Factors affecting the breeding performance of the Antarctic blue-eyed shag (Phalacrocorax atriceps bransfieldensis)

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ABSTRACT

Blue-eyed Shag nestlings at two colonies on Signy Island, South Orkney Islands, have been ringed annually since 1960. By 1979 27 % of the adult population had been ringed, and were of known-age.

More males than females return to the colony and breed for the first time at ages 3-4 years, and most often obtain a mate of the same age, or of one year older than themselves. Age similarities within pairs persist in older age-groups, even amongst changed pairs. In most cases the new mate is one year older than the mate of the previous season.

Pair stability between successive seasons is low, and does not affect, nor is effected by, breeding success. Five nest-site characteristics were found to have no effect on breeding performance. Older males obtain nest-sites which afford a high degree of social contact with their neighbours, usually in the centre and intermediate areas of the colony.

Egg laying is more synchronous than in other shag species, and there is no relationship between female age and laying date. Late clutches are usually smaller and yield fewer fledged young than early and mid-season clutches. The number of chicks hatched and fledged increases up to the age of 5 years, and declined after 10-11 years of age.

Clutch size and nestling survival fluctuate markedly from season to season. In clutches of three, third eggs are smaller, yield lighter chicks and usually hatch within 2-4 days of their siblings. Hatching asynchrony (rather than egg-size differences) promotes chick weight differences, and the early death of third chicks. The daily food consumption of young 3-chick broods is 7-8 times less than that of older, reduced broods, and it is suggested that most adults selectively starve the third chick, causing its early death. Possible advantages of this behaviour are discussed.

FACTORS AFFECTING THE BREEDING PERFORMANCE OF THE ANTARCTIC BLUE-EYED SHAG (*Phalacrocorax atriceps bransfieldensis*)

By

Philip Shaw B.Sc. (Abd.)

Thesis submitted to the University of Durham for the Degree of
Doctor of Philosophy.

February 1984

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.

Philip Shaw.

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APPENDICES

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SECTION I

Introduction

For each bird species there exists an optimal clutch size. If the number of eggs laid exceeds this optimal figure, then as few, or fewer chicks will survive to independence than if the figure is surpassed. In accordance with variation in the food supply or temperature the 'optimal clutch size' may change from one breeding season to the next. This concept, or variations of it, has been repeated by many authors since it was first proposed by Lack in 1954 and 1966. It now forms the basis for a more complex theory - the life history strategy - which seeks to predict when, how often, and to what extent an individual should invest its time and resources, and risk its further survival by breeding (Williams 1966, Ricklefs 1979).

Early evidence for Lack's theory was provided by studies of short-lived species (e.g. on Starlings*: Lack 1948, Robins : Lack and Silva 1949, tits : Lack 1950, and the Great Tit : Perrins 1965). These and other studies revealed that the optimal clutch size may vary throughout each season (e.g. Kluyver 1951, Snow 1958). By this time early studies of long-lived seabird species (e.g. by Richdale 1957, 1963, Coulson and White 1960) began to show the additional effects of laying date, age, and latterly, of mate change and nest-site change, on the individual's clutch size and breeding success. Large scale ringing studies provided the tool for checking the ages and identities of otherwise anonymous colony members, and also for assessing the costs of reproduction in terms of subsequent mortality. An appreciation of the costs and benefits of breeding either early or late in life, annually or in alternate seasons,

*Scientific names are given in Appendix A.

has led to the prediction that each individual should strive to maximise it's lifetime reproductive output (Williams 1966). To achieve this maximum, the individual may at certain times forgo a breeding attempt, or produce fewer surviving offspring than it is capable of doing, if the costs in terms of continued survival outweigh the immediate benefits (Williams 1966, Gadgil and Bossert 1970, Charnov and Krebs 1974). More recently, Curio (1983) has suggested that certain cases where young and first-time breeders show reduced reproductive success should be interpreted not as an effect of breeding constraints (i.e. a lack of experience) but of breeding re<u>straint</u>. Young adults may be capable of producing more offspring, but 'unwilling' to do so at the risk of early mortality. Older adults with fewer breeding seasons left should seek to maximise their breeding output in each season - to make the best of what remains. Note, however, that this theory relies heavily on the existence of a negative relationship between adult age and annual survival. Although adult survival was originally regarded as being stable with respect to age (Lack 1966) this, apparently, is not the case for some species (Coulson and Wooller 1976, Perrins 1979, Pugesek 1981).

The concept of a 'life history strategy', and concomitant ideas on breeding constraints and restraint have almost outstripped the flow of evidence from field studies. This study attempts to answer some of the more basic questions concerning the relationship between age and reproductive success. Mainly based on a ringing programme organized by the British Antarctic Survey, it examines adult annual survival, the age at first breeding, and the effects of age and mate change on the clutch size and reproductive output of a little-known species - the Antarctic Blue-eyed Shag. With the exception of Harris' (1979) study of the

Flightless Cormorant, there has been only one major study of survival and the effects of age on the breeding biology of a Phalacrocorax species. Potts (1966) showed that in a marked population of the European Shag breeding on the Farne Islands the laying period is prolonged and age-graded, that clutch size declines with the date of laying and that nest-site quality varies with the age of the male. Nest site quality was the most important predictor of breeding success (Potts *et al* 1980). Nests were built on cliff edge sites which were extremely variable in size, aspect and the degree of protection afforded. Older males returned to the colony earlier than young males, and obtained better quality sites. For the Blue-eyed Shag, by contrast, return to the colony is often severely disrupted by late winter weather. The laying period - and breeding season as a whole - are very much shorter, and variability in nest-site characters, at least in the colony studied, is much less.

In the 1960s and 1970s a greater appreciation that the gene rather than the individual is the basic unit of selection, led to the formulation of several new theories concerning reproductive fitness (Dawkins 1976). One such is Hamilton's (1964) theory of inclusive fitness, which provided an explanation for the occurrence of sociality in many insect groups (Wilson 1975), and apparent altuism amongst kinship groups of higher animals (Emlen 1978). It has also been used extensively by O'Connor (1978a) to describe the costs and benefits of brood reduction - for the parents, siblings and 'victim' chick. Brood reduction is seen as an adaptation to a fluctuating environment in which an optimal brood size can neither be predicted nor maintained. Consequently, a slightly larger than optimal clutch size may be laid and then, if need be, reduced at the nestling stage. At least in one respect the

Pelecaniformes are particularly well adapted for brood reduction; egg sizes in relation to female weight are extremely small (Lack 1968). Thus, the production of an 'extra' egg to offset egg loss, or to take advantage of an occasional abundance of food, is less wasteful. Brood reduction is common in several of the sulids (Nelson 1978), and pelecanids (Cooper 1980).

Previous studies have emphasised the link between food shortage, sibling competition, and starvation of the last or smallest brood member. Indeed O'Connor (1978a) drew attention to the frequency with which apparent food shortages are recorded amongst species reported to show signs of brood reduction. He emphasised that in some cases it is in the siblings' as well as the parents' best interests to 'eliminate' the weakest chick. Most field workers have made the assumption that chick-loss occurs through sibling competition for a limited resource. This study examines more critically the food requirements of the brood at the time at which mortality is at its highest, and asks whether food availability is necessarily limited by the environment, or by the parents themselves.

SECTION 2

Study Species, Area and General Methods

2.1 Taxonomic Status

The Antarctic subspecies *bransfieldensis* is one of seven subspecies of *Phalacrocorax atriceps* (Behn *et al*, 1955, Devillers and Terschuren 1978) which together occupy a circumpolar range covering the southern tip of South America and many of the sub-Antarctic and Antarctic island groups (Murphy 1936) (Fig. 2.1). *P. atriceps bransfieldensis* has been recorded breeding on many of the island groups around the Antarctic Peninsula (Croxall *et al*, in press) at least as far south as the Faure Islands (68°45'S; pers. obs.) (Fig. 2.2). The taxonomy of the species or species complex, has been reviewed and reinterpreted by several authors since the first description of *P. carunculatus* by Gmelin in 1789 (Gmelin 1789 in Murphy 1936). Early workers regarded the Blue-eyed Shag complex as comprising two (Murphy 1916, Behn *et al* 1955) or five (Murphy 1936, Voisin 1973) species, or, under the generic name *Leucocarbo*, as comprising six species (Derenne *et al* 1976). Such classifications were based mainly on the analysis of plumage characters and soft-part colouration of specimens taken from each of the - largely sedentary - island populations. In particular the presence or extent of the alar and dorsal bars, the position of the black/white border on the face, the colouration of the caruncles, eye-rings and feet were used to distinguish several of the (then) new Antarctic sub-species *bransfieldensis* in 1922 (Bennett in Murphy, 1936).

Most authors have accepted the arrangement suggested by Murphy (1936) - of only two South American Blue-eyed Shag species - *P. albiventer* and *P. atriceps*, but with the inclusion of two subspecies

FIG. 2.1 The distribution of subspecies of *P. atriceps* (after Devillers and Terschuren, 1978).

a. South America, b. Falkland Islands, c. South Georgia,

d. South Sandwich Islands, e. Antarctic Peninsula,

f. Prince Edward Islands, g. Crozet Islands,

h. Heard Island, i. Macquarie Island.

▨ *P. atriceps atriceps*

● *P. atriceps melanogenis*

□ *P. atriceps purpurascens*

○ *P. atriceps nivalis*

▲ *P. atriceps albiventer*

★ *P. atriceps bransfieldensis*

■ *P. atriceps georgianus*

FIGURE 2.1

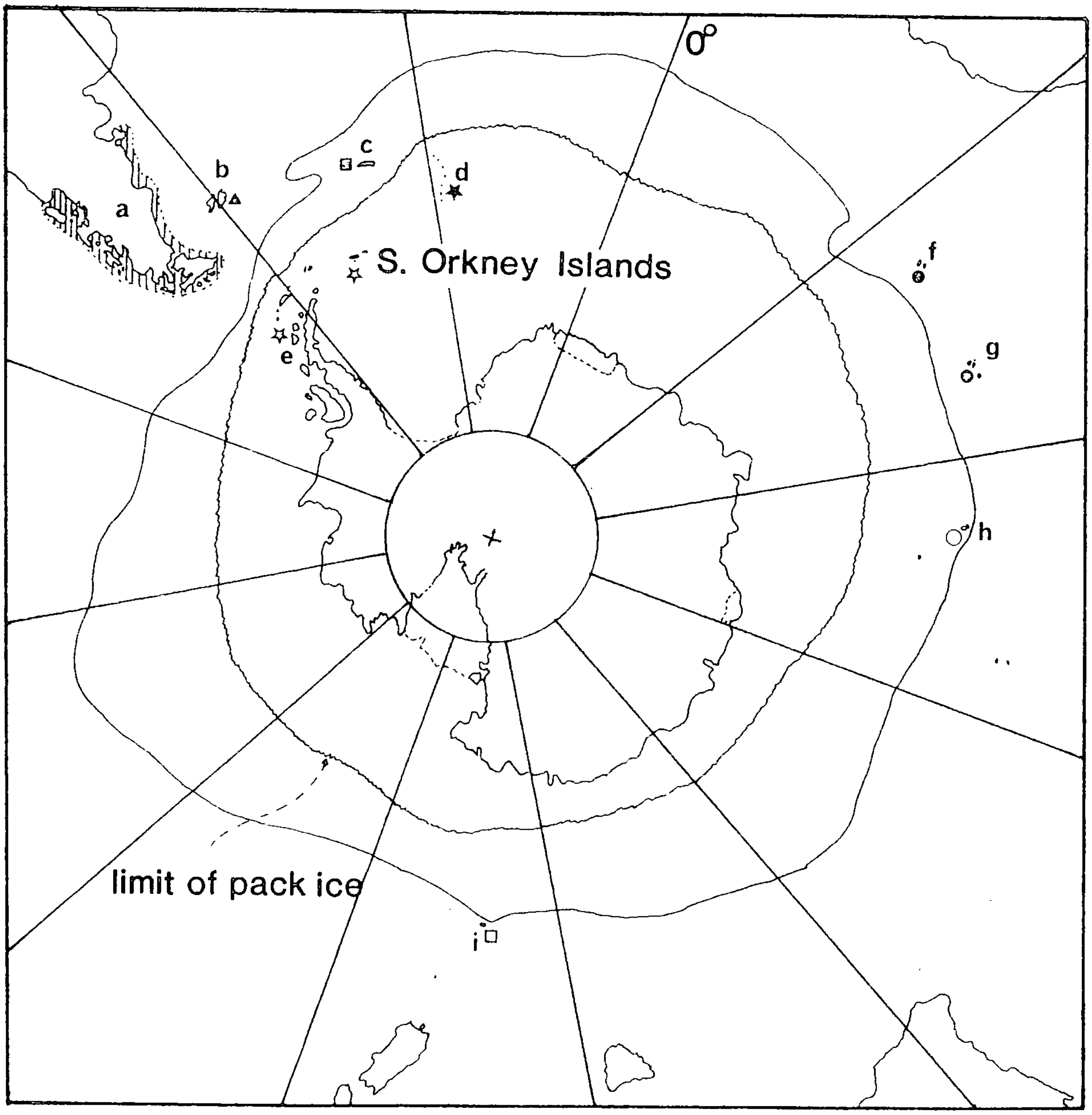


FIGURE 2.2: The distribution of Blue-eyed Shag (*P. a. bransfieldensis*) breeding colonies on the Antarctic Peninsula (after Croxall *et al* in press).

● Shag colonies

○ own observation

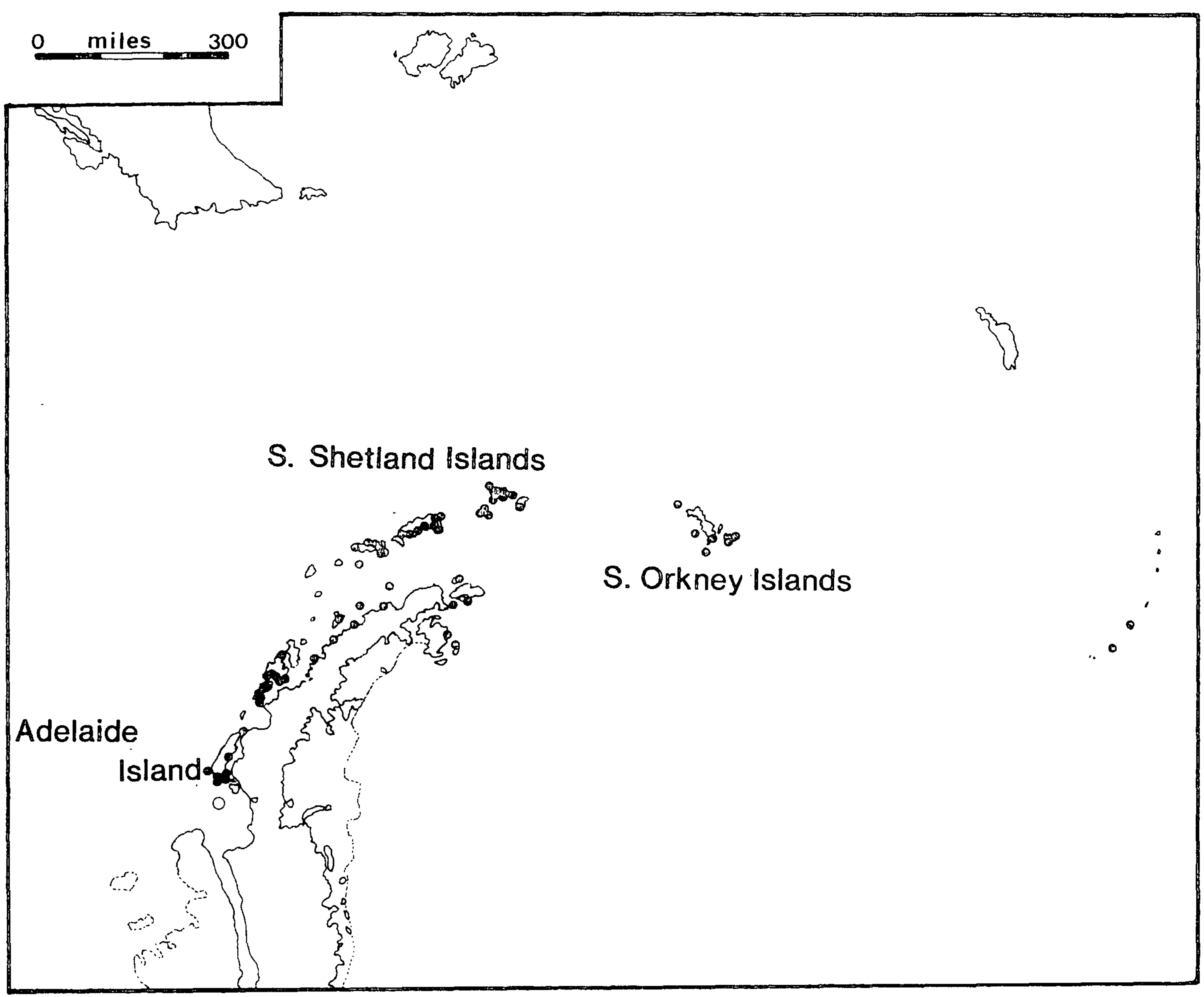

0 miles 300
S. Shetland Islands
S. Orkney Islands
Adelaide
Island

FIGURE 2.2:

in *P. albiventer* (Rand 1956, Watson 1975) and three subspecies in *P. atriceps*. However, pair formation between, and plumage characters of, individuals of '*atriceps*' and '*albiventer*' in a polymorphic population in South America has shown that within sympatric breeding populations wide variation in plumage characters occurs, and that individuals of both plumage types frequently interbreed (Devillers and Terschuren, 1978). Based on these criteria they suggested that *albiventer* should be regarded as a subspecies of the single Blue-eyed Shag species *P. atriceps*, of which they distinguish seven subspecies; *P. atriceps atriceps* (South America), *albiventer* (Falkland Is.) *melanogenis* (Crozet and Marion Is.), *purpurascens* (Macquarie I.), *georgianus* (S. Georgia), *bransfieldensis* (S. Sandwich, S. Orkney and S. Shetland Is.), and *nivalis* (Heard I.) (Fig. 2.1). The substantive names 'Emperor Shag' (Devillers and Terschuren 1978) and 'Imperial Cormorant' (Williams and Burger 1979) have been proposed as alternatives to the more familiar and descriptive name of Blue-eyed Shag. However, this latter name has been retained in the present study and, since many of the breeding adaptations and constraints described here for *P. atriceps bransfieldensis* may be absent or highly modified in the sub-Antarctic and temperate races, the prefix 'Antarctic' has been used in reference to this study species.

2.2 Description of Species

The Blue-eyed Shag is a medium sized phalacrocoracid but is slightly heavier than average, with a degree of sexual dimorphism in weight which falls well within the range of other *Phalacrocorax* species (Table 2.1, Appendix B). In common with most other Southern Hemisphere shags the general body pattern is one of dark to black upper-parts and wings contrasting with pure white underparts (Plate 1). The black feathering on the crown, hind neck, rump and (particularly) the mantle has a blue,

TABLE 2.1 Mean weights of, and degree of sexual dimorphism in 18 phalacrocoracids. Weights in g.

Species	Male	Female	'Adult'	M/F Ratio	Sources
Nannopterum harrisi	3960	2732	-	1.45	Snow, 1966
P. africanus	685	550	-	1.24	Cramp and Simmons 1977
			756		Rand In Burger 1978
P. aristotelis			1750-1930		Bauer and Blotzheum, 1966
	1919	1600	-	1.19	Snow, 1960
	1853	1660	-	1.12	Potts, 1966
			1785		Pearson, 1968
P. atriceps melanogenis	2450	2040	-	1.20	Derenne *et al*, 1976
P. a. bransfieldensis	2883	2473		1.17	This study
P. verrucosus	2000	1600	1700	1.25	Derenne *et al*, 1976
P. auritus	2100	1670	-	1.25	Palmer, 1962
	2233	1861	2047	1.19	Kury, 1968
		1675	-		Ricklefs, 1968
P. capensis	1306	1155	1231	1.13	Berry, 1976
P. carbo carbo	3490	3170	-	1.10	Cramp and Simmons 1977
P. carbo sinensis	2423	2085	1810-2810	1.16	Cramp and Simmons 1977
	2283	1936	1673-2687	1.18	Cramp and Simmons 1977
P. lucidus			2884		Rand In Burger, 1978
P. melanoleucus	820	730		1.12	Serventy In Snow, 1966
P. neglectus			1867		Rand In Burger, 1978
P. olivaceus			1680		Murphy, 1936
			1800		Palmer, 1962
P. pelagicus	2034	1702	1590-2500	1.19	Palmer, 1962
P. pencillatus			2500		Palmer, 1962
P. punctatus			827		Fenwick and Browne,197
P. pygmaeus	650-710	785			Bauer and Blotzheum, 1966
P. sulcirostris	860	696		1.23	Serventy In Snow, 1966
P. urile			2600		Palmer, 1962
P. varius	2200	1716		1.28	Serventy In Snow, 1966

green or violet sheen (depending on the subspecies; blue in *P. a. bransfieldensis*). White alar bars and a dorsal band are also present - but to varying degrees - in four subspecies, the band being absent in *P. a. albiventer* but present in 96 % of Signy Island *bransfieldensis*, the average band width being 3.5 cm (males: n = 28) and 2.9 cm (females: n = 17) (Appendix B). The black/white border on the sides of the face and neck is also variable, crossing the upper, middle and lower edge of the ear coverts in *P. a. bransfieldensis*, *georgianus* and *albiventer* respectively. In *P. a. bransfieldensis* a thin nuchal crest develops during the main moult period (from late December to June, but chiefly in February to April), but in most individuals it becomes worn and inconspicuous by late November. By June a thin white face patch, situated above and behind the eye and consisting of 4 - 8 thin white hair-like plumes also developes in most individuals but is usually lost before the onset of courtship and nest-site attendance in September. Soft-part colouration varies seasonally (as is the case on Anvers Island - Bernstein and Maxson, 1981); the eyelids of mature adults are normally bright cobalt blue throughout August - October (Plate 2) fading to a duller grey/blue during the incubation period in November. Two and three year old birds, which attempt pair formation and nest-building in late December, develop bright blue eyelids which begin to fade by mid-late January. There was no apparent seasonal variation in the colour of the iris (dark grey), gape (bright orange), or feet (flesh pink). Excepting the iris, soft-part colouration fades soon after death.

The species is largely sedentary, monogamous, breeds in compact colonies of about 10 to several thousand pairs (although no single colony of *P. a bransfieldensis* of more than 350 nests was found in the South Orkneys nor at four sites visited on the Antarctic Peninsula),

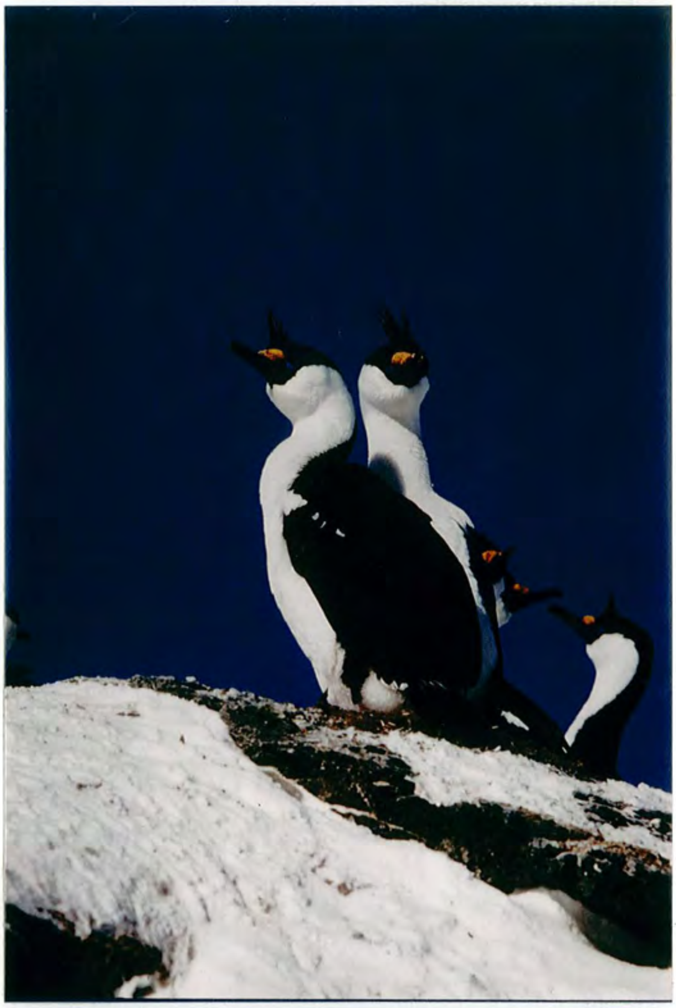


Plate 1. Pair of Antarctic Blue-eyed Shags, October 1980.

Plate 2. Eye and caruncle colouration in October.

and feeds mainly on inshore bottom-dwelling Notothenid fish (Appendix D).

2.3 Study Area and Study Colonies

The South Orkney Islands lie in the Southern Ocean between latitude 60° and 61°S and longitude 44° and 47°W, forming part of the Scotia Arc which connects South America to the Antarctic Peninsula (Fig. 2.1). There are four major islands in the group, the two largest of which - Coronation and Laurie Island - run in an East-West direction, and are approximately 55 km and 27 km long respectively (Fig. 2.3). The nearest Island groups are the South Shetland Islands (380 km to the West). South Georgia (820 km to the North East), and the South Sandwich Islands (850 km to the East).

Signy Island lies about 2 km south of Coronation Island at its closest point. Its outline is approximately triangular, running 7 km north to south and 5.5 km along its southern base, and covering an area of about 25 km^2. It is composed largely of quartz-mica schist and rises to 276 m. Approximately one third of the land area is covered by a permanent ice cap. Much of the coastline is low-lying, with numerous offshore islets (Fig. 2.4).

The climate of the South Orkneys is partly influenced by the west to east passage of depressions which occur to the south of the island group. North west winds prevail; gale force winds occur on an average of 61 days of the year, and some snowfall is recorded on an average of 261 days each year (B.A.S. Meteorological records). The annual temperature cycle shows a fairly low amplitude typical of Antarctic maritime areas. The maximum and minimum temperatures recorded since 1947 have been +19.8°C and -39.3°C; however, maximum and minimum mean monthly temperatures recorded during the period of study (October 1979

FIG. 2.3: Known Blue-eyed Shag breeding colonies and flock sightings in the South Orkneys.

⬤ Breeding colony, 100+ prs.

● Breeding colony, <100 prs.

■ Breeding colony, size unknown

◯ Flock sighting, 100+ birds

○ Flock sighting, <100 birds

Sources

a. Scotia expedition 1906
(Clarke, W.E., 1906)

b. Ardley, R.A.B. 1936

c. Hall, A.B. 1956

d. Scotland, C.D. 1957

e. This study

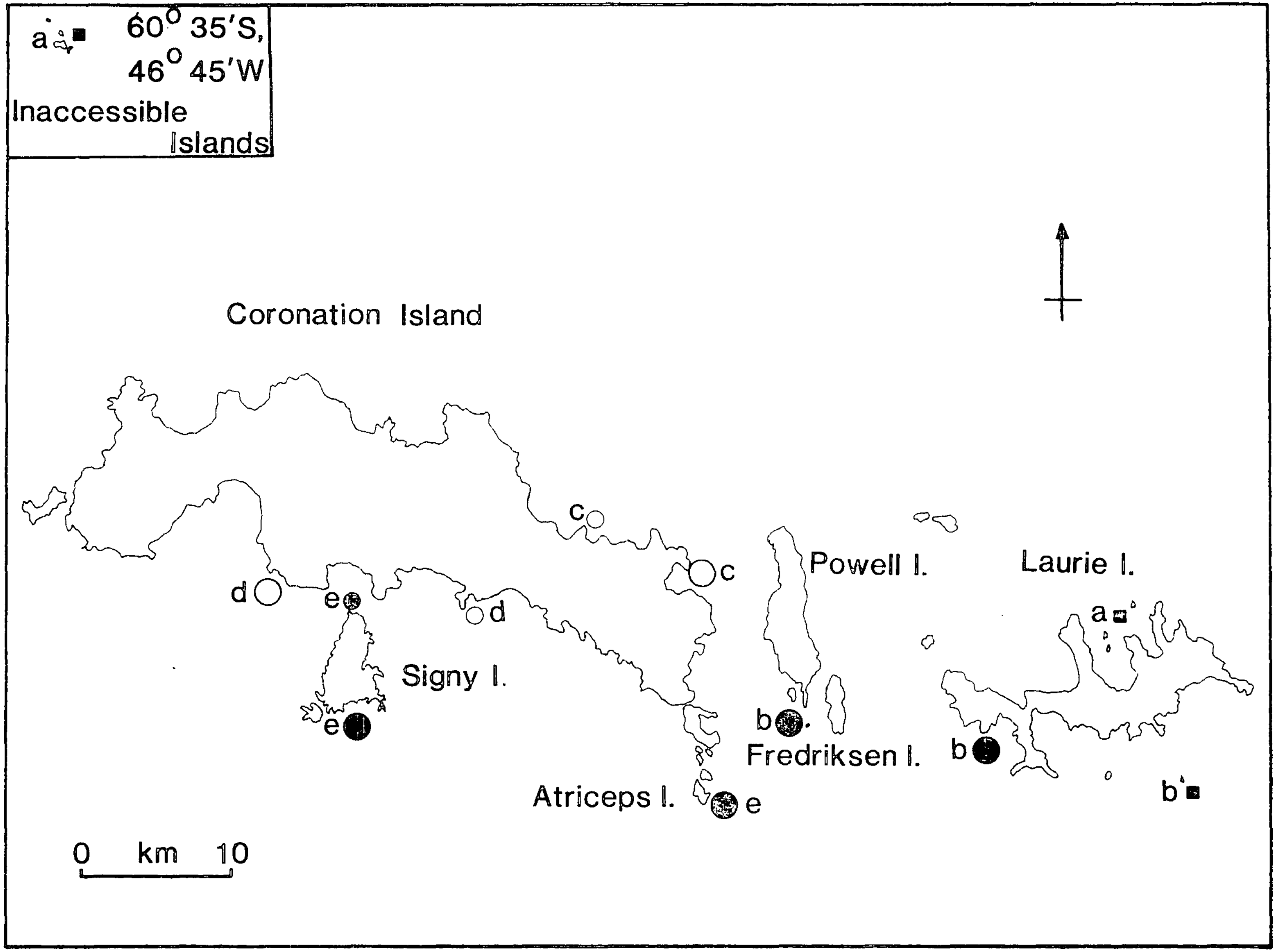
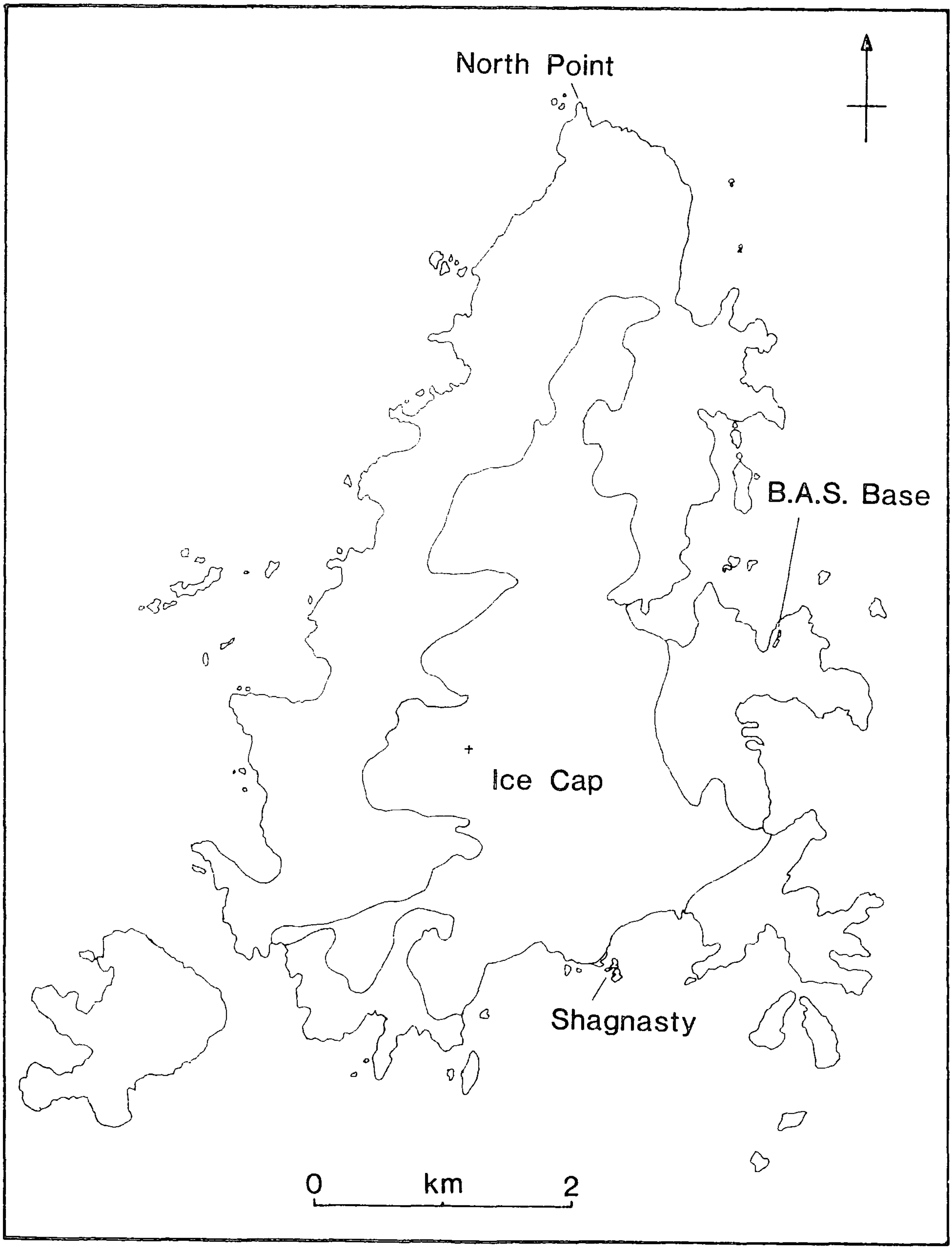

a
60° 35'S,
46° 45'W
Inaccessible Islands
Coronation Island
c
c
d
e
d
Signy I.
e
Powell I.
Laurie I.
a
b
Fredriksen I.
b
b
Atriceps I.
e
0 km 10

FIGURE 2.3:

FIGURE 2.4: Signy Island, showing the position of two Blue-eyed Shag colonies and the B.A.S. base.



to March 1982) were +2.3°C and -17.2°C. Throughout the breeding season (September to March) mean monthly air temperatures ranged from -4.2 to +2.3°C, the warmest month being February (+1.6 to +2.1°C). Temperatures in October (during which pair formation and nest-building occur) and in November (the main period of egg-laying and incubation) ranged from -23.5 to +10.1°C and from -13.0 to +7.7°C respectively. Fig. 2.5 shows the annual air-temperature cycle at Signy Island, and the approximate duration of each breeding event.

Seawater temperatures ranged from about 2.0°C in the summer to -1.9°C in the winter. Pack ice has been recorded in 9 months of the year, and fast ice may occur from April to December though more commonly from May to October.

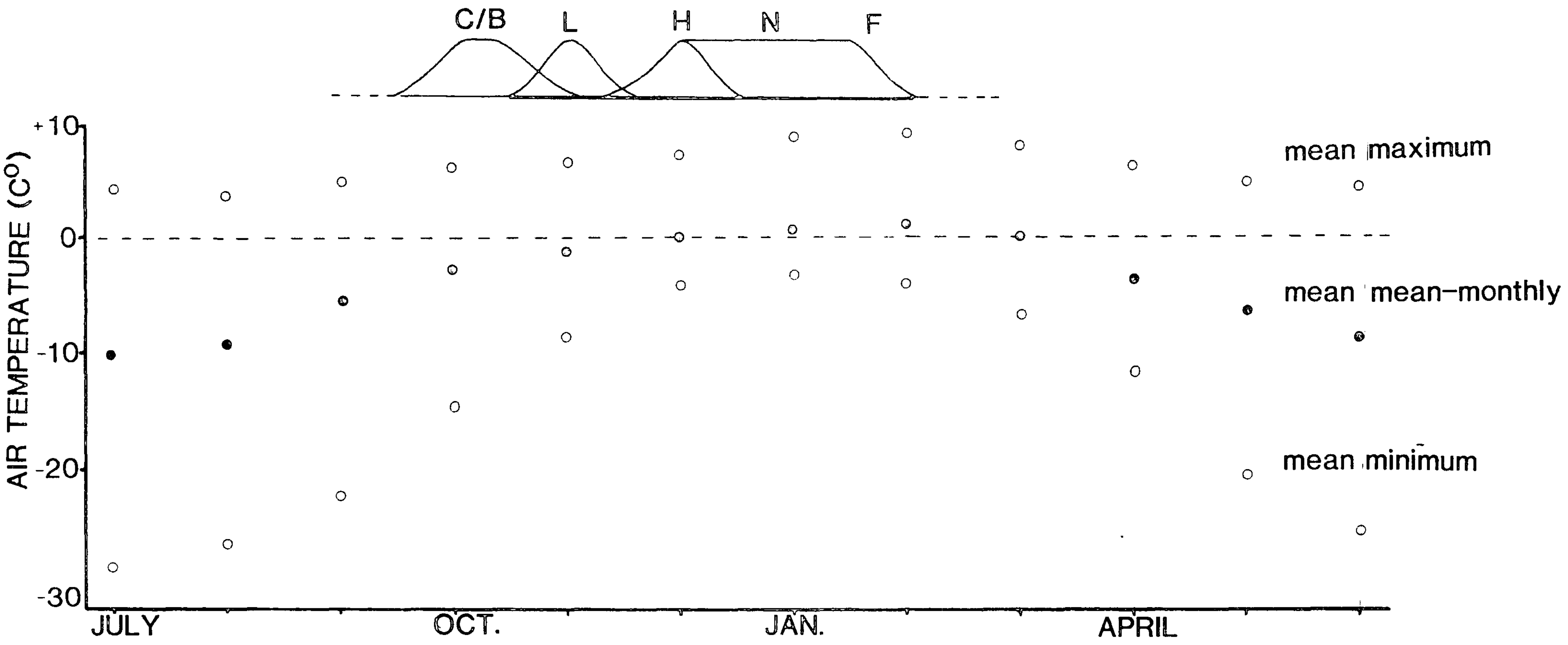
Since 1948 the British Antarctic Survey has maintained a permanently manned base at Factory Cove on the east coast of Signy Island. This provides support and facilities for ecological and physiological studies of the marine, terrestrial and freshwater systems on and around Signy. The island has 16 breeding bird species, comprising 4 penguin species, 6 petrels, 1 shag, 1 sheathbill, 2 skuas, 1 gull and 1 tern. Long-term ringing programmes on four bird species have been maintained since the early 1970s. In the case of the Blue-eyed Shag small numbers of chicks were ringed in most seasons from 1958 to 1969, and an average of 400 chicks have been ringed annually since 1970 (see section 3). Each Austral summer is referred to by the year in which the eggs were laid - e.g. '1980' for the breeding season spanning 1980/81.

Fig. 2.2 shows the positions of all recorded Blue-eyed Shag breeding colonies and (excluding Signy) all notable flock sightings within the South Orkneys. Signy supports two Shag colonies at opposite ends of the island. The largest of these - Shagnasty - has throughout the

FIGURE 2.5; The annual temperature cycle at Signy Island. Each point represents the mean of 34-36 years met. records; the mean maximum temperature each month, the average mean monthly temperature, and the mean minimum air temperature. Superimposed are the approximate timings and spread of each breeding event, as follows :

C/B - courtship/nest building,
L - laying,
H - hatching,
N - nestling period, and
F - fledging.

FIGURE 2.5:


C/B
L
H
N
F
AIR TEMPERATURE (C°)
+10
0
-10
-20
-30
mean maximum
mean mean-monthly
mean minimum
JULY
OCT.
JAN.
APRIL

study been treated as three separate sub-colonies comprising 280, 185 and 305 breeding pairs in 1981. The three sub-colonies are situated on two rocky islets of mica-schist, the shelving surface of which provides shallow sloping areas on which nest density is high. About 50 % of the area is occupied by nesting Chinstrap Penguins.

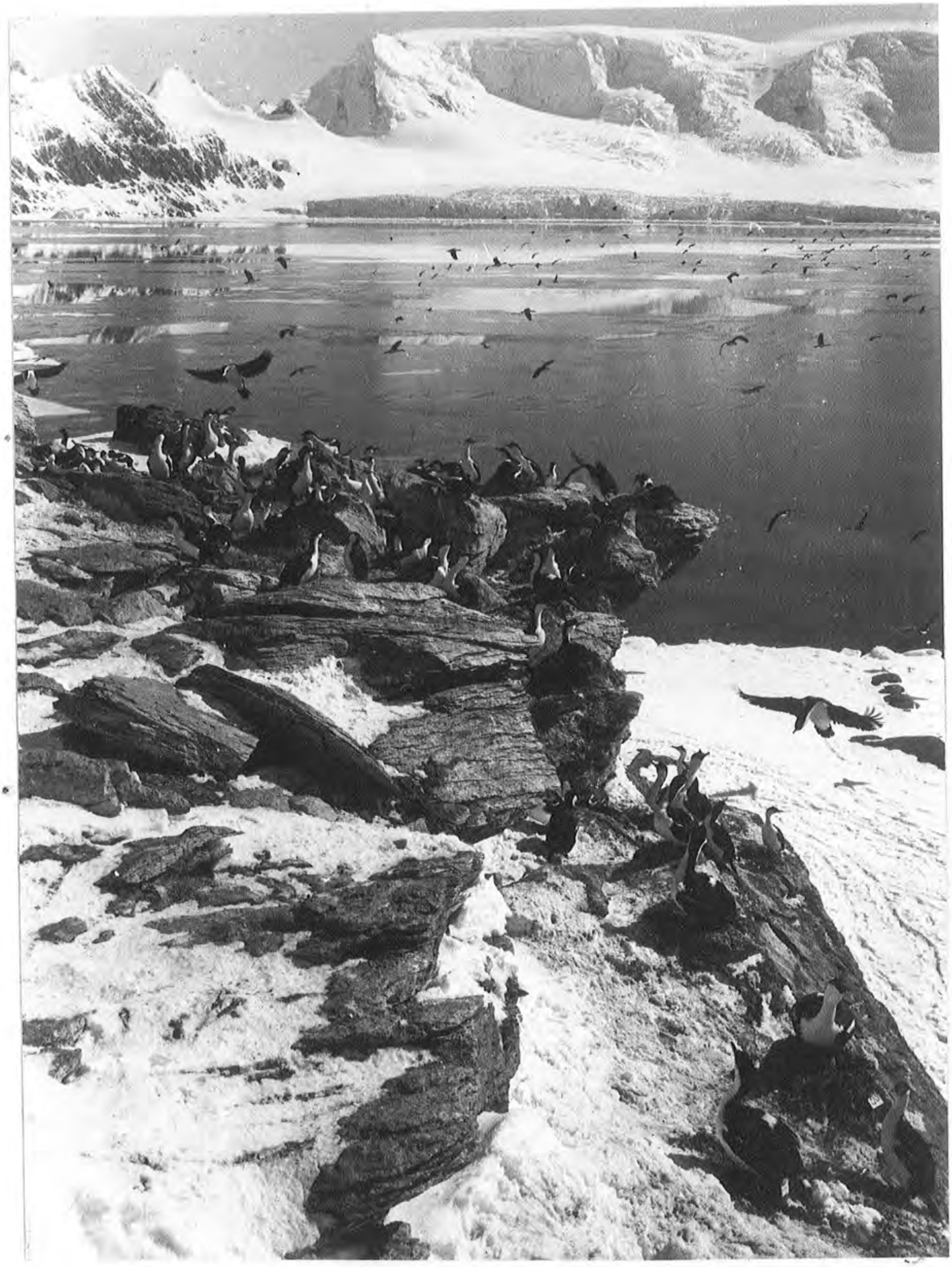
The innermost islet is reached by means of a 50 m long tidal causeway which provides easy access for 2-4 hours each day throughout most of the monthly tidal cycle. More reliable access was gained by erecting a steel cable from the shore to the islet and using this as an anchor point for crossing by means of a two-man dinghy. A large hide was erected on a rocky point opposite the inner islet and used for accommodation and for storing equipment. Access to the area was obtained by erecting a stake-line across the Mcleod glacier (which surrounds the Shag colony and adjoining rock outcrop).

By contrast, the much smaller Shag colony at North Point (Plate 3) - comprising 55 breeding pairs in 1981 - is situated on a low, terraced cliff of quartz-mica schist on the mainland of the island, and is therefore more readily accessible. All nests at both North Point and Shagnasty could be reached for examination and number-tagging.

2.4 Colony Sizes and Rate of Growth

The earliest reliable nest counts at each colony were made in 1948 (North Point) and 1960 (Shagnasty; Appendix C). Several estimates made at Shagnasty between 1948-58 have been disregarded because, at the times at which they were made - in September and early October - the colony was unlikely to have reached its full capacity for that year. Also, it is not clear whether subsequent estimates cover all three sub-colonies, and it is apparent that only sub-colonies I and II at Shagnasty were counted during 1968-78. Due to its small size and accessibility nest

Plate 3. Part of the Blue-eyed Shag colony at North Point.



counts at the North Point colony are likely to have been more accurate and may be used to show the pattern of growth from 1948 to 1981 (Fig. 2.6). Throughout this period changes in colony size have followed a linear progression, with an average annual increment of about 1.46 nests. There is no obvious relationship between colony size and the number of additional nests built in consecutive seasons. The effects of immigration (from the Shagnasty colony) during this period are discussed in section 3, although it is noteworthy that from 1961 to 1981 there was no obvious pattern in colony size changes at Shagnasty (Appendix 2). By 1981 the total number of breeding adults present on Signy was estimated to be *c*.1,664.

2.5 General Methods

Intermittently during 1958 - 1969, and then annually from 1969 onwards, varying numbers of chicks were ringed at Shagnasty and North Point. In 1958 5-figure rings provided by the Falkland Island Dependancies survey were used, but from 1960 onwards 7-figure British Trust for Ornithology rings were applied, normally during the first or second week of January in each season. Thus, by 1979 22 % of the adult population had been ringed as nestlings and were therefore of known age. Throughout the study period such adults were retrapped and, during 1979-81 292 of these were colour-ringed. The purpose of colour-ringing was to facilitate subsequent identification without the need for repeated recapture. Each adult received a unique sequence of 2 or 3 colour rings in conjunction with the existing B.T.O. numbered ring. Each colour ring consisted of a coiled 10X1 cm strip of 0.9 mm thick 'darvic' (rigid polyvinylchloride laminate) of one of 8 colours. In addition, 430 adults which had not previously been ringed, but whose mates were ringed, were also given a unique colour-combination plus B.T.O. ring. In this

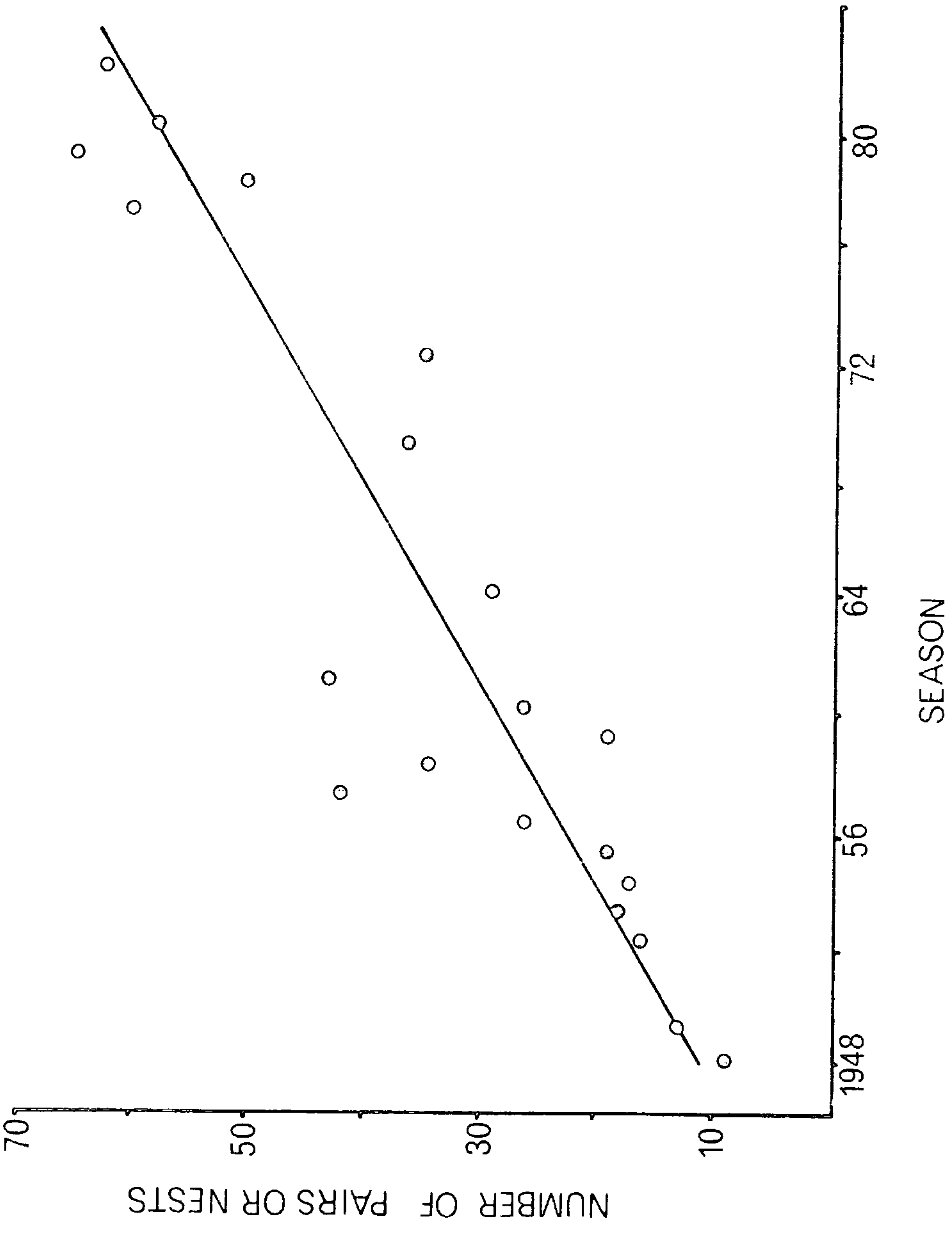
FIGURE 2.6: The number of nests/breeding pairs counted at North Point during 20 seasons from 1948 to 1981. Change in colony size may be described by the formula :

$$Y = 1.46(X) + 10.38,$$

where X = the number of years after 1947 and

Y = the number of pairs or nests.

FIGURE 2.6:



way, pair stability between successive seasons could be monitored.

2.5.1 Sexing

Potts (1966) described reliable sex differences in the voice of European Shags *P. aristotelis* : males produce a 'deep resonant grunt' whilst the only vocal sound produced by females is a 'soft hiss'. Almost identical voice differences occur in *P. atriceps*. Behavioural observations - of nest-site defence and copulation - supported this method of sexing, which was used to derive the sexual differences in body measurements (Fig. 2.7, Appendix B). All adult weights were taken using a 5 kg spring balance and, subsequently, a 5 kg table balance, both accurate to within 20 g. Wing lengths (maximum chord) and tail lengths from the base to the tip of the central tail feathers (on the underside) were measured to within 1 mm using a standard wing rule. Bill depth was measured to 0.1 mm at the angle of the gonys using vernier calipers.

In common with most of the Phalacrocoracids thus far examined, sexual dimorphism in body weight (Table 2.1) and in bill depth (Table 2.2) is evident. Adult males are, on average, 1.10 (*P. carbo carbo*) to 1.45 (*Nannopterum harrisi*) times heavier than adult females. Together with wing length, these characters were used as a guide to sexing when vocalizations were lacking.

Discriminant function analysis was used to estimate the accuracy of sexing by comparison of weight against bill depth, and wing length against bill depth (the measurements themselves being grouped, initially, according to voice differences) (Fig. 2.7). Some 97.2 % of females and 95.7 % of males were separated by the discriminant function :

$$(\text{Bill D.} \times 1.163) + (\text{Wing L.} \times 0.144) = 57.114$$

A comparison of weight against wing length, not surprisingly, gave a

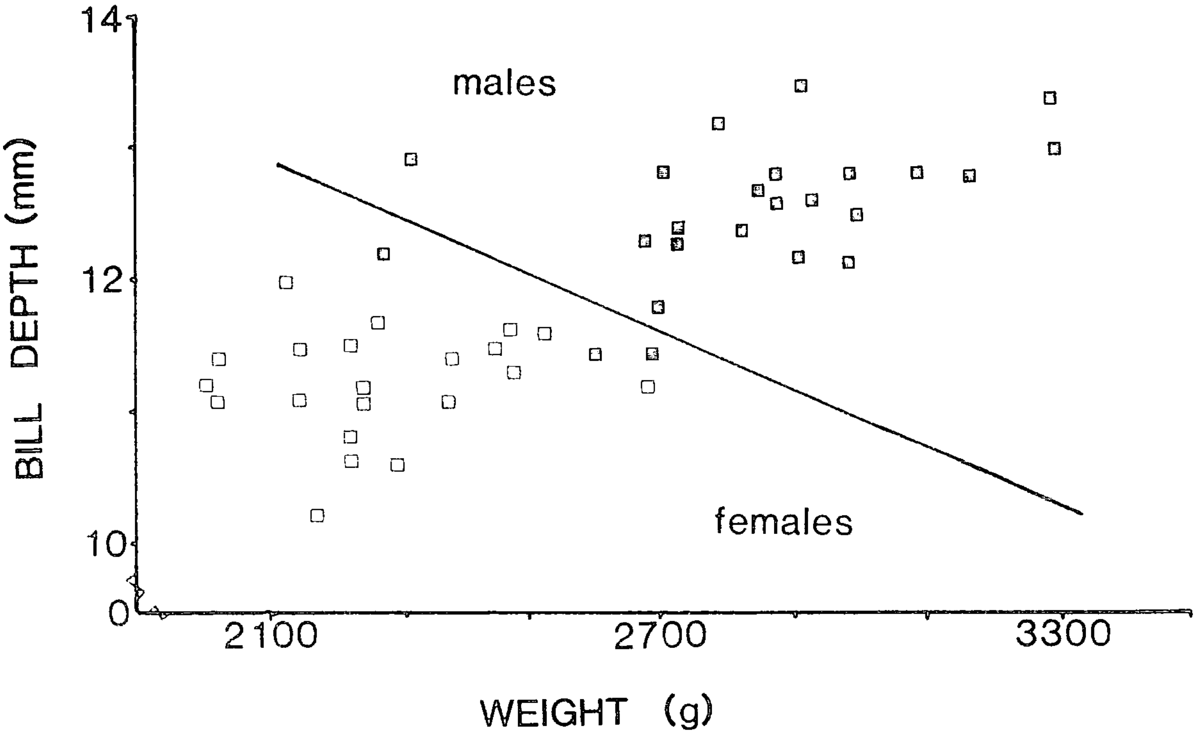
FIGURE 2.7: Sexual differences in weight, wing length and bill depth of a sample of Shags sexed by voice differences alone.

