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Cobley, Norman

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ASPECTS OF THE POPULATION DYNAMICS OF ANTARCTIC BLUE-EYED SHAGS *PHALACROCORAX ATRICEPS* KING.

by

Norman Cobley B.Sc.

Thesis submitted to the University of Durham for the
degree of Doctor of Philosophy

ABSTRACT

Blue-eyed shag chicks have been ringed in almost every year since 1969 at two colonies on Signy Island. In this study, over 40% of breeders (801 pairs in 1987) were ringed and of known age, and during the breeding season adults were readily recaptured. Annual adult survival rates during the study averaged 0.86, although the mean annual survival rate between the early 1980's and 1987 was lower, averaging 0.76. There was no difference in the annual survival rate in relation to sex or breeding experience, but birds older than 11 years showed evidence of decreased survival rates, of about 0.04 annually. The first year survival rate averaged 0.36 but varied widely between 0.03 (in 1979) and 0.69 (in 1984). Low first year survival rates occurred about every four years. Only mean monthly temperature in April and the duration of sea ice were selected as explaining variation in first year survival rates and together they accounted for over two-thirds of the variation. Post-fledging survival rates were independent of hatching order, although only a few last-hatched chicks survived the nestling period.

Although movements to and from neighbouring colonies could not be monitored thoroughly, no ringed birds were seen during searches of the two nearest colonies, and the rate of colony exchange between the two Signy colonies suggested that established breeders exhibited a high degree of faithfulness to their colony, only 0.1% moving each year. Recruits tended to return to their natal colony, and only 2.4% moved away between the two Signy colonies. Blue-eyed shags showed deferred breeding and whilst a few individuals began breeding at two years, most waited until their third and fourth year and some delayed breeding until six years old. The modal age of first breeding varied between years being earliest in 1987 (3 years) when recruitment was also high. Over the age range at which most birds recruited, there was no difference between the sexes in the age of first breeding. Prior to the year in which they first bred, young shags visited the colony to which they subsequently recruited and the number of visits *per* bird increased with age. Older pre-breeding birds also made visits earlier in the season.

Low mate fidelity was normal, only 39% retained the same mate in the following breeding season. Of those which changed mate, divorce accounted for 46%, and the annual rate of divorce declined in relation to increasing age and breeding experience. A comparison of the divorce rates of similar aged birds with different breeding experience showed that recruits were more likely to divorce, suggesting that breeding experience was more important in divorce than age alone. Pairs which divorced in the current year had had lower mean clutches, broods and fledged fewer chicks in the previous year compared with those which kept the same mate. However, pair stability during the previous year had no effect on the breeding performance in the current year. Divorce was associated with further divorce in the following year. Both sexes showed a high tendency to re-nest within 12 m of the previous year's nest, although this was less marked in females. Re-use of the previous year's nest was low. A high proportion of pairs had partners of similar age, 46% being of equal age and 70% differing by a maximum of one year. Nearly twice as many equal aged pairs arose compared with the number expected if mating was random with respect to age, and the proportion of equal aged pairs declined among older birds. With respect to breeding experience and pair stability, experienced pairs and those which changed mates did not form more equal aged partnerships than expected by chance, and only for recruits did more equal aged pairs form than expected. Breeding experience was weakly related to breeding performance and the effect was stronger in 1987 than in 1986. Younger males built poorer quality nests than older birds, but it was not possible to resolve the effects of age and nest quality independently on breeding success.

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.

Dedicated to the men of Signy, 1985-88.

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I would like to thank Dr. John Coulson for supervising this project and in particular for his patience, perceptive advice and encouragement. I also owe a debt of gratitude to Dr. John Croxall for guidance whilst the fieldwork was in progress, and his prompt and helpful replies to questions and results sent from Signy. Without their considerable joint experience, this study could not have been undertaken. Financial support for this study came from the Natural Environment Research Council under the NERC/BAS Antarctic Special Topics award scheme. Professor Bowler kindly made facilities available to me in the Department of Biological Sciences at the University of Durham, and British Antarctic Survey organised my stay at Signy. At Cambridge, I received much help from Dr. Andy Wood who guided my often inept attempts with Oracle, from Peter Rothery who kindly offered statistical help and advice and from Dr. Jonathan Shanklin who generously made available detailed BAS meteorological data from Signy. I would also like to acknowledge Dr. Phil Shaw for many helpful suggestions, advice and constructive criticisms, and at Durham, Dr. Dave Baines, Dr. Steve Percival, Dr. Pat Thompson, Carol Fielding and Cath Todd have all given me encouragement and advice. Last but definitely not least, special gratitude is due to the wintering personnel on base during 1986 and 1987, too numerous to mention individually, but all of whom enriched the experience of wintering in Antarctica. I am especially grateful to Rick Price and Doug Allan, whose combined experience of 10 Antarctic winters proved invaluable, and to the marine assistants Paul Burren and Julian Ashford for help in the field. The boatmen, Pete Macko and Pete Hizzett enabled me to go to many places in search of shags which would be otherwise inaccessible, and their experience was reassuring during the many variations of the Signy weather. I had many stimulating discussions with Jon Pickup and Steve Tucker, both of whom have been influential in shaping my ideas, and received valuable help at the colonies from Ian Lovegrove and Steve Tucker. I would also like to pay tribute to the hard work of past Signy fids, whose efforts resulted in the high proportion of ringed shags, on which this study largely depends.

Thank you.

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APPENDICES

1. GENERAL INTRODUCTION.

During this century most populations of seabirds which breed in the north Atlantic have been increasing, reversing earlier trends (Cramp *et al.* 1974, Evans 1984b). Some of the increases have been dramatic, as in the Fulmar, which in Britain was formerly restricted to St. Kilda but has expanded its range to colonise the rest of the country, and increased at an annual rate of 10% between 1909 and 1939, and 6-7% from 1939 to 1969 (Evans 1984b). Kittiwakes have also experienced population increases since the turn of the century, by about 3-4% annually up to 1969, after which the rate declined to 1% (Coulson 1963, 1983). Gannets in the eastern Atlantic increased by 3% annually (Nelson 1978) and the North sea colonies of European shags by 11-15% over a similar period (Potts 1969, Aebischer 1985). Several explanations for these increases have been advanced, including reductions in human persecution at the end of the nineteenth century which coincided with the passing of bird protection Acts (Coulson 1963, Nelson 1978) and relaxation in human persecution in conjuction with increased food supplies (Evans 1984b). In the Fulmar, where the increase started before the other species, increased food availability in the form of offal, first from whaling and later fishing (Fisher 1952), changes in genotype (Wynne-Edwards 1962) or oceanographic factors (Salomonsen 1965, Brown 1970) have been suggested as likely causes.

The impact of man on seabirds has often been profound, and has led to substantial changes in the populations of some species. Their direct exploitation is mainly for food (Feare 1984), two examples being the hunting of Brünnich's guillemot in Greenland for food and bait, which has produced severe declines in some breeding populations (Evans & Waterston 1976, Evans 1984a), and the decline in North Atlantic Gannets in Scotland and North America during the nineteenth century (Nelson 1978, Brown & Nettleship 1984). Not all exploitation has resulted in declines; in the Short-tailed shearwater ('mutton birds') an increase in population has accompanied extensive harvesting of chicks, suggesting that such cropping is below the maximum sustainable yield (Serventy 1974 cited in Feare 1984). Other forms of interaction between seabirds and man are more subtle. An increase in the use of sophisticated fishing technology has resulted in increased catches and reduced stocks of some fish species, and this trend has brought man and seabirds into conflict. Although evidence for competition between fisheries and seabirds is scarce, some examples are known and more may be expected. Furness & Ainley (1984) have reviewed the species most likely to be affected as a consequence of their ecology and concluded that amongst other characteristics, species with a limited foraging range (inshore feeders such as penguins, auks and cormorants), surface feeding habits and low tolerance to temporal fluctuations in food availability, are especially vulnerable. Examples of overfishing are already evident in some areas, for example the failure of populations of guano seabirds of the Peruvian upwellings to recover after recent El Niño events has been linked to the fishing out of the Anchoveta stock (Duffy 1983b). The problems posed by fisheries are not confined to stock reduction and catching methods have themselves been associated with some seabird declines. The use of fine monofilament nylon nets in such techniques as gillnetting has been responsible for much incidental mortality, especially in diving birds such as auks and cormorants (King 1984, Ogi 1984). Declines of Wandering albatross have been reported at several breeding stations in the southern ocean, and the evidence points to increased adult mortality outside the breeding season when the birds roam the oceans (Croxall 1979, Jouventin *et al.* 1984, Weimerskirch & Jouventin 1987, Croxall *et al.* 1990). This now seems likely to be a direct result of the development of long-line tuna fisheries in areas far removed from the albatross breeding grounds (Weimerskirch & Jouventin 1987, Croxall *et al.* 1990) demonstrating not only that seabirds can be affected by events several thousand kilometers from their breeding colonies, but also that they represent a particularly vulnerable group due to their life history strategy of high annual adult survival rates, low annual reproductive rate and extensive period of delayed recruitment to the breeding population. For the Wandering Albatross, it has been demonstrated that a substantial decline in adult annual survival rates cannot be compensated for by realistic increases in the age at first breeding or fecundity, since they lay single egg clutches without replacement, and a decline of 1% in adult survival rates would require an advance in the mean age of first breeding of 6.5 years (Weimerskirch *et al.* 1987).

Other potential hazards to seabirds include marine pollution and especially the accidental discharge of oil and agricultural and industrial chemicals into the sea. Even in the remote polar regions there is evidence of the effect of human intervention in the marine environment. The increased hunting pressure on Brünnich's guillemots in Greenland (Evans & Waterston 1976) is one direct example, and there are more subtle ones from the Antarctic, where the presence of manned scientific bases has led to decreases in some penguin populations, whilst numbers of skuas have increased due to opportunistic feeding at rubbish dumps (Harper *et al.* 1984). These elevated skua numbers may lead to increased predation on other species, particularly if bases are closed with the subsequent removal of the artificial food supplies (Furness 1987). Organochlorine residues have been detected in a variety of Antarctic seabirds (Sladen *et al.* 1966, Tatton & Ruzicka 1967), and whilst their use has been banned in most developed countries, they are still used in several areas of the third world where indications of their entry into the ecosystem are becoming apparent (Crick 1990). In Antarctic seabirds the highest levels are found in skuas, Giant and Wilsons petrels, species which are pelagic during part of their lives, wandering far from the Antarctic (Conroy & French 1974). Seabirds breeding at Antarctic localities may thus accumulate such residues if they wander into areas where oceanic levels of pollutants are higher, perhaps as a result of river discharge into the oceans. For example, South Georgia Black-browed Albatross spend the non-breeding season off the coasts of South Africa (Croxall & Prince 1980), and may be at risk if the widespread use of organochlorine compounds implicated in the decline of raptorial birds (and associated eggshell thinning) in South Africa (Crick 1990) is entering the offshore environment.

To utilise seabirds as monitors of the marine environment it is desirable to have knowledge of their populations in advance of any changes taking place. Interpretation of changes in seabird numbers requires detailed information on population processes and ecology of each species, which is only realised when more detailed studies are undertaken (Croxall & Prince 1979). As an example of this approach, Croxall & Prince (1979) reported the initiation of regular monitoring of selected species of Antarctic seabirds, in advance of the proposed exploitation of Southern Ocean fisheries and other potential developments (Harper *et al.* 1984). These studies have already revealed substantial increases in the breeding populations of several krill eating species, particularly Adelie and Chinstrap penguins, in additional to the declines in Wandering albatross already discussed. The increases in krill eating species have been attributed to changes in food availability resulting from decreased competition after the reduction of baleen whale stocks (Croxall *et al.* 1981). The complexity of trophic interactions in the South Georgia seabird community has been described by Croxall & Prince (1980), who found that temporal, dietary and geographical differences in foraging were individually important, yet combinations of isolating mechanisms were likely to act in concert to produce the observed partitioning of marine resources. For example, King penguin, Wandering albatross and Grey-headed albatross all feed on squid, the last two feed principally on separate species, and capture prey at the surface. King penguins, in contrast, are deep divers and competition with Wandering albatross is further avoided as the latter breed during the winter, and almost certainly range further during foraging. Grey-headed albatross are biennial breeders during the summer months (Croxall & Prince 1980). These types of segregation mechanisms may be particularly well evolved in high latitude seabird communities since unlike tropical communities, there is probably little opportunity to avoid overlap by altering the timing of breeding owing to the constraints of a shortened summer season (Croxall & Prince 1980).

Since most seabirds are long-lived animals, it is the long-term studies which have provided the most revealing insights into their ecology. Some of the most detailed information currently available is for Kittiwakes, and demonstrates the importance of colony structure (Coulson 1968), pair bond (Coulson 1966, Coulson & Thomas 1983), survival rate differences in relation to age, sex, colony position, breeding experience and time (Coulson & Wooller 1976, Aebischer & Coulson 1990), individual quality (Coulson & Porter 1985), recruitment to the breeding population (Wooller & Coulson

1977, Porter & Coulson 1987, Porter 1988, 1990) and the roles these factors have in influencing lifetime reproductive success (Coulson 1988). Other data exist for a few species, notably Short-tailed shearwater (*e.g.* Wooller *et al.* 1988, 1989, 1990) and Fulmar (Dunnet & Ollason 1978, Ollason & Dunnet 1978, Dunnet *et al.* 1979).

Lack (1968) has emphasised the difference between inshore feeding seabirds, such as gulls and terns, and offshore feeding species like the Procellariiformes, and linked their feeding habits with other adaptations. Whilst almost all seabirds breed in colonies, inshore species tend to nest in smaller colonies which are closer together, have larger clutch sizes, higher chick growth rates and begin breeding at earlier ages than their offshore feeding counterparts. Applying these arguments to the South Georgia seabird community, Croxall & Prince (1980) found that there was corroboration when some pairs of similar species were considered. Comparing Gentoo penguins, an inshore feeder, with offshore feeding Macaroni penguins, they found that the latter bred in large widely spaced colonies, rears a single chick, has longer incubation spells and foraging trips and delays first breeding until six years of age. However consideration of other species-pairs produced only weak agreement with the theory, which the authors attributed to the generalised nature of the theoretical arguments. Seabirds feeding close to their colonies are likely to experience increased intraspecific competition resulting in a reduction in breeding success and recruitment to the breeding population (Ashmole 1963). In a study of five Southern Ocean albatrosses, Weimerskirch *et al.* (1987) have suggested that minor differences in adult survival rates may be due to intraspecific competition. Two demographic trends can be identified; annual breeders such as Black-browed and Yellow-nosed albatross have relatively low annual adult survival rates (0.91-0.92) and breed in large colonies, whereas biennial breeders like Wandering albatross and the two species of Sooty albatross have higher rates (0.95-0.97)and breed in smaller colonies. These two strategies are reflected in the ways in which the species utilise marine resources, Black browed and Yellow nosed albatrosses being confined to highly productive shallower water, upwellings or convergence fronts, whilst the more pelagic species range more widely (up to 1500 km in the case of breeding Wandering albatross (Jouventin

& Weimerskirch 1990)) owing to their dispersed oceanic food supplies. Thus, within a group of seabirds normally associated with offshore habits, variation in life-history traits may be associated with differences in exploiting marine resources in a similar manner to that suggested for the inshore-offshore division, by Lack (1968).

Studies on European shags have indicated that populations in the North sea have continued to increase since the early part of the century, as yet without any apparent limitation (Potts 1969, Potts *et al.* 1980, Aebischer 1985). At the Farne Islands, the breeding population is affected by two principal factors. The regular immigration of birds into the colony from other areas has allowed an accelerated colony growth rate and facilitated rapid recovery from a period of high adult mortality caused by a 'red-tide' episode. Reproductive success is a function of nest site quality, and young birds tend to occupy less suitable sites than more experienced breeders. As population size increased the mean nest site quality declined (Potts *et al.* 1980). By contrast, at the Isle of May colony immigration was low and the colony is presently increasing without density-dependent regulation (Aebischer 1985). Short term factors which affect the colony are principally climatic, and affect first year survival rates, recruitment and breeding success. Food availability is a potentially limiting factor, since a temporary reduction in the normally rich food supplies triggered extensive non-breeding by the adult population and was associated with increased first year mortality and low fledging success (Aebischer 1985, 1986). Boekelheide & Ainley (1989) have shown that in an inshore marine habitat demonstrating considerable annual variation in productivity, Brandt's cormorants appear to have adapted by adopting a variable age at first breeding with the potential to begin breeding at 2 years old in some years, a low mate fidelity and by not breeding in every year as adults. These characteristics are also found in the Flightless cormorant, also an inhabitant of fluctuating but unpredictable environment (Harris 1979).

This study aimed to determine the factors affecting the population dynamics of the Blue-eyed shag, a species which inhabits the maritime Antarctic zone, and where due to the annual formation of sea ice, food availability is likely to fluctuate.

2. STUDY AREA, STUDY SPECIES, COLONIES AND GENERAL METHODS.

2.1 Study area and climate.

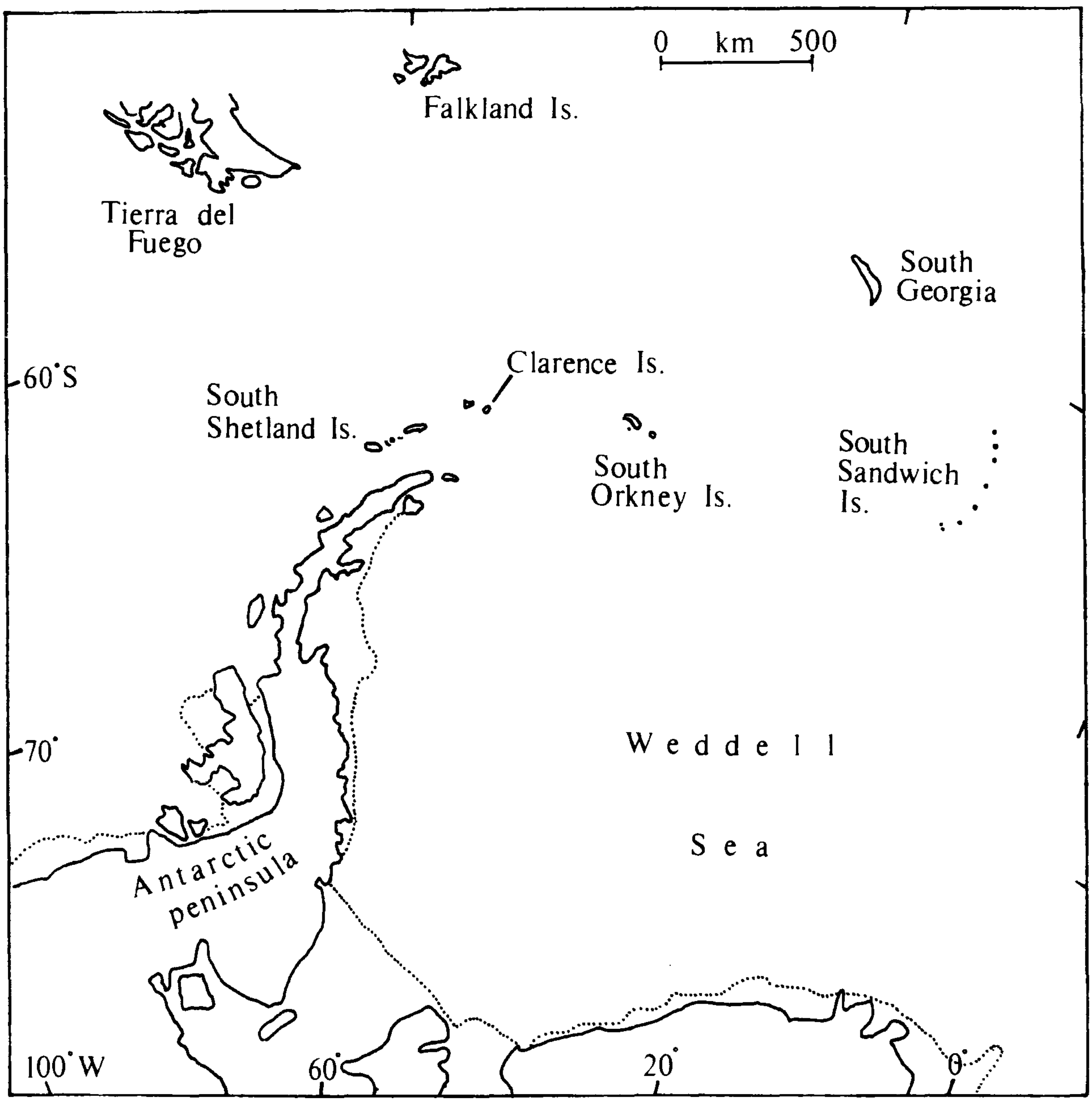
The South Orkney Islands are situated south of the Antarctic convergence on the Scotia arc, a submarine ridge connecting South America with the Antarctic mainland. They lie 1300 km south-east of Cape Horn, 640 km north-east of the Antarctic peninsula and the nearest land, Clarence Island in the South Shetlands group, is 354 km to the west (Figure 2.1)

Signy Island (60° 45′ S, 45° 36′ W) is the most southerly of the South Orkney Islands, and is unusually low lying and ice free having a maximum elevation of 284 m and permanent ice cover only over one third of its area. It is a triangular shaped island 7.5 km along its north-south axis and just over 5 km from east to west, at maximum. Geologically, it comprises regionally metamorphosed sedimentary rocks, mainly quartz-mica-schists with amphibolites and marbles (Matthews & Maling 1967).

Lying in the maritime Antarctic zone, Signy Island experiences a polar climate modified by the surrounding ocean and local topography (Holdgate 1964). The dominant feature of the weather pattern is the westward tracking depressions which are responsible for the prevailing westerly winds and frequent cloud cover, which results in only 14% of the maximum possible sunshine being recorded (Rootes 1988a, B.A.S. meteorological records). The climate is modified locally due to the proximity of Coronation Island, a large, montane and heavily glaciated island one kilometre north of Signy Island. Periodically, katabatic winds from Coronation Island sweep south across Signy creating rough sea conditions and are associated with rapid rises in temperature. Orographic cloud formation also often occurs under these conditions, and contributes to the reduced amount of sunshine recorded.

The mean monthly surface air temperatures, windspeed and hours of sunshine for

FIGURE 2. 1 LOCATION OF THE SOUTH ORKNEY ISLANDS.



each year between 1948 and 1987, were averaged and are shown in Figure 2.2a-c. A pronounced trough of low temperatures, windspeed and number of hours of sunshine is apparent during the winter months, but in the shags breeding season (from mid-October to February) the temperatures are higher, owing to the influence of the increased number of hours of sunshine. The windspeed cycle shows a bimodal pattern with two periods of relative calm, one in winter (June and July) and the other during the summer (December and January). The highest mean monthly windspeeds usually occurred in September and October and often caused the breakup of the sea ice. Figure 2.2d relates the date of sea ice breakup to year. Nearly half of the records indicated that the sea ice broke up during the windy period in September or October (91-152 days after 1 June), which coincides with the start of courtship by the shags.

During the study period (December 1985 until February 1988) the highest mean monthly maxima and the lowest mean monthly minima for surface air temperatures were -0.7 °C and -15.5 °C respectively and the surface seawater temperatures ranged from $+2.0$ °C to -1.7 °C (B.A.S meteorological records). Pack ice was first sighted in April in 1987 and May in 1986, and sea ice (which has formed every winter since 1947 with the exception of 1956) developed in May (1987) or June (1986), and broke out of Factory Cove by September (1986) or November (1987).

2.2 Study colonies.

There are two Blue-eyed shag colonies on Signy Island (Figure 2.3). The smaller is at North Point (72 breeding pairs in 1987) where the birds nest both on the top and on ledges of a low (9 m) cliff. By contrast, Shagnasty Island, situated 50 m offshore from the south coast, is ten times larger (729 breeding pairs in 1987) and the shags nest on the flat tops and shallow inclines of the island. During this study two subcolonies were recognised at Shagnasty, separated by about 70 m and on adjacent islets. The subcolony nearest mainland Signy Island is referred to as Shagnasty I/II (this was split into two by Shaw (1984), termed Shagnasty I and Shagnasty II), and the outer one as

FIGURE 2. 2 THE ANNUAL CYCLE OF a) WINDSPEED, b) TEMPERATURE AND c) SUNSHINE. POINTS REPRESENT THE MEAN OF ALL MEAN MONTHLY RECORDS BETWEEN 1948 AND 1987, VERTICAL BARS ± 1 SE.

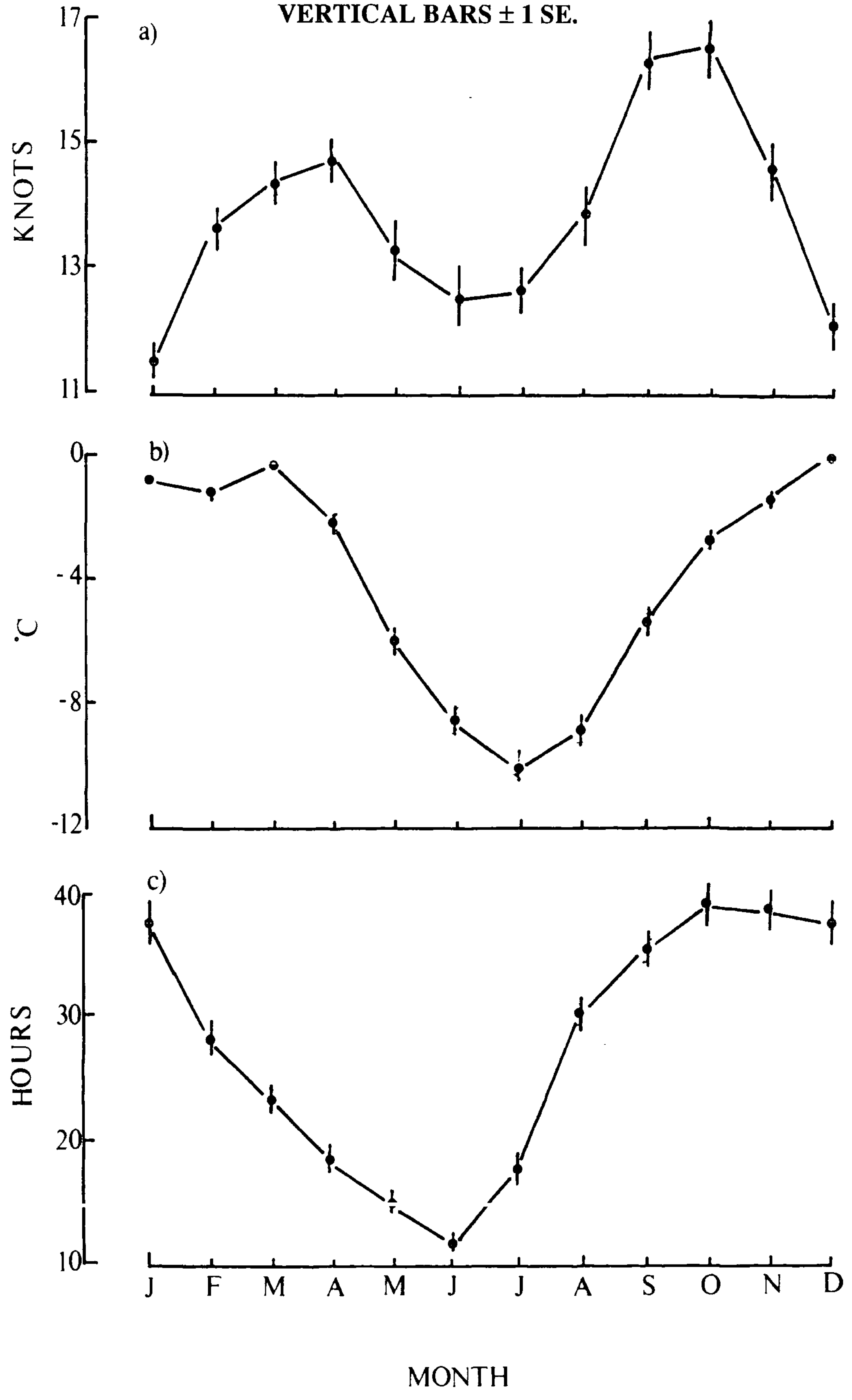


FIGURE 2. 2 cont THE DATE OF SEA ICE BREAKOUT IN FACTORY COVE IN EACH YEAR BETWEEN 1948 AND 1988.

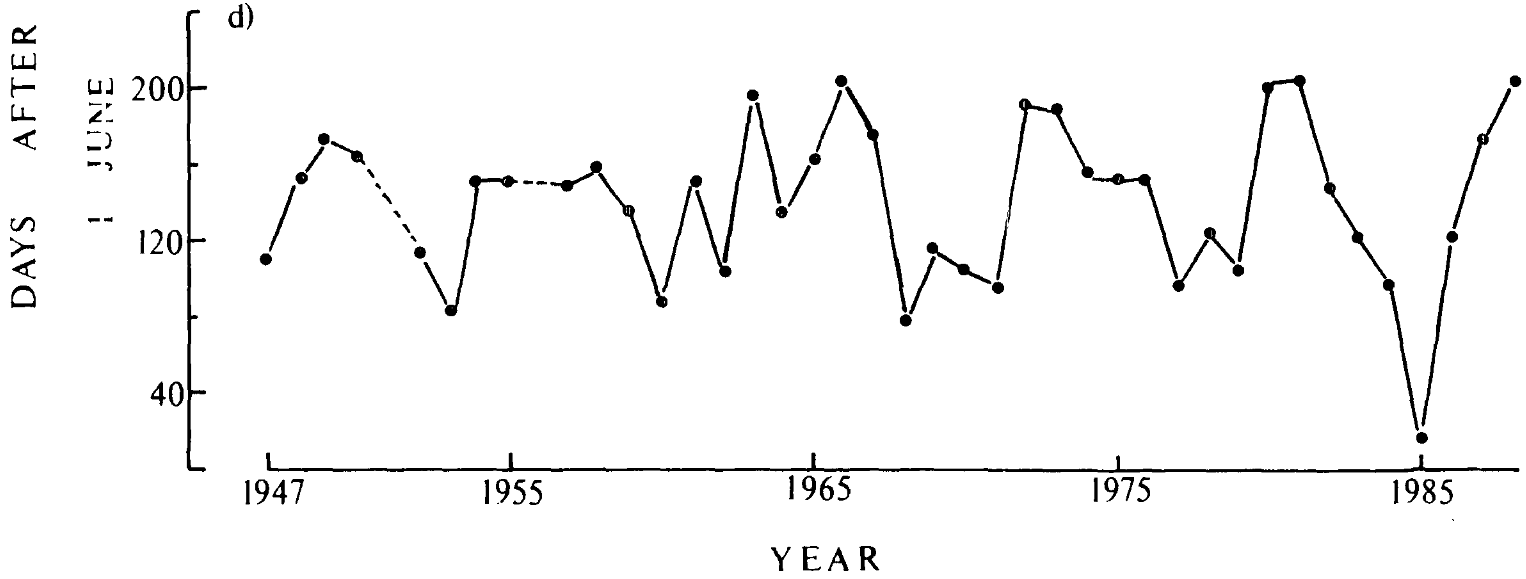
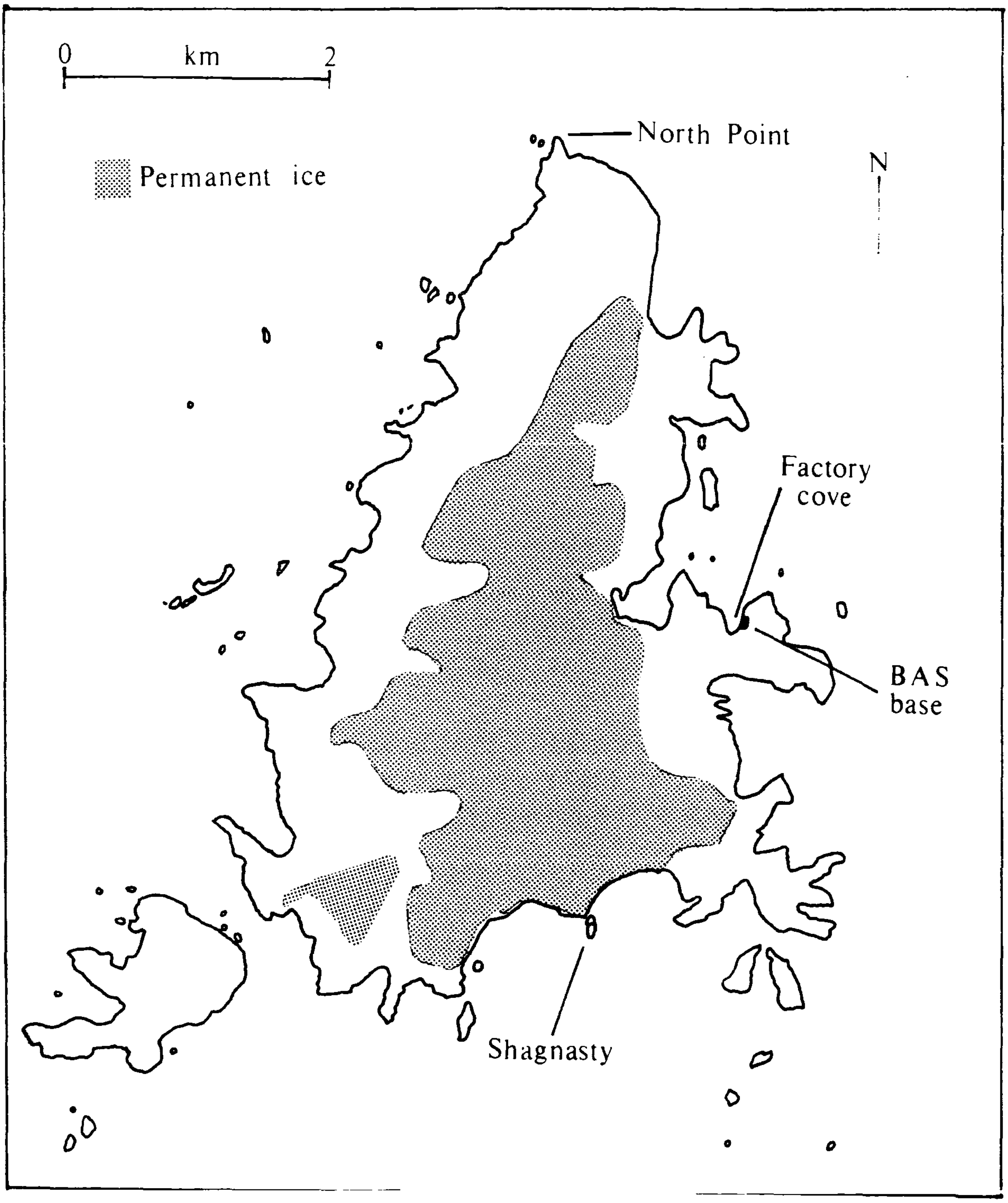


FIGURE 2. 3 SIGNY ISLAND SHOWING THE LOCATION OF NORTH POINT AND SHAGNASTY.



Shagnasty III (as in Shaw (1984)). The term 'colony' refers to North Point or the whole of Shagnasty. However, in some analyses it was convenient to consider North Point, Shagnasty I/II and Shagnasty III as equal units, and for simplicity, the term 'colony' was applied to all three areas, although it has been made clear that the Shagnasty subcolonies are being considered separately. During the summer months, access to the vicinity of Shagnasty was gained by walking along a stakeline erected on the McLeod glacier. The colony itself was reached at low tide by walking along a causeway connecting it to the mainland. At high tide, a small inflatable dinghy was pulled across on a steel cable when weather and sea conditions permitted. North Point could be reached on foot throughout the year and it was possible to drive to both colonies on the sea ice during winter using skidoos. All the nests at both colonies could be reached for examination.

Both colonies have been counted in most years since 1948 (at Shagnasty the counts were intermittent until 1968) although some of the early figures need to be regarded with caution because they were made during September or early October when the colonies might not have been fully occupied. Prior to 1968, all the counts on Shagnasty were made from the shoreline, where about a third of the colony is obscured and it is often not clear if the counts included both colonies (Shaw 1984). At North Point the colony has increased from 9 pairs in 1948 to 58 pairs in 1988 (Figure 2.4). There was a suggestion that in recent years the rate of growth had slowed, and the overall linear regression, colony size $= -2300 + 1.19$ year, fitted the data well ($F_{1,22} = 75.07$ $P<0.001$). Figure 2.5 shows that no overall pattern of change was apparent at Shagnasty I/II between 1960-88 ($r = 0.178$ df $= 15$ NS). Although the size of this subcolony appeared to fluctuate markedly between 1960-77 the accuracy of some of the counts was probably low. From 1977 until 1987 the counts were more accurate and Figure 2.5 shows that there is agreement in the direction of the changes between Shagnasty I/II and North Point. The Shagnasty III subcolony had not been regularly counted until 1982, although since then the number of breeding pairs has varied similarly to the other areas.

FIGURE 2. 4 COLONY SIZE AT NORTH POINT BETWEEN 1948 AND 1988.

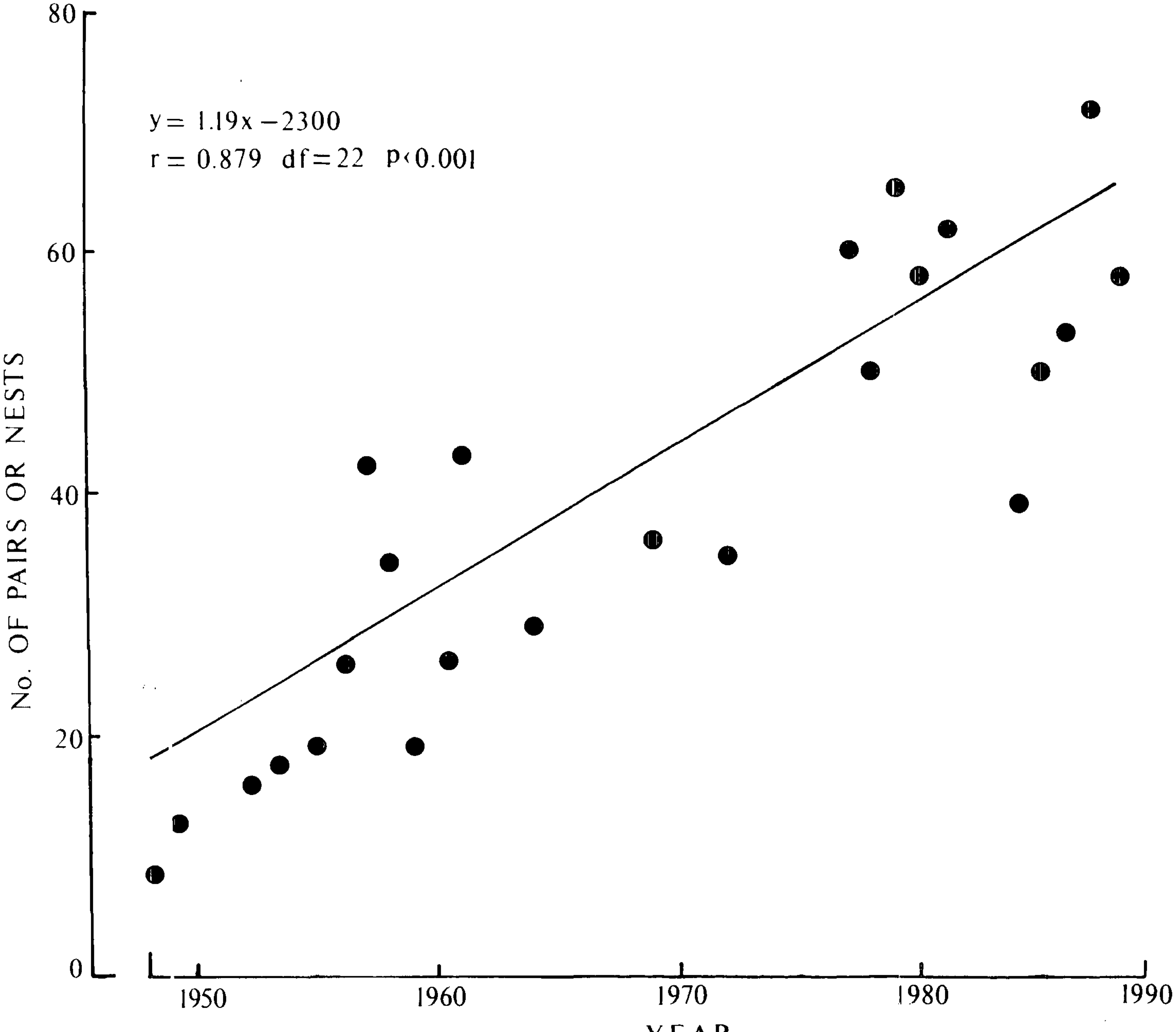
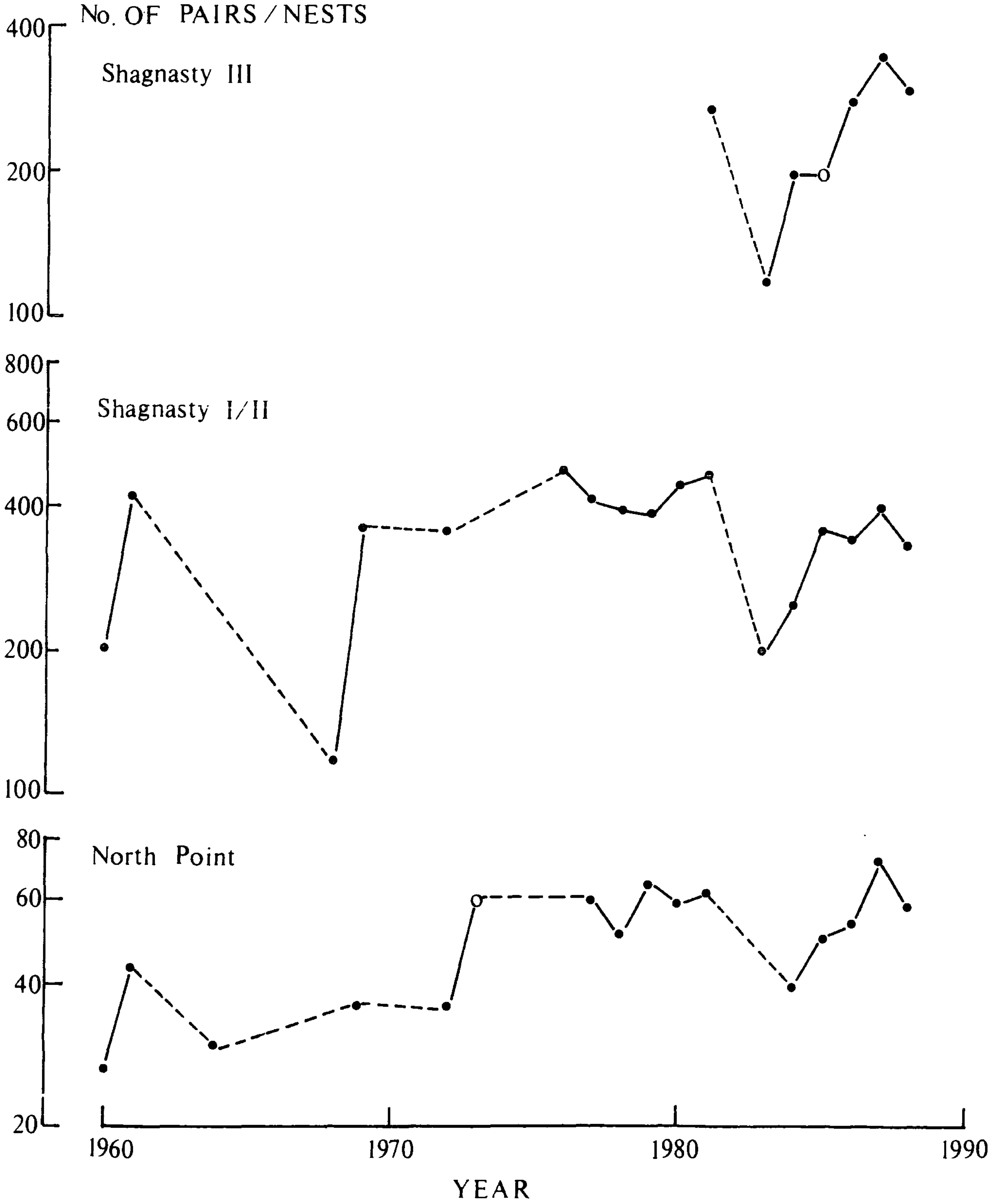


FIGURE 2. 5 COLONY SIZE AT NORTH POINT AND SHAGNASTY BETWEEN 1960 AND 1988. NOTE: LOG SCALE, SOLID LINES JOIN CONSECUTIVE YEARS, BROKEN LINES COVER PERIODS OF NO COUNTS, OPEN CIRCLES INDICATE ESTIMATES.



2.3 Study species.

2.3.1 Systematics of Blue-eyed shags.

The Blue-eyed shags occupy a circumpolar distribution on subantarctic islands and they also penetrate south along the Antarctic peninsula as far as 68°S (Shaw 1984) and extend north along the Pacific coast of South America to 37°S. The relationship between the various taxa is controversial and to some extent unresolved. The first Blue-eyed shag was described by Gmelin (in Murphy 1936) as *Phalacrocorax carunculatus*, a New Zealand species, although it is similar to South American shags in appearance (Murphy 1936).

Murphy (1936) argued that the South American members of the group comprise two species, *P. atriceps* and *P. albiventer*, and their sympatry in the Fuegian region seemed to confirm this idea (Behn *et al.* 1955). Most of the island populations are allopatric and have been given subspecific or specific status (or reclassified into a new genus with three subgenera (Voisin 1973)) on the basis of morphology and plumage pattern. Key distinguishing features are the position of the demarcation line between the black and white feathering on the side of the head and the presence of white alar bars and dorsal patches. Where authors have given these populations subspecific status they have been assigned either to *albiventer* (*purpurascens* on Macquarie Island; *melanogenis* on Crozet and Marion Islands (Rand 1954, Falla 1937)) or to *atriceps* (*nivalis* on Heard Island; *georgianus* on South Georgia; *bransfieldensis* on the Antarctic peninsula, South Shetlands and South Orkneys (Murphy 1936, Behn *et al.* 1955, Devillers & Terschuren 1978)).

During a study of mixed *atriceps* and *albiventer* colonies in Patagonia and the Magellanic region, Devillers & Terschuren (1978) found mixed pairs and numerous individuals with intermediate plumage characters. They concluded that *'atriceps'* and *'albiventer'* should be regarded as conspecific in their zone of overlap and united in a single species, *P. atriceps*. Subsequent studies have supported this conclusion, indicating the absence of behavioural isolation between *'atriceps'* and *'albiventer'* at mixed colonies (Siegel-Causey 1986) and the variability of the plumage and soft parts with season (Bernstein & Maxson 1981). In addition, Rasmussen (1986) has drawn attention to the cheek patterns of juvenile *'atriceps'* which are initially similar to those of *'albiventer'*. This latter point may explain the confusion regarding the identity of the type specimen (Devillers & Terschuren 1978) but still leaves unanswered the question of the status of Blue-eyed shags in other areas (Croxall 1984) and it is likely that a satisfactory solution awaits critical comparative ecological and genetic studies.

Since it is still unclear how Antarctic Blue-eyed shags are related to other forms, the subspecific name *bransfieldensis*, which has sometimes been applied to Antarctic populations, including those in the South Orkneys Islands, has not been used in this study and references to other populations are indicated by their locations. The vernacular name Blue-eyed shag is used in preference to the synonyms Emperor shag and Imperial cormorant since this is the most frequently used name in the literature (*e.g.* Clarke 1906, Murphy 1936, Behn *et al.* 1955, Voisin 1973, Devillers & Terschuren 1978, Bernstein & Maxson 1981, Croxall 1984, Shaw 1986, Siegel-Causey 1986, Rasmussen 1988a, 1988b).

