Studies on the biology of sea birds with particular reference to the Eider (Somateria mollissima)

Flowers, Anne

Studies on the biology of sea birds
With particular reference to the
Eider (*Somateria mollissima*)

by

Anne Flowers, B.Sc.
(St. Mary's College.)

.... being a thesis presented in candidature for the degree of Master of Science in the Durham Colleges in the University of Durham, March, 1964.

ACKNOWLEDGEMENTS

The writer wishes to express her thanks to Dr. J.C. Coulson for direction, encouragement and advice during the course of this work.

Thanks are also due to the members of the Department of Zoology especially Mr. J. Warner who gave so much assistance with the field work.

Mrs. G. Hickling for assistance with ringing recoveries.

The National Trust allowed access to the birds of the Farne Islands and this is gratefully acknowledged.

The work was carried out whilst holding a Department of Scientific and Industrial Research Studentship.

Abstract from the thesis "Studies on the biology of sea birds with particular reference to the Eider Somateria mollissima" by A. Flowers.

The thesis has been divided into three parts, Part A is concerned with the biology of the Eider, Part B deals mainly with the distribution and movements of the Eider around the Farne Islands and the coasts of Northumberland and S.E. Scotland. The mortality rates of Black headed gulls and Gannets and their causes of mortality have been studied in Part C.

The biology of the Eider was studied under the following headings: pre-laying behaviour, breeding season, laying frequency and time of laying, clutch size, incubation period, desertion, hatching and hatching success, activity, tidal rhythm and sex ratio.

In Part B. it has been shown that there is a local distribution as well as a moult migration in the Eider, particularly in the males, which move to the Firth of Forth from the Farne Islands, to moult.

From the data examined in Part C it has been found that the cause of mortality in Black headed gulls varies throughout the life history, young birds being more prone to shooting than adults. The mortality rate was found to be 17.8 per cent. Gannets also were found to have a varying cause of mortality throughout their life history, though in this case young birds were more likely to be caught in fishing nets. Using the same method to calculate the mortality rate an impossible result was obtained and this was thought to be due to biased ringing. Recoveries from the South African Gannet were used in the calculations and a new mortality rate of 5.3 per cent was found which is a more realistic value.

An appendix of the numbers of Eiders counted during the twelve month period July 1961, to June 1962, along the coasts of Northumberland and South East Scotland have been included at the back of the thesis, also further data on clutch size.

CONTENTS.

PART A.

Introduction.

The Eider ducks of the genus Somateria are marine living birds which are widely distributed in the northern hemisphere. The Common Eider, Somateria mollissima, subsequently referred to as the Eider, has an extensive geographical range, breeding in coastal areas in both the North Pacific and North Atlantic Oceans. On the eastern side of the North Atlantic, Great Britain is at the southern extremity of its range, except for a rapidly increasing population in the Netherlands, and a few which breed (or used to breed) in the Brittany region of France.

The Eider has been, and in many areas still is, of considerable economic importance. Wild populations are 'farmed', particularly in Iceland and elsewhere. Despite extensive literature related to this economic importance there is still a considerable amount of the duck's ecology and general biology which requires study. Down production has been studied by Lewis (1926) in Canada, Muller (1906) in Greenland and Gudmundsson (1938) in Iceland. Rolnik (1943, 1955) has made detailed studies on the incubation period of the Eider eggs. A general description of Eider farming in Iceland, including the methods used to attract and protect the breeding ducks has been given by Munro (1961).

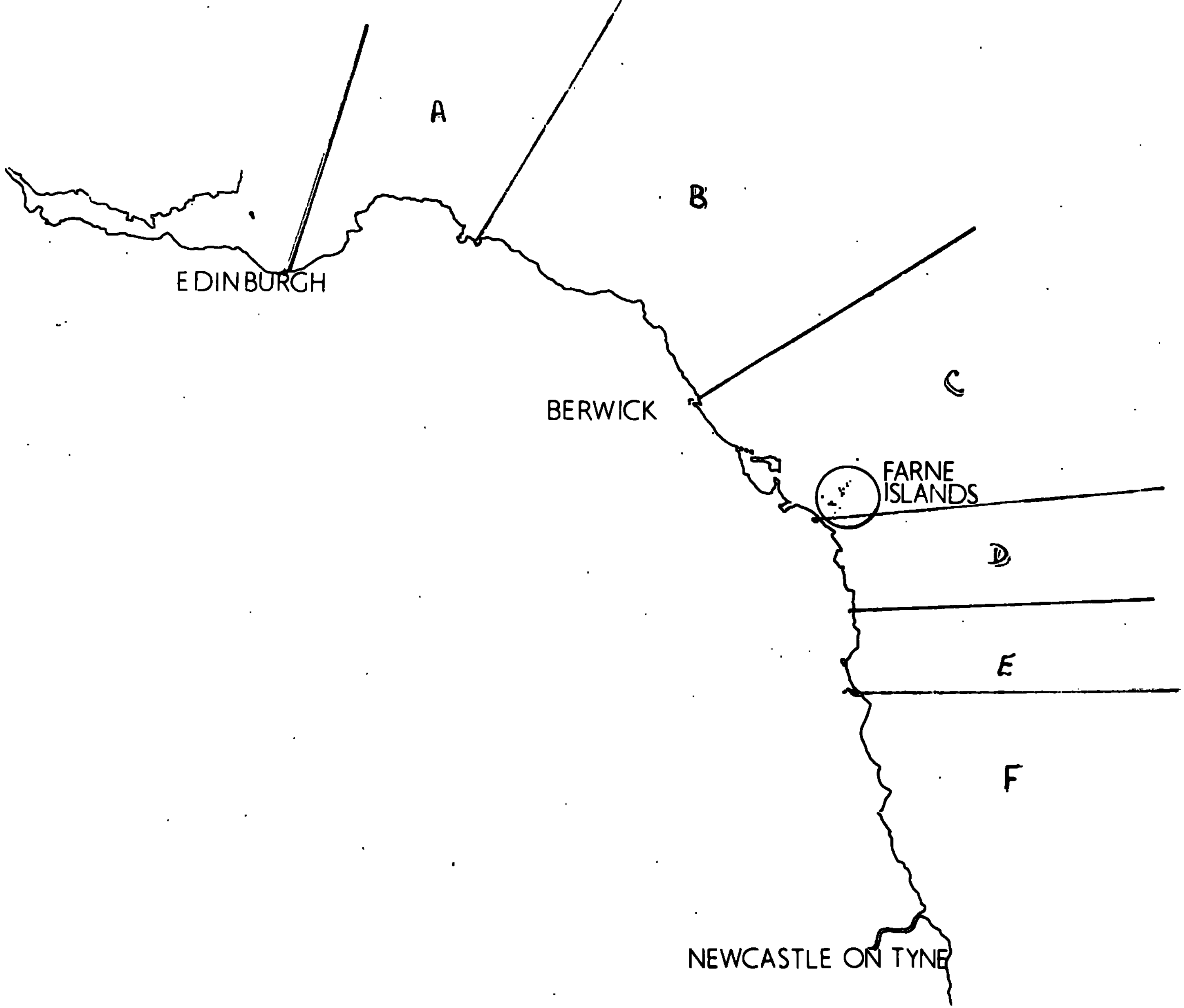
The compilation of Millais (1913) gives a comprehensive account of the general biology and natural history of the Eider, while Best and Haviland (1913) have produced additional information on the biology of the duck in the Outer Hebrides, More recently Gross (1944) has reviewed the status of the Eider on the Main Coast of U.S.A. and Kenyon (1961) has commented on their general biology on Amchitka Island, Alaska.

There is extensive, but often uncritical data on the clutch size of the Eider. Jourdain (1922) has given details of clutches found in Spitzbergen, while Gross (1938) and Lewis (1939) have given quantitive data for the U.S.A. and Canada. Further information from U.S.A. has been published by Paynter (1951). Belopolskii (1957) has collected data on several thousand Eider clutches from arctic Russia, showing that even over a relatively small geographical range, considerable differences can exist in the mean clutch size.

The food of the Eider has been the subject of several studies, the most recent being those of Madsen (1954) and Belopolskii (1957) and Gerasimora (1954) in arctic Russia. These studies have shown that the diet of the Eider consists mainly of molluscs, often the Common Mussel Mytilus edulis, and crustacea, usually small crabs.

In the present study, observations have been made on the breeding biology of the Eider on the Farne Islands, Northumberland in 1962, where

Fig. 1. Shows the position of the Farnes and the areas into which the coastline was divided for the distribution work.


A
B
C
D
E
F
EDINBURGH
BERWICK
FARNE ISLANDS
NEWCASTLE ON TYNE

particular attention was paid to the egg production in relation to breeding area and the period in the breeding season. In addition, investigations were made on the movements of Eiders along the coast of Northumberland and south east coast of Scotland, where evidence was obtained of a moult migration to the Firth of Forth.

The opportunity was also taken to analyse ringing recovery data from the British Trust for Ornithology, for the Gannet, Sula bassana and the Black-headed gull, Larus ridibundus, to obtain estimates of the adult mortality rate, using a new method which did not become biased due to ring wear and loss. Too little data are available on the Eider to make an analysis of ringing recoveries profitable.

Study Area.

The Farne Islands lie off the Northumberland coast (Fig. 1), the nearest island lying about one and a half miles from the nearest point on the mainland. They represent the last eastern outcrop of the Great Whin Sill. Faulting, erosion and weathering have broken the outcrop into a group of 17 small islands, the largest of which is the Inner Farne (16 acres)(Fig. 2). The Eider breeds on several of these islands (Inner Farne, Brownsman, Longstone, Staple, Wideopens and Wamses) but the largest numbers occur on the Inner Farne (Fig. 3).

The Eiders breeding on the Inner Farne were intensively studied throughout May and June, 1962, to obtain information on the breeding biology and ecology of the Eider. The movements of the Eider along the coasts of Northumberland, Berwickshire and East Lothian were followed during the year July, 1961, to June, 1962, and data was obtained on the distribution and movements of this species throughout the twelve month period.

Methods.

Each Eider nest in the study area was marked with a wooden stake and a number. These nests were visited four times daily and each new egg was marked with the date, number of the nest and the number of the egg in the clutch sequence. A wax pencil was used as biro or graphite pencil marks were quickly obliterated. Many of the nesting ducks were individually marked with paint on the head or bill, so that each individual did not have to be disturbed for identification, as would have been the case if colour-rings had been used. The tameness of many of the ducks readily facilitated such markings without causing the bird undue disturbance. The total number of nests in the Study Area was 174, and in all, 536 clutches were started on Inner Farne. Throughout May and

June, counts of non-incubating birds around the Inner Farne, were made four times daily to obtain data on the fluctuations of the sex ratio and diurnal or tidal rhythms of activity.

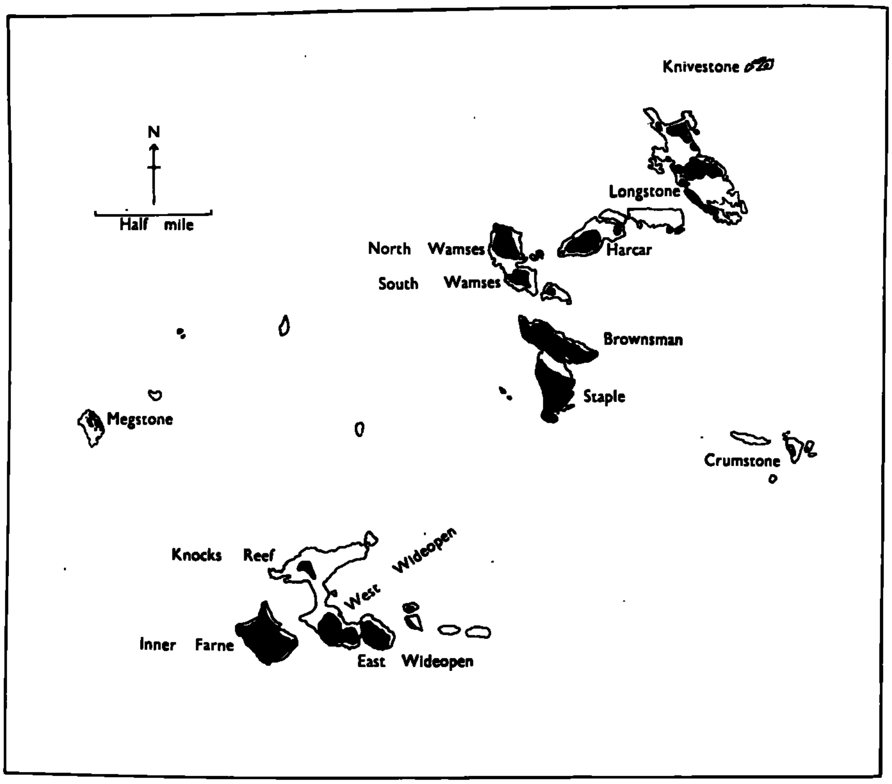
Three censuses of the nests and contents on the whole of Inner Farne were carried out so that comparisons could be made with the results obtained in the Study Area.

The nests within the Study Area were accessible without undue disturbance to other nesting species; and they could also be observed from the top of the tower (Fig. 3).

<u>History of the Eider on the Farnes.</u>

Protection of the Eider duck is by no means a modern development: the Eider having had periods of protection and molestation throughout its recorded history on the Farne Islands. The Eider is also known as St. Cuthbert's Duck, this is supposedly due, not only to the fact that it has long been associated with the Farnes on which St. Cuthbert lived, but also to the legend that St. Cuthbert gave the duck his blessing and forbade visitors to molest it in the breeding season (Watt 1951). St. Cuthbert's blessing has not always been observed. Not until the 19th Century references have any details of numbers been found. Numbers of Eiders on the Farnes decreased according to Selby (1833) but in 1857 he reported that due to protection the population had increased while Hancock (1874) stated that only small numbers of Eiders were nesting on the Farnes. Not until after Hancock's report did the observers begin to record a definite island as the favourite nesting place of the ducks. Up to 1874 the reports were couched in general terms: Wallis (1769) records that Eiders were breeding on the Inner Farne, but in 1887 Nelson stated that Brownsman was the most popular breeding site for the Eider and that there were no nests on the Inner Farne. Backhouse (1898) found that the Wideopens were the next 'centres' for the breeding population of Eiders. An increase in the population was also found, compared with Hancock's (1874) "several pairs breeding on the Farne Islands" and Nelsons (1887) "more than a dozen nests on the Brownsman". This increase in numbers continued and in 1924 the favourite nesting place was the Inner Farne where there were 100 nests. By 1932, due to careful protection there were between 200 or 300 nests there. Numbers increased generally on the Farne Islands according to Goddard (1946). During the war period, however, the Eider population suffered; eggs were taken, sitting ducks shot and ducks and ducklings used as targets for the machine guns at Seahouses. By 1945 there were few ducks around the Farnes but in 1946 there were 70 nests on the Inner Farne. In 1947 large areas of the Inner Farne were closed to visitors to further protect the breeding birds and in one period 1948-9 there were 210 nests, Watt (1949). In 1950, 200 nests

Fig. 2. The Farne Islands.