▤ males

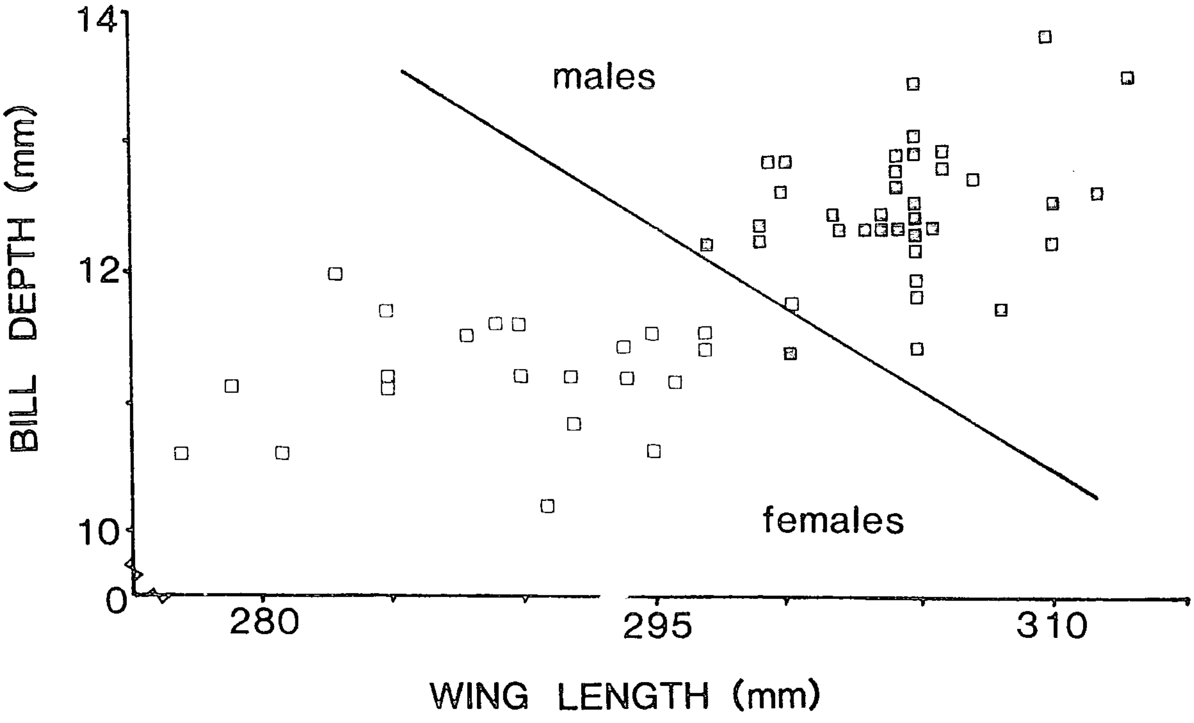
□ females

Boundaries estimated by discriminant function analysis (see text).

FIGURE 2.7:



14
12
10
0
BILL DEPTH (mm)
males
females
2100
2700
3300
WEIGHT (g)



14
12
10
0
BILL DEPTH (mm)
males
females
280
295
310
WING LENGTH (mm)

TABLE 2.2: Sexual differences in bill depths (mm) of four Shag species

Species	Mean bill depth		Ratio	Sample	Source
	Males	Females	M/F		
P. aristotelis aristotelis	12.1	10.4	1.16	238*	Potts 1966
	11.9	10.1	1.18	37	Cramp and Simmons 1977
	11.6	9.9	1.17	25	" " "
	10.5	9.2	1.14	19	" " "
P. a. desmarestii	10.6	9.5	1.11	10	Potts 1966
	10.0	8.7	1.15	10	Cramp and Simmons 1977
P. atriceps bransfieldensis	12.5	11.1	1.13	64*	This study
P. bougainvillei	10.8	9.7	1.11	12	Potts, 1966
P. carbo carbo	17.3	14.6	1.18	10*	" "
	16.3	14.1	1.15	12	Cramp and Simmons 1977
P. c. sinensis	14.0	11.8	1.18	48	" " "

*live specimens; other results from museum skins.

less reliable separation ; although the discriminant function boundary segregated 100 % of all females, it isolated only 87 % of predicted males, based on the formula :

(Bill D. x 1.236) + (Weight x 0.0027) = 21.988

These differences are reflected in the eigenvalues for the two functions, which were 3.42 and 2.70 for Bill D./Wing L. and Bill D./Weight respectively.

2.5.2 Pair Identification and Nest Tagging

Adult Blue-eyed Shags returned to roost at both colonies throughout the winter period, mainly during brief thaw periods or during the temporary local loss of sea-ice. The swift return of up to 52 % of the breeding population, within 1 - 2 days of the onset of each thaw (in June to August), indicated that they were in residence in the vicinity of Signy Island throughout the Winter. The presence of a large, recurring polynya in the Lewthwaite Strait (East of Coronation I. ; about 24 km from Signy I.) has been noted during a number of winter visits since the base was founded, and was recorded in 1980 and 1981. It seems likely that this, and possibly other open water areas to the North of Coronation and Laurie Islands, may sustain the South Orkneys' Shag population in most winters.

During frequent visits to the colony, and from a distance of about 50 m (using a 25X50 Kowa telescope), a large proportion of the colour-ringed birds were identified. Remaining colour-ringed adults, and a high proportion of B.T.O. ringed birds were identified throughout the incubation period in November. Most sitting birds were sufficiently tame to allow examination of their ring by hand, without undue disturbance.

Following the identification of one or both adults at a given site, a wooden numbered nest-tag (8 cm x 2½ cm) was attached to the nest by means of a metal rod. Missing ('off-duty') partners were identified during subsequent visits.

2.5.3 Egg marking and the determination of laying and hatching dates

In order to ascertain the dates and order of laying within each clutch, Shagnasty colonies I and II were visited daily throughout the period 29 October to 10 December 1980. Each egg in 246 study nests was marked (by indelible felt pen) with the date of laying and laying-order within the clutch (i.e. 'A', 'B' or 'C'). Except during the peak period of egg production almost all new (unmarked) eggs were weighed (to 1 g with a Pesola balance) and measured (length and breadth to 0.1 mm using vernier calipers) on the day on which they were first found, and in practice complete clutches in almost all study nests were weighed and measured. Particular care was taken to avoid chilling the eggs during examination in cold weather (at between $0^{o}C$ and $-15^{o}C$).

Eggs in each clutch were laid at 2 - 3 day intervals (section 6), and in 1979 and 1980 their respective laying dates were taken as the day on which they were first found. In 1981 however, most of the laying dates were estimated (by the B.A.S. marine assistant R. Forster) from visits made at intervals of 2 - 3 days, and are considered accurate to within ±1 - 2 days. Consequently the laying order within each clutch could not be determined throughout 1981. Clutches begun during a visit interval of greater than four days have been omitted from analysis pertaining to laying-date effects. In those cases where the hatching date - but not the laying date - was determined to within ±1 day, the laying date was estimated by subtracting 29 days (the mean laying to hatching period).

The hatching date and hatching order was determined using methods essentially the same as for laying dates above; the date on which each chick was first found was taken as it's hatching date - day 1. For newly hatched broods visited at an interval of 2 - 3 days the hatching order was obtained by noting the markings on each of the remaining eggs or - where two chicks had hatched in the interim period - by comparing their respective weights. It was found that body-weight almost doubled within three days of hatching. Where the weights of two siblings indicated that they had hatched on the same day, they were both assigned the position of 'A/B' within the brood. 'A' and 'B' chicks normally weighed 2.0 and 1.5 times that of 'C' chicks at the time of the latter hatching. Thus, since the relative difference in chick weights was at its highest at this time, there were seldom difficulties in determining the hatching order within each brood. Approximately 6 - 7 days after the 'C' chick hatched the 'A' chick developed sufficient down to facilitate paint-marking. Thereafter, 'A' and 'B' chicks received a white paint mark on the back and rump respectively. This was renewed if necessary up until about 21 days, after which the majority of chicks were ringed. The hatching order could not be determined in 1981 due to the need to alternate visits to the two colonies.

During 1980 chicks were weighed using appropriate balances accurate to 0.6 % of capacity.

2.5.4 Measurement of chick survival and fledging age

In 1980 survival within each brood was monitored by checking nest contents at intervals of 1 - 2 days during the first three weeks of life. The death or disappearance of one or more chicks from each brood was noted, and the identity of the surviving chick(s) was determined from their paint marks or ring numbers. A high proportion of 'C' chicks died during their first week and, at this age, could be easily and reliably distinguished from their siblings by the former's very much smaller size and emaciated condition prior to death. In most cases the surviving siblings were weighed to confirm their respective ages and hatching positions.

By age 4 - 5 weeks chicks became increasingly mobile and would often wander onto neighbouring nests at the approach of the observer. Thus it would have been impossible to record subsequent survival on the basis of nest occupancy alone. By ringing each chick at 3 - 4 weeks of age it's subsequent death (but not its continued survival) could be detected from ringing recoveries. Because of the flat nature of the colony it was considered that, prior to fledging, only a very small proportion of deaths were likely to occur outside - or fall outside - the colony area, and hence pass undetected. Thus continued survival was assumed in the absence of a recovery. The number of chicks fledged per brood was determined only for broods in which all chicks had been ringed.

Snow (1960), Palmer (1962), and Potts (1966) have described the prolonged post-fledging period of dependence of chicks of *P. aristotelis*, *carbo* and *auritus* on their parents. In the Blue-eyed Shag, chicks began to leave the nest site for increasingly longer priods from the age of 40 days (though they remained partially dependent on their parents for at least 4 - 5 weeks longer) and thus became less amenable for further study or for accurate measurement of mortality rates. Also, for most chicks, down-loss is completed by between 60 and 70 days - the age at which catching became almost impossible (Fig. 2.8). Thus, 65 days was taken as the age of successful fledging, and the parents' breeding success was scored accordingly - even though the chick may have been recovered dead several days later.

The data were filed on the Newcastle Computer Facility Michigan

Fig. 2.8: The pattern of down loss in known-age nestlings. (Sample sizes shown in brackets).

Down loss was graded as follows :

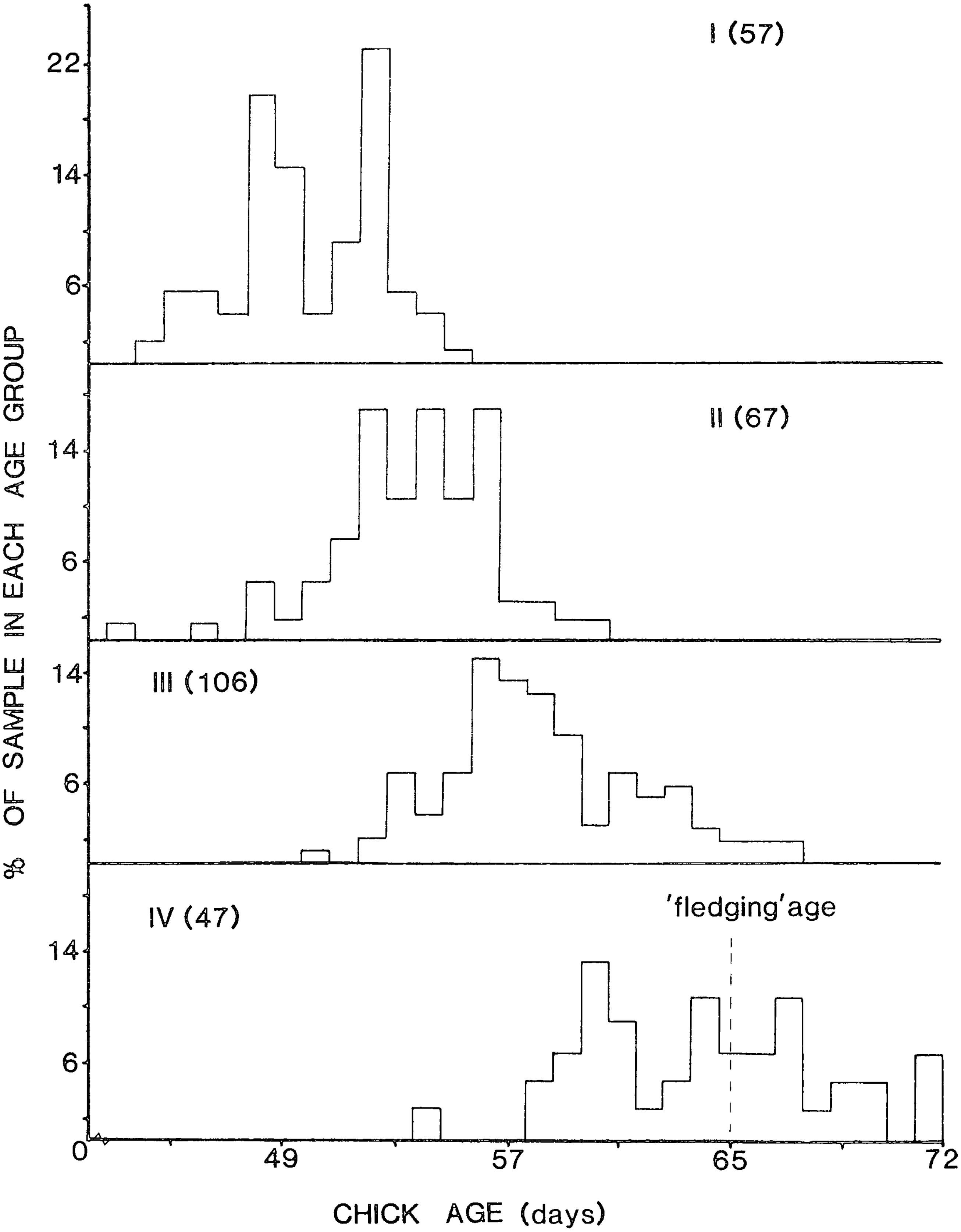
I. 1/3 of underparts (vent and lower belly) showing traces of white, 1^{o} and 2^{o} feathers exposed.

II. 1/3 - 2/3 of underparts white, on wings down adhering to 2^{o} coverts only.

III. Underparts white, wings fully exposed, little down on mantle/back, head (excluding ear coverts) and neck still downy.

IV. Little or no down remaining - on head or neck only.

FIGURE 2.8:


I (57)
II (67)
III (106)
IV (47)
'fledging'age
22
14
6
14
6
14
6
14
6
0
49
57
65
72
% OF SAMPLE IN EACH AGE GROUP
CHICK AGE (days)

Terminal System, and analysed using MIDAS (Michigan Interactive Data Analysis System (Fox and Guire 1976), and SPSS (Statistical Package for the Social Sciences; Nie *et al* 1970). Growth data were analysed using the Maximum Likelihood Programme (MLP) (Ross *et al* 1980).

SECTION 3

Survival, recruitment and philopatry

Introduction

Whilst there may be marked differences in the average lifespan and reproductive rates of temperate and tropical landbird species (Lack 1949, Skutch 1949, Ricklefs 1980), both temperate, tropical and high latitude seabirds are, in the main, long-lived, and have low reproductive rates (Ashmole 1963, Potts 1969, Harris 1973, Perrins *et al* 1973, Chabrzyk and Coulson 1976, Dunnet 1979, Croxall 1982).

At a time when few studies of long-lived species had been made, Lack (1966) suggested that the adult annual survival rate of birds may be constant - or near-constant - with respect to age. A re-appraisal of more recent survival data has tended to undermine this argument (Botkin and Miller 1974), as have the results of those few studies in which sample sizes of the oldest cohorts have been sufficiently large to show statistically significant differences in the annual survival of young and old adults (Coulson and Wooller 1976, Perrins 1979, Pugesek 1981). There is as yet little evidence as to whether or not the effects of age on adult survival are widespread in bird populations (Coulson and Wooller 1976). This point is important in the present study, since if life-expectancy declines with age, and if the stresses of breeding adversely affect adult survival, then old breeders will have less to lose (in terms of future reproductive output; Gadgil and Bossert 1970) whilst young breeders, with a higher life expectancy, may reduce the stresses of breeding by attempting to rear fewer young in a given season (Pugesek 1981, Curio 1983). In the absence of apparent senility effects, one may assume that any age-related differences in breeding performance (see Sections 6 & 7) are due to differences in experience or 'ability', rather than due to differences in 'willingness' to maximise the current breeding output.

On Signy Island 6,196 Blue-eyed Shags have been marked with monel rings since 1960, and of these 1,080 have been recaptured in subsequent years. Throughout this period the population has increased in size by a factor of between 1.5 and 2. Only two recaptures have been made outwith Signy Island but opportunities to visit other breeding colonies in the South Orkneys - and hence to assess the level of emigration - have been few, due to the nature of the environment.

In some cases recaptures made in either 1980 or in 1981 have been pooled. These results are referred to as the number caught in '1980 + 1981'.

3.1 Adult and first-year survival

Proportionately fewer 10 and 11 year-olds were re-identified in 1980 than 4 and 5 year-olds. Beyond this, there was no general decline in the proportion surviving with age (Table 3.1). The mean annual survival rate for all cohorts older than 4 years in 1980 was 0.7653, giving an expectation of further survival of 3.76 years. The two youngest breeding cohorts - ringed in 1975 and 1976 - show a much higher rate of return than those in all previous years, this difference being significant in the case of 5 year-olds ($\chi^2_1 = 53.7$; $P < 0.0001$). Members of all cohorts prior to that of 1975 show very low survival rates, and this is particularly so of those of the 1971 to 1974 cohorts. This step-wise progression in survival rates from 1968-74 to 1975-76 may be explained by a) unusually high mortality between the 1974 and 1975 season, affecting members of all 1969-74 cohorts, or, by b) a low survival rate affecting the 1971-74 cohorts only (annual survival for

TABLE 3.1: The number of nestlings ringed in each year and recaught in 1980.

Year of ringing	No. Ringed	Proportion caught 1980+81	Age	Annual Survival	±S.E.✿
1969	98	0.133	11	0.8324	0.0195
1970	481	0.147	10	0,8255	0.0090
1971	600	0.096	9	0.7707	0.0106
1972	100	0.100	8	0.7498	0.0281
1973	550	0.091	7	0.7100	0.0135
1974	280	0.082	6	0.6591	0.0219
1975	393	0.346*	5	0.8087	0.0112
1976	532	0.248*	4	0.7057	0.0133
1977	495	0.153	3	0.5348	0.0189
1978	423	0.075	2	0.2738	0.0234

Annual survival was calculated from :

$$\frac{Nx^{\frac{1}{y}}}{Ni}$$

where N = Number ringed, i = year of ringing, x = year of recapture, and y = number of intervening years.

*0.70 and 0.85 of adults are recruited by ages 4 and 5 years. Thus, the expected proportion live (both caught and uncaught) in 1980 are 0.353 and 0.407 respectively.

✿See Appendix E for method of calculation.

the 1969-70 cohorts being slightly higher : Table 3.1). In the latter case low first-year survival (or low nestling survival following ringing) is implicated, leaving adult survival for the 1969-70 cohorts unaffected.

From the proportions of each cohort recaptured in 1980 + 1981 combined, survival rate estimates and their standard errors were calculated by the method of iteratively reweighted least-squares (see Finney 1952) using the principle of maximum likelihood (Fisher 1925). (The proportions of birds caught from the 1976 and 1975 cohorts were first adjusted to take account of low recruitment at ages 4 and 5 years: Table 3.1).

Under the conditions of the first hypothesis described above, (a), the adult annual survival rate was estimated to exceed 1.0. When the conditions described by the second hypothesis (b) were applied, an estimate of adult annual survival of 0.8704 (±0.0148 : S.E.) was obtained. The survival rate for first-year birds was estimated to be 0.5844 (±0.0492), except during 1971-74 when the first-year survival rate was estimated to have been only 0.2284 (±0.0310) that of the 'normal' level. There were no significant differences between the adult survival estimate obtained above, and those calculated for adult European Shags (86 ± 9 % (1 S.E.) (Coulson and White 1957) and 83 ± 0.70 % (1 S.E.) (Potts *et al*, 1980).

Only 52.1 % of Blue-eyed Shags caught in 1979 were resighted in 1980, and 67.1 % of 1980 retraps were seen in 1981. These low estimates may have four possible explanations. 1) That the adult mortality rate was unusually high during the study period, 2) that ring-loss was high, 3) that the efficiency of recapture in 1980 and 1981 was inadequate, or 4) that a proportion of adults did not attempt to breed, or to return to the colony in each year. These possibilities will be considered in detail in Section 3.2.

One further estimate of the adult survival rate was made. During the three seasons 1976-78, 65 - 100 known-age adults were caught in each season. The proportions of these samples recaught in 1980 + 1981 combined provide an estimated annual survival rate of 0.7510 (Table 3.2). There was no relationship between age in the year of capture (i.e. whether of 5 years or younger, or older than 5 years) and the proportion which survived to 1980-1981.

It is unlikely that the first-year survival rate should vary independently of the adult survival in any particular year. However, since almost all chicks were ringed at 2-4 weeks of age, 'first-year survival' will encompass a period of high pre-fledging mortality (at 30 - 50 days; Section 7) which, from hatching to fledging varied from 44 - 83 % over 1979-1981.

3.2 Evidence of intermittent breeding

If a proportion of the population does not attempt to breed in each season, the recapture rate - and hence the apparent survival rate - between consecutive seasons will be low. Of those adults identified in 1979, 148 (47.9 %) were not seen in the following year. Similarly, 237 (32.8 %) of adults identified in 1980 were not recorded as present in 1981 (Table 3.3). Part of this shortfall may be accounted for by re-sightings made two years after the year of recapture. Thus, 30 of the 1979 sample were resighted in 1981 (having been missed in 1980), raising the annual survival rate for 1979-1980 to 0.6181. The numbers of birds missed in each season have been estimated in Table.3.4. The maximum estimates obtained - of 78 birds missed in 1980 and in 1981 - would account for 53 % and 33 % of the shortfall in resightings in the two seasons (if all had been ringed). Their addition to the numbers re-identified would raise the 1979-80 and 1980-81 survival estimates to

TABLE 3.2: The proportions of those adults caught in 1976-1978, which were re-caught in 1980 + 1981.

	Caught in :		
	1976	1977	1978
Adults caught	100	65	75
Percentage recaught (1980 + 1981)	43.0%	32.3%	57.3%
Annual survival rate	0.8097	0.6862	0.7572

Mean annual survival : 0.7510

TABLE 3.3: The proportion of birds caught and re-identified in successive study-years.

	Caught in :	
	1979	1980
Number	309	721
Re-identified in 1980	161 (72.1 %)	-
Re-identified in 1981	171 (55.3 %)	484 (67.2 %)

TABLE 3.4: Estimates of the number of ringed birds missed at each colony in 1980 and 1981.

1980 At Shagnasty I, II + North Point :

Total birds at study nests* : 664

No. missed : 18 (2.71 %)

Total birds at all nests : 1008

Total missed : *c.* 27

Ringed birds seen but not identified : 10

*Since at most study nests only one partner was ringed, the number of ringed birds amongst those which were missed (i.e. 27) is unknown. The minimum and maximum number of ringed birds not identified was therefore 10 to 10+27.

At Shagnasty III :

Total birds at all nests : 534

Proportion ringed : 0.27

Estimated number ringed : 144

Number identified : 103

Estimated number missed : *c.* 41

Minimum and maximum number of ringed birds not identified in 1980 : 10 to 37+41

: 10 to 78

Equivalent figures for 1981 : 23 to 78

0.7734 and 0.7799 respectively.

It might be argued that the effects of catching, measuring and colour-marking were sufficient to discourage the return of a sizeable proportion of breeders in the following year. The small number of new recaptures (of birds identified in 1979) made in 1981 does not support this. Moreover, the proportion of colour-ringed birds sighted in successive seasons was higher than the proportion of metal-ringed birds re-identified (Table 3.5). This may be partly due to the comparative ease with which colour-ringed birds were re-identified, but strongly suggests that the process of catching and colour-ringing at least did not discourage a return to the colony in the following season.

The likelihood of breeding in each year may be influenced by whether the individual attempted to breed in the previous year. A breeding attempt in year 'n' may adversely affect the individual's 'condition' throughout the subsequent winter, to the extent that it is less likely to attempt to breed in year 'n+1'. However, this does not appear to be the case : birds which bred in 1980 were no more or less likely to breed or to attempt to breed in 1981 than those for which there was no record of breeding in 1980 (Table 3.6). Unfortunately, the number of birds which survived (to 1980+1981) in either group, but failed to return to the colony, cannot be ascertained.

A much higher proportion of those birds which bred in 1980 was re-identified in 1981, than of those for which there was no breeding record in 1980 (Table 3.6). This may indicate a difference in the likelihood of birds returning to the colony - non-breeders showing less attachment to the site at which they were first caught. Alternatively, there may be a real difference in the survival rates of the two groups - this difference being the reverse of that predicted above.

TABLE 3.5: The proportion of birds recaught or re-identified in year 'n+1', in relation to whether metal-ringed or colour-ringed in year 'n'.

1979	Colour-ringed	Metal only
Number caught	281	28
Re-caught n+1	149	12
Percentage	53.0 %	42.8 %

$\chi^2_1 = 1.05$; N.S.

1979	Colour-ringed	Metal only
Number caught	459	159
Re-caught n+1	337	96
Percentage	73.4 %	60.4 %

$\chi^2_1 = 9.56$; $P<0.01$

Table 3.6 The proportions of breeders and non-breeders of 1980 which were re-caught and which bred in 1981.

	Total	Caught 1981	Percentage
Bred	514	385	74.9
'non-breeder'	164	104	63.4

$\chi^2_1 = 8.18$; $P < 0.01$

	Total	Bred 1981	Percentage
Bred	514	383	74.5
'non-breeder'	164	102	62.2

$\chi^2_1 = 9.24$; $P < 0.01$

Age-related differences in the occurrence of intermittent breeding have been described for the Kittiwake (Wooller and Coulson 1977), in which the tendency to miss one breeding attempt is more pronounced in the year following first breeding. A similar situation in the Blue-eyed Shag would lead to an increase in the frequency of intermittent breeding amongst 4 - 6 year-olds, given that the tendency is independant of the age of first breeding.

There was no apparent relationship between age, breeding status and the likelihood of recapture in the following year. Of those cohorts undergoing recruitment (the 2 - 5 year group), as high a proportion were recaught or reidentified in the following year as amongst the established year-classes (6-11 years), suggesting that for most birds the chance of surviving a year after the first breeding attempt was the same as that for subsequent years (n = 285 breeders, 126 non-breeders; analysis by χ^2).

Figure 3.1 shows the relationship between age and the proportion of birds which were known to have bred in the year of recapture. Both sexes showed significant differences in the proportion of known breeders caught throughout the age span (males : $\chi^2_2 = 6.65$; $P<0.05$, females : $\chi^2_2 = 18.51$; $P<0.001$). However, amongst males this result was largely due to differences between the two end-groups (3 - 4 years versus 10 - 11 years : $\chi^2_1 = 5.28$; $P<0.05$), whilst for females significant differences occurred between each major age-grouping (3 - 4 years/5 - 9 years : $\chi^2_1 = 4.49$; $P<0.05$, 5 - 9/10 - 11 years $\chi^2_1 = 10.58$; $P<0.01$, 3 - 4/10 - 11 years : $\chi^2_1 = 19.19$; $P<0.001$). Such differences may be due to age-effects on the proportion which breed, or to age-effects on the chances of re-identifying young birds once they become established as breeders. If young breeders are more wary of recapture at the nest, then age-related differences should be more pronounced amongst metal-ringed birds (requiring recapture, or at least close examination) than amongst those with colour-combinations.

Unlike males, colour-ringed females showed a significant degree of variation throughout the age-range ($\chi^2_2 = 28.57$; $P<0.001$), as did non colour-ringed females ($\chi^2_2 = 19.64$; $P<0.001$). However in the latter case the recapture rate was lower amongst 6 - 9 year-olds than for 4 - 5 year-olds. There were no significant differences with respect to male age. Thus, there is no evidence that young adults were any less easy to recatch when breeding than were older, more experienced breeders.

The results in Fig. 3.1 may be taken to indicate that the proportion of each year-class which bred increased after the age of 4 years, and again after 9 years. However, since the modal age at recruitment for males and females was 4 and 5 years respectively (Section 3.3) it seems unlikely that intermittent breeding - rather than merely a failure to recruit - would explain the low breeding proportions of 3 - 4 year-olds.

3.3 Recruitment

Age at recruitment was estimated firstly by comparing, within each cohort, the number of birds first caught at age n and n+1, and secondly, by assessing the age at first recorded breeding for each individual.

The proportion of each age-class in attendance at the colony was obtained from :

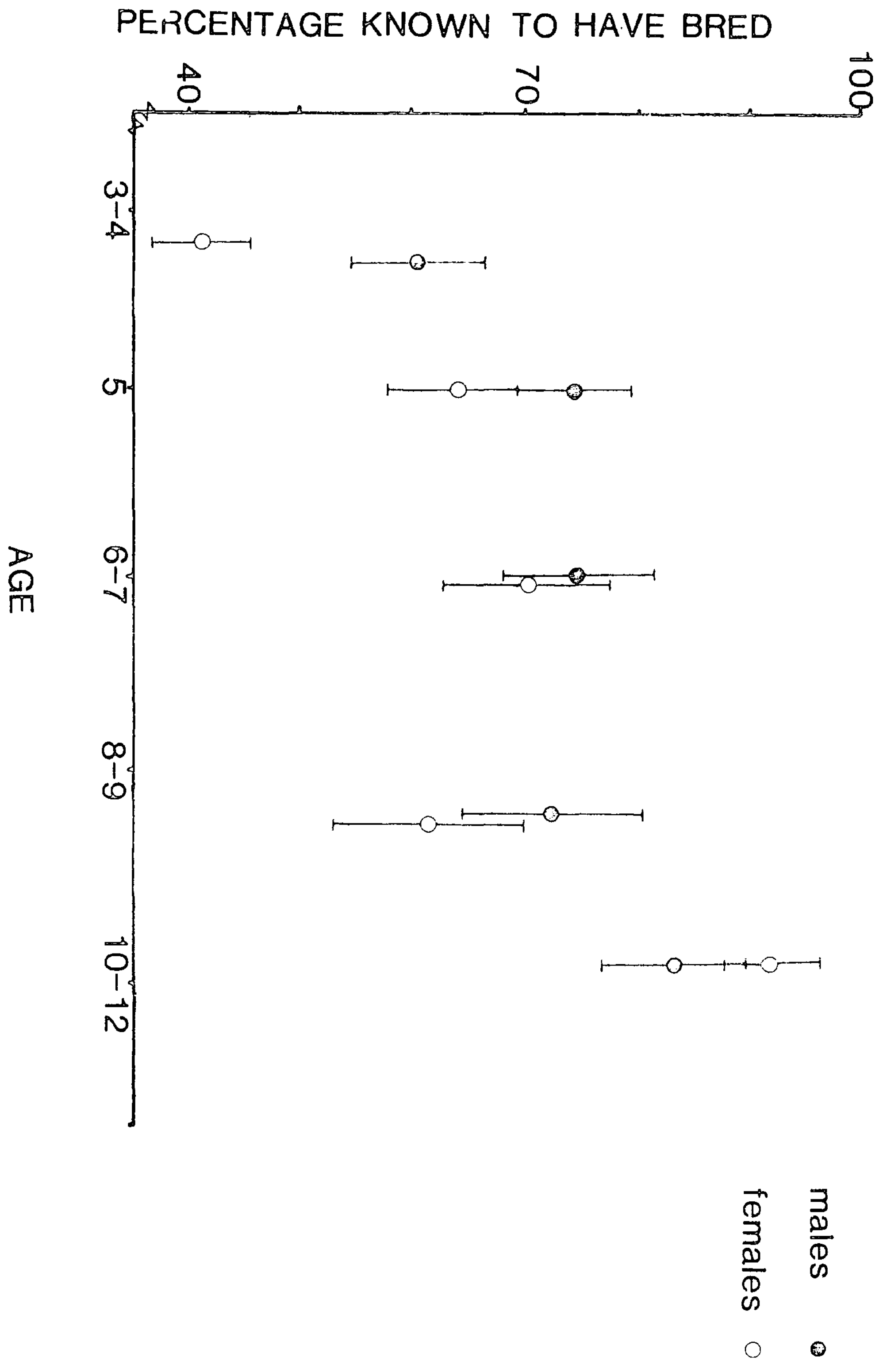
$$\frac{Ni80}{Ni80 + N(i + 1)81}$$

where Ni80 = the number of birds caught in 1980 at age i, and

N(i + 1)81 = the number of birds first caught in 1981 at age i + 1.

FIGURE 3.1: The relationship between age and the proportion of birds caught in 1980 + 1981 which were known to have bred.

Proportion ± 1 S.E. shown.


PERCENTAGE KNOWN TO HAVE BRED
40
70
100
3-4
5
6-7
8-9
10-12
AGE
males ●
females ○

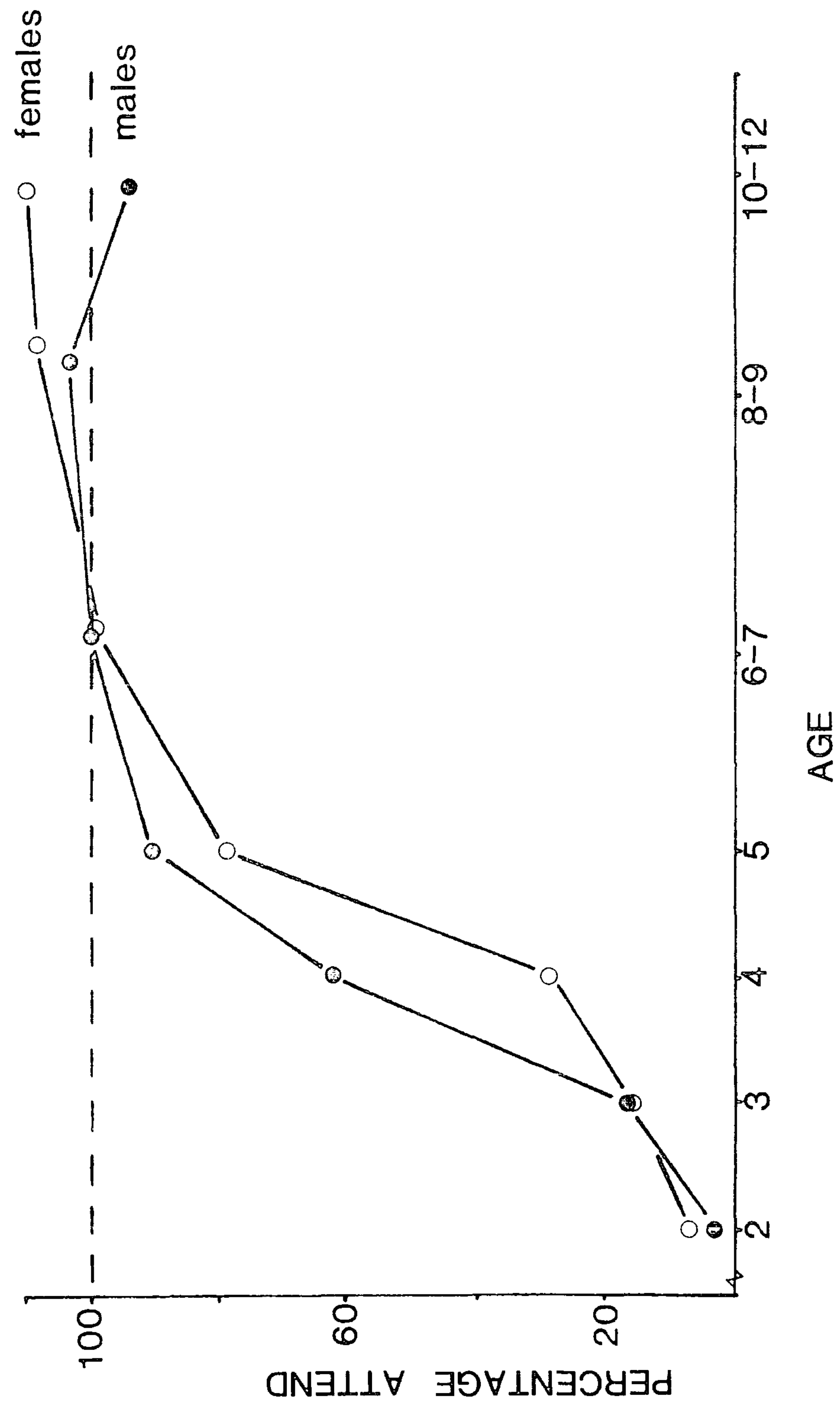
'N' was adjusted to take account of the estimated recapture efficiency (0.87) and, for 1981, the estimated adult survival rate (0.78).

Underestimation of the recapture efficiency, or overestimation of the annual survival rate will, in some cases, produce an estimation of colony attendance which exceeds 1.0. This has occurred for both sexes at 8 - 9 years, and for females at 10 - 11 years. Thus, the colony attendance curves shown in Fig. 3.2 should be used for comparing sex-related and (with caution) age-related variation in colony attendance rather than as an absolute measure of the proportion present from each year-class. As in the European Shag (Potts 1966) males tend to return to the colony at a younger age than females. First return to the colony began at 2 years and was complete at 6 years, the largest intake of males occurring at 4 years (46 %) and of females at 5 years (50 %). The mean ages of entry into the colony were at 4.33 years (males) and 4.77 years (females). Significantly more males than females were present at age 4 years ($\chi^2_1 = 10.95$; $P<0.001$; from the original data).

A further estimate of the mean age of first breeding was obtained from the earliest recorded breeding attempt of each individual. The mean ages at which 281 males and 206 females were first recorded breeding were at 5.00 and 5.42 years (range 3 - 9 years) respectively. There was a significant difference in the proportions of first-time breeders in each age class, for either sex ($\chi^2_6 = 13.18$; $P<0.05$). Since a number of birds evade recapture on their first and in subsequent breeding seasons, the spread of ages for the 'first recorded breeding' will be unrealistically wide and the estimated mean age at first breeding is high.

The highest intake of recorded first-time breeders occurred at

FIGURE 3.2: The estimated proportion of birds present at the colony in each age group.



5 years for both sexes (35.1 % of males and 28.7 % of females). However, differences in the percentage of males and females caught at ages 4 and 5 were less pronounced than indicated in the previous analysis. Also, differences in the cumulative percentage of birds caught at each age persisted to ages 6 - 8 years (Fig. 3.3). The proportion of breeders first caught in each year-class differed significantly only at age 8 years (d = 2.13; P<0.05; Arcsin transformation).

Both sexes showed a lower mean age at first breeding at North Point than at Shagnasty. This difference was significant for females (Table 3.7). Two further points are noteworthy : sexual differences in the age of first recorded breeding were more pronounced at Shagnasty than at North Point, where the tendency for earlier breeding by males was reversed (Table 3.8).

Differences in the age of recapture as a breeder may simply reflect differences in the recapture efficiency or prior ringing effort at the two colonies. Since at North Point ringing of nestlings did not begin until 1972 (three years later than at Shagnasty) the oldest breeders (excluding immigrants) caught there in 1976 would only have been 4 years old. Throughout the recapture period (1976-81) a higher proportion of females were recorded breeding first at 7 - 9 years at Shagnasty (27 %) than at North Point (5 %)(P = 0.001; Fisher's Exact Test). However, the proportion of males caught in this age-group was equal at the two colonies. These results suggest that the significantly higher first-breeding age of Shagnasty females may have been due to a high proportion of apparent late breeders - i.e. old birds (of 7 - 9 years) which had almost certainly bred before. However, within the 3 - 6 year range significantly more females were recorded breeding first at 3 - 4 years

FIGURE 3.3: The cumulative percentage of birds first recorded breeding by each year-class for Shagnasty only.

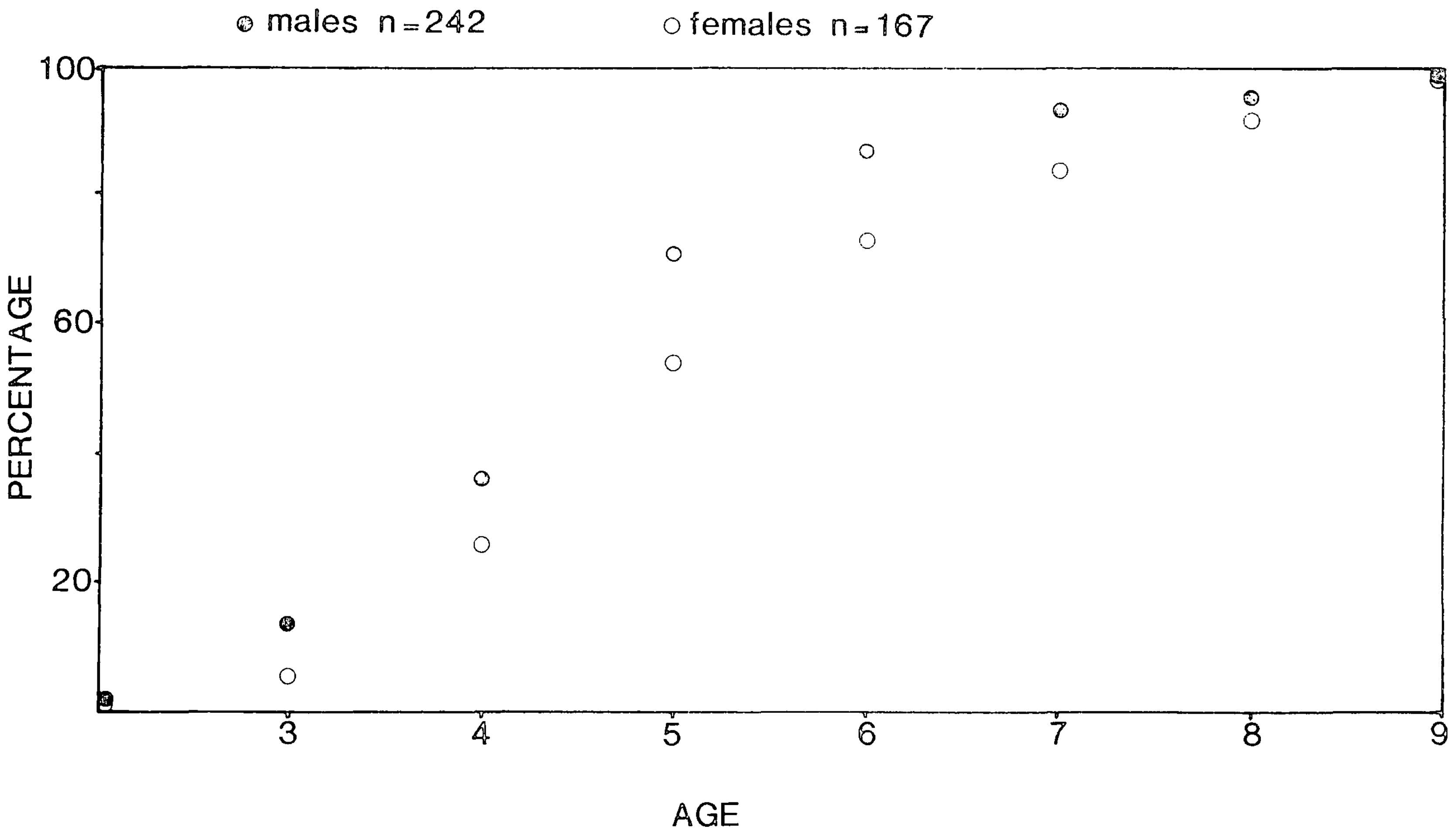


FIGURE 3.3:

TABLE 3.7: The age at first recorded breeding at each colony in relation to sex.

	Males				Females			
	Shagnasty		N. Point		Shagnasty		N. Point	
Age	n	Percentage	n	Percentage	n	Percentage	n	Percentage
3	32	13.2	5	13.1	8	4.8	9	23.1
4	56	23.1	13	34.2	35	20.9	14	35.9
5	85	35.1	11	28.9	48	28.7	10	25.6
6	39	16.1	4	10.5	31	18.5	4	10.2
7	15	6.2	2	5.3	19	11.4	1	2.5
8	3	1.2	3	7.9	13	7.8	0	0
9	12	4.9	0	0	13	7.8	1	2.5
	242		38		167		39	
Mean age:	5.02		4.84		5.65		4.43	

χ^2 results (with probability values) :

	Shagnasty Males	North Point Females
Shagnasty Females	24.27 6 df (<0.001)	18.80 3 df (<0.001)
North Point Males	2.68 4 df (NS)	1.81 3 df (NS)

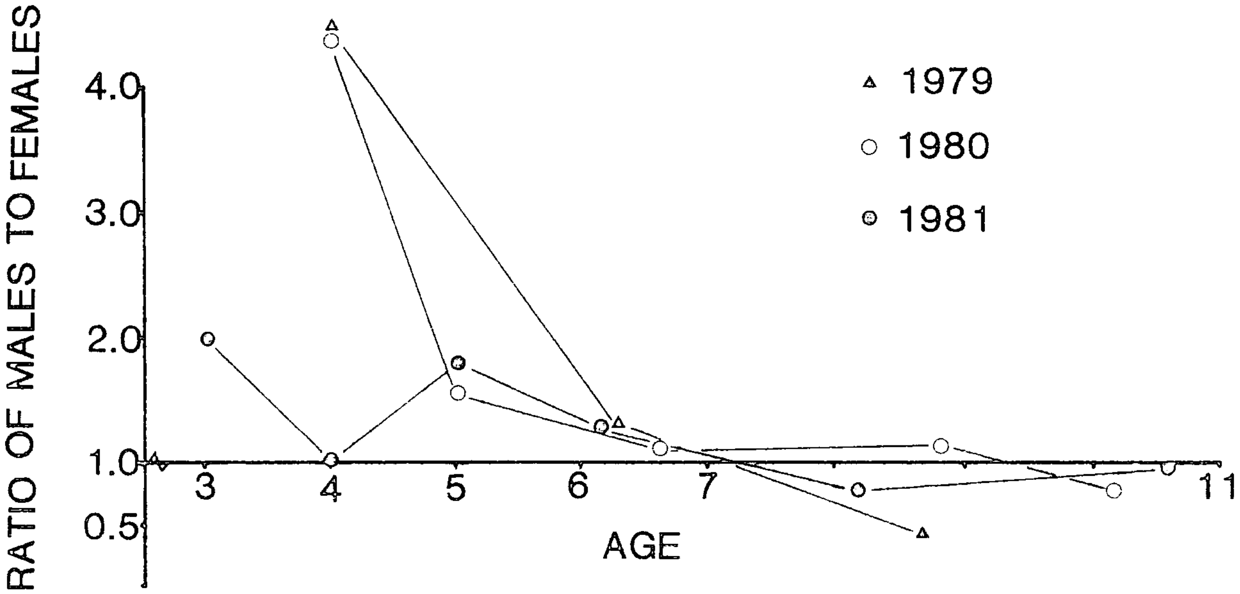
at North Point, and fewer at 5 - 6 years, than at Shagnasty ($\chi^1_1 = 8.47$; $P<0.01$). Although this comparison does not exclude possible bias due to earlier ringing at Shagnasty, it supports the contention that the average age of first breeding was lower there than at North Point.

3.4 Survival in relation to sex

The sex ratio of breeding European Shags varied significantly with age. Males greatly outnumbered females at 2 - 3 years, whilst females outnumbered males at ages 5 - 7 years. Beyond 7 years the sex ratio approached parity (Potts 1966). The early predominance of males reflected their earlier recruitment, which occurred mainly at 2 years, compared with 2 and 3 years for females. By contrast, Blue-eyed Shag males and females recruited mainly at 4 and 5 years respectively, producing a much higher proportion of males to females, particularly at ages 3 - 5 years (Fig. 3.4).

From the estimated age of full recruitment (6 - 7 years) onwards, the sex ratio was approximately equal, although with a slightly greater number of surviving females. This excess may have been due to an increased mortality rate amongst early-breeding males, although the results in Section 3.1 do not support this. The proportion of 3 - 5 year-old males recaught in consecutive years was slightly - but not significantly - lower than that of 6 - 11 year-olds. Potts (1966), by contrast, found evidence of a pre-breeding surplus of female European Shags. This persisted for 2 - 3 years beyond the age of full recruitment, but declined (and was eventually reversed) as a result of a higher female mortality rate.

FIG. 3.4: Variation in the sex ratio of breeders with respect to age.



χ^2_1 tests for a departure from parity (sample sizes in brackets) :

	Age					
Year	3	4	5	6-7	8-9	10-11
1979	-	4.45* (11)	-	N.S. (14)	N.S. (28)	-
1980	-	16.95^{+} (43)	N.S. (78)	N.S. (45)	N.S. (40)	N.S. (62)
1981	N.S. (30)	N.S. (66)	8.98** (107)	N.S. (109)	N.S. (36)	N.S. (95)

* $P<0.05$

** $P<0.01$

\+ $P<0.001$

3.5 Philopatry and Dispersal

In the present study the extent of movements to and between neighbouring islands in the South Orkney group could not be measured. On Signy Island Shagnasty, separated by *c.* 7 km from North Point, has been treated as a discrete colony. More females than males were recaptured breeding at a colony other than the one in which they hatched (Table 3.8). The difference is proportionally greater than that found in European Shags on the Farne Islands: 80 % of males bred first at their natal colony, compared with 75 % of females (n = 250 and 194 respectively) (Potts 1969). The percentage of birds which moved was much lower than that of the European Shag, possibly reflecting the much shorter distance (*c.* 90 m) separating the European Shag study-colonies. Surprisingly, the proportion of birds which moved from the small to the large colony (North Point to Shagnasty) was almost four times greater than for movements in the opposite direction (Table 3.8). Again, the tendency to move from either colony was sex-linked, significantly so for birds ringed at Shagnasty.

Having bred at one colony, significantly more females than males were recorded breeding elsewhere in a subsequent season; 5.0 % of females changed colonies after at least one breeding attempt, compared to 1.5 % of males (n = 199 and 194; P = 0.29; Fisher's exact test).

The proportion of breeders which changed colonies <u>per annum</u> was calculated from the number of changes made between consecutive seasons, divided by the total number of 1 year intervals recorded. (The results obtained should be treated with caution since the number of year-intervals recorded per individual varies).

TABLE 3.8: Sex-differences in the proportion of Shags first recovered breeding at the natal colony.

a) Regardless of colony.

	Same	Different	n	Percentage
Males	324	3	327	0.92
Females	256	10	266	3.76

χ^2_1 (Yates' correction) on sex-difference : 4.28; $P<0.05$

b) With respect to natal colony.

	Same	Different	n	Percentage
S.N. Males	284	1	285	0.35
N.P. Males	40	2	42	4.76
S.N. Females	217	7	224	3.31
N.P. Females	39	3	42	7.14
Total S.N.	501	8	509	1.57
Total N.P.	79	5	84	5.95

P values (Fisher's Exact Test):

	S.N.Males	N.P. Females	Total S.N.
S.N. Females	0.014	N.S.	-
N.P. Males	0.042	N.S.	-
Total N.P.	-	-	0.021

On Signy Island 2.4 % of breeding Blue-eyed Shags changed colonies each year (n = 673 year intervals), compared with less than 1 % of breeding European Shags on the Farne Islands (Potts 1966). However this latter figure does not include movement within the Farne Islands group - and so is not directly comparable.

A higher proportion of females changed colonies each year than males : 3.6 % of females and 1.5 % of males (n = 308 and 340 year-intervals; P = 0.05; Fisher's exact test). Also, the tendency to change colonies was much greater at North Point (5.8 % of breeders per annum) than at Shagnasty (1.5 % per annum) (n = 138 and 527 year-intervals; P = 0.006; Fisher's Exact Test).

A summary of the main results of section 3 is given in Table 3.9.

Discussion

The interpretation of age-related effects on the timing and success of breeding is dependent on whether adult survival varies with age. If young adults have a greater life expectancy than older birds, then they may invest less effort in breeding, thus avoiding possible breeding stress (Curio 1983). However, in this study there was no evidence of age-related variation in adult survival. Thus, variation in breeding performance described in Sections 6 and 7 may be interpreted as being due to a difference in breeding experience or ability rather than to breeding 'restraint' by young adults.

The age at first breeding varies widely both within and between seabird species (Croxall 1982). Whilst individual Wandering Albatross may show a 9-year difference in the age at which they first attempt to breed (Croxall 1982), for most species the mean age of first breeding covers a range of 3 - 5 years. Not surprisingly, shorter age-ranges are characteristic of species which breed first at younger ages, and, in most cases, are associated with lower annual survival rates. In the Adelie Penguin (Ainley and DeMaster 1980), Short-tailed Shearwater,

TABLE 3.9: A summary of the main results from Section 3

Estimate of adult annual survival	0.87	0.01 (S.E.)
Estimate of first year survival	0.58	0.05
Estimate of adult survival between :		
1979 - 1980	0.77	
1980 - 1981	0.78	
Survival in 1980 to 1981 of those which :		
bred in 1980	0.75	
did not breed in 1980	0.63	

	MEAN	MODE	RANGE
Age at return to the colony :			
Males	4.3	4	2 - 6
Females	4.7	5	2 - 6
Age at first breeding record :			
Males	5.0	5	3 - 9
Females	5.4	5	3 - 9
Percentage of birds breed at natal colony :			
Males		99.1	
Females		96.2	
Percentage of birds change colony after breeding :			
Males		1.5	
Females		3.6	

McCormicks Skua, Wandering Albatross (Croxall 1982) and Gannet (Nelson 1978), females first attempt to breed at a younger average age than that of males, whilst in the Laysan Albatross (Fisher 1975), Southern Giant Petrel (Conroy 1972), Kittiwake (Wooller and Coulson 1977), Red-billed Gull (Mills 1973), and European Shag (Potts 1966), the reverse is true. Since the majority of Blue-eyed Shag males first return to the colony at age 4 years, and females at 5 years, pairs in which the male is younger predominate, at least up to the sixth year class. Age similarities within pairs may persist however, through a different cause, as described in Section 4.

Philopatry in birds is sex-linked. Usually more males than females return to breed at the natal colony, or in the vicinity of the territory in which they hatched (Greenwood 1980). Amongst seabirds a male bias towards philopatry has been recorded in the Laysan Albatross (Fisher 1975), Manx Shearwater (Brooke 1978), and in three gull species (Mills 1973, Chabrzyk and Coulson 1976, Wooller and Coulson 1977).

In the European Shag no such bias was recorded (Potts 1969), although movements between colonies within the Farne Islands were not described. Similarly, no sex-related differences in movements were recorded for the Flightless Cormorant, adults of both sexes being extremely sedentary (Harris 1979). However, both adult and immature Blue-eyed Shags must, due to the encroachment of sea ice, move widely within the island group (and perhaps also to neighbouring island groups). Thus, before reaching breeding age, members of both sexes are likely to have an equal opportunity to visit, and join, other breeding colonies. The movements of adults within colonies - in relation to age and sex - is described in Section 4.

SECTION 4

Age, pair stability and breeding performance

Introduction

Several seabird studies have examined the relationship between age, pair stability and the timing of laying (LeResche and Sladen 1970, Coulson 1972, Mills 1973, Ollason and Dunnet 1978, Lloyd 1979, Coulson and Thomas 1983). In some species at least, the timing of laying is age-related; older, more experienced adults begin laying before 'middle-aged' birds, whilst first-time breeders tend to lay at the tail end of the season (Coulson 1966, Potts 1966, Mills 1973). The degree of synchrony within age-groups may thus influence pair formation and stability if each bird tends to mate with a partner of similar breeding condition to itself - and hence of a similar age. However, if nest-site tenacity is strong, established breeders may retain the same site and mate in successive seasons, forcing unestablished first-time breeders to select new or unused sites, and partners of a similar age and status.

Thus there are two contrasting mechanisms for pair formation and maintenance; pairs may split up and re-assort frequently, but, through the influence of age on the timing of each breeding event the age differential (within pairs) is small. Conversely, if 'available' first-time breeders most often pair together and through strong site tenacity pair stability is high, a similar result would obtain.

