Studies on a marked population of the shag (Phalacrocorax aristotelis), with special reference to the breeding biology of birds of known age

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Studies on a marked population of the Shag, (*Phalacrocorax aristotelis*), with special reference to the breeding biology of birds of known age.

by

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St. Cuthberts' Society

...being a thesis presented in candidature for the degree of Doctor of Philosophy in the University of Durham, 1966.

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INTRODUCTION

In recent years an increasing amount of attention has focused on the population dynamics of the higher animals. The central and controversial theme of these studies concern the extrinsic and intrinsic mechanisms by which populations function as dynamic systems. The cibernetics of animal populations are as fascinating as they are fundamental for the more we understand the interdependence of production, recruitment and mortality of species or other populations, the more successful will be the inevitable attempts to control, exploit, conserve, or in turn, appreciate them.

The temporal dimension of an animal population can be considered to have two bases, that of the life of an individual, and that of the length of generation turn over. Though the behaviour (sensu lato) of individuals can be studied within the time scale of the former, the behaviour of populations and the evolution of their organisation can only be studied in the second, which is, excepting inference, outside the scope of this study. For example, it is generation (or cohort) turn over which is intimately related to the age distribution so that variations in the rate of increase of the population affect the relative size of the age classes. Thus the behaviour of an age class (e.g. the proportion which breed) may well be dependent on the rate of increase, if the increase is dependent on the density of the population and if the intra specific competition which enables this, is age specific.

It is because the result of natural selection on an entire cohort operate in the time scale of generation turn over that the implications of the present short term study, in so far as it concerns age specific behaviour in the period 1962-1965, on the understanding of the evolution of age specific behaviour, are limited. Conversely the behaviour of individuals during any finite period can be examined in detail. This last facility is essential if one is to examine organisation beyond that of the individual or pair in colonial animals.

Whilst Darling (1938 a),Austin (1945),Tinbergen (1953 a),Fisher and Lockley (1954),Lack (1954),Coulson and White (1960) and Wynne-Edwards (1962) each consider that various animals gain socially facilitated advantages from their colonial breeding or gregarious habits in general, the last author differs from the others since he considers that the initial advantage to the individual is eventually subordinated to that of the group as a whole. Wynne-Edwards clearly regards this subordination as a social rather than a mechanical device (of age structure, density dependent mortality <u>etc.</u>) which, being socially induced, affects the reproductive rate rather than the mortality rate.

Accepting that sea-bird populations are regulated intrinsically (i.e. intrinsic process, not intrinsic cause) it is difficult to understand how the adult mortality rate could be density-dependent, whilst it is easy to imagine that the reproductive rate could be regulated, though inefficiently, by social organisation on the breeding grounds. To investigate this last kind of regulation it is necessary to eliminate other important variables concerning the individuals' performance within and between sub-populations or breeding groups. Perhaps the most important of these variables, as far as social organisation and its relation to individual status, fecundity and fertility are concerned, is the age of the individual and its previous breeding experience.

If these effects can be eliminated it will be possible to compare sub or even micro-populations in much the same way that Darling (1938 a) did in the Herring Gull, but with a much more rigorous method.

There have been only three major studies of age specific behaviour in sea-birds. The eighteen year study by Richdale (1951,1957) on the population of the Yellow-eyed Penguin on the Otago peninsula, New Zealand was the most detailed study. At first this population which was small and fragmented, declined to 25 pairs, however in the latter half of the study period a recovery began, so that 82 pairs were found in 1952-1953. Even in later years, the numbers of birds in each age class were too small to analyse within population effects or to comment adequately on annual variables.

In the period 1922 to 1955, some 250,000 Common Tern chicks were ringed on Cape Cod, Massachusetts, U.S.A., in an area generally occupied by about 8,000 pairs. The "content of banded birds" in this colony varied between 44 and 59 per cent, though this 'trappable' population did not include 'trap shy' birds, most of which were one or two years of age. Austin (1945,1947,1949) and Austin and Austin (1956) have analysed the results of their work on this population.

In 1949, the Kittiwake began to nest on a warehouse at North Shields (Northumberland) and since that time a colony of just over a hundred pairs has formed. J.C. Coulson (earlier in conjunction with E. White) has regularly ringed the birds throughout the last thirteen years or so and almost all individuals are of known breeding history, though few are of known age, and recruitment from various year classes cannot be studied.

There is a considerable amount of scattered evidence supplementing that of the above studies, in the studies of the Arctic Skua (Williamson 1959, Davis 1961 b) and Herring Gull (Drost,Focke and Freytag 1961). In addition age specific breeding behaviour has been described in the Cormorant (Kortlandt 1942) the Heron (Verwey 1930) and in the White Stork (e.g. Hornberger 1943), and in several passerines, in particular, the Song Sparrow (Nice 1937) and Great Tit (Kluijver 1951, Perrins 1965) and in certain wildfowl (in Delacour and Scott 1964). In general these studies show that behaviour in the reproductive cycle stabilises with age or breeding experience, and that this stability is associated with increased breeding efficiency.

The four year study of the Lundy Shag population by Snow (1960,1963) is of especial comparative interest to the present work. This was the first thorough study of the breeding biology of this species and as such, laid the foundation of the present study. Certain factors such as the seasonal decline in breeding success of the Lundy population begged the conclusion that age and breeding experience were the underlying causes, but few of her breeding birds were ringed and less than half a dozen were of known age. The main advantages of the present study population is that the birds are tame and easily marked and that they have been intensively ringed for more than twelve years. In addition there are now sufficient numbers (400 pairs) to enable multi-variable analysis. However, like the populations studied by Richdale (1957), Coulson and White (1958 a),(1960), Kortlandt (1942), it is increasing, and thus some enviromental pressures (which may act in an age specific manner) are at present relaxed.

The aim of the present work is to provide an analysis of the effects of age on breeding behaviour in the Shag, so that, in due course, other variables such as the social structure of breeding groups, can be examined by eliminating age specific effects.

SECTION ONE

METHODS

Study Area

The Farne Islands, off the north Northumberland coast, are low quartz dolerite outcrops, part of the Whin Sill, a Tertiary intrusion. The highest point is less than sixty feet above high water mark and the scarp slope of the outcrops face south east. This scarp slope is eroded by gullies or clefts around which most of the Shags breed. Out of these gullies the aspect is very exposed, especially to the south and east. A map showing the main islands is given in Fig. 1 and an aerial photograph Plate 1 indicate the essential features. A map showing the location of adjacent breeding areas is given as Fig. 2 .

Accomodation is available on Inner Farne and on Brownsman, but the last is reserved for the 'watchers' or wardens employed by the National Trust, to guard Staple and Brownsman. Access is by boat from Seahouses, two and a half miles south south west of Inner Farne, or by dinghy in good weather, between the islands.

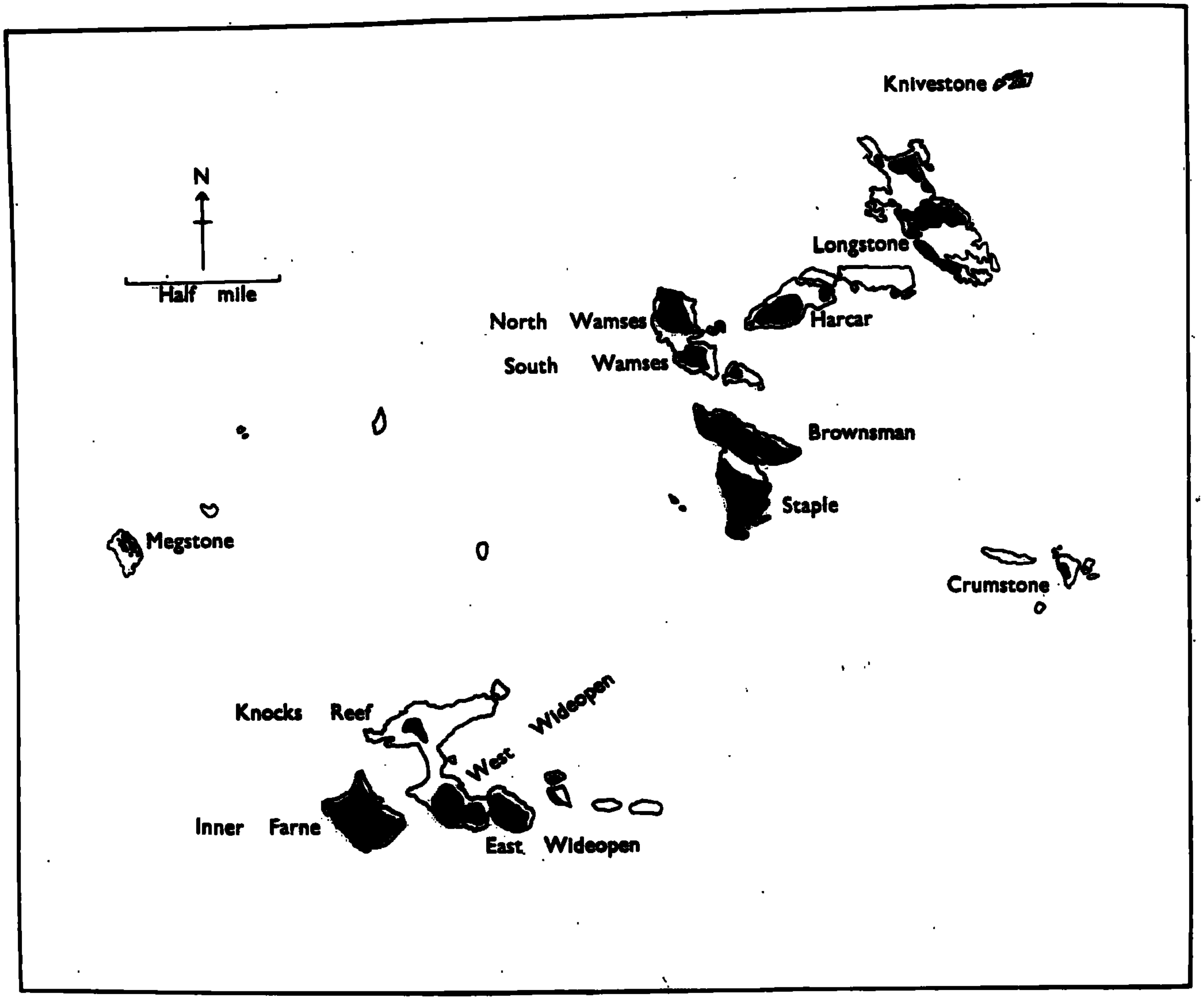
Fig. 1

[illegible]

[illegible]

THE FARNE ISLANDS

dark areas = rocks above MHWM



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

PLATE 1.

AERIAL VIEW OF STAPLE (foreground) AND BROWNSMAN

Numbers of Shag nests in indicated areas are given in Table 26 page 92

...... Photograph by Philipsons' Studios Ltd.

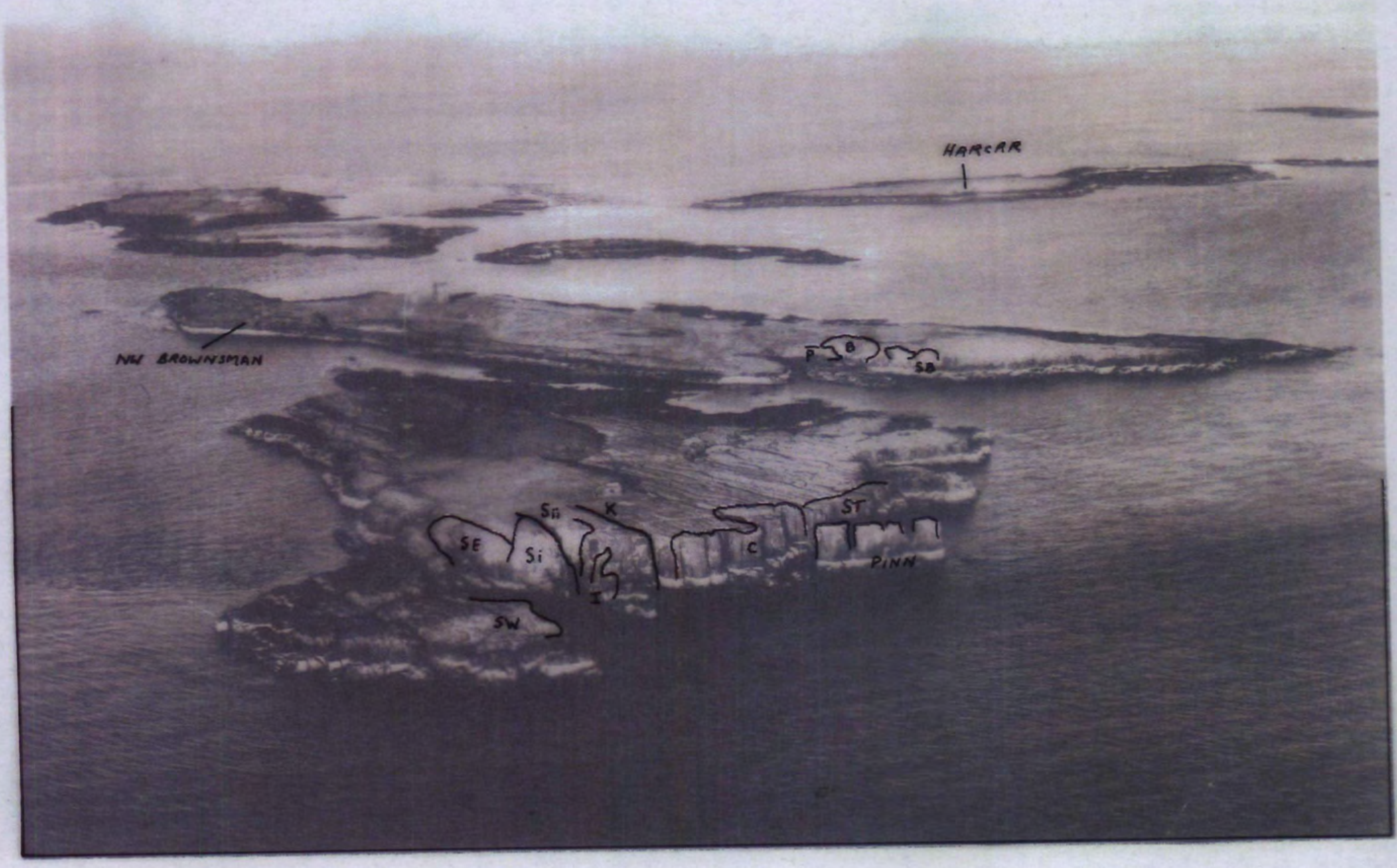
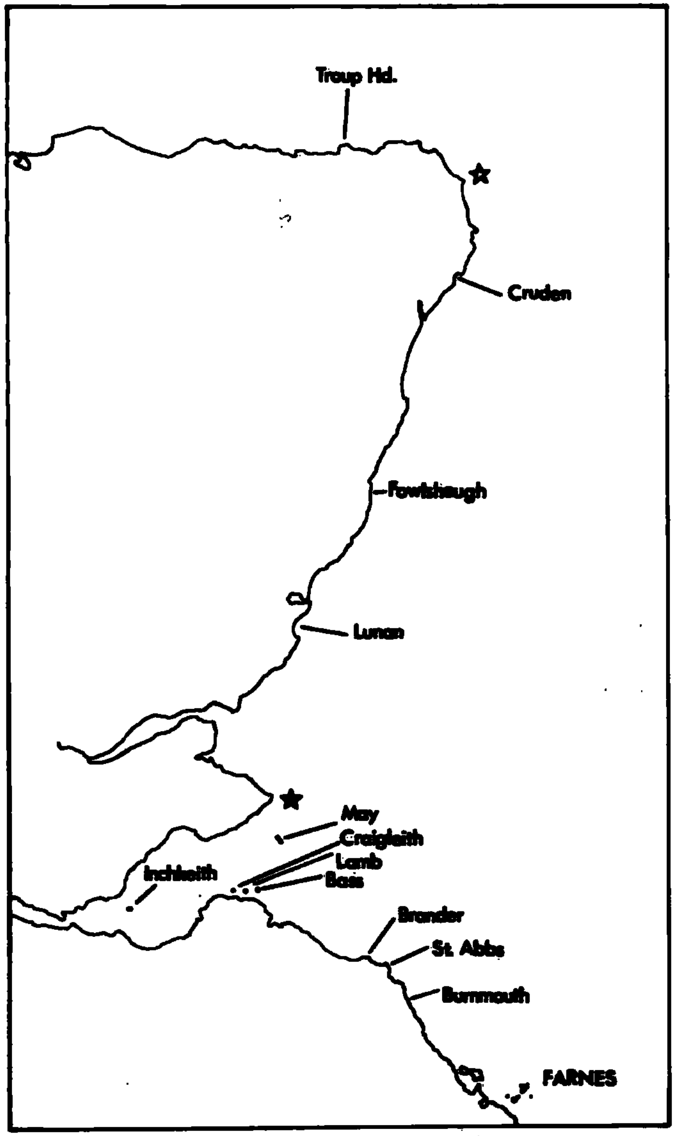
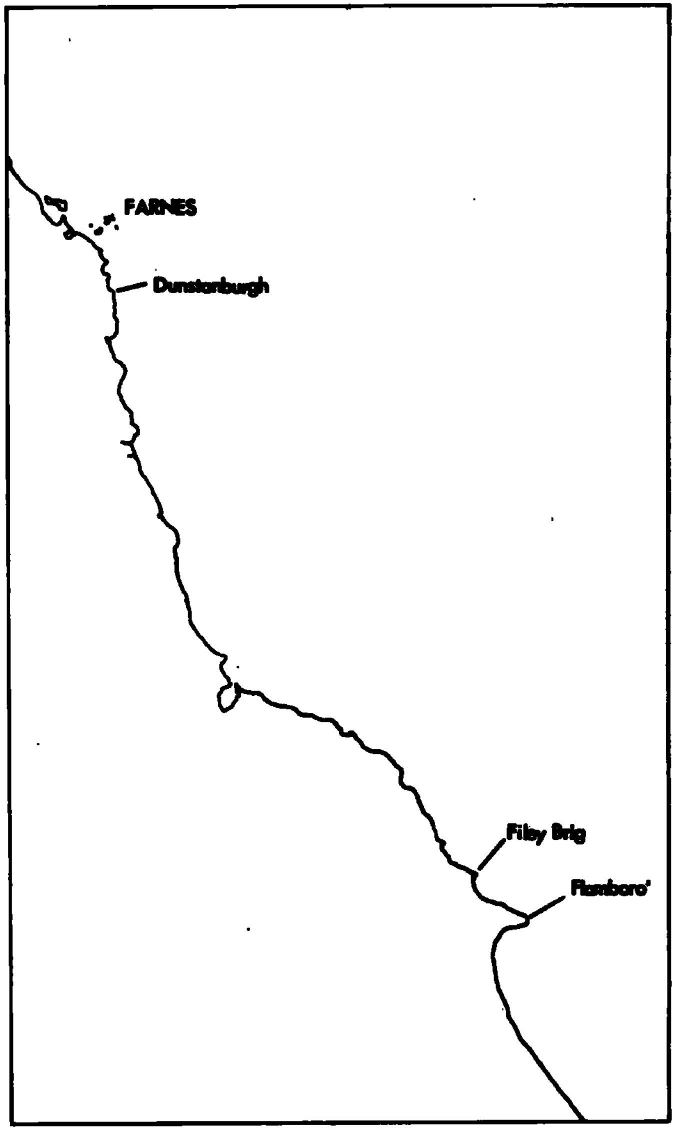

HARCAR
NW BROWNSMAN
P
B
SB
SE
Sii
K
Si
I
C
ST
PINN
SW

Fig. 2

THE FARNE ISLANDS AND ADJACENT COASTS, SHOWING MAIN BREEDING AREAS OF SHAG

Open star	Rattray Head
Filled star	Fife Ness


Troup Hd.
Cruden
Fowlsheugh
Lunan
May
Craigleith
Lamb
Bass
Inchkeith
Brander
St. Abbs
Burnmouth
FARNES


FARNES
Dunstanburgh
Filey Brig
Flamboro'

Marking

Population studies of animals in their natural habitat can only be maintained if two conditions are fulfilled:-

1. An unbiased sample of the animals must be marked in such a way that the animals behave normally.

2. It must be possible to verify the methods of observation subsequent to marking _i.e._ it must be shown that the observations are not biased, or, if they are, the bias must be allowed for.

1. The method of marking

All the marked birds used in this study carried numbered metal rings issued by the British Trust for Ornithology. Until 1958-1959 these rings were of the 'clip' design, and were made of aluminium. This metal is relatively soft and is thus easily abraded. The 'mean expectation of life' of the inscription on these rings is approximately constant at 2.1 years (Calculated from Coulson and White (1957)), though the 'mean expectation of life' of a breeding Shag is 5.7 years.

The diameter of the aluminium 'clip' ring is 20mm which is _c_5mm wider than the tarsus of a male and _c_8mm wider than the tarsus of a female. Two per cent of the recoveries obtained from the use of aluminium rings were of the ring only, and in the majority of these cases it was clear that the rings had fallen off, certainly this would be the fate of the old, worn rings. Ring loss and wear has similarly been described in the Herring Gull (Poulding 1954, Olsson 1958), the Kittiwake (Coulson and White 1955), the Arctic tern (Austin and Austin 1956), the Fulmar (Dunnet, Anderson and Cormack 1963) and the Manx Shearwater (Harris 1964 b), (see also p 178 where the loss of rings from the Shag is calculated).

Shag ringing was started on the Farnes in 1947 by J.S. Ash and the Hon. M. Ridley but from 1951 the Northumberland and Durham Natural History Society organised all of the ringing (Table 1). This has been part of the National Scheme which to the end of 1963 had ringed more than 18,000 Shags (Table 2). The recoveries resulting from this marking were kindly made available for use in the present work.

In 1958, an experimental butt-ended monel ring was adopted for use on the Farnes. These are much harder and have a useful life which approaches that of the birds. However, the inscriptions are difficult to read with binoculars or a telescope and most of the original batch are now being renewed. Almost 25 per cent of those used in and before 1961 required replacement in 1965. However, none of the rings developed electrolytic crevice attack such as noted in the monel rings used on the Sandwich Tern

Table 1

Shag Ringing on the Farne Islands

Year	Pulli ringed	Pulli per pair(1)	Adults ringed for first time	Adults ringed for first time as % of all (2) breeding adults	
1947	"few"	-	>1	-	
48	3	-	"	-	
49	22	-	?	-	
50	12	-	?	-	
51	37	.43	13	7.5	
52	50	.52	39	20.1	
53	61	.53	55	23.7	
54	100	.79	30	11.9	
55	101	.73	82	29.7	
56	133	.88	62	20.4	
57	177	1.10	72	22.4	
58	145	.84	36	10.4	
59	197	1.06	75	20.3	
60	202	1.03	65	16.6	
61	301	1.41	47	11.0	
62	297	1.23	52	10.8	
63	328	1.19	48	8.8	
64	358	1.16	26	4.2)	6.1
65	442	1.24	60	8.2)	
Total 1951-1965	2929	-	762	-	

Total recorded approx. 3730

(1) = maximum number of nests in that season

(2) = 2 x (1), (1) derived from Fig. 13

Table 2

The B.T.O. Ringing and Nest Record Schemes

Annual Statistics for the Shag

Year	No. of Nest Record Cards		No. of Pulli ringed
	Individual	Colonial	
1947	2	0	+)
48	2	0	+) not
49	0	0	+) published
50	5	0	119
51	9	1	174
52	30	1	265
53	48	5	292
54	33	5	376
55	13	3	527
56	38	2	453
57	38	6	832
58	7	3	805
59	9	7	1,256
60	50	2	1,490
61	10	10	2,173
62	57	3	2,797
63	21	6	2,517
64	160	1	?
Totals	532	55	14,076('50-'63)

The Grand Total of Adult and Pull. Shags ringed to 1963 is 18,031 (*c.f.* Cormorant 7,330) and Eider. In 1962 a 'clip' monel ring similar to that used on Swans was introduced, with a deeper inscription. However the numbers are much more difficult to read than those on the aluminium rings or even of the butt-ended monel. Chrome plating on one batch has worn irregularly and flaked off making the inscription especially difficult to read.

Finally, in 1964, a Ni-O-Nel butt-ended four digit (instead of the cumbersome, but usual, seven) ring was specially made for use in the present study. This ring combines the large clear inscription of the aluminium rings with a durability in excess of the monel. The number is repeated twice, horizontally, so that it is not necessary to wait for the individual to turn around to read the number on a live bird. Since there is no clip the ring offers a minimum obstruction and in general, appears to be highly satisfactory. It is possible to read the number on the new ring at 80 yards using a x 60 telescope. Even so, it will be obvious that clearly distinguishable colour-rings would be a much quicker,less arduous and therefore more efficient method of identifying the birds in the field. The colour-rings now used (described by Coulson (1963 c)) allow the identification of any marked bird at any distance normally required, depending only on an uninterrupted view of both legs. The colour-rings were made of 'Darvic' and the adhesive used is 'Tensol cement No. 7' both manufactured by I.C.I. (The manufacture of the rings has been described by Coulson (1963 c) except that 'Evostick' is no longer considered a suitable adhesive) Celluloid rings were used in 1961 and replaced later. They were discontinued since they abrade quickly and the colours fade (Owen and Phillips, 1956; Coulson 1963 c).

The numbers of adults colour-ringed on the Farnes each year are given in Table 3 . Before embarking on such a programme it was first necessary to survey existing colour-ringing schemes but it was found that there was no overlap with other work. A few adults were colour-ringed on Inner Farne in 1954 by M.J. Cullen but soon lost their rings.

A small number of the colour-rings used early in this study became cracked, allowing expansion. Unfortunately, expanded rings jam on the knee or above it, on the thigh, and if the ring becomes permanently jammed there, the bird is crippled. Normally however, the colour-rings and metal rings do not interfere with the birds behaviour in any way, and the few that were affected in the early part of this study do not change the results of the work since they were withdrawn from the analyses.

Table 3

Number of Shags identified for the first time in successive seasons

Season	Colour-ringed for first time	Ring number read for first time
1961	16	0
1962	315	10
1963	156	54
1964	88	58
1965	92	63
Total	667	185

Note: Many of the birds in the second column are caught in succeeding seasons, therefore the two columns can not be added

Routine observations

The various requirements of the methods of site identification were met by using sketch maps of the nesting areas with each site numbered. This method has the following advantages:-

1. Permanent

2. Independent of nest (to record defended sites, and because labels tied to nest material are moved from nest to nest by the birds; this is especially true of a nest which is under construction)

3. Suitable for identifying inaccessible sites

4. Did not involve marking the rocks in any way, this is best avoided in a bird sanctuary.

5. Weather has no effect on method (i.e. even if nest is washed off)

6. Recording of nest number did not involve unecessary approach, or climbing

The disadvantage of this method is that it can only be used accurately by someone completely familiar with the nesting pattern, for in different seasons nests are built in slightly different positions, or embrace two sites, and the three dimensional nature of the nesting areas is difficult to represent on a map. The routine observations were:- site number,contents of nest,identification of birds present. Eggs were labelled (with biro) and measured on the more accessible sites. This routine was supplemented by hide observation and weighing of chicks, in a special study area of about 60 nests on Brownsman. Separate records of birds seen away from the nest, were kept. The Farne Islands Committee of the National Trust kindly allowed the author to stay on Brownsman until the regular watchers arrived in early May. Thereafter access was restricted during periods of high seas. Visits throughout the breeding season were at, on average, intervals of about three days.

Identifying the sexes

From measurements made by J.C. Coulson in 1962 the bill depth, but not bill length or wing length, was found to be bi-modally distributed. Further work on museum skins showed that the bill depth of the male Shag is significantly greater than that of the female throughout its fledged life (Table 4). First autumn birds have been less deep bills but thereafter there is no significant change. The standard deviations (S.E. is given in Table 4) were greater in the first autumn females and a scatter diagram indicated that some may have been incorrectly sexed. It is of interest to note that the bill of the museum skins had shrunk by significant amounts during their storage. Males had deeper bills in each of the other <u>Phalacrocrax</u> <u>spp</u>. (Table 4).

Having established that the two modes of the bill depth frequency distribution were sex determined, the two distributions were separated following the methods of Harding (1949). The results are given in Table 5 and the following 'sexing' procedure was drawn up in the form of a key.

1. Bill greater than 12.0 mm, no conflict with 'sexing' of mate = ♂

2. Bill less than 10.5 mm, " " " " of mate = ♀

3. Bill less than 11.3 mm, " " " " of mate = ♀

Table 4

Sex and Bill depth in P. aristotelis and other species (in mm.)

Museum	♂	♀	Sample
First Autumn	10.76 ± 0.11	9.96 ± 0.76	26
1* Other Immatures	10.95 ± 0.49	10.01 ± 0.45	48
2* Adults	11.38 ± 0.10	10.01 ± 0.45	44
Field			
3* Adults	12.11 ± 0.03	10.42 ± 0.03	238
Museum other species			
P.a. desmarestii	10.6	9.5	10
P. atriceps	12.3	11.2	23
P. bougainvillei	10.8	9.7	12
Field other species			
P. carbo (shot Lune estuary Lancs.)	17.3	14.6	10

1* retaining some juvenal-post juvenal plumage

2* nuptial plumage

3* measured by J.C. Coulson; others by author

Table 5

Separation of the combined frequency distribution of male and female bill depths (after method of Harding 1949)

Bill depth	Total percentage frequency	Percentage male	Percentage female	Probability of male
10.50	18.1	0.1	18.0	.005
10.75	15.4	0.4	15.0	.026
11.00	10.3	1.3	9.0	.126
11.25	8.7	3.7	5.0	.425
11.50	10.6	8.5	2.1	.802
11.75	14.6	14.0	0.6	.959
12.00	20.3	20.0	0.3	.985

4. Bill greater than 11.3 mm, no conflict with 'sexing' of mate = ♂

Pairs with both birds in categories 3 or 4 and birds not sexed at this stage referred to Fig. 3 , any still doubtful, were then sexed from age of mate. Fig. 3 was drawn up from the data of Table 4 and Table 6 , the lines a,b being the regression lines (x on y) for each sex. This somewhat gross method worked well when checked against other sex specific characters in succeeding seasons, namely:-

1. Call

Male a deep resonant croak or grunt

Female a hissing sound

2. Nuptial display

Male, unlike female, has a conspicous 'throwback display' used for soliciting females (see Appendix D)

3. Nesting behaviour

Male brings nesting material

4. Appearance and weight

If both birds of a pair are seen on the nest together the bill of the male appears both shorter and thicker and the neck and body generally of the male appears larger. Of the seventeen adults weighed by Show (1960), nine males averaged 1,919 gm, and eight females averaged 1,600 gm. Of seventeen adults weighed by J.C. Coulson and T.H. Pearson in 1962 on the Farnes, twelve males averaged 1,853 gm, and five females averaged 1,660 gm.

Fig.3

METHOD OF SEPARATING THE SEXES FROM BILL AND WING MEASUREMENTS

(a) ♂ regression bill depth on wing length, reducing x errors

(b) ♀ regression bill depth on wing length, reducing x errors

x = bill depth mm (from gonys)

y = wing length mm. straight chord (carpal joint to tip 9th pp)

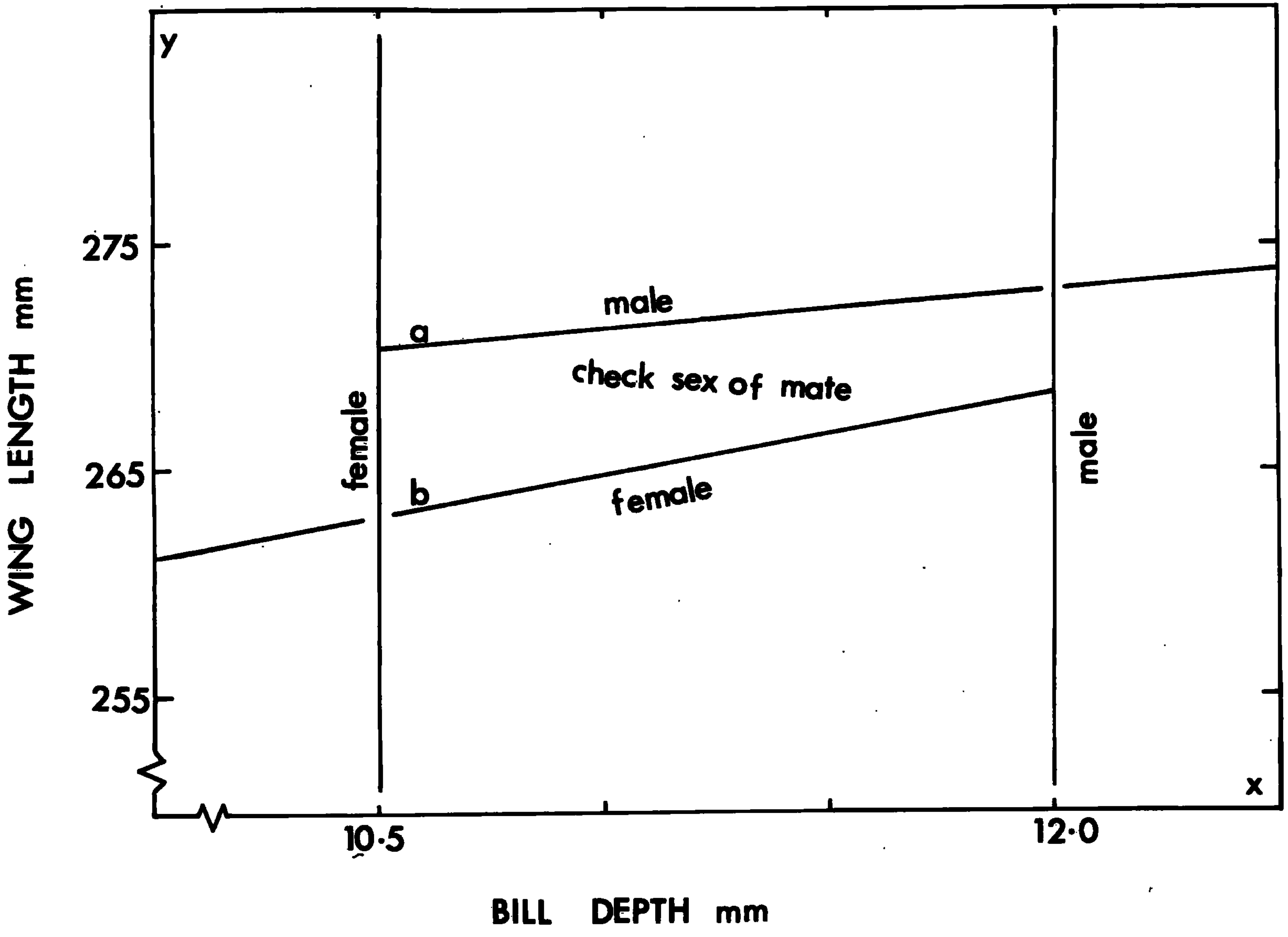

y
275
265
255
WING LENGTH mm
female
a
male
check sex of mate
b
female
male
x
10·5
12·0
BILL DEPTH mm

Table 6

Correlation of bill depth and wing length for 37 pairs each of known sex in 1962

♂ $r = +0.48$ $p = <0.01$ ♀ $r = +0.50$ $p = <0.01$

x = bill depth y = wing length (carpal joint to tip 10th Primary, straight chord)

♂ $y = 8.77x + 167.0$ $(S_y = 1.74)$

♀ $y = 7.00x + 190.5$ $(S_y = 1.42)$

♂ $x = 0.026y - 58.37$ $(S_x = 0.26)$

♀ $x = 0.032y - 72.82$ $(S_x = 0.26)$

Mean wing length ♂ = 272.94 ± 6.23 (SD) mm

Mean wing length ♀ = 263.49 ± 5.05 (SD) mm

Mean bill depth ♂ = 12.2 ± 0.34 (SD) mm

Mean bill depth ♀ = 10.4 ± 0.34 (SD) mm

Finally it should be pointed out that 'reversed' copulation is frequent and this behaviour could not be used to separate the sexes.

Each of the 667 captured Shags are of known sex as were most of the identified birds seen at nests. In addition all dead colour-ringed Shags were sexed by examination of the gonads and these have confirmed the field methods listed above.

Sex of the chick

Snow (1960) considered that male chicks were heavier than female, and that chicks could be, tentatively, 'sexed' from their weight from about the 33rd day. In the present study the weights of 37 chicks of this age are available. The last weighings of each chick beyond the 33rd day were found to form a bi-modal frequency distribution. Since there is a significant sex difference in the bill depth of chicks in their first autumn (Table 4) these measurements were also obtained from the weighed chicks. The correlation between bill depth and weight in these 37 chicks was found to be significant ($r = +.72$ $p = < 0.05$). A plot of bill depth(y) against weight(x) (Fig. 4), about the y on x regression line accentuates the bi-modality of the apparently sex determined distribution. No correlation was found between the modes and weight variation within or between broods of various sizes. (The scatter in Fig. 4 includes known third hatched chicks from three chick broods, separately indicated). The regression line of y on x was used as a base of the scattered distribution. Each point was projected to its 90° intercept with the line, to form a frequency distribution of points along the line. The modes of this distribution were separated according to the methods of Harding (1949). The method appeared to be satisfactory, but confirmation, or otherwise, will not be forthcoming until the chicks breed. Until then the 'sexing' must be regarded as tentative.

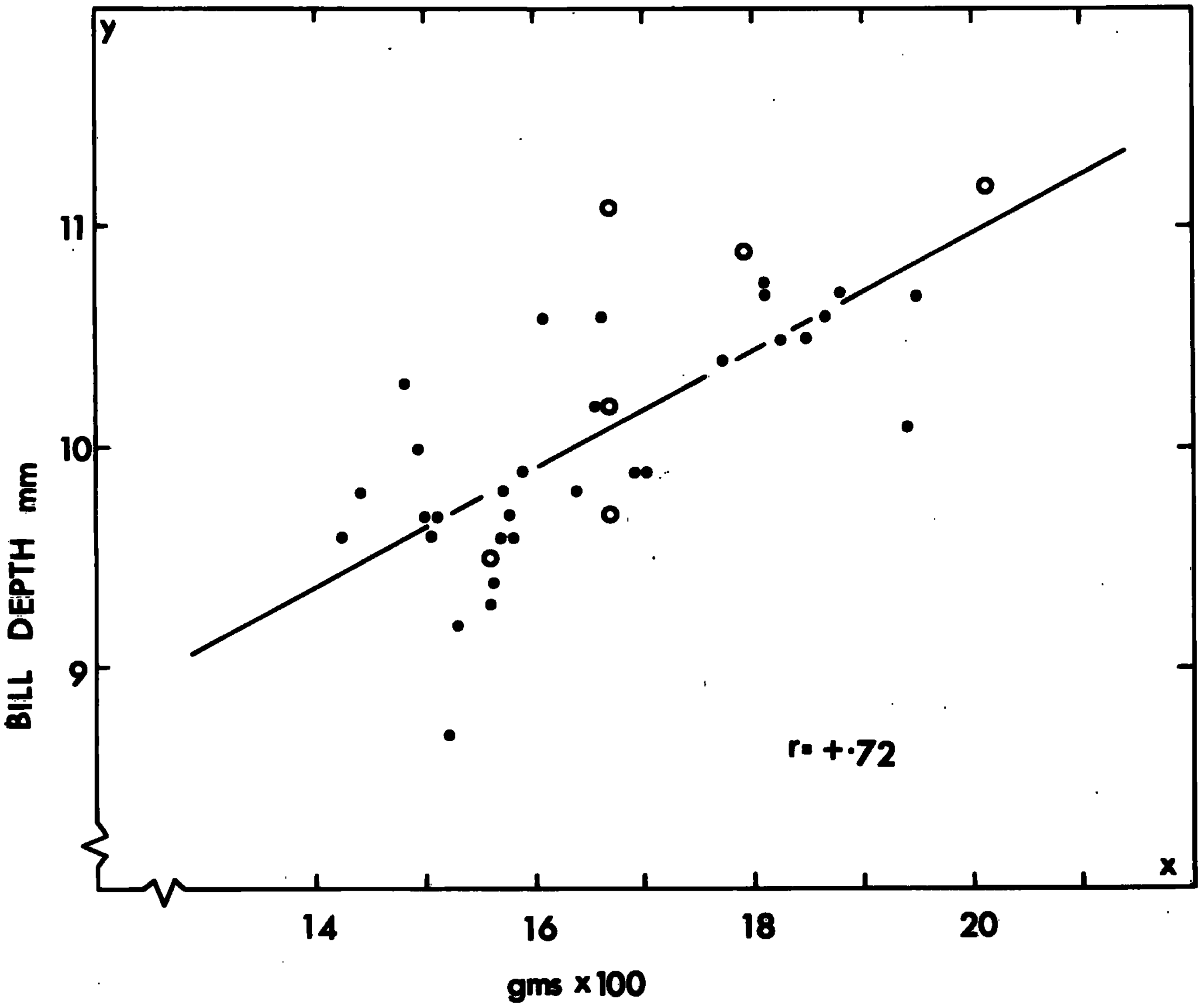
Fig. 4

CORRELATION OF BILL DEPTH AND WEIGHT OF CHICK

Regression line y on x <u>i.e.</u> reducing y errors open circles third hatched chicks from broods of three

x = gms.(hundreds)

y = bill depth mm.


y
x
11
10
9
BILL DEPTH mm
14
16
18
20
gms x 100
r= +·72

The study population, individually recognised, or aged as a proportion of the total population

In 1963, 335 occupied nesting sites were recorded, and allowing two birds in each case, 69 per cent (462) of the nesting populations were recognised individually, or aged (*i.e.* 1,2,>2). In 1964, 395 nest sites were recorded and 75 per cent (596) of the nesting population, were used in this study. The improvement in 1964 concerned all areas. More than half of the birds missed were in two areas which account for 35 per cent of the total nest sites and in the special study area on Brownsman as few as 3 per cent (1964) of the birds were missed. Most of the birds missed in the well covered areas were associated with brief and unsuccessful nestings, and would quickly move to other sites. In general the cover was similar in both seasons and supports, for example, comparison of mortality in the two years based on sight records. Though colour-ringed birds are far more conspicuous than other birds and form a negligible part of the 'missed' birds, a few were missed, and a small correction factor for this is introduced into the calculations of mortality. The most serious form of bias is that females breeding for the first time are especially shy compared with males of similar age. This is discussed later, but at this stage it must be pointed out that two year olds (*i.e.* breeding for the first time) in general can easily be recognised by their plumage and that they need not be captured. Thus the study methods do not exclude shy birds breeding for the first time as two year olds, if they can be seen from a distance.

Estimation of age in unringed Shags

The practical difficulties of marking an adequate sample of the recruits to any wild population of birds at a stage during which age can readily be estimated (e.g. as pulli) are such that birds of unknown age will form a substantial part of the recruits to the breeding population. The proportion of 'un-ringed' Shags in the colour-ringed population on the Farnes is decreasing as the result of using more durable rings, ringing a higher proportion of the young, and because few 'non-ringed' breeding adults are missed each year. Thus the percentage 'unringed' entering the breeding group in 1962 was 64; in 1963, 56 and in 1964, 51. In the oldest age group used in this study however 87 per cent had been originally ringed as 'adults' rather than as 'pulli'. If these 'adults' could not be studied as birds of known age only ten instead of 79 birds would be available in this old age group. Methods of integrating these birds, first ringed as adults, is needed so that, where possible, they can be reliably placed into age categories.

Age and Plumage

Prior to this study, Coward's (1918) conclusion "most writers have no real knowledge of the changes of dress in the Shag" was still valid. However, Witherby et al (1940) stressed the amount of individual variation and described two pre-adult plumages; the adult plumage being reached in the third year. The terminology of Murphy (1936) forms the basis of that used here, since it has greatly clarified the study of moult in other Shag species (Turbott 1956) i.e.:-

1. Juvenile plumage, a downy nestling plumage which is completely shed by the 35th day.
2. Juvenal plumage, the plumage of the fledged young.
3. Post Juvenal, a sub adult plumage completely replacing the Juvenal.
4. Nuptial, the 'final' plumage of Coulson (1959 a) and the 'adult' plumage of Witherby et al 1940.

This plumage is tri-phasic

(i) pre nuptial

(ii) nuptial

These phases are not distinct in aristotetlis, in contrast to P. atriceps and P. punctatus (Murphy and Turbott respectively loc cit)

(iii) post nuptial. This is well developed in some species (G. van Tets in litt.) in which there is a temporary reversion to an immature type of plumage at the end of the breeding season, but in aristotelis this is confined to the aquisition of a brown chin and loss of the crest.

Plumage of the underparts

A study of 180 musuem skins and field work on the Farns is combined to establish the progress of the post juvenal and nuptial plumages, the time courses of which are given in Fig. 5 . The diagrams showing typical ventral breeding

Fig. 5

PLUMAGE CYCLE OF VENTRAL PLUMAGE AND AGE, BASED ON MUSEUM SKINS

The score refers to the proportion of the underparts between bill and vent which has been replaced by the new plumage. E.g. score of 9, nine parts complete, one part still to moult.

The final section of the nuptial plumage is extrapolated, since that proportion which complete the moult are indistinguishable from adults. See Fig. 6

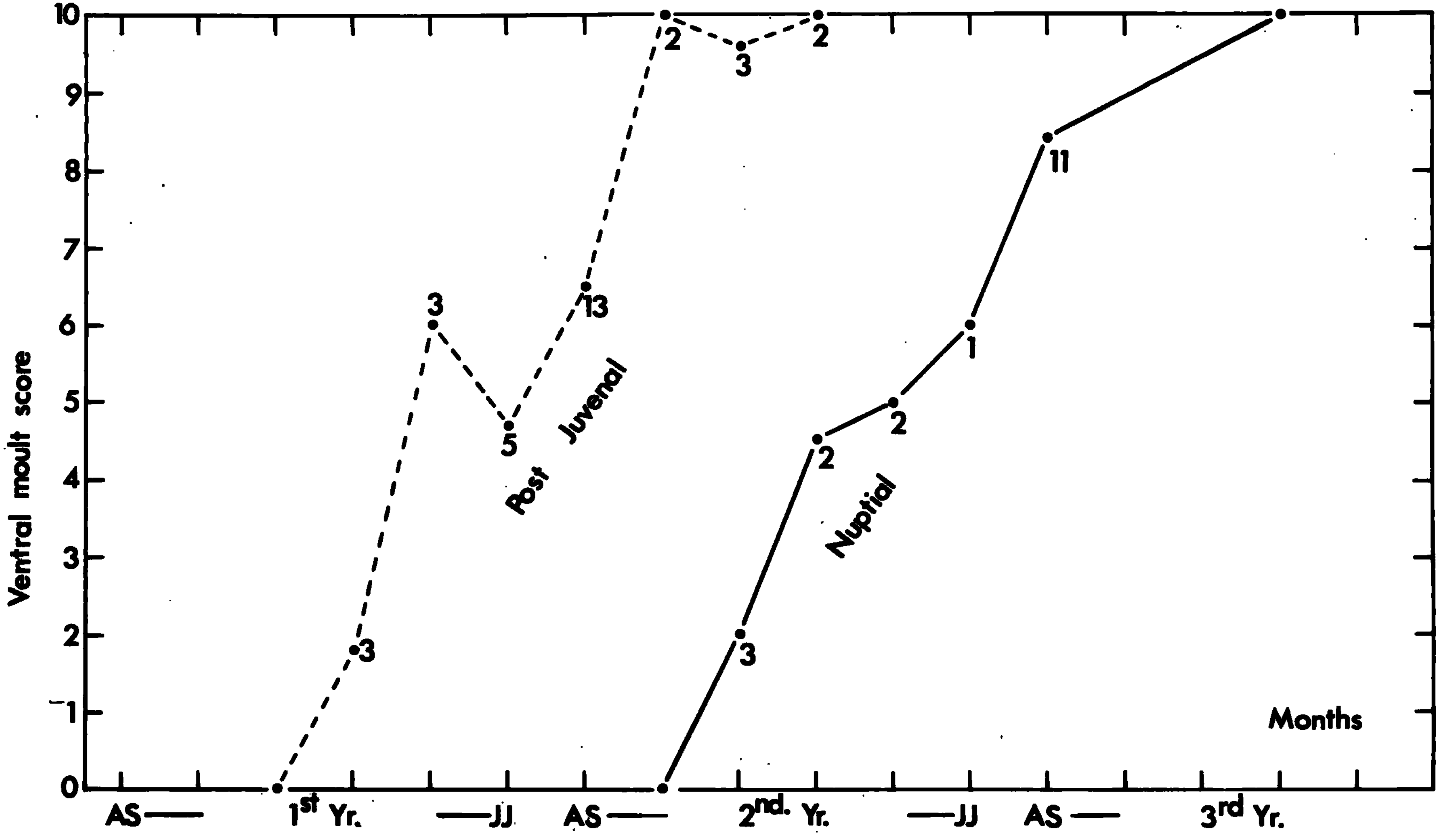
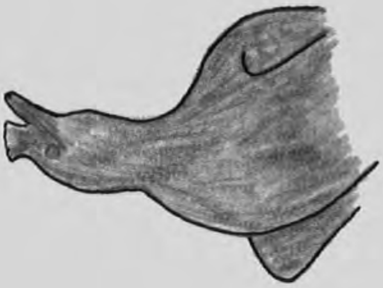

Ventral moult score
10
9
8
7
6
5
4
3
2
1
0
AS ——
1st Yr.
—— JJ
AS ——
2nd. Yr.
—— JJ
AS ——
3rd Yr.
Months
Post Juvenal
Nuptial
3
3
5
13
2
3
2
3
2
2
1
11

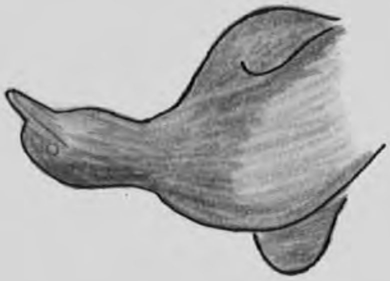
Fig. 6.

ONE YEAR

TWO YEARS

FULL ADULT





season plumages of birds aged 3,12,24 and 36 months are also given in Fig. 6 . Separation of age groups on the ventral plumage is easy and experience of the 1961 and 1962 cohorts suggests that birds can be aged (in years) , as 0,1,2 and >2 with an error in each group of less than two per cent. One breeding three year old had an index rating of 10, but had a considerable amount of juvenal plumage around the vent and under tail coverts and this is why the maximum index does not include the very last stages of moult, see Fig. 5 . The only two year old which had moulted all the ventral juvenal feathers,had however, retained a juvenal primary.

The Primaries

A preliminary investigation in 1962 by J.C. Coulson suggested that the primary moult might be a useful age specific factor, enabling the separation of immature and older birds.

The Primary moult begins with the first primary (that nearest the carpal joint) and ends with the eleventh. The progress of the moult is followed by a score similar to that used by Dorward (1962) and Ashmole (1962) except that the decimal part of the individual score was eliminated. A completely moulted wing would score 11 whilst the intact wing of a first autumn bird would score 0, and the progress, of the moult was averaged for the birds in each bi-montly age group and plotted for the first two years in Fig. 7 . The progress beyond the second year is too complicated to sort out using the skins alone, for in some birds there are three primary moult cycles present at one time, and the age of the birds is not known. There are little data for Farne birds outside the breeding season and so the progress of the nuptial primary cycle is not discussed further.

The post-juvenal primary moult begins in the Shags first Spring and some of the birds have completed the moult by October. The latter birds have a moult cycle length of about eight months or 22 days per primary. This compares with 14 days in the Glaucous Gull (Johnstone 1961) and about 24 days in the Black Noddy (Ashmole 1962).

Primary feathers not moulted by October-November of the Shags second autumn are retained until the second i.e. nuptial cycle gets under way (Fig. 8), six months later. The birds which show this overlapping of moult cycle generally retain the tenth primary which appears very worn and bleached in the breeding season. Juvenal or post-juvenal primaries are brown and dark brown respectively, whereas the nuptial primaries are black with a green sheen. The proportion of birds of various ages from the 1963-1964 ringed recruits with retained immature tenth primaries can be calculated from Fig. 8 . On average it would appear that 63 per cent retain the juvenal primary and 25 per

Fig. 7

THE PRIMARY MOULT CYCLE AND AGE

Open circles ♀

filled circles ♂

Score is average numbers of primaries completed per individual. There are 11 Primaries.

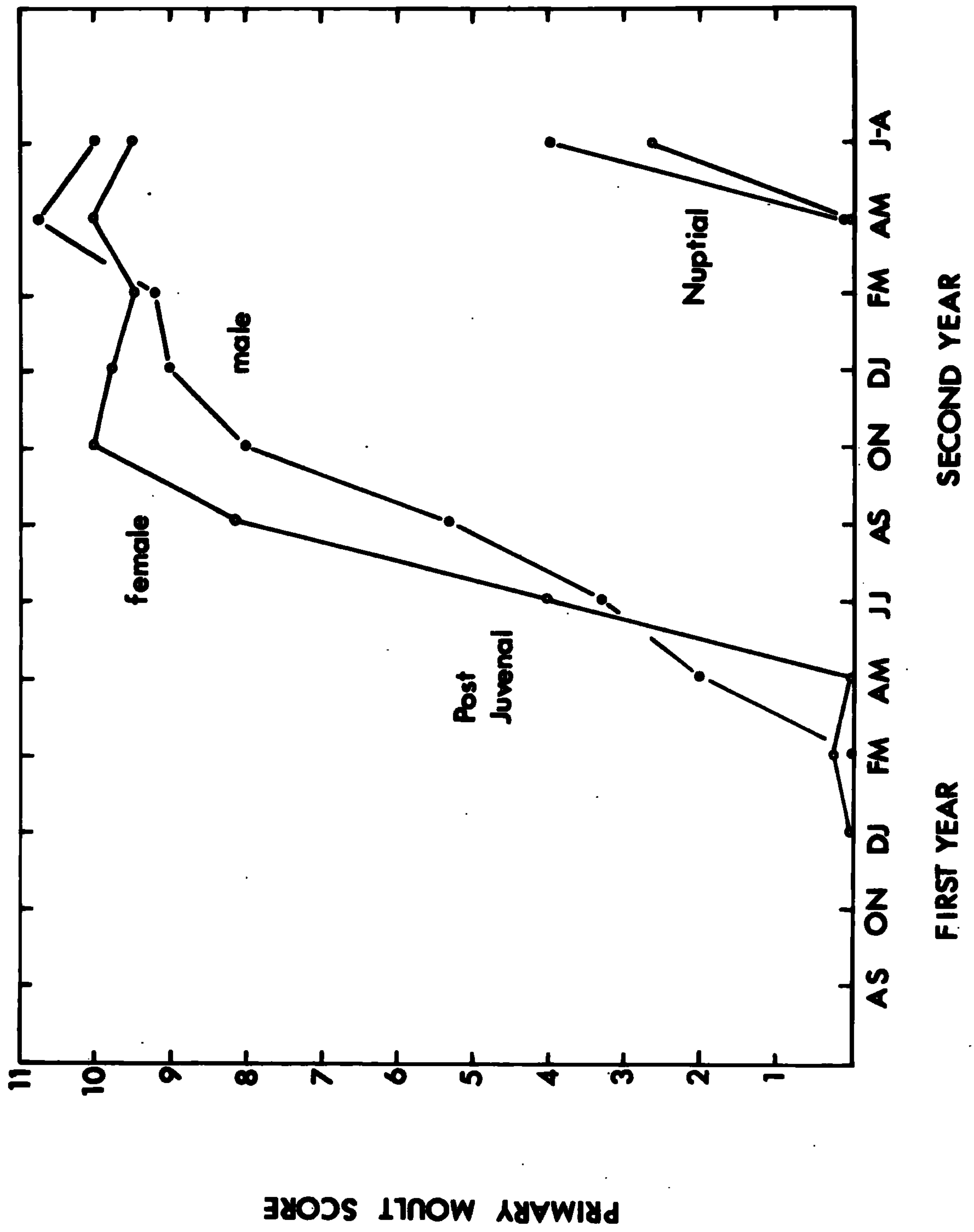
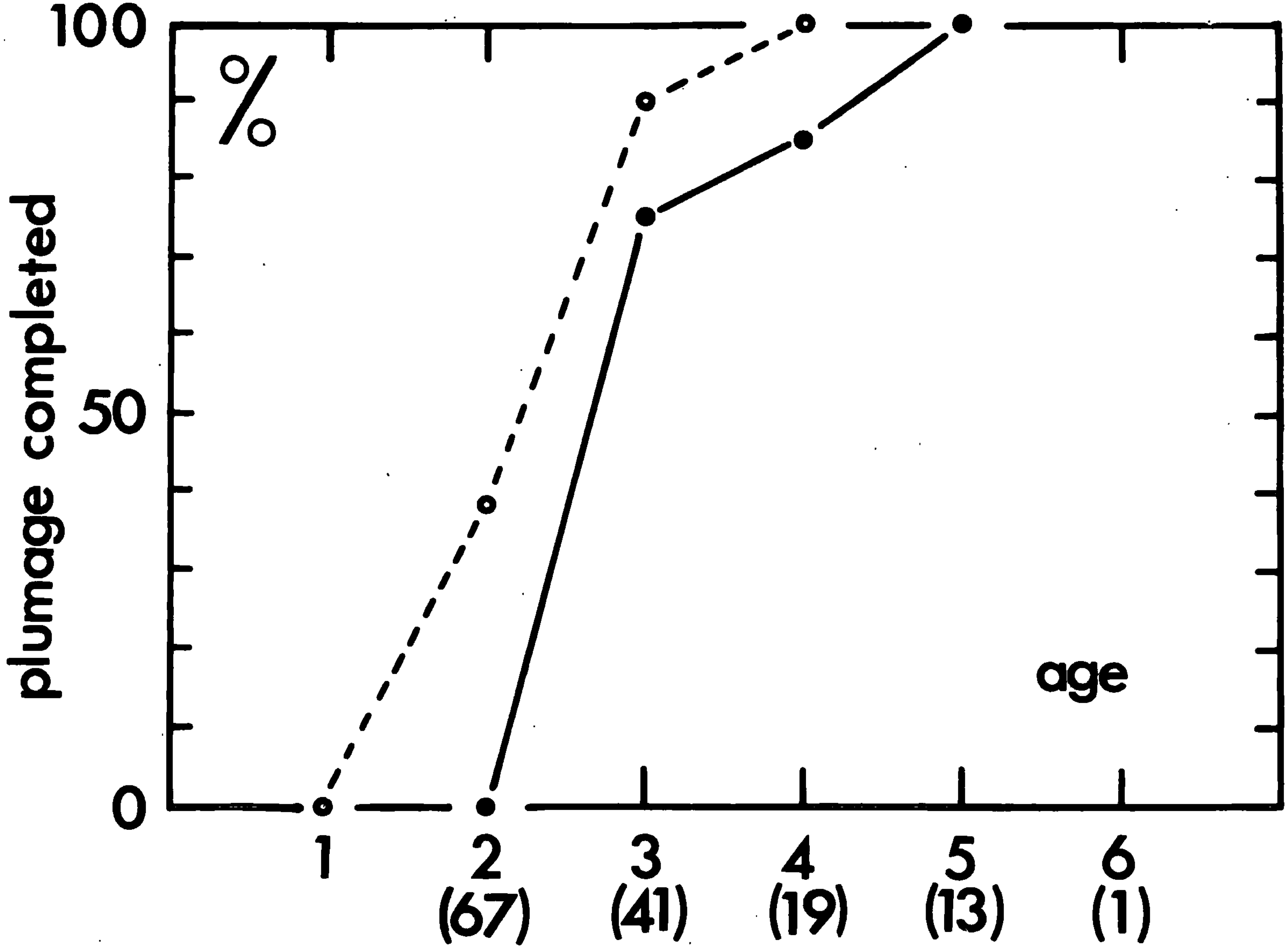

PRIMARY MOULT SCORE
11
10
9
8
7
6
5
4
3
2
1
AS
ON
DJ
FM
AM
JJ
AS
ON
DJ
FM
AM
J-A
FIRST YEAR
SECOND YEAR
female
male
Post
Juvenal
Nuptial

Fig. 8

THE PERCENTAGE OF EACH AGE GROUP WITH JUVENAL, POST JUVENAL OR NUPTIAL PRIMARIES ON FIRST CAPTURE.

