The breeding ecology of great skuas <u>Catharacta</u> <u>skua</u>
in Shetland over a period of declining sandeel stock

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This thesis is dedicated to two people who will never read it: to Louise Hiom, who fell from a cliff and drowned while catching guillemots in 1988, and to my father, who died of cancer, aged sixty, in 1990.

CANDIDATE'S DECLARATION

I declare that the work recorded in this thesis is entirely my own, unless otherwise stated, and that it is of my own composition. No part of this work has been submitted for any other degree.

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CONTENTS

ABSTRACT

A discriminant function was generated to determine the sexes of great skuas on Foula, Shetland from external measurements. The accuracy of the function was assessed and its possible future applications were discussed.

Changes in the breeding ecology of great skuas on Foula were examined over a sixteen year period covering a major reduction in stocks of sandeels around Shetland. Results were discussed with particular reference to the predictions of life history theory.

Ring recovery data and annual returns of colour-ringed adults to the great skua colony on Foula were used to examine possible changes in survivorship over the period of declining sandeel stocks.

Data from breeding adults of known age were used to assess whether breeding performance improved with age during a period of food shortage, and to test predictions of life history theory concerning age-specific differences in reproductive effort.

Several hypotheses were tested concerning individual, seasonal and year to year variation in the aggression displayed by great skuas during brood defence.

Samples of feathers taken from breeding adults were used to examine whether accumulation of mercury by great skuas on Foula effected their breeding performance or success during a period of food shortage. The results were discussed in terms of possible implications for future work on the effects of pollutants upon breeding performance.

CHAPTER 1

General Introduction

Skuas (Family Stercorariidae) are most closely related to gulls (Family Laridae), but are distinguished by several features. The toes have strong, hooked claws; the rhamphotheca (the nail on the distal part of the upper mandible) is complex and prominent; their central tail feathers project beyond the rest of the tail; they have hard scales, or scutes, on the legs; they show reversed sex size dimorphism (Furness 1987).

Hartert (1912), Moynihan (1959) and Anderson (1973) classified all skuas in a single genus, largely on the basis of behaviour. Schnell (1970) adopted the same classification on the basis of skeletal structure. On the other hand, consideration of distribution, body size and plumage led Peters (1934), Wynne-Edwards (1935) and Bannerman (1963) to divide the family into small skuas (Genus Stercorarius) and large skuas (Genus Catharacta). This is the classification favoured by Furness (1987) and adopted in this thesis.

Skuas almost certainly evolved in the northern hemisphere (Furness 1987), and the breeding distribution of small skuas is confined to the Arctic and sub-Arctic. Large skuas, in contrast, breed mainly at equivalent latitudes in the southern hemisphere. Fisher & Lockley (1954) considered that a form of skua colonised the south from an ancestral stock in the northern hemisphere, which later became extinct. Southern skuas then separated into distinct taxa, which Furness (1987) placed in three species. Two of these, Catharacta maccormicki (the south polar skua) and C. chilensis (the Chilean skua) remained confined to the southern hemisphere. The third, C. skua, recolonised the north, giving rise to the nominate great skua or bonxie. This event probably occurred comparatively recently (possibly as late as the end of the 15th century; Furness 1987).

The present-day population of great skuas is approximately 35,000 individuals, with a breeding population of about 13,000 pairs (Furness 1987). They breed mainly in Iceland, the Faeroes and northern Scotland, with less than fifty pairs in each of Spitzbergen, Bear Island, Hopen and north Norway. Approximately 7,000 pairs breed in Scotland, 70% of these (c. 5,000 pairs) in Shetland, 200km north of the Scottish mainland. Half the great skuas in Shetland (c. 20% of the world population) breed on the island of Foula, 22km west of the nearest point of Shetland mainland.

Foula is a small island, 5km from north to south and 4km from east to west, but has the second, third and fourth highest peaks in Shetland and the highest sheer cliff in Britain. Most of the island is composed of old red sandstone, with a small area of highly metamorphosed pre-Cambrian strata in the extreme north-east (Mykura 1976). Parts of the low-lying eastern side of the island have been fenced and cultivated, but outside these areas the land is covered with peat, often to considerable depth. Drainage is poor, resulting in many small pools and areas of damp, marshy ground.

The population of great skuas on Foula was reduced by hunting and egg collecting during the 19th century to three pairs in 1860. It increased at a rate of 7% per annum from 1900 to 1975, to reach a peak of approximately 3,000 pairs. It has since declined to around 2,500 pairs. There is some illegal shooting of great skuas by crofters on Foula, but this is unlikely to have been the cause of this decline (Furness 1987). Great skuas now nest over most of Foula apart from the cultivated areas and active peat cuttings.

Great skuas disperse throughout the North Atlantic Ocean

during the winter months, although on average, adults spend the winter closer to colonies than do immature birds (Furness 1978a). Adults breeding on Foula generally return to their territories during April, and egg-laying commences in early May (Furness 1977). Over 90% of breeding females lay two eggs. Three-egg clutches are virtually unknown, and probably result from two females laying in the same nest (this is comparatively common in brown skuas C. skua lönnbergi; Burton 1968; Young 1978).

Incubation, performed mainly by females, lasts twenty-nine days on average, and chicks hatch asynchronously (Cramp & Simmons 1983). The young are semi-altricial, and are guarded mainly by the female. Males obtain most of the food for the young, which are fed by complete regurgitation. Fledging occurs after an average of forty-four days, and young become independent between two and twenty days after fledging (Cramp & Simmons 1983).

During the 1970s, great skuas on Foula fed their young largely (up to 95%) on sandeels Ammodytes marinus, which they obtained by 'plunging to surface'. These have a higher calorific content than other items in their diet, and appeared to be the preferred food (Furness & Hislop 1981). Adults spent a comparatively small proportion of their time foraging (six hours per day on average during the period of maximum food requirement of chicks, for adults with broods of two), and experienced pairs never left their chicks unguarded.

The main causes of breeding failure during this period were 'addling' of eggs (the result of infertility or embryo death) and egg predation, undertaken entirely by conspecifics (Furness 1984). These together accounted for 26% of eggs laid, while a

further 4% either rolled from the nest or died during hatching. This is a similar rate of egg loss to those found in brown skuas and south polar skuas (Furness 1984).

93% of great skua chicks which hatched at study nests on Foula during the 1970s went on to fledge. This resulted in a mean breeding success of 1.24 chicks per pair (Furness 1984). This generally exceeds fledgling production in south polar skuas and brown skuas (Procter 1975; Moors 1980; Furness 1984; Ainley, Ribic & Wood 1990), although there are exceptions (Young 1978; Hemmings 1984). The low mortality of chicks and consequent high breeding success of great skuas on Foula during the 1970s was attributed to the availability of an abundant food supply in the form of sandeels (Furness 1984).

Sandeels are numerically one of the most abundant fish species on the continental shelf of north-west Europe (Bailey et al. in press). As well as supporting large industrial fisheries they are important in food chain dynamics, and many predators (large fish, seabirds and marine mammals) prey heavily upon them. During the 1970s and early 1980s sandeels formed the base of the seabird food pyramid in Shetland (Ewins 1985; Ewins et al. 1988). Furness (1990) estimated that seabirds in Shetland consumed around 47,000 tonnes of sandeels per year in 1981-83.

A sandeel fishery was established in Shetland in 1974 and reached a peak in 1982 with a landing of 52,000 tonnes (Bailey et al. in press). Stocks of sandeels around Shetland declined markedly during the 1980s (Gauld, McKay & Bailey 1986; Hudson & Furness 1988; Kunzlik 1989; Monaghan, Uttley & Okill 1989; Bailey et al. in press), and this has been attributed to possible overfishing (Royal Society for the Protection of Birds, press release 3, August 1988; Avery & Green 1989). However,

important environmental changes have occurred in the North Sea and north-east Atlantic during the last twenty to thirty years. These include a progressive delay in the initiation of the spring phytoplankton bloom, an increase in numbers of the dinoflagellate Ceratium fuscus and an increase in stocks of herring Clupea harengus (Aebischer, Coulson & Colebrook 1990; Harris & Wanless 1990).

The available fishery-based research data support the view that environmental factors rather then overfishing are responsible for the decline in sandeel stocks. The spawning stock of sandeels in 1986 was still more than 60% of the maximum recorded (in 1984), according to Virtual Population Analyses conducted by the Department of Agriculture and Fisheries for Scotland (Kunzlik 1989). The decline in total stock during the 1980s appears to result from a series of years when relatively few young sandeels recruited into the population, despite the apparent presence of a large spawning stock. Recruitment of sandeels around Shetland is determined by factors acting in the first six months of life (Bailey et al. in press), and Kunzlik (1989) postulated that adverse environmental factors could be influencing the survival of larvae and/or the movements of larvae in and out of the Shetland area.

The responses of seabirds to changes in prey availability show considerable variation. For example, very low marine productivity during El Niño events in the tropical Pacific resulted in large-scale adult mortality (Barber & Chavez 1983; Duffy 1983; Schreiber & Schreiber 1984; Duffy & Merlen 1986), but adult survivorship can remain high during a prolonged period of food scarcity (Mills 1981). Similarly, the growth of seabird chicks may be sensitive to the availability of local food

resources (Dunn 1975; Lloyd 1979; Birkhead & Nettleship 1981; Ricklefs, Duffy & Coulter 1984; Ewins 1985), but several studies have suggested that chick growth rates are intrinsically determined, and not related to food availability except when food is extremely scarce (Prince & Ricketts 1981; Ricklefs et al. 1985; Shea & Ricklefs 1985). Nonetheless, seabird responses to prey availability have been hypothesised to follow a set of general principles, although these have not been widely quantified (Cairns 1987a).

Time devoted to foraging is likely to increase as food availability decreases (Barrett & Runde 1980; Gaston & Nettleship 1982; Schreiber & Schreiber 1984). However, the allocation of time to foraging may be constrained by requirements for other activities (Burger 1981; Birkhead, Johnson & Nettleship 1985; Diamond et al. 1986) and by an upper limit to daily expenditure (Drent & Daan 1980). The extent to which activity budgets are affected by changes in prey availability therefore depends not only upon the degree of change but also upon the initial prey abundance.

Changes in chick growth and fledging weight, breeding success and adult survival are all thought to show a similar dependance upon both the magnitude and the range of changes in food supply (Cairns 1987a). Reductions in prey availability generally result in poorer chick growth (Harris 1969; Barrett & Runde 1980; Cairns 1987b) and lower maximum chick weights (Gaston 1985). Breeding success declines as food supply decreases (Lid 1980; Anderson, Gress & Mais 1982; Schaffner 1986; Springer et al. 1986) and complete breeding failures due to food shortage have occurred in many regions (e.g. Lid 1980; Duffy 1983; Schreiber & Schreiber 1984). Chick growth is

generally more sensitive than breeding success to reductions in prey availability. Adult mortality increases only in conditions of very poor food supply (Cairns 1987a).

Most seabirds breed in large mixed-species colonies, where the potential exists for inter- and intraspecific competition for food (Ashmole 1963; Cody 1973; Whittam & Siegel-Causey 1981; Squibb & Hunt 1983; Birkhead & Furness 1985; Hunt, Eppley & Schneider 1986). Competition among animal communities is very difficult to demonstrate (Krebs 1978). However, seabirds often consume substantial proportions of fish stocks around colonies (Schaefer 1970; Wiens & Scott 1975; Furness 1978b; Furness & Cooper 1982; Montevecchi, Birt & Cairns 1988). Evidence concerning depletion of prey (Birt et al. 1987) and distributions of colonies (Furness & Birkhead 1984) suggests that in some cases at least they do compete for food. A reduction in food supply should increase competition, and consequently the partitioning of food type and size between species. The diets of seabirds in the Barents Sea showed little evidence of such a change following a major decrease in stocks of capelin Mallotus villosus (Barrett & Furness 1990). However, changes in the diets of seabirds have been recorded in association with reductions in prey availability (Hislop & Harris 1985; Montevecchi et al. 1988).

The effects of reduced prey availability upon seabirds are likely to vary according to the breeding ecology of each particular species. The features which are likely to make species more susceptible to perturbations in their food supply were listed by Furness & Ainley (1984). They are:

1. Surface feeding habits,
2. Specialized and inflexible feeding habits,

3. Limited foraging ranges,

4. Limited ability to increase time spent foraging,

5. Energetically expensive food-searching techniques.

The recent decline in stocks of sandeels around Shetland has affected the breeding ecology of most of the seabird species breeding there. These effects include changes in diet (Martin 1989; Furness 1989; Bailey et al. in press) and major reductions in breeding success (Ewins et al. 1988; Heubeck 1989; Monaghan et al. 1989; Bailey et al. in press). However, not all species have been affected equally. Guillemots Uria aalge and shags Phalacrocorax aristotelis maintained high proportions of sandeel (95% or more) in their diet and had similar breeding success in all years recorded between 1975 and 1988 (Bailey et al. in press). This appears to reflect their ability to forage at greater depths than other species (Barrett & Furness 1990), possibly taking sandeels from the seabed (Wanless, Burger & Harris in press).

The proportion of sandeel in the diets of gannets Sula bassana and great black-backed gulls Larus marinus declined from 45% or more during the early 1980s to virtually zero in 1988, without any change in breeding success (Bailey et al. in press). This presumably reflects their ability to switch to alternative prey, such as herring (gannets) and whitefish discards (great black-backed gulls) (Hudson & Furness 1988; Furness 1989; Heubeck 1989; Martin 1989).

Arctic terns Sterna paradisaea are comparatively small seabirds which spend a high proportion of their time foraging (Pearson 1968). They showed reduced breeding success in Shetland in years when other species were apparently unaffected, and have suffered virtually complete breeding failure in Shetland every

year since 1983 (Monaghan et al. 1989).

Great skuas are a comparatively large species, and during the 1970s they spent a small proportion of the available time foraging (Furness & Hislop 1981). Furthermore, they are highly adaptable feeders, taking whitefish discards when sandeels are not available (Furness & Hislop 1981; Hudson & Furness 1988) and the large colonies of other seabirds on Foula provide abundant alternative prey. Furness & Hislop (1981) predicted that great skuas might respond to any decline in the availability of sandeels around Shetland by increasing their predation upon other seabirds, and this would have important implications for seabird conservation within Shetland.

Recent declines in sandeel availability would also be expected to lead to an increase in the time and effort great skuas spend in foraging. However, foraging can be costly to adults (Reznick 1985; Ricklefs 1990) and according to life history theory, long-lived iteroparous species should not prejudice future breeding opportunities for the sake of a single breeding episode (Goodman 1974; Pianka 1976). Great skuas on Foula would thus not be expected to increase their reproductive effort beyond any ability to buffer themselves against reduced survival or lower future breeding success.

The long-term studies of great skuas on Foula, which started during a period of rapid population growth and high breeding success, have provided detailed data on the breeding ecology of this population at a time of apparently abundant food supply. In addition, large-scale ringing of great skua chicks on Foula meant that by 1987 about half the adult great skuas breeding on Foula carried British Trust for Ornithology monel rings, from which their age could be determined. This background

provided an opportunity to study the changes in ecology that occurred as sandeel stocks in Shetland declined. In particular, it provided the opportunity to examine the breeding ecology of birds of different ages at a time when reduced food supply caused a large reduction and an increased variance in breeding success.

It is important to point out that great skuas on Foula had exceptionally high breeding success in the 1970s compared with other skua populations. The situation that has arisen in the late 1980s, where their breeding success is lower, is probably more typical for skuas.

The following chapters deal with different aspects of the breeding ecology of great skuas on Foula over the period of declining sandeel stocks. An ability to distinguish males and females was considered important for this work, and Chapter 2 describes the methods used to sex great skuas. Chapter 3 gives details of changes in breeding ecology over a seventeen-year period from 1973 to 1989, and examines them in terms of the predictions of life history theory. Chapter 4 assesses whether there is any evidence of a decline in survivorship of great skuas during the 1980s. Chapter 5 concerns the influence of age upon the responses of adults to changes in food supply. Chapter 6 explores the opportunity which recent changes in Shetland provide for novel insights into the factors determining the degree of brood defence displayed by great skuas, and tests several hypotheses concerning variation in brood defence. Chapter 7 assesses whether, under the conditions of stress associated with a major decline in food supply, the breeding performance of great skuas on Foula is affected by the relatively high tissue mercury concentrations which they are

known to exhibit. Finally, Chapter 8 discusses the findings of the previous five chapters in the context of responses of seabirds elsewhere to reductions in prey availability.

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CHAPTER 2

Sexing Great Skuas by discriminant analysis
using external measurements

This chapter constitutes a paper entitled "Sexing great skuas <u>Catharacta</u> <u>skua</u> by discriminant analysis using external measurements" by K.C. Hamer and R.W. Furness, in press in <u>Ringing</u> <u>&</u> <u>Migration</u>.

2.1 SUMMARY

A discriminant function used to sex great skuas at Foula, Shetland correctly classified 87.5% of the sample from which it was derived, and several lines of evidence suggest that it performed similarly with a sample of live birds caught over a three-year period. There was no evidence that any of the variables used in the analysis changed during the period of the study or were affected by conditions at the colony during birds' development. However, this may not be the case with birds caught in future years.

Culmen length was correlated with age, and so was not suitable for inclusion in the analysis. The discriminant function derived by one worker performed comparatively poorly with a sample of birds measured by a different worker, despite the fact that their measurements were in close agreement with each other. Great caution should be applied in the use of discriminant functions, particularly when a function has been derived by a different worker.

2.2 INTRODUCTION

Discriminant analysis is a very effective technique for categorising unknown individuals (Klecka 1975; Norusis 1988), and is widely used as a means of determining sex in species of bird with monomorphic plumage (e.g. Dunnet & Anderson 1961; Anderson 1970; Mills 1971; Fox, Cooper & Ryder 1981; Green 1982; Reese & Kadlec 1982; Scolaro, Hall & Ximenez 1983; Coulson et al. 1983; Maran & Myers 1984; Brothers 1985; Hanners & Patton 1985; Monaghan & Metcalfe 1986; Scolaro 1987; Wood 1987; Kavanagh 1988; Malacalaza & Hall 1988; Okill, French & Wanless 1989). The technique involves measuring several morphometric variables for birds of known sex (usually determined by internal examination) and using discriminant analysis to combine and weight the variables in such a way that males and females are statistically as distinct as possible. It does this by forming a linear combination of variables, termed a discriminant function, which can then be used to predict the sex of unknown cases (Norusis 1988).

The effectiveness of the discriminant function is generally assessed from the proportion of cases of known sex which were classified correctly by the analysis (Norusis 1988). However, this can be misleading if certain assumptions concerning the comparability of data in the groups of known and unknown sex are not met (Fox et al. 1981), and there are few studies which test the applicability of discriminant functions to novel sets of data.

If morphometric variables change with age, then the classification of individuals by the analysis may be influenced more by age than by sex. Growth of morphological characters between age classes has been demonstrated in the case of bill

depth (Coulson et al. 1981) and wing length (Pienkowski & Minton 1971; Jones 1987), and Allaine & Lebreton (1990) found slight evidence for an increase with age in one index of body size among adult black-headed gulls Larus ridibundus.

The sizes attained by adults also depend in part upon conditions during development (Batt 1980; Coulson et al. 1981), so that individuals raised in different locations or in the same location in different years may have different morphological characteristics. Furthermore, characters such as weight and wing length, which are partially non-skeletal, can change in individuals with season (Pienkowski & Minton 1973; Johnson 1985) and in response to changes in environmental conditions (Coulson, Duncan & Thomas 1982).

Another problem arises from the fact that differences in the biometrics of males and females are often sufficiently small for systematic errors to be introduced to an analysis as a result of even slight differences in observers' measuring techniques (Barrett et al. 1989).

This paper presents the results of a discriminant analysis used to sex great skuas Catharacta skua, and assesses the reliability of the analysis for determining the sex of live birds measured in different years and by different observers, accounting for the effects of age and conditions during development.

2.3 METHODS

All samples of great skuas were obtained from the largest British colony, at Foula, Shetland. A sample of 40 corpses was obtained from 32 birds shot under licence by crofters and 8 found freshly dead (with little or no dehydration of soft

tissues) at the colony in May or June of 1988. In addition, 199 adults from 186 nests were trapped during incubation between 1988 and 1990 using a clap-net (Spencer 1984) placed at the nest.

All birds were measured by K.C.H. The measurements taken were of the wing (maximum flattened chord), tarsus, culmen, gonys (bill depth at the gonys perpendicular to the cutting edge) and head plus bill, using a stopped wing-rule or Vernier callipers. Wing measurements were made to the nearest 1.0mm, while all others were made to the nearest 0.1mm. Wing and tarsus measurements were both recorded on the right-hand side of the body, to account for possible bilateral asymmetry (McNeil & Martinez 1967; McNeil et al. 1971). In addition, all live birds were weighed to the nearest 50g using a Pesola spring balance.

To assess the measurer's consistency (in accordance with the procedure recommended by Barrett et al. 1989), independent duplicate measurements were taken from a sample of seven non-breeders caught in 1989 with a cannon-net (Spencer 1984) plus three birds caught twice on eggs in different years.

Corpses were sexed by internal examination, and live birds were sexed by a discriminant analysis of morphometric variables. The analysis requires that data are homoscedastic and normally distributed (Norusis 1988), and these were tested using Bartlett's tests and Kolmogorov-Smirnov one-sample tests respectively. To allow variables measured on different scales to be weighted equally by the analysis, all variables were standardized to have sample means of nought and standard deviations of one (Norusis 1988).

Birds' ages and natal colonies were determined where possible from British Trust for Ornithology ring number. For

birds which hatched on Foula after 1974, conditions during development for different cohorts were assessed from indices of chick growth in different years. These compared the weights of chicks of known ages between 13 and 34 days old with those expected from a logistic curve describing the growth of chicks at Foula during the 1970s (Furness 1987). The index produced was the mean difference between the weights of individual chicks and the expected weight derived from this curve. This method is not biased by differences in the mean ages of samples, and no sample differed significantly in its median hatching date (see Hamer, Furness & Caldow in press).

All birds trapped on eggs were given a unique combination of four coloured plastic leg rings. Their sexes were determined, in addition to using discriminant analysis, by comparison in the field of size and plumage with those of their mates (females are generally paler and almost invariably larger than their partners; Furness 1987). The sexes of birds at 52 territories were assessed by this method on three occasions, and only cases where all three assessments were in accordance were used in subsequent analyses.

To assess the applicability of the discriminant function derived from this study to samples of Great Skuas measured by other workers, the function was used to classify a sample of 41 adults shot at Foula in 1980 and measured and sexed by internal examination by R.W. Furness (data presented in Furness 1982). The comparability of measurements taken by K.C.H. and R.W.F. was determined by independent measurement of a sample of live Great Skuas caught with a cannon-net at Foula in 1989.

2.4 RESULTS

Table 2.1 shows mean values and ranges for each variable, for males and females of the 40 birds which were sexed by internal examination. Wing and tarsus length showed a significant difference between sexes (t-tests using pooled variance estimates; t = 5.3, P < 0.01 and t = 2.5, P = 0.02 respectively, with 38 degrees of freedom in each case). However, all variables showed considerable overlap between males and females (Table 2.1).

TABLE 2.1. Morphometric data for male and female great skuas used in a discriminant analysis to determine sex. All measurements are in mm.

	Female			Male			
	mean	S.D.	range	mean	S.D.	range	r
wing	422.4	5.1	412-435	414.8	5.8	404-424	0.87
tarsus	70.5	1.4	67-72	69.4	1.3	67-71	0.54
head+bill	111.4	2.5	108-119	110.6	2.4	107-116	0.20
culmen	48.9	1.5	46.7-52.3	48.2	1.3	46.5-52.1	0.21
gonys	17.7	0.5	16.7-18.7	17.6	0.7	16.4-19.0	0.27

n = 22 females plus 18 males. r is the coefficient for pooled within-groups Pearson correlations between each morphometric variable and the discriminant function giving maximum separation of sexes.

All data were homoscedastic and normally distributed (P > 0.05 in all tests). The analysis was able correctly to classify 35 (87.5%) of the birds of known sex, according to their scores on the following discriminant function, with the vector of the function set at D = 0:

D = 0.41tarsus + 0.17wing - 0.17head - 79.1

where $\underline{D}$ is Mahanalobis distance (Norusis 1988) and head is head+bill length. Birds with positive scores were classified as female (great skuas show reversed sex size dimorphism), and those with negative scores as male. The negative coefficient for head+bill length does not indicate that this variable is shorter in females, but that they have smaller values relative to wing or tarsus lengths; i.e. it reflects a difference in shape rather than size.

Culmen and gonys lengths were omitted from the equation, because they did not add to the discrimination between males and females in the sample of known sex (neither produced a significant decrease in Wilks' lambda; Norusis 1988). The ability of a variable to discriminate between sexes depends in part upon its correlations with other variables, and a better indication of discriminating ability than its inclusion or omission from the equation is given by the correlation between a variable and the discriminant function (Table 2.1). These indicate that wing length is the most powerful variable, followed by tarsus, gonys, culmen and head+bill respectively.

TABLE 2.2. Original and duplicate measurements from ten live great skuas.

	first		duplicate		difference		proportion of
	mean	S.D.	mean	S.D.	mean	S.D.	original (%)
wing	422.2	11.3	423.2	12.3	2.60	2.12	0.6
tarsus	67.3	1.7	67.7	1.6	0.80	0.41	0.6
head+bill	110.1	1.7	109.9	1.3	0.88	0.74	0.7
culmen	50.6	2.2	50.1	1.7	0.77	0.65	1.5
gonys	17.6	0.6	17.6	0.6	0.07	0.11	0.4

S.D. is the standard deviation of each mean.

