Studies of Recruitment in the Great Skua

Nicholas Ignatius Klomp

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CANDIDATE'S DECLARATION

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

Nicholas I. Klomp

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SUMMARY

1. Recruitment is defined as the whole process whereby individuals join the breeding group of a population. Various factors which can potentially influence recruitment in seabirds were described and discussed. Great Skuas were considered to be particularly suitable for a study of recruitment in seabirds for several reasons, but mainly because of the tendency for nonbreeders to frequent traditional, fixed club-sites. Some background information on the biology of the Great Skua population on Foula was presented to enable a study of recruitment in Great Skuas to be conducted with a general understanding of the dynamics of the population on Foula.

2. A technique for the accurate determination of the age of adult Great Skuas and other birds was described and validated using twelve known-age birds. The technique, involving counting endosteal lamellae in sections of tibiae taken from dead birds, was also validated independently by three naive observers. Various possible applications for this technique were proposed.

3. Various external measurements were taken of 863 adult Great Skuas by two observers from 1974 to 1990. An analysis of a sample of these measurements revealed that the variability of linear measurements of adult Great Skuas was greater between the two observers than within each observer's repeated measurements of the same birds. However, the measurements taken by the two observers correlated significantly, such that one set of measurements could be transformed to equate to the other set,

thus allowing valid comparisons to be made between years, age, sex and breeding status.

4. Adult female Great Skuas were significantly larger than males in all of six morphometric variables measured. Values of some morphometric variables appeared to increase with age, although the variation with age within a sex was generally small compared to differences between sexes. The mean sizes and weights of nonbreeding Great Skuas decreased over the breeding season, and this was mainly attributed to older nonbreeders arriving at the colony earlier in the season than younger birds. However, 4 and 5 year-old nonbreeders trapped relatively early in the season were heavier and heavier for their wing length than later arriving birds of the same age. Also, individual nonbreeders were found to decline in weight over a season. Weight, and weight for wing length, of breeding Great Skuas were significantly less during 1988-1990 than prior to this period, coinciding with a period of reduced prey availability and increased foraging effort in the late 1980s.

5. Ring recovery data were used to describe the dispersal of Great Skuas from Foula from 1963 to 1990. In general, the dispersal patterns and causes of recoveries had not changed since they were first described by Furness (1978) up to 1977. However, recoveries of 1-4 year-olds had increased since 1977 and recoveries of first-year birds were greater after 1986 than for all previous years combined.

6. Ring recovery data and observations of individually colour-ringed birds provided several lines of evidence suggesting that levels of immigration and emigration in the Great Skua population on Foula were very low. Great Skuas also

displayed a high degree of micro-philopatry, generally choosing clubs and breeding sites within areas on the island from which they originated.

7. An analysis of Great Skua chick-ringing data on Foula from 1975-1990 revealed that median hatching dates differed significantly among years and areas on the island. Relative and calendar hatching date appeared to influence chick weight, survival and dispersal of an individual in its first year, and subsequent adult survival up to six years after hatching. Chicks that hatched earlier had greater chick weight, greater first-year post-fledging survival, dispersed shorter distances in their first year of life and were heavier as 3-6 year-old nonbreeders, compared to chicks that hatched later in the season. These findings were most easily and consistently explained in terms of inheritable parental quality.

8. Diurnal and seasonal variations in numbers of nonbreeding Great Skuas on Foula were monitored during the 1975, 1976, 1988, 1989 and 1990 breeding seasons. The accuracy and use of daytime and night-time counts were compared. Night-time counts represent the total number of nonbreeders attending the colony on a given date, whilst daytime counts were more variable, although consistently timed afternoon counts were able to provide useful diurnal and seasonal comparisons. The mean number of nonbreeders attending the colony between May and August was significantly less in 1988 (732 individuals), 1989 (662 individuals) and 1990 (656 individuals) than in 1975 (approximately 1949 individuals).

9. Numbers of nonbreeders at the colony correlated with

seasonal changes in diet that appeared to indicate changes in food availability. A reduced afternoon attendance by nonbreeders in 1989 (40%) and 1990 (38%), compared to 1976 (67%), reflected unusually poor Great Skua breeding seasons on Foula during 1988-1990.

10. The number of breeding Great Skuas on Foula was determined by counting Apparently Occupied Territories (AOTs) during the 1988 and 1990 breeding seasons (2400 and 2340 AOTs, respectively, representing 20% of the northern hemisphere population).

11. Both the number of breeders and the peak number of nonbreeders declined from 1977 to 1990, although the peak number of nonbreeders decreased much more (nonbreeders by 80%, breeders by 22%). The rapid decrease in numbers of nonbreeders appears to be due to increased recruitment as a consequence of a reduction in adult survival rate, since age at first breeding and breeding success did not change before 1987.

12. Numbers of nonbreeders attending the colony were considered to be early and sensitive indicators of environmental changes having adverse effects on the population, both within a season and over a longer term, since nonbreeders act as a buffer to the breeding population.

13. Two methods were used to determine the total number of nonbreeding Great Skuas that frequented Foula during the breeding seasons. Totals of 4013 (S.E.=479) and 3303 (S.E.=243) nonbreeding Great Skuas were estimated to frequent Foula in the 1989 and 1990 breeding seasons, respectively. These totals were far greater than indicated by individual

counts, due to each bird staying in the colony an average of only 16-21 days.

14. Nonbreeding Great Skuas on Foula consistently attended one of 15 clubs when frequenting the island during the breeding season. More than 90% of nonbreeders on Foula were 3-7 years old. The age structure of the nonbreeders at clubs varied during the season due to older birds arriving earlier than younger birds. This was facilitated by individual nonbreeders arriving earlier to the colony each successive year.

15. Recruitment rates of approximately 14% of the pool of nonbreeders frequenting Foula in the preceding year were recorded in each year 1989-1991. This rate was not sufficient to maintain the breeding population at a constant level.

16. The mean and median age at first breeding was 7 years, with a range of 4 to 10 years. This was similar to the mean age at first breeding recorded in the 1970s, despite a reduced nesting density in the colony in recent years.

17. Clubs were found to play a pivotal role in the recruitment process of Great Skuas. Birds spent at least one season and an average of three seasons at club-sites prior to breeding. Most birds were faithful to one club. First-time breeders generally chose territories in the vicinity of the club-site most frequented in previous years. New recruits probably selected partners at the club-site prior to holding breeding territories.

18. A comparison of population parameters of different colonies in Shetland revealed correlations between numbers of breeders, nonbreeders and clubs, and between growth rates of colonies and the ratio of breeders to nonbreeders present.

19. First-time breeders held smaller territories (nearest nest distance), incubated a higher proportion of one-egg clutches and were less successful at raising chicks than established breeders.

20. New recruits incubating two-egg clutches had greater mean wing lengths than those incubating one-egg clutches. Young recruits (5 or 6 years old) had smaller territories than older first-time breeders.

21. Three types of breeding territories of first-time breeders were described. First-time breeders recruiting at the edge of the established colony ('periphery' territories) held larger territories than those recruiting into established breeding areas ('colony' territories), whilst birds that first bred within 40m of the centre of a club-site ('club' territories) held even smaller territories. 'Club' and 'periphery' first-time breeders were probably lower quality recruits. Evidence for this was that 'club' and 'periphery' recruits had smaller mean wing lengths, a greater proportion of one-egg clutches and lower breeding success than new recruits in the rest of the colony.

22. In the second year of breeding, birds generally held larger territories and 'club' breeders generally nested further away from the club-sites.

23. A model of the process of recruitment in Great Skuas is proposed, based on the results of this research.

CHAPTER 1

General Introduction

Some authors consider all skuas (Family Stercorariidae) to belong to a single genus. This classification is usually based on behaviour (Hartert 1912, Moynihan 1959, Andersson 1973) or skeletal structure (Schnell 1970). Other authors regard the family as having two separate genera, *Stercorarius* (small skuas) and *Catharacta* (large skuas), based on differences in distribution, body size and plumage (Peters 1934, Wynne-Edwards 1935, Bannerman 1963). This is the classification favoured by Furness (1987a) and adopted in this thesis.

The genus *Catharacta* consists of three species. Two of these, *Catharacta maccormicki* (South Polar Skua) and *C. chilensis* (Chilean Skua), are confined to the southern hemisphere. The third species, *C. skua*, includes three southern hemisphere subspecies: *C. s. hamiltoni* (Tristan Skua), *C. s. lönnbergi* (Brown Skua) and *C. s. antarctica* (Falkland Skua). *C. skua* also includes a subspecies found only in the northern hemisphere: the Great Skua *Catharacta skua skua*, or Bonxie (Furness 1987a).

Great Skuas breed in Iceland, the Faeroes and northern Scotland, plus approximately thirty pairs breeding in each of Spitzbergen and Bear Island, and a total of less than ten pairs breeding in Hopen and North Norway (Furness 1987a). The world population of Great Skuas was estimated to be approximately 35,000 individuals in the mid-1980s, with a breeding population of about 12,500 individuals (Furness 1987a). Approximately 5000 pairs breed in Shetland, 200km north of the Scottish mainland, and around half of these breed on the island of Foula, 22km west of the nearest point of Shetland mainland. Hence, Foula contains about 20% of the world population of Great Skuas (Furness 1987b), making the island an important breeding station for this Red Data Book species (Batten et al. 1990).

Foula is a small island 5km long and 4km wide. The population of Great Skuas was reduced by hunting and egg collecting during the nineteenth century to three pairs in 1860. It increased by a rate of 7% per annum from 1900, reaching a peak of approximately 3000 pairs in 1975, and has since declined (Furness 1986). Breeding Great Skuas generally return to their territories on Foula during April, and egg-laying commences in early May. Around 90% of the clutches consist of two eggs, the remainder being single-egg clutches (Furness 1977, Hamer et al. 1991). Incubation lasts an average of 29 days and is performed by both sexes but with females generally taking the larger share. Hatching is asynchronous. The young are semi-altricial and are guarded mainly by the female (Cramp & Simmons 1983). Chicks are fed mainly by the male, by complete regurgitation. Fledging occurs after an average of 44 days (Cramp & Simmons 1983). During winter months, Great Skuas disperse widely throughout the North Atlantic Ocean, with younger birds generally travelling further from their natal colony than older birds (Furness 1987a). Young birds generally do not attend a colony for three or more years after fledging.

During the 1970s, Great Skuas on Foula had exceptionally high breeding success compared with other skua populations. In the 1975 and 1976 breeding seasons, an average of 93% of Great Skua chicks on Foula fledged, resulting in a mean breeding success of 1.24 chicks per pair (Furness 1984). Adults spent a comparatively small proportion of their time foraging, and experienced pairs never left their chicks unguarded. Chicks were fed largely on Sandeels (scientific names and authorities of all species mentioned in the text are given in Appendix I). Sandeels and whitefish (discarded from fishing trawlers) constituted more than 95% of the diet of breeding and nonbreeding adult Great Skuas (Furness & Hislop 1981). Sandeels have a higher calorific content than other items in their diet, and appeared to be the preferred food (Furness & Hislop 1981). The low chick mortality and high breeding success of Great Skuas on Foula during the 1970s was attributed to the availability of an abundant food supply, particularly that of Sandeels (Furness 1984).

During the 1970s and early 1980s, Sandeels formed the basic food of most seabirds in Shetland (Ewins 1985, Ewins et al. 1988), with an estimated 47,000 tonnes consumed by seabirds each year during 1981-1983 (Furness 1990). A Sandeel fishery was established in Shetland in 1974 and reached a peak in 1982 with a landing of 52,000 tonnes (Bailey et al. in press). Stocks of Sandeels have declined markedly since the mid-1980's (Kunzlik 1989, Monaghan et al. 1989a,b, Bailey et al. in press), and it has been suggested that this may be due to overfishing (Avery & Green 1989). However, the available fisheries-based data suggest that adverse environmental factors could be influencing the survival and/or movements of Sandeel larvae, thereby reducing the number of young Sandeels recruiting into the population (Kunzlik 1989, Bailey et al. in press).

Long-term studies of Great Skuas on Foula commenced during a period of rapid population growth and high breeding success. This research has provided detailed data on the ecology of the breeding population at a time of apparently abundant food supply (Furness 1977, 1984, 1987a). In addition, some data were obtained on the diet and activities of nonbreeding Great Skuas on Foula during this period (Furness 1977). During 1988-1990, Hamer (1990) studied aspects of the ecology of breeding Great Skuas on Foula in a period of declining Sandeel stock. He recorded a greatly reduced breeding success compared to that seen in the 1970s (an average of 0.18 chicks per pair in 1988 and 1989), probably caused by a reduced nest attendance by adults (due to increased foraging effort) resulting in increased chick predation and a low mean fledging success (13%). There was also evidence of a sharp decline in the annual survival rates of Great Skuas more than one year old, from 93% per annum in the 1970s to 80% per annum in the late 1980s (Hamer 1990). Similar reductions in breeding success were also recorded in other Great Skua colonies and for many other seabird species in Shetland. Also, recent declines in numbers of Shetland seabirds have been recorded after many decades of continuous increase (Heubeck 1989). The unprecedented breeding failures and declines in population sizes of seabirds in Shetland have been attributed to the decrease in stock biomass and availability of Sandeels. The reduced availability of Sandeels has led to Great Skuas killing more seabirds and depending more heavily on discarded small whitefish obtained at fishing boats (Hudson & Furness 1988).

It is not clear how such declines in food availability, breeding numbers, breeding success and adult survival affect the recruitment of young birds into breeding populations.

Indeed, very little is known about the process of recruitment in seabirds or in any animal with overlapping generations and deferred maturity (Ollason & Dunnet 1983, Furness & Birkhead 1984, Porter & Coulson 1987).

So, what is recruitment? In its broadest sense, recruitment is the process by which prebreeders join the breeding population, i.e. become breeders. Such a process involves many stages, from fledging to first-time breeding, and is potentially influenced by many variables. Some authors ~~only~~ consider only the final 'step' of this process to be recruitment, i.e. the addition of new birds to a given population in a given year (Duncan 1978, Ollason & Dunnet 1983, Danchin et al. in press). In this context, recruiting birds may not necessarily be first-time breeders (i.e. new recruits) but may have bred previously, either in another colony, or in the same colony but not in the immediately preceding year. It can be seen that recruitment is a complex parameter encompassing such factors as levels of philopatry (the degree to which birds return to breed at the natal colony), breeding site-fidelity and intermittent breeding (Ollason & Dunnet 1983). A knowledge of the process of recruitment, including the behaviour and movement of pre-recruits, is basic to a greater understanding of population ecology, because the number of birds recruiting into a colony each breeding season can be a major determinant of changes in breeding population size from year to year (Ollason & Dunnet 1983, Porter & Coulson 1987). Although there are several important studies of recruited birds, including removal experiments that altered recruitment rates and age at first breeding in seabird colonies (eg. Coulson et al. 1982), the difficulty in studying pre-recruits has resulted in few investigations being attempted. Studies of recruitment are hampered by the inability to determine accurately the ages of adult birds (Caughley 1977) and the general inability to identify individuals in a colony. These problems have been overcome somewhat by extensive marking programmes in a few studies of recruitment in Herring Gulls (Duncan 1978), Fulmars (Ollason & Dunnet 1983) and Kittiwakes (Coulson & Thomas 1985). However, the recruitment process, as a whole, remains poorly understood (Porter 1990).

In studies of recruiting birds, the rate of recruitment at a colony in a given breeding season has been calculated in various ways. Ollason & Dunnet (1983) could not directly identify recruiting Fulmars, so used four different 'indices of recruitment' based on numbers of nest-sites and the proportions of ringed and unringed birds at the colony. However, in studies where new recruits could be identified within a colony, the recruitment rate is usually calculated from the number of first-time breeders, expressed as a proportion of either (1) the total number of breeding birds at the colony (e.g. Duncan 1978, Porter & Coulson 1987), or (2) the total number of birds produced from the population in previous years that had not yet been recorded breeding (e.g. Ratcliffe _et al_. 1988, Court _et al_. 1989, Croxall _et al_. 1990), or (3) the number of birds probably capable of breeding (e.g. of breeding age) that had previously associated with the colony but not bred (e.g. Porter 1988, Owen & Black 1991).

The rate of recruitment has been shown to be one of the most important factors determining changes in the breeding population from year to year in both seabirds (e.g. Fulmars:

Ollason & Dunnet 1983) and other long-lived birds (e.g. Sparrowhawks: Newton in press, Eiders: Coulson 1984). Also, changes to the process of recruitment in seabird colonies can alter the genetic structure of the population through changes in gene frequencies. This can occur if changes in individual survivorship, juvenile dispersal or levels of philopatry change sufficiently to alter the genetic quality of recruits (Cooke et al. in press). Besides recruitment potentially having such important effects on breeding populations, studies of recruitment can also provide clues to the overall health of a seabird colony. Porter & Coulson (1987) found that a decline in the number of nonbreeders attending a Kittiwake colony was the first indicator of a decline in the well-being of the breeding population.

The process of recruitment in a seabird colony can be influenced by a wide variety of variables. Even before young hatch, the probability that they will recruit into a breeding population may have been influenced by parental quality or other factors. Ratcliffe et al. (1988) showed that a significantly greater proportion of young Snow Geese recruited from mothers aged 5-7 years than from younger or older mothers. They also showed that the year of hatching strongly influenced the relative timing of recruitment of the young. Many studies have shown that fledging success is less in young birds (see Perrins & Birkhead 1983) and in very old birds (e.g. Great Tits: Perrins & Moss 1974, Fulmars: Ollason & Dunnet 1978). There are also many studies that have shown relationships between some measure of parental quality (generally age) and laying dates (e.g. Wooller & Coulson 1977, Nelson 1978a), and among laying dates, fledging weight and fledging success (e.g. Birkhead & Harris 1985). Further, post-fledging survival in some seabird species has been shown to decline with fledging ~~weight~~ date (Perrins 1966, Parsons *et al*. 1976) and increase with chick weight (e.g. Brooke 1990). Whilst these latter variables will obviously affect the number of potential recruits in future populations, it is not clear whether any of these variables result in sustained differences in the quality of individuals and their chances of recruitment. However, some long-term studies have shown that only a small minority of individuals in a population produce offspring that live to reproduce themselves (e.g. Newton 1989).

First-year mortality is a strong influence on numbers available to recruit into a seabird population because it is generally much higher than the mortality rate of older birds (Chabrzyk & Coulson 1976, Harris 1983, Ainley *et al*. 1990, Croxall *et al*. 1990). The high rate of mortality of newly fledged young may be due to the lack of foraging and flying experience, but is known to be influenced by climatic conditions - such as autumnal storms causing wrecks of young seabirds - and food availability (e.g. Furness 1978, Hudson, 1985).

After fledging, young seabirds generally disperse widely often becoming largely pelagic for one or more years. The wide dispersal patterns of these young birds probably provide the opportunity for these individuals to first visit a colony (or other potential breeding site), other than their natal colony. Such dispersal patterns may be part of the mechanism of species to extend their range. In most seabird species, individuals do not begin to breed until they are 3-8 years old (Bradley & Wooller in press, Danchin et al. in press). Several studies have shown that prebreeders frequent a colony for one or more years before attempting to breed (e.g. LeResche & Sladen 1970, Pickering 1989, Ainley et al. 1990). In many colonies, nonbreeders (mostly prebreeders, but also other adults not breeding in that season) mix with established breeders on ledges, or may gather on rocks below colonies, e.g. Kittiwakes and Guillemots (Birkhead & Hudson 1977, Cramp & Simmons 1977). Gulls, Gannets, Great Skuas and other seabirds sometimes gather into 'clubs' within or near breeding colonies (Tinbergen 1953, Nelson 1978a,b, Furness 1987a). The sites of these clubs are often transitory, moving according to wind direction, although some favoured localities are regularly attended. Great Skua clubs, however, are at fixed, traditional sites (Furness 1987a). Most authors consider clubs to be only attended by prebreeding birds, based on evidence from time-budget studies and studies of the behaviour of known breeders (Tinbergen 1953, Young 1972, Nelson 1978a, Furness 1987a). All nonbreeding Great Skuas attending a colony frequent these clubs, and they are all present at a club at night (Bayes et al. 1964), although this is not necessarily the case for other seabird species that form clubs (e.g. Gannets: Nelson 1978a). Seabird clubs are not the gatherings or communal roosts described for other birds (e.g. corvids: Coombs 1978, and other birds: Zahavi 1971), nor is there any evidence that they are formed for reasons of territory acquisition (as in the Magpie: Birkhead & Clarkson 1985) or as information centres for finding food (Ward & Zahavi 1973). Clubs are not known to be dominated by one sex or by closely related individuals, as in some flocks of corvids

(Coombs 1978). Seabird clubs are often intensely active congregations of nonbreeders in which individuals display the full range of territorial and sexual behaviour including copulation (Nelson 1978a, Furness 1987a). Some young Herring Gulls and Great Skuas at clubs even attempt to breed, laying eggs in shallow scrapes on the edges of club-sites (Tinbergen 1953, Furness 1974), although the chances of fledging a chick under these circumstances must be close to zero (Furness 1987a).

Porter & Coulson (1987) suggested that nonbreeders associated with a colony could be considered to be a 'pool of potential recruits'. This pool of nonbreeders varies in size and composition from colony to colony, even within the same species, and over the breeding season. In general, prebreeders arrive at the colony later than breeders and leave earlier. There is evidence of a flow of individuals through a colony within a season, with older prebreeders arriving before younger ones (e.g. Furness 1977). Whilst numbers of nonbreeders at a colony at a given time are relatively easy to determine, especially in species that form clubs, very few studies have attempted to estimate the total number of nonbreeders frequenting a colony over a whole season, and only ever in relatively small colonies (e.g. Porter & Coulson 1987, Pickering 1989). Sigfússon (1990) estimated that the number of Fulmars visiting a colony in Orkney was between two and five times as many as bred there.

Very little is known about the patterns of colony attendance of nonbreeding seabirds, or how such patterns affect the process of recruitment (Ollason & Dunnet 1983), although recent studies have revealed relationships between attendance patterns and recruitment in some species (Porter 1988, Pickering 1989). In the past, most authors considered colonial seabirds as intensely philopatric (e.g. Tinbergen 1953, Wynne-Edwards 1962). However, this assumption was mostly based on seabirds which were ringed as chicks and subsequently breeding in the same (natal) colony, without consistent search effort in other colonies (Bradley & Wooller in press). Coulson & Nève (in press) estimated that 36% of young Kittiwakes were philopatric, casting serious doubts on previously held views of almost total philopatry in colonial seabirds. There is also much evidence, for birds of various species, of sexually related differences in philopatry and dispersal (Greenwood 1980, Greenwood & Harvey 1982). Since the period in a colony, prior to breeding, would allow a prebreeder to obtain information about local food supplies and environmental conditions (Nelson 1978a), as well as mate and site availability and local breeding success, one might expect prebreeders to visit several sites or clubs within several colonies to select where to breed. However, although prebreeders of some seabird species are known to move intermittently among different colonies (Mainwood 1976, Harris 1984), the prevalence of this behaviour and the extent to which it affects the degree of philopatry in seabirds remains unclear. A few studies have shown that most non-philopatric recruits come from nearby colonies (e.g. Bradley et al. 1991). Recent studies have shown that the degree of philopatry can be related to differing environmental and breeding conditions at different colonies (e.g. Danchin & Monnat in press).

In many seabird species there is considerable individual variation in the age at first breeding. Recent studies have shown that physiological maturity in Wandering Albatrosses is achieved up to three or four years before breeding is first attempted (Hector et al. 1986, 1990). It is generally thought that physiological immaturity is not the main reason for the long prebreeding period and deferred breeding seen in seabirds. Other reasons for this might be related to foraging inexperience in young birds (Lack 1966) and a trade-off between annual production of young and annual survival rates to achieve maximum lifetime reproductive output (e.g. Wooller & Coulson 1977). However, most authors consider that social limitations play the most important part in restricting the age at first breeding, operating through both the requirement to learn social skills (e.g. displays) and the competition for socially limited resources within the colony (Wooller & Coulson 1977, Ainley 1978, Nelson 1978a, Bradley & Wooller in press). Recruitment rates and ages at first breeding have been shown to vary in some seabird species with varying population densities, competition for nest-sites and other environmental factors (Harris 1973, Duncan 1978, Coulson et al. 1982, Owen & Black 1991).

The process of mate and site selection in seabirds remains relatively unclear. It appears that pairs are formed at nest-sites in most seabird species, although some seabirds are known to arrive at the colony after pair formation has taken place (e.g. Sandwich Terns: Veen 1977). Breeding pairs are also known to be formed at club-sites or elsewhere in the colony away from the subsequent breeding site, often one or more years prior to breeding (e.g. Tinbergen 1953, Porter 1988, Pickering 1989). Breeding pairs are generally formed between individuals of similar ages (e.g. Coulson 1966, Furness 1984). Coulson & Thomas (1983) found that Kittiwakes about to breed for the first time select partners also without previous experience (and, hence, generally of similar age), mainly as a result of these birds arriving relatively late to the colony once experienced breeders had already formed pairs. This conclusion was also drawn by Mills (1973) in a study of Red-billed Gulls. However, Shaw (1985) found that the Blue-eye Shag also formed pairs of similar-aged breeders, despite that an average of 77% of pairs are not continued from one season to the next in this species. Shaw (1985) argued that these birds were probably able to estimate the age of potential mates from behavioural or physical cues, and choose the oldest (and probably most experienced) mate they could attract, with older birds more capable of attracting older mates than younger birds.

In the year following first-breeding, breeding success and mate- and site-fidelity increase markedly in most seabirds (e.g. Coulson 1966, LeResche & Sladen 1970, Mills 1973, Weimerskirch 1990). These birds return to the colony earlier, sometimes occupy better quality sites, and breed earlier (Perrins & Birkhead 1983, Furness 1984). Nelson (1978a) found that laying dates in Gannets became progressively earlier for the first four breeding attempts. It is possible that older birds are able to attain breeding condition earlier than younger birds (Birkhead & Harris 1985), since older, more experienced birds are more proficient at feeding (e.g. Dunn 1972). This is consistent with Porter's (1988) finding that recruits were in better physical condition (heavier for their size) than non-recruits, although Ollason & Dunnet (1978) suggested that higher body-weight might be a consequence of reproductive condition. Breeding site-fidelity in established breeders is usually very high (Bradley & Wooller in press), except in cases of extreme disturbance (Coulson & Nève in press). The occurrence of intermittent breeding probably declines as birds become more experienced (Dunnet 1991).

Several authors call for further study of the whole process of recruitment in seabirds, including an increased knowledge of the origin, distribution, mobility, behaviour and individual variation of nonbreeders, to elucidate the processes of becoming established in a breeding colony (Ollason & Dunnet 1983, Porter & Coulson 1987). In many ways, Great Skuas are especially suitable for a study of recruitment because, during the breeding season, nonbreeders settle at traditional club-sites in and around the colonies. All nonbreeding Great Skuas attending the colony settle in these clubs at night. Although there are no obvious plumage differences between breeders and nonbreeders, colour-ringing and time-budget studies (Furness & Hislop 1981, Furness 1987a, Hamer et al. 1991) have confirmed that breeding Great Skuas rarely, if ever, attend clubs. These features allow the nonbreeding component of a Great Skua colony to be studied as a distinct unit, and allow birds to be trapped and individually marked whilst still nonbreeders; advantages generally acknowledged as requirements for a thorough study of recruitment in seabirds (Ollason & Dunnet 1983, Porter & Coulson 1987). Other advantages of choosing Great Skuas to study the process of recruitment include the facts that they are long-lived, they are highly site-faithful as breeding adults, their populations tend to be stable, they are rather little affected by variations in weather, and adults are able to exploit a wide variety of foods (Furness 1987a). Hence, Great Skua populations are less responsive to short-term fluctuations in conditions than many other seabird species (e.g. Arctic Terns: Monaghan et al. 1989b).

This thesis presents studies of various aspects of the ecology of nonbreeding Great Skuas, in an attempt to describe some of the many factors involved in the process of recruitment in this species. These studies were conducted in Shetland, mainly on Foula, during 1988-1991. A Shetland-based study of recruitment in Great Skuas had the advantage of a large proportion of the world population being present within a relatively discrete group of colonies. Extensive research of Great Skuas on Foula over the last twenty years afforded an opportunity to study recruitment in a colony with previous population changes, breeding successes and mortality rates well documented. Also, information on nonbreeding Great Skuas on Foula collected in the 1970s (Furness 1977) allowed useful comparisons to be made with this study. A consistent chick-ringing effort since the mid-1960s resulted in a large proportion of the birds on the island carrying British Trust for Ornithology (BTO) monel rings, from which their age and origin could be determined. Studies of breeding Great Skuas during 1988-1990 (Hamer 1990, Hamer & Furness 1991, Hamer et al. 1991) allowed this research to be conducted during known breeding and survival conditions in the colony.

The following chapter broadly describes the methods adopted during this study, although more specific methods are described at the beginning of each chapter. Chapter 3 presents a technique for determining the age of adult Great Skuas, and other birds. Chapter 4 presents an analysis of morphometric data of Great Skuas, the results of which are used, as required, throughout the thesis. Chapter 5 describes the dispersal and levels of philopatry in Great Skuas. The effects of hatching date on chick weight, post-fledging survival and dispersal, and subsequent adult weight are discussed in Chapter 6. Chapter 7 describes variations in the numbers of nonbreeding Great Skuas attending Foula and the influence of inferred prey availability. Chapter 8 presents a study of the total number of nonbreeders frequenting the island. The role of clubs and other aspects of the process of recruitment in Great Skuas are described in Chapter 9. Finally, the General Discussion, Chapter 10, presents a tentative model of the process of recruitment in Great Skuas, based on the results of the previous six chapters. The principal findings of this research are listed in the Summary at the beginning of the thesis. The results of the author's research on seabirds, conducted during 1988-1991, that were not presented in this study are appended at the end of the thesis.

Most chapters of the thesis have been written as discrete papers and some have already been published or accepted for publication. The adoption of such a format has resulted in some repetition, particularly in the introductory sections of some chapters. However, this has been kept to the minimum considered appropriate.

CHAPTER 2

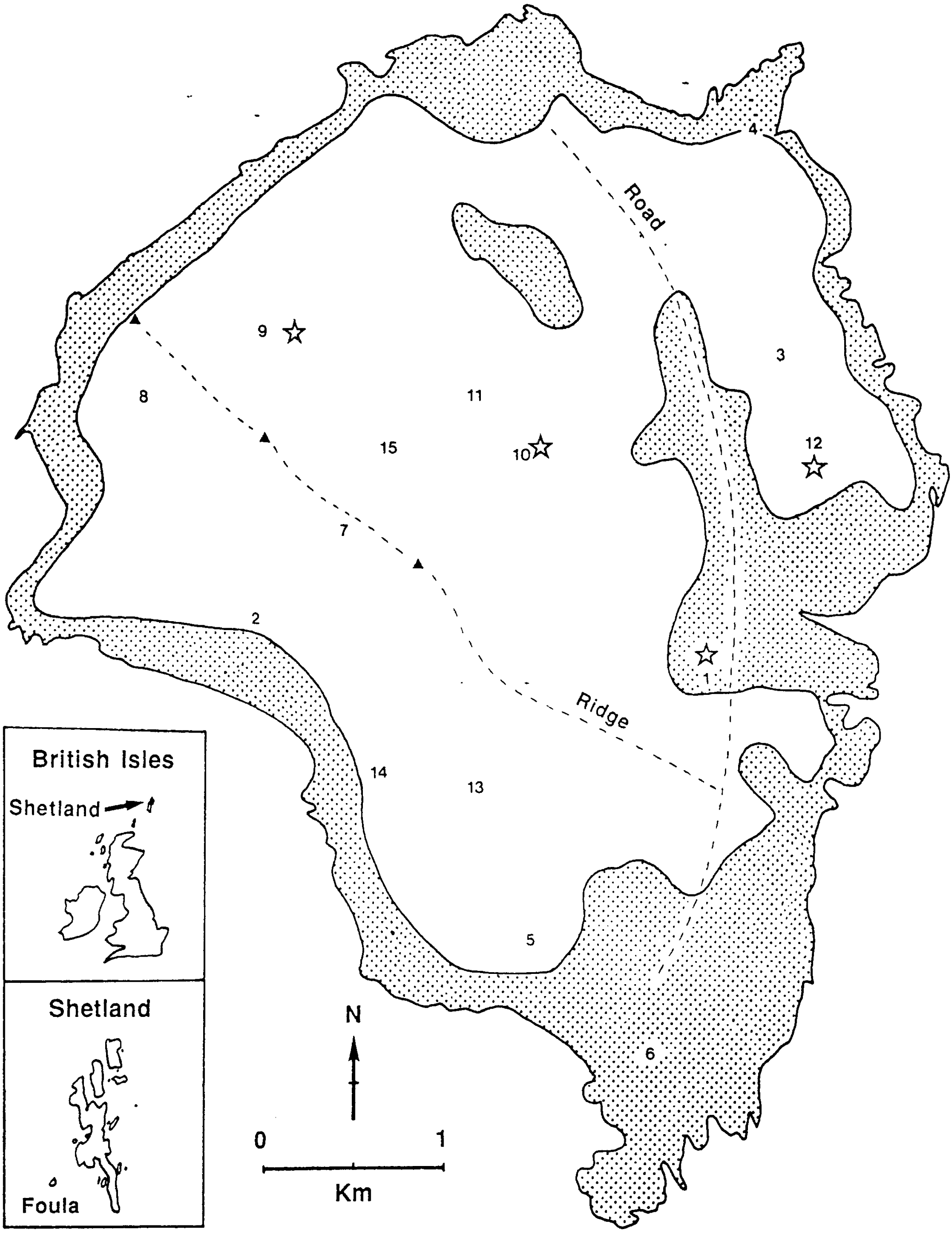
General Methods

This research was conducted in the Shetland Islands, 200km north of the Scottish mainland during the 1988-1991 breeding seasons (May - August). R.W. Furness conducted all the pre-1988 research presented in this text, unless otherwise stated. Most of the data were collected at the Great Skua colony of Foula, an island 22km west of the nearest point of Shetland mainland, although some fieldwork was also done at the colonies of Bressay, Fair Isle, Fitful Head, Fetlar, Hermaness and Noss (see Figure 2.1).

Foula, 60°08'N 2°05'W, is 5km long from north to south and 4km from east to west, and has the second, third and fourth highest peaks in Shetland and the highest sheer cliff in Britain. Most of the island is composed of old red sandstone, with a small area of highly metamorphosed pre-Cambrian strata in the extreme north-east (Mykura 1976). Parts of the low-lying eastern side of the island have been fenced and cultivated, but outside these areas the land is covered with peat, often to considerable depth. Drainage is poor, resulting in many small pools and areas of damp, marshy ground. The island is currently inhabited by only 35 permanent residents, with small numbers of tourists arriving in the summer. Residents and tourists rarely leave the well-worn paths or road when out of doors, so the wildlife on the island is relatively undisturbed, as it has been for many years.

Breeding Great Skuas nest on grassy ground over most of the inland areas of Foula. The colony can be divided into three main areas, based on geographical boundaries and Great Skua breeding history on the island, as shown in Figure 2.1. The

FIGURE 2.1. Map of Foula showing the area occupied by breeding Great Skuas in 1990 (not shaded). The club-sites are numbered from 1 to 15 and the locations of the four bathing sites are indicated by stars. Area 1 (see text) is south-west of the ridge joining the three main peaks on the island (triangles), Area 2 is between the ridge and the road and Area 3 is east of the road.


Road
Ridge
1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
British Isles
Shetland
Shetland
Foula
N
0
1
Km

oldest part of the colony (Area 1) has been occupied since the 18th Century, whilst the newest part of the colony (Area 3) was established in the 1970s (Furness 1987a). Nonbreeding Great Skuas present on the island attend traditional club-sites located in and around the colony. Of the 15 club-sites on Foula, four are associated with bathing sites, where both breeders and nonbreeders bathe and preen, although the nonbreeding component (club) of such sites is usually quite separate (see Figure 2.1). 'Temporary clubs' are formed when nonbreeders gather in additional, previously unavailable areas, usually at the end of the season, when some territories have been vacated by failed breeders.

Between 300 and 2900 Great Skua chicks on Foula were ringed with individually numbered BTO monel rings, every year from 1963 to 1990; a total of nearly 35,000 chicks. From 1975, most chicks ringed were also weighed with a Pesola spring balance to the nearest 5g and their wing lengths were measured to the nearest millimetre using the maximum chord technique (Spencer 1984), excluding the down on very small chicks. The location of these chicks on the island was usually recorded. In addition, from 1968-1974, 400-1400 chicks were colour-ringed each year in combinations unique to the year.

From 1974 to 1990, a total of 644 adult Great Skuas were trapped on Foula using clap-nets placed at nest-sites, or cannon-nets placed at club-sites or bathing sites, or using other non-injurious techniques (see Spencer 1984). Of these birds, 496 were caught at five club-sites on Foula during the 1988-1990 breeding seasons, and all but two were ringed with three or four plastic colour-rings in individual colour-combinations. A separate study of individually colour-ringed breeding Great Skuas on Foula was also conducted during 1988-1990 (see Hamer 1990). During 1974-1990, 219 birds were found freshly dead on Foula, and the sex of most of these was revealed by internal examination. All birds handled, dead or alive, were measured and weighed, as described in later chapters.

Regular thorough searches of the clubs and breeding territories allowed the attendance and behaviour of individually colour-ringed birds to be monitored throughout the 1988-1990 breeding seasons. Counts of birds on all clubs were made regularly in these seasons, both in the afternoon and at night, as described in later chapters. The size of the breeding population of Great Skuas on Foula in 1988 and 1990 was determined by counting Apparently Occupied Territories (AOTs), which equate approximately to the number of breeding pairs, following methods described by Furness (1982).

The six largest Great Skua colonies in Shetland, after Foula, were regularly searched for colour-ringed birds during the 1988-1991 breeding seasons. Also, incidental searches were conducted at other colonies at Shetland and Orkney. During these searches more than 8000 bird-sightings and checks for colour-rings were made.

Diets of nonbreeding Great Skuas were monitored throughout the 1988-1990 breeding seasons by collecting regurgitated pellets from club-sites, as described by Furness & Hislop (1981). Ring recovery data supplied by the BTO were used to determine the age, origin and dispersal of birds recovered on and away from Foula.

All statistical tests used in this thesis are either from Sokal & Rohlf (1969), using statistical tables in Rohlf & Sokal (1969), or were computed using the Statistical Package for the Social Sciences (SPSS) on a personal computer. For statistical methods, limitations and assumptions in SPSS programmes see Norusis (1986). All times in the text are quoted as GMT.

CHAPTER 3

Accurate Determination of the Age of Adult Great Skuas and Other Birds

A condensed version of this chapter constitutes a paper entitled 'A technique allowing accurate determination of the age of adult birds' by N.I. Klomp and R.W. Furness, submitted for publication in the Journal of Wildlife Management.