In the second year 63 per cent have not shed all the juvenal primaries, 37 per cent have completed the post juvenal moult, but none have completed the nuptial. In the following year the proportion (ten per cent) which have still not completed the juvenal moult, is approximate. In the fourth year it is assumed that none of the primaries is juvenal. It is frequently impracticable to distinguish 3 year old juvenal and worn and bleached post juvenal primaries in the third year.



%
plumage completed
100
50
0
age
1
2
(67)
3
(41)
4
(19)
5
(13)
6
(1)

cent retain the post juvenal. However 15 per cent still have a post-juvenal primary (and frequently its covert) at the age of four years. This implies that some birds were overlapping two complete cycles. This is supported by the fact that some museum and field specimens of all ages beyond the aquisition of the nuptial plumage simultaneously showed signs of three moult cycles, whereas two is normal in a bird with a retained primary. This overlapping of cycles is probably more extensive in adult White Boobies which Dorward (1962) describes as having "three spaced concurrent cycles". It is noteworthy to add that a Shag showing these three concurrent cycles will have retained at least one primary for a little over three years. Since it is a simple matter to separate the one and two year olds, by their plumage, no further consideration of them is required here. It is possible to detect some 15-20 per cent of three and four year olds (virtually 15-20 per cent of recruits), from their especially retarded primary moult, but it is likely that these retarded birds may be a biased sample of their age group in other ways (see p8)

Age and Capture

Male

Fig. 9 gives the number of birds of various known ages caught for the first time in the period 1961-1965. The age of birds older than two, caught for the first time 1963-1965

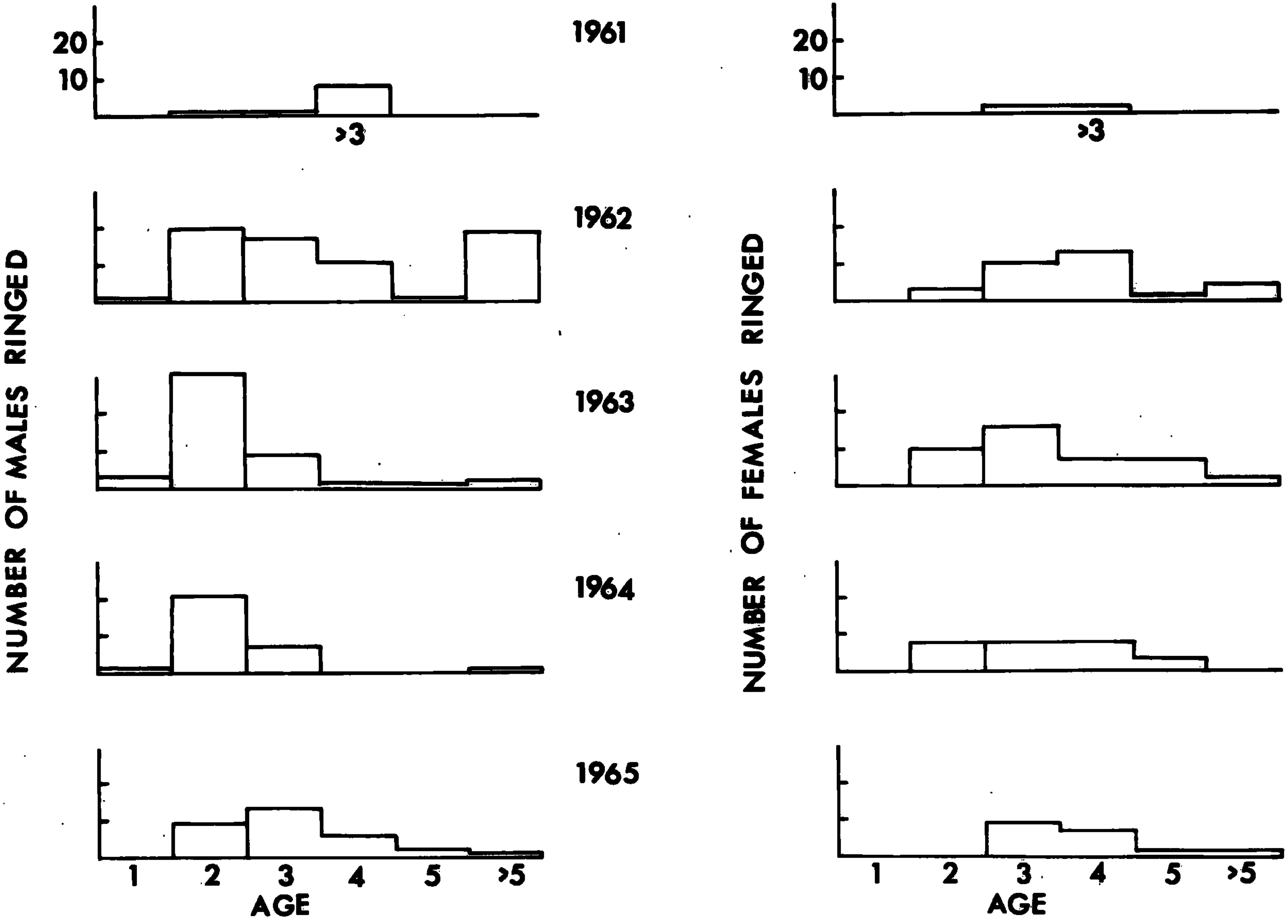
Fig. 9

THE NUMBER OF SHAGS CAUGHT FOR THE FIRST TIME AND

OF KNOWN AGE *i.e.* RINGED AS PULLI

(BUT SEE TEXT FOR 1965).

Note that males are caught at an earlier age than females.



NUMBER OF MALES RINGED
20
10
>3
1961
1962
1963
1964
1965
1
2
3
4
5
>5
AGE
NUMBER OF FEMALES RINGED
20
10
>3
1
2
3
4
5
>5
AGE

shoud give a measure of the age of non-ringed birds likely to be caught for the first time during these years. In each case it will be seen that the majority of birds belonged to the third year group. This was not so apparent in 1962 when more old birds were caught, partly because of increased ringing effort (Table 1 p10) and partly because few ringed birds were recaptured in 1961. Un-aged males form a small group however in any one season since most are caught at age two (this is not apparent from Fig. 8 in 1965, when many ringed two year olds were captured but not colour-ringed). If we assume that the un-aged males are all aged three, they form only 18 per cent of the age group for the year 1962-1965, thus introducing a small potential error of mis-ageing. This potential error however, would be higher in the 1950's when ringing pressure was lower, and therefore some of the oldest birds' estimated age would be too low. Throughout this work six age groups of male are considered:-

1yr: One year old)
Negligible 'ageing' error
2yrs: Two year old)

3yrs: Three years old 'ageing error' in years 1962-1965 of less than ten per cent, or about half the potential eighteen per cent, mentioned earlier in this paragraph.

4-5yrs: Age four or five years, some birds slightly older than five, a carry over of the error in the previous section, offset slightly by the ringing of undetected two year olds prior to 1962.

6-8yrs: Aged, six seven or eight years, error greater than in previous age group. This is slightly offset by adoption of seven as the mean, since this is greater than the weighted mean of the age class.

8+yrs: Aged nine or more. Most birds are of minimum age, offset by the fact that this is a comparatively homogenous group. No marked age specific trends within this group were found in preliminary analysis and none appears likely.

The aim of this grouping (as with the females) has been to provide a group of at least 30 birds of known age which is tangible in both statistical and biological methods. For these practical purposes the groupings can be considered as having mean ages of 1,2,3,4½,7 and 11, years respectively.

Female

Proceeding exactly as in the male, Fig. 8 shows clearly that females are caught at a later age than the male. The majority of non-two year olds are not caught at three years, but at an average age of about four. In addition pre 1962 bias due to the catching of un-detected two year olds is very much less than in the male, and is almost negligible. Two year old females unlike the males, are difficult to catch unless they are defending young or nearly hatching eggs and some escape ringing, probably to be caught as three or four year olds. Thus unringed females are recruited at a higher rate than unringed males, since fewer of the unringed proportion are aged from plumage. If we assume the age of an unringed female is four then 64 per cent(c.f. 18 per cent in the male) of the four year olds enter the colour-ringed population as 'unaged' birds. Before estimating the age of this 64 per cent, an independent method will be considered.

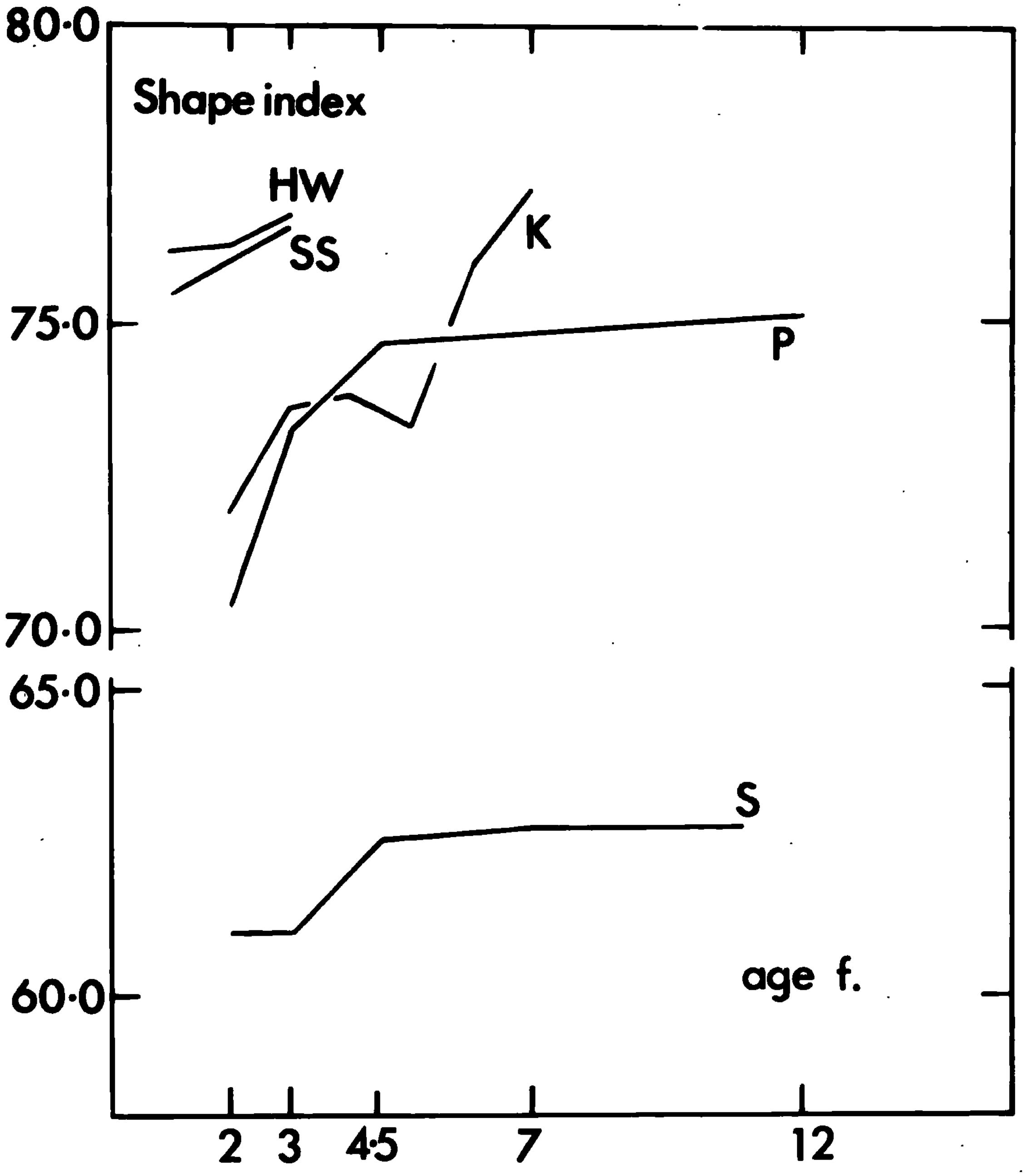
Shape of egg and age of female

Nice(1937) found that year old Song Sparrows lay narrower eggs than older birds and investigated this as a means of estimating the age of unmarked females. However she found that this size difference was also influenced by the size of the female, by the number of eggs laid, and by individual variation. Unfortunately she was unable to separate these various effects. Kendeigh,Kramer and Hamerstrom (1956) found a similar age specific variation of shape in the House Wren using a shape index; $(\frac{\text{breadth}}{\text{length}} \times 100)$. Coulson (1963 b) found that older female Kittiwakes tend to lay eggs with a higher shape index (broader eggs), though these changes became less marked in successive breeding seasons. A comparative study of age and shape index in five species (Fig. 10) indicates that the shape index could be used to indicate the mean age of a group of birds in earlier age groups but that the age specific effect is less in the Shag than in either the Yellow-eyed Penguin (from Richdale 1957;

Fig.10

MEAN SHAPE INDEX OF EGGS IN FIVE SPECIES

S	Shag (this study)
H.W.	House Wren (Kendeigh, Kramer and Hamerstrom 1956)
S.S.	Song Sparrow (from Nice 1937)
K	Kittiwake (C/2 only, Coulson 1963b)
P	Yellow-eyed Penguin (by this author from Richdale 1957)


80·0
Shape index
HW
SS
K
75·0
P
70·0
65·0
S
age f.
60·0
2
3
4·5
7
12

calculated by this author) or the Kittiwake.

The age of female estimated from ringing as 'pulli' and from year of first ringing as 'adult', assuming that such an adult is four years old when first captured, is given with the respective shape index in Fig. 11 . There is no significant difference in the group of four and five year old birds ringed as 'pulli' and those ringed as adults in 1963 suggesting that the estimation of age of the 'adults' was sound. In 1964, the difference was more marked, despite the fact that the ageing error was known to be less, for fewer old, un-caught birds remained to be caught in 1964. Since the 4-5 year old adults in 1964 have a higher shape index than the 9-16 year group, it appears that the shape index can vary from one season to the next. This conclusion is supported by the indices from birds of known age(Fig. 11).

Shape index cannot be used to estimate the age of an individual since there is so much individual variation. However X the between clutch (= individual) variance is significantly greater than the within clutch variance; (for two year olds with no laying history in 1963, F = 3.20;0.05 >P>0.01) and this fact was useful in sorting out some of the double layings in one nest, mentioned later.

The female age class groupings finally adopted were:-

1 yr)
aged as in male, negligible error
2 yr)

3 yr: birds of known age i.e. ringed as pulli, no error

Fig. 11

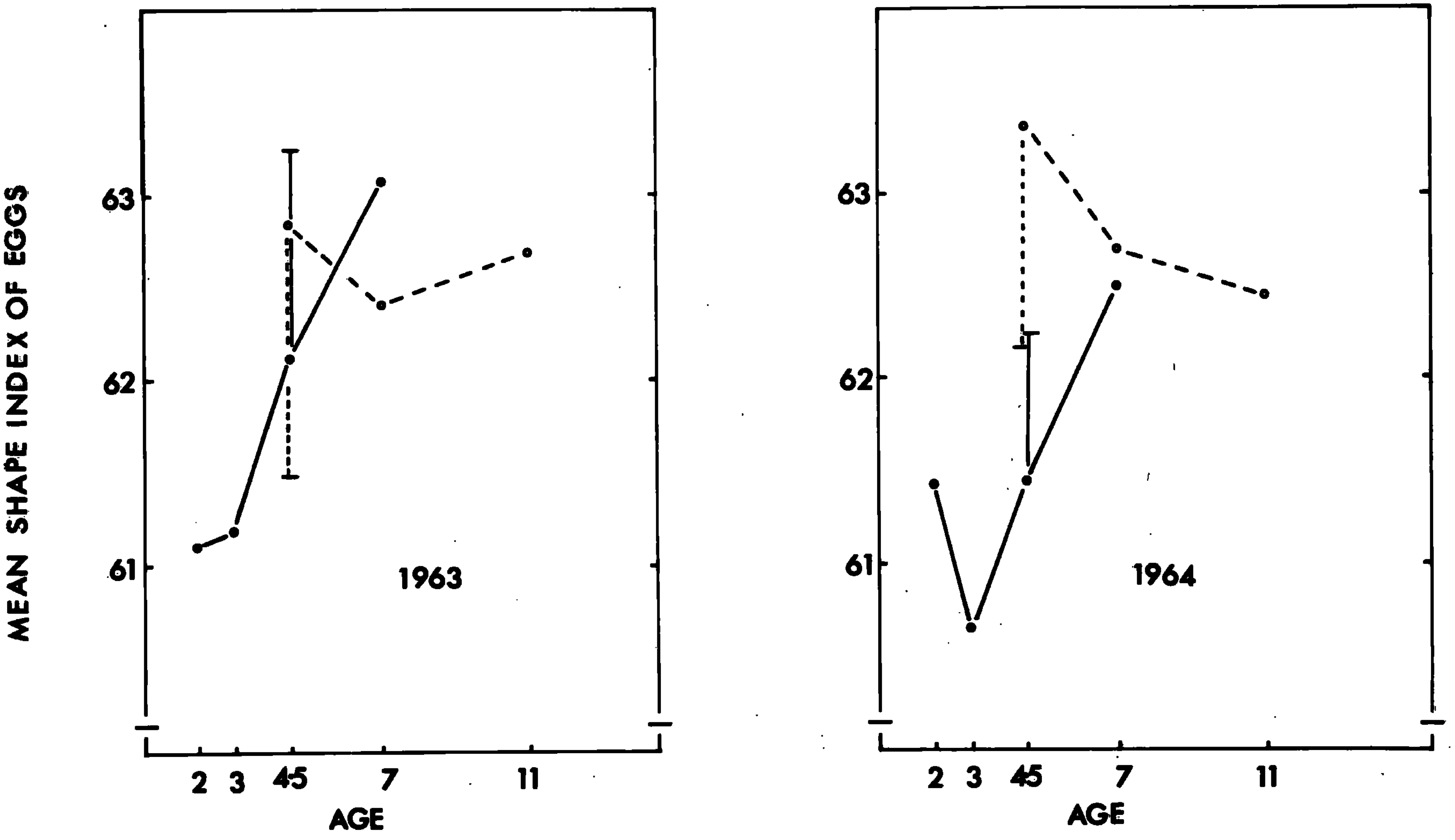
MEAN SHAPE INDEX OF EGGS AND AGE IN THE SHAG

Solid line birds of known age

Broken line estimated age from year of capture

The index of each egg laid by the female is averaged to give an individual index, these indices are then averaged. In this way most individual females could be sampled; the within clutch variation of shape index is small.

limits ± 2SE


MEAN SHAPE INDEX OF EGGS
63
62
61
1963
2
3
45
7
11
AGE
63
62
61
1964
2
3
45
7
11
AGE

4-5 yrs: a heterogeneous group consisting of about $\frac{1}{3}$ birds of known age (4 or 5 years old) and $\frac{2}{3}$ birds of average age four, but with a small number of three year olds. The average age of the group is approximately four and half years.

6-8 yrs: A similar group, but with an average of two and a half further breeding seasons breeding experience. The minimum age is five but a negligible number are of this age.

8+ yrs: On average represents another four seasons breeding experience, a very small number (less than 10 per cent) are of known age. This is a homogenous group however as far as age specific behaviour is concerned.

Prior to each grouping of the two sections of the 'aged' population, they were analysed separately, in each case supporting the above grouping method. Examination of trends disclosed one notable source of bias in the 3-5 female age group since the sample was almost entirely a 'caught' one. (A similar bias was known to occur in the two year age class but this did not matter since all the two year olds would be 'aged' from their plumage). The bias was due to the fact that young females can only be caught late in the incubation cycle or defending young, and birds with high egg loss are not usually caught. This bias was in the study of egg survival and another age class was used <u>i.e.</u> Age Class 4. This was classes 3, and 4-5 years combined plus those monel ringed females in easily accessible sites (to the ringer) which laid and which were never caught because they were too shy, or which lost eggs before they could be caught.

In older age groups this bias was negligible since their breeding success was much higher and fewer birds escaped ringing. Only a bird which had consistently been missed and therefore was unlikely to have reared young for more than three seasons could cause bias in the 7 year age class sample. Some of these birds were found (they were quite conspicous since they nested early and lacked colour-rings); and where possible, their ring numbers were read.

Whilst these groups form adequate working samples the fact that the male grouping was more satisfactory than that of the female was kept in mind, and checks using birds of known age only were made where necessary. It must be stressed that remaining errors of 'ageing' are errors of underestimation. This is especially true of the oldest age group, which is, however, a homogenous one since age specific effects do not occur to a marked extend beyond the ninth year. One of the best checks is the detection of an age specific factor which decreases with age (this could not happen if old birds were frequently being caught for the first time. Since such factors are found among the females the detection of other age specific variables can be attempted with some confidence. Finally it should be metioned that one population characteristic helps the methods outlined above. This is the increase of the population which reduces the average age of a bird caught at random in any one year.

Comma
X

Since most of the 'non-aged' birds are confined to inaccessible areas, it is possible to age three-quarters of the breeding population in any one season; with very little bias.

SECTION TWO

HISTORY AND GROWTH OF THE FARNE ISLANDS POPULATION

Introduction

There are at least four practical ways in which we can use the word 'population', to indicate the number of Shags in a particular area. The word is used in the following ways:

1. The breeding Shags on the Farne Islands during any one season (excluding non-breeders since these are spread out over the Forth-Farnes coast and freely mix with Shags from other areas). = Farnes population
2. Breeding Shags on the coast between Fife Ness and Flamborough in any period of time. = Forth-Farnes population
3. Breeding Shags outside the areas concerned in (1) and (2).
4. Non-breeding products of each or any combination of these populations in any proportion at any place. Hence the best use of 'population' is the precise "a group of Shags" using a prefix if a more precise definition is intended, or a suffix if another species is concerned.

Nowhere in this account does the word 'population' itself imply any assumption of age structure or other animal population characteristic. Used in this way 'population' is however, a convenient term referring to the inhabitants of a particular area.

The following survey of the population changes on and near the Farnes was made in order to establish the possible geographical origin of the birds which spread to the Farnes and as a background to more immediate studies such as immigration, emigration and choice of nesting areas. It is essential to examine changes in the adjacent populations so that the intrinsic dynamics of the study population can be evaluated. It is difficult to fix an arbitrary sphere of influence of these populations, but for present purposes they are defined as, those which breed on the coast between Moray Firth and the Humber. There is undoubtedly some genetic and physical exchange between populations north and south of the Moray Firth, but the populations in the north do not release an important contingent of immigrants to the Farnes and there is a gap in breeding distribution between the colonies to the north and west of the Pentland Firth and those in the Forth-Farnes area.

All estimates of pairs or nests in the remainder of this section refer to the maximum number of nests counted between mid May and mid June (Fig. 12). The estimates are thus more in the nature of an index. Later in this work (p. 169) the relation of this index to breeding strength will be described.

Fig. 12

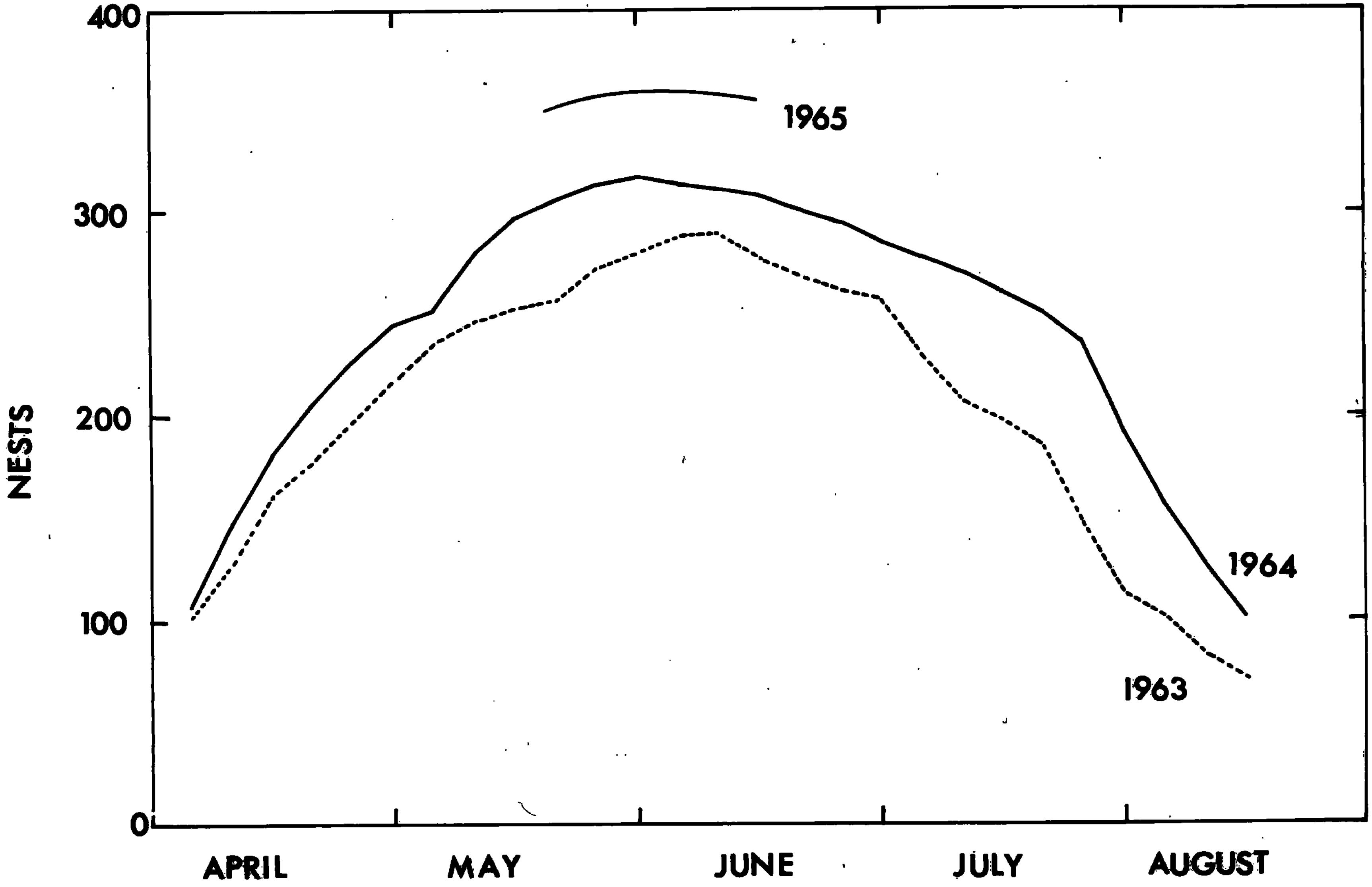
[illegible]

[illegible]

[illegible]
[illegible]

THE NUMBER OF OCCUPIED SHAG NESTS ON THE FARNE ISLANDS 1963-1964.

(The number of nests is given for each five day period) nests on Megstone and East Wideopens, are excluded.


400
300
200
100
0
NESTS
APRIL
MAY
JUNE
JULY
AUGUST
1965
1964
1963

Farnes

Little is known about the status of the Shag on the Farnes, or elsewhere, during the eighteenth and early nineteenth centuries for it was almost inextricably confused with that of the Cormorant. Nevertheless, Watt (1951) summarised the status of the Shag on the Farnes as follows: "from about 1760 to 1830 a few pairs bred on the islands (probably either on Staple Island itself, or on the Pinnacles), although it is not certain that this was an annual occurence. From 1830 to 1840 one or two pairs nested annually on Staple Island but by 1857 Shags no longer nested and were, indeed, rarely seen". From 1857 to 1912 one (but two in 1892) nest was recorded in six of the 55 years. "There was definitely no nesting between 1902 and 1912". Little information is available about the period between 1912 and 1925, when Goddard first visited the islands but Millar (1918) could not find any nests and Goddard (1934) states..."it is only since 1931 that they have commenced to nest annually". In fact there appears to be only one certain breeding record during the period 1912 to 1931 and that concerns a record of a Shag sitting on a nest on a ledge of the west face of the Inner Farne on 11 June 1928 (Temperley 1928).

The increase in the number of pairs (= nests) counted on the three main islands of Staple, Brownsman and Inner

Farne is shown in Fig. 13 . Estimates prior to the present study have been published in Watt (1951) and Farne Island Reports (1950-1962) and are summarised in Table 7 with corrections in 1961 and 1962. These counts were plotted individually on log (base 10) scale and curves were drawn to smooth out the small annual variations for the purposes of Fig. 13 . This latter procedure is plausible since there is no evidence of a simultaneous variation on more than one island, and other variation would be expected since the counts were not carried out at similar stages of the breeding cycle.

The Inner Farne population declined during the disturbed 1939-1945 period, and again from 1956 to 1960. The latter was a progressive decrease and was probably due to excessive disturbance, to counteract which, part of the cliffs were fenced off. In several seasons, especially 1959, Shags have suffered disturbance from tourists and others on Staple and Inner Farne, for example, at least 40 of the Shag nests on Staple had been robbed by the end of April 1959, stones being thrown at birds on inaccessible nests.

The years with high yearling loss referred to later in this work (Section Six), might (*e.g.* the 1957 year class) have resulted in lower numbers of breeding birds (*e.g.* in 1959 and 1960) but the relatively high yearling mortality in 1959,1960 and 1961 was not followed by changes in the number of nesting pairs. The smooth growth curve of the Farne

Table 7

The number of Shag nests on the Farne Islands

1930 - 1965

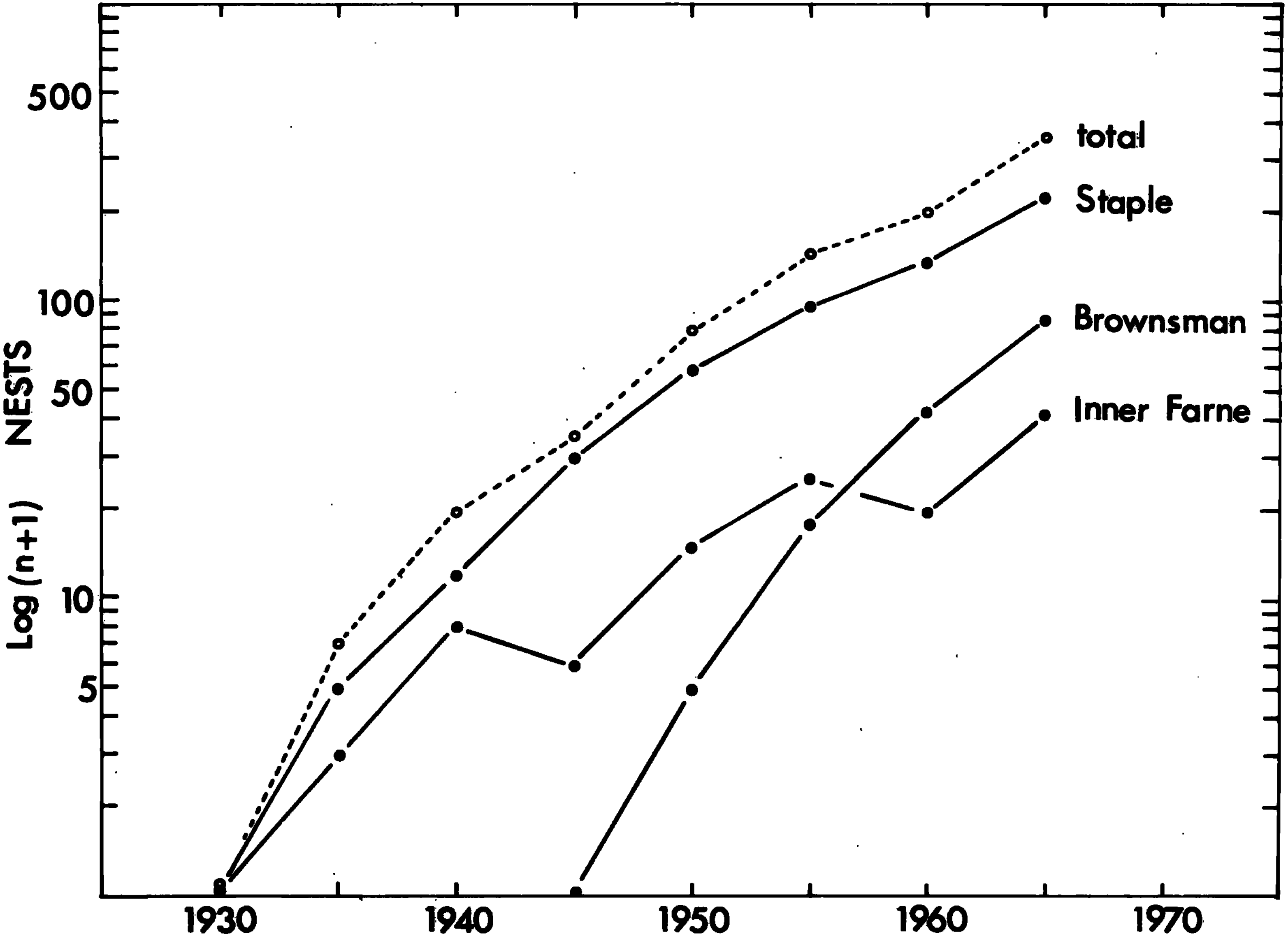
Year	Staple	Inner Farne	Browns.	Other islands	Total
1930	-	-	-	-	-
31	1	-	-	-	1
32	3	-	-	-	3
33	2	1	-	-	3
34	4	1	-	-	5
35	2	2	-	-	4
36	5	2	-	-	7
37	+	2	-	-	+
38	7	3	-	-	10
39	8	7	-	-	15
40	+	+	-	-	+
41	+	+	-	-	+
42	+	+	-	-	+
43	+	+	-	-	+
44	+	+	-	-	+
45	33	5	-	-	38
46	35	6	-	-	41
47	40	9	-	-	49
48	40	+	-	-	+
49	50	13	1	-	64
50	42	14	3	-	59
51	+	+	+	-	85
52	71	17	8	-	96
53	67	25	16	-	108
54	73	26	10	1	110
55	85	25	17	-	127
56	108	22	23	-	153
57	117	22	25	1	165
58	123	18	30	-	171
59	127	17	37	-	181
60	134	20	38	-	192
61	141	25	52	-	218
62	150	27	54	1	232
63	191	32	67	5	295
64	219	35	74	4	332
65	234	42	88	3	367

Fig. 13

GROWTH OF THE SHAG POPULATION ON THE FARNE ISLANDS

1930-1965

Estimates for each year where available, are on page 42.


NESTS
Log (n+1)
500
100
50
10
5
1930
1940
1950
1960
1970
total
Staple
Brownsman
Inner Farne

population as a whole suggests that the breeding sector of the population is buffered against high yearling loss, even in three successive seasons, and without affecting the surplus which supports the rate of increase.

The tendency to a slower over-all rate of growth Fig. 13 is not as pronounced as on the Isle of May or Bass Rock Fig. 16 and it is possible that the level of immigration at the colonies will have differed sufficiently to account for this. At the present time the bulk of the increase on the Farnes is the result of immigration, for at least 26 per cent of the two year olds recruited to the population are immigrants (Table 8).

The recruitment to the population equals the annual mortality rate (.15) plus the rate of increase of the population (.12), of this recruitment (.27), some .27 x .26 (the proportion of immigrants see Table 8), = .07, are immigrants. Now the rate of increase of the native population must exclude the latter. Since .07 of the population are immigrants this must be subtracted from the rate of increase of the Farnes population to give the rate of increase due to the native birds. This is .12 - .07 = .05 or 5 per cent per annum. If the rate of emigration remained the same as at present and immigration ceased, the rate of increase of the Farne population would therefore, fall from 12 per cent to 5 per cent.

Table 8

The Proportion of Immigrants in Two year old nesting Shags

Year	Sample	Proportion Not Ringed
1962 (1960 cohort)	Captured 27 Seen 0	.33 -
1963 (1961 cohort)	Captured 48 Seen 27	.38) .56) .44
1964 (1962 cohort)	Captured 20 Seen 82	* .55) .33) .37
1965 (1963 cohort)	Captured 49 Seen 0	.35 -

* known to be biased in favour of immigrants, but this does not apply to estimate as a whole. The samples are not added since they are heterogeneous.

Proportion of Immigrants = (1963 Proportion not ringed + 1964 Proportion not ringed/2) minus n.r.

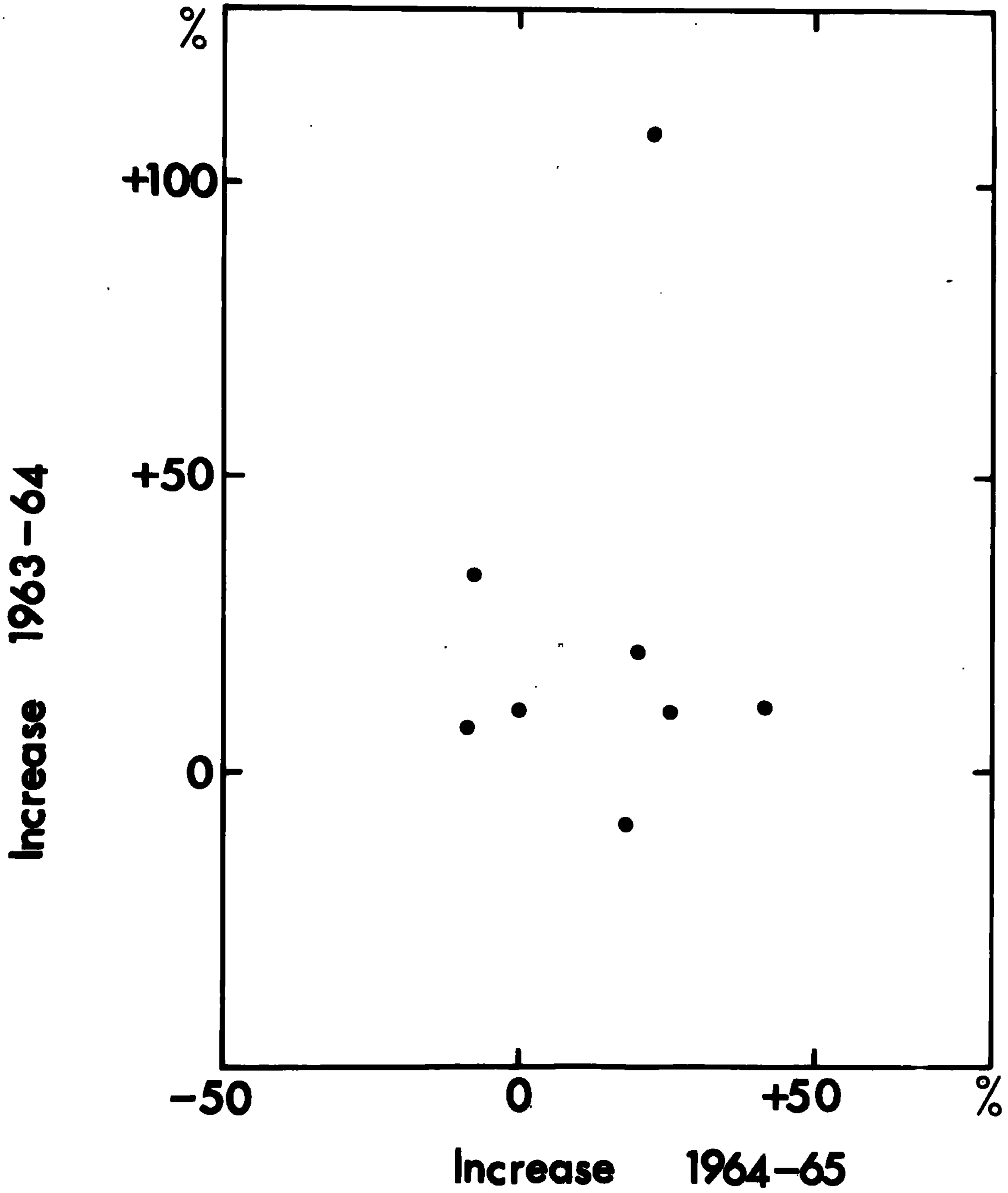
Where n.r. = 0.14 = Annual production on Farnes which are not ringed. Most of these are on Inner Farne or Pinnacles, since pulli tend to return to their natal island, the Proportion of Immigrants is underestimated rather than over-estimated. (In the 1963 cohort n.r. = 0.09, due to intensive ringing effort and high mortality of chicks on Pinnacles, this was the lowest value of n.r. so far on the Farnes).

Study of the rates of increase between 1961-1964 and 1964-1965 indicated that the rates of growth had not stabilised in any of the various parts of the occupied islands. Thus the channelling of growth into new areas continued alongside renewed growth in old established areas. Shag gully showed no increase from 1949 when Watt (1951) counted 33 nests until 1964 when there were 31 nests, but in 1965 the number of nests increased by 42 per cent. It follows that since the rate of growth in one year is not closely correlated with that in the next (Fig. 14), that there are now no clearly defined zones of growth. Partly however this conclusion results from annual fluctuations and further consideration (p91) indicates that renewed growth is not, <u>on average</u> occurring in some areas. If the growth of each of the areas was independent after the initial immigration, renewed growth would not occur and the first established areas would have stabilised long ago. The fact that renewed growth is occurring in some areas does not demonstrate that the limiting factors in these areas have been overcome to the extent that renewed growth is occurring in them, for the resilience of local limiting factors is of little importance when the overall increase is supported by non-local (<u>i.e.</u> Firth of Forth) conditions. The resilience of the prime local limiting factor, namely a shortage of good nesting sites is increasing, and may already have halved the 'native rate of increase' of the

Fig. 14

RATE OF INCREASE BETWEEN ONE YEAR AND THE NEXT, FOR VARIOUS PARTS OF SHAG COLONY ON THE FARNE ISLANDS, IN 1963-1964 and 1964-1965

There is no simple correlation between the increase one year, and that in the next; this is largely a result of annual variations from area to area (see page 91).


%
+100
+50
0
Increase 1963–64
−50
0
+50
%
Increase 1964–65

Farnes population. Evidence of a shortage of good nest sites, generally, on the Farnes is also demonstrated by the dispersal to new (*i.e.* non natal) nesting areas. This dispersal from the island of hatching is found to be linearly related to the growth of the population (Fig.15). This is at least partly (see p89) because some of the prospecting population return to their natal island, and are then forced to search elsewhere by a lack of nesting sites. However, it should be pointed out that most of the individually identified Forth immigrants on the Farnes were first seen on the Farnes prior to the age (two years) at which they would be prospecting. It is thus unlikely that these birds could have been affected by the density of birds in their native area.

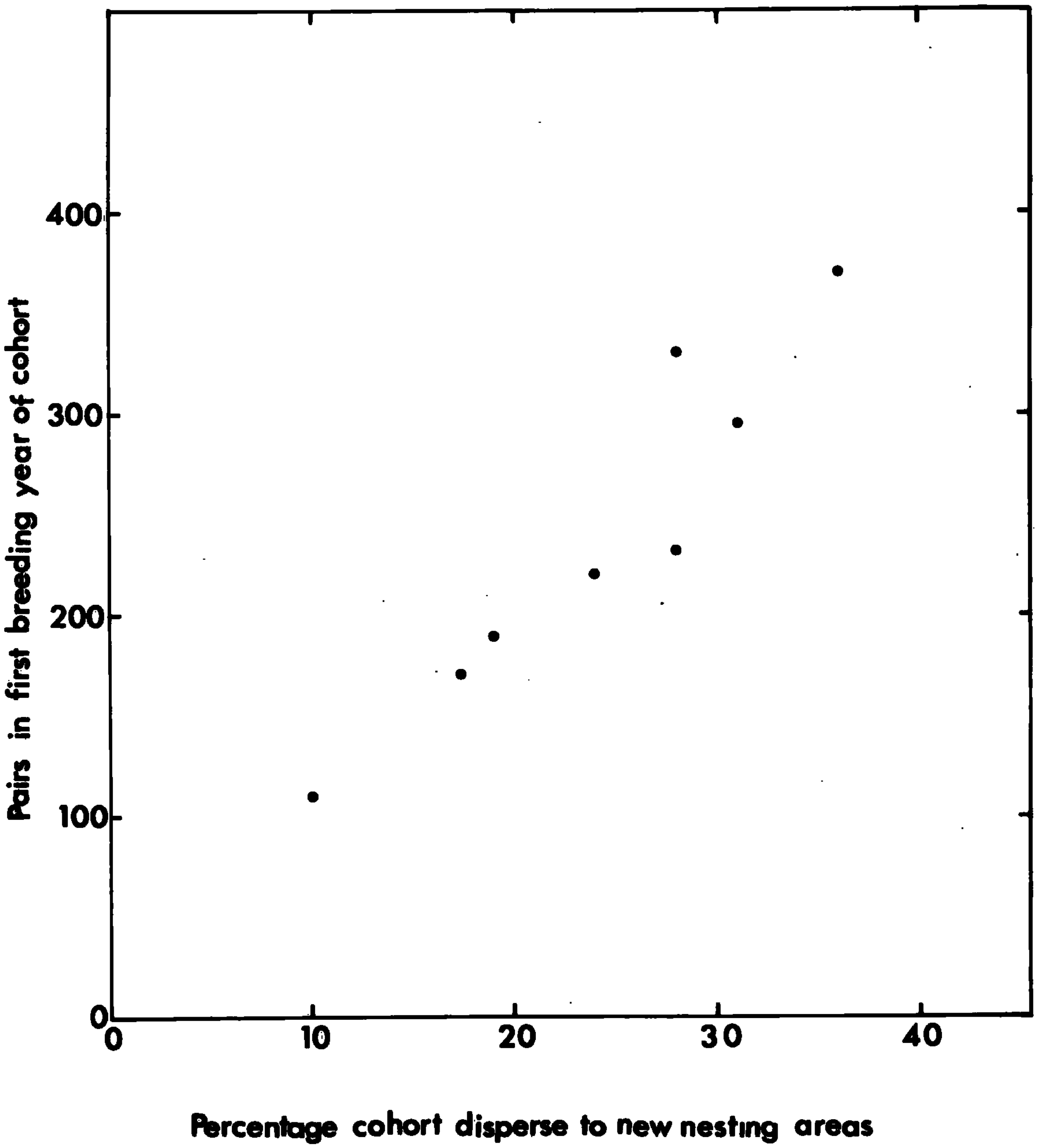
Nesting on the Farne Islands other than the main three has occurred (Table 7) but had only been successful on the Megstone until 1965 when two young were reared on East Wideopens. In 1960, two young were also reared on the low NW cliff of Brownsman but this area has not been used since. Nelson (1887) commented on his visit to the Megstone in 1886 "I think a clutch belonged to the Green Cormorant (*Phalacrocorax graculus*) of which there are *one or two pairs supposed to nest on the Megstone*." It is doubtful if Watson's (1922) record of "2 or 3 pairs of Shag on the Megstone on 13 May 1921" refers to actual breeding birds, though in view of

Fig. 15

DISPERSAL FROM NEST SITE OF HATCHING TO NEST SITE OF FIRST BREEDING

Dispersed - those which leave their island of hatching

cohort - those Shags in one year class which were ringed as pulli on the Farnes <u>e.g.</u> 1953 cohort does not include Shags not ringed as pulli, or those from elsewhere.


Pairs in first breeding year of cohort
400
300
200
100
0
0
10
20
30
40
Percentage cohort disperse to new nesting areas

the date it seems probable and is certainly implied in his account. The adult Cormorants and Shags fly off this rock as soon as landing takes place, and unless one is especially looking for them, the odd Shag nest, clutch or chick are easily overlooked. Successful breeding took place at the NW corner above the steep sided gut in 1962 and 1963 but no young were reared in 1964. It is not known if the breeding was successful in 1965.

Adjacent Populations

The preceding survey of the growth of the Farnes population was extended to all areas (see the Map, Fig. 2) between the Moray Firth and Flamborough Head, inclusive. The detailed account of this survey, for each area is given in Appendix A, where the estimated maximum number of nests for each year is given, where this is known. This survey enables a comparison of the growth curves for each population in the surveyed area (Fig. 16). The total population for each five year period is also calculated from the curves, showing that the population has increased steadily since about 1920.

A similar search was extended to Lundy (Fig. 17) since Snow (*pers. comm.*) did not do this, and as a background to the many comparisons made between the Lundy and Farnes populations. By contrast to the Farne population, the Lundy

Fig. 16

[illegible]

[illegible]

[illegible]

[illegible]

GROWTH OF FORTH-FLAMBOROUGH HEAD SHAG POPULATION 1900-1965.

Details of the counts used in this graph are given as Appendix A., which is a full account of the population growth.

The recent decline in Berwickshire is due to shooting

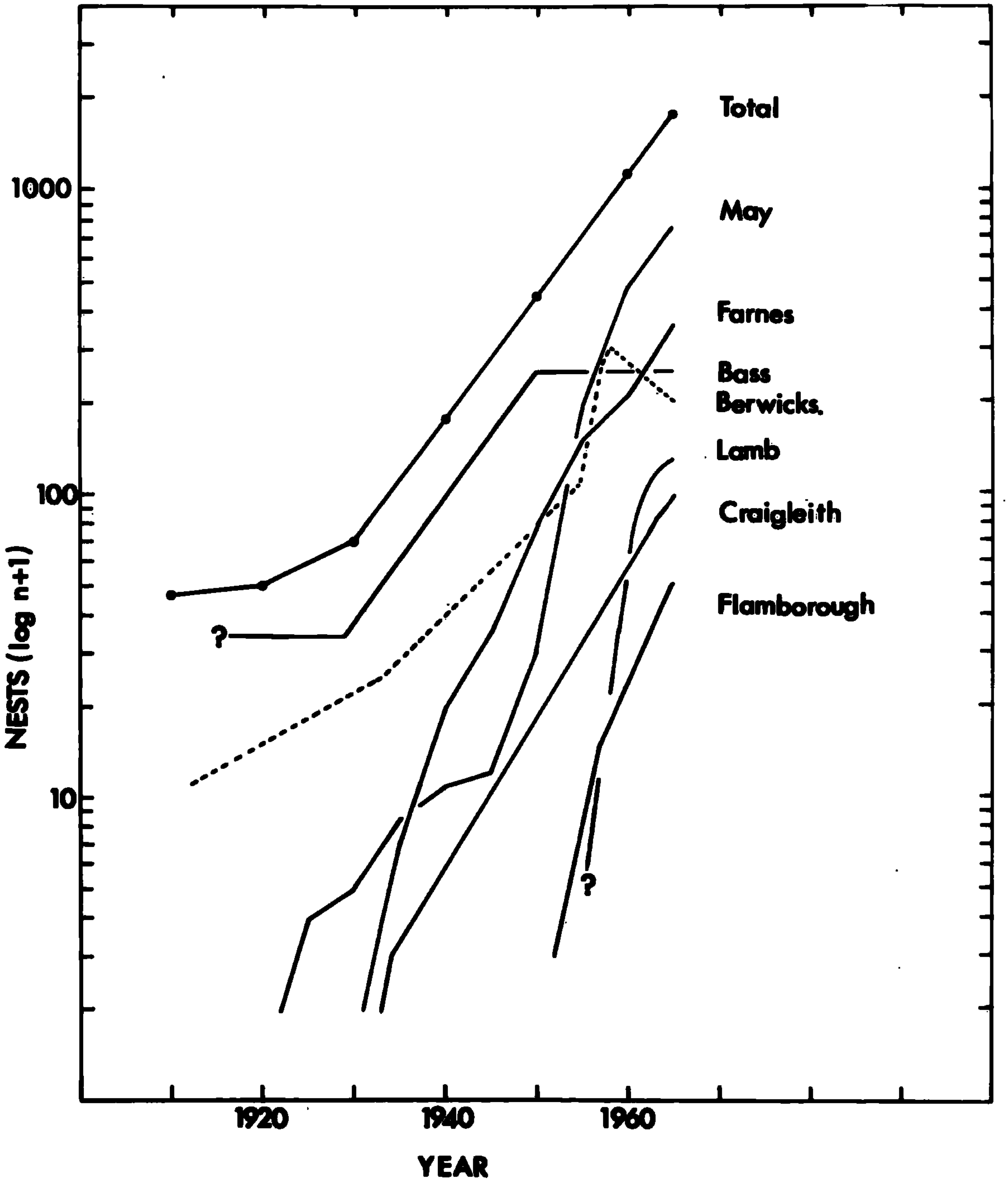
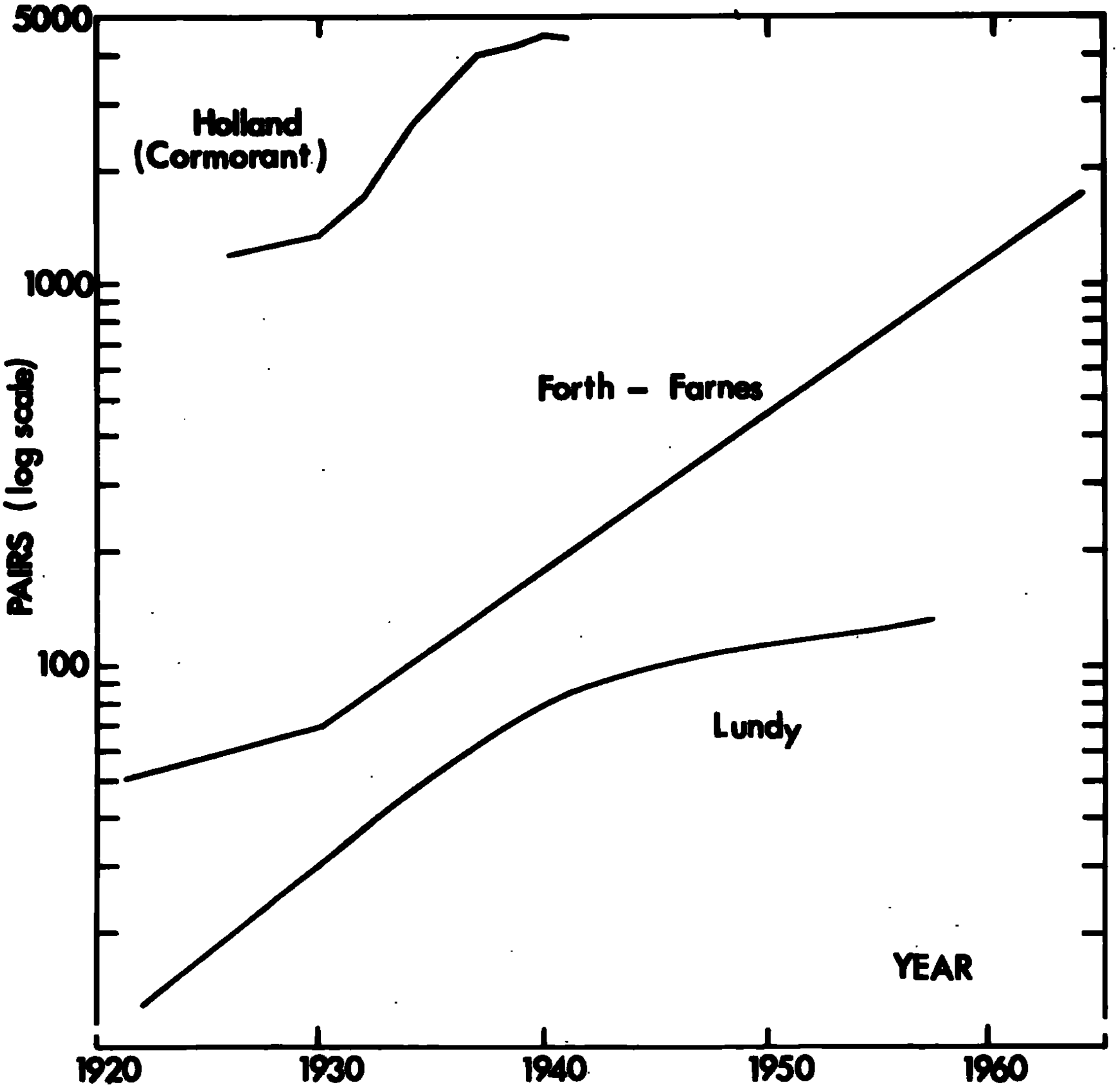

Total
May
Farnes
Bass
Berwicks.
Lamb
Craigleith
Flamborough
1000
100
10
NESTS (log n+1)
?
?
1920
1940
1960
YEAR

Fig. 17

THE GROWTH OF THE CORMORANT POPULATION IN THE NETHERLANDS (FROM KORTLANDT 1942) AND SHAG POPULATION ON LUNDY (APPENDIX C) AND FORTH+FLAMBOROUGH.