The differences between first and duplicate measurements of live great skuas were calculated for each bird on a pair-wise basis, and the mean differences are presented in Table 2.2. No difference was greater than 1.5% of the original measurement.

Table 2.3 shows the function score and sex obtained from the two sets of measurements for each bird. In every case, the classification according to original and replicate measurements was the same.

TABLE 2.3. Function score and sex derived from a discriminant analysis for two independent sets of measurements from ten live great skuas.

Case	First		Second	
Number	Score	Sex	Score	Sex
1	1.66	Female	1.57	Female
2	0.40	Female	1.83	Female
3	2.31	Female	2.58	Female
4	2.72	Female	4.62	Female
5	-1.93	Male	-1.18	Male
6	-0.84	Male	-0.60	Male
7	-0.60	Male	-0.60	Male
8	-1.33	Male	-1.42	Male
9	-1.92	Male	-3.01	Male
10	-4.29	Male	-2.98	Male

The analysis classified all cases with positive scores as females and those with negative scores as males.

Table 2.4 shows weights and wing lengths of live birds in each year. There was no difference between years in weights (one-way analysis of variance; F ratio = 1.05, n = 199, P = 0.35) or in wing lengths (Kruskal-Wallis analysis of variance with heteroscedastic data; Chi-square = 1.31, n = 199, P = 0.52).

TABLE 2.4. Wing length in mm and weight in g for great skuas caught on eggs in different years.

Year	n	wing		weight	
		mean	S.D.	mean	S.D.
1988	120	424.8	8.4	1402.1	101.8
1989	55	426.8	12.7	1425.5	104.3
1990	24	427.2	8.8	1410.4	73.6

S.D. is the standard deviation of each mean.

Of the 239 birds in this study, 105 had been ringed as chicks, all on Foula. Table 2.5 shows the coefficients and associated probabilities for Pearson correlations between each morphometric variable and age. There was a significant correlation in the case of culmen length, which decreased with age. None of the variables measured were correlated with chick growth index (Table 2.5).

TABLE 2.5. Coefficients and associated probabilities for Pearson correlations between morphometric variables and age or chick growth index.

	Age		Chick growth index	
	n = 105		n = 72	
	r	P	r	P
wing	0.12	0.23	0.06	0.64
tarsus	-0.14	0.20	0.07	0.59
head+bill	-0.17	0.09	0.05	0.65
culmen	-0.21	0.04	0.07	0.56
gonys	0.03	0.83	0.13	0.28
weight	0.02	0.82	-0.10	0.41

n is the sample size. See text for method of determining chick growth index.

The numbers of birds classified respectively as females or males by the discriminant analysis were 70 and 50 in 1988, 31 and 24 in 1989, and 16 and 8 in 1990. There was no difference between years in sex ratio (Chi-square = 0.76, P = 0.68 with 2 degrees of freedom). Over all three years, 117 birds were classified as females and 82 as males. This ratio is significantly different from 1:1 (Chi-square = 6.16, P = 0.01 with one degree of freedom).

Of the 199 birds caught on eggs, 26 were at nests where both adults were caught in different years. The two partners at a territory were assigned different sexes by the analysis in all but two cases (i.e. at 84.6% of territories). Both cases of non-accordance were at nests where both partners were classed as males.

An attempt was made to determine the sexes of colour-ringed birds by multiple comparisons of size and plumage shade between partners at 52 territories. No clear difference was discernible between partners in 13 cases. Of the remaining 39, replicate observations were in agreement with each other in 36 cases (92.3%), of which 31 (86.1%) were in accordance with the discriminant analysis. Cases of non-accordance had lower absolute function scores (whether positive or negative) than those where the two methods were in agreement (mean score = 0.6 and 1.5 respectively; t-test using separate variance estimate, t = 4.83, P < 0.001 with 23.1 degrees of freedom).

A sample of 24 great skuas was caught with a cannon-net in 1989 and measured independently by K.C.H. and R.W.F. The mean difference between measurers was 0.3mm for wing length, 0.2mm for head+bill and -1.1mm for tarsus length (the negative difference indicates that measurements taken by R.W.F. were the

longer of the two). Data presented by Furness (1982) do not include head+bill length, and a discriminant analysis using wing plus tarsus length for birds shot in 1988 was able correctly to classify 82.5% of cases. However, its success with the sample of birds shot in 1980 and measured by R.W.F. was only 70.7%. Most of this difference in success was due to the discrepancy between measurers in tarsus length, since wing length alone was able correctly to classify similar proportions of both samples (77% and 73% respectively) and achieved higher success than a combination of wing and tarsus length with the sample measured by R.W. Furness (73% as opposed to 71%).

2.5 DISCUSSION

Non-passerine migratory species diplay seasonal variation in characters such as weight and wing length, which are not wholly skeletal (Pienkowski & Minton 1973; Johnson 1985). All birds in this study were caught or killed during May or June. Such characters can also alter as a result of changing conditions at the colony (Coulson et al. 1982). The size and density of the great skua colony on Foula did not change during the period of the study and there were no differences in the weights or wing lengths of birds caught in different years (Table 2.4). Furthermore, the small sample (three individuals) of birds which were caught twice in different years were classified similarly on each occasion (Table 2.3).

There was no evidence that the morphometrics of birds caught as adults between 1988 and 1990 have been affected by conditions during their development (Table 2.5). This probably reflects the fact that they all hatched in years of abundant

food supply and high breeding success (Furness 1987; Hamer et al. in press).

Culmen length decreased significantly with age (Table 2.5). While the biological significance, if any, of this relationship is unclear, it suggests that culmen length is not a good variable to use in a discriminant analysis with birds of different ages. Culmen length was not included in the discriminant function.

The analysis classified significantly more birds as female than as male (see results). This presumably reflects the fact that female great skuas spend more time incubating than males (Furness 1987) and so are more likely to be caught on eggs.

There were no differences in the ratios of sexes as determined by the analysis in different years (see results). This suggests that the discriminant function based upon birds sampled in 1988 was not systematically misclassifying birds in succeeding years. This view is supported by the accordance in the sexes ascribed by the analysis to partners caught in different years, which was within three percent of the proportion of birds of known sex which were classified correctly by the analysis (see results). Two partners ascribed different sexes could both have been classified incorrectly, but this is unlikely. The fact that both cases of non-accordance were at nests where both birds were classified as males suggests that the discriminant function was biased slightly against females.

For those cases where partners could be distinguished clearly on the basis of size and plumage colour, this method of sexing was in agreement with the discriminant analysis on 86.1% of occasions. This further indicates that the discriminant function was able to classify new birds approximately as well as

those of known sex. It is not certain whether, even in cases where partners can be clearly distinguished, sexing by comparison within pairs is perfectly accurate, although Ainley, Spear & Wood (1985) found with south polar skuas Catharacta maccormicki that in every case the bird they identified as the larger of a pair was the female.

Cases with smaller function scores are more likely to be misclassified (by definition), and were more likely to disagree with the sex determined by comparison of partners (see results). This does not necessarily suggest that comparing mates is a more accurate method, but it does indicate that the two methods may be used in conjunction to identify individuals which are most at risk of being misclassified. These can then be selected for further study involving a more detailed and time-consuming analysis of behaviour (Pierotti 1981; Burger 1987).

While the evidence from this study indicates that the ability of the discriminant function to sex live birds was similar to its success with birds of known sex, this may not be the case with birds caught in the future or measured by other workers. The discriminant function based upon birds measured by K.C.H. achieved comparatively poor success (12% lower) with a further sample measured by R.W.F., despite the fact that wing lengths measured on the same birds were almost identical and tarsus lengths differed on average by only 1.1mm between measurers (see results). Furthermore, great skuas on Foula have recently experienced a series of years with poor chick growth and low breeding success (Hamer et al. in press), and this might be expected to affect both the wing lengths of established adults and the sizes of adults recruiting to the colony in future years. I therefore advocate great caution in the use of

discriminant functions, particularly when a function has been derived by a different worker.

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CHAPTER 3

The effects of changes in food availability on the
breeding ecology of Great skuas in Shetland

A condensed version of this chapter constitutes a paper entitled "The effects of changes in food availability on the breeding ecology of great skuas Catharacta skua in Shetland" by K.C. Hamer, R.W. Furness and R.G. Caldow, in press in Journal of Zoology London.

3.1 SUMMARY

Great skuas on Foula, Shetland have responded to a decline in the availability of sandeels since the late 1970s by increasing the proportion of other items in their diets. This change is correlated with the annual recruitment of sandeels in Shetland waters. Since 1983 there has been a ten-fold increase in predation by great skuas upon other seabirds, as Furness & Hislop (1981) suggested might occur in response to a low availability of sandeels.

Changes in diet have been accompanied by a 50% reduction in adult territorial attendance as adults increased their foraging effort, such that between 1987 and 1989 breeding adults were probably working as hard as they were able to. Despite this, breeding success was less than 40% in 1987 and less than 15% in 1988 and 1989.

The major cause of breeding failure was predation of unguarded chicks by adults from neighbouring territories. The willingness of adults to expose their chicks to high predation risk is probably maintained because of a positive correlation between chick pre-fledging growth and post-fledging survival, which is expressed up to the age of two years and which will place a strong pressure upon adults to feed their chicks as well as possible.

The high expenditure of effort by adults in 1987 and 1988 did not affect the weights of those birds incubating eggs in 1988 and 1989, but there was a slight (3%) decrease in egg size between the late 1970s and the late 1980s. Changes in the age structure of the breeding population and the absence in 1989 and 1990 of almost a third of adults colour-ringed during incubation

in the previous year suggest an increase in the rate of egress since the 1970s. These changes probably represent an increase in the long-term costs of reproduction to adults at this colony.

3.2 INTRODUCTION

Life-history theory envisages reproduction as a costly process, in which breeding individuals need to balance the demand for allocating resources to rearing young against the demands of maintaining body condition (Williams 1966; Gadgil & Bossert 1970). Optimal reproductive tactics should serve to maximise each individual's life-time reproductive success (Pianka 1976), and there should be an inverse relationship between reproductive effort in any one year and the expectation of future offspring, if reproduction subjects breeding individuals to risk (Goodman 1974). Several empirical studies (reviewed by Reznick 1985) support the notion of costs to high levels of reproductive effort, although Tuomi, Hakala & Haukioja (1983) suggested that adults can often buffer themselves against the demands of reproduction, for instance by storing food reserves for use during breeding. Manipulation of brood sizes in birds (Nur 1984; Reid 1987) has produced evidence of increased costs to adults in terms of lower survival after increased reproductive effort. However, Pettifor, Perrins & McCleery (1988) shed doubt upon Nur's results, and other manipulative experiments (Browne 1982; Feifarek, Wyngard & Allen 1983) have suggested that reproduction may be costly only when adults are subjected to extra stress, or when food availability is limited.

Great skuas Catharacta skua in Shetland enjoyed high breeding success and steady population growth in the 1970s (Furness 1987), due mainly to an abundance of sandeels Ammodytes

<u>marinus</u> (Furness & Hislop 1981; Furness 1987). During this period, adults spent a small proportion of the available time foraging (Furness & Hislop 1981). Since the 1970s there has been a marked decline in the availability of sandeels around Shetland (Gauld, McKay and Bailey 1986; Hudson & Furness 1988; Monaghan, Uttley & Burns 1988; Harris & Wanless 1989) and great skuas may be expected to respond to this decline in resource availability by increasing the foraging component of their reproductive effort. However, they are a long-lived iteroparous species, and so should not increase their effort in one season beyond their ability to buffer themselves against reduced survival or lower future breeding success.

This chapter presents up to 16 years of data on various aspects of the breeding ecology of great skuas in Shetland. It examines the ways in which adults have responded to changes in sandeel availability, and the repercussions of these changes upon annual breeding statistics and long-term reproductive potential.

3.3 METHODS

Data were collected from the largest British colony of great skuas, at Foula, Shetland. Data for 1987 were collected mainly by R.G. Caldow, for 1988 - 1990 by K.C. Hamer and for all other years mainly by R.W. Furness. Each worker used essentially the same methods, with some slight differences in protocol (see Furness 1977 and Caldow 1988).

Nests situated in an area of approximately 350 hectares in the north-east of the island (Fig. 3.1) were located between 10th May and 10th June each year, by searching within territories of birds behaving aggressively towards the observer,

42

FIG. 3.1. Map of Foula, showing 100m contours, settlements, residences used during the study (solid squares) and study area (hatched).

400

300

200

100

Ham

Hametoun
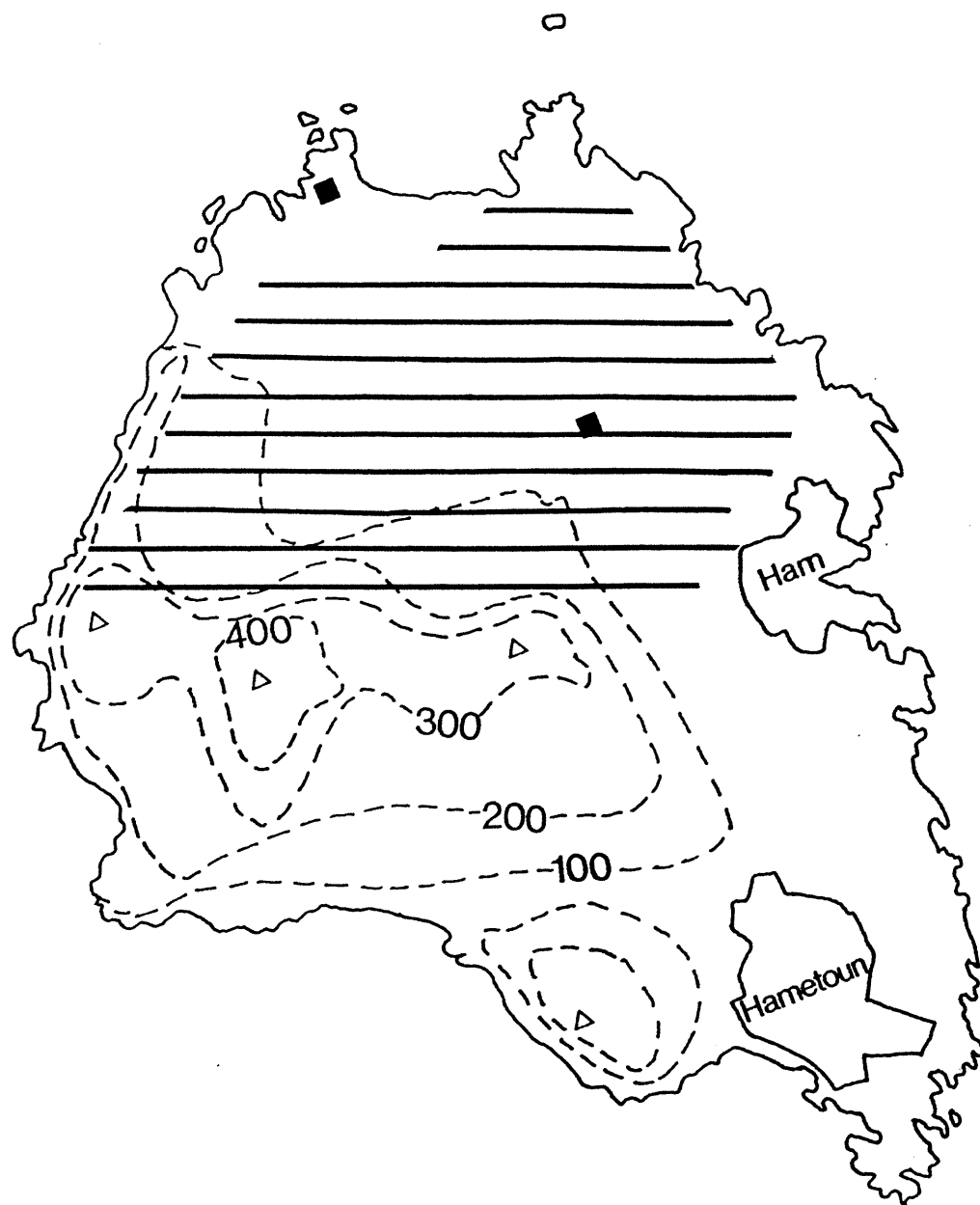
0 ━━━━━━ 1km.

and by watching from a distance through binoculars for birds incubating eggs. Once located, nests were marked with a numbered cane placed at least 5m from the nest cup. To reduce disturbance, no attempt was made to locate all the nests in an area.

Information regarding the diets of both chicks and non-breeders was obtained for every year except one between 1973 and 1989 while data regarding the diets of breeding adults were obtained in 1989. The diets of great skuas on Foula show considerable seasonal variation (Furness & Hislop 1981), and comparisons between years were made on the basis of data collected between 1st and 15th July each year. This corresponds with the middle of the chick-rearing period.

The diets of chicks were determined from samples of food regurgitated during handling, and identified as sandeel, whitefish (mainly gadoids) or bird meat. Diets of adults and non-breeders were assessed by collection and identification of regurgitated pellets containing the non-digestible elements of their food. These were gathered on a weekly basis from marked areas of non-breeder gathering sites (clubs) and, in 1989, from marked territories. Breeding adults exclude other birds from their territories, and other species very rarely use club sites, so there is little chance of mistaking the source of pellets collected at territories or clubs (Furness & Hislop 1981). Pellets containing feathers or fur are more durable than those consisting of fish bones, and this bias was minimised by collecting pellets at weekly intervals (Furness & Hislop 1981).

Each pellet generally contained only one food type. Those containing fish remains usually included otoliths (sagittae), which provide accurate determination of fish species (Harkonen

1986). Otoliths have been widely used to assess the proportions of different fish species in the diets of seabirds (Ainley, Anderson & Kelly 1981; Duffy, Wilson & Wilson 1987; Gales 1988), but can underestimate the representation of fish with small otoliths (Johnstone et al. 1990). Fish remains regurgitated by great skuas were identified, from otoliths and other bones, as either sandeel or whitefish. Otoliths comprised a small proportion of the material in each pellet, so that cases where otoliths were not regurgitated were not excluded by this method.

Eggs were identified to species from shell colour and pattern, and bird remains were identified at least to family level from feather shape and colour. The few pellets containing remains of rabbits Oryctolagus cuniculus, house mice Mus domesticus, barnacles Lepas sp. or mussels Mytilus edulis were easy to identify.

The relationship between chick diet and sandeel availability was examined using data from The Department of Agriculture and Fisheries for Scotland concerning sandeel recruitment in Shetland waters (Kunzlik 1989).

Most of the time which great skuas spend away from their territories is used for foraging (Furness 1987). The attendance of adults at their territories can therefore be used as an index of the ease of obtaining food (Furness & Hislop 1981). Territorial attendance of adults was determined at three stages of the breeding season in 1987, 1988 and 1989 and at one stage in 1976. These were during incubation, the first two weeks post-hatching and the rest of the pre-fledging period. Attendance was determined by walking round marked study territories and counting the number of adults at each one. This was facilited by the fact that great skuas defend their

territories agressively against intruders (see Chapter 6), and the identity of adults was confirmed, where possible, from colour-ring combinations (see below). In the few cases where the number of adults present could not be readily determined in this way (where adults did not defend their territories against the observer), attendance was determined by observation, from a distance and using binoculars, of adults settling in their territories. Detailed analysis of time-budgets indicated that this method gives an accurate measure of territorial attendance (Furness & Hislop 1981). Data were used to produce a mean value for the number of adults attending territories with live chicks, and the proportion of occasions when both adults were absent from a territory simultaneously.

To assess whether this method gave an accurate representation of adult territorial attendance, a sample of 30 marked teritories was observed with a telescope throughout an eight-hour period during chick-rearing in 1988. The number of adults present at each territory was noted at hourly intervals between 10 a.m. and 5 p.m.

Breeding success of great skuas was determined in 1975, 1976, 1987, 1988 and 1989, using methods described by Furness (1983; 1984). Where laying sequence was known, eggs at marked nests were marked 'A' or 'B' with a non-toxic indelible marker; where unknown, they were marked 'a' or 'b'. Single eggs were revisited at intervals of 1-3 days for up to a week to determine whether a second egg had been laid. All eggs were measured (maximum length and maximum width to the nearest 0.1 mm, using Vernier calipers).

The median hatching date for eggs of great skuas on Foula is around the middle of June (Furness 1987). All study nests

were visited during the first week of June each year, and at 5-10 day intervals thereafter, to determine hatching success. Eggs which disappeared before 1st June were assumed to have suffered predation, and this was generally confirmed from the presence of broken egg shell and egg contents in or near the nest cup. Predation was also assumed in all cases where an egg disappeared more then five days before its sibling hatched, or where remains of eggs which had appeared healthy on the previous visit to the territory were found in the vicinity of the nest, or where no chicks were ever seen and the parents ceased to be aggressive after their clutch disappeared.

Pairs which suffered clutch predation were visited along with other territories throughout the breeding season, to determine whether they laid a replacement clutch. If so, its fate was followed in the same way as for other clutches.

The viability of eggs was assessed during the later stages of incubation by shaking them gently, to determine whether their contents were reasonably solid, and so viable, or liquid, and so 'addled' (infertile or the result of embryo death). Eggs in the latter category were also identified by the appearance of pale spots on the shell surface, and by adults continuing to incubate eggs well beyond the normal incubation period of 26-32 days (Cramp & Simmons 1983).

Hatching dates were determined by direct observation or from the ages of recently-hatched chicks. These were obtained from a table of conversions of maximum wing chord, excluding down (Furness 1977).

All chicks with wing lengths greater than 30mm were fitted with a British Trust for Ornithology ring, to allow identification of individuals. The identity of unringed chicks

was determined from proximity to a nest and its contents, the identity of the adult(s) defending it (if colour-ringed) and the agreement between the two methods of determining its hatching date.

Study territories were visited at intervals of 10-20 days during chick-rearing, to search for chicks. Searching continued until all chicks which had hatched and not definitely died had been found, or until the territory had been thoroughly covered. Chicks found were measured (maximum wing chord, excluding down, to the nearest mm, with a stopped rule) and weighed to the nearest gram using a Pesola spring balance.

Ringed chicks found dead were noted and age at death determined from wing length or straightened leg length (from the inner angle of the intertarsal joint to the tip of the centre toe nail, used in cases where only legs were found) by reference to tables of conversions (Furness 1977). Chicks which were not found on at least three consecutive visits to territories where the parents had ceased to be aggressive were assumed to be dead (Furness 1984). Chicks which were first unfound on the penultimate or ultimate rounds of nests were revisited the day after the last round each year to confirm that they were absent. The period from hatching to fledging for great skuas is 40-51 days (Cramp & Simmons 1983), and chicks were regarded as having fledged if they flew off when approached or if they were older than 46 days (as determined from wing length).

Variations between years were examined in terms of chick growth and post-fledging survival as well as chick production and survival to fledging. In excess of 10,000 great skua chicks were weighed and measured on Foula between 1975 and 1989, and only chicks between 13 and 34 days old (i.e. on the linear part

of their growth curve; Furness 1983) were used to compare weights of chicks of similar ages in different years.

Poor growth as a chick may have repercussions after fledging. To assess the relationship between chick growth and post-fledging survival, ring recovery data supplied by the British Trust for Ornithology were used to determine the age-specific recovery rates for cohorts of great skuas ringed as chicks on Foula each year between 1963 and 1987 (the latest year for which all required recovery data were available), after correcting for differences between years in fledging success. These were then compared with each year's data for chick growth.

Possible changes in the body condition of adults at the start of the breeding season were examined by determining the weights of incubating adults during May and June in 1979, 1980, 1988 and 1989. These were caught during incubation at marked territories, using a clap-net (Spencer 1984) placed at the nest. To reduce disturbance, no attempt was made to catch more than one adult per pair in any year or to catch an adult at all marked nests. The net was set only in dry weather, and was kept in place for a maximum of 30 minutes at each nest. The net was not set consecutively at two nests within 100 metres of each other, or at nests where either chick had started to hatch.

Captured birds were weighed and measured, and the measurements used in a discriminant analysis (Norusis 1988) to determine sex by comparison with 40 birds (18 females plus 22 males) found dead on Foula and sexed by internal examination (see Chapter 2). All birds caught were also fitted with a British Trust for Ornithology monel ring or, if already ringed, the ring number was noted. In addition, all birds were given a unique combination of four coloured plastic leg rings, before

being released.

To determine whether the disturbance to the colony caused by trapping adults affected birds' breeding success, a sample of 40 nests in a separate part of the study area were marked in 1989 as a control group, where no adults were trapped (see Chapter 5).

Ringed adults caught in 1988 or 1989 had all been ringed as chicks, and so could be aged accurately from their ring numbers. These were used to assess the age structure of the breeding population, after accounting for differences in the numbers and proportions of chicks ringed in different years.

Adults colour-ringed in 1988 or 1989 were located in 1989 and 1990 by searching the study area on consecutive days during the pre-laying period (5 - 15 May). This was continued until no new birds were recorded. Territories where birds marked in previous years were not seen were then visited on two occasions specifically to search for these birds. Finally, the whole island was searched during June each year, to check whether any marked birds had moved their territories out of the study area.

3.4 RESULTS

Diets

During the 1970s and early 1980s great skuas on Foula fed their chicks mainly on sandeels, which have a higher calorific value and contain a smaller proportion of indigestible material than other items in their diet (Table 3.1; Furness & Hislop 1981). From 1983 to 1984 the proportion of sandeel in chicks' regurgitates fell from 95% to 61%, with nearly all of the difference being compensated for by an increase in whitefish regurgitates. The situation remained more or less unchanged

between 1984 and 1987, with bird meat comprising between 3% and 6% of the diet. From 1987 to 1988, the proportion of regurgitates comprising sandeel fell from 56% to 5%, while the proportions comprising whitefish and bird meat regurgitates rose from 42% to 77% and from 3% to 18% respectively (Table 3.1).

