Aspects of the biology of the shag (Phalacrocorax aristotelis)

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ABSTRACT

On the Isle of May, Scotland, large numbers of Shags have been marked annually since 1962. From 1981 to 1983, this marked population was sampled to investigate retrospectively a catastrophic decline in numbers of breeding Shags between 1974 and 1976. An electrolytic method was developed to read incomplete ring-numbers on abraded rings: it was 94% successful.

The adult annual survival rate before, during and after the decline remained constant at 87%; during the decline, up to 60% of experienced adults refrained from breeding, laying was a month later than usual, chick production and post-fledging survival were both abnormally low. Failure of the fish stocks around the Isle of May probably caused the decline.

Dispersal, pair-bond and reproductive performance with respect to age, timing of breeding and nest-site quality were also examined. Natal and breeding fidelity were strong, and more pronounced in males. Second-year males, breeding for the first time, performed half as well as older males; the effects of other male age categories and female age were unimportant. A strong age-independent seasonal decline in breeding performance was attributable to both environmental factors and individual quality. Four nest-site quality criteria affected reproduction: ledge size, dampness, exposure, and vulnerability to the sea. Experienced Shags bred early and occupied good sites; the social structure forced later-breeding recruits onto poorer sites within the breeding group. Shags which changed sites between years preferred those with a previous history of occupation. Sites occupied continuously were of highest quality.

The study population currently shows no sign of density-dependent regulation; potential future regulatory factors are food and a shortage of good quality nest-sites.

ASPECTS OF THE BIOLOGY OF THE SHAG

(*Phalacrocorax aristotelis*)

By

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licencié ès sciences mathématiques (Lausanne)

A thesis presented in candidature for the degree of
Doctor of Philosophy in the University of Durham.
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I declare that this thesis is original and entirely my own work, except where otherwise stated. No part of it has been submitted previously for a degree at any other university.

To my Parents.

> "Field studies on populations revolve around censuses, the structure of the population by age and sex, the birth-rates and death-rates, movements, as well as the influence on these of outside changes and interrelations."
>
> Charles Elton

Frontispiece

Shags nesting on the Maiden Rocks - Isle of May, 1981.

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Sir Hew Dalrymple kindly allowed me to search the Bass Rock for marked Shags, and the Royal Society for the Protection of Birds gave me permission to visit The Lamb, Fidra and Inchmickery for the same purpose. J. Smith, F.

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1. GENERAL INTRODUCTION.

Over the past 50 years, advances in technology have considerably increased man's impact upon the natural environment. Two examples will illustrate this, and also serve to introduce the reasons for this study. The first is the discovery of organochlorine compounds: these include pesticides such as DDT and dieldrin, commonly used in many countries to control insect pests and boost agricultural productivity, and polychlorinated biphenyls (PCBs) which have a wide range of industrial applications, from electrical equipment to lubricants. The second is the modernisation of fishing techniques, with new methods of detecting, catching and processing fish which have led to a greatly improved yield per unit effort (Hempel 1978). Despite the obvious benefits of these new technologies, they can also have far-reaching effects on natural systems which are crucial to man's survival. A typical case is the contamination of the environment by persistent organochlorines, such as DDT and PCBs, which pass from one animal in a food chain to the next and tend to become concentrated at the same time. Their pervasiveness is such that they are now found throughout the globe, even in areas which, like Antarctica, are far from sources of contamination (Sladen <u>et al</u>. 1966). In Europe and the United States, their introduction during the second world war led to a build-up of residues in top predators which had particularly noticeable effects on birds of prey. Raptors which were not killed outright showed reduced fertility through egg breakage caused by egg-shell thinning and death of the embryo by poisoning (Prestt & Ratcliffe 1972, Newton & Bogan 1974). Ultimately, many kinds of terrestrial pollutants (or their metabolites) end up in the sea after being carried by water run-off, streams and rivers. The sea also receives direct inputs of contaminants from industrial effluent, sewage, military refuse and other sources. The use of the world's oceans as a general dumping ground is a matter of growing concern (e.g. Goldberg & Bertine 1975, Johnston 1976). At the same time, despite the growing efficiency of fishing fleets, there is a tendency to consider the resources of the sea as permanent and inexhaustible. The fallacy of this attitude was amply demonstrated by the collapse of the world's largest fishery, the Peruvian Anchovy industry off the coast of Peru. After 1971, overfishing combined with the climatic phenomenon known as El Niño reduced the standing stock of Peruvian Anchovy from 15 million metric tonnes or more (Idyll 1973) to less than 4 million metric tonnes (Valdivia 1978). The fishery was permanently closed in 1981 (Duffy 1983a).

In many cases, we are still too ignorant of the complex ecology of the seas and the dual effects of pollution and over-exploitation to assess how serious these threats are now, or may become in the future. Seabirds, most species of which stand at the top of the marine food chain, are well placed to detect perturbations to the marine environment. Tovar (1978) reported that the overfishing of the Peruvian Anchovy described above was accompanied by a 70% reduction in the numbers of guano birds (Guanay Cormorant, Peruvian Booby, Chilean Pelican). As regards the effects of, for instance, pesticides, a large decrease in the numbers of Sandwich Terns and Eider Ducks breeding in the Netherlands was traced back to discharges of endrin, dieldrin and telodrin from a factory on the lower Rhine (Koeman & van Genderen 1972, Swennen 1972). As environmental monitors, many seabird species have the advantage of breeding in large, conspicuous groups or colonies, often at traditional sites, where they are relatively easy to find, count and, if necessary, sample from one year to the next. For monitoring to be effective, there is a need for information on two fronts: population changes from year to year, and basic biology of the species.

The first aspect covers routine work such as regular surveillance and ringing. At a selection of colonies throughout the British Isles, the Royal Society for the Protection of Birds and the Seabird Group have together undertaken an "Annual Seabird Census" since 1971, designed to assess changes in the cliff-breeding population of several seabird species (Stowe 1982); strict guidelines have been laid down to ensure uniformity of counting methods (Evans 1980, Harris & Murray 1981). With a few exceptions, the systematic use of ringing as a back-up tool to surveillance has not received the attention it deserves. A notable exception is at the colony of Shags on the Isle of May, where both chicks and breeding adults have been marked annually since the 1950's. This colony provided an opportunity to demonstrate the value of long-term ringing as a monitoring tool. Census data revealed that in the mid-1970's, the number of breeding pairs suddenly declined. The first part of this thesis presents methods which, making use of the ringing records, ringing returns and marked Shags breeding at the colony, enabled the past population dynamics to be reconstructed, and hence provided insight into the causes of the decline. It shows how surveys and ringing complement each other: one displays, as numbers of breeders, the outcome of the complex processes of mortality, natality and dispersal which the other can untangle. In general, abnormal changes in seabird populations are likely to be first detected by regular censusing; regular ringing will then enable the underlying dynamics of the changes to be determined, providing a possible clue as to the ultimate causes of the changes.

The second requirement for effective monitoring is an understanding of the factors associated with breeding and survival, and a knowledge of behaviour under 'normal' conditions. Quantitative data on the reproductive and behavioural characteristics of a species serve as points of reference for detecting future changes, which may be due to extrinsic factors like environmental contamination. The long-term study of the Kittiwake by Coulson and his co-workers is a fitting illustration of this point. Not only did they find that reproductive success varies with breeding experience and age (Coulson & White 1958, 1960), timing of breeding (Coulson & White 1961), position in the colony (Coulson 1968) and pair-bond (Coulson & Thomas 1980), but that consistent individual differences also contribute to much of the variability (Coulson & Thomas in press,a). Despite these complex relationships, they were able to establish that over the 30 years of the study, long-term changes had taken place in both breeding parameters and survival rates, only explicable in terms of changes in the environment (Coulson & Thomas in press,b). Another example of a valuable long-term study is that on the Fulmar by Dunnet and his researchers (Carrick & Dunnet 1954, Dunnet et al. 1963, Ollason & Dunnet 1978, Dunnet et al. 1979, Ollason & Dunnet 1983). The second half of this thesis considers various reproductive and behavioural aspects in the biology of the Shag, again taking advantage of the presence of a ready-marked population at the Isle of May colony to provide information on age classes and individuals.

The first detailed study of the breeding biology and behaviour of the Shag was carried out by Snow (1960, 1963) on Lundy between 1954 and 1958; it provides many points of comparative interest to the present work. Few of her breeding birds, however, were marked and only four were of known age. Meanwhile, Coulson had been in the process of establishing a marked population of Shags on the Farne Islands, and found the average adult annual survival rate to be 86% (Coulson & White 1957). This work paved the way to an analysis of the effects of age on breeding behaviour in the Shag by Potts (1966), Coulson et al. (1969) and Potts et al. (1980). In 1968, the first recorded 'red-tide' off the east coast of Britain, caused by the proliferation of the dinoflagellate Gonyaulax tamarensis Lebour (Wood 1968), resulted in the death of four out of every five Shags breeding on the Farne Islands in that year (Coulson _et_ _al_. 1968). This natural removal experiment enabled young Shags to nest on sites previously occupied by experienced breeders: their breeding success almost doubled, demonstrating that the quality of the nest-site was an important factor influencing reproduction, and showing that the social structure of a Shag colony was normally forcing recruits onto sites of poor quality (Coulson 1971). Potts _et_ _al_. (1980) further showed that mean nest-site quality declined as the population increased, so that the limited number of high-quality sites acted in a density-dependent fashion to reduce young production at high population levels. They predicted that the Farne Islands colony would reach a ceiling at around 900 pairs; the size of the colony in 1983 was 775 pairs (Hawkey & Hickling 1984), so it is still too early to validate their conclusions.

The present study of the breeding biology of the Shag on the Isle of May enables a comparison to be made within the same species at different sites (Lundy, Farne Islands, Isle of May) and at different times (1954-58, 1961-71, 1981-83 respectively). In particular, it has been possible to examine in detail the physical and social components of nest-site quality on the Isle of May, carrying on from the work of Coulson and Potts on the Farne Islands. At the same time, the role of site quality in restraining expansion on the Farne Islands and on the Isle of May, a colony twice the size, can be compared. The final discussion will consider how site quality and the other factors determined in the course of this study fit into the general framework of population regulation.

2. METHODS.

2.1 Introduction to the Isle of May.

The Isle of May ($56^{\circ}11'$N $2^{\circ}33'$W) is situated at the entrance to the Firth of Forth, Scotland. It lies 8km off the Fife coast and the nearest point on the Lothian side is 14km away (Figure 2.1). The island covers an area of 57ha, is 2km long and 0.5km broad at the widest point, and its long axis runs north-east to south-west (Figure 2.2). It is formed of a sloping volcanic sill of hard olivine-dolerite rock (Walker 1936), which results in steep cliffs along the west side rising to 50m, and a tilted plateau sloping gradually to a low rocky shore with off-lying islets to the east. Fault lines running roughly east/west have been eroded to form steep gullies, many of which provide nesting ledges for Shags and other seabirds.

The value of the Isle of May as a seabird colony and migration point was already recognized by Baxter and Rintoul in 1907 (cf. Baxter & Rintoul 1918). In 1934, the Midlothian Ornithological Club established a Bird Observatory on the island which is active to the present day. The Isle of May became a National Nature Reserve in 1956, under a 99-year lease from the Northern Lighthouse Board, and has since been managed by the Nature Conservancy Council in conjunction with the Isle of May Observatory Management Committee. The history of the island, its vegetation and its animal life is well documented by Eggeling (1960, 1974) and further information is given in the management plan prepared by the Nature Conservancy Council (Anon. 1981).

In 1981, I spent a total of seven weeks on the island between mid-May and the end of July. In 1982, 17 weeks were spent on the island, spread

Figure 2.1 Map of the Forth-Farnes area, showing the Isle of May (main Shag colony and study site), and other island colonies referred to in the study. The inset gives the position of the area in relation to the British Isles.

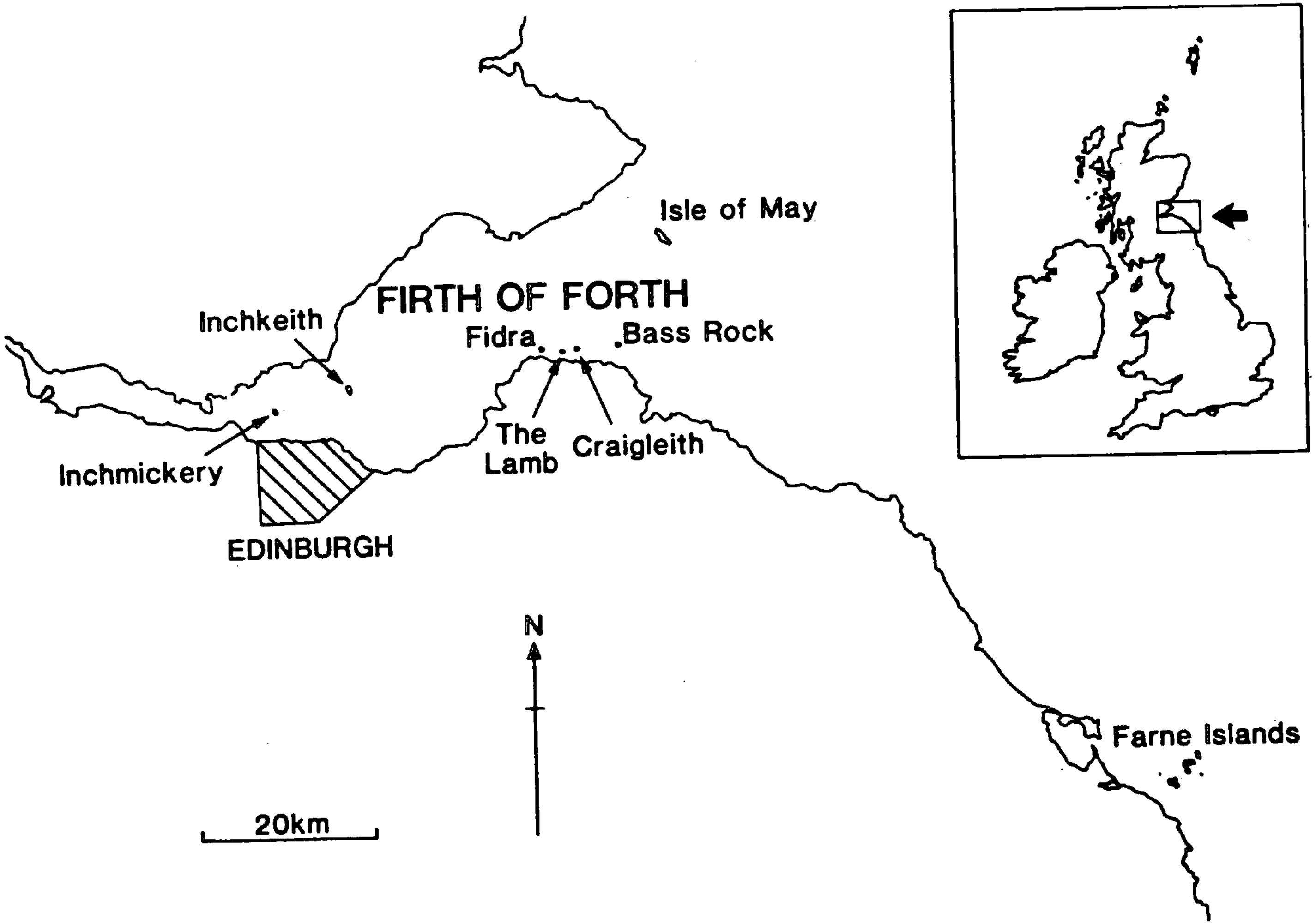
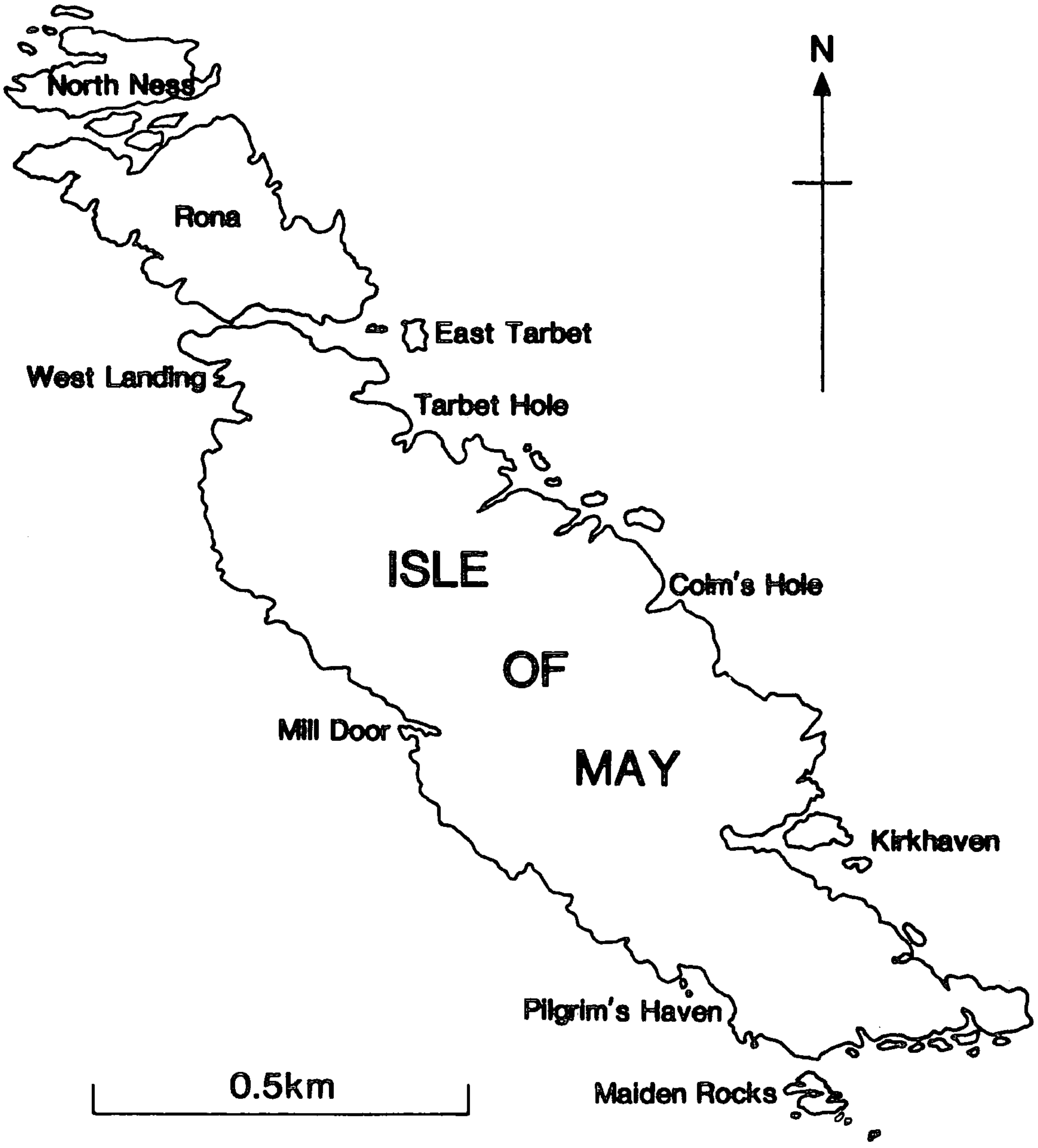


Figure 2.2 Map of the Isle of May, showing the locations of areas mentioned in the text.



between mid-April and mid-September. In 1983, when the emphasis was on visiting the other islands in the Firth of Forth (Figure 2.1), ten days were spent on the Isle of May, split between the second weeks in May and in June.

2.2 Distribution and identification of nest-sites.

Shags nest around most of the perimeter of the island. Areas which remained unoccupied in the course of this study were North Ness, the north and east coastline of Rona, and the stretch of coast between Colm's Hole and Kirkhaven (Figure 2.2). In order to recognize each nest individually, all known breeding areas were photographed during the first week of each field season in 1981 and 1982. The nests were then marked on the photographic prints and assigned a number. Additional photographs were taken in the course of the field season when new breeding sites were discovered which were not visible on the original photographs. The advantages of photographs were that they avoided marking the rocks and could be used to record completely inaccessible nests; they were permanent and independent of the nest itself, so it did not matter if a nest disappeared; they provided an accurate picture of the surrounding topographical features, thereby simplifying the task of locating the nest or nest-site and enabling persons unfamiliar with the area to do likewise; they allowed new nests to be identified as they appeared; they made it possible to compare the sites in one year with those in the next.

2.3 Historical background of Shag rings and ringing on the Isle of May.

The first Shag was ringed on the island by the Isle of May Bird Observatory in 1935. By 1962, nearly 900 Shags had been marked, mostly as chicks. The rings were of the 'clip' design, 20mm in internal diameter, and made of aluminium. Such rings suffered badly from abrasion on rocks due to the softness of the metal, 38% of them becoming illegible after only two years (Coulson & White 1957) Furthermore, ring loss was high due to the large diameter of the ring: on the Farne Islands, 46% of birds ringed as chicks lost their rings before they could be recaptured and reringed after recruiting into the colony (Potts 1966). Similar problems with wear and corrosion of aluminium rings worn by Shags have been experienced in Norway (Johansen 1975).

In 1958, the British Trust for Ornithology introduced the first rings made of monel, a tough cupro-nickel alloy. Monel clip rings were used for Shags on the Isle of May from 1962 to 1965, then replaced by monel butt-ended rings from 1966 onwards. These monel rings had an an inner diameter of 16mm ('K' size), and a serial number comprising seven digits 35mm high. Since 1966, rings other than monel butt-ended ones were used by the Isle of May Bird Observatory in 1979 (31 aluminium clip rings put on Shag chicks) and in 1981 (500 monel clip rings put on breeding birds and chicks). Table 2.1 gives the numbers of Shags marked on the Isle of May since the advent of monel in 1962.

2.4 Identification of ring-numbers and ringing of breeding Shags in 1981 and 1982.

Ring-numbers were read in the field with 10x50 binoculars or a 15-60x telescope. In good light conditions it was possible to read a ring-number at 30m. More often the birds were reasonably approachable, and at close range near-focus lenses were used in conjunction with binoculars or telescope. If a ring was badly abraded, i.e. if any part of the inscription

Table 2.1 Numbers of Shags ringed on the Isle of May from 1962 to 1982.

Year	Chicks	Breeders, unringed	Breeders, reringed	Total
1962	228	11	0	239
1963	377	0	1	378
1964	137	1	0	138
1965	398	45	2	445
1966	193	15	2	210
1967	566	64	0	630
1968	751	21	0	772
1969	610	2	0	612
1970	462	7	0	469
1971	457	91	6	554
1972	723	46	9	778
1973	423	50	3	476
1974	115	115	25	255
1975	68	5	0	73
1976	334	39	0	373
1977	278	4	0	282
1978	311	58	1	370
1979	343	116	9	468
1980	763	88	33	884
1981	620	168	218	1006
1982	993	126	121	1240

Note: 1962 values do not include aluminium rings.

had become obliterated, the Shag was caught (using a crook of 3.5mm fencing wire at the end of a bamboo pole), and the worn ring removed. It was replaced with a ring marked with yellow (1981) or white (1982) PVC tape, which, by enabling caught individuals to be easily recognized and avoided on subsequent visits, minimised disturbance. Abraded rings with incomplete ring-numbers were then treated by electrolysis in the laboratory (see Chapter 3). Twenty-eight illegible rings were treated in 1981, and 58 in 1982; all but six were read (93% success rate). Altogether, 461 Shags which had been ringed in previous years were recorded at the colony in 1981, and 1153 in 1982.

In 1981, an effort was made to ring unmarked second-year birds, so as to increase the number of known three-year olds in 1982. Similarly, if one member of a pair was ringed, an attempt was made to ring its mate in order to increase the number of marked pairs. Initially in 1981, only 17 birds were recorded as chicks ringed in 1979, and only 72 pairs as having both members marked; by the end of the season an additional 17 two-year-olds had been ringed and the number of marked pairs had been brought up to 140. In 1982, the total number of marked pairs was 263 owing to better coverage of the breeding areas.

2.5 Data collection and observations.

In 1981, while most Shags were on eggs or chicks, I concentrated on recording ringed birds and monitoring nest contents. The nests were photographed in mid-May, and recording started at the beginning of June. At each nest, I noted the following features: sex of the bird in attendance, age, presence or absence of a ring, ring-number , number of eggs or chicks if visible, chick size. The maximum period between two successive visits to the same nest was three weeks; on average visits were fortnightly. From the beginning of July onwards, after most of the chicks had fledged, I measured nest-site quality according to the variables described in Appendix 4 (except Density). The photographs themselves were used to obtain additional information on the state of the crest of a bird on its nest, the quality of the nest cup, and the density of nests around the site.

In 1982, the procedure was similar but more detailed. The nests were photographed a month earlier than in 1981. The photographs from 1981 enabled me to start recording nests belonging to two-year-old Shags at the same time, overcoming the problem of young breeders deserting before I had recorded them. They also allowed me to assess the damage to nests inflicted, at the beginning of May, by a freak gale from the west coinciding with a period of spring tides. Extra details noted at a nest were the quality of the nest cup, the stage of chick growth, and, along with the age of the attendant bird, any relevant external features (Appendix 2). Particular attention was paid to identifying both members of a pair. All 28 nest-site variables were scored in the field, and the progress of late nests was checked at fortnightly intervals.

2.6 Coverage of the island.

1981

The total number of nest-sites on the island occupied in the course of the season was 1476, of which 41 were not visible from land. A total of 1169 of these were checked routinely for ringed Shags and monitored for chick production; they were situated round the main body of the island. A further 212 nests were located on the Maiden Rocks, accessible only for two or three hours at low tide. The Rocks were used by St Andrews University as a study area for Herring Gulls, so were only visited twice, to record marked Shags. A number of other nests beneath the south and west cliffs were discovered only at the end of the season or in 1982. The numbers of ringed and unringed Shags on nests in each major area of the island are given in Table 2.2, as are the numbers of birds identified as belonging to one of two age categories, two-year-old or older. The number of nests for each area corresponds to the total number present during the year, including those missed. From the numbers of birds ringed and unringed, it was possible to calculate the proportion of ringed birds in each area, hence the number of ringed birds in each area, and the total number of ringed birds on the island. This worked out at 1129 ringed Shags. Assuming two birds per nest, 38% of Shags breeding on the island were ringed. Of these, 461 were recorded, i.e. 41%. A total of 1323 birds were identified as either two-year-old or older, corresponding to 45% of breeders. Nest-site quality was measured for 832 nests, distributed around the main body of the island (Table 2.2).

1982

The number of nest-sites occupied over the whole island in the course of the season was 1916, of which 47 were visible only by sea. The remaining 1869 were regularly checked, and included the Maiden Rocks. Similar figures to 1981 (Table 2.2) yielded 1532 ringed Shags present, of which 1141 were recorded (74%). The percentage of ringed birds amongst Shags breeding on the island was 40%. In all, 77% of breeding Shags were put into one of the two age categories, two-year-old or older. Nest-site quality was recorded for 1152 nests, again distributed around the main body of the island (Table 2.2).

Table 2.2 Numbers of breeding Shags ringed, unringed, and recognized as second-year or older, and number of nests examined on the Isle of May in 1981 and 1982.

1981	East	South	Rona	West	Maidens	Total
Ringed	67	108	134	68	22	399
Ringed, not identified	20	44	24	56	11	155
Unringed	137	180	160	339	68	884
Second-year	21	13	32	20	-	86
Older	198	229	339	471	-	1237
Number of nests	212	386	247	419	212	1476
Number of nests with nest-site quality recorded	210	119	246	257	0	832

1982	East	South	Rona	West	Maidens	Total
Ringed	226	362	282	131	136	1137
Ringed, not identified	12	28	8	41	8	97
Unringed	303	428	268	486	266	1751
Second-year	126	88	80	74	13	381
Older	427	735	474	632	398	2666
Number of nests	311	481	319	545	260	1916
Number of nests with nest-site quality recorded	311	198	319	324	0	1152

In both 1981 and 1982, the number of individual pairs breeding on the Isle of May was likely to be slightly less than the number of nest-sites, because of Shags which had failed, changed sites and renested. The minimum number of pairs breeding on the island was given by the peak number of nests present at any one time. This peak occurred at the beginning of June in both years, with 1437 nests in 1981, and 1733 in 1982. Subtraction from the total number of nest-sites occupied in each year showed that at most 39 pairs changed site and renested in 1981 (3%), and 136 in 1982 (8%).

2.7 Sexing Shags.

The simplest way of sexing Shags is by voice: the male utters a loud series of croaks or grunts, the female hisses or is silent (Snow 1963).

Alternatively, the male is on average larger than the female, as shown by body weight, wing length and bill depth at the gonys (Table 2.3). Potts (1966) showed that sexing on bill depth was 94% accurate for males and 97% accurate for females, using a separation point of 11.3mm. The results were similar on the Isle of May (see Section 2.9). In addition to depth, the bill of the male often appears yellower than that of the female. The difference due to these two factors was usually clear enough to sex both birds of a pair if they were on a nest together. With experience, they could also be used to sex an appreciable proportion of single birds.

Males could also be sexed from the nuptial display, used for soliciting females. This consisted in drawing the head back over the body and rapidly and repeatedly darting it upwards and forwards, showing the bright yellow gape (Snow 1960, 1963). Copulation was a further means of sexing Shags, although it was observed infrequently. It was not, however, fully reliable, as reverse copulation was noted for certain on two occasions. On Lundy,

Table 2.3 Size differences in male and female Shags on the Farne Islands, with respect to wing length, bill depth at gonys and weight (from Potts 1966)

	Males			Females		
	Mean	S.D.	N	Mean	S.D.	N
Wing length (mm)	272.9	6.2	37	263.5	5.1	37
Bill depth (mm)	12.2	0.3	37	10.4	0.3	37
Weight (kg)	1.85	-	12	1.66	-	5

Snow (1963) saw the female mount the male in three out of 39 mountings.

2.8 Ageing Shags on plumage.

In common with other birds, Potts (1966, 1969) and Potts et al. (1980) have shown that age in Shags can strongly influence various aspects of breeding ecology (pair formation, timing of egg-laying, egg size, hatching and fledging success), and dispersal. This is particularly true of inexperienced breeders, and it is therefore important to be able to recognize the younger age classes at least, in amongst the pool of birds at the colony that are unringed, i.e. that are a priori of unknown age. This is especially relevant when the number of unringed birds is large. On the Isle of May, I estimated that there were 2232 unringed Shags in 1982, of which a proportion were breeding for the first time.

Potts (1966, 1971) was the first who really tackled the problem of ageing Shags on the basis of plumage and moult. He showed that it was possible to identify with a high degree of confidence the juvenile, first-year and second-year age classes on plumage (details in Appendix 1). In what follows, a Shag observed at or around the breeding colony will be called 'first-year', 'one year old' or 'in its first year of life' when it is in its second calendar year; 'second-year', 'two years old' or 'in its second year of life' when it is in its third calendar year, and so on. Shags 'over two' are three years old or older.

Whereas the separation of first from second-year Shags was simple, the distinction between second-year and older Shags was less obvious. A number of second-year Shags were probably confused with older birds at the start of the study in 1981. The accuracy of the identification could be measured by considering the proportions of ringed birds correctly aged. In 1981, 2 out of 19 (10.5%) ringed two-year-olds were recorded as older than two. In 1982, only 4 out of 147 (2.7%) two-year-olds were misidentified; these were probably birds in advanced body moult (Potts (1971) mentions a male in full nuptial plumage at the age of 1 year 10 months). Conversely, a few Shags older than two were misidentified as second-years: one out of 434 (0.2%) in 1981, and four out of 969 (0.4%) in 1982. All five were in fact third-year birds.

The identification of third-year Shags was considerably more difficult. In his work on moult, Potts (1971) found that 2% of males and 4% of females retained the 10th juvenal primary at the beginning of their fourth calendar year. However, this feature was practically impossible to detect in the field, and, in this study, it was only noted once for a bird in the hand.

2.9 Ageing Shags on bill depth.

In the Herring Gull, bill depth has been shown to increase with age (Coulson _et_ _al_. 1981), as well as being sexually dimorphic (Harris & Hope Jones 1969, Threlfall & Jewer 1978). As mentioned earlier, Potts (1966) showed that bill depth at the gonys could be used to sex Shags, but dismissed the effect of age as unimportant. This was examined more closely in the present study, where bill depth was taken as being the minimum height recorded between the base of the bill and the gonys. It was measured to the nearest 0.1mm using Vernier callipers. Although slightly different to the measurement used by Potts, it was equally useful at separating the sexes: 40 males averaged 10.61±0.09mm, and 49 females averaged 9.08±0.05mm (t=14.9 df=87 P[0.001). With the separation point at 9.8mm, only one male (2.5%) and one female (2.0%) were incorrectly classified.

For birds of known age, linear regressions of bill depth against age (Figure 2.3) gave

for males : Bill Depth = 0.05 Age + 10.1 r=0.581 N=26 P[0.05
for females: Bill Depth = 0.01 Age + 9.0 r=0.097 N=29 Not significant.

There was a significant increase in bill depth with age for males; however the increment from one year to the next was so small compared to the scatter around the regression line that it was impossible to age a male accurately by its bill depth. For instance, only 7 out of 19 males over three years of age (37%) had a bill depth greater than that of the largest third-year male. For females there was no significant trend with age. On the Farne Islands, bill depth also increased with age in males, but showed no relationship in females (Coulson, unpublished data, presented in Table 2.4).

Although bill depth was of little value as a means of ageing Shags of either sex accurately, it could serve to compare the average age of two groups of males (chosen, for instance, from different areas).

2.10 Ageing Shags by other characters.

Bill depth had the disadvantage, from the point of view of a possible ageing feature, that it was necessary to capture the Shag in order to record it. A feature which could be recorded without having to capture the bird would be potentially more useful in the field. In a specific attempt to improve the identification of the difficult age group of three-year-old Shags, five characters, described in Appendix 2, were noted if present on Shags over two years of age (according to body plumage) during the 1982

Figure 2.3 Bill depth in relation to age for a sample of male (▲) and female (△) Shags from the Isle of May. For males: y=-0.05x+10.1 (r=0.581 N=26 P[0.05); for females the relationship was not significant (r=0.097 N=29).

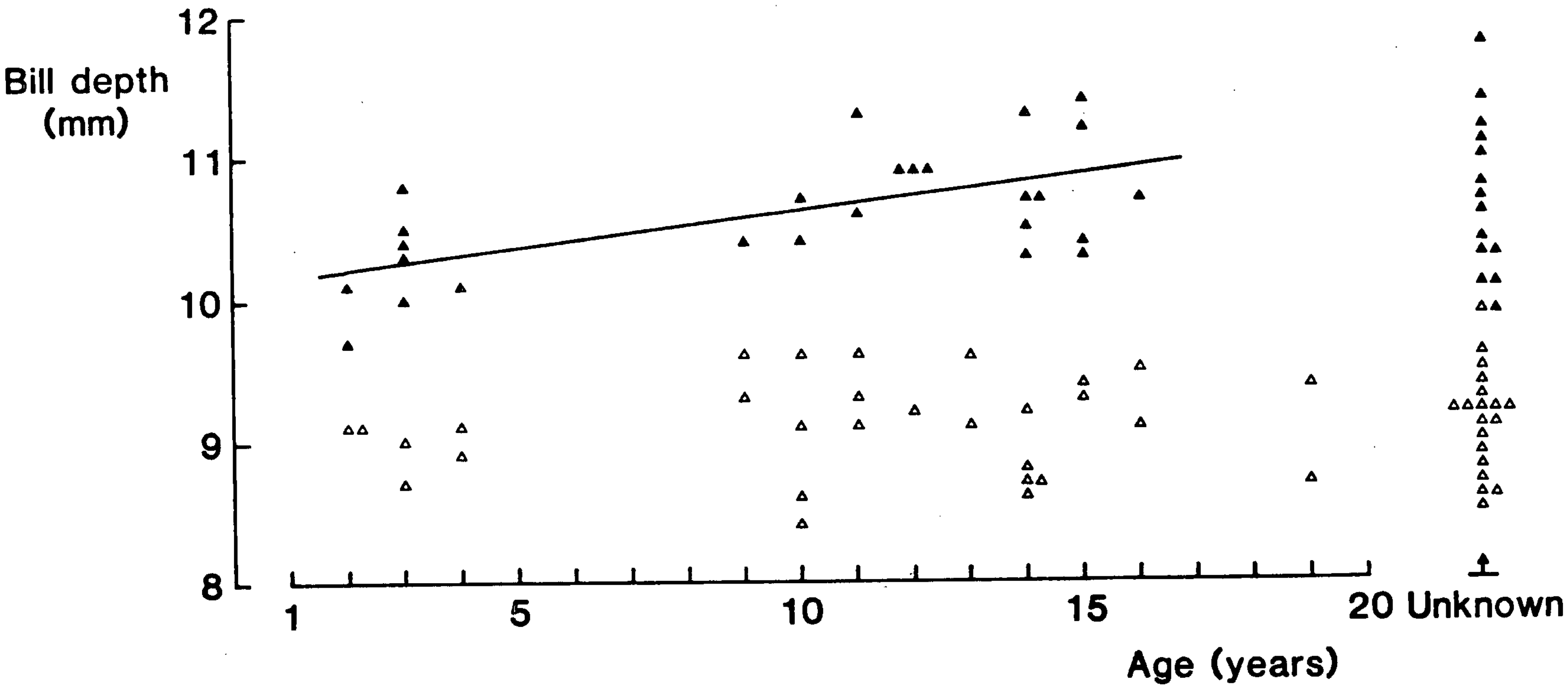


Table 2.4 Age-related differences in bill depth at gonys for Shags of both sexes on the Farne Islands (Coulson, unpublished data).

	Male age (years)				
	2	3-4	5-6	7-8	9+
Mean depth	11.59	11.77	11.92	12.11	11.93
S.E.	0.07	0.05	0.08	0.12	0.09
N	25	26	19	8	21

	Female age (years)				
	2	3-4	5-6	7-8	9+
Mean depth	10.34	10.35	10.37	10.36	10.36
S.E.	0.07	0.07	0.07	0.11	0.12
N	5	19	6	9	9

season:

a) Pale Toe Strips
b) Brown Marginal Coverts
c) Mottled Underparts
d) Unmoulted Primaries
e) White Throat

These five features were analysed with respect to Shags of known age, grouped into two classes: three-year-olds, and older birds. A comparison of the proportions of Shags in each class with and without each character is shown in Table 2.5. All characters occurred significantly more often for third-year Shags than for older ones. The chi-square values indicated that Mottled Underparts was by far the strongest candidate for a useful separation of these classes.

To take into account the fact that a Shag might exhibit more than one character, the technique of Maxwell (1961) was chosen. Out of 32 possible combinations of the five features, 18 were actually observed. Table 2.6 provides details of the analysis, and gives the numbers of individuals for each age group within each combination. Maxwell's method correctly classified 89% of the 36 third-year Shags, and 92% of the 946 older Shags.

Table 2.6 shows that the 10 combinations of features that were assigned to the third-year group comprised all nine ones containing Mottled Underparts. The remaining one, a combination of Pale Toe Strips and Brown Marginal Coverts, was chosen on the basis of only two birds and so should be treated with caution. Classifying on Mottled Underparts alone resulted in 30 out of 34 Shags with the feature (88%) and 874 out of 948 of those without (92%) to be correctly classified. The four misclassified birds with

Table 2.5 Differences between third-year Shags and older ones for the five characters: Pale Toe Strips, Brown Marginal Coverts, Mottled Underparts, Unmoulted Primaries and White Throat (descriptions in Appendix 2).

Character	Character present			Character absent			Chi-square	
	% 3-year	% older	N	% 3-year	% older	N	(1 df)	
Pale Toe Strips	52.9	47.1	51	8.3	91.7	931	97.2	P[0.001
Brown Marginal Coverts	82.4	17.6	17	9.3	90.7	965	86.5	P[0.001
Mottled Underparts	88.2	11.8	34	7.9	92.1	937	218.4	P[0.001
Unmoulted Primaries	50.0	50.0	16	9.9	90.1	966	22.6	P[0.001
White Throat	60.0	40.0	5	10.3	89.7	977	8.2	P[0.01

Table 2.6 Analysis of the separation of third-year Shags and older ones on the basis of the five characters in Appendix 2, according to Maxwell (1961).

Combination u	3-year I	Older II	p(u,I)	p(u,II)	g1.p(u,I)	g2.p(u,II)	Class
00000	57	845	0.548	0.962	0.058	0.860	Older
10000	11	19	0.106	0.022	0.011	0.020	Older
01000	1	1	0.010	0.001	0.001	0.001	Older
00100	10	1	0.096	0.001	0.010	0.001	3-year
00010	1	4	0.010	0.005	0.001	0.004	Older
00001	0	1	0.000	0.001	0.000	0.001	Older
11000	2	0	0.019	0.000	0.002	0.000	3-year
10100	5	2	0.048	0.002	0.005	0.002	3-year
10010	1	1	0.010	0.001	0.001	0.001	Older
10001	0	1	0.000	0.001	0.000	0.001	Older
01100	5	0	0.048	0.000	0.005	0.000	3-year
01010	1	2	0.010	0.002	0.001	0.002	Older
00101	1	0	0.010	0.000	0.001	0.000	3-year
11100	4	0	0.038	0.000	0.004	0.000	3-year
10110	2	1	0.019	0.001	0.002	0.001	3-year
00111	1	0	0.010	0.000	0.001	0.000	3-year
11110	1	0	0.010	0.000	0.001	0.000	3-year
10111	1	0	0.010	0.000	0.001	0.000	3-year
Total	104	878	1.000	1.000	0.106	0.894	

Each character in turn was scored 0 or 1 for absence or presence, so that a combination of characters was described by a sequence of five binary digits. For example, the presence of Mottled Underparts alone was represented by 00100.

p(u,I) is the frequency of combination u within class I (third-year birds);
p(u,II) is the frequency of combination u within class II (older birds);
g1 is the frequency of class I within the total I+II;
g2 is the frequency of class II within the total I+II.

If g1.p(u,I)]g2.p(u,II), elements from pattern u were assigned to class I.
If g1.p(u,I)[g2.p(u,II), elements from pattern u were assigned to class II.
If g1.p(u,I)=g2.p(u,II), elements from pattern u were assigned to class II.

Mottled Underparts were all fourth-year birds, so any effect of misclassification within the third-year group would be lessened by the fact that 'false' third-years would still be young birds. Finally, out of 104 marked third-year Shags, 30 exhibited Mottled Underparts, i.e. Mottled Underparts enabled 29% of them to be successfully identified; there was an equal success rate for males and females (27% for males, 32% for females; chi-square=0.14 df=1 N.S.). The application of this identification feature to the 1982 data increased the sample of third-year birds by 38%, from 104 to 144.

2.11 Ageing Shags by the state of their crest.

The crest of a breeding Shag develops in late winter (Baker 1981) and is rapidly lost once breeding is under way. It was very noticeable that in mid-May at the colony, although most Shags had lost their crests, a certain proportion still retained part or all of it. In parallel with this, Coulson _et al._ (1969) showed that oldest birds tend to breed first, and the young ones several weeks later. The state of the crest in mid-May could therefore be potentially useful as a means of identifying late breeders, and hence young breeders.

In 1982, the state of the crest was recorded for all Shags present at the nest in the middle of May. Any Shags retaining some crest were also noted during the subsequent weeks, up to mid-June. Birds were scored on a 1 to 3 scale:

1 All crest feathers moulted out.
2 Crest partially moulted out.
3 Full or almost full crest present.

The proportions of males and females in each category are given in Table 2.7. Females retained their crests significantly longer than males (chi-square=73.9 df=2 P[0.001). By mid-May, over 20% of females still possessed some form of crest, as opposed to 10% of males. This difference could be due to different timings for the release of sexual hormones, as occurs in the Cape Cormorant (Berry et al. 1979).

The state of the crest in birds of known age (including unringed second-year Shags aged on plumage, and unringed third-year Shags aged by Mottled Underparts) is shown in Table 2.8. For males, the presence of some form of crest was strongly associated with second-year birds (testing presence or absence against age two or three : chi-square=9.83 df=1 P[0.01), although 7% of three-year-old males retained crests. There was no difference between third-year and older males (chi-square=0.64); this could be due to the small sample of six crested birds. Altogether 10% of males older than two retained crests. In females, the difference in crest between two and three-year-old birds was not significant (chi-square=0.64), but that between three-year-old and older birds was highly significant (chi-square=20.2 df=1 P[0.001). Even so, 16% of females retained a crest after three years of age. On average, females therefore retained a crest as third-years whereas males did not; this difference may be the effect of delayed maturity in females, as Potts (1966) found that only 50% of females recruited as second-years compared to 80% of males.

As a means of ageing Shags, crests enabled two-year-old males to be identified with 10% error, but were of little use for males in full nuptial plumage. For females in full plumage, third-year birds could be classified with an error of 44%, which was clearly of little use.

Table 2.7 Proportions of male and female Shags classified according to the state of their crest in mid-May 1982.

	No crest	Some crest	Full crest	N
Males	90.2	7.6	2.2	1087
Females	78.7	10.4	10.9	1013

Table 2.8 State of the crest of male and female Shags in mid-May 1982, in relation to age.

	Males				Females			
Age (years)	No crest	Some crest	Full crest	N	No crest	Some crest	Full crest	N
2	135	40	13	188	25	15	10	50
3	53	2	2	57	22	8	6	36
4	22	1	0	23	13	2	1	16
Older	134	1	0	135	117	3	5	125
Total	344	44	15	403	177	28	22	227

2.12 Ageing Shags according to the age of the partner.

Where a close relationship exists between the ages of the partners, there is a potential for predicting the age of one bird from that of its partner. Such a relationship exists in the Yellow-eyed Penguin (Richdale 1957), the Arctic Tern (Coulson & Horobin 1976), and the Kittiwake (Coulson & Thomas 1980). In the Shag, birds from the 2-8 age group tend to pair with mates of similar breeding experience (Potts 1966). Potts' data show, however, a considerable amount of overlap within this group; the overlap was least for males paired with two-year-old females (15 out of 17 such males were two years old).

Table 2.9 shows the pairings between Shags of known age for 1981 and 1982 (combined) on the Isle of May. Overall, male Shags paired with females that were of the same age or older. Second-year males in particular paired with females of all ages; the largest discrepancy, recorded in 1982, was between a two-year-old male and a nineteen-year-old female. The degree of overlap for pairings of birds aged three or more was such that there was no possibility of accurately predicting a bird's age from that of its mate. However, the overlap was almost non-existent for males paired with two-year-old females: only one such male out of 89 was older than two. Table 2.10 gives the pairings for 1981 and 1982 for just the two age groups, two-year-olds and older birds; Shags ringed as breeders before 1981 have been added to the latter group. Second-year females paired 88 times out of 89 (98.9%) with second-year males; conversely, males over two paired 312 times out of 313 (99.7%) with females over two.

Consequently, in pairs where the age of the female was two and that of male was unknown, the male could be assumed to be a two-year-old; in pairs formed of a male over two and an unknown female, the female could be assumed

Table 2.9 Age of the male and age of the female in paired Shags (1981 and 1982 data together).

		Male age (years)						
		2	3	4-6	7-10	11-13	14+	Total
Female age (years)	2	88	1	0	0	0	0	89
	3	29	9	1	0	0	1	40
	4-6	10	4	3	1	2	0	20
	7-10	2	5	7	13	5	1	33
	11-13	4	4	1	10	6	2	27
	14+	7	3	2	2	5	5	24
	Total	140	26	14	26	18	9	233

Table 2.10 Pairings between two-year-old Shags and older ones in 1981 and 1982.

1981		Males	
		2 years	Older
Females	2 years	7	0
	Older	12	70

1982		Males	
		2 years	Older
Females	2 years	81	1
	Older	61	242

to be over two.

The relationship worked in reverse for sexing according to age: if a Shag over two and of unknown sex was recorded at a nest, the female at that nest was likely to be over two. More interestingly, if a two-year-old bird of unknown sex was recorded, the error on deciding that the male at that nest was a second-year was less than 2%.

2.13 Ageing Shags according to the crest of the partner.

As the presence of a crest was related to the age of the bird (Section 2.11), and, as shown above, the ages of partners were related, it should be possible to age a Shag by the crest of its mate. The nature of the 1981 data did not enable this analysis, but that for 1982 is presented in Table 2.11. In males, 21 out of 34 (62%) crested birds were paired with second-year females, and 27 out of 34 (79%) with females aged two or three. In females, 36 out of 48 (75%) were paired with second-year males, and 40 out of 48 (83%) with males aged two or three. The error was smallest in estimating male age from female crest, but was still only 75% reliable in predicting second-year males. Its use was therefore limited, but it provided a useful guide for 1981, when identification of second-year Shags on plumage was less successful.

2.14 Trios.

Trios have been recorded in several species of seabird, such as Arctic Tern (Cullen 1957b), Gannet (Nelson 1965) and Kittiwake (Coulson & Thomas in press,a). On the Farne Islands, Potts (1966) recorded that on average 4% of male Shags were bigamous, with a range of 1 to 8% depending on the year. On

Table 2.11 Pairings between crested Shags (age unknown) and Shags of known age in 1982.

		Males		
		No crest	Some crest	Full crest
Female age (years)	2	37	17	4
	3	35	4	2
	Older	138	6	1
	Total	210	27	7

		Females		
		No crest	Some crest	Full crest
Male age (years)	2	43	20	16
	3	34	2	2
	Older	134	6	2
	Total	211	28	20

the Isle of May, a male Shag paired with more than one female was noted four times in 1981 (1.2% of known pairs) and 31 times in 1982 (2.2% of known pairs). One of them was promiscuous during three successive seasons (Harris 1982). Although it is likely that the figures for the Isle of May were underestimates owing to the short period of observation at every nest, it would appear that the situation was similar to that on the Farne Islands.

Consequently, the low incidence of non-monogamous pairings was unlikely to affect the accuracy of applying the results from previous sections to ageing Shags of otherwise unknown age.

2.15 Decision procedures for ageing and sexing.

In view of the preceding results, the following procedures were adopted to complete the data sets for 1981 and 1982.

In 1981 and 1982 at each nest:

a) If two Shags identified as older than two (on plumage) were present, sexes unknown, then male and female were considered to be older than two.
b) If two second-years were present, sexes unknown, then male and female became second-years.
c) If female was second-year, male unknown, then male became two years old.
d) If unsexed second-year was present, nothing else known, then male became two years old.
e) If unsexed second-year and unsexed Shag older than two were present, then male became two years old and female became older than two.
f) If male was older than two, female age unknown, then female became older than two.

g) If unsexed Shag older than two was present, nothing else known, then female became older than two.

In 1981, because of the poorer identification of second-year Shags, presence or absence of crest was used to increase the sample of this age class.

h81) If crested Shag was present, nothing else known, then male became two years old.

In 1982, it proved possible to increase the sample of third-year Shags by using Mottled Underparts.

h82) If a Shag exhibited Mottled Underparts, it became three years old.

The outcome of applying these procedures is shown in Table 2.12. All categories increased, the smallest increase being in numbers of males over two (both years) and the largest being in the number of females over two (1981) or third-year females (1982). All increases were consistently smaller in 1982, by a factor roughly of five; this reflected the extra time and effort put into ageing the Shags in 1982.

2.16 Calculation of laying date, hatching date, fledging date and occupation date.

In 1981, the photographs for the individual recognition of each nest were printed only by the beginning of June. As most Shag chicks fledged at the beginning of July, it was not possible to obtain estimates of laying date or hatching date for individual nests.

In 1982, field work started after most Shags had started incubating,

Table 2.12 Improvements, in numbers of Shags aged and sexed, achieved by applying the decision procedures from Section 2.15.

		Before	After	% increase
1981	Males over two	404	447	10.6
	Second-year males	66	122	84.8
	Females over two	448	852	90.2
	Second-year females	9	13	44.4
	Pairs of known age	346	514	48.6

		Before	After	% increase
1982	Males over two	1239	1269	2.4
	Second-year males	290	346	19.3
	Third-year males	64	83	29.7
	Females over two	1427	1622	13.7
	Second-year females	91	97	6.6
	Third-year females	41	63	53.7
	Pairs of known age	1416	1566	10.6

Note: A pair was considered to be of known age if both male and female were known to be either two years old, or older.

but covered the whole period of chick development. The large number of nests present on the island precluded daily visits to each one, so the exact hatching date was known only for nests containing hatching young during a visit. To overcome this difficulty, I needed a scale of chick development in relation to number of days after hatching. A scale based on physical appearance had the advantage of being applicable to chicks in accessible and inaccessible nests alike; by avoiding explicit measuring of the chicks it also saved time and minimised disturbance.

In order to match age against chick development, the physical appearance of chicks from eight nests at Mill Door was monitored daily. For an independent assessment of development, their wing lengths were measured to the nearest millimetre. Recording started at hatching for 15 chicks from 6 nests; of these seven eventually fledged. For the other two nests, containing three chicks each, recording began 25 and 31 days after hatching; all six chicks fledged. This procedure enabled me to obtain a complete record from hatching to fledging for at least six birds at any one day after hatching, in spite of periodical absences from the island. The physical appearance of the growing chicks could be grouped into twelve categories; these are described below and will be referred to as 'growth stages'.

Stage 1. Newly hatched or emerging from egg, skin purplish-black, shiny.

Stage 2. Naked, skin matt black, egg-tooth still present.

Stage 3. Naked, skin matt black, egg-tooth lost, down pins showing through on back.

Stage 4. Downy, down blackish-brown, head bald, black.

Stage 5. Downy, down very dark brown, head bald, black, pins showing through on wings.

Stage 6. Downy, down very dark brown, head downy except maybe for small patch on crown.

Stage 7. Downy, down dark chocolate brown, tail pins projecting beyond tail stump, wispy.

Stage 8. Downy, down dark chocolate brown, remiges starting to sprout.

Stage 9. Downy, down chocolate brown, rectrices 4cm long, no wing coverts showing.

Stage 10. Wing coverts developed, no down on wings, rest of body downy.

Stage 11. Mantle feathers developed, no down left on back, head and neck still downy.

Stage 12. Full juvenile plumage, not fledged.

With experience, it proved possible to assign chicks to intermediate growth stages as well, thus increasing the precision of the method.

A further eight nests, comprising 14 chicks at various stages of development, were surveyed at two to three day intervals at Tarbet Hole. Growth stages were recorded for each chick, and wing lengths were measured on seven of the chicks. This sample provided an independent check on the range in date after hatching and wing length given by the first sample, and the values were extended where necessary. The dates, duration and wing length for each chick growth stage and intermediate stage are shown in Table 2.13, and the range and mean date after hatching for each stage and intermediate stage displayed graphically in Figure 2.4. Each stage or intermediate stage lasted on average 2.7 days; the longest were stages 4 and 8, of mean duration 5.5 and 7.7 days and ranging over a period of 11 and 13 days respectively. As a result, these were of least value in determining the hatching date.

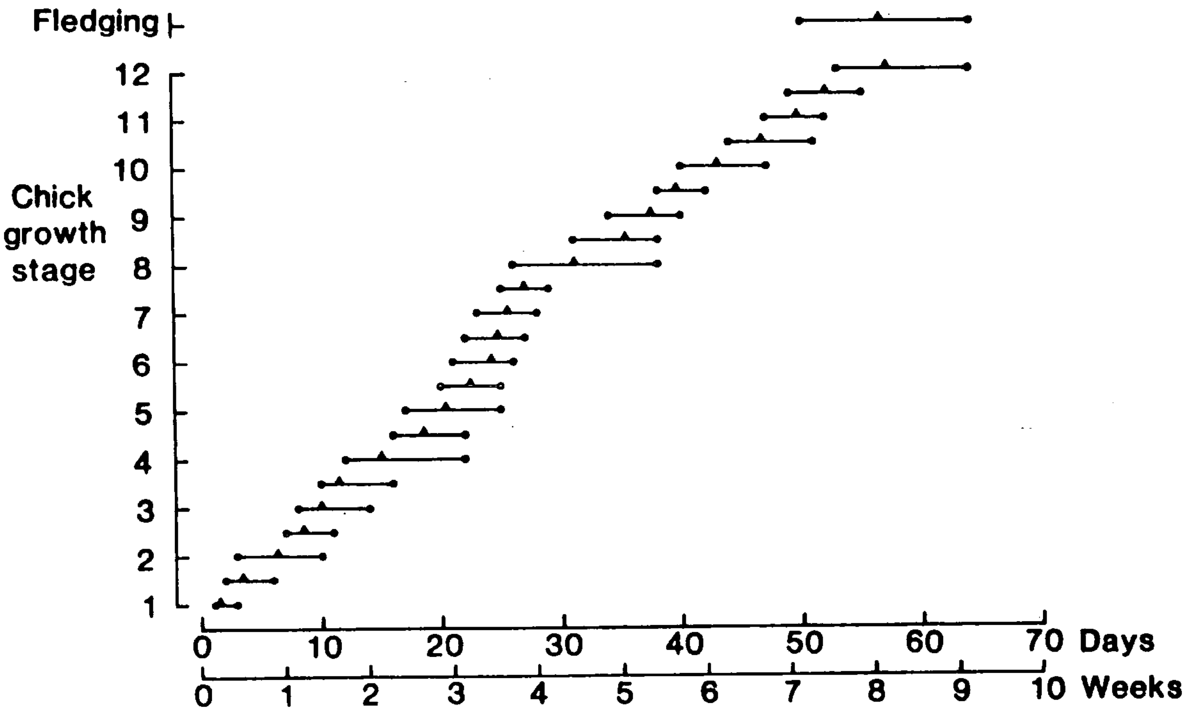
For a given nest, hatching date was calculated on the basis of the

Table 2.13 Date, duration and corresponding wing length for each chick growth stage and intermediate growth stage.

Stage	Date (days after hatching)		Duration (days)	Wing length (mm)		N
	Mean	Range	Mean	Mean	Range	
1	1.0	0-2	2.1	16.3	14-18	12
1/2	3.0	1-5	2.0	18.6	17-21	10
2	5.8	2-9	3.7	23.1	19-28	11
2/3	8.1	6-10	1.0	27.6	24-31	11
3	9.5	7-13	2.0	30.6	25-37	11
3/4	11.1	9-15	1.4	34.8	27-54	11
4	14.5	11-21	5.5	47.8	31-70	11
4/5	18.0	15-21	1.4	62.8	56-72	10
5	20.0	16-24	2.8	74.4	63-100	10
5/6	22.0	19-24	1.1	87.3	74-100	10
6	23.6	20-25	1.8	93.5	81-104	10
6/7	24.3	21-26	1.0	97.9	94-105	8
7	25.1	22-27	1.8	104.3	97-115	8
7/8	26.4	24-28	1.1	114.3	110-121	8
8	30.6	25-37	7.7	141.1	114-168	8
8/9	34.9	30-37	1.9	172.4	162-183	12
9	37.2	33-39	2.2	183.1	162-193	11
9/10	39.3	37-41	2.4	197.1	176-207	6
10	42.5	39-46	3.9	210.9	176-233	6
10/11	46.4	43-50	3.9	223.6	189-241	7
11	49.3	46-51	1.7	232.8	222-245	9
11/12	51.6	48-54	3.4	-	-	8
12	56.6	52-63	6.9	-	-	8
Fledging	55.4	49-63	-	-	-	14

Note: Wing length was no longer measured after day 50, to avoid premature fledging of the chicks.

Figure 2.4 Mean date (▲) and range of dates (●——●), in days after hatching, for each growth stage and intermediate growth stage of Shag chicks. The descriptions of the 12 growth stages are given in Section 2.16.



oldest chick. Usually two to four chick growth stages and corresponding dates were available per nest, giving a number of simultaneous estimates of the hatching date. The hatching date was taken as the average of these estimates, and expressed as the number of weeks from 1 March 1982. Laying date was calculated from the hatching date using the incubation period presented in Potts _et al_. (1980), seasonally adjusted (Potts 1966). Laying date also was expressed as the number of weeks from 1 March. Of 1869 nests present, the week of laying was known for 1512; 1209 of these had been derived from the hatching date as described above, the rest came from direct observations.

This technique was only applicable to nests which succeeded in hatching at least one chick. To accommodate nests which were lost before laying or before hatching, the date of occupation was evaluated for all nests, in terms of the number of weeks from 1 March 1982. It was defined as the date when a male Shag first occupied its site, and was generally known to within a week. Nest-sites already occupied in week 7, when field work began, were given 7 as date of occupation. Altogether, date of occupation was known for 1864 nests.

2.17 Statistical methods and analysis.

The bulk of the data was stored on mainframe computer files, making use of the IBM 370 and IBM 4341 computers at NUMAC (Northumbrian Universities Multiple Access Computer service). The statistical analysis of the data was carried out by means of the packages MIDAS (Michigan Interactive Data Analysis System, Fox & Guire 1976) and SPSS (Statistical Package for the Social Sciences, Nie _et al_. 1975), supplemented by _ad hoc_ programs. Most of the statistical methods referred to in this study are described in Snedecor

& Cochran (1980), Sokal & Rohlf (1981) and Siegel (1956). Details of further references will appear where necessary. For simplicity, when the level of significance of a t-test based on samples with unequal variances was clear-cut, the degrees of freedom were not calculated explicitly, but were expressed relative to their upper bound (if not significant) or lower bound (if significant) defined by the degrees of freedom of the individual samples (Sokal & Rohlf 1981). Abbreviations used throughout this work are df (degrees of freedom), S.D. (standard deviation), S.E. (standard error) and N.S. (not significant); N denotes the sample size.

3. RESTORING THE LEGIBILITY OF THE INSCRIPTIONS ON ABRADED OR CORRODED BIRD-RINGS.

3.1 Introduction.

Any study of birds or other animals involving the use of marked individuals is heavily dependent on the length of time that the marks remain identifiable. Two obvious requirements for identifiability are that the animal retains its mark, and that the mark stays recognizable. In the case of birds, the most widespread form of mark is a metal ring placed round the tarsus and inscribed with a return address and a serial number. The first rings were made of aluminium. In seabirds especially, these were subject to loss and damage to the inscription. Lockley (1942) pointed out that Manx Shearwaters could lose their rings after only two years, owing to wear and corrosion; Poulding (1954) gave evidence for the active removal of rings by Herring Gulls; Coulson & White (1955, 1957) showed that, through abrasion and corrosion, rings on Kittiwakes and Shags could become illegible within two years. The introduction of tougher metals like monel and incoloy has reduced and probably overcome the problem of ring loss, though not that of loss of legibility. Corrosion of the surface (by 'electrolytic' attack in salt or alkaline water) has been noted for monel rings used on terns and Eider Ducks (Coulson 1976). More commonly, illegibility results from abrasion by vegetation, mud, sand or rocks. As the amount of wear shown by a ring increases with time, the problem is particularly noticeable in long-lived birds such as large gulls (Coulson 1976), Puffins (Harris 1980a), and Shags (Galbraith & Furness 1983).

