The age-specific breeding performance of great skuas on Shetland

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Candidates declaration

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

Norman Ratcliffe

December, 1993

Contents

Appendix I

Dedication

This thesis is dedicated to my parents for their support and encouragement throughout my academic career.

Acknowledgements

This research was funded by a studentship from the Natural Environmental Research Council. I am grateful to Professor Graeme Coombs for allowing me access to facilities in the Zoology Department during my three years at Glasgow University.

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I thank the Holbourn family for permission to work on Foula and their continuing co-operation with field workers on the island. I would also like to thank the other islanders, especially Ross and Jim Gear, Brian Taylor and Frank and Penny Millsop, for many a happy night at Leiraback.

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Abstract

The effect of age on the breeding performance of the great skua was examined between 1991 and 1993. There was a linear increase in clutch volume, aggression towards human intruders and fledging success with age while laying date became earlier with age. Clutch size and hatching success improved with age in a non-linear manner; increasing in younger birds before reaching a plateau in older birds. There was no effect of age on inter-nest distance nor on the condition of either the 'A' or 'B' chick. Female age was important in the advancement of laying date while male age was more important in increasing clutch volume. The latter result was possibly due to older males having a higher rate of courtship feeding.

An improvement in food supply between 1989 and 1993 reduced the number of birds deferring breeding on territory, advanced laying date, increased clutch volume and greatly improved fledging success. The increase in clutch volume with improved food supply was statistically independent of laying date. Food supply had an additive effect on age specific laying dates but there was no significant interaction. There was a significant interaction of food supply and age on fledging success; in years of intermediate food supply fledging success improved with age, while in good years the fledging success of younger birds was elevated to a level similar to that found in older ones. This suggests that the fledging success of young birds was constrained by food supply to a greater extent than in older birds.

Breeding experience had an effect on laying date, clutch size and clutch volume but did not affect hatching success. Age and experience were closely inter-related but separating the effects of these factors on breeding performance was not possible due to small samples of birds in which both age and experience were known. Despite this it seems that clutch size improved due to breeding experience rather than age. Improvements in laying date, clutch size and clutch volume were found in individual birds on successive breeding attempts following recruitment suggesting that individual birds improve breeding performance through a maturation process or a learning of skills beneficial to breeding.

There was no evidence for an increase in reproductive effort with age, despite the fact that a decrease in survival was found with old age, which would provide a selective basis for such an increase in effort. There was also evidence to suggest that high fledgling production produced a cost of reproduction in terms of a decline in survival, this only being evident in old birds. Low clutch size and aggression was associated with increased mortality, this finding providing evidence that poor quality breeders have lower life expectation. The high mortality of poor quality birds which laid only one egg was especially evident in first time breeders. This effect could produce and increase in clutch size with age since birds laying a one egg clutch will die early while birds which lay 2 eggs will be represented in the population at older ages.

General introduction

The great skua belongs to the Family Stercorariidae, in the Order Charadriiformes. The combination of features which distinguish skuas from other families in the order are hooked claws, dermal scutes on the tarsi, a prominent nail on the upper mandible, projecting central tail feathers and reversed sexual size dimorphism (Furness 1987).

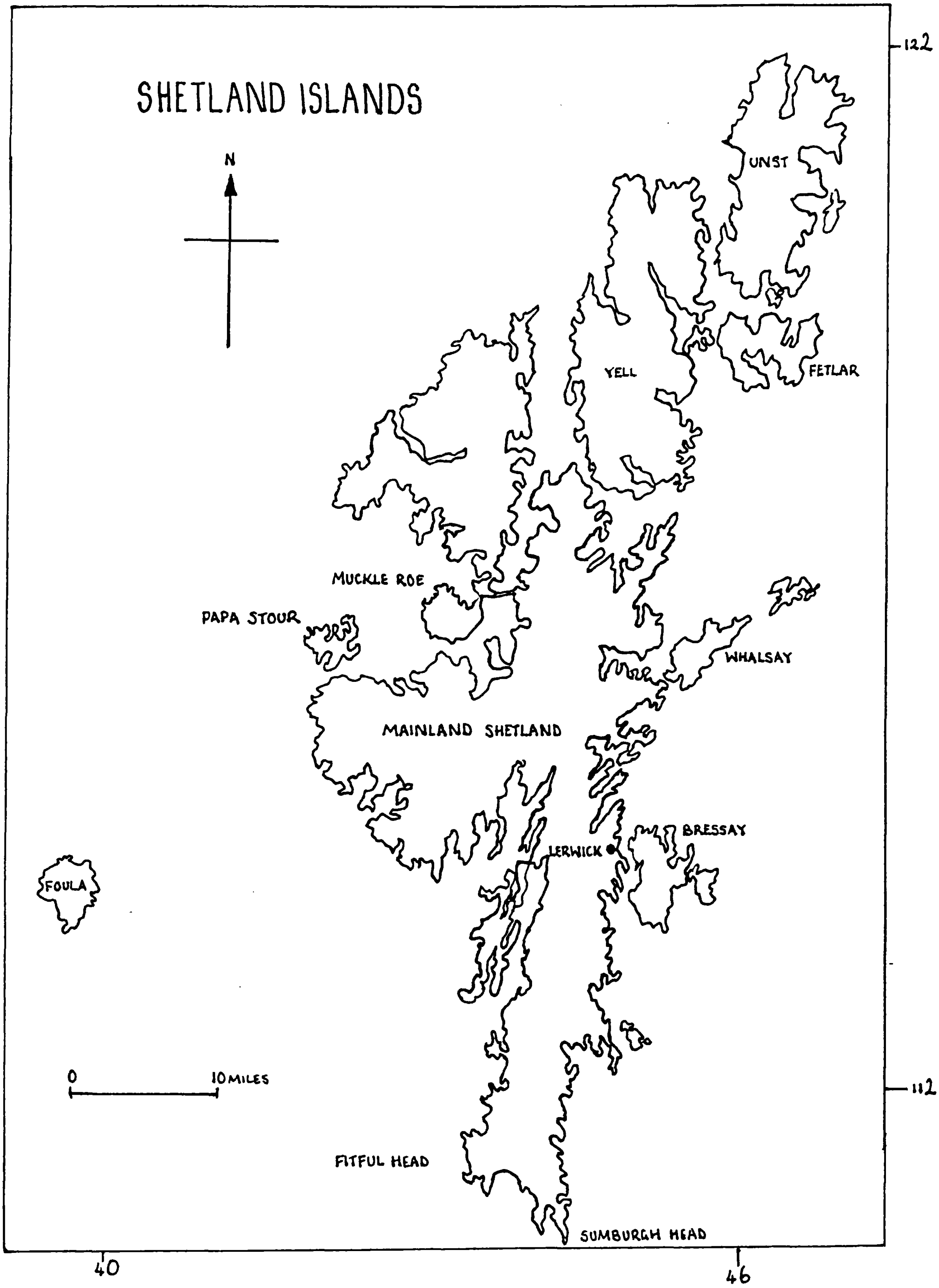
Great skuas are the only members of the genus *Catharacta* to breed in the Northern hemisphere. They have a limited breeding distribution, being confined until recently to the north of Scotland, Iceland, the Faeroes, Spitzbergen and north Norway (Furness 1987) and now also nest in north Russia (BTO news, 1992, pp. 120).

The island chosen for this study was Foula, a small island (5km by 4km) situated 40km to the west of Shetland Mainland (see Map 1). The island is vegetated primarily by short moorland flora (Braythay 1981) on which an estimated population of 3,500 great skuas nest. The study site occupies the low-lying area in the north-east of the island (see map 2).

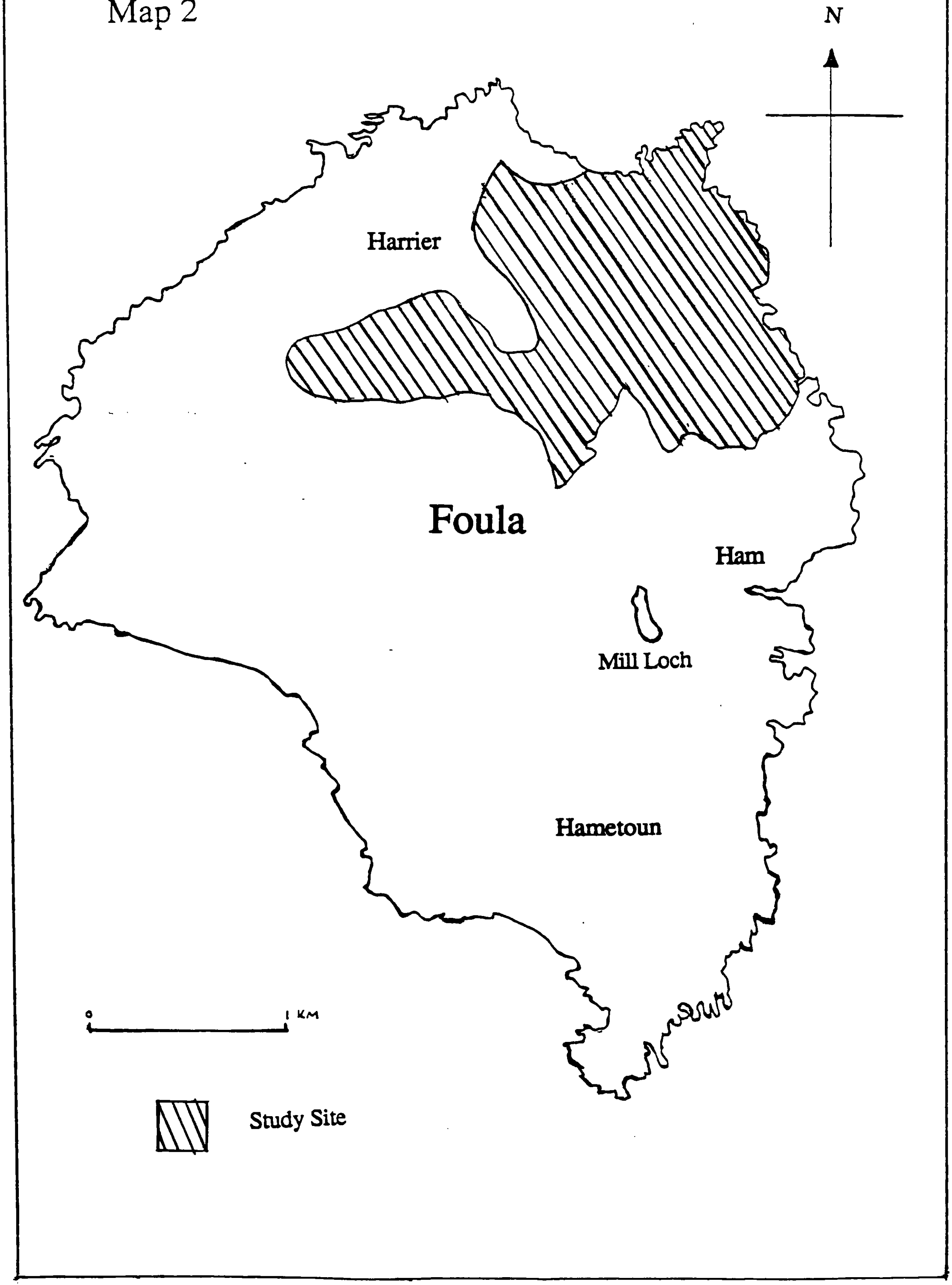
The diet of great skuas in Shetland during the breeding season consists mainly of fish, caught by shallow plunge dives (Furness 1987). In the 1970s sandeel was by far the most common fish in the diet, this food having a high calorific value which promoted chick growth rates (Furness and Hislop 1980). During the mid 1980s sandeel availability was greatly reduced through poor recruitment (Gauld Mackay and Bailey 1986, Monaghan, Uttley and Okill 1989) forcing great skuas to forage for other foods; primarily whitefish discarded by trawlers but seabirds, mammals and marine invertebrates also increased in the diet (Hamer, Furness and Caldow 1991).

This reduction in food availability led to an increase in foraging effort and to a large reduction in breeding success due to a rise in conspecific predation (Hamer, Furness and Caldow 1991). Industrial fishing for sandeel in Shetland waters was suspended on 1 January 1991 and the amount of sandeel increased in great skua diet and the breeding success improved in the summer of that year as stock size increased (see

Map 1


SHETLAND ISLANDS
N
UNST
YELL
FETLAR
MUCKLE ROE
PAPA STOUR
WHALSAY
MAINLAND SHETLAND
BRESSAY
LERWICK
FOULA
0
10 MILES
FITFUL HEAD
SUMBURGH HEAD
122
112
40
46

Map 2



Chapter 3).

Great skuas usually spend the first 2 years of life at sea and normally first return to the colony at the age of 3. They spend the early visits to the colony on club sites: areas within the colony where non-breeding birds gather when not foraging (Furness 1987). Recruitment into the breeding population is usually at age 5-10 with the average being 8 (see chapter 4). Skuas often recruit near or on the club site and move further away from it on successive breeding attempts, though some manage to obtain a territory in the colony proper straight away (Klomp 1991).

Most great skuas return to the breeding colony during April. The site fidelity is very high and birds return to the same territory year after year (Hamer and Furness 1991a). The territories are defended vigorously from conspecifics and conflicts sometimes result in death or injury (pers. obs). Egg laying occurs from early May through to early July. The clutch size is usually two but one egg clutches are not uncommon (about 10% of the nests). The eggs hatch asynchronously, on average 29 days after laying, though some of the eggs fail due to addling (infertility or early embryo death occurs) or they are eaten by conspecifics (Furness 1984) or Arctic skuas (pers. obs., Calvo pers. com).

The chicks are semi-precocial, leaving the nest after 2 or 3 days. The parents provision the chicks by regurgitation of the proventriculus contents. The main cause of chick mortality at this stage is conspecific aggression from neighbouring adults, usually when chicks wander out of the territory or are left unattended by the parents (Hamer and Furness 1991a). The chicks fledge, on average, 44 days after hatching. Both members of the pair are involved in rearing the offspring, though the division of breeding activities is unequal during incubation; females spend more time defending the territory and incubating, while males spend more time foraging to provide food for both themselves and the female (Furness 1987). In the chick rearing period both members of the pair are involved in chick provisioning.

The main aim of this thesis is to make use of the long-term study on the reproduction of known age great skuas on Foula to study age-specific variation in breeding ecology. There are three hypotheses which could explain increases in reproductive output (discussed in chapter 1); the maturation hypothesis which assumes that breeding improves due to a learning of skills advantageous to breeding; the restraint hypothesis which presumes breeding effort increases in response to an age-specific decline in residual reproductive value; and the selection hypothesis which states that age specific trends in reproduction are an artefact of the differential mortality of different quality breeders. In this thesis age is defined as the number of calendar years that a bird has lived to the year of study. In all cases the age of the birds in the partnership was assumed to be the same (Chapter 2), though this was not always the case. However, discrepancies in age in a partnership will weaken rather than reinforce age specific breeding patterns.

The first chapter is a literature review concerning the effect of age on the breeding ecology of birds, the three hypotheses which have been put forward to account for the patterns found and evaluate the evidence which exists in support of each.

The second chapter examines the effect of age on various breeding parameters in the great skua from 1991 to 1993. The discussion emphasises comparison of the findings of this study with the results of similar work by Furness (1984) and Hamer and Furness (1991a).

Chapter three is concerned with the interactive effects of food supply and age on breeding by investigation of age specific breeding patterns during periods of fluctuating food supply and with feeding experiments conducted on known age birds.

Chapter four aims to examine the effect of maturation (the development of skills which improve breeding) on breeding biology. Longitudinal analysis is used to see if individuals improve breeding with age. The relative effects of breeding experience and foraging experience are then examined.

Chapter five is concerned with the residual reproductive value hypothesis as an explanation for the increase in breeding efficiency with age. A brood manipulation experiment was used to examine the effect of different effort loads on age specific foraging effort. The costs of increasing foraging effort in terms of over-winter survival are then examined.

Chapter six discusses the effects of age, reproductive output year and sex on mortality in great skuas.

Finally chapter seven discusses the results of the previous chapters in an attempt to deduce the reasons for the age specific patterns described in this thesis.

The Latin names and authorities for species described by common names in the text can be found in appendix I at the back of this thesis.

Chapter 1

The effects of age on avian reproduction

1.1 Introduction

There is considerable evidence to suggest that the breeding performance of many bird species improves with age, especially in the early years of breeding. There is also some evidence for a slow decline in breeding performance in the oldest age groups. This review includes a summary of the various stages of reproduction which have been demonstrated to change with age in birds. This section is followed by a discussion of the hypotheses which have been put forward to explain these trends and the evidence found for each in the breeding ecology of various bird species.

1.2 The effect of age on breeding performance

The effects of age on the basic parameters of breeding performance are summarised in table 1.1. Those parameters which have received less study are reviewed in the text. The advantages of the age specific improvements described to overall breeding success are also discussed.

Table 1.1: (See overleaf). The effects of age on timing (laying or hatching date), clutch size (Cs), egg size (Es) hatching success (Hs) and fledgling production (Fp). Age refers to either age *per se*, increasing breeding experience or to differences between adults and yearlings. The symbols in the table are (+) breeding improves with age, (-) breeding performance deteriorates with age, (0) no effect of age and (X) not studied.

Species	Timing	Cs	Es	Hs	Fp	Reference
Adeilie penguin	+	+	+	+	+	Ainley *et al.* 1983
Yellow-eyed penguin	0	+	+	X	X	Richdale 1949, 1955
Waved albatross	+	X	X	X	X	Harris 1973
Laysan albatross	+	X	X	X	X	Fisher 1969
Wandering albatross	X	+	X	+	+	Croxall *et al.* 1992, Weimerskisch 1992
Manx sherawater	+	X	+	+	0	Brooke 1978
Short-tailed shearwater	X	X	X	X	+	Wooller *et al.* 1990
Fulmar	X	X	X	X	+	Ollasson and Dunnet 1978
Antarctic fulmar	+	X	+	+	+	Weimerskirch 1990
Gannet	+	X	+	+	X	Nelson 1966
Brandt's cormorant	+	+	X	+	0	Boekelheide and Ainley 1989
Blue-eyed shag	X	X	+	X	+	Shaw 1986
Shag	+	X	+	+	+	Coulson *et al.* 1969 Potts *et al.* 1980
Brown pelican	+	+	X	+	+	Blus and Keahney 1978
White stork	X	X	X	X	+	Zink 1967
Bewicks swan	X	X	X	X	+	Scott 1988
Lesser snow goose	+	+	X	+	+	Hamman and Cooke 1987, Rockwell and Finlay 1993

Snow goose	+	+	X	X	X	Finney and Cooke 1978
Barnacle goose	X	+	X	+	+	Forslund and Larsson 1992
Canada goose	+	+	X	+	+	Ravelling 1981, Aldritch and Ravelling 1983
Nene goose (captive)	+	+	+	X	X	Kear 1973
Mallard (captive)	+	+	X	X	X	Krapu and Doty 1979
Lesser scaup	+	+	X	X	X	Afton 1984
Goldeneye	+	+	X	+	X	Dow and Fredga 1984
Eider	+	+	0	X	X	Baillie and Milne 1982
Sparrowhawk	+	+	X	X	+	Newton *et al.* 1981
Hen harrier	X	–	X	X	0	Picozzi 1984
Kestrel	+	X	X	X	X	Village 1986
Hazel grouse	X	+	X	X	X	Keppie 1975
Willow grouse	0	0	0	0	0	Hannon and Smith 1984
Blue grouse	+	+	X	X	+	Zwickel 1975, 1977
White-tailed ptarmigan	X	+	X	X	X	Geisen *et al.* 1980
Black grouse	X	+	+	0	+	Willebrand 1992
Grey partridge	X	–	X	X	X	Blank and Ash 1960
Coot	+	X	X	X	X	Perdeck and Cave1992
American coot	+	+	X	+	+	Crawford 1980
Semipalmated sandpipier	+	0	+	+	X	Gratto and Cooke 1982

Red-necked phalarope	+	X	X	X	X	Hilden and Vuolanto 1972
Redshank	+	0	+	X	X	Thompson and Hale 1991
Great skua	+	0	0	+	0	Furness 1984
Great skua	+	0	+	+	+	Hamer and Furness 1991
Arctic skua	X	X	X	X	+	Davis 1976
Red billed gull	+	+	X	+	+	Mills 1973
Herring gull	X	X	+	X	X	Davis 1974
California gull	+	+	+	X	+	Pugesek 1983
Glaucous-winged gull	+	+	+	+	0	Reid 1988
Ring billed gull	+	+	X	+	X	Haymes and Blokpoel 1980
Western gull	+	+	X	+	+	Pyle *et al.* 1991
Kittiwake	+	+	X	+	+	Coulson and White 1966
Common tern	+	+	+	+	+	Nisbet *et al.* 1984
Arctic tern	0	+	+	+	+	Coulson and Horobin 1976
Least tern	+	+	X	+	0	Massey and Atwood 1981
White-fronted tern	+	0	+	X	X	Mills and Shaw 1980
Sooty tern	+	X	X	X	X	Harrington 1974
Ural owl	+	0	+	0	X	Pietienan *et al.* 1986 Pietienan 1988
Tengmalms owl	+	+	+	+	+	Korpimaki 1988
House martin	+	+	X	X	+	Bryant 1979

Skylark	+	X	X	X	X	Delius 1966
Tree swallow	+	+	+	X	+	De Steven 1978
Bluebird	+	X	X	X	X	Laskey 1943
Bee eater	+	+	X	0	0	Lessells and Krebs 1989
White wagtail	0	0	X	—	—	Leinonen 1973
Rock pipit	+	X	X	X	X	Askenmo and Unger 1986
Blue tit	+	+	X	0	+	Dhont 1988
Great tit	+	+	X	X	+	Perrins and Mc Leery 1985
Willow tit	X	+	X	X	X	Ekman 1984
Marsh tit	+	+	X	X	X	Smith 1993
Nuthatch	+	X	X	X	+	Enoksson 1993
Pinyon jay	+	0	X	X	+	Marzluff and Balda 1992
Mexican jay	X	X	X	X	+	Brown 1987
Magpie	+	+	+	+	+	Birkhead 1989
Hooded crow	+	+	+	0	0	Loman 1984
Rook	+	+	X	+	+	Roskaft *et al.* 1983
Starling	+	+	X	X	X	Verheyen 1969
Pied flycatcher	+	+	X	X	+	Harvey *et al.* 1984
Prairie warbler	+	+	+	X	+	Nolan 1978
Darwins finch	X	+	X	X	+	Gibbs *et al.* 1984
White-crowned sparrow	X	+	X	X	+	Baker *et al.* 1981
Savannah sparrow	+	+	X	X	X	Ross 1980

Savannah sparrow	+	0	X	0	0	Bedard and La Pionte 1985
Song sparrow	+	+	X	0	+	Nol and Smith 1987
Blackbird	+	+	X	X	X	Desrochers and Magrath 1993
Red-winged blackbird	+	+	+	X	+	Crawford 1977
Yellow-headed blackbird	+	+	+	X	+	Crawford 1977

1.2.1 Arrival at breeding grounds

Afton (1984) found no relationship between age and female arrival date in lesser scaup. Coulson and White (1958) showed that older breeding kittiwakes return the colony before first time breeders who in turn arrives before non breeders. Coulson and Horobin (1976) showed that Arctic terns have a progressive advance in return date from two years old to over eight years old, the oldest returning 17 days earlier than the youngest breeders. In Brandts cormorants arrival date on the colony advances (i.e. becomes earlier) with age (Boekelheide and Ainley 1989).

1.2.2 Timing of breding

Laying date or hatching date have been shown to advance (becomes earlier) with age in 61 species (see table 1.1). Birds breeding earlier in the season generally have a higher fledgling survival so there is a strong selective pressure towards early laying though food supply is a limiting factor (Perrins 1970). Time of hatching is important to the survival of herring gull chicks. Those chicks that hatch earlier have higher survival than those hatching later, especially where conspecific predation is a major cause of mortality (Hunt and Hunt 1976).

However, laying too early can also be disadvantageous. Parsons, Chabrzyk and Duncan (1976) found that hatching too early in herring gulls produces a lower chick survival than chicks hatching during the peak of hatching time. In pinyon jays, older birds lay earlier and as a consequence suffer lower breeding success in years which are very cold early in the season (Marzluff and Balda 1992).

Young birds may be constrained from breeding earlier due to latency in testis or ovary maturation. In mallards ovarian development is earlier in adults than in yearlings (Krapu and Doty 1979). Johnston (1956) found that the testis of immature California gulls developed later and regressed earlier compared with adults. However, if there were a net selective benefit for young birds if they developed the gonads earlier in the season they would do so. Thus late gonad maturation is not the sole reason for young birds laying later, but is a consequence of ultimate factors.

1.2.3 Clutch size and clutch volume.

Clutch size (the number of eggs in a clutch) increased with age in 51 species (see table 1.1). Clutch size is obviously an important component of breeding success since a sub optimal clutch size will produce fewer fledglings.

Increases in egg size with age have been demonstrated in 26 species (see table 1.1). The size of the egg can be an important influence on chick survival, especially in the period immediately after hatching. Davis (1975) showed increasing egg volume improved chick survival in the herring gull. Ankey and Bisset (1976) found an increase in egg mass in the snow goose produced higher gosling survival. In great skuas larger eggs produced chicks with higher survival over the first 4 days (Furness 1983). Galbraith (1988) found that increased egg size in lapwings was primarily due to greater albumin content, and that this produced higher chick survival. Bolton (1991) demonstrated that increased egg volume improved lesser black-backed gull chick survival in the first few days but after this period the quality of the parents was the main factor affecting fledging success. The production of more eggs to produce more young or large eggs to increase survival of the offspring will increase lifetime reproductive success of individuals. However the adult female must have sufficient nutrient reserves at ovulation for the formation of large clutches or egg, without suffering a reduction in condition or survival.

1.2.4 Territory size and quality

Territory quality and location varies with age. In colonial birds older birds occupy the centre of the colony (Haymes and Blokpoel 1980). This reduces the risk from mammalian predation since predators have to pass through the mobbing of peripheral birds to reach the centre. However a central site can increase conspecific predation (Davis 1976). Territory quality has an impact on chick survival. Hunt and Hunt (1976) found increased territory size improved chick survival in herring gulls. Hamer and Furness (1991a) found that high nest density produced higher predation in the egg phase though the reverse was true of the chick stage. Increased territory size could result from increased experience of combat enabling the bird to win conflicts at territorial boundaries. Pugesek and Diem (1983) have challenged the above views on age dependent variations in territoriality. They found territory quality and location had no effect upon breeding success of California gulls if analysed in isolation from age. The distribution of birds of different age was found to be a passive process due to older birds arriving first and younger ones settling around them and not due to older birds being dominant in disputes and excluding young birds from the centre.

1.2.5 Brood defence

The ability to defend the territory and offspring is important can contribute to overall breeding success and there is evidence that it increases with age in several species. On the Bass Rock gannet eggs are eaten by herring gulls, especially after human disturbance. Older birds do not desert the nest as readily as young birds and so the former suffer lower egg predation (Nelson 1966). Aggression towards conspecifics and predators increases with age and improves fledging success in older Canada geese (Raveling 1981). Aggression improved chick survival in great skuas on Foula (Hamer and Furness 1993) and Furness (1984) and Hamer and Furness (1991a) demonstrated an increase in the intensity of brood defense with age. Pugesek (1983) found an increase in territorial defence with increasing age in California gulls and Hannon and Smith (1984) found that adult willow ptarmigan were more vigorous in brood defence than yearlings.

1.2.6 Hatching date and hatching success

An increase in hatching success with age has been documented in 26 species. Hatching success is higher in older birds; possibly because they incubate more efficiently (Coulson and White 1958, Nelson 1966). Absence of the parent from incubation leads to chilling and so retardation and possibly death of the embryo. Addling was found to be higher in inexperienced yellow-eyed penguins (Richdale 1957). Furness (1984) found no age related effects on addling in great skuas during a period of plentiful food supply but Hamer and Furness (1991a) found addling to be higher in younger birds in years when a food shortage resulted in a low food supply. Aldritch and Raveling (1983) found that experienced captive Canada geese improved hatching success by attaining a higher body mass before incubation which increased nest attentiveness. There was a decrease in the nest height of pinyon jays with age and this reduced nest predation by ravens (Marzluff and Balda 1992).

The asynchrony of hatching also decreases with age: older western gulls reduced the difference in hatching date between eggs in a clutch and so reduced the third chicks' competitive disadvantage and consequently increased fledging success (Sydeman and Emslie 1992).

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1.2.7 Fledgling production

Fledgling production increased with age in 42 species. Fledling production is an important component of lifetime reproductive success and therefore a birds genetic fitness (Newton 1989). Post fledging survival depends upon provisioning of the chick in the period just prior to and after fledging (Pugesek 1983, Hamer Furness and Caldow 1991). Pugesek (1983) showed that older California gulls provisioned chicks for a longer period than younger birds thus theoretically increasing post-fledging survival. Perrins and Moss (1974) found that great tits reared by older parents had a higher recruitment the following year than those reared by younger parents but this effect may have been a consequence of higher fledging success in older birds. Lessells and Krebs (1989) showed that the recruitment rate of bee-eater chicks was higher for adult birds than for breeding juveniles, even when analysed as proportion of chicks fledged.

1.3 Hypotheses to explain age-related improvements in breeding

From the studies quoted there can be little doubt that breeding performance improves with age in many species of birds. The reason for this trend, however, is controversial with three hypotheses being debated (reviewed in Nol and Smith 1987). The hypotheses are:

(1) The maturation hypothesis (which can be subdivided into the breeding performance hypothesis and the age hypothesis).

(2) The residual reproductive value hypothesis.

(3) The selection hypothesis.

1.4 The maturation hypothesis.

This proposes that individual birds improve reproductive success due to the learning of skills. Longitudinal studies have demonstrated that individuals do improve breeding performance with age (Dow and Fredga 1984, Hamann and Cooke 1987, Newton 1989, Forslund and Larsson, 1991, Desrochers and Magrath 1993), these improvements often increase rapidly in the initial breeding attempts before reaching a plateau when the skills have been aquired.