Knivestone
N
Half mile
Longstone
North Wamses
Harcar
South Wamses
Brownsman
Staple
Megstone
Crumstone
Knocks Reef
West Wideopen
Inner Farne
East Wideopen

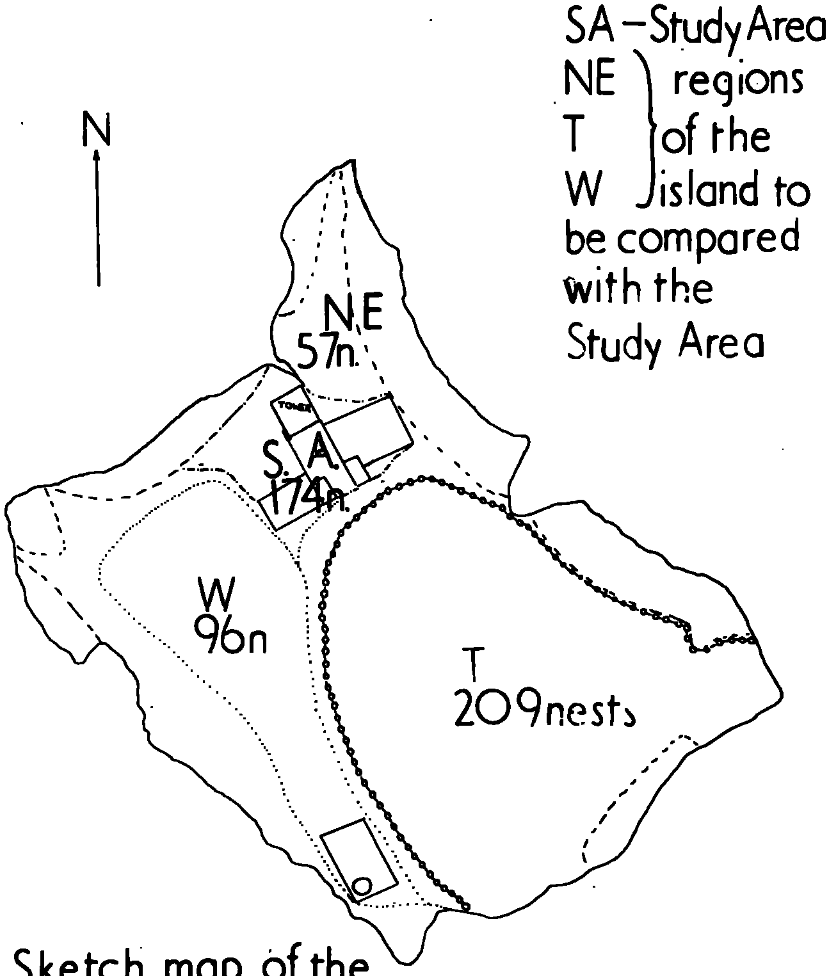


Fig 3 Sketch map of the Inner Farne

were recorded and in 1962, there were 536 nesting ducks on Inner Farne with about another 200 ducks on the remaining islands.

The Eiders on the Farnes have had a chequered history, their association has been a long one, yet at times they seem to have been very near to losing it. The future however with St. Cuthbert's blessing implemented by the present system of protection looks more promising than ever before.

Pre-Laying Behaviour.

At the start of the breeding season, in late April, large flocks of paired Eiders congregated in the sheltered water around the island and came ashore early every morning, just after dawn. The pairs "gaggling" incessantly, proceeded to choose the nesting sites. This choice was made by the female, the male squatting some distance from her while she made the scrape. He gaggled loudly all the time and drove off pairs that approached too closely. Many scrapes were made early in May but some of these were not made into nests until several weeks later. In making the nest, the female first made the scrape and only after a few visits did she settle down and complete the nest with material from the surrounding vegetation. This was formed into a circular nest about 10 inches in diameter. Down is not added immediately, and in most cases not until three or more eggs have been laid. Early nests were often robbed, presumably because there was insufficient camouflage for the eggs. The main predators were probably Herring Gulls, *Larus argentatus*, and Lesser Black-backed Gulls, *Larus fuscus.* If a nest was robbed on average it took 6-7 days before the bird relayed (Table 1). Not all the birds whose nests were robbed relayed. In the Study Area of 11 nests which were robbed 45.5 per cent of the ducks relayed. It should be noted however, that those nets which were robbed were situated on the exposed parts of the Study Area, with very little vegetation, or the eggs had no down over them.

Only occasionally were obvious old nesting sites used, i.e. those scrapes left from the previous nesting season and there seemed to be no special preference for them.

Table 1.

Data on robbing of nests and the time taken for relaying in the Study Area.

Number of eggs in the nest.	B.S.T.	Date of Robbing.	B.S.T.	Date of Relay.	Time lapse in days.
1	06.00	9 May.	21.00	10 May.	2
2	06.00	4 May.	21.00	6 May.	3
1	06.00	3 May.	21.00	7 May.	5
1	06.00	9 May.	21.00	15 May.	7
1	06.00	6 May.	21.00	20 May.	15

Average number of days for the duck to begin to relay is 6.4 ± 2.3

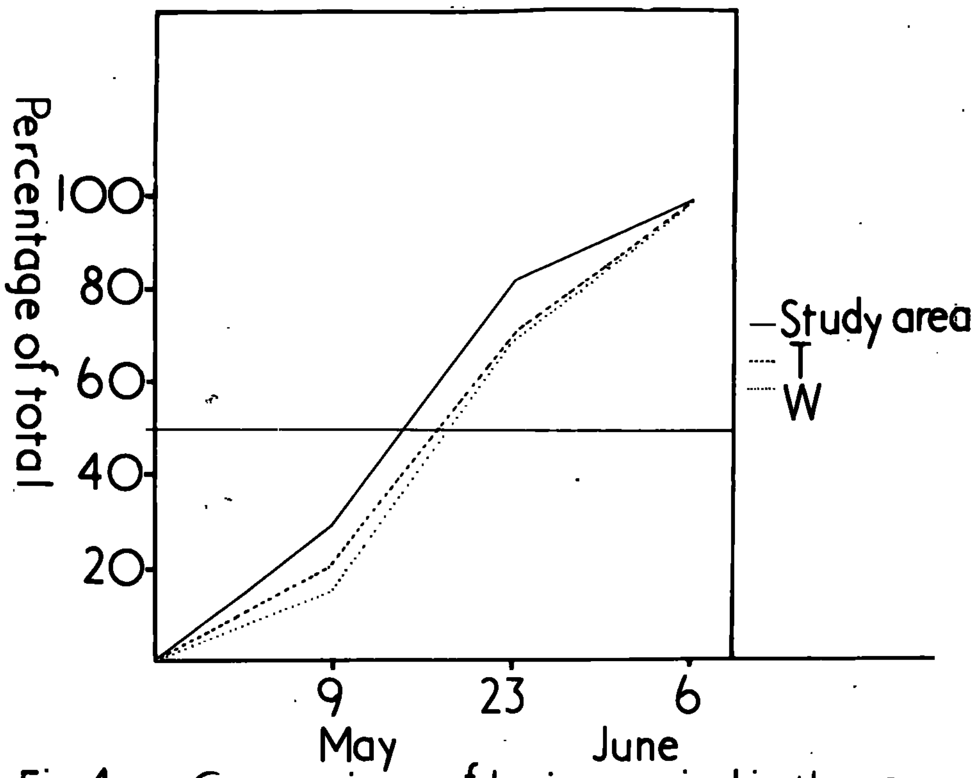


Fig 4 Comparison of laying period in three areas of the Inner Farne

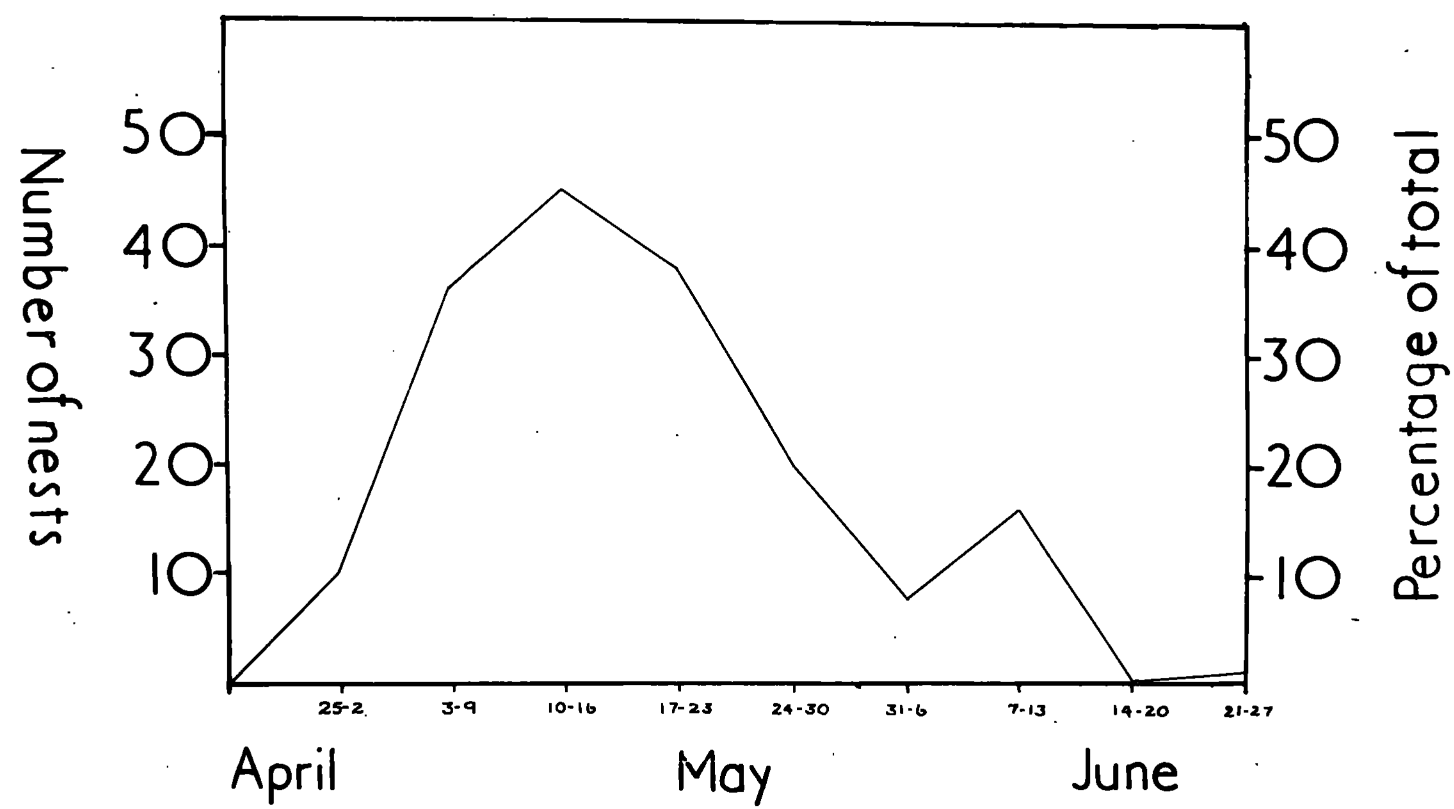


Fig 5 Nesting season in Study Area (174) nests

Breeding Season

The Eiders, males and females, congregated on the north and north eastern rocks of the island, and the parts of the island nearest to these rocks were used first as nesting sites, i.e. the Study Area. Only later did the birds move to the top of the island and then on to the rough open ground (Fig. 4). The first nest with 5 eggs was found on 26 April. The number of new nests with eggs found each day in the Study Area was recorded, and these have been grouped into weekly periods and the accumulative results plotted graphically (Fig. 5). The number of new nests per week increased until the week beginning 16 May and then decreased until 6 June, when a second small increase in laying occurred. This second peak may indicate a replacement clutch in some birds or young birds breeding late. It is unlikely that any of these late clutches could have been second clutches following successful hatching of the first, because those birds which did lay again (two birds) were, when known, identified as unsuccessful breeders of earlier in the season and no record of a bird laying a successful clutch a second time was found. Some Eiders are capable of laying more than one clutch (Belopolskii, 1957) but he does not indicate whether this applies only to birds which have been robbed of their first clutch. From personal observation, one bird made three attempts to lay in early May, deserting each incompleted clutch. Later on 20 June she was found sitting on three eggs but in a nest on the other side of the island. It is not known if all failed breeders made subsequent attempts to relay.

Laying Frequency and Time of Laying.

Eggs were not regularly laid at a particular time of day and they appeared in nests throughout the 24 hour period. However, on analysing the data on laying intervals (Fig. 6) it seems that there was a periodicity in the laying time of each individual duck, at about twelve hours or a multiple of twelve hours. The actual laying of the egg was observed on several occasions and took one and a half to two minutes to complete. At first glance the duck seemed to be looking round prior to take off, with the neck erect. On further investigation, however, the legs were seen to be braced against the ground and the abdomen raised. The egg appeared to be propelled along the oviduct by telescoping movements of the abdomen aided by the regular contraction of the pelvic and leg muscles. The egg appeared at the cloaca and it was only at this juncture that the abdomen was lowered and the egg rolled into the nest. The duck then either sat on the eggs or covered them over and flew off. The Eider egg is large in relation to the size of the female, about 100 ccs. and it was surprising to find that many were laying more than one egg in 24 hours. Some birds were found to have laid as many as three eggs within 24 hours. This could be attributed to parasitation of one bird by another, or of stealing eggs from the nest by neighbouring ducks, but it must be remembered that every egg and every bird