The extent of the problem of lost legibility and the need to overcome it were fully revealed during my study on Shags in the Firth of Forth. Between 1981 and 1983, monel rings on 1536 adult Shags were examined and 243 worn rings replaced. Of these, 12 were clip rings with the ring-number still legible (cf. Galbraith & Furness 1983). On 115 of the remaining 231 butt-ended rings, the ring-number was incomplete owing to the loss of one or more digits. The illegibility of so many ring-numbers constituted a loss of a large amount of information from the older age classes. Consequently the resulting age structure for surviving birds was likely to be biased. It was therefore necessary to develop an effective way of reading all the digits on otherwise illegible rings. This chapter describes and evaluates the technique used.

3.2 Etching techniques: the use of electrolysis.

Loss of legibility of the inscription on a ring is caused by abrasion or corrosion of the surface of the ring to a depth at least equal to that of the inscription. The number or address has, in effect, been filed off (abrasion) or eaten away (corrosion). For this reason, magnifying aids such as a light or electron microscope are of little help, revealing only a maze of scratches or deep pitting. The following method relies on the fact that the inscription has been stamped into the ring, distorting the inner structure of the metal beneath the stamp (the distortion is sometimes visible on the inside of new rings). Even after abrasion or corrosion, the structural differences in the metal persist and can often be revealed by etching techniques. This principle holds for rings of all types of metal. It was applied here to butt-ended rings of monel (nickel and copper alloy) and incoloy (nickel, iron and chromium alloy), by using electrolysis to perform the etching. By removing the metal atom by atom from the surface of the ring, electrolysis produces a ghostly image of the underlying structure created by the stamp. Although dependent on the composition of the metal, the rate of the process is in direct proportion to the intensity of the current passing through the system (Faraday's First Law), and is thus very easy to control. A simple description of the working of electrolysis can be found in Wilson (1971); a more detailed presentation of the theory is in Denaro (1971).

The equipment and materials I used were:

- a variable output intensity generator, such as a battery charger. The one used here was a RS (Radio Spares Components Ltd) nickel-cadmium cell charger providing intensities of 9, 45, 100, 150 and 350mA (approximate cost £25).
- a glass petri dish or similar shallow corrosion-proof container.
- 25% hydrochloric acid (one part concentrated HCl diluted in three parts water). Even though the acid is diluted, it should be prevented from coming into contact with bare skin.
- cupric chloride ($CuCl_2$). Again, to be kept away from bare skin.
- stiff-gauge copper wire (at least 1mm in diameter).
- a timer which can be set to ring after 15 minutes.

The electrolyte was made up of roughly 1g of cupric chloride per 100ml of 25% hydrochloric acid (the exact proportions are probably not important). For a petri dish 9cm in diameter, approximate quantities were 30ml of acid with the equivalent of two pinches of $CuCl_2$ scooped up on the end of a knife.

To treat a ring with illegible digits, the ring was rested vertically on its bottom edge in enough solution to cover the part to be etched. Flattened rings seemed to respond less well than rounded ones, as worn by the bird. A rounded ring also stood up by itself, and the portion projecting above the liquid was easily connected to the generator by a crocodile clip. Warning - any part of the clip touching the solution was also etched.

A schematic layout of the circuit is given in Figure 3.1. The negative pole of the generator was linked to a piece of copper wire bent so that a length of it lay in the solution at one end of the dish. The positive pole was connected to the ring immersed at the other end, with the worn area facing the copper wire. When an electric current passed through the system, bubbles rising from the copper wire gave an indication of the rate of electrolysis. The speed of the reaction could be controlled by the distance between the ring and the wire, and by the output from the generator. A strong reaction attacked the ring too fast for a clear image to form and dissolved the body of the ring. For the best results the etching process needed to be slow, i.e. the stream of bubbles rising from the copper wire had to be perceptible but not intense. With the ring and wire 6cm apart, this corresponded to an output of 45mA from the battery charger; 100mA was excessive. (A continuously variable intensity generator would have been an advantage here.) The process took between 15 minutes and several hours before the ring could be read, depending on the state of the ring (Table 3.1). After 15 minutes of etching, by-products from the reaction had coloured the surface of the ring in brown. At times this could enhance the image of the missing digits; at others the colour needed to be washed off before inspection of the ring. In addition, if the colour was allowed to build up on the ring, it seemed to hinder the etching process. As a result, the following procedure was adopted: every 15 minutes (the timer serving as a reminder), the ring was examined, cleaned under running water and examined again. At the same time the deposit of copper on the wire electrode was removed. The timer was then reset and the procedure repeated until the

Figure 3.1 Schematic layout of the circuit used to etch illegible rings. The ring and the copper electrode bathe in a solution of hydrochloric acid and cupric chloride. Bubbles rising from the copper wire show that electrolysis is taking place.

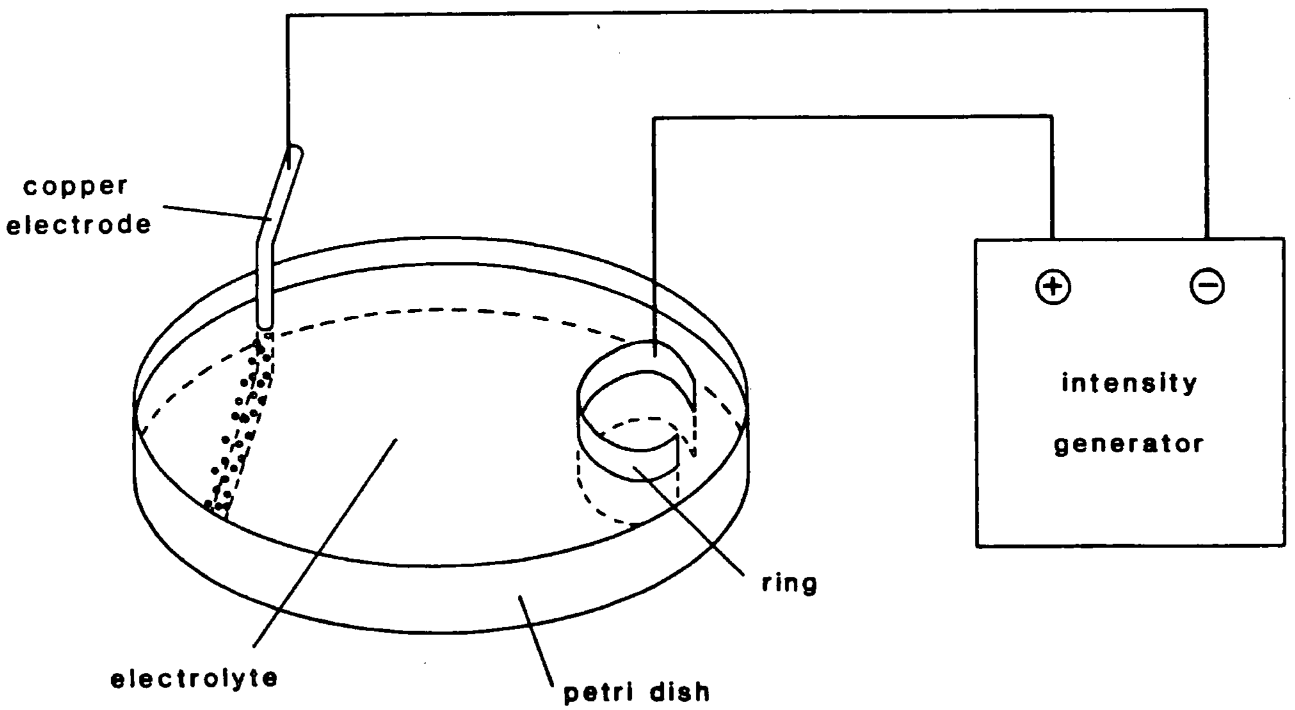


Table 3.1 Time taken to restore the legibility of abraded and corroded rings using electrolysis.

Time required (min)	15	30	45	60	75	90	105	120	]120	Total
Number of rings	17	36	18	11	8	5	1	1	3	100

82% of rings were successfully read in an hour or less.

ring-number was legible. If the process was continued for too long, any missing digits which had appeared started to fade; not all digits appeared simultaneously however, so the 15-minute check allowed each one to be noted down separately as it became visible. If unsuccessful or only partially successful after about one and a half hours of electrolysis, it was possible to rub down the ring with fine emery paper and start again. The number of times this was necessary increased with the overall failure rate; as a guide, approximately one in 10 Shag rings required a fresh start. The same dish of solution lasted for up to five hours of electrolysis. It was renewed when the build-up of impurities seemed to impede the etching process.

The method was extended to treat several rings simultaneously by linking in parallel the same number of petri dishes as there were rings and multiplying the output from the generator by that quantity. In this way three rings required three dishes and an intensity of current of 150mA from the battery charger (the nearest approximation to 3 times 45mA).

There are three ways to control the rate of electrolysis: by varying the intensity of the current, by changing the distance between the ring and the copper wire, and by mounting several circuits in parallel. If only a constant source of current is available, the last two ways provide a means of adjusting the intensity to the level needed to treat a ring.

3.3 Efficiency of electrolysis and other techniques.

X-rays were used in a first attempt at reading worn ring-numbers. Out of a sample of 28 monel butt-ended rings taken off Shags, they revealed the missing digits on only four of them (14%). All four had lacked only one digit, and were among the least abraded in the sample.

The electrolytic technique was then developed, and tried out also on monel butt-ended rings from Shags. It was further tested on monel rings from Razorbills and Guillemots (in this chapter, the term 'auk' will refer solely to those two species), and on a miscellaneous batch of rings ranging in size from those of Ringed Plovers to those from Cormorants. This last sample included incoloy rings as well as monel ones, with no reduction in the success of the method. All rings mentioned so far had lost one to six digits through abrasion. A further 15 monel rings removed from Eider Ducks (10 rings), Redshanks (two rings), Lesser Black-backed Gulls (two rings) and a Sandwich Tern had lost up to five digits by corrosion, presumably as an effect of 'electrolytic' or 'crevice' attack in seawater (cf. Spencer 1976). The ring from the Sandwich Tern was the only one which did not yield to the treatment: corrosion had eaten right through the ring beneath two of the digits. Table 3.2 summarises the results of the different trials. The proportion of illegible rings identified after being treated varied from 65% for auks to 94% for Shags. The overall success rate was 90%, increasing to 94% when auk rings were excluded. This can be contrasted with the attempted use of X-rays, which was successful only in 14% of cases.

The effect of using electrolysis is illustrated in Figure 3.2: a ring from a Mallard was recovered with three digits missing and a fourth nearly gone: GM-8--1. After treatment, the full ring-number GM08571 stands out clearly.

As a result of the technique, the amount of wear on the serial numbers of butt-ended Shag rings can be tabulated according to the age of the ring (Table 3.3). The first incomplete ring-number was recorded after six years on the bird. The proportion remained small up to the ninth year, then increased rapidly; 50% of ring-numbers were illegible after 11 years. Table 3.4 gives the mean weights of rings from the '105xxxx' series on Shags

Table 3.2 Efficiency of electrolysis in restoring the legibility of abraded and corroded rings.

	Number needing treatment	Number identified	% success
Rings from Shags	105	99	94.3
Rings from Razorbills, Guillemots	20	13	65.0
Other abraded rings	16	15	93.8
Corroded rings	15	14	93.3
Overall total	156	141	90.4
Total excluding auks	136	128	94.1

Table 3.3 Age and state of wear of the serial numbers in butt-ended Shag rings.

Age (years)	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16+
Rings examined	158	270	190	87	39	28	25	60	81	104	72	45	56	37	16	10
1 digit missing	0	0	0	0	0	1	0	1	5	5	14	6	9	8	1	0
2 digits missing	0	0	0	0	0	0	0	0	0	2	2	5	6	10	3	4
3 digits missing	0	0	0	0	0	0	0	0	0	0	0	1	6	8	9	4
3 digits missing	0	0	0	0	0	0	0	0	0	0	0	0	2	1	1	1
Total incomplete	0	0	0	0	0	1	0	1	5	7	16	12	23	27	14	9
% incomplete	0	0	0	0	0	4	0	2	6	7	22	27	41	73	87	90

Overall, 115 serial numbers out of 1278 examined were incomplete (9%).

Note: 'age' is taken as the length of time a ring has stayed on a bird (before being replaced).

Table 3.4 Weight loss in butt-ended Shag rings of different ages (105xxxx series).

Age (years)	0	6	11	12	13	14	15	16
Mean weight (g)	6.20	5.80	5.34	5.33	5.28	5.20	5.09	4.82
N	5	1	1	2	11	18	16	7

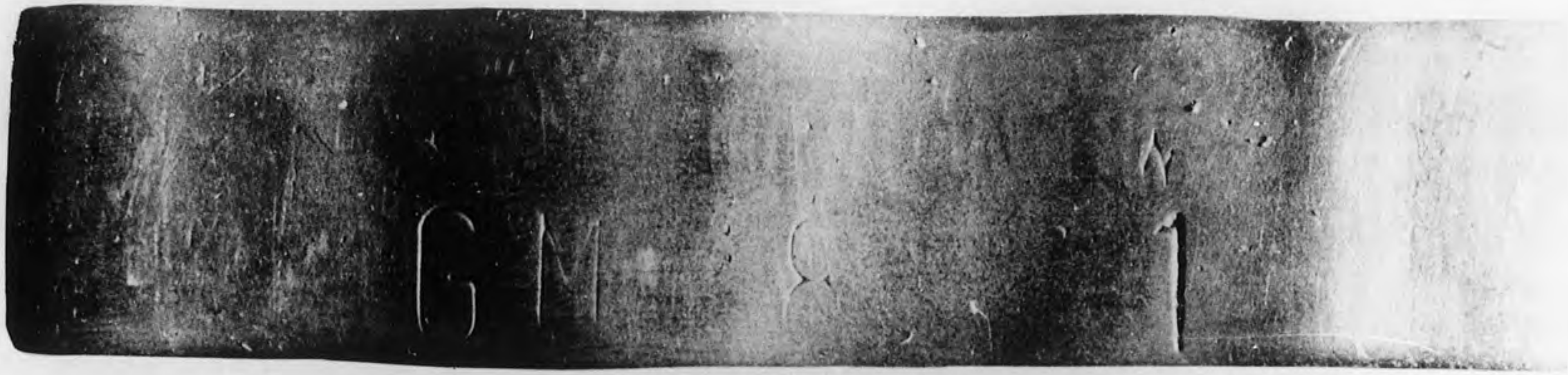
A regression of mean weight against age gives the equation:

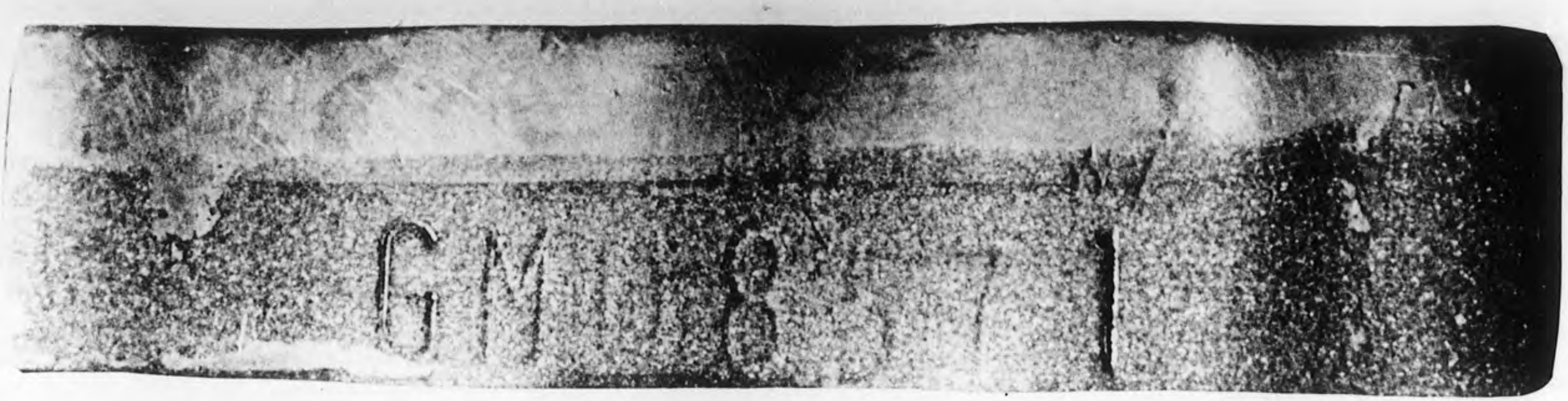
$y = -0.08x + 6.24$ (r=0.98 df=6 P[0.001).

Note: 'age' is taken as the length of time a ring has stayed on a bird (before being replaced).

Figure 3.2

Monel ring GM08571 taken off a Mallard. When recovered (above), three digits were missing and a fourth almost gone. After being treated by electrolysis (below), the ring-number became fully legible.


GM 8 1


GM 8571

followed over a period of time. On average, a ring lost 0.08g per year, equivalent to 1.3% of its initial weight. After 10 years, when illegibility of the ring-number started to increase rapidly, an average ring had lost 13% of its weight.

As regards aluminium rings, a sample of four showed that an effective method was a simple acid bath for 1-2 minutes in a 12.5% solution of HCl. This proved successful for all four rings. Alternatively, Coulson & White (1957) suggest a 5% caustic soda solution after having first removed superficial scratches with fine emery paper. They found that this was successful for 10 out of 11 rings examined.

3.4 Discussion.

Success or failure of the electrolysis probably depends on the amount of structural distortion in the metal. Distortion will be high in the layers immediately below the ring-number and less distinct in deeper layers. As a result, deeply worn rings will respond less well to the treatment than will shallowly worn ones. Rings from Guillemots and Razorbills show a characteristic pattern of wear, i.e. extremely localised and deep, due to these birds shuffling around on their tarsi. Often only a wafer-thin strip of metal remains at the point of abrasion, and the response to etching is correspondingly poor. This is evident in Table 3.2, with 65% of auk rings successfully etched compared to an average of 94% for other rings.

As a general means of reading damaged ring-numbers on monel and incoloy rings, electrolysis has the following benefits:

- it is effective, with a success rate greater than 90% for all species except Razorbills and Guillemots;
- the process is easily controlled by manipulating the electric current;

- it does not require constant attention, but merely needs checking at regular intervals;
- the basic circuit is quick and easy to set up.

The difficulties incurred through ring wear are well documented and discussed in Coulson (1976) and Harris (1980a). Perdeck & Wassenaar (1981) showed that it is possible to reduce loss and damage to the inscription for aluminium rings on Black-headed Gulls by placing the ring on the tibia rather than on the tarsus. This might however affect the rate of return by the public, and is not practicable for all species. The use of harder rings made of monel and incoloy prolongs the life of the inscription, but does not eliminate abrasion or corrosion. Galbraith & Furness (1983) have shown that due to wear on the address, the recovery rate of Shag rings can be affected after only two years (3% illegible), and that 50% of inscriptions (address or ring-number or both) are illegible after eight years. For a study which does not depend on returns from the public, as for example retraps by a ringer, the state of the address is unimportant but legibility of the ring-number is paramount. In this situation, the respite is longer. For Shags, the first incomplete ring-number appeared after six years, and 50% of ring-numbers were illegible after 11 years (Table 3.3). Although this serves short-term studies well, in studies relying upon long-term recaptures the results can be seriously biased by losing the information implicit in worn rings (see e.g. Coulson & White 1955). The etching technique outlined above ensures by its high success rate that loss of information is kept to a minimum. This is helped by the fact that, in most cases, rings of monel and incoloy seem strong enough to be carried for the lifetime of the ringed bird. For instance Coulson (1976) indicated that only a small fraction of Herring Gulls lose their worn monel rings after 8 to 11 years, and certainly in this study none of the 1278 butt-ended Shag rings examined were in any danger of falling off through wear.

Thus, for most species hard metals have probably reduced the problem of ring loss to negligible proportions. That of damage to the inscription persists, but so long as the ring is available for treatment, and with the possible exception of auks, the problem can be overcome by the technique of electrolysis.

4. THE RETROSPECTIVE INVESTIGATION OF AN ECOLOGICAL DISASTER IN THE SHAG: A GENERAL METHOD BASED ON LONG-TERM MARKING.

4.1 Introduction.

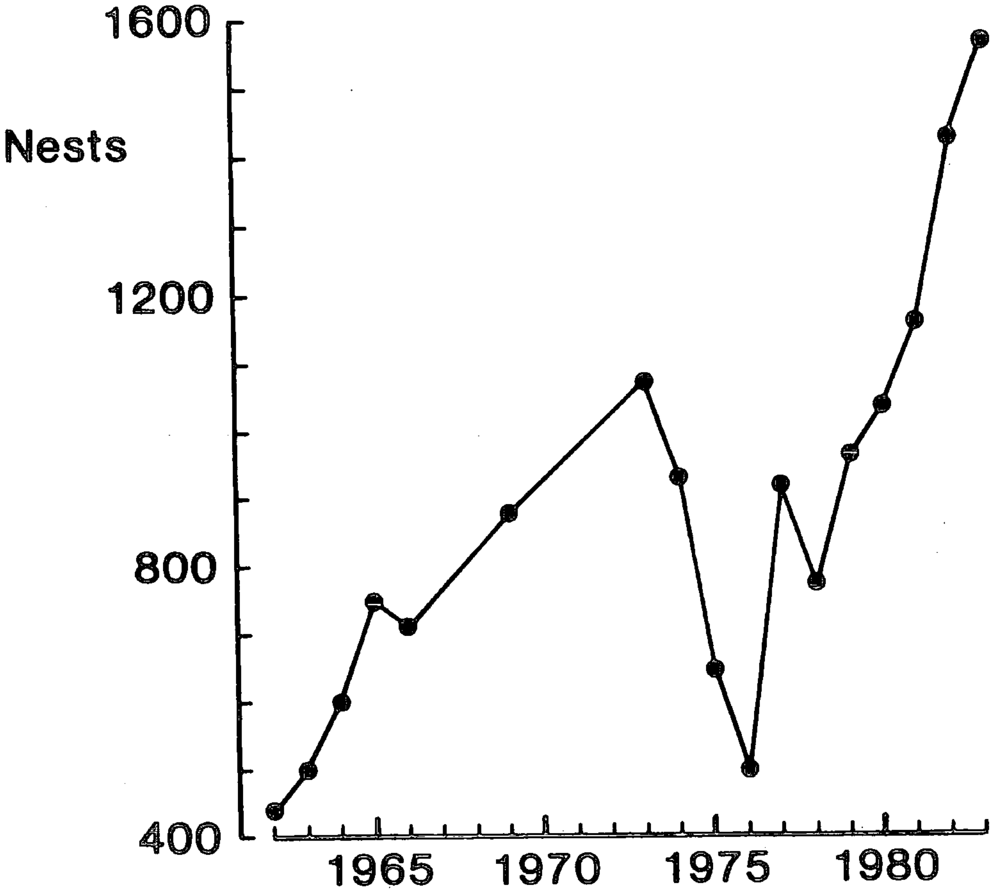
This chapter describes how, after an environmental disaster has occurred, it is possible to examine retrospectively the dynamics of a seabird population before, during and after the critical period. In recent years, there have been many examples of environmental catastrophes involving seabirds. The causes have been identified in some cases. For instance, marine pollution by pesticides resulted in a large decrease in numbers of Sandwich Terns and Eider Ducks breeding in the Netherlands (Koeman et al. 1967; Koeman & van Genderen 1972; Swennen 1972); major oil spills from the Torrey Canyon and the Amoco Cadiz brought about the near extinction of the Puffin at colonies off the coast of Brittany, France (Bourne 1970; Hope Jones et al. 1978); an epidemic of fowl cholera caused high mortality of nesting Eider Ducks in the Gulf of St Lawrence, Canada (Reed & Cousineau 1967); natural toxins produced during dinoflagellate blooms ('red-tides') twice killed over 60% of breeding Shags on the Farne Islands, NE England (Coulson et al. 1968; Armstrong et al. 1978). In other cases, the ultimate causes are less clear, or even unknown. This applies to the mass mortality of King Eiders along the Beaufort Sea coast (Barry 1968), and of Guillemots in Bristol Bay, Alaska (Bailey & Davenport 1972), both attributed to starvation precipitated by severe weather; the Irish Sea disaster in 1969 also involving Guillemots, and tentatively attributed to a combination of weather, the stress of moult, and contamination with organochlorine residues (Holdgate 1971); the spectacular decrease in breeding Guillemots at Søy

Fugløy, Norway, thought to result from human activities (Brun 1979); massive declines in Brünnich's Guillemots in West Greenland, possibly the outcome of shooting pressure and drowning in fishing nets (Evans & Waterston 1976); and the North Sea auk wreck where starvation appeared to be the proximate cause of death, although the ultimate one remained uncertain (Underwood & Stowe 1984). Many other examples exist.

The disaster which was used in this study affected the colony of Shags on the Isle of May, south-east Scotland. After peaking at 1076 breeding pairs in 1973, the number of pairs fell to 933 in 1974 then collapsed to 644 in 1975 and 497 in 1976 (Figure 4.1). This abrupt decline - 54% in the space of three years at a previously expanding colony - will be referred to as the 'crash'. The number of pairs subsequently increased to 921 in 1977, faltered slightly in 1978, then resumed a rapid growth.

A decline of this magnitude is unusual for the Shag, a long-lived species with an average adult survival rate of 83% per annum (Potts et al. 1980). Such a decrease had not previously been recorded on the Isle of May, and only twice have comparable disasters occurred on the nearby Farne Islands, in 1968 and 1975; in each case, they were caused by exceptional outbreaks of paralytic shellfish poisoning, or 'red-tides' (see above). Previous authors have ascribed this crash of Shags on the Isle of May to heavy mortality of adults during the 1975 breeding season and emigration to the Farne Islands in 1976 (Galbraith 1981; Harris & Galbraith 1983). Their evidence for the high mortality stems from Armstrong et al. (1978), who mention that between June and August of 1975, 50 rings of dead Shags marked on the Isle of May were reported compared to 17 in 1976 (these figures, recalculated from the ringing returns, differ slightly from those given by Armstrong et al.). The evidence for emigration of adults to the Farne Islands rests solely on the rapid recovery of that colony after the 1975

Figure 4.1 Annual counts of Shag nests on the Isle of May from 1962 to 1983 (from the Observatory records and personal counts.)



'red-tide'.

Such explanations for the crash are unsatisfactory. Although they provide an interpretation of the changes in the number of Shags nesting on the Isle of May, they offer no clue as to the underlying causes of the crash. Furthermore, the subsequent 85% increase in the number of nests in 1977 is remarkable for a long-lived, slow-reproducing species, especially if, as conjectured, high mortality and emigration of adults had occurred over the two previous years. There was clearly a need for a critical inspection of the dynamics of the Isle of May Shag colony over the last 20 years, in order to reconstruct events before, during and after the crash. This was possible for the Shags on the Isle of May in particular, because of large-scale ringing of chicks and breeding adults carried out in most years since 1962.

In general, to build up a picture of the dynamics of a seabird population before, during and after a disaster, quantitative information is needed on the following:

1) Adult annual survival rates.
2) Annual survival rates between fledging and first breeding.
3) Extent of immigration and emigration.
4) Age at, and rate of, recruitment.
5) Annual number of young fledged.

As this chapter will show, estimates of all these parameters can be obtained as a consequence of regular ringing of adults and young at the same breeding colonies each year. Ringing provides three sources of information concerning the state of the colony from year to year: recovery data from birds found dead and whose ring-numbers were reported; live ringed birds breeding at the colony (either ringed as breeding adults, or ringed as chicks and recruited into the colony); annual brood sizes recorded during chick ringing. The techniques which translate these sources into the parameters listed above are applicable to any population which contains sufficient numbers of marked individuals to give an accurate picture of the survivors from different age classes after a catastrophe. They thus provide a zoological counterpart to the demographic methods developed by Suffling _et al_. (1982) for estimating past age distributions and disturbance rates for boreal forests. Their importance lies as a tool to test specific hypotheses concerning the impact of a catastrophe upon a population. The acceptance or rejection of the hypotheses may indicate where to look for the causes of the catastrophe.

4.2 Study area and methods.

The Isle of May National Nature Reserve lies at the entrance to the Firth of Forth, 8km off the coast of Fife (Figure 2.1); it is approximately 2km long and 0.5km wide. Its value as a migration point and seabird breeding station led to the establishment of the Isle of May Bird Observatory in 1934. The records of the Observatory provide information on the status of breeding birds on the island. The Observatory's main undertaking, however, has been the ringing of resident and migrant birds. The number of Shags ringed between 1962, when short-lived aluminium rings were superceded by more durable monel ones, and 1983 was 11615 birds. These yielded a total of 1191 ringing returns up to 30 June 1983; 1105 recoveries were of Shags ringed as chicks, of which 71% had died during their first or second year of life. Throughout this chapter, the term 'first-year' or 'in the first year of life' refers to the period between fledging and 30 June the following year; the bird is described as 'second-year' or 'in its second year of life' from 1 July to 30 June in the second year after fledging;

thereafter it is called an 'adult'. As the survival rate of Shags ringed as chicks increases during the first three years of life (Potts 1969), the recoveries of such birds are inadequate for estimating adult annual survival rates on a year-to-year basis (Brownie et al. 1978). However, only 81 recoveries were of Shags ringed as breeding adults, too few to provide meaningful estimates of time-specific adult annual survival rates. This problem was overcome by making use of live birds rather than dead ones.

From April to July 1982, Shags on the Isle of May which had been ringed in previous years were sampled by reading ring-numbers in the field with binoculars or a telescope. Shags with abraded rings were caught (using a wire hook at the end of a long pole), and the worn rings replaced. Of 86 abraded rings with illegible ring-numbers, all but six were subsequently read using an electrolytic method to reveal the missing digits (Chapter 3). Altogether, 1141 ring-numbers from Shags ringed between 1963 and 1981 were successfully identified. By recording the presence or absence of rings on adults at each nest, it was possible to calculate the proportion of marked Shags in separate areas of the island. Twice the number of nests in an area multiplied by the proportion of ringed Shags gave the number of ringed Shags in that area. The total number of marked Shags on the island was thus estimated at 1532. Overall, 41% of breeding individuals were ringed, and the sampling efficiency of this study was 74.5%. The initial cohort sizes for each year from 1962 to 1981 are given in Table 4.1. The term 'cohort', as used here, refers both to chicks ringed on the nest before fledging in a particular year, and to adult Shags known to be alive in a given year. The latter comprise unringed breeding Shags caught and marked at the nest, and ringed Shags recorded as breeding in that year ('retraps'). Table 4.1 gives the sizes of the cohorts of adults and chicks in each year. As regards adults, retraps already included in previous cohorts, either because they

Table 4.1 Initial cohort sizes for Shags (chicks and breeding adults) marked or retrapped on the Isle of May from 1962 to 1981.

	Year of marking or retrapping									
	1962	1963	1964	1965	1966	1967	1968	1969	1970	1971
Chicks	92	377	137	398	193	566	751	610	462	457
Breeding adults	-	-	-	48	36	73	27	22	19	105

	Year of marking or retrapping									
	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981
Chicks	723	423	115	68	334	278	311	343	763	620
Breeding adults	63	69	154	4	47	5	56	157	159	345

had been ringed as breeding adults or because they had been retrapped in an earlier year, were ignored in order to retain independence between cohorts.

During the breeding seasons of 1981 and 1982, all except a few Shag nest-sites on the inaccessible west cliffs were photographed for reference purposes and monitored to assess the number of young fledged per nest. In 1983, the Shag nests on the Isle of May were censused in June and July; during the same period, the other Shag colonies in the Firth of Forth (Bass Rock, Craigleith, The Lamb, Fidra, Inchkeith, Inchmickery - see Figure 2.1) were searched for ringed Shags in order to evaluate emigration from the Isle of May. Details of Shags retrapped on the Farne Islands, Northumberland (see Figure 2.1), were supplied by the National Trust and the Natural History Society of Northumbria. In all these cases, the sampling efficiency was approximately 55% (based on proportions of ringed Shags for islands in the Firth of Forth, and on a Lincoln Index on recaptures in 1982 and 1983 for the Farne Islands).

Details of nest counts and dates for the first Shag egg of the season on the Isle of May up to 1981 were extracted from the Observatory records. Several observers inflated their original nest counts by an arbitrary 5% "for nests unseen"; in this chapter, all figures refer to the original counts. The Observatory count for 1981 was made up of five area counts; only one of these areas was counted in 1982, and none in 1983. A regression of the Observatory counts for all six areas ($\underline{y}$) against the corresponding area totals obtained in this study ($\underline{x}$) gave the equation $y = 0.85x + 0.92$ ($r=0.979$, $N=6$, P[0.001), i.e. the Observatory figures were 15% lower than those from this study. Accordingly, the peak number of nests recorded in 1982 and 1983 during this study were reduced by 15% to give counts for 1982 and 1983 comparable to previous ones in the Observatory records.

The Meteorological Office Monthly Weather Reports (H.M.S.O.) provided monthly values for mean air temperature (^{o}C), rainfall (mm) and mean number of hours of bright sunshine (h/day) recorded at Dunbar, and number of hours of wind over 22 knots (39km/h) and over 34 knots (62km/h) recorded at the Bell Rock, from 1961 to 1983. The number of days of easterly (NE-SE) and westerly (SW-NW) winds per month were obtained from the Isle of May Lighthouse returns (copies held at Edinburgh Meteorological Office), and sea temperatures from the Bell Rock log books kept at Leuchars Meteorological Office.

Most statistical tests follow Snedecor & Cochran (1980). The analysis of adult survival involved fitting progressively more complex models to the survivorship data gathered in 1982, and then comparing the models statistically, using maximum likelihood theory. The general structure of survivorship data takes the form $y = r\ s_1\ s_2\ ...\ s_n$, where $\underline{r}$ represents the sampling efficiency, $\underline{s_i}$ is the annual survival rate in year $\underline{i}$, and $\underline{y}$ is the proportion of the original cohort which survived and was sampled in 1982. It is linearised by logarithmic transformation and satisfies the definition of generalised linear models (Nelder & Wedderburn 1972); such models can be fitted to data by the statistical package GLIM (Baker & Nelder 1978), in this case using a binomial error term and a logarithmic link function. In the present study, this approach took into account the large variability in initial cohort sizes (4 to 234) and enabled models to be compared by the likelihood ratio test.

4.3 Colony history and additional information on the crash.

The presence of small numbers of nesting Shags on the Isle of May dates back to the 18th century at least (Rintoul & Baxter 1935). At the beginning of this century, Baxter & Rintoul (1925) noted only 2-3 breeding pairs, but later counts (Southern 1938; Baxter & Rintoul 1953; Eggeling 1960) and the Observatory records show a fast increase from 1918 to 1973 at an average annual rate of 15.6±0.9% (Table 4.2). The colony size subsequently declined by 54% during the crash, from 1974 to 1976. It almost recovered to its former level in 1977, slipped back slightly in 1978, and thereafter resumed a rapid growth at an average annual rate of 14.8±1.1% between 1978 and 1983, very similar to the rate of the pre-1974 increase (Table 4.2).

The changes in numbers of other seabirds nesting on the Isle of May in recent years were not nearly as marked as for the Shag, although Fulmars, Kittiwakes, Guillemots and Razorbills all showed a slight decline in one or both of 1975 and 1976 (Harris & Galbraith 1983). Puffins showed no dip in numbers during the crash period (Harris & Murray 1981). The numbers of Herring Gulls and Lesser Black-backed Gulls reached a low in 1975-1976, but large-scale culls by the Nature Conservancy Council since 1972 overrode the effects of a natural disaster which may have affected them at the same time (Duncan 1978; Coulson et al. 1982).

The period of the 1974-1976 crash was also characterised by particularly late breeding seasons, as measured by the date of laying of the first Shag egg (Figure 4.2). In 1975 and 1976, when the numbers of breeding pairs were at their lowest, Shags began to lay around 20 May, the latest date in the Observatory records. Laying was late in 1974 and 1977 as well, starting at the beginning of May; the only other records of Shags not laying till May were isolated instances in 1936 and 1969.

4.4 Adult annual survival rates.

The calculation of adult annual survival rates was based on cohorts of adult breeding Shags, i.e. birds no longer subject to the high and variable

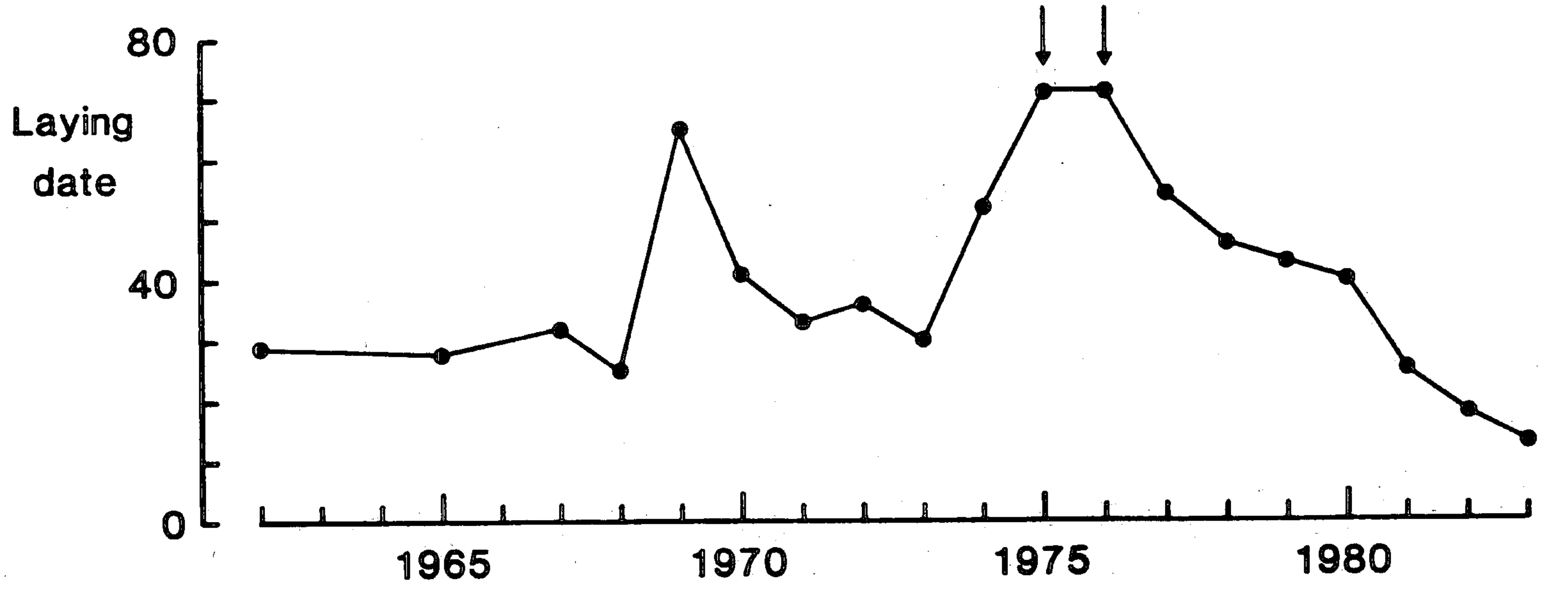
Table 4.2 Counts of Shag nests on the Isle of May from 1918 to 1983, according to Southern (1938), Baxter & Rintoul (1953), Eggeling (1960), the Observatory records and personal counts.

Year	1918	1921	1924	1934	1936	1944	1946	1950	1951	1952	1953
Nests	1	1	2	6	10	6	12	29	50	75	140

Year	1955	1956	1957	1959	1961	1962	1963	1964	1965	1966	1969
Nests	175	185	301	352	526	440	499	600	751	709	880

Year	1973	1974	1975	1976	1977	1978	1979	1980	1981	1982	1983
Nests	1076	933	644	497	921	769	966	1041	1163	1425	1567

Figure 4.2 Timing of breeding for the Shag on the Isle of May from 1962 to 1983, as measured by the date of laying of the first egg (days after 10 March). The arrows indicate the worst years of the crash, 1975 and 1976.



immature mortality rates (Potts 1969). Figure 4.3 presents the proportions of each cohort from 1965 to 1981 which survived to 1982, plotted on a logarithmic scale. A high mortality rate (or emigration rate - the two are confounded) in 1974/75 and 1975/76 would show up on the graph as a sudden break in continuity between 1975 and 1976, with all the proportions of survivors from pre-1976 cohorts shifted down relative to the later cohorts. Inspection of the graph shows no evidence of such a phenomenon, suggesting that the hypothesis of high mortality and emigration during the crash is wrong.

This conclusion was supported statistically as follows. Three progressively more complex models of survival were fitted and compared using the statistical package GLIM. The first and simplest model assumed a constant adult annual survival rate from 1965 and uniform sampling efficiency across all cohorts in 1982. The mathematical form of the model and the estimates of the parameters are given in Table 4.3. The adult annual survival rate was estimated at 85.4%, with at least 97% of birds sampled. The fit of the model to the data was reasonable (chi-square=17.4 df=14 N.S.). However, Figure 4.3 shows that the survival of cohorts from 1965 to 1969 was consistently lower than expected. Instead of a single line of constant slope, the slope appeared to become steeper between 1971 and 1972. Accordingly, the second model assumed a constant annual survival rate between 1972 and 1982, and a second constant survival rate between 1965 and 1971. Compared to the previous model, the improvement in fit was considerable (likelihood ratio test: chi-square=15.5 df=1 P[0.001). The annual survival rate was estimated at 87.4% in recent years, and at 67.9% before 1972; the implications of this will be discussed later. The third model was designed specifically to test the hypothesis that survival during the years of the crash had been abnormally low (or emigration high). It

Figure 4.3 Two models of adult annual survival rates, fitted to the proportions of each adult cohort which survived and were sampled in 1982. Model 1 (– – –) represents a constant annual rate of 85.4%; Model 2 (——) represents the combination of a constant annual rate of 87.4% between 1972 and 1982, and a constant annual rate of 67.9% from 1965 to 1972.

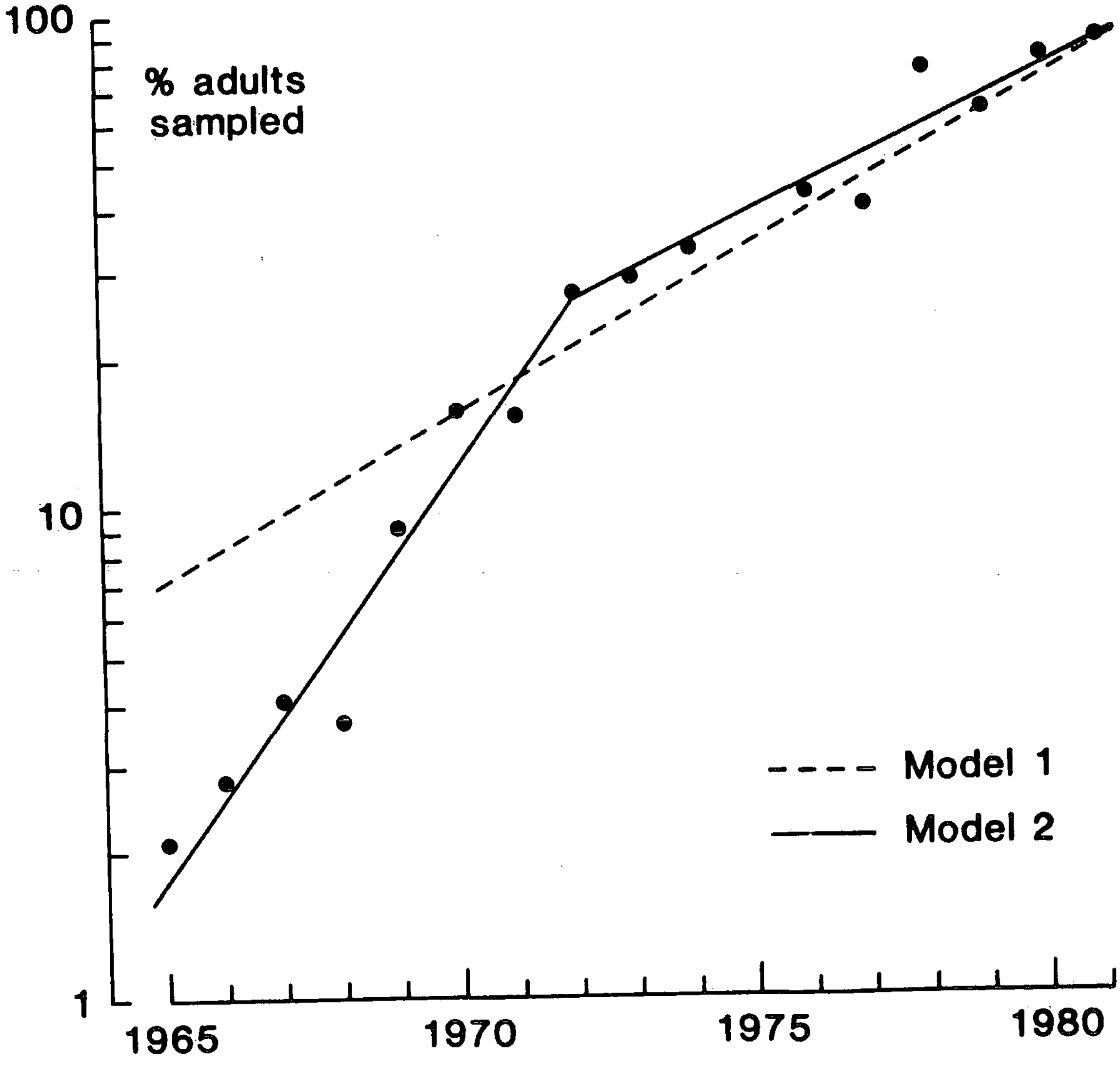


Table 4.3 Three models of adult annual survival for the Shag on the Isle of May, fitted to the cohort data displayed in Figure 4.3.

N_i = initial number of adult Shags in the cohort from year *i*
R_i = number of Shags recorded in 1982 from the cohort of year *i*
r = sampling efficiency

a) Constant adult annual survival between 1965 and 1982 (s):

Model: $R_i = N_i\ r\ s^{82-i}$ for 64[i[82

Parameters	Estimates	95% C.I.	Goodness of fit
s	0.854	0.832-0.877	$X^2_{15} = 17.37$ N.S.
r	1.038	0.967-1.113	

b) Constant adult annual survival between 1972 and 1982 (s_a)
Constant adult annual survival between 1965 and 1972 (s_b)

Model: $R_i = N_i\ r\ s_a^{82-i}$ for 71[i[82

$R_i = N_i\ r\ s_a^{10}\ s_b^{72-i}$ for 64[i[72

Parameters	Estimates	95% C.I.	Goodness of fit
s_a	0.874	0.853-0.895	$X^2_{14} = 7.18$ N.S.
s_b	0.679	0.570-0.807	
r	1.004	0.947-1.065	

c) Constant adult annual survival between 1972 and 1974, 1976 and 1982 (s_a)
Constant adult annual survival between 1965 and 1972 (s_b)
Constant adult annual survival between 1974 and 1976 (s_c)

Model: $R_i = N_i\ r\ s_a^{82-i}$ for 75[i[82

$R_i = N_i\ r\ s_a^{6}\ s_c^{76-i}$ for 73[i[76

$R_i = N_i\ r\ s_a^{6}\ s_c^{2}\ s_a^{74-i}$ for 71[i[74

$R_i = N_i\ r\ s_a^{6}\ s_c^{2}\ s_a^{2}\ s_b^{72-i}$ for 64[i[72

Parameters	Estimates	95% C.I.	Goodness of fit
s_a	0.888	0.853-0.924	$X^2_{13} = 6.67$ N.S.
s_b	0.684	0.582-0.802	
s_c	0.820	0.711-0.947	
r	0.984	0.915-1.057	

differed from the second in that the annual survival rate during the crash (1974/75, and 1975/76) was allowed to vary. The estimated annual rate of survival during the crash was 82.0%, apparently slightly lower than the annual rate of 88.8% in the years after and immediately before it. However, even this slight difference was an artifact of the unusually high survival of the 1978 cohort, which averaged 94.1% over four years: repeating the analysis without the 1978 cohort gave the annual survival rate during the crash as 88.1%, no different to the estimate for other years after 1971. Furthermore, there was no improvement in fit relative to the second model (likelihood ratio test: chi-square=1.00 df=1 N.S.). Thus, contrary to expectation, the rate of adult mortality had remained constant over the years of the crash. The same was obviously true for the rate of emigration, unless emigrant Shags had returned to the Isle of May before 1982; this was highly unlikely in a species where the normal emigration rate of breeders was only 0.5% _per annum_ (Potts 1969).

The greater number of dead Shags recovered in summer 1975 compared to summer 1976 (Armstrong _et al_. 1978) was therefore misleading. As no extraordinary mortality was involved, the proportion of dead birds reported had to be unusually high. Several factors suggest that this was the case. First, the number of days of onshore winds (N-SE) in May and June was 40 in 1975 and only 19 in 1976. In view of the importance of wind drift (Coulson _et al_. 1968; Bibby & Lloyd 1977; Bibby 1981), the predominance of onshore winds in 1975 would substantially increase the number of corpses washed up on the mainland; the same point was made by Armstrong _et al_. (1978). In quantitative terms, Bibby & Lloyd (1977) showed experimentally that differences in wind direction could result in a five-fold difference in the number of corpses recovered; the number of dead Shags recovered in 1975 was not even three times that in 1976. Furthermore, the 'red-tide' alert in

Northumberland led to extensive searches of the coastline in 1975 for dead seabirds; this increased the number of ringing returns. Finally, on the Isle of May itself, there was no difference in the number of ringed Shags found dead in 1975 and 1976: only three were discovered in each year.

The only remaining explanation for the crash was extensive non-breeding amongst experienced adult Shags. The extent of non-breeding was evaluated by simulating the size of the breeding colony of Shags on the Isle of May from 1963 onwards, using further parameters examined in the next paragraphs.

Cohorts marked before 1972 showed a reduction in survival compared to the later cohorts. There are four possible explanations for this.

(a) The proportion of Shags identified in 1982 was smaller for pre-1972 cohorts than for later ones, resulting in an apparently poorer survival of the early birds. This was unlikely: older breeders being considerably easier to approach than young ones, the bias, if any, ought to have been in the opposite direction.

(b) A proportion of rings on earlier cohorts were illegible, so that some old birds were not recognized. A total of 13 ring-numbers from this study were either incomplete (6), or had replaced illegible rings in previous years (7). By considering all combinations for the missing digits, at most another eight birds recorded as breeding adults before 1972 could be accounted for. The deviation from a line with constant 87.4% annual survival represented a shortfall of 28 birds from those years, so that illegible rings contributed only slightly to it.

(c) The survival of Shags in the late 1960s was effectively poorer than in later years. This period coincided with the peak in organochlorine pesticides in Shag eggs (Coulson _et_ _al_. 1972), and by inference in adult Shags. Potts _et_ _al_. (1980) calculated that the average annual survival rate for Shags on the Farne Islands between 1962 and 1971, excluding the 'red-tide' year of 1968, was 82.8±0.7%. Although lower than the present estimate of 87.4% for recent years, it was above the 95% confidence limits of the estimate for early years (57.7%-79.3%). Again, although this may have been a contributing factor, it did not fully explain the difference in survival.

(d) The survival of Shags decreased with extreme age. The Shags recorded as adults before 1972 would have bred for the first time aged two or three, and, on average, would have lived for approximately six years before being caught. Most of these birds, in 1982, would be therefore at least 18 years old. It was not unlikely that, as pointed out by Botkin & Miller (1974), annual mortality increased with old age. Coulson (1984) has recently shown that in the Eider Duck, the adult annual survival rate was approximately constant, at 89.5%, for the first 16 breeding years then declined rapidly. A similar phenomenon in the Shag would lead to the results in Figure 4.3, with a curve of increasing slope being approximated by two straight lines.

4.5 Second-year survival rate.

The survival of Shags during their second year after hatching was calculated from ringing returns of birds which died in their first or second year of life. Intuitively, if a large proportion of a cohort of ringed chicks was found dead during the first year after ringing, mortality over the first year had been high so that the number of birds entering their second year would be small, and the proportion of that cohort reported dead in the second year after ringing would likewise be small. Conversely, a small proportion of returns during the first year was likely to lead to a greater proportion of birds being recovered dead in their second year. This relationship was used to evaluate the survival of Shags during their second year after hatching. Formally, assuming the recovery rate, r, and the second-year survival rate, s_2, to be constant, and the first-year survival, s_{1i}, to vary with year i, then the proportion of chicks ringed in year i and recovered in their first year of life, F_i, is described by $F_i = r\ (1-s_{1i})$. S_i, the proportion of chicks ringed in year i and recovered in their second year of life is described by $S_i = r\ s_{1i}\ (1-s_2)$. Hence $S_i = -(1-s_2)\ F_i + (1-s_2)\ r$, i.e. the negative slope of the regression of S_i against F_i for a number of years will provide an estimate of the second-year mortality rate. For 17 cohorts of Shags ringed as chicks on the Isle of May, the two proportions are plotted against each other in Figure 4.4. Birds shot (40 recoveries, of which 15 in 1965) were omitted from the analysis: the reporting rate of such birds was likely to be much higher than for other causes of death (Potts 1969), so their inclusion would have over-estimated the true rate of mortality. The regression equation was $y = -0.255x + 0.037$ (r=-0.729 P[0.001), where y was the proportion of Shags recovered in their second year of life, x the proportion recovered in their first year of life. The second-year survival rate was 74.5±5.5%.

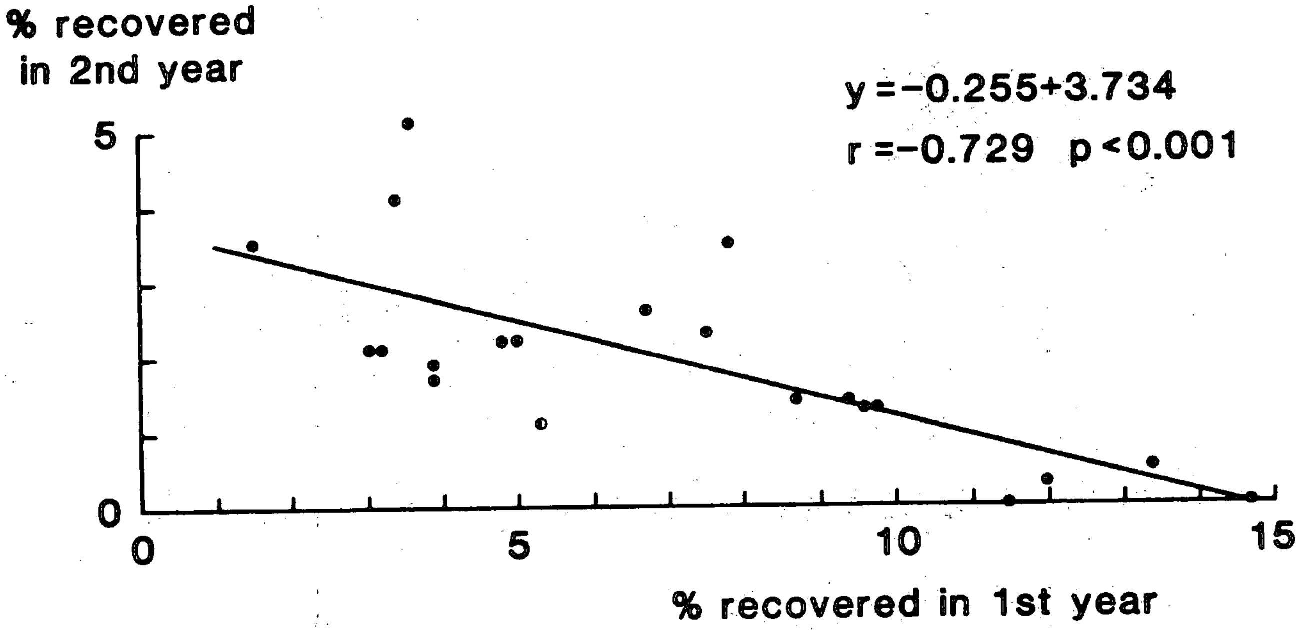
4.6 First-year survival rates.

From the annual adult and second-year survival rates, first-year survival rates for each year from 1963 to 1979 were back-calculated from the proportion of Shags, ringed as chicks in each of those years, which survived till 1982. The relationship between the three rates was given by

$$(\text{1st-year rate})(\text{2nd-year rate})(\text{adult rate})^{n-2} = \text{proportion surviving to 1982}$$

where n was the number of years between 1982 and the ringing of a particular cohort of chicks. The results are presented in Table 4.4. The change in

Figure 4.4 Relationship between the proportion of each annual cohort of shag chicks which was recovered during the first year after ringing, and the proportion of the same cohort which was recovered during the second year after ringing (1961-1981 cohorts).



adult survival, noted earlier, was applied when the birds reached 18 years of age (1963 and 1964 cohorts). The estimates of first-year survival rates obtained in this way obviously did not take into account emigration between fledging and breeding. This is considered in the next section. Their calculation also assumed that Shags ringed as chicks, which returned to breed on the Isle of May and were still alive in 1982, were all recorded during this study (100% sampling efficiency). The proportion of such birds which were effectively identified in 1982 was estimated in the following way. The total number of ringed Shags on the island has been estimated at 1532. In all, 1141 ring-numbers were recorded, of which 691 were Shags ringed as chicks. The estimation of adult annual survival rates gave a minimum sampling efficiency of 95%; it involved 442 Shags ringed as breeding adults. Hence the estimated sampling efficiency for Shags ringed as chicks was 691/(1532-442/0.95) = 0.648, or 64.8%. The difference in sampling efficiency between Shags ringed as chicks and Shags ringed or retrapped as breeding adults can be explained in two ways. First, all Shags ringed or retrapped as adults were ipso facto catchable; it was not unlikely that, as in the Eider Duck (Coulson 1984), some of the Shags ringed as chicks were uncatchable and therefore unapproachable, making it difficult to record their ring-numbers. Also, breeding Shags were very faithful to their nesting area; those which were ringed or retrapped between 1962 and 1981 were nesting in accessible areas, so were accessible for sampling in 1982. Ringed chicks, however, will often recruit into inaccessible areas of the Isle of May, and thus remain unidentifiable. The first-year survival rates corrected for a sampling efficiency of 64.8% are given in Table 4.4. In one instance, the corrected estimate slightly exceeded the second-year survival rate; it was set at the latter value of 0.745. The corrected mean first-year survival rate was 47.8%. Potts (1969) found that the average

Table 4.4 First-year survival rates for Shags reared on the Isle of May from 1963 to 1982: preliminary values and values corrected for a 64.8% sampling efficiency.

Year	1963	1964	1965	1966	1967	1968	1969	1970	1971	1972	1973
Preliminary value	0.525	0.326	0.076	0.458	0.396	0.441	0.291	0.358	0.484	0.469	0.253
Corrected value	0.745	0.502	0.117	0.705	0.610	0.679	0.448	0.551	0.745	0.722	0.390
Cohort size	377	137	398	193	566	751	610	462	457	723	423

Year	1974	1975	1976	1977	1978	1979	1980	1981	1982	Mean
Preliminary value	0.157	0.077	0.089	0.224	0.299	0.394	-	-	-	0.313
Corrected value	0.242	0.119	0.137	0.345	0.460	0.607	0.689	0.650	0.526	0.478
Cohort size	115	68	334	278	311	343	763	620	993	

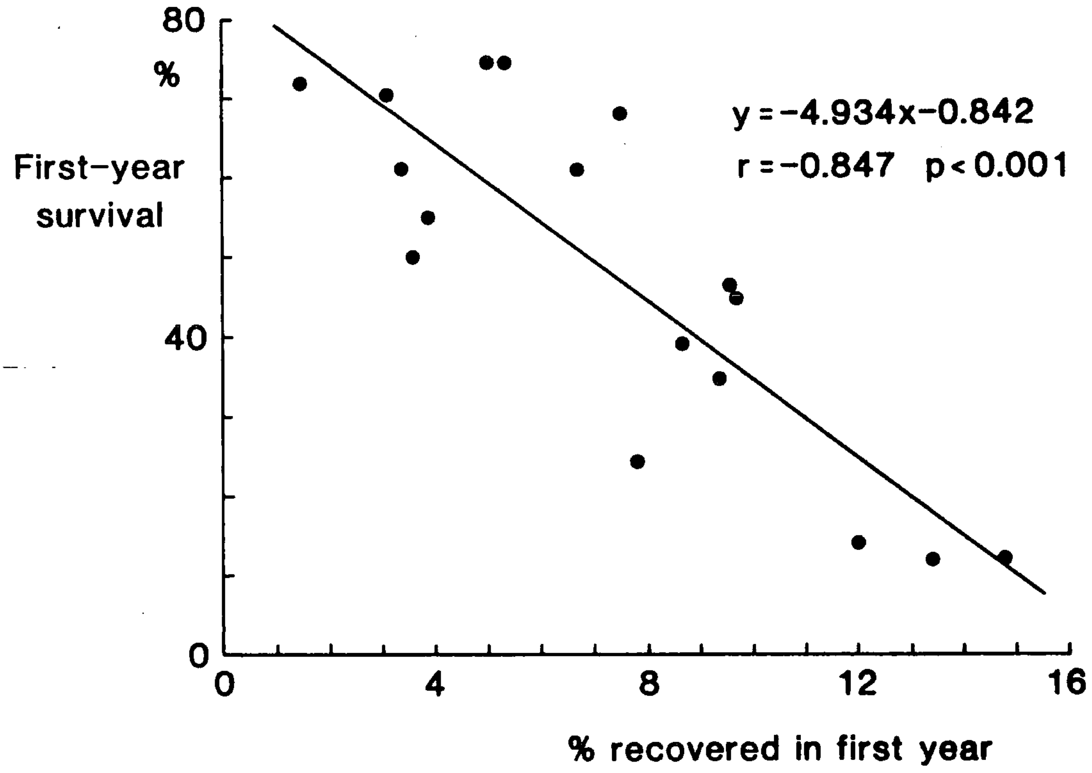
Values for 1980,1981 and 1982 were derived from the proportion of Shags ringed as chicks in those years and recovered dead in their first year of life; the mean values were calculated from the first-year survival rates from 1965 to 1979.

first-year survival rate without emigration for Shags on the Farne Islands was 51%, very close to the corrected mean obtained here.

The validity of the estimates of the first-year survival rates was verified by plotting them against the proportion of Shags ringed as chicks on the Isle of May and recovered dead in their first year of life (Figure 4.5). The two measures of first-year survival agreed well ($r=-0.847$ $N=17$ $P[0.001$). The regression equation, $y = -4.93x + 0.842$, was used to evaluate the first-year survival rates for the 1980 to 1982 cohorts, which had not yet recruited or were in the process of so doing in 1982, when the colony was sampled (Table 4.4). The slope of this equation, -4.93 ± 0.81, meant that on average, one in every five Shags which died in their first year of life was reported.

