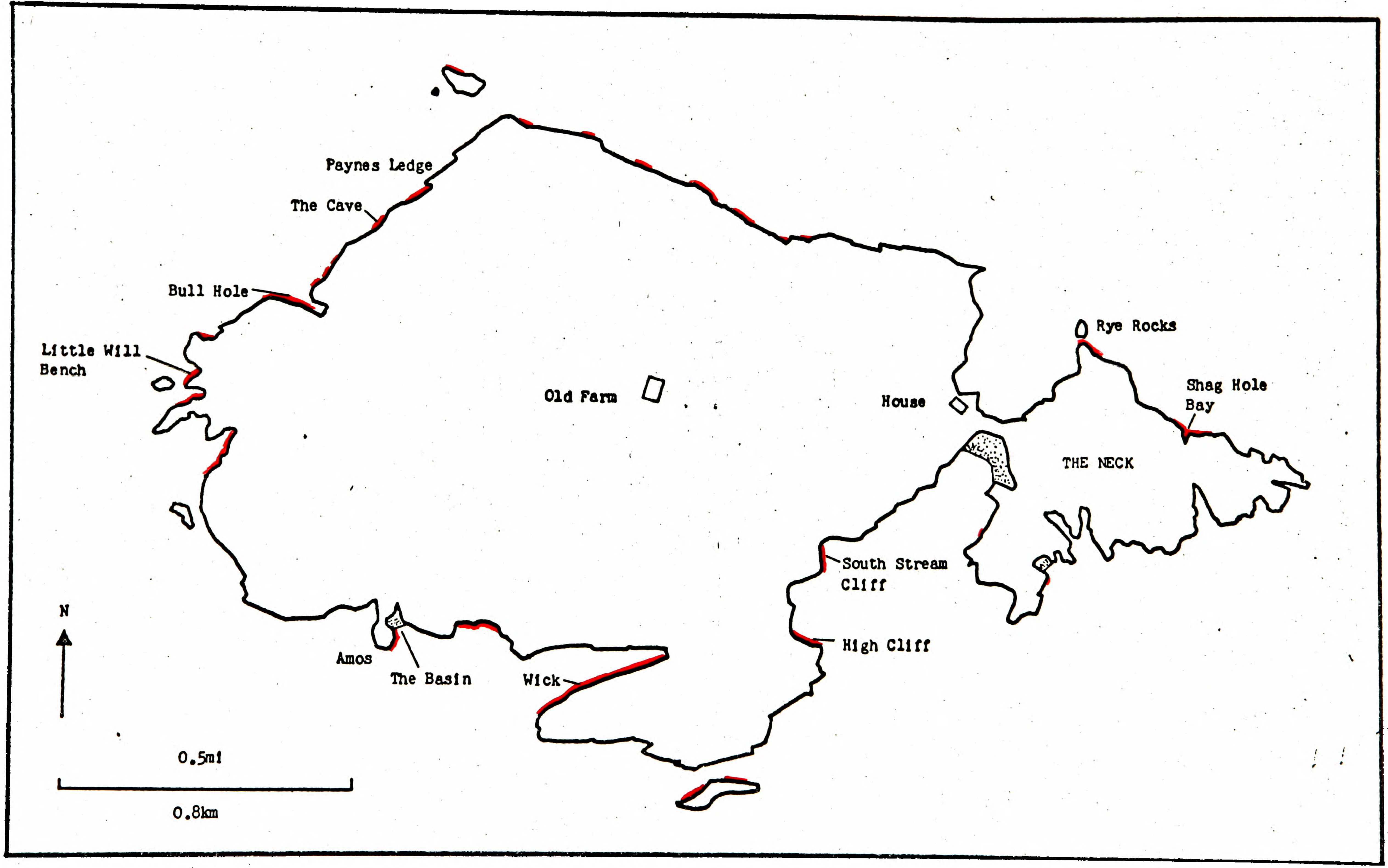


Fig.1.2. Map of Skomer Island showing location of Guillemot colonies (red) and places mentioned in the text.

hardly any frost" (Buxton & Lockley 1950). During the four periods of study, temperatures only once fell below 0°C, and rarely exceeded 25°C.

Skomer Island is a National Nature Reserve and is regarded as an important seabird breeding station. Twelve species breed; Fulmar Fulmarus glacialis (c100prs), Manx Shearwater Puffinus puffinus (c95,000prs), Storm Petrel Hydrobates pelagicus (several hundred pairs), Cormorant Phalacrocorax carbo (10-20prs), Shag P.aristotelis (10-20prs), Great Black-backed Gull Larus marinus (c150prs), Lesser Black-backed Gull L.fuscus (c7000prs), Herring Gull L.argentatus (c2000prs), Kittiwake Rissa tridactyla (c2000prs), Razorbill Alca torda (c1500prs), Guillemot (2000prs) and Puffin Fratercula arctica (c7000prs).

The location of all Guillemot colonies, study areas and places mentioned in the text are shown in Fig.1.2.

Sizes and Subspecies of Guillemots on Skomer

Guillemots breeding on Skomer are of the subspecies albionis (Witherby 1923), which is the second smallest and one of the palest geographical race of the Common Guillemot (Tuck 1960). Data in Tuck indicate that male Guillemots may be slightly larger than females. After colour marking birds on Skomer (see later; Chapter 2) I was able to sex some of them by observing copulations. Size parameters of males and females are shown in Table 1.1. Males differ from females by having larger bills.

Definitions

To avoid ambiguity the following terms are used as defined below:

(1) Population: The Skomer population encompasses all birds associated with Skomer, i.e. either reared on Skomer (but not breeding elsewhere), or breeding on Skomer. The Skomer breeding population does not

Table 1.1. Summary of measurements of breeding male and female Common Guillemots from Skomer Island.

	MALE		FEMALE		t	P	df
Weight	853.1 ± 27.8	(11)	869.8 ± 42.4	(13)	1.11	>0.1	22
Wing length	197.2 ± 2.9	(11)	195.6 ± 5.1	(13)	0.94	>0.1	22
Bill length (l)	46.7 ± 2.7	(11)	45.4 ± 1.5	(14)	1.44	>0.1	23
Bill depth (d)	13.2 ± 0.4	(11)	12.7 ± 0.6	(14)	2.59	<0.02	23
Bill d x l (index)	616.4 ± 31.8	(11)	576.3 ± 20.2	(14)	3.84	<0.001	23

Notes: Measurements are means ± one S.D.

Units; Weight (g), Wingl (mm), Bill (mm).

Sample sizes in parentheses.

t = t value, students' t test.

Bill length and wing length measured as in Pethon (1967), and bill depth as in Storer (1952).

include immature birds, which visit the island but do not breed. Breeding birds are those in which the female of the pair lays an egg during the breeding season in question.

(2) Colony: A cliff-face of Guillemots constitutes a colony. In most Skomer colonies Guillemots were out of sight of conspecifics in other colonies (see Fig.1.2).

(3) Sub-colony: A group of Guillemots within a colony, separated from other sub-colonies by Guillemot-free areas. In many cases birds in sub-colonies within a colony were able to see each other.

(4) Site or nest-site: The two terms are synonymous. An area roughly 25 in^2 (c144cm)^2 in a sub-colony in which the egg is laid.

CHAPTER 2

POPULATION DYNAMICS

Introduction

There have been a number of population studies of seabirds (see reviews by Lack 1966, Ashmole 1971), and these have shown that many species share a number of common features, such as long expectation of life, deferred maturity and low reproductive output.

Guillemot (Uria spp.) populations have long been of interest, because in many areas they constitute an important resource. The birds generally breed in enormous and very dense colonies, and because their eggs and the birds themselves are highly palatable (Cott 1954), they have a long history of exploitation (Martin 1698, Cordeaux 1884, Kaftanovski 1938, Venables & Venables 1955, Fisher & Lockley 1954, Doughty 1971, Dyck & Meltofte 1973). Not surprisingly the intense exploitation at many colonies led to massive reductions in numbers (e.g. Uspenski 1956). Consequently, in areas where Guillemots were considered economically important, attempts have been made to estimate population size and productivity in order that they may be continuously exploited (Krassovski 1937). However, attempts to measure these parameters were largely unsuccessful, due to a number of practical difficulties. These include:

(a) estimating the size of populations in important areas (see Appendix I), where huge numbers of birds occur, often in dense groups. For example, Uspenski (1956) lists five colonies of Brunnich's Guillemots in Novaya Zemlya, estimated to hold over 100,000 pairs, and twenty-two with

10,000-100,000 pairs. On Funk Island, Newfoundland, Tuck (1960) estimated the population of Common Guillemots at 500,000 pairs.
(b) detailed information on adult survival rates and movements from recoveries of ringed birds was precluded because of rapid wear and loss of Guillemot rings. Even with the introduction of harder metal rings (Mead 1974) the problem still exists.
(c) measurements of egg and chick production were probably biased since the presence of man at the breeding colonies each day, to mark and inspect eggs and chicks, causes considerable disturbance, and loss of eggs and chicks (Johnson 1940, Uspenski 1956, Swartz 1966).

The distribution and approximate number of Common Guillemots in the north-east Atlantic are shown in Fig. 2.1 and Table 2.1. Numbers are lowest at the southern limit of their range, in Portugal, and in the north, in northern USSR, where the Common Guillemot is replaced by Brunnich's Guillemot, with which it may compete for resources (Spring 1971). Thus optimal conditions probably occur where the species is most numerous; i.e. between its northerly and southerly limits. The situation is probably analagous with habitat utilization; the best areas are occupied first, and sub-optimal ones later, after the best areas are saturated (Udvardy 1969).

In the southern part of their range in Europe, Common Guillemot numbers have declined during the present century. Areas where decreases have occurred include Skomer Island (the study area), most of southern Britain, France and the Iberian Peninsula. The reasons for the decline are not clear (Cramp et.al. 1974), but there are two main possibilities; (a) oil pollution - the area of population decrease coincides with main tanker lanes (b) oceanographic changes in the north Atlantic (Cushing 1966), which may have resulted in reduced availability of prey species (Coombs 1975).

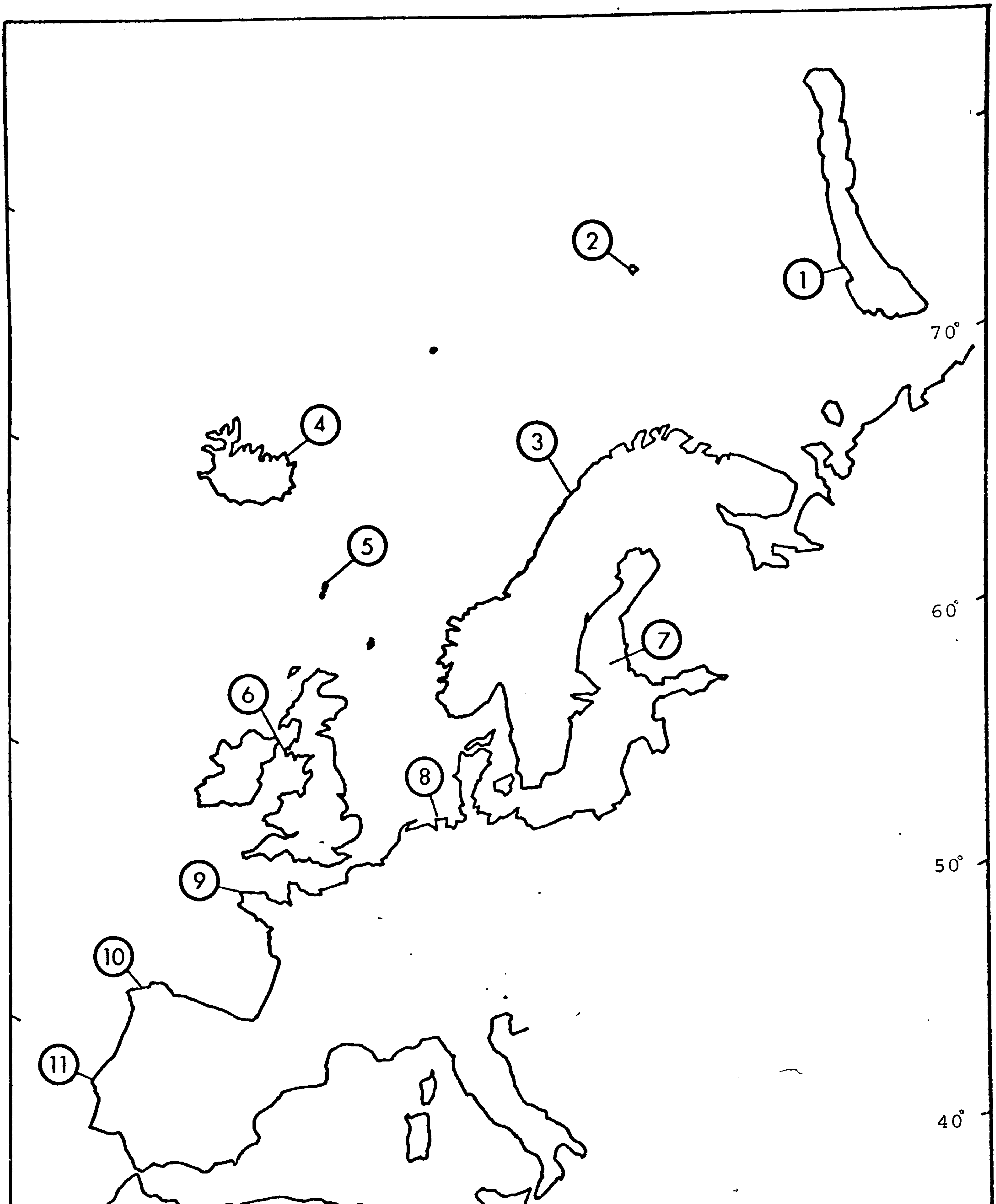


Fig. 2.1. Distribution of Common Guillemots in the north-east Atlantic. See Table 2.1. for figures for each locality.

Table 2.1. Approximate numbers of breeding pairs of Common Guillemots in the north-east Atlantic.

Area	No.of Pairs	Date of count	Source
1. Novaya Zemlya,USSR	1000	1950s	Uspenski 1956
2. Bear Island	300 ,000	1971	Williams 1974
3. Norway	140, 000	1964 - 1968	Brun 1969
4. Iceland	2,000, 000	upto 1970s	T.Einarsson,pers.comm.
5. Faeroes	390, 000	1972	Dyck & Meltofte 1975
6. British Isles	577, 000	1969 - 1970	Cramp *et.al* 1974
7.Baltic Sea	9, 000	1974	Hedgren 1975
8. Heligoland,Germany	2, 000	1940s	Schultz 1947
9. Brittany,France	200	1970	Brien 1970
10.N.W.Spain	300	1940s	Bernis 1949
11.Berlenga Is.Portugal	2, 000	1973	R.Vicente, pers.comm.

Population parameters such as adult survival, age of first breeding, survival to breeding age and breeding success, may differ in different parts of a species' range. Snow (1956) has shown that the age-structure of Blue Tit *Parus caeruleus* populations varied in different parts of its range.

The aim of the present study was to estimate the size of the Skomer Guillemot population, to try to estimate the magnitude of the population decline, and to examine population parameters. Three seasons' work was insufficient to determine the age at which Guillemots first breed, and clearly a larger series of data are necessary before any conclusions can be reached about other parameters such as adult and immature survival rates. This study is therefore a preliminary one; the work is being continued. I have compared my results with those already published; Lewis (1930) made some speculative comments based on ringing recoveries, and Southern *et.al.* (1965) and Mead (1974) have published figures for adult survival. Comparisons are also made with other alcids, mainly the Razorbill (which has been the subject of a population study on the neighbouring island of Skokholm (C.S. Lloyd, (unpubl.), 3km south of Skomer), and Brunnich's Guillemot (from various sources - see later).

Methods

(a) Estimate of Population Size

It is clear from old photographs and personal accounts (R.M. Lockley, pers.comm.) that the Guillemot population on Skomer has undergone a decline (Birkhead & Ashcroft 1975). Photographic material from 1934 is available for a single large Skomer Guillemot colony, known as the Wick. To estimate the size of the population in 1934 I selected areas on the Wick colony where it was possible to count individuals on the photographs. Sample areas were counted by myself and two others; our figures did not vary by more than 15%. The mean values for each sample area are compared with the number of birds counted in the same area in 1975, at the colony (Table 2.2). I suspected that "photographic counts" were under-estimates, so to check this I took photographs of the Wick colony in 1975, counted the birds at the colony at the same time, and later counted the birds on the photograph. This showed that photograph-counts were an under-estimate by 12% (Table 2.3). This enabled me to correct the 1934 colony counts, and to provide an estimate for the size of the Wick colony in that year. Birkhead & Ashcroft (1975) have shown that over the period 1960-1974, on Skomer there was a significant relationship betwen the size of a single colony and the rest of the population, suggesting that all colonies changed in parallel. This means that it is probably safe to extrapolate from the Wick colony to provide an order of magnitude for the size of the population of the whole island in 1934.

(b) Whole Island Counts 1963-1975

Since 1963 the total number of Guillemots present at all colonies has been counted over a number of days during mid-June in an effort to monitor the population (for details see Birkhead & Ashcroft 1975). During 1972-1975 I carried out whole island counts to compare with other population estimates, to determine the level of accuracy of these figures. I have compared Skomer figures with two other South Irish Sea colonies, Great Saltee and Lundy Island, for the period 1962-1973. Data for the latter two colonies were provided by the Seabird Group (C.S. Lloyd, pers.comm.).

Table 2.2. Counts of individual Guillemots from photographs taken in 1934 and 1975: since counts are underestimated by 11.9% (see Table 2.3), the third column presents a corrected 1934 count.

Colony	1934 count	1975 count	1934 count + 11.9%
Wasp/Bee	137	45	153.3
Top Crack	50	6	56.0
Wick Corner	120	65	134.3
Twin area	202	98	226.0
Totals	509	215	569.6

Table 2.3. Differences between counts of individual Guillemots made in 1975 at the colony (column one) and from photographs taken at the same time (column two). The third column shows the percentage difference between these two counts.

Colony	Colony count	Photo count	% difference
1. Lockley	90	78	-13.3%
2. Bee + Wasp	42	45	+ 7.1%
3. Twin	98	88	-10.0%
4. Stony	68	60	-11.6%
5. Hump	60	42	-20.0%
6. Pitchfork	12	10	-16.6%
			-11.9%

(c) The Size of the Skomer Guillemot Population in 1973-1975

Guillemot populations are notoriously difficult to census accurately. The failure to produce reliable figures (e.g. Cramp et.al. 1974) is due to the lack of sufficient ground work on patterns of colony attendance and the variability in these patterns between different colonies. I examined patterns of Guillemot attendance on Skomer in 1973-1975 (Appendix I). The following method was used to estimate the size of the breeding population on Skomer in 1973-1975. At a number of study colonies (where I was recording breeding success - see below) the exact number of breeding pairs was determined by marking the position of each egg, as it was laid, onto a large-scale photograph of the colony. At the same colonies I counted the total number of birds present during the period 1-15 June each year, and plotted the mean number of birds present at each colony against the known number of pairs for the same colonies, thus calculating an average ratio of breeding pairs : birds. It was possible to extrapolate from these data, and provide an estimate of the size of the total breeding population on Skomer, from one count of the total number of individuals, made on a single occasion between 1-15 June each year.

(d) Breeding Success

In order to record laying dates, egg-loss, replacement layings, hatching success, chick-loss and fledging success, a number of colonies were selected where observations could be made without disturbance to the birds. Each study colony was photographed during preliminary observations in 1972, when birds were incubating, and each egg-site was numbered on the photographs. The same sites were used each year and I recorded any sites that were gained or lost. All colonies were visited at least once each day, usually at the same time, from late April until late July, thus spanning the period from the onset of laying in early May until the time when most chicks had fledged, in lated July.

The method I employed here probably differed from earlier workers, in that I took great care not to disturb the birds. Earlier workers, who marked eggs, had to flush incubating birds in order to count eggs, must have caused considerable disturbance, egg and chick-loss (Uspenski 1956, and others).

(e) Adult Survival

Between 1972 and 1974 a total of 156 Guillemots on Skomer were individually colour-ringed and ringed with British Trust for Ornithology (B.T.O.) rings; most birds were marked in 1972. Birds were caught using a wire noose on a long, telescopic (up to 16') pole, from above their breeding ledges. Because of the difficulty of finding areas suitable both for catching birds, and for subsequently being able to observe them without causing disturbance, a smaller sample was used to calculate survival rates. A further difficulty was that birds caught in this way may have been more likely to change breeding site after capture; J.L.F. Parslow (pers.comm.) found this to be the case at a Guillemot colony in Scotland. Only birds which were recorded as breeding adults (i.e. caught while incubating or brooding a chick) were used in this analysis. Colour-marking can only be used to calculate survival if birds are highly site tenacious and there is good evidence that Guillemots are; egg-collectors recorded finding distinctively marked eggs at the same site for up to 15 years (Seebohm 1885, Wade 1903), and several authors recorded ringed individuals using the same site year after year (Lewis 1930, Belopolski 1957, Tuck 1960, Southern et.al. 1965, Tschanz et.al. 1969). Quantitative details of site tenacity on Skomer are presented in Chapter 3. Between 1973 and 1975 a total of 450 hours were spent searching for colour-marked birds.

(f) Mortality Factors

Analyses of ringing recoveries generally consider the ways in which birds die. From the various analyses of Common Guillemot recoveries, I have presented a brief review of the most important factors. Ringed Guillemots may be recovered in a number of ways. One such category is 'found-dead' - this group will almost certainly include some birds dying of oiling, shooting etc., but will contain a high proportion of birds dying of more natural causes. I have used this 'found-dead' category in analyses of adult and immature birds. I have compared the seasonal frequency of adult mortality with a gale-index. Climatological averages for the period 1956-1970, for each month of the year, were obtained from the Meteorological Office, Berkshire. From twenty-two coastal stations around the British Isles I calculated the seasonal frequency of gales, i.e. the mean number of days each month, in which wind speed exceeded 33 knots (timed over a period of 10 minutes).

(g) Survival to Breeding Age

The age at which Common Guillemots first start to breed is not known, since the duration of the present study was only three seasons. The oldest age-class I was able to observe on Skomer was in its third year (referred to here as three years old), i.e. ringed in 1972, observed in 1975. No three year old birds bred. J.L.F. Parslow (pers.comm.) was able to observe marked Guillemots, 4 years old in Scotland, and did not record them breeding. Earlier workers have assumed that Guillemots first breed in their second year (Uspenski 1956) or third year (Tuck 1960, Southern _et.al_. 1965). It has been found that most Razorbills and Puffins first start to breed at about five years old (C.S. Lloyd, unpubl., R.E. Ashcroft, pers.comm.). It seems likely that Guillemots may also start at about the same age, and for convenience I have made this assumption throughout this chapter.

Ringing recoveries from different ringing schemes have been used to calculate a composite survival rate up to the 5th year, using Lack's (1951) method of analysis. Haldane's (1955) maximum likelihood estimator has been used to calculate adult survival rates (see results) since this method allows for some birds still being alive, and I have used Lack's method for calculating survival up to breeding age from recoveries of birds ringed as chicks, since these data are 'complete' in that no records after 1969 (ringing date) have been included. Although there may be differences in the estimates produced by the two methods, the relative differences in survival estimates, between populations will be unaffected by this.

(h) Return of Birds Ringed as Chicks on Skomer

A total of 279 Guillemot chicks was marked with a different colour year-class ring for each year 1972-1975. The yearly totals of chicks ringed were 1972: 87, 1973: 92, 1974: 50, 1975: 50. Observations for resighting birds marked as chicks were made at breeding colonies, particularly those where ringing was conducted and at clubs. For each sighting I noted whether the bird was on the sea, on a breeding ledge or in a club. Guillemot clubs on Skomer consisted of aggregations of birds on tidal rocks beneath breeding colonies (see Fig.5.2a: Chapter 5). Since most club birds were immature, non-breeding birds (see later) I recorded the seasonal changes in numbers in clubs, and on a number of occasions I tried to count the total number of club birds around the island.

(i) Survival of Guillemots to Breeding Age: Mortality Factors

I recorded the behaviour of adults and chicks at fledging, and noted whether fledging chicks were subject to predation. Ringing recoveries were used to examine the seasonal pattern of post-fledging mortality.

Results and Discussion

(a) Estimate of 1934 population size. Table 2.2 shows the number of Guillemots at the Wick colony counted from four sample areas on 1934 photographs, and numbers counted in the same areas in 1975. Table 2.2 also presents corrected 1934 figures to allow for the under-estimate of photograph-counting (see methods). Thus the figures indicate that the population on the Wick (and probably the whole island) has decreased by 62% between 1934 and 1975. This represents an average annual decline of 2.3% although it is not known whether the population declined at a steady rate over the 41 year period, or rapidly over a short period. Some idea of the extent of the decrease can be seen from Fig.3.7(Chapter 3).

(b) Population estimates between 1963-1975. Changes in the whole island population, the total number of individuals counted on a single occasion each year between 1963 and 1975 are shown in Fig. 2.2. These data are compared with counts for Great Saltee and Lundy Island. The sharp decrease in numbers in 1970 was a result of the Irish Seabird Wreck in the autumn of 1969 (Holdgate 1971), in which over 16,000 Guillemots died. The subsequent 'recovery' has been similar in all three colonies (see Table 2.4). The figures for Skomer show that numbers have remained at a similar level since 1972, and the population may have stabilized.

Table 2.4. Changes in Skomer Guillemot Population 1969-1975
This assumes that most immature birds establish
sites on ledges in their 4th year

Years	Percentage Change	Notes
1969-1970	40% decrease	Due to the Irish Seabird Wreck (Holdgate 1971), which killed the following age classes; breeding adults and their still-dependent young (1969 chicks), and birds in their third year and older. In other words first year birds (1968 chicks) and second year birds (1967 chicks) were not involved. Ringing recoveries have shown that first year birds disperse away from the colony in their first summer (Mead 1974), and colour-markin on Skomer (see p.23) has shown that only a small proportion of two year old birds that are alive return to the colony in their second year.
1970-1971	20% increase	Due mainly to four year old birds (1967 chicks), produced by a large population (see Fig.2.2.) entering the population.
1971-1972	16% increase	Due mainly to four year old birds (1968 chicks) entering the population.
1972-1973	9% decrease	Few chicks from 1969 survived to enter the population in 1973.
1973-1974	10% decrease	Adult survival = 93% (high?), survival of 1970 cohort also high?
1974-1975	11% decrease	Adult survival = 88% (low?), survival of 1971 cohort also low?

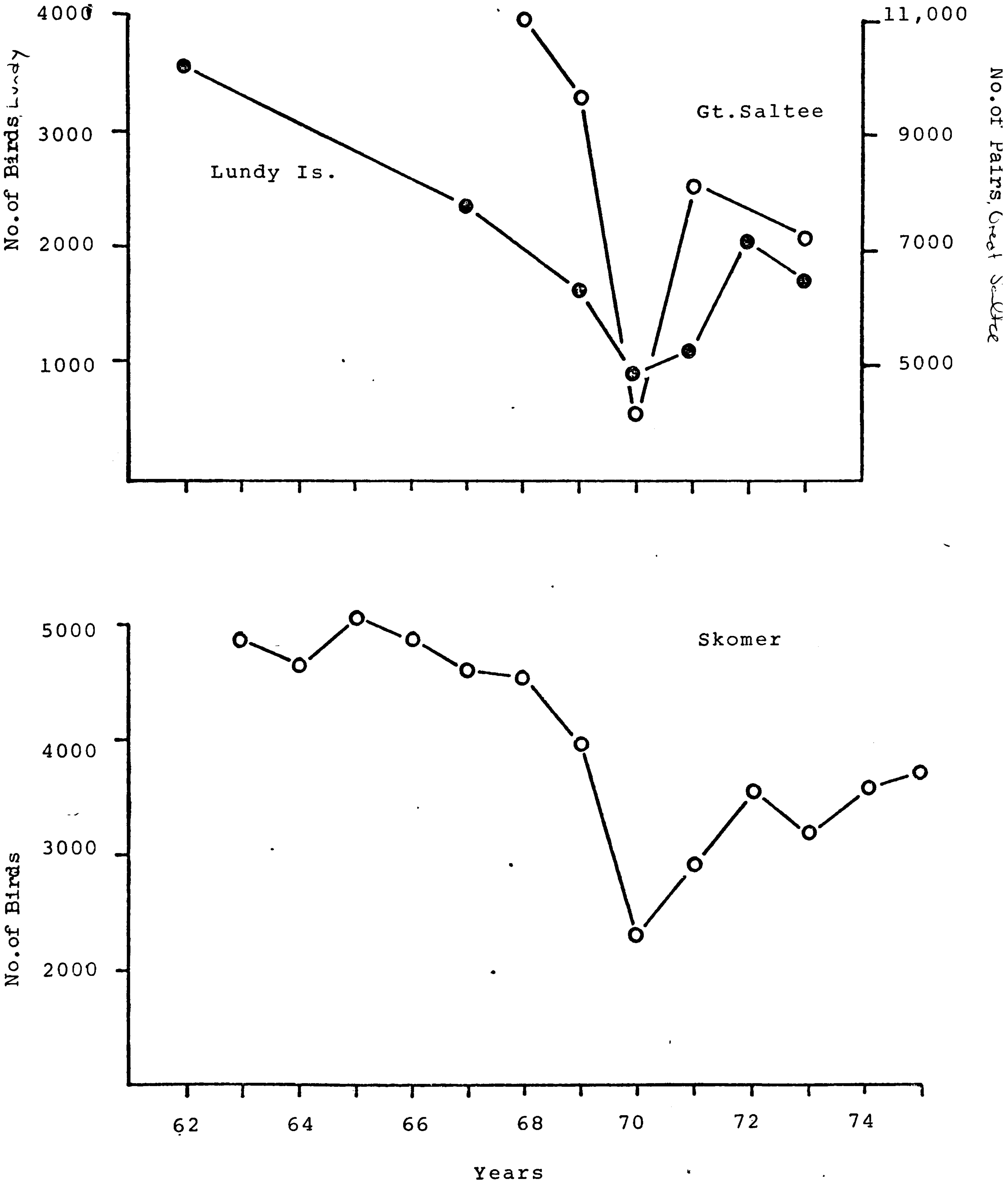


Fig.2.2 Recent changes in the number of Guillemots at three south Irish Sea colonies: Skomer, Lundy Island and Great Saltee.

(c) Size of breeding population in 1973-1975. The relationship between mean number of birds and known number of breeding pairs in three years is shown in Fig.2.3. Table 2.5 shows the total number of individuals counted in whole-island counts 1973-1975, the ratio between breeding pairs and birds, and the calculated breeding population in each year.

Although the calculated number of breeding pairs in 1975 (Table 2.5) is similar to the 1974 figure, there was in fact, a reduction in the breeding population in 1975 (Table 2.6). The discrepancy is due to the high number of individuals counted on 8 June 1975. This illustrates the type of error that can occur in censuses of this type. Thus the breeding population consisted of 2178 pairs in 1973 and 2485 pairs in 1974.

(d) Breeding success. A summary of hatching, fledging and overall breeding succss for a number of study groups between 1973 and 1975 is presented in Table 2.7. The overall mean of breeding success for three years was 0.7 chicks / pair. Breeding success of Common Guillemot is compared with several other alcids' breeding success in Table 2.8.

Replacement layings: At least two factors have been thought to determine whether lost eggs are replaced in *Uria* spp.; these are a) the number of days after laying that egg-loss occurred, and b) the part of the season in which the loss occurred, in relation to median laying date. The mean number of days that eggs had been incubated before being lost and subsequently replaced was 5 days (range 1-13). There was no significant difference between the number of days that eggs had been incubated, between birds replacing them ($\bar{x} = 5.0 \pm 4.1$ S.D. $n = 12$) and those not replacing them ($\bar{X} = 7.8 \pm 8.1$ S.D. $n = 10$) ($t = 1.01$ 20 df. $P > 0.1$). There was however a significant difference between the laying dates of lost eggs which were replaced (May 1 = 1, Median laying date = 24, $\bar{x} = 13.4 \pm 6.0$ S.D. $n = 12$) and those which were not

Fig.2.3 . Relationship between mean number of birds at study colonies between 1-15 June, and the known number of breeding pairs at these study colonies. Means and one S.D. shown. Differences between the slopes of the relationships for each year are not significant.

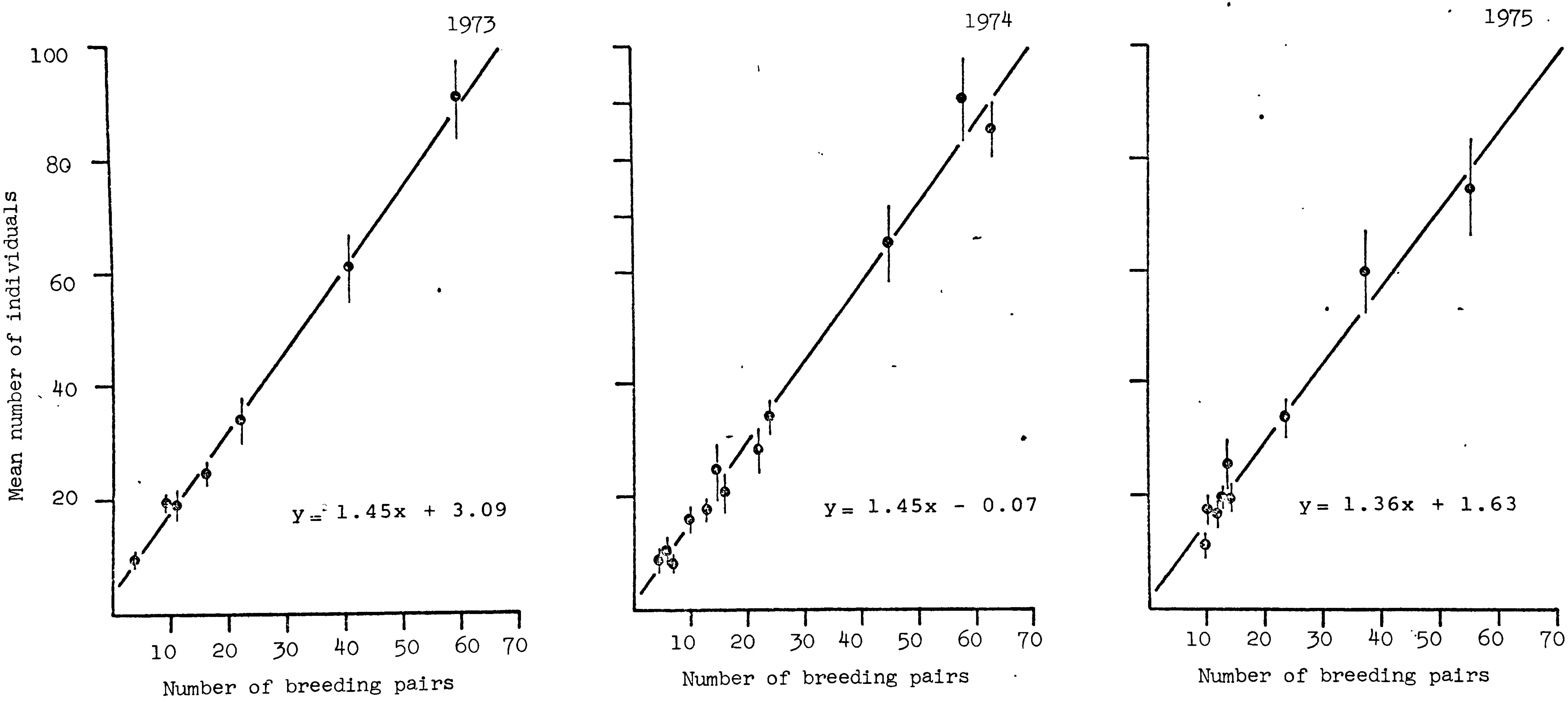


Table 2.5. Calculated number of breeding pairs of Guillemots on Skomer in 1973, 1974 and 1975. The first column shows the total number of birds counted on Skomer on a single occasion. The second column shows the ratio of breeding pairs:birds calculated from Figure 2.3. The third column shows the number of breeding pairs on Skomer.

Year	Total No. of birds counted (a)	Ratio Pairs:birds (b)	Calculated breeding population (a.b)
1973	3251	0.67	2178
1974	3601	0.69	2485
1975	3815	0.65	2480 corrected = 2187

Note: Because of an unusually high count of total birds in 1975 a 'corrected' figure is included. This has been calculated in the following way: since the breeding population on Skomer fell by 12% between 1974 and 1975 (Table 2.6); 2485 - 12% = 2187.

Table 2.6. Changes in the number of breeding pairs at six sub-colonies 1974 - 1975.

Colony	Number of breeding pairs 1974	1975	Percentage change
Bull Hole B	63	56	-11.1
Bull Hole A	14	13	- 7.1
Bull Hole D	12	11	- 8.3
Bull Hole I	15	14	- 6.7
Wick Corner	45	38	-15.5
Wick : Wasp	16	13	-18.7
Totals	165	145	
Mean values	27.5	24.2	-12.1

Table 2.7. Summary of breeding success of Guillemots on Skomer, 1973 - 1975.

Year	No. sub-colonies	Total No. Pairs	No. eggs hatch (% ± S.D.)	No. chicks fledge (% ± S.D.)	Breeding success
1973	3	124	102 (82.6 ± 5.7)	90 (87.6 ± 4.3)	72.5 ± 8.4
1974	6	158	116 (70.1 ± 10.5)	104 (87.8 ± 11.2)	61.7 ± 14.0
1975	10	204	174 (83.4 ± 8.8)	155 (88.3 ± 9.5)	74.2 ± 8.5
Totals	19	486	392 (79.1 ± 10.6)	349 (88.0 ± 9.0)	70.0 ± 11.5

Notes: The number of sub-colonies refers to the number of sub-colonies where data were collected.

Figures for number of eggs, chicks and breeding success include replacement eggs.

[illegible] means

Table 2.8. Breeding success in some Alcid species

Species[a]	Clutch size	Hatching success (%)	Fledging success (%)	Breeding success[b]	Source
Razorbill	1	71.7	93.4	0.69	C.S.Lloyd unpubl.
		76.0	87.6	0.66	Bedard 1969a
Common Gullemot	1	79.1	88.0	0.70	This study
Brunnich's Guillemot	1	67.7	88.5	0.41	Tuck 1960
		84.0	94.0	0.80	A.J.Gaston unpubl.
Black Guillemot	2	83.1	94.9	1.56	A.Petersen unpubl.
Pigeon Guillemot	2	62.0	90.0	1.10	Drent *et al* 1964
Cassin's Auklet[c]	1	82.1	90.2	0.71	Manuwal 1972
Parakeet Auklet	1	67.7	76.2	0.52	Sealy & Bedard 1973
Rhinoceros Auklet	1	90.0	72.0	0.66	Summers 1975
Common Puffin	1	79.0	90.0	0.64	R.E.Ashcroft unpubl.

Notes: a. Order and nomenclature follow Peterson (1934), Latin names - Table 6.1
b. Breeding success : chicks per pair.
c. This species is double brooded in some years.

($\bar{x}$ = 21.9 ± 8.3 S.D. n - 10) (t = 2.77, 20df. $P<0.02$). Thus, on average eggs laid near to, or after the median laying date were less likely to be replaced than those laid and lost earlier in the season. In 1974 12/23 (52.2%) of all birds which lost their first egg replaced it.

The mean interval between loss and replacement on Skomer was 14.8 days ± 1.2 S.D. (n = 9), Tuck (1960:153) obtained a similar figure for Brunnich's Guillemots in Canada, but Uspenski (1956) found that in Brunnich's Guillemots in northern USSR the interval was 15-22 days.

Of the 12 birds which relayed, 9 (75%) successfully hatched their egg, and 7 (78%) fledged chicks, so overall, breeding success was 58.4%. This figure was not significantly different from a sample of 123 birds which did not lose or replace their first egg, whose breeding success was 75.6% (X^2 = 1.69, 1df. NS), but this may have been due to the small sample size for replacement layings.

(e) Adult survival. Ringing recoveries of birds marked as adults have been used to calculate an average annual survival rate. Elsewhere (Birkhead 1974) I presented an adult survival estimate of 87.9% based on ringing recoveries of British ringed Guillemots, and this agreed closely with Mead's (1974) estimate of 87.1% calculated in the same way from recoveries of Heligoland Guillemots. However, ring wear and loss can seriously bias survival estimates calculated in this way (Grosskopf 1964, Kadelac & Drury 1968), and Guillemots probably wear through their rings more rapidly than most other species. Even the resistant 'Monel' rings, introduced in recent years (Mead 1974) rapidly become worn. Thus the two survival estimates calculated from recoveries of British and Heligoland birds, above, are probably under-estimates. There are two possible ways around this problem.

One can do as Mead (1974) has done with British ringing recoveries, which is to use Haldane's method, including only 'middle-aged' birds, before ring-wear has started to occur. In this way Mead estimated adult Guillemot survival to be in the order of 94%. The other method is to use a sample of individually colour-marked birds, and to record the number which survive from one year to the next. In the present study, between 1972-1973, 51/65 (78.5%) marked birds were resighted. Between 1973-1974, 83/89 (93.2%), and 1974-1975, 67/76 (88.2%) were resighted. I have not included the 1972-1973 data to calculate average survival because it was not clear whether the low sighting frequency was due to mortality or to birds changing site after capture (see methods). The average survival rate for the period 1973-1975 was 90.7%. Table 2.9 compares adult survival rates from a number of sources. The figure of 87.0% of Southern et.al. (1965), also from a colour-marked population, agrees well with two Haldane estimates, above, but is lower than my estimate and Mead's (1974) 'corrected-for-ring-loss' estimate. The lower survival rate in Southern et.al.'s study may have been the result of:

(a) a genuinely low adult survival

(b) the small sample size (n = 29), where the loss of one bird constituted 3.4%

(c) because only a limited amount of time was spent each year, searching for marked individuals.

In addition, I found on Skomer, that a small proportion of individuals change their breeding site after capture, so the estimate of 87.0% by Southern et.al. is a mimimum one.

The results of my colour-marking study, and Mead's (1974) survival estimate indicate that Guillemots are long-lived, and survival estimates of

Table 2.9. Adult survival estimates for Common Guillemot, Brunnich's Guillemot and Razorbill, derived from different methods.

Area	Survival estimate	S.E.	Method	Source
COMMON GUILLEMOT				
Skomer Is.Wales	90.5	-	Colour ringing	This study
N.E.Scotland	87.0	-	Colour ringing	Southern *et.al* 1965
British Isles	87.9	2.0%	Ringing recoveries	Birkhead 1974
British Isles	93.7	4.0%	Corrected ringing recoveries	Mead 1974
Heligoland	87.1	2.2%	Ringing recoveries	Mead 1974
BRUNNICH'S GUILLEMOT				
N.E.Canada	91.0	9.0	Ringing recoveries	This study:Tuck & Maher.
RAZORBILL				
British Isles	89.0	1.1	Ringing recoveries	Lloyd 1974
British Isles	91.4	4.0%	Corrected ringing recoveries	Mead 1974
Skokholm Is.Wales	89.0	6.1%	Colour ringing	Lloyd & Perrins,in prep.
Skomer Is.Wales	92.1	4.0%	Colour ringing	Lloyd & Perrins,in prep.

91-94%, which would indicate an average length of breeding-life of 9-16 years, may be of the right order. Table 2.9 compares adult survival rates of Common Guillemot, Brunnich's Guillemot and the Razorbill.

(f) Mortality factors : Causes of adult mortality. The main source of information of adult mortality in Guillemots comes from the recoveries of ringed birds (Holgerson 1961, Tuck 1960, Birkhead 1974, Mead 1974). However, it is well known that ringing recoveries can be biased in this respect. Birds which are killed by man, or caught in fishing tackle are more likely to be handled, and therefore 'recovered', than birds dying of more natural causes. I have tabulated the causes of recovery for four age categories of British ringed birds in Table 2.10; among adult birds the main recovery categories are Found Dead (52%), Oiled (32%) Killed (13%) and Caught in Fishing Tackle (3%). There are, however, marked regional differences in causes of mortality. For example, relatively few birds were recovered oiled in Norwegian waters, but many were recovered shot, whereas in British waters the converse was true. Similarly among Brunnich's Guillemots in west Greenland, most recoveries were of birds which have been shot, but this species occasionally suffers heavy mortality in areas where drift nets are set for salmon (Tull et.al. 1972).

Oiling: Much has been written about the effect of oil pollution on birds (see Aldrich 1938, Moffit & Orr 1938, Clark 1968, Clark & Kennedy 1968, Hope-Jones et.al. 1970, Bourne 1968a,b,1970,1972, Bourne et.al. 1967, Vermeer & Vermeer 1975), and of all species, Guillemots appear to be the most vulnerable. Guillemots feature more frequently than most species in Beached Bird Surveys (Bibby & Bourne 1971,1972). This may be due in part to their being greater numbers of Guillemots than most other species

Table 2.10. Number and percentage of British ringed Guillemots recovered by different methods at different ages.

Recovery method	0 - 1	%	1 - 2	%	2 - 3	%	3 - 4+	%	Total	%
Killed	89	35.3	10	14.1	5	13.5	20	12.5	124	23.7
Oiled	46	18.2	23	32.4	14	37.8	50	31.2	133	25.5
Fishing tackle	7	2.8	8	11.3	0	0	5	3.1	20	3.8
Found dead	103	40.9	30	42.3	15	40.5	80	50	228	43.7
Total	245		63		34		153		535	

Notes: Killed : shot in most cases.

Fishing tackle : on lines or in nets.

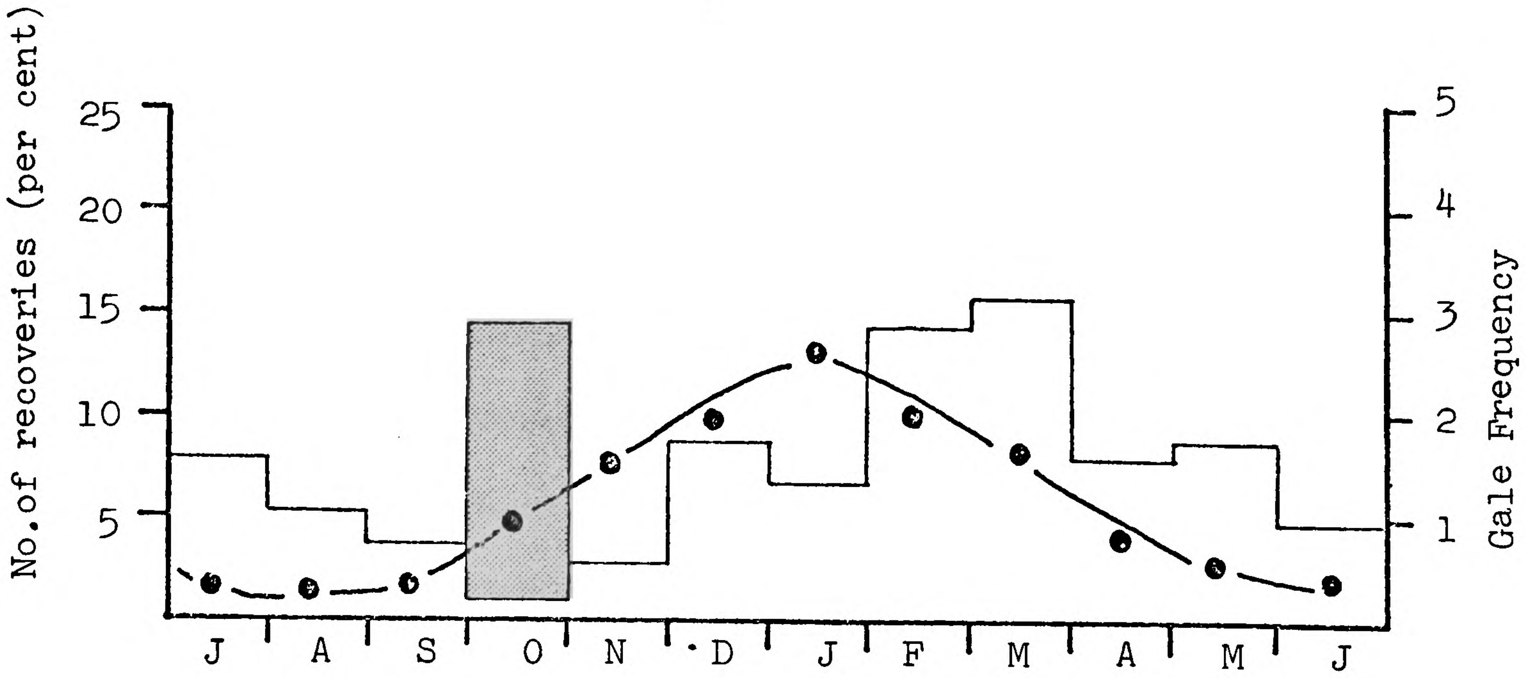
(Cramp et.al. 1974), but the birds' reaction to floating oil may make them especially susceptible (Bourne 1968). Although oil pollution has been implicated in the decline of some Guillemot populations e.g. Farallon Islands, Ainley & Lewis 1974, and on Skomer, Buxton & Lockley 1950), there is no quantitative evidence on this point.

The effects of large spills and chronic small-scale spillages have been discussed by Clark (1968), who concluded that the latter were more damaging to bird populations than infrequent, large-scale incidents (see later).

Over 25% of all recoveries of British ringed Guillemots are oiled (Table 2.10), but Bibby & Bourne (1971,1972) recorded between 80-90% of all Guillemots found during Beached Birds Surveys to be oiled. Although the evidence is circumstantial, it seems likely that oil pollution must reduce adult survival in British waters. Flegg (1975) considers it likely that oil pollution is the reason for the decline in auk numbers in southern Britain.

Weather: Weather can affect Guillemot mortality in two main ways; firstly, an indirect effect in arctic regions is frost shattering of rocks, which results in rockfalls. Tuck (1960), Swartz (1966) and Uspenski (1956) all record Guillemots killed at their breeding colonies by rockfalls. Rockfalls were very infrequent on Skomer. Secondly, probably the most important effect of weather is the way in which it affects birds' foraging. I have shown that heavy seas reduce the rate at which adult Guillemots provision their chicks with food (Chapter 4), and it seems likely that adults also experience difficulty in obtaining food for themselves under stormy conditions. Fig.2.4 shows the pattern of storm frequency each month around the British

Fig.2.4. Number of recoveries of adult Guillemots each month (n = 78)(histogram). The shaded area represents 10 individuals recovered in October 1969 as a result of the Seabird Wreck (see text). Monthly gale frequency average number of days/month with gales is also shown (●-●).



Isles, and the number of recoveries of British ringed Guillemots of four years and older, 'found dead'. Most Guillemot mortality occurs during the winter, when storms are most frequent, but the relationship between these two variables on a monthly basis is poor (r = 0.248 10 df NS). However, the short-term effect of severe sea conditions can sometimes be dramatic, and most of the 'wrecks' of Guillemots that have been recorded, have been preceded by stormy conditions. Bailey & Davenport (1972) estimated that 100,000 Common Guillemots died during April 1970 on the Alaska Peninsula following severe weather. Holdgate (1971) has listed auk wrecks in the British Isles that occurred between 1856-1941, and has discussed the wreck in which over 16,000 Common Guillemots died in the Irish Sea in autumn 1969. In this incident storms preceded most of the Guillemot mortality; but toxic chemicals may also have been implicated in this instance. Wrecks of Common Guillemots associated with storms have also been recorded by Baxter & Rintoul (1953), Austin & Kuroda (1953), Salomonsen (1935), Longworth (in Murie 1959), Jewett et.al. (1953) and Dement'ev et.al. (1968:216), and in arctic regions wrecks and eruptions of Brunnich's Guillemots are often associated with heavy ice formation, which would also disrupt feeding (Fleming 1907, Freuchen & Salomonsen 1958, Preble & McAtee 1923, Snyder 1957, Tuck 1960, Uspenski 1956). There is good evidence that Guillemots experience difficulty in finding sufficient food during stormy conditions (see Chapter 4), and wrecked birds are often emaciated, having lost 25-40% of their weight, and lack fat deposits (Bailey & Davenport 1972, Holdgate 1971). However, the precise relationship between Guillemots and their prey species under stormy conditions, and the factors which determine whether or not birds suffer a heavy mortality, have yet to be elucidated.

Most of the 'natural' mortality of adult Guillemots occurs in February and March (Fig.2.4), after the worst weather is over. Mortality may be high at this time because birds are under a certain amount of pressure to procure sufficient food reserves to enable them to breed.

Predation: A variety of animal species have been recorded preying on adult Guillemots, and large colonies may preferentially attract predators. Table 2.11 presents a list of avian and mammalian predators recorded killing and feeding on Common and Brunnich's Guillemots. The Arctic Fox is the only mammalian predator, and this species may act most often as a scavanger rather than an actual predator. Potts (1969) twice observed Grey Seals *Halichoerus grypus* taking Common Puffins; and although I can find no record of seals taking *Uria* spp., at several colonies on Skomer I noted birds with one foot missing, suggesting predatory attempts by seals or fish. There are a number of records of fish preying on alcids, Bigelow & Welsh (1925), Glegg (1945), Scheffer (1942), Pitman (1957) all recorded marine birds in the diet of various fish species, notably Gadids (Heslington 1894, Tavener 1943) and Angler Fish *Lophius piscatorious* (Bigelow & Welsh 1925). Notwithstanding these records it is difficult to judge the impact of predation on Guillemot populations, but it seems unlikely that predation seriously affects numbers, except on a local scale. In the Baltic, Black Guillemots have decreased because of predation by introduced Mink *Mustela.vison*, but this represents a slightly unusual situation (Olsson 1974).

Toxic chemicals: There is little hard evidence that pesticides or other toxic chemicals have had any effect on Guillemot populations (Gress *et.al.* 1971, Parslow 1973, Scott *et.al.*, in press). Victims of the Irish Seabird wreck in 1969 had high levels of PCBs in their body tissues, but it is not clear

Table 2.11. Predation: animal species recorded preying on adult Guillemots (*Uria* spp.).

Species	Source
Eagle Owl *Bubo bubo*	Willoghs 1974
Sea Eagle *Haliaetus albicilla*	Willoghs 1961
Bald Eagle *H.leucocephalus*	Murie 1940
Golden Eagle *Aquila çrysaeotus*	Wormell 1965, Swartz 1966
Rough Legged Buzzard *Buteo lagopus*	Tuck 1960
Gyr Falcon *Falco rusticolus*	Dement'ev *et.al* 1966
Peregine Falcon *F.peregrinus*	Swartz 1966
Great Skua *Catharacta skua*	Bayes *et.al* 1964
Arctic Fox *Alopex lagopus*	Tuck 1960, Lovenskiold 1954 Murie 1959, Fay & Cade 1959 Uspenski 1956.

whether their presence affected Guillemot mortality (Holdgate 1971, Moriarty 1975).

Other factors: There is no evidence of epidemic disease in *Uria* spp., nor are parasites considered important as mortality agents (Uspenski 1956, Tuck 1960).

(g) Survival to breeding age. The age distribution of Guillemots ringed as chicks and recovered within the first six years of life, for eight sets of data are presented in Table 2.12. The composite survival rates, up to five years old, derived from these data are shown in Table 2.12. Survival values fall between 27% in southern Britain, where numbers are either stable or decreasing, and 41% in Witless Bay, Canada where numbers are increasing (Tuck 1960). As a comparison, I examined ringing recoveries of Brunnich's Guillemots ringed as chicks in Canada (from L.M. Tuck & R.V. Maher, pers.comm.) and Greenland (Salomonsen 1952-1971). Survival up to five years for both sets of data are presented in Table 2.12. This shows that for birds ringed on Bylot Island, Canada, and in Greenland 1958-1962, survival rates are similar to Common Guillemots. However, at Cape Wolstenholme, Canada, survival to five years was high; 53%, while in Greenland 1965-1969 it was low; 19%.

Return of the young birds to Skomer: An alternative method of determining survival to breeding age involves colour-marking chicks at study colonies and recording the number which survive to breed. Since the present study was a short-term one, it was not possible to determine survival by this method. However, the return of young birds prior to breeding, is of some interest. The colour-marking method assumes that young birds are strongly philopatric, and to some extent faithful to the same part of the colony in

Table 2.12. Survival estimates of Common and Brunnich's Guillemots to the fifth year.

Area	No.of recoveries each year					Survival	S.E.	Ringing	Source
	0-1	1-2	2-3	3-4	4-5	Estimate		years	
COMMON GUILLEMOT									
Witless Bay,Canada	169	73	43	13	3	41.1	2.0%	1951-69	This study[a]
First Is.Canada	202	73	23	15	6	37.1	2.0%	1953-58	This study[a]
O.Gannet Is.Canada	32	6	3	2	0	29.5	6.0%	1952-53	This study[a]
Quebec,N.Shore	20	8	2	2	0	36.0	6.0%	1923-43	This study[a]
Southern Britain	51	14	4	0	1	27.0	4.0%	1948-59	This study[b]
Heligoland	117	17	10	3	6	31.3	3.0%	1933-43	Mead 1974
Heligoland	113	12	10	2	6	30.2	3.0%	1955-66	Mead 1974
Norway	117	24	10	5	1	28.6	3.0%	1958-69	This study[c]
BRUNNICH'S GULLEMOT									
C.Wolstenholme,Canada	19	17	14	3	2	52.9	4.0%	1955	This study[a]
Bylot Is.Canada	37	10	2	2	2	34.5	5.0%	1957	This study[a]
Greenland	25	9	5	0	0	33.0	6.0%	1958-62	This study[d]
Greenland	58	8	3	1	0	19.0	4.0%	1965-69	This study[d]

Notes: Survival estimates calculated using Lack's (1951) method.
Data from various sources: a. L.M.Tuck & R.V.Maher pers.comm.b.B.T.O., c.Holgersen 1961 and earlier references. d.Salomonsen (1952-1971).

which they were reared. My observations of colour-marked birds on Skomer show that three year old birds occur in clubs, visit breeding ledges other than those on which they were reared, and obtain sites in the natal colony. For example, two three year old birds returned to their natal ledge as a pair and unsuccessfully attempted to obtain a site there (see Chapter 5 for behaviour details), they eventually settled at a site about two metres away from where they were reared, but did not breed. In the analysis of British ringing recoveries I found only two instances out of 270 chicks ringed, of birds ringed at one colony and recovered at breeding age at another. Both examples were of birds from the Farne Islands, northern England, ringed in 1956. The first recovery was of a bird recaptured on Lundy Island (about 340 miles south west) in June 1966, and the second was recaptured at North Berwick, about 40 miles north, in June 1972. However, the chance of recapturing birds at breeding colonies is low, so that records are biased against colony-interchange information. During the course of the present study I had no sight records of birds marked as chicks from other Guillemot colonies, including nearby Skokholm.

As already stated, immature birds congregate in clubs at the foot of cliffs, below breeding colonies. I recorded two and three year old birds, and on one occasion a four year old bird in clubs. (The four year old was one of ten chicks which had been ringed in 1971 prior to my study; it was not colour-marked, but I was able to read its B.T.O. ring number). A larger proportion of three year olds than two year olds visited Skomer. In 1974 and 1975 a maximum of 3 out of 87 ringed (3.4%) and 2/92 (2.2%) respectively returned at two years old. In 1975 the maximum number of three year old birds seen in one day was 15, which represents a mimimum survival rate of 17.2% of 87 chicks ringed. On one ledge I was able to view birds at close range, and it was possible to read B.T.O. ring numbers of birds ringed as chicks. At this ledge three different individuals out of seven originally ringed (43%) were recorded. Thus survival may generally be much higher than 17%. In addition, it is not known whether all birds return to the colony at three years old; it seems likely that a higher proportion return in their fourth and fifth years. Thus my estimate of 17% survival to the third year is clearly a minimum one.

Three year old birds return to the colony earlier in the year than two year olds, and were recorded in early May, but in 1974 and 1975 two year old birds were not seen until 8 June and 27 May respectively. In 1974 and 1975 two year olds were observed on a total of thirteen occasions, and on only one of these was a bird seen on a breeding ledge. This was towards the end of the season (July 14); the bird appeared nervous and remained on the ledge for only a few minutes before flying off. All other records of two year olds were of birds in clubs or on the sea near clubs. Three year old birds were recorded on breeding ledges, clubs and on the sea, but were observed on ledges with increasing frequency through the season. The relationship between the proportion of all birds seen on ledges (number on ledges / total seen - excluding birds on the sea) and date is shown in Fig.2.5. The relationship was significant ($d = 5.3$ $P<0.001$, Test for linear trend in proportion, Snedecor & Cochran 1967:246). The pattern of return and integration into the colony may be as follows; birds return for the first time at two, or three years, spend most of their first season in clubs, but may make visits to breeding ledges late in the season. Three year old birds, and presumably older age classes spend an increasing amount

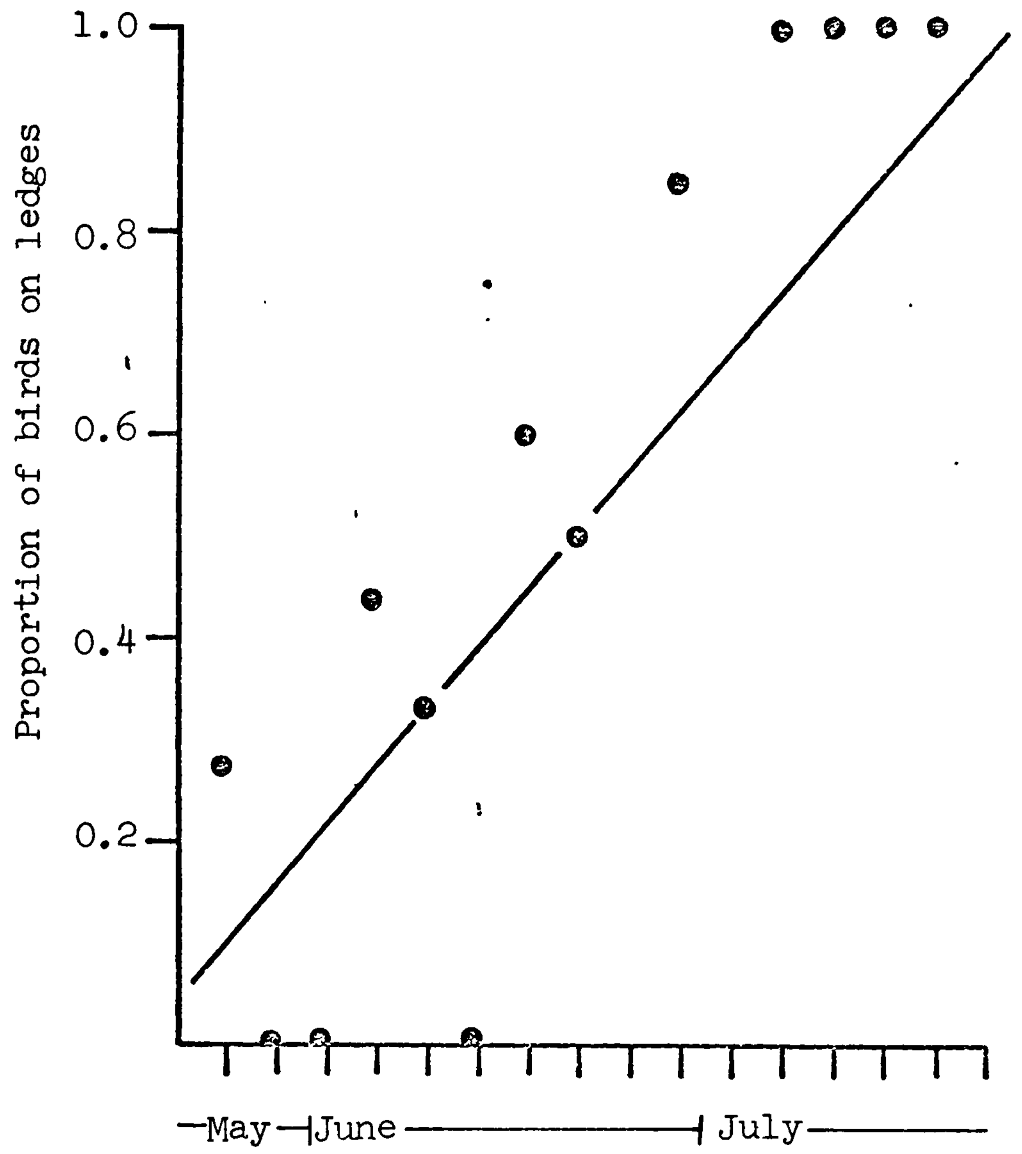


Fig. 2.5. Proportion of three year old Guillemots recorded in clubs and on ledges seen on ledges through the 1975 season. An increasing proportion occur on ledges through the season, and in July all records are of birds on ledges. The relationship is significant: d = 5.3 P<0.001 (test for linear trend in proportion Snedecor & Cochran 1967:246).

of time on breeding ledges and eventually secure a site where they will later breed.

Fig. 2.6 shows the seasonal change in numbers of birds in five main clubs around Skomer. Numbers were lowest early and late in the season, and reached a peak in early June. The decline in numbers after mid-June could have been due in part, at least, to birds moving on to breeding ledges. The total number of club birds around Skomer was recorded on four occasions, the maximum figure was 649, and comprised two, three and four year olds, and possibly older birds. The club population therefore represents the output of earlier years breeding population, and if the age structure of clubs were known, this could provide a useful index of immature survival. In several hundred hours of observations I recorded only two instances of known breeding birds in clubs, in both cases the birds had failed in their breeding attempt. Observations of two and three year old birds far outnumber the records of breeding birds. For example, in 1975 I made a total of 89 sightings of two and three year old birds (out of a total of 87 + 92 = 179 ringed), but only two sightings of adult breeding birds (out of a total of 229 ringed). It seems likely that most individuals in clubs are non-breeding immature birds. To help verify this I captured individuals in clubs during June 1975, and of 18 birds none possessed a brood patch, whereas every bird captured on a breeding ledge (n = 16) during the same period, possessed one.

<u>First year mortality</u>: The first year of a bird's life covers the period from fledging until July 1st the following year.

