Population ecology of Arctic skuas *Stercorarius parasiticus*, on Foula

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This thesis is dedicated to the memory of David Searle

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CONTENTS

SUMMARY

1. The taxonomy, breeding distribution, current status and role of plumage polymorphism in the population dynamics of Arctic skuas are discussed. Information on recent changes in sandeel recruitment in Shetland waters is provided, and some general methods used throughout the thesis are outlined.

2. Both Arctic skua chick growth and fledging success were depressed during the years of low sandeel *Ammodytes marinus* availability, particularly from 1987 to 1990. Adults spent considerably longer foraging in 1987 than they did in 1979, or from 1992 to 1994. However, they were able to breed with moderate success up until at least 1986, in sharp contrast to Arctic terns which failed from 1983 to 1990.

3. The relationships between both chick growth and number of chicks fledged per pair of Arctic skuas, and fisheries-based and avian indices of food availability were better described by threshold effects rather than linear functions.

4. The size of the Arctic skua breeding population in each year and the level of net recruitment (the difference between the observed numbers in a given year and the expected number of breeders surviving from the previous year) correlated with the size and productivity of the Arctic tern breeding population on Foula and an independent fisheries-based index of 0-group and 1-group sandeel abundance in Shetland waters.

5. There was significant annual variation in mean hatching date, clutch size and egg volume, but not hatching success or chick survival to a week. Mean clutch size and egg volume were lowest in 1979 in comparison with 1987 and 1992-1994. Hatching date showed a strong positive relationship with the net recruitment index. It was suggested that these results were a consequence of a change in the age structure of the Arctic skua population since the late 1970s.

6. Analysis of kleptoparasitic interactions of Arctic skuas *Stercorarius parasiticus* foraging within sight of Foula indicated that the skuas were able to switch hosts if

particular species (notably Arctic terns *Sterna paradisaea*) were breeding unsuccessfully in a given year.

7. Breeding Arctic skua adults appeared to be in poorer body condition in 1988, the second year of particularly low sandeel recruitment, and there was also strong evidence that many established pairs deferred breeding in that year and in 1990. Changes in behaviour may therefore act as a buffer allowing Arctic skuas to withstand some degree of reduced prey availability but this appears to involve at least some longer-term costs.

8. From an analysis of individuals processed more than once, it was clear that body measurements were highly repeatable, in several cases across more than a single breeding season. Adult weight recorded during incubation was also highly consistent between years. Morphometrics showed no relationships with adult age.

9. Although ranges overlapped, females were larger than males in all morphometric variables including incubation weight, but with the exception of bill length. Discriminant analyses were used to sex adults on the basis of prior probabilities of group membership of >0.85. A hierarchical system of sex differentiation was developed; sexing by observation, by association or by one of two discriminant functions. Sex was assigned correctly by discriminant analyses to 91.2% of 68 known-sex birds. In total 86.4% of 214 adults measured during 1992-1994 were sexed with a high degree of accuracy.

10. Body weight was closely correlated with body size indices of male and female Arctic skuas (obtained from principal components analyses). Although male body weight (corrected for size) remained reasonably uniform throughout the breeding season, females maintained constant weight (corrected for size) during incubation only, and then showed a sudden stepwise decline when the chicks hatched. It was suggested that this variation was related to sex role partitioning of incubating and chick-rearing duties.

11. Asymmetric declines were observed in the number of occupied Arctic skua territories in different areas on Foula. These were greater at some locations between 1980 and 1986 than would have been expected even if zero recruitment had occured.

12. There were no consistent differences in chick growth or hatching date during 1976-1979 in different areas or when comparing locations where the number of pairs did or did not show a subsequent decline. There was therefore no support for the hypothesis that localised recruitment failures were a consequence of the poor quality of (micro-philopatric) fledglings in previous years.

13. Laying date, breeding synchrony and egg and clutch volume were not related to density in 1992-1994. Chicks in higher density areas with more near-neighbours did grow more poorly in 1992 and 1994. However, the number of chicks hatched increased with increasing density in 1994, and although number fledged was unaffected, post-fledging survival to a week was also better in high density areas. Addling was unaffected by density. These differences were not related to variation in adult age, size or body condition among areas.

14. Egg volume, clutch volume, chick growth, number of chicks hatched and number fledged (but not post-fledging survival) declined seasonally in one or more years, 1992-1994. The incidence of addling increased as the season progressed. Chick growth influenced fledging success in 1993 only, but had no effect on post-fledging survival to a week in 1992 or 1993.

15. An estimated 93% of all new pairs in 1994 could be identified because of movements of adults colour-ringed in 1992 and 1993. Males were much more likely to retain the territory than females in the event of a change of mate. The divorce rate was low - 93% of 27 colour-ringed pairs from 1993 from which both individuals returned were breeding together in 1994.

16. Females identified as being in new partnerships laid later and produced clutches of lower volume than those in the remainder of the population in both 1993 and 1994. They were also more likely to produce a single-egg clutch and to hatch fewer chicks in 1994, and in 1993 single/first-hatched chicks grew more poorly. Birds in known new partnerships formed in 1993 were less likely to be breeding together the following year than those in the remainder of the population.

17. Over 75% of an estimated 45 known-age philopatric adults present on Foula had been trapped by 1994. Around 43% of the population breeding on Foula in 1994 had lived longer than the expected duration of their breeding lifespan on the basis of the 1992-1994 adult mortality rate.

18. There was a significant advance in laying date and, after correcting for pair status, an increase in clutch volume with adult age. Number of eggs laid, chicks hatched and chicks fledged were unaffected by age. Nor did attendance vary with age. There was no evidence of senescence in any aspect of reproductive performance.

19. Arctic skuas breeding on Foula in general showed moderate repeatability in laying dates, moderate to high repeatability in clutch volume and low or insignificant repeatability in chick growth between years, 1992-1994. Females in new partnerships did not show repeatability in laying date or chick growth, and males in new partnerships did not show repeatability in clutch volume or chick growth. It would therefore appear that some attribute of the male determines laying date and of the the female determines clutch volume.

20. Male body condition (weight corrected for size) was negatively correlated with relative laying date, and female body condition (weight corrected for size and stage) was positively correlated with clutch volume. Body size and body condition were unrelated to clutch size or the number of chicks hatched or fledged, and nor were they related to adult over-winter survival between 1993-1994. There was no relationship between size and condition and the difference in laying date and clutch volume between 1993 and 1994.

21. Chick growth but not timing of breeding showed signficant heritability. However, values for heritability exceeded those from repeatability analyses and presumably were slight overestimates. Chick growth and hatching date influenced the probability of survival to recruitment, however neither was related to size or body condition as an adult.

22. A simple model was constructed that estimated the rate of change of the Arctic skua population on Foula using different values for adult mortality, survival to recruitment and fecundity. A separate regression approach, which modelled survival to recruitment as a function of time and various (constant) immigration rates, suggested that juvenile survival declined in the early 1980s but later improved around 1990. The magnitude of this latter increase was heavily dependent on the predicted rate of immigration.

23. On the basis of demographic data collected during 1992-1994 the Arctic skua population was predicted to decline at a rate of 3-4% per year. However, not only have breeding numbers shown a substantial increase or a greater decrease during previous years, but from 1992-1994 they declined at a much greater rate (9% per year). The present rate of decrease was partly attributable to reduced breeding success during the late 1980s, whereas an earlier decline (1979-1987) appeared to be the result of increased adult or juvenile mortality.

24. It was suggested that the rate of immigration had an important influence on population dynamics, particularly as the considerable increase in numbers from 1974-1976 could only have resulted from large-scale immigration. Relatively few recoveries of Arctic skuas ringed as chicks, plus extreme heterogeneity in the recovery rates precluded a quantitative assessment of precise immigration or emigration rates. However, analysis of recovery patterns appeared to indicate that most birds were philopatric and that little movement occured between Orkney and Shetland.

Chapter One. General introduction

"There is a fowl called Scatiullan, of a black colour and as big as a Wild Duck, which doth live upon the Vomit and Excrements of other Fowls, whome they pursue and having apprehended them, they cause them to vomit up what they have lately taken, not yet digested: the Lord` s Works both of Nature and of Grace are wonderful, all speaking forth His Glorious Goodness, Wisdom and Power."

Rev. John Brand (1701)

"...and many other fowles, among which I noted the nature of one, which we called an Allen; who (like the great fishes, which eate up the small, or like some great men, which devoure all the labours of the poore) when some smaller birds have gotten any thing then he leaveth not beating of them, till they have cast up what they have eaten, which he laying hold of devoureth up; and so with little meate in their gorges, and few feathers on their baches, he leaveth them to get more, not for themselves but for him."

Poole (1625)

1.1 Introduction

1.1.1 *Skua taxonomy*

Skuas belong to the family Stercorariidae, closely related to gulls and terns (family Laridae) within the order Charadriiformes. They can be distinguished from Larids by characteristics such as reversed sex size dimorphism, the combination of claws with swimming membranes between the toes, and possession of hard scutes on the legs and a prominent distal nail (the rhamphotheca) on the upper mandible. Pronounced elongation of the two central tail feathers is also apparent in the small skuas (genus *Stercorarius*), although less so in the large skuas (genus *Catharacta*).

There is some dispute as to the phylogenetic relationships within the family Stercorariidae (see Furness 1987 for a discussion). It had appeared that the smaller northern hemisphere *Stercorarius* skuas were separated from the larger, predominantly southern hemisphere (with the exception of the great skua *Catharacta skua skua*) *Catharacta* skuas on the basis of the extensive barring found only on the underparts of juvenile *Stercorarius* skuas (Brooke 1978). This classification has however been disputed both in the past on the basis of behaviour (Andersson 1973), and by recent DNA evidence that suggests, perhaps surprisingly, that the Pomarine skua *Stercorarius pomarinus*, arose from hybridisation between a female great skua and a male Arctic skua *Stercorarius parasiticus* (R.W. Furness and B. Cohen, unpubl. data). On that evidence, all skuas would have to be classified in a single genus. The two genera arrangement however, is the one adopted in this thesis.

1.1.2 *Breeding distribution*

In common with the other *Stercorarius* skuas (Pomarine and long-tailed skua *Stercorarius longicaudus*), Arctic skuas have a circumpolar Arctic breeding distribution (Furness 1987, 1988). Very large numbers (tens to possibly hundreds of thousands) are to be found breeding in Alaska, Canada, and northern Russia in particular. Far fewer, some 3350 pairs in 1985-87, breed in Scotland, although at much greater densities (Lloyd *et al.* 1991). In fact, skuas appear to be better adapted to higher latitude environments. Although all the principal victims of Arctic skua chases are available in large numbers outside its present range, the Arctic skua breeds no further south than Jura within the British Isles (Lloyd *et al.* 1991). Skuas have a high basal metabolic rate and body temperature, a low upper critical temperature and much heavier insulative plumage than other seabirds whose breeding ranges are centred around 60°N (Furness 1988). In addition, across its entire range the southern limit of the Arctic skua's breeding distribution shows a very close correspondence with the 14°C mean July isotherm (Furness 1988). It therefore appears that it is for physiological reasons that they breed no further south.

1.1.3 *Plumage polymorphism*

Skuas (and to an extent also petrels, family *Procellariidae*) are unusual amongst seabirds in that some species exhibit marked ventral plumage polymorphism. All *Stercorarius* skuas and the south polar skua *Catharacta maccormicki*, occur in several colour phases, ranging from dark through intermediate to light, although darker morphs are extremely rare in long-tailed skuas (Ainley *et al.* 1985, Furness 1987). Categorisation can however be somewhat subjective given the degree of gradation within plumage types. For Arctic skuas the ratio of birds of each colour phase shows a distinct cline with latitude, pale phase birds increasing in the population from south to north throughout the breeding range (O'Donald 1983). This implies that an important selective advantage exists for genes associated with the pale colour morph in the north and with the dark form in the southern areas. Numerous hypotheses have been postulated as explanations for the existence of the cline, ranging from sexual selection influenced by assortative mating, regulation of the timing of breeding, the consequence of aggressive camouflage and / or apostatic predator selection during kleptoparasitism (Berry and Davis 1970, Andersson 1976, Arnason and

Grant 1978, Furness and Furness 1980, O'Donald 1983, Rohwer 1983), but in fact none appears particularly convincing (see Furness 1987).

O'Donald and co-workers studying Arctic skuas on Fair Isle found several important demographic correlates of phase (O'Donald 1983, 1987). Dark males bred earlier in the season when they paired for the first time with a new female, apparently as a consequence of sexual selection. However, pale birds recruited at a younger age which partly offset the dark birds' selective advantage. There was also some evidence for assortative mating of the phenotypes but, rather surprisingly, the preference apparently differs depending on colony and year (Bengtsen and Owen 1973, O'Donald 1983, 1987, Furness 1987). In addition, although O'Donald and Davis (1959) considered (in the absence of a more plausible explanation) that the phenotype was determined by the simple mechanism of two alleles at a single genetic locus, the allele for melanic colouration being dominant, population data on offspring and parent phenotypic comparisons do not entirely support this, possibly due to a degree of misclassification (O'Donald 1983). Despite this, by using a modelling approach O'Donald (1983, 1987) concluded on the basis of demographic data that heterozygotes suffered an overall selective disadvantage. Therefore, because the frequency of the pale gene was lower than that which would produce an equilibrium (albeit unstable), pale birds should rapidly be eliminated (O'Donald 1983, 1987). That this had not occured was attributed to a very high immigration rate of pale birds from more northerly populations, thereby balancing their loss via sexual selection.

There was no detectable effect of colour phase on any aspect of the breeding ecology of Arctic skuas on Foula during 1992-1994, including no difference in the laying dates of males of different colour phase breeding with new partners in 1993 or 1994 (Table 1.1). Nor was there any evidence for assortative mating (Table 1.2). It also appears unlikely that the immigration rate onto Foula is anywhere close to the 45% estimated for the Fair Isle population in the 1970s

(Chapter 8). Consequently, the influence of colour-phase on population dynamics of Arctic skuas on Foula is considered to be negligible (at least at present) and is not considered further in this thesis.

Table 1.1. Timing of breeding of male Arctic skuas of different colour phase in new partnerships formed on Foula in 1993 and 1994.

Colour phase	n	Laying date[a]	Relative laying date[b]
Dark	31	28.4±1.3	3.7±1.3
Pale	11	25.4±1.9	0.6±1.8
T-test		t_{40}=1.3, n.s.	t_{40}=1.3, n.s.

[a] - days from 1 May ± 1 s.e., [b] - days relative to the mean in each year ±1 s.e.

Table 1.2. Number of pairs of Arctic skuas of different colour phase breeding together on Foula, 1992-1994. Expected frequencies calculated according to the proportion of dark:pale birds in the population as a whole.

Year		Number:				Observed
		Dark x Dark	Dark x Pale	Pale x Pale	Total	cf. expected frequency
1992	Observed	97	48	10	155	χ^2=1.43, n.s.
	Expected	94.54	53.02	7.43		
1993	Observed	93	41	11	145	χ^2=4.12, n.s.
	Expected	88.90	49.27	6.83		
1994	Observed	84	43	7	134	χ^2=0.23, n.s.
	Expected	83.00	44.93	6.08		

1.1.4 *Status of Arctic skuas in the British Isles*

Within Britain, the Arctic skua is the third rarest regularly breeding seabird after the roseate tern *Sterna dougallii*, and little tern *Sterna albifrons* (Lloyd *et al.* 1991). Around 92% of the population breed in the Northern Isles (Orkney and Shetland), with approximately 2-3% found in each of the Western Isles, Caithness and Sutherland (Lloyd *et al.* 1991). A 1992 census indicated that numbers in Orkney had recently increased by approximately 2% since 1982 to a total of 1056 apparently occupied territories (AOTs), with larger colonies (>75 pairs) found on Papa Westray, Westray, Eday, Rousay, Mainland, Flotta, and Hoy plus South Walls (Ewins *et al.* 1994). In Shetland numbers have declined by 1.8% since 1985-86, to a total of 1878 AOTs in 1992 (Sears *et al.* 1995). Large numbers (>100 pairs) bred on Unst, Yell, Fetlar, Foula and Fair Isle, with Foula holding the third largest colony (Sears *et al.* 1995).

1.1.5 *Feeding habits and adaptations for kleptoparasitism*

In more northerly latitudes (Alaska, Canada and northern Russia), Arctic skuas usually feed by predation, particularly of passerines but also of microtine rodents, on eggs, insects and berries, and only rarely by kleptoparasitism (Maher 1974, Martin and Barry 1978, Birt and Cairns 1987). By contrast, in Britain they obtain food almost solely by kleptoparasitism (Andersson 1976, Furness 1978, 1987, Caldow and Furness 1991). Kleptoparasitism is a somewhat unusual foraging strategy, in which skuas, frigatebirds (Fregatidae), sheathbills (Chionidae) and some Larids and auks may specialise (Brockman and Barnard 1979, Furness 1986, Thompson 1986). A comparison of skuas with gulls however indicates that skuas possess flight muscles with higher levels of oxidative and glycolytic enzyme activity which presumably improves their kleptoparasitic abilities (Caldow and Furness 1993).

1.1.6 *Changes in sandeel availability in Shetland waters*

In Shetland, Arctic skuas obtain sandeels (mainly *Ammodytes marinus*), from Arctic terns *Sterna paradisaea*, puffins *Fratercula arctica*, guillemots *Uria* *aalge*, razorbills *Alca torda*, and kittiwakes *Rissa tridactyla* (Andersson 1976, Furness 1978, 1987, Caldow and Furness 1991). An industrial fishery for sandeels started in Shetland in 1974 and reached a peak in 1982 with a landing of some 52,000 tonnes, although the total catch subsequently showed a considerable decline (Wright and Bailey 1993). During the late 1980s there was a substantial reduction in the recruitment of sandeels to the Shetland stock (Bailey *et al.* 1991, Anon. 1994), and the fishery was closed in 1991. Research surveys undertaken since indicate that very poor recruitment during 1987-1990 (in the last years of the fishery) was followed by relatively good recruitment in 1991, poor recruitment in 1992, moderate recruitment in 1993 and poor recruitment again in 1994 (Anon. 1995). However, some of these estimates (particularly the 1994 value) were based on only a single research vessel index, and few trawls, and so should be treated with caution (Anon. 1995).

Although banned from January 1991 there was little conclusive evidence, given the extreme uncertainties involved in the collection and analysis of fisheries data, that the sandeel fishery had actually caused the recruitment failure (Wright and Bailey 1993). Other large-scale environmental fluctuations have occured in the North Sea and north-east Atlantic in the last 20-30 years. These include an increase in the summer sea-surface temperature around Shetland, progressive delay in initiation of the spring phytoplankton bloom, a decrease in zooplankton abundance, an increase in the dinoflagellate *Ceratium fuscus*, and an increase in the stock of herring *Clupea harengus* (Aebischer *et al.* 1990, Harris and Wanless 1990). In addition, recent studies suggest that all sandeels around northern Scotland form a single large meta-population, with local populations periodically augmented by influxes of larvae and recruiting (0-group) fish (Wright and Bailey 1993). In particular, immigration of Orkney larvae may be important to Shetland year-class strength. It may therefore be nearly impossible to predict probable levels of sandeel biomass and recruitment from year-to-year or to draw conclusions retrospectively as to the agencies responsible for previous changes in numbers. However, regardless of its origin, poor recruitment of sandeels in Shetland waters during the late 1980s was implicated in the widespread breeding failure of many of the seabirds on which the Arctic skua depends (Martin 1989, Monaghan *et al.* 1989, Harris and Wanless 1990, Bailey *et al.* 1991).

1.2 **Aims of the thesis**

On Foula the number of occupied Arctic skua territories increased from the mid to late 1970s but then underwent a substantial decline during the early 1980s until at least 1990, after which there was a slight recovery (see Fig. 2.1). This thesis examines the population ecology of Arctic skuas at Foula with particular reference to recent changes in food supply. Chapter 2 (in press in *Ibis*) investigates the relationship between the changes in sandeel abundance and availability of kleptoparasitic hosts, and parameters such as the population size, net recuitment rate and breeding performance of Arctic skuas on Foula. Changes in the behaviour of Arctic skuas which may have acted to buffer fluctuations in food availability are discussed in Chapter 3 (in press in *Aquatic predators and their prey* edited by S. Greenstreet and M. Tasker). Chapter 4 develops a reliable method for sexing Arctic skuas from external measurements and in addition, examines evidence in support of the adaptive loss of mass by breeding birds, particularly as regards differences between the sexes in their breeding role. Concurrent with the decline in overall numbers of Arctic skuas, there have been pronounced changes in the distribution of territories on Foula. The relationships between density and location, and aspects of reproductive performance as potential explanations for the localised changes in numbers in previous years are discussed in Chapter 5. As a consequence of low productivity in the late 1980s, few recruiting Arctic skuas will have entered the breeding population in the early 1990s. A reasonable proportion of adults on Foula are likely to be relatively old, and the possible influence of age and also the duration of the pair bond on reproduction are discussed in Chapter 6. In addition, recent studies suggest there are marked differences between individuals in lifetime reproductive success. Such variation in adult quality and its effect on reproductive peformance are presented in Chapter 7. Finally, in Chapter 8 ringing recoveries are analysed and a simple model is developed in order to elucidate the mechanism by which changes in adult / juvenile survival, productivity etc. might influence the long-term population dynamics of Arctic skuas on Foula. Chapter 9 is a general discussion. Some general methods used throughout the thesis are described in the remainder of this chapter.

1.3 General methods

1.3.1 *Description of study site*

Foula is a small island approximately 5 x 4 km situated 22km west of the nearest point of Shetland mainland at 60°08′N, 2°05′W (Fig. 1.1). It has the 2nd, 3rd and 4th 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 pre-Cambrian strata in the extreme northeast (Mykura 1976). The substrate is primarily poorly-drained peat moorland with typical short moorland flora. Small areas in the low-lying eastern side are cultivated, mostly around Ristie, Harrier, Ham and Hametoun (see Fig. 1.2), but despite a recent increase in the extent of the island enclosed by fencing, there is little active management of the island. The habitat is influenced most by grazing pressure from several thousand sheep, perhaps 100 Shetland ponies, and one pedigree Shetland cow (although the cow is confined by a peg and a short rope to a rather limited area in south Hametoun). There are around 35 permanent human residents, but numbers are swelled in the summer by the influx of several ornithologists and other regular summer residents, and variable (small) numbers of tourists.

1.3.2 *Early season breeding statistics*

The reproductive performance of the entire island population of Arctic skuas (159, 145 and 134 AOTs in 1992, 1993 and 1994 respectively) was followed between mid May and the end of July during the 1992-1994 breeding seasons.

Territories were visited daily or on alternate days early in the season and the presence of newly-laid eggs established by watching for the initiation of mobbing and/or distracting behaviour by the adults and then locating and checking the nest. Eggs were recorded at all but five AOTs in 1992 and 1993 and all but four AOTs in 1994 - a mean of 96.8% of occupied territories. Most female Arctic skuas lay two eggs, usually with an interval of two-three days between each. Clutch initiation dates could therefore be determined with an accuracy of approximately ± 1-2 days (or less, depending on the frequency of visits) for territories where only a single egg (of a subsequent two-egg clutch) was recorded at first. This was possible for example for over 80% of all two-egg clutches laid in 1994. Only two three-egg clutches were found during the course of the study, one in 1993 and the other in 1994. Nests and eggs were marked, the eggs measured using calipers (length and breadth to the nearest 0.1mm) and the volume (cc) of each egg calculated as 0.00048 x length (mm) x breadth (mm) ^{2} (Coulson 1963).

The fate of all clutches was followed by making repeated visits to territories during incubation and then visits on alternate days, or sometimes daily, around the time of hatching. Although single eggs that disappeared from two-egg clutches were never replaced, if the whole clutch is lost prior to hatching, particularly in the early stages of the season, Arctic skuas will usually re-lay. Replacement clutches (a total of 13, 19 and 13 in 1992, 1993 and 1994 respectively) were also followed and included instead of those pairs' initial breeding attempts in all analyses involving chick growth and survival. To determine hatching success, eggs that were recorded as pipping on the first visit and hatched two days later were assumed to have hatched the previous day, and any chicks found in the nest-cup with their down still damp were assumed to have hatched that day. This allowed the accurate determination of both hatching dates and hatching success. Laying dates were established for any nests that were not located until after clutch completion by subtraction of the appropriate incubation period of 26 days (O'Donald 1983, pers. obs.) from the hatching date of the first or only chick.

1.3.3 *Chick survival*

Recently hatched chicks in two-chick broods were usually marked as either first or second-hatched in 1993 and 1994 using Tipp-Ex on the bill or by clipping the end off the hind nail on one or other foot. All chicks on the island were ringed when they were approximately a week old. Chick survival was followed by visiting territories at every four-eight days in 1992, and generally every eight days in 1993 and 1994. If one or both chicks presumed alive were not recorded on a visit, then the interval before the next visit was reduced, and the territory checked at least twice subsequently for the missing chick(s). Adults cease mobbing and distracting behaviour shortly after the only chick or both chicks in the brood die or disappear, which gave a clear indication of the fate of their offspring.

The average fledging period was around 28 days. For all analyses however, survival to fledging was taken as survival to over three weeks of age. This excludes the mortality which occurs around fledging when chicks begin to stretch their wings and make their first practise flights, becoming vulnerable to predation by great skuas. Time constraints and the risk of scaring recently fledged chicks onto adjacent great skua territories precluded visiting territories sufficiently frequently at this stage to record which chicks fly before they succumb to predation. However, successfully fledged chicks remain permanently on or around their natal territory for at least a week post-fledging. The number of fledglings present one week after the probable fledging date does therefore take account of this mortality and so provides an estimate of immediate post-fledging survival (recorded in 1992 and 1993).

1.3.4 *Chick growth*

At each visit all chicks were weighed to the nearest 5g and the maximum wing chord (excluding the down on very small chicks) measured to the nearest mm. A small number of chicks were of unknown age (23 in 1992, and 11 in 1993), usually because they were the single surviving chick from what were broods of two at hatching, and if unmarked could sometimes be aged only to the nearest two-three days. Logistic growth curves were fitted separately to changes in wing length and weight with age in each year, using all measurements from known-age chicks. The equations were very similar in all years. Those for the 1992 curves (Figs. 1.3 and 1.4) were:

$$wing = \frac{256.49}{1+e^{-0.17762\times(age-13.911)}} \quad \text{(179 chicks, 445 measurements, } r^2\text{=0.99)}$$

$$weight = \frac{406.72}{1+e^{-0.23092\times(age-10.115)}} \quad \text{(179 chicks, 445 measurements, } r^2\text{=0.94).}$$

Unknown-age chicks had their age predicted from the appropriate annual curve, and a hatching date (a mean value if multiple measurements were available) estimated accordingly. A growth index (again a mean value if multiple measurements were available) was calculated for each chick also using the appropriate annual curve. This was the deviation of actual from expected weight expressed as a proportion of the expected value, and standardised relative to a value of one for all points on the curve.

Seven chicks whose weights were between 50-70% of the expected value (they appeared at the time of measuring to be clearly stunted), and a further six chicks from two apparently three-chick broods (i.e. one chick was adopted) were excluded from most analyses. There were no significant differences in growth between first-hatched and second-hatched chicks, and between first-hatched and single chicks in any year (Table 1.3). Consequently the chick growth index of either the first-hatched (in a brood of two) or the single chick raised by a particular pair was used in many analyses.

Table 1.3. Comparison of mean chick growth indices (±1 s.e., (n)) between single, first-hatched and second-hatched Arctic skua chicks on Foula in 1992-1994.

Year	Growth index:			Comparison:	
	(i) First-hatched chicks	(ii) Second-hatched chicks	(iii) Single chicks	(i) cf. (ii) - paired t-test	(i) cf. (iii) - t-test
1992	1.01±0.01 (75)	1.00±0.01 (75)	1.00±0.01 (52)	$t_{74}=1.2^a$	$t_{125}=0.7^a$
1993	1.01±0.01 (69)	0.99±0.01 (69)	0.98±0.02 (45)	$t_{68}=1.3^a$	$t_{73.4}=1.6^a$
1994	1.00±0.01 (62)	1.00±0.01 (62)	0.99±0.02 (33)	$t_{61}=-0.1^a$	$t_{93}=0.3^a$

^{a} - n.s.

1.3.5 *Adult attendance*

The number of adults present was recorded at all visits to marked territories during incubation and chick-rearing. If possible, the identity of any single bird present was also recorded in 1994, as was that of the individual incubating the eggs when both adults were on territory. Timing of visits to different areas of the colony was randomised in order to minimise potential variation arising from possible diurnal feeding rhythms. A maximum of two records per pair per day (possible only for territories which were clearly visible from the road) were used in analysis. These spot attendances were converted to a mean for each territory at four different stages of the season; incubation, 0-9, 10-19 and 20-30 days chick-rearing.

1.3.6 *Adult size and body condition indices*

Breeding adults were trapped using a variety of techniques, ringed and marked in each breeding season, 1992-1994. These birds were sexed by observation, by discriminant analysis or by association with an adult sexed by one of these methods (see Chapter 4 for details). Two separate indices of body size were calculated for each bird using principal components analysis, one analysis separated by sex, and the other using all birds regardless of sex (Chapter 4). These indices were closely correlated, as expected (males r_{75}=0.85, P<0.001, females r_{105}=0.85, P<0.001). Most further analyses in the thesis however, use the former index (which is likely to take better account of possible shape differences between males and females) unless the use of the directly-comparable common body size index is necessitated because of small samples of sexed birds in particular comparisons.

Two indices of body condition were also calculated for each adult (Chapter 4). For females the preferred index was the deviation of the individual's weight from the expected weight for a bird of that size, and at that stage of the season, expressed as a proportion of the expected value. For males there was no seasonal decline in weight and so the index used was the deviation of observed weight from expected weight corrected for male body size only, again expressed as a proportion of the expected value. A common body condition index was also calculated using the common body size index and a similar correction for stage of the season for all measured birds. This obviously overestimates female, and underestimates male condition compared with the separate index as the latter showed no seasonal decline in weight. However, the use of a common index was necessary for some analyses, and the two indices were highly correlated (males r_{72}=0.82, P<0.001, females r_{96}=0.90, P<0.001).

1.3.7 *Statistical treatment*

Data were tested for normality using Kolmogorov-Smirnov one-sample tests, and for homoscedasticity using Bartlett's test. If data did not conform to a normal distribution, log - $\log_{10}(x+1)$, inverse - $1/(x+1)$, or square-root - $\sqrt{(x+0.5)}$, transformations were carried out as appropriate. Most analyses in this thesis were performed using the statistical package SPSS/PC+, and all P values were from two-tailed tests. Any less common tests were generally carried out according to Zar (1984). All chi-square values with one degree of freedom were corrected for continuity (Yates' correction). Details of specific statistical procedures are provided in the Methods sections for each chapter. Unless indicated otherwise, data are presented in all tables as means ± 1 s.e., with sample sizes in parentheses.

Fig. 1.1. Map of Shetland.

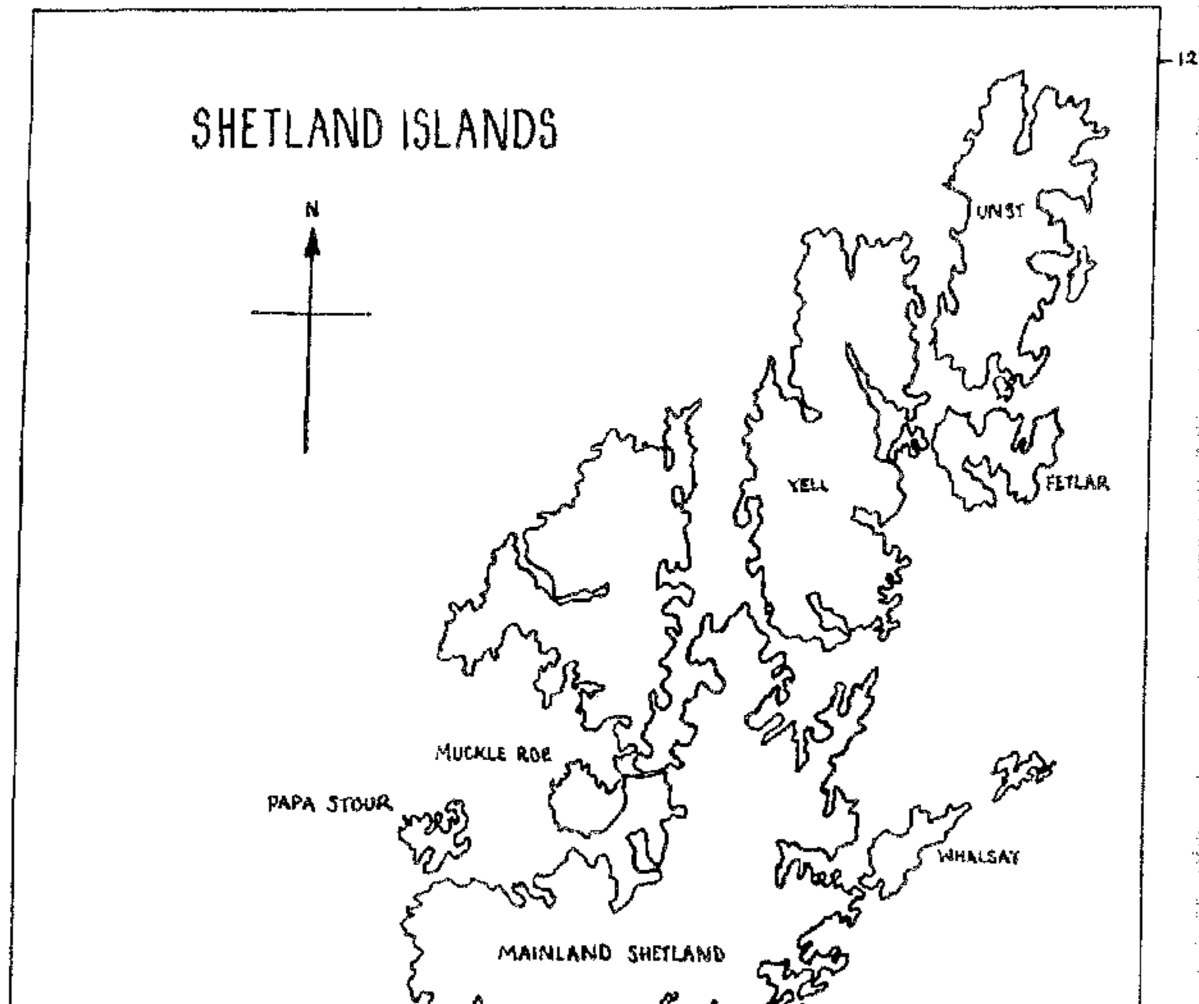


Fig. 1.2. Map of Foula.

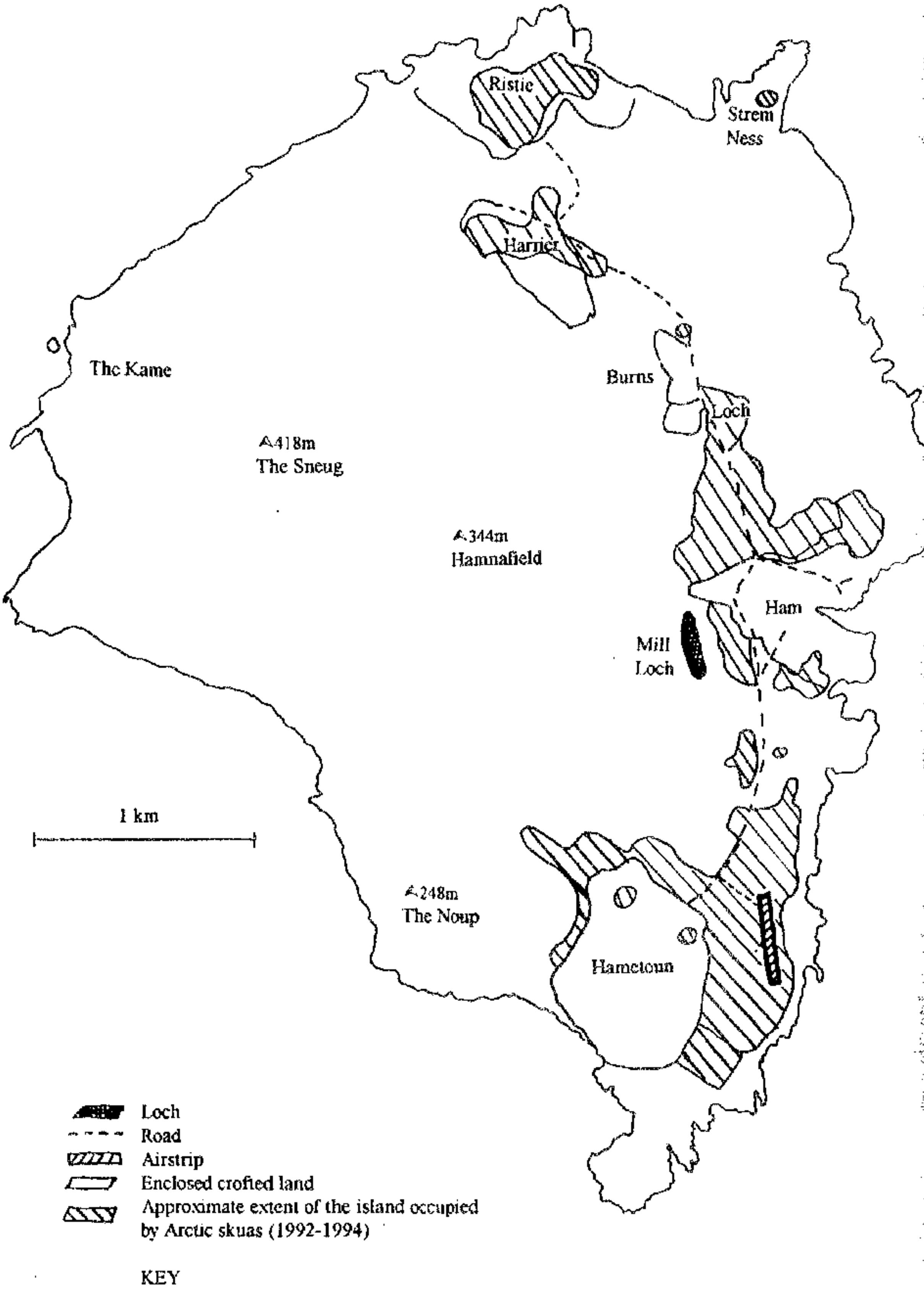


Fig. 1.3. Logistic growth curve fitted to changes in wing length with age of all known-age Arctic skua chicks hatched on Foula in 1992 (n=179 chicks, 445 measurements)

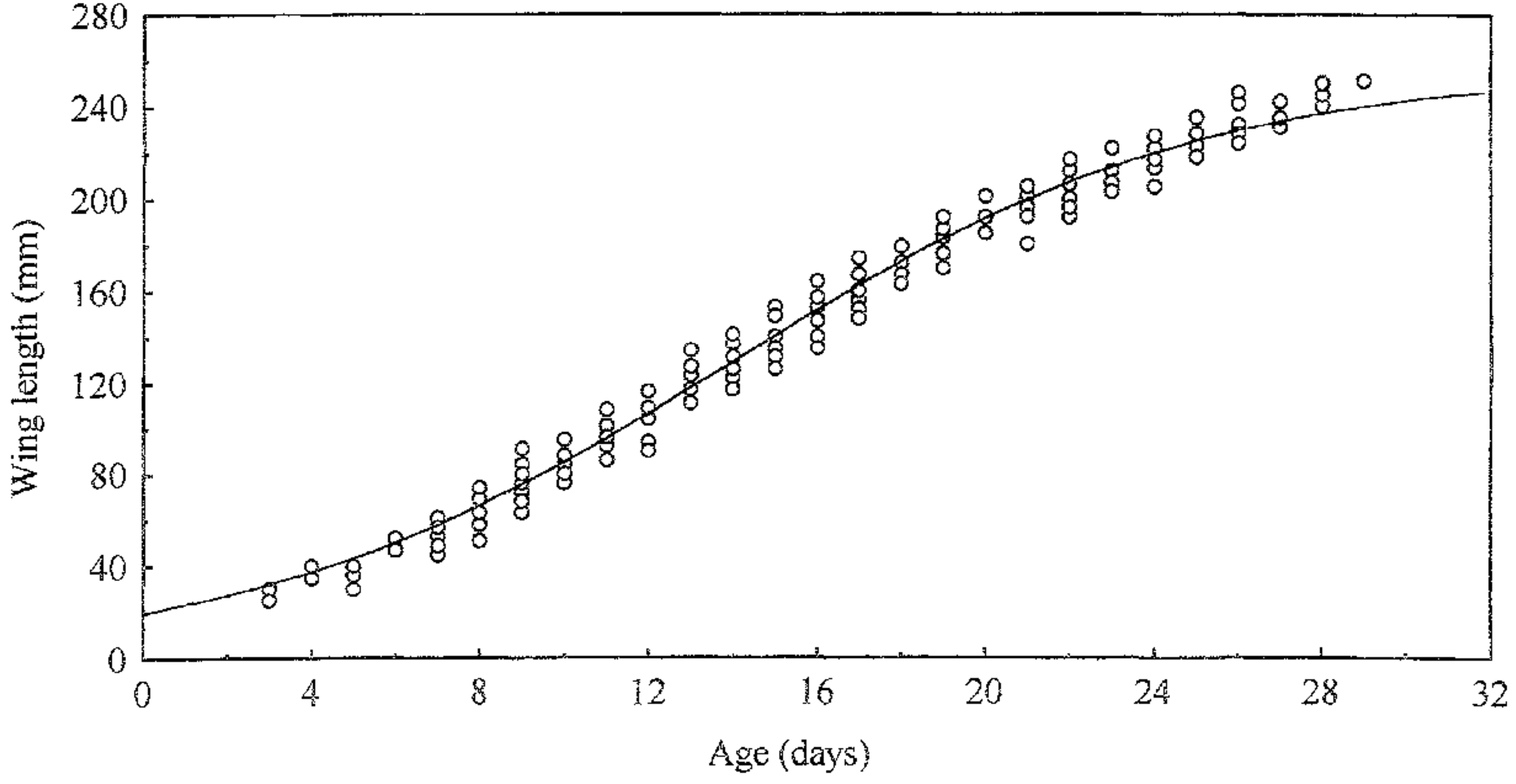
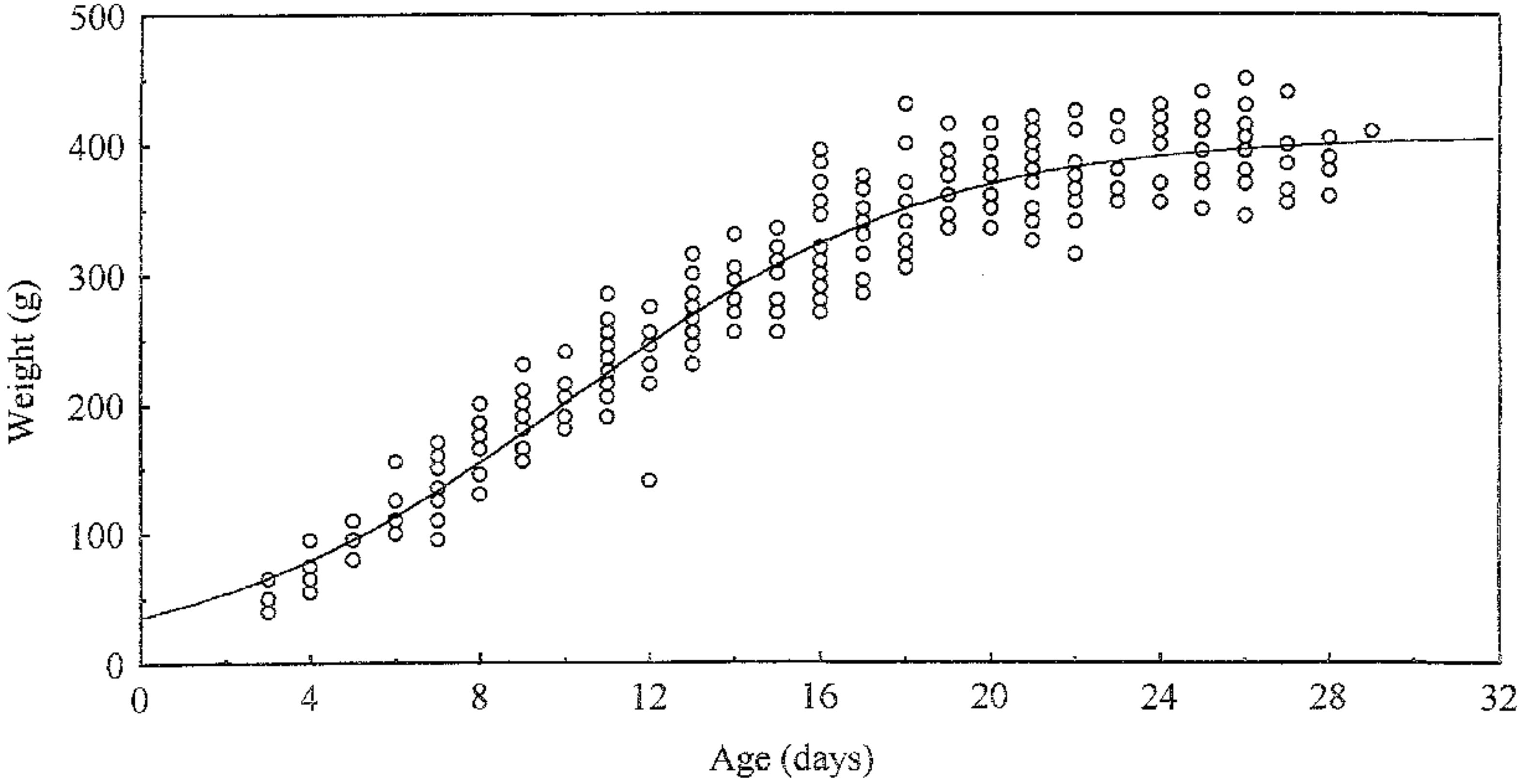


Fig. 1.4. Logistic growth curve fitted to changes in weight with age of all known-age Arctic skua chicks hatched on Foula in 1992 (n=179 chicks, 445 measurements).



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Chapter Two. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*

This chapter is in press in *Ibis*, and appears in the format appropriate for that publication.

The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*

RH. Food and reproductive success of Arctic skuas

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2.1 Abstract

Territorial attendance, chick growth rate and breeding success of Arctic Skuas *Stercorarius parasiticus* in Shetland were lowest in the late 1980s when recruitment of Sandeels *Ammodytes marinus* in the surrounding waters was poor. The relationships between both fisheries-based and avian indices of food availability and annual variation in Arctic Skua chick growth and breeding success between 1976 and 1994 were better described by a threshold effect rather than linear functions. Arctic Skuas conform to the model proposed by Cairns (1987) which predicts the responses of seabirds to changes in prey availability. Skua clutch size, egg volume, hatching success and hatching date were not reliable indices of sandeel availability. However, annual fluctuations in Arctic Skua breeding numbers may be a useful indicator of changes in prey abundance.

2.2 INTRODUCTION

Seabirds exhibit deferred maturity, high adult survival and low reproductive rates, and consequently have moderately stable population sizes (Furness & Monaghan 1987). Large-scale mortality of adult seabirds is rare (Cairns 1987), and generally associated only with dramatic reductions in food availability such as the periodic El Niño Southern Oscillation events (Schreiber & Schreiber 1984). Life-history theory predicts that individuals will try to trade off current against future reproductive potential in order to maximise their contribution to succeeding generations (Stearns 1992). One important factor influencing this trade-off is food supply. Adults should increase their present breeding effort in response to a reduction in prey availability only if it does not jeopardise their residual reproductive value by decreasing their probability of survival or of breeding successfully in later years (Drent & Daan 1980, Reznick 1985).

Increases in breeding effort, for example in the time devoted to foraging, can act to buffer seabirds from environmental pertubation. Such behavioural plasticity may mask the effects of food shortage on chick growth or breeding success (Birkhead & Nettleship 1987, Burger & Piatt 1990, Uttley *et al.* 1994). Cairns (1987) predicted that a reduction in prey availability at a seabird colony would, depending on its severity, sequentially affect several distinct parameters of breeding performance, the most sensitive of which would be behavioural. With a slight limitation of food supply, changes in colony attendance patterns (i.e. total numbers of non-breeding and off-duty birds present), and adult activity budgets would be apparent. Under more restricting conditions, chick growth rates would be reduced and breeding success affected. However, only when food is extremely scarce would any increase in breeder mortality be anticipated. Each of these variables should show a nonlinear relationship with the level of food abundance; responsive only within a specific range of prey availabilities and tending to vary gradually, or not at all, when conditions were good (Cairns 1987, 1992). Many studies that document annual variation in one or more aspects of seabird breeding performance in relation to fish abundance do so for a very limited number of years. To date, none at a single colony has tested rigorously over a broad spectrum of food availabilities whether these proposed nonlinear relationships exist.

Arctic Skuas *Stercorarius parasiticus* breeding in Shetland feed predominantly by kleptoparasitism of Sandeels *Ammodytes marinus* taken from Arctic Terns *Sterna paradisaea*, Puffins *Fratercula arctica*, Guillemots *Uria aalge*, Razorbills *Alca torda* and Kittiwakes *Rissa tridactyla* (Furness 1987). During the 1980s there was a considerable reduction in sandeel recruitment in Shetland waters (Bailey *et al.* 1991), and this was implicated in the widespread breeding failure of a number of these seabird species (Martin 1989, Monaghan *et al.* 1989, Harris & Wanless 1990, Bailey *et al.* 1991). Most attempts to relate such changes in seabird ecology to prey abundance have been hindered by the lack of fish stock assessment data at a local scale. In the case of the Arctic Skua there is the potential, in addition to fisheries data, to quantify annual variation in the availability of fish-carrying hosts and to use this information to create separate, and independent, indices of food availability.

This paper examines the relationships between food supply and the foraging effort, breeding success and size of a population of Arctic Skuas at a colony in Shetland using a long-term data series collected from 1974 to 1994. The validity of the hierarchical set of responses to reduced food supply proposed by Cairns (1987) is assessed. In addition, we test the potential to use annual fluctuations in the size of a breeding population as an indicator of changes in food availability.