3.1 INTRODUCTION

Population biology is an area of research with important theoretical and practical applications (May 1981, Perrins & Birkhead 1983, Hudson & Rands 1988). The ability to determine the ages of animals in a population is an important aspect of such research (Pucek & Lowe 1975, Lamb 1977) and many age determination techniques have been developed for four of the five vertebrate classes. Fish can be aged accurately by counting annuli on the scales and within otoliths and fin rays, by counting vertebrae and by dividing size distributions into age classes (see review by Rounsefell & Everhart 1953). Osteological techniques have been developed to determine the ages of some amphibians and reptiles (see review by Peabody 1961), although the latter are usually aged by size (Caughley 1977). There is a large and constantly increasing number of publications on methods for determining age in mammals, and at least one technique is usually applicable to any given species (Pucek & Lowe 1975). Clues of mammalian age are provided by tooth eruption, tooth wear, size frequency classes, body size, degree of epiphyseal fusion, lens weight, lens protein content, annual growth rings on claws and horns and in teeth and bone, and the number of placental or ovarian scars carried by females (Caughley 1977), as reviewed by Morris (1972), Otero & Dapson (1972) and Pucek & Lowe (1975). Of the five vertebrate classes, only birds remain with no reliable procedure for determining the age of individuals after attainment of sexual maturity or adult plumage. Ornithologists are restricted to dividing birds into juveniles and adults, based on differences in plumage or morphometrics (e.g. Harris 1981, Gaston 1984), and limit accurate ageing to those individually banded as chicks (Caughley 1977).

In the past, various attempts have been made to establish a method of accurately ageing birds. Studies of external morphometrics (e.g. Coulson et al. 1981), lens weight and lens protein content (e.g. Henny & Ludke 1974, and others cited therein) have all failed to provide a method of age determination. Jannett (1983) could not completely separate 2 and 3-year old White Leghorn chickens into correct age classes by discriminant analysis of measurements of 16 different internal body parts.

Layered structures in bones and teeth have long been used to determine the age of amphibians, reptiles and mammals (Peabody 1961), and layered structures in baleen plates and ear plugs are used to provide information on the ages of some cetaceans (Evans 1987). However, despite the suggestion of Van Soest & Van Utrecht (1971) that bone layers may possibly provide information on the ages of individual birds, no previous work has successfully developed an ageing technique for birds using these layers, or established any other method of accurately determining the ages of birds (Larson & Taber 1980).

This study investigates the layered structures in the tibiae of seven known-age Great Skuas, aged 0-16 years, and several other species, and discusses the usefulness of these layers to determine accurately the age of individual dead birds.

3.2. METHODS

Twelve known-age birds, all ringed as chicks with BTO rings and subsequently found freshly dead at varying ages, were used in this study: seven Great Skuas, three Fulmars, one Shag and one Redshank. One tibia was removed from each bird and stored in 10% neutral-buffered formalin (Hopwood 1990). Later, two transverse sections, approximately 1.0mm thick, were cut from each bone using a hand-saw or jeweller's saw. Sections were taken from the proximal end of the diaphysis (central cylindrical shaft) of the bones (Jee 1988).

Several earlier attempts of preparing bone sections for this study were largely unsuccessful. Sectioning bones embedded in resin or ice or sectioning decalcified bones embedded in wax (these and other methods are described in Bancroft & Stevens 1990), all failed to produce the clarity of sections required. Hence, a bone-grinding method (after Page 1982) was adopted for this study.

Two hardened-glass grinding plates were prepared by rubbing together in a circular motion with a small amount of abrasive ('Carborundum 2F'), slightly moistened with water, between the plates. The plates were sufficiently 'sharpened' when they appeared well frosted. They were then washed thoroughly, removing all traces of abrasive. One section at a time was then placed between the glass plates, lubricated with a couple of drops of 70% ethanol, and ground with a circular motion, as above. The section was gently washed in water, relubricated, and turned over every few minutes, and the plates were 'resharpened' with abrasive, as necessary. Each section was ground in this way until it was approximately 20μm thick. This method provided smooth, scratch-free, transparent sections in about 30 minutes. The ground sections were dehydrated by placing them in 70%, 90% and 100% ethanol for two minutes per concentration. The sections were then cleared in xylene for 5 minutes. Sections were mounted on glass slides in natural, filtered Canada balsam.

The sections were photographed through a transmitted light microscope at a magnification of 100X.* Three naive observers were provided with unlabelled, black and white photographs of two different sections of each bone. They were asked to count the maximum number of circumferential lamellae (layers) in the endosteum of each bone, whilst avoiding counting the circular rings of lamellae arranged concentrically around the Haversian canals, as shown in Figures 3.1a,b.

In addition to the tibiae of the twelve known-age birds studied in detail, sections of several other bones were examined, and sections of tibiae from adults of three other species (age unknown) and from juveniles of four different species (i.e. birds less than 12 months old) were all examined. The additional adult birds studied were Manx Shearwaters, Sparrowhawks and Blue Tits, and the juveniles studied were Manx Shearwaters, Sparrowhawks, Blue Tits and Herring Gulls.

* IN EACH SECTION, MOST OF THE ENDOSTEAL DISPLAYED THE SAME (MAXIMUM) NUMBER OF LAMELLAE. IT WAS THESE AREAS OF MAXIMUM ENDOSTEAL LAMELLAE THAT WERE PHOTOGRAPHED, WITHOUT KNOWLEDGE OF THE AGE OF THE BIRDS FROM WHICH THE BONE SECTIONS ORIGINATED.

FIGURE 3.1. a) Diagram of a complete transverse section of cortical bone taken from the tibia of a five year-old Great Skua, showing the location of the periosteum (PER) and endosteum (END). b) Diagram and photograph of an enlarged segment of the same bone section (see boxed segment in Figure 3.1a) showing the remains of the trabecular bone and marrow (Jee 1988) after grinding (TRAB), the circumferential lamellae (CL) and nuclei (NUC) in the endosteum and a Haversian canal (HC) surrounded by concentric lamellae. The endosteal lamellae are numbered in Figure 3.1b.

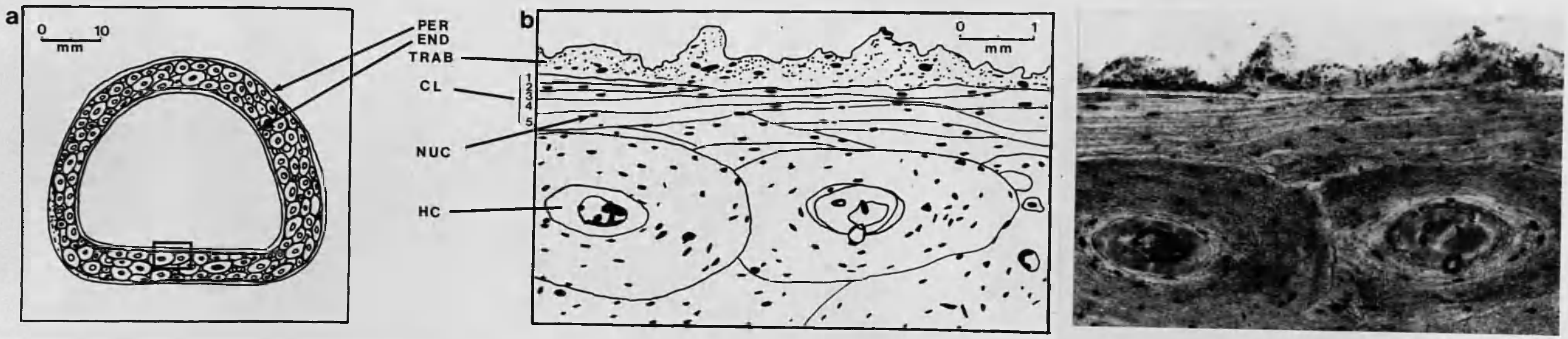
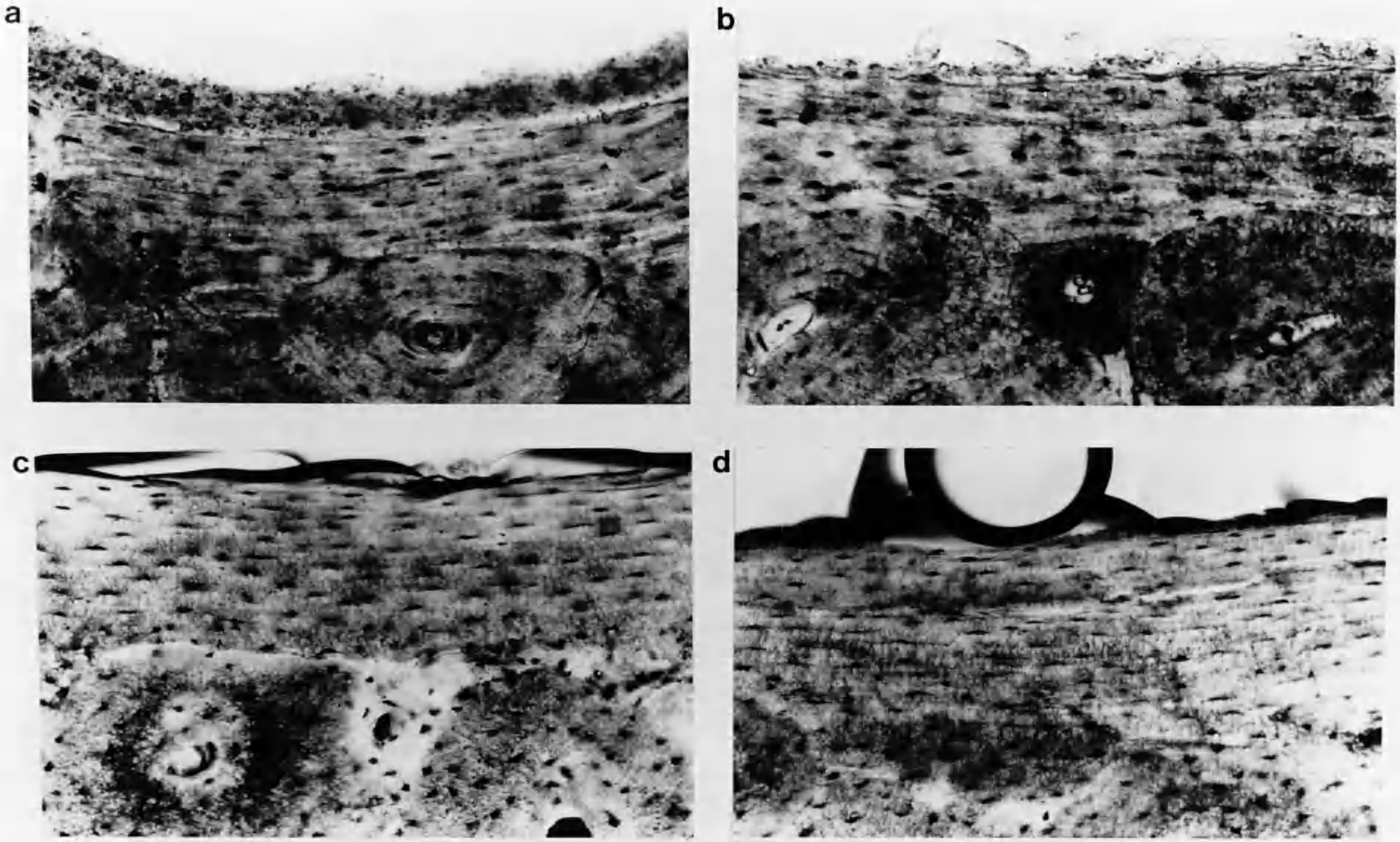

a
0
10
mm
PER
END
TRAB
CL
NUC
HC
b
1
2
3
4
5
0
1
mm

FIGURE 3.2. Photographs of segments of transverse sections of tibiae taken from four adult Great Skuas, showing the circumferential lamellae of the endostea. Scale as indicated in Figure 3.1b. Sections were taken from birds aged a) 8, b) 10, c) 11 and d) 15 years.


a
b
c
d

3.3. RESULTS

The numbers of circumferential lamellae in the endosteum of each bone section were most easily determined by counting the rows of nuclei within the endosteum. The number of endosteal lamellae appeared to vary within some sections, especially where the endosteum was narrowest. However, the number of lamellae was consistent around most of the endosteum of each section, so the maximum number of endosteal lamellae generally could be determined quickly and easily (see Figures 3.1b, 3.2a-d).

Table 3.1 presents the results of the counts of endosteal lamellae by the three naive observers. It can be seen that the number of lamellae related very closely to the age in years of the birds. The slight variation between the number of lamellae counted by the different observers is the result of the subjective decisions of what constituted a separate layer, particularly in older birds with many, closely compacted lamellae. Despite this, the naive observers were always able to determine the age of a bird within one year for birds less than 12 years old, and within two years for older birds. Also, the means of the counts for each bird made by the different observers always equated to the age of that bird, to the nearest year. Endosteal lamellae were also observed in the adult Manx Shearwaters, Sparrowhawks and Blue Tits of unknown age.

The Great Skua chick had no obvious endosteal lamellae (Table 3.1). The juveniles of the other species of birds (Manx

Shearwaters, Sparrowhawks, Blue Tits and Herring Gulls) all known to be less than 12 months old, were found to have largely undifferentiated endostea and Haversian systems, with nuclei apparently dispersed over much of the trabecular bone. Once observed, these types of sections could be determined readily as originating from bones of young birds. However, it was not established when within the annual cycle the bones of young birds formed clear, differentiated endostea.

TABLE 3.1. The number of endosteal circumferential lamellae in sections of a tibia from each of twelve birds, as counted by three naive observers (A, B, C). The means of all the counts of each bone section are given to the nearest year.

Species	Age	Observers / Counts						Mean
		A1	A2	B1	B2	C1	C2	
Fulmar	11	11	12	11	11	11	11	11
	12	11	12	12	12	11	12	12
	14	14	13	15	14	16	14	14
Shag	10	10	10	10	10	10	10	10
Redshank	9	9	10	9	10	9	9	9
Great Skua	0	0	0	0	0	0	0	0
	5	5	6	5	5	5	5	5
	8	8	7	8	9	8	7	8
	10	11	11	9	10	9	9	10
	11	12	11	12	11	10	12	11
	15	13	15	15	16	14	15	15
	16	15	15	16	18	15	17	16

3.4. DISCUSSION

This study presents a method of accurately determining the ages of some birds. The presence of circumferential lamellae in the bones of other species of adult birds, including Grey Herons, Mallards, Chickens, Moorhens, Jays (Van Soest & Van Utrecht 1971) and Canada Geese (Nelson 1976), suggests that this technique may be widely applicable. However, for this technique to be adopted by other workers, the accuracy should be confirmed for each species of bird studied, over a range of ages, using known aged birds (i.e. ringed as chicks). In some mammals, additional layers are sometimes formed, and in some long-lived species the layers laid down in the bone in the early years of life are reabsorbed later (Pucek & Lowe 1975). This process may also occur in some birds, although it is not documented, and this study showed that birds as old as 16 years could still be aged accurately using this method. The accuracy of this technique may also vary slightly among different workers, as shown by the results of the three observers in this study (Table 3.1), so it is important that the technique is validated by each worker, including establishing an ability to recognise sections of bones from juvenile birds. Several counts of the lamellae of the same bone section by different workers may provide a mean that more closely relates to the age than a single count, as seen in this study. Moreover, personal observations revealed that practice of counting lamellae in many different bone sections of a range of known-age birds afforded an ability to accurately determine the age of a given bird quickly and easily.

Each circumferential lamella comprises a longitudinal and transverse bundle of collagen fibres, impregnated with deposits of calcium and other minerals (Jee 1988). This results in the lamellae sometimes appearing as light and dark layers (Van Soest & Van Utrecht 1971). Circumferential lamellae are also present in the periosteum of the bones, and are usually present in similar numbers, although Nelson (1976) and this study found that periosteal lamellae are often more compacted and more difficult to distinguish individually. Since circumferential lamellae are present in most bones (Jee 1988), bones other than the tibia may provide similarly suitable sections for examination.

Future research should determine the timing of the development of the circumferential lamellae. It is possible that seasonal climatic changes, periods of fasting, seasonal migration and/or sexual cycles affect the growth of bone and deposition of calcium (Klevezal & Kleinenberg 1969, Van Soest & Van Utrecht 1971). Hence, studies of bone sections of tropical birds, or birds with non-annual breeding cycles (e.g. Wandering Albatross, Sooty Tern) may reveal different relationships between numbers of endosteal layers and age in those species. Studies of bone formation in birds may be enhanced by the use of a fluorescent bone marker, such as tetracycline, that provides an indication of the location and rate of bone formation (Jee 1988).

An ability to assess accurately the age of birds could have considerable benefit for wildlife management and research, including analyses of 'wrecks' of seabirds found on beaches (Wiens _et al_. 1984), studies of the age structure of populations culled for conservation purposes or harvested by man (Duncan 1978, Coulson _et al_. 1982, Hudson & Rands 1988), studies of pollutant levels in relation to age (Furness _et al_. 1990, Thompson _et al_. in press) and research of other age-related phenomena.

CHAPTER 4

Morphometrics of Great Skuas on Foula

4.1. INTRODUCTION

External body measurements ('morphometrics') have been used extensively by seabird biologists to aid in identifying different groups within a species by sex (e.g. Dunnet & Anderson 1961, Hamer & Furness in press), age (e.g. Harris 1981, Gaston 1984) and possible origin of individuals (e.g. Coulson et al. 1984, Jones et al. 1985). Also, several studies have used differences in external linear measurements and weight to determine differences in 'quality' and 'condition' of individuals (e.g. Coulson & Porter 1985). Porter (1988) suggested that even slight differences in weight and size of individual seabirds may reflect differences in physical or hormonal conditions, which may affect various recruitment factors such as colony attendance and age at first breeding.

However, if differences in morphometrics are to be used to discriminate or compare accurately between groups within a species, all the causes of variation in morphometrics first must be recognised to minimise any interactive effects that may occur. Indeed, differences between measurements among different groups within a population are often marginal, such that any unrecognised causes of variability could cause erroneous discrimination. Barrett et al. (1989) found that the lack of consistency of measurements made by a single observer and the variability of measurements made by different observers could equal differences reported between different populations. Coulson et al. (1982) found that the average weight and size of breeding Herring Gulls changed in response to altered breeding conditions at a single colony.

This chapter examines the morphometrics of Great Skuas on Foula during 1974-1990. Hamer & Furness (in press) used a different set of data to partially discriminate between male and female Great Skuas on Foula, based on the slight sexual dimorphism apparent in the species (females are larger than males). However, that study was based on a relatively small set of measurements of established breeders, and the possible influences of breeding status, age, individual variation, time of season and year remain largely uninvestigated. In this chapter, some proximal causes of variation within measurements of Great Skuas are discussed, in order that such variations can be taken into account in later chapters using these data.

4.2. METHODS

During the 1974-1990 breeding seasons, 644 adult Great Skuas were trapped on Foula using clap-nets placed at nest-sites, or cannon-nets placed at club-sites or bathing sites, or using other techniques (see Spencer 1984). In addition, 219 birds were found freshly dead, with little or no dehydration of soft tissues. These dead birds had generally been shot (see Hamer & Furness in press), although a few were found injured and were subsequently killed by cervical dislocation. The breeding status of these birds was recorded when known (e.g. trapped or killed at a club-site: 'nonbreeder', trapped or killed at a nest-site: 'breeder', trapped or killed at a bathing site or other location: 'unknown'), as shown in Table 4.1. Age was determined for those birds that had been ringed as chicks with BTO rings. Most breeding birds measured were

TABLE 4.1. The numbers and breeding status of birds trapped or found dead on Foula during 1974-1990 that were measured and weighed. All measurements were taken by RWF during 1974-1987 and by NIK during 1988-1990.

Years	Alive			Dead		
	Nonbreeder	Breeder	Unknown	Nonbreeder	Breeder	Unknown
1974-1987	66	5	43	4	66	82
1988-1990	496	34	0	9	5	53
Totals	Alive: 644			Dead: 219		Total: 863

relatively young breeding adults that had been shot at a peripheral and newly colonised area of Foula or nest-trapped in such an area.

Dead birds were usually sexed by internal examination and the sexes of some live birds were known from observations of their behaviour (e.g. copulation) prior to trapping. All birds handled, dead or alive, were measured. The linear measurements generally taken were of the wing (maximum flattened chord), tarsus, culmen, gonys (bill depth at the gonys perpendicular to the cutting edge) and head plus bill ('head+bill'), using a stopped wing-rule or Vernier callipers. Wing measurements were made to the nearest 1.0mm, and all other linear measurements were made to the nearest 0.1mm. Wing and tarsus measurements were both recorded on the right-hand side of the body, to account for possible bilateral asymmetry (McNeil & Martinez 1967, McNeil et al. 1971). In addition, live birds and dead birds that were not obviously emaciated were weighed to the nearest 20g using a Pesola spring balance. During 1988-1990, a total of 13 nonbreeding Great Skuas were trapped and weighed twice within a season. In future analyses, birds' weights are expressed both in grams and as a fraction of wing length ('wt/wing' = weight in grams divided by wing length in millimetres).

Birds were measured by R.W. Furness prior to 1988 and by NIK during 1988-1990. To assess the measuring consistency of each observer and to determine the measurement differences between observers (in accordance with the procedure recommended by Barrett et al. 1989), 31 nonbreeding Great Skuas caught with a cannon-net in 1989 were measured by both RWF and NIK, and seven of these were measured twice, independently, by each observer. This allowed linear measurements taken by RWF to be transformed to equate to NIK's measurements. Incidental repeated weighings of the same bird during 1988-1990 revealed no variation within or between workers. As similar spring balances were used throughout 1974-1990, and these were regularly checked and calibrated, it was assumed that no variation in weights of birds was caused by weighing discrepancies.

An initial inspection of results showed that there were no significant differences in measurements between dead and living birds within groups of birds measured by the same observer and of similar breeding status (ANOVAs, all Ps>0.05). Thus, both groups were pooled in all subsequent analyses.

4.3 RESULTS

4.3.1. Variability of linear measurements

In the sample of 31 nonbreeding Great Skuas measured by NIK and RWF, the differences between the mean values of the first measurements of each observer was significant for gonys and head+bill, as shown in Table 4.2. The coefficients of variation for each morphometric variable differ between each observer, such that NIK's measurements were less consistent than RWF's for some morphometric variables and more consistent than RWF's measurements for others. In a comparison of mean differences between first and second measurements of the same seven Great Skuas by each observer (Table 4.3), it was found that RWF had least discrepancies between repeated measurements

TABLE 4.2. Means, standard deviations (S.D) and coefficients of variation (C.V) of the first measurements of each observer for linear morphometric variables of 31 nonbreeding Great Skuas. All measurements are in millimetres. Mean values obtained by each observer were compared using one-way ANOVAs.

Morphometric variable		Observer		ANOVA	
		RWF	NIK	F-ratio	Prob.
Tarsus	mean	68.7	68.1	1.75	0.190
	S.D	1.7	1.6		
	C.V	2.4	2.3		
Wing	mean	418.1	419.7	0.53	0.471
	S.D	9.1	9.2		
	C.V	2.2	2.2		
Culmen	mean	49.8	49.2	1.07	0.305
	S.D	2.1	1.9		
	C.V	4.1	3.8		
Gonys	mean	17.5	17.9	9.56	0.003
	S.D	0.6	0.6		
	C.V	3.2	3.1		
Head+bill	mean	110.7	109.3	6.88	0.011
	S.D	1.9	2.2		
	C.V	1.7	2.0		

TABLE 4.3. The absolute mean differences (in millimetres) between first and second measurements of the same seven Great Skuas measured by RWF and NIK. The significance of these differences were tested using paired t-tests, as shown.

Morphometric	Observer	Absolute mean difference	Paired t-value	Probability
Tarsus	RWF	0.143	0.23	0.829
	NIK	0.100	0.98	0.366
	Combined	0.121	0.39	0.700
Wing	RWF	0.714	1.11	0.310
	NIK	1.000	1.62	0.156
	Combined	0.143	0.29	0.775
Culmen	RWF	0.986	2.05	0.086
	NIK	0.100	0.48	0.648
	Combined	0.443	1.51	0.155
Gonys	RWF	0.086	1.03	0.341
	NIK	0.014	0.28	0.788
	Combined	0.050	1.05	0.314
Head+bill	RWF	0.214	1.00	0.356
	NIK	0.014	0.10	0.923
	Combined	0.114	0.90	0.383

of wing, and NIK had least discrepancies between repeated measurements of the other linear morphometric variables. However, none of the differences between first and second measurements of either observer for any linear morphometric variable was significant (paired t-tests, see Table 4.3). Furthermore, there were highly significant correlations between RWF's measurements and NIK's measurements; thus allowing regression formulae to be used to transform RWF's measurements so that they could be directly compared to NIK's measurements, as shown in Table 4.4. Future analyses of all RWF's measurements in this chapter have been based on such transformed data.

Tables 4.5a and 4.5b present the mean value of each measurement taken by NIK and RWF (transformed data) in different years from 1974 to 1990, for breeding and nonbreeding Great Skuas. Statistical tests using one-way ANOVAs revealed no differences in mean values of morphometric variables among years or between observers (all Ps>0.1).

4.3.2 Variations due to sex and age

A total of 205 Great Skuas in this study were of known sex: 104 males and 101 females. A total of 268 birds were of known age ranging from 3 to 25 years. Chi-square analyses revealed no differences in the proportion of known males and females in this study from different categories of breeding status, ages, years and time of season (Table 4.6).

It can be seen from Table 4.7 that known female Great Skuas were significantly larger than known males in all linear morphometric variables measured. Females were also

TABLE 4.4. Regression formulae used to transform measurements taken by RWF (R) to allow comparisons to be made to NIK's measurements (N), based on duplicate first measurements of 31 nonbreeding Great Skuas on Foula. The correlation coefficients and their significance are also shown.

Morphometric variable	Formula	Correlation coefficient	Probability
Tarsus	N = 0.829 R + 11.185	0.884	<0.0001
Wing	N = 0.972 R + 13.125	0.961	<0.0001
Culmen	N = 0.838 R + 7.553	0.911	<0.0001
Gonys	N = 0.875 R + 2.63	0.863	<0.0001
Head+bill	N = 0.833 R + 17.065	0.705	<0.0001

TABLE 4.5a. Means, standard deviations (S.D) and sample sizes (N) of linear morphometric variables of breeding Great Skuas on Foula as measured by RWF (transformed data) (1974-1983) and NIK (1988-1990).

Year	Numbers per month		Tarsus	Wing	Culmen	Gonys	Head+bill
1974	July - 1	mean		403.0	51.5		
		S.D		-	-		
		N		1	1		
1975	April - 1	mean	70.5	424.0	48.5	18.5	
		S.D	-	-	-	-	
		N	1	1	1	1	
1976	May - 6	mean		425.1	48.6	18.3	
	June - 3	S.D		7.0	1.4	0.8	
		N		9	9	9	
1979	June - 18	mean	69.7	422.5	49.9	18.2	
		S.D	1.7	9.2	1.3	0.8	
		N	18	18	18	18	
1980	June - 29	mean	68.3	420.3	49.4	18.3	109.7
		S.D	2.2	10.9	1.2	0.6	1.8
		N	19	29	27	28	15
1983	May - 13	mean	67.8	419.4	48.6	18.0	110.5
		S.D	3.1	8.9	1.3	0.7	2.6
		N	13	12	13	13	13
1988	May - 4	mean	68.9	420.9	49.9	18.2	109.4
	June - 19	S.D	1.5	9.0	1.7	0.5	2.4
		N	23	21	23	23	23
1989	June - 6	mean	68.7	424.7	49.4	18.1	109.5
		S.D	1.7	5.0	1.7	0.4	2.3
		N	6	6	6	6	6
1990	May - 1	mean	68.3	421.3	49.6	18.3	110.5
	June - 8	S.D	1.8	7.1	1.4	0.6	1.1
	July - 1	N	10	10	10	10	10

TABLE 4.5b. Means, standard deviations (S.D) and sample sizes (N) of linear morphometric variables of nonbreeding Great Skuas on Foula as measured by RWF (transformed data) (1974-1984) and NIK (1988-1990).

Year	Number per month		Tarsus	Wing	Culmen	Gonys	Head+bill
1974	July - 1	mean		403.0			
		S.D		-			
		N		1			
1976	May - 3	mean		417.4	50.2	17.9	
	June - 1	S.D		7.4	1.1	0.5	
	July - 3	N		7	7	7	
1984	June - 35	mean	68.5	412.7	49.1	17.8	109.8
	July - 27	S.D	1.9	9.7	1.5	0.5	2.2
		N	28	62	28	28	45
1988	May - 2	mean	68.1	413.9	49.3	18.0	110.0
	June - 23	S.D	1.7	8.8	1.8	0.6	2.4
	July - 82	N	112	112	112	112	112
	August - 5						
1989	May - 30	mean	68.3	415.2	49.2	18.0	109.8
	June - 124	S.D	1.8	9.5	1.6	0.5	2.4
	July - 79	N	233	233	233	233	233
1990	May - 22	mean	68.1	414.8	49.2	18.0	109.8
	June - 84	S.D	1.9	9.3	1.6	0.6	2.5
	July - 54	N	158	160	160	160	159

TABLE 4.6. The results of chi-square comparisons of numbers of known males and females in categories from all the birds controlled in this study. The degrees of freedom (df), total sample size of each comparison (N), calculated chi-square value (X^2) and significance (probability, P) are shown.

Categories of comparison	df	N	X^2	P
Breeding status Breeders Nonbreeders	1	80	0.22	>0.6
Years 1974-1986 1987-1990	1	205	0.57	>0.4
Age 3-7 years old 8+ years old	1	80	0.00	1.0
Age Individual years (3-16, 19)	14	80	13.90	>0.4
Time of season April-May June July-August	2	150	1.20	>0.5

TABLE 4.7. Means, standard deviations (S.D) and sample sizes (N) of morphometric variables of known male and known female Great Skuas on Foula. Mean values for each sex were compared using one-way ANOVAs.

Morphometric variable		Sex		ANOVA	
		Male	Female	F-ratio	Prob.
Tarsus (mm)	mean	68.3	69.1	5.0	0.0271
	S.D	2.3	2.0		
	N	88	81		
Wing (mm)	mean	415.2	424.2	68.6	<0.0001
	S.D	8.1	7.2		
	N	102	99		
Culmen (mm)	mean	48.7	49.4	8.5	0.0040
	S.D	1.4	1.5		
	N	103	98		
Gonys (mm)	mean	17.8	18.2	23.2	<0.0001
	S.D	0.7	0.6		
	N	104	99		
Head+bill (mm)	mean	109.6	111.5	19.3	<0.0001
	S.D	2.1	2.2		
	N	54	51		
Weight (g)	mean	1347	1477	59.0	<0.0001
	S.D	104.6	111.2		
	N	85	78		
Wt/wing (g/mm)	mean	3.25	3.48	33.1	<0.0001
	S.D	0.25	0.25		
	N	84	77		

significantly heavier, and heavier for their wing length, than males. Such sex-related differences were evident across most age-groups, although small and missing samples of known-sex birds of each age precluded two-way ANOVAs to be performed. However, despite the small sample sizes, a comparison of mean values of morphometric variables in 3-5 year-old and 10+ year-old males and females (Table 4.8) showed that the mean values of some morphometric variables increased with age in both sexes, although the variations with age within a sex were generally small compared to differences between sexes.

4.3.3. Seasonal and long-term variations

There were significant correlations between several morphometric variables and the date of control (i.e. date trapped or killed) within the breeding seasons. Weight, wt/wing, gonys and head+bill all decreased significantly over the season for nonbreeding Great Skuas, but did not vary significantly with date for breeders (Table 4.9). An examination of the variations of these factors within known-age breeders revealed correlations in similar directions for 3, 4, 5, 6 and 7 year-olds, but none of these correlations were statistically significant. However, an analysis with wt/wing in 4 and 5 year-old nonbreeders (the two largest samples of known-age nonbreeders) revealed that birds controlled in April or May were significantly heavier for their wing length (wt/wing) than birds caught later in the season, as shown in Table 4.10. Also, of the 13 nonbreeders trapped and weighed twice within a season during 1988-1990 (1 to 31 days between

TABLE 4.8. Means, standard deviations (S.D) and sample sizes (N) of morphometric variables of known male and female Great Skuas aged 3-5 years and 10+ years on Foula. Mean values for each group were compared using one-way ANOVAs and Tukey tests were used to determine which groups differed significantly from each other. Lines of asterisks underline those values that do NOT differ significantly from each other (P>0.05).

Morphometric variable		Males		Females	
		3-5	10+	3-5	10+
Tarsus (mm)	mean	68.0	68.8	69.1	69.3
	S.D	1.9	2.1	1.5	1.1
	N	11	15	5	9
			*********	*********	*********
Wing (mm)	mean	415.7	415.8	423.7	426.8
	S.D	5.0	7.5	4.7	5.5
	N	15	16	7	11
		********	********	********	********
Culmen (mm)	mean	49.0	49.2	49.4	49.8
	S.D	1.4	1.5	0.9	1.2
	N	17	16	7	11
		*********	*********	*********	
Gonys (mm)	mean	18.0	18.1	18.2	18.6
	S.D	0.6	0.7	0.6	0.7
	N	17	16	7	14
		*********	*********	*********	
Head+bill (mm)	mean	109.8	110.2	110.8	111.1
	S.D	1.2	2.2	0.9	1.4
	N	8	54	51	7
		*********	*********	*********	*********
Weight (g)	mean	1349	1355	1446	1496
	S.D	83.5	105.7	84.7	109.4
	N	11	14	5	9
		********	********	********	********
Wt/wing (g/mm)	mean	3.24	3.26	3.43	3.55
	S.D	0.22	0.24	0.21	0.26
	N	11	14	5	9
		********	********	********	********

TABLE 4.9. Coefficients (R) and significance (2-tailed probability; n.s - not significant) for correlations of morphometric variables with date of control within the breeding season, for known breeding and nonbreeding Great Skuas on Foula. Sample sizes (N) are shown.

Morphometric variable	Breeders (N=64)		Nonbreeders (N=527)	
	R	Significance	R	Significance
Tarsus	0.154	n.s	0.021	n.s
Wing	0.179	n.s	-0.071	n.s
Culmen	0.148	n.s	0.026	n.s
Gonys	0.158	n.s	-0.137	P<0.01
Head+bill	-0.108	n.s	-0.155	P<0.001
Weight	-0.037	n.s	-0.215	P<0.001
Wt/wing	-0.083	n.s	-0.216	P<0.001

TABLE 4.10. Means, standard deviations (S.D) and sample sizes (N) of wt/wing (weight divided by wing length, g/mm) for 4 and 5 year-old nonbreeding Great Skuas controlled before and after 1 June in each breeding season on Foula during 1974-1990. One-way ANOVAs have been used to compare between early and late controlled birds of each age.

Age in years	Time of season	Wt/wing			ANOVA	
		Mean	S.D	N	F-ratio	Prob.
Four	April-May	3.47	0.26	7	13.1	<0.001
	June-August	3.17	0.20	43		
Five	April-May	3.49	0.26	3	9.2	<0.005
	June-August	3.13	0.19	34		

successive weighings), the latter weights of individual birds were significantly less than the initial weights (paired t=2.88, df=12, P<0.05).

As previously mentioned, there were no significant differences in length measurements of Great Skuas among years (see Table 4.5). However, as shown in Table 4.11, weight and wt/wing were significantly less for breeding birds after 1987 than for those breeders measured before this date. There was no such change in weight or wt/wing in nonbreeders before and after 1987 (Table 4.11).

4.4. DISCUSSION

Analysis of the variability of linear measurements in the same group of Great Skuas revealed that variability of measurements taken by different observers caused more variation in the resultant set of measurements than did the variability within each observer's measurements. Hence, a single observer would have provided more consistent results than two observers. However, many studies compare samples of birds measured by two or more observers, without addressing such problems of inter-observer variability (see Gaston _et al_. 1984). Ideally, the comparisons of measurements between observers would be repeated and checked at regular intervals, although such regular calibrations were not possible in this study. Still, the measurements of each observer in this study were highly significantly correlated and, as no differences in linear measurements among groups of Great Skuas in different years were intuitively expected, the fact that no significant differences

TABLE 4.11. Means, standard deviations (S.D) and sample sizes (N) of weight (g) and wt/wing (weight divided by wing length, g/mm) for breeding and nonbreeding Great Skuas controlled before and after 1987. One-way ANOVAs have been used to compare between these groups.

Breeding status	1974-1987			1988-1990			ANOVA	
	Mean	S.D	N	Mean	S.D	N	F-ratio	Prob.
Breeding								
- weight	1426	144	68	1354	98	39	7.8	<0.01
- wt/wing	3.37	0.31	67	3.22	0.21	37	7.4	<0.01
Nonbreeding								
- weight	1301	104	69	1317	110	502	1.4	>0.2
- wt/wing	3.15	0.22	69	3.17	0.24	502	0.8	>0.3

were found between NIK's measurements and RWF's transformed measurements (Table 4.5) suggest that these transformations were valid and resulted in statistically comparable samples.

In many seabirds, males tend to be bigger than females (Furness & Monaghan 1987). Great Skuas, however, display a reversed sexual dimorphism, with females being the larger sex (Furness 1987a). Such differences in the sizes of males and females within seabird species allow the sexes to be discriminated on the basis of size (see Green & Theobald 1989). However, the discriminants used to sex birds must take into account the possible effects of age and other variables. Some morphometric variables, such as gonys and wing length, have been shown to increase with age in some bird species (see Pienkowski & Minton 1973, Coulson et al. 1981, Jones 1987). Despite small sample sizes, some morphometric variables were also found to increase with age in both sexes, although the differences between the sexes were much greater.

Seasonal reduction in the weight of breeders has been recorded in many seabird species (see Clark 1979 for review). However, this study found no significant seasonal reductions in weight or any other morphometric variables in breeding Great Skuas, although this may be due to the narrow range of dates on which breeders were weighed (75% in June) and the possible confounding effects of the data being collected during nine different seasons.

Weight and some linear morphometric variables reduced over the season in nonbreeders. This suggests that the structure of the nonbreeding population changes within a season. It is known that older nonbreeders arrive earlier at a colony and leave earlier than younger nonbreeders (see Chapter 9), hence the seasonal change in the size of nonbreeding Great Skuas is probably largely related to this seasonal change in the age structure of nonbreeders. However, there was also some evidence of individuals that arrived to the colony earlier in the season being in better condition than later arriving birds of the same age. This was suggested by the fact that earlier controlled 4 and 5 year-olds were heavier for their wing length (wt/wing) than later controlled birds of the same ages (wing did not change significantly with date in these birds). Individual nonbreeders also displayed a significant decrease in weight between first and second weighings. This may imply a 'cost' to nonbreeders in attending the colony. Although such seasonal decreases in weight have been recorded in breeding seabirds (Clark 1979), a seasonal decline in weights of individual nonbreeders has not been recorded previously.

Because weight increases with size, weight alone cannot be used to compare 'condition' of different individuals, so some studies of birds use wt/wing as an 'index of condition' to compare between individuals. For example, Porter & Coulson (1987) used wt/wing to compare the physical conditions of recruits and non-recruits in a Kittiwake colony. However, mean values of wt/wing may be influenced by the sex-ratios of the groups being studied, since this study found significant differences in mean wt/wing values between males and females. Still, the significant difference in wt/wing of birds caught before 1987 and during 1988-1990 is not likely to be a sex-related difference, since there were no significant differences in the proportions of males and females measured during these periods. Hence, the reduction in this wt/wing since 1987 probably reflects a real decline in the condition of Great Skuas on Foula, and is consistent with the reduced prey availability and increased foraging effort reported for Great Skuas on Foula during since 1987 (Hamer et al. 1991). Conversely, Coulson et al. (1982) found that weight and wing increased in a population of Herring Gulls in response to continued culling, and suggested that this was a result of a reduction in intraspecific competition for food.

Wing length also can be affected if the longest primary is moulted, growing or extensively abraded (Coulson et al. 1981). The influence of these latter problems was likely to be minimal in this study because all birds were three years old or older and were trapped or killed during the same time of year, April-August, when no moulting occurs.

Weight, wing and wt/wing are occasionally used in this thesis as measures of size and condition, and any factors possibly affecting these values, as found in this chapter, are addressed appropriately. A more detailed comparison of the morphometrics of nonbreeders that were subsequently determined to be 'recruits' or 'non-recruits' is presented in Chapter 9.