TABLE 3.1. The percentages of different items in food regurgitated by great skua chicks on Foula between 1st and 15th July, for every year from 1974 to 1989.

Year	n	Sandeel(%)	Whitefish(%)	Birdmeat(%)
1974	90	91	9	0
1975	90	70	28	2
1976	95	86	14	0
1977	56	86	14	0
1978	45	71	24	4
1979	49	73	24	2
1980	69	68	28	4
1981	64	88	6	6
1982	21	95	5	0
1983	41	95	2	2
1984	36	61	33	6
1985	58	62	33	5
1986	61	66	30	5
1987	36	56	42	3
1988	22	5	77	18
1989	21	14	76	10

For every year, n is the number of regurgitates and the number of chicks producing them, since every chick produced a single regurgitate. The percentages refer to the proportions of regurgitates containing each food item. Deviations of the summed values from 100% are due to rounding errors.

These changes are closely associated with changes in sandeel abundance, since there is a positive Pearson correlation between the proportion of sandeel in chicks' diet and the number of sandeels recruited to the Shetland population in the previous year ($r = 0.75$, $n = 15$, $P = 0.001$; Fig. 3.2: this parametric test was used because the data for both diet and recruitment

FIG. 3.2. The percentage of sandeel in regurgitates produced by great skua chicks on Foula between 1st and 15th July of every year from 1975 to 1989 against the number of sandeels, in thousand-millions, recruited in Shetland waters in the previous year. Data for sandeel recruitment are from Kunzlik (1989).
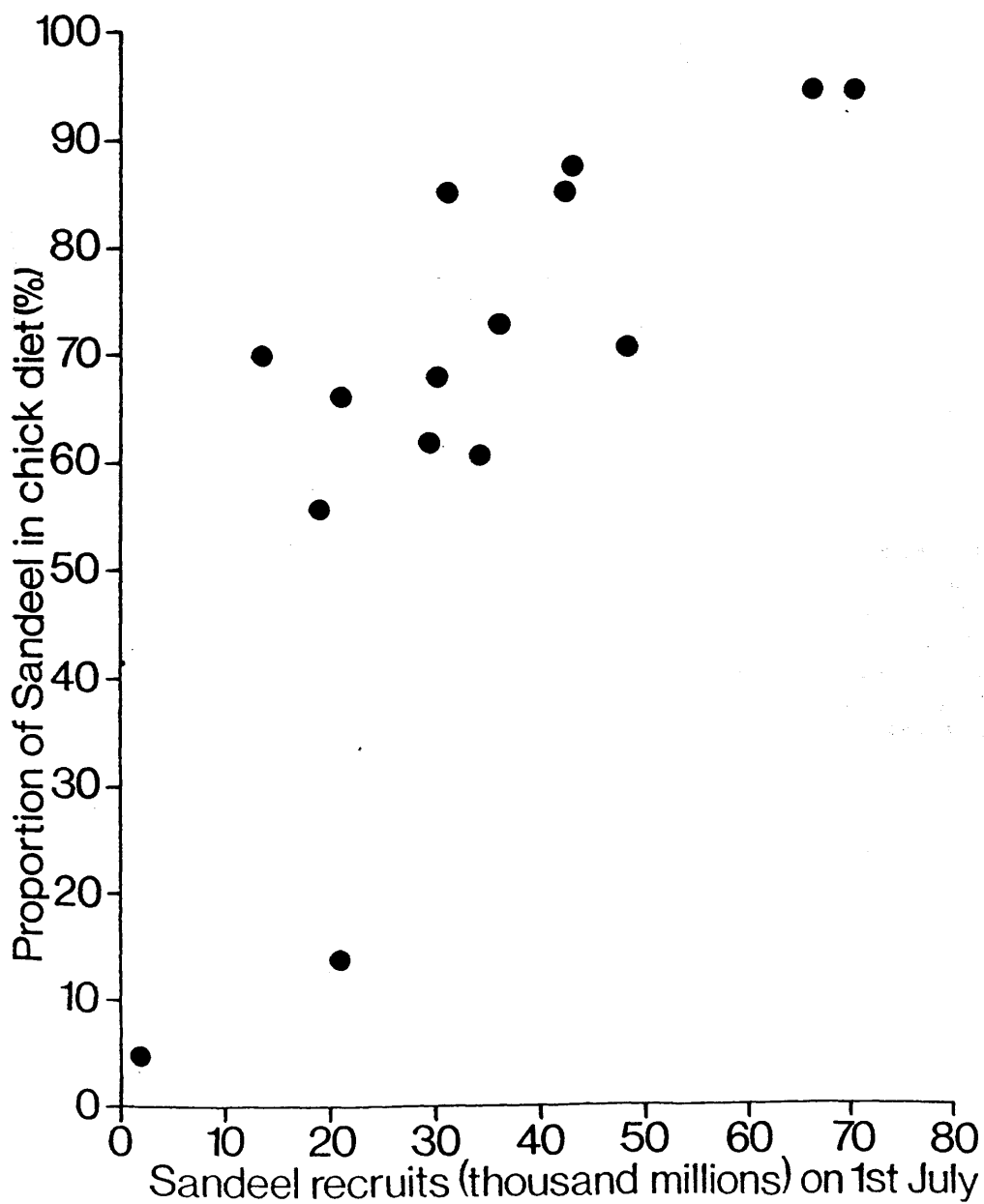
conform to normal distributions, as determined by Kolmogorov-Smirnov one-sample tests. Similar tests were performed on all data before using parametric analyses). Recruitment in the previous year was used because most of the sandeels fed to great skua chicks are one year old (Furness 1987).

TABLE 3.2. Food items in pellets produced by non-breeding great skuas on Foula between 1st and 15th July, for every year from 1973 to 1989 except 1985, and by breeding adults in 1989.

Year	n	Sandeel (%)	Whitefish (%)	Bird (%)	Other (%)
1973	100	71	27	2	0
1974	100	24	71	5	0
1975	100	21	69	6	4
1976	100	72	26	2	0
1977	100	59	35	4	2
1978	100	64	35	1	0
1979	100	41	54	3	2
1980	100	17	74	6	3
1981	100	18	77	4	1
1982	100	13	80	3	4
1983	305	9	70	17	4
1984	100	0	74	23	3
1986	200	0	82	14	5
1987	98	9	77	10	4
1988	200	0	73	24	4
1989	247	4	62	30	4
1989(B)	549	1	69	29	2

For every year, n is the number of pellets analysed. The number of birds producing these pellets is similar to the number of pellets in the case of non-breeders, while the sample for breeding birds was collected from 50 territories. The percentages refer to the proportions of pellets containing each item. 'Other' items were marine invertebrates, rabbits, mice, fulmar Fulmarus glacialis eggs or great skua eggs. 1989(B) refers to breeding adults.

The diet of non-breeders on Foula shows a similar change to that of chicks, with a gradual decline in the representation of sandeel being balanced by an increase in the proportion of whitefish, and latterly of birdmeat, in the diet. The increase in the representation of birdmeat in the diet of non-breeders

was equally marked but occured five years earlier than that in the diet of chicks (Table 3.2). In 1989 the proportions of sandeel and birdmeat in the diet of breeding adults were very similar to those in the diet of non-breeders but not to those in the diet of chicks (Tables 3.1 and 3.2).

Adult territorial attendance

The changes in the diets of chicks between 1976 and 1989 were accompanied by marked changes in the territorial attendance of adults. In 1987, 1988 and 1989, the mean attendance was 1.5 adults per territory during incubation and the first two weeks post-hatching, and 1-1.2 adults per territory during the rest of the pre-fledging period (Table 3.3). Comparison with the same stage of the breeding season in 1976 reveals a 50% reduction in territorial attendance between this year and 1987 (Table 3.3).

TABLE 3.3. Territorial attendances of adult great skuas with live chicks on Foula in 1976, 1987, 1988 and 1989.

Year	n	Stage of Season	Mean No. of Birds Present	% nests with both birds absent
1976	160	3	1.47	0.00
1987	60	1	1.54	0.10
"	60	2	1.54	0.00
"	58	3	1.07	10.34
1988	156	1	1.55	1.28
"	150	2	1.52	1.28
"	32	3	1.03	12.50
1989	194	1	1.51	1.55
"	185	2	1.45	1.08
"	90	3	1.17	11.11

For stages of season, 1=incubation, 2=the first two weeks after hatching, 3=the rest of the pre-fledging period. n is the number of observations producing each mean.

Over the same period of time, the proportion of territories with no adults in attendance following the first two weeks post-hatching increased from nought to 10% (Table 3.3). In a test for a difference in the numbers of territories with nought, one or two adults in attendance in 1976 and 1987-89, Chi-square with two degrees of freedom = 35.57, P < 0.0001.

Breeding statistics

During this period there was a small (3%) but significant decrease in egg size (Table 3.4: in a t-test comparing clutches in 1975 with pooled data for 1987-1989, t with 1493 degrees of freedom = 7.88, P < 0.001). Clutch size and hatching success were unchanged (Table 3.5), while fledging success declined from 91.1% in 1976 to 7.8% in 1988 and 16.5% in 1989, with the value for 1987 intermediate (Table 3.5). Visits to the colony in July of every year from 1977 to 1986 indicated, from the number of pairs with chicks, that breeding success in these years was much closer to the values for 1975 and 1976 than to those for later years.

TABLE 3.4. Sizes of eggs laid by great skuas on Foula in 1975, 1987, 1988 and 1989.

Year	n	Mean Length (mm.)	Mean Width (mm.)	Mean Internal Volume (mm.^{3})	Standard Deviation
1975	749	71.07	50.04	85.42	5.77
1987	52	70.67	49.54	83.25	4.96
1988	307	70.62	49.86	84.34	5.12
1989	387	70.32	49.32	82.18	5.68

n is the sample size. Internal egg volumes were calculated from the equation given by Coulson (1963).

TABLE 3.5. Breeding data for great skuas on Foula, between 1975 and 1989.

Year Studied	No. nests Studied	Mean clutch Size	Hatching Success (%)	Fledging Success (%)	Breeding Success (%)
1975	447	1.87	66.1	95.3	63.0
1976	434	1.93	73.3	91.1	67.5
1987	23	1.95	77.7	61.1	35.6
1988	160	1.93	72.3	7.8	5.7
1989	198	1.95	75.2	16.5	12.4

The differences in breeding success between years are not caused by biases in sampling with respect to laying date or location within the colony, since none of the years differed in their median hatching date (as determined by a Kruskal-Wallis one-way analysis of variance) and the same part of the colony was studied each year. The proximate cause of the low breeding success between 1987 and 1989 was high chick mortality due to predation by adults at neighbouring territories. Of 192 ringed chicks found dead in 1988 and 1989, 35 had previously been found alive with injuries, often severe, resulting from attacks by neighbouring adults, and many more chicks, both ringed and unringed, were found injured than starved. Nearly all dead chicks, including 185 of the 192 with rings, were partially eaten when found. This predation was possible because both parents foraged simultaneously, unlike in previous years, when females stayed on their territories and guarded their chicks (Furness 1987).

Chick growth and post-fledging survival

During the 1970s the growth of great skua chicks on Foula followed a logistic curve (Furness 1987). Table 3.6 shows the

weights of chicks between 13 and 34 days old for every year between 1975 and 1989, expressed in terms of the mean difference between the weights of individual chicks and the expected weight derived from this curve. This method is not biased by differences in the mean ages of samples, and no sample differed significantly in its median hatching date. Chick growth was significantly better in the period 1975-1986 than during 1987-1989 (in a t-test on pooled data, t with 12644 degrees of freedom = 35.32, P < 0.001). Differences between years in chick growth are strongly associated with differences in sandeel availability, since the growth of chicks is positively correlated with the percentage of sandeel in their diets (r = 0.72, n = 15, P = 0.002; Fig. 3.3).

TABLE 3.6. Mean differences in grammes between the observed and expected weights of great skua chicks between 13 and 34 days old on Foula in different years.

Year	n	Mean	S.D.
1975	1049	+30.4	65.6
1976	1171	0.0	99.9
1977	2123	-15.8	78.8
1978	929	+28.4	82.2
1979	366	+26.8	68.0
1980	643	+ 6.6	87.5
1981	1032	-45.0	105.7
1982	629	+ 4.5	51.6
1983	1224	+16.7	74.4
1984	846	+ 4.0	54.8
1985	898	+ 7.2	72.9
1986	777	+ 4.9	60.8
1987	293	-46.0	84.6
1988	466	-134.6	96.8
1989	200	-60.9	84.6

S.D. is the standard deviation of each mean; n is the number of chicks measured each year.

FIG. 3.3. Chick growth index against percentage of sandeels in the diet of great skua chicks between 1975 and 1989. The index is the mean difference between observed and expected weights of chicks (Table 3.6).
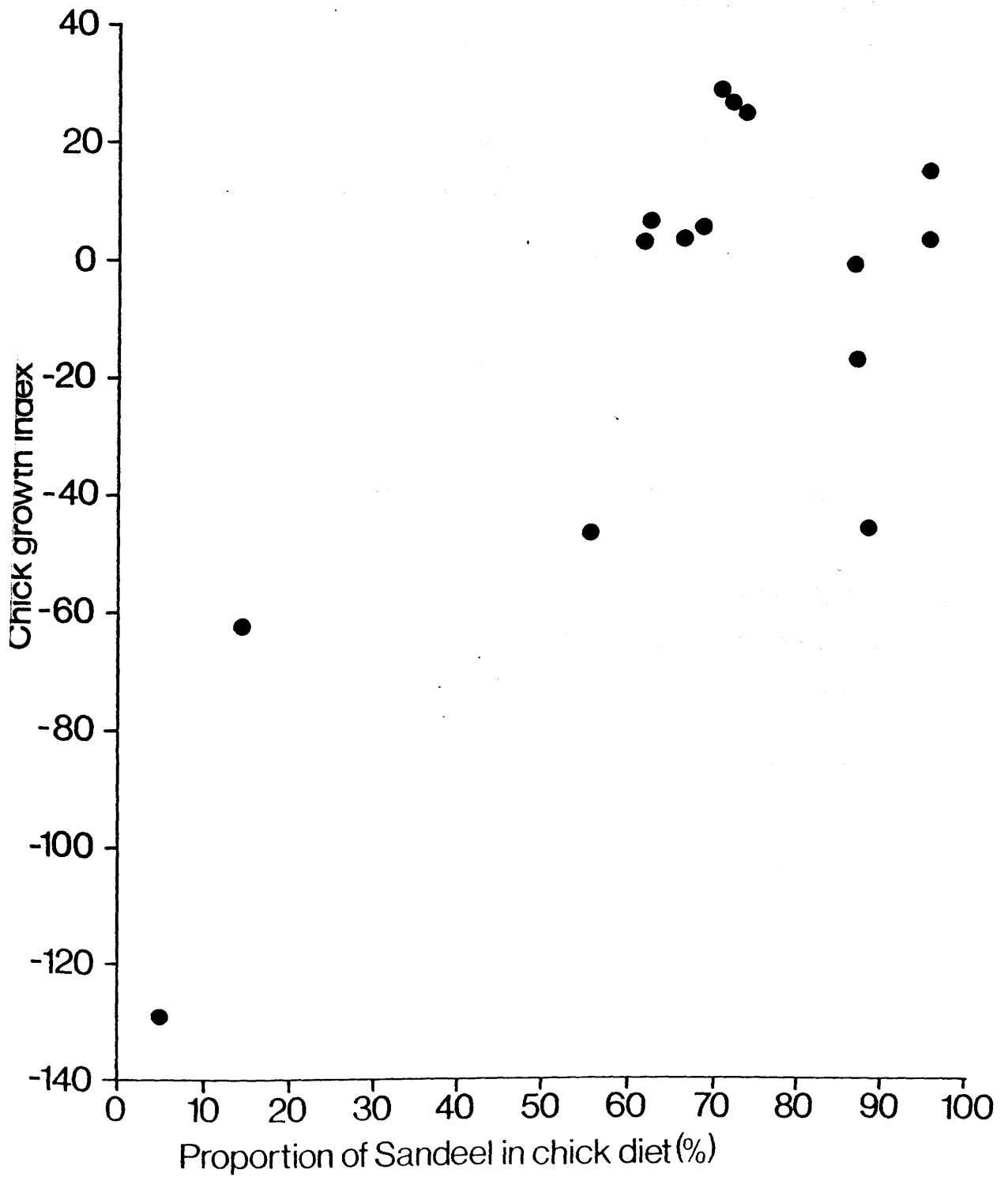
Poor growth of chicks before fledging appears to result in high post-fledging mortality. For cohorts of chicks ringed on Foula between 1975 and 1987, there is a negative Pearson correlation between the mean difference from expected weight for similarly-aged chicks and the proportion of ringed chicks recovered dead away from Foula (i.e. after fledging) in their first year of life (Fig. 3.4; Pearson correlation with normally distributed data, r = -0.60, n = 13, P = 0.03). Furthermore, a cohort which suffers high first-year mortality also suffers high mortality in its second year and third years (in Pearson correlations between recovery rates at age 0 and at ages 1 and 2 for birds hatched between 1963 and 1983, r = 0.69, n = 21, P = 0.001 and r = 0.73; n = 21; P = 0.0001 respectively).

Ages and weights of breeding adults

The high foraging effort exerted by adults in 1987 and 1988 did not reduce the body condition, as determined from weight, of those birds breeding the following season. The weights of samples of incubating adults of both sexes in 1988 and 1989 were no different to those obtained in 1979 and 1980 (Table 3.7).

TABLE 3.7. Weights of incubating female and male great skuas on Foula in 1979, 1980, 1988 and 1989.

Year	n	Female mean weight (grammes)	S.D.	n	Male mean weight (grammes)	S.D.
1979	8	1444	65.2	9	1343	97.2
1980	26	1491	68.8	36	1359	81.4
1988	70	1451	87.7	50	1365	96.7
1989	31	1475	86.7	24	1379	98.3

S.D. is the standard deviation of each mean; n is the sample size.

FIG. 3.4. First year recovery rates of great skua chicks ringed
on Foula between 1975 and 1983 against chick growth index. The
index is the mean difference between observed and expected
weights of chicks (Table 3.6).

Chick growth index
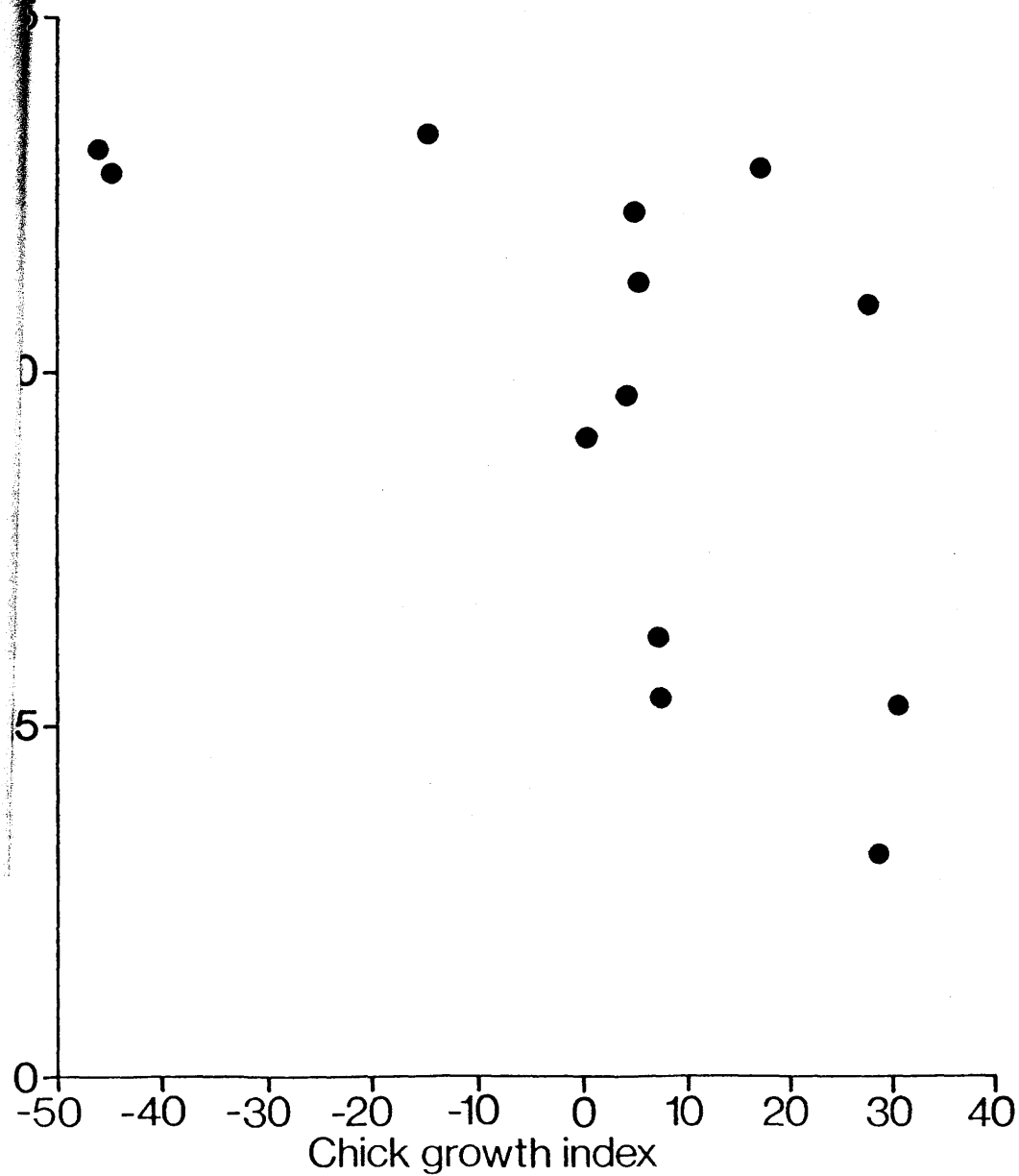
In t-tests comparing pooled data for 1979-1980 with those for 1988-1989, t with 114 degrees of freedom = 1.24, P > 0.2 for females and t with 136 degrees of freedom = 0.78, P > 0.4 for males.

While there was no change in the weights of incubating birds, this increase in foraging effort may have resulted in a higher proportion of adults being unable to recover from the exertions of the previous season and so failing to breed in consecutive years. Evidence in support of this hypothesis was obtained from changes in the ages of breeding birds and in the proportion of adults breeding in consecutive years. Figure 3.5 shows the age structure of the breeding population between 1988 and 1989, as determined from the ages of nest-trapped adults which had been ringed as chicks. The number of adults of each age has been corrected for absolute and relative ringing effort, by dividing by the proportion of chicks ringed each year, and this corrected number has been converted to a percentage of the total over all ages. In 1988-89, 35% of the breeding population were apparently aged eight or less (Fig. 3.5).

Of 120 adults colour-ringed in 1988, 99 were seen on Foula in 1989 and 87 were seen to breed (i.e. incubated or defended eggs), while of 55 marked in 1989, 43 were seen on Foula and 37 bred there in 1990. 74 birds marked in 1988 bred on Foula in 1990, and all but two (i.e. 97%) had been present at the colony in 1989. No adults moved their nests by more than 80 metres between years, and no marked birds which did not breed were seen on the island after mid-June in either year.

