Conservation implications of variation in diet and dietary specialisation in great skuas

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This thesis is dedicated to my mum and dad for being such amazing parents and friends.

Contents

Summary

1. Great skuas *Catharacta skua* are the only member of the genus *Catharacta* in the northern hemisphere. The UK holds around 60% of the World population with 8,000 breeding pairs.
2. Sustained population growth of the great skua in Scotland during the last century appears attributable to an abundant supply of discards (from commercial fisheries) and sandeels *Ammodytes marinus*. In addition great skuas may scavenge or predate other seabirds and their chicks when other prey is in short supply.
3. Following a decline in sandeels in the 1980s there is some evidence that an increase in predation of seabirds by great skuas may be affecting seabird populations. Future measures to reduce the amounts of fish discarded may result in a further increase in predation by great skuas. This highlights the need to quantify the current impact of great skua predation on seabird populations, and monitor any future change.
4. Accurate assessment of great skua diet is fundamental to this type of research. Many studies have used pellets of indigestible prey to assess diet in skuas and gulls, but have not quantified this technique. Captive great skuas were fed a range of fish and birds to try and understand more fully how pellets reflect diet. Feeding trials showed that skuas fed on a diet of birds produced more pellets than when feeding on fish. Fish species strongly influenced the number of pellets produced as well as the proportion and size of otoliths recovered. The numbers of pellets cast also varied significantly among differing species of bird meals. Field trials revealed that only a small proportion of pellets produced are being sampled. This study highlights the need to carefully validate the use of pellets to assess diet, particularly in a species of conservation concern.
5. The diet of great skuas was estimated based on five different techniques (pellets, prey remains, spontaneous regurgitates, observed feeds and water off-loading) and the results compared. The diet composition based on five sampling techniques in a single year

generally showed a good correlation with one another. However comparing the proportion of the three main prey types estimated by four sampling techniques over three years revealed a significant interactive effect of year and sampling technique on the diet composition. While estimates of diet using different sampling techniques may be broadly comparable, technique dependent biases mean that the advantages and disadvantages of each sampling technique need to be borne in mind before conducting diet studies.

6. A small proportion of great skuas breeding at Hermaness, Shetland exhibit distinct dietary specialisation, feeding almost exclusively upon seabird prey. Around half of these "bird-specialists" defend feeding territories within a section of seabird colony, the remainder foraging away from breeding territories. "Bird-specialists" retained their feeding habit and, if present, territory, between years. Time-budgets revealed that "bird-specialists" with feeding territories spent less time foraging than "bird-specialists" without a feeding territory or skuas feeding predominantly on fish. Results of radio-tracking great skuas for the first time suggest that "bird-specialists" have smaller home ranges than "others". In all years "bird-specialists" show similar productivity to "others", but earlier hatching dates (a good measure of quality in great skuas). While we do not know whether high quality skuas feed on seabirds or that feeding on seabirds advances laying date, hatching early is likely to confer an advantage to "bird-specialists". Non-specialist great skuas experienced a reduction in clutch volume and chick condition during 1999, compared with 1998 – presumably due to a reduction in food availability. "Bird-specialists" did not experience a similar decline in clutch volume and chick condition between years, and showed higher clutch volume and chick condition than "others" in 1999. In addition to changes in clutch volume and chick condition, adult non-specialists showed reduced annual survival, compared with "bird-specialists" over the same period. These results suggest that "bird-specialists" not only have earlier hatching dates in all years, but in certain years also gain an advantage in terms of improved chick condition and adult survival that may have implications for

lifetime reproductive success (LRS). Apparent fitness benefits derived from specialising in bird predation may have conservation implications for seabirds colonies in Shetland.

7. Using a bio-energetics model it is estimated that the great skua population at Hermaness requires 428.9 x 10^6 kJ during 1999. 80% of the energy demanded was required by breeding adults with less than 5% being required by breeding adult "bird-specialists". Combining data on energy requirements and prey composition we estimate that great skuas at Hermaness feed on 69.3 tonnes of fish, 6.9 tonnes of seabirds, 2,5 tonnes of rabbit *Oryctolagus cuniculus* and 0.6 tonnes of goose barnacles *Lepas sp*. The number of seabirds estimated to have been consumed by great skuas was over 11,000, the majority being auks (Alcidae) (71%). While "bird-specialists" made up only 5% of the population they consumed 30% of the seabirds. While the number of seabirds being taken by great skuas is large, the impact on populations is not clear. Despite the large numbers consumed, the impact by great skuas is much less severe than has been reported at other smaller skua colonies. Declines in discarded whitefish may result in an increase in seabird predation, but to an unknown extent.
8. In light of likely changes in food availability and concern about the effect that this might have on great skuas preying on other seabird species, we compare the diet of great skuas at two Shetland colonies in three different years. We also compare the proportion of the great skua population which specialise in feeding upon seabirds at three colonies and among three years. While the main component of great skua diet is variable both within colonies and among years, clear trends in a switch away from discarded fish species have not been observed. Similarly while fish species vary among years and between colonies, there are no clear trends in a switch to larger discards. The species of bird prey in the diet varied between "bird-specialists" and non-specialists, between colonies and among years. A decrease in the proportion of black-legged kittiwakes *Rissa tridactyla* in the diet was compensated for by an increase in either auks (Alcidae) or northern fulmars *Fulmarus glacialis*. A consistent proportion of "bird-specialist" pairs at study plots

suggested no increases among three years. The proportion of "bird-specialist" pairs appears to be related to the size of the great skua colony.

9. Future study requires continued monitoring of great skua diets and further investigation into factors regulating numbers of "bird-specialists" at all major great skua colonies. Integrating data on great skua diet and predation with studies of diet and reproductive performance of other seabird populations may indicate the effect of changes in discarding policy more fully.