2.3.2 Sexing Blue-eyed shags.

Blue-eyed shags display several sex-related differences, the most obvious being in their vocalisations. Males utter a resonant croak and females a quiet hissing sound (Shaw 1984) and in this respect they are similar to European shags (Snow 1963, Potts 1966). Other behavioural differences also allow separation of the sexes, particularly the 'gargling' advertisement display of males (see Figure 2(b) in Bernstein & Maxson 1982) and bringing nest material into the colony, which is only carried out by males (Bernstein & Maxson 1985). Observations of copulations and the synchronous sex-linked patterns of colony attendance (Bernstein & Maxson 1984) further aided the decision of a bird's sex. Blue-eyed shags also show sexual dimorphism with respect to bill depth, and with experience this could be used to sex many birds by sight (Plate 1). This technique was verified by measuring the bill depths of 86 birds sexed using the techniques above and only 7% could not be sexed (Figure 2.6). Previously, a discriminant function analysis had indicated the usefulness of bill depth in sexing Blue-eyed shags (Shaw 1984). In practice vocalisations enabled most birds to be sexed and using all the above techniques, together with previous recapture information (where birds had been sexed according to the same principles (Shaw 1984)), only 8 out of 3746 breeding birds examined were of indeterminate sex.

2.3.3 Ageing Blue-eyed shags according to plumage.

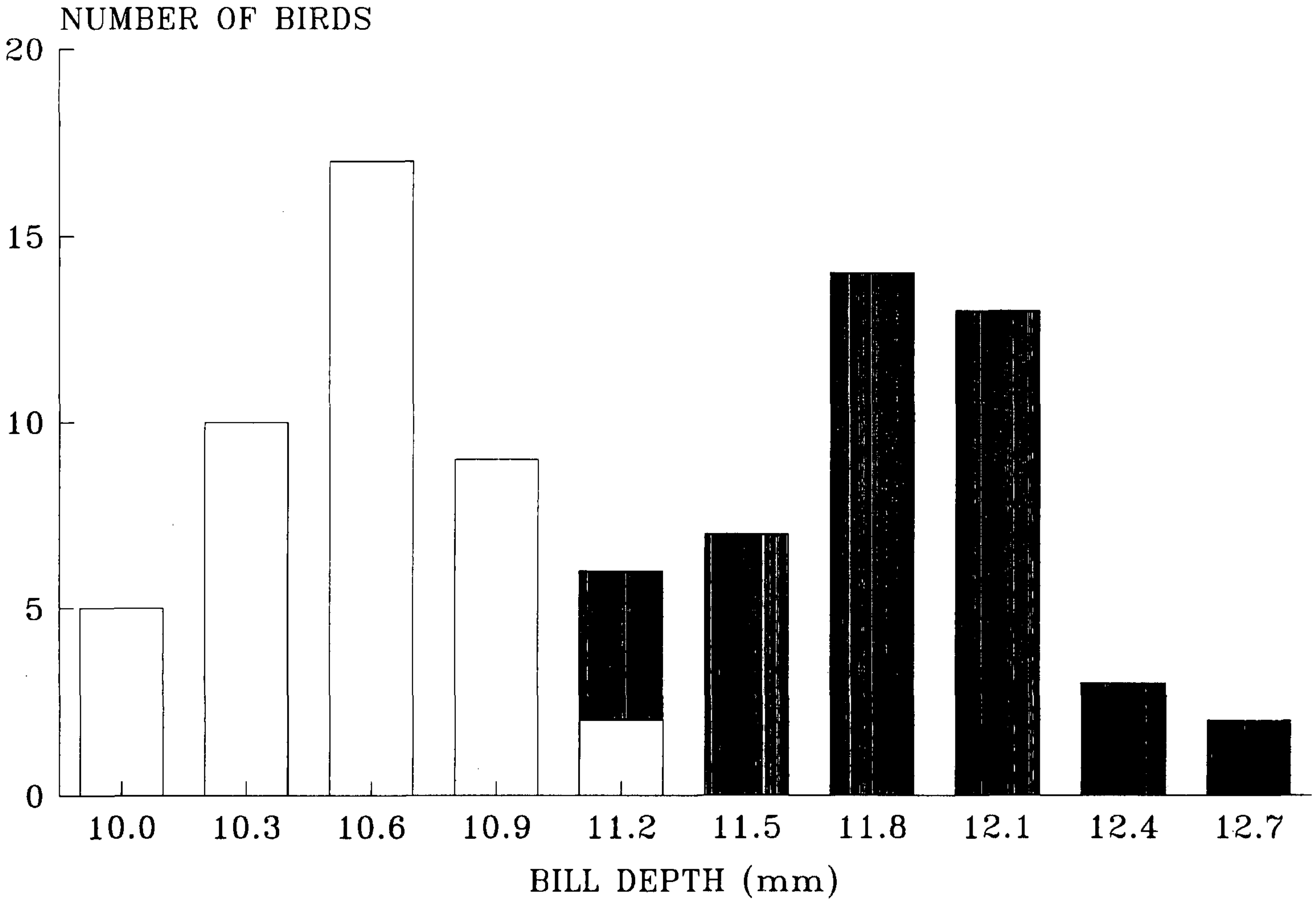
Many long lived birds (*e.g.* gulls, waders, raptors) have distinctive plumages during the pre-breeding period which enables their ages to be deduced (*e.g.* Newton *et al.* 1983). Potts (1966) showed that European shags could be reliably aged up to 2 years on the basis of plumage characters, and Murphy (1936) noted that for Blue-eyed shags, the brown plumage of 'young' birds was replaced by 'adult' plumage in the second year of life.

Since the austral breeding season spans two calendar years, 1 March was used in this study as the date on which a bird's age increases. Whilst this is arbitary it coincides approximately with the end of the breeding season and has the advantage that a bird's age does not change during the course of each breeding season. The term 'one year old' refers to a bird from 1 March after hatching until the next 1 March, when it becomes a 'two year old' bird and so on.

Blue-eyed shags could be aged up to three years old on the basis of retained brown juvenile feathers in their plumage. One year old birds had predominantly brown upper parts and could be distinguished readily from older birds. Two-year-olds resembled adult plumaged birds, from which they could be told apart by brown feathers mixed

PLATE 1 PAIR OF BLUE-EYED SHAGS AT THEIR NEST SITE, MALE ON LEFT. SHAGNASTY, OCTOBER 1987.

FIGURE 2. 6 BILL DEPTH OF MALE AND FEMALE BLUE-EYED SHAGS. SHADED = MALES, UNSHADED = FEMALES.



with the darker adult type on the upperparts, and the presence of unmoulted secondaries which showed as a brown wing patch. In addition, the crest if present, was usually smaller than that of older birds, although this ceased to be a useful guide by January as wear reduced the size of all bird's crests. The brown secondary patch was especially useful because it was visible from a distance, and capture was not necessary.

To assess the reliability of the brown secondary patch as an ageing criterion, a sample of 67 ringed birds were aged as two years old on the presence of the patch, prior to their rings being read. In all except one case the age was correct indicating that this method was 98.5% successful. The bird which was incorrectly aged was three years old and had retained some old secondaries. In 17 birds the number of old feathers forming the patch ranged between 1 and 9, although 15 had 5 or more old feathers. The time of year influences the number of old feathers seen with fewer remaining as the breeding season progresses. Most of the 67 birds above were caught in November, but Blue-eyed shags present at the colonies in January and February still had secondary patches.

By the third year of life, Blue-eyed shags closely resemble older birds although some still retain a few brown feathers in their upperparts, principally the crown and mantle. It was noticed that several three year old birds had a scaled effect on their lesser coverts due to contrast between the pale edges and darker centres of the feathers. These coverts were worn and brown unlike the adult pattern, which can also appear scaled, but in this case because of the contrast between the dark edges and grey centres. A sample of 35 birds aged as three years old on scaled brown lesser coverts was 80% correct, but this method was not subsequently used because it was necessary to catch birds to examine their coverts. Also all of the seven incorrectly aged birds were more than six years old suggesting that some individuals retained a juvenile feather pattern for several years after becoming adults, an occurrence which has been noted in some large gulls (Harris 1962, Cramp & Simmons 1982).

2.4 General Methods.

2.4.1 Ringing.

Until the early 1960's, birds were ringed using aluminium rings which being relatively soft, rapidly abraded becoming illegible and falling off. This problem is particularly acute in seabirds because the majority are long-lived, seawater corrodes their rings, and when on land they often abrade their rings against the substrate (Coulson & White 1955, 1957, Coulson 1976, Harris 1980). After 1962 monel (a nickel-copper alloy) replaced aluminium, but even this harder metal was subject to wear and corrosion (especially electrolytic crevice attack), and long-lived species, such as Herring gulls, or those likely to wear their rings excessively due to their lifestyle (for example burrowing species and those that rest on their tarsi) continued to abrade the inscription (Coulson 1976, Harris 1980). Recently, incoloy (a nickel-chromium alloy) and stainless steel have been used and the serial number double stamped to ensure that the sequence can be deciphered if individual digits are worn. This also facilitates reading the ring number in the field.

Different species of shags vary in the amount of wear which their rings receive and within a species, the degree of wear can vary with ring design as well as other, less discernible factors. In one study of European shags, 50% of the rings removed after eight years were illegible and clip fastened rings were more likely to be legible than the butt ended type (Galbraith & Furness 1983). However in a six year study of the Flightless cormorant, only 1 out of 300 birds had a worn ring (Harris 1980). In no case did abrasion on Blue-eyed shag rings render the inscription unreadable and even the oldest birds (18 years) had perfectly legible rings. This may be due to the snow cover which is present at the colonies throughout much of the year and which would reduce the amount of abrasion received by the rings.

Blue-eyed shags were first ringed on Signy Island in 1959 with aluminium Falkland

Islands Dependencies Survey (F.I.D.S.) rings but these were replaced by monel British Trust for Ornithology (B.T.O.) rings in 1962. Until 1986 B.T.O. size 'L' rings (internal diameter = 19.0 mm) were used which tend to be too big for this species and need to be correctly overlapped. In some years this had not been done and during this study it had been noticed that several rings were opening at the butt ends. From 1986 size 'K' rings (internal diameter = 16.0 mm) were put on.

An examination of 809 birds between 1985-87 revealed 47 cases where the rings had opened, although only 4 of these were considered likely to have been at risk of falling off. Table 2.1 shows that the affected rings were put on over many years but a significantly higher proportion were from 1976-78 than other years ($\chi^2 = 87.5$ df = 2 $P<0.001$). There were no differences with respect to sex in the numbers of birds with opening rings, suggesting that this was unrelated to differences in leg size (in which case females being smaller on average, would be expected to lose more rings), or in behaviour between the sexes. Inter-sexual differences in ring wear and ring loss have been reported in Red-billed gulls (Mills 1972), and in Herring gulls (Coulson 1976). From 93 birds colour-ringed in 1979-80 and recaptured in this study, only three males had lost their metal rings (these individuals were identified because they returned each year to the same nest sites wearing the same combinations of colour rings).

To summarise, only 4 out of 809 birds (0.5%) recaptured during the study period were likely to have been at risk of ring loss, and once fitted, rings remained legible for at least eighteen years. There was a tendency for some metal rings to open after they had been fitted but most of the birds affected were ringed in just three years, 1976-78. Although it was impossible to be certain why this occurred, both sexes were equally affected and the scarcity of opening rings since 1978 (despite an increase in both the number of birds ringed and recaptured) suggests that inexperienced ringers, a faulty batch of rings or a combination of these could have been the cause.

Table 2.2 shows the number of chicks ringed at Signy Island. Between 1959-68, 223 chicks were ringed, but ringing was not carried out annually. From 1969, shag chicks

TABLE 2. 1 NUMBERS OF BIRDS RECAPTURED BETWEEN 1985-87 WITH RINGS OPENING, IN RELATION TO THE YEAR OF RINGING.

Year		1969	1970	1971	1972	1973	1974	1975	1976
Number of opening rings	Males	0	1	1	0	0	0	1	9
	Females	0	1	0	0	1	1	2	5
Number not opening	Males	2	5	3	2	7	1	22	32
	Females	1	7	5	0	6	6	17	21

Year		1977	1978	1979	1980	1981	1982	1983	1984
Number of opening rings	Males	5	5	1	0	4	-	0	1
	Females	4	4	0	0	1	-	0	0
Number not opening	Males	18	14	1	31	128	-	10	109
	Females	21	14	0	36	105	-	12	126

Difference between sexes: $\chi^2_1 = 1.25$ NS

Proportion of rings opening between <1976, 1976-78, >1978: $\chi^2_2 = 87.50$ $P<0.001$

TABLE 2.2 **NUMBER OF CHICKS RINGED AT SIGNY ISLAND**
NOTE: CHICK RINGING AT SHAGNASTY III STARTED IN 1981.

Year	<1969	1969	1970	1971	1972	1973	1974	1975
Number ringed	223*	98	481*	600*	100	550	280*	393

Year	1976	1977	1978	1979	1980	1981	1982	1983
Number ringed	532	495	423	102	436	837	0	232

Year	1984	1985	1986	1987	1988
Number ringed	597	623	888	1107	930

* Indicates years when either North Point or Shagnasty were visited.

have been ringed in every year except 1982, and a total of 9927 were ringed up to 1988. Of these, 57% had been ringed since 1980. An average of 485 chicks were ringed each year, although there was considerable annual variation (range 0-1107 chicks). In 1986, the breeding population was 1342 birds of which 40% were ringed and 34% of known age; the corresponding figures for 1987 were 47% ringed and 43% of known age (n = 1602 birds). Attempts were made to catch as many one and two year old birds as possible in order to follow colony attendance prior to recruitment and facilitate sightings away from the colonies. One year olds were given numbered Darvic rings which could be read from 150m away through 10x50 binoculars thus avoiding the need for subsequent recapture.

2.4.2 Nest tagging and identification of the pair.

Each nest was marked to facilitate identification of the pair and to be certain that every breeding attempt was recorded. In 1985, rectangular plastic tags with painted numbers were used as nest markers and these were fixed to the outside of the nest using welding rods. Neither the tags nor the method of attachment was satisfactory, and in subsequent seasons indelibly numbered plastic cattle tags (Dalton 'rototags') were sewn into the side of the nest using a wire needle and balloon twine. These were much more resistant to theft by neighbouring shags and allowed nests to be quickly located on subsequent visits. Few tags were lost because occupied nests were vigourously defended by the pair, but in 27 cases where the tags had been lost, the numbers of adjacent nests allowed the identity of the nests to be deduced, and additionally in 1986, monochrome photographs showing each site on Shagnasty I/II and North Point aided recognition.

Identification of pairs was easily achieved once nest building had commenced and in the week prior to laying most birds became tame enough to allow examination of their legs for rings whilst they were at the nest. Wary individuals (including failed breeders, first time breeders and immatures) were either caught using a shag hook (a piece of wire shaped in the form of a shepherds crook and fixed to a 1.6m pole) or their rings were read through 10x50 binoculars. The term 'recapture' meant that a bird had been seen or caught, and was known to be either ringed or unringed. Nearly all ringed birds which were recaptured were also individually identified (see section 2.4.3).

In the first year of the study, 1985, no recaptures were made on Shagnasty III and many pairs were not recaptured on Shagnasty I/II because nest tagging could not be carried out until January. Additional recaptures of breeding birds were made by base personnel in 1984 and 1988, and it was possible to incorporate these data in some analyses. Where this extended dataset has been used, it is indicated in the text or tables.

During the study period, some breeding birds were missed because they failed and left the colony before they could be identified and their nests tagged. There are three indications that the numbers of birds which were missed in this way were low, at least at North Point and Shagnasty I/II during 1986 and 1987 :

1. A sample of birds was identified during the pre-breeding period (*i.e.* from the onset of continous colony occupation in August until the first egg was found) and when all the nests had been tagged, some of these birds were not seen at them. At Shagnasty I/II in 1986, from a sample of 121 birds identified, 8 were not subsequently seen at tagged nests. Of these 8, only 3 were seen again in 1987 or 1988. Similarly in 1987, 106 birds were identified, of which 22 were not seen during that breeding season. Only three of these 22 were seen in the following year (Table 2.3). At Shagnasty III in 1986, 23 birds were identified in a pre-breeding sample, and 4 of these were not seen at tagged nests. Three of these birds were seen subsequently. In 1987, 5 out of 22 birds were not seen in that season, and 3 of these were later seen in 1988. Insufficient numbers of birds were identified at North Point during the pre-breeding period to permit analysis.

2. The progress of the first nests to be tagged was monitored until all the nests in the colony were marked. Until 11 November 1986, 70 nests had been tagged on Shagnasty I/II and between then and 9 December (when nest tagging was

TABLE 2. 3 ESTIMATED NUMBER OF BIRDS AND NESTS MISSED AT SHAGNASTY I/II IN 1986 AND 1987 CALCULATED FROM A SAMPLE OF A) PRE-BREEDING BIRDS AND B) FIRST TAGGED NESTS.

A) Pre-breeding sample	Year	
	1986	1987
Number of birds in sample	121	106
Number of sample absent from tagged nests but seen subsequently	3	3
Total birds at tagged nests	666	778
Total birds estimated missed	17	22
B) Tagged nest sample		
Number of nests in sample	70	100
Number failed prior to tagging finished	2	None failed
Total number of tagged nests	333	389
Number nests estimated missed	10	-

completed), 2 pairs had failed and left the colony. In 1987, 100 nests were marked by 10 November and none had been abandoned by 5 December. At North Point in 1986, all nests were tagged on the same day, and in 1987 tagging was accomplished on two days separated by an interval of nine days during which no pairs whose nests had been tagged on the first occasion (n = 27) had failed and left the colony.

3. The temporal pattern of pair failure and nest desertion precluded many pairs being missed. The sample of tagged nests from the early part of the season suggested that few pairs had failed before nest tagging was finished. After its completion at Shagnasty I/II, a further 25 days elapsed in 1986 and 1987 before half of the pairs subsequently known to have failed, had done so (Figure 2.7).

It was unlikely that more than 22 pairs had failed and deserted Shagnasty I/II before their nests were tagged in either year (Table 2.3). In 1987, the remains of 13 untagged nests were found, supporting this conclusion. At North Point nest marking could be achieved quickly and no nests were missed.

Nests on Shagnasty III were always the last to be marked and therefore it is probable that more pairs were missed there. Figure 2.7 shows that when nest tagging was taking place on Shagnasty III in 1986 and 1987, just over half of the pairs known to have failed on Shagnasty I/II, had done so. As an indication of the number of pairs which failed on Shagnasty III in 1987, the remains of 25 nests were found. Although some may have been missed because they were deserted earlier in the season when the tendency to dismantle nests was marked, by the end of December, the appearance of newly hatched chicks coincided with a reduction in nest construction activity. The magnitude of error is likely to be small, because during the early part of the season few pairs failed and deserted the colony (see above), and whilst later the number of pairs which failed increased, the likelihood of their detection was greater, owing to a reduction in the destruction of deserted nests by other shags. This allowed the persistence of empty nests from most pairs which failed. Observations of a few tagged nests which were deserted in mid-December at Shagnasty I/II in 1986 (n = 5) and 1987

(n = 4) and the remains of which were still present a minimum of two weeks after desertion tended to confirm this, although the sample size is small and a possible bias towards more substantial nests, which would be more likely to survive and hence be detected, cannot be excluded.

A further indication supporting the conclusion that few pairs were missed before their nests were tagged is the absence of large gaps between nests. Nest spacing was regular in most parts of the colonies and the failure of many nests would have been noticed. Some pairs which did fail remained at their nests, increasing the chance that they would be identified. Not all birds seen at the deserted nest were from the original pair, but even in these cases, one or both of the original birds sometimes returned in the evening. The presence of one or both birds from the original pair was recorded at 11 nests after failure, including one where the original male was still present 21 days later.

Photographs of Shagnasty I/II and North Point taken during October 1987 showed the number of occupied nest sites, and when these were compared with the number of nests subsequently tagged, there was a good agreement. There were 313 nest sites visible on Shagnasty I/II compared to 317 tagged nests (this is the total number of tagged nests minus 72 nests which were started during tagging, since these mostly belonged to recruits which were unlikely to have been present when the photographs were taken). At North Point, 55 sites on the photograph compared with 49 tagged nests (23 nests started during tagging were deducted from this total).

2.4.3 Recapture efficiency of breeding birds.

The breeding population was equated with the number of tagged nests multiplied by 2. This assumed that all nests were tagged, only one pair bred at each nest in a season and that there was no polygamy. These are reasonable assumptions because very few nests were likely to have been missed before tagging (see section 2.4.2), there were no recorded multiple breeding attempts in one nest and no instances of polygamy were observed. Polygamy was also absent in an earlier study of Signy shags (Shaw 1984) and in a population of shags at Anvers Island (Bernstein & Maxson 1985).

The recapture efficiency of the breeding population (defined as the proportion of the breeding population which were recaptured) at North Point and Shagnasty during the study period, is shown in Table 2.4. Apart from Shagnasty I/II in 1985, more than 90% of the total breeding population at each colony were recaptured every year. There were significant differences in total recapture efficiency between the three colonies in each year of the study. In 1985, fewer birds were recaptured at Shagnasty I/II than at North Point because the visits to the former took place in January, two months later than in subsequent years, and the prevailing climatic conditions limited access (the mean monthly windspeed in January 1986 was 15.9 knots compared to 12.2 knots and 10.1 knots in 1987 and 1988 respectively). Both these factors resulted in fewer visits during the period when many tagged nests were failing and hence a reduction in the proportion of birds identified. At North Point the recapture efficiency was higher because recapture work took place in December, accessibility was guaranteed since it is a mainland site, and its small size enabled the whole colony to be checked in a day. In 1986, the recapture efficiency at Shagnasty I/II was significantly higher than at either North Point or Shagnasty III, reflecting the increased effort in recapturing birds there. About 44 hours were spent identifying birds at Shagnasty I/II compared with 14 hours at North Point and 26 hours at Shagnasty III. Similarly during 1987, the time spent at Shagnasty III was just over a third of that spent at Shagnasty I/II, resulting in a lower proportion of birds recaptured.

Birds which were not recaptured tended to be males except at Shagnasty I/II in 1986 and 1987. Differences between the sexes of unrecaptured birds were significant at Shagnasty I/II in 1985 (χ^2 = 37.0 df = 1 P<0.001), and at Shagnasty III in 1987 (χ^2 = 29.5 df = 1 P<0.001). These differences were probably due to the timing of colony visits rather than differences in the ease of identifying males and females. Visits often took place during the afternoon when males were absent, and in 1987, for example

TABLE 2.4 **RECAPTURE EFFICIENCY OF BREEDING BIRDS BETWEEN 1985-87**
NOTE: 1985 TOTALS INCLUDE UNSEXED BIRDS.

		1985			1986			1987		
		Number recaptured	Number not recaptured	Recapture efficiency (%)	Number recaptured	Number not recaptured	Recapture efficiency (%)	Number recaptured	Number not recaptured	Recapture efficiency (%)
North	males	45	3	93.8	48	5	90.6	69	3	95.8
Point	females	48	0	100.0	50	3	94.3	71	1	98.6
	total	95	5	95.0	98	8	92.5	140	4	97.2
Shagnasty	males	255	92	73.5	337	2	99.4	384	5	98.7
I/II	females	317	30	91.4	337	2	99.4	383	6	98.5
	total	574	124	82.2	674	4	99.4	767	11	98.6
Shagnasty	males	-	-	-	265	14	95.0	292	48	85.9
III	females	-	-	-	267	12	96.0	332	8	97.6
	total	-	-	-	532	26	95.3	624	56	91.7

Difference between sexes 1985 SNI/II $\chi^2_1 = 37$ $P<0.001$
in recapture efficiency: 1987 SNIII $\chi^2_1 = 30$ $P<0.001$

TABLE 2.4 - continued

Differences in total recapture efficiency

a) between years

colony	χ^2	df	P
North Point	3.0	2	NS
Shagnasty I/II	219	2	<0.001
Shagnasty III	5.8	1	<0.05

b) between colonies

year	χ^2	df	P
1985	9.6	1	<0.01
1986	28	2	<0.001
1987	41	2	<0.001

only 1 out of 15 hours spent recapturing birds on Shagnasty III, was during the morning compared to approximately 11 out of 40 hours on Shagnasty I/II. Although observations suggested that females were the more wary sex, the difference was judged insufficient to affect the likelihood of recapture, because of the synchronous pattern of colony attendance and strong nest site tenacity. When the recapture effort was intensified, as at Shagnasty I/II in 1986 and 1987, the bias towards males disappeared.

Apart from lower recapture efficiencies at Shagnasty I/II, for reasons discussed above, and at Shagnasty III, as a result of fewer males being caught because of the timing of colony visits, the absence of differences between years indicated that at each colony the recapture effort was consistent. There were no significant differences in any year at North Point, or in the principal study years of 1986 and 1987 at Shagnasty I/II (Table 2.4).

The number of birds recaptured was subdivided into ringed and unringed birds (Table 2.5). There were significant differences between colonies in the proportion of ringed birds recaptured. The highest proportion of ringed birds, about 70%, was at North Point, and the lowest was about 34%, at Shagnasty III. Between these extremes, at Shagnasty I/II, about half of the birds recaptured were ringed. These differences probably arose from variation in the effort put into ringing chicks, and to a lesser extent adults, at each colony, rather than the differential immigration of unringed birds (see section 3.2.2). Apart from Shagnasty I/II in 1985, there were no significant differences between the sexes in the proportion of ringed birds, although there was a consistently higher proportion of ringed males at both Shagnasty subcolonies in all years. Differences in the number of each sex ringed as adults and recaptured during the study period, could not account for the variation, since equal numbers of males and females ringed as adults were recaptured at Shagnasty I/II in 1985 (n = 38 birds), and the differences at all colonies in other years was small. There was no obvious explanation, unless there was bias towards recapturing ringed males in 1985. This could have arisen because several observers were involved in recapturing birds.

TABLE 2.5 NUMBER OF RINGED AND UNRINGED BIRDS AMONG THE RECAPTURED PART OF THE BREEDING POPULATION, 1985-87. NOTE: 1985 TOTALS INCLUDE UNSEXED BIRDS.

		1985			1986			1987		
		Ringed	Unringed	% Ringed	Ringed	Unringed	% Ringed	Ringed	Unringed	% Ringed
North	males	33	12	73.3	30	18	62.5	48	21	69.6
Point	females	36	12	75.0	36	14	72.0	51	20	71.9
	total	70	25	73.7	66	32	67.3	99	41	70.7
Shagnasty	males	141	114	55.3	167	170	49.6	218	166	56.8
I/II	females	143	174	45.1	153	184	45.4	192	191	50.1
	total	284	290	49.5	320	354	47.5	410	357	53.5
Shagnasty	males	-	-	-	80	185	30.2	122	170	41.8
III	females	-	-	-	72	195	27.0	126	206	38.0
	total	-	-	-	152	380	28.6	248	376	39.7

Difference between sexes in % ringed: 1985 SNI/II $\chi^2_1 = 5.5$ $P<0.05$

TABLE 2.5 - continued

Differences in total percentage ringed

a) between years

colony	χ^2	df	P
North Point	0.9	2	NS
Shagnasty I/II	5.3	2	NS
Shagnasty III	15.4	1	<0.001

b) between colonies

year	χ^2	df	P
1985	18	1	<0.001
1986	74	2	<0.001
1987	54	2	<0.001

There were no differences between years in the total proportion of ringed birds at North Point or Shagnasty I/II (Table 2.5). A significantly higher proportion of ringed birds were recaptured at Shagnasty III in 1987, compared to 1986 ($\chi^2 = 15.4$ df = 1 $P<0.001$), probably reflecting the increased numbers of recruits to the breeding population from the 1984 cohort, in which most of the chicks were ringed. Of relevance, is the proportion of ringed birds at North Point and Shagnasty I/II, which is also higher in 1987 than in 1986, although in neither case was the difference significant. The ringed birds in Table 2.5 can be further divided into those which were individually identifiable because their ring numbers were read, and those only known to be ringed and not identified individually. Table 2.6 shows that most ringed birds were individually identified. The proportions were similar in all years and between all three colonies, except at Shagnasty I/II where fewer were identified in 1985 ($\chi^2 = 19.2$ df = 2 $P<0.001$). Although the samples are small, more males than females were not identified at North Point and Shagnasty I/II, indicating again the influence of the timing of colony visits

2.4.4 Analysis and data storage.

Recapture data was initially stored in a British Antarctic Survey (B.A.S.) microcomputer database. This was transferred to Oracle relational database management software operating on a Digital Electronic Corporation VAX 8350, once back in Britain. Most statistical analyses were carried out using the Minitab statistical package and other statistical procedures follow Sokal & Rohlf (1981), Fowler & Cohen (1986) or Parker (1979). Where Chi-squared tests with only one degree of freedom are used, Yates's correction for continuity has been applied. Measurements are given in S.I. units and the following abbreviations are used: n = sample size, df = degrees of freedom, NS = not significant, SE = standard error, SD = standard deviation, Anova = analysis of variance. The term 'significant' is only used in the statistical sense.

TABLE 2. 6 **NUMBER OF RINGED BIRDS INDIVIDUALLY IDENTIFIED**
NOTE: 1985 TOTALS INCLUDE UNSEXED BIRDS.

		1985			1986			1987		
		Identified	Not Identified	% Identified	Identified	Not Identified	% Identified	Identified	Not Identified	% Identified
North	males	31	2	93.9	26	4	86.7	45	3	93.8
Point	females	35	1	97.2	36	0	100.0	49	2	96.1
	total	67	3	95.7	62	4	93.9	94	5	94.9
Shagnasty	males	129	12	91.5	164	3	98.2	214	4	98.2
I/II	females	137	6	95.8	153	0	100.0	189	3	98.4
	total	266	18	93.7	317	3	99.1	403	7	98.3
Shagnasty	males	-	-	-	79	1	98.8	122	0	100.0
III	females	-	-	-	71	1	98.6	126	0	100.0
	total	-	-	-	150	2	98.7	248	0	100.0

Difference between years: Shagnasty I/II $\chi^2_2 = 19.2$ $P<0.001$

3. EMIGRATION, IMMIGRATION AND INTERMITTENT BREEDING.

3.1 Introduction

It has been suggested that the tendency for animals to move away from their natal or breeding area to other breeding areas (dispersal), is a consequence of the type of mating system they have evolved (Greenwood 1980). Such dispersal usually involves one sex more than the other; in birds it is females which are often the more dispersive sex. Greenwood (1980) argued that because males need to defend fixed resources, such as territories or nest sites, to acquire females, this acts as a constraint on their dispersal.

Seabirds generally show a high degree of colony fidelity once they have become established as breeders (*e.g.* Richdale 1957, Coulson 1966, Potts 1969), although poor reproductive success is associated with dispersal in the Yellow-eyed penguin (Richdale 1957), Puffin (Ashcroft 1979) and Goldeneye (Dow & Fredga 1983). Prior to establishment, however, appreciable dispersal from the natal colony is usual, particularly among females. Avoidance of inbreeding has been postulated as one explanation although evidence for the harmful effects of inbreeding is scarce (Greenwood 1980).

Dispersal has potentially important consequences for the population regulation of Signy Blue-eyed shags. In European shags, immigration was a factor of major importance determining population levels on the Farne Islands, and it allowed a rapid recovery of the population following a period of exceptional mortality caused by 'red-tides' (Potts *et al.* 1980). The assumption, common in population studies, of parity between emigration and immigration, may be unjustified because of differences in emigration rates between colonies. In contrast to the Farne Islands, the Isle of May shag colony showed similarly low levels of both emigration and immigration (Aebischer 1985).

In this chapter, the extent of philopatry (the return of birds to their natal colony to breed), and of colony fidelity among experienced breeding birds is assessed. The influence of sex, age and brood position on dispersal has been investigated as well as the evidence for intermittent breeding by experienced breeders. Emigration, or the failure of part of the adult population to attempt breeding in particular years, can have profound effects on annual adult survival rate estimates, hence an appreciation of the magnitude of these factors is an important prerequisite to survival rate calculations.

3.2 Dispersal between Signy Island and other South Orkney colonies.

3.2.1 Emigration of Signy Island birds.

The emigration of birds from Signy Island to other colonies in the South Orkney Islands could not be measured in detail because of the limited opportunity for travel to other islands in the group. Apart from Signy Island, seven other Blue-eyed shag colonies are presently known from the South Orkney Islands (Figure 3.1), although estimates of colony size only exist for three (Table 3.1).

Atriceps and Grey Islands, at 27 km and 32 km respectively, are the closest to Signy Island. During the 1987 breeding season both islands were visited and a total of 280 breeding shags were examined, representing 26% of the Grey Island colony (n = 157 nests) and 19% of the Atriceps Island colony (n = 524 nests). No ringed birds were seen. Since 1969, these islands have only been visited four times, and the only other recent visits have been to Atriceps Island (one summer and one winter visit), when a single ringed bird was seen, during the winter visit, out of 900 birds present (Forster 1981). However, even this record may be atypical because in 1981, the year of the sighting, the winter was unusually severe. It was the second consecutive winter in which the sea ice had persisted for about 200 days, much longer than the mean duration of 141 days, and the timing of ice breakout, in December, was very late compared with other years (Clarke *et al.* 1988).

FIGURE 3. 1 THE LOCATION OF KNOWN BLUE-EYED SHAG COLONIES IN THE SOUTH ORKNEY ISLANDS. (SEE TABLE 3. 1 FOR KEY).

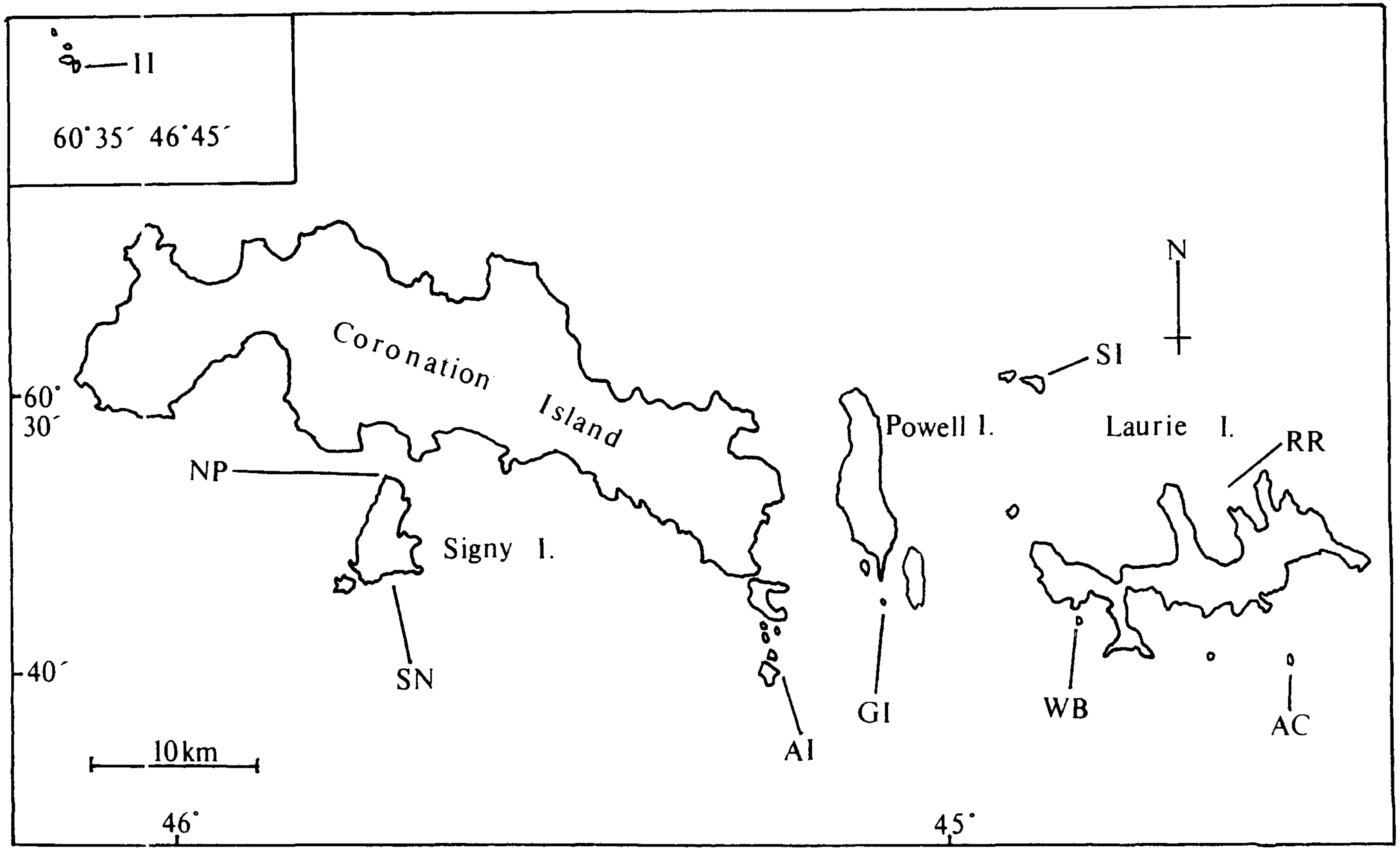


TABLE 3. 1 **KNOWN BLUE-EYED SHAG COLONIES IN THE SOUTH ORKNEY ISLANDS. NOTE: ABBRIEVIATIONS REFER TO FIGURE 3.1.**

Colony	Distance from Shagnasty (km)	Size	Source
Shagnasty (SN)	-	729 pairs	this study
North Point (NP)	6.5	72 pairs	this study
Atriceps Island (AI)	27	524 nests	this study
Grey Island (GI)	32	144 nests	this study
Saddle Island (SI)	42	not known	Clarke (1906)
Wilton bay (WB)	47	180 nests	Ardley (1936)
Inaccessible Islands (II)	48	not known	Ardley (1936)
Rudmose rocks (RR)	52	not known	Ardley (1936)
Ailsa craig (AC)	57	not known	Ardley (1936)

3.2.2 Immigration from other colonies to Signy Island.

The immigration of birds to Signy Island could not be assessed directly because no shags have been ringed elsewhere in the South Orkney Islands. However, there were only two possible sources of unringed breeding birds, those hatched on Signy Island which evaded ringing as chicks, and immigrants from other colonies. Since some unringed birds fledged every year on Signy Island, it is unlikely that immigration alone could account for all the unringed breeding birds, as fidelity to the natal colony was high (section 3.3.2).

Figure 3.2 shows that there was a decrease in the proportion of unringed breeders between 1984-87 and the pattern was generally similar at all three colonies, although a higher proportion of unringed birds occurred in 1988, principally at Shagnasty III. The changes in the numbers of ringed and unringed breeding birds at each colony between 1984-88 are shown in Table 3.2, although only for Shagnasty I/II were the data complete for every year. Since adults were only ringed in 1979 and 1980 and only 51 of these were alive in 1987, almost all ringed birds recaptured during this study were recruits from Signy Island. The total number of breeding birds increased between 1984-87, but the proportion of unringed birds amongst them decreased at all colonies. The combination of a decreasing proportion of unringed breeding birds and a simultaneous increase in the total number of breeding birds, indicated that immigration to Signy Island from other colonies was not the main factor influencing the change in the breeding population during 1985-87. Indirectly, this suggested that immigration to Signy Island was low.

The number of unringed breeding birds in a given year is composed of breeding birds surviving from the previous year, recruiting birds from Signy and, if present, immigrants. To estimate the number of immigrants during 1985, the number of unringed birds remaining after elimination of survivors from the previous year and recruits from the current year, was determined (Table 3.3). Excluding Shagnasty III, in 1985 there

FIGURE 3. 2 CHANGES IN THE PROPORTION OF UNRINGED BREEDING BIRDS BETWEEN 1984-1988.

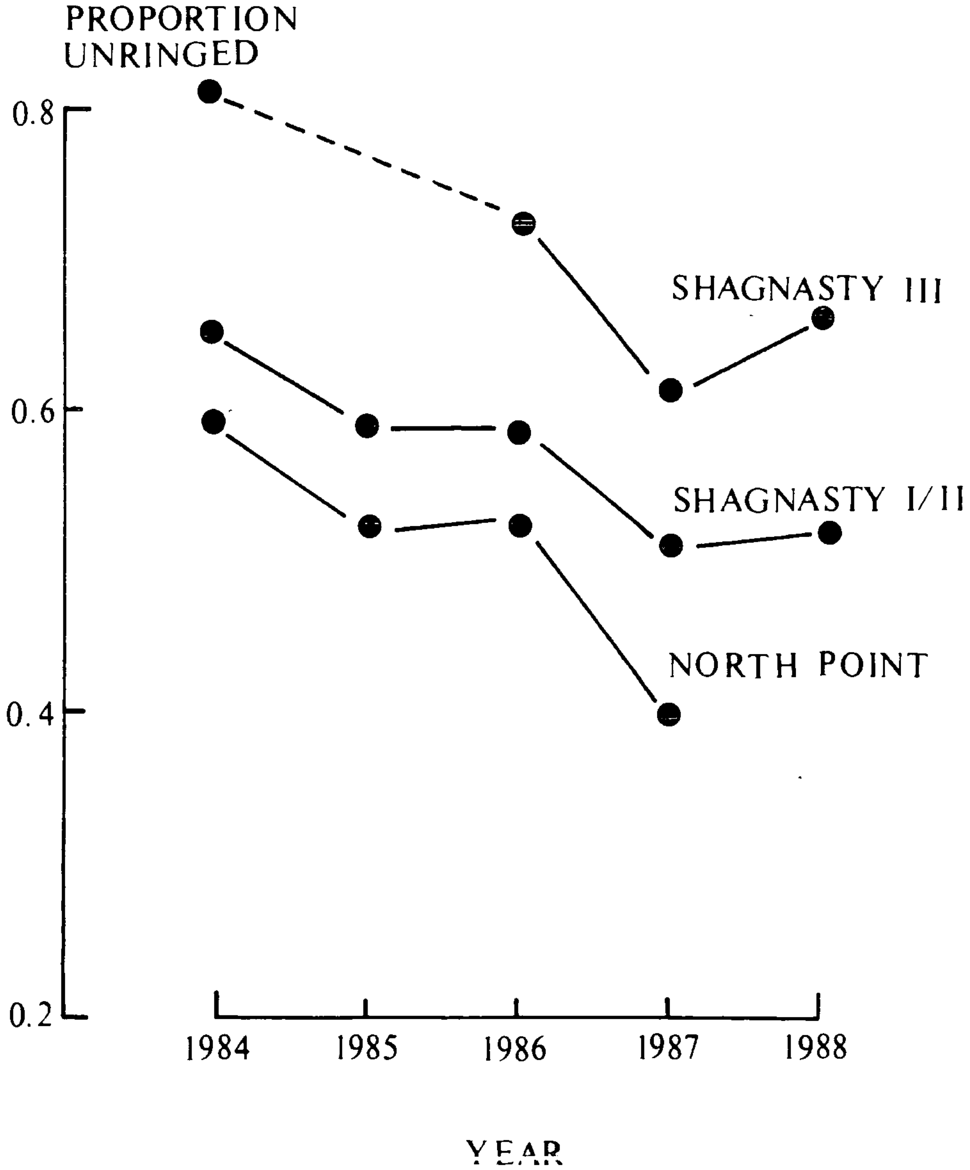


TABLE 3. 2 CHANGES IN THE BLUE-EYED SHAG BREEDING POPULATION ON SIGNY ISLAND BETWEEN 1984-88 WITH RESPECT TO WHETHER RINGED OR UNRINGED. NOTE: BIRDS RINGED AS ADULTS ARE INCLUDED IN THE UNRINGED COLUMN.

	SHAGNASTY I/II			SHAGNASTY III			NORTH POINT		
Year of recapture	Ringed as chicks	Unringed	Proportion unringed	Ringed as chicks	Unringed	Proportion unringed	Ringed as chicks	Unringed	Proportion unringed
1984	164	308	0.65	74	306	0.81	31	44	0.59
1985	228	328	0.59	-	-	-	44	48	0.52
1986	274	397	0.59	144	386	0.73	44	50	0.53
1987	372	388	0.51	241	383	0.61	81	54	0.40
1988	311	332	0.52	157	306	0.66	-	-	-

TABLE 3.3 THE TOTAL NUMBER OF UNRINGED BREEDING BIRDS IN RELATION TO THE ESTIMATED NUMBER OF UNRINGED RECRUITS. NOTE: EXCLUDING SHAGNASTY III IN 1985 AND 1986, ALL COLONIES INCLUDED IN 1987.

Year of Recruitment	Total number of unringed breeding birds	Number of unringed recruits and immigrants	Recruiting cohort(s)	Number of unringed chicks fledged in recruiting cohort(s)	Number of unringed recruits estimated from recruiting cohort(s)	Estimated number of immigrants
1985	376	98	1980 +1981	766	133	(0)*
1986	447	112	1980 +1981	766	107	5
1987	825	88	1984	70	27	61

* Estimated number of unringed recruits exceeded observed unringed recruits and immigrants combined.

were 376 unringed breeding birds of which 278 had survived from 1984, since 352 unringed birds were breeding then, and the survival rate between 1984-85 was 0.791 (Chapter 4). The remaining 98 birds are therefore recruits to the breeding population (*i.e.* Signy birds) and immigrants. The number of recruits can be estimated since 169 out of 170 ringed recruits in 1985 came from the 1980 and 1981 cohorts (Chapter 5), and the number of unringed chicks fledging from Signy can be calculated from this cohort as follows. In 1980, 523 chicks were ringed at Shagnasty I/II and North Point, 85 of which died before fledging, leaving 438 which fledged. The total number of chicks is obtained from Shaw (1984); 504 pairs bred at Shagnasty I/II and North Point, and the mean number of chicks fledged per pair was 1.48, giving 746 chicks fledging in total. The number of unringed chicks which fledged was 746 − 438 = 308. Similarly in 1981, 533 ringed chicks fledged (55 which died prior to fledging have been omitted) at Shagnasty I/II and North Point. The total number of chicks fledging was obtained from 527 pairs x 1.88 chicks per pair = 991 chicks (figures from Shaw 1984), and therefore the number of unringed chicks fledging is 991 − 533 = 458. Combining both cohorts, 1737 chicks fledged in total of which 766 were unringed. Of the 971 ringed birds which fledged in 1980 + 1981, 169 or 0.174 recruited in 1985. Assuming a similar proportion of the 766 unringed chicks fledging in 1980 + 1981 recruited in 1985, gives 133 recruits. However only 98 unringed birds were actually observed, less than expected from Signy recruits alone, suggesting that a negligibly small number of immigrants were present in 1985.

The procedure can be repeated for 1986. Excluding Shagnasty III again, 447 unringed birds were seen, and since the survival rate between 1985-86 was 0.892 (Chapter 4), and the number of unringed breeders in 1985 was 376, 447 − (0.892 x 376) = 112 birds are recruits plus immigrants. The proportion of ringed recruits from the 1980 + 1981 cohorts in 1986 is 136/971 = 0.14, and applying this proportion to the 766 unringed chicks fledging in 1980 + 1981 gives 107 recruits expected in 1986 from these cohorts. The 5 birds remaining after subtraction of the 107 from the 112 seen may have been immigrants, although since 11% of the ringed birds which recruited in 1986 were from other cohorts apart from 1980 and 1981, even these may have originated on Signy.