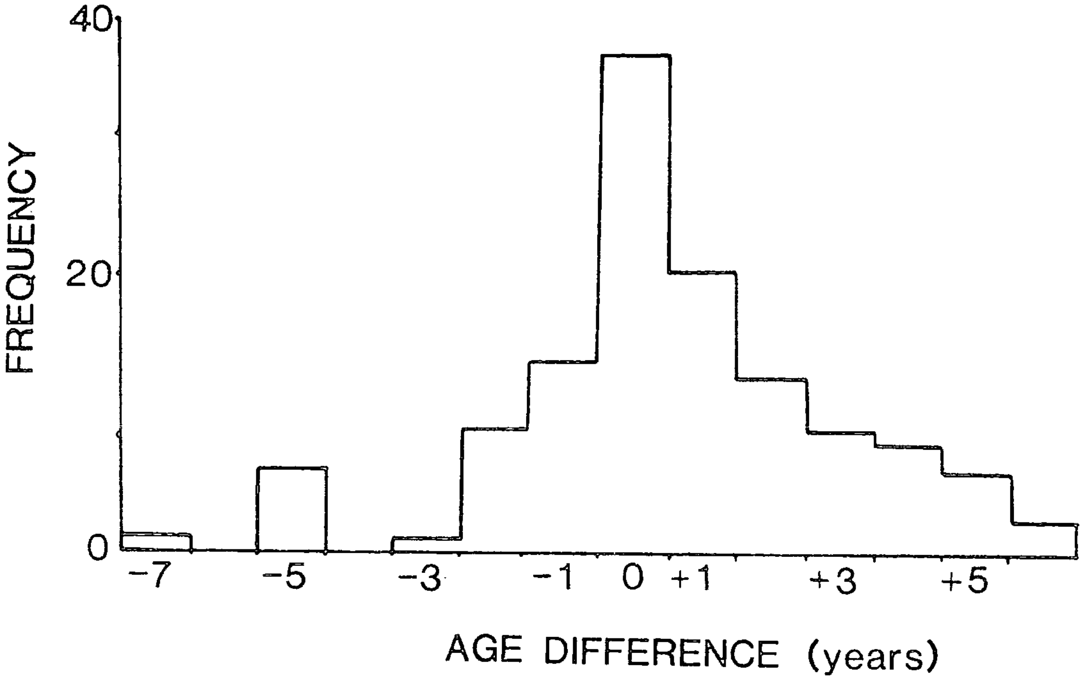
Recent studies by Mills (1973), Ollason and Dunnet (1978) and particularly by Coulson (1972) have shown that successful breeding, site retention and prior breeding experience increase the likelihood of the same pairs reforming in successive years. These stable pairs may spend less time performing pair-bonding displays (Erickson and Morris 1972), begin laying earlier (Mills 1973, Coulson and Thomas 1983), lay larger clutches (Mills 1973, Coulson 1972), and eventually fledge more young (Coulson 1972, Ollason and Dunnet 1978, Wood 1971).

4.1 Age differences within pairs

Of 127 Blue-eyed Shag pairs in which both adults were of known age, 29 % comprised partners of equal age, and in 57 % of pairs partners ages were within ± 1 year of each other. The overall age distribution was slightly skewed, males being on average 0.6 years younger than their mates (Fig. 4.1). However, age differences within pairs varied markedly with absolute age: most males of 3 - 7 years were younger than their respective mates, as were most females of 3 - 5 years (Fig. 4.2). This is to be expected, since the mean age of all males in the sample was 6.18 years, whilst that of all females was 6.79 years. The proportion of younger, equal aged and older partners of adults of 3 - 7 years and 8 - 12 years differed significantly for both sexes; a higher proportion of adults of 3 - 7 years had mates which were older than themselves; $\chi^2_1 = 26.07$; $P<0.005$ (female age in relation to that of the male), and $\chi^2_1 = 10.24$; $P<0.01$ (male age in relation to that of the female). However, if the direction of the age differences are ignored, then the proportion of adults with equal-aged partners is approximately the same: $\chi^2_1 = 0.55$; N.S.

Within the narrow range of ages available for study (3 - 12 years) a high proportion of adults (particularly of young adults) would be expected to obtain a partner of a similar age to themselves through chance alone. To estimate what proportion of pairs would be expected to show age differences of 0, +1, +2 years etc. (given that mate selection occurred at random with respect to age) the following calculations were made : for each male cohort the probability of mating with a female of

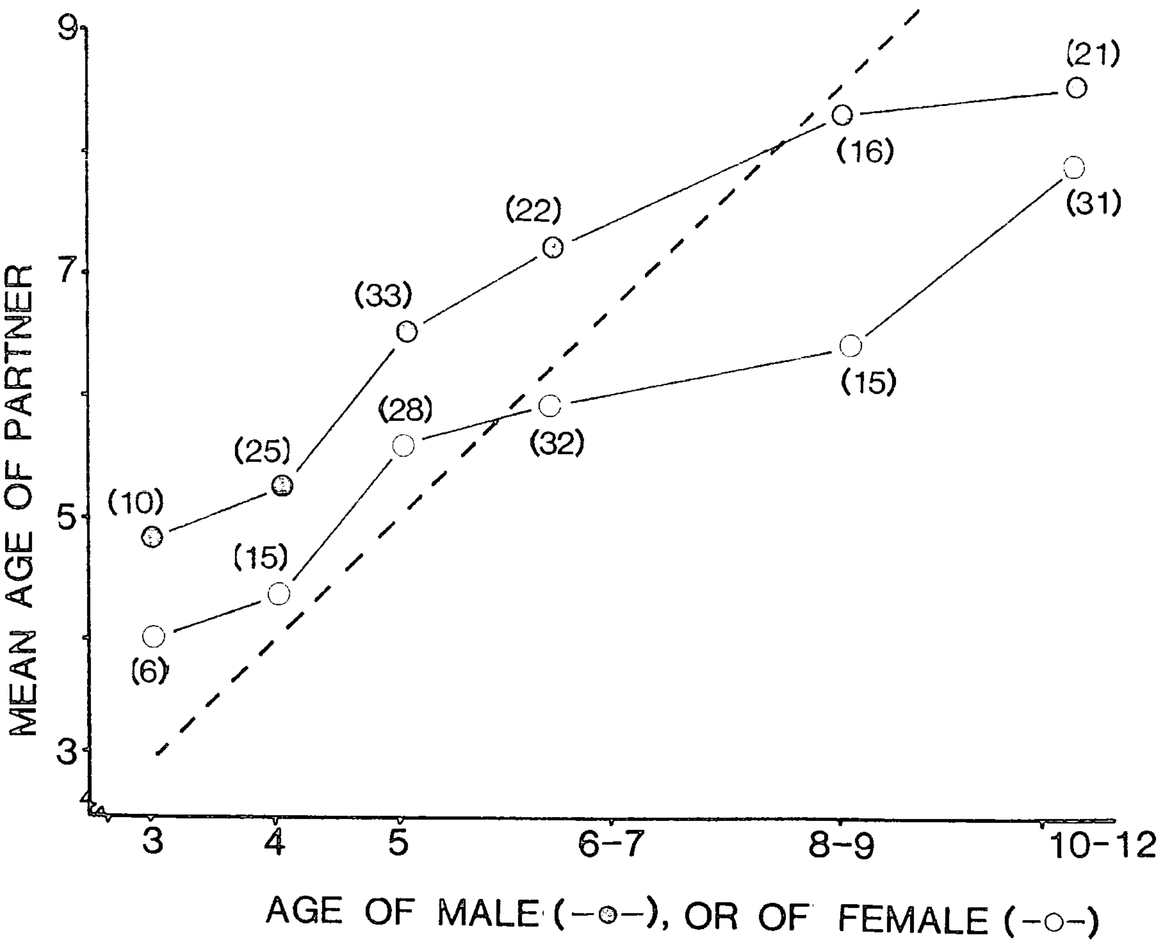
FIGURE 4.1: Age differences in 127 known-age pairs. In each case the age of the male was subtracted from that of the female.



Age of	Female younger								Female older						
male	-7	-6	-5	-4	-3	-2	-1	0	+1	+2	+3	+4	+5	+6	n
3								1	5	2	1			1	10
4							4	6	4	8	1	1		1	25
5						1	1	15	4	2	2	2	6		33
6						2	3	6	2	1	1	2			17
7									1		2	2			5
8						3	1		1		2	1			8
9			1		1	1		2	3						8
10			3			2	2	7	1						15
11			2				2								4
12	1						1								2
n	1	0	6	0	1	9	14	37	21	13	9	8	6	2	127

FIGURE 4.2: The mean age of partners in relation to that of their mate. Solid circles show the mean age of females with respect to that of the male. Open circles show the mean age of males with respect to that of the female. Sample sizes are shown in brackets.

- - - - equal age partners.



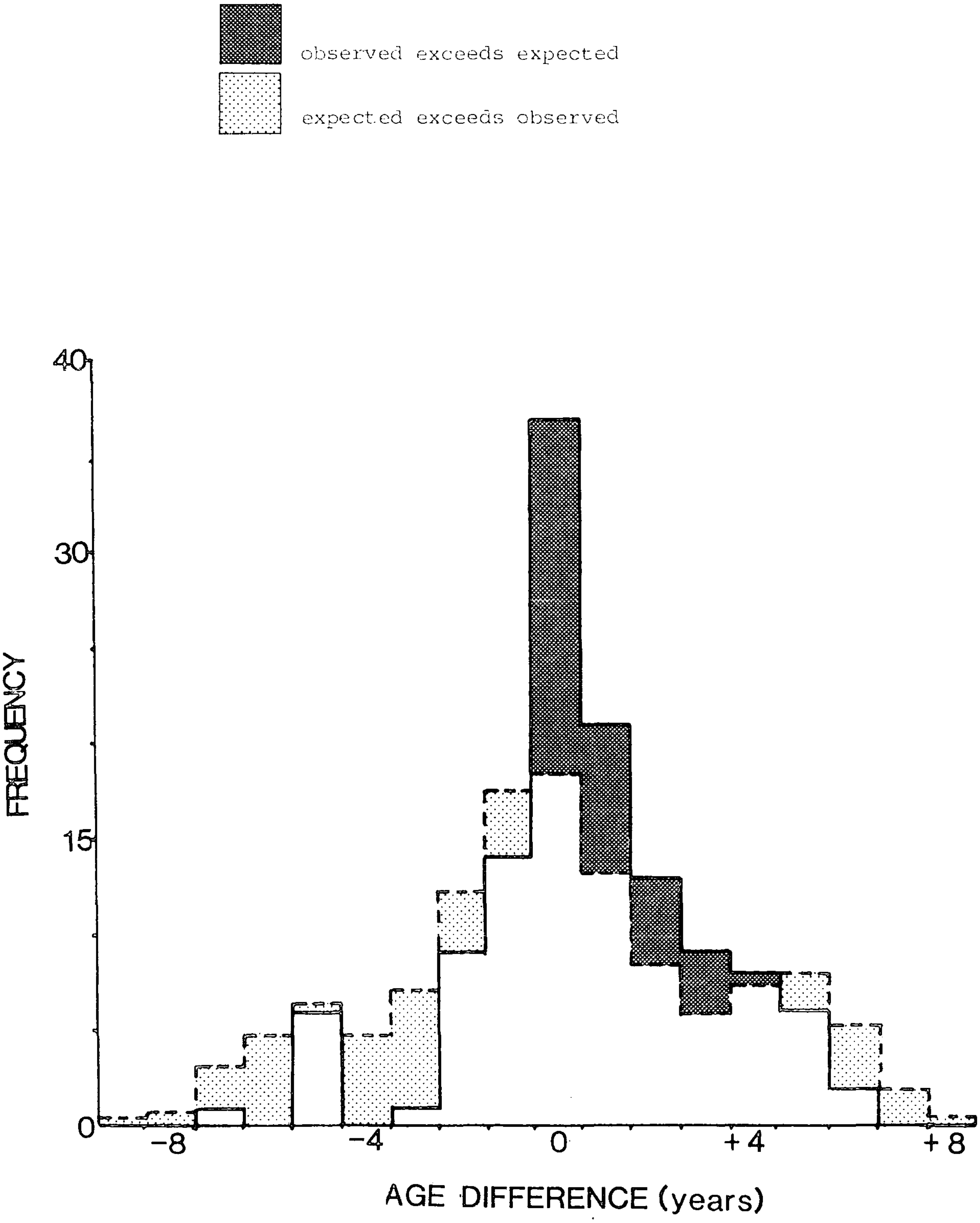
a particular age was estimated directly from the proportion of females recaptured at that age in 1980, and for those recaptured for the first time at one year older in 1981. Thus, if 25 % of female recaptures were aged 5, the probability of a three year old male obtaining a mate of '+2 years' was taken as 0.25. Of the 127 males in known-age pairs only 8 % were aged 3 years. Thus, their contribution to this age difference category was obtained by multiplying 0.25 by 0.08. Similarly, the proportion of 4 year old males (0.19) which obtained a mate of 6 years (0.04 of the female population) was calculated and also added to the age difference category of '+2 years'. This was repeated for each male cohort, and for each age difference category, from -9 to +8 years. The results were summed to give an 'expected' age difference distribution for the 127 pairs. Twice as many equal-age pairs arose (29 %) than would be expected through random mate selection (14 %) (Fig. 4.3). Overall, the observed age distribution showed a significant departure from that predicted through random mate selection : $\chi^2_4 = 18.47$; P = 0.001. This was partly due to the fact that fewer males than expected chose a mate younger than themselves (mean observed age difference = +0.6 years, expected difference = -0.1 years).

4.2 Age differences within 'changed' pairs

In successive years a pair bond may be re-established, or may change, either through the death of one partner, or through 'divorce'. Divorce occurred if both partners of a previous pairing (in 1980) were seen in the same colony (in 1981) but as members of a separate pair or pairs.

If, amongst established breeders, nest-site tenacity is high, first-time breeders are likely to obtain a mate of a similar age and status. This may lead to the observed similarities in partners ages throughout

FIGURE 4.3: The distribution of age differences within pairs. Solid lines show the age differences within 127 known-age pairs. The dashed line shows the expected distribution if mate selection by males occurred at random with respect to age.



the population. However, through death and 'divorce' the initially low age differences amongst first-time breeders would be expected to give way to a preponderance of mis-matched pairs unless a further constraint exists by which older individuals gain a new partner of a similar age to themselves. In the absence of such a constraint age-differences within 'changed' pairs should, on average, exceed that of stable 'same' pairs if the latter consisted originally of first-time breeders. There would be no further tendancy for partners ages to concur, except in the case of the largest cohort. Figure 4.4b shows that, as in all remaining pairs, the proportion of changed pairs (excluding pairs of first-time breeders) in which the partners ages concur (to within ± 1 year) was high; 56 % of changed pairs and 57 % of all other pairs (χ^2_1 = 0.012; N.S.). However, whilst the average age differential of partners in changed pairs was negatively skewed (females being on average younger than their new mates), that of all other pairs was positively skewed - by 0.95 years. A higher proportion of males in 'changed' pairs were older than their mates, when compared with males in 'same' pairs ($\chi^2_1 = 9.81$; $P<0.01$; Table 4.1). This may reflect the older average age within the former group (mean age of males known to have changed = 7.4 years; mean age of all other paired males = 5.7 years).

Thus it would appear that those birds which lose or 'divorce' their previous mate most often obtain a partner of an age close to their own - and to that of their previous mate. This may be further tested by examining the age differences of successive partners of each individual. In 39 cases where the age of each past and current partner is known, 31 % of new partners were one year older than their predecessor, supporting the view that mate selection was in some way age-related (Fig. 4.4c).

FIGURE 4.4: Age differences within a) 'Stable' pairs (i.e. all pairs other than those known to have changed since the previous season) and, b) newly formed changed pairs (excluding pairs of first-time breeders).

4.4c shows, for 'changed' pairs, the relative age of this year's partner with respect to that of last years partner. Age differences shown in years.

FIGURE 4.4:

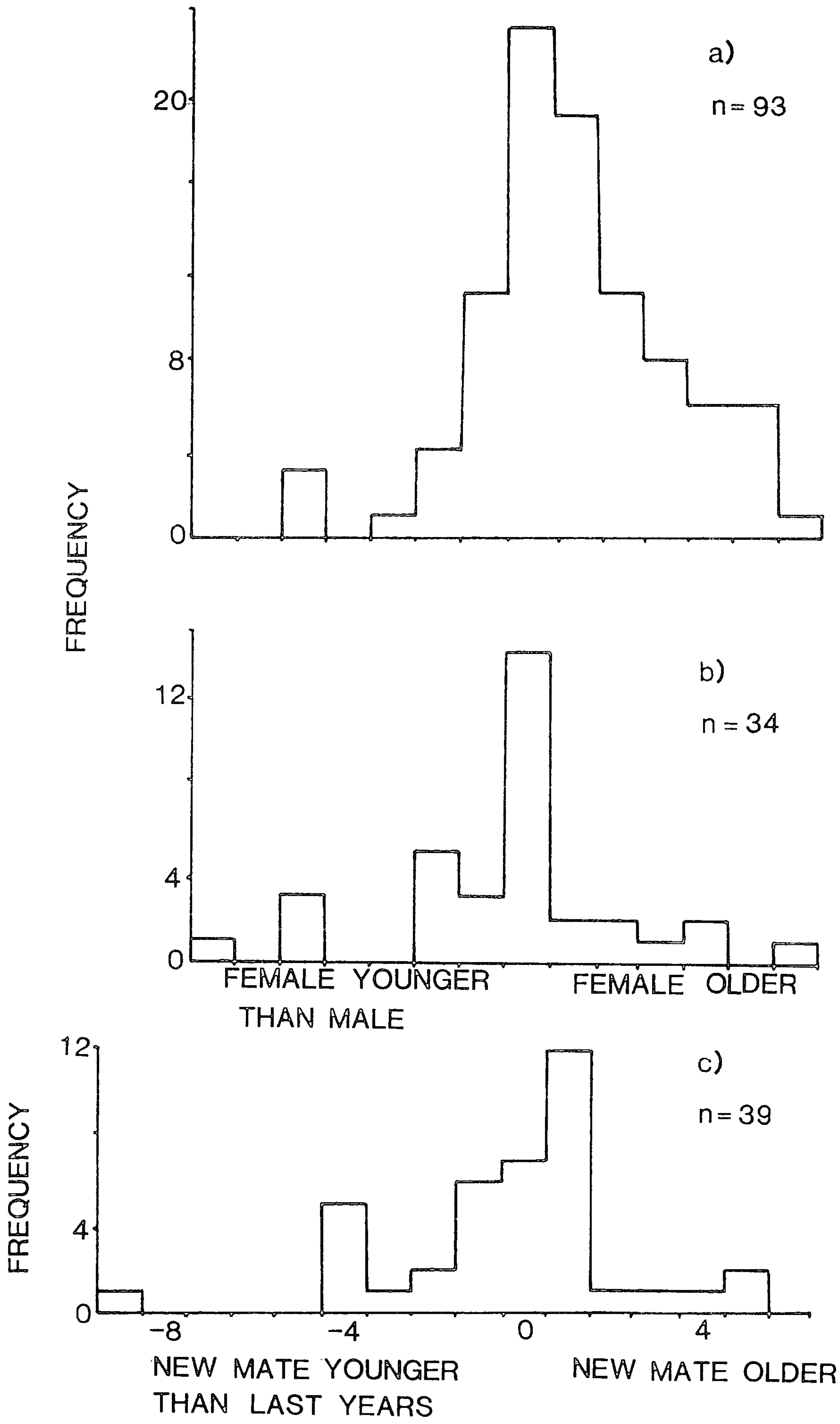

a)
n= 93
20
8
0
FREQUENCY
b)
n = 34
12
4
0
FEMALE YOUNGER THAN MALE
FEMALE OLDER
c)
n= 39
12
4
0
FREQUENCY
-8
-4
0
4
NEW MATE YOUNGER THAN LAST YEARS
NEW MATE OLDER

TABLE 4.1: Age differences within pairs known to have changed between years n and n + 1 (i.e. excluding first-time breeders), in comparison with 'same' pairs.

	Female :			
	younger	same age	older	n
Changed pairs	35 %	41 %	24 %	93
Same pairs	20 %	25 %	55 %	93

Age related variation in the time of return, pairing and laying has been described in a number of long lived species. This in itself may provide the basis for age-related mate selection if prospective partners in each cohort pass through each reproductive stage concurrently. However, in neither 1980 or 1981 was there evidence of a relationship between age and the timing of laying (see section 6.1.2). This does not rule out the possibility of an age effect on the timing of pair formation. Thus the mechanism by which age similarities are sustained within changed pairs remains unclear.

4.3 Pair stability in relation to age

Of 238 pairs which bred or attempted to breed in either year of the study, 77.3 % changed their mates between successive seasons. Variation between 1979-80 and 1980-81 was slight, in spite of the small sample size available in 1979-80 (Table 4.2).

The percentage of pairs which changed was thus significantly higher than that observed for *P. aristotelis* by Potts (1966) (51.9 % of 243 pairs; $\chi^2_1 = 43.62$; $P<0.001$). There was no significant relationship between age and pair stability, although 4 - 6 year-olds of both sexes showed a higher tendency to change their mates than did older birds (Table 4.3).

The death or disappearance of a mate between successive seasons accounted for 56.3 % of pair changes. The remainder were attributed to 'divorce', both partners being present at the colony in the following year (Table 4.4). There was no significant relationship between the age of either partner and the cause of mate change. The proportion of pairs which remated, of those in which both members survived, was 0.40.

TABLE 4.2: The proportion of pairs which change in successive seasons.

	1979-80		1980-81		Total	
	Percentage	n	Percentage	n	Percentage	n
CHANGED MATE	80.8	42	76.3	142	77.3	184
SAME MATE	19.2	10	23.7	44	22.7	54
TOTAL		52		186		238

The difference between 1979-80 and 1980-81 was not significant:

$\chi^2_1 = 0.44$; N.S.

TABLE 4.3: The proportion of pairs which change mates in successive years, in relation to age.

		Age in year 1		
		4 - 6	7 - 9	11 - 12
MALES	Change	82.2	64.3	76.9
	n	45	28	26
FEMALES	Change	85.7	68.7	58.3
	n	21	16	24

Differences with respect to age not significant :

Males, $\chi^2_2 = 2.71$, Females, $\chi^2_2 = 4.05$

TABLE 4.4: The proportion of pair changes attributed to the death or disappearance of one partner, or to 'divorce'.

	Years:		
	1979 - 1980	1980 - 1981	Both Years
Death	0.67	0.53	0.56
'Divorce'	0.33	0.47	0.44
n	34	131	165

The difference between years was not significant :

$\chi_1^2 = 2.20$; N.S.

4.4 Nest site tenacity, age and pair stability

In 1980 a grid of 37 4 x 4 m squares and 10 half squares (4 x 2 m) was marked-out on Shagnasty I and II (see Section 5). The position of each study nest within the colony was then noted from its grid square number. Of 85 males and 61 females relocated in 1981, 64 % and 54 % respectively, renested within their original 4 m area (differences between sexes not significant- Student's t test). For those birds which changed their nest-site square, the distance moved was measured from the centre of the 'old' square to the centre of the 'new' square. The average distance moved by females was similar to that moved by males: 4.96 m by males (n = 31) and 5.04 m by females (n = 28). Differences in the proportions of each sex which moved different distances were not significant (χ^2 analysis).

Age had no apparent influence on the tendency to change nest site squares between successive seasons (Table 4.5). Also, for males, there was no significant relationship between site tenacity and pair stability (Table 4.6). However, of those females which moved site, a higher proportion changed their mate than those which stayed ($\chi^2_1 = 10.51$; $P<0.005$).

The question arises as to whether females lose their previous mate by changing sites, or change sites following mate loss. Table 4.7 shows that there was no significant difference in site tenacity of divorced and bereaved birds. Slightly more <u>males</u> that stayed on their previous site underwent divorce than those which changed sites. For females, twice as many birds changed sites as those which stayed. The ratio was almost the same for bereaved as for divorced females. However this question cannot be resolved without a knowledge of the timing of divorce; if the female returns to an old site to find her partner already

TABLE 4.5: Variation with respect to age group in the proportion of birds which changed nest site squares between seasons.

	AGE GROUP		
	5 - 7	8 - 10	11 - 12
% change squares	42 %	42 %	38 %
n	33	24	13

Differences not significant:

$$\chi_2^2 = 0.065$$

TABLE 4.6: The relationship between site tenacity (the tendency to re-nest in the same 4 m^2 in successive seasons) and pair stability.

	MALES		FEMALES	
	Move site	Stay	Move site	Stay
Change mate	25 %	38 %	40 %	19 %
Retain mate	10 %	27 %	9 %	32 %
	n = 71		n = 53	
	$\chi^2_1 = 1.46$; N.S.		$\chi^2_1 = 10.51$; $P<0.005$	
	No relationship between site tenacity and pair stability.		Mate change and site change are positively related. Mate retention is most often associated with site tenacity.	

TABLE 4.7: The relationship between site tenacity and the occurrence of bereavement and divorce.

	MALES		FEMALES	
	Move site	Stay	Move site	Stay
Divorce	29 %	40 %	41 %	21 %
Bereavement	11 %	20 %	11 %	20 %
	n = 35		n = 29	
	Fisher's Exact Test : P = 0.27; N.S.		Fisher's Exact Test : P = 0.30; N.S.	

paired-off, then divorce in this case will have an equivalent effect to bereavement.

For females, the tendency to move to a new nest square was not influenced by whether she had bred successfully (i.e. had raised at least one young to fledging age) in the previous season. More males however, moved to a new nest square following breeding failure (Table 4.8). For both sexes in the subsequent season neither the laying date, the number of chicks fledged, or the chance of complete breeding failure were influenced by a movement between nest squares.

4.5 Pair stability and laying date

Mate change in the Kittiwake may delay the date of laying (Coulson and Thomas 1983). Females in changed pairs lay at a later average date than they had done in the previous season. This effect did not occur at a statistically significant level in the Blue-eyed Shag. In 1981, female shags which had changed their mate began laying, on average, 1.2 days later than those which had retained their previous mate (Table 4.9a). All females began laying 4.5 days later (on average) in 1981 than in 1980. This difference was greater for females which had changed their mate in the intervening years (5.1 days later) than for females in stable pairs (3.8 days later), though not statistically so (Table 4.9b).

Much of the variation in the timing of laying can be attributed to individual differences; in successive seasons each female shows a high degree of constancy in the date on which she lays. In the Blue-eyed Shag there was a positive correlation between the laying dates of the same females in successive seasons ($r = +0.42$; $n = 115$; $P<0.001$). For females in stable pairs the correlation was slightly stronger than for

TABLE 4.8: The relationship between site tenacity (the tendency to re-nest in the same 4 m square in successive seasons) and breeding success in the first season. 'Successful' pairs are those which produced one or more fledged offspring in 1980.

	MALES		FEMALES	
	Move site	Stay	Move site	Stay
Bred successfully	27 %	57 %	42 %	49 %
Failed	9 %	7 %	7 %	2 %
	Fisher's Exact Test : $P = 0.058$; N.S.		Fisher's Exact Test : $P = 0.14$; N.S.	

TABLE 4.9: Differences in the average laying date of females which change or retain their previous mate.

a) Average laying dates in one season (1981).

	Mean date	S.D.	n
Same pairs	15.1	3.45	37
Changed pairs	16.3	3.98	89

Student's t = 1.77; 124 d.f. N.S.

b) Average change in the laying dates of the same individuals in successive years (1980 and 1981).

	Mean difference in laying date	S.D.	n
Same pairs	+ 3.8 days	7.46	35
Changed pairs	+ 5.1 days	6.69	72

Student's t = 0.87; 105 d.f. ; N.S.

those in changed pairs (r = +0.47 and +0.44 respectively), and this was reflected in the degree of scatter around each regression slope : variance = 0.14 and 0.26 for females in stable and changed pairs respectively; F = 1.90; d.f. = 65, 34; P<0.05. Thus mate change had a disruptive influence on the individual's tendency to lay on or around a particular date.

4.6 Pair stability, clutch size and breeding success

Breeding success may influence, and may in turn be influenced by pair stability. Kittiwakes which fail to produce chicks in one season are more likely to change their mates in the following season than are those which bred successfully (Coulson and Thomas 1983). In the Blue-eyed Shag a similar effect was observed, although the results were not statistically significant. Of 168 males which bred successfully in 1980 76 % changed their partners in 1981, compared with 84 % of 38 males which failed in 1980 (difference not significant; Table 4.10a). Similarly, there was a positive, though non-significant relationship between breeding success and mate retention; 57 % of successful pairs underwent 'divorce' compared with 65 % of failed pairs (Table 4.10b).

Although there is a degree of constancy in the laying dates of different individuals, there was no evidence of individual constancy in clutch sizes between 1980 and 1981 (Table 4.11). Mate change had no apparent effect either on clutch size, brood size (at hatching) or on the number of chicks fledged per pair (Table 4.12). A summary of the main results of Section 4 is given in Table 4.13.

Discussion

For Blue-eyed Shags there appears to be little adaptive significance in maintaining pair stability. Females which changed their mates began

TABLE 4.10: The relationship between breeding success in 1980 and the occurrence of mate-change in 1981. 'Successful' pairs are those which produced one or more fledged offspring in 1980. In a), all pair changes were considered, whilst in b) the frequency of 'divorce' alone was considered.

		Breeding Performance in 1980	
		Successful	Failed
a)	% change by 1981	76.2	84.2
	n	168	38
		$\chi^2_1 = 1.14$; N.S.	
b)	% divorce by 1981	56.9	64.7
	n	93	17
		$\chi^2_1 = 0.34$; N.S.	

TABLE 4.11: Clutch sizes laid by the same females in two successive seasons. There were no clutches of one recorded in the 1981 sample.

		Clutch Size in 1980		
		1	2	3
Clutch sizes from the same females in 1981.	2	2	7	14
	3	0	48	84

$\chi^2_2 = 0.061$; N.S.

$n = 155$

TABLE 4.12: Variation in clutch size, brood size and the number of chicks fledged in 1981 by females which had changed or retained their previous mate from 1980.

		Clutch size, brood size, or the number of chicks fledged					
		0	1	2	3	n	Mean
Clutch size	Same mate	0	0	7	34	41	2.8
	Changed mate	0	0	22	103	125	2.8
					$\chi^2_1 = 0.007$; N.S.		
Brood size	Same mate	1	2	8	23	34	2.5
	Changed mate	1	9	27	64	101	2.5
					$\chi^2_1 = 0.16$; N.S.		
Chicks fledged	Same mate	1	4	17	6	28	2.0
	Changed mate	5	15	40	17	77	1.9
					$\chi^2_2 = 0.87$; N.S.		

TABLE 4.13: Summary of the main results of Section 4

	Percentage of partners of same age.	Percentage of partners of within ± 1 year.
All pairs	29 %	57 %
Same pairs	24 %	57 %
Changed pairs	41 %	56 %
Age similarities expected through random mate selection	14 %	38 %

	Percentage of pairs change annually.
All pairs	77 %
Through death	43 %
Through divorce	34 %
Successful breeders	76 %
Unsuccessful breeders	84 %
Female stays in breeding square	37 %
Female changes breeding square	81 %

	Mean laying date	Mean difference in laying date
Females which change mate	16.3	+ 5.1 days
Females which retain mate	15.1	+ 3.8 days

	r
Correlation between laying dates of same females in successive seasons	+ 0.42
Stable pairs	+ 0.47
Changed pairs	+ 0.44

laying slightly later (on average) than those which had retained their previous mate. Also, mate change was more common amongst pairs which had failed than those which had successfully fledged at least one young in the previous season. However neither of these effects were significant. Nor was there any evidence that mate retention influenced breeding success. Perhaps because of this the proportion of pairs which remate in successive seasons is low : 22.6 % compared with 48.1 % of European Shags (Potts 1966). Amongst the phalacrocoracids only the Flightless Cormorant is known to change partners at a higher rate : 11.9 % of pairs stay together for successive breeding attempts (Harris 1979). Several other seabird species have very much higher rates of mate retention, e.g. : Kittiwakes : 64 % (Coulson 1966), Red-billed Gulls : 82 % (Mills 1973), Fulmar : 90 - 91 % (Ollason and Dunnett 1978), Razorbills : 72 % (Lloyd 1979).

Male Blue-eyed Shags which bred successfully are more likely to remain within their previous breeding square than are those which fail, but are as likely to aquire a new partner as are those which move away. The divorce rate of males which stay is similar to that of those which move. Females, conversely, show no greater tendency to remain within a breeding square following a successful breeding attempt. But if they do remain, they more often retain the same mate. Both divorce and the death of a partner were associated with a reduced chance of the female returning to the same site. These results suggest that whilst males select and defend a site, it is the female which selects a new - or familiar - site and mate. As with pair stability however, site retention did not influence the timing or success of the subsequent breeding attempt.

In most cases of mate change the new partners will be of a similar age. Although it was suggested that age similarities within paris might arise mainly through the pairing of first-time breeders, and might be maintained through strong pair stability, it would appear that the average age differences amongst young pairs were no less than amongst old pairs (Fig. 4.1), and pair stability was low in all age-groups (Table 4.3).

There remains three explanations for the prevalence of age similarities within pairs : firstly, that the timing of pairing (though not of laying; Section 6.1.2) was age-graded. Secondly, that females were able to discern, and then select, partners of a similar age to themselves, or that, throughout the colony, the dispersion of breeders was clumped with respect to age. Potts (1966) has shown that in the European Shag age, the timing of pairing and of laying are inter-related: older birds return and pair early, and also build and lay early. Thus it would seem unlikely that Blue-eyed Shags should show an age-related response to the timing of pairing, but not to laying. If older adults do show an earlier response to, for instance, increasing day length, then the expression of this tendency (for early pairing) would, in most seasons be severely disrupted by poor weather and sea-ice conditions throughout August to October. In 1980 and 1981 each colony was occupied and then abandoned many times during August and September, apparently leaving little scope for the development of an age-graded sequence in site occupancy and pairing.

Though mate selection on the basis of age alone cannot be examined directly from the data available, its occurrence may be inferred if the age distribution throughout the colony was random, rather than clumped. The dispersion of known-age breeders throughout each colony is examined in Section 5.

SECTION 5

The position and quality of the nest site

Introduction

Nest site quality is the main determinant of breeding success of European Shags on the Farne Islands (Potts *et al* 1980). This is because egg and chick mortality - rather than variation in clutch size - strongly influences breeding success, and is in turn dependent on the degree of exposure to rain, and to high seas, and on the capacity of the nest site. High quality nest-sites were in limited supply ; the average nest site quality score declined as the colony grew, and showed a marked increase following a local population crash. The use of low ledges, terraces and gullies undoubtedly contributes towards the high degree of variation in site quality, and is in marked contrast to the type of nest sites used on Signy Island. The three main colonies of Blue-eyed Shags (on Shagnasty) are on flat or gently sloping rock, and show less variation in the degree of exposure to the elements, or in the proximity of the nest sites to the sea. Hence, the contribution made by the quality and position of the nest site to variation in breeding success should be less than in the European Shag.

5.1 Assessment of nest-site quality

Potts *et al* (1980) used a three point scale for assessing nest-site quality of European Shags. Four nest site characteristics were measured: degree of exposure to high seas, and to rain, the capacity of the site, and its access to the sea. These criteria were used in the present study, but with adjustments to the level of scoring in accordance with climatic conditions. The degree of social contact was also assessed on a three point scale. Each site was scored as follows :

i) Degree of social contact with nearest neighbours.

Score:

1. No other pairs nesting within two metres of the site.
2. One pair nesting within two metres on one or two sides of the site.
3. One pair nesting within two metres on each of three or four sides of the site.

ii) Protection from wave damage.

Score:

1. Nest unlikely to be destroyed by wave action in any weather during the breeding season.
2. Nest likely to be effected by wave action when wind stronger than force 8.
3. Wave damage likely, even in moderate sea conditions (less than force 8 wind).

iii) Exposure to wind or snow.

Score:

1. Exposed on one or two sides only.
2. Exposed on three or four sides, but situated in a relatively sheltered hollow, adjacent to a ridge, or below an overhang.
3. Completely exposed on all four sides, no local shelter.

iv) Nest site capacity.

Score:

1. Sufficient room for three large chicks plus one parent.
2. Sufficient room for only one or two large chicks plus parent.
3. Insufficient room for even one large chick plus parent.

v) Access to sea.

Score:

1. Unrestricted : no inhibition from neighbouring sites or local topography, site overlooking water.
2. One or more sites between nest and sea, but nest on raised bluff.
3. Access to sea restricted by neighbouring sites, nest on flat rock.

5.2 Variation in nest site scores between seasons and between colonies.

The consistency of scoring was assessed by comparing results for each colony in successive years. Table 5.1 shows that the agreement between consecutive season's scores within one colony was almost always greater than between colonies in one season. The only instance where a significant difference in the scores for two successive seasons was found, was for nest site capacity at North Point. Here, six nests were assigned a score of '2' in 1981, instead of '1'. With this exception, the results suggest that little or no observer bias occurred between seasons, and hence that the system of scoring was robust.

At North Point the majority of nests were built on ledges and terraces on a small vertical cliff face. In comparison with Shagnasty the degree of social contact between nests was low, but with less exposure to rain and snow, and better access to open water (Table 5.1). Similarly, at Shagnasty III the degree of social contact and exposure to rain were less than at Shagnasty I and II, but with poorer access to and from nest sites. Consequently, in the analyses which follow only the large sample of results for Shagnasty I + II are considered.

TABLE 5.1: Mean scores for each measure of nest site quality at each colony in 1980 and 1981.

		Social Contact	Wind Exposure	Wave Exposure	Site Capacity	Access
Shagnasty I + II	1980	2.59	2.97	1.22	1.01	1.87
	1981	2.54	2.99	1.24	1.02	1.97
	1980+81	2.56	2.98	1.23	1.02	1.92
	n =	527	528	527	528	524
Shagnasty III	1981	2.17	3.00	1.48	1.04	1.66
	n =	102	102	102	102	102
North Point	1980	2.22	2.92	1.62	1.00	1.44
	1981	2.06	2.90	1.60	*1.10	1.50
	1980+81	2.13	2.91	1.61	1.06	1.47
	n =	111	111	111	111	111

*Difference between seasons significant: Fisher's Exact Test on distribution of scores; $P<0.02$.

5.3 Adult age and nest site quality

Most old males occupied nest sites which were in closer contact with neighbouring nest sites than those of younger birds ($\chi^2_2 = 6.43$, $P<0.05$; Age groupings 3 - 5, 6 - 10, 11+ years; Fig. 5.1). No such relationship was evident for females of 3 - 9 years, but there was a significant difference in the 'social contact' scores for females of 3 - 9 years and 10 - 12 years (mean scores = 2.44 and 2.71 respectively, $\chi^2_1 = 11.23$, $P<0.001$). There was no relationship between any other nest site quality variable and the age of either partner.

5.4 Nest site quality, laying date and breeding performance

The mean laying date for each quality score, for each site variable, was compared by analysis of variance. Results for 1980 and 1981 were considered separately since the onset of laying and the distribution of laying dates for the two years differ (Section 6.1.2). There were no significant differences in the mean laying dates at sites with different scores for each variable. Social contact with three or more neighbours (within 2 m) did not advance the date of laying, but was associated with more synchronous laying in 1981 (Table 5.2). A similar trend occurred in 1980, though not to a significant degree. There were no significant differences in clutch size, egg survival, initial brood size or the number of chicks fledged, from nests with different quality-scores (χ^2 analysis).

5.5 The effects of nest site position within the colony

On Shagnasty I + II a grid comprising 37 squares (of 4 m^2) and 10 half squares (each 4 x 2 m) was marked out, and the study nests within each square identified (see Section 4.4). The aim was to assess variation in nest site characteristics, adult age and breeding performance

FIGURE 5.1: Variation in the degree of social contact with neighbouring nest sites, in relation to the age of the male owner. Each nest site was accorded a 'social contact' score (see text), and the mean score calculated for each age group. Sample sizes are shown in brackets. 1 S.E. shown on either side of the mean.

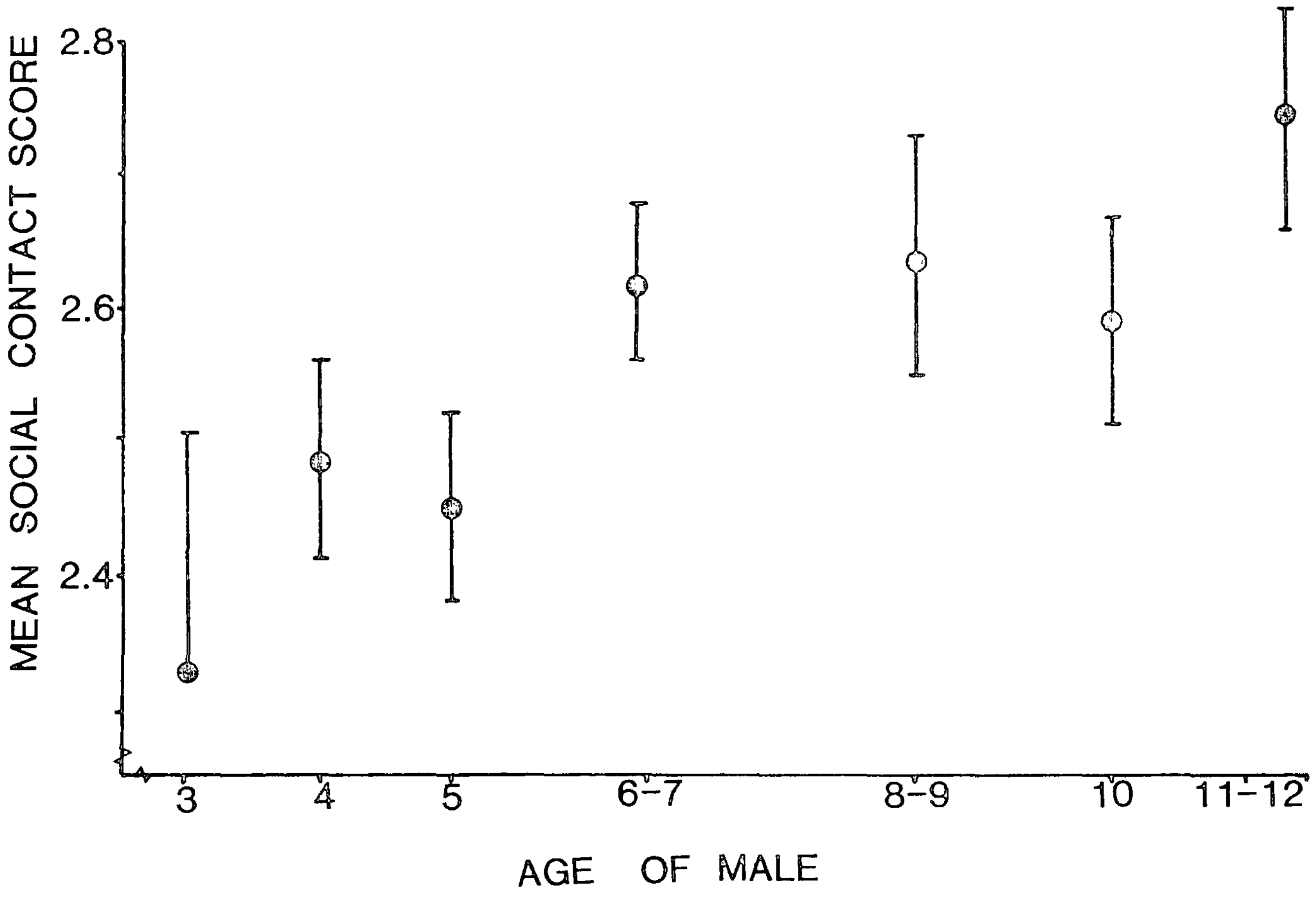

MEAN SOCIAL CONTACT SCORE
2.8
2.6
2.4
3
4
5
6-7
8-9
10
11-12
AGE OF MALE

FIGURE 5.1:

TABLE 5.2: The average laying date at nests with different social contact scores. Those nests with a high level of social contact scored '3', whilst those within the range of little or no social contact scored '1' (see Section 5.1 for details).

There was no significant relationship between laying date and social contact score (Student's t test comparing scores of '2' and '3', and also '1 + 2' and '3').

	Social contact score	Mean laying date	S.D.	n	
1980	1	27.6	5.18	8	F = 1.71;d.f. = 160,7; P = 0.23
	2	24.1	7.70	109	F = 1.29; d.f. = 108,160; P = 0.07
	3	22.9	6.77	161	
1981	1	18.3	5.21	14	F = 1.39; d.f. = 13, 156; P = 0.17
	2	16.8	5.12	147	F = 1.35; d.f. = 146,156; P = 0.03
	3	16.2	4.41	157	

throughout the colony. However, within most squares nest sample sizes were too low to allow statistical comparisons, and so squares were grouped together to provide sample sizes of greater than 30 nests. Each square was thus assigned to one of three groupings, depending on it's position with respect to the 'centre' or 'edge' of the colony. Since there was no obvious centre to Shagnasty I + II, the groups were defined as follows:

a) 'Central' squares : all four sides of the square abut onto an adjacent square.

b) 'Intermediate' : one side of the square forms part of the colony edge.

c) 'Edge' : more than one side of the square forms part of the colony edge.

Figure 5.2 shows the distribution of each square type.

5.6 Variation in nest-site quality throughout the colony

Pairs nesting within 'central' squares experienced a significantly greater level of social contact than those on the 'edge' of the colony (Table 5.3). Although they suffered less from wind and wave exposure, access to and from these sites was more restricted. Differences between central and intermediate areas were less marked, and were significant only with respect to the degree of access shown. Differences throughout the colony may relate to variation in the age or 'quality' of the adults, or in their experience in selecting sites, but are more likely to reflect physical constraints of 'edge', 'intermediate' and 'central' nesting areas themselves.

5.7 Age variation throughout the colony

In Section 4 it was shown that age differences within pairs are, on average, less than would be expected from random mate selection. It

FIGURE 5.2: The distribution of 'central', 'intermediate' and 'edge' 4 m squares at Shagnasty I + II. See text for definition of each type.

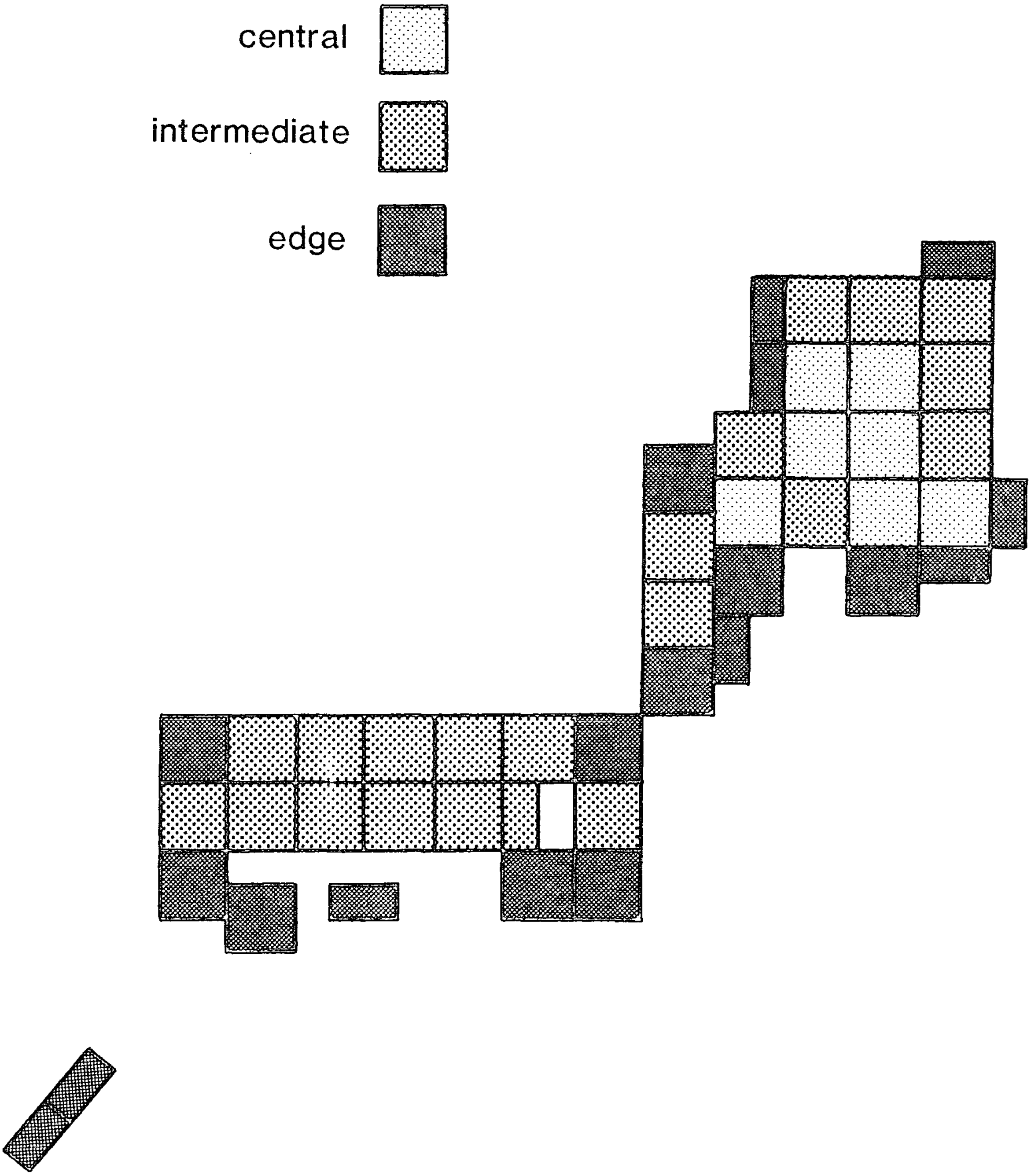


TABLE 5.3: Variation in nest site quality scores with respect to position within the colony. 'Central', 'intermediate' and 'edge' squares are defined in the text. Mean scores given for each group. χ^2 analyses were made of the proportions of each score in 'central', 'intermediate' and 'edge' squares.

	Central	Intermediate	Edge	χ^2	d.f.	P
Social contact	2.76	2.68	2.41	31.73	2	<0.001
Wind Exposure	1.13	1.08	1.42	56.27	2	<0.001
Wave Exposure	1.02	1.02	1.04	Fisher's Exact :		0.05
Site Capacity	1.00	1.00	1.02	Fisher's Exact :		0.18
Access	2.56	1.96	1.58	70.01	4	<0.001
n	59	169	171			

was suggested that in the absence of age-related variation in the time of pair formation, such age similarities might arise through strong site tenacity in conjunction with a "clumped" age distribution. Table 5.4 shows that male age varied significantly between the three colony areas described above, but with a preponderance of older males at the "intermediate" rather than at "central" nest-sites. The same pattern was shown by female age, but not to a significant degree.

To determine whether age similarities occur on a much smaller scale, the age distribution in 4 m squares was examined using a sequence of running means. The ages of breeders within one square were combined with those from its two laterally adjacent neighbours (to increase each sample size) and the mean result attributed to that square. Fig.5.3 shows that squares with similar mean ages were clumped within the colony. However it should be noted that between clumps the difference in the mean age of males is small ; only one year, whilst within clumps the average age span is wide ; 8.07 years. Moreover, an autocorrelation comparing contiguous pairs of squares in sequence failed to show any relationship between the mean ages of males in successive neighbouring squares ($r = 0.28$, 16 d.f., $P = 0.27$). Thus there is no evidence of age-clumping on a small scale, i.e. within the distance normally moved between successive nesting attempts (Section 4.4).

There was no significant variation in the timing of laying, clutch size, initial brood sizes, or in the number of chicks fledged from nests in central, intermediate and edge squares.

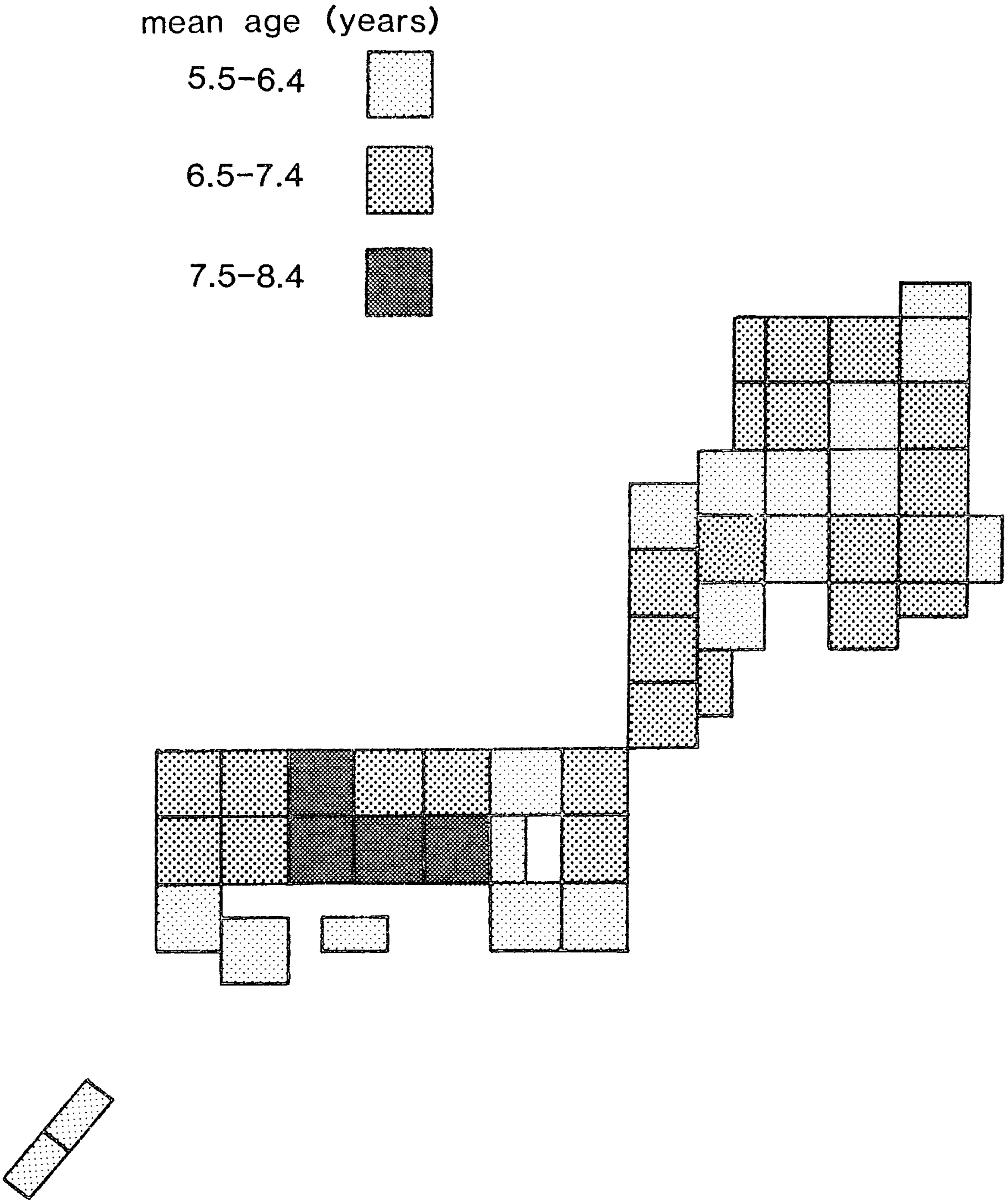
Discussion

Older adults selected, or more successfully competed for, those sites which provided greater opportunities for social contact. Such sites were commonest in the centre and intermediate areas of the colony.

TABLE 5.4: Variation in the age of nest site owners in relation to the position of the nest. For χ^2 analysis three age groups were used : 3 - 5, 6 - 9 and 10+ years.

	Nest Site Square:			χ^2 analysis on the proportions of each age grouping:		
	Central	Intermediate	Edge	χ^2	d.f.	P
Mean age of Male	6.09	7.19	6.44	10.58	4	<0.05
n	31	87	102			
Mean age of Female	7.22	7.51	6.96	2.90	4	N.S.
n	23	61	54			

FIGURE 5.3: Variation in male age throughout the colony. Each mean was calculated from the results from 3 adjacent squares.



Conversely, young adults more often nested on sites with little or no social contact (within 2 metres of their site). Several studies have demonstrated a positive relationship between nest density and the efficiency of breeding (but see Coulson *et al* 1982). The time of return to the colony and the date of laying is earlier in larger, denser colonies of Fulmars (Fisher 1952), Kittiwakes (Coulson and White 1956) and Gannets (Nelson 1978). Also, centrally nesting Kittiwakes, and Brünnichs Guillemots nesting in dense areas within a colony, fledged more young (Coulson 1968, Gaston and Nettleship 1981). At least for the Kittiwake this was due to differences in the 'quality' of centre and edge nesters. These effects have more often otherwise been attributed to 'social stimulation' from neighbouring birds (Darling 1938). Yet there was no evidence that increased social contact between, or central nesting by Blue-eyed Shag pairs led to early laying or an improved breeding output.