The skills learned could be due to experience of either breeding (the breeding experience hypothesis) or of foraging (the age hypothesis). Breeding experience and age are closely inter-related (Saether 1990) with various breeding activities being influenced by either of these learning pathways to different extents. Clearly it is difficult to decipher which of the learned skills influences different breeding parameters.

Many studies have succeeded in separating the effect of age and experience by controlling for one factor and testing the effect of the other. Such an analysis requires that the birds are of both known age and known experience.

1.4.1 The effect of breeding experience controlling for age

In Adelie penguins experience increased hatching and fledging success but not clutch size (Ainley *et al.* 1983). In pied flycatchers first year breeders had smaller clutches and laid later than experienced birds of the same age (Harvey *et al.* 1985). In the western gull, breeding experience was found to improve clutch size and hatching success in females but not males. The trends were non-linear, with gains due to experience being small after the first year of breeding. Forslund and Larsson (1992) found that experience advanced hatching date and increased clutch size in barnacle geese but had very little effect on fledging success when the effects of hatching date and clutch size were controlled for. Experienced Arctic skuas raised more fledglings than inexperienced breeders of the same age (Davis 1976).

Many studies found no effect of experience after controlling for age. Three year old yellow eyed penguins breeding for the first time showed no significant difference in egg weight to birds of the same age breeding in their second year (Richdale 1949). Newton *et al.* (1981) found no difference between the breeding success of similar aged sparrowhawks breeding for first or second time and deduced that hunting skill was more important than breeding experience. Croxall *et al.* (1992) discovered that maternal experience of similarly aged wandering albatrosses had no effect on egg weight or hatching success.

1.4.2 The effect of age controlling for experience

In first time breeding yellow-eyed penguins, age increased the egg weight (Richdale 1946). Similarly in Adelie penguins; clutch size, hatching success and the raising of chicks to crèche increased with age in first time breeders (Ainley *et al.* 1983). Older primiparous breeding pied flycatchers initiated the clutch earlier in the year and had a higher fledging success than younger ones, though clutch size was not affected (Harvey *et al.* 1985). Age independent of experience advanced the timing of breeding in both sexes of the western gull but clutch size, hatching success and fledging success increased in males only. These trends were linear suggesting that age had a constant effect through to the age of 9 years (Pyle *et al.* 1991). Barnacle geese improved both timing and clutch size with age when experience was controlled for (Forslund and Larsson 1992). Age increased egg weight but not hatching success in the wandering albatross independent of experience (Croxall *et al.* 1992).

1.4.3 Does foraging efficiency improve with age ?

The age hypothesis suggests that there ought to be an increase in foraging efficiency with increasing age. Many studies have demonstrated that immature birds are less efficient at food capture than adults, especially if the prey is small, elusive and scarce (Burger 1981). Improvements in foraging efficiency have been demonstrated in Pelicaniiformes (Orians 1969, Morrisson 1978), little blue heron (Recher and Recher 1969), many species of Laridae (Dunn 1972, Buckley and Buckley 1974, Searcy 1978, Greig *et al.* 1983, Carroll and Cramer 1985), turnstone (Groves, 1978) and nuthatch (Enoksson 1988). Evidence exists to suggest that the acquisition of foraging skills increases gradually with age. Mac Lean (1986) compared the foraging efficiency of the various plumage phases of 3 species of gulls and found that feeding efficiency increases gradually with age, the efficiency of the immature in its final year of adolescence being comparable to that of the adult.

Recent evidence suggests variations in foraging success exist in breeding passerines. Jansen (1990) found that, in a population of colour-ringed Heron Island silver-eyes, second-year birds had a lower foraging success than older birds, even though half of the second-year birds were breeding. Desrochers (1992) found that foraging efficiency increased in breeding blackbirds up to the age of 3 years, this being due to improvements in individual performance rather than selection against poor foragers. Whether increases in foraging efficiency occur throughout life in long lived breeding birds, which often have several years of deferred maturity in which to develop feeding methods, is unknown.

1.4.4 Is food a limiting factor in avian breeding?

The age hypothesis also suggests that food is a limiting factor in avian breeding systems, especially to young birds lacking the necessary skills to catch sufficient food. Research has been conducted into the effect of fluctuating food supply on the breeding ecology of known-age populations and have demonstrated that age specific trends diminish in good food years and increase when food is scarce (Furness 1984 compared with Hamer and Furness 1991a, Boekelheide and Ainley 1989, Sydeman *et al.* 1991).

Evidence for experimental feeding improving breeding performance exists for many species including herring gulls (Spaans 1971) great tits (Kallander 1974), kestrels (Drent and Daan 1980), Tengmalms owl (Korpimaki 1989), magpies (Manjit *et al.* 1991) and lesser black backed gulls (Bolton *et al.* 1992). Age-specific feeding experiment have been performed on captive mallard (Krapu and Doty 1979). They found yearlings had lower nutrient reserves, ovarian development and clutch size than older birds. These differences ceased if the yearlings were fed *ad libitum,* suggesting food supply was a constraining factor on reproduction in young birds. Desrochers (1992) found that the supplementation of food advanced the date of clutch initiation in yearling blackbirds but had no effect on the laying date of older birds.

1.5 The restraint hypothesis.

Breeding can be a costly process (Williams 1966), involving physiological stress (Reid 1987) and increased exposure to predation (Ainley and De Master 1980). The costs may be manifested as a decrease in future fecundity or survival, and thus a reduction in lifetime reproductive success and genetic representation in future generations. Life history theory postulates that there is a trade off between the energetic investment in present and future breeding attempts, the balance shifting through a birds lifetime (Partridge 1989). Young birds have a large residual reproductive value (the potential number of future breeding opportunities prior to death) and may refrain from maximum reproductive effort in order to reduce the costs of breeding. In species which suffer age dependent mortality, the cost of greater breeding effort is reduced with age, and so the balance between current and future reproduction will tip in favour of energy investment in the current breeding attempt

(Pugesek 1983). Thus an optimal life history strategy for an individual would be to refrain from high energy output and save reproductive value for future reproductive attempts early in the life history followed by increased effort in the present reproductive attempts when the probability of mortality increases due to ageing (Clutton Brock 1984). Such a strategy would maximise lifetime reproductive success and so would be favoured by natural selection. In order to support this hypothesis it is necessary to demonstrate an increase in breeding efficiency with age, increased effort, a cost of this effort and age dependent mortality.

1.5.1 Do birds show age dependent mortality?

Ringing recoveries demonstrated long ago that survival improved with age over the first few years of life but it was thought that survival did not decrease with old age, a fixed fraction of the cohort dying in each year for reasons other than senescence (Nice 1937, Lack 1954). Since then a decrease in survival rate with old age has been demonstrated in kittiwakes over 7 years (Aebisher and Coulson 1990), fulmars (Dunnet and Ollasson 1978), Temminks stint (Hilden 1978), California gulls over six years old (Pugesek 1987), common gulls over 8 years old (Rattiste and Lilleleht 1987), sparrowhawk over 5 years old (Newton 1989), pied flycatcher (Sternberg 1989), short-tailed shearwaters after 10 years (Bradley *et al.* 1989), dunlin (Jonsson 1991) and wandering albatrosses over the age of 27 (Weimerskirch 1992). No effects of old age on survival have been found in pinyon jays (Marzluff and Balda 1992).

1.5.2 Does effort increase with age?

Separating increased effort from increased efficiency is difficult and requires the study of subtle behavioural traits such as brood defence and foraging activities (Ricklefs 1977). In most studies of foraging, effort is assumed to be a function of the bird's time activity budget (Ryan and Dinsmore 1980) with increased time spent away from the nest being associatied with an increase in energy expenditure.

Pugesek (1981, 1983) demonstrated an increase in foraging effort through time budget studies of California gulls. The older birds fed the young more frequently so increased chick growth rates. Older birds spent more time foraging and less time resting than younger birds, indicating that old birds were working harder to feed chicks. Older birds also spent more time in territorial defence. However Nur (1984) claims the trends shown were due to an increased efficiency in foraging and pair co-ordination. Hamer and Furness (1991a) studied great skua foraging effort using a single spot-observation during the chick rearing stage and found those birds with low territorial attendance were older than those with high attendances.

Roskaft *et al.* (1983) have found decreases in foraging effort with age in the rook, young males foraging for longer, and returning with food more frequently. Despite this the breeding performance was poorer in young rooks and females with young partners spent more time begging than those with old males. A similar result was found in glaucous-winged gulls; young birds left the territory unattended more often and old birds spent more time resting on the territory (Reid 1988a).

There are confounding variables such as chick age and brood size which effect the time budgets of birds, these factors being inter-related with age. Young birds at any point in chick rearing generally have smaller broods of younger chicks compared to older birds. Chick age and brood size should be controlled for in studies of age specific foraging ecology.

1.5.3 Evidence for the costs of reproduction

There are two main methods of assessing the costs of reproduction in terms of survival; correlative studies which allow birds to breed at their chosen rate, and manipulative studies which alter brood sizes of birds. The survival or fecundity of the bird is then examined in the following year in relation to the previous years reproductive output. The latter method controls for the problem of low quality phenotypes having lower survival (see next hypothesis) and so has been more successful in demonstrating costs of high effort (Partridge 1989).

1.5.4 Correlative studies

In short tailed shearwaters high offspring production in older birds correlated with a decrease in survival rate thus indicating a cost of high reproductive effort (Bradley *et al.* 1989). High fledging success was correlated with increased mortality in old age classes of California gulls (Pugesek 1987, Pugesek and Deim 1990). Survival decreased with increasing brood size in great tits (Tinbergen *et al* 1985) and willow tits (Eskman and Askenmo 1986). Double brooded house martins had lower survival than those which raised only one brood in a season (Bryant, 1976). Dow and Fredga (1984) found that female goldeneyes with high breeding success in the first years of breeding suffered increased mortality as a consequence: birds with a lower initial breeding success lived for longer and had a higher lifetime reproductive success. No costs were found in correlative studies of tree swallows (De Steven 1980) and collared flycatchers (Gustaffson and Sutherland 1988).

1.5.5 Manipulative studies

Increased brood size caused a negative effect on survival in glaucous-winged gulls (Reid 1987), male pied flycatchers (Askenmo 1976) and blue tits (Nur 1984). The fecundity in the following year was reduced by increasing brood size in collared flycatchers (Gustaffson and Part 1990), great tit (Slagsvold 1984, Tindbergen 1987), blue tits (Nur, 1988), house sparrows (Henger and Winfield 1987) and rooks (Roskaft 1985).

1.6 The selection hypothesis

This states that improvements in breeding performance with age are a result of differential mortality of the different quality phenotypes. This assumes that birds which breed well are better quality birds which also have a higher survival rate. This means that these good quality birds will represent an increasingly large proportion of the breeding population in successive age classes. Evidence exists to suggest that selection can influence breeding success at a population level. Nol and Smith (1987) found that female song sparrows which bred for only one year raised fewer young than birds which also bred in subsequent years. Bradley *et al.* (1989) found that short-tailed shearwaters which lived for longer had higher breeding success than birds which lived for a shorter period, especially in the first year of breeding. Survival was found to be higher in birds with large brood size in magpies (Hogstedt 1981) and great tits (Den Boer-Haewinkel 1987). Aebisher and Coulson (1990) found that kittiwakes in the colony centre have longer life spans and a higher breeding success than the birds on the colony edge. Marsh tits which laid later in the season were less likely to breed in the following year than those which had early clutch initiation dates (Smith 1993).

These studies suggest that differential selection of phenotypes with different breeding output can account for apparent age specific breeding patterns. However some studies have found no evidence of selection (Newton 1989, Perdeck and Cave 1992, Forslund and Larsson 1992).

1.7 Decreases in breeding performance with old age

A decrease in breeding performance in older birds has been demonstrated in a wide variety of bird species. Declines in clutch volume with old age were found in nene geese (Kear 1973), herring gulls (Davis 1975), Arctic terns (Coulson and Horobin, 1976), ring-billed gulls (Haymes and Blokpoel 1980) and great skuas (Hamer and

Furness, 1991). Old blue and great tits (over the age of 4 and 5 respectively) have later laying dates and reduced nesting success, brood size and post fledging survival (Dhont 1988). Wooller *et al.* (1990) found that fledging success decreased in the oldest age groups of short tailed shearwaters and Haymes and Blokpoel (1980) found lower fledging success in old ring billed gulls. Captive male African village weavers built fewer nests, displayed less often, and had lower paternity at ages of 14-18; the females had smaller clutch size over the age of 9 years and older birds of both sexes spent more time resting (Collias *et al.* 1986).

This decline in breeding performance has been attributed to many factors. Senescence; the deterioration of body condition due to the accumulation of somatic gene mutations with age which reduce fecundity and survival (Newton 1989), is the most probable and widely held view. This theory would predict that individuals would display a decline in reproductive performance with age: this has been found in captive African village weavers (Collias *et al.* 1988) and sparrowhawks (Newton, 1989). The senescence theory would also predict a decline in condition with old age. A decrease in body weight with old age has been found in great tits over 4 years old (Perrins and Mc Cleery 1985) and female wandering albatrosses over 22 years (Weimerskirch 1992) and an increase in arthritis was found in old nene geese (Kear, 1974) and sparrowhawks (Newton *et al* 1981).

Pugesek and Deim (1990) found a decline in the fledging success of old California gulls when analysed cross-sectionally, but a longitudinal analysis of individuals revealed no decline. The reduction in fledging success with old age was an artefact; those birds that adopted a strategy of low reproductive effort had greater longevity than those birds which had high reproductive effort and consequently a higher mortality rate.

Davis (1975) suggests that decreases in clutch volume with old age in herring gulls can be explained by older birds being more efficient at foraging and so can maintain chick survival without producing a large egg. If this theory were true, the fledging success would be expected to be higher in the older birds but this is not the case (Wooller *et al.* 1990, Sydeman and Emslie 1993).

Weimerskirch (1992) suggests that since mortality increases with age the probability of a bird losing its partner will consequently increase. A change of partner has been shown to produce a decrease in breeding performance (Coulson 1966, Mills 1973, Ollason and Dunnet 1978). In birds with high mate fidelity, the likelihood of finding a partner of the same age would be small and so the old bird would be forced to re-mate with an inexperienced bird, which could conceivably increase the effect of a partner change. This increased rate of partner change with old age could result in a decline in breeding output.

Rockwell *et al.* (1993) have suggested that, in birds with a high site fidelity which gain food from the territory, the exhaustion of territorial resources with time, as well as senecence, could account for decreases in breeding performance with old age.

1.8 Conclusion

From the evidence presented it is obvious that age has a major effect upon the breeding ecology of a wide variety of birds. However, the mechanisms for this phenomenon are poorly understood. The evidence suggests that the learning of skills, (those connected with foraging to a greater extent than breeding) is the most important factor in the improvement in breeding in young age groups, selection having a lesser effect. Evidence for an increase in effort with age in middle aged birds is less convincing. The most probable explanation for the decrease in breeding efficiency with age is senescence. The theories are not mutually exclusive and could exert a varying, cumulative influence on different breeding parameters according to species, fitness, environment and stage in life history; thus being inextricably bound.

Chapter 2

The effect of age on the breeding performance of great skuas

2.1 Introduction

Age-specific reproductive success has been recorded in many species of bird, breeding parameters generally improving with increasing age, especially in the younger age classes (see Ryder 1981, Saether 1990 for reviews), in a manner correlated with increased fledging success (Parsons 1970, Birkhead and Nettleship 1982, Amundsen and Stockhard 1990, Bolton *et al.* 1991).

There is a strong selective pressure for all individuals to increase lifetime breeding success in order to maximise genetic representation in future generations. Since age is related to reproductive performance, interactions of age and breeding success will form a major part of a bird's life history strategy (Forslund and Larsson 1992).

This chapter examines the effect of parental age on laying date, clutch size, egg size, brood defence, hatching success, chick condition and fledging success in great skuas. The effect of age on inter-nest distance and adult condition are also investigated.

2.2 Study population and methodology

In every year since 1968 large numbers of great skua chicks have been ringed on Foula. The year in which the bird was a chick is indicated by referring the ring number to the date which it was used to ring a chick and the age of an adult can be determined accurately if it is recaptured. Between 1988 and 1993 efforts were made to trap and colour ring as many breeding known-age birds as possible which resulted in 383 territory-holding known-age birds being caught and marked with a unique combination of four colour rings. Most were captured during incubation with clap nets though some breeding birds were also captured during pre-breeding by dazzling on dark nights, and during the chick stage with an adaptation of the fleyg while the adults were engaged in aggressive behaviour towards the trapper. In addition to these breeding birds, 140 known-age great skuas have been trapped using cannon nets on club sites (Klomp 1991). Of these birds, 55 subsequently recruited and have produced a total of 83 breeding attempts. The age of both partners was only known in a few cases and so is assumed to be the same as that of the known-age study bird in all cases. Even if the assumption is not upheld, differences in the ages of partners will weaken rather than reinforce trends in age specific breeding performance.

2.2.1 The laying period

In 1991 and 1992 the nests of known age birds were usually found within a day of clutch initiation by daily searches of territories. They were marked with numbered, white tipped bamboo canes placed approximately 5 metres to the North of the nest.

The clutch size (1 or 2) was recorded for each nest, a check for remains of egg shell was made around all 1 egg clutches to ensure that they were not 2 egg clutches which had lost an egg to predation or displacement prior to nest discovery. The clutch volume was calculated by measuring the length and breadth of the egg to the nearest 0.05 mm using Vernier callipers and entering these values into the egg index equation (Davis 1975). This equation was formulated on herring gulls and so it is not exact for great skuas, but it forms a good comparative measure of egg size.

2.2.2 The incubation period

In 1991 the distance from the study nest to the nearest neighbour was measured to the nearest metre using a surveyors wheel of 2m diameter. The distance to the nearest neighbour was measured to the nearest metre in 1992 using string knotted at 1m intervals. These measurements were made in the middle of the incubation period at a time when all nests were clearly visible. No measurements of inter nest distance were collected in 1993.

Birds trapped during incubation were weighed in a bag to the nearest 5g using a

1500g Pesola balance; bag weight was subsequently measured and subtracted. Measurements of maximum flattened cord (to the nearest 0.1mm) were taken with a wing rule and the tarsus bone, bill length (from feathers to tip of the hook) bill depth at the gonys and head and bill length (from back of head to hook tip) were measured to the nearest 0.01mm.

Aggression scores were recorded near the hatching time of the pair as this is when birds are at their most aggressive (Hamer and Furness 1992). The scores for the both members of the pair were taken over a 1 minute period whilst standing by the nest cup facing the wind, and the aggression was classed as hit the intruder (me) or did not hit the intruder. Scores were recorded only when both partners were present.

2.2.3 The chick stage

Nests were visited every 3-5 days to determine the fate of the eggs and the hatching date. Chicks were too small to ring at hatching and so an attempt was made to mark 'A' and 'B' chicks until their tarsi had developed sufficiently to take rings. In 1991 permanent marker was used on the webs of chicks feet but this wore off within 2 days and had to be constantly renewed. Liquid paper on the bill was used in 1992 but this also wore off fairly rapidly. Clipping the tip of one of the hind claws was used in 1993 and this was the most successful marking technique employed. There was no harm done to chicks through this technique and the claw grew back in time, but not within 10 days after which the chick could be ringed. In cases where chick asynchrony was successfully recorded up to ringing, the 'A' chick always had a longer wing length than the 'B' chick and so in broods which were of unknown asychrony the chick with the longer wing was classed as the 'A' chick.

Chicks were weighed and measured during the linear growth phase (between 14 days and 30 days). Weight was recorded to the nearest 5g using a 1000g Pesola balance, the maximum flattened cord was measured to the nearest 1mm with a 30cm wing rule. Chick age was calculated from the observed hatching date. Chick condition was estimated by subtracting the observed chick weight from the predicted weight of a chick of the same age according to the logistic equation describing chick growth in the 1970s (Furness 1983).

Study territories were visited every 5 days and the area was searched intensively for 10 minutes. If chicks were absent for 3 visits or more they were classed as dead. The ring numbers on disembodied legs were used to identify which chicks had been killed by conspecifics.

Chicks were classed as fledged if they survived for more than thirty days, unless they were found dead subsequent to this time. Though chicks do not actually fledge at this age, the mortality is negligible once this age is reached. Breeding success is defined as the proportion of eggs which survive to fledging, whereas fledging success is defined as the proportion of hatched chicks which survive to fledging.

2.2.4 Statistical analysis

Adult weight was corrected for body size by summarising the linear biometrics into a single index of size using principle components analysis. Body weight was then regressed against body size and residuals of the birds actual weight compared to its predicted weight from the regression line were calculated.

There were significant effects of year on laying date and clutch volume of 2 egg clutches, (Table 2.2.4). The effect of year was controlled for by standardising the mean for each year as zero and expressing values as residuals of the means before the data were pooled. Differences also occurred in fledging success between years. This difficulty was overcome by ranking the years according to fledging success and entering year as a categorical independent variable along with age in a multiple logistic regression. The effect of age independent of the year effect is quoted in the results.

Table 2.2.4: The effect of year on laying date and the clutch volume of 2 egg clutches of great skuas between 1991 and 199. Values are means with standard errors with sample sizes in parenthesis. The residuals of these means were used for analysis in the results chapter.

Variable	91	92	93	F	p
Laying date	19.1 ± 0.7 (61)	22.3 ± 1.1 (41)	16.0 ± 0.9 (0.9)	11.4	<0.001
Clutch volume	161 ± 16 (62)	166 ± 13 (48)	168 ± 12 (82)	5.22	<0.01

Attempts were made to sex birds using the discriminant equation described in Hamer and Furness (1991b). In order to control for consistent differences in measurment which can affect the accuracy of the discriminant technique, six dead great skuas were measured by both myself and Hamer. I tended to measure wings consistently shorter (a mean of 1.4mm) and measured tarsus and head + bill consistently longer (a mean of 0.4mm and 0.5mm respectively) and these values were used to correct my measurements to match those of Hamer. To test the accuracy of the discriminant technique three tests were used. Firstly, the sexes of birds which were sexed by observation of mating position were compared with the predicted sex from the discriminant technique. This technique sexed 65% (n = 12) of those birds measured by Hamer correctly and 64% (n = 20) of those birds I had measured correctly. Secondly the sex of 24 great skuas which were found dead and were sexed by internal examination were compared to the predicted sex from the equation. In this case the discriminant score predicted 75% correctly. Finally, for pairs in which both birds had been measured, the number of pairs for which the discriminant function classed both birds as female was 42%, meaning that it was only 58% accurate. Clearly the discriminant equation is less accurate than first supposed and this is not due to measurement differences between workers since it classed birds measured by myself and Hamer equally badly. For this reason the analysis was not split by sex except in cases where both birds were captured and measured. A factor score of size was calculated using principle components analysis and the female was classed as the largest bird in the pair since skuas display reversed sexual size dimorphism (Furness 1987).

To maintain independence of data a single observation was taken from each bird, reducing the sample size to 295 breeding attempts, all by individual pairs. Age was analysed as a continuous variable. All data were tested for normality using a Kolmogrov-Smirnoff test. Those data that were normally distributed (laying date, clutch volume, inter-nest distance and chick condition) were examined using regression analysis. The data which were non normally distributed (clutch size, hatching success, aggression and fledging success) were transformed into binary data and analysed using logistic regression. Thus hatching success, for example, was grouped into those that did not hatch a chick and those that hatched one or two chicks. Linear and polynomial models were fitted for both types of regression analysis and the one which best fits the data is presented. Polynomial models were used to test for declines in breeding performance with old age.

2.3 Results

2.3.1 The similarity of ages in a partnership

There was a weak but significant correlation between the ages of the male and the female partners within a pair ($r = 0.49$, $df = 40$, $p<0.05$). The exceptions to this are very old females (over 20) which were more frequently partnered with a young male than an old one (Fig. 2.1).

2.3.2 The egg stage

The date of clutch initiation ranged from 10 May to 30 June and advanced significantly with age (Linear regression; $r^2 = 0.11$, F = 15.07, df = 157, $p<0.0005$, Fig. 2.2). A multiple regression showed that the age of the female was important in determining the laying date (Linear regression; df = 25, $r^2 = 0.26$, F = 4.6, $p<0.02$, Fig. 2.3) while male age had no independent effect.

The size of the clutch was either one or two eggs. Two egg clutches occurred in 86% of nests between 1991 and 1993. The probability of a bird laying a 2 egg clutch increased significantly up to the age of 15 and then reached a plateau in older birds (logistic regression, $r^2 = 0.05$, df =1, Wald = 11.98, $p<0.001$ Fig. 2.4). There is a small but significant increase in the clutch volume of 2 egg clutches with age but there was no evidence for a decline with old age (Linear regression; $r^2 = 0.03$, df = 157, F = 5.9, $p<0.02$, Fig. 2.5). The increase in clutch volume was associated with male age (Linear regression; n = 38, $r^2 = 0.18$, F = 8.02, df = 36, $p< 0.01$, Fig. 2.6) and female age had no effect independently of the age of the male.

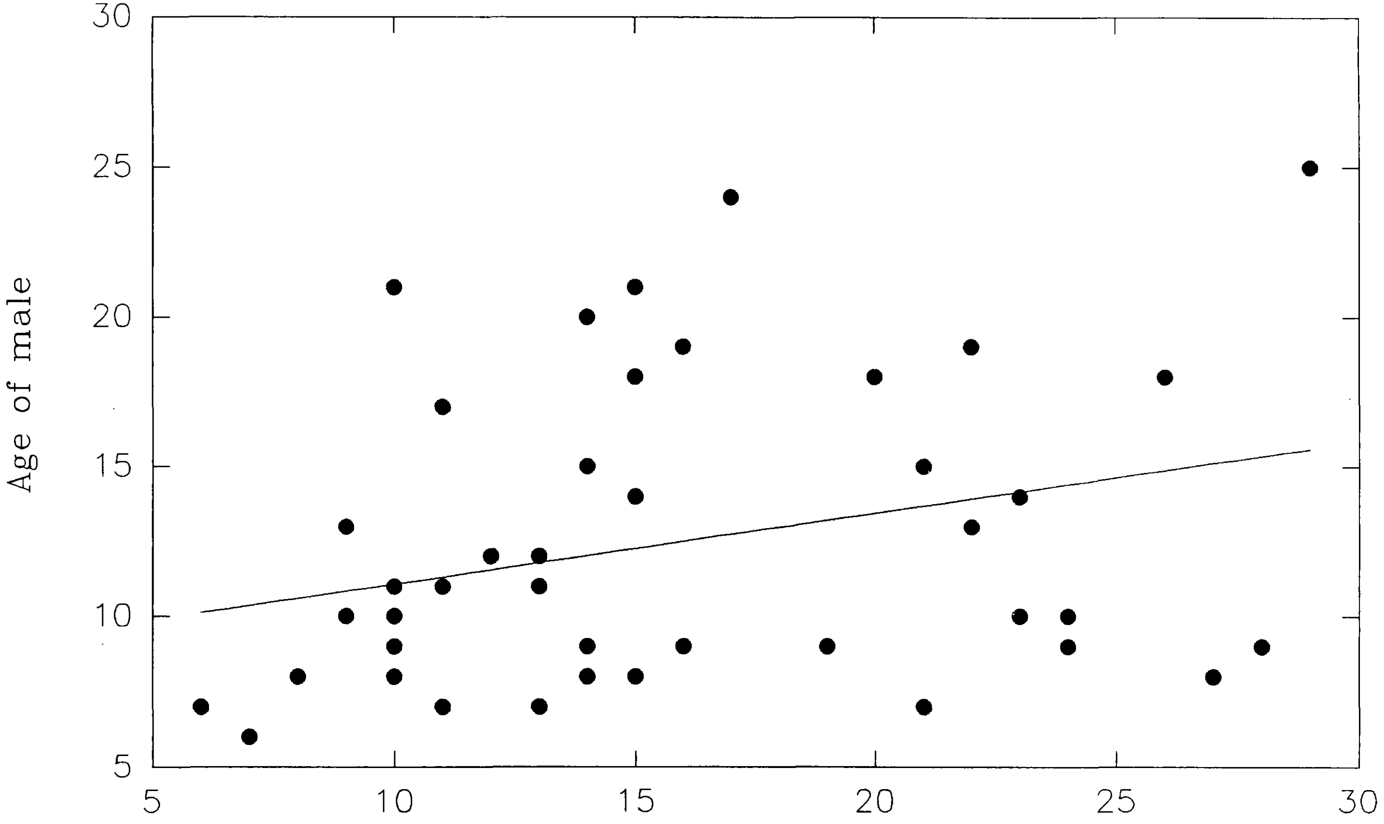
2.3.3 Inter-nest distance

The mean distance between the study nest and its nearest neighbour being 30m (± 1.47) and ranged between 8m and 89m. The inter-nest distance did not vary with age (Regression analysis, n = 80, $r^2=0.00$, F= 0.37, df = 78, $p>0.6$, Fig. 2.7).