The first-year survival rates varied considerably between years, ranging from 11.9% in 1965/66 to 74.5%, the level of second-year survival, in 1963/64 and 1971/72. The next section demonstrates that a low first-year survival rate for a given cohort was not the result of increased emigration from the Isle of May, but represented true mortality. The low first-year survival of the 1965 cohort corresponded to a notorious eruption year for Shags on the Farne Islands; Potts (1969) found that the 1965 cohort of Farne Islands chicks suffered one of the highest first-year mortalities since 1953/54. Table 4.4 shows that the first-year survival of Isle of May Shag chicks was also unusually low for young fledged during the three years of the crash, particularly the worst years 1975 and 1976 (rates of 24.2%, 11.9% and 13.7% respectively). Although the adult annual survival rate remained unaffected over the crash years, the survival of chicks for the first year after fledging was down to a third of the average during the same period. Galbraith _et al._ (1981) showed that these were apparently not eruption years.

Figure 4.5 Correspondence between first-year mortality, as measured through ringing recoveries, and first-year survival, derived from ringed shag chicks which survived and were sampled in 1982.



The seasonal changes in the number of Shags recovered dead in their first year, during the three years of the crash compared to other years, are shown in Table 4.5. The pattern of recoveries was very different in the two periods (chi-square=60.9 df=5 P[0.001). In normal years, when most young fledged in July, only 16% of dead birds were found before November and the peak period for recoveries was from January to April. During the crash, despite fledging occurring over a month later, 45% of dead first-year Shags were found before November, with only a secondary peak in January-February. Having been pooled over several years, these figures are less likely to result from the vagaries of wind, and suggest that post-fledging mortality was heavier shortly after fledging in crash years than in other years.

4.7 Immigration and emigration to and from the Isle of May.

Searches at other colonies in the Forth-Farnes area produced 19 Shags ringed on the Isle of May, of which only one had been either ringed or retrapped on the Isle of May as a breeding adult. Thus emigration from the Isle of May after first breeding was negligible. The distribution according to age of ringing of the 18 other Shags is presented in Table 4.6. The records form two clusters: chicks from 1970 to 1973, and chicks from 1980 and 1981. Strikingly, these intervals correspond to periods of relatively high first-year survival rates (Table 4.4). In particular, none of the emigrant Shags recorded in 1983 belonged to cohorts of chicks ringed from 1974 to 1976, for which the first-year survival rates were calculated as being especially low. These rates therefore represented pure mortality.

Most of the emigrants from the 1970-1973 cohorts were Shags which would have recruited to the Isle of May during 1974-1976. Although it was shown that no abnormal emigration of breeding adults from the Isle of May had

Table 4.5 Seasonal changes in the numbers of Shags from the Isle of May recovered dead during their first year after fledging, in the years of the crash (1974-1976) and in other years.

	July-August	September-October	November-December		
1974-1976	36 (6.7%)	51 (9.6%)	102 (19.1%)		
Other years	2 (3.3%)	25 (41.7%)	7 (11.7%)		

	January-February	March-April	May-June	Total
1974-1976	125 (23.4%)	114 (21.3%)	106 (19.9%)	534
Other years	19 (31.7%)	6 (10.0%)	1 (1.7%)	60

Table 4.6 Shags ringed as chicks on the Isle of May, and found breeding at other colonies in 1983 (by year of ringing).

	Year of ringing on Isle of May									
	1962	1963	1964	1965	1967	1968	1969	1970	1971	1972
Emigrants	0	0	0	0	0	0	0	2	4	5

	Year of ringing on Isle of May									
	1973	1974	1975	1976	1977	1978	1979	1980	1981	Total
Emigrants	2	0	0	0	0	0	0	3	2	18

taken place during 1975 and 1976, it was possible that potential recruits to the island had been deterred and established themselves at other colonies. However, in view of the high first-year survival rates of those cohorts without correcting for emigration, it was unlikely that emigration of young took place on a large enough scale to have much impact on events at the Isle of May.

Immigration to the Isle of May was low. In 1982, only five non-local ringed Shags were recorded, making up less than 0.5% of the marked Shags identified. One of these was a three-year-old male from Craigleith, the only recent immigrant recorded. The other four had been ringed on the Farne Islands, one in 1970, and three before 1968. The latter were the remnants of an influx to the Isle of May of 20 Farnes-ringed Shags after the 1968 'red-tide' off the Northumberland coast (Coulson _et al_. 1968). The sightings of the 20 birds were the result of extensive searching in the years after the 'red-tide'; as most of the Farne Islands Shags had been colour-ringed, searching was effective and few immigrants to the Isle of May were likely to have been missed (Coulson _pers_. _comm_.). Even if all such Shags had arrived on the Isle of May in 1969, they would still only have constituted 1% of the breeding Shags at the colony in that year. With only three other immigrants recorded between 1963 and 1968, it is obvious that immigration before the crash was minimal.

4.8 Age of first breeding and recruitment.

On the Farne Islands, Potts _et al_. (1980) found that about half of the females bred two years after hatching, the remainder waiting to breed for the first time till their third summer. In males, the corresponding proportions were about 80% and 20%, based on 111 Shags colour-ringed as chicks (Potts 1966). In the present study, the rings of 114 two-year-old males and 21 two-year-old females were read in 1982. The number of ringed 1980 chicks expected to be alive and sampled in 1982 (if all had recruited) was 254. Assuming an equal sex ratio, this led to a recruitment rate of 90% for second-year males and 17% for second-year females. The rates for the recruitment of males two years after hatching were similar on the Farne Islands and on the Isle of May; the discrepancy between the female rates may be due to the more timid two-year-old females being more difficult to record than two-year-old males.

4.9 Annual number of young fledged per pair.

In most years, the Isle of May ringing schedules contained information on brood sizes for the Shag chicks which had been ringed. Shag chicks are normally ringed four to six weeks after hatching, and fledge at the age of seven to eight weeks (Snow 1960). In order to examine whether the mean annual brood size at ringing could provide a way of estimating the mean number of chicks fledged per pair (including failed breeders), the mean brood size at ringing for four distinct geographical areas of the Isle of May in 1981 and 1982 was plotted against the mean number of chicks fledged per nest in that area in those years (Figure 4.6). Each point was based on at least 40 broods. Another four points were taken from Potts (1969), corresponding to the years 1963-1966 on the Farne Islands. A linear regression of chick production (y) against brood size at ringing (x) gave the predictive equation $y = 1.60x - 2.11$ ($r=0.897$ $N=12$ $P[0.001$). The annual mean brood sizes at ringing and the associated values for chick production, calculated from the above equation, are presented in Table 4.7. No figures were available before 1965, and for 1972.

Figure 4.6 Relationship between mean brood size at ringing and the mean number of chicks fledged per pair. Eight points were calculated from shag nests monitored on the Isle of May in 1981 and 1982 in different areas of the island; four points correspond to the years 1963-1966 on the Farne Islands (from Potts 1969).

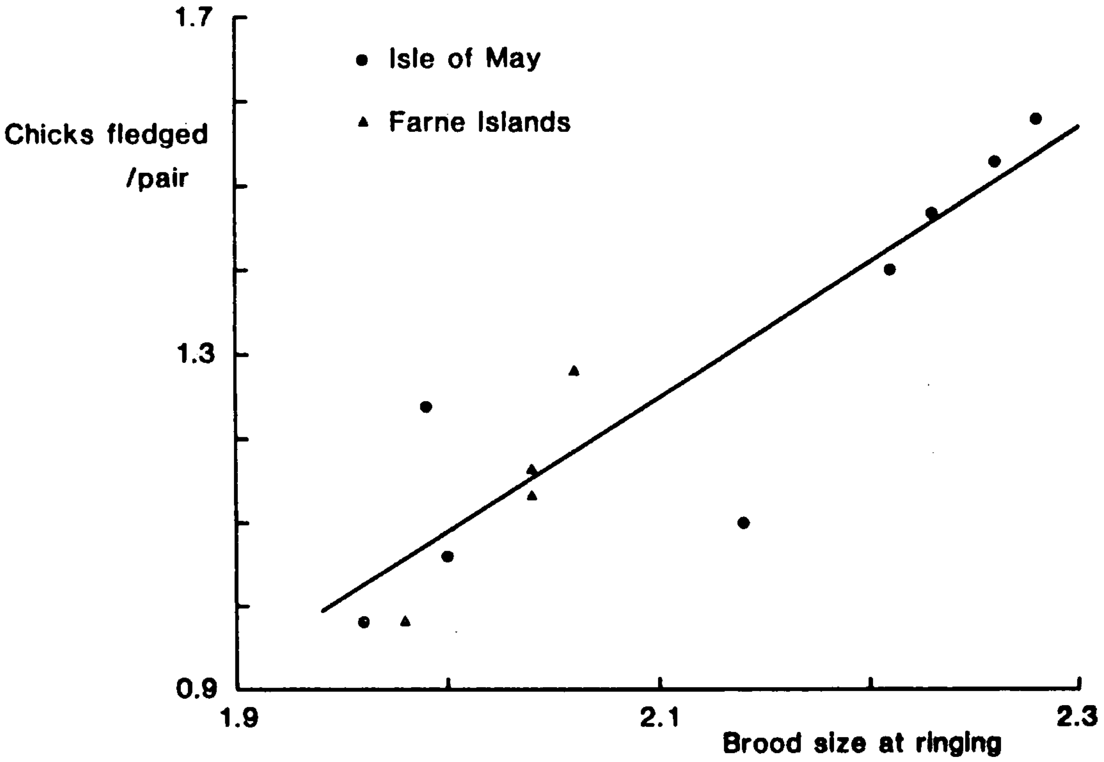


Table 4.7 Mean brood size at ringing and number of young fledged per pair for Shags on the Isle of May, from 1963 to 1982.

Year	1963	1964	1965	1966	1967	1968	1969
Brood size	-	-	2.05	1.87	2.02	2.04	1.90
N	0	0	186	15	198	353	335
No. fledged	-	-	1.17	0.88	1.12	1.15	0.93

Year	1970	1971	1972	1973	1974	1975	1976
Brood size	2.11	1.90	-	2.22	1.81	1.86	1.73
N	204	30	0	59	36	21	187
No. fledged	1.27	0.93	-	1.44	0.79	0.87	0.66

Year	1977	1978	1979	1980	1981	1982	Mean
Brood size	2.03	2.01	1.99	2.21	2.20	2.06	2.00
N	74	165	142	285	276	467	
No. fledged	1.14	1.11	1.07	1.43	1.41	1.19	1.09

Overall, 1.09 chicks were fledged annually per pair. Although isolated cases of below-average production occurred before and after the crash, the number of young fledged per pair was lowest during the three consecutive years of the crash: a pair succeeded in fledging on average only 0.77 young in each of the years 1974 to 1976. Taking into account also the particularly low first-year survival rates during that period, the reproductive success of Shags which bred in those years, in terms of the number of offspring which subsequently bred, was less than 0.1 chicks per pair in a year.

4.10 Simulation of the numbers of Shags breeding on the Isle of May.

Survival rates, recruitment and chick production were brought together in a simple deterministic model simulating the changes in annual numbers of Shag nests on the Isle of May between 1963 and 1983. As the male Shag selects the nest-site and initiates nest-building (Snow 1963), the model equated nests with breeding males and all calculations were performed on cohorts of males. Potts et al. (1980) showed that the annual survival rates for male and female Shags were similar so that the survival estimates calculated earlier remained valid. The model recognized four age classes: chicks of the year, one-year-old Shags, two-year-old Shags, and Shags over two. In 'normal' years, i.e. excluding 1974 to 1976, the transformations applied to each age class to move from one year to the next are illustrated schematically in Figure 4.7. Emigration is already included within the estimates of first-year survival; immigration has been shown to be low, and was ignored. The model was initialised by calculating the number of chicks fledged in 1963, 1964 and 1965 from the actual nest counts in those years, and gradually building up the other age classes according to the steps in

Figure 4.7 One cycle in the simulation model of colony size for Shags on the Isle of May (a normal year). The pathways indicate the transformations applied to each age class to move from one year to the next. Nests are equated with breeding males and all calculations are performed on cohorts of males.

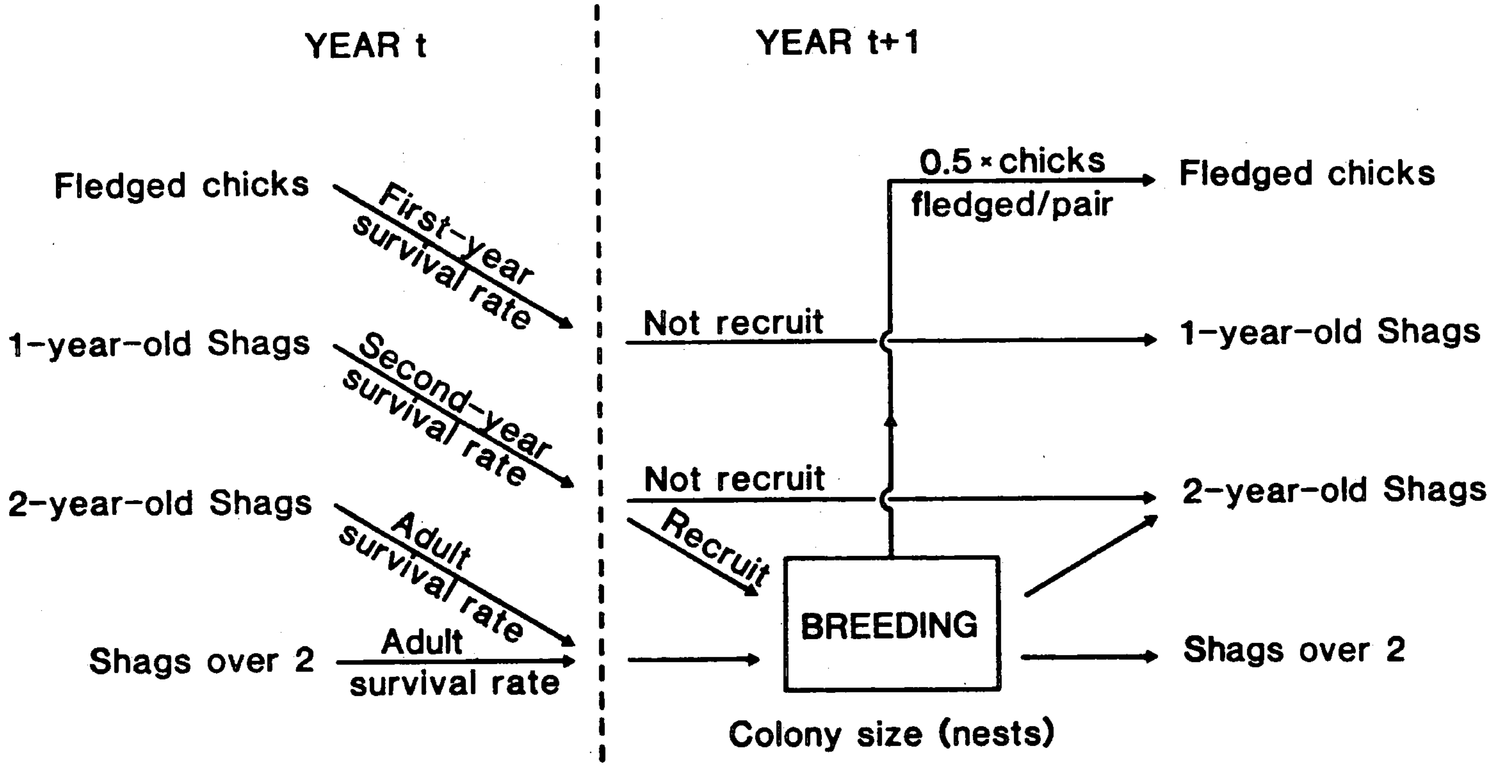


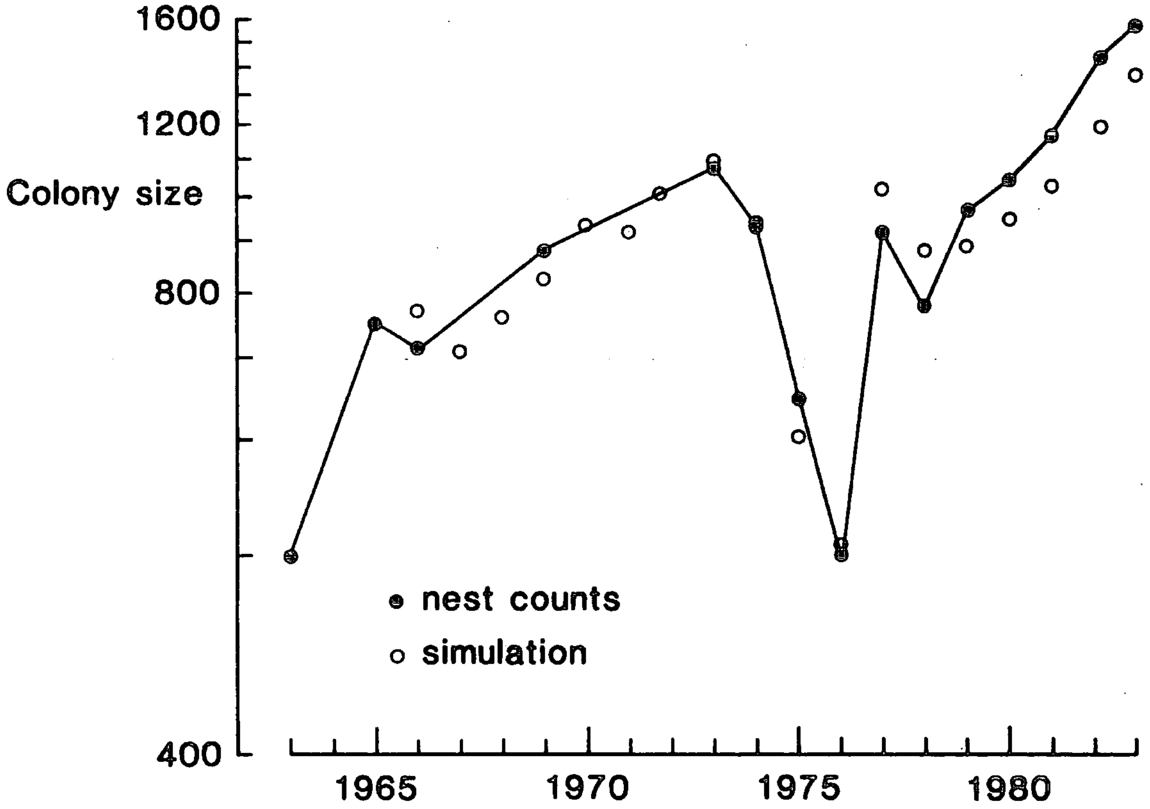
Figure 4.7. In years when the mean brood size at ringing was not available, the mean chick production was set at the overall mean of 1.09 chicks/pair. Male recruitment was put at 85% of two-year-old Shags, 100% of three-year-old Shags.

During the crash years, the extent of non-breeding by experienced Shags was gauged from the model by excluding from the numbers of breeders in those years an increasing proportion of Shags which had bred previously, until the predicted figures approximated the actual nest counts in 1974, 1975 and 1976. The extent of non-breeding depended on that of recruitment in those years: if recruitment was high, a high proportion of non-breeding was necessary to compensate. Maximum and minimum estimates of the proportion of experienced breeders which refrained from breeding during the crash were obtained by setting normal and nil recruitment respectively. In 1977, when the situation apparently returned to normal, all non-recruited adults and non-breeding adults were assumed to have attempted to breed.

A preliminary run of the model with an adult annual survival rate of 87.4% consistently over-estimated the number of nests before the crash. This was rectified by setting the adult annual survival rate at 0.854, the average value over all cohorts obtained from the first survival model (Table 4.3); it was equivalent to including a correction for the lowered survival of the oldest age classes.

The outcome of running the simulation model with no recruitment during the crash years is shown in Figure 4.8. Natural mortality sufficed to produce the decline in nest numbers between 1973 and 1974; the sharp drop in 1975 and 1976 required the proportion of non-breeders among adults which had previously bred to be 25% in both years. With normal recruitment, the proportion of non-breeding adults increased to 30% in 1974, and 60% in 1975 and 1976. Thus the actual figures for non-breeding, in 1974, lay between 0%

Figure 4.8 Simulated colony size and actual nest counts for Shags on the Isle of May from 1963 to 1983. The simulation assumes no recruitment during the years of the crash 1974-1976; in 1975 and 1976, the proportion of non-breeders among adults which had bred in previous years was set at 25%.



and 30% of adults which had previously bred, and in 1975 and 1976, between 25% and 60%. Some experienced breeders may therefore have refrained from breeding for up to three years. With conditions such that experienced adults were opting out of breeding, it was not unlikely that the recruitment of first-time breeders dropped considerably between 1974 and 1976. Many of the potential 1974 recruits may have deferred breeding three years beyond what was normal; they would all have done so in the extreme case of no recruitment.

The model successfully reproduced the pattern of the recovery from the crash, with an initial upsurge in 1977 as non-breeders started nesting again. The slight fall-back in 1978 was produced by a lack of recruits due to the low young production and chick survival during the crash. The relatively poor fit of the model to the counts made in recent years may be due to an increase in immigration. The five Isle of May chicks from 1980 and 1981 found breeding at other colonies in 1983 (Table 4.6) indicated that after a pause, emigration from the Isle of May had started up again. Immigration was probably taking place as well, heralded by the 1979 Craigleith chick found breeding on the Isle of May in 1982, and largely unobserved because of the small number of Shag chicks ringed since 1975 at Forth/Farnes colonies other than the Isle of May and the Farne Islands.

4.11 A summary of the features of the crash.

The features characterising the crash of Shags on the Isle of May, in terms of the dynamics of the colony and the breeding biology of the species, are as follows:

(1) The adult annual mortality rate remained unchanged, at 87.4%.

(2) Up to 30% of adults which had previously bred refrained from breeding in 1974, and up to 60% in 1975 and 1976.

(3) The breeding season was at least a month later than normal.

(4) The number of young fledged per pair was two-thirds that in normal years.

(5) The first-year survival of young fledged between 1974 and 1976 was less than a third of that in other years, and ringing recoveries indicated that mortality was heavier than normal shortly after fledging.

4.12 Possible reasons for the crash on the Isle of May.

The unchanged adult annual survival rate over the period of the crash effectively exonerated causes associated with heavy adult mortality. The available direct evidence fully supports this, and is reviewed below.

4.12.1 'Red-tide'.

The abrupt decline in breeding numbers of Shags on the Isle of May in 1975 was superficially similar to the effects of the 'red-tide' on the Shag colony on the Farne Islands in the same year (Armstrong et al. 1978). However, levels of toxicity in mussels, the standard method of monitoring 'red-tide' outbreaks, around the Firth of Forth in 1975 were "very low" (Howell in litt.), compared to the maximum of 6146 mouse units/100g shellfish tissue recorded off the Northumberland coast (Ayres & Cullum 1978). Furthermore, despite the regular presence of observers throughout the summer, no exceptional Shag mortality nor any of the other characteristic symptoms of a 'red-tide' (Coulson et al. 1968) were noted on the Isle of May in that year.

4.12.2 Water quality.

The general water quality of the Firth of Forth was high (Forth River Purification Board Annual Reports 1976, 1978; Williamson *in litt.*). Average concentrations of lead, copper & cadmium in unfiltered seawater, calculated from Anderson *et al.* (1981) for their easternmost sampling stations, at Seton Sands and Ferny Ness, were 1.42, 1.04 and [0.10 μg/l for the period May 1975-December 1976, and 3.27, 2.72 and [0.10 μg/l respectively for the period November 1978-March 1980. In both sampling periods, the concentrations of cadmium were negligible; those of lead and copper were higher in 1978-1980, after the crash, than in 1975-76, when numbers of breeding Shags were at their lowest.

4.12.3 Pesticide loadings.

The average levels of residues of organochlorine insecticides in Shag eggs (ppm wet weight) from the Isle of May for six years between 1965 and 1971, calculated from Coulson *et al.* (1972), were 0.57 for dieldrin and 1.91 for pp'-DDE. In 1976, when the size of the breeding colony was at its lowest, the concentrations of dieldrin and pp'-DDE were 0.51 and 1.38 respectively, based on a sample of 30 eggs (Coulson, unpubl. data). For both substances, residues in 1976 were lower than in earlier years, thus continuing the downward trend in concentrations noted by Coulson et al. (1972).

Not only did these results confirm the deductions made on the basis of the survivorship data, but they also showed that factors such as pesticides and heavy metals, which might have had a temporary debilitating effect rather than a lethal one, could not be held responsible for the poor breeding success and first-year survival rates during the crash. The other main factors which might be expected to fit the features of the crash were climatic variables and the food supply. These are examined below.

4.12.4 Climate.

In normal years, the first Shag egg was laid in April or even at the end of March. Any delaying effects of climate upon timing of breeding should therefore have been experienced by the Shags sometime during the first three months of the year. The only month to show significant correlations between climatic conditions and the laying date of the first Shag egg was March, the month immediately preceding the usual laying date. The climatic factors involved were the daily mean temperature, the number of hours of bright sunshine per day, the number of days of easterly winds, and the number of days of westerly winds (Figure 4.9). These four factors were strongly intercorrelated. The partial correlations of any three of them with laying date when the fourth was held constant were no longer significant (Table 4.8); this indicated that the four relationships probably had the same underlying cause, which was best represented by the factor showing the strongest simple correlation, the number of days of westerly winds (r=-0.620). As none of the three measures of wind speed was important, it was probable that the ultimate factor coming through was temperature-dependent, westerly winds being associated with warm and easterlies with cold temperatures. The correlations with laying date thus showed that breeding occurred earliest in years of high March temperatures, strong insolation and persistent westerlies, and latest in years when March was cold, overcast, and dominated by east winds. The regression equation of

Figure 4.9

Relationships between the date of laying of the first Shag egg on the Isle of May (days after 10 March) and four March climatic factors: daily mean temperature, number of hours of bright sunshine per day, number of days of easterly winds, number of days of westerly winds. Values are plotted for all years between 1961 and 1983, except 1963 and 1964 when laying date was unknown. Closed circles denote normal years, open ones the crash years (1974-1976).

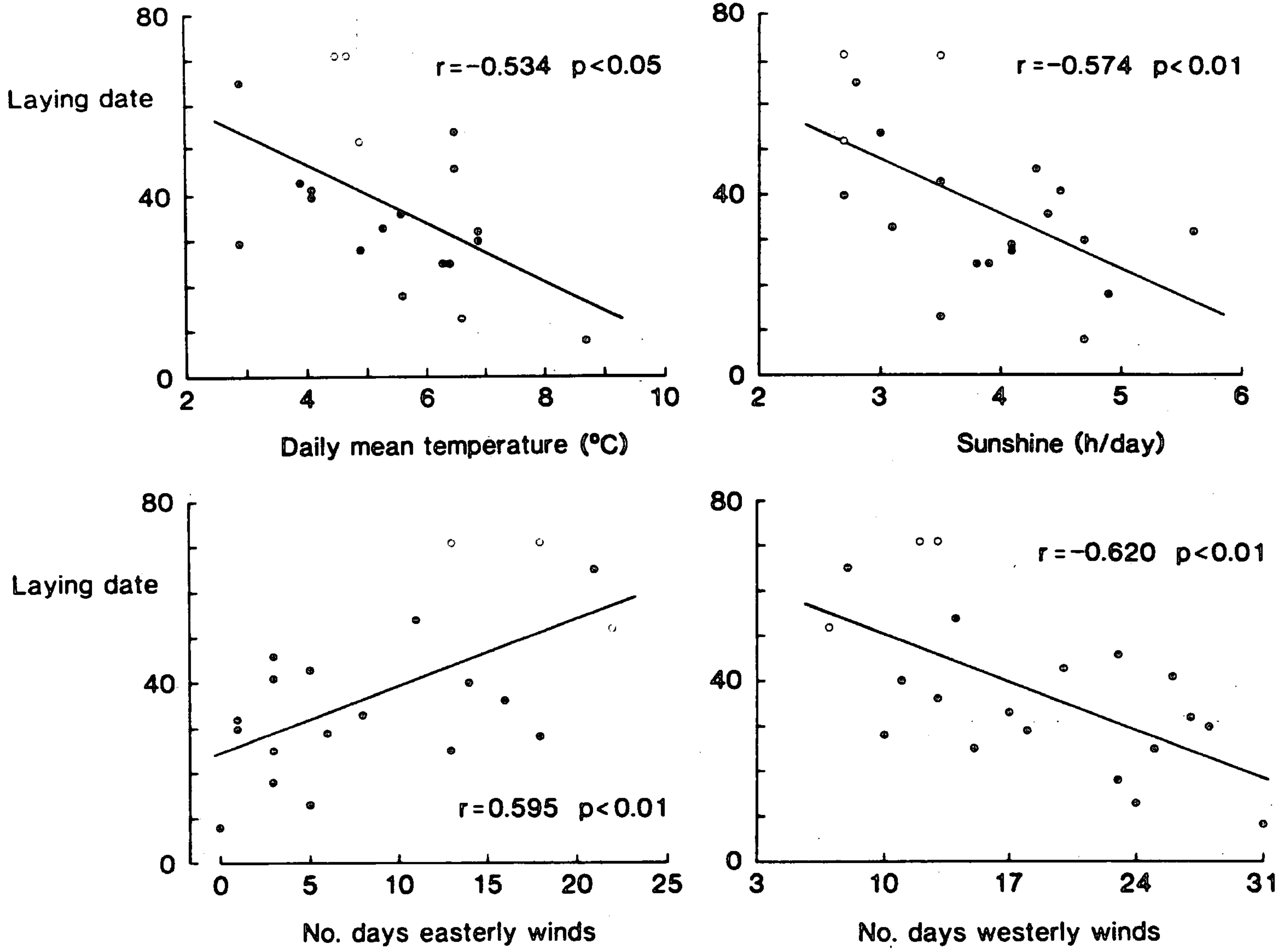

Laying date
80
40
0
r=−0.534 p<0.05
2
4
6
8
10
Daily mean temperature (°C)
80
40
0
r=−0.574 p<0.01
2
3
4
5
6
Sunshine (h/day)
Laying date
80
40
0
r=0.595 p<0.01
0
5
10
15
20
25
No. days easterly winds
80
40
0
r=−0.620 p<0.01
3
10
17
24
31
No. days westerly winds

Table 4.8 Climatic factors in March correlating with the date of laying of the first Shag egg on the Isle of May between 1961 and 1983.

Simple correlations between factors (N=22):

	Sunshine	Easterlies	Westerlies
Daily mean temperature	0.535 **	-0.557 **	0.648 **
Hours of sunshine/day		-0.730 ***	0.790 ***
Days of easterlies			-0.964 ***

Simple and partial correlations of climatic factors with laying date (N=20):

	Simple Correlation	Correlation partialled on			
		Temperature	Sunshine	Easterlies	Westerlies
Temperature	-0.534 *	-	-0.362 N.S.	-0.341 N.S.	-0.256 N.S.
Sunshine	-0.574 **	-0.430 N.S.	-	-0.301	-0.222 N.S.
Easterlies	0.595 **	0.449 N.S.	0.352 N.S.	-	0.010 N.S.
Westerlies	-0.620 **	-0.442 N.S.	-0.357 N.S.	-0.217 N.S.	-

N.S.	Not significant
*	P[0.05
**	P[0.01
***	P[0.001

laying date ($\underline{y}$) against the number of days of westerly winds in March (x) is $y = -1.53x + 60.84$, i.e. an extra week of westerly winds in March advanced the timing of breeding by approximately ten days. It was equivalent to an increase in daily mean temperature of 1.5°C, or to an extra 50min of sunshine per day, or to seven fewer days of easterly winds. There was no evidence that any of the four factors had a cumulative effect upon laying date over March and the preceding two months.

February and March also corresponded to the peak time of first-year mortality in Shags from the Isle of May (Galbraith et al. 1981); there were however no significant relationships between the first-year survival rates and climatic variables in those months.

4.12.5 Food supply.

Shags feed predominantly on fish, the composition of the diet varying locally and seasonally; the main prey groups are Ammodytidae, Clupeidae and Gadidae (Steven 1933; Lumsden & Haddow 1946; Pearson 1968; Rae 1969). Detailed information on the abundance of fish species around the Isle of May is sparse, particularly in years before 1977. The only species for which data are available from the late 1960s onwards is the Herring. Because of the commercial importance of this species, international concern about over-fishing led to annual surveys of its immature stages with a view to managing the stocks. Abundance figures for Herring in their second year of life ('1-ringed') are available as the mean number of fish per hour's trawl for each latitudinal and longitudinal half-degree grid rectangle within the North Sea in February, for each year since 1968 (Postuma 1969; Postuma & Zijlstra 1970; Schubert 1972; Postuma & Kuiter 1973, 1974; Corten 1975, 1976, 1977, 1978, 1979, 1980, 1981, 1982, 1983a, 1983b; Corten & Kuiter

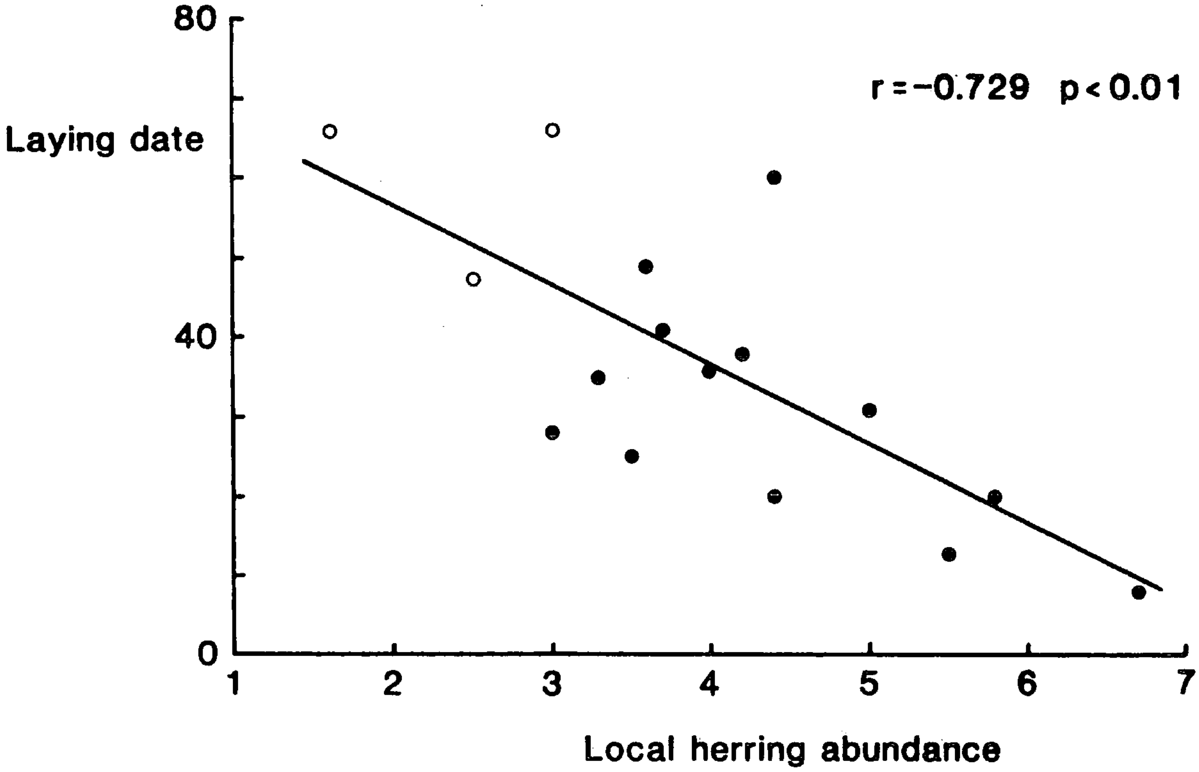
1981). A measure of the local abundance of Herring around the Isle of May was obtained by averaging the logarithm of 1-ringed Herring numbers from the four coastal rectangles situated between 55°30'N and 57°00'N. Figure 4.10 shows that there was a significant relationship between Herring abundance and the date of the first egg laid by Shags on the Isle of May from 1968 to 1983 ($y = -10.00x + 76.56$, $r=-0.729$ $N=16$ $P[0.01)$. On average, halving the abundance of 1-ringed Herring in the area retarded the breeding season by a week. The abundance of young Herring around the Isle of May was especially low during the three years of the crash. In contrast, in 1981, 1982 and 1983, when the first Shag eggs were laid particularly early, it exceeded all levels measured during the previous 13 years.

Between 1968 and 1983, the same climatic factors as in the previous section were significantly correlated with laying date; the number of days of westerly winds again provided the strongest correlation ($r=0.629$ $N=16$ $P[0.01)$. None of these factors were significantly correlated with the abundance of 1-ringed Herring. A multiple regression of laying date ($\underline{y}$) against Herring abundance (x_1) and March westerlies ($\underline{x}_2$) gave the equation $y = -7.86x_1 - 0.1.09x_2 + 86.91$ ($r=0.823$ $N=16$ $P[0.001)$; both variables contributed significantly to the regression, with partial correlations of -0.682 ($P[0.01)$ and -0.556 ($P[0.05)$ respectively. Thus Herring abundance and climate were unrelated, but both appeared to influence the timing of breeding in the Shag.

Herring abundance in February also correlated with the first-year survival rate of Shags fledged in the previous summer ($r=0.539$ $N=16$ $P[0.05)$; in general, high abundance of Herring corresponded to high first-year survival, low abundance to low survival.

The dearth of young Herring around the Isle of May between 1974 and 1976 was supported by the study of changes in the diet of young Puffins on

Figure 4.10 Correspondence between the date of laying of the first Shag egg on the Isle of May (days from 10 March) and the abundance of 1-ringed Herring around the island in February (see text). Values are plotted for all years between 1968 and 1983. Closed circles denote normal years, open ones the crash years (1974-1976).



the island by Hislop & Harris (in press) between 1973 and 1981. They found that Herring was completely absent from the food samples during the first years of the study, whereas by the end, 25% of fish brought in by adult Puffins was Herring. Hislop & Harris also shed some light on the state of the stocks of sandeels, which usually constitute the main prey species of the Shag during the breeding season (Pearson 1968). Most striking was the drop in the percentage contribution of sandeels to Puffin diet, from 93% in 1973 to 21% in 1975, followed by a partial recovery to 50% for the next three years. Furthermore, the mean length of sandeels collected between 1974 and 1976, 67.6±18.8mm (1 S.D.) was significantly less than that of sandeels collected in the other years of the study, 82.9±22.2mm (t=19.6 df]901 P[0.001). Both these facts suggest that sandeel stocks in the area were depressed in the years of the crash compared to previous and later years.

4.13 Discussion.

The techniques used in the present chapter to quantify the dynamics of the Shag on the Isle of May can be applied to any seabird affected by a disaster. The only requirement is a long-term ringing programme which has enabled a marked population to build up. It is vitally important that such a programme includes the marking of breeding adults as well as chicks. Unlike chicks, which suffer high and variable mortality during their first year of life at least, the adult annual survival rate is normally approximately constant (although it probably declines in old age, as suggested here for the Shag). This makes it relatively simple to test for abnormal deviations in certain years from a constant mortality rate. Reliable estimates of the annual adult mortality rates then constitute the key to evaluating the variable post-fledging mortality rates. Many conservation bodies now carry out regular surveys and censuses of breeding seabirds for monitoring purposes (e.g. Nettleship 1977; Folkestad 1978; Munro & Campbell 1979; Stowe 1982). As shown in this study, an annual census of breeding pairs, by itself, may be misleading. Although counts of Shag nests on the Isle of May revealed that a disaster had occurred, the suddenness and amplitude of the crash suggested that the decline was the result of death rather than non-breeding. To gain retrospective knowledge of the situation over the critical period, the large sample of marked Shags alive at the colony was an indispensable back-up.

The proportions of adult Shags ringed or recaptured since 1965 and surviving to 1982 proved conclusively that neither adult mortality nor emigration were the proximate cause of the crash on the Isle of May between 1974 and 1976. Adult annual mortality remained unchanged at 12.6% throughout this period, and, as mortality and emigration were indistinguishable, emigration likewise had remained unchanged. The only explanation left to account for the crash was large-scale non-breeding by adult Shags which had already bred in previous years. Simulation of the colony showed that, depending on the extent of recruitment, the proportion of adult non-breeders lay between 0 and 30% in 1974, and 25-60% in both 1975 and 1976. On the other hand, the first-year mortality of chicks fledged during the years of the crash was exceptionally high, and ringing returns indicated that birds died unusually soon after fledging; on average only 17% of them survived to their second year, compared to 56% in other years. At the same time, the numbers of young fledged per pair in those three years was found to be the lowest of all the values that were calculated; on average a pair fledged only 0.77 chicks in each of 1974, 1975 and 1976, whereas the mean chick production in other years was 1.16 fledglings/pair.

These figures, together with the particularly late breeding during the years of the crash (four to six weeks later then in normal years) pointed strongly towards food being the causative agent behind the events. The idea that food shortage can cause non-breeding is not new (e.g. Bertram _et_ _al_. 1934; Belopol'skii 1961). Few field studies, however, have proved the link between the two. Barry (1962) showed that in female arctic geese, reduced food availability through snow cover at the start of the breeding season led to the resorption of maturing egg follicles, resulting in smaller clutches or non-nesting. In bad years, up to 85% of adult Snow Geese and Canada Geese did not nest. Jones & Ward (1976) obtained similar results for the Red-billed Quelea. They further demonstrated that body condition could in itself provide proximate control of breeding, without the need for environmental releases. For species closely related to the Shag, there is some evidence that food abundance and breeding are indeed related. Berry et _al_. (1979) have shown that for Cape Cormorants, peaks in reproductive endocrine activity coincide with the peak abundance and body condition of their main prey item, the South African Pilchard. The only environmental cues possibly implicated were photoperiod and the seasonal change in wind pattern. For the Little Black Cormorant, an Australian species which breeds irregularly, Miller (1980) was able to explain 85% of the variation in its gonadal cycle by the interaction of a regular, cyclic stimulus such as temperature, the water level of the breeding lakes, and the abundance and availability of food. In two seasons, the latter was apparently the major proximate stimulus triggering gonadal activity. These results are consistent with those obtained for the Shag on the Isle of May: again a climatic factor such as temperature, sun or wind correlated with the onset of breeding, but the major factor explaining the variation in laying date was the abundance of Herring around the Isle of May in February, when birds would normally be coming into breeding condition.

Direct evidence of the importance of Herring in the diet of the Shag in late winter/early spring is lacking. Steven (1933) found that for Shags shot in winter off the Cornish coast, 49% of prey species were clupeids; in spring, by the time adult Shags had returned to their breeding area, clupeids comprised 11% of the diet of immatures sampled in the Clyde Sea area (Lumsden & Haddow 1946). During the summer, clupeids were almost completely absent from the diet of Shags on the Farne Islands (Pearson 1968) and off the east coast of Scotland (Rae 1969); the bulk of fish taken (60-80%) were sandeels. The fact that all sandeel fisheries take place in the summer months (Reay 1970; ICES fisheries statistics) strongly suggests that from October to March, sandeels are less readily available to Shags. Macer (1966) showed that Lesser Sandeels did not grow during the winter, indicating that feeding activity was low, and laboratory experiments by Winslade (1974) showed that the same species overwinters buried in the sand, emerging briefly to spawn in December-January. In contrast, juvenile Herring (0 and 1-ringed) approach close inshore during the winter months (Parrish & Saville 1965), so providing an alternative food source. It seems not unlikely that Shags rely to some extent on Herring before sandeels become available in April; the relationships between the local abundance of Herring in February, the timing of breeding and first-year survival rates of Isle of May Shags may thus be causal. The lack of correlation between young production and Herring abundance is also consistent with the absence of Herring from the summer diet of the Shag. Alternatively, the status of the Herring around the Isle of May each February may act as an indicator of the general suitability of the area in a given year for feeding by a range of fish species on which the Shag might prey. For instance, it was shown earlier that sandeels, the main summer prey, also appeared to have been affected during the period of the crash (from Hislop & Harris, in press). Such an effect might be linked to the overall trends in zooplankton biomass in the North Sea, which has declined steadily between 1948 and 1975 (Colebrook 1978). The decline appears to have reversed in later years, although numbers are still below the long-term mean (Robinson & Budd 1980; Cushing 1982).

Concerning the Herring in particular, one factor now recognized as being at least partly responsible for recent changes in abundance is overfishing: over the whole of the North Sea, the biomass of mature Herring gradually declined between 1947 and 1965, then dropped rapidly to a tenth of its 1965 value in 1975 (Saville & Bailey 1980). Following a complete ban on Herring fisheries from 1977 to 1981, the stock now appears to be recovering (Corten 1984). A combination of overall lower abundance and oceanographic factors may have exacerbated the situation around the Isle of May in the mid-1970s. The decline in stocks of Norwegian Herring during the 1970s has also been implicated in the almost total reproductive failure of the Puffin on Røst, Norway, between 1969 and 1980 (Lid 1980), and is likely to have been the reason for a recent shift in the wintering grounds of Shags from Runde (Johansen 1975).

The evidence therefore points towards a local failure of summer and winter fish stocks as being the cause of the Isle of May disaster. The situation seems comparable, albeit on a much reduced scale, to other cases where oceanic conditions and overfishing by man have adversely affected seabird populations. The most notorious catastrophe involved the guano birds of Peru following the collapse of the stocks of Peruvian Anchovy (Paulik 1971; Tovar 1978; Duffy 1983a). Elsewhere, the declining status of Cape Cormorants, Cape Gannets and Jackass Penguins in certain parts of South Africa has been linked to the decline of the South African Pilchard

(Crawford & Shelton 1978, 1981), and, off the Californian coast, the reduction in numbers of Double-crested Cormorants and Tufted Puffins was probably the result of the near extinction of the Pacific Sardine (Ainley & Lewis 1974).

In conclusion, this chapter demonstrates the value of long-term ringing as a means of analysing a catastrophe after the event. The natural corollary is that the marking of breeding adults and chicks should constitute an integral part of any seabird monitoring scheme, on an equal footing to annual censuses and surveys. In terms of effort, a minimum ringing target probably lies around 50 breeding adults and 500 chicks each year. For monitoring bodies which already include ringing within their remit, the results from the Isle of May provide well-deserved encouragement. For those which do not, it is hoped that the evidence presented here will persuade them of the importance of ringing as a necessary back-up to regular surveillance work.

5. AGE, TIMING OF BREEDING, CLUTCH SIZE, NEST STRUCTURE AND CHICK PRODUCTION.

5.1 Introduction.

In avian literature, many authors have demonstrated a relationship between the success of a bird in rearing young to fledging and its age, degree of maturity or breeding experience (Lack 1966, 1968; Ryder 1980). Invariably, the younger breeders prove themselves less successful than older birds. In passerines, yearling Blackbirds laid smaller clutches and hatched fewer young than older breeders (Snow 1958); clutch size was also smaller in one-year-old Great Tits (Perrins 1965) and Pied Flycatchers (von Haartman 1967). In non-passerines, Richdale (1957) showed that Yellow-eyed Penguins breeding for the first time laid smaller clutches and hatched fewer chicks than older breeders, while Coulson & White (1958) found that in the Kittiwake, first breeders laid fewer eggs. More recently, breeding success has been shown to be lower in young birds than in older ones for such different species as the Fulmar (Ollason & Dunnet 1978) and the Sparrowhawk (Newton et al. 1981). In most species, for example in the ones mentioned above, young birds also breed later than older ones. The difference ranged from only 1-2 days in the Fulmar (Ollason & Dunnet 1978), to over three months in Woodpigeons (Murton et al. 1974). A notable exception to this rule is the Blue-eyed Shag, where laying date is independent of age (Shaw 1984).

Independently of any age effect, the breeding performance of many species varies seasonally. The most usual trend is a decline in one or more reproductive parameters as the season progresses, for instance clutch size in the Kittiwake (Coulson & White 1961) and the Pied Flycatcher (von Haartman 1967), clutch size and nestling survival in the Great Tit (Perrins 1965). Such a tendency has usually been related to changes in food supply (Lack 1966, Perrins 1970). Alternatively, nesting success has been noted as increasing with season in a number of North American passerines (Nolan 1963, Roseberry & Klimstra 1970, Yahner 1983); the main reason put forward was a decrease in predation pressure later in the season. However, small sample sizes meant that these results were based on only three to four seasonal divisions, so that the figures for nesting success early and late in the season may be inaccurate. It is possible that the pattern in fact resembled that found by Patterson (1965) for Black-headed Gulls and by Brown (1967) for Herring Gulls, whereby fledging success increased initially then declined; eggs laid at the peak of the breeding period suffered less predation, as did the chicks from such eggs. In the Herring Gull, this seasonal pattern was confirmed in the detailed study by Parsons (1975) on the Isle of May, although Kadlec & Drury (1968) in New England found a straight decrease in chick production, and Harris (1969) on Skokholm described a straight increase. Thus the seasonal pattern of variation may differ within one species between areas and years.

The Pelecaniformes are, in general, no exception to the trends outlined above. Mature breeders fledge more chicks than young or first-time breeders in the Cormorant (Kortlandt 1942), the European and Cape Gannets (Nelson 1978), the Brown Pelican (Blus & Keahey 1978), and the European and Blue-eyed Shags (Potts et al. 1980, Shaw 1984). These studies, with the exception of Shaw (1984) for the Blue-eyed Shag, also show that the older birds breed earlier than the young ones. Over the colony as a whole, a seasonal decline in the number of chicks fledged per pair occurs for the European and Blue-eyed Shags (Snow 1960, Shaw 1984), and for the White

Pelican (Knopf 1979); when first-time breeders have been excluded, a decrease still takes place for the Brown Pelican (Blus & Keahey 1978), but not for the Gannet (Nelson 1966). The present chapter sets out to examine these relationships for the Shag colony on the Isle of May, and to compare the patterns recorded there with those described above, in particular with those observed for Shags on Lundy by Snow, and on the Farne Islands by Coulson and Potts.

5.2 Parental age and chick production.

The results presented here refer mainly to the more detailed and extensive 1982 data, although the data from 1981 are also included for comparison.

The effect of female age on chick production is shown in Table 5.1. Females were grouped into six age categories (2, 3, 4-6, 7-10, 11-13, 14+ years), and the mean number of chicks fledged per pair was expressed for three groups of male age (2, 3, 4+ years). In 1981, sample sizes were too small for any inferences to be made. In 1982, when three to 10 times more females were available in each class of male age, there was no significant effect of female age on the number of chicks fledged per pair. This agreed well with Potts et al. (1980).

As a result, the relationship between male age and young production could be examined independently of the age of the female partner, with a corresponding increase in sample sizes. The differences in the number of chicks fledged per pair between age classes were highly significant (Table 5.2), and accounted for 26% and 24% of the overall variability in numbers of chicks fledged per pair in 1981 and 1982 respectively. The bulk of the difference lay between second-year and older birds: analysis of variance

Table 5.1 Mean number of chicks fledged per pair in relation to female age, male age constant (sample size in parentheses).

1981

Male age (years)		Female age (years)						F-value
		2	3	4-6	7-10	11-13	14+	
2	Mean	0.86 (7)	0.00 (2)	2.00 (1)	3.00 (2)	2.00 (2)	-	-
	S.E.	0.26	0.00	-	0.00	0.00		
3	Mean	-	2.00 (1)	3.00 (1)	2.00 (3)	-	-	-
	S.E.	-	-	-	0.58	-	-	
4+	Mean	-	-	1.00 (1)	2.59 (17)	2.50 (12)	2.33 (3)	1.72 N.S.
	S.E.	-	-	-	0.15	0.23	0.33	

1982

Male age (years)		Female age (years)						F-value
		2	3	4-6	7-10	11-13	14+	
2	Mean	0.57 (95)	0.81 (27)	0.89 (9)	-	1.00 (2)	0.83 (6)	0.73 N.S.
	S.E.	0.09	0.16	0.39	-	1.00	0.40	
3	Mean	1.00 (1)	1.50 (8)	1.00 (3)	0.00 (2)	2.00 (4)	0.50 (2)	1.62 N.S.
	S.E.	-	0.38	0.58	0.00	0.41	0.50	
4+	Mean	-	1.57 (7)	1.50 (12)	1.93 (29)	1.80 (25)	1.56 (25)	0.63 N.S.
	S.E.	-	0.48	0.31	0.20	0.20	0.21	

Table 5.2 Mean number of chicks fledged per pair in relation to male age.

		Male age (years)						F-value
		2	3	4-6	7-10	11-13	14+	
1981	Mean	1.21 (105)	2.39 (18)	1.92 (12)	2.52 (42)	2.00 (17)	2.00 (6)	13.3 P[0.001
	S.E.	-	-	-	0.58	-	-	
1982	Mean	0.56 (346)	1.37 (83)	1.78 (55)	1.71 (65)	1.75 (55)	1.41 (54)	40.2 P[0.001
	S.E.	0.05	0.12	0.14	0.13	0.15	0.14	

Sample size in parentheses.

showed no difference between age classes over two (1981: F=2.29 df=4,90 N.S.; 1982: F=2.19 df=4,307 N.S.), and the discrepancy between the latter group and second-year birds was the cause of 91% (1981) and 95% (1982) of the total amount of variation explained by age.

In 1982, despite an overall lack of difference between age classes over two, both three-year olds and birds older than 13 appeared to fledge fewer chicks per pair than males aged 4 to 13 (Table 5.2). Chick production for the three age classes included in the latter group was remarkably similar, and averaged 1.74 chicks/pair. This value was significantly higher than that of 1.37 chicks/pair for third-year birds (t=2.57 df=256 P[0.05) and of 1.41 chicks/pair for birds over 13 (t=2.05 df=227 P[0.05). In 1981, the 7-10 age group fledged most chicks per pair (Table 5.2); sample sizes were too small to show up any differences between that group and either the third-year birds or those over 13.

Thus male Shags were at their peak in terms of reproductive output when aged 4 to 13 years; older birds tended to be less productive, as did third-year birds. Similar declines in old birds have been observed in the Kittiwake (Thomas 1983), the Great Tit (Perrins 1979) and the Sparrowhawk (Newton _et al_. 1981). For these species, as for the Shag, the hypothesis that older birds should increase their reproductive output in order to compensate for a shortening lease of life (Williams 1966, Pugesek 1981) was clearly invalid. By far the major difference in the number of young fledged per pair, however, lay between second-year Shags and older ones: in 1981, the performance of young birds was half that of older birds, and in 1982 merely a third. In absolute terms, this difference was of the order of 1 chick/pair in both years. Another way of visualising the difference between second-year Shags and Shags over two is in terms of the proportions of birds in each category which fledged two or more chicks per pair: in 1981, 40% of two-year-old males achieved this, compared to 75% of older males; in 1982, the corresponding proportions were 18% and 51%.

As the differences in mean chick production between the age classes of males older than two were negligible in comparison with that between two-year-olds and older birds, male Shags were divided into two main groups for subsequent analyses. 'Young' breeders comprised the second-year birds, and 'older' breeders encompassed all birds over two years of age. This division had the advantage of corresponding to the two main groups of Shags easily recognisable in the field on plumage (see Section 2.8 and Appendix 1); it was therefore no longer necessary to rely upon the restricted numbers of birds ringed as chicks to provide the age categories. The dichotomy of breeding male Shags according to plumage will be loosely referred to as 'breeding experience' (not strictly correct, as Section 4.8 showed that 90% of males attempted to breed aged two, the remainder waiting until their third year).

5.3 At which stage in the breeding cycle did age-related differences develop?

Only results from 1982 are presented here, as the relevant information was not available for 1981. In keeping with the fact that female age did not influence chick production, Table 5.3 shows that there was no relationship between female age and clutch size (considering clutches incubated for the full term, i.e. known to be complete). This agreed with Potts (1966) and Potts et al. (1980). Thus mean chick production was not dependent upon clutch size.

Between two consecutive visits to a site originally occupied by a nesting pair, it was not infrequent to find that a nest present on the first

Table 5.3 Clutch size in relation to female age in 1982.

	Female age (years)						F-value
	2	3	4-6	7-10	11-13	14+	
Mean	2.77 (39)	2.58 (26)	2.86 (14)	2.89 (18)	2.80 (20)	2.86 (21)	0.56 N.S.
S.E.	0.12	0.11	0.10	0.23	0.16	0.17	

Sample size in parentheses.

visit had disappeared by the second. On a few occasions, the actual process of nest destruction was observed: nests left unattended were raided by neighbouring Shags for nest material, and within a few minutes the whole structure would be dismantled and any nest contents scattered. Such an occurrence is referred to here as nest 'loss'. As nests containing live chicks were constantly attended by at least one of the parents, nest loss after hatching was equivalent to the death of the entire brood some time before the chicks fledged.

Nest loss was strongly related to the breeding experience of the male (Table 5.4). Before laying, before hatching and after hatching, second-year birds lost their nests more often than older ones. For both age groups, the proportion of nests lost was greatest between laying and hatching: 16% of males over two suffered nest loss at this stage, and 44% of second-years. Comparing the proportions of nests lost for the two age groups at each stage in the breeding cycle, the ratio was greatest before laying had taken place: young birds were then four times more likely to lose their nest than older ones (22% of nests lost as opposed to 5%). Of nests containing chicks, the proportion lost stood at 28% in second-year birds, and 15% in older ones.

The precise proportion of fully incubated eggs which hatched could not be directly assessed, as only rarely did visits to a nest coincide with the hatching of its eggs, and the mortality of chicks at and soon after hatching was high (Snow 1960, Potts _et_ _al_. 1980). However, it was possible to consider complete hatching failure, whereby a clutch, although fully incubated, failed to hatch any eggs at all. There was no difference in the proportion of failed clutches between the two age categories, which averaged 7% of fully incubated clutches (Table 5.5). This figure was significantly lower than the comparable one of 12% for Lundy (267 clutches from Snow (1960); chi-square=7.63 df=1 P[0.01), and the minimum one of 13% for the

Table 5.4 Male breeding experience and nest loss before laying, before hatching and after hatching in 1982.

	Second-year			Older			Chi-square	
	Lost	Retained	N	Lost	Retained	N	(1 df)	
Before laying	21.8%	78.2%	275	4.7%	95.3%	509	52.8	P[0.001
Before hatching	44.2%	55.8%	215	16.3%	83.7%	485	60.6	P[0.001
After hatching	28.0%	72.0%	312	14.8%	85.2%	539	11.9	P[0.001

Table 5.5 Number of clutches in 1982 which failed to hatch completely, in relation to male breeding experience.

	No eggs hatched	At least one egg hatched	Total
Second-year	9 (5.2%)	164 (94.8%)	173
Older	80 (7.1%)	1053 (92.9%)	1133
Overall	89 (6.8%)	1217 (93.2%)	1306

Chi-square=0.55 df=1 N.S.

Farne Islands (1026 clutches from Potts (1966); chi-square=22.1 df=1 P(0.001). These differences in the proportions of failed clutches may be the result of different climatic conditions during incubation; the temperature range for optimal development of avian embryos is narrow (Drent 1975), and climate has been found to affect hatching success in Red Grouse (Leslie 1911) and in Zebra Finches (El-Wailly 1966). Alternatively, hatching success in predatory birds is known to be affected by environmental poisons such as organochlorines and PCBs (Prestt & Ratcliffe 1972, Newton & Bogan 1974). The greater hatching success on the Isle of May could well be a result of a decline in the pesticide loadings in Shags following legislation restricting the use of such substances. Table 5.6, based on data from Coulson _et al_. (1972) and Newton (_in litt_.), shows that the levels of organochlorine compounds in Shag eggs in 1981 were significantly lower than those on the Farne Islands at the time of the study by Potts (data for 1965). The reduction in pesticide loadings in 1981 continued the downward trend noted on the Farne Islands and on the Isle of May after concentrations peaked in 1967-1968 for pp'-DDE, and in 1966 for dieldrin (Coulson _et al_. 1972).

Brood size within 10 days of hatching was recorded at 671 nests; of these, clutch size was known for 437. This enabled an evaluation of egg survival from before hatching to approximately one week after hatching, thus spanning hatching success and early chick survival for nests hatching at least one chick. For simplicity, this quantity will be referred to as 'hatching success'. The results are presented, broken down by clutch size, in Table 5.7. For second-year males, hatching success did not vary with clutch size (chi-square=5.85 df=2 N.S.) and neither did fledging success (chi-square=4.32 df=1 N.S.). For older males, there was no variation in the hatching success of clutches of 1, 2, 3 and 4 (clutches of 1 and 2 grouped;

Table 5.6 Mean (geometric) concentrations of organochlorine compounds in Shags eggs on the Farne Islands and on the Isle of May in 1965 and 1971, and on the Isle of May in 1981.

Year	Site	pp'-DDE (ppm)			Dieldrin (ppm)		
		Mean	95% C.L.	N	Mean	95% C.L.	N
1965	Farne Islands	1.49	1.33-1.68	54	0.74	0.71-0.76	54
1965	Isle of May	1.26	0.81-1.97	10	0.68	0.43-1.09	10
1971	Farne Islands	1.10	0.91-1.33	10	0.28	0.23-0.34	10
1971	Isle of May	1.64	1.46-1.84	14	0.34	0.30-0.39	14
1981	Isle of May	0.45	0.37-0.54	10	0.26	0.22-0.31	10

Differences between 1981 concentrations and earlier ones (in above order):

pp'-DDE	Dieldrin
t= 11.2 P[0.001	t= 14.3 P[0.001
t= 4.74 P[0.001	t= 4.29 P[0.001
t= 7.56 P[0.001	t= 0.61 N.S.
t= 12.7 P[0.001	t= 2.82 P[0.01

Table 5.7 Hatching and fledging success of clutches which hatched at least one chick in 1982, in relation to clutch size and male breeding experience.

Second-year males:

	Clutch size						
	1	2	3	4	5	6	Total
Clutches	0	28	74	9	0	0	111
Eggs	0	56	222	36	0	0	314
Chicks at 1 week	0	43	152	19	0	0	214
Hatching success	-	76.8%	68.5%	52.8%	-	-	68.2%
Chicks fledged	0	28	77	13	0	0	118
Fledging success	-	65.1%	50.7%	68.4%	-	-	55.1%

Older males:

	Clutch size						
	1	2	3	4	5	6	Total
Clutches	6	77	203	34	4	2	326
Eggs	6	154	609	136	20	12	937
Chicks at 1 week	6	104	427	87	9	5	638
Hatching success	100.0%	67.5%	70.1%	64.0%	45.0%	41.7%	68.1%
Chicks fledged	5	88	304	45	8	1	451
Fledging success	83.3%	84.6%	71.2%	51.7%	88.9%	20.0%	70.7%

Differences in overall success between second-year males and older ones:

Overall hatching success: chi-square=0.00 df=1 N.S.