Finally in 1987, 825 unringed birds were breeding at all three colonies, of which 833 x 0.885 = 737 were survivors from 1986, leaving 88 recruits plus immigrants. In 1984, 595 ringed chicks and approximately 70 unringed chicks fledged (data from Price 1984), and the proportion of ringed chicks recruiting in 1987 was 230/595 = 0.387. Assuming the same proportion of the 70 unringed chicks also recruited in 1987 leaves 88 − (70 x 0.387) = 61 immigrants. This is probably an overestimate, since as in 1986, recruits came from other cohorts for which there was no information on the numbers of unringed birds fledging.

It is concluded that the population changes between 1984-88 were not principally the result of immigration into Signy Island colonies, and that the changing proportions of unringed breeding birds were consistent with the recruitment of cohorts of birds which had been subject to variable chick ringing effort. During 1985-87 the maximum number of immigrants was likely to have been 61 birds in 1987, which was approximately 5% of the breeding population.

3.3 Movements between Signy Island colonies.

3.3.1 Colony fidelity of breeding birds.

The colony fidelity of birds which had bred previously, was examined at North Point and Shagnasty, 6.5 km apart, and at each Shagnasty subcolony, separated by a mere 100 m. The number of one-year intervals of no colony change was calculated by considering the retrap histories of breeding birds seen in successive seasons at the same colony. For example, an individual known to have bred at North Point in 1985 and 1987 yielded two one-year intervals of no colony change. In calculating the number of yearly intervals of no change for birds which were not recaptured in every year, it has been assumed that after moving, birds stayed at their new colony, unless there was evidence to the contrary. This is a reasonable assumption, since out of 283 birds recaptured in a minimum of three consecutive seasons, only one moved more than once (this individual moved twice and its second movement was excluded from the analysis).

The colony exchanges of experienced breeding birds are shown in Table 3.4. During the study period (1985-87) only one bird moved between North Point and Shagnasty out of 886 breeders. It was a 10 year old female (all ages relate to the year before moving), which moved from Shagnasty I/II in 1986 to North Point in 1987. Considering both Shagnasty subcolonies, four birds from each moved. At Shagnasty I/II, two 4 year old males moved in 1986, and two females, aged 6 and 4, moved in 1987 and 1986 respectively. All four birds which moved from Shagnasty III did so in 1987. Three of these were females, aged 2, 2 and 13, and the other bird was a 5 year old male. The sample is too small to allow comparison between the sexes in the extent of movement between colonies. The annual rate of colony exchange between North Point and Shagnasty during the study period was 1/827 = 0.12%. Between the Shagnasty subcolonies it was 8/707 = 1.13% *per annum*, over nine times higher than the rate between North Point and Shagnasty.

There are no significant differences in the proportions of birds moving each year during 1985-87 or between 1979-84. Only for birds moving from North Point to Shagnasty was there an appreciable difference between the two periods. No birds moved during 1985-87 but previously, six birds had moved. These movements were not obviously clumped in any particular year, two birds each moving in 1980-81, 1981-84, and 1984-85.

Of the 30 birds which moved, 1.76% of females moved *per annum*, compared to 1.06% of males, a difference which is not significant (n = 1040 and n = 1143 year intervals respectively, $\chi^2 = 1.39$, df = 1, NS). Table 3.5 shows that for those birds ringed as chicks, the age range was between 2 and 13 years, but most were under 7 years old. There is a suggestion that more males moved at 4 and 5 whereas females

TABLE 3.4

COLONY EXCHANGE IN EXPERIENCED BREEDING BIRDS DURING 1985-87 AND 1979-84. ALL BIRDS WERE RECAPTURED BETWEEN 1985-87.

Movement		1985 - 1987			1979 - 1984		
		No. moved	Year intervals of no change	Annual change (%)	No. moved	Year intervals of no change	Annual change (%)
From:	To:						
North Point	Shagnasty	0	120	0.00	6	235	2.55
Shagnasty	North Point	1	707	0.14	2	1091	0.18
Shagnasty I/II	Shagnasty III	4	534	0.75	6	845	0.71
Shagnasty III	Shagnasty I/II	4	173	2.31	7	246	2.85

Proportion moving each year 1985-87 *v* 1979-84:		
NP to SN	$P = 0.18$ (Fisher's exact)	
SN to NP	$P = 1.00$ (Fisher's exact)	
SNI/II to SNIII	$\chi 2_1 = 0.06$	NS
SNIII to SNI/II	$\chi^2_1 = 0.00$	NS

TABLE 3.5

COLONY EXCHANGE IN BREEDING BIRDS BETWEEN 1979-87 IN RELATION TO AGE AND YEAR OF RINGING AS CHICKS. NOTE: NO CHICKS RINGED IN 1982.

Age prior to movement	2	3	4	5	6	7	8	9	10	11	12	13
Males	0	1	3	2	1	1	0	0	0	0	0	0
Females	2	0	1	2	5	0	3	0	0	0	1	1

Year of ringing	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1983	1984
No. ringed	481	600	100	550	280	393	532	495	423	102	436	837	232	597
No. moved	1	0	0	2	0	3	2	5	2	0	1	5	0	2

which moved were older, 5 and 6 years, although the sample sizes were small. There was no evidence that birds which moved came from particular cohorts (Table 3.5), and the greater number of birds apparently from 1977 and 1981 reflected high numbers of chicks ringed in these years.

3.3.2 Fidelity to the natal colony.

Table 3.6 indicates the extent of philopatry in birds recaptured breeding during 1985-87. Overall, 25% (207 out of 807 birds) bred away from the natal colony (considering all three colonies separately). There were significant differences between the colonies with respect to the proportion of birds which bred away from their natal colony. Proportionately fewer birds hatched at North Point bred elsewhere, compared with birds from each Shagnasty subcolony (χ^2 = 19.0 df = 2 P<0.001). The movements of North Point birds were mainly towards Shagnasty I/II, with five of the six birds which moved breeding there, although there was no significant difference in the proportion moving to either Shagnasty subcolony (P = 0.21, Fisher's exact test). The highest proportion of birds which bred away from the natal colony came from Shagnasty I/II, where 29% (n = 568 chicks) of the ringed chicks moved, mostly to Shagnasty III (Table 3.6). This pattern was repeated for birds hatched at Shagnasty III, where 34 of the 37 birds which moved, were breeding at Shagnasty I/II.

Considering movements between North Point and Shagnasty only, of 807 chicks, 19 (2.4%) bred away from the natal colony. A significantly higher proportion of North Point chicks moved to Shagnasty than in the opposite direction; 7% (n = 86) from North Point and 1.8% (n = 708) from the whole of Shagnasty (χ^2 = 6.84 df = 1 P<0.01). There were no differences in the proportions of birds hatched at either Shagnasty subcolony which moved to North Point (χ^2 = 0.03 df = 1 NS).

At Shagnasty, 27% (n = 568 birds) of those hatched on Shagnasty I/II, and 22% (n = 153 birds) from Shagnasty III, moved to the other subcolony (χ^2 = 1.25 df = 1 NS). In total, 26% (188) of the chicks ringed at one Shagnasty subcolony moved to the

TABLE 3. 6 FIDELITY TO THE NATAL COLONY OF BREEDING BIRDS RECAPTURED BETWEEN 1985-1987.

	Number of birds breeding at :				
Natal colony	North Point	Shagnasty I/II	Shagnasty III	Birds breeding away from natal colony (%)	NP - SN exchange (%)
North Point	80	5	1	7.0	7.0
Shagnasty I/II	10	404	154	28.9	2.4
Shagnasty III	3	34	116	24.2	2.5

Comparison of proportion breeding away from natal colony.
Between colonies: $\chi^2_2 = 19.0$ $P<0.001$

other.

3.3.3 Variation in philopatry with year and colony size.

Cohorts of birds prior to 1975 were excluded from this analysis because few were recaptured during 1985-87. Additionally, birds ringed in 1979, 1983 and 1985 were excluded because few chicks from the first two cohorts were ringed, and many birds ringed in 1985 were still recruiting at the time of recapture. Table 3.7 shows that the year in which a bird was ringed made no difference to the colony at which it was subsequently recaptured. North Point birds were highly philopatric, with only one individual moving away in most years. At Shagnasty I/II, similar proportions of birds bred away from their natal subcolony in each year ($\chi^2 = 2.87$ df = 6 NS). At Shagnasty III, chick ringing only started in 1981 and there is insufficient data to examine separate years.

There was no relationship between the proportion of birds from Shagnasty I/II which dispersed from the natal colony and the size of the breeding population at Shagnasty I/II in the year of ringing, or with the number of chicks ringed in the cohort. When the number of pairs breeding at Shagnasty I/II three and four years after a cohort of birds was ringed (*i.e.* when most members of the cohort were recruiting), was correlated with the proportion of birds breeding away from the natal colony, there was a suggestion that the size of the breeding population three years later influenced the proportion that moved. Proportionately more birds moved when the breeding population was high, although in neither case was the correlation significant ($r_s = 0.67$ df = 8 for 3 years, $r_s = 0.51$ df = 7 for 4 years). More data are required for a critical examination between the extent of philopatry and the size of the breeding population

3.3.4 Influence of sex, siblings and hatching order on philopatry.

Before investigating sex differences in philopatry, biases due to differences in the

TABLE 3.7 FIDELITY TO THE NATAL COLONY OF BREEDING BIRDS RECAPTURED IN 1985-87 ACCORDING TO THE YEAR OF RINGING

NOTE: NO CHICKS RINGED IN 1982.

		Year of Ringing															
Natal colony	Breeding colony	1969	1970	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1983	1984	1985
North	NP	0	0	0	1	0	0	6	6	2	3	0	6	27	2	23	4
Point	SNI/II	0	0	0	0	0	0	0	1	0	1	0	1	1	0	1	0
	SNIII	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0
Shagnasty	NP	0	0	0	0	0	0	0	0	1	0	0	0	5	0	3	1
I/II	SNI/II	4	12	5	1	8	5	25	34	27	16	1	44	101	6	100	15
	SNIII	1	2	3	0	5	2	6	13	13	8	0	15	39	5	34	8
Shagnasty	NP													1	0	2	0
III	SNI/II						**							19	3	11	1
	SNIII													37	5	63	11

** No chicks were ringed at Shagnasty III before 1981.

Proportion of birds hatched at Shagnasty I/II moving away each year between 1975-1984: $\chi^2_6 = 2.87$ NS likelihood of recapture between the sexes (see Table 2.4) were considered. Table 3.8 shows the number of birds of each sex which were recaptured breeding away from the natal colony between 1985-87. Although in 1985 at Shagnasty I/II significantly fewer males were recaptured, when all birds which were recaptured at Shagnasty I/II in 1985 were eliminated from the analysis, the results were unchanged. Similarly in 1987 at Shagnasty III, a sex bias in recapture existed and again excluding the birds caught there did not affect the results. Accordingly, Table 3.8 shows the complete information from all years during the study. It is apparent that there were no significant differences between the sexes with respect to the overall number moving from the natal colony, and this was also true of each colony separately.

The philopatry of siblings was investigated using 40 sets of siblings which were recaptured between 1985-87. In 10 of these sets, one bird moved, and in another 6 both siblings moved away from the natal colony (only one set of 3 siblings was recaptured and none had moved). Since the overall proportion of birds recaptured breeding away from their natal colony was 0.253, the expected frequency of movement by both siblings of a set can be calculated from the binomial expansion $(p^2 + 2pq + q^2) = 1$, where p is the probability of each bird moving away from its natal colony (0.253) and $q = (1 - p)$ (the probability of each bird remaining at its natal colony). In this expression, p^2 gives the probability of both siblings moving and $2pq$ that of one sibling. The expected and observed frequencies are shown in Table 3.9. There was a suggestion that when siblings bred away from their natal colony, both members of the set tended to move, although the difference was not significant (goodness-of-fit test $\chi^2 = 4.85$ df $= 2$ NS). This probably reflects the small number of sibling sets currently available for analysis, and more data are needed to decide if the effect is genuine.

Where only one bird moved, the sexes were similar in both movers and non-movers, 8 males and 2 females moved, and 5 each remained at the natal colony. Eight birds moved between Shagnasty I/II to Shagnasty III, one from Shagnasty I/II to North Point and another from Shagnasty III to Shagnasty I/II. In the 6 sets where both

TABLE 3. 8

FIDELITY TO THE NATAL COLONY OF BREEDING BIRDS RECAPTURED IN 1985-87 ACCORDING TO SEX.

Natal colony	No. breeding away from natal colony		No. breeding at natal colony		Test of equality between sexes (χ^2, df = 1)
	Males	Females	Males	Females	
North Point	3	3	35	44	-
Shagnasty I/II	91	73	206	198	1.76 NS
Shagnasty III	16	21	50	66	0.43 NS
TOTAL	110	97	291	308	0.70 NS

TABLE 3. 9 OBSERVED AND EXPECTED FIDELITY TO THE NATAL COLONY OF SIBLING SETS.

	Both sibs. moved	One sib. moved	Both sibs. philopatric
OBSERVED	6	10	24
EXPECTED	3	15	22

Goodness-of-fit test $\chi^2_2 = 4.85$ NS members of the brood moved, 5 were males and 7 were females. There was one set of male siblings, two of females and three of mixed sex.

In fifty-five birds, the order of hatching was known and this was unrelated to philopatry (Table 3.10). Among thirteen birds which bred away from their natal colony, there were three sets of siblings, and in two of these sets only one bird moved. Whilst movement was unrelated to hatching order (one A and B chick moved from each set) interestingly, in both sets one bird was first seen breeding a year earlier than the other, and in both sets these early breeders had moved away from the natal colony. In the remaining set where both A and B siblings moved, breeding was first recorded in the same year although since the birds were six years old it was likely that they had bred previously.

To decide if philopatry affected subsequent colony fidelity, the number of birds breeding at the natal colony between 1985-87 and which subsequently changed colonies, was compared with those which bred away from the natal colony and changed. A significantly higher proportion of birds which bred away from the natal colony subsequently changed colonies ($\chi^2 = 3.97$ df $= 1$ $P<0.05$; Table 3.11a). As the sample did not consist entirely of birds breeding for the first time, some individuals may have moved in the interval between recruitment to the breeding population and recapture, although since colony fidelity was high and there was only one case of a bird moving three times, this was unlikely to bias the results appreciably. A further analysis was made by including records of birds first recorded breeding before 1985, and which were recaptured during 1985-87. This confirmed that birds first recorded breeding away from the natal colony were more likely to move subsequently, 7.2% doing so, compared with 1.2% which were first seen at the natal colony (Table 3.11b). All 15 birds which were first recorded breeding away from the natal colony, returned subsequently.

3.4 Intermittent breeding.

The failure of part of the population of experienced breeders to attempt to breed,

TABLE 3.10 FIDELITY TO THE NATAL COLONY IN RELATION TO HATCHING ORDER. A=FIRST HATCHED, C=LAST HATCHED.

	Hatching order		
	A Chick	B Chick	C Chick
Bred away from natal colony	6	5	2
Bred at natal colony	24	17	1

Test of A *v* B chicks moving $\chi^2_1 = 0.01$ NS
Test of A and B *v* C chicks P = 0.14 NS (Fisher's exact)

TABLE 3. 11 **COLONY FIDELITY IN RELATION TO PHILOPATRY A) DURING 1985-87 AND B) DURING 1979-87.**

A)

Colony fidelity after first recorded breeding	First recorded breeding at:	
	Natal	Non-natal
Changed	3	5
Stayed	597	202

Test of proportion moving according to philopatry: $\chi^2_1 = 3.97 \quad P<0.05$

B)

Colony fidelity after first recorded breeding	First recorded breeding at:	
	Natal	Non-natal
Changed	7	15
Stayed	592	193

Test of proportion moving according to philopatry: $\chi^2_1 = 19.04 \quad P<0.001$

has been investigated by looking at the birds seen over three consecutive breeding seasons to detect absence during the middle season. Inevitably, some birds will be missed because they evaded capture, so an estimation of the numbers which would be expected to be missed given the recapture efficiency in that year, is necessary.

In 1985, no visits were made to Shagnasty III, so the sample from 1984 excluded this colony. Some birds which bred at Shagnasty I/II in 1984 might have been missed because they bred at Shagnasty III in the following year. The annual rate of movement of experienced breeders from Shagnasty I/II to Shagnasty III was 0.75% (Table 3.4), and after applying this correction, the estimated number missed was only increased by one bird. A similar situation occurs for the birds missed in 1986 (since the sample was drawn in 1985) and again the difference is only one bird.

A sample of birds seen in year 1 and again in year 3 can be expressed as:

$$N = r + a + b$$

where N is the number of birds that were seen in year 1 and again in year 3, r is the number from N recaptured in year 2, a the number of birds from N not recaptured in year 2, and b the number of birds from N not identified but seen breeding at the colony in year 2. The sum of a and b represents the total number of birds missed in year 2, from which the expected number of birds missed in year 2 can be calculated as in the following example.

To estimate the number of birds which evaded capture in 1985 North Point is considered separately from Shagnasty I/II because there is a significant difference in the recapture efficiency between colonies (Table 2.4). At North Point, 5 birds were not recaptured ('a' term in the above equation) and assuming the ratio of ringed to unringed birds to be similar to those that were recaptured, which is 70/95 = 0.737, then 5 x 0.737 = 3.7 are estimated to be ringed. Among the recaptured birds, the proportion of those which were ringed, from the 1984-86 sample, was (39 − 3)/67 = 0.537 (39 birds seen in 1984 were recaptured in 1986 and 3 were missed in 1985). Applying this correction to the unknown ringed birds, gives the number estimated to have been missed; 0.537 x 3.5 = 1.99 birds. In addition, the three ringed but not identified birds (the '*b*' term), are multiplied by the proportion expected to be in the 1984-86 sample (0.537 x 3) giving a further 1.61. The total number of birds estimated to have been missed because they evaded capture at North Point in 1985 is therefore 1.99 + 1.61 = 3.6 or about 4 birds, close to the observed 3 which were actually missed. The calculation is then repeated for Shagnasty I/II.

The observed and expected numbers of birds missed in each year between 1985-87 is shown in Table 3.11. About 20% of the 1984-86 sample were not seen in 1985, compared with about 5% in the other years. However, the recapture efficiency was lower in 1985 on Shagnasty I/II, where most of the birds sampled were breeding. There is close agreement between the observed and expected numbers missed, suggesting that these birds were breeding at the colony but evaded capture, rather than were not attempting to breed in each year.

3.5 Discussion.

Colony fidelity among breeding birds is usual in most seabird species *e.g.* Kittiwake (Coulson & Wooller 1976), Fulmar (Dunnet *et al.* 1963), Herring gull (Chabrzyk & Coulson 1976), Manx shearwater (Perrins *et al.* 1973), Gannet (Nelson 1966), Buller's mollymawk (Richdale & Warham), European shag (Potts 1969; Aebischer 1985), Flightless Cormorant (Harris 1979). In the European shag, Potts (1969) found that the annual rate of emigration of experienced breeders was about 1% *per annum,* and that 92% of birds returned to the Farne Islands at their first breeding attempt. At the Isle of May colony, 0.3% of breeders moved to another colony and 94% were philopatric (Aebischer 1985). Flightless cormorants were extremely sedentary, with only a few individuals moving away from natal colonies and these birds moved a maximum of 2 km (Harris 1979).

TABLE 3. 12 **OBSERVED AND EXPECTED NUMBERS OF BIRDS MISSED 1985-87.**

Year missed (*i.e.* year 2)	No. seen in year 1 and again in year 3	Observed number missed	Expected number missed
1985	189	39	39
1986	242	6	11
1987	337	16	17

Blue-eyed shags showed similar levels of colony fidelity and philopatry to European shags, although they were perhaps even less inclined to change colonies. In this study only 0.1% of experienced breeders moved between Shagnasty and North Point and 97.6% hatched at one of these colonies returned there to breed. The previous study on Signy Island found an annual exchange rate of breeding Blue-eyed shags of 2.4% (Shaw 1984), and this apparently included movements between the Shagnasty colonies, in which case the corresponding figure from this study, of 1.1%, was not significantly different. ($\chi^2 = 3.02$ df = 1 NS). In both studies about 98% of birds showed philopatry.

Although most other shag colonies in the South Orkney Islands were not searched, it seems unlikely that this would result in underestimation of the extent of movement from Signy, since no Signy birds were found breeding at the two nearest colonies, and they were over six times as far from Signy as North Point and Shagnasty. In the European shag there is an inverse relationship between the extent of movement away from the natal colony and the distance between colonies, and the relationship is apparently independent of colony size (Aebischer 1985). Significantly fewer Blue-eyed shags moved between North Point and Shagnasty than would be expected between two colonies of European shags separated by a similar distance ($\chi^2 = 5.03$ df = 1 $P<0.05$; see Figure 6.1 in Aebischer 1985). However adjacent colonies of both species were similar with respect to philopatry. The proximity of the Shagnasty subcolonies parallels that of Brownsman and Staple Island in the Farnes group, and the amount of exchange was similar, 26% and 22% respectively (Potts 1969).

Shaw (1984) found differences in dispersal between the sexes before and after the first recorded breeding attempt, with females moving more frequently. By contrast, there were no sex related differences in philopatry or colony fidelity in this study and the reasons for this were unclear.

There was no evidence that experienced breeding Blue-eyed shags did not attempt to breed in every year of their reproductive life, although as pointed out by Coulson (1984), detailed studies are required to detect this phenomenon, and the duration of the present study may be too short for intermittent breeding to be apparent. Non-breeding by part of the adult population has been recorded in the European shag on one occasion, apparently in response to aberrant conditions of food shortage (Aebischer 1985). The frequent failure of experienced breeders to attempt breeding, is a feature of Eider population dynamics on Coquet Island, Northumberland where over a 30 year period between 0-60% of adult ducks missed a breeding attempt each year (Coulson 1984).

4. SURVIVAL RATES IN RELATION TO AGE, SEX AND OTHER FACTORS.

4.1 Introduction.

Studies of avian population dynamics have frequently focussed on measuring survival rates and determining the factors which influence them. This is of interest because recent work has indicated that for a variety of species the length of the breeding lifespan and the survival of the young between fledging and recruitment to the breeding population are major components of lifetime reproductive success (Newton 1989). Lack (1954) suggested that the annual survival rates of adult birds is constant with age. This assumption was challenged by Botkin & Miller (1974) who argued that contemporary estimates of annual survival rates led to unrealistic longevity in many species. They concluded that only small annual increases in mortality rates were necessary to fit survivorship curves which agreed with observed values of maximum longevity. Their theoretical arguments have been substantiated by several field studies which have detected decreases in the oldest cohorts of Kittiwake (Coulson & Wooller 1976, Aebischer & Coulson 1990), Fulmar (Dunnet & Ollason 1978, although Buckland (1982) suggested that this may be partly due to an artefact arising from sampling heterogeneity), Eider (Coulson 1984), Black-capped chickadee (Loery *et al.* 1987), Short-tailed shearwater (Bradley *et al.* 1989), and evidence suggesting age-dependent survival rates exists for several more species including Caspian tern (Ludwig 1965), European shag (Potts 1969, Aebischer 1986) and Adelie penguins (Ainley & DeMaster 1980). In Kittiwakes older than 12 years, the annual survival rate decreased by an average of 11% for both sexes combined (Aebischer & Coulson 1990), in Fulmars the decrease was estimated at 0.2% (Dunnet & Ollason 1978), Eider ducks older than 16 years experienced three times the mortality rate of younger individuals (Coulson 1984), in the Short-tailed shearwater the survival rate of 0.91 in 16-20 year old birds fell to 0.80 when they reached 26-30 years old and in European shags birds older than 18 years experienced an annual survival rate of 0.68 compared with 0.87 in younger birds (Aebischer 1986).

Survival rates of birds in their first year of life are invariably lower than in subsequent years (*e.g.* Lack 1954, Potts 1969), a phenomenon usually attributed to inexperience particularly in foraging skills (*e.g.* Orians 1969, Recher & Recher 1969, Dunn 1972, Greig *et al.* 1983). Seabirds, which experience deferred breeding lasting several years, may show a gradual increase in annual survival rate between the end of the first year and recruitment to the breeding population although there is little evidence for this since usually only a few members of each cohort are recaptured prior to first breeding (Nichols *et al.* 1990). In European shags, two year old birds experienced a survival rate of 0.745 compared with the adult rate (*i.e.* older than 2 years) of 0.874 (Aebischer 1985).

Higher mortality rates in birds breeding for the first time have only been established conclusively for a few species. In the Short-tailed shearwater, the mortality rate of recruits to the breeding population was about 13% but this subsequently declined to about 5% in more experienced breeders (Bradley *et al.* 1989). Laysan albatrosses showed an annual mortality rate of 2% in their first breeding season, which was similar to the annual rates of birds in their seventh to ninth breeding seasons, but birds between their third and sixth breeding seasons had higher annual mortality rates, about 6%. However only 75% of birds which first bred aged 6 years survived to their ninth year compared with 92% and 86% of birds which recruited at the usual ages of 7 and 8 (Fisher 1975). There was evidence in a study of Fulmars that first time breeders had lower survival rates than birds with 2-8 years breeding experience (Dunnet & Ollason 1978). However, in both Wandering albatrosses and Kittiwakes there were no differences in the survival rates of first time breeders compared with experienced breeding birds (Croxall *et al.* 1990, Aebischer & Coulson 1990). The failure to detect a difference in mortality rates between first time breeders and experienced birds does not necessarily imply that the cost of breeding is similar in both of these groups. In the Laysan albatross, where the annual mortality rates of recruits and experienced birds is similar, relatively few birds breeding for the first time complete incubation, and by abandoning their attempts at reproduction recruits may maintain low mortality rates (Fisher 1975).

4.2 Adult survival rates.

Adult survival rates were initially investigated by calculating a mean annual survival rate using samples of ringed birds which were first captured breeding in each of the years 1979, 1980 and 1981 and subsequently identified in 1987 (39 birds seen in 1979 had been seen previously, but the important point in the present analysis is that the three samples between 1979-81 were independent). The number of birds recaptured in 1987 was corrected for recapture efficiency as shown in Table 4.1. Since the recapture efficiency at Shagnasty III was lower than in the other two areas (Table 2.4) it was considered separately. The corrected number recaptured differed from the actual number by three birds in the 1980 and 1981 samples and by only one bird in the 1979 sample. Using the corrected values produced survival rate estimates within one standard error of those obtained using the uncorrected value, indicating that the adjustment for recapture efficiency in 1987 was unimportant. Henceforth for simplicity, only uncorrected numbers are considered where recaptures occurred in 1987.

The mean annual survival rates are shown in Table 4.2. A increase in survival rate is apparent in the successive sample years from 0.729 ± 0.017 in 1979 to 0.826 ± 0.015 in 1981, and the rate in 1981 is significantly higher than in the two preceeding sample years. The overall mean annual survival rate, weighted according to sample size, is 0.762 ± 0.013. By using the birds first seen breeding in a particular year, independence between samples was assured, but the proportion of recruits in the sample rose from 10% in 1979 to 82% in 1981. This was because in the last two sample years most of the experienced breeders had been previously recaptured. If younger breeders were experiencing a different survival rate than older birds, then this might account for the observed increase.

TABLE 4. 1 **CORRECTIONS FOR RECAPTURE EFFICIENCY TO THE NUMBER OF BIRDS RECAPTURED IN 1987 FROM BIRDS ORIGINALLY CAPTURED BETWEEN 1979 AND 1981.**

		North Point and Shagnasty I/II	Shagnasty III
No. of birds not recaptured (from Table 2.4)		15	56
Proportion of ringed birds in recaptured sample		0.561	0.397
Estimated no. of ringed birds not recaptured		0.561x15 = 8.4	0.397x56 = 22.3
Proportion of sample in ringed 1987 breeders; sample year =	1979	26/497 = 0.05	no visits
	1980	84/497 = 0.17	before 1981
	1981	41/497 = 0.08	16/248 = 0.06
Estimated no. ringed, unrecaptured birds; sample year =	1979	8.4x0.05 = 0.42	no visits
	1980	8.4x0.17 = 1.43	before 1981
	1981	8.4x0.08 = 0.67	22.3x0.06 = 1.34
Additional no. of ringed unrecaptured birds estimated from ringed but not individually identified (Table 2.6)	1979	12x0.05 = 0.60	all ringed birds individually identified
	1980	12x0.17 = 2.04	
	1981	12x0.08 = 0.96	
Corrected no. of birds recaptured in 1987 from each sample year (uncorrected figures in parentheses)	1979	(26) + 0.42 + 0.60	= 27
	1980	(84) + 1.43 + 2.04	= 87
	1981	(57) + 0.67 + 1.34 + 0.96	= 60

TABLE 4.2

MEAN ANNUAL SURVIVAL RATES OF BIRDS FIRST SEEN BREEDING BETWEEN 1979 - 81 AND RECAPTURED IN 1987. MEANS ± 1 SE[a], N = NUMBER 'AT RISK', TOTALS INCLUDE UNSEXED BIRDS.

Year of first capture	MALES			FEMALES			TOTAL		
	N	Mean	SE	N	Mean	SE	N	Mean	SE
1979	159	0.750	0.022	150	0.713	0.027	326	0.729	0.017
1980	286	0.763	0.015	265	0.766	0.016	569	0.761	0.011
1981	94	0.812	0.022	80	0.839	0.021	179	0.826	0.015
Weighted mean	539	0.768	0.018	495	0.762	0.020	1074	0.762	0.013

Differences between sexes (Z scores)	1979	Z = 1.06 NS	Difference between years (totals)	1979 *v* 1980	Z = 1.58 NS
	1980	Z = 0.14 NS		1980 *v* 1981	Z = 3.49 P<0.001
	1981	Z = 0.89 NS		1979 *v* 1981	Z = 4.28 P<0.001

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[a] See appendix 2a for method of SE calculation.

To investigate this, the samples were divided into recruits (those aged 2-5 years inclusive and seen breeding for the first time) and experienced birds (recorded breeding prior to 1979), and separate mean annual survival rates were calculated for each group. If the increasing proportion of recruiting birds was responsible for the overall trend in survival rates, then when separated, the mean survival rates between years within each group should be similar. Table 4.3 shows that this was not the case. Between groups in each sample year the mean annual survival rate of recruits was higher than the rate for experienced birds, significantly so in 1980 and 1981, indicating that the increased proportion of recruits partly accounted for the trend. However, an appreciable increase in overall mean annual survival rates is still apparent within both groups, although only for recruits between 1980 and 1981 is it statistically significant (Table 4.4). The persistence of this trend in both groups suggested that overall mortality rates were higher in 1979 and 1980 either due to conditions specific to those years or, since the samples were composed of successively more younger birds, as a result of an increased mortality rate with age (see section 4.5). Table 4.5 shows that there were no differences in mean annual survival rates between North Point and Shagnasty in the samples of birds from 1979, 1980 and 1981, or between the Shagnasty subcolonies in 1981.

In addition to mean annual survival rates, it was possible to calculate annual rates between 1984 and 1987 by using the proportion of birds recaptured in successive years and correcting for recapture efficiency (see appendix 1a-c for method). Table 4.6 shows the actual number of birds from the previous year which were recaptured between 1985-87, together with the estimated number alive after correction for the recapture efficiency. Since the calculations were performed separately on each sex and for the totals, the values do not agree exactly. Using the corrected values, the annual survival rate for each year was calculated and is shown in Table 4.7. The overall annual survival rate, weighted for sample size, was 0.864 ± 0.010, and the annual survival rates between 1984-87 were generally higher by about 10% than the mean annual survival rates between 1979-81 and 1987. This may partly reflect the tendency of means to be biassed by a year of unusually high or low survival which may have occurred, but also

TABLE 4. 3

MEAN ANNUAL SURVIVAL RATES OF RECRUITS AND EXPERIENCED BIRDS RECAPTURED IN 1987. TOTALS INCLUDE UNSEXED BIRDS, MEANS ± 1 SE N = NUMBER 'AT RISK'.

Year of first capture	RECRUITS						EXPERIENCED					
	Males		Females		Total		Males		Females		Total	
	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE	Mean	SE
1979	0.777	0.064	0.850	0.052	0.784	0.041	0.741	0.62	-[a]	-	0.651	0.057
	(15)		(11)		(35)		(22)		(34)		(62)	
1980	0.793	0.019	0.793	0.028	0.790	0.017	0.671	0.042	0.722	0.035	0.691	0.026
	(122)		(66)		(193)		(82)		(78)		(173)	
1981	0.829	0.022	0.853	0.022	0.838	0.016	-[a]		0.815	0.051	0.734	0.050
	(80)		(65)		(147)		(14)		(17)		(32)	

Recruits *v* Experienced (Totals)	1979	Z = 1.58 NS
	1980	Z = 3.49 P<0.001
	1981	Z = 4.28 P<0.001

[a] No birds recaptured in 1987

TABLE 4. 4

ANNUAL DIFFERENCES IN OVERALL MEAN ANNUAL SURVIVAL RATE BETWEEN RECRUITS AND EXPERIENCED BREEDING BIRDS, STANDARDISED DIFFERENCE Z - TEST VALUES.

	Recruits			Experienced	
	1980	1981		1980	1981
1979	0.14	1.20	1979	0.64	1.09
1980	-	2.06*	1980	-	0.76

* $P<0.05$
All others NS

TABLE 4. 5 DIFFERENCES BETWEEN COLONIES IN MEAN ANNUAL SURVIVAL RATES. MEANS ± 1 SE, NUMBER 'AT RISK' IN PARENTHESES.

Year of first capture	North Point	Shagnasty I/II	Shagnasty III
1979	0.763 ± 0.037 (96)	0.711 ± 0.022 (229)	-
1980	0.755 ± 0.030 (79)	0.763 ± 0.012 (490)	-
1981	0.833 ± 0.048 (18)	0.800 ± 0.023 (99)	0.830 ± 0.026 (61)

Comparison of means North Point *v* Shagnasty (Z test and t-test)		
	1979	Z = 1.49 NS
	1980	Z = 0.25 NS

1981 North Point *v*
total Shagnasty: $t_{179} = 0.69$ NS
Shagnasty subcolonies: Z = 0.86 NS

TABLE 4.6 **THE NUMBER OF BIRDS RECAPTURED AND ESTIMATED TO BE ALIVE FROM THE PREVIOUS YEAR AFTER CORRECTION FOR RECAPTURE EFFICIENCY BETWEEN 1985-87. NOTE IN ESTIMATED NUMBER ALIVE COLUMN, FAILURE OF TOTAL TO AGREE WITH SUM OF SEXES REFLECTS SEPARATE CALCULATIONS (SEE APPENDIX 1a-c.)**

Recapture year	Number recaptured			Estimated number alive		
	Males	Females	Total	Males	Females	Total
1985	85	87	172	120	98	216
1986	138	146	284	149	150	297
1987	227	217	444	245	224	468

TABLE 4.7 **ANNUAL ADULT SURVIVAL RATE BETWEEN 1984-87. RATE ± SE, NUMBER 'AT RISK' IN PARENTHESES, TOTALS INCLUDE UNSEXED BIRDS. MEAN WEIGHTED ACCORDING TO SAMPLE SIZE.**

Year	Males	Females	Total
1984-85	0.816 ± 0.032 (147)	0.845 ± 0.034 (116)	0.791 ± 0.025 (273)
1985-86	0.931 ± 0.020 (160)	0.872 ± 0.025 (172)	0.892 ± 0.017 (333)
1986-87	0.911 ± 0.017 (269)	0.862 ± 0.021 (260)	0.885 ± 0.014 (529)
MEAN	0.892 ± 0.013 (576)	0.861 ± 0.015 (548)	0.864 ± 0.010 (1135)

Difference between years (totals)	$\chi^2_2 = 16.5$ $P<0.001$
Difference between sexes (all years)	χ^2 - test NS

because birds from the 1979-81 samples were probably showing age-dependent survival rates by 1987, which would result in lower mean survival rates. The survival rate for all birds in 1984-85 was significantly lower than in the succeeding years (χ^2 = 16.5 df=2 $P<0.001$). This might be because during the 1985 breeding season, Shagnasty I/II was not visited until late December. If nests had failed before being tagged, the number of birds alive would have been underestimated.

4.3 Survival rates in relation to sex.

No significant differences between the sexes in mean annual adult survival rates were apparent in the samples of birds captured between 1979 and 1981 (Table 4.2), nor were there consistent differences between the sexes in annual survival rate between 1984 and 1987 (Table 4.7). The proportion of each sex recaptured in consecutive years from the same cohort should indicate if sex-related survival is present, an excess of the sex with the higher survival rate accumulating in later years if there is a difference. As there were significant differences in recapture efficiency between the sexes at Shagnasty I/II in 1985 and at Shagnasty III in 1987 (Table 2.4), these have been excluded from the following analysis. Recaptures made in 1988 and prior to 1984 were also excluded because the possibility of a sex bias in recapture could not be discounted. Table 4.8 shows that for seven cohorts followed between 1984 and 1987 the proportion of each sex did not deviate significantly from parity. In the two youngest cohorts, the proportion of males fluctuated markedly more than in the older cohorts and this may have been due to differences between the sexes in recruitment to the breeding population. However, during this study there was little evidence of a sex-related difference in the age of recruitment, and where a difference was apparent it was the males which recruited at an older mean age (Chapter 5). As no significant difference in survival between males and females was apparent, the sexes were pooled in subsequent analyses.

TABLE 4.8 PROPORTION OF MALES IN EACH COHORT RECAPTURED BETWEEN 1984-87. SAMPLE SIZE IN PARENTHESES, SHAGNASTY I/II AND III EXCLUDED IN 1985 AND 1987 RESPECTIVELY, NONE RECAPTURED FROM 1979, SQUARE BRACKETS INDICATE SAMPLE GROUPED OVER OLDER COHORTS.

Cohort	Year of recapture			
	1984	1985	1986	1987
1981	0.75 (8)	0.55 (22)	0.53 (205)	0.57 (123)
1980	0.43 (21)	0.20 (5)	0.47 (62)	0.45 (44)
1978	0.64 (25)	-	0.52 (27)	0.47 (15)
1977	0.45 (38)	[0.47] (17)	0.47 (38)	0.52 (21)
1976	0.63 (59)		0.61 (51)	0.50 (32)
1975	0.59 (41)		0.60 (35)	0.68 (22)
1974	0.60 (9)		[0.50] (32)	[0.55] (20)
1973	0.61 (15)			
1972-1969	[0.62] (37)			

Test of parity between sexes within cohorts:

Cohort	χ^2	df	
1981	2.19	2	
1980	1.00	2	
1978	1.03	2	
1977	0.52	3	None significant
1976	3.09	2	
1975	2.75	2	
1974-69	1.49	2	

4.4 Survival rates in relation to age.

Table 4.9 shows the mean annual survival rates of breeding birds from each cohort between 1969 and 1978 which were first captured between 1979 and 1981, and subsequently recaptured in 1987. In calculating the mean annual survival rates, the middle year of the initial capture period was chosen as the year on which to base the interval relating to mean annual survival rates (*i.e.* 1980-87). No adjustment was made for recapture efficiency in 1987, since it was previously shown that the difference is unimportant (section 4.2).

There was a significant decline in the proportion of birds recaptured as age increased ($\chi^2 = 24.66$ df=8 $P<0.01$), and hence a decrease in mean annual survival rate with age. Since the survival rate at a given age includes the survival over younger ages, it was assumed that the survival rates operating up to a certain age was constant but then declined as birds grew older. This assumption gave more information on the age-specific survival pattern. To determine if the assumption of a constant survival rate for younger birds was reasonable, the proportion of breeding birds captured in 1984 and recaptured again in 1987 was considered in relation to cohort. It should be noted that birds from cohorts before 1979 are also represented in the sample above which were initially seen during 1979-81 and so these two groups of cohorts on which mean annual survival rates are calculated, are not wholly independent. Of course, birds from cohorts younger than 1978 and recaptured in 1984, do not appear in the earlier group, and it is these birds which should yield the constant annual survival rates.

The mean annual survival rates of both groups are plotted in Figure 4.1 with their standard errors. The survivorship curve, from the 1979-81 data, suggests that a decline in mean annual survival rate starts in cohorts older than 1977, *i.e.* birds in their eleventh year of life in 1987. The relatively flat part of the curve initially, is consistent with a constant annual survival rate until about ten years of age. Age-specific survival rates were calculated by assuming that there was a constant annual survival rate until

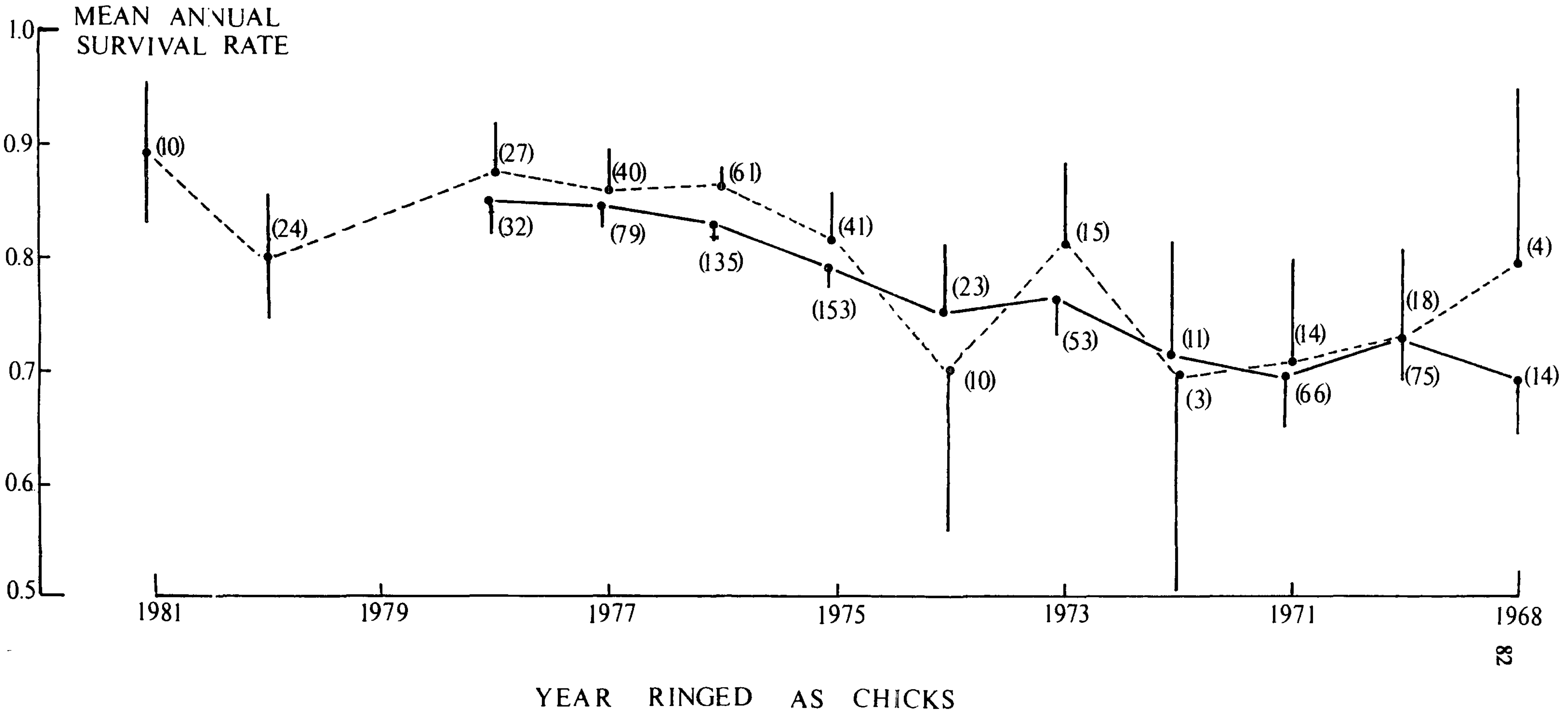
TABLE 4.9 MEAN ANNUAL SURVIVAL RATE OF BREEDING BIRDS FIRST CAPTURED BETWEEN 1979-81 AND RECAPTURED IN 1987, ACCORDING TO COHORT.

	Cohort									
	1978	1977	1976	1975	1974	1973	1972	1971	1970	1969
No. first captured	32	79	135	153	23	53	11	66	75	14
No. recaptured in 1987	10	24	36	29	3	8	1	5	8	1
Proportion recaptured in 1987	0.31	0.30	0.27	0.19	0.13	0.15	0.09	0.08	0.11	0.07
Mean annual survival rate	0.847	0.843	0.828	0.788	0.748	0.763	0.710	0.692	0.726	0.690
S.E.	0.032	0.021	0.017	0.019	0.059	0.036	0.101	0.043	0.035	0.098

Difference between cohorts in proportion recaptured: $\chi^2_9 = 26.31$

FIGURE 4. 1

THE MEAN ANNUAL SURVIVAL RATE OF BIRDS FROM 1969-1978 COHORTS, FIRST CAPTURED BREEDING BETWEEN 1979-81 AND SUBSEQUENTLY RECAPTURED IN 1987 (SOLID LINE), AND OF BIRDS CAPTURED IN 1984 AND SUBSEQUENTLY IN 1987 (BROKEN LINE). VERTICAL BARS ± 1 S.E., SAMPLE 'AT RISK' IN PARENTHESES.



birds were ten. This constant annual survival rate was 0.843, from the proportion of birds from 1979-81 which were recaptured aged 10 in 1987. Table 4.10 shows the age-specific survival rates for birds up to 16 years old, after which the rates varied widely. Although the survival rates showed considerable variation owing to small sample sizes in the oldest birds, the analysis indicated that the survival rate decreased from 0.843 in birds younger than 10 years to about 0.600 at 15-16 years. The survival rate therefore declined by approximately 0.24 over six years or 0.04 each year on average.

The annual survival rate of birds younger than 10 years which were breeding in 1986 and 1987 was investigated by determining the proportion recaptured in the following year. Table 4.11 indicates that between 1986-87 the survival rate of birds breeding for the first time (0 breeding experience in Table 4.11) was similar to that of experienced breeders (χ^2 = 2.0 df=2 NS). Between 1987-1988 the survival rate of first time breeders was significantly lower than that of experienced birds (χ^2 = 86 df=3 $P<0.001$). The survival rate of 0.369 is unusually low compared to all other estimates of adult survival rates and is likely to be due to a lower recapture efficiency of first time breeders in 1988, resulting from less time spent recapturing breeding birds, fewer visits and no recaptures at part of the North Point and Shagnasty III colonies. This would affect first time breeders if they are more likely to fail (birds aged 2-5 years failed to fledge any chicks more often than older birds - see section 6.5.6) or if they are more wary of capture. Both effects will reduce the probability of recapture of young birds. Excluding first time breeders, there was no difference in survival rates between birds with a minimum of 1, 2 or 3 years breeding experience (χ^2 = 3.4 df=2 NS)

4.5 Annual variation in adult survival rates.

Except in 1983, breeding birds were recaptured annually between 1979 and 1987, allowing estimates of annual survival rates to be made using the Jolly mark-recapture technique described by Begon (1979). The results, presented in Table 4.12, indicate that survival in two years, 1979-80 and 1984-85, was particularly low, whereas in

TABLE 4. 10 ESTIMATED AGE-SPECIFIC SURVIVAL RATES IN BIRDS OLDER THAN ELEVEN YEARS WHICH WERE RECAPTURED IN 1987.