CHAPTER 5

Dispersal and Philopatry

5.1. INTRODUCTION

A thorough study of recruitment in a seabird species requires a knowledge of origin, distribution and mobility of nonbreeders, to elucidate the process of becoming established in a breeding colony (Ollason & Dunnet 1983, Porter & Coulson 1987). In the past, most authors have considered colonial seabirds as intensely philopatric (eg. Tinbergen 1953, Wynne-Edwards 1962). However, this assumption was mostly based on studies of seabirds which were ringed as chicks and subsequently seen breeding in the same (natal) colony, without consistent search efforts in other colonies (Bradley & Wooller, in press; Coulson & Nève, in press). Although prebreeders of some seabird species are known to move intermittently among different colonies (Mainwood 1976, Harris 1984), the extent to which this behaviour affects the degree of philopatry in these species remains unclear. More recent studies have revealed the degree of philopatry in some seabirds may be related to differing conditions at the different colonies (Danchin & Monnat, in press). Coulson & Nève (in press), using a combination of direct observations and ring recovery analysis, estimated that only 36% of young Kittiwakes were philopatric, casting serious doubts on previously held views of almost total philopatry in colonial seabirds.

The movements of Great Skuas ringed as chicks have been described previously by Furness (1978), based on recovery data up to 1977. Since then, the breeding population on Foula has been steadily declining, which may reflect or cause changes in the dispersal and recruitment patterns. This chapter presents a largely descriptive analysis of the ring recovery data of Great Skuas up to 1990, focussing particularly on those aspects that may influence recruitment in the species, and uses ring recovery data and observations of colour-ringed birds to determine the degree of philopatry in Great Skuas that hatched on Foula.

5.2 METHODS

Between 300 and 2900 Great Skua chicks were ringed with individually numbered monel rings on Foula each year from 1963 to 1989; a total of nearly 35,000 chicks. The location of these chicks on the island was often recorded at the time of ringing, particularly since 1975. Ring recovery data up to the end of 1990 were analysed to determine levels of dispersal and philopatry, taking into account the various biases sometimes found with recoveries of ringed seabirds (Coulson & Brazendale 1968, Coulson 1976, Coulson & Wooller 1976). Ring recoveries prior to 1963 were excluded from this study because the aluminium rings used then were lost extremely rapidly, thereby not allowing an accurate determination of the movements of adult Great Skuas. However, Furness (1978) found that excessive wear or loss of monel rings on Great Skuas was 'most unlikely' to occur during a bird's lifetime. Only Great Skuas ringed as chicks were included in this study, thus all recoveries were of birds of known age. Ages of birds were calculated from 1 July in the year of ringing as a chick. Ringed chicks that were known not to fledge were excluded from the ring recovery data set.

5.2.1. Dispersal

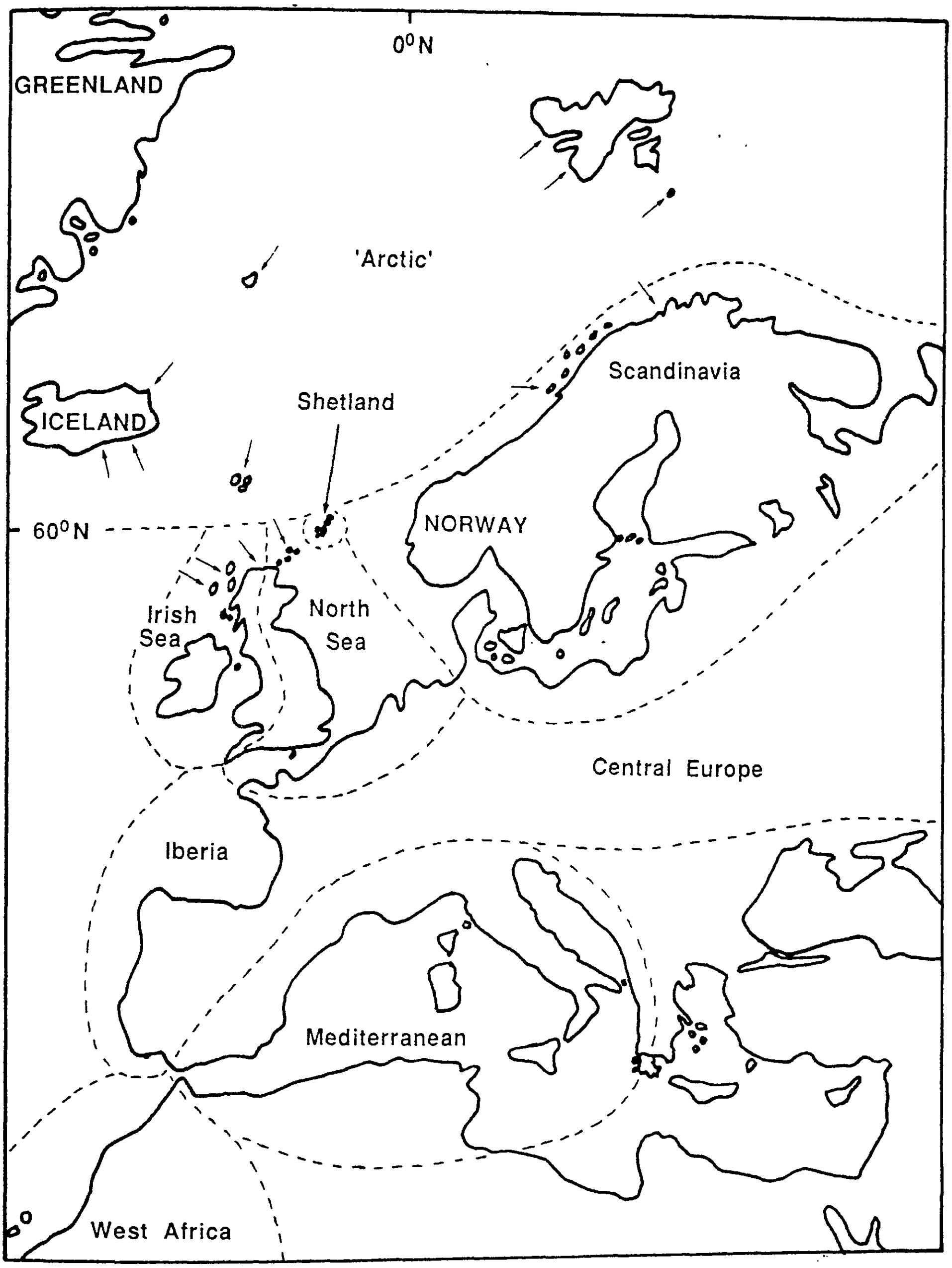
Recovery locations were grouped into ten geographical regions, as shown in Figure 5.1, and causes of recovery were defined as below (after EURING 1979):

1. INTENTIONAL - intentionally by man (shot, hunted, trapped, poisoned, etc.).
2. UNINTENTIONAL - unintentionally by man (pollution, fishing gear, collision with unnatural objects, etc.).
3. NATURAL - not influenced by man (disease, starvation, predation, physical injury, exhaustion, etc.).
4. UNKNOWN - recovery circumstances unknown or not reported.

5.2.2. Philopatry

To determine the occurrence of birds from Foula breeding away from Shetland (emigration), the ring recovery data set was restricted to birds recovered between 1 May and 31 July at an age of six years or older (ie. consistent with possible breeding or colony attachment, see Chapter 9), following ring recovery analysis procedures described by Coulson & Nève (in press). The error induced by breeding birds being recovered at some distance from their breeding colony when on feeding journeys or by being drifted in the sea when ill or after death was minimised by considering all recoveries within 100km of Great Skua colonies (hence, considering Shetland as a whole). Only ring recoveries from birds known to be alive or 'freshly dead' were included in this emigration analysis.

FIGURE 5.1. Map of Europe showing the geographical regions referred to in the text. The region of 'Americas' is not shown, but includes North and South America and surrounding waters. The small arrows indicated the location of Great Skua colonies, irrespective of size or number.


0°N
GREENLAND
'Arctic'
ICELAND
Shetland
Scandinavia
NORWAY
60°N
Irish Sea
North Sea
Central Europe
Iberia
Mediterranean
West Africa

Levels of immigration and micro-philopatry (ie. return to the natal area within the natal colony) were determined from data collected when adults were controlled on Foula during 1988-1990. In 1988, 120 breeding Great Skuas were nest-trapped on the island, and any monel rings present on the birds were recorded, revealing a range of ages from 4 to 25 years (Hamer et al. 1991). As more than 80% of all Great Skua chicks ringed in Britain were ringed at Foula (Furness, unpubl.), any immigration into Foula would result in a dilution of the proportion of ringed birds breeding on Foula. Emigration can not affect these calculations, as unringed birds are presumably as likely to emigrate as ringed birds.

During 1988-1990, 494 Great Skuas were trapped at clubs on Foula using cannon-nets and these birds were individually colour-ringed and the presence of any monel rings recorded. Regular, thorough searches of the clubs and breeding territories allowed individually marked birds to be monitored throughout the breeding seasons.

The five largest Great Skua colonies in Shetland, after Foula, were regularly searched for colour-ringed birds during the 1988-1991 breeding seasons. Also, incidental searches were conducted at other colonies in Shetland and Orkney. During these searches, more than 8000 bird-sightings and checks for colour-rings were made. Hence, it is likely that birds colour-ringed at Foula and subsequently frequenting other colonies would have been observed.

5.3. RESULTS

5.3.1. Dispersal

A total of 1148 Great Skuas ringed as chicks on Foula during 1963-1989 were recovered and reported to the BTO up to the end of 1990. Table 5.1 shows the proportion of recoveries in each geographical region for different ages of birds. There were significant differences in the number of recoveries in the different regions for both first years ($X^2_1 = 87.1$, $P<0.0001$) and for older birds combined ($X^2_1 = 269.6$, $P<0.0001$). Most first-year and one year-old birds were recovered in Iberia and the North Sea, and these regions continued to be well represented in recoveries of most age-classes. No first-years and very few one year-olds were recovered in 'Arctic', yet recovery rates of 2 and 3 year-olds in 'Arctic' were very high. From age four onwards, most recoveries were from Shetland, and most of these were during the summer.

The recovery rate of first year Great Skuas (28.9% of all recoveries) was four or five times greater than that for any other age (Table 5.1). If the probability of recovery was constant with age after the first year, then the number of recoveries from each age should show a progressive decline, as can be seen for three year-olds and older. The recovery rates of one and two year-olds were significantly lower than that of three year-olds ($X^2_2 = 13.3$, $P<0.0001$); this may be due to the mainly pelagic existence of one and two year-old Great Skuas (Furness 1978). These results will be slightly influenced by reduced fledging success after 1986, and the lack of

TABLE 5.1. Percentages of recoveries of Great Skuas of different ages in each geographical region between 1963 and 1990. See text for definitions of ages and regions.

Region	Age when recovered (years) (Percentage of recoveries for each age)								
	0 (28.9)	1 (5.8)	2 (7.1)	3 (9.9)	4 (7.8)	5 (7.4)	6 (7.1)	7 (5.0)	8+ (21.0)
Arctic	0	3.0	27.2	18.4	3.4	4.7	3.7	1.8	0.8
Shetland	14.2	6.0	9.9	18.4	44.9	50.6	46.3	61.4	57.7
Scandinavia	10.2	7.5	7.4	9.6	10.1	5.9	9.8	3.5	7.1
Irish Sea	6.0	4.5	6.2	3.5	5.6	2.4	3.7	3.5	3.7
North Sea	35.2	17.9	21.0	28.1	10.1	12.9	15.9	15.8	17.8
Iberia	18.4	44.8	18.5	11.4	11.2	14.6	13.4	10.5	6.2
Central Europe	6.9	1.5	1.2	0	1.1	1.2	1.2	0	0.4
Mediterranean	2.4	1.5	3.7	1.8	3.4	1.2	2.4	0	2.1
West Africa	4.8	10.4	4.9	7.9	10.1	4.7	3.7	3.5	4.1
America	1.8	3.0	0	0.9	0	1.2	0	0	0
Total - %	100	100	100	100	100	100	100	100	100
- N	332	67	81	114	89	85	82	57	241

opportunity for Great Skuas that fledged in the last few years to be included in the recovery rates of older age-classes. However, there have been comparatively low numbers of chicks ringed in recent years, so any effects will be minimal and are unlikely to mask obvious trends in the dispersal patterns of Great Skuas.

Table 5.2 shows the causes of recoveries of first-year and older Great Skuas from Foula. The majority of recoveries from nearly all regions were due to unknown or unreported causes. This may possibly mask significant variation in the causes of recoveries in different regions. First year birds were more susceptible to being killed intentionally by man in Iberia than older birds (X^2_1= 5.0, $P<0.05$), and this region also had a high recovery rate of birds caught in fishing nets in both first-year and older birds. The proportions of first-years recovered due to natural causes in Iberia and Central Europe were also higher than for older birds, although this trend was not statistically significant. Most of the 'Arctic' recoveries were of one and two year-olds shot in Greenland and the Faeroes prior to 1980. Since then, fewer recoveries have been reported, which coincides with the introduction of laws limiting the shooting of birds in Greenland (Evans 1984), although this may simply be a result of less recoveries being reported.

The recovery rates of first-year Great Skuas in each month following fledging and for each region are presented in Table 5.3. Most of these birds were recovered in the first few months after fledging, particularly in October. This table provides an insight into the general movements of Great Skuas following fledging. It can be seen that the majority of recoveries were

TABLE 5.2. Numbers of Great Skuas recovered in each geographical region between 1963 and 1990, and the causes of such recoveries (see text): 1 - intentional, 2 - unintentional, 3 - natural, 4 - unknown.

Region	Age when recovered	Number of recoveries	Causes of recoveries			
			1	2	3	4
'Arctic'	First year	0	0	0	0	0
	Older	58	44	3	0	11
Shetland	First year	47	0	0	0	47
	Older	328	52	14	12	250
Scandinavia	First year	34	6	2	3	23
	Older	63	6	8	4	45
Irish Sea	First year	20	3	0	3	14
	Older	33	2	4	3	24
North Sea	First year	117	10	10	13	84
	Older	146	5	14	11	116
Iberia	First year	61	19	14	8	20
	Older	113	17	20	6	70
Central Europe	First year	23	4	1	5	13
	Older	6	2	1	0	3
Mediterranean	First year	8	2	3	0	3
	Older	17	5	3	3	6
West Africa	First year	16	6	2	0	8
	Older	48	5	22	4	17
America	First year	6	2	0	0	4
	Older	4	1	0	0	3
Total	First year	332	52	32	32	216
	Older	816	139	89	43	545
Grand total		1148	191	121	75	761

TABLE 5.3. Percentages of recoveries of first-year Great Skuas in the months following fledging in each geographical region between 1963 and 1990. Percentages of recoveries in each time period are calculated from a total of 332 first-year recoveries.

Region	Months following fledging (Percentage of recoveries in each time period)						
	Aug (11.4)	Sep (19.3)	Oct (23.5)	Nov (11.7)	Dec (8.7)	Jan (8.1)	Feb-May (15.1)
'Arctic'	0	0	0	0	0	0	0
Shetland	76.4	3.1	5.1	5.1	0	0	5
Scandinavia	2.6	15.6	16.7	15.4	10.4	0	1
Irish Sea	2.6	17.2	6.4	2.6	0	3.7	1
North Sea	13.2	42.2	51.3	46.1	44.9	18.5	16.0
Iberia	2.6	4.7	10.3	20.5	34.5	59.3	30.0
Central Europe	2.6	12.5	6.4	10.3	3.4	3.7	6.0
Mediterranean	0	1.6	0	0	3.4	0	12.0
West Africa	0	3.1	3.8	0	3.4	11.1	12.0
America	0	0	0	0	0	3.7	10.0
Total - %	100	100	100	100	100	100	100
- N	38	64	78	39	29	27	50

from Shetland in August, from the North Sea during September-December, and from Iberia during January-May. The progressive southward movement from Shetland appears to be mainly via the North Sea, with comparatively few birds being recovered in the Irish Sea. By April, these first-year Great Skuas were often dispersed from the North Sea to the equator. The fastest recorded movement was of an unfledged chick ringed on 20 June and caught on 19 August in Portugal. It must have averaged 143km/day after fledging. Furness (1978) found a similar maximum rate in an analysis of ring recoveries from 1938 to 1977. The dispersal distances of first-year Great Skuas are further discussed in Chapter 6.

The recovery rates of first-year and 1-4 year-old Great Skuas are presented for each year of ringing in Table 5.4. Although there was no significant difference in the overall recovery rate of first years in 1963-1977 compared to 1978-1986 (X^2_1= 0.1, P>0.5), the recovery rate of 1-4 year-olds in 1978-1986 was higher than that of 1963-1977 (X^2_1= 7.2, P<0.01). Also, from 1986 to 1989, the recovery rate of first-years was significantly higher than that of all previous years combined (X^2_1= 8.4, P<0.01).

5.3.2. Philopatry

Altogether, 130 Great Skuas ringed as chicks on Foula and aged six years or older were recovered alive or freshly dead between 1 May and 31 July between 1963 and 1977 (see 5.2.2). Of these, 8 birds (6%) were recovered outside Shetland and within 100km of another Great Skua colony: four birds within 100km of

TABLE 5.4. Recovery rate of first-year and 1-4 year-old Great Skuas ringed on Foula between 1963 and 1989. Recovery rates (%) are calculated from the number of ringed chicks that were estimated to survive to fledge (1963-1986: 96% of chicks ringed, 1987: 65% of chicks ringed, 1988: 8% of chicks ringed, 1989: 20% of chicks ringed; after Furness 1984, Hamer 1990).

Year of ringing	No. of chicks ringed	No. of ringed chicks that fledged	Recoveries of first-years		Recoveries of 1-4 year-olds	
			No.	%	No.	%
1963	822	789	24	3.04	0	0
1964	317	304	3	0.99	2	0.66
1965	975	936	8	0.86	5	0.53
1966	1264	1213	10	0.82	4	0.33
1967	1071	1028	13	1.27	10	0.97
1968	513	492	2	0.47	14	2.85
1969	1539	1477	21	1.42	13	0.88
1970	1310	1258	22	1.75	12	0.95
1971	1661	1595	10	0.63	13	0.82
1972	1736	1667	19	1.14	14	0.84
1973	1354	1300	4	0.31	20	1.54
1974	1795	1723	16	0.93	14	0.81
1975	2224	2135	8	0.37	20	0.94
1976	2110	2026	17	0.84	24	1.19
1977	2874	2759	30	1.09	27	0.98
1978	1000	960	14	1.46	21	2.19
1979	1862	1788	19	1.06	23	1.29
1980	2051	1969	12	0.61	19	0.97
1981	1348	1294	15	1.16	11	0.85
1982	968	929	12	1.29	7	0.75
1983	1330	1277	17	1.33	21	1.64
1984	996	956	8	0.84	13	1.36
1985	1000	960	4	0.42	12	1.25
1986	950	912	11	1.21	11	1.21
1987	748	486	9	1.85	-	-
1988	715	57	1	1.75	-	-
1989	356	71	1	1.41	-	-

the north-western islands of Scotland, two within 100km of the Faeroes and two around Orkney. The proportion of these recoveries after 1977 did not differ significantly from that of earlier recoveries (X_1^2= 0.53, N=138, P>0.1).

Sixty of the 120 breeding Great Skuas nest-trapped on Foula in 1988 had been ringed as chicks (ie. 50%), and all of these had originated from Foula. This equals the expected proportion of ringed birds on Foula if no immigration had occurred (as calculated in Table 5.5).

Of the 494 birds trapped and individually colour-ringed at clubs on Foula, 129 already carried monel rings (ie. ringed as chicks), five of which (3.9%) had fledged in a colony other than Foula (two from Orkney, two from Noss and one from Bressay). Of the remaining 124 birds, the hatching location within Foula was known for 121 birds. All of these birds hatched in Areas 2 and 3 (as described in Chapter 2). As described in Chapter 9, nonbreeding Great Skuas on Foula are generally faithful to one club and most colour-ringed birds consistently used one of the five clubs within these areas (Clubs 8 and 12 in Area 2 and Clubs 2, 3 and 14 in Area 3). The proportion of birds that chose a club within their natal area is significantly greater than that expected by chance (X_1^2= 30.53, P<0.0001). By the end of 1990, a total of 64 birds of known hatching location within Foula were breeding. The proportion of these birds that chose a breeding territory within their natal area was significantly greater than that expected by chance (X_1^2= 9.72, P<0.001).

Only one of the 494 birds (0.2%) colour-ringed at clubs on

TABLE 5.5. The breeding population (pairs or AOTs) of Great Skuas on Foula from 1963 to 1984 (after Furness 1987b), the number of chicks that fledged each year (based on a mean clutch of 1.90 eggs and a mean breeding success of 65.25%, except where indicated, after Furness 1984), and the number of chicks ringed each year that survived to fledge (96% of all chicks ringed each year, after Furness 1984).

Year	Breeding population	No. of chicks fledged	
		Total	Ringed
1963	900	1116	789
1964	1000	1240	304
1965	1150	1426	936
1966	1300	1612	1213
1967	1450	1798	1028
1968	1600	1984	492
1969	1800	2232	1477
1970	2000	2480	1258
1971	2200	2727	1595
1972	2400	2975	1667
1973	2500	3099	1300
1974	2500	3099	1723
* 1975	2705	3354	2135
* 1976	2980	3694	2026
1977	2980	3694	2759
1978	2950	3657	960
1979	2800	3471	1788
1980	2670	3310	1969
1981	2650	3285	1294
1982	2600	3223	929
1983	2600	3223	1277
1984	2550	3161	956
Total:		59,860	29,875

Mean proportion of fledglings ringed during 1963-1984

$= {}^{29,875}/_{59,860} = 0.50$ (50%).

* 1975: Mean clutch = 1.87 eggs, mean breeding success = 63%

* 1976: Mean clutch = 1.93 eggs, mean breeding success = 67.5%

Foula was recorded at any other Great Skua colony (at a club on Hermaness).

5.4. DISCUSSION

5.4.1. Dispersal

The dispersal patterns of Great Skuas from Foula presented in this section are based entirely on ring recovery data. Hence, these patterns are subject to any biases inherent in the interpretation of reported recoveries. For example, the particularly high proportion of birds shot in Greenland and the Faeroes (Arctic) and birds caught in fishing nets in Spain and Portugal (Iberia) will over-emphasise the occurrence of Great Skuas in these regions, as the chances of a ringed bird being reported are very much higher with these causes of death than for individuals which do not die in association with man (Furness 1978). Ring recovery analysis also requires the birds to be recovered within a short time and distance of death, yet the lag times of auk recoveries were experimentally determined to be often of several weeks duration, although mostly less than a month (Jones et al. 1970). As a large proportion of Great Skua recoveries are of birds found exhausted, killed or caught, the average time lag between death and recovery will be very short in this species. Furness (1978) considered the differences in recovery rates from different areas to reflect the dispersal patterns of Great Skuas from Shetland, at least in part, and were only partly obscured by recovery chances.

The highest recovery rate and, hence, probably the greatest level of mortality of Great Skuas from Foula occurs during the first few months following fledging. The comparatively high recovery rate of exhausted first-year Great Skuas in 'wreck areas' such as Iberia and Central Europe (Furness 1978) is consistent with these birds being affected by autumnal storms, many being blown far inland. These young birds are probably more affected by climatic conditions than older birds because of their inexperience of flying and their incomplete physical development. The lack of experience of foraging in first-year birds may also be responsible for the tendency of these birds to be shot or caught in fishing nets more often than older birds. The recoveries of Great Skuas from Foula aged four years and older tended to be mostly from Shetland in the summer and the North Sea and Iberia in the winter. The establishment of this stable migration pattern coincides with the earliest breeding age and the peak age of colony attendance by nonbreeders (see Chapter 9).

The analysis of ring recoveries in this section has yielded similar results to those found by Furness (1978) in an analysis of recoveries from 1938 to 1977. In general, the dispersal patterns and causes of recoveries have not changed markedly since 1977. However, two changes since 1977 of particular relevance to the study of recruitment in Great Skuas have been disclosed. (1) The significant increase in the recovery rate of 1-4 year-olds since 1977 suggests an overall increase in mortality in this age-class. This coincides with a dramatic decrease in the number of nonbreeders frequenting Foula in the late 1980s compared to the mid-1970's, and may be partly responsible for the decline in the breeding population since 1977 (see Chapters 7 and 8). This result is consistent with

Hamer's (1990) finding that annual survival rates of Great Skuas more than one year old decreased from 93% in the 1970s to 80% in the 1980s. (2) The significantly increased recovery rate of first-years ringed on Foula from 1986 to 1989 will have further effects on the size of the pool of prebreeding Great Skuas. As cohorts that suffer high mortality in their first-year also tend to suffer high mortality in their second, and perhaps later, years (Furness 1978, Hamer et al. 1991), this increased rate of mortality of first-years may be coupled with a further increase in the mortality rate of 1-4 year-olds. An increase in prebreeder mortality since 1977 and an increase in mortality of first-years (and perhaps older birds) in recent years, coupled with a dramatically decreased breeding success since 1987 (Hamer et al. 1991), will result in reduced numbers of birds available to recruit, and significant declines in breeding numbers of Great Skuas can be expected in the near future, if no other variables altered appreciably.

5.4.2. Philopatry

The results from this study suggest that Great Skuas from Foula are highly philopatric. Using the analysis of ring recoveries adopted by Coulson & Nève (in press), 6% of ring recoveries (8 out of 130) were from birds that were deemed 'likely' to have been breeding outside Shetland, although four of these eight ring recoveries were from birds less than or equal to the mean age at first breeding of 7 years (see Chapter 9), so these birds may not all have been breeding in the area where they were recovered. Nevertheless, small numbers of Great Skuas colour-ringed as chicks on Foula between 1968 and 1974 have been found breeding in Spitzbergen, Bear Island and

Norway (R.T. Barrett, pers. comm.). This particular technique only addresses possible emigration of Great Skuas from Foula to colonies outside Shetland. Within Shetland, some emigration of Foula birds to other colonies has been recorded in the past, from observations of birds colour-ringed as chicks (Furness 1987a). Small, rapidly expanding, colonies (such as Fair Isle and St Kilda in the 1970's) apparently attract new recruits from other colonies more readily than larger, established colonies (Furness 1987a). However, these levels of emigration are low, since only a few individuals from Foula have been found at each of the small colonies in northeast Scotland.

Levels of immigration of Great Skuas into Foula are clearly very low. None of the sixty known-origin breeders trapped on Foula in 1988 were from outside Foula. The lack of difference between the expected (with no immigration) and observed proportions of ringed and unringed birds in the breeding population on Foula in 1988 also suggests a very low immigration rate into Foula. Further, the maximum possible emigration rate from Foula must also be low, as there is only a slight imbalance between the number of Great Skuas frequenting the island and the number expected from calculations using life tables (see Chapter 8). The numbers of Great Skuas colour-ringed as chicks on Foula and found breeding in other colonies can be explained by an emigration rate of 1-2%. The five nonbreeders from other colonies recorded on Foula during 1988-1990 does indicate a small level of immigration to Foula.

Breeding Great Skuas on Foula are highly site-faithful (Furness 1987a). No marked breeders on Foula have ever been reported breeding, or even visiting, at another colony, and the maximum recorded movement of a nest site between breeding seasons is 80m (Hamer et al. 1991). It appears from this study that the colony fidelity displayed by Great Skuas is not restricted to breeders, but also includes nonbreeders, as very little movement occurred of individually marked nonbreeders among colonies during 1988-1991.

The micro-philopatry of Great Skuas on Foula to their natal areas within the colony is reflected in their choice of the club-site individuals frequent most and the location of their breeding sites. However, the location of breeding sites may simply be a result of proximity to previously frequented clubs, as discussed in Chapter 9, and may not be directly influenced by natal area.

In many seabird species, individuals are known to frequent a colony for one or more years before attempting to breed. This period in the colony, prior to breeding, affords experience and knowledge of local food supplies, breeding success of established pairs, availability of potential mates and levels of competition for territories. Hence, one might expect birds to visit several clubs or colonies to select where to breed. It is surprising, therefore, that Great Skuas show such a high degree of philopatry, club-site and breeding site fidelity and micro-philopatry. There are several lines of evidence suggesting that levels of immigration and emigration are very low, and no evidence was gained to suggest that prebreeders sample a range of colonies. Similar studies of a variety of seabirds may show that different species exhibit behaviours in different places on a continuum from the high club-site and breeding site fidelity and natal area and colony philopatry in

Great Skuas to the regular inter-colony movements of prebreeding Puffins (Harris 1984) and the extreme 'wandering' behaviour of prebreeding British Storm-petrels (Mainwood 1976). Such levels of philopatry and site fidelity may also vary within a species at different colonies and at different times. Much more information on philopatry in a variety of seabirds would be needed before species differences could be related to ecological or evolutionary pressures, but it seems reasonable to expect that such patterns exist.

CHAPTER 6

The Effect of Hatching Date on Chick Weight, Post-fledging Survival and Dispersal, and Adult Weight in Great Skuas.

A condensed version of this chapter constitutes a paper entitled 'The effect of hatching date on chick weight, post-fledging survival and dispersal, and adult weight in Great Skuas' submitted to Journal of Animal Ecology.

6.1. INTRODUCTION

In many seabird species, individuals that lay their clutch relatively early in the breeding season have been shown to be more successful in fledging chicks, often at greater fledging weights, than later breeders (Perrins & Birkhead 1983, Wanless & Harris 1988). Post-fledging survival in some seabird species has been shown to decline with fledging date (Perrins 1966, Parsons *et al*. 1976, Brooke 1990) and increase with chick weight (Brooke 1990, Hamer *et al*. 1991). However, long-term studies of some seabird species have not revealed such relationships (e.g. Guillemots: Hedgren 1981, Puffins: Harris 1984). The sizes attained by adult seabirds have been shown to depend in part upon conditions during development (Batt 1980, Coulson *et al*. 1981). However, it is not known to what extent this occurs, and no studies have shown effects of different hatching conditions within a season to result in any sustained differences (> 2 years) in the sizes or conditions of individual adults.

This paper describes relationships between hatching date and chick weight, post-fledging survival and subsequent adult weight, based on a study of Great Skuas over a period of 16 years (1975-1990). A considerable chick-ringing effort on the island over the last 20 years has made data available for more than 20,000 chicks, although parents of individual chicks were not identified. These data and BTO ring recovery data also were used to carry out an *a posteriori* examination of the relationship between hatching date and post-fledging dispersal distance.

6.2. METHODS

During each breeding season 1975-1990 between 350 and 2600 Great Skua chicks were weighed with a spring balance to the nearest 5g and their wing lengths (maximum chord, after Spencer 1984) were measured to the nearest millimetre, excluding the down on very small chicks. Some chicks were weighed twice in a season. The location within the colony where individual chicks were ringed was usually recorded and grouped into one of the three areas on the island (Areas 1, 2 or 3), as described in Chapter 2. Chicks were only ringed if they were large enough (usually greater than 4 days old), but smaller chicks were weighed and measured also.

The hatching date of each chick was estimated from the length of the wing on the date of measurement, based on the known growth rate of Great Skua chicks' wings (after Furness 1983). Preliminary analysis revealed that the growth rate of the wings of chicks did not differ significantly over the period of study (see 6.3.1.1). Only one set of measurements from each chick (the first set for chicks measured more than once in a season) was used to determine the distributions of hatching dates for each year and area. To avoid possible bias caused by different timing and effort in the measurement of chicks in different years and areas, only chicks measured within a narrow time period (1-15 July each year) were used to determine the distributions of hatching dates (Table 6.1). The distributions of hatching dates for all ringed chicks are slightly different from those of chicks measured during 1-15 July in each year (as presented in Table 6.1), because (a) very small chicks were not

TABLE 6.1. The modal and median hatching dates (June) and range of hatching dates of all chicks measured on Foula during 1-15 July, 1975-1990. The significance of the differences among median hatching dates of chicks from the three different areas on the island were determined for each year using median tests (after Siegel 1956). * = P<0.05, n.s = P>0.05.

	Sample		Overall		Medians			
Year	size	Range	Mode	Median	Area 1	Area 2	Area 3	Significance
1975	1419	3 June - 13 July	15	17	16	17	22	*
1976	693	3 June - 8 July	13	15	15	15	18	*
1977	1827	5 June - 8 July	20	18	18	18	19	*
1978	589	5 June - 6 July	22	20	19	19	21	n.s
1979	536	9 June - 10 July	21	21	-	21	21	n.s
1980	1101	2 June - 5 July	13	14	14	15	15	n.s
1981	1055	2 June - 9 July	15	20	20	20	20	n.s
1982	786	2 June - 30 June	15	17	-	17	17	n.s
1983	1318	3 June - 3 July	10	13	14	12	13	*
1984	840	2 June - 27 June	12	13	12	13	14	*
1985	1113	9 June - 11 July	23	21	18	21	22	*
1986	1025	7 June - 11 July	16	20	19	19	21	*
1987	647	5 June - 6 July	17	18	16	18	19.5	*
1988	491	9 June - 4 July	19	21	-	22.5	19	*
1989	68	10 June - 3 July	22	20	-	20	19	n.s
1990	203	9 June - 5 July	18	20	-	20.5	19	*
All	13711	2 June - 13 July	16	18	16	18	19	*

large enough to be ringed, although still measured, and (b) the distribution of hatching dates of ringed chicks includes chicks ringed and measured on all dates, not just 1-15 July. Hence, the distributions of hatching dates for all ringed chicks from the different areas and years are used throughout this chapter although, in practice, there are only slight differences between the distributions of hatching dates of these two samples.

Individual chicks were classified as either above-average weight or below-average weight for their wing length (i.e. 'wt/wing'), based on growth curves derived for each year (after Furness 1983, Hamer et al. 1991).

A total of 103 adult Great Skuas (3-6 years old) that had been ringed as chicks were nest-trapped or caught at clubs on Foula during the 1988-1990 breeding seasons. These birds were weighed with a spring balance to the nearest 10g and their wing-lengths (maximum chord) and head+bill (tip of the upper mandible to the back of the skull) were measured. The birds were classified as either above-average or below-average for their weight, wing-length, wt/wing and head+bill based on the mean values of these variables for each age-group and year of control.

Information on the survival of individuals was obtained from two sources: (a) birds ringed as chicks on Foula and subsequently controlled as adults, as described previously, and (b) ring recovery data supplied by the BTO. Analysis of survival of individuals based on ring recovery data was restricted to those birds ringed as chicks at an age of 21 days or older, because a lower proportion of birds ringed at less than 21 days was recovered than of birds ringed at 21 days or older (see 6.3.1.2). Few chicks died when older (Furness 1984).

Ring recovery data supplied by the BTO were also used to determine the post-fledging dispersal of individuals away from Foula. As Great Skuas occasionally return to their natal colony at 2 years of age (see Chapter 9), post-fledging dispersal was considered only for birds ringed as chicks on Foula and recovered elsewhere (usually dead) in their first year of life after ringing.

As the hatching dates in most years were not normally distributed, only nonparametric statistical tests were used for their analysis, following procedures described by Siegel (1956) and Sokal & Rohlf (1969).

6.3. RESULTS

6.3.1. Preliminary analysis

6.3.1.1. Growth rates. The growth rate of the wings of Great Skua chicks measured twice in a season in 1985-1990 did not differ significantly from the rate recorded in 1975 on Foula (Furness 1977), based on the linear period of the growth curve (ie. wings 60-260mm long). The mean growth of wings was 9.4mm/day (S.E.=0.34mm/day, N=518), in 1975 (after Furness 1977) and 9.2mm/day (S.E.= 0.74mm/day, N=96) in 1985-1990 (Student's t=0.25, df=612, P>0.5).

6.3.1.2. Survival of ringed chicks. A significantly lower proportion of birds ringed at less than 21 days of age was recovered than of birds ringed at 21 days or older (X^2_1=6.25, N=19,584, P<0.02). This is probably due to some birds ringed at less than 21 days of age dying before fledging. However, there was no effect of age at ringing on recovery rate for chicks ringed after 21 days of age.

6.3.1.3. Hatching date distributions. Table 6.1 presents various parameters describing the distributions of hatching dates of all Great Skua chicks measured on Foula between 1 July and 15 July from 1975 to 1990. It can be seen that the median hatching dates were statistically different among the areas in ten of the sixteen years studied, resulting in an overall difference among areas (median tests among areas in each year). The different median hatching dates of each area and year are controlled for, where appropriate, throughout this study.

The median hatching dates were also statistically different among years (X^2_{15}=1716.7, N=13,711, P<0.001), ranging from 13 June to 21 June (overall: 18 June), whilst the peak (modal) hatching dates ranged from 10 June to 23 June (overall: 16 June). The distributions of hatching dates in each year were skewed. The modal hatching dates were generally earlier than the median hatching dates. There were no statistically significant relationships between first, modal or median hatching dates and range or skewness of hatching dates among years.

6.3.1.4. Repeated chick weighings. Of the 364 chicks that were measured twice within a season during this study, a greater proportion of chicks with above-average wt/wing at their first handling also had above-average wt/wing at their second handling than would be expected by chance (X^2_1=78.70, N=364, P<0.0001). A similarly significant result was obtained if the analysis was restricted to only those birds that were measured for the second time at least one week after their first measurement. This was also true when the analysis was restricted to those birds with hatching dates that fell within a narrow time interval (e.g. median hatching date ± one week: 11-25 June).

6.3.2. Chick weight

There was no significant difference in the proportions of chicks with above-average wt/wing in the different areas on Foula (X^2_2=2.62, N=379, P>0.25). A greater proportion of chicks with 'relative early' hatching dates (i.e. hatched on or before the median hatching date for their area and year) had above average wt/wing than those chicks that hatched later (X^2_1=6.02, N=393, P<0.02). Analysis of the effect of 'calendar' hatching date on chick weight revealed that a greater proportion of chicks that hatched prior to 16 June (overall modal hatching date) in any year had above-average wt/wing than those chicks that hatched later (X^2_1=4.20, N=393, P<0.05). It was not possible to detect any statistically significant influence of either relative or calendar hatching date within any single year, although there were trends in the same direction in most years.

6.3.3. Post-fledging survival

There were no differences in the proportions of birds known to have survived more than one year (i.e. past 1 July in the year following fledging) and less than one year, in the different areas on Foula (X^2_2=1.72, N=378, P>0.4). The proportion of chicks hatching on or before the median hatching date in their particular year and area that survived past their first year was greater than that of later hatching chicks (X^2_1=5.46, N=392, P<0.02). Within individual years, this influence of relative hatching date was significant only for 1977 (X^2_1=5.14, N=70, P<0.03) and 1985 (X^2_1=7.14, N=21, P<0.01). Again, the proportion of chicks hatching before 16 June in any year and known to survive more than one year was greater than that for later hatching chicks (X^2_1=6.93, N=392, P<0.01), although this effect in individual years was only statistically significant in 1985 (X^2_1=6.59, N=21, P<0.05). Survival of an individual beyond its first year was not influenced by its relative or calendar date of hatching.

There was no overall difference in the proportion of birds with above-average wt/wing as chicks that survived more than one year, and that of birds with relatively low wt/wing as chicks (X^2_1=0.71, N=338, P>0.4). However, this effect was found to be significant in one year of the study: 1977 (X^2_1=8.94, N=56, P<0.005).