5000
1000
100
PAIRS (log scale)
Holland
(Cormorant)
Forth - Farnes
Lundy
YEAR
1920
1930
1940
1950
1960

population during Snows' 1954-1958 study was stable.

Population growth

The steady rate of increase of the population on the coast between Fife Ness and Flamborough, despite the non-parallel growth of the individual colonies, suggests that the colonies form one unit, since this is precisely what has happened within the Farnes group, and on the Isle of May. The most obvious links are the initial immigrants supplied to new areas by populations which are, stabilising in the way that the Isle of May increase is now confined to certain areas (Appendix A). It is apparent that much of the dispersal to new breeding sites is regulated by relative saturation of the various breeding areas. Other links are complex because the Farnes population shows concurrent immigration and emigration (Section Six).

Thus similar processes are involved in the differential growth of various parts within a colony such as the Farnes and that between various colonies. The corollary of this is that the increase will continue, other factors apart, until the whole population is poised with the opposing environmental forces and population pressure balanced throughout. Only then could the highest possible numbers be maintained. It is interesting to reflect that as one reduces such a population the effective reproductive capacity of theremaining individuals will increase just as it must decrease during stabilisation.

The cause or causes of the steady increase are not known but, the increase can be temporally related to similar increases in other species. There is no doubt (e.g. the History of the Eider) that the welfare of birds on the Farnes is intimately connected with their protection which dates (apart from odd lapses) from about 1885, (Watt 1951). The increase in the Shags began later than in other species such as the Guillemot (Watt 1951), Kittiwake (Coulson 1963 a) and Cormorant (Table, 8), probably because the spread to the Farnes had to await a build up further north which was somewhat later i.e. the increase in Berwickshire did not begin until after 1910.

Whilst there is good evidence that the Shag declined in the nineteenth century in Berwickshire (Bolam 1912) and in Yorkshire (Bunce and Fenton 1956), there is no evidence of a large population on the Farnes prior to the present increase. Either the decline occurred before 1760 and before that of the Kittiwake, or the present numbers are unprecedented. Unless further evidence becomes available, and since there was a decline (from one or two to none) it appears that the present population is at least partly a revived one and that the increase is a recovery after human predation was relaxed. It is not known what result significant predator pressure would have had on the population. Whilst the Herring Gulls continue to increase on Staple and Brownsman Islands and as the Shags nest in more exposed situations this may become a factor of some importance. Inter specific competition for nest sites (Section Four) may also influence the final outcome.

Yet another interesting aspect of the growth of the Shag populations is that the initial increase builds up from a very small number of pioneers, generally one pair, albeit accompanied by numerous non-breeding birds. This is contrary to the fluctuations in the Cormorants (P. auritus and P. carbo.) which have generally colonised and abandoned areas in groups (Lewis 1927),Watt (1951),Baxter and Rintoul (1953),Smith (1961).

The overall rate of increase of about 10 per cent per annum, is the same as in the colony of Cormorants studied by Kortlandt (1942), and in the colonies of Kittiwake near the mouth of the Tyne (J.C. Coulson pers. comm.). Fisher and Venables (1938) calculate the rate of increase of the Gannet on Noss where there was thought to be little, if any, immigration, as 12 per cent. The rate of increase of the Great Skua in the Faroes was about 8 per cent in the period 1900-1961 (Potts unpublished) and the Fulmar population over the whole British Isles was increasing at about 7 per cent per annum (Fisher 1952).

SECTION THREE

SEX-RATIO AND PAIR BOND

SEX-RATIO

Two main factors determine the sex-ratio (here the number of females per male) of a Shag breeding population:-

1. sex-ratio on hatching
2. subsequent sex specific mortality rate

The practical difficulties of sexing the chick prior to the 33rd day (see p 23) were not overcome in this study. (Practised observers can sex chicks of the Common Fowl from the appearance of the cloaca, but considerable skill is involved and the chicks must be less than half a day old. The method was not tried in the present study, though in theory it should be possible).

The chick

At present only 37 chicks have been tentatively sexed (Table 9), but a sex-ratio of 1.47 indicates a surplus of females.

First year

First year skins collected throughout the British Isles (Table 9) indicate a surplus of females, though the sex-ratio, 1.78, may be slightly too high since there is evidence that some first autumn Shags were wrongly sexed by the taxidermists, or collectors. Subsequently, however the skins show a bias (Table 9) which may be

Table 9

Sex Ratio in the Shag

	Total	Females	% Females	Sex Ratio$\left(\frac{♀}{♂}\right)$	Probability of 50:50 sex ratio, or number required to show that it is significant at P = .05
Farnes					
Chicks(see text p 23)	37	22	60	1.47	200
Adults caught for first time at age >2,1962-65	128	97	76	3.13	P<.05
1958-59 cohorts which have bred to 1965 inclusive	80	46	58	1.35	* 250
(1)1958-61 cohorts which have bred to 1965 inclusive	209	113	54	1.18	1,000
Total	337	210	62	1.65	P<.05
Museum					
First Year	64	41	64	1.78	100
Remain. Immatures	47	20	43	0.74	-
Adults	34	12	35	0.54	-
Total	145	73	50	1.01	-

* From Davis & Zippin(1954)

a shooting bias. A similar result in a shot sample of Barred Doves obtained by Schwartz (1950 discussed in Lack 1954 p.110), might indicate a similar bias.

The breeding population

If the sex of each bird from each cohort is scored from the time it is first determined (i.e. when the bird first breeds), notwithstanding subsequent mortality, it is found (Fig.18) that the cohort gradually shows a surplus of females, showing that the females breed for their first time at a greater age than the male, and that there must have been a surplus of females in the cohort, from the start. In fact if we consider the 4-5 year old group of females in 1965 there is a marked surplus of females (sex-ratio = 1.40). This latter surplus is indicated by point x in Fig.18), whilst y and z are the 'sex-ratio' of succeeding age groups. Now line x to x (i) is the expected 'sex-ratio', calculated from the sex specific mortality rate of the adults (p197). Thus it appears that there is a surplus of females in the pre-breeding population and that this still persists into the early breeding age groups, despite the later breeding of the females. Subsequent age classes show a decline in the strength of their female component, due to sex specific mortality rate.

Each of the samples indicate a surplus of females in the pre-breeding Shag population. This is also reflected in the sex-ratio of the recruits, though subsequently sex

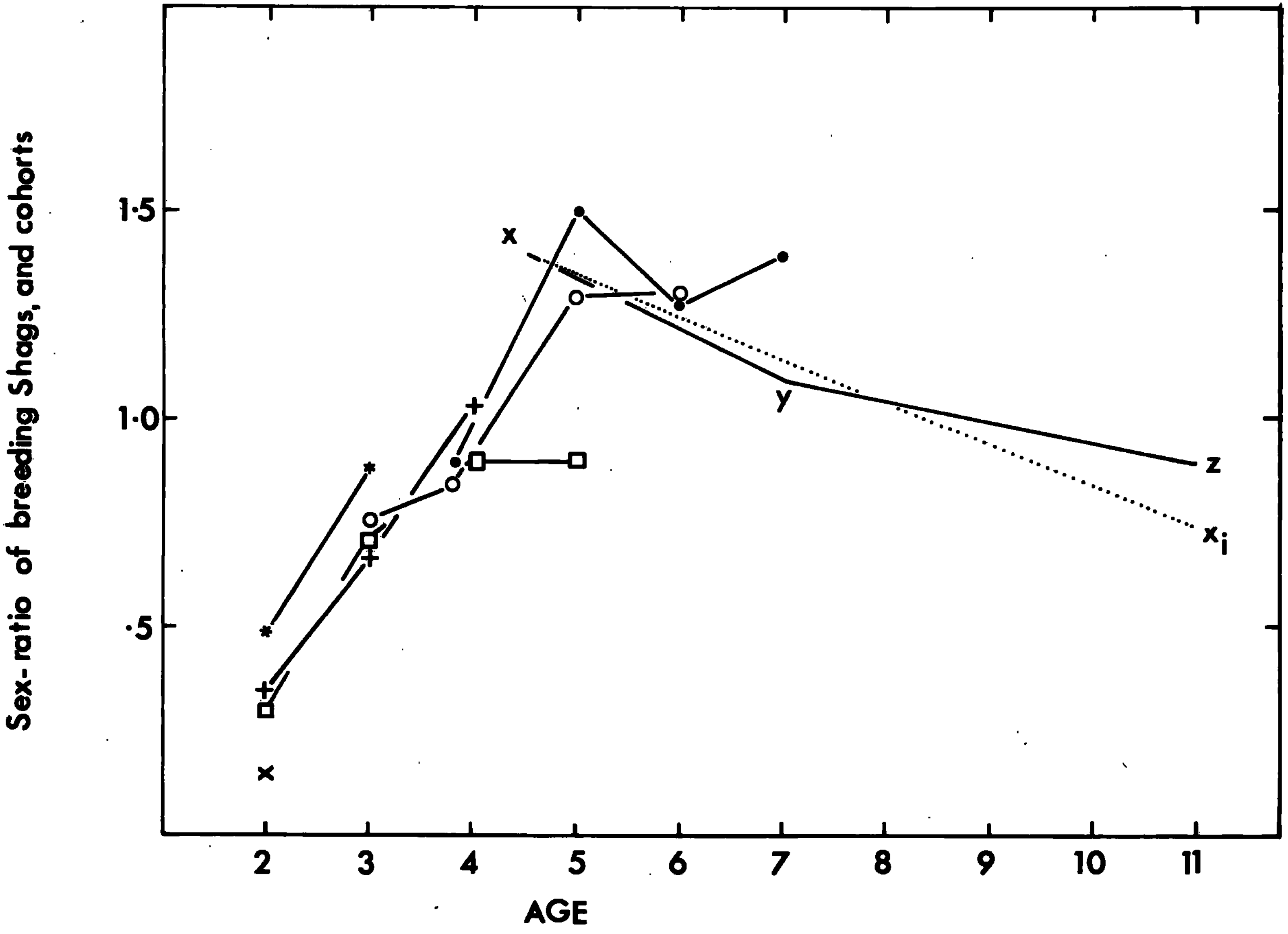
Fig.18

REALISED SEX-RATIO AND AGE OF COHORT

Sex-ratio (females per male) is that which is realised i.e. the number of ringed pulli in the year class recruited to a point in time, according to sex. No account is made for mortality except in lines of x y z (the actual sex-ratio of extant birds at a point in time) and line x to xi(the predicted sex-ratio in subsequent years given x, and assuming no further differential recruitment of the sexes).

Note that the total number of females eventually recruited is greater than that of the males, indicating that the sex-ratio prior to recruitment was also disturbed, in favour of the females.

Filled circle	1958	cohort
Open circle	1959	"
Open square	1960	"
+	1961	"
Asterisk	1962	"
⋈	1963	"



Sex-ratio of breeding Shags, and cohorts
1·5
1·0
·5
2
3
4
5
6
7
8
9
10
11
AGE
x
y
z
x_i

specific mortality erodes the surplus until finally it is eliminated. In the oldest age groups there is a slight surplus of males. Lack (1954) concludes "In birds the sex-ratio is normally about equal in the young"....but "There is perhaps an unequal sex-ratio at birth in icterids and the Sparrowhawk", (the last is based on only 27 individuals). Though it is difficult (Table 9) to conclude, conclusively that there is an unequal ratio in the Shag at birth, the limited evidence suggests that this is the case. In the adult breeding population however there was (in the period 1963-1965 at least) a surplus of females which had various effects on the breeding biology, of the birds, despite the fact that females have a higher mortality rate. Mayr (1963) points out that "...natural selection will normally tend to equalise the parental expenditure devoted to the production of the two sexes". Later in this work two other populations with a disturbed sex-ratio (assuming 50:50 to be the norm) are described, in both of them this was associated with rapid population increase (p133). In view of the rapid increase of the Farne population it may be that the sex-ratio is more disturbed on the Farnes than in a steady population, and it is interesting to reflect that a balanced sex-ratio is (as Mayr points out) of benefit to the population as a whole, rather than to its individuals.

PAIR BOND

Introduction

The mated pair is the basic unit in a breeding population of most birds and mammals and it is the purpose of this section to examine the bond between the members of this unit in the Shag in order to understand its viability and performance. Since a pair is a unit the members must subordinate their individuality and replace this with complementary purpose. On *a priori* grounds such co-operation is probably sensitive to the experience, maturity, and inviduality of its members and thus their success will reflect any disparity within the pair. Consequently, pairs must, on average, be the result of a matching of complementary or similar individuals and evolution will have favoured behavioural and physiological mechanisms which bring this about. It is salutory that in much recent work on pairing behaviour the comparative individuality of the partners has been neglected. Alternatively Howard(1920) comments:- ".... the longer the period over which the process of pairing can be spread, the greater chance will females have of discovering mates, the less severe will be the competition tend to become, and, consequently, the smaller the percentage of individuals that fail to obtain suitable partners".

(1) The Breeding Pair

Following the terminology of Richdale (1957), but without the prefix "mated" since this is the condition of any pair which continually associate and in which copulation takes place, and replacing this by "breeding", which is what Richdale means i.e. "Two birds of opposite sex which are definitely known by the observer to have begun family life together, constitute a mated pair". In the present work "family life" is interpreted as "the laying of at least one egg".

(2) Stable pair

A pair which is intact from one season to thenext. An unstable pair is one which breaks up during or between one season and the next.

(3) Trio

As "Breeding pair" except that two females and one male are concerned i.e. simultaneous polygyny at one nest.

(4) Divorce

Richdale (1957) has described a very confusing distinction between his terms'divorce' and'separation' as follows:-

"Divorce:- When two birds of a pair mated in the previous season return to their breeding place after the non-breeding season, and at least one of them mates with a third bird, a divorce has occurred".

"Separation:- Occasionally one member of a mated pair moves away from its former breeding place to a more distant one even though the second member of the former mated pair may remain there. This is rather different from a 'divorce' and is known as a 'separation'." In fact Richdale has confused the discrete issues of site tenacity and pair bond. In this work the term 'separation' is not used and the term 'divorce' is defined as:-

A change of mate which is not the result of death of one of the partners. There are thus only two kinds of rupture of the pair bond, namely 'divorce' and 'replacement' of a mate which has died.

Relative Ages of Partners

There is a close relationship between the respective ages of the partners, though there are patterns within this relationship (Table 11), Fig.19) which deserve comment. Firstly, males are recruited to the breeding population at an earlier age than the females (Table 10). This explains the tendency for young males breeding for the first time to pair up with older females, which nevertheless will also be breeding for the first time. It is interesting to note that the precise converse of this is found in the Yellow-eyed Penguin (Richdale 1957). Thus birds in the 2-8 years age group tend to pair up with mates of similar breeding experience. Secondly, the oldest birds pair with relatively younger mates. It will be apparent (Table 11 and Fig.20)) that the distributions of the partners' ages are skewed somewhat and that this is what would be expected if there was some random mating. The skew changes sign

Table 10

Age of first breeding (ringed as pulli)

(breeding = member of pair which nested, and laid eggs)

Age of first breeding		1961 cohort		1962 cohort		1963 cohort	
		♂	♀	♂	♀	♂	♀
(1)	2	35	15	55	26	34	7
(2)	3	7	11	12	25	-	-
(3)	4	2	6	-	-	-	-
Total		44	32	(67)	(51)	((34))	((7))

(1) virtually all ringed two year olds are included.

(2) Number caught or seen not known to have bred in second year.

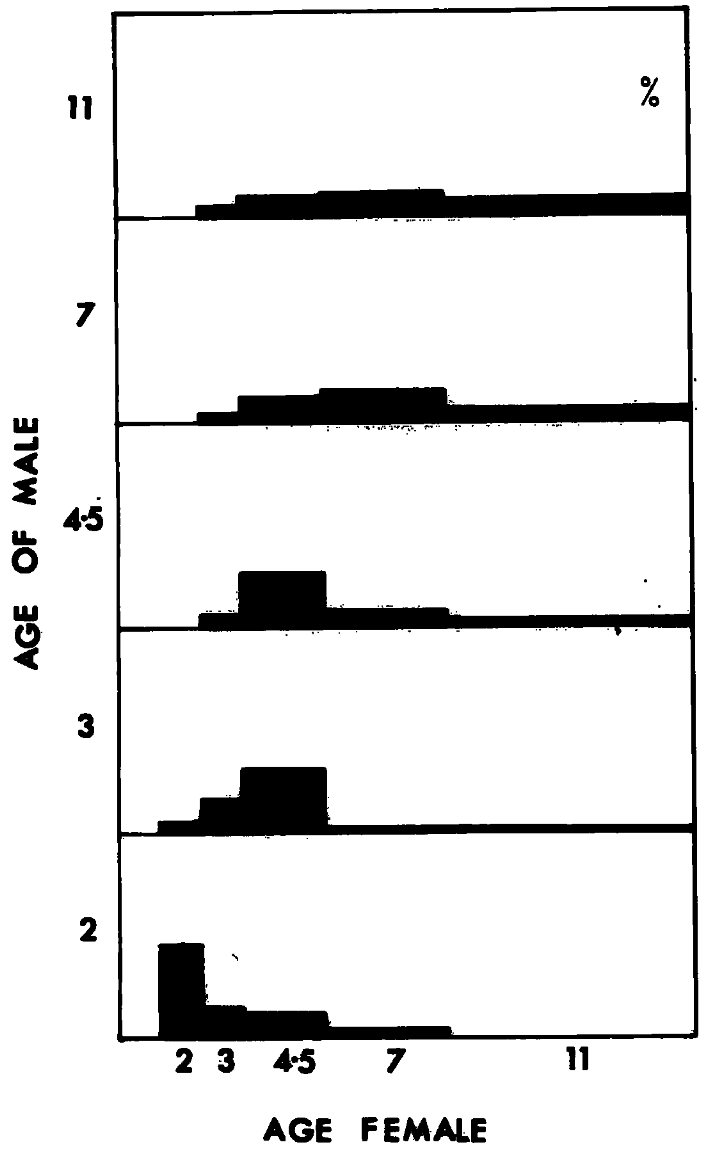
(3) Some known to be non-breeders in second and third years, others probably belong to this category.

Note that the total number of females identified to the end of the fifth year is greater than the number of males (Fig. 18). The percentage recruited as 2 year olds from the respective cohorts, allowing for mortality was 46,49 and 23.

Fig. 19

CORRELATION BETWEEN THE AGE OF MALE AND AGE OF FEMALE IN THE PAIR

Left. The number of females of various ages are plotted as percentages of the total number of females mated with the males of each age group, according to the females' age.


%
AGE OF MALE
11
7
4·5
3
2
2
3
4·5
7
11
AGE FEMALE

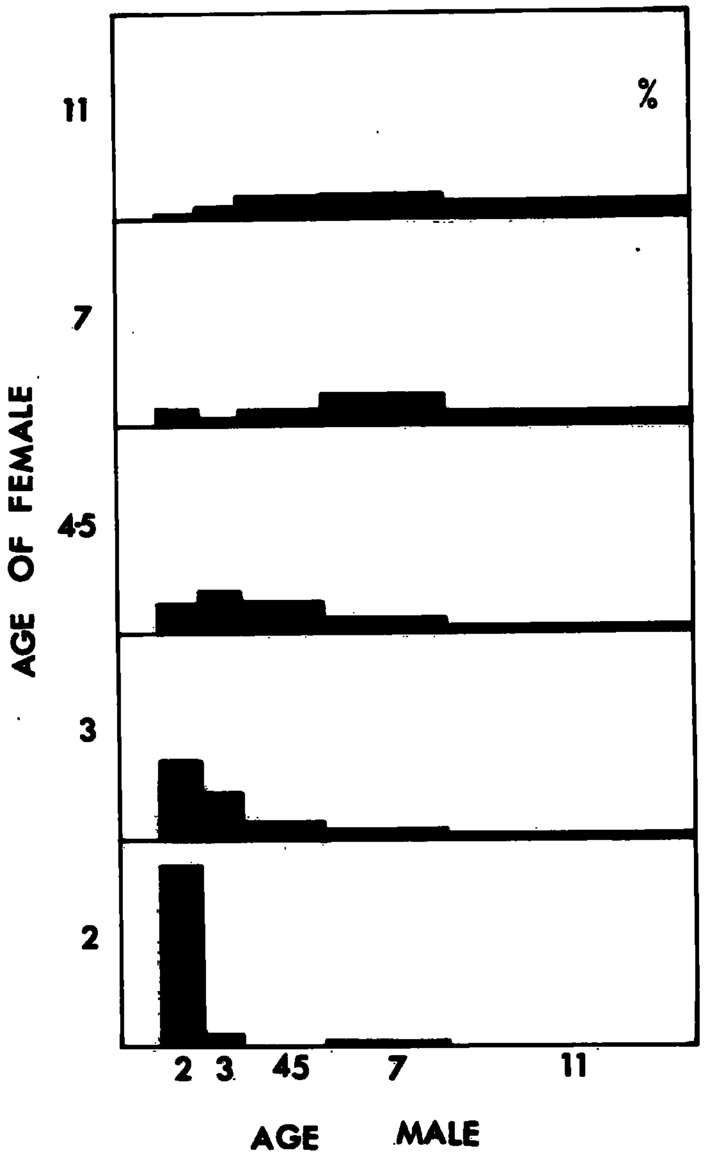

%
AGE OF FEMALE
11
7
4·5
3
2
2
3
45
7
11
AGE MALE

Table 11

Age of Female and Male in Pair; Colour Ringed Adults in 1963

Age of Female	Age of Male								
	2	3	4.5	7	11	Pairs	Mean Age ♀ and St.Dev.	Median Age ♀	Skew
2	15 .88	1 .06	0 -	1 .06	0 -	17	2.4 ± 1.2	2.6	+.2
3	5 .38	3 .23	2 .15	2 .15	1 .08	13	3.9 ± 2.4	2.5	-1.4
4.5	8 .14	11 .20	17 .30	12 .21	8 .14	56	5.0 ± 2.7	4.1	-.9
7	4 .08	2 .04	7 .14	23 .46	14 .28	50	7.2 ± 3.0	7.6	+.4
11	1 .02	2 .05	9 .21	14 .33	17 .39	43	7.6 ± 2.8	8.0	+.4

Table 12

Age of Male and Female in Pair; Colour-Ringed Adults in 1963

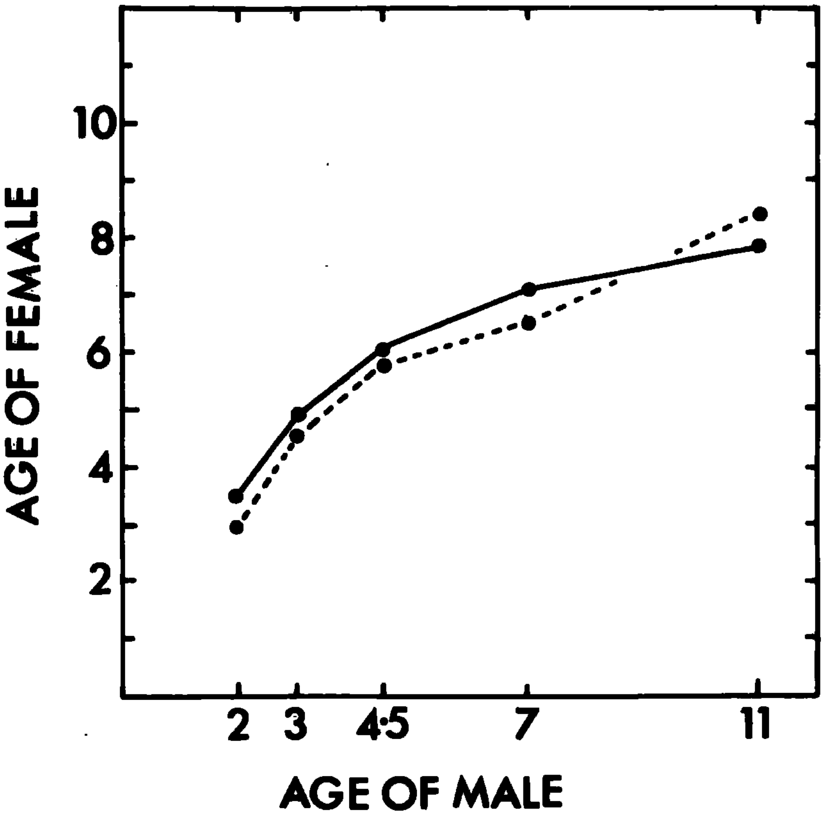
	♀	♀	♀	♀	♀				
	2	3	4.5	7	11	Total ♂	Mean Age ♀ and St. Dev.	Median Age ♀	Skew
♂ 2	15 .45	5 .15	8 .24	4 .12	1 .03	33	3.5 ± 1.9	2.8	-.7
♂ 3	1 .05	3 .16	12 .63	1 .05	2 .10	19	4.9 ± 2.4	4.6	-.3
♂ 4.5	0 -	2 .06	18 .51	8 .23	7 .20	35	6.2 ± 2.4	5.7	-.5
♂ 7	0 -	2 .04	13 .25	23 .44	14 .27	52	7.2 ± 2.2	6.5	-.7
♂11	0 -	2 .05	8 .20	13 .32	17 .43	40	7.9 ± 2.8	8.3	+.4

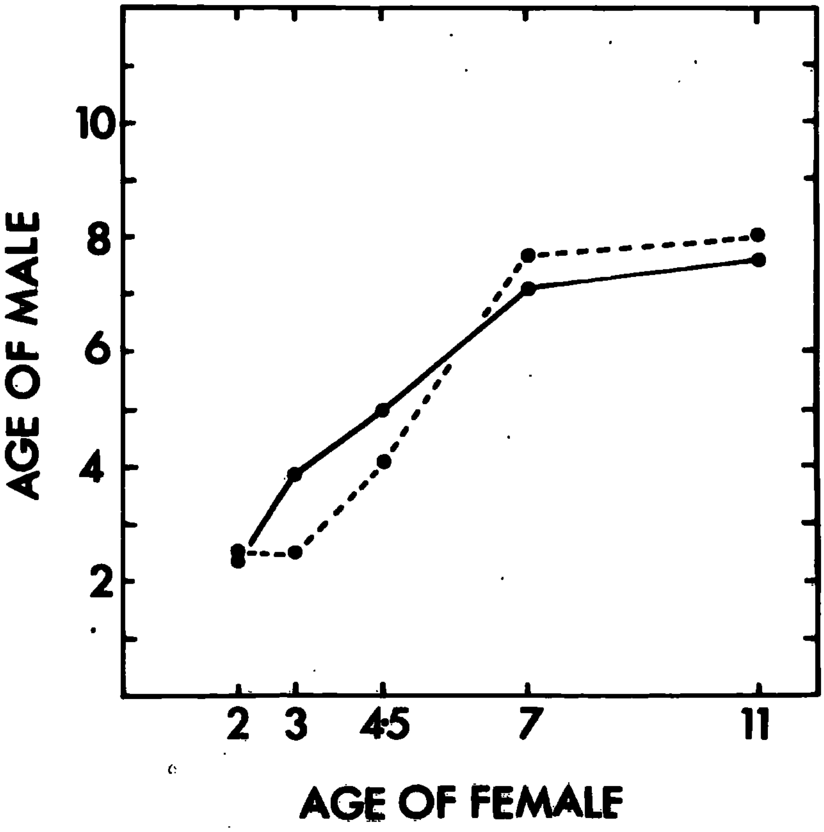
Fig. 20

CORRELATION BETWEEN AGE OF PARTNERS IN THE PAIR

Solid line mean

Broken line median


10
8
6
4
2
AGE OF FEMALE
2
3
4·5
7
11
AGE OF MALE


10
8
6
4
2
AGE OF MALE
2
3
4·5
7
11
AGE OF FEMALE

because the random matings must be within the total age distribution across which the medians gradually shift.

This analysis reveals that there is some mechanism for controlling pairing activities so that birds of similar age breed together. The most likely explanation for this is that the whole process is carried through a seasonal breeding schedule governed by age, a schedule parallel to those discussed at length in Section Five.

Stability of the Pair Bond

For the present, matings and pairings outside the "Breeding Pair" are ignored, thus we are concerned with the strength of bonds already sufficiently secure to allow laying. It is very unlikely that the pair bond remains intact in the autumn after the young are independent and before the breeding sites are re-occupied, and no pair has been sighted together after the young have dispersed, though observations on this were confined to October,1964. A most stringent test of the bond then,would be its stability from one season to the next, among surviving partnerships.

It is clear that older birds formed more stable partnerships (Table 13). The increase in stability of the pair according to the age of the male is threefold. Only 19 per cent of the pairs in the youngest age group are stable whereas 59 per cent of the pairs in the oldest age group are stable. It must be pointed out that such a marked difference could not be due to a difference in mortality

Table 13

Stability of the Pair bond in relation to the age of the male partner

(Pairs recorded in 1961 (8) 1962 (76) and 1963 (159))

Age of male	Number of males	Number keeping mate in following year	Percentage keeping mate
2	26	5	19.2
3	29	13	44.8
4.5	52	19	36.5
7	82	48	58.5
11	54	32	59.2
Total & mean	243	117	48.1(43.6 un-weighted)
* 1963 only	159	74	46.5 ± 4.0

* since the total and mean is biased towards older birds.

rates of the birds, since (especially) the two year old colour-ringed birds which form the above sample have a mortality rate very similar to that of adjacent age classes.

Similar increases in stability of the pair bond have been found in the Yellow-eyed Penguin (Richdale 1957), Kittiwake (Coulson and White 1958a) and in the Arctic Skua (Williamson 1959,Davis 1961b). There is also some correlation between mortality rate and stability of the pair between species (Table 15). If the mortality rate = .10, then .10 - $(.10)^2$ or .09 of the pairs would lose one member, and these members must re-mate with the .90 survivors. Expected instability is therefore .09/,90 = .10. Thus, the direct effect of mortality can be estimated by assuming that the proportion of pairs which would be unstable is equal to the mortality rate. Knowing the age composition of the pairs in 1963-1964 and their mean mortality it is possible to calculate the expected instability due to the direct effect of mortality; this is given in Table 14. The information shows that 68 per cent of instability is due to divorce, but instability of the pair and the proportion of pair change due to divorce decrease markedly with age. Whereas 78 per cent of pair change in young pairs due to divorce, only 54 per cent of the oldest age group which change pairs do so through divorce. Divorce represents a large part of instability and changes of this part are out of proportion to the change in mortality

Table 14

The significance of divorce as a factor in the stability of the pair bond

(1963-1964 data)

Age male survivor (in 1963)	Number pairs	Unstable pairs	*Expected number unstable pairs	% Instability due to Divorce
2	22	18	4	78
3	21	12	4	67
4.5	29	17	5	71
7	52	25	8	68
11	35	13	6	54
Totals and means	159	85	27	68

n.b. The direct method of calculating the expected instability from mortality data (see Table 16) was not used since in 12 instances the female was not identified individually.

* Estimate for ♀♀ from Appendix K. *i.e.* M*a* = .16

(Table 14), both in the Shag and between species (Table 15) suggesting that some other major factors (or factor) are involved.

Two methods of pair re-formation seem likely:-

(1) Individual recognition,

(2) Site tenacity

(1) <u>Recognition</u>

Tinbergen (1953 b) found that Herring Gulls spend the winter as flocks of individuals; no pair bonds remaining intact. The pairs form prior to the occupation of the nesting territories and frequently at some distance from them, on a 'club' which was not divided up in any way. Tinbergen gave evidence that the ability of the birds to recognise their mates was based mostly on the call and was a means by which pairs could reform. The ability of birds to recognise individuals was confirmed much earlier by Lorenz (1938) who found that the birds could recognise every one of about 25 Jackdaws in a flock and that the recognition of individuals persisted, even after birds were absent for at least six months.

(2) <u>Site</u>

Howard (1920, in a study mainly on the Reed Bunting) referred to the territory in these terms:- "the position occupied by the male acts as a headquarters to which the bird can always repair, and becomes a bond of union, which is serviceable in that it prevents any possibility of their

Table 15

Stability of the Pair and Adult Mortality Rate in Various Species of Sea Bird

Species	Area	Adult Mortality Rate(per annum) %	Pairs changing (per annum) %	Authority
Yellow-eyed Penguin	South Island New Zealand	14.4	30.3	Richdale(1957)
Gannet	Bass Rock	6	13	Nelson(1965)
Shag	Farne Islands	15.0	46.5±4.0	Author
Herring Gull	Wilhelmshaven	10	20	Drost,Focke & Freytag(1961)
Kittiwake	North Shields	12	34	Coulson in press
Common Tern	Cape Cod	25	[*21]	Austin & Austin (1956) and Austin(*1947)

drifting apart". Similarly in the Manx Shearwater, Lockley (1942) considered that recognition of the burrow was the only way in which the birds of a pair could renew contact at the beginning of the season.

If the stability of Shag pairs is examined with respect to site tenacity it is apparent that the pair bond is reinforced threefold by site attachment (Table 16). However pairs do change site and remain together, even when moving to another island suggesting that individual recognition is also present from one season to the next. Divorce is six times as likely if the male moves site, but this is not due to site tenacity of the females because, unlike the Gannet (Nelson 1965), they do not show site tenacity (Table 17).

Effect of pair bond rupture on age of partner

Later in this work an attempt is made to assess the significance of the viability of the pair bond, measured through its stability. Before one can compare "changed pairs" with "intact pairs", for example, the effect of change of mate on the age of the partner must be examined.

The analysis in(Table 18) shows that there are differences in the age structure of pairs depending on their formation. Since there appears to be no consistent trend in these differences when related to the method of pair change, changed pairs as a whole will be compared with the stable

Table 16

Stability of the Pair Bond in relation to Age and Site tenacity

(i) Males which keep site 1963-1964

Age 1963	Number of ♂♂	% Keeping mate	% Divorce	% Mate dies
2	5	60.0	20.0	20.0
3	10	70.0	0	30.0
4.5	13	76.9	0	23.1
7	30	63.3	13.3	23.4
11	21	90.5	9.5	0
	79	* 73.4	8.9	17.7

* means are weighted

(ii) Males which change site 1963-1964

Age 1963	Number of ♂♂	% Keeping mate	% Divorce	% Mate dies
2	14	7.1	78.6	14.3
3	9	22.2	66.7	11.1
4.5	13	15.4	76.9	7.7
7	19	42.1	42.1	15.8
11	13	23.1	61.5	15.4
	68	23.5	63.2	13.2

Totals	147	50.3	34.0	15.6

Table 17

Site Tenacity of Divorced Females

1963 - 1964

Age 1963	Number of females	Retaining site
2	12	0
3	6	1
4.5	10	4
7	12	0
11	10	0
	50	5(10%)

Table 18

Age of Partner, according to age and status of male(Age as in 1963)

	2 Yr. ♂	3 Yr. ♂	4.5 Yr. ♂	7 Yr. ♂	11 Yr. ♂
Keep mate (Stable pair)	2.75 ± 0.42 (4)	4.56 ± 0.28 (9)	6.91 ± 0.92 (11)	6.65 ± 0.48 (26)	8.27 ± 0.55 (22)
Divorce	3.00 ± 0.50 (12)	4.83 ± 0.92 (6)	4.60 ± 0.64 (10)	6.33 ± 0.82 (12)	4.89 ± 1.04 (9)
Replacement	2.67 ± 0.27 (3)	6.50 ± 1.59 (4)	5.00 ± 0.94 (4)	5.29 ± 0.80 (7)	5.50 ± 1.06 (2)
Divorce and Replacement together	2.93 ± 0.41 (15)	5.50 ± 0.89 (10)	4.71 ± 0.55 (14)	5.95 ± 0.61 (19)	5.00 ± 0.87 (11)
Difference between Stable and Changed Pairs(Age ♀)	+1.8	+0.9	-2.2	-0.7	-3.3
Probability that each difference due to chance	>.8	>.5	>.2,<.3	>.5	<.2

(sample (number of pairs) is given in brackets) pairs. There is a tendency for the partner of the changed pair to be nearer to the population mean than it would be if it were similar to that of the mate of stable pairs. This trend is significant in the case of the older group (11 years) and is an explanation for the downward trend in this group shown in Fig 20. Richdale (1957) found a similar pattern in the Yellow-eyed Penguin and his data are summarised in Table 19, though he has not supplied details for the whole population of pairs, i.e. he has only looked at pairs as they were established for the first time.

Trios

It became apparent in 1963 that two females were at times seen on a nest together. In 1963 at least nine trios existed. Three of these persisted in 1964 in which season seven other trios were recorded. There was a tendency for the males involved to be older than average, and many of the females involved were breeding for the first time though no two year olds were involved, (Table 20), almost certainly because the older males stop soliciting before the young females are advanced sufficiently to respond. (Most trios are formed at the beginning of the season). The most likely reason for the trio is that the females manage to tolerate each other, since principle females normally fight intruding females. There is no evidence to suggest that the males which formed trios solicited

Table 19

Age of Partner in Yellow-eyed Penguin

(Age of Pairs formed for the first time)

(from Richdale(1957))

Age ♂ in Years	Number of ♀	Age ♀ (Mean)
2	10	2.7
3	47	3.5
4+5	55	4.0
6-8	40	4.2
9-19	44	5.3

Table 20

<u>The number of Shags involved in the trios, according to sex and age in 1963 and 1964</u>

Age	Number males	Males in trios	♂ %	Number females	Females in trios	%
2	61	0	-	18	0	-
3	74	1	1.3	34	1	2.9
4.5	98	3	3.1	158	18	11.4
7	108	7	6.5	119	7	5.9
11	89	7	7.9	88	11	12.5
All	430	18	4.2	417	*37	8.9

* not 36 <u>i.e.</u> 2x number males, because two succesive trios, involving three females and one male occurred at a site in 1963.

<u>n.b.</u> that 'trio' does not include pre-egg laying bonds.

especially vigorously. Many males were 'promiscuous', one to the extent of accepting at least nine individual females, whilst his female was away feeding. Each time the returning female (this was a'stable pair') returned the intruding female was ousted. Another male in a 'stable pair' in the special study area on Brownsman immediately paired up with another female (each time the same individual) when the female belonging to the 'pair' was away. On the other hand, one case of co-operation between the three birds was recorded in 1964 when all three birds were frequently present together and successfully reared 2 young.

One factor emerging from the study of trios was that the males concerned generally occupied a good site or one which was difficult to defend in some way, suggesting that they may be more aggressive in nest site selection. Further study of this aspect is desirable since Jenkins (1965) has shown that hormones which cause increased aggression in the Red Grouse males also tended to promote the formation of trios.

It should perhaps be pointed out that this kind of polygyny which appears to have no adaptive significance whatever (Section Five) is quite different from that described in the Snow Bunting (Tinbergen 1939) and the Bishop Bird (Lack 1935) in which the male courts only one female at a time. It is also different from the situation described in the Corn Bunting (Ryves 1934) in which the females occupy different nests, even though their laying is often synchronous. However, Cullen (1957) described what he called "triangular marriages" in the Arctic Tern and Nelson (1965) describes "triangular and multilateral associations" in the Gannet (as occurs in the Shag in this study) some of which persisted after the egg laying.

SECTION FOUR

THE NEST-SITE AND THE NEST

The Nest Site

The first tangible evidence of attempted breeding of the birds studied in this work has been their nest-site selection. No study of the physiological or histological development which precedes this, was carried out.

The sites are selected on the initiative of the male which then solicits for a mate from the site. If unsuccessful in this, the male will normally move elsewhere. However if the site is concealed from the females which would be standing in the general area of the colony at the time, then the male must solicit first and then lead his mate to the site. On Lundy this latter procedure is usually followed (Snow 1963), as it is on parts of Inner Farne and Staple Island. It was found convenient to rank the sites -1,0,+1 according to each of four requisites.

1. Access to the Sea

-1	More than one nest between site and sea
0	one nest between site and sea
+1	no nests between site and sea

2. Protection from heavy seas

-1	nest washed away at least twice during 1963 and 1964
0	nest washed away once during 1963 and 1964
+1	nest not washed away

3. <u>Exposure, other than to heavy seas</u>

-1 360°, fully exposed in horizontal plane

0 90 to 360° exposed in horizontal plane

+1 less than 90° exposed in horizontal plane or covered by overhanging rock

4. <u>Capacity of Site</u>

-1 completely unsuitable, too small to hold a proper nest

0 obviously inadequate for three young, unless these could wander safely, elsewhere

+1 adequate capacity

A calibration of this scale in terms of breeding potential is not attempted. One cannot use breeding output to do this until a full range of conditions at each site has been studied and when all the other important factors could be taken into account.

It has been clear throughout this study that nest sites can be described in terms of this classification and ranking, which in turn has great bearing on the birds breeding behaviour.

Access to the Sea

One of the striking characteristics of the nests built early in the breeding season is that they have uninterrupted access to the sea. For example, on the 'Shag Flat' area of Brownsmam where the rock is relatively uniform the distribution of nests is shown in Table 21 .

Table 21

(i) Access to the sea from Shag nests in the "Special Study" Area

	Access to sea from nest		
Built:-	-1	0	+1
Prior to 12-4-64	0	1	9
After 12-4-64	14	8	3

(ii) The height of Shag nests above the sea

Height above sea (ft.)	Unst	Cape Clear
0 - 10	5	4
10 - 20	73	
20 - 30	34	
30 - 40	9	34
40 - 50	5	
50 - 60	-	
60 - 90	-	19
90 -120	-	7
120 -150	-	2

What is the advantage of such access?. Firstly, it is an advantage during disturbance, when the birds on the edge have simple escape routes and can dive directly into the sea.

Secondly, and more important on the Farnes, a site on the edge of a sheer drop is easily defended from other Shags which are looking for nest material or for the site itself. The maximum angle which needs defending on the edge is 180°, but a few feet away from the edge it becomes twice this, and a difficult proposition, unless there is a rock behind to help. On Sule Skerry the nesting pattern is somewhat different and the nests are built "all over the island, in some cases under big boulders 200 yards from the sea..." (Tomison 1905). On Lunga in the Treshnish Isles, Harvie Brown and Buckley (1892) also found a colony of "rather unusally placed nests - not overhanging water" and Fraser Darling (1938) estimated that the nests there were "as far as a hundred yards from the sea". Such observations suggest that on completely undisturbed areas, access to the sea may not be so vital.

One of the difficulties of nesting 'inland' on the Farnes is that some of the birds are disturbed by tourists. When the tourists are about ten yards away the disturbed bird will make for the safety of the cliff~~s~~ edge and during the owners absence, less timid birds will tear the nesting material apart for their own ends; eggs and newly hatched young in such nests are ignored. Lewis (1927)° found, after a 24 hour vigil in a P. auritus colony:- "not only had a good deal of material been shifted from one nest to another, but.... this colony of 56 nests had lost 10 eggs in 24 hours. That the Cormorants have any idea of eating such eggs I do not believe; their object is to secure their neighbours nesting material and they appear to remove the eggs because they are in the way". Similarly the author has seen Shags remove other Shags' eggs or Kittiwake eggs before plundering the actual nests.

Protection from Heavy Seas

The most obvious requirement of a site is that it should not be swept by heavy seas, during the nesting season. The highest point on the Farnes is only 57 feet above M.H.W.M., and many nesting sites are swept by seas, especially those resulting from ESE to SSE gales. Northerly and westerly gales can only affect about six nest sites, but a SE gale on a spring tide would wash away at least 40 nests at the height of the nesting season (Table 22). A severe SE gale has not occurred whilst the author has been on the islands, nor during the summer since at least 1960 and so it is difficult to estimate what the effects of such a catastrophe would be.

The easiest way of avoiding heavy seas is to build higher up the cliffs or in a gully and indeed this is what most of the birds in the (-1) category do at their next attempt. On Lundy, where there is no shortage of adequate nest sites and thus no 'pressure' on low edges, the effect of heavy seas, other than spray drift at a few of the nests on the south west side, is negligible (Snow 1960,1963). Most nests on Lundy are built from 50 to 200 feet above sea level and are in addition,protected by a cliff face from spray. On the exposed cliffs at Cape Clear (Cape Clear Bird Observatory) the nests are built higher than on a sheltered site at Clibberswick,Unst, (Machell 1964) Table 21. On the Isle of May, several nests were near the top of the 150 feet cliffs. The species nests to 300 feet on Foula (Brathay Trust Foula Expedition Report 1960) and on Hoy (Serle 1934). The latter appear to be the upper limit for the species which we can conclude nests as close to the sea as the rock structure and exposure will allow.

Exposure other than to heavy seas

During the 19-20 June 1963 the rain was prolonged (about 18 hours) and the wind was NW force 7, in this same period 28 Shag chicks died on the Farnes. The temperature was low, (6°C). All the dead chicks were between 12 and 26 days old. Smaller chicks escaped because the adults brooded them and larger ones had sufficient juvenile feathers to prevent the down 'matting' with water, also they could move more easily to sheltered places. All the dead chicks were from nests exposed to the NW and none from other nests succumbed. Similarly in late July 1965 at least ten chicks, mostly about 15 to 20 days old, died during prolonged rain.

It is of interest to note that the sites on the Farnes are, very exposed compared to those elsewhere, except on Les Minquiers in the Channel Islands (Dobson 1951).

It is estimated that 75 per cent of the nests in the Scilly Islands are under cover and that on some islands all are under cover (Cornwall Bird Watching and Preservation Society Report 1947). In this case it is thought that the main advantage of cover is protection from the Greater Black-backed Gull which frequently takes eggs from the more exposed sites. On the Maidens (Isle of May) where Herring Gulls and Shags nest almost side by side, suspected Herring Gull predation took place at the more exposed sites. Table 22 shows the classification of nests on the Farnes according to their exposure. There is only one cave site and one nest under a boulder and only 27 per cent of the nests on Brownsman and Staple can be described as sheltered - despite the fact that Shags, as we have seen, generally prefer sheltered situations.

Capacity of the Nesting Site

On Lundy 38 per cent of nest sites were on cliff ledges with vertical drops below them but 48 per cent of the chicks which were lost between the age of 11 and 50 days were from this kind of site. Since only 30 per cent of the corpses were found in the nest, compared with 80

Table 22

The relative significance of the various categories of the nest-site

(359 sites, Brownsman and Staple)

	Rank order and number of sites			Mean rating
	-1	0	+1	
Access to sea	20	72	267	+.69
Protection from heavy seas	44	44	271	+.63
Exposure	107	225	27	-.22
Capacity	14	32	313	+.83
Totals	185	373	878	+.48

per cent at non-cliff sites it appeared that the higher loss was due to the young birds falling from the ledge (Snow 1960). Non-cliff sites which are too small to hold broods adequately are of little or no importance since the young merely wander to a better position. Cliff sites on the Farnes are directly over the sea and if a large chick falls it can, if it is older than about 30 days, swim to a lower ledge where it may still be fed. Since successful 'fledging' (defined p. 161) varies between 43 and 68 days (Mean = 55 ± 6.0 days (SD)) it is difficult to estimate mortality, because fatal premature 'fledging' is most likely among chicks which are at the wing excercising stage.(No corpses have been found on the Farnes, suggesting falls from the nest but most of the chicks would fall into the sea). Many cliff sites can support 3 chicks but not 4, though since 4 chick broods are unusual (Section Five) they can be ignored in this respect. Several sites in the -1 category were too small to hold a nest, others were obviously inadequate for 3 young (0 category). One problem is that an especially well constructed nest can outweigh the disadvantages of a precarious site. It has been assumed that from the viewpoint of capacity that the bird could build a normal nest. Nelson (1965) has pointed out that Shags do not cement their nests, unlike the Gannet and Kittiwake, the

Shag in this respect is not adapted to cliff nesting.

The capacity of the site is less important than the other qualities discussed (Table 22), however, there were several conspicuous attempts to nest in completely unsuitable positions. Such attempts cannot be ignored in any discussion of the complimentary roles of experience and physiological development in production.

Nest-site quality and Age of the Male

It is clear that the probability of the site holder rearing young successfully will be related to the suitability of the nest site and it is apparent (Table 22) that good nest sites are in short supply since nests are built on unsuitable sites. It has already been shown that the first birds which take up their nesting sites in the Spring, occupy the better sites (e.g. see Table 21). It was apparent that old birds began nest building earlier than the younger birds. In 1964, the oldest birds began nest building in mid January, so that 21 per cent of the birds in the oldest age group (11 years) had nests on the 9 February (Table 23). The two year olds began nesting in May and the year old Shags began building in July. Thus

XX [illegible] the age determined nest-site selection schedule is spread out over seven months. In 1965, the schedule was of much the same length though one pair may have maintained a nest throughout the winter. In 1962-1963 nesting probably did not begin until later, since the nesting

Table 23

Age of the male and time of nesting : the age of males with nests on 9 February 1964

Age ♂	* Number ♂ alive	Number with nest	Percentage with nest
2	35	0	0
3	31	0	0
4.5	50	3	6
7	53	7	13
11	42	9	21
	211	19	9

* approximate

areas were frequently awash, to this extent the schedule is plastic.

Table 24 summarises the results of an analysis which shows quite clearly that birds which are breeding for the first time (<u>i.e</u>. 2 year olds) are occupying sites of inferior quality. In the following year they occupy much better sites and thereafter they will settle in more suitable sites until finally the oldest birds will be in the best sites.

The progression of birds up this gradient of nest site quality is measured by their site tenacity Fig. 21 and it is clear that this increases with the quality of the site. The factor which causes movement to another site is connected with failure Fig. 21 ; the unsuccessful birds move more frequently. Thus a bird which occupies a poor site and is consequently unsuccessful, will move on. In the following year it is able to occupy a site earlier in the season and it will be able to adopt a better site.

It will be interesting to examine this progress of the unsuccessful birds in the next year or so in relation to the approaching shortage of good sites. Conversely, in earlier years the quality of the nest selected in reaction to age may have been unimportant. Old photographs shows that the best sites were generally utilised first, during the history of the colony.

Table 24

Quality of site occupied by individual males of known age in 1963 and 1964

Brownsman

Age ♂	Number ♂♂	Index 1963	Number ♂♂	Index 1964	Overall
2	10	1.1	-	-	1.1
3	8	2.0	10	2.2	2.1
4.5	10	1.9	12	2.1	2.0
7	13	2.5	15	2.1	2.35
11	5	2.4	9	2.5	2.45
Total and mean	46	2.0	46	2.2	2.1

Staple

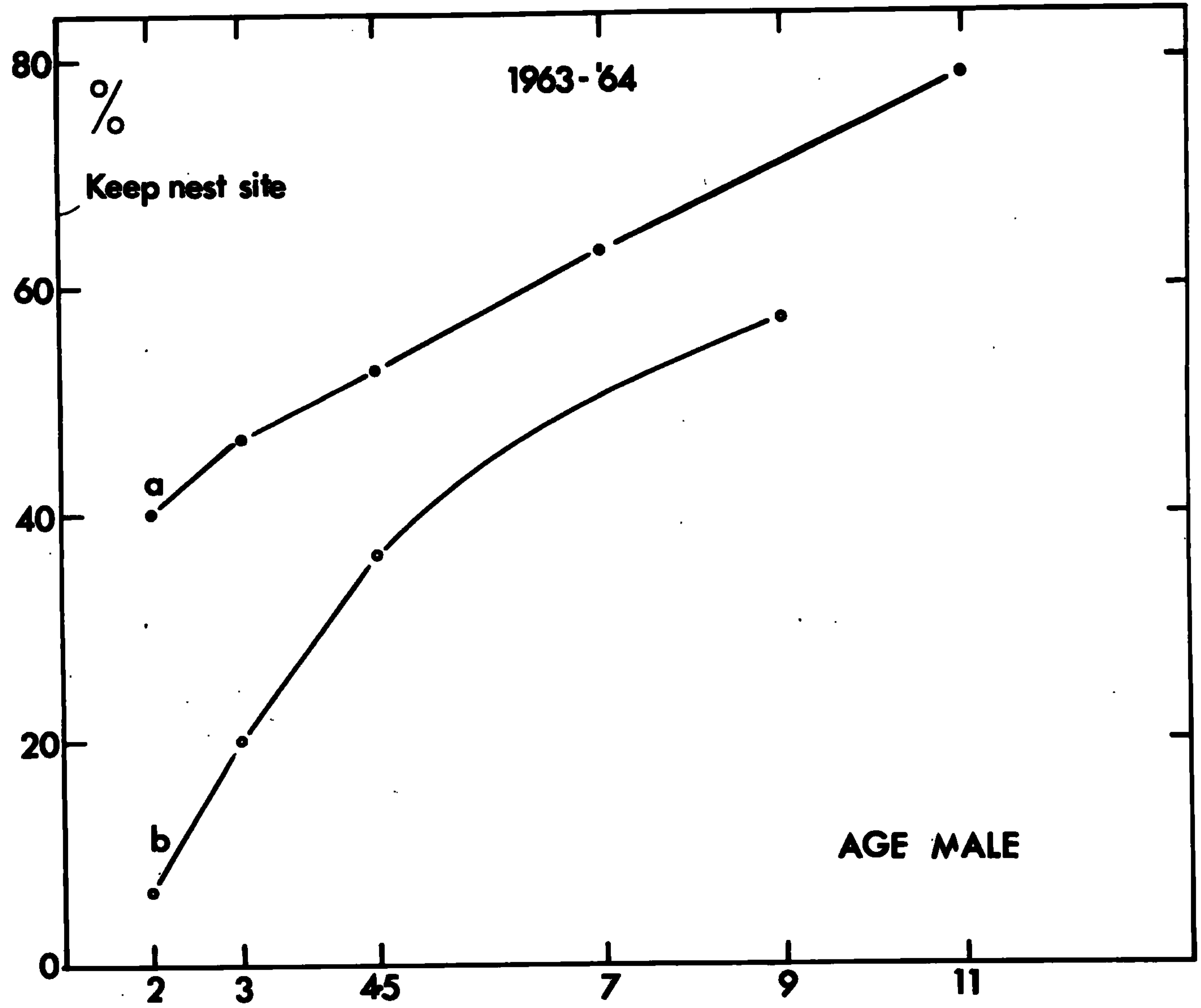
Age ♂	Number ♂♂	Index 1963	Number ♂♂	Index 1964	Overall
2	11	1.8	-	-	1.8
3	15	2.1	11	2.1	2.1
4.5	20	2.3	24	2.1	2.2
7	28	2.2	32	2.2	2.2
11	26	2.5	33	2.5	2.5
Total and mean	100	2.2	100	2.3	2.25

Fig. 21

SITE TENACITY AND SUCCESS AT SITE

a. rear young

b. do not rear young (since so few old Shags do not rear young grouping has been necessary).


1963 - '64
%
Keep nest site
a
b
AGE MALE
80
60
40
20
0
2
3
45
7
9
11

Since most site occupation is spread over a period of some four months, overt competition for sites is greatly reduced and rarely observed, except among recruits in relatively flat areas.

The location of the chosen site is to some extent influenced by the location of the natal site (Table 25) though this is less true than formerly (Fig. 15). The 1964 pulli which returned in 1965 as prospecting birds indicated that some birds may return to the immediate vicinity of the nest-site, for 7 out of 17 (41%) returned to within 20 yards of their natal nest-site, whereas 7 out of 36 (19%) in the previous cohort finally nested there. (cohort:- pulli ringed on the Farnes in the year of this age class)

Table 25

First site chosen by nesting Shags in relation to its natal site. Males of 1963 cohort in 1965 season i.e. when aged two years

Movement of 36 males:-

Type of Movement	Number males	Percentage males
Moved less than 20 yards	7	19
Stayed in same part of island	14	39
Stayed on same island	24	67
Moved island	12	
Moved away from Farnes	2(1)	33
Total males	36	

(1) All areas could not be searched, hence this is a minimum figure

PLATE 2.

SHAG GULLY, STAPLE 29 MARCH 1965

Rate of increase and quality of nest site

Earlier (p45) it was found that there was very little correlation between the rate of increase of breeding Shags in various parts of Staple and Brownsman in the two periods 1963-1964 and 1964-1965. However this is somewhat confused because there are local annual variations. If the growth rates for the two periods are averaged, it is found that some areas sustained little, if any, growth, during this study. Reference to scattered information from earlier years showed that these are the areas with the better nesting sites, which were occupied first in the history of the colony. In fact if the average nest-site quality for each of the areas detailed in Table (these are separate geographical areas such as a particular gully etc.) is plotted aginst growth rate it is found,(Fig. 22) that growth is not now occurring in the optimum areas, nor in the especially poor areas, but in the sub-optimum areas. The implications of this is that nest-sites are in short supply for two reasons:-

1. there are none left in the earlier occupied areas
2. in the poor areas, especially those susceptible to heavy seas, further expansion is prevented by the inadequacy of the sites.