Chapter one

General introduction

Introduction

While each chapter in this thesis has been written as an independent piece of research, it is intended that they address specific elements of great skua diets and dietary specialisation. It is hoped that these can be integrated to provide a better understanding of the dynamics between great skuas and the species they prey upon. In this general introduction I will provide a brief historical overview of the great skua, some information on skua taxonomy, recent population level and trends, and some reasons for these changes. I will then go on to outline why this research was started in the first place. Finally I shall go on to introduce each chapter and reasons for their conception.

Skua taxonomy

Skuas belong to the tribe Stercorariinae, part of the much larger family Laridae (Sibley & Ahlquist 1990, Larson & Olsen 1997). They are closely related to the gulls but possess a number of features which make them quite distinct from gulls. Skuas are generally dark plumaged with distinct colour morphs in a number of species, show a unique combination of claws as well as swimming membranes between the toes, hard scutes on the legs, a prominent distal nail on the bill (rhamphotheca) as well as reversed sexual dimorphism. They comprise at least seven species divided into two groups, four large *Catharacta* skuas and three smaller *Stercorarius* skuas. While division of skuas into two genera has been a matter for debate, evidence for treating the two separately is strong. *Stercorarius* skuas are relatively small-bodied, show distinct adult plumage (usually pale bellied with elongated central tail feathers) as well as juvenile plumage (heavily barred throughout) and all three have an Arctic circumpolar distribution and migrate long distances to winter in the southern oceans. By contrast, adult and young of the large-bodied *Catharacta* skuas are similar in appearance, they lack distinctly elongated central tail feathers and breed predominantly on Antarctic or Sub-Antarctic coastlines, with the exception of great skuas in the north Atlantic (Furness 1987, Cohen *et al.* 1997).

There are three species of *Stercorarius* skua, pomarine *S.pomarinus*, Arctic *S.parasiticus* and Long-tailed *S.longicaudus*. They are all taxonomically very distinct from one another, and with the exception of a debatable treatment of two subspecies of long-tailed into nominate *S.l.longicaudus* and *S.l.pallescens*, they are monotypic (Olsen & Larsson 1997). However, on the basis of mtDNA comparisons and ectoparasites, pomarine skua is apparently more closely related to *Catharacta* skuas than the other two *Stercorarius* skuas, possibly as a result of a *Stercorarius* and *Catharacta* pairing in the past (Cohen *et al.* 1997). More recently cladistic analysis of behaviour, genomic and parasitological evidence, support hybridisation as explaining similarities between pomarine and *Catharacta* skuas (Andersson 1999a,b). Furthermore Andersson (1999a) suggests that pomarine should be given the generic name *Catharacta*, or that skuas be placed in a single genera, *Stercorarius*.

The taxonomy of *Catharacta* skuas has been widely debated and is yet to be fully resolved. Devillers (1977), Cramp & Simmons (1983), & Furness (1987) recognise three species; Chilean *Catharacta.chilensis*, south polar *C.maccormicki*, and polytypic brown skua with four subspecies; great *C. skua skua*, brown *C.s.lonnbergi*, Tristan *C.s.hamiltoni* and Falkland skua *C.s.antarctica*. More recently brown skua has been split into two separate species, great, and the polytypic brown (subantarctic skua *C.a.lonnbergi*, Tristan skua *C.a.hamiltoni* and Falkland skua *C.a.antarctica*) (del Hoyo, Elliot & Sargatal 1996, Olsen & Larsson 1997). A split of brown skua into just *C.lonnbergi* ('brown skua') and *C.antarctica* ('southern skua') has also been proposed (Sibley & Monroe 1990). In this thesis I follow the taxonomy of del Hoyo *et al.* (1996) and Olsen & Larsson (1997).

Distribution and status

Of the four species of Catharacta skua, three occur in the southern hemisphere; brown skua *C. antarctica* Chilean skua *C.chilensis* and south polar skua *C.maccormicki*, and great skua in the northern hemisphere. Southern hemisphere skuas breed throughout the southern oceans in Antarctica, southern South America, Falkland Islands, Patagonia, Tristan da Cuhna and Gough island (del Hoyo *et al.* 1996). Great skuas breed in Iceland, the Faroes and northern Scotland, with smaller numbers found in Spitzbergen, Bear Island, Hopen and north Norway (Furness 1987). Of an estimated global population of ≈13,600 breeding pairs, there are 8000 breeding pairs of great skuas in northern Scotland (Lloyd, Tasker & Partridge 1991, del Hoyo *et al.* 1996). The largest colony in the world is at Foula with 2500 pairs in 1987, followed by Hoy, Orkney with 1573 occupied territories in 1982 (Lloyd *et al.* 1991) and the third largest colony is at Hermaness, Shetland, with ≈650 pairs in 2000 (based on Rodger 2000). Smaller numbers are found throughout Orkney and Shetland, with fewer still in the Western Isles and Sutherland, although there are increasing large colonies at St Kilda (Phillips *et al* 1999a) and Handa, Sutherland (R.W.Furness *pers comm*).

Population trends and reasons for change

In keeping with many other north Atlantic seabirds, the great skua has shown a marked increase in breeding numbers over the last century (Furness 1987, Lloyd, Tasker & Partridge 1991). The current great skua population has been reached from only around 25 pairs in Scotland at the beginning of the 20th Century (Furness 1987). After initial rapid growth at the source population in Shetland, rates of increase slowed, but with new colonies being established in Orkney and the Outer Hebrides from Shetland recruits (Furness 1987). Currently the population in Shetland appears to have become approximately stable with little expansion (Sears *et al.* 1995), whereas colonies on the Outer Hebrides are continuing to increase (Phillips *et al.* 1999a).