Overall fledging success: chi-square=16.8 df=1 P[0.001

Note: Hatching success covers survival of the chick at hatching and during approximately the first week of life.

chi-square=1.96 df=2 N.S.), as found for young males. However, it fell from an average of 69%, to 44% for clutches of 5 and 6 (chi-square=7.91 df=1 P[0.01). Such abnormally high clutches were the result of two females laying in the same nest; the reduced hatching success could be due to Shags being ill-adapted to incubating more than four eggs, or to aggression within the trio disrupting incubation (Harris 1982). Fledging success decreased as clutch size increased, from 85% in clutches of 1 and 2, to 71% in clutches of 3 (chi-square=7.41 df=1 P[0.001), and 53% in larger clutches (chi-square=11.0 df=1 P[0.001). As brood size increased with clutch size, from 1.00 for clutches of 1, to 2.53 for clutches of 4 or more (calculated from Table 5.7), the higher chick mortality at higher clutch sizes was equivalent to a higher chick mortality at higher brood sizes. There was no evidence of chick mortality due to starvation, which would have been expected to affect the chicks of larger broods more than ones in small broods. However, the most obvious cause of mortality in chicks over a week in age was exposure to heavy rain (see Section 8.7 and Tables 8.12, 8.13). Taking broods which comprised at least one chick a week after hatching, i.e. broods old enough to be affected by severe weather, the proportion of chicks found dead of exposure was lowest in broods of one and highest in broods of 3 and 4: 2% as opposed to 21% respectively (Table 5.8). The period of peak mortality was 20-37 days after hatching (see Table 8.12). At this age, chicks were still clad in down, but too large to be adequately sheltered from the elements unless occurring in small broods.

Table 5.7 shows that overall, there was no difference in hatching success between the two age classes, but that fledging success varied significantly, from 55% for second-year males to 71% for older ones. The mean brood sizes and numbers of chicks fledged per pair for the full sample of 671 nests is shown in Table 5.9. On this larger sample, the mean brood

Table 5.8 Death of chicks due to exposure in 1982, in relation to brood size within 10 days of hatching.

	Brood size				
	1	2	3	4	Total
Chicks dead of exposure	2 (1.9%)	17(10.1%)	36(21.3%)	2(22.2%)	57
Other chicks	106(98.1%)	151(89.9%)	133(78.7%)	7(77.8%)	397

Brood of 1 x Brood of 2 : chi-square=5.78 df=1 P[0.05

Brood of 2 x Brood of 3,4: chi-square=7.33 df=1 P[0.01

Table 5.9 Mean brood size at 10 days and corresponding number of chicks fledged per pair in 1982, in relation to male breeding experience.

	Second-year			Older			T-value	
	Mean	S.E.	N	Mean	S.E.	N		
Brood size	1.95	0.07	132	2.21	0.03	539	3.25	P[0.01
Chicks fledged/pair	1.10	0.09	132	1.55	0.04	539	4.50	P[0.001
Difference	0.85	0.08	132	0.66	0.04	539	2.12	P[0.05

size at ten days for inexperienced birds was 88% that for older ones, with a difference of 0.26 chicks/pair. By fledging, the discrepancy had increased to 0.45 chicks/pair, as a result of greater chick mortality between 10 days and fledging for the younger birds.

Second-year Shags therefore performed less well than older birds at most stages of the breeding cycle, with the heaviest incidence of nest loss occurring before hatching. The pattern was very similar to that observed on the Farne Islands (Potts 1966, Potts et al. 1980), except perhaps as regards chicks over 10 days old, whose survival they found to be independent of parental age. Coulson et al. (1969) and Potts et al. (1980) further noted that egg volume, not measured in this study, was smaller for two-year-old females than for older ones. Parsons (1970) and Nisbet (1973,1978) have shown that in the Herring Gull and the Common Tern, chick survival in the first few days after hatching increased with the size of the egg. As, in Shags, second-year females were paired with second-year males (Section 2.12), this could be another cause of reduced breeding success in the younger age class.

5.4 Occupation date, laying date and parental age.

The relevant information on occupation date and laying date was available only for 1982; recording started in mid-April (week 7). From mid-April onwards, the time elapsed between the occupation of the site and the date of first laying decreased through the season (Table 5.10). Birds occupying sites in weeks 8 and 9 laid approximately two weeks later, whereas those occupying sites after week 13, i.e. from the beginning of June, laid about one week later. The trend was the same for both inexperienced and experienced breeders, although the differences were significant only for the

Table 5.10 Interval between occupation of the site and egg-laying in 1982, in relation to male breeding experience.

Week of occupation	Second-year			Older			T-value	
	Mean	S.E.	N	Mean	S.E.	N		
8-9	1.90	0.18	48	2.38	0.55	24	0.83	N.S.
10-11	1.44	0.08	79	1.75	0.13	60	2.03	P[0.05
12-13	1.47	0.21	32	2.30	0.45	10	1.67	N.S.
14+	1.11	0.35	9	1.32	0.21	22	0.51	N.S.
	F=3.19 P[0.05			F=2.21 N.S.				

first category. At all times, the interval between occupation and laying date was greatest for the older age group, although in only one case was it significantly so. Coulson et al. (1969) observed that on the Farne Islands, the interval between the start of nest-building and egg-laying in the Shag also decreased through the season.

The date on which male Shags started defending nest-sites (occupation date) varied according to the age of the birds (Table 5.11). By mid-April (week 7), 90% of males over two years of age were already on their sites. This was in marked contrast to second-year males, of which only 31% had taken up sites by that time (chi-square=231 df=1 P[0.001). Within the group of older birds, the proportion of three-year-olds on sites before mid-April was also lower than that of older birds, being 80% and 93% respectively (chi-square=14.4 df=1 P[0.001); this difference was much less than that between second-years and third-years. There was no difference between the age categories of Shags older than three (chi-square=7.46 df=3 N.S.).

Correspondingly, laying started earlier on nests occupied by older Shags, the effect being noticeable for both sexes (Table 5.12; nests known to contain replacement clutches have been omitted). Again, the change was greatest between the youngest age classes: second-year females laid on average 3.9 weeks later than older ones, and at nests belonging to second-year males, laying occurred on average 3.7 weeks later than for older males. A multiple regression of laying date against the natural logarithm of male and female age gave the equation

$$\text{Laying date} = -\,1.51\ \ln(\text{male age}) - 1.64\ \ln(\text{female age}) + 13.78$$

with N=167, r=0.666, P[0.001. The contribution of each of the two predictor variables was highly significant (P[0.001), and between them they accounted for 44% of the variation in laying date. Male and female age were also found to be highly correlated with laying date on the Farne Islands (Potts

Table 5.11 Occupation date in relation to male age in 1982.

Male age	Week of occupation					
(years)	[8	8-9	10-11	12-13	14+	Total
2	107 (31.0%)	77 (22.3%)	103 (29.9%)	44 (12.8%)	14 (4.0%)	345
3	66 (80.5%)	2 (2.4%)	11 (13.4%)	0 (0.0%)	3 (3.7%)	82
4-6	48 (87.3%)	1 (1.8%)	5 (9.1%)	0 (0.0%)	1 (1.8%)	55
7-10	63 (96.9%)	2 (3.1%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	65
11-13	54 (98.2%)	0 (0.0%)	0 (0.0%)	0 (0.0%)	1 (1.8%)	55
14+	47 (90.4%)	3 (5.8%)	0 (0.0%)	1 (1.9%)	1 (1.9%)	52

Table 5.12 Mean laying date in relation to parental age in 1982.

	Male age (years)					
	2	3	4-6	7-10	11-13	14+
Laying date	11.2	8.7	7.2	6.4	7.3	7.4
S.E.	0.2	0.4	0.4	0.2	0.5	0.5
N	234	66	43	52	42	41

F=53.7 df=5,472 P[0.001

	Female age (years)					
	2	3	4-6	7-10	11-13	14+
Laying date	11.9	9.8	8.1	7.6	7.0	7.3
S.E.	0.3	0.1	0.5	0.4	0.4	0.4
N	73	49	35	49	49	41

F=33.3 df=5,290 P[0.001

Note: Week 1 starts on 1 March. Layings known to be replacement clutches have been excluded.

et al. 1980); in that study, two further variables contributed significantly to the regression in a given year, namely whether or not the male and the female were breeding for the first time. On the Isle of May, the closest approximation to the additional variables was provided by the categories of birds aged on plumage as two, or older. A stepwise multiple regression of laying date against the four variables showed that, unlike the situation on the Farne Islands, only female age and male breeding experience (coded 0 or 1) made significant contributions to the regression, resulting in the equation

$$\text{Laying date} = -\,2.61\ \text{male experience} - 1.45\ \ln(\text{female age}) + 12.76$$

with $N=167$, $r=0.686$, $P[0.001$. The role of female age had not changed (the coefficient of female age was within 1 S.E. of that calculated previously), but the role of male age was reduced to one of breeding experience. The effect of male age upon laying date thus closely matched its effect upon chick production. The proportion of variation accounted for by the regression increased to 47%, which compared favourably with the 55% explained on the Farne Islands by four age variables plus five measuring yearly variation.

The seasonal changes in the relative numbers of inexperienced pairs, i.e. pairs comprising a second-year male, and experienced pairs (male over two) laying in a given week are presented in Table 5.13. Nests known to contain replacement clutches are omitted. During the first four weeks, laying was predominantly by experienced pairs; the proportion of inexperienced pairs laying then increased sharply from 10% to a plateau of ca 60% over the subsequent weeks. After mid-June (week 15 onwards), only 39 pairs laid, and the proportion of inexperienced breeders decreased. Such pairs, mostly experienced birds, were probably renesting after losing their first clutch; they had not been recognized as such, either because they had

Table 5.13 Changes, with relation to week of laying, in the proportions of pairs comprising a second-year male in 1982.

	Week of laying						
	4	5	6	7	8	9	10
Total number of pairs laying	32	152	224	153	150	77	61
Pairs with second-year male	0	1	6	7	16	21	33
% with second-year male	0.0	0.7	2.7	4.6	10.7	27.3	54.1

	Week of laying					
	11	12	13	14	15-16	17-21
Total number of pairs laying	60	99	39	25	24	15
Pairs with second-year male	40	53	28	15	10	4
% with second-year male	66.7	53.5	71.8	60.0	41.7	26.6

lost their first nest before being recorded, or because the birds were not ringed, and so were not individually identifiable.

5.5 Occupation date, laying date and chick production.

In the analyses that follow, nests known to contain replacement clutches have been omitted; the breeding performance of pairs which laid replacement clutches will be examined in Chapter 7.

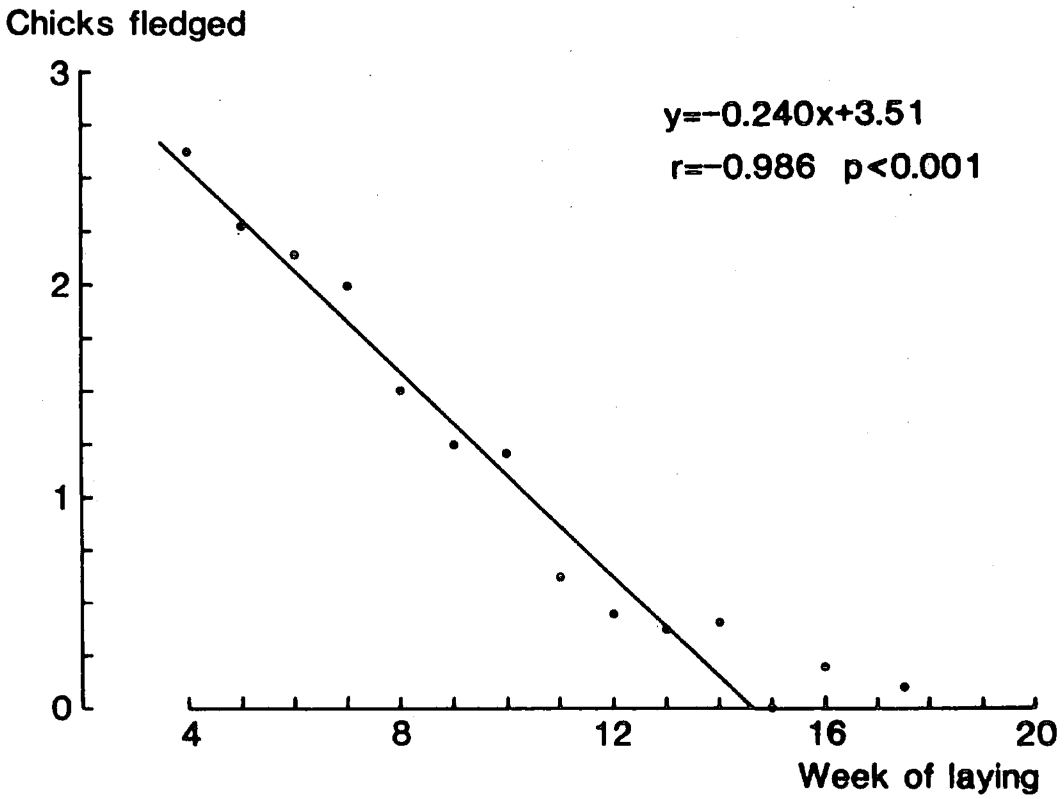
As second-year males fledged fewer chicks and bred later, on average, than older males, it would be expected that, at the colony as a whole, chick production would decline as laying date became later. The mean number of chicks fledged per pair is plotted against week of laying in Figure 5.1. All points were based on a minimum of 10 nests; where necessary (at the end of the season), data from adjacent weeks were pooled and the mean plotted against the average date. Mean chick production decreased strongly with laying date: the decrease was linear until mid-June (week 15), then flattened out. As explained for Table 5.13, many of these very late nests probably belonged to pairs which, although not identified as such, were renesting after the failure of an earlier breeding attempt. The decrease in chick production up to week 15 is well described by the relationship

Chick production = - 0.240 laying date + 3.51

with r=-0.986, N=12, P[0.001. The slope of -0.24±0.01 (1 S.E.) was similar to that derived from Snow (1960) for Lundy (-0.22±0.02) and from Potts (1966) for Unst (-0.18±0.03); it was significantly steeper than that of -0.14±0.03 from the Farne Islands (Potts 1966; t=3.16 df=18 P[0.01), probably because the latter included Shags renesting late in the season.

Was this seasonal decline in young production entirely accounted for by the later breeding of young males, or did a seasonal effect occur

Figure 5.1 Mean number of Shag chicks fledged per pair in 1982, in relation to laying date (measured in weeks from 1 March).



independently of breeding experience? If no independent seasonal effect were present, then splitting the data from Figure 5.1 into the two categories of male breeding experience would result in two horizontal lines. As shown in Figure 5.2, this was not the case. For both categories, the regressions of chick production against laying date (up to week 15) were highly significant; the slopes were equal (t=0.20 df=15 N.S.) and, with a value of -0.22±0.01, were slightly less steep than the slope of -0.24±0.01 from the pooled data in Figure 5.1. The difference is not more pronounced because of the closeness of the two lines in Figure 5.2. Although second-year males fledged on average about 1 chick/pair less than older males (Section 5.2), after adjusting for laying date the mean numbers of chicks fledged per pair were 1.03±0.06 for second-year males, and 1.33±0.05 for older males (t=3.84 df=16 P[0.005). Thus for young and old Shags breeding at the same time, the difference in chick production reduced to an average of 0.3 chicks/pair, i.e. much of the difference in young production between the two categories was due to the difference in timing of breeding. Referring back to the original data, breeding experience and laying date between them accounted for 38% of the variability in the number of young fledged per pair; of this, 79% was attributable to laying date.

Chick production declined also with date of occupation (Figure 5.3). The regressions did not include the points for week 7, as values for that week included all nests occupied earlier as well. For both age categories, mean chick production in week 7 was higher than that in any of the subsequent weeks. From week 8 onwards, the rate of decrease was the same for second-year and older males (t=1.16 df=10 N.S.); although the mean number of chicks fledged per pair, adjusted for occupation date, was lower for younger males than for older ones (0.28 and 0.34 respectively), the difference was not significant (F=0.67 df=11 N.S.). In contrast, the mean

Figure 5.2 Mean number of Shag chicks fledged per pair in 1982, in relation to laying date (measured in weeks from 1 March); values for second-year males and older males are plotted separately. Second-year males: $y=-0.22x+3.13$ ($r=-0.954$ $N=8$ $P[0.001)$; older males: $y=-0.22x+3.49$ ($r=-0.981$ $N=11$ $P[0.001)$.

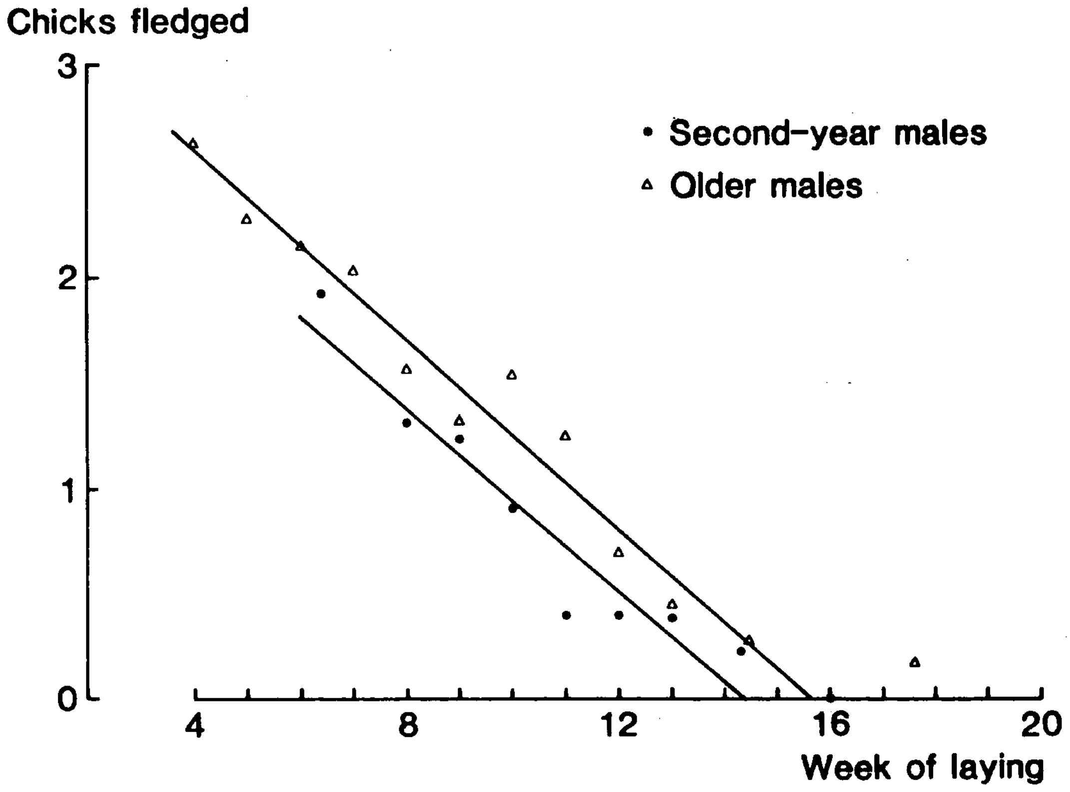
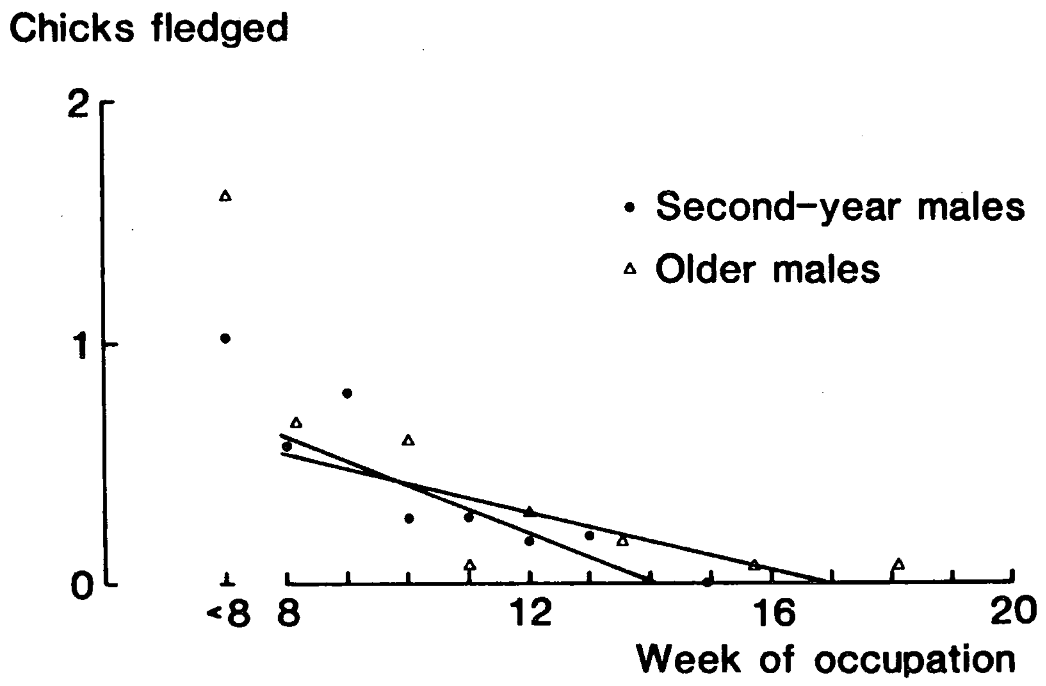


Figure 5.3 Mean number of Shag chicks fledged per pair in 1982, in relation to date of site occupation (measured in weeks from 1 March); values for second-year males and older males are plotted separately. Second-year males: y=-0.10x+1.41 (r=-0.861 N=7 P[0.05); older males: y=-0.06x+1.02 (r=-0.784 N=7 P[0.05).



number of chicks fledged per pair from nests occupied before week 8 was 1.02 and 1.61 respectively ($t=6.00$ $df=1208$ P[0.001). As shown in Section 5.4, older birds occupying sites after week 7 constituted the last 10% of all males over two which attempted to breed in the 1982 season. The lack of a clear-cut difference between young males and late older males, contrasting with the very marked difference between the age categories early in the season, suggests that older males late in occupying a site were of poorer quality than earlier birds in the same age category.

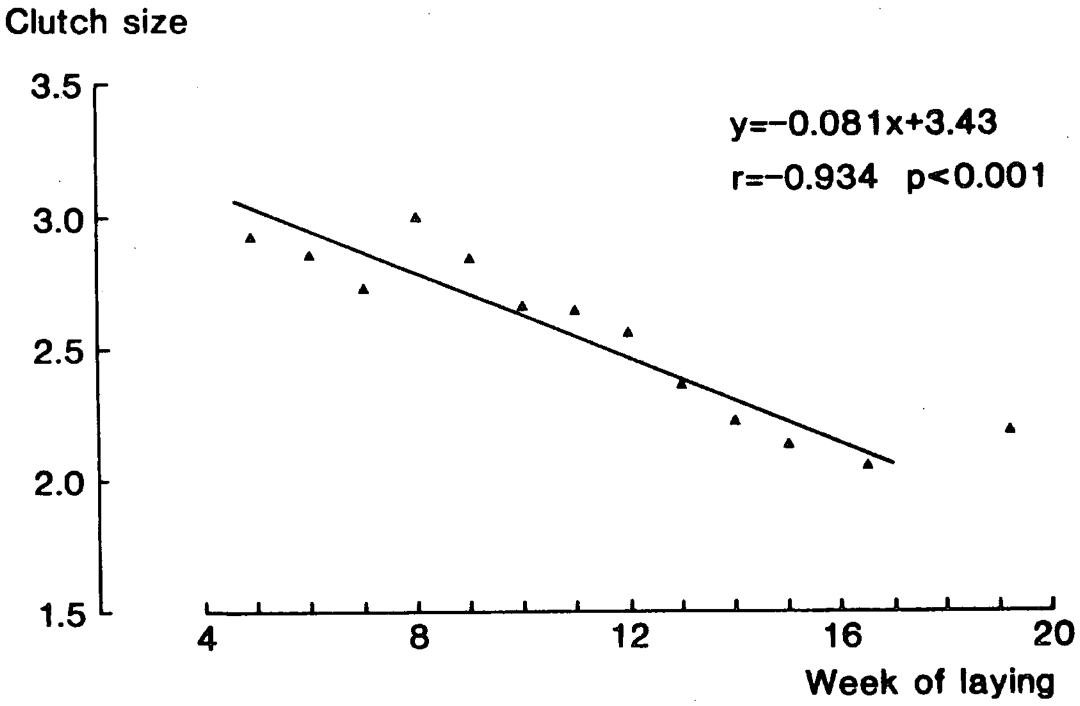
5.6 Mechanisms producing the seasonal decline in chick production.

The variation in clutch size with the week of laying is shown in Figure 5.4. As clutch size did not vary with age (Section 5.3), data from all nests were pooled (excluding known replacement clutches). Each point was based on at least 10 nests, with adjacent weeks grouped where necessary; in such cases, mean clutch size was plotted against the average laying date. Clutch size showed an approximately linear decline with the time of laying, with a suggestion of a plateau at the beginning of the season. The mean clutch size of the latest nests was higher than expected from the preceding trend; as before, such nests were likely to contain replacement clutches which had remained unrecognized. The regression equation for clutches laid before the end of June (up to week 17) was

Clutch size = - 0.081 laying date + 3.43

with $r=-0.934$, $N=12$, P[0.001. The slope of -0.08 ± 0.01 was similar to that of -0.10 ± 0.01 calculated from Snow (1960) for Shags on Lundy. On the Farne Islands, however, Potts (1966) and Potts _et al_. (1980) found no significant variation in clutch size through the season. The difference in results may be due to the greater accuracy of the data from the Farne Islands, where

Figure 5.4 Mean clutch size of Shags in 1982, in relation to date of laying (measured in weeks from 1 March).



nests were checked on average every three days; on the Isle of May, visits were fortnightly, and eggs could have been lost before clutch size was recorded. The frequency of visits on Lundy were not known. Comparing the slopes for the declines in clutch size and chick production for the Isle of May (0.08 and 0.24 respectively), the decrease in clutch size contributed to a third of the seasonal decrease in young production. Coulson et al. (1969) also observed that independently of age, late-breeding Shags on the Farne Islands produced eggs which were on average 4.5% smaller than eggs laid early. They suggested that, as the interval between site occupation and egg-laying decreased through the season, late-laying birds had insufficient time for the reproductive system to develop fully.

The changes in the proportions of nests lost in different time periods through the season, before laying, before hatching and after hatching, are shown in Table 5.14. Linear trends were examined using chi-square with one degree of freedom (Maxwell 1961). The proportion of nests lost before laying were compared for four periods of time defined by date of occupation (since week 8); there was no seasonal trend for either second-year males or older ones. For the proportions of nests lost during incubation and after hatching, the time periods were based on laying date to provide a wider coverage of the breeding season. Nest loss during incubation was examined for nests in which laying took place from week 7 onwards (nests with eggs laid earlier might have been lost before recording began); no eggs hatched before week 7, so that nest loss after hatching was known even for the early nests. For males over two, the proportion of nests lost in each of five time periods increased significantly through the season, both before and after hatching. The relationship was strongest during the incubation stage: only 1% of early nests were lost, increasing to 67% at the end of the season. During the post-hatching stage, 6% of the earliest nests were lost,

Table 5.14 Seasonal changes in the proportions of nests lost before laying, before hatching and after hatching in 1982, according to male breeding experience (sample sizes in parentheses).

Loss before laying:

	Week of occupation				Linear trend
	8-9	10-11	12-13	14+	Chi-square (1 df)
Second-year	23.4% (64)	21.7% (92)	27.5% (40)	30.8% (13)	0.44 N.S.
Older	20.5% (39)	5.9% (51)	35.7% (14)	25.0% (28)	1.38 N.S.

Loss before hatching:

	Week of laying					Linear trend
	7-8	9-10	11-12	13-14	15+	Chi-square (1 df)
Second-year	25.0% (12)	16.2% (37)	49.4% (83)	59.0% (39)	92.3% (13)	25.1 P[0.001
Older	1.3% (79)	11.8% (51)	18.2% (55)	62.5% (16)	66.7% (27)	66.5 P[0.001

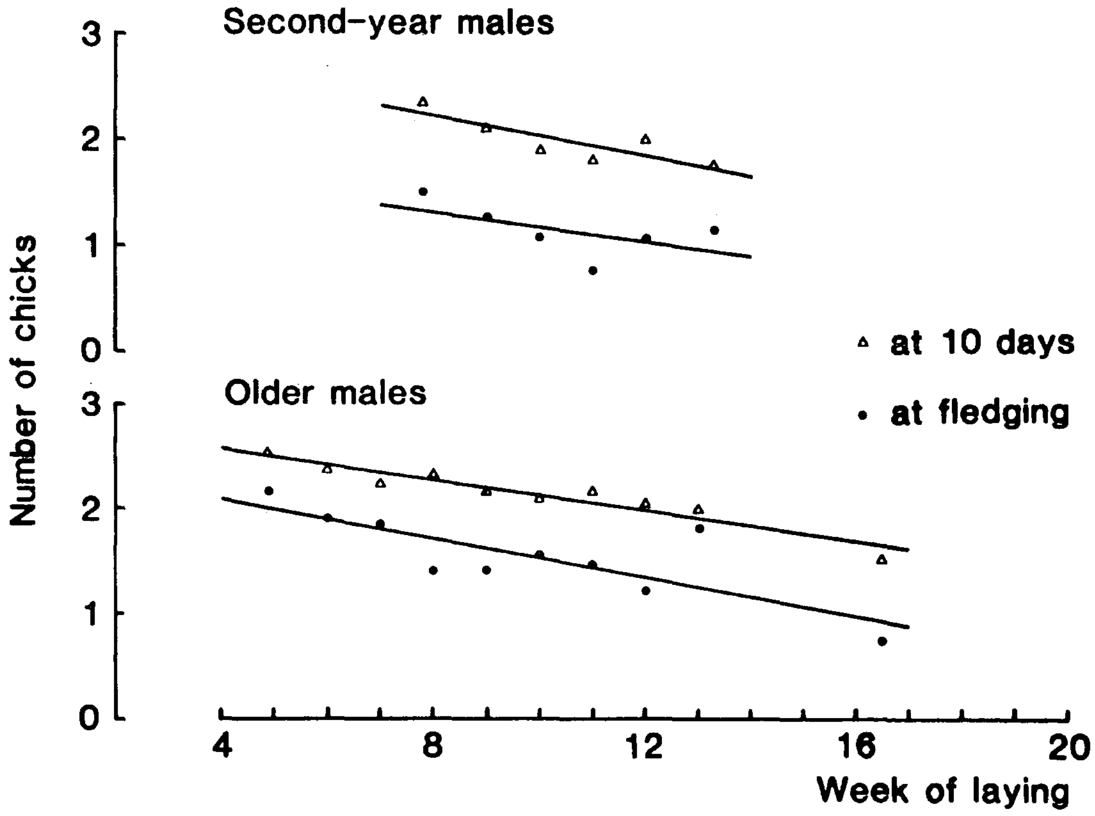
Loss after hatching:

	Week of laying					Linear trend
	4-6	7-8	9-10	11-12	13+	Chi-square (1 df)
Second-year	- (0)	14.3% (14)	27.3% (44)	37.5% (40)	26.7% (15)	1.21 N.S.
Older	6.3% (112)	13.6% (162)	14.1% (71)	20.9% (43)	22.2% (9)	6.80 P[0.01

and 22% of the latest ones. In second-year males, the proportion of nests lost between laying and hatching also increased markedly, from 25% early in the season to 92% at the end of the season. There was no significant seasonal trend in the proportion of nests lost after hatching; on average 29% of nests were lost at this stage in breeding.

The number of nests for which clutch size, brood size and the number of chicks fledged were all known were too few to examine seasonal trends in hatching and fledging success directly. However, it was possible to draw certain conclusions from nests where the brood size and number of chicks fledged were both known, using the same presentation as for chick production (Figure 5.2). Brood size at 10 days decreased through the season (Figure 5.5), with no difference in slope for second-year males and older males (F=0.71 df=1,12 N.S.). The pooled slope of -0.08±0.01 was the same as the slope of the seasonal decline in clutch size (Figure 5.4), i.e. the absolute difference between clutch size and brood size at 10 days remained constant throughout the season. The progressive decrease in clutch size entailed that this difference was proportionately larger as the season progressed, i.e. that the survival of eggs from before hatching to 10 days after hatching declined. This could be a result of poorer hatching success, or poorer chick survival during the first few days after hatching, or a combination of both. Figure 5.5 also shows the mean number of chicks fledged per pair from the same nests. For both age categories, there was no difference in the slopes calculated for brood size and number of chicks fledged per pair (second-year males: F=0.20 df=1,8 N.S.; older males: F=0.61 df=1,16 N.S.), indicating a lack of seasonal effect upon the absolute numbers of chicks lost per pair between 10 days and fledging. However, the seasonal reduction in brood size entailed that the number of chicks lost per pair was proportionately greater as the season progressed, i.e. the survival

Figure 5.5 Comparison of mean brood size at 10 days and at fledging for the same nests in 1982, in relation to laying date (measured in weeks from 1 March); values for second-year males and older males are plotted separately. Brood size at 10 days: second-year males, y=-0.09x+2.98 (r=-0.838 N=6 P[0.05); older males, y=-0.07x+2.86 (r=-0.949 N=10 P[0.001). Brood size at fledging: second-year males, y=-0.07x+1.86 (r=-0.571 N=6 N.S.); older males, y=-0.09x+2.47 (r=-0.800 N=10 P[0.001).



of chicks from 10 days to fledging declined seasonally.

The age-independent decline in young production was therefore the result of similar mechanisms for both age categories. The causes noted from this study were a decrease in clutch size, an increase in the proportion of nests lost through the season, particularly between laying and hatching, a decline in hatching success or early chick survival, and a decline in the survival of chicks between 10 days and fledging.

5.7 Structure of the nest.

Most of the nest-material is collected by the male (Snow 1963). Typically, a Shag's nest on the Isle of May was constructed from seaweed (wracks *Fucus* spp. and kelps *Laminaria* spp.), often intermingled with dried stems of Dock *Rumex crispus* and Sorrel *R. acetosa*, sticks and other debris. The nest was lined with finer material such as grasses, Sea Campion *Silene maritima* or scurvy-grass *Cochlearia* spp. The composition of the nest was similar to that on the Farne Islands (Potts *et al.* 1980), but on Lundy, the seaweed was usually replaced by dried Bracken *Pteridium aquilinum* or Heather *Calluna vulgaris* (Snow 1960).

Three categories of nest were recognised, and recorded each time a nest was visited:

1. A few strands of seaweed, scurvy-grass or Sea Campion.
2. Enough material to form a platform hiding the nest ledge, but with little or no cup.
3. A substantial nest with a well-formed cup.

In both 1981 and 1982, the nest structure score assigned to a nest for the purpose of the analysis was the one recorded on the visit closest to the time eggs were laid in the nest, or, for nests lost before laying, on the last visit when the nest was present.

The change in the distribution of nest structure scores in relation to laying date in 1982 is given in Table 5.15, where nests from categories 1 and 2 have been grouped under the heading 'poor nests'. The table does not include replacement nests, or nests where laying began before the start of fieldwork (in mid-April, week 7). For both experienced and inexperienced breeders, the proportion of poor nests increased through the season (tested for linear trend by chi-square), from 0% initially, to 11% in old breeders and 36% in young ones. Furthermore, the rate of increase, as expressed by the slope of the regression, was significantly higher for the second-year group (d=3.10 P[0.01). Thus after week 8, the proportion of poor nests belonging to young birds was, over equal periods of time, systematically greater than in old birds, with the difference increasing over the season.

As none of the 303 nests where eggs were laid in weeks 7 or 8 were incomplete, and as the proportion of incomplete nests increased as the season progressed, early nests in which laying started before their nest structure had been recorded were considered to have been complete. It was likely that the same held in 1981, when laying date was not known. Table 5.16 presents data for both years on nest structure in relation to breeding experience: in 1981 and 1982, only 1% of nests belonging to males older than two were poorly built, compared to 15% of second-years' nests. This agreed with Snow (1960), Potts (1966) and Potts et al. (1980). Poor nest-building in young breeders of related species has also been noted for the Gannet and the Brown Pelican (Nelson 1978, Blus & Keahey 1978), and also in Grey Herons (Milstein et al. 1970), Kittiwakes (Thomas 1980) and various passerine species (Thorpe 1963).

Reproductive success was also linked to the structure of the nest in both age categories (Table 5.17). Chick production was very low for poorly

Table 5.15 Seasonal changes in the structure of nests at laying in 1982, according to male breeding experience.

Week of laying	Nests of second-year males		Nests of older males	
	Substantial	Poor	Substantial	Poor
7-8	23 (100.0%)	0 (0.0%)	280 (100.0%)	0 (0.0%)
9-10	49 (90.7%)	5 (9.3%)	84 (100.0%)	0 (0.0%)
11-12	83 (89.2%)	10 (10.8%)	63 (96.9%)	2 (3.1%)
13-14	28 (66.7%)	14 (33.3%)	20 (90.9%)	2 (9.1%)
15+	9 (64.3%)	5 (35.7%)	32 (88.9%)	4 (11.1%)
Linear trend (1 df)	chi-square=18.0	P[0.001	chi-square=29.9	P[0.001

Table 5.16 Structure of nests at laying in relation to male breeding experience in 1981 and 1982.

		Substantial	Platform	Strands	Chi-square (1 df)	
1981	Second-year	85 (85.9%)	12 (12.1%)	2 (2.0%)	27.4	P[0.001
	Older	315 (98.8%)	1 (0.3%)	3 (0.9%)		
1982	Second-year	238 (85.3%)	40 (14.3%)	1 (0.4%)	104.5	P[0.001
	Older	1145 (98.7%)	12 (1.0%)	3 (0.3%)		

Note: In calculating chi-square, the last two columns were grouped.

Table 5.17 Chick production in relation to the structure of the nest in 1981 and 1982.

	Substantial			Platform			Strands			
	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N	F-value
1981										
All pairs	1.69	0.04	689	0.45	0.17	29	0.00	0.00	11	28.7 P[0.001
1982										
2-year males	0.78	0.06	249	0.01	0.01	68	0.00	0.00	26	33.2 P[0.001
Older males	1.51	0.03	1220	0.04	0.04	25	0.00	0.00	15	37.0 P[0.001

built nests, with a total of only 15 chicks reared from 174 such nests in the two years combined. This was due to many more of the poor nests being lost than of the well-built ones (Table 5.18). In 1982, over half of the poorly built nests were lost before laying in both age categories. In most cases, this was simply a consequence of the nest being deserted shortly after building had started. However, 15% of inexperienced breeders and 3% of older ones laid eggs before the nest was complete. Furthermore, in marked contrast to the incomplete nests, only 1% of completed nests were lost. This suggests that birds which had successfully built a substantial nest were less willing to desert. In view of the relatively high energy cost invested in collecting material, shown by Williams (1978) for the Cape Cormorant, such a strategy would make sense. Table 5.18 also gives the proportion of nests lost between laying and hatching. During this period too, nests which were incomplete at laying were far more likely to be lost than complete nests (80% loss as opposed to 18%). As regards differences between second-year males and older birds, it is already known that nest loss was greatest in younger birds; Table 5.18 confirms this for each category of nest structure, before and after laying.

5.8 Discussion.

In the introductory paragraph, I gave several examples of how aspects of reproductive output in different species were related to age and timing of breeding. This study was no exception: young male Shags performed less well, when compared to older breeders, at all stages of the reproductive cycle (including nest-building). At the same time, reproductive success declined seasonally; part of the decline was caused by young Shags breeding later than old ones, but the main effect was age-independent.

Table 5.18 Structure of nests lost before laying and before hatching in 1982, according to male breeding experience.

Nest before laying:

	Second-year males		Older males	
	Retained	Lost	Retained	Lost
A few strands	1 (3.8%)	25 (96.2%)	4 (26.7%)	11 (73.3%)
Platform	40 (59.7%)	27 (40.3%)	15 (62.5%)	9 (37.5%)
Well-built	212 (96.8%)	7 (3.2%)	738 (99.9%)	1 (0.1%)
Chi-square (2 df)	156.4 P[0.001		414.1 P[0.001	

Nest before hatching:

	Second-year males		Older males	
	Retained	Lost	Retained	Lost
A few strands	0 (0.0%)	1 (100.0%)	1 (25.0%)	3 (75.0%)
Platform	6 (15.0%)	34 (85.0%)	5 (33.3%)	10 (66.7%)
Well-built	137 (64.6%)	75 (35.4%)	645 (87.4%)	93 (12.6%)
Chi-square (1 df) (first two lines combined)	32.9 P[0.001		43.4 P[0.001	

Many reasons have been proposed to explain the relative inefficiency of first breeders. Lack (1968) suggested that young breeders had not had time to acquire the necessary foraging skills to raise a family, and that the deferred maturity observed in long-lived birds, from two years in the Shag (Section 4.8) to up to 16 years in the Wandering Albatross (Croxall 1982), had evolved as a consequence of this. Although contrary to the view of Wynne-Edwards (1962), who held that breeding was deferred in long-lived species in order to reduce the rate of reproduction and prevent over-population, there is considerable evidence in favour of Lack's theory. Post-fledging care is developed in seabirds (review by Burger 1980), which typically have a long lifespan; some have been noted feeding juveniles several months after fledging - six months in Royal Terns (Ashmole & Tovar 1968), nine months in Flightless Cormorants (Harris 1979), and up to a year in Red-footed Boobies (Verner 1961). The advantage to the young birds is obvious; the parent birds, however, are only likely to benefit from such an adaptation if, by their continued investment, they increase the chances of survival of their offspring. Such would be the case if young birds had difficulty in feeding themselves: the high mortality rates of many birds over their first, and often subsequent, years of life provide indirect evidence of the lesser ability of young birds to fend for themselves (examples in Lack 1966). In the present study, the average first-year mortality rate of the Shag was found to be 52%, decreasing to 25% in the second year and 13% thereafter (Chapter 4). Direct evidence of inefficiency in feeding and catching prey is available for newly fledged juveniles of Little Blue, Great Blue and Grey Herons (Recher & Recher 1969, Quinney & Smith 1980, Cook 1978), Black-winged Stilts (Espin et al. 1983), Brown Pelicans (Orians 1969) and Olivaceous Cormorants (Morrison et al. 1978); for juveniles of Sandwich and Royal Terns about six months old (Dunn 1972, Buckley & Buckley 1974); for immature Glaucous-winged Gulls up to the age of two years (Searcy 1978), and for Herring Gulls up to the age of four years (Greig et al. 1983). The deleterious effect of a poorer foraging ability of younger birds on the weights of their chicks, independently of their breeding experience, was illustrated by Ainley & Schlatter (1972) for Adélie Penguins.

However, the role of breeding experience per se on reproductive success cannot be disregarded. Bruggers & Jackson (1981) found that yearling male Mandarin Ducks performed the courtship display and mounting less well than experienced drakes, and Lehrman (1955) and Lehrman & Wortis (1960) showed that experience increased the responsiveness of Barbary Doves to incubation and feeding of newly hatched young. This is of relevance to cormorants, as in the Shag and the Flightless Cormorant, the parents, especially the larger male, have difficulty in feeding chicks newly out of the egg (Snow 1963, 1966). Lawton & Guindon (1981) demonstrated that in the Brown Jay, a cooperatively breeding species, both foraging ability and aptitude to care for chicks was not only lower in nest attendants, usually first-year birds, than in the parents, but that the young birds improved their performance as nest attendants on both counts in the course of the breeding season.

An alternative theory for lowered reproductive success in young breeders and for deferred maturity is that of reproductive restraint (Williams 1966, Curio 1983). Wooller & Coulson (1977), Ainley & DeMaster (1980) and Croxall (1983) found that the annual survival rate was adversely affected by the first breeding attempt for the Kittiwake, the Adélie Penguin and the Wandering Albatross respectively, so there appears to be a cost associated with breeding. In the Laysan Albatross (Fisher 1971a, 1975), a decline in survival occurred only in the third to sixth year of breeding, corresponding to the point when the birds started breeding in earnest; prior to that, relatively few completed incubation. The high failure rate of young breeders before hatching, as also observed in the Shag, could be a means of ensuring survival to the following year. By refraining from either breeding at all, or from expending a large parental effort, young birds would thus forestall the associated risk of dying and increase their future prospects of breeding. The alternative theories presented here are by no means exclusive, and the evidence suggests that both may in fact be relevant.

The photoperiodic and physiological adaptations regulating avian breeding cycles have been reviewed by Lofts & Murton (1968) and Murton & Westwood (1977). They concluded that in temperate zones, seasonal changes in daylength provide the most reliable environmental information heralding the approach of a suitable breeding season, and that the photoperiodic responses are modified by environmental inhibitors and accelerators such as climate, food supply and behavioural interactions. They considered that temperature was probably the most important modifier of the gonadal cycle, and its effects have been demonstrated experimentally in a number of species (Burger 1948, Farner & Mewaldt 1952, Engels & Jenner 1956). Moreover, Delius (1965) found that in Skylarks, individual females appeared to respond to different temperature thresholds. In the present study, the timing of breeding in the Shag was correlated with a temperature-based factor, but the main influence on timing of breeding seemed to be food-related: the date of laying of the first Shag egg was strongly correlated with the abundance of Herring around the Isle of May in February (Chapter 4). This agrees with Marshall (1951) and Perrins (1970), who proposed that the availability of food to form eggs was a major proximate factor affecting the timing of breeding. Cavé (1968) showed experimentally that the growth rate of ovarian follicles in the Kestrel was inhibited in poorly nourished birds, and the study of Red-billed Queleas by Jones & Ward (1976) demonstrated that body condition alone could provide the proximate control of breeding. Yom-Tov (1974) and Högstedt (1981) further proved that additional food before breeding advanced the laying date in the Carrion Crow and the Magpie. The role of food in controlling the timing of breeding also provides one explanation for the generally later breeding of young birds compared to older ones. As discussed earlier, young birds are generally less efficient at feeding themselves than older birds; as a result, food may effectively be less readily available to them, even when plentiful in absolute terms. The seasonal delay in breeding of younger birds has, however, also been shown to have a physiological component. In young Red-billed Gulls, the development of the gonads takes place two to three weeks later than in older breeders (Mills 1973), and first-year female Woodpigeons do not enter breeding condition until July, three months after laying begins in mature birds (Murton et al. 1974).

Although little is known about the factors determining seasonal trends in clutch size (Klomp 1970), the seasonal variation in reproductive success which occurs independently of age has usually been attributed to seasonal variations in food supply as well, acting upon either egg formation or upon the survival of the chicks (Perrins 1970). In the Shag, clutch size declined over the breeding season in the present study, and egg volume showed a progressive decrease on the Farne Islands (Coulson et al. 1969). As early breeders were successfully feeding young at the time when late breeders were laying, it seemed unlikely that food shortage was acting upon egg formation in late breeders. Because of this, Perrins (1970) argued that in general, reduction of the clutch must have evolved in response to the adverse effects of food shortage late in the season. This is supported in the Shag by the seasonal decrease in chick survival between 10 days and fledging, a period when food requirements are high. Back-up information on changes in the abundance of fish on which Shags prey during the breeding season is sparse. Pearson (1968) showed that 81% of fish taken by breeding Shags were sandeels: fisheries catches of sandeels peak in June, then rapidly decline to virtually nil in August (Reay 1970, ICES Bulletins Statistiques); this may be because they enter an overwintering phase buried in the sand (Winslade 1974). Sandeels may thus be less available to Shags towards the end of the breeding season, but it is not known to what extent the birds could change their diet to compensate.

An alternative explanation for the seasonal decline in clutch size, and also in chick production, is that late breeders generally may be less efficient at foraging than early breeders. The argument is similar to the one put forward for the later breeding of young birds: not only would inefficient feeders take longer to enter breeding condition than efficient feeders, but they would also be less successful at catching food for their offspring. This study also showed that Shags breeding late were more prone to abandon their nests than earlier ones, particularly between laying and hatching. Furthermore, males over two which occupied sites late in the season reared as few chicks to fledging as second-year males, in marked contrast to the early breeders. These two results suggest that the later Shags, lacking sufficient reproductive drive to see them through breeding, were of poorer quality than the early ones. A poorer foraging efficiency could result in poorer quality birds by restricting food intake and thereby affecting reproductive condition. Individual quality and foraging ability might thus explain the seasonal decline in breeding success in the absence of actual changes in food supply.

Another factor progressively reducing chick production by Shags was a decline in combined hatching success and early chick survival. Parsons

(1970) and Nisbet (1973, 1978) showed that in Herring Gulls and Common Terns, chick survival during the first few days after hatching was positively correlated with egg volume. As discussed above, egg volume was shown to decrease seasonally in the Shag on the Farne Islands (Coulson _et al_. 1969), so a similar effect on the Isle of May could explain part at least of the observed decline in combined hatching success and chick survival.

The speculative nature of much of the above shows that the fundamental processes underlying the age-related and particularly the seasonal changes in avian breeding biology are still poorly understood. There is clearly a great need for further research into this subject; in view of its complexity, advances are most likely to be made through a multi-disciplinary approach, bringing together the physiological, ecological and behavioural aspects which have been touched upon in this discussion.

6. PHILOPATRY, SITE TENACITY AND PAIR-BOND STABILITY.

6.1 Introduction.

Philopatry, or faithfulness to the natal area, is a trait characterising many species of animals. Salmon, for instance, return to breed in their stream of origin after a year or more in the open sea (Jones 1959), and, in the spring, the flattened remains of frogs and toads which were returning to spawn at traditional breeding ponds are a common feature of certain roads (Savage 1961, van Gelder 1973). Greenwood (1980) has reviewed philopatry and dispersal in birds and mammals. Whereas males usually disperse more than females in mammals, the converse is true of birds. Fewer female than male Pied Flycatchers returned to breed in their natal area (von Haartman 1949), and the same held for colonial species such as Herring Gulls (Chabrzyk & Coulson 1976), Kittiwakes (Wooller & Coulson 1977) and Manx Shearwaters (Brooke 1978) with regard to the natal island. Once these birds had bred, the distances moved between breeding sites or territories in subsequent years were usually much shorter than the distances from the natal site to the locality of first breeding (Harvey et al. 1979). The retention of the nesting site or territory from one year to the next is often linked to the maintenance of the pair-bond in consecutive seasons, although the exact nature of the relationship is difficult to elucidate and seems to depend upon the social organisation of the species. Delius (1965) considered that site change was responsible for divorce in the Skylark, whereas Coulson & Thomas (1980) decided that in the Kittiwake, divorce was the main reason for a change of site.

A study bearing upon the behavioural aspects outlined above relies above all on marked animals. On the Isle of May, over 10'000 Shags have been marked with monel rings since 1961 (Table 2.1). A further 2'000 Shags have been marked in the south of the Firth of Forth, mostly by the Edinburgh and Tay Ringing Groups (Appendix 3). On the Farne Islands, 6'500 Shags were ringed under the auspices of the National Trust (Appendix 3). This has made it possible to consider movements to as well as from the Isle of May, and also between other colonies of Shags in the region. On the Isle of May, Shags of both sexes ringed in 1981 and identified again in 1982 have led to the investigation of site tenacity, mate retention, their causes, consequences and interactions.

6.2 Emigration and movements between colonies.

In addition to recording ringed Shags breeding on the Isle of May during 1981 and 1982, I visited six other Shag colonies in the Firth of Forth during May and June 1983 (Bass Rock, Craigleith, The Lamb, Fidra, Inchkeith and Inchmickery; see Figure 2.1). My aim was to determine the extent of movements between the islands by sampling the marked birds breeding at each colony. Retrap records of Shags breeding on the Farne Islands in 1982 and 1983 were provided by the Natural History Society of Northumbria. The average annual emigration rate from a given colony was calculated as the number of emigrants recorded at other colonies, over the total number of Shags marked at the original colony and recorded breeding during the census period. To avoid biasing the estimates, it was necessary that the proportion of Shags sampled in relation to the total number of ringed Shags breeding ('sampling efficiency') be the same at each colony. The values for sampling efficiency on the six islands in the Firth of Forth visited in 1983, for the Isle of May in 1982, and for the Farne Islands over the two years 1982 and 1983 are given in Table 6.1. An estimated 55% of ringed Shags (178 individuals) were identified at the six small Firth of Forth colonies, with little difference in sampling efficiency between them; this was comparable to the estimate of 58% sampling efficiency (275 individuals recorded) for the Farne Islands. Sampling had been 74% efficient on the Isle of May; for comparability with the totals from other colonies, totals of marked Shags from the Isle of May were multiplied by 0.55/0.74, equivalent to reducing the sampling efficiency to 55%. The only other colony of any importance in the Forth-Farnes area was that around St Abb's Head in Berwickshire, comprising ca 400 pairs in 1982 (Warman 1983); it was, however, inaccessible. The census period for all the islands under consideration spanned the two years 1982 and 1983; this was unlikely to affect the outcome of the analysis, as the average annual survival rate of Shags (87%) was high with respect to the average annual emigration rate (see below).

Table 6.2 shows how Shags ringed as chicks distributed themselves amongst the colonies. Overall, 4.9% of Shags were found breeding at a colony other than their natal one. As the survey of Shag colonies in the Forth-Farnes area had not been complete, this figure was not markedly different from the 8% annual emigration rate calculated by Potts (1969) for the Farne Islands. On the whole, Shags displayed a very strong fidelity to the natal colony. Inspection of Table 6.2 reveals that there were considerable differences in movements between islands (chi-square=56.0 df=4 P[0.001). In particular, chicks which moved from one of the group of four islands on the south side of the Firth of Forth (Bass Rock, Craigleith, The Lamb, Fidra - henceforth referred to as 'south Forth group') were nine times more likely to move to another island in the group than to move outside the group: of 20 emigrants, 18 remained within the group (compared with a 50:50

Table 6.1 Sampling efficiency of ringed Shags on the six island colonies in the Firth of Forth visited in 1983, on the Isle of May in 1982, and on the Farne Islands in 1982 and 1983 combined.

	% ringed	(N)	Total nests	Total ringed	Number identified	Sampling intensity
Bass Rock (*)	11.0	(236)	176	39	25	64.1%
Craigleith (*)	21.5	(660)	356	153	83	54.2%
The Lamb (*)	19.0	(379)	284	108	58	53.7%
Fidra (*)	11.4	(175)	67	15	9	60.0%
Inchkeith (*)	20.0	(5)	5	2	0	0.0%
Inchmickery (*)	8.3	(108)	42	7	3	42.9%
All six together	17.4		930	324	178	54.9%
Isle of May (**)	40.3	-	-	1532	1141	74.5%
Farne Islands(***)	-	-	-	472	275	58.3%

(*) Sampling efficiency calculated from colony size and the proportion of ringed breeders.

(**) Figures taken from Section 2.6.

(***) Figures calculated from a Lincoln Index on two years' retrap data.

Table 6.2 Inter-colony movements of Shags ringed as chicks.

Breeding colony	Natal colony				
	Isle of May	Bass Rock	Craigleith	The Lamb	Farne Islands
Isle of May	496	0	1	0	3
Bass Rock	1	9	1	0	0
Craigleith	5	1	32	8	0
The Lamb	2	0	3	28	0
Fidra	2	0	3	2	1
Inchmickery	2	0	0	1	0
Farne Islands	6	0	0	0	256
Total emigrated	18	1	8	11	4
Total recorded	514	10	40	39	260
% emigration	3.5%	10.0%	20.0%	28.2%	1.5%

distribution by Binomial Test: P=0.001). As a result, the difference between the proportions of Shags emigrating from the natal islands in the south side of the firth and the proportions of Shags emigrating from the Isle of May or the Farne Islands was highly significant (Table 6.3); when the south Forth islands were considered as one colony, the difference vanished. At the same time, the exchange rate between islands in the south Forth group, 19.8%, was not significantly different from the 22% exchange rate calculated by Potts (1969) between the islands of Staple and Brownsman, Farne Islands, separated by only 100m (chi-square=0.02 df=1 N.S.). Thus the Farnes colony and the south Forth group were behaving in a similar fashion.

The proximity of the four south Forth islands to each other was the obvious factor characterising the group: the mean inter-island distance was 4.8km, whereas the next nearest colony, the Isle of May, was 16km away. Within the south Forth group, the interchange was greatest between the two closest islands, Craigleith and The Lamb (1.6km apart), which between them accounted for 11 out of 18 movements (61.1%). Considering the 17 birds which moved from either Craigleith or The Lamb, but remained within the south Forth group, a comparison with random movement showed that the 11 birds which effectively moved between the two islands were significantly more than expected by chance (Binomial Test: P=0.008).

It was plain from what precedes that the proportion of Shags which bred away from their natal island declined as the distance between the natal colony and the breeding colony increased. Figure 6.1 brings together the information from all the colonies. If Shags from colony A were recorded at colony B, then the proportion of Shags from colony A which were recorded at or beyond colony B was plotted against the distance between A and B. Thus each point represents the proportion of Shags from a particular natal colony recorded breeding beyond the corresponding distance on the X axis. The

Table 6.3 Emigration rates of Shags ringed as chicks from three main sites of ringing.

a) Including movements between the south Forth islands:

	Natal area			
	Isle of May	South Forth	Farne Islands	Mean
% emigration	3.5%	22.5%	1.5%	4.9%
N	514	89	260	863

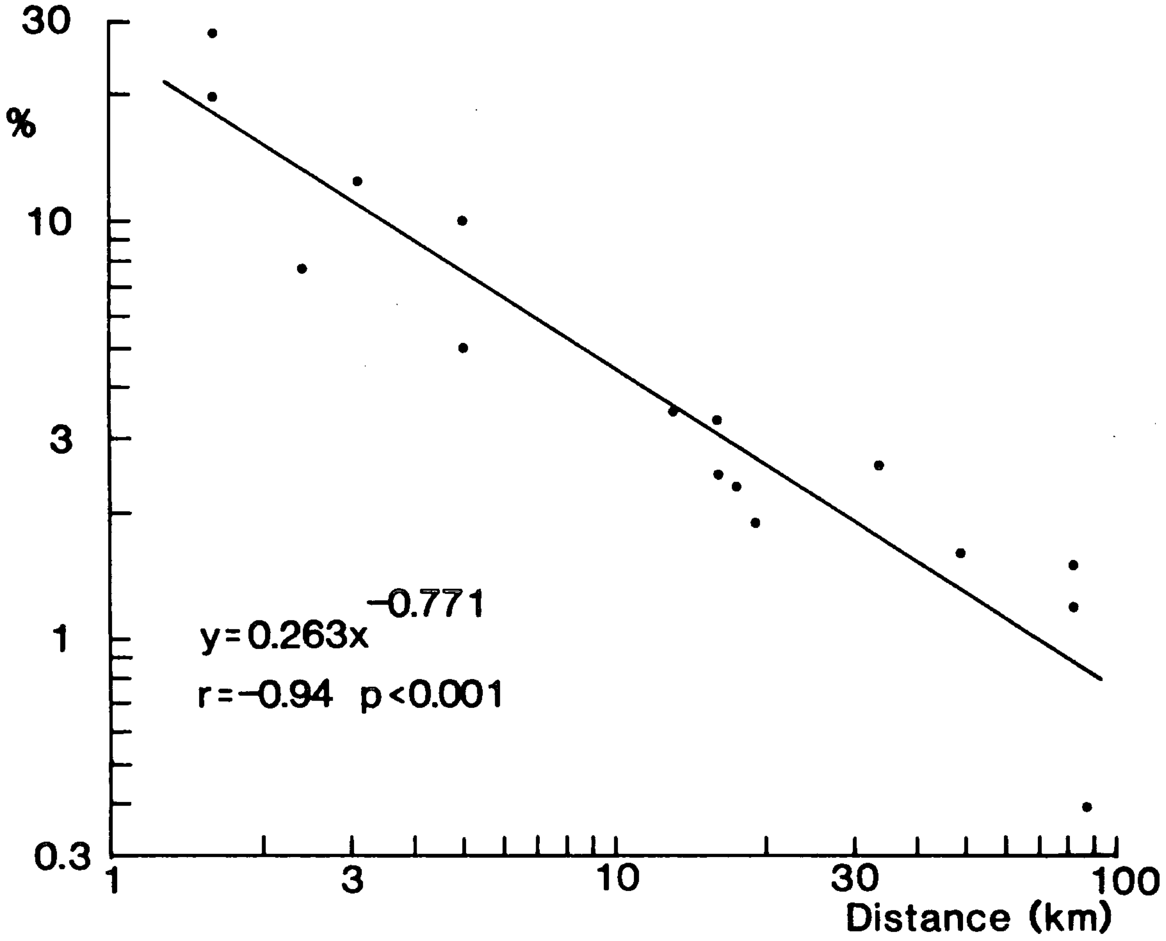
Chi-square=67.9 df=2 P[0.001

b) Excluding movements between the south Forth islands:

	Natal area			
	Isle of May	South Forth	Farne Islands	Mean
% emigration	3.5%	2.2%	1.4%	2.8%
N	514	89	260	863

Chi-square=2.57 df=2 N.S.

Figure 6.1 Relationship between distance away from a colony and the proportion of Shags, hatched from that colony, recorded breeding at or beyond that distance. The graph brings together the data on emigrants from five natal colonies (Isle of May, Bass Rock, Craigleith, The Lamb, Farne Islands) found at seven breeding colonies in 1982-1983 (the previous five, plus Fidra and Inchmickery).



curve was straightened by expressing both axes on a logarithmic scale, giving the equation:

$$y = 0.263\ x^{-0.771} \qquad (6.1)$$

where $\underline{x}$ = distance from the natal colony, and $\underline{y}$ = proportion of Shags from that colony breeding beyond distance $\underline{x}$ (N=16 r=-0.94 P[0.001). The exponential form of the equation signifies that, given bands of equal width around the natal colony, the proportion of birds entering a band which remain within it is large close to the colony, but declines as the distance from the colony increases. Between about 10km and 100km, the decline is so slight that the curve approximates to the pattern of dispersal in Cormorants, whereby a constant proportion of birds entering a band remains within it, irrespective of distance from the colony (Coulson & Brazendale 1968). It is interesting to note that, in spite of pooling information from different colonies, the fit to the regression line (Figure 6.1) was remarkably good. It appears that within the range of distances considered (1 to 100km), the same relationship held independently of the size of the natal colony, and also of the size and proximity of other colonies. Table 6.3 shows that there were no differences in the proportions of Shags recorded breeding more than 16km away from the natal colony for the Isle of May, the south Forth group and the Farne Islands. It would seem that the presence (south Forth group) or absence (Isle of May, Farne Islands) of other colonies near to the natal colony did not affect the proportion of emigrants which bred further afield. It appears that, in the absence of other colonies nearby, potential emigrants return to the natal colony rather than move further away.