Table 26

The Maximum number of Shag nests found in various parts of the Breeding Areas, 1963 - 1965

(see Map 1 page 7)

Area	1963	1964	1965
P	12	15	16
B	44	36	44
SB	11	23	28
Brownsman	67	74	88
ST	14	14	15
C	17	20	20
Pinn	5	6	5
K	39	42	38
S(i)	38	51	47
I	11	12	10
S(ii)	28	31	44
SE	32	34	43
SW	7	9	11
SN	-	-	1
Staple	191	219	234
IF	32	35	42
Others	5	4	3
TOTAL	295	332	367

Fig. 22

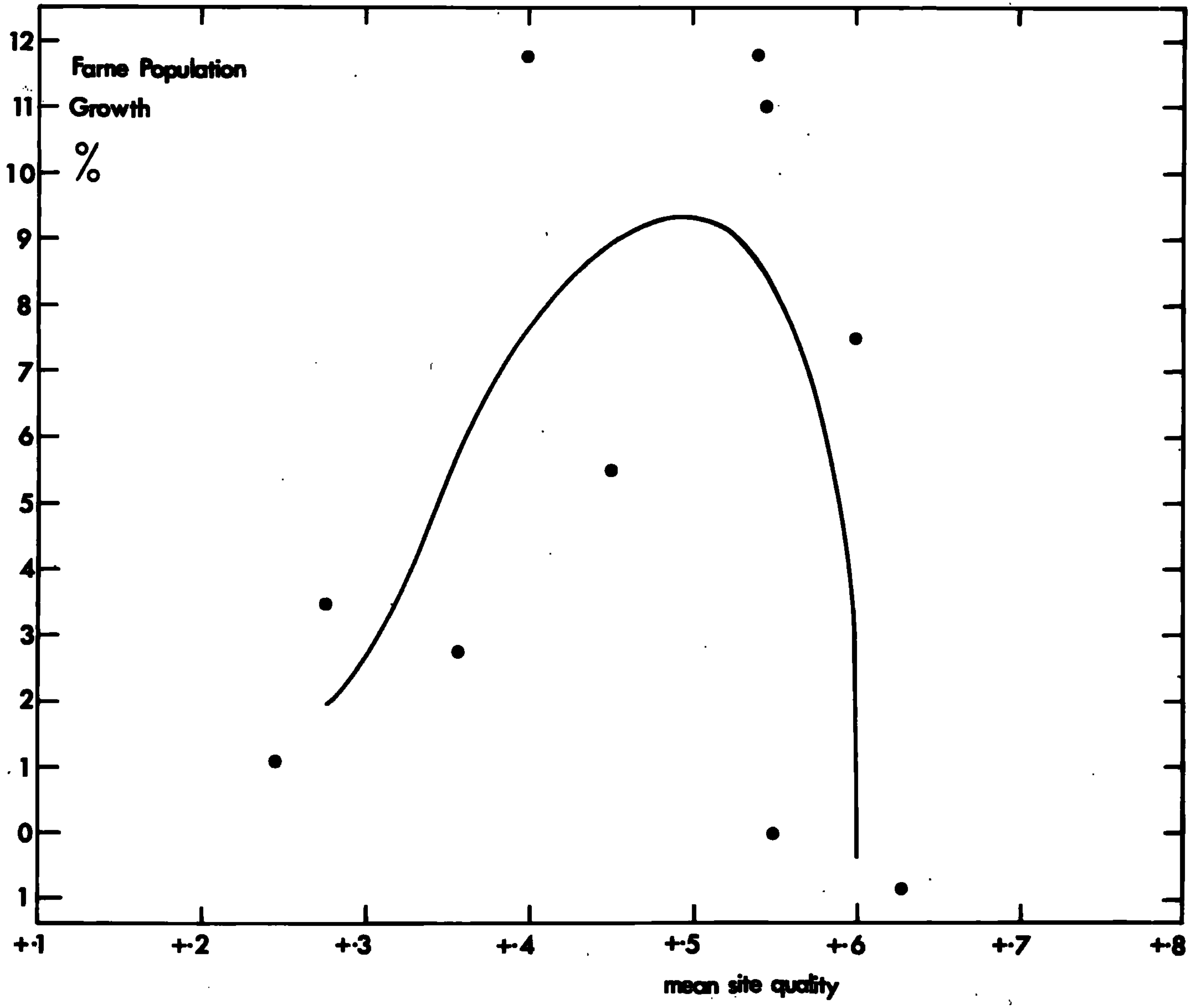
GROWTH OF SHAG POPULATION AND QUALITY OF NEST SITES FOR VARIOUS PARTS OF FARNES

Growth

The mean increase 1963-1964 and 1964-1965 as a percentage of the total increase (for all Farnes) 1963-1965.

Site rating

Mean for all nests in area (Table 26) for 1964.


Farne Population
Growth
%
12
11
10
9
8
7
6
5
4
3
2
1
0
1
+·1
+·2
+·3
+·4
+·5
+·6
+·7
+·8
mean site quality

THE NEST

The male collects virtually all the nest building material and females have only been seen to collect material if it was taken from a neighbouring nest. The bringing of nest material by the male occurs from the time the pair bond is first formed until the chicks are well grown and the offering of nesting material to the female forms a large part of the ritualised behaviour during the formation of the pair bond. The male brings nesting material after short excursions for that purpose or after feeding. The short excursions are especially frequent after the female has been solicited, and again throughout the season, before the first feeding trip of the day. If both birds were to leave any of the better sites early in the season the site would be rapidly occupied by new birds or at least, the nesting material would be quickly incorporated into other nests. The distribution of nests in space and time is thus a measure of pair formation patterns since deserted nests are quickly removed.

Quality of the nest and age of the birds

Since the male brings the material and since the actual building is very simple and partly carried out by the male, the age of the male is likely to be the most important factor and is thus considered here. The prime function of the nest is that it should hold the clutch i.e. it should be cupped, the lining does not matter very much since the eggs are incubated on top of the webbed feet. Three categories of nest are recognised:-

1. a few strands of wrack
2. a platform
3. a cupped nest

These were recorded at the time of laying of the first egg.

The older birds build more suitable and well developed nests while many of the two year old birds build poor nests and indeed, carry out much of the building after the first egg is laid (Table 27). Fourteen platform nests have been built by one year old Shags, nine of them in 1963 but most of these could have held clutches successfully only if they were much improved before incubation were to begin.

Kortlandt (1940) found that young Cormorants begin to show nesting behaviour at an age of two weeks. At first the twigs used were not firmly attached, but after 4 or 5 weeks they became caught up in the nest and later still the young accepted twigs from the male and worked these into the nest. Much the same process has been described

Table 27

The structure of the nest, at the start of the first laying of the season, in relation to the age of the male

1963

x Rank number	Age of ♂(Colour Ringed only)				
	2	3	4.5	7	11
1	10	3	2	3	1
2	8	4	4	5	1
3	4	9	24	34	31
Mean rank	1.73	2.37	2.73	2.74	2.91

(143 nests)

1964

Rank number	Age of ♂(Colour Ringed only)				
	2	3	4.5	7	11
1	16	4	3	2	4
2	9	4	8	2	9
3	8	18	26	37	21
Mean rank	1.81	2.54	2.62	2.85	2.50

(181 nests)

1964 "Study Area" (B+P)

Rank number	Age of ♂ (+ All 2 yr. olds)				
	2	3	4.5	7	11
1	7	0	2	0	1
2	5	1	1	0	2
3	0	7	5	9	8
Mean rank	1.42	2.87	2.38	3.0	2.64

(48 nests)

x1 = scraps, very poor nest, egg in contact with rock
2 = platform, egg likely to roll out
3 = cup nest

Eggs laid on bare rock are excluded(see text). The study area 1964 is kept separate since the sample is complete, (all males are included) and this is an area where sites are in short supply.

in the Shag (Snow 1963) and occurred on the Farnes.

Thorpe (1964) considers it probably "that many cases of improvement in nest building in older birds which are regarded as being due to experience are, in fact, merely cases of rising hormone level, first year birds tending to build clumsy nests because their hormone secretions have not reached the required level" but "further study is necessary to resolve such problems". The Song Sparrow female "builds her first nest as expertly as her last", "for the nest is a simple affair" (Nice 1937). This would appear to be the case in the Serin which possesses the innate capability to build an adequate nest at the first attempt (Thorpe 1964). On the other hand Nice quotes observers who describe how birds which build elaborate nests such as Orioles,Oropendolas and Ploceine weavers improve their techniques as they "grow older".

From his work on doves, Lehrman (1959) considered that the presence of nesting material and of the nest, and/or participation in nest building behaviour contributed to the advancement of the reproductive cycle, probably by stimulation of the luteinising hormone secretion of the pituitary. There are several reasons for thinking that this is not the case in the Shag. Firstly, the first eggs of young birds are frequently laid before the nest is adequate and thus precede the presence of a nest as such. Secondly the period of time which elapses between nest construction and egg laying is very variable, and is modified by weather conditions, (Table 28).

In the Brownsman Special Study area (51 nests) in 1964 it was found that there was a close correlation ($r = +.96$) between y(the percentage of nests with eggs) and x(the percentage of nests built (as percentage of maximum):- The regression being

$$y = 2.73x - 176$$

Thus no eggs were laid until about 65 per cent of the nests were complete, but 83 per cent of the nests held eggs when 95 per cent of the nests had been built. Indicating that the time between the start of nest building and start of laying decreases through the season. Since the older birds nest earlier, the time between nest building and egg laying is therefore inversely related to the age of the birds. Though it is clear that the nesting of young birds is inadequate, this does not appear to reflect lack of skill since a minimum of this is required, nor does it appear to reflect lower hormone levels, unless these are independent of the ovulation cycle.

Table 28

Seasonal variation in the nesting cycle

Percentage nests started:-

DATE	1963	1964	1965
1st Jan.	0 **	0	0
1st Feb.	0 **	4.8	9.5
1st March	0 *	9.0**	21.8
1st April	25.4	27.1	47.7
1st May	74.6	69.3	76.3
1st June	100	100	100
Date of 1st Egg	3rd April	17th April	4th April

* = disturbed weather and seas

SECTION FIVE

EGG AND CHICK

Geographical Variation in the Laying Period

Compared with other European sea-birds, the Shag has long been known to have an unusually variable and extended breeding season, (Jourdain 1913). Indeed it has frequently been considered to raise two broods in the year (*e.g.* Forrest 1907). The evidence for this has been the finding of fresh eggs in nests vacated by fledglings and the finding of fresh eggs and fledged chicks on the same date (Jourdain *loc. cit.*).

More than 3,200 nest records from 14 areas (apart from the Farnes) collected over a number of years and supported by other evidence have been examined (Appendix E).

The shape of the breeding season (egg laying) curve appears to be similar throughout the British Isles, being negatively skewed by about 8 days in each case (Fig.23). With the exception of the Isle of Man (see Fig.23), the early colonies are in areas of higher sea temperature. Lundy is later than would be expected on this basis but the population there is migratory and it is likely that other~~s~~ factors are involved in this instance.

Except on the Calf of Man (Appendix F), February layings are unusual in Britain, but in Cyprus (Bannerman and Bannerman 1958) and Corsica (Jourdain 1912) the

Fig. 23

THE SPREAD OF LAYING IN VARIOUS GEOGRAPHICAL REGIONS OF THE BRITISH ISLES ACCORDING TO SEASONAL VARIATION IN THE LAYING PERIOD

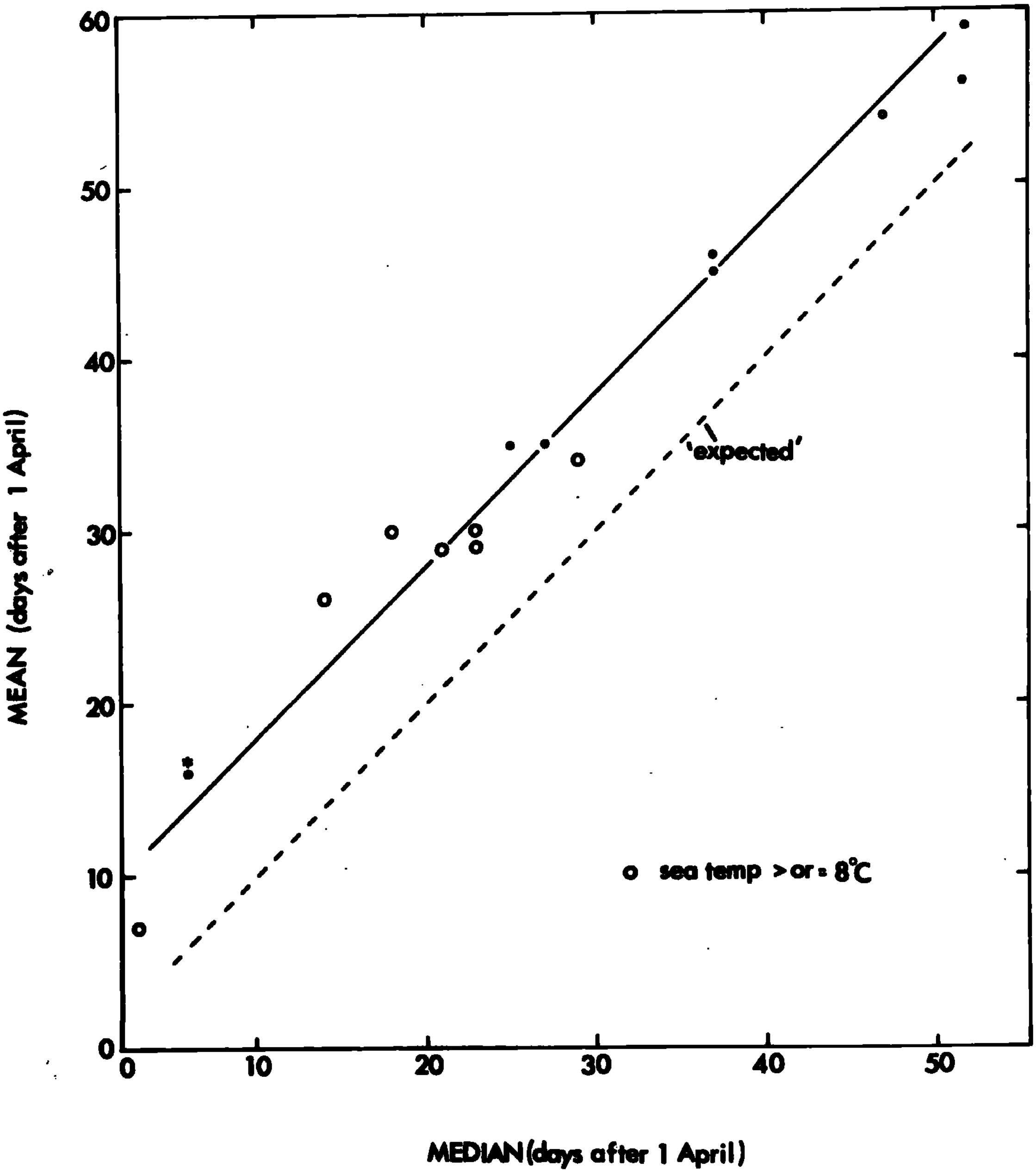
If the spread of laying were a normal curve then the Mean and Median would coincide (the broken line). Since the observed values are parallel to this 'expected' line the shape of the laying curve is similar regardless of the date of laying from 3 April (Isle of Man) (see asterisk) to the 51st day (21 May Shetland).

Sea temp. mean monthly top 30 m. (Min)

Open circles > or = 8° C

Filled circles < 8° C

Asterisk Isle of Man


60
50
40
30
20
10
0
0
10
20
30
40
50
MEAN (days after 1 April)
MEDIAN (days after 1 April)
'expected'
*
○ sea temp > or = 8°C

Mediterranean sub-species starts laying in early January whilst on Kharlov Island in the Murman sea laying begins in mid May (Belopolskii 1961).

Elsewhere other Phalacrocorax spp have very variable nesting seasons. Though P. carbo is strictly seasonal on the equator (Marshall and Roberts 1959), it breeds only after suitable rains in parts of Australia (Serventy 1955) and in New Zealand there are two laying periods, one in May the other in September (Falla, in Serventy 1955). The marine P. varius on the coastal islands of Australia usually breed in autumn and early winter, though in one group of islands breeding is in late spring (Serventy loc. cit.). Again Turbott (1956) describes groups of P. punctatus which breed several months apart, though in the same geographical area. It would appear that the Isle of Man is especially out of phase within the British Isles with regard to the timing of the breeding season, but this also applies to the period of yearling mortality, though there is no correlation between the two factors elsewhere. The laying season on the Farnes is near the average for the whole of the British Isles. The median date of laying is 27 April ± 12.5 days (Stand Dev.)

Seasonal Variation in the start of laying on the Farnes

As a preliminary to an examination of the internal parameters of the egg laying period, some consideration of its modification by proximate factors (after Baker 1938) is required since the onset of laying varies considerably from season to season.* Thus the first eggs have been recorded on the Farnes from the 16 March (1961) to 28 April (1958) a period of 43 days.

Once started, the spread of breeding is practically uniform from season to season. The only exceptions to this are possibly late seasons (e.g. 1958) when the laying is less synchronised (Fig. 24), but it is interesting that this 'late season effect' does not apply to inter-colony (grouped according to sea area), comparisons (Fig. 23), since the degree of skew is similar in early and late breeding areas.

Age and date of first breeding

Use of the Median rather than Mean

Accepting the fact that age influences the laying date some measure of central tendency of date is needed. Since the frequency curves are negatively skewed, the median (the date by which 50 per cent had laid) is a more useful guide than the mean which is subject to the irregular behaviour of the extreme late values. Fig. 25 gives the frequency distribution for all age groups and shows the irregular positive tail. In small samples, the median is even more reliable since one extreme (late) value may shift the mean considerably but does not alter

---

[*] In 1960-1965, according to mean March air temperature.

Fig. 24

ANNUAL VARIATION IN THE SHAPE OF SEASONAL LAYING CURVE

One Shag (Inner Farne) laid on 16 March 1961 calculated from T.H. Pearson _in litt_. Whereas the next laid on 22 March. If the first exceptional record is included there is a suggestion that laying tends to be more synchronised in seasons which begin about the average date. Certainly the late (1958) season was very spread out. (The closer the Mean to the Median the more synchronised the season). The medians were calculated by plotting ogives of 1st egg dates against season and graphically interpolating the 50 per cent mark:- The ogives were plotted on Arithmetical - probability paper (1959 (open circle) from date of 1st egg only).

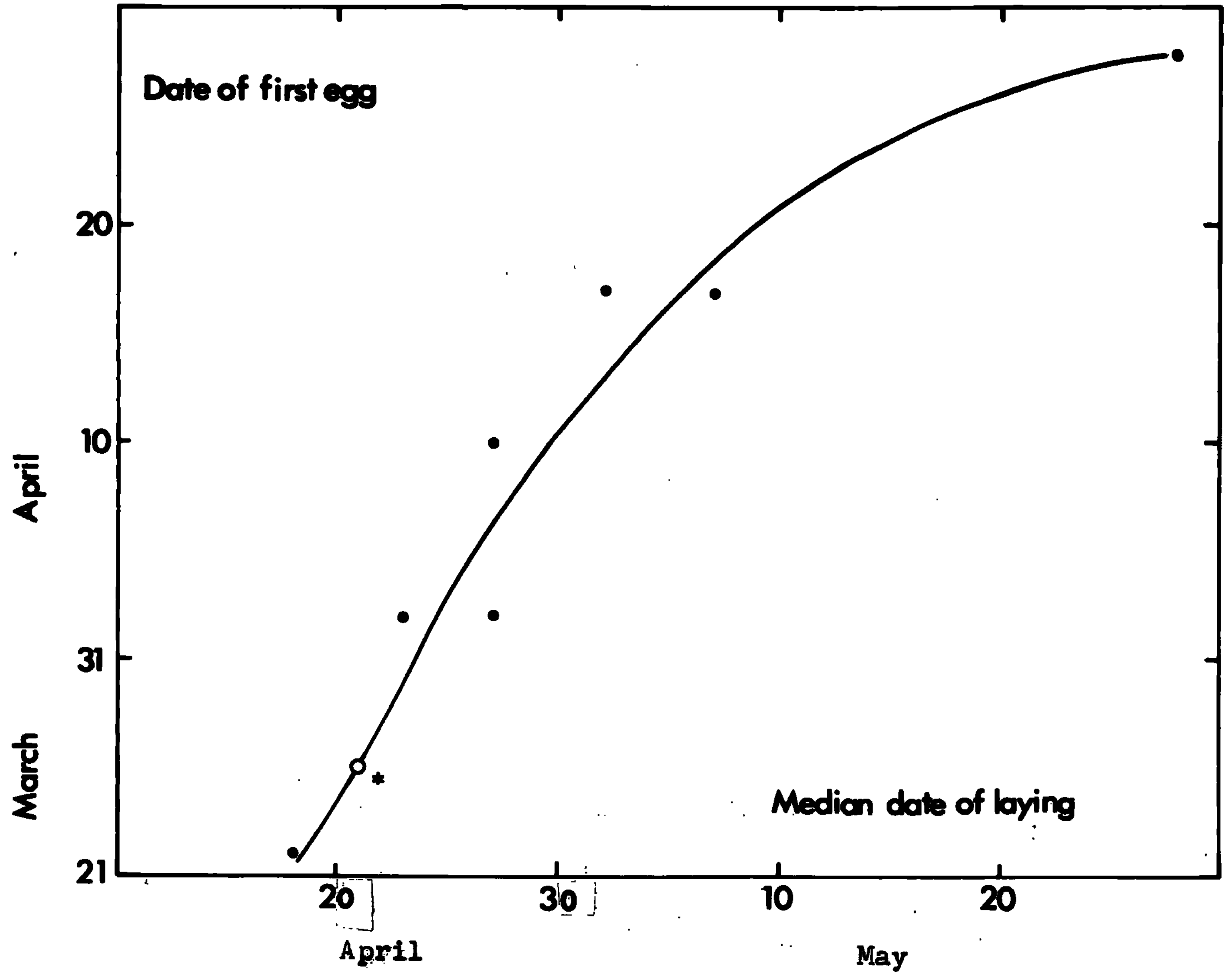
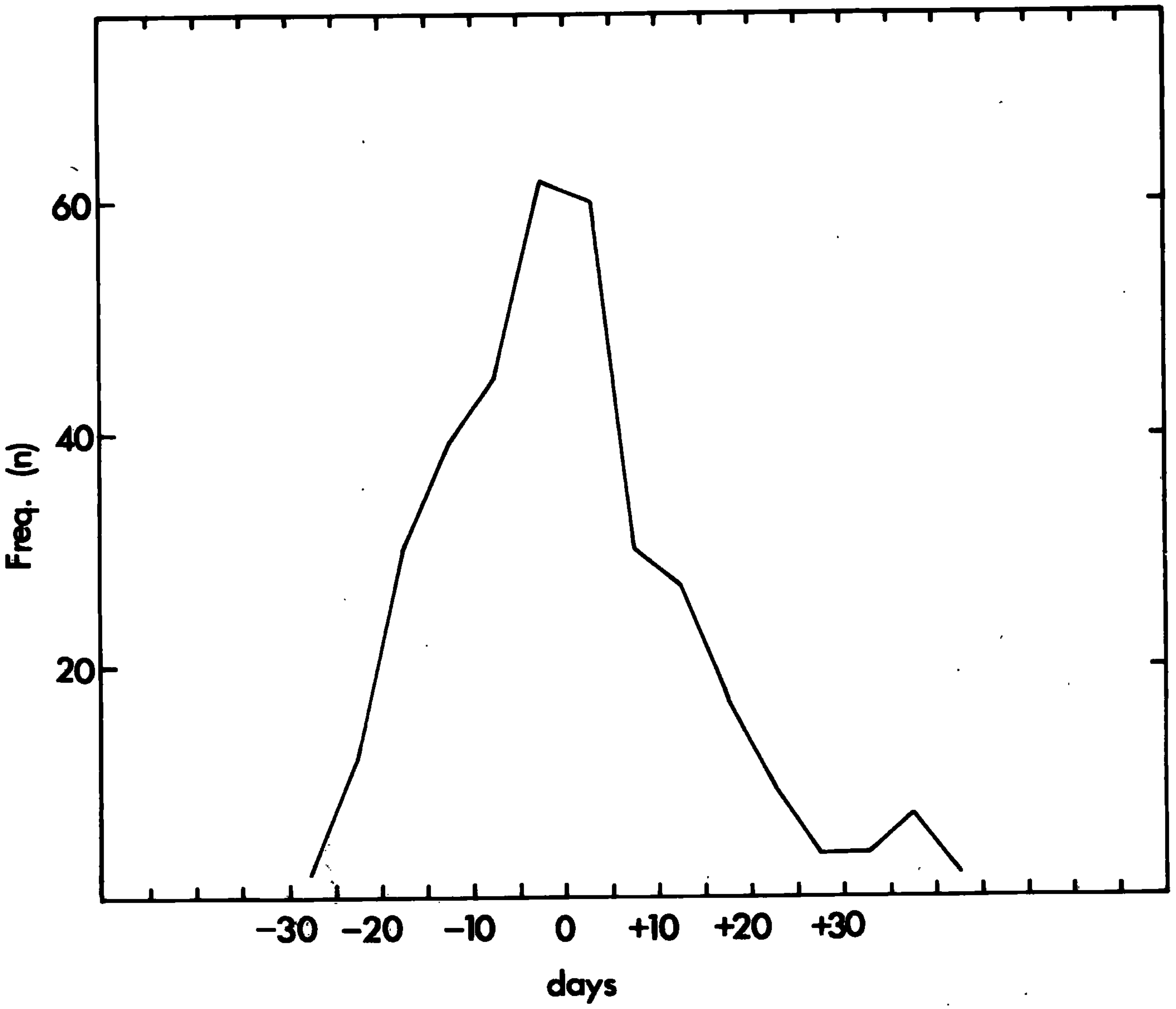

Date of first egg
20
10
31
21
April
March
Median date of laying
20
30
10
20
April
May
*

Fig. 25

SYNCHRONY WITHIN AGE GROUPS IN SEASONAL ONSET OF LAYING

The mean date is compared to the actual date of laying. If the individual was early then the difference was negative. The distributions for each season (1963 + 1964) are added; the total distribution is negatively skewed.


60
40
20
Freq. (n)
−30
−20
−10
0
+10
+20
+30
days

the median. Whilst the median is in this case a more accurate measure of central tendency than the mean, normal statistics require that it is considered 25 per cent less efficient in dealing with the whole distribution and its standard error = SE of the mean x 1.25

The influence of age and status on the date of egg laying

It was found that age had a marked effect on the median date of laying of the females in 1963 (Fig.26) Table 29. For example the median date of the 11 year old group of females was 22 April, and the 2 year olds, 23 May. The one year old birds did not lay but began nest building in early July.

In 1964, the order was much the same except that the oldest group was delayed (Fig.27) since the onset of laying was two weeks later (Table 28). The laying date of the 2 year olds was 24 May and not significantly different from that in 1963. In 1964, it was found that the schedule was not merely determined by age but that at least three 'status groups" modified the effects:-

a. birds laying for first time
b. birds which have changed mates
c. birds which keep mate from one season to next

That each of these has a bearing on laying date is clear from Fig.27. Within each of the three groups age has consistent effect (though less marked in group b). Age

Fig. 26

DATE OF LAYING OF THE FIRST EGG IN 1963, ACCORDING TO AGE OF THE FEMALE

Median ± 2 SE (see text p 101).

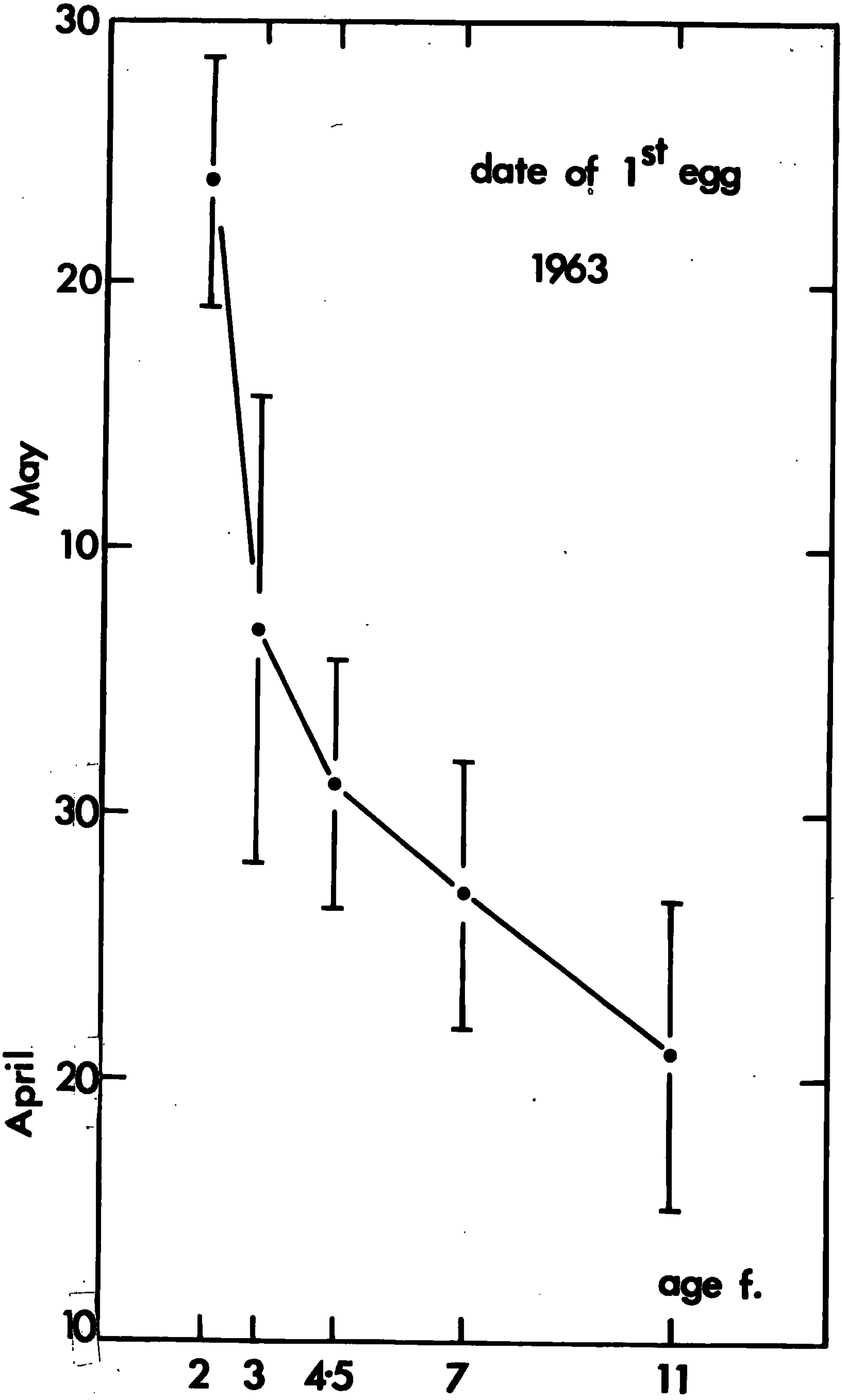
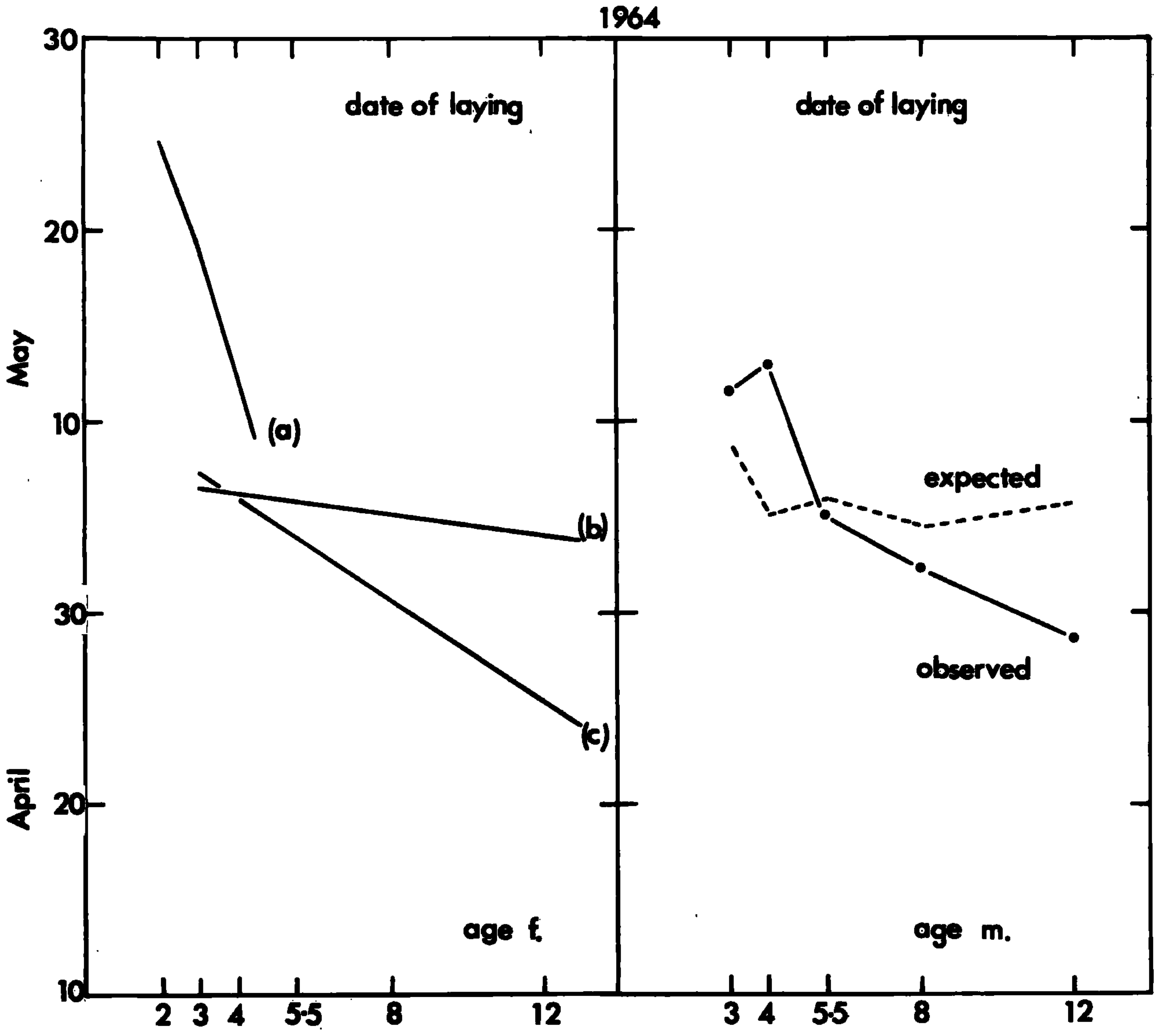

date of 1st egg
1963
May
April
30
20
10
30
20
10
age f.
2
3
4·5
7
11

Fig. 27

AGE,STATUS AND LAYING DATE (FIRST EGG) IN 1964

Medians

(b) and (c) are regression lines reducing y errors, the relationship was approximately linear for full explanation see text.


1964
date of laying
date of laying
May
April
30
20
10
30
20
10
(a)
(b)
(c)
expected
observed
age f.
age m.
2
3
4
5·5
8
12
3
4
5·5
8
12

is closely related to the time of laying; the older birds laying earlier.

In 1964, there was no significant difference between the laying dates of four year old females which had and had not, bred in a previous year (Fig.27). However, the laying date of the three year olds which had bred before was 14 days earlier than those of the same age which were breeding for the first time, but because of the small sample the difference was not significant at the 5 per cent level (see Table 30).

In 1964, there was a delay in the date of laying among the females which had changed their mate, a delay which became more marked as the age of the birds increased. It has been shown that changed pairs have a different age structure from established pairs and that the difference becomes more marked among older birds (Table 18).

The slope (c) (Fig.27) was taken as the standard to obtain the median date of laying of females of known age in 1964. This slope (c) was compared with the average age of the partner of changed pairs, working from the age of the male as in Table 18 . It was then assumed that the date of laying of a changed pair could be estimated knowing only the age of the female. The estimates are given in (Fig. 27) and form an 'expected' series of values, which are compared to the observed laying date of the changed pairs. It is clear that some other influence is present since the expected and observed values differ and the difference is exactly what we should expect if the males also had a breeding schedule graded according to age, and if the date of laying was some sort of compromise between the schedules of the respective partners. Thus the young females in changed pairs (those of old mates) are laying earlier than expected from their age, and the old females in changed pairs (those of the young males) are laying later than expected i.e. they are accomodating to the schedule of the male. Of course, this is not an unexpected conclusion since the function of much pairing behaviour is to fix such a compromise, but it does demonstrate the need to bear in mind that breeding is the result of a combined effort of two birds.

It might well be imagined that individuals would have peculiar laying dates and that the birds which changed mate tend to have an inherently different laying schedule. That this is not so is demonstrated by the information in Table 29 . which gives the laying date of changed and stable pairs (kept mate) in 1963, the season before they changed. The delay in laying of changed pairs is then a result of the different age structure of changed pairs.

Table 29

Median date of laying of females in 1963

Age ♀	Total females	Median date	Females change mate[*]	Median date
2	16	23 May	5	22 May
3	17	7 May	7	11 May
4.5	61	1 May	24	3 May
7	56	28 April	16	30 April
11	39	22 April	9	20 April

[*] 1963-1964

Synchrony within age groups

Apart from the delay in the median date of egg laying, the spread of breeding of birds of lower status may a priori be greater. In particular the birds which change mate are known to be a heterogenous group since some have divorced their mates whilst others are replacing dead mates (see p 61) and this may be reflected in their breeding schedule in this way.

The relevant information is given in Table 30 where the indices of spread have been reduced to a common base as far as possible for ease of comparison. There is no significant difference between the male and female standard indices and no consistent difference between the two status classes of females. It is clear that the male spread of breeding is greater in the old birds which take new mates and that the differential involved, increases with age of the male, until in the oldest group the stable males have a much more closely synchronised season than the males of lower status ($P = <.05$). Here is confirmation that the age of the male is intimately connected with the laying date of the female, since their schedule (unless upset by pair change) is better synchronised than that of the female (which is not upset by change).

There is no trend in the degree of synchrony between age groups, thus the old birds are no more or less on 'schedule' than the young.

Table 30

* Coefficient of Variation of the onset of laying in Shags according to status and age, in 1964

		Status of Females			Status of Male	
Age	Keep mate	Change mate	First time	Keep mate	Change mate	First time
2	-	-	27	-	-	25
3	-	21	20	29	17	22
4	29	13	30	25	19	-
5.5	32	31	-	44	54	-
8	39	37	-	25	32	-
12	43	29	-	27	47	-

* $\frac{100\,SD\left(\frac{n}{n-1}\right)}{\text{mean}}$ (i.e. with Bessel's correction for sample size)

There is no significant difference in the variation with age or between the sexes, but the onset of laying is more variable in males older than five which change mate ($P = < 0.05$, $f = 3.21$)

Intervals between Eggs

Gibb (1946) was the first to amplify the belief of Witherby et al (1941), "that the interval......is apparently more than one day", when he studied interval in six clutches at Trewarvas Head, Cornwall. Snow (1960) states "the interval between the laying of successive eggs was ascertained for a considerable number of nests. Normally eggs are laid every third day, so a complete clutch takes a week to produce". Clearly there was need for a more accurate account, so that the date of laying of the first egg (used in previous sub section) could be calculated if the date of laying was known for the third egg only. But first some consideration of egg laying as a circadian rhythm is needed.

Incidental observations yield the laying time for nine eggs. Eight of these were laid before sunrise, but after dusk. New laid eggs are warm and have a mucus coating and can easily be detected if they have been laid less than half an hour. In the author's experience (involving for example measuring well over 1,000 eggs during the laying period, daily visits etc.) there is no suggestion that the eggs are laid during the main part of the day. The only instance recorded was the ninth egg which was laid at 1100 B.S.T. The egg laying behaviour itself is a fairly conspicuous affair and can be recognised from some distance. The strict laying rhythm had distinct advantage since the male attended the observed layings and the females would not have to defend the nest in her mates' absence during this period of maximum vulnerability, but it is interesting that some of the Laridae (e.g. see Barth 1955) do not possess such a rhythm. Snow (1960) found that eggs were laid "either at night or very early in the morning". "The time of one egg was found to be" ..(Earlier than).. "0445 G.M.T.". The aims of the present study do not justify a more objective study since the amount of disturbance would be great. However there are reasonable grounds for considering the error on the measurements of egg intervals, made on daily visits as being much less than ± 12 hours.

The laying intervals are given in Table 31 and the statistical tests on the intervals in Table 31 . The eggs of a two egg clutch are laid 3.57 days apart, the eggs of a three egg clutch are laid 3.11 days apart and the eggs of a four egg clutch are laid 3.03 days apart. This shortening of the interval according to clutch size is possible since the early intervals in the laying sequence can be compressed whilst the interval between the penultimate and ultimate egg appears to be fixed. Throughout this work extrapolations of egg laying dates have assumed a fixed 3.0 day interval.

Table 31

Laying Intervals according to clutch size

Clutch Size (±SD)	Interval between eggs in days		
	1st 2nd(a,b)	2nd 3rd(b,c)	3rd 4th(c,d)
2	3.57 ± 1.35 (6)		
3	3.01 ± 0.72 (110)	3.21 ± 0.77 (97)	
4	2.92 ± 0.92 (13)	3.07 ± 0.83 (14)	* 3.20 ± 0.93 (29)

n.b.

* Incorporates data on B.T.O. nest records from Gt. Saltee

1. Coefficient of variation for C/3 a,b and C/3 b,c is 23.92 and 23.99 respectively i.e. these laying intervals are equally variable about their mean
2. The probability of differences in the intervals of the eggs is as follows:-

Values of P

C/4	a,b	b,c (0.8)	c,d (0.9)
C/3	-	a,b(0.05)	b,c (0.3)
C/2	-	-	a,b

Thus C/4 c,d C/3 b,c and C/2 a,b are of similar length and C/4 b,c and C/3 a,b are of similar length. The corollary of this is that the interval between eggs decreases with clutch size.

Clutch Size

There does not appear to be a satisfactory definition of clutch size in the ornithological literature, probably because the broad concept is so simple. For example, one would have little hesitation in saying that the clutch size of the Wood Pigeon was two eggs. This broad concept is inadequate for measurement and interpretation of variation in clutch size within a species and within each laying season. Thompson (1964) considers a clutch to be "the complete number of eggs laid by one female, that are brooded simultaneously", which is a dubious improvement of the definition "a set of eggs" given in the Oxford Shorter English Dictionary. Monk (1954) defined the clutch as "the maximum number of eggs found on two consecutive visits more than 24 hours apart", and when Snow (1955) studied clutch size in various _Turdidae_ he used this definition and found "no reason why sources of error should have more effect in one part of the breeding season than another". This last conclusion would not stand, if, for example, older females laid earlier in the season (as they do in the Blackbird (Snow 1958)) and if egg loss was an age specific effect, (both of which are found in the Shag). The proximate factors governing the extent to which an individual is a deterministic or indeterminstic (lays until finite clutch size is reached) layer may also vary within a season.

Parkhurst and Lack (1946) found that error, probably due to partial predation, reduced the clutch size of the Yellow Hammer, estimated from nest records started after laying had ceased. However, Lack (1948) found that this type of error was negligible in the Robin.

Bearing in mind these difficulties, the following definition of clutch size was used throughout this study, and various additional measures were also used:-

A Clutch:- is that number of eggs which is laid in one nest by one female, if no eggs were lost during the laying period, if the last egg was added at an interval of less than eight days, and if the maximum number of eggs persisted for at least five days. Since C/1 and C/5 are so rare they have been incorporated in C/2 and C/4 respectively to ease statistical analysis.

The interval of eight days was introduced since the interval between egg c and d is irregular (Table 32).

Seasonal Variation in Clutch Size

On Lundy (Snow 1960) found a progressive decline in clutch size from the beginning of the season, but in each of the other four samples (Fig. 28) this was not evident. These seasonal patterns imply that clutch size is related to age on Lundy if the breeding schedule of the various age groups is the same there as on the Farnes, but elsewhere support the conclusion that clutch size is not related to age since the steady plateau part of the

Table 32

Interval between third (c) and subsequent (d) eggs in nests which eventually contained four eggs

	Days after laying of c egg											
	1	2	3	4	5——	10	11	12	13——	27——	30——	34
Number of instances	2	2	12	5	3——	2	1	2	1——	1——	1——	1
Status of egg			d					?			?	
Used in Analysis of Clutch Size			Yes					No			No	

Fig. 28

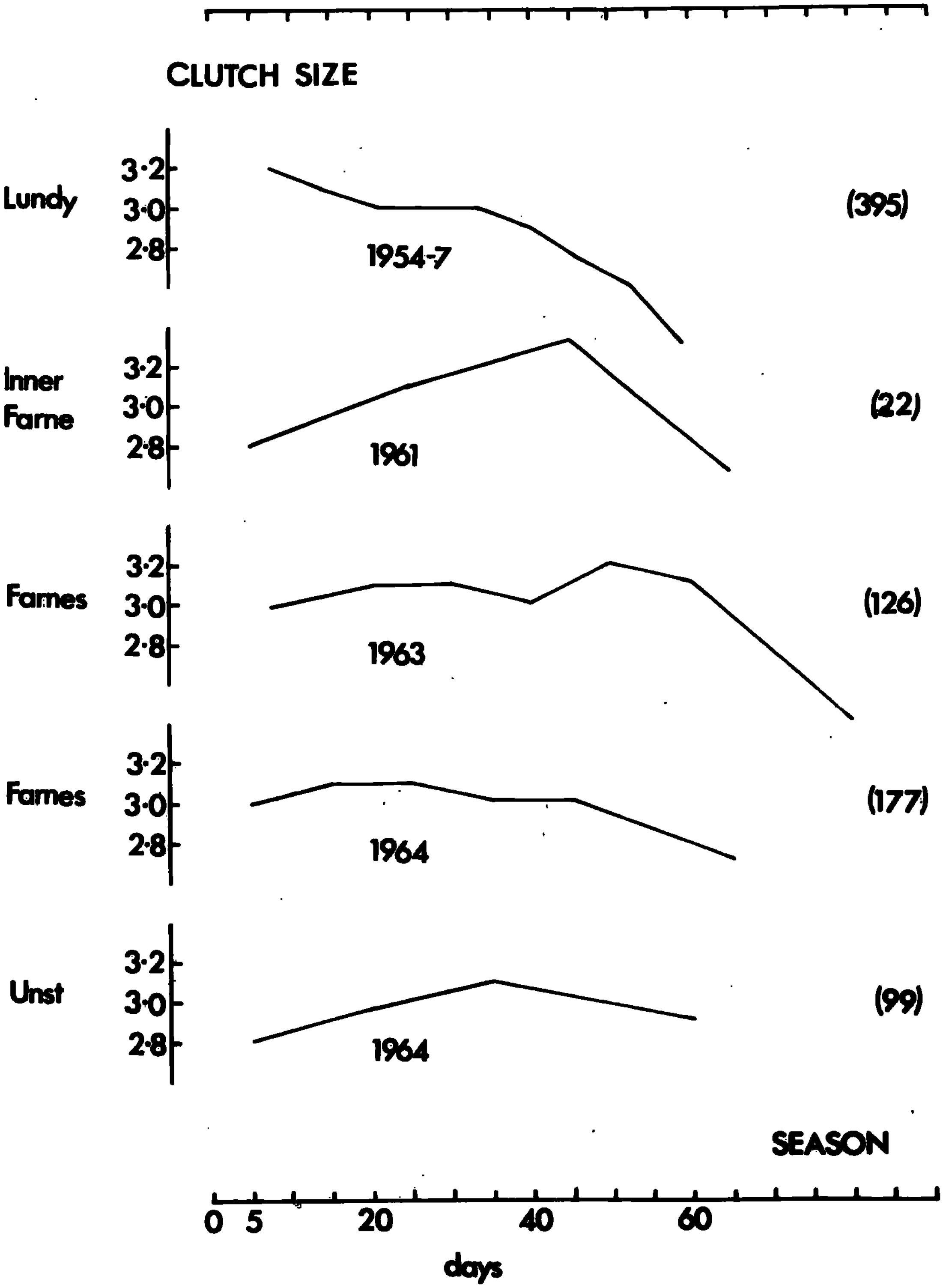
SEASONAL VARIATION IN CLUTCH SIZE

Season - days after 1st eggs, grouped according to sample size (approx.)

The continual decline on Lundy (Snow 1960) is apparently atypical but the data needs re-examining (see text)

Unst from Machell (1964)

Inner Farne 1961 from Pearson *in litt*.


CLUTCH SIZE
Lundy
3·2
3·0
2·8
1954-7
(395)
Inner Farne
3·2
3·0
2·8
1961
(22)
Farnes
3·2
3·0
2·8
1963
(126)
Farnes
3·2
3·0
2·8
1964
(177)
Unst
3·2
3·0
2·8
1964
(99)
SEASON
0
5
20
40
60
days

seasonal trends occur during peak laying. The 1961 season on Inner Farne is the earliest known on the Farnes, but the overall seasonal trend is little different from the others showing (as also the 1963 cf - 1964 (later season) trends) that the absolute date of laying is not important. It would be interesting to compare seasonal trends in a year of high clutch size but Snow's (1960) data are not separated according to season. Since Snow (loc. cit) used weighted mean clutch size, and since the distribution of laying in seasons of high clutch size was more negatively skewed, her data should be re-examined.

Annual Variation of the Clutch Size

Broadly speaking, annual variation in the production of fledged young is due to variation in the number of eggs incubated, and to mortality of the nestlings. Since significant annual variation in the production of young does occur in the Shag (p170) it is especially pertinent to examine the magnitude and frequency of clutch size variation in this species since the fledging success is usually very high (p150). In addition the following brief study shows that the clutch size in 1963 and 1964 on the Farnes was average for the species, thereby supporting the general conclusions from a study of these years.

Methods

One method of estimating clutch size which has frequently been excercised in earlier observations on

Shags has been the counting of the number of eggs per nest on a single day visit. Normally this information cannot be compared directly with that obtained in the normal way, but during this work a method of doing this was devised. If the spot count has been at any time from the 25th to 50th day after the first egg has been laid in the colony, then an estimate of clutch size can be obtained by multiplying the mean spot count by 1.26. In 1964 on the Farnes the absolute error of this method was of the order of ± 5 per cent but since it has not been applied elsewhere with known accuracy, the following statistical tests have been applied to the raw data, not the extrapolated values, which are indicated separately in Fig. 29. Since the spot counts and most estimates of clutch size involved only three or four class intervals and since the data were not distributed symmetrically about the mean, normal statistics are unsuitable and a test more sensitive than the t test is desired. Newall (in litt.) has supplied details of a linear trend test which has proved suitable, using three frequency classes.

Results

The estimates given in Fig. 29 are described by mean 3.085 ±.059 (SE- (see Table 33 for other *Phalacrocorax* spp.)

The clutch size in SE Ireland in 1952-1953 appeared to be high but the figures are based on a relatively small

Fig. 29

ANNUAL VARIATION IN CLUTCH SIZE FOR VARIOUS GEOGRAPHICAL AREAS

from B.T.O. nest records, Machell (1964), Snow (1960), J.C. Coulson (*in litt.*), T.H. Pearson (*in litt.*) and *pers. obs.* (Isle of May 1965, Farnes 1963-1965).

Estimates from number of eggs in nests on single visits given as vertical lines. Estimates from regular inspection of nests given as 'pins'. The horizontal line is the 1964 standard (see text).

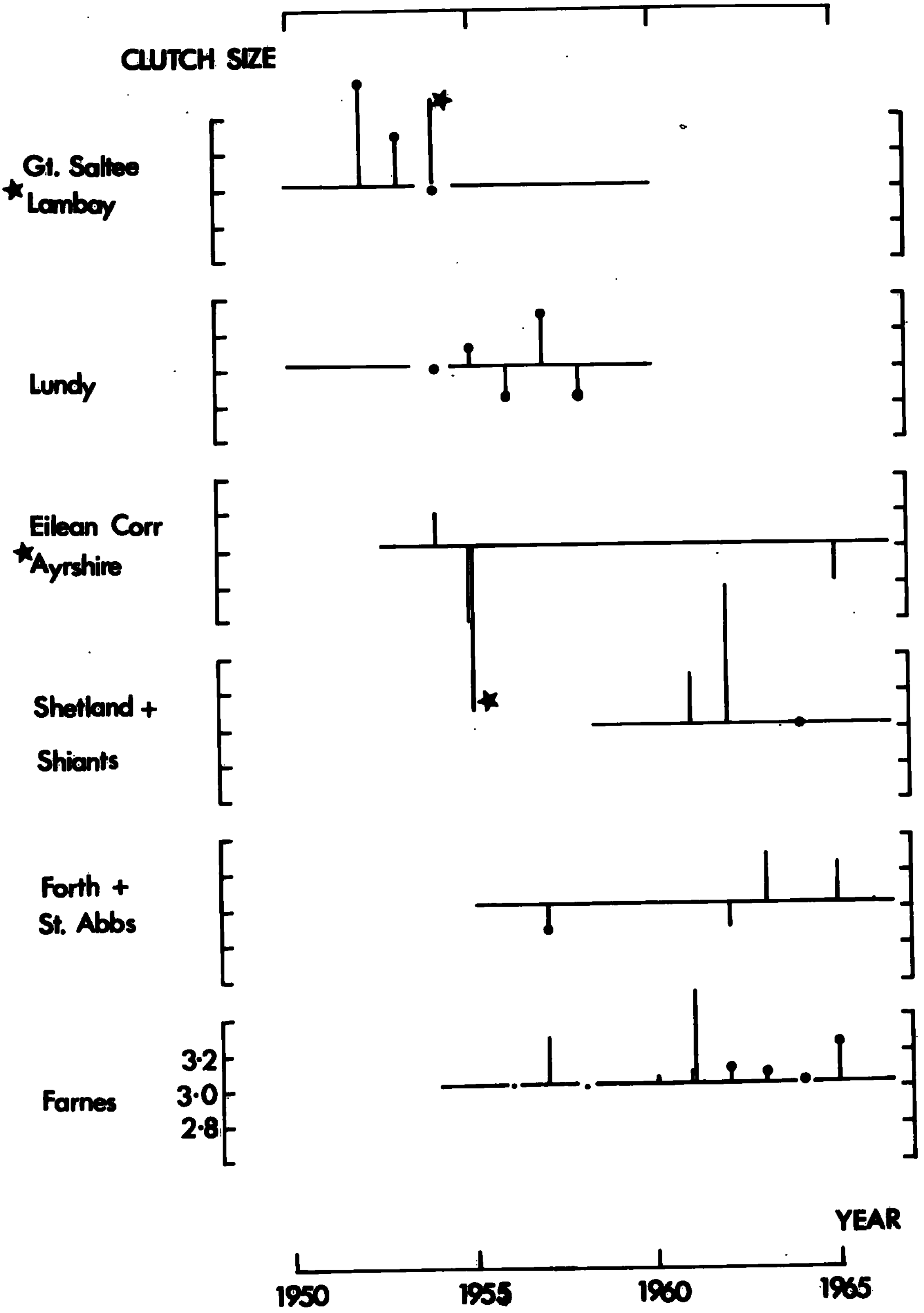

CLUTCH SIZE
Gt. Saltee
★ Lambay
Lundy
Eilean Corr
★ Ayrshire
Shetland +
Shiants
Forth +
St. Abbs
Farnes
3·2
3·0
2·8
YEAR
1950
1955
1960
1965

Table 33

Clutch size in Phalacrocorax spp.

		Authority
P. aristotelis	3.085 ± 0.059	This author
P. bougainvillei	3.13 ± 0.10	Vogt in Hutchinson(1950)
P. auritus	3.46 -	Palmer (1962)
P. penicillatus	3.09 -	Palmer (1962)
P. carbo	*3.63 ± 0.15	This author

* Fifteen per cent higher than Shag, but mean number of eggs in 905 nests on Farnes (1932-1965) was 2.650 ± 0.034 or nine per cent higher than Shag; 2.44 B.T.O. nest record cards and in 1964 the mean number of eggs in Cormorant nests was 2.58 compared to 2.40 in the Shag. The estimate of 3.63 was based on 19 'study nests' on the North Wamses in 1964.

colony at Great Saltee (Ruttledge 1963). Whilst the Saltee estimate agrees with that on Lundy in 1954 the Lambay figure is somewhat higher. None of the differences are significant at the 5 per cent level.

The two lowest recorded clutch size occur in the same year (1955) in the same sea area. Neither was due to mid season re-laying and it seems likely that these estimates did reflect a poor laying season. The difference between their total frequency distribution and that for the Farnes in 1964 is significant ($P = <.001$).

The clutch size of 2.86 in 1956 on Lundy is significantly lower than that of 3.27 in 1957 ($P = <.001$). A similar, high clutch size was recorded on the Farnes in 1957 but the difference between the 1957 mean 3.30 and the 1964 standard (3.03) is not significant (P = approx. ·25). The greatest irregularity in the Forth-Farnes comparisons occur in 1963 but this difference is not significant($.50 > P > .30$) and the two areas appear to vary in concert. The highest clutch size (3.80) was recorded from Shetland in 1961, but it is not significantly different from the 1964 standard ($.5 > P > .2$) being based on sample of only 18 nests. It is the high brood size in 1961 on the Farnes which largely prompted this study, but it is from that year that particularly confusing estimates are available for the Farnes. A spot count by T.H. Pearson(<u>in litt</u>.) on the Brownsman indicates a clutch size of 3.52 which is the highest recorded for the Farnes and which is significantly different from the 1964 standard ($P<.05$). However study throughout 1961 on Inner Farne indicated a normal clutch size of just over three (T.H. Pearson see Fig.28). It is however very unlikely that this reflected the situation on Staple (no counts available) since the mean brood size there indicated a clutch size of about 3.5 (Fig.30). Whilst low brood sizes are not necessarily an indication of a low clutch size a high brood size does indicate a similarly extended clutch size.

The correlation between clutch size and subsequent brood size (as far as possible) is given in Fig.30 and is highly significant ($P = <0.01$) indicating that much of the annual variation in the production of young is related to similar variation of clutch size, and conversely that the survival of small young does not vary much from year to year. (Brood sizes are of young older than 10 days).

Age of Female and Clutch Size

A χ^2 homogeneity test of the two seasons clutch size and age analysis, from the frequency of C/2's cf. C/3's yielded a value $\chi^2 = 1.33$ with 4 df. i.e. $90>P>.80$. Thus the two seasons 1963 and 1964 can be considered together

Fig.30

[illegible]

[illegible]

[illegible] (ii)

[illegible] (iii)

[illegible]

CORRELATION OF BROOD SIZE AND CLUTCH SIZE IN THE SAME SEASON FOR VARIOUS GEOGRAPHICAL AREAS.

y = <u>Brood size</u> of chick 10-30 days, at same time or in same season as clutch size measured.