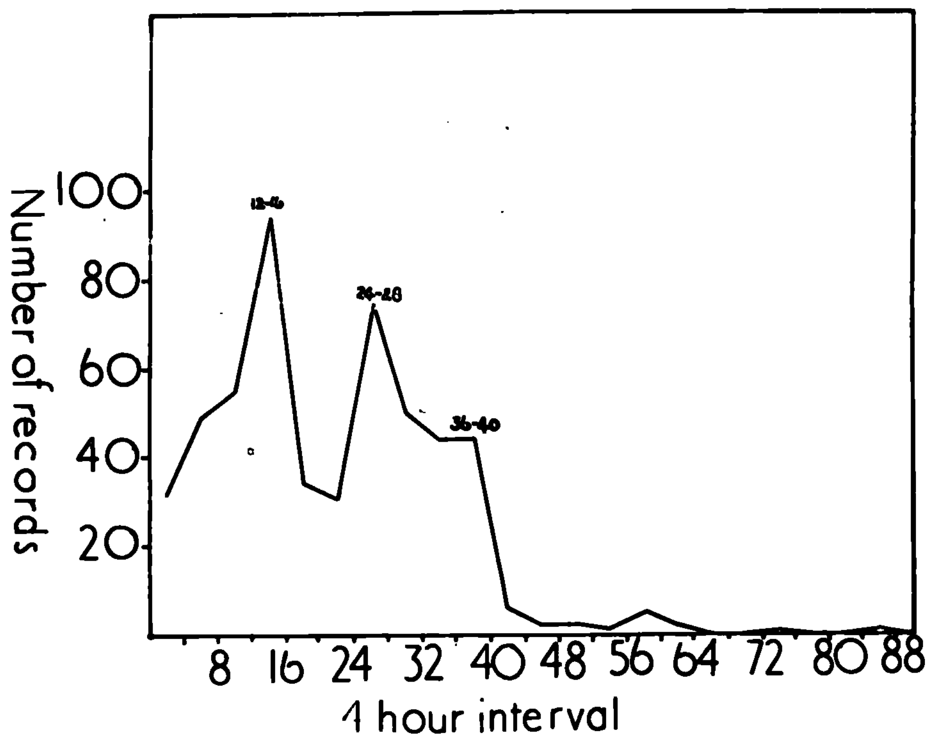


Fig 6 Frequency distribution of laying intervals grouped every four hours

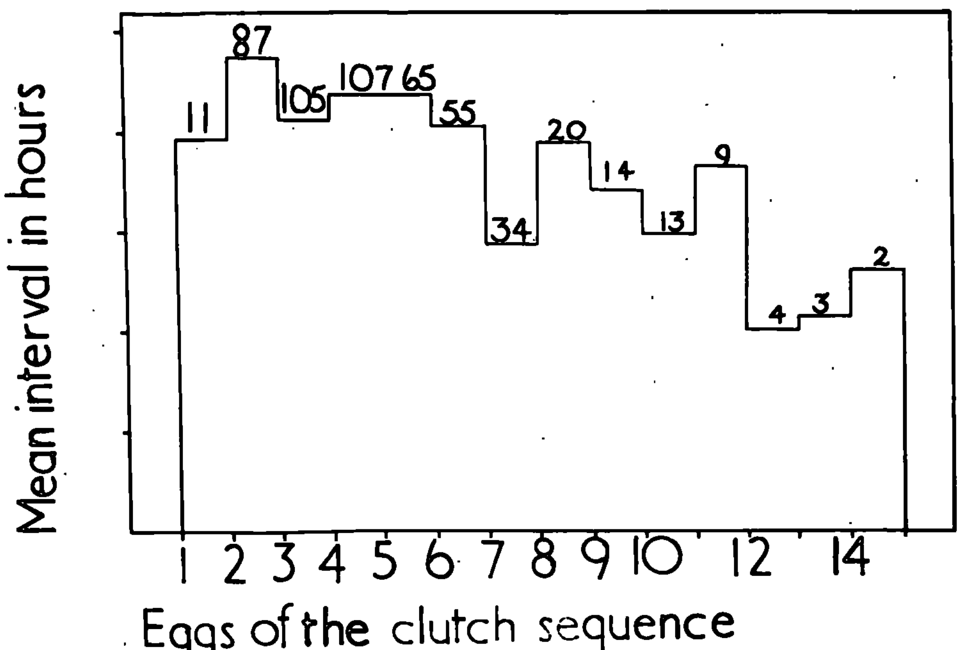


Fig 7. Laying interval between eggs in the clutch sequence.
(Numbers of instances are shown on the histogram.)

in the Study Area was marked, and although stealing, 13 per cent, or parasitation, 16 per cent, was the cause in some cases, in many others 71 per cent, it was not. By visits to the nests at regular intervals, or by almost continuous observation from the tower, it was shown that the same bird sat throughout the day and laid all the eggs found in the nest. If another bird had been laying in the nest it would have been seen, at least in the vicinity of the nest.

Within a clutch it seemed that as the number of eggs increased the interval between laying eggs decreased (Fig. 7) but it was equally possible that this was the result of the time interval between eggs, being shorter in larger clutches, than in smaller ones.

To test the latter possibility a scatter diagram was prepared showing the relationship between clutch size and the average interval between successive eggs. As can be seen from Fig. 8 and Table 2 there is a suggestion that large clutches are produced by ducks laying eggs at shorter intervals.

Table 2.

The relationship between clutch size and the interval between eggs.

	Clutch size.						
	3	4	5	6	7	8	over 8
Number of observations.	6	4	38	18	22	11	16
Average interval between eggs (hrs.)	34.7	33.3	26.1	26.5	21.7	15.8	17.4
Average time to complete clutch after laying the first egg. (hrs.)	104.1	133.2	130.5	159.0	151.9	126.4	191.4

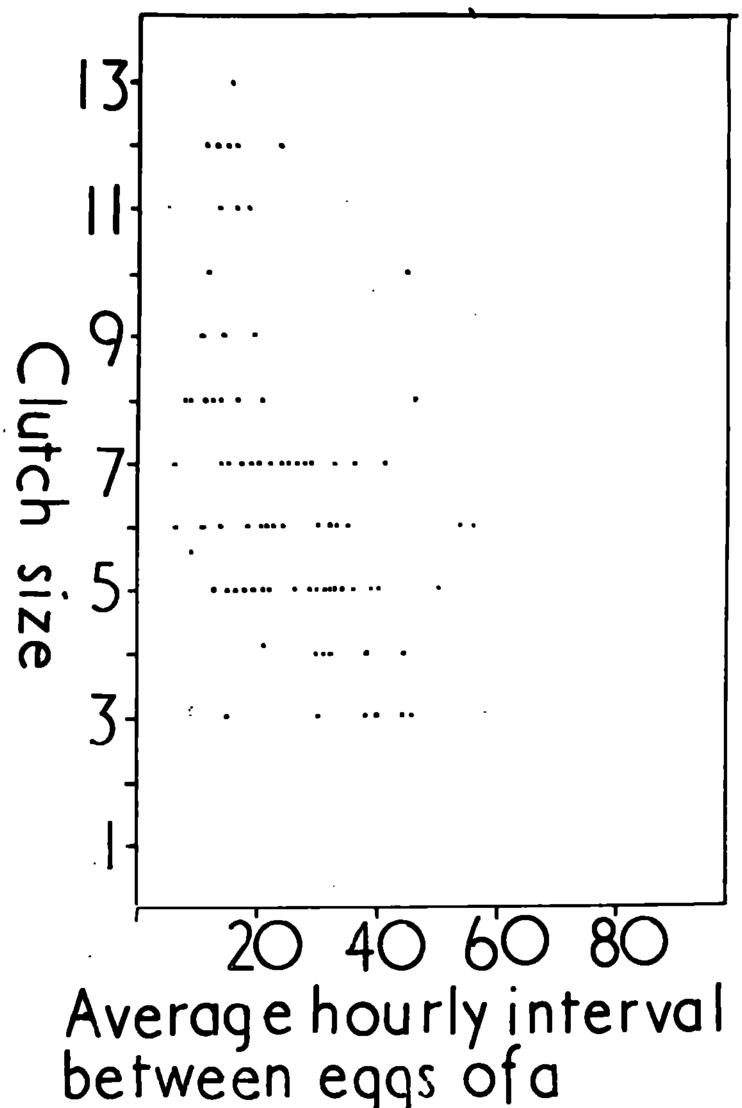


Fig 8 Scatter diagram showing the relationship between clutch size and average interval between successive eggs

Table 3.

Comparison of clutch size of the Eider in different regions in the Northern Hemisphere.

Authority.	Place.	Clutch size.
Millais	Britain	4 - 5
Lewis	America	4·04
Paynter	Kent Island U.S.A.	3·53 ± ·09
Belopolskii	White and Barents Sea	3·13 - 4·69
Kenyon	Alaska	3·7

Table 4.

Clutch size frequency of the Eider duck on the Inner Farne, 1962.

Clutch size	Number of nests.	Percentage of total.
1	6	1.1
2	26	5.0
3	62	11.8
4	127	24.2
5	142	27.1
6	75	14.3
7	35	6.7
8	23	4.4
9	6	1.1
10	5	1.0
11	6	1.1
12	6	1.1
13	1	0.2
14	1	0.2
15	3	0.6
16	1	0.2
TOTAL	525	100.1

Average clutch size = 5.09 ± .09

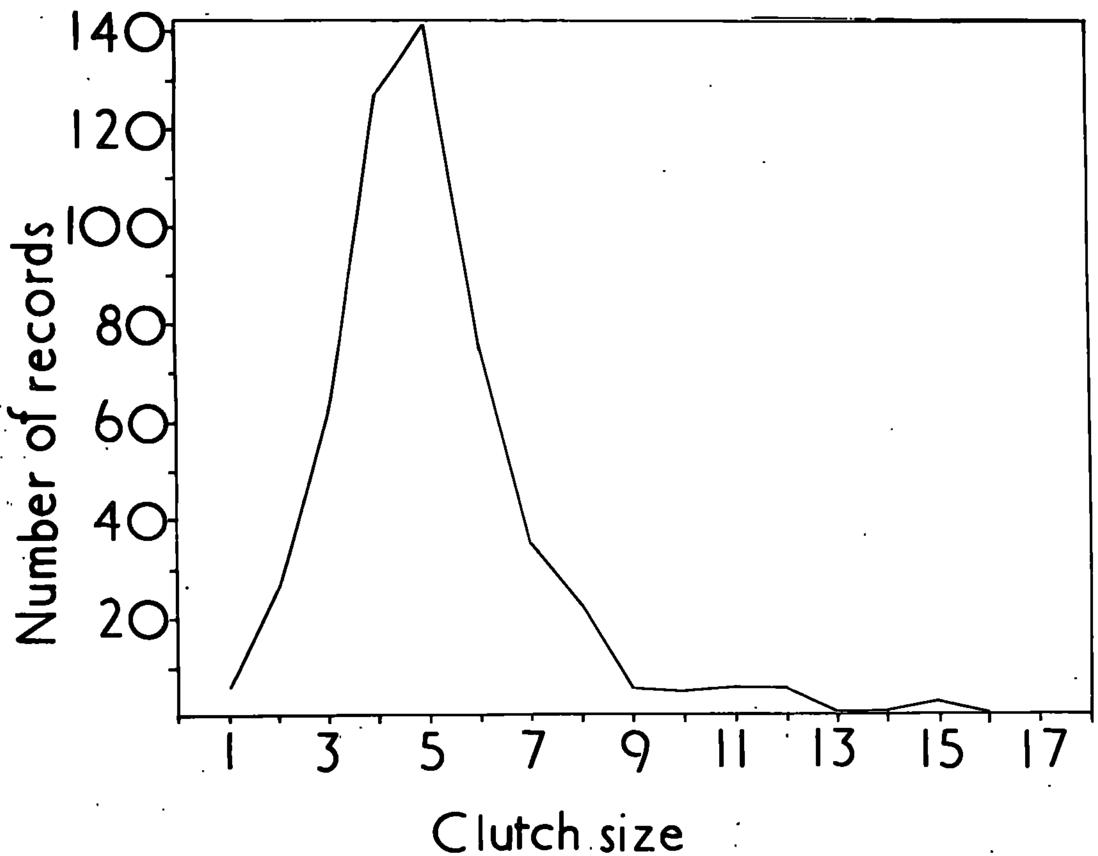


Fig9 Clutch size frequency for the Inner Farne

Clutch size.

The clutch size of the Eider varies geographically (Table 3). The average clutch size for the Inner Farne was 5·09 ± ·09 (Table 4) but the distribution is positively skewed (Fig. 9) with clutches at all sizes between one and sixteen eggs. The clutch size had a seasonal trend as shown in Fig. 10 in weekly periods. The clutch size started at a maximum of over 7 eggs per nest after which it progressively declined for the rest of the season, ending with a mean of 4 eggs per nest.

Coulson (1960) has remarked that many single brooded birds have a seasonal trend in clutch size which starts off at a maximum and progressively decreases as the breeding season advances. However, Lewis (1939) and Belopolskii (1957) suggest that in the Eider the clutch size starts low, gradually increases to a maximum and then declines as the breeding season progresses.

A complete census was made of all nests on the Inner Farne on three occasions to ensure that all completed clutches were recorded and these have been grouped by area viz. (see Fig. 3).

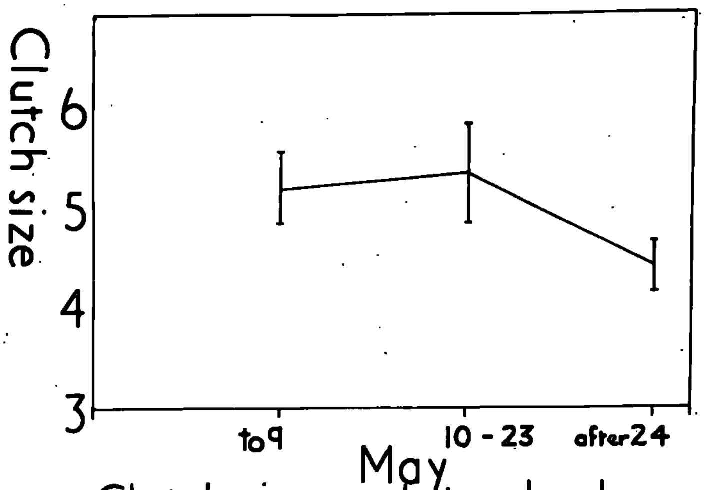
1. the Study Area.
2. Area T.
3. Area N.E.
4. Area W.

These areas have different vegetation types:

1. Short grass with nettles, Urtica sp. in clumps.
2. Mainly tall Dock, Rumex sp. and nettles.
3. Tall nettles with Sea Campion, Silene sp. and dock.
4. Rough pasture.

The size of clutches completed before each of these visits is given in Table 5. Only in the Study and NE areas (the latter really being an extension of the Study Area) was there a pronounced seasonal change in clutch size. The persistently higher clutch size of the Study Area as compared to the other areas is of interest as this exhibits a correlation with the average density of nests. This is discussed later. (see Table 5). It should also be noted that there is also a correlation between the seasonal change in the clutch size and density.

Although the average clutch size, is 5.09 for the Inner Farne, large clutches, exceeding 8 eggs were found to make up more than 5 per cent of the total. Belopolskii (1957) suggested that large clutches in the White and Barents Sea region, were caused by more than one bird laying in the same nest, stealing eggs, or, a different bird laying in a deserted nest. On the Farne where clutches of 14, 15 and 16 eggs were found, it was sometimes due to two birds laying in the same nest, indeed, two birds were



Clutch size and standard error for the Inner Farne

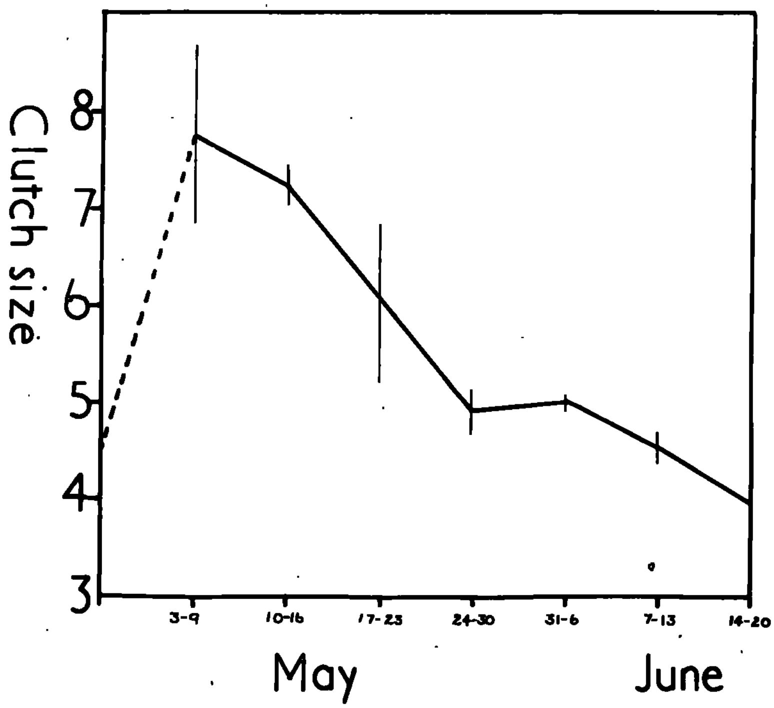


Fig 10 Clutch size and standard error of Eider ducks on the Study Area of the Inner Farne

actually found sitting side by side on one large nest with eight eggs in it. By marking each egg it was found that ducks nesting less than two feet apart, regularly interchanged eggs, as many as five eggs being taken from one nest and transferred to the nest of the other. Two eggs were taken from the nest on the 9 May, two on the 10 May and one on the 12 May. As the Eider drives off any birds that approach too closely to the nest, this interchanging of eggs is further evidence (see page 12) that the ducks leave their nests during incubation, and it is at such times that the stealing takes place. On only two occasions did birds lay in deserted nests. However, in early June, when several clutches had hatched off, these old nests were quickly taken over by late nesting birds.