<u>Losses at fledging</u>: During four seasons I observed a total of 145 chicks fledging, of these only three (2.1%) failed to fledge successfully. Two were predated by Great Black-backed Gulls, and one fell in among rocks at the foot

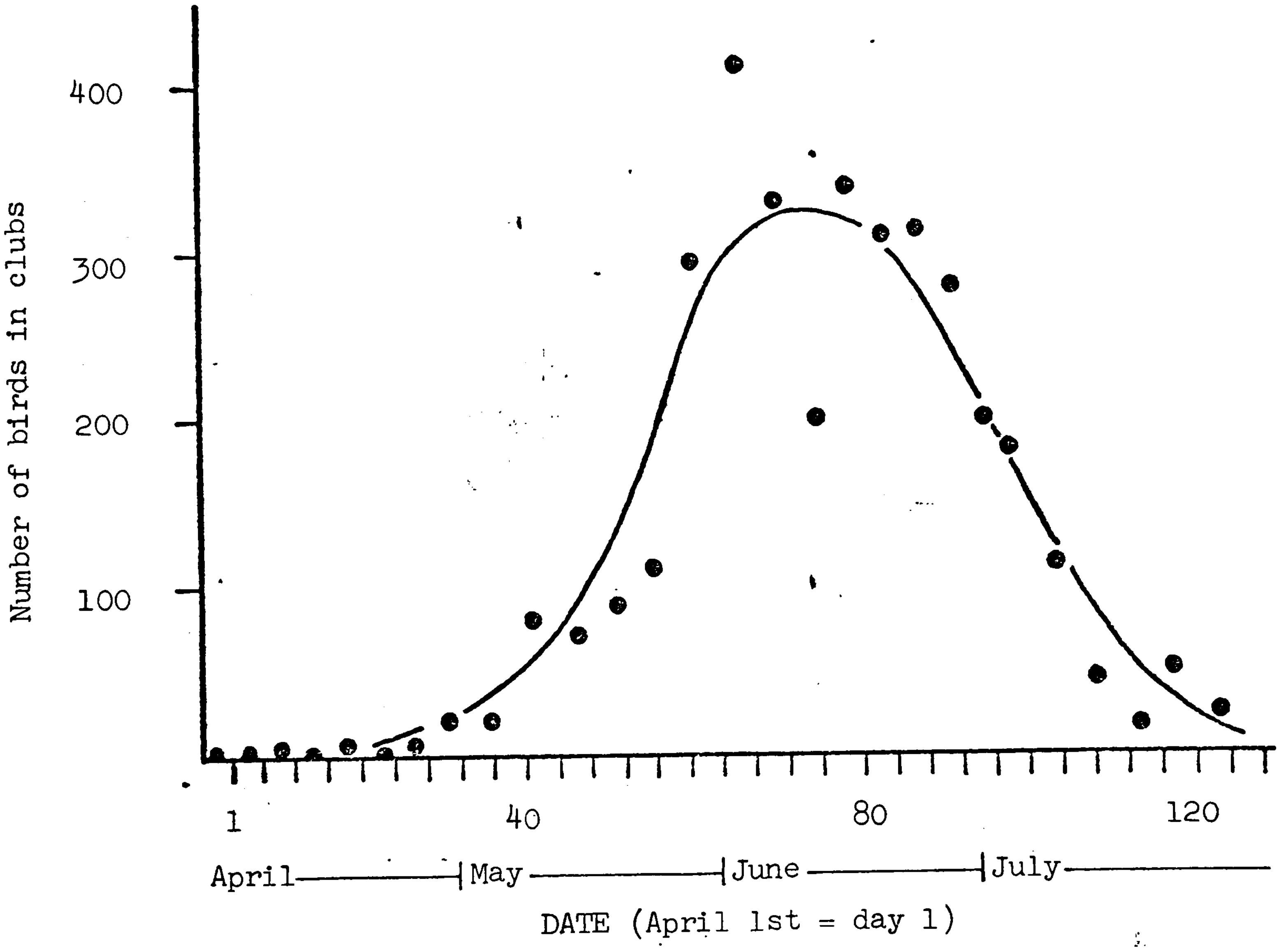


Fig.2.6. Seasonal changes in the number of birds counted in five main clubs around Skomer throughout the season. Each point represents a four-day average.

of the cliff and did not reappear. Thus losses through predation at fledging were low (c.f. Greenwood 1964, Williams 1975). Swartz (1966) and Greenwood (1964) recorded that the most common cause of chick-loss at fledging was due to parents and off-spring failing to link up on the sea; I recorded only five instances where chicks were unattended by adults. These birds (not included in the 145 total above) were not observed fledging, and may have been knocked from the ledge rather than having gone through the normal pre-fledging behaviour (Greenwood 1964). When chicks fledged I recorded the number of adults accompanying them out to sea. Depending upon light conditions, chicks could be watched for distances up to 0.5 miles (0.8km), as they left the vicinity of the colony. In 145 observations of chicks 137 (95%) were accompanied by a single adult, 6 (4%) by two adults, and 2 (1%) by three adults. Although several adults generally showed interest in chicks on the water, all but one bird (presumably the chick's parent) usually lost interest as they swam away from the colony out to sea. There is good evidence that this bird is the male parent (see Chapter 4), and the two may remain together for as long as 12 weeks (see Chapter 4).

I have presented the seasonal distribution of recoveries of Guillemots ringed as chicks and 'found dead' in the first 12 months of life (Fig.2.7). This shows that there is a peak of recoveries during August, September and October. This suggests that most mortality occurs while chicks are still dependent upon their parent, or shortly after they have become independent. Mortality of young birds while still dependent on the adult may occur if the male parent, which is flightless while undergoing moult during this period (see Appendix II) experiences difficulty in obtaining sufficient food for

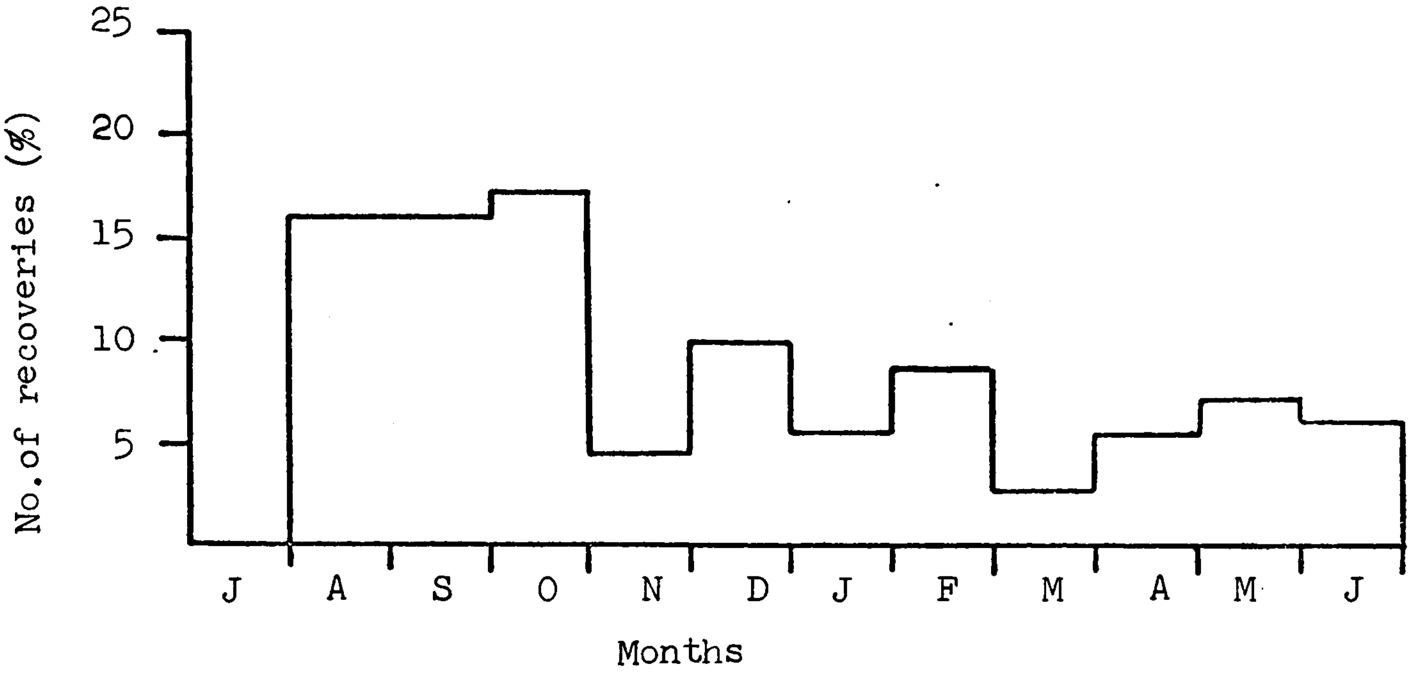


Fig. 2.7. Seasonal changes in the number of recoveries of Guillemots ringed as chicks, and recovered during their first year of life (n = 110).

itself and its growing chick. Some chicks may fail to make the transition from dependence to independence, because they find difficulty in obtaining food (Recher & Recher 1969, Orians 1969, Dunn 1972). This effect would be exacerbated by the seasonal increase in storm frequency (see Fig.2.4).

Synthesis

The main results relevant to this section can be summarized as follows; breeding success on Skomer over three years averaged 0.7 chicks/pair. Adult survival on Skomer varied between 88-93%. Survival of birds to breeding age, calculated from ringing recoveries varied between 27% in southern England to 41% in Canada. Guillemot populations in southern Britain have declined, and may either be declining or stable at present; in contrast, numbers have increased in north east Canada.

I have calculated the survival rate of birds to breeding age for a number of different levels of adult survival (assuming breeding-success to be 0.7 chicks/pair), Fig.2.8 for (A) a population increasing at 5% p.a., (B) a stable population, and (C) a population decreasing at 5% p.a. For example, if adult survival is 90% 100 pairs of Guillemots must produce 70 chicks and 20 (28.5%) of these must survive to maintain a stable population. However, if adult survival is 94% only 12 birds (17%) need survive to breeding age to maintain stability.

Thus, since we know that the Skomer population is stable at present, and that adult survival is 90-94%, and breeding success is 70%, survival to breeding age must be in the order of 17-28%. A schematic representation of the Skomer population is shown in Fig.2.9. These figures emphasize the important role of adult survival in determining population changes. The

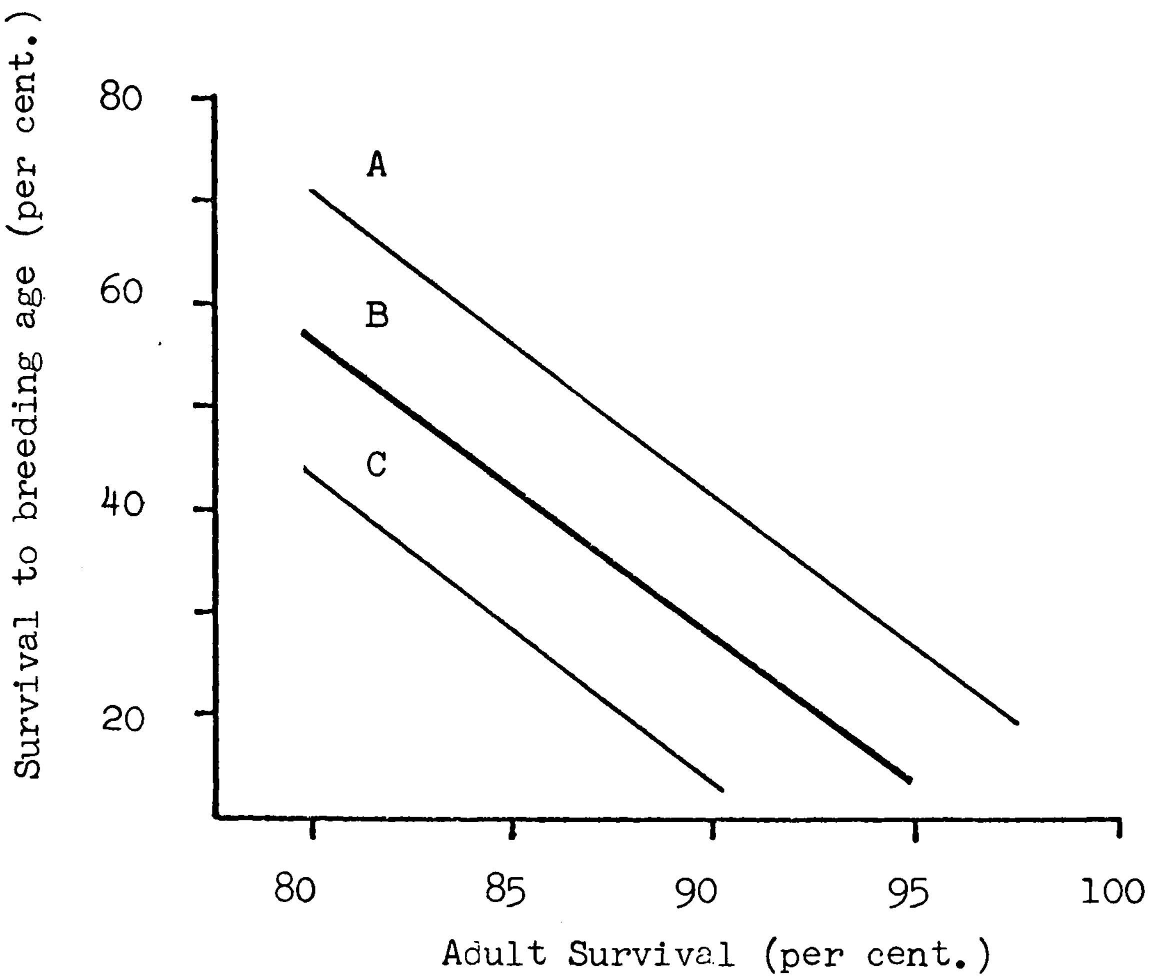


Fig.2.8 . Relationship between adult survival and survival to breeding age (5), assuming a breeding success of 0.7 chicks/pair, at three population states:- (A) Increasing at 5% pa., (B)Stable,and (C) Decreasing at 5% pa. As an example, in the stable population (middle heavy line:B),if adult survival=90%,survival to breeding age must be 28% to maintain stability. If the population was declining at a rate of 5% pa (lower line:C) and adult survival was 90%, survival to breeding age must be about 12%.

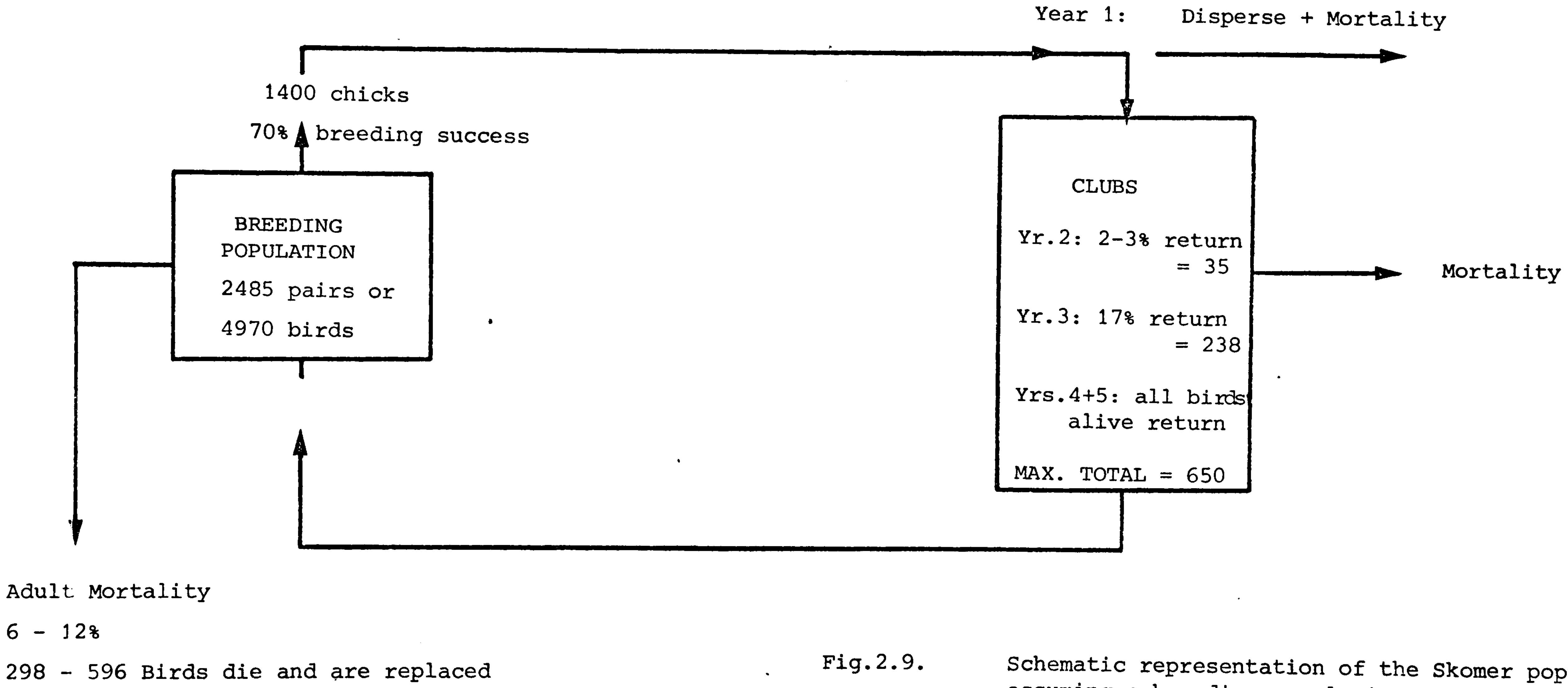


Fig.2.9. Schematic representation of the Skomer population, assuming a breeding population of 2485 pairs, and that numbers are stable (based on data for population parameters presented in the text)

situation on Skomer in 1975 serves as a good example. The breeding population fell by about 12% between 1974 and 1975. This reduction may have been due to a doubling of mortality rate between 1973-1974 (6%) and 1974-1975 (12%), or to low recruitment. Adult survival may have been reduced by a relatively small oil spill around Skomer in late April 1975 (Evans 1975), in which a minimum of 100 Guillemots died. Incidents of this nature, occurring say, every few years may be sufficient to reduce adult survival to such a level that recovery of the Skomer population is prevented.

Population Changes in Other Areas

During the present century Common Guillemots have shown spectacular increases in two regions; the Farallon Island, California (Ainley & Lewis 1974) and off Newfoundland (Tuck 1960). Guillemot numbers were at a low of an estimated 6000-7000 birds in the 1920's on the Farallons. Numbers subsequently remained similar until 1959 when they increased rapidly, so that by 1972 a total of 20,500 birds were counted. This increase represents an average annual increase of 9.2%. On Funk Island, Newfoundland, numbers were estimated at 10,000 pairs in 1936, increasing to 500,000 in 1959; an average annual increase of 19.3%. Similarly, on Green Island, Newfoundland, Guillemots first started to breed in 1936 and by 1950 numbers had reached 10,000 pairs, and by 1959 were estimated at 50,000 pairs; the increase between 1950-1959 averaged 16.6% per year.

Ringing recoveries of Common Guillemots from the Witless Bay area, Newfoundland, for the period 1951-1969 (Table 2.12) show that survival up to 5 years was higher than any other area, at 41%, and was nearly as high at First Island, Witless Bay, at 37%. This must have been an important factor mediating the increase in Guillemot numbers in this area. Unfortunately, there are insufficient recoveries of adult Guillemots from these areas to calculate adult survival - but from what has already been said, it follows that it must have been high.

I have already presented a number of population parameters for Common Guillemots in different areas, and it is possible to calculate intrinsic rates of increase from these figures, (see Leslie 1966) and to determine whether the observed increases in North America are due to intrinsic increase or to immigration. Using population parameters presented earlier, the highest values would result in an average annual percentage increase of 6% (Adult survival : 94%, Survival to 5 years : 45%, Breeding-success : 70%) (see Fig.2.8). This figure is lower than those for increases in Newfoundland, but is similar to that for the Farallons. Moreover, if adult survival was marginally higher, and if individuals commenced breeding at an earlier age (as has been recorded in some pinnipedia (Kenyon & Scheffer 1954, Carrick _et.al._ 1962), an intrinsic rate of increase of 9% may be feasible. The observed increases on Funk and Green Island are considerably higher than this, suggesting that immigration from other areas may have contributed to the increases.

Conclusions

Breeding success in Guillemots on Skomer is similar to that recorded for other alcids, chicks fledge at weights which are at least as good as in other areas (see Chapter 4), and losses at fledging are small. Mortality of immature birds is high in the first few months after fledging, and is higher than adult breeding birds. As yet there is little information on the survival of birds to breeding age or the age at which Guillemots first start to breed. Figures for immature survival are probably less important than those for adult survival in affecting population changes. A small change in adult survival can rapidly affect the rate and direction of population change.

Lack (1954) considered food to be the most important density-dependent factor in population regulation, and Ashmole (1971) suggested that in seabirds competition and density-dependent mortality may occur outside the breeding season when adult and immature birds compete for food: adults may be more proficient and dominant to immature birds at feeding sites, eventually resulting in a higher mortality of younger birds. However, there is little evidence, either for or against density-dependent regulation of seabird numbers (Ashmole 1971).

Nest-sites clearly are not limiting on Skomer (see Chapter 3), and neither predation nor disease appear to be important mortality agents. ~~However, oiling may operate in a density dependent manner~~. Minor oil-spills around Skomer during the breeding season are not infrequent, and during the last 12 years have occurred at a rate of about one per year (Skomer Island records). Small-scale oil incidents of this type resulting in a small decrease in adult survival could prevent the population from increasing.

A further factor which may be important in maintaining a stable population on Skomer at the present time, is the age at which birds first start to breed. Since the population is reduced one might expect young birds to commence breeding at an earlier age than in areas where numbers are high (Carrick et.al. 1962). Clearly more data on adult and immature survival rates are necessary to provide a better understanding of Guillemot population changes on Skomer.

Summary

Between 1934 and 1975 an estimated 62% decrease in the Skomer Guillemot population occurred. The population in 1975 was estimated at about 2,200 pairs.

Data for a number of population parameters for the Common Guillemot are presented. These are derived from a study of marked birds on Skomer, and from recoveries of birds ringed in different parts of the species' range. Results are compared with those for other alcids, particularly Brunnich's Guillemot and the Razorbill.

Breeding success on Skomer over three years averaged 0.7 chicks per pair. Adult survival on Skomer was 93% in 1974 and 88% in 1975. The lower rate in 1975 may have been due to a small oil spill early in the year. Mortality factors are reviewed; two main possibilities for the reduction in numbers in southern Britain occur; oil pollution and changes in the marine environment resulting in a reduction of prey species.

The age at which Common Guillemots first start to breed is not known, but it is thought to be at about five years. Survival rates for birds up to five years old were calculated from ringing recoveries, and varied between 27% in southern Britain (where numbers are stable or decreasing) and 41% in north-east Canada (where numbers may be increasing). Guillemots first return to Skomer in their second year, and a higher proportion in their third year. These birds congregate at specific 'club' sites at the foot of breeding cliffs. Three year old birds spend an increasing amount of time through the breeding season on breeding ledges.

It is calculated that with an average adult survival rate of 90% on Skomer, 100 pairs of Guillemots must produce 70 chicks and 20 (28.5%) of these must survive to breeding age to maintain a stable population.

CHAPTER 3

THE EFFECT OF HABITAT AND DENSITY ON BREEDING SUCCESS IN GUILLEMOTS

Introduction

A large number of factors have been shown to contribute to breeding sucess. These include; age and physical condition of individuals, timing of breeding, and in colonial species position in the colony, colony size and density. Other factors include food availability, competition, predation, social factors, nest-site and habitat quality (Young 1963b, Horn 1968, Perrins 1970, Coulson 1971, Tenaza 1971). Many of these factors are inter-correlated, for example, among Shags on the Farne Islands, young birds attach themselves to the periphery of groups and are forced to nest in sub-optimal areas where they produce less offspring than older birds. A massive reduction in the population enabled young birds to take over high quality sites which had been left vacant, and as a result increased their breeding success to a level similar to older birds (Coulson 1970). Thus in this situation age, social factors and nest-site quality interacted to determine the level of breeding success achieved.

The relationships between habitat and breeding success are not well known and the factors which determine a species' optimal breeding habitat have been investigated for only a few species. For example, the Grey Partridge Perdix perdix (Blank & Southwood 1967, 1969), and the Common Puffin (Nettleship 1972). In the Puffin breeding success was highest among those individuals breeding on sloping habitat and lowest among those on level ground. On the sloping ground Puffins were less vulnerable to disturbance and predation of eggs by gulls during incubation, and later to robbery of food brought in for the chicks.

The object of the present study was to examine the relationship between habitat, group density and breeding success in the Common Guillemot.

Common Guillemots breed in large colonies at high densities, and have been recorded breeding on flat tops, on stacks and low-lying islands, on broad and narrow ledges, and less frequently, under boulders, in crevices and caves (Tuck 1960, Parslow 1966, and see Chapter 5). Maximum densities are achieved on broad flat areas. The adaptive nature of high density nesting in the Common Guillemot has been commented on by Belopolski (1957), and others, and Kaftanovski (1938) provided some data which indicated that Common Guillemots were most productive at high densities. I decided to make a more detailed study of breeding success and density to test Kaftanovski's hypothesis. Thus the first question I wanted to answer was: 'at what densities are Guillemots most productive?'. This involved an investigation of factors which determined the most productive density. The second question, which is related to the first, concerned differences in the distribution of Guillemots within Skomer colonies between the relatively high population level in 1934, and the lower 1975 level. There is good evidence that a change in distribution accompanied or followed the decline in numbers (see Chapter 2). Since the second question is only really answerable after dealing with the first, this chapter is divided into two parts, which deal with each question in turn.

Section I : Breeding Success at Different Densities

Methods

(a) Breeding success. Details of the methods used to record breeding success, and other aspects of breeding biology have been presented in Chapter 2. These are briefly as follows; I used a large-scale photograph of each colony and plotted the position of eggs and recorded the date as eggs were laid. Study colonies were visited at least once a day throughout the period April - late July, and the fate of eggs and chicks recorded. Thus, I had information on the onset and pattern of laying, spread of laying and breeding success. At all colonies I took great care not to disturb the birds. In some areas I was able to examine ledges through a telescope at distances which did not affect the birds. In other areas I used hides, which enabled me to make close inspection of the ledges, and which I could enter without disturbing the birds. In very dense colonies, where birds were packed close together, it was not easy to collect information since birds standing around either at the edge of the colony or beside their mate obstructed my view. To overcome this difficulty I visited dense colonies at dusk in the evening when all non-incubating or brooding birds had left the colony (see Appendix I). With less birds at the colony it was possible to make observations more easily.

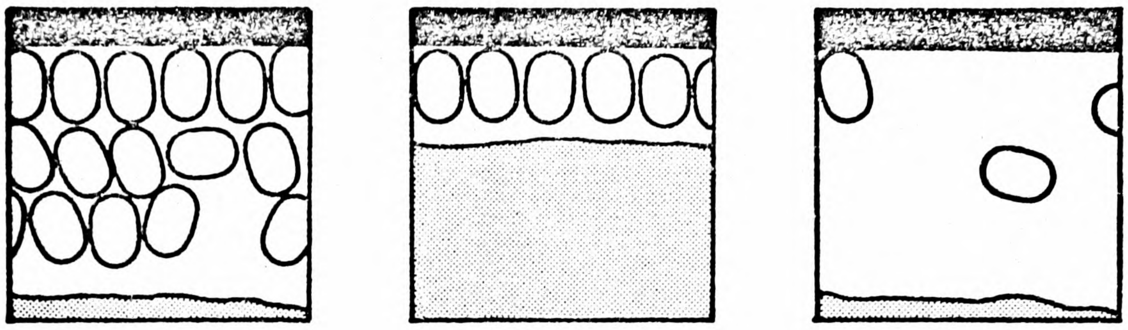
Because of the difficulty of placing each individual Guillemot nest-site into some sort of category regarding its characteristics, such as number of neighbours, location of neighbours, etc., I have compared the breeding success of complete sub-colonies breeding at different average densities, on more or less uniform habitat. Observations were made of Guillemots breeding in three broad, but distinct categories: (a) at high densities on broad ledges

(b) at high densities on narrow ledges, and (c) at low densities on broad ledges. The spatial distribution in each situation is shown in Fig.3.1. These will be referred to as (a) Dense (b) Medium and (c) Sparse, respectively. Breeding success was recorded at two Dense groups, one on the Wick, containing 31 pairs, and the other, called Little Will Bench, at the north-west end of the island, with 113 pairs. Three Medium groups were all situated on the Main Wick ledge (Fig.3.2) and contained 40, 59 and 70 pairs respectively. A single Sparse group contained 26 pairs, and was located on the south-west part of the island.

The density of incubating birds breeding in Medium density groups was measured from photographs, taken from above the groups. On broad ledges for both Dense and Sparse groups I estimated the density of birds in terms of incubating birds per unit area of ledge. The densities in the three different categories were as follows; Dense: more than 10 birds / m^2, Medium: 5.5 birds / m^2, and Sparse: 2.5 birds / m^2. In each case 'birds' refer to incubating individuals for density measurements.

For reasons which I will discuss later (see Discussion), Medium groups were the most frequent on Skomer, and both Dense and Sparse were infrequent.

(b) Factors affecting breeding success. A number of workers have commented on the predation of Guillemot eggs by avian predators, mainly Larus gulls, but also Corvids (Johnson 1938, 1941, Kaftanovski 1938, Swartz 1966). Large numbers of gulls breed on Skomer. The numbers of Great Black-backed Gulls have been controlled sporadically since 1946 and regularly since 1960, and numbers have remained at about 100-150 pairs since 1946. I made observations for over 100 hours at a Guillemot colony on the north coast of Skomer, and



DENSE MEDIUM SPARSE

Fig.3.1. Spatial distribution of Guillemots at three different densities viewed from above. Oval shapes = incubating birds, black area = cliff wall, white area = ledge, stippled area = sea. Dense = more than 10 birds/m^2, Medium = 5.5 birds/m^2, and Sparse = 2.5 birds/m^2.

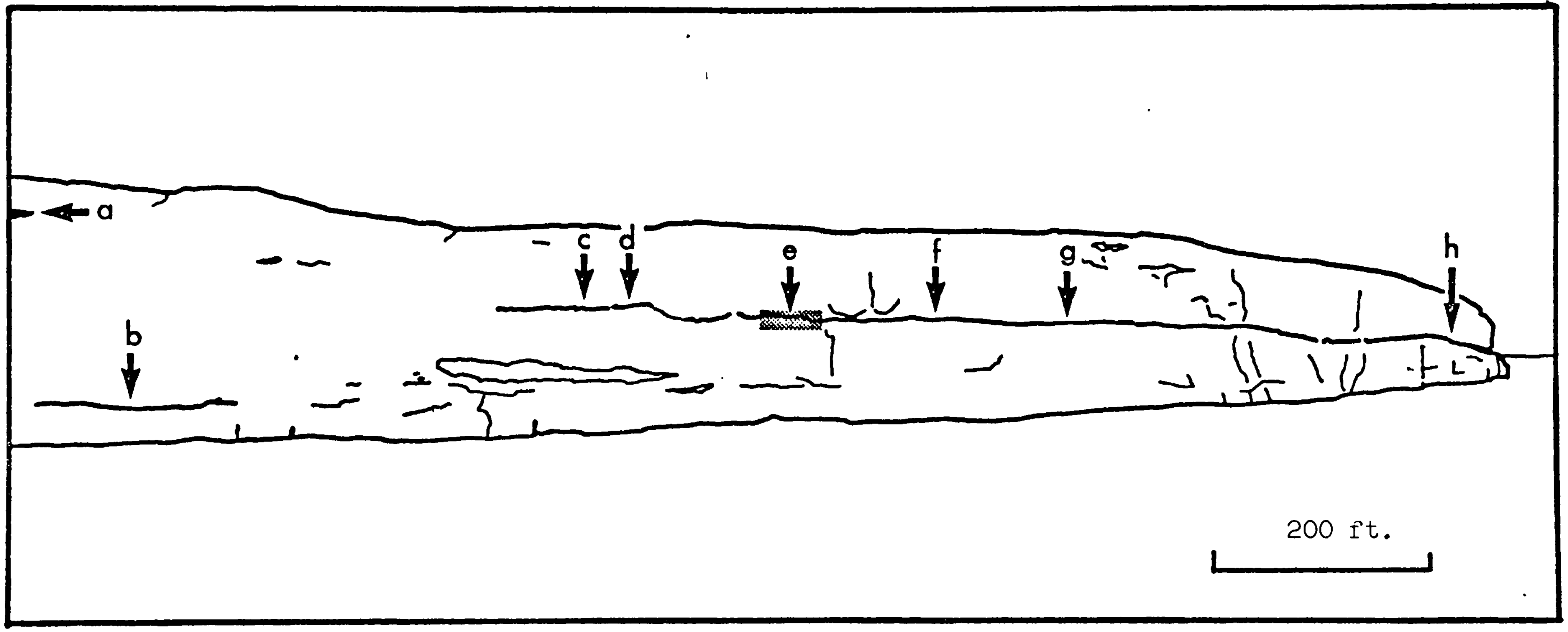


Fig. 3.2. The Wick Guillemot colony viewed from the side,looking south. Arrows pinpoint sub-colonies mentioned in the text; (a) top crack, (b) Wick Corner, (c) Bee, (d) Wasp,(e) Twin,(f) Lockley, (g) Hump, (h) Wick Blind. Sub-colonies c - h all lie on the Main ledge, and all of these are Medium density groups, except for (h) which is a Dense group. The shaded area around sub-colony (e) is the area shown in Fig.3.7.

recorded the method employed by Great Black-backed Gulls to predate Guillemot eggs. In addition I made a total of 30 and 40 hours observations at one Dense study group and the Sparse group, respectively, where both Great Black-backed Gulls and Herring Gulls were observed near breeding Guillemots.

In order to measure a number of aspects of the birds' behaviour which might affect breeding success, I made the following observations:-

(a) Casual observations indicated that the last chick to fledge from a ledge, if left alone with its parent, was more likely to disappear during the day, indicating that it had been predated or had fallen from the ledge, than chicks surrounded by neighbours earlier in the nestling period. To test this I compared the number of chicks that disappeared during the day in two situations a) the last chick on the ledge, and b) in the mid-nestling period, before any chicks had fledged. The data for the 'control' b) were from the same medium density colonies as a), and were from the mid-nestling period 24-28 June (5 days) 1974. Thus, the sample was 111 chicks x 5 days = 555 chick-days. The sample for last-chicks a) was 11 chicks over 11 days = 11 chick-days.

(b) On a small number of occasions (15 in 3 years) I recorded birds leaving their eggs unattended; this happened as a result of the close approach of a boat or human, and sometimes for no apparent reason. I compared the length of time that exposed eggs survived in two different situations; first, among other birds at Medium density (seven observations), and second, at Sparse density, where eggs were left exposed virtually on an open ledge (eight observations). Birds left their eggs in the second situation in response to some disturbance, and I have only included those observations where I actually observed the bird leave. In the first situation it was more usual to notice the unattended egg, between neighbouring birds, as I made daily checks. Thus, in this situation the egg may have been exposed for as long as 24 hours before I noticed it. It was not clear why a single bird incubating among a line of others should desert its egg. I did not record any instances of birds in Dense groups abandoning eggs.

(c) The results of these observations (b, above) suggested additional ways in which I could investigate the role of density and the behaviour of Guillemots. Since Guillemots are reluctant to leave their eggs or chicks unattended, they have been variously referred to as confiding, tame or stupid (Bent 1919 and others), but it has generally been assumed that this is an anti-predator adaptation (Belopolski 1957). In order to investigate differences in 'nervousness' and tenacity of incubation among Guillemots breeding at different densities, I made observations of birds in Dense and Sparse groups. Observations were made for two 50 minute periods, on separate days at both groups. In each minute I watched one incubating bird and recorded whether it spent time sleeping or whether it performed Alarm-bowing (see Chapter 5). Alarm-bowing was recorded as a direct measure of 'nervousness', and in contrast, sleeping as a measure of 'contentment'. It seems unlikely that birds would spend much time sleeping if they were particularly nervous, or constantly on the look-out for predators. The same bird was not watched for two consecutive minutes, but during a fifty minute period the same bird may have been observed for a total of up to four minutes. As a control I made similar observations at another low-density colony. This colony differed from the Sparse group in that birds bred on very small, narrow ledges, in much the same sort of sites that Kittiwakes used. Observations at all three groups were made in the middle part of the day, and were conducted during overcast conditions, since I got the impression that Guillemots spent more time sleeping in direct sunlight.

Results

(a) Breeding success. I have compared the extent of egg or chick loss in Guillemots breeding at three different densities: Dense, Medium and Sparse. Data from different colonies of the same density have been combined in each case, and results are presented in Table 3.1. It can be seen from Table 3.1 that the greatest losses occurred in the Sparse group (70%), and least in the Dense group (12%). The differences between each group are statistically significant ($P < 0.01$). Overall breeding success, in terms of chicks fledged / pair (as a percentage) was 30% in the Sparse group, 74% in the Medium group and 88% in the Dense group.

(b) Reasons for differences in breeding success. In a number of species there is a relationship between breeding success and laying date, and birds which lay late in the season are less likely to produce offspring than early laying individuals. To test this I compared the overall breeding success of two Dense groups, Little Will Bench and Wick Blind (Table 3.2), which were the latest and earliest groups, respectively, to lay on Skomer in 1975. There was no significant difference in breeding success ($X^2 = 0.29$ 1df NS) between the groups. This indicates that the overall breeding success of groups does not decline through the season. Thus, I do not consider the median

Table 3.1. Breeding success at different densities.

Density	No.of pairs	No.of eggs/ chicks lost		Breeding Success (%)
		n	%	
Dense	144	18	12.5	87.5
Medium	169	44	26.0	73.9
Sparse	26	18	69.2	30.8

Notes: The difference in breeding success between each density was siginificant; chi-squared values for one d.f. = Dense vs Medium = 8.96 $P<0.01$, Dense vs Sparse = 42.5 $P<0.001$, Medium vs Sparse = 19.4 $P<0.001$.

laying date of different groups to be important in the present investigation.

However, within the breeding groups, birds which laid late were generally less successful than early birds (Fig.3.3). This is probably, in part at least, an artefact of the late layers being in a sparser, and therefore more vulnerable situation, towards the end of the season as successive birds lose or fledge chicks.

There is no relationship between density of breeding groups and onset of laying; two Dense groups were the earliest and latest, respectively, to lay, and the Medium and Sparse groups fell between these two extremes (Table 3.3). However, there was a marked relationship between group density and the spread of laying within a colony. I have used the period in which the mid 80% of all eggs were laid, in each study group, as a measure of synchrony. Fig.3.4 shows the relationship between spread of laying and density of breeding birds. Dense groups laid over the shortest time span, and the low density groups over the longest, the spread of laying in the low density groups being nearly twice that in the Dense groups. In Fig.3.4 I have included data from an additional low density colony, where birds bred on small, narrow ledges, as a comparison. Like the Sparse colony this also showed a large spread of laying.

(c) Predation. Observations on a single pair of Great Black-backed Gulls at a colony on the north coast of Skomer, showed that they were particularly adept at removing incubating or brooding Guillemots from their egg or chick. A single gull approached Guillemots incubating on open sites, where they could get within grabbing range without being pecked by the potential victim or any of its neighbours. Guillemots threatened and lunged at approaching gulls, and the gull frequently waited several minutes before rapidly striking

Table 3.2. Comparison of breeding success in two groups of Guillemots breeding at similar densities (Dense), but with different laying dates.

Group	Median laying date	No.of eggs laid	No.of eggs or chicks lost	Breeding Success (%)
Wick Blind	10th May	31	3	90.3
Little Will Bench	19th May	113	15	86.7

Notes: The difference in median laying dates was significant (X^2 = 20.18 1df $P<0.001$).

The difference in breeding success was not significant (X^2 = 0.28 1df NS).

Table 3.3. Breeding success at different sub-colonies in relation to density.

Site	Density	Median laying date	No.of pairs	No.of fledged chicks	Breeding success (%)
Little Will Bench	D	19th May	113	98	86.7
Wick Blind	D	12th May	31	28	90.3
Wick: Twin	M		59	45	76.3
Wick: Lockley	M		70	53	75.7
Wick: Hump	M		40	27	67.5
Inca	S	17th May	26	8	30.8

Notes: D = Dense, M = Medium, S = Sparse. The location of Wick sub-colonies are shown in Fig.3.2.

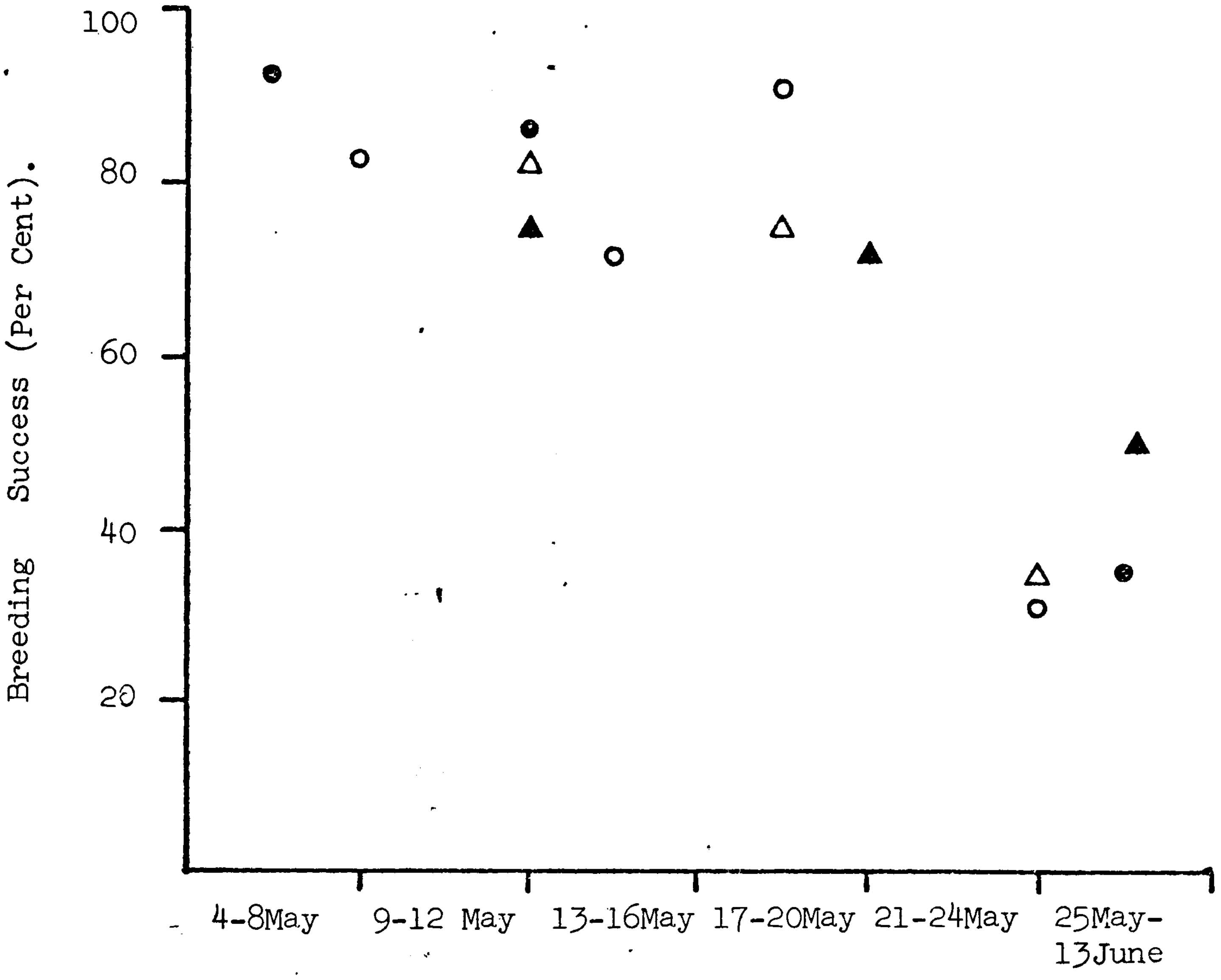


Fig.3.3. Breeding success in relation to laying date for two Medium density colonies in two years. Triangles = Bull Hole, Circles = Wick Corner, open symbols = 1974, closed = 1975 data. Sample sizes are greater than 10 for each point earlier than 25 May, after this sample sizes are between 2 - 8.

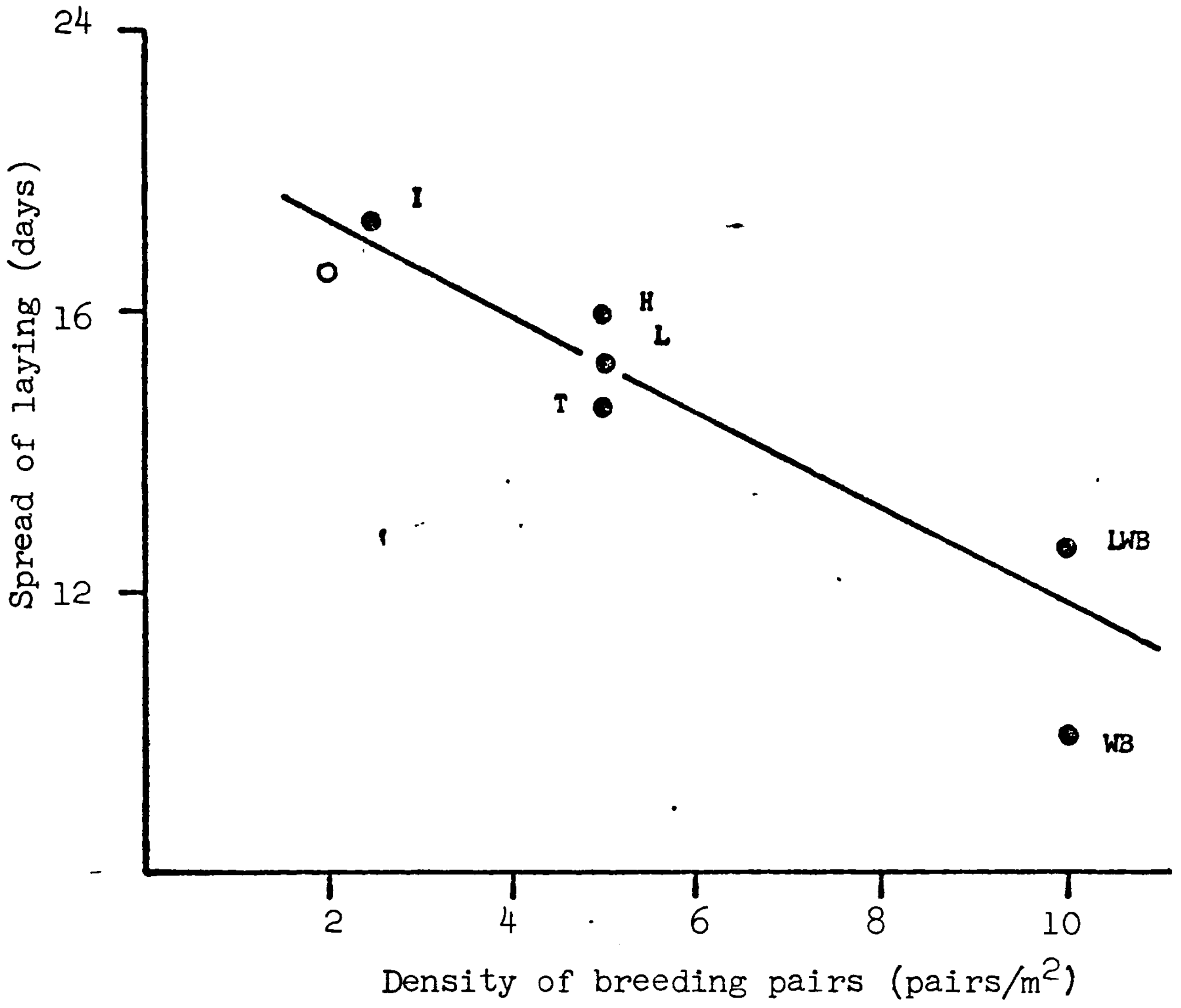


Fig.3.4. Relationship between breeding density and number of days over which 80% of the eggs in each group were laid. Regression equation: $y = -1.14x + 22.5$ ($r = -0.937$ $P<0.001$ $n = 7$). Closed symbols refer to breeding groups; I = Inca (Sparse),H,L and T = the Wick groups,Hump,Lockley and Twin,respectively (Medium), and LWB and WB = Little Will Bench and Wick Blind, respectively (Dense). The open symbol = a further low density group which differed from the Sparse group in that birds were on small,narrow ledges (see text).

out in an effort to grab the Guillemot. Gulls generally grabbed Guillemots by the wing, tail or, more rarely, back feathers. As the gull grabbed the Guillemot, it pulled it quickly towards it and as the egg came into view, the gull dropped the Guillemot, and picked up the egg. The gulls usually took eggs to a Guillemot-free area in order to consume them. Guillemot chicks were taken in the same way.

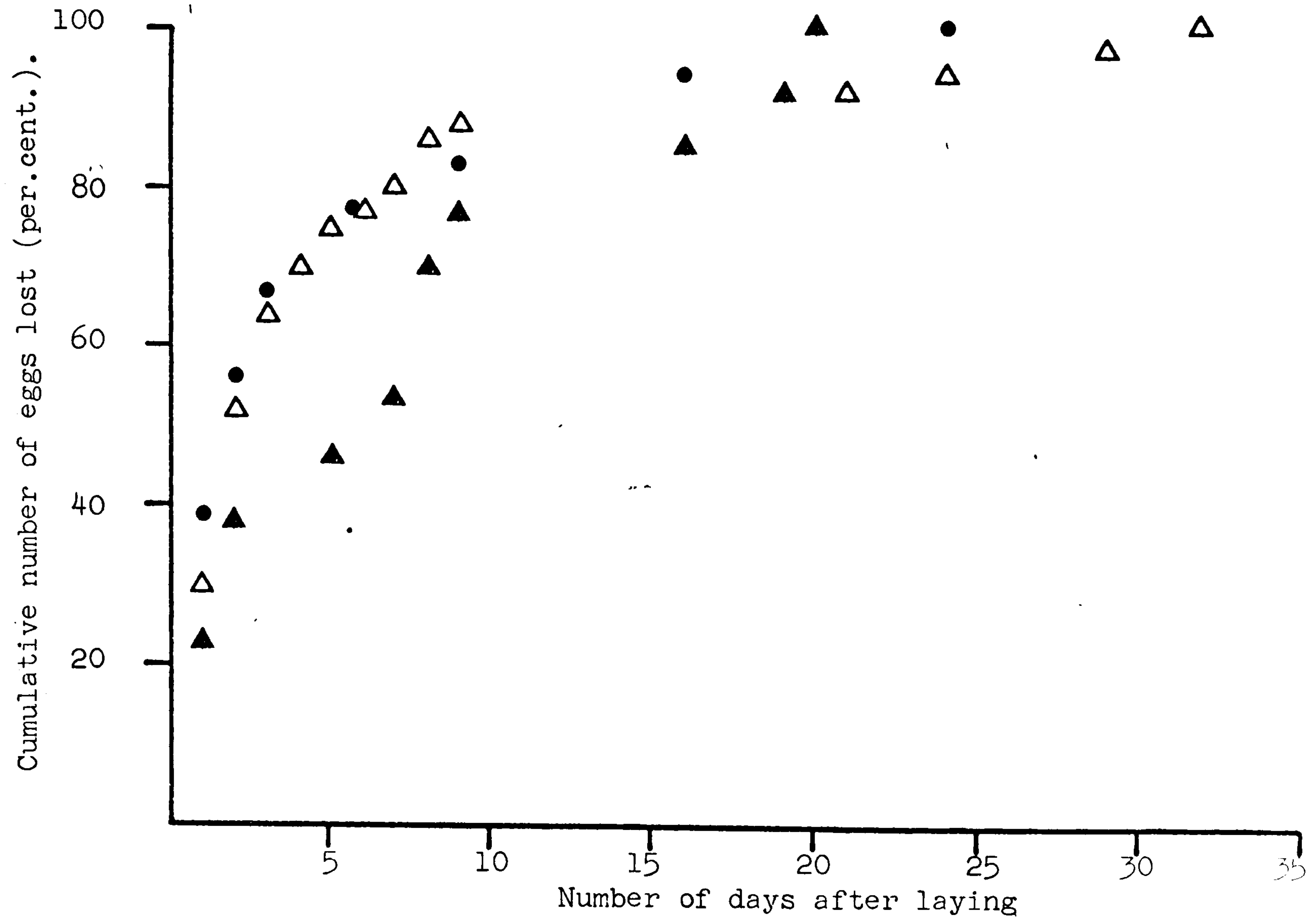
At other colonies I observed Herring Gulls taking Guillemot eggs. This species was less adept at displacing Guillemots from their eggs, and usually spent time near incubating Guillemots, until the Guillemot shifted its position slightly and exposed the egg. The Herring Gull then made a rapid grab at the egg. I only recorded Herring Gulls pulling Guillemots off their eggs on four occasions.

I observed Ravens eating Guillemot eggs on cliff-tops, but I did not determine how they displaced Guillemots. Eggs left unattended were also eaten by Carrion Crows and Jackdaws, but I did not record either species removing Guillemots from their eggs. Carrion Crows appeared to be wary of the Guillemots' lunging bills, but in contrast, they were able to remove Razorbills from their isolated nest-sites comparatively easily. This suggests that the presence of neighbours in the Guillemot helped to protect them from predation by Crows.

Observations at Dense and Sparse groups demonstrated the effectiveness of dense nesting in Guillemots. I spent a total of about 40 hours at Wick Blind (Dense group) and during this time recorded no incidents of predation, although both Herring and Great Black-backed Gulls spent time in the vicinity of this group. The large numbers of Guillemots and their lunging bills apparently deterred gulls, since they were very wary of approaching too close. During a total of 30 hours observation at the Sparse group I recorded six incidents of predation by Herring Gulls. A single gull alighted on the ledge and edged towards incubating birds, which attempted to defend themselves and their egg. The outcome in each case was for the Guillemot to expose its egg in its effort to avoid the gull; exposed eggs were rapidly taken by gulls. Earlier workers stated that Guillemots lack any anti-predator behaviour, other than tenacious incubation (e.g. Kaftanovski 1938). However, I consider that a large number of Guillemots lunging at an approaching larid or corvid acts as a deterrent.

These observations, together with differences in breeding success at different densities, strongly indicate that birds nesting on open ledges at low densities were more vulnerable tp predation than those nesting in Dense groups. Birds in groups have the advantage that gulls cannot approach too closely because of the lunging by nearby Guillemots. The situation in Sparse groups is paralleled on other ledges for a short period as laying commences, and towards the end of the season when most chicks have fledged. The first bird of a group to lay may be more vulnerable to predation than birds which lay later, surrounded by neighbours that have already laid. The data on egg-loss in relation to number of days after laying support this (Fig.3.5). Data for each density group are too few for statistical analysis, although it is clear that in Medium and Sparse groups, most egg-loss occurs within the first few days of laying. The pattern is less clear cut in the Dense group because a greater proportion of birds lose eggs later; this is to be expected if laying is highly synchronized. Reduced egg-loss in the first few days after laying in Dense groups may contribute to the relationship between

Fig.3.5. Cumulative egg-loss in different density groups in relation to number of days after laying. Triangles = Dense, Open triangles = Medium, circles = Sparse.



synchrony and breeding success. In groups where the spread of laying is short, the chance that two or more birds may lay on the same day are increased. A further advantage of synchrony is that it means that most chicks fledge over a short period of time, and the chances that a single bird guarding a chick will be left on a ledge at the end of the season are reduced.

Chicks which disappeared during the day were either predated or fell from the ledge. In eleven cases of a single chick left on a ledge, eight (73%) disappeared during the day. In comparison a control group, consisting of chicks surrounded by neighbours, before any birds had fledged in the same colonies, lost 4 chicks (0.72%) in 555 chick days. A 2 x 2 chi-square test comparing the total lost against those not lost in each category, showed that last-chicks were significantly more likely to disappear than control chicks ($X^2 = 269.5$ 1df $P<0.001$).

(d) Fate of unattended eggs. Seven eggs which were abandoned (either temporarily or permanently) in between other birds in Medium density groups remained on the ledge for an average of 6.3 days (range 4-10 days). In eight cases where I observed birds leaving their egg unattended in 'Sparse' situations, the eggs were all taken by gulls or corvids in less than an hour. The difference between the two groups is significant (Mann-Whitney U test $P<0.001$). In Medium density groups the survival time is probably an under-estimate since most of the eggs were probably knocked off the ledge by neighbouring Guillemots, rather than taken by predators or scavengers. I recorded both gulls and corvids attempting to collect eggs in this situation, but always unsuccessfully. In Sparse situations I probably missed a great many losses of this kind, since I was not present when the bird left the egg, and because eggs disappeared so rapidly. On such ledges, birds left their egg unattended apparently in response to the close approach of a boat or human, and I suspected that birds breeding in these sites were more nervous and ready to leave their eggs, than birds breeding in Dense groups (see next section).

(e) Differences in "temperament" among birds breeding at different densities. Table 3.4 shows the differences in time spent Alarm-bowing and sleeping in Dense and Sparse groups. The difference between the groups was highly significant; the Sparse group spent more time bowing and less time sleeping than the Dense group ($P<0.001$, Table 3.4).

To determine whether the nervousness among birds in Sparse groups was due to a) simply the lack of near neighbours, or b) the birds' vulnerability to predation, I recorded the amount of time spent Alarm-bowing and sleeping by birds in a control group. In the control group Guillemots nested on small, narrow ledges (similar to those used by Kittiwakes), in other words the birds were nesting at low densities but because the ledges were small they were not vulnerable to gull predation. There was a significant difference in sleeping and Alarm-bowing between the Sparse and control group (Table 3.4); the control group spent more time sleeping and less Alarm-bowing than birds in the Sparse group . There was no difference in the frequency of Alarm-bowing between the control group and the Dense group ($X^2 = 3.04$ ldf $P>0.1$), but birds in the Dense group spent a significantly higher proportion of their time sleeping than birds in the control group ($X^2 = 5.13$ ldf $P<0.05$), although this is not important in the present study. The comparison between the Sparse and control groups indicate that a Guillemot's nervousness in Sparse groups is a result of its potential vulnerability, rather than the proximity of conspecifics *per se*.

Table 3.4. Time spent sleeping and Alarm-bowing at different densities.

Values are number of minutes out of 100 in which a bird performed sleeping or Alarm-bowing.

Group	Sleeping	Alarm-bowing
Dense	56	3
Sparse	0	44
Control	40	0

Notes: Data are from two 50 min.observation periods for each site;these have been combined.

Chi-squared values (all 1 df): Sleeping: Dense vs Sparse $X^2 = 77.8$ $P<0.001$, Dense vs control $X^2 = 5.1$ $P<0.05$, Sparse vs Control $X^2 = 50.0$ $P<0.001$.

Alarm-bowing: Dense vs Sparse $X^2 = 46.7$ $P<0.001$, Dense vs Control $X^2 = 3.0$ $P>0.1$, Sparse vs Control $X^2 = 56.4$ $P<0.001$.

For definitions of each density group see text.

Discussion

The main findings relevant to this section are (a) Breeding success is positively correlated with nesting density. The main advantage of nesting at a high density is as an anti-predator strategy; a number of Guillemots are able to deter predatory gulls by lunging at them. At low densities on broad ledges (Sparse groups) gulls were able to walk directly up to incubating birds, displace them and steal their egg. (b) Breeding success within sub-colonies is not related to laying date, but is related to synchrony of laying. Dense groups had a shorter spread of laying than Sparse groups. A short spread of laying minimizes the number of birds at the beginning and end of the season whose breeding is out of phase with the rest. Birds which were out of phase were more vulnerable to predation. (c) Birds in Sparse groups were more nervous and spent more time Alarm-bowing and less time sleeping than birds in Dense groups. Birds in Sparse groups probably spent more time watching for potential predators than birds in Dense groups.

Thus, high breeding success is achieved by two methods (1) clumping in space (maximization of breeding density): see below, and (2) clumping in time (synchronization of breeding activities).

(a) High density breeding as an anti-predator strategy

Colonial breeding in animals may have several functions (Emlen 1973). One function of coloniality is that it reduces the risk of predation if groups of animals are better able to repel predators than individuals (Wilson 1971, Kruuk 1964, Patterson 1965). Coloniality in itself could operate an an anti-predator device since a colony of animals in an area is less likely to be encountered by a predator than are the same number of animals dispersed over the same area (Edmunds 1974). On the other hand colonies are often conspicuous and may attract predators (Ward & Zahavi 1973). As a result there have been selection pressures favouring colonial breeding in inaccessible sites. Allee *et.al.* (1949) and Lack (1968) have discussed the selection of inaccessible sites for breeding by colonial birds. The least accessible sites include islands and sea-cliffs; Guillemots *Uria* spp., together with most seabirds are restricted to such sites. The only terrestrial mammal which commonly preys on *Uria* spp. is the Arctic Fox (Chapter 2), and in many areas this species may be important in determining the limits of breeding distribution (Bertram & Lack 1938). Man may have also exerted a similar effect in many areas, since Guillemots have a long history of extensive exploitation. By breeding on cliff-ledges, stacks and islands Guillemots are able to avoid most terrestrial predators, but not avian predators. There are numerous records of avian predators taking Guillemot eggs and chicks. Swartz (1966), Tschanz (1972) and myself recorded Corvids as predators of Guillemot eggs. Most predation is by large *Larus* gulls, equal or larger in size than *Uria* spp. In the north Atlantic Great Black-backed Gulls (Kaftanovski 1938, Johnson 1938, Perry 1940, Belopolski 1957, Lockley 1958), Herring Gulls (Kaftanovski 1938, Perry 1940, Tschanz 1972, Anon. 1974) and Glaucous Gulls *L.hyp~~o~~eboreous* (Bertram & Lack 1938, Tuck 1960, Lovenskiold 1964) are the main predators, and in the Pacific: Glaucous-winged Gulls *L.glaucescens* (Murie 1959) and Western Gulls *L.occidentalis* (Taylor 1887, Loomis 1896, Kaeding 1903, Ray 1904, Chaney 1924). In all cases gulls prey opportunistically on Guillemot eggs and chicks, and even though some individuals may specialise on Guillemot eggs, the *Larus* gulls as a whole are not Guillemot specialists.

Young (1963a,b, 1970) reached the same conclusion with regard to skua-penguin interactions.

Allee et.al. (1949) have discussed spacing in animals, and have shown that, predictably, each species has an optimum density. This point has been confirmed in several seabird studies, notably studies of larids (Parsons, in press, Davis & Dunn, in press, Fordham 1964, Coulson 1971). The results of this study show that in Common Guillemots breeding success is positively correlated with nesting density and that birds breeding at the highest density are the most productive. Thus, the most productive density for Common Guillemots approaches the maximum attained by any avian species. My results confirm the suppositions of earlier workers (e.g. Johnson 1938, Kaftanovski 1938, Belopoloski 1957) that high density nesting is the most successful, and this agrees with results obtained in another study of Common Guillemots on Lundy Island, England (Anon. 1974).

The data show that Guillemots preferentially breed in close proximity to conspecifics (Fig.3.10), and that individuals breeding in Sparse groups are particularly uneasy. Previous workers have also noted differences in 'nervousness' among Guillemots breeding in different situations. Storer (1952) recorded that group size was proportional to the amount of disturbance necessary to make Guillemots panic. He also noted that, like Johnson (1938), birds were very dependent on their neighbours for 'reassurance'. The Guillemots in the small colonies that Johnson (1938) observed were particularly nervous, and the approach of man resulted in birds panicking and deserting the nesting area. In contrast, at larger, denser colonies, such as Walrus Island, Bering Sea, Bent (1919) found that birds were 'exceedingly tame or stupid and would allow a near approach' and only when the birds were 'hard pressed' would they leave the nesting area. D.N. Nettleship (pers.comm.) recorded a similar situation at the huge, dense colony at Funk Island. Tenaza (1971) recorded the same sort of situation in Adelie Penguins *Pygoscelis adeliae*; birds breeding at low densities were more nervous than those surrounded by other individuals, and a similar effect has also been recorded in other species which normally feed in flocks (Murton *et.al.* 1971, Lazarus 1972, Powell 1974). This may be a widespread reaction among social species.

Section II : Why are Relatively Few Guillemots on Skomer Breeding at High Densities?

Methods

(a) Distribution of Guillemots within a colony. Casual inspection of the distribution of Guillemots in the largest colony on Skomer, known as the Wick (see Figs.3.2 and 3.6), indicated that birds were concentrated on to the narrowest parts of the ledge. The Wick contains over one-third of the island's population of Guillemots and consists of a vertical cliff-face about 60m (200') high and about 450m. (1350') in length. Most Guillemots breed on one ledge (the 'main' ledge) which runs horizontally along 200m of the Wick's length, at about 30m above sea-level. Since the Wick is almost vertical and does not permit easy access to the main ledge, the width of breeding areas and of Guillemot-free areas was measured by photographing as much of the ledge as possible from the top of the Wick. In areas where no Guillemots were breeding I lowered a piece of wood 1m long on to each section

Fig.3.6. The Wick Guillemot Colony

of the ledge before photographing it so that I could measure the ledge dimensions directly from the photographs. In areas where birds were breeding I photographed the ledge, and later estimated the dimensions of the ledge from the size of birds in the photographs. Measurements of ledge width were made at approximately 1m intervals along the length of the main ledge; a total of 63m of Guillemot breeding areas, and 52m of Guillemot-free areas.

One of the main reasons for using the Wick as a study colony is that there is a series of photographs of the colony taken in 1934 when the population was much higher (see Chapter 2), showing the distribution of birds on the Wick. The 1934 photographs, taken by R.M. Lockley, show that birds occupied both broad and narrow ledges (Fig.3.7), and at that time the entire length of the Main ledge was occupied by Guillemots (see also Birkhead & Ashcroft 1975). Buxton & Lockley (1950) later noted that in 1946 a number of gaps had subsequently appeared in the line of Guillemots breeding along this ledge. This occurred as numbers declined (see Chapter 2), and as numbers continued to decrease up to about 1970, the number of gaps and isolated groups also increased. To test whether the distribution of Guillemots on the Wick was non-random I measured the distance between incubating birds from photographs, and compared the inter-bird interval with a random expectation (for method, see Chapter 4). Two groups of data were examined in this way; first, a large sample from the main ledge on the Wick, and second, a smaller sample from a ledge known as Wick Corner ledge, which lies at the eastern end of the Wick. This ledge is approximately 0.3m. wide along its entire length. Photographs of Wick Corner taken by Lockley in 1934 show that, like the main ledge, numbers were much higher at that time, and that the entire

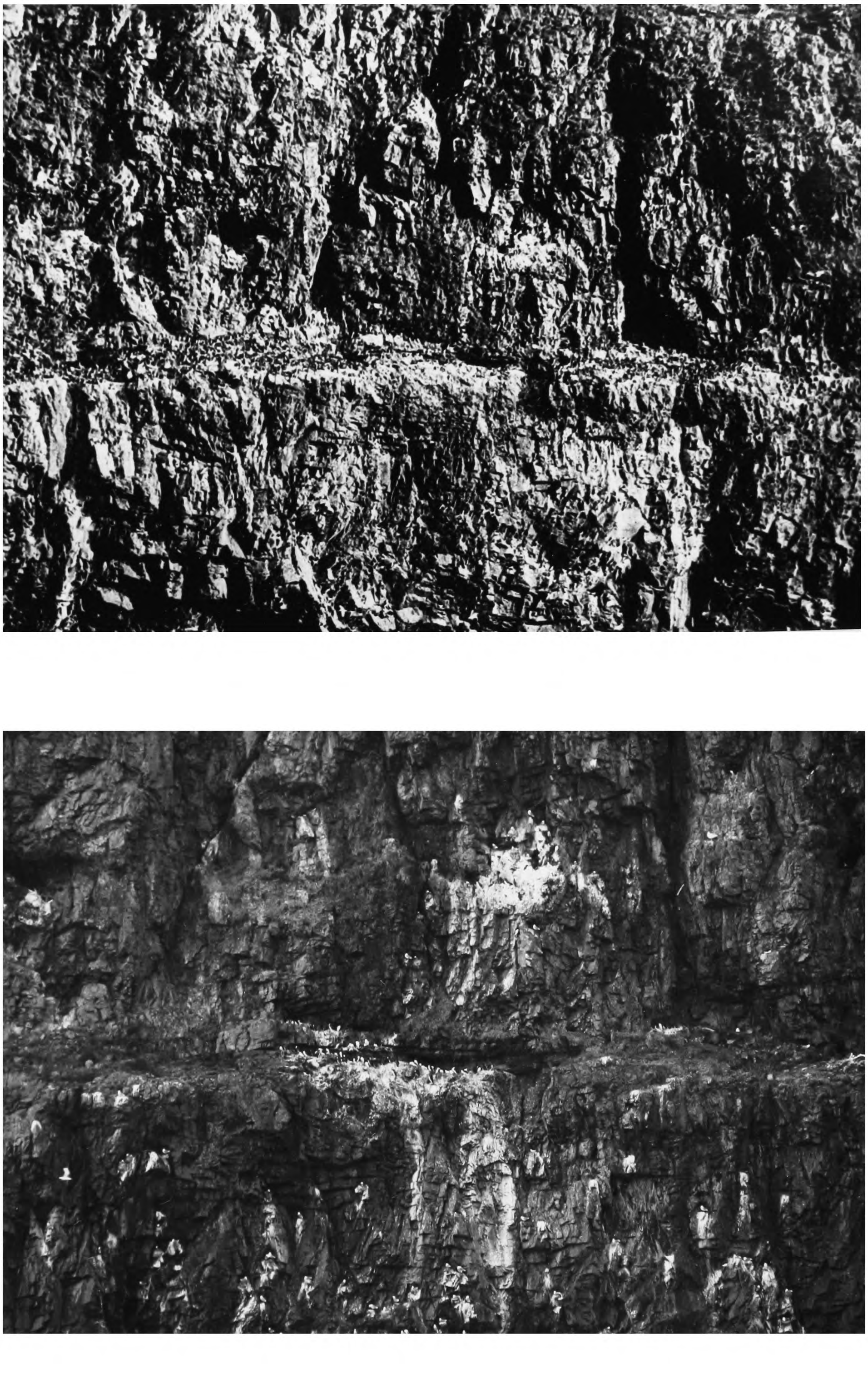


Fig.3.7. Part of the Wick Guillemot colony known as Twin area. The upper photograph shows the area in 1934, with Guillemots occupying broad and narrow ledges. The lower photograph shows the same area in 1975; with reduced numbers of Guillemots, restricted to the narrow parts of the ledge

ledge was used by Guillemots. I used Wick Corner data for two reasons, first to verify the main ledge results, and second, because I had detailed observations over three years on the number of breeding pairs, and distribution of birds on this ledge.