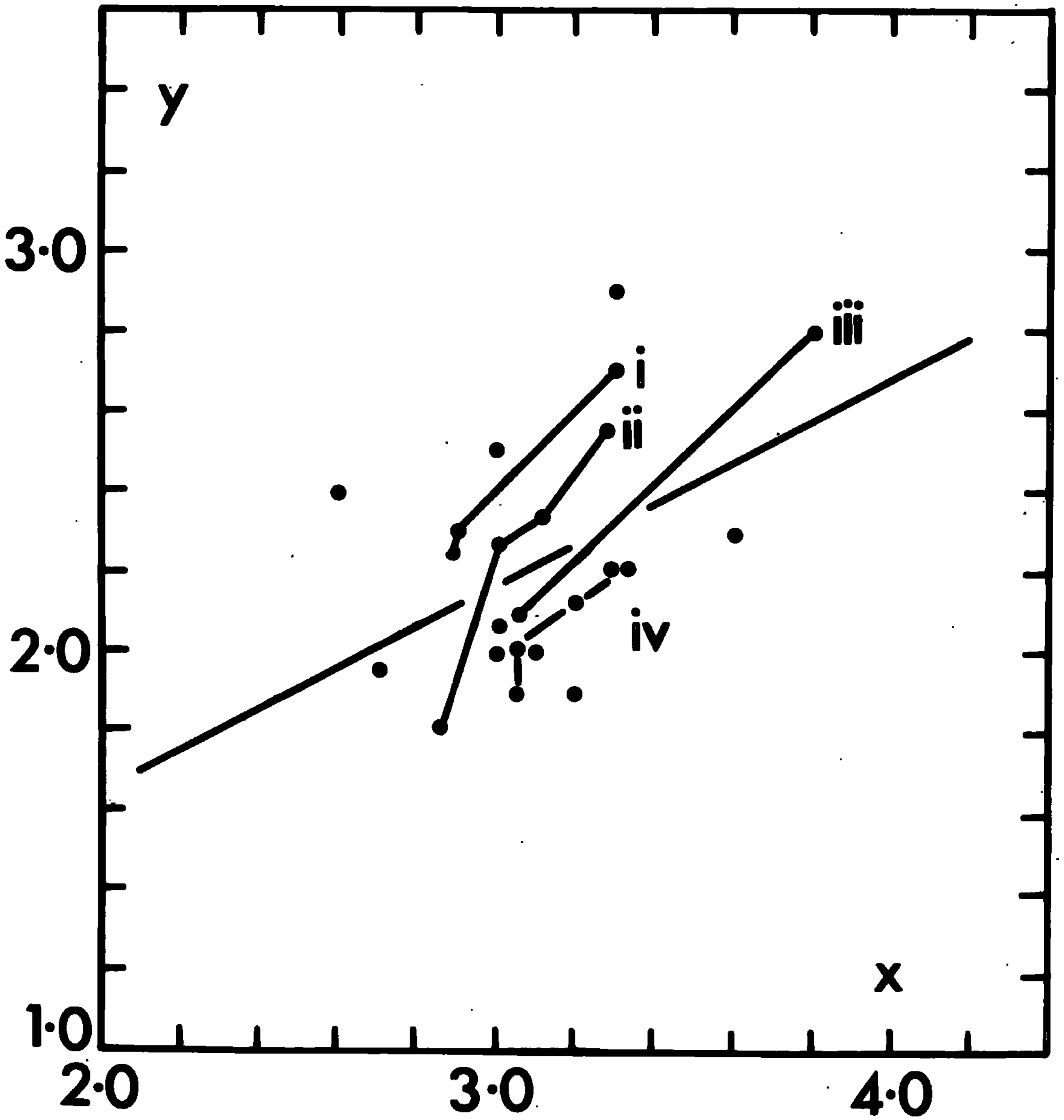
x = <u>Clutch size</u> from Fig.29.

The regression line is given by the expression

$y = 0.52x + 0.61$ ($P = 0.01$)

(i) Forth
(ii) Lundy (Snow *in litt*.)
(iii) Shetland
(iv) Farnes

Other areas Saltee and Argyll;- there is no correlation, judging from present data.


y
3·0
2·0
1·0
x
2·0
3·0
4·0
i
ii
iii
iv

since clutch size varied with age in a significantly similar manner (see Appendix H).

Taking the two seasons together, gradient (a) in Fig.31 gives the clutch size for the various age groups of female. The age group "2 years" is a small one (18) but the others are large samples:- 84,70 and 42 respectively, and it appears that there is a downward trend in clutch size. However, the trend was not significantly different from zero (.70>P>.50), comparing the oldest group of females with females 3,4 and 5 years of age. The trend was similar in the two years and in each season and 1961 , thus old birds (which lay earliest) have produced smaller clutch sizes (Fig. 28).

It will be noted that the above sample sizes are small and that a great amount of material had been excluded by the rigorous definition of clutch size. Therefore another kind of clutch CLUTCH (B) is introduced as follows:-

CLUTCH(B):-

Concerns only those exempted by the definition on p.112 of CLUTCH. It is the maximum number of eggs remaining in the nest when laying has finished. They must be laid by one female and not added to at intervals greater than eight days. A small amount of arbitration has been used in choosing the nests at which this kind of clutch size was measured, depending on the frequency of visits.

Fig. 31

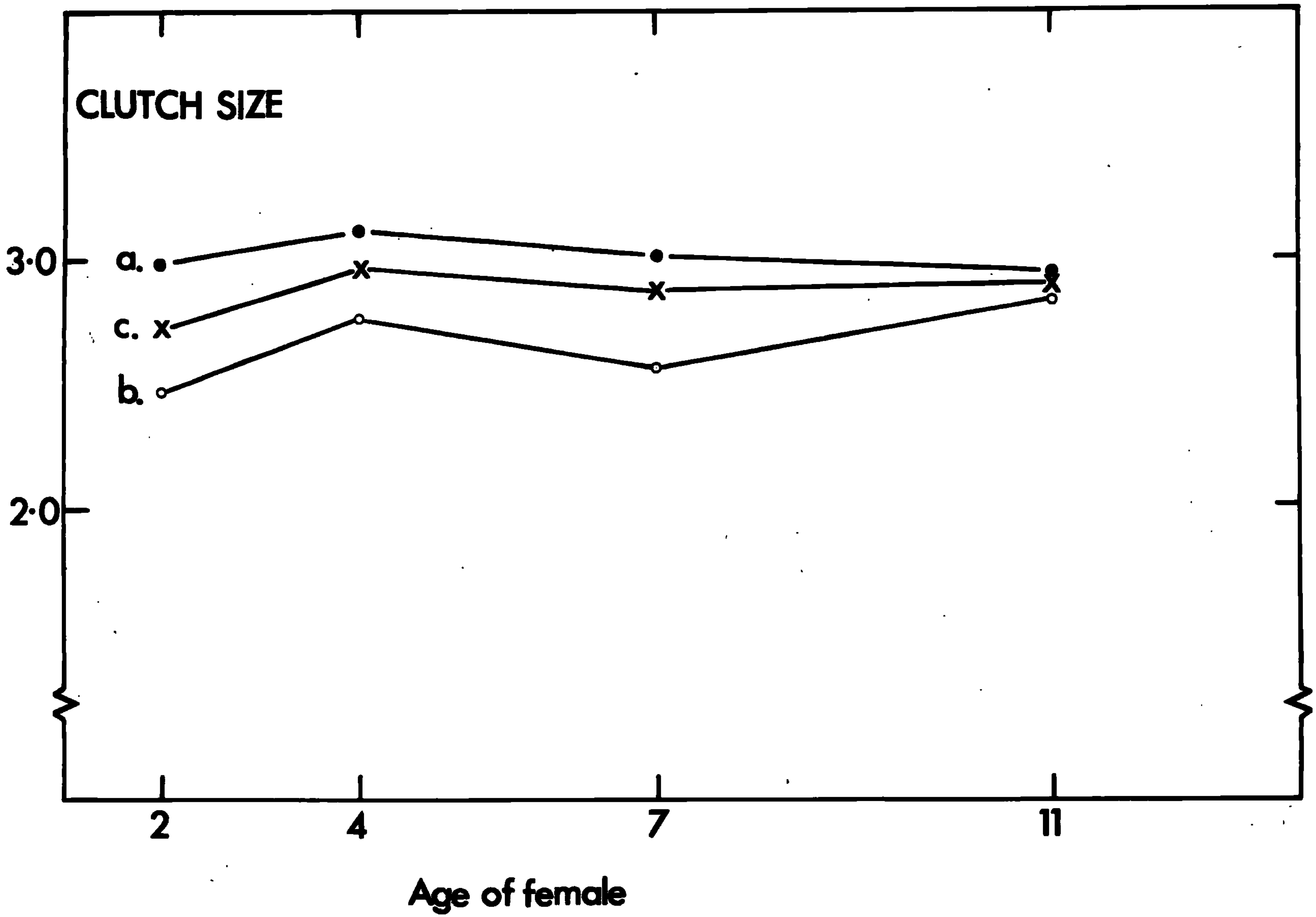
VARIATION IN CLUTCH SIZE OF THE SHAG, ACCORDING TO AGE OF THE FEMALE.

a. clutch size (page 112)

b. clutch B (" 119)

c. weighted mean of a and b.

There is no significant variation of clutch size with age.


CLUTCH SIZE
3·0
2·0
a. ●
c. x
b. ○
2
4
7
11
Age of female

Clutch(B) is processed as other clutch data and the comparable estimates (b) given in Fig.31,(c) represents the weighted mean. (b) is lower, showing that the Shag is not a completely indeterminate layer, it probably depends which egg is lost. (Only eggs lost during the first "5 days" of life could affect the discrepancy). In general (b) supports the conclusions derived from consideration of (a). It can now be justifiably concluded that age has no important effect on clutch size on the Farnes, but this may not be the case at the end of the incubation period.

Excepting those species which lay one egg per clutch the relationship of age and clutch size is not clear. Amongst non-passerines we have at least three species of <u>Laridae</u> (including terns and skuas) and the Yellow-eyed Penguin which show an increase of clutch size with age whilst on the other we have the White Stork (Hornberger 1943) and the Shag which do not show an age-specific variation in clutch size.

Intermittent and non-laying

Intermittent breeding is almost entirely confined to the females. In 1962-1964 nearly seven per cent of the females which had laid in previous seasons were non-layers. However only two instances (half of one per cent) of males non-breeding were recorded (Table 34).

Of those females which laid in 1963 but not 1964 all had either survived their partner or the mate had moved site. The tendency to intermittent laying becomes more marked with age and it appears that some older females may have difficulty finding mates. This is also reflected in the fact that older birds of both sexes, tend to change to a younger partner, (Table 11,12). In the Yellow-eyed Penguin Richdale(1957) found that intermittent breeding was almost entirely confined to the males, and it thus appears that the difficulty of finding a mate in the Shag and Penguin is much greater among birds which are surplus because of a slightly unequal sex-ratio. There is no record of a non-paired bird of either sex in three consecutive seasons and only two in two successive seasons. However three paired Shags have not laid in three consecutive seasons (1963-1965). The evidence of non-laying in one of these three pairs is overwhelming, but in the other two, eggs may have been eaten soon after laying. The 'non-laying'

Table 34

Intermittent Laying of Females

	Age Groups (years)				Total
	2 + 3	4.5	7	11	
Total Adults	91	139	115	88	433
Paired but not laying	?	0	1	2	3 (0.7 per cet)
Non laying in both seasons	0	0.5*	3.0	1.5	5 (1.1 per cent)
Non laying females	0	7	11	12	30 (6.9 per cent)
Per cent non laying	0	5	10	14	-
c.f. intermittent breeding males	1	0	1	0	(.5 per cent males)

* one female involved, in one age group in 1963 and in another in 1964.

among two paired females was not changed when they mated with different males, suggesting that the females' condition was the cause.

To summarise, intermittent breeding in the Shag is largely confined to the older females which have survived their mates and is of a temporary nature.

Egg Survival

The description of age or season specific variation in clutch size is somewhat of an academic excercise, unless it is also shown that such variations are reflected in the number of eggs available for the full term of incubation. Throughout the present study the author has been impressed by the proportion of eggs lost by the study population, more especially since egg predation is negligible.

One factor contributing to egg loss and which is age specific is the loss of entire clutches during high seas which wash the lower sites, occupied by predominantly younger birds (see p. 85). This factor is eliminated from the following analysis which is designed to relate survival to the more immediate behaviour of the birds. In addition, this facilitates why direct comparison with the Lundy population, where nests were not washed away.

After the elimination of about 40 nests which were washed out in each season, the information concerning 454 females and 1,643 eggs remains suitable for consideration. Throughout it has been found that the survival curves of the eggs were approximately exponential and thus the means are geometric. The estimated survival is the result of the interaction of egg replacement and egg loss. The more rapid egg replacement will, other factors equal, result in a lowered estimate of survival, and the number of eggs laid per female in 1963 was a little higher than that in 1964 (Table 35). Since the period during which egg replacement can take place is more extended in the older birds, their survival may reflect a differential between first and repeat laying sequences, but in this analysis the influence of the repeat clutch (defined on p. 112) is very slight because they are mostly a result of storms. It is possible that some eggs could be lost by the Shags before the observer had recorded their presence. However such 'lost' eggs generally leave traces such as egg shells and yolk.

Survival of Eggs and Age of Male and Female

The geometric mean survival rates of eggs laid by females of various age are given in Fig. 32. It is clear that there is a marked improvement after the first season, and some improvement thereafter. The two seasons are plotted separately showing that survival was consistently better in 1964 than in 1963.

Table 35

Sample size and number of eggs recorded per female, used in analysis of egg survival

Age of female	1963		1964	
	Number of females	Number of eggs recorded *	Number of females	Number of eggs recorded *
2 + 3	22	3.2	35	3.1
4.5	85	3.8	79	3.6
7	44	3.8	50	3.5
11	31	3.9	35	3.3

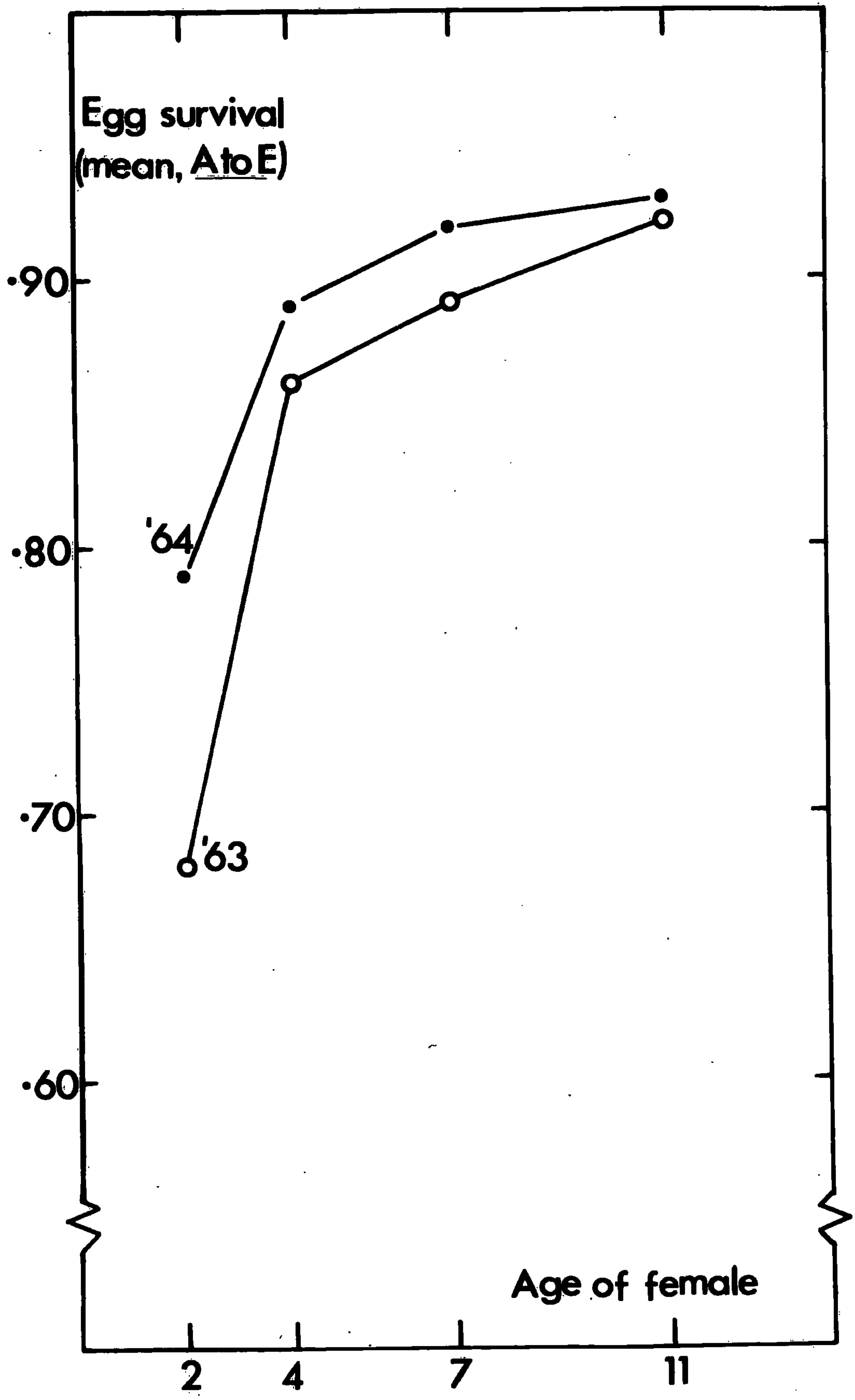
* N.B. This does not denote clutch size because some eggs were missed.

The egg survival is measured from the eggs alone, not from the number of eggs per female, since in certain cases samples per females were used (i.e. where eggs were probably missed). An annual difference in the number of eggs recorded, despite similar methods, indicates an actual difference in the number of eggs laid.

Fig. 32

OVERALL SURVIVAL OF EGGS ACCORDING TO AGE OF FEMALE AND YEAR

Survival = mean (geometric) for each 5 day period A to E note that egg survival increases with age of female and was higher in 1964 than 1963.



Egg survival
(mean, A to E)
·90
·80
·70
·60
'64
'63
Age of female
2
4
7
11

The means were worked out for each permutation of age combination, within pairs, and the data subjected to a partial regression analysis. In Fig.33 the complementary parts of this analysis are shown separately. In the first section of Fig.33 the age groups of female are considered separately and compared with the male (each gradient thus representing that of one age group of females with different aged males). Since the birds of a pair tend to be of similar age some grouping of the data was needed. The first part of Fig.33 is a plot of the egg survival of the females of various age groups when mated to males of a specific age, whilst the second part is a plot of the egg survival of the males of various age groups, when mated to females of a specific age. In this way the partial effect of age of each mate can be separated. Thus (Fig.33) the female egg survival changes according to the age of the male partner, not the age of the female itself. In this way the relative unimportance of the age of the female, becomes apparent.

Thus much of the material graphed in Fig.32 really referred to the age of the male partner.

The overall trend in Fig.32 parallels that in Table 27 which gives the quality of the nest and the age of the male and it is quite clear that part, at least of this

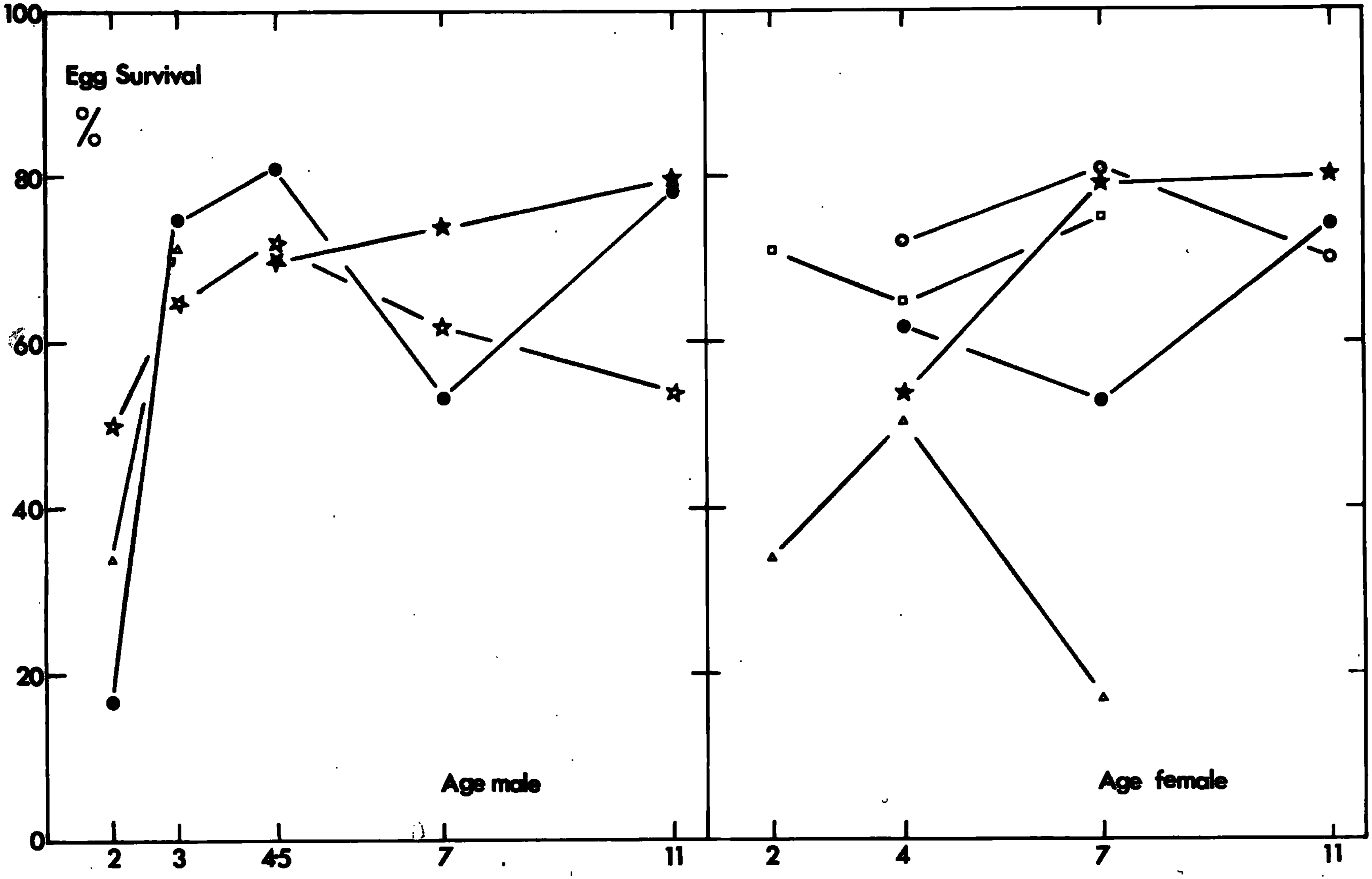
Fig.33

A COMPARISON OF THE INFLUENCE OF THE AGE OF THE MALE AND AGE OF THE FEMALE ON EGG SURVIVAL

Age	
Open Triangles	2 Yrs.
Open Square	3 Yrs.
Open Stars	4 Yrs. (♀)
Open Circle	4.5 Yrs.
Filled Circle	7 Yrs.
Filled Stars	11 Yrs.

right Example: 2 Yr. ♂ 7 Yr. ♀ survival 18% (this being geometric mean for periods A to E, see page 127).

left Example: 7 Yr. ♂ 2 Yr. ♀ also 18%


Egg Survival
%
100
80
60
40
20
0
2
3
4.5
7
11
Age male
2
4
7
11
Age female

result stems from their poor nests, which will not adequately retain eggs.

The incubation period has been divided into five sub-periods from which the geometric mean survival rate has been calculated and used in the previous section. The sub-periods have been regarded as of equal duration but in fact:-

A. From date of first egg laid to date of last egg laid plus five days. Thus:-

egg a is at risk for 3 + 3 + 5 days = 11
" b " " " " 3 + 5 days = 8
" c " " " " 5 days = 5
" d " " " " 2 days = 2,

in a nest with no egg loss. If eggs are lost then the total number or eggs during the formation of a clutch(B) or laid and lost before this was possible is added and divided into that number (including 0) which survive the laying period to give the survival rate over period A.

The next four periods (B to E) are of five days duration, and for present purposes this is also taken to be the period of A. Preliminary analysis indicated that three groups of birds required detailed analysis.

1. Survival per nest occupied by trio
2. Survival per female aged two years
3. Survival per female of all pairs

(1) it is clear that the survival of eggs laid by females in trios is disastrously low (Fig.34). Almost half disappear during each five day period and the mean survival of the 130 eggs laid by these females was 6.9 days. (2) the two year olds show a poor survival consistently below that of the mean for all age groups (Fig.34). There is a tendency for this differential to increase after laying is complete, probably a measure of the incubation drive, which is likely to be less in these young females. (This has been described in Black-tailed Godwits,probably breeding for the first time,(Lind (1961)). However many of the losses were of complete clutches and it appears that the birds may not have been able to defend the site for the full term of incubation. The 177 eggs laid by two year old females had an expectation of life of 11.7 days, still far short of the full term of incubation . (3) The pairs are all grouped together (for a comparison with the trios). The 1,513 eggs studied, had a mean survival of 40.4 days, though even in this group much of the egg loss took place during the first five days(Fig.34)

The magnititude of this egg loss is best realised in a comparison with Snow's (1960) data. Of 921 eggs laid on Lundy 4.2 per cent were predated and 93.0 per cent survived the incubation period; of the 1,513 eggs laid by pairs on the Farnes <0.5 per cent were predated but only 60.4 per cent survived the incubation period.

Fig.34

[illegible]

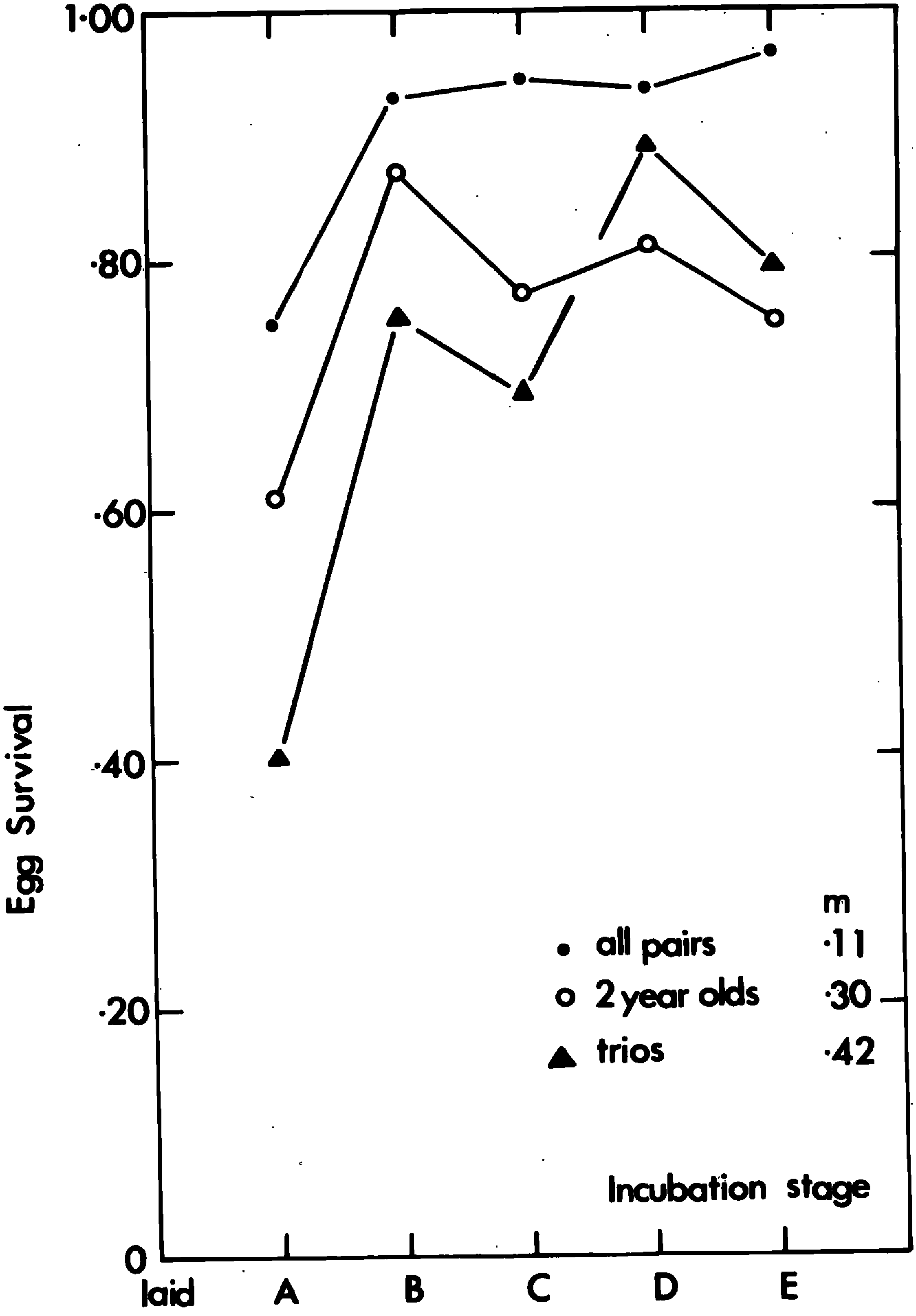
[illegible]

[illegible]

[illegible]

EGG SURVIVAL DURING SUCCESSIVE STAGES OF INCUBATION FOR 2 YEAR OLD FEMALES, ALL FEMALES IN PAIRS, AND FOR TRIOS

m = mean mortality rate per 5 days.


1·00
·80
·60
·40
·20
0
Egg Survival
laid
A
B
C
D
E
Incubation stage
m
● all pairs ·11
○ 2 year olds ·30
▲ trios ·42

Since eggs lost in heavy seas were omitted from this analysis it is probable that the differential attributable to 'parental care' is of the order of 37 per cent. Parental care is used here in a wide sense and would include effects of the shortage of adequate nesting sites on the Farnes.

In a trio, one female was seen to break open an addled egg with her beak, soon after the other female was captured for marking. In another nest a two year old male removed the first egg almost as soon as it was laid. When this egg was replaced by the author, the bird repeated the ejection, this time breaking the egg. A six year old female picked up her egg and broke it on the rock nearby. Another egg was found and put in the nest and it too was ejected. Finally, an unaged adult Shag was seen to to stand on and crush its egg which was laid on bare rock. At these and other nests, yolk was 'splattered' on the surrounding rock in a manner quite uncharacteristic of any predator. Instances in which the birds appear to have 'deliberately' broken their eggs are summarised in Table 36, according to the age of the female. The information suggests that egg breaking is not age specific in cases in which the eggs were broken inside the nest cup, excluding recorded interference by a third bird.

Females frequently (even when members of stable

Table 36

Incidence of egg breaking habit in females in 1963-1964

	Number of females and age				Total
	2+3	4.5	7	11	
Total	90	121	108	77	396
'Egg breakers'	4	5	10	4	23
Percentage females affected	4	4	9	5	5.8

bonds or bond which are intact from one season to the next) move from male to male before egg laying. For example, one male which was re-mated to the female of the previous year accepted at least eleven other females during her absence. For three years (1963-1965) one female continually mated to the same male at and after egg laying, associated with several other males. The fighting frequently observed at nest sites generally concerns rival females, and if such female wandering continues after egg laying, albeit at low intensity, the resulting fights would cause much egg loss. Supporting evidence for such wandering is the spasmodic laying noted in Table 32 .

Since all known human interference has been excluded and since the frequency of egg loss did not differ between the breeding areas on Staple (frequently visited) Brownsman (only the author) we can rule this factor out. In fact the vast majority of 'lost' eggs were found broken or pushed out of the nest in circumstances which suggested that the Shags themselves were 'responsible'.

Another species which has high egg loss is Brünnichs Guillemot in which only 38 per cent of eggs hatched at Cape Hay in 1957 (Tuck 1961), though Kartashew (1960) considers that the degree of egg loss in this species varies with colony size, being lowest in the colonies of high density. The Black Guillemot also has high egg loss with a hatching success of only 42 per cent, but this includes eggs lost during storms (Winn 1950). On the other hand, egg loss due to 'parental failure' was almost negligible in the Song Sparrow (Nice 1937) and Yellow-eyed Penguin (Richdale 1957) and is unusual in the Kittiwake (Coulson _pers_. _comm_.). Whilst egg loss is not a serious drawback as far as overall production is concerned (since early egg loss and complete egg loss later in the incubation period is normally replaced), it affects the breeding efficiency of the population a great deal and some consideration of the factors which could bring about such a reduction of efficiency is needed.

In recent years there has been much discussion of the possible causes of egg breaking in birds, a problem in which this study has considerable bearing. Armstrong (1947) reviewed some of the recorded observations of birds which had destroyed their own nests or eggs, and considered that such behaviour was a result of "emotional stress" such as results from disturbance at the nest site. Armstrong cites a record of Caspian Terns which, when they were disturbed, hovered over their nests and struck their eggs with their beaks, breaking at least a quarter of the eggs in the colony. In the American

Tri-coloured Redwing and in the Sandwich Tern egg piercing preceded desertion of the colonies (Lack and Emlen 1939, Norfolk Naturalists Trust 1938). However spasmodic egg eating, or 'puncturing' has been reported in the Common Tern (Palmer 1941), Arctic Tern (Pettingill 1939, B.P. Springett pers. comm.) and in the Jay (Goodwin 1956). Little is known of the habit of parental egg eating in birds, but it has been shown that in the Herring Gull (Tinbergen 1953b) the habitat is suppressed as laying commences, though Kirkman (1937) has shown that it is revived when eggs are accidently broken. In Kirkmans' colonies of Black-headed Gull it was generally the "outside" birds or strangers which broke eggs though occasional rogues were sometimes responsible. In the Common Fowl (pers obs.) and possibly in the Peregrine (Meeson, in Nethersole Thompson 1942) damaged or accidentally broken eggs are eaten but this is (at most), unusual in the Shag.

Treleavan (1961) noted breakages of eggs at Peregrine nests, mostly since 1955. He pointed out "the crux of the matter is the appearance of a second adult falcon (i.e. female) at the eyrie while the owning female is sitting". In his summary he states "there is an excess of females in the population" which he thought might be a product of the recent upheaval in the Peregrine population; namely the wartime persecution and subsequent rapid recovery.

Similarly Balfour (1957) had written of the Hen Harrier "This peak (of population) coincided with an outbreak of bigamy by the males due to an unbalanced sex-ratio with females predominating. Isolated cases of bigamy had been recorded before: first in 1931 and again in 1944 and 1945, but by 1953 it had become widespread". Supermormal layings and associated adverse effects on breeding success may have been due to "emotional upsets, particularly where the male is bigamously mated".

This work has clearly shown that high egg loss is associated with bigamy in the Shag in which it appears that the eggs are removed by the surplus female of each attempted clutch. That this may also occur in the Gannet is probable since Nelson (1965) records that egg loss is frequently associated"with a third bird". These third birds are referred to as parasitic hens in the Canvasback (Hochbaum 1944) and Redhead (McKinney 1954). These parasitic hens frequently fight (though they will sit side by side), resulting in high egg loss. Haverschmidt (1949) similarly found that eggs of the White Stork are thrown out of nests when there is a change of mate at the nest though this does not appear to have been the cause of similar egg ejection in the Swift (Lack, 1956).

Wynne-Edwards (1962) regarded egg breaking as a "positive act of intervention, carried out at a particular point in the reproductive cycle, cutting down the effective output in accordance with the latest revised homeostatic information" and gives the Peregrine as an example of a species which demonstrates this behaviour. This hypothesis is especially difficult to test in the field since Lockie (1955) has shown that egg loss increases during food shortage in the Short-eared Owl, but that this is the result of increased predation whilst the birds are away hunting. In essence Wynne-Edwards theory was long preceded by that of Oliver who suggested that "pricklings" were "done by the Sandwich Terns themselves possibly as a sort of measure of birth control to prevent the colony from becoming overcrowded" (Marples and Marples 1934).

Ratcliffe (1963) has collected much circumstantial evidence which indicates that "the frequent destruction of their eggs by Peregrines themselves could be explained as abnormal and pathological behaviour due to the physiological upset produced by sub-lethal doses of poison". He showed that there had been a wave like spread of decline in the Peregrine, that this coincided with the pattern of use of organic pesticides, and considered that egg eating was a "first sympton of decline".

Herbert and Herbert (1965) discuss the disappearance of eggs at Peregrine eyries on the Hudson and conclude

"It seems possible that such birds eat their eggs or otherwise dispose of them when disturbed, in the same fashion as frightened mammals.....occasionally eat their young" "On the Hudson it was always a fairly fresh egg and never a long incubated egg that disappeared in instances which suggest egg eating, usually however "it is a bleached or addled egg that disappeared, giving rise to speculation as to whether the Peregrine may have some 'knowledge' of the progress of the egg or may notice its colour".

Ratcliffe (1963) clearly, if reservedly, regards much of this egg breaking as being linked to the presence of toxic chemicals in Peregrines. It is however most unlikely that any record prior to 1955 could be related to the use of the chlorinated hydrocarbons, since by far the most toxic of these dieldrin and heptachlor (De Witt and George 1959) were not in use until 1955 and 1956 respectively (Cook 1964, Moore 1965).

There are however many records of egg breaking prior to 1955. For example Lewis (1938) noted two cases at about this time in the Iceland Falcon and (Ryves 1948) noted two cases of disappearing eggs (1932 and 1937) in Cornwall. Harper-Hall (1958) noted egg loss and egg eating at one site in Canada during the years 1942-1952. Ratcliffe (1958) found one instance of breakage in a total of 35 eyries examined in the period 1949-1950 showed evidence of egg breaking. Thus a certain amount of polygyny in the Peregrine might account for some of the increase of breakages prior to the late 1950's which have been attributed to toxic chemicals, and Treleavans (1961) theory is supported by experience with the Shag and Hen Harrier. Ratcliffe (*pers. comm.*) has however, found that egg breaking has continued in declining and very sparse populations. Accepting that a surplus of females could cause this, it is interesting (and confusing!) to find that the susceptibility to certain chlorinated hydrocarbons is partly sex specific, to the males in the Pheasant and American Robin and that there are sex specific differences in uptake or susceptibility in the Pheasant, American Robin, House Sparrow and rat, (Rudd and Genelly 1956, Wurster *et al* 1965, Datta *et al* 1965).

Incubation Period

One of the basic, if ill defined, parameters in the structure of the breeding cycle in birds is the length of the incubation period, and as such it has been an important tool throughout this work from which other information has been freely extrapolated. There has been no thorough study of the incubation period of the Shag until the present work even though the methods used in this work do not lend themselves to such a study. Nevertheless in 1963 and 1964 the incubation periods for 112 eggs from clutches of three were determined. (There is insufficient information to comment on the clutches of two and four).

Definition of incubation period

Several discrete measurements shelter under the term "incubation" and some consideration of these is essential. Swanberg (1950) reviews the concept of the incubation period especially in relation to his studies on the Nutcracker, and concludes that 'incubation period' is equivalent to the period of development; whilst the 'total brooding time' is an expression he uses to cover the period from the beginning of brooding or covering of the eggs until the time the last egg has hatched. As Barth (1955) points out it would be unfortunate if these terms were used synonomously since, usually it is uncertain at what stage in the egg laying period the bird begins to incubate. One of the most important aspects of incubation is the onset of brooding in relation to the progress of the laying period. Herein lies one mechanism of regulating the hatching of the brood. In certain nidicolous species it has been suggested (Lack 1954) that asynchronous hatching is a buffer against food shortage in the nestling period. Alternatively, almost perfect synchronisation of hatching in nidifugous species can be achieved by delay of the 'pipping' period (Vince 1964). If we measure the incubation period as suggested by Swanberg (<u>loc</u>. <u>cit</u>), that is by following Heinroths practical rule <u>i.e</u>. "the time elapsed from the laying of the last egg until the last young has left its egg shell", the function of variability in the incubation period will escape us. If on the other hand we follow Barth (1955) or Kendeigh (1963) and use thermocouple recorders to determine the "total brooding time" or "cumulative heat required" or follow Delvingt (1963) and determine the 'sitting' index (sitting index = i = $\frac{100\ a\ +\ r}{a}$)

where a = attentive period, a = sitting per day, r = total time the eggs deserted per day, determined using automatic recording apparatus attached to nest boxes) we are lost in a wealth of technical exhuberance.

Whereas, simple determination of the 'time between laying of the egg and emergence of the chick', for the individual eggs will suffice.

Incubation period in the Shag

The incubation period for the Shag has been given by Groebbels (1937), quoted in Belopolskii (1961) as 24-28 and 28 days whilst Witherby et al (1940) gives 24-28 days and Fisher and Lockley (1954) give 24 days. Snow's (1960) fifteen estimates indicated a minimum period of 30 days and that the earlier figures were erroneous, but were too meagre for use in the present study. Three similar estimates for third eggs, accrued from Modestev's (1941) study on Khariov island and Belopolskii (1961) noted that these were longer than the estimates of Groebbels, and considered this to be a result of the arctic enviroment.

The period determined on the Farnes in 1963 and 1964 are given in Table 37. These were in clutches of three, first egg 36 ± 2 days, second egg 33 ± 2 days, and third egg 31 ± 2 days (SD). If the observed spacing of the second and third eggs 3.01 and 3.21 days is compared with the spacing of the corresponding chicks (2.78 and 2.07 respectively) the resulting proportion .92 and .64 respectively indicate that some effective brooding of the egg occurs before the second egg is laid, but that this is

Table 37

Incubation Period

(i) Three egg clutch

	Number eggs	1 Days between laying of eggs	2 Days between laying and hatching(+SD)	3 Days between chicks	3/1
First Egg	37	-	36.05 ± 2.25	-	-
	-	3.01	-	2.78	0.92
Second Egg	41	-	33.27 ± 1.93	-	-
	-	3.21	-	2.07	0.64
Third Egg	34	-	31.20 ± 1.95	-	-

(ii) Season

Date 1st egg	Number eggs	*Length of incubation period
3 - 20 April	28	37.5 days
21April - 5 May	56	36.2 days
6 May - 1 June	28	34.6 days

* as 1st egg equivalent, working from (i), see text

intensified after the second egg is laid. Thus the third chick will hatch some time after the other two in the way that Lack (1956) described for the Swift.

It is possible that brooding would be more efficient in older birds. All the incubation periods were equated with respect to their position in the clutch and then examined for seasonal trends since this yields the maximum amount of information. There is apparently a seasonal decline in length of the incubation period, showing that the (later breeding, younger birds) have a shorter and therefore more efficient incubation cycle, possibly because the length of the period is related to the ambient temperature.

Fertility

Pearl (1928) defined "fertility" as the "number of progeny produced per female" and this was followed by Richdale (1957) because it was "something which could be measured exactly". Richdale proceeded as follows:-

$$\text{Proportion of fertile eggs} = \frac{\text{young hatched(i.e. progeny)}}{\text{eggs fully incubated}}$$

Unfortunately fertility used in this sense could not be assessed in this study because the mortality of the chick on and soon after hatching was high (Table 39). For example small dead chicks were sometimes thrown out of the nest, or incorporated in it, so that in all, 14 per cent (11 per cent in the special study area on Brownsman) of the fully incubated eggs were unaccounted for. These eggs had either hatched, in which case the chick had died and been lost, or had not hatched, in which case they had been broken or removed. Neither Richdale (1957) or Snow (1960) mentioned this and they assumed that eggs which did not produce chicks, were infertile. Since Richdale visited his areas mainly at weekends his method could not have measured fertility exactly. In this study an infertile (or addled) egg is either unfertilised, or contains a dead embryo.

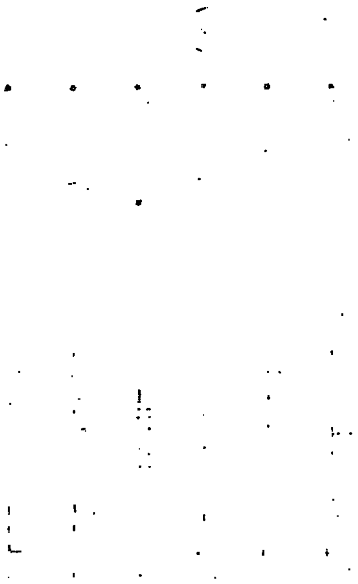
There are two peaks of embyro mortality in the Common fowl i.e., just after laying and just before hatching (Hartmann and Vickers 1950), though embyros may also die before the egg is laid (Munro and Kosin 1945). In addition, some dead embryos in Shag eggs do not 'shake' and therefore pass undetected. In view of this, no attempt is made to separate 'liquid' from 'dead embyro' eggs in the present study.

It is reasonable to assume, however, that the infertile eggs which are detected reflect an unbiased <u>sample</u> of actual infertility, where infertility rate equals $\frac{\text{detected addled eggs}}{\text{eggs survived incubation}}$.

<u>The effect of age on the infertility rate</u>

The proportion of eggs which survived the normal period of incubation and which were then found to be infertile is higher in two year old birds (29 per cent) compared with about 12 per cent in older birds, (Fig. 35), (Table 38). The highest rate of infertility is found in the pairings of two year old females and this age specific effect is virtually confined to them, though there is some evidence (7 females, no infertile eggs) that two year old females mated to older birds have an improved fertility. Two year old males mated to two year old females have an infertility rate of 29 per cent but males of the same age mated to 4 year old females have a 16 per cent infertility rate, ($\chi^2 = 3.36$, P = approx. 0.05).

Fig.35



COMPARISON OF THE INFLUENCE OF THE AGE OF THE MALE AND FEMALE ON INFERTILITY RATE

Open triangles	2 Yrs.
Open squares	3 Yrs.
Open stars	4 Yrs. (♀)
Open circle	4.5 Yrs.
Filled circle	7 Yrs.
Filled stars	11 Yrs.

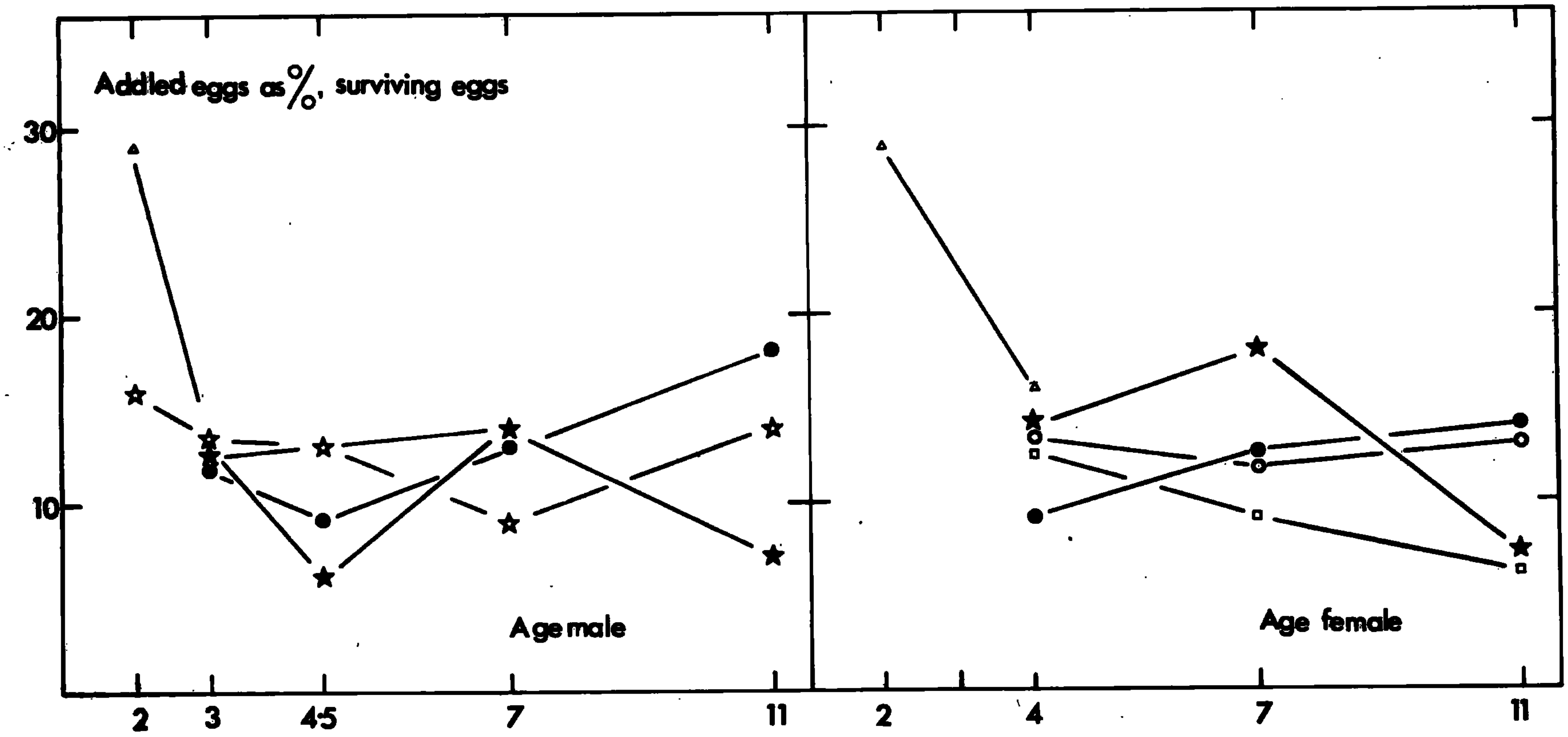

Addled eggs as %, surviving eggs
30
20
10
Age male
2
3
4·5
7
11
Age female
2
4
7
11

Table 38

Infertility rate and age of male and female*

		Age ♂				
		2	3	4.5	7	11
	2	.29 (52)	0 (8)		-	-
Age ♀	4	.16 (77)	.13 (100)	.13 (97)	.09 (65)	.14 (21)
	7	-	.12 (24)	.09 (34)	.13 (85)	.18 (55)
	11	-	.13 (15)	.06 (33)	.14 (44)	.07 (82)

Number of eggs surviving incubation period in brackets

* see page 144.

In the Yellow-eyed Penguin, three year old males mated to two year old females had an infertility rate of 75 per cent, whereas three year old males mated to three year old females had an improved performance, with an infertility of 32 per cent. Finally, three year old males mated to females at least four years old had an infertility rate of 17 per cent (Richdale 1957). It would appear therefore, that infertility in the Shag and Penguins is determined by the age structure of the pair since the performance of individuals of the same age improved with increasing age of the other bird, especially the female, in the pair. Much of the age specific infertility in both species is confined to pairs in which both birds are breeding for the first time at the earliest age. There is a suggestion of improvement with age after the fourth year in the Yellow-eyed Penguin, but not in the Shag. In addition Richdale describes an 'aged' category in which birds at least fourteen years of age had a reduced fertility rate (92 to 77 per cent). This was largely due to an increase of partial infertility and it seems likely (though Richdale did not investigate this) that these old birds were more affected by pair change than younger birds since it was these that changed to a much younger partner (pp67 and 70). Similarly there is a tendency in the Shag (though not significant) for older males (especially) and females to have a decreased fertility if mated to younger partners (Fig.35). If this is the case, Richdale's only evidence of senility in the Penguin (he says "my nearest approach to impaired fertility in 'aged' birds") need not imply the malfunctioning of the reproductive cycle one would expect in a senile animal. The percentage infertile eggs can be estimated, (in aged birds) as follows:-

% Addled eggs = -0.378 age ♂ - 0.906 age ♀ + 21.54, where the partial regression coefficients show that the age of the female is more than twice as important as the age of the male, and that in general, the proportion of addled eggs decreases with age (this assumes a non-curved relationship - this is not so see Fig.36).

Correlation of egg fertility and egg survival

Two groups of nests were considered and the egg survival in them was studied:-

Group 1. At least one egg survives to the end of period E, (i.e. the normal incubation term see p 127), but none hatch,

Group 2. At least one egg survives to end of period E, and at least one chick is known to have hatched.

In both cases, trios, two year old females and repeat clutches were not considered, since egg loss and infertility are both especially high in these groups.

A total of 29 (58 per cent) of the 50 eggs considered in Group 1 survived the normal incubation term in contrast to 794 (72 per cent) of 1,108 eggs recorded in Group 2. The difference in survival is not quite significant(χ^2 = 2.33 (after Yates' correction, P = 0.10) and moreover, in the first group the survival during successive five day periods was .70, .88, 1.00, .97 and .97. Since most of the egg loss was in the first and second periods, the loss occurred before the eggs could be distinguished as addled or non addled by this observer and, presumably by the birds themselves. Thus there is no support for the widespread belief that birds can recognise and remove addled eggs, a belief held by many pigeon fanciers, cage bird breeders and poultry keepers. This conclusion is supported by the fact that Shags will sit on completely addled eggs for two or even three times the normal incubation period with no egg loss (this study and Snow 1960,1963).

Alternatively it would appear that birds which are careless incubators are more likely to have addled eggs and more likely to lose them. This is probably one reason why infertility is higher among the two year olds. On the other hand egg loss early in incubation may reflect a lack of harmony within the pair, such that the eggs are not properly fertilised.

Comparison of fertility on the Farnes with that on Lundy

This section is concerned only with eggs which survive to the end of the normal incubation term. In view of the difficulties mentioned earlier, of detecting addled eggs, fertility is conveniently expressed as follows:-

$$\text{Fertility} = \frac{\text{Number of eggs which produce ten day old chicks}}{\text{Number of eggs which survive incubation period}}$$

$$\text{Fertility on Lundy} = \frac{600}{833} = .72 \text{ or } 72 \text{ per cent}$$

$$\text{Fertility on Farnes} = \frac{868}{1541} = .56 \text{ or } 56 \text{ per cent}$$

$$(\chi^2 = 5.65 \; P = <.02)$$

Of the 724 eggs from clutches in which at least one egg hatched 87 per cent hatched on Lundy whereas only 79 per cent of 1,237 comparable eggs from the Farnes have hatched. Survival of the chick from 0 to ten days was 95 per cent on Lundy, 93-94 per cent on Inner Farne and 89 per cent elsewhere on the Farnes (Table 39). Since survival of the chick during this period is influenced by the age of the parents (p 151) it is interesting to calculate the difference in the population mean of a factor which is age specific, when the age distributions are different. If it is assumed that the only difference between the Farne Islands and Lundy age distribution was a result of the rate of increase then a life table of breeding birds based on an annual adult mortality rate of 15 per cent can be calculated. It is then further assumed that the age specific care of the young (Fig.36) holds for Lundy and that it is experience specific rather than age specific. Since the Farne population has more young birds in it than that on Lundy, the overall mean 'care of the young'

Table 39

The Viability of Eggs Surviving the Incubation Period, From Clutches in which at least one egg hatched

		Lundy 1954-57	Inner Farne 1961	Inner Farne 1963-64	Staple * +S.B.(Br) 1963	Staple +S.B.(Br) 1964	'Study Area' 1963-64	Unst 1964	Total and Arithmetic Unweighted Means
	Eggs Survived	724	42	153	370	429	245	197	2,160
* (a)	Per Cent Hatch	87	79	80	78	79	78	80	80.1
(b)	Alive at 10 Days	95	94	93	89	89	89	84	90.4
Per Cent	Survival 10 to 28 Days	96	100	96	94	98	97	97	96.9
	Survival 28 to 60 Days	98	100	98	85	97	98	98	96.3
	Per Cent Fledge	77	74	70	55	66	66	64	67.4
(c)	(a).(b)	82±1.3	74±6.8	74±3.5	69±2.4	70±2.2	69±2.9	67±3.5	72.1±0.9

* (c):as (a) is underestimated (b) compensates, thus (c)is virtually unaltered by the differences in the methods of the four observers involved.

* *Plate 1.*

will be 4.4 per cent lower, assuming 17 to be the upper age limit (likely since the Lundy population did increase during the 1930's (Fig. 17)).

It seems likely that some of the difference in survival of the young chick could be explained in this way and this is supported by the higher chick survival on Inner Farne, than on Staple or Brownsman (Table 39), which has had a slower rate of increase than the Farnes as a whole and therefore proportionately more older birds (Fig. 13). If this is the case, then the main difference between fertility on Lundy and on the Farnes is to be found in the higher (12 per cent higher) proportion of eggs which do not hatch on the Farnes. The information summarised in Table 40 indicates that there has been no marked rise in infertility on the Farnes in the period 1963-1965 and probably 1961-1965, and that about 13 per cent of clutches produce no young, because they are infertile.

Age of parents and survival of the chick

(1) The first five days

Whereas chick mortality in the first five days is at least 9.6 per cent, it is only 2.7 per cent in the following five days. From the fifth day, until fledging, chick mortality is independent of the age of the parents (Table 43).

The newly hatched Shag chick requires warmth and a

Table 40

The annual proportion of completely infertile clutches on the Farne Islands

Locality	Year	Pairs laying	Infertile clutches	% infertile [x]
[+]Inner Farne	1961	25	3	12.0±6.5
Farnes	1963	301	37	12.3±1.9
Farnes	1964	333	45	13.5±1.8
Farnes	1965	367	50	13.6±1.8
Total		1026	135	13.2±1.1

x A % maximum number of nests recorded with eggs, since egg loss prior to the point at which infertility can be established is not known in 1965.

+ From T.H. Pearson *in litt*.

great deal of care. Snow (1963) points out:- "Parents experience some difficulty in feeding newly hatched chicks, often many unsuccessful attempts are made before a feed is accomplished.....If the chick is not begging, the parent will take its recumbent head in the tip of its mandibles, which stimulates it to start begging". Similarly of the Gannet, Nelson (1965) writes "The newly hatched chick is also brooded in this position (*i.e.* on top of the webs, as in the Shag chick and egg) and in four observed cases aberrant behaviour resulted in its death, the adult continuing to incubate the hatching egg or new chick under foot. Of 13 other cases, eight *eggs disappeared around their due hatching date*, and five chicks disappeared at less than five days. Of the 17 cases referred to above, seven were first time breeders a disproportionately high number".

In this study the care of the newly hatched chick (= care of the young) was calculated as follows:-

$$\text{care of young} = \frac{\text{Number of young surviving at least five days}}{\text{Number of eggs recorded just prior to hatching - minus number addled}}$$

....for the nests in which hatching was known to have occurred, and for which the age of both parents is known.

A partial regression analysis revealed that the care of the young is uninfluenced by the age of the female, but that it is a function of the age of the male:-

care of young (as %) = 2.31 age ♂ + 0.01 age ♀ + 68.6

This analysis suggests that in 1963 and 1964, the age of the male was 200 times as important as the age of the female, since the high multiple correlation coefficient ($r = +0.95$; $P = <0.02$) demonstrates that variation in the care of the young is largely determined by age. The care of the young by the male (Fig. 36) (Table 41) is more highly age specific than any other variable detected in this study, and this in turn, suggests that useful experience is gained with each succeeding brood throughout the average breeding life, and that the behaviour involved is confined to the male. Curiously enough however, 10 of 12 feeds to newly hatched chicks at three nests on Lundy (Snow 1963) were given by the female and on the Farnes the female is especially vigorous in nest defence at this time. In the Bittern too, the young chicks are fed by the female (Hosking and Newberry 1944) but in general little work has been done on the subject in fish eating birds. (Methods on the Farnes do not allow an adequate study of this problem, but it could be done elsewhere since the parents can readily be sexed). Division of labour during the care of the young chick is found in many predatory birds (Witherby _et_ _al_ 1940) and in the Great Skua (Potts unpublished) in which the male collects the food for the chick and passes it to the female but this does not occur in the Shag.

