

Ecology and Behaviour of Great Skuas Breeding on Foula (Shetland)


Paulo X. Catry

Presented in candidature for the degree of Doctor of Philosophy, to the Faculty of
Science, University of Glasgow.

1997

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.

A handwritten signature in black ink, appearing to read 'Paulo Catry', with a stylized flourish at the end.

Paulo Catry

1997

This thesis is dedicated to my parents, for their support and encouragement.

Acknowledgements

This research was funded by Junta Nacional de Investigação Científica e Tecnológica (Programa Praxis XXI BD/2556/93). I am grateful to Professors Graeme Coombs and Felicity Huntingford for allowing me access to facilities in the Zoology Department during my stay at Glasgow University.

I thank Bob Furness for giving me the opportunity to work with such fantastic birds in such a fantastic island, and for supervising this research.

Many thanks to Keith Hamer, Nick Klomp and Norman Ratcliffe for catching and colour-ringing so many birds, and allowing me to use the data they collected on those individuals, without which this thesis would have been very different.

Thanks to the Holbourn family for permission to work on Foula, and to the Foula islanders, particularly Frank and Penny Millsop, for making me feel welcome. To Tony Maiwood for telling us about interesting migrants in the island, and for the excursions to the Back of the Noup to catch storm petrels.

I am grateful to Graeme Ruxton for invaluable help in creating the models in Chapter 6, and for always being so enthusiastic about research.

To Dr James Curren for showing me JMP and providing statistical advice.

Thanks to all researchers in Bob's group, Belen Calvo, Fiona Stewart, David L. Thompson, David R. Thompson, Richard Phillips, Stuart Bearhop, Geoffrey Hilton, Brendan Godley (and Annette Broderick), Ragnar Palsson, Luís Monteiro, José Pedro Granadeiro, Ben Ross and Kenny for creating such a friendly and lively environment, in the office and away from it.

To Belen for friendship from the very first day I arrived in Glasgow.

To Richard and Fiona, for moral support when everything went wrong in my first field season. To Richard for long discussions about seabird ecology, skuas, statistics and dreams about distant places, for collaborative work, for reading and making suggestions on some of my manuscripts, for encouragement and for always making jokes about (our) ecological research.

To Stuart Bearhop, for unbelievable patience during a long enclosure on Foula under very rough weather conditions, for showing me a wood warbler (amongst many others) and for, together with Brendan, making a decisive

contribution to transform lunch breaks in the office into moments of relaxation and good laugh.

To Brendan for reading and editing almost every chapter in this thesis. And for very good friendship and moral support every time it was needed.

To José Pedro for never agreeing with anything I said, and forcing me to think carefully about it.

Thanks to Catarina, Paula, Mário and Alexandra, for helping to make my stay in Glasgow so enjoyable.

To my friends and family back in Portugal, particularly Rui Rebelo, José Pedro, Vanda Magalhães and my sisters, Teresa and Inês, for encouragement, for keeping me informed about people, weather and birds, and for always making me feel like going back, when time comes.

Contents

Abstract	
General Introduction	1
Chapter 1: Territorial intrusions and copulation behaviour in the great skua.	15
Chapter 2: Partnerships and mechanisms of divorce in the great skua.	32
Chapter 3: The influence of hatching date on life-history stages of great skuas.	50
Chapter 4: Egg volume and within-clutch asymmetry in great skuas: are they related to adult quality?	66
Chapter 5: Influences of age and size on the inferred foraging ability of breeding great skuas: an experimental study.	79
Chapter 6: Short-lived repeatabilities in long-lived birds: Implications for the study of individual quality.	102
Chapter 7: The evolution of reversed sexual size dimorphism in skuas: a test of hypotheses.	120
Chapter 8: The incidence of non-breeding by adult great and Arctic skuas from Foula, Shetland.	145
General discussion	160
Summary	165

Abstract

Aspects of the ecology and behaviour of Great Skuas breeding on Foula were investigated by studying individually marked birds.

Pre-incubation behaviour of Great Skuas was described and predictions that arise from theories of territorial intrusions and copulation behaviour in birds were tested.

Partnership composition and behaviour associated with mate change were studied. In particular, an attempt was made to test which of two alternative theories provides a better explanation for the occurrence of divorces in species where mate change is associated with a (short-term) measurable cost.

Investigations were made to evaluate the effect of hatching date on different life-history stages in Great Skuas, including chick growth, survival to fledging, post-fledging survival and reproductive performance. The implications for the optimal timing of breeding in adults were analysed.

Clutch characteristics, including total volume and within clutch asymmetry, were analysed in relation to parental age and breeding performance.

An experiment was designed to infer foraging ability from territorial attendance of adult skuas, and detect small individual differences in those patterns. Results were analysed in relation to adult age and body size.

Mathematical models were built to allow simulations of the effects of age on the study of individual repeatability in a breeding parameter: laying date. The consistency of individual laying dates over long time intervals was assessed. Results were discussed in relation to the concept of a permanent individual quality.

Studies of the behaviour and breeding performance of individual skuas were analysed in relation to sex and body size. Results were discussed in relation to specific predictions made by several theories that explain the evolution of reversed sexual size dimorphism in the Stercorariidae and other birds with a raptorial lifestyle.

General Introduction

Based on concepts of natural selection and optimality, there is a well developed theory of how long-lived animals should behave. This "life-history theory" predicts, for example, that iteroparous long-lived animals with a low annual reproductive output should refrain from investing so much effort into current reproduction as to risk future survival. (Stearns 1992). Testing predictions of life-history theory as they relate to long-lived animals is only possible if data can be obtained from long-term studies of populations of marked individuals. In addition, it is helpful if the ecology and behaviour of the study species is well known. Few suitable study populations exist. One of which, selected for this research programme, is the population of Great Skuas *Catharacta skua* in Foula, Shetland, where there are many marked adults, a large proportion of which of known-age and where long-term studies have provided a large body of knowledge on the ecology of the species.

Great Skuas belong to the family Stercorariidae (Order Charadriiformes). Skuas are thought to have diverged from their closest relatives, the gulls (Laridae), about 10 million years ago (late Miocene). They are distinguished from other Charadriiformes by their hooked claws, dermal scutes on the tarsi, a prominent nail in the upper mandible and reversed sexual size dimorphism (Furness 1987, 1996).

The Stercorariidae are a small family, formed by seven extant species, distributed in two genera, *Catharacta* (four species) and *Stercorarius* (three species; Furness 1996a). Traditionally, Great Skuas have been regarded as conspecifics with three related taxa from the sub-Antarctic seas: *Catharacta (s.) antarctica*, *C. (s.) hamiltoni* and *C. (s.) lonnbergi* (Furness 1987). Recent research (Cohen et al. 1997) has shown that these three taxa are closely related (all subspecies of *C. antarctica*; Furness 1996a), while *C. skua* stands out as the most genetically distinct of all the large skuas, suggesting that it was the first to diverge from the ancestral line, possibly evolving in the northern hemisphere while all other *Catharacta* (*C. antarctica*, *C. maccormicki* and *C. chilensis*) remained in the South. One puzzling question concerns the historical distribution of Great Skuas. There is compelling negative evidence indicating that they were absent from most or all of their current breeding range during pre-historic times, and also during the Viking expansion in the North Atlantic (Furness 1987). Only more recently did great skuas become abundant in

Scotland, the Faeroes and Iceland. Apart from recent colonisations of other locations in the North-East Atlantic by a few individuals (e.g. Svalbard, Bear Island, North Norway and North Russia), Great Skuas are unknown to have bred anywhere else in the world. Current world population is thought to be around 14,000 pairs, the vast majority of which breed in Scotland (mostly in Shetland and Orkney) and Iceland (Cramp & Simmons 1983, Furness 1996a).

Great Skuas are seabirds that only come to land to breed. They mostly nest in small islands or remote places in larger land masses. To establish their breeding territories they select areas with short vegetation, often in moorland. Although they can nest in steep slopes, they tend to occur at highest densities in flat ground, and never use cliffs or rocky substrates. Outside the breeding season, they are pelagic and actively avoid coasts. They winter mostly around Iberia, with birds occasionally reaching more distant locations like the Cape Verde Islands and Brazil to the South, and Newfoundland to the West (Furness 1978, Klomp and Furness 1992).

The island where this study took place was Foula, the most remote of the Shetland Islands, located 25 Km to the west of the nearest point in the remaining archipelago. Foula is a small (5 Km by 4 Km) mountainous island, with hills reaching 400 m, and covered with short moorland vegetation. The human population is around 35 to 50 persons. Land use is almost exclusively confined to grazing by sheep and a few Shetland ponies. With around 2500 pairs of Great Skuas during the last two decades, Foula is the largest colony in the world for this genus (Furness 1987, Sears et al. 1995). Studies with colour-marked birds were carried out only in a defined study area (2 Km by 1 Km) in the north-east of the Island. Human disturbance or interference with these birds (apart from disturbance by researchers) was almost non-existent.

Food habits of Great Skuas are mostly known from studies on the breeding grounds (e.g. Furness 1978, 1979, 1996b, Furness and Hislop 1981, Phillips et al. in press). Feeding techniques include surface-diving for fish, scavenging discards behind fish trawlers, and kleptoparasitism and predation of other seabirds. Some individuals can be very bold, and with their strength they can rob or kill larger birds

such as Shags *Phalacrocorax aristotelis*, Gannets *Morus bassanus* or Great Black-backed Gulls *Larus marinus*. In Shetland they feed mostly on sandeels (Ammodytidae) they catch themselves or on other fish (mainly Gadidae) discarded by fishermen. Most individuals eat some bird meat, either taken live or as carrion, but a few specialise and are mostly predators, at least during the breeding season. Goose barnacles (*Lepas*) are also regularly taken in small amounts from flotsam at sea, particularly when other food is scarce. Behaviour at sea is little known. On Foula, during chick rearing, typical foraging trips last for several hours (up to seven, at least, but probably much more). When feeding conditions are poor, adults may leave chicks unattended, which often results in predation by conspecifics (Hamer et al. 1991). Apart from that, skuas have few predators. On Foula, Ravens *Corvus corax* and very occasionally Arctic Skuas *Stercorarius parasiticus* take some eggs. Shetland sheep have also been seen eating eggs (in 1996, one single ram destroyed five clutches of birds I was studying!).

Great Skuas start arriving on Foula in late March, and almost all birds are back by the end of April. Skuas usually reoccupy previous territories that have strictly defended boundaries and are usually around 30m in diameter in the Foula colony (Furness 1987). Females rely on courtship feeding by their partners to provide most of their nutritional requirements in the two weeks before laying. Laying usually extends from the second week in May to mid June. Clutches are mostly (>90%) formed by two eggs, laid with two or three days interval. One-egg clutches are mostly typical of young inexperienced breeders (Ratcliffe 1993). Three-egg clutches are very rare (one seen in about one thousand nests during this study), and they rarely hatch chicks (Furness 1987, pers. obs.). Incubation is by both sexes, but more so by females, and lasts 29 days on average. Hatching is asynchronous, but when food is abundant both chicks often survive (Furness 1984). Chicks are semi-precocial, leaving the nest after two or three days. It is not uncommon for chicks to wander out of their territories and be adopted by neighbours (pers. obs.). This can happen when they are very small, and probably results from errors by both chicks and adults, when feeding conditions are apparently good. Later in the season, large chicks also get adopted by neighbours, and this could be a strategy of the chicks to get better feeding resources when parental provisioning is insufficient (Hébert 1988). During incubation

and early chick rearing, males do most of the foraging for the pair. As the chicks grow, females progressively increase their relative contribution to the total time spent foraging. Adult birds are very aggressive in defending their nests and broods from potential predators. Many of the individuals on Foula will readily swoop towards humans and strike them vigorously in the head (Hamer and Furness 1993). Chicks fledge when around 46 days old. After 3 to 4 years at sea, young birds return to the colony for the first time (Klomp and Furness 1991). They arrive late in the season and stay for only a few weeks, gathering in clubs, which are well demarcated and stable areas where non-breeders associate. After a first visit, young birds will come back in the following years, arriving progressively earlier until they recruit and breed (Klomp and Furness 1991). Great Skuas from Foula are highly philopatric, generally recruiting in the general area of the island where they were born. Few birds emigrate from Foula, and immigration from other colonies has never been recorded (Klomp and Furness 1992). Age of first breeding is generally between 5 and 9, on average 7.9 (Klomp and Furness 1991). Great Skuas are unknown to change colonies after settling and breeding in one place. They are long-lived, and the oldest known-age bird is a female that was alive and breeding on Foula in 1997, at the age of 34.

Long-term Studies of Great Skuas in Foula: A Brief Historical Overview.

In 1958, members of the Brathay annual expedition to Foula started ringing Great Skua chicks in large numbers. This was done with the primary objective of collecting information on the patterns of migration and dispersal in this population. At first, rings were made of aluminium, and would wear and fall off after only a few years. From 1962, some ringing was done using long-lasting monel rings that remained in good shape even after 20 or 30 years without replacement. From 1968 until 1996, between 500 and 2,900 Great Skua chicks were annually ringed in the island. In 1971, Bob Furness made his first visit to Foula, as a member of the Brathay expedition. He went back each year since, started systematic research on the species and coordinated all investigations that were to follow. Two long field seasons for detailed studies on Great Skua breeding biology, in 1975 and 1976, provided most of the data that were to be the basis of his PhD thesis (Furness 1977). Before this, little was known about the biology of Great Skuas, and the most important studies had

concentrated on the description of behaviour (Perdeck 1960 - who carried out part of his observations in Foula - and Andersson 1976a, b). With his early studies, Furness (1977, 1978a,b, 1979, 1983, 1984, 1987; Furness and Hislop 1981) provided detailed descriptions of the ecology of the species, including breeding statistics and factors affecting nesting success, food habits and kleptoparasitism, migration patterns and survival rates of adults and immatures. With the help of some colour-ringed birds that could be assigned to specific cohorts (but that were not identifiable as individuals) he did the first analyses on the effect of age on breeding performance of this species (Furness 1984). Early investigations on Foula (Furness and Hutton 1979) also started a long series of studies on pollutant levels in skuas, with wider implications for the mechanisms of accumulation and dynamics of pollutants in seabirds, their effects on the biology of these organisms, and their usefulness for environmental monitoring (e.g. Muirhead 1986, Thompson et al. 1991, 1992, Stewart et al. 1997).

In Spring 1986 and 1987, Richard Caldow was on Foula collecting data on the ecology and behaviour of Great Skuas. This field work was aimed at gathering a better understanding of skua feeding behaviour, in particular of kleptoparasitism, which was the main subject of his PhD thesis (Caldow 1988). The data he collected were also used later in the long-term study that analysed annual variations in breeding performance in relation to food supplies (Hamer et al. 1991).

In 1988, Keith Hamer started marking Great Skuas with unique combinations of colour-rings that allowed ready identification of individuals in the field. A large proportion of the individuals he caught had been ringed as chicks on Foula and so their age could be accurately determined. In the three years he spent on Foula, he was to colour-ring just under 200 skuas. It was found that, as in other birds, several breeding parameters improved with increasing age. However, clutch volume decreased after reaching a peak in mid-aged skuas (Hamer and Furness 1991). Hamer et al. (1991) also described the dramatic effects on Great Skuas of the crash in sandeel stocks in Shetland waters during the late 1980s. Breeding success was very low in those years, and there was some evidence of increased mortality in adult birds. Hamer (1990) provided the first survival estimates of adult great skuas based on sightings of colour-ringed birds at a colony, a method usually more accurate than the analysis of ringing recoveries from dead birds. Parental investment was also studied,

by analysing patterns of aggression by adult birds when defending their chicks (Hamer and Furness 1993). Distinction between the behaviour of males and females was made possible by the existence of colour-ringed individuals for which sex could be determined by discriminant analysis of measurements or by observed behaviour.

It was also during 1988-91 that Nick Klomp did his research on the recruitment of Great Skuas (Klomp 1991 and references above). Nick marked numerous immature birds on clubs. After recruitment, those birds became part of the long-term study of individually marked skuas. Because their date of recruitment was known, the separate effects of adult age and breeding experience could be studied in the following years. This was the work of Norman Ratcliffe, who was on Foula in the summers of 1991 to 1993. He used colour-ringed birds left by the two previous researchers, and marked many more by introducing the flick-net as an invaluable tool to catch large numbers of birds. Norman focused exclusively on the effects of age and experience on breeding and survival of adult Great Skuas, testing several predictions from theories that explain maturation in birds and life-history strategies (Ratcliffe 1993).

Aims of this thesis.

Currently available theoretical and empirical evidence suggest that evolutionary processes are driven by selection that operates at the level of individuals. The general idea of fitness maximisation, as the ultimate target of all individuals irrespective of species or environment, provided the fundamental framework that allowed bridging the gap between evolutionary, behavioural and ecological sciences, creating the discipline of evolutionary ecology (where behavioural ecology can be included). More recently, the importance of looking at individuals within populations has been reinforced by the realisation that individuals differ, genetically and phenotypically, to such an extent that they may follow different strategies to maximise their own fitness (e.g. Coulson 1968, Pettifor et al. 1986). Looking at individuals not only reveals new patterns, but also improves our understanding of phenomena that had previously been described.

As briefly summarised above, our general knowledge of the natural history of Great Skuas breeding on Foula is very good. Furthermore, when this particular

project was initiated, there was a large number of individuals on Foula for which data on breeding performance had been collected for several years. Many of these birds were known-age, some known-sex. The general aim of the research presented in this thesis is to use those birds (after having expanded the data sets, through additional fieldwork) to test current ideas about bird ecology and behaviour. Little emphasis was put in questions related to the effects of age on the ecology of adult birds, since this has been extensively investigated before (but see below). However, information on the age of the birds studied has been used in the analysis of the data to help clarify other patterns of interest. During fieldwork, I did not limit myself to expanding existing data files, but instead introduced new practices that changed qualitatively the information available for analysis. I shall quote some (more important) examples:

(1) Initially, in the long-term study of colour-ringed individuals, birds were sexed by means of a discriminant function using external measurements (Hamer and Furness 1991b). This later proved to be rather inaccurate (Ratcliffe 1993). Ratcliffe sexed a few birds by observation of copulations, but his samples were small. From 1994 to 1996, I did systematic watches and sexed approximately 400 colour-ringed skuas by observation of copulations and courtship feeding. This proved essential for most analyses presented in this thesis.

(2) Hamer and Ratcliffe tended to catch only one adult in each pair as it proved much more difficult to catch both birds. A special effort was made in this study to trap and mark as many birds in partnerships as possible. This allowed studies of divorce, assortative mating, and copulation behaviour, not previously possible.

(3) A small area was selected for studies of pre-incubation behaviour. As many birds as possible were marked in this area, and systematic observations were carried out in 1995 and 1996.

(4) All measurements of body size presented in this thesis were taken by myself, to avoid serious potential problems arising from inter-observer inconsistencies in measuring techniques. This also required a large investment into catching and measuring as many adult skuas as possible.

Each of the chapters in this thesis were designed as independent pieces of research, and as such can be read in isolation, without needing any kind of cross reference.

This approach was followed to expedite publication of my work. Each chapter attempts to provide answers for specific questions that might contribute to a better understanding of some aspects of bird evolutionary ecology or behaviour. However, the different chapters of this thesis are all investigations of the adaptive significance of Great Skua morphology or behaviour, with particular interest in aspects of life-history theory and questions of individual quality. The subjects treated in this work are presented below:

Chapter one describes aspects of the pre-incubation behaviour of Great Skuas and tests predictions that arise from theories attempting to explain territorial intrusions and copulation behaviour in birds.

The second chapter describes partnership composition and behaviour associated with mate change in Great Skuas. In particular, it attempts to test which of two alternative theories provides a better explanation for the occurrence of divorces in species where mate change is associated with a (short-term) measurable cost.

The third chapter investigates the effect of hatching date on different life-history stages in Great Skuas, including chick growth, survival to fledging, post-fledging survival and reproductive performance. The implications for the optimal timing of breeding in adults are analysed.

In the fourth chapter it is asked whether clutch characteristics correlate with individual quality of the parents. In particular this chapter examines the proposition that the degree of within-clutch asymmetry (last egg smaller than the first) reflects the ability of individuals to gather resources for reproduction, under natural conditions.

Chapter five presents the results of an experiment designed to infer foraging ability from territorial attendance of adult skuas, and detect small individual differences in those patterns. The aim was to study the influence of age and body size on foraging ability, and analyse the implications of the results for current theories that attempt to

explain age-specific breeding performance and, on a different issue, the evolution of reversed sexual size dimorphism in skuas.

Chapter six presents mathematical models that allow us to simulate the effects of age on the study of individual repeatability in a breeding parameter: laying date. With the help of this tool, we study the consistency of individual laying dates, over a long time interval, to determine if individual quality is a fixed trait of the individuals after correcting for age-effects.

In chapter seven, information from the Great Skuas is pooled with results from a study of Arctic Skuas on Foula (Phillips 1995) to test predictions related to the evolution of reversed sexual size dimorphism in the Stercorariidae and other birds with a raptorial lifestyle.

Chapter eight quantifies the incidence of intermittent breeding in Great and Arctic Skuas on Foula, and attempts to identify the factors that are responsible for such behaviour.

Finally, the last chapter is a brief general discussion of the importance of long-term studies of individually recognisable birds for a better understanding of their ecology and behaviour.

All chapters (except the general discussion) have been submitted for publication and appear in the formats required by the respective journals.

References

- Andersson, M. 1976a. Social behaviour and communication in the Great Skua. - Behaviour 58: 40-77.
- Andersson, M. 1976b. Predation and kleptoparasitism by skuas in a Shetland seabird colony. Ibis 118: 208-217.
- Caldow, R.W.G. 1988. Studies on the morphology, feeding behaviour and breeding biology of skuas with reference to kleptoparasitism. - Unpublished PhD thesis, University of Glasgow.
- Cohen, B.L. and 15 co-authors 1997. Enigmatic phylogeny of skuas (Aves: Stercorariidae). - Proc. R. Soc. Lond. B 264: 181-190.
- Coulson, J.C. 1968. Differences in the quality of birds nesting in the center and on the edges of a colony. - Nature 217: 478-479.
- Cramp, S. and K.E.L. Simmons (eds) 1983. The Birds of the Western Palearctic. Vol. III. Oxford University Press, Oxford.
- Furness, R.W. 1977. Studies on the breeding biology and population dynamics of the Great Skua (*Catharacta skua* Brunnich). - Unpublished PhD thesis. University of Durham.
- Furness, R.W. 1978a. Movements and mortality rates of Great Skuas ringed in Scotland. - Bird Study 25: 229-238.
- Furness, R.W. 1978b. Kleptoparasitism by Great Skuas and Arctic Skuas at a Shetland seabird colony. - Anim. Behav. 26: 1167-1177.
- Furness, R.W. 1979. Foods of Great Skuas at North Atlantic breeding localities. - Ibis 121: 86-92.
- Furness, R.W. 1983. Variation in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. - Journal of Zoology, London 199: 101-116.
- Furness, R.W. 1984. Influences of adult age and experience, nest location, clutch size and laying sequence on the breeding success of the Great Skua *Catharacta skua*. - J. Zool., Lond. 202: 565-576.
- Furness, R.W. 1987. The Skuas. T&AD Poyser, Calton.

- Furness, R.W. 1996a. The Stercorariidae. pp 556-571. *In*: del Hoyo, J., Elliot, A. & Sargatal, J. (eds). Handbook of the Birds of the World. Vol. 3. Lynx Edicions, Barcelona.
- Furness, R.W. 1996b. The impact of predation by Great Skuas on other seabird species, with particular reference to special protection areas in Shetland. Unpublished report to S.N.H.
- Furness, R.W. and Hislop, J.R.G. 1981. Diets and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. - *J. Zool. Lond.* 195: 1-23.
- Furness, R.W. and Hutton, M. 1979. Pollutant levels in the Great Skua. *Environ. Pollut.* 19: 261-268.
- Hamer, K.C. 1990. The breeding ecology of great skuas *Catharacta skua* in Shetland over a period of declining sandeel stock. - Unpublished PhD thesis, University of Glasgow.
- Hamer, K.C. and Furness, R.W. 1991a. Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. - *J. Anim. Ecol.* 60: 693-704.
- Hamer, K.C. and Furness, R.W. 1991b. Sexing Great Skuas *Catharacta skua* by discriminant analysis using external measurements. - *Ringing & Migration* 12: 16-22.
- Hamer, K.C., Furness, R.W. and Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. - *J. Zool., Lond.* 223: 175-188.
- Hamer, K.C. and Furness, R.W. 1993. Parental investment and brood defence by male and female Great Skuas *Catharacta skua*: the influence of food supply, laying date, body size and body condition. - *J. Zool., Lond.* 230: 7-18.
- Hébert, P.C. 1988. Adoption behaviour by gulls: a new hypothesis. - *Ibis* 130: 216-220.
- Klomp, N.I. 1991. Studies of recruitment in the Great Skua. - Unpublished PhD thesis, University of Glasgow.

- Klomp, N.I. and Furness, R.W. 1991. Recruitment in long-lived birds: studies of nonbreeding Great Skuas. - Acta XX Congressus Internationalis Ornithologici. Christchurch, New Zealand.
- Klomp, N.I. and Furness, R.W. 1992. The dispersal and philopatry of Great Skuas from Foula, Shetland. - Ringing & Migration 13: 73-82.
- Muirhead, S.J. 1986. The accumulation, storage and elimination of metals and orghanochlorines in the Great Skua *Catharacta skua skua* and metal accumulation in Atlantic Procellariiformes. - Unpublished PhD thesis, University of Glasgow.
- Perdeck, A.C. 1960. Observations on the reproductive behaviour of the Great Skua or Bonxie *Stercorarius skua skua* in Shetland. - Ardea 48: 111-136.
- Pettifor, R.A., Perrins, C.M. and McCleery, R.H. 1986. Individual optimization of clutch size in Great Tits. - Nature 336: 160-162.
- Phillips, R.A. 1995. Population ecology of Arctic Skuas *Stercorarius parasiticus* on Foula. - Unpublished PhD thesis, University of Glasgow.
- Phillips, R.A., Catry, P., Thompson, D.R., Hamer, K.C. and Furness, R.W. (in press). Inter-colony variation in diet and reproductive performance of great skuas. - Marine Ecology Progress Series.
- Ratcliffe, N. 1993. The age-specific breeding performance of great skuas on Shetland. - Unpublished PhD Thesis, University of Glasgow.
- Sears, J., Ellis, P.M., Suddaby, D. and Harrop, H.R. 1995. The status of breeding Arctic Skuas *Stercorarius parasiticus* and Great Skuas *S. skua* in Shetland in 1992. - Seabird 17: 21-31.
- Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press, Oxford.
- Stewart, F.M., Phillips, R.A., Catry, P. and Furness, R.W. (1997) Influence of species, age and diet on mercury concentrations in Shetland seabirds. - Marine Ecology Progress Series 151: 237-244..
- Thompson, D.R., Hamer, K.C. and Furness, R.W. 1991. Mercury accumulation in Great Skuas *Catharacta skua* of known age and size and its effects upon breeding and survival. - J. Appl. Ecol. 28: 672-684.

Thompson, D.R., Furness, R.W. and Walsh, P.M. 1992. Historical changes in mercury concentrations in the marine ecosystem on the north and north-east Atlantic ocean as indicated by seabirds. - *J. Appl. Ecol.* 29: 79-84.

Chapter 1

Territorial Intrusions and Copulation Behaviour in the Great Skua

Published as:

Catry, P. & Furness, R.W. 1997. Territorial intrusions and copulation behaviour in the great skua *Catharacta skua*. *Animal Behaviour* 54: 1265-1272.

Applied Ornithology Unit, IBLS, University of Glasgow, Glasgow G12 8QQ, U.K.

ABSTRACT

Territorial intrusions are performed by birds of many species in order to obtain extra-pair copulations (EPCs), and frequent within-pair copulations (WPCs) are thought to be a response to cuckoldry where mate guarding is not possible. Great skuas are colonial birds in which females are left alone in the breeding territory while males forage for the pair. Opportunities for cuckoldry are therefore numerous, and it could be predicted that sperm competition should be intense in this species. This study tested several hypotheses that attempt to explain territorial intrusions by female great skuas. Few intrusions coincided with the main fertile period and extra-pair copulations were almost never solicited, and therefore the sperm competition hypothesis was rejected. EPCs represented only 0.9% of the copulations observed (n=339). Thus opportunity for cuckoldry is a very poor predictor of the intensity of sperm competition, in spite of the relevance given to this factor in the literature. Of three EPCs observed, two involved unpaired territorial males. This suggests that genetic benefits were not the aim of unfaithful females. All three EPCs were preceded by courtship feeding, while only 26% of WPCs followed successful food begging. This statistically significant difference constitutes evidence for a trade of copulations for food in a monogamous bird. Evidence is presented supporting hypotheses that territorial intrusions by females are performed in order to induce males to give away some food, and to become familiarised with potential partners for future breeding seasons.

Sperm competition may determine or constrain several patterns of bird behaviour before clutch completion (Birkhead & Møller 1992), including breeding dispersion and territoriality (Møller 1987; Morton et al. 1990; Birkhead & Møller 1992). Coloniality can promote sperm competition simply because of the physical proximity of a large number of conspecifics (Gladstone 1979; Møller & Birkhead 1993). Courtship feeding means that males are unable to guard their mates during long periods while foraging, also creating opportunities for extra-pair copulations (Birkhead et al. 1987). Given the opportunity, male birds are expected to seek extra pair copulations (EPCs) as a relatively inexpensive way of increasing their reproductive output. The advantages of EPCs for the females are less clear, but genetic improvement of the offspring, in terms of quality and diversity, is generally thought to be the most likely advantage (Birkhead & Møller 1992; Møller 1992).

Great skuas Catharacta skua Brünnich are colonial seabirds in which there is a pronounced division of labour in breeding pairs. Males forage at sea and courtship feed their mate while females remain in the territory (Furness 1987), a situation that presents a potential for intense sperm competition to develop (Birkhead & Møller 1992). On the other hand, the "constrained female hypothesis" predicts that females should not seek EPCs when paternal care is essential for successful breeding (Gowaty 1996) because they cannot afford the risk of their partner reducing parental investment (Dixon et al. 1994). This might apply to great skuas, where care by two adults, from laying to fledging, is essential for a successful breeding attempt. Eggs or chicks left alone by foraging parents suffer a high risk of predation (Hamer et al. 1991). Frequent territorial intrusions by female great skuas occur in the pre-laying season, in spite of the fact that this is a strongly territorial species, but the function of such behaviour has never been assessed.

Three hypotheses have been presented to explain territorial intrusions in birds (Møller 1987). (1) The sperm competition hypothesis suggests that intruders are individuals trying to gain extra-pair copulations (Ford 1983). (2) The territory establishment hypothesis maintains that intrusions occur early in the breeding season, while territorial boundaries are being defined. Intrusions occur because birds are unaware of territorial limits or because they are trying to expand territories. (3) The non-territory holder hypothesis claims that intruders are individuals searching for

vacant territories. Møller (1987), reviewing studies on a wide range of birds, including colonial species, found extensive support for the sperm competition hypothesis, but not for the other two. Best supporting evidence comes from the fact that most intrusions are limited to the fertile period and frequently copulations are obtained by intruding males.

Our observations led us to propose two other hypotheses to explain certain territorial intrusions. These hypotheses are not incompatible with those cited above: (a) the male deceiving/food stealing hypothesis states that intruding birds (females) are trying to obtain food in the visited territories, either by foraging there or by begging/stealing from the resident male, (b) the potential mate assessment hypothesis suggests that visitors are searching for potential future mates. This hypothesis differs from the non-territory holder hypothesis because intruders are not searching for a vacancy, but are familiarising themselves with possible partners for future breeding seasons.

In this paper we assess the potential presented by current ideas on sperm competition to explain the occurrence of territorial intrusions and copulation behaviour in great skuas during the pre-incubation period. If opportunities of access to (extra-pair) sexual partners is the main constraint limiting the occurrence of sperm competition, then we would predict that EPCs during the fertile period should be common in the great skua. If, however, females are constrained in their choice by the prospect of male retaliation to EPCs by reducing parental investment, then we would expect few or no EPCs in this species where paternal care is essential for successful breeding. We also test hypotheses concerning territorial intrusions that do not involve sperm competition.

METHODS

The study area was in Foula, a small island (5×4 km.) 30 km west of the Shetland mainland, Scotland. The island is mountainous, with peaks reaching 400m, and is covered with short moorland vegetation. The great skua colony occupies most of the island and comprises *c.*2500 breeding pairs. Skuas nest on the ground and have non-overlapping territories with few empty spaces amongst them. Average distance between nest sites at Foula is around 30m (Furness 1987).

Studies on pre-incubation behaviour were carried out between 20 April and 20 May 1995 and 1996. Observations were made from a fixed point on a slope, high above a flat area with a high density of breeding pairs with many individually marked birds (colour-ringed in previous seasons). Birds always seemed unconcerned by the presence of the observer. In 1995, 35 pairs (13 with two colour-ringed birds and 22 with one) were observed. In 1996 thirty four pairs were studied, of which 32 had both partners colour-ringed. Only two pairs that were not marked, ignored for the purpose of the study, bred within the study plot. Also, the majority of the birds that bred immediately outside the boundaries of the study plot were colour-marked and of known-sex and so could be identified if they visited the study territories.

Observations were made on 52 days (27 in 1995 and 25 in 1996), for an average of 2.3 hours.day⁻¹ (range 1-6), a total of 118 hours of observation (4071 pair-hours). During each observation period we recorded all copulations seen and the identity of the birds involved. When computing the relative frequency of EPCs and within-pair copulations (WPCs), we only included copulations by birds belonging to pairs with both members colour-ringed. For a random sample of copulations we recorded duration (to the nearest second) and the number of cloacal contacts achieved. Because on most occasions it was difficult to see whether a cloacal contact had happened or not, we assumed that it happened each time the male rested his wings on the ground, the only position in which the birds seem to successfully copulate (Perdeck 1960). This assumption may have resulted in an overestimation of the rate at which sperm transfer was achieved. To calculate the proportion of EPCs, and in order to increase the total number of copulations observed, we also recorded all copulations seen that involved colour-marked birds breeding elsewhere in the colony, in 1995 and 1996.

More intensive observations were made simultaneously for a sub-sample of 20 pairs. For each pair we recorded which birds were present (including visits from strangers to the territory), the time of arrivals and departures, and the occurrence of begging behaviour, courtship feeding and nest building displays ("squeaking ceremony", Perdeck (1960), Andersson (1976)). Territorial intrusions and associated behaviour were also studied in this core area.

RESULTS

Description of Territorial Intrusions.

We observed two clearly distinct types of territorial intrusions. Peripheral intrusions involved birds trying to create new territories at the expense of already established ones. This kind of intrusion occurred very rarely and was easily identified because it was associated with aggressive displays and frequently with fighting. The intruders, either single males or pairs, stood mostly at the edge of the intruded territories, when trying to expand their own. Peripheral intrusions are clearly explained by the territory establishment hypothesis and will not be considered in the discussion of other hypotheses. The other type of intrusion occurred when a single bird (always a male, $n=30$) was present in its territory and another bird (intruder) joined it. In 24 of 30 visits, the sex of the intruder was known and it was always female (16 different birds involved). Because several intrusions started before and/or ended after our observation time periods, only a minimum estimate of intrusion duration could be made. Intrusions lasted 56 minutes on average (s.d. = 45.6; range: 3-180+; $n = 30$). In a typical intrusion, after landing the female walked up to the male and stood or sat by his side, sometimes begging for food. Often males slowly walked away, usually being followed by the females. Males were never seen reacting aggressively towards the intruder nor attempting to copulate with them. On three occasions out of 30, a "squeaking ceremony" was performed, this behaviour being more usually associated with nest building, but not with copulation or courtship feeding (Andersson 1976; Furness 1987). However, most of the time of the visits was spent with the birds simply sitting or standing side by side.

There were two cases (one in 1995 and another in 1996) where paired females made daily visits to an unpaired territorial male (different individuals in each year), during most of the pre-incubation period. These females were regularly fed by the unpaired males and we recorded one EPC by each of them. One unsuccessful EPC occurred 32 days before the female laid her first egg. In the other case, there was an apparently successful EPC 8 days before laying. These females regularly performed squeaking ceremonies and always begged for food during the intrusions. Because these long interactions were qualitatively distinct from the remaining intrusions, we excluded them from all summarising statistics below.

Hypotheses Explaining Territorial Intrusions.

Hypothesis 1: The sperm competition hypothesis.

Prediction 1: This hypothesis predicts that most intrusions should occur when the probability of egg fertilisation is high. Excluding the particular case of the two females that regularly visited unpaired territorial males, almost no intrusions were recorded in the 15 days prior to laying (Table I). Presumably, it is in this period that fertilisation probability is higher (Birkhead & Møller 1992), and within-pair copulation rates peaked at this time (Fig. 1). Pair copulations also increased in duration as laying date approached ($r=0.40$, $n=119$, $P<0.0001$) resulting in an increase in the proportion of copulations with at least one cloacal contact (logistic regression: Wald=13.2, $n=118$, $P<0.001$). These data suggest that the two weeks preceding laying are the most important ones for fertilisation, yet intrusions were timed to precede the fertile period and females ceased intruding when fertilisation might have occurred (Table I).

Prediction 2: Intruders should attempt to obtain EPCs.

Although Møller (1987) states that the sperm competition hypothesis predicts that intruders should be males, recent studies show that females visit other territories to solicit EPCs (Smith 1988; Kempenaers et al. 1992; Graves et al. 1993). All skua intruders were females, but in only 1 out of 30 visits to paired males was there solicitation (by the female) of an EPC. Also, this occurred long (17 days) before laying by that female, and in spite of many opportunities, we never recorded her making territorial intrusions again. Including EPCs with unpaired males, we recorded 3 EPCs and 336 within-pair copulations (involving 55 different pairs). EPCs represented 0.9% of the copulations. EPCs occurred at 32, 17 and 8 days before laying. All 3 EPCs were preceded by begging for food and courtship feeding, while such a pattern only occurred with 26% (21/82) of the within-pair copulations. To avoid pseudoreplication, we randomly selected one copulation per study-pair to test if WPCs were less likely to be preceded by courtship-feeding than EPCs. In this subsample, only five out of 21 WPCs followed courtship feeding. The difference

between EPCs and WPCs is statistically significant (Fisher Exact Test, $P=0.028$). Males were never seen trying to initiate copulations.

Hypothesis 2: The territory establishment hypothesis.

Prediction 1: Intrusions should be made mostly by newly established pairs, and territory owners should react aggressively with displays and physical threat.

Only peripheral intrusions (see above) supported this hypothesis. A single pair recruited and established a territory in the study area during the observation period. However, the hypothesis cannot explain the vast majority of intrusions because all 20 studied territories maintained common boundaries unchanged from the previous breeding season. Almost all marked individuals living in those territories survived from 1994 to 1995 (annual survival rate = 95%) and from 1995 to 1996 (survival rate = 92%), reoccupied the same territories, and therefore were familiar with previous boundaries.

Prediction 2: Intruders should be neighbours.

Only four out of 20 (20%) of the intrusions (excluding multiple visits of one female to the same territory and peripheral intrusions) were made by neighbouring individuals.

Hypothesis 3: The non-territory holder hypothesis.

Prediction: Intrusions should be made by non-territorial birds.

All individually identifiable intruders ($24/30=80\%$) were females already paired with territory holding males.

Hypothesis 4: The male deceiving/food stealing hypothesis.

Prediction: Intruders should be females and they should beg for food, at least sometimes successfully.

Out of 30 intrusions, 11 (37%) involved begging for food and in a further three (10%) visits to one particular territory the female fed on sheep carrion lying there. Extra-pair food-begging success ($2/10=0.20$) was roughly similar to within-pair

begging success at the same time of the season ($7/39=0.18$), but the sample sizes are small.

Courtship feeding rates (Fig. 2) and food-begging success (Table II) were much higher in the two weeks immediately before laying, when intrusions were rare. We suggest that females did not try to make territorial intrusions at that time because general female attendance increased considerably (Fig. 3), leaving very few males alone in their territories. In contrast, females visiting unpaired males continued to deceive them until close to egg laying and enjoyed a high food-begging success ($13/20=0.65$).

However, in 53% (16/30) of the intrusions we did not see any attempt by the female to forage or beg for food.

Hypothesis 5: The potential mate assessment hypothesis.

Prediction: Territorial intrusions should be made in the range of distances (from territory of origin) similar to the distances moved when changing partners.

Most females changing mates paired with new partners only 1 to 3 territories away from the previous one (Fig. 4). Territory availability increases exponentially with distance from territory of origin, and there are over 2000 skua territories in this colony. Clearly, females are very strongly biased to choose territories close to those where they have previously bred. If potential mate assessment is the function of territorial intrusions, then we would expect that territories selected for intrusions should be a similarly biased sample of the total available in the colony. This prediction was supported by our data as most intrusions were made to territories very close to the point of origin (Fig. 4).

DISCUSSION

The Function of Territorial Intrusions.

The non-territory holder hypothesis was clearly rejected by the data because most intruders were paired territorial birds. The territory establishment hypothesis explained only a small number of behaviourally distinct intrusions, clearly associated with territorial conflicts. Møller (1987) also found little evidence in favour of these two hypotheses in a wide review of the subject.

The sperm competition hypothesis received almost no support from our observations. The vast majority of the territorial intrusions occurred early in the season, when the probability of egg fertilisation must have been very low. Also, copulation attempts were almost never recorded. The sperm competition hypothesis has been regarded as the best general explanation for territorial intrusions in birds (Møller 1987), and sperm competition has been suggested to have a role as a selective pressure on the evolution of territoriality (Birkhead & Møller 1992). Obviously, our findings do not invalidate these ideas, but do demonstrate some limits to their generality.

The two new hypotheses (male deceiving/food stealing and potential mate assessment) received some support from our data. This is not surprising since they were inspired by our observations of great skua behaviour. However, our tests have limited power and no firm conclusions should be extracted. The power of these hypotheses to predict other species' behaviour needs to be assessed. The male deceiving/food stealing hypothesis might apply to ospreys Pandion haliaetus, for example, where females have been observed intruding into territories and successfully begging from unfamiliar males (Poole 1985; Birkhead & Lessells 1988). This hypothesis is likely to be appropriate only among birds where females receive a substantial proportion of their food from males in the pre-laying period.

Sperm Competition in the Great Skua.