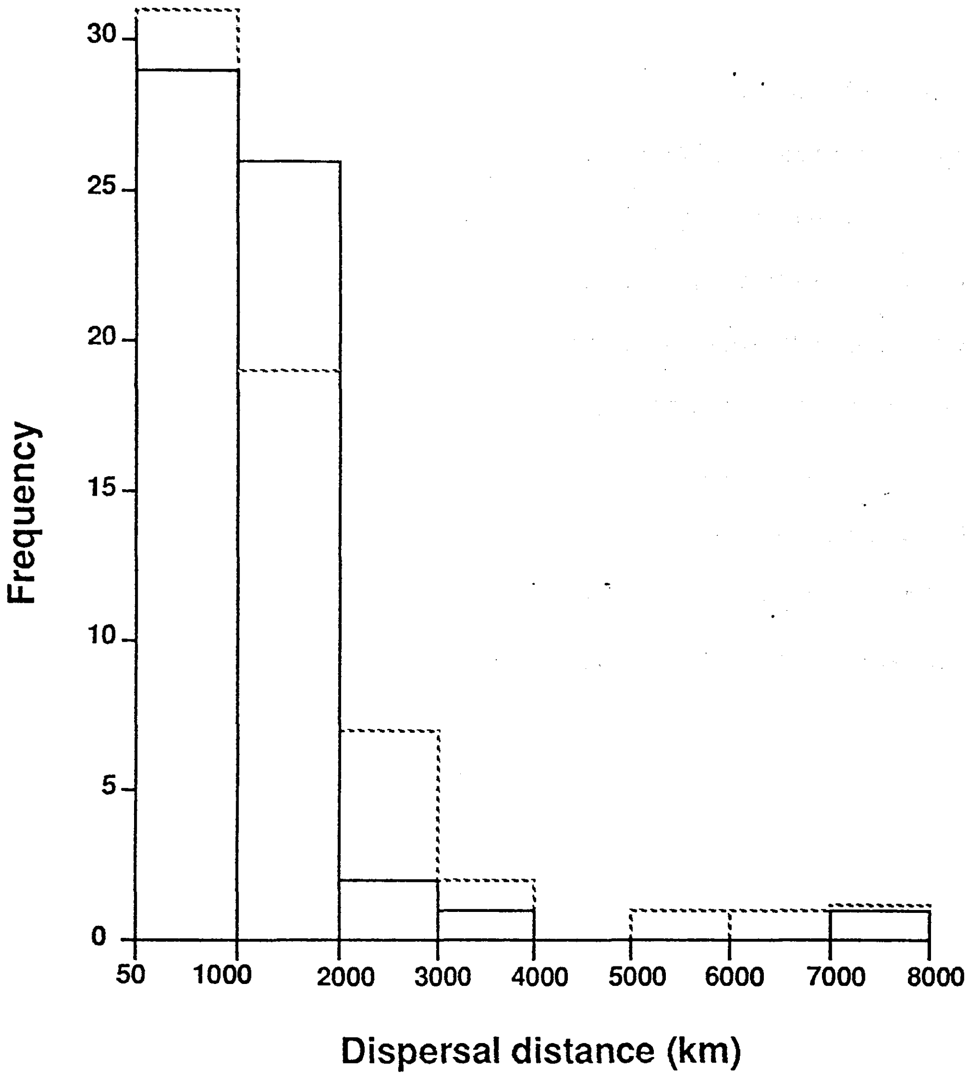
6.3.4. Adult weight

Of the 103 birds ringed as chicks on Foula and subsequently controlled on the island at 3-6 years of age, a significantly greater proportion that hatched on or before the median hatching date for their area and year had above-average wt/wing as adults (controlling for age and year) than that of later hatching birds (X^2_1=4.21, N=103, P<0.05). The proportion of chicks hatching before 16 June in any year with above-average wt/wing as adults was also significantly greater than that of later hatching chicks ($X_1^2=5.22$, $N=103$, $P<0.03$). A significantly greater proportion of those adults with greater than average weight for (a) age and (b) wing length had come from chicks that were also heavier than average for their wing length, than did adults with less weight for age or wing length (a: $X_1^2=8.49$, $N=103$, $P<0.01$; b: $X_1^2=7.55$, $N=103$, $P<0.01$). There was no difference in the proportions of adults with above-average wt/wing that had hatched in the different areas ($X_2^2=0.18$, $N=101$, $P>0.9$). The proportion of birds with above-average weight, wing-length and head+bill (uncombined variables) were not significantly different for early and late hatching birds or for birds from different areas.

6.3.5. Post-fledging dispersal distance

Figure 6.1 presents a frequency distribution of distances away from Foula at which individually ringed Great Skuas were found (usually dead) in their first year. It can be seen that the distributions are slightly different for relatively early and relatively late hatching birds. *A posteriori* examination revealed a greater proportion of relatively late hatching birds (after the median hatching date for their area and year) were found more than 2000km away from Foula than that of birds that had hatched earlier within a season ($X_1^2=4.17$, $N=119$, $P<0.05$). However, such a statistical test is not strictly valid because there was no *a priori* reason to test for variations of post-fledging dispersal distance with hatching date. There were no significant differences in the dispersal distances of first-year

FIGURE 6.1. Frequency distribution of distances away from Foula at which individual Great Skuas were found prior to 1 July in the year following their year of fledging. The solid lines represent those birds that hatched on or before the median hatching date for their area and year, and the dotted lines represent birds with later hatching dates.


Frequency
30
25
20
15
10
5
0
50
1000
2000
3000
4000
5000
6000
7000
8000
Dispersal distance (km)

birds from the three different on the island.

6.4. DISCUSSION

6.4.1. Variations in hatching date distributions

The differences between median hatching dates in the different areas on Foula were statistically significant, so area effects were controlled for in all appropriate analyses in this chapter. However, whilst this study revealed effects of hatching date on chick weight, post-fledging survival and dispersal and subsequent adult weight, there was no evidence of area effects on these variables. Also, Furness (1984) found that differences in nesting density in different areas on Foula did not affect hatching date. Hence, although statistically significant, the small differences in hatching dates among the different areas may not be biologically significant.

Since Great Skuas on Foula start incubating their eggs as soon as they are laid (Furness 1984), resulting in a consistent interval between laying and hatching in all eggs, and since clutch loss is infrequent (Furness 1983, Hamer et al. 1991), the distributions of hatching dates of Great Skuas in this study are likely to be similar - only temporally shifted - to the distribution of laying dates. The hatching date distributions for most years in this study were markedly skewed to the right. Generally there was a rapid increase in the number of chicks hatching followed by a more gradual decrease. This is similar to the laying distributions seen in many seabird colonies (Gochfeld 1980). Gaston & Nettleship (1981) suggested that a skewed pattern of laying occurs because some birds, capable of laying, defer laying to optimise the time of the chick-rearing period, or so that they lay when most other birds lay. Birkhead & Nettleship (1981) found that when laying was late in a colony of Brünnich's Guillemots in any given year, laying synchrony was also reduced, probably because once the optimal egg-laying date is past birds cannot afford to delay laying in order to synchronise their breeding with other colony members (Birkhead & Harris 1985). However, there was no relationship between first, modal or median hatching dates and range or skewness of hatching dates among years in this study.

The timing of egg-laying and hatching often varies greatly among years in seabird colonies (Perrins & Birkhead 1983). The range of median hatching dates over the 16 years of this study was small (8 days) compared to many seabird species. Climatic conditions are known to be responsible for annual variations in laying and hatching dates in some seabirds (Lloyd 1979, Hedgren 1979). One reason for the relative consistency in inter-year hatching dates in this study may be that Great Skuas on Foula do not appear to be unduly influenced by climatic conditions (Furness 1987a) and are never prevented or delayed in laying by snow or ice or flooded nests, as reported in several other seabird species (e.g. Harris 1984).

This study showed that ~~the influence of~~ hatching date, relative to hatching dates in the same area and year, had a greater influence on a chick's weight, post-fledging survival and subsequent adult weight than its calendar hatching date. Parsons (1975) also found that relative laying date had a greater influence on Herring Gull breeding success than calendar laying date, and Wanless & Harris (1988) found that relative laying date influenced a variety of breeding parameters in a colony of Guillemots.

Hamer et al. (1991) reported a positive correlation between chick growth and post fledging survival, up to the age of two years, among cohorts of Great Skuas. The influence of chick-weight on post-fledging survival also has been reported in other seabird species (see Brooke 1990), although it is not true for all seabirds (Harris 1984). It seems sensible that a heavier fledgling, independent of its parents and reliant on its energy reserves and untried foraging ability, should survive better than less heavy fledglings, although this effect was only observed in one year of this study and was not significant across all years. However, the strong relationships between hatching date and chick weight, post-fledging survival and dispersal and subsequent adult weight seen in this study are more difficult to explain directly, and may be a result of other factors such as food availability, and/or parental quality.

Birds that produce a single clutch in a breeding season may time their egg-laying so that they rear young as close as possible to the seasonal peak of food availability (Lack 1954, Perrins 1979, Perrins & Birkhead 1983). Although a thorough investigation of the influence of food availability on the timing of egg-laying and hatching was beyond the scope of this chapter, inter-year variation in prey availability may explain why hatching date influenced the chick-weight and survival of individuals more in some years than in others, in this study. There are two ways in which food availability may influence laying date: (a) adults may require certain energy reserves before they commence laying, and/or (b) adults may predict future levels of food availability in order to determine the optimal laying date. Even if food availability is a factor in determining hatching date and success of young, the differences in parental quality such as their energy reserves or their ability to predict prey availability, may also contribute to the observed influences of hatching date.

The possible effect of hatching date on dispersal is also difficult to explain, but may be a result of the timing of fledging. Late hatching and fledging young may have less opportunity to disperse with other fledglings, and may disperse greater distances as individuals.

6.4.2. Parental quality.

This chapter has presented evidence that chick weight, post-fledging survival and dispersal and adult weight are all correlated with hatching date. Many ornithological studies have shown that fledging success is also influenced by hatching date (see Birkhead & Harris 1985). These observations may be explained by differences in parental quality. Adults which lay late may be poor quality individuals, and less likely to rear good quality young. In many species, including Great Skuas, older individuals breed earlier in the year than those breeding for the first time (Perrins & Birkhead 1983, Furness 1984). Nelson (1978a) found that laying dates in Gannets became progressively earlier for the first four breeding attempts. It is possible that older birds are able to attain breeding condition earlier than younger birds (Birkhead & Harris 1985), since older, more experienced birds are more proficient at feeding (e.g. Dunn 1972). The pair-bond of breeding birds may also influence laying date since birds that change mates tend to lay later in that year (e.g. Brooke 1990).

This study showed that individual chicks that display an above-average weight for size (wing length) at one point in the season, tend to continue in such a condition later into the season. Harris (1984) also found that adult Puffins tended to rear consistently big, heavy chicks or small, light chicks. This suggests that some adults are consistently better at provisioning their chicks than others. Such a difference among adults may be due to experience, as discussed, or may be due to genetic differences (Harris 1984). Grant (1991) suggested that the relationship between chick size at hatching and chick survival in Whimbrels could be controlled to a large extent by inheritance. This study has revealed that the earlier hatching Great Skua chicks are heavier for their size and better survivors. Whilst these effects may also be explained by inheritance, they may equally be explained by adult experience and/or food availability. However, the effect of hatching date on a chick's subsequent adult weight (for wing-length) up to six years later is difficult to explain by prey availability or parental experience in the year of hatching. Although adult female Great Skuas have a greater mean wt/wing than males (see Chapter 4), the effect of hatching date on adult wt/wing is unlikely to be a result of sexual dimorphism, as the sex-ratio of hatching chicks is unlikely to change over a breeding season. Also, there were no differences in the proportions of birds with above average wing-length or head+bill that were early or late hatchers, despite Hamer & Furness (in press) finding that these measurements were good indicators of sex in Great Skuas.

Hence, the effect of hatching date on subsequent adult weight (for wing-length) is most easily explained in terms of parental quality inheritance. It is possible that better quality parents lay earlier in the year, produce better quality offspring that are better provisioned as chicks, either because of their parents' foraging efficiency or as a result of the prey availability during their rearing period. After fledging, these chicks have higher chances of survival due to their greater energy reserves and, perhaps, greater inherent abilities. This inherent difference could result in the observed differences in adult weight between early and late hatched birds. Wanless & Harris (1988) also concluded that heritability of laying dates in Guillemots most easily explained observed influences of laying date with a variety of breeding parameters.

It is not clear whether heavier adults are more successful breeders although, clearly, adults that produce longer surviving chicks are more successful breeders than adults producing chicks with a lower juvenile survival. It would appear possible, from this study, that certain chick-rearing circumstances - perhaps from a better quality parent - could lead to increased chances of future reproduction. This would support the few recent studies that have shown that only a small minority of individuals in a population produce offspring that live to reproduce successfully themselves (e.g. Newton 1989).

CHAPTER 7

Variations in Numbers of Nonbreeding Great Skuas Attending the Colony and the Influence of Inferred Prey Availability

A condensed version of this chapter constitutes a paper entitled 'Variations in numbers of nonbreeding Great Skuas attending a colony' by N.I. Klomp and R.W. Furness, published in Ornis Scandinavica 21: 270-276.

7.1. INTRODUCTION

Very little is known about the patterns of attendance of nonbreeding seabirds in colonies, or how such patterns relate to recruitment (Porter & Coulson 1987). Studies of seabirds as indicators of environmental conditions, as reviewed by Cairns (1987), have failed to include nonbreeders, or distinguish between numbers of breeders and nonbreeders, present in the colony. Yet, population modelling has highlighted the need for further information about the behaviour and movements of potential recruits (e.g. Ollason & Dunnet 1983).

This chapter provides a detailed description of diurnal, seasonal and long-term variation in numbers of nonbreeding Great Skuas on Foula and relates the diets of the nonbreeders and other ecological factors to these diurnal and seasonal patterns. A study of the effect of prey availability on the movements of nonbreeding seabirds is considered particularly relevant in the light of recent breeding failures and population declines of many seabird species that signal ecological changes in food supplies that may be related to human exploitation of fish stocks, e.g. Shetland (Heubeck 1989), Norway (Lid 1981, Anker-Nilssen 1987), and elsewhere (e.g. Burger & Cooper 1982). The breeding population of Great Skuas on Foula is known to have declined from a peak of nearly 3000 pairs in 1977 (Furness 1987a) to 2500 pairs in 1987 (Furness 1987b). Since then, greatly reduced breeding successes in 1987-1990 have occurred. This chapter presents estimates of the size of the Great Skua breeding population on Foula up to 1990. Finally, it is proposed that studies of nonbreeder attendance may be of value as an indicator of the health of the population and its marine environment.

This chapter only compares numbers of nonbreeding Great Skuas on Foula at given points in time. The duration of stay at the colony by individual birds and the total number of nonbreeders frequenting the island over an entire season are discussed in Chapter 8.

7.2. METHODS

The numbers of Great Skuas at a club-site (no. 4) on Foula were recorded on alternate hours on four dates in 1976, 11 dates in 1989 and 8 dates in 1990, between May and July in each year. In 1988 the numbers of birds at, arriving at and departing from, two club-sites (no.'s 3 and 11) on Foula were monitored continuously over three 24-hour periods during June and July.

Twelve "afternoon counts" (during "afternoon attendance", 13:00-15:00 GMT) of the Great Skuas at all club-sites were made throughout the breeding season in 1975. Afternoon counts of birds on one club-site were made every day from mid-May until early August, 1976. In 1988, two daytime counts and ten "night counts" (between 22:30 and 01:30 GMT) of all clubs were made over a similar time of year. In 1989 and 1990, afternoon and night counts were made on 10 dates each year during May-July. Birds bathing adjacent to the club were excluded from afternoon counts where possible. In addition, several incidental daytime counts and observations were made.

The size of the breeding population of Great Skuas on Foula in 1988 and 1990 was determined by counting Apparently Occupied Territories (AOTs), which equate approximately to the number of breeding pairs, following methods described by Furness (1982).

Diets of nonbreeding Great Skuas were monitored throughout the 1988, 1989 and 1990 breeding seasons by collecting regurgitated pellets from club-sites, as described by Furness and Hislop (1981), who also presented similar data for the 1975 and 1976 seasons.

All data collected prior to 1988 are from Furness (1977), unless otherwise stated.

7.3. RESULTS

7.3.1. Diurnal variations

Figure 7.1 presents examples of typical diurnal variation in numbers of Great Skuas on different club-sites in 1976, 1988, 1989 and 1990. It can be seen that the number of birds at a club can change markedly during the daytime, but that there are no changes in numbers of birds at any club between the hours of 22:30 and 01:30 (darkness). During the three 24-hour observations of clubs, no birds were observed arriving at or leaving the clubs during this period.

Incidental daytime counts of Great Skuas on the clubs were found to be highly variable. Table 7.1 shows the variation in numbers of birds on the club-sites when counted at the same time of day (±30 minutes), but on different days, one week apart in 1988. It can be seen that large differences in numbers of birds

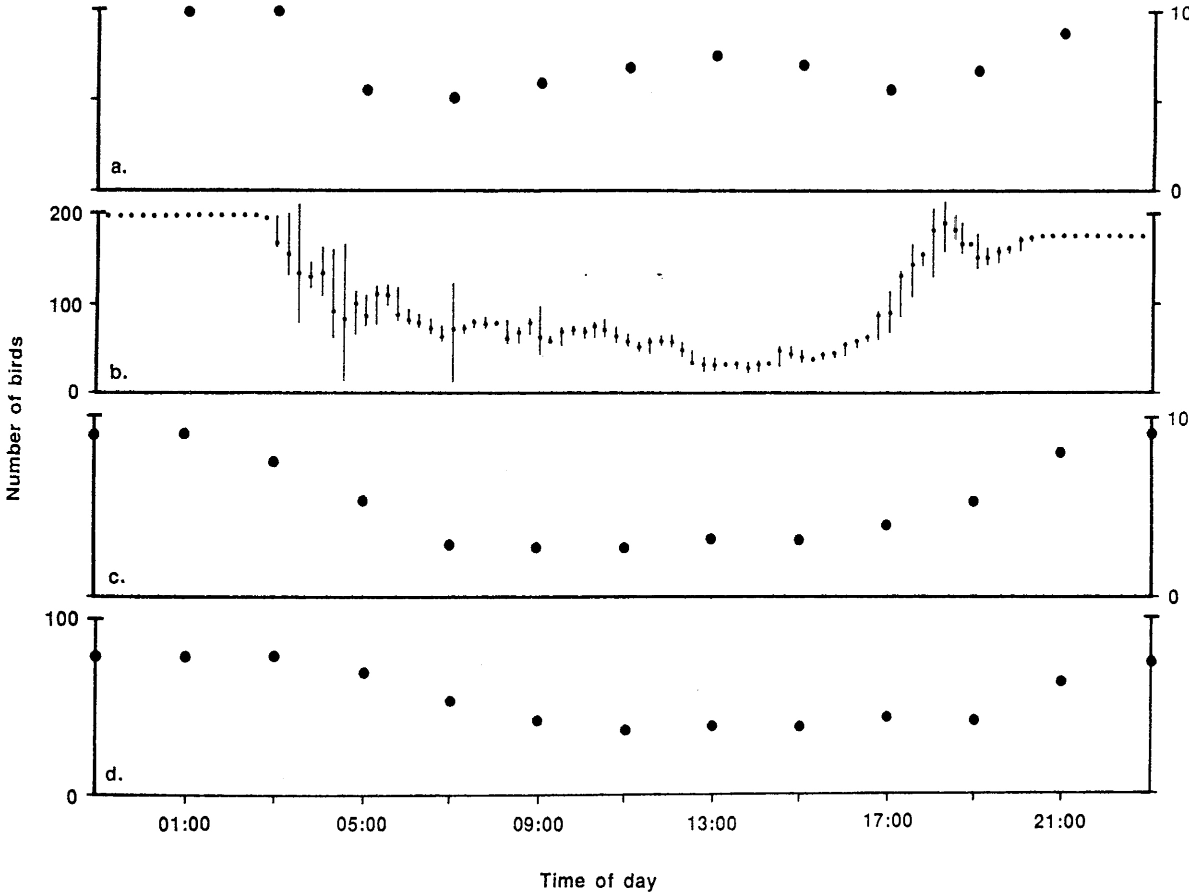
FIGURE 7.1. Typical diurnal variation in numbers of Great Skuas at different sites on Foula, at similar times of year in 1976, 1988, 1989 and 1990.

a. Counts made every two hours over 24 hours at a club-site on 15 June 1976 (club no. 4).

b. Counts made every 15 minutes over 24 hours at a club-site on 3 June 1988 (club no. 11). Vertical bars show movement of birds into (below circles) and out of (above circles) the sites during the preceding 15 minute interval.

c. Counts made every two hours over 24 hours at a club-site on 17 June 1989 (club no. 4).

d. Counts made every two hours over 24 hours at a club-site on 10 June 1990 (club no. 4).



100
0
200
100
0
a.
b.
c.
d.
100
0
100
0
Number of birds
01:00
05:00
09:00
13:00
17:00
21:00
Time of day

TABLE 7.1. The number of Great Skuas present at the different club-sites on Foula, on two different dates in the 1988 breeding season. The percentage differences reflect the counts of 5 June when compared to those of 29 May. Locations of the club-sites are given by Furness (1987a). The four club-sites associated with a bathing site are indicated by asterisks.

Club No.		Time of day ($\pm$30 mins)	Counted on: 29 May	Counted on: 5 June	Percentage differences
1*	Mill Loch	11:00	62	32	- 48.4%
2	Liorafield	14:00	43	21	- 51.2%
3	Bottle	10:00	34	21	- 38.2%
4	Strem Ness	09:00	64	65	+ 1.6%
5	Noup	12:30	26	30	+ 15.4%
6	South Ness	12:00	0	0	0.0%
7	Hamnafield	14:45	19	43	+126.3%
8	Kame	15:00	21	14	- 33.3%
9*	Flick	16:30	106	108	+ 1.9%
10*	Overfandal	16:00	49	88	+ 79.6%
11	Netherfandal	17:00	43	38	- 11.6%
12*	Rossies	10:30	36	32	- 11.1%
13	Daal	13:00	25	69	+176.0%
14	Smallie	13:15	35	23	- 34.3%
15	Ouvra Valley	16:00	0	0	0.0%
All sites combined:			563	584	+ 3.7%

at any given club can occur between different days, although the totals are comparable.

The small differences between numbers of nonbreeders at a club-site at midnight on one day and midnight on the following day (Figure 7.1) are probably due to the movement of small numbers of birds between clubs. A decrease in the number of nonbreeders at one club due to human disturbance often was found to correspond to an increase at other clubs. Toward the end of the season, nonbreeding Great Skuas are less confined to the traditional clubs because some breeders have either left the island or are no longer defending their territories. During 1988-1990 nonbreeders gathered in two or three additional areas (temporary clubs) at the end of the season, which were previously within breeding territories.

Table 7.2 presents the means, variances and coefficients of variation of numbers of birds on club-sites in 1988, from counts made every 15 minutes during night counts, afternoon counts and counts made throughout the remainder of the day. Night counts have a variance of zero, while afternoon counts have significantly smaller variances than counts during the remainder of the day.

7.3.2. Seasonal and long-term variations

The overall seasonal variations in numbers of nonbreeders on Foula in 1975, 1976, 1988, 1989 and 1990 are compared with seasonal changes in the diets of nonbreeders during those years in Figure 7.2. The seasonal variations followed similar trends at each club. The numbers of nonbreeding Great Skuas peaked

TABLE 7.2. The means, variances and coefficients of variation (C.V.) of the numbers of birds on club-sites, counted every 15 minutes during three 24-hour periods in 1988, at night-time (night counts), during afternoon attendance (afternoon counts) and throughout the remainder of the day. The differences between variances of afternoon counts and counts during the remainder of the day were tested using the variance ratio test. Night counts all had variances of 0, so could not be statistically compared.

Club-site number (Date)	Statistical parameter	Night counts (n=13)	Afternoon counts (n=9)	Remainder of day (n=74)
11 (3 June)	Mean	198	35.7	111.7
	Variance	0	44.50	3017.30
	C.V.	0	18.68	49.18
	Significance		F_{Max}=8.23,	p<0.01
11 (9 July)	Mean	69	21.8	29.6
	Variance	0	16.94	355.32
	C.V.	0	18.90	63.68
	Significance		F_{Max}=4.58,	p<0.05
3 (16 July)	Mean	72	9.6	25.0
	Variance	0	1.74	334.52
	C.V.	0	13.75	73.16
	Significance		F_{Max}=13.82,	p<0.01

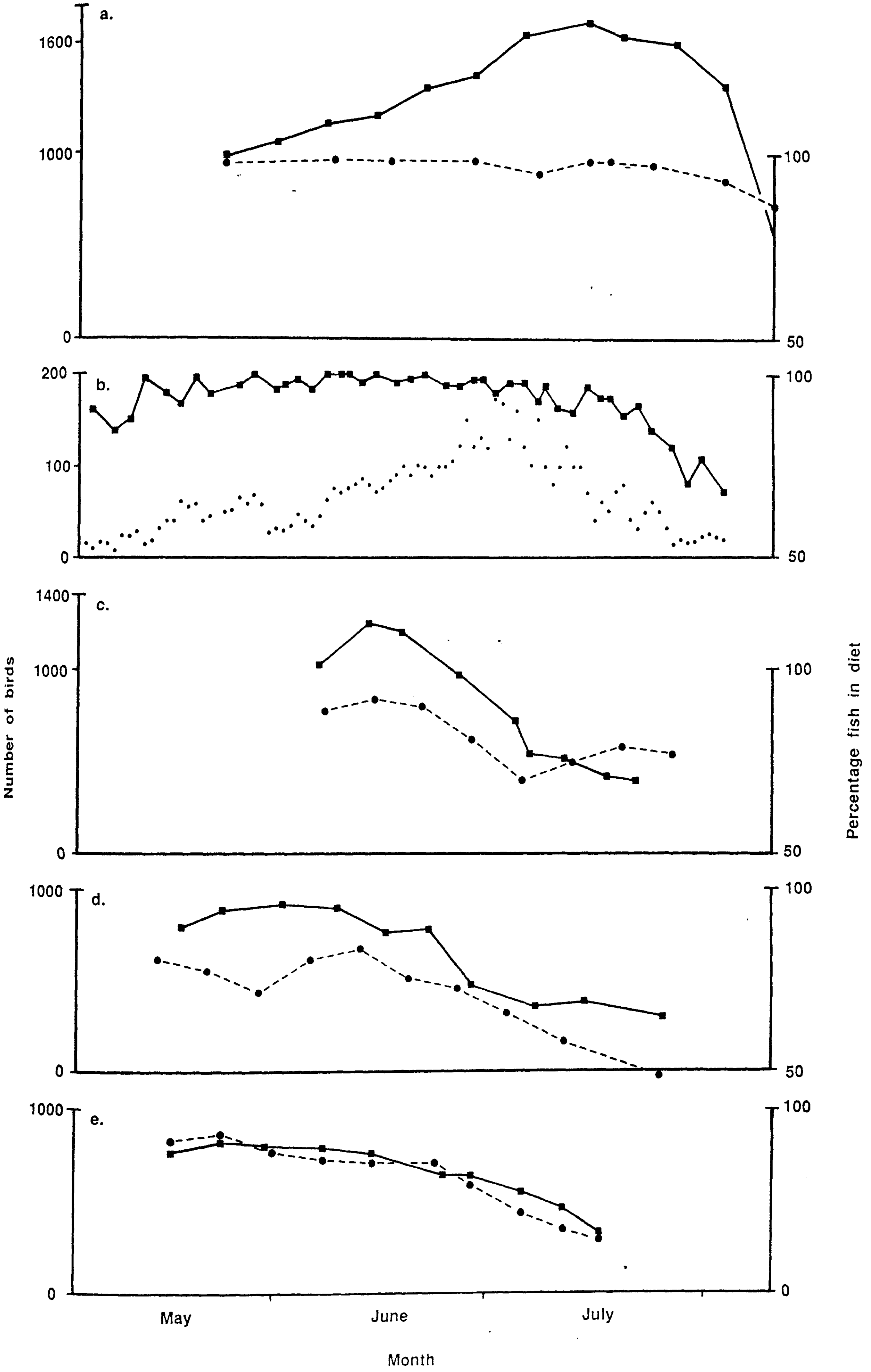
FIGURE 7.2. The seasonal variation of diets and numbers of nonbreeding Great Skuas on Foula.

SQUARES: a. Total numbers of birds on all club-sites during afternoon attendance (ie. afternoon counts: 13:00 - 15:00 GMT) on different dates in 1975.

b. Numbers of birds at a club-site (no. 4) during afternoon attendance in 1976.

c,d,e. Total numbers of birds on all club-sites in 1988 (c), 1989 (d) and 1990 (e) as counted at night (22:30 - 01:30 GMT).

CIRCLES: Percentage of diets composed of fish (sandeels or white-fish discarded from trawlers) as determined from pellet analysis; 1975 and 1976 data obtained from Furness and Hislop (1981).


a.
b.
c.
d.
e.
1600
1000
0
200
100
0
1400
1000
0
1000
0
1000
0
100
50
100
50
100
50
100
50
100
0
Number of birds
Percentage fish in diet
May
June
July
Month

earlier during 1988-1990 than in the mid-1970's, and the subsequent decline in numbers coincided with a change in the diets of the birds each year. Breeding and nonbreeding Great Skuas on Foula feed largely on Sandeels and discarded white-fish from trawlers between April and August (Furness & Hislop 1981). The numbers of nonbreeders on Foula on dates between mid-May and early August correlated significantly with the proportion (arcsine $\sqrt{p}$) of fish in their diet, in each year studied (1975: R=0.59, df=8, $P<0.05$; 1976: R=0.41, df=42, $P<0.01$; 1988: R=0.87, df=6, $P<0.01$; 1989: R=0.81, df=8, $P<0.01$; 1990: R=0.95, df=8, $P<0.01$).

Figure 7.1 suggests that the birds present on the club-sites during afternoon attendance represented a greater proportion of the night-time total in 1976 than in 1989 and 1990. The full results reveal that the birds present at a club-site (no. 4) at 13:00 in 1976 averaged 67% (S.E.=7.5%, N=4) of the following night-time total. This proportion is significantly greater than for 1989 and 1990 ($X^2_2=29.2$, $P<0.0001$), when the number of birds on the same club-site at the same time of day averaged 40% (S.E.=2.4%, N=11) and 38% (S.E.=4.9%, N=8) of the following night-time totals. If the afternoon counts in 1975 also represented, on average, 67% of the night-time totals (as in 1976), then the mean number of nonbreeders attending the colony between 20 May and 10 August in 1975 (afternoon counts transformed to night-time totals by multiplying by 1.492, hence: $\bar{x}=1311 \times 1.492 = 1957$, N=12) and in 1988-1990 (night counts: $\bar{x}_{1988}=732$, N=10; $\bar{x}_{1989}=667$, N=10; $\bar{x}_{1990}=656$, N=10) were significantly different (one-way ANOVA, $F_{3,39}=37.8$, $P<0.0001$). Indeed, even without transforming the

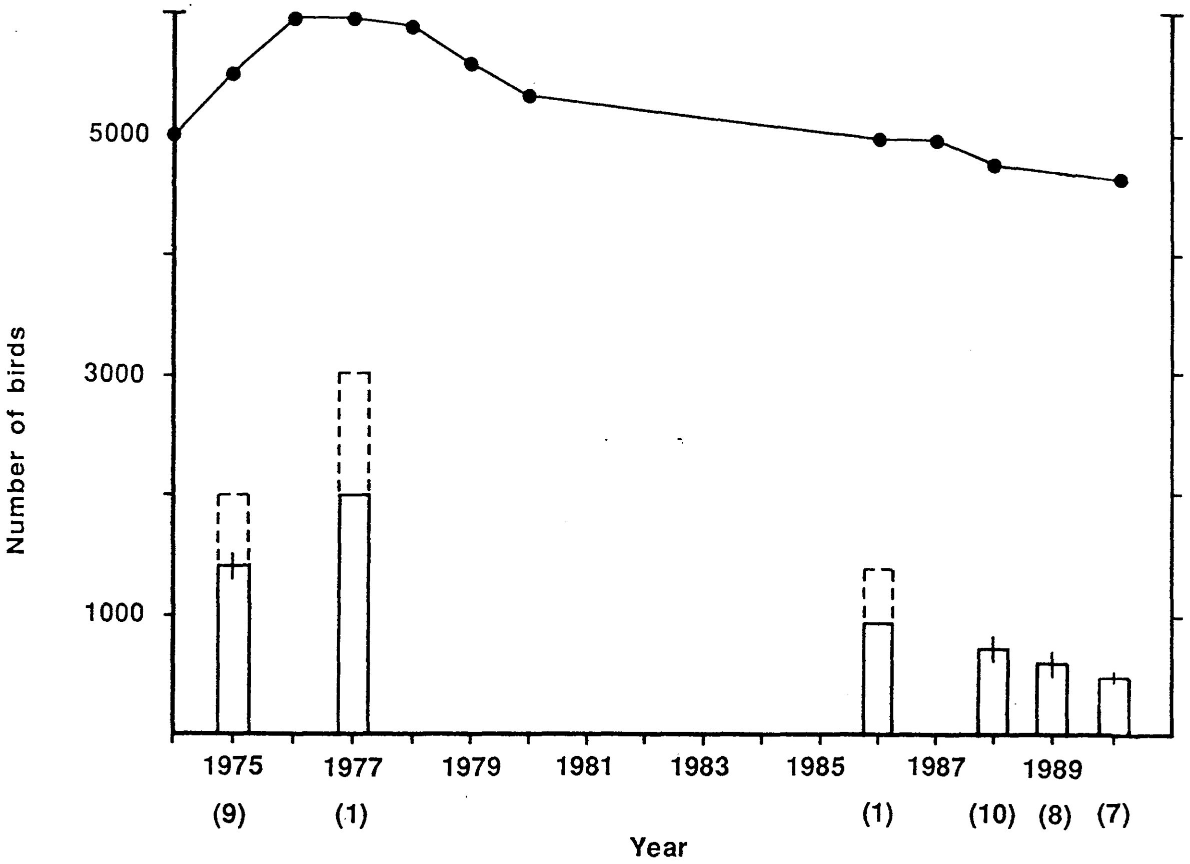
1975 data, the mean number of nonbreeders on Foula in 1975 (afternoon counts) was still significantly greater than in 1988, 1989 and 1990 (night counts) ($F_{3,39}$=13.8, P<0.0001). The number of nonbreeding Great Skuas at all clubs on Foula during afternoon attendance in June 1977 was determined to be 2020 by Furness (1987a), suggesting a night-time total of around 3015 birds in that year (estimation derived from similar transformation).

7.3.3. Long-term changes in numbers of breeding and nonbreeding Great Skuas on Foula.

A total of 2400 and 2340 Great Skua AOTs were recorded on Foula in June of 1988 and 1990, respectively. It can be seen from Figure 7.3 that the number of breeders has declined since the mid-1970s. The breeding population has declined by 22% from 1977 to 1990, an average of 1.9% per year. It can also be seen from Figure 7.3 that the decline in numbers of nonbreeding Great Skuas on Foula coincided with the breeding population decline (R=0.99, df=3, P<0.05), although nonbreeder numbers have decreased much more (breeders by 22% from 1977 to 1990, nonbreeders by 80%). The peak number of nonbreeders present in 1990 (819) was significantly lower than the number expected (1619) on the basis of the breeder/nonbreeder ratio prevailing in 1977 (X^2_1=395, P<0.0001). Such comparison is based on an afternoon count in 1977, and is therefore conservative, because the total number of nonbreeders in 1977 would be greater still.

FIGURE 7.3. LINE: The numbers of breeding Great Skuas on Foula, as determined by twice the number of AOTs (after Furness 1982) from 1974-1990. Data from Ewins _et al._ (1986), Furness (1987a,b), this study.

BARS: The mean number (± S.E., where N>1) of nonbreeding Great Skuas on Foula during June and July in 1975, 1977, 1986, 1988, 1989 and 1990. Sample sizes are shown in parentheses. Values for 1975, 1977 and 1986 represent counts made during afternoon attendance. Total numbers for these years have been estimated by multiplying values by 1.492 (ie. 1/67%, see text), and are shown by dotted bars. The numbers of breeders and nonbreeders correlate similarly for both actual counts (solid bars) and counts transformed into total numbers, where appropriate (R=0.99, df=3, P<0.05).


Number of birds
5000
3000
1000
1975
1977
1979
1981
1983
1985
1987
1989
(9)
(1)
(1)
(10)
(8)
(7)
Year

7.4. DISCUSSION

7.4.1. Diurnal variations and repeatability of counts

It can be seen from Figure 7.1 that the numbers of Great Skuas at club-sites during afternoon attendance are relatively stable, but are lower than numbers present at night. The numbers of birds on a club-site during the rest of the day are highly variable. Although most birds go to sea to feed in early morning, the timing of foraging trips does not appear to follow a set pattern. Table 7.2 shows the variation in numbers of birds during peak afternoon attendance to be much lower than for the rest of the day. Further, the numbers of birds at clubs between the hours of 22:30 and 01:30 are stable (i.e. all variances = 0). During this period, the birds sleep; no birds forage or bathe, and breeders are at their nests (Furness 1987a). As very few birds are seen flying around the colony during this period (pers. obs.) it is reasonable to assume that the birds present at the clubs at this time represent all nonbreeders in the colony at this date. This was also concluded by Bayes *et al*. (1964), who studied a Great Skua colony in the Faeroes. The birds present at bathing sites at night are only those associated with the clubs at those sites (i.e. nonbreeders).

It is clear from Table 7.1 and Figure 7.2 that the numbers of nonbreeding Great Skuas can vary considerably over a few days and at different times of day. Hence, counts of nonbreeding seabirds made at different clubs at different times or on different days, are likely to be inaccurate as estimates of the total number of nonbreeders attending the colony.

The numbers of nonbreeders on a club-site can vary markedly within a 15 minute interval (Figure 7.1b). Such movements of birds to and from the clubs are sometimes caused by disturbance (e.g. people or grazing sheep), but often groups of birds fly in or out of a club-site for no apparent reason. Thus counts of nonbreeders during the daytime will be less reliable and reproducible than counts made at night. Although numbers also vary during afternoon attendance, the variances are significantly less than at other times of the day. Thus, counts made at all the clubs on the same day during this period can be used as an indication of the total numbers of nonbreeders attending the breeding colony. However, using afternoon counts, alone, could be inaccurate, because the proportion of the total number of nonbreeders present at the clubs during afternoon attendance may change between years. This study found that, on average, 67% of the total number of nonbreeders were at a club during afternoon attendance in 1976, but only 38-40% were present during 1989-1990. Also, the afternoon counts are likely to be affected by the presence of breeders bathing at sites adjacent to club-sites, that are inadvertently included in the counts of nonbreeders. This does not happen in night counts, because no birds bathe then, and breeders are at their territories during this time (Furness 1987a).

7.4.2. Nonbreeders and the health of the colony

Great Skuas and other seabird species breeding around the Shetland Islands feed largely on Sandeels and discarded whitefish from trawlers during the summer (Heubeck 1989). Several recent studies have shown that the diets of these seabirds reflect prey availability (eg. Martin 1989, Monaghan *et al*. 1989a,b, Hamer *et al*. 1991). The apparent dispersal or change in the feeding habits of these seabirds toward the end of July may be associated with a decline in the availability of Sandeels at this time (Tasker *et al*. 1985). Sandeels and discarded whitefish from trawlers are also the principal food of breeding and nonbreeding Great Skuas on Foula between April and August. An increase in the presence of other prey in their diet (e.g. crustacea, mussels, bird eggs and meat) is thought to reflect a decline in the availability of preferred food (Furness & Hislop 1981). This change in the diets of Great Skuas and other seabirds occurred unusually early during 1988-1990, and has been blamed for the unusually poor breeding seasons in those years (e.g. Hamer *et al*. 1991).