(b) New breeding sites. A detailed record of all birds breeding on Wick Corner ledge was made over three years. The ledge was visited each day of the breeding season in each year, to record egg-laying and breeding success. The exact position of each breeding pair on the ledge was recorded by photographing the ledge on a number of occasions each year and plotting the positions of birds on the photographs. In this way I was able to record changes in numbers from one year to the next and the position occupied by birds breeding for the first time.

(c) Site tenacity. The precise location of colour-marked birds' breeding sites was recorded by plotting sites on to photographs of colonies. Nearly all marked birds were breeding in 'Medium' density colonies and none in Dense or Sparse colonies. I was able to compare the breeding sites of these birds in subsequent years from the photographs. As a check, in case birds moved over large distances, say between colonies on Skomer, I tried to examine all the birds at breeding colonies on two or three occasions each year.

Results

(a) Distribution of Guillemots on the Wick. The mean width of the main ledge on the Wick was 0.85m ± 0.75 S.D. The mean width of sections occupied by breeding Guillemots was 0.29m ± 0.14 S.D., which was considerably narrower than the Guillemot-free areas; 1.51m ± 0.63 S.D.; the difference between the two was highly significant ($t = 15.3$ 113 df $P<0.001$). The distribution of ledge width for breeding areas and Guillemot-free areas is shown in Fig.3.8.

A comparison of inter-bird spacing and the calculated expected values shows that on both the Main ledge and on Wick Corner ledge, birds tend to occur in clumps; that is, there are many more spaces of 5cm or less than would be expected if birds were distributed at random. Also, because sub-colonies were separated by a few long stretches of ledge, the number of inter-bird spaces greater than 31cm was smaller than expected. Fig.3.9 shows observed and expected values for both sets of data; on the Main ledge and Wick Corner observed values differ significantly from expected (Main Wick ledge; $X^2 = 1609.3$ 6df $P<0.001$, and Wick Corner $X^2 = 101.6$ 6df $P<0.001$) (see Table 3.5). Thus, birds occur in discrete groups (= sub-colonies) on the narrow parts of the Main Wick ledge, and on Wick Corner ledge birds occur in 'clumps', or 'sub-colonies'.

(b) New breeding sites at Wick Corner. Changes in the Skomer Guillemot population have been presented in Chapter 2. Between 1972 and 1975 the population remained at a more or less similar level, with small fluctuations between years. Numbers increased between 1973 and 1974 (Table 2.5, Chapter 2) and as a result, a number of new sites were occupied in 1974. Guillemot numbers on Wick Corner increased from 41 to 45 pairs between 1973 and 1974. Fig.3.10 shows the location of the new sites in relation to the 1973 population; this shows that Guillemots preferentially selected sites near to other Guillemots, at the ends of existing groups. Fig. 3.10 also shows some further observations from 1974 and 1975 of non-breeding birds which occupied sites but did not lay; these also selected sites next to established birds. The areas between groups

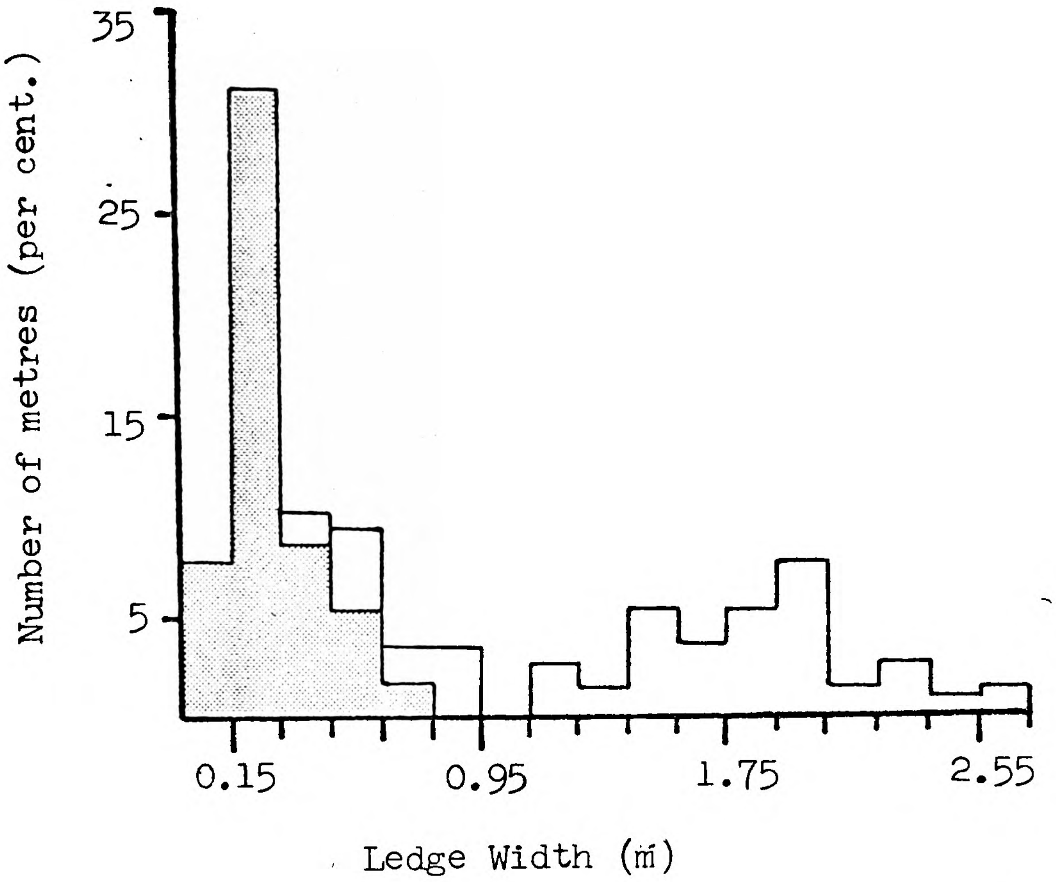


Fig. 3.8. Distribution of ledge width on the Main ledge of the Wick. The shaded area shows the areas occupied by Guillemots in 1975. The y axis is the number of meters of each width along the main ledge.

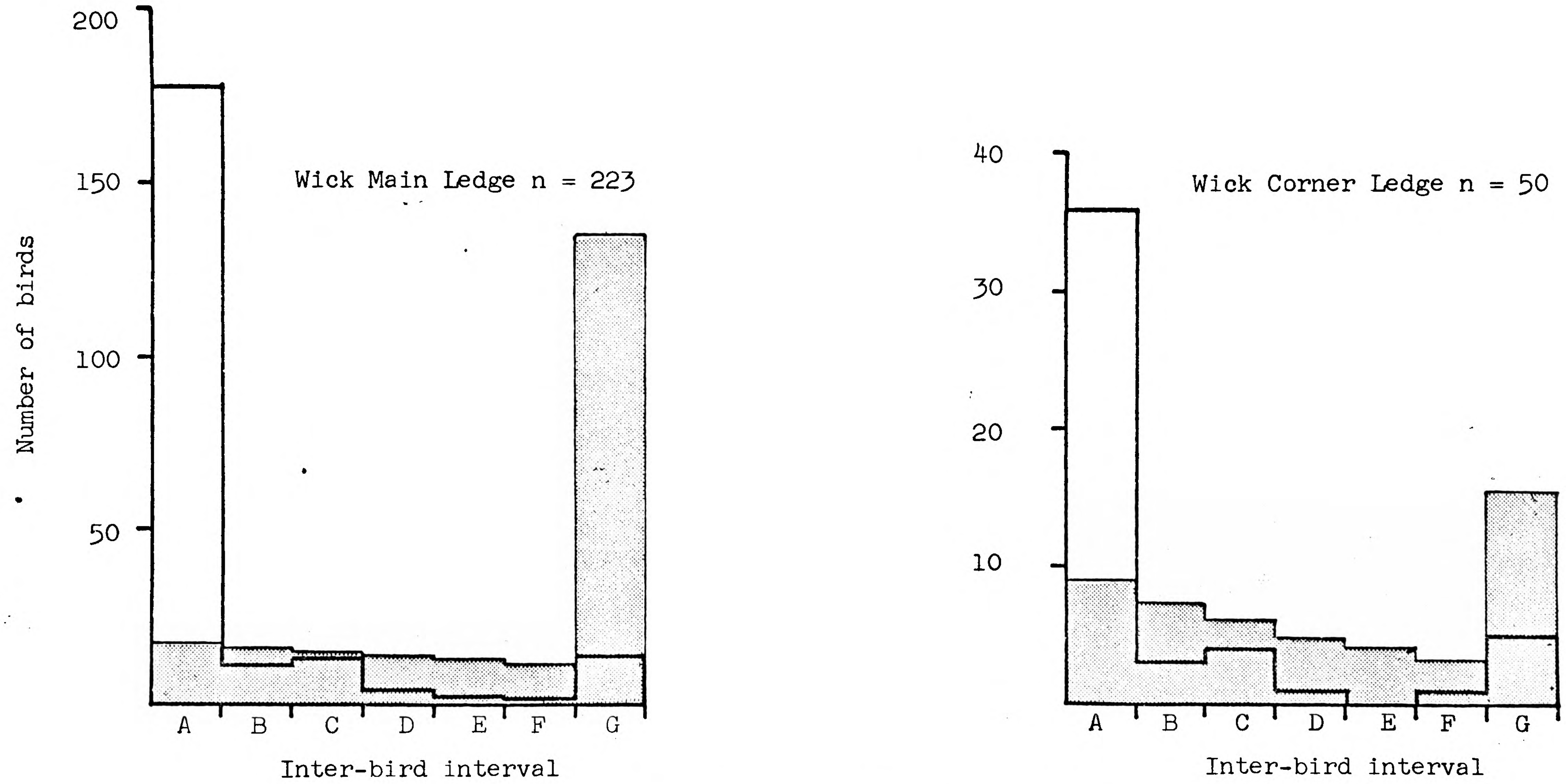


Fig.3.9. Distribution of observed and expected (shaded area) inter-bird intervals. The observed distribution shows the distance to nearest neighbour among incubating Guillemots. Intervals: A: 0 - 5, B: 6 - 10, C: 11 - 15, D: 16 - 20, E: 21 - 25, F: 26 - 30, G: greater than 31 cm. (see also Table 3.5.).

Table 3.5. Inter-bird intervals (cm) on The Wick, on the Main Ledge (excluding Wick Corner) and Wick Corner.

THE WICK							
Intervals	0 - 5	6 - 10	11 - 15	16 - 20	21 - 25	26 - 30	31+
Observed	178	11	13	4	2	1	14
Expected	17.5	16.2	14.9	13.7	12.6	11 .6	136.5
Total X^2 value	1609.3	6 df P<0.001					
WICK CORNER LEDGE							
Observed	36	3	4	1	0	1	5
Expected	8.9	7.3	6.0	4.9	4.1	3.3	15.5
Total X^2 value	101.6	6 df P<0.001					

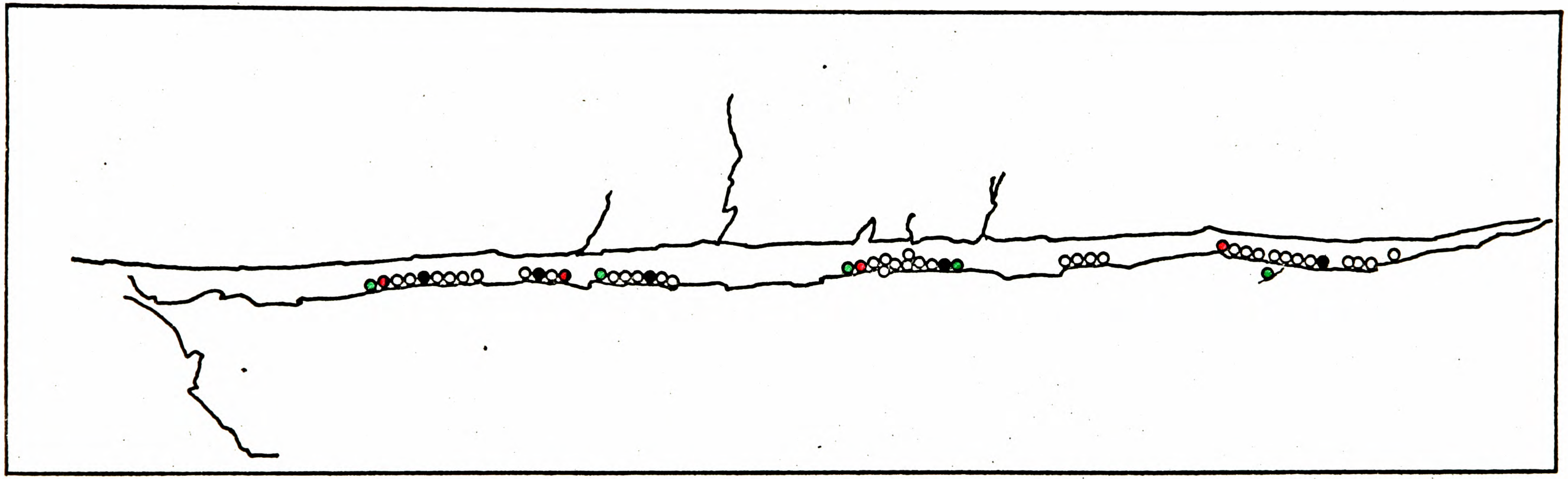


Fig.3.10. Wick Corner Ledge (drawn from photograph) showing distribution of nest-sites in 1973 - 1975. o = nest-site occupied by breeding birds in 1973, 🔴 = site occupied by new breeding birds in 1974, 🟢 = sites occupied by non- breeders in 1974 and 1975, ● = sites not used in 1975. None of the sites occupied by non-breeders in 1974 became breeding sites in 1975.

were not utilized. In contrast, when numbers decreased from 45 in 1974 to 38 in 1975 birds disappeared apparently at random, from the groups.

(c) Site tenacity. Guillemots on Skomer were faithful to their nest-site from one year to the next. Over 95% of birds recorded breeding at one site returned to the same site the following year (Table 3.6). Of the birds which changed site, one individual moved from a small isolated colony to a Medium density colony about 200m away. The other two individuals moved less than 0.5m from their original site, remaining within the same sub-colony. The latter two birds may simply have changed mates.

At another colony, known as the Cave colony, where I was able to trap most breeding birds, three birds moved to new colonies. One moved 3km south to the neighbouring island of Skokholm, the other two moved 600m and 400m, respectively to Medium density colonies. I have not included birds from the Cave colony in Table 3.6, since there was some evidence that trapping birds in this way caused considerable disturbance. This suspicion was partly confirmed when the Cave colony diminished in size over the period of study and after one or two annual trapping sessions, when a 'new' colony, which contained a number of marked birds from the Cave colony, was discovered about 30m away in another cave-like situation, in late July 1975.

Discussion

The main findings can be summarised as follows; (a) The Guillemot population on Skomer has decreased during the period 1934 (or earlier) to 1970 (see Chapter 2). (b) The present distribution of Guillemots in a large colony is non-random; Guillemots occur in discrete clumps (= sub-colonies) on the narrowest parts of the ledges. Photographs taken in 1934 show that at

Table 3.6. Site tenacity of Guillemots on Skomer.

Years	No.of birds marked	No.of birds that return			
		to same site		to different site	
		n	%	n	%
1973 - 1974	34	33	97.1	1	2.9
1974 - 1975	40	38	95.0	2	5.0
Total	74	71	95.9		

that time there were no discrete clumps and both broad and narrow ledges were used for breeding. (c) Birds breeding for the first time join existing groups of birds and do not settle in the spaces between sub-colonies, in other words, new birds breed as close to other Guillemots as possible. (d) In Medium density sub-colonies, site tenacity is highly developed, over 95% of all birds return to the same site from one year to the next.

(a) Changes in population and distribution. The decrease in the Skomer Guillemot population was accompanied, or followed by, a change in the distribution of birds on the Wick colony. It seems a reasonable assumption that as numbers declined birds disappeared from breeding sites in a random (Fig. 3.10) manner, so that a similar proportion from both broad and narrow ledges disappeared. Thus, as numbers decreased the density of birds on broad ledges would have become reduced. Eventually a point would be reached where gulls were able to steal eggs and chicks; in the way I recorded at the Sparse group in the present study. It may be significant that in 1946, when the population was undergoing its decline, Buxton & Lockley (1950) commented on the regular predation of Guillemot eggs by gulls. The gull population in 1946 consisted of about 60 pairs of Great Black-backed Gulls, 700 pairs of Herring Gulls and 1000 pairs of Lesser Black-backed Gulls (Buxton & Lockley 1950).

There are two ways that the present distribution of Guillemots may have come about; (1) Mass movements of adult birds, or (2) Without mass movements of adults.

(1) Although Guillemots exhibit a high degree of site tenacity at Medium densities, it seems probable that after a succession of years with low breeding success birds would be more likely to change site. Birds breeding on

narrow ledges may not have been subject to as much gull predation and may have maintained their breeding sites. Unsuccessful Guillemots moving from broad ledges probably joined the groups on narrow ledges, thus filling the gaps that had occurred there. I have no information on the relation between site tenacity and breeding success in Guillemots, and do not know whether birds which are regularly unsuccessful in their breeding attempt are more likely to move than those which raise chicks. However, Johnson (1938) found that in an area where small Guillemot groups were subject to heavy gull predation, birds abandoned nesting areas and reformed elsewhere, after a certain proportion of eggs had been taken by gulls. In addition, in other species, individuals which are unsuccessful are more likely to change site, for example, Yellow-eyed Penguins Megadyptes antipodes (Richdale 1957), Adelie Penguins (LeResch & Sladen 1970). There is also evidence that individuals will move to better quality sites if vacancies occur there. This has been recorded in House Sparrows Passer domesticus (Dawson 1972), Kittiwakes (Coulson 1968), Shags (Coulson 1971) Great Tits Parus major (Krebs 1971). However, in most cases the individuals which changed sites were young ones. There are fewer records of adult birds changing site, but Corkhill (1970 and pers.comm.) found that after artificially reducing breeding success in Herring Gulls in one year, as part of a control programme, the gulls abandoned the 'control' colonies and settled elsewhere the following season. In addition, it has been shown in several species that if birds were disturbed (by humans) when breeding they were more likely to change breeding site than individuals which bred undisturbed and successfully (Dawson 1972, Myrberget 1961). The same was true of Common Guillemots on Skomer, and my observations show that although most birds show strong site fidelity, large-scale movements may occur, as in the

Cave colony (already mentioned). Disturbance may be an important factor contributing to low quality sites, so that if birds move to areas where they are not disturbed they are effectively moving to better sites.

(2) An alternative hypothesis, which does not involve adult birds changing breeding site, which could account for the changes in distribution of Guillemots on the Wick, is suggested by the work of Bendell & Elliot (1966a, 1966b) on Blue Grouse Dendragapus obscurus. These workers found that birds occurred in two habitat types; Open and Dense, and that young birds preferentially settled in Open habitat. Once a grouse established itself in Open habitat it remained there, even if vegetation changes occurred, which eventually altered Open to Dense habitat. The number of grouse in Dense habitat decreased with time, not because birds moved out into Open habitat, but as a result of natural mortality, and because new recruits did not move into Dense habitat. A similar situation may have occurred in Guillemots on Skomer. As the total number of Guillemots breeding on Skomer declined, the density of birds on broad ledges was reduced, but birds which had originally established themselves on broad ledges remained there. The reduction in density and associated gull predation would eventually result in decreased production of young from these sites, compared with birds on narrow ledges. Immature birds returning to the colony prior to breeding may have preferentially selected narrower ledges because most of them were raised in this habitat. The change in distribution from broad to narrow ledges, assuming that adults were highly site tenacious and that few or no young birds settled on broad ledges during the period of population decline, would have taken over 20 years, that is, until all birds breeding there had died (see Chapter 2 for adult survival rates). However, an increase in the adult mortality rate seems a

likely reason for the decline in numbers between 1934 and 1975 (Chapter 2). Moreover, a high rate of loss from the breeding population would increase the likelihood that both members of a breeding pair would die in the same year, and this would tend to 'open-up' Dense groups to gull predation. It seems likely that during periods of population stability or increase, adult mortality is sufficiently low that the chances of both members of a pair dying in the same year are slight. Consequently, birds are able to re-mate and maintain the density of breeding groups.

Some observations made on the declining population of Common Guillemots on the Farallon Islands, during the period 1880-1920 are of interest. An account of the Guillemots' fortunes on the Farallons is given by Ainley & Lewis (1974). Numbers started to decrease after 1850, as a result of excessive egg-collecting, and later oil pollution accelerated the decline. In the 1920s numbers were at their lowest level, but increased subsequently. Guillemots breeding on the Farallons do so in an open, flat-top situation. A reduction in numbers, and presumably density, may have resulted in large-scale predation by Western Gulls since several authors commented on Guillemot-gull interactions (Taylor 1887, Loomis 1896, Kaeding 1903, Ray 1904, Chaney 1924), for example, Taylor (1887) recorded gulls attacking Guillemots and stealing eggs from them. Chaney (1924) noted that when the population was at its lowest level, birds were breeding in crevices and not on the flat-top as they had done previously, and suggested that Guillemots had selected these protected sites to avoid gull predation. Thus, a similar situation may have occurred on the Farallons as on Skomer, during a period of population decline.

This leads to the question of habitat selection in Common Guillemots. Hilden (1965) has said, that birds will choose the 'best habitat', which is defined as the one in which the greatest number of progeny are produced. In Guillemots the best habitat clearly varies according to the population level and density of breeding birds. At high population levels and density, broad ledges or flat-tops are more productive than similar sites at low densities. Kaftanovski (1938) and Belopolski (1957) also concluded that the high density broad ledge situation was the 'best' for Common Guillemots. At low population levels narrow ledges are the best sites. An examination of Guillemot distribution in relation to ledge width on Skomer, with no prior information on population level, would indicate that the preferred habitat consists of ledges 16-31cm wide (Fig.3.8), since most birds are breeding there. However, as Nettleship (1972) has pointed out, abundance alone is not always a reliable index of habitat suitability. The results of the present study show that birds on narrow ledges are less productive than birds on broad ledges at high density, but both situations are superior to broad ledges at low density. Nettleship (1972) goes on to say, "density could be low, not for reasons of poor habitat, but because few animals were available for invading the habitat. If habitat selection is an adaptive activity, then the only measure of habitat quality during the breeding season is breeding success". Thus, on Skomer, most birds breed on narrow ledges at Medium density, but the greatest levels of productivity are achieved in the few Dense groups. However, Common Guillemots apparently do not have the behavioural repertoire permitting them to coalesce into a few high density groups on broad ledges.

An examination of the habitat and density of Common Guillemots in various parts of their range shows that in many areas a high proportion breed on broad ledges or on flat-tops. For example, Farne Islands, northern England

(Vaucher 1960), Funk Island, Newfoundland (Tuck 1960), Farallon Islands, California (Bent 1919), Walrus Island, Bering Sea (Bent 1919, Peterson & Fisher 1955), Seven Islands, Barents Sea (Belopolski 1957:278). However, in some areas Guillemots may be restricted to narrow ledges. This may occur for several reasons: a) absence of predator-free broad ledges, b) because of a population decrease, as on Skomer, and c) because of extensive egg-predation by man, where man acts in the same way as other predators, as in a) above. Moreover, unless colonies are increasing rapidly in size, it may take many years for birds to occupy or re-occupy broad ledges and flat-top areas. Since it seems unlikely that Guillemots will colonize these sites if they can settle near other Guillemots, there must be a gradual spread from narrow ledges to broader ones. One way in which this can occur is shown in Fig.3.11. In this way the risks of predation during the spread on to broad areas are reduced.

Like the Common Guillemot the North Atalantic Gannet Sula bassana breeds both on cliff ledges and on flat-tops. Nelson (1967) has suggested that the Gannet is primarily a cliff-nester which has the ability to breed on flat-tops, since when Gannets colonize new areas, they first breed on ledges and later spread on to flatter areas. The same type of spread from ledges to flat areas probably occurs in Common Guillemots, and it may be argued that Common Guillemots are primarily cliff (= narrow ledge) nesters. However, I belive that Common Guillemots select 'safe' sites on narrow ledges or against a cliff-wall, when first occupying an area to reduce the risks of predation. Gannets, as very large seabirds rarely suffer from predation (Nelson 1966). Moreover, Common Guillemots are most productive at high densities and show a number of behavioural adaptations to high density nesting (Chapter 5),

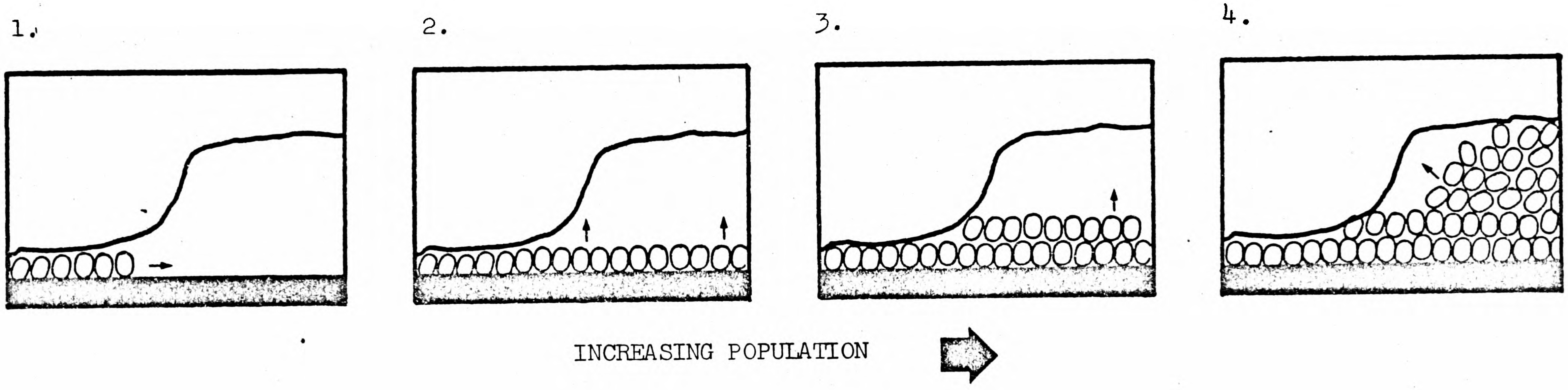
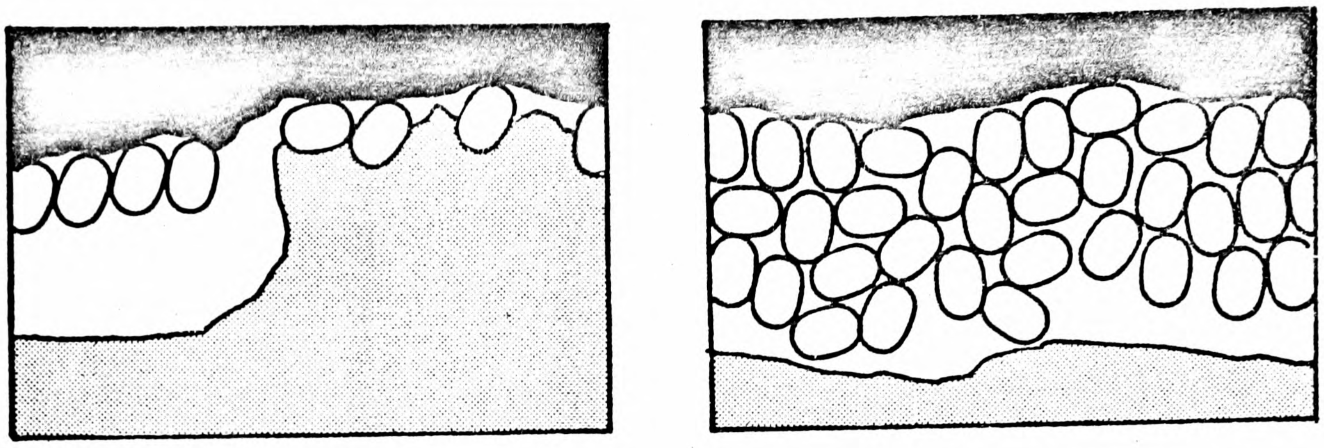


Fig.3.11. Ledge utilization in response to increasing population. Oval shapes = incubating Guillemots, black area = cliff wall, small arrows = direction of spread. At a low population level (1) birds occupy only the narrow parts of the ledge, but as numbers increase they spread along the cliff-wall onto broader parts of the ledge (2). As the population increases further, the ledge space adjacent to the cliff-wall becomes fully occupied, so birds settle next to established birds, eventually occupying much of the broad ledge (3,4).



BRUNNICH'S GUILLEMOT COMMON GUILLEMOT

Fig.3.12. Differences in habitat utilization between Common and Brunnich's Guillemots. Black area = cliff-wall oval shapes = incubating Guillemots, stippled area = sea. Brunnich's Guillemots form lines of individuals on broad ledges, but only against the cliff-wall and do not breed at as high densities as Common Guillemots. Brunnich's Guillemots also occupy narrow ledges, small ledges and crevices large enough for only one bird. (From Tuck 1960, Williams 1974 and others).

which can only be achieved on broad ledges or flat-tops.

The Common Guillemot's preference for broad ledges is most pronounced where it occurs sympatrically with Brunnich's Guillemot. Although there has been no quantitative study of habitat selection in Uria spp. where Common and Brunnich's Guillemot occur together, several workers have commented on the intracolony distribution of the two species (Jourdain 1922, Lack 1934, Kaftanovski 1938, Duffey & Sergeant 1950, Foster et.al. 1951, Belopolski 1957, Williams 1974). In general Common Guillemots occupy broad ledges and flat-tops at high densities and Brunnich's Guillemots occupy narrow ledges and sites similar to Razorbills (see Chapter 5), never exceeding Medium densities. Discussing site selection in Uria, Williams (1974) has said that in Brunnich's Guillemot the presence of a rock-face is the main prerequisite. Williams also pointed out that Common Guillemots apparently occupy vacant sites on a rock-face, before spreading over adjacent flat areas (see Fig.3.11). The differences between the two species are shown diagramatically in Fig.3.12.

Summary

The chapter is divided into two sections, in the first I tried to answer the question 'At what densities are Guillemots most productive?'. Breeding success was highest in Dense groups and lowest in Sparse groups. Breeding success was not related to laying date, but was related to synchrony of laying. Dense groups had a shorter spread of laying than Sparse groups, and a short spread of laying minimized the number of birds at the beginning and end of the season whose breeding was out of phase with the rest. Birds which were out of phase were more vulnerable to gull predation. Moreover, in Dense groups several Guillemots lunging at a gull were able to deter it, but in the Sparse group a gull could readily displace an incubating Guillemot and steal its egg. Birds in Dense groups spent more time sleeping and less time Alarm-bowing than birds in Sparse groups, indicating that they were less nervous and spent less time looking for predators.

The second question I tried to answer was 'Why are relatively few Guillemots on Skomer breeding at high densities?'. The Skomer Guillemot population has shown a marked decline during the present century. It is assumed that mortality of adult birds was high during the decline, and that they disappeared from the ledges at random, thus reducing the density of breeding groups and leaving them open to gull predation. Because of site tenacity and the tendency for new breeders to attach themselves to existing groups, and because Medium density groups are more productive than Sparse groups, Medium density groups have persisted. In other words, Guillemots exhibit a sort of behavioural conservatism, preventing the reduced population from coalescing into a few Dense groups.

CHAPTER 4

FEEDING ECOLOGY

Introduction

Guillemot numbers on Skomer and other parts of southern Britain have declined during the present century and it is generally believed that this is a result of either a) oil pollution, or b) a change in the marine environment (see Chapter 2). If there has been a decrease in the quality of feeding conditions during the Guillemots' breeding season, this may manifest itself in a number of ways; (a) the size and species of fish prey (b) the provisioning rate of chicks by parent birds, and (c) the growth and development of nestlings. Thus, the aim of this study was to examine these parameters on Skomer, and to compare my results with other studies carried out in areas where Guillemot numbers have not declined.

I was also interested in the provisioning rates of chicks by adults under different environmental conditions, since this would provide some information relevant to adult birds' foraging and factors which affect their feeding rates.

Several workers have suggested that sociality in birds has evolved as a strategy for exploiting unevenly distributed food sources (Sergeant 1951, Fisher 1954, Crook 1965, Ward 1965, Horn 1968). These ideas have been crystallized into the 'information centre' hypothesis of Ward & Zahavi (1973). These authors suggest that breeding colonies and communal roosts act as centres for information exchange and that unsuccessful individuals follow successful ones from the colony or roost to good feeding areas. In the present investigation I have examined some aspects of this hypothesis relevant to Guillemots.

A final, rather minor objective was to collect information on the distribution of Guillemots and two sympatric auk species, the Razorbill and Puffin at sea. This information was collected to compare with results presented by Cody (1973) in a controversial paper (Bedard 1975) on ecological segregation in alcid species.

Methods

(a) Prey size and species. The size range and species of fish fed to chicks were determined:

(i) From direct observation of birds feeding chicks. The size of fish was estimated by comparing the size of the fish with the Guillemot's bill-length (45-50mm). This method allowed me to estimate the length of a larger sample of fish than the next method.

(ii) Food items were collected from ledges during visits to ledges to measure or ring chicks. Fish which had partly decomposed or had dried up were measured but not weighed. In all cases fish length was measured from the tip of the snout to the tip of the tail. Only specimens which I judged to be fresh were weighed.

(b) Food intake of chicks. Observations were made:

(i) Over the entire daylight period on two occasions.

(ii) Between 1400-1800hrs (all times B.S.T.) on 22 occasions, and

(iii) On 8 occasions between 0400-0800hrs., during late June and early July. During these periods the number of feeds to chicks of known age, the species and estimated size of fish were recorded.

(c) Chick growth. Chicks were weighed using a 'Pesola' 300g balance, and wing length was measured from the carpal joint to the tip of the longest 'primary' using a steel rule. Thus, wing length consists of a skeletal and a feather component. Measurements were taken to the nearest gram and the nearest mm.

In order to check that growth rates of those chicks which were weighed regularly in small, isolated colonies did not differ from those in larger (undisturbed) groups, I compared weight and wing length of a larger sample (114) of chicks measured on a single visit with regularly disturbed chicks.

Because the close approach of humans to Guillemot colonies causes disturbance, which can result in chick (and egg) loss, the measurement of Guillemot chicks was conducted in areas where birds nested in small, isolated groups and under boulders, to minimize risks to chicks. Despite these precautions, in 1972 only 4 out of 25 (16%) study chicks survived to fledging (other workers have reported similar losses; Johnson 1944, Johnson & West 1975). By selecting only the 'safest' sites in 1975 only one out of nine study chicks failed to fledge. As a further precaution chicks were measured every second day.

(d) Weather and feeding. Observations were conducted under a number of weather conditions between 1400-1800hrs, to determine the rate at which adult Guillemots provided (known age) chicks with food (see earlier). The following envirnomental parameters were recorded during each observation period; wind speed (estimated using the Beaufort Scale (Met. Office 1956: 15-16)). Sea conditions (ranked from 1-3; calm, medium and rough), and cloud cover (ranked from 1-8 cover, where 1 = clear and 8 = completely overcast) (Met. Office 1956: 35-36).

(e) Distribution of birds at sea. A total of five transects was made between Skomer and the island of Grassholm - which lies approximately six miles (9.6km) west of Skomer, between late May and mid July. Transects were made in the M.V. 'Lord Hurcomb', travelling at an average speed of 4 nautical miles / hr, under clear, flat-calm conditions. The number of Guillemots, Razorbills and Puffins on the sea was recorded in each mile between Skomer and Grassholm. The size of Guillemot groups was also recorded. A bird was considered to be part of a group if it was within about 30m of another Guillemot.

To determine to what extent Guillemots fed in mixed species flocks a record was kept of all feeding flocks seen from Skomer during May-July 1974 and 1975. All flocks were estimated to be within 1-2 miles (1.6 - 3.2km) of the shore. The number of each species in the flock was recorded.

(f) Distribution of prey species. As an example of clupeid (Sprat) distribution, an echo-trace made near Grassholm in July 1970, by MAFF workers, and unpublished material supplied by P.O. Johnson (MAFF Lowestoft) are included.

(g) Duration of feeding trips. To provide some sort of estimate of the distance that Guillemots flew to feeding areas, where possible I recorded the time of departure of parent Guillemots and their subsequent return with fish. Data were collected during morning and afternoon feeding watches.

(h) Pattern of departure from colonies. To determine whether the pattern of departures from a colony was non-random, I recorded the time interval between subsequent departures from a large colony, containing 600-800 pairs of Guillemots. Since the inter-departure interval was often very short a tape-recorder was used to record information in the following way. The tape-recorder was started, and for 30 minutes I noted when a bird flew past a specific point on its way out of the colony. Later, the inter-departure interval was measured using a stop-watch. Measurements were made to the nearest second. The formula used in the analysis of this data, to calculate expected values, in order to determine whether departures from the colony were non-random using a chi-square, was as follows:-

$$(- \text{Exponential}^{-\lambda X_1} + \text{Exponential}^{-\lambda X_o})n = \text{Expected}$$

Where, X_1 = top interval, and X_o = lower interval of inter-departure interval categories. The intervals between subsequent departures have been grouped into five second periods; 0-5, 5-10, 10-15, etc.,

$$\lambda = \frac{\text{Total number of events (n)}}{\text{Total time}}$$

Expected values have been combined when they were less than 5.

(i) Flight directions from colonies. If Guillemots leaving the colony for feeding areas are following each other, departures should be a) clumped in time (see above), and b) clumped spatially. To test b) I recorded the direction that birds departed from their colony. This was conducted by following birds through 13 x 60 binoculars mounted on a tripod until they disappeared from view. The direction in which they had flown and disappeared from view was determined using a compass and was plotted on to a map. By following some birds as they flew south of Skomer, towards Skokholm (2 miles / 3.2km away) I estimated that Guillemots could be observed for nearly two miles in good light. The sea area, roughly forming a semi-circle, adjacent to the colony where observations had been made, was divided into nine 20° sectors (Fig.4.15), and the number of Guillemots falling into each sector was recorded. Observations were carried out at two separate colonies, one on the north coast of Skomer and the other on the south, in 30 - 60minute periods over three days within two hours of each other on each day.

Results

(a) Chick Diet. The composition of Guillemot chicks' diet was similar in each of the three years of the study (Table 4.1), with clupeids, mainly Sprats *Clupea sprattus*, forming 95.4% of the total prey items, and 99.2% of all identifiable prey items. Since Ammodytidae made up such a small proportion of the chicks' diet, they have usually been ignored in the following sections.

The number of prey items collected from ledges over four seasons is small (n = 46), because most fish which Guillemots dropped were eaten by other species (Appendix III). The size distribution of clupeid prey fed to chicks is shown in Fig. 4.1. The results obtained by direct observation and from fish taken from ledges are presented separately. However, it is clear from Fig.4.1 that I tended to under-estimate the size of clupeids in visual observations, probably because it was often difficult to determine how much of the anterior portion of the fish was down the adult bird's throat.

Table 4.1. Fish families fed to Guillemot chicks on Skomer in three seasons.

Year	Clupeids	(%)	Ammodytes	(%)	Unidentified	(%)	Totals
1973	232	(96.2)	3	(1.2)	6	(2.5)	241
1974	700	(94.9)	3	(0.4)	34	(4.6)	737
1975	203	(95.7)	3	(1.4)	6	(2.8)	212
Totals	1135	(95.4)	9	(0.7)	46	(3.9)	1190

Note: Unidentified category were fish which were not seen for long enough to determine family.

Total number of specimens identified = 1144, clupeids constituted 99.2% (1135) of these.

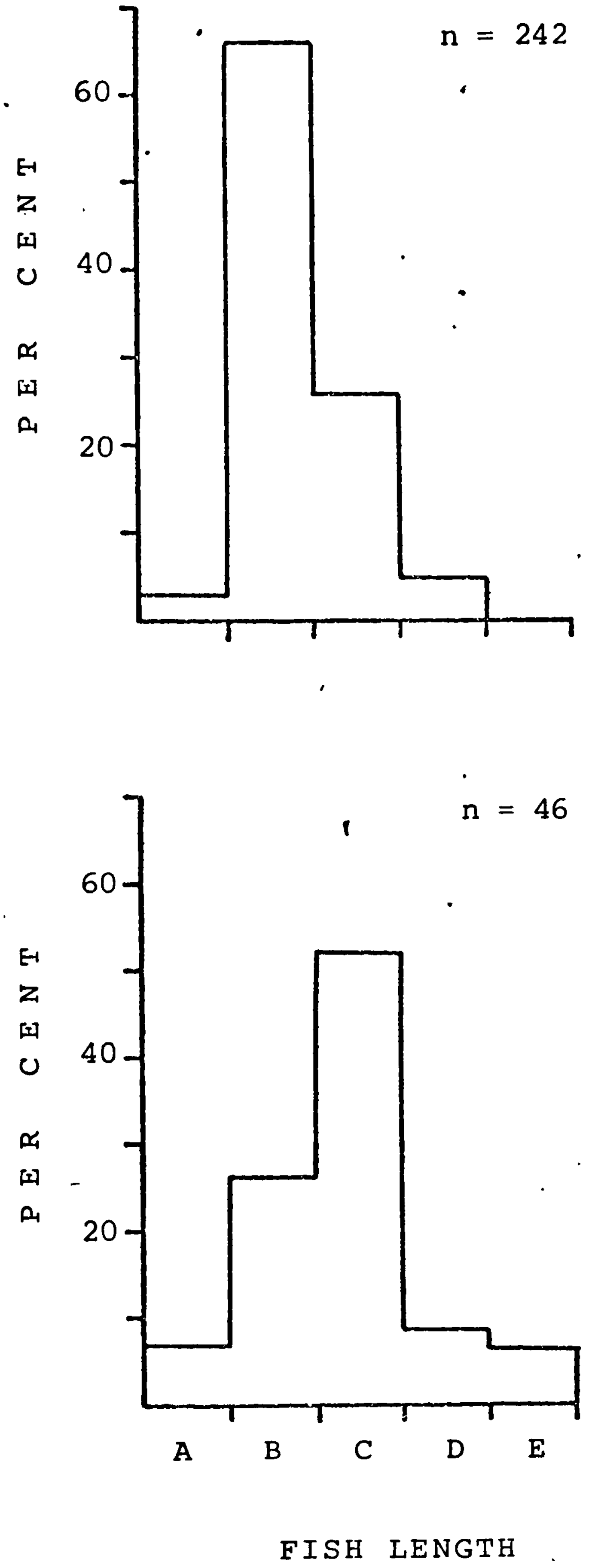


Fig.4.1. Size range of Guillemot clupeid prey. Upper figure is from visual estimates (size estimated on sliding scale - see below). Lower figure (mean = 10.4 ± 0.9 S.D.)is derived from measurements of fish collected from ledges. Size categories (cm.) are: A: 8.1 - 9.0, B: 9.1 - 10.0, C: 10.1 - 11.0, D: 11.1 - 12.0, E: 12.1 - 13.0 cm.

The weight of prey items is plotted against prey-length in Fig.4.2, derived from measurements of fish collected from ledges. The two variables were highly correlated and the relationship could be used to estimate the weight of prey items from their length. Thus, the mean weight of clupeids taken from ledges was 8.8g and the mean length 10.4cm.

There was some evidence that Guillemots selected not only fish of a certain species, but also fish of a certain size to feed to chicks. Throughout the breeding season Guillemots performed a fish-presentation display (see Chapter 5), and on some days at least, the proportions of different fish species involved in fish-presentation differed from that fed to chicks. For example, on July 6 1973, Guillemots brought 98 clupeid and 1 Ammodytes spp. to feed to chicks, and 31 clupeids and 16 Ammodytes for fish-presentation, over the daylight period. The difference in the proportion of the two species for chicks and fish-presentation was significant ($X^2 = 33.8$ 1df $P<0.001$). Most Ammodytes for fish-presentation were estimated to be 5-7cm (therefore weighing approximately 1g; R.E. Ashcroft, unpubl.).

Since a large proportion of the fish involved in fish-presentation are likely to be dropped (see Appendix III) one might argue that the samples of fish collected from ledges may be biased. However, most of the samples from ledges were taken from under or beside chicks, and Guillemots with chicks did not perform fish-presentation (see Chapter 5), so it seems likely that most specimens I collected were fish that adults or chicks had dropped during chick-feeding.

Food species fed to Common Guillemot chicks have been recorded by a number of workers. Table 4.2 shows the range of species utilized; all the important ones are mid-water schooling species (see also Tuck 1960,

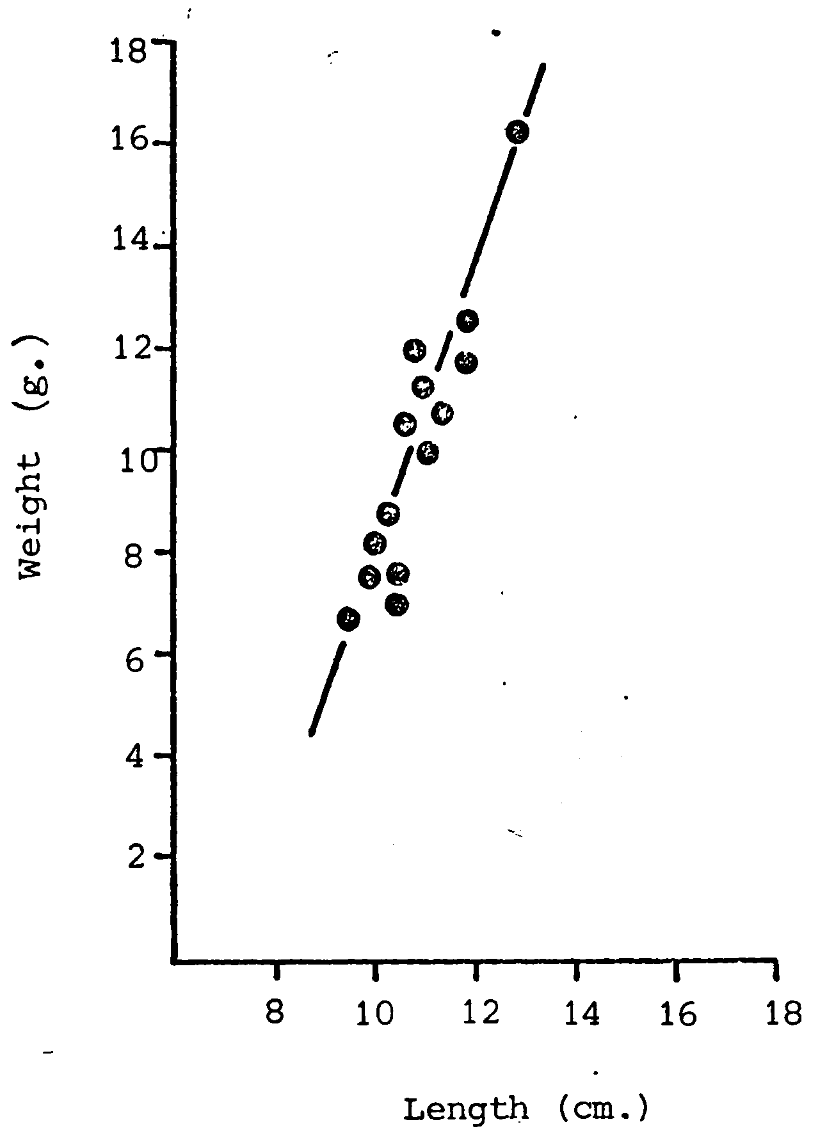


Fig.4.2. Relationship between weight and length of clupeids caught by Guillemots. The regression equation is:
$y = 2.79x - 19.9$ ($n = 16$).

Table 4.2. Fish families fed to Guillemot chicks in different areas. Fish are arranged (l - r) in order of importance.

Locality	Ammodytidae	Clupeidae$_1$	Clupeidae$_2$	Gadidae$_1$	Gadidae$_2$	Engraulidae	Osmeridae$_1$	Osmeridae$_2$	Serranidae	Cottidae	Scombridae	Pholidae	Authority
Skomer Is. Wales	+	*											This study
Farne Is. G.B.	*	+										+	Pearson 1968
Lundy Is. G.B.	+	+									+		Perry 1940
Faeroes		*											Salomonsen 1935
Iceland				*									Taning (in Salomonsen 1935)
East Murman, USSR	*		+	+	+								Kaftanovski 1938
Barents Sea, USSR	*		*	*			*						Belopolski 1957
Novaya Zemlya, USSR	+			+	*		+			+			Uspenski 1956
Western USA						*		*					Scott 1972
Western USA	*					*		*	+				Cody 1973
Cape Thompson, Alaska	*				*								Swartz 1966

Notes: * = recorded as important part of diet, + = present in diet.
Common names to fish families from left to right = Sandeels, Sprats, Herring, Cod, Arctic Cod, Anchovies, Capelin, Smelts, Sea Bass, Sculpins, Mackrel, Gunnels.

Scott 1972). The length and weight of items for chick consumption on Skomer are similar to those recorded in other studies (Pearson 1968, Scott 1972, Cody (1973 and pers.comm.). However, Uspenski (1956) recorded that in Novaya Zemlya Brunnich's Guillemot chicks were fed fish which averaged 15g and Tuck & Squires (1955) found that most prey species in the diet of Brunnich's Guillemot in Canada weighed 25g.

Adult Common Guillemots have been recorded feeding on invertebrates (Swartz 1966, Scott 1972), and I recorded them using squid for fish-presentation displays on Skomer, which indicates that they may utilize them for self-maintenance. Invertebrates have rarely been found in the diet of chicks however. The same is also true of Brunnich's Guillemot. Although invertebrates consititute a greater part of the adult's diet (Swartz 1966), the chicks are fed almost exclusively on fish (Tuck & Squires 1955, Uspenski 1956, Swartz 1966). Tuck & Squire found that one Brunnich's Guillemot chick which they attempted to hand rear on a diet consisting solely of the amphipod Gammarus, failed to increase in weight and died.

(b) Chick Development.

1) Food intake. This section examines food consumption by Guillemot chicks, first with respect to time of day, and second, with respect to age. On two occasions when observations throughout the daylight period were conducted, there was a small peak of chick-feeding soon after first light (Fig.4.3). The mean feeding rate in the morning was 1.03 fish/chick/4hrs ± 0.20 S.D. (n = 8) and in the afternoon was 0.77 fish/chick/4hrs ± 0.11 S.D. (n - 12) (t = 3.74 18df $P<0.002$).

The food consumption of a total of 60 chicks (average age 9.9 days ± 4.9 S.D. ; range 1-20) over the entire daylight period averaged 3.23 fish/chicks/day ± 1.42 S.D.

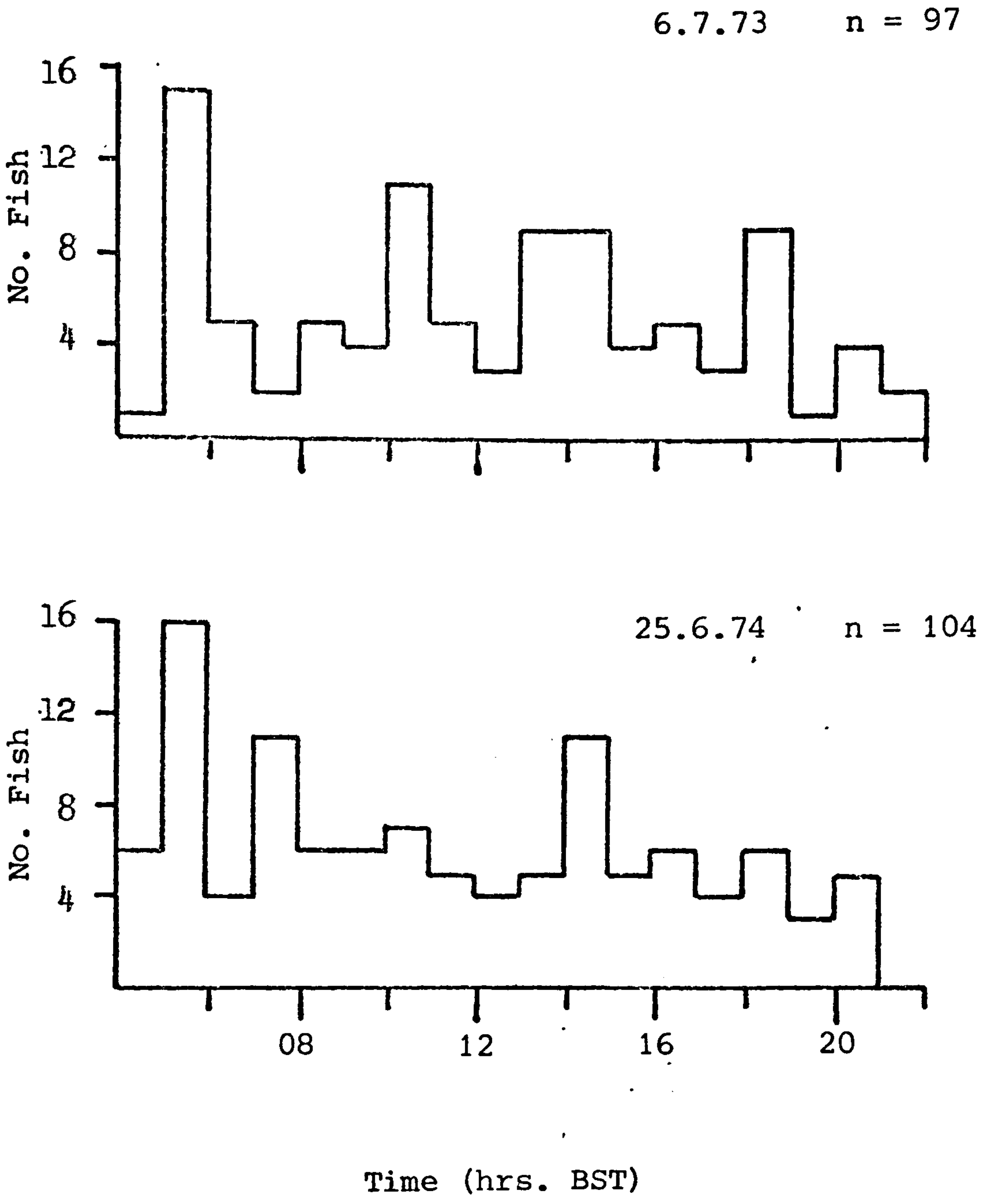


Fig.4.3. Diurnal pattern of chick-feeding at groups of chicks in two years. Histograms show hourly totals of fish broght to chicks between first light (about 0400hrs) and dark (2200hrs).

Using data from early morning and afternoon observation sessions, the mean number of fish fed to chicks during a four hour period for all observation sessions is shown in Fig.4.4. The data in Fig.4.4 are for afternoon (4.4a) and morning (4.4b) sessions. Fig.4.4 shows that there was a decrease in feeding rate with increasing age, and if one and two day old chicks are excluded (since their feeding rate was apparently lower, and because they were sometimes fed smaller fish than older birds - see below), there is a significant negative relationship in both sets of data.

The afternoon feeding data confirm the estimate for No.feeds/chicks/day from whole day watches (presented above). The overall mean from Fig.4.4a is 0.73 feeds/chicks/4hrs which = 0.18 feeds/chicks/hr, with an average of 18 hours of daylight during late June and July; this gives a mean feeding rate of 3.24 feeds/chick/day. The true estimate would probably be slightly higher, since this calculation does not take into account the small early morning peak. Nevertheless, this estimate agrees well with the one already presented.

There was no evidence to suggest any change in the size of prey items presented to older chicks, based on visual estimates. However, it may be significant that the only chicks I observed to be fed small sandeels (Table 4.1) (5-7cm) were less than three days old.

From the data presented it is possible to estimate roughly the food intake of Guillemot chicks, in terms of grams of fish per day. The mean length of fish fed to chicks was 10.4cm, weighing about 8.8g. With an average of 3.23 feeds/day to the average daily food intake of chicks of all ages was 28.4g.

2) Provisioning rate and weather conditions. The rate at which parent Guillemots brought food to chicks in 22 separate 4-hour observation periods was compared under different weather conditions using a step up multiple linear

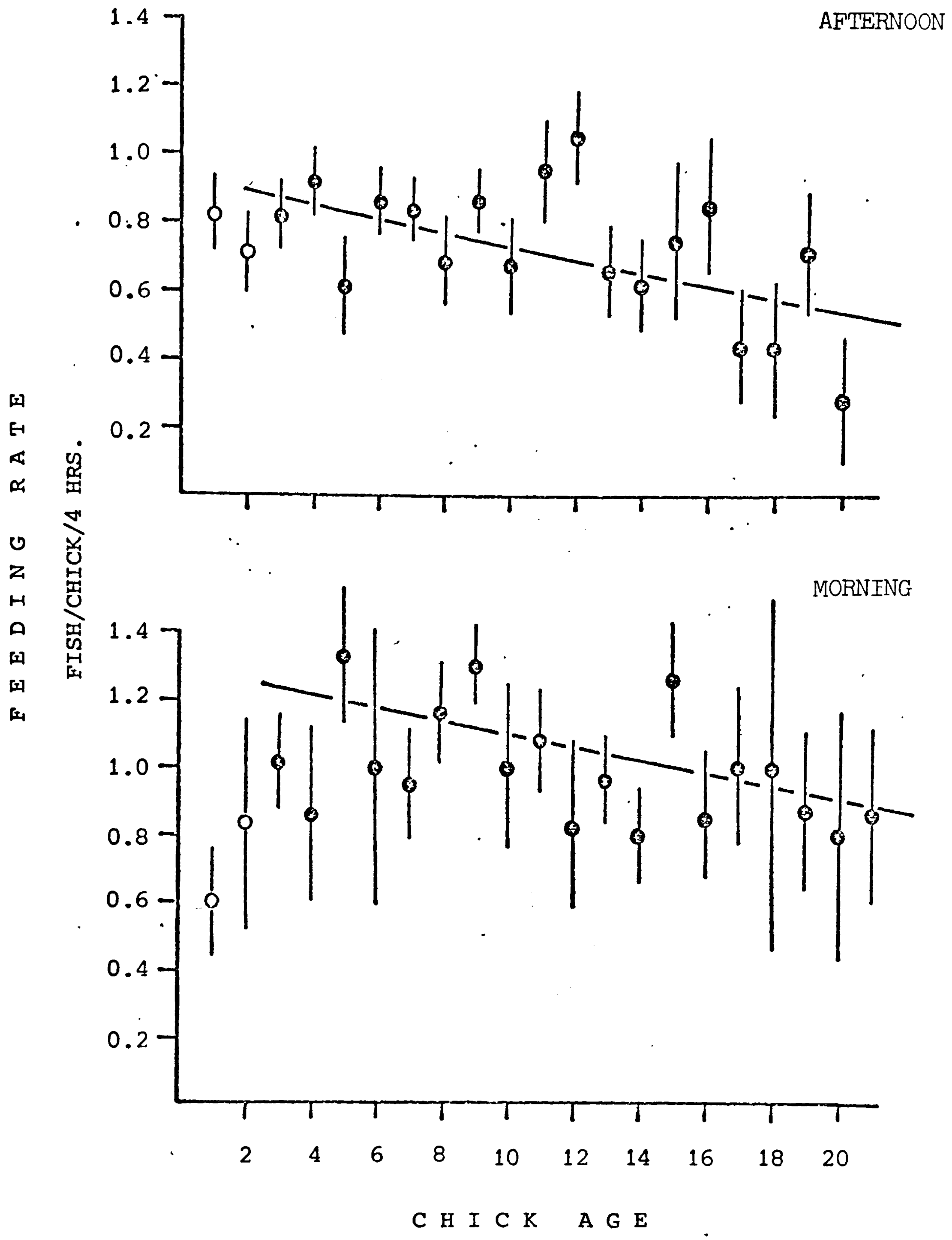


Fig.4.4. Relationship between feeding rate and chick-age (days) ± one S.D. Open symbols = chicks one and two days old, these are not included in the calculation of regression lines. Upper figure is based on afternoon observations regression equation: $y = -0.021x + 0.964$ ($r = -0.551$ 16 df $P<0.02$). Lower figure is based on morning observations; regression equation: $y = -0.0133x + 1.160$ ($r = -0.466$ 17 df $P<0.05$).

regression analysis. The values for three independent and one dependent variables are presented in Table 4.3. The results of this analysis showed that there was a significant negative relationship between feeding rate and sea conditions (X_2) ($r = 0.563$ $P<0.01$) (Fig.4.5), which accounted for 32% of the variation in provisioning rate (see Table 4.4). Thus, provisioning rate of chicks is highest during calm sea conditions, suggesting that the ability of adult Guillemots to capture food is greatest under these conditions.

3) Chick growth. A number of different growth parameters have been presented for Guillemot chicks in Tables 4.5 and 4.6, but the instantaneous growth rate (R) is the most accurate (Manuwal 1972, Ricklefs 1973). R is calculated from the formula originally presented by Brody (1945:508) modified by Banks (1959:103). The formula is:-

$$R = \frac{2.3 \log W_2 - \log W_1}{t_2 - t_1}$$

Where W = weight and $t_2 - t_1$ = time interval (days), 2.3 is a factor used to convert Logs to the base 10, to natural logs. The instantaneous growth rates in Table 4.5 are derived from combined data. That is, because my sample size on any one day is small, I have combined data in two-day periods, e.g. 2+3, 4+5 etc., (see Figs.4.6 and 4.7). The overall mean value for weight and wing length was obtained by calculating the mean rate for each two-day period of the nestling period.

The fledging period of Guillemots on Skomer averaged 21 days (Table 4.7). I have compared my data for weight increase with Pearson's (1968) from the

Table 4.3. Guillemot chick-feeding rates and weather conditions

Date	Feeding Rate Y	Wind X_1	Sea X_2	Cloud X_3	Sample Size
21.6.74	0.71	5	2	0	24
22.6.74	0.72	3	2	0	25
23.6.74	0.82	2	1	8	24
24.6.74	0.72	1	1	8	26
25.6.74	0.71	2	1	3	24
26.6.74	0.83	1	1	8	24
27.6.74	0.58	3	2	4	24
27.6.74	0.77	3	2	4	31
28.6.74	0.69	1	1	8	29
28.6.74	0.90	1	1	8	31
29.6.74	0.69	6	3	4	13
1.7.74	0.61	2	3	0	23
2.7.74	0.85	4	2	8	34
4.7.74	1.00	3	2	8	29
7.7.74	1.00	2	1	8	17
15.6.75	0.67	2	1	0	15
17.6.75	0.94	2	1	0	18
19.6.75	0.48	6	3	8	21
20.6.75	0.58	2	2	8	19
21.6.75	0.89	1	1	0	18
23.6.75	0.87	2	1	5	15
27.6.75	1.07	2	1	8	13

Notes: For wind, sea and cloud estimates see methods section.

Mean number of chicks observed (sample) = 22.6

Feeding rate (Y) = mean rate/4 hr period (1400-1800hrs) for chicks 3 - 16 days old.

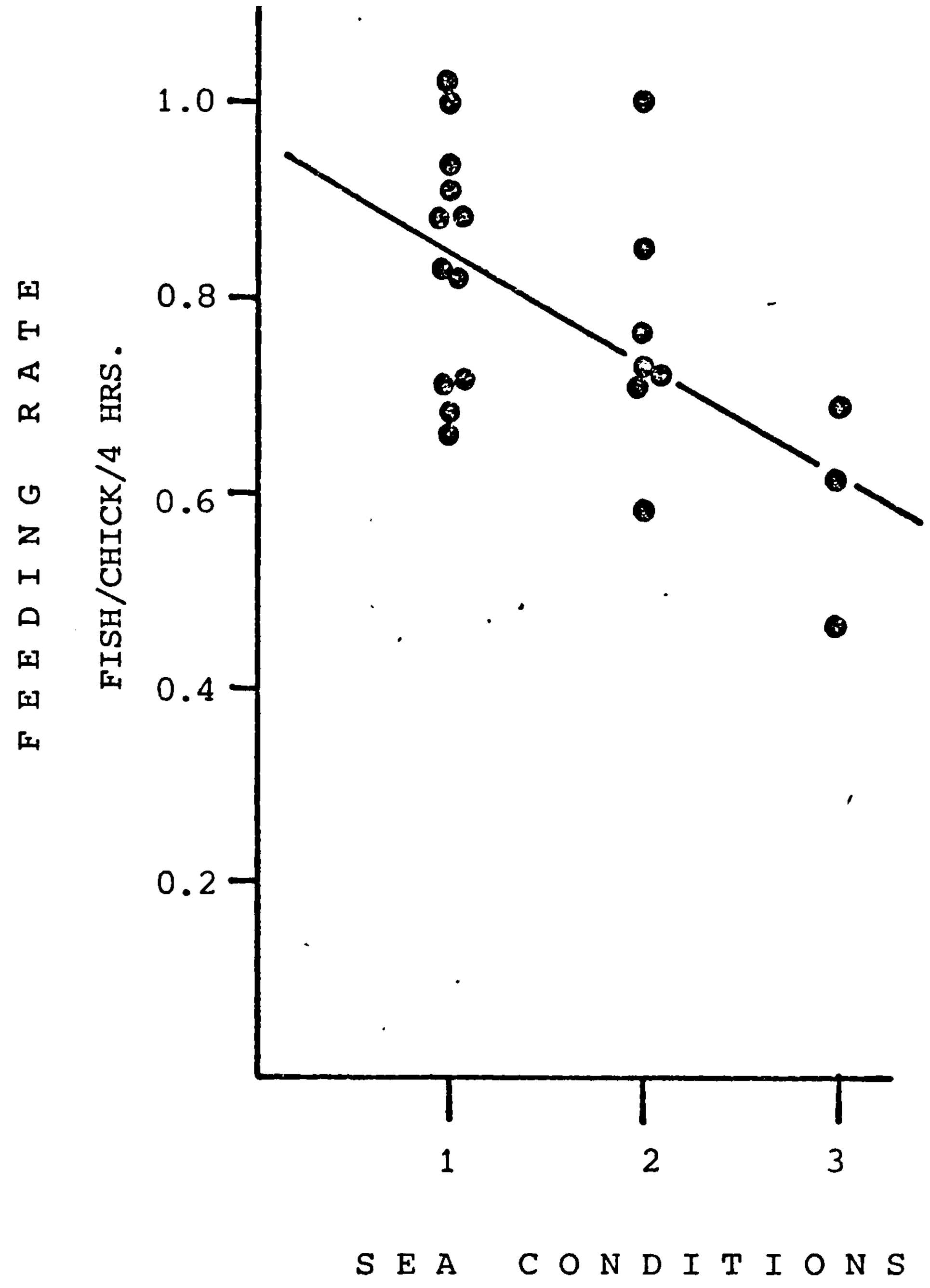


Fig.4.5 Relationship between the rate at which adults feed chicks, aged 3 - 16 days old, and seå conditions. The regression equation is: $y = -0.118x + 0.966$ ($F_{1,20} = 9.3$ $P<0.01$).