2.3.4 Adult condition

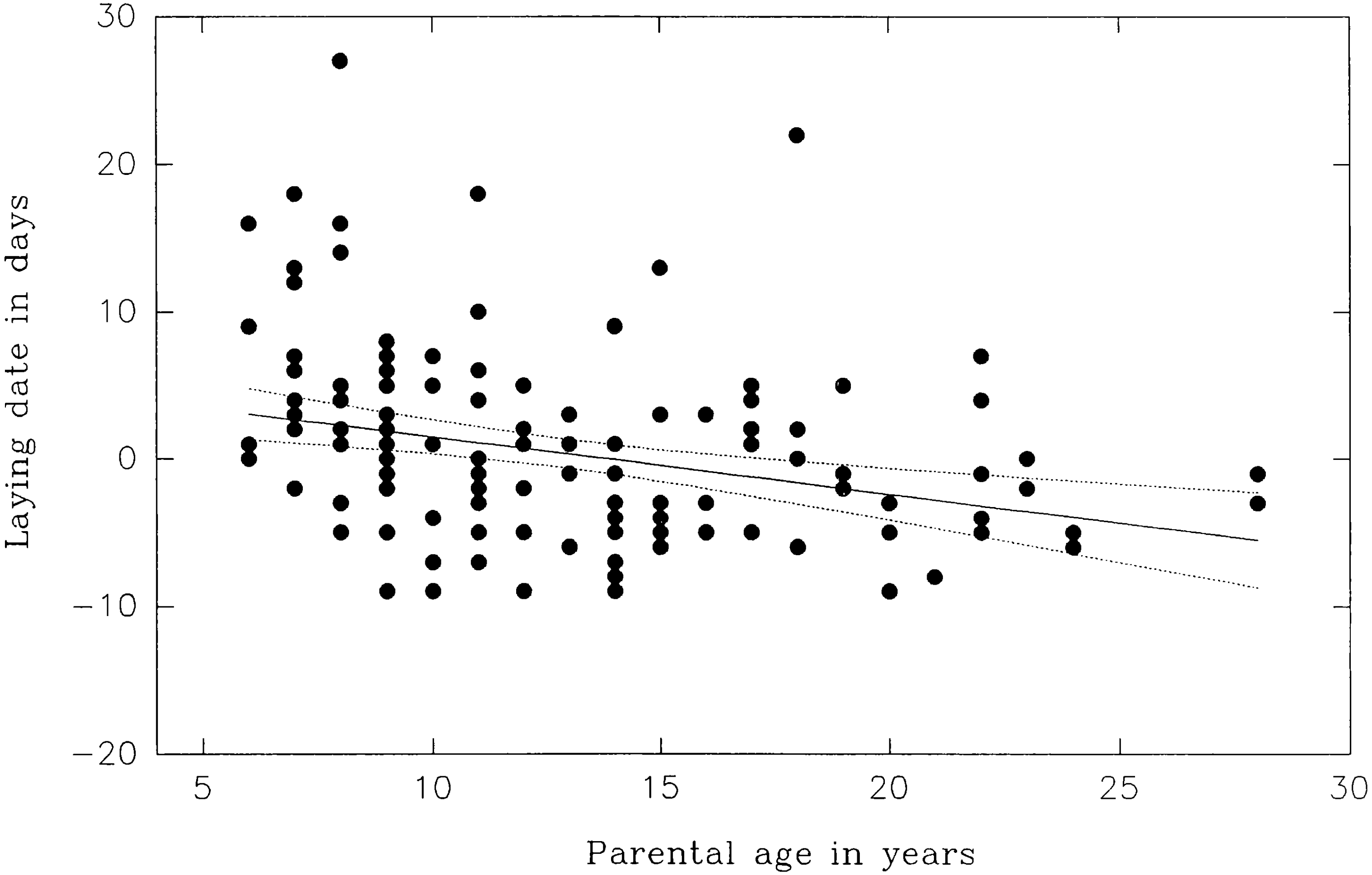
There was no significant effect of sex on adult condition (T-test; df = 1, t = -1.24, $p>0.2$) so data were pooled for analysis. The condition of a bird was not related to date of capture (Linear regression, n = 169, $r^2 = 0.00$, df = 167, F = 1.43, $p>0.2$).

Fig. 2.1: The relationship between the age of males and females within great skua partnerships.



Correlation analysis: n= 42, r = 0.49, df=40, $p<0.05$,

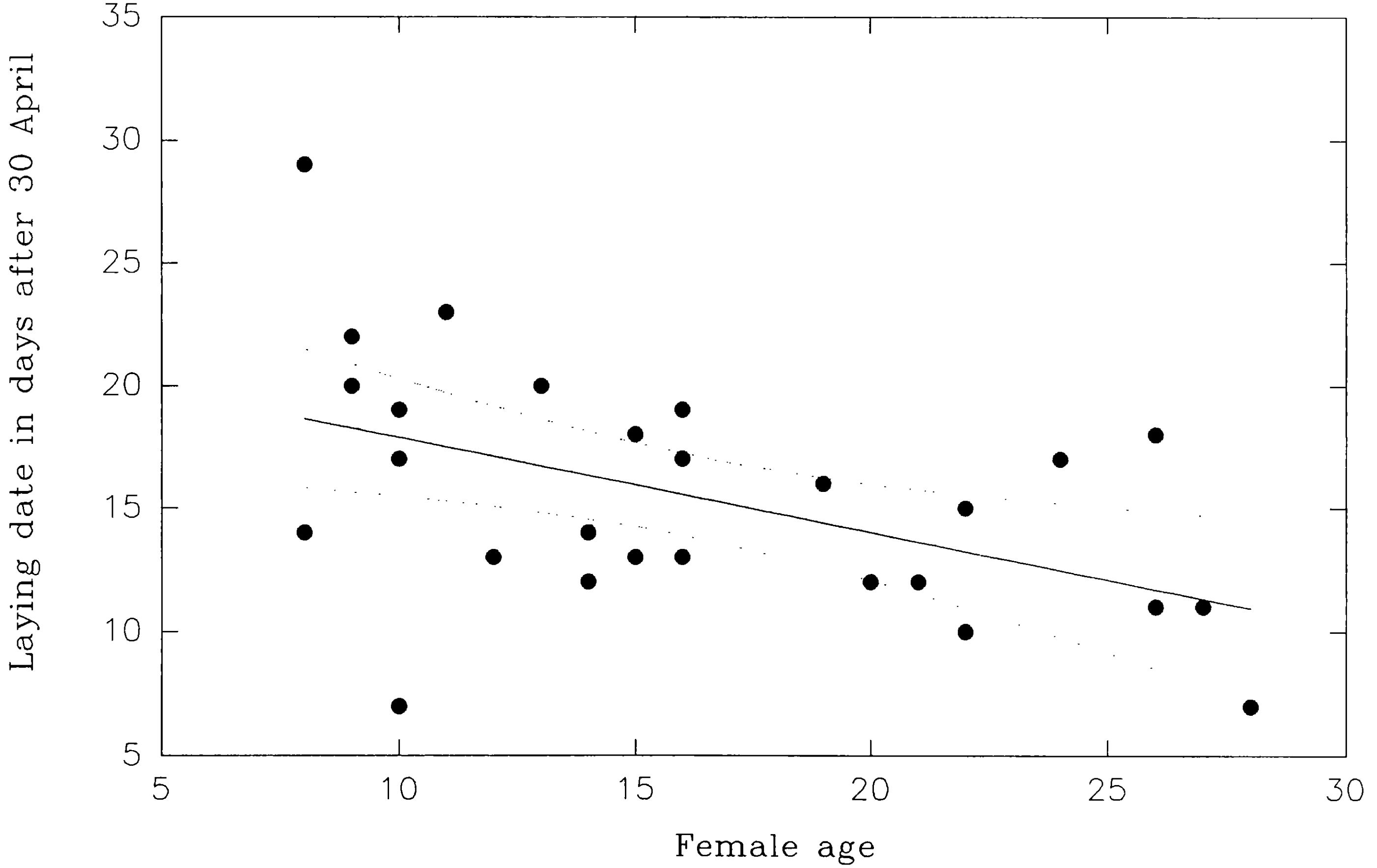
Fig. 2.2 The effect of age on the laying date of great skuas between 1991 and 1993. Values are days after the first of May which are standardised as residuals of yearly means.



Regression analysis; n=159, r^2=0.11,, F=18.16, p<0.0001.

Equation of the line: Laying date = −0.42age+5.6.

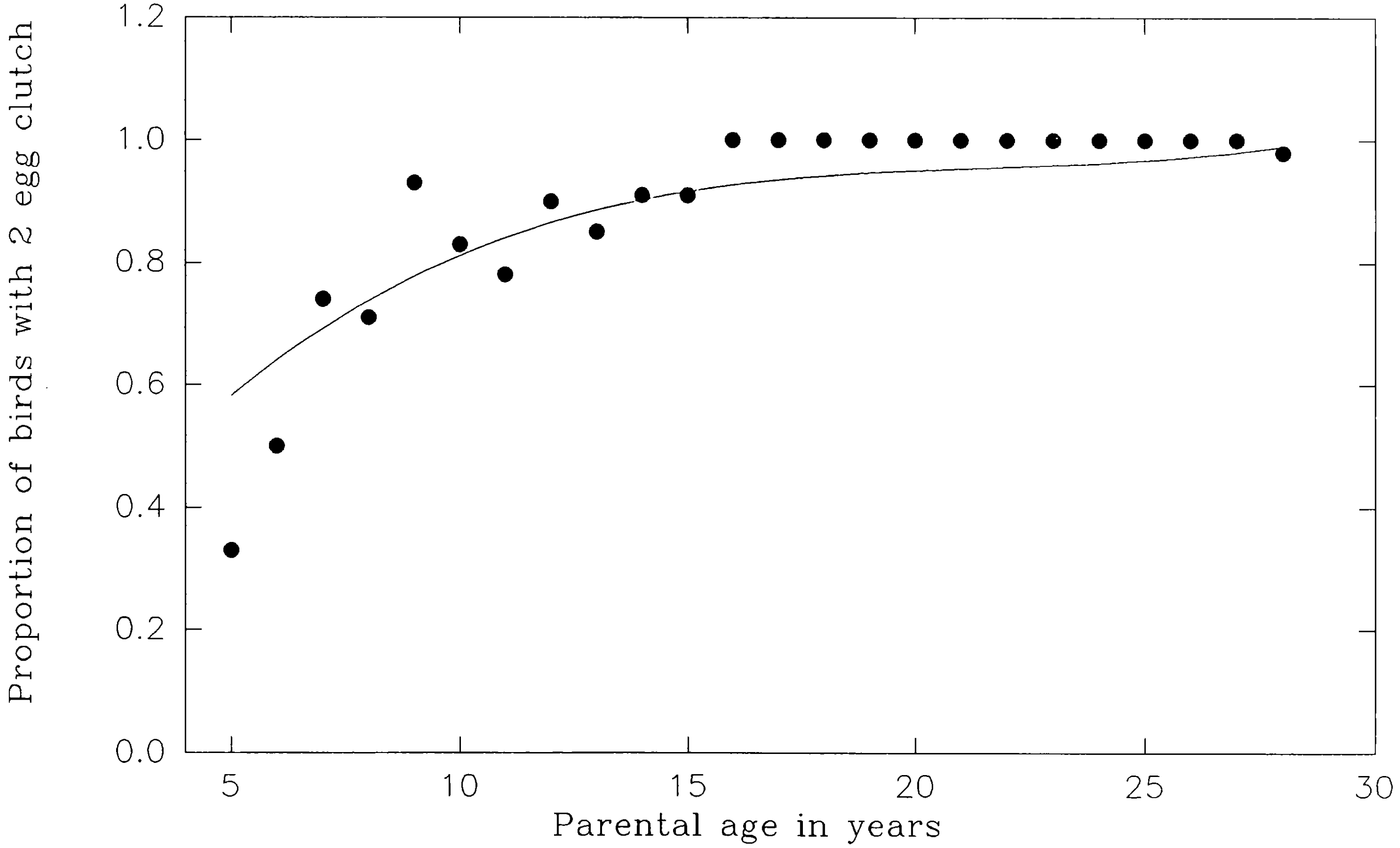
Fig. 2.3: The effect of female age on laying date of great skuas.



Linear regression analysis: $n = 27$, $r^2 = 0.26$, $F = 4.6$, $df=25$, $p<0.02$.

Equation of the line: laying date = 0.9age + 7.8.

Figure 2.4: The effect of age on the probability of a bird laying a 2 egg clutch the line represents the predicted clutch size from the logistic equation and the points are the percentage of birds that laid a 2 egg clutch in each age class

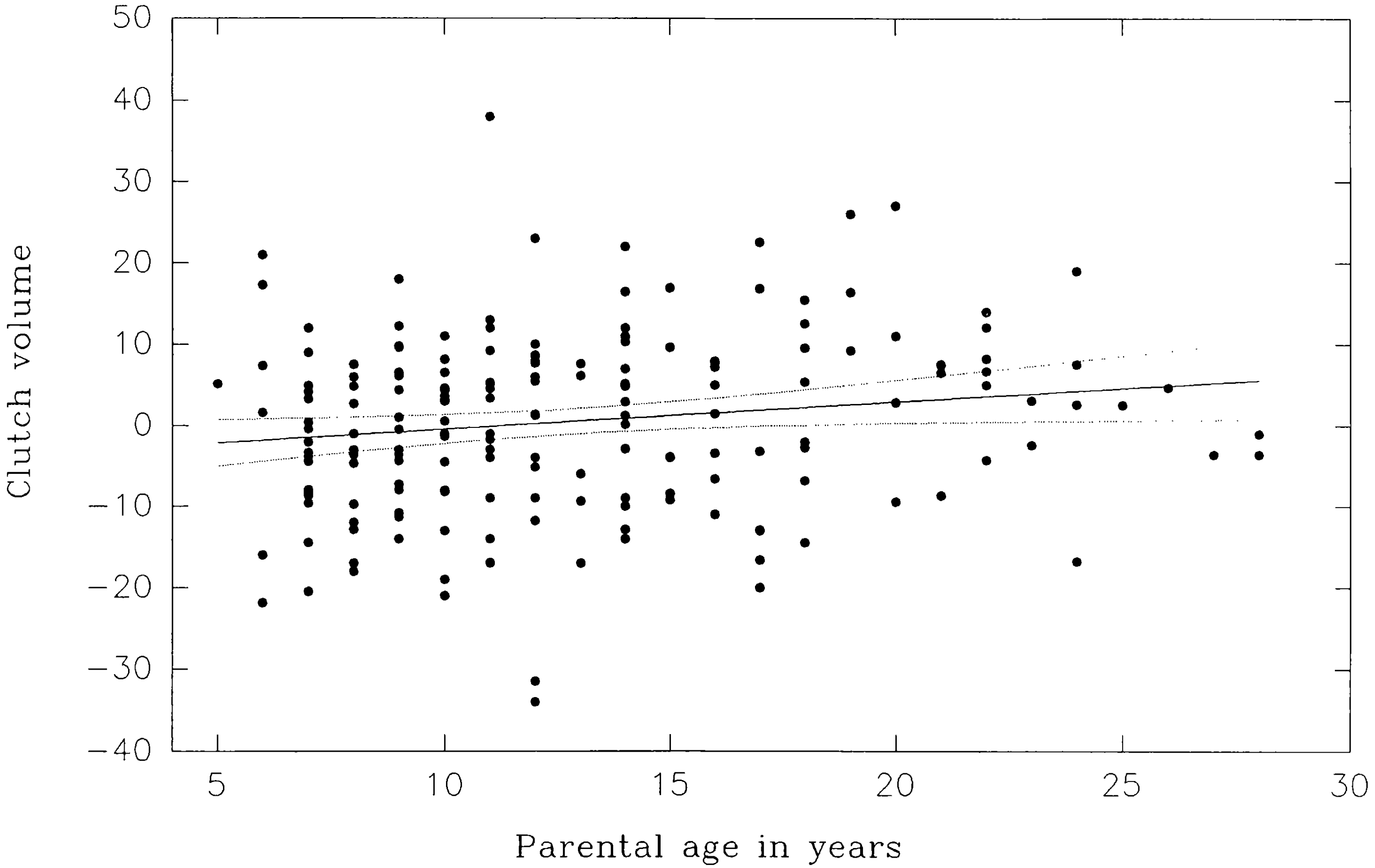


Logistic regression analysis: $r^2=0.05$, Wald=11.98, df=1, $p<0.001$

Equation of the line = $1/1+e^{-(0.15\text{age}-0.03)}$

Fig. 2.5 The effect of age on the internal clutch volume of 2 egg clutches.

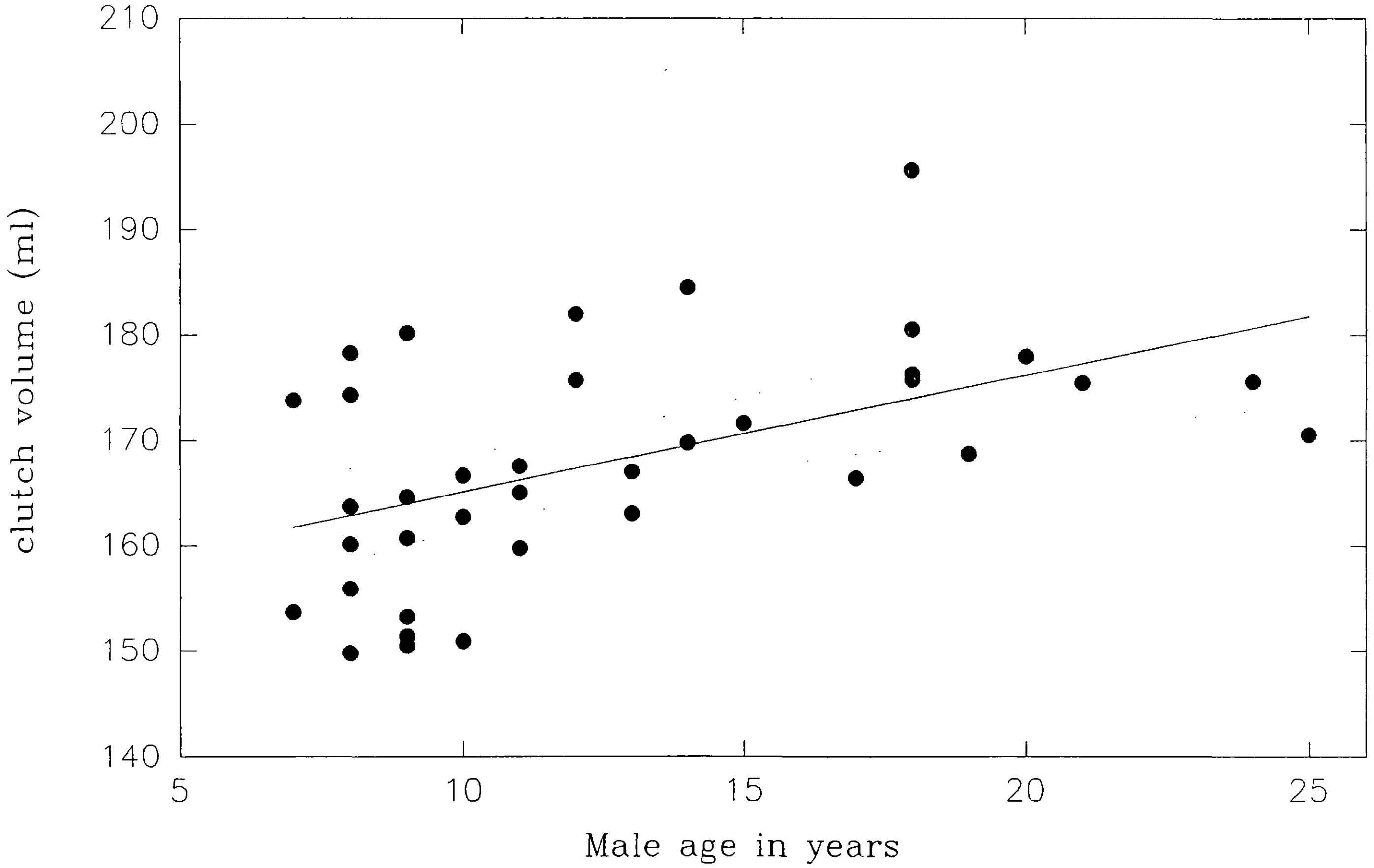
Values are expressed as standardised residuals of yearly means



Regression analysis, n= 159, $r^2 = 0.03$, F=5.9, df=157, $p<0.02$.

Equation of the line: clutch volume = 38.3age−504.

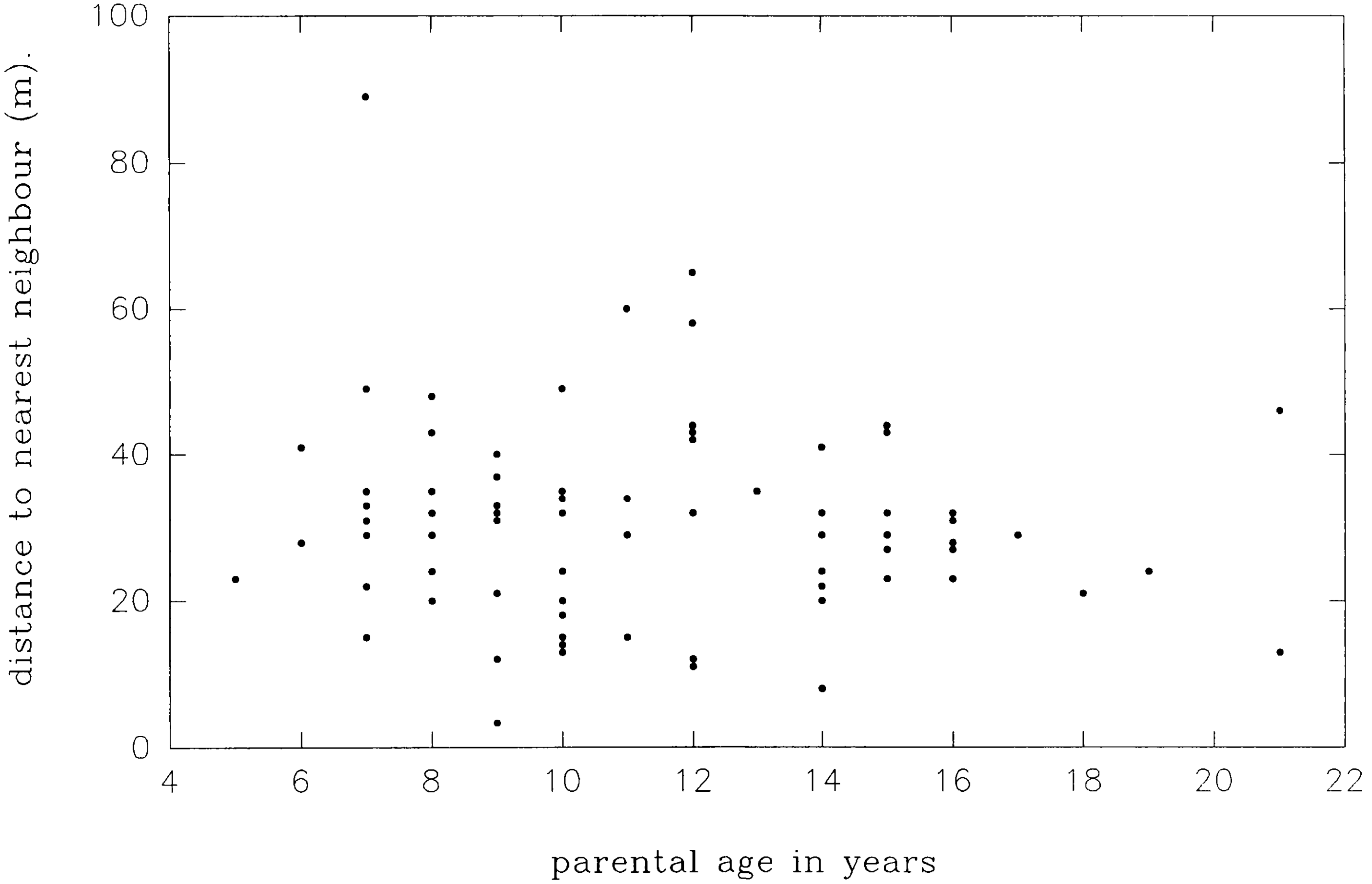
Fig. 2.6: The effect of male age on the clutch volume of 2 egg clutches



Linear regression analysis: $n = 38$, $r^2 = 0.18$, $F = 8.02$, $df=36$, $p<0.01$

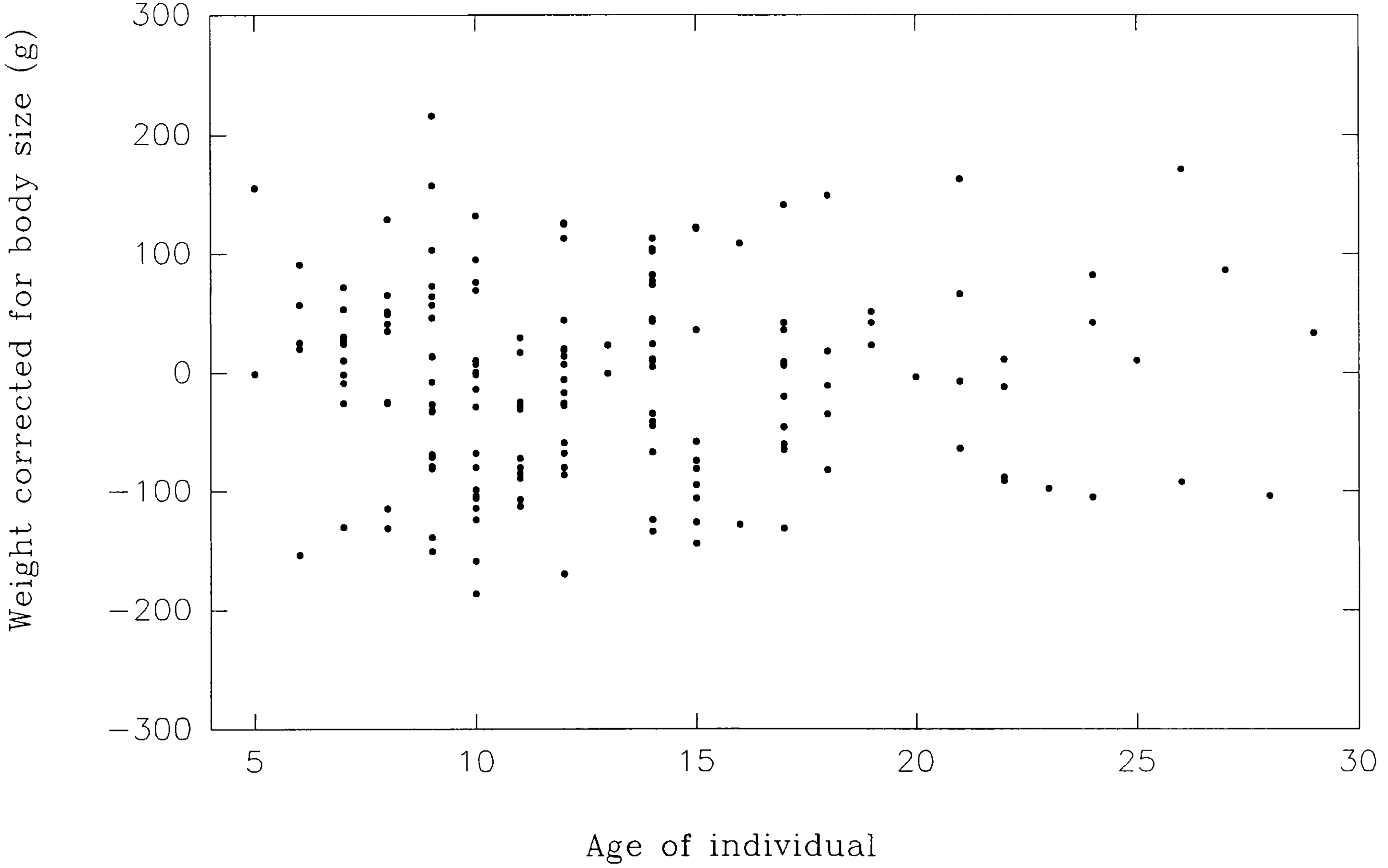
Equation of the line: clutch volume = 1.19age − 15.7.

Fig. 2.7: The effect of age on the distance between a study nest and its nearest single neighbour.



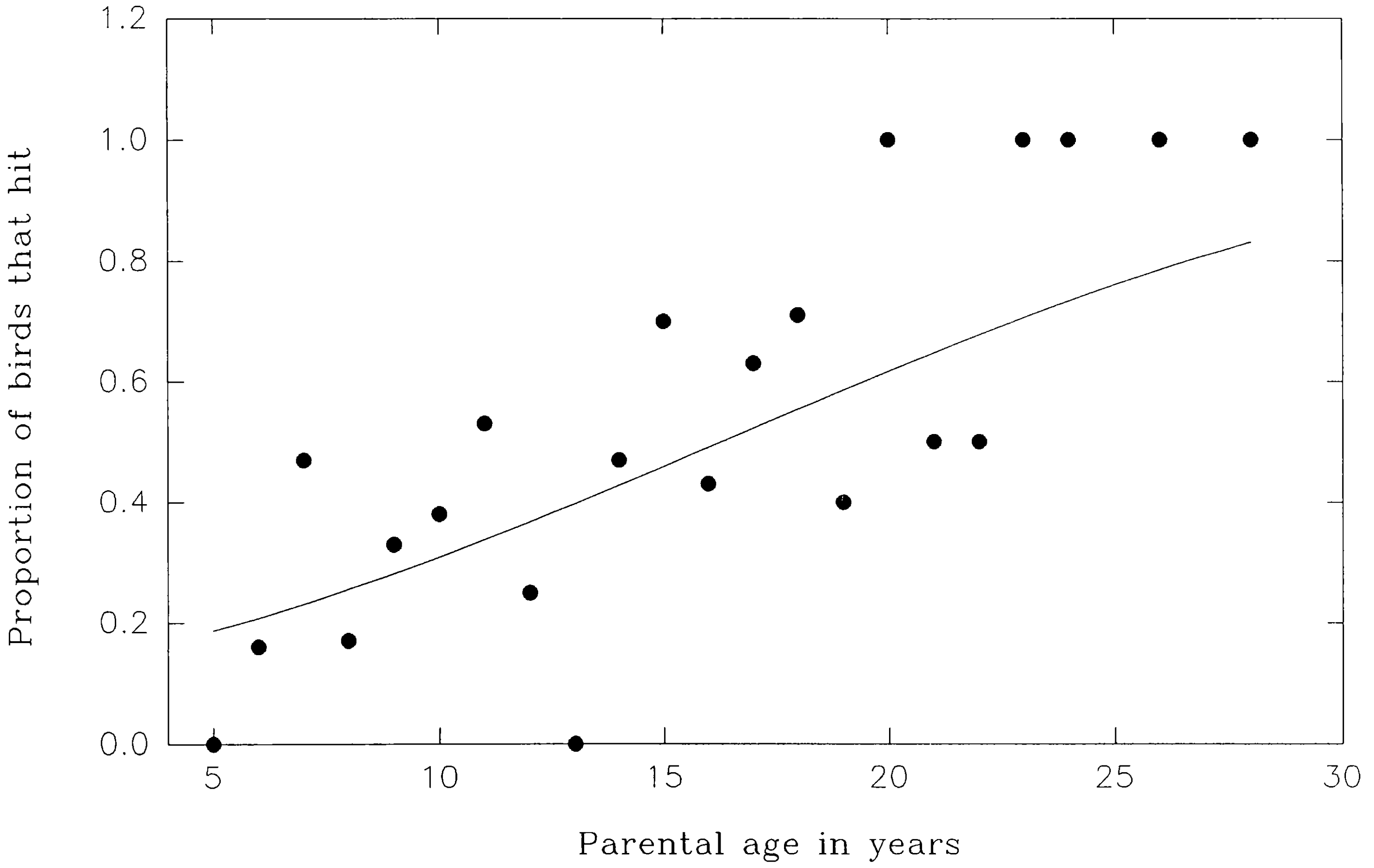
Regression analysis: n= 80, $r^2 = 0.00$, F=0.3, df=78, $p>0.7$

Fig 2.8: The effect of age on the body condition of great skuas.