From these results it seems that no one cause can be attributed to these large clutches. Evidence has been given for parasitation, stealing and laying on deserted clutches, and there is also the possibility that the same bird may be capable of laying as many as ten eggs. Therefore it is suggested that in most cases large clutches are due to one bird producing all the eggs. (Table 6).

Table 5

Comparison of the clutch size of the Eider within four areas of the island and the average density of nests and percentage of nests containing more than six eggs.

Laying period.	Study Area.	NE.	T.	W.
A Before 9 May	7.45	5.61	4.36	4.31
B 9-23 May	6.58	5.42	4.96	4.11
C After 24 May	4.97	4.03	4.64	4.24
Average clutch size.	6.35	5.02	4.65	4.22
Average change in clutch size A-C	-2.52	-1.58	+0.28	-0.07
Average nest density per acre.	87	57	23	22
Percentage of clutches over six.	45.7	31.5	25.2	10.0

Therefore it would appear that there is a correlation between nest density and clutch size, the greatest number of large clutches being found in the most densely populated areas.

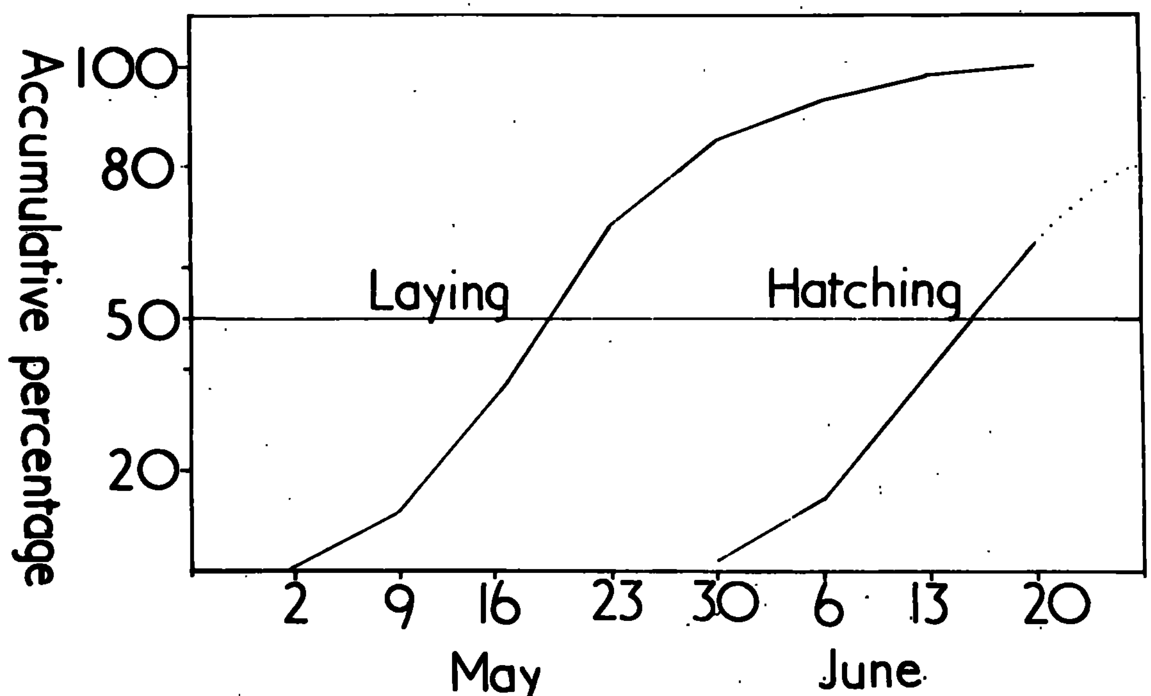


Fig 11 Incubation period: at the 50% level the difference between laying & hatching

Table 6.

The causes of large clutches (over 8) in the Study Area.

	Stealing	Parasitation by other Ducks.	Laying on deserted clutch.	Same bird laying all the time.
Number of instances	5	6	2	27
Percentage of total.	12.5	15.0	5.0	67.5

(Total of 40 clutches).

Incubation Period.

Millais (1913), Witherby et al (1938) and Rolnik (1943) state that the incubation period of the Eider is 28 days. Belopolskii (1957) found that his birds incubated eggs between 22 and 26 days. He also claimed that the incubation period varied with clutch size, being shorter for small clutches, of four or less. Because continuous observations were made only on the Study Area nests, this data alone has been used in the calculations of the incubation period. The mean incubation period for all clutches was found to be 28.5 ± 1.8 days. The incubation periods for small and large clutches were also calculated and compared. For small clutches, four eggs or less, the mean was 28.50 ± .14 days, for large clutches, four or larger, the mean was 28.48 ± .32 days the very small difference is not significant. A frequency distribution of the incubation period has been produced (Table 7) and the most frequent records appear at 28 and 29 days. Another measure of the incubation period can be obtained by plotting a graph of accumulative laying and accumulative hatching against time (Fig. 11). This difference at the 50 per cent level between these values suggests that the average incubation period was about 28 days. As most eggs hatch within a few hours of each other, a difference in incubation period between large and small clutches is hardly to be expected unless incubation starts before the completion of large clutches. Observations suggest that the Eider incubates continually only when the clutch is complete, and therefore, a clutch of three should take the same time to hatch from the completion of the clutch as one of five.

When Eiders are incubating, they sit for long periods but regularly leave their nests for about ten minutes, at least once a day, to drink at one of the brackish or fresh water pools. Belopolskii (1957) states that his ducks never fed during the incubation period and this was proved by the collapsed condition of the gut and complete dehelminthisation at the end of the incubation period. Gross (1944) working on the Eider in America, claimed that his ducks regularly left their nests to feed. The Farne birds left their nests about once a day to feed (in addition to drinking) during the first fortnight of incubation but, as hatching time approached, they appeared to sit tight and rarely left their nests. As the Russian birds did not leave their nests, it may be that this intense incubation is an adaptation to overcome extreme Arctic conditions. When the Eiders were disturbed they often defaecated over the eggs and this took place even toward the end of the incubation period therefore this suggests that the Farne birds were feeding.

During incubation, the eggs were turned regularly, every 20 or 30 minutes. If an egg was accidently broken, the duck picked it up in its bill, flew off and dropped it some distance from the nest.

Table 7.

Incubation Period of Eiders on the Inner Farne: Frequency Distribution.

Number of Days	Number of Birds.	Percentage.
23	1	2.0
24	0	0.0
25	0	0.0
26	3	5.9
27	9	17.7
28	13	25.5
29	13	25.5
30	9	17.7
31	1	2.0
32	0	0.0
33	2	3.9
Total	51	
Average	28.47 $\pm$ 1.82 (S.D.) days	

Desertion.

In the densely populated parts of the Inner Farne, when a duck hatched its eggs, it seemed to induce others in the vicinity to desert their nests. These ducks usually left their nests for short periods at first, then the absences became longer until finally they did not return at all. The majority of these birds deserted within the first week after completion of the clutch. It is interesting to note that most of the birds covered their eggs with down before leaving them for the last time.

Hatching.

When the ducklings hatched they remained in the nest for about 24 hours. They were usually taken down to the water in the early morning or evening. Instead of the ducklings being taken directly into the sea, the ducks usually led them to the large brackish pools that had formed on the rocks above high water mark. Here, they swam about, feeding on the algal growths of these pools. Consequently, large rafts of mothers and ducklings were formed. During the morning the ducklings were taken down to the sea and usually had started their journey to the mainland by late morning or early afternoon,

Hatching Success.

Although insufficient data were collected to give an accurate value for the hatching success on the Inner Farne in 1962, an estimate has been calculated. (Table 8).

The hatching success is very low but this may be due to the fact that the investigation was terminated before all the clutches had been incubated.

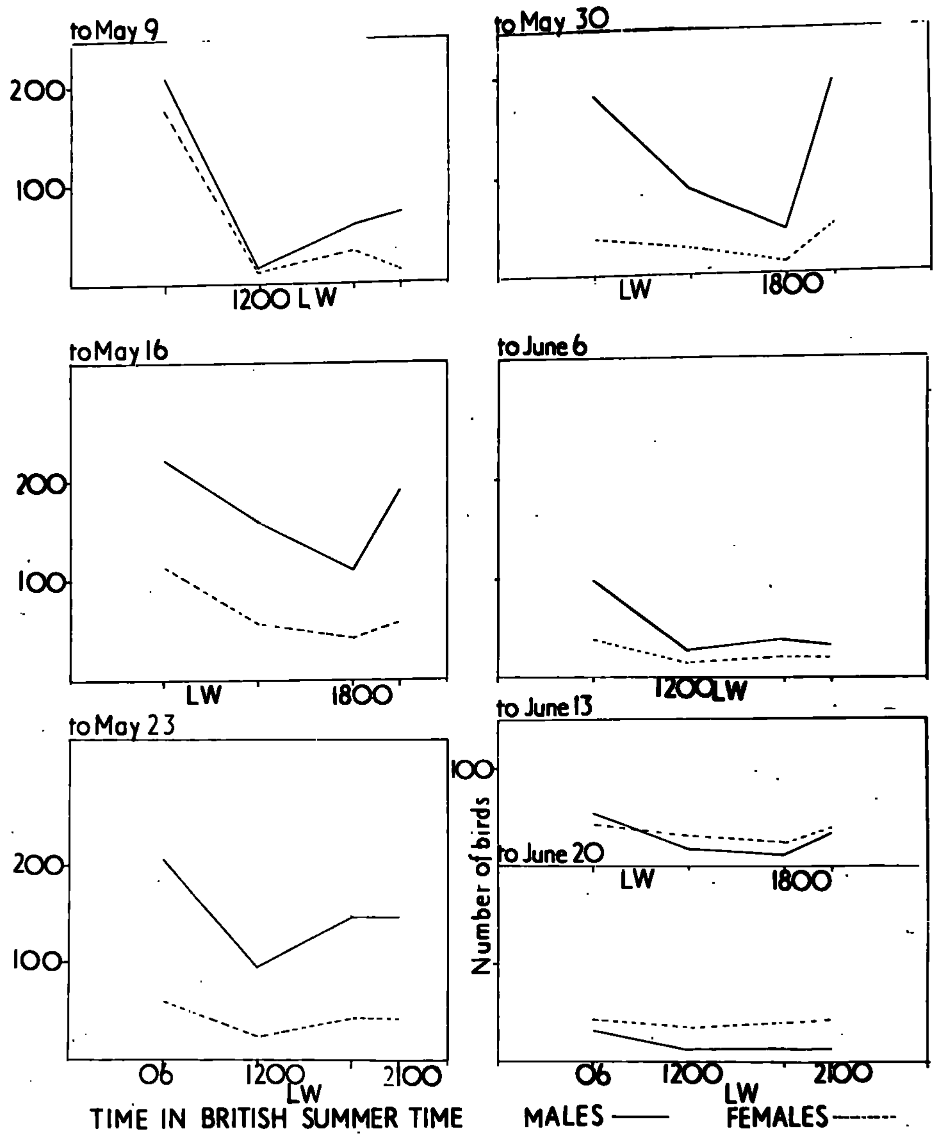
The Eider ducks seem to have evolved a "social system", in that those which are non-breeding birds, or those which have lost their own ducklings, often return to the Island as "aunties". The aunties help protect the duck with her brood. In recent years the Eiders of the Farne have been intensively ringed. Very few of these aunties are ringed, (no more than 10 per cent) so it would appear that the majority of the aunties are young birds. Only in the last two years have ducklings been ringed. Late in the season several aunties were recognised as birds which had successfully reared ducklings and they must therefore, have lost them, probably by predation by gulls.

Table 8.

A comparison of the four areas of the island for hatching success.

	% successful nests.	% eggs which hatch.
Study Area	31	28.1
T	19.9	15.8
W	17.6	18.0
NE	15.8	16.7
Whole Island	22.7	20.9

Fig. 12. Daily counts of the Eider on and around the Inner Farne, grouped into weekly periods and showing a tidal rhythm.



to May 9
200
100
1200 LW
to May 30
LW
1800
to May 16
200
100
LW
1800
to June 6
1200 LW
to May 23
200
100
06
1200
LW
2100
to June 13
100
Number of birds
to June 20
LW
1800
06
1200
LW
2100
TIME IN BRITISH SUMMER TIME
MALES ——
FEMALES --------

Activity

Throughout the study period, counts were made four times daily of the numbers of males, females, immatures and later ducklings. These counts show the tidal rhythm and the gradual change in the sex-ratio of birds present throughout the breeding season. Nesting birds were not counted, primarily because the majority of them, outside the Study Area were virtually invisible from the top of the tower, and in any case, only a few were off their nests at the time the counts were made.

The largest numbers of Eiders could be seen around the Inner Farne early in the morning and a similar, though less pronounced, increase in numbers occurred late in the evening. The morning peak was usually the time that pairs visited the nest site, while the evening peak was probably the accumulation of birds ready for the early morning movement ashore.

Tidal Rhythm.

By splitting the counts into alternate weekly periods so that the state of the tide is similar in each group and graphing the numbers, (Fig. 12), it will be seen that there is evidence of a tidal rhythm in addition to the diurnal rhythm. Most birds leave the vicinity of the Inner Farne in order to feed near the mainland, on the ebb tide. Thus in Fig. 12, the low tide is during the afternoon on the graphs at the left side, and during the morning and late evening on those on the right side.

Sex-Ratio.

It will be seen, Fig. 13, that most of the females began incubating on or after 16 May. The number of males began to decline after this date, presumably because the breeding urge began to decrease. The movements of the males and females are discussed later. By the time the majority of eggs were hatching (mid June) there were very few drakes around the Island.