If opportunity for extra-pair encounters was the main constraining factor determining the occurrence of EPCs, then birds like great skuas, and also colonial raptors and gulls, where courtship feeding is important and females are left alone for long periods during the fertile period, should display frequent promiscuous behaviour. However, that is not the case (Fitch & Shugart 1984; Chardine 1986; Craig et al. 1994; Koga & Shiraishi 1994; this study). We suggest that in the great skua EPCs are rare for two main reasons: (1) females are larger than males and are very aggressive and well armed birds. Any male skua adopting a strategy involving forced EPCs would incur great physical risk, and would probably be unsuccessful. In several other colonial

species, including gulls, attempts to force copulations by males are not uncommon, although they can only rarely be successful without some co-operation of the female after mounting (MacRoberts 1973; Burger & Beer 1975; Fujioka & Yamagishi 1981; Aguilera & Alvarez 1989; Mills 1994). (2). Female great skuas almost never seek EPCs. However, we do not know why this is so. It is now well established that, in some species and populations, females can recognise males of better phenotypic quality than their own partners, and voluntarily copulate with those birds (Smith 1988; Houtman 1992; Kempenaers et al. 1992; Møller 1992; Graves et al. 1993), presumably gaining genetic advantages for their offspring. Why is it then that, in some species, females only rarely “shop for good genes”? It could be that intrapopulation variance in genetic quality, or the ability of females to assess it, varies from species to species. Gowaty (1996) presented the “constrained female hypothesis” which predicts that females should not seek EPCs when paternal care is essential for successful breeding, a condition applying to great skuas. Males might retaliate by reducing parental investment. Our observations add to accumulating evidence suggesting that the “constrained female hypothesis” might indeed successfully explain an important part of the interspecific variability in the frequency of extra-pair paternity and EPCs (Birkhead & Møller 1996). Males could also retaliate to EPCs by divorcing (Gladstone 1979). Retaliation by divorce would be particularly costly in species where reproductive success is positively related to the duration of the pair bond (Møller 1992). This could be an alternative explanation for the positive correlation reported by Cezilly and Nager (1995) between extra-pair parentage and divorce rates. Female great skuas sometimes engage in fights for mates/territories that result in physical damage, suggesting the existence of strong female-female competition and consequently a possible basis for divorce to be an efficient infidelity deterrent. Gulls also show a low divorce rate, frequently a female biased sex ratio leading to female-female competition (Kovacs & Ryder 1983; Johnston & Ryder 1987), and rare unforced EPCs. We suggest that the rarity of unforced EPCs in great skuas (and other colonial long-lived birds like gulls) could be maintained because the cost of male retaliation, through reduced parental investment and/or divorce, is too high for females, in comparison to the genetic benefits to be gained from extra-pair paternity (see also Mills 1994).

Møller and Birkhead (1993) showed that coloniality significantly increases the probability of the occurrence of EPCs. It is now clear, however, that opportunity for cuckoldry is a very poor predictor of the intensity of sperm competition. The “constrained female hypothesis”, on the other hand, predicts a low frequency of EPCs for birds like great skuas, as observed in our study.

From Figure 1, it can be estimated that peak great skua copulation rates are around 2.5 copulations per day per pair, and that the average number of copulations per clutch is around 35. According to Birkhead et al.’s (1987) definition, these are high copulation rates, used as a paternity assurance strategy by species where effective mate guarding is not possible (Møller & Birkhead 1992). However, as we have seen, there is no evidence of intense sperm competition in this population. The same pattern of high rates of within-pair copulations in populations with low levels of EPCs has been found in other species, demanding an explanation for frequent copulation rates, complementary to the paternity assurance hypothesis (Hunter et al. 1993; Negro et al. 1996).

In spite of their relatively low frequency, we did observe some EPCs in our study, the function of which is not very clear. We believe that the most commonly accepted benefit of EPCs for females, the improved genetic quality of offspring, is unlikely to apply to this skua population. Two of the three males involved in EPCs were unpaired territory holders, and the females could have divorced their own partners if they were of inferior quality. The remaining EPC involved a paired male. However, this occurred 17 days before laying, probably too early for fertilisation. The fact that all EPCs were preceded by courtship feeding (a pattern significantly different from the one in within-pair copulations), suggests that females might be trading copulations for food. Females also indulged in other behaviours with extra-pair partners such as the “squeaking ceremony”, and this could help to stimulate males to keep providing them with food. Wolf (1974) and Poole (1985) described observations of birds trading (probably unsuccessful) copulations for food in purple-throated Carib hummingbirds *Eulampis jugularis* and ospreys, respectively. Birkhead

and Møller (1992) dismissed, on the basis of lack of evidence, the hypothesis that nutritional advantages act as a motive for female involvement in EPCs in monogamous birds. Our results suggest however that this hypothesis could explain female great skua behaviour. More research in other species should focus on this hypothesis, before we can assess its importance in determining avian pre-incubation behaviour.

REFERENCES

- Aguilera, E. & Alvarez, F. 1989. Copulations and mate guarding of the spoonbill (*Platalea leucorodia*). Behaviour 110, 1-22.
- Andersson, M. 1976. Social behaviour and communication in the great skua. Behaviour, 48, 40-77.
- Birkhead, T.R. & Lessells, C.M. 1988. Copulation behaviour of the osprey *Pandion haliaetus*. Anim. Behav., 36, 1672-1682.
- Birkhead, T.R. & Møller, A.P. 1992. Sperm Competition in Birds. Evolutionary Causes and Consequences. London: Academic Press.
- Birkhead, T.R. & Møller, A.P. 1996. Monogamy and sperm competition in birds. In: Partnerships in Birds. The Study of Monogamy (Ed. by Black, J.M.). Oxford University Press.
- Birkhead, T.R., Atkin, L. & Møller, A.P. 1987. Copulation behaviour of birds. Behaviour, 101, 101-138.
- Burger, J. & Beer, C.G. 1975. Territoriality in the Laughing gull (*L. atricilla*). Behaviour, 55, 301-320.
- Cezzily, F. & Nager, R.G. 1995. Comparative evidence for a positive association between divorce and extra-pair paternity in birds. Proc. R. Soc. Lond. B, 262, 7-12.
- Chardine, J.W. 1986. Interference copulation in a colony of marked black-legged kittiwakes. Can. J. Zool., 64, 1416-1421.
- Craig, D.M., Anthony, I., Lambert, D.M., Stapleton, P.M., Bergman, C.C., Bellamy, A.R. & Young E.C. 1994. Patterns of reproductive success determined by DNA fingerprinting in a communally breeding oceanic bird. Biol. J. Lin. Soc., 52, 31-48.
- Dixon, A., Ross, D., O'Malley, S.L.C. & Burke, T. 1994. Paternal investment inversely related to degree of extra-pair paternity in the reed bunting. Nature 371, 698-670.
- Fitch, M.A. & Shugart, G.W. 1984. Requirements for a mixed reproductive strategy in avian species. Amer. Nat., 124, 116-126.
- Ford, N.L. 1983. Variation in Mate Fidelity in Monogamous Birds. Current Ornithology 1: 329-356.

- Fujioka, M. & Yamagishi, S. 1981. Extramarital and pair copulations in the Cattle egret. Auk, 98, 134-144.
- Furness, R.W. 1987. The Skuas. Calton: T & A.D. Poyser.
- Gladstone, D.E. 1979. Promiscuity in monogamous colonial birds. Amer. Nat., 114, 545-557.
- Gowaty, P.A. 1996. Battles of the sexes and origins of monogamy. In: Partnerships in Birds. The Study of Monogamy (Ed. by Black, J.M.). Oxford University Press.
- Graves, J., Ortega-Ruano, J. & Slater, P.J.B. 1993. Extra-pair copulations and paternity in shags: do females choose better males? Proc. R. Soc. Lond. B, 253, 3-7.
- Hamer, K.C., Furness, R.W. & Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas Catharacta skua in Shetland. J. Zool., Lond. 223: 175-188.
- Houtman, A.M. 1992. Female zebra finches choose extra-pair copulations with genetically attractive males. Proc. R. Soc. Lond. B, 249, 3-6.
- Hunter, F.M., Petrie, M., Otronen, M., Birkhead, T. & Møller, A.P. 1993. Why do females copulate repeatedly with one male? TREE 8, 21-26.
- Johnston, V.H. & Ryder, J.P. 1987. Divorce in Larids: a Review. Colonial Waterbirds, 10, 16-26.
- Kempnaers, B., Verheyen, G.R., Van den Broeck, M., Burke, T., Broeckhoven, C.V. & Dhondt, A.A. 1992. Extra-pair paternity results from female preference for high-quality males in the blue tit. Nature, 357, 494-496.
- Koga, K. & Shiraishi, S. 1994. Copulation behaviour of the Black Kite Milvus migrans in Nagasaki Peninsula. Bird Study, 41, 29-36.
- Kovacs, K.M. & Ryder, J.P. 1983. Reproductive performance of female-female pairs and polygynous trios of ring-billed gulls. Auk, 100, 658-669.
- MacRoberts, M.H. 1973. Extramarital courting in Lesser black-backed and Herring Gulls. Z. Tierpsychol., 32, 62-74.
- Mills, J.A. 1994. Extra-pair copulations in the red-billed gull: females with high-quality, attentive males resist. Behaviour, 128, 41-64.

- Møller, A.P. 1987. Intruders and defenders on avian breeding territories: the effect of sperm competition. Oikos, 48, 47-54.
- Møller, A.P. 1992. Frequency of female copulations with multiple males and sexual selection. Amer. Nat., 139, 1089-1101.
- Møller, A.P. & Birkhead, T.R. 1992. A Pairwise comparative method as illustrated by copulation frequency in birds. Amer. Nat. 139, 644-656.
- Møller, A.P. & Birkhead, T.R. 1993. Cuckoldry and sociality: a comparative study of birds. Amer. Nat., 142, 118-140.
- Morton, E.S., Forman, L. & Braun, M. 1990. Extrapair fertilizations and the evolution of colonial breeding in purple martins. Auk, 107, 275-283.
- Negro, J.J., Villarroel, M.; Tella, J.L.; Kuhnlein, U.; Hiraldo, F.; Donázar, J.A. & Bird, D.M. 1996. DNA fingerprinting reveals a low incidence of extra-pair fertilizations in the lesser kestrel. Anim. Behav., 51, 935-943.
- Perdeck, A.C. 1960. Observations on the reproductive behaviour of the great skua or bonxie Stercorarius skua skua (Brünn), in Shetland. Ardea, 48, 111-136.
- Poole, A. 1985. Courtship feeding and osprey reproduction. Auk, 102, 479-492.
- Smith, S.M. 1988. Extra-pair copulations in the Black-capped chickadees: the role of the female. Behaviour, 107, 15-23.
- Wolf, L.L. 1975. "Prostitution" behaviour in a tropical hummingbird. Condor, 77, 140-144.

Table I - Frequency of territorial intrusions (total number of intrusions per hour of observation of twenty pairs) in the pre-laying period. Includes all visits of females to males in the study site, when the birds could be individually identified and their laying date was known. In males, "days before laying" refer to their partner

	Days before laying					
	26+	25-21	20-16	15-11	10-6	5-0
Visitors (females)	0.27	0.58	0.34	0.13	0	0
Visited (males)	0.20	0.83	0.57	0.38	0.15	0

Table II - Proportion of successful begging for food ("successful" means male responding with courtship feeding) by the female, in relation to laying date. (The effect of relative date on begging success is highly significant: logistic regression, Wald=28.2, n=142, p<0.0001)

	Days before laying					
	30-26	25-21	20-16	15-11	10-6	5-1
% successful begging	14	21	17	63	80	90
n (sample size)	7	14	18	41	40	21

Figure 1.1.- Copulation rates (3-day running means of the number of copulations per hour) of great skuas in the pre-laying period.

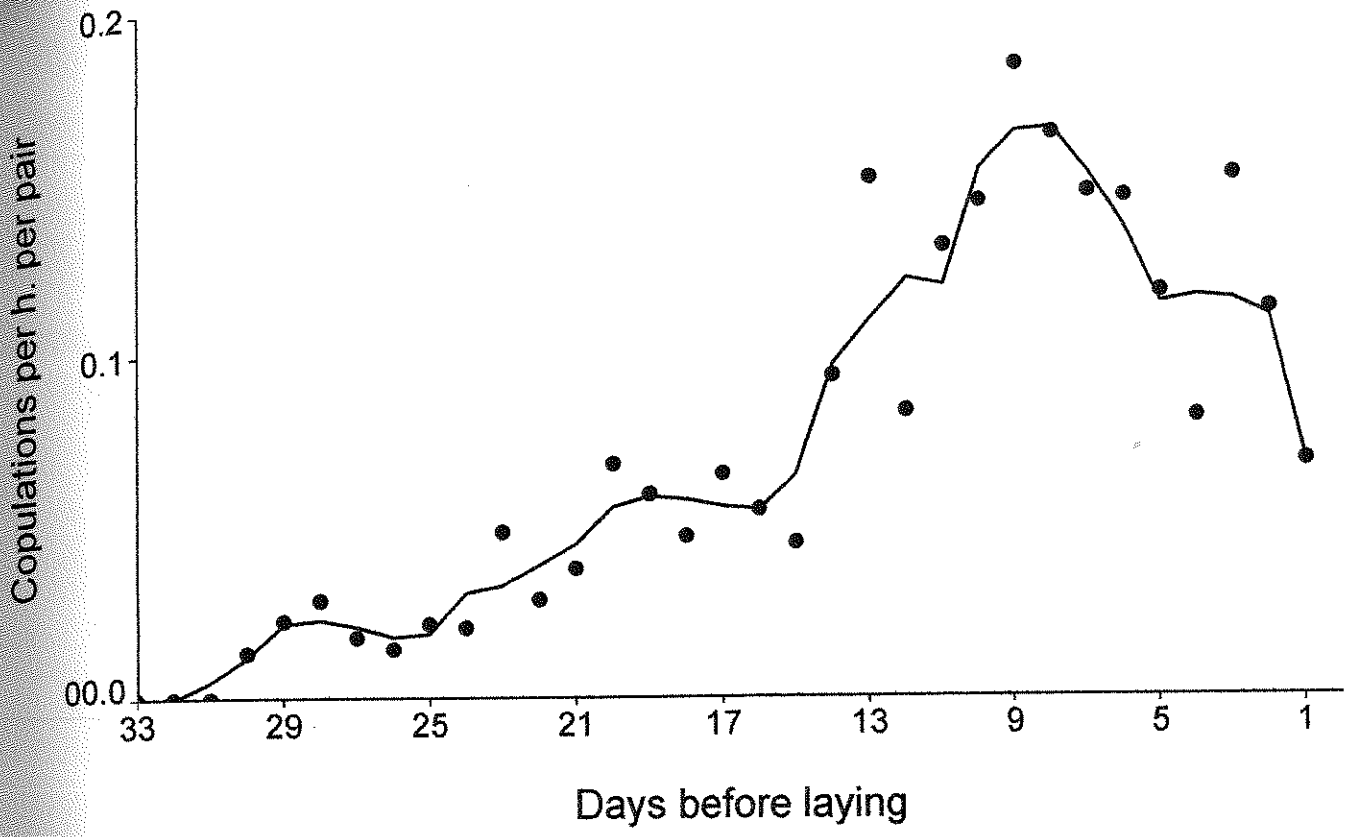


Figure 1.2.- Courtship feeding rates (3-day running means of the number of feeds per hour) of great skuas in the pre-laying period.

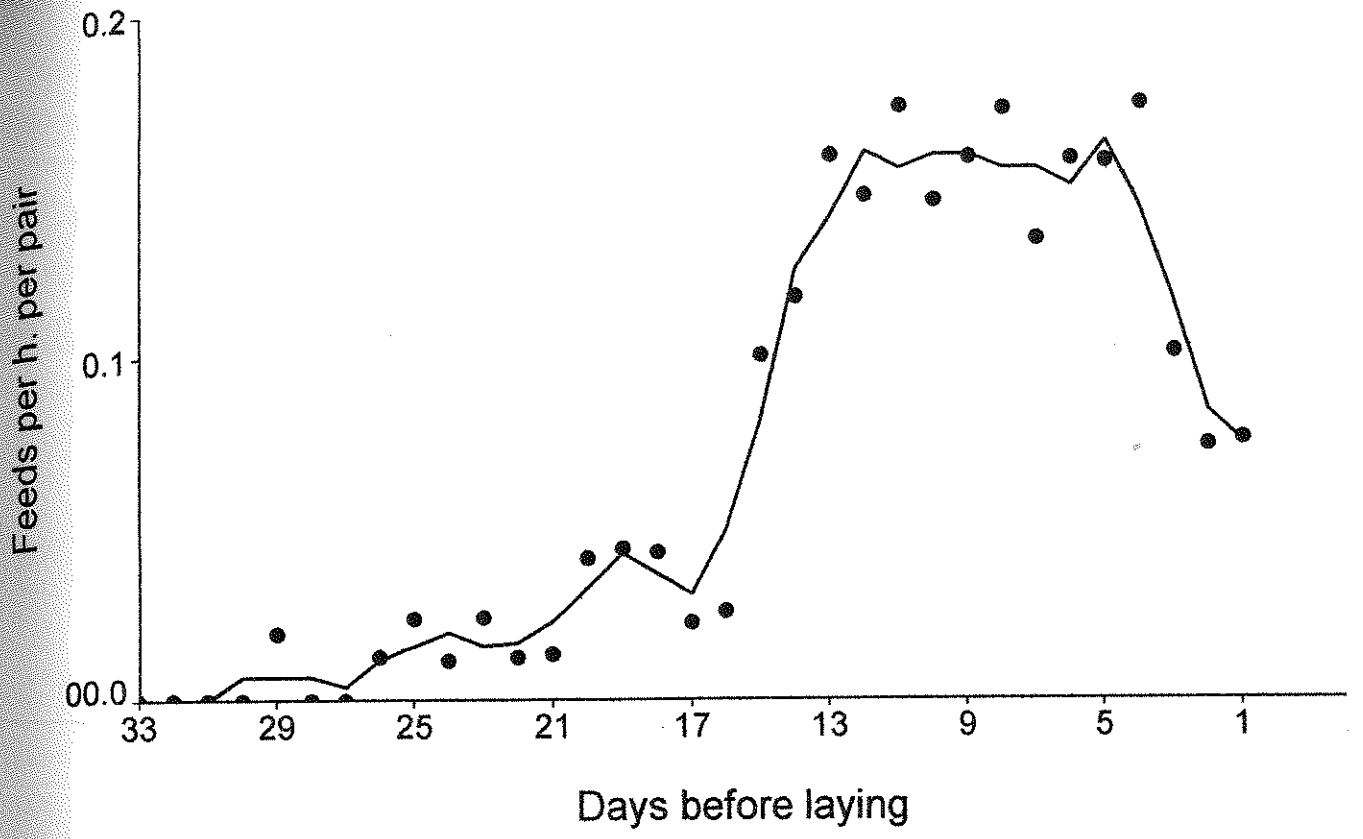


Figure 1.3.- Attendance (3-days running means of the proportion of daytime spent on the territory) by female and male great skuas in the pre-laying period. Circles represent female and squares represent male values.

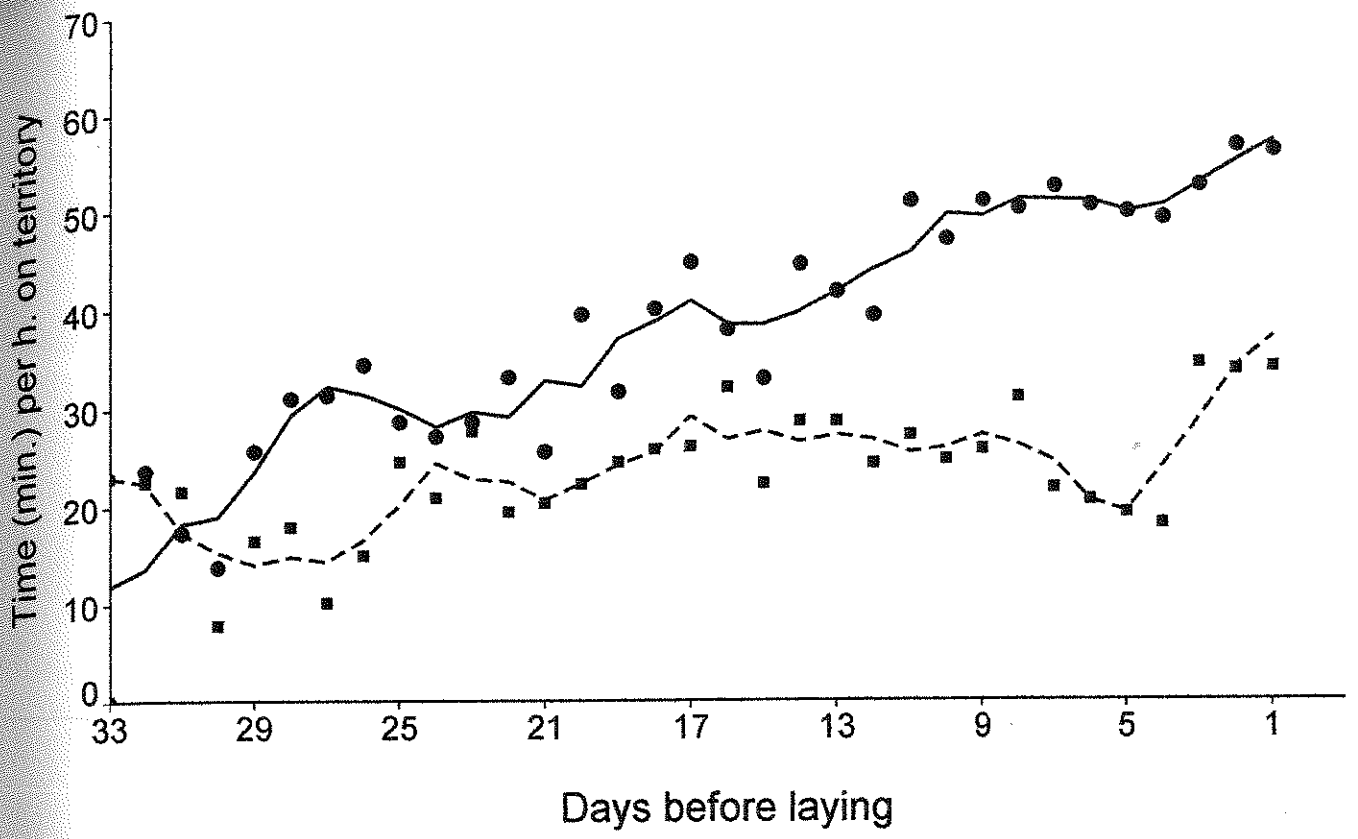
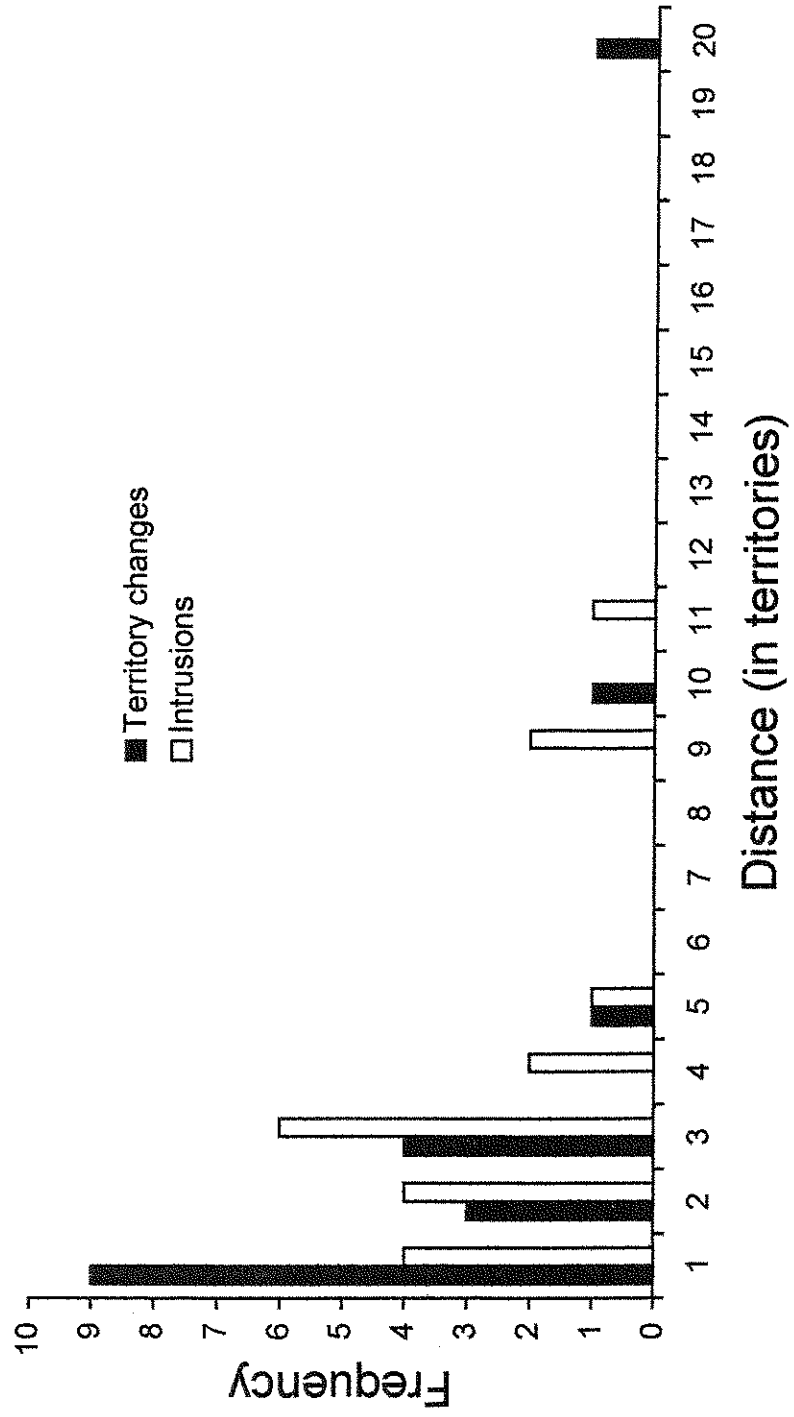


Figure 1.4.- Distance (in number of territories) moved by females when changing territories and when making territorial intrusions (note that territory availability increases exponentially with distance).



Chapter 2

Partnerships and Mechanisms of Divorce in the Great Skua

In press as:

Catry, P., Ratcliffe, N. & Furness, R.W. Partnerships and mechanisms of divorce in the great skua *Catharacta skua*. *Animal Behaviour*.

ABSTRACT

Great skuas *Catharacta skua* breeding in Foula (Shetland) displayed a poor correlation ($r_{50}=0.28$, $P<0.05$) between the ages of partners in breeding pairs. Twenty two percent of the partners differed in age by 10 years or more. Mate fidelity in this population is high, with an annual divorce rate of only 6.4% ($n=20/311$). Death is responsible for three times more interruptions of partnerships than divorces. Three types of divorce were detected: (1) Females deserted their partners, leaving them temporarily unpaired. This represented the majority of divorces where the mechanism could be identified. (2) One female was recorded being forced to desert her partner by an usurper. (3) One female deserted her partner after they lost their breeding territory to another pair. Mate changes had a direct cost, because new pairs (of experienced birds) laid later in the season and raised fewer chicks. After mate loss, 26% ($n=61$) of the individuals did not breed, while faithful pairs always laid eggs. Males, but not females, had a higher probability of remaining unpaired after being divorced than after becoming widowers. There was no difference between the sexes in the probability of re-pairing after losing a mate due to its death. Results suggest that divorces that are initiated by birds within the pair are better explained by the "better option hypothesis", as opposed to the "incompatibility hypothesis".

Partnerships in birds are rarely, if ever, random collections of members of a population. Differences in temporal and spatial distribution of individuals, together with some degree of mate selection, result in patterns in the composition of pairs or breeding groups of birds. Sexual selection and mate choice were already recognised by Charles Darwin, but their role in determining pair composition, mate fidelity and divorce in birds remains poorly understood (Reid 1988, Ens et al. 1996). Long-lived seabirds typically display an improvement in breeding performance with age (Wooller et al. 1992). If there is assortative mating in relation to breeding competence, then we would expect a correlation between the ages of the birds in pairs, a pattern shown to occur frequently (Reid 1988). This is relevant for the study of partnerships and breeding performance in relation to age.

Seabirds also display high site and mate fidelity, which is believed to be the combined effect of a cost of mate change together with high survival rates (e.g. Johnston & Ryder 1987). However, there is no theoretical framework capable of predicting, to any reasonable degree of accuracy, the interspecific variation in divorce rates in birds (Ens et al. 1996). Our lack of understanding is partly the result of the scarcity of empirical studies which attempt to assess the causes and consequences of divorce (Choudhury 1995). In particular, there is a need for behavioural studies to determine which birds (within or outside the partnerships) initiate the divorcing process, and what are the costs and benefits to the individuals involved.

There are two main theories attempting to explain divorce as an adaptive decision for at least one of the members of the pair. The "incompatibility hypothesis" (Coulson & Thomas 1983) states that birds separate because they are unsuccessful breeders as a pair, although their individual characteristics are not negative *per se*. Divorce comes about as an initiative of both individuals to search for a more compatible mate, allowing an improvement in breeding success. The "better option hypothesis" (Ens et al. 1993) suggests that divorce is usually initiated by one of the birds (the "chooser") in search of a "higher quality" partner (or territory). Contrary to the "choosers", "victims" of the divorce are not expected to, on average, improve their breeding performance after mate change. Most attempts to test these ideas found

some support for the better option hypothesis (e.g. Dhondt & Adriansen 1994, Orell et al. 1994, Otter & Ratcliffe 1996). The only solid evidence for the importance of mate compatibility to the fitness of the pair comes from a study of barnacle geese Branta leucopsis (Choudhury et al. 1996). It was found that, although large birds of either sex were usually more successful breeders, small individuals had a higher breeding output if paired with a small (more compatible) partner.

Skuas (Stercorariidae) have been subject of several long-term studies (O'Donald 1983, Furness 1987, Ainley et al. 1990, Hamer & Furness 1991, Pietz & Parmelee 1994, Phillips et al. 1996), but little detailed information has been published regarding partnership composition (in relation to age), divorce rates or the causes of divorce in these birds, and none for the North Atlantic great skua Catharacta skua. In this study we describe partnership composition and behaviour associated with mate changes in great skuas. In particular, we attempt to test the incompatibility and the better option hypotheses as explanations for divorces initiated by birds within the pair.

METHODS

Fieldwork was carried out in the island of Foula (Shetland), the largest great skua colony in Europe with approximately 2500 breeding pairs. The colony is continuous and covers almost the whole surface of the island, from sea-level to 400m. The study area (one single block) covers one quarter of the total surface of the colony. Great skuas breed in strictly defended territories with little space in between. Mean inter-nest distance is around 30 meters (Furness 1987). Since 1988, adult great skuas have been caught and colour-ringed for individual recognition. Age could also be determined when birds had been ringed as chicks (Hamer & Furness 1991). Adults were sexed by observation of copulation and courtship feeding. From 1991 until 1996, there were enough pairs in which both partners were colour-marked to allow a study of mate fidelity. During these years, fieldwork started before egg laying and extended until the vast majority of the chicks were 30 days old. At the beginning of each breeding season, the study area (where birds had been colour-ringed) was visited to locate surviving birds and identify established partnerships. Intensive coverage of

the study area and surrounding sectors assured that resighting probability of live breeding birds was effectively one. Clubs (nonbreeder aggregations) were regularly checked for marked birds that were not breeding. Great Skuas from Foula display a strong degree of breeding philopatry and colour-ringed birds have never been recorded in other skua colonies after nesting in this island (Klomp & Furness 1992). Around laying date, territories were visited daily until one egg was laid. After clutch completion, eggs were measured to the nearest 0.1mm and volumes calculated as $0.48 \times \text{length} \times \text{breadth}^2$ (Coulson 1963). Most (>90%, varying with year) clutches were composed of two eggs. We did not analyse clutch size as a breeding parameter because it was difficult to assess if apparent one-egg clutches were in fact two-egg clutches that had lost one egg to predators (mostly ravens *Corvus corax*). After hatching, chicks were ringed, as soon as their size allowed, and their fate was monitored until they were 30 days old. Great skua chicks fledge when around 46 days old (Furness 1987), but few chicks die between 30 and 46 days, and survival to 30 days is a suitable measure of fledging production for the purposes of this study.

In 1994 and 1995, 118 hours were spent making behavioural observations (covering around 40 territories) during the pre-laying period. This fieldwork was primarily for a different study, but together with other opportunistic observations made around the colony, provided valuable qualitative information on mating behaviour and divorces in the study population.

In this study, a divorce is said to have occurred when two birds that bred together in year A are alive and present in the colony in year A+1, but not breeding together.

In comparisons of the ages of birds that divorced with birds that remained faithful, each individual was included only once in the analysis by randomly selecting one year/age for each bird. All known ages at divorce were included, but only one known-age bird was recorded divorcing twice. When comparing laying dates and clutch volumes from different groups of birds, we standardised the variables to account for annual differences in the means. Laying dates were normalised by log-

transformation. Hatching success and fledgling production did not vary significantly among the years covered by the cases used in the analysis. All tests are two-tailed.

RESULTS

Ages in Partnerships.

There was only a weak correlation between male and female ages in great skua pairs ($r_{50}=0.28$, $P<0.05$). Males were older than females in 26 pairs, and younger in 20 (Chi-square test: $\chi^2_1=0.78$, NS). In 26% of the pairs ($N=50$) the age of the partners differed by one year or less. On the other hand, in 22% of the pairs there was an age difference of 10 or more years (males were older in six cases and females in five; maximum difference was 18 years).

Mate Fidelity and Divorces.

During the entire study, on average 79.3% of the pairs ($N=367$ pairs) remained united from one year to the next. Partnerships were terminated mostly due to the disappearance of one of the birds (73.7% of the cases), and to a lesser extent as a result of divorces (26.3%). Of 28 pairs with both partners colour-ringed in 1991, six were still breeding together six years later. The weighted mean annual divorce rate was 6.4% (Table I). Divorce rates did not differ between years (comparing the three years with larger sample sizes, Chi-square test: $\chi^2_2=4.42$, NS).

Median age of birds (sexes pooled) that divorced (13, $N=15$) was not significantly different from the age of birds that remained faithful (14, $N=74$; Mann-Whitney U-test: $Z=-0.24$, NS). On average, faithful birds were only 0.6 years older than birds involved in divorces.

On eight occasions the direct causes or mechanism of the divorce could be determined and three types could be identified: (1) Females apparently abandoned their partners in six cases. These females re-paired immediately after separation while their partners invariably took longer to attract a new mate. In all 6 cases males retained their territory, while females moved away. (2) On one occasion a female was chased away by an usurper that bred with the male territory holder. In the last case,

(3) a male lost its territory to another pair, and its partner mated with a third male. Two of the females that abandoned their partners were seen, in the days preceding mate change, to regularly visit their future mates and obtain food regurgitates from them, suggesting that they might have been evaluating both males before making a final decision. Other females were observed performing similar behaviours, but retaining their mates. Besides the case described above, where a divorce was forced by a female usurper, we saw several other conflicts between females, competing for a male, that ended with the resident female winning. Fights could last (intermittently) for days, with several combats and long breaks. Sometimes the usurper managed to temporarily exclude the first female from the territory (for up to 3+ days), only to be forced to abandon it on a later date. Males were never seen to take an active part in these disputes, although they were usually present. Females are known to have been mortally injured during these fights. It is interesting to note that, in two cases, there were unpaired territorial males in territories neighbouring the ones where the fights were taking place. In one case, the losing female paired with one of these neighbouring males.

Early in the breeding season, when many birds were still arriving from their wintering grounds, birds apparently waiting for their mates in their former territories sometimes accepted new partners that started visiting them regularly. Both sexes were recorded to be in this position, although in most cases males arrived at the breeding colony before their partners. None of these temporary partnerships were recorded to last after the arrival of the former partner.

Overall, we detected more territory changes by females (N=19) than by males (N=7) after divorce or mate loss (Chi-square test: $\chi^2_1=5.5$, $P<0.05$). In most territory changes skuas moved only a short distance, with the females showing a greater (non-significant) tendency to settle in adjacent territories (Table II). On two occasions, pairs of birds moved together to vacant neighbouring territories, abandoning the previous one. Out of 72 males breeding in one sector where all territories were carefully mapped, in 1995 and 1996, only one (1.4%) changed territory (together with its mate). In the same area, four females out of 80 (5%) changed territory.

Consequences of Mate Change.

After mate loss through death or divorce, 26% (N=61) of the birds did not breed in one year, but all the pairs that remained united from the previous season (N=222) laid eggs (comparing the two groups, Chi-square test: $\chi^2_1=56.9$, $P<0.0001$). For both sexes together the frequency of non-breeding after divorce (9/23=0.39) was more than twice the frequency of non-breeding after mate loss by death (7/38=0.18), but the difference is not significant (Fisher's exact test: $P=0.13$, Table III). The frequency of non-breeding after death of the partner was similar for females and for males (Fisher's exact test: $P=0.4$, Table III). After divorce, however, males were much less likely to breed than females (Fisher's exact test: $P<0.005$, Table III). Probability of females not breeding after divorce was not significantly different from the probability of not breeding after mate loss. This result could be a consequence of small sample sizes. Out of 11 cases, females bred immediately after divorce on 10 occasions. The only exception was when a female was forced to abandon her partner after losing a fight with another female. Males were more likely not to breed after divorce than after losing their partner due to death (Fisher's exact test: $P<0.005$, Table III). Of the eight males that did not breed after divorce, three had lost their territories (either before or after the divorce). Even if these 3 cases are eliminated, the probability of males not breeding after divorce (5/8=0.63) remains higher than the probability of not breeding after mate loss through death (Fisher's exact test: $P<0.05$) and also higher than the probability of females not breeding after divorce (Fisher's exact test: $P<0.05$).

Females in new partnerships (N=38) laid, on average, 5 days later than females that retained the partner from the previous breeding season (N=157; t-test: $t_{193}=5.6$, $P<0.0001$). The magnitude of the difference (5 days) is maintained when we restrict the analysis to new pairs that were constituted by birds known to have previous breeding experience (N=17; t-test: $t_{172}=4.2$, $P<0.0001$). When comparing first and second breeding attempts of individual pairs, a similar difference was found. Laying date on the first breeding attempt was 5.4 days later in the season than on the second breeding (paired t-test: $t_{10}=2.3$, $P<0.05$). Females that divorced laid only 0.34

days earlier than those that lost their partners, the difference not being significant (t-test: $t_{17}=1.46$). Not enough data existed for males to allow a similar comparison. After mate death, mean laying date of surviving males and females was the same (N=15 males, N=10 females).

New pairs (N=40) also had slightly smaller eggs (2.2% smaller clutch volume) than faithful ones (N=151, t-test: $t_{189}=2.1$, $P<0.05$), but the difference disappeared when we restricted the analysis to new pairs formed by experienced birds (N=16).

New and old pairs did not differ in the number of eggs hatched (Chi-square test: $\chi^2_2=1.68$, NS), but there was a significant difference in the number of chicks raised to 30 days old (Chi-square test: $\chi^2_2=6.0$, $P=0.05$), with faithful pairs being more successful (Table IV). New pairs with two experienced birds (N=12) raised only an average of 0.42 chicks, which was not better than the average of all new pairs (0.62 chicks; Table IV).

DISCUSSION

The members of breeding pairs of birds are frequently of similar age (Reid 1988). In gull and tern populations (Laridae and Sternidae, the closest relatives to skuas) it is commonly found that above 60% of the birds in pairs have an age difference of one year or less between them (Mills et al. 1996). In contrast, great skuas breeding in Foula display only a very poor correlation between ages, only 27% of the ages in pairs differ by one year or less, and age differences of 10 or more years are not uncommon. Age correlations between partners are not necessarily a product of mate selection, because they could arise, for example, as a result of similarly aged birds arriving at the breeding colonies (and pairing) at the same time of the season. Reid (1988) documented a tendency for birds of species with low levels of pair stability to display a stronger preference for mates with a similar age, but the causes underlying such pattern are unknown. A poor correlation in ages of partners in great skuas could be due to a lack of ability to assess the age or experience of potential mates. It could also be that individual variation in quality or condition (Coulson & Thomas 1985) is

relatively more important than age, for the outcome of a breeding attempt, and therefore any choice of mates is preferentially based on such attributes.

In any single year, partnerships in great skuas are 3 times more likely to be terminated by death of one of the birds than by divorce. Divorce rates in great skuas (6.4%) are higher than in South Polar skuas Catharacta maccormicki (1.5%, 4/267) studied at Cape Crozier, Antarctica (Wood 1971). Large (Catharacta) skuas seem to be amongst the seabirds with higher mate fidelity, only being surpassed by some auks (Alcidae) and petrels (Procellariiformes) (Ens et al. 1996). The factors that determine interspecific differences in divorce rates of birds are very poorly understood (Ens et al. 1996). Low divorce rates should be expected in species where breeding performance improves with the duration of the partnership, or, put in a different way, when there is a direct cost associated with mate change. We found that after mate change great skuas laid later in the season and raised fewer chicks, even when only considering new partnerships of birds that had previous breeding experience. This was not an age effect since divorcing birds were not younger than faithful ones. Delays in breeding, presumably due to the fact that it takes at least some days to attract a new partner, also occur in South Polar (Wood 1971) and Arctic skuas Stercorarius parasiticus (O'Donald 1983). Part of the cost of laying late in the great skua is the result of a relatively low post-fledging survival for late hatched offspring (Klomp 1991), a pattern commonly found in seabirds (e.g. Spear & Nur 1994). Sometimes a new partner cannot be attracted rapidly enough, and the chance to breed in that season may be lost altogether (Pietz & Parmelee 1994, this study), adding to the cost of mate switching. Jouventin and Guillotin (1979) reported an improvement in breeding up to the fifth year of a partnership in South Polar skuas, but they did not correct for the expected effect of increasing individual age and experience. Increasing familiarity between partners apparently influences the breeding success of short-tailed shearwaters Puffinus tenuirostris beyond the second year of a partnership, independently of age change (Bradley et al. 1990). If this was the case in skuas, then the cost of mate change would be even greater. However, in long-lived birds, like skuas, it might pay to incur the costs of mate changing, if a better partner can be

found, because each breeding attempt makes a relatively small contribution to lifetime reproductive success (Newton 1989).

In a minority of cases, divorce was not a preferred option by the individuals involved, but was forced by other birds, either because a female was chased away by an usurper or because both birds lost a territory. It is not known if a bird can encourage an usurper, but behavioural observations in great skuas (this study) and in oystercatchers Haematopus ostralegus (Ens et al. 1993) suggest that "bystanders" do not assist usurpers in chasing their partners from the territory. In oystercatchers, most divorces are a result of territory or partner loss due to the action of a third bird or of a neighbouring pair (Ens et al. 1993). The lower frequency of this type of mate change in great skuas could be a result of the fact that skuas are very aggressive, well armed and frequently inflict severe injuries during fights. Potential usurpers may be deterred by the risk involved in trying to impose a divorce.