Table 6.4 presents similar data on the movements between colonies of Shags ringed as breeders. Compared to Shags ringed as chicks, breeding

Table 6.4 Inter-colony movements of Shags ringed as breeding birds.

Breeding colony	Colony where ringed				
	Isle of May	Bass Rock	Craigleith	The Lamb	Farne Islands
Isle of May	325	0	0	0	1
Bass Rock	0	10	0	0	1
Craigleith	0	0	29	1	0
The Lamb	0	0	0	20	0
Fidra	0	0	0	1	0
Inchmickery	0	0	0	0	0
Farne Islands	1	0	0	0	12
Total emigrated	1	0	0	2	2
Total recorded	326	10	29	22	14
% emigration	0.3%	0.0%	0.0%	9.1%	14.3%

birds were four times less likely to move from the colony where they were ringed (chi-square=9.25 df=1 P[0.01). The highest emigration rate (14%) was found for the Farne Islands. This was probably the result of the 'red-tide' outbreaks in 1968 and 1975 (Coulson et al. 1968, Armstrong et al. 1978). The first outbreak increased the emigration of breeding birds: the retrap records from the Isle of May Bird Observatory show that, despite considerable searches, only four Farnes-ringed Shags were found breeding on the island up to 1968; the following two years saw 17 immigrants from the Farne Islands nesting there, of which three were known to have bred previously on the Farne Islands. The two individuals recorded as Farnes emigrants in 1983 (Table 6.4) were both in fact ringed while nesting on the Farne Islands in 1967. The one breeding on the Isle of May was discovered breeding there in 1970 already, after having been recorded for the last time on the Farne Islands in 1968, before the 'red-tide'. No new immigrants were observed on the Isle of May after the 1975 'red-tide'. The 'red-tides' also caused the death of 82% and 62% of all Shags breeding on the Farne Islands in 1968 and 1975 respectively. The differential mortality of birds which emigrated before 1975, compared to those which did not, reduced the size of the cohorts which produced the emigrants (of 327 breeding birds ringed on the Farne Islands before 1975, only one was recorded on the Farne Islands in 1982-1983). As the calculation of the average annual emigration rate was based on the sum of cohort sizes, the reduction in size of the pre-1975 ones would lead to an inflated estimate of the rate. The magnitude of the error depends on the size of the cohorts ringed after 1975. Only 10% (37) of birds ringed as breeders were marked after 1975, so the error was likely to be large. On the other hand, chick ringing continued unabated after 1975 (1903 marked up to 1981), so the error was likely to be less on the estimate of average annual emigration rate for Shags ringed as chicks. This may explain why there was no apparent 'red-tide' effect observed in the latter case (see Table 6.2). Excluding the Farne Islands, the average annual emigration rate of breeding Shags became 0.8%.

Too few Shags ringed while breeding changed colonies to be able to compare the behaviour of males and females (three males, two females). The only Shags ringed as chicks for which emigrants and non-migrants were consistently sexed at all colonies where they occurred were those originating from the south Forth group of islands - 86 birds. Although nearly twice as many females as males emigrated, the difference was not significant (28.9% compared to 16.7%; chi-square=1.21 df=1 N.S.). Despite this, the proportion of females among non-migrant Shags (40.3%) was very close to that of 44.0±3.0% observed on the Farne Islands by Potts et al. (1980). The same was true of the proportion of females in Shags which emigrated (57.9%, compared to 61.3±2.3%). It was therefore likely that the figures resulting from this study reflected a real difference, with, as on the Farne Islands, a greater proportion of females changing colony than males.

Another way of testing whether more females change colony than males is to consider the relative dilution, by unringed immigrants, of the proportion of Shags ringed as chicks among all non-migrant Shags. If immigration of males and females to a colony were equal, the ratios of ringed non-migrants to unringed Shags of both sexes at the colony would also be equal. On the Isle of May, as at other colonies, it was not possible simply to compare the proportions of breeding males and females which were ringed, because the marking of breeders was biased towards males (more easily caught than females). The problem did not arise when considering only second-year birds, which were breeding for the first time. On the Isle of May, 365 second-year Shags of known sex were recorded in 1982; 32.6% of females were ringed, compared to 48.6% of males (chi-square=6.31 df=1 p[0.05). In other words, a greater proportion of females than males had immigrated to the Isle of May in that year class, i.e. more females than males changed colony. This was in keeping with the general trend prevalent amongst birds (Greenwood 1980).

6.3 Fidelity to the specific natal area and breeding area on the Isle of May.

The ringing records of the Isle of May Bird Observatory contained information about the areas where particular rings had been used on chicks, especially from 1977 onwards. The names of the areas followed those recommended by Eggeling (1960). On average, a name designated approximately 100m of coastline; certain names indicated a site precisely (e.g. Colm's Hole), and the least accurate description was provided by 'Rona', comprising around 300 nests along 300m of coastline. Breeding Shags aged two to five were grouped into four categories, according to their fidelity to the area where they had fledged. These categories were defined as follows:

1. Good fidelity: the breeding area was the same as the natal area (on average, breeding site within 100m of fledging site).
2. Moderate fidelity: the breeding area was adjacent to the natal area (within 300m of it).
3. Poor fidelity: the breeding area was at least 300m from the natal area, on the same side of the island.
4. Very poor fidelity: the breeding area was at least 600m from the natal area, or on the opposite side of the island.

The results are presented in Table 6.5. The pattern of fidelity to the natal area in males was the same for the second-years (1980 cohort) as for

Table 6.5 Fidelity of male and female Shags breeding on the Isle of May to their area of birth. The categories are explained in Section 6.3.

Males:

	Area fidelity				
	Good	Moderate	Poor	Very poor	Total
1980 cohort	53	11	7	21	92
1979 cohort	18	0	3	9	30
1978 cohort	12	3	2	4	21
1977 cohort	7	0	2	3	12
Total	90	14	14	37	155
	58.1%	9.0%	9.0%	23.9%	100.0%

Females:

	Area fidelity				
	Good	Moderate	Poor	Very poor	
1980 cohort	8	1	2	8	19
1979 cohort	12	1	2	10	25
1978 cohort	7	1	4	10	22
1977 cohort	6	0	1	3	10
Total	33	3	9	31	76
	43.4%	4.0%	11.8%	40.8%	100.0%

Male x female totals: chi-square=9.21 df=3 P[0.05

the older birds (chi-square=2.76 df=3 N.S.). The same was true of females when comparing second and third-years, grouped to overcome the small sample sizes, with older birds (chi-square=0.86 df=3 N.S.). This suggested that once Shags of either sex had recruited to a given area, most of them bred in that area in subsequent years. Ringed individuals which bred in 1981 and returned to breed in 1982 did indeed prove extremely faithful to their breeding area. A total of 267 out of 268 males (99.6%), and 187 out of 190 females (98.4%) returned in 1982 to the area where they had bred in 1981; the four birds which moved travelled relatively far, to the side of the island opposite to the one where they nested in 1981.

Approximately half the Shags which fledged from the Isle of May and returned there to breed showed a clear attachment to the precise area where they were hatched (Table 6.5). This fidelity was significantly stronger in males: 58% of males returned to the area of fledging, and only 24% bred more than 600m away from their natal area, whereas the corresponding figures for females were 43% and 41% (Table 6.5). There was no difference in the proportion of individual males and females breeding in 1981 which moved to a new area in 1982 (Fisher's Exact P=0.31).

6.4 Re-occupation of nest-sites from one year to the next, and site tenacity.

The results from the previous section demonstrated the practically total fidelity of a breeding Shag not only to the colony, but to the part of the colony where it nested. In fact, a striking characteristic of the Isle of May colony was that many of the nest-sites were re-occupied from one year to the next. Either the old nest was renovated and added to, or a new nest was built nearby; a new nest was considered to be on the same site as the old one when, as judged from the photographs of the colony from the previous year, the two nests would have overlapped.

In 1982, 928 of the 1169 sites surveyed in 1981 were re-occupied in the course of the season (79%), and in 1983, a nest census in mid-May revealed that 1378 of the 1869 sites occupied in 1982 held breeding pairs (74%). Taking into account failed and late breeders that were not recorded in 1983, these two proportions were very similar. Of the initial 1169 sites from 1981, a total of 817 were occupied also in the two following years (70%). An inspection of site re-occupation in relation to the breeding experience of the previous owner showed that, in both 1981 and 1982, sites belonging to young males were less often re-occupied in the following year than sites owned by older males: on average, 57% of 'second-year' sites were re-occupied, compared to 85% of 'older' sites (Table 6.6). Considering only the parts of the Isle of May where nests were surveyed in 1981, 42% (646 out of 1536) of the nests built in 1982 were on sites not used in 1981. Such sites will be referred to as 'new' sites; in contrast, 1982 sites previously occupied in 1981 will be called 'established' sites. As suspected by Snow (1960) on the basis of the quality of the nest structure and the number of young fledged, a high proportion of new sites were occupied by young breeders, namely 48%, whereas the proportion for established sites was only 9% (Table 6.7). A correspondingly high proportion of the new sites (44%) was not re-occupied in the following year, whereas only 11% of the established sites were left empty in 1983. The more frequent re-occupation of sites previously held by older males, noted in Table 6.6, remained valid for both new and established sites (Table 6.7).

Although the occupation of a site during two consecutive years did not entail that the occupants were the same in each year, it seemed likely that young males changed site more frequently than older males. The sample of

Table 6.6 Re-occupation of nest-sites from 1981 to 1982, and from 1982 to 1983, in relation to the breeding experience of the previous male occupant.

1981 occupant	1981 sites		1982 sites	
	Used in 1982	Not used	Used in 1983	Not used
Second-year male	82 (67.2%)	40 (32.8%)	184 (53.2%)	162 (46.8%)
Older male	386 (86.4%)	61 (13.6%)	1066 (84.0%)	203 (16.0%)
Chi-square (1 df)	22.8 P[0.001		145.9 P[0.001	

Table 6.7 Occupation of new and established sites in 1982 according to male breeding experience, and their re-occupation in 1983.

	New 1982 sites used by		Established 1982 sites used by	
	Second-year	Older	Second-year	Older
Used in 1983	117 (40.8%)	170 (59.2%)	52 (7.1%)	684 (92.9%)
Not used in 1983	129 (56.3%)	100 (43.7%)	20 (22.5%)	69 (77.5%)
Chi-square (1 df)	11.7 P[0.001		21.8 P[0.001	
Total	246 (47.7%)	270 (52.3%)	72 (8.7%)	753 (91.3%)

New x Established sites: chi-square=264 df=1 P[0.001

ringed individuals breeding in 1981 provided the means of examining site tenacity more closely. Table 6.8 gives the numbers of individual males and females which in 1982 returned to their old site or changed sites. In both sexes, site tenacity increased significantly with age. In males, only 17% of second-years retained their sites, as opposed to around 70% of birds seven years or older; in females, none of those which had been second or third-year birds returned to their original site, whereas about 60% of birds over 10 did. The change in site tenacity with age was also noticeable in Shags of both sexes ringed as adults, with more of the birds ringed in earlier years returning to the same sites. In both males and females, the site tenacity of the youngest age group was significantly lower than that of older birds, confirming what had been suggested by general inspection of site re-occupation.

Table 6.8 includes data from Shags which were paired in 1981, so the proportions of males and females which changed site were only comparable if site tenacity in the two sexes was independent of the pair-bond. However, for males and females which were paired in 1981 and returned to breed in 1982, Table 6.9 shows a close association between whether or not a male changed site and whether or not his partner changed site. In Shags, the male selects the nest-site and attracts the female (Snow 1963), so that the observed association was the result of a causal relationship, with females responding to the action of the male. Thus 83% of females whose male retained the 1981 site returned to that site, whereas only 7% of females whose mate had moved returned to their old site. It was clear that the attachment shown by females for their old site was due almost entirely to their attachment to the male at that site. Further evidence for this was provided by birds whose mate was not recorded breeding in 1982. The proportion of males whose female partner had disappeared and which changed

Table 6.8 Site tenacity between 1981 and 1982, in relation to age in male and female Shags.

Site	Male age (years)						Males ringed as adults in			Total
	2	3	4-6	7-10	11-13	14+	1981	1979-80	1965-78	
Same	4	6	5	30	13	6	25	26	32	147
Change	20	10	6	13	4	3	31	20	14	121
% same	16.7	37.5	45.5	69.8	76.5	66.7	44.6	56.5	69.6	54.9

Second-year x Older males: chi-square=13.9 df=1 P[0.001

Linear trend in males of known age: chi-square=20.7 df=1 P[0.001

Site	Female age (years)						Females ringed as adults in			Total
	2	3	4-6	7-10	11-13	14+	1981	1979-80	1965-78	
Same	0		1	12	10	4	30	14	13	84
Change	7		5	18	7	2	36	20	11	106
% same	0.0		16.7	40.0	58.8	66.7	45.5	41.2	54.2	44.2

Second+third-year x Older females: Fisher's Exact P=0.02

Linear trend in females of known age: chi-square=9.95 df=1 P[0.001

Table 6.9 Male and female Shags paired in 1981: correspondence between whether a male changed site between 1981 and 1982, and whether his mate changed site.

Females in 1982	Males in 1982			
	Same site	Change site	Total breeding	Disappeared
Same site	54	3	57	0
Change site	11	41	52	6
Total breeding	65	44	109	
Disappeared	10	11		2

Association between whether a male changed site and whether his mate changed site: chi-square=58.1 df=1 P[0.001

In all, the members of 109 pairs breeding in 1981 were recorded breeding in 1982. The males from 6 pairs and the females from 21 pairs were not recorded in 1982; neither male nor female from another two pairs were recorded in 1982 (such birds are referred to above as 'disappeared').

site was no different to that of males whose mate from 1981 was breeding in 1982 (chi-square=0.61 df=1 N.S.); this confirmed that males did not depend on the female for the choice of the site. In contrast, all females whose partner disappeared changed site, behaving differently overall to those females whose mate from 1981 was breeding in 1982 (Fisher's Exact P=0.01), but very similarly to the subset of females whose previous partner had changed site (93% of them moved).

Considering independent groups of ringed males and females, i.e. excluding ringed pairs, site tenacity in males was greater than in females. Of 137 males and 74 females which returned to breed in 1982, 53% of males re-occupied their previous site, and only 35% of females (chi-square=5.18 df=1 P[0.05). This matches what would be expected from the previous paragraph: bereavement induced females to change site, but did not influence the site tenacity of males; also a certain proportion of females were separated from their previous mates even though they occupied their old sites.

It was noted earlier that approximately three-quarters of the sites were occupied in successive years: were the same birds re-occupying their old sites or were different ones appropriating them? Table 6.10 shows that a considerable amount of appropriation occurred, with no difference in the proportion of males and females which moved to a previously occupied ('established') site. On average, 59% of birds which changed site moved to an established site; this proportion was almost identical to the proportion of established sites occupied in the colony in 1982 (57%). It would seem that the birds which moved selected sites at random from the pool of sites available to them. However, many sites not occupied in 1982 were suitable for nesting Shags, for instance the 241 sites occupied in 1981 and not in 1982, and another 410 sites newly occupied in 1983. With such sites

Table 6.10 Nest-site selection by individual Shags which changed site between 1981 and 1982: a Shag could either move to a site previously occupied in 1981, or to an entirely new site.

Site occupied in 1982	Paired in 1981			Total	1981 partner unknown		Total
	Males	Females	Stable pairs		Males	Females	
1981 site	16	24	12	52	40	29	69
New site	19	13	9	41	25	19	44
% 1981 site	45.7	64.9	57.1	55.9	61.5	60.4	61.1

Chi-square=2.69 df=2 N.S.

Chi-square=0.01 df=1 N.S.

Note: For Shags paired in 1981, the columns headed 'males' and 'females' refer to birds which were breeding separately in 1982.

included, the proportion of established sites out of those available reduced to 41%. As this figure did not cover the unknown number of sites which, although suitable, were not occupied in the course of the study, it constituted a maximum estimate. Even so, birds which changed sites now demonstrated a significant preference for the established sites (chi-square=34.4 df=1 P[0.001). There was no change in preference with age (Table 6.11).

Although three quarters of the sites were occupied from one year to the next, some of those sites had changed owners. The figures from Tables 6.8 and 6.10 reveal that out of 215 sites occupied in 1981 and re-occupied in 1982, 68 (32%) were taken over by a different male in 1982. In spite of the continuity in the occupation of sites from one year to the next, a transfer of ownership took place on nearly a third of the sites between years.

6.5 Distance between the nest-sites of an individual Shag in consecutive years.

Individuals which changed site between breeding attempts in consecutive years remained within the general area of their first breeding attempt, as demonstrated in Section 6.3. The distances moved were thus relatively short; Table 6.12 shows that in the case of the 121 ringed males which changed site from 1981 to 1982, 92% moved less than 16m (median distance moved: 4.1m). Similarly, 85% of the 106 ringed females stayed within the same radius (median: 6.0m). There was no apparent relationship between age and distance moved in either sex. Table 6.12 includes data from 21 pairs which bred together at a different site in 1981, and from 20 pairs which split up in 1982, with each member moving to a separate site. There was no relationship between the distances moved by each partner for the latter

Table 6.11 Nest-site selection in relation to age for individual Shags which changed site between 1981 and 1982 (sexes combined).

Site occupied	Age (years)					Ringed as adults in			Total
in 1982	2	3	4-6	7-10	11+	1981	1979-80	[1979	
1981 site	10	2	6	6	4	25	11	12	76
New site	12	8	3	16	5	30	25	10	109
% 1981 site	45.5	20.0	66.7	27.3	44.4	45.5	30.6	54.5	41.1

Chi-square=6.19 df=4 N.S.   Chi-square=3.61 df=2 N.S.

Note: Males and females paired in both 1981 and 1982 have not been included in the analysis.

Table 6.12 Distance moved by Shags which changed breeding sites between 1981 and 1982, in relation to age. The data include males and females which were paired in 1981.

Distance moved	Male age (years)					Males ringed as adults in			Total	%
	2	3	4-6	7-10	11+	1981	1979-80	[1979		
Up to 4.0m	8	6	3	6	2	21	7	7	60	49.2
4.1-8.0m	3	2	2	4	1	5	7	5	29	23.8
8.1-16.0m	6	1	1	3	1	2	6	2	23	18.9
Over 16.0m	3	1	0	0	3	3	0	0	10	8.2

Distance moved	Female age (years)					Females ringed as adults in			Total	%
	2	3	4-6	7-10	11+	1981	1979-80	[1979		
Up to 4.0m	2		2	6	4	10	7	6	37	34.9
4.1-8.0m	2		1	5	3	8	7	1	27	25.5
8.1-16.0m	2		2	6	1	8	5	2	26	24.5
Over 16.0m	1		0	1	1	10	1	2	16	15.1

pairs (r=-0.06 df=18 N.S.), so the relative distances moved by males and females were compared in Table 6.13, after removal of the stable pairs. Even within the small range of distances considered, males and females differed significantly. Almost half the males moved less than 4m, whereas just over a quarter of the females did likewise. Conversely, twice as many females than males (18% versus 9%) moved further than 16m.

It was shown in Section 6.4 that significantly more males than females returned to the same site from one year to the next. When considering birds which returned to their sites as well as those which changed sites (excluding stable pairs), 71% of males remained within 4m of their old site compared to 46% of females (chi-square=17.9 df=1 P[0.001); the corresponding median distances moved were 1.5m for males, and 5.0m for females. The pattern observed in recruiting birds, whereby females bred further away from their natal area than males, persisted therefore after recruitment, albeit on a much reduced scale.

In 1981, no Shags, and in 1982, 13 males and five females were recorded as changing site between breeding attempts in the same year. Of these, nine males and four females moved less than 8m, i.e. again, distances moved were usually short. One interesting exception was a third-year male which moved twice in the course of the season: the first time he moved 50m, the second, 175m.

6.6 Stability of the pair-bond.

Of the 138 marked pairs in 1981, 75 (54%) were recorded breeding together again in 1982. This value was similar to that of 48% noted by Potts (1966) on the Farne Islands (chi-square=1.12 df=1 N.S.). A substantial number of pairs which broke up did so through the death or

Table 6.13 Distance moved by male and female Shags which changed breeding sites between 1981 and 1982.

	Distance moved (m)				Total
	Up to 4.0	4.1-8.0	8.1-16.0	Over 16.0	
Males	48 (48.0%)	23 (23.0%)	20 (20.0%)	9 (9.0%)	100
Females	25 (29.4%)	21 (24.7%)	24 (28.2%)	15 (17.6%)	85

Chi-square=8.04 df=3 P[0.05

Note: Males and females paired in both 1981 and 1982 are not included.

disappearance of the partner: out of 27 pairs from 1981, the partners of 6 females and 21 males were not recorded breeding in 1982, and neither member of another two pairs from 1981 was recorded in 1982. Of the remaining 109 pairs from 1981, 34 split up despite both partners being present in 1982, i.e. the rate of divorce (separation not due to the disappearance of a member of the pair) was 31%. Divorce thus accounted for just over half of pair changes.

The relationship between divorce rate and the age of the male in 1981 is shown in Table 6.14. The rates for birds three years old or more were similar, averaging 28%. That for second-year birds was almost three times as high (75%), again following the pattern observed by Potts (1966) on the Farne Islands. Similar increases in the stability of the pair-bond with age have been noted for Yellow-eyed and Adélie Penguins (Richdale 1957, LeResche & Sladen 1970), Kittiwakes (Coulson & White 1958), Arctic Skuas (Williamson 1959), and Red-billed Gulls (Mills 1973).

The effect of male site tenacity upon the rate of divorce is demonstrated in Table 6.15, which incorporates the distance moved by males which changed sites. The rate of divorce increased fourfold, from 17% for males which remained faithful to their old site, to 75% for males which moved more than 8m. That females could recognise the male they had paired with the previous year is evident from Table 6.9, which shows the very strong association between the presence of the previous year's male on his old site, and the return of the female to the same site. A mere 6% returned in his absence, as opposed to 83% in his presence. The female was choosing the male, and not the site. Furthermore, 21 times out of 44, females paired up again with their previous year's mate even though he had moved site. This again indicated that the female recognised the male and choose to pair preferentially with him. However, the greater the distance moved, the less

Table 6.14 Pair stability between 1981 and 1982 in relation to the age of the male.

	Male age (years)						Males ringed as adults in			Total
	2	3	4-6	7-10	11-13	14+	1981	1979-80	[1979	
Same mate	2	6	3	14	6	3	13	9	19	75
Change mate	6	0	0	5	2	0	13	4	4	34
% change	75.0	0.0	0.0	26.3	25.0	0.0	50.0	30.8	17.4	31.2

Second-year x Older males: chi-square=5.67 df=1 P[0.05

Table 6.15 Pair stability between 1981 and 1982, in relation to male site tenacity and distance moved.

	Distance moved (m)					Total
	Nil	Up to 4.0	4.1-8.0	8.1-16.0	Over 16.0	
Same mate	54	12	6	2	1	75
Change mate	11	8	6	6	3	34
% change	16.9	40.0	50.0	75.0	75.0	31.2

Test for linear trend (last two columns grouped): chi-square=19.3 df=1 P[0.001.

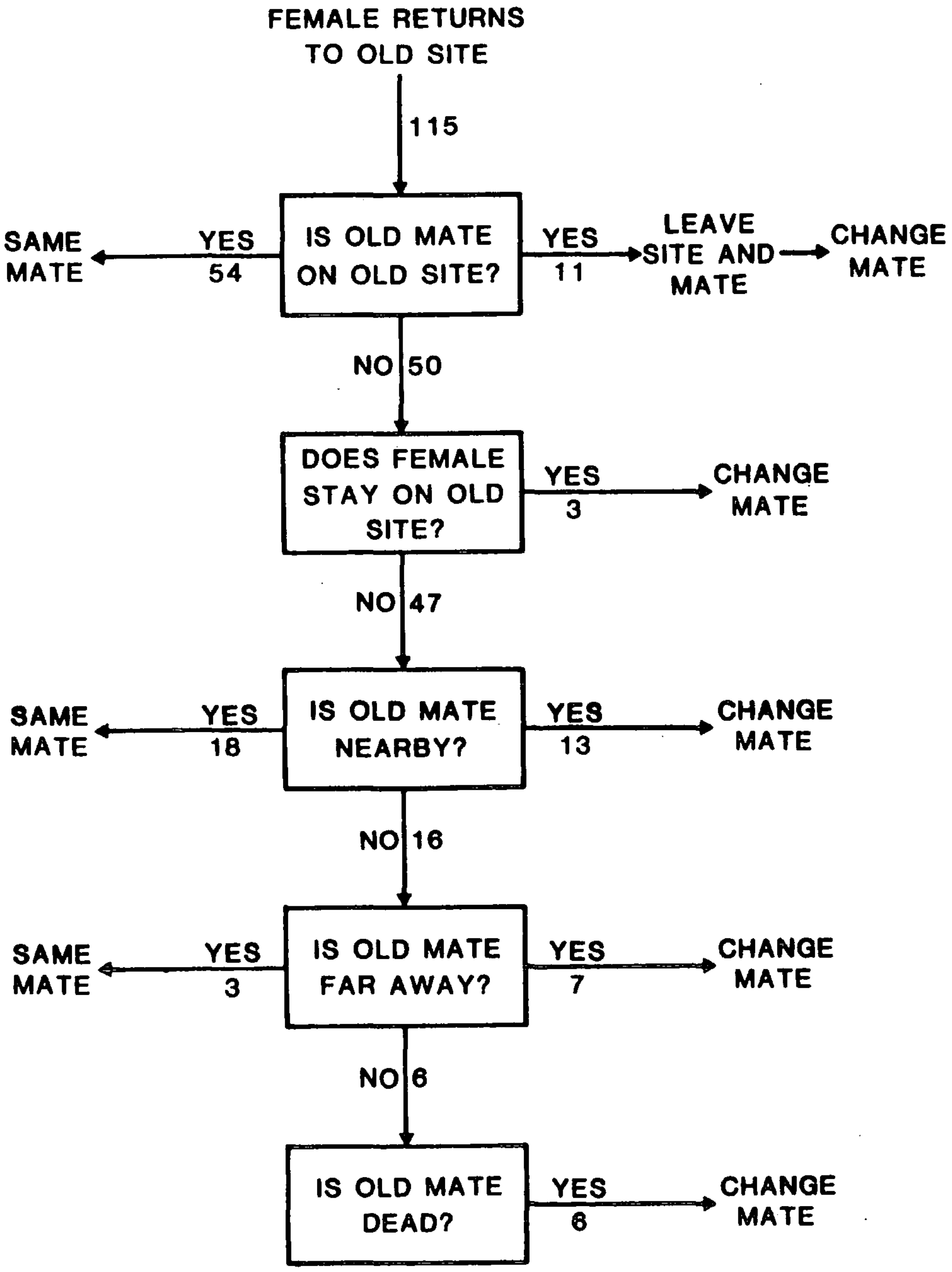
Note: The table includes three females which bred on the same site as in 1981, their previous mates having moved 3.5m, 8.5m and 9m respectively.

likely this became.

The above results can be explained satisfactorily if pair formation of Shags which bred in the previous year proceeded along the lines described schematically in Figure 6.2. It is proposed that the female returned initially to the site where she bred the year before. If it was occupied by her old mate, the two would renew the pair-bond. If a strange male was present on the site, the original male being either dead or having moved, the female would search the adjoining area for her old mate; her success depended on the distance he had moved (if alive and breeding), which obviously influenced the amount of coastline to be searched. It is clear that the Shags did not follow this proposed pattern rigidly: the diagram gives the actual numbers of birds which followed the different pathways, starting with 115 ringed females. For instance, 6% of females whose previous mate was absent from the old site stayed and paired with a stranger on that site. Furthermore, 17% of females did not return to a male which retained his old site. Although this could possibly be due to active avoidance by the female, it could equally well stem from the male having already paired with another female. A consequence of the high proportion of breeders pairing up again the next year is that should young breeders pair together, the ages of birds in mature pairs will tend to be similar; the very fact that a pair which bred in the previous year will tend to breed together again dictates that young males will pair with young females. The net outcome is that pairs will be formed of partners of a similar age, with a blurring imposed by mortality. This is exactly what was observed in Section 2.12 (Table 2.9).

Of the 17 birds recorded as changing sites during the 1982 breeding season, 10 were paired on the first site and stayed together after changing sites; they moved 1.2m, 1.7m, 5m, 7m and 17m respectively. The partners of

Figure 6.2 Schematic model put forward to describe the mechanism of pair formation in Shags which bred in the previous year. The numbers refer to the actual numbers of females which followed the different pathways in 1982.



the remaining seven birds were either unringed or not known; two males with unringed females on the first site paired with ringed females on the second site, i.e. changed mates; one had moved 5m, the other 10m. The data were too few to draw any conclusions about the relationship between pair-bond and distance moved within the same season.

6.7 Site tenacity, pair stability and breeding success.

Failure of the breeding attempt in one year is known to lead to a change of site or territory in the following year in the Yellow-eyed Penguin (Richdale 1957), the Goldeneye (Dow & Fredga 1983), the Puffin (Ashcroft 1979) and passerines such as the Pied Flycatcher (von Haartman 1949) and the Grey Catbird (Darley et al. 1977). It has also been shown to relate to subsequent divorce, as in the Fulmar (Macdonald 1977), the Kittiwake (Coulson & Thomas 1980) and the Skylark (Delius 1965).

In the case of the Shag on the Isle of May, nearly twice as many males changed site from 1981 to 1982 after reproductive failure than after a successful breeding attempt (Table 6.16). As expected on the basis of the association between male site tenacity and female site tenacity, a similar relationship held for females. There was no relationship between success or failure of the nesting attempt in 1981 and subsequent divorce, either when males returned to their old sites or when they moved (Table 6.17). There was thus no evidence of a female rejecting a male which proved a poor breeder in the previous year.

In 1982, both males and females which retained their 1981 sites bred earlier (as shown by the date of laying) than birds which changed sites (Table 6.18). In both sexes, the average difference was about a week. In order to dissociate the effects of changing site and changing mate, Shags

Table 6.16 Nest-site tenacity between 1981 and 1982 in relation to success or failure of the breeding attempt in 1981.

	Males		Females	
1982 site	Same	Change	Same	Change
Success	132 (57.1%)	99 (42.9%)	73 (47.4%)	81 (52.6%)
Failure	7 (20.6%)	17 (79.4%)	5 (19.2%)	21 (80.8%)
Chi-square (1 df)	5.78 P[0.05		6.09 P[0.05	

Table 6.17 Pair stability between 1981 and 1982 in relation to success or failure of the breeding attempt in 1981.

	Male on same site		Male changed site	
	Success	Failure	Success	Failure
Same mate	51 (98.1%)	1 (1.9%)	17 (85.0%)	3 (15.0%)
Change mate	10 (100.0%)	0 (0.0%)	21 (91.3%)	2 (8.7%)
	Fisher's Exact P=0.84		Fisher's Exact P=0.65	

Table 6.18 Date of first laying in 1982 in relation to site tenacity between 1981 and 1982.

Males:

	Week of laying				Mean week
	4-5	6-7	8-9	10+	
Same site	30 (26.8%)	56 (50.0%)	18 (16.1%)	8 (7.1%)	6.7
Change site	15 (17.0%)	38 (43.2%)	19 (21.6%)	16 (18.2%)	7.6

Chi-square=8.38 df=3 P[0.05

Females:

	Week of laying				Mean week
	4-5	6-7	8-9	10+	
Same site	15 (21.1%)	38 (53.5%)	13 (18.3%)	5 (7.1%)	6.9
Change site	11 (15.5%)	25 (35.2%)	18 (25.4%)	17 (23.9%)	8.1

Chi-square=10.65 df=3 P[0.05

Note: Week 1 starts on 1 March 1982.

which had been paired in 1981 and bred in 1982 were grouped into four categories corresponding to the combinations of site and mate retention (Table 6.19). For each sex, there was no difference in the timing of breeding attributable to site change when mate fidelity was kept constant; site was not important, so the categories were regrouped accordingly. Shags which retained their mate bred significantly earlier than those which changed mate: whereas 60% of stable pairs had laid by mid-May, only 34% of males and 29% of females which changed mate had eggs by that time. The apparent relationship in Table 6.18 between site tenacity and laying date was therefore the consequence of the changes in mate taking place at the same time. In general, Shags which changed mate paired with a bird younger than their previous mate. In six cases where the ages of a male's old and new female partner could be compared, the female was younger in five. For females, the new male partner was younger in six out of nine cases. As laying date was negatively correlated with both male and female age (see Section 5.4), this could explain why birds which changed mate bred later than those which did not.

Similar differences in laying date between newly formed pairs and stable pairs have been noted for the Kittiwake (Coulson 1966, 1972), the Red-billed Gull (Mills 1973) and the Fulmar (Ollason & Dunnet 1978). In these species as well as in the Barbary Dove (Erickson & Morris 1972), the Snow Goose (Cooke et al. 1981), the Manx Shearwater (Brooke 1978) and the Arctic Tern (Busse 1983), site tenacity and pair stability led to an increase in reproductive output. The effect of site tenacity upon the breeding success of the Shag is shown in Table 6.20. The failure rate for females which changed site was over twice that of sedentary birds, and chick production was reduced by a quarter; the result for males, although not reaching statistical significance, followed the same pattern as for the

Table 6.19 Timing of breeding in 1982 in relation to site tenacity and pair stability between 1981 and 1982.

		Males		Females	
		Early	Late	Early	Late
Same mate:	Same site	26 (60.5%)	17 (39.5%)	26 (60.5%)	17 (39.5%)
	Change site	9 (60.0%)	6 (40.0%)	9 (60.0%)	6 (40.0%)
		Chi-square=0.00 df=1 N.S.		Chi-square=0.00 df=1 N.S.	
Change mate:	Same site	5 (31.3%)	11 (68.7%)	0 (0.0%)	2 (100.0%)
	Change site	8 (36.4%)	14 (63.6%)	7 (31.8%)	15 (68.2%)
		Chi-square=0.11 df=1 N.S.		Chi-square=0.02 df=1 N.S.	
Totals:	Same mate	35 (60.3%)	23 (39.7%)	35 (60.3%)	23 (39.7%)
	Change mate	13 (34.2%)	25 (65.8%)	7 (29.2%)	17 (70.8%)
		Chi-square=5.27 df=1 P[0.05		Chi-square=5.42 df=1 P[0.05	

Note: The timing of breeding was considered 'early' if a pair laid its first egg before mid-May (week 7), 'late' if it occurred after that time.

Table 6.20 Success or failure of the nesting attempt and chick production in 1982, in relation to site tenacity between 1981 and 1982.

	Males		Females	
	Failed	Successful	Failed	Successful
Same site	24 (16.3%)	123 (83.7%)	10 (11.9%)	74 (88.1%)
Change site	26 (21.5%)	95 (78.5%)	32 (30.2%)	74 (69.8%)
	Chi-square=0.85 df=1 N.S.		Chi-square=8.07 df=1 P[0.05	

	Same site	Change site	Same site	Change site
Mean no. chicks fledged/pair	1.78 (0.08)	1.54 (0.10)	1.83 (0.11)	1.42 (0.12)
	t=1.78 df=266 N.S.		t=2.52 df=188 P[0.05	

	Same site	Change site	Same site	Change site
Mean adjusted for laying date	1.80 (0.08)	1.71 (0.08)	1.73 (0.10)	1.74 (0.09)
	t=0.80 df=253 N.S.		t=0.07 df=174 N.S.	

Note: Means expressed with 1 S.E. in parentheses.

females. After adjusting chick production for laying date, however, the differences became negligible. It was probable that the differences observed originally resulted from the proportion of Shags which had changed site and also mate, thereby breeding later and subject to the seasonal decline in breeding success described in Section 5.5. Table 6.21 shows the breeding success of male and female Shags for each of the four categories of site and mate retention. Overall, there was no detectable difference between categories. With site fidelity kept constant, the proportion of failed breeders varied little in relation to mate fidelity. Grouping the latter categories, 15% of males which retained their sites failed as opposed to 20% for those which moved, and corresponding figures for females were 14% and 31%. Although in both cases birds which changed site failed more often than those which did not, for neither sex was the difference significant. Combining the sexes (counting paired males and females as one), 26% of birds which changed site failed compared to 14% of birds which retained their site; again the difference was not significant (chi-square=3.01 df=1 N.S.). Regarding chick production, the mean values for males were again similar if site fidelity was held constant, with males faithful to their site fledging on average 1.80 chicks, and those which moved fledging 1.56 chicks (t=1.25 df=128 N.S.). For females, the mean values were closest at constant mate fidelity, with females paired to their old mate rearing 1.73 chicks, and newly paired females rearing 1.32 chicks (t=1.82 df=113 N.S.). None of these results decided in favour of site tenacity or of pair stability as the main factor causing the differences observed in Table 6.20. The covariation with laying date, which eliminated the differences in Table 6.20, itself pointed strongly towards mate as the main influence, especially as it showed no trend with respect to site. It was likely, therefore, that reproductive success was mainly affected by mate change.

Table 6.21 Success or failure of the nesting attempt and chick production in 1982, in relation to site tenacity and pair stability between 1981 and 1982.

Site	Mate	Males		Females	
		Failed	Successful	Failed	Successful
Same	Same	8 (14.8%)	46 (85.2%)	8 (14.8%)	46 (85.2%)
Same	Change	3 (14.3%)	18 (85.7%)	0 (0.0%)	3 (100.0%)
Change	Same	5 (23.8%)	16 (76.2%)	5 (23.8%)	16 (76.2%)
Change	Change	6 (17.6%)	28 (82.4%)	13 (35.1%)	24 (64.9%)
		Chi-square=1.00 df=3 N.S.		Chi-square=4.13 df=3 N.S.	
Same	-	11 (14.7%)	64 (85.3%)	8 (14.0%)	49 (86.0%)
Change	-	11 (20.0%)	44 (80.0%)	18 (31.0%)	40 (69.0%)
		Chi-square=0.32 df=1 N.S.		Chi-square=3.83 df=1 N.S.	

		Mean chicks	S.E.	N	Mean chicks	S.E.	N
Same	Same	1.78	0.14	54	1.78	0.14	54
Same	Change	1.86	0.22	21	1.33	0.33	3
Change	Same	1.62	0.26	21	1.62	0.26	21
Change	Change	1.53	0.18	34	1.32	0.21	37
		F=0.58 df=3,126 N.S.			F=1.22 df=3,111 N.S.		

6.8 Breeding success of individuals in consecutive years.

Coulson & Thomas (in press,b) showed that in the Kittiwake, females which had a high chick production in one year were likely to do well in the next year. As part of the 1981-1982 comparison, this was examined in the Shag (Table 6.22). No evidence of a similar trend was discernible for individuals of either sex. However, when considering the breeding unit to be the pair rather than the individual (Table 6.22), a trend became apparent, indicating that certain pairs were consistently more efficient at rearing their offspring than others. The trend was independent of the age of the birds: those fledging one or no chicks in both years were aged three or more (the youngest bird of known age was four years old), and the same was true of those fledging three chicks in 1981 and 1982 (the youngest bird of known age was three years old, and two were aged four). The consistency of individual pairs could result from a stronger pair-bond between members of certain pairs, or a degree of incompatibility between others. A similar effect was noted by Ashcroft (1979) for the Puffin: significantly more pairs reared chicks in the three years of his study or in none of those years than would be expected by chance. He concluded that the pair itself was the most important determinant of breeding success. The question remains open, however, as to why certain partners who consistently produced few or no offspring did not separate in an attempt to improve their life-time reproductive success.

6.9 Discussion.

The importance of dispersal is obvious as a means of promoting gene flow between separate groups of individuals. It has also been identified as

Table 6.22 Number of chicks fledged by individual males, females and stable pairs in two consecutive years.

	Males				Females				Stable pairs			
Fledged	Fledged 1982				Fledged 1982				Fledged 1982			
1981	0	1	2	3-4	0	1	2	3-4	0	1	2	3-4
0	5	7	8	4	8	3	8	7	2	1	1	0
1	4	7	14	7	6	6	7	5	2	2	3	2
2	21	21	26	29	14	17	22	14	5	6	9	7
3-4	14	24	33	32	10	15	19	20	3	7	9	13

Test for linear trend:

For males : chi-square=1.69 df=1 N.S.

For females: chi-square=1.34 df=1 N.S.

For pairs : chi-square=5.17 df=1 P[0.05

having a role in population regulation of certain species (Lidicker 1975) and Taylor & Taylor (1977) considered it an essential adaptation to exploiting a patchy and fluctuating environment. In Shags, the extent of dispersal from natal site to breeding site was found to be inversely related to the distance between neighbouring colonies. Because of the apparent continuity in the relationship, it is difficult to decide what boundaries to put on a colony, vaguely defined by Thomson (1964) as "a number of birds breeding gregariously". For convenience, all breeding groups of Shags isolated from their nearest neighbour by more than 1km will be called colonies (these include each of the four south Forth islands); the Farne Islands, traditionally regarded as a single unit by Coulson and Potts, will be referred to as one colony. The proportion of Shags which emigrated beyond 15km from their natal colony (in the case of the Isle of May or the Farne Islands, this was equivalent to the full emigration rate) averaged 3.1%, on the basis of birds identified at eight colonies comprising the bulk of the breeding Shags in the region. Even if this figure were doubled to take into account emigrants to colonies that were not sampled, it would still imply that 94% of birds returned to breed within 15km of their natal colony, or to the natal colony itself in the case of the Isle of May or Farne Islands. Such a return rate was much higher than the 35% calculated for the Herring Gull on the Isle of May (Chabrzyk & Coulson 1976), but similar to the figures of 89% and 92% for Puffins and Shags respectively on the Farne Islands (Harris 1976, Potts 1969). When Shag colonies were close together, the movement of birds between them increased: on average 23% of birds emigrated from one of the four islands on the south side of the Firth of Forth, and nine times out of 10, these emigrants were recorded breeding on a different island in the same group. Furthermore, over 50% of Shags which returned to breed on the Isle of May settled in the same geographical area from which they fledged. Thus not only did Shags recognise their natal colony, but certainly also their specific natal area and maybe even natal site. In the same way, Nelson (1978) observed that 95% of young Gannets returning to the Bass Rock came back to their area of origin, and certain individuals returned to the actual ledge where they were born.

The attachment of seabirds to the natal colony appears to develop in the nest. By moving eggs and chicks between islands, Serventy (1967) showed that there was no hereditary basis for Short-tailed Shearwaters returning to the natal colony; however, the young seemed to become imprinted before fledging. In Laysan Albatrosses, the survivors of chicks exchanged between islands at 3-4 weeks returned to the point of release; only 17% of chicks exchanged as fledglings did so, the remainder returning to the point of origin (Fisher 1971b). In territorial species, dispersal is usually considered to be a consequence of competition with established territory holders, particularly when the breeding habitat is in short supply (Watson & Moss 1970). In colonial seabirds, competition for nesting space is often intense. The spatial pattern of recruitment to the breeding colony is dictated by the availability of space in the Gannet (Nelson 1978), and inter-specific competition, as between Peruvian Boobies, Chilean Pelicans and Guanay Cormorants, can determine the local distribution of the species on the breeding grounds (Duffy 1983b). It was possible that similar pressures acted on the Shag on the Isle of May, preventing half the recruits from breeding in their natal area. However, it is doubtful that competition prevented recruits from breeding at their natal colony when, as in the Shag, over 90% of them succeeded annually in establishing themselves there. An extreme case of tenacity to the natal colony despite intense competition for nesting sites is provided by the Great Shearwater on Nightingale Island: unable to acquire nest burrows, thousands of birds laid their eggs on the surface of the ground rather than move to neighbouring, sparsely colonised, Inaccessible Island (Rowan 1965). If competition was not the cause of Shags breeding away from the natal colony, what was? Without sophisticated tracking equipment monitoring the exact movements of individuals after fledging, it is possible only to speculate. On the basis of ringing recoveries, Galbraith et al. (1981) showed that after fledging, Shags from the Isle of May dispersed during the winter (66% recovered at least 100km from the island in February), then gradually returned to the vicinity of the colony as first-year non-breeders (62% recovered within 50km in June). It may be during this summer period that certain of the immature birds become attached to a colony other than their natal one, particularly if the two are close together. There would thus seem to be two mechanisms at work: one governing the return to the natal colony, and the other, the competitive process of establishing a site there.

The female-biased dispersal observed in Shags, and in birds in general, is thought to be a consequence of the mating system (Greenwood 1980). In species where the male defends a resource (territory or nest-site) in order to acquire a mate and reproduce, it would be to the male's advantage to establish himself in a familiar area rather than undergo the costs of discovery. Once established, competition would provide an incentive to retain a site rather than move to a new one: 55% of breeding male Shags kept their site from year to year, and of those that moved, the majority nested within 16m of their old site. Females, on the other hand, need not suffer the costs of establishing the territory. Instead, they are in a position to choose between the available males, perhaps on the basis of the quality of each male's resource. Being less tied, they disperse further both before and after breeding.

One measure of the quality of a site is whether or not a pair succeeds in rearing young there. If the site proved to be poor, i.e. if reproduction failed, Shags were twice as likely to seek a new one than if breeding was successful. In the same way, a site which was once occupied and tested was potentially of better quality than an untried site; accordingly, Shags which moved did so preferentially to former established sites. The observations suggest that Shags were capable of assessing the quality of a site, and moved from substandard ones to ones that were likely to be of better quality. The characteristics of a good or poor quality site and the role of site quality within the social organisation of the Shag will be examined later.

The mechanism linking the stability of the pair-bond and site tenacity, presented in Section 6.6 (Figure 6.2), is not incompatible with the mating system described above. The results in Tables 6.15 and 6.9, which showed that 48% of female Shags paired up with their former male even though he had changed site, and that only 7% returned to their old site in the absence of their former mate, indicated however that the female was attracted to the male as an individual, i.e. that mate quality was more important than site quality. Morris & Erickson (1971) showed that Barbary Doves were able to recognise their mate after being separated for up to seven months. Members of experienced pairs were less aggressive towards each other, more responsive to courtship and hatched more eggs than birds which were not familiar with each other (Erickson & Morris 1972, Erickson 1973). Mate quality apart, there were thus other benefits in having experience of the same mate: a reduction in the time taken to establish the pair-bond and a better coordination of parental responsibilities. In the Shag, established pairs bred earlier than newly-formed pairs, thereby rearing more chicks. Shags separated from their former mates tended to pair with younger birds which bred later; nevertheless, the effect would be reinforced by lack of familiarity between the partners.

Two of the factors causing the dissolution of the pair-bond in the Shag were death and a change of site by the male. Excepting these events, 17% of females divorced from their former mate for no obvious reason. In the Kittiwake, Coulson & Thomas (1980) proposed that divorce occurred as the result of the two members returning to the colony at very different dates. They found that the difference between return dates of Kittiwakes which reformed the same pair averaged 10 days, in contrast to 22 days for pairs which divorced. Asynchrony of return to the rookery also appeared to be the primary factor causing divorce amongst Adélie Penguins (Penney 1968). It was probable that female Shags, returning late to the colony, found their previous mate already paired and were forced to move elsewhere. Male Shags which returned late were likely to find their sites usurped by another male - especially as Shags moved preferentially to established sites; they would be obliged to move away, thereby increasing their chances of divorce if their former female were still unattached. In Puffins, over half the divorcees were displaced by another bird; the remaining separations were caused by the mate changing burrow (Ashcroft 1979). As younger Shags returned later than established breeders (see Section 5.4), the chances of a young male losing his site were greater than for established males, and this in turn would increase his chances of divorce. Similarly, a young female would be more likely to find a strange female beside her former male than would an experienced one. As young females typically pair with young males (Section 2.12), she was also more likely to find a strange male in possession of her previous site. In short, not only did differential return times provide a satisfactory explanation of divorce, but also accounted for the greater site tenacity and pair stability observed in the older age classes.

7. THE EFFECTS OF A GALE IN LATE SPRING ON THE BREEDING OF THE SHAG.

7.1 Introduction.

From 1 to 4 May 1982, the wind blew strongly from the west, reaching gale force 9 on the Beaufort Scale during most of 3 May (Isle of May Lighthouse records). This corresponded to a sustained wind speed of 41-47 knots (75-88km/h). On the same day, the Forth Bridge and Bell Rock weather stations recorded their highest hourly wind speed for the month, 41 knots (76km/h) and 42 knots (78km/h) respectively (Meteorological Office Monthly Weather Reports, H.M.S.O.). In comparison, the maximum hourly wind speed at the Forth Bridge in May 1981 was 25 knots (46km/h), and no hourly wind speeds above 40 knots had occurred in May since 1976, when a speed of 41 knots was recorded. The high winds in 1982 coincided also with spring tides; the combination produced a devastating effect on seabirds nesting on the western side of the Isle of May.

Owing to the direction of the winds, the eastern side of the island was practically unaffected by the heavy seas. It served as a control in assessing the short-term and long-term effects of the gale on the reproduction of the Shags, as did also the breeding data from 1981. In this context, the 'east' side was defined as stretching from East Tarbet to Pilgrim's Haven via Kirkhaven, and the 'west' side denoted Rona and the cliffs between West Landing and Pilgrim's Haven (see Figure 2.2). Although there was no difference in the mean number of chicks fledged per nest on the east and west sides in 1981 (Table 7.1), in 1982 chick production on the west coast was 25% lower than on the east. It was clear that the gale did not simply provide a momentary check on breeding, but that the perturbation

Table 7.1 Mean number of Shag chicks fledged per nest from the east and west sides of the Isle of May in 1981 and 1982.

	East	S.E.	N	West	S.E.	N	T-value	
1981	1.53	0.06	382	1.52	0.05	645	0.03	N.S.
1982	1.30	0.04	787	0.97	0.04	814	5.90	P[0.001

it caused to the breeding Shags was sufficiently large to be reflected in the reproductive success later in the season.

The next section will quantify the destruction of Shag nests by the gale. I shall examine whether this alone accounted for the difference in the mean number of young fledged per nest on the east and west sides of the island, and how the gale was the source of other, more subtle, effects.

7.2 Immediate consequences of the gale.

Table 7.2 shows the extent of the damage caused by the gale to the nesting Shags. Out of 658 nests present on the west coast, over 50% were affected: three quarters of these were completely washed away, the remainder were damaged and the eggs lost. On the east side, only 24 nests out of 615 were affected (4%); they were all on the westernmost part of the south coast, in the area known as the Chatterstones. The degree of damage caused by the gale on the west side was related to the vertical height of the nest above the upper barnacle limit (measured to the nearest 0.1m); this approximated to the level of mean high water of spring tides (Russell 1964). The mean elevation of nests which were completely washed away was 3.9m; the highest-placed nest to be washed away was situated at 10.0m (Table 7.3). Damaged nests averaged 5.2m (maximum 12.0m) above mean high water of spring tides, and unaffected nests 6.4m.

The subsequent history of the 658 nests on the west side is given in Table 7.4. A week after the gale, 23% of the sites where nests had been completely washed away were deserted, whereas only 3% of damaged nests had been abandoned (chi-square=15.7 df=1 P[0.001); none of the undamaged nests was deserted.

Most Shags retaining sites affected by the gale started rebuilding or

Table 7.2 Proportion of Shag nests affected by the gale in 1982.

	Unaffected	Damaged	Washed away	N
East side	591 (96.1%)	10 (1.6%)	14 (2.3%)	615
West side	310 (47.1%)	89 (13.5%)	259 (39.4%)	658

Table 7.3 Gale damage to Shag nests on the west side in relation to their height above the level of mean high water of spring tides.

	Unaffected	Damaged	Washed away
Geometric mean height (m)	6.4	5.2	3.9
95% confidence limits	6.0-6.9	4.6-5.8	3.7-4.2
Range	1.5-30.0	1.6-12.0	0.6-10.0
N	233	79	204

F=55.4 df=2,513 P[0.001 (heights normalised by logarithmic transformation)

Table 7.4 Nest desertion and laying on the west side after the gale in 1982.

	Unaffected	Damaged	Washed away
Nests present just before gale	310	89	259
Nests or nest-sites still occupied a week later	310	86	200
% deserted	0.0	3.4	22.8
Nests where pair laid or relaid after gale	32	81	177
% nests with eggs, of nests not deserted after gale	10.3	94.2	88.5

repairing their nests as soon as the wind abated. Amongst pairs which did not abandon their sites, there was no difference in the proportion that laid replacement clutches on sites where the nest had been washed away, and on sites where the nest had only been damaged (89% and 94% respectively; chi-square=1.60 df=1 N.S.). On sites which had not been affected by the gale, most birds had already laid. Only 10% of them laid after the gale, and these eggs represented the pairs' first clutch of the season; most such laying occurred shortly after the gale (Table 7.5). The distribution of laying was markedly different for birds on affected nests, the majority of which were laying replacement clutches. Two-thirds laid during the third week after the gale, and the mean laying date was 19 days (2.7 weeks) after the gale. This agrees well with Snow (1960), who found that in 10 nests where the eggs were lost at or near completion of the clutch, the interval between the laying of the first egg of the first clutch and the first egg of the second clutch averaged 17.3 days (range 8-29), and in two nests where the eggs were lost after 20 and 26 days' incubation, the intervals between loss and re-laying were 21 and 22 days.

7.3 Effects of the gale on reproductive success.

To investigate how the gale had affected chick production, the total number of chicks fledged from the east and the west coast of the island was broken down into four components, corresponding to four categories of nests (Table 7.6). The first category, which fledged no chicks, comprised the nests which were abandoned as a result of the gale. Excluding these, the mean value of 1.09 fledged chicks/nest on the west side was still considerably lower than that of 1.31 on the east side (t=3.89 df]724 P[0.001). Nests occupied after the gale constituted a second category, and

Table 7.5 Distribution of laying on the west side after the gale in 1982.

	Week of laying (after gale)								
	1	2	3	4	5+	Total	Mean	Adjusted mean	
Unaffected nests	11	12	5	2	2	(310)	-	-	
Damaged nests	4	8	54	9	6	81	3.22	2.72	2.69
Nests washed away	1	24	123	18	11	177	3.18	2.68	

As regards week of laying, week 1 is the first week after the gale. The mean laying date was adjusted by taking the mid-point in each week rather than the end-point, i.e. by subtracting 0.5.

Table 7.6 Breakdown of chick production for the east and west coasts in 1982.

East side	Nests	Chicks	Chicks/nest	S.E.
Occupied before gale, unaffected by gale	591	963	1.63	0.05
Occupied before gale, affected by gale, deserted or lost before laying	5	0	0.00	0.00
Occupied before gale, affected by gale, relaid	19	16	0.84	0.22
Occupied after gale	172	44	0.26	0.04
Overall	787	1023	1.30	0.04

West side	Nests	Chicks	Chicks/nest	S.E.
Occupied before gale, unaffected by gale	310	464	1.50	0.06
Occupied before gale, affected by gale, deserted or lost before laying	90	0	0.00	0.00
Occupied before gale, affected by gale, relaid	258	288	1.12	0.06
Occupied after gale	156	38	0.24	0.04
Overall	814	790	0.97	0.04

fledged 0.26 and 0.24 chicks/nest on the east and on the west coast respectively (t=0.35 df=326 N.S.). These two values are so close that nests occupied after the gale were obviously not responsible for the east/west difference in chick production which persisted after exclusion of nests abandoned as a result of the gale. The difference could therefore be caused only by east/west differences amongst production from the remaining nests, all of which had been present at the time of the gale. The effect of the gale upon Shag reproduction reached beyond the obvious one of causing birds to abandon their sites.

The nests present during the gale, excluding abandoned sites, fell into two further categories: those unaffected by the gale, and those, damaged or washed away, which subsequently held replacement clutches. Unaffected nests on the west side fledged on average 1.50 chicks/pair, compared to 1.63 on the east (t=1.66 df]309 N.S.). Although not significant, the t-value was high (it exceeded the 0.1 probability level): inspection of the proportions of failed clutches amongst those incubated for the full term of 32-36 days showed that a significantly higher proportion of complete clutches failed on the west side than on the east (9.4% and 4.9% respectively; chi-square=5.33 df=1 P[0.05). The lower chick production from unaffected nests on the west side was not the effect of chance. The last category, that of replacement clutches, showed no significant east/west difference (t=1.23 df[257 N.S.), and averaged 1.10 fledged chicks/nest. However, this value was much lower than those of 1.50 and 1.63 obtained for unaffected nests on the west and east sides (west side: t=4.71 df]276 P[0.001). The Shags sitting on replacement clutches had occupied their sites at the same time as those whose nests were not affected by the gale; the main difference between the clutches laid by the two groups was one of laying date. The median week of laying for replacement clutches was week 12 (the third quarter of May), 5 weeks later than that for clutches in unaffected nests (week 7 - mid April). Any effect of male breeding experience could be discounted, as the proportions of second-year male parents were the same in the two groups (replacement clutches: 14.0%, unaffected nests: 14.2%; chi-square=0.01 df=1 N.S.). The difference in chick production between the two groups was an age-independent effect of laying date, as described in Section 5.5. The seasonal decline in chick production affected the category of nests which were occupied after the gale even further: such nests fledged on average 0.25 chicks/nest, significantly less than the 1.10 chicks/nest fledged from replacement clutches (t=12.7 df]276 P[0.001).

Thus the breakdown of the mean number of chicks fledged per nest on the east and west coasts, presented in Table 7.6, showed that the overall lower success on the west side arose solely from nests present during the gale. The chick production from those nests was influenced in three ways: pairs on nests which showed no outward sign of damage hatched fewer clutches; a number of pairs on nests which were washed away or damaged abandoned their sites; the remainder, which laid second clutches, raised fewer chicks.

By causing 277 pairs to lay replacement clutches, the gale effectively set up a natural experiment eliminating the difference in timing between late breeders, i.e. Shags which did not lay until after the gale, and a sample of early breeders, whose original clutch was laid about mid-April. These two groups will be referred to as 'late' and 'repeat' respectively. For both groups, week 12 (the third quarter of May) was the median week of laying. Male age structure in the two groups differed markedly: only 14% of repeat males were two years old, compared to 58% of late males (chi-square=109.5 df=1 P[0.001). Consequently, results for second-year males and older males were considered separately. In each age category, the mean number of young fledged per pair was significantly higher for repeat breeders than for late breeders (Table 7.7). Snow (1960) observed that 10 replacement clutches laid by Shags on Lundy were slightly more successful than 32 first clutches laid at the same time; she ascribed it to differences in individual quality, late birds being possibly less fit for breeding. Table 7.7 also shows that the proportion of clutches which were lost during incubation was greatest for late breeders. Amongst older males, four times as many late breeders lost their clutches as did repeat breeders. The proportion of repeat second-year males which lost their clutches (29%) was similar to that of late older males, whereas nearly half of late second-year males lost their clutches. The lack of statistical difference between the proportions of repeat and late two-year-olds which lost their clutches was probably the result of the small sample of repeat breeders in this age group. After excluding clutches lost during incubation, the difference in chick production between repeat and late older males was no longer significant, but it remained so in younger males (Table 7.7). The principal cause of egg loss was other Shags, which raided an unattended nest for its nesting material regardless of contents. The main difference between repeat and late pairs from the older age group lay, therefore, in better attention to the nest and better defense of the site during incubation. The same was true, to a lesser extent, of pairs comprising a second-year male; in the latter case, repeat breeders were also more skilled at rearing chicks to fledging. Finally, Table 7.7 shows that repeat breeders laid on average significantly larger clutches than late breeders (2.88 and 2.71 eggs/clutch respectively), with no difference in clutch size between the two age groups. The overall conclusion to be drawn from the comparison of repeat and late breeders was that repeat breeders were, in general, of better quality than late ones.

Table 7.7 Comparison of clutch size and chick production between repeat and late nests, in relation to male breeding experience.

Clutch size (sample of 331 nests):

	Repeat clutches			Late clutches		
	Mean	S.E.	N	Mean	S.E.	N
Second-year males	2.95	0.13	21	2.72	0.07	81
Older males	2.87	0.06	142	2.71	0.07	82
Overall	2.88	0.05	163	2.71	0.05	163

Second-year x older (repeat clutches): t=0.56 df=100 N.S.
Second-year x older (late clutches) : t=0.10 df=222 N.S.
Repeat x late clutches (overall) : t=2.40 df=324 P[0.05

Chick production (all 553 nests):

		Second-year males		Older males	
		Repeat	Late	Repeat	Late
Number of nests		35	175	215	128
% clutches lost	(a)	28.6%	48.0%	8.4%	31.3%
Chicks fledged/nest (1 S.E.)	(b)	1.00(0.16)	0.46(0.05)	1.15(0.06)	0.83(0.08)
Same, excluding lost clutches	(c)	1.40(0.17)	0.89(0.08)	1.25(0.06)	1.20(0.09)

	Second-year males			Older males		
(a)	Chi-square=3.70	df=1	N.S.	Chi-square=28.3	df=1	P[0.001
(b)	t=3.22	34[df[174	P[0.01	t=3.20	df=341	P[0.01
(c)	t=2.71	df=114	P[0.01	t=0.46	df=341	N.S.

7.4 Effects of the gale in relation to breeding experience.

Considering nests on the west side only, the gale affected nests belonging to second-year Shags more than nests built by older birds (Table 7.8). Although there was no difference in the proportions of nests of second-year birds which were either unaffected by the gale or else simply damaged, the proportion of nests washed away that belonged to young birds was almost twice that of unaffected nests. There was a corresponding difference in the mean elevation of nests belonging to the two age groups: the geometric mean height above sea level of nests of young breeders was 4.6m (95% confidence limits 4.2-5.1m), compared to 5.2m (5.0-5.5m) for nests of older ones (t=2.20 df=549 P[0.05). In general, young birds were nesting on sites more exposed to wind-driven seas than were the older, more experienced birds.

In the case of the sites on the west side which were affected by the gale, 11 out of 52 sites (21%) occupied by second-year males were subsequently abandoned, against 8 out of 222 sites (4%) for older males (chi-square=17.5 df=1 P[0.001). The recruitment of second-year males into the breeding colony was also affected (Table 7.9). The proportions of two-year-old males which recruited to the east and west sides of the island before the gale were similar to those in 1981, with more birds recruiting to the west side (56% on average) than to the east (44%). After the gale, the trend was reversed: 64% of breeding attempts by young birds took place on the east side, and only 36% on the west. This can be explained in two ways: either the potential recruits to the west side moved round to the east, or else they were deterred from breeding at all in that year. It was shown in the previous chapter that males tended to nest close to their natal area; if recruits did indeed move from the west to the east side after the gale, the

Table 7.8 Gale damage to nests on the west side in relation to the breeding experience of the male.

	Two-year male	Older male	Total
Nests unaffected	39 (13.5%)	249 (86.5%)	288
Nests damaged	7 (8.0%)	80 (92.0%)	87
Nests washed away	45 (24.1%)	142 (75.9%)	187

Nests unaffected x nests damaged : chi-square=1.40 df=1 N.S.