Figure 2 shows the seasonal variation in numbers of nonbreeding Great Skuas on Foula during 1975-1990. It can be seen that the peaks in numbers of nonbreeders on Foula became progressively lower and earlier with 2600 birds (transformed data) on 13 July 1975, 1198 on 19 June 1988, 917 on 2 June 1989 and 819 on 25 May 1990. The declines in numbers of nonbreeders at the colony correlated significantly with the decrease in fish in the diets of nonbreeders.

As previously mentioned, the proportion of the total number of nonbreeding Great Skuas present at a club during afternoon attendance was significantly less in 1989 and 1990 than in 1976. This is probably due to nonbreeders spending more time foraging in 1989 and 1990, and may reflect the relative difficulty in obtaining food (Furness & Hislop 1981). This interpretation is supported by the dietary indications of reduced food availability in the latter halves of the 1989 and 1990 breeding seasons. Breeding Great Skuas on Foula also spent more time away from breeding territories, apparently foraging, during 1988-1990 than in the mid-1970's (Hamer et al. 1991). However, young birds are likely to be even more sensitive to poor foraging conditions than more experienced adults (Gaston & Nettleship 1982). The apparent reduction in the time nonbreeders spent at clubs during 1988-1990 may affect future population sizes as recruitment could be reduced if individual nonbreeders have less opportunity to select mates and sites because of an overall decreased club attendance.

The presence and size of the nonbreeding population associated with a Great Skua colony may reflect the health of that colony, rapidly expanding colonies tending to have many more nonbreeders and clubs than declining breeding colonies (Furness 1987a). This observation is supported by the results of this study. The breeding population of Great Skuas on Foula peaked at nearly 3000 pairs in 1976 and 1977, and has since been declining. This decline correlated with a significantly reduced nonbreeding population over the same period. It can be seen from Figure 7.3 that the peak numbers of nonbreeders on Foula at any one time between 1977 and 1990 has declined faster than the total number of breeders on Foula. Breeding failures cannot have caused this reduction in numbers of nonbreeders up to 1990, since Great Skua breeding success remained high until 1986, and there has been no change in the age-structure of the nonbreeding population since the mid-1970's (see Furness 1987a and Chapter 9). No one year-old birds and very few two year-old birds return to the colony, so most club-birds are 3 to 7 years old (see Chapter 9). However, recent breeding failures can be expected to lead to decreases in the nonbreeding population of Foula after 1990. It is thought that the increased mortality of 1+ year-old Great Skuas since the mid-1970s (Hamer 1990) is the principal cause of the reduction in the nonbreeding population on Foula, since there is no evidence of greater emigration (Chapter 5) or a reduced age at first breeding (Chapter 9), although an increased recruitment rate, due to increased breeder mortality, may also be a cause (see Chapter 8).

The continued presence of nonbreeders at a colony may also be dependent upon available food supplies, as suggested by the significant correlations between numbers of nonbreeders and their diets. Whilst breeding birds have reasons to remain with their nest for as long as possible, nonbreeders may leave a colony in search of more profitable areas more readily, as seen during 1988-1990. Also, nonbreeders are, on average, less experienced at foraging than breeders, and therefore may be affected more by reduced food availability (e.g. Dunn 1972).

It is possible that similar patterns of movement may be present among nonbreeders of other seabird species. Whilst long-term changes in a nonbreeding population may reflect the potential growth of the colony, diurnal and seasonal movements of nonbreeders may be good indicators of current food availability around a colony. Indeed, the movements of nonbreeders may be a more sensitive indicator of environmental conditions than the activities of breeding birds, because nonbreeders can respond directly to changes, are not restrained by breeding commitments, and may be more sensitive to poor foraging conditions. Although there have been no previous attempts to monitor environmental changes through observations of nonbreeding seabird activities, the results of this chapter suggest that such counts could be usefully added to current programmes monitoring populations of breeding seabirds.

CHAPTER 8

Numbers of Nonbreeding Great Skuas Frequenting Foula

A condensed version of this chapter constitutes a paper entitled 'Nonbreeders as a buffer against environmental stress: declines in numbers of Great Skuas on Foula, Shetland, and prediction of future recruitment' by N.I. Klomp and R.W. Furness, in press in Journal of Applied Ecology.

8.1. INTRODUCTION

A decrease in the recruitment, stock biomass and availability of Sandeels to seabirds in Shetland has caused unprecedented breeding failures of many species, and declines in colony sizes after many decades of continual increase (Heubeck 1989, Hamer et al. 1991, Lloyd et al. 1991). Decreased availability of Sandeels has led to Great Skuas depending heavily on killing seabirds and scavenging for discarded small whitefish obtained at fishing boats (Hudson & Furness 1988). The possible harmful effects of skua populations on sheep productivity in Shetland have led to granting of licences to cull small numbers of Great Skuas in recent years (Furness 1986). Close monitoring of Great Skua populations is essential, therefore, if informed recommendations are to be made for the management of this species in Shetland. This is also required by international agreements on conservation since the United Kingdom has a major responsibility to safeguard this Red Data Book species (Batten et al. 1990).

Recruitment of nonbreeding seabirds into a breeding colony is one of the most important factors in determining changes in breeding numbers from year to year (Ollason & Dunnet 1983). It has also been suggested that a decline in the number of nonbreeders associated with a colony can be the first indicator of a decline in the well-being of a seabird population (Porter & Coulson 1987). Yet very little inquiry has been made into the size of nonbreeding seabird populations that form the pool from which recruitment occurs. No previous study has attempted to estimate the total number of nonbreeding Great Skuas frequenting a colony in a breeding season.

Chapter 7 discussed diurnal, seasonal and long-term changes in numbers of nonbreeding Great Skuas present on Foula at given times. However, for a thorough understanding of the dynamics of the entire population on the island, a knowledge of the total number of nonbreeding Great Skuas frequenting the island throughout each season is required. This will provide an estimate of the size of the pool of potential recruits associated with the Great Skua population on Foula. This chapter describes different methods of estimating the total number of nonbreeders that visit the colony in a season. The relationships between breeder and nonbreeder population sizes are discussed and the probable future changes in breeding numbers as a consequence of the depleted pool of potential recruits in the local population are considered. Finally, the proposal of Porter & Coulson (1987) that studies of nonbreeders at seabird colonies may provide a sensitive signal of environmental stress is discussed in light of the results obtained.

8.2. METHODS

From 1988-1990, a total of 494 Great Skuas (see Table 8.1) trapped at clubs on Foula with cannon-nets were ringed with three or four plastic colour-rings in individual colour-combinations. Regular, thorough searches of the clubs and breeding territories allowed the attendance and behaviour of individually marked birds to be monitored throughout the breeding seasons. Counts of all birds on clubs were made weekly

TABLE 8.1. Numbers of nonbreeding Great Skuas individually colour-ringed at clubs on Foula in 1988 1989 and 1990, and the factors affecting the numbers of 1988 and/or 1989 colour-ringed birds theoretically available for observation at clubs in 1989 and 1990.

	Year of colour-ringing			Total
	1988	1989	1990	
No. of nonbreeders individually colour-ringed at clubs:	111	229	154	494
No. ringed as chicks with individually numbered rings:	27	65	37	129 (26%)
No. known to have fledged from another colony:	3	1	1	5 (4%)
Total no. of nonbreeders colour-ringed in 1988 and 1989:	111	229		340
Mortality[1] - 1988-1989:	22			22
- 1989-1990:	(15	46)		61
No. of colour-ringed birds that bred for the first time				
- 1989:	13 (14.6%)			13
- 1990:	(16	26 (14.2%))		42
No. of 1988/1989 colour-ringed birds seen in other colonies:	1	0	0	1
No. of 1988 colour-ringed birds available for observation at clubs in 1989:	75			
No. of 1988/1989 colour-ringed birds available for observation at clubs in 1990:				201

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[1] Mortality of nonbreeders is estimated to be 20% per year during 1988-1990 (after Hamer 1990).

in 1989 and 1990, both in the afternoon and at night, as described in Chapter 7.

Observations of colour-ringed birds were used to estimate the number of days individuals spent at the colony in 1989 and 1990. Sightings of colour-ringed birds at all clubs were recorded twice every week in 1989 and once per week in 1990. Hence, the time spent at the colony by any given bird was calculated by adding either 3 days (1989) or 6 days (1990) to the time between first and last sightings of that bird, thus accounting for the time a bird may have spent at the colony before its first sighting and after its last sighting. Individual nonbreeding Great Skuas do not appear to prospect at different colonies in a given season (see Chapter 5), and all nonbreeders attending a colony settle at the club-sites at night (Bayes _et al_. 1964, Chapter 7). Hence, individuals are considered to be present at the colony every night between first and last sightings.

In order to estimate the total number of nonbreeding Great Skuas that visit Foula during a breeding season, two different methods were employed, as described below. These methods both assume that colour-ringed birds behave in the same way as birds not ringed and so are able to be observed equally. There was no evidence from this study to suggest that this assumption is unwarranted. These methods also assume that no unrecorded colour-ring loss occurred. Of 784 colour-rings placed on 196 breeding Great Skuas (4 rings per bird) in a separate study during 1988-1990 (Hamer 1990), only two rings were lost, still leaving these two birds individually identifiable. Using the same type of colour-rings in this study, none of the 494 nonbreeding birds ringed was observed to have lost any colour-rings. Hence, the assumption of no colour-ring loss is accepted.

8.2.1. Method 1

The Lincoln Index (Lincoln 1930; Blower *et al*. 1981) was used to estimate the number of nonbreeders frequenting the island in the 1989 and 1990 breeding seasons. Other mark-recapture estimates of population size, such as the use of multiple marking methodologies (see Blower *et al*. 1981), were not appropriate for this study. Lincoln Index calculations were based on the number of birds individually colour-ringed and the proportion of colour-ringed birds subsequently observed at all clubs. Because numbers colour-ringed varied between clubs, resighting visits were made to every club so that coverage for resightings was uniform. Standard errors of the estimates were also derived. This method assumes that ringed birds mix thoroughly with unringed birds at each club-site. This assumption is considered valid for three reasons: (a) the colour-ringed birds were caught and marked on many different dates throughout each breeding season, (b) the colour-ringed birds were subsequently observed with unringed birds at the clubs, and (c) the ratio of ringed to unringed birds within pairs of first-time breeders suggested non-assortative mating and, hence, thorough mixing of ringed and unringed birds. Estimations using the Lincoln Index can only be conducted on a 'closed' population, with any ingress or egress taken into account (Blower *et al*. 1981). For this reason, the nonbreeding population in 1989 was only estimated using observations of 1988 colour-ringed birds, and the 1990 nonbreeding population was estimated using sightings of birds colour-ringed in 1988 and 1989 only. Immigration, emigration and adult mortality within a given season are very low (Furness 1987a, Chapter 5). The calculations allow for the known mortality, recruitment and emigration from 1988 to 1990.

8.2.2. Method 2

The number of nonbreeding Great Skuas visiting Foula was estimated using the results of calculations of the mean number of days individual nonbreeders spent at the colony in 1989 and 1990. The total number of bird-days of nonbreeders on Foula (determined from weekly night-time counts of all nonbreeders throughout the breeding seasons) was divided by the mean number of days these birds spent at the colony. This quotient provided an estimate of the number of nonbreeders visiting Foula in each season. This method assumes the times birds spent at the colony each year were normally distributed; this was confirmed before these and all statistical calculations were performed.

8.3. RESULTS

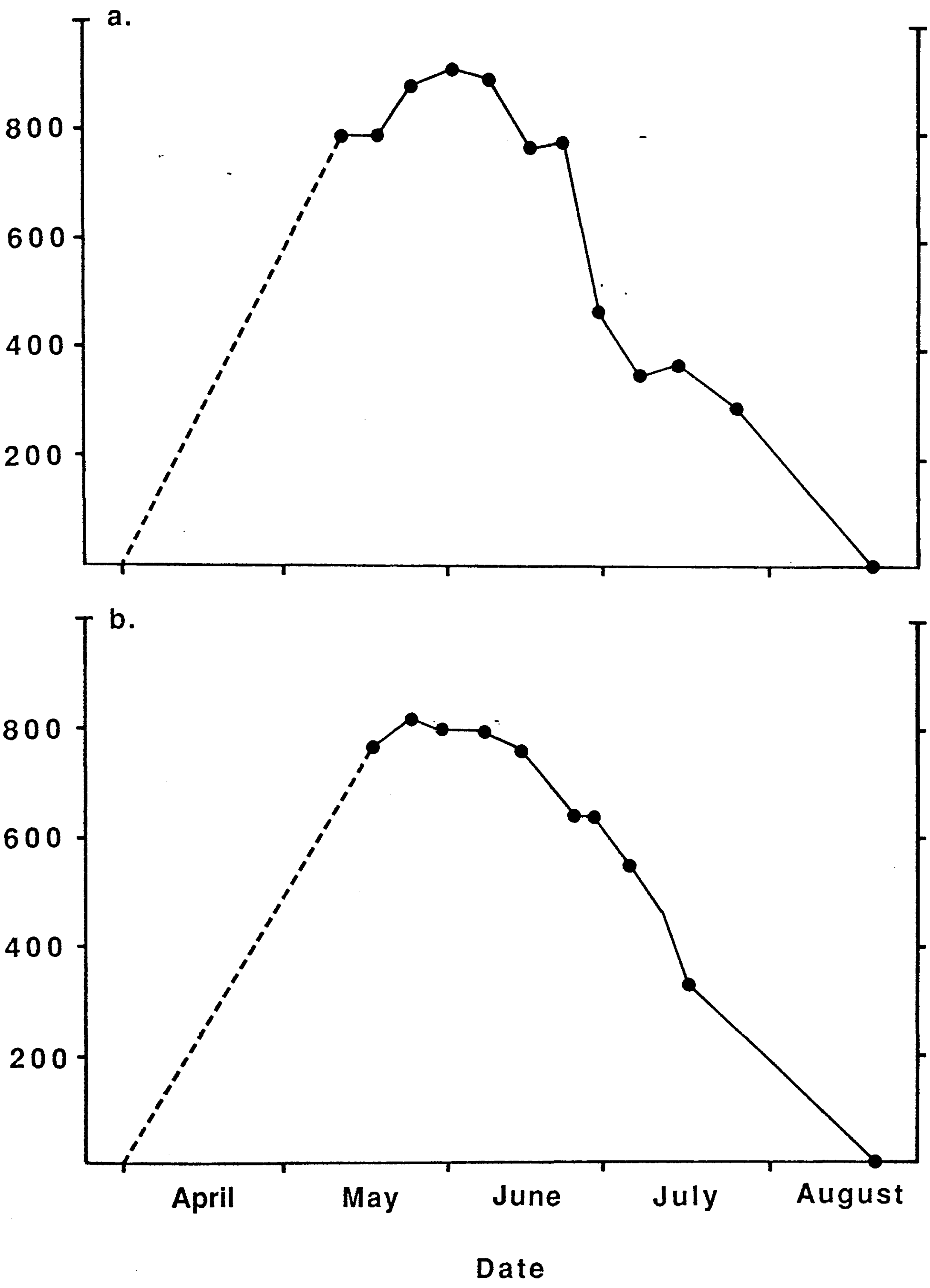
Table 8.1 summarises the ringing and resighting data for nonbreeding Great Skuas in this study. Only one bird of 494 birds colour-ringed on Foula as nonbreeders, was subsequently seen at another colony (Hermaness, Shetland), as described in Chapter 5.

The total number of nonbreeding Great Skuas attending a colony on a particular date can be determined by counting the birds in all the clubs in the colony during the night (see Chapter 7). This then allows the seasonal variation in numbers of nonbreeders at a colony to be monitored. Nonbreeding Great Skuas start arriving back at clubs on Foula in April and have all left by mid-August each year (Furness 1987a). The peak number on the island, however, does not represent the total number of nonbreeders that visit the colony in a season, but only the maximum number on the island at any one time. Figures 8.1a and 8.1b show the seasonal variation in numbers of nonbreeders at the colony in 1989 and 1990, respectively. The areas under these curves represent the total number of nonbreeding bird-days on Foula in each year.

8.3.1. Duration of stay

If the results of every second search of the clubs in 1989 are temporarily omitted from the calculations - thus equating the search efforts in the two years - the mean time spent at the colony by those birds recorded more than once in a season on Foula was not significantly different between years (Student's t=1.78, df=46, P>0.05). There was still no significant difference between the mean durations of stay in the two years when all the 1989 data were included (Student's t=1.83, df=51, P>0.05), despite twice the search effort in 1989. This suggests that the observed durations of attendance were not affected by the different search efforts in 1989 and 1990 and, therefore, were probably close to the actual mean durations of stay of individual nonbreeders in the colony. There was no evidence of older or younger birds, nor earlier or later

FIGURE 8.1. The seasonal variations in total numbers of nonbreeding Great Skuas on Foula over the 1989 (a) and 1990 (b) breeding seasons, as determined by night counts of birds at all clubs (Chapter 7). These graphs have been extrapolated to include the estimated date of first arrival (1 April), as based on observations in previous years (Furness 1987a). The areas under the curves are 70,000 bird-days (1989) and 67,000 bird-days (1990).


a.
800
600
400
200
b.
800
600
400
200
April
May
June
July
August
Date

arriving birds, showing any difference in their duration of stay at the colony. The mean length of stay by all observed, individually marked Great Skuas at clubs (single and multiple sightings) was calculated as 17.8 days (S.D.=16.0 days, n=31) for 1989 and 18.8 days (S.D.=16.0 days, n=72) for 1990. These results were not significantly different between years (Student's t = 0.29, df = 101, P>0.5). The distribution of times spent at the colony in each year did not differ significantly from normality.

8.3.2. Number of nonbreeders

In 1989, 3692 bird-sightings at the clubs resulted in 69 sightings of birds colour-ringed in 1988. In 1990, 2859 bird-sightings resulted in 174 sightings of 1988 and 1989 colour-ringed birds. Some of these sightings were of the same birds, but it is likely that the ratio of single and repeated sightings is the same for both ringed and unringed birds. During 1989, 75 birds colour-ringed in 1988 were available for observation at the clubs on Foula, and 201 1988/1989 colour-ringed birds were available for observation in 1990 (see Table 8.1). Thus, using Method 1, 4013 birds (S.E.= 479 birds) and 3303 birds (S.E.= 243 birds) were calculated to have frequented clubs on Foula in 1989 and 1990, respectively.

The number of nonbreeding Great Skuas visiting Foula was calculated for each year by dividing the number of bird-days (the areas under the curves: Figures 8.1a and 8.1b) by the mean number of days individuals spent at the colony, as described by Method 2. Hence, the number of nonbreeders frequenting the colony was calculated as 3933 birds (70,000 ÷ 17.8) in 1989 and 3564 birds (67,000 ÷ 18.8) in 1990.

8.4. DISCUSSION

ESTIMATES OF TOTAL NUMBERS OF NONBREEDERS IN THIS CHAPTER ARE BASED ON SEVERAL IMPOR
ASSUMPTIONS, NOT THE LEAST OF WHICH IS THE ASSUMPTION MADE IN CHAPTER 7 THAT ALL NONBRE
ASSOCIATED WITH A COLONY ON A GIVEN DATE ATTEND THE CLUBS AT NIGHT. THESE ESTIMATES W
BE WRONG IF SUCH ASSUMPTIONS ARE INVALID.

8.4.1. Nonbreeding Great Skuas frequenting Foula

Porter & Coulson (1987) provide strong evidence for the existence of a pool of potential recruits associated with a seabird colony. However, the total number of nonbreeding seabirds frequenting a colony has rarely been estimated, and only ever in studies of relatively small (<200 breeding pairs) colonies (Porter 1988, Pickering 1989). Despite using two different methods, the estimates of the large number of nonbreeding Great Skuas frequenting clubs on Foula in this study provided relatively consistent results, well within the confidence limits derived from the Lincoln Index calculations (Method 1). Hence, the number of nonbreeding Great Skuas frequenting Foula in 1990 is considered to be approximately 3300 birds (95% confidence limits: ±476 birds). The standard error of the 1989 estimate was relatively large (±479 birds), mostly due to the small number of ringed and retrapped birds, so the estimate of 4013 birds for that year must be considered with some caution, although the results of Method 2 also support this estimate. The number of nonbreeders frequenting Foula in 1989 is considered to have been greater than that in 1990, based on the peak numbers seen in the colony in each year and the population estimates derived from Methods 1 and 2.

The mean duration of stay of nonbreeding Great Skuas on Foula was not significantly different between 1989 and 1990.

However, the mean durations of stay of nonbreeders may be slightly under-estimated in this study, because during the day not all birds are present to be observed. Hence, the estimate of the number of nonbreeders frequenting the colony, using Method 2, may be a slight over-estimate, as is reflected in a comparison to the results of the Lincoln Index calculations. Another estimate of the length of stay of nonbreeding Great Skuas on Foula can be obtained by dividing the total number of bird-days (areas under curves, Figures 8.1a and 8.1b) by the results of the Lincoln Index calculations. In this way, an estimate of 16.7 days and 21.2 days is obtained for 1989 and 1990, respectively. So it is likely that the average duration of stay in 1989/1990 was between 16 and 21 days.

The use of life-tables can provide an indication of the total numbers of birds alive of given ages. Based on known population sizes, previous breeding success and survival rates of Great Skuas on Foula (after Furness 1987a; Hamer 1990), there should be 3500 birds alive that fledged from Foula and were aged 3-7 years in 1990 (see nonbreeder age-structure, Chapter 9). This result coincides closely with the number of nonbreeders estimated in this study. The slight difference between this theoretical number alive and the estimated number of nonbreeders frequenting the colony may be partly due to some birds not returning to the colony until four or five years of age (Furness 1978), although this may be partly or wholly compensated for by the presence of some birds more than seven years old at the clubs. The small difference between the theoretical number alive (calculated from life tables) and the estimated number of nonbreeders frequenting Foula in 1990 may also reflect a net emigration from the colony. This is supported by the fact that a few smaller colonies had been increasing faster than that on Foula and included birds ringed as chicks at Foula (Furness 1987a). However, as ringing analysis has shown that the immigration rate into Foula is very low (Chapter 5), the maximum possible rate of emigration from Foula must also be low, as this study suggests that there is only a slight imbalance between the number of nonbreeders alive and number present on Foula.

Casual counts of nonbreeders present in a colony often do not provide reproducible results (Chapter 7). Regular counts at night were found to show total numbers of nonbreeding Great Skuas present in a colony on a given date, but this number varied over the season. This study has shown that even the peak number of nonbreeders attending the colony at one time (see Figures 8.1a and 8.1b) only represents 20-25% of the total number estimated to have frequented the colony in 1989 and 1990, due to birds only staying approximately 16-21 days, on average. Hence, there is a considerably larger pool of nonbreeders associated with a colony than might be apparent from casual or even regular surveys. This finding has serious implications for management and conservation when considering future population sizes, food consumption in the area, the effect of Great Skuas on sheep productivity and predation of other seabird species.

8.4.2. Past, present and future recruitment

As previously mentioned, very little is known about the patterns of attendance of nonbreeding seabirds in colonies, or how such patterns affect the process of recruitment (Porter &

Coulson 1987), although recent studies have revealed relationships between attendance patterns and recruitment rates in some seabird species (Porter 1988, Pickering 1989). The attendance and population data presented in this study can be used to model recruitment in the breeding population.

There is no evidence to suggest that first-year survival (80%, S.E.=2%), or rates of immigration or emigration changed significantly from the mid-1970's to the late-1980's (Furness 1977, 1978, 1987a; Hamer 1990). The mean age at first breeding (7-8 years old) has also remained unchanged (Furness 1977, Chapter 9). However, annual survival rates of Great Skuas more than one year old apparently decreased from 93% (S.E.=1%) p.a. in the 1970's, to 80% (S.E.=2%) p.a. in the 1980's (Hamer 1990). This change in the mortality rate of birds more than one year old can be shown to be largely responsible for the decline in numbers of nonbreeders on Foula.

For example, in order to maintain a breeding population on Foula of 2980 pairs in 1976 (Furness 1986), approximately 500 nonbreeders would have recruited into the colony in 1977 to balance breeder mortality. An average of 1.2 chicks per pair per year fledged successfully in the mid-1970's (Furness 1984), resulting in approximately 2200 Great Skuas surviving to the minimum age at first breeding of 4 years old. Hence, the comparatively large number of nonbreeders frequenting the island in the mid-1970's. However, the number of new recruits required to allow the 1989 breeding population (2400 pairs) to be maintained into 1990 had almost doubled to approximately 960 recruits in that year, due to the increase in breeder mortality. The nonbreeders, themselves, are apparently also subject to this increased mortality rate (Hamer 1990), so it is not surprising to find a huge reduction in the peak number of nonbreeders in the colony in any year (Chapter 7), reflecting the reduction in the size of the entire nonbreeding pool, since 1977.

The breeding success of Great Skuas on Foula remained high until 1986, and has since declined to an average of 0.3 chicks per pair per year during 1987-1990 (Hamer et al. 1991). Hence, based on chick production alone, the number of birds joining the nonbreeding pool after 1990 will be only 25% of the previous rate. It is the increased breeder mortality rate, resulting in an increased rate of recruitment, that has largely caused a reduction in the numbers of nonbreeders frequenting Foula in recent years. The decreased breeding success since 1987 could only now begin to affect the number of nonbreeders. However, further, and more rapid, decreases in numbers of nonbreeders on Foula are to be expected over the next few years. As breeding and nonbreeding Great Skuas show a particularly high level of colony fidelity (Chapter 5), it is likely that the pool of potential recruits on Foula will dry up and breeding numbers will decline at an increased rate after 1991.

In retrospect, had data to show the increased rate of adult mortality not been available, it would still have been possible to detect and interpret changes in numbers of nonbreeders at the colony as a signal of a decline in the health of the population. Although highly sensitive to any further changes in adult survival rate, the decline in numbers of breeders and nonbreeders on Foula is unlikely to be arrested until at least three years after breeding success improves substantially above the 1987-1990 levels and so signals a considerable and prolonged decrease in numbers of one of the rarer North Atlantic seabirds.

Monitoring of the numbers of immature birds (nonbreeders) attending seabird colonies would provide a valuable early warning of environmental stress affecting seabirds, and would be especially valuable for the majority of populations, where adult survival rates are not assessed. However, nonbreeding Great Skuas at clubs are almost all prebreeding birds (see Chapter 9), and counts of nonbreeders may be more difficult to interpret in species where nonbreeders include birds that have taken a season off after previous breeding years.

CHAPTER 9

The Role of Clubs in Recruitment of Great Skuas

Parts of this chapter constitute a paper entitled 'Recruitment in long-lived birds: studies of nonbreeding Great Skuas' by N.I. Klomp & R.W. Furness, in press in the Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

9.1. INTRODUCTION

Recruitment is a major determinant of changes in breeding populations from year to year, yet the process whereby individuals are recruited to the breeding segment of the population is poorly understood (Ollason & Dunnet 1983, Furness & Birkhead 1984, Porter & Coulson 1987). Long-lived birds do not normally commence breeding until they are several years old (Lack 1968), and many seabird studies have documented the presence of young adults at the colony in one or more years before they breed, as well as the presence of birds of breeding age which do not breed (e.g. Gannets: Nelson 1966, Shearwaters: Perrins et al. 1973, Herring Gulls: Chabrzyk & Coulson 1976, Kittiwakes: Porter & Coulson 1987, Wandering Albatrosses: Pickering 1989).

A knowledge of the behaviour and movements of potential recruits in a seabird colony is basic to a greater understanding of the recruitment process in seabirds (Ollason & Dunnet 1983). Although there are several important studies of recruited birds, including removal experiments that altered recruitment rates and age at first breeding in seabird colonies (eg. Coulson et al. 1982), the difficulty in studying pre-recruits has resulted in few investigations being attempted.

As previously mentioned, Great Skuas are particularly suitable for studies of pre-recruits and recruitment because, during the breeding season, nonbreeders gather in traditional clubs in and around the colonies. Previous chapters in this thesis have discussed various factors that may influence recruitment in Great Skuas, even prior to an individual first returning to a breeding colony. This chapter addresses various aspects of the final steps in the process of recruitment: once individuals first frequent the colony, prior to breeding. The pool of nonbreeding birds that frequent Foula and the ways in which they attempt to become established as breeders are examined, with particular reference to the role of clubs in the recruitment of Great Skuas.

9.2. METHODS

Between 300 and 2900 Great Skua chicks were ringed with individually numbered BTO rings on Foula every year since 1963. Most chicks ringed were also weighed and measured, as described in Chapter 2. In addition, from 1968 to 1974, 400 to 1400 chicks were ringed each year with plastic colour-rings in combinations unique to the year. During the 1973 and 1974 breeding seasons (May to August), the proportions of birds in a club with different colour-ring combinations were monitored regularly. In 1988, 1989 and 1990, 494 birds that were trapped at five different club-sites were measured and ringed using individual colour-ring combinations, as described in previous chapters. In addition, twenty birds breeding within 40m of the centre of club-sites were nest-trapped and individually colour-ringed in 1988. A separate study of individually colour-ringed breeding Great Skuas was also conducted during 1988-1990 (see Hamer 1990).

Regular, thorough searches of the club-sites and breeding territories allowed individually marked birds to be monitored throughout most of the 1988-1990 breeding seasons, although only a short field season was conducted in 1991. Nonetheless, all breeding attempts by known individuals in 1988-1991 were considered to have been recorded, since all marked first-time breeders were located within the first 12 days of searching each season, and no other known new recruits were located after this initial period, despite continued searching effort. The location and size of their breeding territories (nearest nest distance) and the number of eggs laid were recorded in each year, and the success of breeding attempts ~~were~~ was recorded in 1989 and 1990. Eggs were measured in many of the nests monitored, and clutch volume was calculated from equations provided by Coulson (1963). Breeding sites were divided into three groups: 'club' (nest-sites within 40m of the centre of a club-site), 'periphery' (nest-sites on the edge of the established breeding colony) and 'colony' (all other nest-sites within established breeding territories. In addition, all breeding attempts at all club-sites in 1988-1990 were recorded.

The total area occupied by breeding Great Skuas on Foula in 1988 and 1990 was determined by mapping peripheral territories.

9.3. RESULTS

9.3.1. Great Skua club-sites

Great Skua gathering sites can be divided into three groups: 'club-sites', 'bathing sites' and 'temporary clubs'. Figure 2.1 shows the location of the 15 club-sites on Foula, although only 14 were frequented by Great Skuas in 1988 and only 13 were used by the birds during 1989-1991. Of the 15 club-sites, four are associated with bathing sites, where both breeders and nonbreeders bathe and preen, although the nonbreeding component (club) of such sites is usually quite separate (see Figure 2.1). The concentrated trampling and defaecation by the skuas eroded the peat and encouraged dense swards of grass, making the sites easily identifiable. The club-sites were usually 30-70m in diameter (mean=49.0m, S.D.=17.9m, N=15) and did not change in physical size from 1988 to 1990. Temporary clubs were formed when nonbreeders gathered in additional, previously unavailable areas, usually at the end of the season, when some territories had been vacated by failed breeders. Such gatherings sometimes lasted only a few hours, although one temporary club formed at the end of the 1988 breeding season was used as a permanent club-site (no. 15) in 1989-1991.

All nonbreeding Great Skuas attending the colony settled at the club-sites at night (see Chapter 7). Although there are no obvious plumage differences between breeders and nonbreeders, colour-ringing and time-budget studies (Furness & Hislop 1981, Furness 1987a, Hamer <u>et</u> <u>al</u>. 1991, this study) have confirmed that breeding Great Skuas rarely, if ever, attended the clubs.

Established breeders that did not breed in a particular year generally continued to defend their breeding territories (Hamer <u>et</u> <u>al</u>. 1991), although 8 such individuals were recorded at club-sites in 1989 and 1990 following particularly harsh breeding conditions in 1988 and 1989 (see Hamer 1990). This only represented 1.6% of the total number of birds colour-ringed at club-sites and less than 4% of all colour-ringed breeders (after Hamer 1990). Also, these eight birds were each recorded only once at club-sites; significantly fewer observations than of other colour-ringed birds in clubs (X^2_1=9.59, N=101, P<0.01).

Nonbreeding Great Skuas were generally faithful to one club. The limited size of club-sites, confined by surrounding breeding territories, and the aggressive nature of Great Skuas, even in clubs, gives a finite limit to the number of birds that can stand side by side (Furness 1987a). Up to 300 birds have been recorded at one time in a club, but during 1988-1990, the mean number of birds in the clubs at the diurnal and seasonal peaks of nonbreeder attendance during 1988-1990 was 76.4 (S.D.=50.4, N=40).

Great Skua clubs were found to be sites of intensive behavioural interactions between nonbreeding birds. The full behavioural repertoire of the species (as described by Perdeck 1960) was observed at these sites, including copulation, and some breeding attempts were made at the edges of the clubs. Nest-sites on the edges of club-sites are considered in more detail in later sections.

Chapters 7 and 8 described the diurnal and seasonal variations in numbers of nonbreeding Great Skuas on Foula. Numbers of birds at clubs were maximum and stable at night. The proportion of this night-time total present during the afternoon appeared to be relatively constant within years, but may have been related to differences in prey availability and, hence, foraging effort among years. Total numbers of nonbreeders in a colony also varied seasonally, with the peak and subsequent decline apparently coinciding with changes in food availability. The numbers of nonbreeders also correlated with the numbers of breeders on Foula over the 1970s and 1980s. Based on observations of known individuals, the mean time nonbreeding Great Skuas spent at Foula in 1989 and 1990 was estimated to be 16-21 days. There was no evidence of older or younger birds, nor earlier or later arriving birds showing any difference in their duration of stay at the colony. The total number of Great Skuas frequenting the club-sites throughout the 1989 and 1990 breeding seasons was estimated from retrap data to be 4013 (S.E.=479) and 3303 (S.E.=243) individuals, respectively.

9.3.2. Age-structure and sex-ratio of the nonbreeding population

Figure 9.1 shows the age-structure of 129 Great Skuas ringed as chicks with BTO rings and trapped at clubs during 1988-1990, corrected for the different ringing efforts in the different years the birds were ringed as chicks (as if 1000 chicks were ringed on Foula each year). The majority of birds present on the clubs were 3-7 years of age. The presence of birds older than nine years was rare.

Although no seasonal variation in the age-structure of nonbreeders was observed in 1988-1990, possibly due to relatively small sample sizes, observations of larger samples of known age birds in a club (no. 9) in 1973 and 1974 revealed a distinct seasonal pattern (see Figure 9.2). Younger birds (2-4 years old) were present at the club in greater numbers later in the season, and more older birds were at the club earlier in the year. This seasonal variation in age-structure of club-birds could arise if the nonbreeders generally return to the colony earlier each year until they recruit into the breeding

FIGURE 9.1. Frequency histogram of known ages of Great Skuas caught at clubs during 1988-1990, corrected for the different ringing efforts in the different years the birds were ringed as chicks (as if 1000 chicks were ringed on Foula each year).

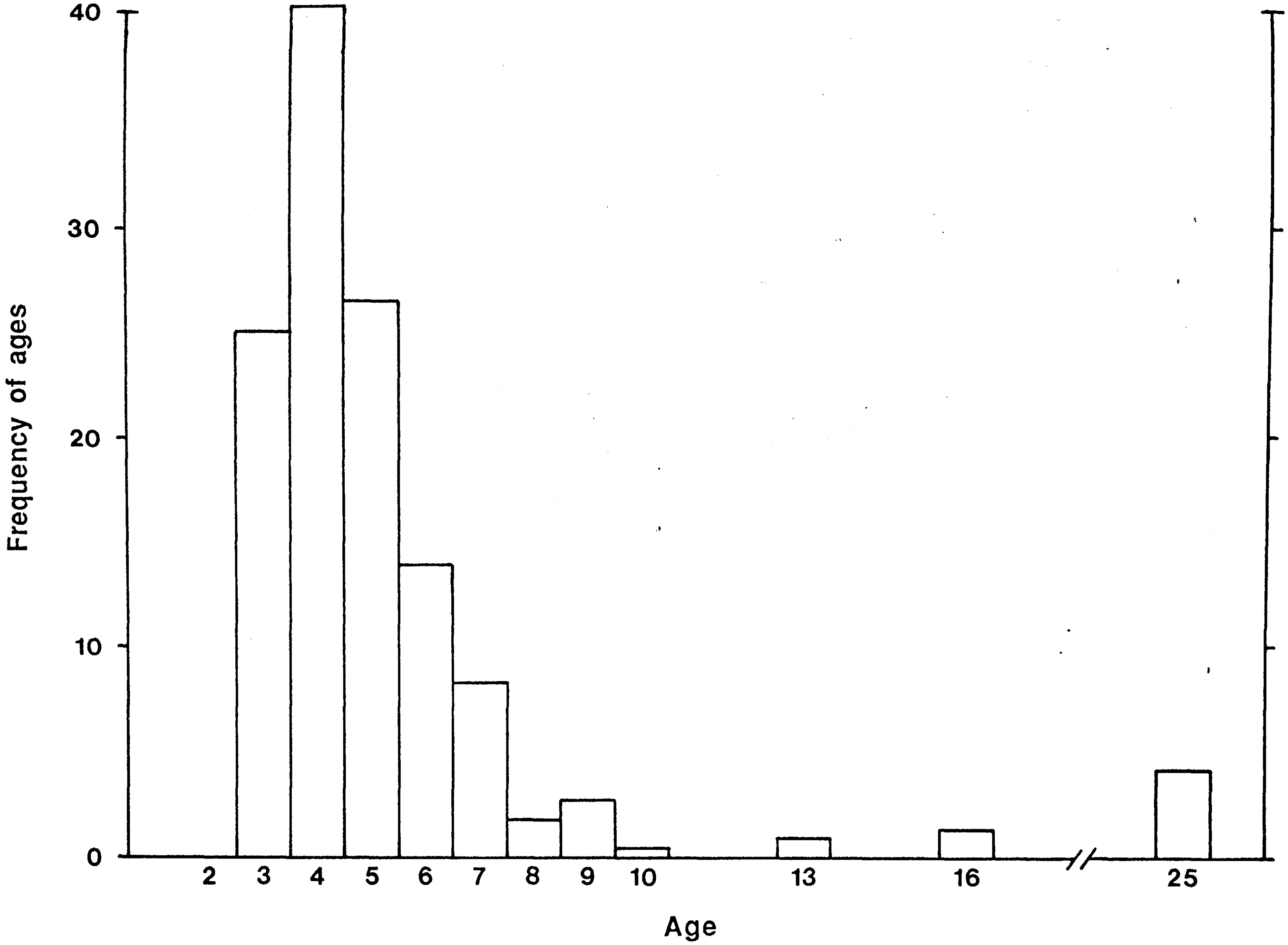

Frequency of ages
0
10
20
30
40
2
3
4
5
6
7
8
9
10
13
16
25
Age

FIGURE 9.2. The frequency of birds aged 2 to 5 years at a club on Foula in 1973/1974, corrected for ringing effort (as if 1000 chicks were ringed on Foula each year) and observational effort (as if 100 birds were observed in each time period).