Some studies on seabirds have shown that mate fidelity can be a by-product of territorial or nest fidelity (Morse & Kress 1984, Cuthbert 1985), but recent investigations clearly demonstrate that birds like shags Phalacrocorax aristotelis and kittiwakes Rissa tridactyla can display high mate fidelity when switching nesting sites or even colony (Aebischer et al. 1995, Fairweather & Coulson 1995). In common with other studies involving skuas (Wood 1971, O'Donald 1983, Parmelee & Pietz 1987, Pietz & Parmelee 1994) we detected few territory changes in great skuas, the majority involving females. Males seem to be the territory owners because when failing to pair and breed they keep trying (often successfully) to defend their territory, sometimes for more than one breeding season. Non-breeding females rarely defend a territory alone. However, they can occupy their former territory when waiting for their previous partner, and re-pair with a new bird in that territory if he fails to return (see also O'Donald 1983, Parmelee & Pietz 1987, Ainley et al. 1990). We found that birds in a pair can move together to a new territory. Ainley et al. (1990) reported that South Polar skua pairs can move long distances together (up to 800 meters). Although high breeding area fidelity in skuas probably makes a decisive contribution to maintain high pair fidelity, it is clear that, like kittiwakes (Fairweather

& Coulson 1995), skuas recognise mates and maintain partnerships as a result of previous experience of being together. Great skua territories within each area in Foula are usually very similar, and as most territorial changes involve short movements, it seems unlikely that divorces could arise as a result of some birds seeking better territories.

Incompatibility or Searching for a Better Option?

Choudhury (1995) has argued that distinguishing whether a new mate has been chosen because it is more "compatible" or of a "higher quality" may be difficult: in both cases it will still be the "best option". However, there is some evidence that deserted birds are of relatively poor quality, independently of the interactions with their deserting mates. Female willow tits Parus montanus were found to desert males relatively younger than their new mates (Orell et al. 1994). Female black-capped chickadees Parus atricapillus divorced their mates to pair with birds of higher social rank (Otter & Ratcliffe 1996). In the blue tit Parus caeruleus, Dhondt and Adriaensen (1994) showed that females, but not males, improve reproductive success after a divorce, compared to birds that remained faithful. All these studies with tits indicate that females are the deserting (choosing) sex. The existence of a chooser and a victim is a condition for the better option hypothesis. Both studies with oystercatchers (Ens et al. 1993) and great skuas provide further evidence that it is generally females that desert their mates, changing territory in the process. After divorce all female skuas bred (except in the case of usurpation) but most males remained unpaired. Divorced male skuas are often seen attacking the new pairs. It seems likely that, in great skuas, deserted males are of relatively poor quality because they have a significantly lower probability of re-pairing than widowed males, sometimes remaining unpaired for more than one year. Prospecting females seem to be able to assess male quality, at least to a certain extent, because they engage in fights for males with established females while other territorial males remain available (unpaired). Ens et al. (1993) provide further evidence that divorced males are somehow inferior: divorced male oystercatchers often lost their territories, while widowed males rarely lost their breeding status.

Choudhury (1995) identified another difficulty when trying to distinguish between the incompatibility and the better option hypotheses. Although the incompatibility hypothesis predicts that both members of a pair should benefit from a divorce, in practice this may not happen if a strong intrasexual competition in one of the sexes prevents the birds from realising their preferred option. This could result in only one of the sexes improving breeding performance after divorce, as reported for the blue tit (Dhondt & Adriaensen 1994), giving the impression that birds from one sex are choosers and the others victims. We believe this confounding factor does not affect our results because there is evidence suggesting that there are no large differences in mate availability for the two sexes in this skua population. After death of the partner, the probability of re-pairing and breeding was similar for males and females, a pattern significantly different from that occurring after divorce (Table IV). Also, there was no difference in laying dates of pairs with recently widowed males versus females, suggesting that time taken to find a new mate and get into breeding condition was independent of gender.

In conclusion, the results from this study show that most divorces in great skuas result from female desertion. Males that are victims of divorce have difficulty in re-pairing, which suggests that they are of poor quality, not merely incompatible with their deserting mates. Therefore, the "better option hypothesis" receives support from these data, but the "incompatibility hypothesis" does not.

REFERENCES

- Aebisher, N.J., Potts, G.R. & Coulson, J.C. 1995. Site and mate fidelity of shags Phalacrocorax aristotelis at two British colonies. Ibis 137, 19-28.
- Ainley, D.G., Ribic, C.A. & Wood, R.C. 1990. A demographic study of the South Polar skua Catharacta maccormicki at Cape Crozier. J. Anim. Ecol. 59, 1-20.
- Bradley, J.S., Wooller, R.D., Skira, I.J. & Serventy, D.L. 1990. The influence of mate retention and divorce upon reproductive success in short-tailed shearwaters Puffinus tenuirostris. J. Anim. Ecol. 59, 487-496.
- Choudhury, S. 1995. Divorce in birds: a review of hypotheses. Anim. Behav. 50, 413-429.
- Choudhury, S., Black, J.M. & Owen, M. 1996. Body size, fitness and compatibility in barnacle geese Branta leucopsis. Ibis 138, 700-709.
- Coulson, J.C. 1963. Egg size and shape in the kittiwake (Rissa tridactyla) and their use in estimating age composition of populations. Proc. Zool. Soc. Lond. 140, 211-227.
- Coulson, J.C. & Thomas, C.S. 1983. Mate choice in the kittiwake gull. In: Mate choice (Ed. by Bateson, P.). Cambridge University Press.
- Coulson, J.C. & Thomas, C.S. 1985. Differences in the breeding performance of individual kittiwake gulls, Rissa tridactyla (L.). In: Behavioural Ecology (Ed. by Sibly, R.M. and Smith, R.H.). Oxford: Blackwell Scientific Publications.
- Cuthbert, F.J. 1985. Mate retention in caspian terns. Condor 87, 74-78.
- Dhont, A.A. & Adriaensen, F. 1994. Causes and effects of divorce in the blue tit Parus caeruleus. J. Anim. Ecol. 63, 979-987.
- Ens, B.J., Choudhury, S. & Black, J.M. 1996. Mate fidelity and divorce in monogamous birds. In: Partnerships in Birds. The Study of Monogamy (Ed. by Black, J.M.). Oxford University Press.
- Ens, B.J., Safriel, U.N. & Harris, M.P. 1993. Divorce in the long-lived and monogamous oystercatcher, Haematopus ostralegus: incompatibility or choosing the better option? Anim. Behav. 45, 1199-1217.
- Fairweather, J.A. & Coulson, J.C. 1995. Mate retention in the kittiwake, Rissa tridactyla, and the significance of nest site tenacity. Anim. Behav. 50, 455-464.

- Furness, R.W. 1987. The skuas. Calton: T & A.D. Poyser.
- Hamer, K.C. & Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in the great skuas Catharacta skua. J. Anim. Ecol. 60, 693-794.
- Johnston, V.H. & Ryder, J.P. 1987. Divorce in Larids: a review. Colon. Waterbirds 10, 16-26.
- Jouventin, P. & Guillotin, M. 1979. Socio-écologie du skua Antarctique à Pointe Géologie. Terre Vie. Rev. Ecol. 33, 109-127.
- Klomp, N.I. 1991. Studies of recruitment in the great skua. PhD Thesis, University of Glasgow.
- Klomp, N.I. & Furness, R.W. 1992. The dispersal and philopatry of great skuas from Foula, Shetland. Ringing & Migration 13, 73-82.
- Mills, J.A., Yarral, J.W. & Mills, D.A. 1996. Causes and consequences of mate fidelity in red-billed gulls. In: Partnerships in Birds. The Study of Monogamy (Ed. by Black, J.M.). Oxford University Press
- Morse, D.H. & Kress, S.W. 1984. The effect of burrow loss on mate choice in Leach's storm-petrel. Auk 101, 158-169.
- Newton, I. 1989. Lifetime reproduction in birds. London: Academic Press.
- O'Donald, P. 1983. The Arctic skua. a study of the ecology and evolution of a seabird. Cambridge University Press.
- Orell, M., Rytönen, S. & Koivula, K. 1994. Causes of divorce in the monogamous willow tit Parus montanus, and consequences for reproductive success. Anim. Behav. 48, 1143-1154.
- Otter, K. & Ratcliffe, L. 1996. Female initiated divorce in a monogamous songbird: abandoning males for mates of higher quality. Proc. R. Soc. Lond. B 263, 351-354.
- Parmelee, D.F. & Pietz, P.J. 1987. Philopatry, mate and nest-site fidelity in the brown skuas of Anvers Island, Antarctica. Condor 89, 916-919.
- Pietz, P.J. & Parmelee, D.F. 1994. Survival, site and mate fidelity in South Polar skuas Catharacta maccormicki at Anvers Island, Antarctica. Ibis 136, 32-38.

- Phillips, R.A., Caldow, R.W.G. & Furness, R.W. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic skuas *Stercorarius parasiticus*. *Ibis* 138, 410-419.
- Reid, W.V. 1988. Age correlations within pairs of breeding birds. *Auk* 105, 278-285.
- Spear, L. & Nur, N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *J. Anim. Ecol.* 63, 283-298.
- Wood, R.C. 1971. Population dynamics of breeding South Polar skuas of unknown age. *Auk* 88, 805-814.
- Wooller, R.D., Bradley, J.S. & Croxall, J.P. 1992. Long-term population studies of seabirds. *Trends Ecol. Evol.* 7, 111-114.

Table I.- Great skua divorce rates in Foula (two birds are said to have divorced when they cease to breed together in spite of being both alive and present at the colony)

	Years					Total
	1991-92	92-93	93-94	94-95	95-96	
% divorced	5.6	5.6	12.1	5.3	4.3	6.4
# Pairs studied	18	36	66	76	115	311

Table II.- Distance moved (in number of territories) by male and female skuas when changing territory

	Distance					
	1	2	3	4	5	6+
Females	9	3	4	0	1	2
Males	1	1	1	2	2	0

Table III- Frequency of breeding and non-breeding after mate loss through divorce and partner death

	Fate after partner death		Fate after divorce	
	Breed	Not breed	Breed	Not breed
Females	12	4	11	1
Males	19	3	3	8

Table IV- Hatching success and number of chicks raised to 30 days old per pair in relation to mating status

	Number of eggs hatched				Number of chicks raised			
	0	1	2	mean	0	1	2	mean
Old pairs	12	29	116	1.66	44	49	48	1.03
New pairs	3	10	23	1.64	13	10	3	0.62

Chapter 3

The Influence of Hatching Date on Different Life-history stages of Great Skuas

In press as:

Catry, P., Ratcliffe, N. & Furness, R.W. The influence of hatching date on different life-history stages of Great Skuas. *Journal of Avian Biology*.

Abstract

We investigated the effect of hatching date on chick body condition, chick survival, post-fledging survival and eventual breeding performance as an adult (laying date and clutch volume) of Great Skuas in Foula (Shetland). In most years (10 out of 16) there was a seasonal decline in chick body condition. In the remaining seasons, there was no detectable effect of hatching date on chick condition. Differences among years were statistically significant. Chicks in early broods survived better than late hatched chicks in four years, and no trend could be detected in one season. Annual variation in the seasonal pattern of chick growth and survival, and of adult territorial attendance, suggest that environmental conditions play a role in determining the seasonal decline in performance. Post-fledging survival in relation to hatching date was studied by analysis of ringing recoveries. Hatching date affected post-fledging survival, but only in the first-year of life. Breeding parameters of birds of known hatching date were studied when they came back to breed in Foula. Hatching date of an individual did not affect its laying date or volume of the clutches laid later in life. This suggests that laying date has a low heritability, or none at all. Birds that laid early in the season produced more future recruits than later birds. After an early breeding attempt, skuas had a higher overwinter survival probability than after a late season. These results suggest that laying date is an indicator of individual quality in skuas, in the sense that early birds apparently are more competent at gathering resources for reproduction and survival.

Introduction

Birds hatching early in the season frequently display better growth and have a greater survival to fledging (Daan et al. 1988, Spear and Nur 1994). This advantage can result from a seasonal decline in food availability, causing early chicks to grow more rapidly and to have a lower mortality rate (Brinkhof and Cavé 1997). Another explanation for seasonal declines in chick condition and survival is that birds that lay early in the season are of higher quality, and therefore provide better parental care to their offspring (Brouwer et al. 1995). Early fledged chicks can display higher post-fledging survival (Perrins 1965, Hochachka 1990), which has been attributed to a better body condition (Perrins 1965) or to a direct seasonal effect where early birds have an advantage in social contests with late birds from the same cohorts (Garnett 1981, Spear and Nur 1994). Some studies, however, have found a variable effect of hatching date on chick growth (Cichon and Lindén 1995) and in recruitment probability (van Noordwijk et al. 1981), while other authors have reported no effects of hatching date on post-fledging survival (Ross and McLaren 1981). Longer term effects, with the exception of adult body size (Boag 1987, Richner et al. 1989), have more rarely been investigated, but they include influences on recruitment probability (Spear and Nur 1994), egg size (Leeson and Summers 1987), clutch size (Haywood and Perrins 1992, Sedinger et al. 1995) and social status (Richner et al. 1989).

Studies with seabirds have also found seasonal declines in chick condition (Hedgren and Linnman 1979, Furness 1983) and in fledging success (Wanless and Harris 1988, Spear and Nur 1994, *but see* Hatch 1990). Few investigations have addressed the effect of hatching (or fledging) timing on fitness correlates after fledging, except for immature survival. A higher post-fledging survival amongst chicks that grew early in the season has been documented in Manx Shearwaters *Puffinus puffinus* (Perrins 1966), Cape Gannets *Sula capensis* (Jarvis 1974), Shags *Phalacrocorax aristotelis* (Harris et al. 1994), Herring Gulls *Larus argentatus* (Parsons et al. 1976), Western Gulls *Larus occidentalis* (Spear and Nur 1994) and Guillemots *Uria aalge* (Harris et al. 1992). The absence of an effect has also been reported, for example in Guillemots (Hedgren 1981) and Puffins *Fratercula arctica* (Harris and Rothery 1985). In many of the studies above, post-fledging survival rates in relation to hatching or fledging date were estimated from recapture data at the

colony of origin, and therefore it was not possible to discriminate between mortality and emigration. Differential philopatry in relation to performance during growth has been demonstrated in birds (Verhulst et al. 1997), but few studies on the effects of seasonal trends on post-fledging mortality have avoided this problem by relying in recoveries or sightings of birds on a wide geographical area.

In this study with Great Skuas *Catharacta skua* we investigated the effect of hatching date on (1) chick body condition, (2) chick survival, (3) post-fledging survival as indicated by ringing recoveries by the public and (4) breeding parameters (laying date and clutch volume). Great Skuas normally first breed when 4 to 9 years old (Furness 1987) and tend to recruit close to their natal territory (Klomp and Furness 1992). Our main aims were to investigate the existence of annual variations in the influence of hatching date (perhaps mediated by varying trends in food availability), to determine how long-lasting might be any effects of hatching date on the life of Great Skuas, and discuss the implications of the relationship between laying date of the parents and their fitness.

Methods

This study was carried out in Foula (Shetland), the largest breeding colony of Great Skuas in the North Atlantic. Between 1975 and 1990, the island was visited annually during the chick rearing period. Chicks were caught, measured (wing chord and weight) and fitted with British Trust for Ornithology (BTO) monel-rings. Chick age was estimated from wing length (Furness 1983) and this provided an estimation of hatching date (with a standard error of 1.8 days for individual estimates; In each year most chicks hatched during a time interval of c. 35 days). An index of body condition was calculated for chicks aged between 13 and 34 days old (i.e. on the linear part of their growth curve; Furness 1983). This index is given by the difference between measured body weight and weight as predicted by wing length, calculated from data collected on Foula in 1975, a year when breeding success was very high (Furness 1983). The regression line of weight on wing is given by the following equation ($r^2=0.88$, $n=877$, $P<0.0001$):

$$\text{Weight} = 58.48 + 6.38\text{Wing} - 0.01\text{Wing}^2$$

To correct for differences in laying dates between years, hatching dates were standardised in such a way that mean hatching date for each year was equal to zero. There were no significant differences among years in the variance of the distribution of hatching dates. Throughout this paper, hatching dates refer to relative hatching dates, unless stated otherwise. In the analysis of chick body condition in relation to hatching date, each chick contributed with one single condition measurement.

We used territorial attendance of adults as a measure of the ease of obtaining food (Furness and Hislop 1981, Hamer et al. 1991, Bukacinska et al. 1996, Monaghan 1996), and measured its temporal variation throughout the breeding seasons of 1994, 1995 and 1996. Attendance was recorded between 08.30 and 12.30h, B.S.T., by walking past 50 to 90 territories in each sampling day, and recording the number of adult birds per territory. At least one adult from each of these territories was individually colour-ringed. Skuas were never observed flying away as a response to observer approach. It is assumed that most time spent away from territories is used for foraging because breeding Great Skuas have never been seen resting outside their territories, except for relatively brief periods when bathing (Furness 1987, Hamer et al. 1991). Furthermore, few birds bathe in the morning, when observations were made. Attendance can conceivably also vary as a result of predation risk, making attendance levels hard to interpret in relation to food availability (Monaghan 1996). Except for Ravens *Corvus corax* that take some skua eggs early in the season, Great Skuas have few or no predators in Foula. Extensive cannibalism can occur, but only when chicks are left unattended as a result of severe food shortages (Hamer et al. 1991).

We investigated the effect of hatching date on chick survival to 30 days, in Foula, from 1991 to 1995. Great skua chicks fledge when around 46 days old (Furness 1987). Because very few chicks die when 30 to 46 days (pers. obs.), survival to 30 days is a reasonable measure of fledging success. Chick fate was monitored as the number of members of a given brood that survived from hatching. We correlated hatching date of the first chick in a brood with the number of chicks fledged per brood. Within broods, Great Skua chicks usually hatch within 48 hours of one another. The vast majority (>90%, varying with year) of pairs laid two egg clutches,

and we restricted our analysis to nests that hatched two chicks. Not enough pairs hatched only one chick to enable a complementary analysis.

Ring recoveries of birds found dead by the public away from Foula, and reported to the BTO until 1990, were used in this study to estimate longevity in relation to hatching date. Birds reported as having been found after being dead for a long time were excluded from the analysis. An index of survival rate in the first year (for groups of birds with different hatching dates) was calculated by dividing the number of birds recovered when older than 365 days by the total number of birds recovered and reported dead in each group. Since some birds of the studied cohorts are known to be still alive, and therefore cannot be recovered, this index is likely to be an underestimate of first-year survival. Great Skua dispersal patterns are age-dependent (Klomp and Furness 1992), and since recovery probabilities vary geographically, our indices of first-year survival might be further biased. However, this should affect all birds of a given age in a similar way, independently of hatching date, allowing comparisons to be made.

Between 1991 and 1996 we caught ringed adults of known hatching date that were breeding in Foula. Upon capture, these birds were colour-ringed with unique combinations and subsequently sexed by observation of copulation or courtship feeding. Breeding performance of these birds was studied in each spring after capture. Territories were visited daily until the first egg was laid. When clutches were complete, eggs were measured to the nearest 0.1mm and volumes calculated as $0.00048 \times \text{length} \times \text{breadth}^2$ (Coulson 1963). We correlated hatching dates of adult male and female skuas with their laying dates as breeders. For each adult, we calculated the average standard laying date in the years studied after correcting for age effects (Hamer and Furness 1991) by taking the residuals from regressions computed for each year. The same procedure was used for the analysis referring to clutch volume. Clutches with only one egg were rare and often could not be distinguished from two egg clutches that had lost one egg to predators. One egg clutches were therefore excluded from the analysis.

The relationship between parental laying date and subsequent overwinter survival was studied between 1991 and 1996. Survival of colour-ringed birds was assessed from territory attendance determined during daily inspections in each

breeding season. Clubs (sites where immatures and non-breeders congregate) were also checked for the presence of non-breeders. Resighting probabilities for live adult great skuas in the study area were almost equal to one (unpublished data). Each individual was included in the analysis only in the years when its laying dates had been determined. The effect of laying date on the probability of an individual surviving to the next breeding season was analysed by the use of logistic regressions. Significance was assessed using likelihood-ratio tests (Norusis 1994). The logistic regression coefficient (β) is presented together with the test statistics.

Results

The chick stage.

Early hatched chicks had, on average, a better body condition than late hatched chicks, in 10 out of 16 years studied. In the remaining 6 years, hatching date had no detectable effect on condition (Table 1). There was a significant year effect on the slopes of the regressions (ANCOVA, $F_{15,12801}=7.26$, $p<0.001$), indicating that the effect of hatching date on body condition differed significantly among years.

To investigate the possibility that there could be annual differences in the pattern of food availability through the breeding season, we studied territorial attendance of breeding Great Skuas as a measure of the ease of obtaining food. Seasonal variation in attendance patterns varied dramatically from one year to another (Figure 1). Attendance in the second half of June 1995 (early chick rearing) was much higher than in the same periods of 1994 and 1996. During incubation and late chick rearing, attendance levels were similar in all three years (Figure 1).

In four of five years studied there was a significant negative correlation between hatching date of the first chick in the brood and the number of chicks surviving to 30 days in broods where two chicks hatched (Table 2).

Post-fledging survival.

The number of days from estimated fledging date to death in the first year, for those birds that left Foula, was not correlated with hatching date (Spearman $r_{128}=0.12$, ns). Considering birds that died in the first year of life versus birds that survived, there was a significant effect of hatching date on survival probability in the first year, with

early hatched birds having a higher survival (Logistic regression, $G^2_1=7.46$, $n=420$, $\beta=-0.054$, $p<0.01$, Figure 2). Using absolute hatching date instead of relative hatching date produced a non-significant relationship (Logistic regression, $G^2_1=3.38$, $n=420$, $\beta=-0.032$, $p=0.07$).

After the first year, longevity (in days) was not correlated with hatching date (Spearman $r_{292}=0.02$, ns). There was no significant difference in hatching dates between birds that died between one year old and minimum recruitment age (4), and birds that were known to have recruited to the breeding population ($t_{452}=0.36$, ns).

Males that survived to breed had a slightly earlier mean hatching date ($x = -2.25 \pm 0.56$, $n=67$) than adult females ($x = -0.81 \pm 0.63$, $n=75$), but the difference was not significant ($t_{140}=-1.69$, $p=0.09$).

Breeding.

Female hatching date had no effect on subsequent laying time when adult ($r_{75}=0.04$, $p=0.75$), and the same was true for male hatching date and laying timing of their partners ($r_{66}=0.01$, $p=0.92$). Hatching date and clutch volume were not correlated in females ($r_{74}=-0.07$, $p=0.55$) or males ($r_{65}=-0.06$, $p=0.61$). The same analysis was performed using absolute hatching date (not standardised for year) and also year by year. All results were non-significant.

Laying date and adult survival.

Our results indicated that early laying parents produced more recruits per breeding attempt and we decided to test if early layers were suffering a cost that might counterbalance their apparent advantage. We tested the hypothesis that early layers had a higher subsequent mortality by studying the effect of laying date on overwinter survival. Contrary to the prediction, early layers had a higher survival than late layers (Logistic regression, $G^2_1=5.03$, $n=1051$, $\beta=-1.81$, $p=0.025$; Figure 3).

Discussion

Birds that are of high quality often lay early in the season and are also better food providers to their offspring (Coulson and Porter 1985; Coulson and Thomas 1985).

This could result in early breeding pairs having chicks with better body condition and higher survival to fledging, as reported in this study. On the other hand, food resources can start declining before most birds have completed their breeding activities in spring and summer, and as a result individuals breeding late face a less favourable environment (Daan et al. 1988). Sandeels constitute the main prey of breeding Great Skuas in Shetland (Furness and Hislop 1981). Sandeels also display a seasonal variation in Shetland surface waters. Fish older than 0-group generally decrease in availability (by moving into the sediments) from July onwards (Kunzlik 1989). A seasonal reduction in food availability could therefore be contributing to the seasonal decline in chick condition and survival to fledging of Great Skuas. It is interesting to note that, in the late eighties, when sandeel was scarce and represented a small proportion of the diet of Great Skuas (Hamer et al. 1991) we could not detect a seasonal decline in chick body condition. Variation in patterns of adult attendance during chick rearing also suggest an increase in foraging time that, at least in 1995, was too abrupt to be a result of greater nutritional demands of growing chicks (there were no noticeable changes in weather conditions during the drop of attendance).

The relative advantage of early chicks in body condition and survival varied from one year to another. If adult quality was the only factor affecting the development of chicks, we would not expect yearly changes in the seasonal trend. Patterns of territorial attendance of adults in different seasons also suggest that the seasonal trends in resource availability are variable for the study population. This does not eliminate the possibility that factors related to parental quality may also contribute to individual differences in chick growth rates and survival.

Great Skua chicks hatched early in the season had higher post-fledging survival, a pattern already found in other seabirds (e.g. Spear and Nur 1994). This could be due to the fact that early chicks have larger body reserves, but hatching date explains only a very small proportion of the variance in body condition. Also, there was no effect of hatching date on longevity of birds that died away from the colony in the first year, suggesting that there was no differential survival immediately after fledging, when body reserves would be most likely to make a difference.

The effect of hatching date on the lives of Great Skuas did not seem to extend beyond the first year. Longevity and breeding parameters (laying date and clutch

volume) were independent of hatching date. Few studies reported an influence of developmental factors on adult birds, and those that do generally document weak effects (*e.g.* Haywood and Perrins 1992). The absence of a correlation between hatching date and subsequent timing of breeding of adult Great skuas suggest that laying date is not heritable, or has a very low heritability, in this species. These results should be interpreted with caution because our samples were not very large and because the hatching date of a bird might be a poor estimate of parental values for laying dates. Laying dates are commonly believed to be heritable (*e.g.* Price et al. 1988). Individual laying dates are usually repeatable, but there are few heritability estimates based on parent-offspring regressions, and most of them involve passerines (Boag and van Noordwijk 1987). Perdeck and Cavé (1992) found laying dates not to be heritable in the Coot *Fulica atra*, and it is possible that this applies to other species, as suggested for the Great Skua.

Neither clutch size nor hatching probability increased as the seasons progressed in the study population (unpublished data), and therefore pairs laying early had a higher annual production of future recruits than late breeders. This pattern seems to be common among birds (*e.g.* Harris et al. 1994), although there are well documented exceptions (van Noordwijk et al. 1981). Great Skuas laying early were not, compared to late birds, paying a high reproductive cost. In fact, after an early breeding, the overwinter survival probability was higher than following a late nesting attempt. This does not mean that there is no cost of laying too early. It is likely that such costs exist, varying with individuals, and must prevent late birds from breeding earlier (Nilsson 1994). Clearly, Great Skuas that lay early are of high quality, in the sense that they are more competent at gathering the resources necessary for breeding and survival. Therefore, laying date can be a good indicator of individual quality in this species.

References

- Boag, P.T. 1987. Effects of nestling diet on growth and adult size of Zebra Finches (*Poephila guttata*). - *Auk* 104: 155-166.
- and van Noordwijk, A.J. 1987. Quantitative Genetics. - in Cooke, F. and Buckley, P.A. (eds.). *Avian Genetics. A Population and Ecological Approach*. Academic Press, London.
- Brinkhof, M.W.G. and Cavé, A.J. 1997. Food supply and seasonal variation in breeding success: an experiment in the European Coot. - *Proc. R. Soc. Lond. B* 264: 291-296.
- Brouwer, A., Spaans, A.L. and Wit, A.A.N. 1995. Survival of Herring Gull *Larus argentatus* chicks: an experimental analysis of the need for early breeding. - *Ibis* 137: 272-278.
- Bukacinska, M., Bukacinski, D. and Spaans, A.L. 1996. Attendance and diet in relation to breeding in Herring Gulls (*Larus argentatus*). - *Auk* 113: 300-309.
- Chicon, M. and Lindén, M. 1995. The timing of breeding and offspring size in Great Tits *Parus major*. - *Ibis* 137: 364-370.
- Coulson, J.C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. - *Proc. Zool. Soc. Lond.* 140: 211-227.
- and Porter, J.M. 1985. Reproductive success of the Kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. - *Ibis* 127: 450-466.
- and Thomas, C. 1985. Differences in the breeding performance of individual Kittiwake Gulls, *Rissa tridactyla* (L.). - in Sibly, R.M. and Smith, R.H. (eds.). *Behavioural Ecology*. Blackwell Scientific, Oxford.
- Daan, S., Dijkstra, C., Drent, R. and Meijer, T. 1988. Food supply and the annual timing of avian reproduction. - *Acta XIX Congressus Internationalis Ornithologicus*, Ottawa.
- Furness, R.W. 1983. Variations in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. - *J. Zool. Lond.* 199: 101-116.
- . 1987. *The Skuas*. - T & AD Poyser, Calton.

- and Hislop, J.R.G. 1981. Diets and feeding ecology of Great Skuas *Catharacta skua* during the breeding season in Shetland. - *J. Zool. Lond.* 195: 1-23.
- Garnett, M.C. 1981. Body size, its heritability and influence on juvenile survival among Great Tits, *Parus major*. - *Ibis* 123: 31-41.
- Hamer, K.C. and Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. - *J. Anim. Ecol.* 60: 693-704.
- , Furness, R.W. and Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. - *J. Zool. Lond.* 223: 175-188.
- Harris, M.P. and Rothery, P. 1985. The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. - *Ibis* 127: 243-250.
- , Halley, D.J. and Wanless, S. 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. - *Ibis* 134: 335-339.
- , Buckland, S.T., Russel, S.M. & Wanless, S. 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. - *J. Avian Biol.* 25: 268-274.
- Hatch, S.A. 1990. Individual variation in behaviour and breeding success of Northern Fulmars. - *Auk* 107: 750-755.
- Haywood, S. and Perrins, C.M. 1992. Is clutch size in birds affected by environmental conditions during growth? - *Proc. R. Soc. Lond. B* 249: 195-197.
- Hedgren, S. 1981. Effects of fledging weight and time of fledging on survival of Guillemot *Uria aalge* chicks. - *Ornis scand.* 12: 51-54.
- and Linnman, A. 1979. Growth of Guillemot *Uria aalge* chicks in relation to time of hatching. - *Ornis Scand.* 10: 29-36.
- Hochachka, W. 1990. Seasonal decline and consequences of nestling condition in Song Sparrows. - *Ecology* 71: 1279-1288.
- Jarvis, M.J.F. 1974. The ecological significance of clutch size in the South African Gannet (*Sula capensis* (Linchenstein)). - *J. Anim. Ecol.* 43: 1-17.

- Klomp, N.I. and Furness, R.W. 1992. The dispersal and philopatry of Great Skuas from Foula, Shetland. - *Ringing & Migration* 13: 73-82.
- Kunzlik, P.A. 1989. Small fish around Shetland. - *in* Heubeck, M. (ed.) *Seabirds and Sandeels: proceedings of a seminar held in Lerwick, Shetland, 15-16 October 1988*. Shetland Birds Club: 30-37.
- Leeson, S. and Summers, J.D. 1987. Effect of immature body weight on laying performance. - *Poultry Sci.* 66: 1924-1928.
- Monaghan, P. 1996. Relevance of the behaviour of seabirds to the conservation of marine environments. - *Oikos* 77: 227-237.
- Nilsson, J.Å. 1994. Energetic bottle-necks during breeding and the reproductive cost of being to early. - *J. Anim. Ecol.* 63: 200-208.
- Norusis, M. J. 1994. *SPSS Advanced Statistics*. - SPSS Inc., Chicago.
- Parsons, J., Chabrzyk, G. and Duncan, N. 1976. Effects of hatching date on post-fledging survival in Herring Gulls. - *J. Anim. Ecol.* 45: 667-675.
- Perdeck, A.C. and Cavé, A.J. 1992. Laying date in the Coot: effects of age and mate choice. *J. Anim. Ecol.* 61: 13-19.
- Perrins, C.M. 1965. Population fluctuations and clutch size in the Great Tit (*Parus major*). - *J. Anim. Ecol.* 34: 601-647.
- 1966. Survival of young Manx Shearwaters *Puffinus puffinus* in relation to their presumed date of hatching. - *Ibis* 108: 132-135.
- Price, T., Kirkpatrick, M. & Arnold, S.J. 1988. Directional selection and the evolution of breeding date in birds. - *Science* 240: 798-799.
- Richner, H., Schneiter, P. and Stirnimann, H. (1989). Life-history consequences of growth rate depression: an experimental study on Carrion Crows (*Corvus corone corone*). - *Funct. Ecol.* 3: 617-624.
- Ross, H.A. and McLaren, I.A. 1981. Lack of differential survival among young Ipswich Sparrows. - *Auk* 98: 495-502.
- Sedinger, J.S., Flint, P.L. and Lindberg, M.K. 1995. Environmental influence on life-history traits: growth, survival and fecundity in Black Brant (*Branta bernicla*). - *Ecology* 76: 2404-2414.

- Spear, L. and Nur, N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in Western Gulls. - *J. Anim. Ecol.* 63: 283-298.
- van Noordwijk, A.J., van Balen, J.H. and Scharloo, W. 1981. Genetic variation in the timing of reproduction in the Great Tit. - *Oecologia* 49: 158-166.
- Verhulst, S., Perrins, C.M. and Riddington, R. 1997. Natal dispersal of Great Tits in a patchy environment. - *Ecology* 78: 864-872.
- Wanless, S. & Harris, M.P. 1988. The importance of relative laying date on breeding success of the Guillemot *Uria aalge*. - *Ornis Scand.* 19: 205-211.

Table 1- Regressions of chick body condition (weight corrected for wing-length) on hatching date for each year between 1975 and 1990.

Year	Slope	Intercept	r²	n	Signif.
1975	-2.7	-9.0	0.07	1141	p<0.0001
1976	-1.3	-45.4	0.01	1218	p<0.001
1977	-1.6	-56.1	0.01	2143	p<0.0001
1978	-1.5	-11.9	0.01	940	p<0.01
1979	-1.2	-10.0	0.01	379	n.s.
1980	-2.7	-35.3	0.05	656	p<0.0001
1981	-1.3	-84.7	0.01	1031	p<0.05
1982	-1.2	-33.7	0.01	629	p<0.05
1983	-4.1	-20.5	0.07	1224	p<0.0001
1984	-2.3	-33.7	0.03	848	p<0.0001
1985	0.6	-35.0	0.00	825	n.s.
1986	-4.5	-34.3	0.08	777	p<0.0001
1987	1.6	-14.3	0.01	219	n.s.
1988	0.8	-107.7	0.00	444	n.s.
1989	1.0	-45.6	0.01	156	n.s.
1990	-0.6	-37.8	0.00	253	n.s.

Table 2.- Effects of hatching date on the number of chicks surviving to 30 days old per brood, as determined by ordinal logistic regression. Confidence limits for the slopes of the resulting models are presented. Note that models with positive slope indicate a seasonal decline in the number of chicks fledged.

Year	95% conf. lim.			G ²	n	r ²	p
	Slope	Low.	High.				
1991	0.14	0.01	0.27	4.8	53	0.04	<0.05
1992	0.21	0.09	0.33	11.4	65	0.12	<0.001
1993	0.12	0.04	0.20	8.4	80	0.05	<0.005
1994	-0.01	-0.08	0.08	0.1	93	0.00	n.s.
1995	0.12	0.02	0.22	5.1	118	0.02	<0.05

Figure 3.1- Seasonal variation in adult territorial attendance as an estimation of foraging effort.

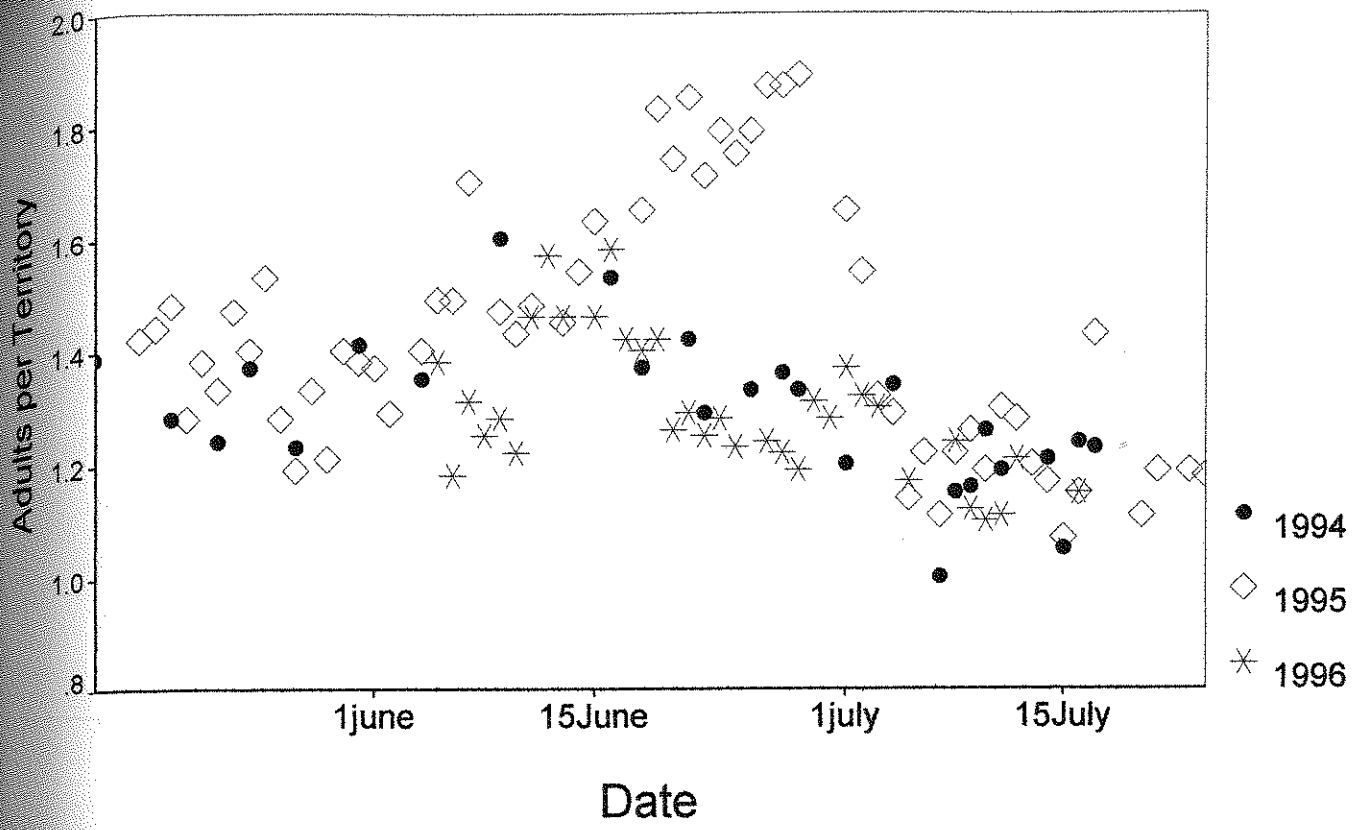


Figure 3.2- The effect of hatching date on post-fledging survival, as determined by ringing recoveries outside the colony of origin. The logistic regression (linear) line of best fit is shown. Note that linear effects on a logistic model can produce non-linear lines when plotted in a graph. Data points represent grouped data. Analyses were of the ungrouped data. Numbers for each point are sample sizes.

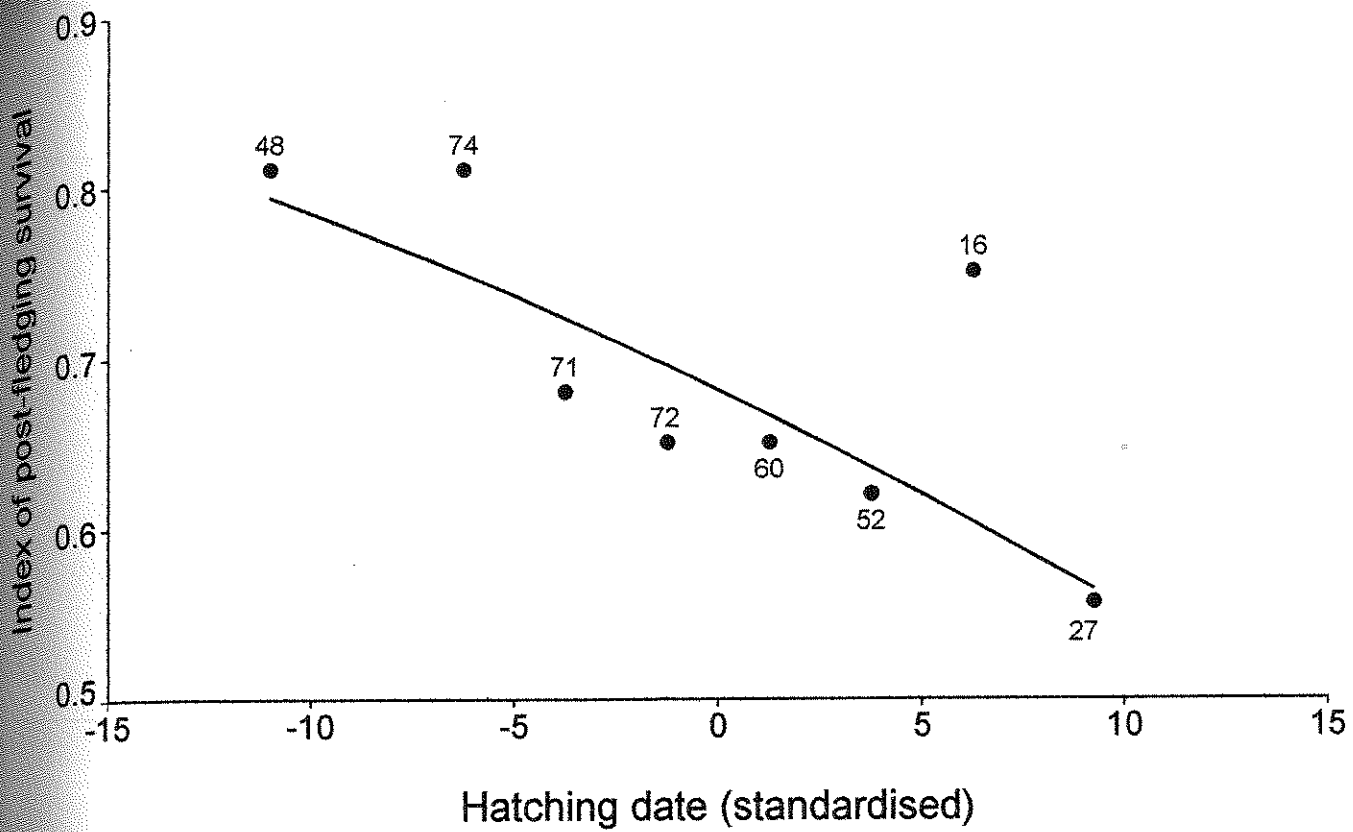
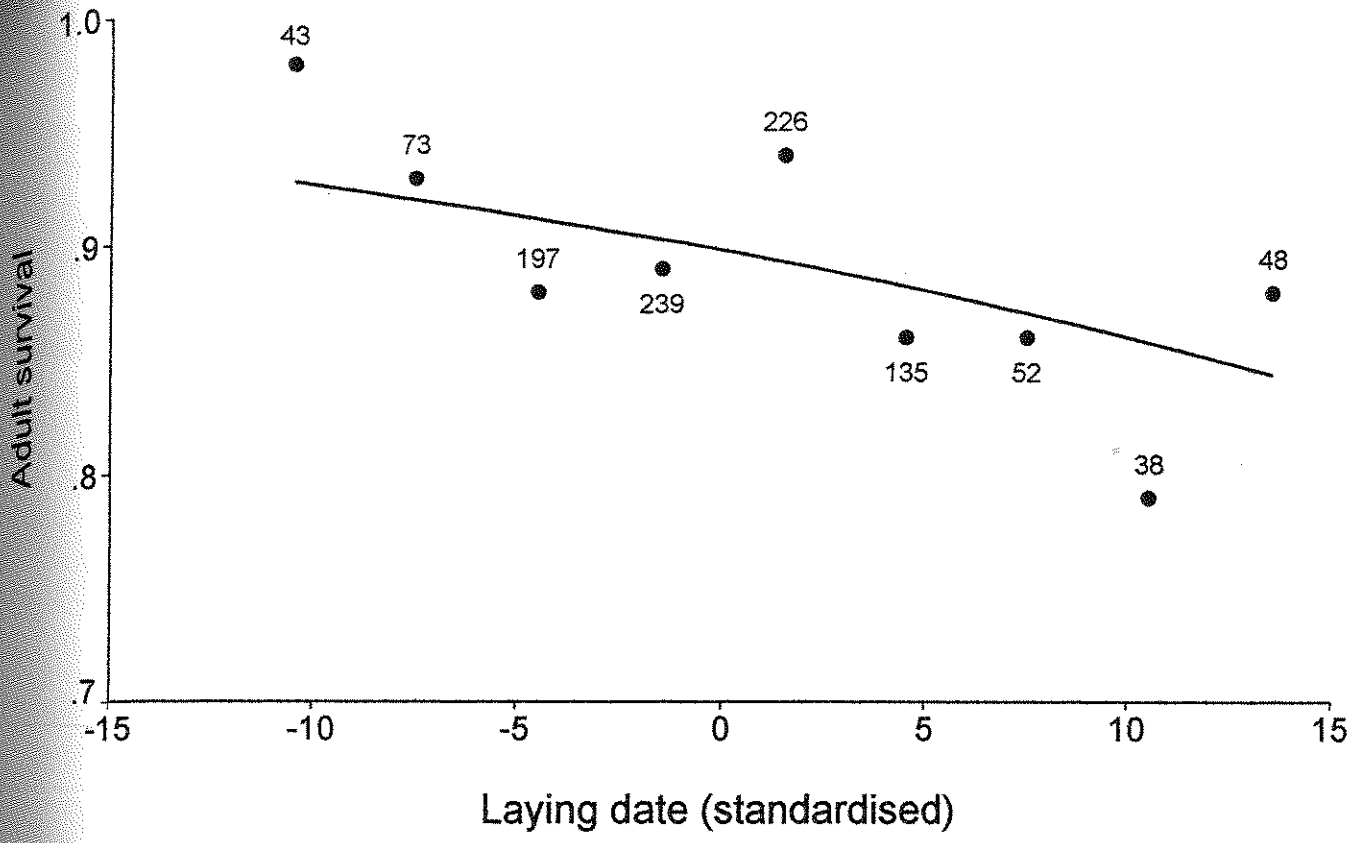


Figure 3.3- Annual survival rates of adults in relation to laying date in the previous spring. The logistic regression (linear) line of best fit is shown. Note that linear effects on a logistic model can produce non-linear lines when plotted in a graph. Data points represent grouped data. Analyses were of the ungrouped data. Numbers for each point are sample sizes.