Age in 1987	Proportion recaptured	Age-specific survival rate
10	$P_{10} = S_{10}^7$	0.843
11	$P_{11} = S_{10}^6.S_{11}$	0.743
12	$P_{12} = S_{10}^5.S_{11}.S_{12}$	0.599
13	$P_{13} = S_{10}^4.S_{11}.S_{12}.S_{13}$	0.580
14	$P_{14} = S_{10}^3.S_{11}.S_{12}.S_{13}.S_{14}$	0.976
15	$P_{15} = S_{10}^2.S_{11}.S_{12}.S_{13}.S_{14}.S_{15}$	0.508
16	$P_{16} = S_{10}.S_{11}.S_{12}.S_{13}.S_{14}.S_{15}.S_{16}$	0.702

Note: P_i = Proportion recaptured at age i in 1987.

S_i = Annual survival rate at age i

TABLE 4.11 **ADULT ANNUAL SURVIVAL RATE OF BIRDS YOUNGER THAN TEN YEARS IN RELATION TO MINIMUM NUMBER OF YEARS BREEDING EXPERIENCE. NOTE: 0 YEARS BREEDING EXPERINCE SIGNIFIES BIRDS BREEDING FOR THE FIRST TIME.**

		Survival during 1986-87			Survival during 1987-88	
Breeding experience	No. at risk	Survival rate	S.E.	No. at risk	Survival rate	S.E.
0	139	0.827	0.032	268	0.369	0.029
1	127	0.843	0.032	132	0.727	0.039
2	77	0.772	0.046	105	0.819	0.038
3	-	-	-	37	0.703	0.075
		$\chi^2_2 = 2.0$ NS			$\chi^2_3 = 86$ P<0.001	

TABLE 4. 12 ESTIMATES OF ANNUAL SURVIVAL RATES USING THE JOLLY METHOD FOR ALL BIRDS, AND FOR BIRDS WHICH WERE YOUNGER THAN TEN YEARS BETWEEN 1979 AND 1985. NOTE: ESTIMATE FOR 1982-84 CALCULATED OVER TWO YEARS, MEAN ANNUAL RATE IN PARENTHESES.

	All birds			Young birds		
Year	No. 'at risk'	Survival rate	S.E.	No. 'at risk'	Survival rate	S.E.
1979-80	313	0.332	0.007	34	0.717	0.055
1980-81	730	0.728	0.011	197	0.781	0.026
1981-82	700	0.930	0.059	300	0.844	0.088
1982-84	208	0.538 (0.733)	0.038	70	0.530 (0.728)	0.054
1984-85	282	0.430	0.020	128	0.822	0.029
1985-86	159	0.884	0.018	73	0.852	0.026

1981-82 and 1985-86 survival rates were high. Since the Jolly method of estimating survival rate assumes age-independent survival and this appeared to contradict the findings in section 4.5, an estimate of the survival rate was made using birds known to be younger than 10 years old between 1979 and 1986. The sample of birds used was therefore largely independent of age. The results (Table 4.12) confirm that the survival rate was high between 1985-86 and 1981-82 and low between 1979-80. Comparing the annual survival rates between the two groups, there are marked differences in 1979-80 and 1984-85. The reason for this is not clear although it may be related to biases in the estimates. Such biases may arise as a result of violation of some of the assumptions of the model (*e.g.* the assumption that all members of the population under study have an equal probability of capture), and Begon (1979) has recommended caution in assigning precision to such estimates. Here, the aim of estimating annual survival rates of adults is to indicate variation between years, hence it is the comparison between rates which is emphasised rather than their absolute values. The estimates of survival rate using young birds all lie in the range of rates calculated in the previous section, whereas three of the rates from the sample using all birds were outside this range, suggesting that the former are more realistic.

4.6 First year survival rates.

Since Blue-eyed shags did not breed until two years old, and most recruitment occurred after this age, it was not possible to measure the survival rate during the first year of life directly. Instead, it was assumed that the survival rate of all birds older than one was similar to the adult rate, and that the proportion of each cohort recaptured as breeding birds, was the product of a first year survival rate and an annual adult rate experienced over the remaining interval, corrected for a decrease of 0.04 each year after 10 years of age. In two cohorts, 1983 and 1984, birds were still recruiting to the breeding population in 1987, and it was assumed that all members of the 1983 cohort and 82.7% of the 1984 cohort had recruited by 1987. This was based on the numbers of birds from these cohorts which first bred in 1988 (section 5.5). One further assumption was that no emigration occurred between fledging and breeding.

The interpretation of these first year survival rates requires caution, since the time between chick ringing and fledging is included and hence 'first year survival rate' incorporates some nestling mortality. No attempt was made to compensate for ringed chicks which died prior to fledging because the data were only available for a few years and since corrections could not be applied to all cohorts, this would bias comparisons between them. As an indication of the magnitude of error resulting from the inclusion of nestling mortality, the number of ringed chicks found dead at the colonies in 1979, 1980 and 1981 was 57, 96 and 65 respectively, representing 56%, 22% and 8% of the ringed chick totals in each year. In 1979, chick mortality was particularly high and this appears to be abnormal, judging from the numbers of chicks ringed in other years (section 2.4.1). In view of the flat nature of Shagnasty, it was unlikely that dead chicks were missed because they rolled off the edge of the colony. Some carcases may have been removed by scavenging Brown skuas, Dominican gulls and Sheathbills, although the first two were rarely observed at shag colonies (two occasions each in three years, despite the constant patrolling of adjacent penguin colonies by skuas during the breeding season), and sheathbills tended to drag carcases to their nests where they were piled up outside the entrance. These piles were easily located and searched for ringed chicks.

The assumption of an adult survival rate after the first year may be unjustified. In European shags, Aebischer (1985) has shown that two year old birds have a survival rate of 0.745 compared with the adult rate of 0.874. A similar situation in Blue-eyed shags will lower the apparent adult survival rate (since the true adult rate will not apply until the third year), leading to higher first year survival rate estimates. For example, if the second year survival rate of Blue-eyed shags is a similar proportion of the adult survival rate as in the European shag, then it will equal 0.745/0.874 x 0.843 = 0.719. For the 1981 cohort, the first year survival rate is $0.2246/0.843^4$ x

0.719 = 0.619, higher than the estimate of 0.528 in Table 4.13.

Table 4.13 shows that the first year survival rates are highly variable and range from 0.032 in 1979 to 0.691 in 1984 although as previously indicated above, the 1979 estimate was likely to include a substantial proportion of nestling mortality. Overall the mean first year survival rate weighted according to cohort size, is estimated to be 0.355 ± 0.046. Years of low survival rates occurred approximately every four years, in 1974, 1979 and 1983, and were particularly low were in 1974 and 1979. The incidence of birds which were recaptured with rings opening and the fidelity to the natal colony did not influence the estimates of first year survival rate (Table 4.14). Neither factor was correlated with first year survival rates ($r = -0.455$, $r=0.012$ $df=11$ N.S.; arcsine transformation of both axes).

4.7 The effect of climate and sea ice on first year survival rates.

Since estimates of adult annual survival rates were only available for a few years no attempt was made to analyse the effects of climate on adult survival rates. The effects of windspeed, number of hours of bright sunshine, barometric pressure and air temperature at sea level on first year survival rates were assessed by correlation analysis. Monthly averages for the climatic variables (obtained from B.A.S. meteorological records), were averaged over three month periods to produce quarterly means. An additional mean was calculated over the winter period by averaging the mean monthly value of each variable for June, July and August. This coincided with the period of most extreme climatic conditions and hence when the survival of shags might be most affected. Survival rates were arcsine transformed prior to correlation to preserve assumptions of normality. The requirement for transformation was indicated by the low variance mean quotient of 0.09 (Fowler & Cohen 1986). Care was taken to align the meteorological data and the period over which first year birds were 'at risk' of dying, so for example, the 1980 cohort was 'at risk' during the 1981 calendar year. During the first quarter of the period 'at risk' (*i.e.* January to March) the birds were still in

TABLE 4.13 **ESTIMATED FIRST YEAR SURVIVAL RATES OF BIRDS RINGED AS CHICKS BETWEEN 1971-1984. NOTE: MEAN WEIGHTED ACCORDING TO NUMBER 'AT RISK', NO CHICKS RINGED IN 1982, SEE APPENDIX 2b FOR S.E. CALCULATION METHOD, RECRUITMENT IN 1983 AND 1984 ASSUMED TO BE 100% AND 82.7% RESPECTIVELY (TABLE 5.11).**

Cohort	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1983	1984	MEAN
No. 'at risk'	600	100	550	280	393	532	495	423	102	436	837	232	580	(5560)
Survival rate	0.236	0.182	0.204	0.096	0.507	0.425	0.244	0.204	0.032	0.371	0.528	0.151	0.691	0.355
S.E.	0.105	0.181	0.067	0.055	0.091	0.064	0.047	0.042	0.032	0.045	0.034	0.031	0.029	0.046

TABLE 4.14

ESTIMATED FIRST YEAR SURVIVAL RATES IN RELATION TO THE PROPORTION OF BIRDS RECAPTURED BETWEEN 1985-87 WITH OPENING RINGS AND FIDELITY TO THE NATAL COLONY. NOTE: NO CHICKS RINGED IN 1982, SAMPLE SIZE IN PARENTHESES.

Cohort	1971	1972	1973	1974	1975	1976	1977	1978	1979	1980	1981	1983	1984
Survival rate	0.236	0.182	0.204	0.096	0.507	0.425	0.244	0.204	0.032	0.371	0.528	0.151	0.691
Proportion recaptured with opening rings	0.13 (8)	0.00 (2)	0.08 (13)	0.17 (7)	0.08 (39)	0.25 (53)	0.23 (39)	0.31 (28)	1.00 (1)	0.00 (67)	0.02 (233)	0.00 (22)	0.00 (235)
Proportion breeding away from natal colony	0.38 (8)	0.00 (2)	0.38 (13)	0.29 (7)	0.15 (37)	0.26 (54)	0.36 (43)	0.32 (28)	0.00 (1)	0.24 (66)	0.28 (230)	0.38 (21)	0.22 (238)

Survival rate and opening rings (both axes arcsin transformed) $r_{11} = -0.455$ NS
Survival rate and philopatry (both axes arcsin transformed) $r_{11} = 0.012$ NS

the nest, fledging being completed by about mid-February. However, as 'first year survival rate' included nestling survival between ringing and fledging, and nestlings were mostly ringed from mid-January onwards, this is unlikely to obscure a relationship between survival rates and climatic variables.

Table 4.15 indicates that there were significant negative correlations between first year survival and barometric pressure during the July to September quarter, and with temperature during the January to March quarter. Survival was positively correlated with temperature in the April to June quarter and with 'winter' temperature (June, July and August). There was no significant relationship with the number of hours of bright sunshine or windspeed and survival rates. Since climatic events during the winter are influenced by the arrival of pack ice from the Weddell Sea, the analysis was extended to investigate the influence of the timing of pack ice arrival and the formation and duration of sea ice. The variables used were defined as:

1. Pack ice arrival; the number of days after 10 April when pack ice was first sighted.
2. Sea ice formation; the number of days after 10 April when walkable sea ice was formed in Factory cove (see Figure 2.3 for location of place names).
3. Sea ice breakup; the number of days after 1 June when the sea ice broke up in Factory cove.
4. Duration of sea ice; the time elapsed, in days, between sea ice formation and sea ice breakup.

Ice variables were transformed prior to correlation analysis using a $\log_{10}(x+1)$ transformation because all variances were more than twice the mean, indicating a clumped distribution (Fowler & Cohen 1986). First year survival rates showed a significant positive association with the date of arrival of the pack ice and with the duration of sea ice, and a negative association with the date of sea ice breakup (Table 4.16). Since the climatic variables and ice factors were likely to be functionally interrelated,

TABLE 4. 15 **RELATIONSHIP BETWEEN FIRST YEAR SURVIVAL RATES, BAROMETRIC PRESSURE AND MEAN AIR TEMPERATURE AT SEA LEVEL.**

		Barometric pressure (mB)					Temperature (^oC)				
Cohort	First year survival rate	Jan-Mar	Apr-Jun	Jly-Sep	Oct-Dec	Winter	Jan-Mar	Apr-Jun	Jly-Sep	Oct-Dec	Winter
1971	0.236	989.9	996.3	995.9	990.4	998.5	-0.1	-6.5	-9.8	-2.8	-11.2
1972	0.182	987.8	987.0	995.4	992.1	993.8	-0.4	-9.0	-8.5	-0.1	-10.4
1973	0.204	992.8	997.4	991.8	996.0	998.3	-1.7	-6.8	-9.2	-1.1	-10.4
1974	0.096	988.9	995.1	994.2	988.7	955.1	-0.6	-8.1	-11.5	-1.0	-13.8
1975	0.507	992.9	990.4	986.1	999.5	987.6	-1.2	-4.3	-9.4	-0.5	-9.9
1976	0.425	990.5	991.8	994.8	992.3	998.1	-1.5	-1.7	-7.1	-1.2	-6.3
1977	0.244	993.8	996.7	996.2	990.0	993.2	-0.8	-3.0	-7.9	-1.2	-8.5
1978	0.204	995.2	990.9	993.2	993.5	991.2	-1.2	-6.5	-7.0	-2.3	-9.0
1979	0.032	992.3	992.6	995.8	991.4	993.3	-0.9	-8.8	-12.8	-2.0	-13.8
1980	0.371	991.9	995.9	995.0	988.1	995.9	-1.2	-4.0	-8.7	-2.8	-9.1
1981	0.528	991.3	995.7	992.8	991.0	996.7	-2.0	-1.6	-9.7	-2.1	-8.9
1983	0.151	990.6	991.7	999.3	992.1	997.3	-0.8	-6.2	-5.7	-1.5	-8.8
1984	0.691	991.4	998.8	990.5	989.7	994.6	-1.5	-5.7	-3.4	-1.1	-6.7
	r_{11} =	0.100 NS	0.313 NS	-0.611 $P<0.05$	0.084 NS	0.099 NS	-0.589 $P<0.05$	0.625 $P<0.05$	0.547 NS	0.082 NS	0.699 $P<0.01$

TABLE 4. 15 cont RELATIONSHIP BETWEEN FIRST YEAR SURVIVAL RATES, AND THE NUMBER OF HOURS OF BRIGHT SUNSHINE AND WINDSPEED BETWEEN 1971-81.

		Sunshine hours (hours and tenths)					Windspeed (Knots)				
Cohort	First year survival rate	Jan-Mar	Apr-Jun	Jly-Sep	Oct-Dec	Winter	Jan-Mar	Apr-Jun	Jly-Sep	Oct-Dec	Winter
1971	0.236	40.6	19.5	58.8	81.0	41.2	10.1	12.7	11.3	11.0	10.5
1972	0.182	49.5	20.9	45.5	70.8	23.6	14.1	10.4	11.6	11.3	9.6
1973	0.204	44.0	19.3	63.4	76.5	47.7	13.1	11.8	12.9	13.0	10.2
1974	0.096	33.6	26.0	64.8	82.5	42.6	12.6	10.1	10.7	14.8	9.0
1975	0.507	41.8	22.1	54.3	97.4	34.3	10.9	11.9	14.6	15.1	12.7
1976	0.425	41.1	11.4	39.6	74.1	27.9	12.5	15.2	13.7	14.4	12.9
1977	0.244	48.0	31.2	40.3	60.1	26.3	14.0	15.5	16.4	17.3	16.7
1978	0.204	45.7	28.3	39.7	72.3	28.1	12.5	13.5	13.6	11.9	12.6
1979	0.032	53.0	13.5	48.2	74.1	31.9	11.1	11.1	11.0	12.7	10.9
1980	0.371	50.0	19.7	29.1	67.3	20.2	13.7	14.3	14.0	15.7	13.7
1981	0.528	65.1	17.6	40.8	56.5	25.5	14.1	13.0	12.3	10.7	11.3
1983	0.151	30.5	16.4	34.7	56.0	24.4	14.2	14.4	17.2	14.1	14.3
1984	0.691	35.3	16.5	36.3	57.9	22.6	14.4	13.9	18.2	15.4	15.0
	r_{11} =	0.078 NS	-0.233 NS	-0.361 NS	-0.171 NS	-0.379 NS	0.249 NS	0.389 NS	0.511 NS	0.209 NS	0.418 NS

TABLE 4. 16 RELATIONSHIP BETWEEN FIRST YEAR SURVIVAL RATES AND ICE VARIABLES. NOTE SURVIVAL RATES WERE ARCSINE TRANSFORMED AND ICE VARIABLES $\mathrm{LOG}_{10}(x+1)$ TRANSFORMED PRIOR TO CORRELATION.

Cohort	First year survival rate	Pack ice arrival (days after 10 Apr)	Sea ice formation (days after 10 Apr)	Sea ice breakup (days after 1 Jun)	Sea ice duration (days)
1971	0.236	21	40	193	204
1972	0.182	5	34	190	207
1973	0.204	2	4	156	203
1974	0.096	25	59	152	144
1975	0.507	41	58	154	147
1976	0.425	93	97	97	51
1977	0.244	80	85	123	89
1978	0.204	28	44	109	116
1979	0.032	8	36	201	216
1980	0.371	45	48	208	211
1981	0.528	81	90	149	110
1983	0.151	7	58	95	88
1984	0.691	52	66	15	1
	r_{11} =	0.623 $P<0.05$	0.366 NS	-0.627 $P<0.05$	0.694 $P<0.01$

the next step in the analysis was to identify at which time the strongest relationship was apparent by using monthly means for each quarter which had yielded a significant correlation. Table 4.17 indicates the months in which the mean monthly temperature was significantly correlated with first year survival rates. Apart from two winter months, April and July, which both showed a positive correlation with survival, the only other month showing a significant correlation was January. Since the mean monthly barometric pressure in July was also correlated with first year survival (Tables 4.15 and 4.18), as were the ice factors indicated above, this suggested that it was conditions during the winter which were affecting the survival of birds in their first year rather than events during January when the birds were still nestlings. This was confirmed by the lack of an association between survival rate and January temperature in the calendar year following fledging (r= −0.232 df=11 NS). The inverse correlation between January temperature and survival may have been spurious or, alternatively, high January temperatures suggest increased precipitation which may promote nestling mortality through chilling. This would be reflected in the first year survival rate because it incorporates a proportion of nestling period (between ringing and fledging). Accordingly, January temperature was excluded from subsequent analysis (as an additional check, including January temperature in the subset of climatic variables described below did not result in its selection by stepwise multiple regression analysis), and the remaining variables, time of pack ice arrival, time of sea ice breakup, duration of sea ice, mean barometric pressure in July and mean air temperature in April and July, were investigated to determine which explained most of the variation in first year survival. Table 4.19 is a correlation matrix between the climatic and ice variables significantly associated with first year survival, showing the extent of intercorrelation. Where climatic or ice variables were significantly correlated, the variable with the lowest correlation with survival rate was replaced by the higher one. This resulted in a subset of three variables, April temperature, July barometric pressure and the duration of sea ice, which were analysed by stepwise multiple regression. Mean monthly temperature in April and the duration of sea ice were selected and together accounted for over two-thirds of

TABLE 4. 17 RELATIONSHIP BETWEEN FIRST YEAR SURVIVAL RATES AND MEAN MONTHLY AIR TEMPERATURE BETWEEN JANUARY AND AUGUST. NOTE: SURVIVAL RATES WERE ARCSINE TRANSFORMED PRIOR TO CORRELATION.

		Temperature (^{o}C)							
Cohort	First year survival rate	Jan	Feb	Mar	Apr	May	Jun	Jly	Aug
1971	0.236	-0.3	-0.1	0.2	-1.5	-4.8	-13.1	-9.4	-14.9
1972	0.182	0.5	-1.0	-0.6	-3.5	-10.5	-13.0	-9.8	-8.3
1973	0.204	-1.5	-1.5	-2.0	-2.8	-7.8	-9.7	-9.3	-12.2
1974	0.096	-0.8	-1.6	0.5	-1.3	-8.1	-15.0	-13.2	-13.2
1975	0.507	-1.0	-2.2	-0.5	-0.2	-3.0	-9.6	-10.4	-9.6
1976	0.425	-2.1	-1.7	-0.7	-0.3	-1.8	-3.0	-8.5	-7.5
1977	0.244	-0.8	-1.6	0.0	-1.8	-2.0	-5.1	-13.4	-7.0
1978	0.204	-1.1	-1.6	-0.8	-0.7	-7.4	-11.3	-9.4	-6.2
1979	0.032	-1.1	-1.9	0.4	-6.7	-8.4	-11.2	-17.2	-12.9
1980	0.371	-0.7	-1.7	-1.2	-1.2	-3.8	-7.1	-9.2	-10.9
1981	0.528	-2.3	-2.1	-1.7	-0.4	-0.5	-4.0	-13.4	-9.4
1983	0.151	-0.6	-1.7	-0.1	-2.4	-3.8	-12.3	-10.0	-4.2
1984	0.691	-2.7	-1.4	-0.3	-0.5	-5.7	-10.8	-4.6	-4.7
	r_{11} =	-0.678 $P<0.05$	-0.210 NS	-0.355 NS	0.675 $P<0.05$	0.544 NS	0.473 NS	0.574 $P<0.05$	0.381 NS

TABLE 4. 18 **RELATIONSHIP BETWEEN FIRST YEAR SURVIVAL RATES AND MEAN MONTHLY BAROMETRIC PRESSURE BETWEEN JULY AND SEPTEMBER. NOTE: SURVIVAL RATES WERE ARCSINE TRANSFORMED PRIOR TO CORRELATION.**

Cohort	First year survival rate	Barometric pressure (mB) Jul	 Aug	 Sep
1971	0.236	996.1	1003.1	993.0
1972	0.182	1002.6	990.8	992.9
1973	0.204	991.5	996.4	987.5
1974	0.096	997.1	989.5	995.9
1975	0.507	985.3	984.3	988.7
1976	0.425	1000.5	997.9	985.9
1977	0.244	1002.0	988.8	997.8
1978	0.204	992.3	992.5	994.7
1979	0.032	997.3	995.2	994.8
1980	0.371	1001.3	992.3	991.4
1981	0.528	989.0	996.9	992.6
1983	0.151	1000.8	993.7	1003.3
1984	0.691	988.6	989.3	993.5
	r_{11} =	-0.560 $P<0.05$	-0.205 NS	-0.394 NS

TABLE 4. 19 CORRELATION MATRIX BETWEEN FIRST YEAR SURVIVAL RATE (ARCSINE TRANSFORMED), PACK ICE ARRIVAL, SEA ICE DURATION, SEA ICE BREAKUP (ICE VARIABLES $\mathrm{LOG}_{10}(x+1)$ TRANSFORMED), MEAN MONTHLY TEMPERATURE IN APRIL AND JULY AND MEAN BAROMETRIC PRESSURE IN JULY. NOTE: DF= 11.

	Survival rate	Ice arrival	Ice duration	Ice breakup	April temperature	July temperature
Ice arrival	0.623*	-	-	-	-	-
Ice duration	-0.694**	-0.386	-	-	-	-
Ice breakup	-0.627*	-0.290	0.985***	-	-	-
April temperature	0.675*	0.681*	-0.369	-0.358	-	-
July temperature	0.574*	0.091	-0.590*	-0.621*	0.571*	-
July pressure	-0.560*	-0.135	0.302	0.322	-0.368	-0.188

* P < 0.05
** P < 0.01
*** P < 0.001
All others NS

the variation in first year survival rates ($r^2 = 69\%$), and the relationship is described by the regression, $y = -0.20X_1 - 0.06X_2 + 0.81$, where y is the arcsine transformed first year survival rate, X_1 is $\log_{10}$ duration of sea ice and X_2 is the mean monthly temperature in April.

First year survival rates were therefore linked to climatic and ice factors during the winter months, particularly April temperatures and the duration of sea ice. The way in which these factors influence survival is not clear, but the arrival of pack ice in April, which is associated with lower temperatures, and the formation of sea ice, is likely to restrict fishing opportunities for all shags although the effects are likely to be felt more by the youngest and least experienced birds, some of which may have fledged only six weeks earlier.

4.8 The effect of hatching order on post-fledging survival.

The variation in survival of 335 chicks of known hatching order which fledged in 1980 was determined from the number recaptured between 1985-87. Fifty-five birds were recaptured, and since only two were seen in 1985 alone and recapture efficiency was high in 1986 and 1987, the figures have not been adjusted for recapture efficiency. Table 4.20 shows the initial sample sizes of nestlings, the number surviving to fledge and the number recaptured alive in 1985-87 (initial number of nestlings from Shaw 1985a, Table 2). Few C chicks (A = first hatched, C = last hatched) survived to fledge, but the order of hatching made no difference to the subsequent survival ($\chi^2 = 0.46$ df= 1 N.S.). The number of A, B, and C chicks recaptured were divided by sex and more female B and C chicks survived than males, although the difference was not significant ($\chi^2 = 2.6$ df=1 N.S., Table 4.21). Five sets of siblings were recaptured, 3 were from broods of two chicks and 2 were from broods of three. From one of the latter broods, an A chick and a B chick survived and the C chick died before fledging. In the other brood, all three fledged but only the A and C chicks survived to be recaptured in 1985-87.

TABLE 4. 20 THE EFFECT OF HATCHING ORDER ON SUBSEQUENT SURVIVAL. [1]SOURCE: SHAW (1985a) TABLE 2.

	Order of hatching		
	A	B	C
Initial sample[1]	208	180	81
Number surviving to fledge	182	144	9
Number recaptured 1985-87	30	22	3

Difference in number recaptured. (A and B chicks grouped: $\chi^2_1 = 0.46$ NS

TABLE 4. 21 **THE EFFECTS OF HATCHING ORDER AND SEX ON THE NUMBER OF CHICKS RECAPTURED BETWEEN 1985-87.**

	Order of hatching		
	A	B	C
Males	18	9	0
Females	12	13	3

Test of equality
A *v* B and C $\chi^2_1 = 2.6$ NS

4.9 Discussion.

The annual adult survival rates found in this study are similar to the value of 0.87 reported by Shaw (1984) during a previous study at Signy. At Macquarie Island, Brothers (1985) found that the mean annual survival rate of King shags determined over five seasons was 0.87 for males and 0.79 for females. Blue-eyed shag survival rates corresponded with those of three other Phalacrocoracids, Flightless cormorant; males 0.82, females 0.91 (Harris 1979), European shag; 0.83, 0.87 (Potts *et al.* 1980, Aebischer 1985) and Brandt's cormorant; males 0.82, females 0.79 (Boekelheide & Ainley 1989). In general, these rates are lower than in pelagic seabirds such as Cape pigeon 0.94, Snow petrel 0.93-0.96 (Hudson 1966), Fulmar 0.97 (Dunnet & Ollason 1978), Short-tailed shearwater 0.93 (Wooller *et al.* 1988) and Wandering albatross 0.94 (Croxall *et al.* 1990), but are more typical of inshore feeding species like Razorbill 0.90, Arctic tern 0.87 (Furness & Monaghan 1987), most penguins 0.61-0.87 and Common diving petrel 0.75 (Croxall 1982).

Several factors have been shown to influence the survival rates of seabirds including age, sex, breeding status and year. In Blue-eyed shags, survival rates varied with age averaging 0.36 over the first year of life, increasing to 0.82 by the age of breeding before declining after about 11 years by approximately 0.04 each year. In 1986 and 1987, 6% and 8% of the known age breeding birds (n=529 and n=745 respectively) were older than 11 and likely to be affected by reduced survival rates. In European shags the first year survival rate is 0.48-0.51 (Potts *et al.* 1980, Aebischer 1986), and older birds show reduced survival rates. At the Isle of May, the survival rate in shags older than 18 years was 0.68, (Aebischer 1986) whilst in Farne Islands shags the reduced survival rates only affected one age group and then after 10 years of age (Potts 1969). In addition to confirming a reduction in the survival rate in old birds, Aebischer & Coulson (1990) also found evidence of long-term changes in survival rate of breeding birds and suggested that apparent age-dependent survivorship could arise as a result of such shifts. It was not possible to decide if this explains the age-related pattern of survival in Blue-eyed shags because annual survival rates are only available for a few years. At Shagnasty the colony size has apparently remained unchanged since 1960 and since immigration is probably low and there seems to be no shortage of space into which the colony could expand, a change in colony size would be predicted if a trend in adult survival rate was occurring.

The length of the minimum previous breeding experience of Blue-eyed shags did not influence annual survival rates although only a limited range of breeding experience was available for analysis since few adults were recaptured between 1982 and 1983. After their first breeding attempt birds survived the following year as well as experienced breeders. This may be explicable in terms of reproductive costs in long-lived birds; if first time breeders are more likely to fail in their reproductive attempts than older birds they may be maximising their survival rate (and hence subsequent reproductive chances) at the expense of the current reproductive attempt (Fisher 1975, Curio 1983). Kittiwakes breeding for the first time show similar survival rates to experienced breeders (Aebischer & Coulson 1990), but assessment of the costs of reproduction is obscured by variation in the quality of individuals (Coulson & Porter 1985). If a similar explanation holds for Blue-eyed shag, then the individuals observed recruiting to the breeding population at a particular age may be higher quality and experience similar survival rates to experienced breeders.

5. RECRUITMENT TO THE BREEDING POPULATION.

5.1 Introduction.

Long-lived birds commonly show a lag of several years between becoming independent of their parents and first attempting to breed. Lack (1966) suggested that delayed breeding has been evolved in these species because the cost of breeding is high, and birds attempting to breed at younger ages would leave fewer descendents. This would occur if young breeders were less successful than more experienced birds and if breeding carries a risk of increased mortality. Wynne-Edwards (1962) explained deferred breeding in terms of group selection with social behaviour being the mechanism regulating the population size to avoid over-exploitation of food resources. Ashmole (1963) suggested that in tropical seabirds recruitment to the breeding population occurs in a density-dependent manner, and that competition for food around the colony is the main cause of variation in recruitment rates.

Theoretical studies have indicated that in long-lived species such as seabirds, maximising lifetime reproductive output requires a compromise between breeding as early as possible and avoiding an increased risk of mortality (Williams 1966). Since each annual reproductive effort represents a small proportion of the total number of potential reproductive attempts during the early part of an individual's breeding career, if there is a cost in terms of increased mortality, then long-lived birds at the start of their reproductive lives should show restraint, since they still potentially have many breeding opportunities remaining.

In common with many birds, seabirds breeding for the first time are less successful than more experienced breeders, and typically produce fewer young. Kittiwakes which bred for the first time fledged fewer chicks per pair than in subsequent seasons irrespective of the age at recruitment or the position in the colony, although the difference was most marked in birds breeding at the centre (Wooller & Coulson 1977). In the

Short-tailed shearwater, the improvement of reproductive performance with experience has two components, breeding experience and the number of previous mates. At their first breeding attempt with their first mate, birds produced 0.31 chicks *per* pair on average; after three breeding attempts with the same mate, productivity had risen to 0.64 chicks *per* pair. However, if at the first breeding attempt the mate is their third one or more, the initial productivity is 0.50 chicks *per* pair rising to 0.71 chicks *per* pair after three or more breeding seasons with the same mate (Wooller *et al.* 1988). In the European shag, two year old males breeding for the first time fledged about one chick fewer *per* pair than older birds, and the effect of female age was unimportant (Aebischer 1985).

Most ideas about why seabirds take several years to breed for the first time include the acquisition and development of skills, and particularly foraging skills. Differences in foraging ability between young and old birds have been demonstrated for several species with delayed breeding including Herring gulls (Verbeek 1977, Ingolfsson & Estrella 1978, Greig *et al.* 1983), Sandwich terns (Dunn 1972), Brown pelican (Orians 1969), Little blue heron (Recher & Recher 1969) and Olivaceous cormorant (Morrison *et al.* 1978). In addition, a comparison of three species of gulls linked the development of foraging expertise with the age of first breeding (Maclean 1986). A study of Royal terns indicated that there were no differences between adults and juveniles with respect to their success rates in prey capture, but juveniles had lower dive rates and obtained less food per unit time than adults (Buckley & Buckley 1974, cited in Burger 1988). However, the improvement of foraging skills alone cannot explain the time taken by some of the larger species to begin breeding, nor does it explain the differences in the age of recruitment between the sexes found in several seabirds (Nelson 1988).

Nelson (1988) emphasised the role of behavioural development in site acquisition and pair bonding. The availability of nest sites at most seabird colonies does not appear to be a limiting factor, although the acquisition and defence of sites may require skills which young birds have to develop prior to first breeding. In the Sooty tern, pre-breeding birds are prevented from landing in the colony by the presence of breeding adults and older pre-breeding birds on the ground (Harrington 1974), and adult male Kittiwakes incur an increase in mortality rate between January and March apparently as a result of site defence (Coulson & Wooller 1976). Whilst nest sites may not be limiting *per se*, there may be a shortage of high quality sites. Young European shags bred at nest sites of poorer quality than older breeders and this contributed to their lower breeding performance (Potts *et al.* 1980). Furthermore, it was apparent that young shags could discriminate between nest sites of differing quality but were unable to acquire high quality sites in normal years because these were already occupied by the time they arrived at the colony. The prolonged courtship period observed in some species may serve to strengthen the pair bond and ensure that the breeding efforts of the pair are coordinated. For example, in the Wandering albatross, the incubation spells are long, and a strong pair bond may provide the necessary impetus for the off-duty bird to return to its mate (Nelson 1988). However there is much variation in the length of the period of association prior to first breeding but this does not correlate with the complexity of pair-bonding behaviours. It seems unlikely that the mechanics of site acquisition and pair related behaviour alone can explain deferred breeding (Nelson 1988)

It has sometimes been assumed that during the pre-breeding years young birds are physiologically immature (*e.g.* Skutch 1953, Lack 1968). There have been few studies of the development of physiological maturity in seabirds, but in Adelie penguins some non-breeding males aged four or more had mature testes yet did not breed (Ainley 1975 cited in Nelson 1988), and pre-breeding Sooty terns developed active brood patches which were linked to gonad maturation (Harrington 1974). Endocrine studies of Albatrosses, which show some of the longest periods of deferred breeding, indicate that males are physiologically mature several years prior to breeding for the first time, whereas females are inhibited from egg formation by progesterone secretion until they are 7 years old (Hector *et al.* 1986). Therefore in some species at least, physiological maturity is not a constraint on first breeding.

5.2 The age of first breeding in relation to year, colony and sex.

The age at which Blue-eyed shags first bred was determined from the number of birds first seen breeding at each age between 1985-87. This method overestimates the age of recruitment to the breeding population because some birds are not recaptured at their first breeding attempt. In this study, the recapture efficiency of breeding birds was high, particularly in 1986 and 1987, and this is unlikely to seriously bias the results. In the following sections, the term 'recruitment' is taken to mean recruitment to the breeding population.

Table 5.1 shows the number of birds which were first recorded breeding between 1985-87 with adjusted totals allowing for recapture efficiency. In general, these adjustments made little difference to the totals, although there are larger differences for 3 year olds in 1987 and 4 year olds in 1985. The minimum age of first breeding was two years, and few individuals were first seen after the age of six. In 1985, 3% (n = 152 birds) were first recorded breeding when older than six, and in the other years of the study even fewer of these older birds were seen for the first time, 1.3% (n = 155 birds) in 1986 and 0.6% (n = 323 birds) in 1987, suggesting that these birds had bred in previous years but were not recaptured. The two birds seen in 1985 and 1986 which were in the age category ' > 7 years', were 10 and 11, and 12 and 13 years old respectively and had almost certainly been missed in previous years. In the following analyses, it has been assumed that no birds recruited to the breeding population after six years of age.

The main age range of recruits was between 3-5 years, a minimum of 74% of the birds breeding for the first time in these age classes in any year. Since no chicks were ringed in 1982, the mean age of first breeding is biassed by the absence of birds from this cohort. In 1985 and 1986, the mean age of first breeding is likely to be overestimated due to the absence of ringed 3 and 4 year old birds, and the absence of ringed 5 year olds in 1987 has probably resulted in an underestimation of the mean. The mean age

TABLE 5. 1 THE AGE OF FIRST BREEDING BETWEEN 1985-87 IN RELATION TO YEAR AND SEX. NOTE: MEANS AND SE EXCLUDE BIRDS OLDER THAN SIX YEARS, ADJUSTED TOTALS ARE CORRECTED FOR RECAPTURE EFFICIENCY, NO DATA FROM 1982 COHORT, TWO YEAR OLDS IN 1987 INCLUDE 30 UNRINGED BIRDS AGED ON PLUMAGE.

		Age(years)								
Year		2	3	4	5	6	7	>7	Mean	SE
	Males	0	-	51	11	1	1	0	4.21	0.056
	Females	0	-	54	18	0	2	2	4.25	0.051
1985	Total	0	-	105	29	1	3	2	4.23	0.038
	Adjusted total	0	-	133	36	1	3	2	4.23	0.033
	Males	0	2	-	59	13	0	0	5.12	0.061
	Females	4	11	-	49	9	0	2	4.66	0.124
1986	Total	4	13	-	108	22	0	2	4.89	0.071
	Adjusted total	4	13	-	113	23	0	2	4.90	0.069
	Males	35	100	7	-	11	1	0	3.03	0.078
	Females	33	118	1	-	1	1	0	2.81	0.040
1987	Total	68	218	8	-	12	2	0	2.92	0.044
	Adjusted total	71	230	8	-	12	2	0	2.92	0.042

Difference between sexes (Z scores):

1985 Z = 0.35 NS
1986 Z = 3.13 P<0.01
1987 Z = 2.25 P<0.05

of first breeding (all ± 1 SE) for all birds between 1985-87 was 3.7 ± 0.04 years. However, the mean age of first breeding varied each year between 2.9 ± 0.04 years in 1987 and 4.9 ± 0.07 years in 1986 (comparison of adjusted totals for 1986 and 1987; $Z = 24.5$ $P<0.001$), and the modal age of first breeding was 4 years in 1985, 5 years in 1986 and 3 years in 1987. Table 5.2 shows that there were significant differences in the proportion of birds which recruited from each age class in relation to year. In 1986, only 11% of 153 recruits were younger than five compared with 79% of 169 recruits in 1985 and 96% of 321 recruits in 1987 ($\chi^2 = 374$ df=2 $P<0.001$). A more detailed comparison between 1986 and 1987 indicated that a higher proportion of 2 and 3 year old birds first bred in 1987, whereas the greatest proportion of recruits in 1986 were aged 4-5 (Table 5.2b).

The age at which a bird first bred was not related to the colony or subcolony at which it bred (Table 5.3). Since birds showed a high fidelity to their natal colony when returning to breed (see section 3.3.2), this implies that the influence of natal colony and subcolony on the age of recruitment is also minor. The mean age of first breeding for all males is 3.82 ± 0.07 years and for all females 3.61 ± 0.06 years, a difference which is significant ($Z = 2.26$ $P<0.05$). Within years, there was a significant difference between the sexes with respect to the mean age of recruitment in 1986 and 1987; the mean age of males being higher in both years (Table 5.1). Considering the numbers of males and females which recruited at each age (Table 5.4), in 1985 there was no difference between the sexes. In both the remaining years significantly different numbers of males and females recruited, but closer investigation revealed that in 1986 this was due to birds in one age class only, the 2 year olds, of which all four were females. Similarly in 1987, it was the birds in the age classes 4 and 6 years which were producing a significant difference. Reanalysing the numbers of recruiting birds in 1986 excluding 2 year olds, which only accounted for 3% of all recruits, there was no difference in the number of either sex which recruited at each age. Likewise in 1987, excluding birds in the age classes 4 and 6 years, which formed 7% of the recruits, there was no difference between the sexes in the numbers which recruited. In conclusion, there was no difference

TABLE 5. 2 **AGE OF FIRST BREEDING IN RELATION TO YEAR: A) BETWEEN 1985-87 AND B) BETWEEN 1986-87.**

A)

	Age(years)		
Year	2-4	5-6	% aged 2-4
1985	133	36	78.7
1986	17	136	11.1
1987	309	12	96.3

Difference between years: $\chi^2_2 = 374$ $P<0.001$

B)

	Age(years)				
Year	2	3	4-5	6	% aged 2-3
1986	4	13	113	23	11.1
1987	71	230	8	12	92.8

Difference between years: $\chi^2_3 = 330$ $P<0.001$

TABLE 5. 3 **THE AGE AT WHICH BIRDS WERE FIRST RECORDED BREEDING IN RELATION TO COLONY OR SUBCOLONY BETWEEN 1985-87. NOTE: NO BIRDS WERE RECAPTURED AT SHAGNASTY III IN 1985.**

	Year									
	1985			1986			1987			
	Age(years)			Age(years)			Age(years)			
Colony/ subcolony	2-4	5-6	% 2-4	2-4	5-6	% 2-4	2	3	4-6	% 2-3
North Point	22	2	91.7	2	8	20	6	26	3	91.4
Shagnasty I/II	111	35	76.0	6	46	11.5	27	109	6	95.8
Shagnasty III	-	-	-	9	82	9.9	38	95	11	92.4
Difference between colonies:	$\chi^2_1 = 2.11$ NS			$\chi^2_2 = 0.95$ NS			$\chi^2_4 = 5.08$ NS			

TABLE 5.4 THE AGE AT WHICH BIRDS WERE FIRST RECORDED BREEDING IN RELATION TO AGE AND SEX BETWEEN 1985-87.

	Year								
	1985		1986			1987			
	Age(years)		Age(years)			Age(years)			
Sex	4	5-6	2-3	5	6	2	3	4	6
Males	51	12	2	59	13	35	100	7	11
Females	54	18	15	49	9	33	118	1	1
Test of equality between sexes:	$\chi^2_3 = 1.29$ NS		overall: $\chi^2_5 = 11.59$ $P<0.05$			overall: $\chi^2_7 = 14.38$ $P<0.05$			
			excluding 2 years: $\chi^2_5 = 7.88$ NS			excluding 4 and 6 years: $\chi^2_3 = 1.55$ NS			

between the sexes in recruitment over the age range in which most of the birds recruited.

5.3 Influence of parental age and reproductive parameters on the age of recruitment.

The age of recruitment of the 1981 cohort in relation to the age of their parents is shown in Table 5.5. For parents in each age class, there was no difference in the proportion of their offspring which first bred when aged four or five years. To determine if there were differences within each age of recruits with respect to the ages of their parents, I tested the null hypothesis that equal numbers of four and five year old recruits came from parents in each age class (Table 5.6). There were no significant differences, indicating that at either age of recruitment birds did not come from parents of a particular age. A more restricted dataset for birds hatched in 1980 and 1985 also indicated that there was no tendency for the age of recruitment to be linked to the ages of their parents (Table 5.7).

The number of birds hatched in 1981 and which bred for the first time aged 4 and 5 was examined in relation to clutch size, brood size, number of chicks fledged and their parents pair status (Table 5.8). There was no indication that any of these factors influenced the age of recruitment, at least in the 1981 cohort. In addition, the survival rate in the year following recruitment was similar for birds which recruited when 4 years and 5 years old (Table 5.9). These survival rates were corrected for recapture efficiency by including birds known to be alive during the period 'at risk' but not actually recaptured then. This method was used here instead of the direct estimate of the number of birds not recaptured employed previously, because the latter produced unrealistically high survival estimates, suggesting that the corrections for recapture efficiency were overestimating the number of birds actually missed. The hatching order of birds in 1980 did not affect the numbers of 5 and 6 year old birds recruiting (Table 5.10). It was not possible to extend the analysis to include 4 year olds because no adults were recaptured in 1983 and the recapture effort in 1982 was

TABLE 5. 5

THE NUMBER OF BIRDS HATCHED IN 1981 AND FIRST BREEDING AT FOUR AND FIVE YEARS IN RELATION TO THE AGE OF THEIR PARENTS.

		Male parent age (years)				Female parent age (years)		
Age at first breeding	No. breeding	3-5	6-8	9-12	No. breeding	3-5	6-8	9-12
4	40	17	15	8	39	7	19	13
5	45	17	13	15	37	14	11	12
Proportion breeding at 4 years		0.50	0.54	0.34		0.33	0.63	0.52
Comparison of 4 and 5 year recruits:		$\chi^2_2 = 1.99$ NS				$\chi^2_2 = 4.46$ NS		

TABLE 5.6

THE EFFECT OF PARENT AGE ON THE NUMBER OF BIRDS WHICH RECRUITED AGED 4 AND 5 YEARS FROM THE 1981 COHORT.

		Male parent age (years)				Female parent age (years)			
Age at first breeding		No.	3-5	6-8	9-12	No.	3-5	6-8	9-12
4	Observed	40	17	15	8	39	7	19	13
	Expected	40	13.3	13.3	13.3	39	13.0	13.0	13.0
5	Observed	45	17	13	15	37	14	11	12
	Expected	45	15.0	15.0	15.0	37	12.3	12.3	12.3

Test of each age class χ^2 - test 2 df:

Recruitment age	Male parent	Female parent
4	3.36 (NS)	5.54 (NS)
5	0.53 (NS)	0.38 (NS)

TABLE 5. 7 THE EFFECT OF PARENT AGE ON THE NUMBER OF RECRUITS AGED 2 AND 5 YEARS FROM THE 1980 AND 1985 COHORT.

Cohort	Sex	Age		3-5	6-11	Observed *v* Expected
1980	Male	5	Observed	5	5	
	Female	5	Observed	2	9	
			Corrected expected	5.5	5.5	$\chi^2_1 = 0.78$ NS
1985	Male	2	Observed	2	3	
			Corrected expected	2.5	2.5	P = 1.0 (Fisher's exact)
	Female	2	Observed	6	3	
			Corrected expected	4.5	4.5	$\chi^2_1 = 0.22$ NS

TABLE 5. 8

AGE OF FIRST BREEDING OF BIRDS HATCHED IN 1981 IN RELATION TO CLUTCH SIZE, BROOD SIZE, NUMBER OF CHICKS FLEDGED AND PARENT PAIR STATUS. NOTE: PAIR STATUS RELATES CURRENT MATE TO THAT IN PREVIOUS YEAR.

	Clutch size				Brood size			No. of chicks fledged			Current pair status	
Age at first breeding	1	2	3	4	1	2	3	1	2	3	Change mate	Same mate
4 (1985)	1	10	67	1	1	21	43	4	42	18	30	11
5 (1986)	1	10	80	0	3	16	53	7	41	20	28	7
Comparison of ages:	$\chi^2_1 = 0.02$ NS				$\chi^2_1 = 0.59$ NS			$\chi^2_2 = 0.82$ NS			$\chi^2_1 = 0.18$ NS	

TABLE 5.9

ANNUAL SURVIVAL RATES IN THE YEAR OF RECRUITMENT FOR BIRDS HATCHED IN 1981 AND RECRUITING WHEN 4 AND 5 YEARS OLD.

	Males			Females		
Age at Recruitment	No. 'at risk'	Survival rate	S.E	No. 'at risk'	Survival rate	S.E.
4	51	0.922	0.038	54	0.907	0.040
5	59	0.915	0.037	49	0.918	0.040
Difference between ages: (Fisher's exact)		P = 1.0			P = 1.0	

TABLE 5. 10 **THE EFFECT OF HATCHING ORDER ON THE AGE OF RECRUITMENT OF BIRDS FROM THE 1981 COHORT. NOTE: 'A' = FIRST HATCHED, 'B' = SECOND HATCHED (3 'C' CHICKS EXCLUDED).**

	Hatching order			
	Age 5		Age 6	
	A	B	A	B
Recruiting	14	11	12	5
Not recruiting	2	3	17	15
Test of difference:	P = 0.64 NS (Fisher's exact)		$\chi^2_1 = 0.77$ NS	

poor. Consequently all birds aged 4 breeding in 1984 were seen for the first time, although they may have bred previously.