The reasons for these population changes in skuas as well as other seabirds, are thought to be a combined result of a cessation in persecution at the turn of the century and changes associated with developments in commercial fisheries. The activity of commercial fisheries has proved advantageous to seabirds in a number of ways. Reductions in the stocks of herring *Clupea harengus* and mackerel *Scomber scombrus* may have resulted in increases in the stock of ecological competitors like sandeel *Ammodytes marinus* and sprat *Sprattus sprattus* (Anderson & Ursin 1977). In addition to this, quantities of discarded undersize fish and offal have provided seabirds with access to a plentiful and easily accessible novel food resource (Furness, Hudson & Ensor 1988, Hudson & Furness 1988, Dunnet *et al.* 1990, Oro & Ruiz 1997, Garthe *et al.* 1999). The combination of a massive increase in abundance of small, shoaling and lipid-rich fish, like sandeels, and readily available discards will have assisted seabirds to proliferate.

In addition to reduced persecution and an increased availability of sandeels and discards, great skua success during this period was also greatly enhanced by their ability to exploit a wide range of foods. They are able to scavenge successfully at fishing boats, steal fish from other seabirds, fish for sandeels and predate or scavenge other seabirds, their eggs and chicks (Furness 1987).

Impact of changes in fisheries policy

In order to maintain sustainable fisheries, reduce waste and limit environmental damage a reduction in discarded fish is desirable. Current and future measures to reduce fishing effort and general discards, as well as increasing the mesh size used in fishing gears may have important implications for scavenging seabirds. Reductions in discards and offal are likely to effect seabirds in a number of different ways. An overall reduction in the quantity of fish discarded may result in increased competition between bird species that regularly scavenge at fishing boats. Large species like northern gannets *Morus bassanus* and great black-backed gulls *Larus marinus* are more successful competitors for discards compared with smaller species like great skuas, fulmars *Fulmarus glacialis* and black-legged kittiwakes *Rissa tridactyla* (Hudson & Furness 1988). These less effective scavengers may suffer food shortages directly. Also with increased competition, rates of kleptoparasitism may increase and further disadvantage smaller, weaker species (Tasker, Becker & Chapdelaine 1999). In the event of an increase in mesh size the amounts of smaller discards are likely to decrease (Furness 1992), which will lead to a reduction in feeding opportunities for the smaller seabird species. Also because young birds tend to be less effective at foraging (Greig, Coulson & Monaghan 1983), these age groups of all species may experience a reduction in food availability.

Reductions in the overall quantity of discards and increased competition may result in seabirds switching their diet or suffering declines in reproductive success or numbers. Herring gulls *Larus argentatus* in Canada responded to a reduction in food availability associated with a long-term fishery moratorium by predating more eggs and chicks of conspecifics (Regehr & Montevecchi 1996). Closure of fisheries in Mediterranean colonies caused Audouin's gulls *L.audouiini* and yellow-legged gulls *L.cacchinans* to increase aggressive interactions and kleptoparasitism between each other (Gonzalez-Solis 1997, Oro, Pradel & Lebreton 1999). Similar declines in fishing activity which reduce the availability of discards, have manifested in a depression of reproductive success or colony size for several species of larids (Noordhuis & Spaans 1992, Oro, Bosch & Ruiz 1995, Oro 1996, Oro, Jover & Ruis 1996).

Response of great skuas to fluctuations in food supply

A dramatic decline in the availability of sandeels in waters around Shetland during the 1980s resulted in large numbers of seabirds suffering a reduction or complete failure of reproductive output (Monaghan *et al.* 1989, Monaghan 1992). While great skuas suffered a reduction in reproductive output over the same time period (Hamer, Furness & Caldow 1991), they were able to buffer the effects somewhat by increasing the amount of bird prey in their diet (Hamer *et al.* 1991). Subsequently sandeel stocks have recovered somewhat but the percentage of great skuas taking other seabirds has remained relatively high (Furness 1997).

Concern about the impact of great skuas on seabird populations in Shetland began to be expressed by researchers throughout Shetland. Changes in the distribution and population of certain species like black-legged kittiwakes were thought in part to have been caused by predation by great skuas (Heubeck & Mellor 1994, Heubeck, Mellor & Harvey 1997, Heubeck *et al.* 1999). While the authors accept that the role of great skuas in these declines is largely circumstantial, regular observations of heavy predation by great skuas on black-legged kittiwakes, including some skuas specialising in feeding almost exclusively on seabirds (Anderson 1976, Boulinier 1992), the evidence is certainly compelling. At another large great skua colony, St Kilda, Outer Hebrides, concern has also arisen about the impact of great skuas on seabird populations. The continued growth of the skua population (Phillips *et al.* 1999a) as well as an apparently higher level of bird prey in the diet compared with skuas on Foula (Phillips *et al.* 1997), raised concerns that seabirds may be taken in large numbers at St Kilda. Using a bio-energetics model, Phillips, Thompson & Hamer (1999b) estimate that over 40,000 seabirds may be consumed by great skuas at St Kilda – a number which suggests that great skua could have a considerable impact on the internationally important seabird populations there.

Aims of the thesis

The current level of great skua predation on Shetland is not known. Given the circumstantial evidence currently available, there is a clear need to quantify the impact of great skuas on seabird populations. If changes in discarding policy further reduce the availability of this important food resource for great skuas, diet switching may occur and further increase predation pressure on Shetland's seabirds.

In this thesis I aimed to develop techniques for monitoring the impact of great skua predation as well as investigating aspects of their foraging behaviour that may influence seabird predation. Using these findings a quantitative assessment of seabird predation was made. Over the three years of this study any evidence of dietary switching was monitored. Although I have aimed to set this research into a framework of ecological theory and principles, my primary objective has been to increase the understanding of great skua natural history in the context of the conservation of seabird biodiversity.

Pellets are widely used in the study of great skua diet and provide a very convenient dietary sampling tool for monitoring this. In **Chapter 1** I studied the rate and quantity of pellets produced by captive great skuas which were fed a wide range of foods. I also investigated the rate at which otoliths errode in the gut of skuas, as these are important indicators of the fish component of their diet.

Chapter 2 continues the study of diet in a great skua colony in Shetland. Using five different techniques I investigate possible error and biases associated with a range of different dietary sampling techniques. The aim is to help researchers to select an appropriate sampling tool for use in future monitoring.