Regression analysis: n=169, r^2=0.00, F= 0.0, df=169, p>0.9

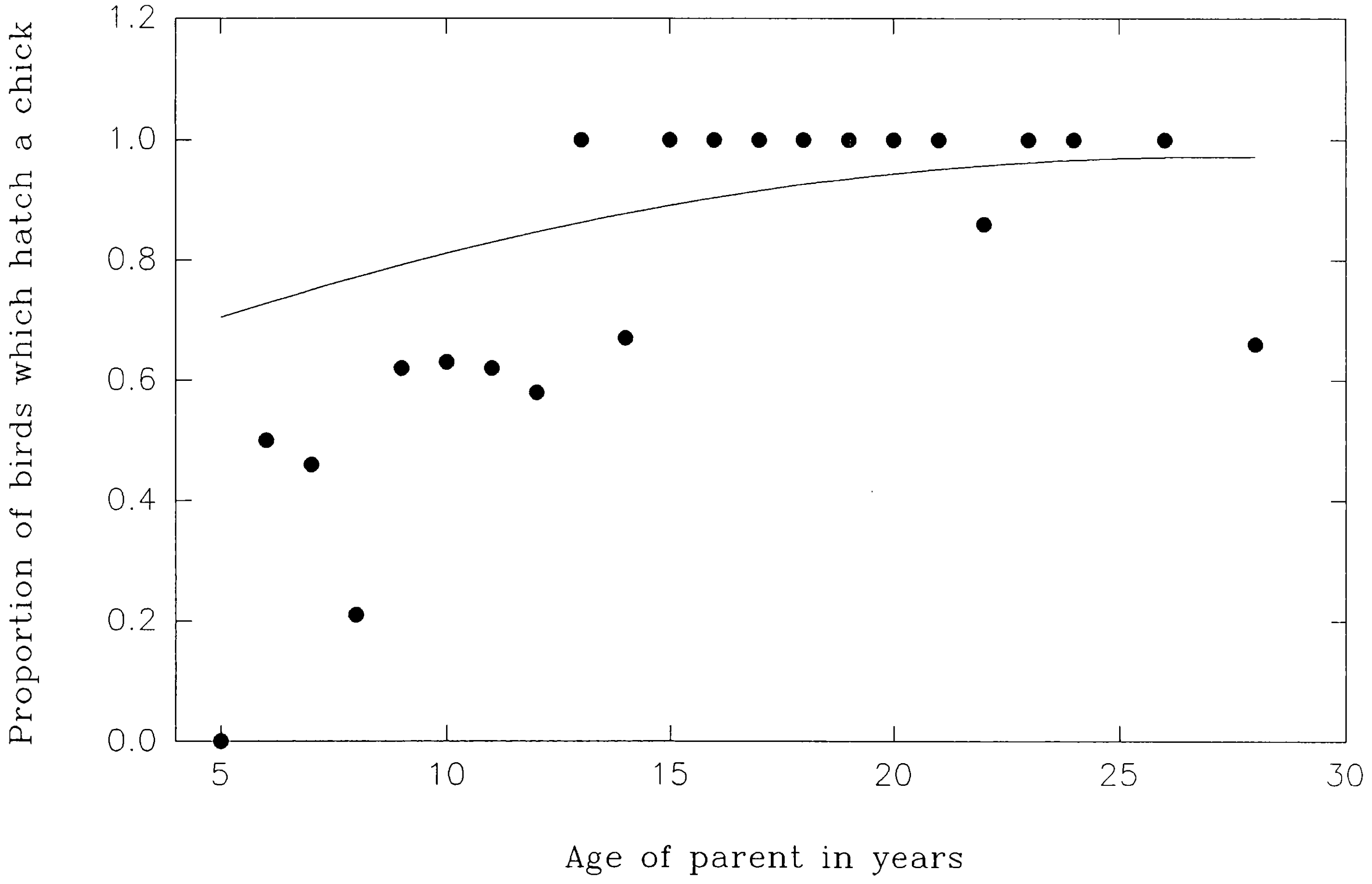
Fig. 2.9: The effect of age on the probability of a pair hitting a human intruder



Logistic regression analysis: $n = 186$, $r^2 = 0.06$, Wald $= 15.96$, df $= 1$, $p<0.0001$

Equation of the line $= 1/1+e^{-(0.13\text{age}+2.16)}$

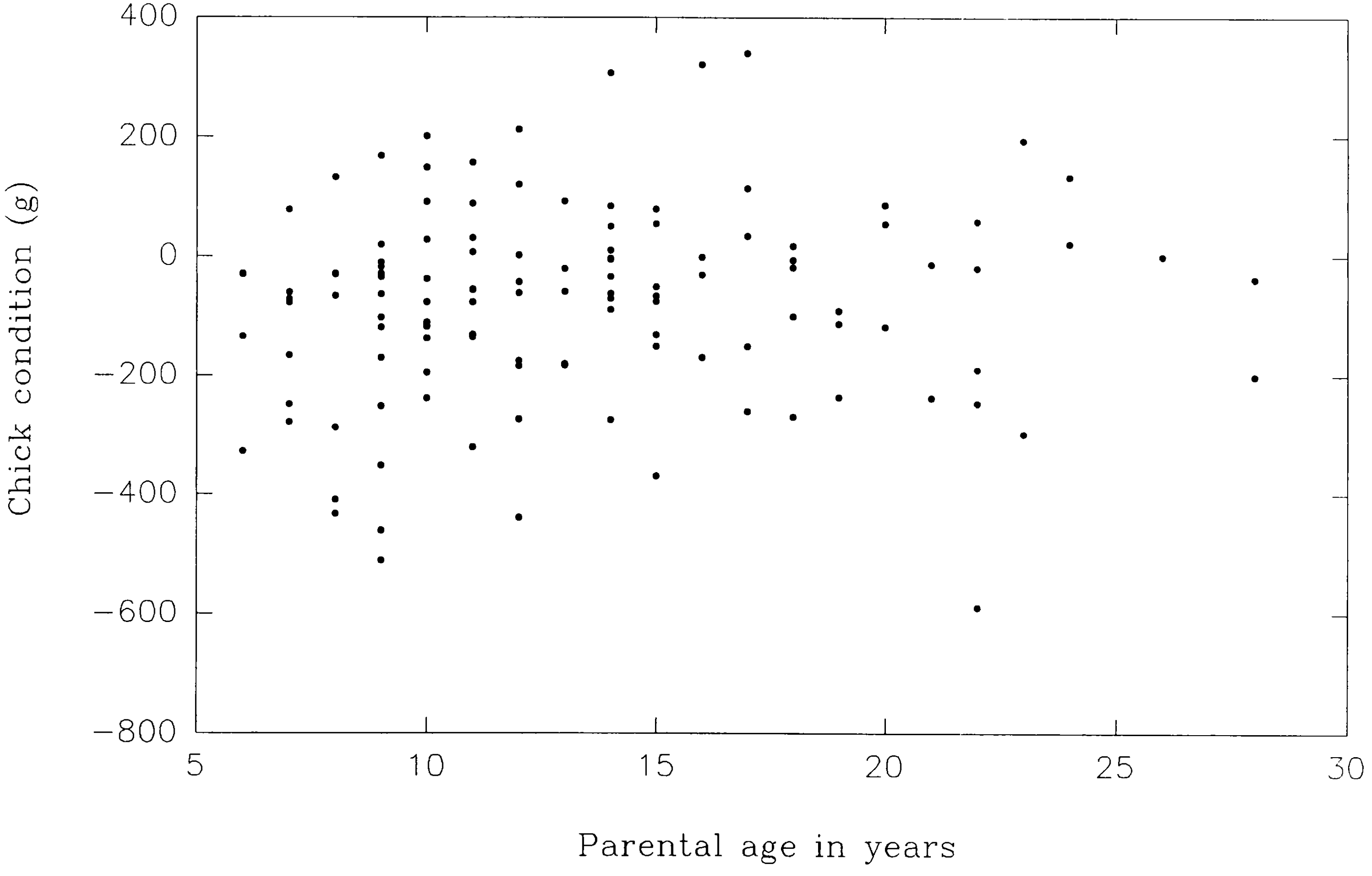
Figure 2.10: The effect of age on the proportion of birds that successfully hatch a chick



Logistic regression analysis: $n = 215$, $r^2 = 0.02$, Wald $= 6.77$, $df = 1$, $p<0.02$

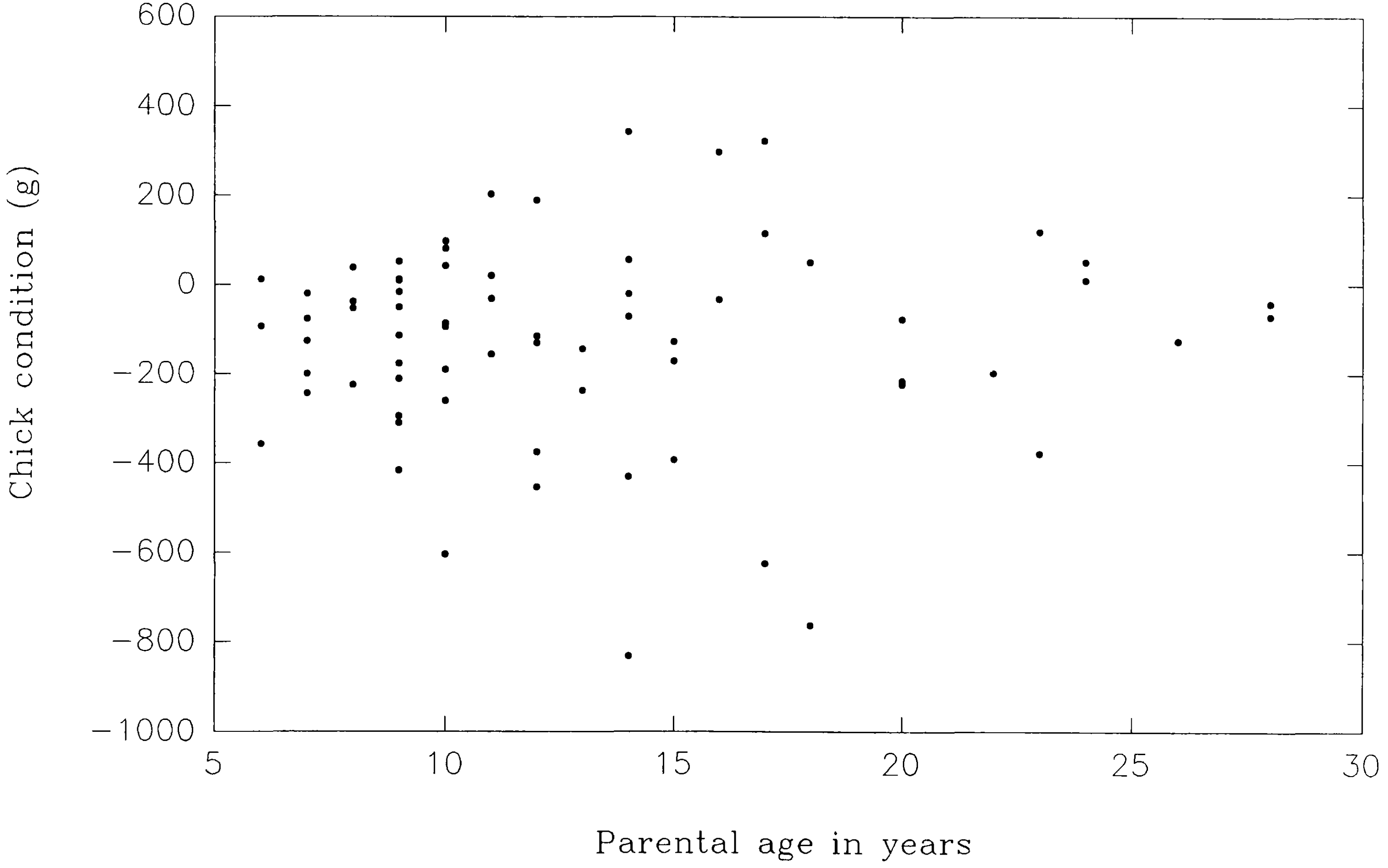
Equation of the line: $1/1+e^{-(0.21age+0.13)}$

Fig.2.11 The effect of age on the condition of the 'A' chick. Values are expressed as residuals from the growth curve in Furness (1983)



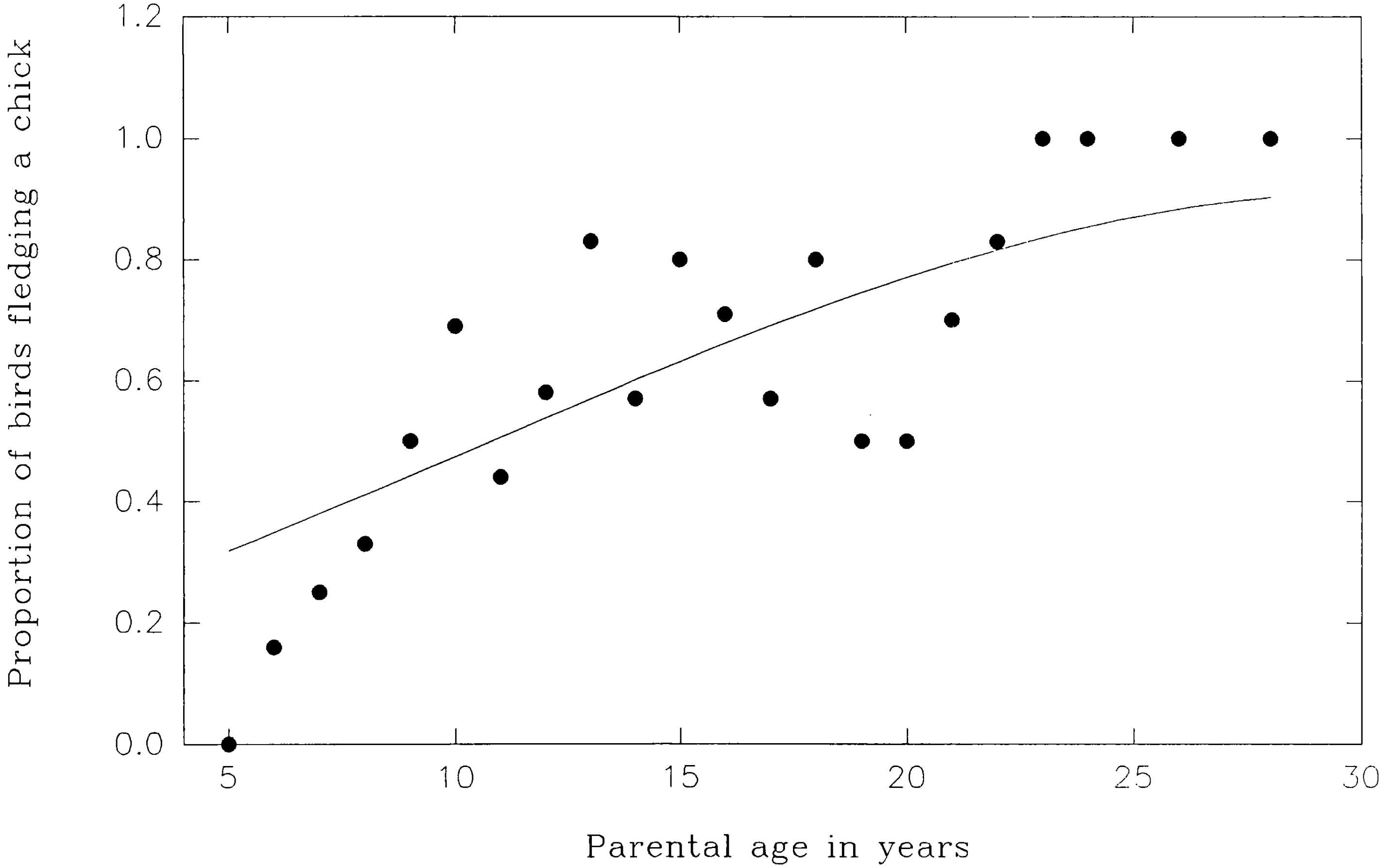
Regression analysis; n= 124, r^2 = 0.00, F= 0.77, df= 122, p>0.3

Fig. 2.12: The effect of age on the condition of the 'B' chick. Values are expressed as residuals from the growth curve in Furness (1983)



Regression analysis; n=70, $r^2 = 0.00$, F= 0.04, df=68, $p>0.8$

Figure 2.13: The effect of age on fledging success. The points represent the proportion of birds which fledged one or more chicks and the line is described by the logistic regression equation



Logistic regression analysis: $n = 168$, $r^2 = 0.05$, Wald = 12.49, df = 1, $p<0.0005$

Equation of the line = $1/1+e^{-(0.13\text{age}-1.42)}$

The age of a bird did not significantly affect its condition (Linear regression, $n = 169$, $r^2 = 0.00$, $F = 0.0$, $df = 167$, $p>0.9$, Fig 2.8).

2.3.5 Aggression

The proportion of birds that would hit a human intruder was 38% and physical contact increased highly significantly with age (logistic regression; $n=186$, $r^2 = 0.06$, Wald = 15.97, $df = 1$, $p<0.0001$, Fig. 2.9).

2.3.6 The hatching stage

The fates of eggs in 215 study nests were determined between 1991 and 1993. The hatching success was 80%, with egg losses being due to predation by conspecifics or Arctic skuas (pers obs) and also by addling (infertility or early embryo death). There was a significant increase with age in the probability of a bird hatching a chick (logistic regression; $n=215$, $r^2 = 0.02$, Wald = 6.77, $df = 1$, $p<0.02$, Fig. 2.10).

2.3.7 Chick condition

The 'A' chick in a brood was in significantly better condition than the 'B' chick (Paired T-test; $df = 1$, $t = 2.4$, $p<0.02$) by an average of 26g ± 1.2g. There was no difference between single chicks and the 'A' chick of 2 chick broods (t-test; $t = -0.18$, $df = 1$, $p>0.8$) and so they were grouped for analysis.

There was no significant effect of parental age on the condition of 'A' and single chicks (linear regression, $n = 124$, $r^2 = 0.00$, $F = 0.77$, $df = 122$, $p>0.3$ Fig. 2.11) nor 'B' chicks (linear regression, $n=70$, $r^2 = 0.00$, $F = 0.04$, $df = 68$, $p<0.87$, Fig. 2.12).

2.3.7 Fledging success

The main cause of chick death was apparently predation by conspecifics, as all chicks found dead were partially eaten and many live but wounded chicks were also found. The chicks were usually found dead on their own territory and time budget studies (see chap 5) showed that it was the chicks parents that were feeding on them, rather than neighbouring great skuas as had previously been assumed. Fledging success increased highly significantly with age (logistic regression, n=168, $r^2 = 0.05$, Wald = 12.49, df=1, $p<0.0005$, Fig. 2.13) but there was no evidence of a decline in fledging success with old age.

Increases in fledging success with age could result from inter-correlations between age and other variables earlier in the breeding season. There was no effect of clutch volume, inter nest distance nor chick condition on fledging success (logistic regression; all Wald values <0.2, p values >0.6). Fledging success improves significantly with the advancement of laying date (Logistic regression; Wald = 16.27, df=1, $p<0.0001$) and increased aggression (Logistic regression; Wald = 14.57, $p<0.0001$) both of which improve with age. The increase in fledging success with age could result from them laying earlier and being more aggressive. However multi-variate analysis shows that the effects of age and aggression on fledging success are independent (Multiple logistic regressions: Age, Wald = 7.73, df=1, $p<0.01$; Aggression, Wald = 9.10, df=1, $p<0.005$). The effects of laying date and age are also independent (Multiple logistic regression: Age, Wald = 5.30, df=1, $p<0.05$; Laying date, Wald = 10.98, df=1, $p<0.001$).

2.4 Discussion

There was a weak correlation between the ages of birds within a pair. Age similarities within pairs have been documented in many species (Richdale 1957, Ainley *et al.* 1983, Nisbet *et al.* 1984, Newton *et al.* 1984, Thompson and Hale 1991). This suggests that pairing is non random and birds will attempt to mate with an older bird to increase breeding success, with the net result that ages within pairs will be similar (Shaw 1985). Age similarities could also result from the partners recruiting at a similar age and then maintaining a pair bond for a number of years (Perrins and Mc Cleery 1985, Reid 1988b). Great skuas have a low mortality (see Chapter 6) and a high mate fidelity (90%) and so age similarities at recruitment could be preserved in the absence of non-random mating. The tendency for females over the age of 20 to mate with males less than 10 years old suggests that mating is random rather than selective with regard to age. Mougin *et al.* (1988) found that mating was random in Corys shearwaters, with the proportion mated with partners of a similar age decreasing as birds became older. Similarly, in many Charadriiformes very old birds tend to mated with young ones (Coulson 1966, Mills 1973, Davis 1976, Coulson and Horobin 1976). This effect can be due to females having a higher suvival rate than males, forcing them to mate with a young male after their former partner has died (Mills 1973). This effect will be enhanced by the high mate fidelity in great skuas which will reduce the number of older males available for pairing (Reid 1988b). An alternative explanation is that, since senescence may occur in old females, males will no longer select them since they will reduce breeding output (Reid 1988b).

The advancement of laying date with age in great skuas is the most consistent of the breeding variables recorded, this difference being evident even in the 1970s when a super abundant food supply removed all other age-specific differences in breeding (Furness 1984). Laying date advances with female age rather than male age a similar finding to other studies (Perdek and Cave 1992, Desrochers and Magrath 1993). There is a selective basis for and advancement in laying date since early laying improves overall breeding success (Parsons 1970, Perrins 1970, Hunt and Hunt 1976, Moss *et al.* 1981).

Single egg clutches are infrequent in great skuas and were formerly attributed to poor quality breeders (Furness 1984). The probability of single egg clutches decreased with age up to the age of 16 before increasing in older birds, probably due to senescence (Davis 1975, Haymes 1980, Wooller *et al.* 1990).

The clutch volume of 2 egg clutches increased with age but no decline in clutch volume with old age could be found, despite the fact that Hamer and Furness (1991a) found a decline after the age of 14. However the proportion of the variation in clutch volume explained by age was very small in both studies (<1%) and so the biological significance would be minimal. Male age rather than female age is important in improving clutch volume, probably due to improved foraging skills in older males allowing them to increase the amount of courtship feeding which is an important factor in egg formation (Slazer and Larkin 1990).

The lack of increase in territory size with age contrasts with the findings of Pugesek and Deim (1983). In many species increased territory size is associated with increased chick survival (Hunt and Hunt 1976) but there is no evidence for this in great skuas. It seems there is no real selective advantage to increasing territory size which accounts for the lack of age-specific increases in inter nest distance.

Hatching success increased with age, though the separate effects of predation and addling could not be separated. This suggests that old birds promote hatching success by improving fertility of eggs, incubation and clutch defence. Older birds were certainly more vigorous in clutch defence than younger ones (see results, Hannon and Smith 1984, Raveling 1981, Hamer and Furness 1991a) and the increased aggression improves hatching success and fledging success (see results, Hamer and Furness 1993).

There was no decrease in the condition of a bird as the season advances, suggesting that there is no physiological cost of reproduction in terms of weight loss (Askenmo 1977, Reid 1987) nor an adaptive decrease in wing loading in response to increased foraging demands (Freed 1981, Norberg 1981). Condition would be expected to decrease with age as older birds are expected to have a higher foraging effort (Clutton Brock 1984) which will deplete somatic reserves. There is no evidence for such a decline in condition with age in this study. Alternatively, condition could increase with age since older birds are more efficient at foraging (Aldritch and Raveling 1983, Willebrand 1992).

The 'A' chick was in better condition than the 'B' chick in all years studied, which shows that asychronous hatching gives the 'A' chick a competitive advantage over its sibling. There were no differences between single and 'A' chicks in broods of 2, a contrast to the findings of Furness (1983) who found 'A' chicks were in better condition than single ones due to single chicks ceasing to beg for food when satiated whereas 'A' chicks will continue to eat regurgitates solicited by their siblings.

There was no effect of age on condition of either chick, this finding being concurrent with that of Hamer and Furness (1991a). Chick condition did not improve fledging success in this study, though Hamer Furness and Caldow (1991) found an increase in fledging success and also with post-fledging survival for up to 3 years with improved chick condition. Old birds would be expected to improve chick condition to increase fledging success, however young birds were able to elevate chick growth to the level found in older birds by increased foraging effort (see Chapter 5).

Chick death was primarily due to conspecific predation from neighbouring pairs and this accounts for the lack of relationship between chick condition and fledging success. Death could result from chicks wandering from their territory and being killed by agonistic behaviour from neighbouring birds (Hunt and Mc Loon 1975). However most chicks were found dead on their own territory, being consumed by their own parents. It seems that neighbouring birds killed chicks when both parents are away foraging attempting to maintain chick growth (Hamer Furness and Caldow 1991).

Fledging success improved with age (see results, Hamer and Furness 1991a) and this effect was not only due to the inter-correlations of age and laying date, a similar result to Enoksson (1993). Age specific improvements in fledging success were due to age-specific variations in the trade off between chick provisioning and chick defence (Martin 1987). Young birds invested time in chick provisioning at the expense of defence while older birds synchronised guard duties more efficiently (see chapter 5) and defended chicks more vigorously (see results).

2.5 Conclusions

This chapter shows that age affected the breeding ecology of the great skua on Foula during the years studied. The proportion of variation in breeding parameters which was explained by age was small and results are inconsistent between years (Compare findings of this chapter with Furness 1984, Hamer and Furness 1991). However, since skuas are long-lived species age specific breeding patterns could play significant role in the life history strategy and total reproductive success of a bird. The following chapters discuss the possible reasons for age specific patterns in reproduction.

Chapter 3

The effect of age and food availability on breeding in great skuas

3.1 Introduction

The availability of food is thought to be an important factor in avian reproductive biology in terms of parental condition and lifetime reproductive strategy. Research into the effect of food supply on breeding has been by correlative studies, which examine changes in breeding parameters in years with varying food supply, and experimental studies in which supplementary food is provided, usually during the pre-laying period. These studies have demonstrated that improved food supply can advance the age of first breeding and decrease the proportion of birds taking years off (Pietiainen 1988, Boekelheide and Ainley 1989), advance laying date (Kallander 1974, Daan and Dijsktra 1988, Korpimaki 1989) increase clutch and egg size (Korpimaki 1991, Bolton *et al.* 1992) and improve chick condition and fledging success (Manjit *et al.* 1991, Sydeman *et al.* 1991).

It is widely documented that young birds have lower breeding success than older ones (see Ryder 1981 and Saether 1990 for reviews) a trend which has also been shown in great skuas (Hamer and Furness 1991a). Despite the fact that many studies have been conducted on the effects of age and nutrition independently, very few have examined the inter-relationships between the two factors, with only two correlative studies (Boekelheide and Ainley 1989, Sydeman *et al.* 1991) and two manipulative studies (Krapu and Doty 1979, Desrochers 1992). These studies have demonstrated that age specific differences in reproduction are most evident when food abundance is low.

One of the reasons that has been used to account for this trend is that young birds cannot forage as efficiently as older ones (Searchy 1978, Caroll and Cramer 1985, Mac Lean 1986, Desrochers 1992) and so in conditions where food supply is poor they lack the necessary foraging skills needed to breed successfully. Alternatively, in years of poor food supply the amount of foraging effort invested in breeding will be higher and this increased effort can produce a cost in terms of survival (Hamer, Furness and Caldow 1991). In such a situation, young birds may reduce the amount of effort they invest in breeding and conserve their reproductive value until conditions improve, while old birds should maintain high effort to maximise offspring production in their final breeding attempts. This explanation has been used to account for the interactions of food supply and age found in Brandts cormorant (Boekelheide and Ainley 1989) and Western gulls (Sydeman *et al.* 1991) but the findings could be equally well explained by lower foraging efficiency in young age groups.

This chapter tests the hypothesis that improved food supply will improve breeding performance and reduce age specific differences in breeding performance. Firstly the correlative approach is used by examining the breeding ecology of known age birds in relation to sandeel abundance. Sandeel was the favoured food-fish of great skuas in the early 1980's, with a high calorific value which promoted chick condition (Furness and Hislop 1980). The abundance of sandeel was reduced drastically in Shetland waters in 1984-1990 which was correlated with a reduction in the breeding success of great skuas on Foula (Hamer, Furness and Caldow 1991). In 1991 the sandeel stocks improved and by 1993 had returned to levels found in the 1970s. This increase in sandeel populations is interpreted as an improvement in food supply. Secondly, this chapter adopts an experimental approach and investigates the effect of supplementary feeding on egg production in known age birds.