5.4 The age of recruitment in relation to year of hatching.

The ages at recruitment for six cohorts are shown in Table 5.11. The number of birds seen recruiting at each age have been corrected for recapture efficiency using direct estimates of the number of birds not recaptured. In 1984 and 1988, the recapture efficiencies used were calculated from unpublished B.A.S. records (Price 1985 and Ashford 1988) and the calculation of the corrections are shown in appendices 3 and 3a. In 1988, it was not clear whether all 2-5 year olds recaptured were breeding and all birds in this age class have been included. This gives an inflated estimate of recruitment and the error may be considerable, since none of the 28 two year olds were known to be breeding, and 43% of the three year olds (n=77 birds) and 53% of the four year olds (n=43 birds) were breeding for the first time. No five year old birds recruited in 1988, probably because the 1983 cohort had completely recruited in previous years (see below).

Although there is no cohort for which all the information is complete, it is apparent that few individuals join the breeding population before the age of 3 and after 5; overall, 10% and 4% of recruits were younger than 3 years and older than 5 years respectively (n=754 birds). There were marked differences between cohorts in the pattern of recruitment. A significantly higher proportion of birds hatched in 1984 recruited at 3 years of age than those from 1981 or 1983 ($\chi^2 = 221$ df=2 $P<0.001$), and proportionately more birds recruited at 4 years from the 1981 cohort. When the 1980 and 1981 cohorts were considered with respect to the recruitment of 4 and 5 year olds, a higher proportion of 4 year olds and a lower proportion of 5 year olds recruited from birds hatched in 1981 than from 1980 ($\chi^2 = 10.85$ df=1 $P<0.001$).

There were no differences between the sexes in the pattern of recruitment within a cohort of birds except for those hatched in 1983, when proportionately more females

TABLE 5. 11 THE AGE OF RECRUITMENT ACCORDING TO COHORT. NOTE: FIGURES FOR 1988 MAY INCLUDE BIRDS NOT ATTEMPTING TO BREED (SEE TEXT). FIGURES ADJUSTED FOR RECAPTURE EFFICIENCY, DASHES INDICATE YEARS WHEN NO RECAPTURES WERE MADE OR BIRDS WHICH HAVE NOT YET RECRUITED, RECRUITS UNSEXED IN 1988.

				Age (years)			
Cohort		2	3	4	5	6	Equality between sexes
1980	Males	-	-	5	16	14	$\chi^2_5 = 2.13$ NS
	Females	-	-	9	20	9	
1981	Males	-	6	71	59	11	$\chi^2_7 = 10.18$ NS
	Females	-	2	60	49	1	
1983	Males	0	2	7	0	-	$\chi^2_1 = 6.23$ $P<0.05$
	Females	0	11	1	0	-	
1984	Males	0	106	48	-	-	$\chi^2_1 = 0.64$ NS
	Females	4	119		-	-	
1985	Males	38	83	-	-	-	$\chi^2_1 = 0.23$ NS
	Females	33		-	-	-	
1986		28	-	-	-	-	

Cohort *v* age (sexes grouped) 1981, 1983, 1984; 3 and 4 years: $\chi^2_2 = 220.9$ $P<0.001$

1980, 1981; 4 and 5 years: $\chi^2_1 = 10.85$ $P<0.001$

first bred at 3 years and proportionately more males aged 4 (Table 5.11). However, only 21 individuals from this cohort survived to recruitment, much lower than in the other years.

5.5 Variation in the recruitment of individual cohorts.

After correcting for recapture efficiency, the number of ringed birds from each cohort which recruited (from Table 5.11) was expressed as a percentage of the number of chicks ringed. The proportion of each cohort which recruited is shown in Table 5.12, and varies between 46% recruitment for birds hatched in 1984 and 9% for those from 1983. The latter year yielded the lowest contribution of recruits to the breeding population of any year in which sufficient time had elapsed for most of the individuals to have bred and been identified. The differences between cohorts in the proportion of recruits each contributed were significant, even after the removal of the 1983 birds from the analysis (χ^2 = 417 df=4 P<0.001). Since first year survival rates are highly variable, more so than the adult survival rates which are assumed to apply after the first year, it is likely that this is the main cause of variation in the pool of potential recruits, with the number attempting to breed being adjusted by the conditions during a particular breeding season and the quality of the individual bird. Clearly, in a cohort where few individuals survive the first year of life, the number of potential recruits will be reduced, whereas a high first year survival rate is more likely to result in a large number of birds available for recruitment.

5.6 The number of recruits in relation to the size of the breeding population.

The number of recruits and experienced birds breeding between 1984-88 are shown in Table 5.13. In 1986 and 1987, a significantly higher proportion of birds recruited at Shagnasty III compared with North Point and Shagnasty I/II. Comparing the Shagnasty subcolonies in 1984 and 1988, a higher proportion of recruits again bred at

TABLE 5. 12 PERCENTAGE RECRUITMENT TO THE BREEDING POPULATION IN EACH COHORT BETWEEN 1980 AND 1986. NOTE: NO CHICKS RINGED IN 1982, * RECRUITMENT NOT YET COMPLETE THESE FIGURES ARE MINIMUM RECRUITMENT.

Cohort	Chicks ringed	Recruits	Recruitment (%)
1980	436	73	16.7
1981	837	259	30.9
1983	232	21	9.1
1984*	597	277	46.4
1985*	623	154	24.7
1986*	888	28	3.2

Comparison of cohorts:

Overall: $\chi^2_5 = 455$ $P<0.001$

Excluding: $\chi^2_4 = 417$ $P<0.001$
(1983)

TABLE 5. 13 **THE NUMBER OF RECRUITS AND EXPERIENCED BREEDING BIRDS IN RELATION TO COLONY, BETWEEN 1984-88. NOTE: SHAGNASTY III NOT VISITED IN 1985, NOT POSSIBLE TO RELIABLY DISTINGUISH RECRUITS AT NORTH POINT IN 1988.**

		Year					
		1984	1985	1986	1987	1988	Propn. of recruits *v* years
North Point	Experienced	48	67	62	94	-	
	Recruits	10	23	10	33	-	$\chi^2_3 = 5.38$ NS
	Propn. of Recruits:	0.17	0.26	0.14	0.26	-	
Shagnasty I/II	Experienced	192	266	317	403	276	
	Recruits	21	148	53	137	55	$\chi^2_4 = 85.3$ $P<0.001$
	Propn. of Recruits:	0.10	0.36	0.14	0.25	0.17	
Shagnasty III	Experienced	71	-	150	240	125	
	Recruits	11	-	91	130	38	$\chi^2_3 = 24.1$ $P<0.001$
	Propn. of Recruits:	0.13	-	0.38	0.35	0.23	
Propn. of recruits *v* colony:		$\chi^2_2 = 2.60$ NS	$\chi^2_1 = 2.99$ NS	$\chi^2_2 = 49.4$ $P<0.001$	$\chi^2_2 = 10.79$ $P<0.01$	$\chi^2_1 = 2.78$ NS	

Shagnasty III, although the differences in these years were not significant. Shagnasty III was more attractive to recruiting birds than either Shagnasty I/II or North Point, possibly because it was flatter and there was more space around the edges of the colony where new birds could nest.

Table 5.14 indicates that there is no correlation between the number of birds which recruited and the number of experienced breeders in the same year ($\log_{10}$ transformation of both axes; $r = 0.769$ df=3 N.S.), nor was the number of recruits related to the number of experienced breeding birds in the previous year, although only a few years data were available ($\log_{10}$ transformation of both axes; $r = -0.306$ df=2 N.S.). To increase the sample size, the number of recruits and experienced breeders from 1979-81 was incorporated into the analysis. No significant correlations were found between the number of recruits and experienced breeders in the same year ($\log_{10}$ transformation of both axes; $r = 0.700$ df=6 N.S.), or the number of recruits in one year and the number of experienced breeders in the previous year ($\log_{10}$ transformation of both axes; $r = -0.225$ df=4 N.S.). There was no association between the mean age of recruitment and the proportion of recruits each year between 1984-88 (arcsine transformation of recruits $r = -0.221$ df=4 N.S.).

These results are not consistent with a simple density-dependent mechanism of recruitment such as nest-site availability. The high positive correlation coefficients ($r > 0.70$) for the numbers of recruits and experienced birds breeding in the same year indicates that in years when the population of experienced breeders is high, recruitment is also high, and conversely it is low in those years when there are fewer experienced breeders.

TABLE 5.14 **THE NUMBER OF RECRUITS AND EXPERIENCED BREEDERS, MEAN AGE AT FIRST BREEDING AND DIFFERENCE IN RECRUITMENT BETWEEN THE SEXES. NOTE: IN 1986 AND 1987 MALES HAD HIGHER MEAN AGES OF RECRUITMENT, ^{A} SHAGNASTY III NOT VISITED; ^{B} RECRUITS WERE NOT SEXED; ^{C} NOT CALCULATED SEPARATELY IN EACH YEAR (FROM SHAW (1984)).**

	Year							
	1984	1985^A	1986	1987	1988	1979	1980	1981
No. of experienced breeders	311	333	529	737	401	62	225	306
No. of recruits	42	171	154	300	93	35	188	150
Propn. of recruits	0.12	0.34	0.23	0.29	0.19	0.36	0.46	0.33
Mean age of recruitment	4.5	4.2	4.9	2.9	3.3	-^{C}	-^{C}	-^{C}
Difference between sexes in mean age of recruitment	No	No	Yes	Yes	-^{B}	-^{C}	-^{C}	-^{C}

	1984 - 1988	All years
Correlation between experienced breeders and recruits (both axes Log_{10} transformed)	1) same year: $r_3 = 0.769$ NS	$r_6 = 0.700$ NS
	2) previous year's experienced and current year's recruits: $r_2 = -0.306$ NS	$r_4 = -0.221$ NS

Correlation between mean age of recruitment and proportion of recruits (arcsine transformed): $r_3 = -0.225$ NS

5.7 Factors affecting the recruitment of pre-breeding birds.

5.7.1 Colony attendance during pre-breeding years in relation to subsequent recruitment.

The attendance of pre-breeding birds at North Point and the Shagnasty subcolonies was related to the colony at which they first bred, also according to the natal colony. Only birds from the 1984 and 1985 cohorts are included in the following analyses (one record included refers to a bird hatched in 1983), because the number of birds hatched in 1986 which had started breeding by 1988 was uncertain. Table 5.15 shows that for birds hatched at Shagnasty I/II, 78% (n=36 records) of the sightings during the pre-breeding years were at the colony to which recruitment occurred. At North Point, 75% of pre-breeding sightings were at the colony of recruitment (n=4 records), and only one out of three visits made by birds hatched at Shagnasty III was at the colony to which they subsequently bred. Combining all colonies, 74% of the 43 visits made by pre-breeding birds (n=37 birds) were to the colony or subcolony at which they recruited.

If the natal colony is ignored, there is a significant difference in the colony attendance of pre-breeders between the two Shagnasty colonies (Table 5.16). Only 14% of sightings during the pre-breeding years of birds which eventually bred at Shagnasty I/II (n=29 records) were at other colonies, compared with 64% (n=11 records) of birds which bred at Shagnasty III (χ^2 = 7.70 df=1 P<0.001). All three sightings of birds which bred at North Point were from that colony, and there was no difference in the number of sightings of birds away from the breeding colony between those which bred at either North Point or Shagnasty I/II (P=1.0, Fisher's exact test).

Since the sightings of birds prior to first breeding were opportunistic, it is likely that the number of individuals sighted was related to the amount of time spent by the observer at each colony, and since more time was spent at Shagnasty I/II than at

TABLE 5. 15 **ATTENDANCE DURING THE PRE-BREEDING YEARS IN RELATION TO NATAL AND SUBSEQUENT BREEDING COLONY. NOTE: FIGURES REFER TO SIGHTINGS NOT INDIVIDUAL BIRDS (N = 37 BIRDS).**

		No. of colony visits by pre-breeding birds to:		
Natal colony	Breeding colony	NP	SNI/II	SNIII
North Point	North Point	3	0	0
	Shagnasty I/II	0	0	0
	Shagnasty III	1	0	0
Shagnasty I/II	North Point	0	0	0
	Shagnasty I/II	0	24	3
	Shagnasty III	1	4	4
Shagnasty III	North Point	0	0	0
	Shagnasty I/II	0	1	1
	Shagnasty III	1	0	0

TABLE 5. 16 ATTENDANCE DURING THE PRE-BREEDING YEARS IN RELATION TO COLONY OF FIRST BREEDING. NOTE: FIGURES REFER TO SIGHTINGS NOT INDIVIDUAL BIRDS (N = 37 BIRDS).

		No. of colony visits by pre-breeding birds to:		
Breeding colony		NP	SNI/II	SNIII
North	Observed	3	0	0
Point	Expected	1	1	1
Shagnasty	Observed	0	25	4
I/II	Expected	7	13	9
Shagnasty	Observed	3	4	4
III	Expected	3	5	4

Goodness-of-fit test:

SNI/II $\chi^2_2 = 20.9$ $P<0.001$

NP and SNIII $\chi^2_1 = 0.13$ NS

North Point or Shagnasty III, it is necessary to consider the effect this might have on the observations. An expected distribution of sightings of pre-breeding birds was obtained as indicated below, based on the proportion of all sightings of pre-breeders made at each colony. All records of pre-breeding birds visiting the colonies were used irrespective of subsequent recapture as breeders, but birds which had been ringed as pre-breeders were excluded. Out of 255 visits made by pre-breeders to the Signy colonies, 58 (23%) were at North Point, 116 (45%) were at Shagnasty I/II and 81 (32%) were at Shagnasty III.

From the resulting expected distribution, shown in Table 5.16, it is clear that for birds which eventually bred at Shagnasty I/II, there were significantly fewer sightings during the pre-breeding period at either North Point or Shagnasty III. The apparently wider distribution of sightings for birds breeding at Shagnasty III was no greater than expected according to the time spent in resighting pre-breeders at each colony ($\chi^2 = 0.13$ df=1 N.S.), and there were insufficient records to test the distribution of birds breeding at North Point. A goodness-of-fit test of the observed distribution of visits to the colonies for birds which were hatched and bred at Shagnasty I/II (Table 5.15), indicated that these birds were less likely than expected to be seen at a colony other than Shagnasty I/II as pre-breeders ($\chi^2 = 22.0$ df=2 $P<0.001$).

The pattern of visits by pre-breeding birds to the colonies paralleled the pattern of recruitment of birds in relation to the natal colony (*cf* Table 3.5), with most of the visits by pre-breeders being to the natal colony, at least at North Point and Shagnasty I/II (Table 5.15). Only three records relate to sightings between North Point and Shagnasty, and this reflects the 93% and 98% fidelity to the natal colony by breeding birds found at North Point and Shagnasty respectively.

5.7.2 Frequency and timing of colony attendance.

The frequency of colony visits made by pre-breeding birds aged between one and

TABLE 5. 17

THE FREQUENCY OF PRE-BREEDING COLONY VISITS MADE BY BIRDS AGED 1-3 YEARS IN RELATION TO THE AGE OF RECRUITMENT.

		Age at recruitment					
		3 years			4 years		
		No. of birds	No. of visits to colonies	No. of visits *per* bird	No. of birds	No. of visits to colonies	No. of visits *per* bird
Age at pre-breeding colony visits (years)	1	5	5	1.0	1	1	1.0
	2	24	27	1.1	0	0	0
	3	-	-	-	9	15	1.7

Test of departure from 1 visit *per* bird
1 year *v* 2 years (Goodness-of-fit test): $\chi^2_1 = 0.31$ NS   1 year *v* 3 years: $\chi^2_1 = 3.61$ NS

three years is shown in relation to the age of recruitment in Table 5.17. Whilst the number of birds visiting the colonies increased with their age, there was no significant increase in the number of visits *per* bird, although an appreciably higher frequency of visits was found for individuals which visited the colonies in their third year of life and subsequently bred in the following year. Since multiple resightings of pre-breeding birds were rare, the true pattern of colony visits by pre-breeders may have been obscured by the relatively high number of birds which were only resighted once. To overcome this problem, the individual recapture histories of 8 birds, which were resighted on more than two occasions, were considered (Table 5.18). Two of these birds recruited and the remaining six did not. Although there is an appreciable increase in the number of visits made *per* bird, both for each individual and collectively as their age increased, the difference was not statistically significant (χ^2 = 2.66 df=2 N.S.).

The timing of pre-breeding visits to the colonies by birds aged between 1 and 4 years is shown in Table 5.19. Apart from 4 year olds, which are only represented by a small number of observations, there is a significant tendency for birds to visit the colonies earlier as they become older. Only 8% and 6% of one and two year olds which were seen, visited the colony before November, whereas 20% of 3 year olds did so. In January and February, the youngest pre-breeding birds were the most frequent visitors, 62% aged one compared with 40% and 32% of two and three year olds (χ^2 = 18.89 df=4 $P<0.001$). The distribution of visits shown by 4 year old birds in Table 5.19 is probably misleading as these individuals were all resighted in 1988 when no observations were made prior to December. During 1986 and 1987, the colonies were observed from August onwards, and pre-breeding birds were recaptured at every opportunity. It is therefore likely that the observations of colony visits by birds accurately reflect the timing of visits by pre-breeders rather than variable recapture efficiency.

The timing of colony visits in relation to recruitment suggested that in the year prior to recruitment more visits occurred between August and December than for birds seen two years prior to breeding (Table 5.20). An appreciably higher percentage of visits

TABLE 5. 18 THE FREQUENCY OF PRE-BREEDING COLONY VISITS MADE BY BIRDS AGED 1-3 YEARS AND RESIGHTED MORE THAN TWICE, A) ARRANGED BY INDIVIDUAL, B) SUMMARISED FOR ALL 8 BIRDS.

A)

Individual	Total No. of visits	Age at pre-breeding visits (years) 1	2	3	Age at recruitment
5096855	3	1	2	0	3
5107839	5	1	0	4	4
5107942	4	1	3	0	-
5125701	4	1	1	2	-
5107688	5	2	0	3	-
5107686	5	1	0	4	-
5096873	7	1	1	5	-
5107940	9	2	7	0	-

B)

	Age at pre-breeding visits (years) 1	2	3
No. of visits:	10	14	18
No. of birds:	8	5	5
No. of visits *per* bird:	1.25	2.80	3.60

$\chi^2_2 = 2.66$ NS

TABLE 5. 19 TIMING OF COLONY VISITS BY PRE-BREEDING BIRDS ACCORDING TO AGE (N = 183 BIRDS).

			Percentage of visits in:		
		No. of visits	Sep-Oct	Nov-Dec	Jan-Feb
Age at each visit	1	53	8	30	62
	2	133	6	55	40
	3	44	20	48	32
	4	9	-	89	11

Test of difference between 1-3 year olds: $\chi^2_4 = 18.89$ $P<0.001$

TABLE 5. 20 TIMING OF COLONY VISITS BY PRE-BREEDING BIRDS IN RELATION TO RECRUITMENT. NOTE: YEAR 0 IS THE RECRUITMENT YEAR AND RECRUITING BIRDS FIRST SEEN AFTER DECEMBER WERE ASSUMED TO HAVE BEEN PRESENT IN DECEMBER.

			Percentage of visits in:		
		No. of visits	Aug-Oct	Nov-Dec	Jan-Feb
Years before recruitment	0	50	18	82	0
	1	44	7	68	25
	2	5	0	20	80

Test of difference between no. of visits in year 0 and year 1 (Aug-Oct *v* Nov-Dec):	$\chi^2_1 = 0.66$ NS
Difference between year 1 and year 2 (Nov-Dec *v* Jan-Feb):	P = 0.03 (Fisher's exact)

were made during the period August-October by birds which subsequently bred in that year, compared with birds in the year before recruitment.

5.7.3 Dispersal of pre-breeding birds away from the colonies.

Opportunities to assess the dispersal of pre-breeding birds away from the colonies were limited, but visits were made to the nearby Coronation Island coastline, and in addition to sightings made around Signy Island, 29 individuals were sighted (Figure 5.1, Table 5.21). It was apparent that birds from both North Point and Shagnasty wandered widely within an 11 km radius of Signy, and individuals seen at Coronation Island did not come only from the adjacent colony of North Point. The extent of dispersal is unknown, and the 11 km radius merely represents the limits of boat access. Observations of shags leaving the colonies on fishing trips suggest that a more extensive area is utilised. Both pre-breeding and breeding birds use similar areas, at least during the breeding season, because two adults with nests (one containing chicks) at North Point and Shagnasty, were seen at Cape Vik and Gerd Island, 9 km and 11 km from Shagnasty respectively.

5.8 Discussion.

Some Blue-eyed shags first bred when 2 years old, one year earlier than previously indicated for the Signy population (Croxall 1982, Shaw 1986), but similar to the minimum age at Macquarie Island (Brothers 1985). Most birds in this study recruited when older than two, but the age range was wide spanning four years. Shaw (1984) found a similar variation in the age of first breeding but suggested that this may have been unrealistically wide owing to birds which evaded capture. In this study the recapture efficiency was high (section 2.4.3.), as confirmed by the low numbers of birds seen for the first time when older than six years, yet the variability in recruitment ages persisted. In addition, there was marked year to year variation in the proportion of

FIGURE 5. 1 DISPERSAL OF PRE-BREEDING BIRDS AROUND SIGNY ISLAND. SEE TABLE 5. 21 FOR KEY.

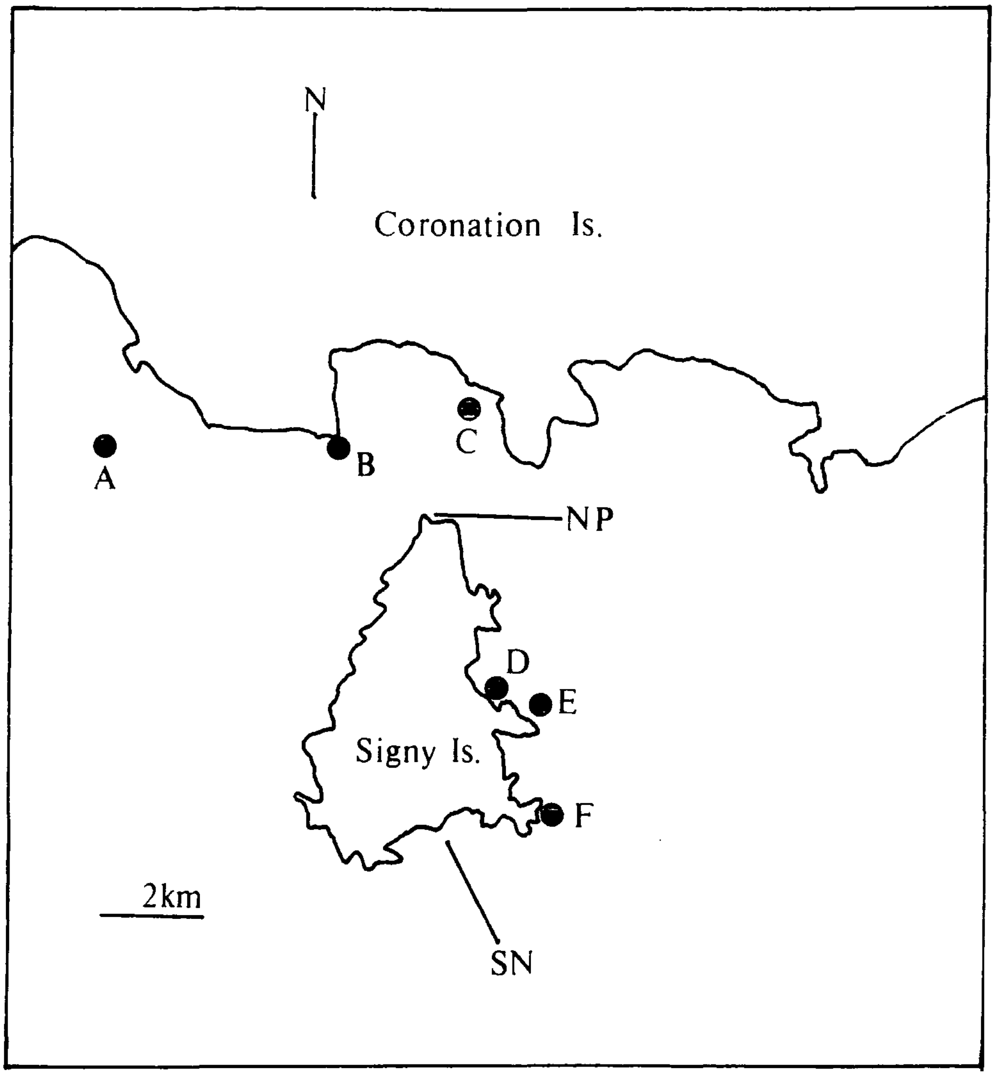


TABLE 5. 21 NUMBER OF PRE-BREEDING BIRDS OBSERVED AWAY FROM COLONIES (N = 29 BIRDS).

Locality (letters refer to Fig 5.1)		Distance from SN (km)	Month of visit	Natal colony		
				NP	SNI/II	SNIII
A	Gerd Is.	11	Jan	1	2	1
B	Cape Vik	9	Jan	2	0	0
			Oct	0	4	1
C	Lynch Is.	9	Jan	2	6	4
D	Factory cove	3	Feb	0	1	1
E	Outer Island	3	Dec	0	1	0
			Feb	0	1	0
			Mar	0	0	1
F	Pantomime Point	2	Dec	0	0	1

birds first breeding at a particular age. This contrasts with the process of recruitment in the European shag which is condensed into 2 years and showed little variation between years (Potts 1966). In the latter species there is also a consistent sex specific recruitment pattern, with 80% and 20% of males recruiting when aged 2 and 3 respectively, and 50% of females recruiting at each age (Potts 1966, Potts *et al.* 1980). This was not shown by Blue-eyed shags in this study, similar proportions of both sexes being seen in all age groups with the exception of 4-6 year olds in 1987, although these birds only accounted for 7% of the recruits. Shaw (1984) found that male Blue-eyed shags returned to the colony at a younger age than females, the modal ages of first breeding being 4 for males and 5 for females. In contrast to this study, he also found a difference in the age of recruitment between North Point and Shagnasty, earlier breeding occurring at North Point. The differences may be accounted for by a lower recapture efficiency of breeders in Shaw's study (0.87), the lower age of recruitment at North Point would then reflect the more thorough coverage at this colony due to its small size and location. Aebischer (1985) suggested that the unexpectedly low proportion (17%) of 2 year old female European shags recruiting at the Isle of May compared with the 50% recruitment found by Potts (1966), arose from a reduced probability of recapture as a result of their greater timidity.

A similar variation in the age of first breeding has been described for Brandt's cormorant, a Pacific endemic which experiences marked fluctuations in food availability arising from the El Niño southern oscillation (Boekelheide & Ainley 1989). In this species recruitment ranges from 2 to 7 years, with the modal age class being 4 for males and 2 for females. There is a link between the age of first breeding and food availability, a higher proportion of younger birds breeding in years when food is abundant, and much lower proportions in El Niño years, when food is scarce. Boekelheide & Ainley (1989) have suggested that flexibility in Phalacrocoracid reproductive strategy is a consequence of breeding in an annually fluctuating environment. The traits which they identified as responsible for reproductive flexibility were a possible young age at first breeding, wide variation in the age of first breeding between years, low mate fidelity and the failure of experienced breeders to attempt to breed in poor years. Comparing Brandt's cormorant with other species, they pointed out that the Flightless cormorant exhibited all these traits, and Blue-eyed shags showed low mate fidelity and first bred when three years old. Both these species were considered likely to experience annual fluctuations in food availability, arising from El Niño events in the case of the Flightless cormorant, and from the presence of pack ice for Blue-eyed shags. In contrast, European shags showed a higher mate fidelity and less variation in the age of first breeding, the latter trait being shared with the Cormorant. Both species inhabit more stable environments (Boekelheide & Ainley 1989).

The age of Blue-eyed shag parents did not influence the number of offspring which survived after reaching independence to recruit into the breeding population. This is consistent with the earlier finding that parental age did not affect clutch size, and was only weakly related to the number of chicks fledged per pair (Shaw 1986). Clearly, parental breeding experience does not influence the survival or eventual recruitment of birds once they have become independent. This contrasts with the Short-tailed shearwater, in which the proportion of young which returned to breed increased as the reproductive experience of both parents increased (Wooller *et al.* 1988). In other seabird species, an increase in reproductive performance has been linked to increased parental breeding experience, for example in Kittiwake, Manx shearwater and Fulmar (Coulson 1966, Brooke 1978, Ollason & Dunnet 1978), although a conventional measure of reproductive success, such as the number of chicks fledged per pair, may not reliably indicate the eventual recruitment of the offspring if variation in the quality of fledgelings relates to subsequent survival, as in the Manx shearwater (Perrins *et al.* 1973).

Prior to recruitment, 74% of the visits made by Blue-eyed shags were to the colony at which they subsequently bred, and 65% of these visits were to the natal colony (Table 5.15). This is comparable with the 75% fidelity to the natal colony of breeding birds (section 3.3.2) but much lower than the 99% fidelity to the breeding colony shown by experienced breeding birds (section 3.3.1). The timing of colony visits was age-related, with older individuals arriving earlier. In the year of recruitment birds were seen appreciably earlier than when visiting the colony as prospectors, and there was an increase in the frequency of visits in the year before recruitment. In the Kittiwake, all birds which recruited during a three year period had also been seen in the year prior to recruitment, and prospecting birds arrived increasingly earlier in the season and left later as they got older (Porter 1988).

As some Blue-eyed shags first bred at two years of age, they are capable of physiological maturity after the first year of life. The failure of most individuals to recruit at this age is unlikely to reflect the ease of nest site acquisition since the numbers of experienced breeding Blue-eyed shags was not inversely correlated with the extent of recruitment, suggesting that nest site availability was not limiting recruitment. Further evidence for the availability of nests sites comes from observations of 2 year old pre-breeding pairs standing on deserted nests and at nest sites in other parts of the colonies. This indicated that potential recruits could not only acquire sites but could defend them also. At least some of these pairs were present at the same time that other pairs commenced breeding; nest site acquisition did not always occur so late in the season as to preclude a breeding attempt. Some development of breeding skills may be a prerequisite to successful recruitment, and the relationship between experience and breeding success is examined in the next chapter. Alternatively, environmental constraints, particularly food availability, may be determining the numbers of recruits. There was a positive correlation between the numbers of experienced breeders and recruits, which suggests that similar factors may be influencing the numbers of both experienced birds and recruits breeding at the colonies.

In the Kittiwake, Porter (1990) found three patterns of recruitment to the breeding colony which were related to the ability of individual birds to compete for nest sites in the denser areas of the colonies. Some recruits arrived early in the season and paired with experienced birds whose previous mates had either died or divorced. Others arrived later during the season and paired with recruits and either nested immediately in poorer locations, or delayed breeding until the aggressive behaviour of established pairs had subsided and nested in the denser areas.

6. PAIR STABILITY, AGE DIFFERENCES WITHIN PAIRS AND BREEDING PERFORMANCE.

6.1 Introduction.

Many seabirds show high mate fidelity once established as breeders, and in some species the retention of familiar mates over the reproductive career of the pair has been associated with an increased breeding success and implied benefits to lifetime reproductive success and fitness. For example, in the Kittiwake, Coulson (1966) has shown that in females the mean date of laying is advanced if they paired with the same mate in a previous year, and that it is mate retention rather than breeding experience (excluding birds breeding for the first time) which influences the laying date. In addition, birds which retained their mate laid larger clutches and, independent of clutch size, experienced a high breeding success. Mate change between seasons resulted in birds only achieving three-quarters of their reproductive potential. In the Short-tailed shearwater, Wooller *et al.* (1989) found that the mean annual number of fledged young produced by a pair was initially lower following mate change, but then returned to previous levels after a further two years of breeding experience with the new mate. Also, in pairs which remained together longer the initial breeding performance was higher, suggesting that individuals which formed the most stable pairs were of higher quality (Bradley *et al.* 1990). Increased breeding success with mate retention is a feature of the biology of several other species including Fulmar (Ollason & Dunnet 1978), and Manx shearwater (Brooke 1978) and Snow goose (Cooke *et al.* 1981), and whilst the breeding success of female Red-billed gulls was unaffected by mate change they bred earlier and laid smaller clutches resulting in a drop of 13% in their reproductive potential (Mills 1973). In some of these studies it was difficult to separate the effects of mate and site fidelity but high attachment to both resulted in a higher breeding performance. In contrast, there was no evidence that mate change in Puffins affected the number of chicks fledged in the subsequent season (Ashcroft 1979).

In view of the importance of mate retention and the low mortality rates of seabirds, the breakup of pairs has attracted considerable interest, particularly where this occurs as a result of divorce. It has been suggested that divorce has adaptive value as an alternative to persistent failure in incompatible pairs, allowing them to improve their chances of successful breeding (Coulson 1966), and the divorce of pairs following breeding failure has been recorded in Kittiwake (Coulson 1966), Red-billed gull (Mills 1973), Fulmar (Macdonald 1977), Manx shearwater (Brooke 1978), Adelie penguin (Davis 1988) and Short-tailed shearwater (Bradley *et al.* 1990) in addition to several other species.

In comparison with other seabirds, the Phalacrocoracidae show high divorce rates, and pair stability appears to have little influence on, or be affected by breeding performance. Studies on the European shag have shown that the divorce rate is between 44% (Potts 1966) and 31% (Aebischer 1985), and there was no relationship between divorce and breeding success in the previous breeding season, although there was a suggestion that mate change influenced the reproductive success in the subsequent season (Aebischer 1985). In Brandt's cormorant, most pairs did not persist for more than one season, although nest site fidelity was high among males (Boekelheide & Ainley 1989), and a similarly high divorce rate between seasons was found in the Flightless cormorant (Harris 1979). The divorce rate of Blue-eyed shags has previously been estimated to be 34%, and breeding failure in the previous year did not promote divorce subsequently. The remating of pairs had no effect on subsequent breeding success (Shaw 1986).

6.2 Pair stability.

Of 351 pairs of breeding birds captured in one year with at least one partner alive in the following year, between 1984-88, 138 (39%) retained the same mate from the previous season (Table 6.1). From the remaining 213 which changed mates, 98 (46%) divorced their original partner (both members of the pair were alive and paired with other birds in the following year), and the partners of the other 115 were not seen

TABLE 6.1 **MATE FIDELITY IN RELATION TO YEAR BETWEEN 1984-88. NOTE: DIVORCE RATE IS THE PROPORTION OF DIVORCEES AMONG ALL PAIRS KNOWN TO HAVE SURVIVED, MORTALITY RATE ASSUMES ALL MATES WHICH DISAPPEAR ARE DEAD, * EXCLUDING 15 PAIRS OF UNKNOWN OUTCOME.**

		No. of pairs alive in next year with:				
Year	No. of pairs	Same mate	Changed mate due to:		Divorce rate (%)	Mortality rate (%)
			Disappearance	Divorce		
1984-85	44*	21	10	13	38	11.4
1985-86	69	32	18	19	37	13.0
1986-87	117	42	37	38	48	15.8
1987-88	121	43	50	28	39	20.7
TOTAL	351	138	115	98	42	16.4

Divorce rate *v* year: $\chi^2_3 = 1.84$ NS subsequently. The permanent disappearance of birds was equated with their death, and expressing the number of birds which disappeared as a percentage of the total number of birds at risk gives an overall mortality rate of 16.4% (range 11-21%) which is similar to 13.6% (χ^2 = 2.53 df=1 NS) calculated from the proportion of all ringed birds which disappeared between years, given in Table 4.7. Since the number of partners which disappeared has not been adjusted for recapture efficiency, this mortality estimate is a maximum, although as recapture efficiency was generally high (section 2.4.3) this makes little difference. For example applying the proportion of recaptured birds from the total estimated to be alive during the principal years of the study, shown in Table 4.6, the adjusted mortality rates for 1984-5, 1985-6 and 1986-7 are 14.8%, 13.7% and 16.7% compared with those in Table 6.1 for the respective years. There was no significant difference between the sexes in the number of birds which disappeared (χ^2 = 0.63 df=3 NS). The overall annual divorce rate was 42% and did not differ significantly between years (χ^2 = 1.84 df=3 NS), and therefore in subsequent analyses data from all the different years (*i.e.* 1984-88) were combined. Table 6.2 indicates that the annual divorce rate of birds which did not change colonies, was similar at all three colonies (χ^2 = 1.66 df=2 NS). Only one individual in the sample (n=232 pairs) changed colony between years and was excluded.

The annual divorce rate decreased significantly with age in both sexes (Table 6.3). Males aged 2-5 years had a rate of 53% which declined to 32% after they reached 9 years, and similarly in females, the rate dropped from 65% among 2-5 year olds to 34% in birds aged 10-17 years old. Within each age group there was no significant difference between the sexes in annual divorce rate, and overall birds aged 2-5 years experienced a divorce rate of 59% each year, whilst in the age classes 6-9 and 10-17 years the annual divorce rates were 36% and 33% respectively. The effect of breeding experience on the likelihood of divorce in the following year was investigated by dividing the sample according to whether birds were recruiting, had one year's breeding experience (*i.e.* birds which had recruited in the previous year), or had more than one year's breeding experience (*i.e.* birds which had recruited more than one year previously) during the

TABLE 6. 2 **THE ANNUAL DIVORCE RATE WITH RESPECT TO BREEDING COLONY. NOTE: SHAGNASTY III NOT VISITED IN 1985.**

Colony	No. of pairs	Retain mate	Divorce mate	% Divorce
North Point	43	29	14	33
Shagnasty I/II	159	90	69	43
Shagnasty III	30	18	12	40

Difference between colonies: $\chi^2_2 = 1.66$ NS

TABLE 6. 3

THE INFLUENCE OF AGE IN THE CURRENT YEAR AND SEX ON THE DIVORCE RATE IN THE FOLLOWING YEAR.

	Age (years)								
	Males			Females			TOTAL		
	2-5	6-9	10-17	2-5	6-9	10-17	2-5	6-9	10-17
Total no. of pairs	77	82	41	85	64	35	162	146	76
No. which divorced	41	31	13	55	21	12	96	52	25
Divorce rate (%)	53	38	32	65	33	34	59	36	33

Difference between age groups (totals): $\chi^2_2 = 23.0$ $P<0.001$

Difference between sexes (all NS):

2-5 years $\chi^2_1 = 1.75$
6-9 years $\chi^2_1 = 0.20$
10-17 years $\chi^2_1 <0.001$

current year. For each category the proportion of pairs which had divorced by the following year was determined. The results were combined for all years between 1984 and 1988, although because no adult shags were recaptured in 1983, it was impossible to decide how many recruits and birds with one year's breeding experience were present in 1984, and therefore in the latter year, 2 pairs in which at least one partner was younger than 6 years were excluded from the analysis, and the remaining 32 pairs were assumed to have more than one year's breeding experience. Table 6.4 indicates that there was no significant difference between the sexes with respect to the divorce rate in each category of breeding experience, and that overall significantly fewer birds (35%) with more than one year's breeding experience divorced. In comparison, birds which had recruited in the current year or during the previous year, were much more likely to divorce, 55% doing so. There was no significant difference in the annual divorce rate between pairs in which both birds were recruiting and those where only one partner was a recruit (χ^2 = 0.93 df=1 NS).

Since recruitment was spread over about four years (chapter 5), some birds of similar age are likely to differ in breeding experience, and this was used to establish whether age or breeding experience was more important in pair stability. Table 6.5 shows that within a category of breeding experience, birds of different ages did not differ significantly in their divorce rates, although the analysis was not extended to birds with more than one year's breeding experience because for most of these individuals the exact amount of breeding experience was unknown. When birds of similar age but with different levels of breeding experience were considered (Table 6.6), it was apparent for birds of 5 and 6 years that recruits had a significantly higher rate of divorce than birds with one or more years breeding experience. For birds aged 2-4 years, there was no significant difference in the divorce rate in relation to breeding experience, but most birds were recruits and the sample size of more experienced breeders was low. Overall the results suggest that a birds breeding experience during the current season was more important in influencing the likelihood of divorce in the following year than it's age. The difference in divorce rate with age in Table 6.3 presumably reflects the concurrence

TABLE 6. 4 THE INFLUENCE OF BREEDING EXPERIENCE IN THE CURRENT YEAR ON THE DIVORCE RATE IN THE FOLLOWING YEAR.

	Breeding experience								
	Males			Females			TOTAL		
	Recruit	1 year	> 1 year	Recruit	1 year	> 1 year	Recruit	1 year	> 1 year
Total no. of pairs	59	14	164	63	17	156	122	31	320
No. which divorced	30	7	60	36	10	52	66	17	112
Divorce rate (%)	51	50	37	57	59	33	54	55	35

Divorce *v* experience (totals): $\chi^2_2 = 15.83$ $P<0.001$

Difference between sexes (all NS):

Recruits $\chi^2_1 = 0.27$
1 year $\chi^2_1 = 0.02$
> 1 year $\chi^2_1 = 0.24$

TABLE 6. 5 **THE INFLUENCE OF AGE IN THE CURRENT YEAR ON THE DIVORCE RATE OF BIRDS WITH SIMILAR BREEDING EXPERIENCE DURING THE FOLLOWING YEAR.**

		Breeding experience					
		Recruits				1 Year	
Age	Retain mate	Divorce mate	Divorce rate (%)	Age	Retain mate	Divorce mate	Divorce rate (%)
2-3	16	19	54				
				4-5	9	8	47
4	13	19	59				
				6	8	6	43
5	16	31	66				
Divorce rate *v* age:		$\chi^2_2 = 1.17$ NS				$\chi^2_1 = 0.02$ NS	

TABLE 6.6 **THE INFLUENCE OF BREEDING EXPERIENCE IN THE CURRENT YEAR ON THE DIVORCE RATE OF BIRDS OF SIMILAR AGE DURING THE FOLLOWING YEAR.**

Age

2-4 Years

Breeding experience	Retain mate	Divorce mate	Divorce rate (%)
Recruit	28	40	59
Experienced	1	7	88

5-6 Years

Breeding experience	Retain mate	Divorce mate	Divorce rate (%)
Recruit	12	31	72
1 year	19	13	41
2-4 years	47	31	40

Divorce rate *v* experience:

2-4 Years: P=0.14 NS (Fisher's exact)

5-6 Years: $\chi^2_2 = 12.75 \quad P<0.01$

of age and breeding experience in many birds which recruit at similar ages.

The effect of the previous year's breeding performance on pair stability during the current year was investigated by looking at both overall breeding success and three components of reproduction; clutch size, brood size and the number of chicks fledged. The effect of successfully rearing a chick to the age of ringing (approximately 50-60 days old) in the previous year on the likelihood of divorce is shown in Table 6.7. Recruits and experienced birds were considered separately, since the former may be more likely to fail and to divorce due to inexperience, rather than because successfully rearing a chick directly influenced divorce rates. However, owing to the low number of failed breeding attempts recorded, it was necessary to compare the divorce rates across categories of breeding experience using only successful pairs. If successful chick rearing was related to divorce rate then comparing successful recruits and experienced pairs should yield similar divorce rates. Table 6.7 shows that this was not the case and that recruits which bred successfully during one year experienced a higher divorce rate in the following year (76%) than successful experienced birds (31%), suggesting that in successful breeders at least, it was breeding experience rather than success which influenced the divorce rate. This analysis cannot eliminate success as a potential influence on divorce because there were not enough failed pairs to investigate if their divorce rates were similar regardless of breeding experience. Excluding pairs in which one partner was breeding for the first time, the proportion of pairs which divorced was not significantly related to clutch size, initial brood size or the number of chicks fledged by the pair in the previous year (Table 6.8). However, pairs which remained intact did have significantly higher mean clutch sizes, initial brood sizes and on average fledged more chicks in the previous year than pairs which divorced. Analysis of the effect of pair stability in the previous year upon breeding performance in the current year indicated that there was no association with overall breeding success (Table 6.9), nor did it influence mean clutch size, brood size or the mean number of chicks fledged in the following year (Table 6.10). Table 6.11 shows that pair stability in the preceeding year has a significant effect upon pair stability during the current year, 28% of pairs which remained together in the previous

TABLE 6. 7 THE EFFECT OF BREEDING SUCCESS IN THE CURRENT YEAR ON DIVORCE RATE IN THE FOLLOWING YEAR.

	Breeding success			
	Recruits		Experienced	
Pair stability	Success	Fail	Success	Fail
Retain mate	4	0	31	1
Divorce mate	13	3	14	1
Divorce rate (%)	76	-	31	-

Comparison of divorce rate among successful birds; recruits *v* experienced: $\chi^2_1 = 8.56$ $P<0.01$

TABLE 6. 8

THE EFFECTS OF CLUTCH SIZE, INITIAL BROOD SIZE AND THE NUMBER OF CHICKS FLEDGED IN THE PREVIOUS YEAR UPON DIVORCE RATE IN THE CURRENT YEAR. NOTE: DATA ON BREEDING SUCCESS ARE FROM 1986 AND 1987 COMBINED.

Factor	Pair stability in current year	Clutch size, brood size or no. of chicks fledged in previous year			Mean	Test of means
		1	2	3		
Clutch size	Retain mate	0	14	55	2.80	$F_{29,68} = 2.73$
	Divorce mate	3	5	22	2.63	$P<0.01$
	Divorce rate (%)	-	26	29		
Brood size	Retain mate	9	23	20	2.21	$t_{39} = 2.25$
	Divorce mate	7	11	3	1.81	$P<0.05$
	Divorce rate (%)	44	32	13		
Chicks fledged	Retain mate	16	37	6	1.83	$t_{103} = 4.25$
	Divorce mate	11	13	3	1.70	$P<0.001$
	Divorce rate (%)	41	26	33		

Divorce rate	clutch size, 2 *v* 3:	$\chi^2_1 = 0.19$ NS
	brood size:	$\chi^2_2 = 4.74$ NS
	chicks fledged:	$\chi^2_2 = 1.79$ NS

TABLE 6. 9 THE EFFECT OF PAIR STABILITY ON BREEDING SUCCESS IN THE NEXT YEAR. NOTE: PAIRS IN WHICH ONE OR BOTH PARTNERS ARE RECRUITS ARE EXCLUDED.

	Success in rearing a chick	
Pair stability	Success	Fail
Retain mate	39	3
Divorce mate	33	3
Divorce rate (%)	46	-
Comparison of divorce rates: (Fisher's exact)	P = 1.0	

TABLE 6. 10 THE EFFECT OF PAIR STABILITY IN THE PREVIOUS YEAR ON CLUTCH SIZE, INITIAL BROOD SIZE AND THE NUMBER OF CHICKS FLEDGED IN THE CURRENT YEAR. NOTE: DATA ON BREEDING SUCCESS ARE FROM 1986 AND 1987 COMBINED, PAIRS WITH EITHER PARTNER A RECRUIT ARE EXCLUDED.

		Clutch size, brood size or no. of chicks fledged in current year				
Factor	Pair stability in previous year	1	2	3	Mean	Test of means
Clutch size	Retain mate	3	8	40	2.73	-
	Divorce mate	2	6	29	2.73	-
	Divorce rate (%)	40	43	42		
Brood size	Retain mate	6	18	10	2.12	$t_{58} = 0.18$
	Divorce mate	3	17	7	2.15	NS
	Divorce rate (%)	33	49	41		
Chicks fledged	Retain mate	14	21	7	1.83	$t_{69} = 0.95$
	Divorce mate	4	23	3	1.97	NS
	Divorce rate (%)	22	52	30		

Divorce rate

clutch size(1 and 2 grouped): $\chi^2_1 = 0.07$ NS

brood size: $\chi^2_2 = 0.77$ NS

chicks fledged: $\chi^2_2 = 5.40$ NS

TABLE 6. 11 **THE EFFECT OF PAIR STABILITY IN THE PREVIOUS YEAR ON PAIR STABILITY DURING THE FOLLOWING YEAR. DATA ARE FROM 1984-1988.**

	Current year		
Previous year	Same mate	Divorce mate	Divorce rate (%)
Same mate	38	15	28
Divorce mate	6	10	63

$\chi^2_1 = 4.83$ $P<0.05$

year divorcing in the current year, compared with 63% of pairs which had divorced in the previous year.