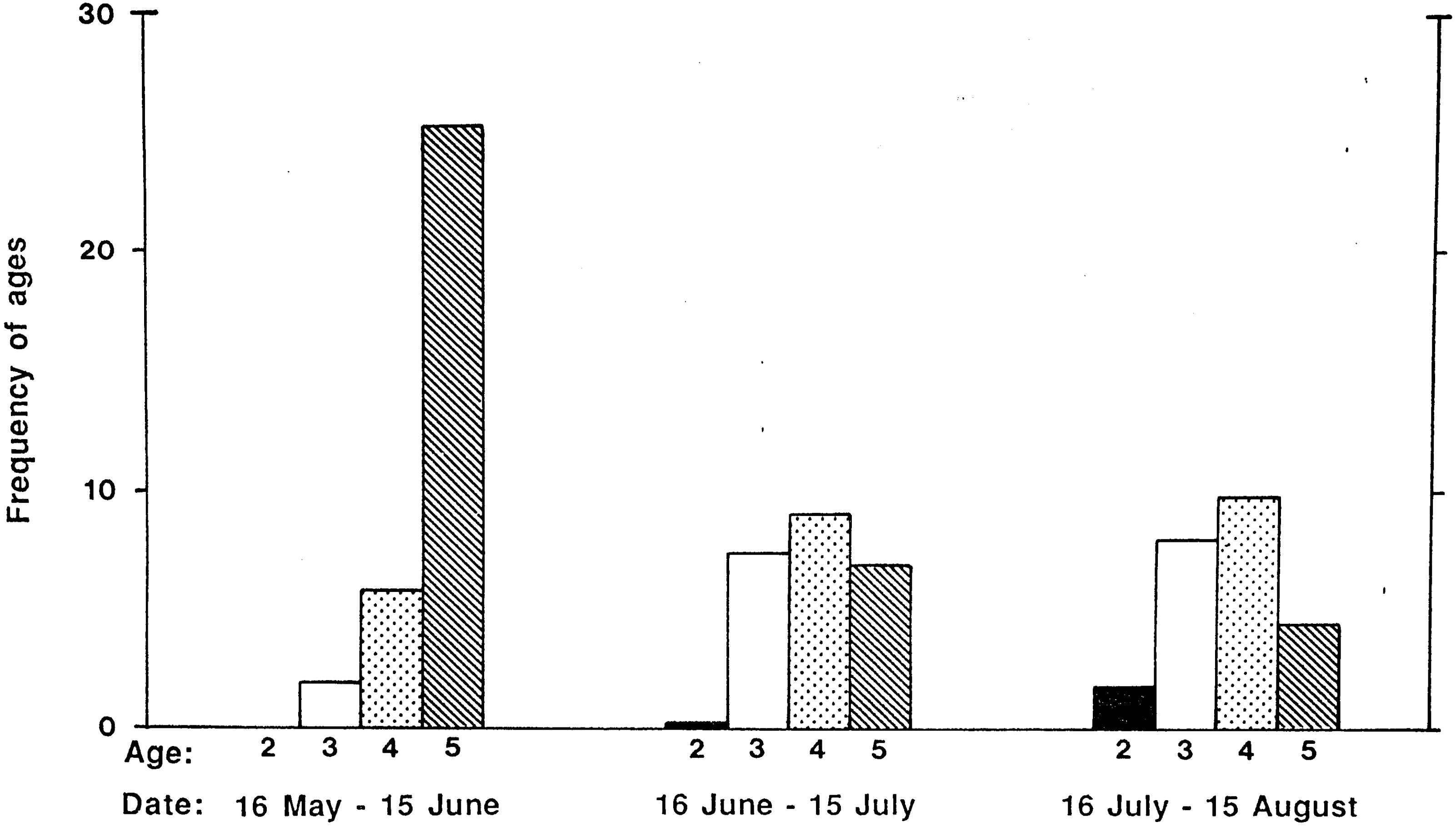
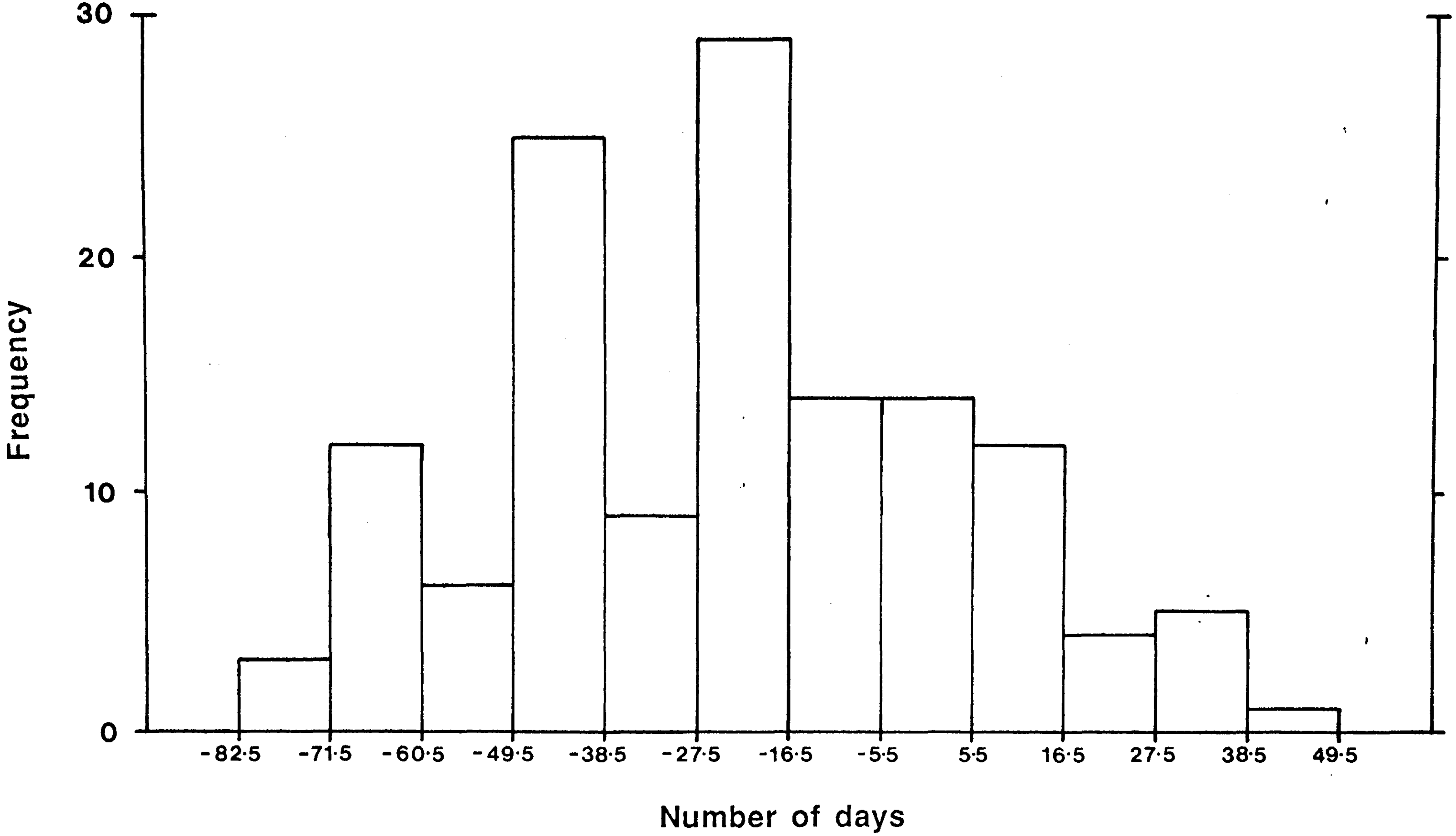

Frequency of ages
30
20
10
0
Age:
2
3
4
5
2
3
4
5
2
3
4
5
Date:
16 May - 15 June
16 June - 15 July
16 July - 15 August

FIGURE 9.3. Frequency histogram of the time differences between first sightings of individual birds in clubs in 1989/1990 and first sightings of the same individuals in clubs in the preceding year.


30
20
10
0
Frequency
-82·5
-71·5
-60·5
-49·5
-38·5
-27·5
-16·5
-5·5
5·5
16·5
27·5
38·5
49·5
Number of days

population. Indeed, it can be seen from Figure 9.3 that in 1989 and 1990, known individuals were first sighted on the clubs significantly earlier than in the previous year (Paired t-test, $t=9.8$, $N=104$, $P<0.001$).

There were only 13 sightings of 2-year old birds at a club in 1973 and 1974 (representing between 1 and 13 birds), despite approximately 1600 chicks having been colour-ringed on Foula two years prior to the observations. No two year-olds were recorded on clubs in 1988-1990. It is clear from Figures 9.1 and 9.2 that most birds first arrived at the colony at 3-5 years of age.

Of the 219 adult Great Skuas sexed by internal examination (see Chapter 4), only 22 were known to be nonbreeders (generally shot at club-sites). Of this sample, 10 were females and 12 were males, a ratio not significantly different from parity ($X^2_1=0.18$, $P>0.5$).

9.3.3. Recruitment

9.3.3.1. Recruitment rates. Of the 494 Great Skuas trapped at club-sites on Foula during 1988-1990 and individually colour-ringed, a total of 117 bred during 1989-1991 (i.e. 24% over three years). However, this proportion does not represent fairly the recruitment rate in the colony during 1989-1991, because some birds were colour-ringed one or two years after others, and would have been, on average, one or two years younger and less likely to recruit. A valid method of calculating the rate of recruitment for each year is shown in Table 9.1. For each year 1989-1991, the number of individually colour-ringed birds that recruited in a given year (Year R) and had been colour-ringed in the previous year (Year R-1) was expressed as a percentage of the total number of birds colour-ringed in Year R-1 that were 'available' for recruitment in Year R, allowing for mortality and emigration of the colour-ringed birds from Year R-1 to Year R. This provides an estimate of the proportion of birds from the pool of nonbreeders frequenting Foula that recruited into the breeding population. The recruitment rates were calculated as 14.6% in 1989, 14.2% in 1990 and 13.8% in 1991.

9.3.3.2. First-time breeders. Of the 117 first-time breeding Great Skuas recorded during 1989-1991, three bred with a known established partner and four pairs were formed where both partners were new recruits. Hence, a total of 113 nests were recorded where at least one partner was a known new recruit. Of the 117 new recruits, 33 had been ringed as chicks with BTO rings, so their age and hatching condition were known. There were no significant relationships between relative or calendar hatching date (see Chapter 6), of these 33 birds, with age at first breeding, number of eggs or volume of first clutch, nearest nest distance or type of territory (club, periphery or colony) held when first breeding. Nor were there any relationships between chick weight (for wing length) with any of the above first-time breeding parameters (chi-square tests and one-way ANOVAs, as appropriate, all Ps>0.1).

All known-age new recruits were 5-10 years old. The median age at first breeding was 7 years (mode=7 years, mean=7.2 years, S.D.=1.4 years, N=33). When corrected for chick-ringing effort in each year, the mean age at first breeding was 7.1

TABLE 9.1. Numbers of nonbreeding Great Skuas individually colour-ringed at club-sites on Foula in 1988, 1989 and 1990, and the recruitment rate from each cohort, expressed as a percentage of the number of birds that were 'available' for recruitment from the birds colour-ringed in the previous year (i.e. allowing for mortality and emigration).

	Year of colour-ringing		
	1988	1989	1990
No. of nonbreeders individually colour-ringed at club-sites:	111	229	154
Mortality* 1988-1989:	22		
No. of colour-ringed birds that bred for the first time - 1989:	13 (14.6%)		
No. of colour-ringed birds seen in other colonies:	1	0	0
Mortality* 1989-1990:	15	46	
No. of colour-ringed birds that bred for the first time - 1990:	16	26 (14.2%)	
Mortality* 1990-1991:	9	31	31
No. of colour-ringed birds that bred for the first time - 1991:	19	26	17 (13.8%)
No. of nonbreders not accounted for by the end of 1991	16	100	106

*Mortality of adult Great Skuas is estimated to be 20% per year during 1988-1991 (Hamer 1990).

years (S.D.=1.5 years). Hence, ringing effort did not alter appreciably the perceived average age at first breeding. One breeding Great Skua, nest-trapped at the edge of a club-site, was 4 years old.

Of the 117 new recruits recorded in 1989-1991, there were no significant differences among the mean values of weight, wing, wt/wing and head+bill as measured in the year of colour-ringing, one to three years prior to recruitment, for first-time breeders of different ages (one-way ANOVAs, all Ps>0.1). A total of 56 birds recruited in the year following colour-ringing, and 115 birds were recorded at a club-site, but did ~~and~~ not ? breed~~ing,~~ in the year following colour-ringing. A comparison of these two groups revealed a significant difference between the mean ages ('recruits'=7.2 years, S.D.=1.8, N=14; 'non-recruits'=5.5 years, S.D.=2.6, N=24; Student's t=2.16, df=36, P<0.05), but no differences between the mean values of weight, wing, wt/wing or head+bill (one-way ANOVAs, all Ps>0.1).

There were no significant differences in the ages of first-time breeders incubating one-egg and two-egg clutches, or in the ages of birds recruiting into any of the three different types of territories (one-way ANOVAs, all Ps>0.1). However, first-time breeders that incubated two-egg clutches had significantly greater mean wing lengths, in the year of colour-ringing (mean=418.0, S.D.=9.09, N=44), than first-time breeders that were responsible for one-egg clutches (mean=422.0, S.D.=9.09, N=73; Student's t=2.31, df=115, P<0.05). First-time breeders aged 5 or 6 years had significantly smaller territories (nearest nest distance) than older recruits

($mean_{5,6}$=17.8, S.D.=4.43, N=10; $mean_{7+}$=23.7, S.D.=8.63, N=23; Student's t=2.05, df=31, $P<0.05$).

Clutch volume was not significantly associated with age at first breeding, sizes and weights of recruits, type of territory or nearest nest distance (all $Ps>0.1$).

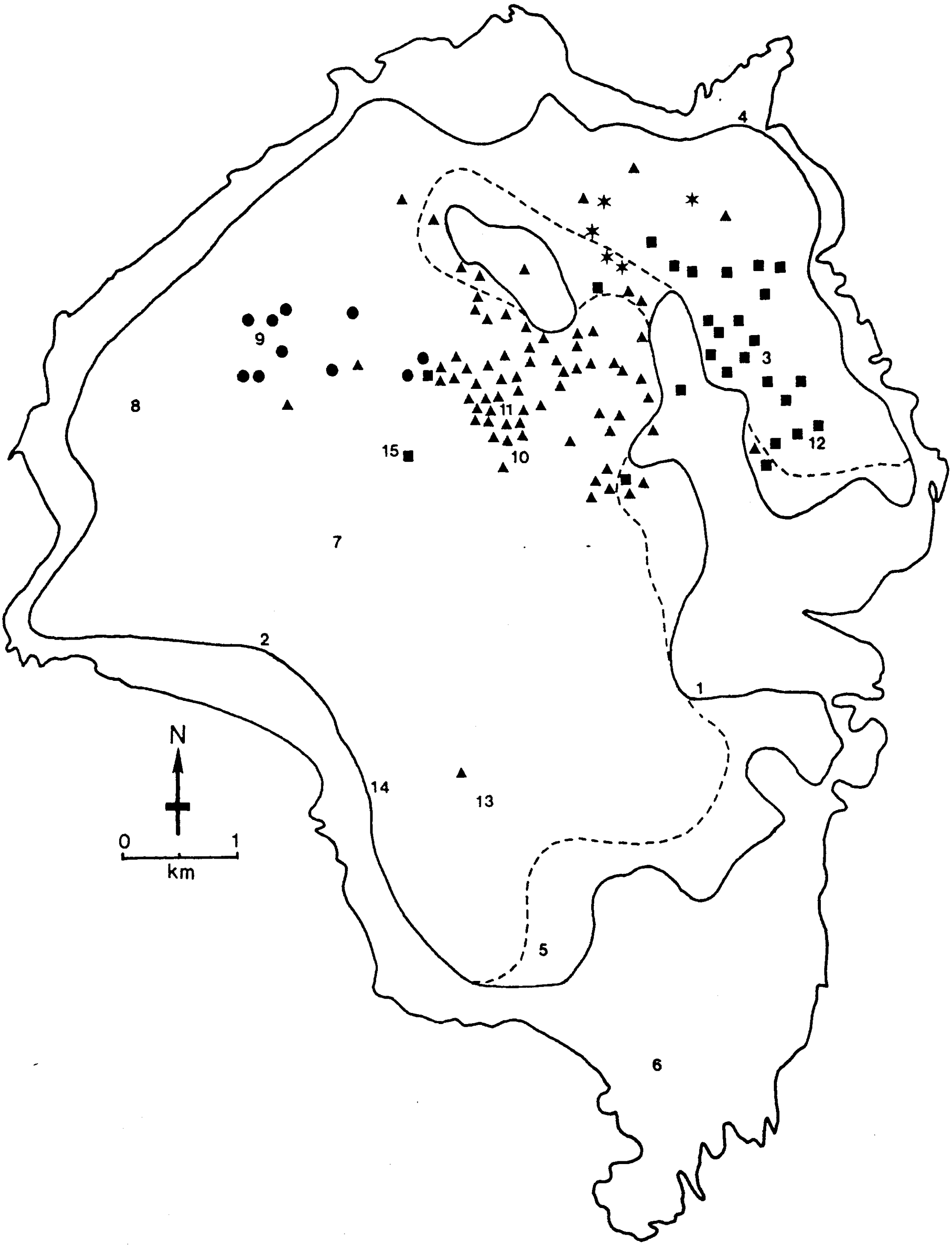
9.3.3.3. Comparison with established breeders. Breeding success of known first-time breeders was only recorded in 1989 and 1990, during a time of low fledging success throughout the colony (see Hamer et al. 1991). Of 53 pairs comprising at least one known new recruit, 77.4% failed to raise a chick to fledging, whereas 67.9% of pairs failed in the colony overall (see Hamer 1990). During 1989-1990, pairs comprising at least one known new recruit had a significantly higher proportion of one-egg clutches (15 out of 53 clutches) than the rest of the breeding population (14 out of 336 clutches; X_1^2=38.7, $P<0.0001$). During 1989-1991, mean nearest nest distance for nests of pairs comprising at least one new recruit was 23.0m (S.D.=11.5m, N=113), a significantly smaller distance than that of 100 randomly selected territories throughout the established breeding colony during the same period in the same areas of the island (mean=38.7, S.D.=17.6, N=100; Student's t=7.79, df=211, $P<0.0001$).

9.3.3.4. Site and mate selection. Only 14 individually colour-ringed birds were observed holding breeding territories, without breeding, for one season. Of these, four bred in that territory and six were recorded back at club-sites in the following season. Hence, in most cases, new recruits were first recorded at a territory in the year that they first bred. No birds bred in the same year that they were first recorded in the colony (i.e. the year that they were trapped at club-sites and colour-ringed).

Figure 9.4 shows the location of the 113 nest sites of pairs comprising at least one known new recruit. It can be seen that these birds generally bred within the vicinity of the club they frequented in previous years. Of these 113 breeding sites, 16 were classed as 'periphery' territories, 14 were within 40m of the centre of a club-site and 73 were within established breeding territories. The mean nearest nest distance of first-time breeders at periphery nests (mean=35.0m, S.D.=16.6m, N=16), club nests (mean=13.6m, S.D.=5.0m, N=14) and nests in the rest of the colony (mean=22.7m, S.D.=9.4m, N=83) were significantly different (one-way ANOVA, $F_{2,111}$= 17.4, P<0.0001). Much of the increase in Great Skua breeding area on Foula from 1988 to 1990 (Figure 9.4) was due to several first-time breeders occupying these outer edges of the colony.

Club and periphery first-time breeders had smaller mean wing lengths (mean=417.4, S.D.=7.59, N=31) than birds first breeding within established breeding areas (mean=421.3, S.D.=9.52, N=76; Student's t=2.05, df=115, P<0.05), and were responsible for a greater proportion of one-egg clutches (16 out of 30 clutches) than new recruits in the rest of the colony (27 out of 83 clutches; X_1^2= 4.05, P<0.05). In 1989 and 1990, none of the club breeders (first-time breeders or others) fledged a chick. Club and periphery first-time breeders produced significantly less chicks that survived for at least 14 (1 out of 21 chicks hatched) days than those birds first

FIGURE 9.4. Map of Foula, Shetland, showing the location of club-sites (1-15). The edge of the Great Skua breeding colony is indicated for 1988 (dotted line) and 1990 (solid line). The locations of 113 nests of 117 colour-ringed first-time breeders in 1989, 1990 and 1991 are shown with symbols, indicating the club mainly or solely attended in previous years: clubs 3 (squares), 4 (stars), 9 (circles) and 11 (triangles).


4
9
3
8
11
12
15
10
7
2
1
N
14
13
0
1
km
5
6

breeding within the colony (13 out of 32 chicks hatched; $X_1^2=8.39$, N=53, $P<0.05$).

Since 1975, only 8 breeding pairs of Great Skuas were known to comprise birds where both partners were of known age (from my, RWF's and K. Hamer's studies). Of six pairs all under nine years of age, three pairs were the same age and three pairs differed by only one year. The remaining two pairs were 14/17 and 21/24 years old. Of the four pairs where both partners were known new recruits in this study, the partners of three of the pairs had been seen together in the clubs in previous years.

9.3.3.5. Subsequent breeding attempts. All 13 new recruits that bred in 1989 also bred in 1990. However, of the total 55 new recruits in 1989 and 1990, 22 (40%) were not recorded on the island in 1991, despite exhaustive searches.

Only four cases were recorded where a change in partners from one season to the next was known. Two of these cases were of the same bird having three different partners in three years.

Of 42 nests of pairs where at least one partner was a known new recruit, the nearest nest distance increased in successive years in 35 cases (83%): a proportion significantly greater than expected by chance ($X_1^2=8.0$, $P<0.01$). Of the 18 individually colour-ringed Great Skuas that bred within 40m of the centre of a club-site in consecutive years (but were not necessarily first-time breeders), all but three birds nested further away from the centre of the club-site in the second year; a proportion significantly greater than expected by chance ($X_1^2=8.0$, $P<0.01$).

There was no difference in the number of eggs per clutch or the mean clutch volume between known first-year and second-year breeding attempts (all Ps>0.2).

9.4. DISCUSSION

In many seabird species, prebreeders are known to frequent a colony for one or more years before attempting to breed. Prebreeding Kittiwakes and Guillemots, for example, mix with established breeders on ledges or gather on rocks below colonies (Cramp & Simmons 1977, Birkhead & Hudson 1977). This period in the colony, prior to breeding, affords experience of local conditions and foraging. It also enables a breeding partner and site to be chosen.

However, prebreeding Great Skuas do not mix with established breeders in the colony, probably due to the aggressive nature of breeding birds. Thus, in order to frequent a colony prior to breeding, the nonbreeders gather into clubs where their location, or sheer numbers, protects them from attack by breeding birds. This study revealed that most Great Skuas in these clubs were aged 3-7 years (Figure 9.1). The ~~reducing~~ reduction in frequency of birds older than four years is partly explained by yearly mortality, but can mostly be attributed to birds leaving the clubs and recruiting into the breeding population. The age-structure of birds in clubs suggests that most birds leave the clubs between 6 and 9 years of age. This agrees with the known ages of first-time breeders (median=7 years), and suggests that prebreeders spend an average of three years in the colony prior to breeding. Of 129 known-age birds in clubs, only 5 were older than 10 years. Hence, Great Skua clubs can be considered mainly to comprise prebreeders.

In each year 1989-1991, approximately 14% of birds present at club-sites in the previous year recruited into the breeding colony. These results suggest that the recruitment rate was lower than the breeder mortality rate during the period of the study. For example, a recruitment rate of 14% from a pool of 4,000 nonbreeders frequenting Foula in 1989 would result in 560 new recruits. However, the mortality rate of breeders (20%, after Hamer 1990) would suggest a reduction from 1988 (2400 AOTs, or approximately 4800 individuals) to 1989 of 960 birds. Although such calculations are very generalised, the results are consistent with the decline in breeding numbers since 1975 (Furness 1987a) and the decline in breeding numbers recorded in this study from 1988-1990.

Although an increase in breeder mortality in seabird colonies can result in a decreased average age at first breeding (e.g. Coulson et al. 1982, Porter & Coulson 1987), the mean and median age of known new recruits in this study (7 years) was similar to the mean age at first breeding on Foula in the mid-1970s (Furness 1987a). Although the number of breeders on Foula decreased from 1988 to 1990 (see Chapter 7), the total breeding area on the island increased (Figure 9.4), resulting in an overall reduction in the breeding density over these years. However, the recruitment rate (approximately 14%) did not change appreciably over this period. These results suggest that young Great Skuas on Foula are not constrained from breeding by social pressures or lack of space (e.g. Monaghan 1980, Furness

& Monaghan 1987), but by other factors such as the need to develop foraging skills (e.g. Burger 1980, Greig et al. 1983).

All of the eight largest Great Skua colonies in Shetland are known to contain club-sites frequented by nonbreeders. Table 9.2 shows the numbers of nonbreeders and clubs associated with these colonies in 1974/5 and 1985/6 (see Table 9.2 for sources of data). There were significant, positive correlations between the number of breeding birds and the number of nonbreeders ($r_s=0.83$, N=8, $P<0.05$) and clubs ($r_s=0.74$, N=8, $P<0.05$) in a colony. Also, the percentage growth of the colonies from 1974/5 to 1985/6 was positively correlated to the ratio of numbers of nonbreeders to breeders in the colony in 1985/6 ($r_s=0.67$, N=8, $P<0.05$). Although these correlations are based on few data, collected in different years, they suggest that larger colonies have more nonbreeders and clubs associated with them. This is likely to be due to prebreeders generally returning to their natal colonies. However, it also appears that faster growing colonies have proportionally more nonbreeders than slower growing colonies, which may indicate that colonies vary in attractiveness to prebreeders and that differential rates of emigration exist between colonies.

The results of this study suggest that clubs play a pivotal role in the recruitment process of Great Skuas. The clubs are at traditional, fixed sites. Prebreeders appear to frequent these clubs for at least one year prior to breeding, although some birds were recorded in clubs for four consecutive years without breeding. Breeding sites are selected in the vicinity of the clubs individual birds frequented most in previous years, and there is some evidence suggesting that

TABLE 9.2. Population parameters of the eight largest Great Skua colonies in Shetland. The number of Apparently Occupied Territories (AOTs) in 1974/5 and 1985/6, the number of clubs in 1985/6 and the number of nonbreeders present on the clubs in daytime in 1985/6 were all determined using similar counting methods at similar times of year. Data after Furness (1986), Ewins et al. (1987) and Bird & Cable (1988). The ratio of the number of nonbreeders to breeders (twice the number of AOTs) is based on 1985/6 data. The percentage change in the number of AOTs per year was calculated using the following formula, despite some colonies increasing and then declining within this period:

$$\text{\% change per year} = \left(\text{antilog} \; \frac{\log_e Y_1 - \log_e Y_0}{\text{no. of years}} - 1 \right) \times 100$$

Colony	AOTs		Clubs	No. non-breeders breeders	Average % change in AOTs per year	Ratio
	1974/5	1985/6				
Foula	2131	2495	13	858	+ 1.32	0.172
Hermaness (Unst)	786	819	6	145	+ 0.38	0.089
Noss	255	378	2	161	+ 3.64	0.213
Saxavord (Unst)	250	355	2	58	+ 3.24	0.082
Lamb Hoga (Fetlar)	129	139	1	40	+ 0.62	0.144
Bressay	160	115	1	35	- 2.96	0.152
Fitful Head (Mainland)	30	95	1	35	+ 10.08	0.184
Fair Isle	17	84	2	54	+ 14.24	0.321

mates are selected from the same club. By frequenting clubs within a colony, prebreeding Great Skuas have the opportunity to experience local environmental conditions and learn foraging skills. The continual interaction with other birds probably also allows social skills to be learnt, such as displays (e.g. Nelson 1978a). Some birds attempt to breed at the edges of the clubs, although these birds and periphery breeders may be lower quality recruits, as they have smaller mean wing lengths, more one-egg clutches and a lower breeding success than other recruits. Still, clubs provide an avenue for such birds to recruit into the colony, and in the following year these birds nest further away from the club-sites and further into the general colony.

A model of the process of recruitment in Great Skuas is proposed in Chapter 10.

CHAPTER 10

General Discussion

A model of recruitment in Great Skuas

Based on the results of this research, a model is proposed to describe the general process of recruitment in Great Skuas. As environmental conditions and other factors can affect the recruitment of seabirds into breeding populations, this model can only be assumed to describe the recruitment of Great Skuas on Foula during 1988-1991, although it probably closely resembles the recruitment process in other Great Skua colonies. Also, since several data obtained in this research were consistent with those obtained in studies of recruitment in other seabird species, it is likely that many aspects of the proposed model of recruitment will be similar to aspects of recruitment in other seabirds.

At a

A hatching Great Skua chick has already inherited certain traits from its parents. The most obvious indicator of the quality of parents and chicks may be the chick's hatching date. An earlier hatching chick is likely to be heavier during chick-growth and more likely to survive its first year than later hatching chicks.

Great Skua fledglings disperse south from Foula. They are more likely to die in their first year, particularly in their first few months following fledging, than in subsequent years. Many will be shot, or killed in fishing nets, particularly in the North Sea and Iberia. Young Great Skuas are largely pelagic for their first two years of life. These prebreeders begin to display stable migration patterns when they start frequenting breeding colonies in the summer.

Great Skuas that fledge from Foula generally return to that colony at 3 or 4 years of age. Of those prebreeders that are not faithful to their natal colony, rapidly expanding colonies may be more attractive than slower growing or declining colonies. The birds spend at least one breeding season (generally 2-4 seasons) in the colony, at clubs, without breeding. Prebreeders generally join a club near their natal area within the colony and are generally faithful to that club. During these prebreeding years they develop skills necessary for breeding (e.g. foraging and social skills). Prebreeders spend an average of 2-3 weeks in the colony each breeding season. They forage at sea during much of the day and spend the night at one of the club-sites on the island.

During these few weeks at the colony, the prebreeders decline in weight. Such weight loss suggests a cost to these birds in attending the colony. This may explain why prebreeders do not spend longer at the colony each breeding season. Although young birds would gain more experience and have greater opportunity to recruit if they spent most of each season at the colony, they can only stay each year as long as body reserves permit. This would also explain why a decline in the prey availability around the colony tends to coincide with an exodus of nonbreeders.

Each year, individual birds arrive at the colony earlier than in the previous year. Because they are generally faithful to one club, they tend to mix with the same individuals each breeding season. After a few years the birds choose a breeding site, generally within the vicinity of the club frequented in previous years. Mates are probably chosen from the same club.

Most birds first breed at seven years of age, although extremes of four and ten years have been recorded. Recruiting birds have four possible choices in selecting a breeding site:

1. A bird can attempt to breed for the first time on the edge of a club-site, probably with another club-bird. In this case, only a small territory will be defended and the breeding attempt will probably fail. In the following years the bird will defend an enlarged territory, further away from the club-site.

2. A recruiting pair can establish a territory on the edge of the breeding colony. This allows a larger territory to be held. Such breeding attempts are also generally unsuccessful. It is possible that 'club' and 'periphery' first-time breeders are lower quality recruits and unable to establish a territory in the established breeding areas. These new recruits have smaller mean wing lengths and produce smaller clutches.

3. A pair of new recruits can defend a territory within established breeding areas, and attempt to breed, perhaps after a delay of one year. Most recruits appear to adopt this strategy and many of these birds breed successfully in their first year.

4. A bird that breeds for the first time in the established breeding area may do so with an established breeder that has lost or abandoned its previous partner. This is likely to be the most successful mode of recruitment because a territory is already established. It is possible that many first-time breeders recruit into the colony in this way, particularly in a

colony of limited physical size and stable population. However, based on known pairs and the ages of partners, it appears that many recruits select partners from the club they frequented in previous years. It is unlikely that any first-time breeders that breed on the edges of club-sites or at the periphery of the colony are paired with established breeders, because of the site-faithfulness of established breeders and the changing periphery of the colony (see Figure 9.4), and the movement of the territories of club-breeders away from clubs in successive years.

Overall, first-time breeders hold smaller territories, incubate a higher proportion of one-egg clutches and are less successful at raising chicks than established breeders. Larger first time breeders tend to produce larger clutches, and young first-time breeders (5 and 6 year-olds) hold smaller breeding territories.

It is not clear whether the influence of hatching date on the subsequent size of Great Skuas 3-6 years later can also affect recruitment parameters such as age at first breeding, type of breeding territory first held, or breeding success. However, the effect of birds returning to breed near their natal territory could promote differences in breeding parameters in different areas on the island, and may increase the likelihood of recruits breeding with close relatives, thereby promoting inherent differences in the quality of their offspring.

One of the most unexpected findings of this research has been the high degree of fidelity of young birds to the colony and their natal area. This strategy would not appear to be consistent with maximising lifetime productivity. Indeed, one might have expected prebreeders to sample a range of clubs and colonies in order to determine the best colony and area in which to breed. This strategy would have been particularly appropriate in recent years when there were variances in breeding success and adult survival rates among Great Skua colonies. One explanation of such site-fidelity in prebreeders might be that the Great Skua is still adapted to sub-Antarctic environments where the food sources, mainly petrel and penguin eggs and chicks, remain relatively stable from year to year. As suggested previously, different seabird species may exhibit behaviours in different places on a continuum from the high site-fidelity of prebreeding Great Skuas to the colony-visiting behaviour of Puffins (Harris 1984) and British Storm-petrels (Mainwood 1976). However, to thoroughly elucidate the reasons for differing levels of prebreeding site-fidelity, studies of individual species over a range of ecological situations are required.

LITERATURE CITED

Ainley, D.G. 1978. Activity patterns and social behaviour of non-breeding Adelie Penguins. *Condor* 80: 138-146.

Ainley, D.G., Ribic, C.A. & Wood, R.C. 1990. A demographic study of the South Polar Skua *Catharacta maccormicki* at Cape Crozier. *Journal of Animal Ecology* 59: 1-20.

Andersson, M. 1973. Behaviour of the Pomarine Skua *Stercorarius pomarinus* Temm. with comparative remarks on Stercorariinae. *Ornis Scandinavica* 4: 1-16.

Anker-Nilssen, T. 1987. The breeding performance of Puffins *Fratercula arctica* on Røst, northern Norway in 1979-1985. *Fauna Norvegica Series C, Cinclus* 10: 21-38.

Avery, M. & Green, R. 1989. Sandeel fishing and seabird deaths. *New Scientist* 123, 1674: 28-29.

Bailey, R.S., Furness, R.W., Gauld, J.A. & Kunzlik, P. (in press). Recent changes in the population of sandeel *Ammodytes marinus* Raitt at Shetland in relation to estimates of seabird predation. *Rapportes et Proces-verbaux des Reunions Conseil International pour l'Exploration de la Mer*.

Bancroft, J.D. & Stevens, A. (eds.). 1990. *Theory and Practice of Histological Techniques*. Churchill Livingston, New York.

Bannerman, D.A. 1963. *The Birds of the British Isles*. Vol. XII. Oliver & Boyd, Edinburgh.

Barrett, R.T., Peterz, M., Furness, R.W. & Durinck, J. 1989.

The variability of biometric measurements. Ringing & Migration 10: 13-16.

Batten, L.A., Bibby, C.J., Clement, P., Elliot, G.D. & Porter, R.F. 1990. Red Data Birds in Britain: Action for Rare, Threatened and Important Bird Species. Poyser, London.

Bayes, J.C., Dawson, M.J. & Potts, G.R. 1964. The food and feeding behaviour of the Great Skua in the Faroes. Bird Study 11: 272-279.

Bird, D.R. & Cable, S. 1988. Noss National Nature Reserve Wardens' Annual Report. Unpublished report to the Nature Conservancy Council, Lerwick.

Birkhead, T.R. & Clarkson, K. 1985. Ceremonial gatherings of the Magpie Pica pica: territorial probing and acquisition. Behaviour 94: 324-332.

Birkhead, T.R. & Harris, M.P. 1985. Ecological adaptations for breeding in Atlantic Alcidae. In: Nettleship, D.N. & Birkhead, T.R. (eds). The Atlantic Alcidae. Academic Press, London.

Birkhead, T.R. & Hudson, P.J. 1977. Population parameters of the Common Guillemot Uria aalge. Animal Behaviour 26: 321-333.

Birkhead, T.R. & Nettleship, D.N. 1981. Reproductive biology of Thick-billed Murres Uria lomvia: an inter-colony comparison. Auk 98: 258-269.

Blower, J.G., Cook, L.M. & Bishop, J.A. 1981. Estimating the Size of Animal Populations. George Allen and Unwin, London.

Bradley, J.S., Skira, I.J. & Wooller, R.D. 1991. A long-term study of Short-tailed Shearwaters Puffinus tenuirostris on Fisher Island, Australia. Ibis 133, Suppl. 1: 55-61.

Bradley, J.S. & Wooller, R.D. In press. Philopatry and age of first-breeding in long-lived birds. Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

Brooke, M. 1990. The Manx Shearwater. Poyser, London.

Burger, A.E. & Cooper, J. 1982. The effects of fisheries on seabirds in South Africa and Namibia. In: Nettleship, D.N., Sanger, G.A. & Springer, P.F. (eds.). Proceedings of the Pacific Seabird Group Symposium, Seattle, Washington, 6-8th January 1982. Canadian Wildlife Service Special Publication. pp. 150-160.

Burger, J. 1980. The transition to independence and postfledging parental care in seabirds. In: Burger, J. (ed.). Behaviour of Marine Animals. Plenum Press, New York. pp. 367-447.

Cairns, D.K. 1987. Seabirds as indicators of marine food supplies. Biological Oceanography 5: 261-271.

Cambell, A.C. 1976. The Seashore and Shallow Seas of Britain and Europe. Hamlyn, Middlesex.

Caughley, G. 1977. Analysis of Vertebrate Populations. Wiley, Chichester.

Chabrzyk, G. & Coulson, J.C. 1976. Survival and recruitment in the Herring Gull Larus argentatus. Journal of Animal Ecology 45: 187-203.

Clark, G.A. 1979. Body weights of birds: a review. Condor 81: 193-202.

Cooke, F., Rockwell, R.F. & Lank, D.B. In press. Recruitment in long-lived birds: genetic considerations. Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

Coombs, F. 1978. The Crows - A Study of the Corvids of Europe. Batsford, London.

Corbet, G.B. & Southern, H.N. (eds.). 1977. The Handbook of British mammals. Blackwell, London.

Coulson, J.C. 1963. Egg size and shape in the Kittiwake (Rissa tridactyla) and their use in estimating age compositions of populations. Proceedings of the Zoological Society of London 140: 211-227.

Coulson, J.C. 1966. The influence of the pair bond and age on the breeding biology of the Kittiwake Gull Rissa tridactyla. Journal of Animal Ecology 35: 269-279.

Coulson, J.C. 1976. An evaluation of the reliability of rings used on Herring and Lesser Black-backed Gulls. Bird Study 23: 21-26.

Coulson, J.C. 1984. The population dynamics of the Eider Duck Somateria mollissima and evidence of extensive non-breeding by adult ducks. Ibis 126: 525-543.

Coulson, J.C. & Brazendale, M.G. 1968. Movements of Cormorants ringed in the British Isles and evidence of colony-specific dispersal. British Birds 61: 1-21.

Coulson, J.C., Butterfield, J., Duncan, N., Kearsey, S., Monaghan, P. & Thomas, C. 1984. Origin and behaviour of Great Black-backed Gulls wintering in northeast England. British Birds 77: 1-11.

Coulson, J.C., Duncan, N. & Thomas, C. 1982. Changes in the breeding biology of the Herring Gull (Larus argentatus) induced by the reduction in the size and density of the colony. Journal of Animal Ecology 51: 739-756.

Coulson, J.C., Duncan, N., Thomas, C.S. & Monaghan, P. 1981. An age-related difference in the bill-depth of Herring Gulls Larus argentatus. Ibis 123: 499-502.

Coulson, J.C. & Nève de Mévergnies, G. In press. Where do young Kittiwakes Rissa tridactyla breed, philopatry or dispersal? Ardea 79.