Nests unaffected x nests washed away: chi-square=7.92 df=1 P[0.01.

Table 7.9 Recruitment of second-year male Shags to the east and west coasts of the Isle of May in 1981 and 1982.

	East side	West side	Total
1981	47 (38.5%)	75 (61.5%)	122
1982 before the gale	85 (48.0%)	92 (52.0%)	177
1982 after the gale	99 (64.3%)	55 (35.7%)	154

1981 x 1982 before the gale: chi-square=2.27 df=1 N.S.

1982 before the gale x 1982 after the gale: chi-square=8.18 df=1 P[0.01.

proportion of second-year males ringed as chicks on the west side and breeding on the east should increase after the gale. Before the gale, 6 out of 22 (27%) two-year-old males ringed as chicks on the west side recruited to the east side, compared to 3 out of 13 (23%) after the gale. Not only was the difference between the two proportions not significant (chi-square=0.08 df=1 N.S.), but even the direction of the difference was wrong. The reduced recruitment to the west side after the gale was due to young males abstaining from breeding rather than moving to the east side. An estimate of the numbers of second-year males which abstained from breeding can be derived from the figures in Table 7.9. In normal circumstances (1981, and 1982 before the gale), 44% of recruiting second-year males nested on the east side. After the beginning of May 1982, i.e. after the gale, 99 second-year males recruited to the east side of the island. If 1982 had been a normal year, a total of 99/0.44=225 second-year males would have recruited to the island as a whole after the beginning of May, and the number of second-year male recruits to the west side would have been 126. Only 55 did in fact attempt to breed after the gale, hence an estimated 71 abstained (56%). This figure represents a third of the potential number of recruits to the west side at the beginning of the season.

7.5 Discussion.

Several authors have commented on the destructive impact of storms and heavy seas on breeding seabirds. Already in 1902, Tomison (in Baxter & Rintoul 1953) mentioned that 200 Shag nests had been washed off the cliffs of Sule Skerry, Orkney. More recently, Winn (1950) showed that stormy seas were the primary cause of egg loss for Black Guillemots, and Crawford *et al.*

(1980) described the loss of 400 Cape Cormorant chicks through heavy swell. Similarly, most of the main colony of Kittiwakes on Kjör, south-west Norway, was washed away in stormy weather (Munkejord & Folkedal 1981). For birds in general, rain, hail and snow storms constitute a recognized source of nesting failure (Ash 1951, Myres 1955, Jehl & Hussell 1960, White et al. 1976, McNicholl 1979) and even adult mortality (Kennedy 1970, Dow 1972, Ojanen 1979). Few studies, however, monitor the aftermath of such disasters in terms of subsequent breeding success and impact upon population numbers. This requires detailed information on the situation before the catastrophe. In McCormick's Skuas, hatching success after high winds and snow in one year was only 58%, compared to an average of 78% in two normal years (Spellerberg 1971); in one extreme season, 75% of eggs were lost (Ensor 1979). An eight-year study on the same species showed that heavy chick losses during blizzards reduced the number of chicks fledged per pair by two-thirds, from an average of 0.44 in good years to 0.14 in unfavourable ones (Wood 1971). In contrast, Temminck's Stints caught in a blizzard hatched 76% of fully incubated eggs and produced 1.94 young/pair, in spite of abandoning the eggs for one or more days (Hildén 1979).

On the Isle of May, the Shags showed themselves to be well able to cope with the disruption to their breeding cycle. 75% of pairs which had been affected rebuilt their nests and laid replacement clutches, the majority within three weeks of the gale. The presence of nest material provided a powerful stimulus to continue breeding on the old site: only 3% of damaged nests were deserted in the week following the gale, whereas 23% of nests completely washed away were deserted.

In spite of the ability of the Shags to repair loss or damage to their nests, by the end of the breeding season the side hit by the gale reared only 0.97 chicks/nest, as opposed to 1.30 chicks for the sheltered side. It is striking that a mere third of this difference was due to nest desertion following the gale: excluding deserted nests, the west side still only produced 1.09 chicks/nest. The remaining discrepancy stemmed from two factors: reduced hatching success for nests apparently unaffected by the gale, and reduced chick production of nests with replacement clutches.

The first factor was probably the result of the chilling effect of wind-driven sea-spray, which blasted nests out of reach of the sea itself. Ward & Burger (1980) showed experimentally that immersion in cold sea-water for only 30 minutes adversely affected the hatchability of domestic chicken and Herring Gull eggs. Similarly, the greatest loss of production from wild ducks and geese, whose breeding grounds had been flooded, resulted from lowered viability of the eggs and not from destruction of the nests (Hansen 1961).

The second factor corresponded to a typical seasonal decline, as described in Section 5.5. Pairs whose nests were unaffected by the gale reared on average over 0.4 more chicks to fledging than pairs which had started to breed at the same time, but which had been forced to lay replacement clutches. There was no reason to suppose that, in the absence of a gale, the delayed breeders would have performed any less well than the others. Thus the difference in chick production between the two groups was probably due to differences in the quality of the environment rather than to differences in the quality of the birds. However, delayed breeders proved on average better parents than late breeders (birds whose first clutch was laid after the gale), particularly with respect to nest attendance and defence. The overall progressive decline in chick production with season reported in Section 5.5 appeared to be partly related to environmental quality, but also in part to individual quality, with the more able Shags breeding earlier.

The gale also affected the recruitment of second-year males to the colony. Not only were the nests of young males, which had recruited before the gale, more vulnerable to destruction, but the birds themselves were more liable than older breeders to abandon their breeding attempt if their nest had been damaged or washed away. As for second-year males which had been potential recruits to the west side of the island, but which had not started breeding before the advent of the gale, over half of them were deterred from breeding altogether in that year. This reduced overall recruitment of second-year males to the west side of the island in 1982 by a third. The drop in the number of recruiting Shags brought about by the gale showed an interesting parallel with changes in the recruitment of Herring Gulls to the Isle of May caused by culling. A six-year study by Duncan (1978) showed that, since the start of an annual cull in 1972, the numbers of recruiting Herring Gulls was only about a third of the level predicted from the near-constant rate of increase between 1907 and 1972. The timing of the culls was similar to the timing of the gale in 1982, in that they coincided with the peak of incubation for Herring Gulls and Shags respectively. In both instances, a few days of large-scale disruption to the breeding cycle was enough to discourage an appreciable proportion of young birds from joining the breeding colony.

8. NEST-SITE QUALITY AND REPRODUCTIVE SUCCESS.

8.1 Introduction.

Along with factors such as timing of breeding, parental experience and pair-bond, reproductive success has been shown to vary also with habitat for many bird species. For instance, Blackbirds, Great Tits and Blue Tits breeding in gardens on average laid smaller clutches and reared fewer nestlings from unpredated nests than their conspecifics in woodland, the difference probably being due to differing food availability (Snow 1958, Perrins 1965). Differences in prey abundance also provided a likely explanation for the greater brood sizes of Great Tits in oak rather than pine woodland (van Balen 1973), and of Sparrowhawks in small valley woods rather than hill forest (Newton 1976). Conversely, differences in predation pressure meant that for Blackbirds, 50% of nests started in gardens resulted in fledged young compared to 14% in woodland (Snow 1958), and urban Woodpigeons fledged up to six times more young than those on farmland (Tomiałojć 1980).

When the notion of 'habitat' is restricted to the area at and immediately surrounding the nest, excluding that used for foraging, again certain features have been found to relate to breeding success. For example, Blackbirds building nests low down suffered greater predation than those that built higher up (Osborne & Osborne 1980); predation varied again according to height, and also to vegetation type, in Red-winged Blackbirds (Goddard & Board 1967, Caccamise 1977) and Woodpigeons (Tomiałojć 1978). The amount of plant cover correlated with a loss of eggs by predation in gulls (Brown 1967) and ducks (Dwernychuk & Boag 1972). In colonial species, birds nesting in the centre of the colony often perform better than those at the edge: in the Kittiwake, this seems due to the quality of the birds (Coulson 1968), but in Black-headed Gulls, predation was responsible (Patterson 1965). In Adélie Penguins (Tenaza 1971) and Double-crested Cormorants (Kury & Gochfeld 1975), peripheral nesters were more sensitive to disturbance, and hence to predation; alternatively, flooding affected Ring-billed Gulls nesting away from the colony centre, on low ground (Dexheimer & Southern 1974). Many topographical aspects of nest location also relate to nesting failure, via exposure to weather, predation or other hazards. Auks provide several examples: flat ground (poor success) versus sloping or cliff ground in the Puffin (Nettleship 1972), open ledges versus rocky overhangs or sheltering walls in Brünnich's Guillemot (Gaston & Nettleship 1981), ledge versus burrow or boulder sites in the Razorbill (Hudson 1982). A last feature worth mentioning is density: in Guillemots and Puffins, success was highest in dense areas (Birkhead 1977, Harris 1980b). In the Herring Gull, birds nesting at the most common density fledged most chicks: at the lowest density, as in the two previous species, success was reduced by predation, whereas at the highest density, intra-specific aggression increased chick mortality (Parsons 1976). All the features described above are components of nest-site quality. Although not exhaustive, the list demonstrates the variety of ways in which nest-site characteristics can affect breeding performance, by modifying the pressures due to predation, exposure, disturbance and social effects.

In the case of the Shag, the breeding habitat covers a range of rocky, usually inaccessible, coastal sites: rugged cliffs, sea caves, boulder beaches, rocky ledges (Witherby _et_ _al_. 1940, Lack 1945, Baxter & Rintoul 1953). On the Farne Islands, Potts (1966) was the first to show that site quality, defined in terms of exposure, size and access to the sea, affected the reproductive success of the Shag. In 1968, a natural experiment demonstrated its importance. A proliferation of the dinoflagellate Gonyaulax tamarensis Lebour, or 'red-tide', off the Northumbrian coast (Robinson 1968, Wood 1968), resulted in the death of 82% of breeding Shags on the Farne Islands in 10 days (Coulson et al. 1968). After the red-tide, the average nest-site quality of the Shags on the Farne Islands increased markedly, with a corresponding increase in the number of young reared per pair (Coulson 1971).

My aim here was to identify , from a range of 28 variables describing the physical and social make-up of a site, the characteristics which might influence reproduction in the Shag. The ultimate measure of site quality was the number of chicks fledged from that site (corrected for other modifying factors). The situation on the Isle of May could then be compared to that on the Farne Islands.

8.2 Description of nest-sites on the Isle of May.

In order to describe a nest-site in relation to its physical and social surroundings in as much detail as possible, a total of 28 variables were examined. They are given below, with details in Appendix 4.

1.	Protection from the Sea.	Scored 1-5.
2.	General Topography.	Scored 1-5.
3.	Local Topography.	Scored 1-5.
4.	Gully.	Scored 1-5.
5.	Proximity to Cliff Edge.	Scored 1-5.
6.	Overhang.	Scored 1-5.
7.	Ledge Size.	Scored 1-5.

8.	Damp.	Scored 1-5.
9.	Immediate Exposure.	Scored 1-8.
10.	Driving Exposure.	Scored 1-8.
11.	Departure Angle.	Scored 1-8.
12.	Sea View.	Scored 1-2.
13.	Attack from Above.	Scored 0-8.
14.	Level Attack.	Scored 0-8.
15.	Attack from Below.	Scored 0-8.
16.	Overall Attack.	Scored 0-8.
17.	Human Accessibility.	Scored 1-5.
18.	Wave Reach.	Scored 1-2.
19.	Cliff Top.	Scored 1-2.
20.	Height above Sea.	Metres.
21.	Distance to High Water.	Metres.
22.	Distance to Low Water.	Metres.
23a.	Density at Occupation.	No. nests within 4m.
24a.	Nearest Neighbour Distance at Occupation.	Metres.
25a.	Second Nearest Neighbour Distance at Occupation.	Metres.
23b.	Maximum Density.	No. nests within 4m.
24b.	Minimum Nearest Neighbour Distance.	Metres.
25b.	Minimum Second Nearest Neighbour Distance.	Metres.

Where possible, variables were scored in such a way that the highest score corresponded to what was intuitively felt to be the best quality. This was the case for variables 1 to 8, 12, and 17 to 19. For variables 9 to 11 and 13 to 16, which measured angles (exposure to weather or attack, departure angle), the scoring was directly related to the relevant angle or arc: a low score represented a small angle or arc, a high score a wide one.

In this case, high quality would be expected to correspond to low scores. Similarly, for distance and density variables, a high value corresponded to a large distance or number of nests; this was not necessarily synonymous with high quality.

The distributions of values for all distance variables were markedly skewed towards the bottom end of the range. For statistical analysis, the transformation ln(x+0.1) reduced the tails, restored normality, and enabled the transformed values to be easily related to the original ones. The density variables fell into two replicate groups, corresponding to different times in the breeding cycle (Appendix 4). Analysis was performed twice, using the first 22 variables and one or other of the two density groups. Results were the same in both cases, so are reported only for the first group.

8.3 Topographical differences between the east and west coast.

The geological configuration of the Isle of May - a volcanic sill slanting down towards the east - results in a very different topography on the east side of the island and on the west. The most obvious difference between the two sides is the presence of high sheer cliffs on the west, and the gently shelving aspect of the east. The effects this had on the mean scores of the 25 nest-site variables in 1982 are summarised in Table 8.1. The results for 1981, being very similar, are not shown. Practically all variables showed significant differences between east and west. The high sample size contributed to the sensitivity of the tests, but even so, over half the significance levels were below 0.001. Many differences stemmed directly from the high west cliffs, for instance General Topography, Local Topography, Gully and Human Accessibility. Other well-marked differences

Table 8.1 Mean scores for 25 nest-site variables (geometric mean for distances) for 509 nests on the east coast and 643 on the west in 1982.

	East		West			
	Mean	S.E.	Mean	S.E.	T-value	
Protection from the Sea	4.70	0.02	3.88	0.05	15.23	P[0.001
General Topography	2.81	0.02	3.41	0.04	13.42	P[0.001
Local Topography	2.59	0.03	2.89	0.03	7.07	P[0.001
Gully	2.73	0.04	2.16	0.04	10.08	P[0.001
Cliff Edge	4.33	0.04	4.54	0.03	4.20	P[0.001
Overhang	1.23	0.03	1.31	0.03	1.89	N.S.
Ledge Size	4.84	0.02	4.67	0.03	4.71	P[0.001
Damp	2.69	0.03	2.81	0.02	3.33	P[0.001
Immediate Exposure	3.11	0.08	3.44	0.08	2.92	P[0.01
Driving Exposure	3.19	0.07	3.61	0.08	3.95	P[0.001
Departure Angle	1.20	0.07	1.30	0.06	1.08	N.S.
Sea View	1.98	0.01	1.98	0.01	0.00	N.S.
Attack from Above	1.07	0.06	0.83	0.04	3.33	P[0.001
Level Attack	2.79	0.07	2.55	0.06	2.60	P[0.01
Attack from Below	0.81	0.04	0.94	0.05	2.03	P[0.05
Overall Attack	4.67	0.08	4.32	0.07	3.29	P[0.01
Human Accessibility	2.69	0.03	3.30	0.05	10.46	P[0.001
Wave Reach	1.98	0.01	1.87	0.01	7.78	P[0.001
Cliff Top	1.88	0.01	1.83	0.01	3.54	P[0.001
Height above Sea (m)	5.68	0.10	5.01	0.11	4.51	P[0.001
Distance to High Water (m)	5.18	0.21	1.83	0.06	15.34	P[0.001
Distance to Low Water (m)	15.97	0.58	6.30	0.29	14.91	P[0.001
Density (nests within 4m)	5.66	0.15	5.07	0.15	2.78	P[0.01
Nearest Neighb. Dist. (m)	1.61	0.04	1.64	0.04	0.53	N.S.
Second N. N. Distance (m)	2.30	0.06	2.52	0.06	2.59	P[0.05

were associated with the sea: although the difference in mean Height above Sea was only 0.7m, there was a 3.4m difference in Distance to High Water, increasing to 9.7m at Low Water. Thus nests on the east side were further from the sea, and therefore likely to be better protected. This was confirmed by the differences in Wave Reach and Sea Protection. Although the differences in variables referring to the sea might be the result of the May gale, the brunt of which was borne by the west side, the east side itself was subjected periodically during the breeding season to heavy swell off the North Sea. It was obvious that in most sites the force of the waves was tempered by shoaling water and offshore islets; no easterly gales struck the island during the period of study, so it was not possible to assess the added effect of high wind.

8.4 Observations on analytical technique.

One of the problems when dealing with a large, complex body of data is understanding the inter-relationships between the variables and how they can affect subsequent analysis. Table 8.2 presents the correlation matrix for all 25 nest-site variables in 1982. The correlation matrix for the 1981 variables was almost identical, so has not been given. Each correlation coefficient was expressed to two decimal places and multiplied by 100. With the 1982 sample size of 1152 nests, a correlation coefficient greater than 0.058 exceeded the 0.05 probability level. One variable correlated with another at r=0.058 would, however, explain only 0.3% of the variation in its correlate, so the biological significance would probably to be small. In Table 8.2, a correlation coefficient was starred (*) if it exceeded 0.22 (5% of variation explained), and double-starred (**) if it exceeded 0.50 (25% of variation explained). The most striking feature of the table was the

Table 8.2 Correlation matrix of 25 nest-site variables in 1982. A star (*) denotes a correlation coefficient which exceeds 0.22 (5% of variation explained), and two stars (**) a coefficient greater than 0.50 (25% of variation explained).

	Sea Prot.	General Topog.	Local Topog.	Gully	Cliff Edge	Over-hang	Ledge Size	Damp	Imm. Exp.	Driv. Exp.	Dep. Angle	Sea View
Sea Protection		-06	-00	34*	-07	-04	-01	-11	-19	-14	18	-09
General Topog.	-06		39*	-42*	29*	27*	-20	07	-26*	-47*	-11	06
Local Topography	-00	39*		-16	63**	01	-25*	11	-04	-07	-11	18
Gully	34*	-42*	-16		-16	-05	08	-14	06	17	36*	-20
Cliff Edge	-07	29*	63**	-16		01	-18	19	-03	-03	-14	22
Overhang	-04	27*	01	-05	01		-03	11	-26*	-37*	-06	-06
Ledge Size	-01	-20	-25*	08	-18	-03		-01	15	15	-05	-05
Damp	-11	07	11	-14	19	11	-01		17	12	-01	09
Immediate Exp.	-19	-26*	-04	06	-03	-26*	15	17		69**	-09	07
Driving Exposure	-14	-47*	-07	17	-03	-37*	15	12	69**		01	06
Departure Angle	18	-11	-11	36*	-14	-06	-05	-01	-09	01		-23*
Sea View	-09	06	18	-20	22	-06	-05	09	07	06	-23*	
Attack Above	05	-19	-15	06	-17	-19	05	-06	-03	20	06	00
Level Attack	-02	-16	-14	-01	-06	-15	39*	12	48*	34*	-11	08
Attack Below	-05	-03	02	-06	02	-08	-08	04	19	12	-02	02
Overall Attack	-01	-30*	-22	-00	-16	-32*	34*	09	54**	53**	-07	06
Human Access	-19	78**	31*	-46*	25*	37*	-16	08	-25*	-49*	-19	10
Wave Reach	62**	-20	02	36*	-09	-14	-01	-08	-03	06	13	-06
Cliff Top	04	33*	12	-23*	17	14	-10	-06	-31*	-48*	-07	03
Height above Sea	48*	18	24*	-03	03	02	-13	-05	-12	-10	01	02
High Water	26*	-32*	-32*	23*	-29*	02	09	-10	-05	-06	07	-09
Low Water	45*	-23*	-24*	33*	-17	02	11	-08	-08	-04	14	-10
Density	15	-37*	-23*	02	-21	-24*	05	-08	15	26*	-01	-01
Near. Neighb. D.	-09	19	10	02	11	13	-01	07	-09	-17	-03	-02
Second N.N.D.	-13	25*	13	03	13	18	-02	06	-09	-20	00	-02

Table 8.2 continued. Correlation matrix of 25 nest-site variables in 1982. A star (*) denotes a correlation coefficient which exceeds 0.22 (5% of variation explained), and two stars (**) a coefficient greater than 0.50 (25% of variation explained).

	Attack Above	Level Attack	Attack Below	Overall Attack	Human Access	Wave Reach	Cliff Top	Height Sea	High Water	Low Water	Density	NND	SNND
Sea Protection	05	-02	-05	-01	-19	62**	04	48*	26*	45*	15	-09	-13
General Topog.	-19	-16	-03	-30*	78**	-20	33*	18	-32*	-23*	-37*	19	25*
Local Topography	-15	-14	02	-22	31*	02	12	24*	-32*	-24*	-23*	10	13
Gully	06	-01	-06	-00	-46*	36*	-23*	-03	23*	33*	02	02	03
Cliff Edge	-17	-06	02	-16	25*	-09	17	03	-29*	-17	-21	11	13
Overhang	-19	-15	-08	-32*	-37*	-14	14	02	02	02	-24*	13	18
Ledge Size	05	39*	-08	34*	-16	-01	-10	-13	09	11	05	-01	-02
Damp	-06	12	04	09	08	-08	-06	-05	-10	-08	-08	07	06
Immediate Exp.	-03	48*	19	54**	-25*	-03	-31*	-12	-05	-08	15	-09	-09
Driving Exposure	20	34*	12	53**	-49*	06	-48*	-10	-06	-04	26*	-17	-20
Departure Angle	06	-11	-02	-07	-19	13	-07	01	07	14	-01	-03	00
Sea View	00	08	02	06	10	-06	03	02	-09	-10	-01	-02	-02
Attack Above		-18	-09	48*	-22	07	-11	-04	09	05	14	-13	-14
Level Attack	-18		-36*	56**	-12	-02	-15	-05	04	11	04	-02	-02
Attack Below	-09	-36*		24*	-03	-04	-03	-05	00	-05	10	-09	-10
Overall Attack	48*	56**	24*		-28*	01	-23*	-11	09	10	20	-16	-18
Human Access	-22	-12	-03	-28*		-36*	37*	02	-26*	-20	-42*	23*	30*
Wave Reach	07	-02	-04	01	-36*		-08	58**	35*	36*	21	12	17
Cliff Top	-11	-15	-03	-23*	37*	-08		03	-04	02	-13	05	06
Height above Sea	-04	-05	-05	-11	02	58**	03		43*	25*	-01	-05	-07
High Water	09	04	00	09	-26*	35*	-04	43*		56**	07	-02	-06
Low Water	05	11	-05	10	-20	36*	02	25*	56**		05	-02	-06
Density	14	04	10	20	-42*	21	-13	-01	07	05		-56**	-67**
Near. Neighb. D.	-13	-02	-09	-16	23*	-12	05	-05	-02	-02	-56**		83**
Second N.N.D.	-14	-02	-10	-18	30*	-17	06	-07	-06	-06	-67**	83**	

paucity of high correlations: only 12 out of a total of 300 (4.0%) exceeded 0.50, and a further 60 exceeded 0.22 (20.0%). These showed that, to some extent, Proximity to Cliff Edge and Local Topography were measuring the same physical characteristics. The definitions of the two variables (Appendix 4) indicate why this was so: nests with an expanse of flat ground in front of them (Local Topography 1) were necessarily set back from the cliff edge (Cliff Edge 1-3), and nests halfway up a cliff (Local Topography 4-5) were usually built right on the edge of the nesting ledge (Cliff Edge 5). In the same way, other pairs showing similar physical characteristics were Immediate and Driving Exposure, Sea Protection and Wave Reach, General Topography and Human Accessibility, Immediate Exposure and Overall Attack, Driving Exposure and Overall Attack, Level Attack and Overall Attack, Wave Reach and Height above Sea, High Water and Low Water, and the three measures of density. If any one of these variables correlated with breeding success in the Shag, then the correlated counterpart of the variable would be likely to do so as well. Thus there may be several ways of interpreting an observed effect.

Principal Components Analysis was used in an attempt to reduce the large number of variables to a smaller number of variables containing as far as possible the same amount of information. However, no obvious number of components satisfactorily represented the dataset: the first two components accounted for only 30% of the variation within it, and the choice of a larger number of components would be purely arbitrary. As pointed out by Green (1979), the smaller components were difficult to interpret (they could simply be an expression of randomness within the data), and furthermore, a large amount of the variation, as represented by the first components, could be irrelevant to the study anyway. In order to avoid loss of information and interpretability, the best policy was to retain the original variables.

The analysis of the relationships between the nest-site variables and chick production was carried out by stepwise multiple regression. At each step, the variable which made the greatest contribution to the coefficient of determination (r-square) was added to the regression equation; the level for inclusion was set at P=0.1. This technique is strongly recommended by Draper & Smith (1981). It has the advantage of adjusting at each step both the dependent and the independent variables not yet in regression for their relationships with the independent variables already entered. It thereby takes into account the intercorrelations within the body of independent variables.

8.5 Chick production in relation to each nest-site characteristic.

For all nest-site variables quantified on an ordinal scale, the mean number of chicks fledged per pair was calculated at each level; continuous variables such as distances were first grouped and then treated as ordinal. The results, with 1981 and 1982 superimposed, are presented in Figures 8.1, 8.2, and 8.3. The correlation coefficients calculated between chick production and the 25 nest-site variables in 1981 and 1982 are given in Table 8.3. Several clear trends emerge from the figures and the table. There was a progressive increase in chick production with an increase in Protection from the Sea in 1982 (in 1981 it seemed instead to be an all or nothing effect). Ledge Size and Damp showed strong increases in production with quality in both years. For Overhang, Immediate Exposure, Driving Exposure, Level Attack and Overall Attack in 1981, the mean number of chicks fledged per pair declined as exposure increased, and the same was true, to a lesser extent, in 1982. A difference occurred in Wave Reach in both years. Height above Sea, Distances to High and Low Water showed strong correlations

Figures 8.1, 8.2 and 8.3

Mean number of chicks fledged per pair in relation to each of 25 variables describing the physical and social characteristics of a nest-site (see Section 8.2 and Appendix 4), in 1981 (- - - -) and 1982 (———). For nest-site variables taking values on an ordinal scale (Figures 8.1 and 8.2), the mean chick production was calculated at each level of the scale; continuous variables such as distances (Figure 8.3) were first grouped and then treated as ordinal. Sample sizes are given for points based on fewer than 20 nests.

Figure 8.1

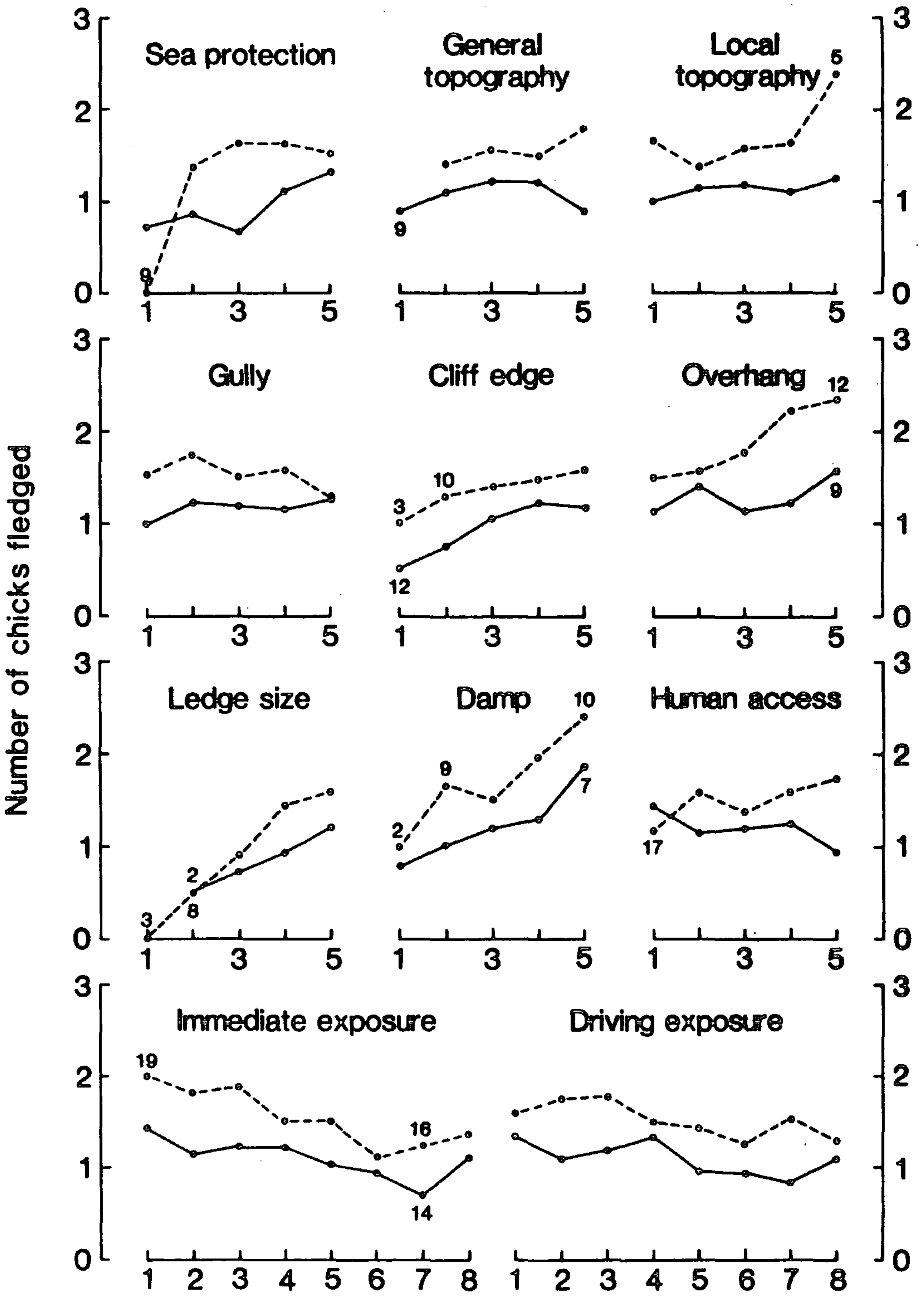

Number of chicks fledged
Sea protection
General topography
Local topography
Gully
Cliff edge
Overhang
Ledge size
Damp
Human access
Immediate exposure
Driving exposure
0
1
2
3
1
3
5
1 2 3 4 5 6 7 8
9
5
12
10
3
2
8
17
19
16
14
7

Figure 8.2

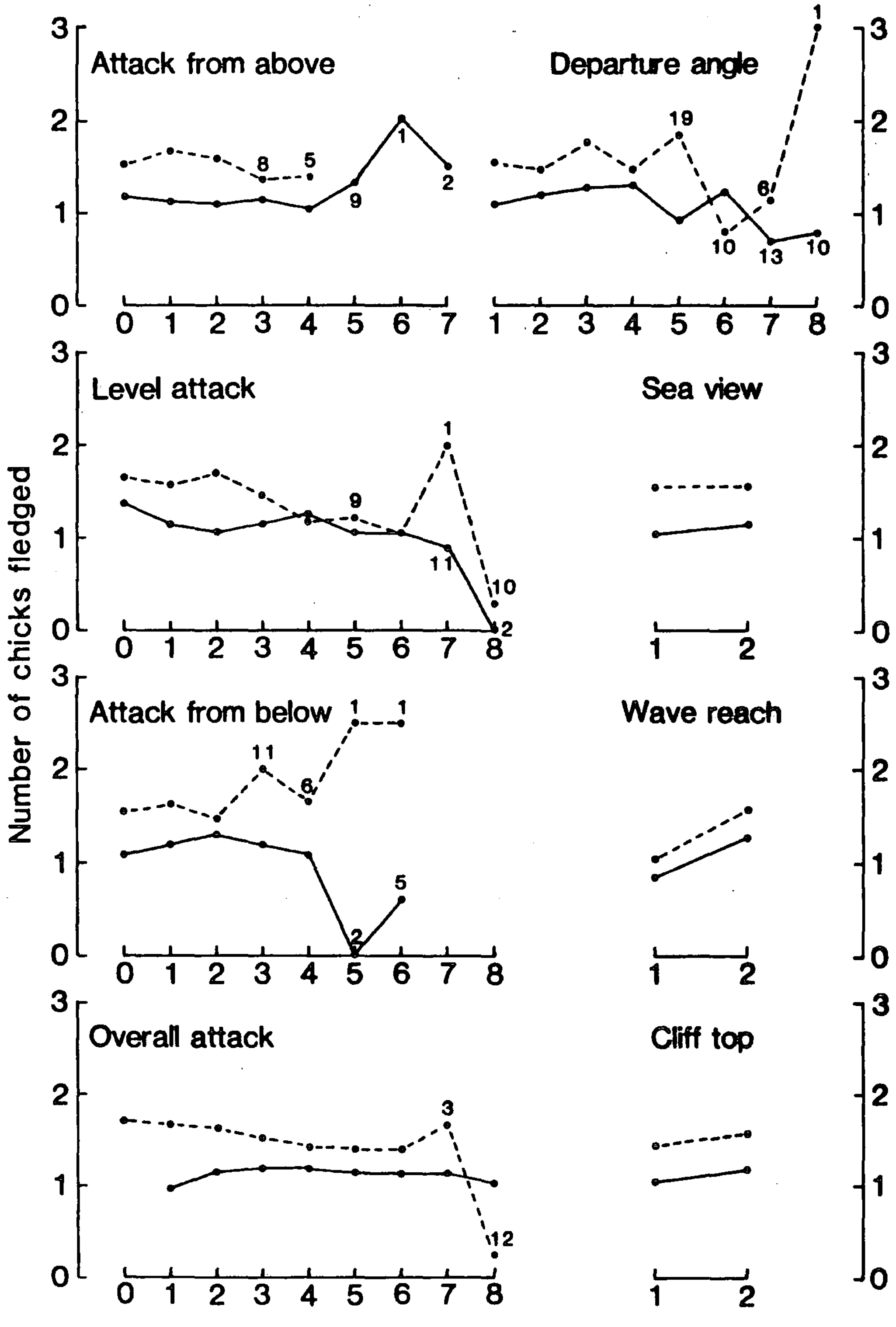

Number of chicks fledged
Attack from above
8
5
9
1
2
0 1 2 3 4 5 6 7
Departure angle
1
19
6
10
13
10
1 2 3 4 5 6 7 8
Level attack
1
9
11
10
2
0 1 2 3 4 5 6 7 8
Sea view
1 2
Attack from below
1
1
11
6
5
2
0 1 2 3 4 5 6 7 8
Wave reach
1 2
Overall attack
3
12
0 1 2 3 4 5 6 7 8
Cliff top
1 2
0
1
2
3

Figure 8.3

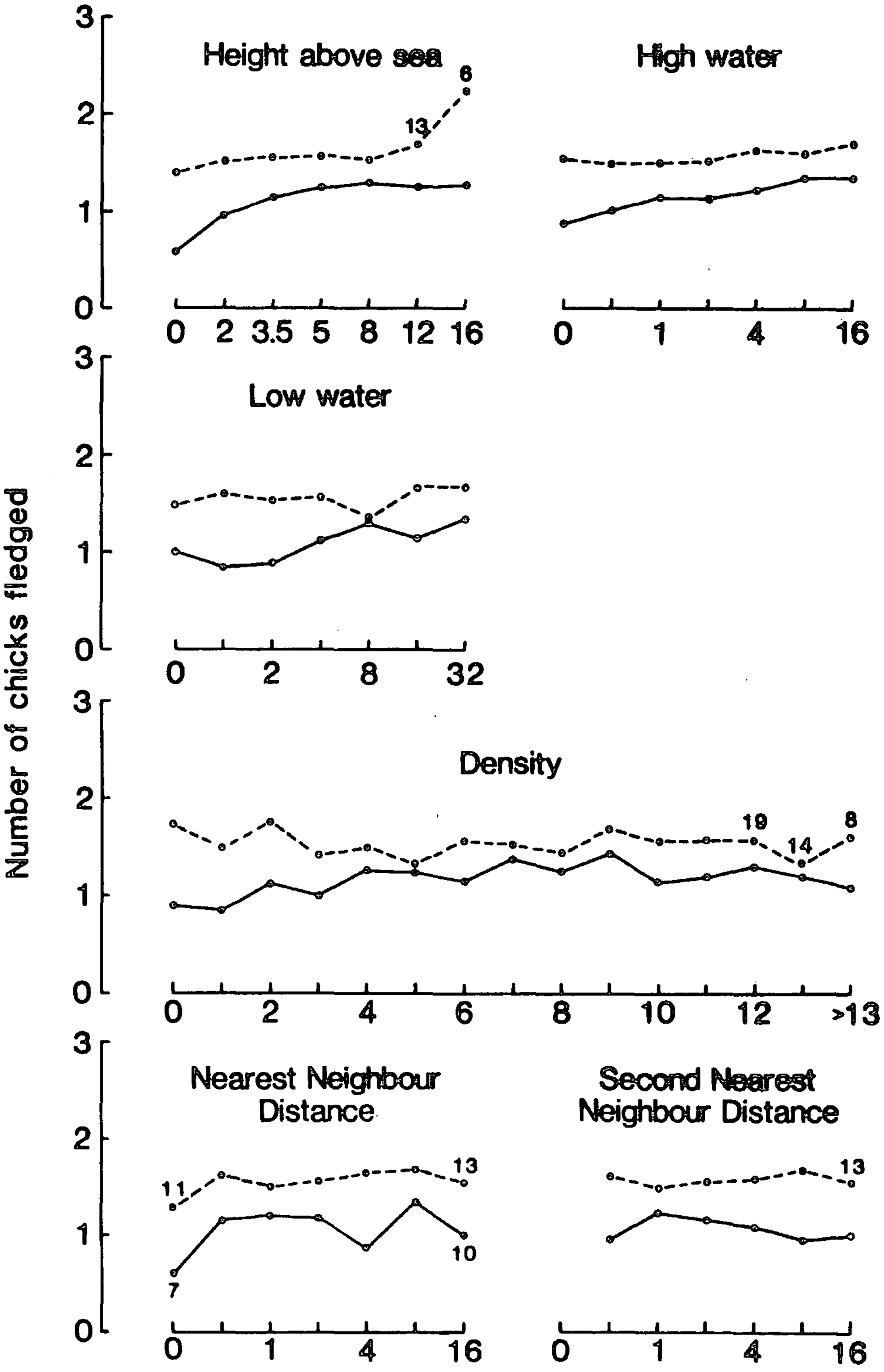

Number of chicks fledged
Height above sea
High water
Low water
Density
Nearest Neighbour Distance
Second Nearest Neighbour Distance
0
1
2
3
0 2 3.5 5 8 12 16
0 1 4 16
0 2 8 32
0 2 4 6 8 10 12 >13
6
13
19
14
8
11
7
10
13
13

Table 8.3 Correlations between chick production and 25 nest-site variables, in 1981 (N=759) and 1982 (N=1152).

	Sea Prot.	General Topog.	Local Topog.	Gully	Cliff Edge	Over-hang	Ledge Size	Damp	Imm. Exp.	Driv. Exp.	Dep. Angle	Sea View
1981	0.032	0.076	0.057	-0.009	0.070	0.140	0.144	0.117	-0.149	-0.118	-0.002	0.001
	N.S.	*	N.S.	N.S.	N.S.	***	***	**	***	**	N.S.	N.S.
1982	0.183	-0.044	0.034	0.047	0.068	0.044	0.131	0.101	-0.057	-0.065	-0.001	0.014
	***	N.S.	N.S.	N.S.	*	N.S.	***	***	N.S.	*	N.S.	N.S.

	Attack Above	Level Attack	Attack Below	Overall Attack	Human Access	Wave Reach	Cliff Top	Height Sea	High Water	Low Water	Density	NND	SNND
1981	0.015	-0.153	0.020	-0.135	0.060	0.096	0.038	0.051	0.025	0.023	-0.020	0.019	0.008
	N.S.	***	N.S.	***	N.S.	**	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.	N.S.
1982	-0.013	-0.026	0.029	-0.014	-0.062	0.164	0.040	0.130	0.111	0.103	0.086	-0.054	-0.094
	N.S.	N.S.	N.S.	N.S.	*	***	N.S.	***	***	***	**	N.S.	**

Note: N.S. : Not significant
* : P [0.05
** : P [0.01
*** : P [0.001

with chick production in 1982, and similar but less pronounced trends in 1981.

In the majority of cases, the relationships described above were approximately linear. Marked fluctuations, as observed for the higher scores of Attack from Below and Departure Angle, for instance, corresponded to small sample sizes. To assess the impact of non-linearity within the data, the levels of 18 variables from 1981 and 1982 were grouped to linearise the line of mean chick production. This increased the correlation coefficient in only 4 cases, and reduced it in 12 of them. As none of the changes was significant, further analyses were carried out on the original data.

8.6 Major nest-site characteristics correlating with chick production.

The simple correlations reported in the previous section suggest that there was indeed a relationship between certain characteristics of a site and the number of young fledged from that site. In the absence of other factors affecting chick production, the technique of stepwise multiple regression would select the nest-site variables which accounted for most of the variation in chick production explicable in terms of the 25 nest-site characteristics measured. However, the number of young fledged from a site varied according to year, side of the island, male breeding experience and timing of breeding.

It was necessary to find a way of determining the correlations between chick production and the nest-site variables independently of those between chick production and the other factors. This was achieved by dividing the data from 1982 into 'parts' corresponding to each of the combinations of side of the island, male breeding experience and timing of breeding. The two sides of the island were the east and the west coasts. Male breeding experience was presented as two age classes: second-year males and older ones; these accounted for 95% of the variation in chick production due to male age (female age has been shown to be unimportant). Timing of breeding was represented by five time periods based on laying date (and occupation date for nests lost before laying); as second-year males bred later than older ones, the time periods for the younger age class were delayed by two weeks. Analysis of variance showed no significant effect of laying date or occupation date upon chick production within each time period (examined for both age categories separately). By considering only the data for 1982, the effect of year was removed; by dividing the data into parts as described above, the effects of side of the island, male breeding experience and timing of breeding were held constant within each part. In this way, within each part it was possible to look independently at the relationships between chick production and the nest-site variables. As the proposed multiple regression required large sample sizes - it involved 25 nest-site variables - analysis was performed on parts containing over 50 nests. There were seven such parts, characterised as shown in Table 8.4; together they comprised 818 nests. One of the parts (Part 7) consisted of nests from the west side containing eggs laid between mid-May and the beginning of June, most of which were replacement clutches (see Section 7.2); such nests were shown to produce more young than nests with late first clutches, so the possible bias was eliminated by considering only replacement clutches.

To determine which of the nest-site variables were best at explaining the variation in chick production within each of the seven parts simultaneously, the parts were each represented by a dummy variable (coded 1 for nests inside the part, 0 for nests outside), which were included as the initial step of the stepwise multiple regression of chick production against

Table 8.4 Description of the nest groupings ('parts') used in the stepwise multiple regression of chick production against 25 nest-site variables in 1982, in terms of side of the island, male age and timing of breeding. The mean chick production within each grouping is also given.

	Part 1	Part 2	Part 3	Part 4	Part 5	Part 6	Part 7
Side of island	East	East	East	West	West	West	West
Male age (years)	3+	3+	2	3+	3+	2	3+
Week of laying	5-7	8-11	10-13	5-7	8-11	10-13	12-14
Week of occupation (for nests lost before laying)	-	[11	9-12	-	[11	9-12	-
N	192	85	88	149	75	85	144
Mean no. chicks fledged/nest	2.09	1.59	0.45	1.59	1.31	0.60	1.19

Note: Part 7 consists of replacement clutches only.

Week 1 starts on 1 March 1982.

the nest-site variables. This was equivalent to an analysis of covariance model, where each part constituted a 'treatment' (Draper & Smith 1981). The outcome of the stepwise multiple regression is presented in Table 8.5. Four variables were selected, namely Ledge Size, Damp, Level Attack and Wave Reach. An F-test confirmed that, as assumed by the analysis of covariance model, the slope of each of the selected variables was the same for all seven parts (F=0.87 df=24,783 N.S.). This meant that the increase in chick production corresponding to an increase in each of the nest-site variables was the same irrespective of experience, timing and side of the island. The coefficient of determination of the covariates, based on the total sum of squares less that pertaining to the groups of nests, was 0.03 (F=6.29 df=4,807 P[0.001). Potts *et al.* (1980) found that the simple coefficient of determination of young fledged per nest against site quality was also 0.03, based on data from 857 nests on the Farne Islands (see end of this section). The slopes from Table 8.5 were used to compute an overall nest-site rating, according to the formula:

$$\begin{aligned}\text{Overall rating} = {} & 0.259\ \text{Ledge Size} + 0.166\ \text{Damp} - 0.042\ \text{Level Attack} \\ & + 0.230\ \text{Wave Reach}\end{aligned} \tag{8.1}$$

Having selected the four nest-site variables in such a way that the choice was independent of other factors known to correlate with chick production, their importance in relation to chick production was validated on the independent body of data from 1981 (Table 8.6). All four contributed significantly to the multiple regression of chick production against site characteristics, with an overall coefficient of determination of 0.073. This confirmed that Ledge Size, Damp, Level Attack and Wave Reach were indeed related to the number of young fledged from a nest (the causal nature

Table 8.5 Stepwise multiple regression of chick production against all nest-site variables, after inclusion of dummy variables coding for the parts of the 1982 nest data (see text).

Independent variable	Multiple r-square	Significance at entry	Regression coefficient	Standard error
Dummies	0.241	-	-	-
Ledge Size	0.253	0.001	0.259	0.064
Damp	0.259	0.014	0.166	0.062
Level Attack	0.262	0.071	-0.042	0.023
Wave Reach	0.264	0.090	0.230	0.135

Table 8.6 Multiple regression of chick production against Ledge Size, Damp, Level Attack and Wave Reach in 1981.

Independent variable	Partial correlation	Regression coefficient	Standard error	Significance
Ledge Size	0.181	0.384	0.076	P[0.001
Damp	0.094	0.299	0.115	P[0.01
Level Attack	-0.178	-0.125	0.025	P[0.001
Wave Reach	0.088	0.464	0.192	P[0.05

r=0.270 N=759 P[0.001

of the relationship is examined in the next section). Likewise, the overall nest-site rating was highly correlated with chick production in 1981 (r=0.256 N=759 P[0.001). The corresponding correlation coefficient over the whole of the 1982 data was 0.228 (N=1151 P[0.001).

Referring back to Figures 8.1, 8.2, 8.3 and Table 8.3, nine nest-site variables other than those selected by this analysis were correlated with chick production in 1982, and a further four in 1981. The present analysis could have rejected them either on the basis of correlations with the external factors (year, side, experience, timing) or because of correlations with the selected variables. The pattern of correlations within the data used for the analysis is given in Table 8.7. All rejected variables except Overhang were highly correlated with the external factors, and all without exception showed some degree of correlation with the four selected nest-site variables. Both criteria were therefore involved in their rejection.

Table 8.8 compares the slopes from the regressions of chick production against the four selected nest-site variables and against the overall nest-site rating in 1981 and 1982 on the east and west sides of the Isle of May. The slopes for each separate variable were the same in all four subsets of data, when considering each of the four separate variables and the overall rating (Table 8.8). Similarly, in 1981 there were no differences in slopes between young and old breeders (F=2.15 df=4,400 N.S.); the same was already observed in 1982 with regard to experience and laying date. The relationship between nest-site quality and chick production was the same between years, on the east and west sides of the island, for young and old breeders, and for early and late breeders.

On the Farne Islands, Potts et al. obtained 0.03 for the simple coefficient of determination of young fledged per nest against nest-site quality over the period 1963-1971. On the Isle of May, the comparable

Table 8.7 Correlation of external factors (experience, timing, side of the island) and the four selected nest-site variables with those which were not selected by the multivariate analysis despite an overall significant correlation with chick production in 1981 or 1982.

	Sea Prot.	Topog.	Edge	Over-hang	Imm. Exp.	Driv. Exp.	Attack
External factors (multiple correl.)	0.51 ***	0.31 ***	0.20 ***	0.10 N.S.	0.17 ***	0.17 ***	0.19 ***
Ledge Size	-0.04 N.S.	-0.22 ***	-0.17 ***	-0.03 N.S.	0.16 ***	0.15 ***	0.35 ***
Damp	-0.07 *	0.07 *	0.18 ***	0.11 **	0.17 ***	0.11 **	0.08 *
Level Attack	-0.01 N.S.	-0.18 ***	-0.09 *	-0.14 ***	0.47 ***	0.33 ***	0.56 ***
Wave Reach	0.43 ***	-0.07 *	-0.03 N.S.	-0.05 N.S.	-0.05 N.S.	0.02 N.S.	0.06 N.S.

	Human Access	Height Sea	High Water	Low Water	Density	SNND
External factors (multiple correl.)	0.29 ***	0.26 ***	0.49 ***	0.42 ***	0.15 **	0.14 **
Ledge Size	-0.18 ***	-0.17 ***	0.07 N.S.	0.13 ***	0.07 N.S.	-0.05 N.S.
Damp	0.05 N.S.	0.01 N.S.	-0.06 N.S.	-0.08 *	-0.03 N.S.	0.04 N.S.
Level Attack	-0.12 ***	-0.05 N.S.	0.03 N.S.	0.12 ***	0.08 *	-0.05 N.S.
Wave Reach	-0.19 ***	0.43 ***	0.23 ***	0.28 ***	0.11 **	-0.15 ***

Note: N.S. : Not significant
* : P[0.05
** : P[0.01
*** : P[0.001

Table 8.8 Comparison of the slopes from the regression of chick production upon nest-site quality between years and between sides of the Isle of May.

	1981 East		1981 West		1982 East		1982 West	
Variable	Slope	S.E.	Slope	S.E.	Slope	S.E.	Slope	S.E.
Ledge Size	0.368	0.128	0.405	0.094	0.455	0.115	0.221	0.070
Damp	0.336	0.235	0.296	0.132	0.234	0.082	0.276	0.076
Level Attack	-0.135	0.041	-0.121	0.032	-0.081	0.034	-0.078	0.028
Wave Reach	0.826	0.405	0.363	0.217	0.861	0.392	0.422	0.120
R-square	0.067		0.083		0.055		0.053	
Overall Rating	1.821	0.438	1.745	0.287	1.703	0.325	1.159	0.216
R-square	0.053		0.077		0.051		0.043	
N	314		445		509		642	

All regressions significant at P[0.001.

Test for differences in slopes between years and sides:

Four nest-site variables F=0.72 df=12,1890 N.S.

Overall nest-site rating F=1.30 df=3,1902 N.S.

figures based on the whole body of data were 0.084 (four separate variables) and 0.076 (overall rating). In both cases, these were over twice the value from the Farne Islands, suggesting that the measurement of site quality was more accurate in the present study. The two techniques are compared later (Section 8.9). In both studies, the coefficients of determination were low. The analysis was detecting the average effect of nest-site quality, but the variability around the average was large. In this study, the four selected variables were ordinal, so that the overall nest-site rating was made up of discrete values. By considering the mean number of chicks fledged per pair at each value, the variability about the average relationship with nest-site quality was reduced. Figure 8.4 displays mean chick production plotted against the overall nest-site rating, for combinations of the four component variables held by at least 10 nests. The regression against the overall rating accounted for 56% of the variation in chick production; this increased to 67% when the overall rating was replaced by its component variables, with all four making a significant contribution (Table 8.9). The presence of an underlying relationship in the data between chick production and nest-site quality was confirmed, and the importance of the four selected variables highlighted.

8.7 Interpretation of the major nest-site characteristics in terms of physical, environmental and social pressures.

Until now, the analysis has concentrated on discovering which factors best described site quality, where the ultimate measure of the quality of a site was the number of chicks successfully fledged from that site. Having selected the major factors involved, it is important to find out what the link was between a factor and its purported effect on chick production, and

Figure 8.4 Mean number of chicks fledged per pair in 1981 and 1982, in relation to the overall nest-site rating. Each point is based on at least 10 nests, which all have the same scores for Ledge Size, Damp, Level Attack and Wave Reach.

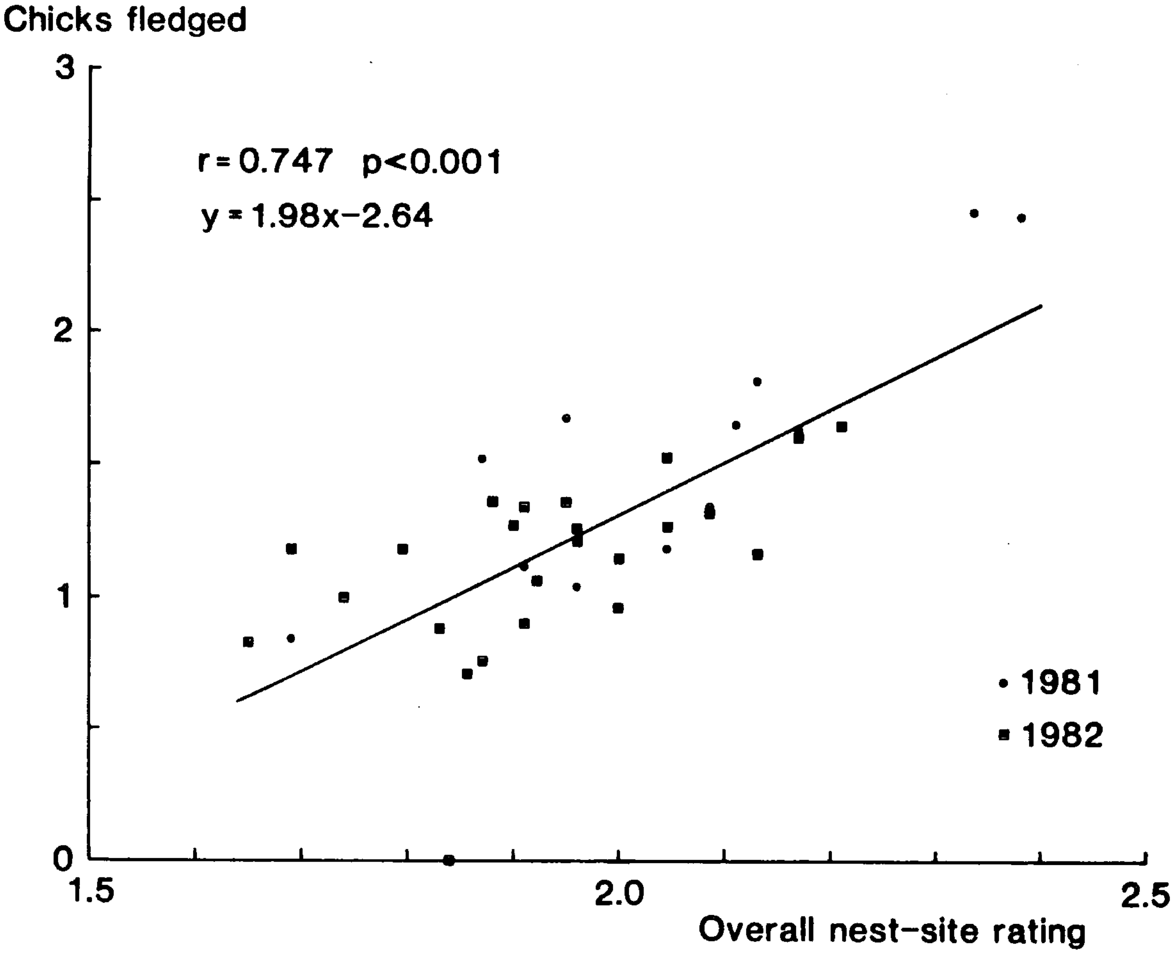


Table 8.9 Multiple regression of mean chick production (each mean based on at least 10 nests) against Ledge Size, Damp, Level Attack and Wave Reach in 1981 and 1982 together.

Independent variable	Partial correlation	Regression coefficient	Standard error	Significance
Ledge Size	0.667	0.402	0.081	P[0.001
Damp	0.748	0.468	0.075	P[0.001
Level Attack	-0.624	-0.120	0.027	P[0.001
Wave Reach	0.413	0.516	0.204	P[0.05

r=0.821 N=36 P[0.001

interpret if possible its action in terms of the Shag's environment.

The effect of Ledge Size upon the number of chicks reared was clear from the definition of this factor (Appendix 4). Shags nesting on a ledge too small to hold a large family would be incapable of fledging as many young as Shags on a spacious ledge. The nest itself was not cemented to the underlying rock, and often disintegrated as the chicks grew; it could not provide an artificial ledge as in the Kittiwake or Gannet. Snow (1960) found that on Lundy, 30% of chick corpses were found on the ledge at or near the nest on narrow cliff sites, against 80% at non-cliff sites, indicating that breeding success at the chick stage was affected by the size of the ledge. On the Isle of May, a four-week-old chick from a brood of three was actually observed to fall off a narrow ledge into the sea below; the nest was inaccessible, so had not been disturbed. For 204 nests where both brood size at 10 days and number of chicks fledged were known, brood reduction occurred twice as often on smaller ledges (Ledge Size scores 1-4) than on the large ones (score 5) on the east side of the island: 68% of nests on smaller ledges lost at least one chick compared to 35% of ones on large ledges (chi-square=7.68 df=1 P[0.01). There was no difference on the west side, probably because the lower hatching success brought about by the gale resulted in fewer chicks per nest than on the east side. Nests could also be dislodged at an early stage from a small ledge, and Table 8.10 shows that nests lost before laying were built on significantly smaller ledges than those which contained eggs, on both east and west sides of the island.

As regards site dampness, Table 8.10 shows that, on both sides of the island, the mean scores for Damp were significantly lower for nests lost before laying and during incubation than for nests which survived the incubation period. Furthermore, considering clutches incubated for the full period, complete failure to hatch was more than twice as frequent on damp

Table 8.10 Mean scores for Ledge Size, Damp, Level Attack and Wave Reach, in relation to nest loss and successful incubation in 1982. Values for the east and the west sides are presented separately.

Nests on the east side:

	Ledge Size		Damp		Level Attack		Wave Reach		
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	N
a) Lost before laying	4.56	0.15	2.56	0.13	3.26	0.31	1.91	0.05	34
b) Lost during incubation	4.83	0.05	2.59	0.07	2.80	0.15	1.97	0.02	93
c) Successful incubation	4.87	0.02	2.73	0.03	2.75	0.08	1.99	0.01	382
Differences between:	a x (b+c)		(a+b) x c		a x (b+c)		(a+b) x c		
T-value	2.02 P[0.05		2.08 P[0.05		1.60 N.S.		2.02 P[0.05		

Nests on the west side:

	Ledge Size		Damp		Level Attack		Wave Reach		
	Mean	S.E.	Mean	S.E.	Mean	S.E.	Mean	S.E.	N
a) Lost before laying	4.31	0.12	2.67	0.07	2.57	0.23	1.90	0.04	58
b) Lost during incubation	4.75	0.05	2.80	0.04	2.84	0.13	1.78	0.04	134
c) Successful incubation	4.69	0.03	2.84	0.03	2.46	0.07	1.89	0.01	450
Differences between:	a x (b+c)		a x (b+c)		(a+b) x c		(a+b) x c		
T-value	3.26 P[0.01		2.07 P[0.05		2.15 P[0.05		2.47 P[0.05		

sites (score 1-3) than on dry sites (score 4-5): the respective proportions on the east side were 9% and 2% (N=341; chi-square=5.14 df=1 p[0.05) and on the west 18% and 8% (N=387; chi-square=6.22 df=1 P[0.05). It was shown that the May gale led to a greater proportion of clutches failing to hatch on the west side (see Section 7.3). The present results strongly suggest that increased dampness, by e.g. wind-driven spray, was the underlying reason.

By observation of nests in the colony, Level Attack appeared to be important in the early stages of breeding. Shags establishing a nest-site or incubating were more timid on open, exposed sites, and often retreated when disturbed or threatened. This left the nest unattended and vulnerable to other, bolder, males, which raided it for nesting material. A similar situation was observed on the Farne Islands (Potts _et al_. 1980), where intra-specific competition for nest material was one of the main causes of nest failure on flat areas where Shags could not easily defend their position. Table 8.10 shows that the mean values for Level Attack, which was a measure of the degree of exposure to other Shags, were indeed highest for nests lost prior to laying and during hatching in 1982 on both the east and west sides, significantly so on the west.

The action of Wave Reach was obvious from the way it was scored: a poor score denoted a nest that was within reach of high waves, i.e. liable to be washed away or at least soaked by sea spray. In 1981, 51% (19 out of 37) of such nests were known to have been washed away. In 1982, only 5% of nests on the west coast which scored poorly for Wave Reach survived the May gale; this contrasted with 50% of high-scoring nests (Table 8.11). Wave Reach was thus a good indicator of the impact of the sea upon a nest.

None of the causes of poor breeding success mentioned so far has dealt with exposure to rain. In the field, it was very noticeable that after a prolonged spell of heavy rain, numbers of sodden, dead chicks were found at

Table 8.11 State of nests on the west side after the May gale in 1982, in relation to their score for Wave Reach.

Wave Reach	State of nests after gale		
	Washed away	Damaged	Undamaged
Within reach	50 (82.0%)	8 (13.1%)	3 (4.9%)
Out of reach	154 (33.8%)	71 (15.6%)	230 (50.6%)

Chi-square=56.5 df=2 P[0.001

or near their nests. The distribution of chicks found dead according to their stage of growth is presented in Table 8.12. 76% of dead chicks were at growth stages 6 to 8, corresponding to 20-37 days after hatching (four to six weeks of age). At this age, chicks were still clad in down, and too large to be effectively shielded from the elements by their parents. Survival increased dramatically as soon as the body feathers started to grow beneath the down (only 4% of dead chicks were at stage 9 or older). The deaths of large downy chicks (stages 6 to 8) due to exposure occurred in three waves (Table 8.13), corresponding to the three periods of heavy rain falling between the beginning of June and mid-August, a time when large numbers of chicks were at a susceptible age. Of the 126 large downy chicks found dead, 119 (94%) were found after these periods of heavy rain.

A comparison of the quality of the sites where chicks were found dead of exposure, with that of other nests known to contain chicks, showed up a difference in only one variable, Level Attack. Only 5.4% of sheltered nests (score 0-1) were noted as having lost chicks through exposure, compared to 12.8% of exposed nests (score 2-8) (chi=square=3.98 df=1 P[0.05). Referring back to Tables 8.2 and 8.7, it can be seen that Level Attack was highly correlated with Immediate Exposure (r=0.48) and Driving Exposure (r=0.34). Thus Level Attack, defined as a measure of exposure to attack by other Shags, provided a measure of how open the site was, and therefore a measure of exposure to weather at the same time.

In summary, the action of the chief nest-site variables could be interpreted as follows: Ledge Size was related to the early loss of nests, and also loss of chicks, through insufficient space; Damp affected nest loss before hatching, and also influenced hatching success; Level Attack was associated with early nest loss through robbing by other Shags, and also provided a measure of exposure of the chicks to heavy rain; Wave Reach

Table 8.12 Numbers of chicks found dead in 1982, in relation to their stage of growth. Shag chicks were assigned to one of 12 growth stages, as described in Section 2.16.