Table 4.4. Provisioning rate and weather conditions, step-up multiple regression course of analysis. The percentage variation accounted for (r^2) by each independent variable is shown.

	Wind Speed X_1	Sea Conditions X_2	Cloud Cover X_3
Alone	14%	32%**	4%
With sea conditions	33%	-	33%

** $P<0.01$

Table 4.5. Instantaneous growth rates (R) of weight and wing length ± one standard deviation (S.D.) of Guillemot chicks on Skomer.

Age	Mean Weight	S.D.	R	n	Mean wing length	S.D.	R	n
1	67.3	5.6	-	15	24.6	0.54	-	5
2-3	85.0	11.1	0.118	8	26.3	1.21	0.032	6
4-5	106.4	16.7	0.108	8	27.6	0.74	0.024	8
6-7	133.8	19.5	0.112	12	29.9	1.52	0.040	10
8-9	153.5	24.6	0.071	11	33.5	3.06	0.057	10
10-11	175.0	24.6	0.069	11	36.8	4.13	0.047	10
12-13	191.5	25.7	0.042	9	40.5	4.21	0.048	8
14-15	194.5	22.0	0.008	13	42.5	3.12	0.024	12
16-17	214.6	24.1	0.047	14	47.5	3.78	0.055	13
18-19	214.2	18.5	-0.001	12	52.6	3.77	0.051	12
20-21	215.4	19.8	0.006	9	56.1	3.97	0.032	7
21-22	202.7	25.8	-	3	54.3	2.31	-	3
Mean			0.058				0.041	
S.D.			0.045				0.012	

Note: Data for days 21-22 are not included in calculated mean R value, since n is only 3.

Table 4.6. Some growth parameters of Common Guillemot, Brunnich's Guillemot and Razorbill.

Locality	Ad.Wt.	Hatch wt. g.	Hatch wt. as % Ad.wt	Growth Rate$_a$	Max. wt.$_b$	Age at max.wt.	Fledging wt. g	Fledging wt. as % Ad.wt	Nestling Period	Source
COMMON GUILLEMOT										
Wales	875	67.3	7.7	9.2	217.8	16-17	214.9	24.6	21.2	This study
England	925	55.5	6.0	10.2	249.7	19	-	-	-	Pearson 1968
U.S.A.	980	95.0	9.7	8.5	274.0	21	274.0	27.9	21	Cody 1973
Alaska	956	c65	6.8	6.2	c210	21	172.1	18.0	22	Johnson & West 1975
Alaska	984	-	-	-	-	-	179.9	18.3	-	Swartz 1966
Canada	965	77.0	7.9	-	-	-	-	-	-	Johnson 1944
USSR	1054	c95	9.0	8.9	274	20	274	26.0	20	Belopolski 1957
BRUNNICH'S GUILLEMOT										
Novaya Zemlya i USSR	967	70.3	7.2	4.3	140	17	140	14	21	Uspenski 1956
ii	975	70.3	7.2	4.8	124	12	124	13	21	Uspenski 1956
iii	944	70.3	7.2	7.2	150	12	150	16	21	Uspenski 1956
East Murman USSR	-	c70	-	11.3	240	15	250	21	24	Kaftanovski 1951
Alaska	989	c67	6.8	8.2	190	15	207.7	21	22	Johnson & West 1975
Alaska	964	-	-	-	-	-	121.5	12.6	-	Swartz 1966
Canada	899	65	7.2	7.9	184	15	200	22	21	A.J.Gaston unpubl.
RAZORBILL										
Wales i	628	c60	9.5	7.7	168	14	157	25	17	C.S.Lloyd unpubl.
Wales ii	628	62	9.8	-	-	-	189	30	18.5	Plumb 1965
Wales iii	628	58	9.2	7.7	173.2	15	164.5	26.3	18	Brun 1958
Canada	701	63	8.9	6.6	155	14	140.3	20	18.2	Bedard 1969d

Notes: a. Growth rate = g./day up to maximum weight.

b. Maximum weight = the point at which weight begins to level-off.

c. Figures preceded by 'c' indicates figures extracted from diagrams and are therefore approximate, as are values derived from them.

d. Novaya Zemlya i-iii for Brunnich's Guillemot; i = 1948, ii = 1949, iii = 1950. Chick hatching weight is mean for three years.

e. Wales i - iii for Razorbill = studies on Skokholm in different years.

Table 4.6. Some growth parameters of Common Guillemot, Brunnich's Guillemot and Razorbill.

Locality	Ad.Wt.	Hatch wt.		Growth Rate$_a$	Max. wt.$_b$	Age at max.wt.	Fledging wt.		Nestling Period	Source
		g.	as % Ad.wt				g	as % Ad.wt		

Table 4.7. Fledging period of 42 Guillemot chicks on Skomer.

No.of days	15	16	17	18	19	20	21	22	23	24	25	26	27
No.of chicks	1	1	1	1	5	8	7	6	4	3	3	1	1
Per cent. chicks	2.4	2.4	2.4	2.4	11.9	19.0	16.7	14.3	9.5	7.1	7.1	2.4	2.4

Overall mean = 21.21 days ± 2.6 S.D.

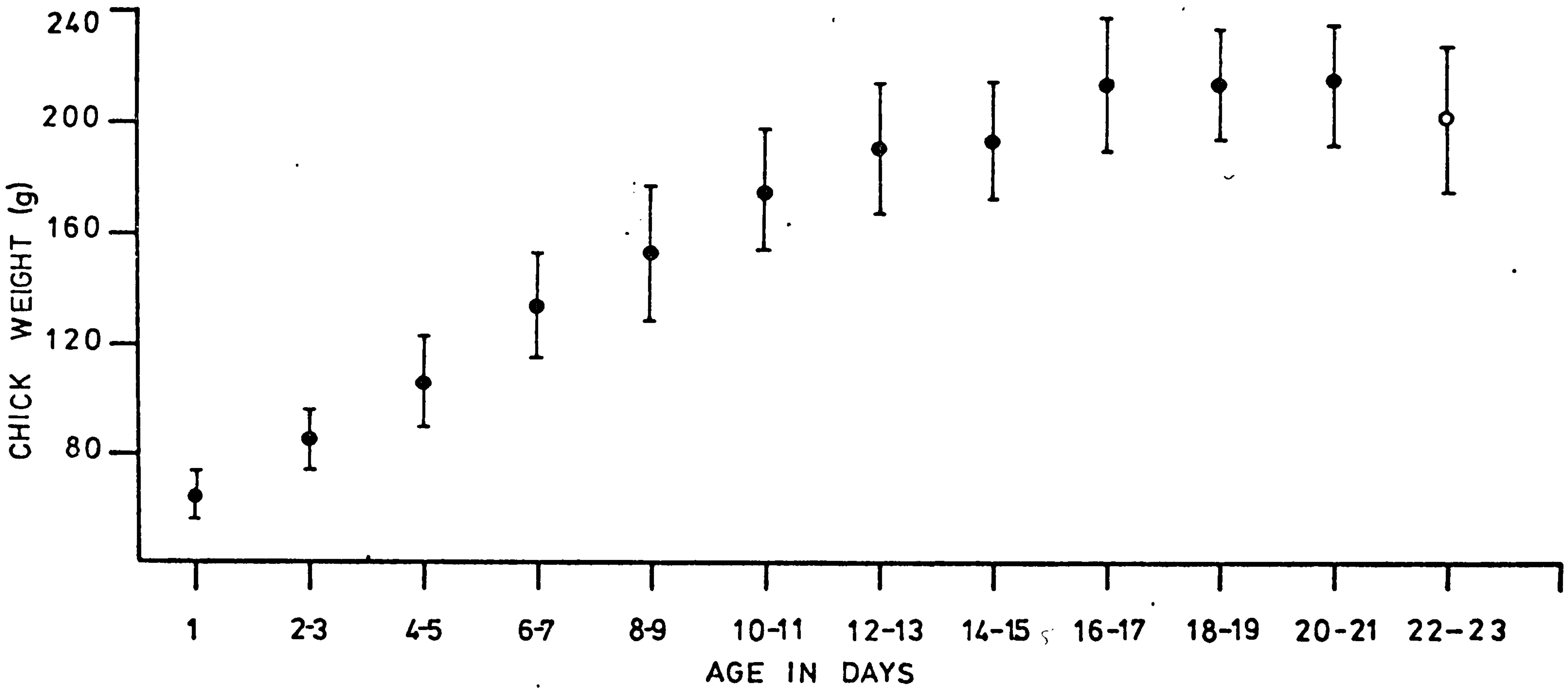


Fig.4.6. Chick weight in relation to age ± one S.D. Except for day 1 (day of hatching) data have been combined into two-day groups; 2+3, 4+5 etc. (n = 12 chicks). Days 22/23 (o) n = 3.

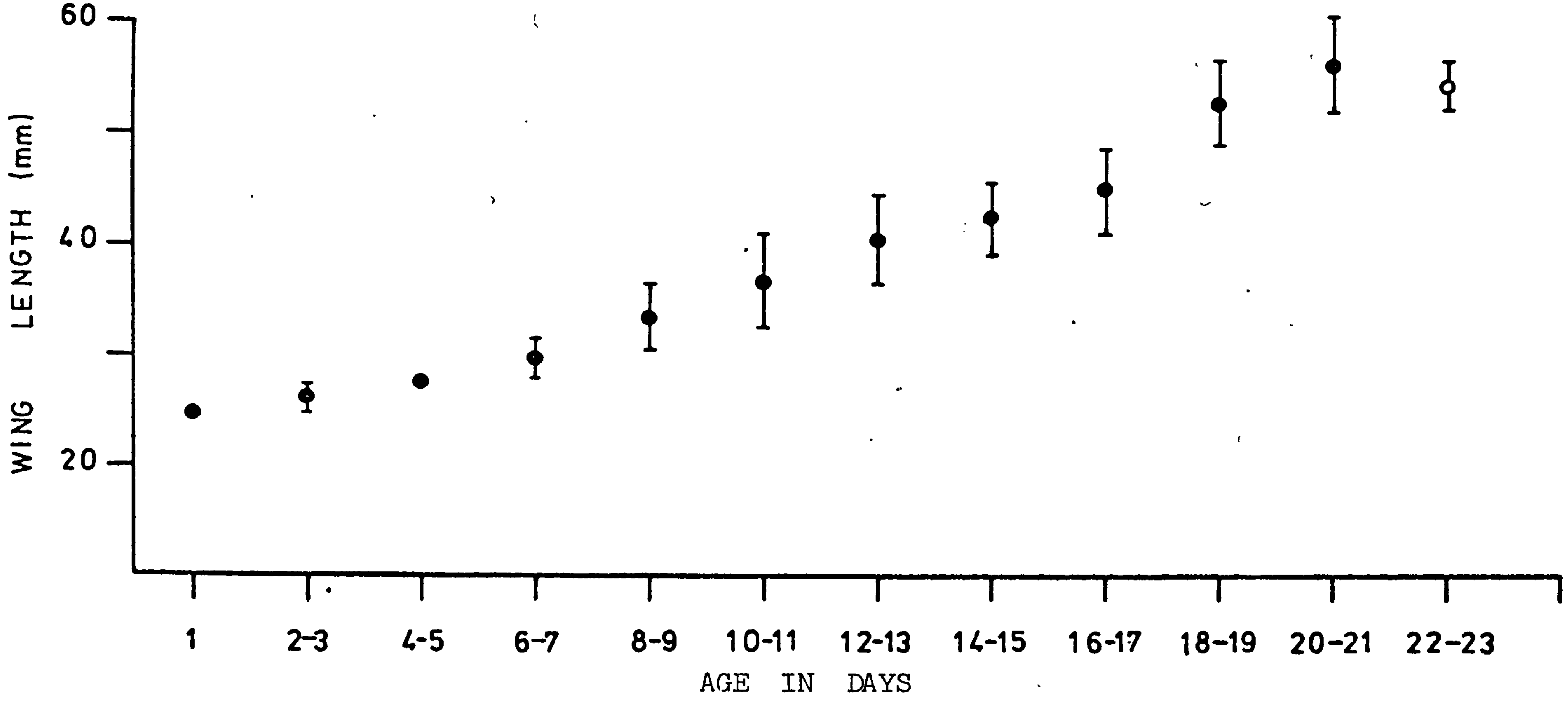


Fig.4.7. Chick wing-length in relation to age ± one S.D. (see also caption to 4.6.).

Farne Islands, northern England ($55^{o}N$). Table 4.8 compares weight increments in two-day periods for the two sets of data. The data indicate different patterns of weight increase, for example, between days 3-5 Skomer chicks increased by about 14 grams on average, but Farnes chicks by over three times this amount; 46 grams. Also, between days 11-13 Skomer chicks increased by 29 grams, but Farnes chicks by 18.5 grams. These differences may be due to either small sample sizes (Skomer, n = 12; Farnes, n = 10), and / or day to day variations in chick feeding rates in the two areas. The growth rate (R) of the two samples on a two-day interval basis during the period of positive weight increase in both samples (taken here as up to day 16/17, see Table 4.8), were not significantly different (t = 0.385 15 df NS). Thus, the pattern of weight increments differed between the two samples, but not the overall rates of growth up to 16-17th day.

Throughout the nestling period one adult normally remains at the nest site and guards and broods the chick. I never observed chicks left unattended (except at fledging, where this is normal) unless disturbed. Regular measuring of Guillemot chicks resulted in the parent birds leaving the nest sites as I approached, and after the first three or four visits, left their chicks at the first alarm calls given by *Larus* gulls - often when I was 20-30m away. Guillemot chicks are unable to maintain their body temperature until the tenth day (Johnson & West 1975), so some chicks, younger than this, may have become chilled. Moreover, as already pointed out, to reduce the risk of losing chicks I selected small, isolated ('safe') sites for regular measurements of chicks. Guillemots nesting in these situations may have been more nervous than birds nesting in larger more 'central' colonies (Chapter 3). In addition, there may also be differences in the 'quality' of birds nesting in 'central' and

Table 4.8. Weight increments per 48 hours of Guillemot chicks on Skomer and the Farne Islands (from Pearson 1968). Mean weight of adult Guillemots on Skomer = 875g and Farnes = 925g.

SKOMER				FARNES		
Age	Mean wt.	wt.change	as % adult weight	Mean wt.	wt.change	as % adult weight
1	67.3			55.5		
3	91.0	23.7	2.71	83.2	27.7	3.00
5	104.8	13.8	1.58	129.5	46.2	4.99
7	135.7	30.9	3.53	148.0	18.5	2.00
9	155.8	20.1	2.30	166.5	18.5	2.00
11	179.4	23.6	2.70	185.0	18.5	2.00
13	208.0	28.6	3.27	203.5	18.5	2.00
15	200.6	- 7.4	-0.84	212.7	9.2	0.99
17	217.3	16.7	1.91	220.0	9.3	1.00
19	216.7	- 0.6	-0.07	249.7	27.7	2.99
21	217.4	0.6	0.07			

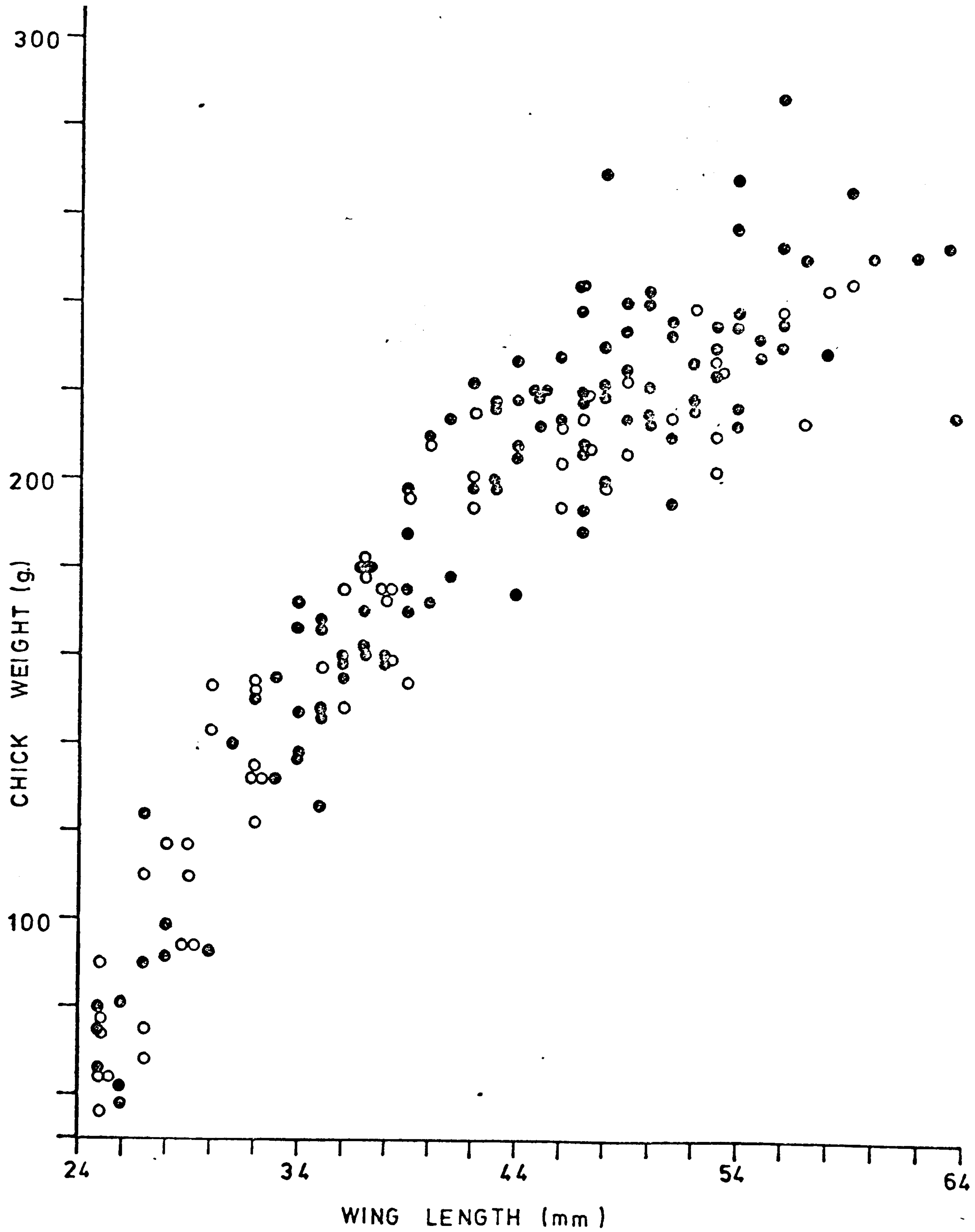


Fig. 4.8. Comparison of weight against wing length of two samples of chicks (see text).Group 1 (●) was measured on● a single occasion (n = 114), Group 2 (o) was measured every second day (n = 12 chicks).

and 'peripheral' sites (Coulson 1968). Therefore, to test whether the sample of birds measured was representative of the Skomer population as a whole, and whether disturbance had any effect, the development of regularly weighed chicks was compared with that of chicks in larger groups visited only once. Since wing length continues to increase throughout the nestling period and is apparently less sensitive to short-term nutritional defficiencies (Ricklefs & White 1975) I have compared the weight of the two groups of chicks in relation to wing length. Fig.4.8 shows the weight and wing length of the two sets of chicks.

Although Fig.4.8 suggests that there was little difference in development of the two groups of chicks, the possibility exists that study chicks had a slower overall growth rate, so that both weight and wing length grew at a slower rate than single-visit chicks. If this was the case, then it would not be possible to detect a difference by this method. However, the fledging weights of study chicks in this study compare favourably with those presented by other workers (Table 4.6), although all studies are subject to the disturbance bias. Also, the highest weights of single-visit chicks in Fig.4.8 are not greatly in excess of study chicks. Even so, the data on this point remain inconclusive.

3) Food intake and weight increase. Between the ages of 3-16 days, during the phase of linear weight increase, the mean feeding rate was 3.35/feeds/chick/day, and the average weight of a meal was 8.8g, thus the mean daily food consumption over this period was 29.5g. During the period of linear weight increase, up to the asymptote at 16-17th day (see Fig.4.6), chicks increased from about 67g to 215g, an increase of 148g in 16 days. This is an average increase of 9.25g/day, thus giving a conversion rate of 31.3%, and 3.2g of fish were

necessary to build one gram of body weight.

(c) Foraging.

1) Distribution at sea. The distribution of Guillemots, Razorbills and Puffins between Skomer and Grassholm is shown in Fig.4.9. Transects between Skomer and Grassholm were carried out under very similar weather conditions; on clear calm days. I estimated that individuals of all three species could be confidently identified up to distances of 200-300m.

A chi-squared test demonstrated that there were significant differences between the distributions of the three species, but there was no clear trend for any species. Consequently I do not consider the data sufficient to form any firm conclusions (but see Discussion).

The distribution of Guillemot group size is shown in Fig.4.10, and this shows that 75/96 (78%) individuals occurred in groups of two or more individuals. Mixed species flocks were recorded between late May and late July. They probably occur after this date, but my observations ceased at the end of July. Table 4.9 shows the relative abundance and frequency of bird species in feeding flocks. In four flocks which I observed forming, Kittiwakes formed the 'nucleus' in two, and Larids (mainly Herring Gulls and Lesser Black-backed Gulls) in the other two. It may also be significant that Kittiwakes and Larids occurred in each flock observed. However, the data may be biased in favour of me noticing these species, since groups of white seabirds feeding in a small area are particularly obvious. This is probably an important point, and other seabirds may use such cues for locating temporarily abundant food supplies (Armstrong 1971). Guillemots occurred in half the flocks observed, although their numbers were generally small

Fig. 4.9. Distribution of Guillemots, Razorbills and Puffins on the sea, in one mile intervals between Skomer Island and Grassholm. Data from five transects, mean ± one standard error are shown.

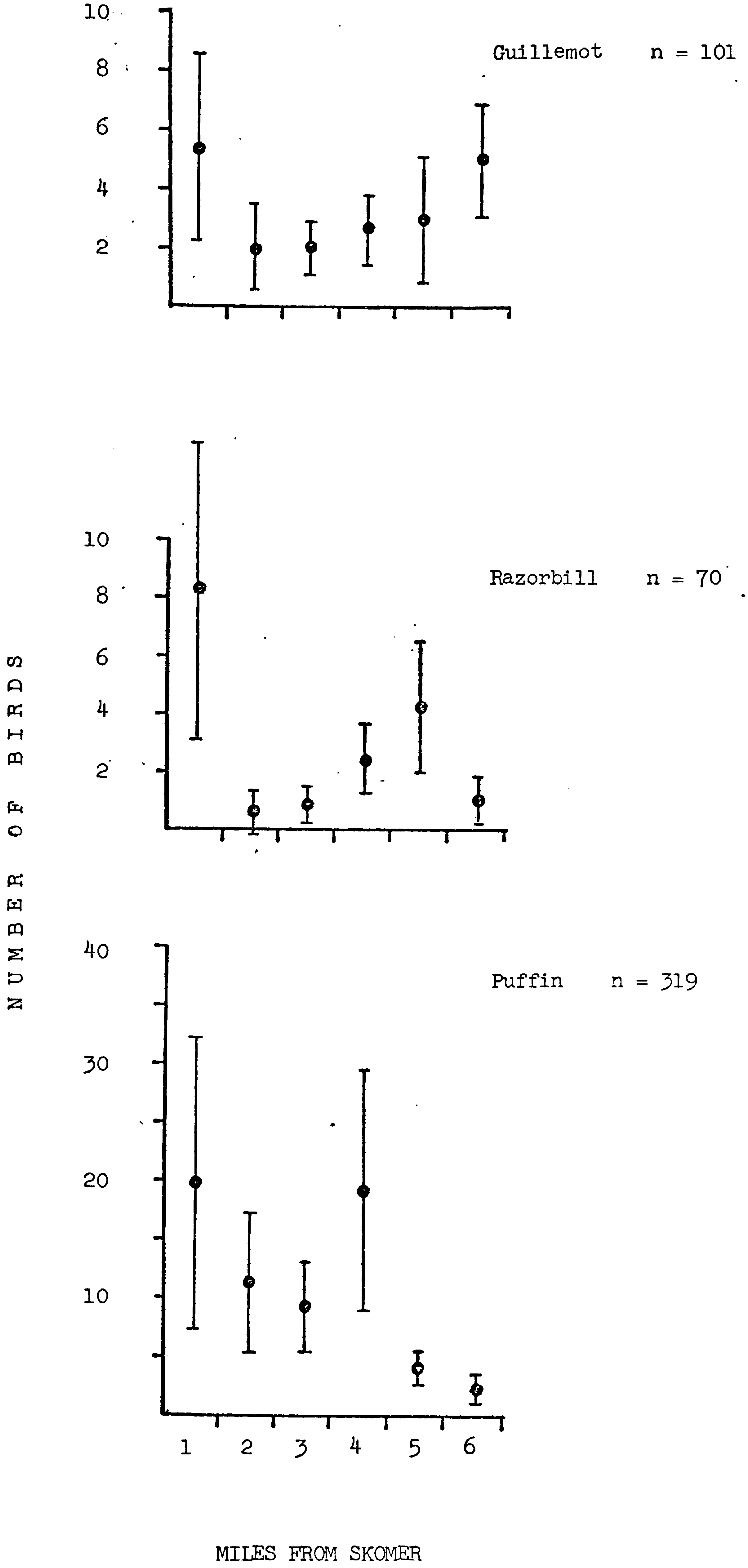

Guillemot n = 101
10
8
6
4
2
Razorbill n = 70
10
8
6
4
2
Puffin n = 319
40
30
20
10
1
2
3
4
5
6
NUMBER OF BIRDS
MILES FROM SKOMER

Fig.4.10. The size distribution of Guillemot groups on the sea between Skomer Island and Grassholm.

Table 4.9. Relative frequency and abundance of seabirds in mixed species feeding flocks off Skomer Island May - July. Total number of flocks = 20.

Species	Frequency		Abundance	
	No.of flocks that contained	% of flocks species	Mean No. of birds/flock	Range
Manx Shearwater	3	15	3	3 - 50
Gannet	1	5	3	-
Shag	1	5	1	-
Larids*	14	70	41.2	3 - 200
Kittiwake	16	80	22.5	5 - 84
Guillemot	10	50	2.5	1 - 20
Razorbill	18	90	15.0	4 - 40
Puffin	10	50	15.0	2 - 120

Notes: * Larids here excludes kittiwakes. Larids or Kittiwakes occurred in all flocks.

(Table 4.9). On the other hand, Razorbills and Puffins occurred in 90% and 50% respectively, of the groups, and with mean numbers of 15 each, were second only to Larus gulls and Kittiwakes.

Mixed species feeding flocks occurred relatively infrequently; in 1975 between mid-May and late July I recorded only 16 flocks, in many hours' observation made during the course of general field-work.

2) Distribution of prey species. Fig.4.11 shows an echo-gram of sprat (clupeid) shoals recorded near Grassholm, about sixteen miles southwest of Skomer, between 1400-1500 hours on 5 July 1970. Data provided by P.O. Johnson (unpublished) for sprat size and distribution off the south coast of Pembrokeshire, in the vicinity of Skomer, show that the mean length and weight of fish was 11.6cm and 11.9g respectively. The mean size of shoals was estimated at $69.3m^3$ (treating the shape of shoals as oblate spheroids), and contained 2000-4000 fish. Fig.4.11 shows that in the middle of the day some shoals occurred near the seabed, at 30-35 fathoms (180-210 feet), and others nearer the surface between 5-10 fathoms (30-60 feet). Johnson's data also showed that small sprats (3-6cm) occur nearer to the shore line than larger fish, and that the largest sprats (13-16cm) were found furthest offshore. It has been shown by other workers that within shoals smaller individuals occur nearer the surface than larger ones (Huntsman 1934, Johnson 1939a, Johnson 1974). It is not known whether there was any difference in the size of shoals or fish within shoals between those near the surface and those near the sea-bed in Fig.4.11.

As with a number of plankton-feeding fish, diurnal, vertical migrations occur (Woodhead 1966); the fish move towards the surface as light intensity decreases in the evening, the shoals disperse near the surface during the hours of darkness, and then reform soon after dawn before moving back to greater

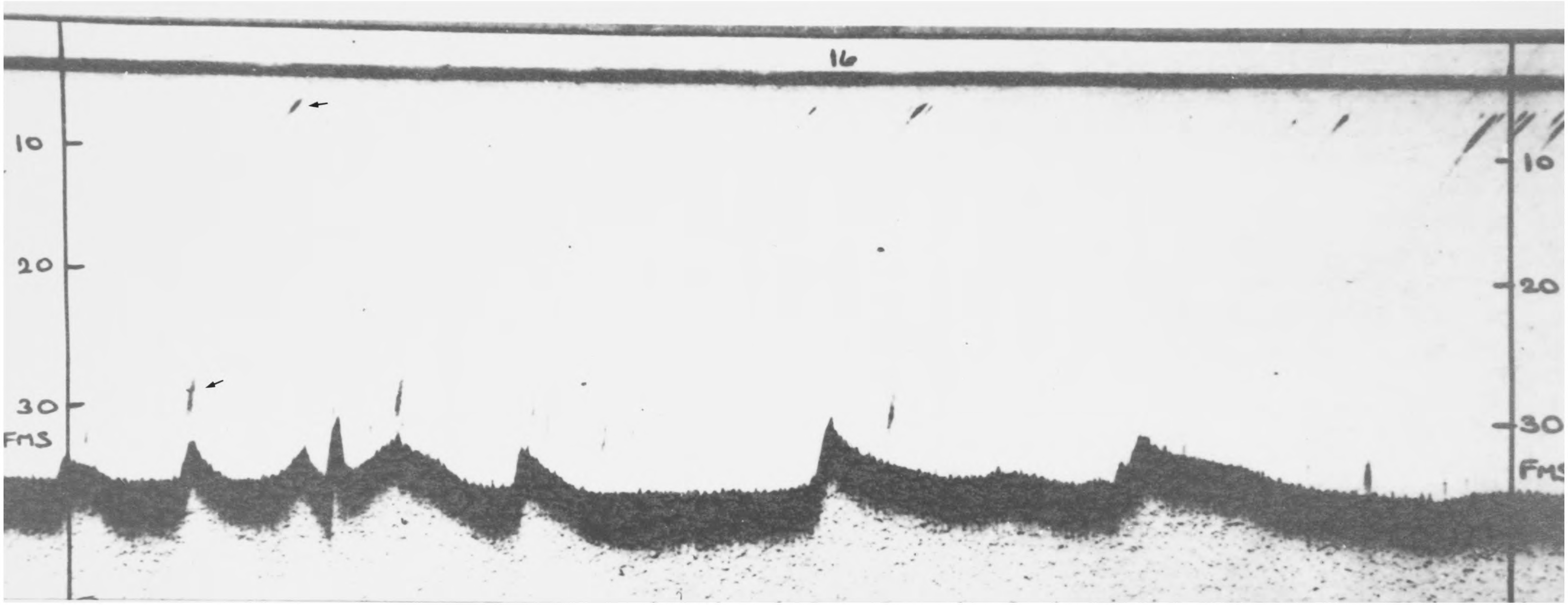


Fig.4.11. Echo-trace of sprat shoals, about 16 miles south-west of Skomer, July 1970; 1400-1500 hrs (B.S.T.). The heavy, dark band near the bottom of the trace is the seabed. The vertical scale (FMS) = fathoms, thus the depth of water is 34 fathoms or about 200 feet. Horizontal scale: 10mm = 247m. Sprat shoals are the cigar-like shapes, two on the left-hand side are marked with arrows. Some shoals are near the surface (especially top, far right) and others near the bottom

depths (P.O. Johnson, pers.comm.).

3) Duration of Guillemot feeding trips. The time interval between an adult Guillemot leaving the colony and returning with fish to feed its chick was recorded on a total of 121 occasions; 62 during the early morning and 59 in the afternoon, (Fig.4.12). Feeding trips were shorter in the morning ($\bar{X}$ = 78.3min ± 46.0 S.D.) than in the afternoon ($\bar{X}$ = 93.5min ± 53.1 S.D.), but this difference was not significant (t = 1.69 119df N.S.). The overall mean of all feeding trips was 85.7min ± 49.9 S.D. The duration of trips varied between 6 and 226 minutes. Very short trips may result if a bird located fish very close to the colony, for example in a mixed feeding flock. Very long trips may result if birds perform self-maintenance activities prior to fishing, or if they spend time sitting on the water with food before feeding chicks. I noted Puffins but not Guillemots actually doing this.

I compared the duration of feeding trips during calm and stormy conditions (seas of rank 1 and 3, respectively), and since there was no significant difference between morning and afternoon results, I have combined the data. Under calm conditions trips were on average 14% shorter (84.1min n = 52) than under stormy conditions (97.6min n = 32), but again this difference was not significant (t = 1.31 82df N.S.).

4) Pattern of departures from the colony. The distribution of inter-departure intervals for 324 Guillemots is presented in Fig.4.13. Data are compared with the random expectation (see methods), and the observed values differ significantly from the expected ones (Table 4.10) (X^2 = 25.7 5df $P<0.001$). Thus, the distribution of inter-departure intervals is non-random, such that more departures than expected occur at less than 5 second intervals. In other words, birds tended to follow one another in rapid succession with the result

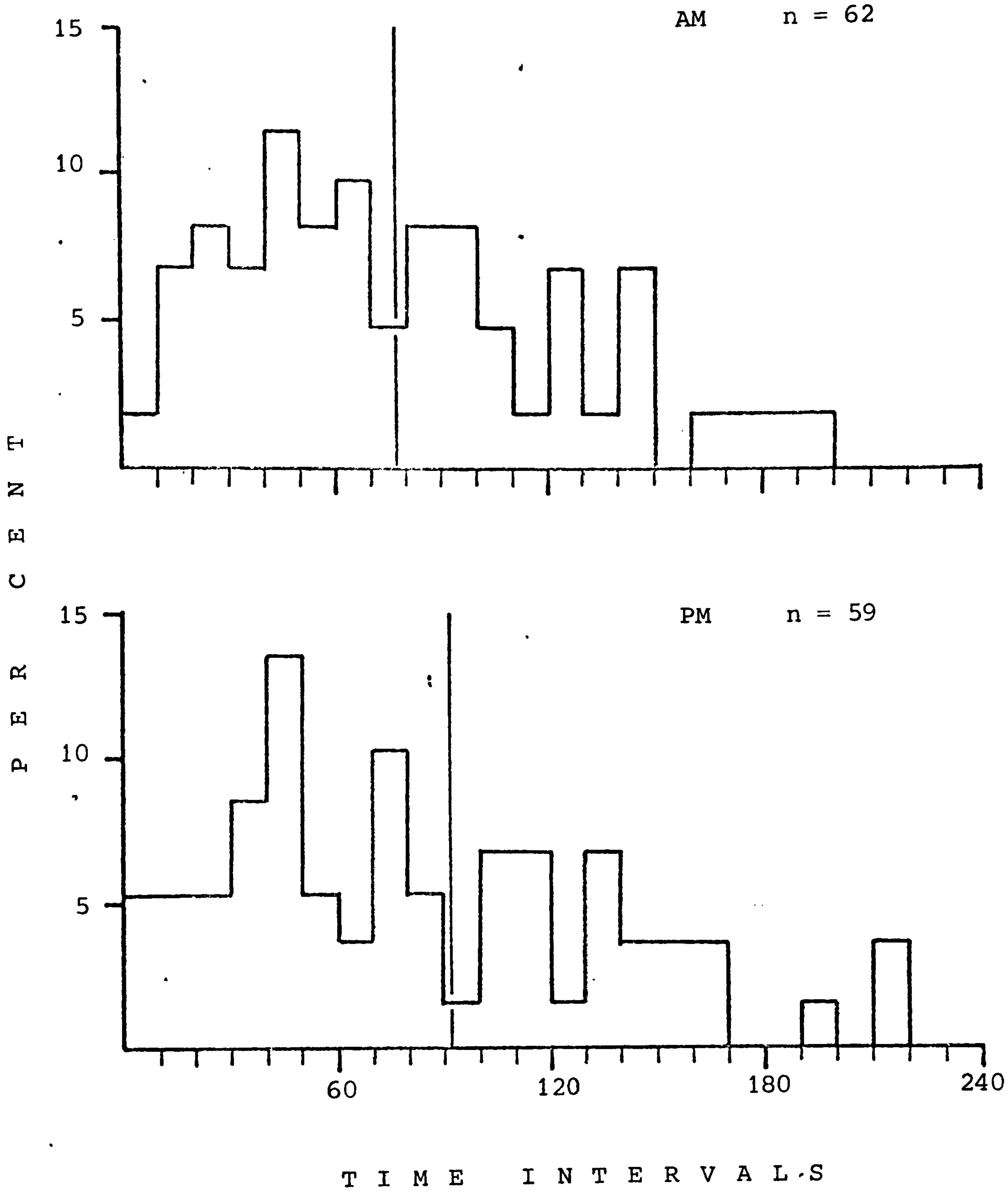


Fig. 4.12. Distribution of feeding trip durations. The scale on the x axis is in 10 minute intervals, ie. 1 - 10, 11 - 20 etc. The upper figure is derived from morning observations (mean = 78.3 min., indicated by vertical bar), lower figure is derived from afternoon observations (mean = 93.5 min.). The number of trips in each 10 min. category is expressed as a percentage of all the observations.

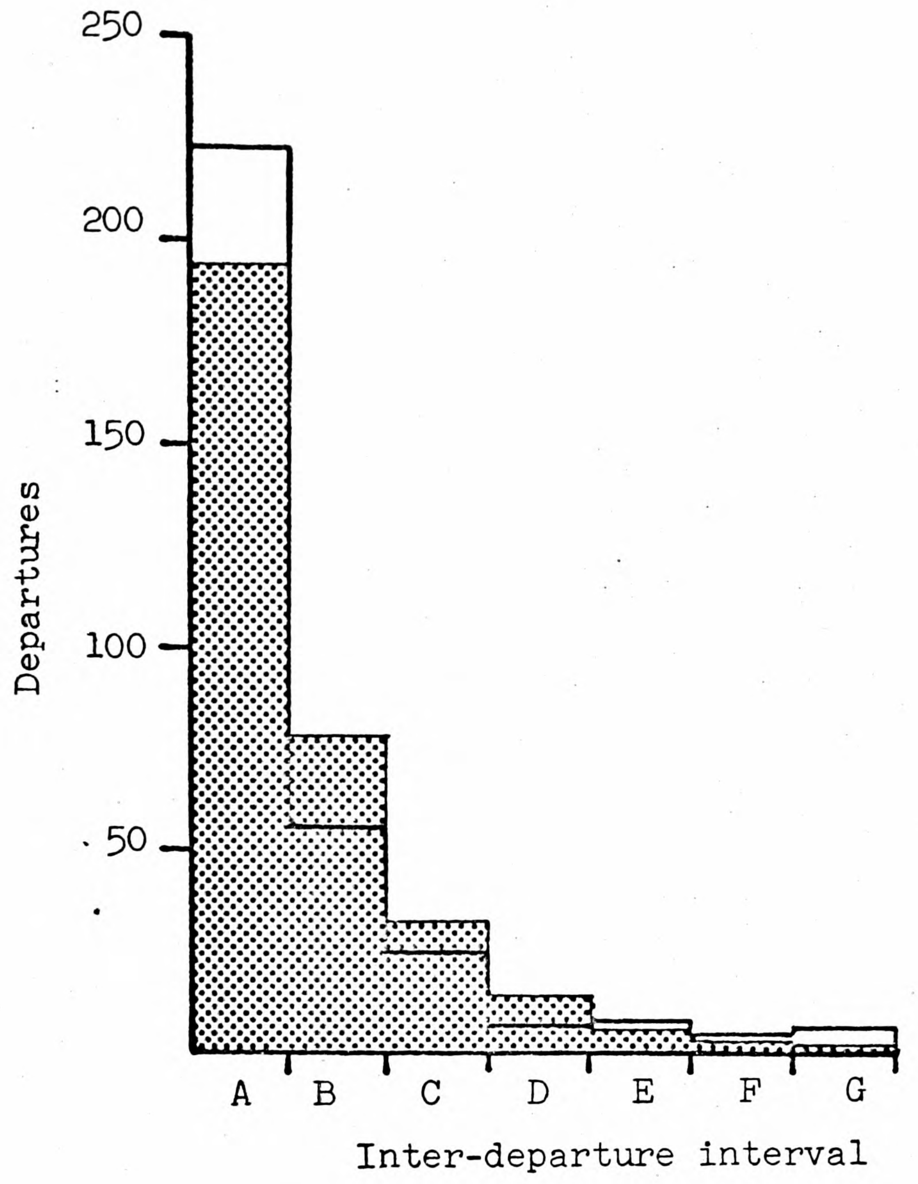


Fig.4.13. Distribution of inter-departure intervals (below heavy line) compared with expected values (shaded) (see text). Total number of observations = 324. Inter-departure intervals in seconds; A: 0 - 5, B: 6 - 10, C: 11 - 15, D: 16 - 20, E: 21 - 25, F: 26 - 30, G: 31+. The difference between the observed and expected is significant (X^2 = 25.7 5 df $P<0.001$).

Table 4.10. Inter-departure intervals of birds leaving a colony (see also Fig.4.13.).

Intervals:	0 - 5	6 - 10	11 - 15	16 - 20	21 - 25	26 - 30	30+
Observed	222	56	24	6	7	4	5
Expected	193.9	78.2	31.5	12.7	5.1	3.4	

Total X^2 values 25.7 5 df $P<0.001$

Notes: Intervals are in seconds.

Departures in categories 26-30 and 30+ have been combined.

that they characteristically departed in groups. On a number of occasions I observed such groups forming; one bird's departure apparently attracted the attention of neighbouring birds, some of which rapidly followed the departing individual(s). The largest group of birds I observed departing in this way was 10 individuals, which formed a compact group at about 500m from the colony. More usually groups were of 2 or 3 birds.

5) Flight directions. The foregoing section suggests that Guillemots follow one another out of the colony; if this is the case then the flight directions of birds leaving the colony should also be 'clumped', that is, non-random. The flight direction of Guillemots leaving a colony on the north coast of Skomer is presented in Fig.4.14, and data from this colony and another one on the south side of the island are presented in Table 4.11. The data show that departures are clumped in space (north coast $X^2 = 29.8$ 8df $P<0.001$, south coast $X^2 = 73.9$ 8df $P<0.001$), and birds also occur in groups on the sea (Fig.4.9).

To determine whether there was a difference in flight directions between the two colonies, I divided the area around the western end of Skomer Island arbitrarily into six sectors, and compared the proportion of birds from each colony whose flight path fell into each sector, when last observed some two miles off-shore. Birds from the two colonies flew in different directions (Table 4.12) ($X^2 = 82.2$ 5df $P<0.001$). The majority of birds from the Bull Hole colony on the north coast flew in a northerly direction, and birds from the Wick colony on the south coast flew in a southerly direction. Some overlap (about 20%) occurred when birds flew in a south-westerly direction (Fig.4.15). However, the comparison of flight directions from the two colonies is not without bias since the land barriers between the colonies formed a constraint

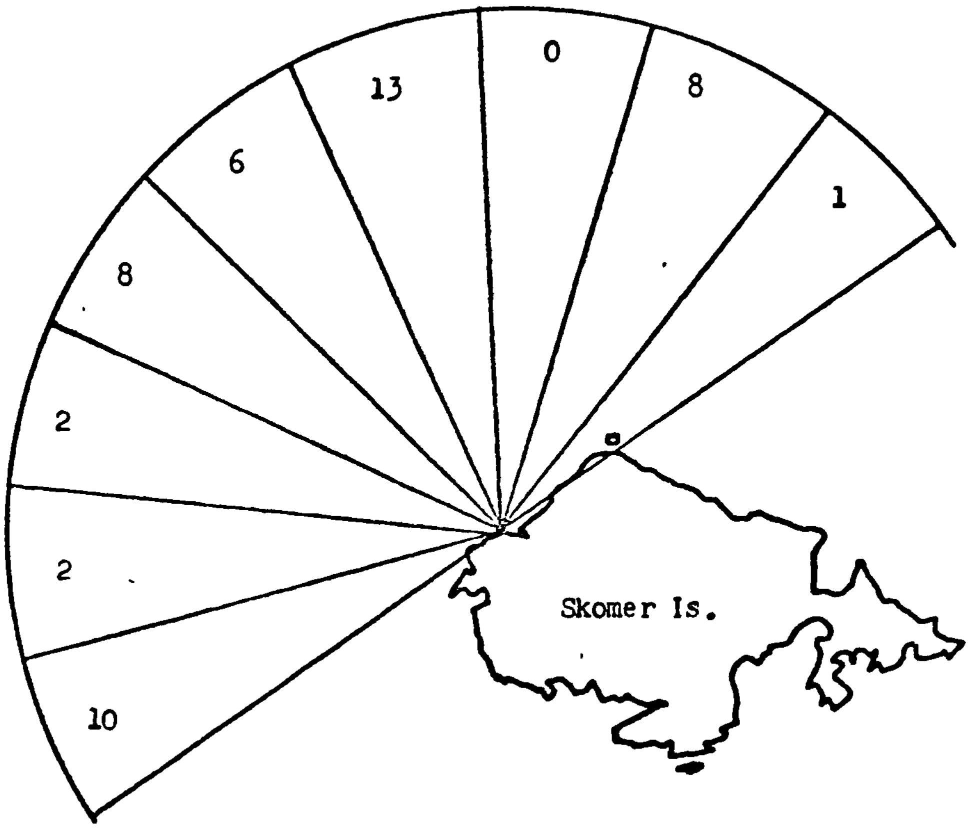


Fig. 4.14. Pattern of departures from Bull Hole Guillemot colony, on the north coast of Skomer. The area is divided into nine 20° sectors (numbered 1 -9 from 1 - r; see Table 4. 11.). The number of birds whose departure flight-lines fell into each sector at about two miles from the shore are shown (total n = 50). The radius of the semi-circle is two miles off-shore from the Bull Hole colony.

Table 4.11. Are flight directions of Guillemots from colonies clumped? The area around two colonies, Bull Hole and The Wick has been divided into nine sectors of equal size (see Fig.4.14.), the number of birds whose departure flight-line fell into each sector at about 2 miles from the shore is shown. Values are compared with equal frequencies (Expected values), ie. since n = 50, expecteds = 50/9 = 5.5.

BULL HOLE										
Sector		1	2	3	4	5	6	7	8	9
Observed		10	2	2	8	6	13	0	8	1
Expected		5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5
X^2 total =	29.8	8 df P<0.001								
THE WICK										
Observed		0	0	3	5	1	22	1	10	8
Expected		5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5	5.5
X^2 total =	73.9	8 df P<0.001								

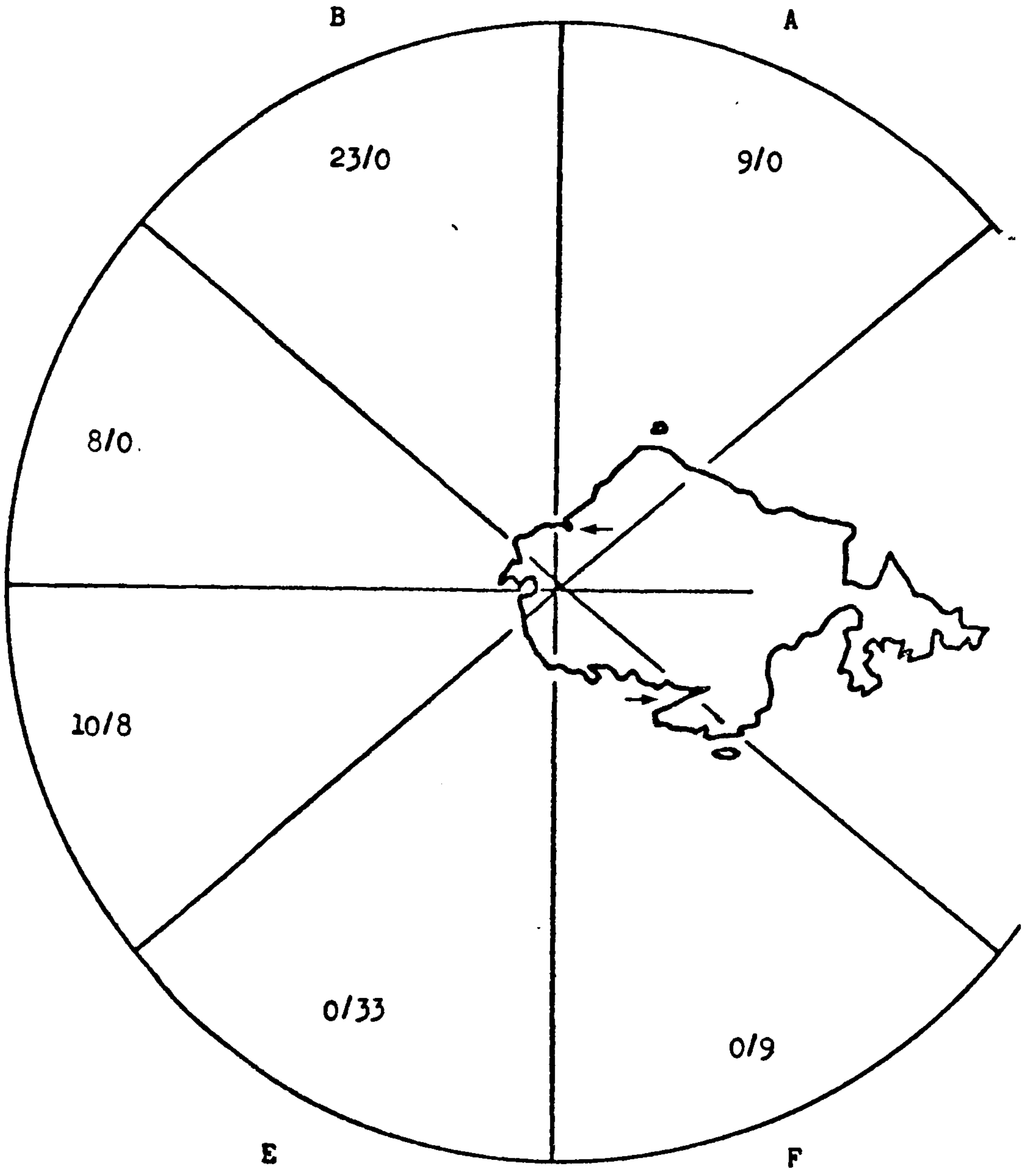


Fig.4.15. Flight departures of Guillemots from two colonies on Skomer, Bull Hole on the north coast and the Wick on the south (colonies pinpointed with arrows). Letters refer to sectors - see Table 4.12.) The first number = number of birds from Bull Hole, the second number = birds from the Wick, whose departure flight-line fell into each sector at about two miles from the shore. The circle describes a radius approximately two miles off-shore from each of the two colonies.

Table 4.12. Comparison of flight directions from Bull Hole and The Wick (see caption to Table 4.11. and see Fig.4.15.).

BULL HOLE

Sector	A	B	C	D	E	F
Observed	9	23	8	10	0	0
Expected	4.5	11.5	4	9	16.5	4.5
THE WICK						
Observed	0	0	0	8	33	9
Expected	4.5	11.5	4	9	16.5	4.5

Total $X^2 = 82.2$ 5 df $P < 0.001$

on the direction in which birds could fly. For example, it could hardly be expected for Guillemots to fly overland in a southerly direction from Bull Hole, or Wick birds to fly north overland. Nonetheless, I consider the observed differences to be genuine, since I was able to follow birds as they left the island for a considerable distance (about 2 miles), and because on nearly all occasions departing birds flew in a straight line away from the colony, making it seem unlikely that they would overlap in their flight directions further off-shore. Moreover, if there was more intermingling between the two colonies, I would have expected there to be a much greater proportion of Wick birds flying around the west end on Skomer in a north-westerly direction, and a greater proportion of Bull Hole birds flying in a southwesterly direction round the west end of Skomer.

There is some further evidence that birds from different colonies fed in different areas; during a minor oil incident in April 1973 I noted that 39/682 (5.7%) of the birds at Bull Hole colony on the north coast had spots of oil on their plumage (Birkhead et.al. 1973), but none of the 1000 or so birds which I examined at the Wick colony, on the south coast had any trace of oil. This suggests that birds from the two colonies were visiting different areas at this time. The feeding areas that birds use in the pre-laying period may be many miles from the colony. For example, two adult Guillemots ringed on Skomer were recovered in late March and April respectively, in south Cornwall, about 130 miles from Skomer. Moreover, during late March and April colony attendance patterns alter, so that instead of returning to the colony each day, the birds remain at sea for 3-5 days at a time, which lends support to the idea that birds feed at considerable distances from the colony at this time. Thus, birds may visit feeding areas several hundred miles apart.

Discussion and Comparison with Other Studies

(a) Food consumption and chick development. There are relatively few data on the food intake of Common Guillemot chicks to compare with my own. Tschanz (1959) recorded that eight chicks (of unknown age, apparently) were fed 30 food items in a 12 hour period, between 0700-1900hrs; a rate which is not dissimilar to that recorded on Skomer. However, Tschanz did not record the size of the fish fed to chicks. Both Tuck (1960) and Uspenski (1956) state that Brunnich's Guillemot chicks are fed 2-3 times a day, and that each feed weighs between 15-25g, indicating a food intake of 30-50g/day. Since neither of these authors provide any data to support their statements, they must be taken as approximate values. Nevertheless, they do suggest a higher consumption rate in Brunnich's Guillemot chicks.

A rough estimate of a Guillemot chick's energy budget has been presented (page 68), and taking the period of linear weight increase (i.e. up to the 16th day), approximately 3.2 grams of fish are necessary for the chick to increase its body weight by one gram. A.G. Gaston (unpubl.) found that over the same period in Brunnich's Guillemots, the ratio was 3:1, and R.E. Ashcroft (pers.comm.) obtained the same figure for the Common Puffin during the first half of the 40 day nestling period. Koelink (1972) found that in the Pigeon Guillemot, Cepphus columba, over the entire nestling period (40 days), 6.5g of food were needed per gram gain in body weight, but conversion of food to body tissue was most efficient in the early stages of the nestling period. Koelink also showed that the ratio of food intake : weight gain was higher (9.1 : 1) in captive birds than wild ones. Tuck & Squires (1955) found that in captive Brunnich's Guillemot chicks the ratio was even higher; 13.4 : 1. However, this estimate is probably too high, since, as Koelink points out, the records for this species did not cover the earliest and presumably the most efficient period of growth.

(b) Growth. Growth parameters from a number of studies of Common Guillemots are presented in Table 4.6. Comparing these data shows that there is some variation, probably due to regional and annual differences. This variation is also apparent in other species (e.g. Brunnich's Guillemot). Ricklefs (1968) estimated that there may be as much as 20% variation in growth parameters within a species with respect to locality and time of breeding season. However, despite the variation, the data in Table 4.6 suggest that overall, growth rate, nestling period and fledging weight recorded in this study are similar to those reported for Common Guillemots in other areas.

I have also compared growth parameters of Common Guillemots with Brunnich's Guillemot and Razorbill, which both show a post-hatching developmental pattern classed as 'intermediate' (Sealy 1973) between precocial and semi-precocial (Table 4.6). The growth rate used here for interspecific comparisons is grams/day up to the asymptotic weight, i.e. the end of the linear phase of growth. Although deciding where the end of the linear growth phase lies is a somewhat subjective decision, this method can be used for intra and interspecific comparison of those species with similar developmental patterns. It cannot be used however to compare 'intermediate' species, with say, semi-precocial ones. This is because semi-precocial species attain 85-90% adult weight prior to fledging (Ricklefs 1973, Sealy 1973), but 'intermediate' species (Uria and Alca) fledge at less than 30% adult weight.

Ricklefs (1973) has used the parameter '% of asymptote attained / day at 15% (and/or 20%) adult wt.', in order to make interspecific comparisons. However, a difficulty with this method is that it selects a specific point (e.g. 15 or 20% of adult wt.) in the chick's development. Comparison of weight increments in Skomer chicks with those on the Farne Islands (Table 4.8), showed that marked day to day differences existed between the two samples. For this reason I have not used Ricklefs method. Moreover, in most cases authors do not provide sufficient data to make more detailed comparisons.

Table 4.6 shows that in the two Razorbill studies, growth rates are of the same order as in Common Guillemots. Brunnich's Guillemots however, show some interesting differences, both between areas (c.f. Novaya Zemlya and East Murman), and between years. Growth rates of Brunnich's Guillemots in Novaya Zemlya (latitude: 73°N) are half those recorded at East Murman (69°N) (Uspenski 1956), and Tuck (1960) also recorded weight differences of a similar order in 21 day-old chicks at different latitudes in N.E. Canada. These differences have been interpreted as the need for chicks raised at low air temperatures to channel more energy into feather growth and maintenance of body temperature rather than into weight increase. The higher rate of food consumption in Brunnich's Guillemot (compared with Skomer data) indicated by Tuck & Squires (1955) and Uspenski (1956) is in accordance with this idea.

It would be interesting to know whether any relationship exists between fledging weight and survival of Brunnich's Guillemot chicks. Perrins _et.al._ (1973) have shown that in Manx Shearwaters _Puffinus puffinus_ individuals fledging early in the season with high body weights have a greater chance of survival than low weight individuals. However, the supra-adult weight attained by

Shearwaters is a fat reserve which is utilized immediately prior to and after fledging (Perrins et.al. 1973). There is no evidence that Uria or Alca deposit fat prior to fledging, but a crucial difference between these alcids and the Shearwaters is that the chicks of both Uria and Alca are dependent on their parents for some time after fledging. The length of this period has not been determined, but M.C. Garnett (pers.comm.) noted Guillemot chicks still with their parents more than eight weeks after fledging, and Keighley & Lockley (1947) noted fully grown chicks calling and following adults as long as twelve weeks after fledging. A period of parental care after fledging may enable chicks fledging at relatively low weights in the arctic to continue growth after leaving the colony.

Because one parent remains with the chick at the nest site throughout the nestling period, only one parent can forage for the chick at any time. The mean feeding rate for parents with chicks aged 3-16 days was 3.35 feeds /day; with feeding trips averaging 86 minutes; this means that about 4.8hrs, or 27% of the daylight period was spent foraging for the chick. The maximum feeding rate I recorded was 7 feeds in one day, when parent Guillemots spent an estimated 56% of the day to provide an 11 day old chick with a mere 62g of fish. Now the maintenance requirements of an adult Guillemot are in the order of 200g fish/day (Sanford & Harris 1967, Marsault 1975). Clearly, if a Guillemot chick was to remain at the nest site until it attained adult weight, its food requirements would rapidly exceed that which its parents could transport. Thus, the short nestling period and low fledging weight (<30% adult weight) enables the adult to take the chick to feeding areas where it can continue its development (Lack 1968, Sealy 1973), while still dependent on the adult (Scott 1972). Cody (1971, 1973) has suggested that predation pressure is an important factor in determining the evolution of short nestling periods, but Sealy (1973) disagreed with this idea. However, it seems likely that one parent Guillemot remains with the chick, at the site, throughout the nestling period to guard it from predation. This means that at any time only one parent can forage for the chick. Thus, the interaction between predation pressure and the ability of adult Guillemots to feed their chick has probably been important in determining the length of the nestling period.

My observations suggest that the male parent takes the chick to sea; in six cases at fledging where the adult bird was individually marked, the parent which departed with the chick was the male. Scott (1972) collected single adult and chick groups at sea and also found that the adults (n = 17) were all males. The male parent must be somehow better equipped to guard the chick at this time.

Scott (1972) suggested additional advantages of taking the chick to feeding areas; a) the adult can exploit a wider variety of prey size and species (see also Royama 1970), and b) the chick can learn to forage while still dependent on its parent. A further advantage, not mentioned by Scott, is that a short fledging period means that adult Guillemots can commence moult soon after fledging occurs, that is, comparatively early in the season, while fish are still abundant, and before weather conditions deteriorate (see Chapter 2). This is important since adults and chicks are both flightless at this time, (see Appendix II, on moult) and are therefore unable to move rapidly from one feeding area to another, and feeding success is probably reduced in stormy conditions (see page 68).

The weight recession. A pre-fledging weight loss occurs in several groups of birds, but particularly in the swallows and swifts, and oceanic species (Ricklefs 1968). Sealy (1973) has reviewed post-hatching developmental patterns in alcids and has drawn attention to the weight recessions that occur in some nidifugous and the intermediate species (Uria and Alca).

The first published figures for weight changes in Common Guillemot chicks were provided by Johnson (1944). This author points out that during his investigation, his visits to the colony to weigh chicks caused considerable disturbance. Moreover, his visits occurred at 3-4 day intervals, which does not permit a detailed examination of growth, particularly the last few days at the colony in which the so-called weight recession occurs. However, Johnson's figures have been extensively quoted by other auk workers. For example, Tuck (1960) used the data to produce a growth curve, and other workers (e.g. Sealy, 1973, Johnson & West 1975) have subsequently quoted Tuck's interpretation of Johnson's figures, stating that a 17% pre-fledging weight recession occurs in this species. However, as already pointed out, Johnson's figures are not sufficiently detailed to allow anything other than a general comment, to the effect that 'some' weight loss may occur prior to fledging. In the present study, the difference between peak weight and fledging weight (Table 4.5) was small, amounting to less than 2% weight loss. Johnson & West (1975) recorded that peak weight was achieved the day before fledging in their study, and that no weight loss occurred. Neither Cody (1973) nor Belopolski (1957) recorded any weight loss prior to fledging apparently, although these authors do not present detailed figures.

Tuck (1960) apparently suspected a pre-fledging weight loss in Brunnich's Guillemots (subsequently quoted as a 7% loss by Johnson & West 1975), but the data Tuck presents are not convincing. Johnson & West (1975) however, did record a 9% weight loss in Brunnich's Guillemots in Alaska. The results of Uspenski (1956) and Kaftanovski (1951) do not indicate weight losses, but they do not publish detailed information. In the Razorbill C.S. Lloyd (unpubl.) recorded no weight change, but Brun (1958) and Bedard (1969d) recorded weight losses of 4.5% and 9.5%, respectively.

Thus, a pre-fledging weight recession is not a consistent or integral part of the growth patterns of these species. However, all three species show similar patterns of weight increase through the fledging period; weight reaches an asymptote and then levels off shortly before fledging (see Table 4.5), and any weight loss which does occur at this stage is small. The loss is probably not important, since it has been shown that ~~even~~ small passerines may regularly lose up to 10% of their body weight overnight (Newton 1972). Moreover, since chicks of Uria and Alca are cared for by one parent after fledging, a levelling-off, or small loss in weight prior to fledging is probably unimportant since growth presumably progresses rapidly once the adult and chick are away from the colony. In this respect the pattern of growth in Uria and Alca is probably unique among birds; at the colony weight increases for about two-thirds of the nestling period and then levels off (or occasionally shows a slight decline). After fledging, a similar pattern probably occurs, although no data on the rate of growth or the period of dependence on the parent are available.

(c) Environmental factors and foraging. Chick feeding rates were lowest during stormy conditions, and Tuck & Squires (1955) reported that Brunnich's Guillemots did not even leave the colony to forage for their chicks under these conditions. Pettingill (1939) and Boeker (1967) noted that gale force conditions reduced feeding success in terns, and Dunn (1973) was able to demonstrate a relationship between sea-surface conditions and fishing success in Common and Sandwich Terns. Dunn showed that fishing success was highest in medium seas, when the sea surface was disturbed, and suggested that this was because under these conditions the birds were able to see the fish, but the fish were unable to see the terns. Reduced fishing success in gale-force conditions in those species which hunt, by surface-plunging (see Ashmole 1971) may be due to a) fish moving into deeper water during stormy conditions, and b) the birds experiencing difficulty in hovering and therefore aiming, prior to diving, in stormy conditions (Dunn 1973). Ashmole (1971) classed the Guillemots' feeding method as 'pursuit diving', and clearly the argument b) above, is not applicable here. However, the former argument a) may be.

Data from commercial sprat fisheries (P.O. Johnson, unpubl.) show that catch rates fall off after prolonged bad weather, and echo-survey records show that this is because the sprat shoals disperse. This probably occurs during the night when fish are nearer the surface and are thus within the zone of wind-induced surface currents.

Potts (1969) suggested that rough seas and associated turbidity and possible changes in fish movements reduce feeding efficiency in the Shag, and related this to the eruptive movements observed in shags. Wrecks and eruptions of seabirds are frequently associated with stormy conditions (see Chapter 2), and Uria spp. appear to be particularly prone to such wrecks. Data in the present study show that Guillemots provision their chicks at a reduced rate during these conditions, and this indicates that adult birds may be confronted with a similar problem in provisioning themselves, as suggested by the condition of wrecked Guillemots; such birds are often emaciated and lack fat deposits (Bailey & Davenport 1972, Holdgate 1971), indicating that starvation has occurred.

(d) The problem of the Information Centre hypothesis.

Most of the evidence for Ward & Zahavi's (1973) hypothesis is circumstantial, and one of its main drawbacks is that the authors do not suggest ways in which the hypothesis can be tested. This is an important point, and no subsequent worker has yet devised a rigorous test of Ward & Zahavi's ideas.

Krebs (1974) working at a colony of Great Blue Herons Ardea herodias, investigated some aspects of the information centre hypothesis, and he suggested that in order to demonstrate that colonies act as information centres, two conditions must be fulfilled; a) that birds exploit a clumped and unpredictable food supply, and that different individuals in the colony do not behave independently of each other in their foraging trips, and b) that individuals foraging in groups have a higher food intake than solitary birds. The first of these conditions has been fulfilled (see Figs.4.10, 4.11, 4.13, 4.14), but it was not possible to test the second. However, it still remains to be demonstrated in any species that less successful individuals follow more successful ones to good feeding area as Ward & Zahavi suggest.

My data on flight directions indicate that a) birds from different colonies on Skomer feed at different locations, and suggests that Guillemots have traditional colony-specific feeding areas. Davies (1975) similarly noted that in Herring Gulls, the birds using one particular feeding area were near neighbours in the breeding colony, and Krebs (1974) showed that in herons birds from neighbouring nests tended to leave the colony at the same time and feed in the same area; b) within colonies birds flying to feeding areas did not behave independently of each other.