In 22 males and 12 females (7 of which were members of the same pair) which were identified in each year between 1984 and 1988, the number of partners is shown in Table 6.12 along with the expected number assuming that mate change resulted solely from death of the partner (*i.e.* applying the average annual mortality rate of 0.136 from Table 4.7). Both sexes had significantly more partners than expected from mortality alone, on average males had 2.2 mates and females 1.9 mates and the modal number of mates was 2 in both sexes.

6.3 Nest site fidelity.

Only approximate estimates of nest site retention in successive years were possible since for most pairs the precise location of nests from the previous year was not possible. Fidelity to the nest site area was investigated by dividing Shagnasty I/II into seven sections of approximately 12 m each. The identity of pairs breeding in these sections in 1986 and 1987 was noted and the extent of movement between years was assessed. Of 132 males and 119 females, 98% and 92% renested in the same section in both years (Table 6.13). Eleven individuals moved to a different section in 1987, and a significantly higher proportion of females moved compared with males (χ^2 = 4.12 df=1 P<0.05).

A further indication of re-use of the same nest was obtained using nests tagged in 1986 where both the nest and the tag remained intact in the next year, allowing recognition of the nest. Twenty-one such nests were found in 1987, and fourteen of the 1986 occupants were known to be alive. Of these fourteen, no females and only one male bred at the same nest. Whilst the incidence of re-use of the same nest by pairs appears to be low, birds do not frequently move beyond 12 m. One possible bias in the interpretation of the results obtained using nest tags, is the shag's habit of stealing nest material from other nests, which may lead to a lack of correlation between the true identity of the nest and the information derived from the tag. In the above analysis,

TABLE 6. 12 **THE NUMBER OF PARTNERS OF MALES AND FEMALES WHICH WERE SEEN IN FOUR CONSECUTIVE YEARS BETWEEN 1984-1988.**

	No. of mates					
	1	2	3	4	Total	Mean
MALES						
Observed	3	13	5	1	22	2.2
Expected	19	3	0	0		
FEMALES						
Observed	3	7	2	0	12	1.9
Expected	10	2	0	0		

Goodness-of-fit

Males $\chi^2_3 = 46.8$ $P<0.001$

Females $\chi^2_3 = 17.4$ $P<0.001$

TABLE 6. 13 FIDELITY TO 12 M SECTIONS OF SHAGNASTY I/II BETWEEN 1986 AND 1987 WITH RESPECT TO SEX.

Sex	No. of birds re-nesting in 1987 which were in:		
	Same section	Changed section	Same section (%)
Males	130	2	98
Females	110	9	92

Comparison between sexes: $\chi^2_1 = 4.12$ $P<0.05$

this was avoided by only including records where the tag was found securely embedded in the nest foundation. Previously, a study of nest site fidelity at Shagnasty I/II compared smaller sections, of 4 m, and found that 64% of males and 54% of females renested in the same section (Shaw 1984).

6.4 Age differences within pairs.

The ages of 230 pairs which bred between 1985-87 are shown in Table 6.14, and each pair was included only at the first sighting. There was a high degree of correlation in the ages within pairs ($\log_{10}$ transformation of both axes; $r=0.577$ $df=228$ $P<0.001$), with 46% of partners being of equal age and 70% being one year or less of each other. Whilst in many pairs there was no difference in age, the overall distribution of age differences within pairs was slightly skewed so that the female was younger than the male in more pairs, although this is not statistically significant (Goodness-of-fit test: $\chi^2 = 2.59$ df=1 NS). On average females were 0.2 years younger than their partners. Shaw (1984), also found a skewed age difference distribution but it was skewed so that more females were older than their mates, by 0.6 years on average.

To determine the distribution of age differences within pairs which would be expected if mating was random with respect to age, the method described by Shaw (1985b) was used, in which the proportions of females of each age in the breeding population was multiplied by the proportions of males of each age in the 230 known age pairs and the products were added to the relevant age difference category. For example, from 143 known age females which bred in 1985, $15/143 = 0.105$ were aged 9 years. From the 230 pairs, 41 pairs were seen in 1985 and $1/41 = 0.024$ males were aged 7 years, therefore the probability of a 7 year old male mating with a 9 year old female is $0.024 \times 0.105=0.003$. This is one contribution to the expected age difference category '+2 years' (*i.e.* male age subtracted from female age). Summation of the expected probabilities of '+2 years' across the age range gives the total expected probability of pairings where females are two years older than males. This is repeated for age

TABLE 6. 14 **THE AGES OF MALES AND FEMALES IN 230 PAIRS WHICH BRED IN 1985-87. BOLD FIGURES INDICATE EQUAL AGED PAIRS.**

	Age of female (years)															
Age of male (years)	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
2	**4**	6	0	0	0	0	0	0	0	1	0	0	0	0	0	0
3	6	**46**	2	0	2	2	0	0	0	0	0	0	1	0	0	0
4	2	2	**15**	7	0	0	0	0	1	0	0	0	0	0	0	0
5	0	5	4	**24**	7	0	0	3	0	0	1	0	0	1	0	1
6	0	9	2	9	**14**	3	1	2	0	2	0	1	1	0	0	0
7	0	0	0	0	1	**1**	0	0	0	2	0	0	0	0	0	0
8	0	0	1	2	1	1	**0**	0	1	0	1	0	0	0	0	0
9	0	1	0	1	1	2	0	**0**	1	0	0	0	0	0	0	0
10	1	1	0	1	0	1	2	3	**0**	0	0	0	0	0	2	0
11	0	0	0	1	1	1	1	0	1	**1**	1	0	0	0	0	0
12	0	1	0	0	0	0	0	0	1	1	**0**	0	0	0	0	0
13	0	0	0	0	0	0	0	0	1	0	0	**0**	0	0	0	0
14	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0	0
15	0	0	0	0	0	0	0	0	0	0	0	0	0	**0**	0	0
16	0	0	0	0	1	0	0	0	0	0	0	0	0	0	**0**	0
17	0	1	0	0	2	0	0	0	0	0	0	0	0	0	0	**0**

Correlation of ages within pairs (Log_{10} transformation of both axes): $r_{228} = 0.577$ $P<0.001$

45.7% same age.

differences between −14 and +12 years to obtain an expected age difference distribution in 1985, and the procedure is repeated for 1986 and 1987 to obtain a total age difference distribution between 1985-87. The observed and expected distributions of age differences (male age subtracted from female age) are shown in Figure 6.1 and Table 6.15, and they differ significantly (Table 6.15; χ^2 = 107.1 df=16 P<0.001). For equal aged partners, nearly twice as many more were observed (105) than would be expected (61) if mating was random with respect to age. In addition, fewer pairs with older females were observed than expected if pairing was random with respect to age.

Table 6.16 shows that there were significant differences in the proportion of birds with younger, equal aged and older partners according to age, and that these differences were present in both sexes (male age; χ^2 = 80.45 df=10 P<0.001; female age; χ^2 = 78.41 df=10 P<0.001). The proportion of equal aged pairs fell from 78% in 3 year old males to 32% in 6 year old males, and from 64% in 3 year old females to 47% in 6 year old females. Only 36% of 2 year old males and 31% of 2 year old females formed equal aged pairs, probably because the number of individuals which started breeding at 2 years old was small, reducing the probability of equal aged pairs occurring. The proportion of pairs where the age difference between partners was one year, varied markedly between age categories, being highest in males aged 2 and 4 years, and in females aged 2 and 5 years. There were no significant differences in the proportions of younger, equal aged or older partners for birds within each age class with respect to sex (Table 6.16). The age differences within pairs where both partners had bred previously are shown in Figure 6.2 and Table 6.17. There was no significant difference in the observed age difference distribution of these experienced pairs from that expected if pairing were random with respect to age. However, in pairs where at least one partner was breeding for the first time, the age distribution differed significantly from random (χ^2 = 79.7 df=8 P<0.001) with nearly twice as many equal aged pairs than expected and fewer pairs where the female was the older partner (Figure 6.3, Table 6.18).

Given the high rate of mate change (61%) reported above, these data are consistent

FIGURE 6. 1 AGE DIFFERENCES WITHIN PAIRS. SOLID BARS = OBSERVED, HATCHED = EXPECTED.

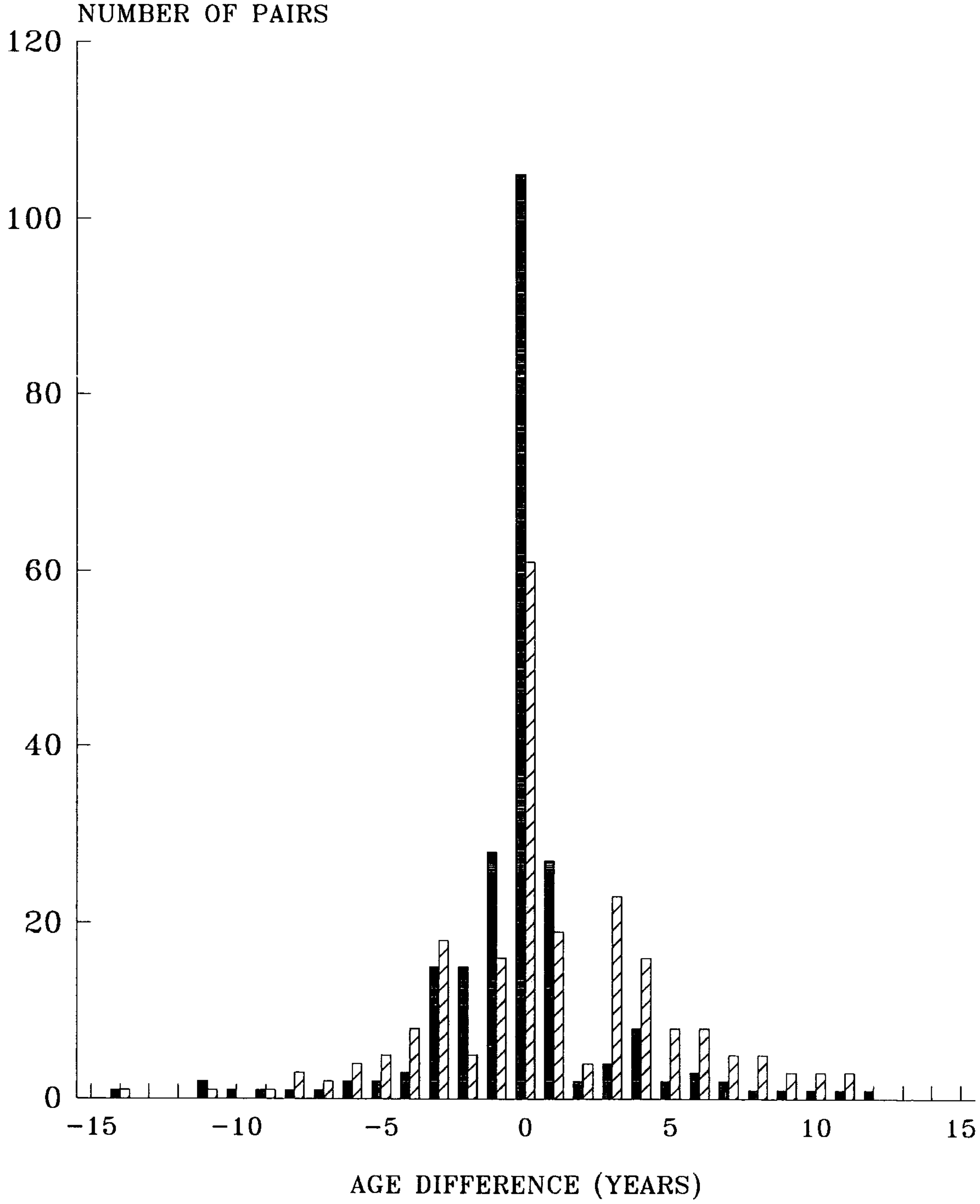


TABLE 6. 15 **COMPARISON OF OBSERVED AGE DIFFERENCES WITHIN PAIRS WITH EXPECTED DISTRIBUTION, ASSUMING RANDOM MATING WITH RESPECT TO AGE. NOTE: N = 230 PAIRS, MALE AGE SUBTRACTED FROM FEMALE AGE.**

	Age difference (years)																										
	-14	-13	-12	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	+11	+12
Observed	1	0	0	2	1	1	1	1	2	2	3	15	15	28	105	27	2	4	8	2	3	2	1	1	1	1	1
Expected	1	0	0	1	0	1	3	2	4	5	8	18	5	16	61	19	4	23	16	8	8	5	5	3	3	3	0

Goodness-of-fit test $\chi^2_{16} = 107$ $P<0.001$

TABLE 6. 16 THE AGES OF PARTNERS IN 230 PAIRS WHICH BRED BETWEEN 1985-87. NOTE: NO BIRDS YOUNGER THAN 2 YEARS RECORDED BREEDING.

		No. of males which were:					No. of females which were:				Difference between sexes		
Age of partner	No.of pairs	Younger	Same	Older	Equal aged (%)	No.of pairs	Younger	Same	Older	Equal aged (%)	χ^2	df	P
2	11	-	4	7	36	13	-	4	9	31	0.02	1	NS
3	59	6	46	7	78	72	6	46	20	64	5.02	2	NS
4	27	4	15	8	56	24	2	15	7	63	0.07	1	NS
5	46	9	24	13	52	45	7	24	14	53	0.28	2	NS
6	44	20	14	10	32	30	9	14	7	47	2.13	2	NS
7-10	28	20	1	7	4	29	14	1	14	3	2.28	1	NS
11-17	15	13	1	1	7	17	15	1	1	6	P = 1.0		NS*

Difference between age groups (excluding 2 years): $\chi^2_{10} = 80.45$ $P<0.001$ $\chi^2_{10} = 78.41$ $P<0.001$

* Fisher's exact test.

FIGURE 6. 2 AGE DIFFERENCES WITHIN PAIRS OF EXPERIENCED BREEDING BIRDS. SOLID BARS = OBSERVED, HATCHED = EXPECTED.

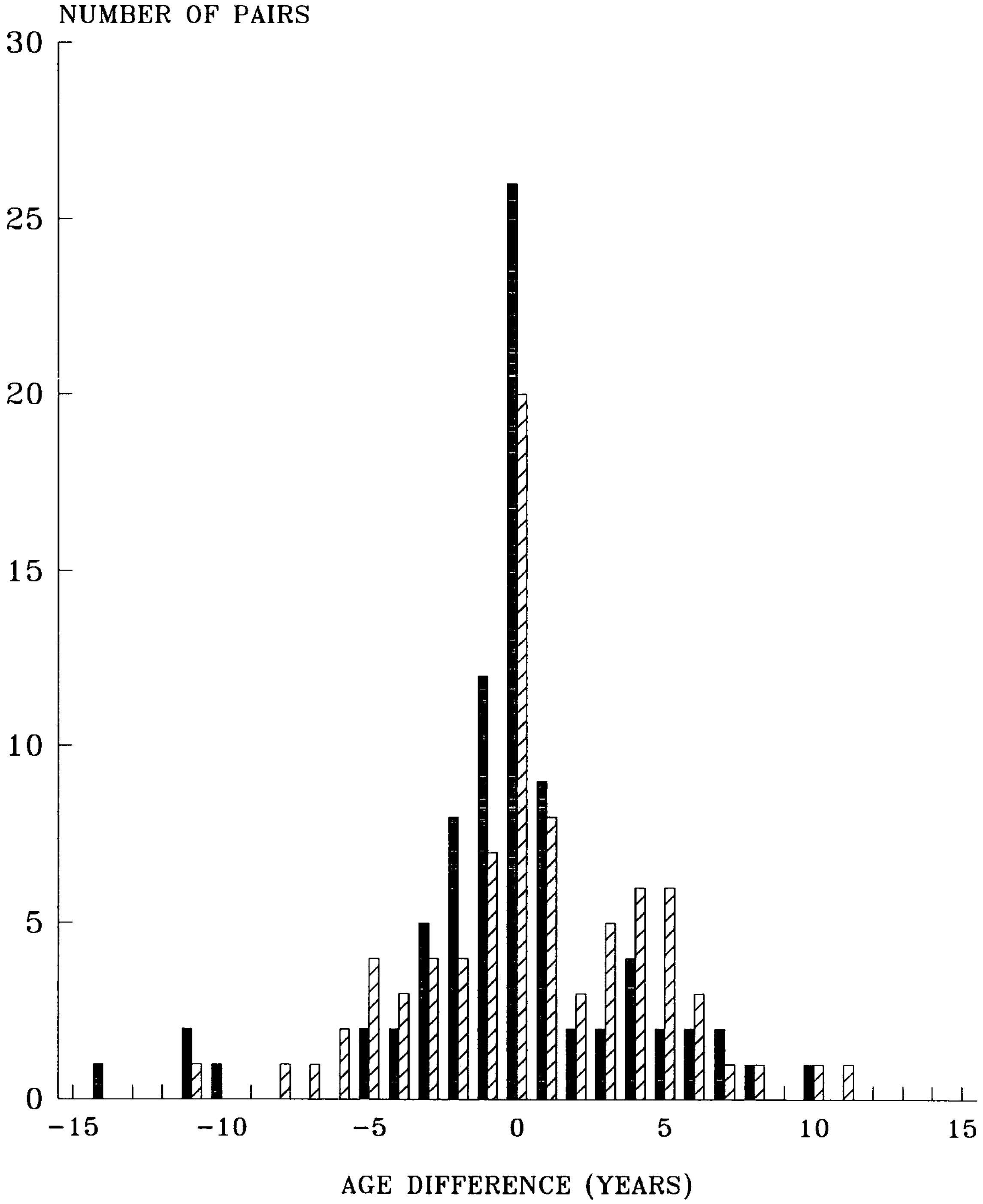


TABLE 6. 17 AGE DIFFERENCES WITHIN PAIRS OF EXPERIENCED BREEDERS, N = 84 PAIRS.

	Age difference (years)																										
	-14	-13	-12	-11	-10	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	+11	+12
Observed	1	0	0	2	1	0	0	0	0	2	2	5	8	12	26	9	2	2	4	2	2	2	1	0	1	0	0
Expected	0	0	0	1	0	0	1	1	2	4	3	4	4	7	20	8	3	5	6	6	3	1	1	0	1	1	0

Goodness-of-fit test $\chi^2_{10} = 15.72$ NS

FIGURE 6. 3 AGE DIFFERENCES WITHIN PAIRS WHERE AT LEAST ONE PARTNER WAS RECRUITING. SOLID BARS = OBSERVED, HATCHED = EXPECTED.

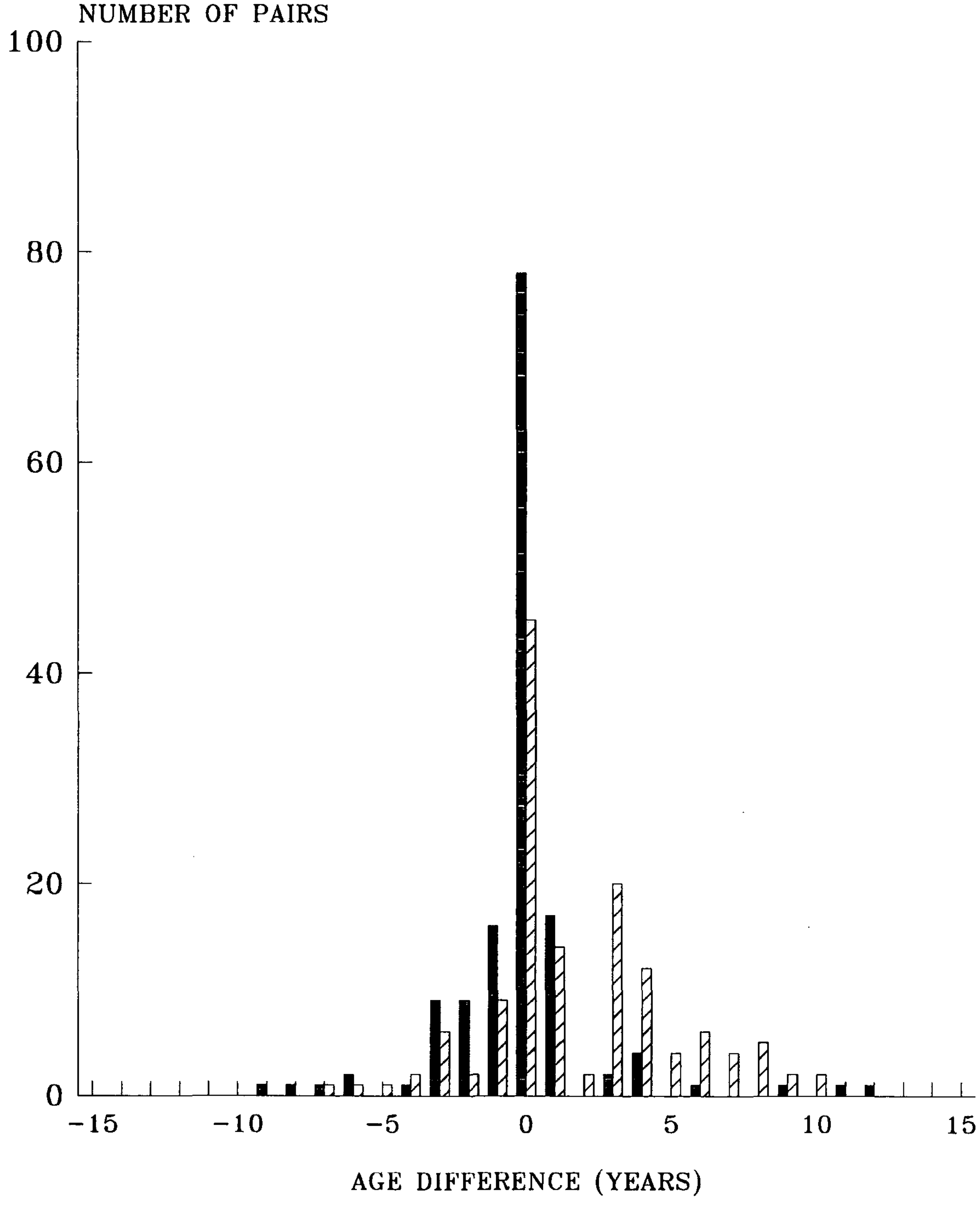


TABLE 6. 18

AGE DIFFERENCES WITHIN PAIRS WHERE AT LEAST ONE PARTNER WAS RECRUITING. N = 145 PAIRS.

	Age difference (years)																					
	-9	-8	-7	-6	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10	+11	+12
Observed	1	1	1	2	0	1	9	9	16	78	17	0	2	4	0	1	0	0	1	0	1	1
Expected	0	0	1	1	1	2	6	2	9	45	14	2	20	12	4	6	4	5	2	2	0	0

Goodness-of-fit test $\chi^2_8 = 79.7$ $P<0.001$

with the explanation that most recruits pair together, but that subsequent pairings are random with respect to age, leading to a breakdown of equal aged pairings. Since a high proportion of recruits during 1985-87 were 3 year olds (see chapter 5), this would account for the high incidence of equal aged pairs among this age class, and the low proportion of pairs with an age difference of one year (Table 6.19). Proportionately fewer birds recruited at 4 and 5 years than at 3, corresponding with the lower proportions of equal aged pairs in these age classes. However, the higher proportion of males and females with an age difference of one year in the 4 and 5 year age category respectively (Table 6.19), suggested an increased discrepancy in the ages of reformed pairs. In older birds the proportion of equal aged pairs is low since no birds are recruiting, although some still form by chance. The proportion of pairs with an age difference of one year is lower in the oldest males and females because most potential mates are younger.

The mechanism causing recruits to pair together is not clear but it may be associated with the timing of pair formation, clumping of birds of similar ages in the colony or both these factors. If recruits are normally denied access to mates older than themselves, then pairs comprising a recruit and an older bird would be expected to arise when the original mate had disappeared (assumed dead) allowing immediate remating between the experienced partner and a (unpaired) recruit. Between 1985-87, 17 pairs formed between a recruit and a bird aged 7 years or older. Since 145 pairs were recorded where at least one partner was a recruit, this suggests that $17/145 = 0.117$ recruits were replacing older partners which had died (some of these partners will have been replaced by older birds also), which compares favourably with the estimated mortality rate of 0.136 during the period (Table 4.7). If correct, this also suggests that there is a temporal component in pair formation related to breeding experience.

Table 6.20 and Figure 6.4 show the age difference distribution of pairs which changed mates, in the year following mate change. There is no significant difference between the observed distribution and that expected if pairing was random according

TABLE 6. 19 **THE PROPORTION OF PAIRS WITH AN AGE DIFFERENCE OF ONE YEAR BETWEEN PARTNERS WITH RESPECT TO SEX. N = 230 PAIRS.**

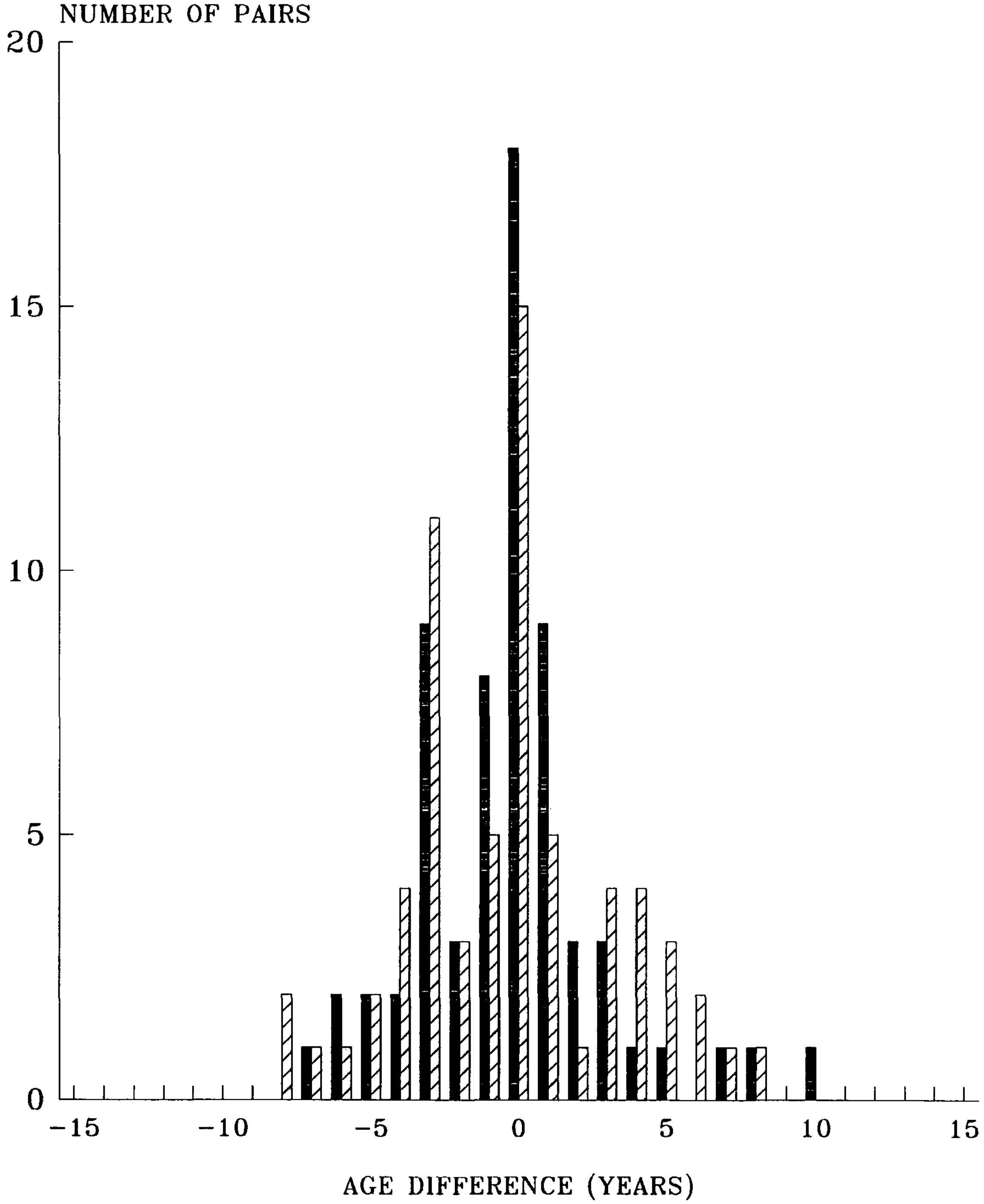
	MALES		FEMALES	
Age	No. of Pairs	Age difference of 1 year (%)	No. of Pairs	Age difference of 1 year (%)
2	11	55	13	46
3	59	14	72	11
4	27	33	24	25
5	46	24	45	36
6	44	27	30	27
7-10	28	21	29	31
11-17	15	20	17	12

TABLE 6. 20 AGE DIFFERENCES WITHIN PAIRS WHICH CHANGED MATES IN THE PREVIOUS YEAR. N = 65 PAIRS.

	Age difference (years)																		
	-8	-7	-6	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	+7	+8	+9	+10
Observed	0	1	2	2	2	9	3	8	18	9	3	3	1	1	0	1	1	0	1
Expected	2	1	1	2	4	11	3	5	15	5	1	4	4	3	2	1	1	0	0

Goodness-of-fit test $\chi^2_7 = 10.18$ NS

FIGURE 6. 4 AGE DIFFERENCES WITHIN PAIRS WHICH CHANGED MATES IN THE PREVIOUS YEAR. SOLID BARS = OBSERVED, HATCHED = EXPECTED.



to age (χ^2 = 10.18 df=7 NS). In 38 pairs which changed mates in successive years between 1984-88, there was no significant difference in the number of new pairs with an increased, decreased or identical absolute age difference (Table 6.21; Goodness-of-fit χ^2 = 3.53 df=2 NS), although in appreciably more of the new pairs there was no difference in age, perhaps reflecting local aggregations of similar aged birds in the colony. The mean age difference within pairs increased from 1.97 years to 2.50 years with each of two consecutive pair changes, as did the variation in age differences (standard deviations; original pair: 2.31 years, second mate change: 2.74 years) although the difference between the means was not significant (Table 6.22). The increase in variance of age differences within pairs after successive mate change is consistent with random pairing with respect to age, since initially recruits tend to pair together but in subsequent years re-pairings are random according to age, and by chance many of these will be to younger birds which are more numerous. The effect of this on the age difference distribution of a sample of pairs followed for several re-matings is to draw out the tails of the distribution (*i.e.* increasing the variance). The proportions of younger, equal aged and older females in changed pairs did not differ significantly in successive pair changes (Table 6.23).

6.5 Breeding performance.

6.5.1 Nest quality.

The external height and width of nest at Shagnasty I/II in 1986 were measured from photographs, using a binocular microscope equipped with an eyepiece graticule. Height was measured from the rim of the nest to the base, at the middle, and width was measured just below the rim as indicated in Figure 6.5. For 14 nests which were built on steeply sloping ground this provided an intermediate value of height (Figure 6.5b). For each nest the width was divided by the height to yield a nest size ratio, higher ratios indicating low, wide nests (platform type), and low ratios indicating tall,

TABLE 6. 21 **ABSOLUTE AGE DIFFERENCES WITHIN NEW PAIRS COMPARED WITH AGE DIFFERENCES IN THE ORIGINAL PAIR DURING THE PREVIOUS YEAR. N = 38 PAIRS.**

	Age differences in new pairs		
No. of pairs	Greater	Same	Less
Observed	11	18	9
Expected	12.6	12.6	12.6

Test of equality: $\chi^2_2 = 3.53$ NS

TABLE 6. 22 MEAN AGE DIFFERENCE WITHIN PAIRS IN RELATION TO SUCCESSIVE MATE CHANGE.

Pair status	No.of pairs	Mean age * difference	S.D.
Original pair	38	1.97	2.31
After first mate change	38	2.29	2.50
After second mate change	6	2.50	2.74

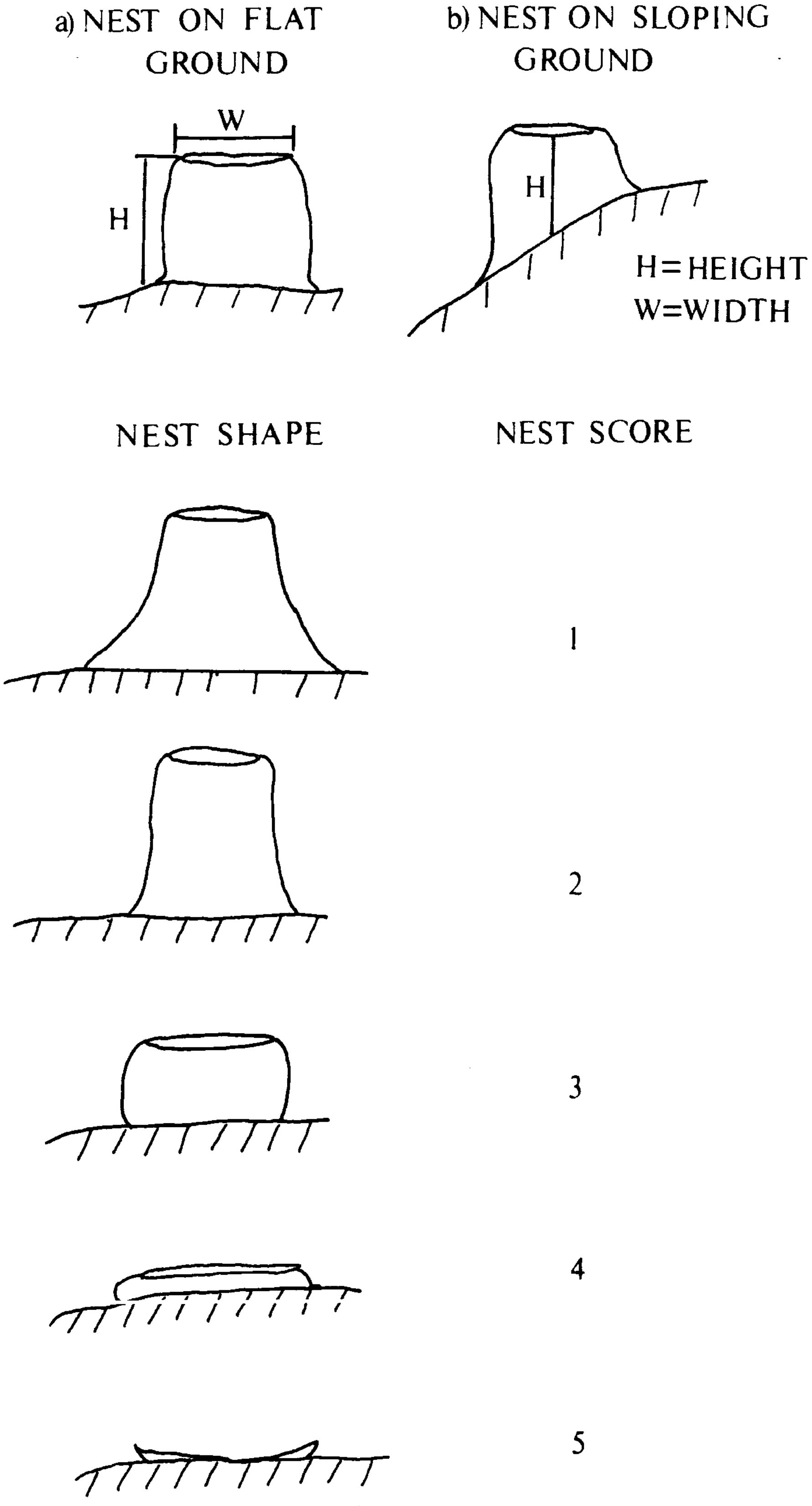
* None of the means are significantly different from the others. t - tests Log_{10} transformed.

TABLE 6. 23 AGE DIFFERENCES WITHIN CHANGED PAIRS IN RELATION TO SEX.

		Female partner in new pair:		
Pair status	No.of pairs	Younger	Same	Older
Original pair	38	14	10	14
After first mate change	38	13	10	15
After second mate change	6	3	2	1

Original pair *v* first and second grouped: $\chi^2_2 = 0.04$ NS

FIGURE 6. 5 MEASUREMENT OF NEST SIZE DIMENSIONS AND NEST SHAPE SCORES.



narrow nests (column type). In addition, the overall shape was assessed by giving each nest a shape score of between 1 and 5, according to the shapes shown in Figure 6.5.

Since the nests were photographed on six days between 7 November and 18 December, a comparison of the means of nest size ratios was undertaken to determine if they varied with time. Table 6.24 indicates that significant difference between mean nest size ratios did occur ($F_{5,176} = 3.02$ P=0.01), although there is no obvious trend in nest size with time, and nests photographed on consecutive days (21 and 22 November) show one of the greatest differences between means. The means were reanalysed omitting those for 21 November and 16 December and there were no significant differences ($F_{3,140} = 1.20$ NS), although a trend of decreasing mean nest size ratios with time was discernible, suggesting that the addition of new nest material was causing nests photographed later in the season to appear higher, and hence result in lower nest size ratios. It may be that the original, significant differences in nest size ratios resulted from particular groups of nests which were photographed on the same day and differed because of the local terrain in that part of the colony. Subsequent analyses were performed on the four groups of nests whose means did not differ significantly.

Table 6.25 shows that there are significant differences in mean nest size ratios in relation to the age of males, the nests of those aged 3-5 years having ratios of 3.58 compared with 3.14 in older bird's nests. Female age had no effect on nest size ratio. This indicated that the nests of young males tended to be wider in relation to their height than those of older males. There were no significant differences between recruits and experienced birds although the latter had appreciably lower nest size ratios. (recruits: mean=3.51 SD=1.13 n=31; experienced: mean=3.25 SD=0.95 n=123; $t_{152} =$ 1.28 NS).

Table 6.26 indicates that nest shape differs significantly in relation to male age ($\chi^2 = 12.01$ df=2 P<0.01). A higher proportion of males aged 2-5 years had nest shape scores of 4 and 5 compared with older males. In contrast, males older than 5 years tended to have scores of 1 and 2. Relating nest scores to the shape, this indicated

TABLE 6. 24 VARIATION OF MEAN NEST SIZE RATIOS WITH DATE OF PHOTOGRAPHY.

		Nest size ratio:	
Date	No.of nests	Mean	S.D.
7 November	21	3.57	1.06
11 November	23	3.44	0.96
21 November	24	2.75	0.76
22 November	37	3.37	1.27
11 December	63	3.15	0.80
16 December	14	2.73	0.57

Difference between means: $F_{5,176} = 3.02$ $P = 0.01$

TABLE 6. 25 MEAN NEST SIZE RATIO IN RELATION TO AGE ANE SEX IN 1986 AT SHAGNASTY I/II.

	MALES			FEMALES		
Age	No. of birds	Mean	S.D.	No. of birds	Mean	S.D
3-5	38	3.58	1.02	35	3.35	1.07
6-16	56	3.14	0.97	51	3.34	1.04
Difference between means	$t_{92} = 2.13$ $P<0.05$				$t_{84} = 0.04$ NS	

TABLE 6. 26 NEST SHAPE SCORE IN RELATION TO AGE IN MALES AND FEMALES.

		MALES						FEMALES				
		Nest shape score						Nest shape score				
Age	No. of birds	1	2	3	4	5	No. of birds	1	2	3	4	5
2-5	44	0	0	26	13	5	38	0	3	23	8	4
6-8	20	1	3	14	2	0	22	0	1	14	7	0
9-10	24	0	5	15	3	1	20	0	1	15	3	1
11-16	15	1	0	9	5	0	13	0	1	10	2	0

Test of proportions at each
nest score.
Nests grouped 1-2, 3, 4-5,
Ages grouped over 6-16: $\chi^2_4 = 12.01$ P<0.01 $\chi^2_4 = 1.10$ NS

that 2-5 year old males possessed flatter, platform-type nests, whereas those of the older birds were more substantial, column or cone shaped nests. This agrees with the above finding on nest size ratio and male age. Female age did not significantly influence the nest shape score. The mean ages of males and females associated with each nest shape score did not differ significantly (Table 6.27), although as expected from the previous analysis, the mean age of males associated with scores of 1 and 2 was appreciably higher than those for males with scores greater than 3. In both sexes, the youngest mean age occurred at nests with scores of 4 and 5. There were no significant correlations between nest shape score and age in either sex (square root transformation of scores, male age: r = −0.167 df=101 NS; female age: r = −0.139 df=91 NS). There was no significant difference between the mean nest shape scores of recruits and experienced breeders (recruits: mean=3.44 SD=0.82 n=34; experienced: mean=3.20 SD=0.73 n=132; difference between means, square root transformed: t_{49} = 1.61 NS), and no correlations between age and nest shape scores for recruits or experienced birds (all scores square root transformed, male recruits: r = 0.01 df=17; female recruits: r = −0.326 df=16; male experienced: r = −0.124 df=84; female experienced: r = −0.178 df=75; all NS)

In a sample of 41 nests, the current year's nest had been built on top of substantial remains of the previous year's nest. This was clearly recognisable in the photographs as a discontinuity in the nest material. The ages of 16 males and 14 females possessing these 'double' nests was known, and the mean age of the males was significantly greater than the mean age of males in the whole sample of 133 photographed nests (Table 6.28). In addition, the variation in the age of males at 'double' nests was less than that for all photographed nests, (SD of 'double' nests=2.24; of all nests= 3.22). There were no significant differences in the mean age of females according to nest type.

6.5.2 Timing of egg laying.

Egg laying was monitored in detail only at Shagnasty I/II and visits were made at

TABLE 6. 27 MEAN AGE OF MALES AND FEMALES IN RELATION TO NEST SHAPE SCORE.

	Male age			Female age		
Nest shape score	No. of birds	Mean	S.D.	No. of birds	Mean	S.D.
1	2	8.50	3.54	0	-	-
2	8	8.63	1.30	6	6.83	2.56
3	64	7.42	2.91	62	7.68	3.15
4	23	7.30	3.30	14	7.00	2.32
5	6	5.67	1.63	5	5.00	2.45

Comparison of means ANOVA, grouped over nest scores 1-2, 4-5: $F_{2,100} = 1.21$ NS $F_{2,90} = 1.29$ NS

TABLE 6. 28 **COMPARISON OF THE MEAN AGES OF MALES AND FEMALES WHICH BUILT THE CURRENT YEAR'S NEST ON RECOGNISABLE REMAINS OF A PREVIOUS YEAR'S NEST ('DOUBLE NESTS') WITH ALL BIRDS IN THE SAMPLE OF PHOTOGRAPHED NESTS AT SHAGNASTY I/II IN 1986.**

	MALE			FEMALE		
	No. of birds	Mean	S.D.	No. of birds	Mean	S.D.
'Double' nests	16	10.31	2.24	14	8.00	3.19
All nests photographed	133	7.77	3.22	121	7.32	3.03
Comparison of means	$t_{23} = 4.05$ $P<0.001$			$t_{15} = 0.76$ NS		

approximately three day intervals during the laying period in 1986 and 1987. This results in a potential error of about three days in the estimates of most dates of first egg laying, so these were grouped into five day intervals for analysis. To estimate the date of laying of the first egg, clutches which were complete when first seen were removed from the analysis since it was impossible to decide when egg laying had finished. In the remaining clutches, the laying intervals were assumed to be 3 days in two egg clutches, and 2 and 3 days between the first and second eggs, and second and third eggs respectively in three egg clutches (Shaw 1984; Table 6.7). Unsoiled eggs with a chalky-white deposit were assumed to have been laid on the day they were found; in a study of European shags, Snow (1960) found that clean eggs were indicative of newly laid eggs. The date on which laying was estimated to have begun was back-calculated from the number of eggs found taking account of the laying intervals, and rounding half-days alternately up and down to avoid bias due to rounding errors. For example, the second egg in a three egg clutch, found on 15 November may have been laid on that day or up to three days previously, (laying interval between the last two eggs in clutches of three is 3 days). Since the laying interval between the first and second egg in three egg clutches is two days, this gives an estimated date of laying of the first egg as between 13 November (which assumes the second egg was newly laid on 15 November) and 10 November (which assumes that the arrival of the third egg was imminent by 15 November), and the mid-point, 11.5, is arbitarily chosen as the first egg date and either rounded up or down. Where visits to the colonies were close together it was often possible to increase the accuracy of the estimated date on which the first egg was laid, and this was incorporated in the analysis

In 1986, the date on which the first egg was laid at Shagnasty I/II could only be determined as between 30 October and 7 November, but in 1987, the first egg was laid at North Point on 30 October and the first egg was laid at Shagnasty I/II between 7-9 November. In the following analyses, day 1 was standardised as 31 October. Figure 6.6 shows the distribution of clutches started at Shagnasty I/II for 33 nests in 1986 and 107 nests in 1987. In 1986, there appears to be a second peak of egg-laying between

FIGURE 6. 6 THE TIMING OF CLUTCHES STARTED IN 1986 AND 1987 AT SHAGNASTY I/II. NOTE DAY 1 = 31 OCTOBER.