2.3 METHODS

The study was carried out on Foula, Shetland (60°08'N 2°05'W). Breeding data were recorded between 1974 and 1994 and related to independent indices of food availability based on avian or fisheries data, primarily (i) the number of chicks fledged by one of the Arctic Skua's principal kleptoparasitic hosts, Arctic Terns, and (ii) the estimated number of recruiting (0-group) plus one year old (1-group) sandeels in Shetland waters on 1 July in each year (data up until 1983 from Bailey *et al.* 1991, and from 1984-1994 from Anon 1994). This latter index was chosen because although Arctic Terns provision their chicks on 0-group sandeels, during the late 1980s, virtually all chases were of Puffins and Guillemots, both of which would have been feeding predominantly on larger, mostly 1-group fish (Furness 1990, Phillips *et al.* 1995). The total number of pairs of Arctic Terns breeding on Foula in each year was also recorded by direct counts of incubating birds in June. The number of Arctic Tern chicks fledged (estimated by counts at the colony in mid to late July) was preferred as the index of host availability for most analyses because, in the absence of more precise data (e.g. on tern hatching success), it was thought to most accurately reflect the numbers of adult Arctic Terns likely to be provisioning chicks during the period when the Arctic Skua chicks were being reared.

The Arctic Skua colony was counted by RWF in most years by recording apparently occupied territories, and in 1979, 1992, 1993 and 1994 by marking nests. The former method may slightly underestimate numbers (Furness 1982). Data for the years 1974-1982 were taken from Furness (1983). Additional counts were made in 1985 and 1989-1991 by S. Gear (unpublished reports to NCC/SNH) and in 1986 by a team of observers (Ewins *et al.* 1988). For these years, and also 1974 and 1975, the numbers were taken as the mean of two independent counts. The size of the Arctic Skua colony in each year was compared with each of the independent indices of food availability.

The changes in Arctic Skua numbers in successive years were examined in terms of annual net recruitment to the breeding population. This was calculated, following the approach of Ollason and Dunnet (1983), as the difference between the observed numbers in a given year and the expected number of breeders surviving from the previous year calculated using an estimate of the annual mortality rate. Colour-ringing of Arctic skuas from 1992-94 indicated a mean annual return rate of 86.4%, with no bird absent in 1993 returning in 1994. There are no mortality rate estimates available for Arctic skuas on Foula prior to the 1990s and so a mortality rate of 13.6% (derived from the colour-ringing data) was used in the model (Phillips *et al.* 1995). Net recruitment is a complex parameter involving not only the recruitment of new breeders to the breeding population, but also intermittent breeding and potential emigration (although this is not recorded in skuas - Furness 1987) of established adults (Ollason & Dunnet 1983). A negative value for net recruitment can therefore be interpreted as a consequence of high mortality or that established birds were absent from the colony or potential first-time breeders were refraining from recruiting, in a given year. The net recuitment index, expressed as a proportion of the population in each year, was compared with the indices of food availability.

Arctic Skuas regurgitate freshly-obtained fish to their mate and chicks after returning from almost all absences from the territory (Furness 1987). Time spent away can therefore be used as an index of foraging effort (Cairns 1987, Monaghan *et al.* 1989, Hamer *et al.* 1991). Comparison among years was made by recording the number of adults present at each visit to marked territories (Hamer *et al.* 1991). The frequency of observer visits was never more than twice daily in 1987 or once daily in other years. Neighbouring adults did not cause confusion in determining attendance as they were chased out by the territory owners. Spot attendances were converted to a mean for each individual territory at four different stages of the season; incubation, and 0-9 days, 10-19 days and 20-30 days after the first chick in each brood had hatched. The mean of these values was then determined for different clutch and brood sizes in each year. In 1979, territories were not visited beyond 20 days after the chicks had hatched and therefore comparison between then and the other years was limited to the first three of these stages.

In six years, eggs were measured (length and breadth to the nearest 0.1mm using callipers) and volumes calculated as 0.00048 x length x breadth^2 (Coulson 1963). Clutch size (either one or two eggs) was recorded. Hatching success and date were monitored in five years by visiting marked nests at intervals from the onset of incubation until the chicks hatched. Chick survival to one week of age was estimated from visits to territories between six and eight days post-hatching. If any hatched chick was not recorded at that time, the territory was checked at least twice subsequently. Counts were made of the number of chicks seen fledged at all territories on the island in 1986 and from 1988 to 1994, and from a sample of 28 nests in the north of Foula in 1987. Although unfledged Arctic Skua chicks are difficult to locate, once they can fly chicks are conspicuously present either on or near their natal territories for at least a week post-fledging. These counts were completed before the end of July, by which time virtually all successful pairs have fledged their chicks.

For all years between 1976 and 1994, except 1990, the wing lengths (maximum flattened chord excluding down) and weights of chicks were measured during chick ringing. In years when chicks were measured only once, this occurred when most chicks were approximately half-way through the fledging period. Logistic growth curves were fitted to changes in wing length and weight with age using all chick measurements from 1992. In each year, all chick ages were predicted from their wing length (Hamer *et al.* 1991) and their hatching date estimated by subtracting the predicted age of each chick from the date of measurement. Possible differences among years in wing growth were investigated using measurements from chicks of known hatching date in 1976, 1979, 1980, 1992, 1993 and 1994. This made it possible to assess error in the use of wing length to estimate age and hatching date. The deviation for each chick from its expected weight predicted from the 1992 curve was calculated and individual chick growth indices expressed as a proportion of the expected value. The annual means of these values were standardised relative to a value of one in the baseline year, 1992. Annual differences in chick growth and hatching date were compared with the avian and fisheries-based food indices.

All data were tested for normality using Kolmogorov-Smirnov one-sample tests, and for homoscedasticity using Bartlett's test. Most analyses, including the fitting of logistic curves, were carried out using the statistical package SPSS/PC+. Nonparametric ranges tests were performed according to Zar (1984). Unless stated otherwise, means are given ± 1 s.e., with sample sizes in parentheses.

2.4 RESULTS

Data for avian and fisheries-based indices of food availability in selected years are given in Table 2.1.

2.4.1 Number of occupied territories

The number of occupied Arctic Skua territories on Foula was at a peak in the late 1970s then fell sharply by 6.6% per year for six years and continued to decline until 1990 (Figure 2.1). There was a slight recovery in 1992, after which numbers again declined. The numbers of territories correlated with total Arctic Tern numbers (r_{17}=0.81, P<0.001), the number of tern chicks fledged (r_{17}=0.68, P<0.002), and the number of 0-group plus 1-group sandeels in Shetland waters on 1 July in each year (r_{16}=0.62, P<0.01). Changes in the net recruitment index also correlated with total Arctic Tern numbers (r_{18}=0.55, P<0.02) and the number of tern chicks fledged (r_{18}=0.54, P<0.02), but not sandeel numbers (r_{17}=0.10, n.s.).

2.4.2 Adult attendance

Variation in foraging effort of adults with different brood sizes might confound the detection of annual trends in attendance patterns. There was a single significant effect of brood size on attendance, in 1979 during days 10-19 of chick-rearing where the attendance of pairs with a single chick was higher (Mann-Whitney U, z=-2.4, n=80, P<0.02). However, there was no difference among years in the relative number of pairs with broods of one rather than two chicks at this stage (χ^2_4=2.4, n.s.) and so the data on attendance in each year were pooled with respect to brood size.

There were significant differences in the mean number of adults present on marked territories between 1979, 1987, 1992, 1993 and 1994 at all stages in the season (Figure 2.2); incubation (Kruskal-Wallis ANOVA χ^2_4=17.4, n=588 territories, P<0.002), 0-9 days chick-rearing (Kruskal-Wallis ANOVA χ^2_4=38.4, n=453 territories, P<0.0001), 10-19 days chick-rearing (Kruskal-Wallis ANOVA χ^2_4=35.7, n=387 territories, P<0.0001), and 20-30 days chick-rearing (Kruskal-Wallis ANOVA χ^2_3=44.4, n=285 territories, P<0.0001). Nonparametric ranges tests indicated that during incubation, 0-9 days and 10-19 days post-hatching, attendance was significantly lower in 1987 than in all other years. Attendance during the middle stage (10-19 days) of chick-rearing was also significantly higher in 1994 than in 1979, 1987 or 1993, but not 1992. During 20-30 days post-hatching, attendance in 1987 was lower than in 1992 or 1994, but not significantly different from 1993, and during this stage attendance was also significantly higher in 1994 than in the other years.

2.4.3 Breeding data

The data on egg measurements indicated a very slight but significant increase in egg breadth (ANOVA $F_{5,1196}$=4.7, P<0.0005) and volume (ANOVA $F_{5,1196}$=3.2, P<0.01) but not length (ANOVA $F_{5,1196}$=0.7, n.s.) since the 1970s (Table 2.2). A ranges test (Newman-Keuls) showed a significant difference in volume, with eggs approximately 2% larger in 1992 and 1994 than in 1979.

There was a significant difference among years in the mean clutch size (χ^2_4=12.3, P<0.02; Table 2.2), with fewer eggs per nest in 1979. However, there was no difference in hatching success (χ^2_4=8.4, n.s.) nor was there a significant difference in chick survival to one week post-hatching (χ^2_3=6.0, n.s.) but the comparison could only be made between 1979, 1992, 1993 and 1994.

Productivity varied greatly between 1986 and 1994 (Table 2.2). Fewer chicks survived to fledging in the late 1980s than in 1986, and far fewer than in the 1991 to 1994 seasons. Logistic curves were fitted to the relationships between the number of Arctic Skua chicks fledged per pair and the number of Arctic Tern chicks fledged ($F_{2,6}=15.1$, $P<0.005$, $r^2=0.83$: Figure 2.3), and between Arctic Skua chicks fledged per pair and the estimated number of 0-group plus 1-group sandeels in each year ($F_{2,5}=29.4$, $P<0.002$, $r^2=0.92$: Figure 2.4). In the former case the logistic curve was a significantly better fit ($F_{1,6}=9.8$, $P<0.05$) than a linear equation (Zar 1984). There was no significant linear relationship between Arctic Skua productivity and sandeel numbers.

Comparing chicks of known age in 1976, 1979, 1980, 1992, 1993 and 1994 (Table 2.3) indicated that Arctic Skua chicks measured in 1979 had wing lengths significantly shorter (by 3-4mm on average) than those of similar aged chicks in the other years (Kruskal-Wallis ANOVA $\chi^2_5=28.2$, $n=650$ chicks, $P<0.0001$). However, only in 1979 was there a significant difference between the predicted and the observed hatching dates (paired t-test $t_{104}=5.4$, $P<0.001$: Table 2.3). The deviation is slight, less than half a day.

Comparing the mean estimated chick hatching date in each year indicated there were annual differences (Kruskal-Wallis ANOVA, $\chi^2_5=362$, $n=1942$ chicks, $P<0.0001$: Table 2.4). In general hatching tended to be later in the late 1970s and 1991. Hatching dates in 1988 and 1994 were also significantly earlier (see Table 2.4). The mean in each year was positively correlated with both the number of pairs of breeding Arctic Terns ($r_{16}=0.56$, $P<0.02$) and the number of tern chicks fledged ($r_{16}=0.48$, $P<0.05$) but not the index of sandeel abundance ($r_{15}=0.19$, n.s.). The mean hatching date also correlated with the net recruitment index ($r_{16}=0.66$, $P<0.005$).

Differences in chick growth showed significant linear correlations with 0-group plus 1-group sandeel numbers in each year (in regression analysis $F_{1,15}=5.6$, $P<0.05$, $r^2=0.27$: Figure 2.5), but not with the number of Arctic Tern chicks fledged (in regression analysis $F_{1,16}=0.8$, n.s., $r^2=0.05$). Logistic curves were fitted to chick growth versus sandeel numbers ($F_{2,14}=4.5$, $P<0.05$, $r^2=0.39$)

and chick growth versus the number of tern chicks fledged ($F_{2,15}=4.6$, $P<0.05$, $r^2=0.38$: Figure 2.6). In the former case however, the logistic curve was not a significantly better fit than the linear equation ($F_{1,14}=2.6$, n.s.).

Table 2.1. Variation in the indices of food availability for Arctic Skuas on Foula.

Year	Sandeel data[a]:		Arctic Tern data:	
	O-group numbers[b]	1-group numbers[b]	Breeding population size (pairs)	Number of chicks fledged
1976	41765	3459	5650	4000
1979	30605	3528	4400	3000
1986	16600	1235	200	0
1987	1288	2013	300	0
1988	1422	157	250	0
1989	3740	204	300	0
1990	1577	554	115	0
1991	54000	261	1010	300
1992	4691	8926	1500	600
1993	18079	775	1500	1100
1994	no data	no data	1000	250

[a] - data provided by the International Council for the Exploration of the Sea

[b] - total numbers of sandeels (in millions) in Shetland waters on 1 July each year

Table 2.2. Breeding statistics for Arctic Skuas on Foula, 1976-1994.

Year	Mean clutch size	Mean egg length (mm)	Mean egg breadth (mm)	Mean egg volume (cc)	Hatching success (%)	Chick survival to one week (%)	Chicks fledged per pair
1976	-	58.8±0.35 (54)	40.5±0.13 (54)	46.3±0.43 (54)	-	-	-
1979	1.81 (186)	58.3±0.12 (323)	40.5±0.06 (323)	45.9±0.18 (323)	71.4 (322)	93.0 (230)	-
1986	-	-	-	-	-	-	0.63
1987	1.93 (28)	58.7±0.28 (52)	40.7±0.15 (52)	46.7±0.44 (52)	74.1 (54)	-	0.21
1988	-	-	-	-	-	-	0.15
1989	-	-	-	-	-	-	0.13
1990	-	-	-	-	-	-	0.09
1991	-	-	-	-	-	-	0.87
1992	1.86 (151)	58.4±0.16 (267)	40.9±0.07 (267)	46.9±0.21 (267)	81.2 (277)	88.4 (225)	0.91
1993	1.91 (140)	58.4±0.14 (260)	40.8±0.08 (260)	46.6±0.21 (260)	76.3 (266)	92.1 (203)	0.97
1994	1.93 (130)	58.3±0.15 (246)	40.9±0.08 (246)	46.8±0.22 (246)	77.7 (251)	87.0 (192)	0.90

Table 2.3. Comparison between actual and predicted hatching dates, and actual and predicted wing lengths of Arctic Skua chicks on Foula. Predicted hatching dates were obtained for each chick by subtracting its estimated age (calculated from chick wing length using the 1992 curve of wing length versus age) from the date of measurement. Wing length residuals were calculated by subtracting the predicted wing length of chicks (predicted from their age using the 1992 curve) from the measured value.

Year	Number of chicks	Mean hatching date[a]: actual	Mean hatching date[a]: predicted	Wing length residual (mm)
1976	9	59.2±2.1	59.2±2.3	-2.2±4.1
1979	105	55.2±0.5	55.5±0.5	-3.4±0.6
1980	10	56.0±1.5	56.5±1.9	-3.2±4.2
1992	179	51.3±0.4	51.2±0.5	0.1±0.5
1993	181	51.9±0.6	51.8±0.6	0.0±0.9
1994	166	48.1±0.4	48.0±0.4	0.3±0.8

[a] days from 1 May.

Table 2.4. Mean estimated hatching dates (days from 1 May) for all Arctic Skua chicks measured on Foula, 1976-1994, using the 1992 curve of wing length versus age to estimate chick age.

Year	Hatching date	Number of chicks	Year	Hatching date	Number of chicks
1976	53.5±0.55	134	1986	51.8±0.77	57
1977	52.5±0.61	82	1987	51.0±0.83	61
1978	53.0±0.41	142	1988	47.3±0.66	96
1979	56.1±0.33	227	1989	49.9±0.59	55
1980	50.9±0.40	120	1990	-	-
1981	50.5±0.45	99	1991	55.7±0.67	46
1982	50.6±0.39	102	1992	51.4±0.44	202
1983	50.0±0.51	73	1993	51.7±0.62	192
1984	49.4±0.65	40	1994	48.0±0.44	166
1985	50.5±0.75	48			

Non-parametric ranges tests (the data were heteroscedastic) indicated that mean hatching dates in (i) 1988 and 1994 were significantly earlier than 1976-82, 1986 and 1991-1993, (ii) 1983-84, 1989 and 1993 were significantly earlier than 1976-79 and 1991, (iii) 1980-82, 1985-87 and 1992 were significantly earlier than 1979 and 1991 and (iv) 1976-78 were significantly earlier than 1991.

Fig. 2.1. Arctic Skua and Arctic Tern numbers on Foula (1974-1994).

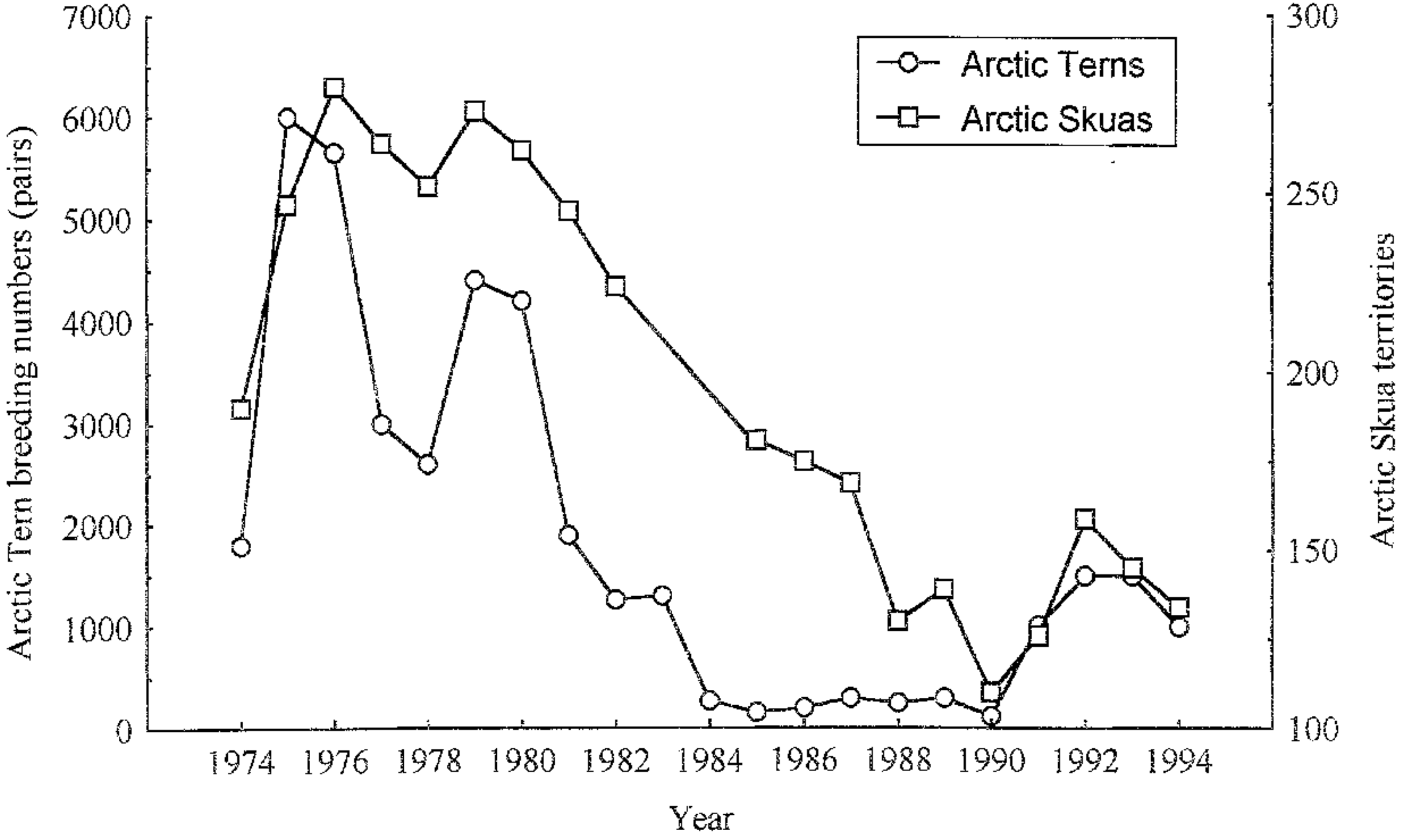


Fig. 2.2. Territorial attendance of Arctic Skuas on Foula in 1979, 1987, 1992, 1993 and 1994. Error bars are +/- 1 s.e.

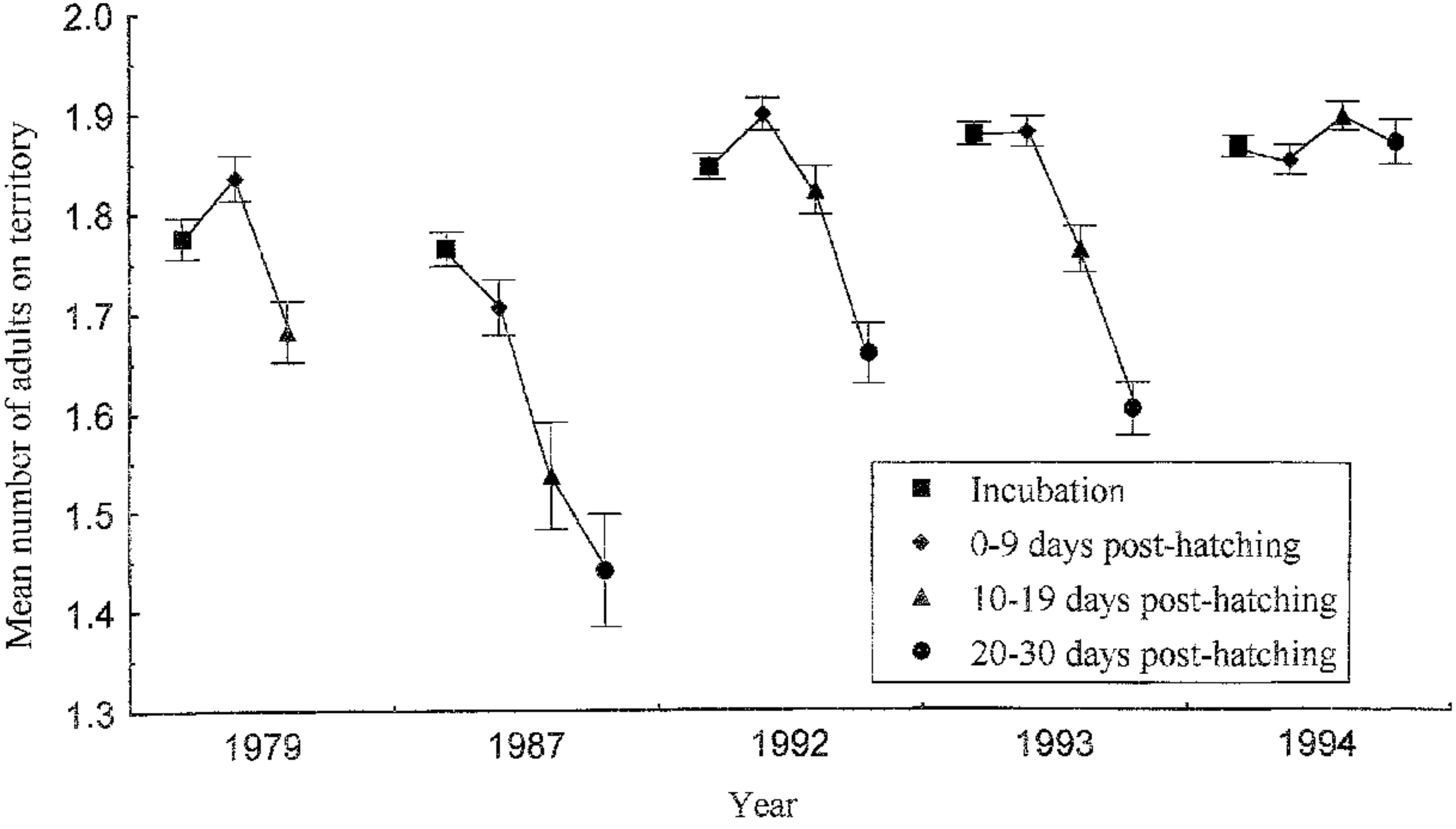


Fig. 2.3. Logistic curve fitted to changes in Arctic Skua breeding success in relation to the number of Arctic Tern chicks fledged on Foula (1986-1994).

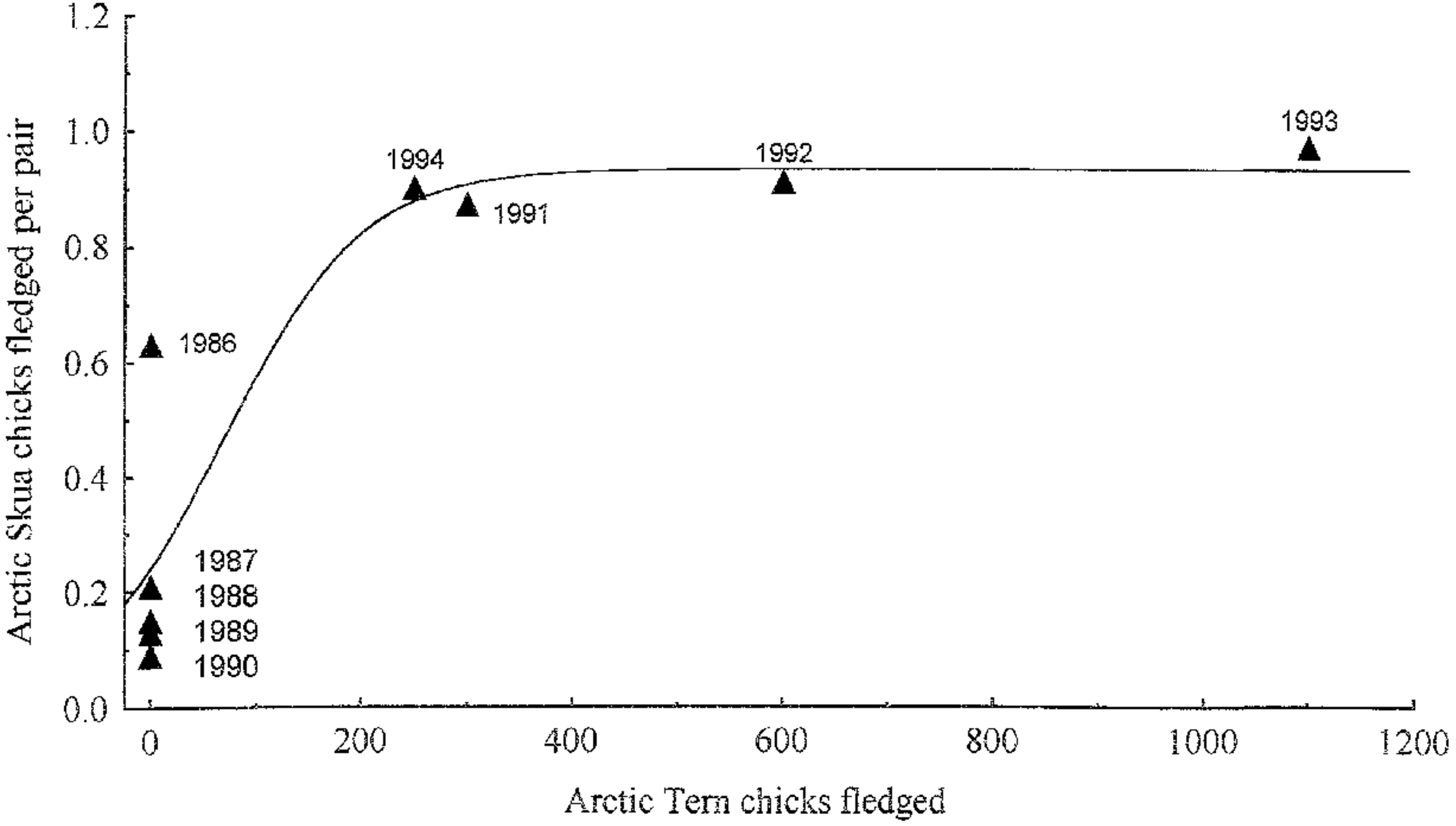


Fig. 2.4. Logistic curve fitted to changes in Arctic Skua breeding success in relation to the numbers of 0-group and 1-group sandeels in Shetland waters on 1 July (1986-1994).

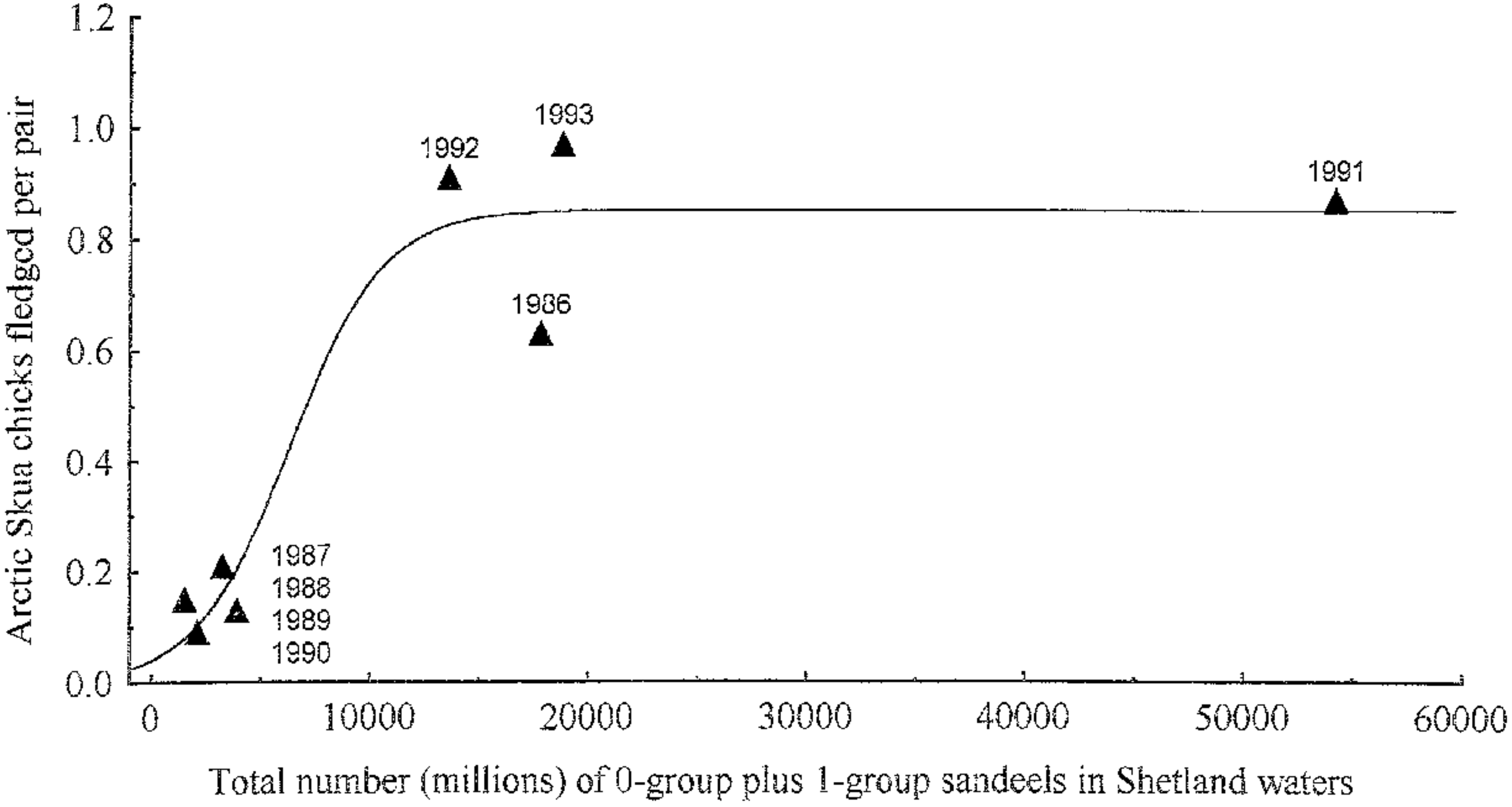


Fig. 2.5. Arctic Skua chick growth on Foula in relation to the numbers of 0-group and 1-group sandeels in Shetland waters on 1 July (1976-1993).

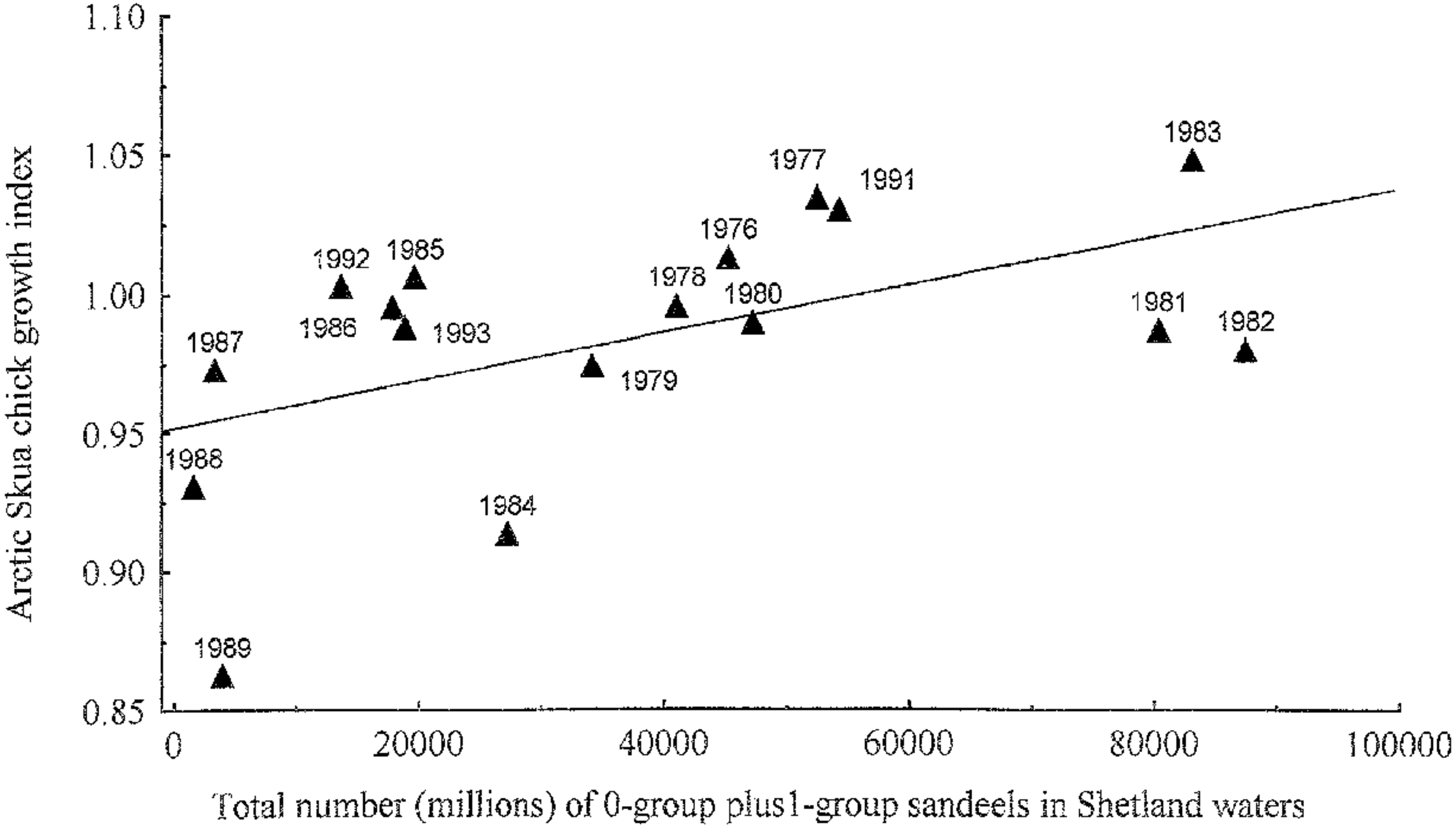
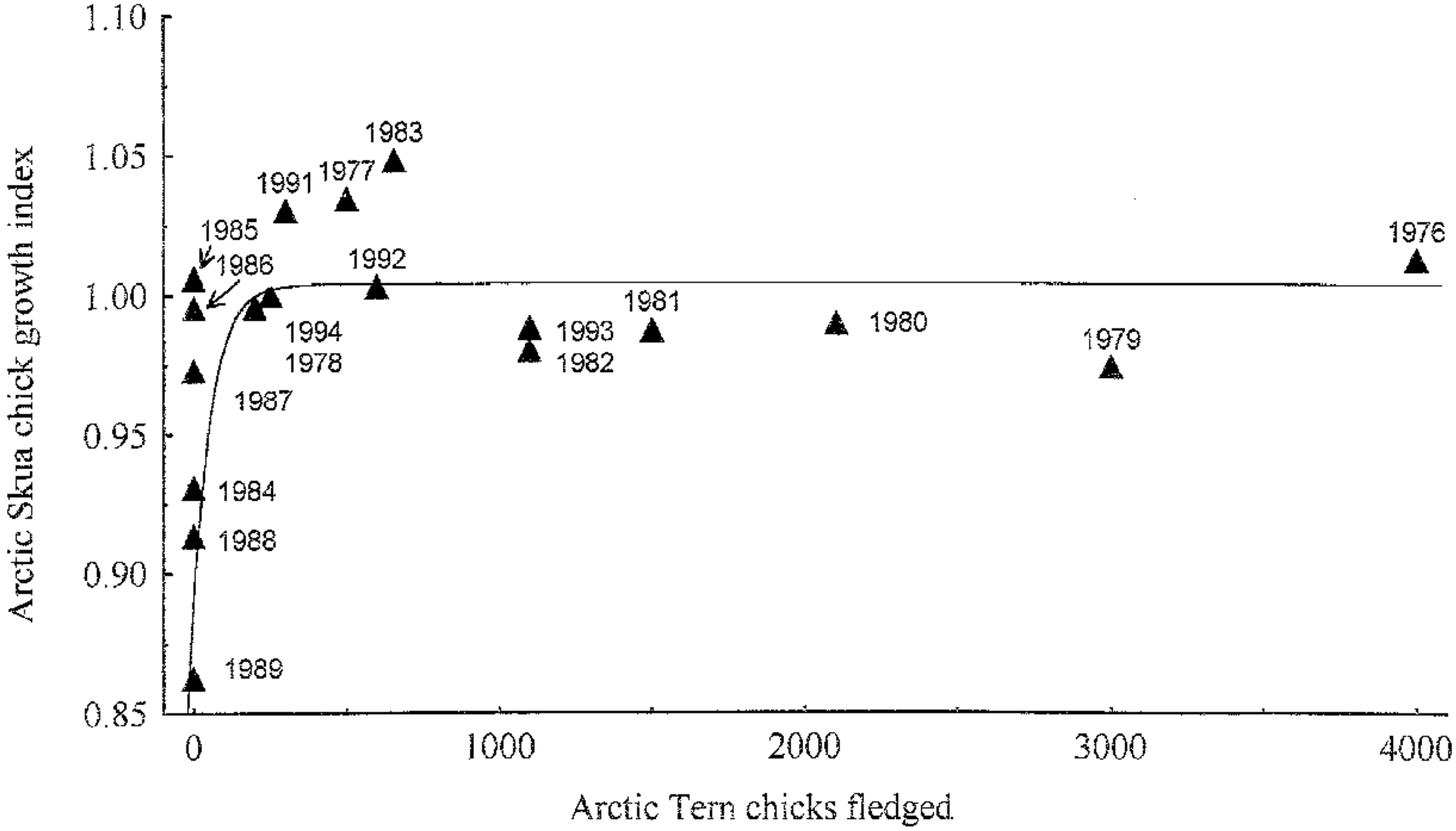


Fig. 2.6. Logistic curve fitted to changes in Arctic Skua chick growth on Foula in relation to the number of Arctic Tern chicks fledged (1974-1994).



2.5 DISCUSSION

2.5.1 *Fluctuations in the size of the breeding population.*

As prey abundance declines, adults would be expected to abandon a breeding attempt once they reach the maximum extent of their buffering capabilities, and before their survival is likely to be affected (Drent & Daan 1980). If this is the case, population sizes, of which adult mortality rate is a crucial determinant (Croxall & Rothery 1991), might be considered insensitive to annual changes in food availability. However, established birds may refrain from breeding in some years (Coulson 1984, Boekelheide & Ainley 1989, Murphy *et al.* 1991). Similarly, potential new recruits may choose not to establish territories if conditions are unfavourable (Boekelheide & Ainley 1989, Coulson 1991). If food availability influences either of these factors, fluctuations in the size of the breeding population might have some value as an indicator of environmental conditions.

Most authors consider population sizes to be inappropriate indicators of environmental change because the time-scale involved is usually long-term (Morrison 1986, Temple & Wiens 1989, Furness & Greenwood 1993). However, both the number of Arctic Skuas breeding, and net recruitment to the breeding population population on Foula over the last 20 years, showed a close correspondence with each index of food availability. Annual variation in net recruitment, and consequently in breeding population size, may therefore be a sensitive response of Arctic Skuas, and possibly of other seabird species, to annual fluctuations in prey availability.

2.5.2 *Cairns' model (1987) and Arctic Skua breeding on Foula.*

Given the uncertainties involved in measuring marine productivity directly, a number of parameters of seabird reproductive performance have been advocated as useful monitors of changes in fish abundance (Cairns 1987, 1992, Montevecchi 1993). One complicating factor in the utilisation of seabird breeding variables for the monitoring of a particular fish stock is the ability of polyphagous species to switch to alternative prey items (Cairns 1987, 1992, Martin 1989, Hamer *et al.* 1991, Montevecchi 1993). An analagous situation existed for the Arctic Skua during the course of this study. Although the food (sandeels) remained the same, the species of kleptoparasitic host changed (Phillips *et al.* 1995). Arctic Terns tended to be the principal host in the mid- to late-1970s, Puffins predominated during the mid- to late-1980s, Guillemots were the most important in 1989, and only from 1991 onwards did Arctic Terns reappear as a major host species. This variation in host selection might go some way in uncoupling Arctic Skua breeding from Arctic Tern reproductive success. However, the assessment of fish numbers is fraught with technical difficulties (Bailey *et al.* 1991). Often the temporal and spatial overlap between the areas monitored by fisheries scientists, and those adjacent to seabird colonies is relatively broad-scale (e.g. Martin 1989, Aebischer *et al.* 1990, Bailey *et al.* 1991, this study). Rarely, as in this study, is there the opportunity to use independent measures of food abundance.

Cairns (1987) considered that the sensitivity of seabird reproductive parameters to fluctuations in food availability would vary, so that their relationship with food abundance would be a threshold rather than a linear function. Breeding success was likely to improve rapidly as food supply rose from poor to moderate, and change only slowly when conditions were favourable. Chick growth rate would follow a similar pattern but remain constant as soon as prey became relatively abundant. Activity budgets would trend in the opposite direction, with time spent foraging exhibiting relative constancy in poor to moderate conditions as adults worked near-maximally, but showing more sensitivity to relatively minor fluctuations when food supply was good. The concurrent reductions in sandeel recruitment in Shetland waters during the 1980s, and consequently in the size and productivity of the Arctic Terns breeding on Foula (Table 2.1), provided an opportunity to test whether Arctic Skuas responded to this decrease in resource availability by modifying their reproductive strategy in the way Cairns' model suggests.

Recent reviewers have suggested that the seabird reproductive parameters most likely to be sensitive to fluctuations in food availability are behavioural (Cairns 1987, 1992, Montevecchi 1993). Seabirds have considerable scope to adjust activity budgets in order to increase the amount of time they spend foraging (Monaghan *et al.* 1989, Hamer *et al.* 1991, 1993, Uttley *et al.* 1994). In accordance with Cairns' model, in 1987 when sandeel recruitment was poor (Table 2.1) breeding Arctic Skuas reduced the amount of time they spent on territory. This higher foraging effort (assuming that individuals prefer to spend discretionary time on territory) was apparent throughout the breeding season including incubation.

Adult attendance was exceptionally high in 1994. Because activity budgets are likely to show most responsiveness to short-term, intra-seasonal fluctuations in food supply, it may be that relatively low foraging effort late in the 1994 season reflected greater sandeel availability during that particular stage. Unfortunately there are no fisheries data available for the waters around Foula to test this hypothesis. If sandeels were more available to Arctic Skuas provisioning older chicks in 1994, the attendance data would corroborate Cairns' suggestion that activity budgets are the most accurate and sensitive indicator of fluctuations in prey abundance when conditions are good.

In 1987, the number of adults present did not drop below a mean of 1.4 per territory and chicks were virtually never left unattended during daylight even though chick growth was relatively poor. By comparison during the late 1980s, Great Skua *Catharacta skua* chicks on Foula were frequently left alone while both parents foraged simultaneously, and they experienced heavy cannibalism as a consequence (Hamer *et al.* 1991). Possibly Arctic Skua adults make a compromise between time spent off-territory collecting food for chicks, and that spent on-territory defending them from predation, in this case by Great Skuas, a major source of chick mortality (Furness 1987). While the risk of predation is certainly one factor, an alternative hypothesis for the continued presence of adults on territory in 1987 when chicks were not achieving maximal growth rates, is one of energetic constraint. Adults might have reached the limit of their potential buffering abilities and no further increase in foraging effort may have been physiologically possible without incurring a cost in terms of body condition (Drent & Daan 1980, Monaghan *et al.* 1989, Hamer *et al.* 1993).

Despite the buffer of increased foraging effort apparent in years with low food availability, there were clear relationships between the indices of food availability and Arctic Skua chick growth. Variations in chick growth have been successfully used as indices of marine productivity in a number of other studies (Ricklefs *et al.* 1984, Safina *et al.* 1988, Monaghan *et al.* 1989, Hamer *et al.* 1991), despite at least two possible confounding influences. Unless chicks are starving, chick wing length growth is usually considered to be relatively independent of fluctuations in food availability (Gaston 1985, Barrett *et al.* 1987), although this is not always the case (Safina *et al.* 1988, Cruz & Cruz 1990). The results presented here indicate a slight retardation of chick wing length growth in some years. If food availability is poor, using wing length would then underestimate actual chick age, and hence, if chicks are lighter than predicted, also underestimate the discrepancy between a chick's observed weight and the weight it would be expected to have reached by that time (which should in fact be that of an older chick). Since the error in estimating the mean hatching date of chicks in 1979, the year in which wing length growth was poorest, was less than half a day (Table 2.3), this is unlikely to be a problem here. However, there is also the factor that lighter chicks in years of poor food availability may experience lower survival, possibly through brood reduction (Williams & Croxall 1991). This has implications for the calculation of annual chick growth indices if differential survival occurs before the chicks are measured. Data on early season chick mortality indicated no difference between 1979, 1992, 1993 and 1994, but in comparison with the late 1980s, sandeel recruitment in Shetland waters in each of these years was high. The data presented in this paper could therefore include overestimations of the mean chick growth rate in the very poor years if more chicks had starved to death before they could be measured.

Regardless of this, the annual variation in chick growth correlated with the estimated number of 0-group plus 1-group sandeels in Shetland waters on 1 July each year. There was no significant linear correlation with the number of Arctic Tern chicks fledged, with this relationship better described by a logistic curve. From Figures 2.5 and 2.6 it is apparent that in 1985 and 1986, when Arctic Tern productivity was nil, mean chick growth was only marginally poorer than that in the baseline year (1992). This was presumably because Arctic Skuas were chasing Puffins as an alternative host (Phillips *et al.* 1995). The shape of the curve in Figure 2.6 implies little improvement in chick growth once food abundance attains a certain threshold level. This is to be expected given that most studies suggest chick growth is constrained by intrinsic factors once food is abundant (e.g. Shea & Ricklefs 1985).

Poor growth of chicks in the late 1980s was associated with depressed breeding success; a decline in the number of chicks fledged between 1987 and 1990, in comparison with 1986 and 1991-1994. Relating this to the independent indices of food availability provided evidence for the suggested curvilinear trends (Figs. 2.3 and 2.4). Breeding success was at an asymptote in 1991-1994. That relatively fewer chicks fledged in 1986, and very few in 1987 (when chicks weighed on average 3% less than predicted), might suggest that minor variation in chick body condition has serious implications. An alternative explanation is that another factor constraining fledging success was also dependent to some extent on food supply. The amount of sandeel in the diet of breeding Great Skuas fell during the 1980s, and was replaced initially by discarded gadid fish and then by bird flesh (Hamer *et al.* 1991), and it is possible that the incidence of predation of Arctic Skua chicks and fledglings may have increased during this period. In that case the situation in 1986-1987 for Arctic Skuas on Foula would be analagous to that described for Arctic and Common Terns *Sterna hirundo* breeding sympatrically on Mousa, Shetland in 1988 (Uttley *et al.* 1989). In that study Common Tern breeding success was nil despite 'normal' chick growth, apparently because specialist predators of terns were unable to feed on Arctic Tern chicks (this species had already suffered reproductive failure) and so turned to Common Tern chicks as an alternative food source.

The positive correlation between mean hatching date and the Arctic Tern indices of food availability in each year is unexpected. Other studies show the opposite and more intuitive result that laying (and presumably hatching) is normally delayed when fish stocks decline (Safina *et al.* 1988, Monaghan *et al.* 1989, Aebischer *et al.* 1990). Data on laying dates are not available for Arctic Skuas on Foula. Using hatching date as an alternative indicator of potential changes in the timing of breeding related to food availability might be confounded by differential survival of early or late-hatched chicks in different years. There is however, little evidence that this was a major factor here; in 1988 for example (the earliest year recorded - Table 2.4), the sample size was sufficiently large that it must have included not just the earliest hatched chicks, and in addition, during the 1991-1994 breeding seasons, despite little variation in Arctic Skua productivity (Table 2.2), there were marked differences in mean hatching date. Annual fluctuations in mean hatching date are likely to have another source. In fact, there was a strong relationship between hatching date and the net recruitment index implying some consequence of changes in the demography of the Arctic Skua population on Foula. In the years when food availability was poor and net recruitment low, few new recruits (and possibly also established breeders that deferred the previous year) were present in the breeding population. As laying date advances with age in skuas (Davis 1976, Hamer & Furness 1991) this would tend to ensure an earlier mean laying / hatching date. An increase in clutch size and egg volume with age (also recorded for skuas - Hamer & Furness 1991) would also explain the lower values recorded for these two variables in 1979. In 1979, the population was at the peak of a recent expansion and was likely to have contained a greater proportion of new recruits or younger birds than in later years. Whatever the explanation, neither clutch size, hatching date nor clutch volume appear to be reliable indicators of any annual changes in prey availability for Arctic Skuas on Foula.

By contrast, variations in chick growth and breeding success provided considerable empirical evidence for the existence of threshold relationships between breeding variables and food abundance.

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Chapter Three. Behavioural responses of Arctic skuas *Stercorarius parasiticus* to changes in sandeel availability

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Behavioural responses of Arctic skuas *Stercorarius parasiticus* to changes in sandeel availability.

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Running headline - Sandeel availability and skua behaviour

3.1 Summary

1. Analysis of kleptoparasitic interactions of Arctic skuas *Stercorarius parasiticus* foraging within sight of Foula, Shetland indicated that the skuas were able to switch hosts if particular species (notably Arctic terns *Sterna paradisaea*) were breeding unsuccessfully in a given year.