3.2 Methods

3.2.1 The correlative study

The breeding success of known age great skuas was studied in years of poor food supply (1989-1990), intermediate years (1991-1992) and a good year (1993) in a similar manner to other studies of this nature (Pietiainen 1988, Boekelheide and Ainley 1989, Sydeman *et al.* 1991). The availability of sandeel in the years was estimated from the proportion of sandeels observed in regurgitates. The regurgitated chick feeds were observed with x8 binoculars or x20 telescope together with samples produced while handling chicks.

Laying dates were estimated by observation of the date on which the first egg was found or back-dated from the hatching date minus the mean incubation period (c 29 days). The number of eggs (1 or 2) in the clutch was counted at clutch completion and a check was made round all nests for eggs which may have been eaten or displaced from the nest cup. The length and maximum breadth eggs were measured to the nearest 0.01 mm using Vernier callipers and these values entered into the egg index equation (Davis 1975) to calculate egg volumes.

The volumes of the 'A' and 'B' eggs were summed to calculate total clutch volume of 2 egg clutches. The proportion of eggs in a clutch which hatched was determined by visiting the nest cup once every 2 days during the hatching stage, the eggs were classed as hatched, eaten or addled. The number of chicks fledged was estimated by the number of chicks which survived for more than 30 days and not found dead subsequent to this period. This value was used to calculate breeding success by dividing it by clutch size and fledging success by dividing it by the number of chicks hatched. Initially the effect of food abundance on breeding was assessed independently of age. The interactions of year and age were studied using Analysis of Covariance for parametric variables and by an interactive logistic regression in the case non-parametric data.

3.2.2 The experimental study

The experiment was conducted on 41 pairs in which at least one bird was of known-age (20 in 1992, 21 in 1993). Experimental birds were fed 400g of 'Whiskas Supermeat' tinned cat-food per pair per day until clutch completion. This provided 34.4g of protein and 1118Kj of energy per day. The basal metabolic rate of great skuas is 543.1Kj (Bryant and Furness in press) and the field metabolic rate is 3.24 times BMR (Birt-Freisen *et al.* 1989). From these data one can calculate that the food supplement provided 30% of the energy requirements for both birds in the pair (this figure is corrected for an estimated 80% food utilisation efficiency). Feeding was initiated approximately 10 days prior to laying to provide nutrition during the rapid follicle growth stage (Brown 1967).

Food was put on the favoured resting area in the experimental pairs territory during the evening when attendance was high. This improved the chances of the pair being present when the food was deposited and made it easy for them to find. Observations were conducted to check that the experimental birds were eating the food. These confirmed that the pair did eat the food and that they defended it vigorously from intruders. The birds soon learned to associate my approach with food and would often begin to feed before I had left the territory. In cases where both birds were absent, the food was hidden by covering it with vegetation on the resting site so that it would be invisible from the air but could be found by the territory holding bird on the ground.

The laying date was determined by daily checks of the territories for nests. The clutch size (1 or 2) was recorded and a search for eaten or displaced eggs was conducted round the nest cup of 1 egg clutches. The egg length and breadth were measured to the nearest 0.05 mm and these values were entered into the egg volume equation (Davis 1975) to calculate the clutch volume. As sample sizes were small in the experimental group, egg production was assessed by analysing total clutch volume of all clutches rather than splitting analysis into clutch size and volume of 2 egg clutches. Laying date and total clutch volume were significantly affected by year (see table 3.2.2) and so residuals of the mean were used for analysis to remove this effect.

Table 3.2.2: The effect of year on laying date and total clutch volume. The values are means with standard errors and the values in parenthesis represent the sample size. Residuals of these means were used in subsequent analyses.

Variable	1992	1993	F	p
Laying date	19.6 ± 0.6 (106)	169 ± 47 (171)	13.1	<0.0005
Total clutch volume	158 ± 0.23 (106)	116 ± 16 (171)	7.21	<0.001

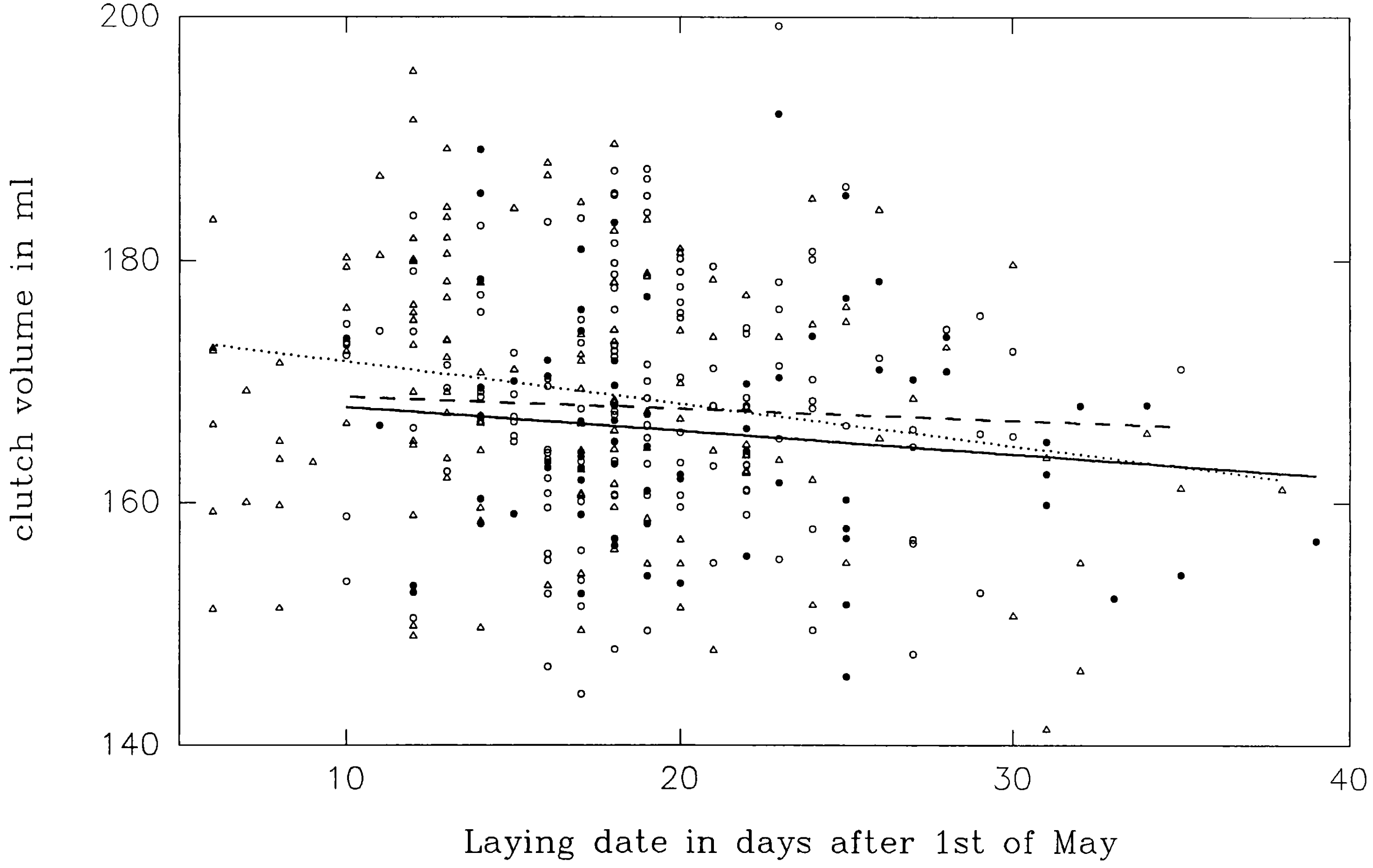
The viability of eggs was estimated from the proportion of eggs in the clutch which were addled. Losses of eggs due to predation were not included in the analysis since the taking of eggs by conspecifics is not affected by egg quality.

3.3 Results

3.3.1 Changes in food abundance

The proportion of sandeel in the diet of great skua chicks increased from 11% in the poor food year to 46% and 60% in the intermediate and good food years respectively, this increase being highly significant ($\chi^2 = 18.25$, df=2, $p<0.0001$). There was an accompanying decline in the proportion of whitefish from 73% in the poor food year to 54% in 1991-1992 and 35% in 1993. Bird meat was greatly reduced in the diet in the latter years, falling from 15% in the late 1980's to negligible levels (only one bird meat regurgitate recorded) in the early 1990s.

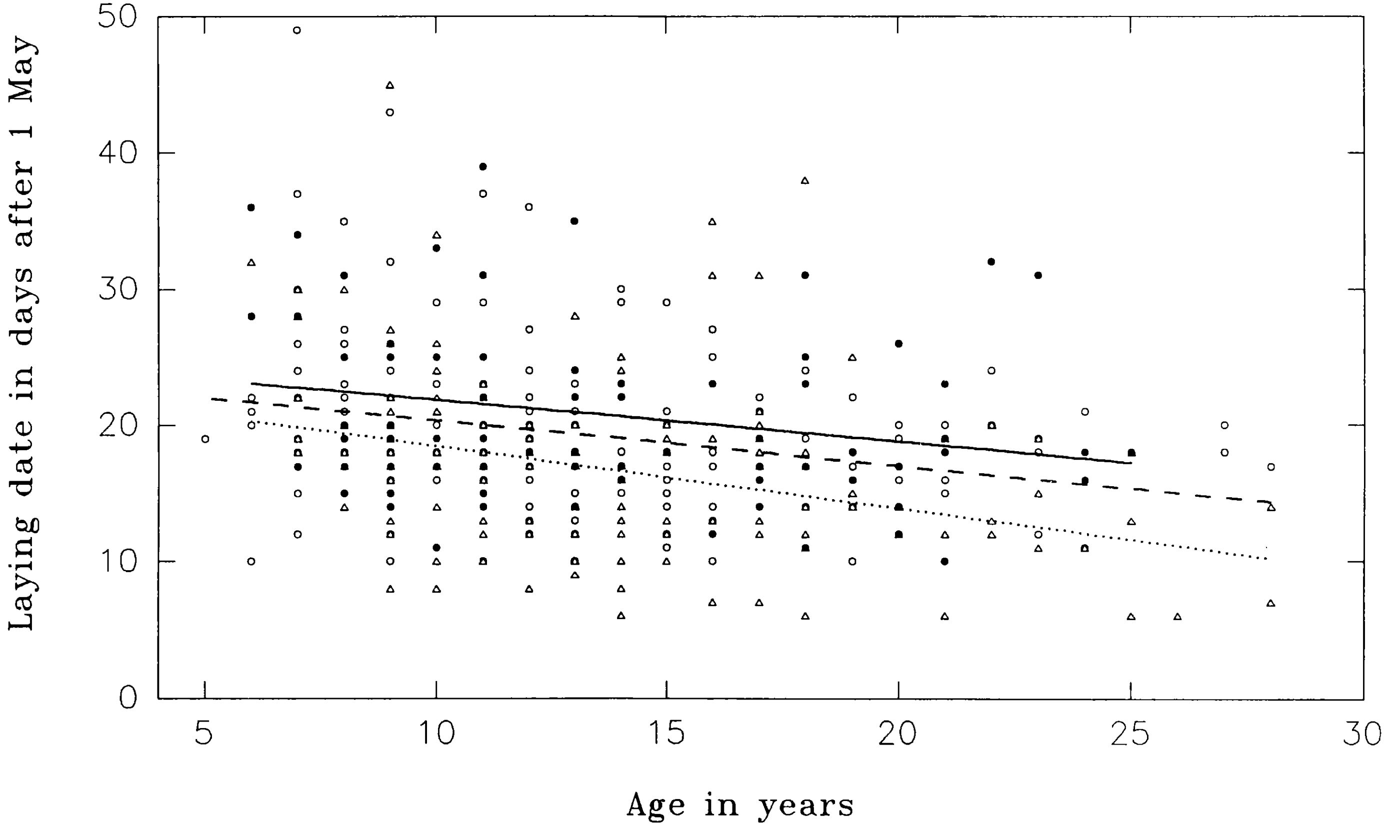
Fig. 3.1 The effect of food supply and laying date on clutch volume



Food availibility: • ——— poor year, ○ ········ intermediate year, △ good year.

Analysis of co-variance: n=433, Year; F= 5.5, df=2, $p<0.05$, Laying date $t = -2.8$, $p<0.005$

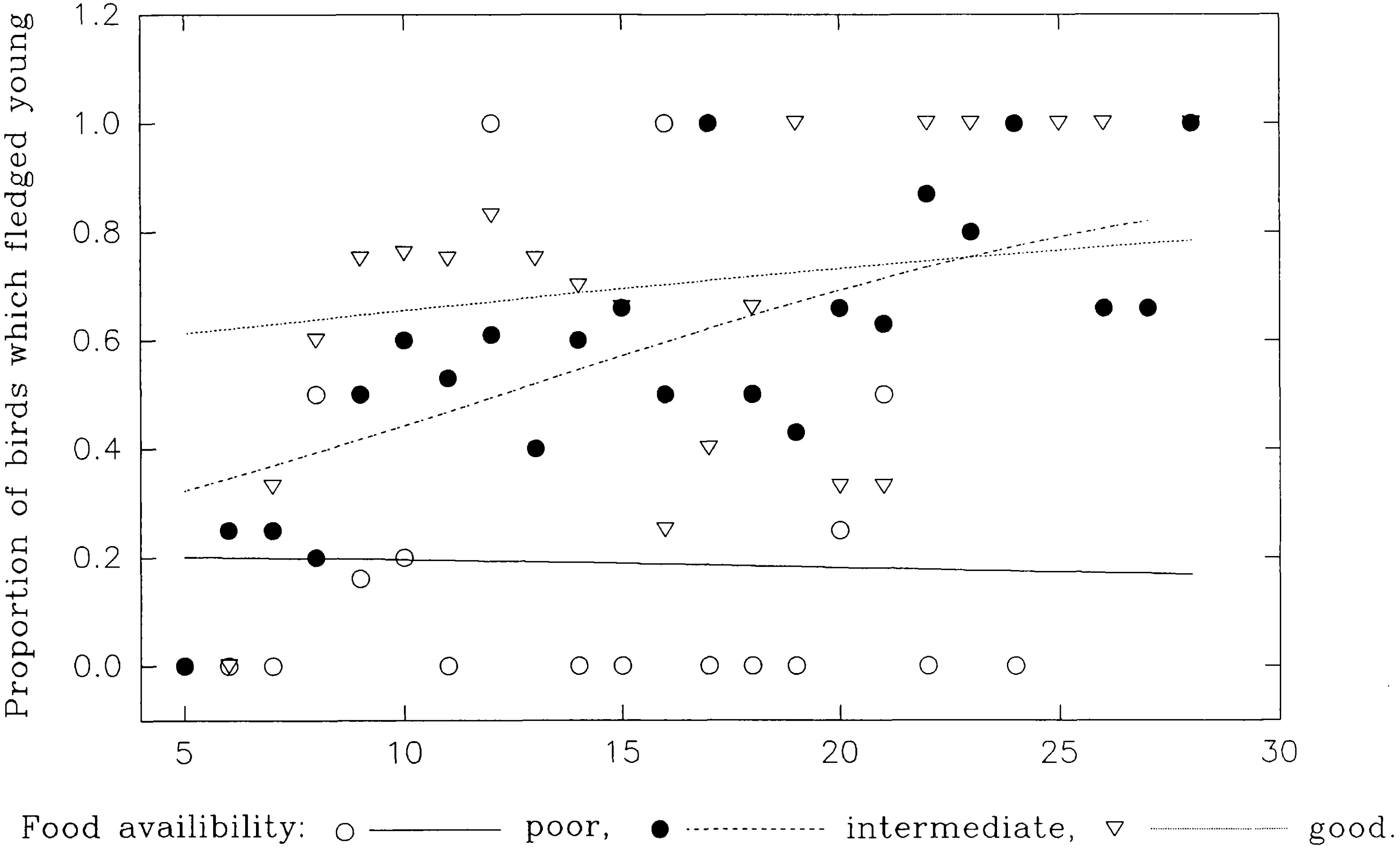
Fig. 3.2 The effect of age and food availability on laying date



Food availability: ——— • poor, - - - - - ∘ intermediate, ... ▵ good.

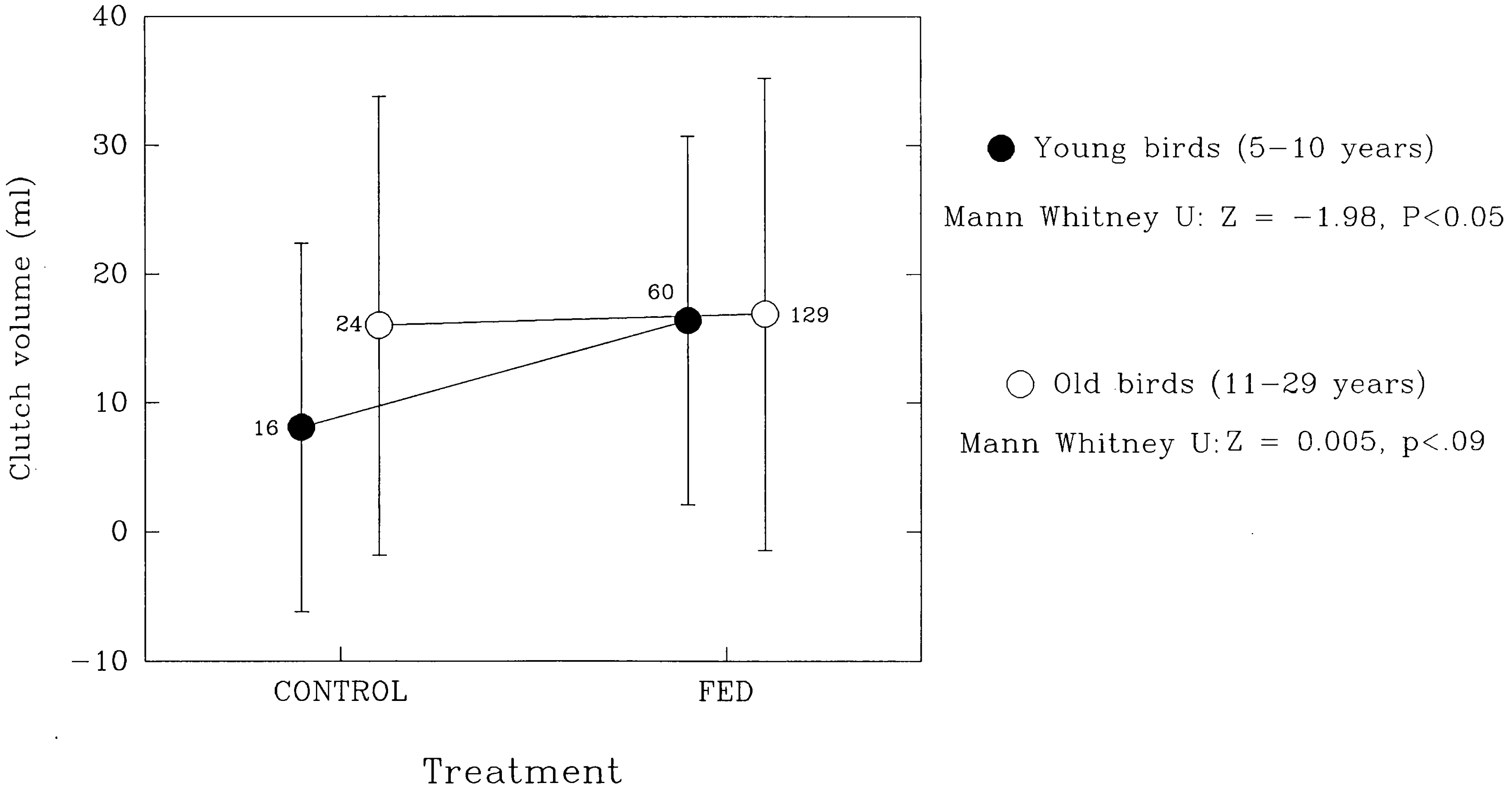
Analysis of co-variance: n=329, F= 7.3, df=2, $p<0.001$.

Fig 3.3: The effect of age on fledging success during periods of variable food availibility



Interactive logistic regression: $r^2 = 0.05$, Wald = 27.6, df=1, $p<0.0001$

Fig. 3.4: The effect of food supplementation on the clutch volume of known age great skuas. Values are medians with inter quartile ranges which were corrected for year effects using residuals of yearly means. Numbers by symbols represent sample size.



3.3.2 The relationship between food abundance and non-breeding

The proportion of birds which took years off breeding whilst holding a territory was higher in the years when food was scarce (10%) than in years in which food supply was intermediate (4%) and abundant (1%). The decline in deferred breeding in response to improving nutrient resources is highly significant ($\chi^2 = 43.3$, df = 2, $p<0.00001$). See Table 3.1 for descriptive statistics.

3.3.3 The effect of annual food abundance on breeding

The laying date advanced highly significantly with improved food supply, this trend being evident between all years (One way ANOVA, F = 11.11, df=2, $p<0.0001$). There were more one egg clutches in the intermediate years than in others, but this difference was not significant ($\chi^2 = 5.1$, df = 2, $p>0.05$). The clutch volume of 2 egg clutches was significantly larger in the good food year than in the poor and intermediate years of food supply (One way ANOVA, F = 10.21, df = 2, $p<0.0001$), but no significant difference was evident between the latter years. There was a significant relationship between laying date and clutch volume This increase in clutch volume in response to improved food supply was independent of laying date (ANCOVA; n=433, F = 5.5, df=2, $p<0.005$, Fig 3.1). Hatching success was not affected significantly by food supply ($\chi^2 = 5.4$, df = 2, $p>0.05$). Fledging success was far lower in poor food years than in good and intermediate years ($\chi^2 = 43.9$, df = 2, $p<0.00001$). See table 3.1 for descriptive statistics.

3.3.4 The effect of age and food supply on breeding

Laying date advanced significantly with age and year significantly affected the elevation of the regression lines (ANCOVA; F = 7.30, df=2, $p<0.001$, Fig 3.2) but there were no significant differences in the regression line slopes (ANCOVA; age by year F = 0.5, $p>0.6$). The improvement of food supply increased the clutch volume of

2 egg clutches (ANCOVA, $F = 9.78$, $df=2$, $p<0.0001$) but age had no significant effect. There was no interaction between age and food supply (ANCOVA: $F = 0.91$, $df=2$, $p>0.4$).

Fledging success increased highly significantly with both age and year (multiple logistic regression: Age; Wald = 11.67, $df=1$, $p<0.001$, Year; Wald = 69.4, $df=1$, $p<0.00005$) and the interaction was highly significant (logistic regression, $r^2 = 0.05$, Wald = 27.58, $df = 1$, $p<0.00001$). Fledging success only improved with age in intermediate years, while in poor years very few birds fledged chicks and in good years birds of different ages raised chicks equally well (Fig 3.3).

Table 3.1: The effect of food availability on non-breeding and breeding performance.

	Food availability				
	Poor **(1989-90)**	**Intermediate** **(1991-1992)**	**Good** **(1993)**	**Test**	**p**
% Non-breeding on territory	10%	4%	1%	$\chi^2 = 43.3$	<0.0001
	(90)	(194)	(194)		
Laying date (days after April 30)	21.6±0.8	19.7±0.4	17.4±0.6	F = 11.1	<0.001
	(88)	(216)	(162)		
Clutch size (% 2 egg clutches)	83%	79%	86%	$\chi^2 = 5.1$	>0.05
	(199)	(388)	(208)		
Clutch volume(ml)	164±0.8	163.9±0.7	168±0.79	F = 10.2	<0.001
	(136)	(273)	(208)		
Hatching success (% birds hatching a chick)	92%	85%	89%	$\chi^2 = 5.4$	>0.05
	(149)	(291)	(194)		
Fledging success (% birds fledging a chick)	20%	53%	63%	$\chi^2 = 39.7$	<0.001
	(81)	(189)	(131)		

3.3.5 The effect of experimental food supplementation on breeding

There was no significant effect of supplementary feeding on laying date (t-test, t = 0.18, df = 1, p>0.8). The total clutch volume of one and 2 egg clutches combined was unaffected by supplementary feeding (Mann-Whitney U test, Z = -1.13, df = 1, p>0.2). The hatching success of eggs (excluding those lost to predation) was not affected by supplementary feeding (χ^2= 0.23, df = 1, p>0.6). See table 3.2 for descriptive statistics.

3.3.6 The interactive effects of age and food supplementation on breeding

There were no interactive effects of age and food supplementation on laying date (Two-way ANOVA; F = 0.34, df = 2, p>0.5). Supplementary feeding significantly increased the total clutch volume in young (5-10 years) birds (Mann-Whitney U test; Z = -1.98, df=1, p<0.05) while there was no effect of age on the clutch volume of older (11-29 years) birds (Mann-Whitney U test; Z = -0.005, df=1, p>0.9, see Fig. 3.4). There was no effect of treatment on the rate of addling within either age group (χ^2 =3.6, df = 1, p>0.05).

Table 3.2: The effect of supplementary feeding on egg production. Laying date is expressed as the mean with standard errors and the total clutch volume (the volume of 1 and 2 egg clutches) is expressed as the median with inter-quartile range (both variables corrected for year effects by calculating residuals of yearly means). Viabilility of the eggs is expressed as the percentage of nests which contained an egg that failed due to addling. Numbers in parentheses represent the sample size.

	Experimental	**Control**	**Test**	**p**
Laying date	18.3±0.7 (40)	-0.34±4.8 (191)	t = 0.18	>0.8
Total clutch vol. (ml)	11.5± 19.2 (40)	15.3± 15.1 (191)	Z = -1.13	>0.2
Viability	82% (40)	83% (191)	$\chi^2 = 0.23$	>0.6

3.4 Discussion

3.4.1 The effects of nutrient resources on breeding

During the 1970s great skuas fed their chicks almost exclusively on sandeels, which have a high calorific value and the lowest proportion of indigestible matter of all prey items in the diet (Furness and Hislop 1980). The proportion of sandeels in the diet was positively correlated with chick condition (Hamer, Furness and Caldow 1991). The sudden increase in the abundance of sandeel in the diet in 1991 compared with the late 1980's and the steady improvement since then can be regarded as an improvement in food supply. The percentage of sandeel in the diet in 1993 is similar to that found in the mid 1980s but is not as high as found in the 1970's, so there may be further scope for improvement in great skua breeding success if sandeel stocks continue to increase.

The proportion of pairs taking years off breeding whilst holding territory decreased as food resources improved. This could be due to birds in poor years being unable to assimilate sufficient reserves for egg formation or due to them refraining from exerting reproductive effort in order to avoid the higher costs of breeding when food is scarce (Boekelheide and Ainley 1989).

Experimental feeding did not advance the laying date significantly, but improved food availability in 1993 advanced laying date highly significantly. The discrepancy in these results may be accounted for by the food supplementation experiment being conducted during years of abundant food supply and so there was no scope for a further advancement. The advancement in laying date in response to improved food supply has been recorded in many species (Yom-Tov 1974, Kallander 1974, Spaans 1971, Korpimaki 1989) and seems to be due to improved body condition allowing follicles to mature at an earlier date (Houston, Jones and Sibly 1983).

There was an increase in the clutch volume of 2 egg clutches in the good food year compared to the poor and intermediate food year, this increase being independent of laying date. Studies of kestrels have demonstrated that the increase in egg production through supplementary feeding is entirely dependent on the advancement of laying date since the number of eggs developed depends on the date of ovary maturation (Meijer, Daan and Dijkstra 1988). Other studies have found that the increases in egg production can be explained by improved food supply independently of laying date (Hoim *et al.* 1991, Korpimakii and Hakkarainen 1991, Bolton *et al.* 1992) and this appears to be the case in great skuas.

It has been suggested (Meijer, Daan and Dijkstra 1988) that the relationship between laying date and egg production would be adaptive in a situation where food supply is predictable through the year. The dependency of clutch size on laying date will be a useful predictor of food supply in the chick rearing stage, allowing egg production to be optimised accordingly . However, if the food supply fluctuates unpredictably the timing of laying will be unrelated to the abundance of food later in the year the best strategy would be maximisation of clutch size with brood reduction relative to food supply later in the season (Bolton *et al.* 1992). This theory could apply to great skuas as sandeels are often abundant in the diet early in the season but there is often a sharp decrease in sandeel availability in the middle of the chick rearing stage.

There was no effect of nutrition on the addling of clutches in either of the studies, suggesting that food supply has no effect on egg viability and that addling is due to infertility or embryo death due to reasons other than the level of nutrition.

Fledging success increased highly significantly with improved food supply, with the death of chicks occurring due to conspecific predation rather than starvation. This arises through parents leaving the chicks unattended in order to forage during poor food years allowing neighbours to kill the chicks in their absence (Hamer, Furness and Caldow 1990) rather than hungry chicks wandering into neighbouring territories (Hunt and Mc Loon 1975).

3.4.2 Interactions of age and food supply

The laying date advanced highly significantly with both age and improved food supply independently. It would be predicted that if young birds are constrained by poor foraging efficiency they would advance laying date to a greater degree than older birds when food supply improves. This is not the case since there is no significant interactive effect of age and food supply on laying date.

The supplementation of food increased clutch volume in young birds but not in old birds, and the food allowed young birds to have similar egg production to older ones. This finding is similar to the one found by Krapu and Doty (1974) and Desrochers (1992) and shows that increases in egg production with age in great skuas are probably due to a constraint of foraging inefficiency in young birds.

Age and food supply had a significant interactive effect on fledging success. Age improved breeding success only in the year of intermediate food supply. In the poor year fledging success was uniformly low across all ages and very few birds fledged a chick due to high levels of conspecific predation. In the year of good food supply fledging success was higher and young birds bred as successfully as older ones. Previous studies have shown that age specific differences in breeding were greatest in situations where food supply is poor, with age having less effect in intermediate years and no effect in years where food is abundant (Sydemann *et al.* 1989). This prediction is in need of modification in situations where food supply is so poor that birds of all ages are unable to meet the nutritional demands of reproduction.