Great skuas that specialise in taking almost exclusively bird prey were first noted at Hermaness by Boulinier (1992). Other specialist *Catharacta* skuas and gulls are important predators of seabirds, and several studies have shown that they gain a fitness benefit from preying solely on seabirds. In **Chapter 3** I compare the reproductive and foraging performance (including radio-tracking great skuas for the first time) of great skuas which specialise in taking seabird prey, with other members of the population.

Despite concerns expressed about the impact of great skuas on seabird populations, there are currently no quantitative estimates of their impact in Shetland. Combining data on dietary studies as well as aspects of dietary specialisation, in **Chapter 5** I use a bioenergetics model to calculate the quantity of different prey consumed by great skuas at Hermaness during a single breeding season. This will not only be the first quantitative estimate of seabird predation at Hermaness, but also provide a baseline to measure any potential effect of changes in discarding practices.

Temporal and colony differences in great skua diet formed the basis of **Chapter 6**. Sampling data from two colonies in three separate years, I compare how the broad diets as well as bird and fish prey vary between the two colonies, and among the three years. Only by constant monitoring of diet can changes in food availability or preferences be detected. Differences among colonies may also be highlighted here. I also compare the degree of dietary specialisation in three colonies at a single year to investigate how this trait is maintained at different colonies.

In the General Discussion in **Chapter 7** an attempt has been made to bring together the main points of the thesis and provide an overview of the current relationship between great skuas and their prey populations. I then go on to discuss how the situation may change with time and possible management measures that could be taken to aid the conservation of Shetland's seabirds.

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Chapter two

Pellets as indicators of diet in great skuas *Catharacta skua*

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Several studies have attempted to answer questions about pellet production by conducting feeding trials with captive seabirds (Duffy *et al.* 1983, Johnstone *et al.* 1990, Brugger 1993). Some on Cormorants and Shags *Phalacrocorax* sp have focussed on the identity and number of pellets produced per fish fed and on rates of otolith wear and relation to fish size (i.e. Zijlstra & Eerden, 1995). Few studies have investigated differences in pellet production from a range of different, non-fish, prey types.

Great Skuas *Catharacta skua* breeding in Scotland have increased dramatically in numbers over the past 50 years, probably because of their ability to exploit a wide range of food types including fish, invertebrates, mammals and seabirds (Furness & Hislop 1981, Furness 1987, Furness 1997, Phillips *et al.* 1997). Their predation impact on seabird colonies in northern Scotland (Heubeck *et al.* 1997) has heightened the need to monitor the diet of skuas. Pellets provide a convenient method for sampling Skua diet but there is clearly a need to understand more fully how regurgitated pellets relate to ingested prey.

Captive Great Skuas were used to establish how pellets reflect prey intake; to quantify biases of different food types; to assess how long after a meal pellets are produced and the extent to which fish otoliths are digested. Feeding trials with wild birds in Shetland were conducted in an attempt to place these captive studies into a field context.

Six Great Skua chicks were taken, under licenses from Scottish Natural Heritage and The Home Office, from Hoy, Orkney (58° 50' N, 04° 45' W), and housed individually in Home Office approved aviaries (3m×4m×3m) with fresh water available *ad libitum*. Growing chicks were fed approximately 150g of Sprats *Sprattus sprattus* daily with a vitamin supplement. Once chicks had completed growth and achieved a stable mass, they were fed a particular fish species (Haddock *Melanogrammus aeglefinus*, Whiting *Merlangius merlangus*, Sprat, Sandeel *Ammodytes marinus*, Herring *Clupea harengus* or Mackerel *Scomber scombrus*) daily for 30 days. Pellets were removed daily to prevent repeat observations. Prior to feeding with Haddock one otolith was removed before it was fed to a Skua. All otoliths in pellets were retained and measured, in order to compare lengths in the pellet with the matching intact otolith removed from the same fish.

For the remainder of the study, they were fed 25 Auks *Alcidae*, 12 Terns *Sternidae*, 9 Gulls *Laridae*, 8 Storm-petrels *Hydrobatidae*, 5 Skuas *Stercorariidae*, 5 small passerines and single Gannet *Morus bassanus*, Mallard *Anas platyryhnchos* or Snipe *Gallinago gallinago* for ten days. The Skuas were fed meals of whole bird corpses each day. Each meal was available for 24 hours, after which time any remains were removed and a new meal presented. Meals of small bird species consisted of more than one individual to match the mass of between 50 – 125g (after Furness & Hislop, 1981). Following Phillips *et al.* (1999) larger bird prey was assumed to contain 65% of digestible material, but for species swallowed whole meals were assumed to be equivalent to adult mass of that species. Most carcasses were whole and small birds were presented soaked in water to assist the skuas to swallow them whole. The time of the first pellet was noted at six, 24 and 30 hour periods following feeds.

Six pairs of Great Skuas breeding at Hermaness NNR, Shetland (60° 50'N, 0° 52'W), with large young (four-five weeks old), were fed a range of fish species daily for 13 days. Each fish had a single otolith removed and replaced with a similar sized coloured plastic marker, colour coded to date. Great Skuas aggressively defend breeding territories, so that any pellets found within a territory can be assumed to belong to the resident pair. Territories were checked daily and all pellets with or without markers were noted and destroyed to prevent double counting.

Data analyses was undertaken using SPSS Version 7.5.1 (1996). Alpha level of significance was 0.05 for all tests.