2. Adult Arctic skuas spent considerably longer foraging off-territory in 1987, when sandeel, mainly *Ammodytes marinus*, recruitment in Shetland waters was low, than they did in 1979 or from 1992 to 1994.

3. Both Arctic skua chick growth and fledging success were depressed during the years of low sandeel availability, particularly from 1987 to 1990. However, they were able to breed with moderate success up until at least 1986, in sharp contrast to Arctic terns which failed from 1983 to 1990.

4. Breeding Arctic skua adults appeared to be in poorer body condition in 1988, the second year of particularly low sandeel recruitment, and there was also strong evidence that many established pairs deferred breeding in that year and in 1990.
5. Changes in behaviour may therefore act as a buffer allowing Arctic skuas to withstand some degree of reduced prey availability but this appears to involve at least some longer-term costs.

Key-words - host availability, breeding performance, adult attendance, body condition, deferred breeding.

3.2 Introduction

Seabirds exhibit considerable plasticity both in their behaviour and life-history characteristics (Furness and Monaghan 1987). Generalist seabird predators may switch from previously abundant but subsequently declining target species to others which are more readily obtainable (Montevecchi 1993). Similarly, adults may increase the foraging component of their reproductive effort in order to offset any reduction in their food supply (Cairns 1987, 1992, Montevecchi 1993). This enables them to buffer themselves to an extent from the effects of environmental fluctuations, such as a reduction in prey availability (Cairns 1987, Montevecchi 1993).

Changes in behaviour serve to compensate for short-term variation in fish stocks, and may mask any effects on chick growth rates or fledging success unless food shortage becomes severe. There is a trade-off between adults' investment in energetically expensive activities such as chick-provisioning and the amount of effort they can expend in maintaining their own body condition (Martin 1987). There is likely to be a limit beyond which any further alteration in behaviour, assuming it represented greater reproductive investment, would have serious repercussions. An adult should abandon a breeding attempt if it is likely to decrease the probability of its survival or jeopardise the resources it can devote to future reproduction (Drent and Daan 1980).

Arctic skuas *Stercorarius parasiticus* (L.) breeding in Shetland feed almost entirely on sandeels, mainly *Ammodytes marinus* Raitt, stolen from other seabirds, in particular Arctic terns *Sterna paradisaea* Pontoppidan, Atlantic puffins *Fratercula arctica* (L.), kittiwakes *Rissa tridactyla* (L.) and common guillemots *Uria aalge* (Pontoppidan) (Furness 1987). During the mid- to late 1980s and 1990, fisheries data indicate that sandeel recruitment declined in Shetland waters, with a concomitant decline in the breeding success of a number of surface-feeding sandeel predators, including several of the species on which Arctic skuas depend (Bailey *et al.* 1991). This paper details changes in the reproductive success and behaviour of Arctic skuas between 1975 and 1994, emphasising the effects of variation in adult attendance and in the proportion of chases directed towards particular kleptoparasitic hosts on the skuas' ability to buffer themselves from the consequences of poor breeding success of their principal victims. The possible longer-term consequences of these changes in behaviour are also discussed with reference to adult Arctic skuas' body weights and the likelihood of breeding deferral in the subsequent years of low food availability.

3.3 Methods

The study was carried out on Foula, an island to the west of Shetland mainland at 60°08'N 2°05'W. The number of breeding Arctic terns and the total number of fledged Arctic tern chicks were counted in most years from 1974-1994. This provides an index, the number of fledglings per pair, to compare annual variation in tern breeding success over the years, plus each of these variables give some indication of the availability of this particular host to Arctic skuas.

Variation in Arctic skua breeding performance was examined in terms of the growth of chicks and the number of chicks fledged per pair. Logistic growth curves were fitted to changes in wing length and weight with age using all measurements from known-age chicks in 1992. Chicks in all years were then aged from their wing length (Hamer, Furness and Caldow 1991) using the 1992 curve of wing length versus age. The deviation (or mean deviation if more than one measurement was available) for each chick from its predicted weight (using the 1992 curve of weight versus age) at that age was then calculated, and expressed as a proportion of the expected value. The mean chick growth index was calculated for each year from 1976 to 1994, with the exception of 1990 when no chicks were measured, and used to compare annual variation in chick body condition. Counts were made of the number of chicks seen fledged at all territories on the island in 1986 and from 1988 to 1994, and from a sample of 28 nests in the north of Foula in 1987.

Arctic skuas obtain most of their food by chasing sandeel-carrying hosts within 1 km of the east coast of Foula (Furness 1978). In most years between 1975-80 and 1986-1993 watches were made from a coastal observation site at intervals through June and July (Furness 1978, 1980, Caldow 1988). During each observation period the number of chases of the various host species was recorded. The proportion of chases in each year directed towards Arctic terns was compared (after arcsine transformation) with two indices of that host`s availability, the number of breeding adults and the total number of chicks fledged.

Arctic skuas regurgitate freshly-obtained fish to their mate and chicks after return from almost all absences from the territory and time spent away can therefore be used as an index of foraging effort in each year (Furness 1987, Hamer *et al.* 1991). The number of adults present was recorded at each visit to marked territories in 1979, 1987, and 1992 to 1994. This was converted to a mean for each individual territory at four different stages of the season; incubation and 0-9 days, 10-19 days and 20-30 days post-hatching. The mean attendance was then determined for marked territories at each stage in each year. In 1979 territories were not visited beyond twenty days after the chicks had hatched and therefore comparison between then and the other years was limited to the first three of these stages.

Adults were trapped on the nest while incubating in 1987, 1988, 1992, 1993 and 1994. The mean weights of these birds were compared to investigate whether adult body condition during the early part of the season was lower in the former two years when food availability was poor.

The Arctic skua colony was censused in most years by counting apparently occupied territories (Furness 1982). Counts for the years 1974-1982 are from Furness (1983). The remainder are either by Mrs. Sheila Gear (unpubl. data) or by the authors, with the exception of a 1986 count in Ewins *et al.* (1988). In 1974, 1975, 1985, 1986 and 1989 to 1991, the population size is the mean of two independent counts. These changes in numbers in successive years were also examined in terms of annual net recruitment to the breeding population, here defined (following the approach of Ollason and Dunnet 1983) as the difference between the actual population size in a given year and the expected number of surviving birds from the previous year corrected for an estimate of the annual mortality rate. Colour-ringing of Arctic skuas from 1992-94 indicated a mean annual return rate of 86.4%, with no bird absent in 1993 returning in 1994. There are no mortality rate estimates available for Arctic skuas on Foula prior to the 1990s and so a mortality rate of 13.6% (derived from the colour-ringing data) was used in the model. A negative value for the net recruitment index in any year can therefore be interpreted as a consequence of unusually high mortality or that established birds are absent from the colony or potential first-time breeders are refraining from recruiting in a given year.

3.4 Results

3.4.1 BREEDING DATA

3.4.1.1 *Arctic tern*

Between 1984 and 1990 no Arctic tern chicks fledged from Foula. In addition, less than 0.2 chicks fledged per pair of breeding adults in two earlier years, 1977 and 1978 (Fig. 3.1).

3.4.1.2 *Arctic skua*

There was a highly significant difference among years in Arctic skua chick growth (Kruskal-Wallis ANOVA $\chi^2 = 181$, n=1913, P<0.0001: Table 3.1). Multiple nonparametric ranges tests (Zar 1984) indicated that chick growth was high in 1983 and to an extent also in 1977, was poor in 1979, 1984 and 1987-89 (1984 and 1988-89 in particular) and varied little in most other years. Chicks were not measured in 1990.

Between 1987 and 1990 fewer than 0.25 chicks fledged per pair of breeding adults on Foula. The number of fledglings per pair in 1990 was 0.09. In comparison, from 1991 to 1994 fledgling production was consistent at approximately 0.9 chicks per pair. In 1986, despite this being a poor year for Arctic terns, Arctic skuas fledged 0.63 chicks per pair. These differences correlated with the chick growth index in each year (r = 0.80, n=8, P<0.02: Fig. 3.2).

3.4.2 CHANGES IN KLEPTOPARASITIC HOSTS

There was considerable variation between years in the proportion of chases directed towards the various species of host (Table 3.2). Arctic terns were important hosts in some years in the late 1970s (1975-6 and 1979) and in the early 1990s, but were virtually absent as victims from 1986 to 1990. They were chased relatively rarely in 1978 and 1980, the former being a very poor year in terms of tern breeding performance (Fig. 3.1). In most years when Arctic terns were chased relatively infrequently the hosts tended predominantly to be puffins. Guillemots featured principally in two years, 1989, and 1990. The remainder of the chases were of kittiwakes and razorbills *Alca torda* L., both of which appeared to be relatively unimportant as host species.

There were highly significant correlations between the proportion of chases directed towards Arctic terns and the indices of their likely availability to Arctic skuas; the total tern breeding population on Foula ($r = 0.73$, $n=12$, $P<0.01$) and the number of tern chicks fledged ($r = 0.83$, $n=12$, $P<0.002$: Figs. 3.3 and 3.4).

3.4.3 ATTENDANCE

Table 3.3 shows the data on adult territorial attendance in 1979, 1987 and 1992 to 1994. There were significant differences between these years in attendance at all stages in the season; incubation (Kruskal-Wallis ANOVA $\chi^2 = 17$, $n=588$, $P<0.002$), 0-9 days post-hatching (Kruskal-Wallis ANOVA $\chi^2 = 38$, $n=453$, $P<0.0001$), 10-19 days post-hatching (Kruskal-Wallis ANOVA $\chi^2 = 36$, $n=387$, $P<0.0001$), and 20-30 days post-hatching (Kruskal-Wallis ANOVA $\chi^2 = 44$, $n=285$, $P<0.0001$). There were no data for this last stage from 1979. Attendance was low in 1987, and to an extent also in 1979 in comparison with the early 1990s. 1979 was the year with the lowest recorded sandeel recruitment between the mid 1970s and 1983 (Bailey *et al.* 1991).

3.4.4 ADULT BODY WEIGHT

The weights of the adult Arctic skuas nest-trapped during incubation are shown in Table 3.4. One-way ANOVA indicated that there were no differences among years in adult incubation weights (ANOVA $F_{4,148} = 1.6$, n.s.). However, all six birds trapped in 1988 weighed less than the mean value in all other years (Binomial probability distribution $P=0.016$).

3.4.5 NET RECRUITMENT

The net recruitment index shows considerable annual variation between 1975 and 1994 (Table 3.5). Net recruitment was high in several seasons in the latter half of the 1970s, but was then constant but at a much reduced level through the 1980s until 1987, concurrent with the overall population decline. In 1988 and 1990, net recruitment was negative - highlighted in the table by '**' - but in each following year, 1989 and 1991, was much higher than it had been throughout the 1980s. In 1992, net recruitment was also high in comparison with the very low level in the two subsequent years, 1993 and 1994.

Table 3.1. Arctic skua chick growth on Foula in 1976-1994. The growth index is the mean difference between the observed and the predicted weight of chicks (derived from the 1992 growth curve) expressed as a proportion of the predicted value. Data are means ± 1 SE. Nonparametric ranges tests results indicated that chick growth in (i) 1983 > 1979-80, 1982, 1984, 1987-89 and 1993, (ii) 1977 > 1979, 1984 and 1987-89 (iii) 1976, 1978, 1980-81, 1985-86 and 1991-94 > 1984 and 1988-89 and (iv) 1979, 1982 and 1987 > 1989.

Year	n	Growth index	Year	n	Growth index
1976	134	0.01±0.01	1986	57	-0.00±0.01
1977	82	0.03±0.01	1987	58	-0.03±0.01
1978	142	-0.00±0.01	1988	91	-0.07±0.01
1979	212	-0.03±0.01	1989	55	-0.14±0.02
1980	120	-0.01±0.01	1990	-	no data
1981	99	-0.01±0.01	1991	40	0.03±0.02
1982	102	-0.02±0.01	1992	202	0.00±0.00
1983	73	0.05±0.01	1993	192	-0.01±0.01
1984	40	-0.09±0.02	1994	166	-0.00±0.01
1985	48	0.01±0.02			

Table 3.2. Variation in the species kleptoparasitised by Arctic skuas on Foula - data for 1975-76 from Furness (1978), for 1978 and 1979 from Furness (1980) and for 1986 and 1987 from Caldow (1988).

Year	Percentage of all chases directed towards:					Total chases observed
	Arctic tern	Puffin	Guillemot	Kittiwake	Razorbill	
1975-6	74	12	0	11	3	117
1978	9	76	14	2	0	198
1979	51	39	5	4	1	741
1980	7	80	13	0	0	314
1986	0	76	14	1	9	1326
1987	1	73	15	0	11	469
1988	0	84	15	1	0	664
1989	1	20	68	5	6	50
1990	0	67	33	0	0	18
1991	35	57	2	5	1	127
1992	26	46	8	20	0	204
1993	42	34	5	18	1	116

Table 3.3. Territorial attendance of Arctic skuas on Foula in 1979-94 - data are the mean number of adults present on territory ± 1 SE (n)

Year	Stage of season:			
	Incubation	0-9 days post-hatching	10-19 days post-hatching	20-30 days post-hatching
1979	1.78±0.02 (175)	1.84±0.03 (115)	1.68±0.05 (83)	no data
1987	1.76±0.02 (28)	1.71±0.03 (25)	1.54±0.06 (24)	1.44±0.06 (23)
1992	1.85±0.02 (122)	1.90±0.02 (104)	1.82±0.03 (87)	1.66±0.04 (85)
1993	1.88±0.01 (136)	1.88±0.02 (111)	1.76±0.03 (102)	1.60±0.03 (100)
1994	1.87±0.01 (127)	1.85±0.02 (98)	1.90±0.02 (91)	1.87±0.03 (77)

Table 3.4. Weights (mean ± 1 SE) of incubating Arctic skua adults on Foula in different years.

Year	Number	Weight	Range
1987	9	433.3±13.3	345-475
1988	6	404.3±10.6	360-430
1992	70	442.3±5.0	355-525
1993	49	439.2±6.0	365-530
1994	19	451.1±9.1	375-525

Table 3.5. Annual variation in the net recruitment of Arctic skuas on Foula between 1975 and 1994 assuming an annual mortality rate for established breeders of 13.6%.
[a] - interpolated population size estimates, ** - N.B. negative net recruitment

Year	(1) Total number of pairs	(2) Expected population size	net recruitment index in no. of pairs i.e. (1)-(2)	net recruitment index as a proportion of actual pop. size
1974	190	-	-	-
1975	247	164	83	0.34
1976	280	213	67	0.24
1977	264	242	22	0.08
1978	252	228	24	0.10
1979	273	218	55	0.20
1980	262	236	26	0.10
1981	245	226	19	0.08
1982	224	212	12	0.05
1983[a]	209	194	15	0.07
1984[a]	194	181	13	0.07
1985	181	168	13	0.07
1986	175	156	19	0.11
1987	169	151	18	0.11
1988	130	146	-16**	-0.12**
1989	139	112	27	0.19
1990	110	120	-10**	-0.09**
1991	126	95	31	0.25
1992	159	109	50	0.31
1993	145	137	8	0.06
1994	134	125	9	0.07

Fig. 3.1. Arctic tern breeding success on Foula, 1974-1994.

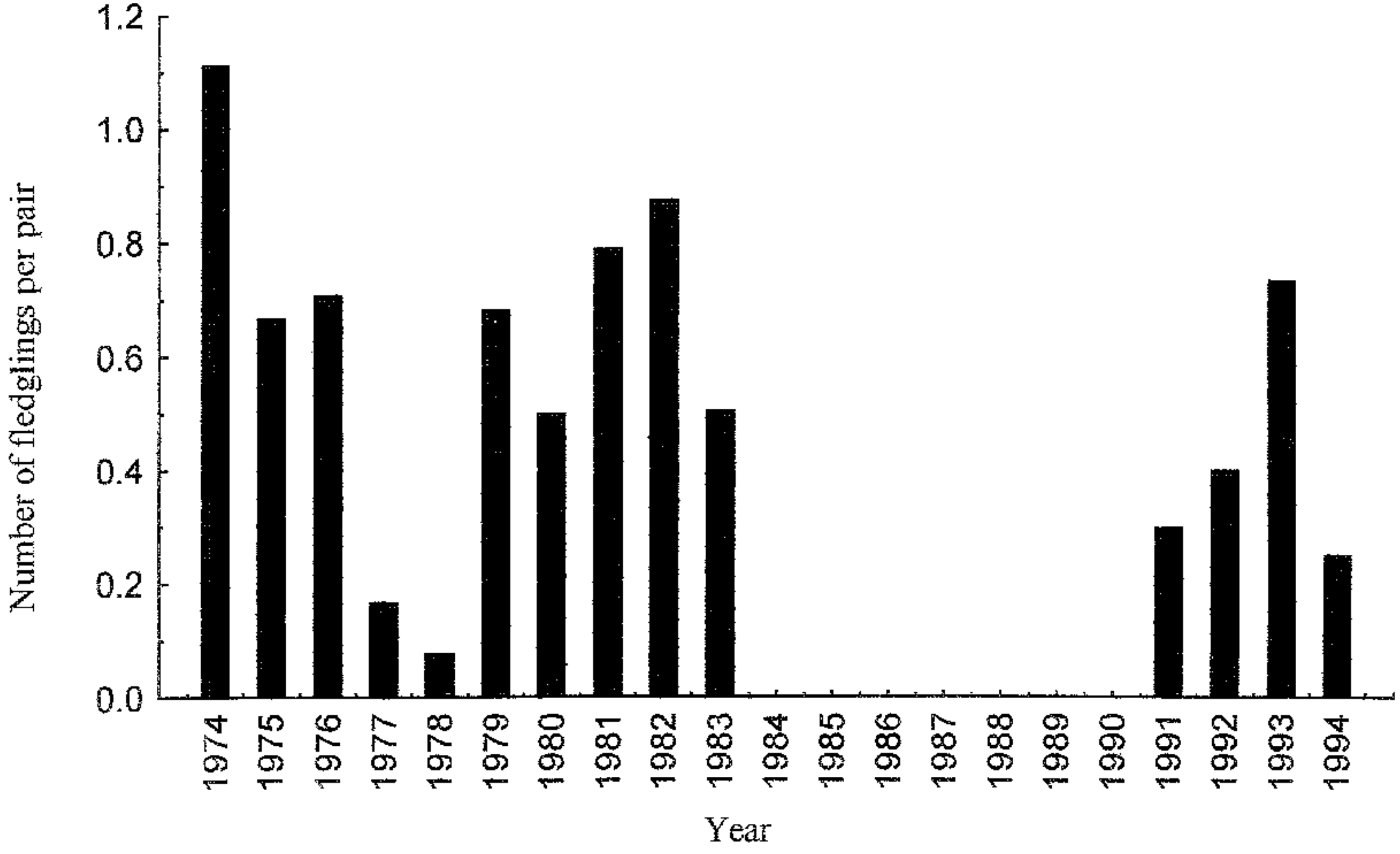


Fig. 3.2. Arctic skua chick growth in relation to fledgling production on Foula.
(r=0.80, n=8, P<0.02)

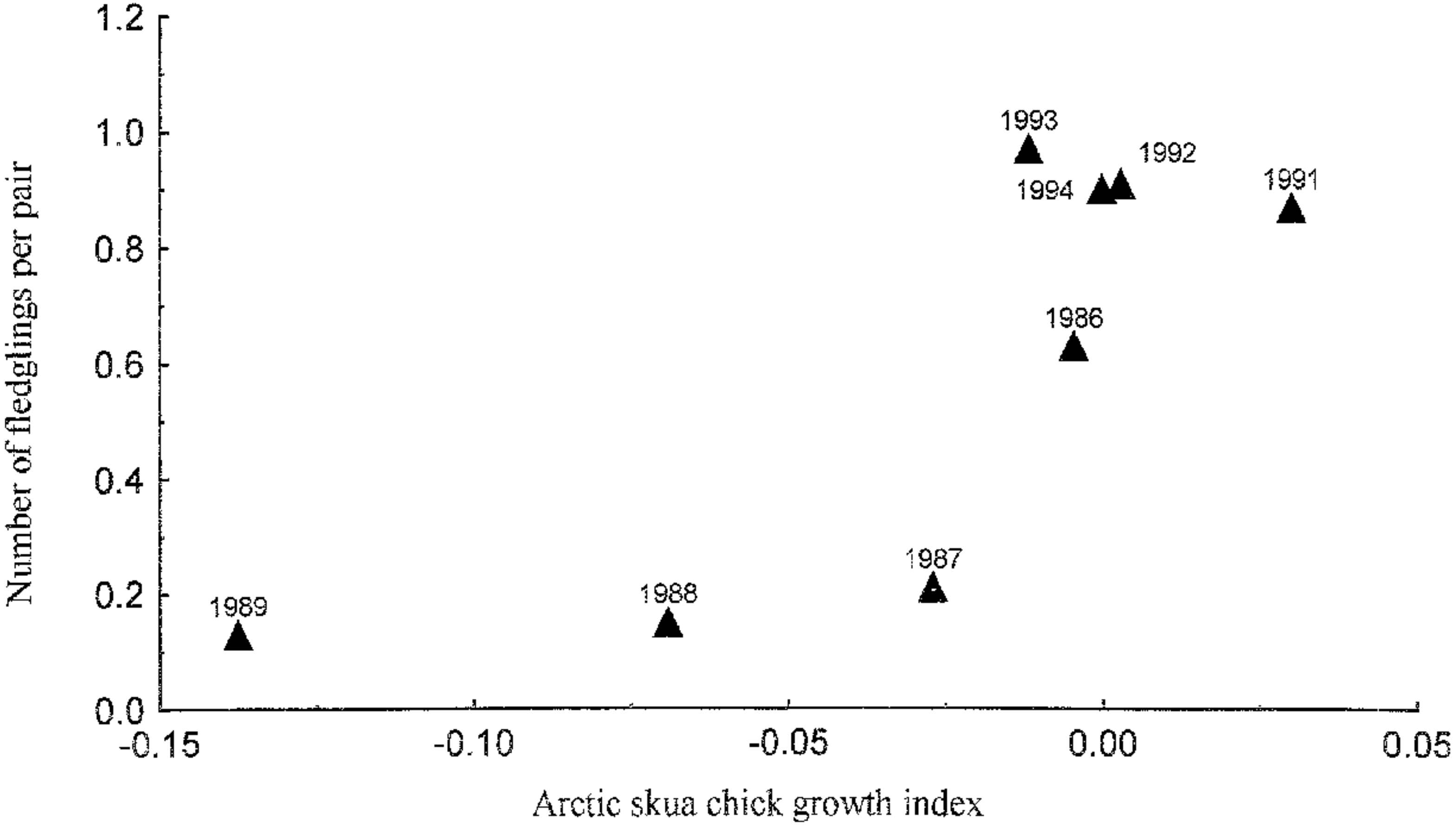


Fig. 3.3. Variation in the proportion of chases directed towards Arctic terns versus the size of the tern breeding population in each year. ($r=0.73$, $n=12$, $P<0.01$)

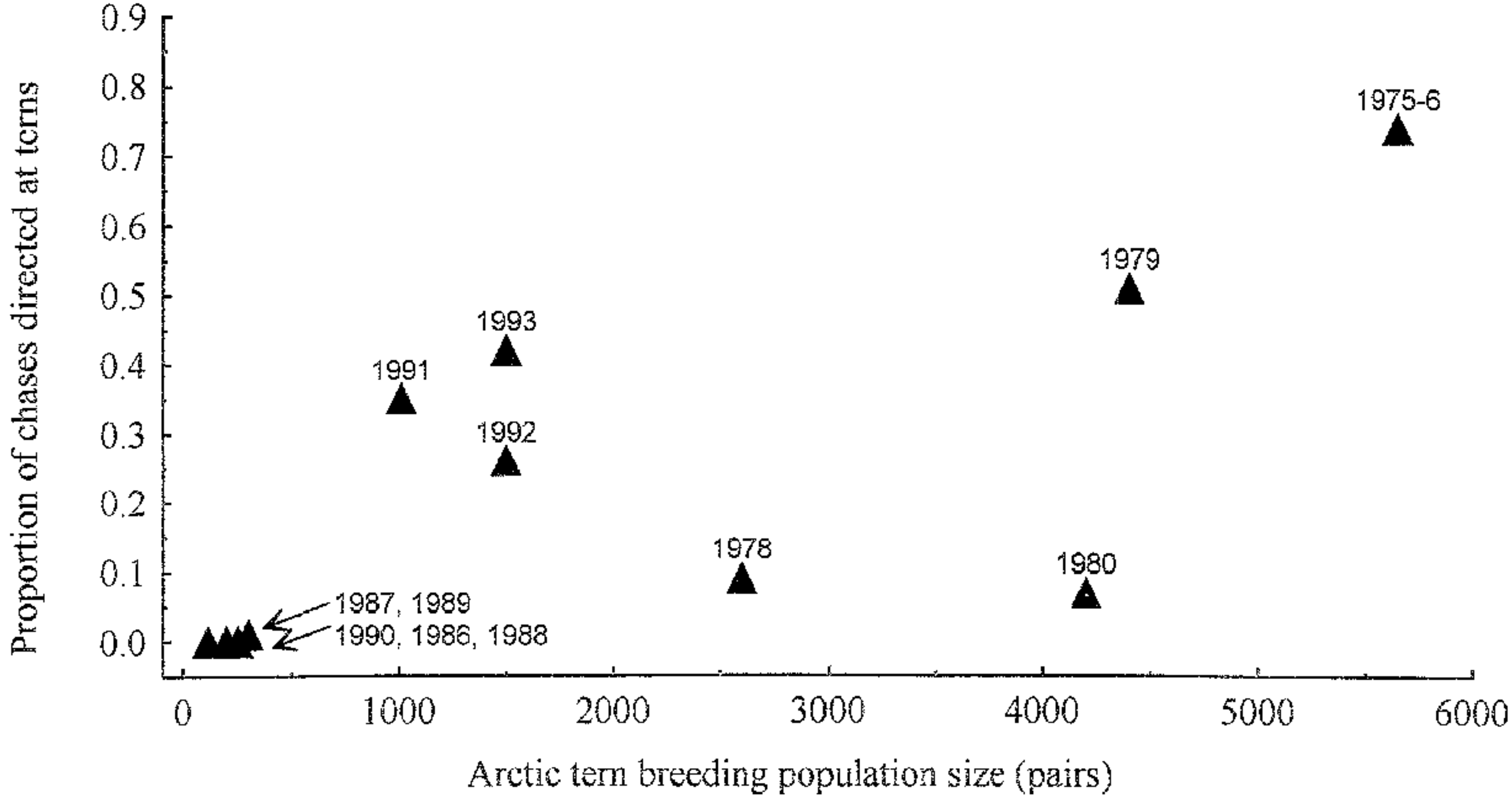
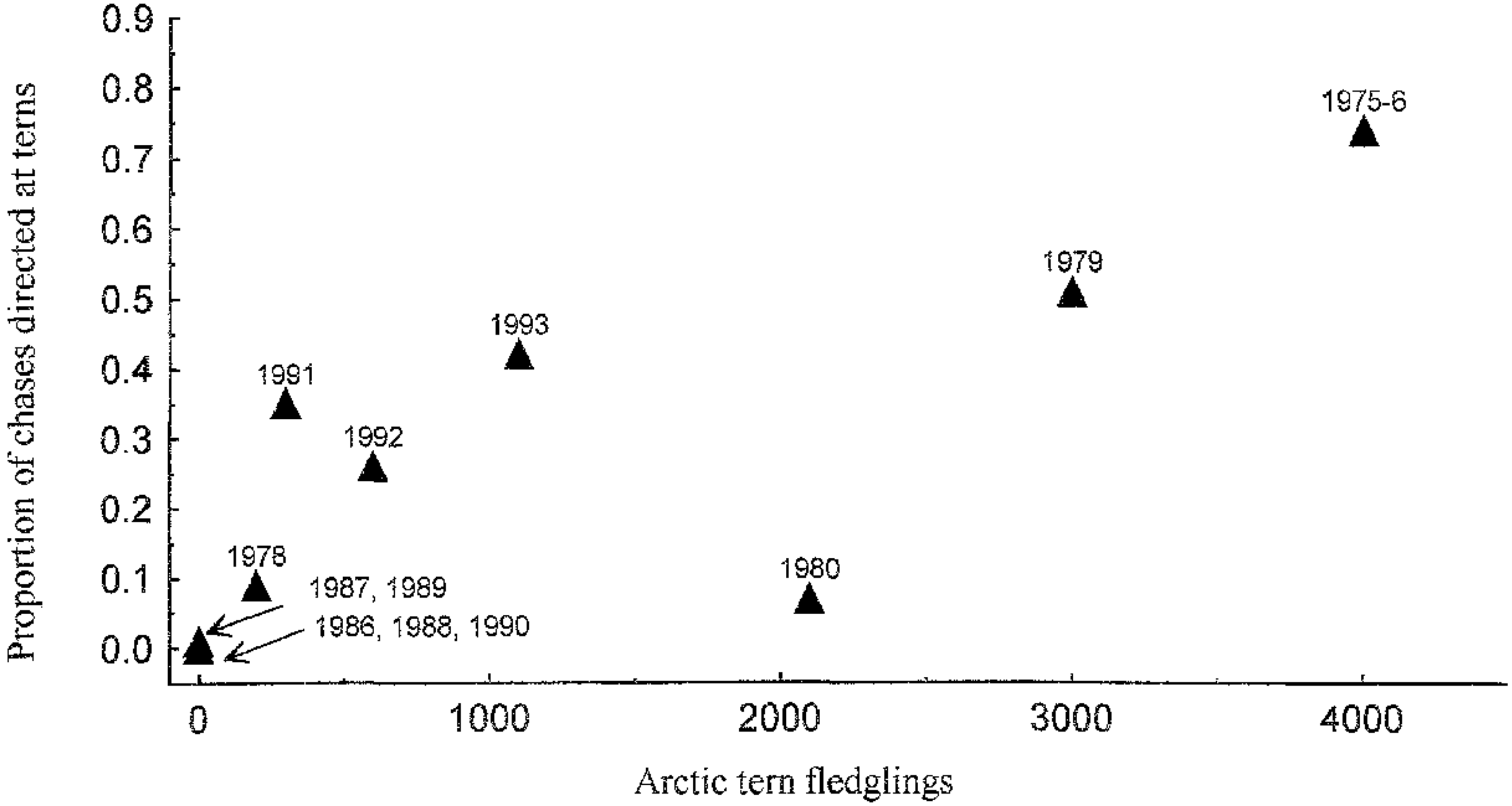


Fig. 3.4. Variation in the proportion of chases directed towards Arctic terns versus the number of tern chicks fledged in each year.

(r=0.83, n=12, P<0.002)



3.5 Discussion

Between 1984 and 1990 there was a complete breeding failure on Foula and elsewhere in Shetland of Arctic terns, one of the Arctic skua's major kleptoparasitic hosts (Monaghan *et al.* 1989). Virtual population analysis using fisheries data indicated a dramatic reduction in sandeel recruitment in Shetland waters during the 1980s, and particularly from 1984 onwards (Bailey *et al.* 1991). Despite this, Arctic skua chick growth was apparently normal in 1985 and 1986, and fledging success was only seriously affected from 1987 to 1990. Given such considerable variation in prey availability, Arctic skua adults must have responded by modifying one or more components of their reproductive or foraging strategies. The considerable temporal gap between the onset of breeding failure for Arctic terns and for Arctic skuas, indicates that, unlike terns, skuas were able to buffer themselves from the effects of declining food availability in these earlier years.

The breeding success of two principal kleptoparasitic hosts of Arctic skuas, Arctic terns and puffins, and less importantly, kittiwakes, was already depressed Shetland-wide because of reduced sandeel availability by 1987 (Martin 1989, Monaghan *et al.* 1989, Harris and Wanless 1990). These former species, as well as guillemots, and to a much lesser extent razorbills, were all chased by Arctic skuas in the mid to late 1970s. During the late 1970s in the years when Arctic terns were breeding successfully, terns were probably chased more frequently than puffins because chases towards them were over twice as likely to be successful (Furness 1978). During the mid 1980s, the majority of chases were directed towards puffins and, particularly in 1989, and also 1990, guillemots. Only from 1991 onwards did Arctic terns and kittiwakes reappear as target species. Puffin breeding success was consistently good on Foula up until 1985, following which there were five very poor years when few adults were observed carrying sandeels to chicks late in the season (RWF, unpubl. data). Guillemot breeding success on Foula was good in 1988, as in 1981-83 (Bailey *et al.* 1991) and their breeding success seems to have been generally unaffected by the reduced sandeel recruitment of the late 1980s. The preference of Arctic skuas for chasing puffins rather than guillemots, despite puffins' relatively poor breeding success in the mid 1980s, was again a likely consequence of differential chase success rate. Chases of puffins by dark-phase skuas (the majority of the population) were consistently almost twice as likely to be successful than those of guillemots (Furness 1978, Caldow and Furness 1991). This was despite an overall decline in success rate towards puffins observed since the 1970s (Caldow and Furness 1991).

Arctic terns feed their chicks predominantly on recruiting (0-group) sandeels, and by comparison guillemots specialise on longer and therefore older (mainly 1-group) fish (Furness 1990). While there is a degree of overlap, kittiwakes and puffins tend to feed on sandeels in the size ranges intermediate to those preferred by the other two species (Furness 1990). As the availability of 0-group sandeels declined during the 1980s, Arctic skuas therefore modified their foraging strategy to chase the host species specialising on progressively older sandeels. This variation in host selection by Arctic skuas is analogous to the dietary switches apparent in other seabird species when relative availabilities of different prey change (Hislop and Harris 1985, Montevecchi, Birt and Cairns 1988, Martin 1989, Hamer *et al.* 1991) and appears to have gone some way in ameliorating the effects of low sandeel availability for Arctic skuas up until 1987.

In addition to the their changes in host selection behaviour, Arctic skuas also have considerable scope to vary the amount of energy they invest feeding themselves and their chicks. In years of below average food abundance, 1987 and possibly also 1979, adult Arctic skuas reduced the amount of time they spent on territory. Such increases in foraging effort in poor food years are a common feature in the behavioural repertoire of seabirds experiencing fluctuations in food availability (Gaston and Nettleship 1982, Monaghan *et al.* 1989, Hamer *et al.* 1991, 1993).

However, according to the predictions of life-history theory, any increase in breeding effort ought not to elicit a cost in terms of future reproductive potential. Altering foraging behaviour should have buffered Arctic skuas from the reduction in sandeel availability, but only until a limit beyond which no further increase in effort was feasible without sustaining such future costs. There is however limited evidence (given the small sample size) that adults were lighter in 1988, the first year subsequent to the decline in adult attendance and also chick growth and fledging success. This may indicate either that sandeels were extremely scarce early in the season in 1988 and adults could not obtain sufficient quantities even to maintain their own body condition, or possibly that birds were suffering repercussions from the energetic costs of more and/or longer foraging trips in the previous year. Similarly, Arctic terns and kittiwakes, but not great skuas, also showed a decline in body condition in years with or following poor food availability (Monaghan *et al.* 1989, Hamer *et al.* 1991, Hamer *et al.* 1993).

The increase in foraging effort in 1987 may also have had considerable bearing on whether adults returned to breed the following year. Net recruitment of breeders to the population was negative in both 1988 and 1990. A net recruitment index of zero in 1988 would have required adult mortality over the 1987-88 non-breeding season to be 23%, twice that recorded for the Foula population between 1993 and 1994. Assuming adult mortality did not increase to that extent during 1988-89 and 1990-91, then established breeders (and possibly also prospective first-time recruits) refrained from breeding in those years. This hypothesis is backed up by the anomalously high net recruitment indices in each year that followed, strongly suggesting that considerable numbers of these deferring adults returned to the colony in 1989 and 1991. There is doubtless a strong selective pressure for adults that have not been able to recover over a single winter from the effects of the previous poor breeding season not to breed the following year. This corresponds to the low body weights recorded for adults that did attempt to breed in 1988.

High net recruitment in 1992, two years after the previously poor breeding season may indicate that potential first-time breeders refrained from recruiting in 1991 until it was clear from the performances of established pairs that conditions had improved. Similarly, experienced adult kittiwakes breeding in the highly variable environmental conditions in Alaska tend not to attend the colony in years when reproductive performance is poor overall (Murphy, Springer and Roseneau 1991). Poor net recruitment recorded in 1993 and 1994 is a consequence of the low fledging success in the late 1980s and it would be reasonable to predict an increase in the number of new breeders in 1995 as adults breed on average aged 4.4 years (O'Donald 1983) and some chicks fledged in 1991.

Arctic skuas appear to have considerable scope in their behavioural repertoire to buffer marked fluctuations in prey (or host) availability. However, increasing reproductive investment in a given year may result in birds being in poor body condition or deferring breeding in the following year. There is also limited evidence that potential new recruits may choose not establish territories until conditions improve.

3.6 Acknowledgements

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Chapter Four. Sexing adult Arctic skuas by discriminant function, and seasonal changes in mass of sexed birds

4.1 Introduction

Patterns of mass change in breeding birds exhibit extreme inter-specific variation (for a recent review see Moreno 1989). Within a species, each sex may have a quite distinct strategy of weight gain and loss at different stages of the reproductive cycle. A distinction has been made between those in which the female loses mass throughout incubation, reaching a minimum weight when the chicks hatch, and those in which mass either remains relatively constant or increases slightly during this early stage of the season (Moreno 1989). The former strategy is generally associated with extreme levels of female attentiveness during incubation in for example gamebirds and ducks. By contrast, incubatory mass constancy tends to occur when the male either supplies food to the female (raptors, owls etc.) or takes a share in incubating the eggs (doves and many seabirds). Once the chicks have hatched, the weights of parents in species with this latter strategy tends to decline until chicks fledge (Moreno 1989).

Depending on the timing of mass changes, general reductions in body weight during breeding have been assumed to be either a consequence of physiological stress (Drent and Daan 1980, Ricklefs 1983), or an adaptive response to minimise wing loading and improve flight efficiency (Freed 1981, Norberg 1981, Moreno 1989). While these hypotheses are not necessarily mutually exclusive, each anticipates that weight reductions occur at relatively different rates and during different stages of the season. The former predicts a gradual decline in condition as the season progresses, whereas the so-called 'programmed anorexia hypothesis' (Jones 1994) predicts an abrupt loss of mass at the time of hatching, just as adults' flight requirements increase in order to cope with the additional demands of chick-provisioning. Such a sudden stepwise reduction in body condition could also be a consequence of physiological stress if brooding is exceptionally demanding (Ricklefs 1983). However this does not appear to be the case, at least in some seabirds (Croll *et al.* 1991, Jones 1994).

Recent work on seabirds provides evidence supporting the programmed anorexia hypothesis (Gaston and Jones 1989, Croll *et al.* 1991, Jones 1994). In these studies on auks, birds were either of unidentified sex or there were no inter-sexual differences in the pattern of mass change. In species such as gulls and skuas, there is unequal sex-partitioning of incubating and chick-rearing duties (Pierotti 1981, Burger 1987, Furness 1987). Selection for flight efficiency of either the male or the female may therefore operate for a more prolonged period or at a different stage of the season, depending on the particular demands of their breeding role.

Discriminant analysis has been widely used to determine sex in species with sexual size dimorphism but monomorphic plumage (e.g. Dunnet and Anderson 1961, Green 1982, Monaghan and Metcalfe 1986, Hamer and Furness 1991, Hatch *et al.* 1993). Such an analysis involves the production of a descriminant function, a linear combination of several morphometric variables which best describes the statistical distinction between samples of adults of known sex, and this is used to predict the sex of unknown birds. The effectiveness of such a technique depends in part on the repeatability of characters employed in the function. Certain morphometrics, for example bill dimensions, may change with age (Coulson *et al.* 1981, Hamer and Furness 1991). Other variables such as weight may change seasonally (Coulson *et al.* 1983, Lima 1986, Monaghan and Metcalfe 1986, Moreno 1989). However, this does not preclude the use of body mass in discriminant analysis if it is measured at the same stage of the season in all individuals and there is limited variation between years.

This chapter attempts to develop a reliable method for sexing Arctic skuas on Foula using discriminant analysis. In addition, it examines the evidence in support of an adaptive loss of mass in breeding birds at the onset of the chick-rearing period. An inter-sexual difference in the pattern of weight variation is discussed in relation to sex role-partitioning of breeding duties.

4.2 Methods

Adult Arctic skuas were trapped on Foula during the breeding season in 1992-1994. Incubating birds were caught on the nest in 1992 using a remote-controlled spring-hinged trap, and in 1993 and 1994 using a string-operated, elastic-powered clap net. Mobbing adults were also caught around hatching and during chick-rearing with an overhead 'flick' net. In addition, in 1993 and 1994 during chick-rearing (when conditions were favourable in terms of wind speed), birds were trapped in a heavy duty single shelf mist-net positioned above a taxidermic mount of a great skua *Catharacta skua*. The stuffed bird was frequently, but not always, mobbed aggressively by the holders of the territory in which it was placed. Occasionally it was also mobbed by other adults flying over the territory. Consequently, weights from six individuals caught by this technique were eliminated from further analyses as they were not breeding in the year of capture. Weights of adults trapped on replacement clutches were similarly excluded from analyses.

Unringed birds were fitted with a standard BTO metal ring and a unique combination of four plastic colour-rings, with the exception of one light-phase individual easily recognisable by the absence of its right tarsus and foot. Adults were weighed to the nearest 5g using a Pesola balance. Wing length (maximum flattened chord) was measured using a stopped wing-rule, and tarsus length, head plus bill length, bill (culmen) length and bill depth (at the gonys, perpendicular to the cutting edge) were measured using Vernier callipers. Both wing and tarsus were measured on the right side of the body (with the exception of the light-phase bird mentioned above!).

Measurements were compared for birds of known age (ringed as chicks on Foula or elsewhere in Shetland) in the year of capture, including four captured as breeders in 1975 which were assumed to have been aged four when first trapped (see Chapter 6 for details). Repeatability analysis was used to assess the reliability of morphometric measurements taken in different years by the same observer, and also the degree of variation between-years in individuals' body weights. Repeatability analysis is a statistical assessment of the consistency of repeated measures of the same character (Zar 1984, Lessells and Boag 1987, Harper 1994). The repeatability value, r_i (the intraclass correlation coefficient) describes the proportion of variance that occurs among rather than within individuals. A value of one would indicate that the character is perfectly consistent with no observer error and no variation between observations. A value of zero indicates that repeated measurements of the same individual are no more similar than those collected from different birds chosen at random from the population. Negative repeatabilities are theoretically possible, but unlikely to occur for morphometric variables (Harper 1994). Harper (1994) suggested that repeatability (r_i) values of less than 0.2 indicate slight repeatability, between 0.2 and 0.4, low repeatability, between 0.4 and 0.7, moderate repeatability, between 0.7 and 0.9, high repeatability, and greater than 0.9, very high repeatability.

Repeatability (r_i) can be calculated using the among-group (s_a^2) and the within-group (s_w^2) variance components derived from one-way ANOVA, such that $r_i = s_a^2/(s_w^2 + s_a^2)$ (Lessells and Boag 1987). These variance components are calculated from the mean square values in ANOVA as follows $r_i = [\mathrm{MS_B} - \mathrm{MS_w}] / [\mathrm{MS_B} + (n-1).\mathrm{MS_w}]$ where $\mathrm{MS_B}$ is the between groups mean square, $\mathrm{MS_w}$ is the within groups mean square and n is a co-efficient taking account of the sample size. If there are the same number of observations in each group, n is simply the size of each sample. If sample sizes are unequal,

$$n = [\frac{1}{k-1}].[\sum_{i=1}^{k} n_i - \frac{\sum_{i=1}^{k} n_i^2}{\sum_{i=1}^{k} n_i}]$$

where k is the total number of individuals (groups), $\sum_{i=1}^{k} n_i$ is the total number of measurements, and $\sum_{i=1}^{k} n_i^2$ is the number of all measurements within each group, squared, and then summed (Zar 1984, Lessells and Boag 1987).

Repeatability values were calculated for morphometrics from 11 individuals first trapped in 1992 and 13 individuals first trapped in 1993, each of which were re-measured in 1994, and two individuals caught on two separate occasions in 1994. Repeatability of adult weight was also calculated for 23 birds caught during incubation in more than one year. Of these, 16 were caught and then re-weighed the following year, and seven were re-weighed two years following their first capture.

Breeding adults were sexed by observation of copulatory position or association with a marked bird of known sex. It was subsequently found that courtship-feeding behaviour also permitted accurate sexing (no males were seen soliciting regurgitations from females, whereas the opposite was commonly observed). Six corpses were sexed by internal examination.

Because incubation weights were consistent among years, and there was no apparent decline in weight of either sex during incubation (see Results), incubation weight was used in discriminant analysis. Two separate discriminant analyses were performed, the first including incubation weight and other morphometrics, and the second excluding weight in order to create a function that could be used to sex adults caught only during chick-rearing. The criterion used for variable selection was Mahalanobis' distance (D^2), which is a generalised measure of the distance between two groups (Norusis 1988). Variables were selected in a stepwise fashion, with those variables with the largest D^2 for the two groups entered first. The effectiveness of each of the discriminant functions was assessed in terms of the proportion of known-sex adults correctly classified.

Principal component analysis summarises covarying patterns of variation in morphometric data to produce independent composite variables which are loosely interpreted as size and shape axes (Rising and Somers 1989, Freeman and Jackson 1990). Separate principal component analyses were carried out for each sex in order to determine the most effective body size index, and in addition the analysis was performed on all birds grouped together in order to create another index useful in comparisons of body size between the members of individual pairs.

Investigation of possible seasonal trends in body condition of males and females was carried out using multiple regression analysis, with weight as the dependent variable and body size index and stage of the season (days since the first egg was laid) as independent variables. Direct comparisons of body condition between incubation and chick-rearing were also carried out using one-way ANOVAs, in an attempt to detect the proposed stepwise decline in mass at hatching.

The attendance of marked adults was monitored during the breeding season in 1994, regardless of whether individuals were of known sex at that time. At routine visits to territories during incubation the identity of the individual that was on the nest was noted, even if both adults were present. In addition, the identity of single birds present on territory was determined during both incubation and chick-rearing.

4.3 Results

In total, 48 colour-ringed birds were sexed by observation of copulatory position and 28 by observation of courtship-feeding behaviour. A further 13 adults were sexed indirectly because of prior or subsequent association with these birds. In addition, six corpses were sexed by internal examination, two of which had colour-ringed partners.

There were no correlations between age and any morphometric variables (Table 4.1). Repeatabilities were highly significant for all morphometric variables recorded twice on individual Arctic skuas (Table 4.2). In the first analysis, most repeatabilities were high, with the exception of tarsus length. Examination of the raw data indicated that there was greatest discrepancy between initial and later measurements of two Arctic skuas trapped first in 1992. Excluding these birds raised the repeatability value from 0.65 (moderate) to 0.87 (high). Adult weight during incubation was highly repeatable.

Although the ranges overlapped, there were significant differences between male and female Arctic skuas of known sex in all morphometric variables recorded with the exception of bill length (Table 4.3). Two separate discriminant analyses were carried out. The first analysis correctly classified 90.5% of the 74 known-sex adults included, according to their score on the following discriminant function, D=0.0820 x wing length + 0.0290 x incubation weight - 39.33, with a cut-off point of -0.168 (Function 1, Fig. 4.1). The second function, in which incubation weight was not available for entry, correctly classified 77.9% of 95 cases, with a cut-off point of -0.072, and a function D=0.134 x wing length + 0.320 x head plus bill length + 1.285 x bill depth - 0.236 x bill length - 73.49 (Function 2). In both analyses, adults with discriminant function scores greater than the cut-off values were classified as female and those with lower scores as male.The negative value for bill length in Function 2 indicates that this character tends to be shorter in females relative to the other variables in the analysis i.e. reflects a difference in shape rather than size between males and females.

Although all cases in a discriminant analysis can be classified on the basis of the absolute value of their discriminant score (D), there is an associated probability that an individual with a particular value for D is, or is not likely to belong to one or other group. This probability is calculated according to Bayes' rule (Norusis 1988). A case is classified according to the value for D, in the group for which the posterior probability value (PP) is greater. It is therefore possible to limit the classification of cases with more equivocal values for D, depending on PP (Hatch *et al.* 1993).

In order to increase the likelihood that adults of unknown sex would be correctly classified (particularly if no incubation weight was available and Function 2 was used), the results of the discriminant analyses for known-sex birds were re-assessed according to PP values. Assigning sex to one or other group using Function 1 only if PP was greater than 0.85, resulted in the correct classification of 93.1% of the 58 adults that were sexed. For Function 2, 87.8% of 41 adults were correctly classified. In 96.8% of the 31 cases to which both functions assigned a sex using PP > 0.85, there was agreement, although sex was incorrectly assigned by both functions in two of these cases. Combining the two functions hierarchically i.e. classifying sex according to Function 1 if PP > 0.85, and according to Function 2 if PP > 0.85, only if Function 1 did not assign sex, correctly classified 91.2% of 68 known-sex birds.

The following hierarchical system of classification was therefore used to assign sex to colour-ringed adults (i) sex by observation, (ii) sex by Function 1 if PP > 0.85, or (iii) sex by Function 2 if PP > 0.85. Birds were also sexed if paired with an individual sexed by one of the above criteria. By this means, sex was assigned to 86.4% of the 214 adults trapped and measured during 1992-1994.

Several authors have suggested that adult skuas can be sexed by relative size within a pair (Ainley *et al.* 1985, Hamer and Furness 1991). Body size and incubation weight were therefore compared between members of colour-ringed pairs sexed by the above criteria. The analysis excluded 5 pairs in which neither bird was sexed. Principal components analysis using all measured birds was used to assess body size, and consequently male and female values for this index are directly comparable. From Table 4.4 it was apparent that within a pair, females were almost always heavier during incubation, and usually also larger, as would be expected from comparison of all birds of known sex (see Table 4.3). However, there was also a significant positive correlation in body size index between males and females within the pair (Table 4.4 and Fig. 4.2). Incubation weights were not correlated.

Multiple regression analysis revealed that body size explained much of the variation in female weight ($r^2_{1,95}$=0.26, P<0.0001; Fig. 4.3), and the number of days elapsed since the first egg was laid ('stage') explained a further 10% ($r^2_{2,94}$=0.36, P<0.0005; Fig. 4.4). There was a also a significant positive relationship between weight and male body size ($r^2_{1,72}$=0.07, P<0.05: Fig. 4.5), but in this case no evidence of a seasonal decline (Fig. 4.6). Considering data from the incubation period only, there was no decline in female weight - in regression analysis only size ($r^2_{1,68}$=0.25, P<0.0001) and not stage was related to incubation weight. Neither of these variables entered the model using data on 50 males weighed during incubation. One-way ANOVA indicated a significant drop in body condition (weight corrected for size) of females at the time of hatching, but no evidence of a seasonal trend for males (Table 4.5).