Of the few studies in which nest site characteristics have been examined, nest density (or the degree of social contact) has been shown to be one of the more important predictors of breeding success. Birkhead (1977) found that densely nesting Common Guillemots lost fewer chicks to predators. Gaston and Nettleship (1981) described an increase in chick production by Brünnichs Guillemots as the number of nearest neighbours increased from 0 to 2, but a reduction for those with 3 neighbours. In the present study egg loss (partly through predation by Wattled Sheathbills) was less common for clutches begun at the middle than at the beginning of laying period (Section 6.3.3). However, although densely nesting Shags (with 3 or 4 nearest neighbours) laid more synchronously than did those with 0 - 2 nearest neighbours, they suffered no less from egg loss.

Perhaps surprisingly, more older adults tended to nest within intermediate squares than in central squares. However, the differences in nest-site quality scores within these two areas were less than between intermediate and edge sites and between central and edge sites.

SECTION 6: Seasonal and age effects on clutch size and egg volume.

6.1 The timing and spread of laying

In birds, hatching is usually timed to coincide with a period of high food abundance (Perrins 1970). Since clutch-initiation must occur in advance of this favourable period, factors which precede high food availability - i.e. changes in the photoperiod, rainfall, water level or ambient temperature - may be used to time the onset of laying.

Laying dates may be further influenced by the availability of food for egg formation, particularly in the case of small birds with large clutches, into which eggs are laid at daily intervals (Perrins 1970). However, amongst seabirds, the eggs are usually laid at intervals of 2 - 3 days, and in the phalacrocoracids egg weights are extremely low in relation to the weight of the adult female (Heinroth 1922, Lack 1968), perhaps due to constraints arising from incubation on the toes and webs. Thus, the demands made on the female's food intake are likely to be much less than for other nidicolous species.

Within the optimal laying period, individuals of colonial species may vary the timing of each breeding event (albeit with less latitude) to coincide more closely with that of their neighbours. This effect may be mediated through 'social stimulation' (Darling 1938), or through a similarity in the ages, experience and breeding condition of various sub-groups within the colony (Coulson and White 1960, Gochfeld 1980).

That the timing of breeding is also at least partly influenced by adult age and experience is now well established in a number of seabird species : the Short-tailed Shearwater (Marshall and Serventy 1956), Kittiwake (Coulson and White 1960), Sooty Shearwater (Richdale 1963), Laysan Albatross (Fisher 1969), Adelie Penguin (Le Resche and Sladen 1970), Red-billed Gull (Mills 1973), Herring Gull (Chabrzyk and Coulson 1976), Manx Shearwater (Brooke 1978) and Fulmar (Ollason and Dunnet 1978).

Within the Pelecaniiformes laying date has been shown to be age-dependent in the Gannet (Nelson 1966), European Shag (Potts 1966) and Brown Pelican (Blus and Keahey 1978).

The breeding ranges of the species listed above collectively span several regions, from North temperate to Antarctic. For those species breeding at high latitudes, a shortened season, and various environmental factors may impose restrictions on the species laying and hatching span, perhaps inducing pairs of all ages to lay as early as conditions will permit (Belopol'skii 1961, Croxall 1983).

6.1.1 Seasonal variation in laying

On Signy Island Blue-eyed Shags normally begin laying during the last week in October. The date on which the first egg in the colony was laid has been recorded in 16 seasons between 1953 and 1981. The earliest recorded laying date was 17 October (1957), and the latest, 10 November (1965 and 1981). Of the 16 dates, 7 fell within a 5-day period. The average date on which laying commenced was 1 November ± 6.67 days (I S.D.) (Table 6.1).

Seasonal variation in the onset of laying (25 days) was thus considerably less than that found for *P. aristotelis* on the Farne Islands by Potts (1966) (43 days between extreme dates; S.D. = 12.50 days) over approximately 20 seasons. At a northern colony of *P. aristotelis* (the Seven Islands, Murmansk, 80°N) variation in the onset of laying was more similar (Range = 28 days ± 5.20; S.D.), but the dates are for only 7 seasons (Belopol'skii 1961).

There was no relationship between the weather during early spring and the earliest laying record in each of 16 seasons. Laying dates were compared with the mean monthly, mean minimum and mean maximum air temperatures for September and October, and also with the number of days

TABLE 6.1: Variation in the date on which the first egg was laid in 16 years between 1952 - 1981.

Laying Date	Number of records	Years
17 October	1	1957
26 October	1	1969
27 October	2	1952, 1958
28 October	1	1980
29 October	2	1955, 1960
30 October	1	1970
2 November	1	1968
3 November	2	1961, 1979
7 November	1	1959
8 November	1	1954
9 November	1	1972
10 November	2	1965, 1981

of snowfall, and of gale-force winds in October. Unfortunately there are insufficient data with which to compare the timing of laying with the degree of sea-ice cover in September - October.

The span of egg laying was short, covering 34 days (S.D = 6.77) and 24 days (S.D. = 4.58) at the large study colony (Shagnasty; 448 and 316 clutches in 1980 and 1981 respectively). At North Point 35 and 44 clutches were laid over periods of 19 (S.D. = 6.77) and 26 days (S.D. = 6.86) in 1979 and 1980. By comparison, at a Blue-eyed Shag colony at Grytviken, South Georgia in 1980 egg laying commenced 9 days later than at Signy Island, and covered a span of 47 days (48 clutches)(P. Lennard-Jones, *pers. comm.*).

These laying periods were each less than half that recorded for the European Shag in the Farne Islands (approximately 70 days) over two seasons, in which the sample sizes were 295 and 332 nests (Potts 1966). Thus, although the timing and spread of laying of Signy Island Blue-eyed Shags was more restricted than that of one temperate congener, the degree of laying synchrony was still slightly lower than that shown by most Antarctic seabirds (Croxall 1983).

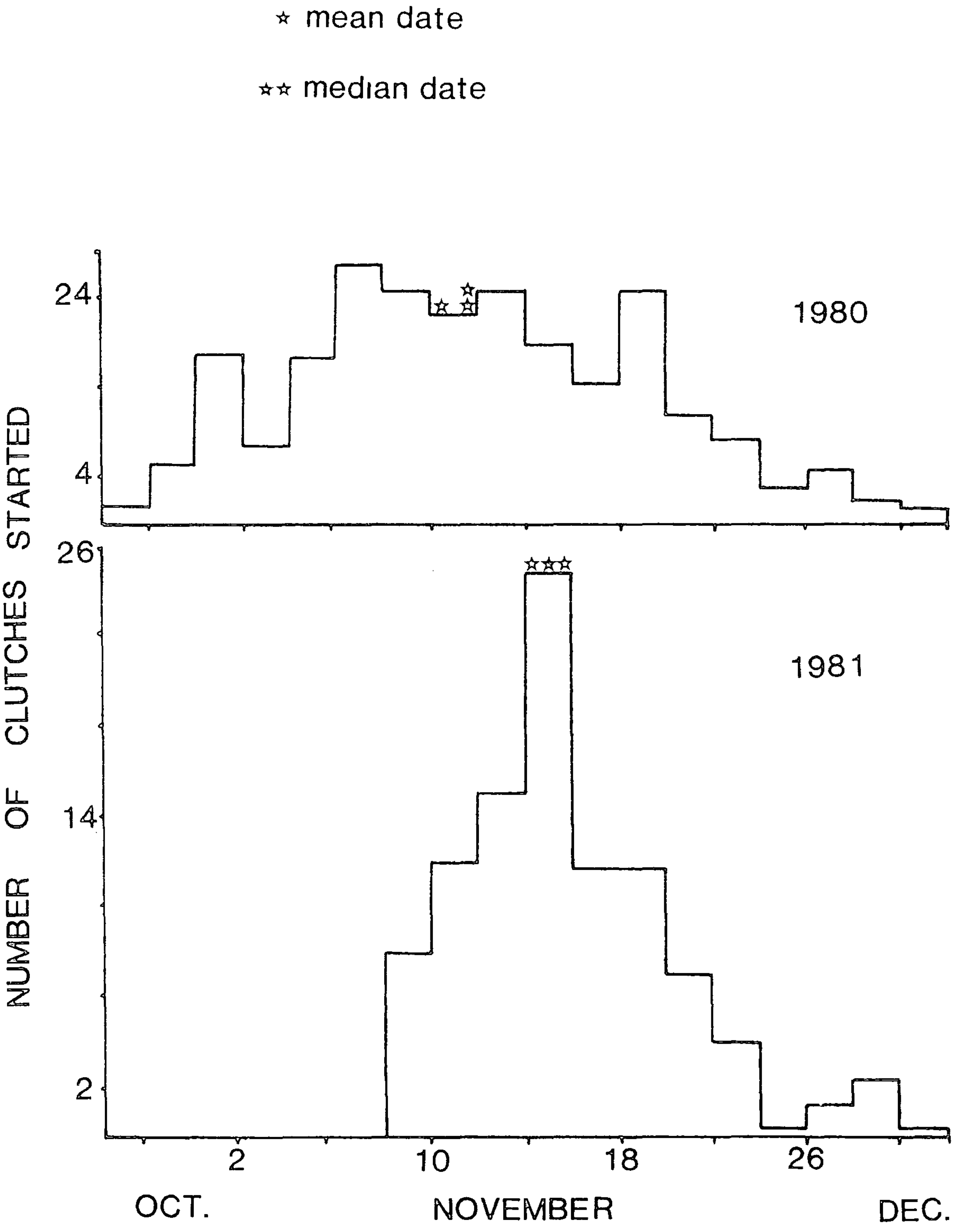
The pattern of egg laying at Shagnasty in both seasons showed a slight positive skew (Fig. 6.1), the degree of skewness shown in the late, shorter season of 1981 being greater than in 1980 (skewness = +0.853 and +0.237 respectively).

6.1.2 Adult age and laying date

For most species in which age-related differences in breeding output have been discerned, at least part of the differential has been attributed to variation in the timing of laying : older age groups may return, pair, nest-build and lay in advance of younger and first time breeders. The advantages of early breeding are various : Perrins (1979)

FIGURE 6.1: Laying date and the number of clutches started at Shagnasty throughout 1980 and 1981.

* = Mean date ** = Median date.



showed that in the Great Tit, mean clutch size declines throughout the season. He suggested that whilst early broods coincide more closely with peak food availability, later clutches are reduced in order to alleviate post-peak food demands and to bring forward the onset of incubation.

There was no discernible relationship between adult age and the date of laying (Table 6.2) when comparing either single or grouped age classes. The mean date of laying of each age class fell within 6.5 days of the colony mean. There was no indication that the mean laying date of older age classes lay closer to the colony mean than those of younger age classes. Although the degree of synchrony within female age groups (measured as 1 standard deviation) increased slightly, the relationship with age was not significant. These results differ markedly from those of Potts (1966), who found that the median date of laying of female *P. aristotelis* declined progressively with age, the difference between the medians of the two extreme age groups (2 to 11 years) being 31 days.

6.1.3 Adult weight and egg laying

Throughout the four weeks preceding the onset of the laying period 99 females and 75 males were weighed after ringing. It was not possible to standardize the time of weighing, although it is known that adult weights fluctuate markedly throughout the day (Appendix F). There was no significant change in the mean weight of either sex throughout this period. The mean weight of females which subsequently attempted to breed (using the definition of 'egg laying' as a breeding attempt) was 2566 g ± 13.73; S.E. (n = 61), significantly higher than that of 38 females for which there was no subsequent record of breeding (mean = 2471 g ± 17.40; S.E.; t = 4.27; $P<0.001$). The mean weight of 28 'non-breeding' males at that time was exactly the same as that of 48 males

TABLE 6.2: The mean and median relative laying dates in relation to age. Results for 1980 and 1981.

MALES									FEMALES								
	1980				1981					1980				1981			
Age	Mean	S.D.	Median	n	Mean	S.D.	Median	n	Age	Mean	S.D.	Median	n	Mean	S.D.	Median	n
3	25.5	-	28	4	20.0	3.39	19	5	3	35.5	-	35	2	19.0	7.14	19	5
4	25.8	7.72	28	27	19.3	6.16	20	26	4	21.2	7,71	21	9	16.9	5.91	16	16
5	24.1	7.76	24	44	16.6	4,36	17	45	5	24.4	6.32	25	26	15.5	4.61	14	24
6	21.6	7.65	21	10	15.9	5.10	15	42	6	28.7	8.03	28	8	18.1	4.32	18	32
7	24.1	7.24	26	20	15.8	3.73	16	10	7	19.6	6.30	19	12	17.8	7.56	18	5
8	23.0	7.58	25	10	16.6	3.81	17	9	8	22.5		22	2	15.7	4.49	16	12
9	21.4	5.88	23	15	21.8	6.30	21	5	9	23.6	5.66	24	19	18.5		18	2
10	25.3	7.55	24	20	16.1	4.26	15	13	10	23,8	6,66	24	23	14.2	3.56	13	13
11+	22.5	-	22	2	14.9	3.56	15	22	11+	22.0	-	22	1	17.0	3.88	17	18
				152				177					102				127

All nests	22.6	7.30	22	492	(1980)
	16.5	4.70	16	363	(1981)

whose mates subsequently laid eggs.

The relationship between pre-breeding body weight and subsequent laying date was examined for 41 females. The mean weight of females which laid before the median laying date of the colony was 2,603 g ± 38.57; S.E. (n = 11). Females which laid after the colony median averaged 2,554 g ± 18.94; S.E. (n = 30). This difference was not statistically significant (t = 1.14, 15 d.f.). Nor was there a significant correlation between female weight and subsequent laying date.

6.1.4 Individual variation in the date of laying

There was a significant positive correlation between the relative laying dates of individual females in two consecutive seasons ($r = +0.42$; $n = 115$; $P<0.001$) and, in Section 4 this was shown to be modified by the effects of mate loss through 'divorce' or mortality. A degree of constancy in the timing of laying has also been described for individual pairs of Herring Gulls (Davis 1975), Manx Shearwaters (Harris 1966) and Swifts (O'Connor 1979), whilst in the Kittiwake individual differences in the timing of laying were shown to account for 39 % of variation within the colony (Thomas 1980).

6.2 Clutch Size

6.2.1 Variation between colonies

Throughout this study 'clutch size' was defined as the maximum number of eggs laid by an individual female between the date on which the first egg was laid and the expected hatching date (Section 6.4).

Although Potts found that 4.2 % of males of the European Shag on the Farne Islands were bigamous, no such 'trios' were found in the present study, in spite of regular visits to each nest, and the high proportion of ringed birds present. In 1981 two clutches of 5 were recorded and, although their parentage was not determined, only one female was identified at each nest throughout the incubation period. Thus, clutch sizes recorded on Signy Island are in almost all cases assumed to be the product of a single female.

There was no significant difference in the clutch-size distributions of 1979 and 1980 (χ^2 analysis). Hence, clutch data for these two seasons have been pooled. Mean clutch sizes recorded during the study period were 2.62 (1979+1980; n = 720) and 2.84 (1981; n = 508). Clutches of 2 and 3 together comprised 98-99 % of all clutches, 3 being the commonest; 64 % and 83 % of clutches in 1979+1980 and 1981 respectively (Table 6.3). Although care was taken to exclude '1 egg' clutches likely to have arisen through through clutch depletion, a proportion of those in the remaining sample may have been included in error. In view of this fact, and the small number of clutches concerned, only 2 and 3-egg clutches will be considered in the statistical analysis, unless otherwise stated.

Mean clutch size at North Point differed significantly between 1980 and 1981 ($\chi^2_1 = 17.35$; $P<0.001$) but not between 1979 and 1980. Similar variation in clutch sizes occurred at Shagnasty, there being a significantly higher proportion of 3-egg clutches there in 1981 than in 1980 ($\chi^2_1 = 36.28$; $P<0.001$), and in 1976 than in 1980 ($\chi^2_1 = 21.16$; $P<0.001$). At North Point proportionately fewer 3-egg clutches were laid than at Shagnasty in 1980 ($\chi^2_1 = 4.84$; $P<0.05$), but this was not the case in 1981.

The degree of variation in clutch size between seven colonies of *P. atriceps* ranging from 46°S to 67°S, in different seasons, was of a similar order of magnitude to that within one colony on Signy Island in different seasons (Table 6.4). Clutch size in the Blue-eyed Shag was consistently lower than for that of most of the *Phalacrocorax* species listed in Table 6.5.

TABLE 6.3: Variation in clutch size at the two colonies on Signy Island, in different seasons.

Colony	1	2	3	4	5	n	Mean	Source
Shagnasty 1976	5	70	289	1	0	365	2.79	Brook, 1976
North Point 1979	3	18	14	0	0	35	2.31	This study
North Point 1980	0	25	28	0	0	53	2.53	" "
North Point 1981	0	7	51	1	1	60	2.93	" "
Shagnasty 1980	10	201	421	0	0	632	2.65	" "
Shagnasty 1981	3	73	371	0	1	448	2.83	" "
Total 1979+80	13	244	463	0	0	720	2.62	" "
% composition	1.8	33.8	64.3	0	0			
Total 1981	3	80	422	1	2	508	2.84	" "
% composition	0.6	15.7	83.1	0.2	0.4			

TABLE 6.4: Mean clutch sizes and clutch composition at Blue-eyed Shag colonies in the Falklands, sub-Antarctic and Antarctic.

Colony/Season	1	2	3	4	5	N	Mean	Source
New Island, Falkland Islands 1979	46	204	1115	28	1	1394	2.81	This study
Beauchene Island, Falkland Islands 1980	5	16	25	0	0	46	2.43	P.A.Prince *pers.comm.*
Bird Island, South Georgia 1979	3	2	20	1	0	26	2.73	S. Hunter *pers.comm.*
Sooty Bluffs, Cumberland Bay, S. Georgia 1980	0	5	40	1	0	46	2.93	P.Lennard-Jones *pers.comm.*
Marion Island, 1976	2	14	24	1	0	41	2.60	Williams and Burger, 1979
Crozet Islands 1973						20	2.90	Derenne *et al* 1976
Avian Island, Marguerite Bay 1978	1	3	46	3	0	53	2.84	Poncet and Poncet, 1979
Signy Island 1979 +80	13	244	463	0	0	720	2.62	This study
1981	3	80	422	1	2	508	2.84	" "

TABLE 6.5: Average clutch sizes of six *Phalacrocorax* species

Species	Mean clutch	Sample Size	Source
P. aristotelis	3.08	-	Potts, 1966
P. aristotelis	3.07	447	Snow, 1960
P. auritus	3.46	-	Palmer, 1962
P. auritus	3.61	57	Pilon *et al* 1983
P. auritus	3.17	138	Pilon *et al* 1983
P. carbo	3.63	19	Potts, 1966
P. carbo	2.65	905	In Potts 1966
P. carbo	4.44	112	Pilon *et al* 1983
P. penicillatus	3.09	-	Palmer, 1962
P. punctatus	2.79	62	Fenwick and Browne, 1975
P. atriceps	2.62	720	This study
P. atriceps	2.84	508	This study

6.2.2 Seasonal variation in clutch size

The relationship between clutch size and laying date differed markedly between the two seasons (1980 and 1981). In 1980, but not in 1981, the proportion of clutches of two and three laid in each quarter of the laying period differed significantly ($\chi^2_3 = 34.4$; $P<0.001$), and the mean laying date of 2-egg clutches was significantly later (by 4 days) than that of 3-egg clutches ($t = 6.82$; 434 d.f.; $P<0.001$). The laying period for clutches of 2 (36 days) was slightly longer than for clutches of 3 (31 days) in 1980, but shorter for clutches of two than three in 1981 (21 and 24 days respectively) (Fig. 6.2). Whilst in 1981 both laying distributions were positively skewed (skewness = +0.832 and +0.913 for clutches of 2 and 3 respectively), in 1980 the laying pattern of 2-egg clutches showed a slight negative skew (skewness = -0.114 and +0.177 for clutches of 2 and 3 respectively).

However it is in the pattern of variation in mean clutch sizes throughout each laying period that more (biologically) significant differences arise ; mean clutch size at Shagnasty in 1980 showed a slight (but non-significant) increase before the mean laying date, and thereafter declined by about 8 % per week. By contrast, mean clutch sizes remained constant (and higher) during the short 1981 season (Fig. 6.3).

A seasonal decline has been found in other seabird species, notably the Herring Gull (5 - 6 % per week throughout the season), Red-billed Gull (3 %) and Ring-billed Gull (2 %) (in Thomas, 1980). A much greater decline in clutch size occurs in the Kittiwake (9 % per week : Coulson and White, 1961). On Lundy Island, European Shags showed a decline of 3.5 % per week (Snow, 1960), but subsequent studies by Potts (1966) on the Farne Islands population, and by Machell on Unst, Shetland (in

FIGURE 6.2: The number of clutches of 2 and 3 started throughout 1980 and 1981.

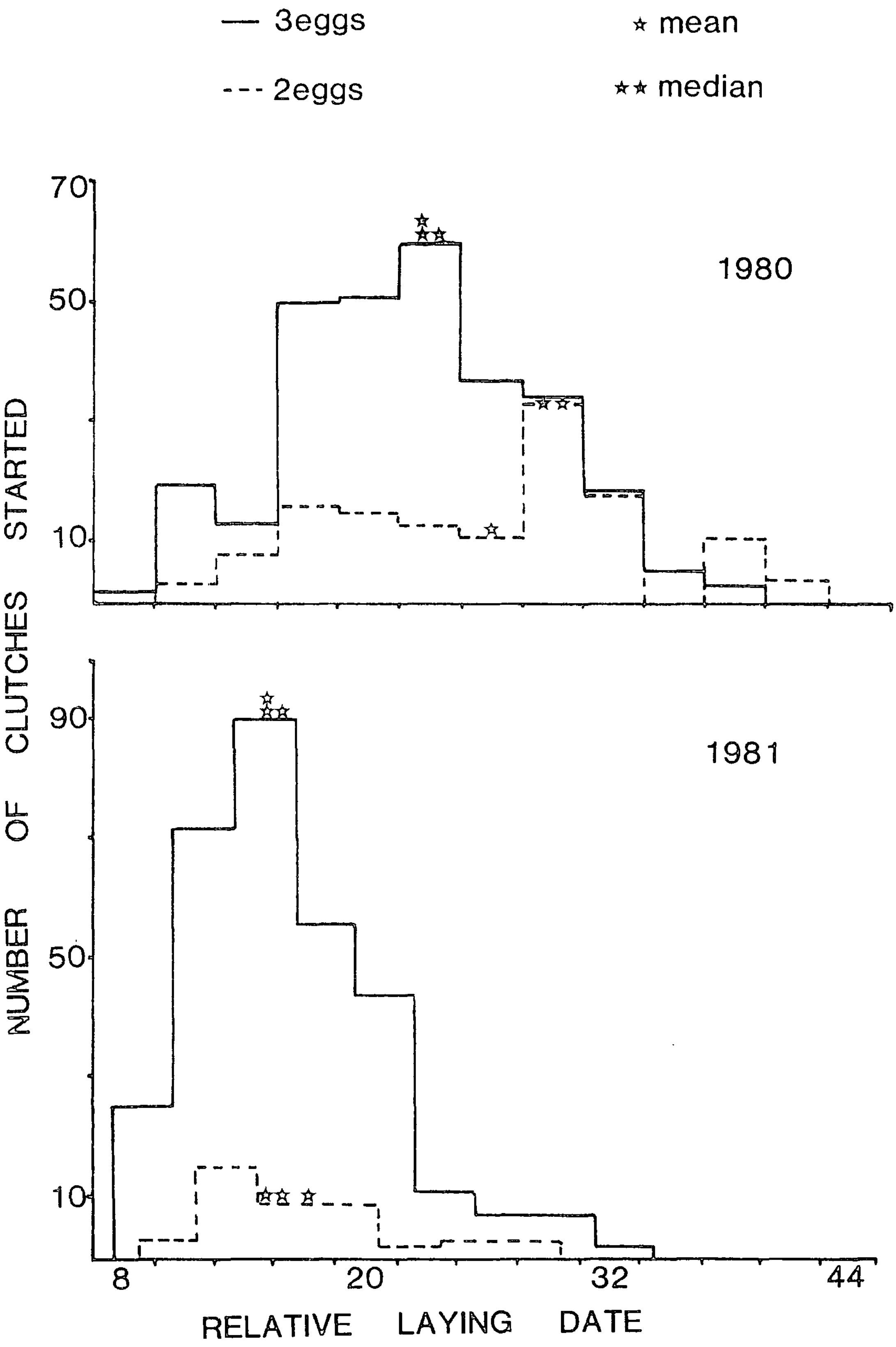


FIGURE 6.3: Seasonal variation in clutch size. Mean clutch sizes were calculated with respect to relative laying dates in each season.

○ = 1980 ○ = 1981

Fitted lines derived from the a) polynomial and b) regression equations :

a) $Y = 0.046(X) - 0.0014(X^2) + 2.388$

b) $Y = -0.004(X) + 2.936$

where X = the relative laying date, and

Y = mean clutch size.

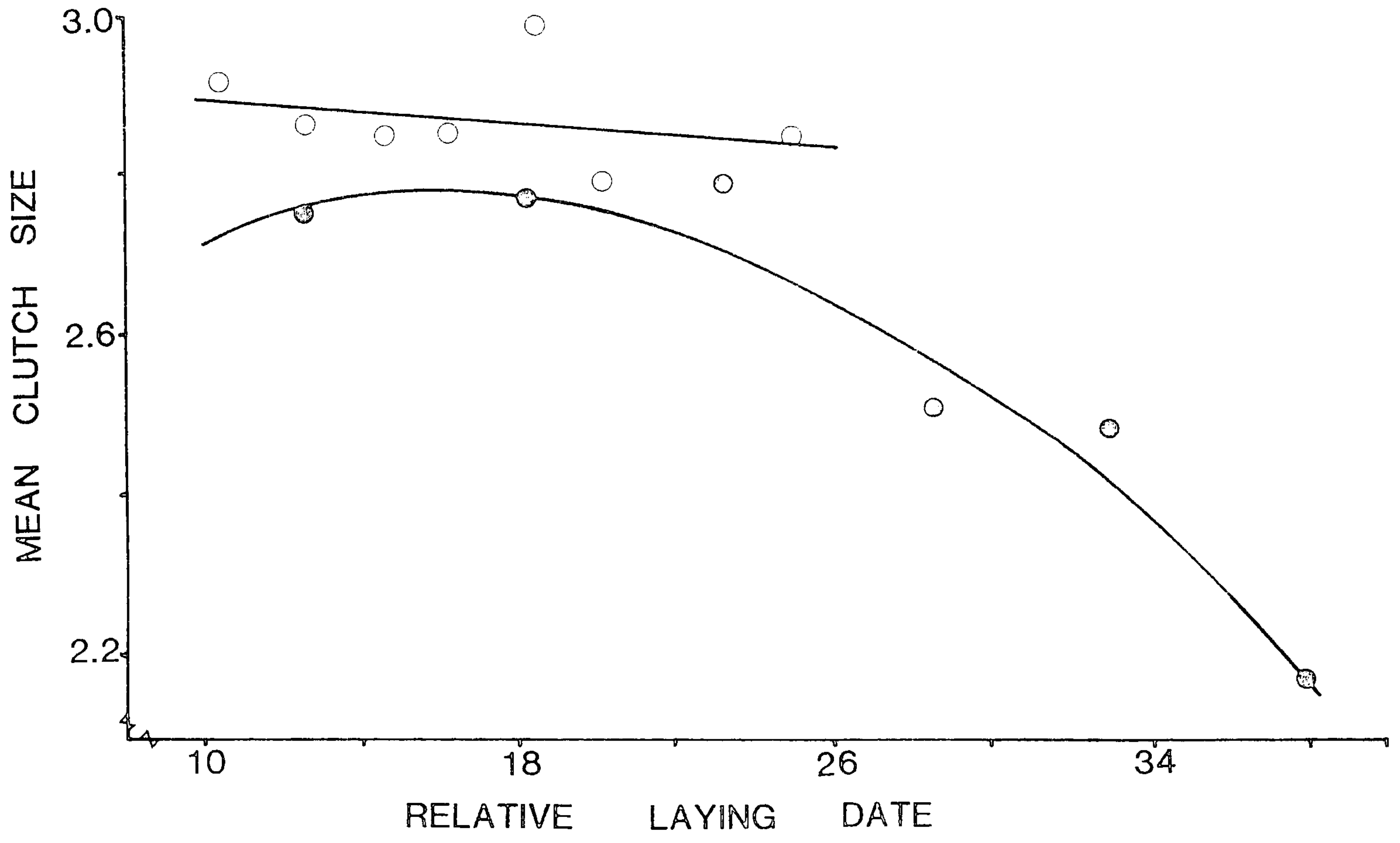


FIGURE 6.3:

Potts, 1966) failed to detect a uniform change in clutch size.

6.2.3 Clutch size and adult age

In 1980 there was no significant relationship between clutch size and female age ($\chi^2_3 = 1.84$; N.S.). However in 1981 a clear, significant relationship between female age and clutch size was apparent : first and second time breeders (3 and 4 year olds) laid smaller clutches, on average, than any other age group - from 0.3 to 0.5 eggs less than females of 6 to 10 years (Table 6.6). The proportions of each clutch size laid varie significantly throughout the age span (3 - 12 years; $\chi^2_4 = 25.69$; $P<0.001$) and also when comparing females of 8 - 10 years with 11 - 12 year-olds ($\chi^2_1 = 5.58$; $P<0.05$). Only 8.8 % of the 8 - 10 year sample laid clutches of 2 eggs, whilst 30.0 % of the 11 - 12 year sample did so (n = 45 and 30 respectively).

6.2.4 Clutch size and pre-laying weight

Of 61 females weighed during 4 weeks prior to the onset of laying 28 subsequently laid clutches of 3, and 33 laid clutches of 2 or 1. There was no statistically significant difference in the mean body weights of the two groups.

6.3 Laying and hatching intervals

6.3.1 Clutch size and laying order

Adjustment of clutch size to seasonal variations in food availability may follow as a response to early environmental cues from which subsequent food levels can be 'predicted' (Perrins, 1970). However, those species for which food levels are unpredictable at the time of laying, will be unable to adjust their clutch sizes to match unusually favourable or inclement conditions at the time of hatching. As an alternative to clutch

TABLE 6.6: Mean clutch size in relation to female age-group (see Appendix G).

Female age	Mean 1980	n	Mean 1981	n
3	2.00	2	2.50	6
4	2.87	8	2.52	27
5	2.57	26	2.72	36
6-7	2.63	19	2.94	50
8-9	2.76	21	2.82	22
10	2.50	24	3.00	23
11-12	-	-	2.70	30

adjustment, brood adjustment - or 'brood reduction' (Ricklefs, 1965) - may follow by the elimination of one or more offspring prior to, or at the time by which food shortage begins to have detrimental effects on the brood as a whole. A disparity in the ages of the chicks within the brood may promote the development of a weight hierarchy (Bryant, 1978) leading to differences in their competitive abilities (Procter, 1975) and subsequent survival chances (Ricklefs, 1965, O'Connor, 1978a, Perrins, 1979). If differences exist within the brood as to the amount of future investment required by each chick to reach independence, the youngest or smallest chick (that which requires the greatest amount of future investment) should be sacrificed in favour of its siblings. Such an age disparity will result if the eggs in each clutch are laid at intervals, are incubated soon after the first egg is laid, and thus hatch asynchronously.

The mean interval separating successive eggs laid in clutches of 3 was significantly shorter than that between eggs in clutches of 2 (Table 6.7). This result would arise if a proportion of the 2-egg clutch sample consisted of 3-egg clutches, from which the middle 'B' egg had been lost - thus producing an apparently long 'A - B' interval. However the mean 'A - B' interval for clutches of 2 in which the 'B' egg volume was greater than 50.4 cc (i.e. greater than the mean weight of 'C' eggs + 2 S.E.; see Table 6.13) was 2.80 days - still significantly greater than that of the 'A - B' interval in clutches of 3. Within clutches of 3, the 'A - B' laying interval was significantly shorter than the B - C interval. On average, C eggs were laid 5.18 days after the A egg, and B eggs were laid slightly closer (in time) to the A than to the C. However, the degree of synchrony at hatching will depend upon the time at which incubation is begun : if the adults begin incubating when the last egg

TABLE 6.7: The average laying interval between successive eggs in relation to clutch size and egg position. Sample sizes are given below each mean.

Clutch size	Laying interval A - B	Laying interval B - C	Laying interval A - C
2	2.97 (142)		
3	2.46 (273)	2.72 (271)	5.18 (268)

Mean laying interval in clutches of 3 = 2.59 (N = 544)

χ^2 tests for differences in laying intervals :

*P<0.05 **P<0.001

	Cl. 3, A-B-C	Cl. 3, A-B	Cl. 3, B-C
Cl. 2, A-B	36.38** 6 d.f.	42.30** 3 d.f.	10.03* 3 d.f.
Cl. 3 A-B			20.77** 3 d.f.

is laid, the hatching span will be much reduced. Conversely, if incubation is begun immediately after the first egg is laid, laying intervals will persist through to hatching.

Table 6.8 shows that the hatching interval in clutches of 2 decreased to a mean of 2.18 days, from a mean laying interval of 2.97 days (from Table 6.7). Similarly, the mean hatching interval between successive eggs in clutches of 3 decreased to 1.98 days from an initial laying interval of 2.59 days. Clearly, in some nests at least, incubation was begun before the clutch was complete. Differences (between clutch sizes) in the mean interval length were also much reduced by the time of hatching, but in two cases remained statistically significant. Indeed, the difference between the 'A - B' interval and the 'B - C' interval increased, indicating that whilst B eggs almost 'caught up' with their predecessor, C eggs did so to a lesser degree. An alternative way of examining changes in the laying to hatching span is to calculate the hatching interval : laying interval ratio (H/L ratio) (Table 6.9). If during the interval between successive eggs being laid the clutch is fully incubated, the H/L ratio will be 1.0 (as the hatching interval will be of approximately the same length as the laying interval). Conversely, if no incubation takes place between consecutive layings, the H/L ratio will be zero.

Table 6.9 shows that, for clutches of 2 and 3, H/L ratios for the first to second laid eggs were 0.70 and 0.65 respectively, suggesting that, on average, A eggs were incubated effectively for about two-thirds of the 'A - B' laying interval. By contrast, C eggs hatched after a delay which was, on average, almost equal to the 'B - C' laying interval, indicating that B and C eggs were usually incubated from the first day of laying. The net result therefore is that whilst 1st and 2nd eggs

TABLE 6.8: The average hatching interval between successive eggs in relation to clutch size and laying position. Sample sizes are given below each mean.

Clutch size	Hatching Interval A - B	 B - C	 A - C
2	2.18 (38)		
3	1.55 (87)	2.41 (89)	3.84 (85)

Mean hatching interval in clutches of 3 = 1.98 (N = 176)

χ^2 tests for differences in hatching intervals:

	Cl.3, A-B-C	Cl.3, A-B	Cl.3, B-C
Cl.2, A-B	N.S.	16.70* 2 d.f.	N.S.
Cl. 3, A-B			39.54* 2 d.f.

*P<0.001

TABLE 6.9: The degree of change between the laying interval and the hatching interval, in relation to clutch size and laying position. The degree of shortening between the initial laying interval by the time of hatching can be calculated as follows :

$$\text{mean interval ratio} = \left(\frac{Hi}{Li}\right) \times \frac{1}{n}$$

where Li = the laying interval between the ith pair of eggs, and

Hi = the hatching interval between the same pair of eggs.

n = the number of pairs of eggs.

Sample sizes (in brackets) and one standard deviation shown.

	Mean H/L interval ratio for:		
Clutch Size	A - B	B - C	A - C
2	0.70 ± 0.28 (38)		
3	0.65 ± 0.24 (84)	0.96 ± 0.40 (82)	0.77 ± 0.21 (77)

Student's t Tests for differences in the mean H/L interval ratio

	Cl.3, A-B-C	Cl.3, A-B	Cl.3, B-C
Cl.2, A-B	N.S.	N.S.	3.50* 118 d.f.
Cl.3, A-B			5.91* 164 d.f.

*P<0.001

hatched with a greater degree of synchrony than their laying dates might predict, the third egg retained its original (laying) time lag.

6.3.2 Seasonal variation in hatching asynchrony

The degree of hatching asynchrony within clutches has been shown to increase with laying date in Roseate and (less reliably) Common Terns (Nisbet and Cohen, 1975), Blue Tits (O'Connor, 1978b), and in Great Tits (Perrins, 1979). In each case, an increased hatching span was regarded as an adaptation against seasonally declining food resources since, by raising the degree of hatching asynchrony within the clutch, any disparity in the competitive abilities of the offspring will be increased, allowing early elimination of the youngest chick.

In the present study, the mean laying span (between A - C eggs) increased throughout the laying period (Figure 6.4), but no significant seasonal increase occurred in the A - C hatching span (for which sample sizes were much smaller), although a positive trend was apparent.

6.3.3 Variation in laying and hatching asynchrony with age

In the absence of an age-related trend in clutch size, age-related differences in the degree of hatching asynchrony might ultimately lead to a reduction in the number of chicks with which young adults have to cope. However, χ^2 analysis of laying intervals, hatching intervals, and the H/L ratio for all* age groups showed no evidence of heterogeneity throughout the 3 - 11 year age span. It would appear that the rate of laying, and the degree of hatching asynchrony in clutches of 3 laid by young females (those in their first 2 - 3 breeding seasons) does not differ from that of the other female age groups combined.

*One 10-day laying interval of an 8 year old female has been ommitted.

FIGURE 6.4: The relationship between the mean laying span, (the interval, in days, between the 'A' to 'C' egg) and the date of laying.

Line fitted derived from :

$Y = 0.02(X) + 4.57$

$r = 0.78; P<0.03$

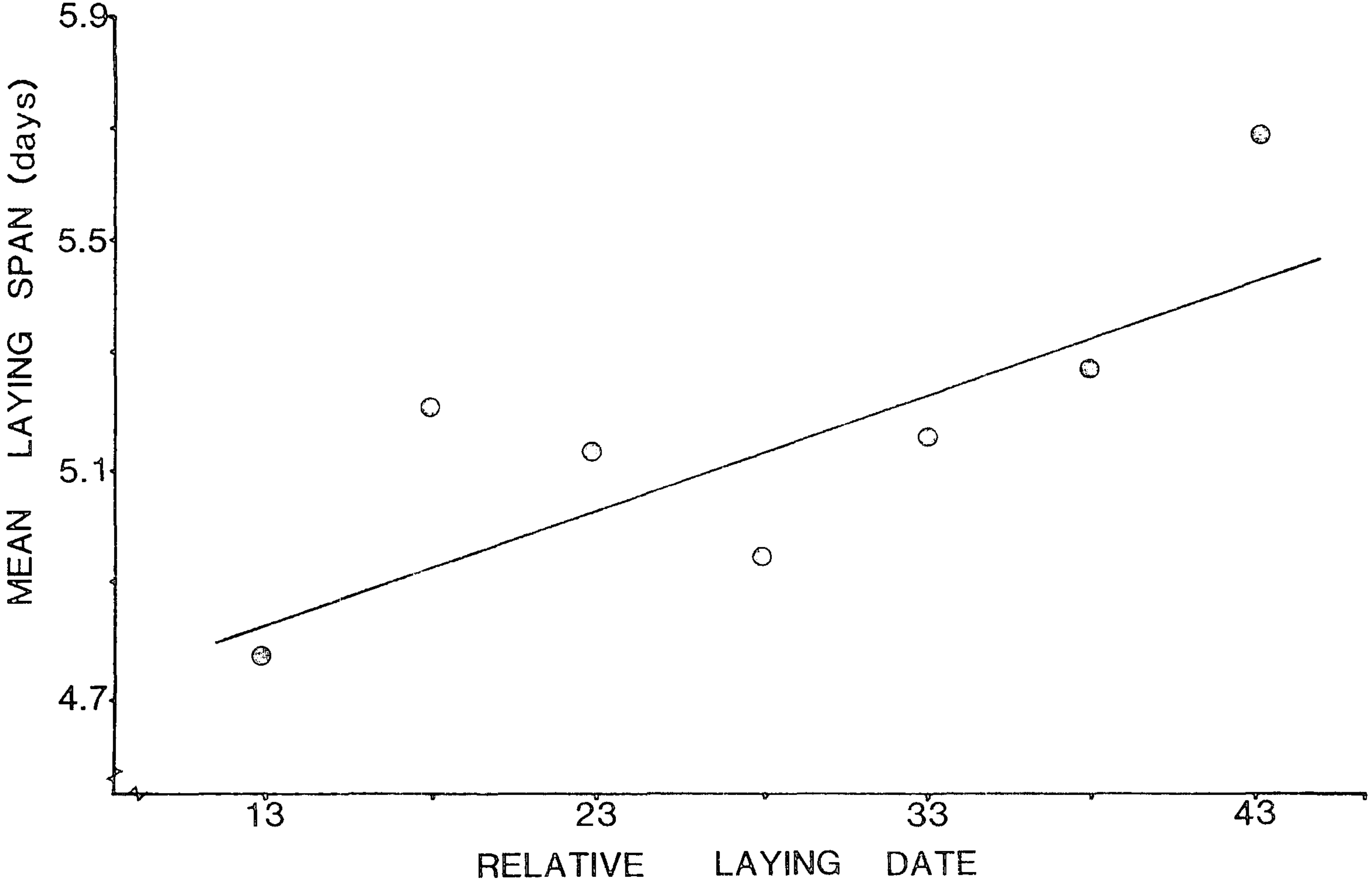

MEAN LAYING SPAN (days)
5.9
5.5
5.1
4.7
13
23
33
43
RELATIVE LAYING DATE

FIGURE 6.4:

Only in clutches laid by females in the oldest age group (of 10 - 11 years) were the laying and hatching intervals consistently shorter than those of other females (of 3 - 9 years inclusive) (Table 6.10). That shorter mean hatching intervals were associated with shorter mean laying intervals is not unexpected. However, analysis of the H/L ratio indicates that the degree of reduction in the laying interval (by the time of hatching) was also greater in the case of older females. The net result is that whilst for most females the first and second eggs hatched closer together (temporally) and the last egg retained its initial lag, for the oldest age group the last egg also 'caught up' to some degree.

6.4 The laying to hatching period

As Beer (1964) pointed out, the term 'incubation period' has been variously interpreted as 'the period between the laying and hatching date of an egg or clutch' or, 'the period during which the adult sits on the nest'. He suggests that the most practical definition is that used by Heinroth (1922) - 'the time from the laying of the last egg of a clutch, to the hatching of that egg'. However, in the present study I am concerned with differences between eggs in relation to their laying order, and will use the term 'laying to hatching period' to describe that period which includes the day on which the egg was laid, but excludes the day on which it hatched. The term 'incubation' is not used here since the time at which incubation began could not be determined.

6.4.1 The mean laying to hatching period

The mean laying to hatching period for all eggs examined was 29.3 days, with a range of 27 - 33 days (n = 372 eggs, Table 6.11). Of these, 95 % hatched within 28 - 31 days. The average laying to hatching period

TABLE 6.10: Mean laying interval, hatching interval and hatching interval/laying interval ratio in clutches of three. Results are shown separately for females of 3 - 9 years and 10 - 11 years.

		Female Age					
		3-9 years	n	10-11 years	n	Mann-Whitney U*	P=
Mean laying interval (in days)	A-B	2.6	40	2.3	14	1.56	0.12
	B-C	2.8	39	2.4	14	1.49	0.14
	A-C	5.3	37	4.7	13	2.07	0.05
Mean hatching interval (in days)	A-C	1.7	22	1.5	6	0.05	0.96
	B-C	2.7	21	2.0	7	3.85	0.0001
	A-C	4.3	21	3.3	6	1.43	0.14
Mean H/L ratio	A-B	0.66	21	0.66	6	0.06	0.95
	B-C	1.12	19	0.74	7	3.98	0.0001
	A-C	0.82	20	0.66	6	2.03	0.04

* Corrected for ties

TABLE 6.11: The number and proportion of each laying-hatching period recorded (in days).

Laying-Hatching Period	Number	Percentage
27	2	0.5
28	68	18.2
29	177	47.6
30	90	24.3
31	23	6.2
32	10	2.7
33	2	0.5
	372	

thus falls within the range of that of most of the *Phalacrocorax* species listed in Table 6.12. A notable exception is that of the European Shag, for which Potts (1966) records a laying to hatching range of 31-36 days, measured in the same way as in the present study.

6.4.2 Clutch position and laying to hatching period

From calculation of the mean H/L ratio (Table 6.9), it was suggested that, on average, A eggs were incubated for about 2/3 of the interval preceding the laying of the B egg (H/L = 0.66 - 0.70) but that B eggs were incubated soon after laying (H/L = 0.96). From these results, the following predictions can be made :

1) That the laying to hatching period for B and C eggs should be approximately equal.

2) That the laying to hatching period for A eggs should be 0.9 days longer than that of B or C eggs, obtained from :

difference = (1 - H/L) x mean A - B laying interval

= 0.35 x 2.46 days (for clutches of 3)

= 0.86 days

or

= 0.30 x 2.97 days (for clutches of 2)

= 0.89 days

Table 6.13 shows that whilst the mean laying to hatching periods of B and C eggs were very similar in length, that of the A egg was 0.9 to 1.0 day longer - a statistically significant difference. Thus, measurement of the laying to hatching period strongly supports the contention that effective incubation was restricted before the second egg was laid.

TABLE 6.12: Incubation and laying to hatching periods* in a range of phalacrocoracids.

Species	Mean (days)	Range	Source
P. africanus	-	23-25	Cramp and Simmons, 1977
P. atriceps melanogenis	28.7 - 30.5	28-32	Williams and Burger, 1979
P. atriceps bransfieldensis	29.3	27.33	This study
P. albiventer	28.8	27-31	Derenne *et al* 1976
P. capensis	-	22-28	Berry, 1976
P. carbo	-	28-31	Cramp and Simmons, 1977
P. punctatus	-	28-31	Fenwick and Browne, 1975
P. pygmeus	-	27-30	Cramp and Simmons, 1977
P. aristotelis	-	31-36	Potts, 1966

* Unfortunately the definitions used for 'incubation period' or 'laying to hatching period' vary - several were unspecified.

TABLE 6.13: Mean incubation length in relation to laying position.

	A egg	B egg	C egg
Mean	29.8	28.9	28.8
Sample size	145	152	80

The mean laying to hatching interval of A eggs was significantly longer than that of B or C eggs :

A : B $\chi^2_3 = 69.8$ $P<0.001$

A : C $\chi^2_3 = 69.5$ $P<0.001$

There was no significant difference between that of B and C eggs.

TABLE 6.14: Seasonal variation in the length of the laying to hatching period with respect to laying position.

Relative Date of laying	A egg	B egg	C egg
1 - 13	30.2 (58)	29.2 (43)	28.9 (18)
14 - 25	29.6 (74)	28.8 (87)	28.7 (54)
26 - 38	29.6 (13)	28.7 (22)	28.7 (8)

Differences throughout the season (proportions of A, B and C eggs equal in each season interval) :

$\chi^2_3 = 16.36$ $P<0.01$

6.4.3 Seasonal changes in the laying to hatching period

The mean laying to hatching period declined with laying date (Table 6.14) although this was due mainly to differences between the first and middle third of the season ($\chi^2_2 = 9.9$, $P<0.01$). There was no significant difference between laying to hatching periods in the middle of last third of the season.

6.5 Egg size and Shape

The range in egg size and shape within a species, although circumscribed by strong physiological and ecological restrictions, may nevertheless account for a large part of the observed variation in chick hatching weight (Schifferli 1973, O'Connor 1979), and, ultimately, chick survival (Parsons 1970, Nisbet 1973, and O'Connor 1979). In this study the following trends should therefore be considered :

Firstly, that egg volume, particularly that of species with asynchronously hatching clutches, may vary with respect to laying position (Ryder 1975, Mills 1979, Thomas 1980). Hence, intra-clutch variation may provide an additional source from which a disparity in chick weights may subsequently arise (Parsons 1975, O'Connor 1979, - but see Howe, 1978, and Ryden 1978).

Secondly, many workers have reported changes in egg volume throughout the laying period (e.g. Coulson *et al* 1969, Perrins 1970 and Mills 1979).

Female age and prior breeding success may, at least in part, influence egg volume (Coulson *et al* 1969, Davis 1975, Lloyd 1979), although for some species the relationship appears to diminish beyond the first few breeding seasons (Richdale 1955, Mills 1979). Pair stability between seasons - itself influenced by the ages of the partners - may also partly effect egg size (Thomas, 1980).

Lastly, various studies have highlighted the relationship between female breeding age and egg shape (or, specifically, egg breadth), established through long term ringing and recapture programmes (Richdale 1955, Coulson 1963, Nelson 1966). Thus, the potential use of egg shape as an indicator of female age group, or as a means of assessing colony age-composition should also be considered (Coulson *et al* 1969).

The formulae used for calculating egg volume and shape index were those described by Coulson *et al* (1969) :

egg volume = 0.51 x breadth x breadth x length (cm)

egg shape index = breadth/length x 100

This calculation was made for each egg. Mean egg volume and egg shape values were obtained from the sum of the original egg volume scores and egg shape scores respectively.

6.5.1 Egg volume, laying weight and hatching weight

Egg volume, laying weight (within 24 hours of laying) and hatching weight (the weight of the chick within 24 hours of hatching) were positively correlated :

r egg volume : laying weight = 0.79; $P<0.001$; n = 619

r egg volume : hatching weight = 0.49; $P<0.001$; n = 132

r laying weight : hatching weight = 0.36; $P<0.001$; n = 88

The slope of the regression relating laying weight to egg volume was steeper than that for hatching weight to volume (Fig. 6.5), the difference being significant ($t = 3.82$; 747 d.f.; $P<0.001$). This result, and the lower correlation value for volume: hatching weight (above) may reflect the fact that newly hatched chicks will have received either zero, one or several meals before their first weighing. Figure 6.5 also shows that large eggs weighed less, and yielded lighter chicks than would be expected if the ratio of egg volume:weight was constant

FIGURE 6.5: The relationship between egg volume and a) laying weight and b) hatching weight. Solid lines derived from :

a) $Y = 0.911(X) + 8.56$, and

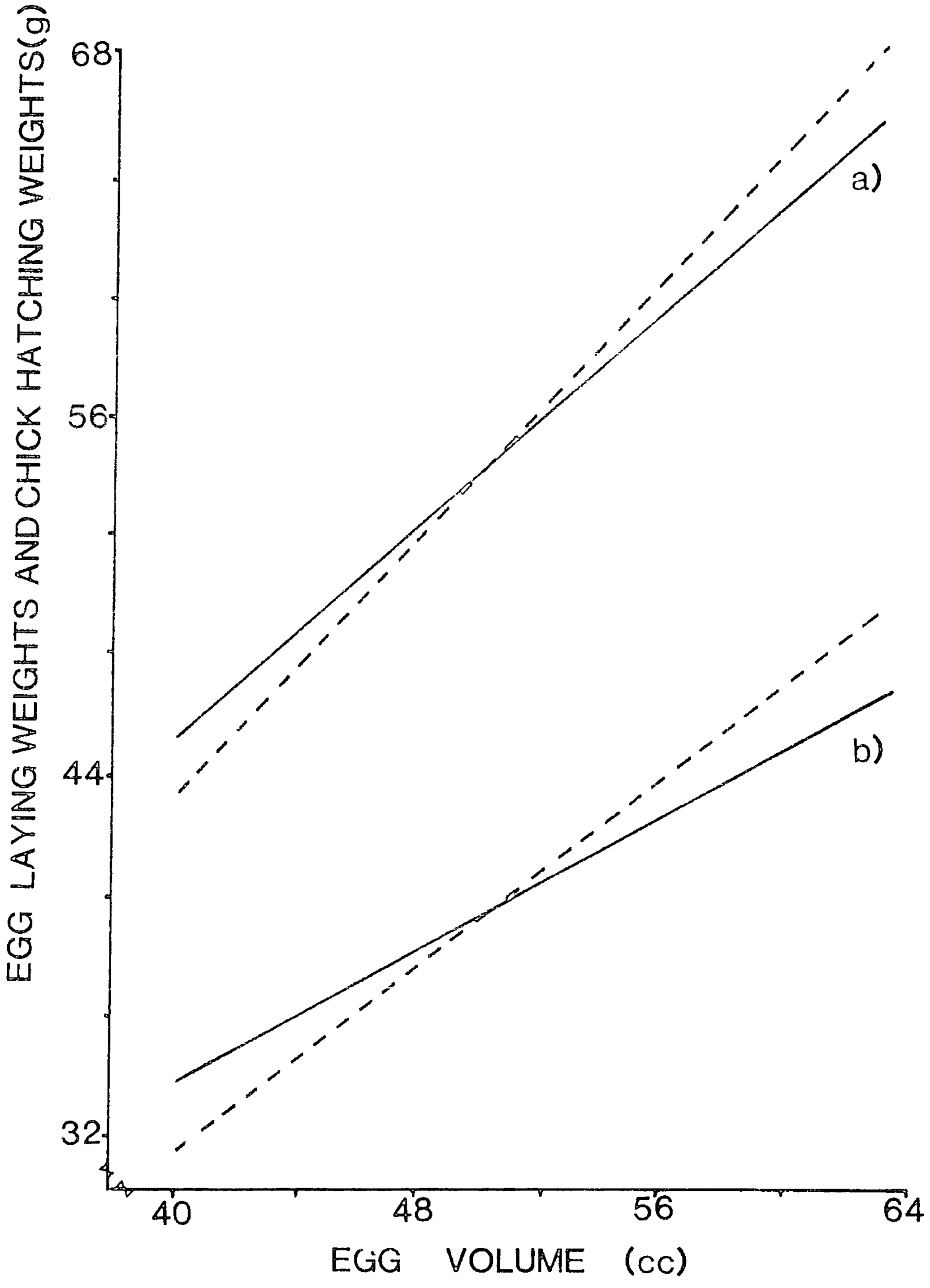
b) $Y = 0.562(X) + 11.14$

Slope SE = 0.027, intercept SE = 1.400

Slope SE = 0.087, intercept SE = 4.415

Dashed line = expected slope if ratio of weight to volume was constant at 1.08 (laying wt.: volume) and 0.78 (hatching wt.:volume). Ratios derived from the mean values for each measure.

FIGURE 6.5:


EGG LAYING WEIGHTS AND CHICK HATCHING WEIGHTS(g)
68
56
44
32
a)
b)
40
48
56
64
EGG VOLUME (cc)

(calculated from the ratio of the mean volume:mean weight). The intercept of each 'constant ratio' slope (i.e. at zero) lay beyond 95 % confidence limits of each regression intercept (volume : laying weight; t = 6.11; 617 d.f.; $P<0.001$, and volume : hatching weight; t = 2.52; 130 d.f.; $P<0.001$).

6.5.2 Egg size in relation to laying position

Eggs in clutches of 1 were, on average, smaller than those in clutches of 2 or 3 (Table 6.15). However, due to the small sample size available, and the possibility of error due to clutch depletion, only clutches of 2 and 3 are considered in the analysis.

Within and between clutches of 2 and 3 there were no significant differences in the mean volume of A and B eggs. In each case the mean weight of A eggs was only marginally greater than that of B eggs. Only the C egg was significantly smaller than the others - by 1.1 to 1.9 cc.

The mean weights of clutches of 2 and 3 eggs were respectively 103.2 and 156.6 g, or 4.0 % and 5.9 % of the average weight of 61 females which bred.

At hatching, chicks from A and B eggs were of a similar weight (Table 6.16), whilst chicks from C eggs were, on average, 3.9 g (10 %) lighter than their siblings. This difference is significant ($P<0.001$). Thus, in clutches of 3 the mean laying weight, hatching weight, and volume of first eggs were greater than those of the last egg. These results agree with the findings of Williams and Burger (1979) at a small colony of *P. atriceps melanogenis* at Marion Island, but differ markedly from the measurements of Coulson *et al* (1969) of egg size in the European Shag on the Farne Islands. In clutches of 3 laid by European Shags the first egg was the smallest, the second egg usually the largest and the third was intermediate (though in some cases larger

TABLE 6.15: Mean egg volume in relation to laying position and clutch size (1980 only). Sample size (in brackets) and 1 standard deviation shown.