Chapter 4

Egg Volume and Within-Clutch Asymmetry in Great Skuas: Are they Related to Adult Quality?

In press as:

Catry, P. & Furness, R.W. Egg Volume and Within-Clutch Asymmetry in Great Skuas: Are they Related to Adult Quality? *Colonial Waterbirds*.

Abstract

In gulls, egg size and clutch asymmetry have been suggested to be suitable variables for assessing individual quality. Skuas, like several other seabirds, generally display within-clutch asymmetry (the second egg in the clutch is, on average, smaller than the first egg). We found no relationship between clutch volume in 2 egg clutches and laying date, hatching success or fledging production of pairs of Great Skuas (*Catharacta skua*) breeding in Shetland. There was a high repeatability (0.72, $p < 0.0001$) in the volume of clutches laid by the same pairs in consecutive years. The influence of adult age on egg size was weak and variable. Unlike clutch volume, clutch asymmetry was not repeatable and showed no relationship with adult age. Furthermore, clutch asymmetry did not correlate with any other breeding parameter. We conclude that, in Great Skuas, clutch characteristics are not suitable indicators of individual quality or environmental conditions over the range prevailing during this study. The results are discussed in comparison with the conclusions from studies with gulls, and it is argued that more research is needed to clarify the factors that are responsible for the existence of within-clutch asymmetry in seabirds.

Egg production appears to be an energetically costly process in birds (Monaghan *et al.* 1995). Individuals with less access to resources, either because they live in poor habitats, during periods of relative food shortage, or because they are less efficient foragers, could be expected to have a greater difficulty in meeting these costs. This can be partly compensated by such individuals laying smaller clutches. However, particularly in seabirds, clutch size shows little or no variability. Even if clutch size is held constant, less successful birds could reduce their costs of laying by producing smaller eggs. However, this can have another cost: lower offspring fitness. Many studies have reported positive associations between egg size and hatching success, chick growth and survival (Williams 1994), but larger eggs are not necessarily always better per se. Clearly, extremely small eggs have lower viability, but, at least in some circumstances, above a certain threshold, hatching success and chick fitness may be independent of egg-size (*e.g.* Smith *et al.* 1995). Most evidence suggests that egg size, corrected for hatching order or adult quality, does affect offspring fitness early in the chick rearing period. However, later in life parental quality becomes more important (Williams 1994). Because parental quality and egg size can themselves be correlated, it is sometimes difficult, without experimental studies, to determine which one of these plays the more important role determining chick fitness (Reid and Boersma 1990, Bolton 1991).

Relatively small eggs can also be adaptive, in relation to laying order. It is commonly found among seabird species that the last egg has a smaller volume (Slagsvold *et al.* 1984). This could be a mechanism to facilitate brood reduction (Slagsvold *et al.* 1984) or to reduce hatching asynchrony. Alternatively, small last eggs could simply be a result of depletion of body reserves, and time constraints, by the end of the laying cycle. The degree to which the last egg is smaller than the first (the within-clutch asymmetry) therefore may be affected by food availability. Studies with gulls (Laridae) have provided some evidence for this. Pierotti and Bellrose (1986) reported that, in a colony where food availability was very high, egg size was independent of laying order in Western Gulls (*Larus occidentalis*). In Herring Gulls (*L. argentatus*) breeding in the Isle of May, Scotland, clutch volume increased as intraspecific competition decreased following a reduction of colony size by culling. Last eggs, in clutches of three, were the ones that benefited from the greatest increase

in volume (Coulson *et al.* 1982). A similar response was obtained from breeding Lesser Black-backed Gulls (*L. fuscus*) in an experiment where birds received supplementary feeding (Hiom *et al.* 1991). Within-clutch asymmetry was found to be negatively correlated with breeding success in a comparison involving ten Herring Gull colonies in Europe (Kilpi *et al.* 1996).

At the individual level, nutritional constraints can not only be affected by environmental conditions, but also by the ability of each bird to access the resources and use them efficiently. It might be expected that efficient foragers, for example, produce larger eggs and clutches with less asymmetry in egg size. Bolton (1991) conducted an experiment to separate the effects of egg size and parental quality on offspring fitness in the Lesser black-backed Gull. After switching clutches, to control for direct egg-size effects on chicks, he found that birds that laid large eggs were also better parents (i.e., they raised more chicks). Bolton concluded that the ability to produce large eggs represent a useful measure of parental quality (see also Mills 1979, Brouwer and Spaans 1994). Following the same argument, we would expect that individuals less constrained by nutritional resources lay more symmetric clutches. Kilpi (1995) reported that Herring Gull pairs that produced more asymmetric clutches had a lower breeding success, which suggests that clutch asymmetry reflects individual quality in this species. In Western Gulls, older individuals lay less asymmetric clutches (Sydeman and Emslie 1992).

Large skuas (genus *Catharacta*, Stercorariidae) are ecologically similar to gull species, their close relatives (Furness 1987). Skuas have a relatively inflexible clutch size, the large majority of clutches being composed by 2 eggs, with the second generally smaller. One-egg clutches are more typical of inexperienced breeders, while three egg clutches are exceptional and usually unsuccessful (Furness 1987). Clutch size is therefore unsuitable as a measure of adult quality. In this paper, we investigate if other clutch characteristics (total volume and asymmetry) are correlated with measures of individual quality of Great Skuas (*Catharacta skua*) breeding in Shetland. For the purposes of this study, "individual quality" is defined as the ability of the individual to reproduce successfully, relative to the rest of the population, as it is affected not only by permanent phenotypic traits (*e.g.*, body size), but also by age, breeding experience and temporary physiological state or body condition.

STUDY AREA AND METHODS

This study was carried out on the island of Foula, Shetland (Scotland), where a large colony of Great Skuas (more than 2,500 pairs) has been subject of a long term study (Furness 1987, Hamer and Furness 1991). As a result of intensive chick banding, in the last 4 decades, many adult breeding birds carry a monel band from which age can be determined. Since 1988, adult birds have been caught and marked with unique color-band combinations so that individuals can be followed for several years and their age determined without recapture. Most pairs studied had only one bird of known-age. When both adults were known-age, we randomly selected the age of 1 of the birds to use in the statistical analysis.

We studied the breeding parameters of this population from 1994 to 1996. In each year, study territories were visited daily until an egg was laid. This allowed accurate determination of laying dates. The first egg was then marked with permanent ink to allow subsequent recognition (only in 1995 and 1996 did we distinguish between first and second egg). After clutch completion, eggs were measured to 0.1mm using calipers and volume (in cm^3) calculated as $0.0048 \times \text{Length} \times \text{Breadth}^2$ (Coulson 1963). Most (>95%, varying with year) clutches were composed of 2 eggs, and 1 egg-clutches were excluded from this study. After hatching, chicks were banded as soon as their size allowed, and their fate was monitored until they were 30 days old. Great skua chicks fledge when about 46 days old, but few chicks die between 30 and 46 days, thus survival to 30 days was a suitable measure of fledging production. Because chicks were followed as members of broods, we could not analyze individual chick survival in relation to egg size. Hatching success and chick survival were only studied in 1994 and 1995. After a preliminary analysis showing inconsistent patterns in the relationship between adult age and clutch volume, we enlarged our data set by including data on these variables from the same study population, collected between 1988 and 1993 (Hamer and Furness 1991, Ratcliffe 1993).

Clutch asymmetry was calculated as the ratio $b\text{-egg} / a\text{-egg}$. The distribution of this variable did not differ from normal (Kolmogorov-Smirnov Test, $N=299$, n.s.). Repeatability, the intra-class correlation coefficient, was calculated following

Lessells and Boag (1987). When calculating repeatabilities we only used data from pairs of individually marked birds that were known to have remained together in both years (1995 and 1996). The number of eggs hatched per clutch and the number of chicks raised per pair can only take the values of 0, 1 and 2. These variables are therefore not continuous or normally distributed. To analyze such parameters in relation to clutch characteristics we used ordinal logistic regression. This allows the dependent variable to take more (ordinal) values than two, as in simple logistic regressions. Significance levels of these regressions were assessed using likelihood-ratio tests (G^2 statistics are presented). Means are presented with standard-errors.

RESULTS

Clutch Characteristics.

Mean clutch volume of 2 egg clutches differed among the years studied (ANOVA, $F_{2,563}=5.72$, $P<0.005$; Table 1). Post-hoc tests (Student-Newman-Keuls) revealed significant differences between 1994 and 1996, 1995 and 1996, but not between 1994 and 1995. In both 1995 and 1996, *a*-eggs were significantly longer than *b*-eggs, and also had a greater volume (Table 2). There were no differences in egg breadth in relation to laying order (Table 2). The *a*-egg had a larger volume in 66% of the clutches ($N=140$) in 1995, and in 65% of the clutches ($N=161$) in 1996. Within clutches, the volume of the first egg was a predictor of the volume of the second egg, in both 1995 (linear regression: $r^2_{140}=0.31$, $P<0.001$) and 1996 ($r^2_{161}=0.60$, $P<0.001$). Between years, Great Skua pairs were consistent in the volume of the clutches they produced (repeatability=0.72, $F_{92,93}=6.21$, $P<0.0001$). Clutch asymmetry was similar in 1995 (0.975 ± 0.005) and 1996 (0.982 ± 0.004) ($t_{298}=-1.10$, n.s.). Unlike clutch volume, clutch asymmetry was not consistent between years, for the same pairs (repeatability=0.15, $F_{63,64}=1.35$, n.s.).

Relationships with Age and Breeding Parameters.

Pooling data from 9 years (1988-1996) shows that there is a quadratic relationship between adult age and clutch volume (Figure 1). An analysis year-by-year revealed that the strength of the relationship is variable (Table 3). In 5 out of 9 years there was no significant effect of age on clutch volume, in spite of large sample sizes. We also

tested for linear effects, but these were always non-significant. Adult age had no effect on clutch asymmetry or size of *b*-egg (testing both linear and quadratic effects), either in 1995 (N=90) or 1996 (N=96).

In none of the years studied was there a significant linear or quadratic relationship between laying dates (independent variable in the regressions) and clutch volume, clutch asymmetry and volume of *b*-eggs. Sample sizes were 146, 138 and 157, respectively for 1994 (there were no data on clutch asymmetry and *b*-egg volume in this year), 1995 and 1996.

In 1994, the number of eggs hatched per pair was 1.59 ± 0.05 (N=164) and the number of chicks raised to 30 days was 0.86 ± 0.06 (N=142). In 1995, the corresponding figures were 1.60 ± 0.05 (N=198) eggs hatched and 1.13 ± 0.06 (N=178) chicks raised per pair. These 2 variables were not associated with clutch volume or clutch asymmetry (Table 4).

DISCUSSION

Previous studies in this Great Skua population described, in accordance with our results, very small (<4%), but significant, annual differences in mean egg volume. There is some evidence that these differences were an effect of varying food availability (Hamer *et al.* 1991, Ratcliffe 1993). We found that most of the variability in clutch volume (in 2 egg clutches) was due to individual (or pair) effects (repeatability was estimated as 0.72). In spite of this high individual consistency, clutch volume did not correlate with any other breeding parameter likely to reflect individual quality (laying date, number of chicks hatched and number of chicks raised). Great Skua pairs that lay early in the season usually have a higher breeding success than late layers (unpublished data). Ratcliffe (1993) found that eggs in early clutches were slightly larger than in later clutches. Such an effect was not apparent between 1994 and 1996. In Brown Skuas *Catharacta (s.) lombergi*, egg weight was not found to be affected by laying date (Williams 1980). Williams (1980) also reported that addled eggs were lighter than eggs that hatched, but we found no relationship between clutch volume and hatching success. Although large eggs can give a slight advantage to chicks, in survival probability in the first 4 days of life

(Furness 1983), fledgling production per pair was found to be independent of clutch volume in 1994 and 1995.

There is a variable relationship between adult age and clutch volume in this population. Pooling all data available, we found that clutch volume increases with age until 16.5 years, and then declines again. However, age accounts for only 2.5% of the total variance. Furthermore, in 5 out of 9 years there was no significant correlation between age and clutch volume, in spite of large sample sizes. An increase in egg volume with adult age is commonly found in birds, and might be a result of older birds having a greater foraging efficiency (Fowler 1995). The decline in size of eggs laid by old birds could result from senescence (Weimerskirch 1992), or it might be that experienced birds do not need to lay large eggs in order to breed successfully (Hamer and Furness 1991). If in years when food supply was good, poor foragers did not suffer from important nutritional constraints during egg laying, then we would expect a variable relationship between adult age and egg volume. However, this does not fit well with the fact that mean clutch volume was the same in 1994 and 1995, and smaller in 1996, while the relationship between age and egg volume could only be detected in 1994.

In Great Skuas, the first egg is, on average, longer than the second egg, but egg-breadth is independent of laying order. This is similar to what has been found in other skua species (Pietz 1987, Peter *et al.* 1990), and it is possible that egg breadth is constrained by the width of the oviduct. Within-clutch asymmetry is therefore mostly an effect of changes in egg length. Pietz (1987) reported that, in South Polar Skuas (*C. maccormicki*), clutch asymmetry was greater in a year with poor food supply than in a year with more abundant resources. However, the samples were very small (5 clutches in each year). We found no differences in clutch asymmetry between 1995 and 1996, in spite of the fact that clutch volume was significantly smaller in 1996. This is in contradiction with the evidence suggesting that, in Herring Gulls, clutch asymmetry is, compared to clutch volume, a variable more sensitive to environmental conditions (Kilpi *et al.* 1996).

We found no relationship between clutch asymmetry and any other breeding parameter or adult age. Furthermore, and in striking contrast with clutch volume, there was no individual consistency in the asymmetry of clutches laid in consecutive

years. It must be concluded that clutch asymmetry cannot be a reliable measure of individual quality of skuas in all circumstances, although the possibility remains that it might indicate quality in some years. Clutch asymmetry in the Great Skua was small when compared to most values obtained from studies in gulls (*Laridae*) and terns (*Sternidae*) (Slagsvold *et al.* 1984, Kilpi *et al.* 1996). It could be argued that our failure to find a relationship between clutch asymmetry and any other variables results from the fact that skuas only lay 2 eggs and therefore suffer from little nutritional constraints during laying. Also, food availability seemed to be high during the years studied, which was reflected in a high breeding success. Within this scenario, however, it is very difficult to see why clutch asymmetry did not disappear, if it is simply a result of nutritional constraints, as previously suggested (Pierotti and Bellrose 1986, Kilpi 1995, Kilpi *et al.* 1996). It could be that, in gulls (and maybe skuas, under more difficult conditions), more asymmetric clutches are laid when food is in short supply because this is the setting where brood reduction is more likely to be necessary, not because individuals are nutritionally constrained at laying.

The difference between our conclusions and those from a study with Herring Gulls (Kilpi 1995, Kilpi *et al.* 1996) should be regarded as an incentive for exerting caution when extrapolating results between taxonomic groups, even if relatively closely related. More studies with seabirds are necessary if clutch asymmetry is to be accepted as a variable indicating individual differences in general breeding competence or ability to cope with nutritional constraints.

REFERENCES CITED

- Bolton, M. 1991. Determinants of chick survival in the Lesser Black-backed Gull: relative contributions of egg size and parental quality. *Journal of Animal Ecology* 60: 949-960.
- Brouwer, A. and A.L. Spaans 1994. Egg predation in the Herring Gull *Larus argentatus*: why does it vary so much between nests? *Ardea* 82: 223-231.
- Coulson, J.C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proceedings of the Zoological Society of London* 140: 211-227.
- Coulson, J.C., N. Duncan and C. Thomas 1982. Changes in the breeding biology of the Herring Gull (*Larus argentatus*) induced by reduction in the size and density of the colony. *Journal of Animal Ecology* 51: 739-756.
- Fowler, G.S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. *American Zoologist* 35: 318-328.
- Furness, R.W. 1983. Variation in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *Journal of Zoology, London* 199: 101-116.
- Furness, R.W. 1987. *The Skuas*. T. and A.D. Poyser, Calton, UK.
- Hamer, K.C. and R.W. Furness 1991. Age-specific breeding performance and reproductive effort in Great Skuas *Catharacta skua*. *Journal of Animal Ecology* 60: 693-704.
- Hamer, K.C., R.W. Furness and R.W.G. Caldow 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. *Journal of Zoology, London* 223: 175-188.
- Hiom, L., M. Bolton, P. Monaghan and D. Worrall 1991. Experimental evidence for food limitation of egg production in gulls. *Ornis Scandinavica* 22: 94-97.
- Kilpi, M. 1995. Egg size asymmetry within Herring Gull clutches predicts fledging success. *Colonial Waterbirds* 18: 41-46.
- Kilpi, M., L. Hillström and K. Lindström 1996. Egg-size variation and reproductive success in the Herring Gull *Larus argentatus*: adaptive or constrained size of the last egg? *Ibis* 138: 212-217.

- Lessels, C.M. and P.T. Boag 1987. Unrepeatable repeatabilities: a common mistake. *Auk* 104: 116-121.
- Mills, J. A. 1979. Factors affecting the egg size of Red-billed Gulls *Larus novaehollandiae scopulinus*. *Ibis* 121: 53-67.
- Monaghan, P., M. Bolton and D.C. Houston 1995. Egg production constraints and the evolution of avian clutch size. *Proceedings of the Royal Society of London B*: 189-191.
- Peter, H.U., M. Kaiser and A. Gebauer 1990. Ecological and morphological investigations on South Polar Skuas (*Catharacta maccormickii*) and Brown Skuas (*Catharacta skua lombergi*) on Fildes Peninsula, King George Island, South Shetland Islands. *Zoologisches Jahrbuch Systematik* 117: 201-218.
- Pierotti, R. and C.A. Bellrose 1986. Proximate and ultimate causation of egg size and the "third chick disadvantage" in the Western Gull. *Auk* 103: 401-407.
- Pietz, P.J. 1987. Feeding and nesting ecology of sympatric South Polar and Brown Skuas. *Auk* 104: 617-627.
- Ratcliffe, N. 1993. The age-specific breeding performance of Great Skuas on Shetland. Ph.D. Dissertation, University of Glasgow.
- Reid, W.V. and P.D. Boersma 1990. Parental quality and selection on egg size in the Magellanic Penguin. *Evolution* 44: 1780-1786.
- Slagsvold, T., J. Sandvik, G. Rofstad, O. Lorentsen and M. Husby 1984. On the adaptive value of intraclutch egg-size variation in birds. *Auk* 101: 685-697.
- Smith, H.G., T.H. Ohlsson and K.J. Wettermark 1995. Adaptive significance of egg size in the European Starling: experimental tests. *Ecology* 76: 1-7.
- Sydeman, W.J. and S.D. Emslie 1992. Effect of parental age on hatching asynchrony, egg size and third-chick disadvantage in Western Gulls. *Auk* 109: 242-248.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the Wandering Albatross. *Oikos* 64: 464-473.
- Williams, A.J. 1980. Variation in weight of eggs and its effect on the breeding biology of the Great Skua. *Emu* 80: 198-202.
- Williams, T.D. 1994. Intraspecific variation in egg size and egg composition in birds: effects on offspring fitness. *Biological Reviews* 68: 35-59.

Table 1- Clutch Volumes of two-egg clutches in 1994, 1995 and 1996.

	Volume (cm ³)	SE	N
1994	167.97	0.77	158
1995	167.11	0.70	195
1996	164.64	0.72	213

Table 2- Measurements of *a* and *b* eggs in 1995 and 1996. Means are presented together with standard errors. Statistical tests are paired t-tests comparing *a* and *b* eggs within years.

	1995		1996	
	<i>a</i> -egg	<i>b</i> -egg	<i>a</i> -egg	<i>b</i> -egg
Length (cm)	7.169±0.021	6.960±0.030	7.119±0.021	6.971±0.025
	t ₁₃₉ =7.45, P<0.001		t ₁₆₀ =7.76, P<0.001	
Breadth (cm)	4.958±0.009	4.962±0.010	4.931±0.009	4.934±0.010
	t ₁₃₉ =-0.37, n.s.		t ₁₆₀ =-0.31, n.s.	
Volume (cm ³)	84.66±0.42	82.48±0.50	83.17±0.41	81.67±0.48
	t ₁₃₉ =5.00, P<0.001		t ₁₆₀ =4.97, P<0.001	

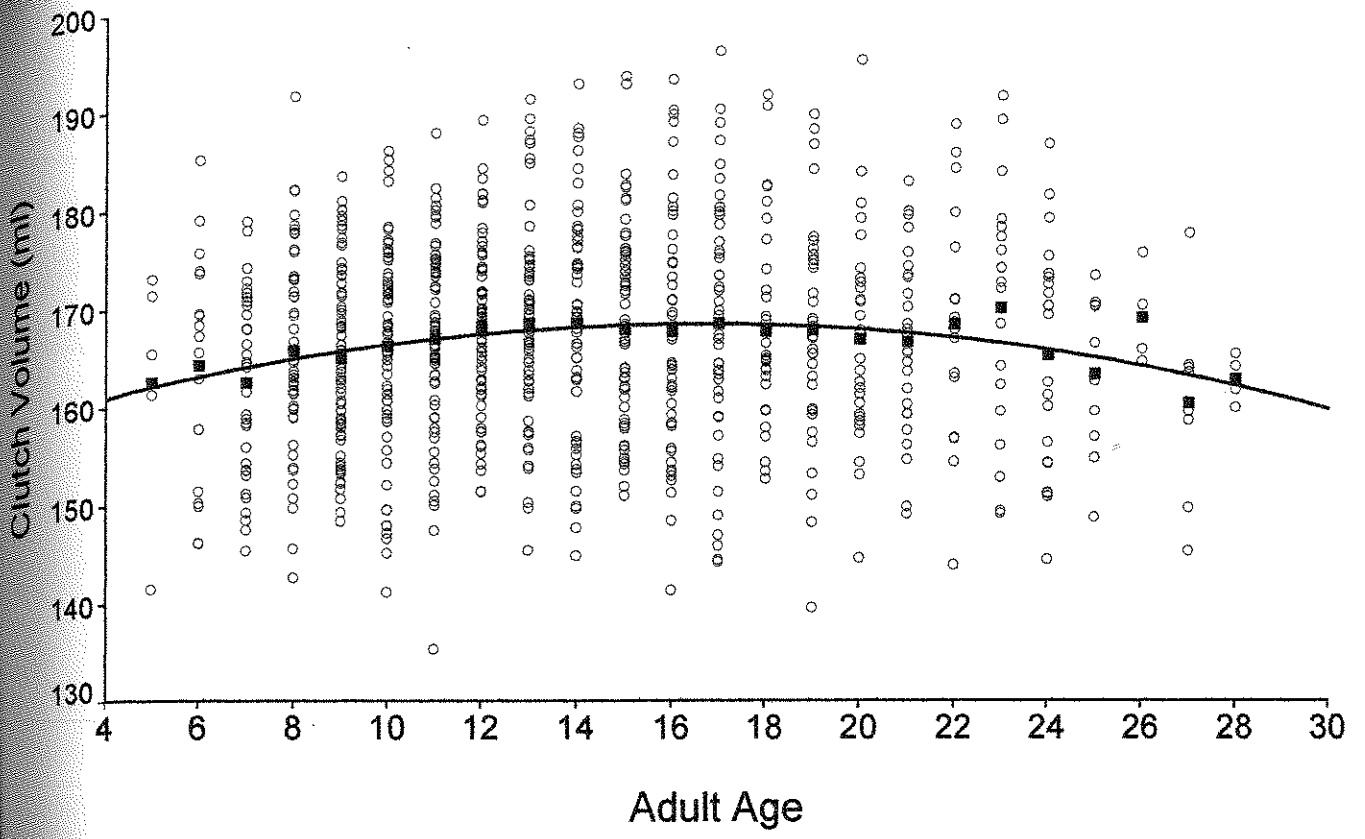
Table 3 - Results from quadratic regressions of clutch volume on adult age (V= clutch volume; A = adult age).

Year	r ²	N	p	Equation
1988	0.14	54	<0.05	$V = 142.96 + 4.33A - 0.15A^2$
1989	0.04	55	n.s.	-
1990	0.09	61	n.s.	-
1991	0.08	80	<0.05	$V = 155.14 + 0.82A - 0.01A^2$
1992	0.01	109	n.s.	-
1993	0.04	177	<0.05	$V = 154.92 + 2.04A - 0.06A^2$
1994	0.10	102	<0.01	$V = 147.62 + 3.12A - 0.10A^2$
1995	0.00	120	n.s.	-
1996	0.01	130	n.s.	-

Table 4 - Likelihood-ratio tests for ordinal logistic regressions assessing the relationship between clutch parameters and hatching and breeding success (measured as number of chicks raised to 30 days old) in 1995.

	Number eggs hatched	Number chicks raised
1994		
Clutch volume	$G^2=1.2, N=150, n.s.$	$G^2=1.4, N=126, n.s.$
1995		
Clutch volume	$G^2=0.7, N=133, n.s.$	$G^2=0.0, N=120, n.s.$
Clutch asymmetry	$G^2=3.1, N=133, n.s.$	$G^2=1.2, N=120, n.s.$

Figure 4.1. The effect of adult age on the volume of 2 egg clutches. Circles represent individual measurements and squares are means for each age. The line is described by the equation: $\text{Volume} = 154.92 + 1.65\text{Age} - 0.05\text{Age}^2$ ($r^2_{888}=0.025$). No probability value is presented as many individuals contribute with more than 1 observation (in different years).



Chapter 5

Influences of age and size on the inferred foraging ability of breeding great skuas: an experimental study.

Submitted for publication as:

Catry, P. & Furness, R.W. Influences of age and size on the inferred foraging ability of breeding great skuas *Catharacta skua*: an experimental study.

Abstract

Individual differences in the foraging ability of birds are often suggested as explanations for age-specific reproductive patterns and differences in timing of breeding. Foraging efficiency dependent on body size could also provide the basis for the evolution of reversed sexual size dimorphism in raptorial species. However, few studies have attempted to measure foraging ability in relation to adult age, time of breeding or body size. We designed an experiment to investigate individual differences in foraging ability of breeding great skuas with similar energy requirements, facing the same environmental conditions. By the means of clutch manipulations, all experimental pairs hatched chicks at the same time. Territorial attendance was then recorded for all pairs. Pairs with one chick had a higher attendance than pairs with two chicks. Attendance declined as chicks grew and food requirements increased. Attendance was not correlated with chick body condition. We concluded that pairs with two chicks displaying higher attendance achieved such levels by being more efficient foragers, and not by provisioning their chicks less well. Pairs with older males had a higher attendance than pairs with younger males. Female age and inferred foraging ability did not correlate. However, older females were less likely to leave their chicks unattended. The results show that age-related differences in the foraging ability of adult long-lived birds clearly exist, and may be responsible for age-specific breeding patterns such as the advancement of laying date with age. Pairs with large birds of either sex had a smaller number of double absences from the territory. This could reflect the greater ability of large birds to fast while their partners forage. The absence of a relationship between male size and attendance questions the validity of the assumption that small males are better foragers, a premise on which several theories on reversed sexual size dimorphism have been built. We suggest that the apparent link between large female size and high attendance could be a result of large females being better competitors for high quality males. This hypothesis was supported by the finding that female size was positively correlated with male age.

Introduction

Individual differences in foraging efficiency are often suggested as an explanation for the age-specific breeding patterns found in most species of birds (Curio 1983). Furthermore, they could help to explain part of the remaining variability found in the "quality" of breeding individuals once age has been accounted for (e.g. Weimerskirch 1990). Differences in foraging efficiency, mediated by body size, are also the basis of several theories that attempt to explain the evolution of reversed sexual size dimorphism in certain groups of birds (Mueller 1990). Although several aspects of breeding performance that could be affected by foraging have been shown to correlate with age (e.g. Hamer and Furness 1991a), and less frequently with size (Hakkarainen and Korpimäki 1991), foraging efficiency itself has rarely been assessed in relation to such parameters. This is probably a consequence of the difficulties in measuring foraging efficiency directly. Some authors have used the variability in chick growth (Ainley and Schlatter 1972) or territorial attendance of adults as indicative of differences in individual foraging ability (Røskoft et al. 1983, Ratcliffe 1993). However, these studies failed to take into account seasonal variation in food availability. If, for example, older birds lay earlier in the season (as found in most studies), then they could exhibit higher attendance or provisioning rates during chick rearing simply because they were facing more benign environmental conditions, in comparison with birds laying later. In a study where timing of breeding was experimentally standardised, no correlation was found between adult age and the amount of time spent foraging (Reid 1988).

Four main hypotheses have been presented to account for the improvement of breeding performance with age in birds (Curio 1983, Forslund and Pärt 1995): (1) constraint hypothesis - young birds are inexperienced and need to learn various skills before they become competent, (2) selection hypothesis - good quality birds are both efficient breeders and have high survival rates, age specific breeding patterns being the result of the progressive disappearance of poor phenotypes from the population, (3) delayed breeding hypothesis - higher quality birds start breeding at older ages and therefore old birds are, on average, more successful than young ones, (4) restraint hypothesis - old birds are more successful because they make a greater investment in the current breeding attempt, a response to their reduced residual reproductive value.

These hypotheses are not mutually exclusive, and evidence suggests that all four factors may explain part of the reported variation in breeding parameters, at least in some populations and at some times (Forslund and Pärt 1995, Fowler 1995, Martin 1995). If foraging skills are important in shaping age-specific reproduction patterns, then the first three hypotheses predict that foraging ability should improve with age in a cross-sectional analysis. While many studies have shown that foraging skills change with age of immature birds and differ between immatures and adults (Marchetti and Price 1989, Wunderle 1991), very few researchers have reported age-specific patterns of foraging efficiency in breeding adults (but see Jansen 1990 and Desrochers 1992 for studies with passerines), and none, to the best of our knowledge, in long-lived birds like seabirds.

A very large number of hypotheses (See Mueller 1986, 1990 for reviews) have been put forward to explain the occurrence of reversed sexual size dimorphism (R.S.D.) in raptors (Accipitriformes, Falconiformes and Strigiformes) and other birds with a raptorial lifestyle, including skuas (Stercorariidae). Most tests of these theories have been theoretical or based on broad interspecific comparisons, and it is clear that results have produced little agreement (Lundberg 1986, Mueller 1990, Ydenberg and Forbes 1991, Paton et al. 1994). Few researchers attempt to document contemporary selective pressures acting on body size within study populations (e.g. Marti 1990, Hakkarainen and Korpimäki 1991), although this could prove to be a powerful test for many of the hypotheses, even in systems at equilibrium (Hedrick and Temeles 1989). All theories predict a correlation between breeding performance and adult size in at least one of the sexes. It is highly unlikely that post-fledging and overwinter survival are independent of body size (Promislow et al. 1992, Owens and Bennett 1994), hence selection pressures at different times should counterbalance each other, and be different from zero (Ydenberg and Forbes 1991).

In this paper we use our observations on attendance patterns by both sexes to test hypotheses that relate size to foraging efficiency and sex role partitioning during breeding. It is not our aim to present a comprehensive review of the hypotheses for the evolution of R.S.D., but only to test empirically some specific predictions. Most theories predict that smaller males should be more efficient foragers, because of lower energy consumption and/or because of increased agility in flight (e.g.

Andersson and Norberg 1981, Safina 1984, Jönsson and Alerstam 1990, Hakkarainen and Korpimäki 1991). We therefore predict that pairs with smaller males (and to a lesser extent females) should need less time foraging to meet the energetic requirements of the family (two adults and two chicks). Some authors have suggested that large individuals are more effective in deterring predators and, after some initial sex role differentiation, females specialised in being good nest guardians (Storer 1966, Andersson and Norberg 1981). We predict that, during chick rearing, in pairs with large females (or large dimorphism) males should do a greater proportion of the total foraging. This pattern is also predicted by a different theory, namely that female dominance excludes males from incubation, brooding and chick guarding and forces them to forage for the family (Cade 1960 quoted in Smith 1982).

In this paper we report the results of an experiment designed to be particularly sensitive to hypothetical age and size-related differences in foraging ability of a long lived seabird, the great skua *Catharacta skua* Brünnich. We assumed that territorial absences reflected time spent foraging (see below for discussion of the validity of the assumption), and studied attendance of birds of known-age and size during late incubation and chick rearing. We standardised food requirements and environmental conditions faced by the birds by experimentally switching clutches so that all study pairs hatched chicks at the same time. Also, we controlled for possible variation in breeding experience and pair bond duration by only including individuals with previous breeding experience that had retained the partnerships from the year before this experiment.

Methods

Rationale: inferring foraging efficiency.

Efficiency (E) is the ratio of benefit (B) to cost (C) (e.g. Stephens and Krebs 1986): $E=B/C$. It follows that if we can have B constant, C is inversely proportional to E. B is usually defined as energy gained, and it is frequently assumed that birds try to maximise this. Under what conditions can benefits be constant? If we have pairs of birds that have roughly the same energy requirements to maintain body condition, and are feeding broods with a similar number of chicks of similar sizes, under the same environmental conditions, then energy requirements should be similar for all

pairs. After meeting these requirements, without allowing brood reduction or deterioration in chick body condition, in order to maximise efficiency, birds are left with the option of minimising costs (C), since B is already maximised. This approach was followed by Bryant and Westerterp (1982) when comparing the foraging efficiency of individual house martins *Delichon urbica*. What currency should be used to measure C? Energy expenditure is the most obvious candidate, but not necessarily the only one (Stephens and Krebs 1986). It could be argued that, for breeding great skuas, time spent foraging is the most important measure. This is because chicks are usually lost not as a result of starvation (insufficient energy), but as a result of predation when parents leave them alone to go foraging (insufficient time)(Hamer, Furness and Caldow 1991, Ratcliffe 1993). In any case, it seems likely that time and energy spent foraging are highly correlated. If some birds spend more energy per unit of time when foraging (for example, because they are less efficient flyers), then they will need more time foraging to meet those requirements. In this case, time and energy spent will not be linearly correlated, but a strong positive correlation would still be expected. In conclusion, when comparing two pairs with the same energy requirements that completely succeed in meeting those requirements (they have the same energy gain $B_1=B_2$) it follows (from $E=B/C$) that foraging costs (C) and foraging efficiency (E) are always inversely related (for example, if $C_1>C_2$, then $E_1<E_2$ is always true). If a time currency is used, then the proportion of time spent resting (one minus the proportion of time spent foraging) directly reflects foraging efficiency (the same argument can be applied to several pairs).

One potential problem remains, with the experimental protocol, when we test the effect of individual characteristics (for example, adult age) on inferred foraging efficiency. This can be caused by our selection procedure when trying to obtain a group of birds that meet the standardised energy requirements (i.e. birds that do not compromise chick growth or survival by reducing the energy gains - B). If we eliminate birds from the analysis that lose their chicks because they are poor foragers, and there are more chicks lost in some adult age classes than in others, then we artificially reduce the variability between different age-classes. If, however, there is not a strong effect of age (or other variable under test) on chick survival, during the experiment, this problem will be negligible. Adult traits, like age, do not have a

measurable effect on chick survival under all environmental circumstances. Age-specific differences in reproduction are more evident when food supply is low (Hamer and Furness 1991a, Sydemann et al. 1991, Ratcliffe 1993).

Study site and general methods.

This study was carried out in Foula, a small island west of Shetland where a large colony (ca 2500 pairs) of great skuas has been under study for the last two decades (Furness 1984, Hamer and Furness 1991a). Many adult birds have been trapped over the last few years and individually marked with unique combinations of colour rings. Birds wearing British Trust for Ornithology rings could be aged accurately if first ringed as chicks. From 1994 to 1996, adults were sexed by observation of copulation and courtship feeding. During these years birds were trapped for measurement of wing chord (to the nearest mm), tarsus and head plus bill length (to the nearest 0.1 of a mm.). All measurements were taken by the same field worker (P.C.). These measurements were used in a Principal Component Analysis, based on a correlation matrix, and PC1 scores were used as an index of body size (Rising and Somers 1989). To avoid distortions caused by sexual differences in body shape (Hamer and Furness 1991b), separate PCAs were performed for males and females.

Study territories were visited daily until the first egg was laid. After clutch completion, eggs were measured (length and breadth) to the nearest 0.1mm.

Experimental Procedures

Seventy two breeding pairs were selected for experimental treatment in 1996. Selection criteria were such as to have an acceptable sample of birds of known-sex, age and/or size in a small area that would allow rapid checks several times a day (see below). All but three birds (not known-age) could be recognised by colour rings or plumage marks and were recorded as breeding in the study plot in 1995. All partnerships were known to have remained unchanged from 1995 to 1996 (except for three pairs, where partnership fate was unknown). All study pairs had laid two-egg clutches.

To obtain synchronised hatching of the study pairs, one week before the estimated modal hatching date of the whole colony (12 June) we switched eggs of

known laying date between experimental nests and nests outside the study plot. This was performed in such a way that all *a*-chicks of experimental pairs hatched between 10 and 14 June, 90.3% of those between the 11 and the 13 June (original laying dates of the *a*-eggs on the study plot ranged between 9 and 26 May). *b*-chicks hatched between 1 and 48 hours after *a*-chicks. Infertile eggs could be identified just before hatching time and were replaced by pipping eggs. After this manipulation, experimental hatching date did not correlate with original laying date ($r_{72}=0.21$, $P=0.08$), male age ($r_{32}=0.21$, $P=0.26$), female age ($r_{31}=-0.01$, $P=0.98$), male size ($r_{50}=-0.26$, $P=0.07$) or female size ($r_{52}=0.22$, $P=0.12$). Any chicks found dead within 24 hours of hatching were replaced by newly hatched chicks, and these were immediately adopted in all cases.

Adult territorial attendance was monitored from three days before hatching of the first chicks until chicks were 31 days old. Territorial attendance was recorded by walking around study territories and noting which birds were present (study birds never flew away as a response to observer approach). One to three observations were made each day, between 8.30h and 20.30h, local time. Observation periods were always separated by at least three hours, and lasted less than one hour each. All territories were visited during each patrol, and a total of 90 observations were made for each territory. No checks were carried out between 12.30h and 17.00h, the time of the day when off-duty birds often went to bathe in the island lochs. Breeding great skuas are never seen resting in or around the island outside their territories, except when they go bathing. Time spent bathing by breeding birds (a few minutes per day; S. Bearhop, pers. comm. and pers. obs.) is trivial when compared to time spent on foraging trips that typically last several hours. Therefore, it is assumed that virtually all the time birds were absent from their territories was used for foraging. This is supported empirically by observations that attendance is lower in pairs with experimentally enlarged broods, and in years with lower sandeel *Ammodytes marinus* abundance (Furness and Hislop 1981, Furness 1987), as well as by our results (see below).

After chicks hatched, we marked the tip of one or two nails, using different combinations of toes, to allow individual chick recognition until the age of ringing. Chick survival was followed by checking territories when chicks were 10, 20 and 31

days old. If one chick was not recorded, we searched the area twice more in the following days until the chick was found or we were confident that it had disappeared. We used chick survival until 31 days old as a measure of breeding success (great skua chicks normally fledge when they are around 46 days old; Furness 1987). Several chicks moved territories and were adopted by neighbouring breeding birds. A naturally high adoption rate in this population (own observations) was probably exacerbated by the fact that many neighbouring broods were constituted by chicks of the same age. In the estimation of chick survival rate, we assumed that chicks that moved in the first 10 days of life (3 cases) did so accidentally and were excluded from the analysis (attendance was high during this stage, no predation was recorded, and it is extremely unlikely that any chicks would be starving). Chicks that moved after 10 days old (2 cases) might have done so as a response to food shortage (Hébert 1988), and therefore their parents were classified as having lost those chicks. In three cases, chicks regularly hid in neighbouring territories, but we were unsure as to which adults fed them, and consequently these pairs were excluded from the study thereafter. Pairs that reared 3 chicks were excluded from the analysis. Three adult birds (two females and one male) disappeared during the course of the experiment and were never seen again (presumed dead). These were also excluded from the analysis from the time they disappeared.