Captive Skuas showed no changes in behaviour during the period of the study with no significant change in weight between the beginning (mean ± SD = 1148g ± 124g) and the end (1156g ± 105g) of the study (paired sample t-test; $t_5 = 0.241$, NS). All birds readily produced pellets following a meal of bird or Gadid fish and we found no evidence of differences among individuals in pellet production (Kruskal Wallis one-way ANOVA; $\chi^2_5 = 6.84$, NS). When fed birds significantly more pellets were produced than when fed Mackerel, Herring and Gadid fish ($\chi^2_6 = 100.83$; $p<0.001$) (Table 1). Birds fed Sprat and Sandeel did not produce any pellets. However when fed Mackerel, Whiting or Haddock they produced approximately one pellet per feed with no significant differences among the three species ($\chi^2_2 = 0.37$; NS). Birds fed Herring produced fewer pellets per fish than when fed on Mackerel, Whiting or Haddock (χ^2_1, Yate's Correction for 1 d.f, = 6.5; $p<0.05$). The recovery rate of otoliths after meals of Whiting (n=19) or Haddock (n=32) was almost 96%. There was no difference in mean length between dissected left otoliths (mean ± SE = 11.98 ±0.32) and otoliths found in pellets of Haddock (11.94 ±0.34) (paired-t $_{22} = 0.07$, NS).

Table 1. The number of pellets produced from meals of bird and fish. Note that for small bird species a meal may consist of more than one individual. Expected values are presented along with the difference between observed and expected values. Note the gross underestimation of pellets produced by fish compared to all birds.

Prey type	**No. meals**	**No. pellets (observed)**	**No. feeds/total feeds x total no. pellets (expected)**	**Observed - expected**
Great Skua chick	4	11	6.2	4.8
Gannet	1	4	1.6	2.4
Large Gull	5	13	7.8	5.2
Storm-Petrel	6	28	9.3	0.7
Auk	24	42	37.3	4.7
Tern	5	24	7.8	16.2
Passerine	1	4	1.6	2.4
Mallard	1	4	1.6	2.4
Herring	17	6	26.4	-20.4
Mackerel	12	10	18.6	-8.6
Whiting	20	20	31.0	-11.0
Haddock	32	32	49.7	-17.7
Total	134	208	208	-

The number of pellets produced per meal was highly variable (Table 2), the differences being significant ($\chi^2_4 = 21.67$; $p<0.001$), Auks were grossly under-recorded and Storm-Petrels over-recorded. Meals of birds eaten whole resulted in the production of significantly more pellets than meals of birds that were not (χ^2_1, Yate's Correction for 1 d.f, = 22.12; $p<0.001$). The mean number of pellets produced per individual bird eaten was calculated separately from pellets produced per meal (Table 3). The bulk of the pellets were produced between six and 24 hours (53%). Over 38% were produced within six hours and almost 9% by between 24 and 30 hours.

During the field trial a total of 27 pellets were collected, 20 being of whitefish. From 76 fish fed to the six pairs of Skuas, eight (12.3%) of the plastic markers were recovered in pellets. No markers were discovered in faeces. Only one otolith was found paired with a plastic marker, and was identical to the otolith removed from the fish.

Table 2. Pellet production and the number of meals of only bird prey. Note that for small bird species a meal may consist of more than one individual. Prey categories are collapsed into the same to cells to equate with prey types identified in field trials (as in Furness 1997, Phillips *et al.* 1999).

Prey type Observed	**Number of meals**	**Number of pellets (observed)**	**Number of feeds/total feeds x total no. pellets (expected)**	**- expected**
Great Skua chick	4	11	10.5	0.5
Gull/Tern	16	47	42.2	4.8
Storm-Petrel	6	28	15.8	12.2
Auk	24	42	63.4	-21.4
Other (Gannet, Mallard, Passerine)	3	12	7.9	4.1
Total	53	140	140	-

Table 3. Mean numbers of pellets produced per bird. These data differ from those presented in contingency tables since they represent pellets produced per individual bird and not per meal of bird.

	Pellets produced per bird		
	n	**Mean**	**se**
Great Skua chick	4	2.5	0.29
Large gull+Fulmar	10	2.5	0.34
Small Gull	6	1.7	0.56
Tern	12	2.0	0.17
Storm-Petrel	11	2.5	0.4
Auk	24	1.8	0.18
Gannet+Mallard	2	4	0

Differences in the numbers of pellets produced when different fish species are eaten have been shown in a number of other seabirds (Duffy & Laurenson 1983, Johnstone *et al.* 1990, González-Solís *et al.* 1997). It is not surprising therefore that the more fragile otoliths and bones of Sandeels, Sprat and to a lesser extent Herring, are more susceptible to wear in the digestive tract of Great Skuas than the more robust hard parts of the larger fish species. Otoliths from Mackerel did not occur in Great Skua pellets suggesting that this species will be under-estimated in field studies. The lack of any significant decrease in the length of Haddock otoliths in pellets compared to those taken from fresh fish contrasts with the high degree of otolith wear found in captive feeding trials of Cormorants (Duffy & Laurenson 1983, Johnstone *et al.* 1990, Zijlstra and Eerden 1995). The reasons for this are not clear but are most likely explained by differences in the rate of pellet production.

Pellets clearly suggest a bias towards bird rather than fish in the estimation of prey in the diet of Skuas, probably due to the resilience of feathers to digestion. Another important factor influencing pellet production appears to depend upon the proportion of the bird prey ingested. By consuming whole Storm-Petrels and small young, pellets may over-estimate these prey compared with those prey plucked or torn apart. While our results were not quite statistically significant, an increase in the intake of indigestible material appeared to result in the more rapid initial production of pellets. This mirrors the situation in Owls that show a decrease in meal to pellet interval when the proportion of indigestible material increases (Duke & Rhoades 1977).

The low recovery rate of markers in the field study suggests that a large number of pellets are going undetected. Plastic markers are assumed to behave in a manner similar to other indigestible material since Warner (1981) reports the wide usage of plastic markers in diet studies and plastic is regularly found in Skua pellets (Ryan & Fraser 1987). So large numbers of pellets are either being deposited away from breeding sites or simply going unnoticed within the breeding territory.