Clutch Size	Mean egg volume (cc.) A eggs	B eggs	C eggs
1	49.7 ± 6.68 (6)		
2	51.8 ± 4.09 (79)	51.4 ± 3.45 (70)	
3	51.6 ± 3.76 (159)	51.1 ± 3.32 (153)	49.9 ± 3.27 (141)

Students t tests for differences in egg volume :

		Clutches of 3 A eggs	B eggs	C eggs
C 2	A eggs	N.S.	N.S.	3.57*
	B eggs	N.S.	N.S.	2.87*
C 3	A eggs		N.S.	4.19**
	B eggs			3.03*

* P<0.002

** P<0.001

TABLE 6.16: Mean chick weights (within 24 hours of hatching) in relation to laying position and clutch size (1980 only). Sample size (in brackets) and 1 S.D. shown.

	Mean chick weights (g) from:		
Clutch size	A eggs	B eggs	C eggs
2	39.4 4.88 (15)	41.2 2.56 (10)	
3	40.0 4.33 (25)	39.9 3.58 (28)	36.2 3.72 (26)

Students t tests for differences in mean chick weight :

		Clutches of 3		
		A eggs	B eggs	C eggs
C 2	A eggs	N.S.	N.S.	2.37*
	B eggs	N.S.	N.S.	3.82**
C 3	A eggs		N.S.	3.40**
	B eggs			3.72**

* P=0.002

** P< 0.001

than the second).

Egg-size variation within clutches of the Blue-eyed Shag were similar to those shown by Common Terns (Gemperle and Preston, 1955), Herring Gulls (Parsons 1975), Ring-billed Gulls (Ryder, 1975), Laughing Gulls (Ricklefs *et al* 1978), Black-headed Gulls (Lundberg and Vaisanen 1979) and Red-billed Gulls (Mills, 1979).

6.5.3 Egg size and laying Date

Several workers have demonstrated a seasonal decline in egg volume which, although often complicated by the extraneous effects of age on egg volume and laying date, may nevertheless persist within age-groups (Coulson 1963, Coulson *et al* 1969). In the European Shag both laying date and egg volume were shown to be partly age-related, and the decline in egg volume throughout the season was large (11 %). In the present study no significant relationship was found between adult age and laying date (6.1.2) nor between egg size and female age (between 3 - 9 years : 6.5.4). Consequently, no attempt has been made to re-partition egg size data with respect to female age.

Considering A and B eggs together from clutches of 2 and 3, and C eggs separately, no linear relationship between egg volume and relative date of laying was found (based on regression analysis, n = 627 eggs). Nor was there evidence (within each egg-class) of heterogeneity in egg volume between 8, 5-day divisions of the laying season (considering C eggs separately from A and B eggs). Both analyses were repeated, separating eggs by clutch size only, but without statistically significant results.

6.5.4 Egg size and female age

Figure 6.6 shows that after an initial increase between the third and fourth year, the mean volume of A and B eggs showed little change until the ninth year, after which there was a marked decline. The mean volume, laying weight and hatching weight of eggs laid by females of 10 - 11 years was, in each case, significantly lower than for eggs laid by females of 4 - 9 years, or of 7 - 9 years (Table 6.17). The values for C eggs were consistently lower, and followed the same trend in relation to female age group as A or B eggs. However, differences in C egg volumes could not be tested statistically due to small sample size.

Egg volume in the European Shag has also been shown to increase with age, but without evidence of a subsequent decline (Coulson *et al* 1969). Results from other studies on age-related variation in egg size have been inconsistent, particularly with regard to the middle, and older age groups. An increase in egg size with age has been reported in Kittiwakes (Coulson 1963), Gannets (Nelson 1966) and Razorbills (Lloyd 1979) and it is suggested that changes in egg volume may be more pronounced in species which show little variation in clutch size with age (Thomas 1980).

6.5.5 The relative difference in egg volume

Egg size variation within broods may thus influence the degree of chick weight disparity at hatching (Fig. 6.5). If initial chick weight disparities directly influence subsequent survival (see Section 7) then one might expect less pronounced disparities - and hence fewer cases of brood reduction - to occur in early than in late broods, and in broods produced by experienced adults than by inexperienced first-time breeders.

The relative difference in egg volume (RDEV; after Bryant 1978) within each clutch of 2 or 3 eggs was calculated using the formula :

$$\mathrm{RDEV} = \frac{\mathrm{Vl} - \mathrm{Vs}}{\bar{\mathrm{V}}}$$

where VI and Vs are the volume of the largest and smallest eggs respectively, and $\bar{\mathrm{V}}$ is the mean volume within the clutch.

FIGURE 6.6: Variation in egg volume in relation to female age. The mean volume of 'C' eggs was consistantly lower than that of 'A' or 'B' eggs, and is shown separately.

o = mean

o = single measurement

± 1 S.E. shown

FIGURE 6.6:

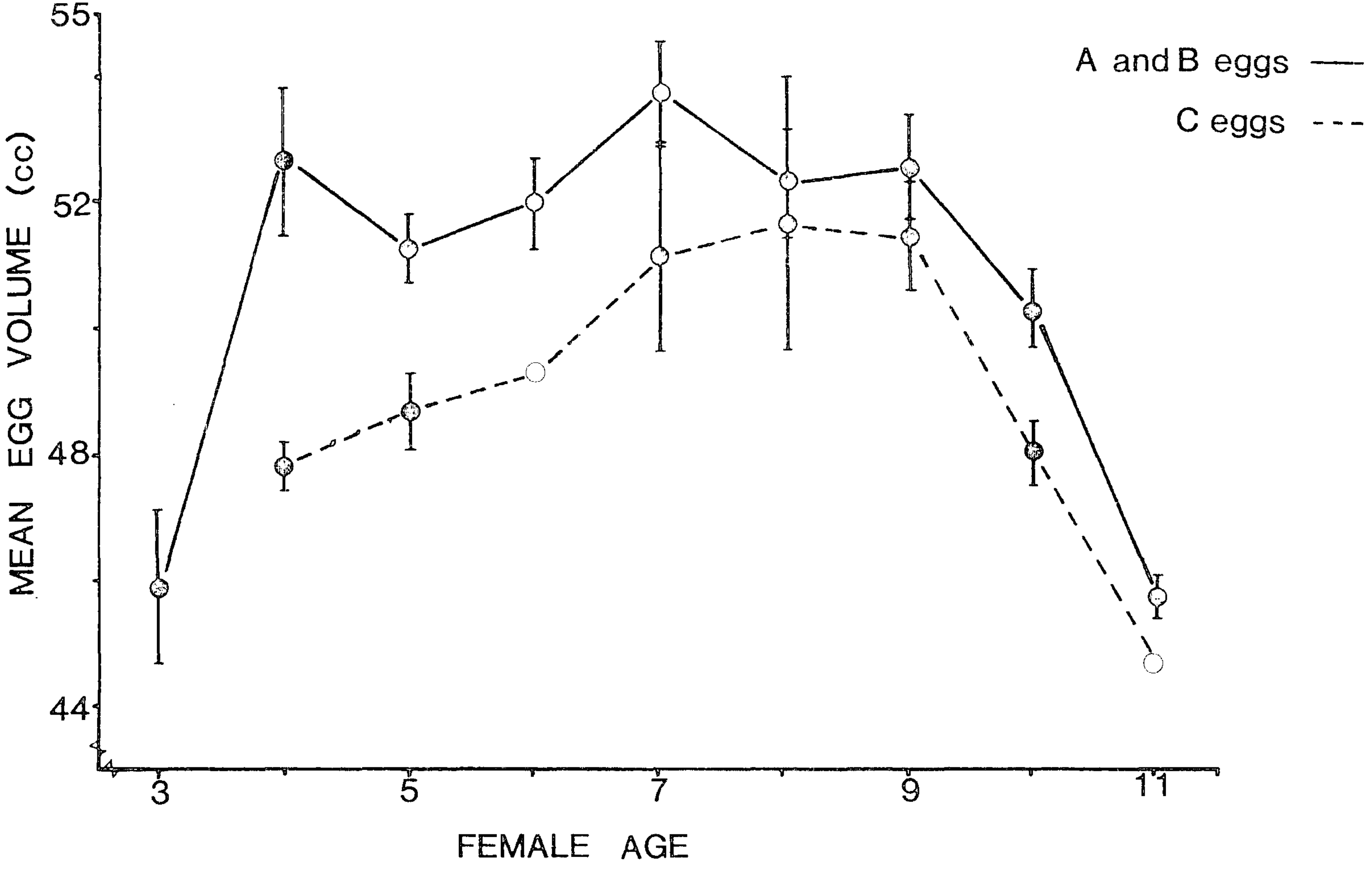

MEAN EGG VOLUME (cc)
55
52
48
44
3
5
7
9
11
FEMALE AGE
A and B eggs —
C eggs ---

TABLE 6.17: Volume, laying weight and hatching weight of A and B eggs, in relation to female age. In each case, results from the oldest age group (10-11 years old) are compared with those from a) females of age 4-9 years, and b) females of 7-9 years inclusive. The values for C eggs were consistantly lower (but show similar trends) and have been excluded. ± 1 S.D. shown.

	Female Age Group		
	a) 4-9 years	10-11 years	b) 7-9 years
Mean egg volume (cc.)	52.2 ± 3.72 (98)	40.1 ± 3.55 (35)	52.7 ± 4.0 (46)
Mean laying weight (g)	55.9 ± 4.00 (87)	53.3 ± 3.61 (32)	56.4 ± 3.9 (45)
Mean hatching weight (g)	42.0 ± 3.42 (20)	38.5 ± 2.38 (10)	42.1 ± 3.0 (9)

Students t tests for differences in egg volume, laying weight and chick hatching weight in relation to female age group.

	4-9 years	- t -	10-11 years	- t -	7-9 years
Mean egg volume		2.88**		3.05**	
Mean laying weight		3.17**		3.46**	
Mean hatching weight		2.81**		2.72*	

* P = 0.014

** P<0.01

However there were no significant differences in the mean RDEV values of clutches laid during each third of the 1980 season (n = 195 clutches), nor with respect to female age (in three groups spanning 3 - 11 years; n = 60 clutches). Clutches of 2 and 3 were considered separately.

6.5.6 Egg 'quality' in relation to egg size

The amount of nutrients or water reserves available to the growing embryo or newly hatched chick increases with egg size, but may vary in their relative proportions (Romanoff and Romanoff 1949, Parsons 1971, Ricklefs 1977, O'Connors 1979). Thus, egg 'quality' - usually taken as the ratio of yolk to albumen - should be considered when assessing the importance of egg size on hatching success, hatching weight and chick survival. Consequently, examination of the relative components, in particular the relative weight of the yolk, in large and small Blue-eyed Shag eggs was necessary in order to show whether large, heavy eggs contain proportionately large yolks, heavier shells or a greater volume of albumen.

Methods

Eighteen eggs were collected from clutches of three (1 egg per clutch) of unringed adults on S.N. III. The eggs were taken as soon after laying as possible. Unfortunately their laying positions (within each brood) were not determined. Each egg was boiled for 10 minutes then stored for later analysis. In the interim period they were kept at -20°C then allowed to thaw at room temperature. Three eggs were discarded due to breakage and partial loss of contents during boiling or thawing. Weight changes as a result of boiling were slight (mean decrease = 2.1 % ± 0.99 %; S.D. of initial weight). Each egg was broken open, the contents extracted, separated and weighed. The egg shells were dried in an oven (60°F for 3 hours) and re-weighed. Care was taken to remove as much of the albumen as possible from the surface of the yolk and from the inner surface of the shell. Egg shell membranes were left in place wherever possible.

In five of the eggs the yolk was greatly enlarged and the embryo well advanced in the mesoblastic stage of development. These eggs were ommitted from further analysis since the object was to measure initial differences in the relative components of the eggs - prior to the enlargement of the yolk and airspace.

Results

Yolk comprised, on average, 18.2 % by weight of the egg contents (excluding the shell; S.D. = 1.82) and 15.7 % of the whole egg (wet) weight. These figures fall within the range of yolk proportions found in eggs of other altricial species : 15 - 20 % by weight (Romanoff and Romanoff 1949). The proportion of yolk present declined significantly with increasing egg weight (Fig. 6.7) and, although there was a slight (statistically insignificant) increase in the absolute weight of the yolk throughout the range of whole egg weights (Fig. 6.8), the regression slope is shallower than that derived from the constant ratio of mean egg weight : mean yolk weight (0.157). The 'constant ratio' slope intercept (at zero) fell beyond the 95 % confidence limits from the regression intercept (at 6.53 g ± 1.58 S.E.; $t = 4.13$; 11 d.f.; $P<0.002$). Clearly, in larger, heavier eggs either the eggshell or the albumen must account for a greater proportion of the total weight. Figure 6.9 shows that whilst shell weight does increase with egg weight, there was no significant departure from the 'constant ratio' shell weight contribution : zero fell within 95 % confidence limits of the intercept (0.96 g ± 1.03 S.E.;

FIGURE 6.7: Variation in the proportion of yolk present in relation to whole egg weight.

Fitted line derived from the equation :

$Y = -0.243(X) + 28.84$

$r = -0.85;\ P < 0.01$

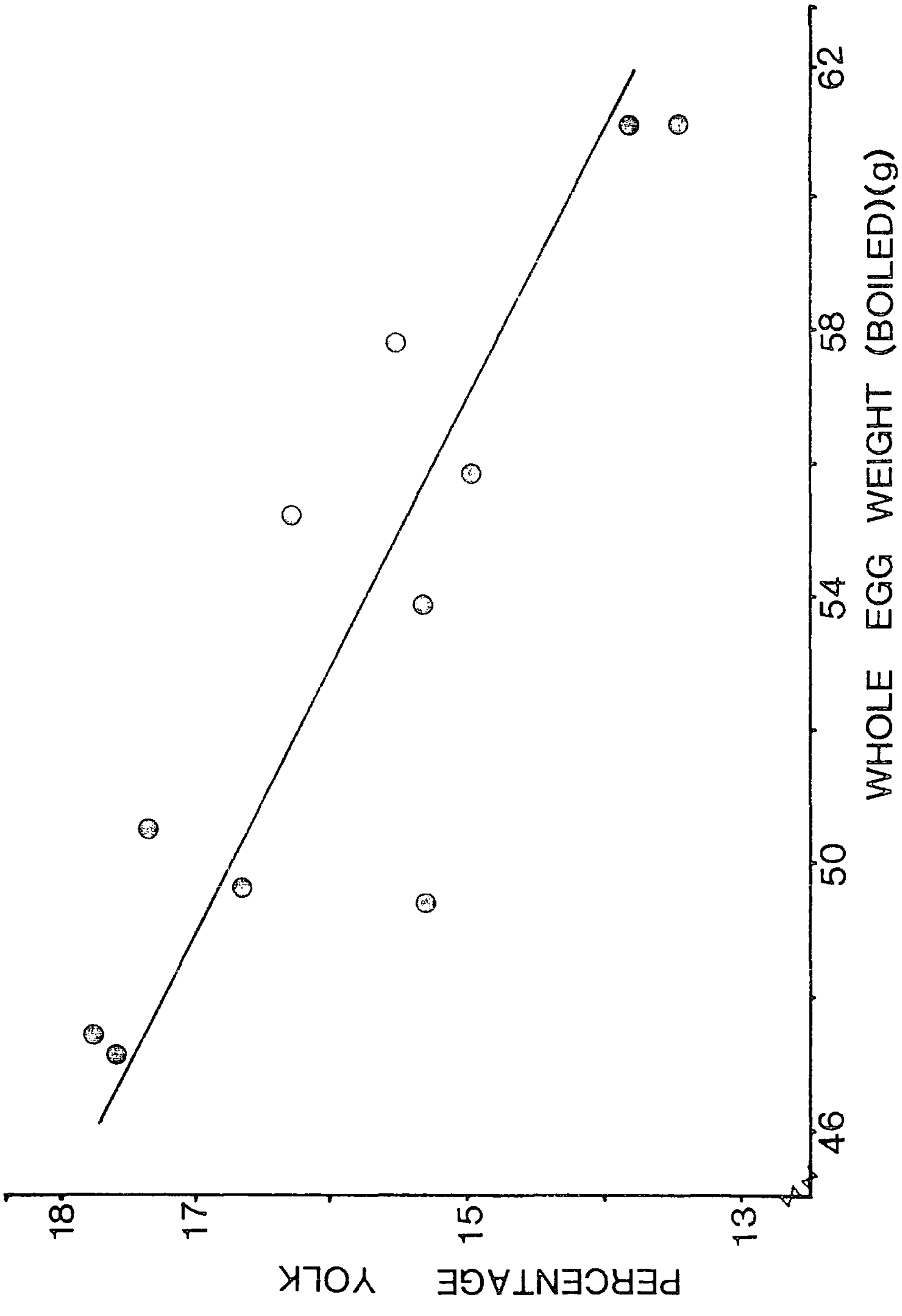


FIGURE 6.8: Variation in yolk weight with respect to whole egg weight. Solid line = least squares regression, dashed line = expected regression if the proportion of yolk present was constant at 15.7 % (the mean value). Fitted line derived from :

$Y = 0.036(X) + 6.53$;

$r = 0{,}36$;

NS. SE of slope = 0.029

SE of intercept = 1.58

FIGURE 6.9: The relationship between dry shell weight and whole egg weight. Solid line = slope of regression, dashed line = expected slope if proportion of weight due to shell is constant at 10.4 % (the mean value). Fitted line derived from :

$Y = 0.086(X) + 0.955$

$r = 0.77$; $P<0.01$

SE of slope = 0.02

SE of intercept = 1.03

FIGURE 6.8

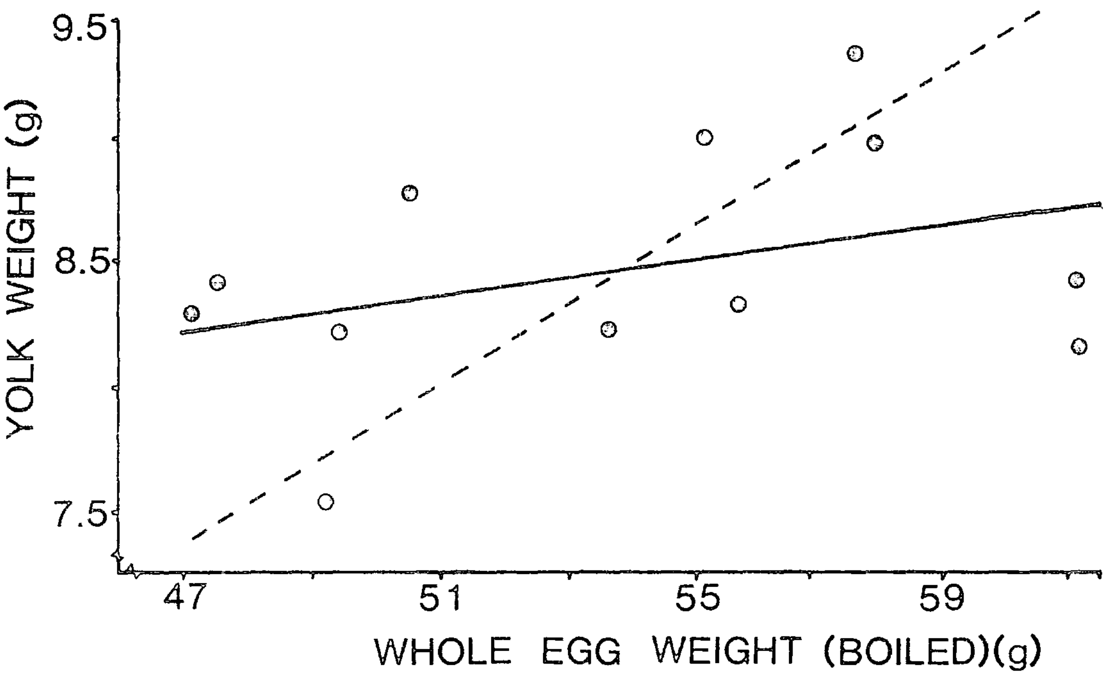
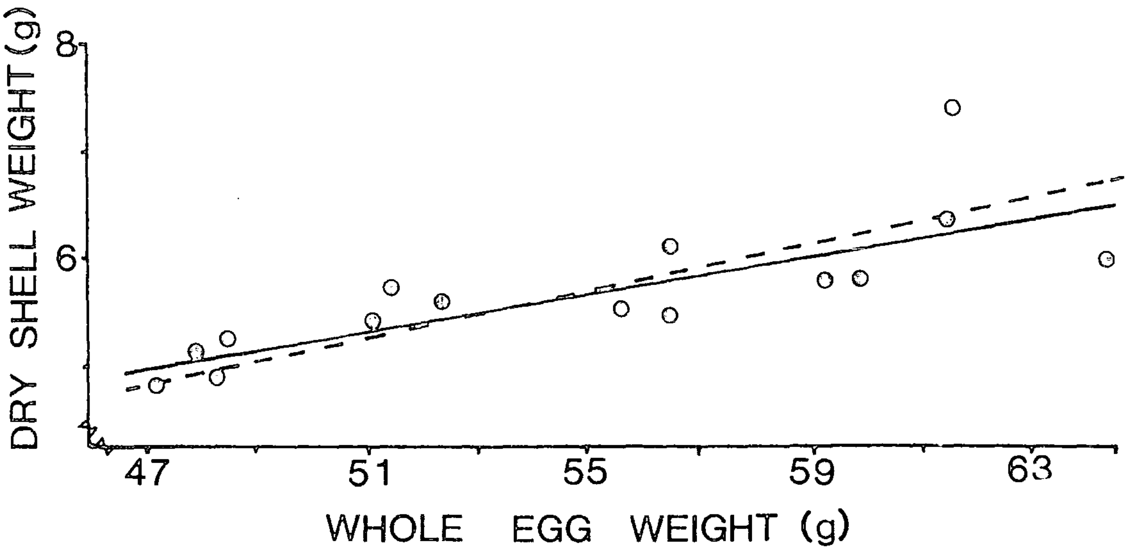


FIGURE 6.9:



t = 0.93; N.S.). Thus, increasing egg weight was largely derived from the presence of a much higher proportion of albumen in large than in small eggs (correlation between percentage albumen and boiled weight = 0.82; 10 d.f.; P<0.01).

A similar relationship was found by Williams and Burger (1979) for 7 eggs of *P. atriceps* on Marion Island.

6.5.7 Egg shape and laying order

The mean shape index of eggs in clutches of 2 did not vary in relation to laying order (Table 6.18). Nor was there any significant difference between the mean shape index of eggs in clutches of 2, and A eggs in clutches of 3. However, both B and C eggs in clutches of 3 had a significantly higher mean shape index than A eggs. These differences were largely due to differences in egg length : B and C eggs were significantly shorter, but, in the case of the B, no broader than other eggs*. C eggs were relatively broader than A or B eggs, but absolutely narrower and shorter. No such differences were evident within clutches laid by European Shags (Coulson *et al* 1969).

6.5.8 Seasonal differences in egg shape

In clutches of 2 there was a significant increase in eggshape index throughout the season (r = 0.263, P = 0.003, n = 125), and a corresponding decline in egg length (r = 0.223, P = 0.013, n = 125). Mean egg breadth did not vary significantly.

No significant changes in egg shape were evident in clutches of 3, although there was a slight (but non-significant) increase in the breadth of C eggs (r = 0.02, P = 0.07, n = 134).

---

* Excluding '1 egg' clutches

TABLE 6.18: Mean egg shape index in relation to clutch size and laying position. (± 1 S.D,).

Clutch size	Egg shape index A eggs	 B eggs	 C eggs
1	65.4 ± 4.20 (3)		
2	63.2 ± 2.82 (66)	63.2 ± 2.78 (59)	
3	63.6 ± 3.23 (137)	64.5 ± 2.97 (135)	64.2 ± 3.10 (122)

Students t tests for differences in egg shape index :

		Clutches of 3 A eggs	 B eggs	 C eggs
C 2	A eggs	N.S.	3.05**	2.52*
	B eggs	N.S.	2.95*	2.43*
C3	A eggs		2.24*	N.S.
	B eggs			N.S.

* P<0.025

** P = 0,0026

6.5.9 Egg shape and female age

The relationship between female age and egg shape, length and breadth is shown in Table 6.19. The egg shape index increased significantly with female age ($r = 0.22$, $P = 0.006$, $n = 178$), indicating that older females laid relatively broader, more rounded eggs. However, this change was due to a shortening of egg length ($r = -0.63$, $P = 0.007$, $n = 178$), whilst egg breadth showed no significant change. When considered separately, C eggs showed no significant change in shape in relation to female age.

6.6 Egg survival and fertility

Differences in the initial brood size should reflect clutch size differences unless egg survival and viability are disproportionately lower in large clutches. Egg survival is here defined as the proportion of eggs laid which survive undamaged in the nest until the time at which they would be expected to hatch - after a period of 31 days. The proportion of eggs 'lost' includes those which were deserted, since, in a number of cases it was not possible to discern whether desertion was itself a result of egg loss or damage (in particular by Wattled Sheathbills), or had occurred through some other factor.

Egg viability was defined as the proportion of eggs which survived undamaged for 31 days, and which subsequently hatched. It was assumed that the proportion of inviable eggs which survived the 31 day period was the same as among those which were lost. That is, that adults did not selectively remove or damage eggs in which embryonic development had ceased - before the average laying to hatching period was complete. By this definition, inviable eggs included those in which no embryonic development had taken place, and those in which the embryo had died as a result of poor egg 'quality' or inattentive brooding by the parents. Thus, the proportion of eggs which hatched was obtained from :

TABLE 6.19 Mean egg length, breadth and shape index in relation to clutch size and female age group.

	Clutches of 3				Clutches of 2			
Age Group	Sample Size	Shape Index	Length	Breadth	Sample Size	Shape Index	Length	Breadth
3	-	-	-	-	2	62.4	61.3	38.3
4	6	62.4	64.1	39.9	2	65.7	61.6	40.5
5	31	62.7	63.1	39.5	15	61.2	64.8	39.6
6-7	25	64.5	62.8	40.5	6	64.4	62.0	39.9
8-9	35	63.5	63.2	40.1	9	64.3	63.0	40.5
10-11	35	54.5	61.8	39.7	9	63.8	62.4	39.7

$$\text{Proportion which hatch} = \frac{\text{No. which survive*}}{\text{No. laid}} \times \frac{\text{No. which hatch}}{\text{No. which survive}}$$

* to at least 31 days

In 1981 fewer visits were made to each colony, and so the relative contributions of inviability and egg-loss to the proportion of eggs which fail could not be determined accurately.

6.6.1 The proportion of eggs hatching at either colony, in each season

Of 645 eggs laid at Shagnasty in 1980, 84.9 % hatched, compared with 90.8 % of 633 eggs laid there in 1981 (a significant difference; $\chi^2_1 = 11.40$; $P<0.001$). At North Point in 1979 a higher proportion of eggs was lost, but a lower proportion proved inviable than in 1980 (Table 6.20). This resulted in a significant difference in the proportion of eggs which hatched, both between seasons, and between the two colonies in one season (1980). Hatching success thus varied from 51.8 % to 84.9 %.

In the European Shag, Potts (1966) found that only 60.4 % of eggs laid on the Farnes survived the incubation period, whilst on Lundy egg survival was much higher - 93 % (Snow, 1960). Potts was able to show that egg survival was indirectly linked to the age of the male, through age-related variation in nest-site quality : he suggested that nests built by young males often could not adequately retain the eggs. In the present study it was found that the average quality of nest-sites used at the North Point colony was lower than that at Shagnasty in terms of the degree of social contact between birds on neighbouring sites, but not with regard to nest-site capacity. The relationship between site quality, and adult age is discussed more fully in Section 5.

TABLE 6.20: Egg survival, viability, and the proportion of eggs which hatched at either colony.

	North Pt. 1979	North Pt. 1980	Shagnasty 1980
Eggs laid	81	131	645
No. lost	38	18	50
% lost	47 %	13.7 %	7.7 %
No. inviable	1	14	47
% inviable	2.3 %	12.4 %	7.9 %
No. hatched	42	99	548
% hatched	51.8 %	75.5 %	84.9 %

χ^2 tests for differences in survival, viability, and proportion of eggs which hatch.

	North Pt. 1979		North Pt. 1980		Shagnasty 1980
Egg survival		28.30**		4.88*	
Viability		+		N.S.	
Proportion hatching		12.59**		6.92*	

* $P<0.05$

** $P<0.001$

+ $P = 0.04$ (Fisher's Exact Test)

6.6.2 Proportion of eggs hatching in relation to laying order and size

Survival in several species has been shown to be slightly greater in large than in small clutches (in Kittiwakes; Coulson and White 1958). However, in the present study there were no significant differences in the survival, viability or hatching rates of A, B, or C eggs overall, nor between clutches of 2 and 3 (Table 6.21). Since C eggs were intermediate between A and B eggs with respect to survival and viability, one might predict that small egg size is unlikely to affect the chances of hatching (C eggs being significantly smaller than A or B eggs : 6.5.2). This prediction is borne-out in Table 6.22 : there is no apparent relationship between egg size, survival and viability.

6.6.3 Seasonal variation in egg viability and survival

In 1980 egg survival and, consequently, the proportion of eggs which hatched overall, declined with laying date (Fig. 6.10). However, only in the case of egg survival was the degree of variation statistically significant; $\chi^2_3 = 8.93$; $P<0.05$. Although in both 1980 and 1981 the proportion of eggs which hatched declined with laying date, in neither year was the degree of variation statistically significant. There was no apparent relationship between viability and laying date (Table 6.23). From these results it would seem unlikely that egg survival was strongly influenced by adult age (which showed no detectable change with laying date).

There was a strong inverse relationship between the proportion of eggs lost and the number of clutches started during each laying period ($r = -0.75$; $P<0.05$), and a similar relationship between egg loss during each laying period and the mean number of clutches 'at risk' per day throughout the 29 day incubation period ($r = -0.74$; $P<0.05$ - 1980).

TABLE 6.21: Differences in egg survival, viability, and the proportion of eggs which hatched, in relation to clutch size and laying position.

a) Order of laying

1980	A eggs	B eggs	C eggs	Sample Size	% Overall
% lost	9.2	5.2	8.7	645	7.7
% inviable	10.1	6.1	6.8	595	7.8
% hatched	81.1	88.7	84.7	645	84.9

χ^2 tests for differences in survival, viability, and proportion which hatched not significant.

b) Clutch size*

	1980			1981		
	C 2	C 3	Sample Size	C 2	C 3	n
% lost	9.3	6.6	642	-	-	-
% inviable	7.7	7.8	594	-	-	-
% hatched	83.6	85.9	642	85.7	92.6	991

Differences with respect to clutch size not significant.

* Clutches of 1 (n = 3) omitted.

TABLE 6.22: The relationship between egg volume and survival, viability, and proportion hatching. Mean ± 1 S.E. shown.

Mean Egg Volume

Survive	51.18 ± 0.25	Lost	50.26 ± 3.75
Viable	51.10 ± 0.26	Inviable	51.98 ± 3.88
Hatch	51.10 ± 0.26	Do not hatch	51.23 ± 2.04

Differences with respect to egg volume not significant

TABLE 6.23: Seasonal variation in egg survival, viability, and hatching rate.

Relative laying date 1980	Sample Size	Percentage survive	Percentage viable	Percentage hatch	Relative laying date 1981	Percentage hatch	Sampl size
1-15	54	94.4	94.1	88.8	1-10	96.7	62
16-20	109	94.4	90.3	85.3	11-12	90.2	113
21-25	182	93.9	93.6	87.9	13-15	93.8	126
26-30	136	92.6	88.0	81.5	16-19	91.2	127
31-35	86	86.0	95.9	82.5	20-22	88.8	108
36-45	44	86.9	95.0	82.6	23-33	90.4	70

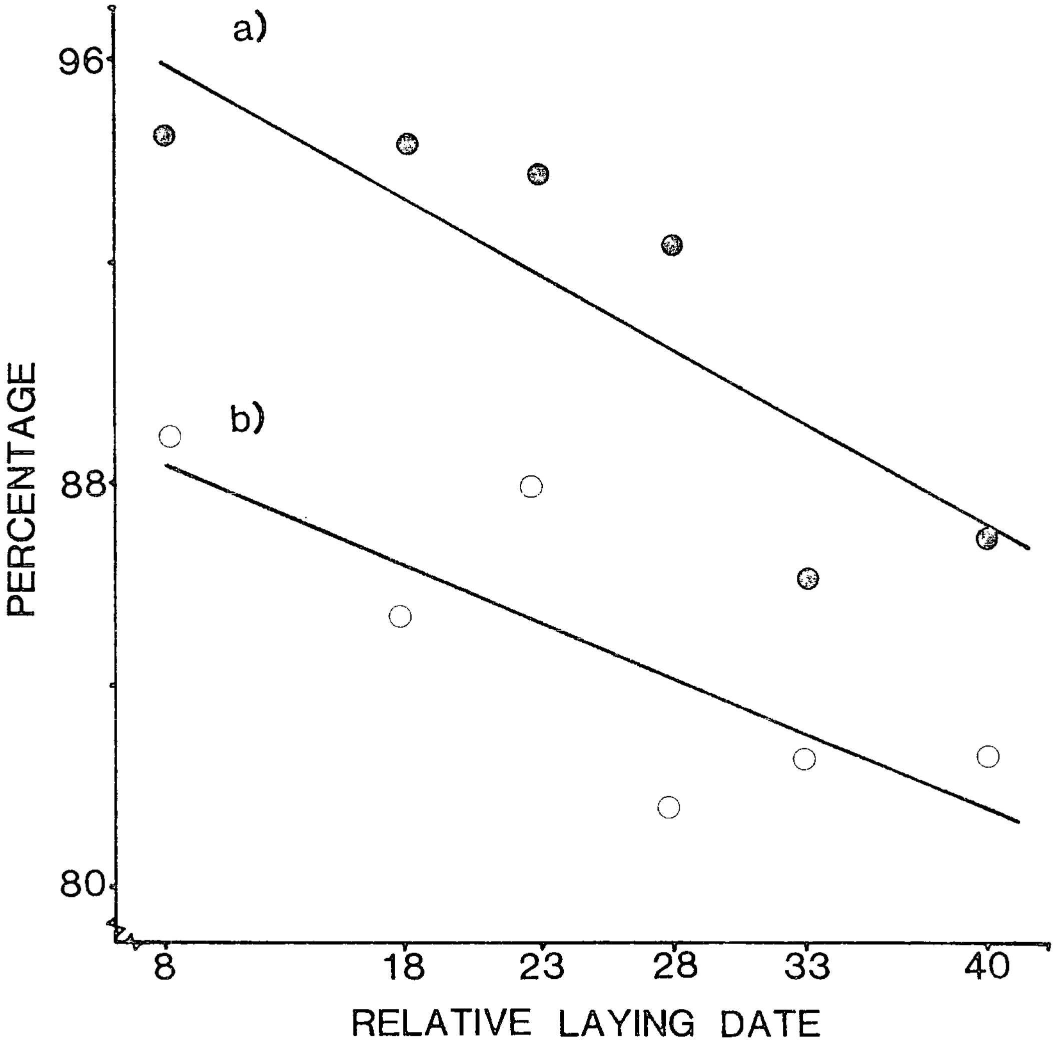
Figure 6.10: Variation in egg survival (Y) and the percentage of eggs which hatch (Y') with respect to laying date (X), described by the regression equations:

a) $Y = -0.287(X) + 98,55$

$r = 0.84;\ P<0.05$

b) $Y' = -0.217(X) + 90.19$

$r = 0.80;\ P<0.05$



Darling (1938) suggested that constant predation pressure would account for a higher proportion of eggs lost before and after the main laying period - as may also be the case for egg-theft (by Wattled Sheathbills and Brown Skuas) on Signy Island.

6.6.4 Egg survival and viability in relation to adult age

There was no statistically significant relationship between the age of either partner, and the proportion of eggs which survived or which proved viable (Table 6.24). Only when comparing 8 - 9 year-old males with those of 10 - 11 years were significant differences evident : proportionately fewer of the eggs laid by partners of the latter group proved viable ($\chi^2_1 = 6.93$; $P<0.01$) and hatched ($\chi^2_1 = 5.36$; $P<0.05$) than of the former group.

6.7 Laying order, seasonal and age-related effects

Table 6.25 summarizes the effects of three variables - laying order, laying date and adult age - on those factors likely to influence the initial brood size of each pair, and the hatching weight of the chick.

Discussion

In contrast to many other studies of age effects on breeding performance, no relationship between age and the timing of laying was evident for the Antarctic Blue-eyed Shag. It may be that age effects on the timing of laying were partly suppressed by the greater degree of laying synchrony shown within each colony. Breeding synchrony may reduce predation effects if at the time of peak laying or hatching, prey availability temporarily outstrips predator requirements (Darling 1938, Gochfeld 1980), as has been shown to occur for a wide range of potential prey-types ; from cicadas (Lloyd and Dybas 1966) to seabirds (Parsons 1971) and ungulates (Wilson 1975). In 1980 the proportion of eggs lost

TABLE 6.24: Variation in egg survival, viability, and the proportion which hatch, in relation to adult age-group.

	MALES				FEMALES			
	1980			1981	1980			1981
	(n = 338 eggs)			(495)	(n = 231 eggs)			(381)
Age Group	Percentage survive	Percentage viable	Percentage hatch	Percentage hatch	Percentage survive	Percentage viable	Percentage hatch	Percentage hatch
3-4	-	-	-	92.2	-	-	-	80.4
4	91.0	88.0	80.0	-	86.6	93.3	82.3	-
5	93.6	92.1	87.0	88.4	84.5	93.5	79.3	92.1
6-7	86.5	92.0	79.3	90.4	95.7	95.5	91.3	94.9
8-9	95.6	97.7	93.2	95.1	92.3	93.8	86.5	94.1
10-11	93.7	83.1	73.0	-	88.0	94.2	82.7	-
10-12	-	-	-	89.2	-	-	-	92.6

TABLE 6.25: The effects of three variables - laying order, laying date and parental age - on those factors most likely to influence brood size and chick survival.

	Effect of :		
on:	Order of Laying	Increasing Laying date	Increasing Adult Age
Laying date	-	-	N.S.
Clutch size	-	Sig. decrease	Sig. increase
Laying interval	Sig. increase	Sig. increase	N.S.
Hatching interval	Sig. increase	N.S.	N.S.
H/L ratio	Sig. increase	N.S.	N.S.
Lay-hatching period	Sig. decrease	Sig. decrease	N.S.
Egg size	Sig. decrease	N.S.	Sig. change
Chick size (hatching)	Sig. decrease	N.S.	Sig. change
Shape index	Sig. increase	Sig. change	Sig. increase
Egg survival	N.S.	Sig. decrease	N.S.
Egg viability	N.S.	N.S.	Sig. change

N.S. = not significant

by Blue-eyed Shags varied throughout the season, being higher when the number of clutches 'at risk' was low. The most likely cause of this was that predation pressure - in this case from Wattled Sheathbills and Brown Skuas - may have a proportionately greater effect on late-laying adults, thus contributing towards the evolution of synchronous laying.

Late laying adults of all age groups produced, on average, smaller clutches than those produced during the first half of the laying span. This finding agrees with that of many other workers, and, where it occurs independently of age effects on the laying date, it is commonly explained in terms of a seasonal decline in the food supply (Perrins 1970). If this is the case, then the high (and relatively constant) mean clutch sizes of 1981 may reflect an abundance of food during that season. However, whilst laying began 12 days later in 1981 than in 1980, it ceased at about the same time in each season, suggesting that the constraint(s) to prolonged laying in 1981 may not have been food availability. Perhaps, had the 1981 laying span been of an equal length a similar decline in clutch size would have occurred.

Seasonal variation in clutch size should preclude age-related effects if the influence of age on the timing of laying is weak or absent. In 1980 a seasonal decline in clutch size was strong and the influence of age was not apparent, whilst in 1981 the converse occurred. By contrast Potts (1966) showed that in the European Shag mean adult age declined with laying date whilst clutch size did not - and thus found no relationship between age and clutch size.

Of the five breeding variables strongly influenced by adult age, three (clutch size, egg volume and male fertility) showed a significant decline at age 10 - 11 years, suggesting that senility had a depressive effect on the mean initial brood sizes of older birds. However, the apparent decline in clutch size and in male fertility was largely dependent on the age groupings used : changing the age pairings by one year removed or reduced 'senility' effects. Only in the case of egg volume was the eventual decline with age found to be independent of the way in which the sample was divided. Evidence of a significant decline in egg size, following an initial increase, has been found in Yellow-eyed Penguins older than 14 years (Richdale 1955), and in Herring Gulls older than 8 years (Davis 1975), whilst a decline in egg size has been noted in Red-billed Gulls over 9 years of age (Mills 1979) and in Ruff, after 2 - 4 years of breeding (Anderson 1953 <u>in</u> Davis 1975).

Perrins (1970) and Mills (1979) have argued that seasonal and age-related variation in egg size reflect differences in foraging ability and food availability at the time of egg formation. Whilst this may be an important factor for species in which the ratio of clutch weight to adult weight is high (e.g. in Red-billed Gulls - 29 - 40 %; Mills 1979, and in Great Tits 40 - 108 %; <u>from</u> Perrins 1979) it is difficult to accept that foraging ability may limit egg size in the Blue-eyed Shag (mean clutch weights = 4.0 % - 5.9 % of female weight), or that older females might become markedly less efficient as foragers in the space of 1 - 2 years.

Few studies have examined the relationship between age and egg shape. Coulson *et al* (1969) described the effects of laying date and age on egg size and shape in the European Shag. Results from the present study differ from his findings on several points. Firstly, within - clutch variation in egg shape in *P. aristotelis* was slight. In both studies egg length declined throughout the season, but whilst egg shape index increased for the Blue-eyed Shag, it decreased for the European Shag.

The most fundamental difference in the results of the two studies lie in egg breadth changes; although both studies show an increase in the shape index with age, in the present study this resulted from a decrease in egg length, whilst in the European Shag increasing egg breadth was the main contributing factor.

In the Blue-eyed Shag, as in most seabirds, the scope for variation in clutch size is slight - each female either lays 2 eggs or 3 eggs, but rarely more or less. In this context it is important to remember that differences in the mean clutch size - in relation to the season, laying date or age - merely reflect differences in the proportion of adults which attempt to hatch either 2 or 3 eggs. For early, late, experienced or first time breeders there exists not a progression in clutch size, but a dichotomy. In terms of the initial breeding investment and the subsequent parental burden the alternatives are therefore limited, although it has been suggested that egg size reduction may be regarded as an intermediate stage in clutch size reduction (Thomas 1980) and, by inference, may provide a continuum between successive clutch sizes. In the Blue-eyed Shag, within-clutch differences in egg volume, and asynchronous hatching lead to differences in hatching weights and subsequent chick-survival, and therefore may be interpreted as adaptations which promote brood reduction. However their acceptance as such is dependant on their frequency and order of magnitude.

Firstly, egg size variation, although strongly correlated with hatching weight, may contribute less to within-brood differences than might be expected. As in the Domestic Hen (Romanoff and Romanoff 1949), large broods contain proportionally small yolks. However, as O'Connor (1979) points out, large Swift eggs produce chicks which are structurally larger - rather than merely possessing larger yolk reserves

- on hatching. Also, large-egg chicks may be physiologically more advanced at hatching (Parsons 1970). Thus, the effects of egg size differences within Blue-eyed Shag clutches may have been more complex than merely to contribute towards chick weight differences at hatching.

The magnitude of this contribution - of 3.5 - 4.0 g difference (9 - 10 % of the mean hatching weight) - was much less than that provided by differences in the timing of hatching. After 4 days (the modal A - C hatching interval) A chicks weighed, on average, 76 g - twice as much as the newly-hatched C chick. At age 5 days C chicks weighed, on average, only a third as much as their A sibling (Section 7).

Assessment of seasonal and age effects on clutch, egg and early brood sizes must therefore take account of variation in interval lengths and egg weight differences. If clutches of 2 are within the rearing capacity of most adults in an 'average' season (Section 7) then 3-egg clutches may represent an attempt to offset egg loss or infertility (both of which are low in the Blue-eyed Shag), exploit unusually favourable (but unpredictable) resources, or perhaps - in the case of adults with few remaining seasons - indicate a much greater commitment to the current, rather than to future breeding seasons. Thus, age or seasonal effects may be reflected by the level of brood reduction invoked as well as by colony-wide differences in clutch size proportions.

Evidence of seasonal variation in laying synchrony by female Blue-eyed Shags was inconclusive, there being no apparent relationship between laying date and hatching intervals, although A - C laying intervals increased by 12 % during the season. Likewise, there was no apparent relationship between age and hatching synchrony, except that older females (of 10 - 11 years) laid and hatched more synchronous broods than all other age-groups. Nor was there any apparent seasonal or age-related variation in the relative difference in egg volume. Thus, it would appear that variation in possible adaptations for brood reduction is so slight as to be insignificant when compared to clutch-size variation, suggesting that the potential for brood reduction may be retained and exploited at a later stage, as experience or food availability dictate.

SECTION 7: Brood size and chick survival

7.1 Introduction

Food availability is, perhaps, the most important constraint to clutch size and chick survival for the majority of temperate and high latitude species (Lack 1968) and probably also amongst tropical species (Ashmole 1963, Ricklefs 1980)(although predation pressure has been strongly implicated in the latter group)(Snow 1970).

A seasonal decline in the food supply, as well as influencing clutch size, may influence chick growth and survival, in late broods of Oystercatcher (but not of Herring Gulls)(Harris 1969), in Guillemots (Hedgren and Linman 1979); in some colonial species late broods suffer proportionally higher predation pressure (Patterson 1965, Spurr 1975, Lloyd 1979). Parental age and experience has also been shown to influence chick growth and survival, notably in Gannets (Nelson 1966), Adelie Penguins (Ainley and Schlatter 1972), Brown Pelicans (Blus and Keahey 1978), Great Tits (Harvey *et al* 1979), Razorbills (Lloyd 1979), and California Gulls (Pugesek 1981).

However, for the individual chick, the effects of each of these variables may be mediated through a single additional variable; its hatching position within the brood. Late hatching chicks may suffer increased mortality within broods of European Shags (Potts 1966), Hen Harriers (Scharf and Balfour 1971), McCormicks Skuas (Spellerberg 1971, Procter 1975), Herring Gulls (Davis 1975, Parsons 1975), Western Gulls (Coulter 1973), Kittiwakes (Thomas 1980), Common and Roseate Terns (Nisbet and Cohen 1975), Great Reed and Reed Warblers (Dyrcz 1974), Great Tits, Blackbirds and Fieldfares (Ryden and Bengtsson 1980), and House Sparrows (Seel 1970). In almost all cases an (initially) small disparity in the weights and, presumably, the competitive abilities of the siblings, may be sufficient to reduce the survival chances of last hatching chicks.

In Chapter 6 brood reduction was described as a means of adjusting the brood size to suit seasonally varying resources. However, it may also be interpreted as a form of insurance against infertility or egg loss. In either situation early elimination of the 'victim' (using O'Connor's (1978a) terminology) will more effectively promote the subsequent growth and survival of those which remain. In support of this, several studies have reported high or peak mortality of chicks during the very early stages of the nestling period. Yet, except in those species in which sibling aggression is common, the means by which early chick-elimination is brought about often remain obscure. Sibling aggression may in itself frequently - or in some species, invariably - cause the death of last-hatched chicks, and is particularly widespread amongst birds of prey (Mayberg 1974), and in the Grey Heron (Owen 1955), Sandhill Crane (Miller 1973), McCormicks Skua (Spellerberg 1971, Procter 1975), and, amongst the Pelecaniformes, in two sulids (Dorward 1962) and the Pink-backed Pelican (Din and Eltringham 1974).

There are also strong theoretical arguments for the possible occurrence of suicide by young, underweight chicks if, through inclusive fitness, the benefits to surviving siblings outweigh the cost to the 'victim' (O'Connor 1978a).

Even in the absence of overt aggression, most studies have emphasised the importance of sibling rivalry in the early elimination of last-hatched chicks, and imply that the amount of food provided by the adults (at the time of elimination) is limited, forcing siblings to compete. This may be the case if the food requirements of young but large broods equal or exceed those of older, but reduced, broods later on. However, it seems more likely that in some species at least, the collective demands of complete broods of young chicks are far less than those of (reduced) older broods, and hence that elimination may in part result through 'selective neglect' of the 'victim' chick by the parents.

In this chapter the effects of parental age, the timing of laying, and hatching order on chick survival are examined.

7.1.1 Clutch size, brood size and the number of chicks fledged

The commonest clutch size - of three eggs - was also the most productive in terms of the number of chicks hatched and fledged. This was the case in all three seasons (Table 7.1). Due to the small sample size available in 1979, only results from 1980 and 1981 will be considered in detail. Clutches of three yielded on average 0.8 - 1.0 more chicks per brood at hatching (reflecting similarities in hatching success for either clutch size) but only 0.4 - 0.6 more chicks per brood at fledging, than from clutches of two (indicating that mortality was greater in the larger brood size).

Differences in the proportions of each brood size hatched and fledged in the two seasons were highly significant (chicks hatched : $\chi^2_2 = 54.6$; $P<0.001$, chicks fledged: $\chi^2_3 = 45.5$; $P<0.001$), as was the difference in the proportion of pairs which failed completely (13.5 % in 1980, 6.1 % in 1981 : $\chi^2_1 = 8.83$; $P<0.01$) or succeeded in fledging three chicks (5.8 % in 1980, 24.8 % in 1981; $\chi^2_1 = 65.5$; $P<0.001$). In total, 57 % of eggs laid in 1980 and 67 % of eggs laid in 1981 yielded chicks which survived to fledge, this difference being significant ($\chi^2_1 = 18.7$; $P<0.001$).

TABLE 7.1: The mean number of chicks hatched and fledged on Signy Island in relation to initial clutch sizes. Sample sizes in brackets.

	Clutch sizes			
1979	1	2	3	Total
Mean no. hatched	-	0.94 (17)	1.64 (14)	1.25 (31)
Mean no. fledged	-	0.35 (17)	0.78 (14)	0.55 (31)
1980				
Mean no. hatched	1.00 (3)	1.68 (106)	2.50 (188)	2.19 (297)
Mean no. fledged	0.75 (4)	1.22 (99)	1.64 (171)	1.48 (274)
1981				
Mean no. hatched	1.00 (2)	1.69 (59)	2.74 (313)	2.26 (374)
Mean no. fledged	0.66 (3)	1.38 (49)	2.00 (241)	1.88 (293)

The proportion of each brood size hatched and fledged from clutches of three differed significantly in the two years (1980 and 1981) (no. hatched: $\chi^2_2 = 21.03$; $P<0.001$, no. fledged: $\chi^2_3 = 28.67$; $P<0.001$). Differences in clutches of two however were not statistically significant.

7.2 Chick Survival

7.2.1 Chick survival at each colony

The proportion of chicks which survived to fledge at North Point from 41 which hatched in 1979 was 44 %, a low value. Unfortunately, comparable data for Shagnasty are not available, although chick mortality there was of a similar level : 98 chicks were found dead at between five to seven weeks old, and only 47 chicks were known to have fledged from 385 nests found. Most of the corpses found were extremely emaciated, and starvation was thought to have been the cause of at least 74 % of deaths at North Point. Of 20 chicks examined from Shagnasty (of five to seven weeks old) only two had food in the gut.

The proportions of chicks which survived from hatching to fledging in 1981 (83 %) was significantly higher than in 1980 (71 %) ($\chi^2_1 = 22.3$; $P<0.001$) which in turn was much higher than at North Point in 1979 (44 %) ($\chi^2_1 = 13.5$; $P<0.001$). Annual variation in chick survival was thus slightly greater than that recorded for the European Shag on Lundy Island (67 - 95 % survival, total sample size = 632; Snow 1963) and on the Farne Islands (78 - 86 % survival, total sample size = 864; Potts 1966). However, chick survival amongst (smaller) samples of *P. atriceps* elsewhere, and in different seasons, was much more variable, and generally lower than on Signy Island; 22 % survival on Marion Island (n = 18; Williams and Burger 1979), 59 % on Crozet Island (n = 44; Derenne *et al* 1976) and 46 - 51 % on Avian Island (n = 91; Poncet and Poncet 1979). On Marion and Crozet starvation accounted for an appreciable proportion of chick deaths : 71 % and 39 % respectively.

7.2.2 Chick survival in relation to brood size and hatching order

In the two years for which large samples are available, significantly fewer chicks in broods of 3 survived than in broods of 1 or 2 (for which survival rates were approximately equal : Table 7.2). However, survival

TABLE 7.2: The percentage of chicks which survived to fledge, in relation to initial brood size.

Percentage surviving at:	Initial brood sizes 1	2	3	n (chicks)
North Pt. 1979	-	45.0	38.0	41
North Pt. + Shagnasty 1980	76.5	80.9	55.7	569
North Pt. + Shagnasty 1981	100.0	90.0	78.1	579

Differences in the proportion of chicks surviving in broods of 3 compared with broods of 2 and 1 combined :

	χ^2	d.f.	P
1979	0.19	1	N.S.
1980	39.59	1	<0.001
1981	13.98	1	<0.001

of A and B chicks in broods of three was of a similar (high) level to that of A chicks in broods of one and two, and of B chicks in broods of two. In 1980, reduced survival in three-chick broods was entirely due to high mortality amongst C chicks, whose survival rates were significantly lower than those of all other hatching position and brood size categories (Table 7.3). It is perhaps significant that in the previous season, during which the overall survival rate was lower, the proportion of A and C chicks which survived was similar to that of 1980, whilst low survival in 1979 was due to high mortality amongst B as well as C chicks. These differences, and the proportion of chicks surviving throughout the nestling period, are illustrated in Fig. 7.1. Thus, in one season in which survival was high, only last hatched chicks suffered high mortality, whilst in the preceding year both last and penultimate chicks suffered high mortality, and first hatched chicks retained a comparatively high survival rate.

7.2.3 Laying date and chick survival

Chick survival may be expected to decline in tandem with food availability - although the effects of a seasonal decline in the mean age of breeding adults may complicate the issue. However, since no relationship between age and the timing of laying was evident in the present study, the decline in nestling survival shown in Table 7.4 may reflect differences in the food supply available to late hatching chicks. In 1981 proportionally fewer chicks of all brood sizes survived in the last third than in the first third of the season. Differences in 1980 however, were not significant.

If the occurrence of brood reduction was at least in part dependent on food availability, then one might expect a more marked decline in chick survival in broods of three than in broods of two. This was not

TABLE 7.3: Chick survival to fledging in relation to brood size and hatching order in 1980 (initial sample size shown below each percentage).

Initial brood size	Hatching Order A chicks	B chicks	C chicks
I	81.5 (27)	-	-
2	83.3 (96)	78.1 (96)	-
3	94.1 (85)	82.1 (84)	11.1 (81)

χ^2_1 for differences in chick survival in relation to hatching position in broods of 2 and 3.

Brood size

		2	3		
		A	A	B	C
2	B	5.14*	4.35*	N.S.	79.17**
	A		N.S.	N.S.	91.60**
3	A			5.84*	115.10**
	B				85.53**

*P<0.05

**P<0.001

FIGURE 7.1: Chick survival from day 1 - 65, in relation to hatching order. Broods of three only.

1979 n = 41

1980 n = 469

Percentage survival is shown on a Log. scale.