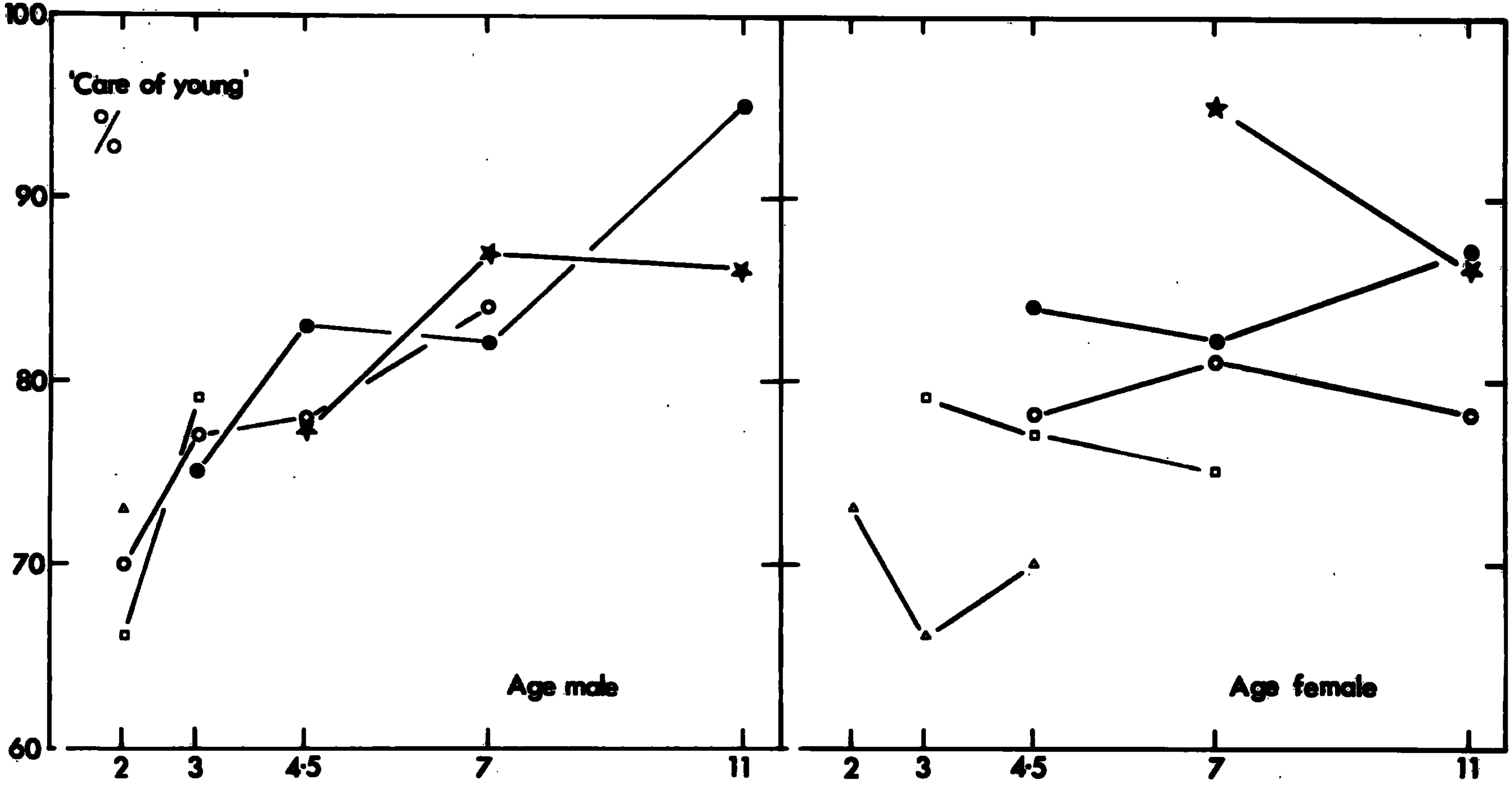
Fig.36

COMPARISON OF THE INFLUENCE OF THE AGE OF THE MALE AND AGE OF THE FEMALE ON CARE OF THE YOUNG (SEE PAGE 153)

Open triangles	2 Yrs.
Open squares	3 Yrs.
Open circles	4.5 Yrs.
Filled circles	7 Yrs.
Filled stars	11 Yrs.

Note that a 4.5 Yr ♂ with a 4.5 Yr ♀ has a success of 78%, and that a 4.5 Yr ♂ with an 11 Yr ♀ has a success of 78%: the same. The success of the young is not influenced by the age of the female.

(full details for both years on page 155).



'Care of young'
%
100
90
80
70
60
2
3
4·5
7
11
Age male
Age female

Table 41

Care of the Young (% Survival) (see text p151)

1963

Age ♂

		2	3	4.5	7	11
Age ♀	2	68(12)	-	-	-	-
	3	53(17)	80(10)	-	-	-
	4.5	57(14)	79(14)	75(53)	86(28)	-
	7	-	-	80(20)	82(38)	91(33)
	11	-	-	-	82(17)	81(42)

1964

Age ♂

		2	3	4.5	7	11
Age ♀	2	78(18)	-	-	-	-
	3	80(10)	78(18)	-	-	-
	4.5	83(12)	75(32)	82(28)	82(28)	[illegible]
	7	-	75(24)	86(21)	83(36)	96(23)
	11	-	-	78(27)	92(24)	91(22)

Mortality and Brood Size in the first five days

The mortality rate of the Shag in the first five days is compared with brood size in Table 42, the mortality rate of B/1 was 14 per cent, of B/2 17 per cent and B/3 20 per cent, there was only a very small number of B/4, but the mortality of the chicks in these (38 per cent) support the conclusion that brood mortality is higher in larger broods. Some other examples of the mortality rate increasing with the brood size are given in Table 42. In the Alpine Swift (Lack 1954) and in the Great Tit (Perrins 1965) it was clear that the main factor which caused the increased mortality was food shortage. However, the newly-hatched Shag chick needs very little food and the mortality could not reasonably be related to the amount of food that the parents could bring. Overall brood mortality was higher in the smaller broods in 1963, Table 44 because the random environmental factors (rain and heavy seas) affected birds on poor sites, tenanted by younger birds which tended to have a lower brood size (see p 85, and p 1964). In 1964 when random factors were not important (Table 43) however, overall brood mortality tended to increase with brood size (Table 44) at first sight lending support to a hypothesis that some large broods might be getting insufficient food. However the difference is less than that which on average, would be residual from the mortality in the first five days.

Table 42

Brood Size and intra-brood mortality in the Shag, Kittiwake, Alpine Swift and Great Tit

% Mortality: Brood Size

Species	B/1	B/2	B/3	B/4	Total individuals at start of risk period	Authority
Alpine Swift	3	13	20	40	2,263	from Lack(1954)
Kittiwake	8	12	28	-	394	Coulson & White(1958)
	B/2-4	B/5-7	B/8-10	B/11-13		
Great Tit	4	8	17	23	403	Perrins(1965)
	* E/1	E/2	E/3	E/4		
Shag 1st 5 days	14	17	20	38	628	This author
	** B/1	B/2	B/3	B/4		
Shag 1963	27	31	20	(50)	423	" "
" 1964	11	12	16	-	441	" "

* Number of eggs just prior to expected hatching date minus number addled.

** $\frac{\text{Number of known chick deaths}}{\text{Number of recorded live chicks}}$, as in other species

Table 43

Cause of chick loss after 5th day, Staple and Brownsman

1963-1964

Cause	1963	1964	Total	Percentage deaths
HEAVY SEAS	34	7	41)	75% Random factors in parental behaviour
RAIN(20-6-63)	25	0	25)	
SITE TOO SMALL	2	6	8)	
PARENT DIES	0	6	6)	
+'DESERTED'	5	1	6)	13% possibly under parental control
*THIN	1	4	5)	
ON FLEDGING	2	1	3)	
UNKNOWN	5	7	12	11%(includes effect of some interference by tourists)
TOTAL	74	32	106	

+Unaccounted for after August 15

*One in each year was fed by same parents

Table 44

Production of independent young in relation to brood size (*i.e.* the number of young first recorded in the nest)

	Brood Size			
	B/1	B/2	B/3	B/4
1963				
Broods	49	83	64	4
Chicks fledged	36	115	153	8
Fledged per brood	0.73	1.39	2.39	(2.00)
Surival in nest	0.73	0.69	0.80	(0.50)
1964				
Broods	54	75	79	-
Chicks fledged	48	132	200	-
Fledged per brood	0.89	1.76	2.53	-
Survival in nest	0.89	0.88	0.84	-
				Total
Total broods	103	158	143	404
Total chicks	84	247	353	684
Fledged per brood	0.82	1.56	2.46	x 1.69
Survival in nest	0.82	0.78	0.82	0.80

x Note that this is not brood size.

Growth of the chick

In 1964 a weight study of some sixty chicks was made on the Brownsman "special study area" using a 4 Kg. 'Mettler' balance. The age of each chick was known, and a mean growth curve was fitted to the data. The weight of each live or fresh dead chick was then divided by the expected weight for a chick of the same age (derived from the curve), according to the number of other chicks (siblings or not) in the nest at the time of weighing.

The deviations (as percentages) were then averaged for each five day period and plotted in Fig. 37). This analysis showed that there was a weight difference between broods of various sizes and that it was apparent from an early age.

Later in the fledging period the difference in weight becomes greater, but the percentage difference becomes less marked. Thus at the age of five days the difference between the broods (13 per cent) amounted to 13 g or 65 per cent of one days weight increase, whilst at the age of thirty days the mean difference between the broods amounted to 26 g and 43 per cent of one days weight increase. This demonstrates that the total food requirement has little bearing on the differences, since as this increases the percentage difference in growth does not become more marked. A percentage difference in weight would be apparent from the earliest age however if the chicks were neglected in some way according to the number of other chicks in the nest. Since feeding is apparently a difficult procedure

Fig.37

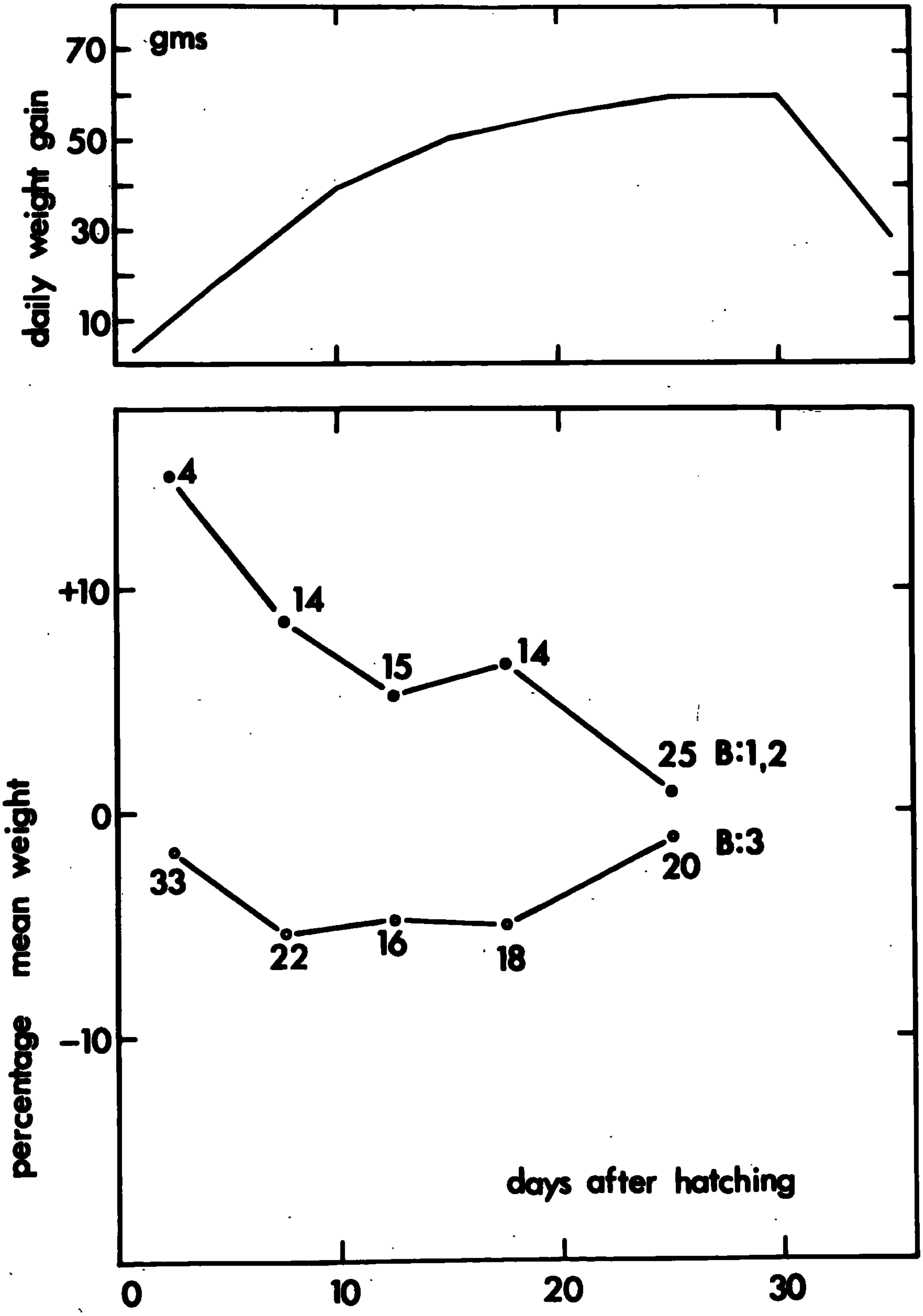
[illegible]

[illegible]

COMPARISON OF WEIGHTS OF CHICKS ACCORDING TO NUMBER OF LIVE CHICKS IN THE NEST

When the weight gain per day is highest, the difference between chicks from various brood sizes is smaller. (This difference is the weight difference as a percentage of the total weight of all chicks of this age).

(Number of live chicks includes non siblings)


gms
70
50
30
10
daily weight gain
4
14
15
14
25
B:1,2
+10
0
-10
33
22
16
18
20
B:3
percentage mean weight
days after hatching
0
10
20
30

it seems that such neglect might be related to the total amount of time that the parents spend feeding their chicks, this would also account for the early intra-brood mortality pattern.

The fledging period

The fledging period is defined here as the mean time spent by chicks in or on the nest. The mean fledging period for non-wandering chicks in 30 broods was found to be 55 ± 6 days (SD) (*i.e.* to hatching date). Many other chicks leave the nest long before 55 days, some at an early age are adopted by other parents but after about 30 days, chicks begin to wander considerable distances, if the nest sites allow this. After older birds have vacated their sites on the edge of a gully or in a more sheltered position, younger parents frequently move their chicks to the better site (some have moved over 30 yards). Similarly in the Brown Pelican, the chicks move into the centre of a breeding group when the earlier chicks from central nests have flown (J. Fisher *pers. comm*). Snow (1960) considered that chicks which had left the nest at an age of 48 days or more had in fact 'fledged', a conclusion supported by the present study.

There was no suggestion of a difference in the length of the fledging period with brood size, but the information is too sparse for any useful conclusions.

On Lundy no young were reared from clutches begun after the ninth week (5 June) from the start of laying in the years 1954-1957 (Snow 1960). On the Farnes however, young were successfully fledged from clutches begun in the 16th week (beginning of August) in 1963 and 1964, (but not 1965). Chicks from these last successfuly clutches fledged during the third week of October. 1964 may have been an exceptional season in this respect since four chicks fledged at St. Abb's during that month and another chick fledged about the 12 November on Muckle Green Holm (Orkney), (E.A. Smith *pers. comm*). What may be the only other November fledging recorded concerns a brood which left their nest on Lewis at the beginning of November 1916 (Baxter and Rintoul 1953). In view of the early end to the season on Lundy it is noteworthy to point out that this is not the case in Scilly or the adjacent Cornwall. For example in 1959 there were eight nests with young on 26 July and a nest with young in mid-September in the Scillies (Cornwall Bird Watching and Preservation Society Report for 1959) and on the Cornish coast a nest was seen with two chicks on 9 September 1963, though this was a "late date" (Cornwall Bird Watching and Preservation Society Report for 1963).

Influence of the age of the male and female on the overall production of independent young

Parent Shags feed fledged chicks for many days after they leave the nest (Selous 1905). Snow (1960) recorded chicks fed at a maximum age of 115 days, though the vast majority were independent at that age. The last recorded feeding took place at the age of 85 days on the Farnes, but little evidence is available on the average age of independence. One exceptional chick was still being fed regularly in the following breeding season along-side chicks hatched in that year . Murphy (1936) relates that Gain found "indication that young (of P. atriceps) which had attained an age of eleven months or more, still showed a tendency to follow and associate with their own parents", but did not record parental feeding. There are only three recoveries of Shags within one hundred days of hatching in 1963-1964 and very few in any year in the period 1952-1965 (see p185) in the first 100 days after the fledging period. Thus the number of fledged young represents the number of independent young.

Since the samples of aged birds in the following analysis are considerably larger than any used so far in this study some further explanation is required:-; if the age of one member of the pair is known the age of the other has been estimated (see p59) and in this estimation, the laying date of the female is considered where the age of the male is two years. Single chicks lost through known human interference have been given the 'benefit of the doubt' as regards survival, and the age of the female for a trio is the average age of the two females. The age of the male and female and the number of young reared are known for 528 nesting pairs in 1936-1964. This sample is slightly biased however, since it contains 78 per cent of all pairs with nests, but 92 per cent of young produced.

The percentage of these nesting pairs which produce young is given by the expression:-

Percentage rear,) = 1.745 age ♂ + 0.781 age ♀ +50.1
at least one young)

(t = 2.05, with 12 d.f.) P = approx. 0.05)

The low multiple regression coefficient of +0.51 reflects the curvi-linear relationship in which maximum production is reached by the fifth year. Bringing in brood size increased this coefficient to +0.62, since brood size itself is related to age (via 'care of the young').

The production of independent young by these nesting pairs is given by the expression

Production of young = 0.12 age ♂ + 0.035 age ♀ + 0.41

(t = 2.71 $P = <0.02$)

The factors resulting in the similar success of the 4.5 year, 7 year and 11 year age groups, (Table 45) despite the steady increase in the 'care of the young' through

Table 45

Production of young in the Shag, according to age structure of the pair

(number pairs given in brackets)

		Age ♂				
		2	3	4.5	7	11
	2	0.52 (69)	-	-	-	-
Age♀	3	0.80 (29)	1.16 (29)	-	-	-
	4.5	1.03 (20)	1.23 (34)	2.03 (57)	1.49 (42)	-
	7	-	0.75 (18)	1.40 (28)	1.33 (51)	1.43 (52)
	11	-	-	1.28 (23)	1.35 (31)	1.60 (45)

these groups is to be found:-

(1) Tendency for older birds to belong to the trios (Table 20)

(2) Tendency for birds at the beginning of the season to lay slightly smaller clutches (Fig. 28)

(3) Tendency for higher partial infertility in older birds (see Fig. 35).

Of especial interest is the comparison of the male and female partial regression coefficients which are 2.2 and 3.4 times as high in the male as in the female, indicating the much greaterimportance of the age of the male. Thus the age of the male is the most important in age specific (1) Egg survival and (2) Care of the young, whilst (3) the female is more important (2.4 times) in the occurence of addled eggs. Thus (4) the production of young, is a result of the combination of (1),(2) and (3), for the most part.

A Comparison of the overall production of young in two populations of Shags

The mean number of young produced (i.e. fledged), by the colony of about 130 pairs (Fig. 17) on Lundy, during the period 1954-1957 was 1.85. Since the number of nests not included in the above sample was very small, and these were excluded because they were inaccesible, the mean probably represents that of the population (Snow 1960,1963, extended in litt and pers. comm). On the Farnes, however, 319 'pairs' in 1963 and 355 pairs in 1964 produced 1.06 chicks per pair. During these periods on Lundy and on the Farnes the clutch size was comparable and, respectively, 3.07 and 3.05. One can thus conclude that the production per pair (see note on bottom of Table 46) on the Farnes is 58 per cent of that on Lundy, a considerable difference which needs explanation.

The mean size of 344 broods (i.e. of chicks 20-30 days of age) on Lundy was 2.27 ± 0.043 (SE) (from Snow in litt.). That of 880 broods (1947-1965) on B.T.O. nest record cards was similar being 2.26 ± 0.026. On the Farnes however brood size in 1963 and 1964 was 1.98 and 2.04 respectively.

On most schedules of Farne Island ringed Shags, broods of 2 or 3 are bracketed, but no distinction is made between groups of young and single broods. However, it was found that a reliable estimate of brood size (y) could be made as follows:-

$y = 0.016x + 1.47$ ($r = +0.92$, ($P<0.02$))

where x = proportion of all broods with three or more chicks as a percentage of broods with more than one chick. Using this information, derived from a study of the B.T.O. nest records together with the Farne data, it has been possible to estimate brood size for each of the years 1951-1965. The mean brood size is 2.04 and there has been no consistent trend over the years, though the five years 1954,56,57,61 and 1965 the mean brood size averaged 2.16. Thus brood size on the Farnes is only about ten per cent less than that on Lundy. Since the age distribution will have an effect on this (p149) it is probable that the small though significant difference (assuming equivalent standard errors) is a result of the stable population on Lundy and the increasing one on the Farnes. This is supported by information from the rest of the British Isles, assuming that, as a whole; it is not increasing at a significant rate. Fertility was found to be 16 per cent lower on the Farnes (p149). Since fertility incorporates brood size this still leaves a considerable remainder to be accounted for. Since the 1963 and 1964 seasons may have been unusual, further analysis has carried out for each of the years 1960-1965, there being insufficient information prior to 1960. The results are given in Table 46 and give a mean production of 1.16 if the

Table 46

Number of young fledged per pair on the Farnes 1960-1965

Year	✱ No pairs	Young fledged (1)	Young per pair	Young per pair as % brood size (2)
1960	216	222	1.01	52
1961	238	331	1.39	66
1962	270	327	1.21	61
1963	319	312	0.98	49
1964	355	401	1.13	55
1965	390	480	1.23	60
		Mean	1.16	

(1) 1960-1962 estimated assuming number of young fledged is ten per cent greater than number of young ringed, this is the average 1963-1965 value, taking into consideration the fact that some areas were ringed in 1963-1965 but not 1960-1962

(2) Best estimate from Table 47.

✱ Represents number of males attempting to breed, this is on average 1.08 times the maximum number of nests, based on 1963-1965.

Table 47

Trends in brood size on Farne Islands 1951-1965

Brood size at age 20 - 30 days

Year	Sample(1)	Brood size A	Sample(2)	Brood sizeB	Sample(2)	Brood sizeC
1951	10	1.80	-	-	-	-
1952	16	1.97	-	-	-	-
1953	22	1.90	-	-	-	-
1954	25	*2.37	-	-	-	-
1955	13	2.08	-	-	-	-
1956	21	(1.93)	20	2.19	58	2.26
1957	21	* 2.16	48	2.10	87	2.07
1958	36	2.00	43	2.00	-	-
1959	47	2.11	-	-	-	-
1960	37	1.71	87	2.05	-	-
1961	85	*2.11	58	2.07	-	-
1962	71	2.22	104	1.97	49	1.79
1963	161	1.98	Present study	2.01	-	-
1964	172	2.04	"	1.98	-	-
1965	181	2.06	"	2.06	-	-
Totals & unweighted means	918	2.03	360+	2.05	194	2.04

Notes (y = brood size)

A. 1951-62 calculated from the expression $y = 0.016x + 1.47$, where x = all broods with three or more chicks as a percentage of all broods with more than one chick. 1963-65 values are the complete samples resulting from the present study.

B. Calculated from the expression $y = 0.91(0.52x + 0.61)$, where x = clutch size (which can be estimated as the mean number of eggs in the nest x 1.26). The constant 0.91 gives the regression line, reducing x errors, as a best fit to the Farnes data (see Fig.30).

C. Mean chicks per nest.
* peak ringing years.

(1) young
(2) nests

possibility that post-ringing loss was higher in the period 1960-1962 than 1963-1965, is ignored. On average then, the production on the Farnes is 63 per cent of that on Lundy. It seems likely that some of the remaining difference could be explained in terms of the more exposed nesting sites on the Farnes. This was undoubtedly true in 1963 when chicks were washed away from the Farnes in heavy seas. If the quality of the sites did account for this difference two effects should be found

(1) The birds nesting at the beginning of the season on the Farnes should have a success equivalent to that on Lundy, since they nest in suitable sites, allowing for the lower fertility on the Farnes.

(2) As the effects of crowding, in relation to the number of good sites increases on the Farnes, the production per pair should decline.

The seasonal trends (see Table 48) do support (1) almost exactly but the annual trends do not, partly because chick loss due to storms cannot be included. However, the storm of the 3-4 June and 20 June 1963 occuring at the same stage of the season in 1965, would have killed a higher percentage of chicks in 1965 than in 1963, judging from the distribution of nests in the two seasons.

Additional to the effects of exposure, infertility and egg breaking, the surplus of females generally, especially, the trios, and an amount of non laying (7 per cent nests 1963 and 1964) (this last is not mentioned by Smow) all combine to account for the lower production on the Farnes, though so far, there is insufficient evidence to show that this is density dependent (i.e. dependent on the availability of good sites, not on the number of Shags). It is especially interesting in this connection to note that the production of the colony on Unst of only 130 pairs was about identical to that on the Farnes. Thus the actual size of the colony is not the important feature (predation can be ruled out of this discussion) but rather, it is the quality of the nesting areas, on Unst rock falls and high seas combine to reduce the production of young. (Current investigation into the effect of the relatively high concentration of insecticide in Shags on the Farnes is reviewed on pp236-42) . It is interesting to compare the overall production of the Shag and Cormorant since the clutch and brood sizes are different on the Farnes. The mean brood size of 271 broods on the Farnes was 2.34 ± 0.123 or 15 per cent higher in the Cormorant, than in the Shag whereas the number of young produced per pair (nest) in 1963-1964 was approximately 1.03 and not significantly higher than in the Shag. This production is similar to that of the tree nesting population of Cormorants in Holland which produced one fledged young per nest, (Kortlandt 1942)(the 'playing nests' mostly built by two year olds are included;

Table 48

Seasonal decline in the Production of Young in the Shag

Week	LUNDY		FARNES 1963		FARNES 1964		UNST 1964		1963-1964 Farnes as % Lundy
	nests	young per nest	nests	young per nest	newts	young per nest	nests	young per nest	
1	32	2.27	19	1.53	19	2.16	3	2.00	81
2	83	2.18	27	1.63	61	1.59	4	1.25	74
3	108	2.22	49	1.29	56	1.61	26	1.73	65
4	75	1.88	48	1.14	54	1.26	21	1.33	64
5	41	1.52	39	1.15	60	0.97	29	0.96	70
6	22	1.20	28	1.04	32	0.75	14	0.64	74
7	23	0.82	27	0.52	11	0.54	5	0.60	65
8	15	0.90	20	0.53	16	0.44	5	0.40	53
9									
10	9	0.60	22	0.32	19	0.37	13	0.39	57
11									
12	No young fledged from eggs laid beyond ninth week								
13			17	0.82	5	0.60	-	-	-
14									
15									
16									
Sample	408	1.85	296	1.05	333	1.20	120	1.07	60.8
All	-	-	319	0.98	355	1.13	(121)	-	57.0

Weeks from date of first egg

Table 48

very few of these contained eggs; Cormorants at least three years old produced 1.25 young per pair, and production of the oldest birds was still higher).

Age specific production of young in Shag and White Stork

Hornberger (1943) carried out a study on 187 White Storks of known age in the Insterburg area of what was then East Prussia. The striking similarity of his results (Table 49) with that of this study is especially interesting since the White Stork (in Europe) is not a colonial species. It might be imagined that the age specific timing of the breeding cycle might be a mechanism for spacing out breeding activities and thus reducing competition for nest sites, and also ensuring that the birds most likely to rear young are least likely to have their attempts thwarted by the effects of having to make do with an unsuitable site. However Hornberger showed that the old White Storks were most likely to be successful and Haverschmidt (1949) in a study of 94 nests demonstrated a progressive and marked seasonal decline in breeding success in which the degree of success was closely correlated with the time of return to the nest. These two studies add up to the same situation described in the Shag and suggest that causes other than those related to colonial organisation are involved in the age determined breeding schedules.

Table 49

Production of young in White Storks and Shags of known age

(1) White Storks(♂+♀)			(2) Shag		
Age	Number birds	% Rear Young	Age	Number birds	% Rear Young
2	-	-(none)	2	187	39.9
3	17	41.2	3	139	60.6
4	53	54.7	4)	261	69.9
5)	82	74.4	5)		
6)			6)		
7)	35	82.9	7)	273	67.4
8)			8)		
9)			9)		
10)			10)		
11)			11)		
11+)			11+)	196	68.9
	187	67.4		1056	62.5

(1) 10 seasons, re analysed from Hornberger (1943)

(2) This study, 1963 + 1964

SECTION SIX

MORTALITY AND MOVEMENT

There are several basic problems concerning the use of ringing recoveries as indicators of mortality and movement.

The Recovery Rate

The higher the proportion of dead birds recovered, the greater the probability that these form a useful sample of the mortality both in space and time. The proportion of ringed Shags which are recovered in their first year of life (August to July inclusive) is given in Table 50, for six ringing stations. The recovery rate of Shags ringed in Shetland is 4 per cent, on Scilly and Lundy 13 per cent and on the Isle of May and Farnes 10 per cent. Davis (1961(a)) considers that the "Sparseness of the human population in the recovery areas" will account for much of the lower recovery rate from the ringing in Shetland. In some years however, the recovery rate of the Isle of May-Farnes group was very low and there is evidently considerable annual variations on this coast. Further, there is a high correlation between the annual recovery rates on the May and on the Farnes (r = +0.90).

Significance of annual variation

One way of testing the biological significance of these annual variations is to examine the corresponding

Table 50

Percentage Recovered in 1st Year of Life (August to July inclusive)

Year	Farnes	Isle of May	Lundy	Scilly	Fair Isle	Foula
1952	16	-	20	-	-	-
1953	21	18	17	-	-	-
1954	15	10	15(11)*	-	-	-
1955	8	5	20(12)	-	-	-
1956	3	6	16(11)	-	-	-
1957	15	13	19(15)	8	3	6
1958	3	6	-	4	2	4
1959	20	-	-	(8)	3	5
1960	11	-	-	19	5	5
1961	16	12	-	12	2	2
1962	5	6	-	13	?	?
1963	4	6	-	7	?	?
1964	4	?	-	6	?	?

* excludes shot category

recruitment from the year classes.

The number of ringed Shags alive in 1965 and surviving from the various cohorts are given in Table . The number of survivors in 1965 divided by S^n where S = the adult survival rate gives the number of Shags recruited as two year olds (Column 3 Table 51).

The number recruited as two year olds is then expressed as a percentage of the number of pulli ringed in that year to give percentage survival to recruitment (Column 5 Table 51). The mean percentage recruited is 15.5 for the year 1951-1957 inclusive in which aluminium rings were used, but 28.8 per cent in the period 1958-1962 when monel rings were used. This suggests that $\frac{28.8-15.5}{28.8}$ or 46 per cent of the Shags lost their aluminium rings before they could be re-captured and re-ringed. The observed percentage recruitment is then divided by the mean recruitment in each of the periods 1951-1957 and 1958-1962 (Column 6 Table 51).

The significant correlation ($r = -0.60, P = <0.05$) between the first year mortality rate and the observed/mean recruitment as represented in the breeding populations in 1965 indicates that the number of recoveries are related to the extent of the mortality since the recruitment is lower where the recovery rate is higher.

Distribution of Recoveries

The next step is to test the temporal association

Table 51

Correlation of Recruitment and first year recovery rate

Year	1	2	3	4	5	6	7
	Alive 1965	s^n	(1/2)	Pulli ringed	(3/4)	Observed mean	% Pulli recovered in first year of life
1962	63	.85	74	297	25%+	.87+	5
1961	50	.72	69	301	23%	.80	16 *
1960	41	.61	67	202	23%	1.15	11
1959	25	.52	48	197	24%	.83	20
1958	25	.44	57	145	39%	1.35	3
1957	3	.37	8	177	5%	.32	15 *
1956	7	.31	26	145	18%	1.16	3
1955	5	.26	19	101	19%	1.23	8
1954	2	.22	9	100	9%	.58	15
1953	1	.19	5	61	8%	.52	21*
1952	1	.16	6	50	12%	.77	16
1951	2	.14	14	37	38%	2.45	7

* 'wreck' years + recruitment still in progress

of death and recovery, so that the recoveries can be used to indicate

1. seasonal mortality variations
2. the movements of the parent population.

If a high proportion of the reported dead birds were not discovered for several months any such association would be obscure, so that one could not, for example, examine the seasonal distribution of mortality, directly.

Independent information referring to the Shag 'wreck' of March 1962 is shown in Fig.38 which supports the use of recoveries as accurate temporal indicators of mortality. Further an examination of all records of Shags, published in the Norfolk Bird Report (1951-1963) and in Payne (1962) shows that there is a correlation between the number of Shags seen in Norfolk and Suffolk and the proportion of recoveries of Farne birds south of Spurn point. (These are independent estimates). This correlation suggests that the annual distribution of Shags can be measured from the pattern of recoveries.

Fig. 38

Top

INDEPENDENT ESTIMATES OF THE TIMING OF THE SHAG 'WRECK' OF MARCH 1962. (1961 COHORT).

Filled triangles , Shags flying south off Yorkshire(see p.189

Open circles , number roosting on Reading Gasometer (Gillmor

Crosses , seen in Norfolk Bird Report area (i.e. includes Cambridge,Ely etc.). This is an index since repeat observati of the same individuals cannot, strictly, be excluded.

Broken line top All Recoveries

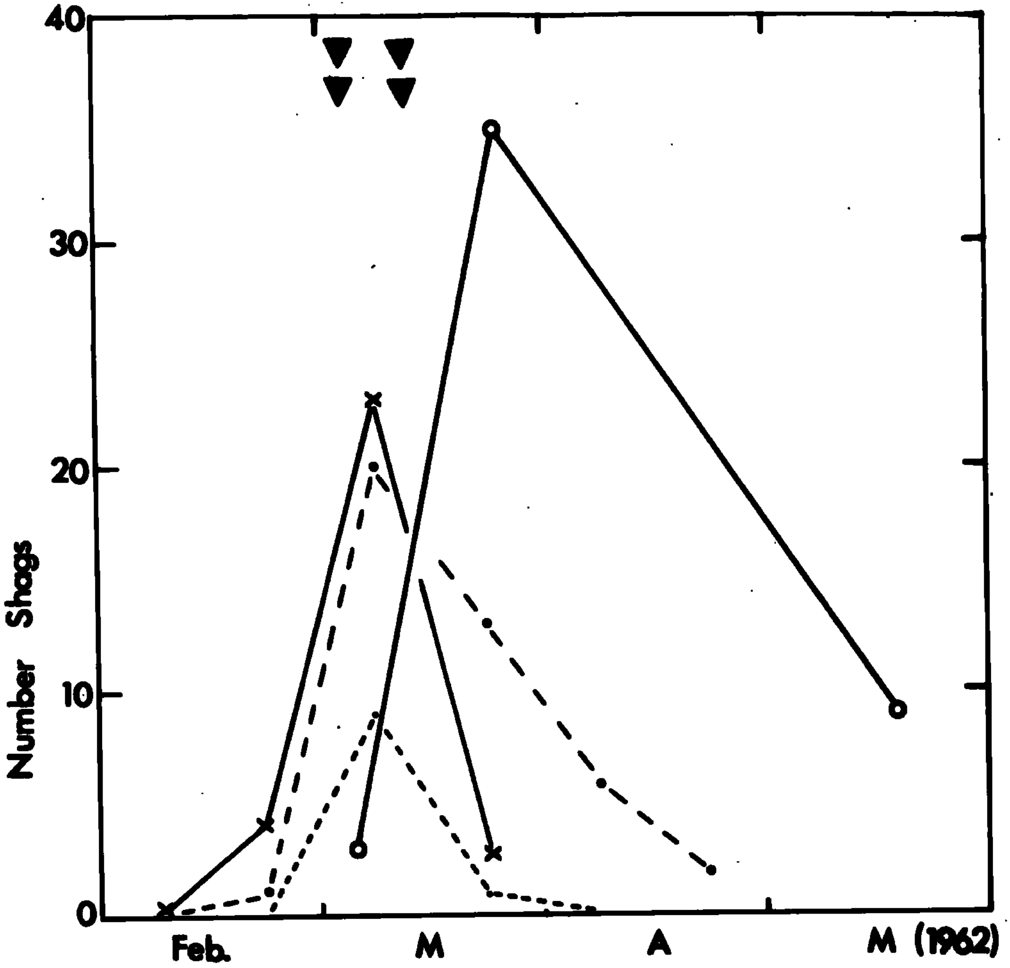
Broken line lower Inland Recoveries

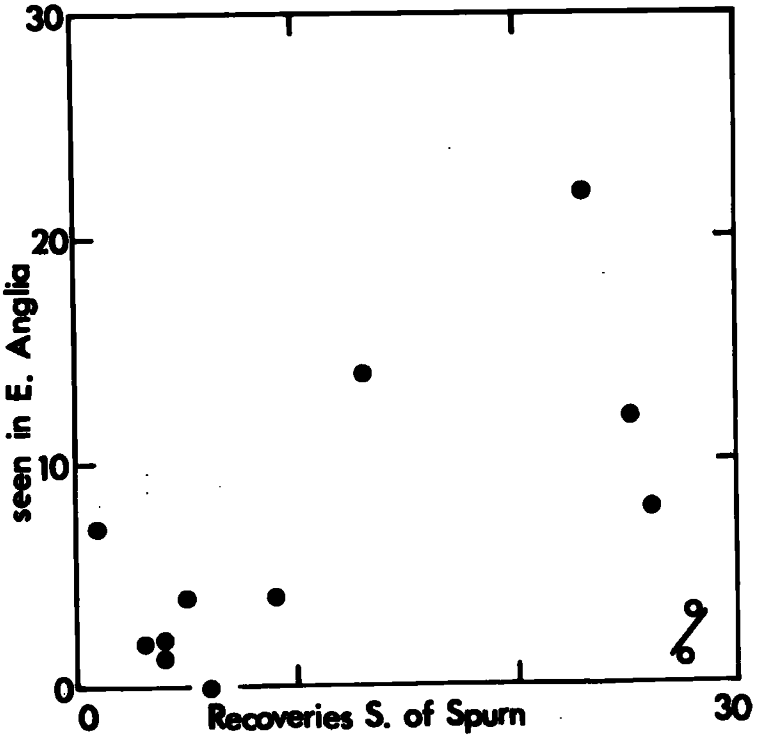
Lower

CORRELATION BETWEEN NUMBER OF RECOVERIES AND NUMBER OF SHAGS IN EAST ANGLIA

Recoveries south of Spurn (Farne birds only, and in first yea

Index of sightings (as before) Norfolk and Suffolk 1951-1962 based on Norfolk Bird Report and Payn 1962.


40
30
20
10
0
Number Shags
Feb.
M
A
M (1962)


30
20
10
0
seen in E. Anglia
0
Recoveries S. of Spurn
30

Seasonal movements in the first year

Monthly 'Shag counts' around the Farnes are given in Fig.39 . These were made from a coble, between 1100 and 1500 GMT. In the period April to August the direct counts used at other times were changed and the estimates for these months are derived by summing twice the maximum number of nests recorded at any one time during the season, and the number of non-nesting Shags both in and away from the breeding areas. The number of non-nesting Shags is best estimated towards dusk, by which time a negligible proportion of the birds will still be on the sea. The September-March counts are under-estimates since some Shags were at sea, fishing. It is not practicable to estimate the number of birds feeding, but is is known that the vast majority of Shags have finished feeding by the time Shag counting starts at least in the relatively calm and clear conditions necessary for a count. Under these conditions it is probably reasonable to assume that the proportion of Shags away fishing during the counts, does not change markedly from count to count, especially since no such changes were apparent in the field. Apart from those feeding during the counts, some Shags move away from the islands, do not return until roosting time, and miss the counts altogether. For example on 18 February 1965, 44 birds were counted flying south off Holy Island to roost on

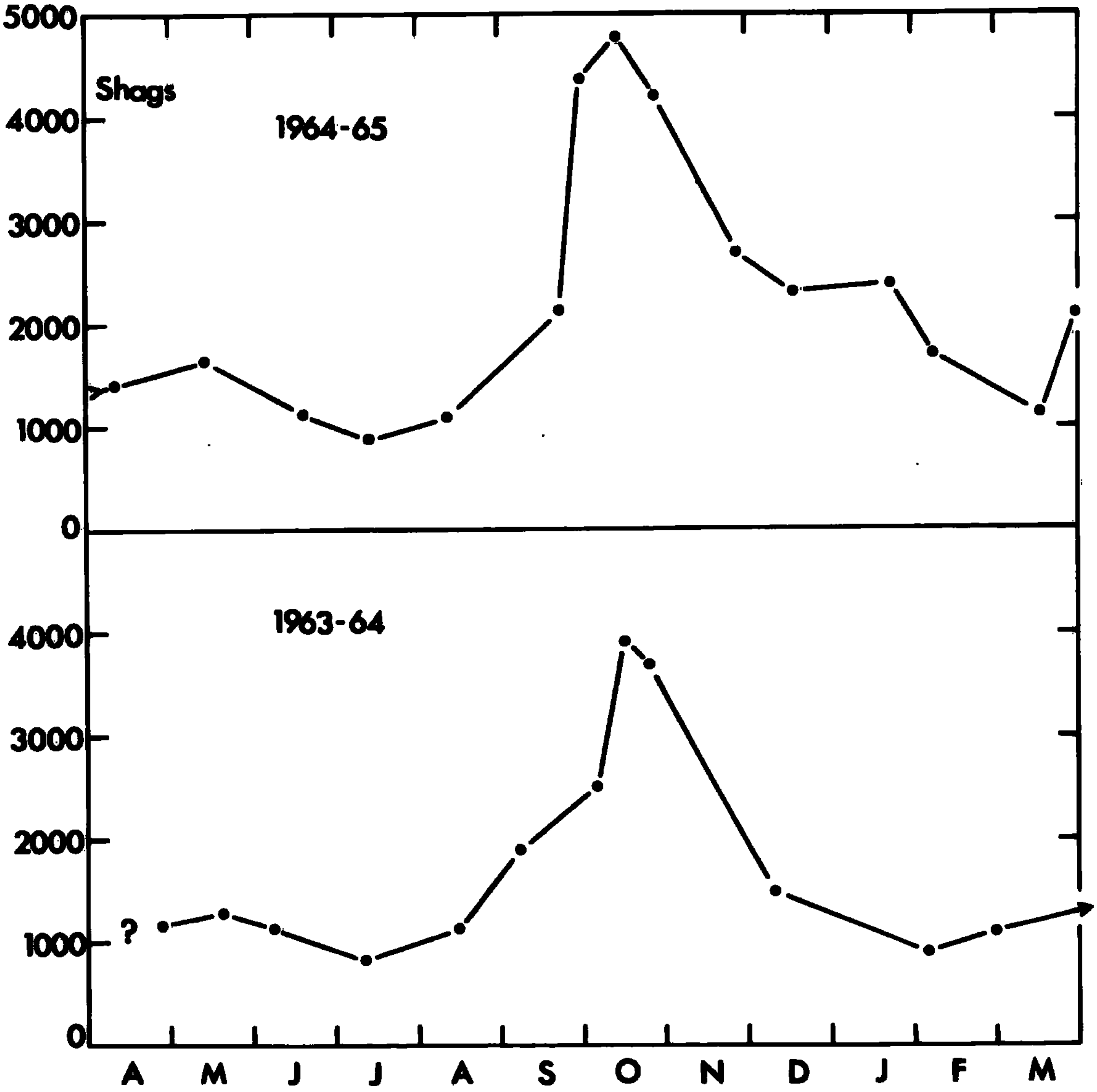
Fig.39

[illegible]

([illegible])

THE NUMBER OF SHAGS ON THE FARNE ISLANDS

(see text page 181)



5000
Shags
1964-65
4000
3000
2000
1000
0
1963-64
4000
3000
2000
?
1000
0
A
M
J
J
A
S
O
N
D
J
F
M

the Farnes. Perry (1946) mentions regular movements of this kind and reported that 'many hundreds' from the Farnes fed off Holy Island in autumn and winter. As Lumsden and Haddow (1946) have pointed out, Shags gather from considerable (up to 18 miles) distances to roost. The Farnes roosting movements are especially complicated since some but not all of the birds on the outlying rocks (see Fig. 1) move into the breeding areas at dusk. At high spring tides or during poor weather the numbers which do this are higher.

It is evident that there are two peaks in the seasonal variation in the number of Shags on the Farnes. Approximately 2500 (75 per cent) of the autumn bulge consists of birds in their first year, reared away from the Farnes. The October influx coincides with the <u>departure</u> of the yearlings reared on the Farnes and that in Spring is associated with their return. Consideration of the recoveries (Fig. 40) together with sightings of ringed birds during this study show that there is a similar autumn dispersal of first year birds from the Forth area and that this progressive dispersal coincides with the autumn peak on the Farnes. The return movement of the Forth birds is not well represented by recoveries and this return is not apparent at all from the Farne recoveries, but it does coincide with the spring peak of numbers on the Farnes. It is also evident that

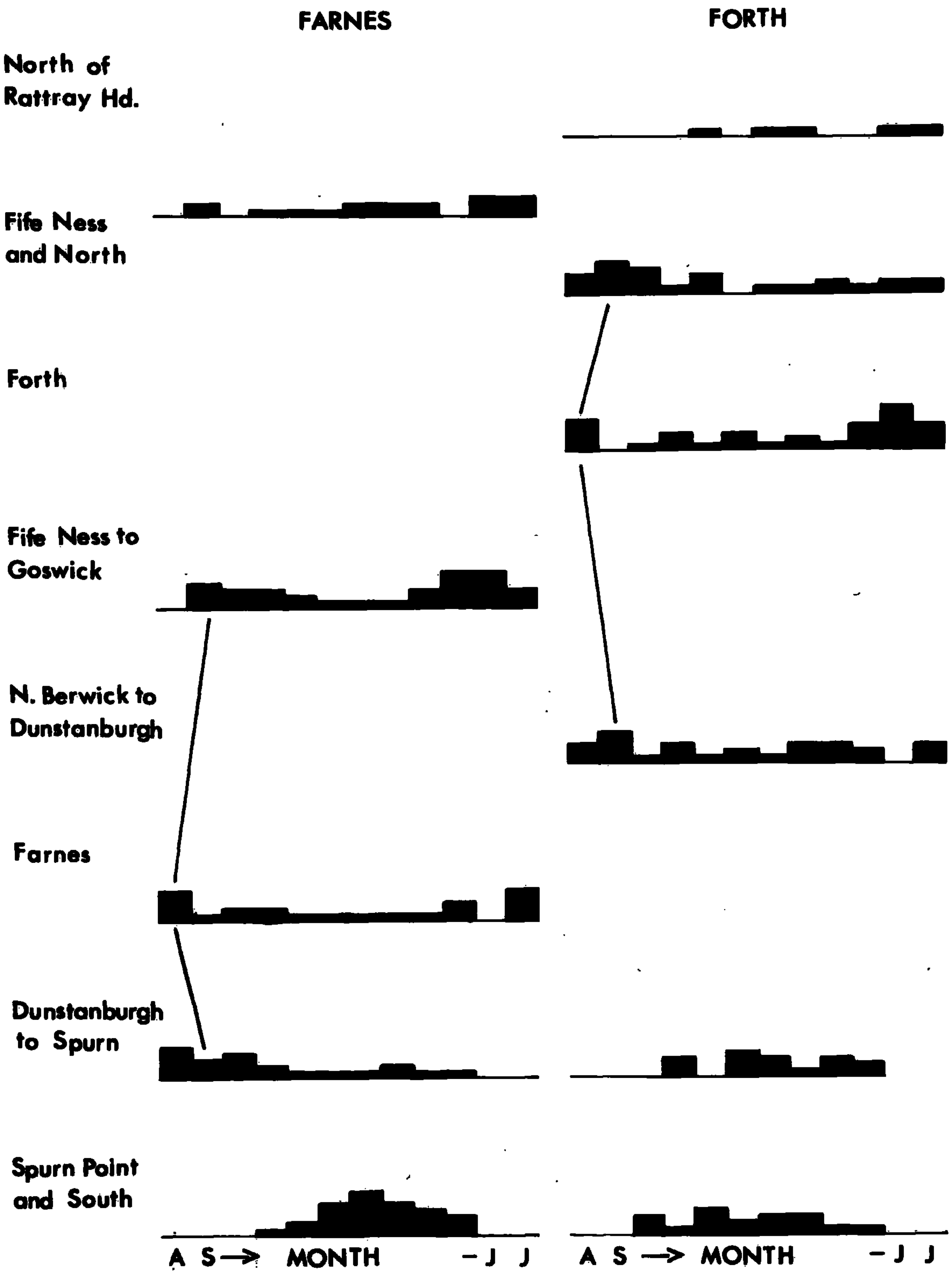
Fig.40

THE PERCENTAGE DISTRIBUTION OF RECOVERIES ACCORDING TO GEOGRAPHICAL REGIONS, DURING THE FIRST YEAR OF LIFE, IN EACH MONTH

Farnes 222 Recoveries to 31 December 1964

Forth 179 Recoveries to 18 November 1964

Lines indicate the post independence dispersal.


FARNES
FORTH
North of Rattray Hd.
Fife Ness and North
Forth
Fife Ness to Goswick
N. Berwick to Dunstanburgh
Farnes
Dunstanburgh to Spurn
Spurn Point and South
A S → MONTH – J J
A S → MONTH – J J

the number of 1st year Shags seen on the Farnes in autumn is too great to be accounted for in terms of the Forth-Farnes population. During the 1963-1964 autumn peaks in which there were at least 2500 non-native 1st year birds, on the Farnes the estimated production (apart from the Farnes) in the Fife Ness-Flamborough area would be on average, only 1500, and of these, not all would be on the Farnes,(e.g. About 20 per cent of Isle of May recoveries in autumn are to the north of the May, see Fig.40).

In other words,half of the non-native first year birds on the Farnes in autumn must come from localities north of Fife Ness. Additional evidence supporting this conclusion comes from the observations of Clarke (1913), Miller (1918),Perry (1946) and Watt (1951), all mentioning large numbers of Shags on the north-east coast of England, before the native breeding populations were large enough to produce them.

Very few Shags have been ringedin Orkney but of 49 ringed on Eynhallow in 1960 one reached Bridlington by October and another two were found in the Forth. It is known that the Farne population at that time moved south of its usual position and this might have also occurred in the Eynhallow population. Recoveries of Shetland birds suggest that 5 per cent of yearlings from this area winter in the Rattray Head-Spurn region, but there have been only seven other recoveries (Calf of Eday(1) Caithness(1) Sutherland(5)) in this region.* One recovery from Caernarvon occurred during a wreck and is thus believed to be exceptional. The fact that many of the yearlings do leave the Orkneys and Shetlands in September and October has been mentioned by Tomison (1905) who commented that it was "rare to see an immature bird after November" on Sule Skerry and by Davis (1961a), but ringing of the Orkney and north Sutherland populations has been too spasmodic and slight to indicate the normal southern limit of their first year birds from recoveries,in autumn. Since there are no large colonies of Shags on the east coast of Scotland north of the May, it is very likely that Orkney and Sutherland Shags regularly winter in the Forth-Flamborough area.

The recoveries shown in Fig.40 do not suggest a large build up of birds on the Farnes in October-November. This is because the mortality rate at this time of year is very low (Fig.41). The dearth of dead birds on the Farnes in the autumns of the 1963 and 1964 compared with April and May of the two years was remarkable, more especially considering the difference in numbers of Shags present at these times.

Thus the autumn build up of Shags on the Farnes is not shown by the recoveries whereas the number of Shags occurring south of Spurn appears to be indicated by the recoveries (p 180).

* See Appendix D

Seasonal and geographical mortality patterns during the first year

The most remarkable feature of the first year mortality patterns is that they vary seasonally from colony to colony (Fig.41), and that these differences are maintained within the same year classes (Fig.42).

Fig.43 shows the ogives (cumulative frequency curves) for the various geographical zones within the range of yearlings from the three breeding areas which have yielded the largest number of recoveries, Farnes(221);Lundy(158) Shetland(142). (Ogives for the Forth colonies are similar to those for the Farnes). The arbitrary areas concerned are:-

Lundy		Farnes	
Li	France	Fi	Dunstanburgh-Goswick inc. Farnes
Lii	Wales and Ireland	Fii	North of Goswick
Liii	Lundy,Cornwall,Devon	Fiii	South of Dunstanburgh

Shetland	
Si	Shetland and <100 miles from natal colony
Sii	elsewhere, mainly Cromarty Firth.

For Lundy and the Farnes the differences between their ogives are negligible and merely represent the influence of the speed of dispersal. For example Lundy Shags do not reach France until September and there is a corresponding effect on the ogive. However, the two steep parts of the curve are marked both in Shetland and in the wider

Fig.41

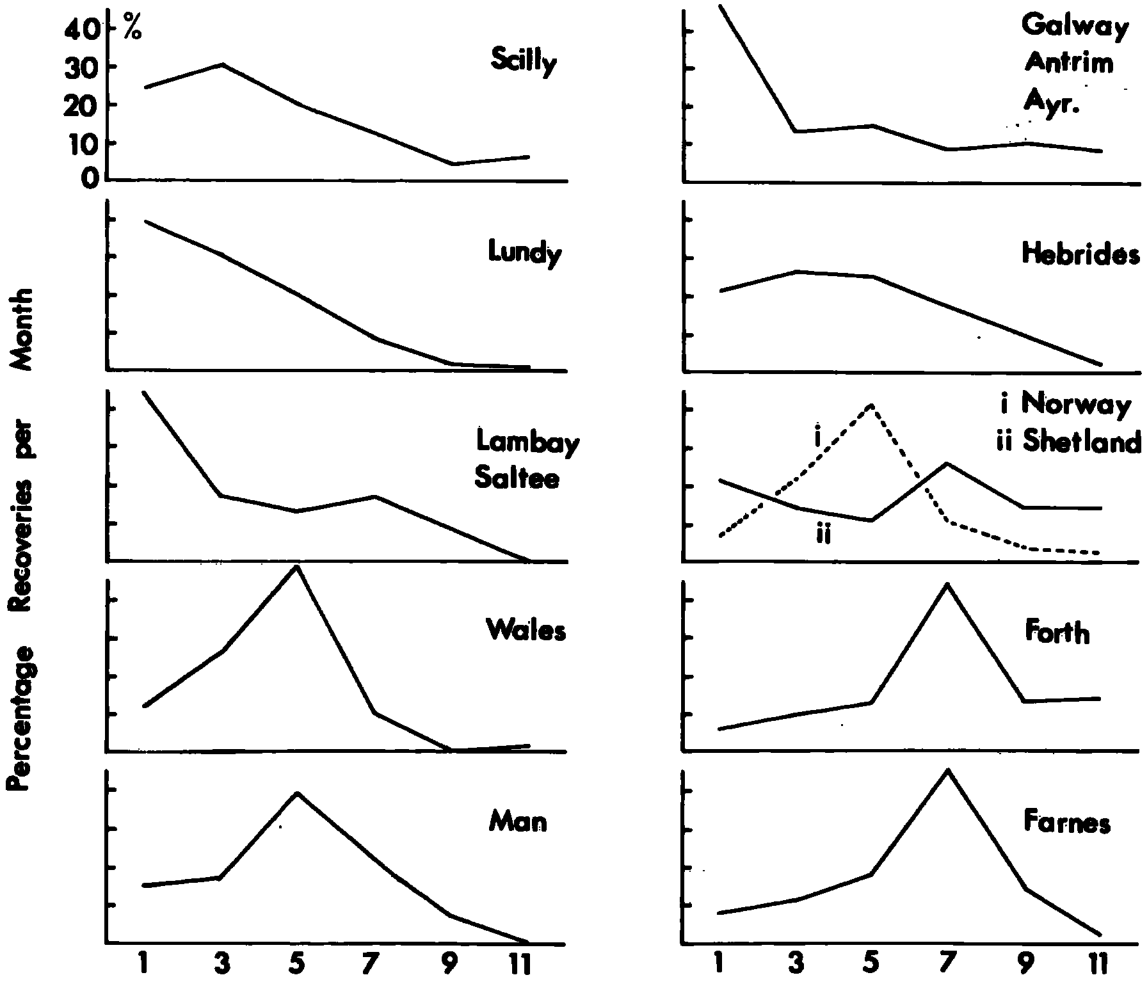
GEOGRAPHICAL VARIATION IN THE SEASONAL PATTERN OF MORTALITY DURING THE FIRST YEAR

(Samples on which percentages calculated)

Scilly	101	recoveries (also in Parslow 1965)
Lundy	158	"
Lambay & Saltee	23	recoveries
Pembroke-Anglesey	42	"
Isle of Man	41	"
Galway Antrim Ayr	39	"
Hebrides	118	"
Shetland	106	"
Forth	179	"
Farnes	218	"
Norway	314	(from <u>Sterna</u> 1958-64 inclusive, reports (for 1957) to 14 (for 1963) of the Stavanger Museum and Norwegian Ornithological Society, compiled by Holger Holgersen)
Total	1339	First year recoveries

<u>Abscissa</u>

Months after fledging <u>i.e.</u> starting 1 August except for Isle of Man and S. Ireland (1 July).