At the age of 20 days, chicks were measured (tarsus length) and weighed to the nearest 10 g.

Analysis

For the purposes of analysis, we divided the study into 3 intervals: Period 1, from 3 days before hatching until half of the a-chicks were 10 days old (42 attendance checks); Period 2, from 11 to 20 days old (28 attendance checks); Period 3, from 21 to 31 days old (20 attendance checks). This division of the study is a consequence of the fact that we only searched for chicks at the end of each of those time intervals (see above). More frequent checks could have resulted in excessive disturbance. All correlations of attendance with parental attributes included only pairs feeding two chicks. Pairs were excluded from the analysis of attendance from the beginning of the

time interval in which they lost or adopted one chick. Two pairs that had three chicks by the end of the first period (due to adoption) were only included in the analysis related to periods 2 and 3 (after removal of the extra chick). This is the cause for some apparent inconsistencies in the number of degrees of freedom in the analysis, when sample size is larger for the third period than for the three periods combined. For each test of the association between variables, we performed correlations using data from the three periods pooled (only pairs that raised two chicks to the end of the experiment) and from each one of the periods separately, to increase sample sizes. Sometimes, samples were too small to test the relationship in individual periods (for example, there were very few double absences from territory in each period, and therefore we only tested the relationship between bird attributes and double absences in the pooled data set).

The proportion of total foraging time undertaken by the male within the pair was estimated by the expression: (number of male absences) / (number of male absences + number of female absences). This statistic was only calculated for pairs that maintained their two chicks alive until the end of the study.

Chick body condition, corrected for size, was calculated as the residual from a linear regression of weight on tarsus length. To analyse chick condition in relation to parental attributes we used the mean condition of *a* and *b* chicks.

Only 3 pairs lost both chicks before they were 31 days old. These were pooled with pairs that lost one chick and compared them with pairs that raised two chicks. The effect of the variables of interest was assessed by the use of logistic regressions. Significance was assessed using likelihood-ratio tests. The logistic regression coefficient (*b*) is presented together with the test statistics.

All variables were tested for normality using the Kolmogorov-Smirnov test. All tests are two-tailed. Means are presented together with standard deviations.

Results

General patterns of attendance.

Attendance (mean number of adults per territory) of the study birds decreased from Period 1 to Period 2 (from $x = 1.44 \pm 0.12$ to $x = 1.29 \pm 0.14$; paired t-test, $t = 8.01$, d.f.=47, $P < 0.001$), and again from Period 2 to Period 3 (from $x = 1.32 \pm 0.14$ to $x =$

1.16 \pm 0.18; $t = 6.30$, d.f.=37, $P < 0.001$). In Period 2, pairs with only one chick had a higher attendance ($x = 1.43 \pm 0.14$, $n=10$) than pairs with two chicks ($x = 1.29 \pm 0.14$, $n=50$; $t = 2.81$, d.f. = 58, $P < 0.01$). The same significant difference was found in Period 3 (one chick, $x = 1.27 \pm 0.16$, $n=15$; two chicks, $x = 1.16 \pm 0.18$, $n=38$; $t=2.16$, d.f.=51, $P < 0.05$). There were too few pairs with single chicks to test this relationship in the first period of the experiment.

The proportion of total foraging time undertaken by the male was $61 \pm 10\%$ ($n=36$) (all periods pooled). Males made a greater contribution than females to total foraging time in 31 of 36 pairs (the difference between the sexes is significant; $\chi^2=16.89$, $P < 0.0001$). To compare relative male foraging time between different periods, we pooled all observations (ignoring pair effects) because sample sizes per pair were small. The proportion of the total time foraging performed by males decreased from 63.8% ($n=1627$) in Period 1, to 57.1% ($n=1125$) in Period 2 and 55.5% ($n=967$) in Period 3.

Age, attendance and breeding parameters.

Male and female ages in the small sample of known-age pairs were not correlated ($r_{12}=0.30$, $P=0.35$). Male age was positively correlated with mean attendance when considering the entire duration of the experiment ($r_{14}=0.65$, $P=0.011$; Fig. 1). The relationship was significant in Periods 2 and 3, but not 1 (Fig. 1). In Period 3, a non-linear model provided a significantly better fit than a linear equation ($F_{1,14}=6.92$, $P < 0.025$; Zar 1984). Female age was not correlated with attendance, either in the pooled data set ($r_{16}=0.14$, $P=0.59$), or in any of the three periods (Period 1: $r_{26}=-0.16$; Period 2: $r_{22}=0.07$; Period 3: $r_{17}=0.21$, all n.s.). The number of double absences from the territory during the whole study was negatively correlated with female age (Spearman $r_{16}=-0.50$, $P < 0.05$), and a similar but non significant trend was found in relation to male age (Spearman $r_{14}=-0.41$, n.s.).

Female age was associated with laying date ($r_{31}=-0.38$, $P < 0.05$), as was male age ($r_{32}=-0.37$, $P < 0.05$). Attendance (all periods pooled) of pairs that raised two chicks to 31 days seemed to be an even better predictor of laying date ($r_{37}=-0.52$, $P=0.001$; Fig. 2). Attendance in Period 1 was correlated with laying date ($r_{60}=-0.40$, $P=0.001$), even though it appeared to be independent of male and female ages (see

above). Laying date was also correlated with attendance in Period 2 ($r_{49}=-0.32$, $P<0.05$) and in Period 3 ($r_{39}=-0.41$, $P<0.01$). In a multiple regression, with male age and attendance (all periods pooled) as independent variables, only attendance remained a statistically significant ($P<0.005$) predictor of laying date. There were not enough pairs with known-age partners to test male and female ages and attendance simultaneously. Neither attendance nor adult ages showed any relationship with clutch volume.

There were no differences in body condition at 20 days between *a*, *b* and *single* chicks (ANOVA, $F_{2,103} = 0.21$, n.s.). Mean chick condition per pair was not affected by adult attendance in Periods 1 and 2 ($r_{48}=-0.11$, n.s.), suggesting that pairs with high attendance were providing their chicks with the same amount of food as pairs expending more time foraging. Mean chick condition was not correlated with male age ($r_{22}=-0.06$, n.s.), female age ($r_{21}=-0.29$, n.s.) or laying date ($r_{50}=-0.08$, n.s.).

Laying date did not affect the probability of both chicks surviving to 31 days (logistic regression: $G^2=0.14$, $b=-0.03$, $n=51$, n.s.), though birds that had laid later were more likely to have left their chicks unattended (Spearman correlation between number of double absences in the whole study and laying date: $r_{37}=0.35$, $P<0.05$). Adult age did not significantly affect the probability of raising two chicks successfully (males: $G^2=1.94$, $b=0.14$, $n=23$, n.s.; females $G^2=2.54$, $b=-0.18$, $n=21$, n.s.).

Adult size, attendance and breeding success.

Contrary to theoretical predictions, male size showed no negative correlation with attendance ($r_{22}=0.23$, $P=0.34$; Fig. 3). This result was unchanged when the analysis was performed period by period, allowing larger sample sizes (Table 1). By contrast, female size showed a significant positive association with attendance on the pooled data set ($r_{29}=0.46$, $P=0.012$, Fig. 4), although this trend was only significant during Periods 2 and 3 (Table 1).

Large birds are expected to be more resistant to fasting, and we predicted that single large birds on the territory would have a greater ability to wait until their partners arrived from the sea, before they left to forage. This would result in pairs with large birds having less double absences from the territory. This prediction held:

male size was negatively correlated with the number of double absences on the territory (Spearman $r_{22}=-0.50$, $P=0.018$) and the same applied to females ($r_{29}=-0.43$, $P=0.021$). Chick survival was not affected by male size (logistic regression: $G^2=0.01$, $b=-0.03$, $n=35$, n.s.) or female size ($G^2=1.17$, $b=-0.28$, $n=36$, n.s.). Adult size and chick condition were not correlated (males: $r_{31}=-0.07$, n.s.; females $r_{34}=-0.19$, n.s.).

Large females did not induce their partners to make a greater contribution to overall foraging effort. Neither female size ($r_{29}=-0.25$, n.s.) nor the degree of pair dimorphism (female size - male size) was correlated with the proportion of time spent foraging by the male ($r_{18}=0.13$, n.s.).

Relationships between age and size.

To investigate whether there was any relationship between age and adult size, we included in the following analysis data from the large sample of birds trapped on Foula from 1994 to 1996 and measured by P.C. There was no relationship between adult age and body size, either for males ($r_{41}=0.16$, n.s.) or for females ($r_{46}=0.16$, n.s.). Because female size was unexpectedly correlated with total attendance, we decided to investigate if this could be a consequence of large females being mated with older males. Indeed, female size and male age within pairs were correlated ($r_{50}=0.38$, $P<0.01$; Fig. 5).

Discussion

Attendance and time spent foraging

The assumption that time spent outside the territory by breeding great skuas is an accurate reflection of time spent foraging (see Methods) was supported by the finding that pairs feeding one chick had a higher territorial attendance than pairs with two chicks. This idea is further supported by the general decrease in attendance as chicks grew older and required more food. A possible seasonal decline in food availability (Furness and Hislop 1981) may also have contributed to the increase in foraging effort. The inferred smaller contribution by females to chick provisioning, increasing throughout the season, is in accordance with typical patterns of sex role partitioning in skuas (Furness 1987), and in raptors (Newton 1979). Alternative explanations for the significance of attendance levels, like investment in chick

protection from predation, do not conform with the fact that pairs with one chick had higher attendance than pairs with two chicks. It also seems unreasonable to suggest that some adults would not try to maximise their attendance levels, and rest at sea instead of the territory, leaving their chicks exposed to risk of predation.

Inferring foraging efficiency.

To infer foraging ability from attendance levels, we needed a group of birds with the same energy gain or benefit (B) in the period used in the analysis (see rationale of the experiment). This sample was provided by those pairs that did not lose chicks, and therefore had constant energy requirements (feeding two adults and two chicks). Benefit would not be constant if chick body condition deteriorated in some pairs but not in others. However, chick condition was independent of the variables under study: attendance, age and adult body size.

It could be that older adult birds were making a greater reproductive investment by increasing attendance at the expense of their own body reserves. If this was the case, benefits (B) would not be constant in relation to age. We have no data to test this hypothesis. However, in this scenario, attendance would be expected to show little or no increase with age amongst young birds (Forslund and Pärt 1995). This is exactly opposite to our results, the largest increase in attendance with age was found amongst younger birds.

The second condition to be met, to allow us to infer foraging efficiency from attendance patterns, is such that pairs selected for the analysis (pairs with constant B) must be an unbiased representation of all pairs, in relation to the traits of interest (age and body size). This condition was fulfilled, as adult age and size did not influence chick survival in any detectable way. Note that the absence of a relationship between adult age and chick survival is not an unreasonable result. Adult age and fledging production in this population are correlated in some years, but not in others. This is not a consequence of changes in sample size, but is probably related to varying food availability (Hamer and Furness 1991a, Ratcliffe 1993). In this study, younger adults left their chicks alone more often than older birds, but a strong random component in the occurrence of predation prevented this to have a measurable effect on the relationship between adult age and chick survival.

We conclude that the experiment was successful in providing a representative pool of pairs where gains or benefits from foraging were constant. Therefore, we can infer foraging efficiency from the attendance levels of those pairs.

Age, foraging ability and breeding parameters.

Pairs with older males had a higher attendance than pairs with younger males, and we regard this as strong evidence that older males were better foragers. The strength and shape of the relationship between age and attendance changed as the season progressed and overall attendance decreased, but there is some evidence for the existence of a reduction of improvement as age increases (Fig. 1d, but see also Fig. 1c). More importantly, variance in attendance did not seem to decrease markedly with increasing age (Fig. 1), which implies that the observed patterns could be a result of learning foraging skills. However, a contribution of selection factors cannot be excluded. It should be stressed that all known-age birds in this study had some breeding experience, and that the youngest male was seven years old. It seems remarkable that these long-lived seabirds could still be improving their foraging skills during their breeding lives. We believe that age-specific differences in foraging ability had never before been shown to exist in long-lived breeding birds.

Female age and attendance were not correlated. This may be because females make a relatively smaller contribution than males to the total foraging effort of the pair and that tests were based on small samples. In addition, all the tests relating attendance to age and laying date are likely to be conservative. This is because early layers (old birds) had a much longer incubation period (up to 2.5 times longer) than the latest breeders, as a result of our clutch manipulations. Increased incubation costs could have had a negative impact on adult body condition and performance during chick rearing (Heaney and Monaghan 1995). It seems unlikely that the pattern of age-related variation in foraging skills differs in some fundamental way between the two sexes, but this question cannot be resolved. That pairs with older females left their chicks unattended less often suggests that other skills besides foraging could be improving with experience. Leaving chicks unattended can be very costly because the risk of cannibalism is high in great skuas (Hamer et al. 1991). It might pay for females to rely on body reserves, wait a little longer for their partner to return, and

try to recover later if feeding opportunities improve. The alternative explanation that older females have better body reserves seems unlikely because no relationship was found between female condition and age in this population (Hamer and Furness 1991a).

Individual differences in adult quality (genetic, age related or others) are commonly believed to influence the timing of breeding, with higher quality individuals normally laying earlier (e.g. Perdeck and Cavé 1992). Early breeding is advantageous because chicks that fledge sooner tend to have higher first-year survival, and many populations face a decline in food availability during chick rearing (Daan et al. 1986). Food supplementation studies in a wide range of species have shown that birds which would otherwise breed later in the season are willing to advance laying date to a limited extent if provided with the necessary resources, but naturally early layers are little affected by experimental treatments (Schultz 1991). Although experiments succeeded in reducing the total variance in laying dates of many populations, synchronisation was far from perfect, suggesting that other factors besides food availability and body condition determine laying dates (Schultz 1991). In the case of gulls and great skuas, food supplementation experiments have produced no detectable changes in laying dates (Bolton et al. 1992, Ratcliffe 1993). In this context, it is interesting to note that inferred foraging ability was strongly correlated with laying date in our study, and in fact, was a much a better predictor of laying date than male or female ages alone. Note also that while attendance was measured with an error (sampling error) and, in addition, after laying had occurred, adult age was accurately determined. This suggests that the decision of when to lay by female great skuas could be mediated by the ability to gather food resources, even if they are *not* nutritionally constrained at the time of laying.

Body size and pair dimorphism effects on attendance.

Several theories of reversed sexual size dimorphism predict that small birds should be better foragers as a result of reduced energy consumption and increased manoeuvrability in flight (Andersson and Norberg 1981, Safina 1984, Jönsson and Alerstam 1990, Hakkarainen and Korpimäki 1991). However, the only empirical evidence supporting this prediction comes from a study on Tengmalm's Owls

Aegolius funereus, where small males, in years with a low food availability, were shown to have a higher fledging production than large males (Hakkarainen and Korpimäki 1991). Great skua foraging is presumed to be energetically highly costly. Foraging trips from Foula normally take many hours and birds were seldom recorded foraging within sight of the colony. Diet was assessed by sampling regurgitates from adults and chicks during our experiment, and consisted mostly of sandeels (*Ammodytidae*) and gadids (unpublished data). Sandeels are caught by splash diving, pecking from the sea surface and to a lesser extent by kleptoparasitising other seabirds. Most other fish were probably obtained as discards from fishing boats (Furness and Hislop 1981, Furness 1987). Kleptoparasitism and competition for discards behind fishing boats are thought to require a high degree of manoeuvrability in flight (Furness 1978, Hudson & Furness 1989). In spite of this, we found no negative correlation between male size and pair attendance at a time when males were the main providers of food. This is in accordance with Newton's (1988) conclusion that no fitness components correlated with male sparrowhawk *Accipiter nisus* body size.

Pairs with large females had a higher attendance than pairs with smaller females, contrary to the trend expected if small size was advantageous for foraging. We suggest that this correlation could be a result of larger females being paired with higher quality males. Great skua females regularly compete for males, sometimes engaging in lengthy fights that can end in injury and death of one of the birds. These fights are resolved on the ground (not in flight) and large size could clearly be important for a successful outcome. The positive correlation between female size and male age clearly supports this hypothesis. Female-female competition has been previously suggested as a selective pressure for large size in species with RSD (Olsen and Olsen 1987, Newton 1988), but Bortolotti and Iko (1992) found no correlation between female size and male condition in American kestrels *Falco sparverius*, a pattern they attributed to weak intra-sexual competition. More research will be necessary to elucidate if large female size regularly confers an advantage in competition for males in species with reversed size dimorphism.

Lundberg (1986) suggested that large incubating or brooding females should be at advantage when intervals between meals are long and unpredictable (the

“starvation hypothesis”), a situation that many raptorial birds may face regularly. Large birds have better fasting endurance and are less vulnerable to cold weather. This idea could apply to seabirds like great skuas, even during chick rearing when females do make a substantial contribution to foraging. We found a negative correlation between both female and male size and the number of times a pair left their chicks unattended. The selection pressure during the whole breeding cycle should be stronger on females, particularly in the pre-laying and incubation periods, because males do the large majority of the foraging. If large birds better resist fasting, then it is likely that they will guard their chicks more efficiently, while their partners forage.

Sex role specialisation is often suggested to be directly linked with RSD in birds. If large birds are more effective in deterring predators, then females could have evolved to become more effective nest defenders by increasing body size, leaving the males to do most foraging (Storer 1966, Andersson and Norberg 1981). Large size in females could also facilitate their dominance over the males, forcing the latter into the role of food providers (Cade 1960 quoted in Smith 1982). If these theories were correct, we could predict that in pairs with larger females, or with larger reversed size dimorphism, males should do a greater proportion of the total foraging. Our results did not support either of these hypotheses.

The adaptive significance of small male size relative to females has perhaps too often been linked to foraging efficiency, and theoretical work has been developed on this premise. However, this assumption has rarely survived the test of empirical studies like our own. Clearly, there is a need for more observational and experimental research on this subject, if our understanding of the evolution of RSD in birds is to make further progress.

References

- Ainley, D.G. and Schlatter, R.P. 1972. Chick raising ability in Adélie penguins. - *Auk* 89: 559-566.
- Andersson, M. and Norberg R.A. 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. - *Biol. J. Linn. Soc.* 15: 105-130.
- Bolton, M., Houston, D.C. and Monaghan, P. 1992. Nutritional constraints on egg formation in the lesser black-backed gull: an experimental study. - *J. Anim. Ecol.* 61: 521-532.
- Bortolotti, G.R. and Iko, W.M. 1992. Non-random pairing in American kestrels: mate choice versus intra-sexual competition. - *Anim. Behav.* 44: 811-821.
- Bryant, D.M. and Westerterp, K.R. 1982. Evidence for individual differences in foraging efficiency amongst breeding birds: a study of house martins *Delichon urbica* using the doubly labelled water technique. - *Ibis* 124: 187-192.
- Cade, T.J. 1960. Ecology of the peregrine and gyrfalcon populations in Alaska. - *Univ. Calif. Publ. Zool.* 63: 151-290.
- Curio, E. 1983. Why do young birds reproduce less well? - *Ibis* 125: 400-404.
- Daan, S., Dijkstra, C., Drent, R. and Meijer, T. 1988. Food supply and the annual timing of avian reproduction. - *Acta XIX Congressus Internationalis Ornithologici*, Ottawa.
- Desrochers, A. 1992. Age and foraging success in European blackbirds: variation between and within individuals. - *Anim. Behav.* 43: 885-894.
- Forslund, P. and Pärt, T. 1995. Age and reproduction in birds - hypotheses and tests. - *Trends Ecol. Evol.* 10: 374-378.
- Fowler, G.S. 1995. Stages of age-related reproductive success in birds: simultaneous effects of age, pair-bond duration and reproductive experience. - *Am. Zool.* 35: 318-328.
- Furness, R.W. 1978. Kleptoparasitism by great skuas (*Catharacta skua*) and Arctic skuas (*Stercorarius parasiticus*) at a Shetland seabird colony. - *Anim. Behav.* 26: 1167-1177.

- Furness, R.W. 1984. Influences of adult age and experience, nest location, clutch size and laying sequence on the breeding success of the Great Skua. - *J. Zool. (Lond.)* 202: 565-576.
- Furness, R.W. 1987. *The Skuas*. - Poyser, Calton.
- Furness, R.W. and Hislop, J.R.G. 1981. Diets and feeding ecology of great skuas *Catharacta skua* during the breeding season in Shetland. - *J. Zool. (Lond.)* 195: 1-23.
- Hamer, K.C. and Furness, R.W. 1991a. Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. - *J. Anim. Ecol.* 60: 693-704.
- Hamer, K.C. and Furness, R.W. 1991b. Sexing Great Skuas *Catharacta skua* by discriminant analysis using external measurements. - *Ringing & Migration* 12: 16-22.
- Hamer, K.C., Furness, R.W. and Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. - *J. Zool. (Lond.)* 223: 175-188.
- Hakkarainen, H. and Korpimäki, E. 1991. Reversed sexual size dimorphism in Tengmalm's owl: is small male size adaptive? - *Oikos* 61: 337-346.
- Heaney, V. and Monaghan, P. 1995. A within-clutch trade-off between egg production and rearing in birds. - *P. Roy. Soc. Lond. B Bio.* 261: 361-365.
- Hebert, P.N. 1988. Adoption behaviour by gulls: a new hypothesis. - *Ibis* 130: 216-220.
- Hedrick, A.V. and Temeles, E.J. 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. - *Trends Ecol. Evol.* 4: 136-138.
- Hudson, A.V. and Furness, R.W. 1989. The behaviour of seabirds foraging at fishing boats around Shetland. - *Ibis* 131: 225-237.
- Jansen A. 1990. Acquisition of foraging skills by Heron Island Silvereyes *Zosterops lateralis chlorocephala*. - *Ibis* 132: 95-101.
- Jönsson, P.E. and Alerstam, T. 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. - *Biol. J. Linn. Soc.* 41: 301-314.

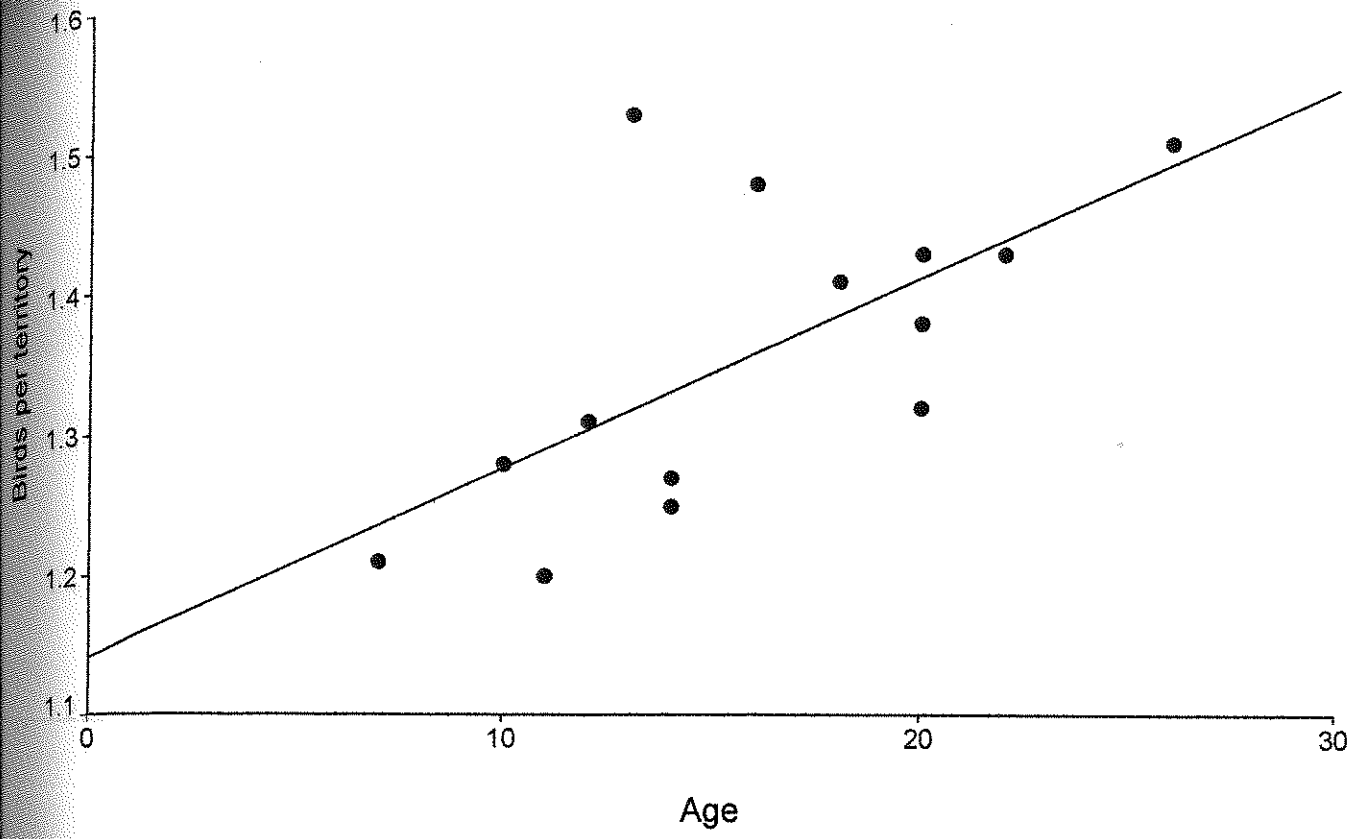
- Lundberg, A. 1986. Adaptive advantages of reversed sexual size dimorphism in European owls. - *Ornis Scand.* 17: 133-140.
- Marchetti, K. and Price, T. 1989. Differences in the foraging of juvenile and adult birds: the importance of developmental constraints. - *Biol. Rev.* 64: 51-70.
- Marti, C.D. 1990. Sex and age dimorphism in the barn owl and a test of mate choice. - *Auk* 107: 246-254.
- Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. - *Am. Zool.* 35: 340-348.
- Mueller, H.C. 1986. The evolution of reversed sexual size dimorphism in owls: an empirical analysis of possible factors. - *Wilson Bull.* 98: 387-406.
- Mueller, H.C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. - *Biol. Rev.* 65: 553-585.
- Newton, I. 1979. Population ecology of raptors. - Poyser, Berkhamsted.
- Newton, I. 1988. Individual performance in sparrowhawks: the ecology of two sexes. - *Acta XIX Congressus Internationalis Ornithologici*, Ottawa.
- Olsen, P.D. and Olsen, J. 1987. Sexual size dimorphism in raptors: intrasexual competition in the larger sex for a scarce breeding resource, the smaller sex. - *Emu* 87: 59-62.
- Owens, I.P.F. & Bennett, P.M. 1994. Mortality costs of parental care and sexual size dimorphism in birds. - *P. Roy. Soc. Lond. B Bio.* 257: 1-8.
- Paton, P.W.C.; Messina, F.J. and Griffin, C.R. 1994. A phylogenetic approach to reversed size dimorphism in diurnal raptors. - *Oikos* 71: 492-498.
- Perdeck, A.C and Cavé, A.J. 1992. Laying date in the coot: effects of age and mate choice. - *J. Anim. Ecol.* 61: 13-19.
- Promislow, D.E.L., Montgomerie, R. and Martin, T.E. 1992. Mortality costs of sexual dimorphism in birds. - *P. Roy. Soc. Lond. B Bio.* 250: 143-150.
- Ratcliffe, N. 1993. The age-specific breeding performance of great skuas on Shetland. - PhD thesis, University of Glasgow.
- Reid, W.V. 1988. Age-specific patterns of reproduction in the glaucous-winged gull: increased effort with age? - *Ecology* 69: 1454-1465.
- Rising, J.D. and Somers, K.M. 1989. The measurement of overall body size in birds. - *Auk* 106: 666-674.

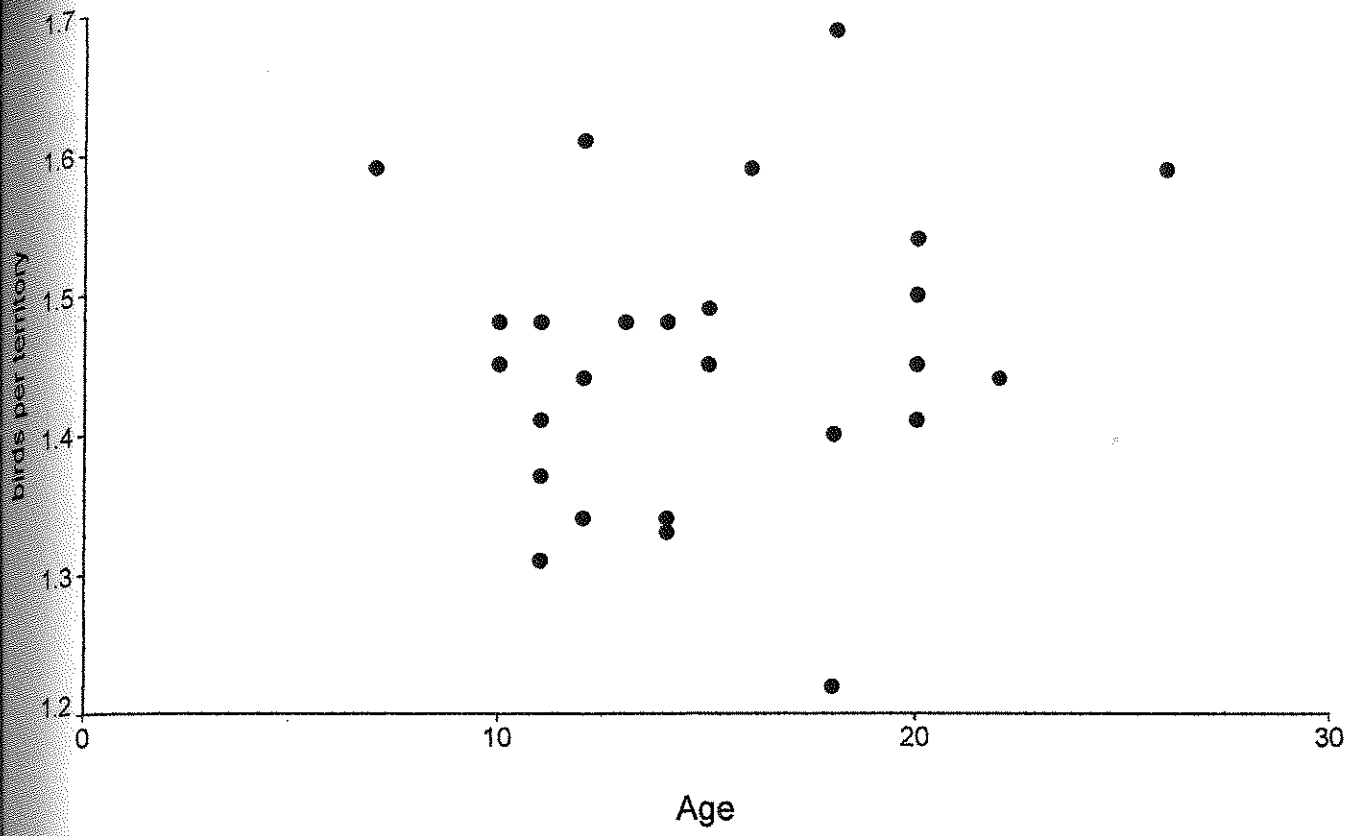
- Røskaft, E., Espmark, Y. and Järvi, T. 1983. Reproductive effort and breeding success in relation to age by the rook *Corvus frugilegus*. - *Ornis Scand.* 14: 169-174.
- Safina, C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. - *Oikos* 43: 159-164.
- Schultz, E.T. 1991. The effect of energy reserves on breeding schedule: is there a saturation point? - *Funct. Ecol.* 5: 819-824.
- Smith, S.M. 1982. Raptor "reverse" dimorphism revisited: a new hypothesis. - *Oikos* 39: 118-122.
- Stephens, D.W. and Krebs, J.R. 1986. *Foraging Theory*. - Princeton University Press.
- Storer, R.W. 1966. Sexual dimorphism and food habits in three North American accipiters. - *Auk* 83: 423-436.
- Sydemann, W.J., Penniman, J.F., Penniman, T.F., Pyle, P. and Ainley, D.G. 1991. Breeding performance in the western gull: effect of parental age, timing of breeding and year in relation to food supply. *J. Anim. Ecol.* 60: 135-149.
- Weimerskirch, H. 1990. The influence of age and experience on the breeding performance of the Antarctic fulmar *Fulmarus glacialisoides*. *J. Anim. Ecol.* 59: 867-875.
- Wunderle, J.M., Jr. 1991. Age-specific foraging efficiency in birds. - In: Power, D. (ed.), *Current Ornithology* Vol 8. Plenum Press, New York, pp. 273-324.
- Ydenberg, R.C. and Forbes, L.S. 1991. The survival-reproduction selection equilibrium and reversed size dimorphism in raptors. - *Oikos* 60: 115-120.
- Zar, J.H. 1984. *Biostatistical Analysis*. - Prentice Hall, New Jersey.

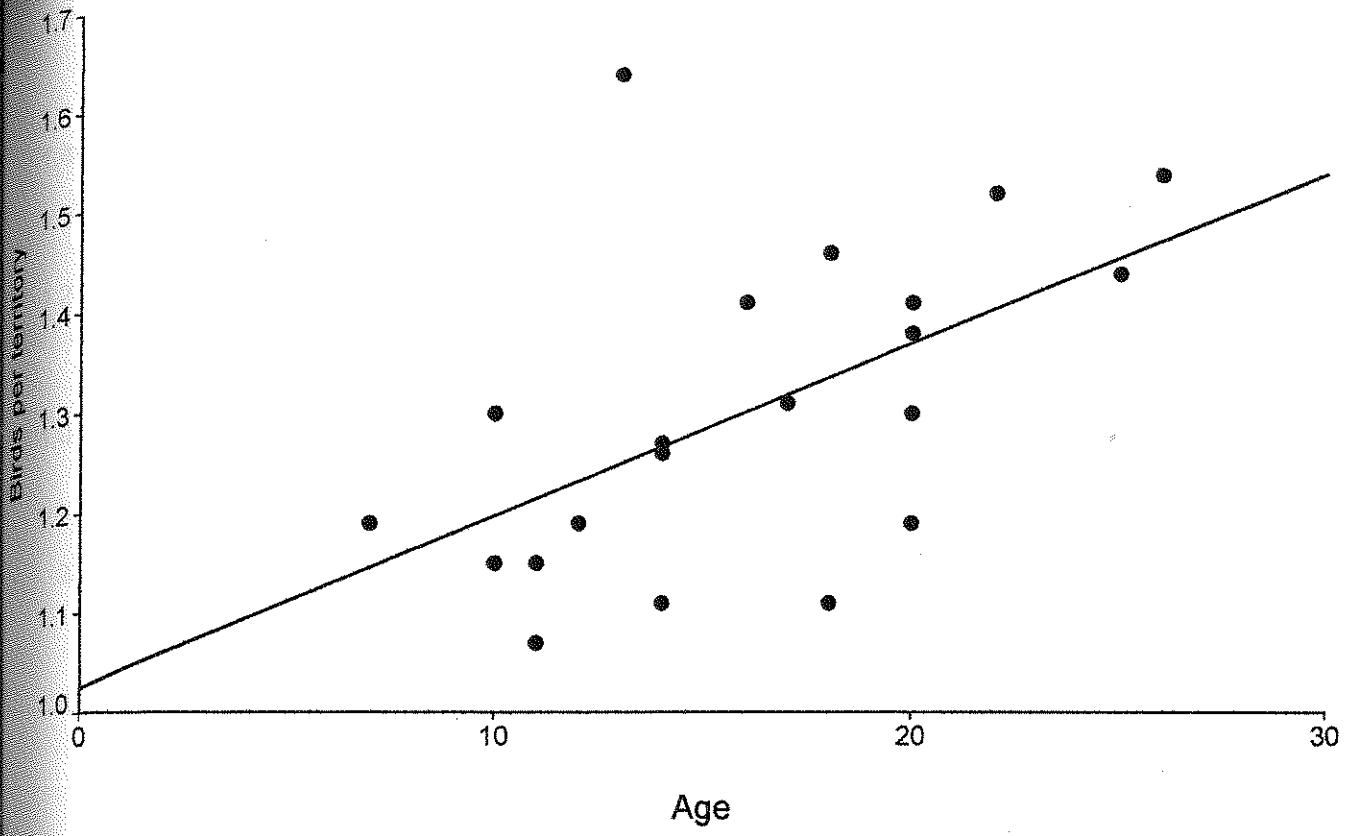
Table 1- Correlations between mean pair attendance per period and male and female size (PC1 scores).

	Period	r	n	p
Males	1	0.26	39	0.11
	2	0.15	32	0.42
	3	0.14	24	0.52
Females	1	0.03	42	0.83
	2	0.49	35	0.003
	3	0.57	30	0.001

Figure 5.1. - Relationship between male age and mean attendance per territory. A) all periods pooled ($r^2=0.42$, $P=0.011$). B) Period 1 (non significant). C) Period 2 ($r^2=0.31$, $P=0.007$). D) Period 3 ($r^2=0.50$, $P=0.002$; model is of the form $y=e^{(a+b/x)}$).







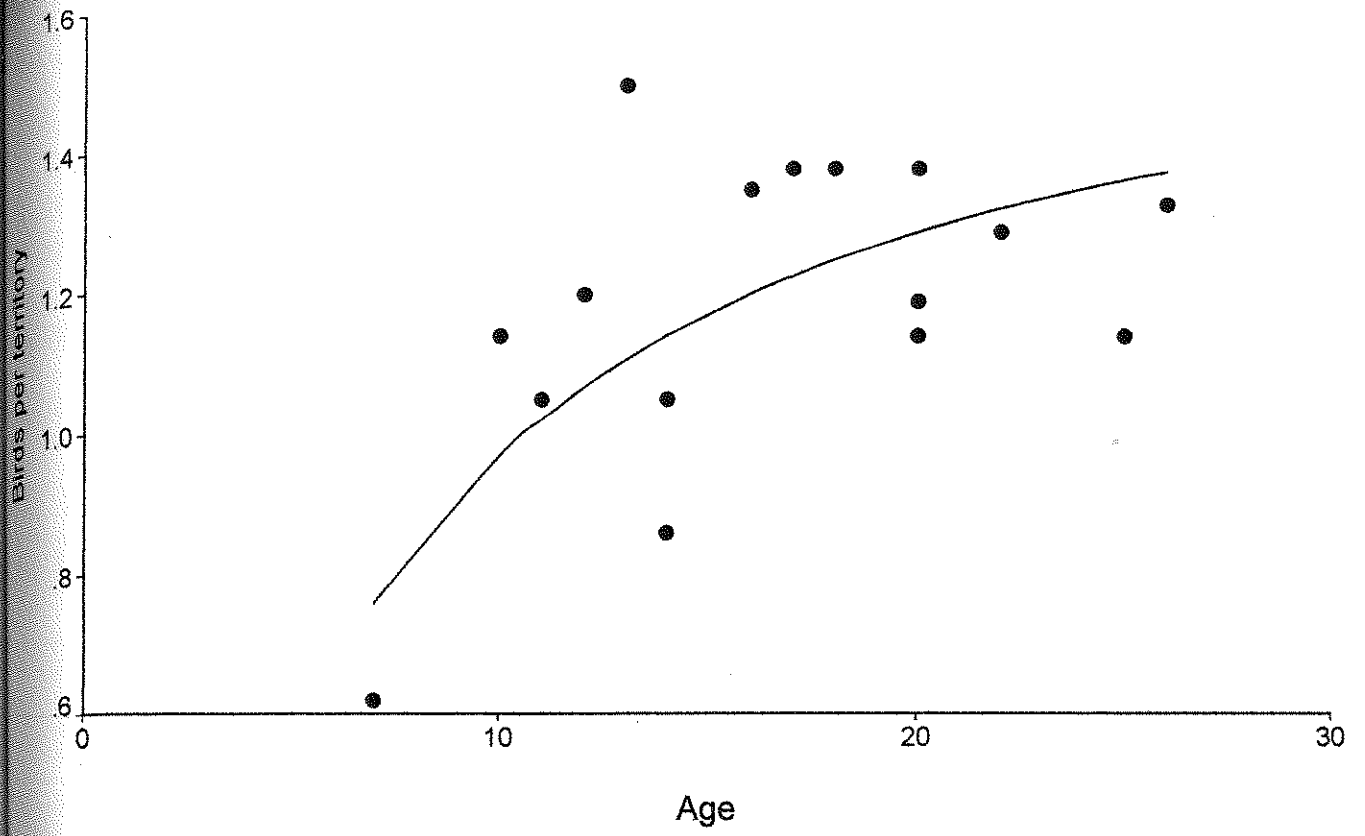


Figure 5.2.- Relationship between pair attendance during chick rearing and laying date.

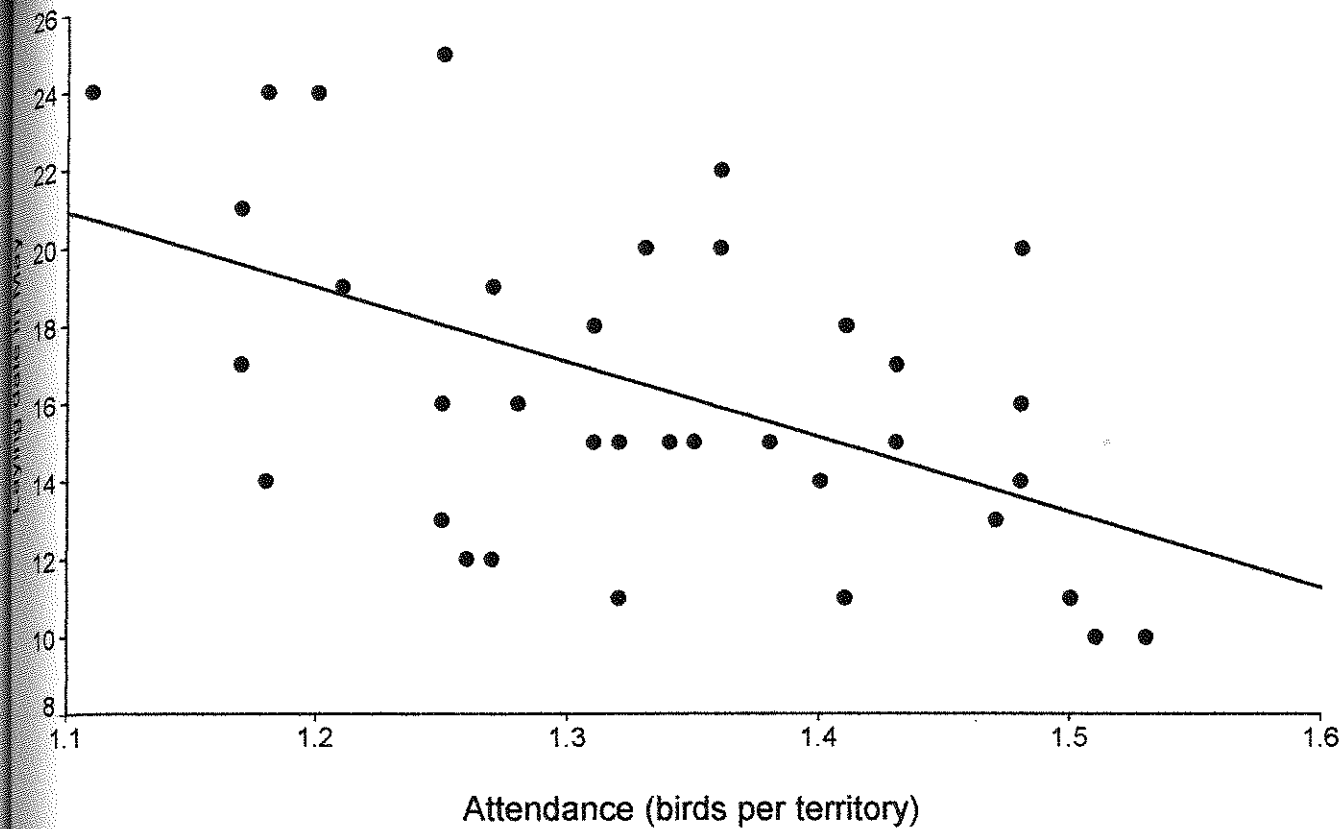


Figure 5.3. - Relationship between male body size and pair attendance during chick rearing.