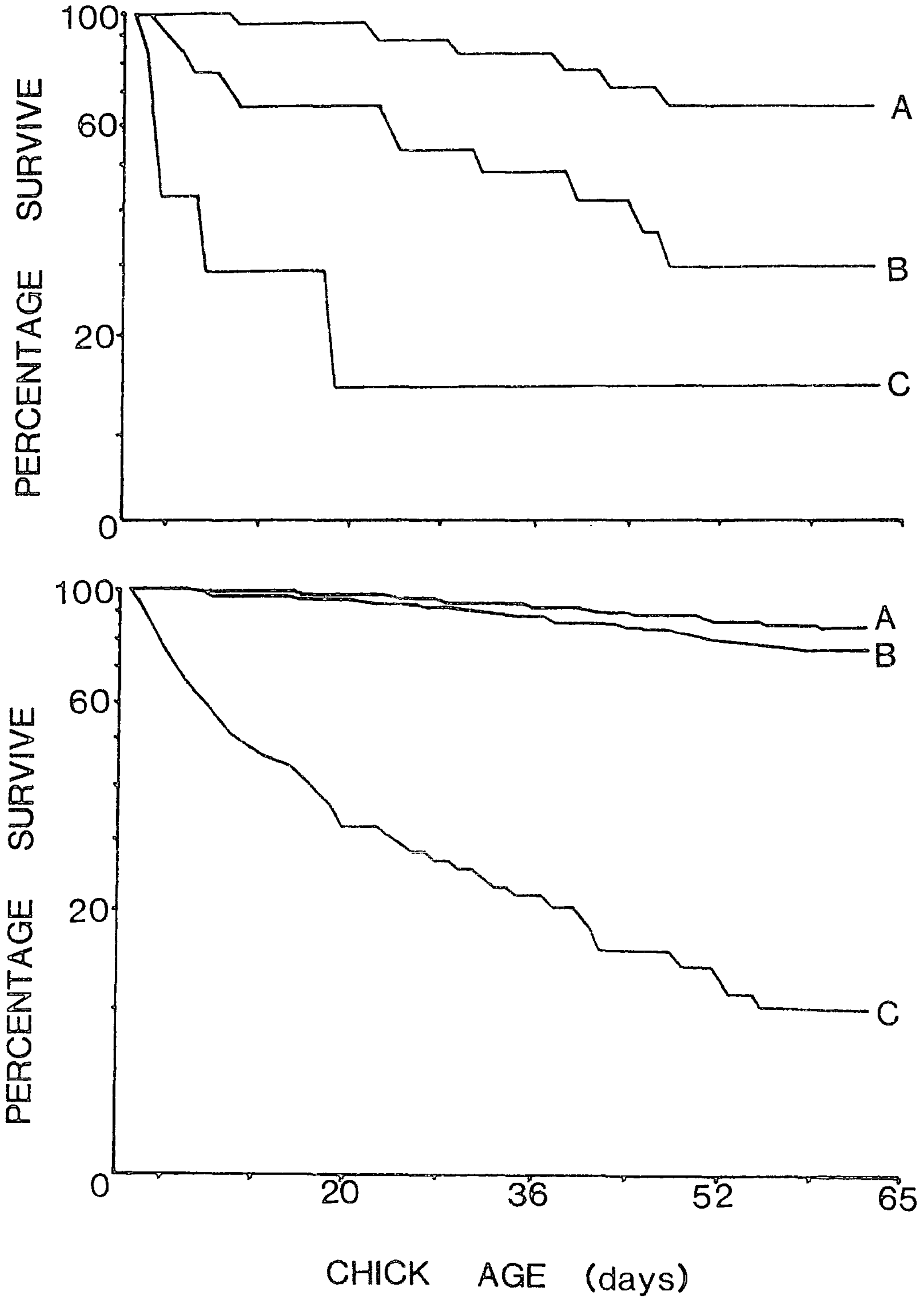


TABLE 7.4: Variation in chick survival in relation to laying date. Since equal time periods would have yielded small sample sizes for the first and last third of the season, data have been partitioned to yield large sample sizes. Figures given are percentage survival (sample sizes in brackets).

1980	Relative laying date				
Brood size	1 - 12	13 - 18	19 - 35	χ^2_2	P
1/2	81.5 (65)	81.2 (85)	77.8 (113)	0.44	N.S.
3	63.1 (114)	65.7 (102)	54.5 (66)	2.19	N.S.
Total	69.8 (179)	72.7 (187)	69.3 (179)	0.58	N.S.

1981					
Brood size	1 - 5	6 - 8	9 - 22	χ^2_2	P
1/2	97.9 (48)	95.4 (44)	83.3 (48)	-	0.005*
3	83.8 (105)	75.2 (105)	70.3 (81)	4.96	N.S.
Total	88.2 (153)	81.2 (149)	75.2 (129)	48.16	0.001

In 1981 although broods of 3 showed no significant variation overall, differences in survival in the first and last third of the sample were significant $\chi^2_1 = 4.83$; $P<0.05$.

*Fisher's Exact Test.

the case : differences in the proportion of chicks surviving in early and late broods of two and three were about the same; a drop of 14.6 % in broods of two and 13.5 % in broods of three.

7.3 Brood Sizes

7.3.1 Brood size and laying date

The mean number of chicks hatched and fledged per pair declined during each season (Fig. 7.2). In 1980, brood size proportions both at hatching and at fledging varied significantly with respect to the laying period (chicks hatched; $\chi^2_6 = 38.3$; $P<0.001$, chicks fledged; $\chi^2_3 = 16.9$; $P<0.001$), but this was only true of the number of chicks fledged in 1981 ($\chi^2_2 = 10.4$; $P<0.01$). In spite of marked differences between seasons in the average number of chicks hatched and fledged, the effects of laying date on breeding success were of a similar magnitude in each year; females which laid towards the end of the season fledged, on average, 0.64 to 0.66 fewer chicks than those which laid during the most favourable period (in 1981 and 1980 respectively). Similar results have been reported for Herring Gulls (Parsons 1975), Adelie Penguins (Spurr 1975), Razorbills (Lloyd 1979) and Kittiwakes (Thomas 1980), whilst in Manx Shearwater (Perrins 1966) and Great Tits (Perrins 1979) fledging success and subsequent survival decline throughout the season. This would also appear to have been the case in 1981, in which the earliest clutches produced the largest broods. However in 1981, laying began 12 days later than in 1980. Thus the period of decline in mean brood sizes at fledging coincided in the two years. Moreover the slope of the decline (calculated from regression analysis) was similar : -0.06 ± 0.04 (S.E.) in 1980 and -0.04 ± 0.06 (S.E.) in 1981.

Similarities in the mean number of chicks hatched and fledged throughout 1980 suggest that chick survival was relatively constant with respect to laying date, whilst a comparison of hatching and fledging

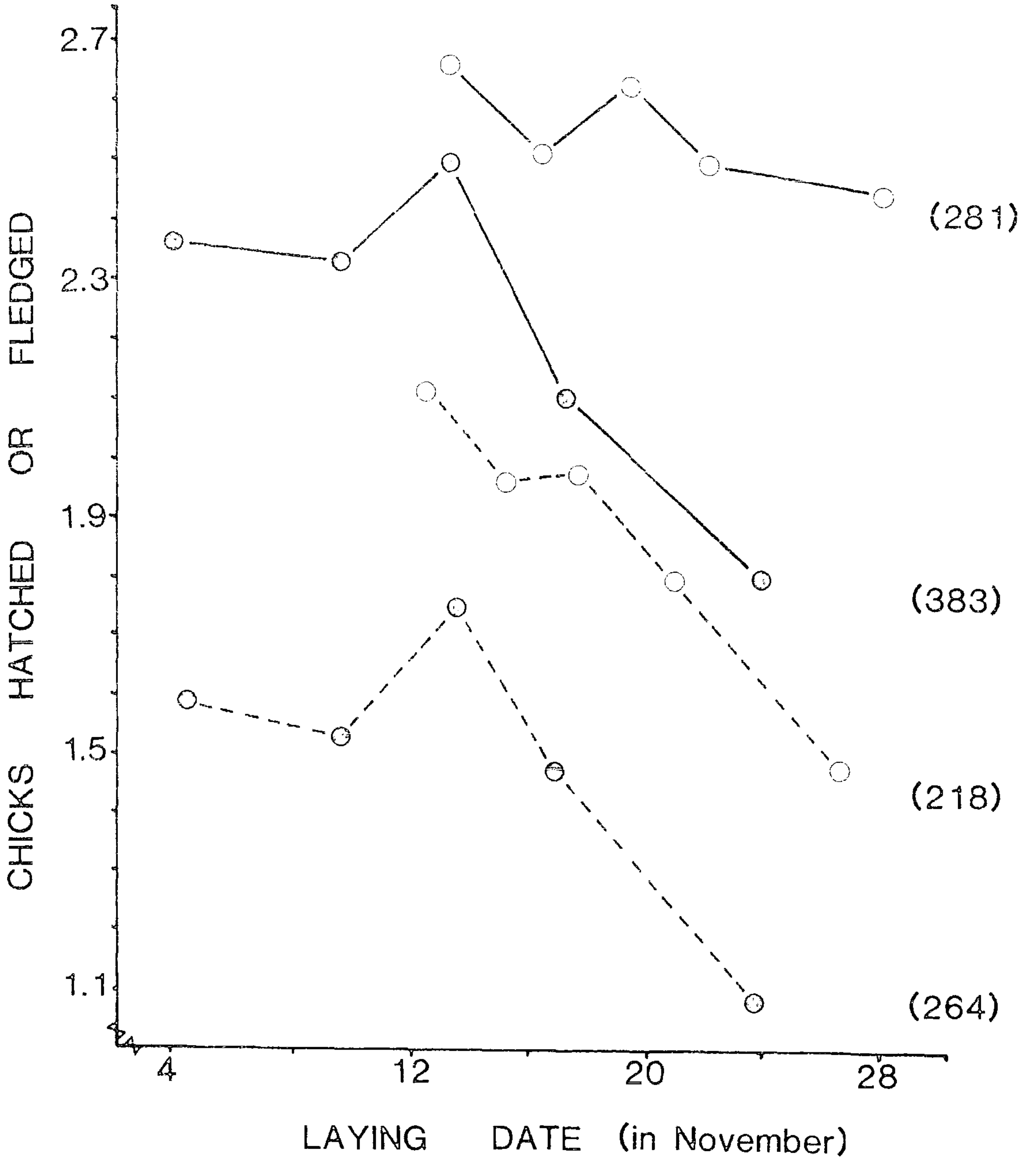
FIGURE 7.2: Variation in the mean number of chicks hatched and fledged in relation to laying date.

——— chicks hatched ● 1980

- - - - chicks fledged ○ 1981

Sample sizes shown in brackets.

FIGURE 7.1:


CHICKS HATCHED OR FLEDGED
2.7
2.3
1.9
1.5
1.1
4
12
20
28
LAYING DATE (in November)
(281)
(383)
(218)
(264)

patterns in 1981 would suggest that chick survival declined throughout the season. These results were confirmed in Section 7.2.3.

7.3.2 Analysis of adult age-effects

In the analyses which follow, the relationship between 'parental' age and, for example, chick death-age was largely derived from examination of breeding pairs in which only one partner was of known age. Analysis of age differences (Section 4) has shown that in most cases the age (and breeding experience) of birds of unknown age is similar to that of their ringed mate. However, where the ages of both partners are known (17.8 % of pairs) only that of the female was used in the analysis since, in this instance female age shows a stronger correlation with the variable (chick death-age) than does male age. The correlation between adult age and the age at death of C chicks and A/B chicks was greater in the case of adult females than males. For either sex the slope coefficient was positive for adult age in relation to C chick death-age,and negative for adult age in relation to A/B death-age(Table 7.5).

TABLE 7.5: The relationship between adult age and the age at death of C chicks and A/B chicks.

		slope	intercept		
Female	r	m	c	n	P
Age A/B	- 0.34	-2.16	47.5	25	-
C	0.36	+2.65	-0.7	22	0.10
Male					
Age A/B	- 0.08	-0.66	39.4	41	-
C	0.27	+1.44	4.2	34	-

7.3.3 Brood size in relation to adult age

The mean number of chicks hatched per pair increased with adult age, and reached a peak at 8 - 9 years in 1980, and at 10 years in 1981 (Fig. 7.3, Appendix H). Throughout the age range the proportions of (initial) brood sizes of 3,2 and 1 varied significantly in both years (1980, χ^2_4 = 12.14; $P<0.05$ and in 1981 χ^2_5 = 17.5; $P<0.01$). However brood size differences in 1980 were more pronounced in the 3 - 5 year age groups; throughout the 5 to 10+ year age groups differences in the number of chicks hatched were not statistically significant. This was not the case in 1981; brood size variation throughout the 5 to 11+ year age group was statistically significant (χ^2_4 = 11.48; $P<0.05$) due mainly to the smaller average brood size hatched by 11 year-olds than by 10 year-olds.

The pattern of age-related variation in the number of chicks fledged reflects initial brood sizes in that the degree of change was greatest during the first three breeding years. Thus, although variation in the number of chicks fledged throughout the age-span was significant (1980, χ^2_4 = 11.38; $P<0.05$, 1981, χ^2_5 = 18.45; $P<0.01$), this was not the case when the two youngest age-groups were omitted.

Broad similarities in the mean number of chicks hatched and fledged by each age-group suggest that the proportion of chicks reared varied little with respect to adult age. This was the case amongst chicks in broods of three, there being only a slight, statistically insignificant, increase in chick survival in relation to adult age (Fig. 7.4). Surprisingly, the proportion of twins and singletons reared from hatching showed a marked increase with adult age (in 1980: χ^2_3 = 14.8; $P<0.01$, but not in 1981; Fisher's exact test), although this result loses its statistical significance if the youngest age-group is omitted. Thus,

FIGURE 7.3: The influence of adult age on the mean number of chicks hatched and fledged in 1980 and 1981.

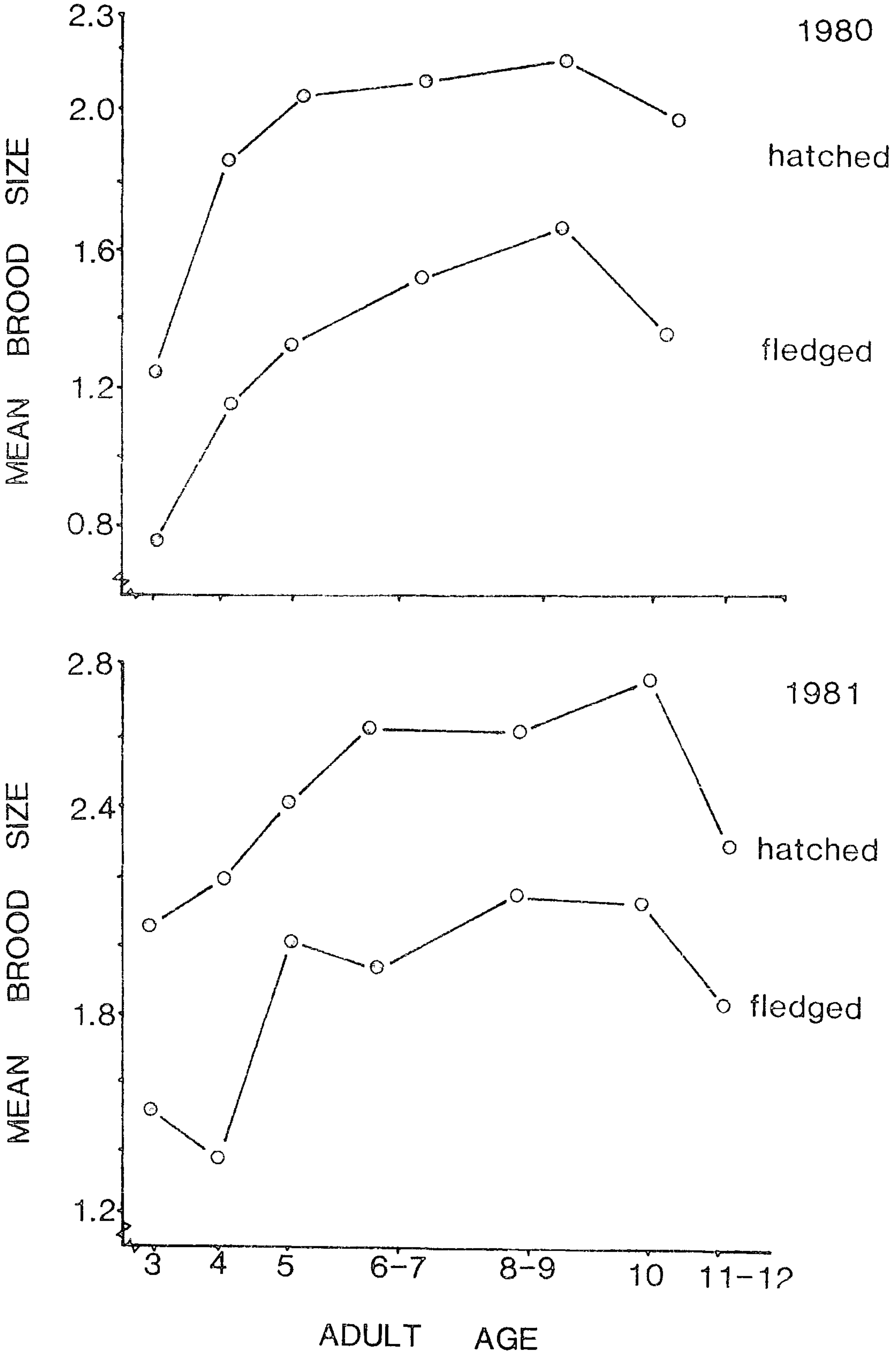
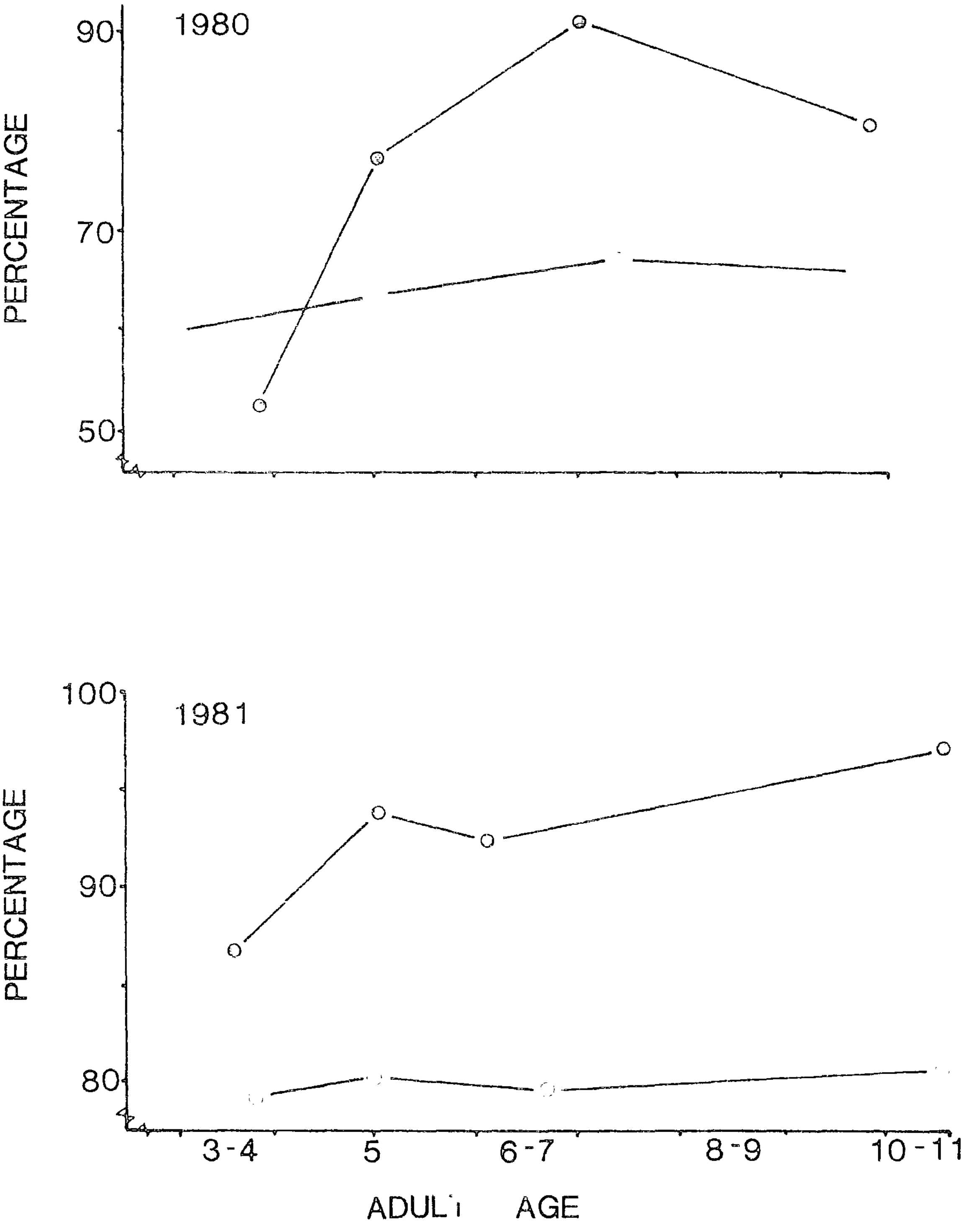


FIGURE 7.4: The influence of adult age on the percentage of chicks reared to fledging from initial brood sizes of 1 - 2 and 3.

o Broods of 1 and 2

o Broods of 3

FIGURE 7.4:


1980
PERCENTAGE
90
70
50
1981
PERCENTAGE
100
90
80
3-4
5
6-7
8-9
10-11
ADULT AGE

beyond the age at first breeding, adult age showed no significant influence on chick survival.

7.4 Chick survival following A or B-egg loss

Where in clutches of three the A or B egg fails to hatch, the C egg chick may have as high a chance of surviving as second hatched chicks in normal broods of two. However, two modifying factors must be considered: firstly, that the small size or the low ratio of albumen to yolk in C eggs may reduce the chick's survival chances regardless of what circumstances it encounters on hatching, and secondly, that any competitive disadvantage suffered by the second hatched chick is likely to be greater if the hatching interval is long (i.e. the B egg is lost) than short (the A egg is lost).

Of 31 chicks from C eggs which, through A or B egg loss, hatched in broods of two, 71 % survived to fledge; significantly more than for C egg chicks in full broods of three (11 % of 81; $\chi^2_1 = 40.11$; P<0.001), but not significantly lower than for B chicks in normal broods of two (78 % of [illegible]; $\chi^2_1 = 0.74$) or in full broods of three (82 % of 84; $\chi^2_1 = 1.69$).

The second assertion - that loss of the B egg and the long hatching delay between A and C eggs should reduce the survival chances of second hatched (C egg) chicks - was not borne out by the results. In 18 broods where the A egg failed, C egg chicks survived less well (67 %) than in 11 broods where the B egg failed (82 %). However this difference was not significant; P = 0.24 (Fisher's exact test). Thus, it would appear that reduced survival of third hatched Blue-eyed Shag chicks in normal three-chick broods stems from the presence of two other chicks in the nest rather than from an intrinsic difference in C egg 'quality'. Moreover, there was no significant difference in the mean volume of eggs from which chicks subsequently survived, or died (Table 7.6).

TABLE 7.6: Chick survival in relation to egg volume.

The mean volume of eggs from which chicks subsequently died or survived is shown with respect to hatching position.

		Mean	Sample	S.D.
A/B chicks, C 1/2	Live	51.0	85	4.27
	Die	49.8	25	3.28
A/B chicks, C 3	Live	51.1	162	3.27
	Die	50.8	26	2.42
All A/B chicks	Live	51.1	247	3.60
	Die	50.4	51	2.89
C chicks*	Live	47.7	7	1.60
	Die	49.9	47	3.54

Differences within each brood size/position category not significant (Students t).

*Mann Whitney U test used ; Z = 1.29; P = 0.09

7.5 Variation in the age at death

The age at which a chick dies should have little bearing on its parents overall reproductive success, except that late-dying chicks will have required a greater amount of (wasted) parental investment than those chicks which die soon after hatching. However, for the siblings which survive, an early rather than a late death by their nest-mate may prove advantageous (both to them, and to their parents) if, whilst alive, the 'victim' chick increases the likelihood of their discovery and predation, or reduces food availability and subsequent survival chances (O'Connor 1978a).

O'Connor (1978a) produced a model which predicts the levels at which increased liability to predation (presumed to be greater for large broods) should outweigh the benefits (to parents and siblings, through inclusive fitness) of the victim chick's continued survival, and lead to its 'elimination' either by its siblings or by its parents, or finally through its own suicide - in that order. In a colonial species such as the Blue-eyed Shag, detection and predation of chicks is unlikely to increase with brood size since there is no attempt by the parents to conceal the nest. Moreover, chicks are brooded continuously until large enough to defend themselves against predators. However, it is conceivable that the risk of brood starvation may be reduced through brood reduction, in the manner described by O'Connor for the reduction of predation risk. In other words, loss (or 'elimination') of the 'victim' chick may <u>precede</u> the period of risk - whether that risk is one of predation or starvation.

In 1980 the mean and median ages at which A and B chicks died (in all brood sizes) differed by about 2 or 3 days. On average, B chicks died slightly earlier (but not significantly so) than A chicks. However the mean and median ages at death of C chicks were less than half those of A or B chicks (Table 7.7), suggesting that the main cause of death, or the chick's sensitivity to that cause, may have differed with respect to hatching position.

On average, chicks of all hatching positions died at a slightly older age in mid-season broods than in early or late broods, although differences were not significant (Table 7.8). This trend may reflect the slightly higher percentage survival of chicks in mid-season broods of that year (Table 7.4).

Examination of seasonal effects was based on the rationale that in times of low food availability - perhaps towards the end of the season - chick deaths may occur at an earlier age than when conditions are more favourable. The same prediction may be applied to adult-age effects; that older adults - with more experience in foraging, and in distributing food to the chicks - may sustain their C chick for longer than do young adults. Table 7.9 shows that the mean age at death of C chicks reared by 'old' adults (of 6 - 12 years) was almost twice that of C chicks reared by less experienced breeders (of 3 - 5 years). A significantly higher proportion of chicks in the latter group died at 15 days or less (the mean death-age of all C chicks) than in the former. Amongst A and B chicks the mean age at death varied little in relation to adult age although, on average, A and B chicks of young adults died at a slightly greater age than those of old adults. Thus, throughout the 65 day span, the cumulative pattern of A/B and C chick deaths shows a much greater temporal separation for the 'young adult' than for the 'old adult' group (Fig. 7.5).

Since the degree of synchrony in laying and hatching was also much greater in clutches laid by older females (of 10 - 11 years; Section 6.3.3) it seems likely that there may have been a direct link between

TABLE 7.7: The mean ages of chicks at death in relation to their hatching position.

	Death-age (days)			
Position	Mean	Sample	S.D.	Median
A	39.6	25	15.97	40
B	33.7	45	16.14	34
C	15.38	72	14.50	9

	t	P
A-B	1.47	N.S.
A-C	6.69	0.001
B-C	6.23	0.001

TABLE 7.8: The mean ages of chicks at death in relation to their laying date. Sample sizes (in brackets) and S.D. shown.

Laying date :	1 - 19	20 - 29	30 - 40
A/B chicks	36.8 ± 23.69 (14)	38.5 ± 14.77 (29)	33.7 ± 12.40 (27)
C chicks	11.5 ± 4.33 (14)	17.5 ± 16.5 (39)	12.1 ± 7.58 (17)

Seasonal differences not significant :

A/B $F_{2,69} = 0.55$

C $F_{2,69} = 1.33$

TABLE 7.9: The average age at death of A/B and C chicks in relation to the ages of their parents. Ages in days.

A/B chicks

Adult age-group	Mean death-age	S.D.	n
6 - 12	30.8	17.2	21
3 - 5	37.0	15.7	31

Difference in the proportion dying at greater than 35 days, or at 35 days or less, not significant ($\chi_1^2 = 0.16$).

C chicks

Adult age-group	Mean death-age	S.D.	n
6 - 12	18.5	14.7	26
3 - 5	10.2	8.7	24

Of those C chicks hatched by young adults, and which subsequently died, 54 % died at 15 days or less, compared with 21 % of C chicks hatched by older adults ($\chi_1^2 = 5.77$; $P<0.05$).

FIGURE 7.5: The cumulative proportion of chick deaths in relation to age, hatching position and parental age.

C/YOUNG = 'C' chick of adults aged 3 - 5 years

AB/OLD = 'A' and 'B' chicks of adults aged 6 - 12 years.

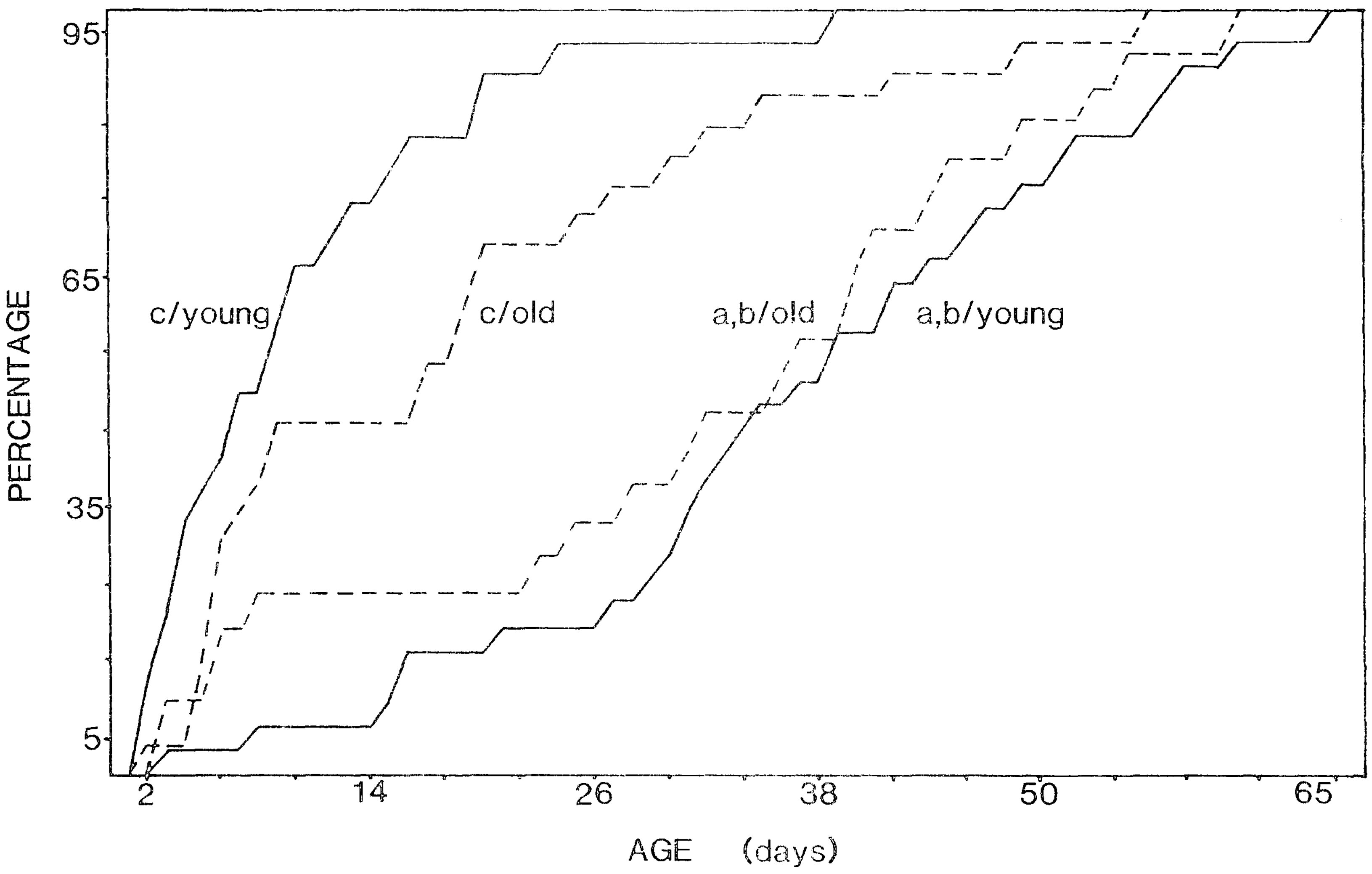

PERCENTAGE
95
65
35
5
c/young
c/old
a,b/old
a,b/young
2
14
26
38
50
65
AGE (days)

FIGURE 7.5:

the hatching interval length and the age at death of C chicks. The results in Fig. 7.6 support this view; on average, C chicks died earlier as the A-C hatching interval lengthened. C chicks which hatched within 2 to 4 days of the A chick died, on average 6.7 days older than C chicks hatched within an interval of 5 to 6 days. This difference was unlikely to have arisen by chance; P = 0.06 (Mann-Whitney U test). The relationship between the age at death, and the B-C hatching interval was not statistically significant. However, of those B chicks hatched within 3 - 6 days of their A sibling, all four died at earlier ages than four B chicks which hatched within 1 - 2 days of their sibling (P = 0.03; Mann-Whitney U test).

The relationship between hatching asynchrony and the proportion of C chicks which survives to fledge was not statistically significant, although the proportion of C chicks which died before fledging age (65 days) was 1.5 times greater in asynchronous broods (hatching over 5 - 6 days) than in relatively synchronous broods (hatching over 1 - 2 days) (Table 7.10).

7.6 Chick survival in synchronized broods

To determine whether, and how, asynchronous hatching effects chick survival, brood survival, and the age at death of chicks in broods of three, the hatching span within each of 15 broods in 1980 and of 17 broods in 1981 was experimentally reduced. Each brood was manipulated so as to comprise 3 chicks of 1 - 2 days of age, with an average weight difference of 4.2 % (heaviest-lightest). This was achieved by exchanging 1 - 2 chicks from each experimental brood with chicks from neighbouring broods. Although hatching dates and the hatching order within each 'donor' brood were not known, the relationship between age and weight

FIGURE 7.6: Hatching asynchrony and mean age at death of the C chick. 1 S.E. shown on either side of the mean.

● A - C hatching interval

○ B - C hatching interval

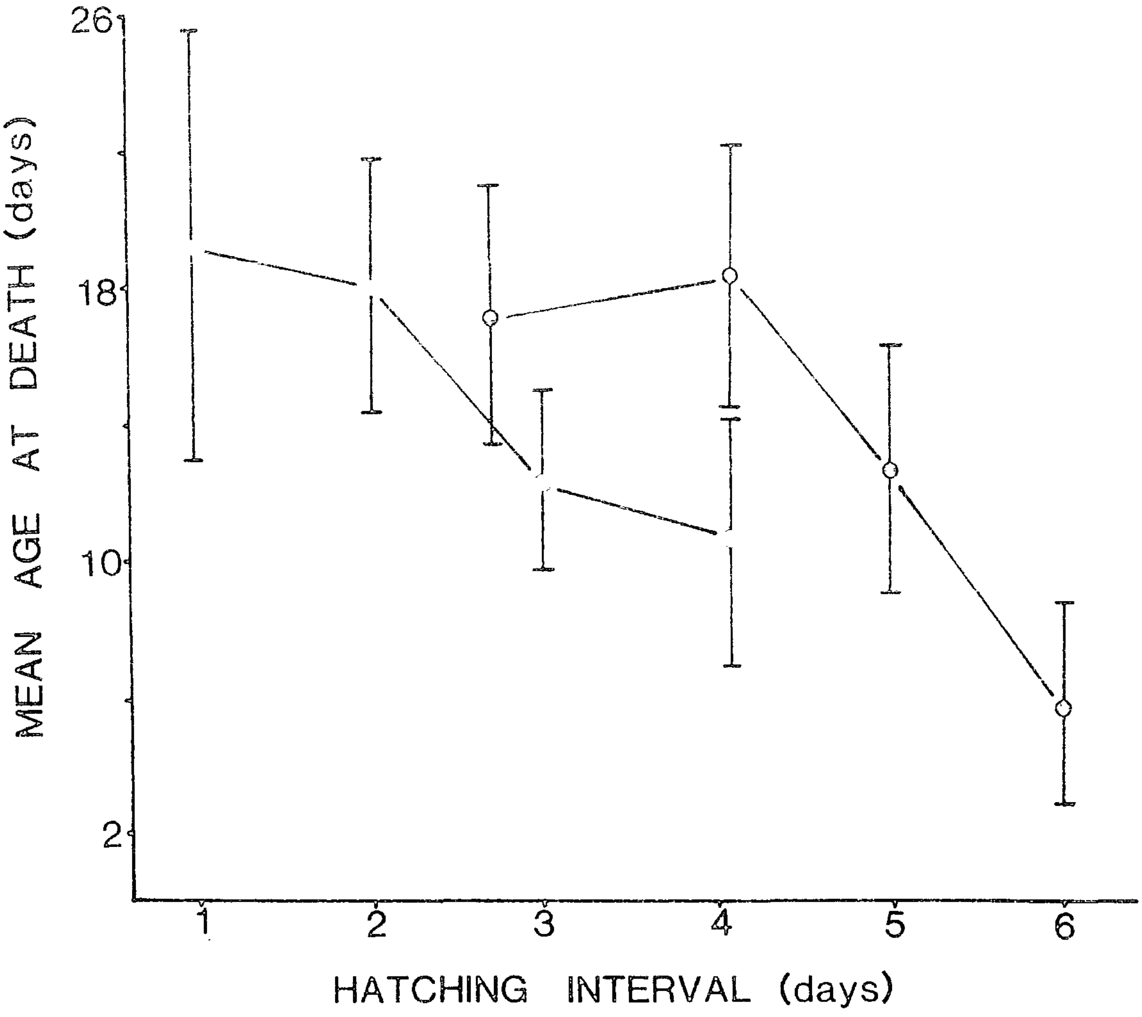


TABLE 7.10: The relationship between the degree of hatching asynchrony within each brood and the proportion of C chicks which subsequently survive to fledge

	A - C hatching interval		
	1 - 2 days	3 - 4	5 - 6
Total hatched	8	29	17
No. survive	3	3	1
Percentage die	62.5	89.6	94.1

during the first 3 - 4 days shows little variation (Section 7.10). Chicks may thus be aged confidently to within 1 day. Moreover, as shown in 7.4.2, the viability of C-egg chicks did not differ significantly from that of A or B chicks when the disadvantage of hatching third is eliminated.

There was no significant difference in the percentage of chicks which survived in synchronized broods compared with normal broods of three, in each season respectively (Table 7.11a). However, the proportion of synchronized broods which failed entirely was significantly higher in 1980 and slightly higher in 1981, than for normal broods, in each year respectively (Table 7.11b). Synchronous hatching was associated with a high chance of total brood loss, but had no apparent influence on the number of chicks produced per successful brood.

There was no significant difference in the average age at death in synchronized broods (27.4 ± 19.34 days (S.D.); n = 16) compared with normal broods of three (25.9 ± 18.3 days; n = 138). The proportion of deaths occurring at 20 days or less was similar for the two groups: 37 % of deaths of synchronized chicks and 45 % of deaths of chicks in asynchronous broods of 3 ($\chi^2_1 = 0.38$; N.S.)

7.7 Sibling weight differences in relation to age

Early mortality of C chicks may have been caused by selective neglect by the parents or through sibling competition. Whilst the latter cannot be observed directly (chicks are brooded continuously up to the age of 12 - 15 days) chick weight disparities may provide a measure of the strength of the dominance hierarchy (Bryant 1978). Figure 7.7 shows that in both normal and synchronized broods of three the absolute difference in weight between the heaviest and lightest chicks in the

TABLE 7.11: Chick survival in normal broods of three and in synchronized broods.

a) Percentage survival

1980	No. hatch	No. Die	Percentage Survive
Normal broods of three	246	99	59.7
Synchronized broods	45	16	64.0

$\chi^2_1 = 0.37$; N.S.

1981			
Normal broods of three	375	79	78.9
Synchronized broods	51	8	84.3

$\chi^2_1 = 0.79$; N.S.

b) Proportion of broods which fail

1980	No. of broods	No. Fail	Percentage Fail
Normal	82	2	2.4
Synchronized	15	3	20.0

P = 0.02; Fisher's Exact Test

1981			
Normal	125	1	0.8
Synchronized	17	1	6.2

P = 0.21; Fisher's Exact Test

brood, increased with age. This is to be expected in view of the large increase in weight required from hatching to fledging (Fig. 7.16). In contrast, the relative difference in chick weight (RDCW; calculated in the same way as for egg volume; Section 6.5.5) declined with age, after reaching a peak at 4 - 6 days (Fig. 7.8). It may be argued that the reduction in the RDCW is due to a change in sample composition; at progressively older age intervals the data are derived from a dwindling sample of broods in which the C chick had survived - perhaps as a result of low RDCW scores throughout. This possibility was eliminated by comparing the mean RDCW scores at ages 1 - 15 days, of those broods in which the C chick died during that period, with those in which it survived to beyond 30 days. There were no significant differences in the mean RDCW scores over the period 1 - 15 days for those broods in which the C chick died at 1 - 15 days (24 broods), 16 - 30 days (13 broods) or at over 30 days of age (24 broods)(Mann-Whitney U). The mean RDCW scores for broods in each category were, respectively, 98.8, 96.6 and 92.4.

The pattern of change in the RDCW score over 1 - 50 days may arise through a combination of two factors: a) the initial hatching asynchrony, and b) variation in the daily weight increment with age. To determine whether the RDCW scores (and hence the growth lag sustained by the C chick) were in accordance with, or greater than that which might be expected from age differences alone, the following calculations were made: the average hatching intervals separating A, B and C chicks (Table 6.8) were used to estimate the average age of A and B chicks on the day that the C chick hatched. Knowing the average age difference, and also the average weight of all chicks at any given age, it was possible to estimate the 'expected' relative difference in chick weight

FIGURE 7.7: The relationship between age and weight differences in broods of three. Each point shows the difference in weight between the mean heaviest and lightest chicks in :

normal broods of three **o**

synchronized broods of three ○

FIGURE 7.7:

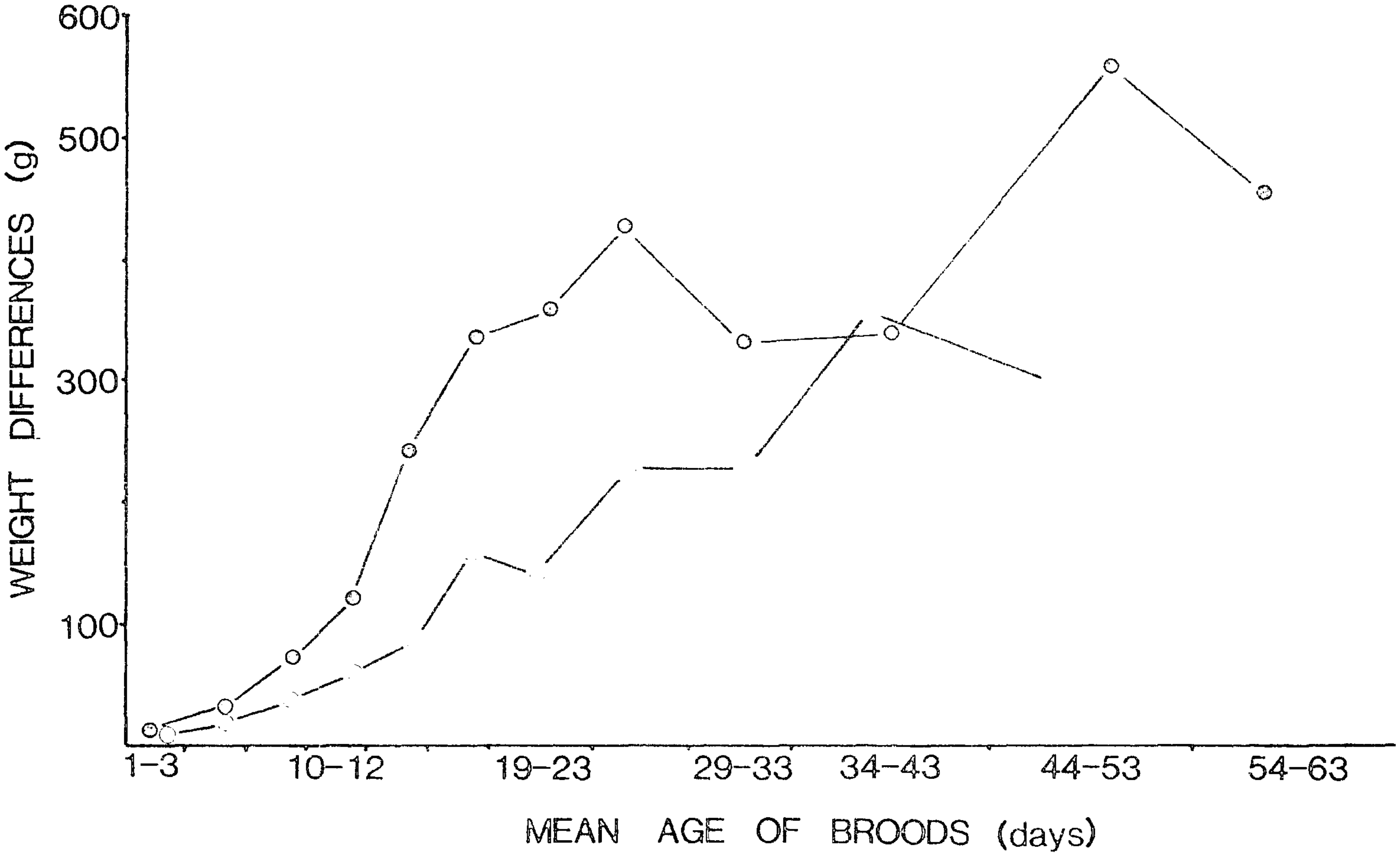
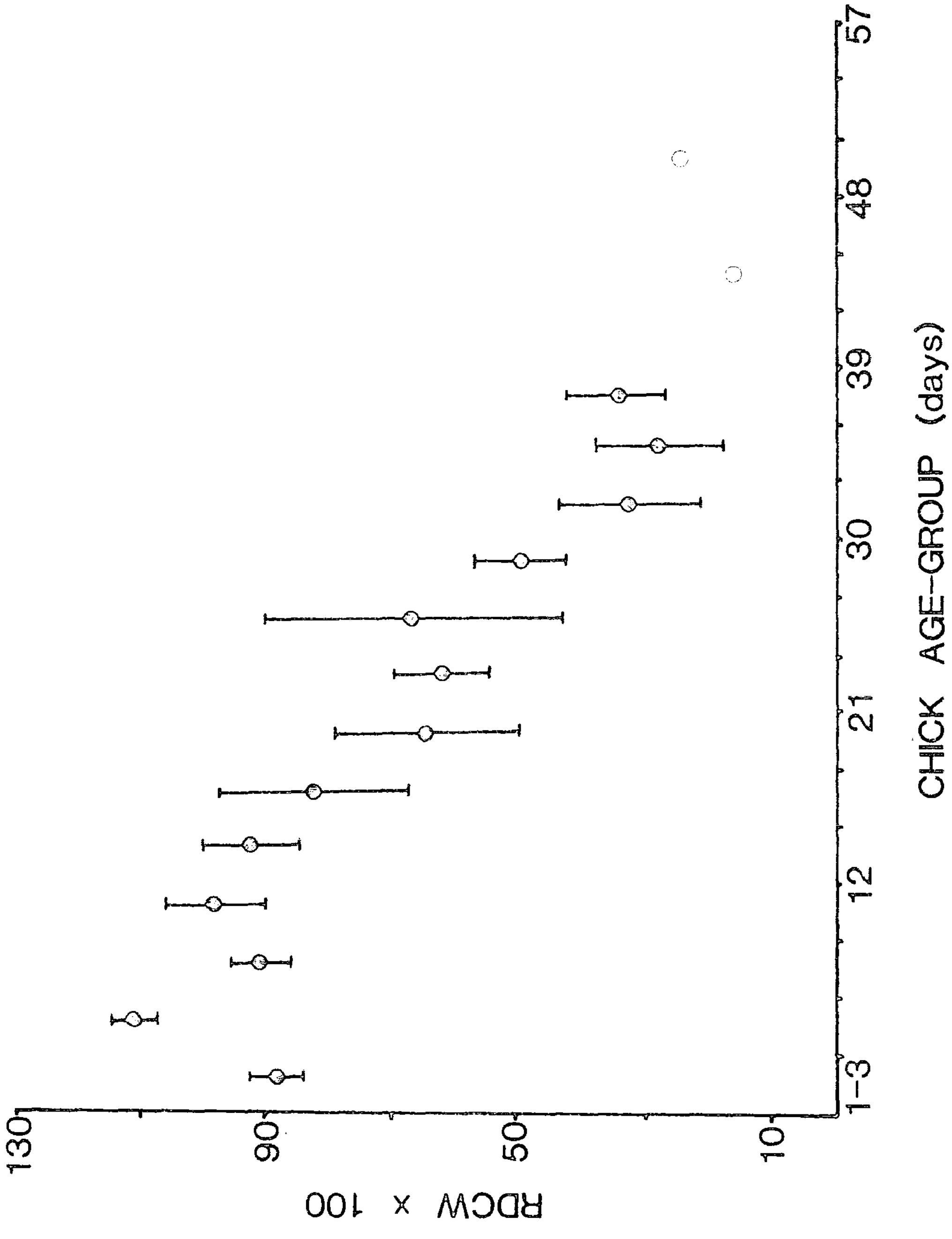

600
500
300
100
WEIGHT DIFFERENCES (g)
1-3
10-12
19-23
29-33
34-43
44-53
54-63
MEAN AGE OF BROODS (days)

FIGURE 7.8: Variation in the mean 'relative difference in chick weight' (RDCW) in broods of three, in relation to age. ± 1 S.E. shown either side of the mean.

$$\text{RDCW} = \frac{\text{heaviest - lightest chick wt.}}{\text{mean wt. of brood}}$$

⊙ Mean   ○ Single observation



within an average brood at ages 1 to 65 days. RDCW scores thus obtained were lower than those obtained from real broods of three (Fig. 7.9). Thus, sibling weight differences within broods were more extreme than might be expected from the degree of hatching asynchrony shown. This discrepancy between observed and predicted RDCW scores was greatest at 14-26 days - just after the average age at death of C chicks (15.4 days: Table 7.7). Thereafter, those broods which had survived intact showed weight differences which more closely reflected their age differences.

As might be expected, weight differences within synchronized broods were much less extreme than in normal broods, and remained approximately constant throughout the nestling period.

7.8 Food consumption

Whilst sibling competition may be the proximate cause of starvation and death of third-hatched chicks, environmental or parental constraints on food availability are likely to be the ultimate cause. To determine whether the demands of a brood of three are likely to impose a strain on the parents' foraging abilities, the amount of food consumed daily by chicks in each age class and brood size was determined.

Methods

1. Feeding Frequency

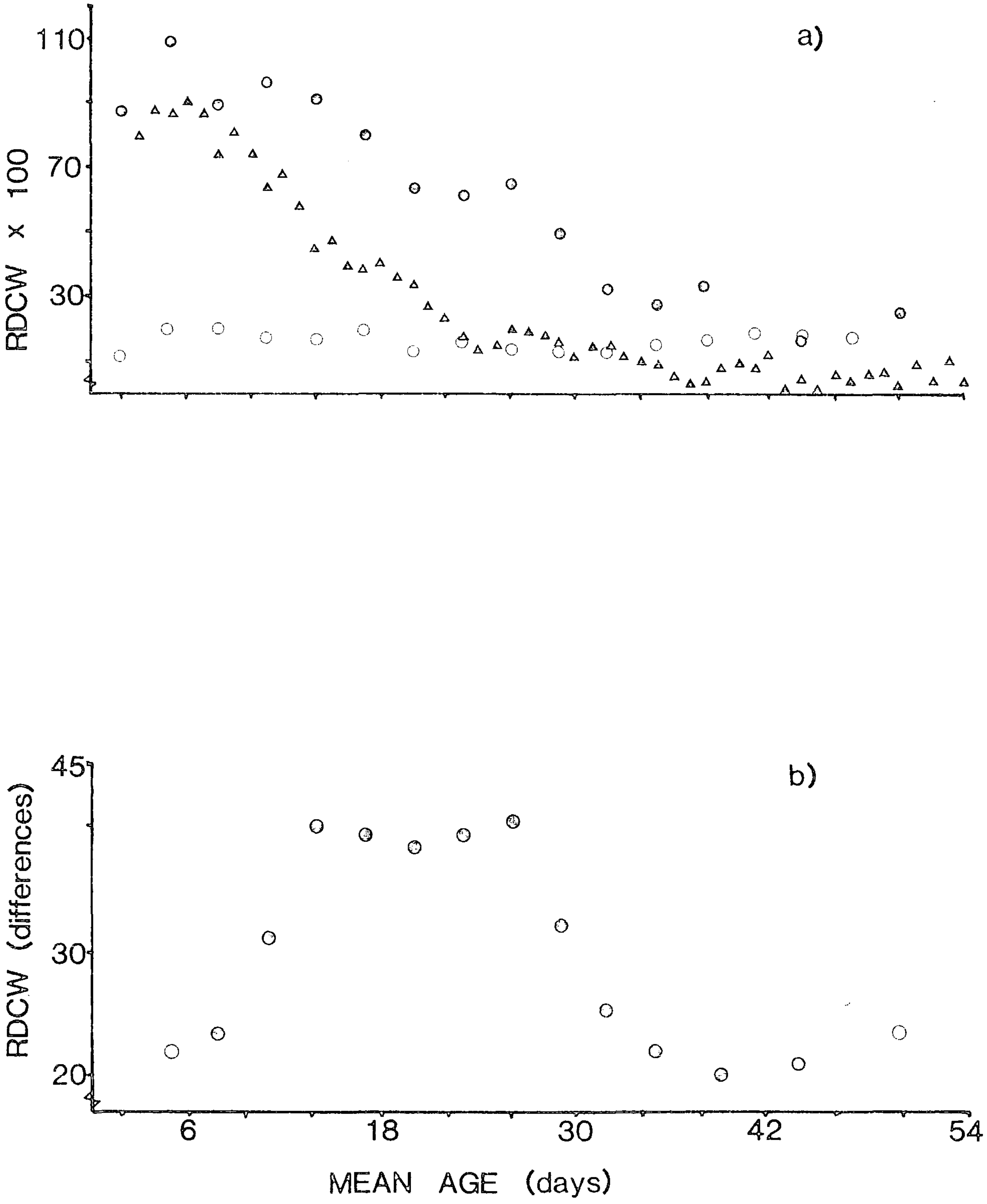
At North Point 23 broods were observed, usually in groups of about 11 for periods of 2 - 9 hours. The approximate hatching date (to within 2 days) was known for each chick, and the mean age of the brood calculated for each observation day. Results for each brood were then grouped in 10 day age-intervals.

Before each observation session chicks in each brood were marked in order of size. Felt pens were used to mark (temporarily) the pale gular

FIGURE 7.9: a) A comparison between the relative difference in chick weight (RDCW) for normal broods of three ○ for synchronized broods of three ○ and an estimate of the RDCW attributable to asynchronous hatching △ Each is shown in relation to chick age.

b) The differences between (observed RDCW) - (predicted RDCW). Each solid point is a running mean obtained from successive groups of three points. Each open circle represents a single point.