Thus, while my data may provide some evidence to support the idea that birds associate in some way for food finding, they are far from conclusive.

A critical test would be to select some measure(s) of 'success', such as, adult body condition, rate of chick growth, size of prey fed to chicks, time interval between successive chick feeds, and see whether birds which are more successful are more likely to be 'leaders' of groups, than 'followers'.

(e) Other aspects of foraging.

1) Spatial distribution. The horizontal distributions of Guillemots, Razorbills and Puffins differed from each other within a 7mi limit of Skomer. In general, the birds were widely dispersed on the sea, although the different species sometimes occurred together in mixed species feeding flocks. However, this is probably an opportunistic method of foraging and the rarity with which I observed such flocks indicates that this is not an important method of food acquisition (see also Sealy 1974).

Although significant differences in the horizontal distribution of auks existed, they did not show any clear trend (c.f. Cody 1973). However, I suspect that the data do not provide a complete picture, for several reasons; a) observations were made only within 7 miles of Skomer, b) relatively few Guillemots or Razorbills were observed (e.g. Guillemots, average is <20 birds / transect), and c) the mean duration of Guillemot foraging trips was 86 minutes, which with an average flight speed of 40-50 mph (pers.obs. and see Tuck 1960: 23) clearly gives the species a much greater range - even allowing for fishing time. On one occasion at approximately 7 miles from off-shore, I observed a colour-marked Guillemot from Skomer fly past Grassholm heading in a westerly direction.

Cody (1973) suggested that a negative relationship between alcid body size and foraging distance from the shore exists, such that the largest species

(Common Guillemot) forage nearest the shore and the smallest furthest off-shore. This is clearly not the case in the present study. It is more likely that birds forage in good feeding areas irrespective of distance from the shore (although, obviously each species will have an upper limit). Alcids in general have short foraging ranges compared with other marine species such as Procellariformes (see Lack 1968:267, Sealy 1972), since their flight energy requirements are high. Good feeding areas will differ in their distribution and distance from the shore in different parts of a species' range. For example, Tuck & Squires (1955) state that in northeast Canada Brunnich's Guillemots foraged within 1-5 miles off-shore and rarely more than 10, while feeding chicks. Swartz (1967) on the other hand found that in Alaska, Brunnich's Guillemots reached their peak between 20 and 40 miles off -shore.

2) Ecological segregation. My data do not permit a detailed discussion of ecological segregation in Skomer auks, but one or two points are relevant here. My observations of fish size and prey species of Guillemots, Razorbills and Puffins on Skomer agree with those of Harris (1970) and Corkhill (1973). That is, Guillemots take the largest and Puffins the smallest prey items. Razorbill prey items fall somewhere between the two, but there is probably greater overlap between Razorbills and Puffins than Razorbills and Guillemots (R.E. Ashcroft, unpubl.). On Skomer, Puffins feed on small Sand eels (33-65mm) and Clupeids (24-65mm) (Corkhill 1973). I recorded only two instances during four seasons' observations, of Puffins with clupeids for chicks which overlapped in size with Guillemot prey. The mean weight of Puffin loads on Skomer in 1970 was 8.4g (Corkhill 1973). However, Puffins are capable of carrying heavier loads than this; for example, Nettleship (1972) recorded Puffins

in Newfoundland carrying Capelin Mallotus villosus up to 180mm and individual loads up to 33g. If Skomer Puffins were able to mimimize their efforts by bringing larger but fewer fish to chicks they would presumably do so. It has been shown that Clupeid shoals may be stratified in the water column, with smaller individuals nearer the surface and larger (older) ones at greater depths (Huntsman 1934, Johnson 1939a, Johnson 1974). If there is a relationship between body size and the depth to which a species is able to dive, as the relatively sparse literature on diving (Kooyman 1972, Kooyman et.al. 1971) suggests, then a likely explanation for the difference in Clupeid prey size between Puffins and Guillemots is that Guillemots which weigh twice as much as Puffins are able to dive to greater depths and thus capture larger prey. Alternatively, since it has been shown that smaller sprats occur nearer the shore than large ones (P.O. Johnson, unpubl.), Puffins may exploit inshore fish because they cannot get at larger fish which occur in deeper water, further off-shore. This would result in Puffins spending less time travelling to and from feeding areas, which may compensate for feeding on smaller prey items. This latter strategy would appear to be the one which Puffins on Skomer employ. Although the data on horizontal distribution of auk species (Fig.4.9) are unsatisfactory in some respects, they do suggest that Puffins feed closer inshore than Guillemots. To support this, R.E. Ashcroft (pers.comm.) found that the average duration of Puffin feeding trips on Skomer was about 50 minutes, considerably shorter than the average Guillemot trip.

Field experiments to investigate the depths to which auks dive for food would be of some interest, and could be a rewarding topic for further research.

Summary and Conclusions

The growth rate of Guillemot chicks on Skomer was similar to those recorded on the Farne Island (Pearson 1968), and fledging weights and nestling periods are comparable with the results of a number of other studies. There was no evidence that Guillemot chicks on Skomer developed any less well than chicks in other parts of the species' range, indicating that food is not limiting during the breeding season. However, the Guillemot population on Skomer has apparently ceased to decline, and has stabilized during the course of this study, so it is not known whether a food shortage was implicated in the earlier decline.

Comparisons with Brunnich's Guillemot, which replaces the Common Guillemot at higher latitudes, revealed some interesting differences. Growth parameters differ with locality, but in general at higher latitudes growth is slower and birds fledge at lower weights.

The post-hatching patterns of development of Uria spp. and Alca torda are unusual among seabirds. The advantages of a short fledging period of post-fledging parental care are discussed.

The main food species fed to Guillemot chicks on Skomer were Sprats (Clupeidae); these averaged 10.4cm in length and 8.8g in weight. There was no annual or seasonal variation in the prey species utilized. Chicks between 3-16 days were fed on average 3.35 times a day. Feeding rates were reduced in stormy conditions. The food intake of chicks decreased towards the end of the nestling period, and this may have accounted for a levelling-off in weight prior to fledging. The 'weight recession' in Uria and Alca is discussed, and it is concluded that recessions in weight prior to fledging are probably unimportant. Usually weight reaches an asymptote some time after the 14th day, and remains similar until fledging on the 21st day.

Some data are presented which support, in part, Ward & Zahavi's (1973) Information Centre hypothesis; i.e. birds leaving the colony do not do so indendently of each other. A more rigorous test of Ward & Zahavi's idea is necessary - although this may not be easy with auks.

The distribution of Guillemots at sea differs from that of two other auks (Razorbill and Puffin) which breed on Skomer. My data for distributions at sea are not conclusive, but do not lend any support for the scheme presented by Cody (1973). Alternatives to Cody's representation are presented and the horizontal and vertical components of ecological segregation in auks are briefly discussed.

CHAPTER 5

BEHAVIOURAL ADAPTATIONS TO HIGH DENSITY NESTING

Introduction

In Chapter 3 I examined an important aspect of the Guillemot's breeding biology, namely, the function of high density nesting. The densities characteristically attained by Guillemots in their breeding colonies are unparalleled by other bird species, but this is adaptive since it enhances breeding success by reducing egg and chick predation. The spacing of individuals of any animal species is brought about largely by the way conspecifics respond to each other (Brown & Orians 1970); this is the subject of the present chapter.

Most bird species defend territories, or at least maintain individual distances (Hinde 1956, Hediger 1950). Guillemots defend only a small area in which the egg is laid (territory type C; Hinde 1956), and characteristically nest in close bodily contact with conspecifics (see Fig.3.1). Since the proximity of conspecifics is an important factor determining levels of aggression (Hinde 1974) the density at which Guillemots breed is likely to require extensive behavioural modifications to the basic alcid plan. The types of problem facing Guillemots in establishing and maintaining high nesting densities are outlined below:-

(1) In order to get to and from their nest sites birds must walk through the territories of other birds; a situation in which the 'trespasser' is likely to be attacked.

(2) Fighting among birds breeding at high densities may be detrimental, a) if a defeated bird is unable to flee, and b) through the loss of eggs and chicks. Birds must therefore achieve a balance between destructive fighting and maintenance of nest-site and mate.

(3) The close proximity of conspecifics may result in promiscuity (Norrevang 1958, MacRoberts 1973).

(4) High density nesting precludes the use of highly mobile or 'long-distance' displays, such as threat or mate attraction.

(5) Nest-site competition may be severe among species nesting at high densities (Nelson 1970), with a premium on site maintenance and fidelity.

(6) High density nesting means that sites will be small and if members of a pair are to spend time together at the site they must do so in close proximity.

The value of comparative behavioural studies has been emphasized (Hinde 1966, 1974) and in this respect seabirds have proved to be particularly fruitful subjects for study (Tinbergen 1959, Nelson 1970). Therefore, in an effort to make a more meaningful investigation of the Guillemot's behavioural adaptations to high density nesting I have made some comparisons with the Razorbill. The Razorbill is generally considered to be closely related to the genus <u>Uria</u> (Storer 1945, 1960), and breeds in the same cliff habitat as the Guillemot - although the two species utilize the habitat in different ways and breed at different densities (see later). The two species are likely to share a number of behaviour patterns, a) because of their phylogenetic affinities, and b) because their nesting sites share a common feature - restricted space. Differences between the two species are likely to be due to differences in their dispersion patterns and degree of contact with conspecifics. Observations on mammalian carnivores indicate that there may be a relationship between a species' repertoire of social signals and the degree of contact between individuals; the more social species exhibiting a more varied repertoire (Schaller 1972, Fox 1974).

There has been no quantitative account of Common Guillemot social behaviour previously, but some general observations have been made by Selous (1901, 1905), Perry (1940), Johnson (1941), Conder (1950), Storer (1952), Norrevang (1958), Tuck (1960) and Williams (1972). General qualitative accounts of Razorbill behaviour have been given by Perry (1940), Paludan (1947), Conder (1950) and Bedard (1969d). The aim of the present study was to a) provide a quantitative account of Guillemot behaviour, and b) to consider Guillemot behaviour in relation to spatial dispersion at breeding colonies.

Methods

Most observations were made on Skomer Island between late March and late July 1973 - 1975. Some additional observations were made during November and December 1974 at Bempton Cliffs, north England (56^{o} 6'N 0^{o} 0.3'W) since Skomer was inaccessible at this time.

In order to provide a quantitative basis for this study, and to obtain some information on the frequency that birds performed certain displays, diurnal and seasonal changes in their frequency were recorded. Behaviour of Guillemots was recorded in two main situations, a) on breeding ledges (Medium density - unless otherwise stated, see Chapter 3), and b) in clubs, where immature birds congregated (see Chapter 2). On ledges I recorded the frequency of some behaviour patterns that members of breeding pairs performed during the course of a minute's observation. A pair was observed for one minute only and to avoid any subconscious bias in the selection of pairs I worked my way through a group of birds from left to right, or top to bottom, observing each pair in turn. Fifty minutes' observation conducted within a 90 minute period was taken as one behavioural unit, using the mean value for each activity as a measure of its frequency. This method was used to provide a general outline of seasonal and diurnal patterns of behaviour. It ignored individual variation and the fact that within any one period, such as pre-laying, incubation, different pairs may have been at different stages of the breeding cycle.

During the winter and pre-laying period I watched pairs of Guillemots at their sites (often using colour-marked individuals), and in the nestling and incubation periods I watched pairs of birds in which one was incubating or brooding. Thus, the observations were divided up into four periods: winter, pre-laying (April), incubation and nestling.

To determine diurnal changes in behaviour, five observation units were made at regular intervals throughout the daylight period on a number of occasions through the breeding season. Seasonal changes in behaviour were recorded by conducting observations during the first two hours of daylight, when there was a peak of activity.

Observations at clubs were made between 1000-1200 hrs and I watched only a single bird for a one minute period. Each bird was watched for one minute and 50 minutes of observations were taken as one unit. It was not practicable to record the behaviour of 'pairs' in clubs, because although pairs did occur there they were often of a temporary nature (see later). Because of this difference in recording methods on ledges and clubs comparison of the frequency of displays must be made with care.

Hinde (1966:253, 1974:65) has outlined the types of evidence that have been used in analysing displays, to suggest their function and causation. In the present study I have used a number of these: a) the situation in which the display occurs, b) behaviour which accompanies the display, or c) precedes or follows the display, d) the nature of the display itself. In the latter case I filmed and photographed displays, and recorded their duration where possible. Calls were recorded using a Sony TC68 portable tape-recorder, and examined using a Kay Sona-Graph 6061B. In addition I have also used an experimental approach to provide further evidence for a specific interpretation of one display (Bowing -see later) derived from observations of type a) - d).

I have used the same methods as those outlined above to investigate Razorbill behaviour. All observations of Razorbills at the nest site were made in areas where birds bred on ledges or restricted ledges and were clearly visible (see Fig.5.1).

Since much of the comparison between Guillemots and Razorbills lies in their different nesting dispersion and utilization of habitat, I have compared the nest sites of each species on Skomer.

The time spent by each species displaying on the sea was also recorded. On seven occasions between 0800-1000 hrs during the pre-laying period I made 'spot' checks in areas where both species were known to breed and recorded, for both species, the number of birds on breeding ledges and on the sea. Observations were made in the morning since Razorbills show a marked diurnal pattern of colony attendance in the pre-laying period, with a peak of

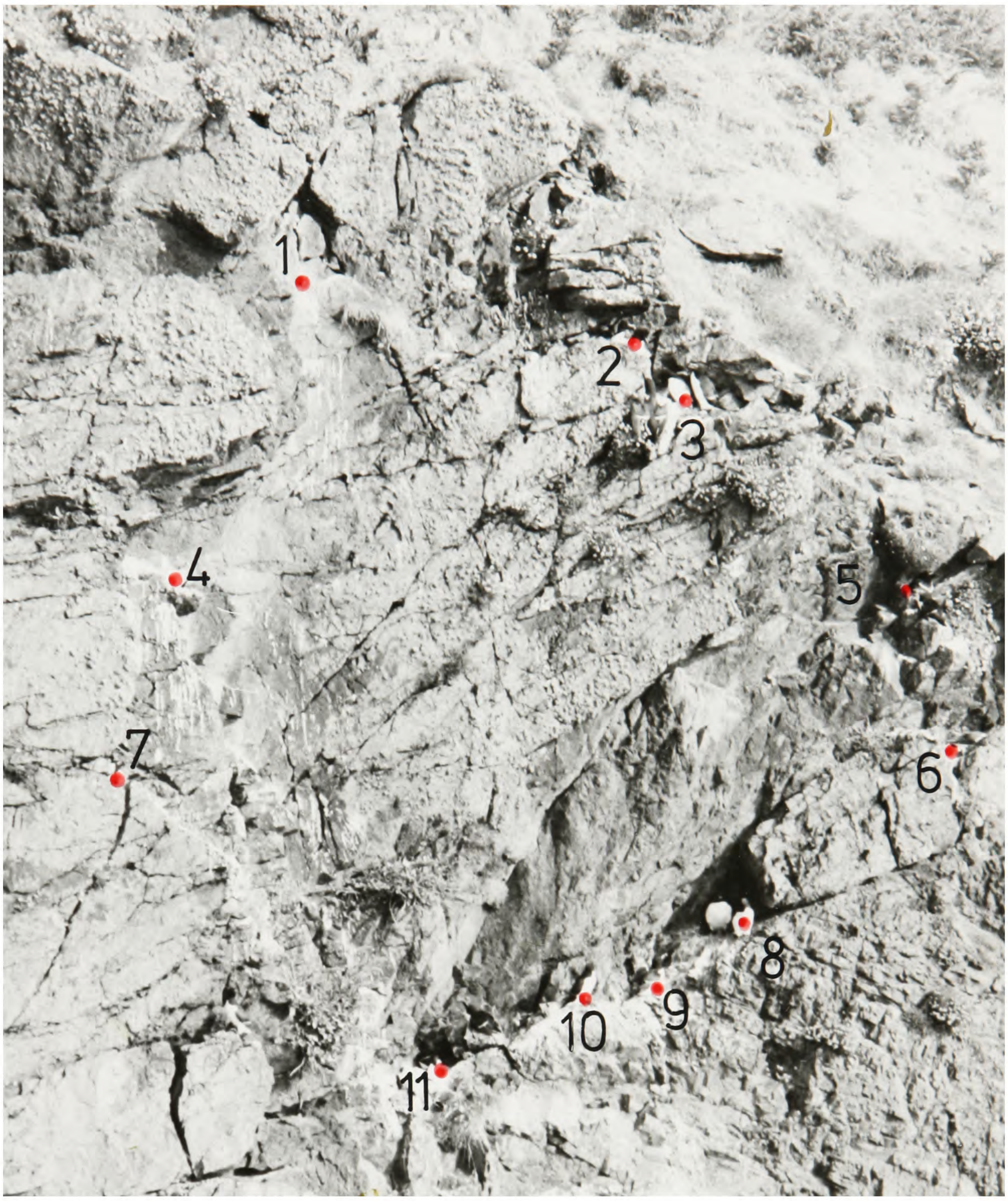


Fig.5.1. Razorbill colony. Nest-sites are marked by red spots and numbered 1 - 11. Note spacing.

numbers in the early morning. I did not record any change in the proportion of birds on ledges and on the sea throughout the day. The behaviour of birds on the sea was recorded using behavioural units as described previously.

The rest of this chapter is set out as follows: first, the postures assumed by Guillemots are described and illustrated; then follows a number of sections describing the situations in which each posture occurs. Comparison with other species are made where this helps to clarify the situation in the Guillemot. A smaller section like that for the Guillemot on Razorbill behaviour follows, and finally a discussion comparing and summarising the behaviour of the two species and outlining the Guillemot's behavioural adaptations to high density nesting.

Results

(a) Habitat and spacing differences between the Guillemot and Razorbill

On Skomer Guillemots and Razorbills utilized five types of nest sites on cliffs (see Fig.5.2).

(1) Ledges. Ledges varied in width from 10cm -250cm, and were generally longer than 50cm (see (2) below; and for further details of Guillemot distribution on ledges see Chapter 3).

(2) Restricted ledges. Sites not generally wider than 20cm or longer than 30cm, in other words usually large enough for only a single bird to incubate or brood a chick. Restricted ledges usually had two or three rock-walls against which an incubating bird could crouch.

(3) Boulders. Birds nested in spaces beneath boulders on sloping cliffs or

Fig.5.2. Habitat types used by Guillemots or Razorbills on Skomer (see also Table 5.1.). The oval shapes represent incubating birds, shaded area = cliff-wall, and in the burrow the stippled area = earth.

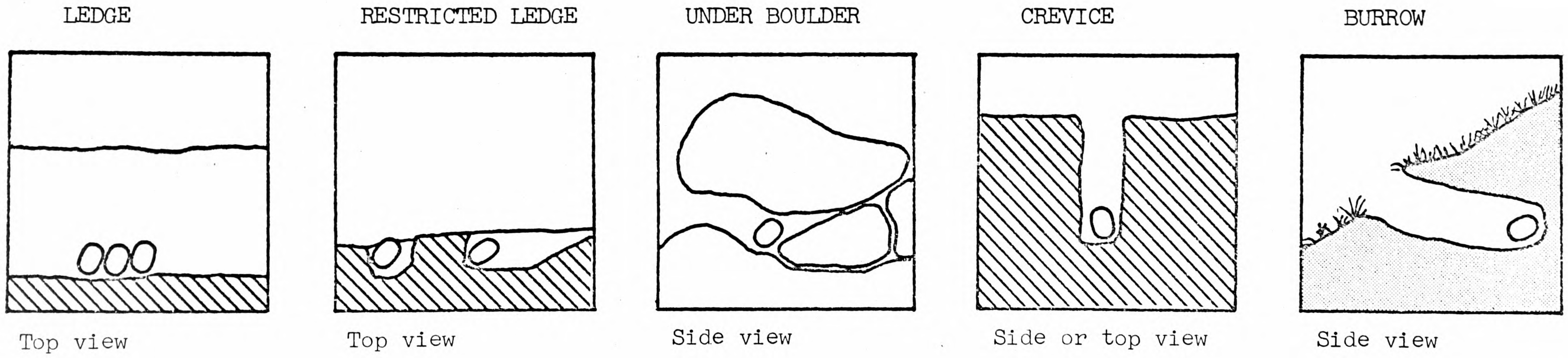


Table 5.1. Habitat differences between Common Guillemot and Razorbill on Skomer.

Nest-site type	Guillemot		Razorbill	
	n	%	n	%
Ledge	740	77.6	5	0.7
Restricted ledge	192	20.1	291	40.9
Boulder site	20	2.1	250	35.2
Crevice	2	0.2	130	18.3
Burrow	0	0.0	35	4.9
Totals	954	100.0	711	100.0

Note: For definitions of nest-site types see Fig.5.2.

at the foot of cliffs above the high water mark. Boulders ranged between 30cm to 20 m in diameter.

(4) Crevices. Crevices were distinct from sites under boulders in that they were vertical fissures with either a lateral or horizontal opening (sometimes both).

(5) Burrows. Burrows occurred in earth at the cliff edge and were generally shorter than those used by Puffins on Skomer (R.E. Ashcroft - unpubl.) rarely exceeding 60cm in depth.

Most Guillemots nested on ledges, and most Razorbills on restricted ledges and under boulders (Table 5.1). A further difference between the two species was the degree of contact between conspecifics; 756/934 (81%) of Guillemots nested touching another Guillemot, but none of 460 Razorbills were nearer than about 15cm to a conspecific. As already pointed out (Chapter 3) Guillemots generally nest in dense groups, but Razorbills space themselves just out of pecking distance of neighbouring birds. Razorbills characteristically incubate against at least one rock surface - usually more, and unlike Guillemots they apparently never nest on broad ledges away from the cliff wall (see Chapter 3). The three largest alcid species, which sometimes nest sympatrically, thus form a series from the densely nesting Common Guillemot, through the less densely nesting Brunnich's Guillemot, to the Razorbill which does not breed in contact with conspecifics.

A further difference between Guillemot and Razorbill concerns 'clubs' and loafing areas. I have already discussed how immature Guillemots congregate at sites, referred to as clubs, on tidal rocks at the foot of cliffs (Fig.5.2a). Very few adult Guillemots occur in such clubs (see Chapter 2), nor do they congregate at other sites. In contrast, adult and immature Razorbills both congregate at the same sites, referred to here as loafing areas. Loafing

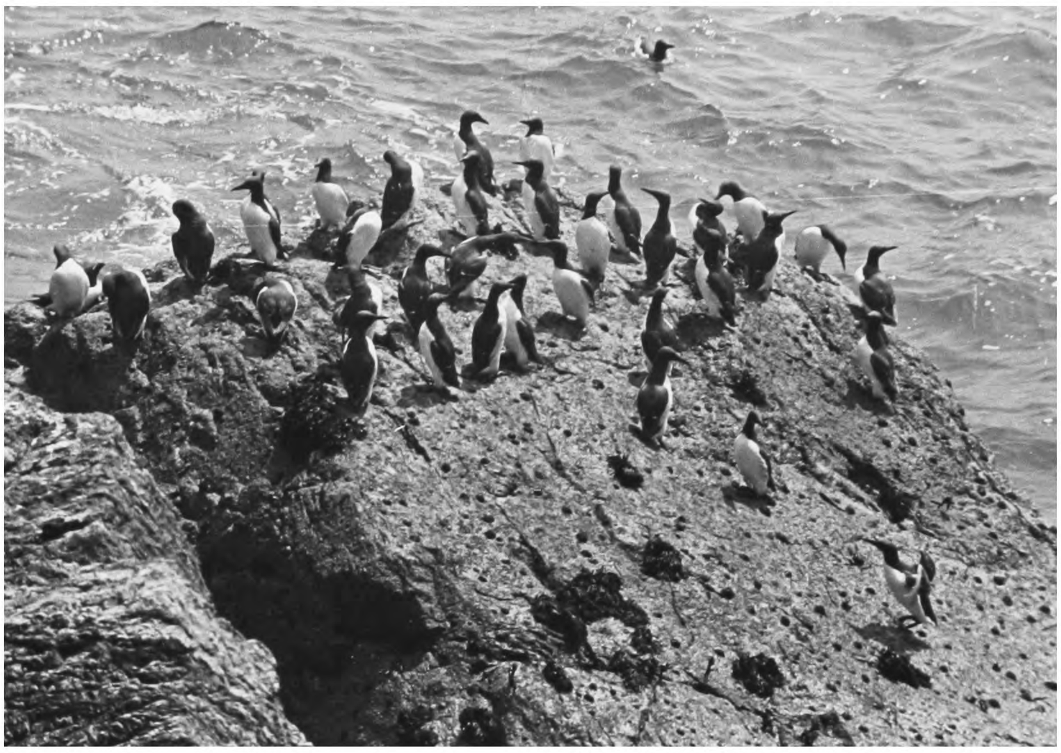


Fig.5.2a. A Guillemot club situated on tidal rocks at the foot of a cliff. This club was the site where most club-observations were made.

sites were generally near breeding areas but usually on cliffs above the level of Guillemot clubs.

(b) Time spent displaying on the sea

Guillemots spent a significantly greater proportion of their time than Razorbills on the breeding ledges, and Razorbills spent more time than Guillemots on the sea below the colony (Table 5.2) ($X^2 = 737.1$ 6df $P<0.001$). Razorbills also spent a greater proportion of their time displaying in groups (see Paludan 1947) on the sea, than Guillemots. Allopreening was used as measure of sexual activity among birds on the sea. Since Billing and Allopreening (see later) in Razorbills were not always distinguishable the measure of activity may include Billing in the Razorbill. However, this is not important in that it does not affect the results: Razorbills averaged 1.31 Allopreens/bird/min. (range for four units = 0.96 - 1.88), but Guillemots were not recorded Allopreening or engaging in any other courtship activity during these observations.

GUILLEMOT BEHAVIOUR

(a) Postures and Movements

(1) Alert (see Frontispiece). The neck was stretched upwards but the head remained horizontal. The bird sometimes looked rapidly from side to side.

(2) Threat (Fig.5.3a). The head and neck were directed forward and upward at about 45°, and the wings were held away from the body. Birds usually countered threat with threat, so that as one bird lunged forward with the head the other withdrew its neck, ready to lunge back and keeping out of

Table 5.2. Number of Guillemots and Razorbills on the sea and on ledges in the pre-laying period

	GUILLEMOT					RAZORBILL				
Date	Ledges	%	Sea	%	Total	Ledges	%	Sea	%	Total
April 7	152	87.3	22	12.6	174	10	10.1	89	89.9	99
April 11[a]	150	95.5	7	4.5	157	18	35.3	33	64.7	51
April 11	78	96.3	3	3.7	81	1	3.9	25	96.1	26
April 11	612	99.7	2	0.3	614	81	72.3	31	27.7	112
April 18	330	98.5	5	1.5	335	49	66.7	20	33.3	60
April 19	700	99.6	3	0.4	703	135	88.8	17	11.2	152
April 19	114	96.6	4	3.4	118	8	19.0	34	81.0	42
Totals	2136	96.2	46	3.8	2182	302	42.3	249	57.7	542

Notes: a. Values with the same date refer to colonies counted within one hour of each other, around the island.

Overall chi-squared value = 737.1 6 df $P<0.001$.

reach of the other. Non-incubating and non-brooding birds usually orientated themselves so that they were standing about 20cm apart, just out of lunging range of each other, with the head directed laterally. The bill was kept closed, but as intensity increased the wings were flicked away from the body, and on some occasions birds called (see Fig.5.4). Threat may develop into fighting, with physical contact between contestants. Threatening encounters varied in duration, lasting from less than one second to a minute or more.

(3) Fighting. Bills were grasped and twisted, and blows delivered with the wings. Fighting usually resulted in one or both birds losing their balance - especially on narrow ledges, and birds often lay with bills locked and wings open. Fights were generally brief, rarely lasting more than one minute. The longest fight I recorded lasted 10.5 min. I recorded only two fights out of several hundred observed, where blood was drawn. In the more severe of the two cases, a bird grasped another by the neck and severed what appeared to be a major blood vessel. The wounded bird also sustained serious injury to one eye.

Both threat and fighting alternated with appeasement postures and displacement activities (see below).

(4) Side-preening (Fig. 5.3b). The head was turned, the bill pointing downwards and the bird preened its scapulars, side of its breast or its back. Sometimes, the bird made intention preening movements, but did not actually touch its plumage. Preening in this situation lasted from a few seconds to several minutes.

(5) Stretch-away (Fig.5.3c). This display, which was performed most frequently by incubating or brooding birds, involved rapidly outstretching

Fig.5.3 a. Threat. Two Guillemots engaged in threat prior to fighting. Note position of the head relative to the body. Not also the wings, which are used to deliver blows.

Fig.5.3 b. Side-preening. The bird pinpointed by an arrow has just alighted and is Side-preening. Note the position of the head and bill.

Fig.5.3 c. Stretch-away. The bird pinpointed by a large arrow is performing Stretch-away; the neck is out-stretched. The bird marked by a smaller arrow is performing Turn-away, turning its head to the right and slightly behind it.

Fig.5.3 a. Threat.

Fig.5.3 b.Side-preening.

Fig.5.3 c. Stretch-away and Turn-away.

Fig.5.3 d. Head-vertical. The bird on the far left is performing Head-vertical towards another (marked by arrow) walking towards it.

Fig.5.3 e. Bill-arring. The right-hand bird has just returned to its mate, at the nest-site. Both birds engaged in Bill-arring. Note that neighbours show considerable interest in the activity.

Fig. 5.3 d. Head-vertical.

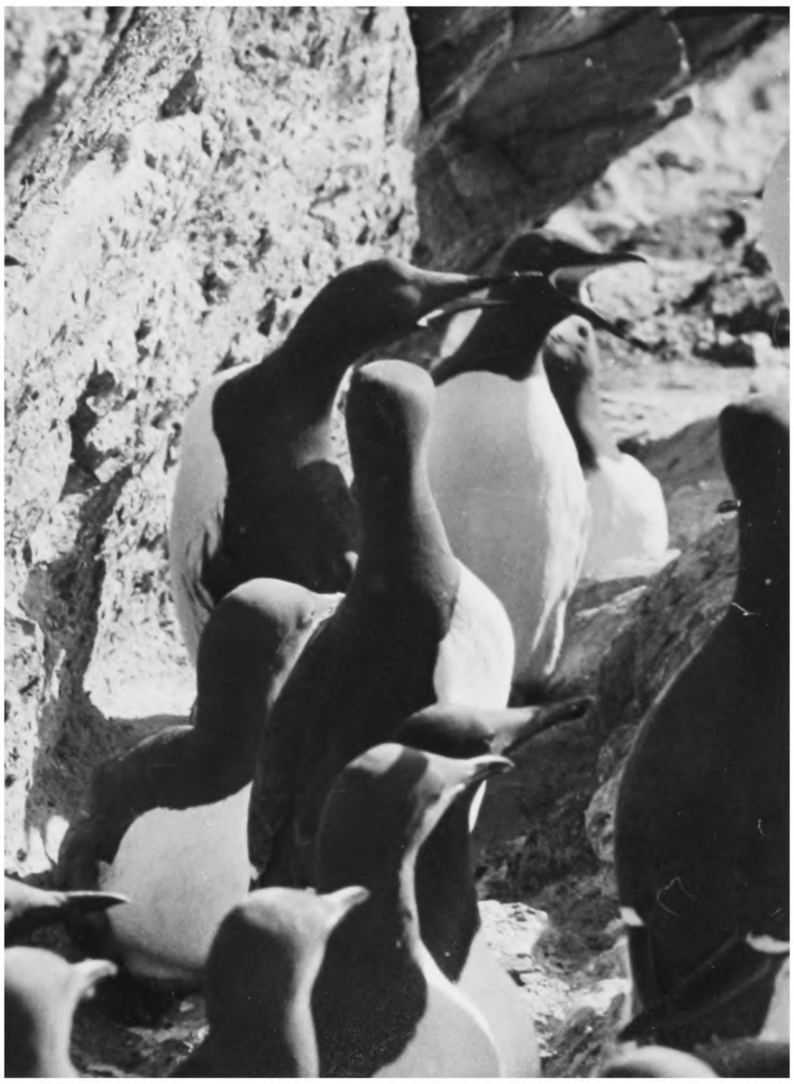


Fig. 5.3 e. Bill-arring.

Fig.5.3 f. Allopreening. The central bird is allopreening its incubating mate. The recipient has closed its eyes.

Fig.5.3 g. Bowing. Both birds have their bills open pointing towards the ground.

Fig.5.3 h. Rape attempt. The male is attempting to hook his neck around the other bird's. The other bird is standing upright,probably in an effort to throw the male off.

Fig.5.3 f. Allopreening

Fig.5.3 g. Bowing

Fig.5.3 h. Rape attempt

Fig.5.3 i. Post-landing display. The bird with its head stretched upwards and wings held above its back has just alighted.

Fig.5.3 j. Ritualized-walking (i). The nearest bird with outstretched and wings held above its back is walking past a group of Guillemots, (compare with Fig.5.3 k - below).

Fig.5.3 k. Ritualized walking (ii). The bridled bird is walking through a dense group of Guillemots, during the pre-laying period.

Fig.5.3 i Post-landing display.

Fig.5.3 j. Ritualized walking (i).

Fig.5.3 k. Ritualized walking (ii).

the neck - sometimes at a slight angle away from a potential aggressor. In most cases the neck was shot out and rapidly withdrawn within less than a second. Less commonly, the neck remained outstretched, away from the aggressor: Prolonged stretch-away.

(6) Turn-away (Fig.5.3c). A bird facing another averted its head through 90° or more, but not exceeding about 150°, thus turning its head 'away' from the other bird.

(7) Foot-looking. The bird simply directed its bill towards the ground and apparently looked at its feet.

(8) Head-vertical (Fig.5.3d). The head and neck were stretched vertically, or almost so. The hyoid may be depressed, producing an unfamiliar outline to the bird's neck. The posture is assumed for 2-5 seconds.

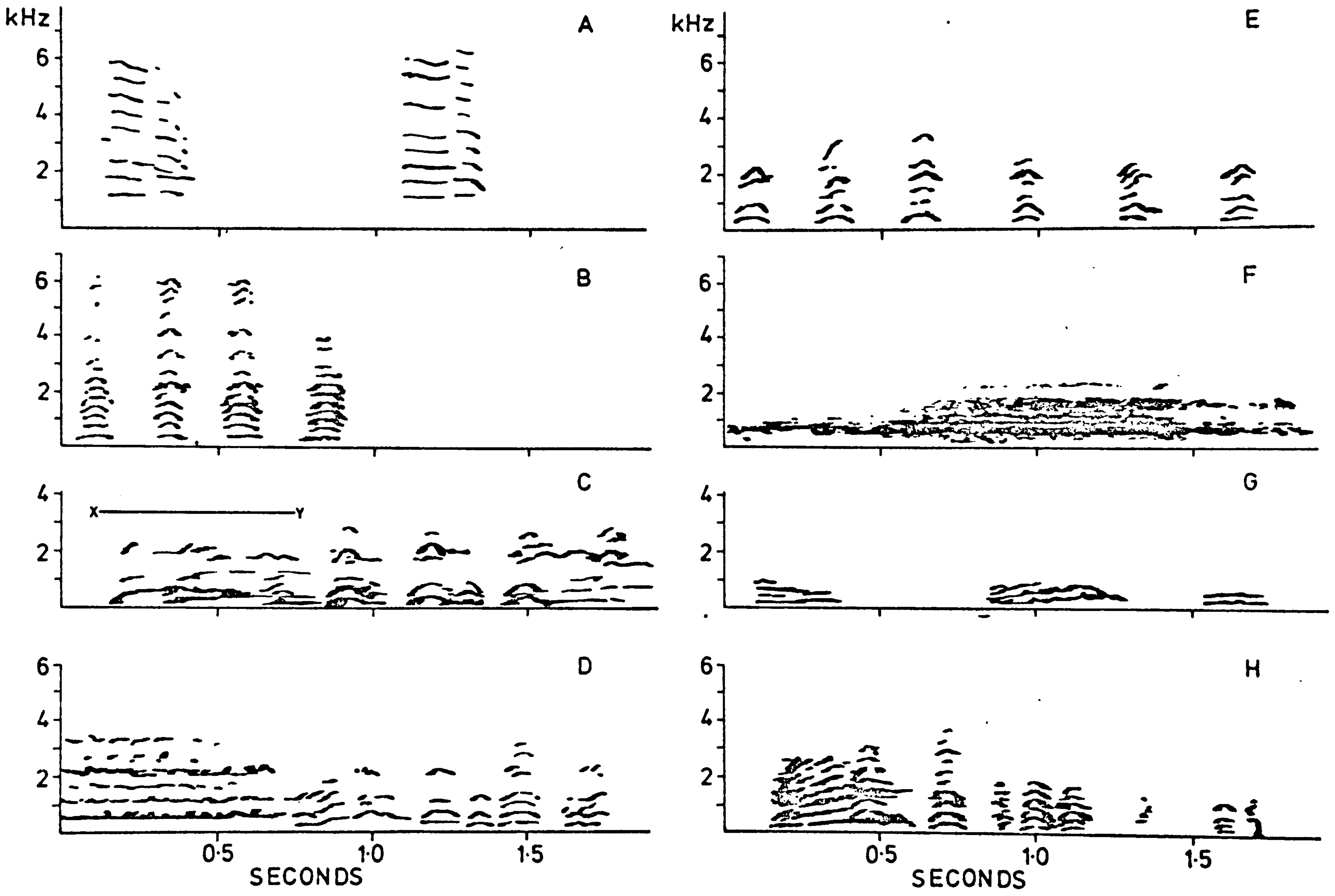
(9) Bill-Arring (Fig.5.3e). This was a display performed between members of a pair. Birds usually faced each other, or faced the same direction, with their necks and bills in close contact. Both birds' bills remained open as they called (see Fig.5.4), exposing the yellow lining to the mouth. The duration of Bill-Arring was 1-10 seconds.

A call similar to that in Fig.5.4 was uttered by single birds (i.e. mate absent or unpaired), in response to other birds fighting or returning to the ledge with a fish.

(10) Allopreening (Fig.5.3f). The head and neck feathers were nibbled by the bill tips of another bird. Among incubating birds the back feathers were also nibbled. The head feathers of the recipient and sometimes the preener were erected or fluffed.

A single bout of Allopreening was treated as one which was separated by a pause of two seconds or more from the next bout. Reciprocal Allopreening was scored as two bouts of Allopreening.

Fig.5.4. Sonagrams of some Guillemot calls. A: Female copulation call. These are disyllabic and occur at about one second intervals. B: Male copulation call; a continuous 'ah ah ah ah' with about four 'ah' calls to every one of the female's calls. C: Bill-arring, greeting call. The section marked x -- y may be as long as four seconds. D: Arring calls uttered during a fight. E and F: calls uttered during Bowing, E is a regular 'ah ah ah' call and F is a drawn-out crooning call. G: call uttered during Alarm-bowing. H: An'arring' call uttered after Bowing.


kHz
6
4
2
A
B
C
x
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D
0·5
1·0
1·5
SECONDS
E
F
G
H

A similar activity to Allopreening was Bill-nibbling, which involved the same sort of mandible movements, but was directed towards another bird's bill tip.

(11) Bowing (Fig.5.3g). This activity was performed by one bird (solitary Bowing), or more usually, by two birds (mutual Bowing). In both cases the birds leant forward and one bird placed its head under its own breast. In mutual Bowing the birds may grasp each other's bills in this position. Single birds may grasp at the substrate or loose material on the ledge. In mutual Bowing bill grasping sometimes developed into Allopreening. A variety of calls were uttered during mutual Bowing (Fig.5.4).

(12) Fish-presentation. A bird returns to its site with a single fish - not intended for a chick. Birds returning with fish with no mate present simply stood holding the fish. Paired birds adopted a bowed position, during which the wings were sometimes drooped, and the fish exchanged at least once between the birds. The exchange generally took place under the breast or between the feet of one of the birds. The activity closely resembled Bowing and chick-feeding. It was not courtship feeding (see later). I was unable to determine whether any call was uttered when birds bowed or exchanged fish.

(13) Scraping. The bird crouched forward onto its breast, the wings hanging loosely at the bird's side, and the feet scraped backwards and forwards across the ledge. The bird sometimes placed its head under the breast while holding a small stone between its mandibles, and placed the stone under its breast. Scraping usually preceded egg-laying (see also Williams 1971). Birds picked at stones during scraping. This behaviour, known as Picking, also occurred independently of Scraping. Birds adopted a posture similar to Foot-looking and repeatedly picked up and dropped stones or other material on the

ledge. In 82% of 110 observations of Picking stones were dropped or thrown between the feet, the rest were dropped elsewhere.

(14) Copulation. During copulation the female threw her head back at regular intervals and uttered a disyllabic call (Fig.5.4). The male drooped his wings while standing on the female's back and sometimes used them for balancing. The male uttered a rhythmical "ha ha ha ha ha" call during copulation (Fig.5.4). The mean duration that 22 males remained on females' backs was 17 seconds (range 4-40), and the mean duration of 18 cloacal contacts was 3.5 seconds (range: 1.9-5.4). Up to four cloacal contacts during one 'mounting' occurred. Copulation was usually initiated by the female adopting the 'Copulation-invitation' posture; crouching forward and simultaneously uttering the copulation call. In cases where the female did not perform Copulation-invitation and males attempted to mount, the male attempted to hook his neck around the female's (Fig.5.3h), presumably in order to stay on, while the female attempted to stand upright, presumably to throw the male off.

Rape is defined as a copulation attempt by a male with an uncooperative female.

(15) Post-landing posture (Fig.5.3i). This posture consists of two components, the head-up and the wing-up components. The head was held up and forward at an angle of about 60°, and the wings were outstretched over the bird's back. This posture was maintained for a duration of about one to four seconds after alighting (but see below).

(16) Ritualized-walking. This also consisted of two components, the angle of the head and the outstretched wings. Ritualized-walking postures were assumed when birds moved past or between conspecifics, and were maintained until the bird stopped moving. The first posture was very similar to the Post-landing one (Fig.5.3k), but the head was sometimes at a greater angle: 70°-90°.

In the second posture (Fig.5.3j) the wings were outstretched above the bird's back and the head directed forward and downwards.

(17) Alarm-bowing. This consisted of a short neck bow while the bird maintained an alert posture. The neck was moved through 90°, while the head maintained either a horizontal or downward-pointing position, and returned to the alert position. The bowing action was a rapid one, and was accompanied by a short duration, low frequency, low amplitude call (Fig.5.4). Alarm occurred in three stages; at the first sign of danger (e.g. gull alarm call, appearance of man) birds became alert. As the intensity of alarm increased the birds performed Alarm-bowing, and some moved to the edge of the ledge, facing the sea. The final stage is taking flight. Incubating and brooding birds are less likely to take flight than other birds.

(d) Diurnal and Seasonal Changes in Behaviour

During the pre-laying period there was a decrease in the frequency of all behaviour patterns (except aggression) through the day (Table 5.3), but this was not the case in the other two periods. This difference is probably due to the patterns of colony attendance at the different stages of the breeding season (see Appendix I). In the pre-laying period all birds arrived at the colony within the first two hours of daylight, and pairs remained on the ledge together throughout the day. A peak of activity occurred soon after birds met, but as they hatituated to each other's presence the frequency of some behaviour patterns decreased. During the incubation and nestling periods the pattern of attendance was different, and birds were leaving and returning to their mates at the site throughout the daylight period, thus obliterating any habituation effect.

Table 5.3. Diurnal changes in the frequency of some Guillemot behaviour patterns at different stages in the breeding season. Values are means for behaviour units expressed as 'activities'/pr./hr.

Time	Pre-laying Period					Incubation Period			Nestling Period		
	Allop.	B-arr.	Agg.	Cop.	Bow.	Allop.	B-arr.	Agg.	Allop.	B-arr.	Agg.
0500-0700	1.46	0.06	0	0.42	0.30	1.48	0	0.04	0.86	0.12	0
0900-1100	1.04	0.06	0	0.04	0.26	1.58	0.06	0	0.74	0.02	0.04
1300-1500	0.96	0.04	0	0.02	0.20	1.26	0	0.04	0.76	0.02	0.16
1700-1900	0.66	0.02	0.02	0.05	0.20	1.52	0	0	0.70	0.12	0.06
2000-2200	-	-	-	-	-	1.54	0	0.04	0.56	0.10	0.14

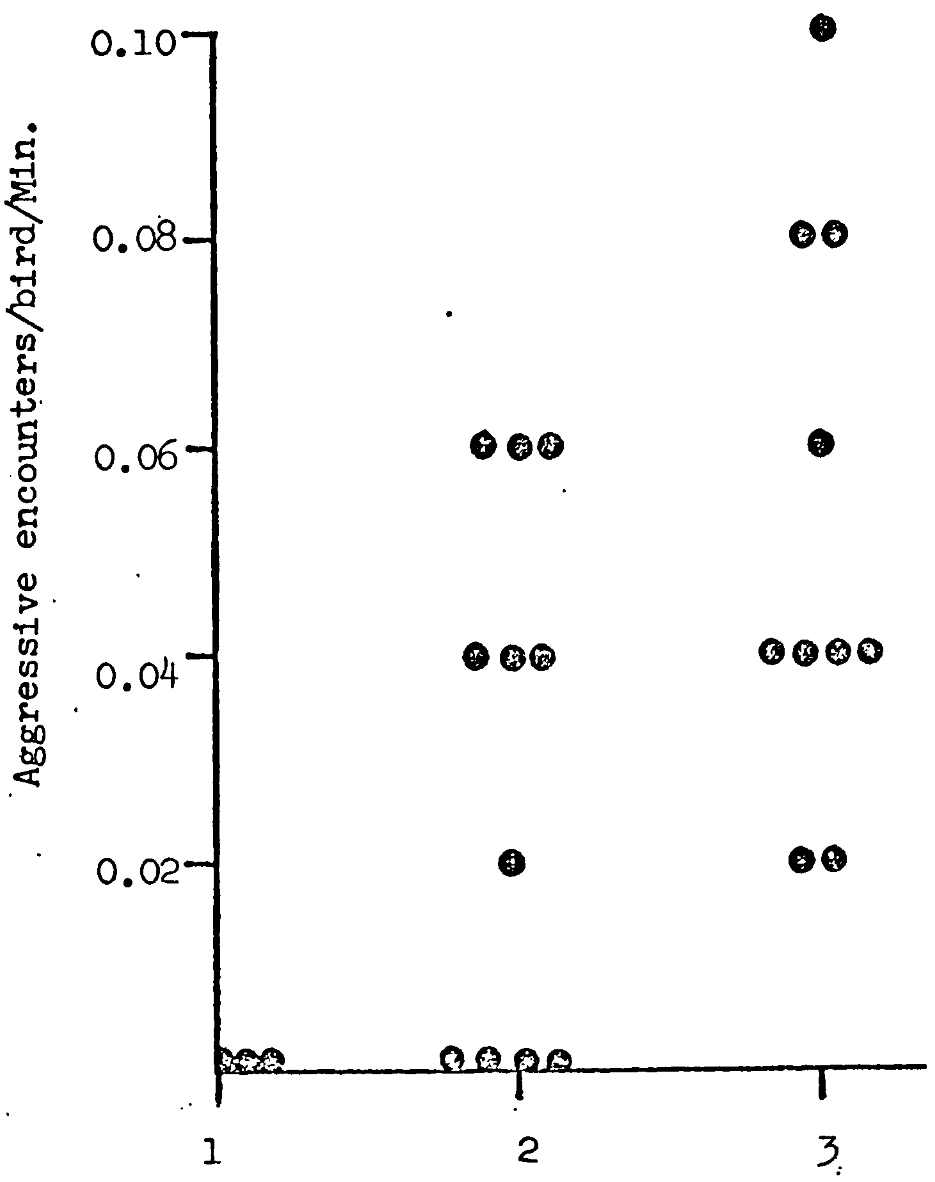
Notes: Copulation and Bowing only occurred during the pre-laying period.
Copulation frequency is expressed as copulations/bird/hr., all other values are activity/pair/hr.
There is no information for 2000-2200 hrs (BST) during the pre-laying period because most birds had left the colony by this time.
Allop.= Allopreening, B-arr = Bill-arring, Agg. = Aggression, Cop. = Copulation, Bow = Mutual Bowing.

(e) Aggression

Levels of aggression and appeasement increased with the density of breeding birds (Fig.5.5). Seasonal patterns of aggression at Medium densities are shown in Fig.5.6, and are significantly lower in the pre-laying period (April) than at other times ($t = 3.88$ 33df $P<0.001$). The higher levels of aggression during the winter may reflect the re-establishment of sites after a period of absence, and this agrees with the idea that one function of an early return to the colony (see Appendix I) is to maintain the site. The increased aggression during the incubation and nestling periods may be due to encounters between breeding birds and site-hunting immatures visiting the ledges, or to 'idle' failed breeders trespassing.

Aggression occurs at different levels among different categories of birds (e.g. breeding birds, their incubating or brooding mates, immatures, etc.) and occurred in the defence of two main resources, the nest site and mate.

Aggression in different categories of birds. Levels of aggression were lower among incubating birds than among their mates. In 30 minutes' observation of six incubating birds and their mates, incubating birds initiated only two encounters, whereas their mates initiated 15, this difference is significant ($X^2 = 9.9$ 1df $P<0.01$). In addition, incubating birds appeared to actively avoid aggression since they performed appeasement postures (Stretch-away) nearly three times as frequently as their non-incubating mates (see below). The response of incubating birds to nearby fights was usually to perform Stretch-away and then to withdraw the neck and keep the head low. Fighting birds could flap and fight all over incubating birds without eliciting any attack from them. In contrast, non-incubating birds standing



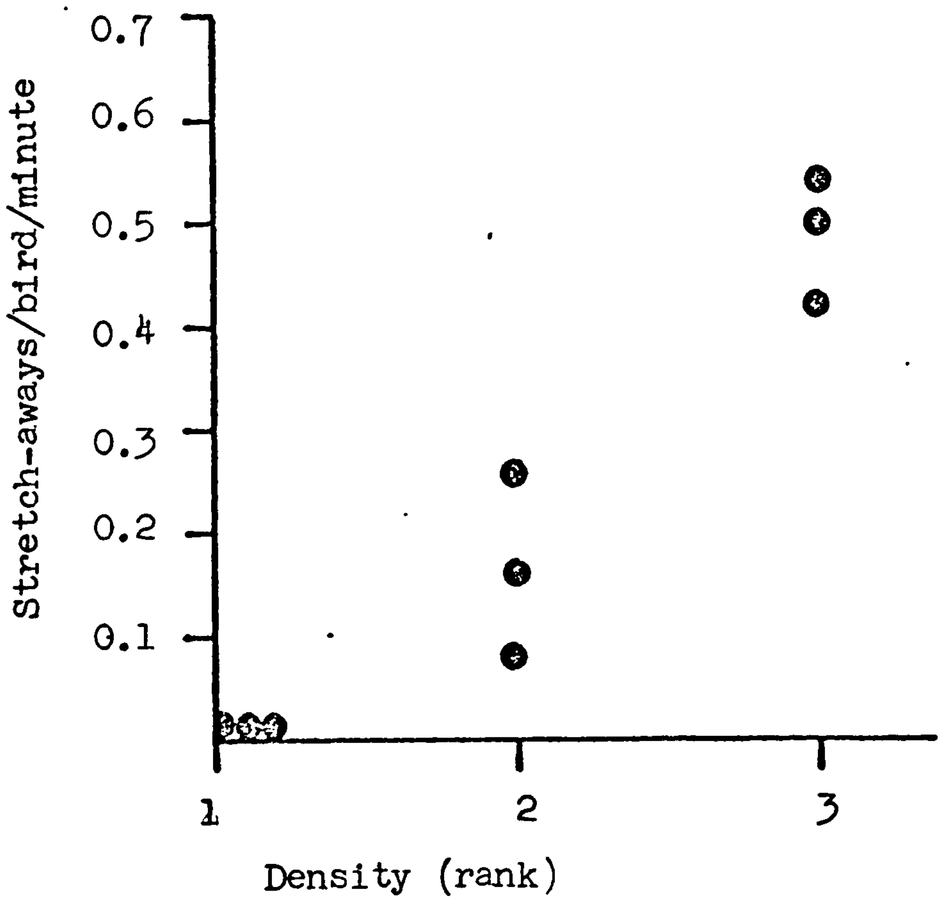
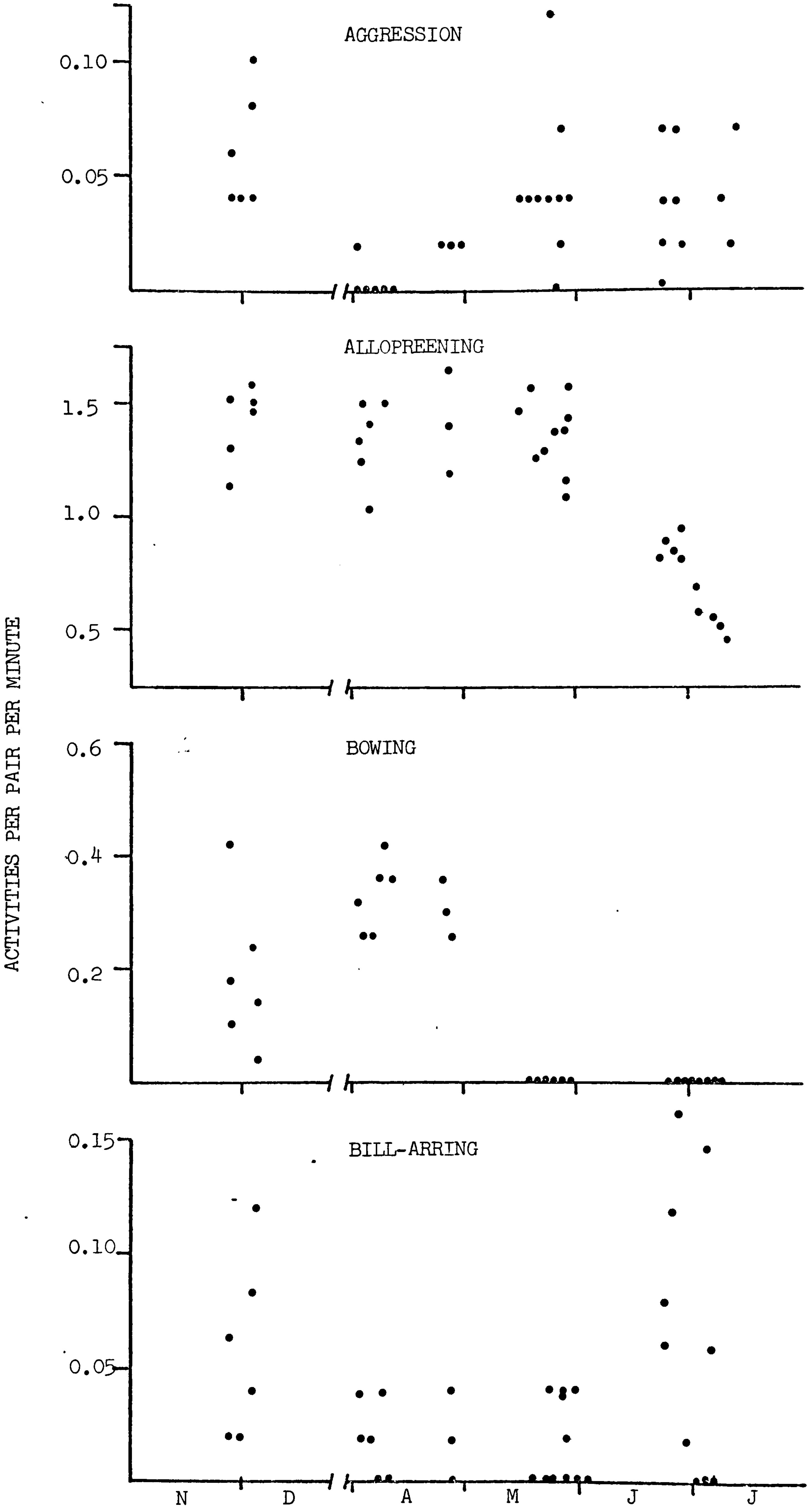


Fig.5.5. Relationship between density of breeding Guillemots and agonistic behaviour. Density 1: less than 3 birds/m^2, 2: c5 birds/m^2, 3: more than 10 birds/m^2. Upper figure is number of aggressive encounters vs density (Spearman Rank r = 0.608 P<0.01). Lower figure is relationship between Stretch-away performance and density (Spearman Rank r = 0.964 P<0.001). Each point in both figures represents one 50 min. observation unit (see text).

Fig.5.6.Seasonal changes in some Guillemot behaviour patterns; from the top: Aggression, Allopreening,Bowing and Billarring. Each point represents one 50 min. observation unit. Observations were made in the Winter months (November and December), pre-laying period (April),Incubation (mid-May to mid-June) and nestling period (late-June and July).


AGGRESSION
0.10
0.05
ALLOPREENING
1.5
1.0
0.5
BOWING
0.6
0.4
0.2
BILL-ARRING
0.15
0.10
0.05
ACTIVITIES PER PAIR PER MINUTE
N
D
A
M
J
J

nearby attempted to peck at those engaged in fighting. In several hundred hours' observation I only once recorded an incubating bird leave its egg unattended during an aggressive encounter in order to attack its opponent. The advantage of avoiding aggression among incubating birds is clear; at high densities where the likelihood of aggression is high, incubating birds run the risk of losing or damaging their egg if they freely engage in fighting.

The second category of birds that showed reduced aggression were (colour-marked) three year olds (see Chapter 2). I was able to observe at close range a pair of three year old birds visiting a ledge and apparently attempting to obtain a site. Numerous qualitative observations of other three year olds elsewhere on Skomer confirmed the results obtained from this pair. The three year olds persistently visited a particular site on the ledge where they were originally hatched, but were attacked by established birds. The three year olds appeared subordinate and nervous of established birds, and were attacked as they moved towards the site and even when they alighted on the edge of a ledge. Observations were made in three one hour periods on consecutive days. On each day I recorded interactions between the pair of three year olds and the other established birds (mean number of established birds = 16). A total of 41 aggressive encounters was observed, and three year old birds were involved in 30 (73%) of these. The mean number of aggressive encounters/bird/hour (not including three year olds) was 0.21, but was 5.0 for three year olds. I did not record three year olds initiating fights. In 9/30 (30%) encounters three year old birds fled, but none of the established birds did this. In only 5/30 (17%) cases did three year old birds retaliate when attacked, whereas all non-incubating established birds retaliated. The three year olds finally acquired a breeding site, but because this was about 2m from the ledge where I had observed them I did not discover this until they had established themselves there.

Aggression in defence of the site and mate. Aggression occurred in the following situations:-

(1) When a bird trespassed into another's territory.

(2) When prospecting birds visited ledges (see above). I have shown earlier (Chapter 2) that there is an increase in the amount of time spent by three year old birds on breeding ledges as the season proceeds, and most sightings of three year olds late in the season were on ledges.

(3) In clubs; the club situation provided additional information regarding the function and causation of aggression. Levels of aggression on the ledges between paired birds and others were generally low, averaging 0.035 aggressive encounters/pair/min over the entire study period (November - July) (Table 5.3). The level of aggression in clubs was about ten times higher than on ledges (Mean in clubs for whole season = 0.35 encounters/bird/minute, compared with the value for birds on ledges, above, $t = 15.7$ 44df $P<0.001$) - not allowing for the difference in recording method. Of 125 aggressive encounters on clubs, 70 (56%) occurred as another bird moved near the 'aggressor', 50 (40%) when the 'aggressor' attacked a neighbour for no apparent reason, and 5 (4%) as a result of a Rape-attempt. Club birds apparently formed temporary territories (often with temporary mates) and defended them against potential or actual trespassers. Levels of aggression were lowest when there were few birds on the club, but levelled out above 14 individuals in the particular club I was watching (Fig.5.7). This effect probably occurred because, up to peak numbers, birds encountered each other, or encroached on one another's

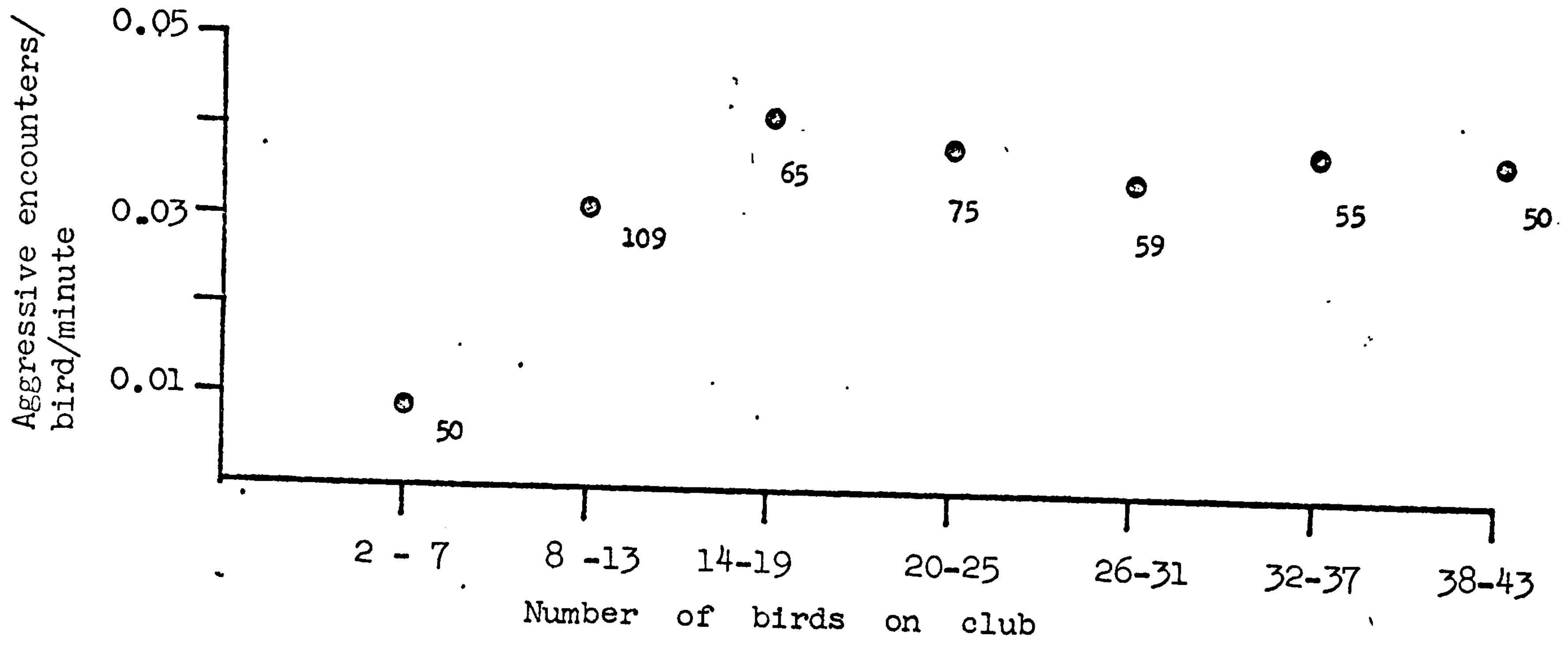


Fig.5.7. The frequency of aggressive encounters among Guillemots in a club, in relation to the number of birds on the club (x axis). The figures by each point show the number of minutes observation on which each point is based.

territory more often the greater the number of birds on the club. There was no seasonal change in aggression on clubs (Fig.5.8a).

(4) Aggression occurred when adults had to re-establish their site boundaries. An experiment was conducted to investigate the function and causation of mutual Bowing. To do this I altered the physical nature of a breeding ledge. This involved 'improving' one half by paving an irregular area with flat stones, and disrupting existing sites, by covering them with rubble - thus simulating a rock-fall (which apparently occur frequently in arctic breeding areas (Tuck 1960), but are probably rare on Skomer). Some evidence suggested that aggression was important in site acquisition and maintenance. To test this hypothesis I recorded the frequency of aggressive encounters in the experimental (ledge change) group and nearby control group, matched for density and number of breeding pairs. Both groups could be observed more or less simultaneously from my observation point. Observations were made in early April before any birds had laid, and were conducted on peak attendance days when most birds were present at their breeding sites. I recorded the number of birds in the experimental group and then recorded the number of aggressive encounters over a continuous ten minute period. Observatio were recorded into a tape recorder. Immediately after completing ten minutes of observation at the experimental group, I conducted the same sort of observation at the control group. Because of the diurnal changes in behaviour during the pre-laying period (Table 5.3) control observations were made directly after experimental group observations, so that records could be treated as paired observations. The results of this experiment, relevant here, showed that although birds did not change site in response to the 'loss' of their breeding sites, they did make small shifts in position, because of the

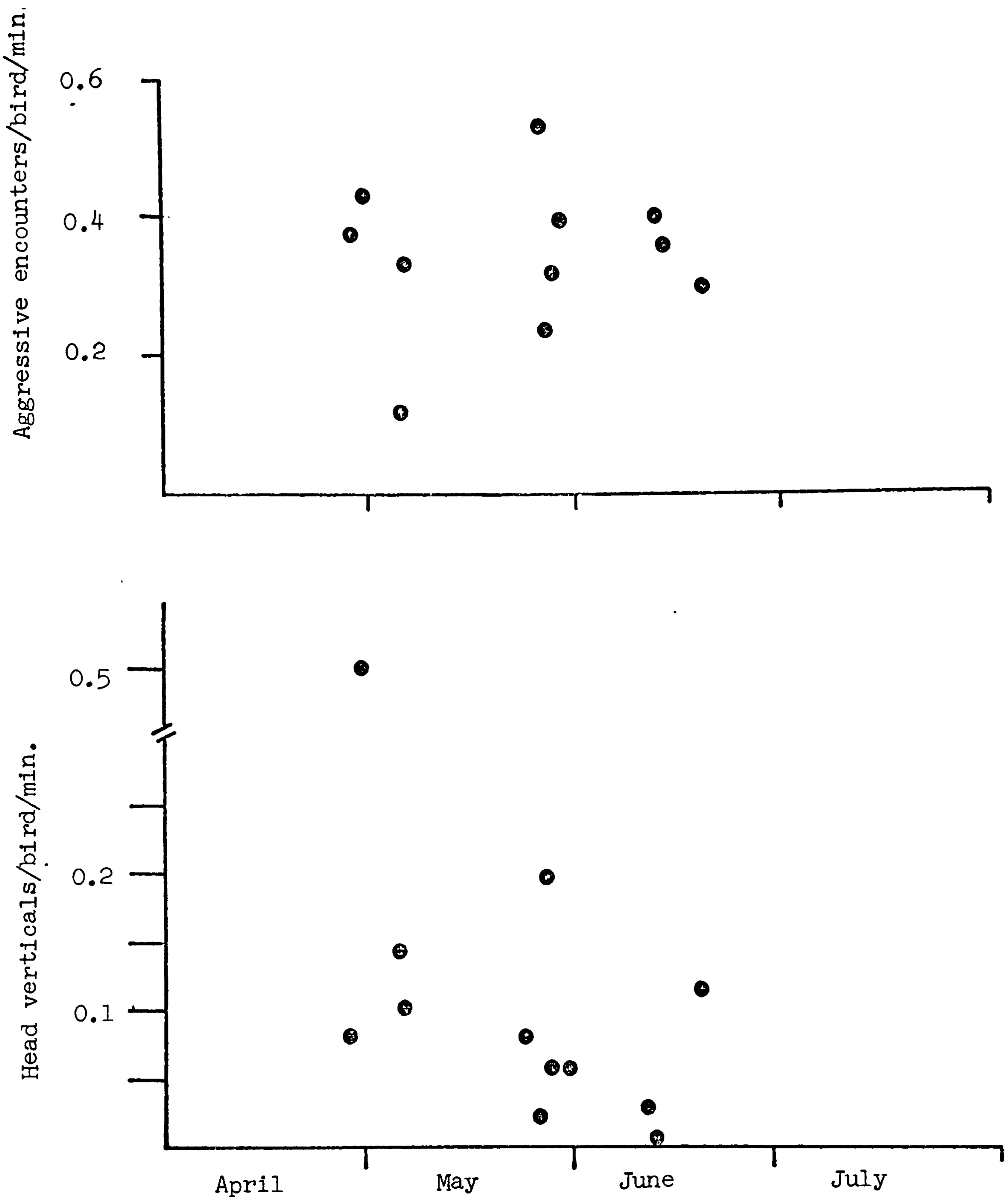


Fig.5.8. Frequency of aggression and Head-vertical behaviour in Guillemots in clubs in relation to date. The upper figure shows the number of aggressive encounters/bird/min. and the lower one, Head-vertical displays/bird/min. Each point = one 50 min. observation unit.

irregularity of the disrupted surface. Notwithstanding the small changes in position, the experimental group's aggressive encounters averaged 0.12 bird/10 min ± 0.127 S.D., and the control group averaged 0.037 aggressive encounters/10 bird/min ± 0.058 S.D. (in both cases n = 28 ten minute observation periods). The difference between the two groups was significant (Wilcoxon Matched Pairs $P<0.001$) (see also section on Bowing).