Coulson, J.C. & Porter, J.M. 1985. Reproductive success in the Kittiwake Rissa tridactyla: the roles of clutch size, chick growth rates and parental quality. Ibis 127: 450-466.

Coulson, J.C. & Thomas, C.S. 1983. Mate choice in the Kittiwake Gull. In: Bateson, P.P.G. (ed.). Mate Choice. Cambridge University Press, Cambridge. pp. 361-376.

Coulson, J.C. & Thomas, C. 1985. Differences in the breeding performance of individual Kittiwake Gulls Rissa tridactyla (L.). In: Silby, R.M. & Smith, R.H. (eds.). Behavioural

Ecology. Blackwell, London. pp. 489-506.

Coulson, J.C. & Wooller, R.D. 1976. Differential survival rates among breeding Kittiwake gulls *Rissa tridactyla* (L.). *Journal of Animal Ecology* 45: 205-213.

Court, G.S., Bradley, D.M., Gates, C.C. & Boag, D.A. 1989. Turnover and recruitment in a tundra population of Peregrine Falcons *Falco peregrinus*. *Ibis* 131: 487-496.

Cramp, S. & Simmons, K.E.L. (eds.). 1977. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. Vol. 1. Oxford University Press, Oxford.

Cramp, S. & Simmons, K.E.L. (eds.). 1980. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. Vol. 2. Oxford University Press, Oxford.

Cramp, S. & Simmons, K.E.L. (eds.). 1983. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. Vol. 3. Oxford University Press, Oxford.

Cramp, S. (ed.). 1985. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. Vol. 4. Oxford University Press, New York.

Cramp, S. (ed.). 1988. *Handbook of the Birds of Europe, the Middle East and North Africa: the Birds of the Western Palaearctic*. Vol. 5. Oxford University Press, New York.

Croxall, J.P., Rothery, P., Pickering, S.P.C. & Prince, P.A.

1990. Reproductive performance, recruitment and survival of Wandering Albatrosses, Diomedea exulans at Bird Island, South Georgia. Journal of Animal Ecology 59: 775-796.

Danchin, É., Cadiou, B. Monnat, J.Y. & Rodriguez Estrella, R. In press. Recruitment in long-lived birds: conceptual framework and behavioural mechanisms. Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

Danchin, É. & Monnat, J.Y. In press. Population dynamics modelling of two neighbouring Kittiwake colonies: implications for management. Ardea 79.

Duncan, N. 1978. The effects of culling Herring Gulls (Larus argentatus) on recruitment and population dynamics. Journal of Applied Ecology 15: 697-713.

Dunn, E.K. 1972. Effect of age on the fishing ability of Sandwich Terns, Sterna sandvicensis. Ibis 114: 360-366.

Dunnet, G.M. 1991. Population studies of the Fulmar in Eynhallow, Orkney Islands. Ibis 133, Suppl. 1: 24-27.

Dunnet, G.M. & Anderson, A. 1961. A method for sexing living Fulmars in the hand. Bird Study 8: 119-126.

Dunnet, G.M. & Ollason, J.C. 1978. The estimation of survival rate in the Fulmar (Fulmarus glacialis). Journal of Animal Ecology 47: 507-520.

EURING (The European Union for Bird Ringing). 1979. Code Manual: New EURING. British Trust for Ornithology, Hertfordshire.

Evans, P.G.H. 1984. The Seabirds in Greenland: their status and conservation. In: Croxall, J.P. Evans, P.G.H. & Shreiber, R.W. (eds.). Status and Conservation of the World's Seabirds. ICBP, Cambridge. pp. 49-84.

Evans, P.G.H. 1987. The Natural History of Whales and Dolphins. Helm, London.

Ewins, P.J. 1985. Growth, diet and mortality of Arctic Tern Sterna paradisaea chicks in Shetland. Seabird 8: 59-68.

Ewins, P.J., Bird, D.R., Ellis, P.M. & Prior, A. 1987. The Distribution and Status of Arctic and Great Skuas in Shetland, 1985-86. Unpublished report to the Nature Conservancy Council, the Royal Society for the Protection of Birds, the Seabird Group and Shell U.K. Ltd..

Ewins, P.J., Ellis, P.M., Bird, D.R. & Prior, A. 1988. The distribution and status of Arctic and Great Skuas in Shetland 1985-86. Scottish Birds 15: 9-20.

Ewins, P.J., Wynde, R.M. & Richardson, M.G. 1986. The 1986 Census of Arctic and Great Skuas on Foula, Shetland. Unpublished report to the Nature Conservancy Council, Lerwick.

Furness, R.W. 1974. The ecology of the Great Skua on Foula. Brathay Exploration Group Field Studies Report No. 25: 1-32.

Furness, R.W. 1977. Studies of the Breeding Biology and Population Dynamics of the Great Skua (Catharacta skua Brünnich). Unpublished PhD thesis, University of Durham.

Furness, R.W. 1978. Movements and mortality rates of Great

Skuas ringed in Scotland. Bird Study 25: 229-238.

Furness, R.W. 1982. Methods used to census skua colonies. Seabird 6: 44-47.

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. 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. Journal of Zoology, London 202: 565-576.

Furness, R.W. 1986. The Conservation of Arctic and Great Skuas and their Impact on Agriculture. Unpublished report to the Nature Conservancy Council, Lerwick.

Furness, R.W. 1987a. The Skuas. Poyser, Staffordshire.

Furness, R.W. 1987b. Assessment of the status of seabirds on the island of Foula, Shetland. Unpublished report to the Nature Conservancy Council, Lerwick.

Furness, R.W. 1990. A preliminary assessment of the quantities of Shetland sandeels taken by seabirds, seals, predatory fish and the industrial fishery in 1981-83. Ibis 132: 205-217.

Furness, R.W. & Birkhead, T.R. 1984. Seabird colony distributions suggest competition for food supplies during the breeding season. Nature 311, 5987: 655-656.

Furness, R.W. & Hislop, J.R.G. 1981. Diets and feeding ecology of Great Skuas Catharacta skua during the breeding season in Shetland. Journal of Zoology, London 195: 1-23.

Furness, R.W., Lewis, S.A. & Mills, J.A. 1990. Mercury levels in the plumage of Red-billed Gulls Larus novaehollandiae scopulinus of known sex and age. Environmental Pollution 63: 33-39.

Furness, R.W. & Monaghan, P. 1987. Seabird Ecology. Blackie, Glasgow.

Gaston, A.J. 1984. How to distinguish first-year Murres, Uria spp., from older birds in winter. Canadian Field Naturalist 98: 52-55.

Gaston, A.J., Chapdelaine, G. & Noble, D.G. 1984. Phenotypic variation among Thick-billed Murres from colonies in Hudson Strait. Arctic 37: 284-287.

Gaston, A.J. & Nettleship, D.N. 1981. The Thick-billed Murres of Prince Leopold Island - a study of the breeding ecology of a colonial high arctic seabird. Canadian Wildlife Service Monograph Series No. 6. 350pp.

Gaston, A.J. & Nettleship, D.N. 1982. Factors determining seasonal changes in attendance at colonies of the Thick-billed Murre Uria lomvia. Auk 99: 468-473.

Gochfeld, M. 1980. Mechanisms and adaptive value of reproductive synchrony in colonial seabirds. In: Burger, J., Olla, B.L. & Winn, H.E. (eds.). Behaviour of Marine Animals. Vol. 4: Marine Birds. Plenum Press, New York. pp. 207-270.

Grant, M.C. 1991. Relationships between egg size, chick size at hatching, and chick survival in the Whimbrel Numenius phaeopus. Ibis 133: 127-133.

Green, P.T. & Theobald, C.M. 1989. Sexing birds by discriminant analysis: further considerations. Ibis 131: 442-447.

Greenwood, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour 28: 1140-1162.

Greenwood, P.J. & Harvey, P.H. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics 13: 1-21.

Greig, S.A., Coulson, J.C. & Monaghan, P. 1983. Age-related differences in foraging success in the Herring Gull (Larus argentatus). Animal Behaviour 31: 1237-1243.

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. & Furness, R.W. 1991. Age-specific breeding performance and reproductive effort in Great Skuas Catharacta skua. Journal of Animal Ecology 60: 693-704.

Hamer, K.C. & Furness, R.W. In press. Sexing Great Skuas Catharacta skua by discriminant analysis using external measurements. Ringing & Migration.

Hamer, K.C., Furness, R.W. & Caldow, R.G. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* Brunnich in Shetland. *Journal of Zoology, London* 223: 175-188.

Härkönen, T. 1986. *Guide to the Otoliths of the Bony Fishes of the Northeast Atlantic*. Danbiu ApS., Hellerup.

Harris, M.P. 1973. The biology of the Waved Albatross *Diomedea irrorata* of Hood Island, Galapagos. *Ibis* 115: 483-510.

Harris, M.P. 1981. Age determination and first breeding of British Puffins. *British Birds* 74: 246-256.

Harris, M.P. 1983. Biology and survival of the immature Puffin *Fratercula arctica*. *Ibis* 125: 56-73.

Harris, M.P. 1984. *The Puffin*. Poyser, Calton.

Hartert, E. 1912. *Die Vogel der Palaarktischen Fauna*. Berlin.

Hector, J.A.L., Croxall, J.P. & Follett, B.K. 1986. The reproductive endocrinology the Wandering Albatross (*Diomedea exulans*) in relation to biennial breeding and deferred sexual maturity. *Ibis* 128: 9-22.

Hector, J.A.L., Pickering, S.P.C., Croxall, J.P. & Follett, B.K. 1990. The endocrine basis of deferred sexual maturity in the Wandering Albatross *Diomedea exulans* L.. *Functional Ecology* 4: 59-66.

Hedgren, S. 1979. Seasonal variation in fledging weight of Guillemots, *Uria aalge*. *Ibis* 121: 356-361.

Hedgren, S. 1981. Effect of fledging weight and time of fledging on survival of Guillemot Uria aalge chicks. Ornis Scandinavica 12: 51-54.

Henny, C.J. & Ludke, J.L. 1974. An attempt to age mallards using eye lens proteins. Journal of Wildlife Management 38: 138-141.

Heubeck, M. (ed.). 1989. Seabirds and Sandeels: Proceedings of a Seminar Held in Lerwick, Shetland, 15-16th October 1988. Shetland Bird Club, Lerwick.

Hopwood, D. 1990. Fixations and fixatives. In: Bancroft, J.D. & Stevens, A. (eds.). Theory and Practice of Histological Techniques. Churchill Livingston, New York. pp. 21-42.

Hudson, A.V. & Furness, R.W. 1988. Utilization of discarded fish by scavenging seabirds behind whitefish trawlers in Shetland. Journal of Zoology, London 215: 151-166.

Hudson, P.J. 1985. Population parameters for the Atlantic Alcidae. In: Nettleship, D.N. & Birkhead, T.R. (eds.). The Atlantic Alcidae. Academic Press, London.

Hudson, P.J. & Rands, M.R.W. (eds.). 1988. Ecology and Management of Gamebirds. BSP, Oxford.

Jannett, F.J. 1983. A quantitative method of age determination of adult birds. American Midland Naturalist 109: 145-151.

Jee, W.S.S. 1988. The skeletal tissue. In: Weiss, L. (ed.). Cell and Tissue Biology. A Textbook of Histology. Urban & Schwarzenberg, Baltimore. pp. 211-254.

Jones, G. 1987. Selection against large size in the Sand

Martin *Riparia riparia* during a dramatic population crash. *Ibis* 129: 274-280.

Jones, P.H., Barrett, C.F., Mudge, G.P. & Harris, M.P. 1985. Examination of corpses of auks beached on East British coasts in February 1983. *Seabird* 8: 9-14.

Jones, P.H., Howells, G., Rees, E.I.S. & Wilson, J. 1970. Effect of 'Hamilton Trader' oil on birds in the Irish Sea in May 1969. *British Birds* 63: 97-110.

Klevezal, G.A. & Kleinenberg, S.E. 1969. Age determination in mammals by layered structure in teeth and bone. (Translated from Russian). In: Sergeant, D.E. (ed.). *Fisheries Research Board of Canada*, *Translation Series* 1024: 1-142.

Klomp, N.I. & Furness, R.W. 1990^{a}. Variations in numbers of nonbreeding Great Skuas attending a colony. *Ornis Scandinavica* 21: 270-276.

Klomp, N.I. & Furness, R.W. 1990^{b}. *The Diets and Numbers of Nonbreeding Great Skuas - A Comparison Among Colonies*. Report to the Nature Conservancy Council, the Royal Society for the Protection of Birds, and the Seabird Group.

Klomp, N.I. & Furness, R.W. In press^{a}. Nonbreeders as a buffer against environmental stress: declines in numbers of Great Skuas on Foula, Shetland, and prediction of future recruitment. *Journal of Applied Ecology*.

Klomp, N.I. & Furness, R.W. In press^{b}. Recruitment in long-lived birds: studies of nonbreeding Great Skuas. Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

Klomp, N.I. & Furness, R.W. In press. Patterns of chick-feeding in Cory's Shearwaters and the associations with ambient light. Biological Oceanography 7.

Klomp, N.I. & Furness, R.W. Submitted. The effect of hatching date on chick weight, post-fledging survival and dispersal, and adult weight in Great Skuas. Journal of Animal Ecology.

Kunzlik, P. 1989. Small fish around Shetland. In: Heubeck, M. (ed.). Seabirds and Sandeels: Proceedings of a Seminar Held in Lerwick, Shetland, 15-16th October 1988. Shetland Bird Club, Lerwick. pp. 38-47.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Oxford University Press, Oxford.

Lack, D. 1966. Population Studies of Birds. Clarendon Press, Oxford.

Lack, D. 1968. Ecological Adaptations for Breeding in Birds. Methuen. London.

Lamb, M.J. 1977. Biology of Ageing. Blackie, London.

Larson, J.S. & Taber, R.D. 1980. Criteria of age and sex. In: Schemnitz, S.D. (ed.). Wildlife Management Techniques Manual. The Wildlife Society, Washington D.C.

LeResche, R.E. & Sladen, W.J.L. 1970. Establishment of pair and breeding site bonds by young known-age Adelie Penguins

(Pygoscelis adeliae). Animal Behaviour 18: 517-526.

Lid, G. 1981. Reproduction of the Puffin on Røst in the Lofoten Islands in 1964-1980. Fauna Norvegica Series C, Cinclus 4: 30-39.

Lincoln, F.C. 1930. Calculating waterfowl abundance on the basis of banding returns. Circular of the U.S. Department of Agriculture 118: 1-4.

Lloyd, C.S. 1979. Factors affecting breeding of Razorbills Alca torda on Skokholm. Ibis 121: 165-176.

Lloyd, C.S., Tasker, M.L. & Partridge, K. 1991. The Status of Seabirds in Britain and Ireland. Poyser, London.

McNeil, R. & Martinez, M.A. 1967. Asymetrie bilaterale des os longs des membres du pigeon Columbia livia et du perroquet Amazona amazonica. Review of Canadian Biology 26: 273-386.

McNeil, R., Rodriguez, S., Figuera, B. & Figuera, D.M. 1971. Handedness in the Brown-throated Parakeet Aratinga pertinax in relation with skeletal asymmetry. Ibis 113: 494-499.

Mainwood, A.R. 1976. The movements of storm petrels as shown by ringing. Ringing and Migration 1: 98-104.

Martin, A.R. 1989. The diet of Atlantic Puffin Fratercula arctica and Northern Gannet Sula bassana chicks at a Shetland colony during a period of changing prey availability. Bird Study 36: 170-180.

May, R.M. 1981. Theoretical Ecology, Principals and Applications. Blackwell, Oxford.

Mills, J.A. 1973. The influence of age and pair-bond on the breeding biology of the Red-billed Gull *Larus novaehollandiae scopulinus*. *Journal of Animal Ecology* 42: 147-162.

Monaghan, P. 1980. Dominance and dispersal between feeding sites in the Herring Gull (*Larus argentatus*). *Animal Behaviour* 28: 521-527.

Monaghan, P., Uttley, J.D., Burns, M.D., Thaine, C. & Blackwood, J. 1989^{a} The relationship between food supply, reproductive effort and breeding success in Arctic Terns *Sterna paradisaea*. *Journal of Animal Ecology* 58: 261-274.

Monaghan, P., Uttley, J.D. & Okill, J.D. 1989^{b} Terns and sandeels: seabirds as indicators of changes in marine fish populations. *Journal of Fish Biology* 35A: 339-340.

Morris, P. 1972. A review of mammalian age determination methods. *Mammal Review* 2: 69-104.

Moynihan, M. 1959. A revision of the family Laridae (Aves). *American Museum Novitates* 1928: 1-42.

Mykura, W. 1976. *British Regional Geology: Orkney and Shetland*. Edinburgh.

Nelson, J.B. 1966. Population dynamics of the Gannet (*Sula bassana*) at the Bass Rock, with comparative information from other Sulidae. *Journal of Animal Ecology* 35: 443-470.

Nelson, J.B. 1978a. *The Gannet*. Poyser, Staffordshire.

Nelson, J.B. 1978b. *The Sulidae: Gannets and Boobies*. Oxford

University Press, London.

Nelson, R.C. 1976. Age Determination of Canada Geese (Branta canadensis maxima) by Layers in the Periosteal Zone. M.S. Thesis. Ohio State University, Columbus.

Newton, I. 1989. Lifetime Reproduction in Birds. Academic Press, London.

Newton, I. In press. The role of recruitment in population regulation. Proceedings of the 20th IOC Conference, Christchurch, New Zealand, 1990.

Norusis, M.J. 1986. SPSS/PC+ for the IBM PC/XT/AT. Spss inc., Chicago.

Ollason, J.C. & Dunnet, G.M. 1978. Age, experience and other factors affecting the breeding success of the Fulmar, Fulmarus glacialis, in Orkney. Journal of Animal Ecology 47: 961-976.

Ollason, J.C. & Dunnet, G.M. 1983. Modelling annual changes in numbers of breeding fulmars, Fulmarus glacialis, at a colony in Orkney. Journal of Animal Ecology 52: 185-198.

Otero, J.G. & Dapson, R.W. 1972. Procedures in the biochemical estimation of age of vertebrates. Researches of Population Ecology 13: 152-160.

Owen, M. & Black, J.M. 1991. Geese and their future fortune. Ibis 133, Suppl. 1: 28-35.

Page, K.M. 1982. Bone and the preparation of bone sections. In: Bancroft, J.D. & Stevens, A. (eds.). Theory and Practice of Histological Techniques. Churchill Livingston, New York. pp. 279-331.

Parsons, J. 1975. Seasonal variation in breeding success of the Herring Gull: an experimental approach to pre-fledging success. Journal of Animal Ecology 44: 553-573.

Parsons, J., Chabrzyk, G. & Duncan, N. 1976. Effects of hatching date on post-fledging survival in Herring Gulls. Journal of Animal Ecology 45: 667-675.

Peabody, F.E. 1961. Annual growth zones in living and fossil vertebrates. Journal of Morphology 108: 11-62.

Perdeck, A.C. 1960. Observations on the reproductive behaviour of the Great Skua, or Bonxie, in Shetland. Ardea 48: 111-136.

Perrins, C.M. 1966. Survival of young Manx Shearwaters in relation to their presumed date of fledging. Ibis 108: 132-135.

Perrins, C.M. 1979. British Tits. Collins, London.

Perrins, C.M. & Birkhead, T.R. 1983. Avian Ecology. Blackie, Glasgow.

Perrins, C.M., Harris, M.P. & Britton, C.K. 1973. Survival of Manx Shearwaters Puffinus puffinus. Ibis 115: 535-548.

Perrins, C.M. & Moss, D. 1974. Survival of young Great Tits in relation to age of female parent. Ibis 116: 220-224.

Peters, J.L. 1934. Check-List of the Birds of the World. Harvard University Press, Cambridge, Massachusetts.

Pickering, S.P.C. 1989. Attendance patterns and behaviour in relation to experience and pair-bond formation in the Wandering Albatross *Diomedea exulans* at South Georgia. *Ibis* 131: 183-195.

Pienkowski, M. & Minton, C.D. 1973. Wing length changes of the Knot with age and time since moult. *Bird Study* 20: 63-68.

Porter, J.M. 1988. Prerequisites for recruitment of Kittiwakes *Rissa tridactyla*. *Ibis* 130: 204-215.

Porter, J.M. 1990. Patterns of recruitment to the breeding group in the Kittiwake *Rissa tridactyla*. *Animal Behaviour* 40: 350-360.

Porter, J.M. & Coulson, J.C. 1987. Long-term changes in recruitment to the breeding group, and the quality of recruits at a Kittiwake *Rissa tridactyla* colony. *Journal of Animal Ecology* 56: 675-689.

Pucek, Z. & Lowe, V.P.W. 1975. Age criteria in small mammals. In: Golley, F.B., Petrusewicz, K. & Ryszkowski, L. (eds.). *Small Mammals: Their Productivity and Population Dynamics*. Cambridge University Press, Cambridge. pp. 55-72.

Ratcliffe, L., Rockwell, R.F. & Cooke, F. 1988. Recruitment and maternal age in Lesser Snow Geese *Chen caerulescens caerulescens*. *Journal of Animal Ecology* 57: 553-563.

Rohlf, F.J. & Sokal, R.R. 1969. *Statistical Tables*. Freeman, San Francisco.

Rounsefell, G.A. & Everhart, W.H. 1953. *Fisheries Science:*

Its Methods and Applications. Wiley, New York.

Schnell, G.D. 1970. A phenetic study of the suborder Lari (Aves), parts I-II. *Systematic Zoology* 19: 35-57, 264-302.

Shaw, P. 1985. Age-differences within breeding pairs of Blue-eyed Shags (*Phalacrocorax atriceps*). *Ibis* 127: 537-543.

Siegel, S. 1956. *Nonparametric Statistics for the Behavioural Sciences*. McGraw-Hill Kogakusha, Tokyo.

Sigfússon, A.P. 1990. *Studies of pre-breeding Fulmars* (Fulmarus glacialis), *their recruitment to breeding populations and intermittent breeding*. Unpublished PhD thesis, University of Aberdeen.

Sokal, R.R. & Rohlf, F.J. 1969. *Biometry*. Freeman, San Francisco.

Spencer, R. 1984. *The Ringer's Manual*. British Trust for Ornithology, Tring.

Tasker, M.L., Jones, P.H., Blake, B.F. & Dixon, T.J. 1985. The marine distribution of the Gannet *Sula bassana* in the North Sea. *Bird Study* 32: 82-90.

Thompson, D.R., Hamer, K.C. & Furness, R.W. In press. Mercury accumulation in Great Skuas *Catharacta skua* of known age and sex, and its effects upon breeding and survival. *Journal of Applied Ecology*.

Tinbergen, N. 1953. *The Herring Gull's World*. Collins, London.

Van Soest, R.W.M. & Van Utrecht, W.L. 1971. The layered structure of bones of birds as a possible indication of age. Bijdragen tot de Dierkunde 41: 61-66.

Veen, J. 1977. Functional and causal aspects of nest distribution in colonies of the Sandwich Tern. Behaviour Suppl. 20: 1-193.

Wanless, S. & Harris, M.P. 1988. The importance of relative laying date on breeding success of the Guillemot *Uria aalge*. Ornis Scandinavica 19: 205-211.

Ward, P. & Zahavi, A. 1973. The importance of certain assemblages of birds as 'information-centres' for food finding. Ibis 115: 517-534.

Weimerskirch, H. 1990. The influence of age and experience on breeding performance of the Antarctic Fulmar *Fulmarus glacialoides*. Journal of Animal Ecology 59: 867-875.

Wiens, J.A., Ford, R.G. & Heinemann, D. 1984. Information needs and priorities for assessing the sensitivity of marine birds to oil spills. Biological Conservation 28: 21-49.

Wooller, R.D., Bradley, J.S., Skira, I.J. & Serventy, D.L. 1990. Reproductive success in Short-tailed Shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology 59: 161-170.

Wooller, R.D. & Coulson, J.C. 1977. Factors affecting the age of first breeding of the Kittiwake *Rissa tridactyla*. Ibis 119: 339-349.

Wynne-Edwards, V.C. 1935. On the habits and distribution of the birds on the North Atlantic. Proceedings of the Boston Natural History Society 40: 233-346.

Wynne-Edwards, V.C. 1962. Animal Dispersion in Relation to Social Behaviour. Oliver & Boyd, Edinburgh.

Young, E.C. 1972. Territory establishment and stability in McCormick's Skua. Ibis 114: 234-244.

Zahavi, A. 1971. The function of pre-roost gatherings and communal roosts. Ibis 113: 106-109.

APPENDICES

I - XVII

Appendix I lists the Latin names and authorities of all species mentioned in this thesis. Appendices II-XVI summarise the results of comparative research performed at various Great Skua colonies in Shetland and on Handa during 1988-1990, as presented in detail in the unpublished report:

Klomp, N.I. & Furness, R.W. 1990^{b}. *The Diets and Numbers of Nonbreeding Great Skuas - A Comparison Among Colonies*. Report to the Nature Conservancy Council, the Royal Society for the Protection of Birds, and the Seabird Group. 143pp.

Appendix XVII is a paper describing the results of research conducted in the Azores whilst studying at the University of Glasgow, although it is not related to the thesis topic. It is in press in *Biological Oceanography*.

APPENDIX I. Latin names and authorities of species mentioned in the text, after Cambell (1976), Corbet & Southern (1977), Cramp (1985, 1988), Cramp & Simmons (1977, 1980, 1983), Härkönen (1986).

Birds

Wandering Albatross	*Diomedea exulans* Linnaeus
Manx Shearwater	*Puffinus puffinus* (Brünnich)
Fulmar	*Fulmarus glacialis* (Linnaeus)
British Storm-petrel	*Hydrobates pelagicus* (Linnaeus)
Gannet	*Sula bassana* (Linnaeus)
Shag	*Phalacrocorax aristotelis* (Linnaeus)
Blue-eyed Shag	*Phalacrocorax atriceps* King
Grey Heron	*Ardea cinerea* Linnaeus
Snow Goose	*Anser caerulescens* (Linnaeus)
Canada Goose	*Branta canadensis* (Linnaeus)
Mallard	*Anas platyrhynchos* Linnaeus
Eider	*Somateria mollissima* (Linnaeus)
Sparrowhawk	*Accipiter nisus* (Linnaeus)
Chicken	*Gallus gallus* (Linnaeus)
White Leghorn Chicken	*Gallus domesticus* (Linnaeus)
Moorhen	*Gallinula chloropus* (Linnaeus)
Whimbrel	*Numenius phaeopus* (Linnaeus)
Redshank	*Tringa totanus* (Linnaeus)
Pomarine Skua	*Stercorarius pomarinus* (Temminck)
Arctic Skua	*Stercorarius parasiticus* (Linnaeus)
Long-tailed Skua	*Stercorarius longicaudus* Vieillot
Great Skua	*Catharacta skua skua* Brünnich
Brown Skua	*Catharacta skua lönnbergi* (Mathews)

APPENDIX I (cond.).

Falkland Skua	*Catharacta skua antarctica* Lesson
Tristan Skua	*Catharacta skua hamiltoni* (Hagen)
South Polar Skua	*Catharacta maccormicki* (Saunders)
Chilean Skua	*Catharacta chilensis* Bonaparte
Herring Gull	*Larus argentatus* Pontoppidan
Great Black-backed Gull	*Larus marinus* Linnaeus
Red-billed Gull	*Larus novaehollandiae* Stephens
Kittiwake	*Rissa tridactyla* (Linnaeus)
Sandwich Tern	*Sterna sandvicensis* Latham
Arctic Tern	*Sterna paradisaea* Pontoppidan
Sooty Tern	*Sterna fuscata* Linnaeus
Guillemot	*Uria aalge* (Pontoppidan)
Brünnich's Guillemot	*Uria lomvia* (Linnaeus)
Puffin	*Fratercula arctica* (Linnaeus)
Meadow Pipit	*Anthus pratensis* (Linnaeus)
Great Tit	*Parus major* Linnaeus
Blue Tit	*Parus caeruleus* Linnaeus
Magpie	*Pica pica* (Linnaeus)
Jay	*Garrulus glandarius* (Linnaeus)
Starling	*Sturnus vulgaris* Linnaeus
Crossbill	*Loxia curvirostra* (Linnaeus)

Fish

Cod	*Gadus morhua* Linnaeus
Haddock	*Melanogrammus aeglefinus* (Linnaeus)
Pollack	*Pollachius pollachius* (Linnaeus)
Saithe	*Pollachius virens* (Linnaeus)

APPENDIX I (cond.).

Whiting	Merlangius merlangus (Linnaeus)
Blue Whiting	Micromesistius poutassou (Risso)
Norway Pout	Trisopterus esmarkii (Nilsson)
Poorcod	Trisopterus minutus (Linnaeus)
Torsk	Brosme brosme (Ascanius)
Hake	Merluccius merluccius (Linnaeus)
Garfish	Belone belone (Linnaeus)
Redfish	Sebastes marinus (Linnaeus)
Bass	Dicentrarchus labrax (Linnaeus)
Sandeel	Ammodytes marinus Raitt
Turbot	Psetta maxima (Linnaeus)
Plaice	Pleuronectes platessa Linnaeus
Dab	Limanda limanda (Linnaeus)
Long Rough Dab	Hippoglossoides platessoides (Fabricius)
Mammals	
Rabbit	Oryctolagus cuniculus (Linnaeus)
Mouse	Mus musculus Linnaeus
Sheep	Ovis (domestic)
Invertebrates	
Mussel	Mytelus edulis Linnaeus
Squid	Loligo sp.
Goose Barnacle	Lepas anatifera (Linnaeus)
Common Shore Crab	Carcinus maenas (Linnaeus)

APPENDIX II. The diets of nonbreeding Great Skuas on Fair Isle in 1989 and 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates	
	1989 (18/6)	1990 (4/7, 12/7, 18/7)
Prey items found in regurgitated pellets		
Whitefish	66	39
Sandeel	0	4
Fulmar	0	19
Kittiwake	0	1
Arctic Tern	0	1
Auk sp.	0	11
Crossbill	0	1
Unidentified bird	16	4
Rabbit	4	3
Others - egg	0	2
- wool	0	1
Total	86	86
Fish species from which otoliths found in whitefish pellets originated		
Haddock	2	3
Whiting	21	37
Norway Pout	5	4
Total	28	44

APPENDIX III. The diets of nonbreeding Great Skuas on Fetlar in 1989, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates	
	June (8/6, 15/6)	July (3/7, 6/7, 19/7, 29/7)
Prey items found in regurgitated pellets		
Whitefish	87	307
Sandeel	26	1
Fulmar	25	24
Kittiwake	1	0
Auk sp.	1	5
Unidentified bird	0	1
Rabbit	8	27
Goose Barnacle	8	11
Others - wool	0	1
- Common Shore Crab	0	1
- vegetation	0	1
- inorganic material	0	1
Total	156	380
Fish species from which otoliths found in whitefish pellets originated		
Cod	3	0
Haddock	67	39
Saithe	32	2
Whiting	101	89
Blue Whiting	8	5
Norway Pout	114	13
Hake	0	2
Long Rough Dab	3	0
Total	328	150

APPENDIX IV. The diets of nonbreeding Great Skuas on Fetlar in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (24/5, 29/5)	June (4/6, 9/6, 16/6, 20/6, 25/6)	July (4/7, 11/7, 18/7)
Prey items found in regurgitated pellets			
Whitefish	20	100	91
Sandeel	1	2	1
Fulmar	2	2	2
British Storm-petrel	0	1	1
Gannet	1	1	0
Kittiwake	1	0	0
Auk sp.	1	0	0
Unidentified bird	0	7	5
Rabbit	0	3	1
Goose Barnacle	1	22	18
Others - Mouse	0	3	1
- wool	2	1	0
- inorganic material	0	0	3
Total	29	142	123
Fish species from which otoliths found in whitefish pellets originated			
Haddock	2	4	16
Whiting	10	16	13
Blue Whiting	0	6	10
Norway Pout	18	11	11
Long Rough Dab	0	4	0
Unidentified	0	2	0
Total	30	43	50

APPENDIX V. The diets of nonbreeding Great Skuas on Fitful Head in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (16/5, 29/5)	June (17/6)	July (13/7, 20/7)
Prey items found in regurgitated pellets			
Whitefish	28	7	61
Sandeel	5	1	0
Fulmar	8	0	30
Kittiwake	0	0	2
Auk sp.	0	0	10
Unidentified bird	5	6	1
Rabbit	1	4	23
Goose Barnacle	4	0	18
Others - Squid	0	0	1
- sea urchin	0	0	1
- Common Shore Crab	0	0	2
- vegetation	0	0	3
- inorganic material	0	0	1
Total	51	18	153
Fish species from which otoliths found in whitefish pellets originated			
Haddock	8	4	20
Whiting	24	18	24
Blue Whiting	0	0	3
Norway Pout	8	6	15
Total	40	28	62

APPENDIX VI. The diets of nonbreeding Great Skuas on Foula in 1988, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (19/5, 25/5)	June (1/6, 8/6, 15/6, 22/6, 29/6)	July (6/7, 14/7, 21/7, 30/7)
Prey items found in regurgitated pellets			
Whitefish	187	690	291
Sandeel	5	32	4
Bird - white feather	6	29	36
- dark feather	6	49	54
Meadow Pipit	0	0	1
Rabbit	0	1	2
Goose Barnacle	2	6	6
Others - egg	0	3	3
- Mouse	0	1	0
- sea urchin	1	14	0
- Mussel	0	0	1
- vegetation	7	9	0
- inorganic material	1	3	0
Total	215	837	398
Fish species from which otoliths found in whitefish pellets originated			
Cod	0	1	0
Haddock	111	141	121
Whiting	228	391	289
Blue Whiting	10	4	6
Norway Pout	68	28	19
Torsk	2	0	0
Hake	2	1	0
Redfish	2	0	2
Bass	0	0	1
Long Rough Dab	1	3	3
Total	424	569	441

APPENDIX VII. The diets of nonbreeding Great Skuas on Foula in 1989, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (16/5, 23/5 30/5)	June (6/6, 13/6, 20/6, 27/6)	July (4/7, 12/7, 18/7, 25/7)
Prey items found in regurgitated pellets			
Whitefish	113	289	204
Sandeel	36	128	11
Fulmar	30	56	55
British Storm-petrel	0	2	5
Arctic Skua	0	0	3
Great Skua	0	0	12
Kittiwake	5	8	18
Arctic Tern	2	6	5
Auk sp.	3	5	32
Rabbit	4	9	10
Goose Barnacle	0	15	25
Others - egg	0	2	0
- Mouse	0	4	1
- Mussel	1	0	1
- Squid	0	0	1
- Common Shore Crab	1	1	6
- meat	0	1	0
- inorganic material	0	0	2
Total	195	526	391
Fish species from which otoliths found in whitefish pellets originated			
Cod	3	21	2
Haddock	9	12	9
Whiting	67	176	81
Blue Whiting	5	40	18
Norway Pout	126	59	38
Torsk	0	1	1
Garfish	1	0	0
Redfish	0	2	0
Bass	0	0	4
Turbot	0	1	0
Plaice	0	5	0
Long Rough Dab	0	12	8
Total	211	329	161

APPENDIX VIII. The diets of nonbreeding Great Skuas on Foula in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (13/5, 18/5 25/5)	June (4/6, 8/6, 15/6, 22/6, 29/6)	July (6/7, 12/7, 17/7)
Prey items found in regurgitated pellets			
Whitefish	62	142	71
Sandeel	85	79	2
Fulmar	9	18	30
British Storm-petrel	4	3	8
Shag	1	0	0
Great Skua	0	0	2
Kittiwake	5	4	6
Arctic Tern	0	1	3
Auk sp.	2	4	13
Unidentified bird	0	0	9
Rabbit	1	10	18
Goose Barnacle	1	38	25
Others - Mouse	0	1	2
- sea urchin	0	1	0
- Mussel	0	1	0
- Common Shore Crab	0	0	1
- meat	0	5	4
- inorganic material	0	0	3
Total	170	307	197
Fish species from which otoliths found in whitefish pellets originated			
Cod	0	1	0
Haddock	2	5	9
Saithe	0	0	1
Whiting	42	61	50
Blue Whiting	3	25	7
Norway Pout	13	27	2
Hake	0	2	0
Dab	0	3	0
Total	60	124	69

APPENDIX IX. The diets of nonbreeding Great Skuas on Hermaness in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (22/5, 28/5)	June (4/6, 10/6, 16/6, 22/6, 29/6)	July (5/7, 12/7, 19/7, 26/7)
Prey items found in regurgitated pellets			
Whitefish	25	117	87
Sandeel	0	0	0
Fulmar	4	4	8
British Storm-petrel	0	1	1
Shag	0	1	0
Kittiwake	0	0	2
Auk sp.	0	3	2
Crossbill	0	1	0
Rabbit	2	3	0
Goose Barnacle	2	13	16
Others - Common Shore Crab	1	1	0
- wool	0	1	0
- vegetation	0	1	0
Total	34	146	116
Fish species from which otoliths found in whitefish pellets originated			
Cod	0	0	1
Haddock	2	1	2
Whiting	5	3	2
Blue Whiting	13	40	2
Norway Pout	5	9	2
Long Rough Dab	4	2	0
Total	29	55	9

APPENDIX X. The diets of nonbreeding Great Skuas at Lumbister, Mid-Yell, in 1989, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates June 1989 (8/6, 16/6, 23/6)
Prey items found in regurgitated pellets	
Whitefish	7
Sandeel	0
Fulmar	3
Kittiwake	1
Auk sp.	3
Rabbit	1
Others - wool	1
Total	16
Fish species from which otoliths found in whitefish pellets originated	
Blue Whiting	2
Norway Pout	4
Total	6

APPENDIX XI. The diets of nonbreeding Great Skuas on Noss in 1989, as determined by the number of different prey items found in regurgitated pellets. No otoliths were collected from Noss in 1989.

	Collection dates	
	June (4/6, 11/6, 18/6, 25/6)	July/August (2/7, 9/7, 17/7 25/7, 1/8)
Prey items found in regurgitated pellets		
Whitefish	103	120
Sandeel	9	8
Fulmar	52	88
Kittiwake	0	4
Auk sp.	6	23
Rabbit	27	43
Goose Barnacle	7	5
Others - vegetation	1	0
Total	205	291

APPENDIX XII. The diets of nonbreeding Great Skuas on Noss in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (17/5, 25/5)	June (1/6, 8/6, 15/6, 23/6, 28/6)	July (6/7, 14/7, 20/7, 28/7)
Prey items found in regurgitated pellets			
Whitefish	51	220	153
Sandeel	10	41	17
Fulmar	16	32	2
Gannet	0	1	1
Great Skua	0	0	4
Kittiwake	7	32	12
Auk sp.	12	25	27
Crossbill	0	4	0
Starling	0	0	3
Unidentified bird	1	51	37
Rabbit	6	59	181
Goose Barnacle	4	73	20
Others - egg	0	9	3
- wool	0	7	2
- Common Shore Crab	1	1	0
- Mussel	0	1	0
- insect	0	0	1
Total	108	556	464
Fish species from which otoliths found in whitefish pellets originated			
Cod	2	2	0
Haddock	23	22	29
Whiting	32	62	60
Blue Whiting	0	4	2
Norway Pout	35	78	10
Torsk	0	4	0
Redfish	0	3	1
Dab	3	0	0
Long Rough Dab	0	3	0
Total	95	178	102

APPENDIX XIII. The diets of nonbreeding Great Skuas on Handa in 1989, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (5/5, 8/5, 11/5, 15/5, 19/5, 23/5, 30/5)	June (6/6, 13/6, 17/6, 21/6, 28/6)	July (5/7, 12/7, 20/7, 24/7)
Prey items found in regurgitated pellets			
Whitefish	19	70	34
Sandeel	27	31	16
Bird	119	81	240
Goose Barnacle	0	2	1
Others - Common Shore Crab	1	0	0
- gastropod	1	0	0
- wool	3	0	0
- vegetation	0	3	1
- inorganic material	1	0	0
Total	171	187	292
Fish species from which otoliths found in whitefish pellets originated			
Haddock	7	12	10
Whiting	6	22	7
Norway Pout	9	29	9
Torsk	0	0	1
Dab	2	0	1
Unidentified	2	4	5
Total	26	67	33

APPENDIX XIV. The diets of nonbreeding Great Skuas on Handa in 1990, as determined by the number of different prey items found in regurgitated pellets, and the number and type of otoliths found in the whitefish pellets.