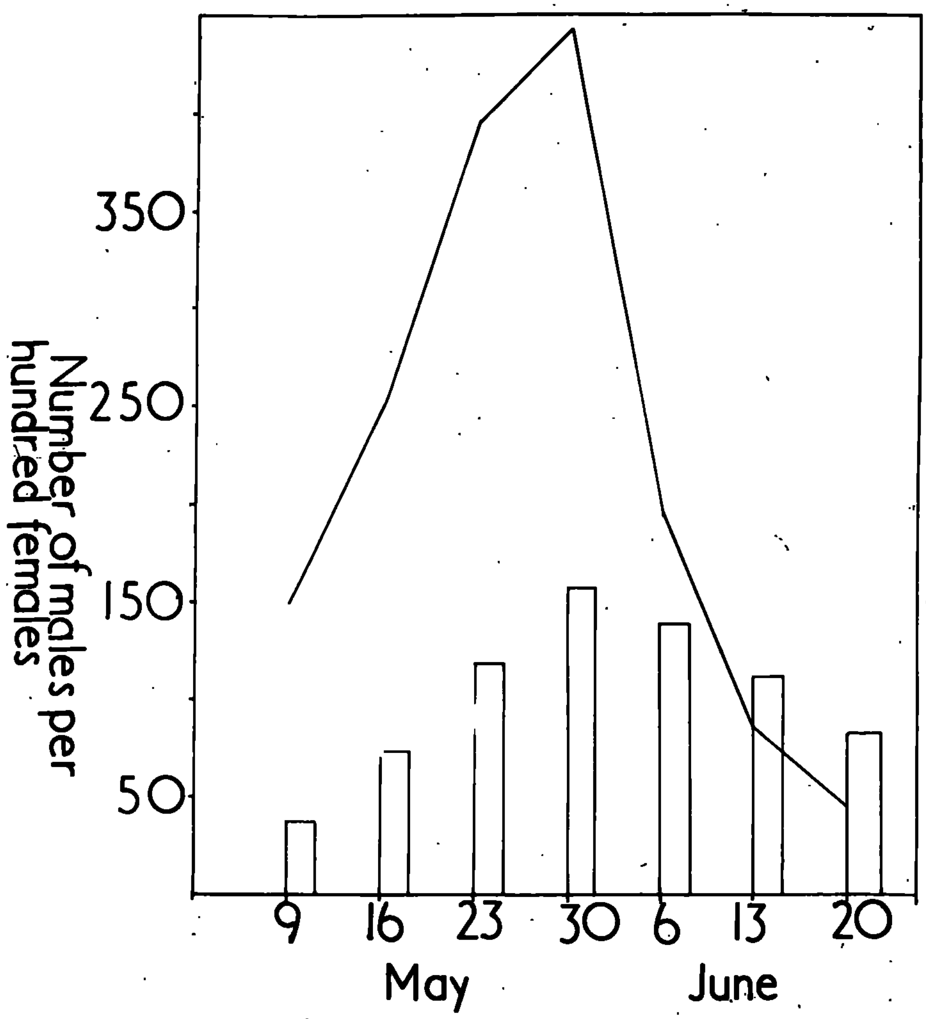


Fig 13 Number of males per hundred non laying females is shown as a straight line graph. The histograms represent the numbers of sitting females.

PART B.

DISTRIBUTION AND MOVEMENTS OF EIDERS.

Introduction.

The movements of the Eider in northern latitudes seem to be governed primarily by weather conditions. In countries near the northern limit of the Eider's breeding range e.g. Spitzbergen, the birds do not stay in the breeding areas throughout the year. This has been attributed to the effects of Polar Ice; the birds moving away from the breeding grounds to avoid being trapped by the ice, (Myers pers. comm.). When the ice recedes, the Eiders return to breed. In the Baltic, where much of the water freezes in winter, the birds also move south in that season. In the North Sea, around the British Isles there is no necessity for such a seasonal movement and the birds were considered to be sedentary, (Witherby et al., 1938), until Taverner (1959) suggested that there was a certain amount of movement within the species. He envisaged the Eider as an expanding species with dispersal points such as the Farne Islands and Holland contributing to the increased numbers on the east, south-east and south coasts of England. The main dispersive units were thought to be immature birds.

Belopolskii (1957), working in the Seven Islands and Merman region of Russia, noted that while many female Eiders remained with their young in the breeding areas, mass departures of drakes were observed all flying in a SE direction. The few drakes that remained began to moult, and he suggested therefore, that the drakes were congregating elsewhere to moult. Coombes (1949, 1950) working on the Shelduck Tadorna tadorna in Morecambe Bay, observed that they disappeared in late summer and on further investigation he found that they were flying across England and proceeding to the Baltic Sea, where they assembled in large numbers to moult.

As long ago as 1923, Evans reported large flocks of Eider on the Firth of Forth. From ringing recoveries in recent years it would appear that some Farne birds move to the Firth of Forth (Fig. 14). Few birds actually breed in the Firth of Forth area (Baxter and Rintoul, 1953), and so it would appear that the large flocks of Eider found in late summer, represent a movement of birds from other areas, possibly from the Scottish and Northumberland coasts. It is likely that it is a moult migration similar to that of the Shelduck but on a smaller scale.

Estimated Breeding Population from the Firth of Forth to South Northumberland.

Based on published records, nest record cards and personal observations, the size of the breeding population (given as breeding females) is as follows.

		BREEDING FEMALES.
1.	Coquet Island, Northumberland.	220
2.	Dunstanburgh and Newton.	10
3.	Farnes, Inner Farne	550
	Other Islands	150
4.	Holy Island and Ross Links.	30
5.	Dunbar area, East Lothian.	50
6.	South Firth of Forth Islands and coast.	40
7.	Inchkeith.	20
8.	Isle of May	50
N.B.	No Eiders nest in Berwickshire.	
	Total	1120

The sex-ratio is about equal so this suggests that there are about 2,200 breeding birds with an additional number of immature birds. Of these, only 240 breeding birds nest in SE Scotland; the great majority nesting in Northumberland. There are no Eiders breeding in E. England, south of Coquet Island.

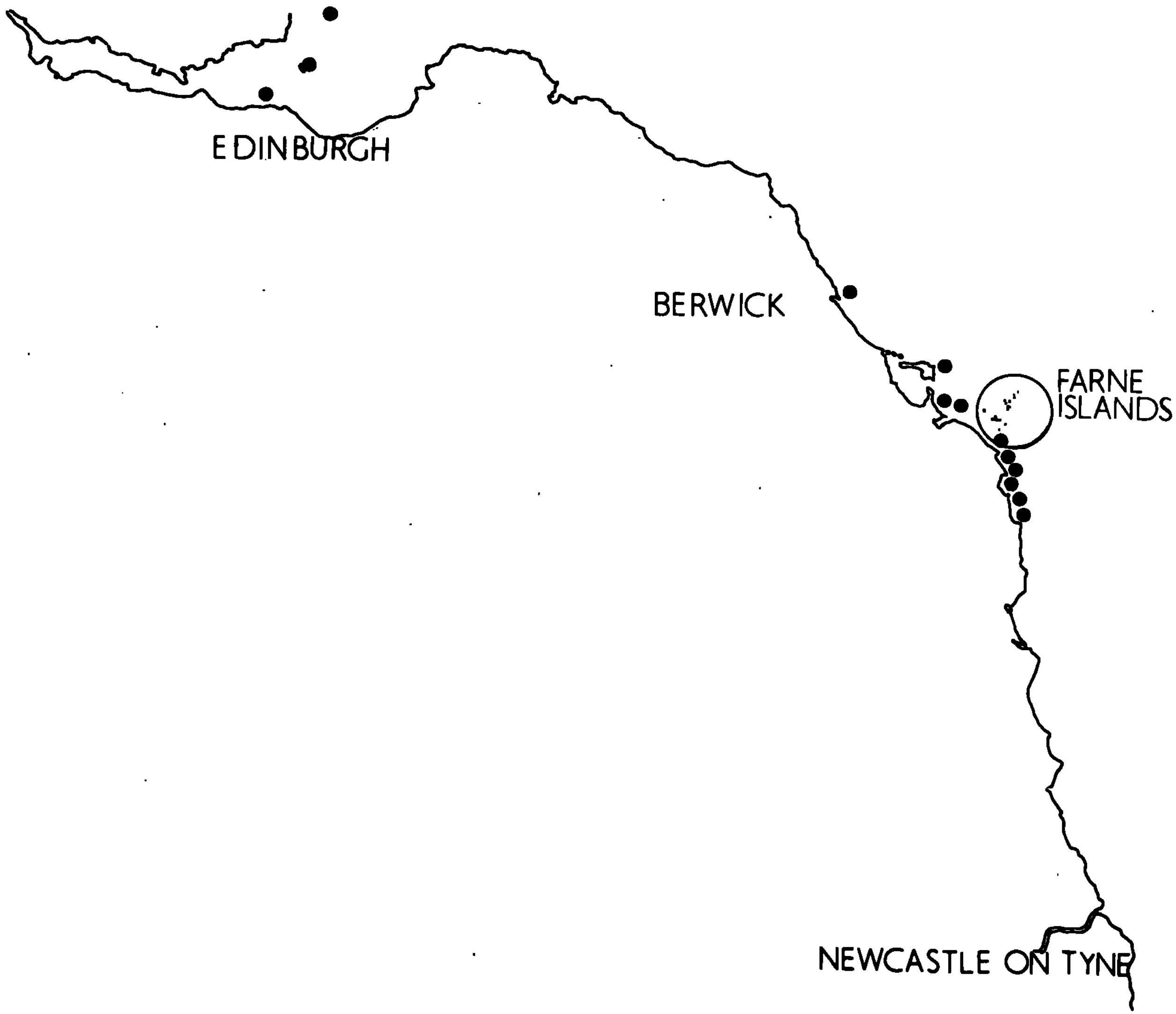
Method.

Counts were made at monthly intervals of the number of Eiders along the Northumberland, Berwickshire, East Lothian and Midlothian coasts, from the Tyne to Edinburgh. It was impossible to survey the whole of this coastline in the time available but it is estimated that by using a Land Rover 80 per cent of this coast was examined and over 90 per cent of the favoured areas were covered regularly. The Eider is essentially a coastal bird and is rarely seen out of sight of the coast.

For convenience of analysis, the coastline was divided into six sections as follows, (Fig. 1).

1. Section A Edinburgh to Dunbar (120 breeding pairs)
2. Section B Dunbar to Berwick (none breeding)
3. Section C Berwick to Budle Bay (30 breeding pairs)

Fig. 14. Recoveries of adult female Eiders outside the breeding season.


EDINBURGH
BERWICK
FARNE ISLANDS
NEWCASTLE ON TYNE

4. Section D Budle Bay to Craster (700 breeding pairs)
5. Section E Craster to Amble (220 breeding pairs)
6. Section F Amble to Tynemouth (none breeding)

From examination of recent Ornithological Reports for County Durham and Yorkshire, it is clear that the Eider is a rare bird in these counties at all times of the year and it is unlikely that an appreciable proportion of the Northumberland breeding population move south of Northumberland. There is only one ringing recovery south of Northumberland, and that only three miles south of the River Tyne.

Local Distribution.

The Eiders obtain their food by diving, finding most of it at depths up to 20 feet. The main food items are Molluscs (51 per cent) and Crustacea (24 per cent), (Witherby et al. (1938). Madsen (1954) recorded mollusca as forming 82 per cent of the Eiders' food in the Baltic area of Denmark. It would appear that mussels, Mytilus edulis, and shore crabs, particularly Carcinus maenas, are the main food animals and these are restricted to rocky areas on the coast. This agrees closely with the distribution of the Eider, which occurred almost exclusively on the parts of the coast which were rocky or where rocky outcrops appeared on a sandy coast.

Distribution and Movements.

The results of twelve monthly counts have been analysed and the data presented in Fig. 15 where the distribution has been expressed as a percentage of the total for the count. The counts started in July 1961 and finished in June 1962. From the known distribution of breeding birds, it might be expected that about 11 per cent of the total birds would occur in Scotland. This agrees with the proportions found between September and April, off the Scottish coast (varying between 30 and 10 per cent).

The distribution was considerably different between June and August, when about half the birds found were in Scotland. This corresponded to a comparable decrease in the absolute number of Eiders found in Northumberland, and it seemed most likely that some of the Farne Islands breeding population had moved into the Firth of Forth area. Similarly there was a return to Northumberland in the early autumn and a decrease in the numbers in the Firth of Forth.

From an examination of the sex-ratios (Fig. 16), this large increase in the Firth of Forth is due mainly to the presence of many drakes. While there is a suggestion of an increase in the number of females in

Fig. 15. Percentage distribution of the Eider along the coasts of Northumberland, Berwickshire, East Lothian and Mid-Lothian between July 1961 and June 1962.