(5) Aggression also occurred when a bird attempted to mount another's mate (Rape), and also between Rapist and victim.

As in many species there was a strong element of fear in aggressive encounters between Guillemots. Threat lunges were often interspersed with appeasement postures (see next section). Fights were usually preceded by threat, although when males were defending their mates from Rapists, 'pure' aggression seemed to dominate. An analysis of birds' behaviour at the end of fights provided some clues to the causation of these behaviour patterns.

There were few cases where defeated birds fled from their opponents after fights, when it was obvious which bird had won. I used the performance of Side-preening by one bird as an indication that the bird had 'lost' the contest. There is some evidence that Side-preening occurs as an appeasement activity (see below), and it is probably reasonable to assume that birds which performed this display had a stronger escape tendency than those not performing it. I have compared the behaviour of birds which won contests with those which lost. A test for heterogeneity between the behaviour of the two groups revealed a significant difference (Table 5.4) ($X^2 = 28.7$ 3df $P<0.001$). Winners performed Bill-arring with their mates more often than losers but losers performed Turn-away more frequently than winners. The lack of difference in Head-shaking between the two categories suggests that it may not

Table 5.4. Comparison of behaviour patterns of 'winners' and 'losers' at the end of fights. Losers were defined as birds which performed Side-preening at the end of a fight (n = 34) see text.

Display	WINNERS		LOSERS	
	Observed	Expected	Observed	Expected
Head-shake	12	16.0	16	11.9
Turn-away	6	1.5	11	7.2
Bill-arr mate	15	9.2	1	6.8
Foot-look	6	4.0	1	2.9

Notes: Total chi-squared value = 28.7 3 df $P<0.001$.

serve any signal function and may be a comfort movement. Ainley (1974) showed that in Adelie Penguins salt secretion accompanying Head-shaking increased during a disturbance such as a territorial dispute. It is possible that hypersecretion of the nasal gland during Guillemot aggression may account for the high frequency of Head-shaking (61/103; 60% of all fights) in this situation. Van Iersel & Bol (1958) found that in terns Sterna spp. displacement activities such as Head-shaking and preening were more frequent the stronger the escape drive. Kruijt (1964) found in the Red Jungle Fowl Gallus gallus, which has no nasal glands, Head-shaking and preening were more frequent in birds which lost encounters.

Turn-away occurred more frequently in losers than winners and this display appears to be a classical appeasement gesture (see Tinbergen 1959), and may be similar to Side-preening in this respect (see later).

There was little difference in Foot-looking between birds which won and birds which lost contests (Table 5.4). The function of Foot-looking is not clear (see Harrison 1965b for review), but it probably occurs as a displacement activity.

Aggression between members of a pair. Fights between pair members were rare. In five out of five cases where I observed aggression between members of a pair, and where I knew the sex (colour-marked) individuals, the male attacked the female, and so may be the dominant partner.

(f) Appeasement

I have divided appeasement displays into two categories; 'active' and 'passive'. Active appeasement is a signal performed in response to an attack, and signals 'please stop pecking me'. Passive appeasement is performed before any attack has been launched, and signals 'please don't peck me'. There were three active appeasement signals; 1) Side-preening, 2) Stretch-away, and 3) Turn-away, although all of these displays were also used as passive appeasement in certain contexts (Table 5.5).

Side-preening. This display was never observed among incubating or brooding birds. Side-preening was used as active appeasement during and at the end of fights (see Table 5.4) both on ledges and clubs, and was performed as passive appeasement 1-3 seconds after the bird had alighted on a ledge, or after it had moved along a ledge. In both of these post-moving situations a bird was more likely to perform Side-preening if other birds were nearby. Thus, it seems likely that Side-preening serves as an appeasement directed towards conspecifics close by (i.e. those birds most likely to attack the bird which recently arrived or moved along the ledge).

In both the post-fighting and post-moving contexts Side-preening occurred more frequently in birds in which the tendency to escape was greater than to attack. Side-preening probably serves as an appeasement by hiding the bill, signalling non-aggressive intent. Although the bill is not directed towards the potential aggressor, nor is it 'facing away' in the strict sense. The bill is directed downwards (see Fig.5.3b) into the bird's plumage, so it seems unlikely that there is any directional component to Side-preening. In 36 cases when fighting birds were positioned so that I could readily decide whether a right or left-hand Side-preen was directed away from or towards the opponent, in 14 cases birds preened 'away', and 11 'towards' their opponent. This difference was not significantly different from an expected 50:50 ratio (X^2 = 1.8 ldf NS).

Stretch-away. This rapidly executed display occurred in four situations (Table 5.5) and was performed significantly more frequently among incubating

Table 5.5. Appeasement behaviour: a summary of frequency and context in which displays occur.

Display	Birds involved	Context	Appeasement	Frequency	
Side-preen.	Non-incubating	(1) Post-landing: mate present	Passive	11/220	(5%)
		mate absent	Passive	118/258	(46%)*
		Mate absent bird alights within 0.5m of a conspecific		76/115	(66%)**
		(2) Walkingpast/through conspecifics	Passive		
		(a) to 'centre' sites:		8/30	(27%)
		(b) to 'edge' sites:		8/116	(7%)***
		(3) Post-fighting:performed by at least one contestant	Active	53/103	(55%)
Stretch-away	Mainly incubating birds	(1) After being pecked or threatened	Active	38/375	(10%)
		(2) After pecking or threatening	Active	27/375	(7%)
		(3) In response to nearby fight	Passive	41/375	(11%)
		(4) In response to movement of nearby bird and/or for no apparent reason	Passive	269/375	(72%)
Turn-away	All birds	(1) After or during fight by at least one contestant	Active	42/103	(42%)
		(2) In response to movement of nearby bird	Passive	-	-

Notes: 'Centre' sites = those where birds are closer than 0.5m to subject, 'edge' sites = where birds are further than 0.5m away.

Chi-squared comparisons: * Comparison of mate present/absent $X^2 = 52.8$ 1 df $P < 0.001$. ** Comparison with birds alighting further than 0.5m away $X^2 = 11.9$ 1 df $P < 0.001$. *** Comparison of 'centre' and 'edge' sites $X^2 = 6.9$ 1 df $P < 0.01$.

birds (n = 135) than their non-incubating mates (n = 48) (X^2 = 41.4 1df $P<0.001$). The frequency of Stretch-away among incubating birds was positively correlated with the density of breeding birds (Fig.5.5) as was aggression.

In about 27% of all observations of Stretch-away the display was performed as active appeasement, and in 83% as passive appeasement (Table 5.5). In 72% of observations Stretch-away occurred in response to a bird moving nearby, and waves of Stretch-away movements occurred in dense groups when a bird attempted to leave the centre of the group, climbing over incubating birds and pushing between non-incubating individuals.

A modified form of Stretch-away is Prolonged Stretch-away. Instead of the rapid in-out movement of the neck, the neck remains extended away from an aggressor. Prolonged Stretch-away occurred infrequently between contestants at the end of a fight. It is not clear why Stretch-away does not function correctly in these situations. However, the Prolonged Stretch-away is adaptive; among incubating birds it signals submission, 'I submit but I am staying here'. Incubating birds cannot flee without risk of losing eggs or chicks (see Chapter 3).

Turn-away. The main contexts in which this display occurs, as active and passive appeasement are shown in Table 5.5. Turn-away appears to be similar to appeasement postures recorded in other species, such as larids (Tinbergen 1959), canids (Fox 1974) and the Spotted Hyena *Crocuta crocuta* (Kruuk 1972).

Conclusions on Appeasement Behaviour

At first sight it may seem unnecessary to have three different appeasement postures. However, each display has a specific function, and the differences between the displays can be summarized as follows; Stretch-away serves mainly as passive appeasement. When it is performed in dense groups it is impossible for a bird to direct its head and neck 'away' from all other birds. For this reason the rapidity of the display is probably important; the display can be performed and completed without eliciting aggression from neighbours. The difference in the meaning of Side-preening and Turn-away in the post-fight/ active appeasement situation is not clear, but the form of the displays provides a clue. In Side-preening the head and bill are directed away from the opponent, and are usually directed towards the performer as it preens its plumage. There is no directional element in Side-preening. As a bird Side-preens it turns its head so that it can no longer see its opponent, and the display may function as a cut-off posture (Chance 1962). In contrast, the Turn-away posture allows the performing bird to signal appeasement, but still keep its opponent in view. Thus, Turn-away may occur as a low intensity or defensive form of Side-preening, and may be used in situations where the bird has a less strong escape tendency, and must keep an eye on its opponent in case of renewed attack.

(g) Post-landing and Ritualized-walking displays: Passive appeasement

Post-landing displays occurred in 418/478 (87.5%) occasions when a Guillemot alighted on a ledge. The display consists of two components; head-up and wing-up. The head-up component was performed in 393/418 (94%) cases, and the wing-up component less often, 279/418 (67%), but rarely without head-up (see Table 5.6).

Alighting birds were more likely to perform Post-landing displays in the proximity of other birds. During the incubation and nestling period one member of the pair was at the site continuously, incubating or brooding. On only one occasion out of 114, during these two periods did a bird not perform a

Table 5.6. Summary of post-landing display components in the Guillemot, with and without mates present at site.

Component	Pre-laying	Incubation	Nestling	Total
Mate Present	n= 106	n= 34	n= 80	n= 220
Head-up	100 (94.3%)	33 (97.0%)	75 (93.7%)	208 (94.5%)
Wing-up	66 (62.2%)	30 (88.2%)	33 (41.2%)	129 (58.6%)
Head-up + Wing-up	63 (59.4%)	30 (88.2%)	33 (41.2%)	126 (57.3%)
No display	0	1 (3.0%)	0	1 (0.45%)
No Mate Present	n=86	n=83	n= 89	n= 258
Head-up	70 (81.4%)	50 (60.2%)	65 (73.0%)	185 (71.7%)
Wing-up	61 (70.9%)	44 (53.0%)	45 (50.5%)	150 (58.0%)
Head-up + Wing-up	59 (68.6%)	42 (50.6%)	42 (47.2%)	143 (55.4%)
No display	11 (12.8%)	27 (32.5%)	21 (23.6%)	59 (22.8%)

Post-landing display.

During the incubation and nestling periods, in cases where no mate was present, significantly more birds alighted without displaying than in the pre-laying period ($X^2 = 7.4$ 1df $P<0.01$) (see Table 5.6). This was probably a result of the increase in the number of non-breeders visiting the colony at this time. To test this I recorded the Post-landing behaviour of immature birds without sites, alighting on a 'loafing area'. As already pointed out, immature birds generally congregated in clubs on tidal rocks at the foot of cliffs, where they simply hopped out of the water onto the rocks. I knew of only two areas on Skomer where immature birds congregated in areas that they had to fly up to. Observations were made at one of these sites. A total of 107 arrivals was observed and of these only 9 (8.4%) performed any Post-landing display. The difference between 'centre' and 'edge' positions (Table 5.7) was similar to that already discussed for other situations. The most striking feature of Post-landing behaviour at this site was the low frequency of displays among non-breeding birds. I have compared the frequency of display in this area with a comparable situation among breeding birds (Table 5.7). The difference between display frequency among birds without sites and breeding birds arriving at their site, when their mate was absent, during the pre-laying period, was significant ($X^2 = 120.4$ 1df $P<0.001$).

Thus, Post-landing displays were performed by site-owning birds when their mate was absent or present, and more frequently when they alighted close to other birds. Post-landing displays have two possible functions, a) as passive appeasement; alighting birds appear at the ledge very suddenly and birds already there become alert and may threaten the arrival. The Post-landing display provides nearby birds with an opportunity to recognize the alighting

Table 5.7. Differences in frequency of Post-landing displays between site-owning breeding birds and immature birds without sites.

Alighting position	Breeding birds		Non-breeding birds	
	Display	No Display	Display	No Display
'Centre' position	54	1	7	63
'Edge' position	21	10	2	35
Total (all data)	75	11	9	98

Notes:

Comparison of breeding and non-breeding birds at centre sites: $X^2 = 95.8$ 1 df $P<0.001$

Comparison of breeding and non-breeding birds at edge sites: $X^2 = 29.8$ 1 df $P<0.001$

bird, and birds from adjoining sites may habituate to each other, thus reducing the likelihood of conflict (Van Tets 1965); b) Site-ownership; Table 5.7 shows that Post-landing displays are performed more frequently by birds with sites than birds wituout sites.

Ritualized-walking.

(1) On each of 50 occasions when I observed birds walking through dense groups of birds, Guillemots assumed a head-up posture, almost identical to the Post-landing posture (Fig.5.3k). In 39 cases the wing-up component also occurred. In some cases birds assumed the head-up, wing-up posture as they alighted and maintained it as they walked between conspecifics to their site or mate.

After egg-laying and during the nestling period birds could not alight at the edge of the group and then walk through or between birds, so at these times arriving birds usually alighted among the dense group of birds as near to their site as possible - often attempting to perform a Post-landing display as they alighted. Similarly, when leaving the group, birds had to scramble over the backs of incubating and brooding birds. In doing this they performed the head-up and wing-up postures; they were frequently threatened by the mates of incubating birds (Williams 1974: Fig.4), but incubating birds simply kept their heads down and did not threaten or attack birds which walked over them.

(2) When birds walked within 0.5m of conspecifics, that is, along-side a group of birds, a different posture was assumed. A head-down wing-up posture was adopted in 142/176 (81%) cases, and in 28/176 (16%) the wing-up component was not included. In the remaining six cases no posture was assumed.

(3) When no birds were nearer than 2m away no display was performed (n = 23).

In both the head-up and head-down versions of this display, the wing-up component helps to make the bird conspicuous, an important factor in drawing attention to the moving bird. The angle of the head in both situations allows the bird to move forward and see where it is going. The need for ritualized, conspicuous movements are clear; a bird which makes a sudden movement, especially in crowded conditions is likely to be attacked by neighbouring birds. Thus, the Ritualized-walking postures probably signal 'I am moving, but have no aggressive intentions'.

It is apparent from this section that Post-landing and Ritualized-walking displays share a number of common features, both in form and in the message transmitted. Similar behaviour patterns in the Pelecaniforms have been reviewed by Van Tets (1965 - but also see Nelson 1967), and Van Tets has shown that in this group the Post-landing displays and 'hop' displays - which are equivalent to Ritualized-walking in the Guillemot, also share a number of common features.

Other Displays

(h) Head-vertical

This display occurred most frequently in the clubs, that is, among non-breeding birds. No seasonal trend in the frequency of Head-vertical in clubs was apparent (Fig. 5.8b). Head-vertical was never recorded among breeding pairs in behaviour-unit observations, and only twice at other times. Head-vertical was observed among non-breeding birds (marked three year olds) on ledges, but all observations recorded in this section were made in clubs.

In 80/162 instances (50%) Head-vertical was performed as another bird approached or walked past the performer. More rarely it was performed after the performer had approached another bird. In general, performing birds remained stationary, apparently on temporary territories, and waited for other birds to approach them.

In 32 cases I was able to sex club birds performing Head-vertical; all were males. On a few occasions when two birds, which had been Allopreening, were standing together, both birds performed Head-vertical. Thus, females may occasionally perform this display.

A characteristic of club birds' behaviour appeared to be the formation of temporary pairs on temporary territories (this has also been recorded in clubs of McCormick's Skua <u>Catharacta macormicki</u>; Spellerberg 1971). In the Guillemot the Head-vertical display appears to be an important preliminary in the formation of temporary pairs, and probably, permanent pairs as well. It seems likely that Head-vertical serves as a distance-reducing display (Tinbergen 1959), that is, a mate-advertising display important in initial contact between two birds. Fig.5.9 shows the sequence of events after a bird (in most cases probably male) performed a Head-vertical display. Of 162 instances, 63 (39%) resulted in 'no further action' - the performer being ignored, and in 16 (10%) cases the other bird retreated or fled. In both situations it may have been either a male, and therefore uninterested in the bird's advertising signal, or an unreceptive female. In 83% of the cases the birds approached each other and stood side by side. In 38% of the cases the male immediately attempted to mount the bird as it came within range. Only rarely did the other bird (female?) cooperate in such copulation attempts, and in most cases (23/32: 72%) it attacked the male. In a few cases (9) it did not attack the male after an unsuccessful mounting attempt, and in 8 of these the male appeared to resume his advancesby performing Head-vertical again.

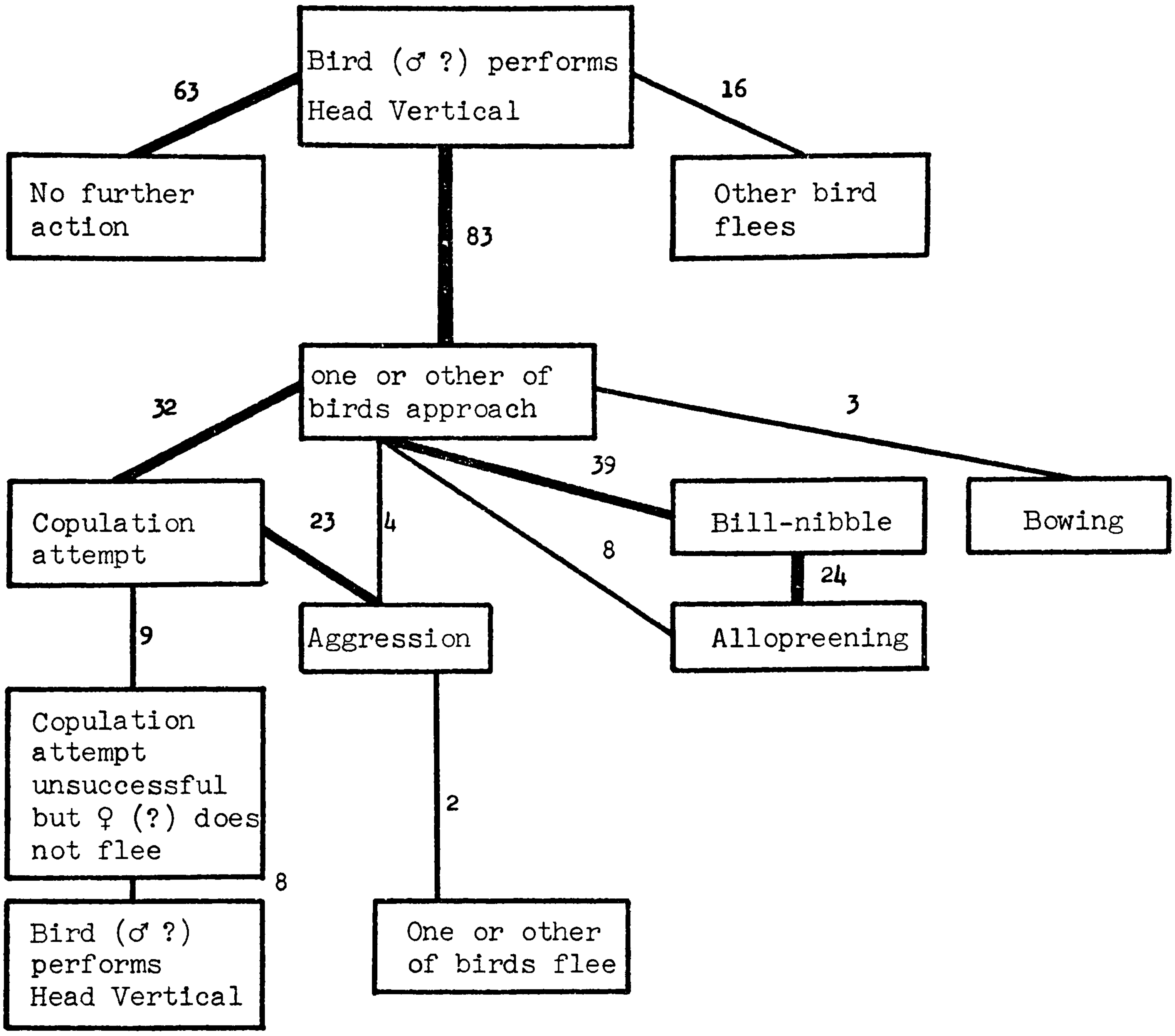


Fig.5.9. A flow diagram showing sequences of pair formation behaviour among birds in clubs, starting with a bird performing a Head-vertical display. The numbers between boxes are the number of occasions that pathway was observed. A total of 162 sequences was recorded. The diagram 'flows' from top to bottom and the thickness of the lines between boxes corresponds to the number of observations.

In those cases (39) where males did not make an immediate copulation attempt, Bill-nibbling was performed. During Bill-nibbling birds stood about 30-40cm apart, with their necks reaching towards each other, making nibbling movements with their bills in contact. In most cases birds gradually moved closer together and eventually nibbling merged into Allopreening, concentrated on the feathers of the head. Club birds spent long periods standing close together performing Allopreening.

Thus, to summarize, the evidence suggests that Head-vertical serves as a male advertising display, and that pair formation occurs in clubs. In one case involving marked three year old birds, the birds first appeared on the ledge (where they eventually obtained a site) as a pair. Clearly though, more data from colour-marked birds on clubs are necessary before we can draw any firm conclusions regarding pair formation.

By pointing the Head vertically, the bill is placed in a non-aggressive position; an important element of a distance-reducing display. At the same time the position is conspicuous, which must be a prerequisite for an advertising display - particularly in the crowded and active conditions on the club. Similar movements, in similar contexts have been recorded for several species of birds, e.g. Grey Heron Ardea cinerea (Baerends & van der Cingle 1962), certain boobies (Nelson 1970) Frigate Birds Fregeta spp. (Nelson 1968, Diamond 1973), Adelie Penguins (Ainley 1975).

(i) Allopreening

Allopreening was the most frequently performed activity between members of breeding pairs throughout the entire period of study (November - July); the average rate was 1.04 Allopreens/pair/minute (35 units). There was no difference in the frequency of Allopreening between winter, pre-laying or incubation periods, but Allopreening was significantly less frequent during the nestling period (Fig.5.6) ($t = 10.3$ 33df $P<0.001$). The duration of Allopreen bouts was greatest during the incubation period (Table 5.8). The reasons for the changes are not clear.

Allopreening occurred spontaneously between pair members, and more predictably in two other situations:-

(1) Following the return of a bird to its mate Allopreening followed mutual Bill-arring in 95/100 occasions in the pre-laying period. Numerous qualitative observations showed that this was also the case at other times.

(2) Allopreening followed Wing-flapping in 86/103 (84%) cases where the Wing-flapping bird was standing beside its incubating mate. In this situation the Wing-flapping birds always Allopreened its incubating mate (the reverse was not observed). Wing-flapping may be potentially threatening - a violent movement close to the incubating partner, and Allopreening may serve as a form of reassurance.

During the pre-laying period at least male Guillemots Allopreen their mates more frequently than females Allopreen their male partners. During 2.5hrs observations over five days during the pre-laying period males Allopreened their partner a total of 180 times; females preened their mates 132 times. ($X^2 = 7.4$ 1df $P<0.01$). There was no difference in bout duration between the sexes (males: 6.2 sec ± 5.6 S.D. n = 104, Females: 5.4 sec ± 4.9 S.D. n =80) ($t = 1.03$ 182df NS). The sexual difference in Allopreening frequency may be related to the fact that males are dominant to their mates (see earlier).

As well as preening their mates Guillemots also Allopreen neighbours. Allopreening among incubating neighbours appeared to be more frequent than among non-incubating birds. The mean frequency of Allopreening among incubating

Table 5.8. Frequency and duration of Allopreen bouts in Guillemots and Razorbills.

	GUILLEMOT						RAZORBILL					
Period	Frequency	S.D.	n	Duration	S.D.	n	Frequency	S.D.	n	Duration	S.D.	n
Winter	1.43	0.16	6	6.80	7.36	45	-	-	-	-	-	-
Pre-laying	1.37	0.18	9	6.32	6.27	180	0.98	0.09	3	6.70	9.21	108
Incubation	1.35	0.16	10	14.31	20.32	152	0.93	0.30	3	9.60	13.19	139
Nestling	0.72	0.18	10	6.39	5.68	119	0.95	0.12	3	5.80	7.62	191
Means	1.14	0.35	29	7.67	12.67	531	0.95	0.17	9	7.2	10.19	438

Notes: Frequency = allopreen/pr/min. Duration = seconds.

No data for Razorbills in winter since this species is not at colony at this time.

Sample sizes for frequency n = number of 50 min.observation units.

neighbours was 0.093 Allopreens/bird/min (three units) - approximately one tenth of the frequency among members of a pair when one bird was incubating (1.35 Allopreens/pair/min). In contrast, the duration of Allopreening among incubating birds is greater (28.3 sec ± 30.2 S.D. n = 67) than between members of a pair during the incubation period (14.3 sec ± 20.3 S.D. n = 152) ($t = 3.47$ 217df $P < 0.001$). However, if an Allopreening index (mean duration x mean frequency) is used to compare incubating neighbours (2.63) and pairs (19.31) it is clear that overall, incubating neighbours spend less time Allopreening than members of pairs.

The frequency of Allopreening among birds on clubs was also lower than between members of pairs (Club: 0.31 Allopreens/bird/min ; Breeding pairs 1.41 Allopreens/bird/min), but the different methods used to obtain these figures precludes statistical analysis (see methods). However, it was possible to compare the duration of Allopreens made by club birds and breeding birds. Club birds: 5.3 sec ± 6.7 S.D. n - 150, Breeding pairs (using the period April - July); 7.7. sec ± 12.7 S.D. n = 531 ($t = 3.04$ 679df $P < 0.01$).

The high frequency of Allopreening and its long seasonal duration indicate important functions among breeding pairs; it is probably also important among immature birds on clubs and incubating neighbours. In breeding pairs the main function is probably pair-maintenance, and also 'reassurance' after an activity such as Wing-flapping. Among club birds Allopreening is probably important in pair formation (see Fig.5.9), and in incubating neighbours Allopreening may help in reducing aggression between birds packed close together.

Allopreening in birds and Allogrooming in mammals are regarded as agonistic activities, but both occur at one end of the continuum of agonistic activities and are generally considered to be 'friendly' behaviour

(Harrison 1965a, Morris 1965, Nelson 1965, Sparks 1967, Ewer 1968). Cullen & Ashmole (1963) have pointed out that Allopreening is common among those bird species with restricted breeding sites. Allopreening may thus help to avoid aggression between pairs, and in Guillemots between incubating neighbours forced into close proximity at the breeding site.

(j) Bill-arring

As a greeting ceremony. Bill-arring occurs throughout the period November - July, when a bird returns to its mate at the site. Between April and July in 220 observations of birds returning to their mates Bill-arring occurred in 205 (93%) cases. There was no apparent seasonal change in the frequency of Bill-arring as a greeting ceremony.

Bill-arring in other contexts. Bill-arring also occurred in other situations unconnected with the arrival of a bird to its mate; in clubs between members of temporary pairs, and on breeding ledges. Among birds on ledges Bill-arring occurred relatively infrequently during the incubation and pre-laying periods (Fig.5.6), but during the nestling period Bill-arring occurred about three times as often ($t = 3.02$ 27df $P<0.01$). This increase may be due to two factors, a) Bill-arring occurs among birds at the end of fights and fight spectators, and b) in response to neighbouring birds returning to the ledges with fish. Both these factors increase during the nestling period (see Figs.5.6 & 5.12).

The Bill-arring response to birds with fish is of some interest. In 100 observations of birds returning with fish for chicks, the brooding bird Bill-arred as the fish bearer arrived, on each occasion, and in 74 cases neighbouring birds also Bill-arred. It is interesting that birds were apparently able to recognize other birds which had chicks. In 98 observations of birds arriving with fish (but not having chicks - see section on Fish-presentation) neighbouring birds called on only 6 (7%) occasions, and this was usually a single bird rather than all immediate neighbours, as in the fish-to-chick situation above. The difference in response to birds with and without chicks was highly significant ($X^2 = 94.7$ ldf $P<0.001$).

The form of Bill-arring and the situations in which it most frequently occurs indicate some links with aggression. I have already pointed out that the arrival of a bird at its mate and the site is a potentially aggressive situation. It seems possible that mutual Bill-arring serves the same function as mutual fencing in the Gannet (Nelson 1966), 'a display in which fear and aggression between the sexes is reduced'. That is, redirected aggression, channelled into a friendly display. However, there are similarities between mutual Bill-arring and fighting (see earlier) and Norrevang (1958) thought that members of a pair fought each time they met at the site. This similarity between aggression and greeting is even more marked in the Razorbill (see later).

(k) Copulation

Copulation has a long seasonal duration, commencing when birds return to the colony in October and November, and continuing until egg-laying. If the egg or chick is lost, or if both parents return to the site after the chick has fledged, copulation recommences. In addition, on several occasions I recorded copulation among pairs which had a large chick. At this time the chicks spent a greater part of the day standing beside their guarding parent than when they were younger, suggesting that incubating and brooding may play a part in inhibiting copulation.

Copulation showed a marked diurnal pattern with a peak during the first few hours of daylight, declining to a lower level 2-3 hours later (Fig.5.10). This pattern was a regular one on Skomer during April, but was also similar at Bempton during the winter. The early morning peak of copulation activity was closely associated with the return of birds to the colony, and mates meeting at the site. Most pairs copulated soon after meeting on the ledge. On one occasion during April I watched 10 pairs of marked birds for 150 min from first light, and all pairs copulated at least once during this period, two pairs three times and one pair four times. On another occasion, I recorded the number of pairs which copulated within a two minute period after their partner had arrived at the site. In 22/24 such observations (92%) the pair copulated.

In 41/48 (85%) cases the female initiated copulation; this figure is significantly different from a 50:50 expected ratio ($X^2 = 24.1$ 1df $P<0.001$).

Non-breeding birds and failed breeders on ledges may copulate throughout the breeding season, and as already pointed out (Fig.5.9) copulation attempts were frequent in clubs.

The performance of copulation throught the winter period and in clubs suggests a function other than insemination (c.f. the Gannet, which is present at its site from December onwards, but first starts to copulate in March (Nelson 1966)). In Common Guillemots copulation frequently occurred when one member of the pair returned to the site. This is just the sort of situation where the male partner, which is probably dominant to the female (see earlier) is likely to be aggressive. If the female arrives when the male is present she constitutes an intruder; if the male arrives second, the female already at the site also constitutes an intruder. Copulation-invitation is probably

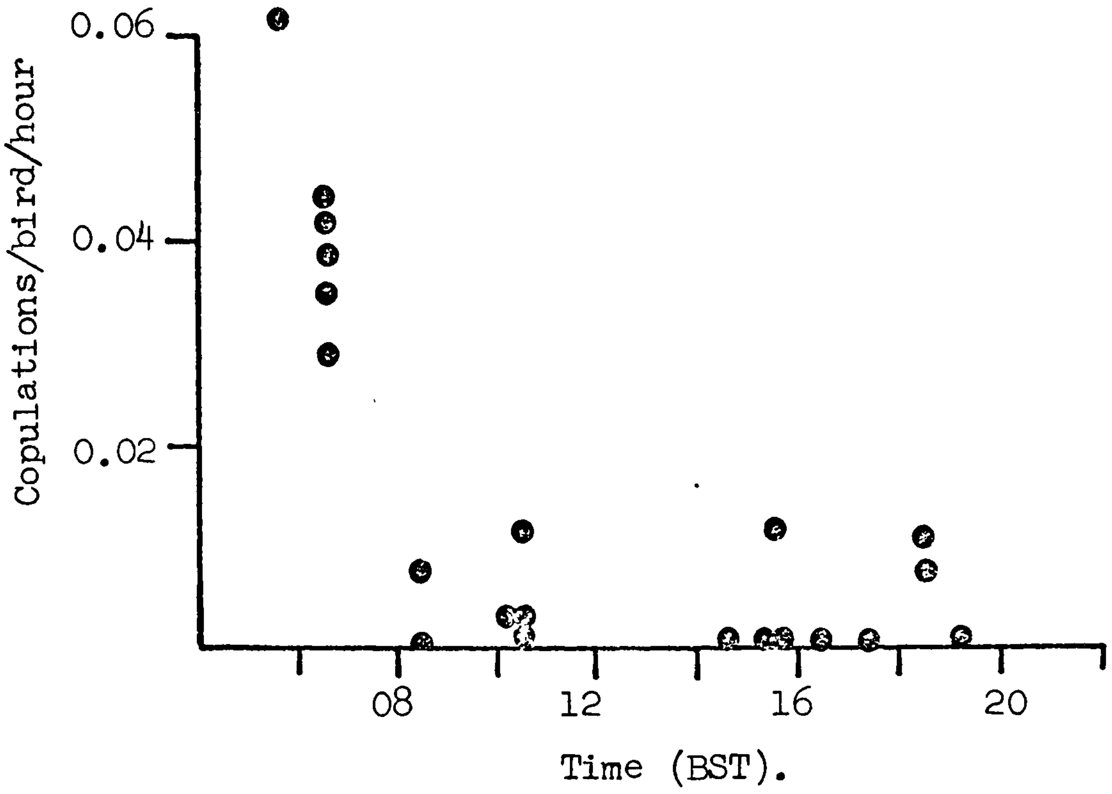


Fig.5.10. Diurnal frequency of copulation in Guillemots. Each point represents one hour of observation of between 20 - 30 birds, expressed as copulations/bird/hour.

performed as an appeasement, directed towards the male. Further evidence for this interpretation comes from the observations in clubs. Here I recorded on 5 occasions the female partner of a temporary pair perform Copulation-invitation during an aggressive encounter; the female suddenly broke off from aggressive Bill-arring, squatted and called, and the male mounted. Both birds then stood up and commenced Allopreening. In both situations, i.e. on ledges and in clubs, copulation appears to offer an outlet for female fear while still maintaining the male's sexual interest, and for the male, copulation may provide an outlet for aggressive and sexual tendencies. Thus, copulation is probably important both in formation (see Fig.5.9) and maintenance of the pair bond.

In Brunnich's Guillemot copulation has become ritualized and the male simply steps on and off the female's back when they meet at the site, in what Williams (1971) calls 'token copulation'. A similar situation to that in Common Guillemots occurs in many primates where subordinates 'present' their hind quarters to indicate submission to a superior partner, potential or actual aggressor (Altmann 1966, Wickler 1967, Kummer 1968). In many species, including Man, copulation is important in maintaining the pair bond (Morris 1967).

(1) Rape

Rape attempts occur in three situations:-

(a) When males attempt to mount nearby females performing Copulation-invitation.

(b) When males approach other birds (of either sex?) and attempt to mount. In this situation males approach potential females in a characteristic posture, uttering a long drawn out 'Arrr' call. Although the female remains in an upright posture males may attempt to mount (Fig. 5.3h).

(c) In clubs, where a copulation attempt appears to be part of a pair formation.

Cloacal contact in any of a) - c) is rarely achieved, although on some occasions I observed Raping males perform what appeared to be successful copulation. This occurred in situation a) when the female had performed Copulation-invitation while her mate was looking in another direction or was engaged in an interaction with another bird. Nearby birds responded rapidly to such females and moved with remarkable agility and speed in order to mount the female. The female, feeling the (Raping) male on her back proceeded with copulation. This type of copulation attempt was usually cut short by the male partner violently attacking the Rapist. If more than one Rapist was involved the resulting fracas often attracted the attention of other birds and on several occasions I saw birds run from 2-4m away to join in the fight. In some cases a bird attempted to mount others which were engaged in the fight lying in a prostrate position.

The regular occurrence of Rape attempts is probably a consequence of dense nesting. If birds are close together males can exploit any Rape opportunity. Promiscuity of this type is probably adaptive since it would facilitate rapid pair formation in the event of one member of a pair dying. Rape attempts can be advantageous to males (see Parker 1970), for example, in unpaired birds, i.e. those that have not had a mate, or birds which have lost their mate - either permanently or temporarily.

The main disadvantage of the regular occurrence of Rape is that paired males must expend time and effort defending their mates from other males (see Parker 1974). In view of this there is probably a strong selective advantage in strong pair bonds between pair members (see Discussion).

(m) Bowing

This display occurs on the ledges only in the period before egg-laying (November - May) (Fig.5.6). Bowing recommences among failed breeders and among pairs returning to their site after the chick has fledged; both these situations are those in which other species show a revival of courtship.

Bowing was performed mutually or singly. Mutual Bowing frequently followed Bill-arring after one bird returned to its mate (21/21: 100% cases), and after copulation (10/10 cases). Club birds performed Bowing comparatively infrequently ($\bar{x} = 0.07$ bows/bird/min) about one quarter as often as ledge birds during the pre-laying period ($\bar{x} = 0.32$ bows/bird/min).

Bowing in Common Guillemots is similar to Bowing recorded by Nelson (1966) in the Gannet, who showed that its main function was as a site-ownership display. To investigate the role of Bowing in the Guillemot I performed a ledge-change experiment (already described - see p.107). This showed that even birds which had to make only a small change in the position of the site performed mutual Bowing over three times as frequently ($\bar{x} = 0.4$ bows/bird/10min period) as a control group, which did not change nest-site ($\bar{x} = 0.12$ bows/bird/10min period) (Wilcoxon matched pairs test $P < 0.001$).

Concurrent with the increase in Bowing in the experimental birds there was a three-fold increase in aggression. This evidence suggests that Bowing in the Guillemot serves as a site-ownership display. The seasonal pattern of occurrence provides further evidence, the site is occupied during much of the winter (when Bowing occurs), but once the egg is laid Bowing ceases. This may be because it is no longer necessary to perform a site-ownership display if there is an incubating or brooding bird continually present at the site. Alternatively, it may be difficult to perform mutual Bowing when one bird is incubating. In addition, club birds, which have only temporary sites to defend perform mutual Bowing at a lower frequency than ledge birds.

The motivation among birds during mutual Bowing is not clear. Tinbergen (1959) has pointed out that bowing and bending over the site is taxonomically widespread in birds, and suggested that in larids the choking display is derived from pecking at nest material or from nest-building. Guillemots frequently peck at their feet, a stone or each other's bills during Bowing, which may indicate a tendency to perform nest-building type activities. However, Nelson (1966, 1970) has interpreted nest-biting (part of the bowing display) in the Gannet, as an aggressively motivated activity. Bowing in Guillemots shares a number of features with other Guillemot displays (Table 5.9), but it most strongly resembles egg-inspection. Not only are the movements performed during the two activities very similar, but I have heard identical calls (at least at my ear) uttered in the two movements. If egg-inspection is the origin of mutual Bowing it is unlikely to be purely aggressive.

(n) Fish-presentation

Fish-presentation is a display performed by birds without chicks, and therefore does not include birds carrying fish to feed chicks. It was rare among club birds.

In 54 observations of birds with fish returning to their mate both birds Bowed in 41 (76%) cases and in 36 (67%) the fish was exchanged at least once between the pair. In only three cases (5%) were fish exchanged without Bowing. In six instances where birds Bowed, at least one bird also drooped its wings. Most fish were eventually dropped, although a few were eaten. Of 24 observations of birds with fish returning to their site, but with no mate present, in

Table 5.9. Relationships between components of different displays.

Display	Components:			
	Head under breast, body crouched	Pick or play with object	Wings drooped	Feet scraped
Bowing	+	Partner's bill, stone or grass	Sometimes	No
Scaping	+	Stone or grass	Yes	Yes
Fish-presentation	+	Fish	Frequently	No
Egg inspection	+	May pick at egg or place stone by egg	No	No
Chick-feeding or inspection	+	Holding fish May allopreen chick	Yes Sometimes	No No

Note: + means component occurs in particular display.

10 (41%) cases the bird Bowed at least once. In all other cases the bird simply stood at the site holding the fish. In this situation 32 birds held the fish for an average of 22.1 min, significantly longer than birds whose mate was present ($\bar{x}$ = 10.3 min n = 69) (t = 3.05 99df $P<0.001$). This suggests that birds arriving at the site with a fish to find their mate absent, waited for it to return.

Fish-presentation showed a marked diurnal and seasonal pattern of occurrence (Figs.5.11 & 5.12). Throughout the season a peak of Fish-presentation coincided with the return of birds to the colony in the first few hours of daylight. I did not record Fish-presentation on two days during November and December at Bempton, although Perry (1940) reported it through the season, from the time the birds first returned to the Lundy colony in late December. There was a significant linear increase in Fish-presentation through the period 3 May - 27 June (r = 0.763 18df $P<0.001$), and this was followed by a further much more dramatic increase in the nestling period.

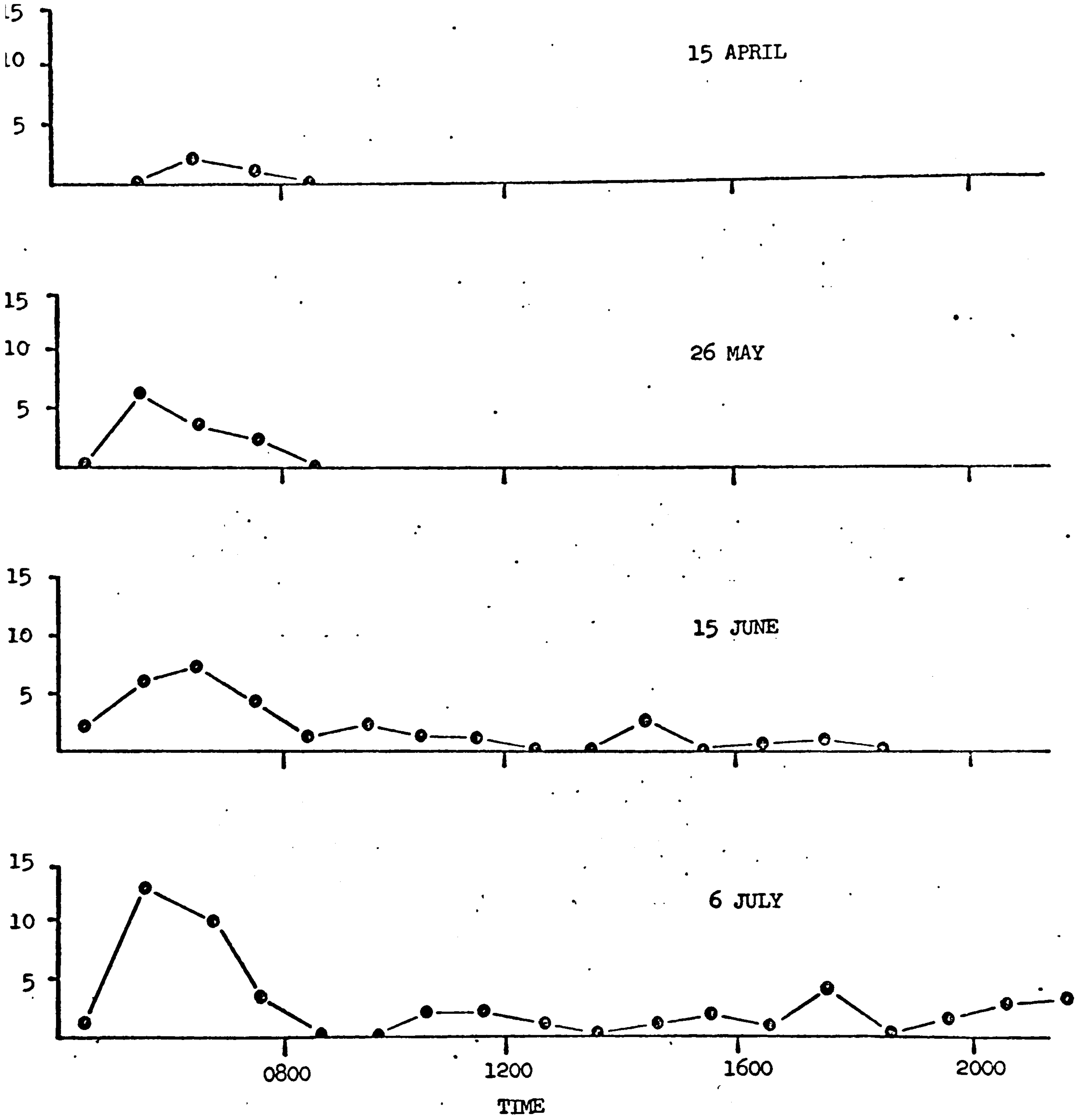
Observations of marked birds showed that breeding birds performed the display during the pre-laying period, but after egg-laying and up to the end of the incubation period Fish-presentation was performed mainly by failed breeders (also noted by Perry (1940)). Non-breeding birds may have performed Fish-presentation, although I never saw three year old birds with fish.

In 28 cases where the sex of Fish-presenting birds was known from marked birds, all were females (Perry 1940, also recorded this).

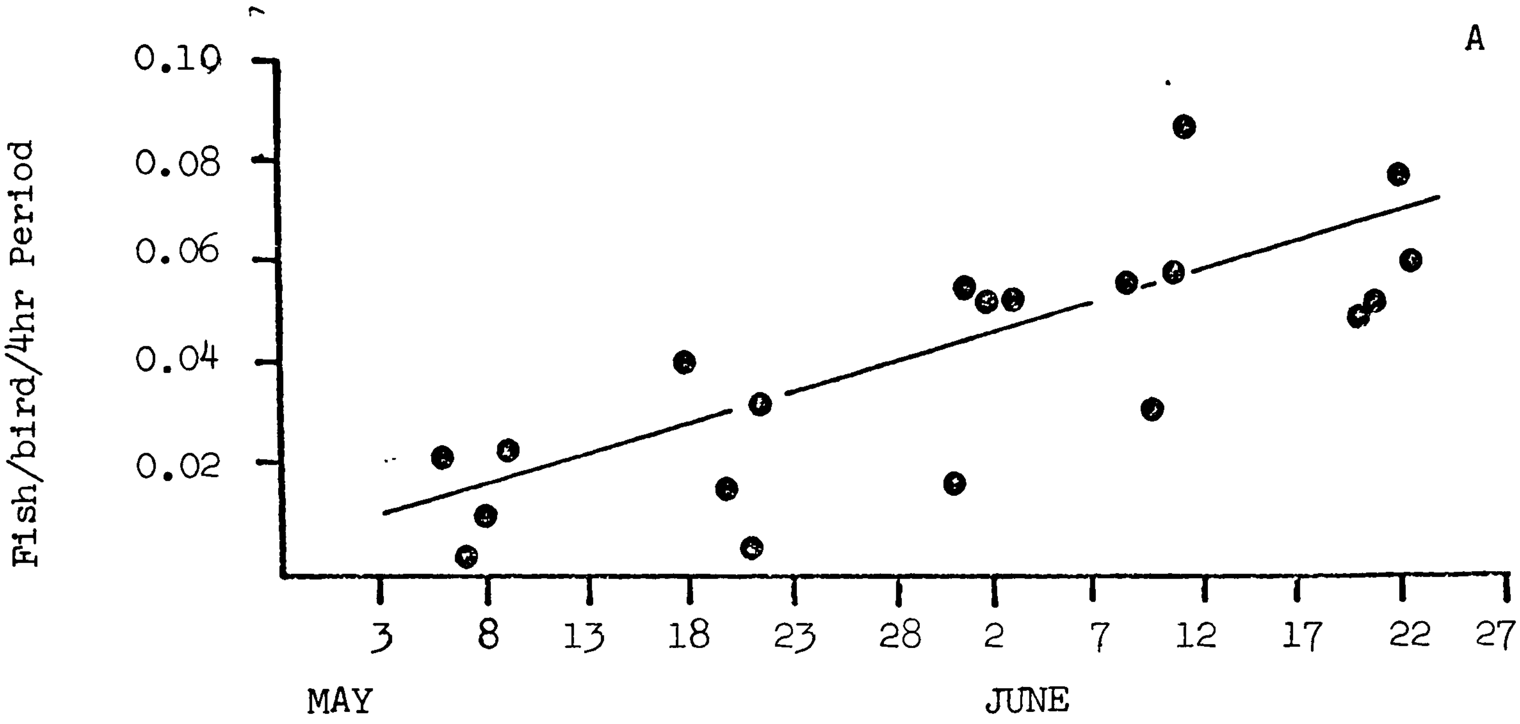
Thus, to summarize, we have a number of clues to the function of Fish-presentation: -

(a) Only females present fish to males.

(b) Fish-presentation is restricted to the site.



.5.11. Diurnal patterns of Fish-presentation, from dawn to dusk, at different stages of the breeding season. April 15 = Pre-laying period, 26 May = incubation period, June 15 and July 6 = nestling period. The same group of birds was watched on each day and the number performing Fish-presentation recorded.



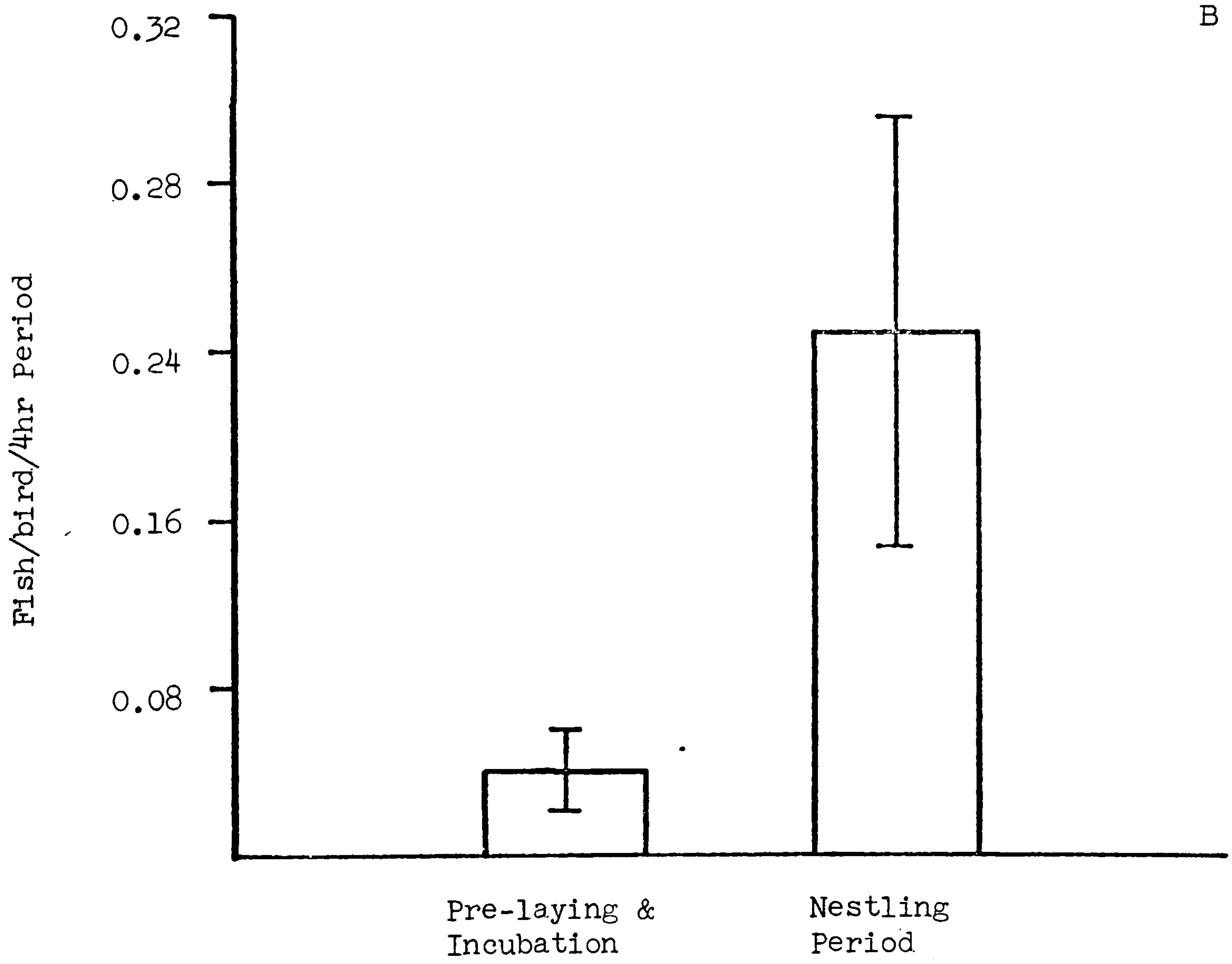


Fig.5.12.Seasonal pattern of fish presentation. Fig.A shows the pattern through the pre-laying and incubation periods.Regression equation: $y = 0.001x + 0.016$ ($r = 0.763$ 18 df $P<0.001$). Fig.B. Shows mean levels ± one S.D. in pre-laying and incubation periods (Data from Fig.A) and nestling period ($t = 4.6$ 24 df $P<0.001$). Data were collected on four consecutive days during the first 4 hours of daylight approximately every 7 days from early May - late June, Fig.A n = 20, Fig.B n = 6.

(c) It is rare among club birds and therefore probably not important in pair formation.

(d) It is infrequent during the pre-laying period and incubation period.

(e) It occurs mainly among failed breeders.

(f) The movements performed during Fish-presentation are similar to those during Bowing and other displays (see Table 5.9).

I have already shown that Guillemots are highly site tenacious (Chapter 3), and have pointed out that there may be competition for nest-sites. It has been shown earlier that Bowing is probably a site-ownership display, and there is a clear similarity in form between Bowing and Fish-presentation. Now Fish-presentation occurs mainly after pairs have failed in their breeding attempt, and since failed breeders attend their site throughout the remainder of the season in order to avoid losing it to other birds, it seems possible that Fish-presentation constitutes a 'high-powered' site-ownership display. It may also help to maintain the pair bond. There have been too few observations recorded during the time when Guillemots first return to their sites after completion of moult, so it is not known whether Fish-presentation is important in re-establishment of pair bonds at this time.

Bowing, Fish-presentation and other activities (Table 5.9) may have a common or similar origin. At fledging the male Guillemot takes the chick away from the colony, and the female usually returns to the site for up to three weeks (see Chapter 4). Fish-presentation may have originally occurred when females returned to the site with a fish and found the chick gone. This occurs in Razorbills (C.S. Lloyd, unpubl.) and Puffins (R.E. Ashcroft, unpubl.).

RAZORBILL BEHAVIOUR

Postures and Movements

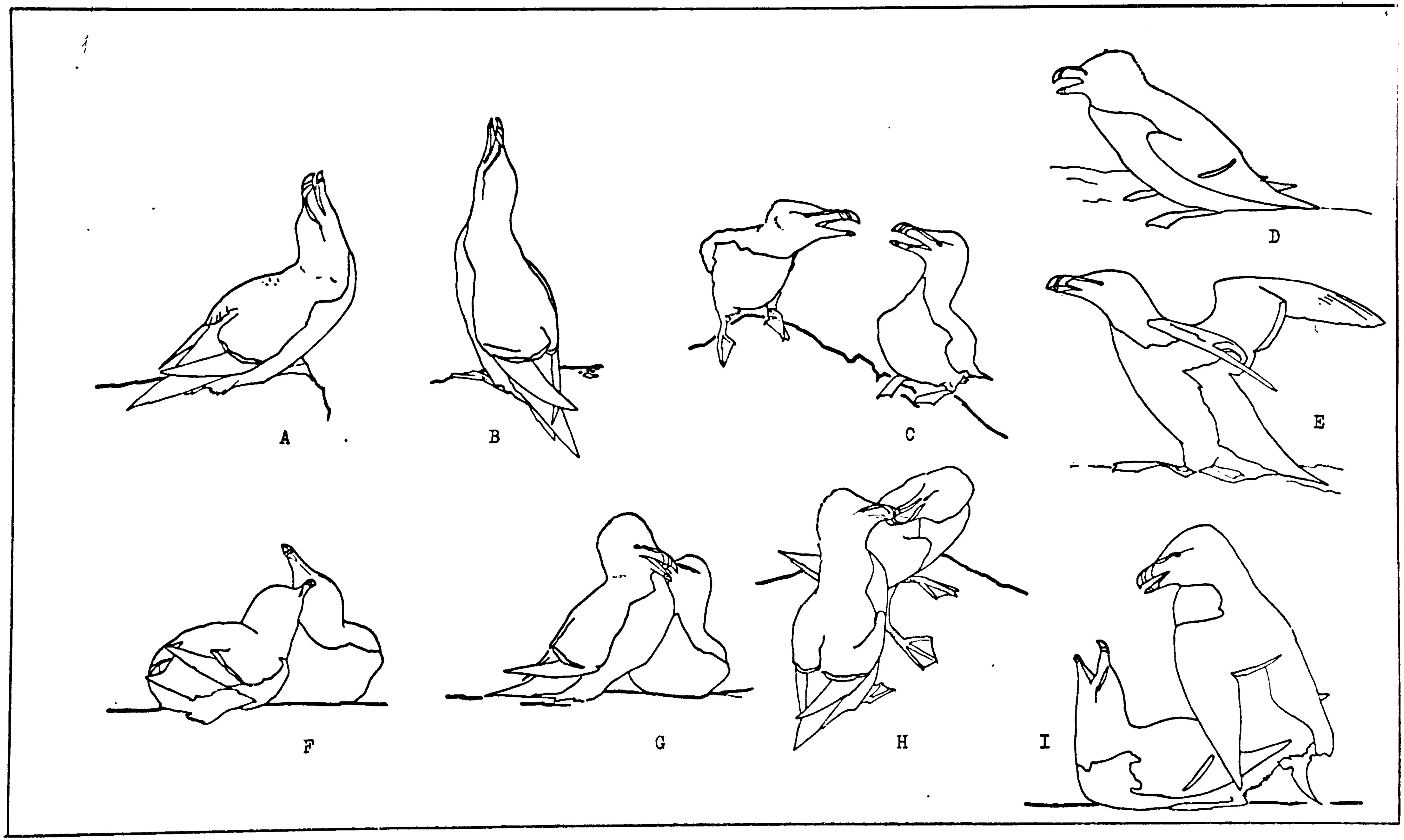
The postures and movements of Razorbills are described below. Further descriptions and illustrations of most of these signals can be found in Paludan (1947), Perry (1940) and Bedard (1969d) and most of those listed below are shown in Fig.5.13.

(1) Alert. Similar to Common Guillemot.

(2) Threat (Fig.5.13). Razorbills threaten conspecifics by stretching the head, with the bill open, towards the opponent. Sometimes the bill is rapidly jabbed towards the opponent. The feathers of the head are often raised during aggressive encounters. A threat may be accompanied by a low pitched growling call. The posture of threatening Razorbills differed from the Guillemot's threat posture in two ways, a) Razorbills generally stretched directly towards opponents, so that they faced each other breast to breast, whereas Guillemots usually stood with their heads turned laterally to face their opponent (see Fig.5.3a), b) Razorbills threaten with an open bill posture, which displays the yellow buccal lining, but Guillemots keep their bill closed unless actually fighting. This difference may be due to the difference in bill shape (which in turn may be related to their feeding habits; see Bedard 1969c). The hooked bill of the Razorbill may be better suited for grasping, rather than stabbing. The Guillemot's stilleto-shaped bill is probably better for stabbing.

(3) Fighting. Fighting in Razorbills is similar to that in Guillemots; bills

Fig.5.13. Razorbill postures. A,B Bill-vibrate. C,D aggression - note the erection of the head feathers. E Post-landing display and Ritualized-walking. F Allopreening. G,H Billing - note erection of head feathers. I copulation.


A
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are grasped and twisted, and the wings are used to deliver blows. Growling calls are uttered during fights (see also Perry 1940:115).

(4) Bill-vibrate (Fig.5.13). This display has been referred to as the 'male's song' (Paludan 1947), the 'ecstatic posture' (Conder 1950, Bedard 1969d) and 'vibrating' (Perry 1940). I have chosen to use Perry's descriptive term. The display consists of two phases; in the first the head is held vertically and the lower mandible is rapidly vibrated against the upper one. After holding the head vertically, the second phase involves sweeping the head down towards the breast with the bill open. The first phase produces a rattling sound as the mandibles rapidly open and close, and draws attention to the white markings on the bill. In the second phase the yellow interior of the mouth is displayed.

(5) Allopreening (Fig.5.13). Allopreening in Razorbills is very similar to Allopreening in Guillemots, except that in Razorbills erection of the head feathers is more pronounced - probably because this species has longer feathers in this region.

(6) Billing (Fig.5.13). The head feathers are erected and the two birds nibble with their bills, often gently grasping each other's bill. Loud growling calls are generally uttered during Billing. In most cases one bird positions itself so that its head is higher than the other bird's and thus has its bill pointed downwards towards the other bird. Billing invariably merged into Allopreening.

(7) Bowing. Bowing movements in Razorbills are similar to those in Guillemots. Bowing also showed similarities with Billing, and it was not clear whether Bowing was a ritualized display in Razorbills or whether it was a form of Billing in

which the birds' bodies were inclined forward in a bowed position.

(8) Scraping. Very similar to the Guillemot - but see Williams (1971) for more details.

(9) Copulation (Fig.5.13). Copulation is similar in form to copulation in the Guillemot; both sexes call, the female utters a growling disyllabic call at regular one or two second intervals, while the male utters a continuous call throughout the time he is mounted on the female.

(10) Post-landing display and ritualized-walking (Fig.5.13). Immediately after alighting and when walking Razorbills adopted a wing-up posture. The angle of the wings, both at the body and at the carpal joint, differed from the Guillemot (Fig.5.3i). Also, in the Razorbill the head and neck were not outstretched as they are in the Guillemot.

(11) Butterfly flight. A display flight, described by Conder (1950). Razorbills perform this flight, in which the wings are beaten in a slow, stiff manner, as they departed from the cliff.

Displays on the water. Razorbills perform the following postures and movements on the water; alert, threat, fighting, Bill-vibrate, Allopreening and Billing (see later).

(a) Aggression and Appeasement in the Razorbill

Aggressive interactions between Razorbills were infrequent (Table 5.10), but were most common in the nestling period, and all encounters were bill-open threats, not fights. The increase in aggression during the nestling period occurred when other Razorbills, possibly prospecting immatures, arrived near the breeding sites of established pairs. The overall mean for the pre-laying, incubation and nestling period was 0.033 encounters/pair/min, about half the rate recorded for Guillemots (0.064 encounters/pair/min) over

Table 5.10. Summary of seasonal changes in the frequency of displays in Guillemots and Razorbills. In Guillemots the number of units was nine for the pre-laying period and ten for each other period. In the Razorbill the number of units was three for each period.

Guillemot	Pre-Laying Period		Incubation Period		Nestling Period	
Display	Mean	S.D.	Mean	S.D.	Mean	S.D.
Allopreening	1.37	0.18	1.35	0.16	0.72	0.18
Bowing	0.32	0.06	0	0	0	0
Aggression	0.01	0.01	0.04	0.03	0.04	0.04
Bill-arring	0.02	0.02	0.02	0.02	0.07	0.06
Razorbill						
Allopreening	0.98	0.09	0.93	0.30	0.95	0.12
Bowing	0.13	0.04	0	0	0	0
Aggression	0	0	0	0	0.03	0.01
Billing	0.04	0.02	0.07	0.04	0.16	0.08
Bill-vibrate	0.01	0.01	0	0	0.14	0.08

the same period.

The difference in frequency of aggression between the two species was almost certainly due largely to differences in their spacing patterns; Razorbills never bred in contact with conspecifics. The situation in Razorbills is the same as that shown in Fig.5.5, for Guillemots breeding at the lowest densities.

I did not record any ritualized appeasement displays associated with aggression among Razorbills. In numerous aggressive encounters that I observed on Razorbill loafing areas no appeasement gestures were observed, and defeated birds simply fled from opponents. However, in 6 cases out of 14 fights observed, one bird commenced preening at the end of the fight. This preening appeared to be less ritualized than the Guillemot's Side-preening, and may have occurred as a displacement activity (see Morris 1956). Preening is not unusual among birds after some form of disturbance (see Delius 1970, van Iersel & Bol 1958).

(b) Bill-vibrating

This display is similar in form to Head-vertical in the Guillemot; as in Head-vertical, Bill-vibrating is performed most frequently by the male bird (Paludan 1947). Bill-vibrating is performed in two main contexts:-

a) By the male at the site when the female returns.

b) Apparently spontaneously between members of a pair at the site.

In most cases only one bird (presumably the male) performed, but in 2/21 observations both birds performed simultaneously.

Bill-vibrating also occurred in two other situations; on the sea during the pre-laying period, and on or near breeding sites late in the season by solitary birds, apparently towards other Razorbills flying or settled nearby.

In the first situation a), taking the season as a whole Bill-vibrating occurred in 42/171 (25%) cases when a bird returned to its mate at the nest-site. Since I rarely knew the sex of the returning bird, the proportion of males which displayed to their mate was probably higher than this. Bill-vibrating was recorded less frequently during the incubation period than at other times; it was observed in only 5/73 (7%) occasions during the incubation period, compared with 20/52 (38%) and 17/46 (37%) in the pre-laying and nestling periods, respectively. This may reflect sexual differences in incubating duties and therefore the sex of birds arriving at the site, or a reluctance to display among incubating birds. Bill-vibrating occurs in this situation as a form of greeting display, and on every occasion that I observed it following the return of one bird to its mate, it was followed by Billing - the usual greeting ceremony (see later). Its precise function remains obscure.

In the second situation b), Bill-vibrating occurred spontaneously between members of a pair, and was most frequent during the nestling period (Table 5.10).

Because immature, non-breeding Razorbills did not form discrete groups on Skomer as immature Guillemots did, it was more difficult to make observations of immature birds. A small number of colour-marked 2, 3 and 4 year old Razorbills were observed on the loafing areas, but these were not recorded Bill-vibrating. However, on six occasions during July I observed solitary Razorbills in areas near breeding sites perform Bill-vibrating towards other Razorbills that flew, or settled nearby. This situation is similar to the performance of Head-vertical in Guillemots (see earlier), and in this situation Bill-vibrating may be used by unmated males to advertise to females.

More data are needed to demonstrate this.

Thus, to summarize, Bill-vibrating may occur as a form of greeting ceremony and also as a male advertising signal. A similar display in the Guillemot, Head-vertical, is used only in the latter context.