FIG. 3.5. Percentage of birds of different ages in a sample of 91 great skuas breeding on Foula in 1988 or 1989. All these birds had been ringed as chicks. Percentages are corrected for differences in annual ringing effort and population size.
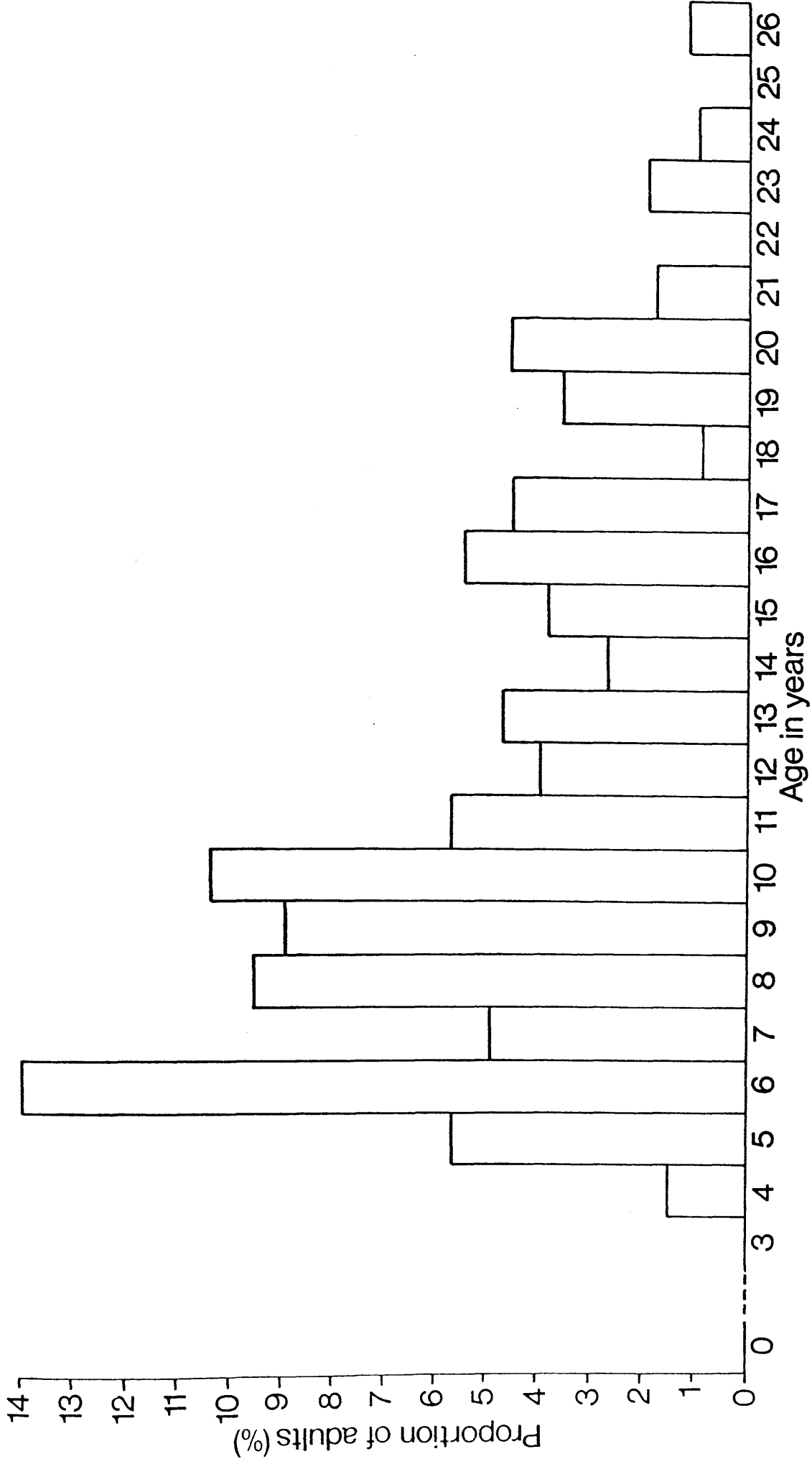
3.5 DISCUSSION

Diet and reproductive effort

Changes in the mean territorial attendance values of great skuas since 1976 (Table 3.3) indicate that between this year and 1987 they greatly increased the time, and presumably the effort, they spent foraging for food. Before 1988 breeding birds were continuing to provide easily-digestible food of high calorific value (sandeels) for their chicks in years when non-breeders had switched to alternative food sources (Tables 3.1 and 3.2). Furthermore, at least in 1989, adults were feeding themselves differently to chicks but in a similar way to non-breeders (Tables 3.1 and 3.2). These data suggest that much of this extra effort was being allocated to reproduction, and not simply to maintaining adult body condition. The importance of maintaining a high proportion of sandeel in the diets of chicks is demonstrated by the positive correlation between dietary representation and chick growth (Fig. 3.3), while the positive correlation between sandeel recruitment and dietary representation (Fig. 3.2) indicates that these changes are directly related to changes in sandeel abundance. A similar link between breeding success and sandeel abundance in Shetland has been demonstrated for Arctic terns _Sterna paradisaea_ by Monaghan, Uttley & Okill (1989) and by Monaghan, Uttley, Burns, Thaine & Blackwood (1989).

Between 1987 and 1988 there was a marked change in chick diets, but this was not accompanied by any further increase in adult foraging effort. Caldow (1988) calculated from time budget data and allometric energetics equations that in 1987 the daily energy expenditure of breeding great skuas on Foula averaged

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five times basal metabolic rate (BMR). The equivalent figure for 1974-76 was about 3.5 BMR. Five times BMR is slightly higher than the putative ceiling (about 4 BMR) suggested by Drent & Daan (1980). Recent labelled water studies with gannets _Sula bassana_ have indicated that daily energy expenditure may equal 6 times BMR during chick rearing in Newfoundland (Birt-Friesen, Montevecchi, Cairns & Macko 1989) but this figure is much higher than found in most seabird studies to date (Birt-Friesen _et al_. 1989). The fact that great skuas had reached 5 BMR in 1987 suggests that in 1988 breeding adults may not have been able to increase their foraging effort further because they were not physically able to do so. Direct measurements of metabolism under the present conditions of food shortage would be interesting in this regard.

This high energy expenditure would not necessarily represent abnormally high parental investment if it simply reflected the fact that adults were devoting their time to energetically expensive foraging rather than energetically inexpensive activities such as chick-guarding (Bryant, Hails & Tatner 1984; Finch 1984). However, since the main cost to adults of an increase in their foraging effort is probably a reduction in the time available to care for themselves, so that they have to use their endogenous reserves (Martin 1987), then an increase in the time spent foraging to feed young probably does represent an increase in parental investment.

The reason why great skuas chose to spend so much time and effort foraging in 1987, 1988 and 1989 probably lies in the inverse relationship between chick growth and post-fledging mortality up to the age of two (Fig. 3.4 and see Results). This will greatly lower the value to adults of chicks which grow

poorly, even if they do fledge, and so will place a strong pressure upon adults to feed their chicks as well as possible. This agrees with the suggestion by Martin (1987) that the consequences of compromises made by adults during previous stages of the breeding season may be clearly expressed by their young after fledging.

The importance of maintaining chick growth rates is indicated by the fact that between 1987 and 1989 adults were prepared to leave their chicks unguarded while both parents foraged (Table 3.3), even though this resulted in many chicks being killed and eaten by adults from neighbouring territories. There is a trade-off between increased foraging effort and an increased probability of chick predation, as suggested by Martin (1987). This may further explain the lack of an increase in foraging effort between 1987 and 1988. The large difference in predation upon chicks between these two years presumably reflects an increase in the willingness of adults to risk attack from neighbouring adults returning from foraging trips.

Long-term costs of reproduction

The high parental investment by adults between 1987 and 1989, in terms of both high energy expenditure and likely increased exposure to risks associated with foraging, is difficult to reconcile with the idea that long-lived iteroparous individuals should adopt reproductive tactics which favour adult survival and maintenance of reproductive potential in preference to the success of any one reproductive attempt. Of course, increased energy expenditure does not necessarily mean an increased cost to adults in terms of survival or resources for future breeding attempts. It is possible that even the high

energy expenditure of adults in these years did not exceed their ability to buffer themselves against these costs, and this is supported by the data for weights of adults of both sexes during incubation, which were as high in 1988 and 1989 as in previous years (Table 3.7). However, mean egg size decreased significantly between 1975 and 1987 (Table 3.4 and see Results) and this may indicate that although adults were able to maintain body weight over this period they were not able to maintain protein reserves, which are much more important than fat reserves as determinants of egg size and quality (Houston, Jones & Sibly 1983). Several studies have demonstrated an affect of adult age upon egg size (Coulson 1963; Coulson, Potts & Horobin 1969; Davis 1975; Coulson & Horobin 1976; Becker & Erdelen 1986; Williams 1990), and this appears to be the case with great skuas (see Chapter 5). A decrease in egg size could therefore result from changes in the age structure of the breeding population. Egg size affects breeding success through its influence upon chick growth and mortality (Parsons 1970; Nisbet 1973; Galbraith 1988), but since the decrease in egg size between 1975 and 1987 was too slight to have any discernible effects upon breeding success it cannot be taken as evidence of a reduction in the reproductive potential of adults at this colony. However, two lines of evidence indicate that some individuals have suffered such a reduction.

In 1988-89, 35% of the breeding population were apparently aged eight or less (Fig. 3.5) whereas in the 1970s the mean age of first breeding at this colony was 7-8 (Furness, 1987). While this is not a direct comparison, it nonetheless strongly suggests a lowering in the age of first breeding, indicative of an increase in adult mortality or emigration (Porter & Coulson

1987), since it is highly unlikely that a third of the birds incubating eggs in 1988-89 were breeding for the first time. The data may be biased by differences in the numbers of chicks fledged each year, but a decrease in annual breeding success would result in greater representation of older birds, not younger ones. The fact that this lowering in the age of first breeding is associated with a decrease in the ease of finding food suggests that young great skuas on Foula were previously constrained by social pressures or lack of space (Monaghan 1980; Furness & Monaghan 1987) rather than the need to develop foraging skills (Burger 1980; Greig, Coulson & Monaghan 1983).

10% of adults colour-ringed in 1988 were present on Foula in 1989 but did not breed, while a further 18% were not seen at all in 1989. Similarly, 11% of birds marked in 1989 failed to breed on Foula in 1990 and a further 22% did not return to the colony. It is very unlikely that any of the birds absent in either year were breeding elsewhere, since great skuas are highly site-faithful (Furness 1987 and see Results) and no marked birds were reported from any other great skua colonies in 1989 or 1990. These data strongly suggest that adult egress (absence from the colony, though not necessarily due to mortality) has increased since the 1970s, and that at least some of this increase is the result of birds failing to breed in some years. It is likely that the birds which breed in a particular season are those which were able to recover sufficiently from the efforts of the previous season, whereas those birds unable to recover are not represented in the breeding population. The decrease in egg size since the 1970s suggests that even among breeding birds this recovery may not be complete.

The increase in adult egress may be related to winter

conditions rather than food supply during the breeding season. However, there is no evidence to suggest that this is so, and it seems unlikely given that the winter dispersal of great skuas extends from Greenland to Brazil (Furness 1978). The increase in egress since 1980, the absence in 1989 of 28% of marked adults breeding in 1988 and the decrease in egg size since 1975, in conjunction with the high reproductive effort of adults between 1987 and 1989, strongly suggest that adults at this colony are now suffering greater long-term costs of reproduction. The described changes in diet and their relationship to changes in sandeel recruitment indicate that this has occured as a result of a decline in food availability during the breeding season.

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CHAPTER 4

Survival rates of great skuas over a period
of declining sandeel stocks

4.1 SUMMARY

Changes in the proportions of pellets of different types regurgitated by non-breeding great skuas on Foula, Shetland between 1973 and 1988 indicate a major reduction in the availability of sandeels after 1983. This is supported by data from mid-water research trawls, which indicate that summer stocks of sandeels in Shetland waters have been very low since 1983.

Analysis of ring recovery data for great skuas ringed as chicks on Foula indicate that annual adult survival was 13% lower in the 1980s than in the 1970s, while first-year survival was unchanged. Estimates of survival derived from recoveries of birds ringed as chicks are sensitive to many possible sources of error, and comparison with estimates derived from annual returns of birds colour-ringed as adults suggests that the analysis of ring recovery data may have underestimated adult survival during the 1980s by as much as 5%. Nonetheless, the two methods together suggest strongly that the survivorship of adult great skuas in Shetland has declined since the 1970s, in association with a decline sandeel stocks around Shetland.

4.2 INTRODUCTION

Great skuas <u>Catharacta skua</u> in Shetland experienced high
breeding success and steady population growth at a rate of
approximately 7% per annum during the 1970s (Furness 1987). This
was considered possible because there was an abundant lipid-rich
food supply in the form of sandeels <u>Ammodytes marinus</u> (Furness &
Hislop 1981; Hamer, Furness & Caldow in press). Adult survival
during this period was estimated from ring recovery data to be
93% per annum (Furness 1978). During the 1980s there has been a
major decline in the availability of sandeels around Shetland
(Gauld, McKay & Bailey 1986; Hudson & Furness 1988; Monaghan,
Uttley & Okill 1989; Monaghan, Uttley, Burns, Thaine & Blackwood
1989; Harris & Wanless 1990; Bailey, Furness, Gauld & Kunzlik in
press). This has resulted in adult great skuas on Foula, the
largest colony in Shetland, increasing the time spent at sea
during chick-rearing and, according to time and energy budget
calculations, working near the limits of their ability in order
to provide food for their chicks (Hamer <u>et al</u>. in press). While
life history theory predicts that long-lived iteroparous species
should not increase their reproductive effort in any one year
substantially beyond their ability to buffer themselves against
reduced survival or lower future breeding success (Goodman 1974;
Pianka 1976; Martin 1987) there is also evidence of increased
absence of adults from the colony (though not necessarily due to
mortality) since the 1970s (Hamer <u>et al</u>. in press).

Over 35,000 great skuas have been ringed on Foula, using
monel rings, since 1963. More than 1500 of these were recovered
after fledging and reported to the British Trust for Ornithology
up to 31st December 1988. These were all recoveries of birds

ringed as chicks, and so of known age and natal colony.

This paper presents an analysis of the recoveries of great skuas ringed on Foula between 1963 and 1988. It examines whether patterns of mortality since the 1970s can be related to the large-scale decline in the availability of sandeels in Shetland in recent years, and assesses the value and comparability of analyses of ring recovery data and annual returns of colour-ringed breeding birds as methods of estimating adult survival rates.

4.3 METHODS

Fishery and research vessel data concerning the abundance of sandeels in Shetland waters for years between 1973 and 1988 were taken from Bailey et al. (in press). In addition, sandeel availability was assessed from the diets of non-breeding great skuas on Foula in every year from 1973 onwards, except 1985. This was done by weekly collection of pellets of non-digestible material deposited at club sites between 1st and 15th July each year, using methods described by Furness & Hislop (1981). This gave an unbiased indication of the diets of non-breeders, which, at least in 1989, were very similar to those of breeding birds (Hamer et al. in press).

Recoveries of rings from birds ringed on Foula as chicks between 1963 and 1988 were analysed with respect to age, location, circumstances, season and year. Birds' ages were calculated from the time elapsed between 1st July in the year of ringing and the date of ring recovery, with every bird entering a new age class on 1st July each year. Survival rates of birds in different age classes were determined from ring recovery data using standard 'life table' or 'maximum likelihood' analyses

(Seber 1972; Lakhani & Newton 1983; Lakhani 1987). These can be highly misleading if the following assumptions, listed by Anderson, Burnham & White (1985) are not met:

1. The ringed sample represents the population of interest,

2. There is no loss of rings,

3. Survival rates are not affected by ringing,

4. Years of recovery are correctly tabulated,

5. The fates of ringed birds are independant,

6. Annual survival is independant of year,

7. The reporting rate is constant over all ages and years,

8. No subgroups have heterogeneous survival or reporting rates.

In addition, these methods rely upon the assumption that survival is constant above a certain age (Lakhani & Newton 1983). The validity and testability of these assumptions was taken into account in calculations of survival rates, which follow methods described by Furness (1978).

Adult survival rates were also assessed from annual returns of birds colour-ringed as breeding adults. Samples of great skuas breeding on Foula were trapped during incubation in 1988 and 1989, using a clap-net (Spencer 1984) placed at the nest, and every adult caught was given a unique combination of four coloured plastic leg-rings. Breeding territories were searched on consecutive days during May of 1989 and 1990 for colour-ringed birds marked in previous years, and this was continued each year until no new birds were recorded. Territories where birds marked in previous years were not seen were then visited on two occasions specifically to search for these missing birds. Finally, the whole island was searched during June of both years, to check whether any marked birds had moved their territories.

Calculation of adult mortality from annual returns of identifiable individuals assumes that no marked birds move to other colonies, and to assess this, wardens and other workers at great skua colonies throughout Shetland were asked to note any colour-ringed birds present during the breeding seasons of 1989 or 1990.

This method also relies upon the assumption that birds breed, or at least return to a breeding colony, every year. The validity of this assumption was assessed from the proportion of birds missing from Foula in 1989 which reappeared in 1990, and from the numbers of marked birds which held territories but did not breed each year.

During this study, two birds lost a single colour-ring, but no bird lost more than one, and so we are confident that colour-ring loss did not affect our survival estimate.

The possibility that catching and marking birds affected their survival or behaviour in future years was assessed from the relative proportions of birds breeding or not breeding one or two years after marking.

4.4 RESULTS

Measures of sandeel availability

Table 4.1 shows data concerning sandeel stocks in Shetland waters and the proportion of sandeel in pellets regurgitated by non-breeding great skuas on Foula, for every year but one between 1973 and 1988. Data from regurgitated pellets indicate that sandeel occurred at a frequency below 10% in the diets of non-breeders in every year recorded since 1983, while mean numbers of sandeels caught in experimental hauls show a decline from a peak of 1368 per haul in 1978 to below one in every year

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since 1983. Fishery-derived data (Table 4.1) also indicate a decline during the 1980s from peaks in 1983, for biomass, and 1982, for numbers of recruits. However, in contrast to the research trawl and skua dietary data, the fishery-derived data indicate that sandeel stocks in 1988 were higher than those in 1974 or 1975.

TABLE 4.1. Percentage of sandeel in the diets of nonbreeding great skuas on Foula between 1st and 15th July, estimated total sandeel stock biomass and number of sandeel recruits in Shetland waters on 1st July, and geometric mean number of sandeels caught per haul by a mid-water research trawl, for years between 1973 and 1988.

Year	proportion in diet		biomass (tonnes)	recruits (millions)	geometric mean
	n	%			
1973	100	71	-	-	242.0
1974	100	24	49.9	13898	25.8
1975	100	21	75.4	32076	1301.0
1976	100	72	100.6	41765	744.0
1977	100	59	116.6	48257	208.0
1978	100	64	99.4	36663	1368.0
1979	100	41	92.1	30605	115.0
1980	100	17	113.6	42783	6.4
1981	100	18	167.4	76083	75.8
1982	100	13	182.6	81180	14.9
1983	305	9	191.5	74926	0.4
1984	100	0	133.3	29188	-
1985	-	-	108.6	21343	0.4
1986	200	0	89.5	19451	0.0
1987	98	9	54.1	2208	0.5
1988	200	0	68.4	20750	0.9

For dietary data, n is the number of pellets analysed each year. Data concerning sandeel stocks are from Bailey et al. (in press).

First-year survival

Figure 4.1 shows the cumulative percentages of birds reported as found dead in successive annual cohorts of great

FIG. 4.1. Cumulative percentages of great skuas ringed as chicks on Foula and reported as found dead at different ages after fledging, for chicks ringed between 1963 and 1976 and recovered up to 1980 (solid circles), and for chicks ringed between 1977 and 1988 and recovered between 1981 and 1988 (solid squares).

Cumulative percentage recovered vs. Age (years)
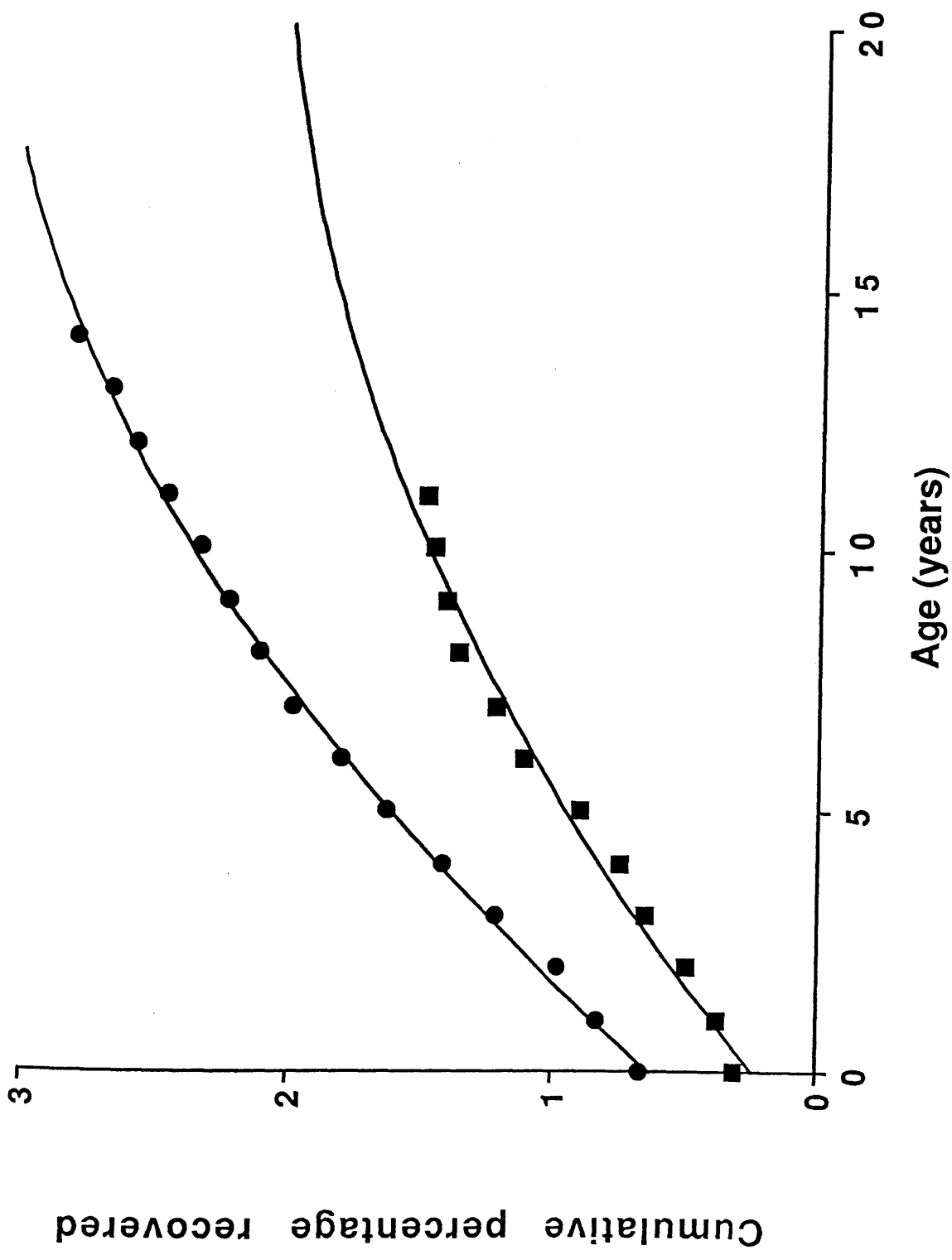
skuas ringed as chicks at Foula between 1963 and 1976, and recovered up to 1980. Projection to an asymptote indicates that 3.2% of all ringed chicks would eventually be reported as found dead. The proportion of recoveries between fledging and one year old (0.66% of chicks ringed) represents 20% of this total, suggesting a survival of 80% in the first year of life (assuming reporting rates to be the same for all ages). If this process is repeated using only recoveries between 1981 and 1988, for chicks ringed after 1976, estimated first-year survival is again 80% (Fig. 4.1).

Adult survival

Figure 4.2 shows log. recovery rate against age for great skuas ringed at Foula between 1963 and 1975, and recovered at Foula between 1968 and 1980 when old enough to be established at the colony (i.e. at ages greater than four years). Annual survival (the antilog. of the slope) is 92%. Figure 4.3 shows log. recovery rate against age for birds recovered away from Foula at ages of three years or above (recoveries at younger ages were excluded because they are biased by the mainly pelagic existence of birds aged one and two years; Furness 1978). From this plot, annual survival is 91%. Since these two estimates are independant, they may be combined to give a single estimate of 91.5%, with a standard error of 1%.

If the procedure is repeated using rings recovered between 1981 and 1988 for birds ringed on Foula after 1975, the two methods give estimates of 78% and 80% respectively (Figs. 4.2 and 4.3). These combine to give an estimate of 79%, with a standard error of 2%. Thus, adult survival during the 1980s appears from these ring recovery data to be significantly lower

FIG. 4.2. Log. recovery rate against age for great skuas ringed as chicks on Foula and recovered on Foula at age five years or more, for chicks ringed between 1963 and 1975 and recovered between 1968 and 1980 (solid circles), and for chicks ringed between 1976 and 1983 and recovered between 1981 and 1988 (open circles).