When only one adult was present on territory during incubation, it was much more likely to be the female (Table 4.6). When both adults were present, there was no difference in the likelihood that one or other sex would be on the nest. There was also no difference in the likelihood that either the male or the female would be alone on territory during chick-rearing (Table 4.6).

Table 4.1. Correlations between morphometric variables and age of Arctic skuas on Foula.

Variable	Correlation
Wing length	r_{43}=-0.07, n.s.
Head plus bill length	r_{43}=-0.17, n.s.
Bill length	r_{43}=-0.23, n.s.
Bill depth	r_{43}=0.07, n.s.
Tarsus length	r_{43}=-0.07, n.s.
Incubation weight	r_{30}=-0.03, n.s.

Table 4.2. Repeatability of morphometrics of Arctic skuas trapped on Foula, 1992-1994.

Variable	n	Mean square: Between, within groups	F ratio	r_i
Wing length	26	90.20, 8.50	10.6, P<0.0001	0.83
Head plus bill length	26	3.94, 0.17	22.6, P<0.0001	0.92
Bill length	26	2.52, 0.24	10.4, P<0.0001	0.82
Bill depth	25	0.18, 0.016	11.8, P<0.0001	0.84
Tarsus length	26	3.91, 0.82	4.8, P<0.0002	0.65
	24[a]	3.81, 0.27	13.9, P<0.0001	0.87
Incubation weight	23	3441.7, 285.3	12.1, P<0.0001	0.85

[a] - excludes two of the adults measured first in 1992.

Table 4.3. Morphometrics of known-sex Arctic skuas trapped on Foula, 1992-1994 and used in discriminant analysis.

	Male	Female	T-test
Tarsus length (mm)	44.5±0.2 (44)	45.2±0.2 (53)	$t_{88.7}=-2.2$, $P<0.05$
range:	41.8-46.8	38.5-48.3	
Wing length (mm)	320.3±0.7 (44)	327.2±0.8 (53)	$t_{95}=-6.1$, $P<0.001$
range:	307-329	314-339	
Head plus bill length (mm)	76.1±0.2 (43)	77.3±0.2 (53)	$t_{94}=-4.0$, $P<0.001$
range:	71.9-79.0	74.3-81.5	
Bill length (mm)	28.6±0.2 (43)	29.0±0.1 (53)	$t_{94}=-2.0$, $P=0.051$
range:	25.3-30.3	26.7-31.3	
Bill depth (mm)	9.5±0.0 (43)	9.7±0.0 (53)	$t_{94}=-4.3$, $P<0.001$
range:	8-9-10.0	9.1-10.5	
Incubation weight (g)	405.0±4.7 (32)	466.8±4.7 (42)	$t_{72}=-9.1$, $P<0.001$
range:	360-470	395-525	

Table 4.4. Size and body condition of adults within pairs of Arctic skuas on Foula sexed by observation or discriminant analysis.

	Body size index	Incubation weight
No. of pairs	65	34
Female	0.52±0.09	473.8±4.5
Male	-0.67±0.10	402.5±3.9
Paired t-test	t_{64}=-10.5, P<0.001	t_{33}=-11.1, P<0.001
Comparison within pairs:	Male larger - 10.8% (7/65) Female larger - 89.2% (58/65)	Male heavier - 2.9% (1/34) Female heavier - 97.1% (33/34)
Correlation	r_{63}=0.31, P<0.02	r_{32}=-0.15, n.s.

Table 4.5. Seasonal changes in Arctic skua body condition on Foula - data are the residual values (in g) from the regression of weight versus male or female body size index for all skuas sexed by observation or discriminant analysis.

Stage	Weight corrected for size:	
	Male	Female
(i) 1st half incubation (days 1-13)	-6.2±7.4 (17)	15.2±4.9 (28)
(ii) 2nd half incubation (day 14 - hatching)	4.8±3.3 (28)	1.7±4.1 (29)
(iii) 1st half chick-rearing (hatching - day 14)	3.5±5.8 (8)	-11.7±7.8 (11)
(iv) 2nd half chick-rearing (> day 15)	-2.8±5.6 (21)	-11.6±5.7 (30)
ANOVA results	$F_{3,70}$=0.95, n.s.	$F_{3,94}$=5.65, P<0.002[a]

[a] - Ranges tests (Newman-Keuls) indicated a significant difference between stage (i), and stages (iii) and (iv).

Table 4.6. Partitioning of incubation and chick-rearing duties by male and female Arctic skuas (sexed by observation or discriminant analysis) on Foula in 1994.

	Number of occasions:		
	Male or female on the nest during incubation (both adults on territory)	Single adult on territory during incubation	Single adult on territory during chick-rearing
Female	235	154	55
Male	222	49	36
Comparison with 1:1 ratio	χ^2=0.32, n.s.	χ^2=53.3, P<0.0001	χ^2=3.56, n.s.
Number of pairs involved	88	69	46

Fig. 4.1. Graphical illustration of the discriminant function used to sex male and female Arctic skuas on Foula - all individuals to the right of the line sexed as females and all to the left sexed as males.

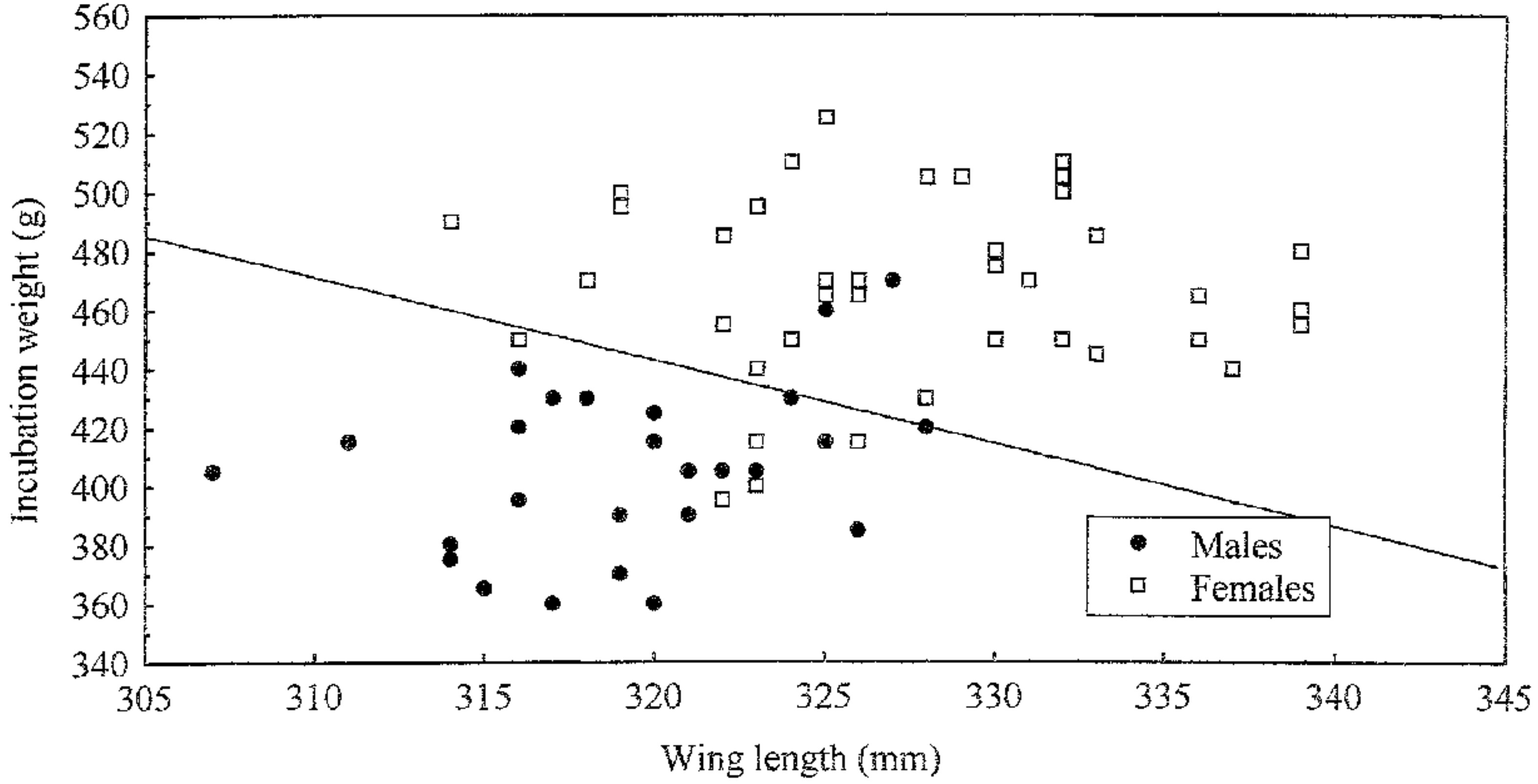


Fig. 4.2. Comparison between the body size of male and female members of Arctic skua pairs on Foula, using a common factor score for body size obtained from principal components analysis.

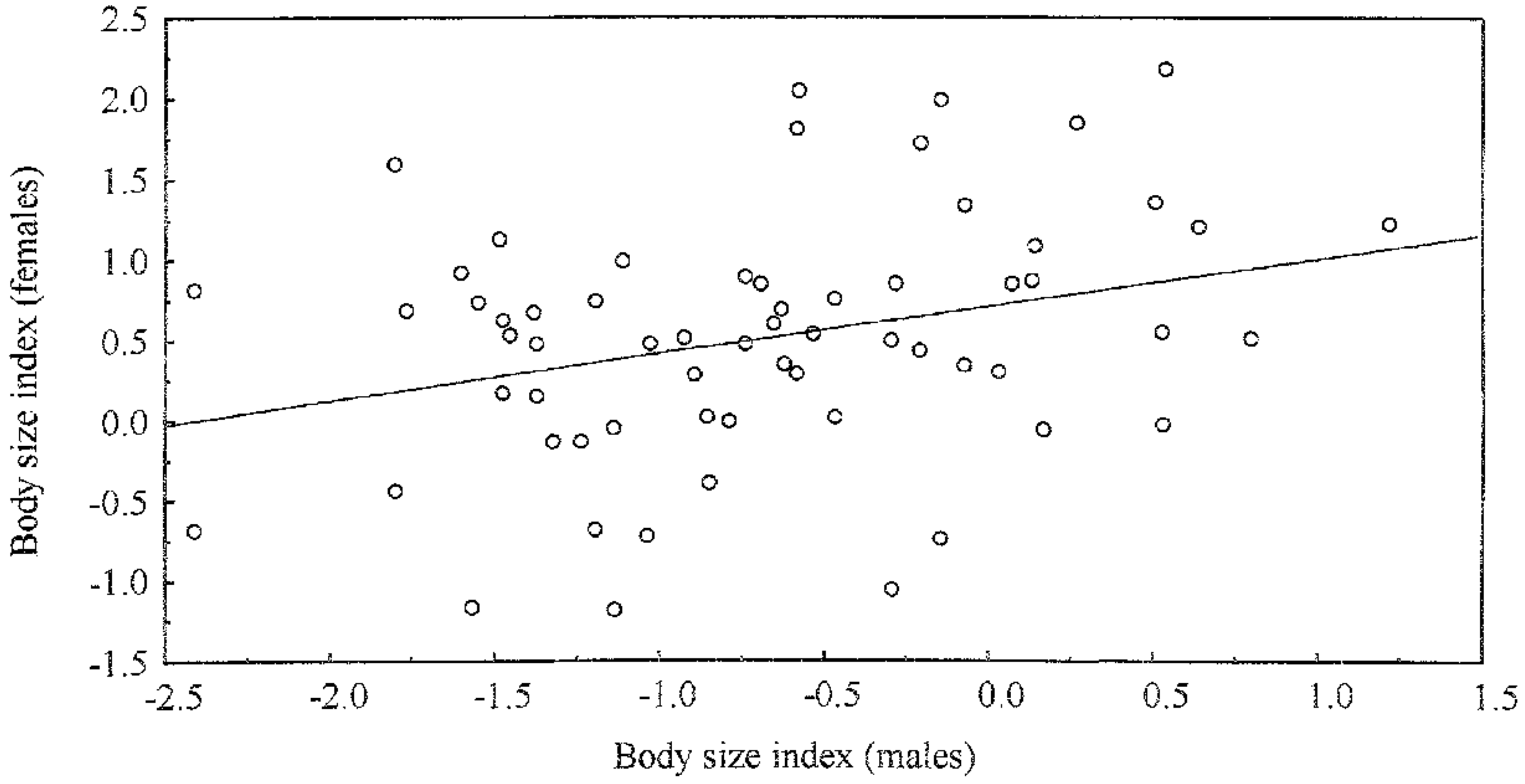


Fig. 4.3. The relationship between size and weight of female Arctic skuas trapped at all stages of the season on Foula.

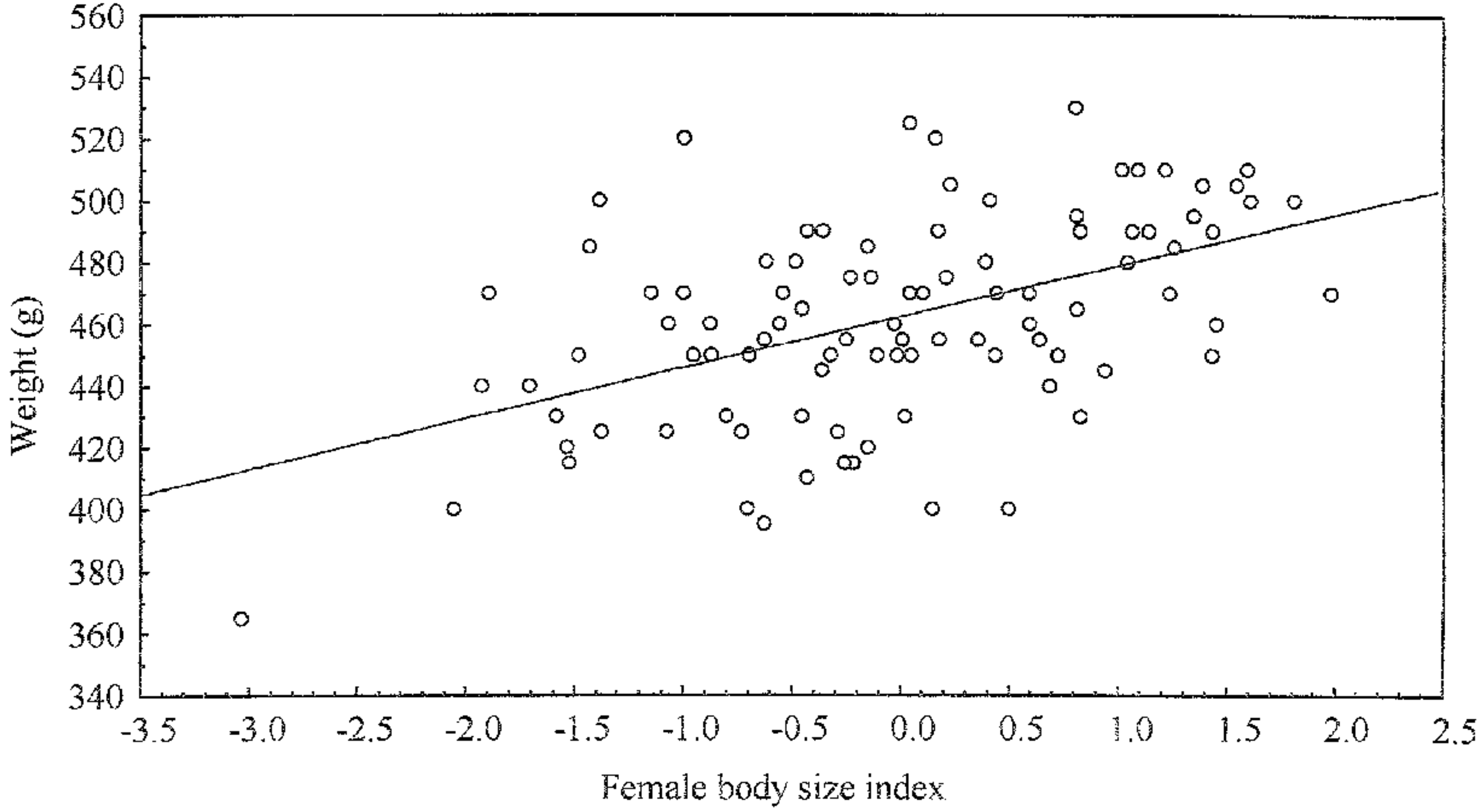


Fig. 4.4. Seasonal decline in body condition of female Arctic skuas on Foula.

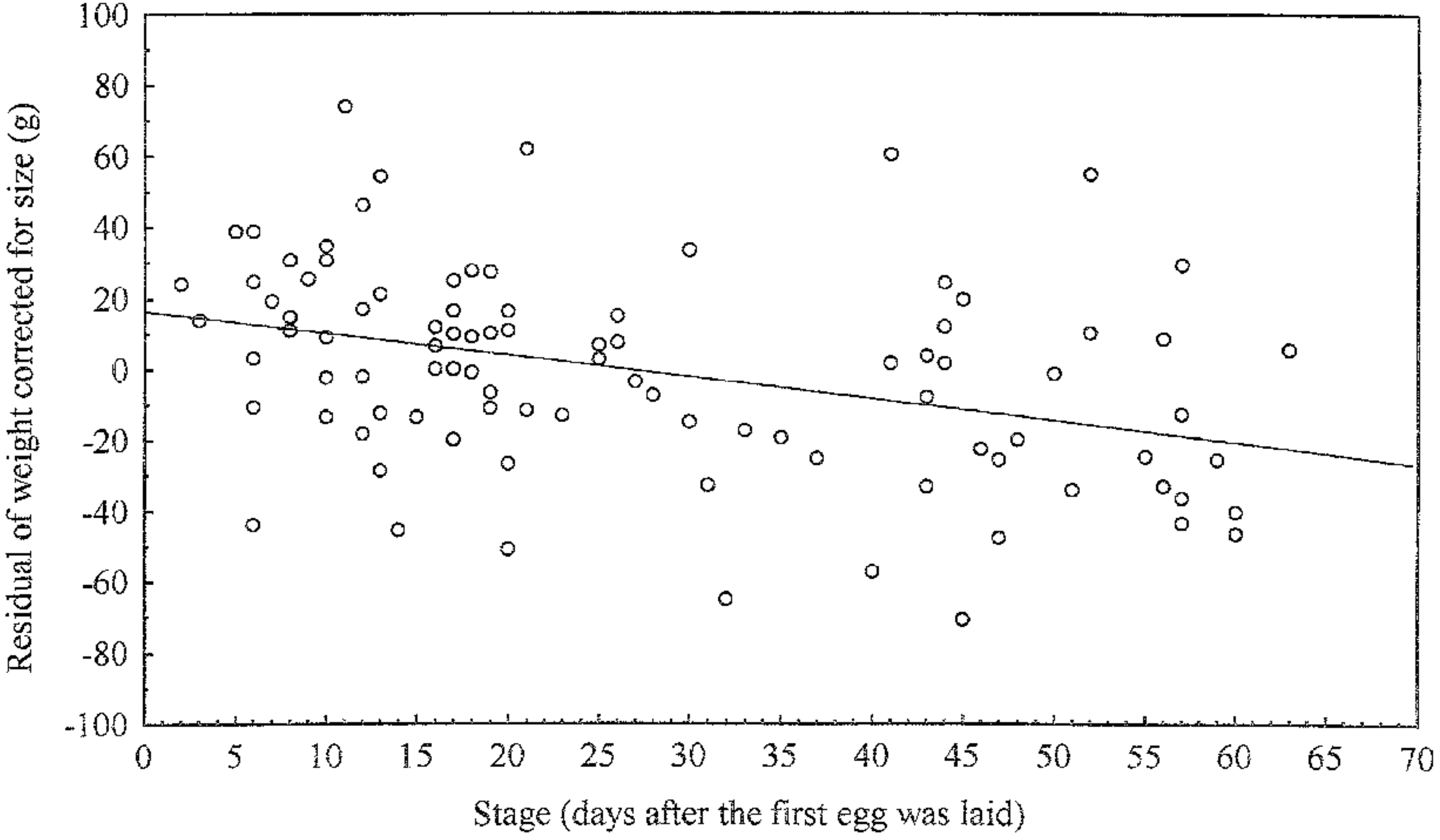


Fig 4.5. The relationship between size and weight of male Arctic skuas trapped at all stages of the season on Foula.

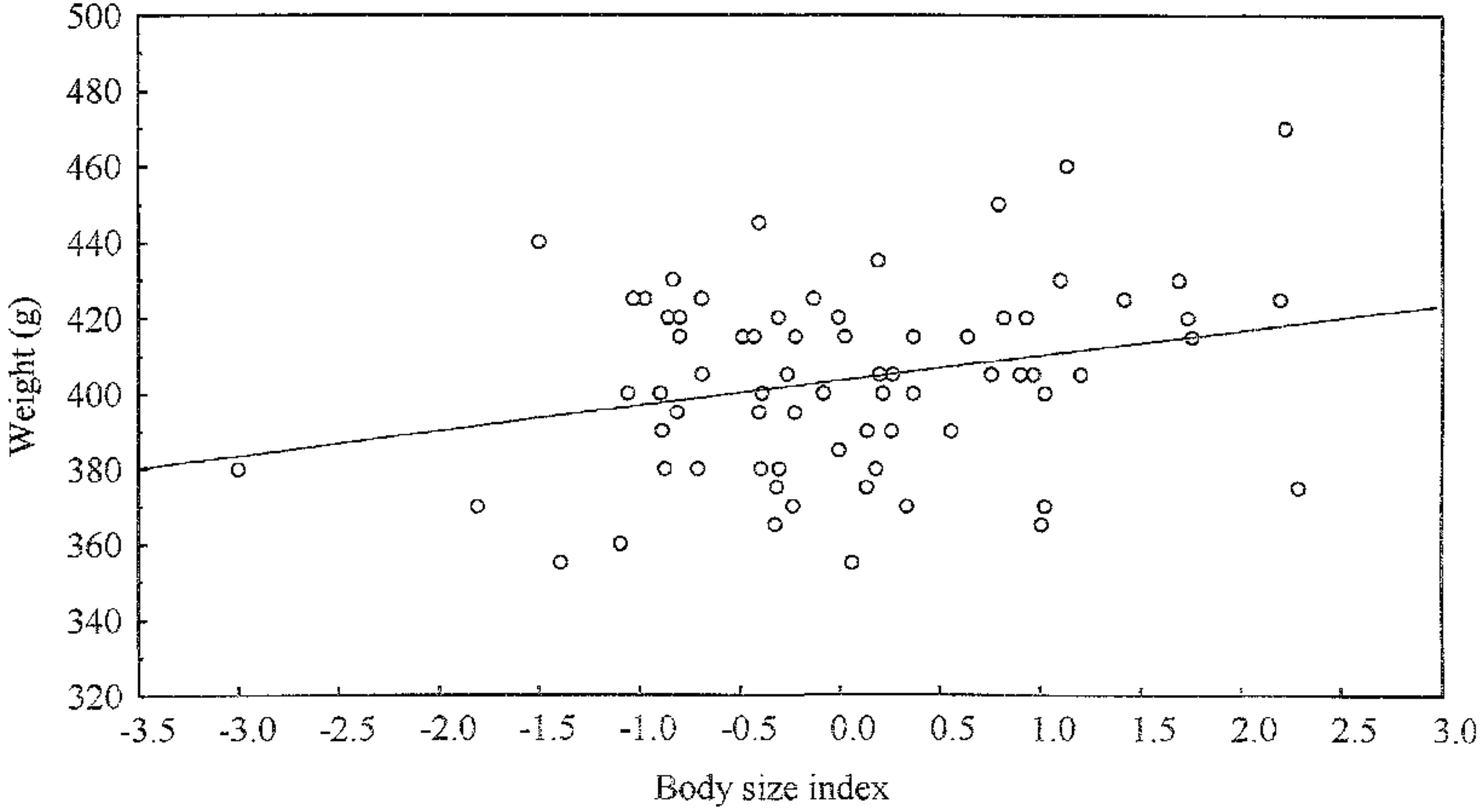
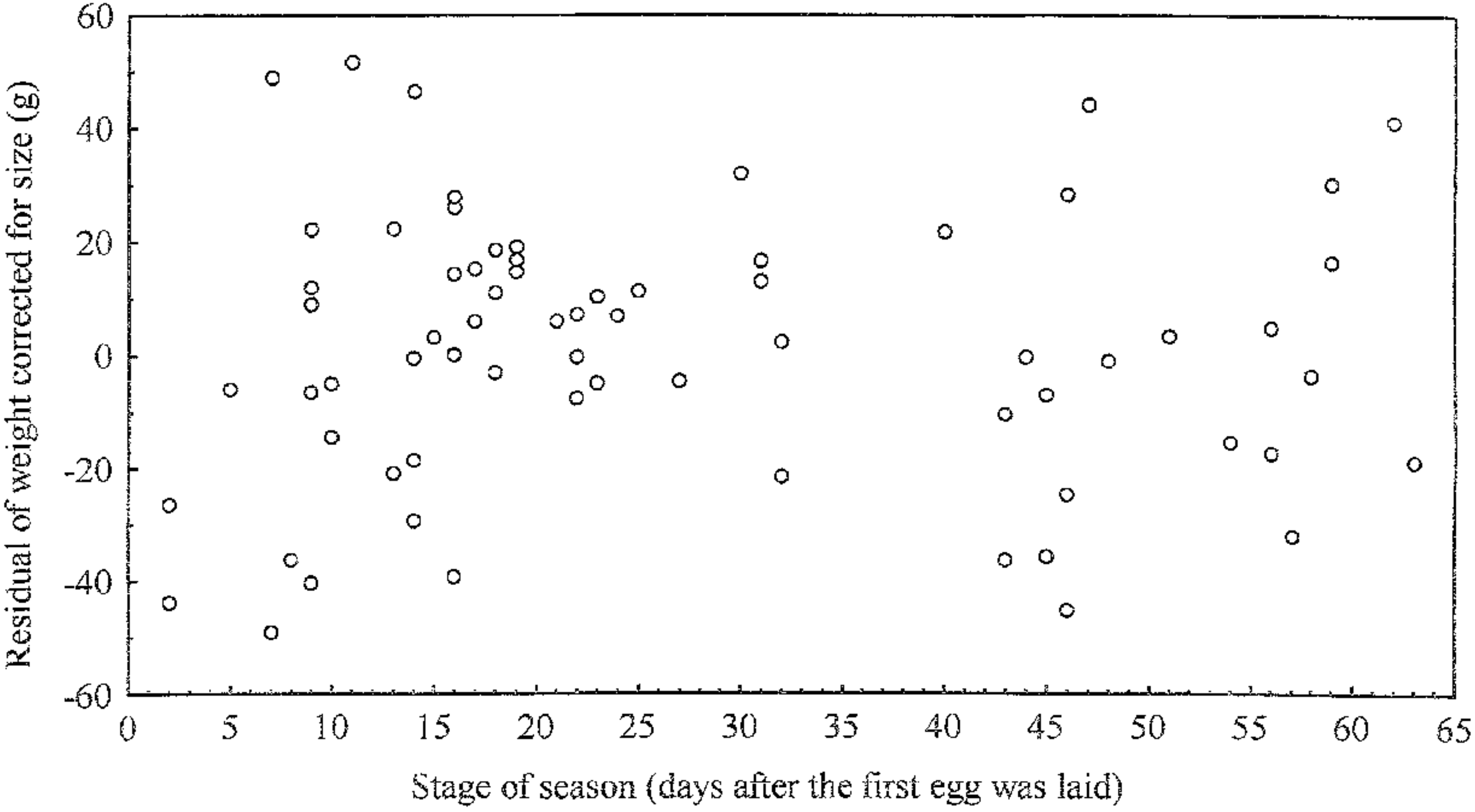


Fig. 4.6. Body condition of male Arctic skuas in relation to the stage of the breeding season on Foula.



4.4 Discussion

4.4.1 *Sexing by discriminant analysis*

Several factors can limit the effectiveness of discriminant analysis as a technique for predicting the sex of unknown cases. Characters such as wing length and bill dimensions can change with age in birds including Charadriiformes (Pienkowski and Minton 1973, Coulson *et al.* 1981, Hamer and Furness 1991, Furness *et al.* 1994), although this was not the case with Arctic skuas over the age-range at this colony (Table 4.1). The consistency, both within and between observers, with which measurements are taken is also likely to limit the reliability of a discriminant function (Barrett *et al.* 1989, Hamer and Furness 1991). This is particularly important when a function has been derived from measurements of an independent sample of birds and is then applied to a novel data set produced by an alternative observer (Hamer and Furness 1991). In this analysis however, all birds were processed by the same observer, RAP, and from the sample of individuals measured more than once it was clear that measurements were highly repeatable, in several cases across more than a single breeding season. This itself further implies that any change in body measurements with age is negligible.

Relatively few studies attempt to use body mass in discriminant analyses, with some exceptions (e.g. Spear 1988, Hatch *et al.* 1993). Yet, in this study adult weight during incubation proved extremely effective as a predictor variable. Although mass may show both annual and seasonal variation, so too do wing length and bill dimensions (Boag and van Noorwijk 1987, Leverton 1989) which are commonly used in discriminant analyses. Some seabirds may show relatively little annual variation in body condition measured at the same stage of the season even if food availability is poor (Hamer *et al.* 1991, but see Monaghan *et al.* 1989, Hamer *et al.* 1993). In addition, longitudinal analysis has indicated that particular individuals may vary little in weight in successive years (Jones 1994, this study). Therefore, if weight is recorded at approximately the same point in the reproductive cycle in different years, and there is no temporal trend during that stage, there seems little reason not to include it alongside other morphometrics in discriminant analysis. It would not, of course, be appropriate to employ a discriminant function using mass to sex adults measured in a different year if there was any evidence of inequalities in body condition.

Numerous studies attempt to resolve inter- and intra-sexual patterns in, for example, breeding success or aggression using data from adults sexed by discriminant analysis (e.g. Brooke 1978, Ollason and Dunnet 1978, 1988, Monaghan and Metcalfe 1986, Hamer and Furness 1991). However, relatively few consider the exclusion of cases for which the results of the analysis may be more ambiguous (but see Spear 1988, Pugesek and Diem 1990, Hatch *et al.* 1993). Unknown sex Arctic skuas were assumed to be either male or female if their probability of group membership using Function 1 or 2 was > 0.85 (see Results). By these criteria, over 91% of all known-sex adults would have been assigned to the correct sex. Based on a hierarchical system of sex differentiation (see Results), over 86% of all measured adults were designated male or female with approximately that degree of accuracy. The exclusion of the remaining unsexed birds was considered reasonable in order to maintain accuracy, especially as sample sizes in most further analyses were still high.

Several authors have suggested that relative size or colour (both observed visually) within breeding pairs of skuas might be of value in determining sex, or of identifying individuals most at risk of being misclassified (Ainley *et al.* 1985, Hamer and Furness 1991). In the study on south polar skuas *Catharacta maccormicki*, no clear size difference was discernible in 12% of pairs (Ainley *et al.* 1985). Hamer and Furness (1991) working on great skuas *Catharacta skua*, were unable to decide which individual was larger in 16 pairs (of a sample of 52), and their conclusions disagreed with those from discriminant analysis for five pairs. Only 31 pairs (60% of the total) observed in the field could therefore be sexed accurately by relative size. The application of this technique therefore appears to be rather limited. No attempt was made to sex Arctic skuas by visual observation of size differences. However, based on measurements it was apparent that within a pair females were virtually always heavier during incubation, and usually larger, as expected from data on all sexed birds within the population. There was also a correlation in body size between members of the pair, suggesting that some assortative mating may have been occuring. However, Boag and van Noordwijk (1987) could find no conclusive examples of assortative mating with respect to a metric trait in birds (but see Meathrel *et al.* 1993). The existence of assortative mating in skuas would further diminish any scope for the use of relative size within the pair as a potential clue to estimate sex.

4.4.2 *Seasonal changes in body mass*

Male and female Arctic skuas appeared to have quite distinct strategies of mass variation during the course of the breeding season. Male body weight remained comparatively uniform throughout incubation and chick-rearing, while female condition, although also relatively constant during incubation (the apparent decline between the first and second halves of incubation was not significant - Table 4.5), showed a sudden stepwise drop at the time when the chicks hatched. Neither sex lost mass during the remainder of chick-rearing.

Although no data were collected on the number or duration of foraging trips by female Arctic skuas on Foula in 1992-1994, figures are available for earlier years. In 1987 females from three pairs each spent 298, 413 and 441 mins. respectively away from their territories in 24 hrs. during chick-rearing (Caldow 1988). Data collected during hide-watches, 1976-1979, indicated that females with medium or large chicks spent 150, 193, 255 or 299 mins. in 24 hrs. off-territory foraging (Furness 1987). Using equation 6 in Norberg (1981), and assuming a cost of flight for Arctic skuas typical of seabirds (approximately 5.25 x BMR - Birt-Friesen *et al.* 1989), the reduction in female weight of around 20g or 4.3% of their incubation weight would have resulted in a saving of between 2.8-8.3% of BMR in 24 hours. This assumes total foraging trip durations in 1992-1994 fell within the range of values recorded in earlier years. This represents a not inconsiderable proportion of daily energy expenditure, in accordance with estimated levels of energy savings found in similar studies (Norberg 1981, Croll *et al.* 1991, Jones 1994).

There is a problem inherent in using mass as an indicator of changes in body reserves during the breeding cycle, as it does not take into account the gradual regression of reproductive tissues after egg-laying. Some studies involving carcass analysis however, have shown that reproductive tissues are almost fully atrophied by the end of incubation in species that do maintain a constant weight during this stage (Ricklefs and Hussell 1984, Jones 1987). The loss of tissue must therefore have been compensated by the simultaneous laying down of other body reserves. As female Arctic skuas do not lose mass until the onset of chick-rearing, and males do not lose mass at all, it is extremely unlikely that regression of reproductive organs is more than a minor component contributing to weight variation.

The data for male or female Arctic skuas provided no evidence that temporal differences in body condition were a detrimental consequence of stress associated with reproductive workloads (Ricklefs 1983). Males showed no seasonal reduction in weight, nor did females lose mass during incubation or, after the initial decline, during chick-rearing. If mass loss were stress-induced a more distinct decline would be anticipated within the chick-provisioning stage as adults begin to cope with the increasing energetic demands of growing chicks, and as their foraging effort rises.

There is an increasing body of evidence suggesting that seabirds are able to finely regulate changes in their body condition. Incubating blue petrels *Halobaena caerulea*, desert once their body weight has decreased to a threshold value, the same level as that maintained during chick-rearing (Chaurand and Weimerskirch 1994a,b). This suggests that during chick-rearing adults are working at a minimum weight in order to minimise flight costs. In addition, although there were significant differences between years in adult ancient murrelet

Synthliboramphus antiquus, weights at clutch completion, the birds lost a variable amount during incubation so that in all years they entered the chick-rearing phase at the same weight (Gaston and Jones 1989). Again, this was presumably an optimum value, despite that during this latter stage in the breeding cycle, adults in fact do very little flying as the young are reared at sea, away from the colony. Finally, although older glaucous-winged gulls *Larus glaucescens*, maintain lower body condition during incubation in comparison with younger birds, provisioning of supplementary food did not result in greater increases in mass in experimental than control birds, suggesting that old adults were not food-stressed but instead were regulating mass at a lower set-point (Reid 1988).

Assuming variation in mass is adaptive, there are a number of possible explanations for the dissimilarity in the pattern of weight variation of male and female Arctic skuas. Skuas show reversed sex size dimorphism and partitioning of reproductive duties, neither of which was found in the studies researching programmed anorexia in auks (Gaston and Jones 1989, Croll *et al.* 1991, Jones 1994). Presumably the retention of extra body reserves by female Arctic skuas during incubation, and the subsequent shedding of these energy stores at the point of hatching, is related to a differing reproductive role from the male.

Females must maximise energy or protein reserves prior to egg-laying in order to produce the optimal number of good quality eggs (Drent and Daan 1980, Houston *et al.* 1983). Adult skuas usually arrive at the colony in good condition following migration (De Korte 1985, Furness 1987) and Arctic skuas often lay soon after (Furness 1987). Females of many seabird species that do not attain a threshold weight usually do not attempt to breed (Shaw 1986, Weimerskirch 1992). Most female Arctic skuas that breed are therefore likely to be in relatively good condition at the onset of incubation. Maintenance of these body reserves throughout the rest of incubation could act as an insurance, buffering natural fluctuations in food availability (Gaston and Jones 1989, Jones 1994). Larger birds are predicted to have lower mass-specific metabolic rates which may allow them to fast for longer periods (Lima 1986, Moreno 1989, Hatch 1990). Female Arctic skuas might therefore retain their reserves until the chicks hatch, when their reproductive workload suddenly increases. At that point flight demands rise, the excess mass is jettisoned, and the female reaches optimum condition in terms of flight performance. This level of condition is maintained steadily during the remainder of the chick-rearing period (Table 4.5). The carriage of supplementary fat reserves has become less necessary, and in addition retaining these reserves would have entailed an added maintenance cost in addition to that related to flight efficiency (Lima 1986).

Male Arctic skuas spend much longer foraging off-territory in order to provision the female during incubation. Because the female appears to be much more constrained in terms of incubation duties, males might also have more scope to increase foraging effort to combat temporary reductions in food availability (for example due to poor weather conditions), while the female is obliged to remain on territory incubating the eggs. Small birds perform better than larger birds of similar shape in terms of flight performance (Andersson and Norberg 1981). The relative cost of flight is also lower for smaller and, after correcting for size, for relatively lighter individuals. This has been proposed to be a valuable consequence of reversed size dimorphism in raptors, although not necessarily an ultimate explanation (Andersson and Norberg 1981). As male Arctic skuas are both smaller and lighter it is energetically more efficient for them to forage more than their partners during incubation. Of course, this alone could not be an explanation for the origin of reversed size dimorphism, as selection could as easily have acted on males for them to become larger and adopt the female's present breeding role.

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Chapter Five. The effects of territory quality on Arctic skua reproduction on Foula and its implications for the long-term changes in territory distribution

5.1 Introduction

Variation in breeding site quality is an important determinant of reproductive success for many colonially-nesting seabirds (e.g. Davis and Dunn, 1976, Potts *et al.* 1980, Pugesek and Diem 1983, Coulson and Thomas 1985). As a result, potential new breeders may be unable or unwilling to recruit into a population if appropriate nest-sites or territories are limited (Porter and Coulson 1987, Klomp and Furness 1992). The availability of suitable breeding space might therefore regulate bird population sizes in a density-dependent or even density-independent fashion irrespective of the overall food abundance (Cairns 1992, Newton 1992, 1994). Bird breeding densities may also be limited by food, predation or parasite pressure (Croxall and Rothery 1991, Hudson and Dobson 1991). The relative importance of these factors is both species- and colony-specific, and probably also exhibits a degree of temporal variation (Cairns 1992, Newton 1994).

Arctic skuas breeding in Scotland defend small territories (mean distance to the nearest neighbouring nest on Foula in 1992/1993 was 72 ± 90 (s.d.) metres, n = 278 nests) around their nest from which other skuas are forcibly excluded (Furness 1987). This colonial-nesting habit contrasts with pairs breeding in the high Arctic which are found at much lower densities (0.02-0.2 pairs per km^2) and defend large feeding territories in which they prey on eggs, small birds or rodents (Furness 1987). In Iceland these two discrete territory types and usages are recorded in spatially-isolated populations (Andersson and Götmark 1980). On Foula, Arctic skua numbers have declined considerably since the late 1970s associated with a drop in sandeel recruitment in the surrounding waters and a reduction in the numbers and breeding success of their kleptoparasitic hosts (Chapter 2). However, this decrease in population size has not been uniform across all breeding locations on Foula. As these birds obtain virtually none of their food within breeding territories, clearly some other attribute of territory location or quality must be important.

A localised reduction in breeding numbers could arise because of an elevation in the adult mortality rate, which would also result in individuals, particularly females, that are unable to aquire a new partner shifting territories (Chapter 6). Alternatively, a local decline in breeding performance might increase the likelihood of divorce, which is more frequent in some species after reproductive failure than success (Mills 1973, Brooke 1978, Bradley *et al.* 1990). It is also possible that potential recruits are able to distinguish and so avoid areas where there is a lot of disturbance or where reproductive performance is poor (Harris 1980, Coulson 1991). Variation in reproductive success of surface-nesting seabirds can be related to one or more of a variety of nest-site or territory attributes, particularly the density, size, location or degree of vegetative cover (Davis and Dunn 1976, Hunt and Hunt 1976, Pugesek and Diem 1983). Some of these factors can have apparently contradictory effects in different species depending on local conditions. The proximate influence of, for example, breeding density may be to confer an advantage to pairs with more neighbours at close proximity because of a collective anti-predator response (Harris 1980, Pugesek and Diem 1983), sometimes enhanced by a degree of breeding synchrony in adjacent pairs (Birkhead 1977, Hatchwell 1991). Conversely, it may be disadvantageous to nest in high density areas if the likelihood of cannibalism or con-specific interference is greater (Hunt and Hunt 1976, Butler and Trivelpiece 1981, Furness 1984). Breeding density appears to be of little consequence in certain situations if predation pressure is mild or absent (Harris and Wanless 1988), so clearly its importance varies.

The spatial location of a nest or territory, which often covaries with density, also influences reproductive performance. Kittiwakes that recruited in the dense 'centre' (defined as the area occupied when the colony was half its maximum size) as compared with the 'edge' of the colony experienced not only higher breeding success but also higher survival (Wooller and Coulson 1977, Coulson and Thomas 1985, Aebischer and Coulson 1990). This was attributed not to any variation in the degree of predation on adults nesting in different areas, but to a segregation at recruitment of better as compared with poorer quality individuals. In several studies the effects of location on egg, chick or adult survival were more direct, particularly if predators had easier access to peripheral nests (Patterson 1965, Spear 1993).

This chapter examines the relationship between territory density and location, and aspects of Arctic skua reproductive performance on Foula during 1992-1994, and also includes data on chick growth and hatching dates in different areas from 1976-1979. It investigates long-term changes in breeding numbers in an attempt to provide an explanation for the asymmetric declines in different areas on Foula since the late 1970s.

5.2 Methods

5.2.1 *Historical data*

The locations of Arctic skua apparently occupied territories (AOTs) on Foula were mapped by R.W. Furness in 1976-1980, 1986, 1987 and 1989, by Sheila Gear in 1985 (in Ewins *et al.* 1986) and 1989-1991, by various observers in 1986 (Ewins *et al.* 1986), and by RAP in 1992-1994. There are therefore two independent sets of data to compare in several years. All AOTs were counted in each of nine geographically discrete areas (see Fig. 5.1), the boundaries of which approximate to those of Ewins *et al.* (1986). The precise timings of most of the annual censuses are unknown, but they all took place after the end of May, by which time virtually all breeders have arrived, and before mid-July, before which very few (and none with chicks) will have departed.

Considerable variation in the rate of decline in different locales was especially evident in the early 1980s. (Results, Table 5.1). The losses in specific areas could be a consequence of locally elevated adult mortality rates in addition to poor recruitment of new breeders. In order to resolve whether the former might have occured, the number of occupied territories in each area in 1986 (for which two sets of corroborating census data were available) was estimated assuming an adult mortality rate of 13.6% per year since 1980 and no recruitment. This mortality rate, the mean annual return rate for marked Arctic skuas on Foula between 1992-1994, is close to that estimated on Fair Isle between 1973-1975 for the relatively unpersecuted population, and is therefore likely to be a minimum value. A positive value for the difference between the observed number of pairs in a given area in 1986 minus the estimated number therefore indicates that at least some recruitment had taken place in the previous six years. Fewer pairs than predicted suggests that the mortality rate in that area was higher than the 13.6% recorded for 1992-1994.

If there is a tendency for adults to recruit in the general vicinity of the territory from which they fledged (e.g. Klomp and Furness 1991, Spear and Nur 1994), low breeding success in some areas in the late 1970s may have had a direct effect on the availability of sufficient individuals for recruitment to those locations in the early 1980s. Early hatching date and a higher growth rate significantly improves the likelihood of a chick surviving to recruitment (Chapter 7). Between 1976-1979 the location, wing length and weight of each chick was recorded during routine chick ringing. This made it possible to investigate whether chicks did hatch later or grow more poorly in certain areas prior to any observed decline in the early 1980s.

Hatching date was estimated, and a chick growth index calculated for all chicks (see Chapter 1, General Methods). In 1976, 1977 and 1978, all chick ages were predicted from a single measurement of their wing length (n.b. differences between years in wing length growth on Foula are extremely slight - Chapter 2) and an estimated hatching date obtained by subtracting the predicted age from the date of measurement. The deviation for each chick from its expected weight at this age was then calculated using the 1992 curve of weight versus age, and individual chick growth indices expressed as a proportion of the expected value.

In 1979, multiple measurements were available for some chicks, in which case the mean value for the estimated hatching date and chick growth index was used.

Two-way ANOVAs were performed to investigate whether there were any significant differences among areas in hatching date or chick growth in 1976-1979, with a further comparison performed with the samples pooled as to whether chicks did or did not come from an area that subsequently declined. From Table 5.1 (see Results), it was apparent that areas 2,3,4 and 6 had declined to one half or less of the late 1970s population level by the mid 1980s, in comparison with areas 1,5,7 and 8 (see Fig. 5.1).

5.2.2 *1992-1994 data*

Data on hatching and fledging success on Foula are not available for the early 1980s. However it was possible to examine what correlates of territory quality were important for breeding performance now, and make predictions as to whether the same factors may have applied during the initial phase of decline. Information on laying dates, egg and clutch volumes, chick growth, and number of eggs laid, chicks hatched and chicks fledged were collected according to Chapter 1, General Methods. Several potential correlates of territory quality, indices of density, territory size and location, were recorded for each pair that laid. It should be noted that in some of the following analyses a considerable number of tests were carried out, thereby increasing the likelihood of spurious correlations. Consequently some results, although statistically significant, should be treated with caution.

All territories were marked on a 1:10,000 Ordnance Survey map. In 1992 and 1993 but not 1994, the distance from each Arctic skua nest to the nearest one and nearest three neighbouring nests (abbreviated to D1N and D3N) was measured either using a string marked at two metre intervals or, if the distance was more than 100 metres, calculated from the map using the point-separation option on a BBC micro digitiser. Because individual territories were rarely bordered by three adjacent territories with contiguous boundaries in the low density areas, some pairs may have been defending on one side from a relatively close neighbour but have unlimited space in the other directions. As a consequence, the distance to the nearest three neighbouring nests (D3N) should be considered as an index of density only, as it may bear little resemblance to the size of the defended area. In all three years, another index of density was calculated from the map as the number of nests within 150 metre radius, abbreviated to NN150.

The distance adults have to fly to transport prey items to their chick(s) can have a significant effect on chick growth and survival (Ens *et al.* 1992). Arctic skuas on Foula appeared to obtain most of their food by chasing sandeel-carrying hosts within a short distance of cliffs either on the east coast or at the north end of the island. Birds nesting in the centre of the island were often seen commuting in the direction of one of these two foraging sites, and chases at sea were rarely observed from elsewhere along the east coast. The straight-line distance (abbreviated to DF) from individual Arctic skua nests to 100 metres out to sea from the centre of what would be the nearest foraging site (see Fig. 5.1) was measured for each pair from the census map using the BBC digitiser. Use of the southerly point may slightly overestimate the closest foraging distance of airstrip pairs which did occasionally chase sandeel-carrying Arctic terns flying over their territories.

Territory density or location effects may only influence reproductive performance in particular circumstances. The following analyses were therefore carried out separately for each year. It should be noted that D1N, D3N and post-fledging survival to a week were not recorded in 1994. Spearman rank correlations were performed between attendance at each stage of the season and D1N, D3N, NN150 and DF. Correlation analysis was also used to investigate the relationships between density (D1N, D3N and NN150) and laying date, egg volume (either the single egg or the larger in two-egg clutches) and clutch volume (two-egg clutches only) of first clutches. The degree of breeding synchrony between adjacent pairs might influence several aspects of reproduction (Hatchwell 1991). Whether such variation existed was investigated by comparing the homogeneity of variance about the mean laying date in different areas using Bartlett's test.

Correlations were performed betwen D1N, D3N, NN150 and two separate chick growth indices, that of single / first hatched chicks, and the mean value for two-chick broods. Chick growth was also compared at territories with different fledging success and post-fledging survival to a week to determine at which stage prior to independence selection might be acting on chicks of poor quality. All chicks, including the poorly-growing chicks excluded from other analyses (see Chapter 1, General Methods) were included if their fate was known. It was not usually possible to distinguish which chick was alive one week post-fledging at territories where two fledged and one died or disappeared. Consequently, mean chick growth was compared in relation to post-fledging survival only if both chicks fledged.

The variables NN150, D1N, D3N and laying date were compared between territories with different numbers of chicks hatched, chicks fledged (assuming at least one hatched) and fledglings alive one week post-fledging (assuming at least one fledged), including data on replacement clutches. Where more than one variable was significantly different between categories, stepwise binomial logistic regression was used to isolate the factor or factors that best predicted the probability of one or two, compared with neither chick hatching, fledging or surviving to one week post-fledging as appropriate. The possibility that density might influence hatching success through an effect on the probability of addling was also tested. The variables D1N, D3N and NN150 were compared between territories depending on whether one or more eggs in any clutch (including replacement clutches) became addled (i.e failed to hatch due to infertility or embryo death). Laying dates were also compared, but with data from replacement clutches excluded from the analysis. Addled eggs were invariably incubated at least until the predicted hatching date and often beyond. Consequently, no pair with an addled egg in the initial clutch produced a replacement clutch.

Differences in breeding performance depending on density or location might be the consequence of variation in age or adult quality (Chapters 6 and 7). Correlations were performed between body size and body condition of colour-ringed adults and the density variables D1N, D3N and NN150. Size and condition of sexed birds were calculated according to Methods, Chapter 4, and individuals were included in the analysis only in the year in which condition was estimated, excluding those trapped on replacement clutches. Pugesek and Diem (1983) suggested that any variation in reproductive success associated with nest-site or territory quality is attributable to the latter's covariation with age. The possibility that adults of different ages tended to nest in different areas on Foula was tested using the ringing retrap-data. There were 39 adults of known-age, and three adults assumed to be older than 23 years (having been ringed as breeding adults in 1975) on Foula in 1994 (see Chapter 6), one of which did not hold territory. Birds were categorised as young (aged 5-8 years), middle-aged (aged 9-18 years) or old (aged >19 years), and the relative number of individuals in each category compared between the high-density airstrip area and the rest of the colony. The proportion of marked breeders in 1993 that returned in 1994 was also compared between the airstrip and elsewhere in the colony.