(c) Allopreening

As in the Guillemot, Allopreening is more frequent (mean frequency + mean duration) in the incubation period than at other times, but in contrast to the Guillemot, the Razorbill did not show any decrease in Allopreening frequency during the nestling period. Taking the pre-laying, incubation and nestling periods together for both Razorbills and Guillemots, there was no significant difference in the frequency of Allopreening (Razorbills $\bar{x} = 0.95$ Allopreens/pair/min ± 0.17 S.D. $n = 9$ units, Guillemots $\bar{x} = 1.41$ Allopreens/pair/min ± 0.35 S.D. $n = 29$ units) ($t = 1.54$ 36df NS), or duration (Razorbills $\bar{x} = 7.24$ sec ± 10.2 S.D. $n = 438$, Guillemots $\bar{x} = 7.67$ sec ± 12.7 S.D. $n = 531$) ($t = 0.58$ 967df NS).

Razorbills at their nest-site were not observed Allopreening birds other than their mates, but it is not clear whether Razorbills Allopreened other birds when on the sea or on loafing areas.

Allopreening is frequent among birds on the sea during the pre-laying period, and at the breeding site throughout the season (see Table 5.10). This suggests that Allopreening is important in re-establishment, formation and maintenance of pair bonds.

(d) Billing

Billing is the Razorbill's greeting display, and in 171 observations of birds alighting beside their mate at the nest-site, Billing occurred in 164

(96%) cases. In some instances Billing was preceded by Bill-vibrating (see earlier). There was no indication of any seasonal change in Billing in this situation; pre-laying period 51/52 (98%), incubation period 69/73 (95%) and nestling period 44/46 (96%) birds displayed.

As in the Guillemot, Billing also occurred between members of a pair outside the arrival/greeting context. The mean values derived from behavioural units showed an increase through the breeding season (see Table 5.10). Thus, the seasonal trend in Billing is similar to the trend in Bill-Arring in Guillemots, although probably for different reasons (see p.120).

Earlier, I pointed out the similarity in form between aggression and the greeting display in the Guillemot; the similarity between these two activities is also striking in the Razorbill. Moreover, the greeting displays of both the Guillemot and Razorbill are similar to those recorded in other species, such as the Kittiwake and the Gannet (see Nelson 1967), which also have restricted nest-sites. In all these species it seems likely that the greeting display is derived from aggression, redirected into a 'friendly' display.

(e) Copulation

There were two important differences between Razorbills and Guillemots in their copulation behaviour:-

a) The difference between Razorbills and Guillemots in the proportion of each sex initiating copulation is highly significant. In Guillemots the female initiated copulation in 41/48 (85%) cases, but in Razorbills males usually initiated it (22/22: 100%) ($X^2 = 45.3$ 1df $P<0.001$).

b) As for Guillemots (see earlier) I recorded the proportion of Razorbills which copulated with their partner within two minutes of one of them returning to their mate at the site; in only 4/36 (11%) cases did copulation occur within this period, but in Guillemots 22/24 (92%) did so ($X^2 = 32.8$ 1df $P<0.001$).

I have no measure of the frequency of copulation in either species, so it is not known whether Guillemots copulate more often than Razorbills or vice versa.

Rape was not observed in Razorbills.

(f) Bowing

As already stated, it is not clear whether mutual Bowing in Razorbills is a ritualized display. Previous workers have not recorded it (Perry 1940, Paludan 1947, Conder 1950, Bedard 1969d), although this does not mean that it does not occur. I recorded Razorbills adopting postures similar to Guillemots performing mutual Bowing, during the pre-laying period, but less frequently than Guillemots (see Table 5.10) (Mann-Whitney U test $P<0.02$).

(g) Post-landing displays

Razorbills performed Post-landing displays in the same situation as Guillemots, but less frequently. In the arrival-to-mate situation, taking the incubation and nestling periods together 105/119 (88.2%) Razorbills displayed, (c.f. Guillemots where 113/114 (99%) displayed ($X^2 = 11.4$ 1df $P<0.001$), and in the not-to-mate situation, 164/266 (61.6%) displayed, (c.f. Guillemot; 124/172 (72%) displayed: $X^2 = 5.05$ 1df $P<0.05$). As in Guillemots, I recorded the frequency of Post-landing displays in relation to the proximity of neighbouring birds. Data were collected during the incubation period only, and for birds which were not arriving beside their mate. Of those birds which displayed on alighting 9/71 (14%) were within 0.5m of other birds. Among birds which did not display 6/42 (17%) were within 0.5m of other birds. This difference was not significant ($X^2 = 0.06$ ldf NS). In contrast, the likelihood of display was enhanced by the proximity of other birds in the Guillemot.

It has already been pointed out that one difference between Guillemots and Razorbills, is the use of loafing areas by off-duty Razorbills. I recorded the Post-landing behaviour of adult, breeding (colour-marked) Razorbills on their loafing rock. In 108 instances only 14 birds (13%) displayed. Making the same comparison that I made for Guillemots, that is, between arrivals at their breeding site and arrivals away from the breeding site, showed that adult birds alighting at their site displayed significantly more often (50/73 (68%)) than loafing birds ($X^2 = 58.8$ ldf $P<0.001$). This result suggests that, as in Guillemots, the Post-landing display serves as a site - ownership display.

Post-landing displays of Razorbills differed from Guillemots in the following ways: a) Razorbills performed these displays less frequently than Guillemots, b) Post-landing displays in the Razorbill were unaffected by the proximity of neighbours, whereas they were performed more frequently in Guillemots if neighbouring birds were nearby, c) In Razorbills the wing-up component only appears to be important, whereas in the Guillemot's Post-landing display both a wing-up and a head-up component were important, d) On a qualitative basis only, the duration of Post-landing displays appeared to be shorter in the Razorbill than in the Guillemot.

(h) Ritualized-walking

As in the Post-landing situation, the angle of the Razorbill's head does not appear to be important in this display.

I compared the frequency of the wing-up posture in walking Razorbills in 'centre' (birds nearer than 0.5m) and 'edge' (birds further than 0.5m away) sites as in Guillemots. In 24 observations at 'centre' sites birds used the wing-up display on 17 (71%) occasions. At 'edge' sites the wing-up posture was used on 32/46 (69%) occasions. The difference between 'centre' and 'edge' positions was not significant (X^2 = 0.05 1df NS). This situation is the same as that for the Post-landing display in Razorbills, but differs from that in Guillemots (see earlier).

I compared the frequency of Ritualized-walking displays in Razorbills and Guillemots. Razorbills displayed in 17/24 (71%) cases, and Guillemots in 170/176 (96%) cases - this difference was significant (X^2 = 23.0 1df $P<0.001$).

Thus, to summarize, Razorbills performed Ritualized-walking displays less frequently than Guillemots, and in different situations. The function of Ritualized-walking in the Razorbill is not clear at present.

Discussion

Many of the differences in behaviour between the Guillemot and the Razorbill stem from their patterns of dispersion. Habitat selection in Guillemots, *Uria* spp. has already been discussed in Chapter 3, but some additional points are relevant here. Within the three largest alcids Common Guillemots form the densest concentrations; birds are often surrounded by and in contact with conspecifics. Brunnich's Guillemot is intermediate between Common Guillemots and Razorbills, and is dependent upon a surface to rest against, so that although it breeds in contact with neighbours, it will only do so with lateral neighbours.

The Razorbill spaces itself so that it does not have to nest in contact with conspecifics. Where all three species occur sympatrically there is apparently little overlap in habitat utilization, but where one species is absent there is a greater degree of overlap. Common Guillemots can utilize broad ledges, narrrow ledges, crevices and boulder sites (i.e. both Brunnich's and Razorbill-type sites). Brunnich's Guillemot can utilize long narrow ledges as well as small (Razorbill-type) sites. The Razorbill is restricted to small ledges, crevices and burrows (Table 5.1), where it breeds out of the reach of conspecifics (Fig.5.1).

As in other species (see Hinde 1974:270) aggression in the Guillemot increases with increasing proximity of conspecifics. The difference in spacing and its effect on aggression is the key to most of the differences in behaviour between Guillemot and the Razorbill. One of the most striking differences between the two species is the lack of any active appeasement, and the reduced frequency of passive appeasement in the Razorbill.

A summary of the behaviour of each species is presented in Tables 5.11 & 5.12. Guillemots perform at least 15 displays, although the number of signals in species' repertoire will depend on the interpretation of different workers (see Moynihan 1970, Hinde 1974:52). Of the 15 signals shown by Guillemots, only nine are performed by Razorbills, and only three of the 15 (Allopreening, Billing, and Bill-vibrate) are performed with equal frequency in both species (Table 5.13). Moreover, several of the Guillemot's displays are more elaborate than the Razorbill's equivalent, for example, the Post-landing and Ritualized-walking displays involve an important angle of head component in the Guillemot but not in the Razorbill.

Table 5.11. Summary of Guillemot behaviour.

Behaviour pattern	Sex	Situation	Suggested Function
Aggression	both	Attempt by another ♂ to rape ♀ partner. Trespasser on territory	Defence of mate and site.
Side-preening	both	Post-fighting and post-moving situation	Ritualized appeasement.
Stretch-away	both	Incubating birds in response to threat, or after threat, or in response to bird moving	Avoidance of aggression, appeasement.
Prolonged stretch-away	♀	Attack by ♂ partner	Submission.
Turn-away	both	Post-threat or fight	Defensive appeasement.
Head-vertical	♂	*Mainly in clubs in* response to bird (♀?) moving nearby.	*Male advertising.*
Allopreening	both ♂ more	Pair at site, also in clubs and between incubating neighbours	Appeasement, aggressive tendencies diverted into preening.
Bowing	both	Pair at site. Particularly in re-establishment of site	Site-ownership.
Bill-arring	both	Bird returns to mate at site. Post-fighting and on seeing parent birds with fish	Greeting ceremony, strengthens pair bond. Aggression diverted into "friendly" display.
Fish-presentation	♀	At the site: failed breeders	Site-ownership? Strengthens pair bond?
Post-landing display	both	On site after landing	Site-ownership.
Ritualized-walking	both	Walking along ledge; different postures at different densities	Appeasement
Alarm-bowing	both	Impending danger	Signals alarm
Copulation	both	Return of bird to site, Long seasonal duration	Maintenance of pair bond, appeasement, insemination.
Rape attempt	♂	After Head-vertical in clubs. On ledges after 'subject' has alighted	Pair-formation, Insemination (rare).
Head-shaking	both	Post-fighting and after Picking	Displacement activity
Picking	both	Post-fighting and nest-building	Displacement and nest-building
Foot-looking	both	Post-fighting	Displacement activity.

Table 5.12. Summary of Razorbill behaviour.

Behaviour pattern	Sex	Situation	Suggested Function
Aggression	both?	Trespasser on territory	Defence of site.
Allopreening	both	Pair at site and on sea	Appeasement, aggressive tendencies diverted into preening.
Bill-vibrate	♂ most	Return of ♀ to site and pair together on sea. ♂ alone near site.	Part of greeting display (Billing) Male advertising.
Bowing	both	Pair at site, pre-laying period	Site-ownership?
Billing	both	Return of partner to site	Greeting ceremony, strengthens pair bond.
Post-landing display	both	Return to site	Site-ownership
Ritualized-walking	both	Walking	Appeasement?
Copulation	both	Pair at site	Insemination, pair bonding?
Butterfly-flight	both	Leaving site	?

Table 5.13. Display types in the Guillemot and Razorbill. + indicates that a display occurs in the species' repertoire, ++ indicates that the display occurs more frequently in that species than the other, - indicates behaviour not observed.

Display type	Guillemot	Razorbill
1. Threat	+	+
2. Fighting	++	+
3. Side-preening	+	-
4. Stretch-away	+	-
5. Turn-away	+	-
6. Head-vertical - Bill-vibrate	+	+
7. Allopreening	+	+
8. Greeting ceremony	+	+
9. Bowing	++	+
10. Fish-presentation	+	-
11. Post-landing display	++	+
12. Ritualized-walking	++	+
13. Alarm-bowing	+	-
14. Copulation	++	+
15. Rape attempt	+	-
16. Aerial display	-	+

The differences between Common Guillemot and Razorbill are shown further in Table 5.14; in this table I have listed the displays used by each species in specific contexts. It is clear that in each case the Guillemot possesses a greater number of displays than the Razorbill. The situation is similar to that recorded in sulids (Nelson 1967, 1970), canids (Fox 1974) and other carnivores (Ewer 1968); more social species possess a more varied repertoire of social signals. However, in the Guillemot and the Razorbill the difference is also one of degree, that is, in frequency of performance. For example, in some displays which are common to both species the Guillemot performs them more frequently than the Razorbill.

One difficulty in recording the number of displays in each of these species' repertoire is that a Razorbill, for example, is unlikely to be observed walking through a dense group of conspecifics, so its response in this situation is unknown.

In the introduction a number of problems associated with dense nesting were outlined. It is now possible to discuss each of these in turn. In doing this the behaviour of the Guillemot and the Razorbill is compared, and the Guillemot's adaptations to high density nesting examined (see Table 5.15).

(1) In dense groups Guillemots must walk through the territories of conspecifics to get to their nest-site.

Ritualized-walking displays are performed in this situation. Guillemots adopt different postures in different situations. These postures may reflect different levels of fear or anxiety associated with the proximity of neighbours in the two situations. Razorbills perform Ritualized-walking, but less frequently than Guillemots. The function of this display in Razorbills is not clear.

Table 5.14. Comparison of behaviour of the Guillemot and Razorbill. UR = Unritualized, R = Ritualised behaviour.

Context	Guillemot	Razorbill
Territorial defence	Aggression frequent;threat and fighting (UR).	Aggression infrequent. Threat (R).
Site-ownership	Bowing (R) Post-landing display (R) Fish-presentation? Early return to colony	Bowing (UR) infrequent. Post-landing display (R).
Appeasement	Three displays (Table 5.5), Side-preening (R) Stretch-away (R) Turn-away (UR)	None: withdrawl - fleeing only. Preening (UR) in post-fight situation may be displacement preening.
Pair bond maintenance	Bill-arring (Greeting (UR?)) Allopreening Copulation Fish-presentation?	Billing (Greeting) Allopreening
Pair formation	Immature birds in clubs perform Head-vertical + copulation/rape attempts	Not in clubs? Bill-vibrate?
Impending danger	Alarm bowing	-
Conflict behaviour	Picking (UR) Head-shaking (UR) Foot-looking (UR)	Picking? Foot-looking (UR)

(2) Aggression in dense groups may be detrimental.

Guillemots have achieved a balance in aggression; too much could be harmful, too little could result in the failure to acquire, or the loss of resources such as a mate and a breeding site. A specific adaptation among incubating birds is reduced aggression and avoidance of aggression by performing a specific appeasement display; Stretch-away.

Common Guillemots possess three different appeasement displays (Table 5.14) which are all associated with the increased likelihood of aggression at high densities. In contrast, the Razorbill, which shows lower levels of aggression possesses no ritualized active appeasement signals.

(3) Close proximity of conspecifics increases promiscuity.

Rape attempts are frequent during the pre-laying period but they were not observed in Razorbills. The increased risk of promiscuous mating may have resulted in a greater level of pair maintenance behaviour in Guillemots (see Table 5.15).

(4) Site competition as a result of high nesting density.

As in other animal species Guillemots use aggression in the acquisition and maintenance of the site (see 2 above). In addition, two ritualized displays, Bowing and Post-landing displays, (see Table 5.15) signal site-ownership. Fish-presentation may also be important as site-ownership display among failed breeders. A further adaptation to site-competition is probably the very early return of Guillemots to their sites soon after the completion of moult (see Appendix I). There is probably a selective advantage

Table 5.15. Behavioural adaptations to high density nesting in the Common Guillemot.

Consequences of high density nesting	Adaptations
1. Increase in aggression	Three appeasement postures: (a)Side-preening, (b) Stretch-away, (c) Turn-away. Incubating birds avoid aggression. Ritualized walking (passive appeasement); different postures used at different densities.
2. Competition for sites	Marked site-ownership; (a) Bowing, (b) Post-landing display, (c) Fish-presentation (?), (d) Early return to colony after moult.
3. Increase in promiscuity	Marked pair bond maintenance behaviour; males guard and defend their mates, protracted greeting display, Allopreeening frequent, copulation frequent and long seasonal duration (not just insemination). Fish-presentation?
4. Restricted space for long-distance displays	Male advertising is performed in clubs by immature birds. Pair formation may occur in clubs.
5. Communal defence against predators (ie.lunging)	Alarm-bowing alerts neighbours of impending danger.
6. Difficulty in being heard	Loud calls.

to return to the site early if this ensures a bird maintaining it. Razorbills return to their breeding colonies 4 or 5 months after the earliest Guillemots, and in this species, site-ownership displays are less numerous and less frequently performed than in the Guillemot.

(5) High density nesting precludes the use of mobile or long-distance signals.

The only 'long-distance' displays in the Guillemot's repertoire is the male advertising, head-vertical display, and this is performed away from the high density nesting area, in clubs.

The Razorbill uses the equivalent display, Bill-vibrating, in two contexts; as a greeting display and probably as a male advertising display. Bill-vibrating is performed on the sea, and at the nest-site where it can be observed by other birds.

In neither Guillemot nor Razorbill are highly mobile displays performed in the vicinity of the site (c.f. some boobies, Nelson 1970). In the Guillemot's case space is restricted by the proximity of other birds, although by breeding on broad ledges there is still sufficient room for both members of the pair to be present and display at the site together (c.f. Razorbill, and Brunnich's Guillemot; Williams 1974). In Razorbills space is restricted by the nature of the site; a small ledge or crevice. This may explain why, in Razorbills, but not Guillemots, a) off-duty adults congregate in loafing areas - away from the site, and b) perform much of their courtship on the sea during the pre-laying period, and c) perform an aerial display.

(6) Restricted nature of the site.

In both species the breeding site is small and restricted, and because of this common feature Common Guillemots and Razorbills might be expected to share a number of behavioural patterns. Cullen (1957) examined adaptations to cliff-nesting in Kittiwakes, and Nelson (1967) subsequently compared the Gannet with the Kittiwake in relation to their restricted, cliff-ledge nesting sites. There have also been a number of other studies which have examined behavioural adaptations to cliff-nesting (Hailman 1965, Smith 1966, Harris 1970, Cullen & Ashmole 1963). Two behavioural features which have been associated with nesting at a restricted site are Allopreening (see Cullen & Ashmole 1963) and a protracted greeting ceremony (Nelson 1967). Both Common Guillemots and Razorbills perform Allopreening and protracted greeting displays.

CHAPTER 6

FINAL DISCUSSION

The purpose of this final chapter is to draw together and discuss some of the results of this study and to consider some of the inter-relationships that exist between different aspects of the Guillemot's biology.

Many different aspects of a species' biology are intimately interwoven. As an example, relationships between social organisation and foraging patterns have been recorded in such diverse groups as insects (von Frisch 1967, Wilson 1971), birds (Crook 1965, Lack 1968), mammalian carnivores (Mech 1970, Kruuk 1972, Schaller 1972) and primates (Eisenberg et.al. 1972). In birds, other factors such as timing of breeding, anti-predator behaviour, clutch-size, recruitment rate and social behaviour may be linked, shaped by natural selection as parts of the species' overall adaptiveness (Nelson 1970). Every feature can probably be explained in terms of the selective forces that shape and maintain it, and when selective pressures affect one part of a system others may be forced to adapt to the change (Lack 1968, Schaller 1972).

Members of the Alcidae are all morphologically adpated for under-water swimming, using their wings (Storer 1960, Spring 1971). They show extensive adaptive radiation (Bedard 1969c, Sealy 1972), for example, the alcids are unique among bird families in that the post-hatching developmental patterns of different species range from being semi-precocial to precocial (Lack 1968, Sealy 1973). In addition the different species vary greatly in body-size; the smallest species, the Least Auklet Aethia pusilla weighs only 90g (Sealy 1972), and the largest, the extinct Great Auk Pinguinus impennis probably weighed about 5000g (Bedard 1969c). The largest living species is the Common Guillemot (Table 6.1), which shows the most extreme morphological modifications for under-water swimming, (the Great Auk showed even greater modifications for diving, which involved the loss of the ability to fly; Blyth 1837). Large size confers several advantages, such as reduced likelihood of predation, and probably in diving species, increased swimming speed and the ability to dive to greater depths. The Common Guillemot has short wings which are adapted for propelling itself under-water as well as for flying, and because of its relatively high body weight is apparently near the upper limit of wing-loading (Blyth 1837, Storer 1960). The Common Guillemot is thus probably near the evolutionary upper size limit of flying alcids.

Because of these morphological features Common Guillemots and other large alcids, lack manoeuvrability in the air. Moreover, their upright posture, which is a consequence of the positioning of the legs for swimming (Storer 1960, Stettenheim 1959) results in their being considerably less agile on land than, say, gulls. This reduction in manoeuvrability on land and in the air means that Common Guillemots are unable to take off from a flat surface and usually have to walk to the cliff-edge to do so. It also means that at the breeding colony Common Guillemots are unable to defend their eggs and young in the same highly mobile way that gulls and terns do (by aerial dive-bombing), and have had to develop another method.

I consider that body-size and morphological adaptations for diving, while maintaining the ability to fly, have been major factors moulding many of the features of Common Guillemot biology.

Table 6.1. Body weight, post-hatching developmental pattern and nest-site type in the Alcidae.

Species	Body Wt.	Semi-precocial	Inter-mediate	Precocial	Nest-site	Source
Great Auk Pinguinus impennis	c5000		?		O	Bedard 1969c, Grieve 1885
Common Guillemot Uria aalge	984		X		O,L	Swartz 1966, This study
Brünnich's Guillemot U.lomvia	964		X		L	Swartz 1966
Tufted Puffin Lunda cirrhata	838	X			B,C	Cody 1973
Razorbill Alca torda	628		X		L,C	C.S.Lloyd, unpubl.
Horned Puffin Fratercula corniculata	599	X			B,C	Sealy 1973
Rhinoceros Auklet Cerorhinca monocerata	518	X			B	Summers 1975
Common Puffin F.arctica	510	X			B,C	Belopolski 1957
Pigeon Guillemot Cepphus columba	450	X			B,C	Drent 1965
Black Guillemot C.grylle	425	X			B,C	Winn 1950
Spectacled Guillemot C.carbo	-	X			B,C	Sealy 1973
Crested Auklet Aethia cristatella	286	X			C	Sealy 1973
Parakeet Auklet Cyclorrhynchos psittacula	280	X			C	Sealy 1973
Japanese Murrelet Synthliboramphus wumizusume	-			X	C	Sealy 1973
Kittlitz's Murrelet Brachyramphus brevirostris	237	X			ET	Bent 1919, Bedard 1969c
Marbled Murrelet B.marmoratum	222	X			T	Sealy 1973, Binford et.al 1975
Ancient Murrelet S.antiquus	206			X	B,C	Sealy 1975
Cassin's Auklet Ptychoramphus aleuticus	167	X			B,C	Manuwal 1972
Little Auk Plautus alle	160	X			C	Norderhaug 1970
Xantu's Murrelet Endomychura hypoleuca	156			X	C	Bent 1919
Craveri's Murrelet E.craveri	151			X	C	Bent 1919
Whiskered Auklet A.pygmaea	118	X			C	Bent 1919
Least Auklet A.pusilla	90	X			C	Sealy 1973

Notes: Species are arranged from top to bottom in order of body weight. Although body weight of the same species varies with latitude, those given are for one area and this does not materially affect the order.

For those species where no weight is given the relative body size has been estimated from museum skins.

O = Open site; flat-top, L = Ledge, C = Crevice, B = Burrow, ET = Exposed terrain, T = Tree branch.

Body weight in grams.

in Uria at least, does not develop until after the tenth day (Johnson & West 1975). Parental brooding is likely to be particularly important in arctic regions.

Whatever the reason for one parent remaining at the nest-site with the chick, this habit introduces a constraint when it comes to provisioning the chick. This, in turn, raises the question 'why don't Common Guillemot chicks form creches?', as are found in some other seabirds and waterfowl (Gorman & Milne 1972), since this would allow both parents to forage simultaneously for their chick, at least some of the time. However, since a relatively high proportion of adults might be needed to guard a number of chicks from a predator at any one time, this may reduce any advantages of a creche system. Although I never saw creches on Skomer both Tuck (1960) and Cody (1973) have observed them, but neither author provides any details.

Therefore, at any one time only one parent can usually forage for the chick. In addition, feeding trips are quite long and a Guillemot carries only a single, relatively small fish back to its chick at a time. With these constraints Guillemots are not adapted for rearing the chick to adult weight at the colony (Chapter 4). Instead, the nestling period is reduced and the adult (male) takes the chick to feeding areas. This has several advantages on a time-energy basis for the parent and chick, but also permits the male parent to commence its post-nuptial moult relatively early in the season.

The relatively high wing-loading of the larger auk species probably determines their pattern of wing-moult (Watson 1968); the flight feathers are dropped simultaneously, and the birds undergo a period of flightlessness (Appendix II). In those bird species with high wing-loading, which are not forced to fly in order to feed (e.g. alcids and waterfowl; Stresemann & Stresemann 1966: c.f. Swifts Apus spp.), it is probably most efficient to drop all flight feathers simultaneously. This is because, if they moulted their primaries one at a time, as most bird species do, the period of feather replacement would be greatly prolonged, but perhaps more important, any gaps in the wings would further increase the wing-loading, thus making flight energetically inefficient. It should be pointed out that in alcids the reduced surface area of the wings during moult does not impair their ability to dive, since selection has favoured large wings for flying and small wings for under-water use, so that even with a full complement of flight feathers, these species must fold their wings when diving to reduce the surface area (Storer 1960).

A number of factors influence the timing and duration of moult in the Common Guillemot:-

a) Because the chick is flightless when it leaves the colony, and for some (unknown) time afterwards, it is probably most efficient for the male parent to moult and be flightless at the same time.

b) It may be important to complete moult as soon as possible since once birds have regained the ability to fly they can extend their foraging range and can also return to the breeding colony (see below).

Common Guillemots apparently replace their flight feathers, and moult into summer plumage earlier than Razorbills (Appendix II); they also return much earlier to their breeding sites than Razorbills.

In boreal regions such as the British Isles, it is not unusual for adult Common Guillemots to visit their breeding colonies more or less continuously from late October onwards. In other words, they remain at sea only during the time it takes to replace the flight feathers. This suggests that there is a strong selective pressure to return to the colony as soon as possible.

Dense nesting indicates that intense competition for sites will occur (Nelson 1970); the proximity of neighbouring Guillemots determines the frequency of aggressive territorial interactions (Chapter 5). The early return of Common Guillemots to the colony may be closely linked with high density nesting. Site-fidelity, which is highly developed in Common Guillemots (Chapter 3) presumably has selective advantages, and birds may return as soon after completion of the moult to ensure that they maintain their nest-site for the following breeding season. Similarly, at the end of the breeding season, after the male has taken the chick away from the colony, the female generally returns to the nest-site for up to three weeks; presumably to defend it from prospecting immatures, which are most abundant on the ledges at this time (Chapter 2).

Finally, dense nesting as an anti-predator strategy has at least two further consequences:-

a) Groups of Guillemots breeding at high densities are highly synchronised in their timing of breeding (Chapter 3). Such synchronisation appears to be important in reducing predation, but may also have implications in foraging behaviour as Ward & Zahavi (1973) and Emlen & Demong (1975) have suggested, thus indicating a link between coloniality and foraging. However, as already pointed out, there is insufficient evidence to support Ward & Zahavi's ideas for any species at present (Chapter 4).

b) Dense nesting has resulted in extensive modifications of social behaviour, notably a tolerance of conspecifics and a wide range of appeasement signals, and evolution of displays which do not involve locomotory or long-distance signals (Chapter 5).

Thus, it is possible to demonstrate links between at least some features of the Common Guillemot's breeding biology and its physical shape and size.

APPENDIX I

APPENDIX I

ATTENDANCE PATTERNS OF GUILLEMOTS AT BREEDING COLONIES ON SKOMER ISLAND

Introduction

A number of studies have shown that many seabirds share broadly similar seasonal patterns of colony attendance, e.g. Manx Shearwater *Puffinus puffinus* (Perrins 1972), Laysan Albatross *Diomedea immutabilis* (Fisher & Fisher 1969), Razorbill *Alca torda* (Lloyd 1972), Gannet *Sula bassana* (Nelson 1966) and Kittiwake *Rissa tridactyla* (Coulson & White 1956). This seasonal pattern is in general as follows: after a period of absence, during which the post nuptial moult usually occurs; the colonies are generally first occupied by experienced breeding birds, followed by immature non-breeders later in the season. The oldest non-breeders may return first, and the youngest latest, usually visiting the colony for a short period towards the end of the breeding season. During the incubation period, and in some species the nestling period as well, one member of each breeding pair may be present at the colony, incubating or brooding. Off-duty partners of breeding birds may spend time at the colony with their mate, or may be away foraging. As the breeding season advances a greater number of birds fail in their breeding attempt, so there is a general increase in the number of failed breeding birds through the season. In many species immature non-breeding birds arrive later and leave the colony earlier than breeding birds, after reaching a peak of numbers late in the season. This generalised pattern of seasonal attendance is presented diagramatically in Fig.A1.

The changes in numbers at a seabird colony, both seasonally and diurnally will depend on the presence or absence of these different categories of birds. In the diurnal Common Guillemot Uria aalge, these are as follows:-

Breeding birds. Pairs in which the female produces an egg during the breeding season in question, are breeding pairs. During the incubation and nestling period they comprise two groups: a) incubating/brooding birds and b) their off-duty mates. Pairs which have failed in their breeding attempt through loss of egg or chick are referred to as failed breeders.

Non-breeding birds. As in many seabirds Guillemots exhibit deferred maturity and birds probably first breed at 5 years or older. Immature birds from 2 years old congregate in special areas known as 'clubs' near the breeding colonies, but as they approach breeding age a greater proportion of their time is spent on the breeding ledges (Chapter 2). Most non-breeding individuals are probably immature birds, but fully mature non-breeding birds have been recorded in some alcid populations; e.g. Cassins auklet, Manuwal (1974) and Common Puffin (R.E. Ashcroft, pers.comm).

The aim of this study was to examine patterns of attendance at some Guillemot colonies on Skomer. This information provides an outline of the seasonal pattern of activity and is connected with other aspects of the study, such as behaviour (Chapter 5) and feeding ecology (Chapter 4). Moreover, details of some aspects of colony attendance are crucial for developing census techniques (Chapter 2).

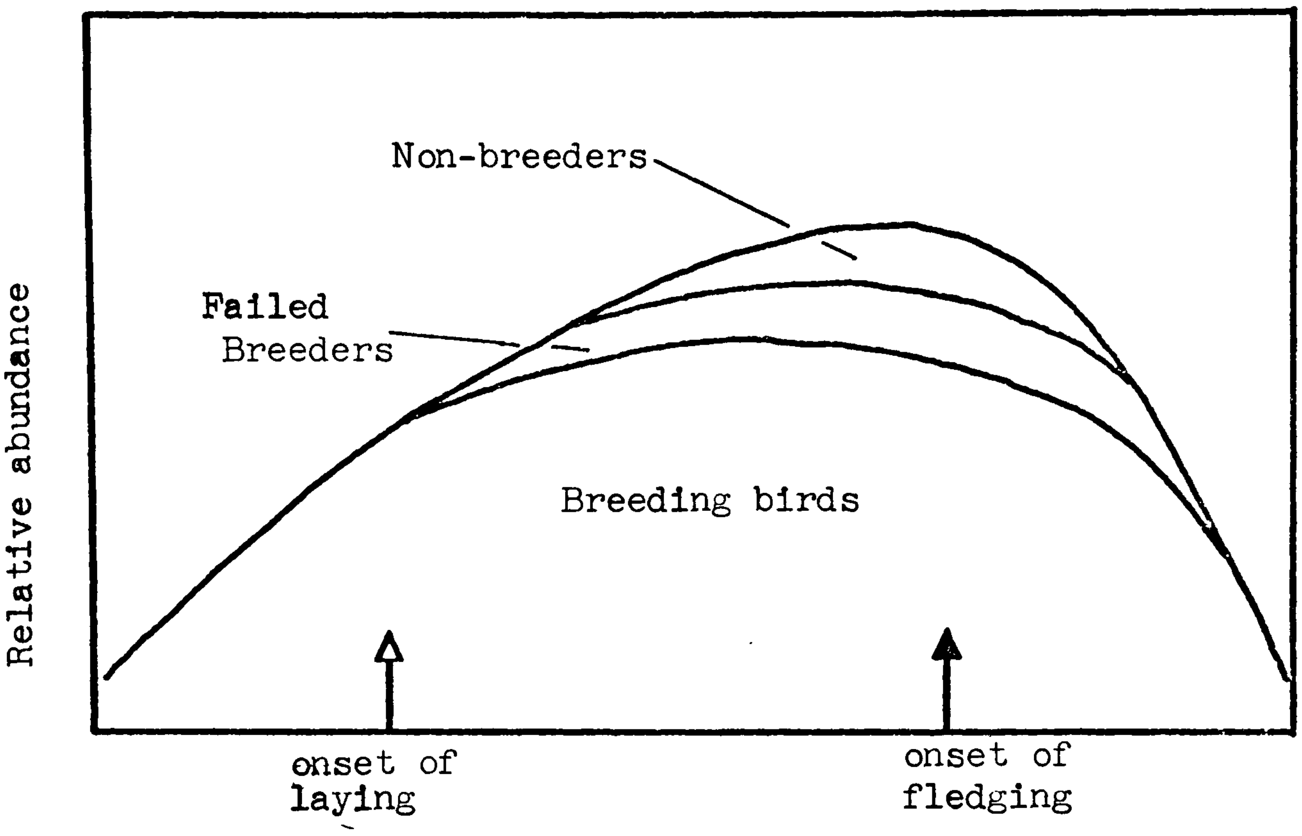


Fig.A.1Generalised seasonal pattern of seabird colony attendance.

Methods

In boreal regions the time that Guillemots spend at their breeding colonies can be divided into four periods: winter (October-March), pre-laying (April), incubation (May-mid-June) and nestling period (mid-June-late July).

Three categories of birds occurred on ledges; a) breeding birds, b) failed breeders, and c) non-breeders, Breeding birds were identified during the incubation and nestling periods by their attachment to an egg or chick at a site. In a few cases breeding birds were colour-marked.

After the loss of the egg or chick it was not possible to positively identify failed breeders - unless they were colour-marked. Nor was it possible to distinguish between breeding birds, failed breeders or non-breeders away from specific nest-sites. For this reason most observations were either of 'all birds' at the colony or breeding birds. However, a small number of birds were colour-marked as chicks and in subsequent years, when they returned, these provided some information on the attendance of immature (non-breeding) birds.

Counts through the season. To determine seasonal changes in numbers, a single count of all birds was made at each of three colonies each day at the same time, from late March until late July 1973. The colonies and the times at which the counts were made are as follows: South Stream Cliff (1000hrs), High Cliff(1000hrs) and Bull Hole (1200hrs) (All times are B.S.T.).

I have used both published and unpublished material to determine the dates when Guillemots return to their breeding colonies in Britain.

Counts over the daylight period. Diurnal patterns of colony attendance were determined by making a single count at 30 minute intervals throughout the entire daylight period, at Bull Hole, High Cliff and South Stream Cliff colonies. Such counts were made on a number of occasions through the season.

Weather records. Records of weather conditions were made each day on Skomer, throughout the period of study; these included wind speed (recorded on a Beaufort Scale) and rain, recorded as wet or dry days.

Results

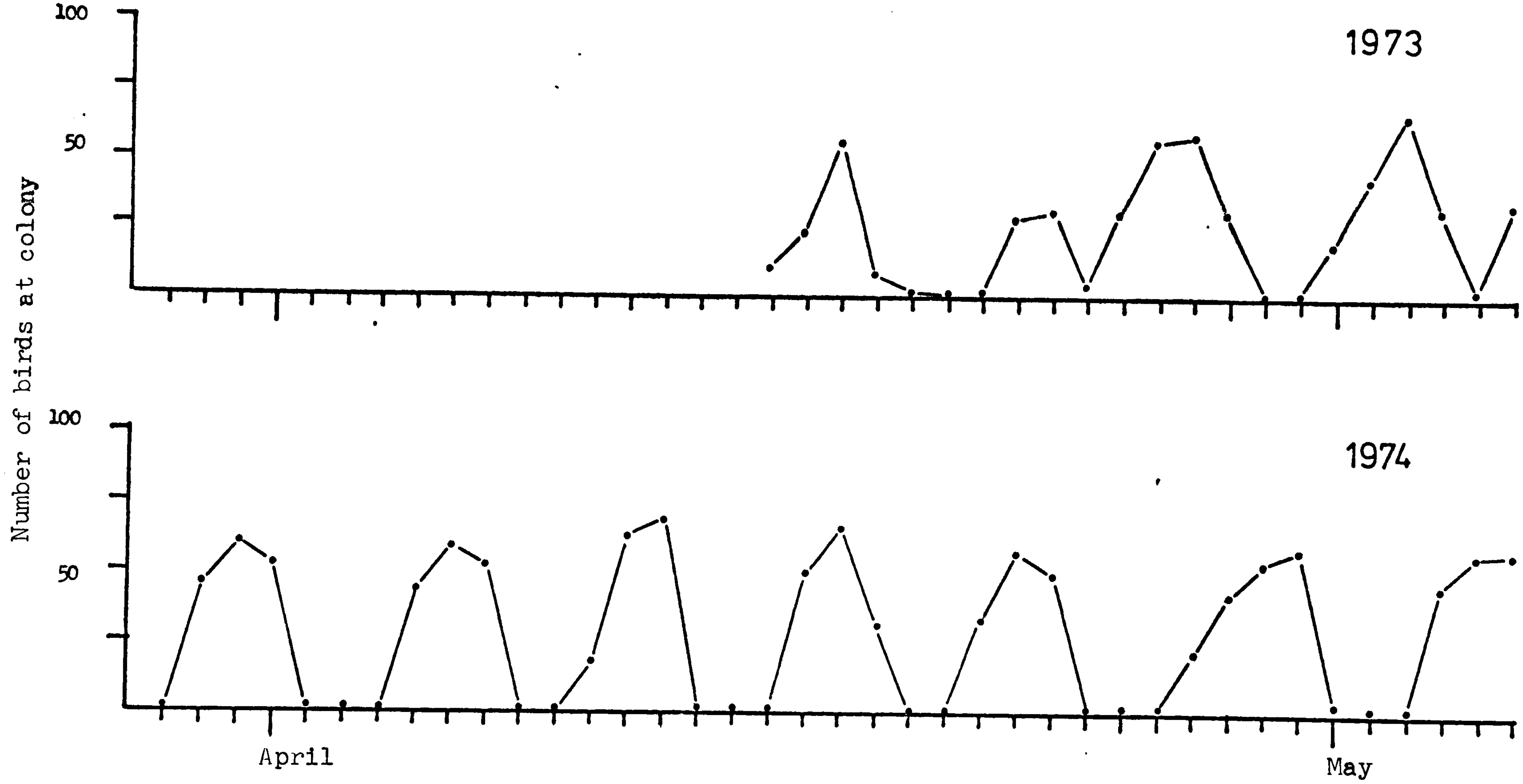
Seasonal pattern of attendance. As long ago as the 1870s Cordeaux (1872) recorded Guillemots visiting colonies in November, but this aspect of the Guillemot seasonal pattern of activity does not appear to have become generally known until more recently (Dennis 1967). Details of the date of return at four colonies for which there are several years' data, are shown in Table A1. Few data are available for changes in total numbers at the colony through the winter period (Bourne & Dixon 1974).

During the pre-laying period on Skomer attendance of Guillemots alternated between high numbers and total absence (Fig.A2). In 1973 an irregular pattern of attendance was recorded and numbers were negatively correlated with wind speed ($r = 0.615$ $P<0.001$ $n=30$); in other words, low numbers or total absence coincided with high wind speeds. In 1974 the pre-laying period was comparatively calm (1974 $\bar{x}$ wind force (rank); 1.9 cf 1973; $\bar{x} = 3.2$, Mann-Whitney U test $z = 3.2$ $P<0.001$) and peak numbers occurred at regular 5-6 day intervals (Fig.A2). This suggests a regular cycle of activity at this part of the season, which is disrupted by high winds. The periods of absence from the cliffs are presumably feeding trips.

Table A.1. Date on which Guillemots were first recorded after the post-nuptial moult at four British colonies.

Location	Year	Month	Day	Source
Fair Isle, Scotland	1966	November	7	Dennis (1967)
	1967	November	19	Fair Is. Rept. 1967
	1968	October	23	" " 1968
	1969	November	8	" " 1969
	1970	October	27	" " 1970
	1971	November	13	" " 1971
	1972	October	26	" " 1972
	1973	October	7	" " 1973
	1974	October	7	" " 1974
Farne Is. N.England	1961	November	8	G.Hickling (pers.comm)
	1962	November	22	" "
	1963	November	19	" "
	1965	November	5	" "
	1970	November	18	" "
	1971	October	26	" "
	1973	October	17	" "
Gt.Saltee, Eire	1954	November	13	Irish Bird Rept.1954
	1955	October	31	" " 1955
	1957	October	13	" " 1957
Dorset colonies southern England	1962	November	7	Dorset Bird Rept.1962
	1965	October	24	" " 1965
	1968	November	5	" " 1968
	1969	November	3	" " 1969

Fig.A.2. Number of birds at South Stream Cliff colony each day in the pre-laying periods of 1973 and 1974. Counts commenced on 12 April 1973 and 29 March 1974. Peaks of numbers were more regular in 1974 than in 1973. Intervals on the x axis are days.

100
50
Number of birds at colony
1973
100
50
1974
April
May

Once egg-laying and incubation commenced the cyclical pattern ceased. The pattern during the rest of the season at one colony is shown in Fig.A3. Despite wide day-to-day fluctuation, this colony and two others showed similar seasonal patterns and were highly correlated with each other on a day-to-day basis (Table A2), which indicates that they were responding to the same factors. As egg-laying proceeded through May the number of birds rapidly increased until early June, and thereafter increased at a slower rate until a peak was reached in the nestling period in late June. The peak of numbers at the colony in late July coincided with peak sightings of immature, 3 year old birds on ledges (see Chapter 2, Fig.2.5).

The total number of birds decreased through July as the adults and fledging chicks and immature birds left the colonies.

Daily variation in numbers. A count of the total number of individuals on the island was made each year between 1-15 June (Chapter 2). Since it was possible to make only a single count around the island each year, it was important to know the sort of margin or error that existed around a single count. Day-to-day variation in numbers was recorded by counting birds at three colonies, at the same time each day, between 1-15 June 1973-1975 (Table A3). These data have been used to calculate the standard deviation for the total island count each year, using the formula:

$$\text{S.D. of } t = \sqrt{\text{Variance of } \bar{x} \cdot \frac{t}{\bar{x}}}$$

Where t = whole island total, and $\bar{x}$ = sample mean. The sample mean was derived from the sum of the numbers at the three colonies counted each day between 1-15 June. This sample constituted about one quarter of the total island

Fig.A.3. Number of Guillemots at South Stream Cliff colony each day from 20 May 1973 to end of the breeding season. Each point is a five-day running mean, thus smoothing the curve.

Table A.2. Correlation coefficients from comparisons of the numbers of Guillemots at three Skomer colonies, counted each day, showing that all colonies followed similar trends.

Comparison	Incubation Period	Nestling Period
Bull Hole vs High Cliff	0.831	0.916
Bull Hole vs South Stream Cliff	0.763	0.850
High Cliff vs South Stream Cliff	0.828	0.895

Notes: All correlation coefficients are significant at the P<0.001 level, and sample sizes are 48 for the incubation period and 23 for the nestling period.

Table A.3. Day to day variation in numbers of Guillemots at three colonies between 1-15 June 1973 - 1975

Colony	1973			1974			1975		
	Mean	S.D.	Range	Mean	S.D.	Range	Mean	S.D.	Range
Bull Hole	517.0	33.3	470-562	511.1	39.6	424-547	475.1	42.5	384-521
High Cliff	317.3	19.9	272-349	321.4	30.3	252-357	307.4	25.4	271-346
South Stream Cliff	103.7	8.1	83-116	102.2	10.8	84-128	96.6	8.9	83-110

population. Table A4 presents whole island counts for each year, the Standard deviation and the sample mean.

Diurnal patterns of attendance. There are few data for the winter period, but these suggest that patterns are variable. My own observations at Bempton (Yorkshire) agree with those of N. Brown made in Scotland (pers.comm.); birds are absent at night, return in the early morning and remain either for only a few hours or until dusk in the evening.

A similar pattern was recorded on Skomer during the pre-laying period. The total number of birds at one colony was counted every 90 minutes over a four day period of attendance (Fig.A4). Birds arrived soon after first light; numbers remained similar throughout the day and declined in the evening. On the third and fourth days of the period of attendance numbers decreased relatively early in the day.

The number of birds on days of peak numbers during the pre-laying period was slightly in excess of twice the number of pairs which were later recorded breeding there (Table A5). This may indicate that some birds visit ledges other than their own at this time, or that a small number of non-breeding birds are present during the pre-laying period.

Diurnal patterns of attendance by all birds during the incubation and nestling period are shown in Fig.A5. The pattern of low numbers early and late in the day, and a more or less constant level during the middle of the day persists throughout the entire season. A similar pattern occurred in each of three years (Fig.A6).

After the onset of incubation day-to-day and seasonal changes in levels of attendance may be brought about in either or both of two ways: a) a change

Table A.4. Standard deviation of whole island counts 1973 - 1975 (see text for methods).

Year	Total Island count	S.D.	Sample Mean	S.D.
1973	3251	118.8	880.0	61.8
1974	3601	110.0	934.7	56.1
1975	3815	93.7	938.1	46.4

Fig.A.4. Number of birds at South Stream Cliff colony on four consecutive days in the pre-laying period, over the entire daylight period. Compare counts at 1000hrs each day with those in Fig.A.2.

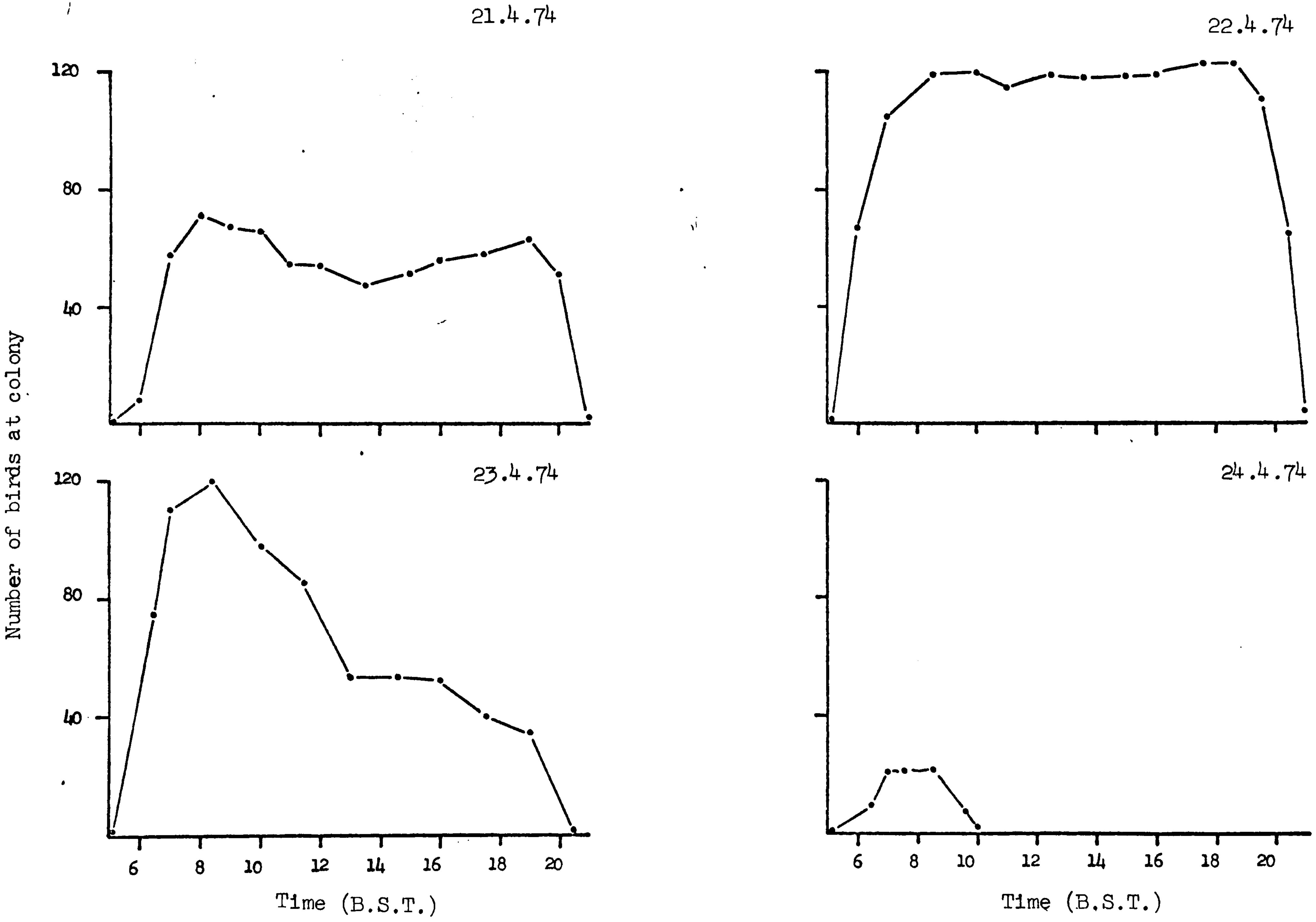

21.4.74
22.4.74
23.4.74
24.4.74
Number of birds at colony
120
80
40
6
8
10
12
14
16
18
20
Time (B.S.T.)

Table A.5. Maximum number of birds recorded at certain sub-colonies during the pre-laying period and the number of pairs which subsequently bred there. All data are from 1973 except B* which is 1974.

Sub-colony	No.of breeding pairs	Maximum number of birds
Bull Hole A	12	36
B	60	132
B*	63	137
C	25	51
D	10	24

Fig.A.5. Number of birds at Bull Hole colony throughout the day on 26 May (incubation period), 15 June (late incubation) and 6 July (nestling period).

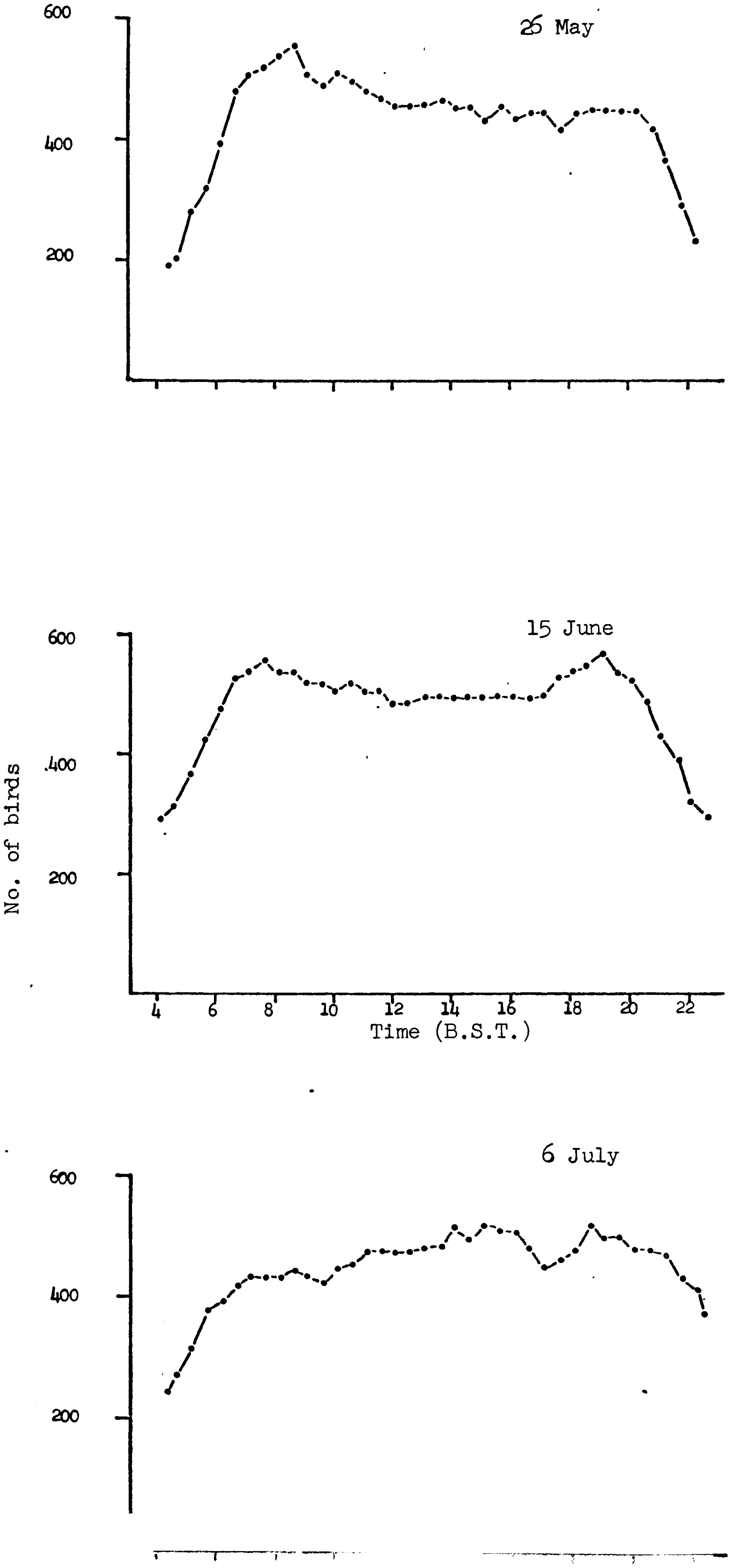
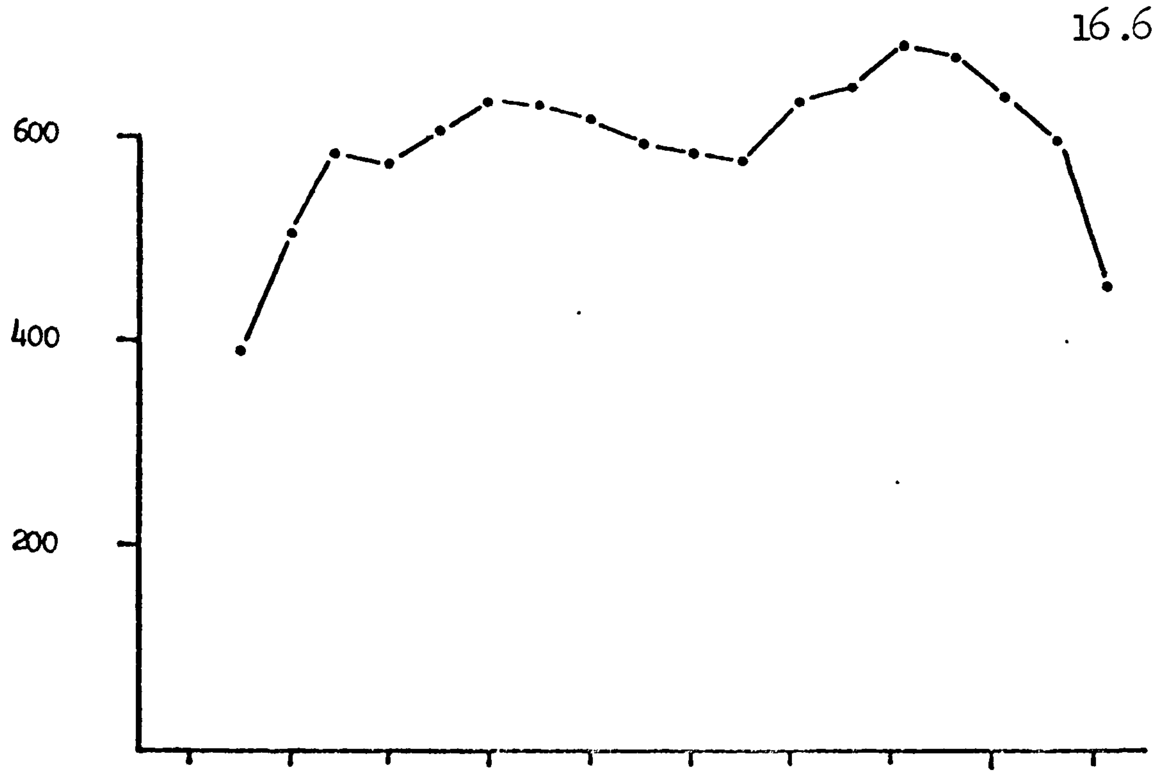
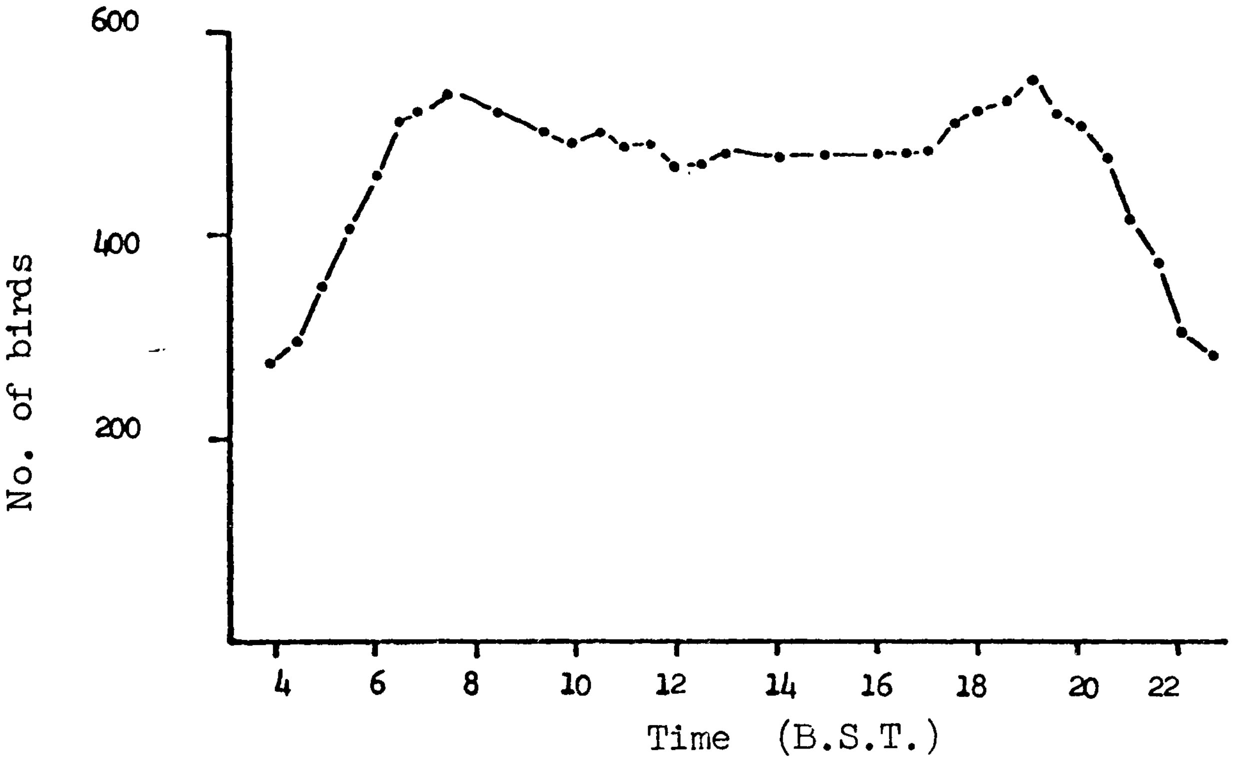

26 May
600
400
200
15 June
600
400
200
No. of birds
4
6
8
10
12
14
16
18
20
22
Time (B.S.T.)
6 July
600
400
200

Fig.A.6. Number of birds at Bull Hole colony on three days in three years during late incubation. Similar diurnal patterns occurred in each year.

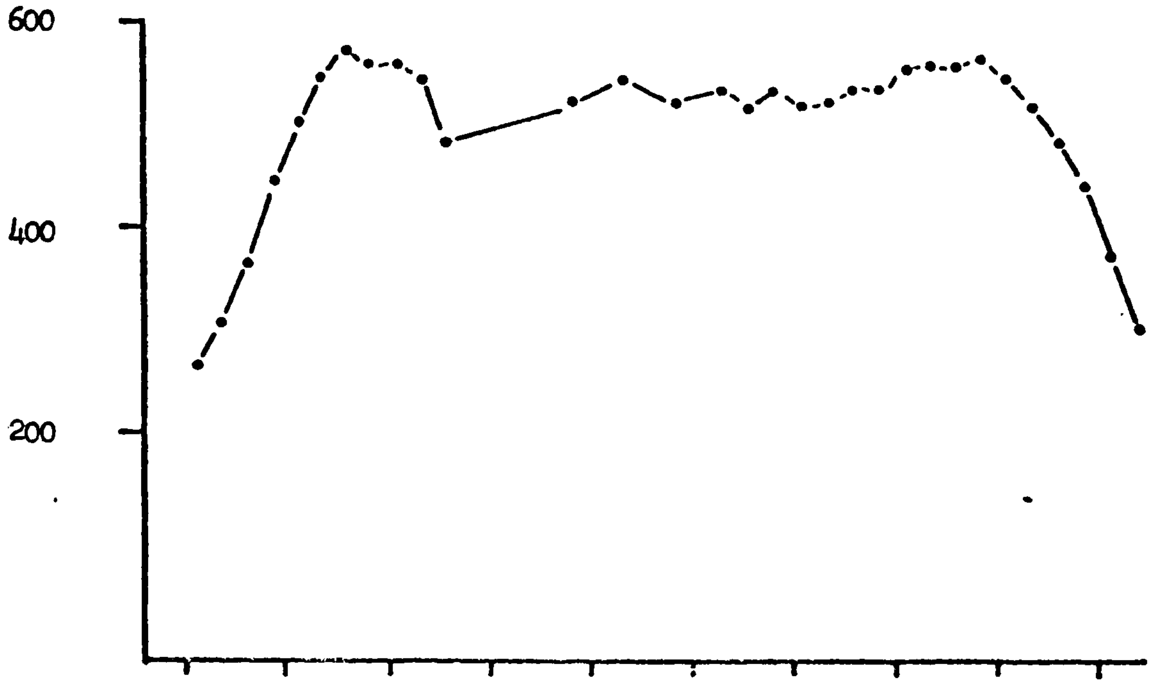
16.6.72



15.6.73



14.6.74



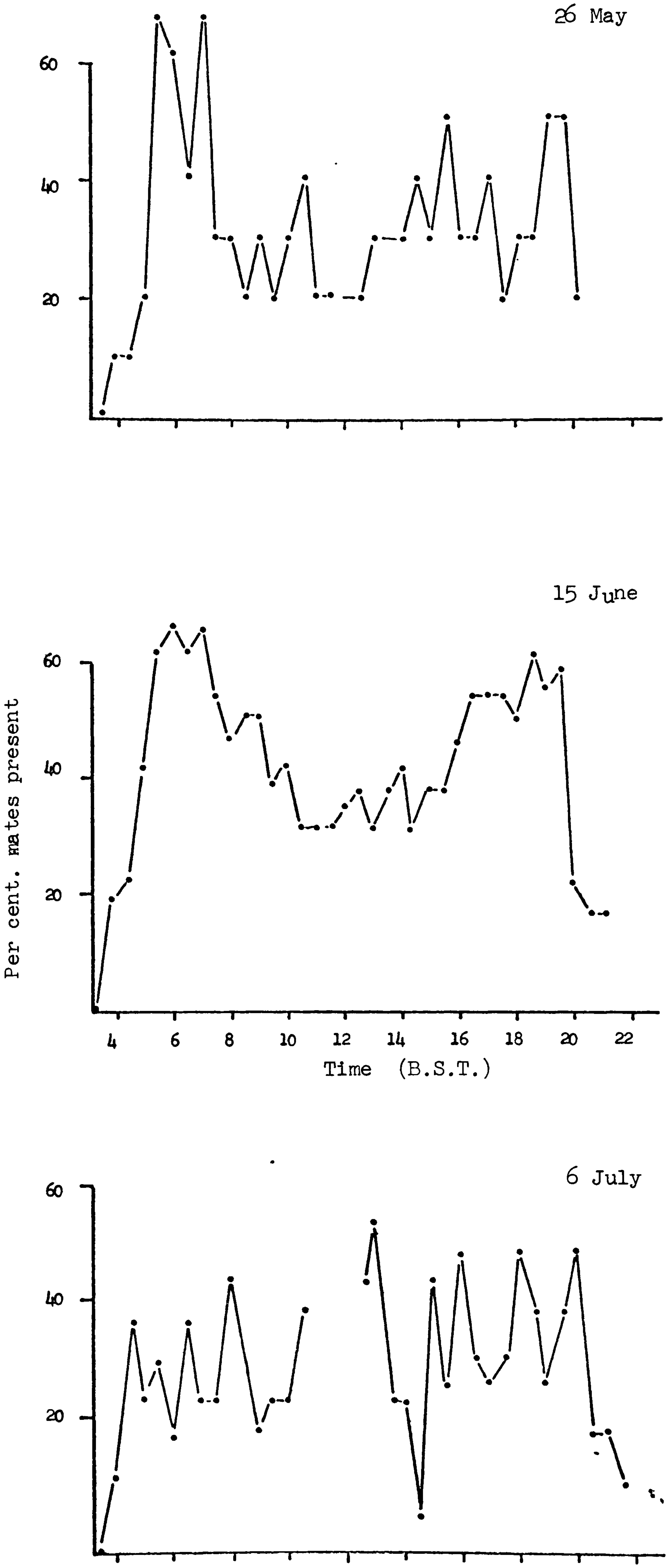
in the total number of birds visiting the colonies, or b) the same number of birds spending different amounts of time at the colony. In fact, both these methods operate (see later), and the next section examines the role of breeding birds in determining diurnal and seasonal attendance patterns.

Attendance of breeding birds. Providing no birds die, the breeding population will remain constant throughout the breeding season, although numbers actually present at the colony may vary. The number of birds incubating eggs increased throughout May, then declined slightly as eggs and chicks were lost, and decreased rapidly once chicks started to fledge in early July. Off-duty partners spent varying amounts of time at the colony. During the incubation period observations made over the entire daylight period on two occasions showed that off-duty birds spent an average of 30% (26 May) and 42% (15 June) of the day at the colony (Fig.A7). During the nestling period observations throughout the day showed that off-duty partners spent 36% of the day at the colony (Fig.A7).

While this suggests little seasonal difference in the total amount of time spent at the colony by off-duty birds, there were marked changes in diurnal patterns of attendance through the season. During the nestling period diurnal attendance by mates of brooding birds was irregular since birds made fishing trips throughout the day to feed their chick.

The bi-modal patterns of mate-attendance was confirmed by repeating counts in 1974. Both the morning and evening peaks represented a period of change-over of incubation duties, but it is not known whether pairs changed over twice each day, or whether some birds changed over in the morning and others in the evening. On average 9/10 (90.0 ± 7.5% S.D.) of incubating birds were visited

Fig.A.7. Diurnal changes in the number of off-duty mates of breeding birds at Bull Hole colony on three days, at different stages of the breeding cycle (see Caption to Fig.A.6). Note the early morning peak in numbers on 26 May and 15 June, and the irregular pattern of attendance throughout 6 July when birds were feeding chicks.