A major assumption in this study is that pellet production in captive birds is an appropriate model for pellet production by wild birds. There are a number of factors which may effect how pellets are produced. Zijlstra & Eerden (1995) showed that captive Cormorants fail to produce pellets following stressful events due to calcium excretion. However our birds were kept in constant conditions, showed no dramatic changes in pellet production over time and since the degree of wear was minimal in Haddock otoliths at least, our birds did not appear to be reacting in the same as way as the Cormorants in that study. Other confounding factors such as lower metabolic rate of captive birds resulting in increased retention time or a reduction in gut size (Hilton *et al.* 2000) cannot easily be corrected for. It is also possible that wild birds may ingest different amounts of feather when feeding on bird prey than our captive birds, especially given that wild birds have probably learned to handle prey more effectively.

Our preliminary values of pellet production presented here would alter bio-energetics model outputs (i.e. Phillips *et al.* 1999) and afford a less severe view on the impact of Great Skua predation on seabird populations. Where diet studies based on pellets are being used to influence issues of conservation concern they clearly need to be carefully validated.

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Chapter three

Assessing the diet of great skuas *Catharacta skua* using five different techniques

Abstract

In this study we assessed the diet of wild great skuas using five techniques (pellets, prey remains, spontaneous regurgitates, observed feeds and water off-loading). The estimates of diet derived from each sampling technique during a single breeding season generally correlated well with one another. However comparing the estimated proportions of the main prey types using four techniques among three years revealed significant and interactive effects of sampling technique and year. It is easy to collect large samples of pellets and remains but they over-estimate the amount of indigestible material in the diet. Prey remains provide a high degree of taxonomic accuracy but may underestimate prey swallowed whole or underestimate large carcasses. Spontaneous regurgitates are useful for assessing chick diet but are difficult to collect systematically and may also overestimate easily egested prey. Observed feeds are time consuming to collect and over-record easily identifiable prey. Water off-loading provides unbiased estimates of chick diet but may stress birds and is labour intensive. While different sampling techniques provide broadly similar estimates of diet, technique dependent biases highlight the need for careful selection of an appropriate sampling method for specific studies.

Introduction

Diets of seabirds may be investigated using a wide range of techniques, but each sampling method is open to certain biases. Regurgitated pellets, prey remains and analysis of faeces typically result in the under estimation of prey with soft body parts; observed feeds may be biased towards large distinctive prey, and certain prey may be more likely to be spontaneously regurgitated than others (Duffy & Jackson 1986). A number of studies have used a range of integrated sampling methods to assess the level of these potential biases (e.g. Harris & Wanless 1993, Brown & Ewins 1996, González Solís *et al.* 1997, Bearhop *et al.* 2001). In each case, the authors have advocated the cautious use of data derived from particular techniques to assess diet, and further systematic review of dietary assessment techniques.

A dramatic increase in the British population of great skuas *Catharacta skua* has prompted research into their diet and feeding ecology (Furness 1979, Furness & Hislop 1981, Hamer, Furness & Caldow 1991, Phillips *et al.* 1997a, Phillips, Thompson & Hamer 1997b) and investigations into interactions with commercial fisheries and other seabird populations (Furness 1996, Phillips, Thompson & Hamer 1999). In these studies, diet was analysed using pellets regurgitated by adults and spontaneous regurgitates of proventriculus contents by chicks, to reflect the diet of adult and young skuas respectively. Other studies of the diet of *Catharacta* skuas in the southern hemisphere have concentrated almost exclusively on the use of pellets and prey remains (Ryan & Moloney 1990, Zipan & Norman 1993, Mund & Miller 1995 and Moncorps *et al.* 1998). However Mund & Miller (1995) also investigated faecal samples. In contrast, Pietz (1987) used a combination of direct feedings, courtship feedings, chick feeds and chick regurgitates, but did not make detailed comparisons between these different techniques.

In this study, we used a range of different dietary assessment techniques to investigate the diet of great skuas. We aimed to investigate biases in dietary assessment according to methods used, and investigated age and time dependence in skua diet. The integration of different sampling techniques, as well as identification criteria to give a more accurate quantitative assessment of diet is discussed.

Methods

Diet was assessed using five standard sampling techniques: regurgitated indigestible material in pellets, prey remains, spontaneous regurgitates, observed courtship/chick feeds and water offloading by gastric lavage.

Data were collected from breeding birds at two large great skua colonies in Shetland, Scotland, both of which are National Nature Reserves managed by Scottish Natural Heritage: Hermaness NNR (60^0 50'N, 0^0 52'W) and Noss NNR (60^0 08'N, 1^0 00'W). Diet was sampled using pellets, remains, spontaneous regurgitates and observed feeds throughout the breeding season (May to September) during 1998, 1999 and 2000. Water offloading was performed, under Home Office Licence, on chicks from June to August 2000.

PELLETS & REMAINS

Pellets consist of indigestible body parts that are coated in mucus and then regurgitated. Prey remains comprised whole animal carcasses caught on or near the territory, or fish regurgitated whole and subsequently picked clean by the chicks or adults. Pellets and remains were collected from 95 marked territories every five to ten days throughout the breeding season. A further 100 and 61 territories were sampled randomly at Hermaness and Noss respectively. Chicks do not produce pellets (Votier unpublished data) and thus pellets give a representation of adult diet only. They were assigned to a prey category in the field, as described by Furness (1997), and then removed.

Fish pellets were classified on the basis of bone structure and general colouration but in addition any otoliths present in pellets were retained, stored dry and assigned to species later. They were also measured to the nearest 0.5mm to calculate fish size (Härkönnen 1986). During

2000 we took a random sample of fish vertebrae from pellets which were collected during the breeding season and these were retained dry for later identification using Watt, Pierce & Boyle (1997).

Pellets and remains of birds were classified to the lowest possible taxon, on the basis of feathers (colour, size, shape and smell) as well as any limbs or skulls. However in cases where specific identification was not possible, pellets were assigned to broader categories such as gull/tern (*Laridae/Sternidae*) or Auk (*Alcidae*). In most cases pellets contained the remains of a single prey type but where multiple prey were discovered each prey type was recorded.