	Chick growth stage											
	1	2	3	4	5	6	7	8	9	10	11	12
No. found dead	6	5	7	8	7	20	38	68	3	1	2	1
% of total dead	3.6	3.0	4.2	4.8	4.2	12.0	22.9	41.0	1.8	0.6	1.2	0.6

76% of dead chicks were between stages 6 and 8, corresponding to 20-37 days after hatching.

Table 8.13 Rainfall and numbers of large downy chicks (growth stages 6-8) found dead of exposure in 1982. Rainfall figures were taken from the Meteorological Office Daily Weather Reports for Dunbar.

Date	10-11.6	25-26.6	14-15.7
Rainfall(mm)	17.2	51.6	25.5
Number of dead chicks	14	71	34

described the destructive potential of the sea.

8.8 Quantitative effects of nest-site quality on chick production, and limiting factors.

The change in chick production with increasing site quality was examined by means of formula 8.1. Table 8.14 shows the difference in the expected number of chicks fledged per pair for nests with the poorest and the highest nest-site rating. The lowest theoretical rating was obtained by taking the worst theoretical score for each of Ledge Size, Damp, Level Attack and Wave Reach, and the highest theoretical nest-site rating was obtained by using the best scores for each variable. The maximum possible difference in chick production between the worst and the best quality sites was 2.3 chicks.

In practice, however, none of the measured sites was extreme with respect to all factors. The sites with the worst overall rating attained the worst score for one only of the constituent variables in 1981 and 1982 (Table 8.14). In contrast, the sites with the highest rating achieved the optimal score for all four variables. There was thus no difference between the theoretical maximum rating and the observed maximum one, and inspection of the observed minimum one showed that the observed values of the overall nest-site rating were located within the upper two-thirds of the range of possible values. Owing to the topographical diversity of the Isle of May, this was unlikely to be due entirely to a shortage of poor quality sites. It is far more probable that the Shags avoided nesting on those sites which were clearly unsuitable. Over the observed range of sites in use, the mean difference in chick production between the worst and the best was approximately 1.4 chicks.

Table 8.14 Nest-site quality scores for the worst and best sites: in theory, and in practice in 1981 and 1982. The differences in mean chick production, calculated from the overall ratings, are also given.

In theory:

	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
Worst site	1	1	8	1	0.32
Best site	5	5	0	2	2.59

Difference in mean chick production: 2.27 chicks.

In practice:

1981	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
Worst site	3	2	4	1	1.17
Best site	5	5	0	2	2.59

Difference in mean chick production: 1.42 chicks.

1982	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
Worst site	2	3	1	1	1.20
Best site	5	5	0	2	2.59

Difference in mean chick production: 1.39 chicks.

As regards the effects of the individual factors involved in nest-site quality, the average change in the number of chicks fledged from a nest per unit change in factor quality was given directly by the coefficients in formula 8.1. All else equal, a Shag seeking to improve its breeding performance by changing site would achieve the maximum effect by improving the quality of the factors with the highest coefficients, namely by selecting a larger nesting ledge (Ledge Size), a site out of reach of waves (Wave Reach) and a dryer site (Damp). Its ability to do so would depend on the availability of sites with optimal factors, and also on its capacity to recognise such sites. Table 8.15 shows that, in fact, an average site was close to the optimal for Ledge Size and Wave Reach. For these variables, an increase in quality from the average resulted in only a small increase in chick production. This led to two conclusions: first that sites of good quality with respect to Ledge Size and Wave Reach were not in short supply, and second that the Shags were capable of recognising such sites, and occupied them in preference to poorer ones.

In contrast, the average scores for Damp and Level Attack differed considerably from the optimal scores, especially Damp (Table 8.15). In the latter case, the potential for improving chick production was over three times that offered by the other variables. As the birds seemed able to select high quality sites with respect to other factors, it was likely that the mediocre average scores for Damp and Level Attack reflected a real lack of sites optimal in these two features. In other words, the dampness of the site and its degree of exposure to weather and attack by other Shags were the limiting factors in nest-site quality.

For a given nest, the dampness, produced by water run-off and seepage, differed according to the rain regime during the breeding season. The variation in dampness with climate would be most pronounced for nests that

Table 8.15 Increases in the mean number of chicks fledged per pair, obtained by maximising each nest-site characteristic individually, compared to the number fledged from an average site.

1981 (N=832)	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
Average site score	4.78	3.07	1.60	1.95	2.13
Best site score	5	5	0	2	2.59
Overall rating obtained by maximising one factor (*)	2.19	2.45	2.20	2.14	
Increase in chicks (**)	0.06	0.32	0.07	0.01	

1982 (N=1152)	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
Average site score	4.74	2.76	2.65	1.92	2.02
Best site score	5	5	0	2	2.59
Overall rating obtained by maximising one factor (*)	2.08	2.39	2.13	2.03	
Increase in chicks (**)	0.06	0.37	0.11	0.01	

(*) Obtained using formula 8.1.

(**) Obtained by subtracting the overall rating for an average site from the maximised rating.

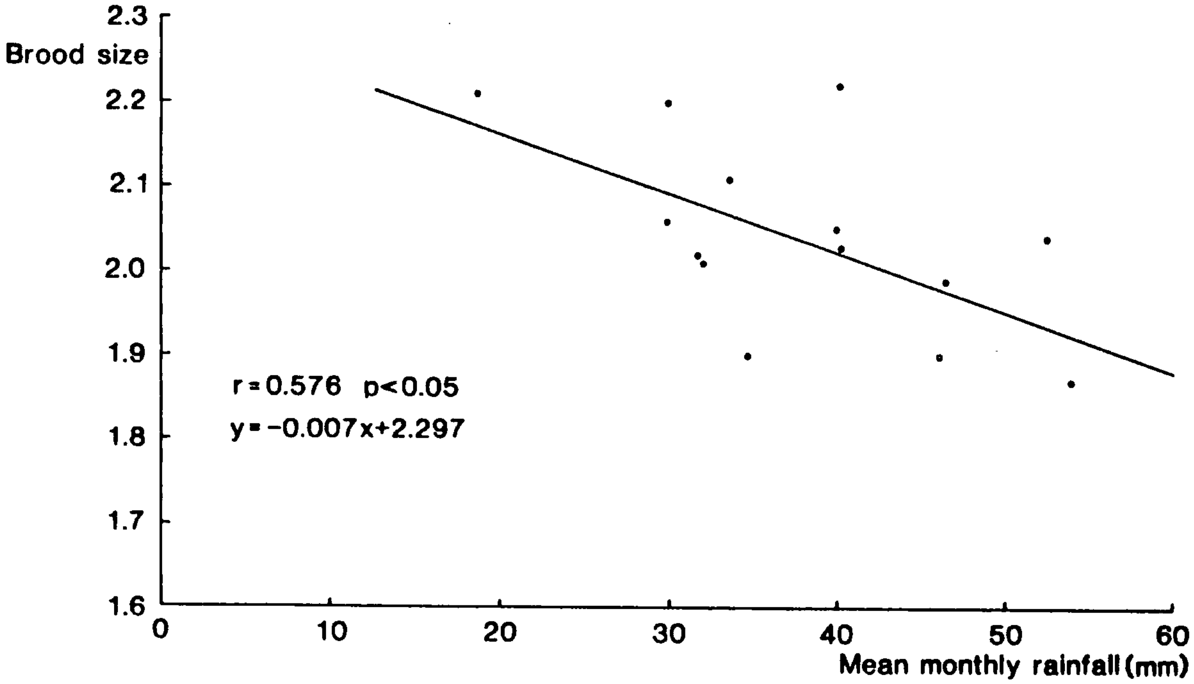
are neither very wet or dry, but intermediate. Seeing that the average nest on the Isle of May scored 3.07 in 1981, and 2.76 in 1982, for a Damp score of 1 to 5, most nests were intermediate in character. Furthermore, it has already been shown that rainfall has a direct effect, through exposure, on the survival of chicks (Table 8.13). The second limiting factor, Level Attack, provided a measure of this exposure. Annual breeding success might be expected therefore to correlate with a measure of rainfall during the breeding season. An estimate of chick production was given by the brood sizes from the Isle of May Bird Observatory ringing schedules from 1965 to 1982 (none recorded in 1972). Rainfall was measured by the geometric mean of the monthly rainfall at Dunbar Meteorological Station over three months, starting with the month in which the laying of the first egg was recorded. This covered the period from nest-building to chick ringing for the majority of nests. The points are plotted out in Figure 8.5. Those corresponding to the years of the crash (1974, 1975, 1976) were aberrant, for reasons associated with the decline (Chapter 4), so were not included in the analysis. There was a significant correlation between mean rainfall and brood size (r=-0.576 N=14 P[0.05), confirming the importance of Damp and Level Attack as factors controlling chick production on the Isle of May.

8.9 Comparison of nest-site quality in the present study with nest-site quality as described by Potts *et al*. (1980).

Potts *et al*. considered four factors to be important in determining nest-site quality on the Farne Islands, on the basis of observations of the behaviour of breeding Shags. They were:

1. Protection from Rough Seas.
2. Amount of Exposure to Rain.

Figure 8.5 Relationship between the annual mean brood size at ringing and mean monthly rainfall (geometric mean over three months, starting with the month the first egg was laid), for the years 1965-1971, 1973, 1977-1982. Brood sizes were not recorded in 1972, and 1974-1976 were the aberrant years of the crash (cf. Section 4).



3. Size of the Site.
4. Access to the Sea.

Each site was ranked -1, 0, or +1 with respect to each factor, and then the scores were summed to form an overall nest-site quality rating. A detailed description of the different categories of each factor, taken from their paper, is given in Appendix 5. These four factors will henceforth be termed "Potts' variables" or "Potts' factors", to distinguish them from the variables used in the present study to describe nest-site quality. The latter will be called "Isle of May variables".

For comparative purposes, the 832 sites scored in 1981 for the 28 Isle of May variables were also graded according to Potts' variables. After the May gale in 1982, it was found that 105 nests had been wrongly graded for Potts' Protection from Rough Seas, so were corrected. Table 8.16 presents the correlations between Potts' variables and the four important Isle of May variables. Potts' Protection from Rough Seas correlated strongly with the Isle of May Wave Reach (r=0.52), which constituted the only sea-related variable amongst the four. Potts' Exposure to Rain was correlated with Level Attack (r=-0.36) and Damp (r=0.29), which were the two Isle of May factors related to exposure. Potts' Site Size was strongly correlated with Ledge Size (r=0.74), and to a lesser extent with Level Attack (r=0.15). Potts' Access to Sea correlated weakly with Wave Reach (r=0.07) and with no others. Apart from Access to Sea, which had no obvious counterpart amongst the Isle of May variables, each of Potts' variables correlated with the Isle of May variable or variables which represented the same kind of factor. Conversely, the Isle of May variables showed an affinity with one at least of Potts' variables, although the correlation was relatively low in the case of Damp. Both sets of variables represented approximately the same factors with regard to site quality. The correlation between the two overall

Table 8.16 Correlations between Potts' variables and the four major Isle of May variables in 1981.

Potts' variables	Isle of May variables			
	Ledge Size	Damp	Level Attack	Wave Reach
Protection from Seas	-0.03 N.S.	0.06 N.S.	-0.11 **	0.52 ***
Exposure to Rain	-0.11 **	0.29 ***	-0.36 ***	-0.05 N.S.
Site Size	0.74 ***	0.06 N.S.	0.15 ***	-0.01 N.S.
Access to Sea	-0.01 N.S.	-0.01 N.S.	-0.05 N.S.	-0.07 *

Note: N.S. : Not significant

* : P[0.05

** : P[0.01

*** : P[0.001

ratings - Potts' obtained by summing the scores of his four factors, the one for the Isle of May derived from formula 8.1 - was 0.39, highly significant (N=832 P[0.001).

In Section 8.6, it was noted that nest-site quality, as defined by the Isle of May variables, accounted for a greater proportion of the variation in Isle of May chick production than Potts' nest-site quality did for chick production on the Farne Islands (8% versus 3%). The relationships between the chick production on the Isle of May in 1981 and the two methods of measuring site quality are compared in Table 8.17. When standardising for the study area, the year and the observer in this way the difference vanished. The regression of young fledged per pair against the component factors of nest-site quality gave coefficients of determination of 0.08 for Potts' factors and 0.07 for the Isle of May ones; the corresponding figures for a simple regression against the overall nest-site ratings were 0.06 and 0.07 respectively.

Thus not only did the variables from the two methods of measuring site quality match up in the factors whose influence they represented (sea, weather, etc.), but, to all intents and purposes, the effect they had on chick production was the same. It is relevant to note that Potts' Access to Sea, the only variable not to have an obvious counterpart amongst the Isle of May variables, was also the only variable which did not contribute significantly to the regression against chick production in Table 8.17.

8.10 Comparison of nest-site quality and its effects on chick production on the Farne Islands and on the Isle of May.

The distribution of nest-sites for Potts' variables on the Farne Islands from 1963 to 1971 (data from Potts et al. 1980) and from the Isle of

Table 8.17 Comparison of the relationship between chick production on the Isle of May in 1981 and nest-site quality, as measured by Potts' variables and the Isle of May variables.

Overall ratings:

	Correlation	Slope	S.E.	Significance	R-square	N
Potts' rating	0.245	0.328	0.047	P[0.001	0.060	759
Isle of May rating	0.256	1.763	0.242	P[0.001	0.057	759

Potts' variables:

	Partial corr.	Slope	S.E.	Significance
Prot. from Seas	0.105	0.264	0.091	P[0.01
Exposure to Rain	0.168	0.330	0.071	P[0.001
Site Size	0.215	0.871	0.144	P[0.001
Access to Sea	0.047	0.134	0.104	N.S.

r=0.286 N=759 P[0.001

Isle of May variables:

	Partial corr.	Slope	S.E.	Significance
Ledge Size	0.181	0.384	0.076	P[0.001
Damp	0.099	0.312	0.114	P[0.01
Level Attack	-0.178	-0.124	0.025	P[0.001
Wave Reach	0.088	0.465	0.192	P[0.05

r=0.271 N=759 P[0.001

May in 1981 is presented in Table 8.18. For each variable, there was a significant difference in distribution of nests from the two areas (chi-square=53, 81, 15 and 119 respectively; df=2 P[0.001 in all cases); the difference was least for Site Size. The proportion of unsuitable nest-sites (i.e. scored -1 or 0) was consistently higher on the Farne Islands, and the mean rank for each factor consistently lower. On the overall nest-site rating, the average on the Farne Islands was 1.78, against 2.59 on the Isle of May. This was higher even than the rating of 2.31 obtained from the Farne Islands in 1969 and 1970 (Coulson 1971), after the death of 82% of the breeding population in 1968 due to the 'red tide' (Coulson et al. 1968). In short, nests on the Farne Islands were more exposed to the sea and the weather, occupied smaller ledges, and were less well placed for access to the sea. On average, a Farne Islands nest-site was of poorer quality than an Isle of May nest-site.

The mean number of chicks fledged per pair in relation to nest-site quality on the Farne Islands from 1963 to 1967 (from Potts et al. 1980), and on the Isle of May in 1981, are compared in Table 8.19. Although the means were similar between the two areas for the lowest quality sites, they were consistently higher for sites scored 1 to 4 on the Isle of May. However, this was likely to reflect a particularly good year for the Isle of May rather than an ability of the Isle of May Shags to produce more young on the better quality sites than Shags on similar quality sites on the Farne Islands. Indeed, Table 8.20, presenting data from Coulson (1971), shows that in 1969 and 1970 chick production on the Farne Islands averaged 1.7 chicks/pair, for a mean nest-site quality of 2.3. This chick production was also considerably higher than expected from the results of 1963 to 1967, and Coulson mentions the good weather in those years as being an additional factor contributing to the high success. This agrees with the relationship

Table 8.18 Rankings and suitability of nest-sites according to Potts' variables, for sites on the Farne Islands from 1963 to 1971 (from Potts *et al*. 1980), and on the Isle of May in 1981.

Farne Islands 1963-1971:

	-1	0	1	Unsuitable	Mean rank
Protection from Seas	77	99	491	26%	0.62
Exposure to Rain	222	393	52	92%	-0.25
Site Size	18	66	583	13%	0.85
Access to Sea	102	110	455	32%	0.53

	-1	0	1	2	3	4	
All factors summed	0	92	164	237	148	26	1.78
	0%	14%	25%	36%	22%	4%	

Isle of May 1981:

	-1	0	1	Unsuitable	Mean rank
Protection from Seas	19	146	667	20%	0.78
Exposure to Rain	135	537	160	81%	0.03
Site Size	5	59	768	8%	0.92
Access to Sea	13	87	732	12%	0.86

	-1	0	1	2	3	4	
All factors summed	0	15	87	220	412	98	2.59
	0%	2%	11%	26%	49%	12%	

Note: 'Unsuitable' sites are those which score -1 or 0.

Table 8.19 Mean number of chicks fledged per pair, in relation to nest-site quality on the Farne Islands from 1963 to 1967 (from Potts *et al.* 1980), and on the Isle of May in 1981.

Quality rating	0	1	2	3	4	Mean fledged
Farne Islands 1963	0.58	0.53	0.92	1.36	1.83	1.04
N	19	60	113	106	24	
Farne Islands 1964	0.39	0.64	1.01	1.39	1.39	1.03
N	31	74	135	121	26	
Farne Islands 1965	0.86	0.85	1.28	1.27	1.26	1.15
N	42	80	148	126	23	
Farne Islands 1966	0.46	0.84	1.02	1.27	1.59	1.03
N	41	82	139	109	22	
Farne Islands 1967	0.67	0.58	0.89	1.21	1.71	0.90
N	58	106	169	104	21	
Isle of May 1981	0.54	1.16	1.33	1.67	2.08	1.55
N	13	76	210	373	87	

Table 8.20 Mean nest-site quality and chick production on the Farne Islands, before and after the population crash in 1968 (from Coulson 1971).

	Before 1968		1969-1970	
	First breeders	Older	First breeders	Older
Nest-site quality	1.61	1.92	2.24	2.31
Chick production	0.90	1.27	1.64	1.73

between brood size and rainfall demonstrated in Section 8.8, and with the fact that 1981 was a year of low rainfall on the Isle of May.

The years 1969 and 1970 were exceptional for the Farne Islands, in that reduced numbers of breeding birds brought about an increase in average site quality; compounded with good weather, this resulted in a very high breeding success. In a more normal situation, with colony size over 300 pairs, as represented by 1963 to 1967, breeding success was very much lower than that observed on the Isle of May in 1981 (Table 8.19). This was not merely an effect of the low rainfall on the Isle of May in that year, as was shown by the 1982 data on chick production: the spring and summer of 1982 were wetter than those of 1981, and owing to the gale which affected the whole of the west coast, it was unlikely that the mean young production of 0.97 chicks/pair could be worse for that side of the island. Even so, it was higher than the worst recorded for the Farne Islands (0.90 in 1967). For the east coast of the Isle of May in 1982, mean young production was 1.30 chicks/pair; in spite of suboptimal weather, this was higher than any of the mean yearly values recorded on the Farne Islands from 1963 to 1967. It would appear that, generally, the production of young was higher on the Isle of May than on the Farne Islands. This accords with the initial observation that the average nest-site quality was higher on the Isle of May than on the Farne Islands.

8.11 Discussion.

Of the 28 variables describing nest-site characteristics and initially considered as potential factors related to reproductive success in the Shag, four were found to be important: Ledge Size, Damp, Level Attack and Wave Reach. These factors embodied the effects of the physical capacity of the site, dampness, exposure to wind, rain and other Shags, and the action of the sea. I shall take each factor in turn, and examine how it fits in with observations on seabirds by other workers.

The destructive action of the sea, through flooding and storm damage, is well documented in, for instance, gulls (Beer 1966, Bongiorno 1970, Burger & Shisler 1980) and terns (Burger & Lesser 1979, Buckley & Buckley 1982, McNicholl 1982, Spendelow 1982). Damage was caused by abnormally high tides as well as wind-driven waves, and the main features of the nests which survived were higher site elevation and greater nest-cup height. Heavy seas caused the loss of 400 Cape Cormorant chicks in one season (Crawford et al. 1980), and in the case of the Shag, already in 1902 Tomison (in Baxter & Rintoul 1953) remarked on 200 nests being washed off the cliffs of Sule Skerry, Orkney. However, not all sea damage was imputable to gales, as on the Isle of May, certain nests were built so low down that the first spring tide destroyed them.

Exposure to wind and rain has been shown to cause the death of gull chicks (Jennings & Soulsby 1958, Harris 1964, Burger 1974, Burger & Lesser 1979) and tern chicks (White et al. 1976, Randall & Randall 1981a), particularly small ones. Much of the exposure was due to the inability of the parents to shield the chicks of large broods (Harris & Plump 1965), and nests in dense vegetation were better protected (Burger 1974, Winnet-Murray 1979). Alternatively, exposure to the sun, resulting in heat stress, affected breeding success in Peruvian Boobies (Vogt 1942), Jackass Penguins (Randall & Randall 1981b) and Herring Gulls (Parsons 1982); the problem was reduced for birds nesting under cover or in rock crevices. The effects of bad weather conditions are well documented at high latitudes (Jehl & Hussell 1966, Ojanen 1979, Hildén et al. 1982). Species nesting in holes or cavities usually suffered only slight loss compared to those nesting in the open (Bengtson 1963, Spjøtvoll 1972). Heavy rain was responsible for the death of 800 Cape Cormorant chicks (Crawford et al. 1980); as on the Isle of May in 1982, they were all in the late downy stage. Similar timing of the mortality of Shag chicks through exposure was reported on the Farne Islands (Potts et al. 1980).

Linked to the problem of exposure is that of dampness of the nest-site, which heavy rain will tend to exacerbate. Certain groups of birds, such as grebes, cormorants, flamingoes, ducks and jacanas, which nest in damp places or have wet underparts when they come onto the eggs, have evolved waterproof coatings for their eggs (Lack 1968). In Laughing Gulls (Burger 1979), Herring Gulls and domestic chickens (Ward & Burger 1980), eggs experimentally immersed in water for various lengths of time showed reduced hatching success. In this study, site dampness also affected the hatchability of the eggs, maybe as a result of reduced gas exchange or cooling through contact with water.

The restrictions imposed by nest size on breeding success have been discussed by Snow (1978), in relation to clutch size in tropical passerines. A positive correlation between clutch size and the size of the nest or the site holding the nest has been demonstrated in tits and flycatchers (Ludescher 1973, Karlsson & Nilsson 1977), Swallows (Møller 1982), but not in Starlings (Karlsson 1978) or Goldeneyes (Eriksson 1979). In seabirds, a main cause of mortality in young Kittiwakes was the collapse of nests built on impossibly small ledges (Cullen 1957a); in the Gannet, mortality of chicks on cliff sites was predominantly due to them falling out of the nest and off the nesting ledge (Nelson 1978). This held also for the Shag on Lundy (Snow 1960), and Potts et al. (1980) noted that loss of nests and eggs occurred on the smaller ledges used by Shags on the Farne Islands.

Thus the factors found to be important for the Shag on the Isle of May have been shown also to affect the breeding success of other bird species, in particular other Pelecaniformes. These factors were compared in a more detailed way with the characteristics used by Potts et al. (1980) to measure the quality of Shag nest-sites on the Farne Islands (see Section 8.9). There was good agreement between the factors selected on the basis of chick production from a wide range of potentially important nest-site descriptors in this study, and those chosen on the basis of observations at the colony on the Farne Islands. A factor omitted by Potts et al. was dampness; however, this was partly covered by Potts' exposure variable. Conversely, Potts' measure of access to the sea, which had no counterpart amongst the factors selected in the present study, was found to be unimportant on the Isle of May. This may be because the average height of cliffs on the Isle of May is greater than on the Farne Islands, so that, on the Isle of May, Shags usually had no difficulty in obtaining sites with good access to the sea.

In terms of comparing the quality of nests on the Isle of May with those on the Farne Islands, it appeared that in conditions of high occupation of the Farne Islands, the quality was lower than that on the Isle of May; chick production was correspondingly poorer. A higher chick production associated with better average sites on the Isle of May would possibly explain the relatively poor fit of the model of the Shag population on the Farne Islands since 1975 (Potts et al. 1980). From 1976 onwards, the predicted values were approximately 100 nests lower than the observed ones. The shortfall would be accounted for if the recruitment of immigrants had been underestimated. This in turn could be a result of underestimating the size of the pool of potential immigrants, to which the Isle of May was and still is a major contributor.

9. NEST-SITE QUALITY IN RELATION TO AGE, TIMING OF BREEDING AND SITE CHOICE.

9.1 Introduction.

The previous chapter cited several instances of different habitat or breeding site types being occupied by the same species, despite certain types being more favourable than others. In particular, this was shown to be true of the Shag. Natural questions arising in such cases are whether any differences exist between the individuals which occupy different habitats or sites, whether the individuals are capable of distinguishing between sites of different quality, and if so, what the mechanisms are which govern site occupation, especially that of the poorer quality sites.

Detailed studies of the behavioural responses of an animal to sites of different quality are few. Wells (1977), working on the territorial Green Frog, ranked territory quality on the basis of cover, vegetation, location and dryness. He found that males on high quality sites were larger than those on poor ones, and that territory quality was strongly correlated with the number of days the site was occupied. Of frogs which changed sites, twice as many moved to a better as to a poorer quality territory, and males invested their greatest effort in active takeovers of high quality sites. In birds, Coulson (1968) showed that Kittiwakes nesting on the less favourable edge sites weighed less than those nesting in the centre of the colony, and Nettleship (1972) found a similar result for Puffins. In many cases, the birds occupying the poorer quality areas were predominantly young ones. For example, young Sooty Terns often bred in more open and featureless areas than older birds (Harrington 1974), most immature-plumaged

Ring-billed Gulls nested on the periphery of the colony (Ryder 1975), and young female Snow Geese nested in areas of the colony which had been only recently colonised or were irregularly available for nesting (Finney & Cooke 1978). In the Pelecaniformes, adult-plumaged Brown Pelicans selected the higher nesting sites whereas immature-plumaged birds nested more often in the low-lying periphery, where two-thirds of nests were subsequently flooded (Blus & Keahey 1978).

Did this mean that young birds were incapable of recognising good sites, and therefore learnt by a process of trial and error? In the above examples, the older birds bred earlier than the young ones; an alternative explanation was that they occupied the better quality areas or sites first so that recruiting young birds were forced onto less suitable ones. Removal experiments on Red Grouse (Watson & Jenkins 1968) and Great Tits (Krebs 1971) showed that vacant, high quality territories were rapidly taken over, usually by yearlings which moved in from marginal habitats. Thus occupation of suboptimal areas, in these species at least, was caused by territorial exclusion from better areas rather than by ineptitude on the part of the young birds. This is the 'buffer effect' described by Brown (1969), whereby a species first occupies its preferred breeding habitat until numbers reach a certain limit dictated by territoriality; the surplus then overflows into second-rate habitat until that too reaches saturation, whereupon any extra birds form a non-territorial body of 'floaters'.

The present chapter makes use of the results from Section 8.6 to investigate the relationships between site quality, age, timing of breeding and site choice for the Shag on the Isle of May. Site quality was shown to be based mainly on four physical characteristics of a nest-site: its capacity (Ledge Size), dampness (Damp), exposure to weather and to other Shags (Level Attack), and vulnerability to the sea (Wave Reach). The components were combined in an overall nest-site rating according to formula 8.1. As there were marked differences in the way these variables were scored, to help comparison and interpretation in the analysis which follows the values were transformed: each variable score was expressed as an equivalent change in the number of chicks fledged per 100 pairs relative to the figure obtained from 100 average nests. For example, the maximum score of 5 for Damp was expressed as an increase, from the average production of 100 nests in 1981, of 32 chicks (see Table 8.15). In what follows, the transformed scores will simply be referred to as 'scores'.

9.2 Age-related differences in nest-site quality.

The mean scores of the four major nest-site variables and the overall rating in 1981 and 1982 are presented for six age classes of males (Tables 9.1 and 9.2). In general, variability between age classes was small. The only variables to show significant differences between age classes were Damp and Level Attack in 1981; after excluding the youngest age class (second-year birds), none of the variables differed significantly between classes. As a result, it was sufficient to consider the two categories identifiable in the field on plumage: second-years and older birds. For convenience, these two categories will be referred to collectively as 'breeding experience' (as in Chapter 5). Tables 9.1 and 9.2 also give the mean scores of the nest-site variables for the two categories of breeding experience. In both years, there was a small difference in the overall rating (significant in 1982), indicating that second-year males held slightly poorer sites than older ones. The scores showed that the difference in site quality was responsible for young Shags producing, on average, only 2-3 chicks per 100 pairs less than older birds. The average

Table 9.1 Mean nest-site variable scores in relation to male age in 1981.

Male age (years)	N	Ledge Size	Damp	Level Attack	Wave Reach	Overall rating
2	106	-0.3 (1.4)	-1.0 (0.3)	-1.6 (0.7)	0.3 (0.4)	-2.6 (1.4)
3	16	-2.3 (3.9)	-1.2 (0.0)	-1.7 (1.8)	1.2 (0.0)	-3.3 (3.7)
4-6	9	0.1 (3.8)	0.6 (1.8)	-0.7 (2.5)	-1.4 (2.6)	-1.4 (5.4)
7-10	39	2.5 (1.7)	-1.6 (1.3)	2.2 (1.0)	0.6 (1.9)	3.7 (2.1)
11-13	14	-3.4 (4.4)	-2.4 (1.2)	2.2 (2.0)	1.2 (0.0)	-2.4 (4.1)
14+	5	-9.7 (6.3)	2.1 (3.3)	5.0 (1.7)	1.2 (0.0)	-1.4 (8.3)
F-value		1.02 N.S.	2.29 P[0.05	2.76 P[0.05	0.62 N.S.	1.34 N.S.
2-year	106	-0.3 (1.4)	-1.0 (0.3)	-1.6 (0.7)	0.3 (0.4)	-2.6 (1.4)
Older	329	0.2 (0.8)	-0.8 (0.2)	0.1 (0.4)	0.5 (0.2)	-0.1 (0.8)
T-value		0.34 N.S.	0.45 N.S.	2.03 P[0.05	0.45 N.S.	1.48 N.S.

1 S.E. in parentheses.

Table 9.2 Mean nest-site quality scores in relation to male age in 1982.

Male age (years)	N	Ledge Size	Damp	Level Attack	Wave Reach	Overall rating
2	272	1.1 (0.9)	-0.9 (0.6)	-1.0 (0.4)	0.0 (0.4)	-0.8 (1.0)
3	74	4.5 (0.8)	0.2 (1.0)	-1.6 (0.7)	0.3 (0.7)	3.4 (1.7)
4-6	39	0.0 (2.6)	1.5 (1.0)	-0.7 (1.1)	0.1 (1.0)	0.8 (2.9)
7-10	42	-0.2 (2.2)	0.8 (1.2)	1.0 (1.1)	0.8 (0.8)	2.5 (2.7)
11-13	26	3.6 (1.7)	-1.1 (1.8)	-0.3 (1.5)	1.9 (0.0)	4.1 (2.3)
14+	24	-2.0 (3.0)	3.3 (1.6)	-0.2 (1.5)	0.9 (1.0)	2.0 (3.6)
F-value		1.48 N.S.	1.42 N.S.	0.96 N.S.	0.62 N.S.	1.16 N.S.
2-year	272	1.1 (0.9)	-0.9 (0.6)	-1.0 (0.4)	0.0 (0.4)	-0.8 (1.0)
Older	746	0.5 (0.5)	0.6 (0.3)	0.2 (0.2)	0.3 (0.2)	1.5 (0.6)
T-value		0.55 N.S.	2.01 P[0.05	2.57 P[0.05	0.89 N.S.	2.12 P[0.05

1 S.E. in parentheses.

difference in chick production between second-year males and older ones was about 1 chick/pair in both 1981 and 1982, i.e. 100 chicks per 100 pairs (Section 5.2). Nest-site quality therefore contributed only mildly to this difference. Considering the component variables of site quality, nests of second-year males were slightly more exposed and damper than those of older birds (Tables 9.1, 9.2). In both years, proportionately more young than old birds built their nests within reach of high waves, but no differences were significant; Ledge Size showed no relationship. Thus the only variables to show significant age-related differences were Damp and Level Attack, which were the two factors found to be limiting on the Isle of May (Section 8.8). In both instances, the better sites were usually occupied by the older males.

These results were consistent with the situation on the Farne Islands, where Coulson (1971) showed that Shags breeding for the first time occupied sites of poorer quality than experienced breeders. Were young Shags therefore incapable of recognising good sites, or were they prevented from occupying them by being competitively excluded by older birds? On the Farne Islands, the destruction of 82% of the breeding Shags during the 'red-tide' in 1968 (Coulson _et_ _al_. 1968) was followed by an increase in mean nest-site quality, particularly for young birds; this was accompanied by an increase in breeding performance (see Table 8.20, from Coulson 1971). It seemed that young Shags were indeed able to recognise good sites, but had been forced to take poorer sites because the older birds occupied the better ones.

9.3 Nest-site quality in relation to the timing of breeding.

If Shags are able to recognise good sites, then it is likely that, irrespective of breeding experience, birds nesting early would preferentially occupy good sites, leaving late breeders to occupy the poorer ones. Table 9.3 presents the mean scores of the nest-site variables for early and late breeders in 1982, where a second-year male was considered 'early' if he occupied his site before 26 April, and an older male was 'early' if he was present on his site when recording started, i.e. before 19 April. In both age categories, mean site quality (overall rating) was significantly higher for early than late birds. In terms of the component variables, early second-year males occupied, on average, sites of higher quality than late ones with respect to Ledge Size, Damp and Wave Reach (significant for Ledge Size). They also appeared to occupy more exposed sites (Level Attack) than late birds; however the difference was minimal and the standard errors large. Males older than two and present early in the season scored, on average, consistently better on all four nest-site characteristics than late birds in the same age category (significantly so for Level Attack and Wave Reach). In general, therefore, the Shags were behaving as predicted by the hypothesis of the best sites being taken by birds which nested early.

Section 9.2 showed that second-year males occupied on average sites of slightly poorer quality than older ones. However, second-year males also occupied their sites later than older males (Section 5.4), so the late arrival might explain the poorer site quality. After correcting the scores of the overall nest-site rating for timing of breeding, the means for the two age categories were practically identical (second-year males: 1.0 ± 1.1, older males: 0.9 ± 0.6). Thus the poorer mean score in young Shags was accounted for solely by the fact that they occupied their sites later than the older ones. The similarity of the corrected mean nest-site ratings meant that, on average, a second-year Shag fared as well as an older one when both took possession of their sites during the same period, i.e. both

Table 9.3 Mean nest-site quality scores for early and late breeders in 1982, presented in relation to male breeding experience.

Second-year males:

Timing	N	Ledge Size	Damp	Level Attack	Wave Reach	Overall rating
Early	131	4.2 (0.7)	-0.7 (1.0)	-1.2 (0.6)	0.5 (0.5)	2.9 (1.2)
Late	141	-1.8 (1.5)	-1.1 (0.8)	-0.9 (0.6)	-0.4 (0.6)	-4.2 (1.7)
T-value		3.58 P[0.001	0.26 N.S.	0.31 N.S.	1.41 N.S.	3.58 P[0.001

'Early' birds occupied their sites before 26 April (week 9), 'late' birds from 26 April onwards.

Older males:

Timing	N	Ledge Size	Damp	Level Attack	Wave Reach	Overall rating
Early	652	0.6 (0.6)	0.6 (0.4)	0.5 (0.3)	0.6 (0.2)	2.3 (0.6)
Late	94	-0.6 (1.5)	0.1 (0.9)	-1.4 (0.7)	-1.8 (0.9)	-3.6 (2.0)
T-value		0.79 N.S.	0.47 N.S.	2.44 P[0.05	2.42 P[0.05	2.68 P[0.01

'Early' birds occupied their sites before 19 April (week 8), 'late' birds from 19 April onwards.

1 S.E. in parentheses.

were equally capable of recognising good sites. It also meant that late arrivals among older Shags failed as much as young ones to obtain good sites - a strong indication that optimal sites were in short supply, and that older males which arrived late were subjected to the same constraints on site availability as younger ones.

9.4 Nest-site quality, site choice and site tenacity.

Being capable of recognising good nest-sites, it was likely that Shags forced onto poorer sites in one year would seek to upgrade their sites in the following year by moving to different ones of better quality. This was examined for ringed individuals breeding in 1981 and 1982 (Table 9.4). There were no differences in this respect between the sexes, so that the data were pooled to increase the sample sizes; stable pairs were regarded as single individuals. In 1981, Shags which subsequently retained their site held on average slightly better sites than those which subsequently changed, with respect to all variables except Ledge Size. The only significant difference was in Level Attack, with retained sites being less exposed than sites from which Shags moved. In 1982, the pattern was identical: the mean scores for retained sites were slightly above those for sites occupied by birds which had moved (except for Ledge Size), and the only significant difference was again in Level Attack. Although the trends were weak, they indicated that it was the Shags on poorer sites which tended to move. In spite of moving, they were apparently unable to improve the quality of their sites to match that of birds which did not move.

Owing to differences in weather conditions which affected the way certain nests were scored in 1981 and 1982 (see Appendix 4), it was not feasible to compare directly the 1981 site quality scores and the 1982

Table 9.4 Mean site quality scores for individuals which retained their sites or changed sites between 1981 and 1982, comparing retained sites with sites from which individuals moved (1981 site quality) and retained sites with sites to which individuals moved (1982 site quality).

1981 site quality:

	1981 site retained in 1982	1981 site from which owner moved in 1982	T-value
Ledge Size	-1.2 (1.2)	1.6 (1.1)	1.72 N.S.
Damp	-1.1 (0.2)	-1.3 (0.3)	0.89 N.S.
Level Attack	1.2 (0.6)	-1.1 (0.5)	3.11 P[0.01
Wave Reach	1.0 (0.2)	0.3 (0.3)	1.34 N.S.
Overall Rating	-0.1 (1.2)	-0.6 (1.2)	0.29 N.S.
N	140	172	

1982 site quality:

	1982 site retained from 1981	Site to which Shag moved in 1982	T-value
Ledge Size	1.8 (0.9)	3.0 (0.9)	0.80 N.S.
Damp	1.3 (0.6)	1.0 (0.5)	0.40 N.S.
Level Attack	1.0 (0.5)	-0.6 (0.5)	2.15 P[0.05
Wave Reach	0.9 (0.4)	0.2 (0.4)	1.06 N.S.
Overall Rating	5.0 (1.1)	3.6 (1.1)	0.93 N.S.
N	146	180	

1 S.E. in parentheses.

scores for birds which changed sites. It was, however, possible to compare 1981 nest scores for Shags which, in 1982, had moved to sites previously occupied in 1981; similarly, it was possible to compare 1982 nest scores for birds which, in 1982, had moved from sites taken over by other individuals in 1982: in both situations, the 1981 and 1982 sites for Shags which changed had been scored for site quality within the same year. Table 9.5 shows that the mean overall rating of the second site was slightly lower (1981 score) or higher (1982 score) than the mean rating of the original site. The differences were not significant, and the mean scores of the component variables showed no obvious pattern. As regards the behaviour of the individuals, 33 out of 93 Shags improved their overall site rating by changing (35%), compared to 40 which moved to sites of worse quality (43%), according to the 1981 scores. The equivalent figures from the 1982 scores were 47% and 44% (based on 126 individuals). Again, no pattern emerged.

In view of the age-related differences in Section 9.2, it might be expected that inexperienced Shags would improve their site quality most. Site quality scores were available for only nine marked individuals aged two in 1981. The mean change in overall site quality was 1.5 ± 7.0 (1981 scores) and 3.0 ± 4.7 (1982 scores). In both cases, these showed stronger improvements than the means for all individuals (-0.5 and 1.6 respectively, from Table 9.5), but again they did not differ significantly from zero.

It may be that the conditions imposed by the need to compare site quality scored within the same year for birds which changed sites were too restrictive to allow any convincing trend to emerge: sample sizes were small, birds which pioneered new sites were excluded from the 1981 analysis, and those whose old sites remained unoccupied were excluded from the 1982 analysis.

Table 9.5 A paired comparison of mean site quality scores of 1981 and 1982 nest-sites for ringed Shags which changed sites between years; nest-site quality scores were not directly comparable between years, so only nests scored within the same year have been compared (see text).

Sites scored in 1981:

	1981 site	1982 site	N	Paired t
Ledge Size	1.1 (1.7)	0.5 (1.4)	93	0.25 N.S.
Damp	-1.0 (0.3)	-1.0 (0.2)	93	0.00 N.S.
Level Attack	-1.9 (0.7)	-1.5 (0.7)	93	0.41 N.S.
Wave Reach	0.2 (0.5)	0.0 (0.5)	93	0.38 N.S.
Overall Rating	-1.6 (1.7)	-2.1 (1.4)	93	0.20 N.S.

Sites scored in 1982:

	1981 site	1982 site	N	Paired t
Ledge Size	2.9 (1.1)	3.7 (0.9)	126	0.82 N.S.
Damp	0.1 (0.7)	1.1 (0.6)	126	1.13 N.S.
Level Attack	-0.4 (0.6)	-1.0 (0.6)	126	0.81 N.S.
Wave Reach	-0.5 (0.6)	-0.1 (0.6)	126	0.53 N.S.
Overall Rating	2.1 (1.4)	3.7 (1.3)	126	1.02 N.S.

1 S.E. in parentheses.

9.5 Nest-site quality and the re-occupation of sites.

A more general way of examining site tenacity in relation to site quality was to compare re-occupied sites with those which were not re-occupied. Section 6.4 showed that three-quarters of sites occupied in one year were re-occupied in the next, suggesting that such sites were on average of better quality than those which were abandoned. This was tested by classifying 1981 nest-sites into three types: 1) those not re-occupied in 1982, 2) those re-occupied in 1982 but not in 1983, and 3) those used in all three years. All variables showed significant differences in mean scores between types (Table 9.6). The overall rating showed that mean quality was lowest for sites not re-occupied after 1981, and highest for sites occupied in all three years. Amongst the component variables, Damp and Wave Reach behaved in the same way. Mean Ledge Size scored slightly worse for sites occupied in 1981-1982 than for sites only occupied in 1981 (t=0.35 N.S.), but the mean scores for both these categories of sites were significantly lower than those recorded for nests occupied in all three years (t=2.06 df=649 P[0.05 and t=2.23 df=728 P[0.05 respectively). The mean score for Level Attack was slightly better at sites occupied in 1981-1982 than at ones occupied three years running (t=0.60 N.S.); both values were significantly better than the mean for sites occupied only in 1981 (t=4.34 df=281 P[0.001 and t=4.95 df=728 P[0.001 respectively). Considering all variables, this meant that site quality was on average greater for sites occupied during the three years of the study than for those abandoned after one or two years, and that it was lower for sites abandoned immediately after the first year than for those occupied for another year at least.

Although certain of the birds on sites abandoned after one or two years may have died, the high survival rate of Shags entails that a majority of

Table 9.6 A comparison of mean quality scores for three categories of 1981 nest-sites: ones not re-occupied in 1982, ones occupied in 1982 but not in 1983, and ones used in all three years.

	1981 only	1981-1982	1981-1983	F-value
Ledge Size	-1.9 (1.4)	-2.8 (1.8)	1.2 (0.5)	5.06 P[0.01
Damp	-1.6 (0.3)	-0.9 (0.6)	0.7 (0.3)	10.91 P[0.001
Level Attack	-2.4 (0.6)	0.5 (0.6)	0.7 (0.3)	13.77 P[0.001
Wave Reach	-1.1 (0.5)	-0.2 (0.5)	0.4 (0.2)	5.96 P[0.01
Overall Rating	-7.0 (1.5)	-3.4 (1.9)	2.9 (0.6)	25.87 P[0.001
N	181	102	549	

1 S.E. in parentheses.

them will have changed sites. In contrast, Section 6.4 showed that two-thirds of re-occupied sites were held by the same male, usually accompanied by the same female (Section 6.6). Thus the majority of re-occupied sites were sites retained by the same pair. The differences in site scores between different site categories (Table 9.6) provides supporting evidence that birds keeping the same site in successive years were in possession of better sites than birds which moved.

In a similar fashion, 1982 nest-sites were classified into four types: 1) sites occupied for the first and only time in 1982, 2) sites occupied in 1981 and 1982 only, 3) sites occupied for the first time in 1982 and used also in 1983, and 4) sites used in all three years. All variables again showed significant differences between types (Table 9.7). In particular, the sites occupied throughout the three years of the study were of higher quality, on average, than the other sites with respect to all variables (significant for all except Damp - Table 9.7a). This matched the results from the 1981 dataset. A comparison of sites abandoned after 1982 (first and second types) with ongoing sites (third and fourth types) showed that the latter were of better quality than abandoned sites, again with respect to all variables (all differences significant - Table 9.7b). As in the 1981 dataset, this indicated that Shags were moving from poor quality sites and holding onto good ones.

Section 6.4 showed that birds which changed site moved preferentially to formerly occupied ('established') sites, suggesting that the quality of such sites was higher than that of 'new' sites (ones not previously used by Shags). A comparison of 1982 sites which were and were not occupied in 1981 (types 1 and 3, 2 and 4 respectively) confirmed that this was true, with established sites scoring better, on average, than new sites for all variables (significant for the overall rating and Level Attack - Table

Table 9.7 A comparison of mean quality scores for four categories of 1982 nest-sites: ones occupied only in 1982, ones occupied in 1981 and 1982 only, ones occupied in 1982 and 1983 only, and ones used in all three years.

	1982 only	1981-1982	1982-1983	1981-1983	F-value
Ledge Size	-2.6 (1.2)	-1.1 (2.0)	0.5 (0.9)	1.0 (0.5)	3.53 P[0.05
Damp	-1.0 (0.7)	-1.9 (1.1)	0.5 (0.6)	0.5 (0.4)	2.60 P=0.05
Level Attack	-1.0 (0.5)	0.3 (0.8)	-0.5 (0.4)	0.6 (0.3)	4.22 P[0.01
Wave Reach	-0.7 (0.5)	-1.1 (0.9)	0.2 (0.4)	0.4 (0.2)	2.78 P[0.05
Overall Rating	-5.4 (1.3)	-3.8 (2.1)	0.8 (1.1)	2.5 (0.7)	12.89 P[0.001
N	239	84	269	560	

1 S.E. in parentheses.

Statistical comparisons of combinations of columns:

	Ledge Size	Damp	Level Attack	Wave Reach	Overall Rating
a) 1981-1983 x others	*	N.S.	**	*	***
b) Abandoned [1983 x Used 1983	**	**	*	**	***
c) New(1982) x Established(1982)	N.S.	N.S.	***	N.S.	***
d) 1982-1983 x 1981-1983	N.S.	N.S.	*	N.S.	N.S.
e) 1982 only x 1982-1983	**	N.S.	N.S.	N.S.	**
f) 1982 only x 1981-1983	**	*	**	*	***
g) Abandoned [1983 x 1982-1983	**	**	*	**	***

N.S.	Not significant
*	P[0.05
**	P[0.01
***	P[0.001

9.7c). Sites newly occupied in 1982 comprised those abandoned after 1982 (type 1) and those re-occupied in 1983 (type 3). The re-occupied sites were almost equal in quality to those occupied three years running: there was no significant difference in the overall rating, and although the mean scores for all variables indicated slightly lower or equal quality, the only significant difference occurred in Level Attack (Table 9.7d). In contrast, sites occupied only in 1982 scored significantly less on the overall rating than those first occupied in the same year and re-occupied in 1983; the mean scores for all component variables indicated lower quality, although significantly so only for Ledge Size (Table 9.7e). When compared to sites occupied three years running, all scores were significantly poorer (Table 9.7f).

In short, sites occupied only in 1982 were on average of poorer quality than sites occupied for the first time in 1982 and re-occupied in 1983; the quality of the latter sites approached that of the best sites (those occupied throughout the study). Referring back to Section 6.4 (Table 6.7), 56% of sites occupied only in 1982 belonged to second-year males, compared to 41% of sites new in 1982 and re-occupied in 1983. As second-year males took up their sites later than older ones, the differences in quality between the two types of site were likely to reflect the competitive exclusion of the younger birds from the better sites, as described in Section 9.3. All second-year males were new recruits, whereas most older males were birds which had already recruited, i.e. most of those occupying previously unoccupied sites in 1982 were in fact birds which had changed sites. As the quality of the new 1982 sites re-occupied in 1983, 59% of which belonged to such older Shags, was significantly higher on all counts than that of sites abandoned after 1982, i.e. sites from which Shags had moved away (Table 9.7f), it strongly suggested that Shags which moved were selecting better sites.

A purer sample of Shags which changed to a previously unoccupied site in 1982 was obtained by considering only males over two which occupied their sites before mid-April. By making use of the earlier timing of breeding in older Shags - birds likely to have bred before, and therefore likely to have changed sites - most of the new recruits were excluded. Compared to the sites occupied throughout the study (Table 9.8), all the differences between variables were small; in two cases (Damp and Wave Reach), the quality exceeded that of the continuously occupied sites; in no instances were the differences significant. Thus the birds which changed sites were moving to ones as good as the continuously occupied ones. The proportion of such newly acquired sites which were re-occupied in 1983 was correspondingly high: 77%, compared to 43% for other sites occupied for the first time in 1982 (N=678; chi-square=60.5 df=1 P[0.001). The figures from Tables 9.6 and 9.7 demonstrate that sites abandoned in the course of the study were of poorer quality than the continuously occupied ones, so that in general terms, Shags changing sites were improving the quality of their sites.

9.6 Nest-site quality and social constraints.

Potts et al. (1980) showed that over a period of nine years on the Farne Islands, mean site quality was negatively correlated with the number of sites occupied in a given year. With the number of high-quality sites in short supply, the presence of large numbers of breeding Shags forced a correspondingly large proportion of them to nest on sites of low quality. On the Isle of May, the quality ratings for 1981 and 1982 were not directly comparable (see Section 9.4), so it was not possible to examine the effects of the increase in number of nests between the two years upon mean site

Table 9.8 Mean quality scores of previously unoccupied (new) 1982 sites which were taken up by males over two before mid-April (mostly Shags which changed sites) compared to sites occupied throughout the study.

	New 1982 sites	Sites occupied 1981-1983	T-value
Ledge Size	-1.1 (1.5)	1.0 (0.5)	1.33 N.S.
Damp	0.8 (0.8)	0.4 (0.4)	0.45 N.S.
Level Attack	-0.1 (0.6)	0.6 (0.3)	1.04 N.S.
Wave Reach	0.9 (0.4)	0.4 (0.2)	1.12 N.S.
Overall Rating	0.5 (1.6)	2.5 (0.7)	1.15 N.S.
N	138	560	

1 S.E. in parentheses.

quality. Section 9.5 showed that 1982 sites which had not previously been occupied were on average of lower quality than those occupied already in 1981: this suggested indirectly that as numbers increased, mean site quality might be decreasing.

An alternative approach was to examine the relationship between site quality and nest density over different areas within a year. The coastline of the Isle of May was divided into 12 areas, each with at least 30 nests in both 1981 and 1982; the correlations between site quality and mean density, expressed as the average number of nests within a radius of 4m of a site being established (see Appendix 4), were -0.482 in 1981, and 0.314 in 1982. Neither was significant (10 df) and the two were of conflicting signs, so there was no suggestion of a trend. It appeared that, on the Isle of May, numbers of breeding Shags had not yet built up sufficiently to exhaust the availability of sites in any one geographical area. This was supported by the speed at which breeding groups of Shags were expanding and new areas were colonised, noticeable already over the three years of this study.

As described by Coulson (1971), Shags recruiting to the breeding colony seemed to need the influence of an established group of breeders to be able to breed themselves. Observations on the Isle of May showed that typically, immature Shags in their first year spent much time in and around breeding groups. Subsequently, most recruiting Shags attempted to nest within established groups - if allowed in by older birds already on their sites - or, more often, on the periphery of such groups. With the good sites already occupied, this should mean not only that new sites would be of poorer quality than established sites (as seen in the previous section), but that the range of potential sites to choose from should be greater on the outskirts of an established group than within it, and greater still away from an established group. On the hypothesis that Shags selected high quality sites when these were available to them, it would be expected that the quality of new sites would be lowest if they were situated within an established group, and highest if situated in previously uncolonised ground. Accordingly, recently occupied 1982 sites were assigned to one of three categories according to their position relative to established groups:

a) Central sites : surrounded by previously occupied sites.

b) Peripheral sites: placed on the periphery of established groups.

c) Pioneer sites : situated in previously uncolonised areas.

Areas such as the west cliffs were not included in the analysis as the range of available sites was limited, and mounting inter-specific pressure for nest ledges from Guillemots, also increasing in numbers (Harris & Galbraith 1983), complicated the situation.

Of the 436 sites assigned to the three categories, only 34 (8%) were pioneer sites; it was obvious that few Shags attempted to breed solitarily. Of the remainder, 58% were peripheral sites and 42% central sites: this illustrated the great attraction of the area within the group, and also the greater difficulty of establishing sites there compared to the edge. There was no difference in the proportions of second-year males and older males which occupied the three categories of sites (chi-square=4.45 df=2); even on pioneer sites, only 57% of males were over two compared to 46% on new sites in colonised areas. The breeding performance of inexperienced and experienced breeders according to site category is shown in Table 9.9. Within each age class, Shags nesting in colonised areas fledged similar numbers of chicks per central nest as per peripheral nest; on average, second-year males fledged 0.5 chicks/pair and older males 1.3 chicks/pair. On pioneer sites, young production doubled to 1.0 chicks/pair for two-year-old males (t=2.13 df=195 P[0.05) and increased to 2.1 chicks/pair for older ones (t=2.82 df=170 P[0.01). Clearly, at least some first-time

Table 9.9 Mean numbers of chicks fledged per pair from newly occupied sites situated within existing groups of breeding Shags, on the edge of them, or outside them (in previously uncolonised areas). Second-year males and older males are presented separately.

	2-year			Older			All Shags(*)		
	Mean	S.E.	N	Mean	S.E.	N	Mean	S.E.	N
Within	0.54	0.10	68	1.25	0.14	72	0.75	0.08	169
Edge	0.47	0.08	116	1.30	0.12	83	0.70	0.06	223
Outside	1.00	0.25	13	2.06	0.23	17	1.41	0.19	34
F-value	2.43 N.S.			4.00 P[0.05			7.47 P[0.001		

(*) Includes birds of unknown age.

breeders were able to reproduce without the influence of established breeders. Furthermore, their success paralleled that of established breeders, again suggesting that the quality of pioneer sites was greater than that of new sites in colonised areas.

The mean quality of the three categories of sites is presented in Table 9.10. The overall rating showed a highly significant difference between categories with, as predicted, central sites scoring on average less than peripheral sites, which in turn scored less than pioneer sites. Inspection of the scores of the component variables revealed that most of the difference was due to Ledge Size, which followed the same pattern as the overall rating. No other differences were significant, although the means varied in approximately the same way: central nests averaged worse for Damp than other nests, and pioneer nests averaged better for Level Attack and Wave Reach than other nests. The difference between the two extreme values of the overall rating was equivalent to pioneer sites fledging 0.11 chicks/pair more than central sites. As shown in Table 9.9, this is in fact an underestimate. The difference may be the result of individual quality: few Shags attempt to breed in isolation, and those atypical individuals which do may be of higher intrinsic quality than those which behave typically.

The data thus support the postulate of Coulson (1971), whereby the social convention of Shags typically nesting in groups resulted in a contrived shortage of good sites available to prospecting birds. The desire to breed colonially often meant that a bird would accept a poor site rather than nest in isolation on a good one, in spite of the existence of good sites outside the breeding group. Some of these would be occupied as the groups expanded. Others required one or two atypical individuals to nest in isolation in order to be occupied. In cases where good sites in uncolonised

Table 9.10 A comparison of mean quality scores for newly occupied sites situated within existing groups of breeding Shags, on the edge of them, or outside them (in previously uncolonised areas).

	Within	Edge	Outside	F-value
Ledge Size	-3.8 (1.5)	1.9 (0.8)	4.3 (1.3)	8.32 P[0.001
Damp	-2.0 (0.8)	-0.1 (0.6)	-0.9 (2.2)	1.85 N.S.
Level Attack	-0.9 (0.5)	-1.2 (0.4)	-0.1 (1.0)	0.38 N.S.
Wave Reach	0.4 (0.4)	0.1 (0.4)	1.2 (0.7)	0.56 N.S.
Overall Rating	-6.3 (1.6)	0.8 (1.1)	4.6 (2.7)	9.97 P[0.001
N	169	233	34	

1 S.E. in parentheses.

areas were clumped, this could lead to subsequent rapid colonisation of the area. On the Isle of May, an example was provided by the old wreck of a trawler, the 'Island', 50m south of Colm's Hole. The battered hull offered a multitude of dry, sheltered sites out of reach of the summer seas. In 1981, no Shags nested along the coastline between Colm's Hole and Kirkhaven (see Figure 2.2). In 1982, two pairs were found at the beginning of the season nesting inside the carcass of the wreck. By the end of the season, the total had risen to six pairs, and the average site quality was equivalent to 24 more chicks than the average number fledged by 100 nests; the corresponding value for all new sites was -3. Over the whole island, only 22 out of 1152 nests (2%) had a nest-site rating higher than the average rating of the wreck nests. In 1983, a count in mid-May revealed 14 nests, and 20 nests were present in mid-June. No nest-sites were scored for quality in 1983, so it is not possible to examine how mean quality evolved with increasing numbers of nests.

From what precedes, it seemed that colony growth in Shags proceeded along two lines: a steady expansion of existing groups of breeders as recruits were attracted to them and established themselves on the periphery, and a sporadic occupation of new, high quality sites outside the existing groups, which formed the nuclei from which new groups developed.

9.7 Discussion.

As in the animal species mentioned in the introduction, younger Shags were shown to occupy, on average, sites of poorer quality than older ones. This proved to be a consequence of the differential timing of breeding in young and old birds, rather than an inability of recruiting Shags to recognise good sites. Old Shags arrived early, occupied the best sites and thereby constrained late birds, comprising mostly young ones, to use sites of poorer quality within the breeding group. A similar mechanism appeared to act in Wheatears (Brooke 1979): older males returned early and preferentially occupied territories which provided better foraging conditions for females, thereby enabling them to lay earlier and fledge more young.

Thus individuals seem capable of recognising sites of high quality, and seek to occupy them in preference to others. For the Shag on the Isle of May, the direct evidence of this (based on a comparison of sites occupied in consecutive years by ringed individuals which changed sites) was inconclusive, owing to the small sample sizes and the need to compare quality scored within the same year. However, strong supporting evidence was provided by considering site re-occupation and large samples of unmarked individuals comprising a majority of birds which changed sites. It was found that in general, Shags which changed sites were those which had previously nested on poorer quality sites, whereas those which retained their sites owned better ones. Furthermore, birds which changed sites moved to sites of high quality, equal to that of sites continuously occupied throughout the three years of the study. Such sites scored consistently higher, with respect to all measures of site quality, than sites occupied during only one or two years of the study. Boag (1976) found that in Ruffed Grouse also, occupancy of territories was strongly influenced by their quality: prime territories, as measured by the number of display sites they contained and the status of the vegetation around those sites, were occupied continuously by a series of different birds over as many as 11 years, i.e. for the full duration of his study. Similarly in Sparrowhawks, Newton et al. (1979) noted that territories defined as high-grade on the basis of frequent occupation were in the best of the various breeding places available in the local landscape; they owed their high grading partly to individuals staying there longer than on low-grade territories, but mainly to rapid re-occupation each time an owner left or died (Newton & Marquiss 1982). Thus in the presence of habitat diversity, recognition of site quality by territorial species translated into sporadic occupancy of low-grade territories and almost continuous occupancy of the high-grade ones, resulting from the movement of individuals from low-grade to high-grade territories as soon as the latter became vacant.

The advantages to an individual of occupying high-grade habitat can be two-fold: a higher survival (Jenkins *et al.* 1963, Boag 1976) and greater reproductive success (see Chapter 8). These factors combined result in a greater lifetime reproductive output. However, in terms of species abundance, a breeding success which varies with habitat quality entails that, even if territory availability *per se* is not limiting, the restricted amount of high-quality habitat will act as a density-dependent mechanism slowing population growth.

In colonial species, this situation is complicated by the social system. The desire to breed in groups - on the Isle of May, 92% of new sites were established in or on the edge of existing groups of Shags - results in an artificial shortage of good sites. This was well illustrated in the present study, when a comparison of site quality in relation to position showed that quality was lowest for new nests established within a group, and highest for individuals nesting in isolation. The social structure evidently constrained individuals to nest on poor sites despite the availability of better sites outside the group. Presumably the disadvantages of using poor nest-sites were offset by the benefits of social breeding. As discussed by Coulson & Dixon (1979), these are considered to be of four kinds: defence against predators, social stimulation, self-regulation and transfer of information. The artificial shortage of good sites produced by the social system means that density-dependent regulation acts before good sites are exhausted. In Kittiwakes, the rate of colony growth decreased as colony size increased (Coulson 1983). In Shags, the model proposed by Potts et al. (1980) for the Farne Islands quantified the curb on colony growth resulting from a shortage of nest-sites; they calculated that growth would cease at 918 pairs. The 1983 total was 775 pairs (Hawkey & Hickling 1984), so it is still too early to verify their results. On the Isle of May, the lack of a relationship between density and site quality, the rapid expansion of existing groups and the colonisation of new areas demonstrated that overall, the shortage of sites had not yet become limiting. It will be interesting to observe how the pressure on nest-sites will develop, and what the ceiling on colony size will be for this potentially very large colony.

10. GENERAL DISCUSSION.

Many of the points raised in this study have been discussed at the end of the relevant chapters. Two points which have only been touched upon so far are the questions of population regulation and of non-breeding. They will be considered below, under separate headings.

10.1 Population regulation.

A population is understood here to be a group of organisms of the same species occupying a particular space at a particular time (Krebs 1978). In the case of the Shags on the Isle of May, the population will be regarded as the group of Shags which are either breeding on the island, or, as immatures, were reared on the island and are likely to breed there in due course; the colony is defined as those birds breeding or attempting to breed on the island. As regards the use of the term regulation, I shall follow Nicholson (1954) in considering that a population is regulated when governed by mechanisms which tend to bring it into a state of equilibrium.