The improvement in fledging success with age in the intermediate year is probably due to young birds being less efficient at foraging, forcing them to spend more time foraging at the expense of chick defence (see chapter 5). In the year of improved food supply fledging success was higher and there was no effect of age. This suggests that the constraint of poor foraging efficiency in young birds had been negated by the fact that food was far more abundant. Alternatively, young birds may be refraining from investing effort during years of lower food supply since this may jeopardise future breeding opportunities, whereas in years where food is plentiful young birds may be able to increase effort within their ability to buffer themselves against reproductive costs (Williams 1966). This suggestion is improbable since there was no effect of fledging success on survival in the years studied and so high fledgling production does not have a discernable cost. Further to this, Hamer Furness and Caldow (1991) found that survival was lower in the late 1980's than in the 1970's owing to increased effort during the period of sandeel shortage. This shows that great skuas do increase effort to the degree that future survival is threatened and so the concept of restraint by young birds seems unlikely.

3.5 Conclusions

This chapter shows that food supply is an important factor in the breeding ecology of great skuas. The improvements in breeding in response to promoted food supply are probably directly due to food allowing improvements in parental condition and chick provisioning rather than birds refraining from exerting high effort in poor years to avoid reproductive costs. Increases in breeding success with age seem best explained by nutritional constraints on younger birds due to foraging inefficiency rather than young birds attempting to exert low effort to conserve future breeding opportunities.

Chapter 4

The effect of age, experience and maturation on great skua breeding ecology

4.1 Introduction

Improvements in breeding performance with age have been demonstrated in many species (Ryder 1981, Saether 1990), including the great skua (Furness 1983, 1984; Hamer and Furness 1991). The maturation hypothesis suggests that such trends are attributable to an increase in parental quality through a process of learning skills which improve breeding efficiency (Forslund and Larsson 1992). This theory would predict that there is an improvement in breeding parameters within individuals as they become older (Nol and Smith 1987) and that the effect of age will be confined to the early years of breeding, since the benefits of learning tend to decrease with increasing age (Pugesek 1984).

The skills acquired could be associated with foraging, which would allow the bird to maintain better condition, enabling it to lay larger eggs at an earlier date, and to provision chicks more efficiently (Newton *et al.* 1981, Korpimakii 1984). As birds will have to forage as soon as they become independent of their parent, foraging skills will be learned with increasing age. The fact that the foraging efficiency of adult seabirds is better than that of immature birds is widely documented in Larids (Dunn 1972, Buckley and Buckley 1974, Searchy 1978, Grieg *et al.* 1983, Carroll and Cramer 1985, Mac Lean 1986) but improvements in foraging in breeding birds have only been examined in passerines (Jansen 1989, Desrochers 1992).

Alternatively, birds may improve on successive reproductive attempts by learning skills which could only be acquired by breeding (Nol and Smith 1987). Experience of laying, incubation, hatching and chick rearing could be important in increasing reproductive success in subsequent years.

The separate influences of age and experience on breeding are highly inter-correlated and difficult to disentangle due to small sample sizes of known age and experience marked birds. The relative contributions of age and experience can be further confused by variations with sex (Pyle *et al.* 1991, Forslund and Larsson 1992).

This chapter examines the effect of experience on breeding in great skuas using cross sectional analysis. The successive breeding attempts of individual birds were then studied longitudinally to determine whether the patterns described in the cross-sectional analysis can be attributed to a learning of skills. The inter-relationships between age and experience were examined in order to discover if the skills learned were associated with foraging or breeding. The implications of these findings on the duration of deferred breeding are also discussed.

4.2 Methods

Between 1988 and 1992 631 non-breeding great skuas were cannon netted on club sites on Foula. All birds were given a unique colour-ring combination by which they could be individually identified in subsequent years. Of these birds 204 recruited between 1989 and 1993 and 109 bred more than once giving a total of 358 breeding attempts

Every breeding attempt of each individual bird which recruited between 1989 and 1993 was recorded. It is unlikely that any breeding attempts were missed since the study area on Foula was checked daily for colour-ringed birds and the repeatability of colour-ring sightings was very high. More extensive searches were conducted outside the study area throughout the breeding season but few birds were found away from the study area due to the high degree of philopatry found in great skuas (Furness 1987).

Breeding birds do not use club sites (over 300 breeders have been colour-ringed but they are not seen on clubs once breeding has commenced) and so the contamination of the sample of known-experience birds by those which have bred before was insignificant.

The laying date, clutch size, clutch volume and hatching success were monitored for all the breeding attempts made by colour ringed birds. Laying date was determined by observation of laying date or hatching date, in the latter case the laying date was calculated by subtracting the mean duration of incubation (29 days).

The clutch size was always either one or two. A search was conducted round one egg clutches to confirm that one of the eggs had not been eaten or displaced from the nest. The length and breadth of the eggs were measured and these values were entered into the egg index equation (Davis 1975) to calculate egg volume. This equation was calculated for herring gulls and is only approximate for great skuas.

The fate of the eggs was determined by visiting the nest every 5 days throughout the incubation period. Losses of eggs were mainly due to predation by conspecifics or due to addling.

There were insufficient data on fledging success in birds of known experience, this being due to field work terminating too early to investigate fledging success in inexperienced birds which lay very late in the season and also to the excessive number of chicks this would involve monitoring.

4.2.2 Statistical Analysis

Of the parameters studied only laying date varied significantly with year if experience was controlled for (all ps >0.05) so the years were pooled for analysis. With respect to laying date, yearly effects within experience were controlled by calculating residuals of the yearly means for each experience group. The effects of experience were first investigated in a cross sectional analysis using one-way anova for normally distributed data and Chi-square tests for ordinal variables. In the longitudinal analysis the first and second breeding attempts of individual birds were compared using Wilcoxon matched pairs tests and the first second and third breeding attempts were compared with a Kendall coefficient of concordance. The independent effects of age and experience were examined using multiple regression for normally distributed data and multiple logistic regression for ordinal data.

4.3 Results

4.3.1 The effect of experience on breeding

The laying date advanced significantly between the first and second breeding attempt but not the second and third (One way ANOVA, df=2, F = 10.12, $p<0.0001$). The number of one egg clutches decreased significantly with experience ($\chi^2 = 26.6$, df=2, $p<0.00001$) with 45% of nests having one egg clutches in the first year of breeding compared to 25% in the second and 10% on the 3rd breeding attempt. The clutch volume of 2 egg clutches increased significantly between the first and second breeding attempt but not the second and third (One way ANOVA, df=2, F = 4.76, $p<0.01$). Hatching success did not vary significantly with experience ($\chi^2 = 2.91$, df=2, $p>0.23$) (see table 4.1 for descriptive statistics).

4.3.2 The effect of experience within individuals

There were no within individual effects of experience on laying date from the first year to the second (Wilcoxon matched pairs test, df=1, Z = -62, $p>0.5$). There were insufficient cases to test the effect of experience on laying date in the first, second and third years (n = 4).

Clutch size increased significantly within individuals with increasing experience between the first, second and the third year of breeding (Kendall coefficient of concordance, df=2, $\chi^2 = 14.69$, $p<0.001$). The percentage of one egg clutches decreased from 40% in recruiting birds to 10% in third time breeders.

The clutch volume of birds that laid 2 egg clutches in all three breeding attempts increased significantly with experience (Kendall coefficient of concordance, $\chi^2 =$

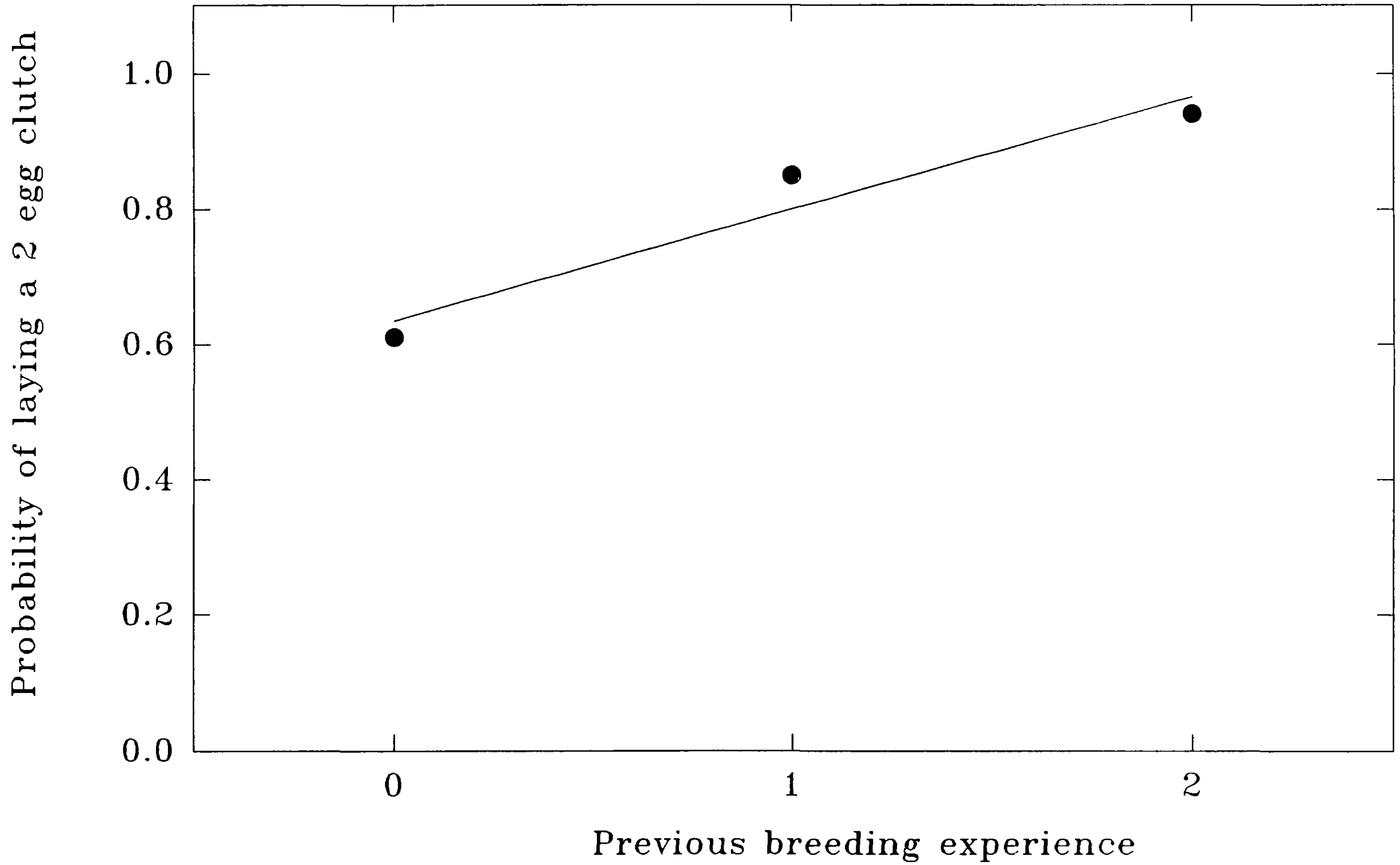
7.53, df=2, $p<0.05$). The clutch volume of birds which laid one egg clutches on both their first and second breeding attempt did not change significantly with experience (Wilcoxon matched pairs test, df = 1, Z = -0.56, $p>0.5$). There were too few cases to analyse the effect of experience on the volume of one egg clutches since most birds increased their clutch size with experience.

There was a longitudinal increase in hatching success with experience between the first and second breeding attempt but it was not significant (Wilcoxon matched pairs test, df = 1, Z = -1.85, $p>0.05$). There was no effect of experience on hatching success in the first three years of breeding (Kendall coefficient of concordance, χ^2 = 4.62, df=2, $p>0.05$) (see table 4.2 for descriptive statistics).

4.3.3 Independent effects of age and experience

There was no significant effect of either age or experience on the laying date of great skuas (multiple regression; r^2 = 0.00, F = 0.25, df = 1, $p>0.7$) but the sample size was small (n = 31). Clutch size increased with experience (multiple logistic regression; r^2=0.02, Wald = 5.69, df = 1, $p<0.02$, Fig 4.1) but age had no effect independent of experience (multiple logistic regression; r^2 =0.00, Wald = 2.12, df = 1, $p>0.1$). The clutch volume of 2 egg clutches did not increase significantly with age nor experience (ANCOVA: experience; F= 1.09, df = 2, $p>0.3$, age; t = -108, df = 45, $p>0.2$). Hatching success was unaffected by both age and experience (multiple logistic regression, r^2 = 0.00, Wald<0.6, df = 1, $p>0.4$).

Fig. 4.1: The effect of experience on clutch size while statistically controlling for age



Logistic regression analysis: $r^2 = 0.05$, Wald =9.08, df=1, $p<0.005$.

Equation of the line=$1/1+\exp^{-(1.3\text{expeience}-0.88)}$

Table 4.1: The effect of previous breeding experience on reproductive performance in a cross sectional analysis. Values are means and standard errors for laying date and clutch volume, clutch size is expressed as the percentage of one egg clutches, hatching success as the percentage of birds which did not hatch all their chicks.

	Years of previous breeding experience					
Variable	**0**	**1**	**2**	**n**	**Sig.**	**p**
Laying date	27.4 ± 1.2	23.9 ± 1.6	17.9 ± 1.2	47	F = 10.12	<0.0001
Clutch size	74%	32%	10%	375	$\chi^2 = 26.6$	<0.0001
Clutch vol.	159.3 ± 2.6	166.5 ± 1.1	167.5 ± 1.6	196	F = 4.76	<0.01
Hatching success	81%	34	81.%	161	$\chi^2 = 2.91$	>0.2

Table 4.2: The longitudinal effect of experience on breeding performance within individual birds. Values are expressed as mean ranks for all variables.

Years of breeding experience

Variable	0	1	2	n	Test	p
Laying date	1.80	2.40	1.80	13	Z = -0.6	>0.5
Clutch size	1.77	1.98	2.26	43	$\chi^2 = 14.69$	<0.001
Clutch vol.	1.74	1.62	2.64	13	$\chi^2 = 7.53$	<0.05
Hatching success	1.91	2.41	1.68	11	$\chi^2 = 4.62$	>0.05

4.4 Discussion

The cross sectional analysis of experience demonstrated that experience improves breeding from the first to the second breeding attempt but not from the second to the third, this pattern conforming to that described in studies of other species (Fisher 1969, Thomas 1983, Dow and Fregda 1984, Furness 1984, Loman 1984). This indicates that the additional benefits of previous breeding experience decrease after the first breeding attempt. This alone does not prove that the learning of skills is responsible for improved reproductive performance, the pattern could also be produced by poor quality breeders deferring or dying between the first and second breeding attempts (see Chapter 6).

The longitudinal analysis showed that the increase in clutch size and clutch volume with experience was due to an improvement in the performance of individual birds. Similar within individual effects have been demonstrated by other studies on wildfowl (Dow and Fregda 1984, Hamann and Cooke 1987, Forslund and Larsson 1992) sparrowhawks (Newton 1989) and blackbirds Desrochers and Magrath 1993). Improvements in the performance of individual birds suggest that a learning process is involved in the improvements in clutch size and volume (Nol and Smith 1987).

Since experience and age are so closely inter-correlated the increases in experience *per se* could be due to age and the learning of foraging skills. Experience of breeding rather than foraging improves clutch size in great skuas (see results) but there was insufficient data on laying date and hatching success to allow the independent effects to be separated. Many similar studies on other species have demonstrated that experience can affect breeding independently of age (Davis 1976, Ainley *et al.* 1983, Forslund and Larsson 1992) while others have shown that age rather than experience improves breeding (Richdale 1949, Ollason and Dunnet 1978, Wooller *et al.* 1990, Croxall *et al.* 1991). Pyle *et al.* (1992) showed that age improved breeding success in males since they do most of the foraging whereas females incubate and guard the nest and so benefit only from experience. This division of labour within the pair is the same as that found in great skuas and so the same could be true for this species.

4.4.2 Deferred breeding

Many species of seabird have prolonged periods of deferred breeding, often lasting for several years. One explanation for this phenomenon is that effort expended in breeding reduces residual reproductive value by increasing mortality (Williams 1966). This loss of future reproductive potential would not be compensated for by the low reproductive success in young breeders (Chabrzyk and Coulson 1976, Wooller and Coulson 1977, Hamann and Cooke 1987, Ainley *et al.* 1990). Great skuas which breed at very young ages have higher mortality rates (see Chapter 6) and so this represents a cost of early recruitment.

On the basis of this theory Pyle *et al.* (1991) predicted that, where reproductive success increased with breeding experience, the optimal reproductive strategy would be to breed at low intensity at an early age to gain benefits of breeding while avoiding reproductive costs. In a situation where age improves breeding rather than experience a prolonged period of deferred breeding would be favoured in order to gain foraging experience to ensure the cost of reproducing is made worthwhile by high breeding success.

In great skuas experience of breeding seems more important than age in determining clutch size. According to theory, the age of first breeding in great skuas will be subject to a trade off between deferring in order to conserve future breeding potential, and breeding at a low intensity to improve clutch size through experience. The final balance will depend on the relative contributions of these parameters to overall breeding success and their costs in terms of survival. The reason for deferred breeding in great skuas is probably a combination of nutritional constraint and adaptive restraint (Curio 1983).

4.5 Conclusions

Experience has significant effects on laying date and egg production, these trends being due to improvements intrinsic to the individual rather than selection against poor quality phenotypes (but see Chapter 6). The improvements in clutch size are due to skills learned through experience of breeding rather than foraging, suggesting that foraging skills are developed prior to recruitment. However there is evidence to suggest that foraging skills are important in chick rearing.

Chapter 5

The effect of age and brood size on the foraging effort of great skuas

5.1 Introduction

Reproduction is envisaged as a costly process in terms of survival and future fecundity, the cost increasing with the effort invested in the current breeding attempt (Williams 1966, Gadgil and Bossert 1970). Energy invested in breeding reduces the resources available for maintenance (Reid 1987) and may increase the risk of injury or predation (Ainley and De Master 1980, Pugesek 1983).

Life history theory predicts that the cost of breeding produces a trade off in the amount of reproductive effort invested in present and future breeding attempts. In species where residual reproductive value decreases with age (due to age-dependent mortality or senescence) the cost of reproduction will be reduced as age increases (Williams 1966, Gadgil and Bossert 1970). There ought to be a selective pressure for reproductive effort to increase with age in order to maximise lifetime breeding success. Evidence for this hypothesis is difficult to obtain since age-dependent mortality, an increase in effort with age and a cost of this effort all need to be demonstrated. The theory has been used to account for the improvement in breeding with age (Pugesek 1981, 1983, Hamer and Furness 1991) though many studies have dismissed it as unimportant (Roskaft *et al.* 1983, Nur 1984, Ried 1988c, Forslund and Larsson 1992, Perdeck and Cave 1992).

The main aim of this chapter is to investigate the effect of a brood size manipulation on the reproductive effort of known-age birds. Life history theory would predict that differences in age-specific foraging effort will be greatest where reproductive demands are high (i.e. where the brood is large and the chicks are old). Young birds ought to conserve their residual reproductive value and opt for a strategy of low foraging effort and brood reduction. Older birds should increase foraging effort in an attempt to rear as many chicks as possible, incurring a cost in terms of increased mortality.

5.2 Methods

An intensive programme of ringing of great skua chicks since the 1970s has resulted in approximately one third of breeding skuas on Foula now being of known-age. Many of these have been subsequently trapped on the nest during incubation using a clap net and were given a unique 4 ring colour combination. In addition to this, cannon netting on club sites (areas where non-breeders gather before recruiting) has resulted in the colour-ringing of many known-age birds which have subsequently recruited into the breeding population. Age ranged from 5 (the earliest recorded breeding age of great skuas) through to 29 years old. Age was grouped into 2 age classes for analysis; young (5-10) and old (11 to 29). The partner is assumed to be in the same age class as the known-age study-bird (see chapter 7).

5.2.1 Brood size manipulations

The brood size of 30 pairs with clutches of 2 was reduced naturally in 1991 by addling of eggs and the predation of eggs and young chicks. This gave sample sizes of 17 one chick broods and 26 two chick broods. In 1992, the brood size (of birds with a clutch size of 2) was manipulated at hatching, creating broods of 1, 2, 3 or 4 chicks. For analysis brood sizes were grouped as reduced (1 chick), control (2 chicks) and enlarged (3 and 4 chicks); the sample sizes were 15, 41, 49 respectively. The brood size was allocated randomly among age groups.

5.2.3 Estimation of foraging effort

The study sample in 1991 comprised 65 pairs in which at least one member of the pair was of known age. In 1992 110 colour ringed pairs were studied, of which 70 contained at least one bird of known age. The attendance of parent birds was monitored from elevated vantage points at the edge of the study area using binoculars and a telescope. Pairs were watched for 60 hours (685 nest hour's) in 1991 and for 65 hours of observation (1538 nest hours) in 1992. Observations were conducted between 10:00 and 17:00 (B.S.T.). The timing of observation was randomised between sites in order to control for daily variations in attendance.

The arrival and departure of birds on their territories was noted to the nearest 1 minute and these data were used to estimate the amount of time the territory had zero, one or two adults on it. These values were used to calculate the proportion of time spent foraging by dividing the total number of bird hours spent away from the territory by the total number of bird hours observed for the nest. These proportions were arcsine transformed for analysis to stabilise the variance.

This assumes that time spent away from territory is spent in foraging activity (Ryan and Dinsmore 1980) rather than loafing off territory. Furness (1987) found that the time spent away from territory was correlated with the quality of chick diet, chick growth and breeding success, indicating that breeders are foraging when away from territory. Breeding colour-ringed birds are never seen on club sites once breeding has started (Furness 1987).

The number of chick feeds were observed during attendance studies and the number of chick feeds per hour were deduced. A single chick feed was classed as any regurgitations occurring after the return of a parent from a foraging trip, regardless of the number of chicks being fed. Only chick feeds in the late chick stage were analysed as too few regurgitations were observed in the early chick stage to warrant analysis. The data were normalised using an arcsine transformation.

Effects of chick age on attendance were controlled for by splitting the chick period into an early chick stage (2 weeks or less) and a late chick stage (>2 weeks). To control for the effect of chick mortality, observations in the late chick stage were based on the brood size at 2 weeks old rather than the initial brood size. Observations were terminated when pairs lost all their chicks.

5.2.4 Estimates of chick survival and condition

The number of days the chicks survived was estimated by intensive searches of the territories every 5 days and by counts of chicks attending chick feeds during time budget observations. The mean chick survival for each pair was calculated for the analysis. An index of fledging success was produced by dividing the number of chicks that survive for 30 days by the initial brood size, exempting those found dead after this time.

The chicks were weighed to the nearest 5g during the linear growth phase, their ages were known from the hatching date. These values were used to produce an estimate of condition by taking residuals from the logistic regression curve of age against weight in Furness (1983).

5.2.5 Statistical analysis

There was no significant effect of year on foraging time in the early chick stage (t-test, t = -0.6, df = 1, p>0.5) nor in the late chick stage if enlarged broods were excluded (t-test, t = -1.34, df=1, p>0.1) so data from both years were combined for analysis.

All attendance data were arcsine transformed to stabilise varience and conformed to a normal distribution (Kolmogrov-Smirnoff goodness of fit test, All ps >0.4) except for the time that the territory was unattended and the number of chick feeds per hour, which were skewed towards zero. These data were analysed using Kruskall-Wallis ANOVA in the case of brood size and were transformed into binary variables for analysis with age interactions of age and brood size. For the number of chick feeds per hour data was categorised according to whether the values were above or below the population mean (0.1). In the case of non-attendance the data were grouped according to whether the pair left the brood unattended or not.

The chick survival, condition and fledging success was significantly lower in 1992 compared to 1991, even when controlling for brood size (See table 5.2.5).

Table 5.2.5: The effect of year on the number of days the chick survived and chick condition (weight corrected for age). The values are means with standard errors and the values in parenthesis represent the sample size.

Variable	1991	1992	F	P
Chick survival	31.2 ± 1.2 (38)	21.4 ± 1.0 (73)	32.61	<0.001
Chick condition	412 ± 0.2 (40)	223 ± 10.9 (62)	70.1	<0.0001

To control for this year effect, residuals of the yearly means were calculated for each case before the data were pooled for analysis . Both chick survival and chick condition conformed to a normal distribution.

5.3 Results

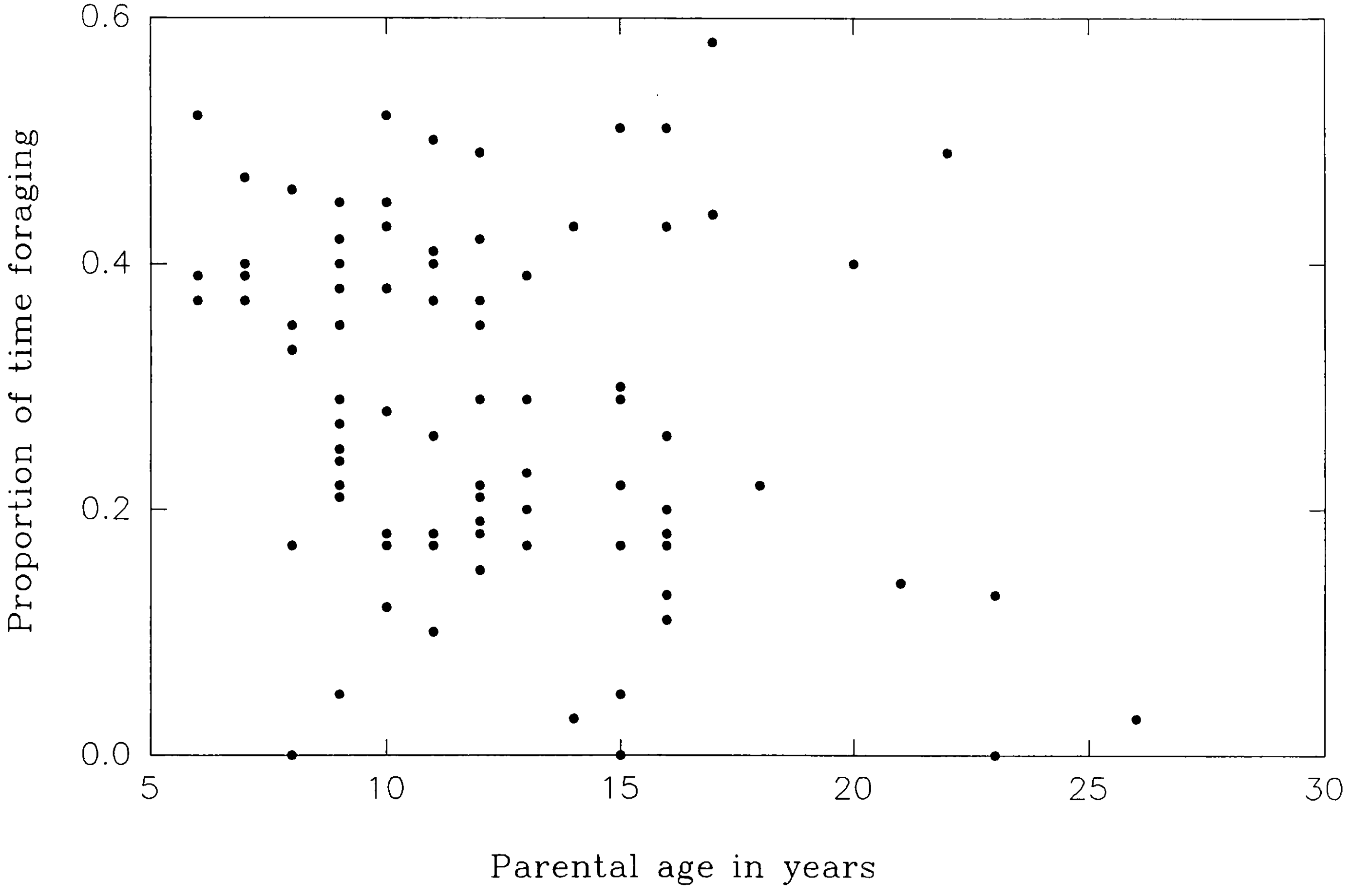
5.3.1 The effects of brood size on foraging effort

Increased brood size had no significant effect on proportion of time birds in a pair spent foraging in the early chick stage (one-way ANOVA; n = 111, F = 1.06, df =2, p>0.3). During the late chick stage, time spent foraging was significantly higher in enlarged broods than in one and two chick broods (One way ANOVA; n = 133, F = 4.80, df=2, p<0.01). Increasing brood size had no effect on the index of chick feeding rate (Kruskal-Wallis ANOVA; χ^2 = 5.43, df=2, p>0.05). The proportion of time that adults left the brood unattended did not vary with brood size during the early chick stage (Kruskal-Wallis ANOVA; $\chi^2 = 1.66$, df=2, $p>0.4$) but increased with brood size during the late chick stage (Kruskal-Wallis ANOVA; $\chi^2=13.1$, $p<0.0001$). For all descriptive statistics see Table 5.1.