5.3 Results

5.3.1 *Long-term changes in territory distribution*

Changes in distribution of Arctic skua breeding territories on Foula between 1976 and 1994 are shown in Table 5.1. Although differences do exist in the number of territories counted in some areas by independent observers in the same year, these were relatively minor. The long-term trend has been for a dramatic reduction in the number of AOTs in most of the northern half of the island i.e. Harrier / Skiordar and Lioag / Sloag (areas 3 and 4), and a virtual elimination of the small breeding group at Ruscar (area 2). The single territory recorded in area 2 from 1989 to 1994 was situated at Strem Ness, some distance north of where the six or so pairs used to nest at Ruscar in the late 1970s / early 1980s. One area in the south, Hametoun Wilse (area 6), has also shown a considerable decline. By contrast, the number of AOTs in most of the remaining southern areas, in particular around the airstrip, have shown much less severe reductions, although area 9 - just south and south-west of the airstrip (Fig. 5.1) - no longer held any territories in 1992-1994.

The predicted number of territories in each area in 1986 is also indicated in Table 5.1. In at least one of the 1986 counts, areas 2,3,4 and 9 contained fewer or in one case the same number of pairs as would be expected assuming an adult mortality rate of 13.6% and no recruitment having taken place since 1980. Both area 2 and area 9 had held a relatively small number of breeding pairs in any case in the late 1970s and were effectively abandoned by 1986.

5.3.2 *Variation in chick growth and hatching date among areas, 1976-1979*

There was no significant difference among areas in mean chick growth index (Two-way ANOVA $F_{3,530} = 1.0$, n.s.: Table 5.2). There was a year effect (Two-way ANOVA $F_{7,530} = 8.8$, $P<0.001$) and also a significant interaction between year and area (Two-way ANOVA $F_{16,530} = 1.8$, $P<0.05$.) indicating that any trends in the area comparisons were not consistent between years. Comparing the chick growth index in areas which subsequently showed a decline in AOTs (i.e. areas 2,3,4 and 6) with the remainder, again shows an effect of year (Two-way ANOVA $F_{3,556} = 9.5$, $P<0.001$: Table 5.3), but not of area (Two-way ANOVA $F_{1,556} = 0.1$, n.s.) and no interaction (Two-way ANOVA $F_{3,556} = 2.3$, n.s.).

There was both a significant effect of year (Two-way ANOVA $F_{3,530} = 16.3$, $P<0.001$) and of area (Two-way ANOVA $F_{7,530} = 5.6$, $P<0.001$) on the mean estimated hatching dates of chicks (Table 5.2). The interaction between year and area was not significant (Two-way ANOVA $F_{16,530} = 1.5$, n.s.). However, oneway ANOVA ranges tests (Scheffe) performed separately for each year indicated that none of the individual differences between areas were by themselves significant at the 5% level. From Table 5.2 it would appear that apart from chicks in the Ristie and Mucklegrind area tending to have hatched slightly earlier, there was no clear or consistent trend. Comparison between the areas of later decline and the remainder indicated no area effect (Two-way ANOVA $F_{1,556} = 0.5$, n.s.; Table 5.3), but a year effect (Two-way ANOVA $F_{3,556} = 14.5$, $P<0.001$) and a significant interaction (Two-way ANOVA $F_{3,556} = 5.0$, $P<0.005$). No consistent differences in hatching dates were therefore maintained on an annual basis between these two area groupings.

5.3.3 *Territorial, location and seasonal effects on breeding performance, 1992-1994*

At no stage in the season were there any significant rank correlations between attendance and the distance to the nearest foraging site (Table 5.4). In 1993 during the middle part of the chick-rearing period, and in 1994 during incubation, there was a significant positive correlation between attendance and density. However, given the large number of tests carried out these results should be treated with caution.

None of the correlations between the laying date of the first egg of first clutches and the various density variables was significant (Table 5.5). Oneway ANOVAs also indicated no significant differences among areas in laying date or the degree of laying synchrony in any year (1992 data using $\log_{10}$ laying date $F_{6,143}=0.6$, n.s. Bartlett-Box $F=1.1$, n.s., 1993 data using 1/laying date $F_{6,129}=1.3$, n.s. Bartlett-Box $F=2.0$, n.s., and 1994 data using 1/laying date $F_{6,122}=1.0$, n.s. Bartlett-Box $F=1.1$, n.s.). There were no significant correlations between density or location (variables as above) and either the volume of the single / larger egg or clutch volume in any year (Table 5.5). However, there were significant correlations between laying date and both egg and clutch volume in all years (only 1994 data illustrated - Fig. 5.2).

One density variable, NN150, was negatively, and D1N and D3N positively correlated with the chick growth index of single / first hatched chicks in 1992 and 1994 (Table 5.5). Chicks in the higher density areas with more near neighbours therefore grew more poorly in both these years. There was also a significant negative correlation between the chick growth index and laying date in both 1992 and 1993, indicating a seasonal decline (only 1993 data illustrated - Fig. 5.3). Stepwise multiple regression analysis for 1992 indicated that once NN150, had entered into the model, no further variation was explained by laying date or the other density variables (Fig. 5.4). The mean growth index in two-chick broods showed similar relationships with density and laying date; significant correlations between growth and NN150 in 1992 and 1994, and a correlation between chick growth and laying date in 1993, although not in 1992 as was the case for single / first hatched chicks in that year.

Pooling the data for all chicks indicates that those that fledged grew significantly better in 1993 but not 1992 or 1994 (Table 5.6). Comparison of survival of fledglings at territories where both chicks survived to fledging indicated no relationship beween the number subsequently seen alive one week later and their mean growth rate in the pre-fledging period (Table 5.6).

There was a significant difference in laying date in 1992 and 1994, and in NN150 in 1994, among territories with different numbers of chicks hatched (Table 5.7). Stepwise logistic regression analysis for 1994 indicated most variation in the likelihood of hatching at least one chick was explained by NN150 (improvement χ^2=12.7, $P<0.0005$), with significant residual variation explained by laying date (improvement χ^2=4.4, $P<0.05$). There were no effects of density on the likelihood of one or more eggs in a clutch being addled in any year (Table 5.8). In 1992 addling was significantly more likely in initial clutches laid later in the season.

The number of chicks fledged at territories where at least one hatched was influenced by laying date in both 1992 and 1993 (Table 5.9). There were no significant effects of any density variable in any year. By contrast, the number of fledglings alive one week post-fledging showed no laying date effects in 1992 or 1993 but a significant effect of the density variables NN150 and D3N in 1992 (Table 5.10). In logistic regression analysis for 1992, NN150 entered the model first (improvement $\chi^2=6.0$, $P<0.02$), and no further variation was explained by D3N.

There were no significant correlations between density and male or female body size or body condition (Table 5.11). Nor was there a difference in the number of birds in each age category between the high density airstrip area and the rest of the island ($\chi^2_2=1.23$, n.s.; Table 5.12). There was no significant difference in the proportion of breeding adults holding territory in 1993 in the airstrip (50/53 = 94.3%) compared with the rest of the colony (75/86 = 87.2%) that returned to Foula in 1994 ($\chi^2_1=1.14$, n.s.), though the inferred mortality rate was only half as great among airstrip birds.

Table 5.1. Changes in the distribution of Arctic skua territories on Foula, 1976-1994.

Year:	1976	1977	1978	1979	1980	1985	1986	1987	1989	1990	1991	1992	1993	1994
Source:	a	a	a	a	a	c	a/b	a	a/c	c	a/c	d	d	d
1. Ristie / Mucklegrind	8	8	7	7	7	5	7/6 [3]	8	?^{e}/8	5	11/4	9	8	7
2. Ruscar / Strem Ness	6	6	6	7	4	3	1/0 [2]	1	?^{e}/1	1	1/1	1	1	1
3. Harrier / Skiordar	49	36	32	39	34	12	11/14 [14]	10	?^{e}/11	8	8/6	7	6	6
4. Lioag / Sloag	77	77	71	79	79	45	37/33 [33]	38	26/35	23	31/21	33	30	26
5. Ham to the Manse	10	11	17	15	17	16	12/11 [7]	13	14/15	12	9/10	11	10	9
6. Hametoun Wilse	22	24	21	22	21	11	16/11 [9]	15	6/9	5	7/5	9	6	6
7. Daal / Noup	17	19	16	25	20	12	22/16 [8]	19	7/10	7	14/8	14	13	12
8. Airstrip / Bankwell	79^{f}	74	82	73	73	71	77/73 [30]	64	48/66	61	59/55	75	71	67
9. Yogins / S. Hametoun	5	6	0	4	6	0	0/0 [2]	1	1/0	0	1/0	0	0	0
10. Others	3	2	1	1	1	0	2^{e}/0	0	20^{e}/0	0	0/0	0	0	0
Total	276	263	253	272	262	175	185/164	169	122/155	122	141/110	159	145	134

^{a} - RWF ^{b} - Ewins *et al.* 1986 ^{c} - Mrs. S. Gear ^{d} - RAP

^{e} - exact distribution unknown ^{f} - estimated number, not from map [ ] - predicted number in 1986 (see text)

Table 5.2. Chick growth and hatching dates in different areas on Foula, 1976-1979.

Year		Area:							
		Ristie / Mucklegrind	Ruscar	Harrier / Skiordar	Lioag / Sloag	Ham to the Manse	Hametoun Wilse	Daal / Noup	Airstrip / Bankwell
1976	Chick growth index:	0.96±0.03 (9)	1.02±0.03 (6)	1.01±0.02 (27)	1.04±0.01 (52)	1.01±0.04 (8)	1.00±0.04 (10)	-	1.00±0.03 (16)
	Mean hatching date:	59.4±2.2 (9)	50.1±1.4 (6)	51.4±0.7 (27)	53.6±0.8 (52)	58.8±5.0 (8)	51.3±1.4 (10)	-	54.5±1.2 (16)
1977	Chick growth index:	-	-	1.07±0.03 (20)	1.03±0.01 (45)	-	0.98±0.03 (5)	-	0.97±0.04 (5)
	Mean hatching date:	-	-	51.3±1.0 (20)	53.2±0.9 (45)	-	50.9±2.2 (5)	-	50.9±2.7 (5)
1978	Chick growth index:	1.01±0.05 (6)	1.03±0.04 (6)	1.01±0.01 (10)	0.97±0.01 (50)	1.08±0.03 (7)	0.99±0.03 (13)	0.95±0.02 (6)	1.01±0.01 (44)
	Mean hatching date:	58.4±1.0 (6)	52.3±1.0 (6)	52.4±1.1 (10)	54.0±0.7 (50)	53.8±2.5 (7)	52.9±1.7 (13)	51.3±1.7 (6)	51.6±0.7 (44)
1979	Chick growth index:	1.02±0.04 (7)	0.91±0.06 (6)	0.98±0.02 (30)	0.98±0.01 (68)	1.00±0.03 (18)	0.95±0.03 (11)	0.98±0.03 (20)	0.96±0.01 (52)
	Mean hatching date:	58.9±1.0 (9)	60.5±1.9 (7)	58.1±1.0 (31)	55.5±0.6 (68)	58.1±1.0 (18)	53.5±1.2 (12)	54.5±0.8 (20)	55.4±0.7 (62)

Table 5.3. Chick growth and hatching dates in the areas on Foula where numbers did or did not decline in the early 1980s.

Year		Area:	
		declined in early 1980s[a]	did not decline in early 1980s[b]
1976	Chick growth index:	0.98±0.02 (33)	1.03±0.01 (95)
	Mean hatching date:	56.9±1.5 (33)	52.5±0.5 (95)
1977	Chick growth index:	1.01±0.02 (12)	1.04±0.01 (70)
	Mean hatching date:	52.9±1.9 (12)	52.5±0.6 (70)
1978	Chick growth index:	1.01±0.01 (63)	0.98±0.01 (79)
	Mean hatching date:	52.4±0.6 (63)	53.5±0.5 (79)
1979	Chick growth index:	0.97±0.01 (97)	0.97±0.01 (115)
	Mean hatching date:	56.0±0.5 (109)	56.3±0.5 (118)

[a] - areas 2,3,4,6 i.e. Ruscar, Harrier / Skiordar, Lioag / Sloag, and Hametoun Wilse

[b] - areas 1,5,7,8 i.e. Ristie / Mucklegrind, Ham to the Manse, Daal / Noup, and Airstrip / Bankwell

Table 5.4. Rank correlations between the mean number of adults present on territory and density / location variables.

Stage	Year	Territory variable:			
		DF	NN150	D1N	D3N
Incubation	1992	r_s=-0.13 (n=122) n.s.	r_s=0.16 (n=122) n.s.	r_s=-0.02 (n=119) n.s.	r_s=-0.04 (n=119) n.s.
	1993	r_s=0.00 (n=136) n.s.	r_s=0.05 (n=135) n.s.	r_s=0.03 (n=136) n.s.	r_s=-0.01 (n=136) n.s.
	1994	r_s=-0.02 (n=127) n.s.	r_s=0.25 (n=127) P<0.005	-	-
0-9 days chick-rearing	1992	r_s=-0.17 (n=104) n.s.	r_s=0.08 (n=104) n.s.	r_s=-0.11 (n=103) n.s.	r_s=-0.11 (n=103) n.s.
	1993	r_s=0.11 (n=111) n.s.	r_s=-0.06 (n=110) n.s.	r_s=0.01 (n=111) n.s.	r_s=-0.02 (n=111) n.s.
	1994	r_s=-0.02 (n=98) n.s.	r_s=0.09 (n=98) n.s.	-	-
10-19 days chick-rearing	1992	r_s=0.12 (n=87) n.s.	r_s=0.04 (n=87) n.s.	r_s=-0.02 (n=86) n.s.	r_s=-0.05 (n=86) n.s.
	1993	r_s=-0.14 (n=102) n.s.	r_s=0.22 (n=101) P<0.05	r_s=-0.22 (n=102) P<0.05	r_s=-0.24 (n=102) P<0.02
	1994	r_s=-0.08 (n=91) n.s.	r_s=0.12 (n=91) n.s.	-	-
20-30 days chick-rearing	1992	r_s=0.11 (n=85) n.s.	r_s=0.02 (n=85) n.s.	r_s=-0.14 (n=85) n.s.	r_s=-0.14 (n=85) n.s.
	1993	r_s=-0.03 (n=100) n.s.	r_s=0.00 (n=99) n.s.	r_s=-0.07 (n=100) n.s.	r_s=-0.09 (n=100) n.s.
	1994	r_s=0.19 (n=77) n.s.	r_s=-0.15 (n=77) n.s.	-	-

Table 5.5. Correlations between laying date, density and breeding parameters recorded for Arctic skuas on Foula, 1992-1994.

	Year	Laying date	Density variable:		
			NN150	D1N	D3N
Laying date	1992	-	r_{149}=0.04, n.s.[c,f]	r_{142}=0.08, n.s.[c,f]	r_{142}=0.02, n.s.[c,f]
	1993	-	r_{134}=0.01, n.s.[d,f]	r_{135}=0.05, n.s.[d,g]	r_{135}=0.01, n.s.[d,g]
	1994	-	r_{128}=0.14, n.s.[d,h]	-	-
Egg volume[a]	1992	r_{141}=-0.31, $P<0.001$[c]	r_{143}=-0.11, n.s.[f]	r_{142}=0.07, n.s.[f]	r_{142}=0.05, n.s.[f]
	1993	r_{131}=0.17, $P<0.05$[d]	r_{134}=0.02, n.s.[f]	r_{135}=0.08, n.s.[g]	r_{135}=0.05, n.s.[g]
	1994	r_{128}=0.24, $P<0.01$[d]	r_{128}=0.05, n.s.[h]	-	-
Clutch volume[b]	1992	r_{118}=-0.29, $P<0.002$[c]	r_{119}=-0.06, n.s.[f]	r_{118}=0.02, n.s.[f]	r_{118}=0.03, n.s.[f]
	1993	r_{117}=0.19, $P<0.05$[d]	r_{120}=0.00, n.s.[f]	r_{121}=0.08, n.s.[g]	r_{121}=0.04, n.s.[g]
	1994	r_{113}=0.20, $P<0.05$.[d]	r_{113}=-0.01 n.s.[h]	-	-
Chick growth index (Single / first hatched)	1992	r_{126}=-0.20, $P<0.05$[c]	r_{126}=-0.34, $P<0.001$[f]	r_{119}=0.20, $P<0.05$[f]	r_{119}=0.29, $P<0.02$[f]
	1993	r_{114}=0.27, $P<0.005$[d]	r_{113}=-0.06, n.s.[f]	r_{114}=-0.12, n.s.[g]	r_{114}=-0.09, n.s.[g]
	1994	r_{96}=0.08, n.s.[d]	r_{96}=-0.30, $P<0.005$[h]	-	-
Chick growth index (Two-chick broods)	1992	r_{73}=-0.13, n.s.[c]	r_{72}=-0.28, $P<0.02$[f]	r_{69}=0.17, n.s.[f]	r_{69}=0.23, n.s.[f]
	1993	r_{67}=0.44, $P<0.001$[d]	r_{66}=-0.01, n.s.[f]	r_{67}=-0.03, n.s.[g]	r_{67}=-0.09, n.s.[g]
	1994	r_{60}=0.07, n.s.[d]	r_{60}=-0.31, $P<0.02$[h]	-	-

[a] - single / larger egg in two-egg clutches [b] - two-egg clutches only, and [c] - $\log_{10}$ laying date [d] - 1 / laying date
[e] - $\sqrt{}$ laying date [f] - $\log_{10}$ (density variable) [g] - 1 / (density variable) [h] - $\sqrt{}$ (density variable) used in the analysis

Table 5.6. Chick growth of Arctic skuas on Foula in relation to fledging success and post-fledging survival.

	Year:		
	1992	1993	1994
Fledged[a]	1.00±0.01 (135)	1.00±0.01 (134)	0.99±0.01 (114)
Did not fledge[a]	1.02±0.02 (26)	0.89±0.03 (12)	0.98±0.03 (15)
	$t_{30.7}=0.73$, n.s.	$t_{23.7}=-3.43$, $P<0.005$	$t_{127}=0.66$, n.s.
Both fledglings alive one week post-fledging[b]	1.00±0.01 (27)	1.03±0.01 (30)	-
One / both fledglings dead one week post-fledging[b,c]	1.00±0.02 (14)	1.00±0.03 (11)	-
	$t_{39}=-0.03$, n.s.	$t_{39}=-0.98$, n.s.	-

[a] - all chicks of known fate included as independent cases

[b] - mean growth index in two-chick broods only from territories where both chicks fledged

[c] - data pooled because of small sample sizes

Table 5.7. The effects of density and laying date on the number of chicks hatched on Foula.

	Number of chicks hatched:			ANOVA results
	0	1	2	
Laying date:				
1992	30.7±2.3 (14)	27.5±1.3 (37)	25.1±0.6(94)	$F_{2.142}$=4.3, P<0.02[a]
1993	30.4±2.3 (16)	26.0±1.3 (33)	25.0±0.9 (85)	$F_{2.131}$=3.0, n.s.[b]
1994	29.0±12.5 (21)	25.0±1.8 (23)	21.5±0.6 (86)	$F_{2.127}$=5.9, P<0.005[b]
NN150:				
1992	6.7±1.4 (18)	7.5±0.9 (37)	7.3±0.5 (94)	$F_{2.146}$=0.53, n.s.[a]
1993	6.7±1.4 (21)	7.2±0.9 (33)	8.1±0.7 (84)	$F_{2.135}$=0.8, n.s.[a]
1994	4.0±1.1 (21)	7.2±1.2 (23)	8.5±0.6 (86)	$F_{2.127}$=6.9, P<0.002[c]
D1N:				
1992	70.6±8.6 (17)	60.1±6.1 (37)	70.4±11.3 (90)	$F_{2.141}$=0.7, n.s.[a]
1993	130.2±45.4 (21)	69.5±7.4 (33)	66.4+5.6 (85)	$F_{2.136}$=0.9, n.s.[b]
D3N:				
1992	101.4±13.5 (17)	88.7±10.8 (37)	98.1±11.8 (90)	$F_{2.141}$=0.5, n.s.[a]
1993	164.2±46.3 (21)	94.2±9.9 (33)	88.8±7.2 (85)	$F_{2.136}$=1.3, n.s.[b]

[a] - $\log_{10}$ (laying date / density variable) [b] - 1 / (laying date / density variable)

[c] - $\sqrt{}$ (laying date / density variable) used in the analysis

Table 5.8. The effects of density and laying date on the likelihood of one or both eggs in any clutch being addled.

	Year	No addling	Addling^{d}	T-test results
Laying date^{e}	1992	24.9±0.5 (136)	28.5±1.1 (12)	$t_{146}=-2.12$, $P<0.05^{a}$
	1993	23.6±0.6 (117)	24.8±1.4 (18)	$t_{133}=0.86$, n.s.^{b}
	1994	21.8±0.6 (117)	21.7±1.1 (13)	$t_{128}=0.45$, n.s.^{b}
NN150	1992	7.2±0.4 (132)	8.4±1.5 (19)	$t_{149}=-0.35$, n.s.^{a}
	1993	7.7±0.6 (117)	7.8±1.3 (22)	$t_{137}=-0.06$, n.s.^{a}
	1994	7.6±0.6 (117)	7.3±1.5 (13)	$t_{128}=-0.08$, n.s.^{c}
D1N:	1992	68.7±8.2 (127)	57.5±8.2 (19)	$t_{144}=0.59$, n.s.^{a}
	1993	78.2±9.2 (118)	67.4±9.6 (22)	$t_{138}=0.03$, n.s.^{b}
D3N:	1992	97.1±8.9 (127)	83.2±12.1 (19)	$t_{144}=0.79$, n.s.^{a}
	1993	101.7±10.8 (118)	98.1±13.6 (22)	$t_{138}=0.59$, n.s.^{b}

^{a} - $\log_{10}$ (laying date / density variable) ^{b} - 1 / (laying date / density variable)

^{c} - $\sqrt{}$ (laying date / density variable) used in the analysis

^{d} - data from territories where at least one egg in the clutch was addled

^{e} - data from first clutches only

Table 5.9. The effects of density and laying date on the number of chicks fledged on Foula, excluding pairs that did not hatch any chicks.

	Number of chicks fledged:			ANOVA results
	0	1	2	
Laying date:				
1992	31.3±2.8 (12)	25.3±0.7 (61)	23.5±0.7 (53)	$F_{2,123}$=6.8, P<0.002[a]
1993	32.2±13.3 (13)	24.3±0.9 (39)	22.6±0.5 (60)	$F_{2,109}$=7.7, P<0.001[b]
1994	22.4±2.1 (12)	21.1±0.6 (36)	19.8±0.6 (48)	$F_{2,93}$=1.8, n.s.[b]
NN150:				
1992	6.7±1.6 (12)	7.2±0.6 (61)	7.6±0.7 (53)	$F_{2,123}$=0.2, n.s.[a]
1993	7.2±1.7 (13)	7.7±1.0 (39)	8.2±0.8 (59)	$F_{2,108}$=0.3, n.s.[a]
1994	8.8±2.1 (12)	7.0±0.9 (36)	9.1±0.8 (48)	$F_{2,93}$=1.5, n.s.[c]
DIN:				
1992	66.4±10.3 (12)	57.1±4.6 (61)	80.5±20.3 (49)	$F_{2,119}$=0.6, n.s.[b]
1993	83.5±17.5 (13)	63.8±5.9 (39)	66.0±7.0 (60)	$F_{2,109}$=0.2, n.s.[b]
D3N:				
1992	98.1±14.0 (12)	85.0±7.3 (61)	107.2±20.8 (49)	$F_{2,119}$=0.6, n.s.[a]
1993	102.9±18.4 (13)	89.1±8.9 (39)	89.4±9.1 (60)	$F_{2,109}$=0.4, n.s.[b]

[a] - $\log_{10}$ (laying date / density variable) [b] - 1 / (laying date / density variable)

[c] - √ (laying date / density variable) used in the analysis

Table 5.10. The effects of density and laying date on the number of chicks alive one week post-fledging excluding pairs that did not fledge any chicks.

	Number of chicks alive one week post-fledging			ANOVA results
	0	1	2	
Laying date:				
1992	23.5±1.3 (13)	22.1±0.5 (45)	21.8±0.6 (28)	$F_{2,83}$=1.0, n.s.^{a}
1993	22.6±1.2 (7)	20.6±0.5 (27)	20.5±0.4 (30)	$F_{2,61}$=1.6, n.s.^{b}
NN150:				
1992	3.8±0.8 (13)	6.4±0.7 (45)	8.5±0.8 (28)	$F_{2,83}$=6.1, P<0.005^a
1993	3.4±0.5 (7)	8.6±1.2 (27)	8.9±1.1 (30)	$F_{2,61}$=1.4, n.s.^{a}
DIN:				
1992	78.5±14.1 (13)	84.5±22.9 (43)	47.3±5.4 (26)	$F_{2,79}$=2.9, n.s.^{a}
1993	58.0±5.2 (7)	63.9±8.2 (27)	68.0±12.7 (30)	$F_{2,61}$=0.5, n.s.^{b}
D3N:				
1992	111.2±17.0 (13)	120.4±23.9 (43)	67.3±7.0 (26)	$F_{2,79}$=4.7 P<0.02^a
1993	85.7±9.5 (7)	87.1±10.5 (27)	89.1±16.0 (30)	$F_{2,61}$=0.7, n.s.^{b}

^{a} - $\log_{10}$ (laying date / density variable) ^{b} - 1 / (laying date / density variable) used in the analysis

Table 5.11. Correlations between density and adult size and body condition.

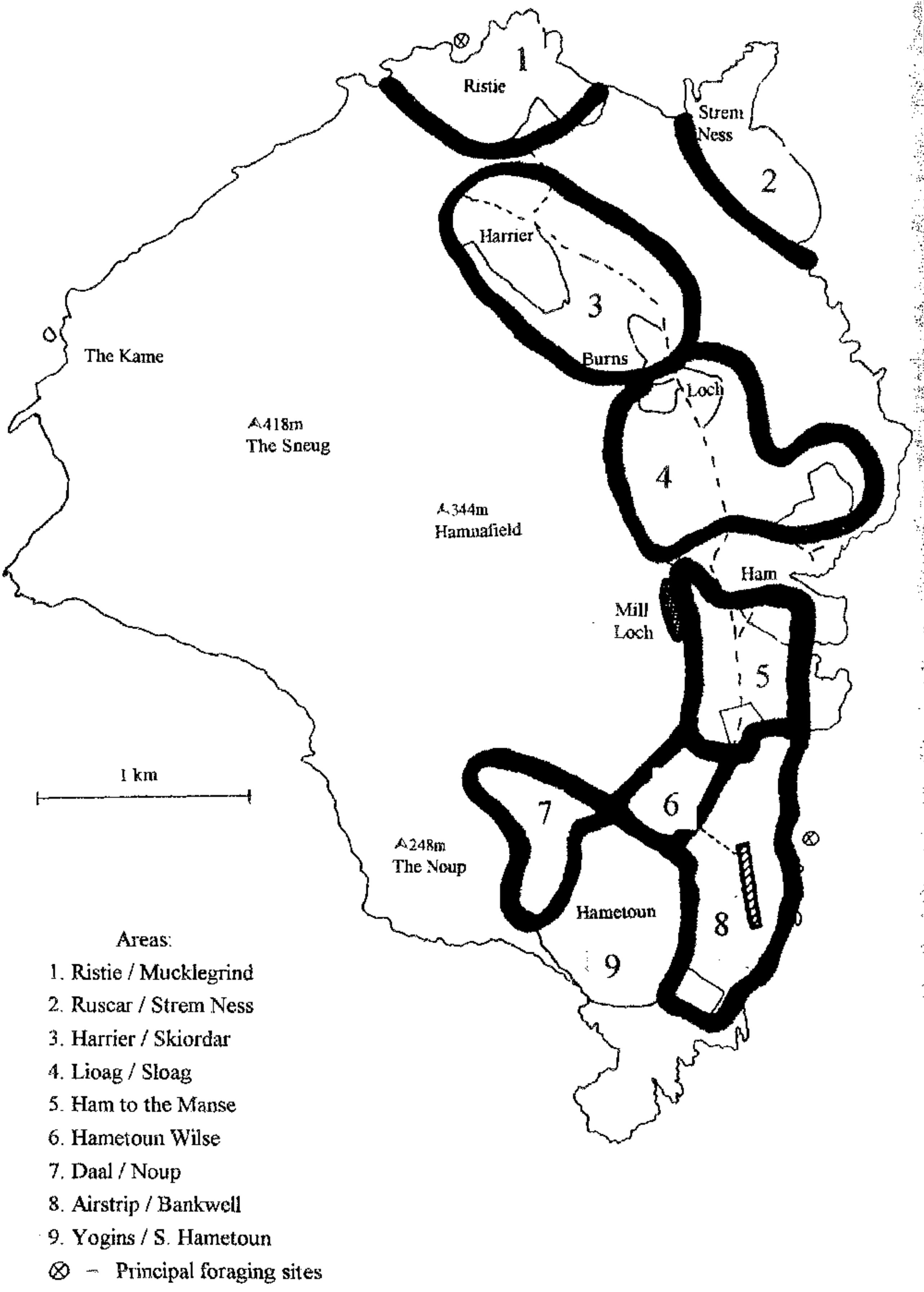
		Density variable:		
		NN150[a]	D1N[a]	D3N[a]
Body size:	male	r_{74}=-0.01, n.s.	r_{57}=0.05, n.s.	r_{57}=-0.02, n.s.
	female	r_{104}=0.05, n.s.	r_{77}=-0.07, n.s.	r_{77}=-0.01, n.s.
Body condition:	male	r_{72}=-0.12, n.s.	r_{56}=0.03, n.s.	r_{56}=0.07, n.s.
	female	r_{96}=0.04, n.s.	r_{71}=0.02, n.s.	r_{71}=-0.03, n.s.

[a] - $\log_{10}$ (density variable) used in the analysis

Table 5.12. Age structure of the Arctic skua population in 1994 in the airstrip compared with the rest of the colony.

Age group	Number of individuals:	
	Airstrip	Outside airstrip
5-8 years	3	6
9-18 years	7	12
> 19 years	7	6
Total	17	24

Fig. 5.1. Map of Foula showing area divisions



Areas:

1. Ristie / Mucklegrind
2. Ruscar / Strem Ness
3. Harrier / Skiordar
4. Lioag / Sloag
5. Ham to the Manse
6. Hametoun Wilse
7. Daal / Noup
8. Airstrip / Bankwell
9. Yogins / S. Hametoun

⊗ – Principal foraging sites

Fig. 5.2. Seasonal decline in clutch volume of two-egg clutches laid by Arctic skuas on Foula in 1994.

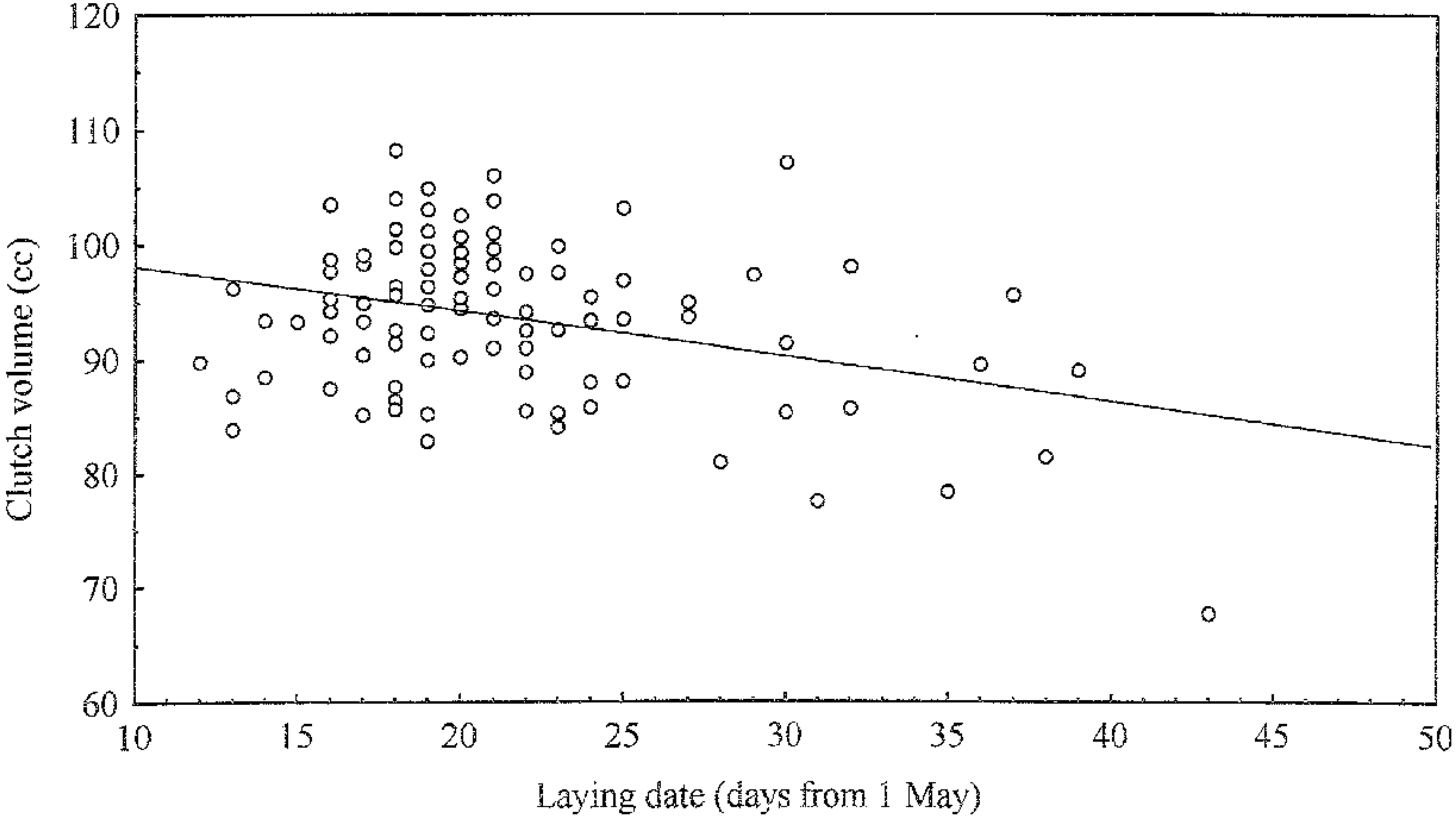


Fig. 5.3. Seasonal decline in growth of single / first hatched Arctic skua chicks on Foula in 1993.

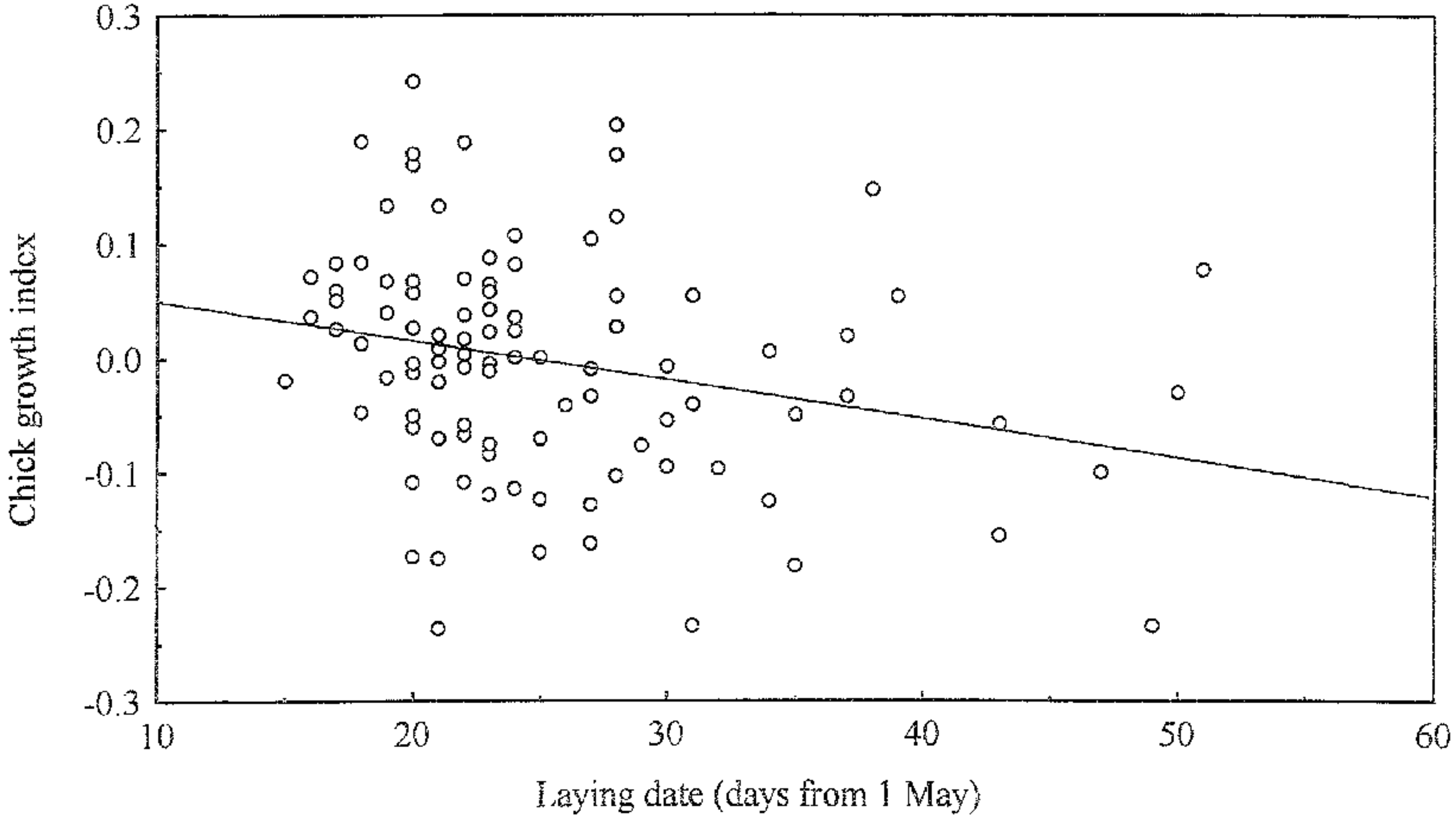
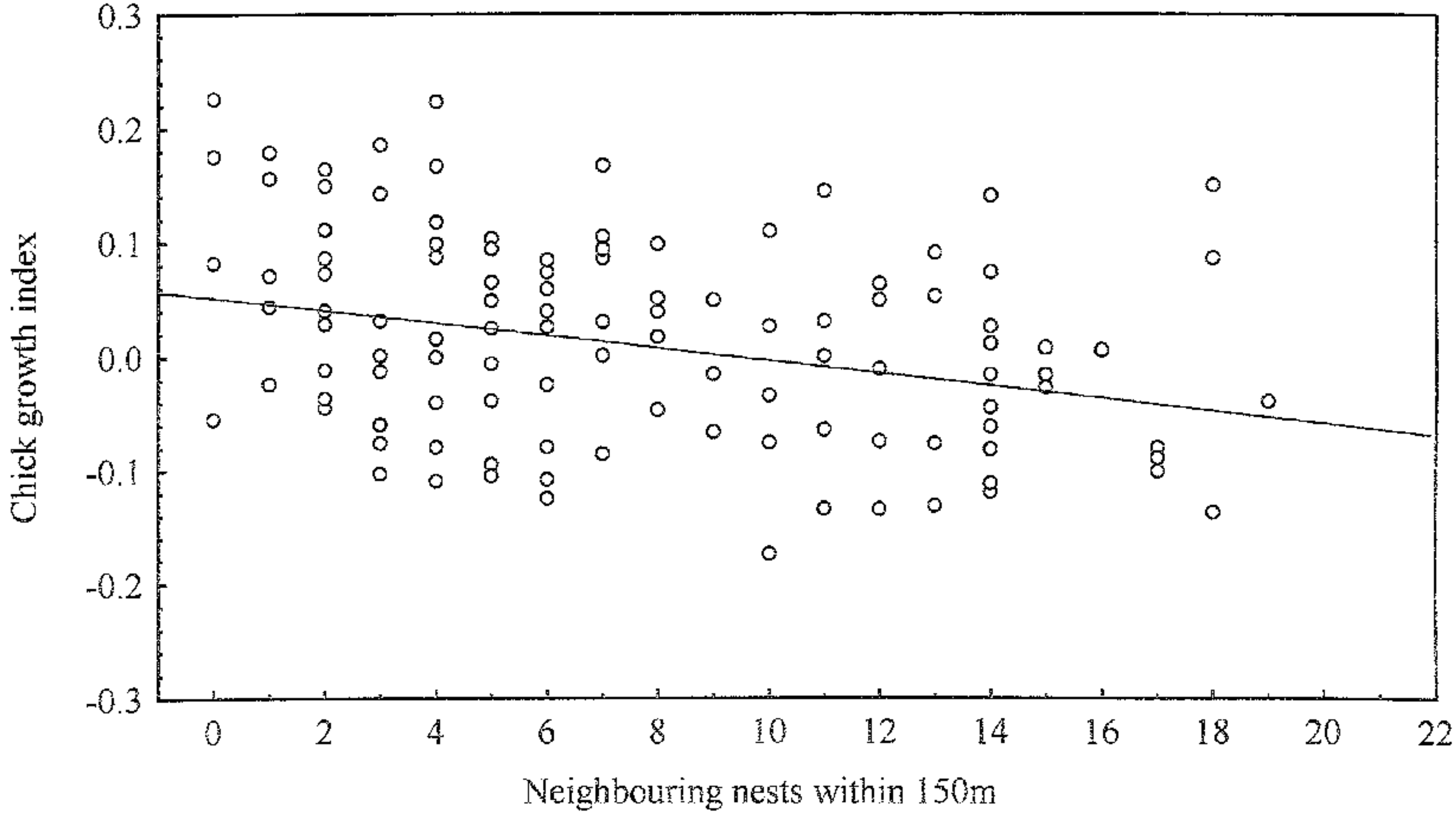


Fig. 5.4. The relationship between density and growth of single / first hatched Arctic skua chicks on Foula in 1992.



5.4 Discussion

Prior to the late 1960s, Arctic skuas on Foula had been breeding in locations considerably further west than those marked in Fig. 5.1 (Furness 1987). The move eastward, which must have occured at some time in the 1960s, was almost certainly a consequence of pressure from the rapidly expanding great skua *Catharacta skua*, colony (Furness 1987). However by 1969 the situation had stabilised, with Arctic skuas occupying much the same range as they do at present, and they began to increase in numbers in the late 1970s, despite a concurrent increase in the great skua population (Furness 1987). Since then however, there have been substantial changes in the relative numbers of occupied Arctic skua territories within their present distribution, the census data indicating that a disproportionately large decline has taken place in most of the northern half of the island (with the exception of Ristie), and also in the Hametoun Wilse area in the south. Such localised changes in demography must be a consequence of variable adult mortality or recruitment patterns in different areas.

The mortality rate of breeders might have increased in some northern areas and Hametoun Wilse (which would also result in the movement of widowed individuals, particularly females out of the area - Chapter 6). The data in Table 5.1 suggest that the loss of pairs from 1980 to 1986 in the areas of decline was indeed faster than would be expected from an adult mortality rate of 13.6%. The factor most likely to operate locally in this way would be mortality as a consequence of inter-specific competition with neighbouring great skua adults. Since their geographic range on Foula stabilised in the early 1970s, the relative proportion of total Arctic skua AOTs in the north which border adjacent high density areas of breeding great skuas has been much greater. This is particularly apparent in contrast with pairs breeding near the airstrip - bordered on one side by the sea, and on the other either by Hametoun (crofted land in which no great skuas have been recorded nesting) or the Hametoun Wilse area, where the number of Arctic skuas has declined. Unfortunately there are no data available on adult mortality rates or mortality factors operating in the early 1980s for any part of Foula. However, great skuas have been observed killing breeding Arctic skua adults in territorial disputes (Furness 1987, S. Gear, pers. comm.) and during the early 1970s, the additional mortality rate as a consequence of territorial competition was estimated at between 3-5% per year (Furness 1987). Although the effect of location on survival of marked breeders in the early 1990s was not statistically significant, mortality around the airstrip was half that recorded elsewhere in the colony. The addition of a few adults killed by predation in the north to the number dying from other mortality factors could easily have a significant effect on breeding numbers there.

Regardless of whether this putative increase in the adult mortality rate in the north of Foula has occured, either there is an apparent dearth of new recruits establishing themselves in the vacant territories, or birds tend to move after their initial breeding attempts. This is in sharp contrast with the area around the airstrip where numbers are presently only slightly lower (Table 5.1) despite the overall size of the Arctic skua breeding population on Foula having halved since the late 1970s. There are a number of possible explanations for this.

There is increasing evidence for both gulls and skuas that if recruits return to their natal colonies they tend to establish themselves in or near the territories from which they fledged (Coulson *et al.* 1982, Ainley *et al.* 1990, Coulson 1991, Klomp and Furness 1991, Spear and Nur 1994). If this is also the case for Arctic skuas, then a depressed recruitment rate in some areas of Foula in the early 1980s might have had a source in poor breeding performance at those locations in the late 1970s. Arctic skuas that hatch earlier or grow better as chicks are more likely to recruit into a breeding population (Chapter 7). Despite the absence of information on the number of chicks that survived to leave Foula, it might be expected that variation in these two parameters affected the survival of cohorts of chicks from particular areas in the late 1970s and so decreased the likelihood that large numbers of surviving birds would return to recruit near their natal territories.

However, although there was some evidence that chicks in one small area tended to hatch later than average, there were no consistent differences in either chick growth or hatching date. This does not therefore provide any support for the hypothesis that the localised recruitment failures on Foula were a consequence of the poor quality of fledglings from previous years. This does not preclude the possibility that another factor, for example chicks succumbing to predation in the pre-fledging or immediate post-fledging stages, might have operated differently in some areas.

The overall number of returning birds does not appear to have been a factor limiting recruitment around the airstrip, so potential recruits were perhaps reluctant to establish themselves elsewhere for some reason, or were more likely to move after establishment. Although inter-colony movement post-recruitment is the exception in seabirds, juveniles of many species prospect a number of colonies before they decide where to breed (Chabrzyk and Coulson 1976, Brooke 1978, Porter and Coulson 1987, Klomp and Furness 1991, Halley *et al.* 1993). Peripatetic Arctic skuas in immature plumage are often seen flying slowly over (and occasionally landing in) the territories of established pairs on Foula (and also at other colonies - Arnason and Grant 1978), apparently tolerated by the residents. They are presumably evaluating local conditions, and there is no reason to suppose that this process of discrimination occurs between colonies without also occurring between different areas within a colony. It is quite plausible that birds use breeding density, or the presence of large young or newly-fledged chicks as a cue to assess their prospective breeding success. Alternatively, low reproductive success in some areas could have a more direct effect on breeding numbers as in some species pairs that perform poorly are more likely to divorce (Mills 1973, Brooke 1978, Bradley *et al.* 1990).

Nest or territory density may have a strong influence on the recruitment rate - very low density areas attract few recruits, while lack of available space may restrict the potential for establishment in very high density areas (Duncan 1978).

As culling began to reduce the breeding population of herring gulls *Larus argentatus*, in certain areas on the Isle of May, it appeared that there was a broad range of mid-value density areas which attracted the maximum number of potential recruits (Duncan 1978). This is probably a species-specific characteristic related to the relative advantage or disadvantage of having large numbers of neighbours. Studies may show either a positive (Davis and Dunn 1976, Birkhead 1977, Harris 1980, Pugesek and Diem 1983, Hatchwell 1991) or a negative (Hunt and Hunt 1976, Furness 1984, Butler and Trivelpiece 1981) relationship between reproductive performance and increasing density, if the major determinant of egg or chick survival is predation by neighbouring pairs or predation by another species.

There appeared to be a positive association between density and reproductive success of Arctic skuas breeding on Foula in the early 1990s, despite the potential disadvantages for such an aggressive species of a likely increase in agonistic behaviour between closely-spaced pairs. There was a strong positive relationship between the number of near neighbours and hatching success but not with the likelihood of addling, indicating that greater density had the benefit of ameliorating the risk of egg predation but had no cost in terms of the likelihood of egg infertility or embryo death, for example through chilling. There was no effect of density on egg or clutch volume (as Harris 1980). Nor was there a relationship between density and the laying date of Arctic skuas, or in the degree of breeding synchrony, despite evidence in some studies that timing of breeding (Davis and O'Donald 1976, Harris 1980, Potts *et al.* 1980, Harris and Wanless 1988) or synchrony (Birkhead 1977, Hatchwell 1991) can be influenced by nest-site quality, density or territory size. Davis and O'Donald (1976) working with Arctic skuas on Fair Isle in the 1970s did find that amongst experienced males breeding for the first time with a new female, those with larger territories bred earlier. However, there was no such relationship with inexperienced males or birds in established pairs, which would be expected to constitute the majority of the population, which is why there may be no such trend in the sample here.

There was a negative correlation between chick growth and the number of near neighbours in two out of three years. This may reflect a requirement for both adults to invest more time in defending their offspring in high density areas, given the possible positive association between attendance and density. There was no evidence that the density effect on growth, or indeed the other differences in breeding performance (which showed the opposite relationship with density), were due to differences in adult age or quality between areas.

In some studies proportionally more younger, and sometimes also lighter or smaller individuals may be found breeding on the edge of a colony than in the centre (Wooller and Coulson 1977, Porter 1990, Klomp and Furness 1991). Often these birds show poor breeding success (Pugesek and Diem 1983, Coulson and Thomas 1985, Klomp and Furness 1991), and occasionally lower survival (Aebischer and Coulson 1990, Spear 1993). Higher mortality may be a direct consequence of breeding on the margins of a colony where they are exposed to a greater risk from predators with easier access to peripheral nests (Patterson 1965, Spear 1993), or alternatively, a consequence of segregation of intrinsically better and intrinisically poorer quality individuals (Aebischer and Coulson 1990). On Foula, the absence of any correlation between density and adult size or body condition, means that such variation in bird quality is an unlikely explanation for the localised differences in breeding performance. Nor were they likely to be due to an effect of segregation of breeders of different ages (suggested by Pugesek and Diem 1983), as there was no appreciable variation in the present age structure of the breeding population attributable to density.

Despite the density effect on growth, and that chicks growing more poorly were less likely to fledge at least in 1993, there were no significant effects of density on fledging success during 1992-1994. This could be related to the extreme crypsis of Arctic skua chicks pre-fledging, with the resulting low mortality rate due to predation in any case. In 1992-1994, 88% (n=524) of chicks that lived to a week i.e. overcame problems related to temperature regulation, the initiation of correct feeding behaviour by adults etc., survived to fledging.