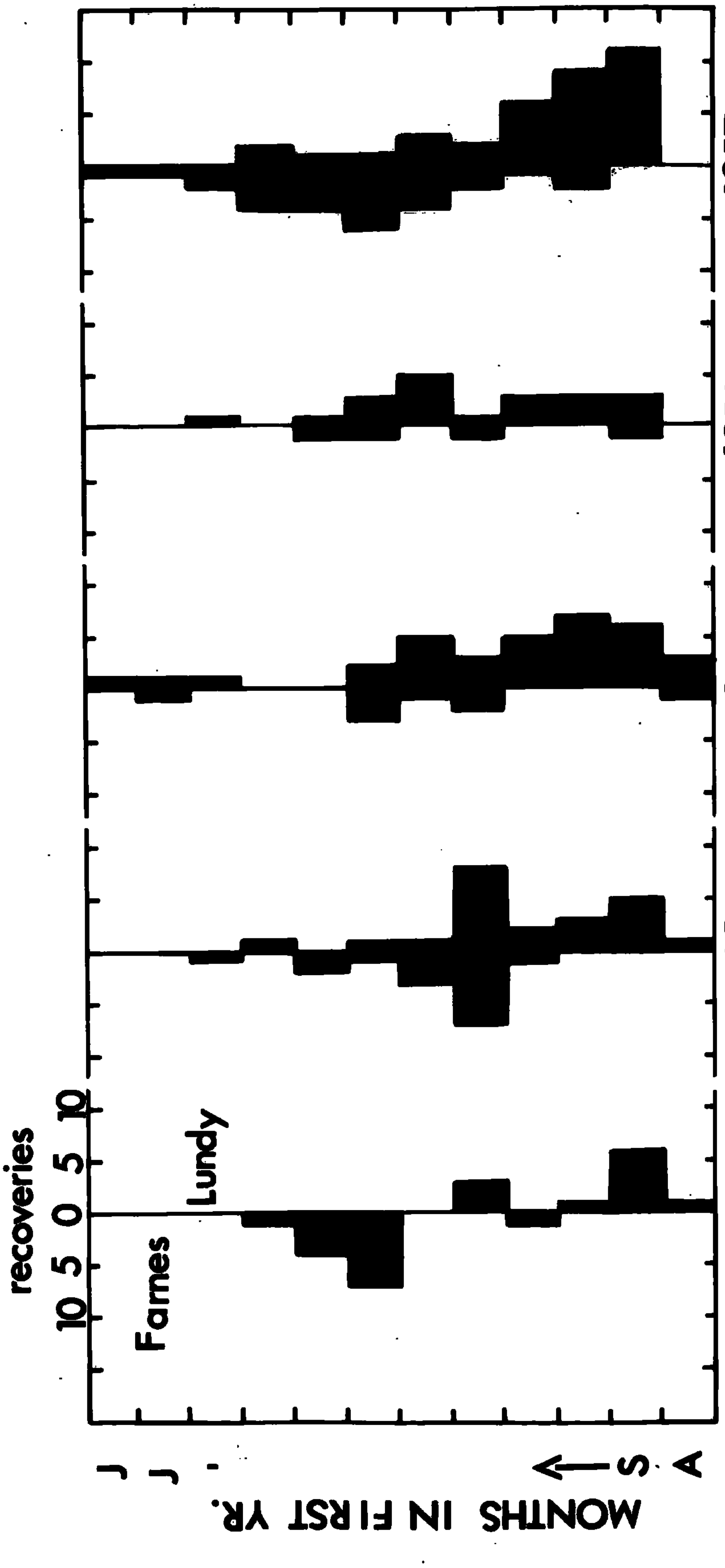
40
30
20
10
0
%
Scilly
Galway
Antrim
Ayr.
Lundy
Hebrides
Lambay
Saltee
i Norway
ii Shetland
i
ii
Wales
Forth
Man
Farnes
Percentage Recoveries per Month
1
3
5
7
9
11
1
3
5
7
9
11

[illegible]

[illegible]

MONTHLY TOTALS OF RECOVERIES IN FIRST YEAR
OF COHORTS 1953-1957, FOR LUNDY AND FARNES,
SHOWING EARLIER MORTALITY IN THE LUNDY AREA

(1954 was one of three early years, for the Farnes
in the period 1951-1965. see text)



recoveries
10
5
0
5
10
Farnes
Lundy
MONTHS IN FIRST YR.
J
J
A
S
1953
1954
1955
1956
1957

Fig. 43

MONTHLY RECOVERY PATTERN IN DIFFERENT AREAS OCCUPIED BY SHAGS FROM THE SAME COLONY

Lundy

Li France (mainly Brittany)
Lii Wales and Ireland
Liii Lundy Cornwall and Devon

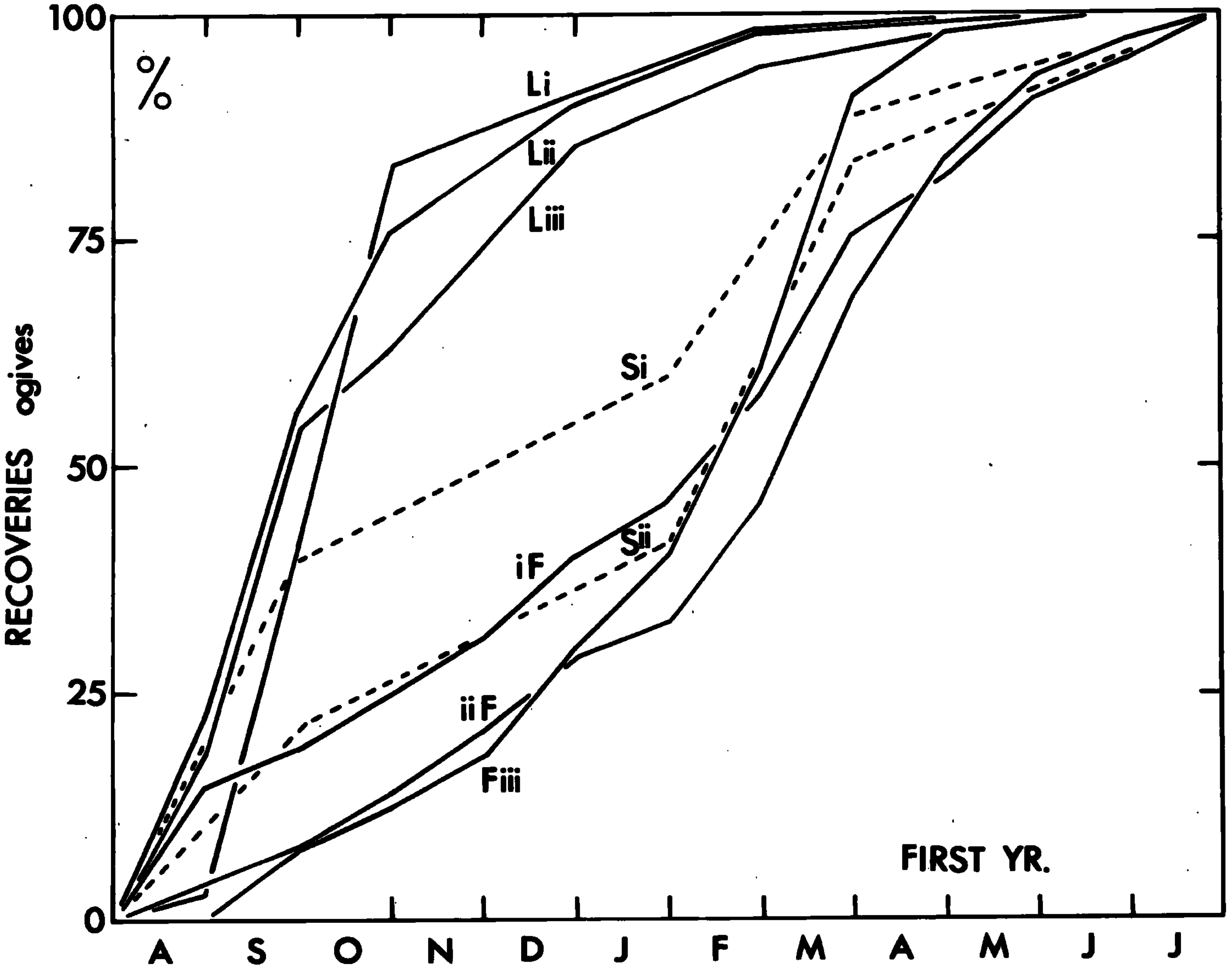
Farnes

Fi Dunstanburgh to Goswick *i.e.* local (< 10 miles)
Fii North of Goswick
Fiii South of Dunstanburgh

Shetland

Si Shetland and <100 miles from natal colony
Sii Elsewhere mainly Cromarty Firth

Note that the L ogives are very similar, and the F ogives are similar, but the S ogives are more different and indicate that Sii is near to the F pattern. If mortality were to spre across the S.W. approaches, or down the North sea, then the L and F curves would be heterogeneous.

%
RECOVERIES ogives
100
75
50
25
0
A
S
O
N
D
J
F
M
A
M
J
J
Li
Lii
Liii
Si
Sii
iF
iiF
Fiii
FIRST YR.

area and the latter (area Sii) shows the March peak typical of the Farne-Forth population. Similarly the second peak of the Lambay-Saltee area (Fig. 41) is confined to the Irish sea.

The mode of first year mortality occurs in September or October in the English Channel, Brittany, south-west approaches north to St. George's Channel and including the west coast of Ireland, the outer Hebrides and Shetland. The mode occurs in December-January in the north Irish sea, Argyll, N. Minch and Norway. Finally in February and March the Shags on the eastern seaboard of the U.K. are involved, but there is considerable evidence (Fig. 43) that the mortality does not spread geographically within the South West Approaches or in the North Sea. In the period 1907-1962 there have been about 14 wrecks of Shags which have included inland movements (_Brit_. _Birds_ 1907-1963) in England. The wrecks in autumn occurred inland from the Severn, those inland from the Wash in late winter, with the Cheshire and Staffordshire area occupying an intermediate position, _i.e_. the wreck pattern agrees with the seasonal pattern worked out from the recoveries. There is some overlap however and the Scilly mortality of the 1961 cohort occurred in January, but this mortality was by far the latest in the nine year period 1957-1965 (Parslow 1965, extended _in litt_). Similarly the 1954, 1960 and 1965 mortality peaks were earlier than usual in the North Sea, but in 10 of the 14 years 1952-1965 the mode of mortality on the North Sea coasts has followed that on the southwest coasts by at least two months.

There is no significant correlation between the recovery rates in the same year between Shetland and Forth-Farnes, Forth-Farnes and Scilly-Lundy or Scilly-Lundy and Shetland. The coefficient of variation of the annual first year recovery rate is 43 per cent in the SW, 42 per cent in Shetland, but 58 per cent on Forth-Farnes indicating that the first year mortality is more variable on the east coast than in the other areas.

The association of mortality with dispersal

The correlation between dispersal and recovery rate in the yearling Shag population is a most striking one (Fig.44). Since mortality in the Forth and on the Farnes is closely related (p 176) the whole of the Forth-Farnes population is involved. In the period July 1960 to January 1966 recoveries of Forth-Farnes Shags have indicated four periods of high mortality. In late October 1960 there was a small 'wreck' of Shags on the coasts of Lincolnshire and East Anglia, in early March 1962 a large scale 'wreck' occurred throughout the eastern seaboard of the British Isles and 25 per cent of the recoveries were from inland localities. At the end of March 1964 a small 'wreck' (Fig.48) occurred on the coasts bordering the Firth of

Fig.44

[illegible] 1

FIRST YEAR MORTALITY AND DISPERSAL IN FARNE ISLAND SHAGS

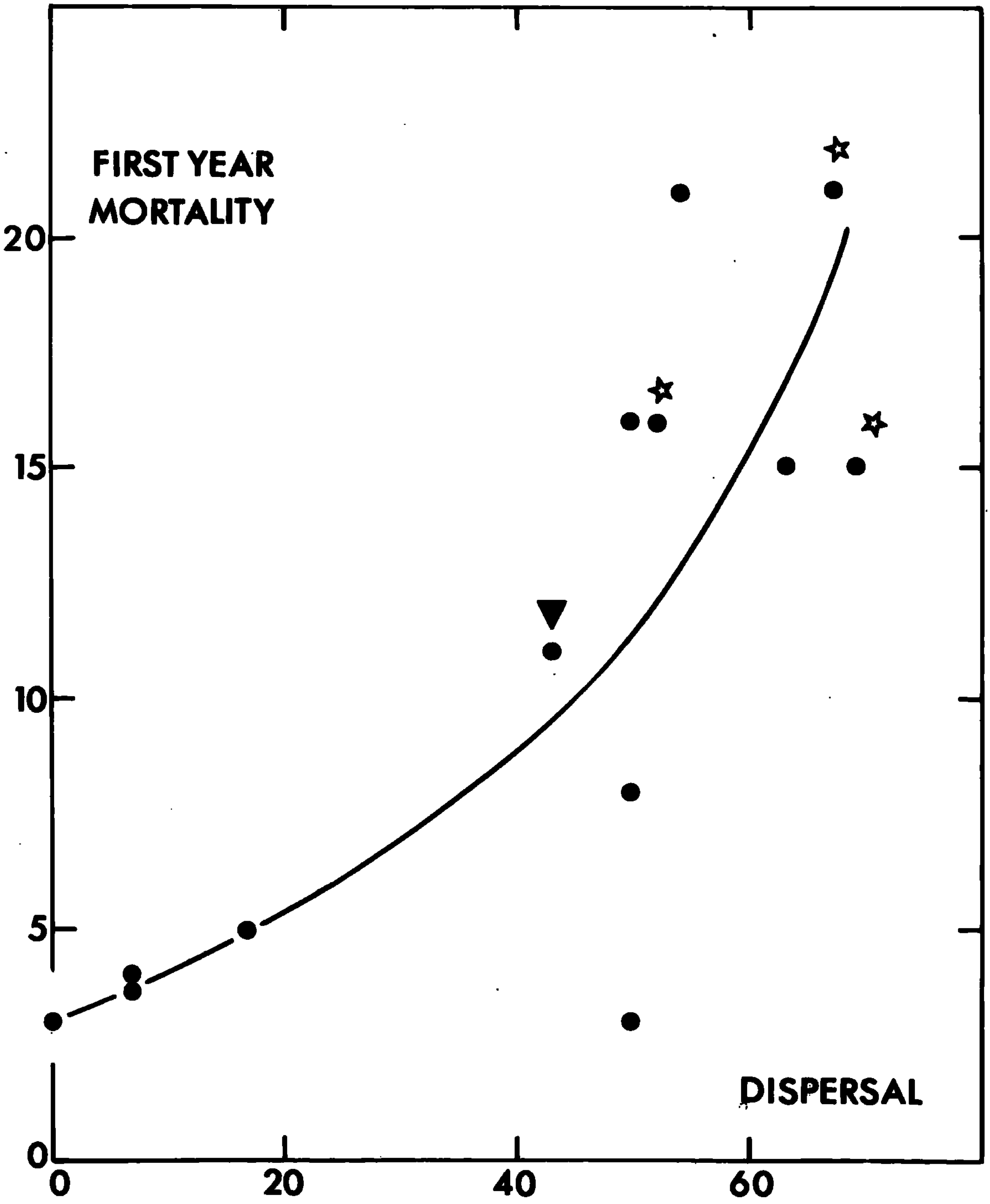
Filled triangle 1960 (see text)

Stars Wreck years (1953,1957 and 1961 cohorts)

$$\underline{\text{First Year Mortality}} = \frac{\text{recovered}}{\text{ringed}} \times \frac{100}{1}$$

Note that the scale of this is exaggerated in terms of mortality (see text).

$$\underline{\text{Dispersal}} = \frac{\text{N. of Fife Ness + S. of Spurn Point}}{\text{Total}} \times \frac{100}{1}$$


FIRST YEAR
MORTALITY
20
15
10
5
0
0
20
40
60
DISPERSAL

Forth and several Shags were found dead inland at Loch Leven. Finally on the 20 November 1965 and in succeeding weeks a large scale 'wreck' occurred, broadly similar to that in 1962. Apart from the March 1964 'wreck' which occurred during a period of very high seas, and which was very small compared with the other 'wrecks', numbers of Shags were seen flying south off the Yorkshire coast but at no other time during the period 1960-1965 inclusive (Table 52).

In earlier years too, the number of birds passing south along the Yorkshire coast was also higher in 'wreck' years (Y.N.U. Reports 1952-1960).

The correlation between recovery rate and dispersal, indicated by the recoveries, is amply confirmed by the fact that the numbers of first year Shags seen south of Spurn is related to the number of recoveries in that area, combined with observations that flocks of Shags were seen flying south from Spurn during the most recent 'wrecks'.

Seasonal variation in mortality rate, according to age

The seasonal distribution of recoveries are given for each of four age groups in Fig.45. The seasonal mode of mortality in the first year was in March, in the second year in April, in the third year in May and June and in subsequent years was spread over the period

Table 52

Shags flying south at Spurn Point or adjacent coast 1960-1965

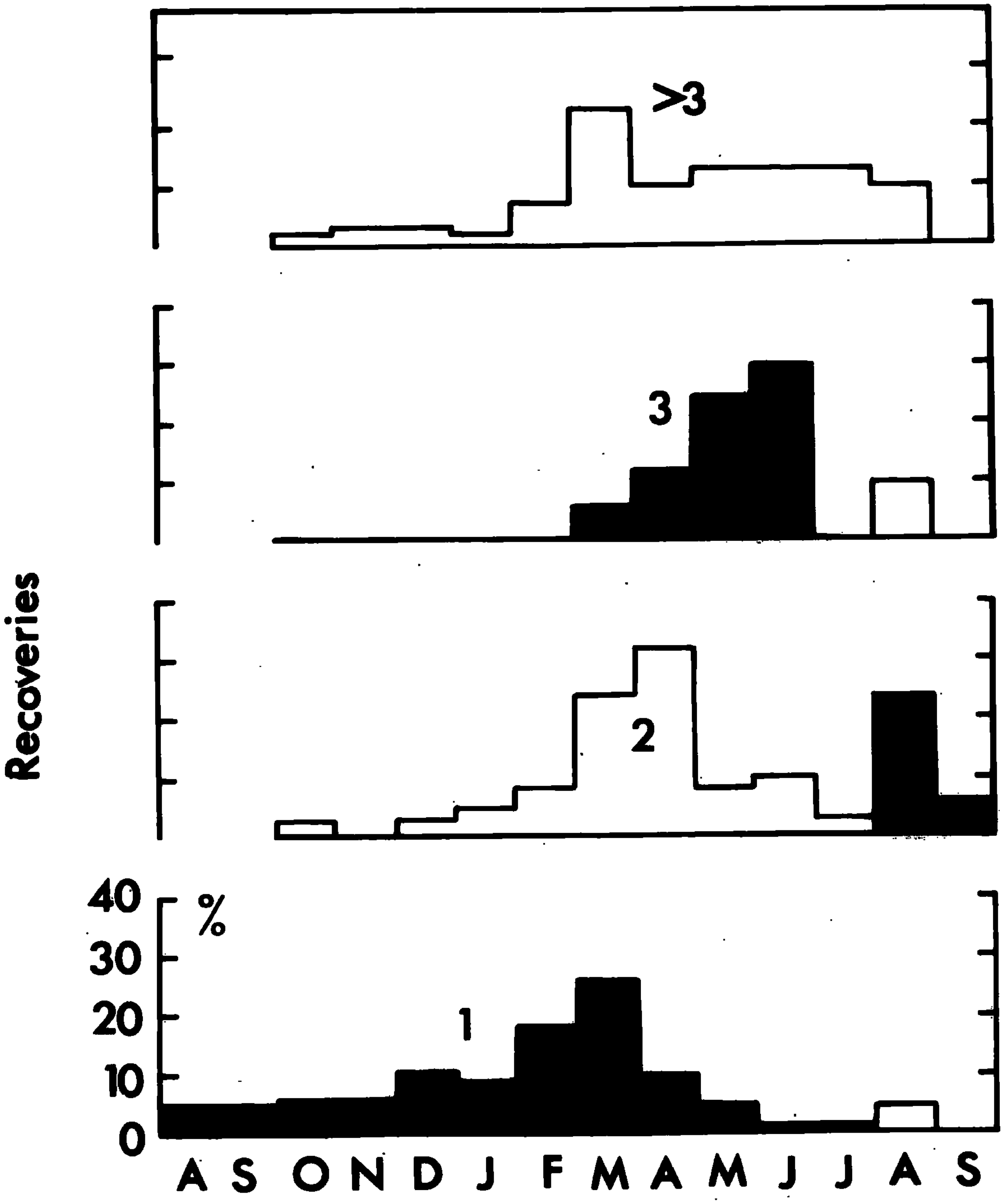
Date	Number of Shags flying south	Observer	Farne Recoveries south of Spurn in following month
29-10-60	30	J.Cudworth	7 (4% of ringed)
3- 3-62	83	J.Cudworth	)23 (8% " ")
11- 3-62	130	YNU(1962)	)
21-11-65	129	J.Cudworth	*22 (5% " ")

* a few more can be expected to come in at date of writing

Fig.45

SEASONAL VARIATION IN RECOVERY RATE WITH AGE

(1 : 1st Yr, 2 : 2nd Yr, 3 : 3rd Yr, >3 : over 3 Yrs.)
Within each year group the percentage recovery per month is calculated. The histograms from different year groups are placed together to indicate the overall periods of mortality.


>3
3
2
1
Recoveries
40
30
20
10
0
%
A S O N D J F M A M J J A S

February-August. It is thus evident that there is a gradual change through the first three years, followed by a return to the first year pattern. It is further evident that the 2nd and 3rd winter birds largely escape the peak period of mortality in the 1st year birds, this was especially notable in the 1965 'wreck'. This mortality is difficult to understand since it becomes later with age during the early years whereas the breeding schedules become advanced. The moult is unlikely to be responsible since the body moult occurs in autumn and in any case the timing of moult is not related to age (p 27).

Geographical distribution of the Farne Island Shags according to age

The distribution of recoveries shows clearly the dispersed nature of the first year population compared to that of birds of breeding age (Table 53). (The geographical distribution of first year and older Farne Island Shags is mapped in Coulson (1961)). There is no evidence of age specific movements after breeding age, or of a difference between the sexes. Certainly in October 1964 a sample of 142 colour ringed Shags was representative of the summer population. Among the birds of breeding age it seemed possible that the birds which included immigrants (*i.e.* ringed as 'adults') might show either a tendency to return to their natal area after breeding, or that they wander more because "their wandering tendency is stronger

Table 53

Recovery Range of Farne Shags

In 1st Year (221 recoveries)

Area

	a	b	'home'	c	d	e
Percentage recovered	14	19	14	9	9	35

Caught as Adults on Farnes(i.e. includes immigrants)

(51 recoveries)

Area

	a	b	'home'	c	d	e
Percentage recovered	2	18	55	23	2	0

Age > 1$\frac{3}{4}$ yrs. ringed as pulli on Farnes

(48 recoveries)

Area

	a	b	'home'	c	d	e
Percentage recovered	0	19	60	15	4	2

Area

a	north of Fife Ness
b	Fife Ness to Goswick
c	Craster - Tees
d	Tees - Spurn
e	Spurn and South
'home'	Goswick to Craster, including Farne Islands

than in their contemporaries which, presumably stay behind, near where they were hatched" (Richdale 1957). Unfortunately it is impossible to separate the birds which might have emigrated before breeding age from the others in the "ringed as pulli" sample. Though this cannot be done directly we can allow for such an effect by calculating the emigrating rate of birds reared on the Farnes.

Emigration and Immigration

The proportion of Farne bred birds which move to other colonies for first breeding cannot be calculated directly, since it would be impracticable to locate all (or a known proportion) of the emigrants on their new breeding grounds. However it is likely that emigration is occurring at the same rate from Shag populations which are increasing at the same rate. Assuming this, and further, assuming that the Flamborough-Forth breeding population is a closed or nearly closed one, at present, then the overall emigration rate from all the colonies in the Flamborough-Forth area will equal the emigration rate from the Farnes to these areas.

The 1961 and 1962 cohorts supplied 55 'non native' birds to the Farnes and 138 natives, as two year olds. These 138 natives represent $\frac{138}{490}$ or 0.28 of the number of 'native' pairs, since a total of 490 nests were recorded on the Farnes in 1961 and 1962. Given that 0.28 (or 678) of the 2420 'non native' pairs return to breed away from the Farnes then $\frac{55}{678 + 55}$ or 0.075 (=7.5 per cent) will have emigrated from the 'non native' pairs. Therefore it seems likely that the emigration rate (of potential recruits) from the Farnes is approximately 7.5 per cent. Four Shags from the 1961-1963 cohorts ringed on the Isle of May have bred on the Farnes. Since the Farnes represents one quarter of the Forth-Farnes population apart from the Isle of May, 4 x 4 or 16 may well have emigrated. Judging from experience on the Farnes 0.28 x 680 (number ringed on Isle of May) or 190 Shags would be expected to return to breed on the May. Thus $\frac{16}{16 + 190}$ or 7.8 per cent represents the proportion of potential recruits to the May, which emigrate to breed for the first time, a result supporting the original estimate of 7.5 per cent. If we then use an estimate of 8 per cent for the emigration rate from the Farnes, this would imply that 34 birds from the 1960-1963 cohorts emigrated. Of these supposed emigrants seven were located, a result which is quite satisfactory in view of the methods used.

Returning to Table 53, it can now be concluded that there is no major difference between the movement of immigrants (i.e. ringed as adults) and natives once they have become established for breeding purposes, since the small proportion of emigrants has negligible effect and, since there is no difference in the geographical distribution of breeding birds consisting entirely of 'natives': this conclusion is supported by a study of the mortality of the unringed recruits 1962-1965.

Observations on the Berwickshire coast in 1964 and 1965 and on the Isle of May in 1965 indicated that about 0.4 per cent of the breeding population there consisted of birds colour-ringed as adults on the Farnes. If this were true over the whole Flamborough-May coast then approximately ten colour-ringed Shags emigrated during the 1962-1965 period, of which 8 would be considered dead using method b(i), since only two were found breeding away from the Farnes. Three colour-ringed adults were found dead away from the Farnes suggesting that they were wandering through or breeding in new areas; further evidence that Ma of is underestimating survival. The emigration rate of the breeding adults is much less than that of the pulli prior to breeding age, since only $\frac{10}{941}$ (941 being the number of adult years of survival) or one per cent emigrated per year compared to 7.5 per cent of the pulli. This must be allowed for when assessing the mortality rate from the annual return of colour-ringed adults.

Mortality rate of the adults

(1) Jacksons' 'negative' mortality method

The first estimate of the annual adult mortality of the Shag was obtained by Coulson and White (1957) who adopted Jackson's negative (mortality) method as interpreted in the formulae of Bailey (1951,52). The 1956 adult recaptures yielded an estimate of 13 ± 9 per cent, the 1959 recaptures 22 per cent and 1962 recaptures 17.5 ± 6.5 per cent.

(2) Return of Colour-marked individuals

The principle method used during the study however is based on the sighting of colour-marked individuals using the formulae:-

$$M\underline{a} = \frac{b - M\underline{b} + c}{a - M\underline{s}} \ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\ldots\text{(i)}$$

where

$M\underline{a}$ = annual adult mortality rate
$\underline{a}$ = colour-marked birds in season $\underline{a}$
b = alive in season $\underline{a}$, seen season $\underline{b}$
$M\underline{s}$ = marked in $\underline{a}$ which died before 31 July $\underline{a}$
$M\underline{b}$ = seen in season $\underline{b}$ but known to die before 31 July $\underline{b}$
c = additions which were later (in season $\underline{c}$ or $\underline{d}$)

shown to have been alive, but un-recorded in season $\underline{b}$.

Since the methods changed slightly to try and eliminate $\underline{c}$ a constant is not used and $M\underline{a}$ 1964-1965 is probably subject to error in the order of not in excess of -2 per cent. Ignoring this last error and that caused by undetected emigration, $M\underline{a}$ for the period 31 July 1962 to 31 July 1965 is 14.8 ± 1.07 per cent, based on 1116 adult years.

Allowing for adult emigration, the best estimate of adult mortality rate is 14 per cent. The mark-recapture analysis of Shags captured in 1959 and 1962 but not 1956 indicate that this estimate is a little lower than the long term average (p195). This compares reasonably with Snows' estimate (re-calculated by this author) of 7 ± 4.82 per cent from only 28 adult years in view of the fact that she considered it an under-estimate, (Snow 1960).

Mortality of the Sexes

Over each period of risk it was noticed that the female mortality rate exceeded that of the male. The combined data for each season are presented in Fig.46. (The raw data are given in Table K, Append.). The difference between the male and female mortality rate is significant ($P < .02$) ; ($t = 4.12$), after Bessels' correction, 4 d.f.). It is this differential mortality which leads to a change in the sex ratio with age and after recruitment had ceased (see p 53).

Thus the male Shag has an annual mortality rate of 11.6, and the female 18.3 per cent (excluding emigration of breeding birds since this is small and is not sex specific). In comparison Kortlandt (1942) found that the mature male Cormorant had a mean annual mortality rate of 9 per cent whilst the mature female had a mortality of 11 per cent. Richdale (1957) also concluded that the female Yellow-eyed Penguin had a somewhat higher annual mortality rate than the males, that of the males being 13.7 per cent, that of the females being 15.3 per cent. Kluijver (1955) gives the mortality of male Great Tits as 50.0 per cent, that of the females as 54.5 per cent, (a significant difference) and Nice (1937) found that the percentage return of female Song Sparrows was generally less than that of the males. The differences described by Lack (1954) for various ducks and gallinaceous birds

Fig.46

[illegible]

[illegible]

([illegible])

ANNUAL ADULT MORTALITY RATE AS A SEX SPECIFIC VARIABLE

(Mortality from return of colour-marked birds)

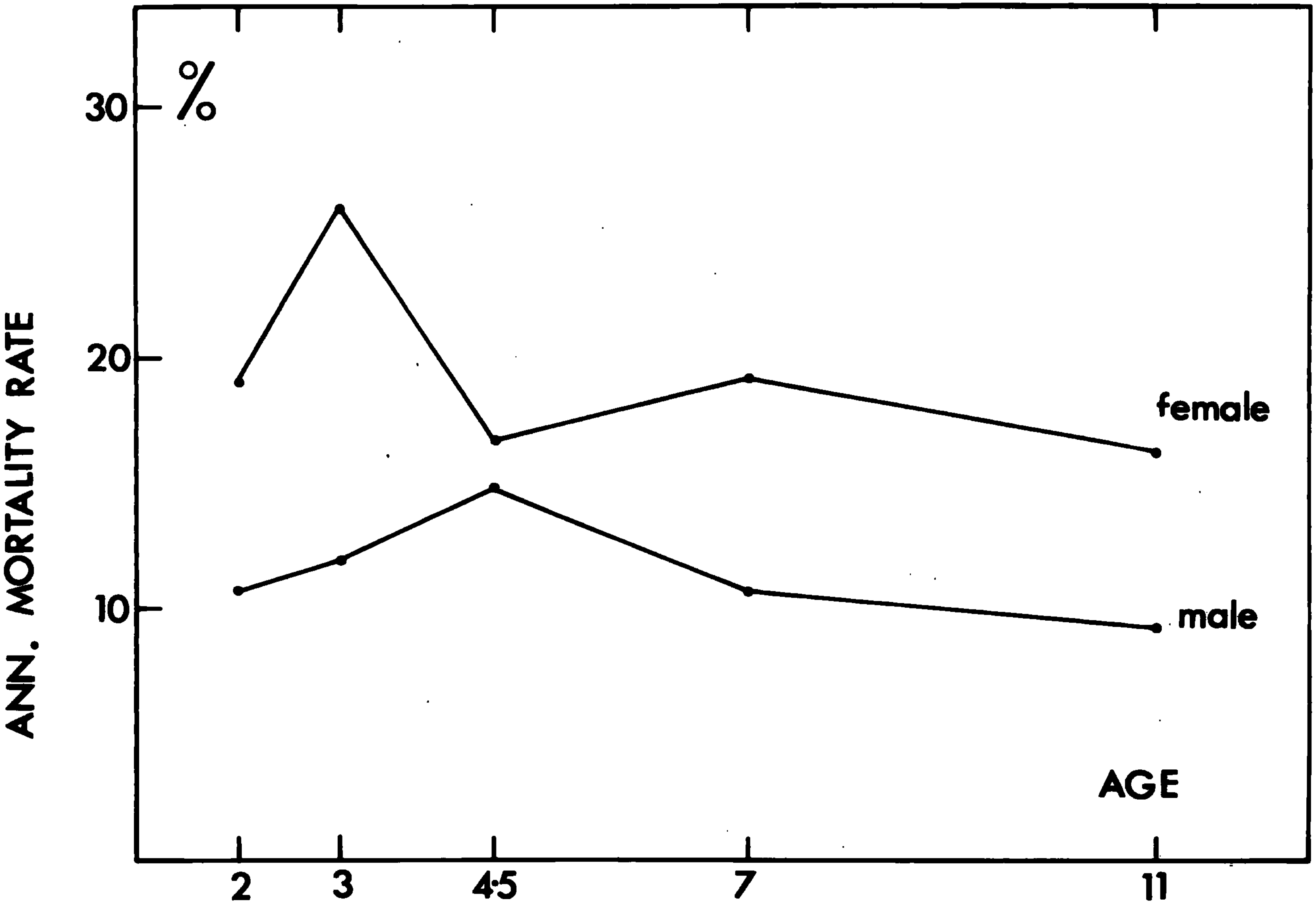

%
30
20
10
ANN. MORTALITY RATE
female
male
AGE
2
3
4·5
7
11

Table 54

Sex ratio of Shags found dead on Farnes 20 December 1965

Age	Total 'sexed'	♂	♀	♀/♂ Ratio
1st autumn	16	6	10	1.7
2nd autumn	11	5	6	1.2
3rd autumn	22	10	12	1.2
3rd autumn +	3	1	2	-
Totals	52	22	30	1.36

are more complicated since they involve possible shooting bias and the sexes have unequal risk during incubation. Since neither of these are involved in the Shag,Cormorant or Penguin other factors must also be involved. It is of interest to note that the differential involved (Fig.46) does not change appreciably with age in the breeding population. A sample of 52 dead Shags on the Farnes on 20 December 1965 (Table 54) however indicated that mortality in the early years may not be sex specific, since the sex-ratio of the samples were similar to those at recruitment age and in the nest,(Table 9).

Annual Variations in Adult Mortality

The annual mortality rate (Ma Formulae 6(i)) in 1962-1963 was 14.7 per cent, from 1963-1964 it was 15.9 per cent and from 1964-1965 it was 14.3 per cent. Whilst these differences are not significant there was a difference in the age specific mortality of 1963-1964 compared with the other two years, (Fig.47), (.01>P>.001); χ^2 homogeneity test with 4 d.f.). Mortality increased with age in 1963-1964, but decreased with age or remained steady in 1962-1963 and 1964-1965.

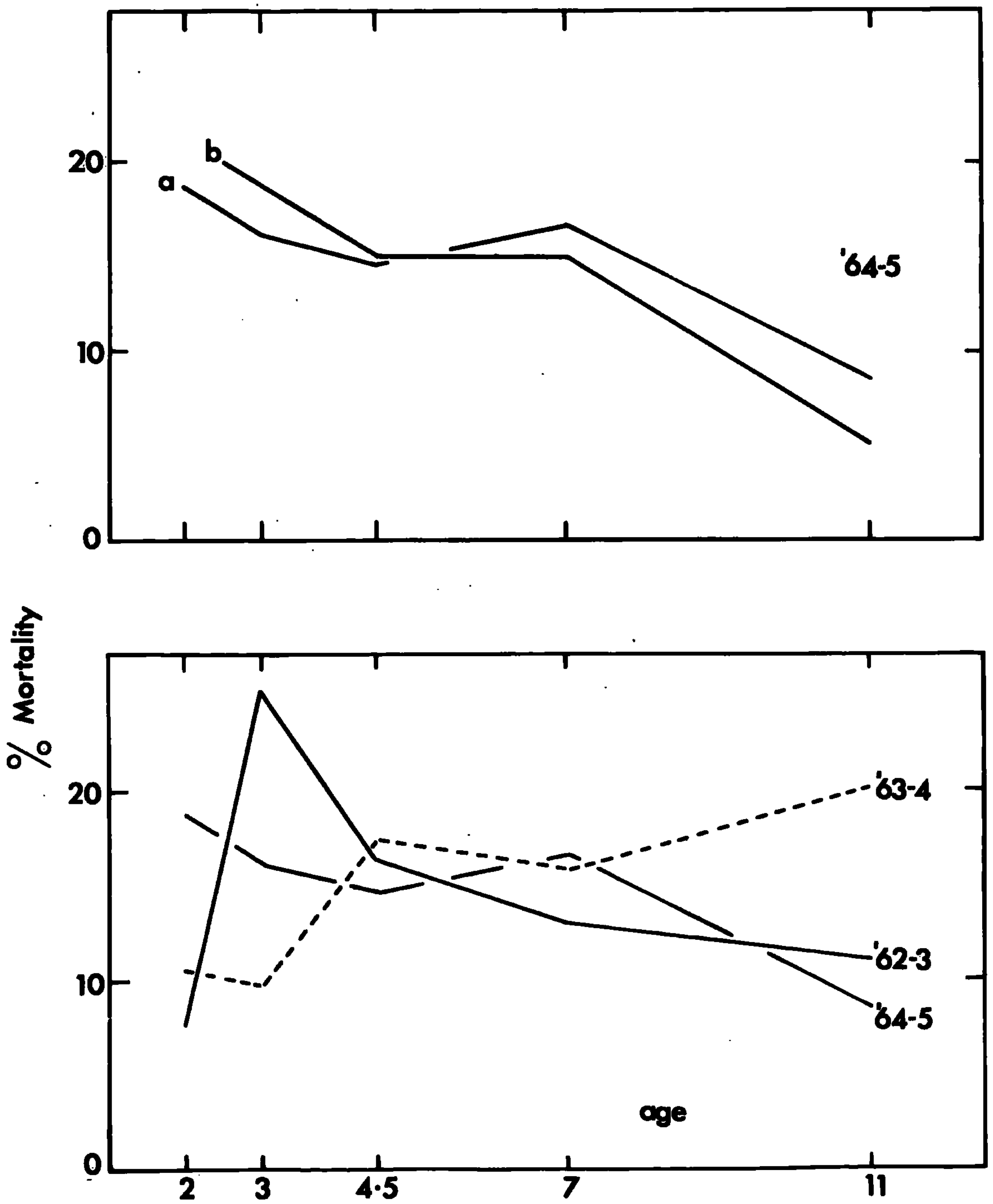
In March 1964 the old birds (many of which were nesting at that time) suffered a higher mortality than in the other years, whilst the younger breeding birds fared better. The last is a puzzling result since there was a minor wreck

Fig.47

AGE SPECIFIC MORTALITY OF BREEDING BIRDS AS AN ANNUAL VARIABLE

Top a 1964-1965 (1 August to 31 July)
b November 1964-1965 (31 July)

Lower - note that the mortality in 1963-1964 tended to increa with age - broken line, whereas it decreased with age in the other two years.


20
10
0
b
a
'64-5
% Mortality
20
10
0
'63-4
'62-3
'64-5
age
2
3
4·5
7
11

of first year birds in the Farnes-Forth area at that time. It thus appears that the youngest and oldest group at risk were involved, but that intermediate groups were not. Similarly in November-December 1965 there were recoveries of 1st year birds and birds of breeding age, but Shags in their second winter and of Farne origin were not recovered. It is especially difficult to understand these mortality patterns since the cause of death is not known, except for a small proportion of the dead birds which are recovered and these represent a negligible proportion of total mortality in adults.

There is no significant difference between the estimate M_a prior to 1962 (by mark-recapture) and since 1962, though there is a suggestion that the mean values are higher (p196). Thus in three years 1962-1965 when the first year mortality was very low, the adult mortality was little different from average, and over a period in which there were seven out of ten years of high first year mortality. Whilst it is very likely that adult mortality will not remain unaltered in wreck years, the breeding adults do not have marked annual variations of mortality rate.

Annual mortality rate in the first year

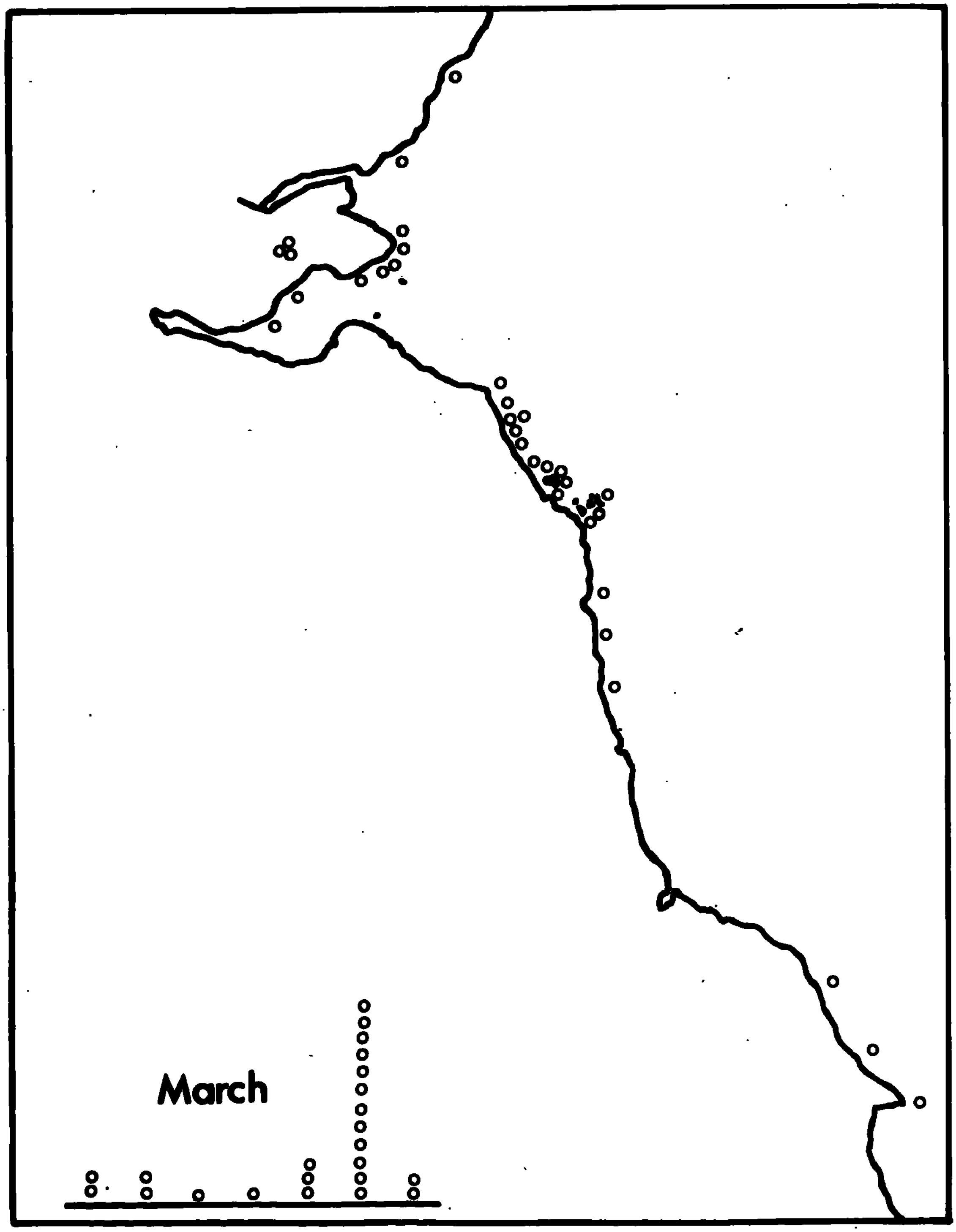
It has been pointed out that one in eight of dead ringed adults were recovered (i.e. found and reported), at least in the period 1962-1965. If this applied to first

Fig.48

RECOVERIES OF SHAGS IN THEIR FIRST YEAR IN MARCH 1964

The lower diagram gives the recoveries per 5 day period (to 4 April) showing that most of the mortality was at the end of March. Several Shags were found dead on Loch Leven.

Forth-Farnes recoveries except Foula (1) and
Faraid Head (1).


March

year Shags the mortality in some years would be estimated as high as 168 per cent.

A characteristic of a year of high first year mortality (Mf) is that the Shags move from predominantly rocky coasts to areas, where the chance of a dead Shag being recovered is higher, thus exaggerating the difference in mortality rate judging from the recoveries alone. After the first year however the chance of a dead Shag being recovered probably does not change much since the areas occupied are similar (Coulson 1961, this study) and the proximate causes of death probably do not change so far that they might affect the recovery rate of dead birds, markedly. This being the case the mortality rate of first year Shags has been calculated from the recoveries, assuming that mortality in the second and third year is equal.

The birds at risk to mortality in their third year can be classified as follows:-

(1) 75 colour ringed birds, mostly males, good breeding performance at age of 2 and average Ma 12 per cent.

(2) 49 B.T.O. ringed birds, mostly females, poor breeding performance or non-nesting and average Ma 43 per cent.

Since colour-ringed birds are easier to identify than B.T.O. ringed birds Ma (2) is known to be an overestimate, but the methods of observation changed so that a correction factor for birds missed in 1965 but which will be seen in 1966 cannot be used. Bearing this in mind, and considering that groups (1) and (2) each represent about half their year class in their third year, and interpolating graphically from Fig.46 an approximate third year mortality rate of 22 per cent appears reasonable. If this is true the third year birds survive less well than fully mature breeding birds. This seems especially likely in 1962-1963 and 1964-1965 when mortality decreased gradually with age, even among the breeding birds. The last conclusion was also reached by Kortlandt (1942) who found that the second and third year Cormorants survived less well than adults (p24). Similarly, the mortality rate of the Heron decreases steadily with age (Olsson 1958). Richdale (1957) estimated mortality rate of the immature Yellow-eyed Penguin from the returned juveniles and concluded that there was no change in survival rate once the birds are 'mature'. In this case 'maturity' was reached at the age 14-18 months, or when the fledged chicks returned. Richdale found it virtually impossible to allow for dispersal of some of these juveniles. Austin and Austin (1956) concluded from the scarcity of recoveries that the second and third year mortality was "probably considerably lower" than that of the breeding population. There was insufficient evidence for the latter conclusion but they considered that the Common Tern is more vulnerable to its enemies while nesting, which might well account for such an effect.

A total fo 301 pulli were ringed in 1961, of which 16 per cent were recovered in their first year. At least 44 males have survived to the third year from this cohort, implying a survival rate to the third year of 44 + 44 x sex ratio (assumed to be 1.35), or 103 Shags. Assuming that M_2, second year of 0.22 then 0.78 would represent the 103 Shags. Thus 132 survived the first year ($\frac{100}{78}$ x 103) and the mortality rate in the first year was not more than $\frac{301-132}{301}$ or 0.56, and the recovery rate of dead ringed birds was $\frac{56}{16}$ or 1 in 3.5.

A total of 297 pulli were ringed in 1962 and 5 per cent were recovered in their first year. Assuming that the proportion of surviving males which breed for the first time in the third year (in this case 1966) is the same as that for the 1961 cohort then at least 70 males and a total of 165 Shags survived to the third year and 211 survived the first year. The mortality in the first year of the 1962 cohort was thus $\frac{297 - 211}{297}$ or 0.29, with a recovery rate of dead ringed birds of $\frac{29}{5}$ or 1 in 5.8.

Since the mean 1961 + 1962 recovery rate (10.5 per cent) was the same as that over the period 1951-1963 then a dead recovery rate of 1 in 4.6 can be assumed. In order to calculate the average first year mortality rate for the Forth-Farnes population it is possible to use the recoveries as indicators of survival by correcting the first and second year (= adult) recoveries for their dead recovery rates. The number of recoveries in the first year is 312 and in the second 52, the corrected figures being 1,435 and 416 respectively. The 416 recoveries thus represent .22 of the second year population which becomes ($\frac{100}{22}$ x 416) 1,891, and the first year population becomes 1,891 + (the recoveries) 1,435 = 3,326, of which $\frac{1,435}{3,326}$ x $\frac{100}{1}$ = 43 per cent die in their first year, compared with 57 per cent using the uncorrected recoveries or 47 per cent using uncorrected recoveries and assuming that the second year mortality was the same as that of the breeding adults 1962-1965 (as did Coulson and White 1959 for the Kittiwake).

Since the number of survivors from the 1961 and 1962 cohorts are known to be underestimates the estimate of 43 per cent may well be overestimated, though the recovery rate of dead ringed adults may vary more than is at present realised, and compensate.

Geographical variation in first year mortality rate

Using a second year mortality of 17 per cent and not-correcting the recoveries for dead recovery rate(since this may vary with dispersal habits and geographically in many ways), Fig.49 clearly shows that the first year mortality rate varies according to the time of peak mortality in various regions. Thus the annual yearling mortality rate is higher if the main period of mortality occurs at an earlier age. This is plausible on the grounds that a month fledged Shag might be expected to be more susceptible to 'stress' than an eight month old. It seems possible that the early peak of mortality may also be supplemented by

Fig. 49

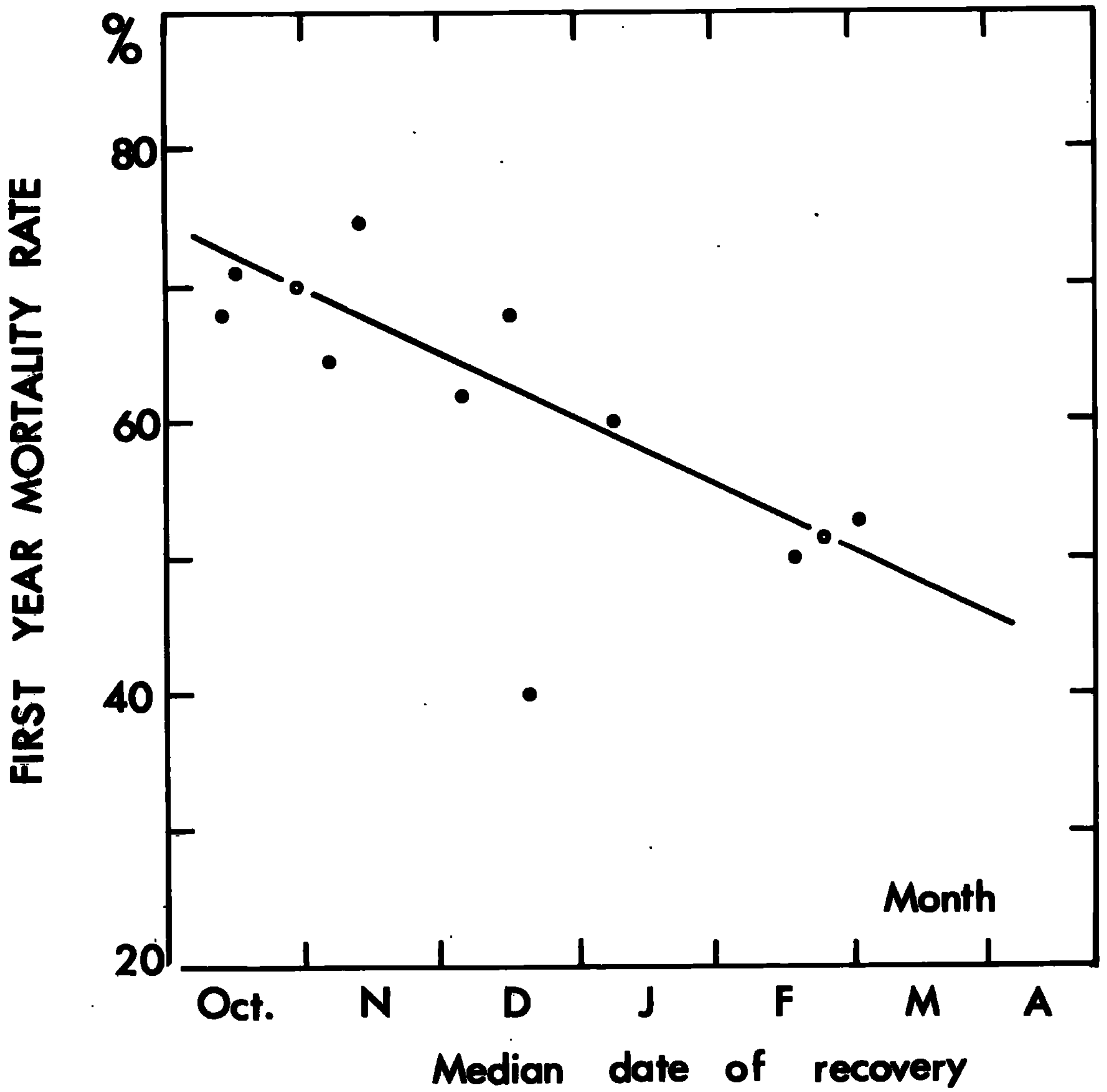
[illegible]

[illegible]

([illegible])

FIRST YEAR MORTALITY RATE AND MEDIAN DATE OF RECOVERY

(Raw data in Appendix J)


%
80
60
40
20
FIRST YEAR MORTALITY RATE
Month
Oct.
N
D
J
F
M
A
Median date of recovery

difficulties arising when the parent-fledged chick bond is broken (see p.163). However on Lundy the peak of mortality occurred well after the chicks had become independent.

Causes of high first year mortality

One of the most interesting aspects of the present mortality study is that the first year mortality is so high and that this is due to the effects of certain 'poor years'.

During the 14 years 1951-1965 the first year birds moved out of its normal winter quarters in eight, and at the same time suffered high mortality. In 1953,1957,1961 and 1965 the cohorts 'wrecked' and about a quarter of the birds came inland.

Periods of high mortality and unusual movements have frequently been reported in maritime *Phalacrocorax spp*. For example Stejneger (in Bent 1922) reports that during the winter of 1876-1877 "thousands and thousands" of *P. pelagicus* were destroyed by an "apparently epidemic disease, masses of dead birds covered the beach". Cobb (in Murphy 1936) found that *P. magellanicus* and *P. albiventer* are found dead or dying along Falkland beaches - "all suggestive of the pandemic type of disease which periodically affects other sorts of colonial cormorants".

Robinson (1913) describes the great *P. aristotelis* wrecks of 1893-1894 when thousands died apparently of starvation in northern Scotland "lost all fear and entered cow byres (where some were eaten alive by rats)". Shed floors near high water mark were strewn with dead. The Shag wreck of 1912-1913 was noted from Lewis (Clyne 1915) Orkney (Robinson 1913) and birds occurred inland throughout the north midlands (Chislett 1954) (Coward 1918) and, judging from various museum collections, over much of SE England. Russell (1913) describes how some of the Shags resorted to eating dead fish when "the sillocks moved to deep water in what Tulloch (1913) considered "an awful succession of gales". The fact that gales are not directly associated with these wrecks was noticed during the 1936-1937 wreck which occurred after the gale had subsided and whilst the sea was calm,(Anon 1937). Subsequent experience show that the more spectacular wrecks do not occur _during_ gales; the effect of gales or other peculiar meteorological conditions is thus probably _via_ some effect such as abundance or distribution of food.

The population of _P. bougainvillii_ has recently been estimated at 20 million (Jordan _in litt_). The wreck or 'peste' of 1957-1958 however resulted in the death of 60 per cent of the total population. The rate of increase was remarkable and during the period 1960-1961 and 1961-1962 increased by 45 per cent. (Jordan 1963 extended _in litt_). Dispersal, measured by the proportion of recoveries from

Chile is a characteristic feature of periods of high mortality, even though the proportion recovered is less than 0.4 per cent (Jordan and Cabrera 1960). The cause of these movements is not understood but is due to "condiciones hidrobiologicas adversas" (Jordan <u>in</u> <u>litt</u>), of which the chief is the distribution of the fish or anchovetas which is dependent on the vigour of the Humboldt (Hutchinson 1950).

The causes of these movements and mortalities in <u>P. aristotelis</u> are not understood, but in 1965, 10 Shags were sent for post mortem. The ten were generally (in some cases extremely) underweight, but in most if not all, disease could be ruled out as a proximate cause of death. Since diseases frequently act in an age specific manner and since Shags are known to carry, at times, pandemic disease organisms (Blaxland 1951), this seemed a possible cause.

In September and October 1965 several Shags were seen far south of their usual position, (there was no wrecks of west coast birds), in Suffolk (<u>Birds</u> Jan. 1966). At the same time the build up of Scottish first autumn Shags was considerably less than in 1963 or 1964, despite a higher production of young. At the end of a series of heavy seas and rainy weather a wreck and extra dispersal of first autumn Shags occurred, lasting at least three weeks, and continuing during spells of westerly or calm weather. Meanwhile numbers of Shags on the Farnes was similar to 1963 and 1964, despite the fact that a considerable proportion of the breeding adults and virtually all the non breeding immatures had dispersed. The fact that weather could be causing the wrecks can be ruled out since this does not explain the geographical variation in the timing of wrecks, or the more prolonged periods of mortality *i.e.* 1957-1958 and 1959-1960, and since the dispersed birds are not driven by gales. Shortage of food (accentuated by severe weather in some cases) seems to be a likely cause, but it implies that the older birds are able to catch sufficient food, whilst their younger company are starving.

In fact the association of mortality and eruptive dispersal in birds has chiefly been described in relation to abundance of food. Sauter (1956) discusses her study of Barn Owl recoveries, using two useful concepts. First is the *Sterbejahr* in which a "mortality burst" (following terminology of Honer (1963)) occurred. Second is the *Wanderjahr* in which owls spread out over the country. Sauter and Honer concluded that the *Wanderjahr* followed a combination of high density of the owls and a falling density of the micro-rodent population, and that a *Wanderjahr* generally resulted in a *Sterbejahr*. In other species *Wanderjahr* have been related to the abundance of lemmings on the tundra, or of seeds in the taiga (Refs. in Lack 1954), but there are no comparable data for cool temperature sea-birds. Nevertheless Sergeant (1952) concluded that gales were not the ultimate cause of Little Auk wrecks in Britain for the birds must have been unusually south of their normal range in the first instance. In future, it would be preferable to attack the problem of sea-bird wrecks from the marine biological or pathological angles rather than the meteorological. In general, simultaneous _Wanderjahr_ and _Sterbejahr_, such as shown by the Forth-Farne Shags, vary according to the relative abundance of some resource. Since the incidence of neither of these has changed during the Forth-Farnes population 'explosion' a simple resource - mortality relationship is probably involved.