5.3.2 The effect of age on foraging effort

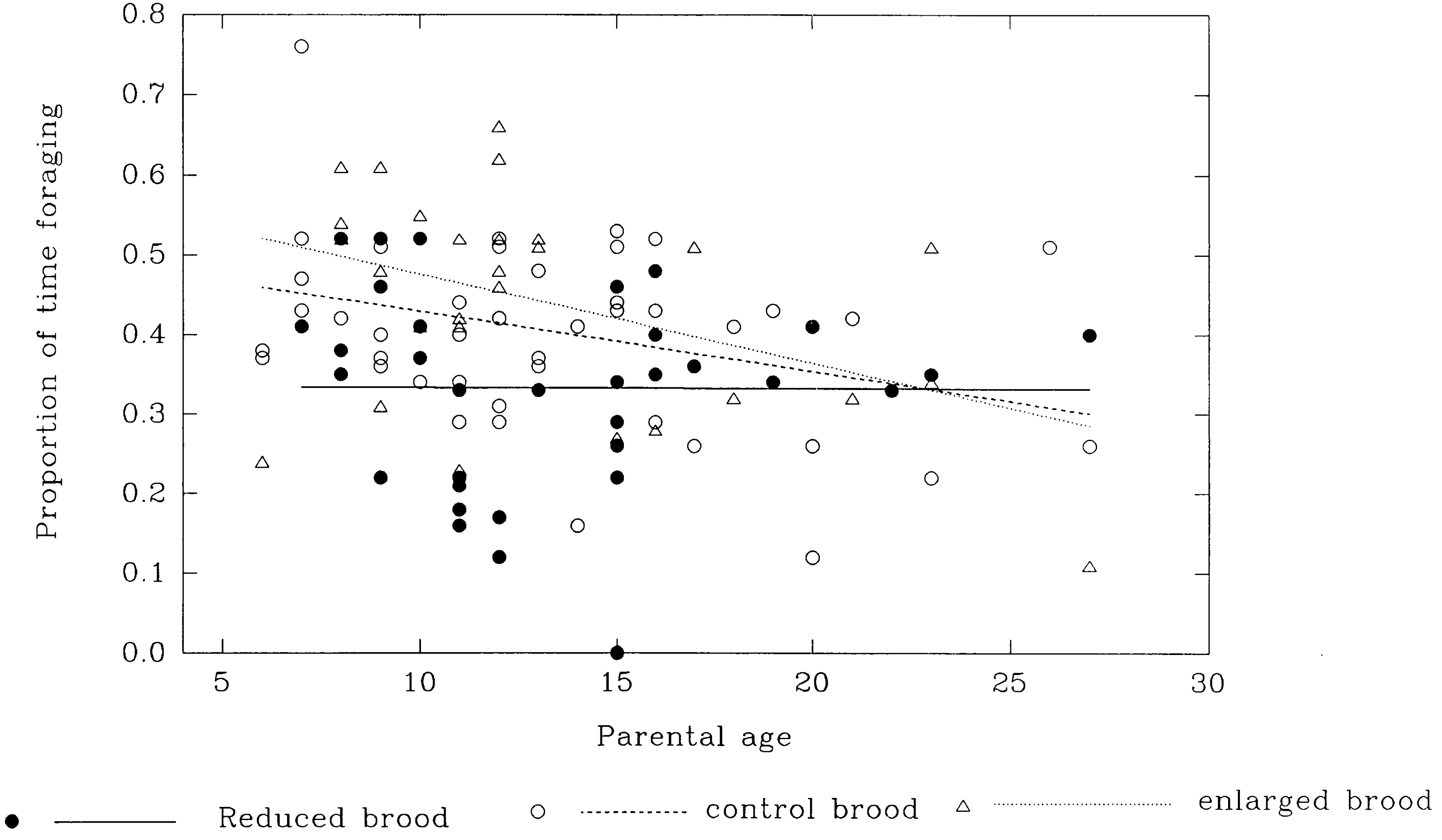
There was no effect of age on foraging effort during the early chick rearing stage (linear regression, $r^2 = 0.00$, F = 0.93, df = 83, $p>0.9$, Fig 5.1). Similarly, during the late chick stage there was no effect of age on foraging effort in pairs with only one chick (Linear regression, $r^2 = 0.00$, F = 0.77, df= 34, $p>0.3$). In contrast, there was a significant decrease in foraging effort with age in pairs with two chicks (linear regression; $r^2 = 0.09$, F = 4.96, df = 46, $p<0.05$) and in pairs with enlarged broods (linear regression; $r^2 = 0.16$, F = 5.76, df=17, $p<0.05$, Fig 5.2). The probability of the pair leaving the brood unattended decreased significantly with age (logistic regression, $r^2 = 0.04$, Wald = 10.61, df=1, $p<0.005$, Fig 5.3). Likewise, the probability of a pair having a high rate of chick feeding also decreased with age (logistic regression, $r^2 = 0.02$, Wald = 5.38, df=1, $p<0.02$, Fig 5.4).

Fig 5.1: Graph showing the effect of age on the proportion of time spent foraging during the early chick stage



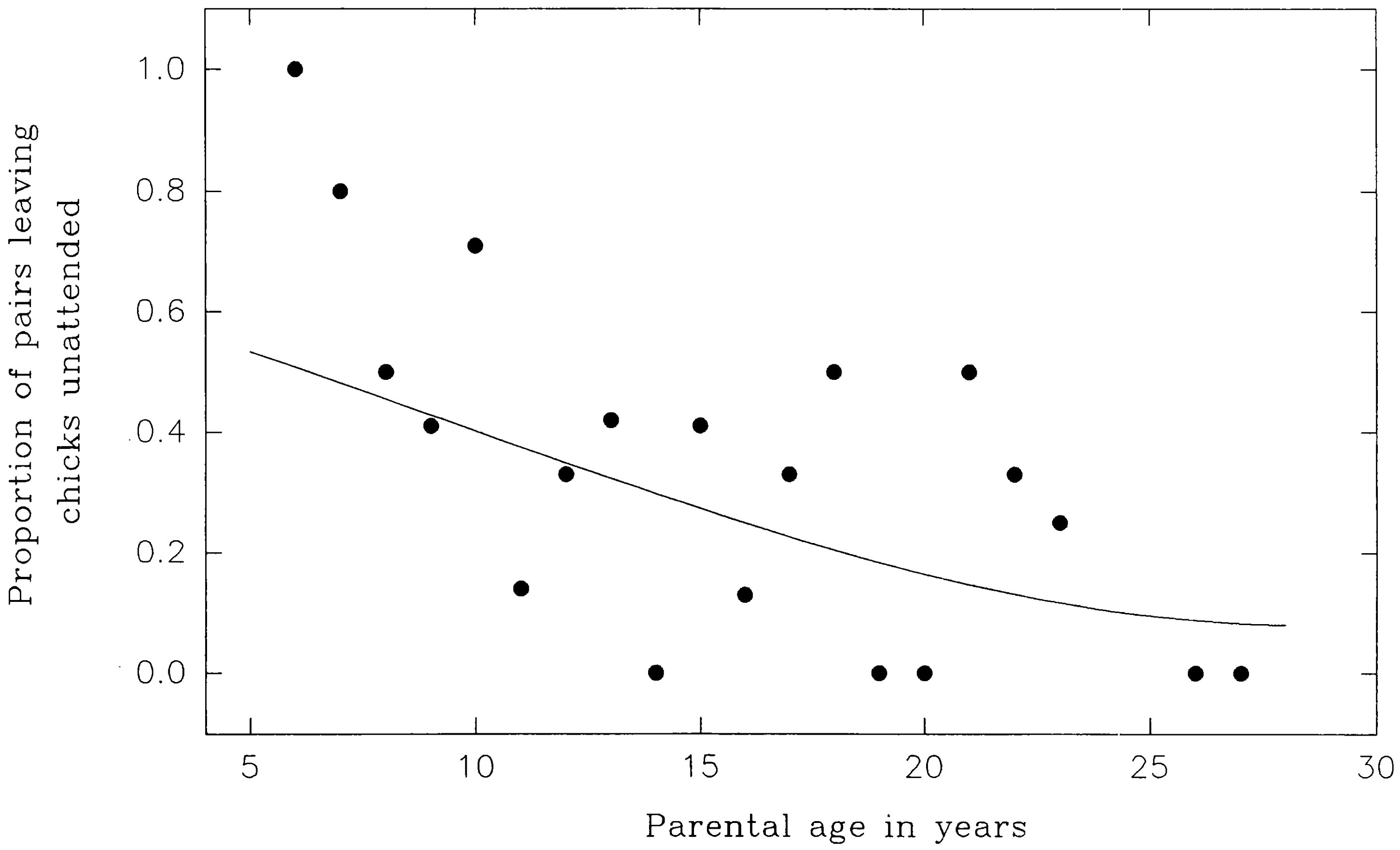
Linear regression analysis: n=85, F= 0.93, df=83, p>0.9.

Fig. 5.2: The effect of age and brood size on the proportion of time spent foraging during the late chick stage



Multiple analysis of varience: interaction of age and brood size; n=113, F =3.22, p<0.05.

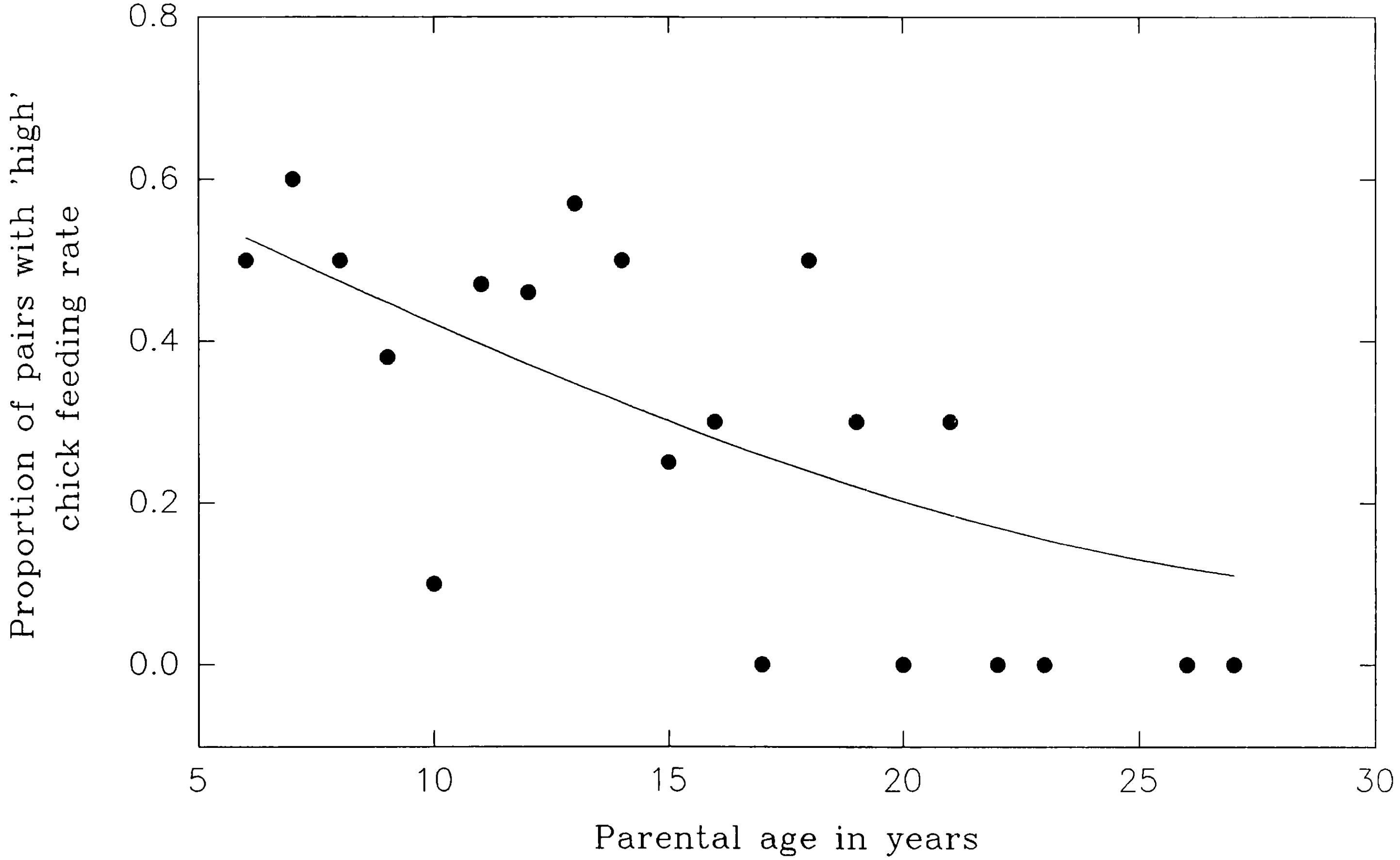
Fig 5.3: The effect of age on the probability of a brood being left unattended during the late chick stage in 1991 and 1992



Logistic regression analysis: $n=113$, $r^2=0.03$, Wald=5.8, $df=1$, $p<0.02$

Equation of the line $= 1/1+e^{-(-0.12\text{age} + 0.76)}$

Fig. 5.4: The effect of age on the rate of chick feeding during the late chick stage in 1991 and 1992



Logistic regression analysis: $n = 121$, $r^2 = 0.03$, Wald= 5.38, df = 1, $p<0.02$

Equation of the line: $1/1+e^{-(-0.12age+0.76)}$

Table 5.1: The effect of brood size (**BS**) on attendance and chick feeding. Values for the proportion of time allocated to foraging (arcsine transformed) during the early and late chick stages are expressed as means ± standard errors and were analysed using an SNK test. The number of chick feeds per hour $^{-1}$ and the proportion of time the territory were analysed using a Kruskall-Wallis analysis of variance.

	BS=1	**BS=2**	**BS=3**	**n**	**Sig**	**p**
Proportion of time spent foraging time in the early chick stage	0.26± 0.03	0.27± 0.02	0.31± 0.21	111	F = 1.1	p>0.3
Proportion of time foraging in the late chick stage	0.36±0.02	0.41±0.02	0.47±0.03	133	F = 4.8	p<0.01
Chick feeds per hour	0.06±0.01	0.09±0.02	0.14±0.02	136	$\chi^2 = 5.4$	p>0.05
Proportion of time territory unattended in the early chick stage	.02±0.02	0.01±0.01	0.02±0.01	111	$\chi^2 = 1.7$	p>0.4
Proportion of time territory unattended in the late chick stage	0.03±0.13	0.04±0.01	0.11±0.03	134	$\chi^2 = 13.1$	p<0.001

5.3.3 The interactive effect of brood size and age on foraging effort

There was no effect of age or brood size on foraging effort in the early chick stage (ANCOVA, $F = 0.48$, $df = 2$, $p>0.6$). In the late chick stage brood size significantly affected the slopes of the regression lines between age and foraging time (ANCOVA, $F = 3.22$, $df = 2$, $p<0.05$, Fig 5.2). Young birds increase foraging effort in response to increased brood size whereas older birds spend a similar amount of time foraging for all brood sizes. There is no interactive effect of age and brood size on non-attendance (logistic regression, $r^2 = 0.00$, Wald = 0.17, $df = 1$, $p>0.6$) nor on the chick feeding rate (logistic regression, $r^2 = 0.00$, Wald = 0.34, $df=1$, $p>0.5$).

5.3.4 The effect of brood size and age on chick condition and survival

Increasing initial brood size significantly reduced mean chick survival, this effect being apparent between all brood sizes (SNK, $n = 128$, $F = 6.35$, $p<0.005$, Table 5.2). Chick condition was not significantly affected by brood size (SNK, $n = 111$, $F = 0.32$, $df=2$, $p>0.7$, Table 5.2). The initial brood size had no significant effect on fledging success (Kruskall-Wallis ANOVA, $n = 125$, $\chi^2 = 0.94$, $df=2$, $p>0.5$, Table 5.2).

Age had no effect on mean chick survival (ANCOVA; $t = 1.66$, $p>0.1$) or mean chick condition (ANCOVA; $t = 0.70$, $p>0.4$). There were no interactive effects of brood size and age on the mean chick survival nor the mean chick condition (ANCOVA; $F< 0.9$, $p>0.4$).

TABLE 5.2: The effect of brood size (**BS**) on the mean chick survival (in days) in a brood, the mean chick condition in the brood and fledging success. Values are expressed as residuals of yearly means with standard errors for survival and condition, and mean ranks for fledging success.

	BS=1	**BS=2**	**BS=3**	**n**	**Sig**	**p**
Chick survival	3.9 ± 1.8	0.6 ± 1.8	- 3.1 ± 1.1	128	$F = 6.35$	<0.005
Chick condition	- 2.3 ± 19.6	11.2 ± 15.4	- 4.1 ± 12.6	111	$F = 0.32$	>0.7
Fledging success	67.90	60.67	61.66	125	$\chi^2=1.04$	>0.5

5.4 Discussion

Life history theory predicts that great skuas should increase foraging effort with age in response to the declining residual reproductive value found in this species (see Chapter 6). Increases in foraging effort with age have been demonstrated in California gulls (Pugesek 1981, 1983) while Roskaft *et al.* (1983) and Reid (1988a) showed a decline in foraging effort with age similar to the one shown in this study.

The decrease in foraging effort with age was only apparent when the energetic demands upon the adults were greatest (during the late chick stage in broods of more than one chick). Young birds increased foraging effort in response to increasing brood size while the old birds spent a similar amount of time foraging for all brood sizes.
The increase in time away from the territory is not due to young birds engaging in non-foraging behaviour since they were returning with food significantly more often

than older birds. Despite the greater rate of chick provisioning found in young birds, there was no decline in chick condition with age as would be expected. It seems that young skuas were spending more time than older ones to meet the nutritional demands of the chicks, probably to offset their lack of foraging experience. Similarly Roskaft *et al.* (1983) found that female rooks with young partners begged for food more often than females with older partners, despite the fact that young males provisioned the female more often. It is possible that young birds spend a greater amount of time obtaining many small regurgitates, while older birds reduced foraging effort by bringing back fewer, larger regurgitates. Foraging efficiency increases with age in many bird species, both in comparisons between immatures and adults (Dunn, 1972, Buckley and Buckley 1974, MacLean 1986) and in breeding adults (Jansen 1989, Desrochers 1992).

The decline in territorial attendance with age could also be attributed to young birds having poor pair co-ordination (Nur 1984). Young birds left the chicks unattended more often than older ones (see results), thus leaving them vulnerable to conspecific predation (Hamer, Furness and Caldow 1991). It may be that young birds forage in response to chick begging even if this leaves the chicks unprotected, whereas old birds stay to defend the chicks until the partner returns. Consequently, through increased time invested in brood defence and increased aggression (see Chapter 2) old parents have a higher fledging success.

One other possible explanation for the decrease in reproductive effort with age is that older birds may be senescent (Collias *et al.* 1986, Newton 1989, Wooller *et al.* 1990) and so are constrained from working harder by somatic deterioration. This theory would predict that there would be a decrease fledging success with adult age, but since no such decline was found in Chapter 2 the senescence theory can be discounted.

5.5 Conclusions

There is a decrease in residual reproductive value with age in terms of survival, thus providing a selective basis for an increase in reproductive effort. There was no evidence to suggest that young birds adopted a strategy of low foraging effort and brood reduction, indeed the reverse appeared true with young birds attempting to maintain larger broods by increasing foraging effort, but at the expense of chick defence. Consequently young birds suffered higher chick predation and lower fledging success. Since effort had no apparent cost in terms of survival (Chapter 6) for young birds, they can work harder without jeopardising residual reproductive value.

I conclude that an increase in effort with age can not be considered as a primary mechanism in age-specific improvements in breeding performance in the years studied.

Chapter 6

The effect of age and reproduction on the survival of great skuas

6.1 Introduction

Early investigations of age-dependent survival rates discovered that the survival rate of the youngest age-classes of birds is lower than in older ones, but assumed that once maturity is reached the survival rate remained constant with age (Lack 1954). Long term population studies of marked individuals have strongly challenged this view and declines in survival with old age have been demonstrated in Charadriiformes (Hilden 1978, Pugesek 1987, Aebisher and Coulson 1990) sparrowhawks (Newton 1989) and in Procellariiforms (Dunnet and Ollason 1978, Bradley *et al.* 1989, Weimerskirch 1992).

According to life history theory reproduction is a costly process in terms of survival and future fecundity, the cost increasing with the effort invested in the breeding attempt (Williams 1966, Gadgil and Bossert 1970). Energy invested in breeding reduces the resources available for maintenance (Reid 1987) and may increase the risk of injury or predation (Ainley and De Master 1980, Pugesek 1983). Both correlational and manipulative studies concerning the effect of reproduction on survival have been conducted, but the results are conflicting (see Reznik 1984, Partridge 1989 for a review). Correlational studies allow birds to breed at their chosen rate and are subject to biases of individual quality, and several studies have demonstrated selection against poor quality individuals with a low breeding success (Nol and Smith 1987). Manipulative studies alter brood size experimentally and so the effects of quality are reduced and as a consequence have been more successful in demonstrating decreases in survival (Reid 1987) and fecundity (Gustaffson and Part 1990) with increased reproductive effort.

The separate effects of selection against poor reproductive phenotypes and the costs of high reproductive effort would be expected to manifest themselves at different ages within a cohort. Selection should occur at an early age, as poor quality breeders are removed from the breeding population after their first few breeding attempts. The costs of high reproductive output should only be evident in older age classes since increasing reproductive effort to the degree that survival is jeopardised would only be adaptive in old birds approaching the end of their reproductive lifetime (Williams 1966, Gadgil and Bossert 1970). This pattern of age-specific mortality in relation to reproductive output has been demonstrated in short- tailed shearwaters (Bradley *et al.* 1989).

The aim of this chapter is to investigate the effect of age and reproductive output on the survival rate of breeding great skuas to see if high effort has a cost in terms of survival.

6.2 Methods

A large number of breeding adults were nest trapped during the incubation period using a whoosh net between 1988 and 1991. Each was given a unique four ring colour combination from which individuals could be identified when subsequently sighted, and a single uniquely numbered B.T.O. monel ring. In addition to these birds, many non-breeders were trapped on club sites (areas where non-breeders gather during the breeding season) using cannon nets, and subsequently recruited into the breeding population. This long-term colour-ringing effort resulted in 322 breeding birds being individually colour marked.

There are many problems inherent in the analysis of survival data arising from the possibility of birds being present on the colony but not being observed, the loss of rings and birds taking years off away from colony and returning again in subsequent years. The following paragraphs address the extent of these problems in this study and the solutions employed to minimise them.

The study site was searched daily for known-age colour-ringed birds using binoculars and a spotting scope in all breeding seasons from 1989 to 1993. Observations were continued through the entire breeding season and the high repeatability of sightings of recorded birds (a minimum of once every 3 days for 3-4 months) along with the small number of new sightings after May (less than 5% of the birds sighted in each year) indicated that recapture rate approached 100%.

Almost all the skuas showed high nest site fidelity and were found on the same territory year after year. So birds were unlikely to be missed due to them moving to another locality. To check for movement from the study site, more extensive searches of the whole island and of other colonies on Shetland were conducted, but no colour-ringed birds which had bred in the study site were sighted elsewhere.

Despite the colour rings being made of durable plastic some ring loss did occur, with 5.9% of marked birds losing one or more rings. This loss was especially evident with rings over 5 years old, since the plastic used in 1988 was of inferior quality (thinner and more flexible) than the 'Codex' plastic rings used in subsequent years. Degradation of the rings included fading and cracking of the plastic, while other rings slipped into one another so that only one was visible. Attempts were made to re-trap birds with missing rings but due to skuas being trap shy for several years after initial capture, the number recaptured was small (37%). Those that were recaptured could be identified using the monel ring, and had all their colour rings replaced. Identification of birds missing one or more colour rings was possible by a process of deduction using the remaining colour rings, the leg the monel ring was on and the position of the territory in the colony. In this manner all birds which had lost colour rings were identified with reasonable certainty as belonging to the territory on which they were located.

Another confounding factor in the analysis of survival rates is that great skuas may take years off breeding. Some birds hold their usual territory but do not breed but others take years off away from the colony. To investigate the proportion of birds which take years off away from the colony 120 birds which were nest trapped in 1988 were examined for 5 years. The study shows that 88.3% of birds did not take years off away from the colony, whilst 8.4% were absent for a single year. Only 3.3% were absent for 2 years and no birds were recorded as being absent for 3 or four years. On the basis of this information, birds which spent more than 1 year away from territory and which were not sighted subsequently are classed as dead for the purposes of analysis.

Death is assumed to have occurred in the first year of absence from the colony since it is this point that represents the end of the bird's reproductive contribution to the population, even if the bird continued to live at sea for a few years before dying.

6.2.1 Analysis

Birds which died were classed as those which were absent from the colony for more than one year. This means that the data set can only include survival from 1989-1992, with data from 1993 being used as a year to check the mortality data for birds which took a year off breeding away from the colony in 1992.

Age-dependent survival rate was examined by analysing the proportion of birds which survived from one age to the next and entering these values into a polynomial regression for analysis. The problem of small sample sizes found in very young and very old ages producing an excessive weight on the curve was overcome by weighting the percentages, so that less importance was attached to proportions derived from small sample sizes. The data were arcsine transformed to stabilise variance.

The effect of breeding output on survival was estimated using a logistic regression procedure in the case of parametric data and Chi-square analysis for binary breeding data. The effects of fledging success on survival within age groups was investigated by categorising the data into young inexperienced birds (birds with less than 2 years of breeding experience and/or an age of 5-10 years) and old experienced birds (birds with more than 2 years breeding experience and or an age of 11-29 years) and examining the costs of reproduction within these groups.

6.3 Results

The annual survival rate of great skuas between 1988 and 1992 was on average 83%. There was no effect of sex on survival to the following breeding season ($\chi^2 = 1.4$, df = 1 $p>0.5$) but the sample of known sex birds was small. There was no significant effect of year on survival between 1988 and 1992 ($\chi^2 = 7.79$, df = 4, $p=0.1$, see table 6.1).

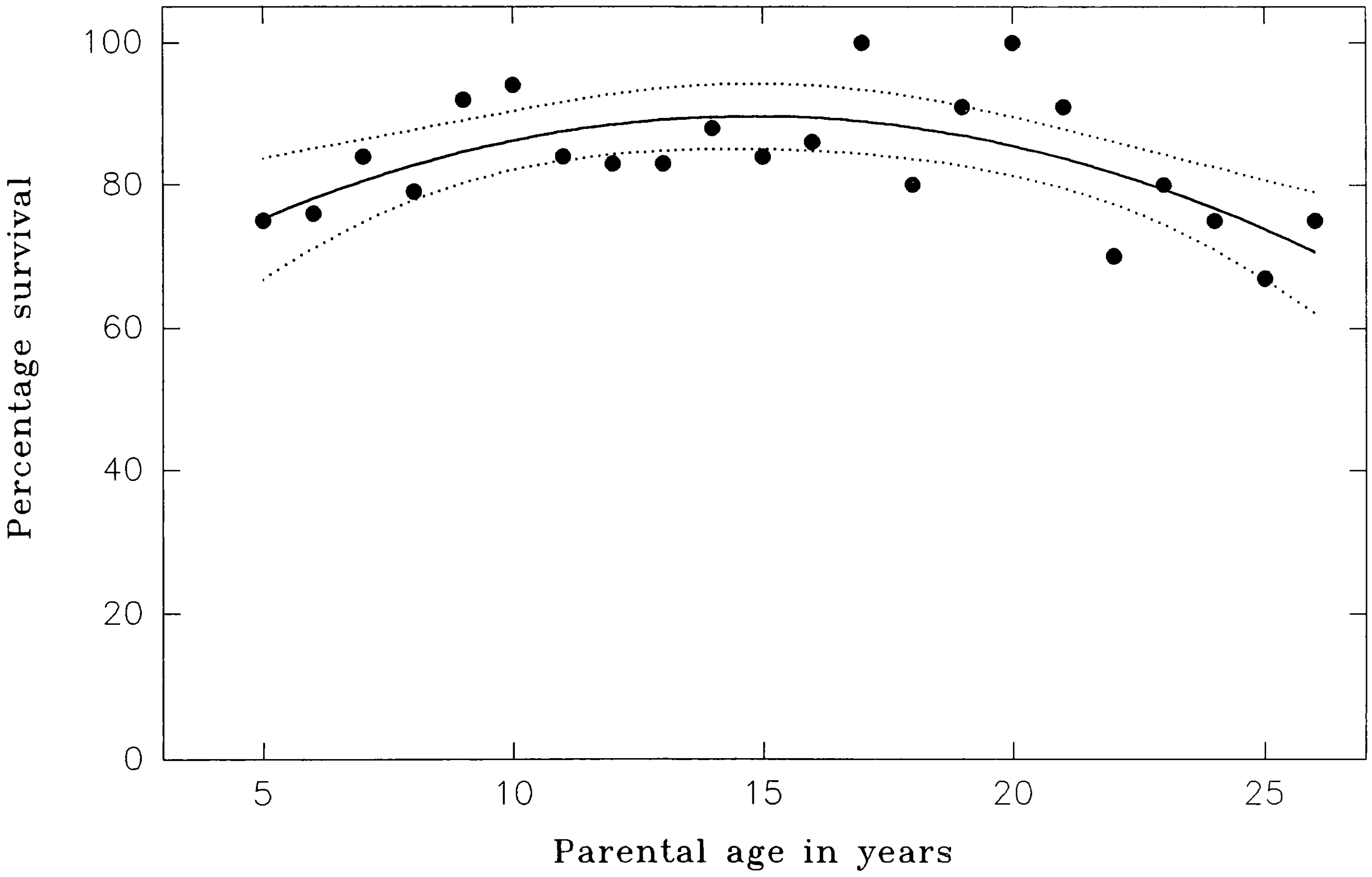
Table 6.1: The effect of year on the survival of known age great skuas between 1988 and 1992. Values are expressed as the percentage of birds which survived from the specified year to the following year. Numbers in parenthesis refer to the sample size.

	1988	**1989**	**1990**	**1991**	**1992**	χ^2	**p**
Percentage survival	78% (54)	89% (67)	81% (86)	78% (130)	87% (163)	7.79	0.1

6.3.1 Age-dependent mortality

The mortality data showed that survival was lower in the youngest birds, increasing to a peak at the age of 14 and then decreasing in older birds. This relationship is highly significant (Polynomial regression, $r^2 = 0.54$, F = 11.52, df = 21, $p<0.001$, Fig 6.1) and explains over 50% of variance in the survival rate of great skuas.