FIGURE 7,9:

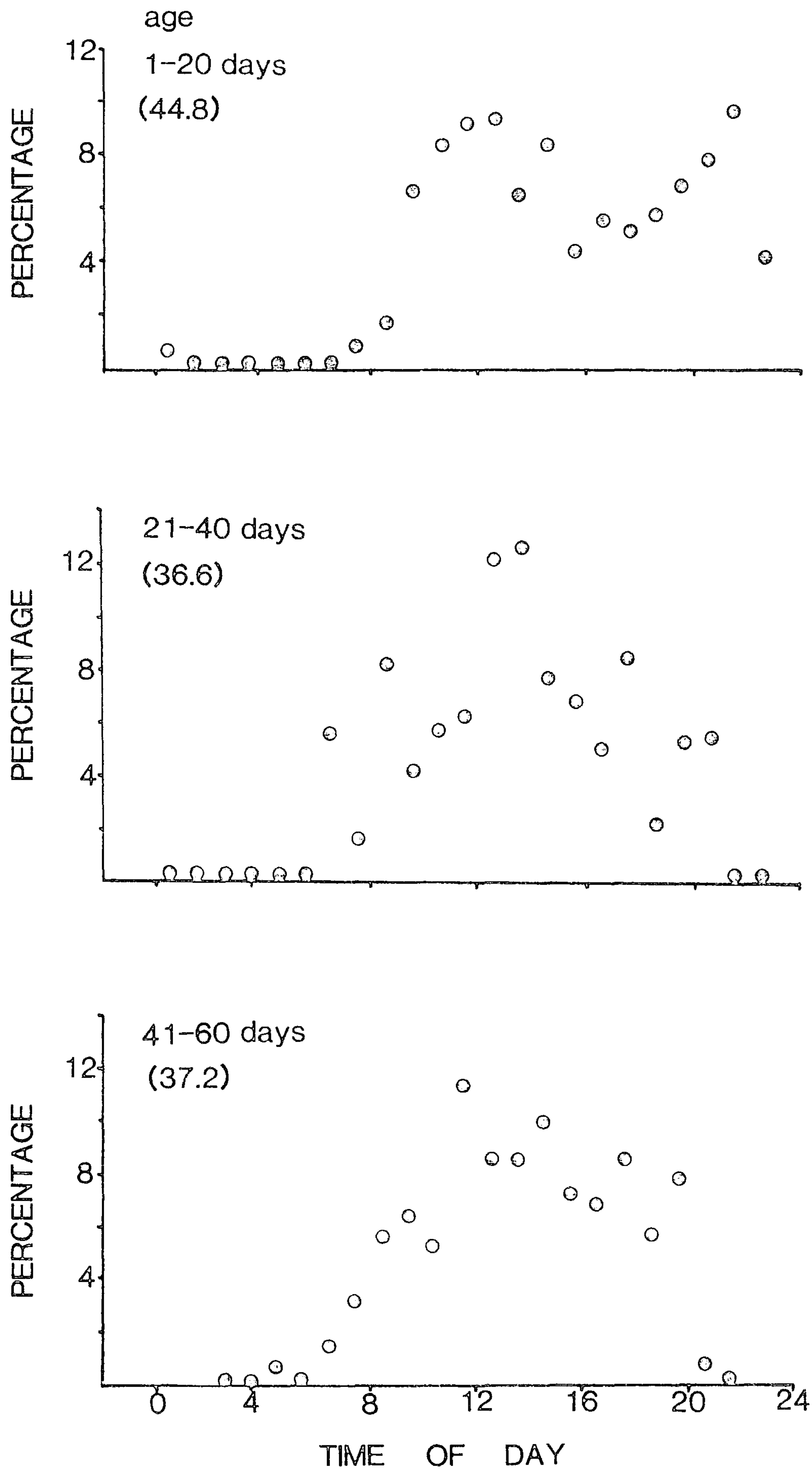

a)
110
70
30
RDCW x 100
b)
45
30
20
RDCW (differences)
6
18
30
42
54
MEAN AGE (days)

flap on each chick. To avoid the possible effects of parental bias towards certain colours used, the order in which the colours were applied was varied in relation to the size order within the brood. Observations were made from a hide situated no more than 15 metres from each nest. The number of feeds received at each nest was recorded during successive 10-minute periods. The colour-identity of each chick was noted immediately after it received a feed. A single 'feed' was defined as a regurgitation in which distinct pumping actions in the adult's throat could be seen. Each insertion and withdrawal of the chick's head was counted as a separate feed.

In total 1374 brood/hours of observations for 48 chicks of up to 65 days of age were made. To obtain an estimate of the mean number of feeds given per 24 hours to each brood size, coverage is required throughout the daylight period (02.00 to 22.00 at midsummer). The mean number of feeds given to each brood size was calculated for each hour of the diurnal cycle and then totalled to give an estimate of the number of feeds provided per 24 hours. These calculations were made separately for chicks in 3 different age-groups (Fig. 7.10). Towards the end of the study period few observations were made between 21.00 and 03.00 (due to encroaching darkness). Previous observations had shown that few or no feeds were given during the period 23.00 to 05.00, and so the number of feeds given during each hour missed during this period was taken to be zero (see Fig. 7.10). The number of feeds given during each hour of observation missed during the active period however, could not be calculated from a standard feeding rate, since daytime fluctuations were marked. Instead, the relative proportion of feeds provided during each hour of the diurnal cycle was calculated for all chicks in each 20-day age group and used to estimate the number of

FIGURE 7.10: The estimated proportion of feeds given in each hour of the diurnal cycle. Figures in brackets indicate the mean number of chicks observed per hour.

FIGURE 7.10:


age
1–20 days
(44.8)
21–40 days
(36.6)
41–60 days
(37.2)
PERCENTAGE
12
8
4
0
4
8
12
16
20
24
TIME OF DAY

feeds given during the observation hours missed for particular brood size and age categories. Thus, if for broods of three, of age 31 - 40 days, no observations were made at 14.00 - 15.00 hours, the proportion of feeds normally given during that hour (12.6 % of the 24 hr total for all chicks of 21 - 40 days) was used to estimate the number of feeds missed for that brood size and age category.

Complete coverage of the 'active' period was obtained for eight out of fifteen brood size and age categories. For the remaining categories an estimate has been made of the proportion of feeds made which went unobserved. These estimated proportions vary from 1 % to 14 % (mean = 9 %), and were calculated knowing the time and duration of observation gaps for each brood size and age category.

Feed sizes

Chicks in samples of up to 14 broods were each weighed once, and then again after each feed. At intervals of up to 3 hours all chicks were reweighed, regardless of the time of their previous weighing. Thus, estimates of feed size and of weight loss rates were obtained in each session. By calculating feed sizes and the rate of weight loss in relation to chick age, rather than to weight, the results should be compatible with observational data (above) and more readily comparable with available mortality data.

When weight losses were plotted against the time interval (between successive weighings) it became evident that a linear (rather than a curvilinear) relationship existed within the short time intervals used (mean interval = 106 minutes ± 6.04 S.E., n = 103). That is, there was no evidence of a decline in the rate of weight loss with time. To verify this, the mean rate of weight loss per minute was compared over periods of less than, and greater than the mean time interval (115 minutes, n = 64) for the most intensively sampled age-group (31+ days). Chicks reweighed after less than 115 minutes had lost weight at a mean rate of

0.86 g/min, ± 0.095 S.E. (n = 29), compared with a mean rate of 0.72 g/min ± 0.154 (n = 30) over longer time periods (difference not significant).

Occasional weight increases (by chicks of 1 - 10 days) were omitted from the analysis, since they indicate that one or more feeds had been given (unobserved) during the interim period, or that there had been an error in the first weighing.

Linear regression analysis was used to estimate the rate of weight loss in each of four age groups (Fig. 7.11). There was no significant difference in the estimated rate of weight loss shown by chicks of 31 - 40 days and 41+ days (t = 0.24; 62 d.f.; N.S.). The data for chicks of over 31 days were combined, and the rate of weight loss calculated by regression analysis. An estimate of the weight of each feed was obtained as follows; food weight estimate = measured increase in weight since the previous weighing + estimated weight loss in the interim period.

Results

Fig. 7.10 shows that, for chicks of 1 to 40 days the feeding rate peaked at between 12.00 and 14.00, and for chicks of less than 20 days there was a second peak at 22.00 (after dark). This latter peak may reflect the adults' ability to retain a store of food - to be dispensed in small amounts to the young brood some time after the last feeding trip. Older chicks however, demand larger feeds and doubtless more rapidly depleted the adults' food resources.

The number of feeds given per 24 hours was highest for chicks of 1 - 10 days old, and declined unevenly thereafter (Fig. 7.12). The greatest change in feeding frequency occurred between the ages of 1 - 10 and 21 - 30 days. At 1 - 10 days the feed frequency was between 1.7 and 3.6 x that for chicks just prior to fledging. Intuitively, one

FIGURE 7.11:

The rate of weight loss by chicks of four age groups, estimated by regression analysis. Y = weight change (g), X = time (min.).

	Correlation coefficient	S.E. of slope	Sample size
a) 1 - 10 days; $Y = -0.03X - 0.29$	-0.64	0.09	17
b) 11- 20 days; $Y = -0.09X - 4.23$	-0.37	2.74	17
c) 31- 40 days; $Y = -0.76X - 3.64$	-0.72	0.61	34
d) 41+ days; $y = -0.61X -11.30$	-0.57	0.16	30

The age group 21 - 30 days was ommitted due to small sample size.

Dashed line shows the weight loss rate of all chicks of 31+ days;

$$Y = -0.72X -5.36 \quad r = -0.68 \quad S.E. = 0.74 \quad n = 64$$

FIGURE 7.11:

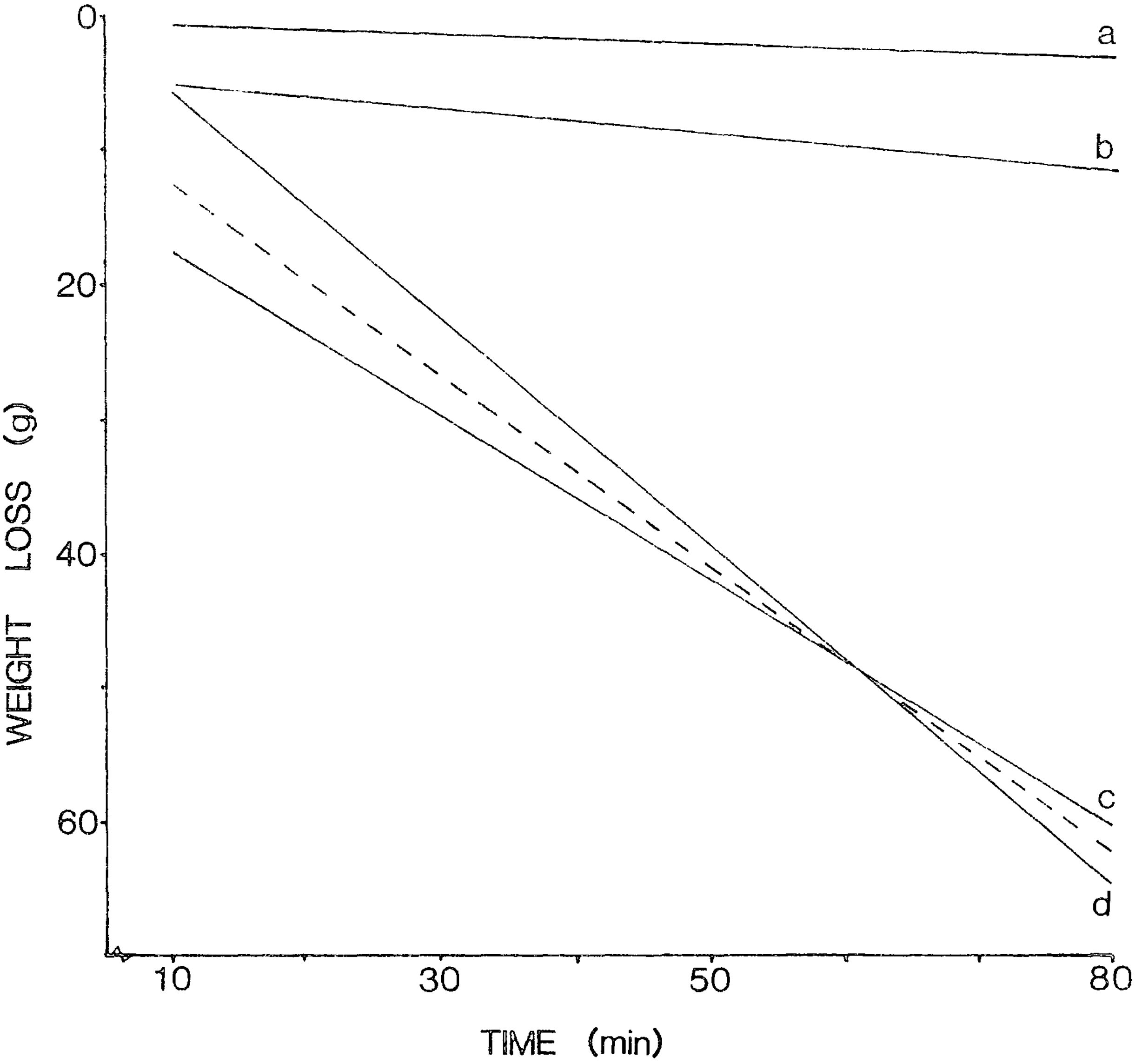
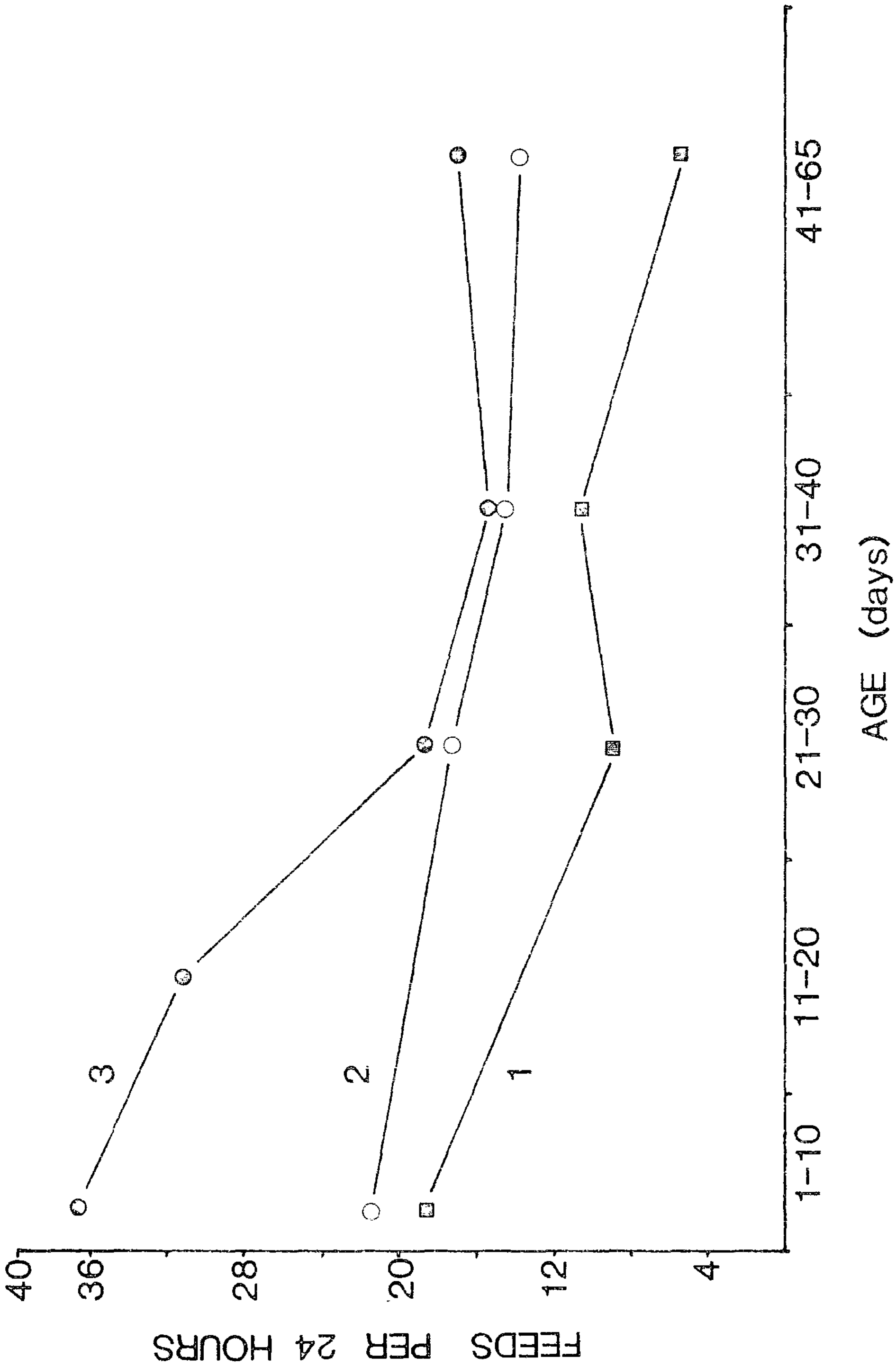


FIGURE 7.12: The relationship between chick-age and the estimated number of feeds brought per 24 hours to broods of 1, 2 and 3.



might expect a feeding rate ratio of approximately 1:2:3 in relation to brood size, however this ratio was not attained : single chicks each received slightly more feeds than twins (up to 1.72 times the frequency) at 1 - 10 days, but proportionately fewer than chicks in broods of 2 or 3 in the 41 - 50 and 51+ day age group (Table 7.12).

Estimates of the amount of food consumed by each brood size will reflect feeding frequencies unless mean feed weights vary with brood size as well as chick age. Fig. 7.13 shows that mean feed weight estimates increased by a factor of 30 from the age of 1 - 10 days to 40+ days. This increase shows a slightly sigmoidal pattern, reflecting the pattern of growth in body weight of the chicks themselves. Unfortunately, for only two age groups - 1 - 10 days and 31 - 40 days - were feed weight sample sizes sufficiently large to allow examination of mean feed weights in relation to brood size. At age 1 - 10 days there was no significant difference in mean weight of feeds given to chicks of brood sizes three and two. Chicks of 31 - 40 days however, received feeds which varied in weight with respect to brood size : estimated mean feed weights for broods of three, two and one were 117.5 g, ±14.29(S.E.), 78.1 g, ±8.58(S.E.) and 68.1 g, ±10.59(S.E.) (n = 13, 26 and 22) respectively ($F_{2,60} = 4.39$; $P<0.025$). Chicks in broods of three each received fewer but larger meals than single chicks. Had they each received meals of the same average weight as those given to singletons, their estimated daily food consumption would have been very much lower : 347 g instead of 600 g.

An estimate of the total weight of food consumed per 24 hrs is given in Fig. 7.14. One aspect of these results is of particular significance; that the amount of food consumed by broods of three at 1 - 10 days was 7 to 8 times less than that consumed by broods of two

TABLE 7.12: The estimated number of feeds received per 24 hours by chicks in each brood size/age category.

	Broods of :					
	1		2		3	
Age (days)	No. feeds	Brood-hrs watched	No. feeds	Brood-hrs watched	No. feeds	Brood-hrs watched
1 - 10	18.5	87	10.7	106	12.2	109
11 - 20	-	-	-	-	10.4	82
21 - 30	8.9	83	8.6	154	6.1	49
31 - 40	10.4	74	7.5	64	5.1	35
41+	5.6	163	6.9	200	5.7	44

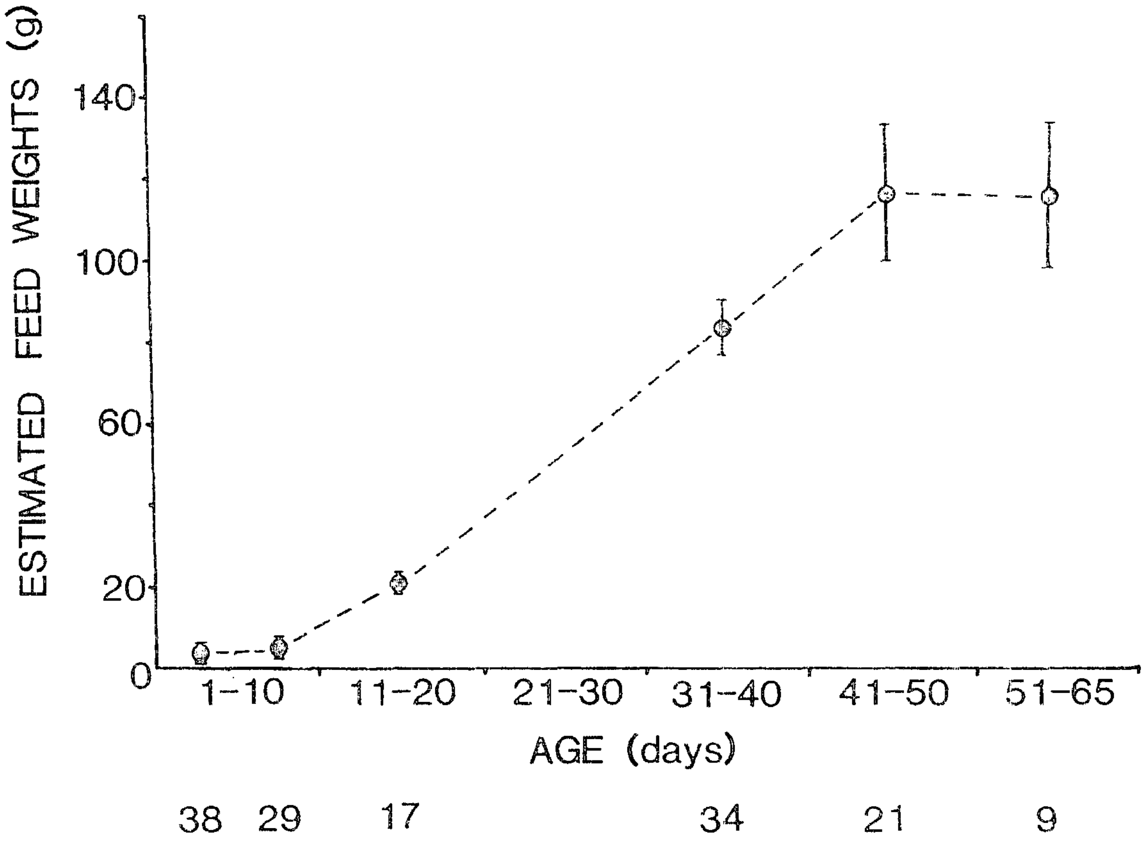
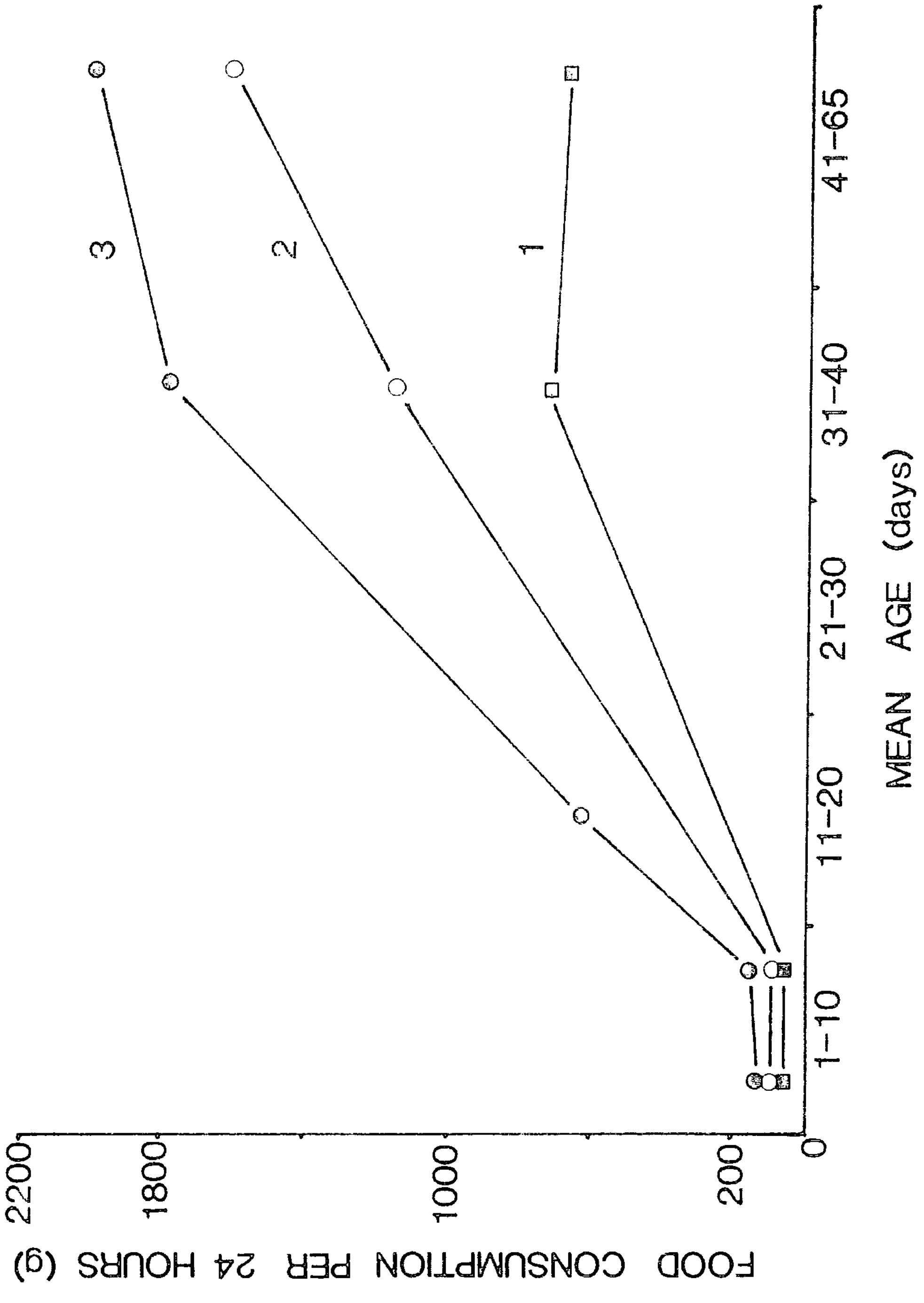


FIGURE 7.13: The relationship between chick-age and the mean estimated weight of feeds given. Each point represents the mean ± 1 SE. Feed sample sizes are shown below the X axis.

FIGURE 7.14: The estimated weight of food consumed by each brood per 24 hrs, in relation to brood size.



at 31 - 40 days, suggesting that unless fish stocks show seasonal changes of a similar magnitude, the requirements of 1 - 10 day old broods of three should remain within the foraging capacity of the parents.

7.9 Food Partitioning

Measurement of food partitioning within young broods of two and three of less than 21 days of age is of particular relevance to this study since it was at this stage that 'C' chick mortality and the RDCW index were at their highest in 1980. Moreover, amongst older broods the weights of first, second and third hatched chicks frequently cross over, suggesting that food partitioning by parents is fairly even by this stage.

Table 7.13 shows that within broods of two,food partitioning between the heavier and lighter chicks was approximately equal. In broods of three however, the smallest chick (which in almost all cases was the 'C' chick) received proportionately fewer feeds than its siblings, at ages 1 - 5 days and 11 - 15 days. In the latter age-group the disparity was significant; the lightest chicks received only 12 % (instead of 33 %) of feeds.

7.10 The pattern of chick growth

Variation in the growth rate or asymptotic weight in relation to brood size and hatching position has been described in the Herring Gull (Harris 1964), House Sparrow (O'Connor 1978b) and Hen Harrier (Scharf and Balfour 1971). As might be expected, last-hatched chicks grow at a slower rate and fledge at a lighter weight than their elder siblings. In several studies, brood size and fledging weight have been shown to have a marked effect on the chances of subsequent survival - or at

TABLE 7.13: The proportion of feeds given to each chick in order of relative weight within the brood. H = heaviest, M = medium, L = lightest, H/M = chicks of approximately equal weights.

	Broods of 2			Broods of 3				
Age	H	L	n	H	M	H/M	L	n
1 - 5	0.44	0.56	18	0.33	0.52	-	0.14	21
6 - 10	0.43	0.57	28	0.36	0.30	-	0.33	93
11 - 15	0.44	0.56	18	-	-	0.88	0.12*	75
16 - 20	0.45	0.55	36	-	-	0.64	0.35	31
21 - 30	0.58	0.42	65	-	-	0.70	0.30	20
31+	0.48	0.52	23	-	-	0.60	0.40	20

$^{*}\chi^2_1 = 15.36$; $P<0.01$

least, of subsequent recapture (Perrins 1965, Nisbet and Drury 1972, Parsons *et al* 1976). Hence, unless conditions are unusually favourable, it may be more adaptive to rear two chicks to a high fledging weight, than to attempt to rear all three chicks. Such an attempt may yield three underweight fledglings or, perhaps, two normal and one underweight fledging. Either result may be less productive or less 'cost effective' for the parents than an attempt to rear two chicks only. Hence, early elimination of the third-hatched chick should be avoided only if the parents are capable of raising it to a normal fledging weight in the conditions prevailing.

This section examines whether hatching position within the brood effects growth rate and fledging weight, and also whether the presence of a 'C' chick effects the growth of A and B chicks in broods of three, compared to those in broods of two.

To compare the pattern of growth shown by chicks of different brood sizes and hatching positions, estimates of the growth rate, growth curve shape and form, and of the asymptotic weight were obtained from 1,900 weighings of 461 chicks. The mean weight per day/age was calculated for each category and a growth curve was fitted using a weighted least squares technique from the maximum likelihood programme (see Ross *et al* 1980). The curve used was derived from the family of curves described by Richards (1959) in which the relationship between body weight (W) and time is described by the equation :

$$W = A(1 + \lambda \exp -k(t-ti))^{1/\lambda}$$

Here, A is the asymptotic weight, λ determines the form of the curve, k is the growth rate, and ti is the time of inflection. The logistic and Gompertz curves are also derived from this equation (Ricklefs 1968).

Richards, logistic and Gompertz curves were, in turn, fitted to the growth data available in the present study. The difference between each of the observed and fitted values (i.e. the residuals) was then weighted by $\sqrt{n}/\sqrt{W}$ (where n = sample size, and W = mean weight at that age). This weighting ensured that the residuals were normally distributed about zero and of equal variance. The goodness of fit provided by each equation was then tested using the variance ratio formula :

$$\frac{(\text{Gompertz RSS} - \text{Richards RSS})}{(\text{Richards RSS})/(\text{Richards d.f.})}$$

Here, RSS = residual sum of squares, and d.f. = degrees of freedom.

For 12 out of 13 brood size and position categories tested, the Richards equation provided a significantly closer fit to the growth data. From the equation, an estimate of the growth rate, asymptotic weight, growth curve form, and the time of inflection were derived. To test for differences in the parameters generated for each of two or three brood size/postition categories a common curve was fitted to each category. The residual sum of squares obtained from such a fit was then compared with the RSS obtained when parallel curves were fitted to each category. The comparison was made by :

$$F_{(d.f.2\,-\,d.f.1),\ d.f.1} = \frac{(RSS2 - RSS1)/(d.f.2 - d.f.1)}{RSS1/d.f.1}$$

where RSS1 = residual sum of squares obtained from the simpler model (i.e. where a common curve was fitted), and RSS2 = Residual sum of squares obtained from the more complex model (i.e. where a series of parallel curves were fitted). Where F is such that $P<0.05$, the more complex model provides a significantly better fit, and the simpler model should be discarded. Parallel curves were fitted to the growth data available for chicks in broods of 1, 2 and 3 separately. Although the three parallel curves fitted have identical estimates for each of the non-linear parameters (growth rate, growth curve form and point of inflection) the asymptotic weight attained by each brood size category differed to such a degree that three parallel curves provided a significantly better fit than would a single common curve ($F_{2,170}$ = 14.73; $P<0.001$). Individual curves (differing on all four parameters), when fitted to the three datasets provided a closer fit than did three parallel curves (differing only in scale); 'individual' RSS = 6.65, 'parallel' RSS = 6.87. However, in this instance the difference was not significant, and so the simpler model was used to describe the data.

7.10.1 The pattern of growth in weight and body measurements

Being relatively small, and nidicolous, the young of most Pelecaniformes show an extremely rapid increase in weight and body size (e.g. the White Booby (Dorward 1962), Gannet (Nelson 1966), Brown Pelican (Schreiber 1976) and Double-crested Cormorant (Dunn 1977, Des Granges 1982). Although the sample size was small (few weighings were made just before and during the asymptotic phase) Dunn (1977) suggested that the growth rate of nestling Double-crested Cormorants is greater in relation to size than for any other species studied with an asymptotic weight of over 500 g.

In this study the average wing length, bill length and outer toe length for each 2-day age interval were calculated from measurements taken on 129 occasions. Wing length was measured initially using vernier calipers and, after the primary feathers had erupted, using a wing rule. Bill length was measured from the 'V' shaped upper edge of the ramphotheca to the tip of the upper mandible. The outer (longest) toe was measured from the tip of the claw to the apex of the adjoining web.

Growth curves shown in Fig. 7.15 are essentially similar to those described for Blue-eyed Shag subspecies on Crozet Island (Derenne *et al* 1976) and on Marion Island (Williams and Burger 1979). Asymptotic weight is attained by 45 - 50 days and shows a slight decline thereafter. Whilst wing length continues to increase up to the age at fledging (65 - 70 days), bill length and, more especially, toe length reach their maximum size at an earlier age (at approximately 40 days and 30 - 35 days respectively). Early development of the legs and feet may assist in begging away from the nest, and, latterly, in swimming and diving before the chick becomes independent of its parents.

7.10.2 Growth rate and fledging weight in relation to brood size and hatching position.

Asymptotic weight varied inversely with brood size (Fig. 7.16a). Although broods of 1, 2 and 3 showed slight differences in their growth rate and time of inflection, there was no significant improvement in the goodness of fit obtained when individual, rather than parallel curves were fitted to the data.

As might be expected, the asymptotic weight attained was also dependent on hatching position : the asymptotic weight of A chicks was 150 g greater than that of B chicks, which in turn was 280 g greater than that of C chicks (Fig. 7.16b). However, whilst A and B chicks differed only in the fledging weights attained, C chicks showed a difference in the growth rate, time of inflection and growth curve form ($F = 6.01$; d.f. = 3, 164; $P<0.001$).

Differences in the asymptotic weights of A and B chicks were significant, both within broods of two and of three (Table 7.14) (2 chick broods; $F = 19.69$; d.f. = 1, 113; $P<0.001$, 3 chick broods; $F = 10.19$; d.f. = 1, 121; $P = 0.0018$). In broods of three the asymptotic weight of

FIGURE 7.15: The pattern of growth in weight, and in three body measurements throughout the nestling period. Each point represents the mean of several weighings for that day-age class. ± 1 SE shown.

a) Weight

b) Wing length

c) Bill length

d) Toe length

FIGURE 7.15:

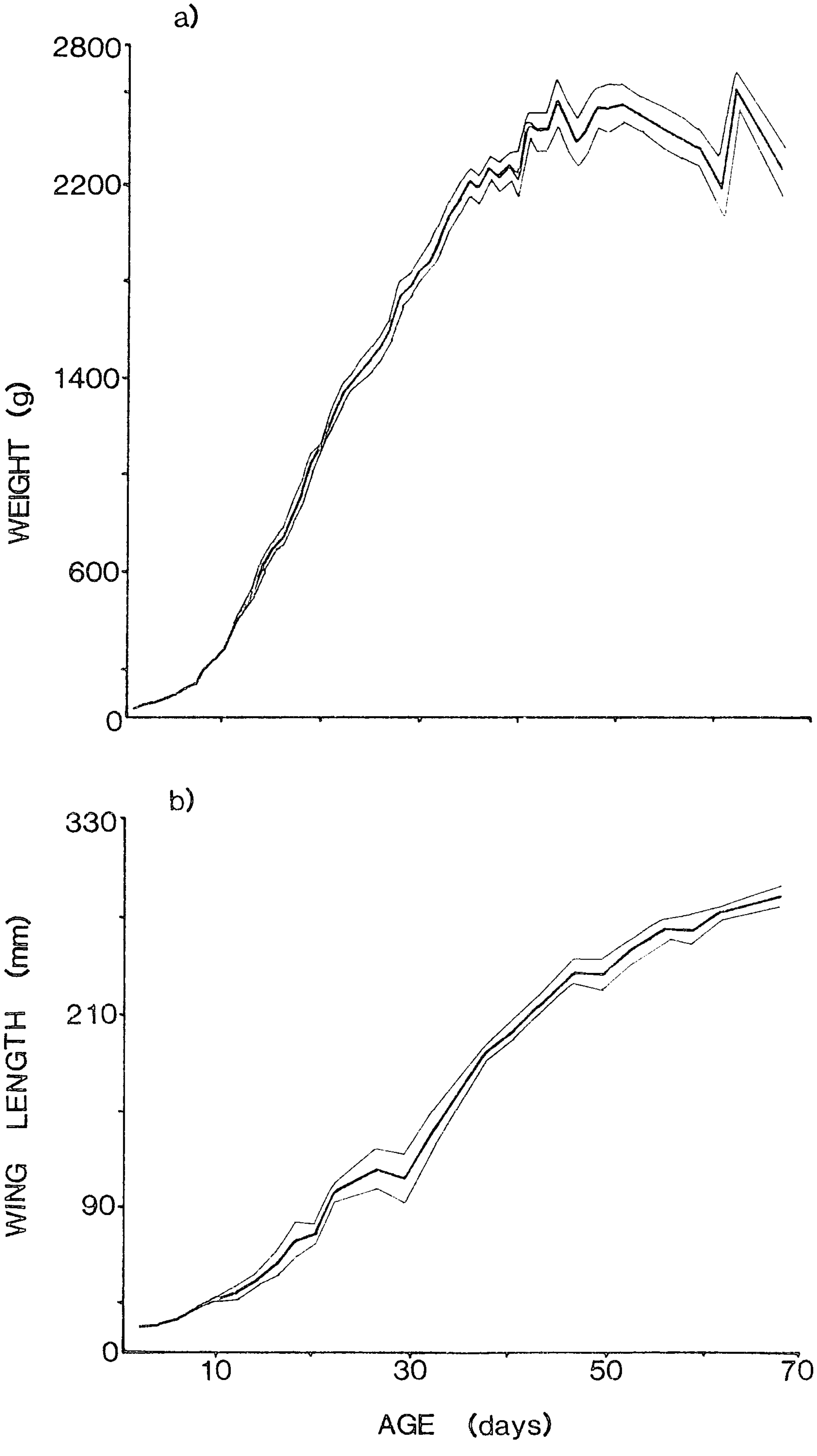

a)
2800
2200
1400
600
0
WEIGHT (g)
b)
330
210
90
0
WING LENGTH (mm)
10
30
50
70
AGE (days)

FIGURE 7.15: (continued)

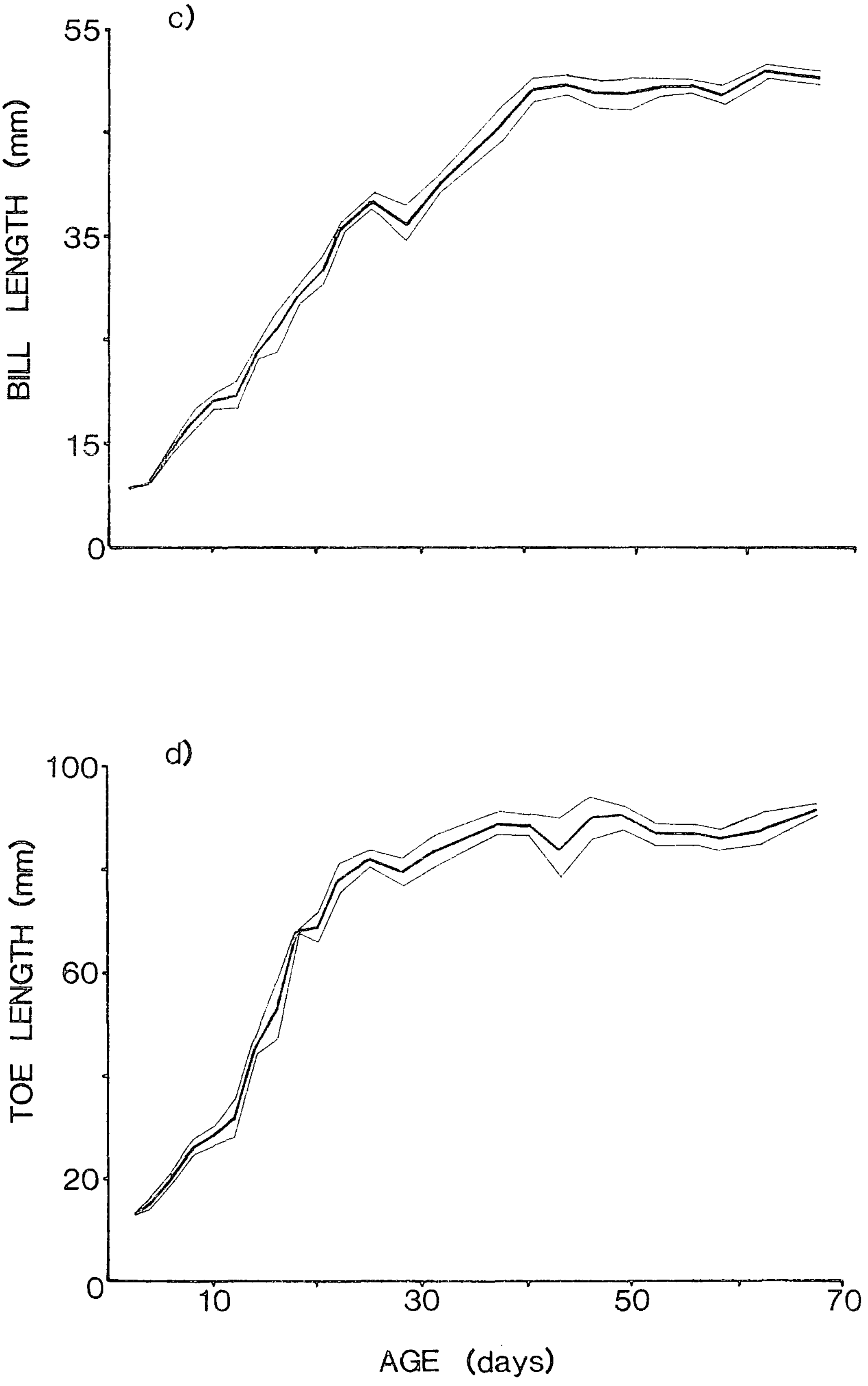


FIGURE 7.16: The pattern of growth shown by chicks in different brood sizes, and of different hatching positions.

a) In relation to brood size

b) In relation to hatching position

c) Brood size ('A' chicks only)

d) A and B chicks in broods where the C chick died at less than, or greater than 20 days.

FIGURE 7.16:

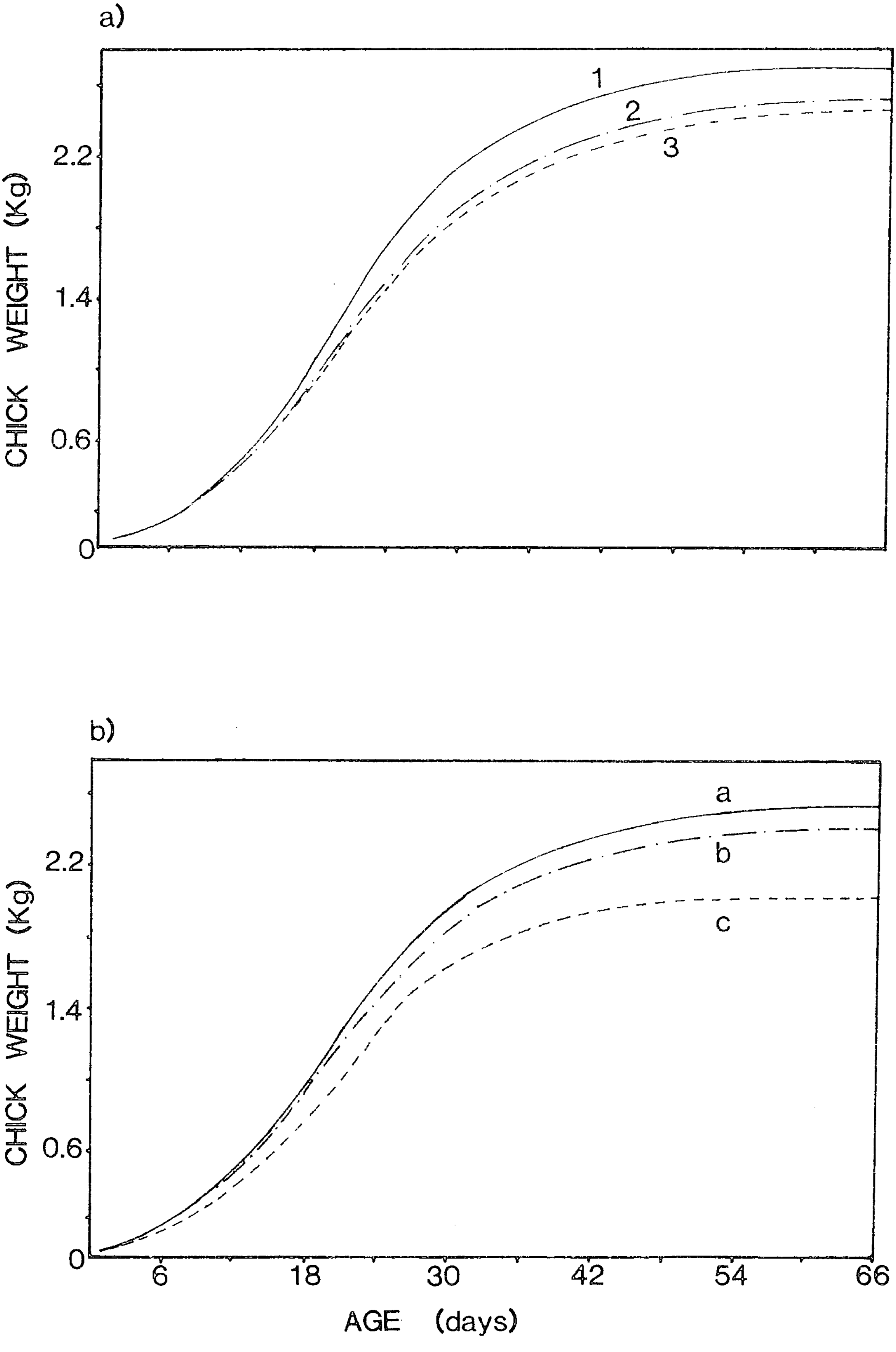
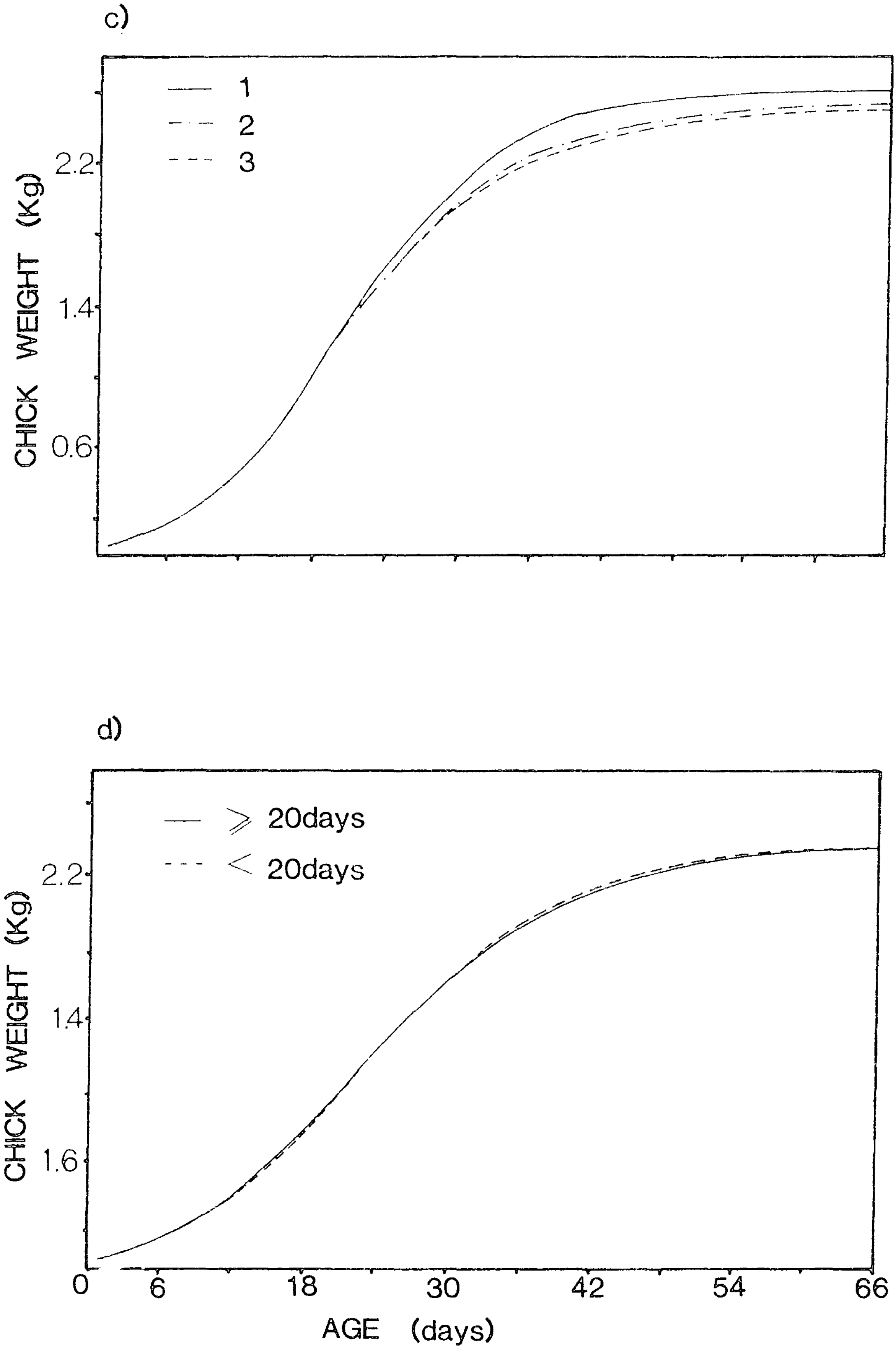

a)
1
2
3
2.2
1.4
0.6
0
CHICK WEIGHT (Kg)
b)
a
b
c
2.2
1.4
0.6
0
CHICK WEIGHT (Kg)
6
18
30
42
54
66
AGE (days)

FIGURE 7.16 (Continued)



B chicks was 90 g less than that of A chicks, whilst in broods of two the difference was of 170 g.

First hatched chicks were also affected by the presence and number of siblings : although there were no significant differences in the growth rate, time of inflection and growth curve form, the asymptotic weights of first hatched chicks declined with brood size (Fig. 7.16c) (F = 3.37; d.f. = 2, 166; P = 0.037).

Thus, at fledging, a weight hierarchy existed within broods of 2 and 3, the difference in weight between the first and third hatched chicks (360 g) being much greater than that between first hatched chicks in different brood sizes (110 g). Parents of three-chick broods reared their first and second hatched chicks to a fledging weight which was as high, or higher than that of chicks in broods of two (Table 7.14), but at the expense of the C chick's normal growth (Fig. 7.16b). One might therefore expect chicks in synchronized broods of three (see 7.6) to attain a fledging weight intermediate between that of A and C chicks in normal broods of three. Table 7.14 shows that the non-linear growth parameters for synchronized chicks did not differ significantly from those of A and B chicks in normal broods of three. Asynchronous hatching thus helped to ensure that at least one chick in a brood of three attained a fledging weight which was close to that attained by A chicks in broods of 2 and 1. Nevertheless, the presence of one, or two other siblings does affect the A chick's final weight (Fig. 7.16c) - in spite of the frequent early death of third-hatched chicks.

Fig. 7.16d shows that the age at death of the C chick (whether occurring at less than or greater than 20 days) had little effect on the growth of its older siblings. In broods in which the C chick died at less than 20 days, the asymptotic weight, and other growth

TABLE 7.14: Growth curve parameters for first and second hatched chicks in broods of two and three, and for chicks in synchronized broods.

BROODS OF TWO:

Hatching Position	Growth Rate	Time of inflection (day-age)	Curve form	Asymptotic weight (Kg)
A	0.120	19	0.30	2.53
B				2.36

BROODS OF THREE:

A	0.118	19	0.29	2.52
B				2.42
Synch.				2.42

parameters of the A and B chicks were almost identical to those of A and B chicks from broods in which the C chick had survived to 20 days or more.

Finally, since there was no detectable difference in the survival rate (in 1980-1981) of those adults which bred or failed to breed in 1980, it seems unlikely that brood size alone would produce a measurable difference in adult survival.

7.10.3 Chick weight differences in relation to sex

Sexual differences in the growth rate and asymptotic weight occur in some species where sexual dimorphism in adults is pronounced. Weight differences may be sufficiently great to allow chicks to be sexed at an early age (e.g. at 16 days in Sparrowhawks; Moss 1979, and at 20 - 30 days in Hen Harriers; Scharf and Balfour 1971). Although in the Blue-eyed Shag sexual dimorphism in weight and other body measurements was small (the average weight of males being 1.17 that of the female), it may have partly obscured chick weight differences in relation to brood size and hatching position. Snow (1960) tentatively sexed European Shag chicks by weight from the 33rd day onwards, and Potts (1966) sexed European Shag chicks by a combination of bill depth and weight differences. However there is no evidence of a bimodal distribution of bill-depth measurements taken from 81 Blue-eyed Shag chicks, aged 45 - 65 days (mean = 56 days). Nor is there evidence of bimodality in the distribution of weights in the same age-range (n = 219 weighings of 146 chicks). (C chicks were ommitted from both analyses because of their much lower asymptotic weights).The two measures were positively correlated ($r = +0.54$, 65 d.f., $P<0.001$), but there was no evidence of sexual dimorphism when chick weights were plotted against bill depth.

Table 7.15 provides a summary of the effects of order of hatching, laying date and parental age on chick growth and survival.

Discussion

Brood reduction may be regarded as the result of a single factor, or a combination of factors, each of which incidentally promote the development of age differences and weight differences within the brood, and which eventually contribute to the early death of the most disadvantaged brood member(s). Many workers however (Lack 1954, Ricklefs 1965, Howe 1978, O'Connor 1978a), view brood reduction as a breeding adaptation which complements, or replaces the strategy of 'clutch adjustment' in species for which the early prediction of food availability is unreliable, or for which the food supply fluctuates throughout the nestling period.

Following the latter interpretation, brood reducing species should, by definition, show greater annual variation in chick survival to fledging than that shown by those species which adjust their clutch in accordance with seasonal changes in food availability. Also, in poor years, increased mortality should fall more heavily on chicks which hatch last and to a lesser degree on the penultimate chick. Both of these criteria were fulfilled in the present study: Blue-eyed Shag chick survival was almost twice as high in 1981 as in 1979, whilst in 1980 eight times as many first-hatched chicks survived as those which hatched third.

However, the results also suggest that third-hatched chicks were not inherently less viable than their older siblings: if for any reason the A or B egg failed to hatch, C egg chicks survived as well as the second hatched chick in a normal brood of two. This underlines the potential of brood reduction as a form of insurance or 'bet hedging'

TABLE 7.15: The effects of brood size, order of hatching, laying date and parental age on chick survival and growth.

	EFFECT OF:		
	Order of hatching	Increasing lay date	Increasing adult age
ON:			
No. of chicks hatched	-	Sig. decrease	Sig. increase
No. of chicks fledged	-	Sig. decrease	Sig. increase
Chick survival	Sig. decrease	Sig. decrease	Sig. increase
Age at death	Sig. decrease	N.S.	Sig. increase
Proportion of feeds received, 11 - 15 days age	Sig. difference	-	-
Growth rates	Sig. decrease	-	-
Asymptotic weight	Sig. decrease	-	-

N.S. = Not significant

which, for some species, (e.g. the Brown Booby and White Booby; Nelson 1978, Herring Gull; Graves *et al* in press), may be the prime, or only benefit gained.

Lack (1954) and O'Connor (1978a) predicted that for species in which brood reduction is common, starvation mortality should be more prevalent in young than old nestlings, and indeed, O'Connor cites 22 studies of species in which mortality was concentrated in the early part of the nestling period. These species range from the Fiordland Crested Penguin (Warham 1974) to the House Sparrow (Seel 1970). Early chick losses should be expected not only as a safeguard against later, wasteful, competition, but also because as chicks age they are able to withstand a much greater proportional weight loss before they succumb (O'Connor 1978a). In this study starvation mortality amongst third-hatched chicks occurred at an early age, thus fulfilling a further criterion for brood reduction. The age at death of the third chick was inversely related to the length of the hatching interval, and positively related to the age of its parents. This finding may reflect the fact that the oldest females (of 10 - 11 years) laid and hatched each clutch with greater synchrony than did younger birds.

The occurrence of early mortality infers (directly) that broods are reduced before the time at which food availability becomes limiting, and (indirectly) that it is the adults themselves that limit the food supply to the young brood - or to certain member(s) of the young brood. This last point should be examined more critically; while most studies have suggested that differences in growth or survival of siblings arise through differences in their competitive abilities (Dyrcz 1974, Bryant 1978, O'Connor 1978b, Ryden and Bengtsson 1980) few have questioned what limits food availability - particularly at a time when the chicks' food demands are comparatively small. Unless resources are restricted, sibling competition (though not sibling aggression) will be ineffective in reducing the brood. Thus the most fundamental question in brood reduction studies is not whether, or how last hatched chicks are out-competed by their siblings, but whether the resources competed for are limited by the environment - or by the parents themselves.

At the age at which most C chick deaths occurred, the daily food consumption of the entire brood was some eight times less than that of most 2 - chick broods prior to fledging. A parallel situation has been reported by Langham (1968) in Common Terns, and by Graves *et al* (in press) in the Herring Gull : because of the spread of hatching dates, young third-hatched Herring Gull chicks in some broods starve to death at a time when relatively large amounts of food are brought to much older (reduced) broods in the same colony. As in the present study, it was suggested that the adults themselves limit the amount of food available to the young brood.