Log percentage recovered
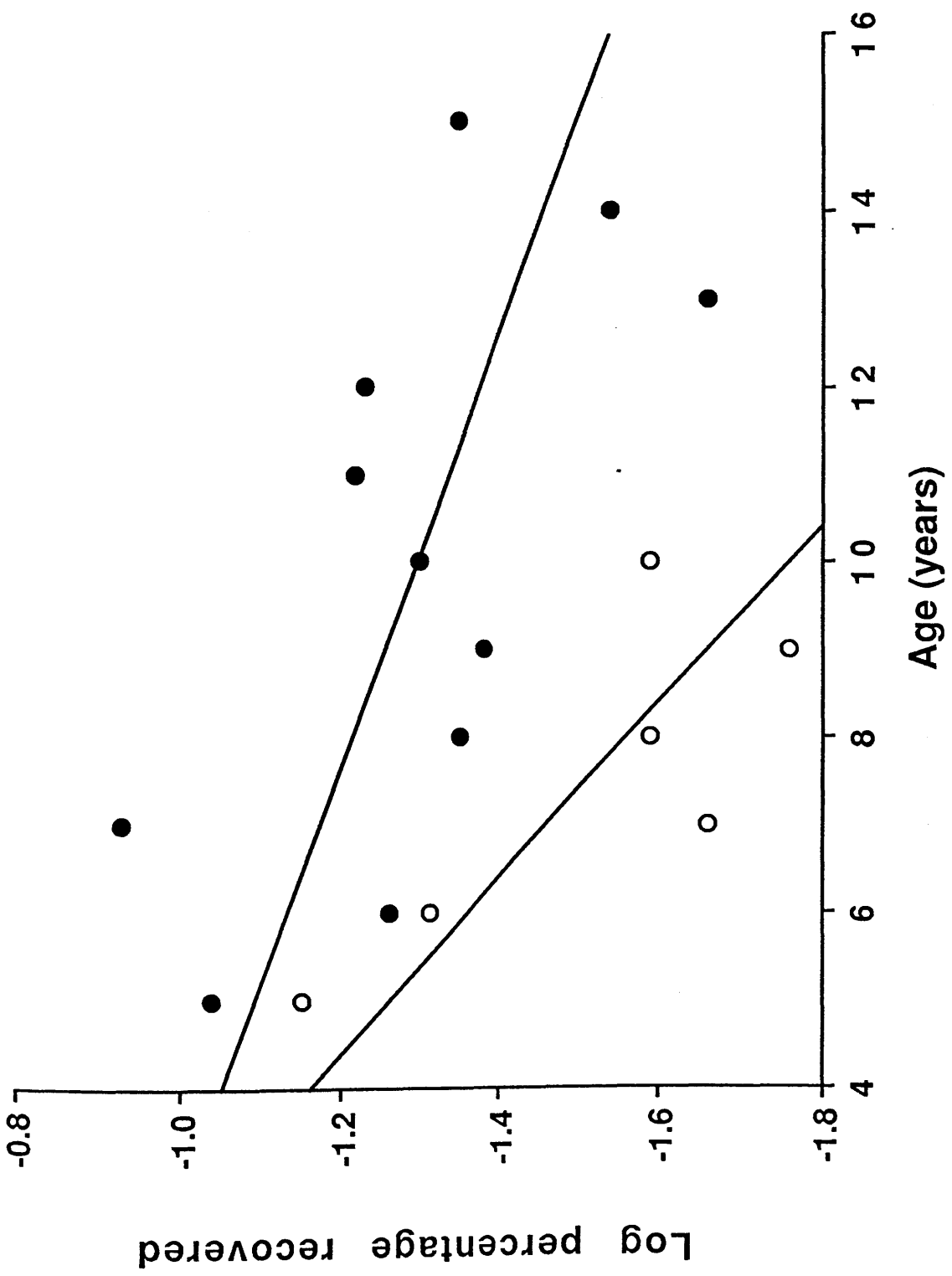
Age (years)

FIG. 4.3. Log. recovery rate against age for great skuas ringed
as chicks on Foula and recovered away from the colony at age
three years or more, for chicks ringed between 1963 and 1975
and recovered before 1981 (solid circles), and for chicks ringed
between 1976 and 1985 and recovered between 1981 and 1988 (open
circles).
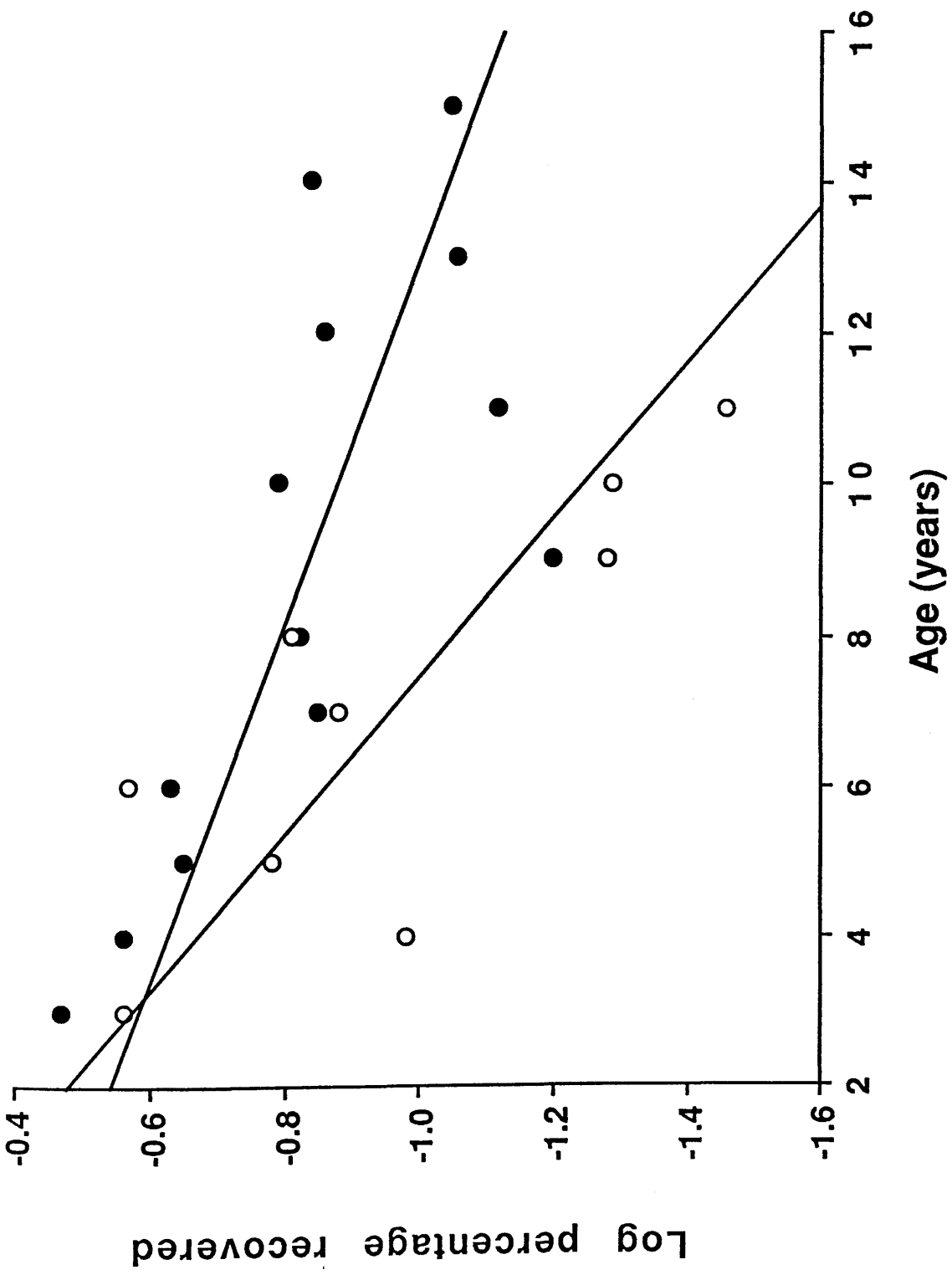
than that prevailing during the 1970s.

Survival of colour-ringed birds

120 adults were colour-ringed at nests on Foula in 1988, and a further 55 in 1989. None of these were seen at any other colonies in Shetland in 1989 or 1990. Table 4.2 shows the numbers of marked birds breeding (i.e. incubating or defending eggs), present but not breeding, or absent from Foula in 1989 and 1990. No adults moved nest sites by more than 80m between years. A total of 83 birds marked in 1988 were present at the colony in 1990 (Table 4.2) and all but 3 of these (i.e. 96%) had also been present in 1989. Of the 74 birds marked in 1988 and breeding in 1990, all but 2 (i.e. 97%) held territories in 1989.

TABLE 4.2. Numbers of colour-ringed great skuas breeding, present but not breeding, or absent from Foula, in 1989 and 1990.

Year marked	1989			1990		
	Breeding	Present	Absent	Breeding	Present	Absent
1988	87	12	21	74	9	37
1989	–	–	–	37	6	12

120 birds were marked in 1988, and a further 55 in 1989. Birds were considered to be breeding if they incubated or defended eggs.

Likelihood of breeding in consecutive years was not affected by capture and marking, since there was no difference between the first and second years after capture in the proportions of birds breeding, present but not breeding or absent from the colony in 1990 (Chi-square = 3.15, n = 175, P = 0.21 with two degrees of freedom).

Of the 120 adults marked in 1988, 102 (85%) were seen at the colony in 1989 or 1990. Since 3% of birds breeding in 1990 failed to hold territories in 1989 (see above), this can be taken as indicating a survival rate for adults of approximately 85% between 1988 and 1989. Of 157 colour-ringed birds definitely alive in 1989 (55 of them ringed that year), 126 (80%) were present in 1990. Assuming a similar proportion (3%) of colour-ringed birds were alive but absent from Foula in 1990, this represents an estimate of 130 birds (83%) which survived from 1989 to 1990. These figures combine to give a mean estimate of 84% annual survival between 1988 and 1990.

4.5 DISCUSSION

Data regarding sandeel stocks and dietary representation (Table 4.1) indicate a major decline in the availability of sandeels in Shetland waters after 1983. This is supported by evidence concerning the breeding success of Arctic terns Sterna paradisaea in Shetland. These feed their young almost entirely on sandeels, are likely to be more sensitive than other species to changes in food supply (Furness & Ainley 1984), and have had consistently poor breeding success in Shetland since 1983 (Monaghan et al. 1989).

Comparison of survival rates for the periods 1963-1980 and 1981-1988, as estimated from ring recovery data, indicates that annual survival of adults was 13% lower during the latter period, while first year survival rates were very similar in both periods (see results). Estimates for first years and adults for the period 1963-1980 agree closely with those recorded by Furness (1978) for recoveries up to the end of 1974.

Age-specific changes in movements and causes of mortality

of great skuas result in survival and ring recovery being heterogeneous with respect to age (Furness 1978), and this can seriously bias estimates of survival rate (Anderson et al. 1985) but this problem is minimised for great skuas by restricting analysis of first year survival to recoveries reported as found dead and of adult survival to recoveries at ages greater than two years (Furness 1978).

For survival rates estimated from ring recovery data to be meaningful, the ringed sample must be representative of the population of interest (Anderson et al. 1983). This is the case with great skuas on Foula, since a large proportion (approximately 50%) of the total population of chicks at the colony was ringed each year. Ring wear, resulting in the loss of rings from older birds, can produce misleading estimates of adult survival (Nelson, Anderson & Burnham 1980; Coulson & Butterfield 1986), but ring loss is not a problem with great skuas (Furness 1978).

Life table analyses also rely upon the assumption that survival is constant above a certain age (Lakhani & Newton 1983). Although this was long thought to be the case with birds (Nur 1984) it is now clear that survivorship of long-lived birds generally decreases with age (Botkin & Miller 1974; Coulson & Wooller 1976; Pugesek 1984; Bradley et al. 1989; Aebischer & Coulson 1990). Higher mortality among older birds would result in their being over-represented in ring recoveries, producing an inflated estimate of survival. While this problem was minimised by omitting recoveries from birds older than 15 years from the analysis, recoveries away from Foula (Fig. 4.3) occurred at a higher rate for birds aged 10 years or older than for nine year olds, suggesting that they may have been over-represented.

However, the survival rate estimated from this plot was very similar to those estimated from Fig. 4.2 and by Furness (1978), neither of which showed evidence for a higher recovery rate than expected for older birds.

Such calculations also rely upon the assumption that reporting and survival rates are constant across all years. This is generally untrue for first year recovery rates (Anderson, Wywialowski and Burnham 1981) and is not the case for first-year great skuas (Hamer et al. in press). Tests of these assumptions for older birds found that they were not met for hunted species (Burnham & Anderson 1979), and in a range of unhunted species, the only group for which these assumptions consistently held was gulls (Anderson et al. 1981). Reporting rates from Foula are likely to have been more or less constant at least since 1981, and the two survival estimates for adults in this period agreed closely with each other (see results). Furthermore, changes in conditions during the winter are unlikely to have widespread affects upon great skuas, since they are widely dispersed outside the breeding season (Furness 1978) and adult survival is very unlikely to differ in years in which more sensitive measures of perturbation at breeding colonies, such as breeding success, are constant (Cairns 1987). Great skuas on Foula experienced consistently high breeding success during the first of the two periods analysed in this study (Furness 1977; Hamer et al. in press), and while adult survival may have declined during the latter period, the aim of this analysis is to examine such a change. While the true difference in adult survival between the two periods may be less than 13%, analysis of ring returns does provide evidence that annual survivorship of great skuas at Foula has declined since the 1970s.

Annual returns of colour-ringed birds produced a survival estimate 5% higher than ring recoveries over a similar period (see results). Colour-ring returns will underestimate survival if some marked individuals move to other colonies between years. However, great skuas are highly site-faithful (Furness 1987), no colour-ringed birds were seen at any other colonies in Shetland, and only 3% of birds were absent in 1989 but reappeared in 1990 (see results). Extensive non-breeding by adults has been recorded in other species (Ollason & Dunnet 1983; Coulson 1984; Weimerskirch 1990), but since in this study 97% of birds marked in 1988 and breeding in 1990 held territories in 1989, whether they bred in them or not (see results), this does not appear to be a large source of error for great skuas.

Annual returns of colour-ringed birds will not give a true indication of survival if the marked sample is not representative of the breeding population. In this study, adults were not trapped if they failed to return to their eggs within 30 minutes of the trap being set over them. This occurred on approximately 20% of occasions, so that the marked sample may have been biased in favour of birds less easily deterred from incubating. If willingness to incubate eggs when the trap was set is an indicator of adult quality, then the survival of marked birds may be an overestimate for the population as a whole, since better quality birds have higher survival (Nol & Smith 1987; Thomas & Coulson 1988; Aebischer & Coulson 1990; Wooller et al. 1990). However, birds colour-marked in this study do not appear to be of better quality than unmarked ones, since they were no more aggressive and had similar hatching success to birds which the trap failed to catch (see Chapters 5 and 6).

Comparison of survival estimates from ring recoveries and

returns of colour-ringed birds suggests that the former method underestimated survival during the 1980s by around 5% (see results). While this is a large discrepancy, it is not sufficiently great to account for the difference in estimated survival rates during the two periods analysed. The estimate for the period 1963-1977 (92%) agrees well with estimates of adult survivorship in a variety of long-lived seabirds obtained using several different techniques (Harris 1970; Chabrzyk & Coulson 1976; Dunnet & Ollason 1978; Hudson 1985; Coulson & Butterfield 1986; Cairns 1987; Ainley, Ribic & Wood 1990; Croxhall et al. 1990). Data from colour-ringed birds thus support the notion that the survivorship of great skuas at Foula has decreased since the 1970s.

Hamer et al. (in press) found evidence that adults at Foula have increased their reproductive effort since the 1970s, and they noted changes in the age structure of the breeding population which were indicative of an increase in egress (absence from the colony, though not necessarily due to mortality). The two methods used to estimate adult survival in this study together produced a strong indication that at least a component of this increase is the result of an increase in adult mortality. Decreases in adult survivorship associated with major reductions in food supply have been described in the tropical Pacific (Barber & Chavez 1983; Duffy 1983; Schreiber & Schreiber 1984) and southern Africa (Cairns 1987), but an increase in the mortality of great skuas ont Foula is perhaps surprising in view of the wide range of potential food sources available to them (Furness & Hislop 1981; Cairns 1987).

While the results of this study suggest that annual survival of great skuas on Foula has decreased since the 1970s,

recovery data from birds ringed as chicks are generally considered to be of doubtful value for calculating survival rates, and while studies of colour-ringed birds, particularly if of known age, can give a much better indication of annual survival (Harris 1970; Chabrzyk & Coulson 1976; Coulson & Butterfield 1986) we cannot compare the survival of great skuas colour-ringed since 1988 with any earlier data. Further study of colour-ringed birds in future years will be required to assess the extent to which egress from Foula represents non-breeding or mortality, and to relate changes in both to the availability of sandeels in the waters around Shetland.

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CHAPTER 5

Age-specific breeding performance and reproductive effort
in great skuas

This chapter constitutes a paper entitled 'Age-specific breeding performance and reproductive effort in great skuas Catharacta skua', in press in Journal of Animal Ecology.

5.1 SUMMARY

During a period of reduced food supply, egg laying dates of great skuas Catharacta skua Brünnich on Foula, Shetland advanced and hatching success increased with age, although breeding success increased with age in only one of the two years studied. Clutch volume increased with age up to fourteen years and decreased with age above this, and could be described by a quadratic equation.

There was no relationship between age and territorial attendance during incubation, but time spent foraging to provide food for chicks increased with age in 1989, while aggression increased with age in both years studied. These are both evidence of an increase in reproductive effort with age.

Older birds may have expended greater reproductive effort simply because they were better able to do so without incurring higher mortality or lower future breeding success. However, return rate between years declined with age for males, which could be a consequence of increased reproductive investment by older birds.

5.2 INTRODUCTION

Many studies of birds have shown that breeding success increases with adult age and experience (see Ryder 1981 for a review; Nisbet, Winchell & Heise 1984; Shaw 1986; Ainley, Ribic & Wood 1990; Weimerskirch 1990; Wooller, Bradley, Skira & Serventy 1990). By contrast, Furness (1983, 1984) found that the breeding performance of great skuas Catharacta skua Brünnich in Shetland during the 1970s showed no consistant relationship with age, other than a tendancy for younger birds to lay later in the season. The lack of differences with age was attributed to the presence of an abundant and reliable lipid-rich food supply in the form of sandeels Ammodytes marinus Raitt (Furness & Hislop 1981), along with competition for territories forcing many birds to defer breeding, so that breeding success was uniformly high among birds able to obtain a territory.

During the 1980s the availability of sandeels around Shetland declined markedly (Gauld, McKay & Bailey 1986; Hudson & Furness 1988; Monaghan, Uttley & Okill 1989; Monaghan et al. 1989; Harris & Wanless 1990; Bailey, Furness, Gauld & Kunzlik in press). One effect of this has been that great skuas at the largest colony in Shetland, on Foula, have had to spend more time foraging and, according to time and energy budget calculations, work near the limits of their ability in order to provide food for their chicks (Hamer, Furness & Caldow in press). The period since the 1970s has also seen an increase in the proportion of young birds breeding on Foula (Hamer et al. in press). Differences in breeding performance between pairs resulting from the greater experience and ability of older birds are much more likely to become apparent under these conditions.

The greater experience of older birds should lead to higher breeding success under the present adverse conditions, and life history theory predicts that reproductive effort will also increase with age whenever residual reproductive value decreases with age (Gadgil & Bossert 1970; Schaffer 1974; Pianka & Parker 1975; Charlesworth & Leon 1976; Charlesworth 1980). Despite statements to the contrary (Nur 1984) survivorship of long-lived birds generally decreases with age (Botkin & Miller 1974; Coulson & Wooller 1976; Pugesek 1984; Bradley, Wooller, Skira & Serventy 1989; Aebischer & Coulson 1990). Furthermore, residual reproductive value may be reduced in the absence of increased mortality by senescence (Curio 1983; Clutton-Brock 1984; Reid 1988), and so, according to life history theory, older birds should invest more in reproductive effort than younger ones (Curio 1983; Pugesek 1983; Reid 1988).

As a result of intensive ringing of great skua chicks on Foula, approximately half the adults now breeding there carry British Trust for Ornithology (BTO) rings, from which their ages can be determined (Hamer et al. in press). This paper examines the relationship between adult age and breeding performance of great skuas during a period of low sandeel availability. It assesses whether influences that were absent or at most inconsistent during a period of high availability become apparent in more adverse conditions, and examines the predictions of life history theory regarding age-specific changes in residual reproductive value and reproductive effort.

5.3 METHODS

Breeding statistics of great skuas on Foula were determined in 1988, 1989 and 1990. Samples of nests were marked in early

May, the eggs laid at them were measured and, in 1988 and 1989, the fates of these eggs were determined by visiting territories containing marked nests at regular intervals until surviving chicks fledged, in late July or early August.

Differences between adults in breeding performance were examined in terms of chick growth as well as production and survival to fledging. Chicks were weighed and measured as described by Furness (1983), their ages were calculated from wing length (Furness 1977) and measurements from chicks between 13 and 34 days old (the period of most rapid daily mass gain; Furness 1983) were used to compare the growth rates of chicks at different territories. Growth was assessed in terms of mean percentage deviation in weight for each brood from the weight predicted by a logistic equation describing the growth of great skua chicks on Foula in the 1970s (Furness 1983).

Ages of breeding birds were determined in 1988, 1989 and 1990 by trapping adults during incubation, using a clap net (Spencer 1984) placed at the nest. Ages were obtained from BTO ring numbers. To limit disturbance, only one adult was caught at each nest. Great skuas usually breed with similarly aged mates (Furness 1984), and nest histories were related to the known age of either parent.

To assess any affects of trapping on breeding success, adults were not caught in either year at approximately a quarter of marked nests. In addition, to examine whether nest-trapping had a general effect upon birds breeding in an area, forty nests in a separate part of the colony were marked in 1989 as a control group, where no adults were trapped.

All adults caught were weighed and measured (maximum wing chord, tarsus length, length of head plus bill, bill length and

bill depth). The measurements were used in a discriminant analysis (Norusis 1988) to determine sex by comparison with forty birds found dead or shot under licence on Foula and sexed by internal examination (Hamer & Furness in press). Measurements and weights were also used to calculate an index of body condition, in terms of body mass corrected for body size (Reid 1988). Size was calculated from body measurements using principal components analysis (Norusis 1988; the index produced by the analysis is the sum of variables standardized to have means of nought and standard deviations of one). The factor score representing body size was then regressed against body mass and the condition of each adult was determined as the residual (observed minus predicted) mass. This was used to determine whether body condition during incubation was related to age or date of capture (in days since 1st May), using multiple regression.

Great skuas forage for most of the time when away from their territories, and the attendance of adults can therefore be used as an index of foraging effort (Furness & Hislop 1981). Territorial attendance of adults was determined on two occasions during incubation and a further two during chick-rearing in 1988 and 1989. Attendance was determined by walking round all marked territories and counting the number of adults at each. For each period of the breeding season, the two scores for attendance were then combined to produce a mean value for the number of adults attending each territory with eggs or live chicks.

Each adult caught was given a unique combination of four coloured rings. Aggression of marked individuals was scored on a five-point ordinal scale, depending upon the reactions of colour-ringed birds to a single intruder (K.C. Hamer) within

their territories (Furness 1984). These varied between leaving the territory, and hitting the observer hard and repeatedly. Only the maximum aggression score recorded during incubation at nests with both adults present was used in future analyses. This controls for possible confounding effects (Furness 1983; Nur 1984).

To examine the interactions among aggression, territory size and breeding success, nest density was determined in 1989 for 151 territories, in terms of the distance between nests and each of their nearest three neighbours (Jones 1986). Distances were measured during incubation, to avoid possible confusion resulting from the presence of disused nests within some territories.

The breeding status of birds colour-ringed at nests in 1988 and 1989 was determined in 1989 and 1990. Likelihood of breeding in consecutive years was then analysed with respect to adult age and sex.

5.4 RESULTS

Breeding success and causes of breeding failure

There were no differences between years in clutch size or volume, hatching success or causes of egg loss (Table 5.1; P > 0.05 in all tests), and so where data were collected in more than one year these were combined for later tests.

Trapping activities did not influence breeding success. There was no difference either in the hatching success of eggs in nests where adults were and were not trapped (Chi-square with 1 degree of freedom = 1.12, n = 271, P > 0.05) or in hatching success at areas where trapping did and did not take place (Chi-square with 1 degree of freedom = 0.34, n = 116, P > 0.05).

TABLE 5.1. Breeding statistics for great skuas on Foula in 1988, 1989 and 1990.

| | Year Studied | | |
	1988	1989	1990
Number of nests studied	160	198	138
Mean clutch size	1.93	1.95	1.97
Mean egg volume (with S.D.)	84.34(5.12)	82.18(5.68)	82.45(6.83)
Hatching Success (%)	72.3	75.2	-
Fledging Success (%)	7.8	16.5	-
Breeding Success (%)	5.7	12.4	-

S.D. is the standard deviation of each mean.

Among all clutches, 26.1% of eggs laid over the two years failed to hatch. 63% of these (16.4% of eggs laid) were 'addled' (the result of infertility or embryo death), 37% (9.7% of eggs laid) suffered predation, and one egg rolled from its nest. The major proximate cause of breeding failure in both years was predation of chicks by conspecifics (Hamer et al. in press).

Influences of adult age

In 1988, fifty-nine of 120 adults caught during incubation were wearing a BTO ring, while twenty-three of fifty-five birds trapped in 1989 and six of thirteen birds trapped in 1990 carried rings. This gave a sample of eighty-eight birds of known ages between five and twenty-four years.

The index of adult body condition during incubation was not related to age (Pearson Correlations; $r = 0.002$, $n = 34$, $P = 0.99$ for males; $r = 0.09$, $n = 54$, $P = 0.50$ for females). Body mass declined during incubation in the case of males (Pearson correlation; $r = -0.26$, $n = 82$, $P = 0.02$) but not females ($r = -0.03$, $n = 106$, $P = 0.72$). Multiple regressions of body size, age and date upon body mass revealed that only size was related

to mass (F = 5.79, n = 34, P = 0.02 for males; F = 11.05, n = 54, P = 0.001 for females). All variables were normally distributed, as determined by Kolmogorov-Smirnov one-sample tests.

The incidence of one-egg clutches did not vary with age (Mann-Whitney U-test; z = -0.34, n = 88, P = 0.74), but only four birds of known age were trapped on single eggs. The volume of two-egg clutches (calculated from the equation given by Coulson 1963) was related to age, but the relationship is not one of straight-forward increase (Fig. 5.1). Clutch volume increased up to 14 years, and decreased beyond 15 years. The relationship is described by the quadratic equation:

Clutch Volume (mls.) = $2.9a - 0.1a^2 + 149$,

where a is adult age in years. The regression is significant (F = 3.26, n = 84, P = 0.04).

Hatching dates differed slightly between years. The first chick to hatch from each successful clutch did so on average 16.3 and 17.7 days after 1st June in 1988 and 1989, respectively. Of the eighty-two clutches incubated by an adult of known age in 1988 or 1989, at least one chick hatched at seventy-four nests. There was a significant negative Pearson correlation between adult age and hatching date relative to the average in the year of sampling (Fig. 5.2; r = -0.35, n = 74, P = 0.002; both variables were normally distributed). Older birds generally laid earlier than younger ones.