Once chicks do start flying however, they become much more conspicuous and considerably more vulnerable to great skua predation. During the 1992-1993 breeding seasons, 61.9% (n=528) of eggs laid resulted in a fledged chick. This corresponds to a loss of approximately 6% of remaining eggs / chicks per week and contrasts with the far greater mortality rate of 19.3% of fledglings (n=233, 1992-1993 data) found dead or disappeared in the first week following fledging. There must be a very strong selection pressure on adults to mitigate against such substantial losses late in the season. This can be acheived by nesting at higher density, even if adults incur a cost in terms of chick growth.

There is a therefore a considerable incentive for birds to move territories in the event of poor reproductive success or post-fledging survival of recently-fledged chicks. The mortality rate of established breeders in certain locations in the early 1980s appeared to be higher, probably because of competition with neighbouring great skuas. If, in addition birds are more likely to divorce and so move out of these areas after breeding failure, and potential recruits do use cues to assess local conditions at possible future breeding sites, that would certainly account for the localised declines in Arctic skua AOTs since the late 1970s.

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Chapter Six. The influence of age and duration of the pair-bond on reproductive success of Arctic skuas

6.1 Introduction

Improvements in reproductive performance with age and the duration of the pair-bond are a common feature of many seabirds' breeding biology (e.g. Ollason and Dunnet 1988, Thomas and Coulson 1988). Within a population the youngest birds may breed later, lay fewer or smaller eggs and have poorer hatching or fledging success (Weimerskirch 1990, 1992, Wooller *et al.* 1990, Hamer and Furness 1991). The same may also be true for the oldest age classes (Reid 1988b, Thomas and Coulson 1988, Wooller *et al.* 1990).

The initial improvement in the first years after recruitment has been attributed to several factors, These include the advantages of cumulative breeding experience (Wooller *et al.* 1990, Pyle *et al.* 1991) and/or an increase in general skills, e.g. foraging abilities with chronological age (Nur 1984, Boekelheide and Ainley 1989, Wooller *et al.* 1990, Pyle *et al.* 1991, Croxall *et al.* 1992). These two effects are often hard to distinguish in statistical analysis (Croxall *et al.* 1992). Unequivocal evidence for the latter is that birds which recruit when older are invariably more successful at their first breeding attempt (Ollason and Dunnet 1978, 1988, Wooller *et al.* 1990, Pyle *et al.* 1991). Studies also find evidence for differential survival of higher quality individuals after the first breeding attempts (Thomas and Coulson 1988, Bradley *et al.* 1989). The cost of reproduction appears to be greater in birds breeding for the first time (Bradley *et al.* 1989). While their survival is not always poorer (Aebischer and Coulson 1990, Weimerskirch 1990, 1992), they are usually less likely than established birds to return and breed the following year (Wooller and Coulson 1977, Weimerskirch 1990, 1992).

Alternatively, a central prediction of life-history theory, that reproductive effort (rather than skill) should increase with age to compensate for declining residual reproductive value (Stearns 1992), would also account for age-specific patterns in reproduction. Data supporting this last hypothesis however, remain limited (Pugesek 1981, 1984, Nur 1984).

In general, individuals breeding together for the first time tend to perform more poorly than those in established partnerships (Davis 1976, Brooke 1978, Ollason and Dunnet 1978, Weimerskirch 1990). Their success usually improves as they accumulate more common breeding experience, sometimes over several seasons (Davis 1976, Bradley *et al.* 1990), and they become less likely to divorce (Coulson and Thomas 1983, Bradley *et al.* 1990). Divorce rates in seabirds are quite variable (Rowley 1983, Johnston and Ryder 1987). If the advantages of cumulative breeding experience mitigate against it, divorce is likely to occur only if there is an element of incompatability or if at least one member can improve its success by deserting and breeding with a better quality partner or at a better site (Johnston and Ryder 1987).

Middle-aged birds retaining their mates are therefore likely to contribute most to the overall productivity of a breeding colony (Thomas and Coulson 1988, Ollason and Dunnet 1988). On Foula poor chick growth and fledging success in the late 1980s and 1990 reduced the potential number of new recruits from 1991 onwards (Chapter 2). Given that Arctic skuas in Shetland normally breed for the first time aged 4 or 5 (O'Donald 1983), the mean age of the population on Foula in 1994 was likely to be higher than in previous years. For this reason, evidence of senescence in the oldest age classes could have important repercussions for the productivity of the colony as a whole, and potentially might limit the likelihood of longer-term recovery. This chapter explores evidence for effects of age and duration of the pair-bond on reproductive success, with such implications for population development in mind.

6.2 Methods

Adults trapped during 1992-1994 were fitted with unique colour-ring combinations (Chapter 4). During 1992-1994, all occupied Arctic skua breeding territories were marked on a 1:10,000 Ordnance Survey map, and the colour-phases of both members of each pair were noted. The location of Arctic skua territories remain constant from year to year asssuming at least one member of the pair survives and retains residency (O'Donald 1983, Furness 1987). It was therefore possible to use information on the establishment of new territories in new locations, on movements of colour-ringed adults, and on the presence of adults of different colour-phase, to identify partnerships involving birds breeding together for the first time. The efficiency with which these pairings were identified was estimated in 1994 by predicting the expected number of new partnerships on the basis of the 1993-1994 adult mortality and divorce rates. The divorce rate was calculated from data on 34 pairs in which both partners were colour-ringed in 1993. The proportion of new partnerships formed in 1993 that were not breeding together on Foula in 1994, presumably because of either death, divorce or breeding deferral, was compared with equivalent data recorded for the remainder of the population.

Colour-ringed individuals in new partnerships were sexed by observation or by a discriminant function (Chapter 4). It was therefore possible to ascertain the gender of the adult retaining the territory in a number of cases. The approximate distance marked individuals had moved from their previous territory was calculated from mapping information. In 1994, one new pairing of colour-ringed birds marked in the previous year appeared to involve the fusion of two adjacent territories, and was excluded from these analyses.

Laying date, clutch size and clutch volume of first clutches were compared between territories where the pair was or was not known to be a new partnership in 1993 and 1994. A similar comparison was carried out on number of chicks hatched, number of chicks fledged, growth of first-hatched/single chicks and mean growth in two-chick broods. Breeding variables were also compared between 1993 and 1994 for all pairs formed in 1993 that were not known to have split by the following year. Data from second clutches were included in the analyses involving hatching success and chick growth and survival. All breeding data were collected as detailed in Chapter 1, General methods.

Fifty adults caught during the 1992-1994 breeding seasons already carried a metal ring. Forty-three of these had been ringed as chicks and so were of known age, and the remainder had been ringed as breeding adults, one in 1988, three in 1987 and three in 1975. Of the 50 birds ringed previously, 46 were present on Foula in 1994, including 39 known-age birds (five of which were immigrants from other Shetland colonies).

By 1994, 65% (173/268) of the territory-holding adults were colour-ringed. In that year 73 other breeders which had not been trapped were checked for the presence or absence of metal rings. This was not feasible for the 22 adults constituting the remainder of the breeding population because these birds would start flying when the observer was still some distance off-territory, and did not mob intruders. It was not possible to get a clear view of these adults' tarsi. The number of birds breeding in 1994 that had been ringed prior to 1992 was estimated. The proportion of these ringed birds that had been captured by 1994 was then calculated in order to estimate how representative of all potential known-age adults on Foula the recorded known-age birds were.

From the above analysis it was clear that a substantial proportion of all the 1994 breeders that had fledged from Foula in previous years had been caught. The number present in 1994 from each cohort of chicks was corrected for the appropriate annual ringing total only, as the proportion dying between ringing and fledging was unknown in most years. This provided a ratio of the relative number present from each year-class. These values, divided by the sum, represent the proportion of the philopatric breeding population in 1994 surviving from each Foula cohort.

Analyses of age-specific patterns in reproductive performance were carried out using breeding data recorded for all known-age adults present on Foula in 1994. The birds ringed as breeders in 1975 were assumed to have been four years old (a minimum estimate) when they were first trapped, and included as 23 year-olds (the oldest age-group) in these comparisons. Both members in six pairs were of known-age. In order to retain statistical independence, data from these pairs were included only once, and in all cases the age of the female was used in the comparisons.

Correlations were performed between age, laying date, and clutch volume of first clutches, and also between age and growth of chicks from first or replacement clutches. Possible differences in adult foraging effort were investigated using attendance data collected during each of four stages in the breeding season. In addition adults were categorised as young (aged 5-8 years), middle-aged (aged 9-18 years) or old (aged 19-23 years). Mean laying date, clutch volume, chick growth and number of eggs laid, chicks hatched, and chicks fledged, were compared between these groups using parametric or Kruskal-Wallis one-way ANOVAs. Because changing partner might confound the detection of age-related trends with these relatively small samples, some analyses were repeated using two-way ANOVAs with age-group and pair status as factors.

6.3 Results

In total, 22 new partnerships were detected in 1993, and 27 in 1994. The efficiency with which these were identified in 1994 was estimated as follows using the 1993-1994 mortality rate of 0.117 (m) derived from colour-ringing data,

$\Rightarrow$ probability of one bird in a pair dying = $2m(1-m)$ = 0.207

probability of both birds dying = m^2 = 0.014

probability of both birds surviving = $(1-m)^2$ = 0.780

Both members from 27 of the original 34 pairs of colour-ringed adults in 1993 were present on Foula in 1994. Individuals from two of these pairs were recorded breeding with new partners - a divorce rate of 2/27 = 7.4% (d). The probability of remaining together if both partners survive is therefore $1-d = 0.926$. The number of surviving pairs from 1993 likely to be together in 1994 equals the total number of pairs in 1993 x $(1-m)^2$ x $(1-d)$ = 145 x 0.780 x 0.926 = 105. The difference between that value and the 1994 population size (134 pairs) i.e. 29, is an estimate of the number of new pairs. The actual number detected was 27 i.e. 93%.

On 21 occasions in 1993 or 1994, the sex of the incoming bird in the new partnership was determined, and on 19 it was a female. This is significantly different from a 1:1 ratio (Binomial Probability test $P<0.0002$). The mean distance moved (± 1 SE) by incoming colour-ringed females from their previous territories was 394 ± 91m. (n=10, range 130-840 m).

In total, 40.9% (9/22) of known new partnerships formed in 1993 were not breeding together (either because of death, divorce or breeding deferral) on Foula in 1994. Only 19.5% (24/123) of pairs in the remainder of the 1993 population were definitely not breeding together the next season. This difference is significant ($\chi^2=4.86$, $P<0.05$).

Results of the comparison of breeding performance between known new pairings and partnerships of unknown status are shown in Table 6.1. In both 1993 and 1994 females laid significantly later and their clutch volume (in two egg clutches) was significantly lower if the pair were breeding together for the first time. In 1994 they were more likely to produce single egg clutches and also to hatch fewer chicks. First-hatched/single chicks raised by adults in new partnerships grew more poorly in 1993.

Although the trend was for an advance in laying date relative to the population mean and for an increase in clutch volume in the new pairs that remained intact, no aspect of breeding performance (with the exception of chick growth) showed a significant improvement from 1993 to 1994 (Table 6.2). However, the sample sizes were quite small.

The proportion of all potentially known-age adults present on Foula in 1994 for which ages were actually recorded was calculated as follows. Forty-six (of 173) colour-ringed adults were already metal-ringed prior to trapping in 1992-1994, and 10 of the 73 unmarked breeders checked also carried a ring. The number in the remainder of the population likely to be carrying a ring = 22 x

[(10+46)/(173+73)] = 5, giving a total of 15 unmarked breeders carrying rings. The number of these birds likely to have been ringed as chicks on Foula in previous years and so of known-age (assuming these occured in the same proportion as they did in the sample of ringed adults already captured) = 15 x (34/46) = 11. The proportion of all known-age philopatric adults available to be trapped on Foula in 1994 that had actually been recorded was therefore 34 / (34+11) = 0.756.

The estimated age structure of the adult population breeding on Foula in 1994 that fledged from there in previous years is shown in Fig. 6.1. Using the mean adult mortality rate, 1992-1994, of 0.136 (Chapter 8) and assuming that adults recruit aged 4.4 years, the expectation of future life at recruitment was 6.9 years (Botkin and Miller 1974). Interestingly, 43% of the adults present on Foula in 1994 were 13 or older i.e. had lived for longer than expected (presumably because so few young birds will have recruited in recent years - Chapters 2 and 3).

The correlation between the ages of members in the known-age pairs was not statistically significant (r_5=0.55, n.s.: Fig. 6.2). The mean difference (± 1 s.d.) in age was 5.4 ± 4.1 years (range 0-12). Both adults were the same age in only one case, and in five out of the remaining six, the male was older than the female.

There was a significant negative correlation between age and laying date (r_{32}=-0.40, $P<0.02$: Fig. 6.3), but no correlation between age and clutch volume (r_{32}=0.25, n.s.: Fig. 6.4). Similarly one-way ANOVA indicated there were significant differences in laying date between the age groups, but not in clutch volume. Two-way ANOVA however, indicated a significant effect on laying date of both age ($F_{2,28}$=4.41, $P<0.05$) and pair status ($F_{1,28}$=10.09, $P<0.005$), and of both age ($F_{2,28}$=3.4, $P<0.05$) and pair status ($F_{1,28}$=13.27, $P<0.002$) on clutch volume (Table 6.3). Small sample sizes in each cell preclude the use of the interaction terms in these ANOVAs.

Age did not show a significant correlation with the growth index of first-hatched/single chicks (r_{23}=0.21, n.s.: Fig. 6.5), nor did a significant difference exist between age groups (Table 6.3). Similarly, the mean chick growth index did not correlate with age (r_{15}=0.14, n.s.). The number of chicks hatched and chicks fledged did not differ between age groups (Table 6.3) and all clutches laid by known-age birds were of two eggs. There were no significant rank correlations between age and attendance during incubation (r_s=0.09, n=34, n.s.), 0-9 days post-hatching (r_s=-0.14, n=25, n.s.), 10-19 days post-hatching (r_s=0.21, n=24, n.s.) or 20-30 days post-hatching (r_s=-0.04, n=20, n.s.).

Table 6.1. Comparison in breeding variables between pairs of different status in 1993 and 1994.

	1993			1994		
	Pair status:			Pair status:		
	Unknown	New		Unknown	New	
Laying date^a	23.0±0.5 (n=116)	28.5±1.5 (n=21)	t-test^b t_{135}=3.9, P<0.001	20.6±0.5 (n=107)	27.2±1.6 (n=23)	t-test^b t_{128}=4.6, P<0.001
Clutch volume (cc)	94.2±0.7 (n=103)	90.1±1.6 (n=20)	t-test t_{121}=2.2, P<0.05	94.9±0.7 (n=99)	89.3±2.3 (n=17)	t-test t_{114}=2.8, P<0.01
A / single chick growth index	1.00±0.01 (n=103)	0.92±0.04 (n=16)	t-test $t_{17.0}$=2.3, P<0.05	1.00±0.01 (n=84)	0.96±0.02 (n=16)	t-test t_{98}=1.8, n.s.
Mean chick growth index	0.99±0.01 (n=63)	0.95±0.03 (n=10)	t-test t_{71}=1.6, n.s.	0.99±0.01 (n=57)	1.00±0.03 (n=9)	t-test t_{64}=-0.3, n.s.
Number of eggs laid	1.91±0.03 (n=118)	1.91±0.06 (n=22)	χ^2_1=0.03, n.s.^{c}	1.93±0.03 (n=107)	1.74±0.09 (n=23)	χ^2_1=6.71, P<0.01^c
Number of chicks hatched	1.50±0.07 (n=117)	1.23±0.19 (n=22)	Mann-Whitney, Z=-1.4, n.s.	1.56±0.07 (n=107)	1.22±0.18 (n=23)	Mann-Whitney, Z=-2.0, P<0.05
Number of chicks fledged	1.23±0.08 (n=114)	0.95±0.19 (n=21)	Mann-Whitney, Z=-1.4, n.s.	1.17±0.08 (n=99)	0.89±0.20 (n=18)	Mann-Whitney, Z=-1.3, n.s.

^{a} - days after 1 May

^{b} - inverse transformed data

^{c} - excluding a single three-egg clutch

Table 6.2. Changes in breeding variables between 1993 and 1994 of new partnerships formed in 1993.

	n	1993	1994	
Relative laying date[a]	13	2.2±1.4	0.4±1.4	Paired t-test t_{12}=1.19, n.s.
Clutch volume (cc)	11	92.4±1.5	94.3±1.3	Paired t-test t_{10}=-2.01, n.s.
A / single chick growth index	7	0.93±0.03	1.00±0.02	Paired t-test t_6=-2.06, n.s.
Mean chick growth index	4	0.97±0.02	1.00±0.02	Paired t-test t_3=-7.35, $P<0.01$
Number of eggs laid	13	2.00±0.00	1.92±0.14	Wilcoxon test z=-0.53, n.s.
Number of chicks hatched	13	1.23±0.23	1.15±0.270	Wilcoxon test z=-0.31, n.s.
Number of chicks fledged	11	1.18±0.23	0.91±0.32	Wilcoxon test z=-1.21, n.s.

[a] - days relative to the mean in each year

Fig. 6.1. The estimated age structure of the population of philopatric adults breeding on Foula in 1994.

Fig. 6.2. The relationship between the ages of each member of known-age pairs on Foula in 1994.

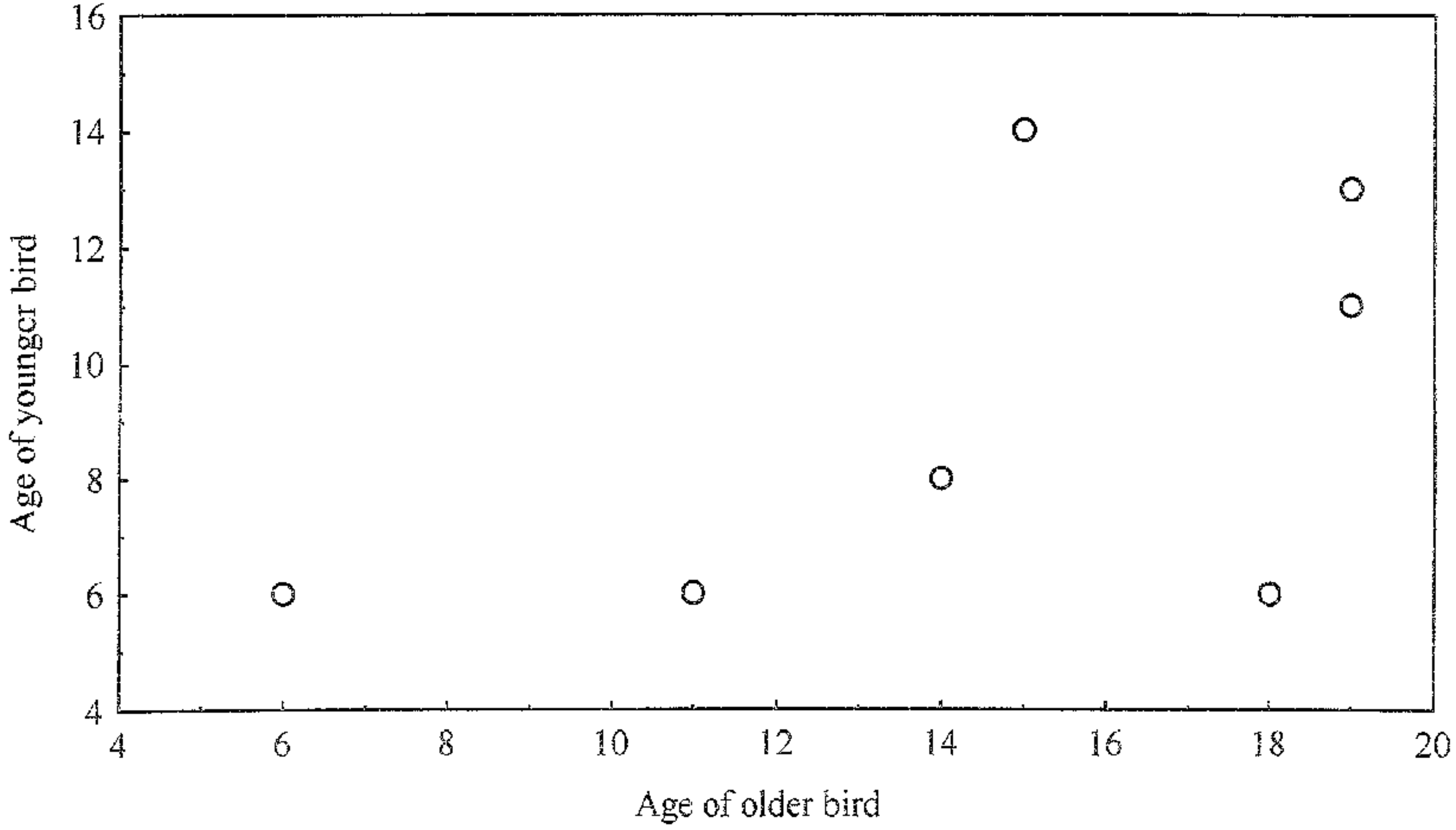


Fig. 6.3. Laying date on Foula in 1994 in relation to adult age and pair status.

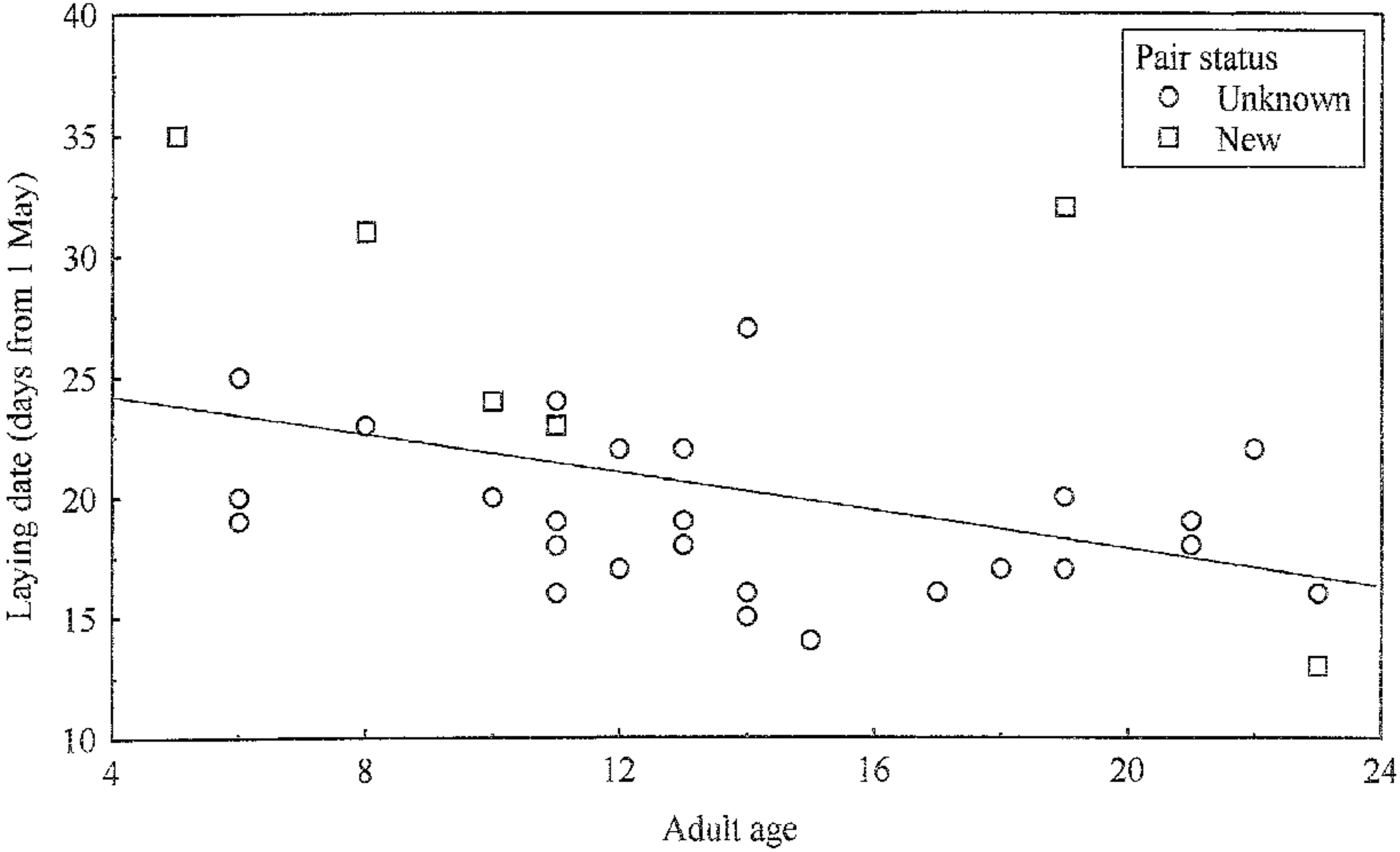


Fig. 6.4. The volume of two egg clutches laid by Arctic skuas of different ages and pair status on Foula in 1994

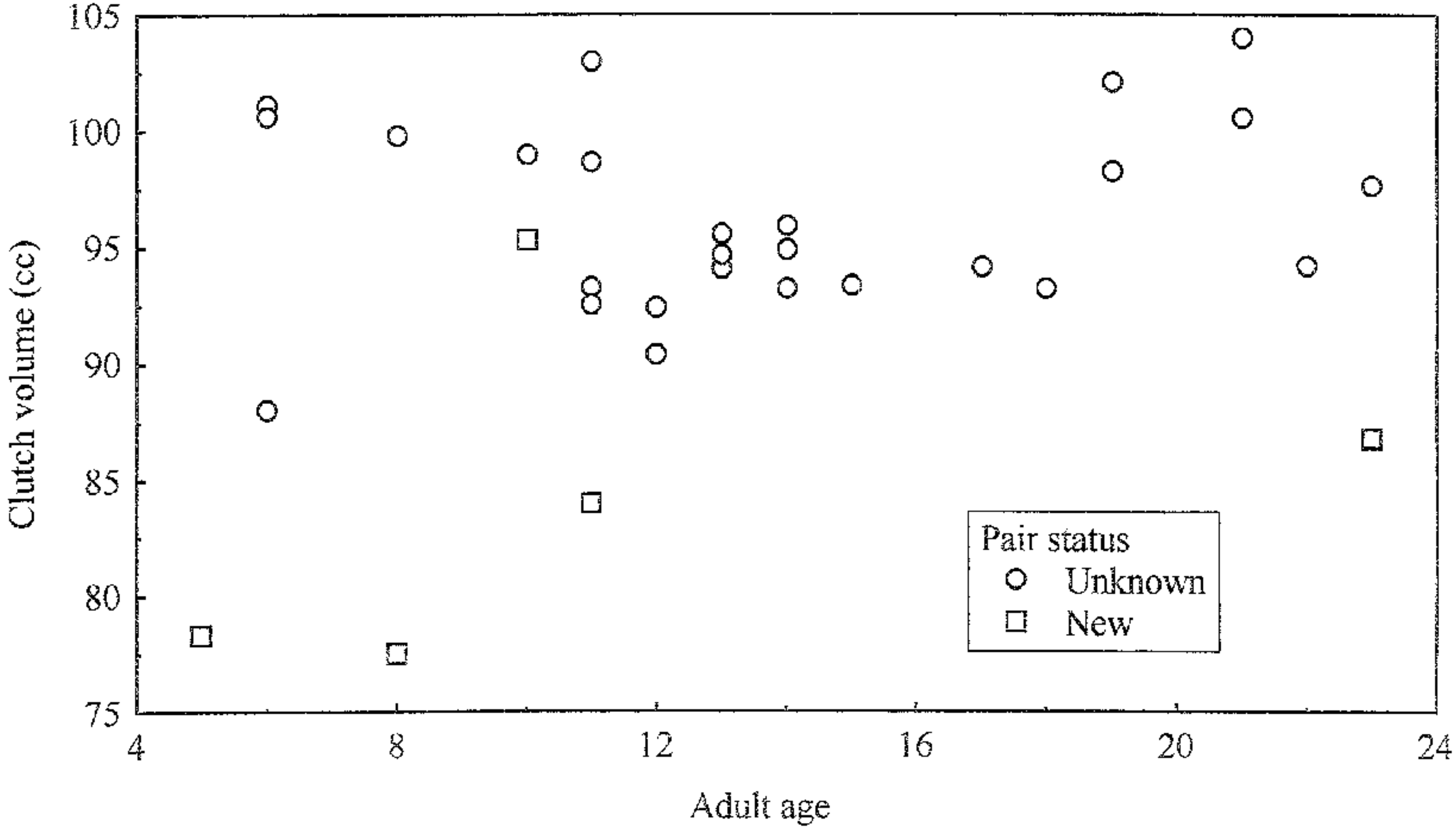
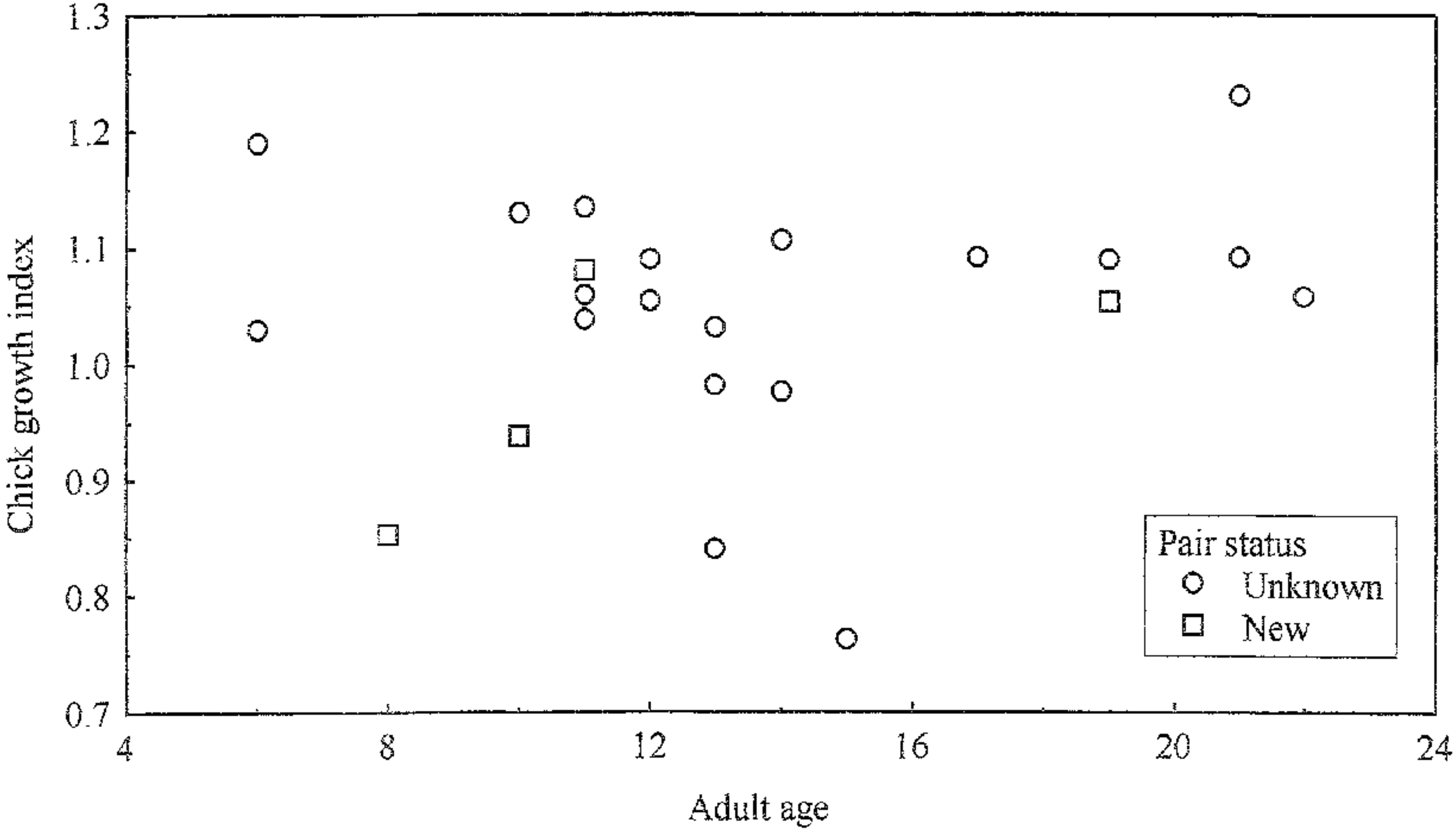


Fig. 6.5. The growth index of first hatched or single chicks raised by Arctic skuas of different age and pair status on Foula in 1994



6.4 Discussion

Females in new partnerships laid later in the season and produced eggs of smaller volume on Foula in both 1993 and 1994. Clutch sizes were smaller and the number of chicks hatched lower in 1994, and chick growth was poorer in 1993. Other studies comparing new with established partnerships find similar effects (Mills 1973, Brooke 1978, Ollason and Dunnet 1978, Coulson and Thomas 1983). Although not observed in this study, frequently the overall breeding success of new pairs is also significantly lower (Mills 1973, Davis 1976, Ollason and Dunnet 1978, 1986, Coulson and Thomas 1983, Weimerskirch 1990).

The previous breeding experience gained by each individual prior to the formation of a new pair-bond has a major influence on performance in their first breeding attempt together (Davis 1976, Ollason and Dunnet 1978, Brooke 1978, Weimerskirch 1990). However, it was not possible to assume a lack of breeding history for any unmarked adult in new partnerships formed in 1994. By the close of the 1993 breeding season, only 50% of established breeders on Foula had been colour-ringed. In addition, modelling of annual differences in the level of net recruitment on Foula suggested that relatively few new recruits entered the breeding population in 1993 or 1994 (Chapter 2). As a consequence, many new pairings recorded in these two seasons were likely to have involved at least one member with previous experience. Perhaps for this reason the number of chicks fledged in 1993 and 1994 by new pairs was not significantly lower than in the rest of the population.

Experienced male Arctic skuas were much more likely to retain the territory, whereas females were more likely to move in order to form a new partnership. Male kittiwakes *Rissa tridactyla*, retained the nest site after divorce, and only if the male died was the female likely to remain resident (Coulson and Thomas 1983). Even in species with very low mate fidelity males are much less likely to move (Boekelheide and Ainley 1989). The inference from this is that males are more active in territory establishment and defence during the earliest part of the season before eggs are laid. This is true for Western gulls *Larus occidentalis*, despite female attendance actually being higher during the pre-incubation phase (Pierotti 1981).

Stability of the new partnerships formed in 1993 was significantly poorer than in the rest of the population. This might reflect either higher rates of divorce or mortality, or a greater incidence of breeding deferral in 1994. In general divorce is much more likely to occur after reproductive failure than success (Mills 1973, Brooke 1978, Coulson and Thomas 1983, Bradley *et al.* 1990, Weimerskirch 1990), and new partnerships certainly performed more poorly. Pair-bond duration also tends to be shorter for younger birds (Bradley *et al.* 1995). If numbers of new partnerships formed in 1993 involved at least one recruiting adult, these birds may have been more likely not to breed the following year. Individuals are less likely to return following their first breeding attempt, either because of lower survival or breeding deferral (Wooller and Coulson 1977, Aebischer and Coulson 1990, Weimerskirch 1990, 1992).

Laying date tends to advance and other aspects of breeding performance improve with increasing duration of the pair-bond (Brooke 1978, Coulson and Thomas 1983, Bradley *et al.* 1990, 1995). However, there were no significant differences in relative laying date or clutch volume etc. for those pairs formed in 1993 that also bred together in 1994. While the data show trends in the right direction, the sample size may not have been sufficient to detect any improvement.

Arctic skuas on Foula divorce relatively infrequently. Divorce rates in seabirds are quite variable, recorded values ranging from zero in some albatrosses to over 40% in Adelie penguins *Pygoscelis adeliae*, and masked boobies *Sula dactylatra* (Rowley 1983). Pair stability can be even lower in species such as Antarctic blue-eyed shag *Phalacrocorax atriceps*, and Brandt's cormorant *Phalacrocorax penicillatus*, living in unstable environments where the advantages of prior breeding experience, and mate fidelity, appear to be slight (Shaw 1986, Boekelheide and Ainley 1989). In general Larids have relatively low levels of divorce, ranging from 5 % for red-billed gull *Larus novaehollandiae*, similar to the value for Arctic skuas, to 29% for Caspian tern *Sterna caspia* (Johnston and Ryder 1987). Divorce can be influenced by environmental factors, and not just pair incompatability (Rowley 1983, Johnston and Ryder 1987). Rates of divorce are highest among young breeders and tend to decrease markedly with age, and also with increasing duration of the pair-bond (Coulson and Thomas 1983, Ainley *et al.* 1990, Bradley *et al.* 1990). The low divorce rate for Arctic skuas on Foula, 1993-1994, might be a reflection of the relative minority in which younger birds were found in the breeding population.

Despite the low divorce rate, there was no significant correlation between the ages of both members of the breeding pair. With a sample of seven pairs in the analysis a correlation coefficient of greater than 0.75 would have been required for statistical significance. In most studies the correlation is around 0.4 to 0.6 (Reid 1988a), i.e. close to the value found for Arctic skuas. The usual explanation cited for the close correspondence in age between individuals in a pair is non-random mate selection (Mills 1973, Shaw 1985). However, a modelling approach (Reid 1988a) suggested that because adults recruited at approximately the same age usually with a similarly aged partner, and mortality and divorce rates were low, typical correlations in field studies could be acheived with random mate choice alone, provided adult survival was greater than 0.8 and pair stability high (Reid 1988a). In species with low mate fidelity, a high correlation coefficient may still be evident if there is assortative mating on the basis of experience alone, and in only two instances did selection on the basis of age appear to have occured (Reid 1988a).

In 1994, laying date advanced and clutch volume increased with adult age, but there were no changes in any other breeding parameter. This age-specific variation was primarily a consequence of the difference between the youngest adults and the rest of the breeding population. Breeding variables often improve with age only during the first few breeding attempts, reaching a plateau after perhaps three or four seasons (Ollason and Dunnet 1978, Thomas and Coulson 1988, Weimerskirch 1990), although changes in breeding performance sometimes occur over more prolonged periods (Pugesek 1981, Wooller *et al.* 1990, Hamer and Furness 1991). Chick growth, number of eggs laid, number of chicks hatched and number of chicks fledged did not change with adult age on Foula. Similarly, Davis (1976) working with Arctic skuas on Fair Isle found hatching date advanced with age, but despite evidence that early laying pairs were more successful, found no correlation between age and the number of chicks fledged.

Although age or experience usually influence hatching success, possibly determined by adults' abilities to co-ordinate incubation shifts (Coulson and Thomas 1983, Weimerskirch 1990), frequently chick growth is unaffected (Reid 1988b, Lequette and Weimerskirch 1990, Hamer and Furness 1991). Fledging (rather than breeding) success *per se* may change little with increasing age or experience (Thomas and Coulson 1988, Boekelheide and Ainley 1989, Weimerskirch 1990). This is not surprising given the lack of direct or even indirect evidence that foraging abilities actually improve beyond the second breeding attempt (Lequette and Weimerskirch 1990, Weimerskirch 1990). The absence of age-specific variation in hatching or breeding success for Arctic skuas on Foula might relate to relative food availability in 1994. Both very good or very poor conditions may have equivalent masking effects on age-related trends in reproductive performance either because young adults are able to perform equally well if food is readily obtainable (Furness 1984), or because reproductive failure occurs *en masse* (Boekelheide and Ainley 1989, Hamer and Furness 1991). Adult attendance on territory in 1994 was exceptionally high, so food was presumably abundant (Chapter 2).

There was no evidence of senescence in any parameter of reproductive performance of Arctic skuas on Foula in 1994. In a cross-section of the breeding population, declines in some aspect of breeding ability (often clutch size or volume) in the oldest age classes were found in some (Reid 1988b, Thomas and Coulson 1988, Pugesek and Diem 1990, Wooller *et al.* 1990, Hamer and Furness 1991, Weimerskirch 1992) but not all studies (Pugesek 1981, Ollason and Dunnet 1988, Croxall *et al.* 1992, Weimerskirch 1992). Longitudinal analysis of individual breeding histories has contradicted cross-sectional evidence for senescence (Pugesek and Diem 1990). However, in another study longitudinal analysis indicated that senescence was related to the proximity of the end of a particular individual's breeding career (Ollason and Dunnet 1988). This would not have been revealed by a straightforward cross-sectional approach.

It is possible that the oldest birds, although breeding as successfully, were having to expend greater reproductive effort than the younger birds in order to offset their declining residual reproductive value (Stearns 1992). Recent studies indicate that the probability of survival is generally lower for the oldest age-classes (Bradley *et al.* 1989, Aebischer and Coulson 1990, Weimerskirch 1992), although this was apparently not the case for the Northern fulmar *Fulmarus glacialis* (Ollason and Dunnet 1988). The cost of reproduction for old individuals could then be higher. Studies have shown that older birds experienced more of a decline in body mass during the course of the breeding season, which was interpreted as evidence of greater reproductive effort (Pugesek 1984, Pugesek and Diem 1990). Reid (1988b) found that while body condition decreased with increasing adult age during incubation, by contrast, older individuals had gained more mass than younger birds by the middle stage of chick-rearing, and suggested this variation reflected neither varying effort nor cost of reproduction, but the ability of older individuals to regulate their weight at a lower set point in order to maintain flight efficiency. In any event, Arctic skua territorial attendance was not related to age at any stage of the breeding season in 1994, nor was there any relationship with body weight during incubation (Chapter 4) providing no indication of an age-specific pattern in reproductive effort. Unfortunately insufficient data exist to test for age-dependent variation in the adult mortality rate.

Although age clearly had some implications for the timing of breeding and the volume of the eggs produced, breeding with a new partner had considerably greater influence on hatching success and chick growth. There was no evidence of senescence in reproductive abilities. It is therefore unlikely that the predominance of middle-aged and older adults breeding on Foula in 1994 has much implication for the colony's productivity as a whole. In fact, it may be a factor contributing to the present low level of divorce. However, the probability of pair-bond termination tends to increase in the oldest age-classes because of elevated levels of adult mortality (Coulson and Thomas 1983, Bradley *et al.* 1995), and the Arctic skua population on Foula does appear to include many quite old individuals.

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Chapter Seven. Individual quality and its effects on Arctic skua reproduction on Foula

7.1 Introduction

Recently, results from long-term studies of seabirds have indicated marked differences among individuals in their lifetime reproductive success (Ollason and Dunnet 1988, Thomas and Coulson 1988, Mills 1989). Birds vary not only in the total number of chicks fledged during their reproductive careers, but even amongst those that do produce fledglings, there is strong evidence that the proportion of these that survive to recruit into future breeding populations, is quite variable (Newton 1989a). Longitudinal data on individual productivity would clearly be the ideal for looking at these differences in adult quality, but it is difficult to collect. An alternative approach is to pinpoint the characteristics of the individual that make the greatest contribution to reproductive performance in the short-term, and make the assumption that these will be important determinants of variation in lifetime reproductive success.

Individuals are frequently very consistent in laying date, clutch size, clutch volume and breeding success from year-to-year, especially if they retain the same partner (Brooke 1978, Coulson and Thomas 1985, Goodburn 1991). Repeatability analysis can be used to assess the consistency in such aspects of individual reproductive performance (Lessells and Boag 1987, Harper 1994), and comparisons of repeatability between different groups also offer the potential to separate the effects of the individual from those of its mate or territory (van Noordwijk *et al.* 1980, Newton and Marquiss 1984, Goodburn 1991). In addition, the value for repeatability sets an upper limit to heritability, the proportion of total phenotypic variance that can be attributed to additive genetic variance (Falconer 1981). Obtaining the necessary data to determine heritability of characters more directly, by parent-offspring regression, is laborious for populations of wild birds (Boag and van Noordwijk 1987), and especially so for seabirds which defer breeding for considerable numbers of years.

Although repeatability analysis can provide evidence that selection pressures exist that lead to individual consistency, it gives no indication which characteristics mediate differences in breeding performance. Both genetic and environmental factors contribute to repeatability according to the formula $r_i=(V_G+V_{Eg})/V_P$, where V_G represents genetic variance, V_{Eg} represents general environmental variance and V_P represents total phenotypic variance (Falconer 1981). This equation excludes special environmental variance or V_{Es}, the "within-individual variance arising from temporary or localised circumstances" (Falconer 1981). Variation in reproductive performance might therefore be a consequence of a combination of genetic factors, inequalities in body size, parasite burdens, energy reserves etc, or a function of breeding or foraging experience. In kittiwakes *Rissa tridactyla*, intrinsic differences in adult quality appeared to determine the ability to secure preferentially-located nest sites.

Female body condition is thought to be an important determinant of reproductive success, with those in better condition laying earlier and producing more, better quality, or larger eggs (Houston *et al.* 1983, Pietiäinen and Kolunen 1993). In species with sex role partitioning of breeding duties, particularly where the male courtship-feeds his partner during the pre-incubation stage, male foraging abilities may also influence timing of breeding and egg production (Nisbet 1973, Newton 1979, Newton and Marquiss 1984, Meijer *et al.* 1990). In addition, because of the direct influence of size on metabolism (Walsberg 1983), it has been suggested that skeletally smaller females could divert a greater proportion of their daily energy intake to breeding and so might become reproductively active ahead of larger birds (Downhower 1976, Murphy 1986). Presumably smaller males would also require less energy for maintenance metabolism and so be able to provide more prey items for their partner and offspring. Consequently male size would be important to productivity. Finally, selection on body size or condition related to the probability of overwinter survival might have more direct implications for lifetime reproductive success (Coulson *et al.* 1983, Monaghan and Metcalfe 1986, Schluter and Smith 1986).

This chapter compares the repeatability between 1992 and 1994 of several reproductive parameters recorded for Arctic skuas on Foula, particularly with regard to possible differences between the sexes and between pairs of different breeding status. It also examines the relationships between adult size, condition, and reproductive performance and survival. The heritability of timing of breeding and chick growth is estimated from parent-offspring regression (Falconer 1981), using data from chicks ringed during 1976-1989 and subsequently trapped as breeding adults. The implications of differences in heritability and repeatability between breeding variables are also discussed.

7.2 Methods

Data on laying date, clutch volume, chick growth, and the number of eggs laid, chicks hatched and chicks fledged, were recorded for marked adults breeding on Foula in 1992-1994 (see Chapter 1, General Methods). Colour-ringed birds were sexed either by observation, by discriminant analysis, or by association with an adult sexed by these techniques (Chapter 4). There were significant differences between 1992, 1993 and 1994 in clutch initiation date, but not in other breeding parameters (Chapter 2). Laying date was therefore expressed either in terms of calendar date - 'laying date' - or standardised as days relative to the mean in each year - 'relative laying date'.

Repeatability, or the intra-class correlation coefficient (r_I) can be estimated using variance components calculated from mean squares values obtained from one-way ANOVA (Lessells and Boag 1987, Harper 1994; see Chapter 4, Methods). Between-year repeatability was calculated for several breeding variables; laying date, relative laying date, clutch volume (two-egg clutches only) of first clutches, and chick growth indices (single/first hatched chicks and the mean in two-chick broods), including chicks in replacement clutches. Repeatability (within-year) was also calculated for clutch volume of first and replacement clutches (if both were of two eggs) produced during the same breeding season. Individuals were included in between-year ANOVAs if appropriate data were available from two or more years.

Repeatabilities were calculated for established partnerships (in which one or both members was colour-ringed in a previous season and where there was no evidence of a change of mate), and separately for birds that had definitely changed partner one or two seasons following marking (termed 'new' pairings). Because of extensive colour-ringing, virtually all partnerships involving birds breeding together for the first time (new pairs) were detected in 1994, and many were also detected in 1993 (see Chapter 6 for details). A number of birds marked in 1992 and included in the established group might have replaced their unmarked partner in 1993, which would have been undetected. However, there was no way of avoiding this complication without a considerable reduction in sample sizes, and it was unlikely the numbers involved would obscure any overall patterns (though they would tend to reduce any real differences).

It was not feasible to calculate repeatability of number of chicks fledged using variance components calculated from mean squares, as the type of data involved (with possible values only of zero, one or two) is inappropriate for one-way ANOVA. However, it is possible to compare the number of years in which particular individuals were successful with an expected frequency distribution based on the assumption that all pairs in the population have the same probability of success in a given year (Hatch 1988). In this study, complete data sets for number of chicks fledged in 1992, 1993 and 1994 were available for 35 adults colour-ringed in 1992 that were not known to have changed partner in the two following seasons i.e established pairs, as above. Three-year data sets existed for only eight birds that had changed partner, and so a comparison between established and new pairs was not possible.

When expected frequencies were calculated for all possible combinations of zero, one or two chicks fledged in each of the three years, i.e. none fledged in any year, one (or two) fledged in one, two or all three years, one in one year and two in one other year etc. (there are ten possible combinations), sample sizes in each expected frequency class were very small. For this reason, an alternative approach was adopted, simply to calculate the frequency distribution of the expected number of years successful, where success in any year was defined as the production of one or more fledglings.

The expected frequency distribution of number of successful years can be calculated by combining probabilities of success or failure in individual years (Hatch 1988). The probabilities of success in 1992, 1993 and 1994 (p_{92}, p_{93}, p_{94}), were equal to the proportions of all breeding pairs that successfully reared one or two chicks. In the population as a whole the proportion of pairs that were successful in 1992 was 117/148=0.79 (p_{92}), in 1993 it was 100/135=0.74 (p_{93}), and in 1994 it was 84/117=0.72 (p_{94}). The probabilities of failure (q_{92}, q_{93}, and q_{94}) were therefore $1\text{-}p_{92}$, $1\text{-}p_{93}$, and $1\text{-}p_{94}$, respectively. Therefore, the probability of failing in all three years, $P(0) = (q_{92} \times q_{93} \times q_{94}) = (0.21 \times 0.26 \times 0.28) = 0.0153$, of being successful in one year, $P(1) = (p_{92} \times q_{93} \times q_{94}) + (q_{92} \times p_{93} \times q_{94}) + (q_{92} \times q_{93} \times p_{94}) = (0.79 \times 0.26 \times 0.28) + (0.21 \times 0.74 \times 0.28) + (0.21 \times 0.26 \times 0.72) = 0.1403$, of being successful in two years, $P(2) = (p_{92} \times p_{93} \times q_{94}) + (p_{92} \times q_{93} \times p_{94}) + (q_{92} \times p_{93} \times p_{94}) = (0.79 \times 0.74 \times 0.28) + (0.79 \times 0.26 \times 0.72) + (0.21 \times 0.74 \times 0.72) = 0.4235$, and of being successful in all three years, $P(3) = (p_{92} \times p_{93} \times p_{94}) = (0.79 \times 0.74 \times 0.72) = 0.4209$.