SPONTANEOUS REGURGITATES

Both adult and young skuas may regurgitate stomach contents when captured and handled. During the course of three breeding seasons (1998-2000) a total of c600 young and 60 adult great skuas were handled (for ringing and measuring), and all spontaneous regurgitates were identified to lowest possible taxon.

OBSERVED FEEDS

Male skuas feed their mate prior to egg-laying, during incubation and to a lesser extent during chick rearing (Furness 1987). These feeds consist of prey regurgitated onto the ground where it is accepted by the female. By observing through a telescope from outside the territory many of these prey items can be identified. Adults feed young either by regurgitating a meal onto the ground in a similar way or for small chicks by carefully feeding them small morsels of food. In both cases it is sometimes possible to identify the food item. During 130 hours of feeding watches (representing 1637 bird-hours), observed feeds were noted and, where possible, identified to lowest possible taxon.

WATER OFFLOADING BY GASTRIC LAVAGE

Stomach contents of 168 skua chicks were sampled on their breeding territories. A plastic catheter was gently inserted into the stomach and water at ambient temperature was introduced to the digestive tract, until water escaped from the sides of the bill. The chick was then inverted over a plastic container and the rib cage and oesophagus gently massaged to induce regurgitation. Only one chick was sampled from each territory visited, and on only one occasion per chick.

Statistical analysis was performed using contingency tables and Fisher's Exact tests for categorical data. Where one fifth of the expected values were less than five, cells were collapsed (Fowler & Cohen 1996). Due to multiple tests performed for Pearson correlations, alpha was altered using a Bonferroni correction (0.05/number of comparisons).

The interactive effect of sampling technique and year was investigated using multi-dimensional contingency tables in logit loglinear analysis (Norušis 1999) with prey category as the dependent variable and sampling regime and year as factors.

Results

The numbers of samples and percentages of prey items found by each different sampling method during 2000 are presented in Table 1. During 2000, pellets were by far the most abundant sampling unit with 1441 collected. Remains were less abundant than pellets, providing 287 samples. As well as 120 food samples obtained by water offloading, a further fourteen samples contained only fragments of vegetation. In addition to this, 34 of the chicks sampled produced no food items when their stomachs were flushed, suggesting an empty stomach (but see Discussion). Adult skuas are regularly observed pulling at sphagnum and grass as part of their nest maintenance and chicks were observed pecking at flower heads. This material seems likely to be incidental in the digestive tract of skua chicks and was not considered to be food. The number of spontaneous regurgitates from chicks was relatively low (9) but even lower for adults with only 5 regurgitates collected. Only small numbers of chick feeds (18), or adult courtship feeds were observed (6) with a further 16 being unidentifiable. Observed feeds were collected over a considerable time period (see Methods), making this was the most labour-intensive sampling method.

Table 1. Total numbers of great skua *Catharacta skua* dietary items from 2000. Totals exclude unidentified prey from observed feeds and vegetation collected from the stomachs of young skuas. WF = whitefish, SE = sandeel (*Ammodytes sp.*).

	Pellets		**Remains**		**Water off-loading**		**Observed feeds**		**Spontaneous regurgitates**	
	Number		Number		Number		Number		Number	
WF	751	52.1%	185	64.5%	79	65.8%	19	79.2%	11	78.6
BIRD	535	37.1%	74	25.8%	16	13.3%	3	12.5%	0	0.0
Mammal	124	8.6%	26	9.1%	2	1.7%	1	4.2%	0	0.0
Invert	19	1.3%	0	0.0	1	0.8%	0	0.0	1	7.2%
SE	4	0.3%	0	0.0	1	0.8%	0	0.0	0	0.0
Egg	4	0.3%	0	0.0	5	4.2%	0	0.0	0	0.0
Herring/ Mackerel	3	0.2%	2	0.7%	13	10.8%	1	4.2%	2	14.3
Other fish	1	0.1%	0	0.0	3	2.5%	0	0.0	0	0.0
Total	1441		287		120		24		14	

SEASONAL EFFECTS

Analysis of pellets sampled at ten day periods from 1st June to the end of July revealed that the proportions of the three main prey categories differed significantly during 1998 (χ^2_{10}=44.0, $p<0.01$) and 1999 (χ^2_{10}=42.9, $p<0.01$), but not during 2000 (χ^2_8=4.05, $p>0.08$). The change in the proportion of prey during 1998 & 1999 (Figure 1 A & B) was largely due to an increase in the proportion of bird pellets in the diet as the breeding season progressed. No similar increase in bird prey was observed during 2000, although sampling did cease ten days earlier than in 1998 & 1999.