Older birds also had a higher hatching success (Table 5.2; Kruskal-Wallis one-way analysis of variance; Chi-square = 7.38, n = 82, P = 0.02) and were less likely to have addled eggs (Mann-Whitney U-test; Z = -2.05, n = 82, P = 0.04). However, the

FIG. 5.1. Clutch volume against adult age for two-egg clutches laid by great skuas on Foula between 1988 and 1990. Internal egg volumes were calculated from the equation given by Coulson (1963).
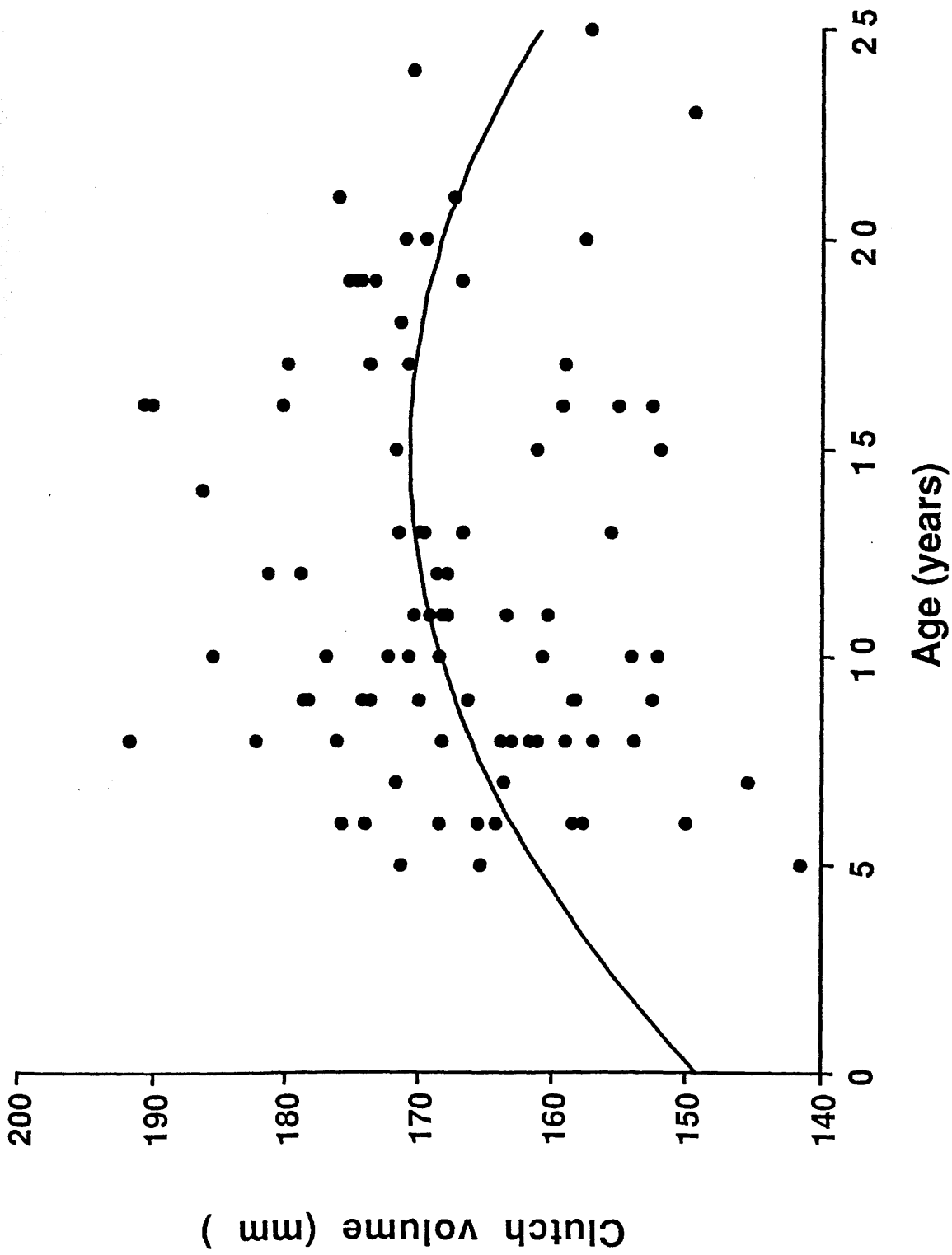
FIG. 5.2. Relative hatching date against adult age for chicks hatched by great skuas on Foula in 1988 or 1989. Relative hatching date is the hatching date of the first chick from each successful clutch relative to the mean in the year of sampling.

Age (years)

Relative hatching date (days)
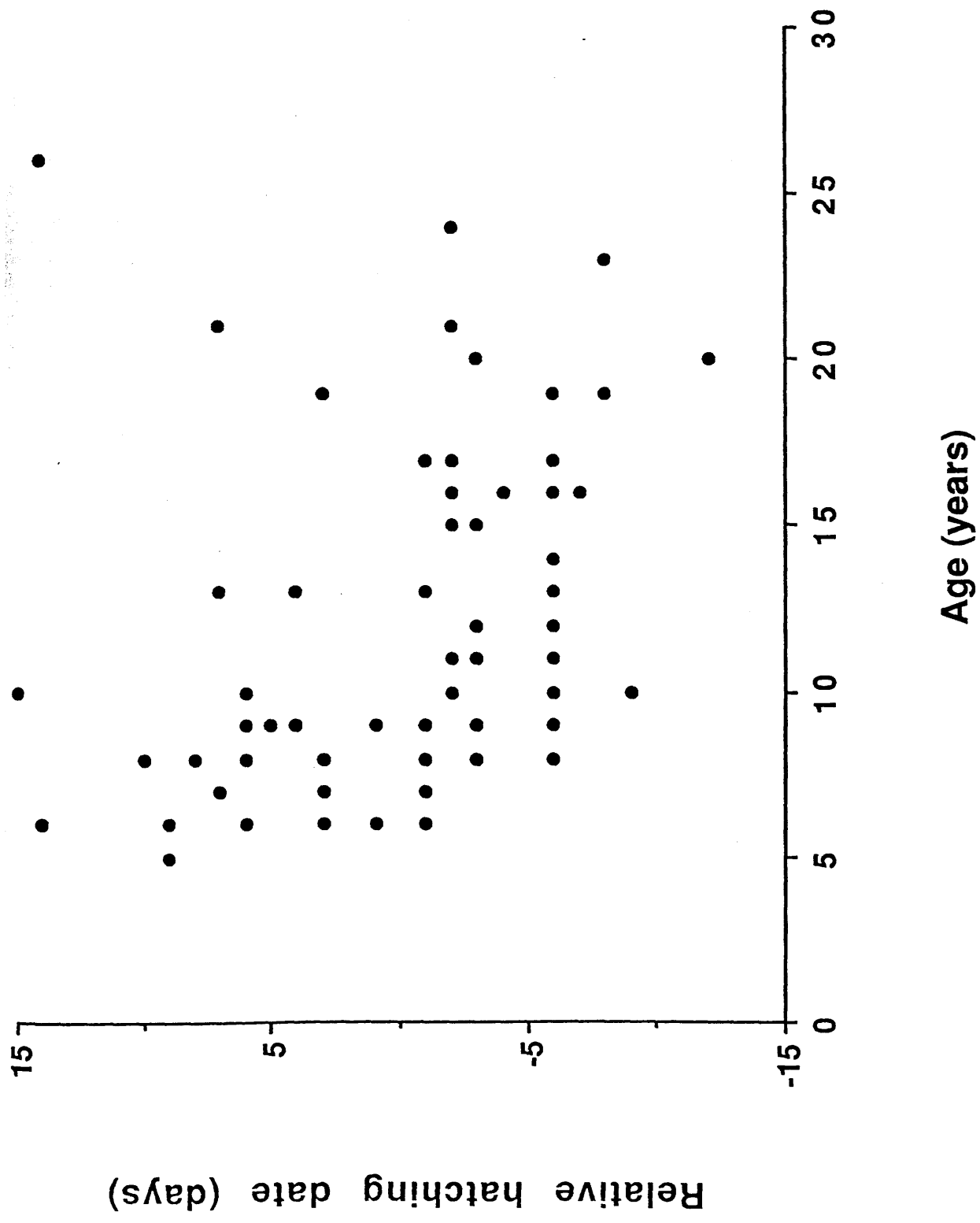
number of eggs taken by predators was not related to adult age
(Z = -0.81, n = 82, P = 0.42).

TABLE 5.2. Ages in years of adult great skuas on Foula with
different numbers of eggs hatched, addled and taken by
predators.

	No eggs			One egg			Two eggs		
	Mean	S.D.	n	Mean	S.D.	n	Mean	S.D.	n
Hatched	9.00	4.35	10	10.53	4.43	19	12.70	5.20	53
Addled	12.31	5.08	61	10.69	4.94	16	8.20	3.96	5
Eaten	11.93	5.18	72	10.89	4.04	9	6.00	–	1

S.D. is the standard deviation of each mean. n is the sample
size.

Older birds had a higher breeding success in 1988 (Mann-Whitney U-test; Z = -2.14, n = 59, P = 0.03) but not in 1989 (Z = -0.70, n = 63, P = 0.50). Chicks in only thirty-four broods raised by an adult of known age survived to be weighed and measured at an age greater than thirteen days, and there was no evidence of a relationship between adult age and chick growth index (Pearson Correlation; r = -0.07, n = 34, P = 0.68).

Older pairs had lower territorial attendance post-hatching in 1989 (Table 5.3; one-way analysis of variance; F Ratio = 6.18, n = 18, P = 0.007; all data were homoscedastic, as determined by Bartlett's test, and were normally distributed) but not in 1988 (F Ratio = 0.01, n = 13, P = 0.98). Pre-hatching attendance was not related to age in either year.

Among 120 breeding birds colour-ringed on Foula in 1988, eighty-seven bred there (i.e. incubated or defended eggs) in 1989, and sixty-four of these (73.6%) did so again in 1990. No

adults moved their nests by more than 80m between years, and despite detailed searching no marked birds that did not breed were seen on the island after mid-June in either year. Twelve birds marked in 1988 were present but did not breed in 1989, and seven of these (58.3%) bred there in 1990; of twenty-one birds marked in 1988 and not present at the colony in 1989, only two (9.5%) were breeding in 1990. This difference is highly significant (Chi-square with two degrees of freedom = 29.15, n = 120, P < 0.0001). Likelihood of breeding in consecutive years was not affected by capture and marking, since there was no difference between the first and second years after capture in the proportion of marked birds breeding, present but not breeding, or absent from the colony in 1990 (Chi-square with two degrees of freedom = 3.15, n = 175, P = 0.21).

TABLE 5.3. Mean ages of adults in years for pairs with different scores for mean attendance at territories during incubation and chick-rearing in 1988 and 1989.

Mean Attendance	Incubation			Chick-rearing		
	Mean	S.D	n	Mean	S.D.	n
1988						
0.5	5.00	–	1	13.00	–	1
1.0	12.56	4.93	9	13.60	5.50	5
1.5	10.75	4.49	32	13.14	6.04	7
2.0	11.31	5.52	16	–	–	0
1989						
0.5	–	–	0	18.00	2.83	2
1.0	10.82	5.33	11	18.00	4.24	2
1.5	11.83	5.04	29	9.33	1.86	6
2.0	12.65	4.45	23	13.25	3.65	8

S.D. is the standard deviation of each mean. n is the sample size.

Of 175 adults colour-ringed in 1988 or 1989, 126 were observed and 111 bred on Foula in 1990. The mean age of males

marked in 1988 or 1989 and breeding in 1990 was 10.82 years (S.D. = 3.85, n = 22), while the mean age of those not breeding in 1990 was 15.33 years (S.D. = 6.25, n = 9). This difference is significant (t-test; t with 29 degrees of freedom = -2.46, P = 0.02; all data were normally distributed). There was no difference in the mean ages of females marked in 1988 or 1989 and breeding (mean = 13.31 years, S.D. = 5.40, n = 36) or not breeding (mean = 12.79 years, S.D. = 3.79, n = 14) in 1990 (t with 48 degrees of freedom = 0.33, P = 0.74).

Interactions among age, nest density and aggression

Sample sizes for adults with different aggression scores were lower than in previous tests because adult attendance at some nests was not sufficiently high for aggression scores to be determined accurately (Table 5.4; see Furness 1984). Aggression scores increased with adult age (Kruskal-Wallis one-way analysis of variance; Chi-square = 13.72, n = 68, P = 0.008).

TABLE 5.4. Ages in years and nest densities for great skuas with different aggression scores.

Aggression Score	Age			Nest Density		
	Mean	S.D.	n	Mean	S.D.	n
1	7.50	2.14	8	18.75	4.68	3
2	9.78	5.14	9	18.70	6.15	15
3	11.66	4.83	35	21.95	7.45	57
4	12.86	4.38	7	23.80	8.85	11
5	16.33	6.50	9	24.67	8.82	9

Nest density is the mean distance in metres to each of the nearest three neighbouring nests. S.D. is the standard deviation of each mean. n is the sample size.

Chick survival, in terms of age at death of the first chick to die in each brood, decreased with increasing distance to the nearest neighbour (Fig. 5.3; Pearson correlation with normally distributed data; $r = -0.36$, $n = 34$, $P = 0.03$), but showed no significant relationship with mean distance to the nearest three.

5.5 DISCUSSION

Breeding performance

Clutch size, egg volume and hatching success between 1988 and 1990 (Table 5.1) did not differ from the values recorded during the 1970s (Furness 1983, 1984; Hamer et al. in press). The proportions of eggs addled and taken by predators were also very similar (within 1.5% of figures recorded by Furness 1984). Breeding success increased with age in 1988 but not in 1989 (see Results). However, laying date, clutch volume (except for birds older than 14 years) and hatching success all changed consistently with age (Figs. 5.1 and 5.2, and see Results) in a direction strongly associated with increased breeding success (Parsons 1970; Perrins 1970; Davis 1974; Parsons, Chabrzyk & Duncan 1976; Nisbet 1978; Galbraith 1988). The lack of a consistently demonstrable relationship between age and breeding success probably resulted from the small numbers of chicks fledged from study nests in 1988 and 1989 (Table 5.1).

The availability of sandeels around Shetland was low in both 1988 and 1989 (Hamer et al. in press), and several aspects of breeding performance were related to age in both these years. Furthermore, of the two years studied by Furness (1984), adult age exerted a slight influence upon breeding performance in the year with lower food availability. It seems that, in keeping

FIG. 5.3. Age at death of the first chick to die from each brood against nest density for great skua chicks which died before fledging on Foula in 1989. Nest density is the distance between each nest and its nearest neighbour.

Age at death (days) vs Distance (m)
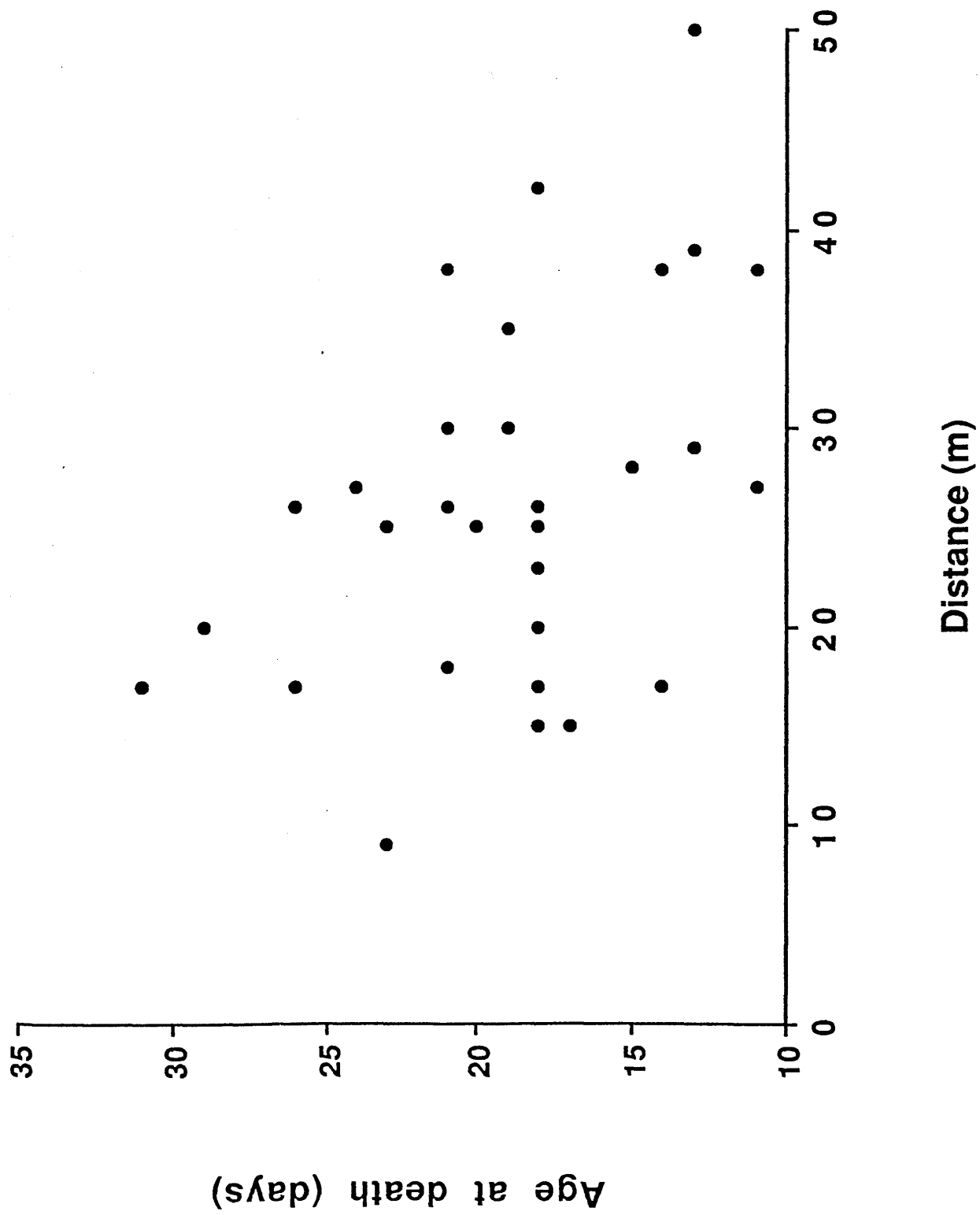
with many other species, adult age has a significant influence upon the breeding biology of great skuas, particularly when food is scarce.

Reproductive effort

Growth and survival of great skua chicks both increase with egg volume (Furness 1983). The decrease in clutch volume for great skuas older than 15 years (Fig. 5.1) may therefore provide evidence of a senescent decrease in fecundity similar to that shown in other species (Coulson & Horobin 1976; Wooller & Coulson 1977; Curio 1983; Reid 1988; Wooller et al. 1990). Egg size is influenced strongly by female protein reserves (Houston, Jones & Sibly 1983). The decline in clutch volume among oldest great skuas probably represents a decrease in reserves available for reproduction, rather than an age-specific change in the allocation of resources. However, clutch volume may be smaller in older birds because they do not need to lay such large eggs in order to achieve similar breeding success.

Time spent foraging during chick-rearing increased with age in 1989 (Table 5.3). This could have been the result of greater investment in reproduction, greater allocation of resources to maintaining body condition or lower foraging efficiency among older birds. Foraging duration during incubation was not related to age (Table 5.3). This strongly suggests that the relationship observed during chick-rearing resulted from differences in response to the increasing demands of growing chicks, rather than differences in foraging efficiency. Furthermore, foraging efficiency generally increases with age (Dunn 1972; Searcy 1978; Burger & Gochfeld 1983; Greig, Coulson & Monaghan 1983; Carroll & Cramer 1985; MacLean 1986), although there is little evidence

that it improves with age among established breeders (Pugesek 1984; Weimerskirch 1990). If the territorial attendance of breeding great skuas was related to foraging efficiency, then higher attendance for older birds would be expected during chick-rearing, but the opposite was found (Table 5.3).

Ainley & DeMaster (1980) found that the oldest Adelie penguins Pygoscelis adeliae (Hombron & Jacquinot) at a colony in South Geogia were the poorest quality individuals. This was the result of high mortality among breeding birds as a result of predation. Age-specific differences in attendance observed in this study are unlikely to result from differences in the quality of adults, since increased foraging duration was associated with increases in several aspects of reproductive performance among older birds (Figs. 5.1 and 5.2, and see results). The lack of a demonstrable relationship in 1988 probably results from the higher and earlier chick mortality that year (Hamer et al. in press; Table 5.1).

Nur (1984) stated that older birds might be expected to have lower scores for territorial attendance if they coordinate their feeding trips better than younger birds. However, they would not be expected to leave their chicks unguarded, and lower territorial attendance of great skuas is closely associated with an increase in the likelihood of both adults being absent from their territory simultaneously (Hamer et al. in press). Furthermore, chicks died earlier in larger territories (Fig. 5.3) which were defended by more aggressive (usually older) birds (Table 5.4). Since predation of chicks was only possible when they were left unguarded (Hamer et al. in press) this indicates that older birds were leaving their chicks more than younger ones. An alternative explanation, that territory size

reflects adult quality (Patterson 1965; Parsons 1976), would predict the opposite relationship. Older birds appeared, at least in 1989, to be more willing to risk predation of their chicks in an effort to maintain chick growth rates. These are closely related to post-fledging mortality at least up to the age of two years (Hamer et al. in press). This may further explain the lack of a relationship between age and breeding success in 1989.

The greater foraging effort of older birds may have been allocated either to reproduction or to maintaining body condition. The fact that adults were continuing to provide their chicks with easily-digestible food of high calorific value (sandeels) while feeding themselves on less nutritious food (Hamer et al. in press) suggests that much of this extra effort was allocated to reproduction.

Hatching and breeding success of great skuas increase with adult aggression (see Chapter 6). The increase in aggression with age recorded here (Table 5.4) is evidence of a greater reproductive effort among older birds, since defence of chicks and breeding territories entails a risk of injury or death (Bryant, Hails & Tatner 1984; Finch 1984; Reid 1988).

Costs of increased reproductive effort

Increases in reproductive effort with age have been interpretated as support for life history theory (Pugesek 1983, 1984). However, the increase in breeding performance with age demonstrated in this and other studies results in part from differential survival of higher and lower quality individuals (Nol & Smith 1987; Thomas & Coulson 1988; Aebischer & Coulson 1990; Wooller et al. 1990). Older birds may therefore be better

able to maintain high reproductive effort without incurring any costs in terms of higher mortality or lower future breeding success. In this case, the higher reproductive effort of older birds may result from every bird, irrespective of age, working as hard as it is able to without incurring any costs. To support life history theory, increases in reproductive effort with age must be demonstrated in association with an increased cost of reproduction among older individuals.

The lack of a decline in body condition with age for great skuas (see Results) does not at first appear to support the notion of increased costs of reproduction among older birds. However, since older birds spent longer foraging than younger birds only during chick-rearing (Table 5.3) then no differences related to foraging effort would be expected during incubation.

Return rate for males, but not females, between 1989 and 1990 decreased with age (see Results). The reason why males were effected more than females is unclear, but coincides with a significant reduction in weight for males, but not females, during incubation, and with a tendancy for males to do much more foraging than done by females (Furness 1987). The lower return rates of older males could be seen either as the selective basis for increased reproductive effort with age (Pianka & Parker 1975; Pugesek 1984) or as evidence of an increase with age in the cost of reproduction; i.e. it could be either the cause or the effect of an increase in reproductive effort with age. The proportion of great skuas of all ages breeding in consecutive years appears to have decreased since the 1970s, in association with an increase in reproductive effort (Hamer et al. in press). This strongly suggests the latter, and supports the view that age-specific patterns of reproductive effort in great skuas are

in keeping with the predictions of life history theory. However, since a decline in residual reproductive value among older birds is both the selective basis and the predicted outcome of an increase in reproductive effort with age, then the predictions of life history theory regarding age-specific reproductive tactics constitute a circular argument.

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CHAPTER 6

Variations in brood defence by great skuas:

a test of hypotheses

6.1 SUMMARY

Individual, seasonal and year to year variations in the
intensity of aggressive brood defence by great skuas Catharacta
skua were used to test six hypotheses relating variation in
brood defence to differences in parental quality and investment,
body condition and sex, and to the risk of predation to adults
and young. Differences in the intensity of aggressive responses
of adults to intrusion within their territories were found to be
related to adult quality, in terms of clutch hatching date, and
to body condition, in terms of mass corrected for body size.
The intensity of adults' responses was also dependant upon the
risk of injury or predation to adults. Further evidence
supported the hypothesis that the post-hatching decline in the
intensity of brood defence found in many nidifugous species
results from mobile young being able to secure their own
protection by hiding.

6.2 INTRODUCTION

Brood defence is one aspect of parental investment (Trivers 1972; Barash 1975; Pierotti 1981) and has been studied in detail in a range of nidicolous bird species (Curio 1975; Greig-Smith 1980; East 1981; Blancher & Robertson 1982; Buitron 1983; Wiklund 1990). Several models have been developed to explain individual, temporal and geographic variation in its intensity (Barash 1975; Andersson, Wiklund & Rundgren 1980; Curio, Regelmann & Zimmermann 1984; Sargent & Gross 1985; Regelmann & Curio 1986), and while some studies have upheld their predictions (Weatherhead 1979; Biermann & Robertson 1981; Regelmann & Curio 1983; Coleman, Gross & Sargent 1985) others have falsified them (Knight & Temple 1986; Wallin 1987).

Six hypotheses, which are not mutually exclusive, attempt to explain variations in brood defence:

1) It increases in intensity with offspring vulnerability. This may explain the post-hatching decrease in brood defence by many nidifugous species (Simmons 1955; Kruuk 1964; Furness 1987) if mobile young are able to secure their own protection by hiding (Barash 1975; Andersson et al. 1980).

2) Parents mob potential predators in relation to the risk of predation to themselves, the intensity increasing when the risk is low (Hudson & Newborn 1990).