Balance of Recruitment and Losses of the nesting Farnes population

The mean annual production of 100 pairs would be 116 young. Of these 57 per cent or 66 would survive the first year and 51 the second. Of the 51 entering the third year, 47 per cent or 24 could be expected to nest, judging from the 1961 and 1962 cohorts. Of the remaining 27, those surviving, 78 per cent = 19), a further year will acount for virtually all further recruitment. Thus, (24 + 19) the recruitment totals 43. These estimates must be regarded as tentative since recruitment varies from year to year and since there is no independent estimate of second year mortality.

The mortality of the 100 pairs would be 15 per cent or a loss of 30 birds. The surplus of 13 birds might be expected to balance the native rate of increase of 5 per cent or 10 birds plus the emigration of potential recruits. The 43 recruits would represent 92 per cent of the total recruits since 8 per cent emigrate. Eight per cent of the potential recruits is 4, and the total losses are 30 + 10 + 4 or 44 birds. The balance of losses (44) and recruitment (43) supports the use of the above parameters.

The age specific mortality rates of the Shag and Cormorant (from Kortlandt 1942) are compared in Table 55, and this indicates a similar pattern in the two species.

Table 55

Age, mortality rates and expectation of further life in Cormorant(1) and Shag

Year of risk	Cormorant*	Expectation of life(yrs)	Shag	Expectation of life(yrs)
1	.36	2.3	.43	1.8
2	.22	4.0	.22	4.0
3	.16	5.7	.22	4.0
4	.10)		.19	4.8
5	.10)		} .16	5.7
6	")		}	
7	")		}	
8	")		} .15	6.2
9	")	9.5	}	
10	")		)	
11	")		)	
12	")		) .13	7.2
13	")		)	
14	")		)	
15	")		)	

(1) Kortlandt (1942)

* $\frac{2 - m}{2m} = \frac{2 - Ma}{2\ Ma}$

(2) at beginning of year of risk

DISCUSSION

Few would disagree with Nicholson's (1958) belief that the most contentious issue in animal ecology at the present time is whether animal populations are self-regulating or not. It has been widely stated that there are two schools of thought on the issue; those believing that only density dependent factors can control populations form one school, whilst the other regards density dependent factors as unimportant or non-existent. Nicholson himself (1933 et seq) is the chief proponent of the former view, whereas Andrewartha and Birch (1954) develop the second. Andrewartha and Birch (loc cit) consider that shortage of material resources (food,nest sites etc.) were least important and shortage of time in which to increase between one catastrophe and another, most important, of possible control mechanisms. Much of the rift between the schools is semantic, however, since the disturbing effects of limiting factors such as weather and the compensatory effects of density dependent mortality have both been considered controlling factors (Varley 1963). Almost all work concerning the above theories had been carried out on insects and the emphasis was consequently on the model or field population as a whole rather than on individuals, which in higher animals, clearly differ according to behaviour,territory size and other factors. Some authors (Howard 1920 Christian 1950) did consider these behavioural aspects, but it was not until the work of Wynne-Edwards (1962) that the importance of behaviour in the ecological approach to population regulation was fully appreciated.

Another consideration in colonial animals is that two kinds of regulation can be expected, one governing colony size, the other the population of some larger geographical area. For practical purposes the last is by definition, a limited area, rather than the entire range of the species, though it must be pointed out that this difference in species with wholly contiguous range, is one of time scale.

The method of growth of the Farne Islands Shag colony is one of its most interesting features. In those areas in which the increase has ceased, the recruits, other than those replacing mortality of the breeding birds are dispersed and this situation prevails throughout the Forth-Farnes area. In view of the fact that the recruits are so efficiently dispersed as to maintain a steady overall rate of increase, the entire Forth-Farnes area can be considered as one, certainly from the standpoint of the dispersed recruits. Thus any discussion of intrinsic control mechanisms, such as envisaged at the start of this study, must involve the adjacent breeding areas.

During autumn and winter the first year Shags from colonies on the eastern seaboard of Britain are so mixed with respect to their natal colonies, that they can be regarded as one population so far as risk to possible density dependent mortality factors is concerned. The 'wrecks' of this first year population would appear equivalent to the 'eruptions' described for many species by (Lack 1954), in which case they could be density governing movements. These first year 'eruptions' are preceded by local build up in numbers, involve young individuals, are associated with high mortality and are spasmodic. There is considerable evidence that there has been no change in the extent of first year mortality during the growth of the Forth-Farnes Shag population, and it is therefore, unlikely that this is a controlling factor, or that it has not been (so far) induced as such.

Even if the first year mortality was to become density dependent it would imply competition between first year Shags from widely separated breeding areas, in 'neutral' territory. The mortality could not therefore be a governing factor regulating colony size since it would remove a similar proportion of birds from a large colony as from a small one and would be independent of local conditions. However in conjunction with some factor that governed relative colony size, the first year mortality could become a mechanism for determining the population over a wide area. In this case the 'wrecks' would be a mechanism for excluding surplus birds and the mechanism has been suggested to operate in the guanay (P. bougainvillei) on the islands off the Peruvian coast. There the guanay populations are regarded by Hutchinson (1950) as self regulating, according to food supply. Maritime Shags are unusual among sea birds in that they have 'wettable' plumage and must roost on land, preferably in sheltered areas with no predation. They are therefore more limited in their feeding areas and the arguments used by Ashmole (1963b) against density dependent mortality outside the breeding season may not apply. Ashmole considered it unlikely that oceanic birds could deplete their available food supply sufficiently to give rise to competition for food, because the areas searched were so extensive, and the total amount of food so great. Though competition for food is eventually likely to occur on the east coast given a continued increase, the Shag population will undoubtedly be subject to or controlled by other environmental pressures.

It is not known whether emigration is determined more by conditions in the natal colony, than by the relative attractiveness of areas visited in the first winter, but it is likely that both kinds of dispersal occur. For example several Scottish immigrants to the Farnes were known to start frequenting their breeding islands on the

Farnes at the end of the first year. On the other hand dispersal from the natal colony (*i.e.* where the bird was hatched) is increasing as a function of the population size, presumably reflecting the increasing difficulty of obtaining a nest site. This second kind of dispersion involves a return to the natal areas, before emigration and this is known to occur in the Shag. Consideration of both kinds of dispersal led Mayr (1963) to conclude "The opposing tendencies for sedentariness and its converse condition, a flow of individuals from population to population have an optimum balance " and "The advantage of a proper balance seems to be for the population as a whole, rather than for the individual".

An individual Shag which cannot find a suitable nest site has two alternatives. It can stay and defer breeding until the following season, or it can move on where it may be successful later in the same season or where its difficulties may increase. Natural Selection will tend to balance these opposing tendencies in the population so that the emigrants and deferred breeders will on average, have similar success and raise a similar number of progeny. The factors which inhibit nesting are not known , but they must be very sensitive since dispersion of potential recruits was increasing long before the Farnes could be regarded as saturated with Shags, and this last condition is still some way ahead.

The pool of potential recruits must vary considerably from year to year, reflecting to some extent the variable first year mortality, and yet there is no evidence that this is reflected in the overall rate of increase. Allowing for mortality, the variable proportion of Shags which breed on the Farnes at the age of two, from one season to the next, indicates that in some years at least, breeding is inhibited. These inhibited individuals form what Wynne-Edwards (1962) would call a "reserve which can be mobilised and brought into action whenever greater reproductive output is called for". On the other hand, Ashmole (1963b) considers it unlikely that such a surplus occurs, "but if it did it need not be interpreted as evidence for a self-regulatory capacity in the population; in many species individuals breeding at the edge of the colony are more exposed to predation than those at the centre, so that in some populations individuals which missed a breeding season rather than breed on the edge might not be eliminated by selection". Ashmole does not explain why birds which missed one season will not still breed on the edge in the second attempt nor does he consider that such attempts are unlikely to be completely unsuccessful. Any attempt to nest which might be successful will always be a selective advantage unless there are compensating factors.

A useful hypothesis at this stage is that the population is controlling its recruitment, but to see how this could be brought about involves consideration of the breeding population.

The old breeding Shags return to the nest site earliest in the season, the earlier the male returns the better the site, the earlier the onset of laying and the greater the number of progeny. Since old stable pairs nest first, and since the older stable pairs produce the most young, they represent the birds at the top of the breeding hierarchy. Since the concept of dominance, essential to the understanding of hierarchial organisation is often "rather loosely applied" (Armstrong 1947) it is here defined as:-

A dominant individual has priority in site selection over a subordinate individual. Individuals are ranked according to dominance and form the hierarchy.

On its breeding grounds the Shag is a very aggressive bird, the only notable exception being that females do not challenge females away from the nest. The general aggressiveness overflows into sexual dominance so that any female is attacked as soon as she approaches a soliciting or advertising male and is driven off, unless she gives the correct appeasement signal (facing away). The aggressive behaviour in the Shag (described by Snow, 1963) is typical of the Pelicaniformes in which the 'signal' behaviour is highly ritualised and conspicuous (van Tets 1965). Nelson (1963b) did not support his contention that Shags "do not have overt aggressive behaviour in any way comparable to the Gannet" and it is quite incorrect. Nelson (loc. cit) may have been thinking of the low level of overt aggressive behaviour relating solely to typical nest site establishment. Shags nesting in flat areas such as those used by the Gannets in Nelson's study area are so aggressive, having to defend 360° around their nests, that a regular dispersed nesting pattern such as shown by non cliff nesting Pelicaniformes seems to this author impossible.

In both Shag and Gannet however the prolonged period of site establishment reduces the opportunity for overt aggression between birds competing for sites. This conclusion, reached in a general way by Howard (1920) is analagous to that of Lorenz (1952) who describes reduced aggression in the Jackdaw social hierarchy in which status is determined by aggression between birds of adjacent rank.

Nelson (1963b,1964b) argues that the present aggressive tendencies of the Gannet are a "response to the "heavy selective premuim placed on the establishment of a suitable site "and subsequently (1965) points out that this heavy selective pressure could be explained if there was" a strictly limited number of sites suitable in all respects". Though Nelson makes no attempt to support this hypothesis, in his studies on the Bass Rock Gannets, it is abundantly clear that the probability of rearing young varies greatly from site to site occupied by the Shags on the Farne Islands, and indeed, elsewhere.

The hierarchial organisation ensures that the individual Shags most likely to rear the maximum number of young are least likely to have their attempt thwarted by non predictable effects such as storms which will affect the breeding performance, on poor sites. The period of site selection in Shag and Gannet is spread over about seven months, but the laying period is mainly concentrated into about six weeks so that any benefit derived from the spread of laying or feeding young is far less important than that relating to the prolonged nature of site establishment itself. A more striking example of this is to be found in the Short-tailed Shearwater, in which laying is spread over about two weeks, but time of return to the colony of non-layers is spread over four months (Serventy 1957). Thus the hierarchial organisation allows the breeding birds the benefit of group organisation.

The question of how the hierarchy is maintained by Natural Selection needs consideration. A selective advantage is required to explain the later nesting by the younger birds. This is unlikely to be connected with the social habit since the Starling (Kluijver 1933, Kessel 1957), Song Sparrow (Nice 1937), Redstart (Ruiter 1941), White Stork (in Europe)(Hornberger 1943, Haverschmidt 1949), Blackbird (Snow 1958) and Great Tit (Kluijver 1951, Perrins 1965), which are non colonial, also have age determined breeding schedules. However the colonial habit may well modify the hierarchy since, in the Kittiwake the time of return to the colonies is related to the density of the colony (Coulson and White 1960). The return is earlier at colonies of high density and therefore earlier where sites may be harder to find and where aggression towards new arrivals may be more intense.

The earlier a Shag occupies the nest site the better will be the chance of success, in so far as the site affects the breeding success. Since there is variability in the time of occupation of site, the early two year olds might be expected to give rise to more progeny and be selected, but the logical extension of this is that site selection would occur at the same time. As Lack (1954) points out, such early breeding young birds would not be able to "avoid conflicts in which the previous owner would probably be successful". Thus still earlier breeding of the two year olds is likely to lead to social disadvantages for the early individual which will compensate the later breeders.

The late breeding of the two year olds is merely an extension of a wider issue, the deferred maturity and non-breeding of all yearlings and some older Shags. The age of first breeding is one of the most important parameters in population dynamics. Its variations can have considerable effect on the number of progeny reared per individual life especially where the breeding life is short, where the animals breed once each year, and where the mortality rate of the progeny is low. Unfortunately Cole (1954) and Capildeo and Haldane (1954), make various a priori assumptions in their mathematical models designed to predict the change in biotic potential with change in age of first breeding. The assumptions do not allow for individual variability in age of first breeding (Cole 1954), age specific production of young, age specific mortality in breeding life,disturbed sex ratio, any interaction between age of first breeding and expectation of life of adults or social factors.

It has been shown that potential recruits are at the bottom of the breeding hierarchy and that at least in some years they cannot find a site suitable for breeding. This combined with a tendency for recruits to nest near other Shags, probably explains why recruitment can be controlled even while the population is increasing and when one would mormally expect recruitment to be un-restrained

The position in the hierarchy is thus partly due to social rank and therefore to social competition. As Wynne-Edwards points out "in so far as the length of adolescence is variable and governed by social competition it must automatically also be density dependent". If this were true then the period of adolescence should lengthen as the number of Shags reaches its population asymptote. In this connection it is interesting to recall that two year olds do not breed on Lundy where the population is now stable. Though on Lundy it is difficult to imagine a shortage of nest sites in the in the strict sense and other factors may well be involved. Nevertheless breeding Shags in immature plumage are at least unusual outside the Forth-Farnes area.

At this stage it must be stressed that the kind of hierarchial organisation occurring in the Shag is fundamentally different from that postulated for many animals by Wynne-Edwards (1962). Wynne-Edwards would presumably regard the nest sites on the Farnes as conventional trophies, but this study has shown that the trophies are highly functional. There is no conflict with Natural Selection and no suggestion of the selection of altruistic individuals, thus the objections on these grounds to Wynne-Edwards' theories (e.g. Maynard Smith 1964) do not apply. A corollary of this is that the total numbers will in general be adapted to the limiting factors directly, and not reduced or held low by artificial competition. As Nicholson (1957) points out the regulating factor is the inimical environment, not the population itself. Dispersal, deferred breeding and reduced output associated with an increase in numbers are induced by the population but the causes are the inimical elements.

A major problem raised by this study is the timing of breeding in individuals. In general it has been shown that it is apparently an advantage to breed early within the overall parameters of the breeding season, but with the exception of the preceeding discussion there has been no satisfactory explanation of the selective advantage in late breeding of young individuals. Perrins' (1965) argument rests on the suggestion that the Great Tit and presumably the Manx Shearwater (Perrins 1966) does not inherit a tendency to breed early or late, but merely a tendency to breed as early as they can. However there is considerable variation in the timing of breeding within the young birds and the early breeding young birds must be less hindered by their physical or physiological apparatus than their fellows. Since the early breeding young birds will have a higher number of progeny then Perrins (1965) implies that these progeny do not have any of the exceptional qualities of their parents and that the progeny will breed on average no earlier than progeny from 'normal' parents. An alternative explanation is that, in the absence of a super abundant supply of dry, ample, protected and natural nesting sites in the Great Tit (since numbers rose when nest boxes were provided, (Kluijver 1951, Perrins 1965) and Manx Shearwater (Harris 1965) then there will surely be intra specific competition for nesting sites such as Kessel (1957) describes in the Starling and thus an advantage is hierarchial organisation in the way that this study suggests for the Shag.

Clearly there is a great need for more research into the inherited nature of time of breeding, socio-economic factors determining status, and the relationship between status and fecundity, especially among the newly recruited members of these populations. As Nice (1937) concludes, "We need a great body of facts intelligently and conscientiously collected before we can safely launch into elaborate theories".

SUMMARY

SECTION ONE (Methods)

1. The main study area was the Farne Islands,Northumberland and the main study period was 1962-1965.

2. A total of 3730 Shags were ringed on the Farne Islands in the period 1947-1965; Ni-O-Nel rings introduced in 1964 probably have a useful life similar to that of a Shag, but rings used in earlier years did not.

3. Colour-ringing started in 1961 and 667 Shags were marked in this way, since it offered the most efficient method of identifying individuals in the field.

4. The sexes could be separated according to bill depth, behaviour,appearance,call,weight and sex of mate. Each of the colour-marked Shags were of known sex.

5. These methods were confirmed by dissection of dead Shags and examination of museum material.

6. A tentative method of calculating the sex ratio of the chick beyond the 33rd day, based on bill depth and weight, is used.

7. The moult of the ventral plumage is described. On year old and two year old Shags can easily be 'aged' by this character. The juvenal plumage is light brown, the post juvenal is dark brown and the nuptial or adult plumage is dark green.

8. The Primary moult is described. This is not a useful method of 'ageing' since only 20 per cent retain juvenal or post juvenal outer primaries in their third and fourth years.

9. Half the newly captured adults in 1964, did not carry rings; this proportion has decreased with increasing ringing effort.

10. Methods of estimating the age of the proportion of these un-ringed adults which are older than 2 years are described, using the year of capture.

11. The shape index of the egg tends to increase with age, (the eggs become broader), and this was found to support the use of year of capture as a measure of ageing the females.

12. These methods were confirmed by comparing data from adults 'aged' by year of capture with information from Shags of known age.

13. The following age categories were used
1 Yr :2 Yrs: 3 Yrs: 4.5 Yrs(4 or 5 Yrs): 7 Yrs(6-8 Yrs): 11 Yrs(> 8 Yrs).

SECTION TWO

(History and Growth of Population)

14. The growth of the Farne Island Shag population from one pair in 1931 to 367 pairs ih 1965 is described. The rate of increase is about 12 per cent per annum at present, but the native rate of increase (*i.e*. increase supported by the Farnes population) is 5 per cent.

15. The remainder of the rate of increase is made up by immigration from the other colonies in the Forth-Flamborogh area.

16. Ninety per cent of the recruitment from each cohort nested on their island of hatching when there were 100 pairs on the Farnes, but only 37 per cent when there were 367 pairs. The relationship between this kind of dispersal and the size of the population is linear.

17. The growth of the adjacent Shag populations, *i.e*. on the coast between the Moray Firth and Flamborough Head is described, and found to have been at the rate of 10 per cent per annum since 1925. The overall rate of increase started between 1900 and 1920.

18. The growth of the small Shag population on Lundy, which has stabilised, and the rapid increase of the Cormorant in Holland in the 1930's is compared to the Forth-Farnes growth.

19. At least part of the present growth in this last area is a population revival after relaxed human persecution.

SECTION THREE

(Sex ratio and Pair bond)

20. Thirty seven unfledged chicks were intentatively 'sexed' and a sex ratio of 1.47 (females per male) indicated a surplus of females.

21. First year museum skins show a sex ratio of 1.78, again a surplus of females, butolder skins show a marked surplus of males, indicating a shooting bias.

22. Recruitment from cohorts indicated an original sex ratio (i.e. before breeding) of 1.35 to 1.47.

23. Sex specific mortality erodes this surplus of females among the recruits, so that the oldest age group of breeding Shags shows a surplus of males.

24. There is a close correlation between ages of partners within the pair. Males are recruited at an earlier age than females, and pairs except in the oldest age group tend to contain birds of similar breeding experience.

25. Divorce represents a large part of instability of pairs. (90 per cent in young pairs, 60 per cent in old).

26. The Pair Bond is reinforced threefold by site attachment, but the females do not show site tenacity and there are a few records of intact pairs moving considerable distances. Stability of the pair increase with age from 19 per cent (2 year olds) to 59 per cent (11 year olds).

27. There is a tendency for the age of the female mated to a male of changed pairs, to be nearer the population mean than it would be if the male had kept the same female for at least one year. In the oldest group the average age of females in stable pairs is 8 years, but 5 years in unstable pairs.

28. There is no significant difference in age of female in pairs which reform through divorce or through replacement.

29. Four per cent of males mate with two females and form trios, these males tend to be older than average age and 8 per cent of the 11 year old group form trios.

SECTION FOUR (Nest and Nest Site)

30. It was found convenient to rank the nest sites according to each of four requisites
    1. Access to sea.
    2. Protection from heavy seas.
    3. Exposure(apart from 2).
    4. Capacity of site.

31. Only 27 per cent of nest sites on Brownsman and Staple, (where most of the Shags nest) were sheltered, despite the fact that Shags generally prefer sheltered sites.

32. The probability of the site holder rearing young successfully is partly related to the suitability of the site.

33. The oldest Shags begin nest building in January or early February, the two year olds in mid May and some yearlings do so in July.

34. Males choose the site and those breeding for the first time generally choose a poor site. In the following year they occupy better sites,until finally the oldest birds occupy the best sites.

35. The factor which causes movement from one site to another is largely dependent on whether or not young are reared, but failure to rear young does not result in movement among the oldest birds.

36. Older birds are able to occupy better sites since they return progressively earlier with age.

37. The location of the nest site chosen by a male breeding for the first time is influenced by the location of the site of hatching. This is less true than formerly. Ninteen per cent return to within 20 yards of their natal site.

38. The growth of the Farnes breeding population is not occurring in the earlier occupied areas, nor in the poor areas, especially those susceptible to high seas. It is concluded that there is an overall shortage of nest sites.

39. The male collects all the nest material.

40. The distribution of nests in space and time, is a measure of the number of pairs, since deserted nests are quickly removed by other Shags and because nest building is part of the ritual associated with formation of the pair bond.

41. The quality of the nest at the time of laying of the first egg of the season was ranked. The mean rank of the nests of 2 year olds was 1.4 to 1.8 but 2.5 to 2.9 in the oldest group.

42. The onset of nesting is promoted by fine weather.

<u>SECTION FIVE</u> (Egg and Chick)

43. The seasonal distribution of egg laying is negatively skewed and similar throughout the British Isles despite

the fact that the median date of laying in fourteen sea areas varies from 3 April to 20 May.

44. The median date of laying on the Farnes is 27 April, but the first eggs have been recorded from 16 March to 28 April.

45. The shape of the egg laying 'curve' is similar whether the season is early or late, but there is a tendency for laying to be more synchronised when the laying starts near the average date.

46. The median date of laying of females in 1963 was:- 2 Yr. olds: 23 May, 3 Yrs : 7 May, 4.5 Yrs. : 1 May, 7 Yrs. : 28 April and 11 Yrs. : 22 April.

47. In 1964 it was found that three 'status' groups modified the effect of age of date of laying
   1. ♀♀ laying for first time.
   2. ♀♀ which have changed mate.
   3. ♀♀ which keep mate.

48. Females which are breeding for the first time breed earlier, according to age <u>e.g.</u> in 1964 2 years:26 May, 4.5 years:9 May.

49. The later laying of changed pairs is correlated with change to a younger partner.

50. The age of the male modifies the laying date of the female.

51. There is very little difference in the variation in date of laying with respect to the mean date for each age and status group, but old males which keep their mate of the previous season are more closely synchronised than those which change mate. This does not apply to the females.

52. The eggs of a two egg clutch are laid 3.57 days apart, the eggs of a three egg clutch are laid 3.11 days apart and the eggs of a four egg clutch are laid 3.03 days apart. The interval between the penultimate and ultimate eggs appears to be fixed.

53. There is no marked variation in clutch size with season, but clutch size in the main period of laying tends to be higher.

54. Significant annual variation of clutch size occurs and is reflected in annual variation in the production of young.

55. Clutch size is not an age specific variable.

56. Intermittant breeding is confined to older females which have survived their mates, and is of a temporary nature. 7 per cent of females aged 4.5 years, 11 per cent aged 7 years and 12 per cent aged 11 years belong to this category.

57. Egg survival is closely correlated with age of the male, but not the female, and is partly a result of the inadequate nests built by young males.

58. The mean survival of eggs laid by females by trios was 6.9 days, of two year old female 12 days but of all pairs together exceeded the mean incubation period. However, much of the egg loss occurred during the first five days.

59. Females appear to have 'deliberatley' broken their eggs at 6 per cent of nests, excluding the trios.

60. High egg mortality in several other species of bird is also associated with a surplus of females.

61. The incubation period is defined as the number of days between laying and hatching, for each egg, and is 36 days for the first egg, 33 for the second and 31 for the third. The third chick tends to hatch one day after the other two.

62. The incubation period appears to be shorter in younger parents, but this is likely to be an effect of ambient temperature rather than more efficient incubation.

63. One measure of infertility is the percentage addled eggs in those which survive at least 25 days. This can be estimated as follows.

    % Addled eggs = -0.38 age ♂ - 0.91 age ♀ + 21.54, (it decreases with age, age of the female is more than twice as important as age male).

64. Fertility is 72 per cent on Lundy, 56 per cent on the Farnes, (the difference is significant) (Fertility = percentage egg survive incubation and produce ten day old chicks).

65. Chick mortality is at least 10 per cent in the first 5 days, but only three per cent in the next 5 days, and still lower thereafter.

66. The care of the small chick was estimated as the percent-

age of apparently fertile eggs which survived at least 25 days and which produced 5 day old chicks. It can be calculated from the regression care of young = 2.31 age ♂ + 0.01 age ♀ + 68.6; the age of the female has no influence on the survival of the young chick. This is not readily explicable from the behaviour of the parents.

67. The brood mortality increases with brood size during the first five days (B/1 14%, B/2 17%, B/3 20%), but not thereafter. In 1963 overall brood mortality was higher in the smaller broods since these belonged to young parents on poor sites.

68. The number of young fledging from broods of one was 0.82, from broods of two;- 1.56 and from broods of three;- 2.46.

69. There was no difference in weights of chicks according to brood size in 1964 that could be attributed to the amount of food, which could be brought to the chicks by the parents.

70. The fledging period varies according to the nature of the nest site, but where chicks could not wander was 55 days. Independence is generally reached during a further 3 weeks.

71. The overall production of independent young by 528 pairs of known age was given by the regression.
Young produced = 0.12 age ♂ + 0.035 age ♀ + 0.41, indicating the greater importance of the age of male; the effect of age of female was on fertility only.

72. The mean annual production of young by the whole colony is 1.16 per pair compared with 1.85 on Lundy, a significant difference.

73. Brood size on the Farnes was 2.04, on Lundy 2.27 and for the rest of Britain 2.26.

74. There has been no change in brood size on the Farnes in the period 1951-1965 and no trend in production of young since 1960.

75. Age specific production of young in the Shag and Cormorant and White Stork follow a similar pattern. Older birds return earlier in the season and produce more young; as they do in many other species.

<u>SECTION SIX</u> (Mortality and Movement)

76. The first year recovery rate of Shags ringed on Shetland is 4 per cent, on Scilly and Lundy 13 per cent and on the Farnes and Isle of May 10 per cent. There is a close correlation (r = + 0.90) between annual variation in this recovery rate for the Farnes and Isle of May.

77. The loss of aluminium rings, before ringed pulli could be captured was 46 per cent.

78. Twenty nine per cent of ringed pulli return to breed and are identified on the Farnes. There is a significant correlation between first year mortality rate and recruitment; the recruitment is lower when the recovery rate is higher, indicating that the number of recoveries is related to the extent of mortality.

79, Independent evidence is provided, indicating that the annual distribution of Shags can be measured from the pattern of recoveries.

80. There is a large autumn and a small spring peak in numbers (max. 5,000 1963-1964), on the Farnes. Approximately 2,500 (75%) of the autumn bulge consists of birds in their first year, reared away from the Farnes. The peak is the result of a dispersal from colonies to the north, including those beyond the Pentland Firth. The Spring peak coincides with the return movement of these first winter birds which pause at the Farne Islands.

81. The native first autumn Shags disperse during this autumn build up on the Farnes.

82. This autumn mix up is not indicated by the recoveries since mortality is very low at this time of year in this area.

83. The mode of 1st year mortality occurs in autumn on the west coast and in late winter around the North Sea. The peak of mortality tends to be later around the coasts starting in the S.W. approaches and the extreme western regions, but there is no evidence of a spread within the areas occupied by Shags from the same breeding areas. In 10 of 14 years the mode of mortality on the north sea coasts has followed that on the SW by at least 2 months.

84. There is no significant correlations between the recovery rate in the same year between Shetland and Farnes, Scilly-Lundy and Farnes, or Scilly Lundy and Shetland. The first year recovery rate is more variable in the Forth-Farnes area than elsewhere.

85. Annual dispersal of Farne birds in their first winter is closely correlated with annual first year mortality rate; the higher the mortality the more move outside the Fife Ness-Spurn Point area.

86. The mode of mortality of Farne Shags is age specific being in March (1st year) April (2nd year) June (3rd year) but March with mortality in breeding season (Adults).

87. There is no evidence of a return movement of immigrants, once they have bred on the Farnes.

88. Eight per cent of potential recruits reared on the Farnes emigrate to breed for their first time, and the emigration rate thereafter is about one per cent per annum.

89. The adult mortality was estimated according to mark-recapture analysis (1956-1962) and from return of colour-ringed birds (1962-1965). The annual adult mortality rate in 1962-1965 was 14.1 per cent (allowing for adult emigration) but is likely to be about 15 per cent on average.

90. The mortality rate of breeding females (including emigration) was 18.3 per cent, but 11.6 per cent in breeding males ($P = <0.02$), but the mortality rate is unlikely to be sex specific prior to breeding, judging from sex ratio of Shags found dead in November,1965.

91. The adult mortality of breeding birds increased with age 1963-1964, but decreased with age in 1962-1963 and 1964-1965.

92. The recovery rate of dead ringed Shags in their first year varies from 1 in 3.5 in a year of high mortality to 1 in 5.8 in a good year; it is only 1 in 8 for breeding birds.

93. The recoveries were corrected for this bias and a mean first year mortality rate of 43 per cent was calculated for Farne Island Shags.

94. The mean first year mortality is higher in areas where the mean period of first year mortality is earlier.

95. The association of mortality and movement in the first year population is due to the occurence of wrecks or

irruptions. Since the incidence of irruptions has not changed during the growth of the Forth-Farnes population a simple mortality - resource relationship is involved. Older Shags are not affected by the irruptions to any significant extent. Possible cause of the irruptions are considered.

96. The Farne Islands population is found to balance gains with losses, using the estimates of this study.

97. The hierarchial organisation of the breeding population is discussed. Much more research is needed into the social and economic factors influencing the date of occupation of the nest site. The present hierarchial system confers group benefits on the populations, but inter group selection is not invoked.

Accumulation of organo-chlorine insecticides in the Shag

In 1964 and 1965 the almost universal contamination of the environment by chlorinated hydrocarbon insecticides and insecticide residues was demonstrated. Traces of organochlorine insecticides were recovered from high altitude air samples (U.S.D.I., 1964), sea birds and their eggs (Moore and Walker 1964, Moore 1965,a,b), oceanic fish (Rudd 1964) and rainwater (Wheatley and Hardman 1965). More remarkably certain, endemic,antarctic species of Seal and Penguin, and a fish (Pagophilus) were found to contain DDT or its metabolites (George 1966)*

Among the sea bird species so far examined, it is evident that the Shag has the highest concentration of insecticide, and that the concentration in this species is higher in the Forth-Farnes area than in S. Ireland (Moore and Tatton 1965). There is evidence that levels of insecticide, equivalent in toxicity to those found in the Shag on the Farnes have had lethal or sub lethal effects in the Peregrine (Ratcliffe 1963,1965,Przygodda 1964), Osprey (Ames and Mersereu 1964), Golden Eagle (Lockie and Ratcliffe 1964) and Herring Gull (Keith 1965, Hickey,Keith and Coon 1965). Detailed field work on the

* George, L.P. (1966) Pesticides in Antarctic Journ. Applied Ecol. 3: (in press)

lethal concentration in tissues has been carried out on the American Robin (Bernard 1963,Wurster et al 1965), supported by lethal dosage studies of other species in the Laboratory (e.g. Genelly and Rudd 1956,U.S.D.I. 1960-1965,Sherman et al 1965); but almost all are game birds. Very little is known of the indirect and long term effects of insecticides in wild populations (see Robinson 1966, Cramp New Scientist 29 Jan. 1966), their decay in the environment as a whole, or their concentration through food chains (Rudd 1964).

Three organo-chlorines occur regularly in Shag tissue on the Farnes; benzene hexa-chloride,DDE (a metabolite of DDT) and dieldrin. The only active (i.e. toxic) compound occurring in significant amount is dieldrin (HEOD).

Analyses of eggs and liver (Table 56) indicate that there is no continual accumulation in individuals, and that the body burden is therefore not age specific, at least after the initial build up which may take about one year. At present there is insufficient data on annual accumulation to warrant useful comment, but there was no apparent change from 1964-1965 in the Shag.

Analyses of eggs indicated that the level of dieldrin was significantly higher in wholly addled clutches (Table 57). After allowing for excessive water loss in some eggs, the difference persists (Table 58), but the samples are too

Table 56

Concentration of Dieldrin in Eggs and Liver of Shags of known age

(i) Eggs and Age of female

Age of female	Number of females in sample	Median conc.(ppm) ⁎ per clutch	Min.	Max.
2	8	1.32	0.98	4.56
3	9	1.06	0.87	2.53
4.5	14	0.91	0.77	2.13
7	7	1.05	0.71	2.80
11	6	1.07	0.81	2.60
All ages	44	-	0.71	4.56

(ii) Liver and Age of Shag

Age	Sample number	Mean conc. ppm	Median conc. ppm	Min.	Max.
1	1	1.53	1.53	-	-
2	3	3.79	3.21	1.84	6.33
3 to 5	6	2.86	1.06	0.42	9.84
6 and over	4	2.09	1.61	0.54	4.61
	14	-	-	0.42	9.84

⁎ parts per million, wet weight, by thin layer and gas-liquid chromatography. (One part per million is approximately one ounce in 32 tons)

Analysis by "Shell" Research Limited, except for six eggs sent to the Government Chemist.

Table 57

Concentration of Dieldrin (HEOD) in Shag clutches

	Clutches		
Conc.	Fertile	Partly fertile*	Infertile
0.0 - 0.5	-	-	-
0.5 - 1.0	6	10 (1)	4 (1)
1.0 - 1.5	2	5	7 (1)
1.5 - 2.0	-	3 (1)	6
2.0 - 2.5	-	3	2
2.5 - 3.0	-	2	4
3.0 - 5.0	-	-	2 (2)

* part of clutch contained healthy embryo.

The number of clutches laid by 2 year old females involved is given in brackets.

The eggs were collected on the Farnes (1964-1965) and Isle of May (1965) but two were collected at St. Abb's in 1963.

Analysis 'Shell Research' and Govt. Chemist, one or more egg from each clutch.

Table 58

Concentration of Dieldrin (HEOD) in Shag clutches*

(Corrected data)

Conc.	Fertile	Partly fertile	Infertile	2 Yr. ♀
0.0 - 0.5	-	-	-	-
0.5 - 1.0	5	2	5	3
1.0 - 1.5	1	3	4	-
1.5 - 2.0	-	2	1	-
2.0 - 2.5	-	-	1	-
2.5 - 3.0	-	-	-	2
3.0 - 5.0	-	-	-	-

* 1965, Farnes. $\frac{\text{Conc. in sample x weight of sample}}{\text{weight of whole egg}}$

weight of whole egg calculated from egg measurements, length x (breadth)^2 x 0.52 assuming Specific Gravity of 1.0. Analysis by Shell Research Limited, Tunstall Laboratory, Sittingbourne, Kent.

small for further analysis. It is possible however that part of the difference in the concentration of dieldrin in fertile and infertile eggs is due metabolsim of dieldrin by the chick, since the level of dieldrin apparently decreased with the growth of the embryo (Table 59). This suggestion cannot be followed by on present data since the metabolites of dieldrin cannot be detected.*

Even allowing for such an effect there is a suggestion that the body burden of dieldrin in some adult Shags is sufficient to cause infertility in their clutches. Such a lethal effect of dieldrin would account for at least part of the significantly lower fertility on Farne Island Shags compared to those on Lundy (p 148), prior to the widespread use of dieldrin.

Much further study both in the field and in the Laboratory is needed to clarify these vital issues.

* I am indebted to Dr. J. Robinson, A. Richardson and N. Crabtree of Shell Research Limited, for carrying out the vast majority of these analyses.

Table 59

Development of embyro and *concentration of Dieldrin in fertile Shag eggs

	length of embryo			
Conc.	<10mm	10-20mm	20-30mm	30-40mm
0.0 - 0.5	-	-	1	3
0.5 - 1.0	2	2	2	1
1.0 - 1.5	2	-	-	-
1.5 - 2.0	-	-	-	-
2.0 - 2.5	-	-	-	-

* Corrected values, see Table 58 .

Appendix A

THE GROWTH OF ADJACENT SHAG POPULATIONS

Note: localities are indicated in the map (Fig. 2)

Moray Firth to Tay

There are no records of Shags breeding on the coasts of Nairn or Moray.

As early as 1895, Serle (in Baxter and Rintoul 1953) found nests at Pennan Head (= Troup Head) and Cruden Bay, but there are no further records from the Banff and Aberdeen coasts until Watson's own in 1947 (Watson 1954):-

3 nests	Hell's Lum	28.5.47
4 "	" "	24.4.48
41 birds	" "	19.8.50
13 nests	" " and nearby in areas not seen in 1947 and 1948	30.6.51

Watson found several nests at Troup Head on 25 July 1954 and commented that up to 150 Shags regularly use the Hell's Lum area as a winter roost. Along the coast between Longhaven and Cruden Bay he found:-

1 nest near Longhaven	June 1954
2 nests Dunbuy Rock	20.6.50

and the Editors of Scot. Nat. 66 add:-

3 nests and 50 adults Dunbuy Rock 24.5.52

Kincardineshire and Angus.

Each time Baxter and Rintoul were at Fowlsheugh they saw Shags "obviously nesting" and in April 1935 L.J. Rintoul visited Lunan where she was told that Shags nested in the caves nearby. Boase records one nest at Lud Castle in 1939 (in Baxter and Rintoul 1953). Since Harvie Brown did not record the species at these places Baxter and Rintoul consider that Shags may have spread into the areas after the turn of the century.

The species is frequently found further south on the rocky headlands such as Prail Castle and Red Head but in the Tay Estuary it is "met infrequently" (Grierson 1963).

The Isle of May, Fife

There are no records of nests on the Fife mainland (Baxter and Rintoul 1953).

Eggeling (1960) reviewed the history of the Shag on the island and (Table 60) is a summary of counts on the island which have been brought up to date (1961-64) and corrected (for 1936,1944 and 1946) by W.J. Eggeling (in litt.). The 1965 count was made on 23/24 May by the author.

It is clear from the counts given in (Table 60) that the rate of increase is now much reduced on the old established cliff areas, but not on the Maidens

Table 60

The increase in the number of Shag nests on the Isle of May

Year	Nests	Year	Nests
1918	1	1952	70-80
1921	1	1953	>140
1924	2	1955	175-200
1934	>6	1957	>315
1936	10	1959	c.400
1946	c.12	1961	>550
1950	c.30	1965	750
1951	c.50		

More detailed information

	1955	1957	1960	1965
Iron Stairs - Mill door	69	92	110	153
Mill door - Pilgrim	64	143	(109)	208
Pilgrim - South Ness	4	36	74	131
Maidens	24	30	52	160
Other areas	0	0	0	98

(the latter except 1965, are extracted from the log of the Isle of May Bird Observatory. Brackets are this authors' insertion, but the total 1960 count was not quoted as an accurate census in the Annual Report of the Observatory.

which are similar in structure to the Farnes. Most of the present increase however is on the low cliffs to the north and east which have been colonised since 1960.

Craigleith

Waterston found the first Shag nest on this island in 1933 and there were two nests the following year (Rintoul and Baxter 1935). Since that time the number of pairs has increased and breeding has began at a site about 100 yards from the shore under boulders covered by Elder (*Sambucus nigra* L.) (Smith 1961, extended *in litt*.). Smith's estimates are summarised in Table 61 .

Inchkeith

The first nest (but no eggs at end of June) was found in 1965 but "numbers of immature birds" have roosted there for "a good number of years" (Smith *in litt*.). This is the first nest in the upper Firth islands.

The Lamb

There are no records of numbers on this island until those of R.W.J. Smith (1961, extended *in litt*.) which are given in Table 61. Baxter and Rintoul (1953) do not mention the island as a breeding place and it seems likely that the island has been colonised recently.

Table 61

The number of Shag nests on the Lamb and on Craigleith, in the Firth of Forth

	The Lamb		Craigleith	
Year	Number of nests	Date	Cliffs	'Inland'
1933	-		1	-
1934	-		2	-
1959	c.35	21-6	>10	-
1960	53	11-6	+	-
1961	87	10-6	+	3
1962	(125)	9-6	+	14
1963	97	8-6	62, from boat	20
1964	+		+	23
1965	128	Late June	55, from top	40

The brackets are included by R.W.J. Smith, who has carried out the 1959-1965 counts for both islands

The Bass Rock

Fleming (1847) quotes from Ray who found Shags breeding on the Bass in August 1661, "The other birds which nestle in the Basse are these; the Scout (Common Guillemot); the Cattiwake, in English Cormorant, the Scart (Shag), and a bird called Turtle-Dove (Black Guillemot), whole footed and the red feet"

In 1774 (Walker, in Fleming (1847)) and in 1807 it was believed that the Shag was resident on the Bass, and an authenticated record dates from 1843 (Baxter and Rintoul 1953). In 1928 Rintoul and Baxter (1935) were told that 30-40 pairs nested on the island whilst in 1962 there were 256 pairs (Nelson 1963a). Smith (1961) considered that the increase on the Bass probably paralleled that on the other islands, but there is no supporting evidence. It seems likely however that this population levelled off its growth earlier than the others in the area since,

1. It contained the bulk of the area's breeding birds in the 1930's.
2. There is evidence that there has been no increase (in the accessible area at least) since 1950, judging from the numbers of young which have been ringed.

If the Bass Rock population increased with the help of immigration this must have been from beyond the Pentland Firth. Since there is no evidence of such immigration it need not be considered for the time being. It is therefore unlikely that the Bass Rock birds increased at the rapid (up to 50 per cent per annum for a time) rate shown by the Isle of May. It is more likely that the population increased at about 10 per cent per annum (See Fig. 16). If this were a correct assumption then the population would have reached its present size in the mid 1940's just when the Isle of May increase was getting under way. There is some evidence of a decline in the war years on the May and on the Inner Farne, so the sequence of these events may have been somewhat disturbed too. If the Bass Rock population was small (30-40 pairs) in the late 1940's, a purely hypothetical surplus population would have to be erected elsewhere and at a distance (along the coast) of some three hundred miles, to account for the rapid increases elsewhere in the Forth area in the early and mid 1950's. It is known that the Bass Rock population has supplied two birds to the Farnes increase, from the 1959 and 1962 year groups.

Berwickshire

In 1832 Selby recorded the Shag breeding at St.

Abbs Head, but it appears that, from the writings of Wallis (1769) the species was much more abundant there in the eighteenth century, than in the nineteenth (Baxter and Rintoul 1953). In 1855 the principal breeding station of the Shag in Berwickshire was at Brander Cove (Hardy, in Bolam 1912). In 1881 Bolam found about 12 nests at Brander Cove and in 1879 he found several nests at Whitteleheugh nearby. At the end of March 1903 Raeburn (1903) found six occupied nests at Brander or St. Abbs (the exact site is not mentioned). By 1911 however the only breeding place was at Brander Cove (Bolam 1912). Despite the fact that there were then only about six pairs in Brander Cove, Evans (1911) considered that a recovery had started. The increase was slow however and in 1933 there were still only about "a dozen pairs at Brander and a similar number at St. Abbs" (Baxter and Rintoul 1953). In July 1937 C.R. Mills visited Brander and ringed chicks from at least five broods, but otherwise nothing is known of the Shags there until July 1955 when Mrs. Irene Waterston counted nests in the area. It seems likely that her estimate of 15 pairs between Petticowick Bay and Pease Bay is well short of the actual total and this should be taken into account when discussing the increase of birds in the area which is very difficult to cover adequately.

Table 62

The number of Shag nests on the Berwickshire Coast

Year	Whiteheugh to Petticowick	Petticowick to Pease Bay	Burnmouth to Eyemouth	Authority
1911	-	c.6	-	Evans(1911);Bolam(1912)
1933	c.12	c.12	-	Baxter & Rintoul(1953)
1955	88	(15)	-	I.Waterston via Patterson
1957	153	114	c.6	Patterson (*in litt.*)
1958	160	125	7	Patterson (*in litt.*)
1964	c.135	+	+	Author
1965	90	105	+	Author

Patterson (in litt.) covered the area thoroughly in the first week of July of 1957 and 1958. His figures and others are summarised in Table 62.

Dunstanburgh Castle Cliff (Northumberland)

Dunstanburgh cliff is only 8 miles from the Farnes and is easily seen from them. One or two pairs bred here, probably continously from 1870 to the 1930's (Bolam 1912,1932). There are apparently no records to 1953 when a B.T.O. Nest Record Card was filed for this site. In 1959 there were three pairs (J.C. Coulson pers comm) and in both 1963 and 1964 at least six nests were seen in the area by the author. It is interesting that the Shag should have persisted here when it was not regularly breeding on the Farnes.

Marsden Rock (Durham)

Coulson (1961b) records a pair which summered on Marsden Rock in 1960 but no nest was built. A report of a "nesting centre" of this species on the Durham coast (Richmond 1932) has never been confirmed.

Filey Brig - Flamborough Head (Yorkshire)

Since the early part of the nineteenth century the Shag has been recorded as a non-breeding bird on the Yorkshire chalk cliffs. However it has now re-established itself in this area and breeding was proved in 1952, though the species may well have been breeding here for a few years prior to this date (Bunce and Fenton

Table 63

The number of Shag nests and Shags on the Yorkshire Coast

Year	Number of nests Filey to Flamborough	Authority
1952	2	Bunce & Fenton(1956)
1957	15	Bunce(1958)
1964	c.45	Bunce(*in litt.*)

Date & Year	Number of Adults & Immatures at Flamborough (Bunce) *
29-6-49	28
11-7-53	25
11-8-53	21
10-8-56	48
24-8-58	39
3-8-59	77
13-9-59	90

* Yorkshire Naturalists Union Annual Ornithological Reports

1956). In 1956 and 1957 a nest was found at Bempton (Yorkshire Naturalists Union, Orn. Reports) and in 1964 (Bunce *pers. comm.*) 20-25 pairs nested there.

Throughout the period 1949 to 1959 the number of juveniles (in 1955 some of latter were still fed by adults on 10 September) and adults seen about Flamborough has increased (Table 63). The fact that these are not all of local origin was first demonstrated by the sighting of two Farne birds at Flamborough in August 1964 by Henry Bunce.

Breeding is now regular at Filey Brig (Bunce *pers. comm.*) where the first nest was found in 1954 (Y.N.U. Orn. Reports). The total of pairs in the Filey to Flamborough area was about 40-50 pairs in 1964 (Bunce *pers comm.*). On 6 April, 1965 this author saw at least 3 Farne ringed Shags in the area and there was another there the previous day.

Other areas

The nearest regular nesting sites, south along the coast from Flamborough, are on Culver Cliffs, Isle of Wight, Hampshire.

Appendix B

Number of Cormorant nests on the Farnes

Year	Number nests	Year	Number nests
1869(1)	70+	1952	350
1885(2)	45	1953	420
1895	90	1954	240
1897	100	1955	200
1907	106	1956	190 *
1910	112	1957	420
1934	120	1958	200
1946	250	1959	180 *
1947	300	1961	190
1949	250	1962	130
		1963(3)	160
		1964	200
		1965	200

(1) Seebohm (1885)

(2) 1885 to 1949 from Watt (1951)

(3) 1963-1965 this author

N.B. In some cases maximum and minimum estimates have been averaged.

* During the late 1950's two adjacent colonies were formed, possibly from Farne stock, they were on the Lamb(Firth of Forth) Smith (1961) and on Marsden Rock (Co. Durham) (Coulson *pers. comm.*)

APPENDIX C

Number of nests of Shag on Lundy

Year	Nests	Authority
1922	12	Loyd (1922)
1930	30	Wynne-Edwards, V.C. et al (1932
1939	110	Perry (1940)
1942	66	*Alexander and others (1945)
1955	124	Snow (1960)
1956	130	"
1957	132	"
1963	77 + (July)	Greenwood (1963)

* 43 where Perry (1940) found 72, total estimate by this author therefore $\frac{43}{72}$ x 110. J. Greenwood pers. comm. suggests that there has recently (i.e. to 1963) been some decline, but his July counts are probably too low.

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APPENDIX D

Shetland Shags Recovered south of Firth of Forth on Eastern seaboard

1.	Fair Isle	1960 pull	shot 7 November 1960 Berwick on Tweed
2.	Fair Isle	1960 pull	found dead 24-3-62 Eyemouth
3.	Fair Isle	1965 pull	shot autumn 1965 Berwick on Tweed
4.	Unst	1965 pull	found dead Holy Island (6 miles north of Farnes)

Also 1 England, (Bucks. April 1962) 1 Holland, 1 France, 2 Denmark

APPENDIX E

Onset of laying in various geographical regions from nest record cards of the British Trust for Ornithology

Area	Number of nests studied	Mean date by which 50% of nests contained eggs
SE Ireland	97	3 April
Isle of Man	126	6 April(& See Appendix F)
Cornwall and S. Devon	29	14 April
Pembroke	57	18 April
Co. Cork(C.Clear)	133(1)	21 April
Channel Islands	21	23 April
Scilly Islands	46(2)	23 April
Anglesey	131	25 April
Lundy	451(3)	29 April(Snow 1960)
Forth and St. Abbs	256	6 May
Hebrides and N. Minch	189	6 May
Argyll	793(4)	16 May
North Channel	108	20 May
Shetland	362	20 May
14 areas	2799	27 April
Farnes	(8 seasons)	27 April

(1) Corrected for observational bias from one season to season to next *i.e.* only one set of Spring observations and three sets status in July.

(2) Independent estimate gives 22 April for Annet 1961-64, derived from J.L.F. Parslow *in litt*.

(3) Includes repeat clutches *c.f*. Snow 1960 Table 3.

(4) Excludes 1965 data.

Appendix F

Summary of Recorded early layings in the Shag

7 Feb* 1964	Calf of Man	A.H.Morley & R.E.Rayment *via* B.T.O.
16 Feb* 1933	Cornwall	Taylor (1933)
20 Feb* 1963	Calf of Man	A.H.Morley *via* B.T.O.
24 Feb 1907	Sule Skerry	Robinson (1908)
27 Feb* 1959	Calf of Man	Brun (1960)
1 March* 1902	St.Tudwal Isles, Cardigan Bay	Aplin in Thearle *et al* (1953)
1 March* 1957	Maughold Head, Man	Anon (1957)
9 March* 1965	Calf of Man	P.Bennett *in litt*
+ 10 March* 1961	Calf of Man	B.T.O.(N.R.C.)
+ 12 March* 1890	Great Saltee	Ussher (1890)
16 March 1914	Scilly Isles	Robinson (1923)
16 March* 1961	Inner Farne	T.H.Pearson *in litt*
20 March 1927	Donegal	Storey (1928)
26 March	Yell	Raeburn in Jourdain (1913)

* extrapolated from hatching dates etc. by the author of this summary.

+ but B.T.O. nest record cards indicate that this is not unusually early for these areas.

Appendix G

Records of two female Shags laying in the same nest, based on circumstantial evidence

	No. of instances	Year	Area	Authority
(1)	1	1895	Yell, Shetland	Jourdain(1913)
(2)	2	<1912	Co. Kerry	" "
(3)	1	1924	Cornwall	Harvey(1924)
(4)	1	*1939(?)	Eynhallow, (Orkney)	Robertson(1939)
(5)	1	*1939	Isle of Man	Williamson(1939)
(6)	1	1943	Sheep Island, Antrim	Kennedy *et al* (1954)
(7)	2	*1952	Gt.Saltee, Wexford	B.T.O.
(8)	1	*1953	" "	"
(9)	1	*1954	Lundy	Snow(1960)
(10)	1	*1957	"	" "
(11)	1	1962	Shiant Islands	B.T.O.
(12)	1	1965	Isle of May	This author
(13)	1	1964	Unst	Machell(1964)

N.B. "B.T.O." refers to the nest record scheme of the British Trust for Ornithology.

* Evidence in addition to clutch size

APPENDIX H

Clutch Size and Age of the female

Age ♀	Number ♀♀	Mean clutch size 1963	Number ♀♀	Mean clutch size 1964
2	10	3.10	8	2.88
3	9	3.22	13	3.23
4.5	25	3.08	37	2.97
7	38	3.05	32	3.00
11	19	2.95	23	2.96
Unweighted mean	-	3.08	-	3.01
? Age	15	3.07	20	3.05
Total females and) Grand unweighted mean)	116	3.08	133	3.02

APPENDIX I

Clutch Size and age of the female

Age ♀	Number of females	Clutch size	Number of females	* Clutch size(b)
2	18	2.99	16	2.5
3	22	3.22)) 3.12	9	2.7
4.5	62	3.03)	48	2.9
7	70	3.02	35	2.6
11	42	2.95	30	2.8
Unknown	35	3.06	23	2.7
Totals & Means (Unweighted)	249	3.05	161	2.7

* see text

There is no significant difference between the clutch size distribution of the oldest females and those in the 2.5 year old group. ($\chi^2 = 0.87$ with 2 d.f,($.70>P>.50$).)

APPENDIX J

First Year Mortality Rate from First and Second Year Recoveries

Site	1st Year	2nd Year	Total	Estimate from Coulson and White (1959)
Farnes	221	38	259	50 %
Forth	91	14	105	53 %
Lundy	158(138	11(9)	169(147)	71 %(* 72%)
Man	44	12	56	39 %
N. Channel	36	3	39	68 %
Scilly	32	2	34	74 %
S. Ireland	21	2	23	65 %
Hebrides	113	13	126	62 %
Shetland	69	8	77	60 %
Wales	36	3	39	68 %

* excluding shot

APPENDIX K

Mortality of Colour-ringed Shags

Raw Data (Die/Total)

Age

Year		2 Yr.	3 Yr.	4.5 Yr.	7 Yr.	11 Yr.
1962-1963	♂	2/23	5/27	4/43	6/51	2/31
	♀	0/3	5/12	12/56	8/57	4/23
1963-1964	♂	3/38	3/31	10/50	3/53	9/42
	♀	2/9	2/20	13/82	14/54	8/42
1964-1965	♂	4/23	4/42	7/48	8/55	2/47
	♀	2/9	5/14	10/70	12/65	6/46

APPENDIX L

Male 'advertising' display

Photographs or drawings of this display are to be found in Carthy (1964),Snow (1963),Armstrong (1947, in Dover Edition 1964). The display differs from that of *Phalacrocorax penicillatus* (Williams 1942), and *P. carbo sinensis* (Kortlandt 1938), since in these species and *P. carbo carbo* (*pers. obs.*), the wings are held out and up.

The display starts with a dart and gape, the head is then thrown back onto the mantle.

The behaviour of Cormorants is discussed by van Tets (1965).

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SYSTEMATIC NAMES OF BIRD SPECIES MENTIONED IN THE TEXT

Auk, Little	Plautus alle
Bishop bird	Euplectes hordeacea
Bittern	Botaurus stellaris
Blackbird	Turdus merula
Booby, Brown	Sula leucogaster
" White	" dactylatra
Bunting, Corn	Enberiza calandra
" Reed	" schoeniclus
" Snow	Plectrophenax nivalis
Buzzard	Buteo buteo
Canvasback	Nyroca valisineria
Crow, Carrion	Corvus corone
Dove, Barred	Geopelia striata
Eagle Golden	Aquila chrysaetos
" White-tailed	Haliaetus albicilla
Eider	Somateria mollissima
Falcon Gyr	Falco rusticolus (as Iceland)
" Peregrine	" peregrinus
Flycatcher, Pied	Muscicapa hypoleuca
Fulmar	Fulmarus glacialis
Gannet	Sula bassana
Godwit Black-tailed	Limosa limosa
Goshawk	Accipiter gentilis
Greenfinch	Chloris chloris
Grouse Red	Lagopus scotius

Grouse Ruffed	Benasa umbellus
Guillemot Black	Uria grylle
" Common	" aalge
" Brunnichs	" lomvia
Gull, Black-headed	Larus ridibundus
" , Common	" canus
" , Glaucous	" hyperboreus
" , Great Black-backed	" marinus
" , Herring	" argentatus
Harrier, Hen	Circus cyaneus
Hawk, Sparrow	Accipiter nisus
Heron	Ardea cinerea
Jackdaw	Corvus monedula
Jay	Garrulus glandarius
Kestrel	Falco tinnunculus
Kingfisher	Alcedo atthis
Kittiwake	Rissa tridactyla
Mallard	Anas platyrhynchos
Merganser, Red-breasted	Mergus serrator
Noddy, Black	Anous tenuirostris
Nutcracker	Nucifraga caryocatactes
Osprey	Pandion haliaetus
Owl Barn	Tyto alba
" Short-eared	Asio flammeus
Pelican, Brown	Pelecanus occidentalis
" White	" erythrorhynchus

Penguin, Adelie	Pygoscelis adeliae
" , Yellow-eyed	Megadyptes antipodes
Petrel, Storm	Hydrobates pelagicus
Pheasant	Phasianus colchicus
Pigeon, Wood	Columba palumbus
Puffin	Fratercula arctica
Razorbill	Alca torda
Redhead	Nyroca americana
Redstart	Phoenicurus phoenicurus
Redwing,tri coloured	Agelaius tricolour
Robin	Erithacus rubecula
" American	Turdus migratorius
Rook	Corvus frugilegus
Serin	Serinus canarius
Shearwater Manx	Puffinus puffinus
" Short-tailed	" tenuirostris
Skua, Arctic	Stercorarius parasiticus
" , Great	Catharacta skua
Sparrow, Song	Melospiza melodia
Starling	Sturnus vulgaris
Stork, White	Ciconia ciconia
Swan, Mute	Cygnus olor
Swift	Apus apus
" , Alpine	" melba
Tern, Arctic	Sterna paradisea
" , Caspian	Hydroprogne tschegrava

Tern, Common	Sterna hirundo
" , Sandwich	Thallaseus sandvicensis
" , Sooty(Wideawake)	Sterna fuscata
Thrush, Mistle	Turdus viscivorus
" , Song	" ericetorum
Tit, Blue	Parus caeruleus
" , Great	" major
Wren House	Troglodytes aedon
Yellowhammer(Yellow Bunting)	Emberiza citrinella