Historically, there are three main schools of thought concerning the factors controlling animal populations:

a) Density-dependent factors. Density-dependent regulation was strongly advocated by Nicholson in particular (Nicholson 1933, Nicholson & Bailey 1935, Nicholson 1947, 1954, 1958), and supported by Varley (1947, 1963), Varley & Gradwell (1963) and Lack (1954, 1966). It rests on the principle that animal populations are inherently stable and, when perturbed, revert to a state of balance through density-dependent mechanisms. These mechanisms, based on competition between individuals for the essential requirements for life and reproduction (e.g. food and living space), tend to depress the population at high densities and to increase it at low densities; they act through, for instance, the reproductive rate, the survival rate, or territorial behaviour.

b) Density-independent factors. The opposite view to Nicholson was put forward by Andrewartha & Birch (1954). They proposed that density-dependent control was unimportant, because animal abundance was primarily determined by the reaction of individuals to the rigours of the environment, especially climate. The shortage of time in which to increase between one catastrophe and another was the overriding mechanism controlling numbers; the heterogeneous nature of the animal's habitat enabled pockets of individuals to survive and recolonise areas after local extinctions.

c) Homeostatic, or self-balancing factors. Homeostasis was developed by Wynne-Edwards (1962), who accepted that populations were density-dependently regulated, and considered that food was the ultimate limiting factor. However, he proposed that animals were capable of restraining themselves from over-exploiting their food resources, thus keeping their numbers at a level below that set by food. This was achieved by substituting conventional goals of competition, e.g. territorial rights or social status, for a direct contest for food.

Other theories exist. For instance, Chitty (1960) proposed that changes in abundance could result from genetic changes in the quality of individuals; Christian (1963) concluded that in higher vertebrates, crowding or "stress" could lead to physiological changes which in turn modified behaviour, reproduction or resistance to disease, with regulatory effects; Pimentel (1968) argued that evolutionary processes could control populations through interspecific interactions and the effects of genetic change in one organism upon the abundance of another ("genetic feedback"); Lidicker (1975) emphasized the role of dispersal as a means of regulating populations.

The two views of Nicholson and Andrewartha & Birch were primarily derived from studies of insects. Accordingly, they were mainly concerned with laboratory or field studies of populations as a whole rather than with the behaviour of individuals; the importance of the latter was stressed by Wynne-Edwards. The applicability of density-dependent theories to vertebrates, and in particular birds, was considered by Lack (1954). Starting with the observation that animals generally fluctuate in numbers between very restricted limits compared to what was in theory possible, he deduced that all populations must be regulated by density-dependent factors. From the available evidence, he decided that the main density-dependent control of numbers probably came from variations in the mortality rate, caused by food shortage, predation or disease. In most species, the most important factor was likely to be food shortage outside the breeding season, acting especially on juveniles.

A study of tropical seabirds led Ashmole (1963) to suggest that food shortage during the breeding season rather than during the winter could be important in controlling numbers. Outside the breeding season, seabirds were free to seek food over the entire ocean, whereas when breeding they were constrained to stay within the vicinity of their nesting areas. A large concentration of birds in one area could lead to a local depletion of food in the surrounding sea, resulting in poor breeding success and a decrease in population size through lack of recruitment. Another possible regulatory factor, stressed by Rowan (1965), was the availability of nest-sites: saturation would place a ceiling on young production, and eventually on population size.

How do the mechanisms described above relate to the Shag on the Isle of May? First of all, the early history of the Shag colony on the Isle of May shows that, in the past, the population was certainly regulated. Throughout the 19th century, the colony remained at around two or three pairs, before starting to increase in the 20th century (Rintoul & Baxter 1935). Similar temporal patterns in changes in abundance were observed for other seabirds around the British Isles, and are well documented for e.g. Fulmars, Gannets and Kittiwakes (Cramp et al. 1974). The reasons most often put forward to explain the change from a small stable population to a rapidly increasing one are a reduction in human persecution, and changes in natural factors such as food supply. Fisher (1952) argued that the expansion of the Fulmar was caused by the new food supply provided by offal from whalers and trawlers, although Wynne-Edwards (1962) regarded the correlation between the available offal and the spread of the Fulmar as weak, and proposed that a genetic change was more likely. As regards the Gannet and the Kittiwake, Nelson (1978) and Coulson (in Cramp et al. 1974) were convinced that human persecution and exploitation, particularly during the 19th century, had depressed numbers to a very low level, from which they were recovering after protective legislation and appropriate conservation measures. Rae (1960) used the same argument to explain the recent increase in numbers of Grey Seals around the British Isles. It is also the most likely explanation for the Shag: numbers of Shags were originally so low along the east coast of Britain that food shortage as a limiting factor was effectively ruled out (Potts 1969). The protection hypothesis is attractive because the increase of the Shag took place concurrently with that of the Gannet, Kittiwake, Herring Gull, Great Skua, Eider Duck and Grey Seal, beginning as soon as protection was afforded at the end of the last century or at the beginning of this one. The relaxation of hunting pressure removed the regulatory factor which had maintained numbers of all these species at a low level; the response was a rapid increase in numbers which, in the Shag on the Isle of May, averaged 15% per annum from the beginning of this century until 1973.

The question arises as to whether a population which apparently increases exponentially can be considered to be regulated. Obviously, if the increase is truly exponential, the answer is no. However, the initial stages of an exponential increase are very similar to the initial stages of a sigmoid increase, which typically describes a regulated process (e.g. Krebs 1978). The reason is simply that at numbers far below equilibrium, the effects of density-dependent mechanisms are minimal; they will be felt more and more strongly as population size approaches equilibrium. In order to determine whether or not a population is regulated, particularly after numbers have been depressed to a very low level, it is necessary to consider growth over a time-span long enough to show a change in the rate of increase. The increase in the number of Shags on the Isle of May, from only a few pairs at the turn of the century, is a good illustration of this problem. The rate of increase remained approximately constant for 56 years, from 1918 to 1973, so that the time-span needed to reveal the presence or absence of density-dependent effects could be of the order of 100 years or more.

The crash in breeding pairs observed between 1974 and 1976 suggested that the population might be limited a lot sooner. The delayed timing of breeding, the large proportion of non-breeding adults, the low breeding success and post-fledging survival of chicks, as well as the available evidence on fish stocks, all point towards food as having been insufficient in those years. Although the adult mortality rate remained unaffected, the near-total lack of recruitment in 1978, resulting from a negligible input of young Shags into the Isle of May population during the crash years, produced an overall drop in colony size which reflected the drop in population size. Food shortage was thus shown to be potentially capable of limiting the Shag population, by acting not during the winter as suggested by Lack (1954), but during the summer as proposed by Ashmole (1963). The question remains as to whether the events on the Isle of May at that time were truly density-dependent. Characteristically, density-dependence would lead to a damped oscillation around the level where numbers and food supply balanced. The renewed increase of the Shag on the Isle of May after 1978, at a similar annual rate to the pre-crash situation, belies that such was the case. It suggests rather an irregularity in the normally rich marine environment in the same way that off the Peruvian coast, temporary oceanographic changes produce a drastic reduction in prey availability for the guano birds (e.g. Vogt 1940, Jordán & Fuentes 1966). Under these conditions, fluctuations in population size are caused by changes between favourable and very poor feeding opportunities, i.e. of a nature typically assigned to density-independent factors, sensu Andrewartha & Birch (1954).

In the Shag, Potts (1969) proposed that such density-independent mechanisms also explained the eruptive behaviour of the Farne Islands population in certain winters: food shortage, caused by prolonged turbulence from onshore gales rather than by depletion of food stocks, resulted in abnormal dispersal of Shags, especially juveniles, away from the colony. Eruptions are also well documented for other bird species such as Waxwing, Crossbill and Nutcracker. The evidence reviewed by Lack (1954) showed that these species usually move in response to food shortage, particularly in years of bad seed-set or poor fruiting. In big eruptions, the proportions of juveniles were particularly high, suggesting that some eruptions acted as a safety-valve to relieve overpopulation resulting from an unusually successful breeding season (Lack 1954, Wynne-Edwards 1962). In Norwegian Lemmings, spectacular emigrations occur during exceptionally high peaks in density (Elton 1942), and in locusts, intense population pressure leads to morphological and behavioural changes resulting in mass emigration by swarming (Key 1950). Eruptions are usually associated with mass mortality, and Potts (1969) found that first-year mortality of Farne Islands Shags increased in eruption years. This study showed that 1965, a notorious eruption year for Shags on the Farne Islands, was a year of very poor first-year survival on the Isle of May as well.

Superficially, the high and variable mortality of young Shags (on average 51% as opposed to 13% for adults, with a range of 11% to 75% - see Chapter 4), most of which occurred before the following breeding season (Galbraith et al. 1981) concurred with Lack's hypothesis that avian populations were predominantly regulated by juvenile mortality during the winter. However, Lack relied on density-dependent competition for diminished winter resources to achieve the extra mortality. In the case of seabirds which disperse from the breeding area and cover a large expanse of sea at a low density, it is difficult to visualise how competition for food can take place. As the explanation of eruptive behaviour suggests, it seems more likely that juvenile inexperience, coupled with variable feeding conditions dependent upon climate, constitute the main source of mortality. Again, this effect cannot be considered density-dependent.

Climate also acts upon experienced birds. In many species, timing of breeding is, for instance, related to temperature (Murton & Westwood 1977) or snow melt (Belopol'skii 1961, Barry 1962). In Chapter 4, a temperature-based climatic factor in March was found to correlate with the timing of breeding in Shags. Late breeders were also found to fledge fewer chicks than early ones (Chapter 5), with only part of the difference due to differences in the quality of individuals (Chapter 7); the remainder was possibly caused by a factor such as seasonal change in food availability. Climate early in the year thus brought about a reduction in overall young production. A similar effect, later in the season, was that of rainfall upon brood size, with chicks being lost from exposure in damp summers (Chapters 5 and 8). In contrast, a harsher example of climatic effects upon breeding Shags was given by the gale which struck the island in May 1982 (Chapter 7). In spite of lasting only three days, its effects upon the colony persisted for the rest of the breeding season: compared to the unaffected east side, breeding success was down by a quarter on the west side of the island, and recruitment of second-year males reduced by a third. Again, these climatic factors are obviously independent of the numbers of Shags breeding on the Isle of May. Furthermore, although they may momentarily check or encourage reproductive output, their long-term effect on the population of a long-lived species like the Shag is minimal.

The factors acting upon the Isle of May Shag population which have been considered so far are density-independent rather than density-dependent. On the Farne Islands, Coulson (1971) found that the quality of the nest-site was an important factor affecting the breeding success of the Shag. As top-quality sites were in short supply, the increasing size of the colony entailed that more and more Shags were forced into nesting on inferior sites (Potts _et_ _al_. 1980). Here was clearly a density-dependent factor at work, reducing the output of young as the colony grew and therefore theoretically halting its growth eventually through lack of recruitment. Unfortunately, it is yet too early to test this prediction as colony size on the Farne Islands is still beneath the predicted maximum. On the Isle of May, the quality of the nest-site was also found to have a direct bearing upon chick production in the Shag, and acted by reducing or increasing susceptibility to climatic conditions and to other Shags (Chapter 8). Clearly, on both the Farne Islands and on the Isle of May, a high-quality site was an asset defended by the pair in occupation, and not a conventional trophy as propounded by Wynne-Edwards (1962). However, this study showed that despite the availability of high-quality sites in parts of the Isle of May as yet unoccupied, many Shags, particularly young ones, were preferentially occupying sites of poorer quality situated in areas which were already colonised. Such Shags appeared to be breeding suboptimally and, by thus reducing the overall growth of the colony, apparently supported the theory of group selection.

The alternative is to examine how this behaviour could benefit the individual. Self-regulation apart, the benefits of social breeding lie in enhanced defense against predators, transfer of information or social stimulation (Coulson & Dixon 1979). Although adult Shags on the Isle of May are free from predators, species such as White-tailed Eagles and Great Skuas have been known to prey on Shags (Willgohs 1961, Furness 1978). There is considerable evidence to show that groups of individuals, from fishes to large mammals, are more successful at detecting or deterring predators than isolated pairs or individuals (e.g. King 1955, Carl 1971, Birkhead 1977, review by Bertram 1978). Such advantages could have shaped the social structure of the Shag through evolution even though the pressure of predation on the Isle of May is momentarily relaxed. Ward & Zahavi (1973) postulated that breeding colonies and other gatherings act as information centres for the efficient exploitation of unevenly distributed food. For instance, colonial nesting by Brewer's Blackbirds is primarily an adaptation to a variable food supply (Horn 1968), and Krebs (1974) found that in the Great Blue Heron, colonial nesting and social feeding were adaptations concerned with finding food. As Shags are essentially solitary feeders, though, it is unlikely that their colonies have this function. Darling (1938) suggested that colonial breeding enhanced the performance of the individual through social stimulation. For Barbary Doves under experimental conditions, the stimulation from the colony was capable of accelerating reproductive condition over and above that induced by daylength and interaction with the mate (Lott et al. 1967). Social stimulation has also been reported as affecting timing or synchronisation of breeding in the Kittiwake (Coulson & White 1960) and the Gannet (Nelson 1978); an increase in stimulation caused by the expansion of the colony enabled young Gannets to breed a year earlier than usual. Both Kittiwake and Gannet are obligate colonial breeders, in which recruits do not even attempt to breed in isolation. In the Shag, the vast majority of recruits nest within or on the edge of existing groups of breeders: presumably most require stimulation by other breeding pairs in order to reproduce successfully, although Chapter 9 showed that certain second-year males, apparently nesting in isolation, succeeded in fledging young. Most such birds were paired with older females, and were at least within sight or earshot of breeding groups of Shags, with which they associated on the water; perhaps significantly, the only known pair of two-year-old Shags which attempted to breed totally out of range of other Shags failed to lay at all, despite the construction of a bulky nest. If, as birds age, the need for stimulation grows less, they would become free to upgrade their sites. In general, Shags which changed site tended to move to sites of better quality (Chapter 9), and Shags breeding for the first time also changed site more frequently before breeding again in the following year (Chapter 6). Certain individuals might then colonise new ground as they moved to high-quality sites; Chapter 9 showed how pioneering provided a mechanism of colony growth other than mere expansion of existing colonised areas, and Nelson (1978) stressed the role of pioneers as an adaptive mechanism in maintaining the success of a species. Overall, the most likely benefits to the Shag of colonial breeding are therefore protection from predators and social stimulation; these factors could explain the relationship between site availability and site occupation in Shags without having recourse to the arguments of Wynne-Edwards.

To summarise, the population of Shags on the Isle of May is currently in a state of rapid increase, with density-dependent controls apparently relaxed. Regulation certainly occurred during the last century, probably through predation (human exploitation and persecution). In the future, two factors are potentially regulatory: food supply during the breeding season, the importance of which was demonstrated by the crash, and a decline in nest-site quality, which was shown to occur at high densities on the Farne Islands. Other, density-independent, factors which affect numbers of Shags only in the short term are climate, acting upon recruitment, chick production and juvenile mortality during the winter, and abnormal fluctuations in fish stocks, which induce adult non-breeding as well as acting upon the same features as climate.

10.2 Non-breeding.

The analysis of the crash in 1974-1976 revealed that up to 60% of experienced adult Shags refrained from breeding, in all likelihood because of food shortage. Such behaviour is aberrant in the Shag: non-breeding by adults was not detected during over ten years of studies on the Farne Islands, and, on the Isle of May, the high recapture rate in 1982 of Shags known to be alive in 1981, 87.0%, was so close to the adult annual survival rate of 87.4% that it precluded non-breeding on the island in 1982.

The direct link between the environment, particularly food supply, and breeding performance was emphasized by Drent & Daan (1980). The crudest level for the role of food in reproductive performance concerns the bird's decision whether to breed or not. Bertram et al. (1934) observed that few arctic predatory species attempted to breed in bad lemming years; the same was true of owls (Southern 1970, de Bruijn 1979) and other raptors (Newton 1979) in years of rodent scarcity. The existence of some threshold value of body condition for breeding to be attempted has been hinted at for arctic geese (e.g. Barry 1962, Ryder 1970), and demonstrated for Red-billed Queleas (Jones & Ward 1976). Antarctic species such as King Penguin and Grey-headed Albatross have evolved biennial breeding cycles which are believed to be due to energetic constraints on birds which feed predominantly on squid, of low calorific value (Croxall 1983, Prince in press). Non-breeding also appears to be a regular feature of other seabird species (Vogt 1940, Belopol'skii 1961, Fisher 1969, Nelson 1978), and Wooller & Coulson (1977) showed that in Kittiwakes, non-breeding occurred predominantly in young birds, after the first breeding attempt. The threshold hypothesis is consistent with the fact that young birds, being less efficient at feeding (see Chapter 5 for examples) require more time to rebuild body reserves after breeding. As foraging efficiency increases over several years, it also provides an explanation for the deferred maturity observed in many species, with efficient individuals breeding sooner than inefficient ones (Ashmole 1963).

An interesting comparison of the incidence of non-breeding can be drawn between the Shag and the Eider Duck. These species are sympatric over much of their range, and are therefore subject to the same climatic stresses. They are both long-lived seabirds, whose young exhibit deferred maturity for approximately two years (Cramp & Simmons 1977). However, the proportion of adult ducks which nest in any one year is highly variable, ranging from 100% to 35%, with non-breeding occurring in practically every year (Coulson 1984). This is in sharp contrast to the Shag, where non-breeding was shown to be exceptional. The reason for this difference probably lies in the cost of breeding. Eider Ducks lay relatively large eggs, and the average clutch size of 4.4 eggs corresponds to 25% of the female body weight before laying; incubating females pass the whole of incubation without feeding (26 days), and lose on average 40% of their body weight during this period (Milne 1974). The cost of breeding is therefore high. In Shags, the eggs are small, the total clutch (3.1 eggs) averages less than 10% of female body weight, incubation is shared with the male, and feeding proceeds normally (Snow 1960, 1963): the cost of breeding is much lower than in the Eider Duck. The differences in frequency of non-breeding in the two species, from common to exceptional, is as would be predicted from the threshold hypothesis. Species subject to high breeding costs would require higher reserve levels to even attempt to breed; this higher threshold would be achieved less often, and non-breeding would thus be more prevalent, then in species with low costs of breeding and low thresholds. In Eider Ducks (Milne 1974) and in arctic geese (Ankney & MacInnes 1978), an attempt to breed when body condition is poor may result in the death of the individual. In such species, non-breeding is therefore an important adaptation to overcome the considerable strains of reproduction; in the Shag, it seems rather that it acts as a safeguard against severe conditions. In both cases, the different thresholds of body condition required for survival and for breeding act as a buffer protecting the individual against environmental fluctuations. The result is a trade-off between survival and breeding performance, ensuring that if the individual does not breed in one year, at least it has a strong chance of surviving to breed in a later year. Obviously, this can only apply to relatively long-lived species. A Starling, for instance, with an annual survival rate of 47%, has a less than even chance of surviving to the following breeding season (Coulson 1960). Accordingly, the species in which non-breeding has been reported, such as those mentioned earlier, have an annual adult survival rate of at least 75%, and as high as 97% for the biennially breeding albatrosses (Croxall 1982).

The corollary to the threshold hypothesis is that, when non-breeding is taking place, those individuals which do breed are those which have been able to build up their condition above the threshold, i.e. the more efficient members of the population. Having achieved breeding condition, it appears worth while attempting to breed even when, as for the Shag on the Isle of May during the crash, only 0.1 chicks/pair survived on average to breeding age (Chapter 4). This figure represented a quarter of the normal value, but - assuming that reproduction did not affect subsequent survival, as suggested by the constancy of the adult annual survival rate - it still meant that the members of one pair out of 10 successfully increased their reproductive fitness. Typically, reproductive success was also very low for breeding Eider Ducks, with only 5% of ducklings normally fledging (Milne 1974). In the presence of non-breeding, the individuals which do breed, being more efficient, are likely to be the older, experienced birds. Thus the mechanism underlying the threshold hypothesis may act in determining age of breeding, timing of breeding and frequency of breeding; it is linked ultimately to food supply, measured both in terms of absolute abundance, and in terms of the ability of the individual to exploit it.

One of the main features which has come out of this study is the importance of the food supply in shaping the breeding biology and population dynamics of the Shag. At the same time, this is an area where relatively little is known about seasonal variation in abundance and quality of different prey species of fish, so that many of the conclusions drawn on the basis of the behaviour of the birds must be tentative. The most obvious way of overcoming this difficulty is for greater collaboration between seabird and fisheries biologists. The recent Young Fish Surveys organised by ICES (Hislop 1979, Holden 1979) are a first step towards building up a detailed map of fish abundance in the North Sea. It is hoped that these surveys signal the start of a future period of joint investigations, leading eventually to the elucidation of the complex interrelationships between a species and its environment.

APPENDIX 1

Identification of age classes in the Shag by plumage.

The following account is drawn from Cramp & Simmons (1977) and Baker (1981), based on Potts (1971) and Bauer & Glutz (1966).

Juvenile:	Underparts pale brown becoming paler towards foreneck, chin almost white. Upperparts and flanks dark brown with faint green gloss, feathers of mantle and scapulars edged dark brown.
1st summer:	Hind neck feathers darker than juvenile with faint green gloss. Back mostly black with green gloss, some bleached wing-coverts and scapulars. Underparts darker brown than juvenile.
2nd summer:	Upperparts and wing coverts black with green gloss, some worn brown immature feathers on wing-coverts. Underparts typically black with green gloss from chin to lower breast, dark brown on belly and vent. Neck with some old brown feathers. Outer primaries sometimes very worn and bleached.
3rd summer:	Similar to adult, occasionally worn brown immature feathers on underparts and wing-coverts.
Adult:	Black strongly glossed metallic green on body, blue-green on head and neck. Dull black primaries and tail. Crest in early spring.

APPENDIX 2

Descriptions of five external characters recorded in Shags, of potential interest in identifying third-year birds.

a) Pale Toe Strips

In most adult Shags, the feet are dull black all over. The colouration is gradually acquired with age. In juveniles and first-year birds, the toes are brown with pale flesh-brown sides and webs; in second-year birds, the feet are typically dull black with broad and conspicuous pale strips along the sides of the toes and the webbing. This colouration is sometimes found in an attenuated form in a full adult, and described here as 'pale toe strips'.

b) Brown Marginal Coverts

In most adult Shags, the marginal coverts (coverts situated on the leading edge of the wing) are black with a green gloss. In some individuals however, one or more of the marginal coverts may show a pale brown edging similar to that of unmoulted juvenile wing coverts found in second-year birds.

c) Mottled Underparts

Between their second and third year, Shags moult out their dark brown belly and acquire full adult plumage. Baker (1981) mentions that third-year birds retain the dark brown feathers around the abdomen and vent, but none of the individuals of known age examined on the Isle of May have shown this feature. However, close examination of the ventral plumage of adult birds showed that some individuals lacked the deep green-black gloss normally found in adults; the gloss was sparse and restricted to the tips of the feathers, and in places the tips of dark brown feathers were showing through, giving a mottled appearance to the underside. This mottling was visible in the field at a distance of 5 to 10m, further in good light conditions.

d) Unmoulted Primaries

According to Potts, 2 to 4% of third-year birds retain one or both of their juvenal 10th primaries. Any unmoulted brown or bleached primary in an adult bird was therefore noted. These were predominantly the 10th primary, sometimes the ninth, and occasionally the sixth or fifth.

e) White Throat

In some birds the feathering at the top of the throat, round the base of the yellow and black gular skin, was off-white instead of black. Although not a characteristic of second-year birds, this too was recorded as being of possible use in ageing.

APPENDIX 3

Numbers of Shags ringed in the Forth-Farnes area from 1961 to 1983 (monel rings).

	Isle of May		Bass Rock		Craigleith		The Lamb		St Abb's		Farne Islands	
	Ad	Ch	Ad	Ch	Ad	Ch	Ad	Ch	Ad	Ch	Ad	Ch
1961	0	0	10	44	0	0	0	0	0	0	47	301
1962	1	92	32	64	0	0	0	0	0	0	55	297
1963	0	377	13	37	0	0	0	0	0	0	48	328
1964	1	137	20	39	0	0	0	0	0	0	26	358
1965	45	398	6	46	0	0	0	0	0	0	60	442
1966	15	193	4	26	0	0	0	0	0	0	26	393
1967	64	566	5	25	0	16	0	3	0	0	38	376
1968	21	751	15	18	0	6	0	0	0	0	1	44
1969	2	610	0	0	0	0	0	0	0	0	4	177
1970	7	462	1	15	0	0	1	75	0	3	15	219
1971	94	457	27	44	0	13	11	144	0	6	7	281
1972	49	723	0	0	0	26	8	192	0	21	0	102
1973	51	423	6	3	11	76	20	181	0	29	0	220
1974	119	115	0	0	22	42	36	177	0	50	0	266
1975	5	68	2	0	11	6	23	98	0	0	3	78
1976	39	334	0	2	4	2	23	0	0	14	26	298
1977	4	278	0	0	1	7	18	17	0	0	0	115
1978	59	311	0	0	0	0	0	0	0	0	3	197
1979	116	343	0	0	8	29	0	0	0	0	3	266
1980	91	763	0	0	8	87	0	0	0	0	0	402
1981	170	620	0	0	10	96	0	0	0	0	0	547
1982	132	993	0	0	11	66	0	0	0	0	0	530
1983	173	936	0	0	-	-	0	0	0	0	2	548

Ad: Shags ringed as breeding adults   Ch: Shags ringed as chicks.

The figures for the Isle of May were derived from the ringing records of the Isle of May Bird Observatory; those for the Farne Islands were provided by the Natural History Society of Northumbria. The numbers of birds marked at the other four sites were extracted from the ringing records kept by the British Trust for Ornithology.

APPENDIX 4

Descriptions of nest-site variables defined in this study.

A total of 28 nest-site variables were measured. Variables 1 to 19 were scored on an ordinal scale, ranging from 1 to 2, 1 to 5, 1 to 8, or 0 to 8. The descriptions of all 28 variables and the features characterising each point on the ordinal scale for variables 1 to 19 follow below.

1. Protection from the Sea

The variable was quantified mainly by direct observation during periods of swell or storms. The wind regimes were different in 1981 and 1982, when, in the latter year, a combination of spring tides and gale force winds destroyed a third of the nests on the west side of the island (see Chapter 7). As a result, the measure of protection from the sea changed from one year to the next for certain nests.

Scale: 1 No protection, washed away at least once.
2 Within reach of high waves.
3 Within reach of spray and very high waves.
4 Rare spray, out of reach of waves.
5 Fully protected: no spray, totally out of reach of sea.

2. General Topography

This variable described the general aspect of the coastline where the nest was situated.

Scale: 1 Flat area.
2 Gentle to medium slope.
3 Low cliff ([10m) or steep slope.

4 Cliff of medium height (10-20m).

5 High cliff (20m or more).

3. Local Topography

This variable described the topography directly in front and beneath the nest-site (as seen by looking forward and down from the nest).

Scale: 1 Flat area.

2 Gentle to medium slope.

3 Low cliff ([8m) or steep slope.

4 Cliff of medium height (8-15m).

5 High cliff (15m or more).

4. Gully

Scale: 1 Exposed to the open sea.

2 At the entrance to a gully, or on a stretch of coast where the wave action was slightly mitigated.

3 In a gully, but less than 20m from the sea, or on a stretch of coast protected from the sea by a string of islets.

4 At the back of a deep gully, or in a gully parallel to the sea and separated from it by a body of land not submerged under high waves.

5 Up a dry gully.

5. Proximity to Cliff Edge

This variable described the ease with which a disturbed bird could escape into the sea.

Scale: 1 On a more or less flat area far from the cliff edge; at least two nests to pass to reach the sea.

2 On a shallow slope with no marked edge; a nest to pass to reach the sea.

3 Over 1m from the nearest cliff edge overlooking the sea, or on a poor ledge on a slope, or with a nest to pass.

4 0.5m to 1m from the nearest cliff edge overlooking the sea.

5 By a well-marked cliff or ledge edge overlooking the sea.

6. Overhang

Scale: 1 No overhang above the nest.

2 A slight overhang, or nest placed against a high vertical cliff.

3 An overhang high above the nest, or a low one sheltering approximately half the nest, or nest placed down a cleft open to rain.

4 A complete overhang above the nest.

5 Nest situated in a cave or cleft fully sheltered.

7. Ledge Size

This variable referred to the size of the ledge and not to the size of the nest itself. It was not unusual for the nest to disintegrate after the chicks had reached a certain size and started to move around, so Ledge Size measured the amount of space available to hold the chicks in such a situation. It also took into account the mobility of the chicks; thus a small ledge extending back to the top of the cliff scored 5.

Scale: 1 Too small to hold one large chick and a parent.

2 Adequate for one large chick and a parent.

3 Adequate for two large chicks and a parent.

4 Adequate for three large chicks and a parent.

5 Plenty of room for four large chicks and both parents.

8. Damp

This variable was recorded after observing the state of nests after a downpour, and by examining the paths taken by water from run-off or seepage. As 1981 was dryer than 1982, certain nests were recorded differently in the two years.

Scale: 1 Waterlogged, with bad to no drainage of rainwater.
2 Wet during rain, poor drainage.
3 Wet during rain, good drainage.
4 Occasionally wetted by rain or run-off.
5 Dry at all times.

9. Immediate Exposure

This variable measured the exposure of the nest in a horizontal plane, relative to the shelter given by the immediate nest backing.

Scale: 1 0 to 45 degrees.
2 46 to 90 degrees.
3 91 to 135 degrees.
4 136 to 180 degrees.
5 181 to 225 degrees.
6 226 to 270 degrees.
7 271 to 315 degrees.
8 316 to 360 degrees, fully exposed.

10. Driving Exposure

This variable measured the exposure of the nest in a horizontal plane in conditions of driving rain and wind, taking into account the shelter given by the surrounding topography.

Scale: 1-8 As for Immediate Exposure.

11. Departure Angle

This variable measured the angle in a horizontal plane between the aspect of the nest and the direction to the sea. It represented the ease with which a bird could fly from its nest to the sea.

Scale: 1 0 to 22 degrees, nest facing the sea.

2 23 to 45 degrees.

3 46 to 67 degrees.

4 68 to 90 degrees.

5 91 to 112 degrees.

6 113 to 135 degrees.

7 136 to 157 degrees.

8 158 to 180 degrees, U-turn to reach the sea.

12. Sea View

Measurements were taken from the point of view of a bird sitting on its nest.

Scale: 1 No view of the open sea from the nest.

2 Open sea in view from the nest.

13. Attack from Above

This variable described the arc through which a nest could be attacked from above by another Shag.

Scale: 0 Inaccessible from above.

1-8 As for Immediate Exposure.

14. Level Attack

This variable described the exposure of the nest to attack by birds at the same level as the nest.

Scale: 0 Inaccessible from a point level with the nest.
1-8 As for Immediate Exposure.

15. Attack from Below

This variable described the degree of exposure to birds attacking from below.

Scale: 0 Inaccessible from below.
1-8 As for Immediate Exposure.

16. Overall Attack

This variable was the sum of values from the three previous variables, and measured the overall vulnerability of a nest to attack by other Shags.

Scale: 0 Inaccessible to attacking birds.
1-8 as for Immediate Exposure.

17. Human Accessibility

Scale: 1 Of easy access, could walk up to nest, no climbing involved.
2 An easy scramble with no hands needed; or a moderate climb but close to a source of disturbance.
3 A moderate climb, or a short pole needed ([2m) or far from a source of human disturbance.
4 A difficult climb, or a moderate climb with minimal disturbance by human beings, or a long pole needed (at least 2m).
5 Inaccessible without a boat or ropes.

18. Wave Reach

This variable was scored after observations during rough weather; owing to the 1982 gale, certain nests had different scores in 1981 and 1982.

Scale: 1 Below the level normally reached by high waves, potentially in danger of being damaged or washed away.

2 Above the level normally reached by high waves, safe from all except extreme sea conditions.

19. Cliff Top

A nest was said to be on the cliff-top if it was situated at most 0.5m down from the top; in this position a Shag would be aware of any activity taking place near the cliffs, and be more susceptible to disturbance than birds nesting lower down.

Scale: 1 Nest on top of cliff.

2 Nest below top of cliff.

The remaining 9 variables were scored on an integer or metric scale. Distances were measured by means of the catching pole, marked off in 0.5m sections (total length 4.5m, including the wire hook). For nests that were totally inaccessible, distances were judged by eye. In 1981, measurements were accurate to the nearest 0.5m; in 1982 to the nearest 0.1m.

20. Height above Sea

Height 0 was taken as the upper limit of the barnacle band, which approximates to the level of mean high water at spring tides (Russell 1964).

Scale: Height in metres.

21. Distance to High Water

This variable measured the horizontal component of the distance to the high water mark, taken during high tide.

Scale: Distance in metres.

22. Distance to Low Water

This variable measured the horizontal component of the distance to the low water mark, taken during low tide. The low water line was taken to start at the belt of *Laminaria* (Russell 1964).

Scale: Distance in metres.

23a. Density at Occupation

This variable recorded the number of nests present within a four-metre radius of the nest being scored, at the time when the site was first occupied (late nests), or photographed (early nests).

Scale: Number of nests within 4m.

24a. Nearest Neighbour Distance at Occupation

This variable measured the distance from the centre of the nest being scored to the centre of the nest nearest to it, at the time when the site was first occupied (late nests), or photographed (early nests).

Scale: Distance in metres.

25a. Second Nearest Neighbour Distance at Occupation

This variable measured the distance from the centre of the nest being scored to the centre of the nest second nearest to it, at the time when the site was first occupied (late nests), or photographed (early nests).

Scale: Distance in metres.

23b. Maximum Density

This variable recorded the number of nests present within a four-metre radius of the nest being scored, at the time when the density around the nest was at its greatest.

Scale: Number of nests within 4m.

24b. Minimum Nearest Neighbour Distance

This variable measured the distance from the centre of the nest being scored to the centre of the nest nearest to it, at the time when the density around the nest was at its greatest.
Scale: Distance in metres.

25b. Minimum Second Nearest Neighbour Distance

This variable measured the distance from the centre of the nest being scored to the centre of the nest second nearest to it, at the time when the density around the nest was at its greatest.
Scale: Distance in metres.

There were two replicate measures of the three density variables, corresponding to two different times in the breeding season: the time the site was first taken up, and the time the area around the nest was most densely colonised. These were the two moments when social pressure or stimulation from surrounding nests was likely to have the most pronounced effect, and hence the most readily detected one, if such an effect existed.

APPENDIX 5

Descriptions of nest-site variables used on the Farne Islands (from Potts _et al_. 1980).

The different aspects of nest-site quality were scored according to four factors, each split into three categories (ranked -1, 0 and +1). The factors and their categories are described below.

1. Protection from Rough Seas

Nests were ranked on the basis of records of nest loss, plus a knowledge of the areas which were covered by waves during storms.

-1 Nest-sites which were covered in rough seas resulting from winds of less than gale intensity. These sites were usually affected several times during a breeding season, except during very fine summers.

0 Nests likely to be destroyed only during rough seas resulting from gales (Beaufort scale 8 or more). Nests were destroyed on these sites to the extent that successful breeding was prevented about once in every 3 years.

+1 Nests not likely to be destroyed by rough seas during the summer.

2. Exposure to Rain

-1 Nest-site on flat area with perimeter exposed for 360 degrees.

0 90 to 270 degrees (approximately) exposed.

+1 Less than 90 degrees exposed, or in a cave or beneath a protecting overhang.

3. Size of the Site

-1 Too small to hold one full-grown young - some even too small to hold an adequate nest.

0 Not big enough for three full-grown young and one parent.

+1 Suitable for the rearing of three young.

4. Access to the Sea

-1 More than one other nest-site between site and sea.

0 One other nest-site between site and sea.

+1 Edge site, no nests between site and sea.

An overall nest-site quality rating was obtained by summing the scores from each factor.

APPENDIX 6

Scientific names of animal species mentioned in the text.

Albatross, Grey-headed	*Diomedea chrysostoma* Forster
Albatross, Laysan	*Diomedea immutabilis* Rothschild
Albatross, Wandering	*Diomedea exulans* Linnaeus
Anchovy, Peruvian	*Engraulis ringens* Jenyns
Blackbird	*Turdus merula* Linnaeus
Blackbird, Brewer's	*Euphagus cyanocephalus* (Wagler)
Blackbird, Red-winged	*Agelaius phoeniceus* (Linnaeus)
Booby, Peruvian	*Sula variegata* (Von Tschudi)
Booby, Red-footed	*Sula sula* (Linnaeus)
Catbird, Grey	*Dumetella carolinensis* (Linnaeus)
Cormorant	*Phalacrocorax carbo* (Linnaeus)
Cormorant, Cape	*Phalacrocorax capensis* (Sparrman)
Cormorant, Double-crested	*Phalacrocorax auritus* (Lesson)
Cormorant, Flightless	*Nannopterum harrisi* (Rothschild)
Cormorant, Guanay	*Phalacrocorax bougainvillei* (Lesson)
Cormorant, Little Black	*Phalacrocorax sulcirostris* (Brandt)
Cormorant, Olivaceous	*Phalacrocorax olivaceus* (Humboldt)
Crossbill	*Loxia curvirostra* Linnaeus
Crow, Carrion	*Corvus corone* Linnaeus
Dove, Barbary	*Streptopelia risoria* (Linnaeus)
Duck, Eider	*Somateria mollissima* (Linnaeus)
Duck, Mandarin	*Aix galericulata* (Linnaeus)
Eagle, White-tailed	*Haliaeetus albicilla* (Linnaeus)
Eider, King	*Somateria spectabilis* (Linnaeus)

Finch, Zebra	*Poephila guttata* (Vieillot)
Flycatcher, Pied	*Ficedula hypoleuca* (Pallas)
Frog, Common	*Rana temporaria* Linnaeus
Frog, Green	*Rana clamitans* Latreille
Fulmar	*Fulmarus glacialis* (Linnaeus)
Gannet (European)	*Sula bassana* (Linnaeus)
Gannet, Cape	*Sula capensis* (Lichtenstein)
Goldeneye	*Bucephala clangula* (Linnaeus)
Goose, Canada	*Branta canadensis* (Linnaeus)
Goose, Snow	*Anser caerulescens* (Linnaeus)
Grouse, Red	*Lagopus lagopus scoticus* (Latham)
Grouse, Ruffed	*Bonasa umbellus* (Linnaeus)
Guillemot	*Uria aalge* (Pontoppidan)
Guillemot, Black	*Cepphus grylle* (Linnaeus)
Guillemot, Brünnich's	*Uria lomvia* (Linnaeus)
Gull, Black-headed	*Larus ridibundus* Linnaeus
Gull, Glaucous-winged	*Larus glaucescens* Naumann
Gull, Herring	*Larus argentatus* Pontoppidan
Gull, Laughing	*Larus atricilla* Linnaeus
Gull, Lesser Black-backed	*Larus fuscus* Linnaeus
Gull, Red-billed	*Larus novaehollandiae* Forster
Gull, Ring-billed	*Larus delawarensis* Ord
Hen, Domestic	*Gallus domesticus*
Heron, Great Blue	*Ardea herodias* Linnaeus
Heron, Grey	*Ardea cinerea* Linnaeus
Heron, Little Blue	*Egretta caerulea* (Linnaeus)
Herring	*Clupea harengus* Linnaeus
Jay, Brown	*Cyanocorax morio* (Wagler)

Kestrel	*Falco tinnunculus* Linnaeus
Kittiwake	*Rissa tridactyla* (Linnaeus)
Lemming, Norwegian	*Lemmus lemmus* (Linnaeus)
Magpie	*Pica pica* (Linnaeus)
Mallard	*Anas platyrhynchos* Linnaeus
Mussel	*Mytilus edulis* Linnaeus
Nutcracker	*Nucifraga caryocatactes* (Linnaeus)
Pelican, Brown	*Pelecanus occidentalis* Linnaeus
Pelican, Chilean	*Pelecanus thagus* Molina
Pelican, White	*Pelecanus erythrorhynchos* Gmelin
Penguin, Adélie	*Pygoscelis adeliae* (Hombron & Jacquinot)
Penguin, Jackass	*Spheniscus demersus* (Linnaeus)
Penguin, King	*Aptenodytes patagonica* Miller
Penguin, Yellow-eyed	*Megadyptes antipodes* (Hombron & Jacquinot)
Pilchard, South African	*Sardinops ocellata* Pappe
Plover, Ringed	*Charadrius hiaticula* Linnaeus
Puffin	*Fratercula arctica* (Linnaeus)
Puffin, Tufted	*Fratercula cirrhata* (Pallas)
Quelea, Red-billed	*Quelea quelea* (Linnaeus)
Razorbill	*Alca torda* Linnaeus
Redshank	*Tringa totanus* (Linnaeus)
Salmon	*Salmo salar* Linnaeus
Sandeel, Lesser	*Ammodytes marinus* Raitt
Sardine, Pacific	*Sardinops sagax* (Jenyns)
Seal, Grey	*Halichoerus grypus* Fabricius
Shag (European)	*Phalacrocorax aristotelis* (Linnaeus)
Shag, Blue-eyed	*Phalacrocorax atriceps* Murphy
Shearwater, Great	*Puffinus gravis* (O'Reilly)

Shearwater, Manx	*Puffinus puffinus* (Brünnich)
Shearwater, Short-tailed	*Puffinus tenuirostris* (Temminck)
Skua, Arctic	*Stercorarius parasiticus* (Linnaeus)
Skua, Great	*Catharacta skua* Brünnich
Skua, McCormick's	*Catharacta maccormicki* (Saunders)
Skylark	*Alauda arvensis* Linnaeus
Sparrowhawk	*Accipiter nisus* (Linnaeus)
Starling	*Sturnus vulgaris* Linnaeus
Stilt, Black-winged	*Himantopus himantopus* (Linnaeus)
Stint, Temminck's	*Calidris temminckii* (Leisler)
Swallow	*Hirundo rustica* Linnaeus
Tern, Arctic	*Sterna paradisaea* Pontoppidan
Tern, Common	*Sterna hirundo* Linnaeus
Tern, Royal	*Sterna maxima* Boddaert
Tern, Sandwich	*Sterna sandvicensis* (Latham)
Tern, Sooty	*Sterna fuscata* Linnaeus
Tit, Blue	*Parus caeruleus* Linnaeus
Tit, Great	*Parus major* Linnaeus
Toad, Common	*Bufo bufo* (Linnaeus)
Waxwing	*Bombycilla garrulus* (Linnaeus)
Wheatear	*Oenanthe oenanthe* (Linnaeus)
Woodpigeon	*Columba palumbus* Linnaeus

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SUMMARY

Methods.

1. Since 1962, over 11'000 Shags have been marked with monel rings on the Isle of May, Scotland. By 1981, 38% of Shags breeding on the island were marked. In 1981, the ring-numbers of 41% of marked breeders were recorded, and 74% in 1982. The total numbers of nests in the two years were 1476 and 1916 respectively.

2. Shags were sexed by voice, size, appearance and behaviour. They could be aged easily as one and two-year-olds on plumage. Two-year-old males could also be identified by the state of the crest in mid-May, with 10% error. The only reliable character found to identify three-year-old Shags was Mottled Underparts; 29% of three-year-olds exhibited Mottled Underparts. In males only, bill depth gradually increased with age (increment of 0.05mm/year).

3. Male Shags tended to pair with females of the same age or older; second-year (two-year-old) females paired almost exclusively with second-year males. Bigamy was negligible.

4. Twelve chick growth stages were recognizable on the basis of physical appearance, and could be recorded even at inaccessible nests. They were used to estimate hatching date and laying date for 1209 nests from the state of development of their chicks.

Restoring the legibility of the inscriptions on abraded or corroded bird-rings.

5. Of 1536 monel rings on Shags examined between 1981 and 1983, 243 were worn and needed replacing. Twelve were clip rings, with the ring-numbers still legible; in 115 of the remaining 231 butt-ended rings, the ring-number was incomplete due to abrasion of one or more digits.

6. The missing digits could be revealed by electrolytic etching: the ring served as one of two electrodes immersed in a solution of hydrochloric acid and cupric chloride. As an electric current passed through the system, etching of the surface of the ring revealed the structural differences in the metal created when the serial number was stamped onto it.

7. The etching process could last from 15 minutes to several hours; 82% of worn rings were successfully read within an hour. The method could be extended to treat several rings simultaneously.

8. The success rate of electrolysis as a means of reading illegible rings was 65% for Guillemots and Razorbills, and over 90% for either abraded or corroded rings of both monel and incoloy for other species; it was 94% for Shags. In comparison, X-rays were successful in only 14% of cases.

9. On Shags, the first incomplete ring-number appeared after six years, and the proportion of rings with incomplete numbers increased rapidly after nine years; 50% of ring-numbers were illegible after 11 years. On average, a ring lost 0.08g of metal a year, equivalent to 1.3% of its initial weight.

The retrospective investigation of an ecological disaster in the Shag: a general method based on long-term marking.

10. From 1918 to 1973, the number of pairs of Shags breeding on the Isle of May increased at an annual rate of 15.6%. After peaking at 1073 pairs in 1973, the colony crashed to 497 pairs in 1976. It subsequently increased to 921 pairs in 1977, faltered in 1978, then resumed a rapid growth at a rate of 14.8% _per annum_. During the period of the crash, 1974-1976, the breeding seasons were about a month later than usual.

11. At least 95% of Shags marked or retrapped as breeders on the Isle of May since 1965 were sampled in 1982. The adult annual survival rate had remained constant immediately before, during and after the crash, at 87.4%. The crash was not due to mass mortality of adult Shags. The only possible explanation was large-scale non-breeding by experienced adults.

12. Shags marked before 1972 showed a reduction in survival compared to later cohorts, which was not accounted for by ring wear. Poorer sampling efficiency of old Shags was unlikely, and the hypothesis of a lower annual survival rate in early years was not sufficient to explain the decrease in survival. The most likely explanation was that the survival of Shags decreased with extreme age.

13. The survival rate during the second year of life of Shags ringed as chicks on the Isle of May was 74.5%. It was obtained from the slope of the regression of the proportion of marked Shags which were recovered during their second year against the proportion of marked Shags which were recovered in their first year, for 17 cohorts of birds ringed as chicks.

14. Of Shags ringed as chicks and breeding on the Isle of May, 65% were sampled in 1982. The first-year survival rates from 1973 to 1979 were back-calculated from the proportions of each cohort which survived and were sampled in 1982. The average first-year survival rate was 47.8%; the annual estimates were strongly correlated with the proportions of Shags ringed as chicks and recovered during their first year.

15. The first-year survival rates were down to a third of the average during the crash years. Although fledging occurred later in those years, 45% of dead first-year Shags were recovered before November, compared to only 16% in normal years.

16. Searches at seven other colonies, comprising the bulk of breeding Shags in the Forth-Farnes area (Isle of May excluded), showed that emigration from the Isle of May was low: only one breeding Shag had emigrated, and amongst Shags ringed as chicks, emigrants were recorded only for the 1970-1973 cohorts and the 1980-1981 cohorts. These years corresponded to periods of relatively high first-year survival rates. No emigration was recorded for chicks fledged during the crash.

17. Five non-local Shags were recorded breeding on the Isle of May (0.5% of marked Shags identified). Only one was a recent immigrant (1979 chick from Craigleith), the others were old birds from the Farne Islands, of which three moved to the Isle of May as a result of the 1968 'red-tide' on the Farne Islands.

18. The recruitment rate of two-year-old males to the Isle of May was 90% in

1982, and 17% for females. The latter is probably an underestimate as two-year-old females were more difficult to record than males.

19. The mean number of chicks fledged in a year was derived from the mean brood size of chicks ringed in that year according to the equation $y=1.60x-2.11$. On average, a pair fledged 1.09 chicks per year; from 1974 to 1976, the number fell to 0.77 chicks/pair.

20. A deterministic model bringing together the survival rates , recruitment and chick production was used to simulate the number of pairs breeding on the Isle of May between 1973 and 1983. It showed that the proportion of adults which had bred in previous years and refrained from breeding lay between 0-30% in 1974, and 25-60% in 1975 and 1976; the exact value depended on the extent of recruitment during those years.

21. The slight fall-back in colony size in 1978 was caused by a lack of recruits due to low fledging success and chick survival during the crash. A relatively poor fit of the model to counts made in recent years may be due to an increase in immigration.

22. The unchanged adult annual survival rate over the period of the crash precluded causes associated with heavy mortality. In particular, the dinoflagellate proliferation ('red-tide') which killed 62% of Shags breeding on the Farne Islands in 1975 was not implicated. Water quality in the Firth of Forth was high; levels of copper, cadmium and lead in the seawater of the Firth during the crash remained unchanged or were lower than in subsequent years. Pesticide residues in Shag eggs from the Isle of May in 1976 were lower than in previous years. These factors were not responsible for the crash.

23. The laying date of the first Shag egg on the Isle of May was correlated with four climatic variables in March, all of which were strongly intercorrelated and probably represented a same, temperature-dependent, factor. First-year survival rates of Shags from the Isle of May were not correlated with climate in February or March, the period of peak mortality.

24. The laying date of the first Shag egg on the Isle of May was strongly correlated with a measure of the abundance of 1-ringed Herring around the island in February. Herring abundance was especially low during the years of the crash, and was independent of climate. Both Herring abundance and climate contributed significantly to a multiple regression against laying date, Herring abundance having the stronger partial correlation. First-year survival rates of Shags from the Isle of May also correlated with Herring abundance.

25. The lack of Herring during the crash was confirmed from the diet of young Puffins on the Isle of May during the same period. Furthermore, the percentage contribution of sandeels to Puffin diet dropped in 1975, and sandeels were smaller between 1974-1976 than in other years.

26. All factors point towards food shortage as being responsible for the crash. Direct evidence of the importance of Herring in the diet of Shags is lacking; Herring may act as an indicator of the suitability of the area for feeding by other fish on which Shags prey, e.g. sandeels, which comprise 80% of the summer diet.

Age, timing of breeding, clutch size, nest structure and chick production.

27. For constant male age, there was no significant effect of female age on chick production. Male age accounted for 25% of the overall variability in numbers of chicks fledged per pair in 1981 and 1982; of this, over 90% was caused by differences between second-year males and older males, with a second-year male fledging less than half the number of chicks fledged by an older male. Males aged 3 performed significantly less well than males aged 4 to 13, as did old males over the age of 13.

28. Clutch size was not related to female age in 1982. Before laying, before hatching and after hatching, second-year males suffered greater nest loss (through pilfering by other Shags) than older males; losses were greatest during incubation (44% of second-years suffered losses at this stage, 14% of older males).

29. In 1982, 7% of complete clutches failed to hatch (no age effect), compared to 12% on Lundy and 13% on the Farne Islands. The differences may be due to different climatic conditions during incubation. Alternatively, hatching success in predatory birds is known to be affected by pesticides, and the pesticide loadings in Shag eggs from the Isle of May in 1981 were lower than those in eggs from the Farne Islands in 1968.

30. In 1982, hatching success and early chick survival (to ca 10 days) averaged 69% for clutches of 1 to 4, 56% for larger clutches (no age effect). Fledging success was 55% for second-year males, 71% for older ones. For older males, mortality of chicks after 10 days increased with brood size: the main reason was exposure to rain when chicks were still downy, but too large to be adequately sheltered when in large broods. Mean brood size at 10 days was 1.95 for second-year males and 2.21 for older ones; the number of chicks subsequently lost before fledging was 0.85 and 0.66 respectively.

31. The interval between nest-site occupation and egg-laying decreased from two weeks at the end of April to one week from the beginning of June in 1982. By mid-April, 90% of males over two were already on nest-sites, compared to 31% of two-year-olds. The proportion of pairs with a second-year male which laid in a given week was less than 10% up to the end of April, and rose to a plateau of ca 60% by mid-June. Only 39 pairs laid after then, and were probably renesting.

32. Second-year females laid on average a month later than older ones in 1982. Both male and female age were important in determining laying date, although the role of male age reduced to being either two or older than two.

33. Mean chick production decreased strongly with laying week in 1982, according to the relationship $y=-0.24x+3.51$ (valid until mid-June). Much of the decline was age-independent, with a slope of -0.22 for second-year and older males separately. The two age categories plus seasonal effects accounted for 38% of the overall variability in chick production, of which 79% was attributable to laying date; the age effect was still significant. For males which occupied their sites late (after mid-April), chick production also declined seasonally, with no difference between age groups.

34. The age-independent decline in chick production in 1982 was the result of a decrease in mean clutch size with laying week ($y=-0.08x+3.43$), an

increase in the proportion of nests lost through the season, particularly during incubation (from 1% to 67% for males over two, and from 25% to 92% for two-year-olds), a decline in hatching success or early chick survival, and a decline in the survival of chicks between 10 days and fledging.

35. In 1981 and 1982, 15% of nests belonging to second-year males were poorly built at laying, and only 1% in the case of older males. In 1982, the proportion of nests poorly built at laying increased seasonally, from 0% initially, to 11% in males over two and 36% in two-year-olds. Over the two years, only 15 chicks were reared from 174 nests which had been poorly built, owing to heavy nest loss: half were lost before laying began, and 80% of the remainder were lost before hatching. Only 1% of completed nests were lost before laying, and 18% before hatching.

Philopatry, site tenacity and pair-bond stability.

36. In 1983, 55% of marked Shags breeding on the Bass Rock, Craigleith, The Lamb, Fidra, Inchkeith, Inchmickery and the Farne Islands were identified. On average, 4.9% of Shags marked as chicks were found breeding at a colony other than their natal one. The proportion of Shags which bred away from their natal island declined exponentially as the distance between the natal colony and the breeding colony increased; over the range considered (1-100km), the relationship held independently of the size of the natal colony, and of the size and proximity of other colonies. More females than males bred away from their natal colony.

37. Excluding the Farne Islands, only 0.8% of Shags ringed as breeders moved to another colony after ringing. The apparent emigration rate of breeders from the Farne Islands was 14%. This was likely to be the result of the 'red-tide' outbreaks in 1968 and 1975: the first boosted emigration, the second reduced the number of Shags which remained on the Farne Islands.

38. Half the Shags ringed as chicks on the Isle of May which subsequently bred on the island returned to their area of hatching; this fidelity was stronger in males. Only 1% of breeders changed area between years. In terms of distance, 71% of males remained within 4m of their old (1981) nest-site in 1982, and 46% of females. The median distances between the 1981 nest-site and the 1982 nest-site were 1.4m for males, and 5.0m for females.

39. Three-quarters of sites were reoccupied from one year to the next, and 70% in three consecutive years. 44% of sites occupied for the first time were subsequently abandoned, compared to 11% of established sites. In both sexes, site tenacity increased with age, with 19% of second-years retaining their old sites as opposed to 70% of Shags over seven; correspondingly, 48% of sites occupied for the first time belonged to second-year males, and only 9% of established sites. Site tenacity was more strongly marked in males. Shags which changed sites moved preferentially to established sites; nearly a third of sites changed owners between 1981 and 1982.

40. 54% of 1981 pairs bred together in 1982; divorce accounted for just over half the pair changes, disappearance of the partner for the remainder. The rate of divorce was 75% for second-year males, and 28% for older ones. The divorce rate also varied with the distance moved by the male when selecting nest-sites in one year and the next: it was 17% for males which occupied the

same site, and increased to 75% for males which moved more than 8m. Females apparently recognized their male from the previous year and chose to mate preferentially with him.

41. Twice as many males changed site from 1981 to 1982 after reproductive failure than after successfully breeding; divorce was not related to breeding success in the previous year. Shags which retained their mate bred earlier than those which changed; the latter tended to pair with younger birds. Breeding success was reduced for Shags which changed sites, probably as a result of mate change and later breeding.

42. There was no relationship between chick production by the same individual in consecutive years. However, certain pairs were consistently more efficient at rearing offspring than others, and the trend was independent of age.

The effects of a gale in late spring on the breeding of the Shag.

43. A gale destroyed or damaged over 50% of 658 nests on the west side of the Isle of May, from 1 to 4 May 1982. The damage was related to the height of a nest above the sea. A week after the gale, 23% of sites where nests had been washed away were abandoned; only 3% of damaged nests and no undamaged nests were abandoned. Over 90% of pairs which retained their sites laid replacement clutches; two-thirds of them laid during the third week after the gale (mean laying date for replacement clutches: 19 days after the gale).

44. In 1981, chick production on the east and west sides of the island was the same (1.52 chicks/pair); in 1982, the unaffected east side fledged 1.30 chicks/pair, and the west side 0.97 chicks/pair. Only a third of the difference was caused by nest-site desertion on the west side after the gale. The remainder was caused by poorer hatching success of apparently unaffected nests on the west side, and poor chick production from replacement clutches, consistent with an age-independent seasonal decline.

45. Replacement clutches averaged 2.88 eggs, compared to 2.71 eggs for late-laid first clutches. Pairs on replacement clutches also fledged more chicks/pair than late breeders nesting for the first time (1.0 versus 0.5 for second-year males, 1.2 versus 0.8 for older ones), mainly because of better attention to the nest and better defense of the site during incubation; second-year males on replacement clutches were also more skilled at rearing chicks to fledging than late-breeding two-year-olds on first clutches. Overall, repeat breeders were of better quality than late ones.

46. In general, second-year males nested lower than older Shags, and were more exposed to the gale. Young males abandoned their nest-sites more readily than older males if the nest had been damaged or washed away during the gale. Recruitment of second-year males to the west side of the island was reduced by a third, owing to the deterrent effect of the gale upon males which had been potential recruits, but had not started breeding before the gale.

Nest-site quality and reproductive success.

47. The physical and social characteristics of a nest-site were described using 28 variables. Nearly all showed significant differences in mean scores between the east and west sides of the island, reflecting the topographical differences between sides.

48. Analysis was carried out by stepwise multiple regression of chick production against the nest-site variables. The effects of male age, timing of breeding and side of the island upon chick production were held constant, during the selection of the major nest-site variables correlating with chick production, by means of dummy variables. The selection was performed on the 1982 dataset, and the procedure validated on the 1981 dataset.

49. Four variables were selected: the size of the nest ledge, which was related to the early loss of nests and also of chicks, through insufficient space; site dampness, which affected nest loss before hatching and hatching success; exposure to weather and to other Shags, associated with early nest loss through pilfering, and with loss of chicks through exposure to heavy rain; vulnerability to the sea, which described the risk of a nest being washed away or damaged by wave action.

50. The technique combined the scores from the four selected variables into an overall nest-site rating. The effects of each variable upon chick production remained the same irrespective of male age, timing of breeding, side of the island or year. Overall, nest-site quality accounted for 8% of the variation in chick production; when individual variability was reduced by considering the mean production from nests of the same quality, the proportion rose to 56% when using the overall rating, and 67% when using the four component variables (each made a significant contribution to the regression).

51. Three-quarters of dead chicks found in 1982 were 20-37 days old. Such chicks were still downy, but too large to be adequately sheltered from bad weather by their parents: 94% of them were found after three periods of heavy rain. Only 4% of chicks were found dead after body feathers had started to grow beneath the down.

52. The quality ratings of sites occupied by Shags were situated within the upper two-thirds of the range of possible values, i.e. Shags avoided highly unsuitable sites. The difference in mean chick production between the worst and best-rated sites occupied by Shags was 1.4 chicks/pair. An average site was close to the optimal with respect to ledge size and vulnerability to the sea, but not for dampness and exposure. The latter factors were likely to be the limiting ones in nest-site quality. This was confirmed by a significant correlation between mean brood size at ringing and a measure of rainfall during the breeding season, over 14 years.

53. In 1981, nest-sites on the Isle of May were also graded according to the four variables used by Potts <u>et al</u>. (1980) on the Farne Islands. Potts' variables and those selected by the regression procedure represented approximately the same factors with regard to site quality, although Potts' Access to the Sea had no counterpart on the Isle of May, and site dampness was correlated, poorly, only with Potts' Amount of Exposure to Rain. The two sets of variables explained the same amount of variation in chick production on the Isle of May in 1981 (7%).

54. Using Potts' variables, the proportion of unsuitable nest-sites was consistently higher, and the mean rank of nests consistently lower, on the Farne Islands than on the Isle of May. Correspondingly, chick production on the Isle of May was generally higher than on the Farne Islands.

Nest-site quality in relation to age, timing of breeding and site choice.

55. Mean site quality was slightly lower for second-year males than for older ones, equivalent to young Shags producing 2-3 chicks per 100 pairs less than older birds; this constituted only 2-3% of the overall difference in chick production between the two age classes. There was no significant difference between mean site quality for different ages of males over two.

56. Sites occupied early in the season, by both second-year males and older ones, were of higher mean quality than sites occupied late. The difference in mean quality for sites occupied by second-year males and older ones vanished after correcting for the differences in timing of breeding. Shags could recognize good quality sites; late breeders were forced onto sites of poor quality because sites of high quality were preferentially occupied by early breeders.

57. Results from marked individuals suggested that Shags which changed site from 1981 to 1982 tended to move from sites of less than average quality; in spite of moving, they seemed unable to improve the quality of their sites to match that of birds which did not move.

58. Taking nests scored for site quality in 1981, mean scores were highest for nests occupied continuously from 1981 to 1983, and lowest for sites abandoned after 1981. Taking nests scored for site quality in 1982, mean scores were again highest for nests occupied continuously from 1981 to 1983. Sites abandoned after 1982 scored less, on average, than sites occupied in 1982 and 1983. In general, this indicated that Shags were moving from poor quality sites and holding onto good ones.

59. Taking nests scored for site quality in 1982, previously unoccupied sites scored worse, on average, than sites occupied already in 1981. The lower average was due to the poor mean quality of sites abandoned after 1982; those reoccupied in 1983 were equivalent in quality to continuously occupied sites. The former belonged mainly to second-year males, and reflected the competitive exclusion of late breeders from good sites, the latter belonged mainly to older males, i.e. birds likely to have changed sites. A purer sample of males which changed sites showed that they moved to sites of quality as good, on average, as that of continuously occupied sites.

60. Only 8% of sites newly occupied in 1982 were situated in previously uncolonised areas (pioneer sites); 58% of the remainder were sites on the edge of established groups of breeders, and 42% were within such groups (no age differences in the proportions). Chick production from sites within or on the edge of established groups was the same, but doubled to 1.0 chicks/pair for second-year males on pioneer sites, and increased from 1.3 to 2.1 chicks/pair for older birds on pioneer sites. Part of the difference at least was due to differences in mean site quality, with pioneer sites scoring highest, on average, and central sites lowest.

61. The results are as would be predicted if Shags were selecting high quality sites when they were available to them, within the constraints of colonial breeding. The desire to breed in a group meant that a Shag would usually accept a poor site rather than nest in isolation on a good one. Colony growth in Shags can proceed by steady expansion of colonised areas, or by atypical, pioneering, individuals founding nuclei of growth in new areas. If good sites are plentiful in such new areas, growth can proceed rapidly: in the case of the 'Island' wreck, two pairs were present early in 1982, six by the end of the season, and 20 by June 1983.

62. During the 19th century, numbers of Shags on the Isle of May were maintained at 2-3 pairs, probably through hunting pressure. The Isle of May Shag population currently shows no signs of density-dependent regulation, although potential regulatory factors, as revealed by this study, are food and shortage of good quality nest-sites.