Indices of body size and body condition (mass corrected for size and for stage of the season, if necessary) were calculated separately for colour-ringed adults of each sex (Chapter 4). Correlations were performed between these indices and relative laying date, clutch volume and chick growth in the season in which the condition index was calculated (not necessarily the year a bird was first captured). Body size and body condition were also compared between birds that had laid different sized clutches, and between those that subsequently hatched or fledged different numbers of chicks.

In addition to a (potentially) direct influence on the value of particular breeding parameters in a particular year, body size or body condition might show a relationship with individual consistency in laying date or clutch volume (these showed moderate to high repeatability - see Results). Correlations were therefore performed between size and condition, and the difference (in absolute terms) between the 1993 and 1994 values for laying date, relative laying date and clutch volume. The equivalent categorisation into male and female and established and new pairs were adopted as in the repeatability analyses.

Of all adults trapped on Foula in 1992-1994, 38 had been ringed there as chicks in previous years. Measurements of wing length and weight were available for 29 of these birds, which allowed an index of chick growth and an estimated hatching date (and also relative hatching date) to be obtained (see Chapter 1, General methods). Heritability (h^2) in timing of breeding can be calculated as twice the slope of the single parent-offspring regression (Falconer 1981), in this case using chick hatching date as a direct indicator of parental laying date. This is a reasonable assumption as there is little variation in the length of the incubation period (pers. obs.). However, laying date varies from year to year, although it is most consistent in established pairs (see Results). Values for (offspring) laying date were therefore excluded if the individual was known to be breeding together with its partner for the first time. This eliminated five birds altogether for which no datum from an established partnership was available. Several regressions were carried out. Hatching date and relative hatching date as a chick (i.e. parental values) were compared with respectively, mean laying date and earliest laying date, and mean relative laying date and earliest relative laying date as an adult during 1992-1994 (i.e. offspring value). In addition, the growth index of an individual when it was a chick (parental value) was compared with the mean growth index of the chicks they themselves reared in 1992-1994 (offspring values). Data from single or first hatched chicks only were included in the calculation of offspring mean values.

Late hatching date or poor growth as a chick might have a deleterious effect on post-fledging survival or the likelihood of recruitment. Arctic skuas in Shetland generally recruit at age four or five (O'Donald 1983). Some individuals ringed as chicks on Foula were recorded at Shetland colonies four years or more after they fledged, including 29 adults nest-trapped on Foula between 1992-1994, and 9 either found dead there in previous years or recovered (BTO ringing recoveries file) at another colony. The growth and hatching dates of these presumed recruits, representing less than 3% of all chicks ringed, weighed and measured between 1976 and 1989, were compared with the remaining chicks that were not known to have survived and recruited at any colony. Growth as a chick was also compared with size and body condition as an adult.

In addition, body size and body condition (if the latter was recorded in 1993) were compared between breeding birds that did or did not return in 1994. Because of small sample sizes for adults of each sex, weights of all trapped birds were included in a regression analysis with a common factor score for body size (obtained from principal components analysis) and number of days after post-laying included as independent variables, in order to create a common body condition index (see Chapter 1, General methods).

7.3 Results

Repeatabilities of laying date, relative laying date, clutch volume and chick growth indices are indicated in Table 7.1. Similar results were obtained when considering unstandardised laying date (i.e. calendar date) compared with relative laying date (days before or after the mean in that year), and also clutch volume, between-years compared with within-years. In general, either index of laying date showed moderate repeatability, clutch volume showed moderate to high repeatability and chick growth showed low or insignificant repeatability (according to Harper 1994). Established pairs had significantly repeatable laying dates, clutch volumes and chick growth indices. Females in new pairings showed moderate repeatability in clutch volume, but no significant repeatability in laying date or chick growth between years. Although males in new pairings also did not show significant repeatability in chick growth, by contrast they did not show significantly repeatable clutch volumes, but did show moderate repeatability in laying dates, and at a similar level to established pairs.

Differences between the observed and expected frequencies of the number of successful breeding attempts by established pairs during 1992-1994 is shown in Fig. 7.1. Although not statistically significant (χ^2_2=2.73, n.s.), it appears that more pairs did tend to be consistently unsuccessful i.e. never fledged a chick or fledged one/two chicks in only one year, or consistently successful i.e fledged one/two chicks in all three years, than might have been expected.

There was a significant negative correlation between male body condition and relative laying date i.e. the partners of males that were relatively heavy for their size had laid earlier in the season (Table 7.2, Fig. 7.2). There was no such relationship between relative laying date and body condition of females (recorded after clutch completion). However, females in better condition had laid clutches of larger volume (Fig. 7.3). Chick growth was unrelated to parental condition, but did correlate with female, but not male, body size. The number of eggs laid, and number of chicks subsequently hatched and fledged did not show a significant relationship with either adult size or body condition (Table 7.3).

Although results in Table 7.1 indicated that laying dates and clutch volumes were repeatable, and in Table 7.3 that each correlated with the body condition of one or other adult, there were no correlations between body condition and the difference (in absolute terms) between the 1993 and 1994 values for these variables (Table 7.4). These differences were also unrelated to variation in male or female body size.

Hatching date as a chick did not show a significant correlation with laying date as an adult regardless of whether mean or minimum, calendar or relative values were used in the comparison (Table 7.5, Fig. 7.4). Although not significant, the heritability of laying date was approximately 0.16-0.30, and of relative laying date approximately 0.56-0.63. By comparison, there was a significant correlation between parental and offspring values for chick growth, with a heritability value of approximately 0.69 (Table 7.5, Fig. 7.5).

Chicks that were known to have recruited into Shetland colonies grew significantly better than those of unknown fate (Table 7.6). Although they did not hatch earlier relative to the mean in their particular year, on average they did hatch on earlier calendar dates i.e. without correcting for annual variation. However, there were no correlations between growth or hatching date as a chick and body size or body condition as an adult (Table 7.7). Nor were there any relationships between body size and body condition of birds breeding on Foula in 1993 and the likelihood of returning there the following season (Table 7.8).

Table 7.1. Repeatabilities of breeding parameters recorded for marked Arctic skuas on Foula during 1992-1994.

Variable	Pair status	Sex	Mean squares[a]	ANOVA results	r_I
Relative laying date	Established	-	43.1, 12.0	$F_{65,102}=3.59$, $P<0.0001$	0.50
	New	Females	41.8, 60.7	$F_{13,19}=0.69$, n.s.	-0.15
		Males	106.6, 33.58	$F_{12,18}=3.18$, $P<0.02$	0.48
Laying date	Established	-	43.1, 13.8	$F_{65,102}=3.12$, $P<0.0001$	0.45
	New	Females	43.5, 63.8	$F_{13,19}=0.68$, n.s.	-0.16
		Males	113.6, 31.4	$F_{12,18}=3.61$, $P<0.01$	0.52
Clutch volume[b,c]	Established	-	89.4, 11.6	$F_{59,85}=7.69$, $P<0.0001$	0.73
	New	Females	57.6, 12.9	$F_{9,13}=4.47$, $P<0.01$	0.60
		Males	44.6, 27.8	$F_{11,16}=1.61$, n.s.	0.21
Clutch volume[b,d]	All birds	-	83.8, 10.2	$F_{17,18}=8.21$, $P<0.0001$	0.78
Chick growth index (single / first hatched)	Established	-	0.010, 0.006	$F_{57,76}=1.83$, $P<0.01$	0.26
	New	Females	0.017, 0.010	$F_{7,10}=1.62$, n.s.	0.22
		Males	0.012, 0.006	$F_{9,12}=2.08$, n.s.	0.33
Chick growth index (mean)[e]	Established	-	0.010, 0.004	$F_{28,35}=2.65$, $P<0.005$.	0.43

[a] - between groups, within groups [b] - two-egg clutches only,

[c] - between year values, [d] - within year values

[e] - sample sizes too low to compare males and females in new pairs

Table 7.2. Correlations between relative laying date, clutch volume (two-egg clutches only), chick growth, and body size and body condition of marked adults on Foula.

	Body size:		Body condition:	
	Female	Male	Female	Male
Relative laying date[a]	r_{103}=-0.00, n.s.	r_{74}=-0.07, n.s.	r_{96}=-0.01, n.s.	r_{72}=-0.32, P<0.01
Clutch volume	r_{96}=0.13, n.s.	r_{72}=-0.01, n.s.	r_{89}=0.28, P<0.01	r_{70}=-0.16, n.s.
Chick growth index (single / first hatched)	r_{91}=0.26, P<0.02.	r_{68}=0.20, n.s.	r_{87}=0.11, n.s.	r_{67}=0.01, n.s.
Chick growth index (two-chick-broods)	r_{58}=0.14, n.s.	r_{39}=0.01, n.s.	r_{55}=0.26, n.s.	r_{38}=-0.20, n.s.

[a] - $\log_{10}$ (relative laying date) used in the analysis.

Table 7.3. Body size and body condition of Arctic skuas in relation to the number of eggs laid, chicks hatched and chicks fledged on Foula.

		Body size index:		Body condition index:	
		Female	Male	Female	Male
Eggs	1	-0.20±0.30 (8)	-0.32±0.39 (2)	0.01±0.02 (7)	-0.08±0.04 (2)
laid:	2	0.02±0.10 (98)	0.04±0.12 (74)	-0.00±0.01 (91)	0.00±0.01 (72)
T-test		$t_{104}=-0.58$, n.s.	-	$t_{96}=0.60$, n.s.	-
Chicks	0,1[a]	0.01±0.18 (28)	0.04±0.22 (24)	-0.00±0.01 (26)	-0.01±0.01 (23)
hatched:	2	-0.01±0.12 (77)	0.02±0.13 (52)	0.00±0.01 (72)	0.00±0.01 (51)
T-test		$t_{103}=0.09$, n.s.	$t_{74}=0.08$, n.s.	$t_{96}=-0.29$, n.s.	$t_{72}=-0.66$, n.s.
Chicks	0	0.22±0.23 (13)	-0.08±0.25 (9)	-0.01±0.03 (10)	0.02±0.02 (7)
fledged:	1	0.10±0.17 (33)	0.04±0.19 (29)	-0.02±0.01 (33)	-0.01±0.01 (29)
	2	-0.11±0.16 (46)	0.11±0.17 (34)	0.01±0.01 (45)	0.01±0.01 (34)
ANOVA		$F_{2,89}=0.71$, n.s.	$F_{2,69}=0.15$, n.s.	$F_{2,85}=2.12$, n.s.	$F_{2,67}=0.88$, n.s.

[a] - data combined because very few pairs hatched no chicks

Table 7.4. Correlations between body size and body condition, and the absolute differences in laying date, relative laying date and clutch volume (two-egg clutches only) of Arctic skuas on Foula between 1993 and 1994.

	Laying date	Relative laying date	Clutch volume
Female body size	$r_{43}=0.11$, n.s.	$r_{43}=-0.01$, n.s.	$r_{35}=-0.03$, n.s.
Male body size	$r_{36}=-0.07$, n.s.	$r_{36}=-0.02$, n.s.	$r_{31}=0.02$, n.s.
Female body condition	$r_{41}=0.17$, n.s.	$r_{41}=0.04$, n.s.	$r_{34}=-0.04$, n.s.
Male body condition	$r_{35}=-0.24$, n.s.	$r_{35}=-0.13$, n.s.	$r_{30}=0.05$, n.s.

Table 7.5. Heritability of timing of breeding and chick growth of Arctic skuas on Foula - values in the table are correlation coefficients (*r*), P values and the slope (*b*) of the regression equation.

	Parental:		
Offspring:	Hatching date	Relative hatching date	Chick growth index
Mean laying date	r_{22}=0.14, n.s. b=0.15±0.23	-	-
Earliest laying date	r_{22}=0.09, n.s. b=0.08±0.19	-	-
Mean relative laying date	-	r_{22}=0.28, n.s. b=0.32±0.23	-
Earliest relative laying date	-	r_{22}=0.25, n.s. b=0.28±0.23	-
Mean chick growth index	-	-	r_{23}=0.48, $P<0.02$ b=0.39±0.15

Table 7.6. The mean chick growth index and hatching dates of Arctic skua chicks ringed on Foula between 1976 and 1989 in relation to their fate

Status	Chick growth index	Hatching date	Relative hatching date
Recruited[a]	1.03±0.02 (n=38)	49.7±0.9 (n=38)	-1.4±0.8 (n=38)
Unknown	0.98±0.00 (n=1275)	52.0±0.2 (n=1298)	0.0±0.1 (n=1298)
	T-test t_{1311}=2.91, P<0.005[b]	T-test t_{1334}=2.65, P<0.01[c]	T-test t_{1334}=1.74, n.s.[b]

[a] - birds trapped or recovered at any Shetland colony aged four or more

[b] - √, or [c] - inverse transformed data used in analysis

Table 7.7. Correlations between body condition (growth index) and hatching date as a chick, and body condition and body size as an adult.

			Chick:		
Adult:		n	Growth index	Hatching date	Relative hatching date
Body condition:	Female	10	*r*=0.15, n.s.	*r*=-0.13, n.s.	*r*=-0.18, n.s.
	Male	15	*r*=-0.03, n.s.	*r*=-0.04, n.s.	*r*=-0.13, n.s.
	All birds	28[a]	*r*=0.11, n.s.	*r*=-0.05, n.s.	*r*=-0.12, n.s.
Body size:	Female	10	*r*=0.15, n.s.	*r*=-0.32, n.s.	*r*=-0.32, n.s.
	Male	15	*r*=0.32, n.s.	*r*=-0.24, n.s.	*r*=-0.32, n.s.
	All birds	28[a]	*r*=0.19, n.s.	*r*=-0.24, n.s.	*r*=-0.14, n.s.

[a] - three birds were of unknown sex

Table 7.8. The relationship between body size and body condition of adults breeding on Foula in 1993 in relation to whether or not they returned there in 1994.

		Absent 1994	Present 1994	T-test results
Body size	Male	-0.11±0.47 (5)	0.19±0.15 (52)	t_{55}=-0.06, n.s.
	Female	-0.11±0.28 (10)	0.07±0.13 (63)	t_{71}=-0.52, n.s.
	All birds[a]	0.07±0.24 (17)	0.06±0.09 (127)	t_{142}=-0.01, n.s.
Body condition	Male	0.03±0.02 (4)	-0.02±0.01 (39)	t_{41}=1.73, n.s.
	Female	-0.02±0.02 (4)	0.00±0.01 (39)	t_{41}=-0.68, n.s.
	All birds[a]	0.00±0.02 (9)	-0.02±0.01 (86)	t_{93}=0.69, n.s.

[a] - not all birds were sexed.

Fig. 7.1. Observed and expected frequencies of the number of successful breeding attempts by Arctic skua pairs on Foula during 1992-1994 (pairs with 0 or 1 successful attempts pooled because of small expected frequencies).

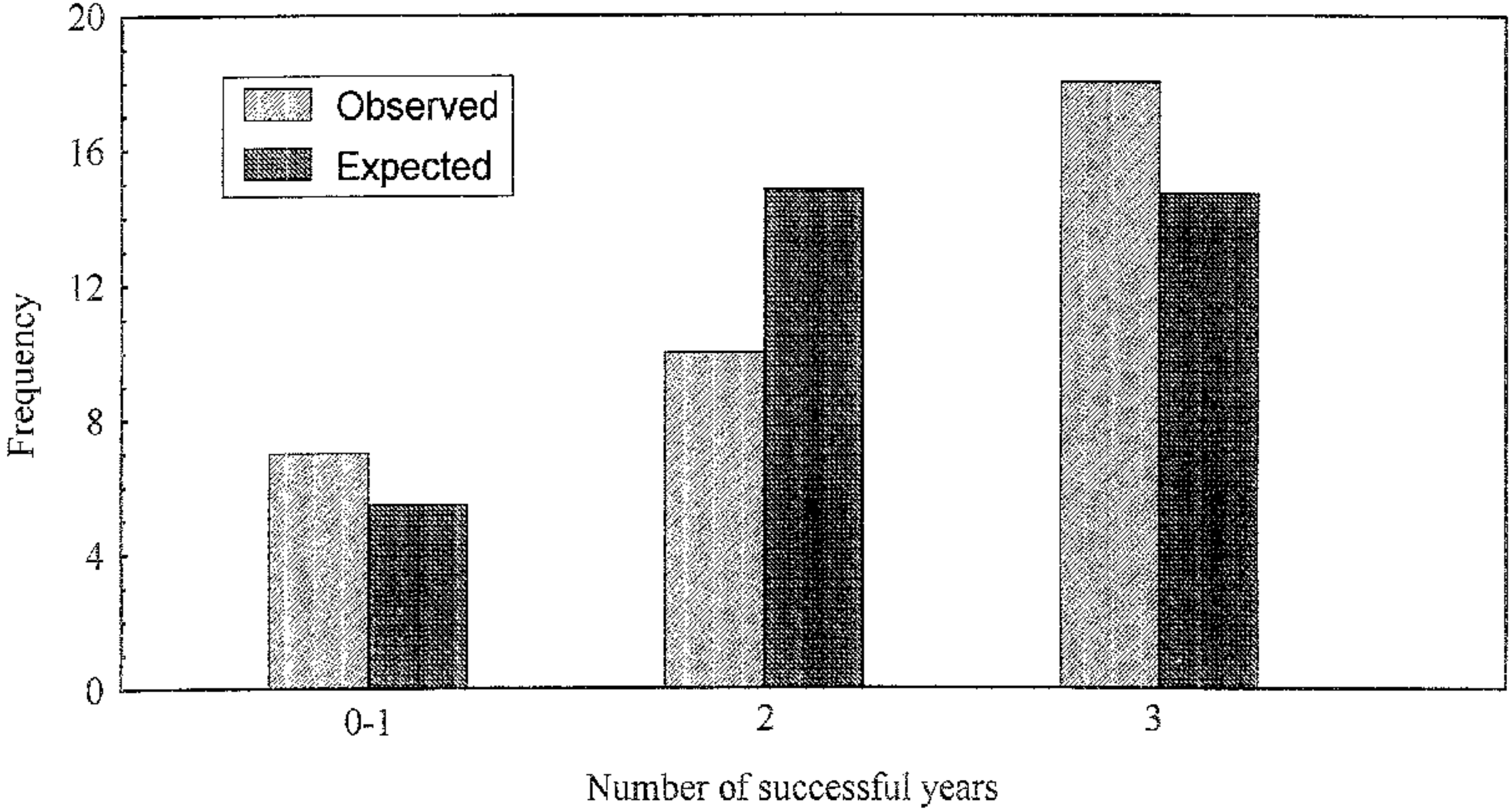


Fig. 7.2. The relationship between timing of breeding and male body condition.

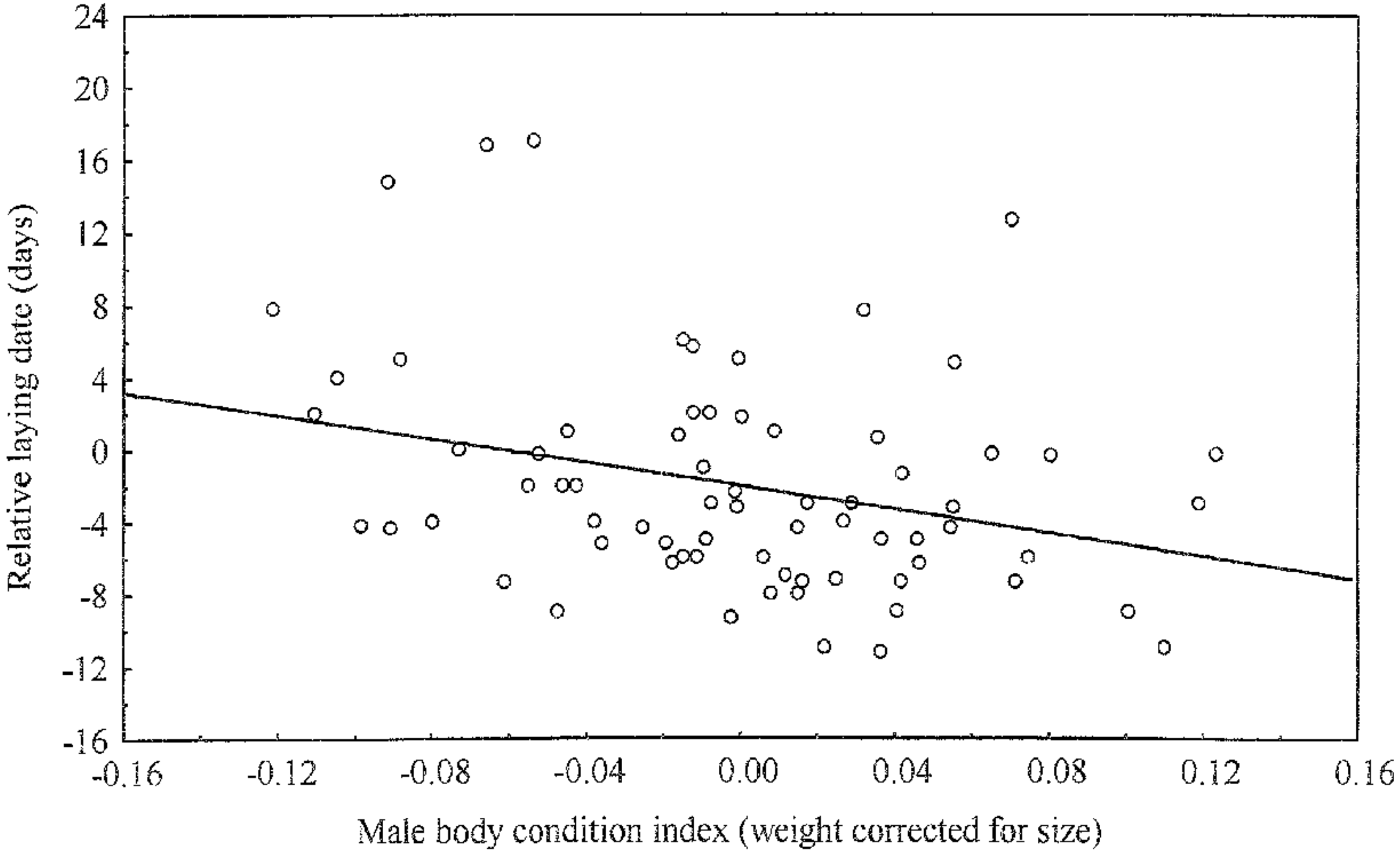


Fig. 7.3. The relationship between clutch volume of two-egg clutches and female body condition.

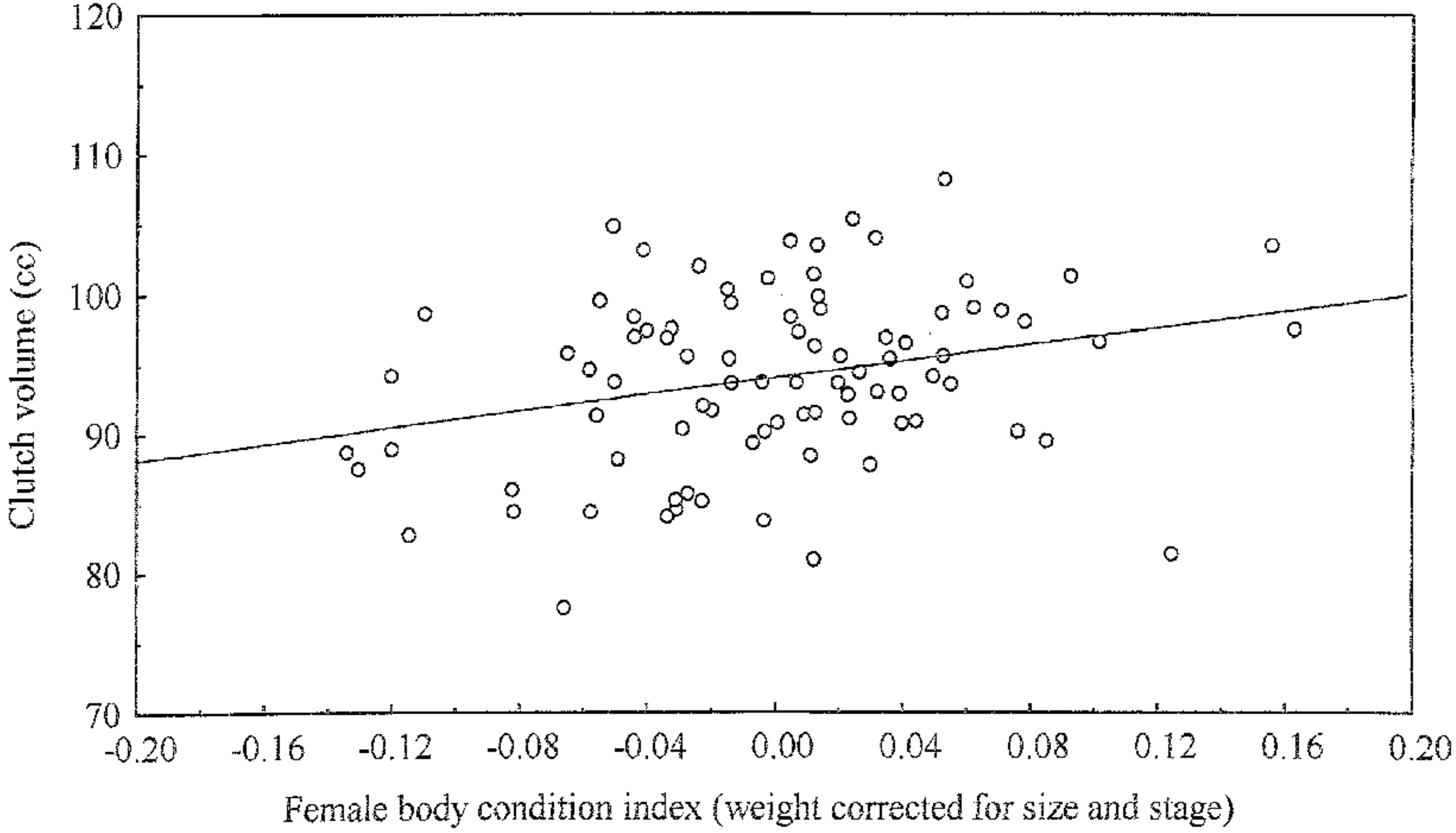


Fig. 7.4. The relationship between parental and offspring values for relative timing of breeding.

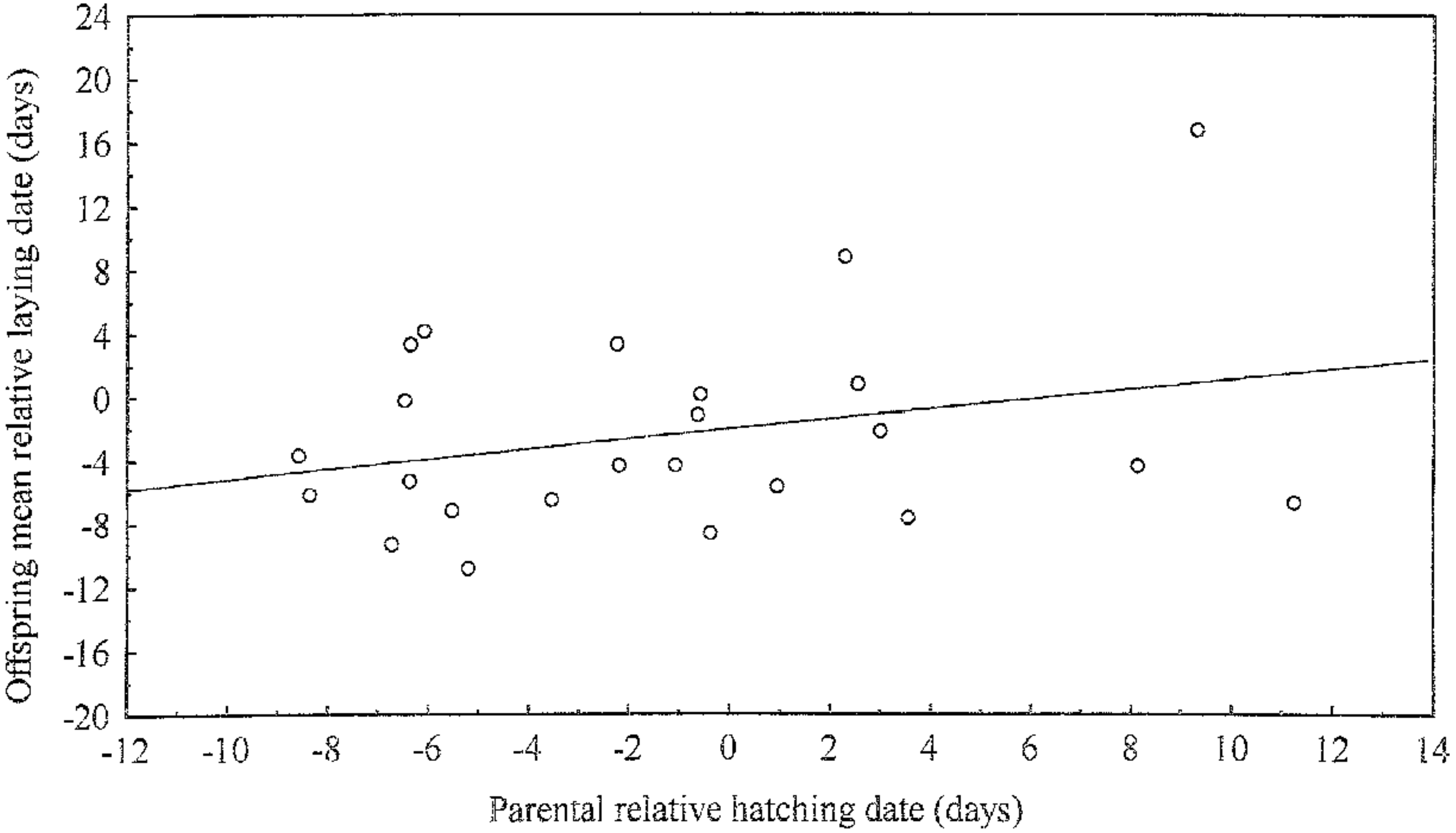
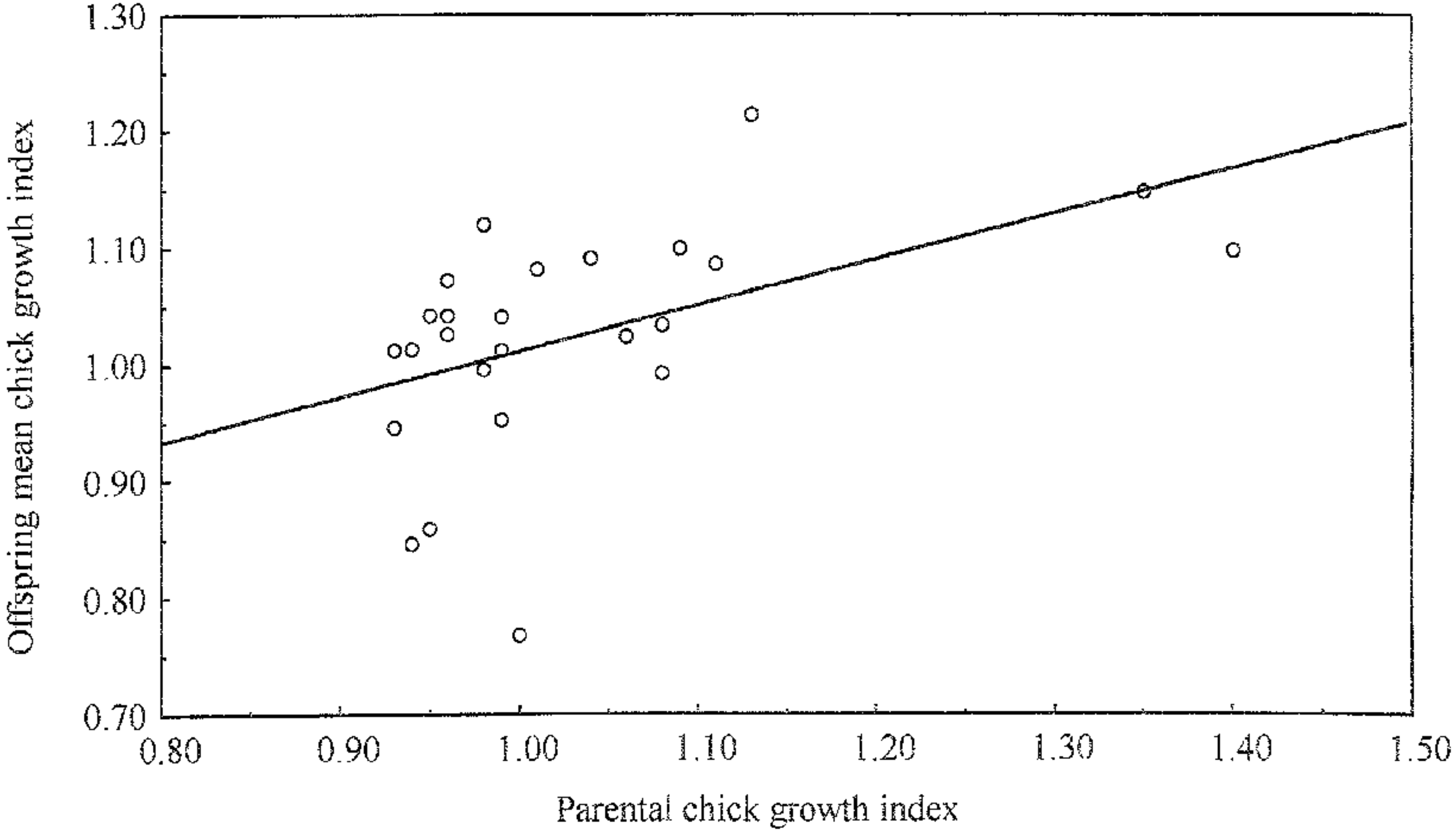


Fig. 7.5. The relationship between parental and offspring values for chick growth index on Foula.



7.4 Discussion

7.4.1 *Repeatability of breeding parameters and the influence of body condition*

Although repeatability is rarely calculated, individuals of many seabird species do appear to show consistency in some aspects of reproductive performance, particularly in laying date, which often correlates in consecutive years (Shaw 1986, Ollason and Dunnet 1988). Consistency in reproductive performance has sometimes been equated with adult quality (e.g. Coulson and Thomas 1985, Goodburn 1991), but for example, a bird that always laid the same number of low volume eggs on the same date late in the season and never fledged any chicks would be extremely consistent, but not of high quality.

Individual Arctic skuas breeding on Foula between 1992-1994 tended towards consistency in reproductive success, although a larger sample size would probably have been necessary for statistical significance. Relatively few seabird studies have examined individual consistency in breeding success, but those that have also tend to find that some pairs are more or less frequently successful at hatching or fledging chicks (Coulson and Thomas 1985, Hatch 1988, Ollason and Dunnet 1988, but see Shaw 1986, Weimerskirch 1990). The calculation of repeatability quantifies the proportion of overall phenotypic variation that can be explained by consistent differences among rather than within individuals (Lessells and Boag 1987). Arctic skuas on Foula showed significant repeatability in timing of breeding (with standardised and calendar date giving comparable results), clutch volume (both within- and between-seasons) and chick growth. The lower values for repeatability of breeding variables recorded for new, in comparison with established, pairs can be attributed to the poorer general performance of adults that are breeding together for the first time (Chapter 6).

Overall, repeatability of laying date in Arctic skuas on Foula was moderate between 1992 and 1994, and compares well with values recorded in some other studies (Table 7.9). Repeatability of clutch volume also fell within the range of typical values of 0.56-0.86 recorded in most species, although it should be noted that many of the estimates are based on repeatabilitity of egg volume within clutches (Boag and van Noordwijk 1987, van Noordwijk 1987, Hendricks 1991). There are few published repeatabilities for chick growth, but it was possible to calculate an approximate value (Lessells and Boag 1987) for the repeatability of fledging weight in Manx shearwater *Puffinus puffinus*, from data in Brooke (1986). This gave a value $r_{\text{approx}} = 0.28$ for chicks raised by 56 unchanged pairs in different years, which is similar to the values for repeatability of chick growth indices in this study. Relatively low repeatabilities for chick growth presumably indicate that strong environmental components, such as annual variation in food availability have an important influence.

The degree of repeatability in laying date was similar for established pairs and for males in new pairs, but was not significant for females in new pairs. It would therefore appear that an attribute of the male, rather than his partner, determines the timing of breeding. Male Arctic skuas tend to retain the territory after death or divorce, whereas females are much more likely to move (Chapter 6). One potential explanation for the variation in repeatability of timing of breeding might have been inequalities in territory quality. In some species, there is considerable variance in prey availability among territories, and consequently differences in repeatabilities arise depending on whether the breeding territory is retained from year to year (Newton and Marquiss 1984, Goodburn 1991). In magpies *Pica pica*, the influence of territory quality appears to be mediated via the male (Goodburn 1991). The repeatability in breeding date at the same territory with a different female was low (r_i=0.19), whereas at the same territory with a different male, it was even lower (r_i=0.06), and not significant . However, Arctic skuas obtain little or none of their food from breeding territories, and there were no apparent effects of territory density or location on laying date or clutch volume in 1992-1994 (Chapter 5), so this seems an unlikely explanation.

It appears that laying date in sparrowhawks *Accipiter nisus*, and tawny owls *Strix aluco*, raptors with relatively high mate and site fidelity, was determined primarily by male rather than female quality (Table 7.9), perhaps related to the greater probability that males will retain the territory from year-to-year (Newton 1979). By contrast, in Tengmalm's owl *Aegolius funereus*, there was no significant repeatability in laying date for either sex (Korpimäki 1990). This was assumed to be a consequence of selection for considerable phenotypic plasticity in this species which lives in an environment where the annual abundance of voles, its principal prey, varies dramatically. In most raptors, males vary in their ability to deliver sufficient prey items to their partner during the pre-laying phase, and this influences the date at which she is able to lay (Newton 1979, Meijer *et al.* 1990). Although female Arctic skuas still forage for themselves prior to egg-laying, the male performs a considerable amount of courtship feeding, both before and after the eggs are laid, a pattern common to most skua species (Furness 1987). Disparities between males in foraging abilities would therefore seem a plausible explanation for the stronger effect of male rather than female quality on laying date, especially as it appears that males that were in better body condition later in the season were those whose partners had laid earlier. This of course need not contradict the requirement for males in general to have a lower wing loading than females as a consequence of the sex-role partitioning of breeding duties (Chapter 4).

By contrast, repeatability of clutch volume was high for all females, regardless of whether they were in established or new pairs, but not significant for males in new partnerships. Female rather than male quality thus appeared to have most influence. There was also a positive correlation between clutch volume and female body condition, a pattern common to many bird species (Loman 1984, Murphy 1986, Meijer *et al.* 1990, Pietiäinen and Kolunen 1993 but see Meathrel *et al.* 1993). Male quality must therefore be important in initially providing sufficient food to get his partner into reproductive condition. In some species, only females that have attained a certain threshold weight will attempt to breed (Shaw 1986, Weimerskirch 1992). However, the volume of the eggs produced by the female was determined by other, more intrinsic factors, which might be the ability to store the resources for egg production (which may not simply be a function of skeletal size, as clutch volume did not correlate with female body size). Egg size can be constrained by the availability of specific nutrients at the time of clutch formation (Bolton *et al.* 1992), and egg quality has been shown to be related to female protein, but not fat reserves (Houston *et al.* 1983). The evidence that egg volume tends to show high repeatability and heritability suggests that environmental factors (which in this case would include the foraging ability of the male) have relatively little influence in comparison with a strong genetic component (Falconer 1981, Boag and van Noordwijk 1987).

7.4.2 *Heritability of timing of breeding and chick growth*

Repeatability of a trait represents the potential upper limit to heritability (Falconer 1981). Heritability can also be estimated from the slope of the regression of offspring versus mean parental value or, more commonly, twice the slope of the offspring value regressed on one parent (Falconer 1981). Although the regression of parental and offspring values for timing of breeding (laying and hatching date, respectively) was not significant for the sample of 24 Arctic skuas, the estimated value of heritability from the gradients of the regression ranged from 0.16-0.30 for calendar date, and 0.56-0.63 for standardised breeding date. However, these latter values exceed slightly the repeatability of relative laying date in breeding adults, and are therefore likely to be overestimates. The Arctic skua is one of the few species for which there is already a published value for heritability of breeding date, from a sample of 22 Arctic skuas breeding on Fair Isle (O'Donald 1983). The criterion for the inclusion of offspring values differed from this study as that analysis was restricted to initial hatching dates of individuals in new partnerships, and included two birds twice in the regression. The heritability value of 0.85 obtained was even greater than that obtained for Arctic skuas on Foula, and is probably also an overestimate unless the repeatability of laying date is much higher on Fair Isle than it is on Foula (and incidentally than it is in other species - Boag and van Noordwijk 1987, and see Table 7.9). Heritability values for clutch initiation date obtained from separate study populations of great tits *Parus major*, similarly showed poor agreement, and the suggestion was that estimates should be regarded with caution unless samples are sufficiently large to ameliorate the effect of outliers (van Noordwijk 1987).

Heritability estimates for chick growth of Arctic skuas on Foula were marginally higher than repeatability values, and were presumably also overestimates. However, there was clearly strong selection related to both chick hatching date and growth acting between fledging and recruitment, although there were no apparent influences of these variables on size or body condition once the individual had attained maturity. In the majority of studies on post-fledging mortality in seabirds, survival generally appears related to fledging date (Nisbet and Drury 1972, Harris *et al.* 1992, Spear and Nur 1994) and to weight at fledging or the mean growth rate of particular cohorts (Perrins *et al.* 1973, Jarvis 1974, Hamer *et al.* 1991), although the latter was apparently not true for auks (Lloyd 1979, Harris and Rothery 1985, Harris *et al.* 1992).

Repeatability or heritability of laying date and some other measures of reproductive performance such as clutch size and chick growth rate are commonly relatively low whereas those for egg volume tend to be much higher (Boag and van Noorwijk 1987, this study). Non-significant parent-offspring regressions in laying date have been recorded in several species (Newton and Marquiss 1984, Boag and van Noordwijk 1987, Mills 1989). This pattern was apparent here and fits with the expectation that traits which are the most strongly related to fitness should show little or no heritability for otherwise they would have long ago been incorporated by selection (Falconer 1981, but see Price *et al.* 1988). For example, most studies find that although egg volume may initially have some influence on chick size or hatching weight, parental quality is invariably much more critical in terms of the likelihood of chick survival (Ollason and Dunnet 1986, Reid and

Boersma 1990, Bolton 1991, Meathrel *et al.* 1993). In addition, there may be little apparent genetic basis for variation in lifetime reproductive success, i.e. no correlation between the number of chicks fledged by the parent during its lifetime and that fledged by its offspring (Gustafsson 1989, Mills 1989, Newton 1989b), and that is undoubtedly one of the better indices of fitness.

4.4.3 *Influence of adult size on reproductive performance, and of size and condition on mortality*

Despite the influence of adult body condition on laying date or clutch volume, neither body size nor condition was of any consequence in terms of the number of chicks hatched or fledged. Female size was correlated with the growth rate of single/first-hatched chicks, which might suggest a slight inherited component of body size. Adult size and condition were unrelated to the difference in laying date, relative laying date and clutch volume between 1993 and 1994, despite the significant repeatability of these variables. Although it has been suggested that smaller females might initiate reproduction at an earlier date (Downhower 1976), several studies have found no effect or a trend in the opposite direction (Loman 1984, Wiggins 1991, this study). This inconsistency can probably be attributed to inter-specific differences in the ability of females to store reserves for egg production (Loman 1984).

The size or body condition of Arctic skuas was not related to the likelihood of overwinter survival. This is probably not surprising as the analysis was only carried out across a single non-breeding season, and selection on body size may act most strongly only when overall mortality is high (Schluter and Smith 1986). In addition, an analysis of mortality patterns in herring gulls *Larus argentatus*, by Monaghan and Metcalfe (1986) found strong evidence of stabilising selection i.e. both extremes in the size distribution experienced greater mortality than intermediate-sized birds, although at different times of the year. This would be impossible to test with the small sample available in this study. The lack of any correspondence between survival and body condition could be attributable to the collection of body mass data predominantly during incubation, given that condition at the end of the season is more likely to show a relationship with mortality (Coulson *et al.* 1983, Monaghan and Metcalfe 1986).

The number of years in which breeding is attempted tends to have the greatest influence on lifetime reproductive success (Coulson and Thomas 1985, Ollason and Dunnet 1988, Thomas and Coulson 1988, Newton 1989a, Pietiäinen 1989). In addition, longitudinal studies mostly indicate a positive relationship between lifespan and fecundity, especially early in an individual's reproductive career (Thomas and Coulson 1985, Coulson and Thomas 1988, Bradley *et al.* 1989, Wooller *et al.* 1990, but see Ollason and Dunnet 1988, Pugesek and Diem 1990). The results presented in this chapter for Arctic skuas on Foula indicated that over the course of three seasons there was consistency in laying date, clutch volume, chick growth, and possibly breeding success, and also showed that adult body condition was an important determinant of laying date and clutch volume. In a study on red-billed gulls *Larus novaehollandiae scopulinus*, the heaviest females hatched more eggs, and the heaviest males fledged more chicks during their lifetime (Mills 1989). In addition, the birds that laid earlier produced the most surviving young, and in the case of females also lived the longest. Parallels between the conclusions of the present study of Arctic skuas on Foula between 1992-1994, and these long-term results underline the relevance of the shorter-term findings to probable variation in lifetime success related to individual quality.

Table 7.9. Repeatabilities of timing of breeding recorded in other species.

Species	Sex	r_i value	Source
Tengmalm's owl	Female	0.03[a]	Korpimäki (1990)
Aegolius funereus	Male	-0.21[a]	
Tawny owl	Female	0.23	Wallin (1988)
Strix aluco	Male	0.52	(cited in Korpimäki 1990)
Ural owl	Female	0.21[b]	Pietiäinen (1989)
Strix uralensis			
Kestrel	Female	0.00[a]	Meijer *et al.* (1988)
Falco tinnunculus			
Sparrowhawk	Female	0.23[c]	Newton and Marquiss (1984)
Accipiter nisus	Male	0.63[c]	
Magpie	Male	0.54[d], -0.34[a,e]	Goodburn (1991)
Pica pica	Female	0.54[d], -0.09[a,e]	
Guillemot	Female	0.49	Wanless and Harris (1988)
Uria aalge			

[a] - non-significant

[b] - standardised value (controlling for variation due to annual and/or age effects)

[c] - corrected values from Lessells and Boag (1987)

[d] - birds that retained territory between seasons

[e] - birds that changed territory between seasons

7.5 References

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Chapter Eight. The demography of Arctic skuas on Foula: a simple model

8.1. Introduction

In recent years, the results of long-term ringing studies and the monitoring of colony productivity have provided estimates of several important demographic parameters for a number of seabirds (Croxall and Rothery 1991, Jouventin and Weimerskirch 1991). In general, changes in adult survival are assumed to have most influence on population growth rates (Croxall and Rothery 1991). However, fluctuations in the size of a breeding colony in theory can arise from a wide variety of sources. For example, in one study of Northern fulmars *Fulmarus glacialis,* variation in net recruitment (a complex parameter which involved recruitment of new breeders as well as intermittent breeding and emigration of established birds) was of greater relevance to annual fluctuations in colony size than were changes in adult mortality (Ollason and Dunnet 1983).

Breeding numbers in any year are a function of the balance between mortality of breeders from the previous year, the incidence of nonbreeding by established birds, and recruitment of new birds from within or outwith the colony. Movement of adults after establishment also influences colony size although this appears to be a limited component in most seabirds' population dynamics (Ainley *et al.* 1990, Harris and Wanless 1991, Prince *et al.* 1994) with some exceptions notably amongst the terns (Cuthbert 1988). These demographic parameters are in turn influenced by numerous factors including food abundance, the availability of suitable breeding sites, predation, or parasite pressure, acting both at the colony and also during the non-breeding season (Croxall and Rothery 1991, Cairns 1992). For example, the recruitment rate is likely to depend on the productivity of the colony as a whole in previous years, juvenile survival prior to establishment, and the degree of philopatry shown by fledglings from different colonies. Juvenile survival may itself have been heavily influenced by food availability during the chick-rearing period (Perrins *et al.* 1973, Hamer *et al.* 1991, Chapter 7), and immigration rates may vary depending on the attractiveness of different colonies (Duncan 1978, Porter and Coulson 1987, Ainley *et al.* 1990).

Monitoring of Arctic skuas breeding on Foula indicates considerable long-term fluctuations in population size. This chapter attempts to describe this temporal variation in breeding numbers using a simple mechanistic model. Initial values for input parameters in the model, including adult mortality rate, survival to recruitment and fecundity (number of female chicks fledged per female holding territory) were estimated from data collected during 1992-1994. Observed changes in the size of the breeding population were then interpreted in the light of the predicted rates obtained by varying these input parameters. In addition, the importance of immigration in population dynamics is discussed.

8.2. Methods

Initial estimates of the value of each parameter to be used in the model were obtained as follows

8.2.1 *Adult mortality rate*

There was no information available on survival of Arctic skuas on Foula prior to the early 1990s. Between 1992-1993, a total of 154 breeding birds were trapped on Foula and each was fitted with a unique combination of four plastic colour-rings, two on each tarsus. Four other birds were individually-recognisable in 1992; one adult missing its right leg below the tibiotarsal-tarsometatarsal joint, one with unique white wing patches (this bird was colour-ringed in 1993) and two which started the 1992 breeding season with two plastic colour-rings (probably as a result of trapping that took place on Foula in 1975), one of which was killed by the plane during the 1992 season. Adults were sexed by observation, by discriminant analysis or by association with an individual sexed by these techniques (Chapter 4).

Throughout the 1993 and 1994 breeding seasons, all territories and the two small club-sites on the island were checked on numerous occasions for the presence of individuals marked in previous years. All marked birds that defended a territory in either year will have been recorded, and it is also extremely unlikely that any bird that spent more than perhaps a week on Foula as a non-breeder will have been missed. In the calculation of survival rates, all individuals were considered to have been marked at the start of the breeding season in the year of first capture, and all those that were recorded the following year to have survived. By this means any that died prior to the close of the first season in which they were marked were included in the mortality figures.

8.2.2 *Number of chicks fledged*

Information on the survival of chicks to one week after their probable fledging date was included in this parameter in order to take account of mortality occuring during the fledging period (see Chapter 1, General Methods). Accurate figures for the proportion of territory-holding pairs that laid, mean clutch size, breeding success and post-fledging survival to a week were available from data collected for the colony as a whole during 1992-1994 (Chapter 1, General Methods).