	Collection dates		
	May (19/5, 27/5)	June (3/6, 10/6, 17/6, 24/6)	July (1/7, 8/7, 12/7, 18/7)
Prey items found in regurgitated pellets			
Whitefish	18	32	40
Sandeel	25	26	12
Bird - white feather	54	82	116
- dark feather	14	24	86
Goose Barnacle	0	1	0
Others - egg	1	2	0
- Squid	1	0	0
- Common Shore Crab	0	0	2
- vegetation	1	0	0
Total	114	167	256
Fish species from which otoliths found in whitefish pellets originated			
Cod	0	0	1
Haddock	12	21	12
Whiting	13	28	7
Blue Whiting	0	0	3
Norway Pout	56	39	10
Hake	0	5	0
Dab	1	0	0
Total	82	93	33

APPENDIX XV. The number of nonbreeders present at all the club-sites in different Great Skua colonies in 1988-1990. "N" represents a count made at night (22:30 - 01:30 GMT) and "A" represents a count made in the afternoon (13:00 - 15:00 GMT), as described in the text.

Colony	Year	Date	Count	Time
Fair Isle	1990	17/6	42	N
		3/7	43	N
		12/7	32	N
		20/7	22	N
Fetlar (Lamb Hoga)	1989	27/5	20	A
		15/6	35	N
		30/6	23	N
		3/7	38	N
		6/7	30	N
		19/7	31	N
Fetlar (Lamb Hoga)	1990	18/5	29	A
		5/6	23	N
		20/6	42	N
		2/7	34	N
		18/7	27	N
Fitful Head	1990	16/5	17	10:30
		29/5	22	A
		13/7	16	A
		20/7	54	10:50
Foula	1988	29/5	563	09:00-17:00
		5/6	584	09:00-17:00
		7/6	1023	N
		14/6	1243	N
		19/6	1198	N
		27/6	975	N
		5/7	715	N
		7/7	534	N
		12/7	513	N
		18/7	408	N
		22/7	389	N
		31/7	321	N
Foula	1989	12/5	791	N
		19/5	793	N
		25/5	889	N
		2/6	917	N
		9/6	898	N
		17/6	767	N
		23/6	783	N
		30/6	472	N
		8/7	354	N
		15/7	375	N
		26/7	294	N

APPENDIX XV (cond.).

Colony	Year	Date	Count	Time
Foula	1990	18/5	767	N
		25/5	819	N
		31/5	798	N
		8/6	795	N
		15/6	762	N
		25/6	640	N
		29/6	638	N
		6/7	550	N
		12/7	463	N
		17/7	330	N
Hermaness	1989	8/6	183	A
		16/6	176	A
		26/6	161	A
		1/7	185	N
		3/7	128	A
		16/7	106	A
		27/7	94	A
Hermaness	1990	16/5	117	N
		22/5	133	N
		27/5	115	A
		8/6	177	A
		10/6	185	A
		20/6	187	N
		5/7	189	A
		15/7	159	A
		23/7	131	A
Mid-Yell (Lumbister)	1989	13/6	28	A
		23/6	14	A
		5/7	11	10:00
		27/7	21	A
Noss	1989	28/5	95	N
		4/6	49	N
		11/6	89	N
		18/6	48	N
		25/6	61	N
		2/7	48	N
		9/7	34	N
		17/7	33	N
		25/7	31	N
		1/8	37	N
Noss	1990	17/5	45	N
		26/5	105	N
		2/6	97	N
		8/6	80	N
		15/6	84	N
		21/6	45	A
		27/6	83	N

APPENDIX XV (cond.).

Colony	Year	Date	Count	Time
Noss	1990	6/7	60	N
		13/7	35	N
		21/7	65	N
Handa	1989	19/5	39	A
		23/5	63	A
		30/5	34	A
		5/6	32	A
		13/6	13	A
		16/6	12	12:00
		20/6	9	A
		25/6	18	A
		5/7	22	12:00
		12/7	22	A
		17/7	30	N
		22/7	7	12:30
Handa	1990	19/5	57	A
		7/6	26	A
		15/6	16	12:00
		19/6	40	12:00
		29/6	20	12:00
		6/7	3	A
		12/7	18	A

APPENDIX XVI. The number of AOT's, number of club-sites, maximum number of nonbreeders recorded at one time (day or night), diet of nonbreeders in July (percentage of certain prey types in the diets) and breeding success (chicks fledged per pair) of Great Skuas at eight colonies during 1988-1990. Those colonies adjacent to large Gannet colonies are shown with an asterix.

Colony	Year	AOT's	Clubs	Non-breeders	Diet in July (%)			Breeding success
					w/fish	Sandeel	bird	
Fair Isle	1989	72	2-3	-	-	-	-	0.79
	1990	73	2-3	43	45.0	5.0	43.0	0.70
Fetlar	1989	157	1	38	80.5	0.5	8.0	0.13
(Lamb Hoga)	1990	-	1	42	78.5	1.0	6.5	0.3-0.4
Fitful Head	1989	-	1	-	-	-	-	0.7
	1990	155	1	54	39.9	0	28.1	-
Foula	1988	2400	13	1243	73.1	1.0	22.9	0.11
	1989	-	13	917	52.2	2.8	33.2	0.24
	1990	2340	13	819	36.0	1.0	36.0	0.40
Hermaness*	1989	896	4	185	-	-	-	1.02
(Reserve only)	1990	-	4	189	70.0	0	11.0	0.69
Mid-Yell (Lumbister)	1989	-	1	28	-	-	-	-
Noss*	1989	388	2	95	41.2	2.7	39.5	0.11
	1990	-	2	105	33.0	3.5	18.5	0.22
Handa	1989	68	2	57	11.6	5.5	82.2	1.20
	1990	80	2	63	15.6	4.7	78.9	1.25

APPENDIX XVII. The following manuscript describes the results of research conducted whilst studying at the University of Glasgow, but not related to the thesis topic. This paper is in press in Biological Oceanography.

Patterns of Chick-Feeding in Cory's Shearwaters and the Associations with Ambient Light

N.I. Klomp & R.W. Furness

Applied Ornithology Unit
Department of Zoology
University of Glasgow
Glasgow G12 8QQ
Scotland

Abstract

We determined meal size frequency and timing of chick-feeding by Cory's shearwaters at a colony in the Azores by weighing chicks every 4 hr. Chicks were fed mainly on fish, but occasionally on cephalopods. Meal sizes delivered to the chicks averaged 60g (S.D.= 32.2g). Overnight positive mass increments ranged up to 180g. Inter-feed mass loss due to respiration and excretion was positively correlated with the chicks' initial masses. The minimum amount of food required by the chicks to maintain constant mass ($44.2g.day^{-1}$) was well surpassed by actual meal sizes received. The mean growth rate of the chicks ($24.8g.day^{-1}$) also suggests the presence of a plentiful and nutritious food supply available to the colony. Most feeds were between 2000 h and 0400 h (GMT). The timing of adult returns was, however, dependent on ambient light conditions. Birds fed their chicks less on moon-lit nights and tended to return to nests later. This response to variations in noctural illumination is in remarkable contrast to the diurnal return of birds of the same species at Selvagem Grande, 1400km distant. The effects of ambient light on food-provisioning behaviour may be related to nocturnal food availability rather than predator avoidance behaviour by adult birds. Comparisons are made with chick-feeding patterns of other pelagic Procellariiformes.

Key words: seabirds, shearwaters, meal sizes, chick-feeding frequencies, ambient light effects, nocturnal illumination, predator avoidance.

Introduction

Procellariiformes (albatrosses, petrels, shearwaters, etc.) are pelagic seabirds and an integral part of oceanic food webs. Little is known of their feeding ecology owing in part to problems associated with studying them at sea. Inferences can, however, be made from studies at breeding colonies. Patterns of food delivery to chicks are related to species-specific foraging strategies and are relevant to the evolution of brood size, chick growth rate, developmental mode, parental brooding period and energy storage patterns of chicks (Ricklefs, 1984; Ashmole, 1971; Lack, 1968). Meal sizes and feeding frequencies may also reflect foraging conditions related to weather, oceanographic and light effects on prey availability close to sea surface waters. However, parental feeding has received little attention in studies of seabirds, despite the information it may provide on distributions and diurnal activities of prey organisms (Brown, 1975; Furness & Monaghan, 1987).

Ricklefs _et_ _al_. (1985) found that food provisioning in Leach's storm-petrels _Oceanodroma_ _leucorhoa_ was regulated by the requirements of the chicks. However, some procellariiform species that return at night to feed their young have been shown to alter their food-provisioning behaviour according to ambient light conditions (e.g. Manx shearwaters _Puffinus_ _puffinus_; Thompson, 1987). Some procellariiforms are believed to have a reduced level of activity at the colony on moonlit nights as an anti-predator stategy (e.g. Leach's storm-petrels; Watanuki, 1986). Alternatively, seabird activity and food-provisioning levels at night may be affected by prey availability which may, in turn, be affected by light conditions, an idea proposed by

Imber (1975) but considered little since.

Meal sizes delivered to chicks can be estimated from the chicks' daily mass increments. Such estimates must allow for loss of mass through respiration and excretion. Meal sizes can be calculated more accurately, therefore, by taking more frequent, regular weighings. This also provides information on feeding frequency and timing of returning adults. This paper adapts techniques described by Ricklefs (1984) and Ricklefs _et al_. (1985) to report such feeding characteristics estimated by mass increments and to determine the effects of ambient light on the chick-feeding behaviour. Imber's (1975) hypothesis that the level of nocturnal illumination affected food availability to some procellariiforms suggests that meal sizes and feeding frequencies would be less on nights of bright moonlight, whereas the anti-predator hypothesis would predict that birds would visit the colony less often on moonlit nights, but that meals delivered to chicks should be no smaller. Other variables such as foraging ranges and adult food loads may also be important factors determining food-provisioning behaviour.

Methods

Fieldwork was carried out on Ilheu de Vila Franca (37° 29' N, 25° 21' W), a small islet one km from Vila Franca do Campo, Sao Miguel, Azores. Commencing 13 August 1989, 16 nests of Cory's shearwaters _Calonectris_ _diomedea_ _borealis_ were monitored every 4 hr from 2000 h until 0800 h (GMT). After two nights one nest was deleted from the study. Nests were monitored for five nights over two study periods: 13-16 August (full moon) and 24-26 August (new moon) 1989. Each nest contained one chick. At the start of the study, chicks were all between 5 and 15 days old, as estimated by plumage characteristics described by

Cramp and Simmons (1977). On each visit chicks were weighed to the nearest 5g using a Pesola spring balance, and the presence of any adults was noted. All study chicks were also weighed at midday on 13 and 24 August, when their wings (maximum flattened chord) were measured. In addition, 73 adults of unknown breeding status and 30 chicks from nests in other parts of the colony were weighed and ringed. Some of these regurgitated food samples which were examined and identified as fish or cephalopod. Statistical procedures follow Sokal and Rohlf (1969).

Results

A total of 23 adults of unknown breeding status and eight chicks regurgitated when handled during this study; 29 regurgitated fish and two regurgitated cephalopod remains. The daily (0800 h to 0800 h) mass change of a chick is referred to as its NET value. The sum of the overnight, positive (≥0) mass increments of a chick is described as its SUM value (after Ricklefs, 1984). The mean values of NET and SUM are presented for the two study periods in August (Table 1).

Meal sizes

The values of SUM are useful indices to the total amount of food received by the chicks. SUMs varied between 0g (by definition) and 180g (Figure 1). The overall mean (± S.D.) SUM of 54 chick-nights was 61.9 ± 50.0g. This represented approximately 10% of the mean mass of chicks (Table 1). No significant correlation was found between initial chick masses and their SUMs, nor between initial chick wing/mass ratios and their SUMs. Consistent differences among pairs of parents in either feeding frequency or meal sizes may be expected to be revealed by a positive correlation among the SUMs of chicks recorded on successive nights. No such correlation was found.

Some of the SUMs presented in Figure 1 undoubtedly represent feeds delivered by both parents. Although our study did not allow for this to be determined directly, it is possible to estimate the number of SUMs that represent feedings by two parents and, therefore, to estimate the average size of a single meal, as described below (after Ricklefs, 1984). SUM values of zero have been excluded from this analysis:

If the probability that a given parent feeds its chick on a given night is P, then the probability that a given parent does not feed its chick on a given night is 1-P. Assuming that individual adults of a pair feed their chick independently, it follows that the probability of neither parent feeding its chick is $(1-P)^2$. This may be estimated from the observed frequency of zero or negative mass increments. During 13-16 August, for example, the number of chick-nights with no positive mass increments was 20, out of 47 chick-nights, or 42.5%. So $(1-P)^2 = 0.425$, hence $1-P = 0.652$ and $P = 0.348$. Further, the probability that both parents feed a given chick on a given night is P^2; in this case, 0.121. Thus the six highest values of SUM (approximately 0.121 X 47 chick-nights) probably represent feedings by both parents in a single night. By deleting these six from the meal size calculations, the average value of SUM represents the average meal size from one parent. Meal sizes have been calculated for both study periods - individually and combined - in this manner (Table 1). Alternatively, an average meal size can calculated by dividing the total amount of SUMs (2010g for 13-16 August) by the estimated number of feeds (in this case, 33: 21 single feeds and six two-parent feeds). This method yields similar results (13-16 August: 60.9g, 24-26 August: 66.8g, overall: 63.1g).

Values of SUM underestimate true meal sizes due to losses of mass by respiration and excretion. Ricklefs (1984) suggested that values of SUM could be adjusted by a constant equal to the average mass loss during a non-feeding, 4-hr interval. Ricklefs, et al. (1985) and Thompson (1987), however, found that rates of chick mass loss were greater in the periods immediately after feeding than in non-feeding (e.g. daytime) periods. This study found that mass loss was also significantly and positively correlated to the mass of the chick at the start of the given time interval ($r_{76} = 0.39$, $P<0.001$). Heavier chicks lost weight faster than lighter chicks. Hence; $L = 0.115W - 59.27$, where L is the mass loss over a given 4-hr interval (in grams), and W is the mass (g) of the chick at the start of that interval.

Although it is possible to adjust estimations of meal sizes by the above methods, such adjustments are tenuous and have little influence on the estimates. The average mass loss of chicks over non-feeding periods throughout this study was 2.5 ± 1.6g/hr, a result similar to other studies (e.g. Ricklefs, 1984), but very small compared to average meal size. Consequently, SUM is considered to be the most useful statistic of meal size, and will be used as such in further discussions.

Timing of returning adults

Adult Cory's Shearwaters were only found in their nests on our 2400 h and 0400 h rounds; of 154 nest-visits at these times, individual adults were present 21 times, and only once were both adults of a pair in a nest. The presence of adults was usually associated with chick mass gains. Of the five occasions when the presence of an adult in a nest was not associated with an increase in its chick's mass, the mass of the chick had not decreased over the preceding 4-hr interval on three occasions. On these occasions, the adult had probably fed the chick a small amount before we disturbed it.

The average mass increments and the proportion of mass increments greater than zero did not differ significantly between the two study periods (Student's t-tests, $P>0.05$). Figure 2 shows that most feeding took place between 2000 and 0400 hr.

The proportion of nests with evidence of adult attendance on the nights of nearly full ("full"), unclouded moon at midnight (14/15 and 15/16 August) is significantly less than that of the other nights ($X^2_1 = 4.30$, $P<0.05$) (Table 2). Comparison of the number of feedings before and after midnight for the two study periods showed that the chicks were fed later during nights of "full" moon at midnight, 13-16 August, than during nights of no moon at midnight, 24-26 August ($X^2_1 = 14.01$, $P<0.05$). Similar results were obtained when adult returns (based on observations and/or chick mass increases) were compared between the two study periods (Figure 3). The timing of adults returning to their nests was related to moon phase and cloud cover.

Meal size and ambient light

Table 2 also presents data on the meal sizes of chicks in relation to the ambient light conditions of each night of the study. The amount of food (mean SUM) delivered to the chicks on the nights of "full", unclouded moon at midnight (14/15 and 15/16 August) is significantly less than that of other nights

(Student's $t_{52} = 3.23$, $P<0.01$).

NET vs SUM

To determine how daily mass gain is related to amount fed, we regressed values of SUM (positive mass increment) with values of NET (daily mass change) for individual chick-nights (after Ricklefs, 1984; Ricklefs, et al., 1985). This was highly significant (14-16 August: $r_{21} = 0.87$, $P<0.001$; 25/26 August: $r_9 = 0.88$, $P<0.01$; overall: $r_{31} = 0.85$, $P<0.001$). Such regressions can provide useful information on the food conversion efficiency and feed size requirements of the chicks. The amount of food required for chicks to maintain constant mass is equal to the intercept of the regression of NET on SUM at the point NET = 0. In this study, such values of SUM were 38.6g and 55.3g for 14-16 and 25/26 August, respectively, the difference being due to the greater mass and energy requirements of the chicks by the latter study period. These 'break-even' values of minimum food required per feeding were well surpassed, as can be seen from the mean amount of food delivered to each chick per night of 73.1g and 86.7g (Table 1).

To calculate the time interval that would result in the observed variation in the masses of chicks, the following method was used (after Ricklefs, 1984):

The S.D. of the initial mass of chicks about its quadratic regression against wing-length was 51.2g and 87.2g for 13-16 August and 24-26 August (Table 1). These correspond to an S.D. in the values of SUM of 47.7g and 97.8g, respectively (S.D. divided by the slope of the regression). Hence, variation in chick masses might be expected to have arisen over the course of 0.8 days and 5.3 days, respectively (the quotients of the corresponding variances of mean SUMs, i.e. $(47.7)^2/(52.2)^2$ and $(97.8)^2/(42.4)^2$). This explains the lack of correlation between the midday masses of chicks on 13 and 24 August ($r_{14} = 0.092$, $P>0.5$).

Discussion

Comparison of feeding characteristics

Food conversion efficiencies and feeding characteristics of some procellariiforms are compared in Table 3. The published and present information suggest that, in terms of adult mass, Cory's shearwaters need to provide the least food to their chicks to maintain chick mass. Average meal size was ~40% greater than this value (Table 1). Also, Cory's shearwaters were found to feed their chicks on fewer nights (58%) than most other birds studied, suggesting that the adults are able to forage for a longer time, perhaps over longer distances, and provide chicks with larger meals. Two estimations of food conversion efficiency of Cory's shearwater chicks in this study are presented in Table 3. Using the slope of the regression of NET on SUM (after Ricklefs, 1984), the estimated food conversion efficiency was found to be extremely and improbably high (96% overall), but, due to small sample sizes, so is the standard error (11%). Alternatively, estimation of the efficiency of chicks to convert food consumed into mass gain can be calculated from data in Table 1. Overall, the average mass of food delivered per chick per day = 78g, or 33.8g more than required to maintain constant mass (44.2g). Over the duration of the study (11 days), chicks increased mass by an average of 24.8g.day^{-1}, suggesting a food conversion efficiency of 73%. Clearly, chicks are able to convert a very large proportion of the food consumed into mass gain. This is consistent with foods of high calorific value, typical of oily fish, found in the majority of samples in this study.

There was large variation in individual meal sizes within the colony, although no consistent differences in meal sizes delivered by given pairs of parents were apparent. This resulted in large variations in chick masses and irregular mass increases. This pattern is probably typical of pelagic feeders due to patchy food distribution at sea (Ashmole, 1971).

Effects of ambient light conditions

There is a surprising lack of literature on the effects of ambient light conditions on the activities of nocturnal, breeding seabirds. The nocturnal habit of the Cory's shearwaters at most colonies may be a response to human persecution (Lockley, 1952) or to predator avoidance (Harris, 1966; Watanuki, 1986; Thompson, 1987; Bretagnolle, 1990). The diurnal return of the same species at Selvagem Grande (Hamer & Read, 1987) is a remarkable contrast to the subtle changes in colony return and chick-feeding in the Azores in response to variations in nocturnal illumination. Alternatively, Cory's shearwaters in this study may have fed more successfully on dark nights than on moon-lit ones due to increased prey availability. This has been seen in petrels that exploit vertically migrating and/or bioluminiscent prey (Imber, 1975). Adults may be more likely to return to their chicks after recent, successful foraging. The finding that meal sizes are significantly greater on darker nights than on moonlit nights (this study) fits this hypothesis, but is difficult to explain in terms of an anti-predator strategy. The reduced feeding frequency seen in Manx shearwaters and altered nocturnal activity in other petrels on moonlit nights can also be explained by this hypothesis, although reduced meal sizes have not been previously described. Nocturnal feeding is very important for many Procellariiformes. For instance, studies of fulmar Fulmarus glacialis diets at St. Kilda and Shetland (Furness & Todd, 1984) suggested that nocturnal feeding was more common in that species than previously thought. Deployment of activity monitors on gray-headed albatrosses Diomedea chrysostoma (Prince & Francis, 1984) and satellite tracking of wandering albatrosses Diomedea exulans (Joventin & Weimerskirch, 1990) have shown that most feeding is done at night in these species. The relative importance of nocturnal feeding in shearwaters is not documented. Clearly, more research into the effect of ambient light conditions on behaviour of nocturnal prey availability and seabird activity is required.

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References

Allan, R.G., 1962. The Madeiran storm-petrel *Oceanodroma castro*. *Ibis* 103b: 274-295.

Ashmole, N.P., 1971. Seabird ecology and the marine environment. In: Farner, D.S. & J.R. King (eds.). *Avian biology, Vol. 1*. Academic Press, New York. pp 223-286.

Bretagnolle, V., 1990. Effet de la lune sur l'activité des pétrels (classe Aves) aux îles Salvages (Portugal). *Can. J. Zool*. 68: 1404-1409.

Brown, W.Y., 1975. Parental feeding of young sooty terns (*Sterna fuscata* (L.)) and Brown Noddies (*Anous stolidus* (L.)) in Hawaii. *J. Anim. Ecol*. 44: 731-742.

Croxall, J.P., H.J. Hill, R. Lidstone-Scott, M.J. O'Connell & P.A. Prince, 1988. Food and feeding ecology of Wilson's storm-petrel *Oceanites oceanicus* at South Georgia. *J. Zool., Lond*. 216: 83-102.

Cramp, S. & K.E.L. Simmons, 1977. *Handbook of the birds of Europe, the Middle East and North Africa. Birds of the Western Palaearctic. Vol. 1*. Oxford University Press, Oxford.

Furness, R.W. & P. Monaghan, 1987. *Seabird Ecology*. Blackie, London.

Furness, R.W. & C.M. Todd, 1984. Diets and feeding of fulmars *Fulmarus glacialis* during the breeding season: a comparison between St. Kilda and Shetland colonies. *Ibis* 126: 379-387.

Hamer, K. & H. Read, 1987. Patterns of return to land in a colony of Cory's shearwaters *Calonectris diomedea* on Selvagem Grande. *Seabird* 10: 3-11.

Harris, M.P., 1966. Breeding biology of the Manx shearwater *Puffinus puffinus*. *Ibis* 108: 17-33.

Imber, M.J., 1975. Behaviour of petrels in relation to the moon and artificial lights. *Notornis* 22: 302-306.

Jouventin, P. & H. Weimerskirch, 1990. Satellite tracking of wandering albatrosses. *Nature* 343:-746-748.

Lack, D. 1968., *Ecological adaptations for breeding in birds*. Methuen, London.

Lee, K. & P. Won, 1988. Breeding biology of Swinhoe's fork-tailed petrel *Oceanodroma monorhis* (Swinhoe) on Chilbal Islet, Korea. *Bull. Inst. Ornithol., Kyung Hee Univ. Seoul, Korea*.

Lockley, R.M., 1952. The birds of the islands of the Berlengas (Portugal), the Desertas and Baixo (Madeira) and the Salvages. *Ibis* 94: 144-157.

Payne, M.R. & P.A. Prince, 1979. Identification and breeding biology of the diving petrels *Pelecanoides georgicus* and P. *urinatrix excsul* at South Geogia. *New Zealand J. Zool.* 6: 299-318.

Prince, P.A. & M.D. Francis, 1984. Activity budgets of foraging gray-headed albatrosses. *Condor* 86: 297-300.

Quinlan, S.A., 1979. *Breeding biology of storm-petrels at Wooded Islands, Alaska*. Ph.D. thesis, University of Alaska, Fairbanks.

Richdale, L.E., 1965. Biology of the birds of Whero Island, New Zealand, with special reference to the diving petrel and the white-faced storm-petrel. *Trans. Zool. Soc. Lond*. 31: 3-86.

Ricklefs, R.E., 1984. Meal sizes and feeding rates of Christmas shearwaters and phoenix petrels on Christmas Island, Central Pacific Ocean. *Ornis Scand*. 15: 16-22.

Ricklefs, R.E., C.H. Day, C.E. Huntington & J.B. Williams, 1985. Variability in feeding rate and meal size of Leach's storm-petrel at Kent Island, New Brunswick. J. Anim. Ecol. 54: 883-898.

Scott, D.A., 1970. Breeding biology of the storm-petrel Hydrobates pelagicus. D. Phil. thesis, Univ. of Oxford.

Sokal, R.R. & F.J. Rohlf, 1969. Biometry. Freeman, San Francisco.

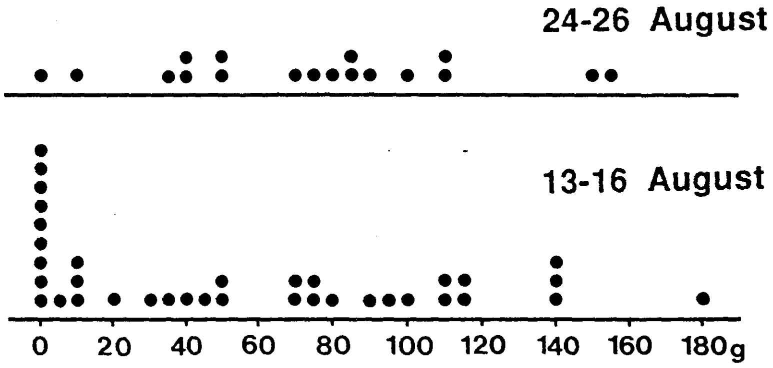
Thompson, K.R., 1987. The ecology of the Manx shearwater Puffinus puffinus on Rhum, West Scotland. Ph.D. thesis, University of Glasgow.

Watanuki, Y., 1986. Moonlight avoidance behavior in Leach's storm-petrels as a defense against Slaty-backed Gulls. Auk 103: 14-22.

Figure 1. Distributions of SUM values for different study periods.

Figure 2. Average mass increments (± S.E.) and proportion of mass increments greater than zero for different time intervals. Pooled data for 13-16 August: solid bars and diamonds, pooled data for 24-26 August: hollow bars and solid circles. Sample sizes are shown in parentheses.

Figure 3. The proportion of nests with evidence of adults having been in attendance (ie. chicks fed or adults present) during different periods of the night. The light conditions (moon phase and cloud cover) for each midnight are described. N.B. Full moon occurred on 17 August 1989.


24-26 August
13-16 August
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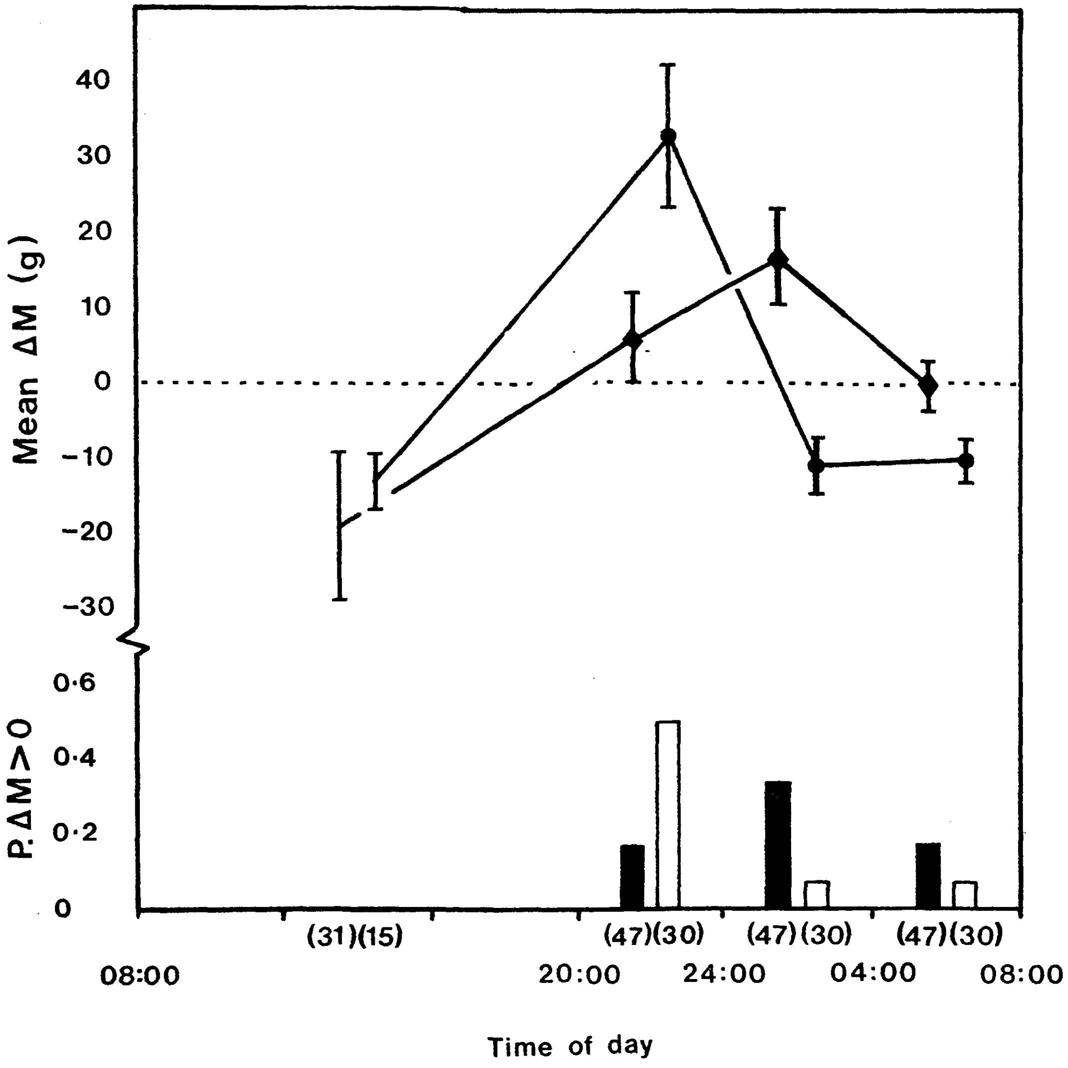
40
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0
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Mean ΔM (g)
0·6
0·4
0·2
0
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08:00
Time of day

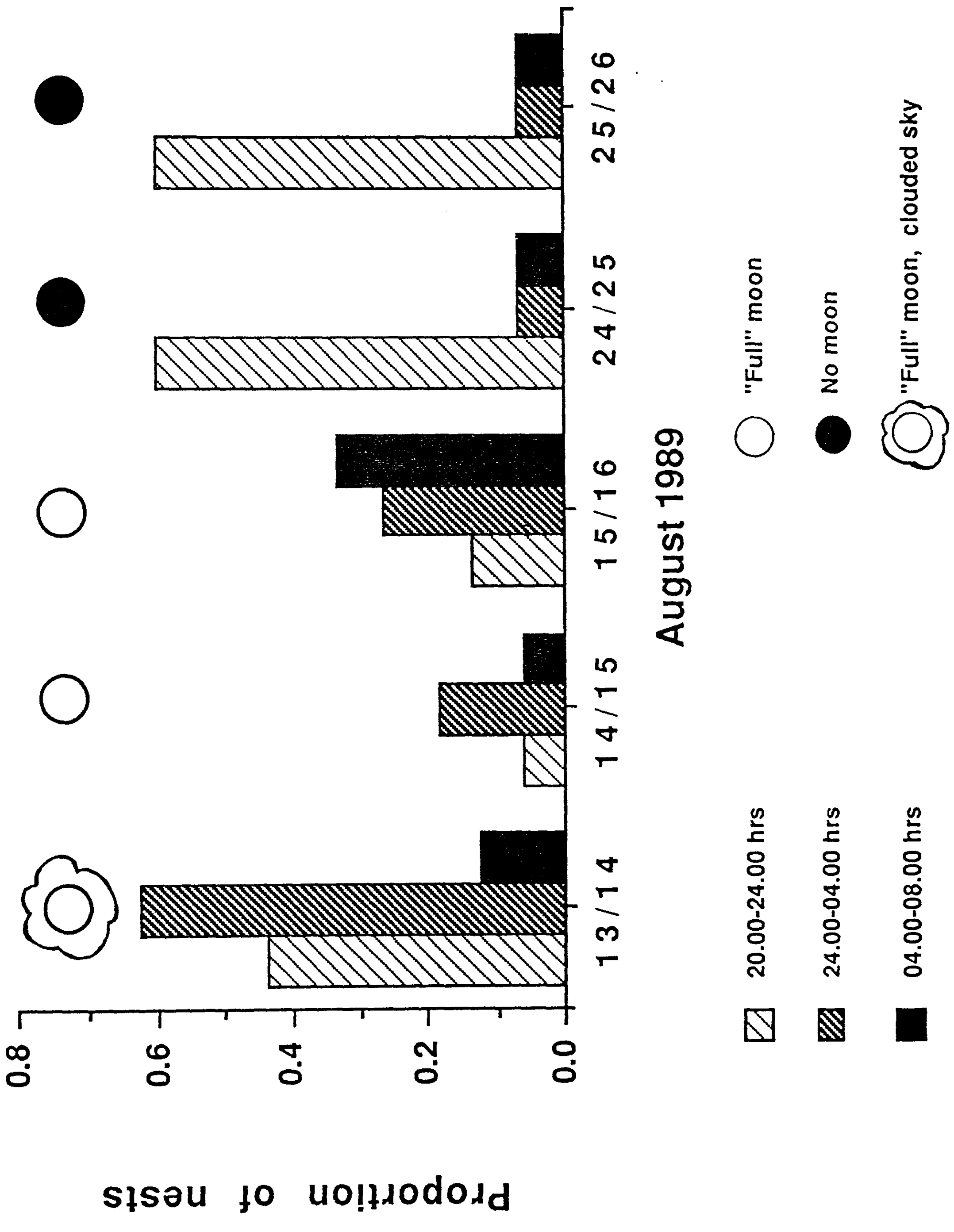
Proportion of nests
0.0
0.2
0.4
0.6
0.8
13/14
14/15
15/16
24/25
25/26
August 1989
20.00-24.00 hrs
24.00-04.00 hrs
04.00-08.00 hrs
"Full" moon
No moon
"Full" moon, clouded sky

Table 1. Growth and feeding characteristics of Cory's shearwaters on Ilheu de Vila Franca (Sao Miguel, Azores) for different study periods in August 1989.

	13 - 16 August	24 - 26 August	Overall
Adult mass (g ± S.D.)	774 ± 80		
Initial chick mass (g ± S.D.)	503 ± 67	770 ± 91	
Range (g)	385 - 610	635 - 955	
Initial chick wing-length (mm ± S.D.)	65.6 ± 5.4	88.1 ± 25.2	
Initial chick wing/mass ratio ($mm.g^{-1}$ ± S.D.)	0.132 ± 0.015	0.124 ± 0.019	
S.D. about quadratic regression of mass vs wing-length (g)	51.2	87.2	80.7
Number of chick - nights	47	30	77
SUM (g ± S.D.)	55.8 ± 52.2	74.2 ± 42.4	61.9 ± 50.0
% of chick mass	11.1	9.6	9.7
Feeding frequency per adult per day	0.65	0.66	0.65
Meal size (g ± S.D.)	56.2 ± 34.6	65.7 ± 28.6	60.0 ± 32.2
% of adult mass	7.3	8.5	7.7
Food (g) delivered per chick per night	73.1	86.7	78.0
NET (g ± S.E.)	- 0.9 ± 11.8	14.5 ± 13.7	3.9 ± 9.1
Slope of NET vs SUM (± S.E.)	1.07 ± 0.16	0.89 ± 0.13	0.96 ± 0.11
Intercept of NET vs SUM (g)	- 41.4	- 49.3	- 42.3
NET = 0, when SUM = (g)	38.6	55.3	44.2

Table 2. Chick-feeding characteristics of the five study nights, in order of decreasing ambient light conditions. Full moon occurred on 17 August 1989.

Conditions at midnight [Light intensity]	Date August 1989	Proportion of nests with evidence of adult attendance	Proportion of chicks fed	Proportion of chicks first fed before midnight (of all chicks fed)	Mean SUM (g)
"Full" moon, clear sky [Bright]	14/15	0.31	0.31	0.20	22.1
"Full" moon, clear sky [Bright]	15/16	0.67	0.60	0.11	45.0
"Full" moon, clouded sky [Dim]	13/14	0.88	0.81	0.46	84.3
No moon, clear sky [Dark]	24/25	0.60	0.47	0.86	77.5
No moon, clear sky [Dark]	25/26	0.67	0.67	0.82	71.5

Table 3. Comparison of food conversion efficiency and feeding characteristics in studies of some Procellariformes with chicks >5 days posthatch and before prefledging mass recession.

Species	Mean meal[1]	Min. meal[2]	Conv. eff.[3]	% nights fed	Source
Cory's shearwater *Calonectris diomedea*	7.7%	5.7%	73-96%	58%	This study
Christmas shearwater *Puffinus nativitatis*	14.2	13.6	42	86	Ricklefs, 1984
Manx shearwater *Puffinus puffinus*	12.5	13.1	58	75-85	Thompson, 1987
Phoenix petrel *Pterodroma alba*	18.2	16.6	77	59	Ricklefs, 1984
Wilson's storm-petrel *Oceanites oceanicus*	13.4-20.0	-	-	55-84	Croxall, *et al.*, 1988
White-faced storm-petrel *Pelagodroma marina*	13.6	-	-	72	Richdale, 1965
British storm-petrel *Hydrobates pelagicus*	23.2	-	-	82	Scott, 1970; after Croxall, *et al.*, 1988
Leach's storm-petrel *Oceanodroma leucorhoa*	22.0	15.0	92	68	Ricklefs *et al.*, 1985
Swinhoe's fork-tailed petrel *Oceanodroma monorhis*	20.9	14.9	78	56	Lee & Won, 1988
Fork-tailed storm-petrel *Oceanodroma furcata*	19.0	-	-	77	Quinlan 1979, after Ricklefs *et al.* 1985
Madeiran storm-petrel *Oceanodroma castro*	15.0	-	-	47	Allan, 1962
Georgian diving-petrel *Pelecanoides georgicus*	31.0	35.0	35	81	Payne & Prince, 1979

1. Average meal size as % adult mass.
2. Minimum meal size required to maintain constant chick mass (value of SUM when NET = 0, for regression equation NET vs SUM) as % adult mass.
3. Food conversion efficiency calculated by methods described in text.