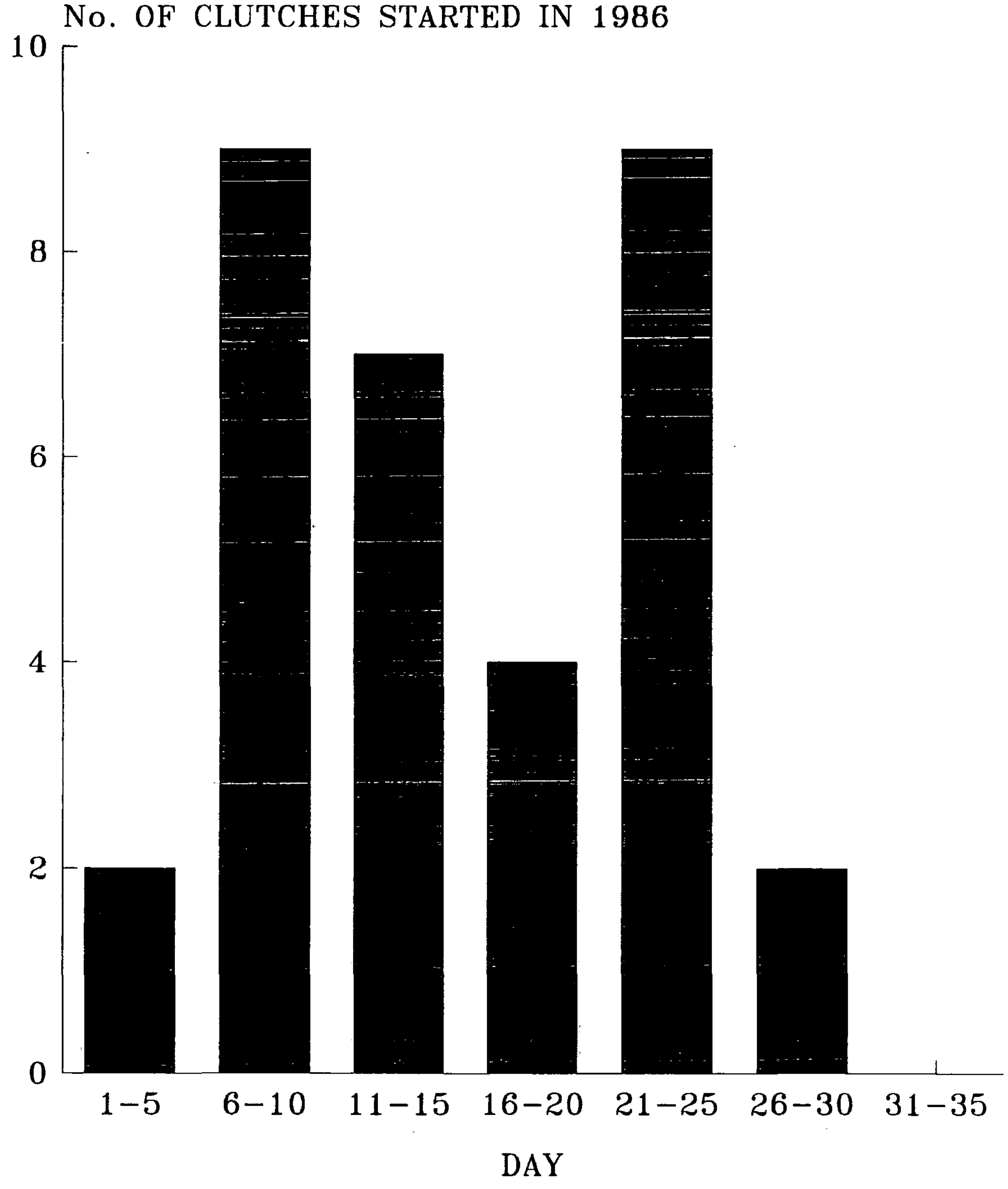
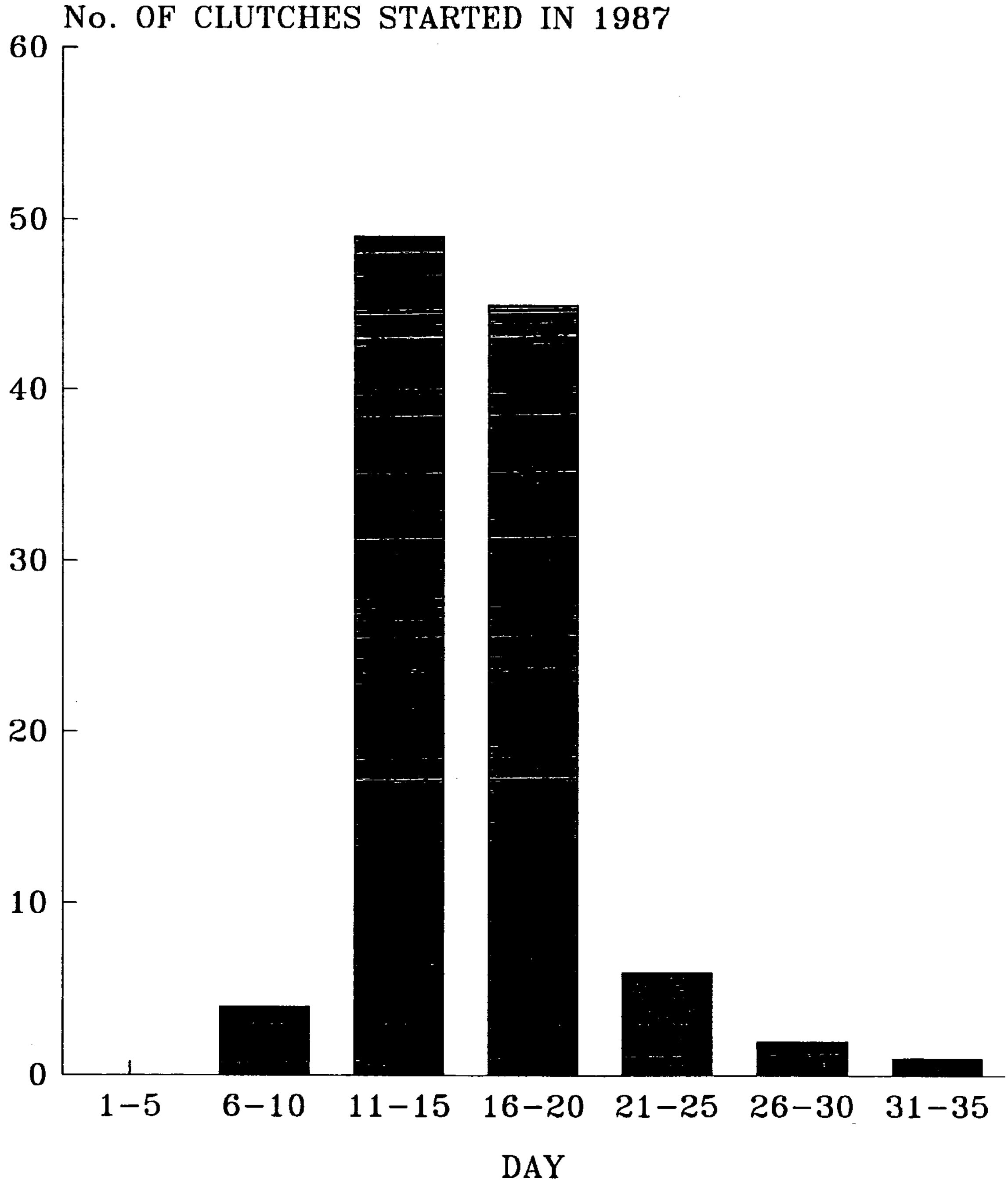


FIGURE 6. 6 - cont.



days 21-25 which may reflect a real difference in the laying pattern or may be an artefact due to the small number of nests sampled. There was no evidence that Blue-eyed shags relaid following the loss of the original clutch and it is unlikely that there would be sufficient time during a breeding season to permit relaying, since in the European shag the interval between egg loss and replacement in 10 nests is 21-22 days (Cramp & Simmonds 1977). If this is similar in Blue-eyed shags, then a pair which failed by 15 November would have relaid at the earliest by 6 December, which is later than the latest clutch was started during 1986-87. In reality, most pairs which failed probably did so after mid-November (see section 2.4.2), further reducing the likelihood of relaying. There was a significant difference in the proportion of clutches started at different times between years ($\chi^2 = 41.9$ df=3 $P<0.001$), with only 33% of clutches in 1986 being started between days 11-20, compared with the same period in 1987 when 88% of egg-laying occurred.

The timing of egg-laying in relation to male and female age is shown in Table 6.29, and there are no significant differences in the proportion of birds which started clutches in the first or second periods of egg-laying, with respect to age. However an appreciably higher proportion of individuals aged 2-5 years started clutches during the later period in both years, and in 1987 a higher proportion of birds older than 10 years started clutches during the first period of laying. In both years the effect appeared to be more marked in relation to male age rather than female age.

6.5.3 Clutch size.

The distribution of clutch sizes in 1986 and 1987 on Signy is shown in Table 6.30. In 1986, no eggs were recorded at six nests (two in each colony), and in 1987 no eggs were seen at two nests at North Point or from three nests at each Shagnasty subcolony. These pairs had almost certainly laid eggs which had been lost prior to the examination of their nest contents, and were excluded from subsequent analyses. In both years there were significant differences between colonies in mean clutch size (1986: $F_{2,621} = 40.9$

TABLE 6. 29 **THE NUMBER OF CLUTCHES STARTED DURING TWO PERIODS IN 1986 AND 1987 IN RELATION TO AGE. NOTE: DAY 1 IS 30 OCTOBER.**

	1987					1986			
	Males		Females			Males		Females	
	Day		Day			Day		Day	
Age	1-15	16-35	1-15	16-35	Age	1-15	16-30	1-15	16-30
2-5	0	5	4	9	2-5	0	3	3	4
6-9	11	9	8	8	6+	6	1	4	3
10+	17	8	4	2	-	-	-	-	-

Difference between ages 1-15 *v* 16-35 days in 1987 (6-10 years grouped):

Males $\chi^2_1 = 2.03$ NS
Females $\chi^2_1 = 1.03$ NS

TABLE 6. 30 CLUTCH SIZE IN RELATION TO COLONY AND YEAR.

Colony	Year	No. of clutches	Clutch size				Mean	S.D.
			1	2	3	4		
North Point	1986	51	1	14	36	0	2.69	0.51
	1987	61	8	18	34	1	2.46	0.74
Shagnasty I/II	1986	331	4	46	280	1	2.84	0.41
	1987	345	21	66	258	0	2.69	0.58
Shagnasty III	1986	242	15	102	125	0	2.45	0.61
	1987	330	13	96	220	1	2.63	0.56

Difference in mean clutch size between colonies (one way ANOVA):

1986: $F_{2,621} = 40.9$ $P<0.001$
1987: $F_{2,733} = 3.99$ $P<0.05$

Difference between years (means):
NP: $t_{109} = 2.10$ $P<0.05$
SNI/II $F_{344,330} = 2.00$ $P<0.01$
SNIII $F_{241,329} = 1.19$ $P<0.01$

$P<0.001$; 1987: $F_{2,733} = 3.99$ $P<0.05$). In 1986, pairs at Shagnasty III had a mean clutch size of 2.45 eggs, lower than at Shagnasty I/II or North Point, and in 1987, the mean clutch size at North Point (2.46) was lower than at Shagnasty. These differences probably reflect variation in the frequency of visits during which clutch size was recorded, since in 1986, only one visit to record clutch size was made during November to North Point and Shagnasty III, and the proportion of 1 and 2 egg clutches found at these colonies was higher (29% and 48% respectively) than at Shagnasty I/II where five visits were made. In 1987 during November, four visits were made to North Point and one visit to Shagnasty III, and again the proportions of 1 and 2 egg clutches at these colonies were higher (43% and 33% respectively) than at Shagnasty I/II where six visits were made. Proportionately three times more clutches of 1 were recorded from North Point than from Shagnasty III in 1987, but it is not clear if this resulted from more incomplete clutches being recorded or greater egg loss from completed clutches before they were found.

Considering Shagnasty I/II, where visits were more frequent and widespread during November, there was a significantly higher proportion of 1 and 2 egg clutches in 1987 compared with 1986 ($\chi^2 = 15.0$ df=2 $P<0.001$), suggesting that the loss of eggs was more rapid in 1987, or that proportionately more smaller clutches were laid. At North Point the clutch size distribution followed a similar pattern over the two years, except in 1 egg clutches which formed only 2% of all clutches in 1986 but 13% in 1987, although this difference was not statistically significant ($\chi^2 = 3.45$ df=2 NS). By contrast, there were higher proportions of 1 and 2 egg clutches in 1986 than in 1987 at Shagnasty III ($\chi^2 = 13.4$ df=2 $P<0.01$). There were significant differences between years in mean clutch size at all colonies, being greater in 1986 than 1987 at North Point and Shagnasty I/II and smaller in 1986 than 1987 at Shagnasty III (Table 6.30). It was not possible to decide whether the observed shifts in the distribution of clutch sizes at North Point and Shagnasty III represented more incomplete nests being recorded or egg loss in completed clutches.

6.5.4 Clutch size in relation to age and breeding experience.

The results in this section and in section 6.5.5. relate only to Shagnasty I/II, where nests were monitored more closely that at North Point or Shagnasty III. There was no significant difference in mean clutch size with age (Table 6.31), although except for females in 1987, birds aged 11-18 years laid appreciably larger clutches on average than those aged 2-5 years. The proportions of 1, 2 and 3 egg clutches (the ages of the pair which laid the 4 egg clutch was unknown) were also similar between 2-5, 6-10 and 11-18 year age classes, although appreciably more birds aged 1-5 years laid 1 and 2 egg clutches than older birds (Table 6.32). With respect to breeding experience (Table 6.33), female recruits in 1986 had a significantly lower mean clutch size of 2.61 eggs compared to the 2.88 eggs laid by experienced females, and pairs in which the male was a recruit had lower mean clutch sizes than pairs with experienced males in both years, although this difference only statistically significant in 1987. Table 6.34 shows that recruiting males and females were associated with a higher proportion of 1 and 2 egg clutches than experienced birds, significantly so for females in 1986 when 35% laid 1 and 2 egg clutches but only 12% of experienced birds did so. Considering the joint experience of both members of the pair, there was no significant difference in mean clutch size of pairs where both birds were recruits or where both were experienced breeders, but the latter did have appreciably higher mean clutch sizes (Table 6.35).

6.5.5 The influence of clutch size on brood size.

The mean brood size which resulted from clutches of 2 and 3 eggs was investigated with respect to breeding experience. Four clutches of 1 egg were excluded from the analysis since these had probably lost eggs before being recorded, and another two nests which failed after eggs had been laid were also omitted. Some clutches of 2 eggs may originally have had a third egg which was lost. Table 6.36 indicates that in pairs where at least one of the partners was an experienced breeder in 1986, the mean number of

TABLE 6. 31 MEAN CLUTCH SIZE IN RELATION TO MALE AND FEMALE AGE IN 1986 AND 1987 AT SHAGNASTY I/II.

FEMALES

	1986			1987		
Age	No. of pairs	Mean clutch size	S.D.	No. of pairs	Mean clutch size	S.D
2-5	54	2.78	0.42	58	2.66	0.55
6-10	58	2.88	0.39	72	2.65	0.61
11-18	19	2.89	0.32	26	2.54	0.71

MALES

	1986			1987		
Age	No. of pairs	Mean clutch size	S.D.	No. of pairs	Mean clutch size	S.D.
2-5	57	2.72	0.53	54	2.57	0.66
6-10	58	2.81	0.44	83	2.63	0.60
11-18	24	2.96	0.20	32	2.75	0.57

Mean clutch size *v* age (ANOVA)	Males:		Females:	
	1986:	$F_{2,136} = 2.43$ NS	1986:	$F_{2,128} = 1.18$ NS
	1987:	$F_{2,166} = 0.93$ NS	1987	$F_{2,153} = 0.40$ NS

TABLE 6. 32 CLUTCH SIZE FREQUENCY IN RELATION TO MALE AND FEMALE AGE IN 1986 AND 1987 AT SHAGNASTY I/II.

FEMALES

	1986				1987			
		Clutch size				Clutch size		
Age	No. of pairs	1	2	3	No. of pairs	1	2	3
2-5	54	0	12	42	58	2	16	40
6-10	58	1	5	52	72	5	15	52
11-18	19	0	2	17	26	3	6	17

MALES

	1986				1987			
		Clutch size				Clutch size		
Age	No. of pairs	1	2	3	No. of pairs	1	2	3
2-5	57	2	12	43	54	5	13	36
6-10	58	1	9	48	83	5	21	57
11-18	24	0	1	23	32	2	4	26

Clutch size *v* age (grouped over 1 and 2 egg clutches)	Males:			Females:		
	1986	$\chi^2_2 = 4.80$	NS	1986	$\chi^2_2 = 3.44$	NS
	1987	$\chi^2_2 = 2.29$	NS	1987	$\chi^2_2 = 0.46$	NS

TABLE 6. 33 MEAN CLUTCH SIZE IN RELATION TO MALE AND FEMALE BREEDING EXPERIENCE IN 1986 AND 1987 AT SHAGNASTY I/II.

FEMALES

	1986			1987		
Breeding experience	No. of pairs	Mean clutch size	S.D.	No. of pairs	Mean clutch size	S.D
Recruit	23	2.61	0.58	48	2.65	0.57
Experienced	108	2.88	0.33	107	2.64	0.62

MALES

	1986			1987		
Breeding experience	No. of pairs	Mean clutch size	S.D.	No. of pairs	Mean clutch size	S.D.
Recruit	26	2.73	0.45	52	2.63	0.76
Experienced	110	2.81	0.46	121	2.68	0.57

	Males:		Females:	
Mean clutch size *v* experience	1986	$t_{134} = 0.78$ NS	1986	$F_{22,107} = 3.09$ $P<0.01$
	1987	$F_{51,120} = 1.78$ $P<0.01$	1987	$t_{153} = 0.10$ NS

TABLE 6. 34 CLUTCH SIZE FREQUENCY IN RELATION TO MALE AND FEMALE BREEDING EXPERIENCE IN 1986 AND 1987 AT SHAGNASTY I/II.

FEMALES

	1986				1987			
		Clutch size				Clutch size		
Breeding experience	No. of pairs	1	2	3	No. of pairs	1	2	3
Recruit	23	1	7	15	48	2	13	33
Experienced	108	0	13	95	107	8	23	76

MALES

	1986				1987			
		Clutch size				Clutch size		
Breeding experience	No. of pairs	1	2	3	No. of pairs	1	2	3
Recruit	26	0	7	19	52	7	11	34
Experienced	110	3	15	92	121	6	27	88

Clutch size v experience(grouped over 1 and 2 egg clutches)	Males:			Females:		
	1986	$\chi^2_1 = 0.94$	NS	1986	$\chi^2_1 = 5.70$	$P<0.05$
	1987	$\chi^2_1 = 0.62$	NS	1987	$\chi^2_1 = 0.01$	NS

TABLE 6. 35 MEAN CLUTCH SIZE IN RELATION TO BREEDING EXPERIENCE OF BOTH MEMBERS OF THE PAIR IN 1986 AND 1987 AT SHAGNASTY I/II.

	1986			1987		
Breeding experience of pair	No. of pairs	Mean clutch size	S.D.	No. of pairs	Mean clutch size	S.D
Both recruits	5	2.60	0.55	21	2.57	0.60
Both experienced	37	2.89	0.31	37	2.65	0.63

Mean clutch size	1986	$t_{40} = 1.77$	NS
v experience	1987	$t_{43} = 0.46$	NS

TABLE 6. 36 MEAN BROOD SIZE IN RELATION TO CLUTCH SIZE AND BREEDING EXPERIENCE OF EITHER OR BOTH PARTNERS IN 1986 AND 1987 AT SHAGNASTY I/II.

1986

	2 egg clutches			3 egg clutches		
Breeding experience	No. of pairs	Mean brood size	S.D.	No. of pairs	Mean brood size	S.D
Recruit	3	2.00	0.00	17	2.06	0.83
Experienced	13	1.69	0.48	97	2.26	0.73

1987

	2 egg clutches			3 egg clutches		
Breeding experience	No. of pairs	Mean brood size	S.D.	No. of pairs	Mean brood size	S.D.
Recruit	8	1.63	0.52	31	1.65	0.66
Experienced	23	1.65	0.49	98	2.09	0.72

Mean clutch size	1986	Experienced	$t_{108} = 2.73$ $P<0.01$
2 *v* 3 egg clutches	1987	Recruit	$t_{37} = 0.08$ NS
		Experienced	$t_{119} = 2.77$ $P<0.01$

chicks hatched by birds with clutches of three was 2.26, significantly higher than the 1.69 chicks hatched from clutches of two eggs. Insufficient numbers of recruits with 2 egg clutches were found to compare mean brood sizes according to clutch size for recruits in 1986. In 1987, there was no difference in the mean brood size of recruits which laid 2 or 3 egg clutches ($t_{37} = 0.08$ NS), whereas experienced pairs again had higher mean brood sizes from 3 eggs than from 2 ($t_{119} = 2.77$ $P<0.01$).

6.5.6 The number of chicks fledged in relation to brood size, breeding experience and nest quality.

The mean number of chicks fledged in relation to brood size at Shagnasty I/II is shown in Table 6.37. Pairs of mixed breeding experience were excluded (n=7 pairs in 1986 and n=12 pairs in 1987), as were broods where no chicks fledged (n=2 and n=13 broods in 1986 and 1987 respectively). In 1986, pairs with 2 and 3 chick broods fledged similar numbers of chicks ($t_{61} = 0.72$ NS), but in the following year pairs with broods of 2 only fledged 1.9 chicks compared with those with broods of 3, which fledged 2.6 chicks ($F_{33,64} = 3.81$ $P<0.01$). Comparing recruits and experienced pairs with broods of 2, similar numbers of chicks were fledged in 1986 but experienced pairs fledged significantly more in 1987 ($F_{16,64} = 2.50$ $P<0.01$).

With respect to breeding experience, the mean number of chicks fledged by successful pairs (*i.e.* those which fledged at least one chick) did not differ between recruits and experienced breeders of either sex in 1986. However, in 1987 recruits of both sexes fledged significantly fewer chicks on average than experienced birds (Table 6.38). The proportion of pairs which failed to fledge any chicks is shown in Table 6.39 according to the breeding experience of the pair. In both years a significantly higher proportion of female recruits did not fledge any chicks, but male breeding experience was not related to breeding success. Comparing the proportion of pairs which failed between years, similar numbers of recruits failed in both years irrespective of sex (comparison of recruits between years (Fisher's exact), females: P=0.1; males: P=0.25). A higher

TABLE 6. 37

MEAN NUMBER OF CHICKS FLEDGED IN RELATION TO BROOD SIZE AND BREEDING EXPERIENCE OF BOTH PARENTS, AT SHAGNASTY I/II. NOTE: PAIRS OF MIXED BREEDING EXPERIENCE ARE EXCLUDED.

Brood size in 1986

	1			2			3		
	No. of pairs	Mean fledged	S.D.	No. of pairs	Mean fledged	S.D.	No. of pairs	Mean fledged	S.D.
Recruits	1	-	-	9	1.67	0.50	0	-	-
Experienced	12	1.00	-	34	1.62	0.49	29	1.72	0.59

Brood size in 1987

	1			2			3		
	No. of pairs	Mean fledged	S.D.	No. of pairs	Mean fledged	S.D.	No. of pairs	Mean fledged	S.D.
Recruits	18	1.00	-	17	1.65	0.49	3	2.00	1.00
Experienced	23	1.00	-	65	1.89	0.31	34	2.59	0.61

Difference between means	1986 Experienced	2 *v* 3 chicks:	$t_{61} = 0.72$ NS
	1987 Experienced	2 *v* 3 chicks:	$F_{33,64} = 3.81$ $P<0.01$
	Experienced *v* recruit	1986 (2 chicks):	$t_{41} = 0.26$ NS
	Experienced *v* recruit	1987 (2 chicks):	$F_{16,64} = 2.50$ $P<0.01$

TABLE 6. 38 **THE MEAN NUMBER OF CHICKS FLEDGED BY SUCCESSFUL PAIRS IN RELATION TO BREEDING EXPERIENCE OF MALES AND FEMALES IN 1986 AND 1987 AT SHAGNASTY I/II.**

1986

	FEMALES			MALES		
Breeding experience	No. of pairs	Mean	S.E.	No. of pairs	Mean	S.E
Recruit	12	1.50	0.151	18	1.33	0.114
Experienced	89	1.37	0.077	84	1.57	0.062

1987

	FEMALES			MALES		
Breeding experience	No. of pairs	Mean	S.E.	No. of pairs	Mean	S.E.
Recruit	44	1.34	0.079	55	1.07	0.077
Experienced	89	1.89	0.068	84	1.93	0.071

Comparison of means; recruit *v* experienced	1986	Males	$t_{100} = 1.66$ NS
		Females	$t_{99} = 0.59$ NS
	1987	Males	$t_{137} = 7.89$ $P<0.001$
		Females	$t_{131} = 4.90$ $P<0.001$

TABLE 6. 39

THE FLEDGING SUCCESS OF PAIRS IN RELATION TO MALE AND FEMALE BREEDING EXPERIENCE IN 1986 AND 1987 AT SHAGNASTY I/II.

		Female breeding experience		Male breeding experience	
Year	Fledging success	Recruit	Experienced	Recruit	Experienced
1986	Fail	7	12	4	14
	Success	12	89	18	84
	% Fail	37	12	18	14
1987	Fail	7	2	6	7
	Success	44	89	55	84
	% Fail	14	2	10	8

Fledging success *v* breeding experience:	1986	Male	P = 0.74 (Fisher's exact)
		Female	P = 0.01 (Fisher's exact)
	1987	Male	$\chi^2_1 = 0.03$ NS
		Female	P = 0.01 (Fisher's exact)

proportion of experienced breeders of both sexes failed during 1986 compared to 1987, 14% of males and 12% of females failed in 1986 against 8% of males and 2% of females in 1987 (comparison of experienced between years: females $\chi^2 = 5.29$ df=1 $P<0.05$; males $\chi^2 = 12.37$ df=1 $P<0.001$).

It was not possible to determine at which stage of the nesting cycle losses occurred because most nests were not visited frequently after laying. However, the breeding success (*i.e.* the proportion of eggs which produced fledged chicks) is shown in Table 6.40. Within each category of breeding experience there was no significant difference between the sexes in breeding success and therefore only the breeding experience of females was considered. Recruits had a lower breeding success than experienced birds in both years, although this was only statistically significant in 1987 ($\chi^2 = 6.45$ df=1 $P<0.05$). Both recruits and experienced birds had a significantly lower breeding success in 1986 than in 1987, and in the latter year all birds fledged about one and a half times more chicks *per* egg than in 1986.

The effect of nest size was investigated by dividing the nest size ratios into groups of approximately equal sample size, and since nest size ratio was approximately normally distributed this resulted in unequal group sizes. There were significant differences in the mean number of chicks fledged according to nest size ratio (Table 6.41). Nests with ratios up to 2.5 fledged 1.8 chicks whereas those with higher ratios fledged fewer chicks. This indicated that more chicks were fledged from tall column-type nests than flatter, platform-type nests, and since nest size ratio was related to male age (section 6.5.1), it was younger males which built flatter nests and achieved lower chick productivity. Analysis of nest shape scores confirmed this, birds which were associated with the flatter nests fledged 0.9 chicks fewer on average (Table 6.42). Twelve out of thirteen pairs with nests which scored 1-2 (column or cone-shaped) fledged two or three chicks. In comparison, only about a third of pairs with nests scored 4-5 (flat, platform-type) fledged more than one chick ($\chi^2 = 12.3$ df=2 $P<0.001$).

TABLE 6. 40 THE BREEDING SUCCESS OF FEMALES ACCORDING TO BREEDING EXPERIENCE IN 1986 AND 1987 AT SHAGNASTY I/II.

	1986			1987		
	No. eggs	No. chicks fledged	Breeding success (%)	No. eggs	No. chicks fledged	Breeding success (%)
Recruit	64	18	28.1	129	59	45.7
Experienced	298	122	40.9	283	169	59.7

Breeding success *v* breeding experience:
1986: $\chi^2_1 = 3.13$ NS
1987: $\chi^2_1 = 6.45$ $P<0.05$

Breeding success *v* year
Recruit: $\chi^2_1 = 4.82$ $P<0.05$
Experienced: $\chi^2_1 = 19.7$ $P<0.001$

TABLE 6. 41 THE MEAN NUMBER OF CHICKS FLEDGED *PER* PAIR ACCORDING TO NEST SIZE RATIO IN 1986 AT SHAGNASTY I/II.

Nest size ratio	No. of pairs	No. of chicks fledged: Mean	S.D.
0 - 2.5	26	1.81	0.49
2.6 - 3.3	45	1.22	0.80
3.4 - 4.0	25	1.16	0.85
4.1 - 7.0	23	1.52	0.59

Comparison of means: (ANOVA) $F_{3,115} = 4.89$ $P<0.01$

TABLE 6. 42 **NUMBER OF CHICKS FLEDGED IN 1986 AT SHAGNASTY I/II IN RELATION TO NEST SHAPE SCORE. NOTE: SEE FIGURE 6.5 FOR EXPLANATION OF NEST SHAPES.**

		No. of chicks fledged:			
Nest shape score	No. of pairs	0-1	2-3	Mean	S.E.
1 - 2	13	1	12	2.08	0.137
3	84	45	39	1.33	0.080
4 - 5	36	23	13	1.19	0.118

Proportion of chicks fledged *v* nest shape: $\chi^2_2 = 12.34$ $P<0.01$

Comparison of means (ANOVA; square root transformed): $F_{2,130} = 4.73$ $P = 0.01$

6.5.7 The number of chicks fledged *per* pair.

The number of chicks fledged *per* pair was estimated by dividing the total number of chicks known to be alive at ringing by the overall number of breeding pairs. The estimates for Shagnasty in 1988 and Shagnasty III in 1986 are minima since not all chicks were ringed and the remainder were not counted. At the completion of chick ringing in 1984, 70 chicks at Shagnasty were not ringed. Subsequently, on a return visit, most of the remaining chicks at Shagnasty I/II were ringed (Price 1984). Since it was not clear how the original 70 chicks were distributed between the Shagnasty subcolonies, it was assumed that half of the chicks were at Shagnasty III, and these 35 were added to the 189 ringed chicks already known there, to yield an estimate of the total number of chicks fledged from which the number of chicks fledged *per* pair could be calculated. This is the value given in Table 6.43, and the maximum and minimum estimates of the number of chicks fledged *per* pair are $(189 - 70)/198 = 0.60$ and $(189 + 70)/198 = 1.31$. Since the estimates of chick productivity rely on chicks seen at ringing, they fail to take into account mortality between ringing and fledging. However, this has been partly corrected for, by excluding all dead ringed chicks most of which were probably found at Shagnasty owing to the flat nature of the colony (see section 4.6). As most chicks at Shagnasty I/II and North Point were ringed, the numbers of unringed dead chicks which were not included in the correction is likely to be small and to have a minimal effect on the productivity estimates.

The mean number of chicks fledged *per* pair in each year between 1984-88 is shown in Table 6.43. At North Point this did not differ significantly, but at Shagnasty I/II significantly more chicks per pair were fledged in 1987, and fewer in 1985. The latter may be an underestimate because Shagnasty I/II was not as closely monitored as in 1986 and 1987, and some chicks may have been missed. Chick productivity may also have been underestimated at North Point in 1987 since the single visit made to ring chicks occurred in mid-January, when some nestlings may have been too small to ring. Within each year there were no significant differences between colonies in the number

TABLE 6. 43 THE OVERALL NUMBER OF CHICKS FLEDGED *PER* PAIR BETWEEN 1984-88, BASED ON THE TOTAL NUMBER OF CHICKS FLEDGING AND THE NUMBER OF BREEDING PAIRS. NOTE: NUMBER OF PAIRS IN PARENTHESES, SHAGNASTY III NOT COUNTED IN 1985, SQUARE BRACKETS DENOTE MINIMUM ESTIMATES - SEE TEXT.

	Year				
Colony	1984	1985	1986	1987	1988
North Point	1.51 (39)	1.52 (50)	1.51 (53)	1.13 (72)	1.22 (58)
Shagnasty I/II	1.44 (243)	1.04 (349)	1.44 (339)	1.67 (389)	[1.43] (327)
Shagnasty III	[1.13] (198)	-	[1.19] (279)	1.67 (340)	[1.35] (295)
Difference between colonies, all NS. (min. estimates excluded):	$\chi^2_2 = 3.96$	$\chi^2_1 = 3.43$	$\chi^2_1 = 0.02$	$\chi^2_2 = 5.49$	$\chi^2_1 = 0.49$

Difference between years (min. estimates excluded): North Point: $\chi^2_4 = 2.70$ NS Shagnasty I/II: $\chi^2_3 = 23.74$ $P<0.001$

of chicks fledged *per* pair.

Table 6.44 shows the overall mean clutch size, brood size and number of chicks fledged *per* pair for a sample of pairs which were monitored in detail at Shagnasty I/II. The mean number of chicks fledged *per* pair is 1.39 in 1986 and 1.70 in 1987 and these values are not significantly different from the estimates in Table 6.43 (1.44 and 1.67 chicks *per* pair respectively) which were obtained by relating the total number of chicks alive at ringing to the number of pairs breeding (1986: χ^2 = 0.08 df=1 NS; 1987: χ^2 = 0.01 df=1 NS). The consistency between methods suggests that an accurate assessment of productivity has been obtained. The mean clutch and brood sizes were significantly greater in 1986 than in 1987, despite this more chicks were fledged by pairs in 1987, indicating that chick mortality was greater in 1986 and resulted in fewer fledging.

6.6 Discussion.

Blue-eyed shags showed a high rate of mate change, 61% taking a new partner in the following season. Compared to the previously reported rate of 77% for this population during 1979-81, this is significantly lower (Shaw 1985b; χ^2 = 17.26 df=1 $P<0.001$), but both rates are higher than in the European shag where 52% of pairs changed (Potts 1966; difference between Blue-eyed shags (this study) and European shags: χ^2 = 4.32 df=1 $P<0.05$). Mate change resulted from disappearance of the partner or divorce, in which case both members of the pair were alive and breeding during the following season. Disappearance of partners can be equated with mortality since the colony fidelity of breeding birds was high (section 3.3.1), there was no evidence of emigration (section 3.2.1) and only a few birds which disappeared were seen subsequently (section 3.4). For the latter, the numbers involved were no higher than expected according to the recapture efficiency.

The divorce rate of Blue-eyed shags was 42%, significantly lower than the 57% divorce rate found by Shaw (1984), χ^2 = 8.54 df=1 $P<0.001$, although similar to the rates of European shags on the Farne Islands, 44%; χ^2 = 0.21, df=1 NS, and on the

TABLE 6. 44 MEAN CLUTCH SIZE, BROOD SIZE AND NUMBER OF CHICKS FLEDGED *PER* PAIR AT SHAGNASTY I/II IN 1986.

	Clutch size			Brood size			Chicks fledged		
	No. of pairs	Mean	S.E	No. of pairs	Mean	S.E.	No. of pairs	Mean	S.E
1986	333	2.82	0.025	213	2.18	0.05	274	1.39	0.045
1987	346	2.67	0.033	251	1.97	0.045	282	1.70	0.048
Comparison of means: (Z scores)		Z = 3.57 P<0.001			Z = 3.10 P<0.001			Z = 4.74 P<0.001	

Isle of May, 31%, $\chi^2 = 2.62$, df=1 NS (Potts 1966, Aebischer 1985). The lower rate of mate change in European shags compared to Blue-eyed shags was not due to differences in divorce rate, and indicated that European shags experience lower mortality rates on average, since the colony fidelity of breeding birds in both species is high. A similar comparison with Shaw's (1984) results suggest that in Blue-eyed shags, both mortality and divorce rates were higher during 1979-81. High rates of mate change have been reported for the Flightless cormorant, (88%; Harris 1979) and Brandt's cormorant, (91%; Boekelheide & Ainley 1989), and since the average annual mortality rates are low, approximately 12% in Flightless cormorants and a minimum of 18-21% in Brandt's cormorant aged 2-7 years, this implies high divorce rates.

The adaptive significance of such high rates of divorce in Blue-eyed shags may lie in allowing rapid pair formation once the season has begun, facilitating breeding at the earliest opportunity. The advantage to early laying pairs in terms of an increased proportion of chicks fledged has been demonstrated by Shaw (1986), although one consequence of divorce is the pairing of experienced breeders with mates of lesser breeding experience. As the number of chicks fledged was higher in experienced pairs than in recruits, and the latter were also more likely to fail to rear any chicks altogether, this could outweigh benefits gained by divorce. However, there was a suggestion of a temporal difference in the timing of breeding between birds aged 2-5 years, most of which were breeding for the first time, and older, more experienced birds, with earlier breeding by the older birds. In addition, the tendency for recruits to pair together is consistent with later arrival, particularly since their nests were not obviously clumped in the colony. In Brandt's cormorant, Boekelheide & Ainley (1989) have suggested that breeding experience is of little importance compared to experience of environmental conditions and in this species the oldest males arrive first at the colony and divorce rates are high.

In both sexes the divorce rate decreased with age and breeding experience, but breeding experience was more important in divorce rates than age. Overall the divorce rate among recruits was 54% compared to 35% in pairs with at least one years previous breeding experience. In European shags, two year old males (*i.e.* recruits) had a 75% divorce rate in contrast to males aged three or more (comprising mainly experienced birds), where the rate was only 28% (Aebischer 1985). A trend towards decreased rates of divorce in older birds has also been demonstrated in other seabirds, notably Yellow-eyed penguin (Richdale 1957), Red billed-gull (Mills 1973), Fulmar (Ollason & Dunnet 1978), Kittiwake (Coulson & Thomas 1983) and Short-tailed shearwater (Bradley *et al.* 1990).

Previous performance did not appear to influence divorce rates in Blue-eyed shags, although it was only possible to investigate this in relation to pairs which had previously bred successfully. In these pairs, recruits still experienced higher divorce rates than experienced birds, indicating that the amount of breeding experience was more important than performance. However, pairs which retained their mates from the previous year had significantly higher mean clutch and brood sizes and fledged more chicks. An appreciably higher proportion of pairs which only fledged one chick subsequently divorced, these effects being independent of breeding experience. Pair stability had no effect on overall success in the following year or on breeding performance indicated by clutch size, brood size and the number of chicks fledged. Shaw (1986) also found no effect of prior breeding success on mate change, although a slightly higher proportion of failed breeders changed mates. Mate change did not affect the mean clutch size, brood size or the number of chicks fledged in the following season either. Breeding success in the previous year was not related to mate fidelity in the Flightless cormorant (Harris 1979) or in the European shag although in the latter there appeared to be a link between mate change and subsequent reproductive success (Aebischer 1985).

In several other seabirds, breeding success and mate fidelity are positively correlated with breeding experience. In the Kittiwake the duration of the pair bond increases the chance of subsequent mate retention. Additionally, there is a decrease in the rate of divorce with the accumulation of breeding experience occurring independently of pair status (Coulson & Thomas 1983). Mate retention has a marked effect on reproductive success in the Kittiwake, resulting in 12% more chicks *per* pair being fledged in pairs which stay together. Short-tailed shearwaters showed an increased breeding success with consecutive pair bonds as well as with increasing duration of each pair bond, indicating that both individual breeding experience and experience of breeding with a particular mate influenced successful reproduction (Bradley *et al.* 1990).

Mate fidelity may arise through strong nest site tenacity rather than mate choice, as shown in Leach's storm petrel (Morse & Kress 1984), although in Fulmars and Gannets high rates of both mate and nest site fidelity prevented a satisfactory resolution (Macdonald 1977, Ollason & Dunnet 1978, Nelson 1978). Aebischer (1985) found that female European shags were choosing the mate preferentially to nest site, and proposed that females returned initially to the nest site of the previous year and searched the adjacent area if her original partner was absent, her success depending on the distance moved by her mate (assuming both partners had survived). Not all individuals followed this pattern, since some females remated on the old nest site despite their original partner having returned to the colony. It was not possible to determine nest site fidelity with a high degree of accuracy in Blue-eyed shags during this study, but previous results indicated that 60% (n=146 birds) nested within 4 m of the previous year's nest site, nest site fidelity was similar between the sexes and a significantly higher proportion of females which change nest sites also changed mates (Shaw 1984). An appreciably higher proportion of males remaining at the previous site divorced, in contrast to those which changed site; in females a higher proportion of birds which changed site underwent divorce, although the differences were not significant for either sex.

Age correlations within pairs of breeding birds have been noted in several species including Kittiwake (Coulson 1966), Red-billed gull (Mills 1973), Arctic tern (Coulson & Horobin 1976), European shag (Aebischer 1985) and California gull (Pugesek & Diem 1986). If pair stability is high and rates of mortality low, and birds breeding for the first time tend to breed together, then similar aged pairs will perpetuate through mate retention. However, in some species pair stability is low, yet similar aged pairs still form. It has been suggested that in these species, similarities may arise as a result of temporal or spatial differences in relation to age. For example, in Kittiwakes pairing between birds of similar breeding experience arose because inexperienced birds most often paired together and an age-related time of return to the colony coupled with high mate fidelity ensured this persisted (Coulson 1966, Coulson & Thomas 1983). However in California gulls, whilst there is also an age-related return to the breeding grounds, considerable variation in reproductive events occurs suggesting an overlap between age groups to an extent incompatible with the observed high age correlation within pairs (Pugesek & Diem 1986).

In the absence of timing or spatial constraints on mate choice, birds may be selecting their partner on the basis of age or breeding experience. Shaw (1985b) suggested that this occurred in Blue-eyed shags because the observed distribution of age differences departed significantly from that expected if mating were random with respect to age. However, Reid (1988) has pointed out that the assumption that each bird is free to mate with every other bird is misleading since the degree of mate retention restricts the choice. In a simulation study, Reid (1988) found that substantially reduced age correlations were obtained even when the frequency of dissolved pairs was low, and concluded that for Blue-eyed shags the deviation between the observed and expected age correlation was so great that even assuming a total preference for experienced breeding birds could not explain the observed correlation. This suggested that mate choice was based on a finer definition of age than experienced or inexperienced birds. However, the demographic parameters used for Blue-eyed shags in Reid's study were incorrect, in particular the value of pair stability (22.7%) is a considerable underestimation since this is the total pair stability and not the stability of pairs where both members survived, which is Reid's definition of pair stability. Recalculation from Shaw (1985b) indicated that the value should be 42.5%. Additionally, the age of first breeding was assumed to be two years old and a constant survival rate with age was used, whereas in this study few birds bred before three, recruitment was spread over several years and there was evidence of a lower survival rate in older birds. In this study the simple approach used by Shaw (1985b) was followed, and a similar high age correlation within pairs was found, 70% of all pairs having an age difference of one year or less. This represented a significant departure from the expected distribution of age differences given random mating with respect to age. When pairs were divided according to breeding experience, the age correlation within pairs of experienced breeders did not suggest assortative mating in relation to age, whereas the age difference distribution within pairs where at least one member was a recruit continued to show preferential mating with similar aged birds despite an overall pair stability of only 59%.

Both nest size ratios and overall nest shape indicated that 2-5 year old Blue-eyed shags built flat platform-type nests which were less substantial than the taller, columnar-shaped nests of older birds. Older birds were also more likely to build on top of existing nests and thus acquire a large mud foundation to their nests. Nest quality was related to the number of chicks produced, platform nests (scores of 4-5) fledging 2-3 chicks less frequently than columnar nests (scores 1-2). This may reflect the influence of age on breeding success, and the sample sizes were insufficient to control for this effect. It seems unlikely that the influence of age on chick productivity would be independent of nest characteristics, and possibly the effect of age or breeding experience is at least partly mediated by nest quality, with younger birds building less substantial nests through inexperience or low breeding drive, which are less likely to fledge chicks. In the European shag, two year old males were associated with a higher proportion of poor quality nests (platform nests or strands of nest material) than older birds, and on average a higher number of chicks were produced from more substantial nests, even within an age category (Aebischer 1985). Potts (1966) found that the interval between the initiation of nest building and egg-laying decreased throughout the season and was therefore inversely correlated with age, since older birds were the earliest nesters. Some recruiting Blue-eyed shags began their breeding attempt later than experienced birds, and in these pairs males may not have sufficient time to collect enough material to build a more substantial nest.

The timing of laying was not significantly related to age, although in both years a higher proportion of younger birds began breeding later. Shaw (1986) also found no relationship between laying date and age, although in older females there was a suggesting of increased synchrony in laying date. Old European shags of both sexes laid earlier than younger birds on the Isle of May, and further analyses revealed that whilst in females age was the factor related to laying date, in males breeding experience was more important (Aebischer 1985). In Brandt's cormorant, the timing of arrival at the colony and laying is strongly age related, the youngest birds arriving and laying later (Boekelheide & Ainley 1989).

Age had no significant effect on clutch size in this study although younger birds of both sexes were associated with an appreciably higher proportion of clutches of two rather than three. When breeding experience was considered in both 1986 and 1987, recruits laid fewer eggs on average than experienced birds and laid proportionately more clutches of 1-2 eggs than clutches of 3. Since nests were not visited daily it is uncertain if these differences arose through clutch size or differential rates of egg loss between the categories. Shaw (1986) found that in one season clutch size increased with increasing age of the female up to 10 years, after which it declined, although there was no relationship in the other season. In the European shag, two studies have confirmed the absence of a link between female age and the clutch size (Potts *et al.* 1980, Aebischer 1985). However, female Brandt's cormorants aged 2 and 3 years laid smaller clutches than those older than 5 years, and there was a similar relationship between male age and clutch size (Boekelheide & Ainley 1989).

There were significant differences in the number of chicks fledged *per* pair at Shagnasty I/II in different years, although this may be partly due to variations in colony monitoring. However, appreciable yearly variation occurred between 1986 and 1987, both years of detailed monitoring and chick ringing. The number of chicks fledged was related to breeding experience, significantly fewer being fledged by recruits in 1987, than by experienced birds. In both years female recruits failed to fledge any chicks more often than experienced females.

The number of chicks fledged *per* pair in this study falls within the range given by Shaw (1984) of 0.55-1.88 chicks *per* pair, although in both studies the value is at the lower end of the range for King shags at Macquarie Island in 1975 of 1.7-2.3 chicks *per* pair (Brothers 1985). Shaw (1986) recorded an increase in the mean number of chicks fledged *per* pair in birds up to five years, but there was no effect beyond this age. In European shags, the number of chicks fledged by a pair is influenced by the timing of breeding as well as age, the latter being a less important cause of variation (Aebischer 1985). In Brandt's cormorant, the youngest birds fledge fewer chicks *per* pair but the breeding success of older birds did not vary with age.

7. GENERAL DISCUSSION.

7.1 Comparison of Blue-eyed shag population demography with other shag species.

When compared with pelagic seabirds, inshore feeding seabirds such as the Phalacrocoracidae have low annual adult survival rates, large clutch and brood sizes, fledge more than one chick at each breeding attempt and begin breeding at younger ages. These differences have been related to the greater food availability in inshore marine environments (Lack 1968).

Using breeding adult Blue-eyed shags first recaptured 6, 7 and 8 years prior to this study, the mean annual adult survival rate was 0.76. Up to about 11 years of age the annual survival rate was probably constant at 0.82, giving a mean expectation of further life of 5.1 years. In older birds the rate decreased by about 0.04 each year. The annual survival rate calculated between 1985 and 1987 indicates a higher value, of 0.86 (chapter 4), suggesting that the survival of adults was better during the study. There was no difference in survival rate between the sexes.

Shaw (1984) estimated the annual survival rate of breeders to be 0.87 between 1960-81, although he found lower rates during 1976-78 of 0.75, and also during the study period, of 0.77 in 1979-80 and 0.78 in 1980-81. Low return rates of breeding Blue-eyed shags have also been reported from the Cormorant Island colony on the Antarctic peninsula (Maxson & Bernstein (1980) in Bernstein (1982) and see below). In the King shag at Macquarie Island, the mean annual survival rate calculated over five seasons was 0.79 in females and 0.87 in males, although the samples used were small (range 12-29 birds at risk (Brothers 1985)). The mean annual survival rate of the European shag on the Farne Islands was 0.83 although this declined to 0.24-0.38 during 'red-tide' years (Potts *et al.* 1980). At the Isle of May the rate was 0.87 between 1972 and 1982 (Aebischer 1985). A reduction in survival rate of older birds was reported in both of these studies; at the Farnes it was only apparent during one season in birds of 8 years or more (Potts 1969), whereas on the Isle of May most individuals involved were over 18 years old (Aebischer 1985). There were no differences in survival rates between the sexes (Potts *et al.* 1980). Brandt's cormorants aged between 2 and 7 years showed a return rate to the colony of 0.82 in males and 0.79 in females (difference not significant) and a reduction in return rates in males and females older than 9 and 7 years respectively. It was not clear if this reduction was related to age rather than due to an El Niño event (Boekelheide & Ainley 1989). Flightless cormorants had an overall mean annual survival rate of 0.87, with a significant difference between the sexes, females 0.91 and males 0.82 (Harris 1979).

Adult Blue-eyed shags therefore had similar annual rates of survival to other species of shags and showed a similar range of annual variation, in contrast to the higher rates typical of many Procellariiform and other Pelecaniform seabirds such as Cape pigeon, 0.94-0.95 and Snow petrel, 0.93-0.96 (Hudson 1966), Fulmar, 0.97 (Dunnet & Ollason 1978), Gannet, 0.95 (Nelson 1978), Short-tailed shearwater, 0.93 (Bradley *et al.* 1989) and Wandering albatross, 0.94 (Croxall *et al.* 1990).