26 May
60
40
20
15 June
60
40
20
Per cent. mates present
4
6
8
10
12
14
16
18
20
22
Time (B.S.T.)
6 July
60
40
20

by their mates during the first four hours of daylight, on 8 days between 25 May-12 June. Thus, the overall increase in Guillemot numbers after first light (Fig.A5) was largely due to the return of off-duty breeding birds which had spent the night on the sea.

During the nestling period one parent continued to remain at the site with the chick, but the diurnal pattern of mate-attendance was slightly different at this time. The increase in numbers of off-duty birds after first light was less marked than in the incubation period (Fig.A.4), but the number of mates visiting their brooding partners during the first four hours of daylight was as high as in the incubation period (91.4 ± 4.8% S.D., based on seven days' observation). However, at this time mates spent less time at the nest-site in the morning, because they were engaged in fishing for the chick, and no build-up in the number of mates occurred.

Factors determining levels of attendance. Daily variations in number are caused by factors operating on the different categories of birds. The mates of incubating/brooding birds make up the largest proportion of the population that varies from day-to-day, therefore the way in which they are affected by different factors will be important in determining levels of attendance.

(a) Disturbance. The presence of predators such as Great Black-backed Gulls or Ravens on Guillemot ledges produced a temporary decrease in numbers. Non-breeding birds and failed breeders were usually first to leave in this situation. Disturbance by man, either by his close approach to the colony on foot, or by close approach in boats or aircraft, resulted in greater decreases of longer duration. Disturbance from man or avian predators affected the number of birds at the colony, but only in reducing numbers.

(b) Environmental factors. Other factors affecting levels of colony attendance include environmental ones, such as weather, sea conditions and feeding conditions. Preliminary observations showed that inclement weather conditions (high winds and heavy rain) resulted in reduced numbers of Guillemots at the colony. Counts of all birds on 18 days between 16 June and 7 July 1972 showed that there was a negative correlation between windspeed and total numbers of birds at the colony ($r = -0.474$ $P<0.05$) - although this explained only 22.5% of the variation in numbers. Similarly, a comparison of the numbers of birds on 3 wet and 5 dry days, when wind conditions were similar (Beaufort scale, force 1-3) between 18 May and 3 June 1973 showed that significantly fewer birds were present at the colony on wet days (Mann Whitney U test $P = 0.018$).

Since birds which were not incubating eggs or brooding chicks left the colony in the evening and returned the following morning, they must have made two sorts of decision each day: 1) whether to attend, and 2) when to attend. There is a highly significant relationship between the number of birds arriving during the first four hours of daylight and the numbers at 1200hrs. ($r = 0.734$ $P<0.001$ $n = 17$), which demonstrates that the level of Guillemot attendance on any day is determined either before first light or shortly afterwards.

Because wind speed appeared to be an important factor affecting attendance, a regression of wind speed (mean value for the period 0100-0400hrs) on the level of attendance (expressed as deviations from a 5-day running mean, thereby eliminating the non-linear effect of seasonal change in numbers) for three colonies in the incubation and nestling periods was carried out. Results are presented in Table A6. Significant negative relationships were obtained for Bull Hole and High Cliff, but not for the smallest colony, South Stream Cliff, during the incubation period. No significant results were obtained for the fledging period.

To examine the effect of wind speed on only the mates of breeding birds I have plotted mean levels of mate attendance, during the period 1-15 June, against different wind speeds (Fig.A8). Only when wind speed exceeded force 5 was there any reduction in attendance. Comparisons between all values at wind speeds of less than force 5 showed no significant differences, but comparisons between the values at force 6 and all others at different wind speeds, in turn, showed a significant difference (Mann Whitney U test, $P<0.05$).

Discussion

To summarize the main results:

(a) At British colonies, where winter observations have been made, Guillemots return in October or early November.

(b) Attendance may be irregular or cyclical during the pre-laying period and on days of peak numbers at this time, the number of birds slightly exceeds twice the number of pairs which later breed.

(c) Total numbers increase through the breeding season and reach a peak in late June, which may be due to non-breeding birds visiting the ledges at this time.

(d) A marked diurnal rhythm occurs throughout the incubation and nestling periods. All non-incubating and non-brooding birds leave the colony in the evening and return again soon after dawn. Numbers remain similar throughout the day. During the latter part of the incubation period (1-15 June) the ratio of

Table A.6. Relationship between wind speed and total number of birds at three colonies during the incubation and nestling periods 1973.

Colony	Incubation Period			Nestling Period		
	r	P	n	r	P	n
Bull Hole	- 0.394	<0.01	47	- 0.152	NS	21
High Cliff	- 0.311	<0.01	47	- 0.166	NS	21
South Stream Cliff	- 0.265	NS	47	- 0.066	NS	21

Notes: r = correlation coefficient, P = probability (NS = not significant), n = number of days.

In calculating the r values number of birds is expressed as deviations from a 5-day running mean (to allow for the non-linear changes in numbers at the colony - see Fig. A.3.). Wind speed is the mean value (expressed as km/hr) for the period 0100-0400hrs, recorded at Milford Haven, about 10 miles east of Skomer.

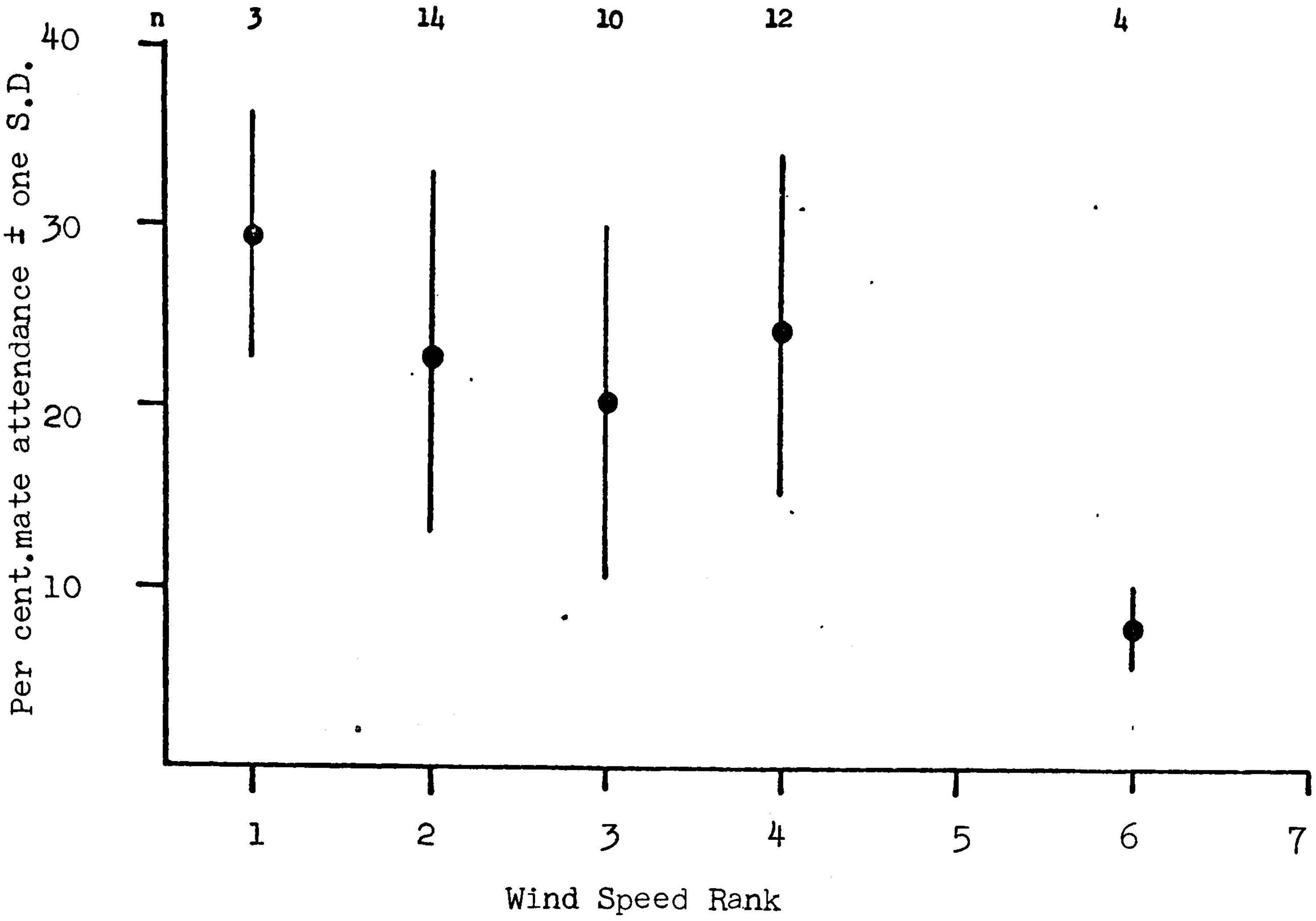


Fig.A.8. Percentage mate attendance (mean ± one standard deviation) at different wind speeds (ranked 1-7 Beaufort scale). Mates were significantly less abundant at wind speeds greater than force 5 (see text). Sample sizes for each point are shown at the top of the figure.

breeding pairs to birds present was 2 : 3 (67%) (see Chapter 2, Table 2.4).
(e) The total number of birds at the colony was reduced during high winds and heavy rain.

I have suggested that the early return of Guillemots to their breeding colonies is closely linked with competition for sites, which is a consequence of high density nesting (Chapter 6). It has also been recorded that at Fair Isle, Scotland, where the population is increasing in size, Guillemots have returned at an earlier date each year (Dennis 1967). This effect has also been recorded in Puffins on the Isle of May, Scotland (M.P. Harris, pers. comm.) and Gannets on the Bass Rock, Scotland (Nelson 1964).

Differences in diurnal patterns of attendance in different parts of a species' range may reflect different feeding situations, such as abundance of prey or distance to foraging areas, which in turn may determine the length of incubation shifts, intervals between chick feeds and the time spent at the colony (Ashmole & Ashmole 1967).

Different patterns of colony attendance have been recorded in various parts of the Guillemots' range. At the Cliffs of Moher, western Ireland, C. Bibby (pers.comm.) found that over the entire daylight period Guillemot numbers fluctuated only by 10% around the mean, with no early morning increase or evening decrease. His data suggest that, in contrast to Skomer and to Ailsa Craig, Scotland (Gibson 1950), birds at Cliffs of Moher, spent the night at the colony.

On Skomer Guillemots may leave the colony at dusk and fly to feeding areas so that they can start fishing early in the morning prior to returning to the colony. They may also feed in the dark, although there is no good evidence for this idea. However, Guillemots do manage to forage in arctic regions where light intensities are very low during winter months.

There may be no advantage in leaving the colony at night if food is close at hand, or if it is not available early in the morning for some reason. Unfortunately, there is no information on Guillemot feeding habits at the Cliffs of Moher. Although Bibby's results differed from the situation on Skomer in overnight attendance, the relative constancy of total numbers during the day was similar to Skomer and the patterns recorded at Ailsa Craig, Scotland (Gibson 1950) and in the Baltic (Hedgren 1975).

The number of Guillemots at the colony was lower during stormy conditions than at other times. I have shown that the rate at which Guillemots provision their chick is reduced during stormy weather (Chapter 3), and presumably the low numbers at the colony reflect the difficulties of foraging under these conditions.

The ratio of breeding pairs : birds present at the colony is of fundamental importance in census procedure. Figures presented for the Skomer colonies (Chapter 2) need not necessarily hold true for other areas. The ratio could be affected in a number of ways: a) High numbers of immature, non-breeding birds, which may occur in increasing populations (e.g. Funk Island, Newfoundland; Tuck 1960:202) may affect the ratio. b) In areas where birds forage close to the colony they may spend more time there, than in areas where feeding places are further away. However, Hedgren (1975) obtained a figure of 0.70 (pairs/birds present) for Common Guillemots in the Baltic - similar to the Skomer figure. A.J. Gaston (unpubl.) obtained a higher value of 0.75 for Brunnich's Guillemot in the Canadian arctic.

Because the ratio of pairs : birds is important in census procedure, other workers have tried to estimate it; Joensen (1963) and Southern et.al. (1965) estimated a 1:1 ratio, and Cramp et.al. (1974) have used this value in the census of the Guillemot population of Britain and Ireland. Dyck & Meltofte (1975) estimated a value of 0.67 and used this in calculating the size of the Faroes Guillemot population. However, since the ratio may vary between populations it is probably important in census work to derive such values from detailed observations, rather than assume that the ratio of breeding pairs : birds in one area is the same as in another.

APPENDIX II

APPENDIX II

MOULT OF THE GUILLEMOT

The timing and sequence of moult in the Alcidae is not well known. Some information on the moult of the Guillemot Uria aalge has been provided by the studies of Verwey (1922, 1924) and Salomonsen (1944). Verwey (1922) has described the partial spring moult of Guillemots from specimens found dead and Salomonsen (1944) has descirbed patterns of post- and pre -nuptial moult from a small sample of museum skins. In common with several other families of birds Guillemots experience a period of flightlessness during the replacement of the remiges. Since moult is undergone at sea, the length of the flightless period is unknown and its consequences have not been examined. The present paper describes the sequence and duration of post- and pre - nuptial moult in a group of captive Guillemots.

A group of nine Guillemots, which had originally been oiled, were cleaned and maintained in captivity. When the study was carried out the birds had been in captivity at least two years and all were at least three years old. They were in good health and three pairs had bred earlier in the year prior to the moult study (Marsault, 1975). The birds were individually marked with numbered rings. Since we knew from previous experience that the Guillemots were averse to frequent handling, they were examined at intervals of about fourteen days on nine occasions between 29 July 1973 and 24 November 1973 and on five occasions between 8 January 1974 and 5 March 1974.

Moult scores were used to record moult of primaries and tail. Primaries were numbered from the inside of the wing to the outer edge, from 1 to 10 (the minute 11th primary was ignored). The method of scoring moult was the same as that used by Harris (1971); each feather was given a score between 0 and 5, so that a fully moulted wing scored 50. Since moult in the two wings is symmetrical the right wing only was examined. The rectrices were scored in the same way, but because there was a total of 12 tail feathers the score for a fully moulted tail was 60. Before moult dorsal feathers were very abraded and pale brown in colour; this is probably caused by the disintegration of some of the cornified cell layers of the feather (Miller 1928). New dorsal feathers were very much darker, almost charcoal grey, and were therefore readily distinguished from old feathers. Thus, it was possible to estimate and rank the proportion of new dorsal body feathers from 0 to 100, where 0 = all old feathers, and 100 = all new. Ventral body surface and head were recorded as 'in progress' when moulting.

Results.

For primary, tail and dorsal body moult, the moult score was plotted against date for each individual, and a regression line fitted. In view of the small number of points for each bird, no refinements over a linear regression were attempted. Since birds were examined at intervals of about fourteen days the duration of moult of the various feathers has been determined by extrapolation from the regression line. Results for each individual are presented in Table A9. The mean duration and standard deviation

Table A.5. Estimated duration of moult of different feather tracts.

Bird No.	Commencement of moult (date)	Primary tract (days)	Rectrices (days)	Dorsal body Plumage (days)
30	28 June	90	78	128
33	12 July	67	80	126
51	20 July	54	53	95
48	7 July	86	60	134
20	20 July	60	35	64
78	20 July	46	53	79
26	20 July	62	86	51
79	20 July	42	50	87
41	20 July	57	54	105
Mean ± S.D.	-	62.7 ± 16.3	61.0 ± 16.7	95.9 ± 28.5

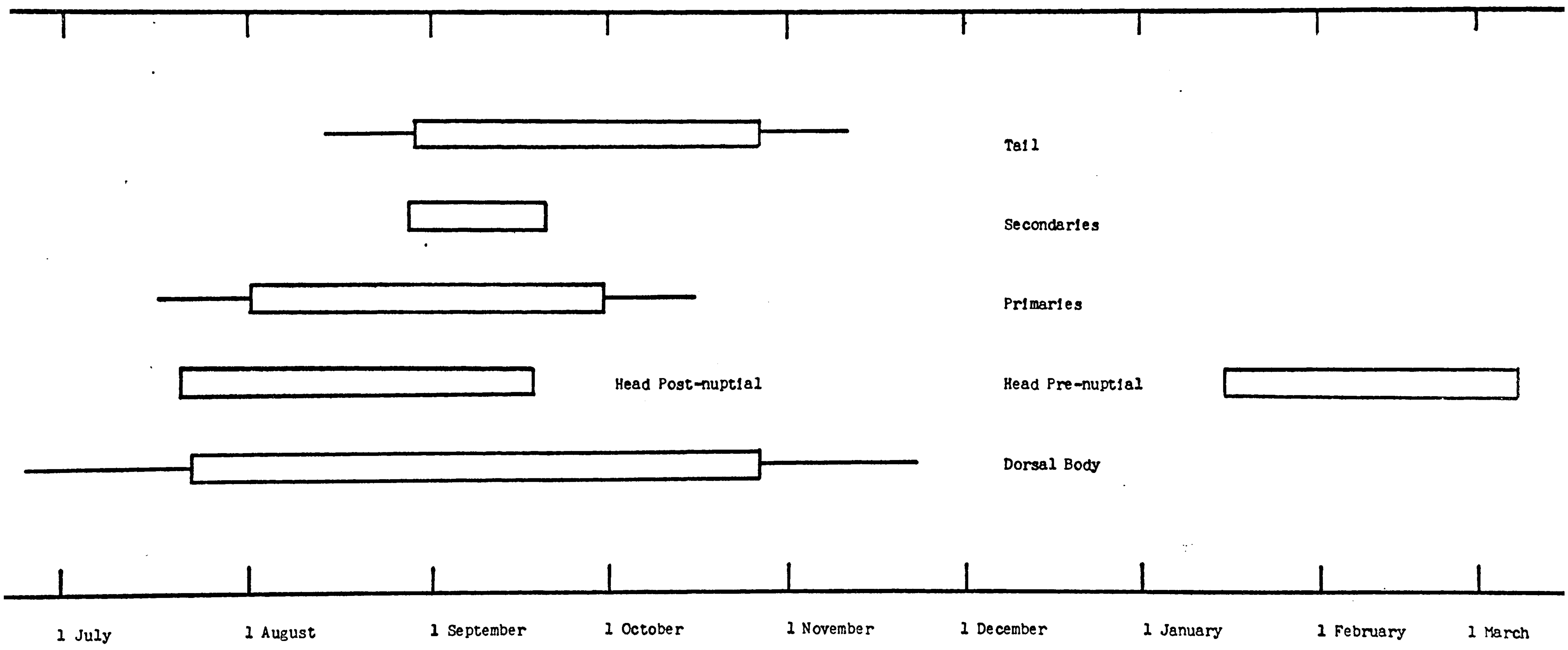
are also presented. The relationship between the moult of different feathers is summarized in Fig.A.5.

Primary Moult. Primaries were all dropped within a few days of each other. One individual dropped its 10th primary last, but another dropped its 9th and 10th primaries first. In all but one bird the 10th primary started to grow later and at a slower rate than the other primaries. Because of this irregularity in the growth of the 10th primary, the regression lines for primary scores were plotted between scores 1 and 45. The rate of primary moult varied markedly between individuals (Table A.9), some birds completing their moult within half the time of others. The average duration of primary moult was 62.7 ± 16.3 days.

Secondary Moult. Secondaries were dropped simultaneously. It was not possible to collect quantitative data on secondary moult because the growth of these feathers was unexpectedly rapid, and in two cases completed within fourteen days. The estimate of the mean duration of secondary growth is therefore a maximum one, of 25.0 ± 8.4 days. It can be seen from Fig.A.5 that the secondaries are not dropped until the primaries are about half grown, indicating that it may be important to maintain the surface area of the wing above a certain size for efficient submarine flight (diving). On average, the growth of the secondaries was completed during the last third of the period of primary growth, and it seems probable that the power of flight is regained at about this time (see Discussion).

Tail Moult. Rectrices were also dropped simultaneously. The moult of the rectrices took on average the same length of time as the remiges: 61.0 ± 16.8 days (Table A.9), despite the fact that (from a dead, wild bird

Fig.A.9. Pattern of moult in the Guillemot. The blocks show the average duration of moult of various feather tracts; horizontal bars = one standard deviation.



we examined) the fully grown tail feathers weighed less than one seventh of the weight of the remiges from both wings. However, tail moult did not start until the primaries were almost half grown, and therefore was not completed until about thirty days after the completion of primary moult. The timing and relatively long duration of tail moult suggest that the Guillemots' short tail plays only a minor role in submarine and aerial flight.

Body Moult. Both Verwey (1922) and Salomonsen (1944) noted that ventral surface body moult continued into the spring and overlapped with the pre-nuptial moult. However, it seems likely that feather growth is completed before breeding commences; no growing feathers were found on the ventral surface of twenty-five wild Guillemots examined during the incubation period (late May) on Skomer Island, S. Wales.

Further observations on wild birds at Bempton, north-east England, indicate that in some birds at least, post - nuptial ventral surface body moult, and head moult, may begin before they have left the breeding colonies, during late July and early August. In the present investigation most ventral body-surface feather growth started at a locus on the upper breast, just after the start of head and primary moult (Fig.A.5) and in most birds lasted at least 250 days. Salomonsen (1944) and Verwey (1922) also commented on the protracted period of ventral surface body moult. The plumage of auks is particularly thick; Kaftanovski (1951) found that alcids had about twice as many feathers as larids. From the birds we examined it was apparent that the feathers on the ventral surface were more densely distributed than on the dorsal surface. Notwithstanding the greater mass of feathers, it is probably important to replace these feathers at a slower rate than the dorsal feathers in order to maintain insulation and waterproofing.

Dorsal body moult started at two loci; one at the nape, the other on the rump. Because some birds retained a small number of old dorsal body feathers for several weeks after the rest of the moult was complete, regression lines for dorsal moult were plotted between scores of 1 and 95. Dorsal body moult lasted 95.9 ± 28.5 days (Table A.9).

<u>Head Moult</u>. Since all birds were at a similar stage of head moult when first examined we assumed that they had started post - nuptial head moult at approximately the same time. In all birds head moult started under the chin, spread back towards the eye and eventually over the sides of the head and crown. Completion of post -nuptial head moult took an average 62 ± 9.3. days. In the present study there was a pause lasting 121.2 ± 23.7 days between completing post - nuptial head moult and commencing pre - nuptial head moult, although this is certainly not always true of wild birds (see Verwey 1924, and Discussion). The estimate of the mean length of time to complete pre - nuptial head moult was a maximum one of 51.7 ± 5.3 days.

<u>Rate of Moult</u>. There was a significant relationship between the rate of primary and dorsal surface body moult and the starting date of moult, for a) primary moult ($r = 0.659$ $P<0.05$ $n = 9$) and b). dorsal body moult ($r = 0.721$ $P<0.01$ $n = 9$), but not for tail moult ($r = 0.151$ $P>0.1$ $n = 9$). Thus, birds which started later moulted primaries and dorsal body feathers more rapidly than those starting earlier. There was no significant difference in the time of starting or the duration of primary, tail or dorsal body moult, between breeding and non-breeding birds in the present study, although the samples are very small.

Discussion.

In many seabird species moulting and breeding are mutually exclusive and in most Alcidae the remiges are dropped after they have left the breeding grounds. Guillemots (Uria spp.) are the largest flying alcids and in order to maintain the compromise between submarine and aerial flight are near the upper limit of wing loading (Storer 1960). As a result it seems unlikely that Guillemots are able to fly until their primaries are 70-80% grown. This means that the period of flightlessness is about 45-50 days. Adult Guillemots have been observed undergoing moult in mid-August off South Wales, while accompanied by young (A.M. Taylor, pers.comm.). Food supplies must therefore be abundant and reliable during the flightless period enabling such birds to attend to their young and undergo moult (with a period of maximum feather growth occurring during the latter half of the flightless period - see Fig.A.5) simultaneously without undue stress. Indeed, in most years there is no peak of adult mortality at this time (Chapter 2). However, during the autumn of 1969 large numbers of moulting Guillemots died in the Irish Sea (Hodgate 1971).

Since the Guillemot's breeding season is approximately one month later in the arctic than in boreal regions, more northerly races of Uria aalge commence post - nuptial moult later than southerly races (Kozlova 1957). However, apparently nothing is known of the rate of moult in the different races. All birds in the present study were of the southern race U.a.albionis except for bird 20, which was of the nominate U.a.aalge. This bird had the shortest overall duration of post - nuptial moult (although only ten days shorter than the most rapid albionis) (Table A.9). Individual albionis varied widely in their rate of moult in the present study, despite being subject to the same environmental conditions and having a constant food supply, and those birds which started primary moult later, moulted at a more rapid rate than early moulting birds. However, it has been found in a number of species that populations at higher latitudes complete moult more rapidly than those at lower ones (Pitelka 1958, Flegg & Cox 1969, Holmes 1971, Salomonsen 1972, Newton 1973, Green & Summers 1975).

Since the origin of all the Guillemots was unknown, one cannot exclude such an effect being responsible for some of the variation observed. This suggests that there are advantages in being able to fly by a certain time. One advantage may be the ability to return to the breeding ledges. There is evidence that adult Guillemots breeding in boreal ice-free regions remain in the vicinity of their breeding colonies throughout the winter, and may visit their breeding ledges from late October onwards (Appendix I). There must, therefore, be strong selection pressures favouring the early return of Guillemots to their breeding colonies, and the timing and duration of their moult, although probably ultimately determined by food availability, enables them to return early. Both Verwey (1922) and Salomonsen (1944) recorded birds which had completed pre - nuptial moult in November, and N. Brown (pers.comm.), recorded that in late November 80% of the birds at a breeding colony in Berwickshire, Scotland, had completed pre - nuptial moult. Thus, some birds must commence pre - nuptial moult almost immediately after completing post - nuptial moult.

Guillemots differ from Razorbills <u>Alca torda</u> and Puffins <u>Fratercula arctica</u> both in their pattern of moulting and their date of return to breeding colonies. Razorbills generally return to their breeding colonies later than Guillemots, usually in February or March, but earlier than Puffins (M.P. Harris, pers.comm.). Salomonsen's (1944) data suggest that Razorbills may drop their remiges later than Guillemots, although more data are needed, and both Salomonsen (1944) and Verwey (1922) have shown that the pre - nuptial moult of the Razorbill does not start until at least three months after the earliest Guillemots. Thus, the early acquisition of pre - nuptial moult in the Guillemot may be associated with an early return to the breeding colonies.

APPENDIX III

Utilization of Guillemot *Uria aalge* colonies by Jackdaws *Corvus monedula*

Birkhead, T. R. Utilization of Guillemot *Uria aalge* colonies by Jackdaws *Corvus monedula*. *Ornis Scand. 5,* 71–81, 1974.

Foraging activity of Jackdaws at a Guillemot colony on Skomer Island, Wales, is described. Colour ringing showed that only a few "specialist" Jackdaws operated at the Guillemot colony, and these fed mainly on fish dropped by Guillemots and on remains of Guillemot and Razorbill eggs predated by other species. Jackdaw success for collection of fish was 2.0 % and overall food item success was 3.5 %. Jackdaws were able to determine the level of fish being brought to the colony by Guillemots, and regulated their behaviour accordingly. Thus, when fish levels were high, Jackdaws increased the amount of time they spent at the colony, and by doing so, increased the number of food items they obtained. The results showed that Jackdaw activity did not seriously affect Guillemot breeding success.

INTRODUCTION

Jackdaws *Corvus monedula* are highly opportunistic feeders. On Skomer Island, south-west Wales, they have been observed predating eggs of Puffins *Fratercula arctica,* and they have learned to intercept and cleptoparasitize Puffins carrying food for chicks (Harris, in Dickinson 1958, Mylne 1960, Corkhill 1973). Tuck (1876), Seebohm (1883), and Wade (1907) also recorded Jackdaws predating Guillemot *Uria aalge* eggs, and both Seebohm (1883) and Birkhead (1973) observed Jackdaws stealing fish from Guillemots.

The number of Guillemots on Skomer is apparently declining, and the present study forms part of a broader programme of work designed to discover factors affecting Guillemot breeding success. Since the Jackdaw population on Skomer in 1973 was probably as high as it has ever been (Birkhead 1974), the aims of this study were to determine the effect of Jackdaws on Guillemots, and to discover to what extent Jackdaws are dependent on Guillemots. Information presented here will go part of the way towards the formation of a management policy for Jackdaws on Skomer.

METHODS

The study area

Both preliminary observations in 1972 (Birkhead 1973) and those of the present study were made at an area known as Bull Hole on the northern side of Skomer. Guillemots and Razorbills *Alca torda* numbered about 500 and 120 individuals respectively at Bull Hole in 1973. One pair of Great Black-backed Gull *Larus marinus,* eight pairs of Herring Gull *L. argentatus* and three pairs of Puffin nested on the grass slopes above the Guillemot ledges. In addition, a pair of Carrion Crow *Corvus corone corone* nested in Bull Hole in 1973. Observations were made from a hide and a blind (Fig. 1), which provided a clear view of the entire cliff-face occupied by Guillemots.

Colour marking Jackdaws

Jackdaws were trapped for colour ringing, so that birds could be recognized individually.

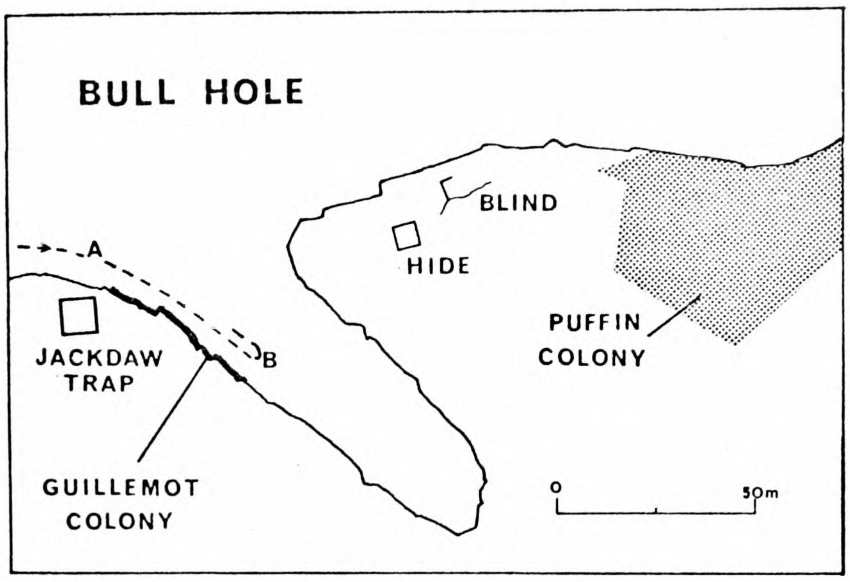


Fig. 1. The study area, north coast of Skomer Island. Broken line A–B defines limits of one Jackdaw patrol.

Birds were caught in a large cage-trap (6′ × 6′ × 4′ 6″) with a ground funnel, using a decoy, with bread and gull eggs as bait. The trap was placed on the cliff top at Bull Hole (Fig. 1). All birds caught were ringed with a B. T. O. ring on the left leg, with a red colour ring and a 2 ring colour combination on the right leg. Trapped birds were measured and sexed on presence or absence of brood patch. A total of 12 birds was caught and ringed, and thereafter observations were made at nearby Jackdaw colonies to determine breeding areas of colour-ringed birds. After the "main" colony of colour-ringed birds was located a further female was caught there.

Method of observation

To determine seasonal and diurnal changes in Jackdaw activity at Bull Hole Guillemot colony, three types of observation session were used.

(a) Whole Day: This involved entering the hide before first light and making observations continuously throughout the day until dark in the evening. Whole day watches were carried out on 15 April, 26 May, 15 June and 6 July.

(b) Mid-day: Every day from 27 May until 23 July 1973 observations were made from the blind, for one hour between 1130 and 1245 hrs. Data from these observations have been grouped into ten day means.

(c) 4 hr/4 Day: On four consecutive days the hide was entered before first light and observations carried out for the first four hours of daylight; this procedure was repeated approximately every 7 days throughout the season. These 4 hr/4 day observation sessions were conducted so that they fell as near as possible in the middle of the 10 day means mentioned above.

Jackdaws regularly followed a similar flight path when patrolling at Bull Hole, and it was possible to quantify Jackdaw activity on this basis. A patrol is defined as a flight from one end of the cliff to the last group of Guillemots at the other, where Jackdaws turned round to retrace their flight-path (Fig. 1).

During observations of types (a), (b) and (c) all Jackdaw patrols were recorded, noting the identity of birds involved. On some occasions, however, it was not possible to identify birds positively; these were recorded as "unknown". Unringed Jackdaws were also recorded. An effort was made to identify all food items by Jackdaws, and virtually all Jackdaws collecting food items could be identified by ring combination. If during a patrol a food item was collected, the patrol was regarded as having been successful. During observations of types (a) and (c) all fish brought to the ledges by Guillemots were recorded so as to determine the proportion that Jackdaws collected.

Food samples

A small number of food samples was collected from nestling Jackdaws, between 25 May and 6 June, using the collar method described by Kluijver (1933). Since none of the nests of colour ringed Jackdaws were accessible, food samples were collected from two colonies on other parts of the island.

RESULTS

Colour-marked Jackdaws

Of 12 Jackdaws caught at Bull Hole, only six were subsequently seen again and found to be breeding. This suggests that the other six may have been temporary visitors or non-breeders. Five colour-ringed Jackdaws were seen patrolling at Bull Hole, and four were breeding in a small colony approximately 400 m to the west of Bull Hole. A female (YW) caught at Bull Hole was not seen patrolling, but was found to be breeding at this colony. Another bird, YO, although observed patrolling, was frequently seen at another colony on the south side of the island and was not proved to be breeding. A further female (GyGy) caught at the colony near Bull Hole was paired to bird GyW, caught at Bull Hole.

The following birds were seen patrolling at Bull Hole: YY male, GyY male, GyW male, OO female, and YO sex unknown. The female OO was only observed patrolling on a single occasion, but was frequently seen foraging in the Puffin colony east of Bull Hole (Fig. 1). Bird YO was only seen on ten occasions (0.63 % of all patrols), and the remaining three males accounted for over 80 % of observations.

Feeding strategy and food items collected by Jackdaws

Patrolling Jackdaws flew slowly over all groups of Guillemots, making use of updraughts. Birds generally patrolled singly, although birds GyY and YY were seen patrolling at the same time, in opposite directions. Interactions between patrolling Jackdaws were rare. Depending upon the proximity of the nearest Guillemot to the food item, Jackdaws had to operate with a certain amount of daring and speed. On some occasions Jackdaws positioned themselves besides Guillemots which were standing very close to dropped fish, apparently waiting for the Guillemot to move. Guillemots generally adopted threat postures and lunged at nearby Jackdaws. In 1972, on three occasions out of 175 patrols, Guillemots holding fish were intimidated by Jackdaws which subsequently collected the fish dropped by the Guillemot (Birkhead 1973). In 1973 behaviour of this sort was observed only twice. This habit probably requires a greater level of skill and daring by Jackdaws. When Jackdaws collected fish they were carried cross-wise in the bill to a Guillemot-free area. The fish was then held in the feet, broken into pieces, and stored in the sublingual pouch prior to being taken to chicks.

Jackdaws occasionally accompanied marauding Great Black-backed Gulls, and were sometimes able to collect fish which Guillemots dropped in their efforts to avoid the gulls. Jackdaws also waited beside Great Black-backed Gulls eating Guillemot and Razorbill eggs, in order to secure bits left by the gull.

On a few occasions apparently nervous Guillemots were flushed from their eggs, for example by the close approach of a boat; on each occasion exposed eggs were taken by either Herring Gulls, Great Black-backed Gulls, or Carrion Crows. Jackdaws were never observed predating Guillemot eggs, although a bird was once observed to eat an unattended Razorbill egg. Jackdaws always examined shells of eggs which had been predated by gulls and left on the ledges, but apparently had difficulty collecting the yolky remains of gull-predated eggs on rock surfaces. It seems likely that the amount of food collected in this way was small.

Table I. Food items collected by Jackdaws at Bull Hole Guillemot colony

Food item	No.
Fish	32
Whole egg (Razorbill)	1
Egg pieces	9
Unidentified	15
Total	57

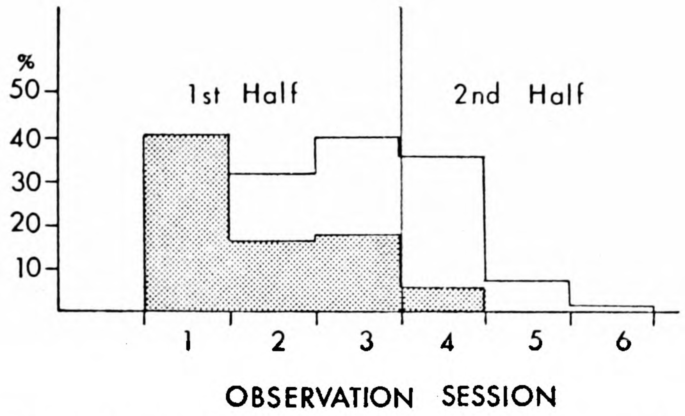


Fig. 2. Seasonal changes in the percentage success of food items collected by Jackdaws. From 4 hr/4 day data. Stippled area = "other" food items, open area = fish. Observation sessions 1 to 6 are the same as those in Fig. 5a (see caption to Fig. 5).

A list of food items collected by Jackdaws at Bull Hole is presented in Table I. With the exception of a single entire Razorbill egg, fish dropped by Guillemots were the largest items collected by Jackdaws. However, a significantly greater proportion of "other" food items were taken during the first half of the season (Fig. 2) (Median Test $P \lesssim 0.02$). As pointed out, unidentified items could have been fish, although there is no reason why fish should have been unidentified more frequently early in the season than later. However, eggs were certainly more abundant early in the season. It therefore seems likely that this was a genuine difference in food items.

It was not possible to reach the nests of any of the colour-ringed Jackdaws to determine the proportion of fish in their chicks' diets. However, a small number of collar samples were collected from nests on other parts of the island. Samples were collected from two regions: one at the eastern end of the island, nearest the mainland, and the other at the south-western end of the island. Samples from the eastern end of the island contained grain, indicating that birds were feeding on the mainland. At the other site, birds were only observed foraging near the colony.

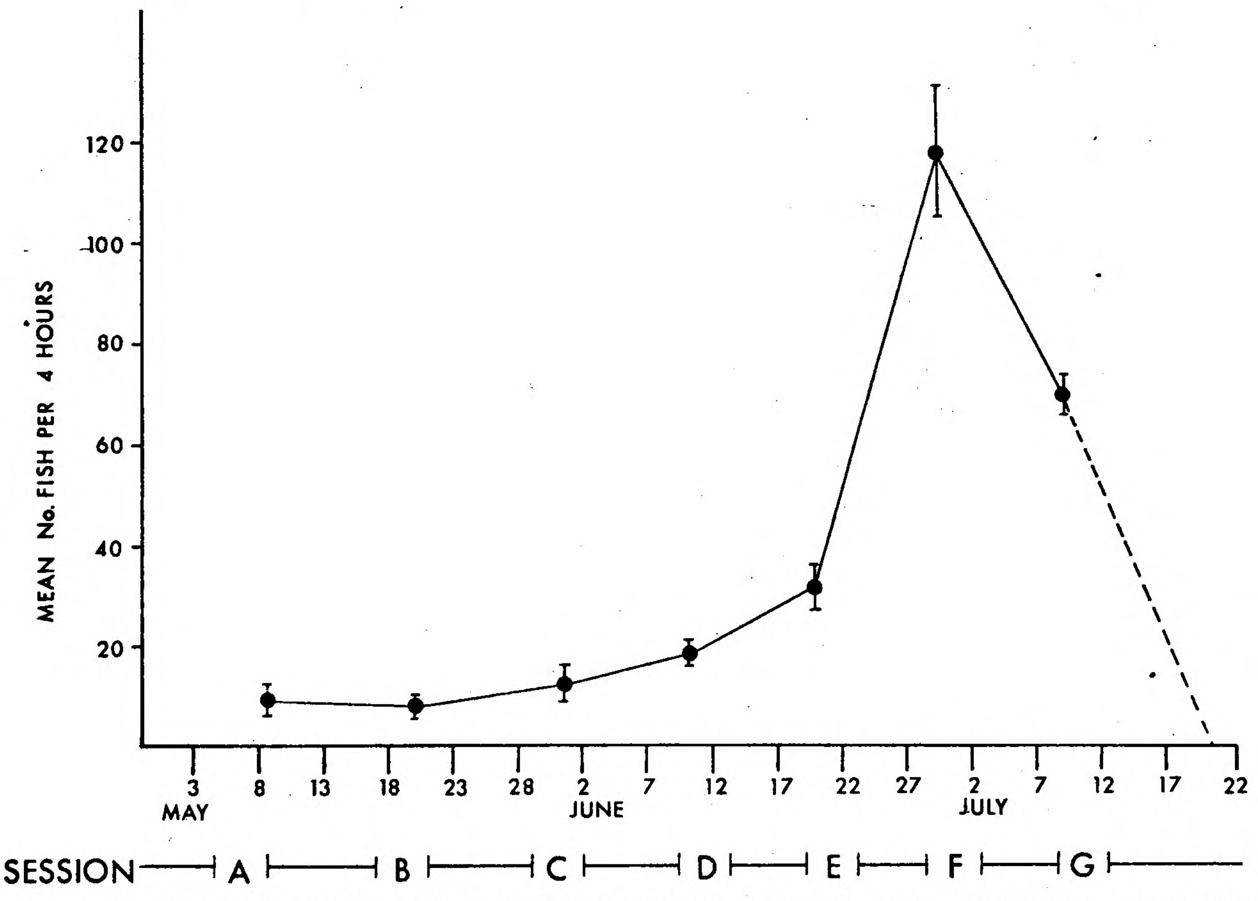


Fig. 3. Seasonal changes in total number of fish brought to the colony by Guillemots ± S. E. Data are from 4 hr/4 day observation sessions. Session A = 6–9 May, sessions B to G correspond exactly with sessions 1 to 6 in Fig. 5a (see caption to Fig. 5). Broken line refers to data based on less than a 4 hr/4 day observation session; by 20 July most Guillemot chicks had fledged.

Fish presentation in Guillemots

A more detailed account of fish presentation in Guillemots is given elsewhere (Birkhead in prep.). During the entire breeding season a small proportion of Guillemots, without chicks, bring fish to the ledges. These were mostly clupeid species, having a mean length of 10.7 ± 0.71 cm (n = 10) and, from samples collected from ledges, weighing about 9 g. The fish were held by Guillemots for an average of 17 minutes (range 1-125 minutes). During the first half of the season, up to the peak of Jackdaw activity (12 June), but before Guillemot chick feeding commenced, 72.7 % of fish brought to the ledges by Guillemots were dropped, and were potentially available to Jackdaws. Most of the remaining 27.3 % were eaten. During the Guillemot chick feeding period it was possible to distinguish those Guillemots carrying fish which were not intended for chicks.

Seasonal changes in the mean number of fish per 4 days, brought by Guillemots, are presented in Fig. 3. The first five points are based on observations of the entire cliff-face. However, during sessions F (peak of Guillemot chick feeding) and G, the volume of fish arriving was such that not all arrivals could be counted; only fish brought to the nearest groups of Guillemots were recorded. Since all groups of Guillemots at Bull Hole were regularly counted, it was possible to extrapolate from the observation group the approximate number of fish brought to the whole group. There was no apparent difference in the frequency of fishing trips on different ledges at Bull Hole.

Fig. 3 shows that the number of fish remained fairly stable until Guillemot chicks first appeared (12 June) and chick feeding commenced. It then rose to a peak at session F and fell again at session G. However, during the period when Guillemots were feeding chicks, the proportion of fish dropped by birds without chicks was 37.9 %, which was significantly lower than before 12 June ($\chi^2 = 6.07, P < 0.02$). I estimated that the proportion of fish dropped by Guillemots or chicks during feeding was less than 2 %. Thus, notwithstanding the increase in total number of fish being brought to the ledges during this period, the number potentially available to Jackdaws was less than before 12 June. Very few fish were being brought in by 20 July, when virtually all chicks had fledged and few birds were present on the ledges.

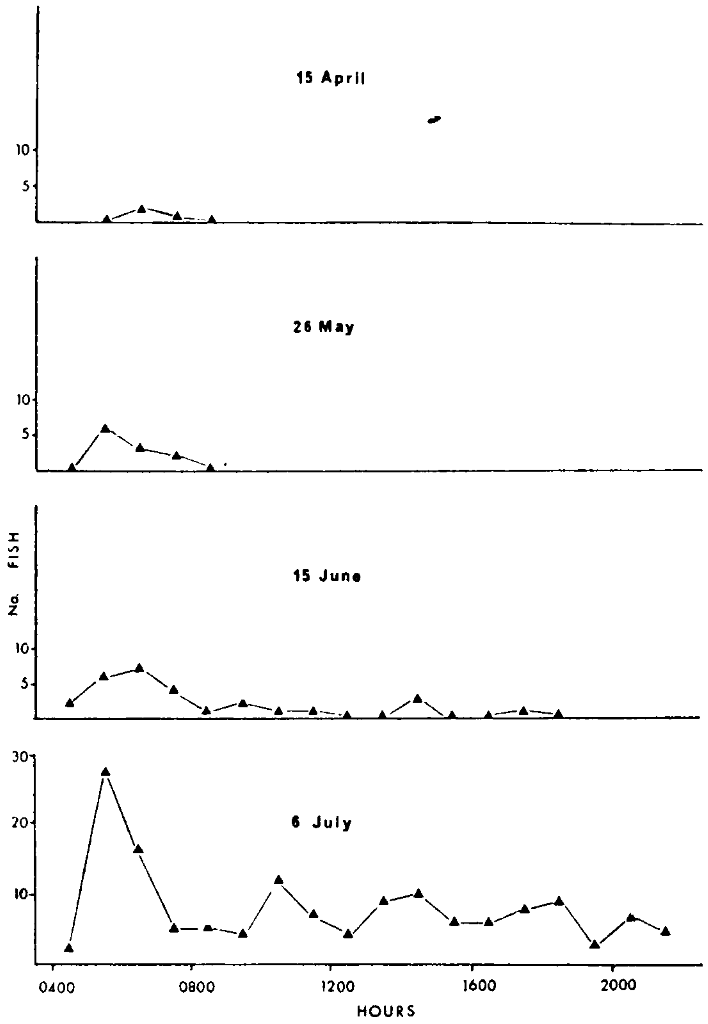


Fig. 4. Diurnal changes in total number of fish brought to the colony by Guillemots. Figures include both fish for chicks and fish not for chicks.

The diurnal patterns of Guillemots arriving with fish are presented in Fig. 4 for four whole day watches. It can be seen that there was a tendency for fish presentation to occur in the early morning during the first part of the season, but it covered a greater part of the day as the season progressed, although still maintaining a peak early in the day.

Seasonal and diurnal patterns of patrolling

To measure Jackdaw activity, a patrolling rate was calculated, based on mean number of patrols per hour for the 4 hr/4 day observation sessions, and the number of patrols during one hour's observations at mid-day, each day.

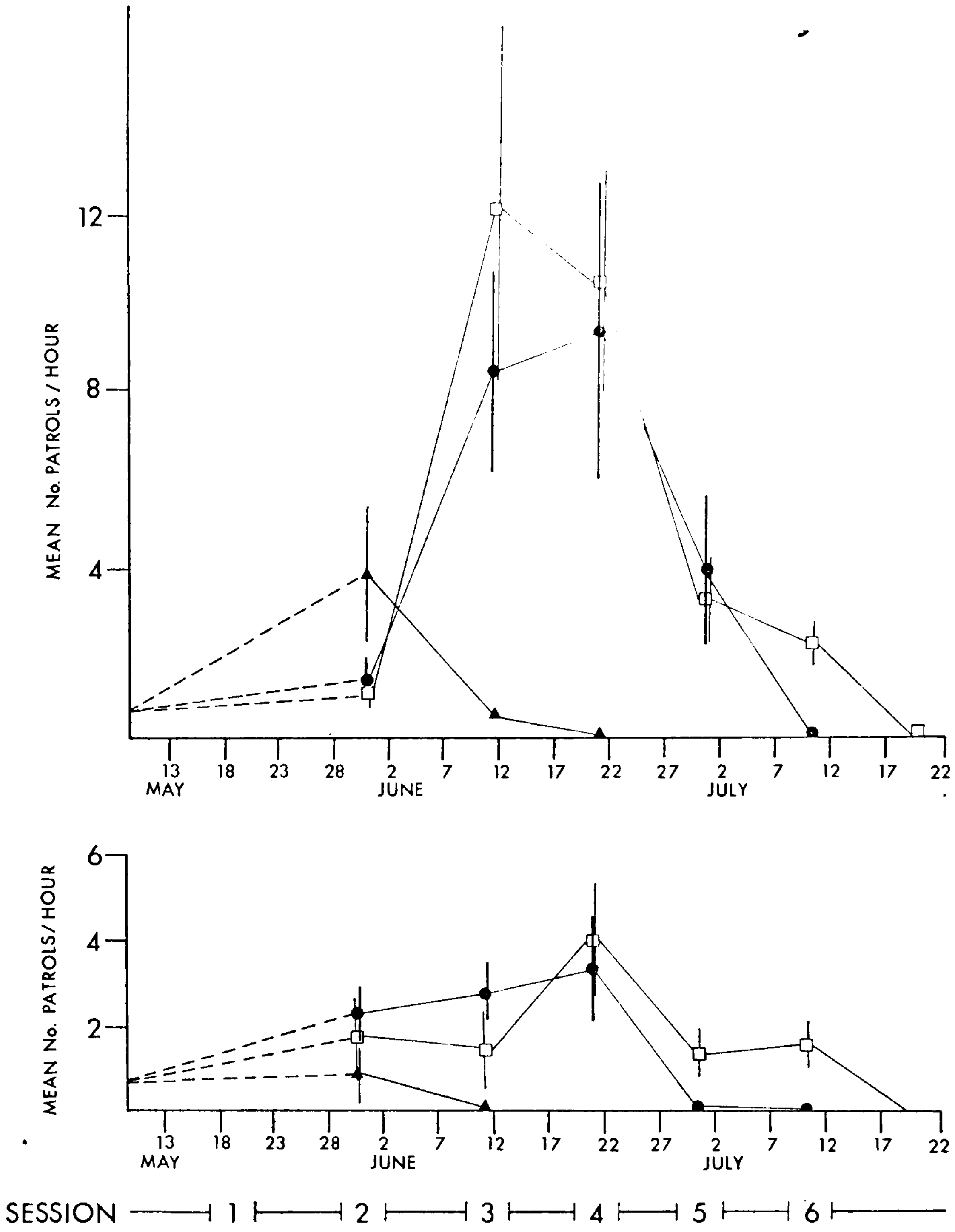


Fig. 5. Seasonal changes in patrolling rate of individual Jackdaws ± S. E. ▲ = bird GyW, □ = bird GyY, ● = bird YY. Broken lines refer to a period when Jackdaws were patrolling, but before birds were marked. *Upper Fig. (5a)* is based on 4 hr/4 day data, and session numbers on horizontal axis refer to 4 hr/ 4 day observation sessions. Session 1 (18–22 May), session 2 (31 May–3 June), session 3 (9–12 June), session 4 (20–23 June), session 5 (29 June–2 July), session 6 (10–13 July). *Lower Fig. (5b)* is based on mid-day data, grouped into ten-day periods. Session 1 (17–26 May), session 2 (27 May–5 June), session 3 (6–15 June), session 4 (16–25 June), session 5 (26 June–5 July), session 6 (6–15 July).

Seasonal changes in patrolling rates of three Jackdaws, using 4 hr/4 day data, are presented in Fig. 5a, and using mid-day data, in Fig. 5b. Three individuals account for over 80 % of all patrols. The seasonal pattern of patrolling by individuals varied. From Fig. 5 it can be seen that bird GyW was only active up to early June, although it was seen near the breeding colony on 21 June. The other two birds, GyY and YY, patrolled throughout the season, with a peak patrolling rate between 9–23 June. Bird GyY covered the greatest time span,

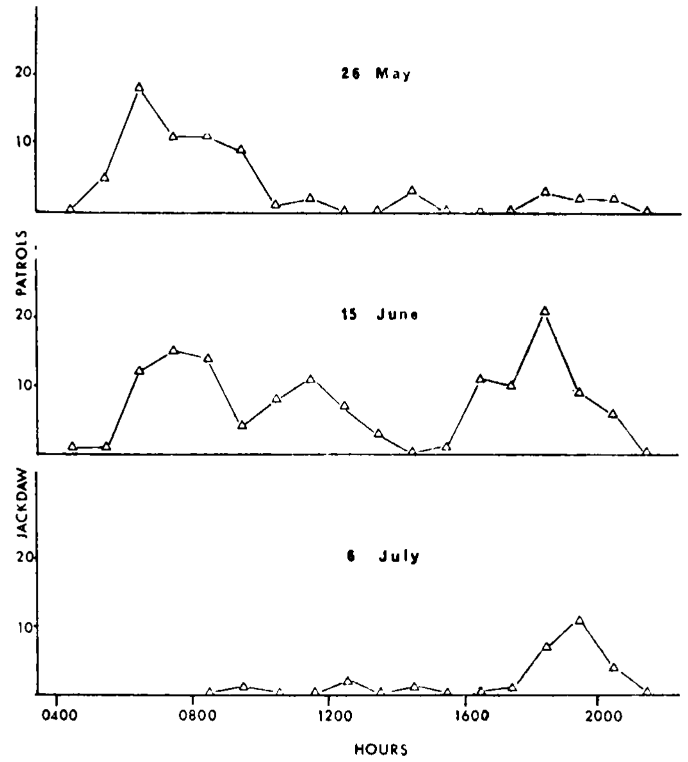


Fig. 6. Diurnal changes in number of Jackdaw patrols irrespective of individual, each hour, throughout the daylight period on three days. On 26 May and 15 June, Jackdaws started patrolling during the first hour of daylight. On all three days Jackdaws were recorded patrolling during the last hour of daylight.

patrolling from 18 May to 13 July. It is not known whether the differences shown by the three individuals are due to the birds being at different stages of the breeding cycle, or to their exploitation of other food sources, since it was not possible to reach any of their nests. Taking all observation periods into account, bird GyW accounted for 7.7 %, bird YY 33.4 %, and bird GyY 40.4 % of all patrols.

Diurnal patterns of patrolling were examined by carrying out four whole day watches. Although the data suggest that diurnal patrolling patterns changed with season (Fig. 6), it was not possible to distinguish between genuine seasonal changes and changes in the activity of individual Jackdaws. On the first whole day watch (15 April) no Jackdaws were observed, although weather conditions were good (see below). In addition, no Jackdaws were observed during early morning watches about this time, suggesting that Jackdaw activity was low at this time of year. On 26 May, when three individuals were operating, patrolling was concentrated in the first six hours of daylight. Bird GyW accounted for 40 % of all patrols, but 36 % were by unidentified birds. However, bird GyW accounted for 66 % of all patrols made by known individuals. The small number of patrols between 1800 and 2000 hrs were made by bird GyY. By 15 June, bird GyW had ceased patrolling, and on this date birds GyY and YY accounted for 35 % and 55 % respectively of all patrols. Both birds patrolled to a similar extent throughout the day. The diurnal pattern of patrolling is similar to 26 May, in that a peak of activity between 0500 and 0900 hrs is maintained, but differs from 26 May in that birds were active, to varying extents, throughout the entire daylight period. It is likely that the early morning was an especially favoured part of the day for patrolling during most of the season (see next section); on 20 days between 18 May and 2 July, the patrolling rate of all marked individuals was significantly higher during the first four hours of daylight than at mid-day (matched pairs "*t*" test, $t = 3.03$, df. $= 39$, P $= < 0.01$). However, on 6 July the patrolling rate was low, and virtually all patrols were made in the evening, GyY accounting for 86 % of these (other patrols were by 3 unringed and one unidentified bird).

Weather conditions affected the amount of time that Jackdaws spent patrolling. During two of the 4 hr/4 day sessions heavy rain occurred on one day out of four in the first case, and on two days out of four in the second (Table II). On these days, the number of Jackdaw patrols made by all individuals was significantly lower than on the dry days (Mann-Whitney *U* test, P $= < 0.02$). It is not clear whether Jackdaws were generally less active in wet weather or if they were exploiting some other food supply. However, Kennedy (1970) has recorded Jackdaws exhibiting rain avoidance behaviour, and I have observed Jackdaws sheltering under cliffs on Skomer during heavy rain.

Success

A successful patrol was one during which a Jackdaw collected a food item. Food items

Table II. Comparison of number of Jackdaw patrols on wet (W) and dry days. Thick mist on 19 May prevented any observations being made

	May					June		
Hour after first light		W			W		W	
	18	20	21	22	31	1	2	3
1st hour	2	0	5	7	2	26	9	29
2nd hour	5	0	24	26	17	36	15	62
3rd hour	3	0	9	29	19	39	16	42
4th hour	10	0	3	2	10	18	14	35
Total	20	0	41	64	52	119	54	168

have been divided into two categories – fish rewards (R) and "other" items. The latter category includes all items which were not fish, and unidentified items which could have been fish (see p. 73–74). Success is expressed as fish rewards per hour/patrols per hour. Table III presents overall success from the 4 hr/4 day data, mid-day and whole-day data, irrespective of individuals patrolling. Mid-day sessions for both types of food item were markedly less successful than either of the other two periods. Overall food item success was 3.5 % and fish success 2.0 %, i.e. on average Jackdaws were likely to obtain some sort of food item approximately once every 30 patrols, and, on average, a fish item once every 50 patrols.

During the first half of the season (up to 12 June) leading to the peak of Jackdaw activity (birds GyY and YY), the patrol rate (P) of all colour-marked birds was positively correlated, first with the number of fish rewards (R) ($r = 0.653$, $P<0.001$), and second, with the number of fish per hour (F) brought by Guillemots ($r = 0.44$, $P < 0.05$).

A multiple regression analysis was used to determine the type of relationship existing between R, as dependent variable, and P and F as independent variables. The best fit was obtained from the linear regression R on P (42.6 % of the variation in R is explained by P) (Fig. 7). In addition, although there is a significant correlation between R and F, the addition of F to the regression does not significantly improve that fit ($F_{1,25} = 0.49$; NS). Thus it appears that Jackdaws increase their patrol rate when more fish are being brought in by Guillemots, and by doing so, increase the number of rewards they obtain.

Table III. Foraging success of colour-ringed Jackdaws at Bull Hole irrespective of individual. Success is expressed as a percentage of the number of successful patrols. Total food items include fish rewards. Mean for the whole day sessions is calculated from the total number of patrols made on each of the three days, on the 3rd whole day session 24 patrols were made by marked Jackdaws. Overall mean is calculated from 4 hr/4 day sessions, mid-day sessions, and whole day sessions-overall mean. Whole day sessions 1, 2 and 3 refer to 26 May, 15 June and 6 July, respectively

	Fish success	Total food item success
4 hr/ 4 day sessions	2.8	4.2
Mid-day sessions	0.5	1.0
Whole day sessions: 1	7.3	14.6
2	1.7	3.4
3	0	0
Whole day sessions – overall mean	2.7	5.4
Overall mean	2.0	3.5

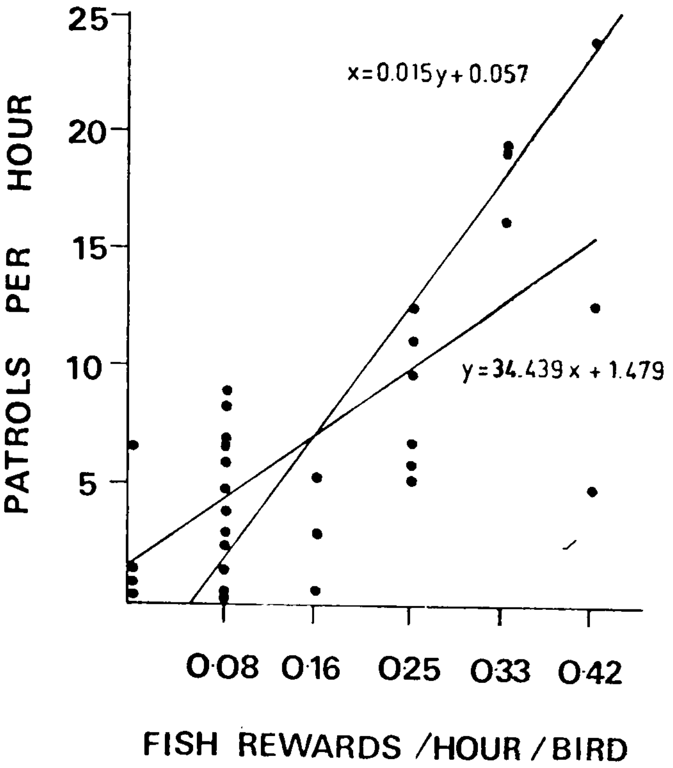


Fig. 7. Relationship between Jackdaw patrol rate and fish rewards per hour/per bird. The figure is based on observations of three colour-ringed Jackdaws (birds GyW, GyY and YY) during 4 hr/4 day observations up to and including 12 June. For the equation: $y = 34.439x + 1.479$, $r = 0.723$, $p < 0.001$, $n = 31$.

It has already been shown that individual Jackdaws spent varying amounts of time patrolling at Bull Hole. The success rates for individual Jackdaws are presented in Table IV. From Table IV it can be seen that Jackdaw GyW was significantly more successful than either of the other two Jackdaws ($\chi^2 = 8.8$, $P < 0.01$), which was due to this bird's significantly better success at collecting "other" food items ($\chi^2 = 15.3$, $P < 0.001$). All three birds had similar fish success. From Fig. 5 it can be seen that GyW patrolled the least number of times, but only during the early part of the season, and this bird's activity accounts for the higher number of "other" food items taken early in the season. By the time birds GyY and YY were reaching their peak of activity, bird GyW had ceased patrolling.

DISCUSSION

It is clear from colour marking Jackdaws that only a small number of birds, which can be regarded as specialists, were involved in utilizing the Guillemot colony at Bull Hole. Corkhill (1973) also noted that a Jackdaw which cleptoparasitized Puffins carrying fish was a highly successful "specialist" individual.

Although both parent Jackdaws feed chicks, the birds operating regularly at Bull Hole were males. The mate of male GyW was colour ringed (GyGy), and was observed flying to the nest site with food but was never observed at Bull Hole. In contrast, the pair of Carrion Crows nesting at Bull Hole frequently foraged together on the Guillemot ledges. Feeding studies of the Jackdaw have been carried out by Lockie (1955), but the role of the sexes in chick feeding is apparently unknown. It is pos-

Table IV. Success of individual Jackdaws over entire observation periods. Success is expressed as a percentage of the number of successful patrols

Bird	No. patrols	No. fish collected	No. "other" items collected	% fish success	% "other" item success	% total food success
YY	526	15	5	2.8	0.9	3.8
GyY	636	12	8	1.9	1.3	3.1
GyW	121	4	7	3.3	5.8	9.1
YO	10	0	0	–	–	–
OO	1	0	0	–	–	–
Unknown	207	1	4	0.5	1.4	1.9
Unringed	72	0	1	0	1.4	1.4
Totals	1573	32	25			

sible to suggest tentatively that male Jackdaws may be more daring than females and therefore better suited to collecting food from Guillemot ledges.

Birds GyY and YY both showed similar seasonal patterns of patrolling, but bird GyW patrolled only during the early part of the season. Since none of these birds' nests were accessible, it was not possible to determine whether GyW was at a different stage in the breeding cycle than the other two. However, Jackdaw activity at Bull Hole before 18 May (before any birds were colour marked) was generally low; prior to 6 May birds were seen only infrequently, but a 4 hr/4 day watch between 6–9 May produced a mean figure of 3.12 patrols per hour. Even if GyW was the only bird involved in these days, its patrolling rate is still considerably lower than either GyY or YY at the peak of their activity. This suggests that bird GyW either failed in its breeding attempt, or turned to exploit some alternative food supply, notwithstanding its high level of success.

Despite the variation of diurnal patterns of patrolling throughout the season (which may reflect individual differences), in general the Jackdaws maintained a peak of patrolling early in the morning during most of the season. Since Guillemots brought fish to the ledges mainly during the morning, this strongly suggests that Jackdaws had learned to patrol more at this time. Moreover, on any particular day the Jackdaws adjusted their patrolling rate according to the level of fish on the Guillemot ledges. Since those Guillemots which are not feeding chicks tend to hold their fish for some time, the number of fish held almost certainly acts as an index on which Jackdaws can base their patrolling rate. Jackdaws increase their patrolling rate when more fish are being brought to the ledges, and by doing so increase the number of fish rewards they obtain. It seems likely that the collection of a reward also reinforces patrolling rate.

It would be of interest to know the overall relative value to chicks of being fed on fish compared with invertebrates or grain. For fish food to be useful, it must be efficiently assimilated by Jackdaw nestlings. The time taken to collect a similar biomass of the different food types probably differed considerably. A patrol took on average 20 seconds, and birds collected fish approximately once every 50 patrols, i.e. one 9 g fish for every 17 minutes of patrolling time. However, a Jackdaw foraging on the mainland may be able to collect 9 g of grain quite rapidly, although the value of this as chick food is probably considerably less than invertebrates or fish. Dawson (1972) found that nestling House Sparrows *Passer domesticus* raised on different food types showed different levels of nestling mortality. It would be interesting to compare growth rates and survival of Jackdaws fed predominantly on fish, invertebrates, or grain. This may show the type of advantage Jackdaws gain from specializing on fish.

Only on a single occasion was a Jackdaw observed predating a whole Razorbill egg. Clearly a reward of this size is of high value both nutritionally and on a patrolling-time and energy basis. During the present study Jackdaws were not seen taking Guillemot eggs. It seems unlikely that Jackdaws ever get an opportunity to predate Guillemot eggs unless the birds are disturbed, since Guillemots' nesting strategy (i.e. incubating in dense groups) is highly effective in the case of most predators. Wade (1907) observed Jackdaws rolling Guillemot eggs off ledges in order to eat them, but from his account it seems likely that this occurred when human egg collectors were operating and the Guillemots had been frightened from the ledges. Since a Jackdaw cannot carry an egg the size of a Guillemot's, in order to successfully predate one, it must either eat it on a ledge devoid of Guillemots or roll it off the ledge as Wade has described. Razorbill eggs are probably much more vulnerable to Jackdaw predation since this species nests individually and apparently leaves its egg unattended on occasions. C. S. Lloyd (pers. comm.) found that Jackdaws were responsible for up to 60 % of all Razorbill egg loss in some areas of the neighbouring island of Skokholm. In addition, casual observation on Skomer indicates that some Jackdaws are particularly adept at collecting eggs from Puffin and Manx Shearwater *Puffinus puffinus* burrows.

Corkhill (1973) suspected that cleptoparasitism by Jackdaws may have reduced the provisioning performance of Puffins in some areas on Skomer. The affect of Jackdaws on Guillemots in the present study is negligible. Virtually all fish collected by Jackdaws were those dropped by Guillemots, and in most cases never intended for chicks. Incidents of fish stealing were rare, and it seems likely that birds vulnerable to cleptoparasitism are those without chicks which are holding fish for long periods. Furthermore, the Jackdaws' breeding season is completed before the peak of Guillemot fish landings, during the chick-feeding period in July. Although Jackdaws do not have an adverse affect on the breeding success of Guillemots on Skomer, Razorbills and Puffins appear to be much more at risk. In addition to Razorbill eggs and Puffin eggs and fish, the Guillemots' habit of fish presentation provides a few specialist Jackdaws with a good food supply during the breeding season.

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