8.2.3 *Age at recruitment*

Unless all birds in the breeding population are marked, thereby facilitating the detection of individuals breeding for the first time, age at recruitment is clearly a difficult parameter to estimate. O'Donald (1983) provided a table detailing the distribution of ages at maturity of Arctic skuas on Fair Isle during two periods, 1948-1959 and 1970-76. Although it is claimed that virtually all birds were marked by the close of every breeding season, comparisons between the size of the breeding population and sample sizes provided elsewhere for calculation of adult survival rates, clearly indicate that 27, 11, 20 and 33 birds remained unmarked in each year, 1973-1976 respectively. An even smaller proportion of the population would have been colour-ringed prior to 1973 when JWF Davis began intensive trapping of breeding adults. Additionally, the relative proportion of recruits breeding at each age was not corrected for bias due to variation in ringing effort in previous years. It is hardly surprising that no birds older than seven were recorded breeding for the first time during 1970-1976 as, with the exception of 1966 when 21 chicks were ringed, a maximum of only ten chicks were ringed annually from 1965-1970 (see Table 8.7). However, there is no information on age at recruitment on Foula during any period. Therefore while bearing in mind the reservations mentioned above, because from the Fair Isle data it appears that many more birds do seem to recruit at age four and five than at age three or six, the former two values were used in calculations.

8.2.4 *Survival to recruiting age*

This was initially estimated independently for each cohort of chicks ringed between 1972-1983 using information on the numbers of birds recorded breeding on Foula in 1994. Cohorts fledged in subsequent years were not included as from 1984 chick growth began to be affected by reduced sandeel availability (Chapters 2 and 3). The number present in 1994 from each cohort was corrected for the proportion of all known-age philopatric birds that had been trapped by 1994 (34/45 - see Chapter 6) and for mortality acting since recruitment (assuming a constant annual rate equal to the 1992-1994 mean value), based on the assumption that birds recruit aged either four or five. The size of each cohort of chicks ringed was corrected for mortality acting between ringing and one week post-fledging. This was done on the assumption that 76% of chicks ringed at two weeks of age survived to one week post-fledging (1992 and 1993 data) as in previous years most chicks were ringed when approximately half-way through the pre-fledging period. Each corrected value for the probable number of recruits was expressed as a proportion of the estimated number of surviving chicks at one week post-fledging.

8.2.5 *Modelling changes in Arctic skua numbers*

The Arctic skua colony was censused in most years by counting apparently occupied territories (Furness 1982). Changes in population size were expressed in terms of the instantaneous rate of natural increase, or r (O'Donald 1983, Stearns 1992). Over a specified interval of time, the rate of population growth, $\lambda = N_t / N_{t-1} = e^r$, where N_t is the number of females in the breeding population in year t. The rate of change of the population expressed as a percentage is then 100 x (e^r-1). Rates of population growth can be measured by λ or r, or by the increase or decrease over the period of one generation, $R_0 = N_{t+T} / N_t = e^{rT}$, where T is the mean duration of each generation (O'Donald 1983). As R_0 is the average number of offspring that an individual contributes to the next generation it can be calculated by the equation $R_0 = \Sigma_x l_x b_x$ where l_x is the probability of surviving from hatching to the beginning of age-class x, and b_x is the expected number of offspring for a female in age-class x. The value of r can be estimated by a power series (see O'Donald (1983), Appendix A for details). If $R_0 = \Sigma_x l_x b_x$, $R_1 = \Sigma_x x l_x b_x$ and $R_2 = \Sigma_x x^2 l_x b_x$ etc. If r is a small quantity, terms in r^2 and higher powers of r can be neglected, in which case $r = \ln (R_o) / (R_1 / R_o)$. A more accurate r can be obtained using additional terms of the power series, such that

$$r = \frac{-1 + [1 + 2(1 - R_0 R_2 / R_1^2) \ln(R_o)]^{0.5}}{R_1/R_0 - R_2/R_1} \qquad \text{(O'Donald 1983).}$$

Assuming that (i) individuals fledge the same number of chicks in every year after they recruit, (ii) that the adult mortality rate remains constant from year-to-year, and (iii) that all birds recruit at the same age then $R_0 = (bs_j) / m_a$, $R_1 = (bs_j) \times [(k\text{-}1)/m_a + 1/m_a^2)$, and $R_2 = (bs_j) \times [(k\text{-}1)^2/m_a + (2k\text{-}3)/m_a^2) + 2/m_a^2]$, where b is the expected number of female chicks per breeding female, s_j is the proportion of fledged chicks that return to the colony to breed, m_a is the annual adult mortality rate, and k is the age at recruitment. This model is clearly based on a number of simplifying assumptions, and also takes no account of movement between colonies. However, it does have the advantage that it allows r to be estimated from demographic data and also from theoretical values, for a comparison with those observed.

Changes in population size were also examined by adopting a regression approach using the non-linear modelling module of SYSTAT (the programming was done by Dr. Simon Wood at St Andrews University). This model included a term for immigration of birds from other colonies. The model was fitted to the folowing equation (on the assumption that birds recruit aged four years)

$$N_t = bS_J(t)N_{t-4} + (1-m_a)N_{t-1} + I,$$

where N is the number of pairs in each year, t, t-1 and t-4 (using interpolated values for 1983 and 1984), I is the number of immigrant pairs (set at 0-18 pairs), and survival to recruitment, $S_J(t)$, is allowed to vary with time. $S_J(t)$ was constrained to lie only between 0 and 1, according to $S_J = e^y / (1+e^y)$, where y = a + bt + ct^2 + dt^3 and t = year-77. Adult mortality was set at the 1992-1994 value (0.136), and fecundity was assumed to equal the 1992-1994 value of 0.45 (see Results) for all years prior to 1983, and also 1985, but was set at 0.075 in 1984, 0.315 in 1986, 0.105 in 1987, 0.075 in 1988, 0.065 in 1989 and 0.045 in 1990 (Chapter 2). These latter values were half the observed number of chicks fledged per pair from 1986-1990 (Chapters 2 and 3), with an estimated value for 1984 on the assumption that because chick growth in that year was close to the 1988 value, breeding success would also have been similar (Chapter 3).

8.2.6 *Immigration and emigration*

Information on all notified recoveries of Arctic skuas ringed in the British Isles was obtained directly from the BTO. This file was checked to ensure that it included details of immigrant birds and birds found dead on Fair Isle which are provided in the annual *Fair Isle Bird Observatory Reports*. All recoveries of chicks at their natal colony prior to the following breeding season were excluded from further analyses, as were three recoveries in the following April/July which had no details or were 'leg only'.

Additional information was available on recoveries of Arctic skuas ringed at Foula and Fair Isle which were younger than the retrap age and which had not moved more than 5km, about which the BTO would not have been informed. These were records of ringed Arctic skuas found dead on Foula or trapped as breeding adults, mostly in 1992-1994. For Fair Isle, this information was less readily available but was estimated from the following information. O'Donald

(1983) states that 38 chicks fledged between 1973-1977 had returned to Fair Isle to breed by 1979. In 1977, the final year in which a large number of breeding adults were trapped, the number of birds of different ages present at the colony was indicated in the annual observatory report. This included 18 adults that had fledged prior to 1973 - eight in 1972, three in 1971, four in 1970, two in 1969 and one in 1968. Previous reports (1973-1976) list fewer birds from these cohorts present as breeders, with the exception of a single bird fledged in 1965. On the working assumption that with the exception of the 1965 chick all those listed in the 1973-1976 reports were alive and breeding in 1977, then a total of 19 birds fledged between 1965-1972 were recovered on Fair Isle between 1968-1977. A further 15 birds from post-1975 cohorts (none from 1976) were found dead or trapped on Fair Isle in later years i.e. from 1980 onwards (BTO recoveries file and observatory reports). In total therefore, an estimated 38 + 19 + 15 = 72 chicks ringed at Fair Isle were later recorded at that colony up until 1993.

In order to correct for variation in ringing effort, RWF inspected all appropriate BTO ringing schedules for the years 1965-1991, and noted ring numbers of all Arctic skua chicks and adults and the ringing site. The total ringed was later counted for each colony in each year. As a check for the accuracy of this procedure, annual totals for Fair Isle were compared with those presented in observatory reports, and for Foula (1965-1982 only) with published totals in Furness (1983). In addition, the totals for all colonies in each year were compared with the BTO's own published figures in *Ringing and Migration*.

Recovery rates for chicks were calculated separately for each colony but all years from 1965-1990 were pooled. These included records of birds found dead or injured, as well as those trapped as breeding adults. It should be noted that this was not intended as a quantitative inter-colony comparison because of the extreme heterogeneity in retrapping effort. Recoveries of adults ringed in previous years were excluded as less durable aluminium rings were in use. Recoveries were grouped by age, distinguishing first-year, second-year, third-year and older birds. For the purposes of analysis, each chick was considered to have been ringed on 1 August, and those recovered within one calendar year from this date described as a one year-old/first-year bird, within two calendar years as a two year-old/second-year bird etc. As few three-year old Arctic skuas attempt to breed (O'Donald 1983), all recoveries of birds in the oldest age group were assumed to be of breeding adults. Some third year birds were trapped as breeding adults and these were also included in the 'presumed breeder' category in an analysis of the distribution of recoveries at or near an Arctic skua colony during the breeding season.

8.3 Results

8.3.1 *Adult mortality rate (m_a)*

No marked bird absent in 1993 returned to Foula in 1994. Of 78 marked adults in 1992, 66 i.e. 84.6% were present on Foula in 1993, and of 145 marked adults in 1993, 128 i.e. 88.3% were present on Foula in 1994. These figures were not significantly different (χ^2=0.32, n.s.), and indicated a mean annual survival rate of 86.4%. Although considerably fewer colour-ringed females (63/73=86.3%) than colour-ringed males (53/58=91.4%) in 1993 returned to Foula in 1994, this difference was not significant (χ^2=0.40, n.s.).

8.3.2 *Expected number of chicks fledged (b)*

Data on breeding statistics collected during 1992-1994 are shown in Table 8.1. On the basis of mean values, the expected number of female chicks per female holding territory that were likely to be alive at one week post-fledging = 0.5 x (0.968 x 1.90 x 0.608 x 0.809) = 0.45.

8.3.3 *Survival to recruiting age (s_j)*

The estimated proportions of chicks from cohorts fledged between 1972 and 1983 that survived from one week post-fledging to recruitment are indicated in Table 8.2. Survival to recruitment as calculated by this method was clearly quite variable. Mean estimates of survival to recruiting age were 21% and 18% depending on whether recruitment is assumed to occur at age 4 or 5 years.

8.3.4 *Modelling changes in numbers*

The number of occupied Arctic Skua territories on Foula increased to a peak in the late 1970s but then fell sharply over the next few years, continuing to decline until 1990 (Table 8.3, Fig. 8.2). There was a slight recovery in 1992 after which numbers again declined. In 1988 and 1990, there was strong evidence that established adults deferred breeding (Chapters 2 and 3), and it is also possible that in 1991 not all of these individuals (and possibly also potential new recruits) (re)joined the breeding population. If these fluctuations in breeding numbers are resolved into several phases, the values for r (the instantaneous rate of natural increase) were 0.19 per year for the increase between 1974-1976, -0.01 for the stable period from 1976-1979, followed by -0.06 per year for the steady decline from 1979-1987. Depending on the level of nonbreeding considered to have occured during the late 1980s, r was equal either to -0.07 per year for the decline between 1987-1991 and 0.20 for the increase from 1991-1992, or -0.01 per year over the entire period 1987-1992. From 1992-1994, r was equal to -0.09.

If adult survival, survival to recruitment and fecundity (number of female fledglings per female holding territory) were set at the 1992-1994 estimates of 86.4%, 21% or 18% (depending on whether birds are assumed to recruit aged four or five) and 0.45, r equals -0.03 or -0.04. This is considerably greater than the observed annual rate during the decline in the Arctic skua population from 1979-1987, and is much greater than r during the decline from 1992-1994, but is less than the value of r from 1987-1992. It is also far less than the value of r per year during the period when the population increased rapidly from 1974-1976.

It is possible to determine the effects of incremental changes in adult survival, survival to recruitment and fecundity on r while keeping the values of two of the three parameters constant (Table 8.4). This indicated that the rate of population increase on Foula from 1974-1976 (r = 0.19) was far greater than would be expected even if adult mortality more than halved (to 5%), survival to recruitment doubled or fecundity increased by 60%. It should be noted that it is not likely that fecundity varied a great deal on Foula prior to 1984. There is a close relationship between chick growth and number of chicks fledged per pair, and growth was 'normal' on Foula from 1976-1983 (Chapter 3). In addition, data on number of chicks fledged per pair indicate that productivity equaled approximately 0.90 chicks per pair even if chick growth exhibited minor fluctuations (Chapters 2 and 3). It is therefore hard to avoid the conclusion that very large-scale immigration must have occured during the mid-late 1970s.

The decline during 1979-1987 could, by contrast, have resulted from an adult survival rate 3-4% lower, a survival to recruitment rate of 14% or a fecundity value of 0.32-0.38 (0.64-0.76 chicks per pair) (Table 8.4). As mentioned above, this last possibility seems unlikely, and so presumably lower survival, either of adults or juveniles is responsible. Interestingly, while data are far from conclusive, mean survival to recruitment from 1977-1983 was 15% according to Table 8.2.

As adult survival was known, for the population to have declined as observed from 1992-1994 either survival to recruitment was around half its estimated level, or fecundity was 0.20-0.22 (from Table 8.4). In fact, fecundity did drop to considerably less than this theoretical value during 1987-1990 (Chapters 2 and 3), which suggests that the population decline should actually have been greater. It is therefore possible either that juvenile survival was actually higher than has been supposed so far, or perhaps again that changes in immigration rate should be taken into account.

The regression models of survival to recruitment assuming various constant immigration rates (set at between 0 and 18 pairs) indicated a decline in survival to recruitment some time around the early 1980s, regardless of the level at which immigration was set (Fig. 8.3). The crude estimate of survival to recruitment based on ringing data (Table 8.2) also showed the same general pattern. In addition, the regression model indicated that survival to recruitment appeared to rise at or around 1990, and as suggested above. However, this was much more dependent on the estimate of immigration, with only a slight improvement in survival to recruitment if immigration was assumed to be close to the upper end of the scale used.

8.3.5 *Immigration and emigration*

The number of Arctic skua chicks ringed at different colonies in each year, 1965-1991, is indicated in Table 8.5. The totals presented for each site were obtained from ringing schedules, with some exceptions. In most years separate totals were provided for adults and chicks ringed on Fair Isle in the observatory reports and those figures were used in the table. Totals for Foula up until 1982 (with the exception of 1972, 1975 and 1981) were taken directly from Furness (1983). In all but one year (after correcting these Foula totals), annual totals for all chicks ringed at all colonies were within ± 10 of BTO figures in *Ringing and Migration* reports. The exception was 1974 when a further 53 chicks were apparently ringed (BTO report) but for some reason cannot be located in the schedules.

Most chicks were ringed at Foula (30.2%), Fair Isle (23.2%), Papa Stour (6.7%), Fetlar (6.4%), Noss (5.2%) and Unst (4.6%) in Shetland. The location of these colonies is indicated in Fig. 8.1. Only 16.9% were ringed in Orkney and very few (0.5%) were ringed outside of the Northern Isles. Although relatively few chicks were ringed in the period between 1965-1971, since 1972 (with the exception of 1987) usually well over 200 chicks were ringed at all colonies in total, although there was evidently a decline from 1984-90. Clearly most ringing took place in Shetland, but particularly in 1990 and 1991, respectable overall totals were attributable mainly to increased effort in Orkney.

The number of Arctic skuas ringed as chicks between 1965 and 1990 and subsequently recovered are indicated in Table 8.6. Overall, recovery rates were low, with a mean of 3.2% of the 6912 chicks ringed. The majority of these

(82.3%) were recovered as presumed breeding adults. Higher recovery rates were apparent for Mousa (although few have been ringed there), Foula and Fair Isle.

Considering only recoveries of birds old enough to be breeding at or near an Arctic skua colony (Table 8.7), the vast majority were at Foula (32.8%) and Fair Isle (52.9%). This reflects the closer monitoring of these two colonies, and particularly the extensive trapping of adults in the mid-1970s on Fair Isle and in 1992-1994 on Foula. Not surprisingly, most recoveries were of birds ringed at these colonies. Of all recoveries at Foula, 87.7% (50/57) were of individuals ringed there as chicks in previous years, and of all those at Fair Isle, 78.3% (72/92) were of chicks ringed at Fair Isle. Of all recoveries of Foula chicks at Shetland colonies, 74.6% (50/57) were at Foula, and of all recoveries of Fair Isle chicks, 92.3% (72/78) were at Fair Isle. A single chick from Orkney was recorded in Shetland (at Noss), and although of the seven recoveries within Orkney only two were at or near the natal colony, movement between Orkney and Shetland appears to be minimal.

Table 8.1. Breeding variables recorded for Arctic skuas on Foula, 1992-1994.

	1992	1993	1994	Mean
Proportion of pairs which laid	0.969 (154/159)	0.966 (140/145)	0.970 (130/134)	0.968
Mean clutch size	1.86	1.91	1.93	1.90
Breeding success (%)	61.8 (168/272)	62.1 (159/256)	58.4 (132/226)	0.608
Post-fledging survival to a week (%)	78.9 (101/128)	82.9 (87/105)	no data	0.809

Table 8.2. Estimated proportions of Arctic skuas fledged from Foula between 1972 and 1983 that returned there to recruit.

Cohort	Number ringed	Corrected ringing effort[a]	Number present in 1994	Estimated number that recruited[b,c]	Estimated proportion that recruited[c]
1972	80	61	1	18 / 16	0.30 / 0.26
1973	92	70	3	47 / 41	0.68 / 0.59
1974	65	49	0	0	0
1975	150	114	3	35 / 31	0.31 / 0.27
1976	159	121	2	20 / 18	0.17 / 0.15
1977	174	132	1	9 / 8	0.07 / 0.06
1978	160	122	0	0	0
1979	228	173	2	13 / 11	0.08 / 0.07
1980	181	138	4	23 / 20	0.17 / 0.14
1981	83	63	3	15 / 13	0.23 / 0.20
1982	107	81	2	9 / 7	0.10 / 0.09
1983	73	55	6	22 / 19	0.40 / 0.34

[a] - corrected assuming a mean proportion of 0.76 of ringed chicks survived to one week post-fledging.

[b] - corrected assuming (i) the number recorded represented 0.76 (34/45) of all known-age ringed birds present in 1994 and (ii) a constant annual adult survival of 0.864 since recruitment.

[c] - two values are presented, assuming recruitment is at age 4 / age 5 years.

Table 8.3. Number of occupied Arctic skua territories on Foula, 1974-1994.

Year	Number	Counted by	Year	Number	Counted by
1974	180	RWF[a]	1986	164	various[c]
	200	JWF Davis[a]		185	RWF
1975	240	RWF[a]	1987	169	RWF
	253	JWF Davis[a]	1988	130	RWF
1976	280	RWF[a]	1989	122	RWF
1977	264	RWF[a]		155	SM Gear[b]
1978	252	RWF[a]	1990	122	SM Gear[b]
1979	273	RWF[a]		98	RWF
1980	262	RWF[a]	1991	110	SM Gear[b]
1981	245	RWF[a]		141	RWF
1982	224	RWF[a]	1992	159	RAP[d]
1985	175	SM Gear[b,c]	1993	145	RAP
	187	RWF	1994	134	RAP

Reference:

[a] - Furness (1983) [b] - reports to NCC / SNH

[c] - Ewins *et al.* (1988) [d] - Sears *et al.* (1995)

Table 8.4. The effect of changes in adult survival, survival to recruitment and fecundity on theoretical values of r.

Fecundity[a]	r[b]	Adult survival[c]	r[b]	Survival to recruitment[d]	r[b]
0.20	-0.09/-0.10	0.75	-0.13/-0.13	0.10	-0.09/-0.08
0.22	-0.09/-0.09	0.76	-0.12/-0.12	0.12	-0.08/-0.07
0.24	-0.08/-0.09	0.77	-0.11/-0.11	0.14	-0.06/-0.06
0.26	-0.08/-0.08	0.78	-0.10/-0.11	0.16	-0.05/-0.05
0.28	-0.07/-0.08	0.79	-0.09/-0.10	0.18	-0.05/-0.04
0.30	-0.06/-0.07	0.80	-0.08/-0.09	0.20	-0.04/-0.03
0.32	-0.06/-0.07	0.81	-0.08/-0.08	0.22	-0.03/-0.03
0.34	-0.06/-0.06	0.82	-0.07/-0.08	0.24	-0.02/-0.02
0.36	-0.05/-0.06	0.83	-0.06/-0.07	0.26	-0.01/-0.01
0.38	-0.05/-0.05	0.84	-0.05/-0.06	0.28	-0.01/-0.01
0.40	-0.04/-0.05	0.85	-0.04/-0.05	0.30	0.00/0.00
0.42	-0.04/-0.05	0.86	-0.04/-0.05	0.32	0.01/0.01
0.44	-0.03/-0.04	0.87	-0.03/-0.04	0.34	0.01/0.01
0.46	-0.03/-0.04	0.88	-0.02/-0.03	0.36	0.02/0.02
0.48	-0.03/-0.04	0.89	-0.01/-0.02	0.38	0.02/0.02
0.50	-0.02/-0.03	0.90	0.00/-0.01	0.40	0.03/0.03
0.52	-0.02/-0.03	0.91	0.00/-0.01	0.42	0.03/0.03
0.54	-0.02/-0.03	0.92	0.01/0.00		
0.56	-0.01/-0.03	0.93	0.02/0.01		
0.58	-0.01/-0.02	0.94	0.03/0.02		
0.60	-0.01/-0.02	0.95	0.04/0.02		
0.62	0.00/-0.02				
0.64	0.00/-0.01				
0.66	0.00/-0.01				
0.68	0.00/-0.01				
0.70	0.01/-0.01				
0.72	0.01/0.00				

[a] - assuming adult survival = 0.864 and survival to recruitment = 0.21/0.18[b]

[b] - assuming birds recruit aged four/five years.

[c] - assuming fecundity = 0.45 and survival to recruitment = 0.21/0.18 [b]

[d] - assuming fecundity = 0.45 and adult survival = 0.864

Table 8.5. Number of Arctic skua chicks ringed at different colonies, 1965-1991.

Year	Yell[a]	Unst	Fetlar	Papa Stour	Mousa	Noss	Burra	Bressay	Whalsay	Mainland	Foula	Fair Isle	Orkney	Others[b]	All colonies
1965	0	1	0	0	0	0	0	0	0	0	27	9	0	0	37
1966	0	0	0	0	0	0	0	0	0	0	29	21	0	0	50
1967	0	2	0	0	0	0	0	0	0	0	17	2	0	0	21
1968	0	4	7	0	0	0	0	0	0	0	30	5	0	0	46
1969	3	18	4	0	0	25	0	0	0	0	45	10	0	3	108
1970	0	13	4	0	4	16	0	7	0	0	90	6	31	0	171
1971	0	0	5	0	0	0	0	0	0	0	33	14	12	2	66
1972	3	30	17	0	3	0	0	0	0	0	80	36	66	1	236
1973	1	17	4	0	0	0	0	11	0	0	92	144	2	1	272
1974	4	64	15	0	0	0	0	25	1	0	65	150	19	2	345
1975	0	6	0	0	0	0	0	0	8	0	150	169	52	0	385
1976	0	27	3	0	1	36	0	20	8	1	159	102	31	0	388
1977	0	21	3	51	1	30	0	36	0	0	174	170	36	0	522
1978	7	30	4	54	0	21	0	8	8	1	160	82	43	1	419
1979	6	15	15	55	0	28	0	1	10	0	228	94	13	0	465
1980	3	6	22	39	0	22	0	0	0	0	181	107	23	4	407

Table 8.5 (cont.). Number of Arctic skua chicks ringed at different colonies, 1965-1991.

Year	Yell[a]	Unst	Fetlar	Papa Stour	Mousa	Noss	Burra	Bressay	Whalsay	Mainland	Foula	Fair Isle	Orkney	Others[b]	All colonies
1981	7	10	58	39	0	23	0	13	15	3	83	60	10	0	321
1982	11	4	52	55	3	27	0	4	28	1	107	23	53	2	370
1983	10	4	212	70	15	17	0	18	15	2	73	62	88	0	586
1984	8	3	0	43	14	7	0	0	3	0	42	54	104	2	280
1985	2	0	0	43	0	33	0	0	2	0	54	48	67	3	252
1986	0	0	4	13	2	25	0	0	1	2	55	42	97	1	242
1987	0	9	5	17	0	5	8	0	0	9	62	33	39	2	189
1988	9	20	19	0	0	26	16	0	3	10	81	74	38	0	296
1989	0	1	1	0	3	11	0	0	0	3	60	88	41	4	212
1990	10	6	3	0	0	7	0	0	0	0	0	26	172	2	226
1991	2	25	13	9	6	19	6	0	1	24	41	73	199	5	423
Total	86	336	470	488	52	378	30	143	103	56	2218	1704	1236	35	7335

[a] - includes chicks ringed on Hascosay

[b] - mostly Western Isles, Handa, Jura and Caithness

Table 8.6. Recoveries of chicks ringed between 1965 and 1990 at different ages.

Colony	Number ringed	Number recovered					
		First year	Second year	Third year	presumed breeders[a]	Total	Overall % recovered
Yell	84[b]	0	0	0	1	1	1.2
Unst	311	0	0	0	77	7	2.3
Fetlar	457	2	0	0	7	8	1.8
Papa Stour	479	0	0	2	4	6	1.3
Mousa	46	0	0	0	2	2	4.3
Noss	359	1	0	0	1	2	0.6
Burra	24	0	0	0	0	0	0
Bressay	143	1	0	0	2	3	2.1
Whalsay	102	1	0	0	0	1	1.0
Mainland	32	0	0	0	0	0	0
Foula	2177	7	1	2	70	80	3.7
Fair Isle	1631	2	2	10	80[c]	94	5.8
Orkney	1037	2	3	2	8	15	1.4
Others	30	0	0	1	0	1	3.3
Total	6912	16	6	18	181	221	3.2

[a] - includes a few third-year birds, [b] - includes chicks ringed on Hascosay, [c] - estimated total (see text)

Table 8.7. Number of Arctic skua chicks ringed during 1965-1990 recovered as breeding adults at different colonies.

Ringed	Recovered:										
	Yell	Unst	Fetlar	P. Stour	Mousa	Noss	Bressay	Whalsay	Foula	F. Isle	Orkney	Total
Yell	0	0	0	0	0	0	0	1	0	0	0	1
Unst	0	2	0	0	0	0	0	0	1	3	0	6
Fetlar	0	1	3	0	0	0	0	1	0	1	0	6
Papa Stour	0	0	0	2	0	0	0	0	1	0	0	3
Mousa	0	0	0	0	0	0	0	0	0	2	0	2
Bressay	0	0	0	0	0	0	0	0	0	2	0	2
Whalsay	0	0	0	0	0	0	0	0	1	0	0	1
Foula	1	0	1	0	0	3	0	0	50	12	0	67
Fair Isle	0	0	1	0	0	1	0	0	4	72	0	78
Orkney	0	0	0	0	0	1	0	0	0	0	7	8
Total	1	3	5	2	0	5	0	2	57	92	7	174

Fig. 8.1. Location of main Arctic skua colonies in Shetland.

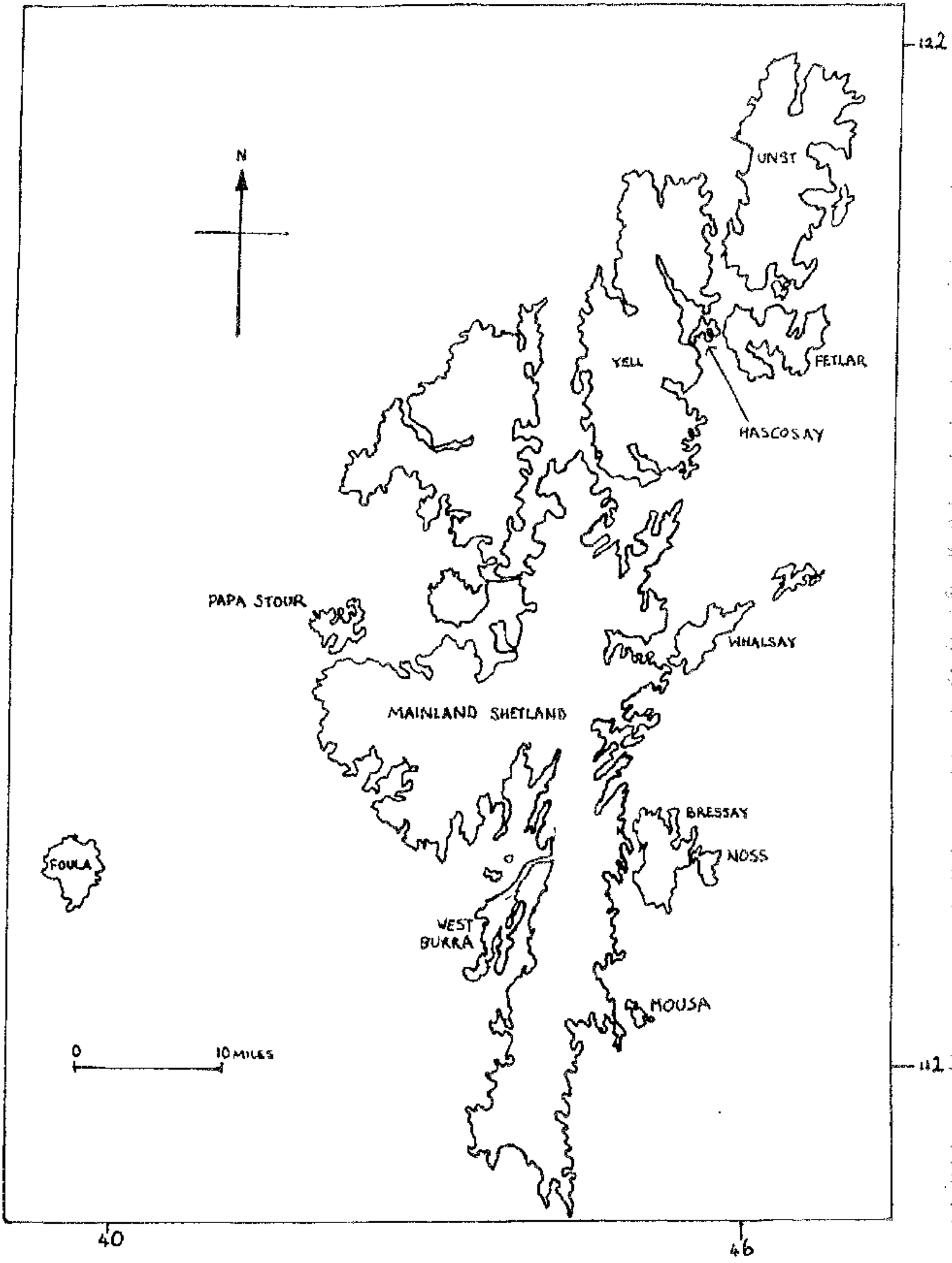


Fig. 8.2. Arctic skua numbers on Foula (1974-1994).

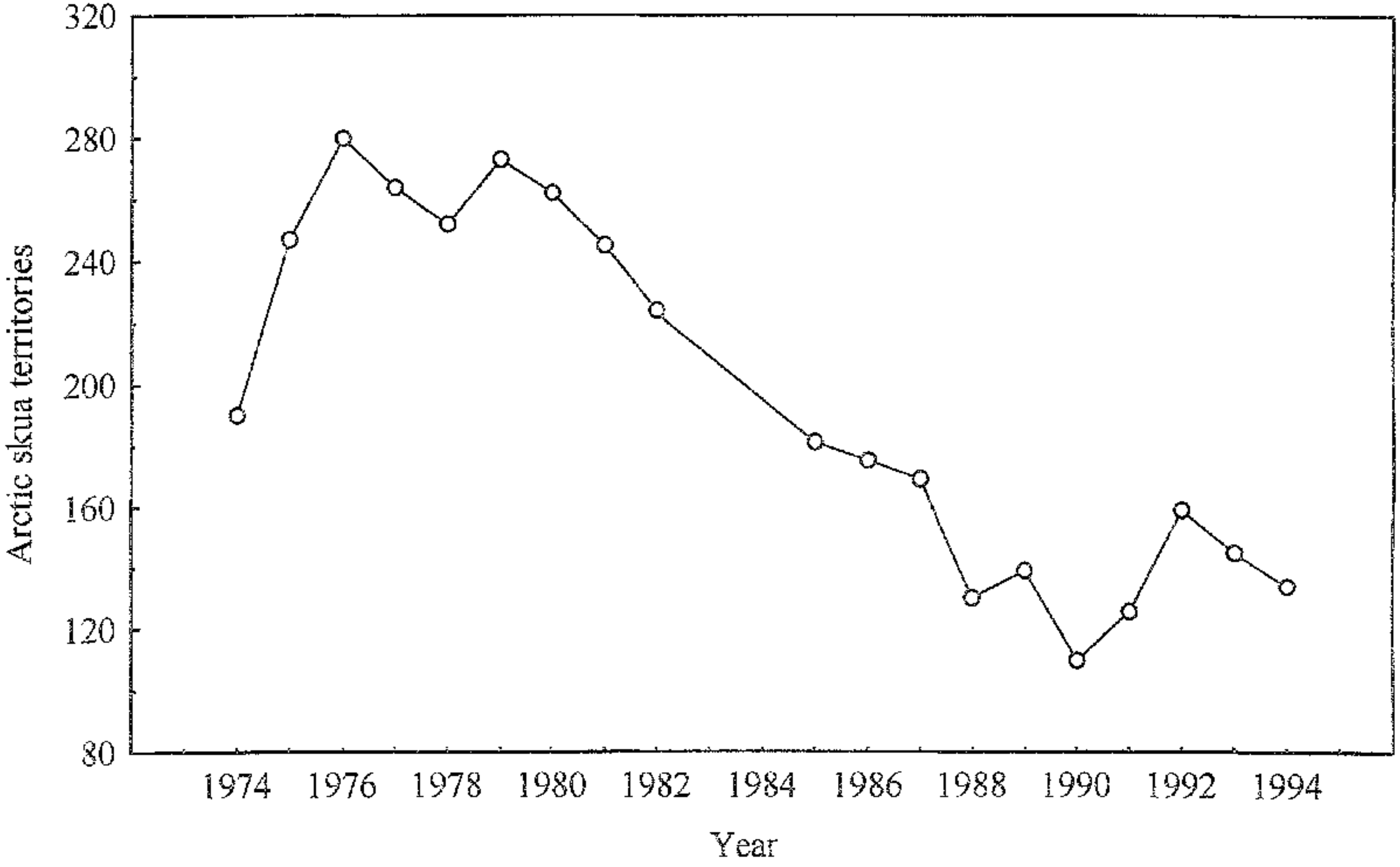
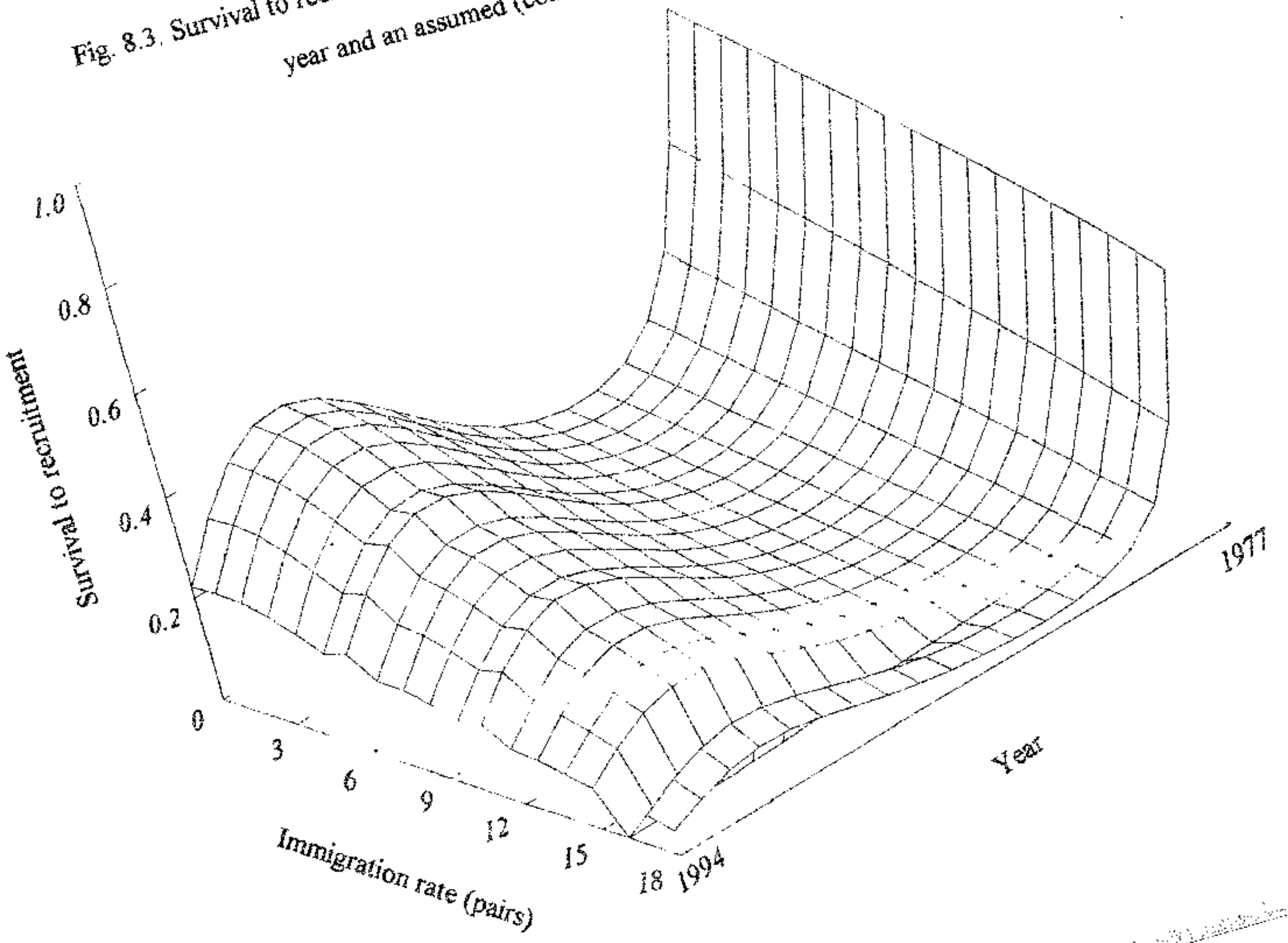


Fig. 8.3. Survival to recruitment (at age four) of juvenile Arctic skuas as a function of year and an assumed (constant) immigration rate.



8.4 Discussion

Modelling changes in population size on the basis of demographic data collected during 1992-1994 indicated that the number of Arctic skuas on Foula should be declining at a rate of 3-4% per year (equivalent to an *r* value of -0.03 to -0.04). In fact, not only has the population shown a substantial increase (1974-1976) or a greater decrease (1979-1987) during previous time periods, but from 1992-1994 declined at a much greater rate (9% per year). There are several explanations for this variation.

The mathematics of the model adopted here were developed by O'Donald (1983). In similar studies to this (e.g. Ainley *et al.* 1990, Hatchwell and Birkhead 1991, Migot 1992, Weimerskirch *et al.* 1992), *r* is calculated according to a Leslie matrix model (Leslie 1945). These models essentially involve the same parameters except that with a Leslie matrix it is also possible to take account of the proportion of individuals that survive to recruit at different ages and to include age-specific rates of adult survival and fecundity. This approach was not used as there was no information on age at recruitment on Foula, and it was felt that the Fair Isle data was not entirely appropriate (see Methods). Although simpler than a matrix model, O'Donald's model functions adequately within the limitation of its assumptions. For example, working from first principles, if the expected population size in year t is given by $N_t = bs_jN_{t-k} + (1-m_a)N_{t-1}$, for losses to be balanced by recruitment it follows that $m_a = bs_j$ If two of the three parameter estimates (0.136 for m_a, 0.45 for b, 0.18 or 0.21 for s_j) are entered into this simple equation, the resulting estimate for the third parameter corresponds to that for an *r* value of approximately 0 (i.e. indicating a stable population) in Table 8.4.

The discrepancy between the decline in numbers of Arctic skuas during 1992-1994 and the predicted rate of change based on demographic data collected during that period is partly explained by a reduction in fecundity on Foula during the late 1980s. The substantial decrease in the number of chicks fledged per pair from 1987-1990 appeared to be a direct consequence of low sandeel availability in surrounding waters (Chapter 2). However, when fecundity was set to the observed values, the model predicted an even greater decline in population size from 1992-1994. This suggests that since adult survival was set at the observed value, either survival to recruitment was greater, or that another factor such as immigration was not being fully considered.

The results of regression modelling (Fig. 8.3) also suggested an improvement in survival to recruitment at some point around 1990, although to a large degree dependent on how much immigration was considered to have taken place. Numerous studies indicate that juvenile survival is extremely variable from year-to-year (e.g. Ainley *et al.* 1990, Harris and Wanless 1991, Weimerskirch *et al.* 1992, Harris *et al.* 1994, Prince *et al.* 1994). However, it seems unlikely that survival to recruitment would be higher during a period of reduced food availability, in light of the strong relationship with chick growth (Hamer *et al.* 1991, Chapter 7). Instead, it seems more probable that there was an increase in the rate of immigration into Foula once conditions had improved, or perhaps potential recruits did not enter the breeding population when conditions were unfavourable during the late 1980s (as suggested in Chapter 3).

Neither O'Donald's model nor Leslie matrix models take possible immigration into account. The crude estimate for survival to recruitment obtained from the number of breeders present in 1994 from each previous cohort of chicks does involve an emigration component, as it was based only on birds recorded on Foula. Several studies using observed values for demographic variables conclude from matrix models that a particular population should be declining, and in some cases, observed immigration rates correspond to the differences between the actual and predicted rate of population change (Ainley *et al.* 1990, Chastel *et al.* 1993).

Unfortunately it would not have been feasible to calculate an accurate immigration rate into Foula (or Fair Isle) without a better estimate of survival to recruitment. Similarly, emigration was impossible to quantify as so few ringed Arctic skuas have been recovered. There was also extreme heterogeneity in the reporting rate, with the majority of birds trapped as breeding adults either on Fair Isle during 1973-1977 or on Foula during 1992-1994. However, it did appear that most birds from Foula and Fair Isle were philopatric and this may apply to the rest of the Shetland population. Movement between Orkney and Shetland also appeared to be limited.

However, given the magnitude of the increase in breeding numbers that occured between 1974-1976, large-scale immigration must have taken place. The Fair Isle population also increased around this period, but that has been attributed to reduced persecution (O'Donald 1983). The Fair Isle population had shown an unexplained massive increase to 180 pairs in 1969, well over double the number counted two years previously (Riddiford 1993). It is possible that such increases were each the result of a wave of immigrants coming perhaps from more northerly populations of Arctic skuas, but this would be difficult to prove. Immigration certainly has considerable bearing on present numbers of Arctic skuas on Foula, with 13% (5/39) of all ringed adults breeding on Foula in 1994 fledged from other colonies.

Regardless of the level of immigration, the question still stands as to why the number of breeding pairs declined at more than the predicted rate from 1979-1987, particularly after an apparent period of stability from 1976-1979. One possibility might be that the adult survival rate was lower from 1979-1987 than 1992-1994. Adult survival could not have overestimated for some reason related to methodology during 1992-1994. There is a tendency in any mark-recapture study to overestimate rather than underestimate mortality because an absent individual is incorrectly assumed dead, but even the likelihood that this occured on Foula was minimal. All territories on the island were checked repeatedly throughout each breeding season and any colour-ringed breeder would certainly have been recorded. In addition, no marked bird missing in 1993 returned in 1994 and it would seem unlikely that more than a very few would be absent from Foula for two years if none were absent for a single season. The adult survival rate during 1992-1994 was also comparable to the 88.6% recorded for the Fair Isle population of Arctic skuas when it was relatively persecution-free from 1973-1975, although lower than in many *Catharacta* skuas (Furness 1978, Ainley *et al.* 1990, Pietz and Parmalee 1994).

There is some evidence that adult mortality may have been higher in some locations on Foula during the early 1980s when the population was declining. It was during this period that substantial reductions in breeding pairs occurred in the northern half of Foula, at rates greater than expected even if no recruitment of new breeders had taken place. This was attributed to predation by great skuas *Catharacta skua*, from adjacent territories (Chapter 5). In addition, regression modelling (Fig. 8.3) and the rather crude estimation based on numbers of known-age birds present in 1994 (Table 8.2) both suggest that survival of juveniles to recruitment may also have declined during this period. Given the close relationship between density/location and survival of fledglings in the immediate post-fledging period, it may be that a large component of this postulated increase in juvenile mortality occurred as a result of predation before Arctic skua fledglings had even left the colony.

In conclusion therefore, it appears that the rate of immigration is an important, though as yet unquantifiable, determinant of changes in breeding population size on Foula. The reduction in number of chicks fledged per pair during the late 1980s was a factor contributing only to recent population decline. There was also some evidence that both adult and juvenile mortality was relatively high during the early 1980s possibly as a result of predation by great skuas. If this was the case it would seem likely that the relative importance of this factor has, and will continue to diminish as the Arctic skuas on Foula become more and more concentrated in the less affected high-density airstrip area in the south of Foula.

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Chapter Nine. General Discussion

9.1 Discussion

The Arctic skua population on Foula has been monitored to a greater or lesser extent since the early 1970s, the information collected forming the background to the present study. The number of occupied territories showed substantial fluctuations over this period and, as the model presented in Chapter 8 indicated, much of this variation could be attributed to changes in adult mortality, survival to recruitment, fecundity and immigration rate. In addition, the simple model presented in Chapters 2 and 3 which described changes in net recruitment suggested that the incidence of non-breeding by established adults should also be taken into consideration. Some of the factors which affect these parameters and which are relevant to the population ecology of Arctic skuas were examined in detail in previous chapters.

The effects of food availability on Arctic skua reproduction (with particular emphasis on breeding performance) were discussed in Chapters 2 and 3. Using long-term data it was clear that the reduction in sandeel recruitment around Shetland during the mid to late-1980s had considerable impact on chick growth and breeding success. However, the relationships between these two variables and indices of food availability were not strictly linear. Both chick growth and number of chicks fledged per pair improved rapidly over a short range as food supply rose from poor to moderate, but showed limited variation thereafter. This was exactly as Cairns' model predicted, and is perhaps the first occasion that this has been shown over a broad spectrum of prey availability at a single seabird colony.

The existence of these thresholds can partly be attributed to the ability of adult Arctic skuas to alter their foraging behaviour and so buffer themselves from less severe reductions in prey availability (Chapter 3). Increasing foraging effort and chasing of alternative hosts allowed them to breed with moderate success in most years until 1987, in sharp contrast with one of their principal kleptoparasitic hosts, Arctic terns *Sterna paradisaea*, which experienced total reproductive failure on Foula from 1983 to 1990. However, breeding adults were conspicuously light in 1988, the second year in which sandeel recuitment was especially poor and some birds must have skipped breeding in that year and in 1990.

The incidence of non-breeding by established adults is a fairly common feature of many seabirds' reproductive biology, but has rarely been shown to be so closely related to food abundance. This was apparent in the relationship between net recruitment of Arctic skuas on Foula and several independent indices of sandeel, or host availability (Chapter 2). Information from marked birds collected during 1992-1994 further underlined the fact that adults do not miss a season if conditions are favourable. Breeding deferral may reflect the trade-off between current and future reproductive potential, and implicit in this is the assumption that reproduction is a costly process. It might therefore be that the relatively high annual mortality rate of Arctic skuas on Foula (in comparison with many other seabirds and the larger *Catharacta* skuas in particular) reflects the stress of annual breeding attempts in all except the worst years of prey abundance.

Concurrent with the overall decline in the size of the Arctic skua population on Foula since the late 1970s, there has been a contraction in the extent of the island occupied by breeding territories (Chapter 5). Adult suvival may have been poorer in the northern half of Foula during the early 1980s because of predation by great skua *Catharacta skua* adults in neighbouring territories. In addition, mortality of chicks as they become vulnerable to predation from the beginning of the fledging period was almost certainly higher, as this showed a strong negative relationship with increasing density in 1992-1994 (Chapter 5). The comparative stability in breeding numbers observed since the mid 1980s may then reflect the diminishing importance of this factor, as the remaining Arctic skuas have become concentrated around the airstrip in an area of very high density.

As the number of chicks fledged per pair was low during the late 1980s, few new recruits will have joined the breeding population in recent years (Chapter

8). One consequence of this is that the present age structure is probably biased towards older age groups (Chapter 6). Had senescence been apparent in any aspect of reproductive performance, this would have had implications for the productivity of the population as a whole. There was however, no evidence for senescence. The only negative effect of the biased age structure would then be if adult mortality is age-dependent, which recent studies have shown to be the case. This would also lead to an increase in the proportion of new partnerships in the population, which does have a negative influence on breeding performance of Arctic skuas (Chapter 6).

A notable characteristic of seabird population ecology, but which has only attracted attention relatively recently, is the effect of individual quality on reproductive performance. Much of the variation in laying date and breeding success etc. may be accounted for by consistent differences between individuals (Chapter 7). In this respect, one interesting feature that emerged was that male quality was the primary determinant of laying date, yet it was female quality that had most influence on clutch volume.

Comparison of seasonal patterns in mass variation showed that this too was related to sex role partitioning of breeding duties (Chapter 4). Only females maintained higher body condition during incubation, but then experienced a sudden stepwise drop in weight at the onset of the chick-rearing period. It was suggested that this reflects the requirement of females to withstand possible short-term reductions in food availability during incubation as they are constrained to remain on territory during that stage. This is the first time that differing strategies of seasonal mass variation by each sex have been observed.

One factor which had important implications for the population dynamics of Arctic skuas, but about which little could be revealed, was the degree of inter-colony movement by potential recruits. It was not possible to quantify immigration or emigration rates because of the paucity of recoveries at colonies other than Foula or Fair Isle, and also the extreme heterogeneity in reporting rate.

It had been proposed (in the past) that the maintenance of the pale colour morph in the Arctic skua population in Shetland was due to a constant, high immigration rate from more northerly colonies. However, there was relatively little movement observed within Shetand, and even less between Orkney and Shetland. In addition, the differing yet apparently quite stable proportions of pale:dark phase birds at different colonies add no credence to the proposition that gene flow occurs continually via extensive immigration.