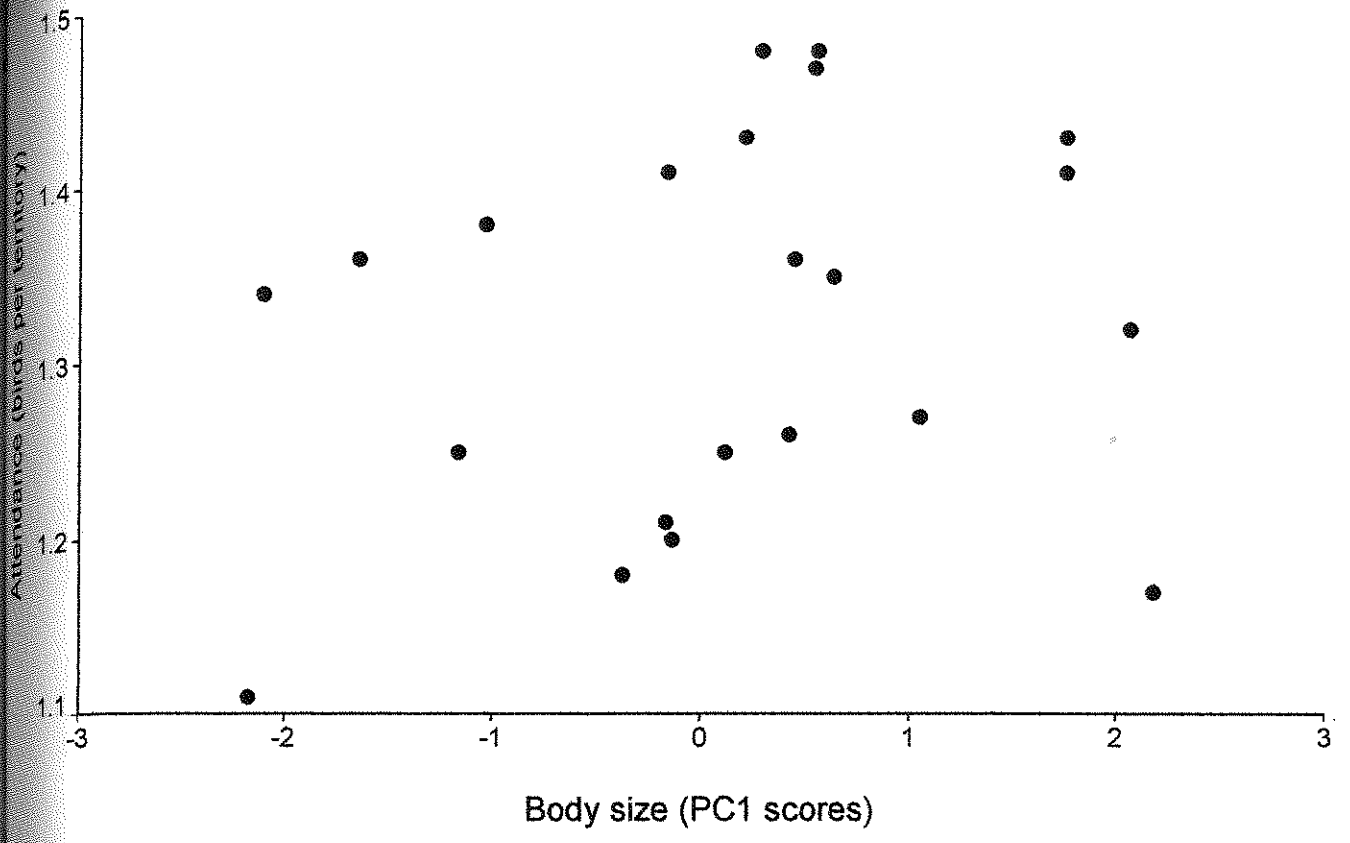


Figure 5.4.- Relationship between female body size and pair attendance during chick rearing

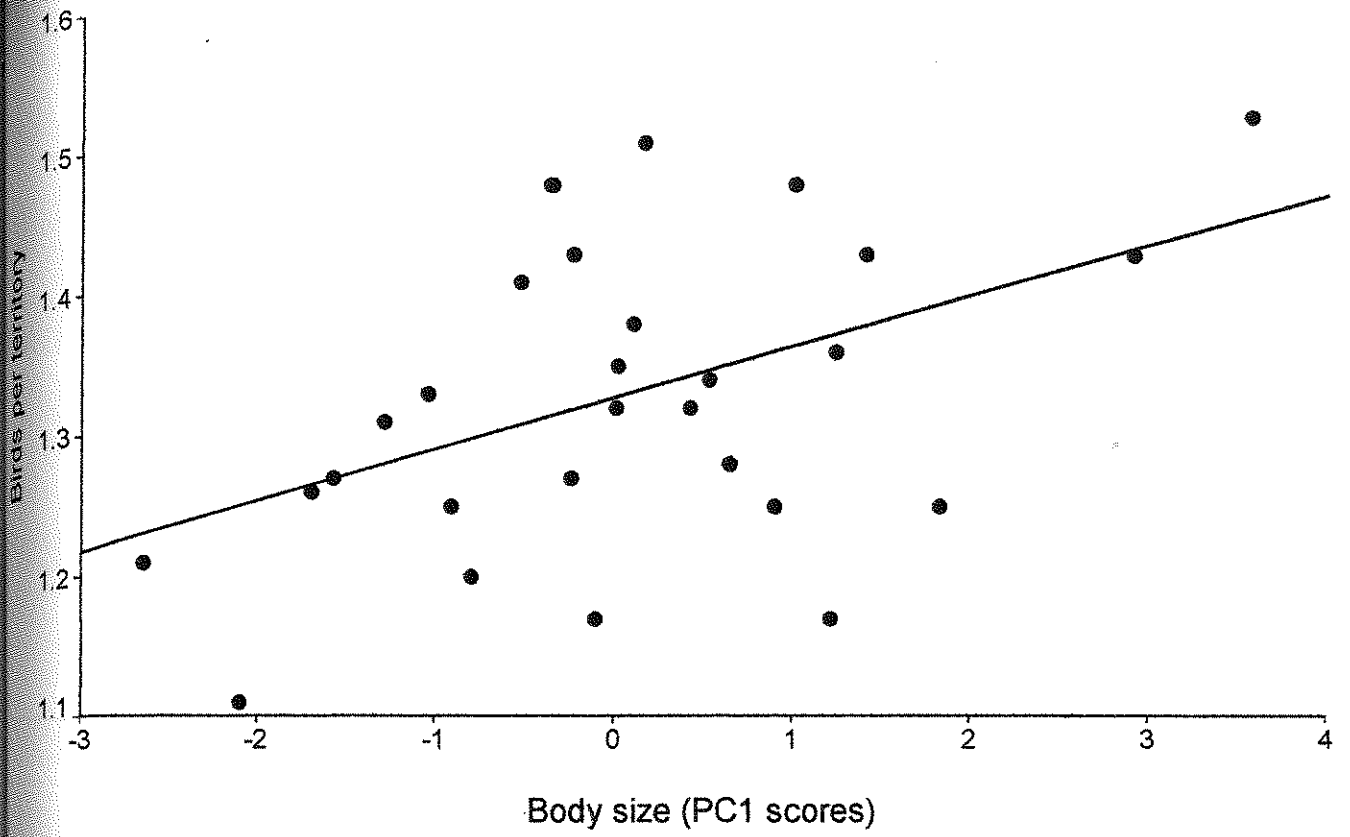
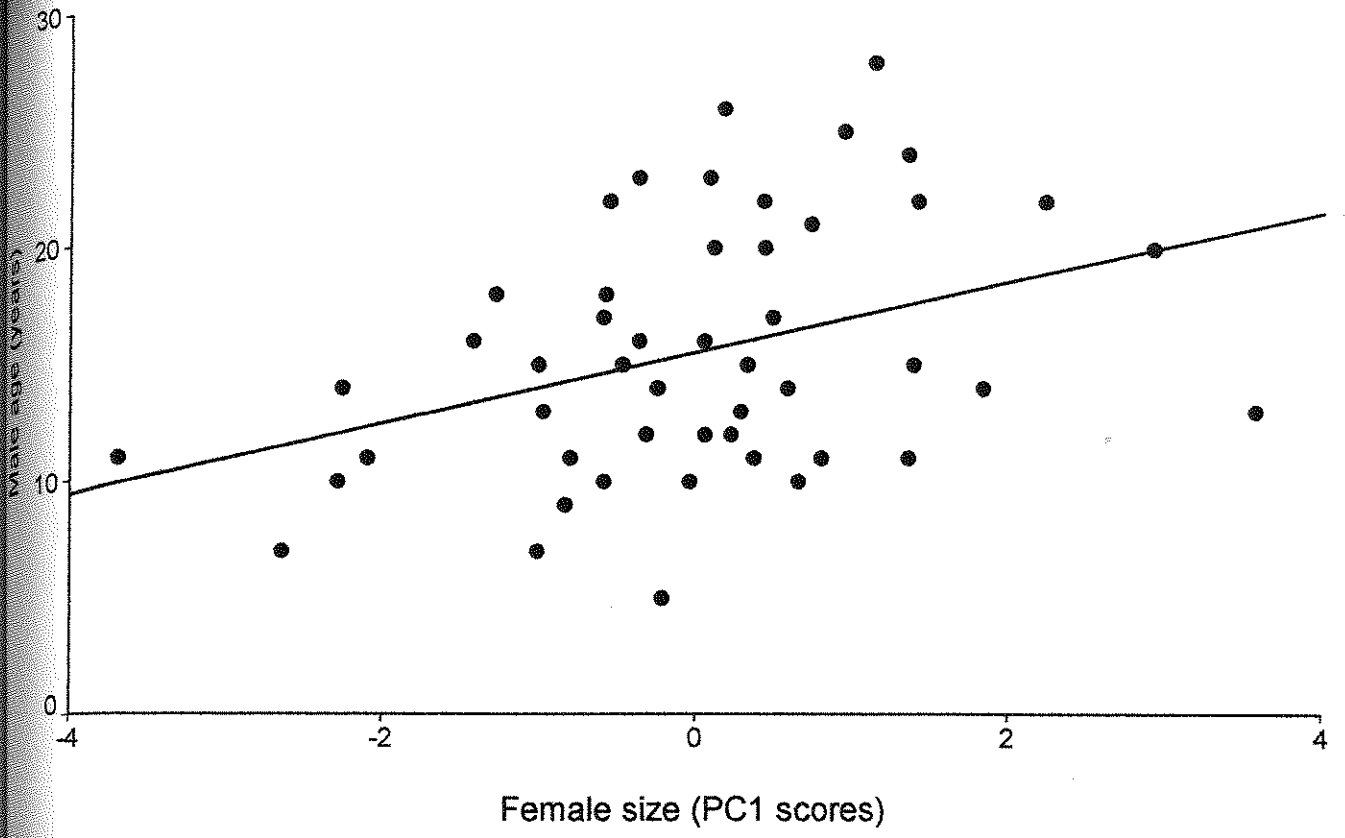


Figure 5.5. - Relationship between female body size and male age within great skua pairs breeding on Foula between 1994 and 1996.



Chapter 6

Short-lived Repeatabilities in Long-lived Birds: Implications for the Study of Individual Quality.

Submitted for publication as:

P. Catry, G. D. Ruxton, N. Ratcliffe, K. C. Hamer & R. W. Furness. Short-lived Repeatabilities in Long-lived Birds: Implications for the Study of Individual Quality.

SUMMARY

Individual variation in reproductive performance and behaviour is believed to be partly explained by differences in the quality of individuals. Excluding age effects, quality is frequently assumed to be a fixed trait. This assumption remains untested. In this paper, we test if apparent quality, expressed in individual consistency in a breeding parameter, is indeed permanent. Most studies of individual consistency in breeding traits have been relatively short-term. This may present two problems, (1) in a short-term study individuals will be consistently young or old and repeatability estimates can be affected by age-specific breeding performance or behaviour and (2) apparent individual quality might change slowly, implying that consistencies could disappear over long time intervals. We assess this possibility by studying the repeatability of laying dates of a long-lived seabird, the great skua *Catharacta skua*. We create mathematical models to evaluate the effect of age-specific timing of breeding on repeatability estimates. Simulations show that, in short-term studies (lasting 2 or 3 years), age-specific laying dates can produce spurious repeatabilities with values ranging between 0.1 and 0.2, when the value should be zero. Field observations show that individual consistency of timing of breeding is high over short time intervals, but disappears over longer periods (4 or 5 years). A comparison between field data and the simulations demonstrated that the high repeatabilities in consecutive years, and the fast subsequent declines, cannot be fully accounted by age effects. The mechanisms underlying this surprising pattern are completely unknown, but results clearly suggest that apparent individual quality is a transient attribute in these birds.

INTRODUCTION

At any given time, individuals in a population show differences in breeding performance or behaviour. Individuals that show a high general competence in breeding are often termed "high quality" individuals (e.g. Coulson 1968, Coulson & Thomas 1985). These can be identified, with a degree of uncertainty, because they display favourable values in several breeding parameters (without evidence of trade-offs between parameters), or because they have values that are consistently better, from one year to another, in comparison to "low quality" individuals. While correlations between breeding traits in one season can arise from temporary attributes (e.g. adult age and breeding experience), consistency over several years should reflect permanent characteristics of the individuals. "Quality" is therefore a term that is generally used in relation to at least two types of phenomenon with very distinct underlying causes. In this text, quality (in relation to a trait of interest) is defined as the value of the individual contribution, as is determined by genotype and by permanent environmental effects, to the measured value of a trait. It is the individuals' value for that trait when unmodified by temporary or localised circumstances. Individual quality is therefore independent of age (although quality may influence longevity). Note that quality is not exclusively determined by genotype. It can be affected by permanent environmental effects like, for example, the ones resulting from conditions experienced during growth. By this definition, individual quality should be unchanged for life. Although other authors almost never define quality explicitly, it is generally implicit that, when age effects are excluded, quality is a permanent attribute. Our main aim is to test whether individual consistency in breeding performance, resulting from quality, is indeed a permanent trait of individuals.

Individual consistency in breeding parameters or behaviour is often studied by estimating repeatabilities, the proportion of variation in a trait that can be attributed to individuals. Repeatability (r) is given by:

$$r = (V_G + V_{Eg}) / V_P, \quad (1)$$

where V_G is the genotypic variance, V_{Eg} the general environmental variance (arising from permanent or non-localised circumstances), and V_P the phenotypic variance (Falconer 1981). Repeatability is the intra-class correlation coefficient (Sokal &

Rohlf 1981) and can also be calculated from the variance components derived from a one-way analysis of variance (ANOVA) as:

$$r = S_a^2 / (S^2 + S_a^2) \quad (2)$$

where S_a^2 is the among-groups variance component and S^2 is the within-group variance component (Sokal & Rohlf 1981, Lessells & Boag 1987). Repeatability provides an upper limit to the value of heritability (Falconer 1981). Furthermore, empirical evidence suggests that repeatability often has a value that is very similar to heritability estimates derived from parent-offspring regressions (Boag & van Noordwijk 1987). Because repeatability is often much easier to estimate than heritability, it can also provide the means to evaluate the feasibility of measuring heritability (Boake 1989). The difference between repeatability and heritability values gives a measure of the importance of non-heritable genetic effects (due to dominance and epistasis) and permanent environmental effects.

Lifetime reproductive success (LRS) has been shown to have a large variance within populations (Clutton-Brock 1988, Newton 1989). It is unclear to what extent such variance is the result of random factors, and what is the role of individual quality in determining LRS. Although LRS is one of the best fitness correlates we can study, its consistency among individuals cannot be assessed because individuals only live once. Other fitness correlates are often studied in order to find how important adult quality is in determining the performance of individuals (for example, clutch size or laying date).

Most studies of individual consistency in breeding performance or behaviour are relatively short-term and many individuals are followed for a small number of years (Spurr 1975, Brooke 1978, Hatch 1990, Sydeman & Eddy 1995). This raises the question of whether the individual effects being measured are truly permanent traits. If birds are long-lived and of unknown age, repeatability values could be an artefact caused by age-specific variation in breeding performance. In a short study, individual birds will be consistently young or old. There is also the possibility that some changes in the environment (affecting phenotype) or in the physiological condition of the individuals are slow enough to allow consistencies to be detected over the short term, but not over longer periods.

In this paper, we study the effect of individual quality on laying date of a long-lived seabird, the great skua *Catharacta skua*, by the means of repeatability analysis. The evolution of timing of breeding in birds and other organisms has been a subject of much interest to evolutionary ecologists (e.g. Perrins 1970, Price, Kirkpatrick & Arnold 1988, Daan et al. 1989, Schultz 1991, 1993). It is commonly found in birds that breeding success declines seasonally. In great skuas, early hatched chicks display better growth rates (Furness 1983), and have higher survival to fledging as well as higher post-fledging survival (Catry & Furness, unpublished). This seasonal patterns have also been found in other skuas, as well as gulls, their close relatives (e.g. O'Donald 1972, 1983, Spear & Nur 1994). Many of our observations come from pairs where one or both birds are of unknown age. To control for this problem, we create mathematical models to assess the effect of the age-specific timing of breeding on repeatability estimates. The models allows us to simulate laying dates for individual great skuas followed during several years. The only deterministic factor of the models is age. The models also include an error component, with a magnitude that is estimated using data derived from field observations. This means that the models provide estimates of intra-class correlation coefficients in an age-structured population with no "true repeatabilities" (as defined in equation 1). We have two models, one where only female age affects laying date and another where both sexes make a similar contribution to the timing of breeding. After analysing the potential effect of age on repeatability estimates, we investigate whether individual influences on laying dates arise from truly permanent traits or if individual quality is subject to changes in the medium or long-term.

MATERIALS AND METHODS

Fieldwork was carried out in the island of Foula (Shetland), the largest great skua colony in the North Atlantic, with approximately 2500 breeding pairs (Furness 1987). As a result of intensive chick ringing in the last three decades, many adult breeding skuas carry rings from which their ages can be determined. From 1988, adults were caught during the breeding season and marked with unique combinations of colour-rings (Hamer & Furness 1991). Birds were sexed by observation of copulation and

courtship feeding behaviour. Between 1989 and 1996, laying dates were determined by visiting the territories daily until one egg was found in the nest. In some cases, laying dates were back-calculated from hatching time.

To correct for annual differences in the timing of breeding, laying dates were standardised by subtracting the annual mean from each individual value and then adding the overall grand mean. All analyses below were performed with this standardised variable. There were no significant differences among years in the variance of the distribution of laying dates. Statistical comparisons of intra-class correlation coefficients were performed following Zar (1984). Means are presented together with standard errors.

Simulations

Models were built based on parameters determined empirically for our study population. Age correlations in pairs and divorce rates were taken from Catry, Ratcliffe & Furness (*in press.*). Relationships between age and laying dates, and data on the age-structure of this population have also been published (Hamer & Furness 1991, Hamer, Furness & Caldow 1991). In more recent years, this original data set has been greatly enlarged. We therefore re-analysed these data to obtain better fits for the relationships of male and female ages and laying dates, and to obtain an estimate of the age-structure of the population based on as large sample as possible (age-structure in 1996). Derived equations and distributions are presented below. Sample sizes and quality of fits are presented in the Appendix.

Model 1

The first simulation begins by randomly selecting the ages of 1000 females. The age-structure of the field population in the last year of the study is well represented by the following distribution

$$\log(\text{age}) = N[1.16, 0.163] \quad (3)$$

where $\log()$ is a logarithm to the base 10, and $N[x,y]$ is a normal distribution with mean x and standard deviation y . Since there is no difference between the sexes in the

age distribution, we assume that equation (3) is a good representation of the female age structure and so assign an age to each individual by sampling randomly and independently from this distribution.

There is also a clear relationship between the ages of males and females making up a breeding pair, described by

$$\log(\text{male_age}) = 0.818 + 0.308 \log(\text{female_age}), \quad (4)$$

with the standard error on individual estimates being 0.178.

Thus to obtain the age of the male paired to a specific female, we first substitute her age into equation 4. The male age obtained is the mean male age of males paired to females of that specific age. We assume that males are distributed about this mean normally with standard deviation 0.178. Hence we sample randomly from this distribution to obtain the actual age of the male paired to a specific female. We now have 1000 pairs where the ages of both partners are known.

The relation between female age and laying date (the number of days after the first of May when the first egg is laid) is

$$\log(\text{laydate}) = 1.12 + \frac{1.58}{\text{female_age}}, \quad (5)$$

with the standard error on individual estimates being 0.107.

Similarly there is a relation between male age and laying date:

$$\log(\text{laydate}) = 1.15 + \frac{1.37}{\text{male_age}}, \quad (6)$$

with the standard error on individual estimates being 0.128.

For each pair, we calculate the predicted laying date from female age using equation 5 to obtain the mean of the normal distribution. Similarly, we use equation 6 to calculate the predicted laying date based on the age of the male bird in the

partnership. In the absence of any data on the correlation between the two estimates, we define the actual lay date for a particular pair to be the arithmetic average of the laying dates predicted on the basis of male and female ages. We thus produce the predicted laying date for each pair in the final year of the (simulated) study.

To obtain the predicted laying date of each of these pairs in the previous year, we make the assumption that we are studying 1000 females which do not die during the course of the study and which always remate if a mate is lost. In the previous year, the age of the female is simply one less than before. However, the male may have changed. We assume that the annual survival rate is 0.9 (Appendix). Even if the male survives, the pair bond may not. Hence, conditional on the survival of both individuals, we assume that the divorce rate is 0.064 (Catry, Ratcliffe & Furness *in press*). If no change in partner occurs (which we determine stochastically) then the male age is simply one less than before, if a change of mate does occur then the age of the new mate is determined using equation 4 and the same procedure as before. Having obtained the ages of both partners in each pair we calculate the laying date in the usual way.

This process can be repeated, yielding predicted laying dates for each female over a number of years. Note that very few birds of each sex reach sexual maturity before five years old (Hamer, Furness & Caldow 1991), thus we stop simulating for any given couple when either of them falls below this age. As a consequence, sample sizes in early years are smaller (see Results) than the final number of females: 1000.

In the field measurements, we do not know that it is the female that remains constant in each study pair, it may equally well be the male. We mimic this in simulations by following 500 males which never die but may acquire new partners and 500 equivalent females. Should a male loose a particular partner then the age of the replacement is calculated from

$$\log(\text{female_age}) = 0.856 + 0.261\log(\text{male_age}), \quad (7)$$

with the standard error on individual estimates being 0.154.

Model 2

Model 2 differs from model 1 in that only females determine laying dates. Again, half of the birds followed are females and half are males.

RESULTS

Simulations

In our first simulation, both sexes contributed to determine laying dates. The age-specific laying dates created an effect strong enough for us to be able to measure highly significant repeatability (r) values where there should be none (Table 1). As expected, as the time interval between measurements relative to the same individuals increased, r values decreased. With an interval of five years, the age-effect is almost non-existent and r is close to zero (Table 1). Results from simulation 2, where only females determined laying dates, are broadly similar to results from simulation 1 (Table 1).

Observed values

Taking all data available for the calculation of the repeatability of timing of breeding of great skuas in Foula, we have 954 records of laying dates, involving 278 individuals (2-8 records per individual). The repeatability value for this sample is 0.467 ($F_{277,676}=4.01$, $p<0.0001$).

To investigate if repeatability was a stable attribute in the years when the study took place, we calculated the (intra-class) correlation coefficient between laying dates of individuals in pairs of consecutive years (1989-1990, 1990-1991, etc.). The mean repeatability value was 0.525 ± 0.0610 ($n=7$, Table 2). In only one case, with a small sample size, was r non-significant (Table 2). There were significant differences between r values among pairs of years (comparing all repeatabilities from Table 1, $\chi^2_6=15.3$, $p<0.025$). No significant differences were found among pairs of consecutive years between 1991 and 1996 (the years used in comparisons below; $\chi^2_4=5.4$, n.s.).

We calculated repeatability values for paired observations in years separated by an increasing time interval (e.g. 1996-1995, 1996-1994, etc.). As the time interval

increased, repeatability decreased ($r^2=0.97$, $n=5$, $p<0.01$), approaching zero (Table 3). This pattern was significantly different from the one resulting from simulations using Model 1 (ANCOVA, $F_{1,6}=44.6$, $p<0.01$; Figure 1) and Model 2 (ANCOVA, $F_{1,6}=32.3$, $p<0.01$). We repeated the analysis using only birds known to have been breeding in 1991 that were still breeding in 1996. This restriction aims to control for the possibility that decreasing repeatabilities with increasing time intervals could be a result of a reduced variability, caused by differential mortality of phenotypes. Sample sizes are relatively small, but the same trend can be detected in the reduced data set (Table 4). Not all birds had their laying dates recorded every year and hence the discrepancies in sample sizes. There were not enough cases to calculate r for 1996-91.

DISCUSSION

Results from simulations based on realistic models of age-dependent timing of breeding show that, as expected, positive repeatabilities in laying dates can result from individual consistency in age during short-term studies. In a species like the great skua, where there is only a relatively weak influence of age on laying date, r values ranging between 0.1 and 0.2 result from age effects in studies lasting two or three years. The effect of consistency in age(-dependent laying date) disappears when the interval between measurements is greater than four years. Results are similar whether laying date is determined by one or both sexes. In short-lived species, like many passerines, it is possible that the opposite effect might be found in relatively long-term studies: age-dependent timing of breeding could create a negative repeatability (at least for individuals with greater longevity). This could also apply to long-lived birds when studying consistency of individuals that were followed for very long periods. Several studies have reported consistencies in breeding parameters of individuals of unknown age (e.g. Spurr 1975, Brooke 1978, Hatch 1990, Sydeman & Eddy 1995). Without correcting for age effects, it is impossible to determine to what extent such patterns are artefactual. It should also be noticed that, even when a study lasts for several years, the contribution of pairs or trios of observations in consecutive years, to the calculation of r , can be disproportionately large. This is because many individuals enter and exit the study populations (through emigration, death, natural

recruitment and "recruitment after capture and marking") during the study, and therefore have only a reduced number of observations contributing to the general data set.

Our results further suggest that short-term studies of individual consistency can be misleading for a second reason: consistency can decrease rapidly over longer time intervals. This effect cannot be fully explained by changes in age, and therefore cannot be corrected simply by studying individuals of known age.

The importance that these two effects can have on a repeatability estimate is illustrated by the data regarding the great skua. When we took all records available to produce a single repeatability estimate for laying dates of individuals (with data coming from an eight-year study), an r value of 0.467 was calculated. Even higher repeatability estimates were obtained when studying pairs of consecutive years (Table 2). However, when analysing pairs of observations separated by four or five years, repeatabilities dropped markedly and became non-significant. Although our samples are not large enough to convincingly demonstrate that laying dates, in the long-term, are not repeatable at all, there can be no doubt that r decreases rapidly over a relatively short time.

In this population, the best predictor of laying date of a bird in year N is laying date in year $N-1$. It is remarkable that such a strong effect dilutes rapidly with increasing time intervals. The mechanisms underlying this pattern are completely unknown. One can speculate that environmental variation may produce changes in plastic phenotypes, altering the ranking order of individual qualities in a population. Slow changes in the physiological condition or semi-permanent changes in phenotype (for example, arising from chronic diseases or long-term injury) would also affect repeatabilities over large time intervals, more so than over short periods. The influence of environmental conditions on repeatabilities is confirmed by the fact that consistency of laying dates in pairs of consecutive years varied during our study. Sydeman & Eddy (1995) also reported that in a year with scarce food resources, during an El Niño event, repeatability of laying dates of guillemots *Uria aalge* breeding in California was low (when compared to other years), and so presumably the "normal laying order" was altered by such conditions.

Individual quality is believed to be one of the most important factors affecting breeding output in some species (Coulson & Thomas 1985, Goodburn 1991). Hochachka (1993) found that, in a situation where several breeding parameters were repeatable, few correlations existed between those parameters and therefore there was little evidence for the existence of "super-parents". This calls for caution when trying to infer overall bird quality from single fitness correlates, like laying date. Our results further highlight difficulties in the use of repeatabilities when trying to assess the importance of individual variation in the outcome of breeding. Part of the problem is a conceptual one. We defined quality as reflecting permanent traits, but it may be that most traits of interest cannot be permanent in a variable environment. It is not enough to define permanent as meaning "lasting for life". Some "permanent" traits in short-lived individuals might only be "semi-permanent" in longer-lived ones. Indeed, that seems to be the case with "laying date values" for individual great skuas.

References

- Boag, P.T. & van Noordwijk, A.J. 1987. Quantitative genetics. In *Avian genetics. A population and ecological approach*. (ed. Cooke, F. & Buckley, P.A.) pp. 45-78. London: Academic Press.
- Boake, C.R.B. 1989. Repeatability: its role in evolutionary studies of mating behaviour. *Evol. Ecol.* **3**, 173-182.
- Brooke, M. de L. 1978. Some factors affecting the laying date, incubation and breeding success of the manx shearwater, *Puffinus puffinus*. *J. Anim. Ecol.* **47**, 477-495.
- Catry, P., Ratcliffe, N. & Furness, R.W. (*in press.*). Partnerships and mechanisms of divorce in the great skua *Catharacta skua*. *Anim. Behav.*
- Clutton-Brock, T.H. (ed.) 1988. *Reproductive success: studies of individual variation in contrasting breeding systems*. Chicago: University of Chicago Press.
- Coulson, J.C. 1968. Differences in the quality of birds nesting in the centre and on the edges of a colony. *Nature, Lond.* **217**, 478-479.
- Coulson, J.C. & Thomas, C. 1985. Differences in breeding performance of individual kittiwake gulls *Rissa tridactyla* (L.). In *Behavioural Ecology*. (ed. Sibly, R.M. & Smith, R.H.) Oxford: Blackwell Scientific.
- Daan, S., Dijkstra, C., Drent, R. & Meijer, T. 1989. Food supply and the annual timing of avian reproduction. *Acta XIX Congressus Internationalis Ornithologicus*, 392-407. University of Ottawa Press.
- Falconer, D.S. 1981. *Introduction to quantitative genetics*. London: Longman.
- Furness, R.W. 1983. Variations in size and growth of great skua chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *J. Zool., Lond.* **199**, 101-116.
- Furness, R.W. 1987. *The skuas*. T & AD Poyser, Calton.
- Goodburn, S.F. 1991. Territory quality or bird quality? Factors determining breeding success in the magpie *Pica pica*. *Ibis* **133**, 85-90.
- Hamer, K.C. & Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. *J. Anim. Ecol.* **60**, 693-704.

- Hamer, K.C., Furness, R.W. & Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. *J. Zool., Lond.* **223**, 175-188.
- Hatch, S.A. 1990 Individual variation in behaviour and breeding success of northern fulmars. *Auk* **107**, 750-755.
- Hochachka, W.M. 1993. Repeatable reproduction in song sparrows. *Auk* **110**, 603-613.
- Lessells, C.M. & Boag, P.T. 1987. Unrepeatable repeatabilities: a common mistake. *Auk* **104**, 116-121.
- Newton, I. (ed.) 1989. *Lifetime reproductive success in birds*. London: Academic Press.
- O'Donald, P. 1972. Sexual selections by variations in fitness at breeding time. *Nature* **237**, 349-351.
- O'Donald, P. 1983. *The Arctic skua. A study of the ecology and evolution of a seabird*. Cambridge University Press, Cambridge.
- Perrins, C.M. 1970. The timing of birds' breeding seasons. *Ibis* **112**, 242-255.
- Price, T., Kirkpatrick & Arnold, S.J. 1988. Directional selection and the evolution of breeding date in birds. *Science* **240**, 798-799.
- Schultz, E.T. 1991. The effect of energy reserves on breeding schedule: is there a saturation point? *Funct. Ecol.* **5**, 819-824.
- Schultz, E.T. 1993. The effect of birth date on fitness of female dwarf perch *Micrometrus minimus* (Perciformes: Embiotocidae). *Evolution* **47**, 520-539.
- Sokal, R.R. & Rohlf, F.J. 1981. *Biometry*. San Francisco: Freeman.
- Spear, L. & Nur, N. 1994. Brood size, hatching order and hatching date: effects on four life-history stages from hatching to recruitment in western gulls. *J. Anim. Ecol.* **63**, 283-298.
- Spurr, E.B. 1975. Breeding of the Adélie penguin *Pygoscelis adeliae* at Cape Bird. *Ibis* **117**, 324-338.
- Sydeman, W.J. & Eddy, J.O. 1995. Repeatability in laying date and its relationship to individual quality in common murre. *Condor* **97**, 1048-1052.
- Zar, J.H. 1984. *Biostatistical analysis*. New Jersey: Prentice-Hall.

Table 1. Results from two simulations to determine the effect of age-specific timing of breeding on estimates of repeatability of laying dates ("true" repeatability is zero in the model) of great skuas breeding on Foula.

(Each individual contributes with two observations, separated by the number of years defined in "interval".)

Interval (years)	Repeat. (<i>r</i>)	L.95%C.L.	U.95%C.L.	Sample size	<i>p</i>
<i>Model 1</i>					
1	0.129	0.067	0.191	982	<0.0001
2	0.150	0.088	0.211	956	<0.0001
3	0.079	0.014	0.143	911	<0.01
4	0.050	-0.017	0.117	855	0.06
5	0.017	-0.053	0.087	786	0.4
<i>Model 2</i>					
1	0.171	0.110	0.232	982	<0.0001
2	0.126	0.064	0.188	956	<0.001
3	0.149	0.085	0.212	910	0.02
4	0.065	0.002	0.131	856	0.03
5	0.007	-0.063	0.077	784	0.4

Table 2. *Repeatability analysis for laying dates of individuals in pairs of consecutive years.*

Years	Repeat. (<i>r</i>)	L.95%C.L.	U.95%C.L.	Sample size	<i>p</i>
1989-90	0.503	0.201	0.717	33	0.001
1990-91	0.203	-0.092	0.465	45	0.09
1991-92	0.466	0.239	0.645	58	0.0001
1992-93	0.657	0.507	0.770	75	<0.0001
1993-94	0.586	0.432	0.707	89	<0.0001
1994-95	0.685	0.584	0.766	135	<0.0001
1995-96	0.577	0.463	0.672	156	<0.0001

Table 3. *Repeatability analysis for laying dates of individuals in pairs of years with an increasing time interval.*

Years	Repeat. (<i>r</i>)	L.95%C.L.	U.95%C.L.	Sample size	<i>p</i>
1996-95	0.577	0.463	0.672	156	<0.0001
1996-94	0.371	0.203	0.518	116	<0.0001
1996-93	0.271	0.062	0.457	84	0.005
1996-92	0.194	-0.094	0.452	47	0.09
1996-91	0.025	-0.276	0.321	42	0.4

Table 4. *As Table 2 but with analysis restricted to birds that were known to have bred in all years between 1991 and 1996 (see text for explanation).*

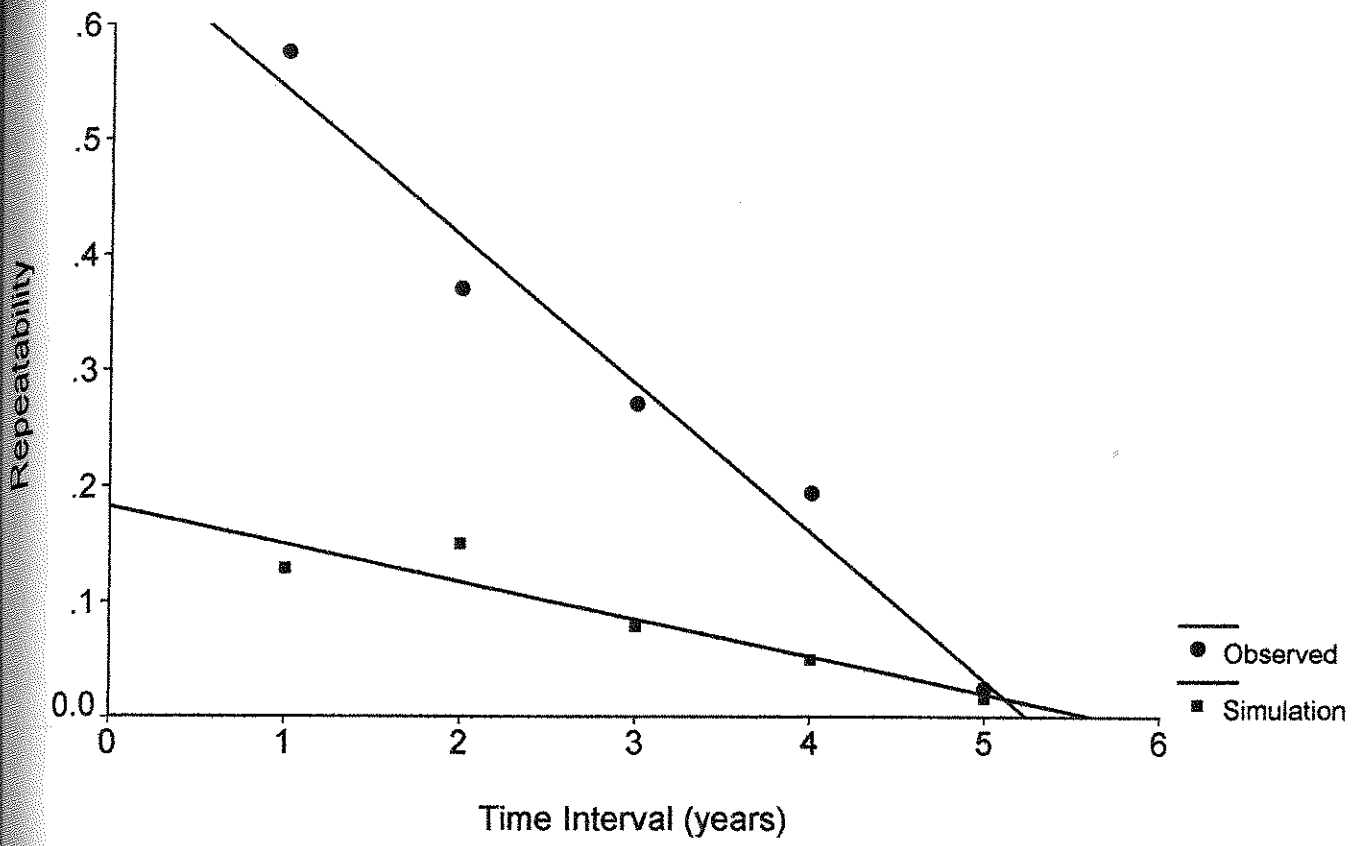
Years	Repeat. (<i>r</i>)	L.95%C.L.	U.95%C.L.	Sample size	p
1996-95	0.475	0.206	0.677	42	<0.001
1996-94	0.270	-0.067	0.552	34	0.06
1996-93	0.181	-0.166	0.487	33	0.2
1996-92	0.172	-0.197	0.499	29	0.2

Appendix - *Sample sizes and quality of fit in parameter estimation for model building.*

Equation	Sample size	r^2	p
3	200	-	-
4 and 7	50	0.08	<0.05
5	110	0.13	<0.001
6	96	0.12	<0.01

The adult survival rate is an average of four annual estimates (1992-1996), with sample sizes varying between 120 and 361 birds.

Figure 6.1. Repeatability estimates, derived from a simulation (Model 1) and from field measurements, for laying dates in pairs of years separated by an increasing time



Chapter 7

The Evolution of Reversed Sexual Size Dimorphism in Skuas: A Test of Hypotheses

Submitted for publication as:

Catry, P., Phillips, R.A. & Furness, R.W. The Evolution of Reversed Sexual Size Dimorphism in Skuas and Jaegers (Stercorariidae): A Test of Hypotheses

ABSTRACT.- Skuas and Jaegers (Stercorariidae), like other birds with a raptorial lifestyle, display reversed sexual dimorphism in size (RSD; females larger than males). This condition is commonly believed to be associated with morphology or behavioural ecology of avian predators, and numerous theoretical explanations have been presented accounting for its evolution. Most tests of these ideas have been theoretical or based on comparative analyses. This paper presents tests of specific hypotheses of RSD based on field studies of two species, the Great Skua *Catharacta skua* and the Parasitic Jaeger *Stercorarius parasiticus*, breeding in Shetland. A comparative analysis of foraging behaviour and degree of RSD within the Stercorariidae is also presented. No evidence was found supporting the popular theories that claim that RSD evolved as a result of specialised roles during breeding. Large females were not more fecund, nor were they the main defenders of the nest. Male body size did not correlate with any breeding parameter. In addition, interspecific comparisons did not support the idea that the degree of RSD is related to foraging behaviour during the breeding season (as opposed to morphology). Female dominance within pairs did not affect any breeding parameters. Support was found for theories that RSD is linked to sexual selection. Large females had an advantage when pairing with older males, which could be a result of intra-sexual competition for mates. There was assortative mating for size, indicating that small males could also have an advantage in pairing, as large males seem to be rejected by small females. Given the disparate results of several studies in the bibliography, we conclude that a large body of empirical evidence will be needed before we can draw firm conclusions about the main selective factors that act to maintain current levels of RSD in natural populations of raptorial birds.

The mechanisms behind the origins and maintenance of sexual size dimorphism in animals are, in general, poorly known (Hedrick and Temeles 1989). Several unrelated groups of birds display reversed sexual dimorphism in size (RSD; females larger than males) suggesting that this condition must have evolved independently on a number of occasions (Jehl and Murray 1986, Panton et al. 1994). Reversed size dimorphism is a common feature of some avian groups with a raptorial lifestyle, principally the diurnal birds of prey (Falconiformes), owls (Strigiformes), skuas and jaegers (Charadriiformes: family Stercorariidae) and frigatebirds (Pelecaniformes: family Fregatidae). This has led to the belief that the evolution of reversed size dimorphism is linked to the morphology or behavioural ecology of avian predators, regardless of its evolutionary origin in other taxa.