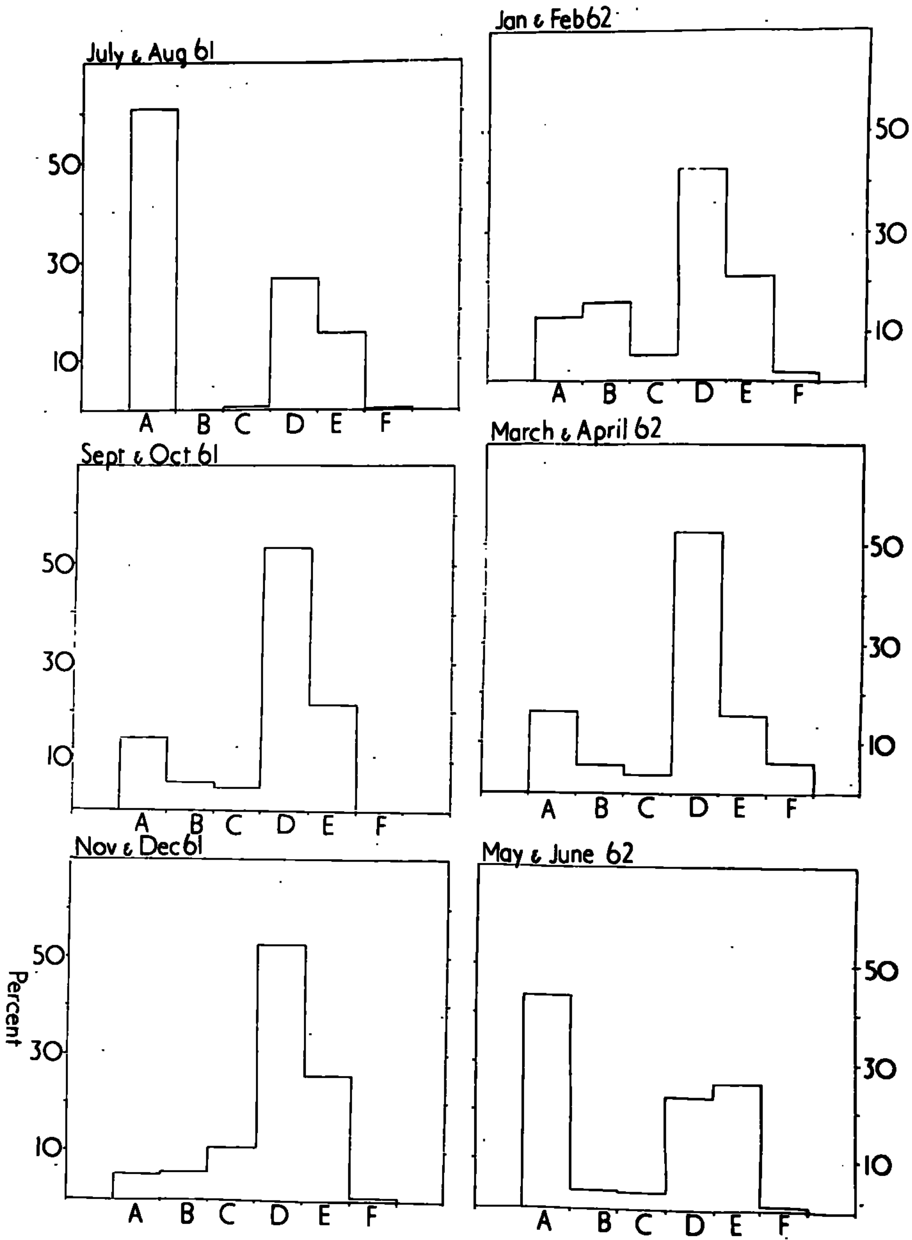
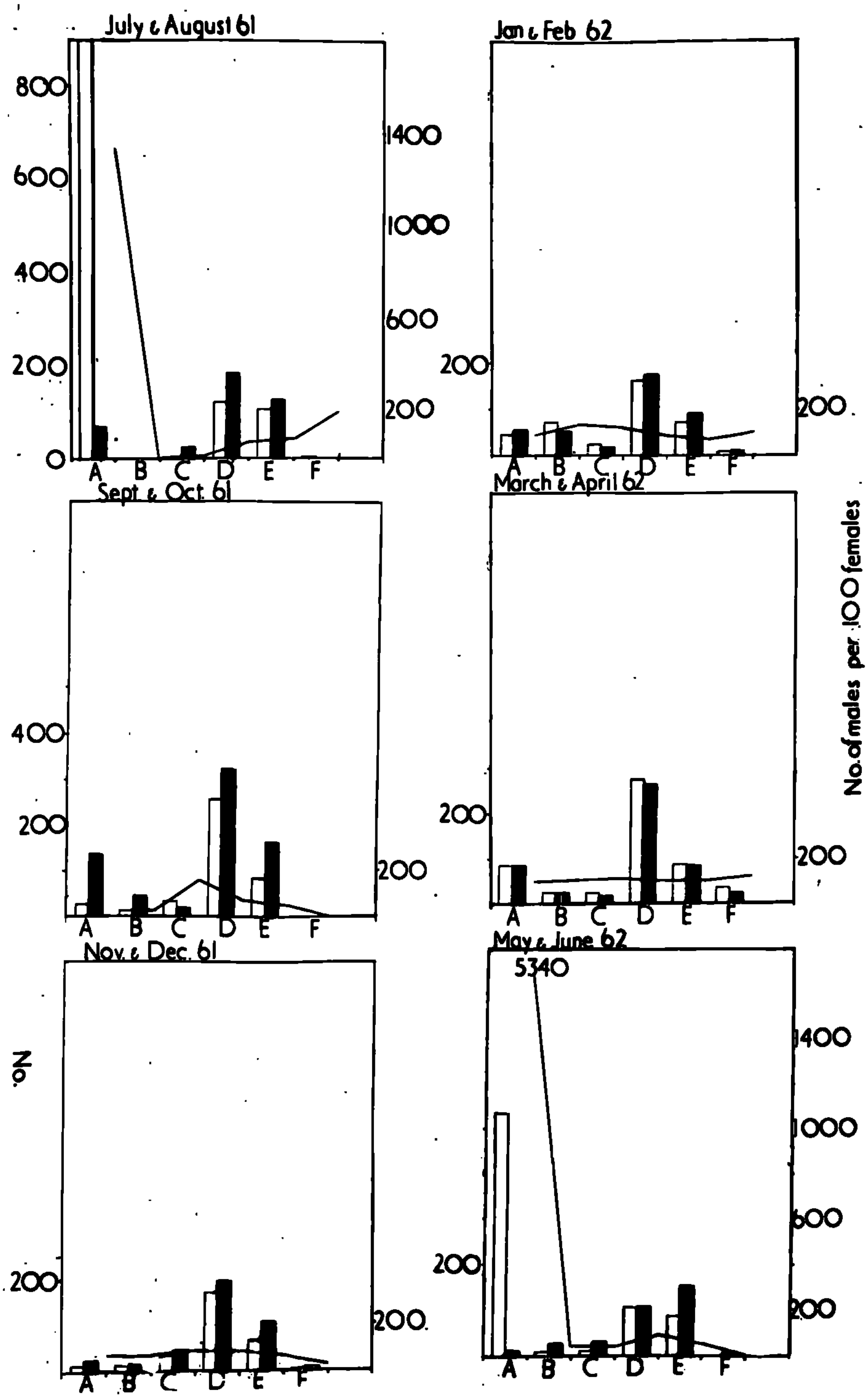

July & Aug 61
Jan & Feb 62
Sept & Oct 61
March & April 62
Nov & Dec 61
May & June 62
Percent
10
30
50
A B C D E F

Fig. 16. Sex Ratio of the Eider along the coasts of Northumberland, Berwickshire, East Lothian and Mid Lothian from July 1961 to June 1962. The sex ratio is shown as histograms, the number of males per hundred females is shown as straight line graphs. (Number of females shown black on the histograms.)


July & August 61
Sept & Oct 61
Nov & Dec 61
Jan & Feb 62
March & April 62
May & June 62
5340
No.
No. of males per 100 females
A B C D E F
0
200
400
600
800
1000
1400

September and October, it appears that the ducks do not enter into this movement to such an appreciable extent. Thus the data suggests that over 80 per cent of the drakes from the Northumberland breeding areas move to the Firth of Forth at the end of the mating season in May and June. This is almost certainly a moult migration since the drakes are flightless during the greater part of the time they are in the Firth of Forth. This area provides an ideal feeding ground, since there are extensive beds of Mytilus edulis in the area and the birds are protected from bad weather. This area is also used by large flocks of Red-breasted Merganser, Mergus serrator, and the Common Scoter, Melanitta nigra, again probably as a moulting area.

This moult movement differs from that reported by Freuchen and Salomonsen (1959) in the King Eider, Somateria spectabilis, in Canada and Greenland. The migration in this species involves a much greater movement but it is similar in that mainly the drakes are concerned.

Proportion of First Year Birds.

The proportion of first year birds in the population, after the initially high mortality in the first few months of life, gives an indication of the adult mortality rate. The proportions were recorded on counts from January to April as it was impossible to separate these birds until the adults had completed the moult.

It is more difficult to separate first year females from adult females than in the case of the males. Nevertheless, the low proportion suggests that the adult mortality is also low, but further information is needed since it is necessary to avoid annual fluctuations in the reproductive success. (Table 9).

The sex ratio is approximately 1:1 and this suggests that both sexes have an equal chance of survival. From an examination of ringing recoveries it would appear that the Eider ducks are long lived and therefore a low breeding success is to be expected if the population is not to increase out of all proportion.

Table 9.

The Proportion of First Year Birds.

	Males	Females	Immatures
January-April	903	896	42

Therefore the percentage of first year birds to adults is 2.33 per cent.

PART C.

MORTALITY RATES OF BLACK-HEADED GULLS AND GANNETS.

Introduction.

Certain aspects of avian populations can be examined by using ringing recoveries. Early studies were made by Kendeigh (1937) on the House Wren, *Troglodytes aedon*, and Nice (1937) on the Song Sparrow, *Melospiza melodia*. Lack (1943, 1946) has been a more recent worker in this particular field and has made a major contribution, analysing data for several species, including that for the Black-headed Gull *Larus ridibundus*. Coulson (1960), has analysed data on both the Starling, *Sturnus vulgaris* and the Blackbird, *Turdus merula.*

In studying population dynamics a certain terminology has been developed. Mean natural longevity is the mean age attained by individuals of a population living under natural conditions, at the time of death. Ideally this should be calculated from the date of hatching, but, it has been found necessary to select an initial date and to express the mean natural longevity or life expectancy from this arbitrary date. Mortality is usually expressed as an annual mortality rate m, which is obtained by dividing the number in a group or sample, which die during the course of a year, by the number alive at the beginning of that year. Similarly, the annual survival rate s is obtained from the number in a group or sample which survives to the end of the year, divided by the number alive at the beginning of the year.

Therefore $s = 1-m$, when s and m are expressed as probabilities or $s = 100 - m$ when given as a percentage.

In order to utilise all the data obtained from ringing recoveries, it is simpler to construct a life table and from this extract information on survival and mortality rates. Both Hickey (1952) and Farner (1955) explain the principles of this, and their methods together with those of Haldane (1955), have been employed on these data, which were obtained from ringing recoveries loaned by the British Trust for Ornithology on the Black-headed Gull, and the Gannet, *Sula bassana*.

The choice of the initial date, from which the age of the birds is to be calculated is still open to discussion. Hickey (1952) stressed the desirability of beginning calculations as near the date of hatching as possible, while Lack and Farner agreed that the first January 1 was the most satisfactory, as this allowed a period of time in which adequate dispersal of young birds could occur. This disagreement arises from a difference in the information which is required since Hickey wished to produce a complete life table, while both Lack and Farner were primarily concerned in calculating the adult mortality rate.

It seemed possible in sea-birds, which often take several years to reach maturity, that the high mortality rate found in the first few months of life may persist so that the young birds do not have a similar mortality rate to the adults until a year or more after fledging.

In this present analysis attempts have been made to calculate the average annual adult mortality rates of the Black-headed Gull and the Gannet. In addition, attention has been paid to the causes of mortality.

Method.

The method presented below has been derived so that errors in estimating mortality rates can be minimised. The loss or illegibility of rings is a major difficulty in using ringing data of sea-birds to measure survival. It is necessary to develop a method which can avoid this bias.

The number of birds recovered in two consecutive years depends upon the number at risk, which in turn depends upon (a) the number ringed and (b) the survival rate $\underline{s}$.

If $\underline{N}$ are ringed then the recoveries in year 1 are proportional to $\underline{N}$, while in the second year the recoveries are proportional to $\underline{Ns}$. (i.e. the number at risk at the beginning of each year).

Thus the proportion $$\frac{\text{Recoveries in year } a+1}{\text{Recoveries in year } a} = \frac{Ns}{N} = s$$

This only applies if the mortality rates in years $\underline{a}$ and $\underline{a+1}$ are similar. Thus the mortality rate $= 1 - \left(\frac{\text{Recoveries in year } a+1}{\text{Recoveries in year } a}\right)$ which can then be multiplied by 100 to give the percentage mortality rate.

This method can be extended to use data concerning additional years and the year groups can be altered to years lived since ringing by substituting $\underline{a+2}$, and $\underline{a+1}$, for $\underline{a+1}$ and $\underline{a}$ in the above equation. These can then be added and the equation becomes:

$$s = \frac{\text{recoveries in year } (a+1) + (a+2) + (a+3) \ldots\ldots\ldots (a+n)}{\text{recoveries in year } (a) + (a+1) + (a+2) \ldots\ldots\ldots (a+n-1)}.$$

This method has an advantage in that some data can be used up to the last complete year before analysis, but a small correction is required since birds ringed in e.g. 1959 will contribute to "Numbers recovered in second year", (i.e. recovered in 1961) but those comparable recoveries in the third year will not be complete until the end of 1962. Thus recoveries are only used up to the end of 1958 although the 1959 recoveries can be used in working out for first year and second year recoveries.

Another advantage of this method over that used by Lack (1946) is that it will work if the number of recoveries of old birds is biased due to ring loss, since the recoveries up to the age of expected ring loss can be used, and there is no need to calculate the "total birds recovered" as in Lack's method.

Example.

Assume that data were obtained from recoveries from 1956 to 1959 and that the recoveries were examined in 1960. It will be obvious therefore, that the number of recoveries for 1960 will be incomplete as the recovery period will not be over until 1961. Thus, this missing mortality will affect the calculations and so a correction has to be made excluding these recoveries. The recoveries are grouped in pairs for calculation, with the corrected total as the denominator, e.g.

$$\frac{\text{year 2}}{\text{year 1 (corrected)}}$$

	1956	1957	1958	1959
Recovered	15	11	8	7
Correction	3	1	0	1

THEREFORE, $\underline{s} = \frac{\text{year 2}}{\text{year 1}} = \frac{11}{15-3}$

$$\underline{s} = \frac{\text{year 3}}{\text{year 2}} = \frac{8}{11-1}$$

$$\underline{s} = \frac{\text{year 4}}{\text{year 3}} = \frac{7}{8-0}$$

The survival rate for years 1 to 4 can be obtained by adding these proportions which are already weighted.

$$\underline{s} = \frac{11+8+7}{12+10+8} = \frac{26}{30}$$

Therefore % mortality = $100\left(1-\frac{26}{30}\right) = 14\%$

Calculation of the Standard Error.

The standard error of the mortality rate can be calculated thus:

Where MR = mortality rate, n = number of years, d1 = recoveries in first year
dn+1 = recoveries in last year.

$$\text{S.E.} = \frac{MR}{n}\sqrt{\left(\frac{d1+dn+1}{d1-dn+1}\right)}$$

Example.

Recoveries in year D1 = 118
Recoveries in year D5 = 24
Mortality rate = 17.8%
Number of years = 5

$$SE = \frac{17\cdot8}{5}\sqrt{\left(\frac{118 + 24}{118 - 24}\right)}$$

$$= \frac{17.8}{5}\sqrt{\left(\frac{142}{94}\right)}$$

$$= \frac{17.8}{5} \times 1.23$$

$$= 4.4$$

Therefore Mortality rate = 17.8 ± 4.4%

Mortality Rate.

From the data examined it became apparent that before any acceptable value for the mortality rate of the breeding population could be calculated two possible errors had to be considered.

1. Many young birds die in the first few months of life soon after ringing and have a higher mortality rate than the adults.
2. Ring abrasion and wear: Rings generally last for several years after which time they are so worn that the inscription and numbers cannot be read, and eventually the rings fall off. This has been discussed by Coulson and White (1955).

To obtain an acceptable value for the mortality rate of the breeding population, it would therefore seem advisable to omit first and second year birds from the calculations and also, those birds of over seven years old, when, from examination of old rings, wear and loss become possible sources of bias in recoveries. With these limitations the mortality rate for the breeding population is 17.8 per cent ± 4.4 (Table 13).

It would appear that the potential longevity of an adult Black-headed Gull can be over twenty years, but the majority will have a breeding life expectancy of between three and ten years, with an overall average of 5.1 years. These estimates would appear to be acceptable and are within the limits imposed by the breeding potential of the Black-headed Gull.