There are two ways in which this deficit may be brought to bear on the third chick: 1) directly, through selective neglect, or 2) by introducing a disparity in the competitive abilities within the brood. In this study the greater the disparity in the siblings' weights, the higher the proportion of C chicks which died. However, these results are equivocal since, although large size differences within the brood may reflect differences in their competitive abilities, they may also serve as a means of 'earmarking' the victim chick for parental neglect.

Weight differences within the brood were high at the outset, but soon increased beyond the level which might be expected to arise through asynchronous hatching alone. By contrast, weight differences within synchronized broods were low, and showed little change throughout the nestling period. Thus, asynchronous hatching apparently acted as a catalyst, promoting further, more extreme differences in weight.

Synchronizing the brood at hatching produced two results of some biological significance. Firstly, as might be predicted, synchronization led to a significantly higher incidence of total brood loss - although in one season only. Secondly, - and perhaps more importantly - the average fledging weight of chicks in synchronized broods was equal to that of B chicks in normal broods of three. If, as suggested by Fretwell (1969), there exists a weight hierarchy amongst each year's offspring, then it may benefit the parents of 3-chick broods to produce one heavy and one medium weight fledgling (i.e. one A and one B chick) rather than to produce three chicks of medium weight.

Section 8a

Final discussion : population dynamics

In a stable population immigration and reproduction must balance emigration and mortality. On Signy Island the breeding colony at North Point is increasing in size, whilst that on Shagnasty has shown no apparent long-term changes. Occasional variation in the number of nests or pairs recorded are likely to reflect differences in the timing of counts, or the inclusion of birds on Shagnasty III. At breeding colonies on neighbouring islands only one ringed bird has been recorded amongst several hundred examined. Hence emigration would appear to be low.

If the Blue-eyed Shag population on Signy is stable, the number of birds recruited into the colony must offset adult annual mortality. Since most birds delay breeding until the ages of 3-5 years, and are subject to first-year and then adult mortality rates during that time, the number of young fledged in each season must, on average, appreciably exceed the number of adults which die. From an estimate of adult and first-year survival rates, the breeding output required to sustain the colony can be predicted. If this prediction exceeds the observed level then either immigration is high, or the adult survival estimates are too low. Methods used to calculate the 'required' breeding output, based on adult survival, first-year survival and the age at recruitment, are described in Table 8.1.

Survival between consecutive seasons, and over a period of 3-4 years, was low (0.75 - 0.77). However, an estimate of adult survival obtained using a maximum likelihood programme was much higher (0.87) and similar to two estimates of adult survival for the European Shag (0.86 ; Coulson and White 1957, 0.83 ; Potts *et al* 1980). Table 8.2a shows that, if adult survival is low (0.77) the average number of fledglings required per pair to sustain the population is high ; 1.74, if all birds begin breeding at 4 years. If

TABLE 8.1: Methods used to calculate the mean number of fledged young required per pair to offset losses due to adult mortality.

Parameters :	Estimates available	Source (Page)
Adult annual survival	0.77 ; 0.87	Section 3.1(19,20)
First-year survival	0.58	" 3.1(20)
Mean age at return to colony	4.3 ; 4.8 yrs	" 3.3(25)
Mean age at first recorded breeding	5.0 ; 5.4 yrs	" 3.3(25)
Estimated proportion of 'non-breeders'	0.24	Table 3.6
Chicks fledged per pair which laid	1.88 ; 1.48 ; 0.55	Table 7.1

Example :

50 breeding pairs, adult survival = 0.77, first-year survival = 0.58

Young fledged per pair = 1.88

Total young fledged = 94

Adults die each year = 23

Number of young survive to breed at 4 years = $94 \times 0.58 \times 0.77^3$

= 24.9

at 5 years = $94 \times 0.58 \times 0.77^4$

= 19.2

Conversely,

the number of young required to offset adult losses :

if recruitment at 4 years = $\frac{23}{(0.58 \times 0.77^3)}$ = 86.9 young

= 1.74 young per pair

if recruitment at 5 years = 2.26 young per pair the age at first breeding is raised, fledgling production must also be higher. In Table 8.2b the mean number of chicks fledged per pair is shown for each of the study years. Only in 1981 was the breeding output sufficiently high to sustain the colony, given that adult survival was 0.77, and that breeding begins at 4 years. In 1979 and 1980 fledgling Production fell a long way short of this required minimum, and may do so in most years. Also, fledgling production was estimated only for those pairs which attempted to breed. Since only 76 % of adults caught in 1980 were known to have bred in that year, the mean number of fledglings produced per birds was considerably less. The production of young by all pairs will exceed that required to sustain the population only if the higher survival estimate (0.87) is used. The discrepancy between this figure, and the lower recapture rates between seasons, suggests that 11-14 % of breeding adults were missed, or were absent from the colony in each season.

TABLE 8.2: Variation in the mean number of fledged young required per pair to offset adult mortality. The calculations used are described in Table 8.1. Most birds first attempt to breed at 4 or 5 years, and the remainder at 6 years. Three estimates of the age at first breeding, and four estimates of adult annual survival are used. First-year survival is estimated at 0.58.

a)

	Age at 1st breeding:		
	4 yrs	5 yrs	6 yrs
Adult annual survival	Fledged young required		
0.75	2.04	2.72	3.63
0.77	1.74	2.25	2.93
0.80	1.34	1.68	2.10
0.87	0.68	0.78	0.90

b)

Mean number of fledglings produced :

	1979	1980	1981
Per pair which bred	0.55	1.48	1.88
By all pairs*	0.42	1.12	1.43

*Given that 24 % of adults caught were non-breeders (Table 3.6).

SECTION 8b

FINAL DISCUSSION : Breeding biology

A fluctuating environment selects for rapid breeding and low adult survival rates, whilst adaptations to a constant environment include small brood or litter sizes and increased longevity (MacArthur and Wilson 1967, Pianka 1972). Yet, many high latitude marine invertebrates (Clarke 1979), birds (Croxall 1982) and mammals (Bowen *et al* 1981, Croxall and Hiby 1983) are relatively long lived, slow breeders. They have evolved highly K-selected strategies to cope with an environment which is both harsh and unpredictable. This apparent paradox was resolved by Schaffer (1974), who suggested that in a fluctuating environment, iteroparous species (those which make several breeding attempts) should invest less in each attempt, and in so-doing increase their reproductive lifespan and (in theory) their lifetime reproductive output.

A long life, and repeated breeding attempts have two important consequences. Firstly, as longevity, and the number of breeding attempts made, increase, so will the complexity of the individual's life history strategy. The more breeding 'decisions' or choices to be made, the greater the chance of attaining the maximum reproductive output through natural selection - rather than through a combination of natural selection and random events. Individuals of a long-lived species may choose between breeding early or late in life, annually or intermittently (Croxall 1982), with the same mate or a succession of mates (Coulson 1966, Rowley 1983), or at the same or a succession of sites (Potts *et al* 1980). As foraging skills improve, so might the capacity to lay and rear larger offspring, or larger broods (Coulson 1972, Mills 1973). This improvement may be mirrored by an increasing commitment to breeding as the costs - in terms of future reproductive output - decline with the expectation of further breeding seasons (Pugesek 1981).

A second consequence of K-selection is that the difference between the number of offspring an individual can and does produce at each attempt may increase with the number of breeding attempts made during an average lifespan. Given the expectation of only one or two breeding seasons (as is the situation for most temperate songbirds and small mammals), the individual should attempt to lay and rear as many offspring as the food supply will allow. Its 'optimal' clutch size will closely coincide with that which yields the largest number of independent young in the prevailing conditions (Lack 1954). By contrast the 'optimal' clutch or litter size of a multiple breeder will fall short of that which it may be possible to rear to independence in each season. This deficit will be offset by an increased reproductive lifespan (Williams 1966).

The first major breeding 'decision' made concerns the age of return to the colony, and at which breeding begins. In the European Shag, breeding may commence at two years (Potts 1966), whilst for Blue-eyed Shags first-breeding is deferred to three years or, for some individuals, to as late as five or six years of age.

Deferred breeding in birds, as in many other groups, may be adaptive if the costs of attempting to breed are outweighed by the probability of breeding failure or of only partial success (Lack 1968). In later life, non-breeding may occur for similar reasons. In the present species, as in many other seabirds, young adults may require several seasons to perfect their foraging skills to the point at which they are able to support themselves, plus one or more offspring, without compromising their own survival chances. Nevertheless, even for one of the most extreme examples of deferred breeding - by the Wandering Albatross, with an average age at first breeding of 10 years - adult survival drops appreciably in the year following the first breeding attempt (Croxall 1983).

Deferred breeding may also result if, for young inexperienced animals, the chances of obtaining a nest site, mate, or a territory with which to attract a mate are slim. Hence, the age at first breeding, and the proportion of animals which attempt to breed at a given age are dependent on the density of the population (Bowen *et al* 1981, Gaskin 1982, Clutton-Brock *et al* 1983), or the degree of crowding at the breeding area (Coulson *et al* 1982). Blue-eyed Shags were recorded breeding at a younger average age at the smaller colony (North Point), at which nest site density was lower.

For promiscuous and polygynous species increased competition for females may also reduce the chance of successful breeding by young, inexperienced males. Hence, young males should delay their first breeding attempt until such time as their chances of obtaining at least one or more successful matings outweigh the increased risk of injury or death (Lack 1968). For young male Elephant Seals this delay may take up to 10 or 11 years, by which time many have attained a sufficiently high body weight to enable them to defend a harem against the established 'beach masters' (McCann 1980). Similarly, in polygynous or promiscuous bird species the onset of maturity, and the development of a bright conspicuous plumage by the male may be delayed, thereby avoiding a (presumed) increased risk of predation (Lack 1968).

Intermittent, or biennial breeding may occur if the food supply fails in one or more seasons (Mikkola 1983) or if the diet is such that chick growth is slow and the breeding season very prolonged. Prince (in press) has suggested that differences in the diet of Grey-headed and Black-browed Albatrosses (which are almost identical in size and weight), may account for differences in the length of their respective breeding seasons. Grey-headed Albatross feed on squid, which has a lower calorific value than the krill taken by Black-browed Albatross. Grey-headed Albatross chicks have a much slower growth rate, and to accommodate this, adults must begin breeding six weeks earlier than Black-browed Albatross at the same colony. The prolonged breeding season almost entirely prohibits annual breeding by the former species, which perhaps as a consequence, has a higher annual survival rate (95 % and 92 % for Grey-headed and Black-browed Albatross respectively) and a greater average age at first breeding (13 and 11 years respectively) (Croxall 1983).

In contrast to other animal groups, some 92 % of bird species are monogamous (Lack 1968). A departure from monogamy is likely if either sex is liberated from parental responsibilities, and if emancipation allows an increase in the reproductive output of the liberated sex (Lack 1968, Orians 1969, Trivers 1972). Females, by definition, invest more in the production of each offspring than do males, and hence usually have fewer opportunities to form additional pair bonds. Clearly, if the reproductive performance of a male which mates with two females exceeds that gained from investing in the offspring of only one female, bigamous or polygynous breeding may result. However, the opportunity for multiple mating will depend on the availability of additional females. It should be in each female's interests to ensure that her mate invests a large amount of time in nest site attendance, nest building, courtship and mate guarding before she lays the eggs (Trivers 1972). Then, in a highly synchronous breeding population few or no additional females will remain for the male to pursue.

The breeding season of Blue-eyed Shags on Signy is curtailed by harsh weather and the formation of sea-ice in April and May. The period required for laying and fledging by the entire colony was 17 to 18 weeks, compared with 24 weeks for European Shags on the Farne Islands. The laying period for each species was of 24 to 33 days and about 70 days duration respectively. Pair formation and nest-building by Blue-eyed Shags occurred mainly in October, with sporadic earlier attempts in August and September, when the weather allowed. It is not known to what extent frequent desertion of the colony (due to bad weather) disrupted the process of pair formation, however during this relatively short period no bigamous trios were recorded. By contrast, pair formation amongst European Shags on the Farnes spanned three months, during which time over 4 % of males mated bigamously (Potts 1966). Flightless Cormorants, breeding near the equator, may form pair bonds and lay in any month of the year. In this situation monogamy prevails, although the female will normally desert her mate and find a new breeding partner before their chicks have reached independence (Harris 1979).

Although amongst the majority of animal groups there are at least some long-lived species, few are monogamous. Fewer still combine these two traits. Long-lived birds are unusual in that they have the opportunity to re-mate with the same individual in successive years. These stable pairs may show higher reproductive success (Coulson 1972), and this is usually attributed to greater coordination of activities between the male and female (Cooke *et al* 1981) and a reduction in the amount of time spent in pre-breeding activities (Coulson 1966, Rowley

1983). Croxall and Ricketts (1983) have shown that Wandering Albatross partners must balance the timing of their foraging trips and incubation shifts in such a way that neither partner is subjected to undue stress - in the form of weight loss - throughout the incubation period. Any incompatability in this respect may seriously jeopardise breeding success, and possibly also subsequent survival.

Mate change through divorce is more frequent in years following breeding failure than after successful breeding (Coulson 1966, Brooke 1978). Those birds which divorce their previous mate must then chose from a pool of available mates at the colony. However, Coulson and Thomas (1983) have shown that a small Kittiwake study colony the pool of 'available' new mates was small.

If the effects of photoperiodicity on hormone levels is influenced by the age or condition of the individual once adulthood is attained (Hutchison and Hutchison 1983), then available new partners may all be of the same or of a similar age. Older birds may be more efficient feeders and might attain breeding condition earlier in the season than young birds. This may explain why, in the European Shag, the timing of laying is age-graded, with two-year old birds laying at the end of the (prolonged) laying period. As mentioned above, the earliest breeding attempts of Blue-eyed Shags were at three years, perhaps because poor weather prohibits late laying. In a highly synchronized breeding colony a much higher proportion of the population will be available for pairing at any given time in the pre-laying period. Thus, even if the effects of age on the timing of pairing is strong the chances of obtaining a mate of the same age will be less than if the pre-laying period is prolonged. Yet, average age differences within 'changed' pairs of Blue-eyed Shags were small, suggesting that the timing of pairing was age dependant, or that partners were selected for their age similarities. Clearly, detailed observations of pre-breeding activities are required.

Mean clutch sizes throughout 1980 followed a pattern which has been noted in other bird species; there was little change during the first half of the laying period, followed by a marked decline. This pattern may reflect the change in food availability later in the season; optimal brood sizes should be preceded by an adjustment in the clutch size. Average clutch sizes were much higher in 1981, and with no evidence of a decline towards the end of the laying period. Either food availability and the optimal brood size were 'expected' to change in 1980, but to remain constant in 1981, or else clutch size differences in the two seasons merely reflected variation in the amount of food available to each female during the time of egg formation. However this latter suggestion seems unlikely in view of the relatively small eggs and small clutches laid by Blue-eyed Shags.

If older birds are more efficient feeders, and are more efficient at rearing their chicks, then old females would be expected to lay large clutches, and hence support larger broods. Also, for reasons mentioned earlier, breeding effort may increase with age if adult annual survival declines. Since, from egg laying onwards, the male contributes an almost equal amount to incubation and chick rearing (Bernstein 1982), it may be to the female's advantage if she can assess the age and experience of her partner, and vary her clutch size accordingly. To either sex, an older partner may be more 'attractive' than a partner of the same age or younger. If this is so, and if age can be assessed by behavioural cues, then it would be advantageous for young adults to mimic the behaviour patterns of older birds, in an attempt to secure an older mate.

To attain an optimal clutch size in a given season three attributes are required : 1) the capacity to predict the level of food available later in the season, 2) the capacity to gauge one's own efficiency at chick rearing (and perhaps that of one's mate), and 3) the capacity to adjust the clutch finely. In common with most seabird species, Blue-eyed Shags lay small clutches, and so the capacity to vary the clutch size to suit the food supply is limited. Also, sea-ice conditions and, perhaps, the locality of fish stocks near the colony, are difficult to predict. The former is certainly true, and the latter may be inferred from variation in the mortality of chicks (through starvation) in the three study seasons. Brood reduction may be seen as a late alternative to clutch adjustment. Although less efficient, it need not be unduly wasteful if the death of the last-hatched chick occurs at an early stage and if, as in the Blue-eyed Shag, the amount of nutrients invested in egg production is very low.

The question remains as to whether egg size differences and hatching asynchrony are pre-adaptations for brood reduction, and if so, to what extent the parent's behaviour after hatching can modify or reverse these effects. Firstly, egg size differences, and subsequent chick weight differences in broods of three were small in magnitude. At hatching, C chicks were only 10 % lighter than their siblings had been. Also, hatching weight had no influence on subsequent survival when the effects of hatching position were removed. Perhaps more importantly, C egg chicks in broods of two (from which the A or B egg or chick had been lost or had died) survived as well as B chicks in normal broods of two, in spite of their weight 'handicap'. Clearly, egg weight differences on their own were ineffective in reducing the C chick's survival chances. This is not always the case. In two-egg clutches laid by Fiordland

Crested Penguins the first egg hatches earlier than the second, but yields a much smaller chick, which rarely survives (Warham 1974). In the Common Grackle, egg weight increases with laying order in clutches of five and six. These differences were sufficient to partly offset the effects of hatching asynchrony, to the extent that although brood reduction did occur, chick deaths normally occured late in the nesting period (Howe 1978). Egg weight differences in the Blue-eyed Shag may result from the depletion of nutrient reserves, or may be an attempt to save expenditure on a chick which is unlikely to survive in any case. Again, both of these interpretations seem unlikely in view of the relatively small eggs laid by Blue-eyed Shags.

Hatching asynchrony was the main cause of sibling weight differences. These differences must severely impair the C chick's ability to compete with its siblings - if the need for such competition arises. Yet although the majority of C chick deaths occurred when relative differences in chick weights were at a peak, there is no evidence that these weight differences alone caused the death of the third chick. The mean RDCW score in broods in which the C chick survived was similar to that for broods in which it died. Adults of the latter group must either have been extremely inefficient at sustaining the (young) brood, or may have used clutch-size differences as a means of identifying (and then neglecting) one individual within the brood of three. 'C' chick deaths during the first ten days cannot be explained satisfactorily by food shortages. At the time at which many late-hatching broods of three lost their C chick, many older, larger chicks in broods of two were thriving. This is in spite of the much greater food requirements of the latter group. O'Connor (1978a) has suggested that early mortality may arise if adults experience greater difficulty in catching small prey items for tiny chicks, than in catching larger items for older chicks. It may well be that the size of prey taken by Blue-eyed Shags increased with chick size, to the extent that newly hatched C chicks were unable to cope with prey items which were more appropriate for their larger siblings. However this seems unlikely, since shag chicks are fed on intact and partly digested fish in the parent's gullet, and appear to extract mouthfuls from this soft, almost homogeneous bolus of food. Also, as noted above, C egg chicks in broods of two survived well, even if the other sibling was several days older and much larger than it.

The most likely explanation for early brood reduction in this species is that the parents selectivity neglect the last hatched chick, thereby avoiding further investment in a chick whose asymptotic weight and chance of reaching adulthood are low. By laying a third egg however, they reduce the effects of egg loss.

This study has provided answers to some of the more basic questions concerning the effects of age on clutch size, laying date and chick production by a moderately long lived seabird. Theoretical models predict that the lifetime reproductive output of an individual depends on a fine balance between many inter-related factors. These include the age at first breeding, the selection of a compatible mate, the position of the nest site, the date of egg laying or of birth, and the production of a clutch or litter which in each season yields the maximum number of healthy surviving offspring which the food supply will allow, but with the minimum of effect on the parents subsequent survival or breeding condition. The few studies which have tested these predictions include those of Coulson on Kittiwakes (e.g. Coulson 1966, 1968, 1972, Coulson and Thomas 1983), Perrins on Great Tits (Perrins 1965, Perrins and Jones 1974, Perrins and Moss 1974), Cooke on Lesser Snow Geese (Finney and Cooke 1978, Cooke *et al* 1981, Cooke and Davies 1983), and Clutton-Brock *et al* on Red Deer (Clutton-Brock *et al* 1982).

SUMMARY

Study species, area and general methods

1. The study species, the Blue-eyed Shag *Phalacrocorax atriceps*, comprises seven subspecies. On Signy Island (South Orkney Islands) intensive ringing of *P. a. bransfieldensis* nestlings has been carried out by British Antarctic Survey since 1969. Much smaller samples of nestlings were ringed between 1960 and 1968. Counts of breeding birds at the two colonies have been made since 1947.

2. The smaller colony (at North Point) has increased in size from 9 to 62 pairs during 1948 to 1981. Data for the larger colony (at Shagnasty) are less reliable. By 1981 the colony comprised 770 pairs.

3. Adults were sexed by a combination of voice and bill-depth differences. Sexual dimorphism in bill-depth is similar to that of other *Phalacrocorax* species.

Survival, recruitment and philopatry

4. Of 6,196 Blue-eyed Shags ringed during 1960-1981, 1080 have been recaptured. Adult and first-year survival during this period was estimated at 0.87 and 0.58 respectively. Adult annual survival during 1976-1978 was lower : 0.75. During the study period the estimated survival rate in successive years was also low : 0.77 (1979-80), and 0.78 (1980-81).

5. If an individual bred in 1980 its chances of recapture or resighting in 1981 were increased. 74.9 % of individuals which bred in 1980 were recaptured in 1981, compared with 63.4 % of non-breeders in 1980.

6. The estimated mean age at return to the colony was 4.3 years (males) and 4.8 years (females). Most males returned at age 4 years (46 %) and most females at age 5 years (50 %). The earliest and latest age of first return to the colony was at 2 and 6 years.

7. The proportion of birds known to have bred in 1980 and 1981 increased with age, at least up to 10 years. The estimated mean ages at which breeding was first recorded were 5.00 and 5.42 years for males and females respectively. For both sexes the commonest age at which breeding was first recorded was 5 years (35.1 % of males and 28.7 % of females; range = 3.9 years, both sexes). Females were first recorded breeding at a younger average age at North Point than at Shagnasty.

8. Because males returned at a younger average age than females, many more males than females were recaptured at ages 3 - 5 years. Thereafter the sex ratio of recaptures was close to parity.

9. Very few adults were recaptured breeding at a colony other than the one at which they hatched; 0.9 % of males and 3.7 % of females. A higher proportion of males which hatched at North Point bred at Shagnasty then vice versa. After at least one breeding attempt the proportion of females which moved to a different colony was almost three times greater than that of males. The tendancy to change colonies was greater at North Point (5.8 % of breeders per annum) than at Shagnasty (1.5 % per annum).

Pair stability

10. 29 % of pairs comprised partners of an equal age, whilst in 57 % of pairs, partner's ages were within ± 1 year of each other. 50 % of these 'same age' pairings would be expected to occur through chance alone.

11. The majority of males of 3 - 7 years, and of females of 3 - 5 years chose partners which were older than themselves. The opposite was true of males of more than 8 years, and females of more than 6 years.

12. 56 % of birds which changed their mate chose a new mate of within ± 1 year of their own age. In 31 % of cases the new mate was 1 year older than the mate of the previous season.

13. On average, 77 % of birds changed their mates in successive seasons. 56 % of these mate changes were due to the death or disappearance of the mate.

14. In successive seasons, 64 % of males, and 54 % of females re-nested within the same 4 m area. The average distance moved by males was 4.9 m, and by females was 5.0 m. Site retention was more often associated with mate retention, for females, but not for males.

15. A change of partner delayed the date of laying (though not significantly so) and had a disruptive effect on the female's tendancy to lay on or around a particular date.

16. A slightly, but not significantly higher proportion of failed breeders changed their mate in the subsequent season (84 %) than those which reared at least one young to fledging (76 %). Beyond this, mate change had no effect on clutch size, brood size or the number of chicks fledged.

The position and quality of the nest site

17. More older males occupied nest-sites which were in close contact with 3 - 4 neighbours, than did young males. However, there was no relationship between age and any other nest site quality variable measured; i.e. the degree of protection from wave damage, exposure to wind, ease of access to the sea, or the capacity of the site.

18. Within the colony, laying was more synchronized at nests with 3 or 4 neighbours within a distance of 2 m, than at those with fewer or no neighbours. With this exception, there was no relationship between any measure of nest site quality and either the laying date, clutch size, egg survival, brood size or the number of chicks fledged.

19. Nest site quality varied throughout the colony. Pairs nesting in 'central' and 'intermediate' squares experienced a greater level of social contact, less wind and wave exposure, and reduced ease of access compared with those in 'edge' squares.

20. The mean age of males nesting in 'intermediate' squares was greater than that in 'central' or 'edge' squares. However there was no evidence of age 'clumping' on a finer scale within the colony.

Laying date, clutch size, egg size and hatching success

21. Over 16 seasons the average date on which laying commenced was 1 November (S.D. = 6.7 days, range = 25 days). Neither the temperature, snowfall or average wind speed in October affected the date of laying.

22. In each colony the span of egg laying was short, covering 34 days (S.D. = 6.8) and 24 days (S.D. = 4.6) at Shagnasty (in 1980 and 1981 respectively). At North Point the laying span was shorter : 19 days (S.D. = 6.8) and 26 days (S.D. = 6.9).

23. There was no relationship between age and the timing of laying for either sex. Nor did the degree of laying synchrony within age groups vary with the age of the female.

24. During the four weeks prior to egg laying the mean weight of 61 females which bred was significantly greater than that of 38 females which did not attempt to breed (mean weights = 2566 g and 2471 g respectively). There was no relationship between weight and subsequent laying date.

25. There was a strong positive correlation between the relative laying dates of individual females in two successive seasons.

26. On average, clutches were smaller at North Point in 1979 than in 1980 (means = 2.3 and 2.5). At both North Point and Shagnasty, clutches were on average, significantly larger in 1981 than in 1980 (1981, means = 2.9 and 2.8, 1980 means = 2.5 and 2.6). Blue-eyed Shag clutch sizes were lower than those recorded for four out of six other *Phalacrocorax* species.

27. In 1980 mean clutch size showed no significant change during the first half of the laying period, but declined at a rate of 8 % per week during the second half. By contrast, mean clutch sizes remained constant and higher throughout the much shorter 1981 laying period.

28. Average clutch size increased with female age in 1981, though not in 1980. 10 year-old females laid an average clutch of 3.0 eggs, compared to 2.5 eggs laid by 3 and 4 year olds. A higher proportion of females of 11 and 12 years laid clutches of 2 eggs (30 %), than did those of 8 - 10 years (9 %). There was no significant relationship between body weight prior to laying and the number of eggs laid.

29. The average interval separating successive eggs in clutches of two (3 days) was significantly longer than that between successive eggs in clutches of 3 (2.6 days). Within clutches of 3, the mean B-C laying interval (2.7 days) was significantly longer than the A-B laying interval (2.5 days).

30. The average hatching interval in clutches of two (2.2 days) was not significantly longer than that in clutches of three (2.0 days). By hatching, the A-B interval was, on average, 1 day less than it had been at laying, whilst the B-C interval was 0.3 of a day less than it had been at laying.

31. In two-egg clutches the hatching interval separating A and B chicks was 0.7 times the length of the laying interval, whilst in three-egg clutches the ratio was 0.6. The interval between B and C eggs at hatching was, on average, 0.9 - 1.0 times the length of the B-C laying interval. This suggests that A eggs were incubated for two-thirds of the A-B interval, whilst B and C eggs were most often incubated from the date of laying.

32. The mean laying span in clutches of 3 increased significantly throughout the laying period. Although the hatching span showed a similar increase this was not significant.

33. In 3-egg clutches laid by females of 10 - 11 years, the laying and hatching intervals were shorter than in clutches laid by 3 - 9 year olds. These results were significant for : A-C laying intervals, B-C hatching intervals, and for the ratio of laying:hatching interval lengths (B-C eggs and A-C eggs).

34. The average period separating laying and hatching was 29.3 days, with a range of 27 - 33 days. 95 % of eggs which hatched did so within 28 - 31 days. The mean laying to hatching intervals for A, B and C eggs in clutches of 3 were 29.8, 28.9 and 28.8 days respectively.

35. On average, the laying to hatching period was approximately half a day shorter during the first half of the laying season, than during the final two-thirds.

36. Egg volume, laying weight and the weight of the chick at hatching were intercorrelated. However, large eggs weighed less and yielded lighter chicks than would be expected if the ratio of egg volume:weight was constant. This was because yolk weight showed an absolute increase, but a relative decrease with whole egg weight.

37. The average weights of two and three egg clutches were 103.2 g and 152.6 g respectively. This represents 4.0 and 5.9 % of the mean weight of 61 females which bred.

38. A and B eggs in clutches of two and three did not differ significantly in volume. However, C eggs were, on average, significantly smaller - by 1.1 to 1.9 cc. Similarly, at hatching, A and B chicks did not differ significantly in weight, but were both, on average, significantly heavier than C chicks.

39. The mean volume, laying weight and hatching weight of eggs laid by females of 10 - 11 years were significantly lower than for eggs laid by females of 4 - 9 years or of 7 - 9 years. The relative difference in egg volume in clutches of two or three did not differ significantly with laying date or female age.

40. B and C eggs were significantly shorter and, in the case of C eggs, broader than A eggs. In clutches of two there was a significant increase in egg breadth throughout the laying period. Older females laid relatively broader, more rounded eggs. This was due to a shortening of egg length, whilst egg breadth showed no significant change.

41. A significantly higher percentage of eggs hatched at Shagnasty in 1981 (90.8 % of eggs laid) than in 1980 (84.9 % of eggs laid). At North Point a higher percentage hatched in 1980 (75.5 %) than in 1979 (51.8 %). There was no significant variation in egg survival, viability or hatching success in relation to egg size, clutch size or laying position.

42. Egg survival declined significantly with laying date in 1980. A similar, but non-significant decline in survival occurred in 1981. In both years hatching success showed a significant inverse relationship with the number of other clutches 'at risk' throughout the incubation period.

43. Egg viability and hatching success were lower for males of 10 - 11 years than for those of 8 - 9 years.

Chick growth rates and survival

43. The mean number of chicks fledged per brood in 1979, 1980 and 1981 was 0.5, 1.5 and 1.9 respectively. 57 % of eggs laid in 1980, and 67 % of eggs laid in 1981 yielded chicks which survived to fledge.

44. Chick survival (from hatching to fledging) in 1979, 1980 and 1981 was, respectively, 44 %, 71 % and 83 %.

45. Overall, chick survival was higher in broods of one and two, than in broods of three. This difference was due to low survival by 'C' chicks. Only 11.1 % of C chicks survived to fledge, compared to 78.1 % - 94.1 % of chicks in other brood size and position categories.

46. Chick survival in late broods in 1981 was lower than in early broods of that year. Both the number of chicks hatched and fledged per brood declined with laying date in 1980. Only the number of chicks fledged declined during the 1981 season. On average, in 1980 and 1981, late layers produced 0.7 and 0.6 chicks fewer than early layers.

47. The mean number of chicks hatched and fledged per pair increased with adult age up to the age of 5 years, varied little from between 5 and 10 years of age, and then showed a slight decline. In 1980 and 1981 8 - 9 year old fledged 0.9 and 0.7 more chicks per pair on average, than those of 3 - 4 years. This mainly reflects differences in the number of chicks hatched per pair, rather than variation in chick survival with parental age. Egg size had no effect on chick survival.

48. In clutches of three, if the A or B egg failed to hatch, then the C egg chick had as high a chance of surviving as A or B egg chicks in normal broods of two or three.

49. The mean age at death of A and B chicks was at 40 and 34 days, whilst that of C chicks was 15 days. On average, C chicks reared by parents of 6 - 12 years died at 18 days, compared with an average age of 10 days for those reared by 3 - 5 year olds.

50. There was an inverse relationship between the A-C hatching interval and the age at which the C chick died. C chicks which hatched within 2 - 4 days of the A chick survived for 6.7 days longer than those which hatched within 5 - 6 days of the A chick. However, the hatching interval had no significant effect on the proportion of C chicks which survived to fledge.

51. Chick survival in two samples of artificially synchronized broods of three did not differ from that in normal broods of three. However, synchronized broods suffered an increasedrisk of total brood loss.

52. In broods of three, absolute differences in weight between the heaviest and lightest chicks increased with age, whilst relative differences in weight declined. Relative differences in chick weights within broods were greater than could be explained by asynchronous hatching alone.

53. Chicks were fed most frequently between 12.00 and 16.00, the feeding rate being highest for chicks of 1 - 10 days of age, and declining thereafter. Average meal size increased sigmoidally throughout the nestling period. The amount of food consumed by broods of three at 1 - 10 days (the age at which most C chicks die of starvation) was 7 to 8 times less than that consumed by broods of two at 31 - 40 days.

54. In broods of three, the smallest chicks received proportionally fewer feeds than their siblings at ages 1 - 5 days and at 11 - 15 days.

55. Bill and toe lengths reached their maximum size at approximately 40 days and 30 - 35 days respectively, whilst wing length continued to increase up to the age at fledging (65 - 70 days).

56. In broods of three, the asymptotic weight of A chicks was, on average, 150 g greater than that of B chicks, which in turn was 280 g greater than that of C chicks. C chicks differed from A and B chicks

in their growth rate, time of inflection and growth curve form. 'A' chicks in broods of one, two and three differed significantly in their asymptotic weights. However, survival of the C chicks beyond 20 days did not adversely effect the asymptotic weights of its elder siblings.

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APPENDIX A: Scientific names of species mentioned in the text.

Albatross, Black-browed	*Diomedea melanophris* Temminck
Albatross, Grey-headed	*D. chrysostoma* Forster
Albatross, Laysan	*D. immutabilis* Rothschild
Albatross, Wandering	*D. exulans* (Linnaeus)
Blackbird	*Turdus merula* Linnaeus
Booby, Brown	*Sula leucogaster* Boddaert
Booby, White	*S. sula* Linnaeus
Cormorant, Double-Crested	*Phalacrocorax auritus* (Lesson)
Cormorant, Flightless	*Nannopterum harrisi* (Rothschild)
Deer, Red	*Cervus elaphus* Linnaeus
Fulmar	*Fulmarus glacialus* (Linnaeus)
Fieldfare	*Turdus pilaris* Linnaeus
Gannet	*Sula bassana* (Linnaeus)
Goose, Lesser Snow	*Chen caerulescens* (Linneaus)
Grackle, Common	*Quiscalus quiscula* (Linnaeus)
Guillemot, Brünnichs	*Uria lomvia* (Linneaus)
Guillemot, Common	*U. aalge* (Pontoppidan)
Gull, Black-headed	*Larus ridibundus* Linnaeus
Gull, California	*L. californicus* Lawrence
Gull, Herring	*L. argentatus* Pontoppidan
Gull, Laughing	*L. atricilla* Linnaeus
Gull, Red-billed	*L. novaehollandiae* Forster
Gull, Ring-billed	*L. delawarensis* Ord

Harrier, Hen	*Circus cyaneus* (Linnaeus)
Hen, Domestic	*Gallus domesticus*
Heron, Grey	*Ardea cinerea* Linnaeus
Kittiwake	*Rissa tridactyla* (Linnaeus)
Martin, House	*Delichon urbica* (Linnaeus)
Oystercatcher	*Haematopus ostralegus* Neumann
Pelican, Brown	*Pelecanus occidentalis* Linnaeus
Pelican, Pink-backed	*P. rufescens* Gmelin
Penguin, Adelie	*Pygoscelis adeliae* (Hombron and Jacquinot)
Penguin, Chinstrap	*P. antarctica* Forster
Penguin, Fiordland Crested	*Eudyptes pachyrhynchus* (G.R. Gray)
Penguin, Yellow-eyed	*Megadyptes antipodes* (Hombron and Jacquinot)
Petrel, Southern Giant	*Macronectes giganteus* (Gmelin)
Razorbill	*Alca torda* Linnaeus
Robin	*Erithacus rubecula* (Linnaeus)
Ruff	*Philomachus pugnax* Linnaeus
Seal, Elephant	*Mirounga leonina* Lydekker
Shag, Blue-eyed	*Phalacrocorax atriceps* Murphy
Shag, European	*P. aristotelis* (Linnaeus)
Shearwater, Manx	*Puffinus puffinus* (Brünnich)
Shearwater, Short-tailed	*P. tenuirostris* (Temminck)
Shearwater, Sooty	*P. griseus* Gmelin
Sheathbill, Wattled	*Chionis alba* Gmelin
Skua, Brown	*Catharacta skua* Hagen
Skua, McCormick's	*C. maccormicki* (Saunders)

Sparrow, House	*Passer domesticus* (Linnaeus)
Sparrowhawk	*Accipiter nisus* (Linnaeus)
Starling	*Sturnus vulgaris* Linnaeus
Tern, Common	*Sterna hirundo* Linnaeus
Tern, Roseate	*Sterna dougallii* Montagu
Tit, Blue	*Parus caeruleus* Linnaeus
Tit, Great	*P. major* Linnaeus
Warbler, Great Reed	*Acrocephalus arundinaceus* (Linnaeus)
Warbler, Reed	*A, scirpaceus* (Hermann)

APPENDIX B: Body measurements and weights

P. atriceps, Signy Island

	Males			Females		
	Mean	S.D.	n	Mean	S.D.	n
Weight	2883.2	255.26	130	2472.7	154.50	101
Wing Length	304.5	3.60	36	289.6	6.16	23
Bill Depth	12.5	0.51	39	11.1	0.44	25
Tail Length	137.0	11.11	36	128.6	4.89	24
Dorsal Band Width*	3.5	1.09	28	2.9	0.92	17

* The width of the white band across the centre of the back.

The mean of three measurements was taken for each individual.

Frequency of occurrence of the white dorsal band :

Location	% with dorsal band	n	Sub-species	Source
South Orkney Islands	96	64	*P.a.bransfieldensis*	This study
Bird Island, South Georgia	49.1	57	*P.a.georgianus*	I.Hunter, *Pers.comm.*
Beauchene Island, Falkland Islands	0.0	Large sample from 5000-10,000 pairs	*P.a.albiventer*	P. A. Prince, *Pers.comm.*
New Island, Falkland Islands	0.0	1394	*P.a.albiventer*	*Pers.obs.*

P. atriceps albiventer, Beauchene Island, Falkland Islands (information from P. A. Prince)

	Mean	S.D.	n
Weight	2433.4	154.2	16
Wing Length	294.1	8.75	16
Bill Depth	11.5	0.76	16
Bill Length	63.7	2.48	16

APPENDIX C: Estimates of the number of breeding pairs and of nests at North Point and Shagnasty (colonies I and II only) during 1947-1981. Counts made during September - early October, and estimates (at Shagnasty) from the shoreline are less likely to have been accurate, and are indicated by an asterisk. pr = pairs, n = nests, b = birds.

Season	North Pt.	Shagnasty I and II	Source: B.A.S. Reports
1947	-	175 pr (?)*	Anderson, J.H. 1948
1948	9 pr	86 pr*	Laws, R. 1949
1949	13 pr	142 pr*	Jones, N.V. and Pinder, R. 1961
1952	16 n	-	Base Journal 1952
1953	18 n	'200-300'b*	Tritton, A.G. 1953
1954	17 pr*	-	Tickell, W.L.N. 1956
1955	19 pr	-	" " "
1956	26 pr	-	" " "
1957	42 n	-	Scotland, C.D. 1957
1958	34 n	600 n*	Richards, P.A. 1958
1959	19 n	-	Pinder, R. 1961
1960	26 n	200 n	" " "
1961	43 n	424 n	Jones, N.V. and Pinder, R. 1961
1962	25+ pr*	-	Topliffe, F. 1962
1964	29 n	-	Burton, R.W. and Howie, C.A. 1965
1968	-	115 n	Census form
1969	36 n	360 n	" "
1972	35 n	356 n	" "
1973	60 pr*	-	Base Journal
1976	-	469 n	Brook, J. 1976
1977	60 n	419 n	Rootes, D. 1978
1978	50 n	396 n	Rootes, D. 1979
1979	65 n	385 n	Price, R. 1980
1980	58 n	446 n	This study
1981	62 n	465 n	" "

APPENDIX D: Analysis of regurgitated food.

In 1980 and 1981, 84 regurgitated food samples were collected from adult Blue-eyed Shags. Many adults regurgitate when handled and, in some cases, when approached at the nest. Each sample was collected in a separate polythene bag and deep frozen within 3 - 4 hours of collection. The total weight and mean weight of samples collected in the two seasons were similar (Table D.1). Fish comprised 96.2 % of the weight of food collected.

Intact fish remains were identified by pectoral and dorsal fin ray counts, and by head shape (Norman 1938, and North *pers. comm.*). Notothenids comprise 96.9 % by weight of identifiable prey remains (Table D.2) *Notothenia neglecta* being the most abundant species in the diet. 13 individuals of 3 species were aged by A.W.North (British Antarctic Survey), by counting scale annuli (Table D.3).

Invertebrate species identified are listed in Table D.4

TABLE D.1: The weights and composition of food samples collected in two seasons.

				Percentage by weight				
Season	No. of samples	Total weight	Mean weight (± S.D.)	Fish	Poly-chaeta	Cepha-lopoda	Crustacea	Others
1979								
10.1.80- 27.6.80	42	3262.5g	77.1±56.1g	95.6%	2.5%	0.6%	1.3%	0
1980								
4.10.80- 6.2.81	42	3195.2g	76.1±46.3g	96.7%	2.1%	0.5%	0.5%	0.2%

APPENDIX D (Continued)

TABLE D.2: The species composition of identifiable fish remains.

Species	No. of Food Samples	% by weight of identified remains	No. of intact individuals	Mean weight of intact individuals (± S.D.)	Range
Notothenia neglecta	13	42.4	13	102.5±82.5g	1.3-201g
N. rossii	8	13.4	6	58.2±37.4g	18-115g
Trematomus newnesi	5	3.6	5	25.6±12.6g	9.3-41g
Unidentified *Notothenia/ Trematomus* spp.	32	37.5	14	43.23±47.4g	4.5-165g
Harpagifer bispinus	2	0.7	11	2.3g –	–
Parachaenichthys/ Chaenocephalus spp.	3	2.3	33	2.5g –	–

APPENDIX D: (Continued)

TABLE D.3: The age distribution of 13 fish from regurgitated food samples.

Age	*N. neglecta*	*N. rossii*	*Notothenia* spp.	*T. newnesi*	All species
1 year	1				1
1-2 years		1		1	2
2-3 years	2			2	4
3-4 years		1			1
4-5 years			1		1
5-6 years	3		1		4

TABLE D.4: Invertebrate prey species in regurgitated food samples.

Polychaeta	Cephalopoda	Crustacea	Asteroidea
Aglaophanus sp.	Squid sp.	*Antarctomysis maxima* *Bovallic gigantea* *Glyptonotus antarcticus*	*Turqueti cryptasterias*

APPENDIX E.

The standard error on each survival estimate (Table 3.1) was calculated using a formula derived from Paradine and Rivett (1960):

$$Sz = \frac{1}{Y} \cdot \frac{1}{X^{\frac{Y-1}{Y}}} \cdot Sx$$

where : Sz = S.E. of survival estimate,

Y = number of years between ringing and recapture,

X = the proportion of birds recaptured, and

Sx = Binomial standard error

APPENDIX F.

Diurnal variation in adult weights, and in colony attendance

Seasonal variation in the mean weights of adult males and females is shown in Table F.1. There was no distinctive pattern of weight changes throughout the breeding season. However, any changes which occurred may have been obscured by differences in the time of day at which weights were taken. Bernstein (1982) described sex differences in the timing of feeding by Blue-eyed Shags at Anvers Island; almost all females left the colony to feed during the morning, and almost all males were absent from about 12.00 onwards. This pattern became less distinct during the nestling period, and especially by the age at which chicks fledge.

On Signy Island sex differences in the timing of feeding were also evident, although data are only available for the pre-laying period (Fig. F.1). At this time both partners roosted at the nest site. Females left within one hour of sunrise and returned 4½ to 5 hours later. On October 21, 1980 almost the entire complement of 437 females returned within a 20 minute period, at between 09.00 and 10.00. Then they took-over nest guarding activities from their mates and, apparently, had no further opportunities to feed during the 24 hour cycle. Most males left within one hour of their mate's return, and spent approximately 4½ hours away from the colony. They returned in small groups from 15.30 onwards.

With minor variations, this cycle of activities occurred throughout the incubation and early nestling stages, and is reflected in the diurnal pattern of weight change shown by males (Fig. F.2). This shows an increase in the proportion of males which had fed before being weighed, rather than a gradual increase in the weight of males throughout the day. There was no distinct pattern of variation in female weights, perhaps because no

TABLE F.1; Seasonal variation in body weight.

	Males			Females		
Date	Mean	S.D.	n	Mean	S.D.	n
1-15 January, 1980	2936	300.6	13	2322	144.2	16
16-31 January, 1980	2920	155.6	13	2377	191.9	19
1-7 October, 1980	2941	154.4	15	2569	73.1	14
8-15 October, 1980	2948	184.0	15	2519	109.1	43
16-31 October, 1980	2878	215.9	40	2520	139.6	37
29 November - 14 December, 1980	2798	256.1	5	2417	131.7	10
15-31 December, 1980	3113	242.7	24	2518	149.3	24
31 December, 1980	3115	258,6	16	2560	150.0	12
1-15 January, 1981	2803	199.6	22	2412	125.1	24
15-31 January, 1981	2774	259.9	27	2363	176.9	17
1-15 February, 1981	2918	209.4	22	2614	123.1	17

FIGURE F.1: The percentage of adults present at Shagnasty I and II, and the percentage of adults in pairs, from sunrise to sunset. 21 October 1980.

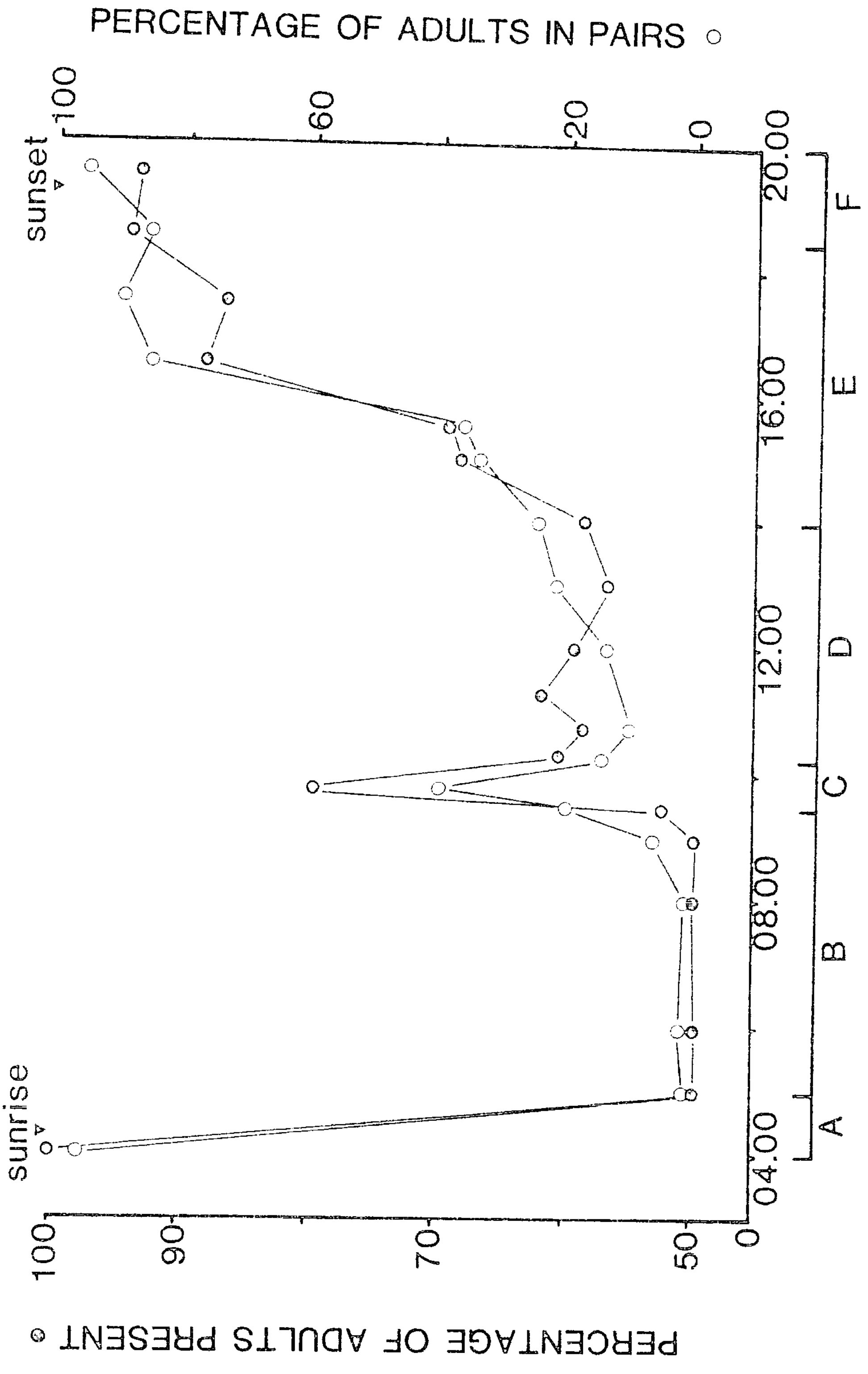


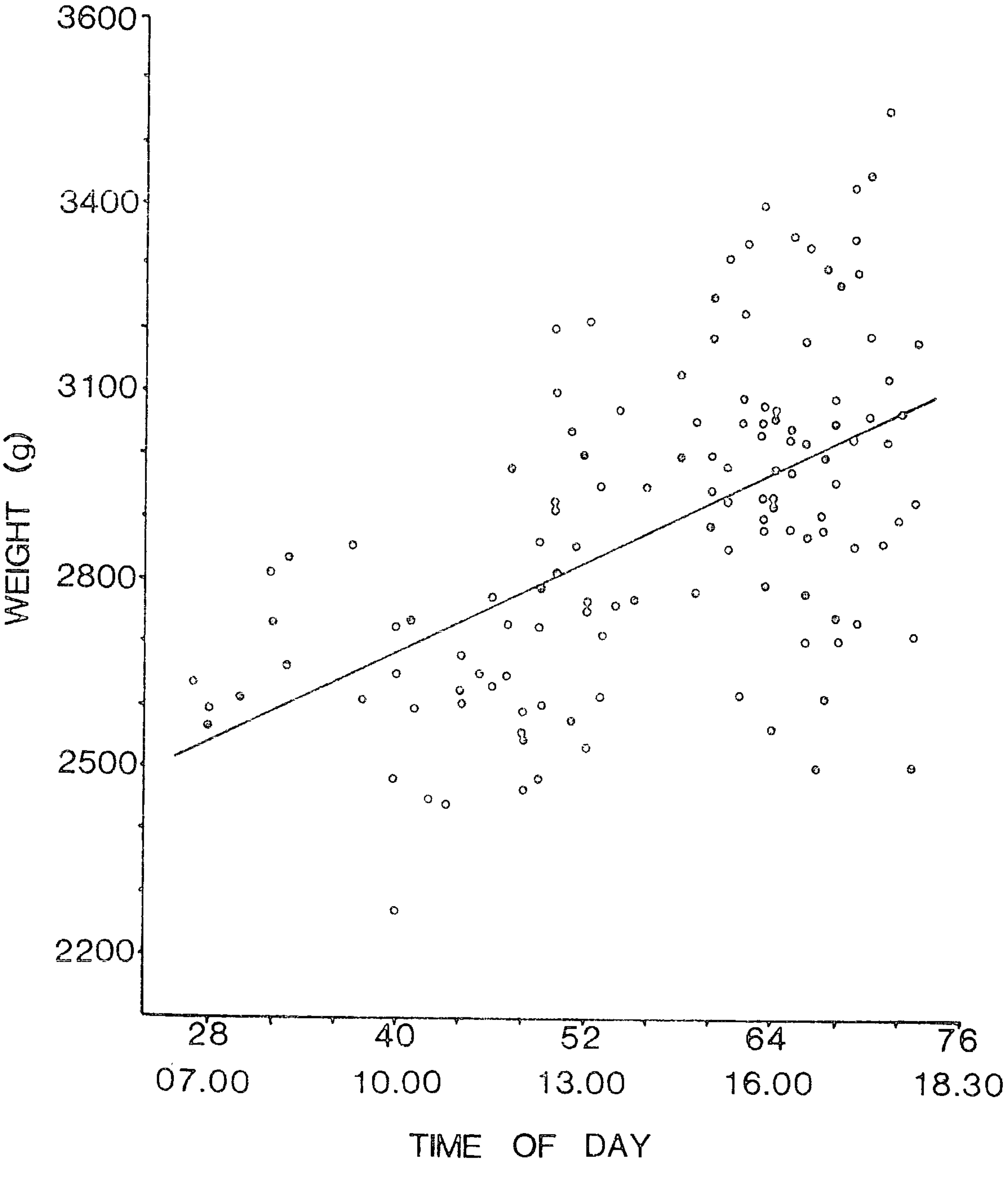
FIGURE F.2: Variation in the weight of male Blue-eyed Shags in relation to the time of day. Fitted line derived from the regression equation :

$Y = 11.9(X) + 2271.2$; 129 d.f.;
$r = 0.55$; $P<0.001$,
where 'X' = number of 15 minute intervals after 24.00.

Figure F.1: The letters below the X axis denote the following :

A	Females leave
B	Males guard nest
C	Females return
D	Females guard nest
E	Males return in small groups
F	Almost all adults present

FIGURE F.2:


3600
3400
3100
2800
2500
2200
WEIGHT (g)
28
40
52
64
76
07.00
10.00
13.00
16.00
18.30
TIME OF DAY

birds were weighed before they left to feed (at 04.00 to 05.00), and throughout the mornings.

Between 07.00 and 18.30 males showed a weight gain of 524 g (estimated from the regression equation; Fig. F.2). This represents 18.2 % of the average weight of male Blue-eyed Shags. However, at weighing, a proportion of males will have partly, or completely assimilated the food taken that day, and so this figure is an underestimate of the total weight of food consumed. However it is unlikely that male Blue-eyed Shags consume more than 600 - 700 g per day on average. This estimate falls short of that of Bernstein (1982); 1209 g of food per day (40 % of body weight).

APPENDIX G;

Clutch size in relation to female age.

1980

Clutch size:

	1	2	3	4	n
Age					
3	0	2	0	0	2
4	0	1	7	0	8
5	0	11	15	0	26
6	0	4	3	0	7
7	0	3	9	0	12
8	0	0	2	0	2
9	0	5	14	0	19
10	2	8	14	0	24

1981

3	1	2	2	1	6
4	1	11	15	0	27
5	1	8	27	0	36
6	0	3	41	0	44
7	0	0	6	0	6
8	0	4	16	0	20
9	0	0	2	0	2
10	0	0	23	0	23
11	0	9	16	0	25
12	0	0	5	0	5

APPENDIX H;

Brood sizes at hatching, and at fledging, in relation to adult age. Where both numbers of a pair are of known age, the female's age was used.

1980

Brood size at hatching :

Age	0	1	2	3	n
3	1	1	2	0	4
4	1	4	9	9	23
5	4	9	28	22	63
6	2	2	5	1	10
7	1	1	14	12	28
8	1	2	4	3	10
9	0	3	12	10	25
10	3	6	16	10	35
11	0	1	1	2	4

1981

3	0	2	9	3	14
4	1	6	9	14	30
5	0	10	14	37	61
6	0	2	17	45	64
7	0	0	4	7	11
8	0	0	5	16	21
9	0	1	2	3	6
10	0	0	5	22	27
11	2	5	10	19	36
12	0	1	0	5	6

APPENDIX H (Continued)

1980

	Brood size at fledging:			
	0	1	2	3
Age				
3	2	1	1	0
4	6	9	7	1
5	9	22	28	0
6	2	4	3	0
7	3	3	20	0
8	2	3	5	0
9	0	6	19	1
10	8	10	12	3
11	0	1	2	0
15	0	0	1	0

1981

3	1	3	7	0
4	4	12	9	3
5	1	9	33	13
6	4	4	25	13
7	1	2	6	0
8	0	2	11	6
9	0	1	3	0
10	2	4	9	12
11	2	7	17	5
12	0	1	2	3