3) Brood defence varies as a function of parental condition, with birds in better condition being less at risk of injury or capture, and so mobbing more intently (Bergerud 1970).

4) Level of brood defence is related to the cost of reaching the same stage of the breeding season after the loss of an offspring (Dawkins & Carlisle 1976; Harvey & Greenwood 1978).

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5) Brood defence varies as a function of adult quality.

6) Intensity of brood defence differs between sexes. Males are generally more aggressive and engage in more brood defence than females (Pierotti 1981; Wiklund & Stigh 1983; Regelmann & Curio 1986; Burger 1987; Breitwisch 1988; Burger & Gochfeld 1990). This may result from size-specific differences in risk of injury (Knapton 1984) or from selection favouring males which reduce an initial inequality in reproductive effort between the sexes (Trivers 1972; Burger 1987; Wiklund 1990).

Brood defence by great skuas Catharacta skua takes the form of mobbing, directed towards conspecific and other intruders, with the aim of driving them from their territories. It shows considerable individual and seasonal variation, generally reaching a peak around hatching and declining throughout chick-rearing (Furness 1982; 1984; 1987).

During the 1970s, adults at the largest colony of great skuas, on Foula, Shetland spent little time foraging (Furness & Hislop 1981) and enjoyed high breeding success with almost no predation upon chicks (Furness 1983; 1984). This was considered to be possible because there was an abundant food supply in the form of sandeels Ammodytes marinus (Furness & Hislop 1981; Furness 1984). Since the 1970s there has been a major decline in the availability of sandeels around Shetland (Gauld, McKay & Bailey 1986; Hudson & Furness 1988; Monaghan, Uttley & Okill 1989; Monaghan et al. 1989; Harris & Wanless 1990; Bailey, Furness, Gauld & Kunzlik in press), and this has had profound effects upon the breeding ecology of great skuas on Foula. Adults have increased their work rate to a level close to the limits of their ability (Hamer, Furness & Caldow in press) and this represents an increase in parental investment, both in

terms of expenditure of time and energy (Knapton 1984) and in time and energy required to replace lost offspring (Dawkins & Carlisle 1976). Adults have also suffered an increase in chick predation from less than 5% to a frequency in excess of 80% of chicks hatched, while egg predation has remained at approximately 10% of eggs laid (Hamer et al. in press). These changes provide an opportunity to test hypotheses relating brood defence to parental investment and to risk of brood predation under the conditions of a 'natural experiment'.

This chapter presents information on the factors associated with variation in brood defence by great skuas, and tests the predictions of six hypotheses concerning individual, seasonal and year to year variations in brood defence.

6.3 METHODS

Samples of great skua nests on Foula were marked in early May of 1975, 1976, 1988, 1989 and 1990. The numbers of nests marked in each of these years were 447, 434, 160, 198 and 138 respectively. Breeding statistics and adult attendance at marked nests were determined using methods described by Furness (1983; 1984) and Hamer et al. (in press). Territorial attendance patterns give a good indication of work rate, since most of the time which great skuas spend away from their territories is spent foraging (Furness & Hislop 1981). Clutch size and adult work rate, as reflected by territorial attendance, were used as measures of adults' investment in reproduction. This allowed two independant tests to be made of the hypothesis that brood defence varies with parental investment, one comparing individuals in the same year, the other comparing individuals at the same colony in different years. Hatching date was used as an

index of adult quality since, as with most other birds, breeding success decreases monotonically with hatching date in great skuas (Furness 1983; 1984; 1987).

To test hypotheses relating brood defence to adult sex, size and body condition, adults were trapped during incubation at samples of nests chosen at random from those marked in 1988 and 1989, using a clap net (Spencer 1984) placed at the nest. Only one adult was trapped at each nest, and no attempt was made to trap an adult at all marked nests. All adults caught were weighed and measured (maximum wing chord, tarsus length, length of head plus bill, bill length and bill depth), and the measurements were used in a discriminant analysis (Norusis 1988) to determine sex by comparison with 40 birds found dead or shot under licence on Foula and sexed by internal examination (see Chapter 2). Measurements and weights were also used to calculate an index of body condition, in terms of body mass corrected for body size (Reid 1988). Size was calculated from body measurements using principal components analysis (Norusis 1988; the index produced by the analysis is the sum of values for tarsus length, maximum wing chord and length of head plus bill, standardized to have sample means of nought and standard deviations of one). The factor score representing body size was then regressed against body mass, and the condition of each adult was determined as the residual (observed minus predicted) mass.

Every adult caught was given a unique combination of four coloured leg rings. Study territories were visited on two or three occasions during incubation and a further three during chick-rearing. Frequency and intensity of brood defence by marked individuals was scored on a five-point increasing scale,

depending upon the level of aggression exhibited in the reactions of colour-ringed birds to a single human intruder within their territories. For other study territories, where neither adult had been trapped, the score recorded was that of the more aggressive partner. In 1975 and 1976, territories were visited at intervals of two to three days, and the response of the more aggressive partner was recorded in each case. In 1990, separate scores were determined for both adults at each territory. Adult aggression score was determined using the following criteria (from Furness 1984):

1. adult left territory

2. adult circled above territory but did not swoop

3. swooped at intruder but did not hit

4. swooped regularly but hit only rarely or lightly

5. swooped regularly and hit hard on most swoops

Aggression scores were recorded only at territories with eggs or live young and when both parents were present. The modal value obtained during incubation was used to describe the aggressiveness of each bird. This gives a consistent measure, and correlates with aggressiveness in other contexts (Furness 1984).

Aggression scores recorded during incubation and chick-rearing were used to test whether brood defence varied within a season with the risk of predation of offspring. As an independant test of the hypothesis that brood defence declines during incubation in nidifugous species because mobile chicks become harder to find as they grow (Simmons 1955; Barash 1975; Andersson et al. 1980), the time taken to find chicks in marked territories was recorded during the chick-rearing period of 1989. In each case, a single observer (K.C.H.) commenced

searching at the nest and recorded the time taken to find
chicks. The identity of chicks was determined from British Trust
for Ornithology rings, fitted shortly after hatching, and chick
age was determined from wing length (Furness 1977).

6.4 RESULTS

Aggression scores and breeding statistics

120 adults were trapped during incubation in 1988 and a
further fifty-five5 in 1989. The low attendance of adults at
their territories in these years (Hamer et al. in press) meant
that aggression scores were recorded at only 129 nests. There
was no difference between aggression scores at nests where an
adult was or was not caught (Mann-Whitney U-test; Z = -0.52, n =
168, P = 0.61). The discriminant analysis allowed the sexes of
trapped birds to be determined to a high degree of accuracy
(approximately 90% of the cases of known sex were classified
correctly by the analysis).

Table 6.1 shows mean numbers of eggs hatched, addled and
eaten by predators plus mean numbers of chicks fledged at
territories defended by adults with different aggression scores
in 1988 or 1989. Aggression scores did not differ between years
(see below). Hatching success increased with aggression
(Kruskal-Wallis analysis of variance; Chi-square = 14.88, n =
129, P = 0.001) while numbers of eggs addled and suffering
predation both decreased with increasing aggression (Kruskal-
Wallis; Chi-square = 6.64, n = 129, P = 0.04 and Chi-square =
7.57, n = 129, P = 0.02, respectively). Fledging success
increased with aggression (Kruskal-Wallis; Chi-square = 9.77, n
= 129, P = 0.008).

TABLE 6.1. Egg and chick survival for great skuas with different aggression scores in 1988 or 1989.

Aggression Score	n	Number of eggs						No. of chicks	
		Hatched		Addled		Eaten		Fledged	
		mean	S.D.	mean	S.D.	mean	S.D.	mean	S.D.
1	8	0.88	0.99	0.50	0.53	0.63	0.74	0.00	0.00
2	17	1.12	0.86	0.65	0.86	0.18	0.39	0.00	0.00
3	66	1.56	0.61	0.26	0.51	0.17	0.41	0.14	0.43
4	24	1.58	0.58	0.25	0.44	0.08	0.28	0.29	0.69
5	14	1.71	0.46	0.21	0.43	0.00	0.00	0.50	0.76

means are per pair of adults. n is the sample size and S.D. the standard deviation of each mean.

Aggression and parental investment

Table 6.2 shows the numbers of birds with different aggression scores in different years. Despite significant changes in adult attendance (Table 2; Hamer et al. in press), there were no differences between years in median aggression scores (Kruskal-Wallis one-way analysis of variance; Chi-square = 4.06, n = 1069, P = 0.26). Nor was there a relationship between clutch size and aggression (Mann-Whitney U-test for marked adults at nests with one or two eggs; Z = -1.07, n = 129, P = 0.28).

Aggression and risk of brood predation

In 1988 and 1989, over 80% of hatched chicks suffered predation, while egg predation occurred at a frequency of approximately 10% (Table 6.2; Hamer et al. in press). Despite this, aggression scores of individual pairs were higher during incubation than during chick-rearing (Wilcoxon matched pairs test; Z = -2.25, n = 22, P = 0.02; the comparatively small sample size reflects the small number of occasions when both adults were present at territories with live chicks).

TABLE 6.2. Aggression scores, hatching success, fledging success and adult attendance for great skuas on Foula, between 1975 and 1989.

Aggression score	1975 n	%	1976 n	%	1988 n	%	1989 n	%
1	24	5.0	28	7.0	5	3.9	2	3.2
2	105	22.0	68	16.9	14	11.0	10	15.9
3	165	34.6	182	45.3	66	52.0	37	58.7
4	145	30.4	105	26.1	27	21.3	8	12.7
5	38	8.0	19	4.7	15	11.8	6	9.5
Hatching	477	66.1	434	73.3	160	72.3	198	75.2
Fledging	315	95.3	318	91.1	116	7.8	149	16.5
Attendance	–	–	160	1.47	156	1.03	194	1.17

See text for method of determining aggression score. Hatching is the proportion of eggs which successfully hatched; fledging is the proportion of chicks which fledged; attendance is the mean number of adults per territory. n is the number of territories studied in each case.

Time taken to find chicks was positively correlated with chick age (Spearman correlation, r = 0.37, n = 317, P < 0.001). Great skua chicks are not very mobile for the first day or two after hatching (Furness 1987), so to test whether this correlation was independant of the effect of finding very young chicks in their nests, the analysis was repeated using only chicks with an age greater than two days. The result was the same (r = 0.32, n = 241, P < 0.001).

Comparisons between sexes

Table 6.3 shows aggression scores for incubating males and females at different nests in 1988 or 1989. There was no difference between sexes in median scores (Mann-Whitney U-test; Z = -1.48, n = 129, P = 0.14). Nor was there a difference between aggression scores of individual males and females at the same territories (Wilcoxon matched pairs test; z = -0.92, n = 53, P = 0.36). However, there was a correlation between the

aggression scores of the two members of each pair (Spearman correlation; r = 0.33, n = 53, P = 0.02).

TABLE 6.3. Aggression scores for incubating male and female great skuas.

Aggression score	male n	%	female n	%
1	2	3.8	6	7.8
2	6	11.5	11	14.3
3	26	50.0	40	51.9
4	9	17.3	15	19.5
5	9	17.3	5	6.5

n is the number of adults in each case.

Aggression and adult size, body condition and quality

Table 6.4 shows mean values for size and body condition indices for incubating males and females with different aggression scores. Aggression was not related to size (Kruskal-Wallis analysis of variance; Chi-square = 6.01, n = 77, P = 0.20 for females; Chi-square = 2.48, n = 52, P = 0.65 for males). However, aggression increased with body condition for females (Kruskal-Wallis; Chi-square = 9.89, n = 77, P = 0.04). Aggression of males was also related to body condition, but by a reciprocal relationship. Males which struck the observer (scores of 4 and 5) had significantly lower values for body condition than those which did not (Mann-Whitney U-test; Z = -2.04, n = 52, P = 0.04).

Hatching dates differed slightly between years. The first chick to hatch from each successful clutch did so on average 16.3 and 17.7 days after 1st June in 1988 and 1989 respectively.

TABLE 6.4. Size and body condition index for incubating male and female great skuas with different aggression scores.

Aggression Score	males					females				
	n	size mean	S.D.	condition mean	S.D.	n	size mean	S.D.	condition mean	S.D.
1	2	0.3	0.2	45.9	48.0	6	1.3	3.3	-92.2	35.2
2	6	-1.0	1.7	28.2	80.7	11	-0.2	1.3	20.4	95.5
3	26	0.2	1.8	13.5	92.3	40	0.2	0.2	-4.7	86.8
4	9	0.4	1.6	-14.3	87.2	15	0.0	0.8	31.5	97.2
5	9	0.3	1.5	-26.7	62.1	5	1.5	0.2	45.4	138.1

n is the number of adults and S.D. the standard deviation of each mean. See text for method of deriving body condition index.

Table 6.5 shows the mean hatching date of the earlier-hatched chick in each brood, relative to the mean in the year of sampling, for marked adults with different aggression scores.

TABLE 6.5. Relative hatching date for incubating great skuas with different aggression scores.

Aggression Score	n	mean	S.D.
1	2	4.0	7.1
2	9	3.1	5.5
3	57	0.3	4.9
4	23	-2.3	3.5
5	13	-4.0	3.3

Relative hatching date is the difference in days between the hatching date of the earlier-hatched chick at each nest and the mean hatching date in the year of sampling. It has a negative value for dates before the mean. n is the number of nests and S.D. the standard deviation of each mean.

The parents of chicks which hatched earlier were significantly more aggressive than those with later-hatching chicks (one-way analysis of variance; F ratio = 5.12, n = 103, P = 0.001; all data were homoscedastic, as determined by Bartlett's test, and

normally distributed, as determined by Kolmogorov-Smirnov one-sample tests). The smaller sample size in this test was due to egg failure, mainly of birds with low aggression scores (see Table 6.1).

6.5 DISCUSSION

Collection of data

Trapping adults did not alter their aggression, since there was no difference in the scores at nests where an adult was or was not trapped (see Results). The two sets of data were collected in slightly different ways, since at nests where an adult was trapped the score recorded was for the marked bird, regardless of whether or not it was the more aggressive partner. This would introduce a bias into the comparison if the two members of a pair differed in their aggressiveness. However, this was not the case, since there was no systematic difference in the scores for males and females, and the responses of each member of a pair were correlated (see Results).

Frequent exposure to the same stimulus may cause either a decline in the intensity of adults' responses through habituation (Hinde 1954; Burger & Gochfeld 1983) or an increase through reinforcement (Knight & Temple 1986). Lemmetyinen (1971), in a study of Arctic terns _Sterna paradisaea_ and common terns _Sterna hirundo_ considered intervals of two days between exposure to be sufficient to overcome this problem. In this study, territories were visited at intervals of two to three days in 1975-76 and approximately ten days in 1988-90. Furthermore, all but one of the comparisons made in this study were between birds with similar previous exposure to the observer in terms of numbers of visits to their territories.

Aggression and breeding success

Several studies have documented the effectiveness of aggression in deterring predators (eg. Lemmetyinen 1971; Montevecchi 1977, 1979; Veen 1979; Bildstein 1982; Shields 1984). In this study, egg and chick survival both increased with adult aggression (Table 6.1). This may be the direct effect of potential predators being deterred by the aggressive responses of adults, or it may reflect an association between adult quality and aggression. The lower proportions of addled eggs and earlier hatching dates of more aggressive birds (Tables 6.1 and 6.5 respectively) both support the latter, while the lower frequency of egg predation among more aggressive birds (Table 6.1) suggests that higher aggression in itself increases egg survival. Although most chick mortality was the result of predation, the higher fledging success of more aggressive birds (Table 6.1) probably reflects adult quality rather than direct deterrence of potential predators, since most chicks were killed as a result of neighbouring conspecifics attacking unguarded chicks when both parents foraged simultaneously (Hamer et al. in press).

Parental investment

Hudson & Newborn (1990) found no support for the hypothesis that the intensity or frequency of distraction displays by red grouse Lagopus lagopus scoticus depend upon the level of parental investment. In this study, there was no relationship between the cost of replacing a brood, in terms of either its size or the work rate required to reach the same stage of the breeding cycle, and the intensity of aggressive brood defence by

adults (Table 6.2 and see Results). Aggression increased throughout incubation, but declined during chick-rearing, despite the fact that parental investment continued to increase during this period (Trivers 1972; Burger & Gochfeld 1990). The lack of a relationship between parental investment and intensity of brood defence is perhaps not surprising for a long-lived iteroparous species (great skuas have an annual adult survival of 93%; Furness 1978) in which investment in any one year represents only a small proportion of lifetime investment in reproduction.

Risk of brood predation

Aggression was higher during incubation than during chick-rearing regardless of whether egg or chick predation occurred at a higher frequency (Table 6.2 and see Results). This does not support the hypothesis that brood defence varies with risk of brood predation. However, since most chick predation occurred when chicks were left unguarded (see above), the risk of chick predation occurring while one or both parents were present may not have been related to the overall frequency of predation. Search times for chicks increased significantly as chicks grew (see Results), probably because their mobility increased with age (Furness 1987). Although the time it took a human observer to find chicks increased with their age, this may not have been the case for the main predators of chicks at this colony (neighbouring conspecifics). However, since the best indicator of the location of chicks is likely to be proximity to a nest, it is reasonable to assume that as chicks increase their mobility they will be less easy for any predator to locate (Hunt & Hunt 1976).

Comparisons between sexes

There was no difference in the intensity of brood defence by male and female great skuas, whether comparing median aggression scores for samples of nests or aggression scores within individually identifiable pairs (Table 6.3 and see Results). Burger (1987) found that male herring gulls Larus argentatus were more aggressive than females, but that pairs with more similar levels of aggression reared more young. Wiklund (1990) found a similar relationship between equitability of brood defence and breeding success in merlins Falco columbarius. The lack of a difference in aggression scores of male and female great skuas lends some support to the idea that their behaviour is the result of selection for equal investment in reproduction (Burger 1987). However, brood defence is only one aspect of reproductive effort, and this question requires further examination. Knapton (1984) suggested that greater aggression of males may result from their being larger and so at less risk of injury. This leads to the prediction that since female great skuas are larger than males (Furness 1987) they should be more aggressive. However, this was not the case (see Results).

Risk to adults

There was a significant correlation between the aggression scores of males and females at each territory (see Results). This suggests that brood defence varies with the risk of injury or predation to the parents, since the risk to either parent will be lower if its mate is present and displaying at a high intensity (Hudson & Newborn 1990). An alternative explanation,

that aggressive displays facilitate choice among prospective partners (Curio, Regelmann & Zimmermann 1985; Wiklund 1990) is unlikely to apply to established pairs in long-lived species with high mate fidelity. Further support for a relationship between brood defence and risk to parents comes from the lower aggression scores of adult great skuas in the absence of their partners or in the presence of more intruders within their territories (Burton 1968; Furness 1984, 1987) and from the higher aggression displayed towards intruders such as sheep Ovis (domestic) which have little capacity to harm adults (Furness 1987). Furthermore, great skuas in the Antarctic and sub-Antarctic, which have received little human persecution, are much more aggressive than populations in the northern hemisphere, which have been highly persecuted (Furness 1987). Knight, Anderson, Bechard & Marr (1989) recorded a similar correlation between aggression and history of persecution in red-tailed hawks Buteo jamaicensis, which they regarded as being due in part to learning. However, the lack of a difference in aggression between males and females (see above) does not support the hypothesis that aggression is related to the risk to adults if larger birds are less at risk of injury, as suggested by Knapton (1984).

Adult size, body condition and quality

Aggression was not related to adult size, but varied significantly with body condition for both sexes (Table 6.4). However, while it increased with condition index for females, the opposite was true for males. Condition indices may have little value if they are based on a single measure of size or if they fail to account for seasonal or sex differences in size and

body proportions (Ormerod & Tyler 1990). The index used in this study was based upon several morphometric variables recorded at the same stage of the breeding season in each case.

The adaptive value of high or low body condition, as measured in terms of body mass, is likely to change during a bird's lifetime (Reid 1988; Ormerod & Tyler 1990). In the case of great skuas, selection may favour females which maintain high body mass during the breeding season, since they generally spend more time on the territory defending the brood (Furness 1987). Males, in contrast, spend more time foraging (Furness 1987) for which low mass will be an advantage in terms of reducing energy expenditure and increasing agility (Pennycuick 1972; Norberg 1981; Lima 1986). There will be a constraint upon reduction in mass by males if they need to maintain a reserve of fat as a buffer against prolonged exposure to poor feeding conditions (Reid 1988) so that males able to maintain lower body reserves while breeding may be better quality birds, at least in terms of foraging efficiency.

The relationships between body condition and aggression scores of male and female great skuas probably reflect an increase in aggression with adult quality for both sexes, rather than any relationship between body condition and risk of injury or capture, as proposed by Bergerud (1970) and Lima (1986). This is supported by the earlier hatching dates of more aggressive birds (Table 6.5), since laying date (and hence hatching date) is a good index of adult quality (Furness 1983, 1984). Furthermore, aggression increases with age in great skuas (Hamer & Furness unpublished data) and changes with age in several aspects of breeding performance are associated with differential survival of high and low quality individuals (Nol & Smith 1987;

Thomas & Coulson 1988; Aebischer & Coulson 1990; Wooller, Bradley, Skira & Serventy 1990).

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CHAPTER 7

The effects of mercury accumulation by great skuas upon their breeding and survival

7.1 SUMMARY

Great skuas Catharacta skua Brünnich have among the highest tissue mercury concentrations of British seabirds, and many of the birds breeding on Foula in 1988 and 1989 had concentrations well in excess of those known to affect reproduction adversely in some terrestrial bird species. Comparison of mercury concentrations in feathers of great skuas collected before 1900 and in 1988-89 indicates a significant increase during this century, which is assumed to be due to anthropogenic activities (Thompson 1989).

There was no relationship between diet during the breeding season and feather mercury concentration, either comparing mercury concentrations in different years covering a period of major change in diet at the colony, or comparing different birds with markedly different diets in the same year. Great skuas disperse widely during the winter, and differences in exposure to mercury during this period may be more important than differences in diet during the breeding season.

Despite evidence of increased mercury pollution (Thompson 1989), there was no evidence of a relationship between the mercury concentrations of individuals and their breeding performance or survival.

7.2 INTRODUCTION

The adverse effects of high doses of mercury upon various aspects of the breeding biology and survival of captive terrestrial birds have been well documented (Borg et al. 1970; Fimreite 1971; Fimreite & Karstad 1971; Thaxton, Parkhurst & Cogburn 1973; Heinz 1974; Scott et al. 1975; Heinz 1983). The findings of such studies are difficult to relate to seabird populations, which are likely to be adapted to some extent to the relatively high naturally-occurring concentrations of mercury present in marine ecosystems. Fimreite (1974) noted elevated mercury concentrations (up to 6.5 µg g^{-1} fresh weight) in the eggs of common terns Sterna hirundo L. experiencing reduced breeding success, and Becker, Ternes & Russel (1985) suggested that similarly high egg mercury concentrations (up to 5.7 µg g^{-1} fresh weight) in a population of the same species on the German North Sea coast may be endangering their successful breeding. However, Connors et al. (1975) found no significant differences between mercury concentrations in samples of tissues from common terns taken from different localities where birds were experiencing differing breeding successes, and Vermeer, Armstrong & Hatch (1973) noted mercury concentrations of up to 16 µg g^{-1} fresh weight in a sample of eggs from a population of herring gulls which showed normal hatching success. The disparity of these findings might reflect differences between species in sensitivity to mercury. Furness & Hutton (1980) noted a high frequency of addled eggs produced by great skuas at Foula, Shetland in association with somewhat elevated concentrations of mercury in eggs (up to 1.3 µg g^{-1} fresh weight) and high concentrations of PCBs. However, no data were

available in any of these studies for mercury concentrations and breeding success of the same individuals.

In common with gannets Sula bassana L., great skuas tend to have higher mercury burdens than other British seabirds (Walsh 1988; Thompson & Furness 1989; Thompson, Stewart & Furness 1990). Analysis of feathers from museum study skins has shown that mercury concentrations are now about double those in the nineteenth century, presumably due to anthropogenic release of mercury into the environment (Thompson 1989). Feather mercury concentrations are highly correlated with those in liver and muscle tissue, and so reflect current body burdens or mercury (Thompson, Hamer & Furness in press). The colony at Foula has been studied intensively since 1975 (Furness 1987) and approximately half of the adults breeding there were ringed as chicks, and so can be aged from their ring numbers. Great skuas at Foula have recently been affected by a major reduction in sandeel Ammodytes marinus Raitt availability, resulting in a several-fold increase in the proportion of bird meat in their diets during the breeding season (Hamer, Furness & Caldow in press). This is likely to have led to an increase in dietary exposure to mercury, since seabirds generally contain mercury at concentrations far in excess of those in fish (Thompson 1990). Recent reductions in food supply have also placed adults at the colony under stress (Hamer et al. in press), and potentially deleterious effects of elevated mercury burdens would be more likely to be manifested under such conditions.

This paper examines whether recent major changes in food supply and diet during the breeding season have altered the exposure of adults at this colony to mercury, to an extent that can be detected by analysis of feather samples, and whether the

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high tissue mercury concentrations accumulated by adults in Shetland have produced any discernible effects upon their breeding biology or behaviour during the recent period of major food shortage. This study provides the first analysis of the breeding success and survival of individual free-living birds for which mercury concentrations have also been determined.