Lack (1943) attempted to determine the annual mortality rate of Black-headed Gulls from British Trust for Ornithology ringing recoveries and found it to be over 30 per cent. This value is impossibly high as the

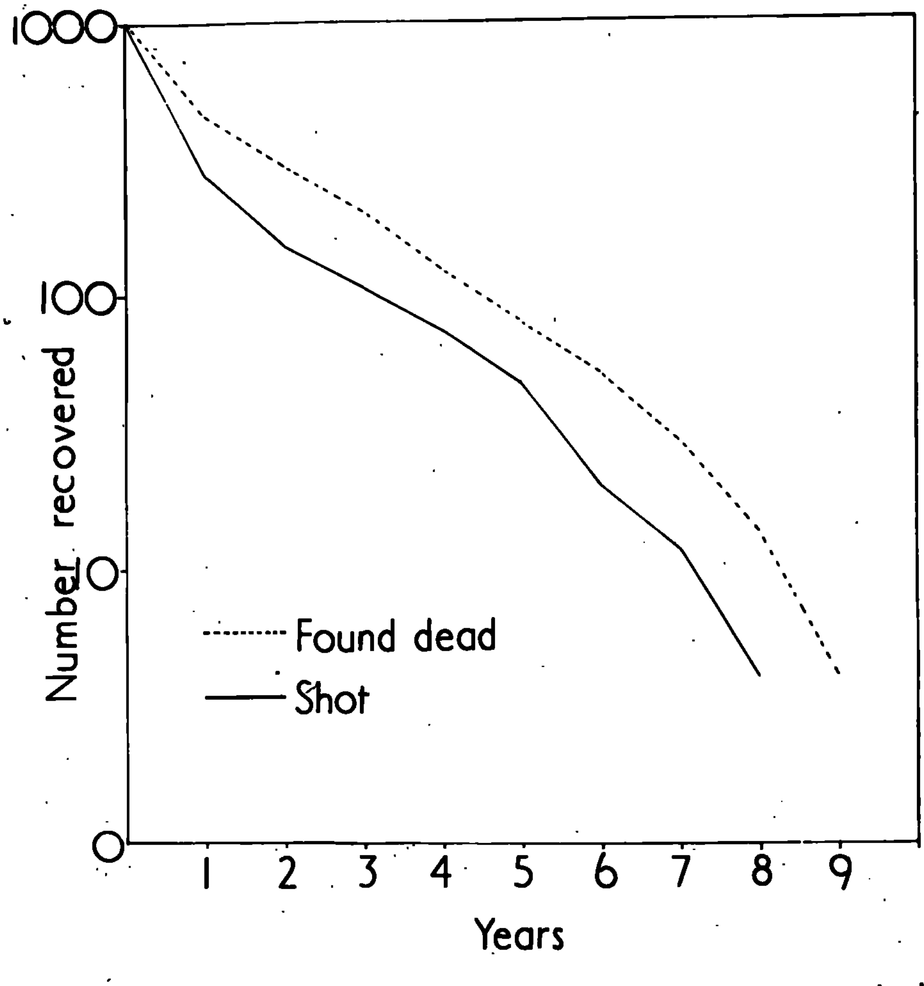


Fig 17 A comparison of the survival of black-headed gulls recovered as 'found dead' and shot. The slope of the graph indicates the mortality rate (log scale)

average clutch size and breeding success are not sufficient to compensate for this high mortality rate. Therefore the ringing recoveries from 1909 to 1959 have been analysed by the method already described and the data used in the subsequent calculations. The recoveries were divided into three major groups, (a) young, those ringed as nestlings; (b) juveniles, those ringed as full grown fledgelings; and (c) adults.

For young and juveniles the first August 1 after ringing, and the first January 1 after ringing were selected as initial dates for analysis. The initial date for ageing adults was taken from the first April 1 as most of them were ringed in the winter months, and as this date also gave the maximum amount of information.

Causes of Mortality.

The majority of recoveries are reported as "found dead", "shot", "caught", and "drowned". Each of these groups is ill defined, for a corpse "found dead" could quite easily have been shot. "Caught" is vague and because of this these recoveries have not been included in the calculations.

From Table 10 it will be seen that a high percentage of the birds ringed as young and "found dead" are first year birds, and 72 per cent of those "shot" are first year birds. Lack (1943) concluded that first year birds are shot more often than older birds. However, Coulson (1960) working with data on the Starling, Sturnus vulgaris, suggests that this high first year mortality by shooting may be misleading. In certain areas birds may be more prone to shooting and therefore a high mortality rate results. This certainly happens with Starlings, and also Cormorants, Phalacrocorax carbo, in places where they are considered pests, e.g. Berwick on Tweed. The difference in the proportion of first year and older birds shot is significantly different (Table 11). These data and those "found dead" have been plotted on a log scale, against year groups (Fig. 17) and it will be noticed that in first year birds the graphs for "found dead" and "shot" diverge in the first year and then run parallel in subsequent years, which indicates a different mortality within these two categories for the first year of life, and is in contrast to the graphs for the Starling which continues to diverge after the first year. Table 10 also shows the data for adult birds, and it is interesting to note that there is apparently a high mortality in the first year after ringing. There is no obvious explanation for this result, unless ill birds are more likely to be caught.

When the time of recovery is grouped in a bi-monthly series (Table 12) it seems that most young birds die in the period July to October, while the peak of deaths in adult birds occurs in the breeding season, May to August, presumably due to the additional risk associated with breeding.

Table 10.

A: Ringed as young or juveniles, year of recovery starting ... after ringing.

RECORD OF DEATH	YEAR OF RECOVE...											
	1	2	3	4	5	6	7	8	9	14...20		TOTAL
Found Dead	611	175	107	85	52	31	26	16	12	[illegible]	1	1123
Shot	180	30	12	8	7	7	2	2	0	0	0	249
Caught	26	14	8	4	2	2	2	0	0	0	0	58
Drowned	0	1	0	0	1	0	0	0	0	0	0	2
TOTAL	817	220	127	97	62	40	30	18	12	1	1	1432

% of first year birds.

Found dead 54
Shot 72
Caught 45
Drowned 0

B: Ringed as young or juveniles, year of recovery starting ... 1 after ringing.

RECORD OF DEATH	YEAR OF REC...											
	1	2	3	4	5	6	7	8	9	14...20		TOTAL
Found Dead	235	155	101	61	45	24	29	14	10	0	1	680
Shot	43	20	12	4	7	12	3	0	1	0	0	102
Caught	9	9	10	5	3	3	1	0	0	0	0	40
Drowned	0	0	0	0	0	0	0	0	0	0	0	0
TOTAL	287	184	123	70	55	39	33	14	11	0	1	822

% of first year birds.

Found Dead 35 Shot 42 Caught 23 Dro...

N.B. Table 5

For more detail concerning clutch size within the four areas of the island see Appendix 2.

Table 10.

Cause of Mortality of Black-headed Gulls.

C: Ringed as adults, year of recovery starting at first April 1 after ringing.

RECORD OF DEATH	YEAR OF RECOVERY.													
	1	2	3	4	5	6	7	8	9	10	11	12 ... 19	20	TOTAL
Found dead.	32	9	3	9	4	4	2	3	0	2	2	0 ... 1	0	71
Shot.	2	3	3	1	1	0	1	0	0	0	0	0 ... 0	0	11
Others.	NIL													
TOTAL	34	12	6	10	5	4	3	3	0	2	2	0 ... 1	0	82

% of first year birds.

Found dead	45
Shot	18

Table 11.

Cause of mortality of Black-headed Gulls according to age, year of recovery calculated from the first of August.

RECORD OF DEATH	1st year.	2nd year & 3rd year	4th year or older
Found dead	75%	81%	86%
Shot	22%	12%	10%
Other	3%	7%	4%
Total Recoveries	817	347	268

The difference between the percentage shot in the first year and subsequent years (11% $\pm$ 2.2%) is highly significant.

Table 12.

Bi-monthly distribution of recoveries of Black-headed Gulls.

	July & August	Sept. & October	November & Dec.	Jan. & Feb.	March & April	May & June.
First year birds	240	158	68	78	34	32
Older birds	85	75	85	66	76	135
TOTAL	325	233	153	144	110	167
% First year birds	73.8	67.8	44.4	54.2	31.0	19.2

Older birds are more than one year old.

Table 13.

Mortality rate of Black-headed Gulls.

Year of recovery beginning at the first August 1 after ringing.

	YEAR OF RECOVERY.									
	1	2	3	4	5	6	7	8	9	10
Number recovered	848	227	132	112	71	45	31	23	12	8
Corrected total	771	192	118	98	62	41	24	19	5	6

Mortality rate calculated from the third to the seventh year: $1 - \frac{282}{343}$

Therefore % mortality rate = $100 \left(1- \frac{282}{343}\right) = 17.8$

S.E. = 4.4

GANNET

Introduction.

Fisher and Vevers (1943, 1944) conducted a world census of the Gannet, Sula bassana, population. They concluded that the population of the species was increasing, and this they attributed to the protection of these birds in recent years. Human predation was extensive at the end of the 19th Century, due to the Gannet being a source of meat, fat, and eggs. The Gannet population was therefore at a relatively low level at that time. Following this the birds were protected and consequently increased in numbers, and apparently this increase is still going on. The Gannet is restricted to the north Atlantic Ocean; outside of the British Isles it breeds on the Faroes, Iceland, and along the east coast of Canada, from the Magdalen Islands in the Gulf of St. Lawrence and on to Funk Island in New Foundland. Around the British Isles the largest colonies include Grassholm, Ailsa Craig, St. Kilda, Shetlands, Orkneys and the Bass Rock. The clutch consists of a single egg and the young Gannet does not attain maturity for at least four years (Witherby et al. 1938).

An attempt has been made to estimate the mortality rate and the causes of mortality from ringing recoveries. The mortality rates were calculated by the same method employed for Black-headed Gulls (p. 25). The breeding season of the Gannet is over by the end of August, and so the first September 1 after ringing was selected as the initial date from which the age of the birds was calculated.

By September 1 most of the fledgelings have left their nests and would all be subject to recovery by the general public. The mortality rate for the breeding population has been calculated for each of the major British colonies. Broekhuysen et al. (1961) in a paper on the South African Gannet, Morus capensis, include several lists of recaptures, and from these it has been possible to obtain a mortality rate, and this is compared to that calculated from the British recoveries. Although the South African Gannet is usually distinguished specifically from the North Atlantic Gannet, both are closely related, and, may represent geographical forms of the same species as has been suggested by Broekhuysen et al. (loc. cit.)

Causes of Mortality.

It would appear that the reported causes of mortality in Gannets are consistent, namely, "found dead", "shot" and "caught" in nets, and the ringing recoveries have been grouped into these three categories. Table 14 shows that in all the recoveries in these three categories, first year birds represent more than 50 per cent of the total in each case. This shows that a high first year mortality occurs, indeed 72 per cent of all the birds "caught" are first year birds. Table 14 also gives the data for adult birds and it is interesting to note that a high mortality occurs in the first year after ringing, and, as in Black-headed Gulls, there is no obvious explanation. Data are presented in Table 15 on the age of the birds and the causes of mortality. The proportion caught decreases as the age groups become older. The difference between first year and older birds "caught" is significant (difference is 11% ± 3.5% P $\angle$.01) and this may be due to their feeding habits. In the case of the young birds, they see fish trapped in the fishing nets or on lines, dive from a height of about 50 feet and become entangled. By the time the nets or lines are hauled the birds are drowned. It would appear that the older birds are better able to avoid becoming caught in this manner. (Fisher & Lockley, 1954).

While a large proportion of young Gannets winter off the coast of North Africa, the great majority of adults remain off the European coast. This differential movement could affect the recovery rate (possibly higher in Europe than in North Africa) and could lead to biased mortality estimates. This is examined in more detail later.

Table 14.

A: Data from recoveries of young and juvenile birds whose age has been calculated from the first September 1 after ringing.

RECORD OF DEATH	YEAR OF RECOVERY											
	1	2	3	4	5	6	7	8	9	10	11	TOTAL	% of first year birds.
Found dead	303	69	41	30	12	5	0	1	1	1	0	463	65.4
Shot	22	11	7	0	0	0	1	0	1	0	0	42	52.4
Caught	90	19	10	6	0	0	0	0	0	0	0	125	72.0
Total dead	415	99	58	36	12	5	1	1	2	1	0	630	65.9

B: Data from recoveries of adult birds whose age has been calculated from the date of ringing.

RECORD OF DEATH	YEAR OF RECOVERY											
	1	2	3	4	5	6	7	8	9	10	11	TOTAL
Found dead	25	14	12	2	7	6	0	0	2	0	1	69
Shot	1	0	0	0	0	0	0	0	0	0	0	1
Caught	5	4	0	0	0	1	1	0	0	0	0	11
Total dead	31	18	12	2	7	7	1	0	2	0	1	81

Table 15.

Relationship between Cause of Mortality and Age.

	PERCENTAGE OF THE TOTAL FOR A PARTICULAR YEAR GROUP.		
Age	Percentage found dead	Percentage Shot	Percentage Caught.
First Year.	73.0	5.3	21.7 ± 2.0
Second Year.	69.7	11.1	19.2 ± 4.0
Third & Fourth years.	75.5	7.4	17.0 ± 4.1
Over five years including adults	86.4	2.9	10.7 ± 2.9

Difference between percentage caught in first year and adults is significant:

Difference is 11% ± 3.5% $P < .01$

Mortality Rate.

There seemed to be two possible sources of error in attempting to estimate the adult mortality rate of the Gannet from the ringing recoveries of birds ringed as young. In the first place, there is a high mortality in the first months after fledging, and it is, therefore, necessary to ignore the recoveries in the first and possibly the second year after ringing. Secondly, there is a possibility of ring wear and loss (for which reason the present method of analysis has been developed).

In Table 17 the mortality rates have been calculated using recoveries over varying periods of time. It is clear that all estimates using first year data are excessively high. The estimate starting with the second year data gives a similar result to that starting with the third and fourth years. It seems reasonable therefore, to omit recoveries of young only during the first year of life. An examination of a collection of rings which have been on Gannets for periods up to seven years, suggests that the inscription but not the numbers may be difficult to read after five years. Therefore, only recoveries between two and five years have been used.

In the case of birds ringed as adults, recoveries from the time of ringing until the end of the fifth year have been used.

Having made these limitations, the best estimate of the adult mortality is 37 ± 10 per cent per annum.

Based on recoveries of birds ringed as adults, the annual mortality rate is 31 ± 8 per cent.

These estimates are impossibly high. Capildeo and Haldane (1954) have given a Table from which it is possible to estimate reasonable mortality rates, knowing the age at maturity and the breeding success. They give as an example a value of 13 per cent annual mortality for the Gannet, (not based on actual data) and this produces an almost static population.

An adult mortality rate of 36 per cent implies that of every 100 pairs of Gannet 72 birds die between one breeding season and the next, during which time the 100 eggs laid by the pairs must produce 72 young which eventually survive to maturity (probably four years). It is inconceivable that during the first four years of life the Gannet should suffer only a 28 per cent mortality (including egg and chick mortality), since the mortality of immature birds is usually more than four times that of the adults.

Therefore, there is reason to suspect a bias in the ringing recoveries. Two explanations are possible:

1. The adults which are ringed are usually on the edge of a colony. It is possible that these are young birds, or less vigorous birds which have a higher mortality rate than the rest of the population.

2. That there is a differential recovery rate for young and old birds. This could arise from the fact that there is an age difference in the migration, and also from adults and young birds dying from different causes. A bird which is caught in a net is much more likely to produce a recovery than one which dies of disease or infection.

Of these two possibilities, the second seems more likely, as data has already been presented which suggest that the causes of death may well change with age (Table 15).

The mortality rates for the three major British Colonies of Sula bassana were also calculated but these did not differ significantly from each other, or from the calculated value for the breeding population and did not warrant further discussion.

When the recoveries are grouped in a bi-monthly series, and first year birds are separated from older birds, it is seen that the majority of first year birds die in the September to December period. This may indicate that the high proportion of deaths in September and October is due to the peculiar development of the young Gannet which leaves the breeding grounds before it is fully fledged, (Table 16).

Table 16.

Bi-monthly distribution of recoveries of the Gannet.

AGE	MONTH OF RECOVERY.					
	S&O	N&D	J&F	M&A	M&J	J&A
Older birds	52	35	37	20	37	27
First year birds	221	69	23	6	7	30
TOTAL	273	104	60	26	44	57
% of first year birds	81.1	64.3	38.4	22.5	13.6	54.0

Table 17.

Mortality rate of Gannets.

A: Year of recovery beginning at the first September 1 after ringing data from recoveries of young and juvenile birds.

	YEAR OR RECOVERY									
	1	2	3	4	5	6	7	8	9	10
Number recovered	415	98	58	36	12	5	1	1	2	1
Corrected total	388	89	53	30	10	4	1	1	2	1

Mortality rate calculated from the second to the fifth year: $1 - \frac{111}{182}$

Therefore the % mortality rate = $100 \left(1 - \frac{111}{182}\right) = 39\% \pm 11$

B: Data from recoveries of adult birds, year of recovery beginning from the date of ringing.