There are many hypotheses attempting to explain RSD in birds of prey (*see reviews in* Mueller and Meyer 1985, Mueller 1990). Proposed advantages of large female size include greater ability to produce eggs, incubate, protect the nest and take care of offspring (Andersson and Norberg 1981, Wheeler 1983, Lundberg 1986, Jönsson and Alerstam 1990), and superiority in intra-sexual competition for mates (Olsen and Olsen 1987, Newton 1988). It has also been suggested that small males have greater foraging efficiency (Andersson and Norberg 1981, Lundberg 1986, Jönsson and Alerstam 1990, Hakkarainen and Korpimäki 1991) or superiority in territorial contests or nuptial displays (Widén 1984, Safina 1984). Another group of hypotheses state that it is the relative asymmetry within pairs that is advantageous, not male or female size *per se*. Female dominance resulting from RSD should facilitate rapid pairing (Smith 1982) and could help females to relegate their partner to the role of food provider (Cade 1960 quoted in Smith 1982).

All the above theories predict a correlation between body size, and mating or breeding success, in at least one sex. This would be counterbalanced by differential mortality of phenotypes, since it is unlikely that the optimal size from the perspective of breeding role specialisation would be the same as that which maximises post-fledging and overwinter survival (Owens and Bennett 1994). Nonetheless, it should be possible to detect directional selective pressures on body size operating during the breeding season (Hedrick and Temeles 1989, Ydenberg and Forbes 1991).

In comparison with the vast theoretical bibliography and comparative analyses published on this subject, few studies with raptorial species have attempted to relate body size to the performance of individuals during reproduction in a single species. Several authors have looked at mating in relation to size (Newton et al. 1983, Bowman 1987, Marti 1990, Bortolotti and Iko 1992, Plumton and Lutz 1994, Hakkarainen et al. 1996) but attempts to relate breeding success and foraging efficiency to body size are scarce, and have produced mixed results (Newton 1988, Hakkarainen and Korpimäki 1991, 1995, Hakkarainen et al. 1996). Given that the adaptive values of phenotypes are likely to change in variable environments (Hakkarainen and Korpimäki 1995), and that contemporary selective pressures might be weak, a large body of empirical evidence will be needed before any firm conclusions can be extracted from this type of study.

All seven species in the family Stercorariidae display reversed sexual dimorphism in size (Furness 1996), unlike their close relatives, the Laridae (gulls). In a similar way to birds of prey, skuas and jaegers also have a pronounced division of roles between the sexes in the breeding season (Pietz 1986, Furness 1987, 1996, Phillips and Furness in press b). Males courtship feed their partners during egg formation and do most of the foraging during incubation and chick rearing. Unlike some raptors, they also carry out a substantial part of the incubation. As the season advances, females progressively increase their contribution in terms of foraging effort, and after the first days or weeks of chick rearing, they spend almost as much time gathering food as their partner. Skuas and jaegers feed mostly on fish, birds and small mammals. As a group, they are versatile in the foraging techniques they use, acting as predators, scavengers and kleptoparasites (Furness 1987, Phillips et al. 1996). Some species, such as the great skua *Catharacta skua*, have an ecological niche very similar to that of the large gulls (*Larus* spp.). One important difference between skuas and gulls is morphological. Skuas and jaegers have hooked claws, allowing them to grab birds in flight or hold them on the ground, although not to carry them (Furness 1987, 1996).

Often breeding colonially (although defending small territories), skuas and jaegers are particularly suited for tests of hypotheses of RSD. A large number of pairs can be studied simultaneously, and because in many populations there are no feeding

territories, territory quality is not usually a confounding factor when analysing mate preferences or breeding performance. The large number of conspecifics in a small area could also allow birds to be more selective in their choice of partner. This paper incorporates field observations of skuas of known size to test hypotheses related to RSD. We studied two species, one of each genus (*Catharacta* and *Stercorarius*) in the family. We also present a comparative analysis of foraging behaviour and degree of RSD within the Stercorariidae using published information. It is not our aim to present an extensive review and discussion of all current hypotheses for the evolution of RSD in raptorial birds, nor to draw any general conclusions. Instead we concentrate our efforts in trying to evaluate hypotheses for which our data allow robust tests of specific predictions.

STUDY AREA AND METHODS

Breeding data were collected in Foula, Shetland (60°08'N, 2°05'W) for Parasitic Jaegers *Stercorarius parasiticus* between 1993-1994 and for Great Skuas between 1994-1996. Territories of individually colour-ringed birds were visited daily or on alternate days early in the season and the presence of newly-laid eggs established by watching for the initiation of mobbing by the adults (or distraction behaviour in the case of Parasitic Jaegers) and then locating and checking the nest. Most females lay two eggs, usually with an interval of two-three days between each. Laying dates for nests which were not located until after clutch completion were back-dated from hatching dates of the first or only chick, assuming an incubation period of 26 days for Parasitic Jaegers and 29 days for Great Skuas.

Nests and eggs were marked, the eggs measured using vernier callipers and the volume (ml) of each egg calculated as $0.00048 \times \text{length (mm)} \times \text{breadth}^2 \text{ (mm)}$ (Coulson 1963). Hatching success and chick survival were recorded by visiting marked nests at regular intervals throughout incubation, every one to two days around hatching, and at approximately six to ten day intervals during chick-rearing. Adult skuas and jaegers show high survival and low divorce rates and consequently breeding data collected in consecutive years from the same pairs cannot be considered statistically independent. Most of the following analyses were therefore carried out separately for each year.

Large numbers of adult Parasitic Jaegers and Great Skuas were trapped, weighed and measured during the breeding season. All Great Skuas were measured by PC, and Parasitic Jaegers by RAP and RWF. Great Skuas were sexed by observation of courtship feeding and copulations. Arctic Skuas were sexed by observation, by a hierarchical combination of two discriminant functions based on the prior probabilities of group membership (with an accuracy of over 91% for birds classified), by dissection of birds found dead at the colony or by association with a partner sexed by one of these methods (Phillips and Furness in press a). For each sex and each species, separate principal component analyses (Rising and Somers 1989) incorporating the morphometric variables wing-length, tarsus-length and head plus bill-length were used to produce single factor scores (PC1 scores) representing body size. Body mass was not used as a measure of size because it also reflects body condition. Ages of breeding Great Skuas that had been marked as chicks were determined from their British Trust for Ornithology ring numbers.

Male and female morphometric and composite body size indices were compared within pairs to test whether there was any evidence for assortative mating with respect to size. Differences in structural size among males or females or in the degree of dimorphism within the pair may be important determinants of breeding phenology and success. Correlations were performed between laying date and clutch volume (two-egg clutches only), and adult size and dimorphism indices (female value minus male value). Number of chicks fledged was compared with adult size and pair dimorphism using ordinal logistic regression. This allows the dependent variable to take more (ordinal) values than two, as in simple logistic regressions. Significance levels of these regressions were assessed using likelihood-ratio tests (G^2 statistics are presented). The taxonomic classification of the Stercorariidae used here follows Furness (1996).

Relative aggressiveness of male and female Great Skuas in marked pairs was assessed at four stages of the season, and only when both partners were present. For each pair we recorded (1) which of the birds was the more aggressive (i.e. came closer to the observer while swooping) and (2) whether or not each of the birds hit the observer in the head. The intensity of mobbing and distraction behaviour of male and female Parasitic Jaegers was compared in the population as a whole at two stages

of the season, again only when both birds in a pair were present. Distraction intensity was scored on a scale of 0 to 5; 0 - no distraction, 1 - walking away, possibly bowing, wings not extended, 2 - standing with outstretched wings, or occasional flapping, 3 - walking with outstretched wings or occasional flapping, 4 - walking or standing with vigorous flapping, 5 - running with vigorous flapping. In addition, the total number of swoops by marked Parasitic Jaegers was recorded while the observer walked from the edge of the territory, stood at the nest for 60 s and then walked off-territory.

RESULTS

Female and male sizes in the study populations

Few studies documenting the degree of size dimorphism in skuas have been based on large sample sizes. Measurements of live Great Skuas and Parasitic Jaegers are presented in Table 1. Incubation weights were compared for Parasitic Jaegers since females, but not males, show a stepwise reduction in mass shortly after chick-hatching (Phillips and Furness *in press b*). Females were significantly larger than males in all traits studied.

Assortative mating in relation to size

Female and male body size were correlated within pairs of Parasitic Jaegers ($r_{65} = 0.28$, $P = 0.027$). A similar positive correlation was found in Great Skua pairs ($r_{61} = 0.22$, $P = 0.085$), but failed to reach statistical significance.

In Great Skuas, female size and male age were positively correlated (Spearman $r_{50} = 0.38$, $P < 0.01$) and so were male size and female age (Spearman $r_{44} = 0.32$, $P < 0.05$). Not enough known-age birds were available to test these relationships in Parasitic Jaegers. Adult age and size are not correlated in individual jaegers and skuas (Phillips and Furness *in press a*, and unpubl. data for Great Skuas). Birds providing data for the tests above were between 5 and 29 years old.

Body size, dimorphism and breeding performance

In both species, neither female nor male size affected laying date during this study (Tables 2 and 3). Only female body size had an effect on clutch volume, large birds laying larger eggs, although the trend in Great Skuas was not significant in every year

(Table 3). In general, body size had no effect on hatching or breeding success (Table 4). In 1995 only, there was a negative correlation between body size of male Great Skuas and number of chicks hatched. However, this did not result in higher overall productivity by small males in that year (Table 4). We repeated all the analyses above using univariate measurements (wing, tarsus and head plus bill length) instead of PC1 scores, but the results were unchanged.

Pairs of Parasitic Jaegers with a large dimorphism index tended to lay early in the season in 1993 (Table 5). Apart from this effect, the degree of size dimorphism within pairs did not correlate with laying date, clutch volume, hatching success or fledging production, in either of the two populations studied (Tables 4 and 5). Again, the same results were obtained when we repeated the analyses using univariate morphometric measurements instead of composite body size indices.

Male and female roles in nest defence

We compared male and female Great Skua aggression levels at four different stages of the nesting cycle (Table 6). There were more pairs where the male rather than the female was the more aggressive nest-defender, than vice versa (females more aggressive), in periods 1 ($\chi^2_1 = 59.1$, $P < 0.0001$), 2 ($\chi^2_1 = 12.2$, $P < 0.001$) and 3 ($\chi^2_1 = 6.2$, $P < 0.05$). The difference was not significant in period 4 ($\chi^2_1 = 2.7$). There was a progressive increase in relative aggression levels of female great skuas from egg-laying to hatching ($\chi^2_6 = 40.7$, $P < 0.001$; Table 6). In a sample of 14 pairs, females increased absolute aggression levels (from not-swooping to swooping) from period 1 to period 2 in seven cases, while males did so only once (comparing the sexes: Fisher exact test, $P = 0.02$). There were no significant differences between male and female Parasitic Jaegers in the intensity of distraction behaviour or in the number of swoops at the observer at either stage of the season (Table 7).

RSD and foraging behaviour in different species of the Stercorariidae

It is well known that in diurnal raptors, species that usually catch relatively agile prey (e.g. birds versus mammals or mammals versus insects) show greater size dimorphism (Newton 1979). It is often suggested that RSD has evolved because small size confers the advantage of greater aerial agility to the sex (males)

undertaking the bulk of food provisioning for their mate and brood. Small size would also lower seasonal energy consumption for birds spending long periods in flight. In table 8 we present a brief summary of the foraging techniques and degree of RSD in different skua and jaeger species. We could not find enough suitable data for the Chilean Skua *Catharacta chilensis* or the Falkland Skua *C. antarctica antarctica*. It appears that skua and jaeger species exhibit a similar level of wing and weight dimorphism in spite of marked differences in foraging style (Table 8).

DISCUSSION

Are large females better parents?

It has been suggested that in species with RSD, larger females should be more fecund, or should deliver better parental care to offspring (Andersson and Nörberg 1981, Wheller 1983, Lundberg 1986). Skuas and jaegers have an inflexible clutch size, with the vast majority of clutches being composed of two eggs (Furness 1987, 1996). We report that large females lay slightly larger eggs. However, this effect is also found in species with normal size dimorphism (e.g. Loman 1984) and cannot, by itself, explain RSD in the Stercorariidae. In addition, egg size had only a weak effect on Great Skua chick survival in the first four days after hatching (Furness 1983). Other possible advantages of large female size include a greater ability to store energy reserves, carry the breeding increment and protect developing ovarian follicles. Larger females could also be better at incubation, either because of an improved ability to physically cover the eggs or a higher resistance to fasting while their partners forage. If these hypotheses were correct, large females would lay early in the season, produce eggs of high quality and/or incubate more efficiently, with a resultant increase in hatching success. However, we found no significant relationships between female size and laying date or hatching success in either Great Skuas or Parasitic Jaegers, despite large sample sizes.

It has also been suggested that large female raptors are more efficient at dismembering prey and feeding it to young. This hypothesis cannot apply to the Stercorariidae because, when prey needs to be dismembered, both birds in a pair work together to tear it apart (Andersson 1971).

In both raptors and skuas and jaegers, females spend more time on territory during incubation and chick-rearing than males, and it could be that large female size has evolved because of their crucial role in the defence of eggs and young. This hypothesis assumes that large birds are more efficient when deterring predators. We found that within pairs of Great Skuas, it is the males that generally display the more aggressive behaviour towards humans, coming closer to the observer (and hitting more often as a result) during threatening attacks. There were no differences in the level of nest defence (either mobbing or distraction behaviour) by male and female Parasitic Jaegers. Female Great Skuas were particularly unaggressive towards humans immediately after egg laying, at the time when they undertake the greater share of incubation duties. Studies with diurnal and nocturnal raptors also showed the male to be the primary defender of the nest (Wiklund and Stigh 1983, Andersson and Wiklund 1987). It is quite possible that small size and increased manoeuvrability of males allows them to come closer and strike potential predators with a reduced risk from a potential retaliatory attack (Andersson and Wiklund 1987). Although large female size could still be favourable when intimidating or fighting some kinds of predators, it seems unlikely that this advantage would be large enough to compensate for their generally lower level of aggressiveness.

Are small males better parents?

In skuas, jaegers and raptors, males undertake the bulk of food provisioning for their partner and brood. Several authors have suggested that small males should be better parents because they are more efficient at foraging (e.g. Andersson and Norberg 1981). This increased efficiency would result either from greater agility in flight due to a low wing-loading, reduced energy consumption during flight and lower requirements for self maintenance, or a combination of these. Two studies, with Tengmalm's Owls *Aegolius funereus* and Euroasian Kestrels *Falco tinnunculus*, have provided some evidence that small males are indeed better at supplying prey (Hakkarainen and Korpimäki 1991, Hakkarainen et al. 1996). We found no relationship between male body size and breeding success in Great Skuas and Parasitic Jaegers in either of two years. If small males were better food providers in these species, we could also expect male size to influence clutch volume and laying

date, since females rely heavily on male courtship feeding in the two weeks before laying, when egg formation takes place (Furness 1987, Catry and Furness in press). However, no relationship was found between male body size and clutch volume or timing of breeding in the study populations despite very large samples. Similarly, Newton (1988) failed to find an effect of male body size on any fitness components of European Sparrowhawks *Accipiter nisus*, a species with particularly pronounced RSD.

Inter-specific comparisons provide another line of evidence that militates against the hypothesis that small male size has evolved for efficient foraging during breeding. Given that the proposed benefits of small size for males are related primarily to reduced wing-loading (thereby increasing agility and reducing flight costs), we can predict that in species where breeding males do not forage or chase their prey on the wing, the selective advantage of reduced male size would not exist, and therefore RSD should be reduced or might disappear altogether. Inter-specific comparisons within the Stercorariidae suggest otherwise. The species with the largest degree of wing dimorphism is the Pomarine Jaeger *Stercorarius pomarinus*, which specialises in predation on lemmings, catching the rodents in flight patrols or from the ground, often digging open their burrows (Cramp and Simmons 1983, Furness 1987). From its foraging mode, we would expect Pomarine Jaegers to have one of the smallest dimorphism indexes, yet this species shows one of the largest (Table 8). It is particularly interesting to compare Great and Brown Skuas *Catharacta antarctica*, two species that are morphologically very similar, even though Great Skuas diverged from the remaining species at a relatively early stage in the evolution of the *Catharacta* skuas (Cohen et al. 1997). Brown and Great Skuas show virtually the same degree of dimorphism in spite of strikingly different foraging techniques during the breeding season (Table 8). Brown Skuas (particularly the Tristan Skua *Catharacta antarctica hamiltoni*) forage mainly by walking around their territories, scavenging or pouncing on prey, mostly Procellariiformes that come ashore during the night (Furness 1987, Young et al. 1988). By contrast, Great Skuas search and catch food exclusively on the wing, in the main by splash-diving onto surface shoals or competing for discards behind fishing vessels, but also by kleptoparasitism and predation of seabirds (Furness 1987, Phillips et al. in press). Over all species, there

seems to be no relationship between foraging behaviour and RSD in the Stercorariidae (Table 8). This contradicts the small efficient male hypothesis, but fits well with behavioural hypotheses (see below) that state that it is morphology, and not diet, that correlates with dimorphism in birds with a raptorial lifestyle (Smith 1982).

Does female dominance (or large RSD) improve breeding success?

More efficient sex-role partitioning should be achieved when females can readily force males into the role of food providers, while preventing them from taking a greater role in incubation or brooding activities (Cade 1960 quoted in Smith 1982). In our study, the degree of dimorphism within pairs did not correlate with any breeding parameters, with the exception of laying date in Parasitic Jaegers in one of two years. There is therefore no clear support for this hypothesis, although it should be stressed that our tests are not very powerful because of the comparatively small number of pairs in the study populations in which both birds were measured.

Theories that suggest that inter-sexual competition for food occurs in feeding territories during the breeding season also predict that a high degree of size dimorphism within the pair should be advantageous (e.g. Newton 1979, Andersson and Norberg 1981). If this hypothesis were correct, we would predict lower RSD in skua and jaeger species that feed mostly outside their breeding territories (e.g. Great Skua and South-Polar Skua *Catharacta maccormicki*). However, RSD in these species is not particularly small when compared to other skuas or jaegers (Table 8). At southern colonies, Parasitic Skuas also feed by kleptoparasitism outside their breeding territories (Phillips et al. 1996) but this is rare in the northern part of their range where the great majority of birds breed. In addition, it is difficult to see how body size differences between sexes could contribute to niche partitioning in species such as the Pomarine Jaeger, in which both parents feed almost exclusively on a single kind of prey (small rodents).

Is RSD related to intra-sexual competition or pair formation?

If small males are more agile, they can perform better aerial displays during courtship, which might facilitate the acquisition of mates. This hypothesis has been presented as an explanation for RSD in some waders (Charadrii) and in raptors

(Widén 1984, Jönsson 1987). Large *Catharacta* skuas seldom perform aerial displays during courtship (Furness 1987), and therefore the hypothesis cannot apply to these birds.

Parasitic Jaegers display assortative mating in relation to size, and there is an indication that the same might apply to Great Skuas, implying that small females avoid pairing with large males. This conforms with behavioural theories that propose that RSD evolved to facilitate pair formation. Female dominance is particularly important in species where aggressive and well armed males could easily inflict injuries during hostile contacts at the initial stage in pair establishment (Smith 1982). This would tend to explain the large RSD in species that feed on relatively large and fast-moving prey (birds, mammals) because these are the species better equipped to inflict serious injury (Smith 1982). However, studies with European Sparrowhawks (Newton et al. 1983), American Kestrels *Falco sparverius* (Bowman 1987, Bortolotti and Iko 1992) and Barn Owls *Tyto alba* (Marti 1990) failed to find any correlation between the sizes of males and females in mated pairs. Clearly, there is a need for more studies of assortative mating in relation to size in raptors and skuas and jaegers.

If large within-pair RSD facilitates pair formation, then we would expect RSD to correlate with timing of breeding, at least in newly formed pairs. Because survival rates and mate fidelity are high in the species studied, there were not enough new pairs to test this relationship in new partnerships only. Including all pairs, no such effect was found in Great Skuas, but in one of two years, Parasitic Jaeger pairs with large RSD laid relatively early in the season. This is similar to a study on Red-backed Sandpipers *Calidris alpina*, a wader that displays RSD, but which obviously has a non-raptorial lifestyle (Jönsson 1987).

Large female size could also result from intra-sexual competition for mates, an hypothesis that could apply to raptorial birds (Olsen and Olsen 1987). Female Great Skuas regularly engage in fights for males. In Great Skuas, and possibly in other species, such fights are resolved on the ground, contests are violent and sometimes cause fatal injuries (Catry et al. in press). If large females have an advantage, then we would expect them to be paired with better quality males, and this is supported by the fact that female size is positively correlated with male age. Newton (1988) found that large female European Sparrowhawks bred at a younger

age than smaller birds, a pattern that could also result from female-female competition for mates and/or territories. Large female Great Skuas paired with better quality males need not necessarily achieve a higher breeding success. It is quite possible that above a certain point, large size could become disadvantageous when performing breeding duties, even though it permits birds to compete for males.

It might be argued that if large females win intra-sexual contests, they should also select small males, if one accepts that RSD facilitates pairing. However, large females may be able to establish dominance easily over any partner, and therefore might not be constrained by male size in their choice of mate. Assortative mating by size could simply result from medium-sized or small females avoiding pairing with large males.

Conclusions

This study provides evidence against theories claiming that male and female body size differences in skuas and jaegers evolved because of specialised roles during breeding. Large females in the study populations were not more fecund, nor were they the main defenders of the nest. We could find no evidence that small males were more efficient at foraging. In addition, inter-specific comparisons did not support the idea that the degree of RSD is related to foraging behaviour during the breeding season (as opposed to morphology), or that small male size evolved to reduce wing-loading. Female dominance within pairs did not affect any breeding parameters. There was some support for theories that maintain that RSD is linked to sexual selection; large females seem to have an advantage in pairing with older males. The same could be true for small males, if large birds are rejected by small partners, as suggested by evidence of assortative mating for size in the study populations.

The origin and maintenance of RSD in several groups of birds (generally, but not exclusively predatory species), has been subject of considerable debate and hypothesis-testing. The question is far from settled, nor is there yet agreement over fundamental issues such as whether or not RSD in different groups is a consequence of similar selective pressures. The problem is extremely complex. Our study does not provide any definitive answers, not even for the particular family of birds that we studied, and despite large sample sizes in most cases, but we believe that only as the

number of detailed field studies such as this gradually build up will it ultimately be possible to provide convincing evidence on the selective pressures that currently act to maintain RSD in natural populations.

LITERATURE CITED

- Andersson, M. 1971 Breeding behaviour of the Long-tailed Skua *Stercorarius longicaudus* (Viellot). *Ornis Scandinavica* 2: 35-54.
- Andersson, M. and R.A. Norberg 1981. Evolution of reversed sexual size dimorphism and role partitioning among predatory birds, with a size scaling of flight performance. *Biological Journal of the Linnean Society* 15: 105-130.
- Andersson, S. and C.G. Wiklund 1987. Sex role partitioning during offspring protection in the Rough-legged Buzzard *Buteo lagopus*. *Ibis* 129: 103-107.
- Bortolotti, G.R. and W.M. Iko 1992. Non-random pairing in American Kestrels: mate choice versus intra-sexual competition. *Animal Behaviour* 44: 811-821.
- Bowman, R. 1987. Size dimorphism in mated pairs of American Kestrels. *Wilson Bulletin* 99: 465-467.
- Cade, T.J. 1960. Ecology of the Peregrine and Gyrfalcon populations in Alaska. *Univ. Calif. Publ. Zool.* 63: 151-290.
- Catry, P. and R.W. Furness In press. Territorial intrusions and copulation behaviour in the Great Skua *Catharacta skua*. *Animal Behaviour*.
- Catry, P., N. Ratcliffe and R.W. Furness In press. Partnerships and mechanisms of divorce in the Great Skua *Catharacta skua*. *Animal Behaviour*.
- Cohen, B.L. and 15 co-authors. 1997. Enigmatic phylogeny of Skuas (Aves: Stercorariidae). *Proceedings of the Royal Society of London B* 264: 181-190.
- Coulson, J.C. 1963. Egg size and shape in the Kittiwake (*Rissa tridactyla*) and their use in estimating age composition of populations. *Proceedings of the Zoological Society of London* 140: 211-227.
- Cramp, S. and K.E.L. Simmons (eds) 1983. *The Birds of the Western Palearctic*. Vol. III. Oxford University Press, Oxford.
- Furness, R.W. 1983. Variation in size and growth of Great Skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *Journal of Zoology, London* 199: 101-116.
- Furness, R.W. 1987. *The Skuas*. T&AD Poyser, Calton.
- Furness, R.W. 1996. The Stercorariidae. pp 556-571. *In*: del Hoyo, J., Elliot, A. & Sargatal, J. (eds). *Handbook of the Birds of the World*. Vol. 3. Lynx Edicions, Barcelona.

- Hakkarainen, H. and E. Korpimäki 1991. Reversed sexual size dimorphism in Tengmalm's Owl: is small male size adaptive? *Oikos* 61: 337-346.
- Hakkarainen, H. and E. Korpimäki 1995. Contrasting phenotypic correlations in food provision of male Tengmalm's Owls (*Aegolius funereus*) in a temporally heterogeneous environment. *Evolutionary Ecology* 9: 30-37.
- Hakkarainen, H., E. Huhta, K. Lahti, P. Lundvall, T. Mappes, P. Tolonen and J. Wiehn 1996. A test of male mating and hunting success in the Kestrel: the advantages of smallness? *Behavioural Ecology and Sociobiology* 39: 375-380.
- Hedrick, A.V. and E.J. Temeles 1989. The evolution of sexual dimorphism in animals: hypotheses and tests. *Trends in Ecology and Evolution* 4: 136-138.
- Jehl, J.R. and B.G. Murray 1986. The evolution of normal and reverse sexual size dimorphism in shorebirds and other birds. *Current Ornithology* 3: 1-86.
- Jönsson, P.E. 1987. Sexual size dimorphism and disassortative mating in the Dunlin *Calidris alpina schinzii* in Southern Sweden. *Ornis Scandinavica* 18: 257-264.
- Jönsson, P.E. and T. Alerstam 1990. The adaptive significance of parental role division and sexual size dimorphism in breeding shorebirds. *Biological Journal of the Linnean Society* 41: 301-314.
- Loman J. 1984. Breeding success in relation to parent size and experience in a population of the Hooded Crow. *Ornis Scandinavica* 15: 183-187.
- Lundberg, A. 1986. Adaptive advantages of reversed sexual size dimorphism in European owls. *Ornis Scandinavica* 17: 133-140.
- Marti, C.D. 1990. Sex and age dimorphism in the Barn Owl and a test of mate choice. *Auk* 107: 246-254.
- Mueller, H.C. 1990. The evolution of reversed sexual dimorphism in size in monogamous species of birds. *Biological Reviews* 65: 553-585.
- Mueller, H.C. and K. Meyer 1985. The evolution of reversed sexual dimorphism in size. A comparative analysis of the Falconiformes of the Western Palearctic. *Current Ornithology* 2: 65-101.
- Newton, I. 1979. *Population Ecology of Raptors*. T&AD Poyser, Berkhamsted.
- Newton, I. 1988. Individual performance in Sparrowhawks: the ecology of two sexes. *Acta XIX Congressus Internationalis Ornithologici*, Ottawa.

- Newton, I. 1983. Weights, breeding, and survival in European Sparrowhawks. *Auk* 100: 344-354.
- Olsen, P.D. and J. Olsen 1987. Sexual size dimorphism in raptors: intrasexual competition in the larger sex for a scarce breeding resource, the smaller sex. *Emu* 87: 59-62.
- Owens, I.P.F. and P.M. Bennet 1994. Mortality costs of parental care and sexual size dimorphism in birds. *Proceedings of the Royal Society of London B*: 257: 1-8.
- Panton, P.W.C., F.J. Messina and C.R. Griffin 1994. A phylogenetic approach to reversed size dimorphism in diurnal raptors. *Oikos* 71: 492-498.
- Phillips, R.A. and R.W. Furness In press a. Predicting the sex of Parasitic Jaegers by discriminant analysis. *Colonial Waterbirds* 20.
- Phillips, R.A. and R.W. Furness In press b. Sex-specific variation in the loss of mass by breeding Arctic Skuas. *Journal of Avian Biology* 28.
- Phillips, R.A., R.W. Furness and R.W.G. Caldow (1996) Behavioural responses of Arctic Skuas to changes in sandeel availability. In *Aquatic predators and their prey* (eds. S. Greenstreet & M. Tasker). Oxford: Blackwell Scientific.
- Phillips, R.A., P. Catry, D.R. Thompson, K.C. Hamer and R.W. Furness 1997. Inter-colony variation in diet and reproductive performance of Great Skuas *Catharacta skua*. *Marine Ecology Progress Series*. In press.
- Pietz, P.J. 1986. Daily activity patterns of South Polar and Brown Skuas near Palmer Station, Antarctica. *Auk* 103: 726-736.
- Pietz, P.J. 1987. Feeding and nesting ecology of sympatric South Polar and Brown Skuas. *Auk* 104: 617-627.
- Plumton, D.L. and R.S. Lutz 1994. Sexual size dimorphism, mate choice, and productivity of Burrowing Owls. *Auk* 111: 724-727.
- Rising, J.D. and K.M. Somers 1989. The measurement of overall body size in birds. *Auk* 106: 666-674.
- Safina, C. 1984. Selection for reduced male size in raptorial birds: the possible roles of female choice and mate guarding. *Oikos* 43: 159-164.
- Smith, S.M. 1982. Raptor "reverse" dimorphism revisited: a new hypothesis. *Oikos* 39: 118-122.

- Wheeler, P. 1983. The evolution of reversed sexual dimorphism in birds of prey. *Oikos* 40: 145-149.
- Widén, P. 1984. Reversed sexual size dimorphism in birds of prey: revival of an old hypothesis. *Oikos* 43: 259-263.
- Wiklund, C.G. and J. Stigh 1983. Nest defence and the evolution of reversed sexual size dimorphism in Snowy Owls *Nyctea scandiaca*. *Ornis scandinavica* 14: 58-62.
- Ydenberg, R.C. and L.S. Forbes 1991. The survival-reproduction selection equilibrium and reversed size dimorphism in raptors. *Oikos* 60: 115-120.
- Young, E.C., P.F. Jenkins, M.E. Douglas and T.G. Lovegrove 1988. Nocturnal foraging by Chatham island skuas. *New Zealand Journal of Ecology* 11: 113-117.

Table 1. Measurements of live Great Skuas and Parasitic Jaegers from Foula and statistical comparisons between the sexes (all linear measurements in mm; Samples do not include birds sexed by discriminant analysis).

	Sample Size		$\bar{x} \pm \text{s.d.}$		Comparisons	
	Males	Females	Males	Females	<i>t</i>	<i>P</i>
Great Skuas						
Wing chord	112	127	416.8±7.1	427.4±7.1	11.5	<0.001
Tarsus	112	127	68.89±1.55	70.32±1.72	6.7	<0.001
Head	112	127	109.89±1.68	111.49±1.82	7.0	<0.001
Weight (g)	112	125	1271.5±69.4	1409.2±75.0	14.6	<0.001
Parasitic Jaegers						
Wing chord	44	53	320.3±5.0	327.2±5.9	6.1	<0.001
Tarsus	44	53	44.50±1.13	45.17±1.81	2.2	<0.05
Head	43	53	76.09±1.55	77.35±1.53	4.0	<0.001
Weight (g)	32	42	405.0±26.8	466.8±30.2	9.1	<0.001

Table 2. Correlations between male body size and laying date and clutch volume. (All correlations are non-significant).

	Laying Date				Clutch Volume			
	1993	1994	1995	1996	1993	1994	1995	1996
Great Skuas								
PC1	-	-0.16	-0.10	-0.18	-	-0.23	-0.06	0.00
<i>n</i>	-	42	91	99	-	39	91	89
Parasitic Jaegers								
PC1	-0.18	-0.05	-	-	-0.07	-0.02	-	-
<i>n</i>	56	68	-	-	54	62	-	-

Table 3. Correlations between female body size and laying date and clutch volume.

	Laying Date				Clutch Volume			
	1993	1994	1995	1996	1993	1994	1995	1996
Great Skuas								
PC1	-	0.08	-0.10	-0.10	-	0.18	0.31**	0.16
<i>n</i>	-	61	100	100	-	50	89	90
Parasitic Jaegers								
PC1	0.16	0.02	-	-	0.30*	0.23*	-	-
<i>n</i>	70	87	-	-	64	77	-	-

* $P < 0.05$ ** $P < 0.01$

Table 4. Effects of male and female sizes and pair dimorphism on hatching and fledging success. (Analyses non-significant unless indicated otherwise).

	Number of chicks hatched		Number of chicks fledged	
	1994	1995	1994	1995
Great Skuas				
PC1 males	$G^2 = 0.30$	$G^2 = 6.73^*$	$G^2 = 0.07$	$G^2 = 1.23$
<i>n</i>	41	93	37	90
PC1 females	$G^2 = 0.16$	$G^2 = 1.01$	$G^2 = 0.12$	$G^2 = 1.29$
<i>n</i>	56	98	47	91
Dimorphism	$G^2 = 1.23$	$G^2 = 1.11$	$G^2 = 0.00$	$G^2 = 0.70$
<i>n</i>	28	46	25	44
Parasitic Jaegers				
PC1 males	$G^2 = 0.00$	$G^2 = 0.34$	$G^2 = 0.04$	$G^2 = 0.33$
<i>n</i>	56	68	53	62
PC1 females	$G^2 = 0.32$	$G^2 = 1.06$	$G^2 = 0.14$	$G^2 = 0.80$
<i>n</i>	71	87	68	77
Dimorphism	$G^2 = 1.74$	$G^2 = 0.00$	$G^2 = 0.00$	$G^2 = 0.70$
<i>n</i>	33	56	31	52

* $P < 0.01$; small males hatched more chicks

Table 5. Correlations between within-pair dimorphism index of skuas and jaegers and laying date and clutch volume.

	Laying Date				Clutch Volume			
	1993	1994	1995	1996	1993	1994	1995	1996
Great Skuas								
PC1	-	-0.20	0.07	0.02	-	-0.27	-0.27	-0.17
<i>n</i>	-	30	47	49	-	24	39	40
Parasitic Jaegers								
PC1	-0.5**	-0.12	-	-	-0.08	-0.08	-	-
<i>n</i>	33	56	-	-	32	51	-	-

** $P < 0.01$

Table 6. Relative aggression levels of males and females in pairs of Great Skuas.

Period	More aggressive bird in the pair is			<i>n</i>
	Male	Neither	Female	
1- After laying one egg	91.4%	7.1%	1.5%	70
2 - After laying two eggs	59.4%	34.4%	6.2%	32
3 - Half way into incubation	49.1%	32.1%	18.8%	53
4 - At hatching	51.1%	21.1%	27.8%	47

Table 7. Relative aggression levels of male and female Parasitic Jaegers. Sample sizes in parentheses.

Period	Intensity of distraction display		Mann Whitney U test
	Male	Female	
1- Half way into incubation	2.1±1.9 (64)	2.1±2.0 (82)	Z = 0.00, ns
2- At hatching	1.6±2.0 (46)	2.0±2.1 (55)	Z = 1.15, ns
	Mean number of swoops at observer		
Period	Male	Female	
1- Half way into incubation	3.4±5.6 (63)	3.8±5.8 (81)	Z = 0.13, ns
2- At hatching	5.9±6.0 (46)	5.4±6.3 (55)	Z = 0.79, ns

Table 8. Main foraging modes during the breeding season and degree of size dimorphism of different skua and jaeger species. Degree of dimorphism is the difference between the sexes as a percentage of male size. (All morphological data from Furness (1987), except when indicated. Behavioural data from Cramp & Simmons 1983, Furness 1987, 1996, Pietz 1987, Young *et al.* 1988, Phillips *et al.* 1996, Phillips *et al.* 1997).

Species	Foraging mode during breeding			Dimorphism index	
	Walking	Flying	Aerial chases	Weight	Wing
<i>Catharacta skua</i>		+	+	11.1 (11.1)*	2.7 (2.5)*
<i>C. maccormicki</i>	+	+		11.0	1.4
<i>C. antarctica</i>					
<i>hamiltoni</i>	+			10.7	2.7
<i>lonnbergi</i>	+			13.0	1.6
<i>S. pomarinus</i>	+	+		13.6	3.0
<i>S. parasiticus</i>		+	+	16.5 (15.3)*	1.8 (2.2)*
<i>S. longicaudus</i>		+		12.1	1.3

*this study

Chapter 8

The incidence of non-breeding by adult Great and Arctic Skuas from Foula, Shetland.

Submitted as:

Catry, P., Phillips, R.A., Hamer, K.C., Ratcliffe, N. & Furness, R.W. The incidence of non-breeding by adult Great and Arctic Skuas from Foula, Shetland.

ABSTRACT

Several recent studies of seabirds have found high levels of non-breeding by experienced adults. By contrast, just 8.9% (range 4-14%, in 8 years) of experienced Great Skuas *Catharacta skua* in the Foula population deferred breeding in each year, 1989-96. For Arctic Skuas *Stercorarius parasiticus* a corresponding value of 5.5% (range 3-8%, in 2 years) was found. Only 3% of the territorial pairs of Arctic Skuas (including new recruits) failed to lay eggs. Higher incidence of non-breeding in Great Skuas was found in years when laying was late, eggs were small and fledging production was low. Loss of mate due to death or divorce was the main direct cause of non-breeding. Loss of territory was also important for male birds. In Great Skuas, more males missed a breeding season than females, but the same did not apply to Arctic Skuas. Very young and very old Great Skuas were more likely to defer breeding than mid-aged birds. Evidence is presented that the decline in breeding frequency of old birds was due to senescence, as opposed to increased frequency of mate-changes resulting from a high mortality of old partners.

Seabirds are particularly long-lived, and several studies have reported delayed age of first breeding coupled with intermittent breeding in experienced birds (Furness & Monaghan 1987, Wooller et al. 1992). Non-breeding can result from a complete inability to do so (e.g. from lack of a breeding site at the colony) or from a decision aimed at maximising residual reproductive value, avoiding paying the costs of reproduction at a stage when they might be potentially too high. The incidence of non-breeding at the population level has been found to correlate with environmental conditions, including weather and food availability (Schreiber & Schreiber 1984, Murphy et al. 1991, Chastel et al. 1993, Crawford & Dyer 1995), and high numbers of non-breeders are often associated with years of poor breeding performance (Coulson 1984, Boekelheide & Ainley 1989, Aebischer & Wanless 1992). The birds most likely to defer breeding tend to be young or less experienced and lower quality individuals (Wooller & Coulson 1977, Wooller et al. 1990, Calladine & Harris 1997). Non-breeding can also be socially induced, for example resulting from loss of a mate or nest site (Harris & Wanless 1995). In species with long reproductive cycles, breeding performance in the last attempt can influence the probability of nesting in the following season (Chastel 1995). Comparatively little is known about interspecific variation in the incidence of non-breeding, although this should be expected to correlate with other life-history traits.

The existence of potentially large and variable numbers of non-breeders has important implications for population dynamics. Non-breeders can provide a buffer against environmental stress by replacing lost breeders during periods of increased adult mortality or after periods with a reduction of breeding success (Klomp & Furness 1992). The relative incidence of non-breeding has implications for population modelling and monitoring (O'Connell et al. 1997).

The dynamics and behaviour of inexperienced Great Skuas *Catharacta skua* attending a colony before recruitment has been described (Klomp & Furness 1990, 1992). In this study, we investigated the incidence of non-breeding by individually-marked adult Great Skuas and Arctic Skuas *Stercorarius parasiticus* on Foula, Shetland, concentrating on birds that had at least one year of previous breeding experience. Our objectives were (1) to quantify the incidence of non-breeding and its annual variations, (2) to relate the incidence of non-breeding to various reproductive

parameters that might reflect environmental conditions, (3) to identify the factors that are directly responsible for non-breeding, and (4) to examine the influence of sex and age on the probability of non-breeding. Several of these analyses could be performed only for Great Skuas, because the Arctic Skua data set was much less detailed.

STUDY AREA AND METHODS

This study took place on Foula (60°08'N, 2°05'W), a small island (5km by 4km) situated 25 km west of Shetland Mainland. Around 2500 Great Skua and 150 Arctic Skua pairs regularly nest there. We followed the entire population of Arctic Skuas, but Great Skuas were studied in a demarcated area that covered only part of the colony. Skuas of both species were trapped and fitted with unique combinations of colour-rings allowing individual identification. The ages of Great Skuas that had been ringed as chicks on this island could be determined precisely (Hamer & Furness 1991). Great Skuas were sexed by observation of copulations and courtship feeding. Arctic Skuas were sexed by observation, by a hierarchical combination of two discriminant functions based on the prior probabilities of group membership (with an accuracy of over 91% for birds classified), by dissection of birds found dead at the colony or by association with a partner sexed by one of these methods (Phillips & Furness in press). Most Great Skuas were only sexed in the latter years of the study.

In each year (1989-1996 for Great Skuas and 1992-1994 for Arctic Skuas) observers walked regularly around the study area, starting before egg laying, searching for colour-ringed individuals. Searches of other parts of the Great Skua colony failed to locate any of the colour marked adults at other territories. After the birds were located (most individuals kept the same territory as in previous years), visits were made daily or on alternate days until eggs were laid. Territories where eggs were not found were checked regularly until well after the end of the laying period. For Great Skuas between 1994 and 1996 and for Arctic skuas in all years, records were kept on whether non-breeding birds were paired or not. Clubs (aggregations of non-breeders) were checked regularly to search for non-territorial birds. The study areas were visited again in 1995 and 1996 (for Arctic Skuas) and 1997 (Great Skuas), following the end of the intensive study periods, to check for the presence of colour-marked individuals that had been alive but absent (non-breeders)

in previous years. Only one Great Skua absent in 1996 was found in 1997. During this study it was exceptional for adults of either species to be absent from the colony for two consecutive years and therefore we are confident that a further search for missing Great Skuas in 1998 would have no effect in our conclusions.