In contrast to adults, the survival rate of first year Blue-eyed shags of 0.36 ± 0.05 was low and highly variable, ranging from 0.03 in 1979, the year of particularly low fledging success, to 0.69 in 1984. Since first year survival rates include some nestling mortality, these may be reflecting variations in nestling mortality rather than differences in mortality during the rest of the first year. The rate reported in this study is appreciably lower than the overall rate of 0.58 ± 0.05 found by Shaw (1984), but the latter may be an overestimation because a smaller number of cohorts were available for analysis. During 1971-74 a lower survival rate of 0.13 was found (Shaw 1984). Brothers (1985) estimated the survival rate of birds between fledging and three years old to be in the range 0.273 to 0.367. Assuming an adult survival rate equal to 0.82 and effective after the first year, this indicates a first year survival rate of 0.41-0.55, which overlaps with the rate obtained in this study. First year survival rates of European shags have been estimated as 0.51 ± 0.12 (Potts *et al.* 1980) and 0.48 (Aebischer 1985).

During the Isle of May study, the first year survival rate varied between 0.11 and 0.75 and peak mortality occurred between January and April in most years. During the principal 'crash' years, first year survival rates fell to 0.12-0.14 although adult rates remained unaffected, and peak mortality occurred before November suggesting heavier losses immediately post-fledging compared to other years (Aebischer 1985).

In the Flightless cormorant, extensive non-breeding by adults, increased mortality of juveniles (and probably adults also) and reductions in breeding success and recruitment to the breeding population have been reported during years of abnormally low marine productivity due to El Niño southern oscillation events (Harris 1979, Valle & Coulter 1987). Harris (1979) suggested that the high rates of mate and nest site change between breeding attempts which occurred irrespective of previous breeding success, was an adaptation to the special conditions which Flightless cormorants experience in the Galapagos and allowed a rapid response to conditions which were favourable for reproduction. Boekelheide & Ainley (1989) have also suggested that a flexible breeding strategy characterises some shag species, and suggested that this has evolved as a response to a variable food supply. The characteristics they listed include a wide variation in the age of first breeding with the potential to breed at a young age, low mate fidelity and the ability to abandon or miss breeding attempts entirely. These features allow a rapid response to favourable conditions whilst maximising survival at the expense of breeding effort in years when the food supply was poor. Brandt's cormorant illustrates these adaptations since like the Flightless cormorant, it inhabits a highly productive inshore marine habitat which nevertheless is subject to periodic collapses in productivity resulting from El Niño events. Although capable of breeding at 2 years, the age of first breeding varied between 2 and 7. In years of high food availability 64% (n=11) of recruits were aged 2 compared with none in El Niño years when food availability was low. Mate fidelity between seasons was also low, allowing an individual to start breeding as soon as it returned to the colony without having to wait for its partner of the previous year. Given the low mate fidelity, the breeding experience of a bird was insignificant in determining subsequent breeding success after the first attempt. During years of low food availability a lower proportion of the colony attempted to breed compared with ‘good’ years. This was partly because the youngest breeders only attempted breeding in ’good’ years when food was abundant.

Blue-eyed shags showed most of these characteristics. The age of first breeding varied between 2 and 6 years, and the proportion of birds first recorded breeding at each age differed between years (chapter 5). This contrasts with the European shag in which birds were always recorded first breeding when 2 or 3 years (Potts 1966). Mate fidelity of Blue-eyed shags was low and was unaffected by previous breeding success, although breeding performance was related to previous breeding experience, with older birds fledging significantly more chicks *per* pair. There was no evidence of intermittent breeding or abandonment of the breeding attempt at Signy during this study, but occupied shag colonies with no eggs or chicks during the summer have been noted at Cockburn Island, James Ross Island (I. Hawes and K. Richards personal communication; B.A.S. Annual Report 1988-89), and at Zavadovski Island, South Sandwich Islands (Cobley 1989). At the former locality, poor breeding success was also reported for Adelie penguins and Antarctic terns. Abandonment of an entire colony by King shags has been recorded at Macquarie Island (Brothers 1985). In the absence of annual ringing and recapture of adult shags on Signy, intermittent breeding would almost certainly be undetected especially if, as in Brandt’s cormorant, it only affected a proportion of the colony.

Low reproductive success in Blue-eyed shags was reported in 1974 and 1979 at Cormorant Island. In the latter year, low return rates of breeders (30% of 60 birds failed to return), failure of eggs to hatch, nest abandonment and low chick survival were observed and probably indicated food shortage (Parmelee *et al.* 1977 and Maxson & Bernstein 1980 both in Bernstein 1982). Low chick survival in 1976 compared with other years at subantarctic Marion Island was attributed to starvation, and may have been due to heavy seas preventing adults from foraging (Williams & Burger 1979). At Signy in 1979, only 47 chicks fledged from 385 nests at Shagnasty I/II and many chicks were found dead in the nest apparently having died from starvation (Shaw 1984). However the date of sea ice breakup was 17 September, a typical date (Rootes 1988a). Conversely, in the 1980-81 breeding season, ice conditions at Signy were unusually severe, the winter sea ice persisted until 18 December, and even after breaking up remained inshore for most of the summer causing high chick mortality among Adelie and Chinstrap penguins (Lishman 1985). Despite this, the reproductive performance of Blue-eyed shags was unaffected, an average of 1.5 chicks fledging *per* pair which compares favourably with values found during this study. The effect of inclement climatic and ice conditions also had little effect on shags at Antarctic peninsula colonies. During 1976-77, Blue-eyed shags bred normally despite heavy late summer storms, and in the following season ice remained frozen to the shore yet both penguins and shags bred normally (Parmelee *et al.* 1978). In 1981, following the latest recorded date of sea ice breakup (25 December) and one of the longest durations of sea ice at Signy, Blue-eyed shags had a high breeding success, 1.88 chicks fledged *per* pair and more pairs bred than in the previous two seasons. At Signy, the date on which the sea ice broke up explained only 24% of the variation in the start of egg laying in 15 years between 1958-88 ($\log_{10}$ transformation of ice breakup: $r= 0.486$ $df=13$ NS), although due to biases in assessing sea ice conditions (*e.g.* observations confined to one sheltered inlet, lack of information on the extent of offshore leads) it is probably misleading to dismiss the role of sea ice in determining shag breeding schedules without further evidence. During the 1981 and 1987 breeding seasons, egg laying started later and was more synchronous than in 1980 or 1986 (Shaw 1984, this study), and this coincided with the persistence of sea ice for longer than normal. In all four breeding seasons egg laying finished at the end of December, suggesting that whilst the termination of laying is fixed, its start is flexible and responsive to ice conditions or factors which correlate with ice conditions, such as food availability.

Clearly, an abnormal persistence of sea ice into the breeding season has less effect on shags than on penguins, and this probably reflects the relative difficulties of walking over loose blocks of ice packed together by wind compared with flying over it. The effects of early and late sea ice breakup on the breeding success of Adelie penguins in two consecutive seasons at an Antarctic mainland colony indicates that in years when the breakup occurred early more birds attempted to breed, the mean date of clutch completion was a week earlier, the breeding success was higher because proportionately more birds laid the maximum clutch (2 eggs) and fledging success was higher (Ainley & LeResche 1973). These authors stressed the critical role of windy weather, which caused the sea ice to break up, and suggested that early sea ice break up affected the body condition of Adelie penguins at the start of the breeding season by allowing a rapid return to the rookeries and reducing the distance birds had to travel to replenish fat reserves. Changes in the timing and synchrony of reproduction in response to climatic and biological factors have been noted in the Antarctic fur seal at South Georgia. In 1987, when the winter was colder and more prolonged than normal and the limit of the pack-ice extended unusually far north, the occupation of territories by bulls and the arrival of cows was later and more synchronous (Duck 1990). In two species of Australian cormorant, egg laying was synchronous within colonies despite fluctuations in the water levels of the lakes at which they bred. However, during unfavourable drought conditions Little Black cormorants did not lay eggs due to a shortage of inundated trees in which to nest, whereas Little Pied cormorants laid in every year, delayed the onset of laying in the drought year until suitable nesting trees became available, but in some years abruptly terminated the breeding attempt with widespread nest abandonment resulting in heavy losses of eggs and chicks (Miller 1980).

7.2 Population regulation.

Opinions about the population regulation of birds owe much to the work of Lack (1954, 1966) who argued that bird populations are regulated since whilst they vary about an equilibrium value, this is much less than the variation which is theoretically possible. Lack regarded regulation as a consequence of density-dependent mortality which arises from competition for food outside the breeding season. Wynne-Edwards

(1962) argued that density-dependent regulation resulted from social behaviour imposing restraint on the population size to avoid over-exploitation of resources, chiefly food. Since the latter argument may require group selection to explain why individuals conform, it is currently considered unlikely that self-regulation is responsible for controlling bird populations (*e.g.* Murton & Westwood 1977). In seabirds, Ashmole (1963) suggested that in stable populations of tropical oceanic seabirds, the numbers are regulated by a density-dependent reduction in productivity resulting from competition for food during the breeding season. He reasoned that since seabirds are widely dispersed outside the breeding season, their numbers are unlikely to be controlled by food supplies at this time, but when constrained to the same area by breeding requirements, competition for food resulted in reductions in breeding success and recruitment to the breeding population. Evidence for the factors involved in the regulation of seabird populations has been reviewed by Birkhead & Furness (1985), who found that limitations in the availability of colony sites and of high quality breeding sites within colonies were important in the local regulation of some species. In two cormorant species which inhabit rich marine upwelling areas, the Guanay cormorant of the Peruvian Humbolt current and the Cape cormorant of the Benguela current, the provision of additional safe breeding areas enabled substantial expansions of the population; in Guanay cormorants, Peruvian boobies and Peruvian brown pelicans the numbers increased from 2 million birds to 20 million birds (Duffy 1983a, Crawford & Shelton 1978). The negative relationships found between colony size and several breeding parameters indicated the importance of intraspecific competition during the breeding season (Birkhead & Furness 1985), and in Double-crested cormorants depletion of fish stocks around two colonies was reported by Birt *et al.* (1987).

Studies on the population dynamics of European shags in the North sea have identified several factors potentially involved in population regulation, although these populations have not yet reached stability. In common with Kittiwakes, Gannets, Fulmars and other seabirds in the North Atlantic, the numbers of European shags have been increasing throughout most of this century probably owing to the relaxation of human persecution (Cramp *et al.* 1974). At the Isle of May, a crash in the number of breeding pairs between 1974 and 1976 was apparently related to a marked reduction in prey availability. Although this was a potentially limiting factor, the shags continued to increase subsequently indicating that regulation had still not been achieved (Aebischer 1985). The crash was an anomaly which probably arose because of a temporary reduction in normally abundant food supplies, and resulted in non-breeding by up to 60% of adult shags. Those individuals which did attempt to breed delayed their timing of breeding, experienced lower breeding success and their chicks had poorer post-fledging survival (Aebischer 1985). In the Farne Islands population, density-dependent competition for high quality nest sites reduced the number of chicks which fledged. High adult mortality which resulted from the 1968 'red-tide' created a natural removal experiment in which young birds were shown to be capable of selecting the high quality nest sites but were normally prevented from doing so due to their prior occupation by older birds (Potts *et al.* 1980). This population had not reached equilibrium during this study (*i.e.* where the level of recruitment to the breeding population equals the adult mortality rate), and since there is net immigration this will be achieved at a much higher level than would otherwise have been the case. Immigrants also promoted a rapid recovery of the population following the 'red-tide' mortality and counteracted the shortfall in recruits from the Farnes during the low productivity of the 'red-tide' years (Potts *et al.* 1980).

Although there is insufficient information to determine reliably the factors regulating the Signy Blue-eyed shag population, because detailed monitoring has only occurred in a few years and no data exist on changes in food availability, some elements likely to be involved in population regulation can be assessed. Unlike European shag populations, there is no evidence that the population at Shagnasty has changed since 1960, suggesting that the numbers there are regulated. However, at North Point the colony has increased by an average of 1.3% (or one additional pair) each year since 1948 (Figure 2.4). Could this increase be met by North Point birds recruiting at their natal colony alone or is immigration necessary to sustain the increase? Table 7.1a

TABLE 7. 1 MODELS OF COLONY SIZE CHANGE AT NORTH POINT ASSUMING A) NO EMIGRATION OR IMMIGRATION AND B) NET IMMIGRATION FROM SHAGNASTY.

	A) North Point recruits alone:	B) North Point recruits and net immigration from Shagnasty:	
		Recruit at 3	Recruit at 4
Year	No. of[3] pairs	No. of pairs	No. of pairs
1949[1]	13	13	13
1950[2]	13	13	13
1955	12.3	24.8	21.8
1960	11.6	37.0	29.9
1965	10.8	55.9	36.6
1970	10.2	63.2	41.9
1975	9.5	71.5	46.1
1980	9.0	78.9	49.5
1985	8.4	84.9	52.3
1988	8.1	88.7	53.6

[1] 13 pairs were observed in 1949

[2] Colony not counted; estimated at 13 pairs

[3] Not rounded off

shows that using a simple model of population change in which the annual adult survival rate was 0.82 (see above) and was applied to birds older than one year, the first year survival rate was 0.36 (Table 4.13), the number of chicks fledged *per* pair was 1.35 (Table 6.38; weighted average for North Point between 1984-88) and all birds first bred at 3 years, the colony size decreased. It was assumed that no emigration or immigration was occurring and that all adults attempted to breed in every year. Starting with the observed 13 pairs in 1949 (Shaw 1984) and assuming that there were also 13 pairs in 1950 and 1951, when the colony was not counted, the breeding population was estimated to decline to about 8 pairs by 1988. If these calculations are repeated allowing the observed rates of emigration of North Point birds (7% of chicks emigrated each year and no experienced breeders moved; Tables 3.6 and 3.4) and the immigration of Shagnasty birds (2.4% of Shagnasty chicks which survived to recruitment and 0.14% of experienced breeders moved to North Point each year; Tables 3.6 and 3.4), the colony size increases. To calculate the number of immigrants, it was assumed that the Shagnasty population was stable and equal to 740 pairs, this being the average colony size of Shagnasty I/II between 1960-88 multiplied by 2, since the size of the Shagnasty III subcolony was assumed to be the same as Shagnasty I/II (this assumption appeared reasonable since between 1984-88 Shagnasty III was 80-90% the size of Shagnasty I/II). One further assumption was that the number of chicks *per* pair fledged at Shagnasty was 1.40, the unweighted average at Shagnasty I/II between 1984-88 (the weighted average differed by only 0.01, Table 6.38). If recruitment occurs at 3 years then each year 2.4% of $(740 \times 1.40 \times 0.36 \times 0.82^2)=6.0$ chicks from Shagnasty survive and recruit at North Point along with $740 \times 0.14\% = 2.07$ experienced breeders which also move, hence 8.09 immigrants from Shagnasty breed at North Point each year. Although 7% of North Point chicks move to Shagnasty, there is net immigration into North Point and the colony size increases to about 90 pairs by 1988 (Table 7.1b), a little above the observed maximum of 72 pairs in 1987. If recruitment is assumed to occur at 4 years then there are 7.0 immigrants from Shagnasty every year and the colony size at North Point still increases, although at a lower rate, reaching 54 pairs by 1988. In reality, recruitment occurred at both 3 and 4 years giving an estimated population size in between the two modelled values. These models give an oversimplified idea of colony change at North Point because they fail to incorporate variable first year mortality rates, chick productivity or a wider spread in age at first breeding. However they do suggest that the observed colony increase at North Point is unlikely to result solely from the recruitment of North Point birds, and that the observed level of immigration from Shagnasty is sufficient to explain the increase.

The availability of colony sites appears not to be a limiting factor since there are several islands similar to Shagnasty around the Signy coast and ice-free headlands occur both on Signy and on the adjacent coastline of Coronation Island. Despite this, no other shag colonies have been found in the vicinity and since frequent visits are made around Signy and to Coronation Island, it is unlikely that colonies would remain undetected. A shortage of breeding sites within the colonies also seems unlikely to govern population size since between 1984 and 1987 an additional 146 nests were built at Shagnasty I/II, bringing the 1987 total to 389 and the highest nest count, 469 nests in 1976 has not been equalled since. Interspecific competition for nesting areas with Royal and Rockhopper penguins has been suggested as a factor limiting colony expansion of King shags at Macquarie Island (Brothers 1985). At Signy Island there are Chinstrap penguin rookeries adjacent to both shag colonies and since they are able to compete successfully with similarly sized Adelie penguins for nest sites (Trivelpiece & Volkman 1979) it might be expected that they would have a regulatory effect on Blue-eyed shag colonies. However, at both Shagnasty and North Point the number of breeding Chinstrap penguins has declined between 1978 and 1987, by 624 and 2313 nests respectively (B.A.S. records), but this has not been paralleled by an overall increase in the number of Blue-eyed shags at Shagnasty or by an increase in the rate of colony growth at North Point. Furthermore, the boundaries of both Blue-eyed shag colonies have not changed since 1979 (P. Shaw personal communication). There was no indication that a shortage of high quality nest sites was an important factor in the Signy Blue-eyed shag population since nest site quality was unrelated to breeding success (Shaw 1986). This contrasts with European shag populations in which the quality of the nest site is the principal factor determining the number of chicks fledged by a pair and as the population size increases, the mean nest site quality declines and there is a shortage of high quality sites (Potts *et al.* 1980).

Other factors which have been implicated in the regulation of some seabird populations are human persecution and predation. Neither of these factors are likely to affect the Signy Blue-eyed shag population. Human interference, which has been held responsible for the past reductions of North Atlantic seabirds including European shags, Kittiwakes and Gannets (Potts 1969, Coulson in Cramp *et al.* 1974, Nelson 1978), has not occurred in the South Orkney Islands. Adult Blue-eyed shags appear to have no natural predators and although there are records of King shag remains from Leopard seal stomachs (Pitman 1957), this probably represents opportunism by a predator noted for a catholic diet. Recent stomach analyses involving larger samples of Leopard seals indicate that birds form only a quarter of the items in the diet, and mainly penguins are taken (Laws 1984). Predation on eggs and chicks has been observed at some colonies. At Macquarie Island, Brown skuas preyed upon chicks (Brothers 1985) and at the Crozet archipelago, Dominican gulls took 64% of all eggs which failed and equal importance was attributed to predation and food shortage in explaining chick mortality (Derenne *et al.* 1976). By contrast, at Marion Island starvation was the main cause of chick mortality and predation appeared to be unimportant (Williams & Burger 1979). Shaw (1984) noted predation of eggs by Brown skuas and Greater sheathbills at Signy but during this study the only loss of eggs in this way occurred when shags had been disturbed by observers. Kleptoparasitism of adult Blue-eyed shags around the colony by South Polar skuas was recorded at Antarctic peninsula colonies (Maxson & Bernstein 1982) but this did not occur at Signy, presumably because there are only 9 breeding pairs of South Polar skuas (Rootes 1988b).

SUMMARY

Methods.

1. Two colonies of Blue-eyed shags at Signy Island were studied between 1985 and 1987. These were situated at North Point (72 breeding pairs in 1987) and Shagnasty (729 breeding pairs in 1987). Counts of breeding birds have been made in most years since 1948 at North Point and since 1969 at Shagnasty. The size of the colony at North Point has increased from 9 pairs in 1948 to 72 pairs in 1987. There was no change in colony size at Shagnasty between 1960 and 1988.

2. The systematic relationships among Blue-eyed shags are poorly understood. Formerly two species were recognised, the King shag *Phalacrocorax albiventer* and the Blue-eyed shag *P. atriceps*, each with several allopatric island races. These 'species' freely interbreed in a area of sympatry in South America, and most workers now accept one species, the Blue-eyed shag *P. atriceps* although the systematic position of the island forms is not clear.

3. Blue-eyed shags can be readily sexed by voice, behavioural differences such as advertisement display and nest material gathering (both of which are performed only by males), bill depth and the synchronous sex-linked pattern of colony attendance during the breeding season until the chicks are well grown. This pattern results in males being present almost exclusively during the morning whereas during the afternoon females predominate.

4. Birds could be aged until they were two years old on plumage characters, specifically the pattern of retained brown juvenile feathers. A few three year old birds could be aged although this was unreliable for certain individuals. Beyond three years old, birds of different ages were indistinguishable.

5. Annual ringing of Blue-eyed shag chicks has occurred at Signy Island in each year since 1968 except in 1982. Up to 1988, 9927 chicks have been ringed. No illegible rings have been detected and only three rings were known to have been lost.

Although several rings were observed to be opening up during the study period, these were mostly put on between 1976-78. It is suggested that this phenomenon is confined to these years, perhaps as a result of incorrect fitting or inadequate rings. Since 1978 there has been an increase in the number of chicks ringed but only 7 rings were found to be opening during the study period. Ring loss was only likely to have affected 0.5% of the 809 ringed birds recaptured during this study.

6. Each nest was tagged for identification. Using a sample of birds identified during the pre-breeding period and the pattern of nest failure both in a sample of the first tagged nests and overall, it was unlikely that more than 22 pairs had failed before the nests were tagged in either 1986 or 1987. Few empty nests or gaps between nests were found supporting this conclusion. The number of occupied sites on photographs of both colonies taken in October tallied with the number of nests subsequently tagged, omitting nests which were started during tagging. The latter were likely to belong to recruiting birds which were absent from the colonies earlier in the season when the photographs were taken. The number of tagged nests in 1986 and 1987 was likely to be an accurate indication of the number of breeding pairs. There were no records of polygyny or multiple broods.

7. The recapture efficiency of the breeding population was more than 90% except in 1985 at Shagnasty I/II when it was 82%. Males were less likely to be recaptured than females but this was due to the timing of recapture efforts during the day rather than behavioural differences.

Emigration, Immigration and Intermittent breeding.

8. Apart from Signy Island, seven other Blue-eyed shag colonies are currently known in the South Orkney Islands. During this study it was only possible to visit the two closest, Atriceps and Grey Islands. At both these colonies about 20% of the estimated breeding population was examined and no ringed birds were seen. Previously, a ringed bird from Signy Island was sighted during the winter at Atriceps Island.

9. The immigration of shags to Signy Island was assessed by investigating changes in the proportion of unringed breeders. After allowing for the survival of unringed Signy Island breeders from the previous year and the number of unringed Signy Island recruits, the number of unringed birds remaining which may have been immigrants was small, at maximum 5% of the breeding population in 1987.

10. During this study the annual rate of colony exchange of experienced breeding birds between North Point and Shagnasty was 0.1%. Between the Shagnasty subcolonies, 100 m apart, it was 1%. Considering movements during the period 1979-1987, there was no clumping of movement in any year. Similar numbers of males and females moved.

11. Overall, 25% of birds bred away from the natal colony, most of the movement being between the Shagnasty subcolonies. Considering movement between Shagnasty and North Point, 2.4% (n=807 chicks) bred away from the natal colony. A significantly higher proportion of North Point chicks moved to Shagnasty than in the opposite direction. Similar proportions of chicks moved between each Shagnasty subcolony, overall 26% hatched at one subcolony moved to the other.

12. Philopatry was not related to the year of ringing, the number of breeding pairs in the year of hatching or the number of chicks fledging in the year of hatching. There was a weak correlation between philopatry and the size of the breeding population at the time of recruitment. The sex of a bird did not influence its philopatry. When siblings bred away from the natal colony there was a suggestion that both birds moved. The order of hatching was unrelated to philopatry. Philopatry was related to subsequent colony fidelity, birds which bred away from the natal colony being more likely to change colony subsequently.

13. The number of birds not recaptured breeding each year between 1985-87 was similar to the number expected according to the recapture efficiency. This suggested that these birds had attempted to breed but were not recaptured.

Survival rates in relation to age, sex and other factors.

14. The mean annual survival rate of breeding birds captured between 1979-81 and recaptured in 1987 was 0.762. There was a trend of increasing mean annual survival rate from 0.73 between 1979 and 1987, and 0.83 between 1981 and 1987. This was independent of breeding experience. The lower rates may reflect lower survival in certain years, be due to a higher proportion of older birds (which experienced a decreased survival rate) or may be a combination of both factors.

15. The mean annual survival rate between 1984 and 1987, based on the proportion of breeding birds recaptured in successive years, was 0.864. There were no differences in survival rates between colonies or between males and females.

16. Older birds showed a decrease in the mean annual survival rate. This is effective after about 11 years old. Age specific survival rates were calculated assuming a constant rate up to 10 years. This indicated that the constant survival rate was 0.843 which declined on average by 0.04 annually after 11 years.

17. There was no difference in the annual survival rates of recruits and experienced breeding birds between 1986 and 1987, although between 1987 and 1988 recruits survived significantly less well. This was probably due to a reduced probability of recapture for young birds breeding in 1988.

18. Mark-recapture estimates of annual survival rates between 1979 and 1987 indicated that survival rates were low during 1979-80 and between 1984-85, but were high in 1981-82 and 1985-86.

19. First year survival rates were highly variable and ranged between 0.03 and 0.69. The overall mean survival rate for birds in their first year from cohorts between 1969 and 1984, was 0.355 (weighted according to sample size). The low survival estimate in 1979 is likely to include a substantial component of nestling mortality, about 56%. In 1980 and 1981, 22% and 8% of the total number of chicks ringed were found dead before fledging, and therefore 'first year survival rate' may include

a variable amount of nestling mortality and should be regarded as a minimum estimate. Years of low survival rate occurred approximately every 4 years. First year survival rates were not associated with philopatry or the frequency of birds recaptured with opening rings.

20. First year survival rates were considered in relation to windspeed, temperature, number of hours of bright sunshine, barometric pressure and ice variables using stepwise linear regression methods. Only mean monthly temperature in April and the duration of sea ice were selected. These two factors together accounted for two-thirds of the variation in first year survival rates.

21. The order of hatching did not affect post-fledging survival rates although few 'C' chicks (last hatched) survived to fledge.

Recruitment to the breeding population.

22. The minimum age at first breeding was 2 years and a few birds were still recruiting when aged 6 years. In any of the three study years a minimum of 74% of birds first bred when aged between 3-5 years.

23. There were significant differences in the age at first breeding in different years, the modal age being 4 years in 1985, 5 years in 1986 and 3 years in 1987. In 1986, most recruits were older than 4 years, whereas in 1987 most were 3 years or younger.

24. The mean age at recruitment was 3.82 years in males and 3.61 years in females, a significant difference. In 1986 and 1987 the mean age of recruiting males was significantly higher than for females, but there was no difference between the sexes in 1985. However, in 1986 and 1987 the difference depended upon a small percentage of recruits at the extremes of the age range; excluding these individuals indicated that there was no difference in the age at recruitment of males or females in either year.

25. The age of the parents did not influence the age at recruitment of the 1981 cohort, nor was the recruitment age of these birds affected by the clutch size from which

they hatched, the brood size whilst they were nestlings, the number of chicks which fledged from their nest or the mate fidelity of their parents. The hatching order of birds in 1980 did not affect their age of recruitment, considering those which recruited at 5 and 6 years.

26. The survival rate in the year following recruitment was similar for birds which first bred when aged 4 or 5 years in the 1981 cohort.

27. Proportionately more 3 year old birds recruited from the 1984 cohort than from either the 1981 or 1983 cohorts, and more birds aged 4 years came from the 1981 cohort.

28. Except for birds hatched in 1983, there was no difference with respect to sex in the proportion of birds recruiting at each age within a cohort. In 1983, only 21 birds survived to recruitment, and proportionately more females bred when aged 3 years.

29. The proportion of each cohort which survived and recruited varied between 46% in the 1984 cohort and only 9% in the 1983 cohort. There were significant differences between cohorts, even after excluding birds hatched in 1983, which had the lowest proportion of recruits.

30. A higher proportion of birds recruited at Shagnasty III than at Shagnasty I/II in each year between 1984 and 1988. In 1986 and 1987, 38% and 35% of breeding birds at Shagnasty III were recruits, significantly more than at either North Point or Shagnasty I/II. The attractiveness of Shagnasty III to recruits may be related to the ease with which they could obtain nest sites in the colony.

31. There was no significant relationship between the number of birds recruiting and the size of the breeding population in the same year or in the previous year, suggesting that the number of recruits was not regulated in a density-dependent manner through nest site availability.

32. At all colonies, 74% of 43 visits made to the colonies by 37 birds prior to re-

cruitment (pre-breeding birds) were to the colony or subcolony at which they eventually recruited. Ignoring natal colony, 64% of birds which recruited to Shagnasty III were seen at other colonies before recruitment compared with only 14% of those which recruited to Shagnasty I/II. However, when the effort put into re-sighting pre-breeding birds at the different colonies was allowed for, birds breeding at Shagnasty III were no more likely to have been seen at other colonies prior to recruitment than expected. Most visits by pre-breeders were to the natal colony and only three visits away from the natal colony relate to sightings between North Point and Shagnasty.

33. The number of pre-breeding birds visiting the colonies increased with age, and 3 year old birds which bred at 4 years, made slightly more visits *per* bird than younger birds (not significant). Considering the resighting histories of 8 individuals which were seen on more than 2 occasions, the number of visits *per* bird increased appreciably from 1.3 in 1 year olds to 3.6 in 3 year olds.

34. Between 1 and 3 years of age, pre-breeding birds visited the colonies significantly earlier in the season, 8% and 6% of 1 and 2 year olds being seen before November compared with 40% and 32% of 2 and 3 years olds. An appreciably higher proportion of visits made during August-October were by birds which attempted to recruit in that season compared with birds in the year prior to recruitment.

35. The timing of colony visits was unlikely to merely be reflecting the effort put into resighting pre-breeders since this was similar throughout the season, particularly in 1986 and 1987 when attempts were made to locate pre-breeding birds on every occasion between August and February.

36. Both Shagnasty and North Point shags used most of the Signy coastline and were also known to use fishing areas on the Coronation Island coast up to 11 km away from Signy Island. The 11 km boundary represents the limits of access from Signy Island and it is likely that the shags travel further to other fishing areas currently unknown.

Pair stability, age differences within pairs and breeding performance.

37. Out of 351 pairs, 39% retained the same mate in the following year, and of those which changed mates 46% divorced. Overall, the mean annual divorce rate between 1984 and 1988 was 42% and did not differ significantly between years.

38. Annual divorce rate decreased significantly with age, being 53% in 2-5 year old males but only 32% in 9 year olds. In females, the rate changed from 65% in 2-5 year olds to 34% in 10-17 year olds. There were no differences in divorce rate between the sexes in each age group. With respect to breeding experience, recruits had a 55% divorce rate compared with that of 35% in experienced breeders.

39. In similar aged birds with different levels of breeding experience divorce was related to experience. Recruits had higher rates than more experienced individuals, although this effect was not detected in birds aged 2-4 years, probably owing to the low sample size of experienced breeders.

40. In pairs which bred successfully in the previous year, recruits divorced more often (76%) than experienced birds (31%) in the current year. Insufficient numbers of failed breeders were observed to analyse divorce rates in relation to failure.

41. Excluding recruits, the proportion of pairs which divorced was not related to clutch size, brood size or the number of chicks fledged *per* pair during the previous year. However, pairs which divorced did have significantly lower mean clutch and brood sizes and fledged fewer chicks on average than those which retained their mates.

42. Pair stability in the previous year had no effect on overall breeding success or clutch size, brood size or the number of chicks fledged during the current year.

43. Sixty-three percent of pairs which divorced in the previous year, divorced again in the current year compared with 28% which remained together in the previous year.

44. Both sexes had significantly more partners than expected from mortality rates

alone.

45. At Shagnasty I/II, 98% of males and 92% of females renested within 12 m of the previous years nest. Females were significantly more likely to move than males.

46. Re-use of the same nest was low, as indicated by 21 nests in 1987 where the tag from the previous year was intact allowing identification of the pair in both years. From these nests, 14 of the previous years occupants were still alive in 1987 and only one individual (male) re-used the old nest.

47. There was a high correlation in the ages of 230 pairs, 46% being of equal age and 70% having mates of the same age or up to one year different. On average, females were 0.2 years younger than their partners. Almost twice as many equal aged pairs arose than expected if mating was random with respect to age.

48. The proportion of equal aged pairs fell from 78% among pairs in which males were 3 years, to 32% in pairs with 6 year old males, and from 64% in pairs with females aged 3 to 47% in those with 6 year old females. Only 36% and 31% of 2 year old males and females formed equal aged pairs. This was probably because only a few individuals began breeding at this age. The proportion of pairs in which the age difference was one year was highest in birds aged between 2 and 4 years.

49. There was no significant difference in the proportion of younger, equal aged or older partners within each age class with respect to sex.

50. Among experienced breeders, there was no significant difference between the observed age distribution within pairs and that expected if pairing was random with respect to age. However, among pairs where at least one partner was a recruit, nearly twice as many equal aged pairs formed compared with the number expected on the basis of random mating with regard to age. Pairs which changed mates had an age difference distribution which did not differ significantly from random.

51. The observed patterns of age differences within pairs is consistent with recruits pairing together, but then subsequent matings being random with respect to age.

Given the high rate of mate change, this results in a reduction in the number of equal aged pairs after the year of recruitment. A temporal separation of pairing according to breeding experience may be responsible for the pattern of age difference distribution within pairs.

52. The number of experienced birds whose mates were replaced by recruits was similar to the expected mortality rate of their mates. This was consistent with recruits only being able to pair with a few more experienced birds later in the season after their mates had died.

53. Male age was significantly related to nest size ratio and nest shape scores, those aged 3-5 years having significantly higher ratios and scores (indicating low platform-type nests) than older birds. Female age was unrelated to nest size ratio or nest shape score. The mean age of males which built nests on top of the previous years nest was significantly greater than the mean age of all males in the sample of nests measured (n=133).

54. There were significant differences in the pattern of egg laying in 1986 and 1987. In the latter year laying was more synchronous and started later. No replacement clutches were laid following egg loss, and calculations based upon the timing of replacement eggs in European shags indicated that there was unlikely to be sufficient time available in a breeding season for Blue-eyed shags to lay replacement clutches.

55. No significant relationship in the timing of laying with age was present, although appreciably more birds aged 2-5 years laid later than older birds. This effect was more marked in relation to male age than female age.

56. Mean clutch size was significantly different at different colonies in both years, but this probably reflected variation in the frequency of colony visits by observers. This was particularly so at Shagnasty III in 1986 and at North Point in 1987, the less frequent visits coinciding with lower mean clutch sizes being recorded.

57. At Shagnasty I/II there was a significantly higher proportion of 1 and 2 egg clutches in 1987 compared with 1986. The situation was similar at North Point although the differences were not statistically significant. By contrast, at Shagnasty III there were proportionately more 1 and 2 egg clutches in 1986 than in 1987. There was insufficient evidence to decide if this difference arose due to differential recording of incomplete clutches or greater egg loss.

58. Mean clutch size was not significantly related to female age, although with only one exception (11-18 years olds in 1987) older females laid larger clutches. With respect to breeding experience, female recruits in 1986 laid significantly smaller clutches on average than experienced females (2.61 compared with 2.88 eggs). In 1987, both recruits and experienced females had similar mean clutch sizes which were as low as the mean clutch size of recruits in 1986. Thirty-five percent of clutches of female recruits were of 1 and 2 eggs compared to only 12% of those of experienced females. Male breeding experience was associated with mean clutch size, significantly in 1987.

59. In pairs where at least one partner was an experienced breeder, the mean number of chicks hatched in 1986 from clutches of 3 (2.26 chicks) was higher than the number hatched from 2 egg clutches (1.69 chicks). In 1987, experienced pairs hatched more chicks on average from clutches of 3 than from clutches of 2, but the mean brood size did not differ between 2 or 3 egg clutches.

60. In 1986, pairs with 2 and 3 chick broods fledged similar numbers of chicks, but in 1987 pairs with broods of 2 fledged 1.9 chicks compared to 2.6 chicks fledged by pairs with 3 chick broods.

61. Breeding experience did not affect the number of chicks fledged in 1986 from 2 chick broods, but in 1987 experienced pairs with broods of 2 fledged significantly more chicks.

62. Among successful pairs, the number of chicks fledged was not related to the breed-

ing experience of either sex in 1986, but in 1987 recruits of both sexes fledged fewer chicks.

63. A higher proportion of female recruits failed to fledge any chicks compared with experienced breeders. Fledging success was unrelated to male breeding experience. A higher proportion of experienced breeders of both sexes failed to fledge any chicks in 1986 than in 1987.

64. Recruits experienced a lower breeding success (the proportion of eggs which produced fledged young) than experienced birds in both years, but this was only significant in 1987.

65. Regardless of breeding experience, pairs had a higher breeding success in 1987, fledging about 1.5 times more chicks *per* egg than in 1986.

66. Nests with low nest size ratios and scores (tall column-type nests) were associated with higher chick productivity, although since nest size and shape was also related to male age, it was not possible to distinguish between these effects. It was considered likely, that part of the variation in chick productivity with breeding experience results from the construction of poorer quality nests by younger (inexperienced) birds.

67. The mean number of chicks fledged *per* pair at Shagnasty I/II between 1984-88 varied significantly, being 1.67 in 1987 and only 1.04 in 1985. Using a sample of pairs monitored in more detail at Shagnasty I/II in 1986 and 1987, the mean number of chicks fledged *per* pair was estimated to be 1.39 and 1.70 respectively. Mean clutch sizes and brood sizes were larger in 1986 but more chicks were fledged by pairs in 1987, suggesting that chick mortality was higher during 1986.

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APPENDIX 1a CALCULATION OF THE CORRECTION FACTOR FOR ESTIMATION OF TOTAL ANNUAL SURVIVAL RATE.

	1985		1986		1987	
	NP	SNI/II	NP	SNI/II	NP and SNI/II	SNIII
1. Number of birds not recaptured:	5	124	8	4	15	56
2. Proportion of ringed birds in recaptured segment:	0.737	0.495	0.673	0.475	0.561	0.397
3. Estimated No. of ringed birds unrecaptured:	3.69	61.38	5.38	1.9	8.42	22.23
4. Proportion of ringed birds from initial sample recaptured among all ringed birds recaptured:	0.67	0.48	0.82	0.73	0.64	0.50
5. Estimated No. of birds from initial sample not recaptured in following year:	2.47	29.46	4.41	1.39	5.39	11.11
6. Estimated No. of initial sample among those ringed and not identified:	2.01	8.64	3.28	2.19	7.68	None identified
7. Estimated No. of sample missed due to movement between SN subcolonies (1985,86 only):	-	1.49	-	1.86	-	
8. Rounded correction:	4	40	8	5	13	11
9. Estimated number alive:	**49**	**167**	**61**	**237**	**329**	**133**

APPENDIX 1b CALCULATION OF THE CORRECTION FACTOR FOR ESTIMATION OF MALE ANNUAL SURVIVAL RATE.

	1985		1986		1987	
	NP	SNI/II	NP	SNI/II	NP and SNI/II	SNIII
1. Number of birds not recaptured:	3	92	5	2	8	48
2. Proportion of ringed birds in recaptured segment:	0.733	0.553	0.625	0.496	0.587	0.418
3. Estimated No. of ringed birds unrecaptured:	2.20	50.88	3.13	0.99	4.70	20.06
4. Proportion of ringed birds from initial sample recaptured among all ringed birds recaptured:	0.71	0.488	0.92	0.70	0.63	0.53
5. Estimated No. of birds from initial sample not recaptured in following year:	1.56	24.83	2.88	0.69	2.96	10.63
6. Estimated No. of initial sample among those ringed and not identified:	1.42	5.89	3.68	2.10	4.41	None identified
7. Estimated No. of sample missed due to movement between SN subcolonies (1985,86 only):	-	0.81	-	0.90	-	-
8. Rounded correction:	3	32	7	4	7	11
9. Estimated number alive (by year):	**120**		**149**		**245**	

APPENDIX 1c CALCULATION OF THE CORRECTION FACTOR FOR ESTIMATION OF FEMALE ANNUAL SURVIVAL RATE.

	1985		1986		1987	
	NP	SNI/II	NP	SNI/II	NP and SNI/II	SNIII
1. Number of birds not recaptured:	0	30	3	2	7	8
2. Proportion of ringed birds in recaptured segment:	-	0.451	0.720	0.454	0.540	0.380
3. Estimated No. of ringed birds unrecaptured:	-	13.53	2.16	0.91	3.78	3.04
4. Proportion of ringed birds from initial sample recaptured among all ringed birds recaptured:	0.66	0.46	0.78	0.77	0.66	0.48
5. Estimated No. of birds from initial sample not recaptured in following year:	0	6.22	1.69	0.70	2.49	1.46
6. Estimated No. of initial sample among those ringed and not identified:	0.66	2.76	0	0	3.30	0
7. Estimated No. of sample missed due to movement between SN subcolonies (1985,86 only):	-	0.62	-	0.96	-	-
8. Rounded correction:	1	10	2	2	6	1
9. Estimated number alive (by year):	**98**		**150**		**224**	

APPENDIX 2 CALCULATION OF STANDARD ERRORS.

1. Mean annual survival rate.

$$SE = 1/k.1/p^{(k-1/k)}.\sqrt{(p.q)/n}$$

where

k = interval between capture and recapture
p = proportion of birds recaptured
q = (1-p) (proportion not recaptured)
n = number at risk.

2. First year survival rate

$$SE = R.1/S_A^{(k-1)}.\sqrt{(p.q)/n}$$

where:

R = recapture efficiency (assumed to be 100% in 1987)
S_A = adult annual survival rate. Assumed to be 0.843 up to 11 years and then to decrease by 0.04 annually.
k = interval between ringing and recapture
p = proportion of birds recaptured
q = (1-p)
n = cohort size at fledging

APPENDIX 3

A) 1984 RECAPTURE DATA

	Ringed	Unringed	Ringed not identified	Not recaptured
North Point	58	15	1	4
Shagnasty I/II	213	259	7	7
Shagnasty III	82	298	0	16

Source: Price (1984)

B) CALCULATION OF CORRECTIONS TO NO. OF RECRUITS SEEN IN 1984

	Shagnasty I/II	Shagnasty III	North Point
No. not recaptured:	7	16	4
Propn. ringed:	0.45	0.22	0.79
Estim. no. ringed and not recap:	3.16	3.45	3.18
3 years	0.0047	0.049	0.052
Estim. no. not recaptured:	0.01	0.17	0.16
Estim. no not identified:	0.03	0	0.052
Correction:	None	None	None
Total	**1**	**4**	**3**
4 years	0.042	0.012	0.069
Estim. no. not recaptured:	0.13	0.04	0.22
Estim. no. not identified:	0.29	0	0.009
Correction:	None	None	None
Total	**9**	**1**	**4**

APPENDIX 3a

A) 1988 RECAPTURE DATA

	Ringed	Unringed	Ringed not identified	Not recaptured
North Point[1]	-	-	-	-
Shagnasty I/II	331	312	9	2
Shagnasty III	163	300	11	116

Source: Ashford (1988)

[1] It is not possible to ascertain the number of breeding birds at North Point in different categories from the available information. As the author of the report indicated that most of the breeding birds were likely to have been recaptured, it has been assumed that the recapture efficiency at North Point was 100%.

B) CALCULATION OF CORRECTIONS TO NO. OF RECRUITS SEEN IN 1988

	Shagnasty I/II	Shagnasty III	North Point
No. not recaptured:	2	116	-
Propn. ringed:	0.51	0.35	-
Estim. no. ringed and not recap:	1.03	40.6	-
2 years	0.006	0.01	-
Estim. no. not recaptured:	0.006	0.406	-
Estim. no not identified:	0.054	0.11	-
Correction:	None	0.52	-
Total	**2**	**3**	**23**
3 years	0.094	0.092	-
Estim. no. not recaptured:	0.097	3.73	-
Estim. no. not identified:	0.873	1.01	-
Correction:	0.97	4.74	-
Total	**32**	**20**	**31**

APPENDIX 4 SCIENTIFIC NAMES OF SPECIES MENTIONED IN THE TEXT.

Albatross, Black-browed	*Diomedea melanophris* Temminck
Albatross, Buller's	*Diomedea bulleri* Rothschild
Albatross, Grey-headed	*Diomedea chrysostoma* Forster
Albatross, Laysan	*Diomedea immutabilis* Rothschild
Albatross, Wandering	*Diomedea exulans* Linnaeus
Albatross, Yellow-nosed	*Diomedea chlororhynchos* (Brandt)
Black-capped chickadee	*Parus atricapillus* Linnaeus
Booby, Peruvian	*Sula variegata* (Tschudi)
Cape pigeon	*Daption capense* (Linnaeus)
Cormorant, Brandt's	*Phalacrocorax pencillatus* (Brandt)
Cormorant, Cape	*Phalacrocorax capensis* (Sparrman)
Cormorant, Double-crested	*Phalacrocorax auritus* (Lesson)
Cormorant, Flightless	*Nannopterum harrisi* (Rothschild)
Cormorant, Guanay	*Phalacrocorax bougainvillii* (Lesson)
Cormorant, Little Black	*Phalacrocorax sulcirostris* (Brandt)
Cormorant, Little Pied	*Phalacrocorax melanoleucos* (Vieillot)
Cormorant, Olivaceous	*Phalacrocorax olivaceous* (Humboldt)
Eider	*Somateria mollissima* (Linnaeus)
Fulmar	*Fulmarus glacialis* (Linnaeus)
Gannet	*Sula bassana* (Linnaeus)
Goldeneye	*Bucephala clangula* (Linnaeus)
Goose, Snow	*Anser caerulescens* (Linnaeus)
Gull, California	*Larus californicus* Lawrence
Gull, Dominican	*Larus dominicanus* Litchenstein
Gull, Herring	*Larus argentatus* Pontoppidan
Gull, Red-billed	*Larus novaehollandiae scopulinus* Forster

Guillemot, Brünnich's	*Uria lomvia* (Linnaeus)
Heron, Little Blue	*Egretta caerulea* (Linnaeus)
Kittiwake	*Rissa tridactyla* (Linnaeus)
Krill	*Euphausia superba* Dana
Pelican, Brown	*Pelecanus occidentalis* Linnaeus
Penguin, Adelie	*Pygoscelis adeliae* (Hombron & Jacquinot)
Penguin, Chinstrap	*Pygoscelis antarctica* Forster
Penguin, Gentoo	*Pygoscelis papua* Forster
Penguin, King	*Aptenodytes patagonica* Miller
Penguin, Macaroni	*Eudyptes chrysolophus* (Brandt)
Penguin, Rockhopper	*Eudyptes crestatus* (Miller)
Penguin, Royal	*Eudyptes schlegeli* Finsch
Penguin, Yellow-eyed	*Megadyptes antipodes* (Hombron & Jacquinot)
Peruvian anchovy	*Engraulis ringens* Jenyns
Petrel, Common diving	*Pelecanoides urinatrix exul* Salvin
Petrel, Leach's	*Oceanodroma leucorhoa* (Vieillot)
Petrel, Snow	*Pagodroma nivea* (Forster)
Petrel, Southern giant	*Macronectes giganteus* (Gmelin)
Petrel, Wilson's	*Oceanites oceanicus* (Kuhl)
Puffin	*Fratercula arctica* (Linnaeus)
Razorbill	*Alca torda* Linnaeus
Seal, Antarctic Fur	*Arctocephalus gazella*
Seal, Leopard	*Hydrurga leptonyx* (Blainville)
Shag, Blue-eyed	*Phalacrocorax atriceps* King
Shag, European	*Phalacrocorax aristotelis* (Linnaeus)
Sheathbill, Greater	*Chionis alba* (Gmelin)
Shearwater, Manx	*Puffinus puffinus* (Brünnich)
Shearwater, Short-tailed	*Puffinus tenuirostris* (Temminck)

Skua, Brown	*Catharacta lönnbergi* Mathews
Skua, South Polar	*Catharacta maccormicki* (Saunders)
Tern, Arctic	*Sterna paradisaea* Pontoppidan
Tern, Caspian	*Sterna caspia* Pallas
Tern, Royal	*Sterna maxima* Boddaert
Tern, Sandwich	*Sterna sandvicensis* (Latham)
Tern, Sooty	*Sterna fuscata* Linnaeus