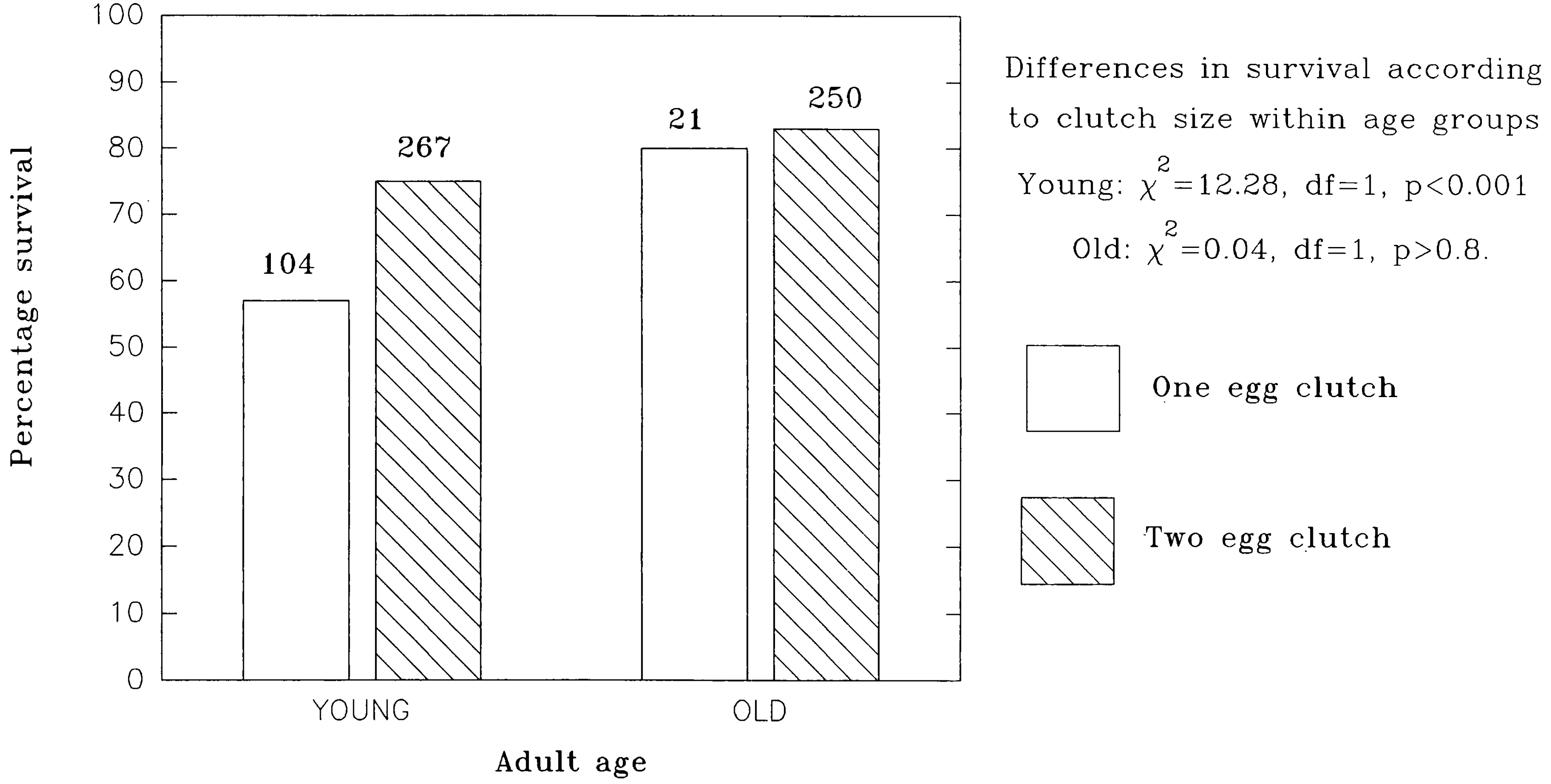
Fig 6.1 The effect of age on survival of breeding adults between 1988 and 1991. Values are expressed as the proportion of birds which survived from the specified age to the next.



Polynomial regression; n = 22, $r^2 = 0.54$, F = 11.52,df= 21, $p<0.001$.

Equation of the line survival = $4.46\text{age} - 0.015\text{age}^2 + 56.4$.

Figure 6.1: The effect of age and clutch size on adult survival of great skuas between 1989 and 1992. Bars represent percentage survival and the numbers above the bars represent sample size

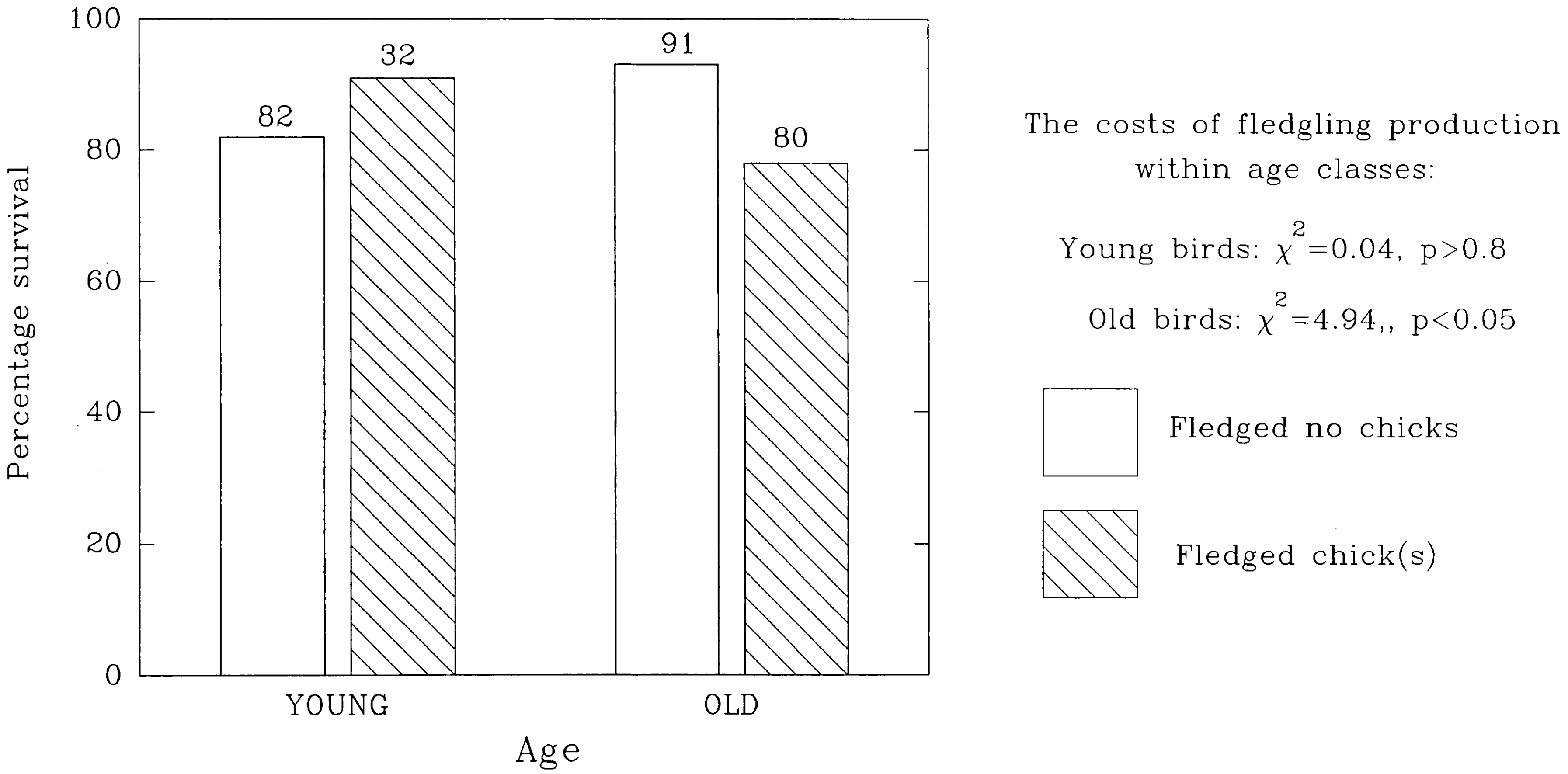


Differences in survival according to clutch size within age groups

Young: $\chi^2 = 12.28$, df=1, $p<0.001$

Old: $\chi^2 = 0.04$, df=1, $p>0.8$.

Fig. 6.2: The effect of age and fledgling production on the survival of great skuas between 1989 and 1991. Bars represent percentage survival and numbers above bars represent the sample size.



6.3.2 The costs of reproduction

See table 6.1 for descriptive statistics. There was no effect of laying date on survival to the following breeding season (logistic regression, r^2 =0.00, Wald = 0.1, df=1, p>0.7). Birds which laid single egg clutches had a lower survival than those which laid 2 egg clutches (χ^2 = 15.00, df=1, p<0.0001). The lower survival of birds with one egg clutches was only evident in young, inexperienced birds (χ^2 = 12.28, df = 1, p<0.001) with no effect being evident in older, experienced birds (χ^2 = 0.04, df=1, p>0.8, Figure 6.2).

There was no effect of clutch volume on survival (logistic regression, Wald = 2.45, df=1, p>0.1), similarly hatching success had no effect on survival (χ^2 = 0.71, df=1, >0.3). Birds which were less aggressive (i.e. did not hit human intruders entering the territory) had a lower survival rate than more aggressive birds (χ^2 = 5.69, df=1, p<0.02). There was no effect of fledging success on survival to the following year (χ^2 = 1.5, df=1, p> 0.2). However, there was a significant effect of fledging success on survival within age groups. Old experienced birds had significantly lower survival if they produced fledglings than if they did not (χ^2 = 4.94, df=1, p<0.05) while in young birds there was no effect (χ^2 = 0.04, df=1, p>0.8, see Fig 6.3).

Table 6.1: The effect of reproductive output on survival to the following year.

Key: Clutch size: 1 = 1, 2 = 2; hatching success: 1 = hatched no chicks, 2 = chick(s) hatched; aggression: 1 = did not hit the intruder, 2 = hit the intruder; fledging success: 1 = fledged no chick, 2 = fledged chick(s).

	1	**2**	**n**	**Chi-square**	**p**
Clutch size	62%	78%	732	$\chi^2 = 15.0$	<0.0001
Hatching success	85%	81%	582	$\chi^2 = 0.71$	>0.3
Aggression	77%	88%	324	$\chi^2 = 5.69$	<0.02
Fledging success	83%	79%	375	$\chi^2 = 0.66$	>0.4

6.4 Discussion

There was no effect of year on survival of great skuas between 1989 and 1992 despite the fact that food supply improved during this time period. Hamer, Furness and Caldow (1990) documented a decrease in survival rate of great skuas in response to a decline in abundance of sandeels. The improvement of food availability would be expected to promote survival of breeding adults, perhaps because of the reduced foraging effort during times when food supply is improved. This was not the case, however, suggesting that great skuas are still paying long-term costs of high reproductive effort exerted during the late 1980s.

In contrast to kittiwakes in which males have lower survival than females, (Aebischer and Coulson 1990) there were no detectable differences in the survival of the sexes. The data on relative ages of birds in a partnership (Chapter 2) suggested that male survival may be lower than that of females.

Many species of bird exhibit age-dependent mortality (Hilden 1978, Bradley *et al.* 1989, Newton 1989, Stenberg 1989, Weimerskirsch 1992), survival often being lower in the youngest and oldest age classes. The long-term data set from 1989 to 1992 demonstrates a very similar pattern, with survival rate increasing up to the age of 14 and then declining in older birds. This decline in residual reproductive value provides a selective basis for an increase in reproductive effort with age. Despite this, no evidence of such an increase in foraging effort has been found (see Chapter 5).

Survival was lower in birds with 1 egg clutches or low aggression scores, the reverse of what would be expected if reproduction was costly. This trend is due to poor quality phenotypes with low breeding output also having higher mortality. This increased mortality of poor quality birds can obscure reproductive costs (Partridge 1989). Poor quality birds will probably suffer mortality early in the life history and will produce increases in clutch size and aggression with age (Nol and Smith 1987). This was evident in the case of clutch size, where lower survival in birds which laid one egg clutches was manifested only in young inexperienced breeders, with no effect being apparent in older birds. However, increased clutch size with age are not purely due to selection since increases also occur within individuals (see Chapter 4).

Many studies have demonstrated costs of fledgling production (Reid 1987, Bradley *et al.* 1989) as feeding older chicks is probably the most energy intensive part of the breeding cycle. The cost of fledgling production in terms of reduced survival was apparent only in old birds while in younger ones there was a tendency for birds which produced chicks to have higher survival, a similar pattern to that found in California gulls (Pugesek 1987) and short-tailed shearwaters (Bradley *et al.* 1989). Clearly the conflicting effects of selection against poor phenotypes with low reproductive output and the costs of reproduction can obscure the relationship between survival and fecundity in more simplistic analyses (Partridge 1989). The fact that young birds which produced chicks showed no reproductive costs suggests that there is no selective pressure for young birds to refrain from high reproductive effort in order to increase survival and future breeding opportunities.

6.5 Conclusions

Survival improves with age up to the age of 14 and then declines in older birds. The low survival in younger birds is probably due to the death of poor quality birds while in older birds it is due to somatic deterioration. The decline in survival with age provides a selective basis for an increase in reproductive effort with age. However, young birds had higher foraging effort than old ones. Life history theory would predict that young birds should avoid increasing effort since this could reduce future breeding opportunities. However, there is no evidence that fledgling production affects survival in young birds and so it seems that young birds increase effort within their abilities to buffer themselves against the costs.

Chapter 7

General Discussion

This study has demonstrated that increased age improves laying date, clutch size, clutch volume, aggression towards human intruders, hatching success and fledging success and so show a similar trend to many other species of bird (see Ryder 1981, Saether 1990 for reviews). Laying date and clutch size were affected by age in a non-linear manner; increasing in young birds before reaching a plateau. No declines in breeding performance with old age such as the ones documented previously in great skuas (Hamer and Furness 1991) and Larids (Davis, 1974, Haymes and Blokpoel 1980, Pugesek and Deim 1990) were evident.

There is a lack of consistency between the findings of this study and the findings of similar studies conducted on great skuas on Foula by Furness (1984) and by Hamer and Furness (1991). The reason for these discrepancies is probably due to the fluctuations in food supply. During the 1970s when the first study was conducted great skuas had high breeding success due to a super-abundance of sandeels in the diet (Furness and Hislop 1980) which resulted in little effect of age on breeding since birds of all ages had sufficient nutrient resources to breed successfully. From 1988 to 1990 there was a severe shortage of sandeels (Hamer, Furness and Caldow 1991) and this resulted in very low breeding success. There has been a steady increase in sandeel availability since 1990 (see chapter 3) and breeding success has improved as a consequence. Under such fluctuating conditions of food availability and breeding success it would not be expected for the same pattern of age specific breeding performance to emerge on successive studies. Also the age structure of the population will have an effect on the results of an age specific study; an increase in recruitment such as the one described in Hamer, Furness and Caldow (1991) will increase the number of very young birds in the sample size and will thus increase the chance of detecting age-specific improvements in breeding performance.

The main aim of this study was to examine possible mechanisms by which age could improve breeding performance. The maturation hypothesis suggests that individual birds improve breeding by learning skills which are beneficial to reproduction

(Hammann and Cooke 1987). The relative benifits of learning decrease rapidly (Pugesek 1984, Pyle *et al.* 1991) and so improvements in breeding due to maturation ougt to be confined to young birds with a plateau in older birds that have aquired all the neccessary skills for breeding. There is evidence that improvements in clutch size, laying date and hatching success follow such a pattern with age (Chapter 2). Similarly, the data in Chapter 4 demonstrated that improvements in laying date and clutch volume with experience were evident only evident between the first and second breeding attempts.

These skills could be associated with improving foraging (Mac Lean 1973, Desrochers 1991); a skill which would be refined as soon the bird first became independent of its parents. Alternatively they could be associated with experience of breeding itself, and so could only be learned after the bird had recruited into the breeding population. Age and experience are closely inter-correlated and separating their individual effects is difficult (Pyle *et al.* 1991, Croxall *et al.* 1992).

This study has demonstrated that individual great skuas do improve their breeding performance on successive breeding attempts, thus supporting the maturation hypothesis. Although this effect was demonstrated for breeding experience it could be equally well be accounted for by age since the two are so closely related. An investigation of the separate effects of age and experience was hampered by the small sample size of marked birds which were of both known age and experience. However, analysis suggested that clutch size was affected by experience independently of age. Experience rather than age affected breeding success in female western gulls (Pyle *et al.* 1991).

Improved foraging skills do have the potential to improve the breeding performance of great skuas. Studies of great skua breeding performance under fluctuating food supply have shown that breeding is related to food availability (Hamer, Furness and Caldow 1990, Chapter 3). A study of age specific breeding patterns under conditions of varying food availability showed that the fledging success of young birds was depressed to a greater degree than older ones by a reduction in food supply. This suggests that young birds are constrained because they have poor foraging skills. Similar results to this have been found in western gulls (Sydeman *et al.* 1991) and Brandts cormorant (Boekelheide and Ainley 1990) during fluctuating food availability in the California current. Alternatively, young birds may have been refraining from exerting high effort in chick production during poor years in order to conserve potential reproductive value. Older birds which have a lower expectancy of future breeding due to a reduction in survival with age (Chapter 6) would be expected to maintain effort even in poor years in an attempt to increase lifetime reproductive output prior to death. This explanation has been used to account for the age-specific patterns of reproduction under fluctuating food availability found in western gulls (Sydeman *et al.* 1991) and Brandts cormorant (Boekelheide and Ainley 1990).

Similarly, a food supplementation experiment showed that young birds which were given daily supplements to their diet had similar clutch volumes to older birds, while young control birds had lower clutch volumes than older ones. This suggests that providing food removes the effect of poor foraging efficiency on egg production and allows young birds to produce clutches similar to the ones found in older birds. Krapu and Doty (1979) found that yearling mallards which were fed *ad libitum* produced clutches of similar size to older females and Desrochers (1992) showed that food supplements allowed young blackbirds to lay as early as older ones.

Another hypothesis which has been put forward to explain increases in breeding performance with age is the restraint hypothesis. This suggests that reproduction is a costly process in terms of survival (Williams 1966) and so young birds should refrain from exerting maximum effort in reproduction in order to conserve future breeding opportunities (Partridge 1989). As expectation of life decreases due to age-dependent mortality, there will be an increase in effort in order to maximise reproductive success before the terminal event (Clutton-Brock 1984).

The survival rate of great skuas increased with age up to the age of 15 before it declined in older birds. Declines in survival rate with old age have been found in many species including fulmar (Dunnet and Ollasson 1978) sparrowhawk (Newton 1989) California gull (Pugesek 1987), common gull (Rattiste and Lillehet 1987) and short-tailed shearwater (Bradley *et al.* 1989).

This decline in survival with old age provides a selective basis for an increase in effort with age. Despite this there was no evidence for an increase in foraging effort with age in great skuas, indeed the reverse appeared to be true with young birds spending more time away from territory (in pairs with 2 or 3 chick broods) and having a higher rate of chick feeding. Similar decreases in foraging time with age have been shown in glaucous-winged gulls (Reid 1988a) and rooks (Roskaft *et al.* 1983). Despite the higher foraging time and chick feeding rate in young birds, they did not have heavier chicks and had a lower fledging success, which suggests that they were less efficient at foraging than older birds (i.e. had lower returns in terms reproductive gain for unit time spent foraging). Fledging success was probably lower in young birds since they left their brood unattended more often in order to go foraging and as a consequence the chicks were killed by neighbouring birds (Hamer, Furness and Caldow 1991).

There was little evidence to suggest that high reproductive effort had a cost in terms of subsequent survival. However, the production of fledglings in older birds produced a decrease in survival which could represent a reproductive cost. Since this effect is only apparent in older birds which have higher fledging success, it could possibly represent a cost of increased effort with age. A similar result was found by Pugesek (1987) in California gulls and Bradley *et al.* (1989) in short-tailed shearwaters, who found that increased fledgling production was associated with a lower survival rate in older birds but not younger ones.

The final explanation which could account for the improvement in breeding performance with age is the selection hypothesis which predicts that poor quality birds which have a low breeding performance also have a lower survival rate and so will be eliminated from the breeding population at a relatively early age (Nol and Smith 1984). In contrast good quality birds with high breeding performance have a higher survival rate and so are represented in the breeding population for far longer, giving the impression of an increase in breeding performance with age.

There is evidence to suggest that great skuas which lay a one-egg clutch have a lower survival rate than birds which lay a 2 egg clutch, this effect being especially evident in first time breeders. This could produce an apparent increase in clutch size with age as birds which lay one egg will be eliminated from the breeding population. Nol and Smith (1987) found that female song sparrows which bred for only one year raised fewer young than birds which also bred in subsequent years. Similarly, Bradley *et al.* (1989) found that short-tailed shearwaters which lived for longer had higher breeding success than birds which lived for a shorter period, especially in the first year of breeding.

In conclusion, the real reason for the increase in breeding performance with age is probably due to a combination of the three factors all acting to different extents at various stages of the reproductive season and the individuals life history (Wooller *et al.* 1990). Maturation is probably the main cause of the increases in breeding performance with age in great skuas but whether these improvements are due to a development of foraging or breeding techniques is unclear. Clutch size and aggression could improve with age due to the lower survival of birds which have one egg clutches and are unaggressive. There is little evidence for an increase in effort with age despite there being a decline in survival with old age. However the higher cost of increased fledgling production in older birds could indicate that they have higher reproductive effort than younger ones.

Summary

1. Great skuas which were ringed as chicks were nest trapped on Foula and were given unique colour ring combinations. The age of these birds was calculated from the date the bird was ringed as a chick. Also, non-breeding birds were captured and colour ringed on club sites and the breeding experience of these birds was followed.

2. The effect of parental age on the laying date, clutch size, clutch volume, adult body condition, hatching success, brood defence, inter nest distance, chick condition and fledging success of great skuas on Foula was investigated.

3. There was a weak but significant correlation between the ages of birds within a pair. Very few partnerships contained two birds of known age. In cases where only one was of known age, the age of partners was assumed to be the same. Although this assumption is only weakly supported any differences between ages of partners will weaken rather than reinforce age-specific patterns in breeding performance.

4. Laying date, clutch size and hatching success were related to age in a non-linear manner, improving in younger birds and then reaching a plateau. Laying date was influenced by female rather than male age.

5. Clutch volume, aggression and fledging success increased with age but there was no evidence for a decrease in older birds. The increase in clutch volume with age was due to male age rather than that of the female, possibly due to an increase in courtship feeding in older males.

6. The increase in fledging success with age was independent of laying date and aggression towards human intruders.

7. There was no effect of age on the inter-nest distance, nor on the body condition of

adults and chicks.

8. Increased food supply advanced laying date and increased clutch volume and fledging success, but had no significant effect on clutch size and laying date.

9. Age and improved food availability advanced laying date independently but there was no significant interaction between these factors.

10. There was a significant interactive effect of food availability and age on fledging success: age had no effect on fledging success in years when food was scarce (uniformly low at all ages) and when food was abundant (uniformly high at all ages) but there was an increase in fledging success with age in years of intermediate food availability. This shows that food is a constraining factor in young birds more than old ones, probably due to young birds having poor foraging skills.

11. A food supplementation experiment improved clutch volume in young birds but not old ones. This provided further support to the theory that young birds are constrained from breeding as well as old birds due to lower foraging efficiency.

12. Breeding experience advanced laying date and increased clutch size and clutch volume but it had no effect on hatching success. The benefits of experience decreased after the first breeding attempt.

13. The increase in clutch size and clutch volume with age was apparent within individual birds, suggesting a learning process improves breeding performance.

14. Breeding experience rather than age was important in increasing clutch size. This suggests that foraging efficiency is unimportant in egg formation though the feeding experiment and studies of clutch volume with changing food availability

suggest otherwise.

15. The time budgets of known-age great skuas were investigated by a series of 2-4 hour observations. Data collected were the proportion of time spent foraging, the number of chick feeds per hour and the proportion of time chicks were left unattended. To control for the fact that young birds have fewer, chicks a brood size manipulation was used so that young birds had similar effort loads to older ones. The interactions of age and brood size were also investigated. The effects of chick age were controlled for by allocating chicks to early and late chick categories.

16. There was no effect of parental age or brood size on foraging effort when chicks were young. The chicks were almost never left unattended and the rate of feeding was low since chicks of this age have low nutritional demands.

17. During the late chick stage, increased brood size produced a marked increase in foraging effort. There was a decrease in foraging effort with age in brood sizes of two or three, possibly due to young birds having to forage for longer in order to compensate for their lack of foraging efficiency. Chick feeding rate also decreased with age, suggesting that the increase in foraging time was not due to inefficiency, however since chick condition did not decrease with age it may be that young birds bring back smaller meals more often. The time that chicks were unattended decreased with age and as a consequence younger birds had increased chick predation and lower fledging success.

18. The above findings suggest that there is no increase in effort with age as suggested by life history theory. Instead there is a decrease in foraging effort with age due to poor foraging efficiency and pair co-ordination in young birds.

19. The survival of adult great skuas improves with age up to the age of 16 years and

declines in older birds.

20. Survival is lower in birds that have one egg clutches and in birds that are unaggressive to intruders. This is probably due to poor quality phenotypes with low breeding output being selected against and having lower survival. This could account for increases in clutch size and aggression with age since poor quality birds will die at young ages while good quality birds will continue to breed for many more breeding seasons.

21. Survival was lower in old birds that fledged young birds than in old birds that fledged no young and this could represent a cost of reproduction. In young birds there was no effect of fledging success on survival.

22. The conclusions of this thesis is that age does affect the breeding ecology and survival of great skuas, though the magnitude of the effects are often small. The reasons for the increase in breeding success with age is best explained by a learning process within individual birds associated with experience of both breeding and foraging. There is also evidence that poor phenotypes have lower survival which could also produce an apparent increase in breeding performance with age. There is no evidence for an increase in effort with age despite the age dependent mortality and a cost of reproduction in older birds.

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Appendix 1:. List of systematic names of species mentioned in the text.

Sandeel: *Ammodytes marinus.*

Adelie penguin: *Pygocelis adelie.*

Yellow-eyed penguin: *Megadyptes antipodes.*

Waved albatross: *Diomedea irrorata.*

Laysan albatross: *Diomedea immutablis.*

Wandering albatross: *Diomedea exulans.*

Fulmar: *Fulmaris glacialis.*

Antarctic fulmar: *Fulmaris glacioides.*

Manx shearwater: *Puffinus puffinus.*

Short-tailed shearwater: *Puffinus tenuirostris.*

Corys shearwater: *Calonectris diomedea.*

Shag: *Phalacrocorax aristotelis.*

Antarctic blue-eyed shag: *Phalacrocorax antriceps.*

Brandts cormorant: *Phalacrocorax penicillatus.*

Brown pelican: *Pelecanus occidentalis.*

Gannet: *Sula bassana.*

White stork: *Ciconia ciconia.*

Little blue heron: *Florida caerulea.*

Bewicks swan: *Cygnus columbianus.*

Snow goose: *Anser caerulenscens.*

Lesser-snow goose: *Anser caerulecens caerulecens.*

Barnacle goose: *Branta leucopsis.*

Canada goose: *Branta canadiensis.*

Nene goose: *Branta sandvicensis.*

Mallard: *Anas platyrhynchos.*

Lesser scaup: *Athyna affinis.*

Eider: *Somateria mollissima.*

Goldeneye: *Bucephela clangula.*

Kestrel: *Falco tinnunculus.*

Sparrowhawk: *Accipiter nisus.*

Hen harrier: *Circus cyaneus.*

Blue grouse: *Dendragopus obscurus.*

Hazel grouse:*Dendragopus canadensis.*

Black grouse: *Tetrao tetrix.*

White tailed ptarmigan: *Lagopus leucrurus.*

Willow ptarmigan: *Lagopus lagopus lagopus.*

American coot: *Fulica americana.*

Coot: *Fulica atra.*

Lapwing: *Vanellus vanellus.*

Dunlin: *Caladris alpina.*

Redshank: *Tringa totanus.*

Red-necked phalarope: *Phalaropus lobatus.*

Semi-palmated sandpipier: *Caladris pusilla.*

Turnstone: *Aenaria interpres.*

Arctic skua: *Stercorarius parasiticus.*

Great skua: *Catharacta skua.*

California gull: *Larus californius.*

Lesser black backed gull: *Larus fuscus.*

Common gull: *Larus canus.*

Glaucous-winged gull: *Larus glaucescens.*

Red-billed gull: *Larus novaehollandiae scopulinus.*

Ring-billed gull: *Larus delwarensis.*

Western gull: *Larus occidentalis.*

Herring gull: *Larus argentatus.*

Laughing gull: *Larus antricilla.*

Kittiwake: *Rissa tridactyla.*

Royal tern: *Sterna maximus.*

Sooty tern: *Sterna fuscata.*

White fronted tern: *Sterna striata..*

Least tern: *Sterna antillarum.*

Common tern: *Sterna hirundo.*

Arctic tern: *Sterna paradesia.*

Ural owl: *Strix uralensis.*

Tengmalms owl: *Aegolius funereus.*

Skylark: *Alauda arvensis.*

Rock pipit: *Anthus spinoletta.*

White wagtail: *Motacilla alba.*

Tree swallow: *Iridoprocne bicolor.*

House martin: *Delichon urbica.*

Bee-eater: *Merops apiaster.*

Bluebird: *Sialia sialis.*

Nuthatch: *Sitta europaea.*

Great tit: *Parus major.*

Blue tit: *Parus caeruleus.*

Willow tit: *Parus montanus.*

Marsh tit: *Parus palustris.*

Pied flycatcher: *Ficedula hypoleuca.*

Collared flycatcher: *Ficedula albicollis.*

Heron island silvereye: *Zosterops lateralis chlorocephala.*

Blackbird: *Turdus merula.*

Starling: *Sturnus vulgaris.*

Magpie: *Pica pica.*

Hooded crow: *Corvus corone cornix.*

Rook: *Corvus frugilegus.*

Pinyon jay: *Gymnorhinus cyanocephalus.*

Mexican jay: *Aphelocoma ultramarina.*

Raven: *Corvus corax.*

Prarie warbler: *Dendroica discolor.*

Darwins finch. *Geospiza fortis* and *G. scandens.*

House sparrow: *Passer domesticus.*

African village weaver: *Ploceus cucullatus.*

Song sparrow: *Zonotrichia melodia.*

White crowned sparrow: *Zonotrichia leucophrys.*

Savannah sparrow: *Zonotrichia sandwichensis.*

Red-winged blackbird: *Agelaius phoeniceus.*

Yellow headed blackbird: *Xanthocephalus xanthocephalus.*

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