	YEAR OF RECOVERY											
	1	2	3	4	5	6	7	8	9	10	11	12
Number recovered	31	18	12	2	7	7	1	0	2	0	1	
Corrected total	30	16	12	2	7	7	1	0	2	0	1	

Mortality rate calculated from the first to the fifth years: $1-\frac{46}{67}$

Therefore the % mortality rate = $100 \left(1-\frac{46}{67}\right) = 31\% \pm 7.80$

Combining calculations A. and B.:
The % mortality rate = $100 \left(1-\frac{157}{249}\right) = 37\% \pm 10$

Data on the recoveries (live recaptures) of the South African Gannet and the annual adult mortality rate. (Data after Broekhuysen et al. 1961).

	YEAR RINGED		
	1951	1952	1953.
Number ringed	129	1366	3865
Number recaptured. 1954-57. (including multiple recaptures)	89	904	2423
Proportion recovered.	69.0%	66.2%	62.7%
Mortality rate (per annum)	4.1% (1951–1952)	5.3% (1952–1953)	

The adult gannets ringed in 1952 have had one year's more mortality than those ringed in 1953 and one year's less than those ringed in 1951. Thus the difference in the "proportion" of recoveries is proportional to the mortality rate and can be calculated as follows:

1951 and 1952 ringing.

$$\text{Survival rate} = \frac{129}{89} \times \frac{904}{1366} = 95.9\%$$

Therefore Mortality rate = 4.1%

$$\text{1952 and 1953 ringing} = \frac{1366}{904} \times \frac{2423}{3865} = 94.7\%$$

Mortality rate = 5.3%

Pooling this data and weighting it according to the recapture available, the mortality of the South African Gannet is 5.0 per cent ± 1.7 %. This a much more realistic value and it would seem reasonable to assume that a similar rate applies to the European Gannet.

SUMMARY

The thesis has been divided into three parts. Part A. deals with the breeding biology of the Eider, Part B. with the distribution and movements of the Eider throughout the year and Part C. with the mortality rates of the Black-headed Gull and Gannet.

Part A.

Investigations were carried out on the Farne Islands off the coast of Northumberland, from May to the end of June, 1962. The Inner Farne was divided into four sections, one of which was chosen as the Study Area due to its accessibility. Prenesting behaviour deals with the initial choice of the nest, and the preparation of the nest.

The first nest was found on the 26 April and the number of clutches started increased until the week beginning 16 May and then decreased until 6 June when a small second increase in numbers occurred.

It seemed that there was a periodicity in the laying of eggs by a particular duck, at about 12 hours or a multiple of 12 hours, but they were not laid at any particular time in the 24 hour period. Some birds laid more than one egg in 24 hours but in some cases the increase was attributable to parasitation and stealing of eggs. It seemed that as the number of eggs increased the interval between eggs was shorter for large clutches than for small ones.

The average clutch size was found to be 5.09 ± .09 for the Inner Farne. Large clutches, of 8 or more were found and it seems that this cannot be attributed to any one cause. In some cases the reason for this was parasitation, stealing or laying on an already deserted clutch, but these were relatively unimportant and it was found that in the majority of cases one bird laid all the eggs. There was a close correlation between nest density and clutch size, and the greatest number of large clutches was found in the most densely populated areas.

The mean incubation period was found to be 28.5 days. Early in incubation the Eider left the nest to feed and drink, but as the hatching time approached, the duck sat without leaving the nest. Nest desertion was thought to be influenced by ducks hatching off in the vicinity.

When the ducklings hatched they remained in the nest for about 24 hours. They were not taken directly to the sea, but spent some time in the fresh water pools above high water mark.

Hatching success was low (22.7%) but this was thought to be due to lack of data.

The Eider ducks have evolved a social system whereby non-breeding birds or birds which have lost their broods, help protect other broods.

There is a definite tidal rhythm of feeding; most birds left the Farne on the ebb tide to go to the mainland coast to feed.

The sex ratio varied from 1:1 at the beginning of the breeding season to virtually no males at the hatching period (mid-June), The breeding success of the Eider seemed to be low, only 20.9 per cent.

Part B.

From the study of the distribution of the Eider it has been concluded that there is probably a moult migration from the Farnes to the Firth of Forth though in the main only the males seem to take part. In this respect the Eider is similar to the King Eider.

Moreover, it has been found that there is a local distribution, in that the Eider only occurs on those stretches of coast that are rocky.

Part C.

The mortality rate of Black-headed Gulls was found to be 17.8 per cent ± 4.4 per cent. The reported causes of mortality were found to be similar in both Black-headed Gulls and Gannets. In the case of the former, the young birds were more prone to be shot than older birds, and in the latter, it was found that being "caught" by fishermen decreased with age.

Using the same method to calculate the mortality rate of Gannets the mortality was found to be 37 per cent ± 10. This is an impossible value. Using the results on the South African Gannet the mortality rate was calculated at 5.3 ± 1.7 per cent, which is a more realistic value.

BIBLIOGRAPHY

BACKHOUSE, (1898) Notes on the Sandwich Tern. Naturalist 1898: 73-74.

BAXTER, E.V. & RINTOUL, L.J. (1953) The Birds of Scotland: their History Distribution and Migration. Edinburgh and London.

BELOPOLSKII, (1957) Ecology of Sea Colony Birds of the Barents Sea. Moscow - Leningrad.

BEST, G.S. & HAVILAND, M.D. (1913) Notes on the breeding habits of the Common Eider (Outer Hebrides) Brit. Birds 7: pages 101-104.

BROEKHUYSEN, G.J. LIVERSIDGE, R. & RAND, R.W. (1961) The South African Gannet, Morus capensis. 1. Distribution and Movement. Ostrich, 32: 1 - 19.

CAPILDEO, R. & HALDANE, J.B.S. (1954) The mathematics of bird population growth and decline. J. Anim. Ecol. 23: 215 - 223.

COOMBES, R.A.H. (1949) Shelducks: Migration in Summer. Nature 164: 1122

COOMBES, R.A.H. (1950) The moult migration of the Shelduck. Ibis 92: 405-418.

COULSON, J.C. (1960) A study of the mortality of the starling based on ringing recoveries. J. Anim. Ecol. 29: 251 - 271.

COULSON, J.C. & WHITE, E. (1955) Abrasion and loss of rings among Sea birds. Bird study 2: 41-4.

EVANS, W. (1923) The Eider Duck, Somateria mollissima in the "Forth Area". Scot. Nat. 1923: 147 - 152.

FARNER, D.S. (1955) Birdbanding in the Study of Population Dynamics in "Recent Studies in Avian Biology." University of Illinois Press (397 - 450).

FISHER, J. & LOCKLEY, R.M. (1954) Sea Birds. London.

FISHER, J. & VEVERS, H.G. (1943, 1944) The breeding distribution, history and population of the North Atlantic Gannet (Sula bassana) J. Anim. Ecol. 12: 173 - 213, 13: 49 - 62.

FREUCHEN, P. & SALOMONSEN, F. (1959) The Arctic Year. London.

GODDARD, T.R. (1946) The Farne Islands - Ornithological Report. Farne Islands Committee of the National Trust.

GROSS, A.O. (1938) Eider ducks of Kent Island. Auk. 55: 387 - 400.

GROSS, A.O. (1944) The present status of the American Eider on the Maine Coast. Willson Bull 56: 15-26.

GUDMUNDSSON, F. (1938) Aedarvarp og duntekja a Islandi. pamphlet Gutenberg 19pp.

GERASIMORA, T.D. (1954) Ecology of the Eider on the Murmansk Coast and methods for the rationalisation of eider breeding. Scientific notes of the Moscow Pedagogical Institute, 28: 155 - 191.

HALDANE, J.B.S. (1955) The calculation of mortality rates from ringing data. Acta XI Congr. Internat. Orn.: 454 - 8.

HANCOCK, J. (1874) A catalogue of the birds of Northumberland and Durham. Nat. Hist. Trans. Northumberland and Durham Vol. VI.

HICKEY, J.J. (1952) Survival studies of banded birds. U.S. Dept. Int. Fish & Wildlife Serv. Special Scient. Rept. Wildlife 15: 177 pages.

JOURDAIN, F.C.R. (1922) Birds of Spitzbergen and Bear Island. Ibis 1922: 159 - 179.

KENDEIGH, S.C. (1937) Factors affecting yearly abundance of passerine birds. Ecol. Monogr. 7: 91 - 124.

KENYON, K.W. (1961) Birds of Amchitka Island, Alaska. Auk. 78: 305-326.

LACK, D. (1943) The age of some more British birds. Brit. Birds 36: 193-7, 214 - 21.

LACK, D. (1946) Do juvenile birds survive less well than adults? Brit. Birds 39: 258 - 264.

LEWIS, H.F. (1926) Producing Eiderdown. Ottawa National Parks Service.

LEWIS, H.F. (1939) Size of sets of eggs of the American Eider. J. Wildlife Management 3: 70 - 73.

MADSEN, F.J. (1954) On the food habits of the diving ducks in Denmark. Danish Rev. Game Biol. 2: 157 - 266.

MILLAIS, J.G. (1913) British Diving Ducks. London: 1 - 32.

MULLER, R. (1906) Vildet og Jagten i Sydgrønland. Copenhagen (Hagerup) : 89 - 113.

MUNRO, D.A. (1961) The Eider farms of Iceland. Canadian Geographical Journal. August 1961. 1 - 7.

NELSON, T.H. (1887) A Naturalist's Ramble on the Farne Islands. Naturalist 1887 : 116 - 128.

NICE, M.M. (1937) Studies on the Life History of the Song Sparrow. I. Trans. Linn. Soc. N.Y. 4 : 247 pp.

PAYNTER, R.A. (1951) Clutch size and egg mortality of Kent Island Eiders. Ecology, 32 : 497 - 507;

ROLNIK, V.V. (1943) Instructions for the incubation of Eider Duck eggs. Journal of Wildlife Management 7 : 155 - 162.

ROLNIK, V.V. (1955) Inkubatsiya yaits gagi (Somateria mollissima) Zool. Zhur. 34 (v.4) : 885 - 897.

SELBY, P.J. (1833) Illustrations of British Ornithology, Edinburgh.

SELBY, P.J. (1857) Catalogue of the birds which inhabit or resort to the Farne Islands. His. Berwick Nat. Club Vol. III : 238 - 241.

TAVERNER, J.H. (1959) The spread of the Eider in Great Britain. Brit. Birds 52: 245 - 258.

WALLIS, J. (1769) The Natural History and Antiquities of Northumberland and of so much of the County of Durham as lies between the Rivers Tyne and Tweed. 2 vols. London.

WATT, G. (1949) The Farne Islands - Ornithological Report. Farne Islands Committee of the National Trust.

(1951) The Farne Islands, their history and wild life. London.

WITHERBY, H.F. et al (1938) The Handbook of British Birds. London.

APPENDIX.

Counts of Eiders along the Northumberland, Berwickshire, East Lothian and Mid-Lothian coasts during the twelve month period from July 1961 to June 1962.

The coastline has been divided into six regions:

A - Edinburgh to Dunbar

B - Dunbar to Berwick

C - Berwick to Budle Bay

D - Budle Bay to Craster

E - Craster to Amble

F - South of Amble

July and August, 1961.

Area	Males	Females	Immatures	Total
A	913	69	28	1010
B	0	0	0	0
C	1	24	11	36
D	120	186	35	341
E	107	127	29	263
F	4	2	0	6

September and October, 1961.

Area	Males	Females	Immatures	Total
A	57	267	0	324
B	31	93	2	126
C	63	40	0	103
D	513	649	8	1170
E	163	305	0	468
F	0	1	0	1

November and December, 1961.

Area	Males	Females	Immatures	Total.
A	15	20	1	36
B	17	19	1	37
C	34	40	1	75
D	165	194	3	362
E	68	105	7	180
F	1	4	1	6

January and February 1962.

Area	Males	Females	Immatures	Total
A	24	27	2	53
B	36	25	1	62
C	23	19	0	42
D	165	173	4	342
E	69	89	13	171
F	7	8	0	15

March and April, 1962.

Area	Males	Females	Immatures	Total
A	84	84	2	170
B	28	27	2	57
C	20	19	1	40
D	273	266	2	541
E	76	75	11	162
F	33	28	3	64

May and June 1962.

Area	Males	Females	Immatures	Total
A.	534	10	6	550
B	10	24	16	50
C	12	30	1	43
D	105	108	76	289
E	88	152	85	325
F	0	4	0	4

AREA W

a) Up to May 9

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Number of Instances	-	2	1	5	6	2	-	-	-	-	-	-	-	-	16

Total number of eggs = 69   Number of nests = 16

b) 9 - 23 May

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	Total
Number of Instances	3	2	6	18	19	3	-	-	-	-	-	-	-	-	51

Total number of eggs = 210   Number of nests = 57

c) After 23 May

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	Total
Number of Instances	-	2	8	7	7	4	-	1	-	-	29

Total number of eggs = 123   Number of nests = 29.

AREA T

a) Up to 9 May

	Clutch Size											
	1	2	3	4	5	6	7	8	9	10	11	Total
Number of Instances	1	1	3	17	14	2	-	1	-	-	-	39

Total number of eggs = 170 Number of nests = 39

b) 9 – 23 May

	Clutch Size											
	1	2	3	4	5	6	7	8	9	10	11	Total
Number of Instances	1	8	12	22	25	19	9	5	-	1	2	104

Total number of eggs = 515 Number of nests = 104

c) After 23 May

	Clutch Size											
	1	2	3	4	5	6	7	8	9	10	11	Total
Number of Instances	-	3	11	18	17	8	3	2	-	-	1	63

Total number of eggs = 292 Number of nests = 63

STUDY AREA.

a) Up to May 9

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
Number of Instances	-	-	-	3	7	3	-	1	1	1	1	-	-	-	2	1	20

Total number of eggs = 149 Number of nests = 20.

b) From May 9 - 23

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	Total
Number of Instances	-	2	3	11	24	11	15	10	5	2	2	5	1	1	1	-	94

Total number of eggs = 620 Number of nests = 94

c) After 23 May

Clutch Size.

	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	Total
Number of Instances	1	4	5	5	9	9	4	2	-	-	-	1	-	-	-	40

Total number of eggs = 199 Number of nests = 40

APPENDIX 2

Data concerning the clutch size frequency within four areas of the island, the Study Area, T, W, and NE(Fig 3) during the three periods up to May 9, May 9 to 23, and after May 23.

AREA NE.

a) Up to 9 May

	Clutch Size.										
	1	2	3	4	5	6	7	8	9	10	Total
Number of Instances	-	-	1	2	4	3	2	-	-	1	13

Total number of eggs = 73 Number of nests = 13

b) 9 - 23 May

	Clutch Size.										
	1	2	3	4	5	6	7	8	9	10	Total
Number of instances	-	-	1	3	3	4	2	1	-	-	14

Total number of eggs = 76 Number of nests = 14

c) After 23 May

	Clutch size.										
	1	2	3	4	5	6	7	8	9	10	Total
Number of Instances	-	2	8	12	3	5	-	-	-	-	30

Total number of eggs = 121 Number of nests = 30