7.3 METHODS

Sample collection, preparation and storage

Adult great skuas were trapped in 1988 and 1989 during incubation using a clap-net (Spencer 1984) or at club sites (well-defined areas frequented by non-breeding great skuas; Furness 1987) using a cannon net. A sample of six body feathers was taken from between the scapulae of every ringed bird trapped in 1988 and every bird trapped, whether ringed or not, in 1989. Feathers were also obtained from birds shot or found dead, but in a fresh condition, on the island in 1980, 1983, 1987 and 1988. All feathers were stored in mercury-free polythene bags. Prior to mercury analysis, feathers were dried at ambient laboratory temperature (c 22°C).

A sample of 18 whole sandeels was obtained from auks (Alcidae) carrying prey back to the colony on Foula during the 1987 breeding season. Fish lengths were measured (to 0.1 cm) and fish were maintained deep-frozen at c -20°C to await further treatments. Prior to mercury analysis, the fish were oven-dried at 50°C to constant weight and subsequently homogenised using an electric grinder. Fresh weights of sandeels were calculated using the equation W=0.00209L$^{3.148}$ where W = total fresh body weight in g and L = total body length in cm (Harris & Hislop 1978), since fish carried by seabirds are known to suffer a

degree of dehydration (Montevecchi & Piatt 1987) with further dehydration occurring during frozen storage.

Analysis of mercury concentrations

Total mercury and extracted methyl mercury concentrations were determined by a cold vapour technique using a Data Acquisition Ltd. DA 1500-DP6 Mercury Vapour Detector, preceded by a standard acid digestion of samples (Furness, Muirhead & Woodburn 1986). The accuracy and reproducibility of the mercury determination method were tested by analysing International Atomic Energy Agency horse kidney Reference Material H-8 (Thompson & Furness 1989). Mercury concentrations are expressed in terms of fresh weight (Thompson 1989).

Collection of breeding statistics and dietary data

The ages of those adults wearing British Trust for Ornithology rings when trapped during incubation in 1988 and 1989 were determined from their ring numbers. Every adult caught was fitted with a unique combination of four coloured plastic leg rings, to allow identification of individuals, and weighed and measured (maximum wing chord, tarsus length, length of head plus bill, bill length and bill depth). These measurements were used in a discriminant analysis (Norusis 1988) to determine sex by comparison with 40 birds (18 females plus 22 males) shot on Foula in 1988 and sexed by internal examination. This allowed sex to be determined with a high degree of accuracy (approximately 90% of the birds of known sex were classified correctly by the analysis).

All eggs laid at study nests in 1988 and 1989 were measured (maximum length and breadth) to the nearest 0.1 mm using Vernier

callipers. Laying dates, hatching success and breeding success were determined at all marked nests in both years using methods described by Furness (1983, 1984). Ages of chicks at death were determined, where possible, from either wing length or straight, flattened leg length (Furness 1977).

Great skuas generally respond aggressively to intruders within their territories (Furness 1987). The level of aggression displayed by colour-ringed adults in 1988 and 1989 was determined using methods described by Furness (1984). Aggression was recorded as a ranked score between one and five, depending upon the reactions of adults to one observer (K.C.H.) entering a territory and searching for chicks. A score of one was recorded if the adults did not swoop the observer, two if they swooped occasionally but not closely, three if they swooped frequently and/or closely, four if they struck the observer occasionally and/or lightly and five if they struck frequently and with force.

The diets of study adults were determined in 1989 by weekly collection and identification at 40 territories of regurgitated pellets containing the indigestible portions of their food (Furness & Hislop 1981). Pellets were also collected each year at nonbreeder club sites during 1-15 July. Possible diet-related changes in feather mercury concentrations during the 1980s were assessed by comparing mercury concentrations in samples of feathers collected from adults in 1980, 1983, 1987, 1988 and 1989 with diet composition shown by pellets collected in these seasons.

7.4 RESULTS

It can be seen from the data presented in Table 7.1 that, in general, fish exhibit muscle mercury concentrations (c 0.05 μg g^{-1} fresh weight) at least an order of magnitude lower than those which might be expected in seabird muscle (c. 0.2-0.7 μg g^{-1} fresh weight). This difference is greater still (up to two orders of magnitude) when seabird liver methyl mercury concentrations (c. 1.0 μg g^{-1} fresh weight) are considered.

There were no significant differences in feather mercury concentrations between 1980, 1983, 1987, 1988 and 1989 (Table 7.2; one-way analysis of variance, F = 0.87, n = 197, P = 0.48; the five samples in the analysis were homoscedastic, and normally distributed).

In all, 65 females and 42 males, as determined by discriminant analysis, were caught on nests during incubation in 1988 or 1989. Incubating male and female feather mercury concentrations were not significantly different (Table 7.3; Mann-Whitney U-test, Z = -0.34, n = 107, P = 0.74).

A total of 895 pellets were collected from 40 territories of breeding birds in 1989. One pair, whose chicks had died, deserted their territory during the sampling period, leaving a sample of 39 territories. The proportions of pellets deposited at these territories that contained bird prey varied between zero and 75%, and were not correlated with feather mercury concentration of the one adult caught at each territory (Spearman Correlation, r_S = -0.06, n = 39, P = 0.71).

Of the 120 adults colour-ringed on Foula in 1988 (from which 58 were sampled for feather mercury), 72% bred on the island in 1989, 10% returned to the colony but did not breed,

TABLE 7.1. Mercury concentrations ($\mu g \ g^{-1}$ fresh weight) in seabirds and fish from Shetland. Values are means with standard deviations in parentheses.

Fish species	Number sampled	Whole fish	Muscle	Source
Sandeel *Ammodytes marinus*	18	0.04 (0.01)	----	1
Cod *Gadus morhua*	79	----	0.05 (0.02)	2
Whiting *Merlangius merlangus*	20	----	0.07 (0.02)	2
Plaice *Pleuronectes platessa*	25	----	0.03 (0.01)	2

Seabird species	Number sampled	Feather	Liver	Muscle	Source
Fulmar *Fulmarus glacialis*	12	1.1 (0.3)	0.5 (0.2)	0.2*	3
Kittiwake *Rissa tridactyla*	14	2.4 (0.6)	1.0*	0.3*	4
Razorbill *Alca torda*	16	2.1 (0.3)	0.9*	0.3*	4
Common guillemot *Uria aalge*	17	1.5 (0.4)	0.6*	0.2*	4
Puffin *Fratercula arctica*	10	5.2 (2.7)	2.2*	0.7*	4

* Concentration determined using the 7:3:1 feather:liver:muscle mercury concentration ratio. See Thompson et al. (1990).

1. This study; 2. Clark & Topping (1989)

3. Thompson et al. (1990); 4. Thompson & Furness (1989)

while a further 18% did not return to Foula in 1989. Birds with high feather mercury concentrations in 1988 were as likely both to return and to breed in 1989 as those with low mercury concentrations (Table 7.4; Kruskal-Wallis One-way analysis of variance for birds breeding, at the colony but not breeding, or absent from the colony, in 1989; Chi-square = 1.16, n = 58, P = 0.56). Combining those birds absent from the colony with those present but not breeding does not alter the outcome (Mann-Whitney U-test; Z = -0.40, n = 58, P = 0.69).

TABLE 7.2. Feather mercury concentrations of great skuas on Foula in different years between 1980 and 1989.

Year	n	mean	S.D.
1980	17	5.80	3.86
1983	7	7.30	4.27
1987	6	6.20	2.48
1988	109	7.44	4.92
1989	58	6.45	5.87

n is the sample size and S.D. the standard deviation of each mean.

TABLE 7.3. Feather mercury concentrations of female and male great skuas incubating eggs in 1988 or 1989.

Sex	n	mean	S.D.
Female	65	7.13	6.07
Male	42	5.89	3.24

n is the sample size and S.D. the standard deviation of each mean.

There was no relationship between the feather mercury concentration of females and either laying date or clutch volume. In a Spearman correlation between feather mercury

concentration and hatching date of the earlier-hatched chick in each brood, relative to the mean hatching date at the colony in the year when the feather sample was taken, $r_S = -0.0007$, n = 60, P = 0.99. Similarly, in a Pearson correlation between feather mercury concentration of females and clutch volume, relative to the mean in the year when each sample was taken, r = -0.01, n = 65, P = 0.92 (both variables were normally distributed, as determined by Kolmogorov-Smirnov one-sample tests).

TABLE 7.4. Feather mercury concentrations of great skuas caught during incubation in 1988 and breeding on Foula, present but not breeding, or absent from Foula, in 1989.

Status	n	mean	S.D.
Breeding	42	7.31	4.67
Present	7	7.83	4.73
Absent	9	5.39	2.16

n is the sample size and S.D. the standard deviation of each mean.

Of the 214 eggs laid in 1988 and 1989 in nests where an adult was caught and sampled, 163 (77.1%) hatched. Of the 49 eggs which failed to hatch, 29 were 'addled' (the result of infertility or embryo death) and a further 20 suffered predation. Females with addled eggs had feather mercury concentrations no different to those of females which successfully hatched their clutches (Table 7.5; Mann-Whitney U-test, Z = -1.37, n = 65, P = 0.17) and overall hatching success of females was not related to their feather mercury concentrations (Kruskal-Wallis One-way analysis of variance for females which hatched nought, one and two eggs; Chi-square =

2.95, n = 65, P = 0.23). Hatching is also dependent upon

successful incubation, in which males play an important role

(Furness 1987). The analysis of hatching success was repeated

with both males and females included, with a similar outcome

(Chi-square = 1.79, n = 107, P = 0.41). In both 1988 and 1989,

clutch size and hatching success at the colony were normal, but

chick survival was very low (Hamer et al. in press). Chick

survival was not related to adult feather mercury concentration

(Spearman correlation with age at death of the younger chick in

each brood; r_S = -0.08, n = 22, P = 0.73).

TABLE 7.5. Feather mercury concentrations of female and male great skuas with different hatching success and numbers of eggs 'addled'.

		Female			Male	
Hatched	n	mean	S.D.	n	mean	S.D.
0	4	10.93	14.38	5	5.67	2.04
1	16	4.90	2.93	17	6.27	3.81
2	45	7.59	5.76	20	5.60	3.00
Addled						
0	56	7.18	5.39	27	6.31	3.32
1	8	7.15	10.39	12	5.34	3.32
2	1	4.14	-	3	4.42	1.58

n is the sample size and S.D. the standard deviation of each mean. Addled eggs resulted from infertility or embryo death.

The responses of adults at this colony to an intruder

entering their territory varied between flying away and hitting

the intruder hard and repeatedly. The level of aggression

displayed by adults was not related to their feather mercury

concentrations (Table 7.6; Kruskal-Wallis One-way analysis of

variance; Chi-square = 8.63, n = 81, P = 0.07)

TABLE 7.6. Feather mercury concentrations of incubating great skuas with different aggression scores in 1988 or 1989.

Aggression	n	mean	S.D.
1	8	7.22	3.77
2	12	6.32	2.29
3	42	6.71	5.05
4	10	4.28	2.22
5	9	9.99	6.69

n is the sample size and S.D. the standard deviation of each mean.

7.6 DISCUSSION

The proportion of bird meat in the diets of great skuas on Foula showed a five-fold increase during the 1980s (Hamer et al. in press), but this had no discernible effect on the concentrations of mercury in feathers of adults at this colony. Approximately half the bird pellets analysed for this study contained remains of adult auks and fulmars Fulmarus glacialis L. These would be expected to exhibit muscle mercury concentrations at least an order of magnitude greater than those found in fish muscle (Table 7.1).

The lack of any relationship between diets of individuals and their feather mercury concentrations (see Results) is unlikely to result from the fact that feather mercury concentrations represent the previous year's accumulation of mercury (Thompson et al. in press), since birds with high feather mercury concentrations one year are likely to have similarly high concentrations the following year (Thompson et al. in press), and individual specializations in diet are unlikely to change from one year to the next. The two members of each pair are likely to have similar diets, since males

regurgitate food for their mate in their territory (Furness 1987). Pellets deposited in territories are very unlikely to be deposited by birds other than the occupiers, since adults defend their territories vigorously against intruders. Great skuas are widely dispersed outside the breeding season (Furness 1978) and it may be that differences in diet and dispersal during the winter are more important factors determining exposure to mercury in this species.

The highest concentrations of mercury in the livers of great skuas shot on Foula between 1980 and 1988 (Thompson et al. in press) were in excess of those shown to have pronounced effects upon the behaviour of red-tailed hawks Buteo jamaicensis (Gmelin) (Fimreite & Karstad 1971) and pheasants Phasianus colchicus L. (Borg et al. 1969). Reproduction is affected by much lower concentrations of mercury than those required to produce gross toxic effects (Borg et al. 1969; Fimreite et al. 1974), but even so, the accumulation of mercury in tissues of great skuas on Foula in 1988 and 1989 produced no discernible effects upon their reproductive performance. Such effects are often difficult to distinguish in wild populations (Newton, Bogan & Haas 1989), but this study examined possible effects upon several aspects of reproduction involving egg size and quality, chick survival and adult behaviour. Furthermore, the study took place under conditions of food shortage and associated stress (Hamer et al. in press), when any subtle effects are more likely to be shown. Trapping adults on their eggs did not adversely affect their breeding performance, since the hatching success of nests where an adult was caught was no different from that at control nests recorded by Hamer et al. (in press).

The use of feathers, taken from recognisable individual birds, to monitor the possible effects of mercury upon breeding success has several advantages. Since feather mercury concentrations correlate well with those of internal tissues (Thompson et al. in press), the need for an invasive sampling technique is removed. The use of eggs to assess mercury burdens with respect to reproductive parameters is prone to several drawbacks. The laying sequence of eggs should be known since mercury concentrations decrease from the first to the last-laid egg (Becker, Conrad & Sperveslage 1989). Furthermore, the use of addled eggs to determine mercury concentrations may introduce bias to the results whilst the use of viable eggs for this purpose reduces the scope for following the breeding success within a particular clutch. Newton & Haas (1988), in a study of breeding success in merlins Falco columbarius L., analysed mercury concentrations of eggs taken randomly from nests but took no account of laying sequence. Their suggestion that mercury adversely affected breeding success in this species would appear somewhat overstated, especially since the negative relationship between brood size and egg mercury concentration was found to be stronger when birds with the highest egg mercury concentrations were removed from the regression (Newton & Haas 1988).

Perhaps most importantly, mercury concentrations in eggs of seabirds appear to reflect mercury concentrations in the diet immediately before egg-laying and not the body burden of mercury stored in the female (Becker et al. 1985), so that mercury accumulation in winter might affect female survival or behaviour but not be recorded in egg mercury concentrations. By contrast, feather mercury concentrations appear to reflect overall annual

uptake rather than mercury concentrations in the diet at a particular time in the year (Furness et al. 1986; Honda et al. 1986; Braune & Gaskin 1987).

Associations between tissue mercury concentrations and decreases in some aspect of reproductive performance at a population level do not necessarily demonstrate cause and effect (Furness & Hutton 1980; Furness et al. 1989). An 'individual' approach to the potentially adverse effects of relatively high pollutant levels upon breeding success would be more likely to demonstrate such effects, if they existed.

The lack of any effect of mercury upon the reproduction of great skuas on Foula is in keeping with the results of similar studies (at a population level) of gannets (Fimreite, Kveseth & Brevick 1980) and herring gulls (Vermeer et al. 1973), and emphasises the difficulty in inferring toxicity in one species from described effects in another (Ohlendorf, Risebrough & Vermeer 1978), although it seems reasonable to conclude that seabirds appear better adapted than terrestrial birds to deal with relatively high concentrations of mercury.

It is clearly useful to draw attention to possible links between mercury pollution and reduced breeding success in wild populations. However, the lack of any association between mercury and breeding performance in this study, at a colony which does nonetheless exhibit high mercury concentrations and poor breeding success, emphasises the need for rigorous methods which examine mercury accumulation and breeding performance on an individual basis and eliminate possible effects of confounding variables.

7.7 REFERENCES

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CHAPTER 8

Discussion

The recent large-scale decline in sandeel stocks around Shetland (Gauld, McKay & Bailey 1986; Hudson & Furness 1988; Kunzlik 1989; Monaghan, Uttley & Okill 1989; Bailey et al. in press) has had a profound and deleterious effect upon most species of seabird breeding there (Bailey, Furness, Gauld & Kunzlik in press). However, there is clearly much information to be gained by studying the details of their responses to this major reduction in food supply.

The responses of great skuas at a population level were generally in accord with those of other species, both in Shetland (Furness 1989; Heubeck 1989; Martin 1989; Monaghan et al. 1989; Bailey et al. in press) and in other regions (see Furness & Ainley 1984, Cairns 1987, Furness 1987 and Montevecchi, Birt & Cairns 1988 for reviews) where seabirds have experienced reductions in prey availability. Because great skuas are opportunistic feeders, the proportions of items other than sandeel in the diets of non-breeders and chicks increased over the period of declining sandeel stock (Chapter 3). Adults increased their predation upon other seabirds, as Furness & Hislop (1981) predicted might occur in response to a decline in the availability of sandeels. This has important implications for seabird conservation within Shetland, particularly as it coincides with major reductions in the breeding success of most species of seabird there, and merits further study into its likely impact.

Adult territorial attendance, chick weight growth and breeding success all declined over the period of declining sandeel stock (Chapter 3), indicating that a high abundance of sandeels had been an important factor in determining the breeding success of great skuas on Foula during the 1970s.

Some aspects of the responses of great skuas to the decline in prey availability were not in keeping with expectations. The willingness of adults to leave their chicks exposed to high risk of predation (Chapter 3) would not have been intuitively predicted. Furthermore, life history theory would not predict that breeding adults would increase their work rate to such an extent that it reduced their future breeding potential (Goodman 1974; Pianka 1976), yet there is some evidence that this was the case (Chapter 3).

The availability of a large number of birds ringed as chicks, and so of knowable age, presented a rare opportunity to examine age-specific differences in the responses of individuals to a reduction in food supply. The data presented in Chapter 5 indicate that adult age has a similar influence upon the breeding performance of great skuas to that seen in other species (see Ryder 1981 for a review; Nisbet, Winchell & Heise 1984; Shaw 1986; Ainley, Ribic & Wood 1990; Weimerskirch 1990; Williams 1990; Wooller, Bradley, Skira & Serventy 1990), when food is scarce. Increases with age in time spent foraging and aggression displayed in brood defence (Chapter 5) are in keeping with the predictions of life history theory regarding age-specific changes in reproductive effort (Pugesek 1983; Curio 1983; Reid 1988), although not to the exclusion of other hypotheses. Further study of age-specific differences in time and energy budgets and in likelihood of breeding in successive years should throw important light on this subject.

Increased adult mortality resulting from failures in food supply have been recorded elsewhere (Barber & Chavez 1983; Duffy 1983; Schreiber & Schreber 1984; Duffy & Merlen 1986), but adult

great skuas would not be expected to starve as a result of a reduction in sandeel stocks, since they are highly versatile feeders and there is a plentiful supply of alternative food around Foula. However, there is evidence that the mortality of great skuas on Foula increased during the 1980s (Chapter 4). Further study of the annual returns of colour-ringed birds should be able to confirm or refute this indication, and give a better indication than has been possible to date of the extent to which absence from the colony is due to mortality.

The usefulness of marking birds individually is further indicated by their use in Chapter 6 to test hypotheses concerning individual, seasonal and year to year variation in brood defence. The fact that body condition, in terms of body mass corrected for body size, had an opposite relationship with aggression displayed by males and females indicates that the adaptive value of high or low body mass is likely to differ between individuals. This has an important bearing upon the use of body mass as an indicator of general body condition and quality (Norberg 1981; Lima 1986; Reid 1988; Ormerod & Tyler 1990).

The value of collecting data for recognizable individuals is further emphasised by the results of Chapter 7. These indicate that although feather mercury concentrations of great skuas on Foula are among the highest recorded for British seabirds (Thompson & Furness 1989; Thompson, Stewart & Furness 1990), and were recorded in conjunction with low breeding success, the relationship is not one of cause and effect. This has important implications for future studies of the effects of pollutants upon breeding performance and reproductive success.

The timing of the changes in different aspects of breeding

ecology (Chapter 3) may reflect differences in their usefulness as monitors of the marine environment (Cairns 1987; Furness 1987). Large-scale reductions in chick growth and breeding success occurred only after a major reduction in sandeel stock. On the other hand, the proportion of sandeel in the diets of great skuas on Foula started to decline before other effects became apparent. The diets of non-breeders gave the earliest indication of a decline in sandeel availability, probably because non-breeders were not constrained by the need to provide suitable food for chicks. This suggests that where birds can switch to alternative food sources in response to a decline in prey availability, the diets of non-breedes may be the most sensitive indicators of such a decline. For great skuas, collection of suitable data is comparatively straightforward, since non-breeders gather at discrete sites, to the exclusion of other birds, where they regurgitate pellets from which their diets can be assessed.

The relative ease of obtaining data concerning diets and other aspects of the breeding ecology of great skuas, their high site fidelity and the presence of a large sample of colour-ringed adults, approximately half of them of known age, all mean that great skuas on Foula provide an outstanding opportunity for further study of the responses of individuals, either through a prolonged period of food shortage or during a period of recovery in sandeel stocks.

8.1 References

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SUMMARY

1) A discriminant function used to sex great skuas on Foula, Shetland correctly classified 87.5% of the sample from which it was derived, and several lines of evidence suggest that it performed similarly with a sample of live birds caught over a three-year period. There was no evidence that any of the variables used in the analysis changed during the period of the study or were affected by conditions at the colony during birds' development. However, this may not be the case with birds caught in future years.

2) Culmen length was correlated with age, and so was not suitable for inclusion in the analysis. The discriminant function derived by one worker performed comparatively poorly with a sample of birds measured by a different worker, despite the fact that their measurements were in close agreement with each other. Great caution should be applied in the use of discriminant functions, particularly when a function has been derived by a different worker.

3) Data from mid-water research trawls indicate that summer stocks of sandeels in Shetland waters have been very low since 1983.

4) Great skuas on Foula have responded to a decline in the availability of sandeels by increasing the proportion of other items in their diets. This change is correlated with the annual recruitment of sandeels in Shetland waters. Since 1983 there has been a ten-fold increase in predation by great skuas upon other seabirds.

5) Changes in diet have been accompanied by a 50% reduction in adult territorial attendance as adults increased their foraging

effort, such that between 1987 and 1989 breeding adults were probably working as hard as they were able to. Despite this, breeding success was less than 40% in 1987 and less than 15% in 1988 and 1989.

6)   The major cause of breeding failure was predation of unguarded chicks by adults from neighbouring territories. The willingness of adults to expose their chicks to high predation risk is probably maintained because of a positive correlation between chick pre-fledging growth and post-fledging survival, which is expressed up to the age of two years and which will place a strong pressure upon adults to feed their chicks as well as possible.

7)   The high expenditure of effort by adults in 1987 and 1988 did not affect the weights of those birds incubating eggs in 1988 and 1989, but there was a slight (3%) decrease in egg size between the late 1970s and the late 1980s. Changes in the age structure of the breeding population and the absence in 1989 and 1990 of almost a third of adults colour-ringed during incubation in the previous year suggest an increase in the rate of egress since the 1970s. These changes probably represent an increase in the long-term costs of reproduction to adults at this colony.

8)   Analysis of ring recovery data for great skuas ringed as chicks on Foula indicates that annual adult survival was 13% lower in the 1980s than in the 1970s, while first-year survival was unchanged. Estimates of survival derived from recoveries of birds ringed as chicks are sensitive to many possible sources of error, and comparison with estimates derived from annual returns of birds colour-ringed as adults suggests that the analysis of

ring recovery data may have underestimated adult survival during the 1980s by as much as 5%. Nonetheless, the two methods together suggest strongly that the survivorship of adult great skuas in Shetland has declined since the 1970s, in association with a decline sandeel stocks around Shetland.

9)   During a period of reduced food supply, egg laying dates of great skuas on Foula advanced and hatching success increased with age, although breeding success increased with age in only one of the two years studied. Clutch volume increased with age up to fourteen years and decreased with age above this, and could be described by a quadratic equation.

10)   There was no relationship between age and territorial attendance during incubation, but time spent foraging to provide food for chicks increased with age in 1989, while aggression increased with age in both years studied. These are both evidence of an increase in reproductive effort with age.

11)   Older birds may have expended greater reproductive effort simply because they were better able to do so without incurring higher mortality or lower future breeding success. However, return rate between years declined with age for males, which could be a consequence of increased reproductive investment by older birds.

12)   Individual, seasonal and year to year variations in the intensity of aggressive brood defence by great skuas were used to test six hypotheses relating variation in brood defence to differences in parental quality and investment, body condition and sex, and to the risk of predation to adults and young. Differences in the intensity of aggressive responses of adults

to intrusion within their territories were found to be related to adult quality, in terms of clutch hatching date, and to body condition, in terms of mass corrected for body size. The intensity of adults' responses was also dependant upon the risk of injury or predation to adults. Further evidence supported the hypothesis that the post-hatching decline in the intensity of brood defence found in many nidifugous species results from mobile young being able to secure their own protection by hiding.

13) Great skuas have among the highest tissue mercury concentrations of British seabirds, and many of the birds breeding on Foula in 1988 and 1989 had concentrations well in excess of those known to affect reproduction adversely in some terrestrial bird species.

14) There was no relationship between diet during the breeding season and feather mercury concentration, either comparing mercury concentrations in different years covering a period of major change in diet at the colony, or comparing different birds with markedly different diets in the same year. Great skuas disperse widely during the winter, and differences in exposure to mercury during this period may be more important than differences in diet during the breeding season.

15) Despite evidence of increased mercury pollution, there was no evidence of a relationship between the mercury concentrations of individuals and their breeding performance or survival.