In each year, all Arctic Skua territories in the island were mapped, including those with unmarked birds, and checked regularly for indication of a breeding attempt. For Great Skuas, only territories with colour-marked birds were targeted. Breeding statistics (laying dates, clutch volume of two-egg clutches and productivity) of a sample of the Great Skua population were collected in a standardised fashion (following Hamer et al. 1991). Number of chicks fledged per pair was recorded in six of the eight years. The annual incidence of non-breeding was compared with population mean values for these parameters in each year. The incidence of non-breeding was also compared with adult survival rates calculated from re-sightings of colour-ringed birds (unpublished data). We used one-tailed tests when comparing the incidence of non-breeding with breeding parameters. This is because we predicted *a priori* that a high incidence of non-breeding should always be associated with values reflecting poor breeding conditions (i.e. late laying, small eggs, few chicks raised). A one-tailed test was also used when correlating the incidence of non-breeding with survival rates in the previous year, because low survival rates are associated with more mate changes, which might induce non-breeding (see below). We tested for the effect of adult age on the probability of non-breeding using quadratic logistic regressions. When individuals failed to breed for two or more consecutive years after having bred, we defined this as chronic non-breeding. We evaluated the influence of adult age on chronic non-breeding by testing for the effect of age on the probability of non-breeding for birds that had not nested in the previous season. To avoid pseudoreplication, individual non-breeders only contributed one case to the data set. The significance of the logistic regressions was assessed by the use of likelihood-ratio tests. Means are presented with standard-errors.

RESULTS

Great Skuas

During this study, an average of $8.9 \pm 1.4\%$ ($n = 8$ years) of the Great Skuas with previous breeding experience did not breed (Table 1). The annual incidence of non-breeding was negatively correlated with clutch volume ($r_6 = -0.63$, $P = 0.05$, one-tailed test) and with productivity ($r_4 = -0.94$, $P < 0.005$, one-tailed test, Figure 1). There was a positive correlation with laying date that just failed to reach significance ($r_6 = 0.61$, $P = 0.06$, one-tailed test). The incidence of non-breeding was negatively correlated with adult survival rates from the previous to the current breeding season ($r_6 = -0.68$, $P < 0.05$, one-tailed test).

A total of 25 different males and 14 females with some breeding experience did not breed in at least one year. This is significantly different from the sex ratio of colour-ringed birds in the study population where 47% of the individuals sexed were males ($\chi^2_1 = 5.7$, $P < 0.05$). On a year-by-year basis, only in 1995 were males more likely not to breed than females, but samples were generally small (Table 1). Considering birds that missed at least one breeding season, males failed to nest on average 1.4 times during the study, while the corresponding value for females was 1.3. Among experienced Great Skuas, very young or very old birds were less likely to breed than mid-aged birds (quadratic logistic regression: $G^2_2 = 6.7$, $n = 1081$, $P < 0.05$, Figure 2). A similar effect of age was found on the incidence of chronic non-breeding ($G^2_2 = 11.0$, $n = 63$, $P < 0.01$, Figure 3). Both quadratic models provided a significantly better fit than linear alternatives.

Most cases (85%) of non-breeding where the cause could be determined (all in 1994-96) were associated with loss of partner (either due to death or to divorce) or with loss of territory (Table 2).

Arctic Skuas

On average, 5.5% of the Arctic skuas with previous breeding experience did not breed in each year (Table 3). In total, 8 different females and 1 male were recorded not breeding. This is not significantly different from the sex ratio of the colour-marked population ($\chi^2_1 = 2.5$, n.s.). All 25 pairs that remained united from the previous year laid eggs. Out of nine cases of non-breeding by birds known to be

alive, there were only two occasions when the individual in question was not recorded at the breeding colony. Of the seven birds seen on the island, three held a territory and were paired while the remaining four were only seen on clubs.

Between 1992 and 1994, all Arctic skua territories were mapped on Foula and in each year no eggs were laid in 3% of those territories (Table 4).

DISCUSSION

Both Arctic and Great Skuas displayed a low incidence of non-breeding during this study. In 1993 and 1994, only 3% and 8% respectively of Arctic skuas with previous breeding experience failed to nest. Excluding years when breeding success was very low in the Great Skua (when non-breeding reached 14%), in general less than 10% of experienced adults failed to breed in each season. These figures contrast with some recent studies on gulls (*Laridae*, the closest relatives to skuas) where around a third of the adult experienced birds failed to lay eggs in any one season (Calladine & Harris 1997, Pugesek & Diem 1990), even when breeding success in the colony was not particularly low. Between 1992 and 1994, only 3% of the territorial pairs (including new recruits) of Arctic Skuas on Foula failed to lay eggs. In a similar study with Lesser Black-backed Gulls *Larus fuscus*, 27% of pairs did not produce eggs, with no evidence that this was a result of food shortage (O'Connell et al. 1997). Studies with auks (*Alcidae*) have revealed, in a similar way to skuas, very low incidence of non-breeding among experienced individuals (Ashcroft 1979, Harris & Wanless 1995), but most other seabirds display a higher incidence of non-breeding, in at least some years (e.g. Coulson 1984, Boekelheide & Ainley 1989, Wooller et al. 1990, Aebischer & Wanless 1992, Williams & Rodwell 1992, Chastel et al. 1993, Chastel 1995). The factors responsible for large interspecific variation in non-breeding are poorly understood. A high incidence of non-breeding is particularly surprising in some species when environmental conditions seem to be favourable, and when no simultaneous failure in breeding performance has been reported. In some years, skuas living in the Arctic tundra, particularly Long-tailed Skua *Stercorarius longicaudus* and Pomarine Skua *Stercorarius pomarinus*, display extensive non-breeding affecting the majority of their local populations, but this results from periodic crashes in

lemming numbers, which form their main prey during the nesting season (Andersson 1981, Furness 1987).

The low incidence of non-breeding amongst adults in the study populations, as well as the very small number of occupied territories where breeding was not attempted, suggests that a correction factor is not necessary either when attempting to census breeding skuas in Shetland or in estimating parameters for the purposes of population modelling.

Intraspecific variation in the annual incidence of non-breeding in seabirds has been linked with environmental conditions. Correlations between the percentage of non-breeders and various breeding indices of performance have been found in several seabird species (e.g. Coulson 1984, Boekelheide & Ainley 1989, Murphy et al. 1991, Chastel et al. 1993, this study). This suggests that factors such as food availability or weather might be affecting both non-breeding and breeding birds. There is evidence for links between non-breeding and fish stocks or weather patterns in a wide variety of seabirds, from polar regions to the tropics (Schreiber & Schreiber 1984, Aebischer & Wanless 1992, Chastel et al. 1993, Crawford & Dyer 1995). Increases in non-breeding frequency in response to unfavourable environmental circumstances could result from an inability of some individuals to reach a high enough body condition prior to egg laying, by a prudent restraint by birds that are unable to make an investment in a potentially difficult breeding attempt without compromising survival and future breeding prospects, or both. An individual might have enough energy reserves to lay eggs but still refrain from nesting if body condition was below a threshold value which would indicate a minimum level of food availability. Of course, environmental conditions at the time of egg laying might not be accurate predictors of conditions later on. This might explain why so many Great Skuas nested in years where breeding success was very low. For example, in 1989, as a result of sandeel (*Ammodytidae*) scarcity in Shetland waters, the mean number of chicks fledged per pair that laid eggs was 0.21 (Hamer et al. 1991), but 86% of the birds still attempted to nest (Table 1). Given that 4 to 6% of experienced adults did not nest even in good years, under 10% of the population responded to the unusually unfavourable conditions by not laying.

Annual survival rates of adult Great Skuas on Foula in the late eighties were low, not only in comparison with other years, but also with other large *Catharacta* skuas (Ainley et al. 1990, Hamer 1990, Unpublished PhD thesis, University of Glasgow, and unpublished data). If social factors, particularly mate change, influence non-breeding (see below), then the correlation between breeding parameters and the incidence of non-breeding in Great Skuas could at least partly be a consequence of increased mortality, forcing more birds to find new partners during the poor years. Overwinter survival rates did correlate with the incidence of non-breeding in the following season, lending support to this hypothesis. Low survival rates could reflect the cost of reproducing under unfavourable conditions. In conclusion, the evidence suggests that very few Great Skuas deferred breeding as a direct response to environmental stress. Although non-breeding might represent a strategy in some species to maximise residual reproductive value when conditions are poor (Schaffer 1974), it seems likely that the unpredictability of the marine environment prevents this strategy being finely tuned in birds like Great Skuas.

In general, more experienced male than female Great Skuas failed to breed, suggesting that there might be a slight excess of experienced males in this population. The same does not apply to Arctic Skuas where no significant difference between sexes was found. Between 1994 and 1996, which were years with a low incidence of non-breeding in Great Skuas, careful behavioural observations allowed us to determine the causes of non-breeding, which in most cases (59%) appeared to be mate loss. One quarter of the Great Skuas that lost their mates failed to breed in the same season, but all the pairs that remained united laid eggs (Catry et al. in press.). This is similar to the situation in South Polar Skuas *Catharacta maccormicki* (Ainley et al. 1990). New mates are probably difficult to find, and experienced birds in new partnerships lay significantly later in the season than pairs that remain together (Catry et al. in press). If a new partnership takes too long to form, breeding may simply be postponed until the following season. The second most common cause of non-breeding in Great Skuas was loss of territory (26% of cases). After losing a territory, some males failed to establish a new one for several years. One particular male was without a territory for at least four consecutive years, not because of overcrowding (new territories were being established by other birds in empty areas in the same

period) but because in each year this bird attempted to recover its former territory. In conclusion, most cases of non-breeding were socially induced, and not simply a result of birds "deciding" to reduce their reproductive investment (see also Harris & Wanless 1995).

Non-breeding was more prevalent among very young (but experienced) or very old Great Skuas. One potential explanation for this pattern could be that, because these are the age classes expected to have higher mortality (and maybe divorce rates in young birds), more cases of mate loss are to be expected, resulting in a greater incidence of non-breeding. However, we find this unlikely for several reasons. Great Skuas display a poor correlation of ages within partnerships ($r=0.28$) and no tendency for younger birds to have greater divorce rates was found in a previous study (Catry et al. in press.). More importantly, very young and particularly very old birds had a greater probability of deferring breeding after one year off, in comparison to mid-aged birds in similar circumstances. This result can only be explained, in what concerns old birds, by some form of senescence. It is possible that very young and old birds have greater difficulty in holding territories or attracting new mates. A higher incidence of non-breeding among younger or less experienced individuals has been described for other species (Wooller and Coulson 1977, Wooller et al. 1990). Weimerskirch (1992) also reported an increase between nesting intervals in very old Wandering Albatrosses *Diomedea exulans*, but this was attributed to a higher probability of loss of mate amongst old individuals. Senescence can be difficult to demonstrate in wild birds, particularly in long-lived species (Newton & Rothery 1997). We believe that our results clearly show that very old Great Skuas experience increasing difficulties in meeting all the conditions necessary to breed. At an anecdotal level, however, it must be said that the oldest living Great Skua ever known, a female aged 34 years, was incubating a clutch in the spring of 1997.

Acknowledgements: We thank the Holbourn family for permission to work in Foula and Sheila Gear and Tony Mainwood for access to Arctic Skua re-sighting data in 1995 and 1996.

References

- Aebischer, N.J. & Wanless, S. 1992. Relationships between colony size, adult non-breeding and environmental conditions for Shags *Phalacrocorax aristotelis* on the Isle of May, Scotland. *Bird Study* 39: 43-52.
- Ainley, D.G., Ribic, C.A. & Wood, R.C. 1990. A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. *J. Anim. Ecol.* 59: 1-20.
- Andersson, M. 1981. Reproductive tactics of the Long-tailed Skua *Stercorarius longicaudus*. *Oikos* 37: 287-294.
- Ashcroft, R.E. 1979. Survival rates and breeding biology of Puffins on Skomer Island, Wales. *Ornis Scand.* 10: 100-110.
- Boekelheide, R.J. & Ainley, D.G. 1989. Age, resource availability, and breeding effort in Brandt's Cormorant. *Auk* 106: 389-401.
- Calladine, J. & Harris, M.P. 1997. Intermittent breeding in the Herring Gull *Larus argentatus* and the Lesser Black-backed Gull *Larus fuscus*. *Ibis* 139: 259-263.
- Chastel, O. 1995. Influence of reproductive success on breeding frequency in four southern petrels. *Ibis* 137: 360-363.
- Chastel, O., Weimerskirch, H. & Jouventin, P. 1993. High annual variability in reproductive success and survival of an Antarctic seabird, the Snow Petrel *Pagodroma nivea*. *Oecologia* 94: 278-285.
- Catry, P., Ratcliffe, N. & Furness, R.W. in press. Partnerships and mechanisms of divorce in the Great Skua *Catharacta skua*. *Anim. Behav.*
- Coulson, J.C. 1984. The population dynamics of the Eider Duck *Somateria mollissima* and evidence for extensive non-breeding by adult ducks. *Ibis* 126: 525-543.
- Crawford, R.J.M. & Dyer, B.M. 1995. Responses by four seabird species to a fluctuating availability of Cape Anchovy *Engraulis capensis* off South Africa. *Ibis* 137: 329-339.
- Furness, R.W. 1987. The Skuas. T. & A.D. Poyser, Calton.
- Furness, R.W. & Monaghan, P. 1987. *Seabirds Ecology*. Blackie, Glasgow and London.

- Hamer, K.C. & Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. *J. Anim. Ecol.* 60, 693-704.
- Hamer, K.C., Furness, R.W. & Caldow, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of great skuas *Catharacta skua* in Shetland. *J. Zool., Lond.* 223, 175-188.
- Harris, M.P. & Wanless, S. 1995. Survival and non-breeding of adult Common Guillemots *Uria aalge*. *Ibis* 137: 192-197.
- Klomp, N.I. & Furness, R.W. 1990. Variations in numbers of non-breeding Great Skuas attending a colony. *Ornis Scand.* 21: 270-276.
- Klomp, N.I. & Furness, R.W. 1992. Non-breeders as a buffer against environmental stress: declines in numbers of Great Skuas on Foula, Shetland, and prediction of future recruitment. *J. Appl. Ecol.* 29: 341-348.
- Murphy, E.C., Springer, A.M. & Roseneau, D.G. 1991. High annual variability in reproductive success of Kittiwakes (*Rissa tridactyla*) at a colony in western Alaska. *J. Anim. Ecol.* 60: 515-534.
- Newton, I. & Rothery, P. 1997. Senescence and reproductive value in Sparrowhawks. *Ecology* 78: 1000-1008.
- O'Connell, M.J., Coulson, J.C., Raven, S. & Joyce, S. 1997. Nonbreeding and nests without eggs in the Lesser Black-backed Gull *Larus fuscus*. *Ibis* 139: 252-258.
- Phillips, R.A. & R.W. Furness In press. Predicting the sex of Parasitic Jaegers by discriminant analysis. *Colonial Waterbirds* 20.
- Pugesek, B.H. & Diem, K.L. 1990. The relationship between reproduction and survival in known-age California Gulls. *Ecology* 71: 811-817.
- Schaffer, W.M. 1974. Optimal reproductive effort in fluctuating environments. *Amer. Nat.* 108: 783-790.
- Schreiber, R.W. & Schreiber, E.A. 1984. Central Pacific seabirds and the El Niño Southern Oscillation: 1982 to 1983 perspectives. *Science* 225: 713-716.
- Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition and survival in the Wandering Albatross. *Oikos* 64: 464-473.
- Williams, T.D. & Rodwell, S. 1992. Annual variation in return rate, mate and nest-site fidelity in breeding Gentoo and Macaroni Penguins. *Condor* 94: 636-645.

- Wooller, R.D. & Coulson, J.C. 1977. Factors affecting the age of first breeding of the Kittiwake *Rissa tridactyla*. *Ibis* 119: 339-349.
- Wooller, R.D., Bradley, J.S. & Croxall, J.P. 1992. Long-term population studies of seabirds. *Trends Ecol. Evol.* 7: 111-114.
- Wooller, R.D. Bradley, J.S., Skira, I.J. & Serventy, D.L. 1990. Reproductive success of Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. *J. Anim. Ecol.* 59: 161-170.

Table 1 - Incidence of non-breeding by Great Skuas with previous breeding experience.

Year	Incidence of nonbreed (%)	Birds studied	Number of non-breeding	
			males	females
1989	14	105	-	-
1990	12	151	-	-
1991	9	80	2	2
1992	14	132	4	4
1993	5	145	1	3
1994	6	82	5	1
1995	4	140	11 *	2
1996	7	185	12	7
x ± s.e.	8.9 ± 1.4			

(Between 1994 and 1996 the sum of males and females non-breeding is higher than the total number of non-breeders as calculated from the two first columns. This results from the inclusion of known-sex birds from outside the main study plot that were known to have failed breeding in those years).

* significantly more males than females, $p < 0.05$

Table 2 - Causes of non-breeding by experienced Great Skuas on Foula in 1994-96.

	Males	Females	Total
Loss of mate	11	5	16
Loss of territory	7	0	7
Not seen at colony	0	1	1
Unknown (paired, with territory)	2	1	3

Table 3 - Incidence of non-breeding by Arctic Skuas with previous breeding experience.

Year	Incidence of nonbreed (%)	Birds studied	Number of non-breeding	
			males	females
1993	8	66	1	4
1994	3	130	0	4

Table 4 - Percentage of occupied Arctic Skua territories on Foula where a breeding attempt was not recorded.

Year	Territories occupied	Territories where no eggs were laid (%)
1992	159	3.1
1993	145	3.4
1994	134	3.0

Figure 8.1- The negative relationship between the incidence of non-breeding in experienced Great Skuas and the number of chicks raised per nesting pair.

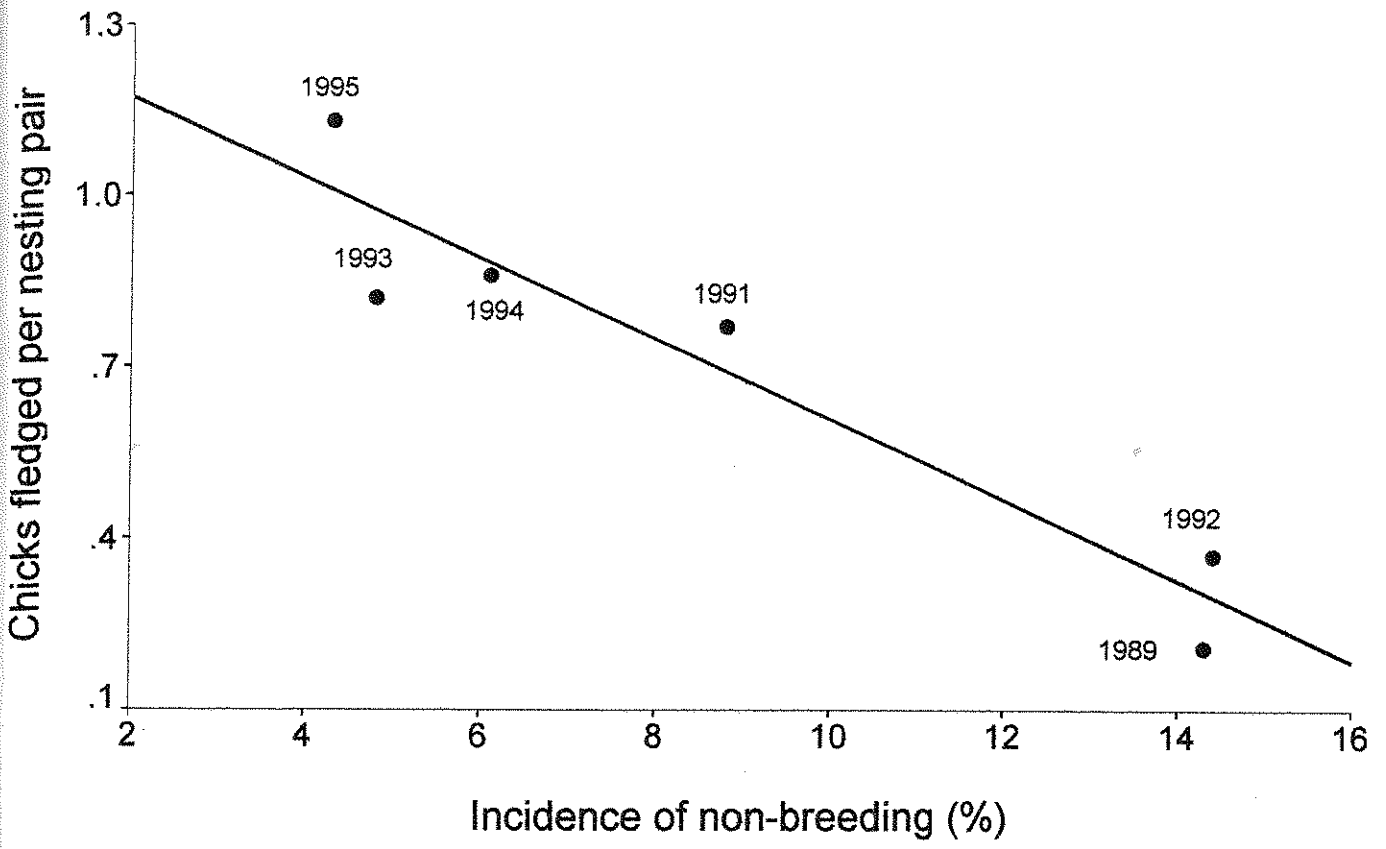


Figure 8.2- The influence of age on the probability of breeding in a particular year by Great Skuas. The line represents the best fit by a quadratic logistic regression. Dots are observed frequencies. Ages between 5 and 7, and 29 and 31 were pooled in one single dot for each group. Analysis was of the ungrouped data. Note that this analysis does not presuppose that the fitted relationship will follow a quadratic equation.

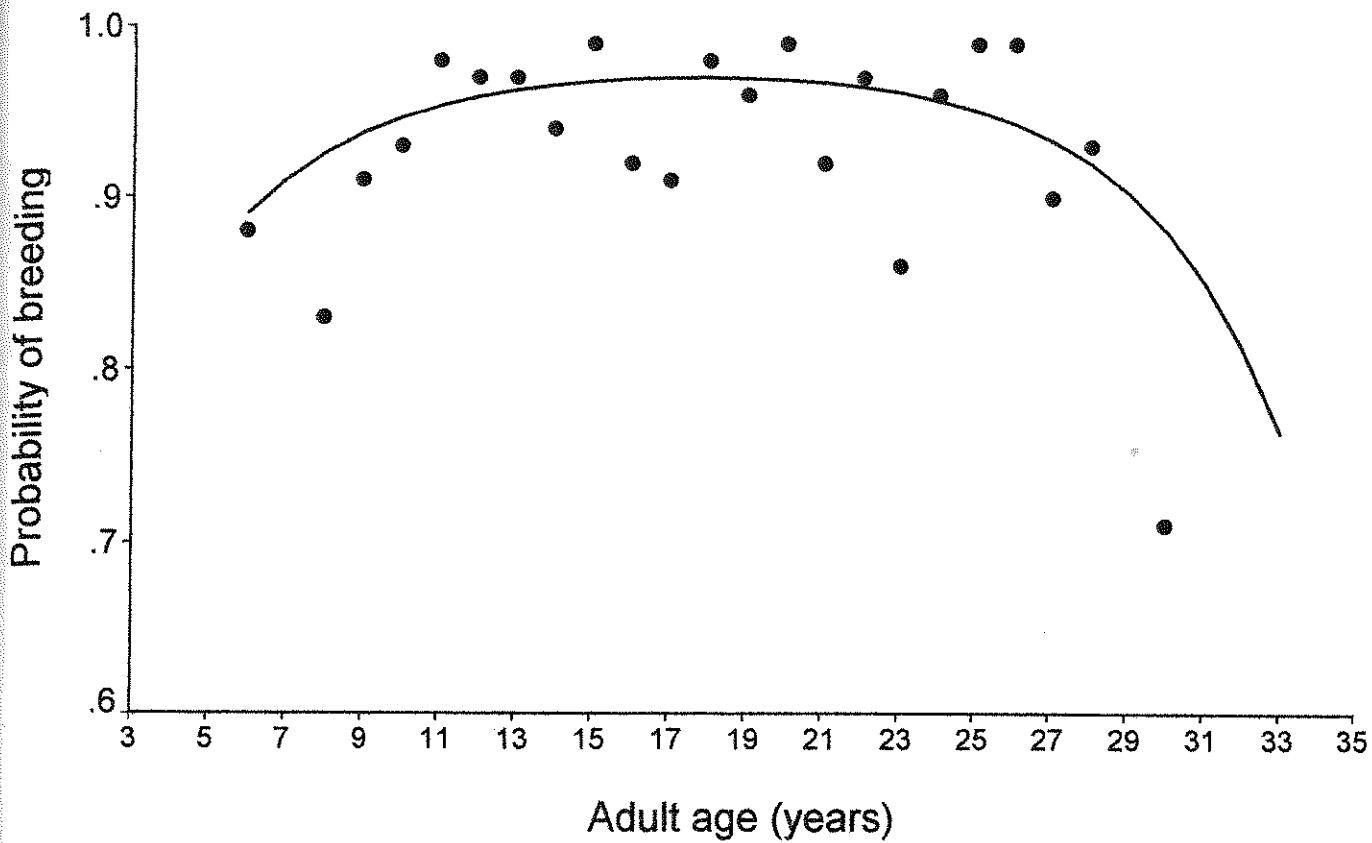
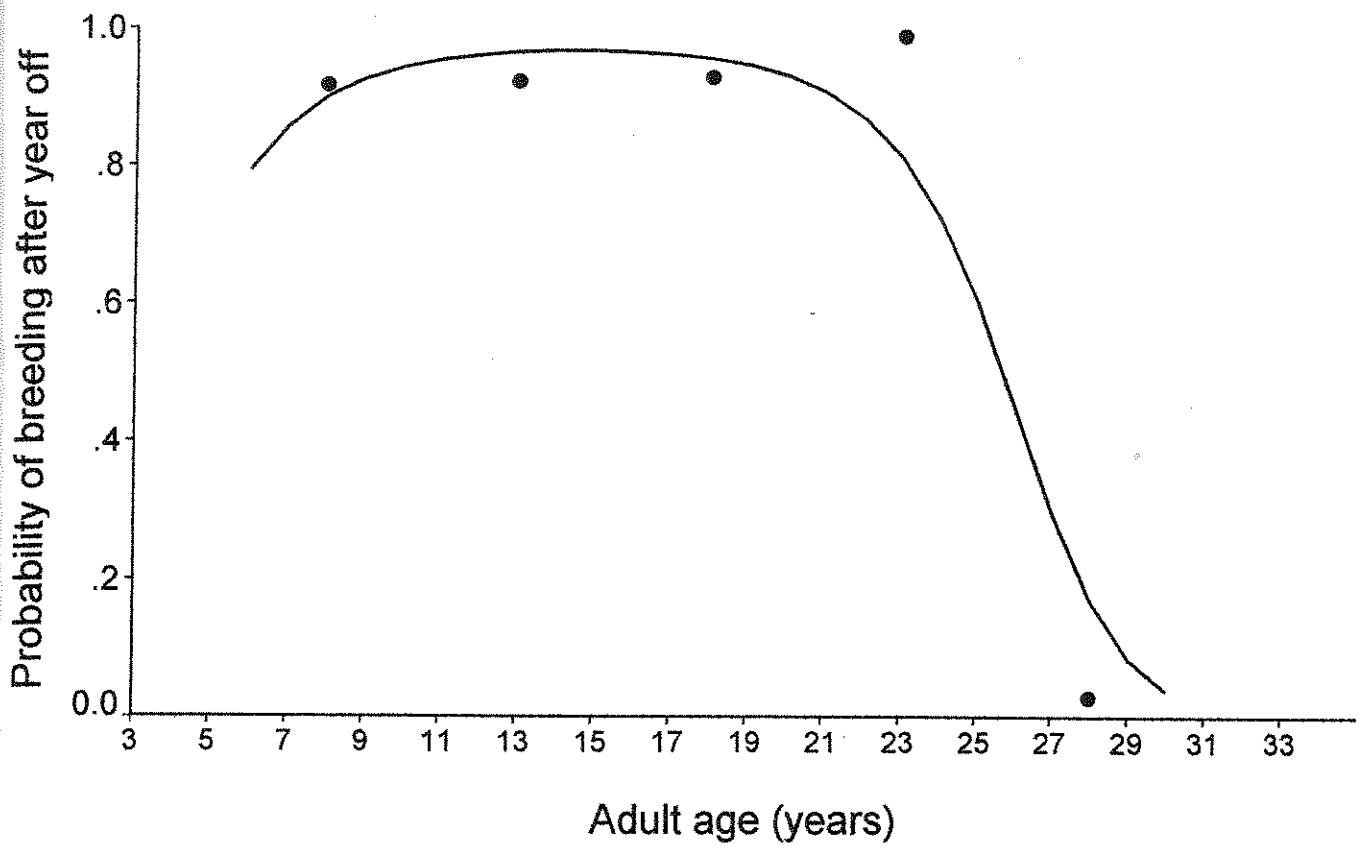


Figure 8.3- The influence of age on the probability of breeding after taking one year off in Great Skuas. Dots represent grouped data for better visual display. Line fitted on ungrouped data. Other details as in fig.2.



General Discussion

In this section, I will not attempt to provide a synthesis of the conclusions that derive from each individual chapter, since they are mostly independent of one another, and are discussed fully within each chapter. Instead, I will briefly discuss some issues related to the costs and benefits of conducting long-term studies on individually marked birds, underlining the potential they present to identify patterns, test hypotheses and eventually make a contribution to ecological theory.

Some studies of wild birds are long-term simply because the rate of data acquisition is, for logistical reasons, slow. Although this is not what makes long-term studies unique and valuable, a long-term study might start for that very reason, and that is possibly the case of the research on Great Skuas in Foula. Initially, skuas were ringed with the main objective of discovering their migration routes and wintering areas. Although each bird carried a ring with an unique number, effectively this was more of a "population marking" than a system to recognise individuals. Extensive ringing on Foula made a decisive contribution to the understanding of the distribution of Scottish Great Skuas during the non-breeding season. Ringed chicks only became more "individualised" after they were measured and weighed at ringing, permitting estimation of parameters like hatching date or an index of body condition. With these data, it became possible, for example, to compare survival rates of groups of fledglings hatched at different stages of the season. It can be argued that, in a way, ringed chicks only became full individuals (from the point of view of the researchers) after being recaptured, when they returned to their breeding colony, and were fitted with unique colour combinations of rings. Then, they were measured and their age accurately determined. Further observation was necessary to establish their sex, and identify their partners. With all this information, interesting patterns could be identified just from following the fates of such individuals over the years, without need for more recaptures. Breeding success could be studied in relation to adult age, breeding experience, body size and partnership duration, amongst others. The evolution displayed by the Great Skua study illustrates the point that assigning a number or a code to anonymous birds is not the only step necessary to get a population suitable for research centred on the observation of individuals. In general, the more characteristics or attributes measured, distinguishing each individual in the

study population (the more *individualised* they are), the greater the potential value of the population for research.

There are many aspects of bird ecology than can only be investigated by long-term studies of marked individuals. The following ones are just a few examples. Lifetime reproductive success is maybe the most obvious one. Given that this is one of the best measures of fitness one can study, and that much ecological research is ultimately focused on the effects of proposed specific adaptations on fitness, lifetime reproductive success could hardly be a more important (but difficult) parameter to measure in natural populations. The effects of age, experience and maturation on breeding and survival, and their implications in life-history theory, form another field of major importance that requires empirical evidence from long-term studies. Population dynamics can also only be properly analysed in longitudinal studies. An interesting but complicated difficulty is emerging from studies with marked individuals. Population fluctuations can be accompanied by shifts of their age-structure, or even of their "quality-structure". Only the use of marked individuals will allow determining adequate parameters for modelling population dynamics, with all the obvious consequences in fields like environmental monitoring and conservation biology. Particularly long-term studies are necessary to research questions relating to long-lived organisms. It is simply not good enough to replace them and ask the same questions using shorter-lived species, since those will be subject to different selective pressures, or the same ones but acting with different intensities.

In most of its important aspects, the long-term study of Great Skuas on Foula did not result from a carefully designed strategy of research. It just happened. Except for the invaluable effort of sustained annual ringing of large numbers of chicks for over three decades, the study can maybe better be described as a succession of opportunistic ideas that capitalised on the investments involved in previous research. That is undoubtedly the case for the part of the study focusing on colour-ringed individuals. None of the researchers (including myself) planned his research with a possible medium or long-term project in mind. That inevitably reflects on the quality of the data at our disposal. Emerging problems, like the occurrence of progressive ring-loss in the birds that were marked in the early years, have not been dealt with. Without a long-term perspective, it would always be too costly, for any individual

researcher, to make a special effort to trap wary skuas in order to replace lost rings. After all, we know our birds, and can recognise them even with a few rings missing. In the future, that could mean disaster, were the project to continue.

One very specific (non-scientific) question related to long-term marking of large numbers of individuals, using tags or colour-rings, is the impact they produce as forms of visual pollution. This is by no means a localised problem. In the whole of south-west Europe, it is virtually impossible to observe a small to medium sized flock (say, two dozen individuals) of Flamingos *Phoenicopterus ruber* or Spoonbills *Platalea leucorodia* that does not include one or more colour-ringed individuals. In 1995, on Foula, I did not manage to obtain a good photograph of an Arctic Skua with nice natural dark legs. All the tame birds I found had been marked. I suspect this question will soon be regarded as an issue, as the public increases its demand for "truly natural" experiences of wildlife.

Given the way most ecological research is currently funded, with emphasis on pre-defined short-term objectives, one might be surprised by the number of long-term studies of individuals that actually take place (see Clutton-Brock 1988 and Newton 1989 for remarkable collections of successful examples). In the absence of broad scientific targets, it seems pointless to attempt to discuss if these are, or not, enough. Evidence suggests that valuable long-term studies can be built as collections of short projects, in spite of the difficulties presented by this strategy. However, it could be that only the studies with the highest quality and sustained investment are likely to survive long enough to become long-term. It is possible that funding agencies will see this process of selection as a "natural system" that does not require further regulation or support. As I write (June 1997), adult skuas that were colour-ringed in 1988 and studied each year ever since, are nesting on Foula. For the first time in a decade, their breeding performance is not being monitored. Perhaps the good thing about a lost opportunity is that we cannot know what is being missed.

The experiment described in chapter five was first imagined and designed in the middle of the field season in 1996. Just over a month later, all the data had been collected. An estimation of the necessary investment in previous field work that made

this possible would certainly prove much harder. One would need to quantify the effort required to ring thousands of chicks over some 30 years, and the effort to trap, measure, colour-mark and sex hundreds of adult Great Skuas. Given the costs and benefits, it seems most unlikely that any agency would ever consider financing such a project. Of course, one of the problems of writing a research proposal for a long-term study is that, while the (large) cost can be estimated, it is impossible to anticipate the benefits, as these could only be predicted if we had any idea of the hypotheses to be tested within the framework of future ecological theory. Coming back to chapter five, some people will argue (two already did) that the results are not fully conclusive anyway. Although that is not the main point, I do agree that many others would certainly, given the same conditions, design a much better experiment. It is even possible that I would have designed a better one myself, had I not spent all that (good) time trapping, measuring and sexing difficult birds. In any case, the birds of known-age/sex/size are still there, available for research, and waiting. Or, to be more precise, slowly going, at a current rate of 8% a year.

References

- Clutton-Brock, T.H. (ed.) 1988. Reproductive success: studies of individual variation in contrasting breeding systems. - Chicago: University of Chicago Press.
- Newton, I. (ed.) 1989. Lifetime reproductive success in birds. - London: Academic Press.

Summary

1) A long term study of Great Skuas on Foula provided large numbers of known-age and individually recognisable birds that were used for tests of ecological hypothesis. Previous studies with these individuals concentrated on the effects of age on breeding and survival, and therefore this particular aspect received little emphasis in this work.

2) Territorial intrusions are performed by birds of many species in order to obtain extra-pair copulations (EPCs), and frequent within-pair copulations are thought to be a response to cuckoldry where mate guarding is not possible. Great skuas are colonial birds in which females are left alone in the breeding territory while males forage for the pair. Opportunities for cuckoldry are therefore numerous, and it could be predicted that sperm competition should be intense in this species. EPCs represented only 0.9% of the copulations observed ($n=339$). Thus opportunity for cuckoldry is a very poor predictor of the intensity of sperm competition, in spite of the relevance given to this factor in the literature. Of three EPCs observed, two involved unpaired territorial males. This suggests that genetic benefits were not the aim of unfaithful females. All three EPCs were preceded by courtship feeding, while only 26% of WPCs followed successful food begging. This statistically significant difference constitutes evidence for a trade of copulations for food in a monogamous bird.

3) Besides the sperm competition hypothesis, territorial intrusions have been suggested to result from birds trying to establish new territories at the expense of others, or trying to find vacancies within previously established territorial boundaries. The fact that most intrusions were made by females already paired with territorial males excluded this hypothesis. Evidence is presented supporting hypotheses that territorial intrusions by females are performed in order to induce males to give away some food, and to become familiarised with potential partners for future breeding seasons.

4) Great skuas displayed a poor correlation ($r_{50}=0.28$) between the ages of partners in breeding pairs. Twenty two percent of the partners differed in age by 10 years or more. Mate fidelity in this population is high, with an annual divorce rate of only

6.4% (n=20/311). Death was responsible for three times more interruptions of partnerships than divorces.

5) Mate changes had a direct cost, because new pairs (of experienced birds) laid later in the season and raised fewer chicks. After mate loss, 26% (n=61) of the individuals did not breed, while faithful pairs always laid eggs.

6) Three types of divorce were detected: (1) Females deserted their partners, leaving them temporarily unpaired. This represented the majority of divorces where the mechanism could be identified. (2) One female was recorded being forced to desert her partner by an usurper. (3) One female deserted her partner after they lost their breeding territory to another pair. Males, but not females, had a higher probability of remaining unpaired after being divorced than after becoming widowers. There was no difference between the sexes in the probability of re-pairing after losing a mate due to its death. Results suggest that divorces that are initiated by birds within the pair are better explained by the "better option hypothesis", as opposed to the "incompatibility hypothesis".

7) In most years studied (11 out of 16) there was a seasonal decline in chick body condition. In the remaining seasons, there was no detectable effect of hatching date on chick condition. Differences between years were statistically significant. Chicks in early broods survived better than late hatched chicks in four years, and no trend could be detected in one season. Annual variation in the seasonal pattern of chick growth and survival, and of adult territorial attendance, suggest that environmental conditions play a role in determining the seasonal decline in performance.

8) Post-fledging survival in relation to hatching date was studied by analysis of ringing recoveries. Hatching date affected post-fledging survival, but only in the first-year of life. Breeding parameters of birds of known hatching date were studied when they came back to breed on Foula. Hatching date of an individual did not affect its laying date or volume of the clutches laid later in life. This suggests that laying date has a low heritability, or none at all. Birds that laid early in the season produced more

future recruits than later birds. After an early breeding attempt, skuas had a higher overwinter survival probability than after a late season.

9) Skuas, like several other seabirds, generally display within-clutch asymmetry (the second egg in the clutch is, on average, smaller than the first). No relationship was found between clutch volume in 2 egg clutches and laying date, hatching success or fledging production. There was a high repeatability (0.72, $p < 0.0001$) in the volume of clutches laid by the same pairs in consecutive years. The influence of adult age on egg size was weak and variable. Unlike clutch volume, clutch asymmetry was not repeatable and showed no relationship with adult age. Furthermore, clutch asymmetry did not correlate with any other breeding parameter. It was concluded that, in Great Skuas, clutch characteristics are not suitable indicators of individual quality or environmental conditions over the range prevailing during this study.

10) An experiment was designed to investigate individual differences in foraging ability of breeding great skuas with the same energy requirements and facing the same environmental conditions. By the means of clutch manipulations, all experimental pairs hatched chicks at the same time. Territorial attendance was then recorded for all pairs. Pairs with one chick had a higher attendance than pairs with two chicks. Attendance declined as chicks grew and food requirements increased. Attendance was not correlated with chick body condition. It was concluded that pairs displaying higher attendance achieved that by being more efficient foragers, and not by provisioning their chicks less well.

11) Pairs with older males had a higher attendance than pairs with younger males. Female age and inferred foraging ability did not correlate. However, older females were less likely to leave their chicks unattended. The results show that age-related differences in the foraging ability of adult long-lived birds clearly exist, and may be responsible for age-specific breeding patterns such as the advancement of laying date with age.

12) Pairs with large birds of either sex had a smaller number of double absences from the territory. This could reflect the greater ability of large birds to fast while their partners forage. The absence of a relationship between male size and attendance questions the validity of the assumption that small males are better foragers, a premise on which several theories on reversed sexual size dimorphism have been built.

13) Individual variation in reproductive performance and behaviour is believed to be partly explained by differences in the quality of individuals. Excluding age effects, quality is frequently assumed to be a fixed trait. We tested if apparent quality, expressed in individual consistency in a breeding parameter (laying date), is indeed permanent. We created mathematical models to evaluate the effect of age-specific timing of breeding on repeatability estimates. Simulations showed that, in short-term studies (lasting 2 or 3 years), age-specific laying dates can produce spurious repeatabilities with values ranging between 0.1 and 0.2, when the value should be zero.

14) Field observations showed that individual consistency of timing of breeding was high over short time intervals, but disappeared over longer periods (4 or 5 years). A comparison between field data and the simulations demonstrated that the high repeatabilities in consecutive years, and the fast subsequent declines, could not be fully accounted by age effects. The mechanisms underlying this surprising pattern are completely unknown, but results clearly suggest that apparent individual quality is a transient attribute in these birds.

15) Tests of specific hypotheses explaining the evolution of reversed sexual size dimorphism in the Stercorariidae are presented. Tests are based on field studies on Great Skuas and Arctic Skuas. A comparative analysis of foraging behaviour and degree of RSD within the Stercorariidae is also presented. No evidence was found supporting the popular theories that claim that RSD evolved as a result of specialised roles during breeding. Large females were not more fecund, nor were they the main defenders of the nest. Male body size did not correlate with any breeding parameter.

In addition, interspecific comparisons did not support the idea that the degree of RSD is related to foraging behaviour during the breeding season (as opposed to morphology). Female dominance within pairs did not affect any breeding parameters.

16) Support was found for theories that RSD is linked to sexual selection. Large females had an advantage when pairing with older males, which could be a result of intra-sexual competition for mates. There was assortative mating for size, indicating that small males could also have an advantage in pairing, as large males seem to be rejected by small females. Given the disparate results of several studies in the bibliography, it is concluded that a large body of empirical evidence will be needed before we can draw firm conclusions about the main selective factors that act to maintain current levels of RSD in natural populations of raptorial birds.

17) Non-breeding by Great Skuas *Catharacta skua* with previous breeding experience affected an average 8.9% (range 4-14%, in 8 years) of the Foula population in each year. For Arctic Skuas *Stercorarius parasiticus* a corresponding value of 5.5% (range 3-8%, in 2 years) was found. Only 3% of the territorial pairs of Arctic Skua (including new recruits) failed to lay eggs.

18) Higher incidence of non-breeding in Great Skuas was found in years when laying was late, eggs were small and fledging production was low. Loss of mate due to death or divorce was the main direct cause of non-breeding. Loss of territory was also important for male birds. In Great skuas, more males missed a breeding season than females, but the same did not apply to Arctic Skuas. Very young and very old Great Skuas were more likely to defer breeding than mid-aged birds. Evidence is presented that the decline in breeding frequency of old birds was due to senescence, as opposed to an increased frequency of mate-changes resulting from a high mortality of old partners.