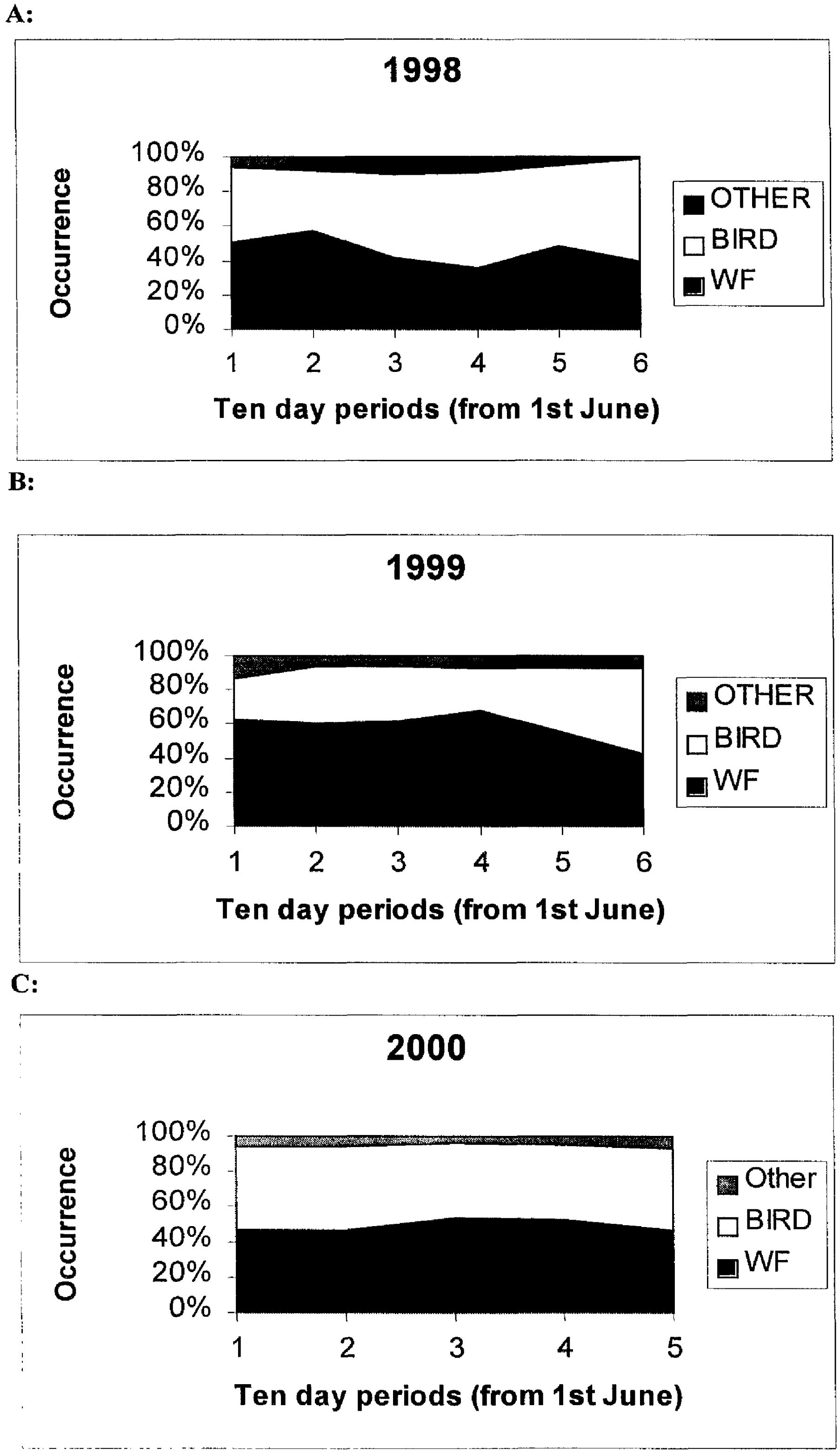

Figure 1. Relative proportions of three main prey categories found in the pellets of adult great skuas during three breeding seasons, 1998, 1999 & 2000. WF = whitefish. During 1998 & 1999 the proportions of the three prey categories differed significantly among ten days periods throughout the breeding season, there was no significant seasonal effect during 2000.

COMPARING FIVE SAMPLING METHODS

Using data pooled from 2000 only (Table 1), we compared the proportion of different dietary items as estimated by the five sampling techniques. Once the data had been arcsine transformed, Pearson correlations revealed that the results of all sampling regimes were strongly correlated with one another (Table 2). Only the relationship between pellets and spontaneous regurgitates was not statistically significant, though with *r*=0.76 this lack of statistical significance may be attributed to small sample size for spontaneous regurgitates.

Table 2. Results of comparisons between the proportion of dietary items as identified by five techniques. Pearson correlations were performed on arcsine transformed data. Due to multiple comparisons, standard alpha level of significance (0.05) was divided by the number of comparisons (4) and set to 0.0125.

	Pellets	**Remains**	**Water off-loading**	**Spontaneous regurgitates**	**Observed feeds**
Pellets	-	r=0.96 n=9 p<0.001	r=0.87 n=9 p=0.002	r=0.76 n=9 n.s.	r=0.87 n=9 p=0.002
Remains	-	-	r=0.97 n=9 p<0.001	r=0.90 n=9 p=0.001	r=0.97 n=9 p<0.001
Water off-loading	-	-	-	r=0.97 n=9 p<0.001	r=0.99 n=9 p<0.001
Spontaneous regurgitates	-	-	-	-	r=0.97 n=9 p<0.001
Observed feeds	-	-	-	-	-

COMPARISON OF FOUR SAMPLING TECHNIQUES IN THREE YEARS

Using logit log-linear models for multi-dimensional contingency tables we tested the null hypothesis that the effect of year and sampling regime on the proportion of the three main prey types (whitefish, bird and "other") (Table 3) were mutually independent of one another. However only the fully saturated model including the interaction between year and sampling regime was an adequate fit for the data ($\chi^2_{12}=32.8$, $p=0.001$). Therefore year and sampling regime had significant and interactive effects on estimates of prey composition.

Annual variation in diet as detected by pellets was however reasonably slight among years, the only apparent change being an increase in the amount of whitefish recorded during 1999. Remains showed higher annual variation than pellets, particularly reflected in a dramatic increase in the proportion of bird remains in 2000. Observed feeds showed similar trends among years although small sample sizes in 1999 resulted in bird and other being unrecorded. Spontaneous regurgitates showed the least consistent estimates of annual diet compared to other methods. Comparing between sampling regimes, pellets tended to estimate lower proportions of whitefish prey and higher proportions of bird prey than in all the other techniques.

Table 3. Numbers of three main prey categories of great skuas *Catharacta skua* obtained from four different sampling regimes during 1998, 1999 & 2000.

Year	Prey	Pellets		Remains		Observed feeds		Spontaneous regurgitates	
1998	WF	559	48.7%	138	82.1%	19	86.4%	36	94.7%
	Bird	515	44.9%	23	13.7%	2	9.1%	0	0.0
	Other	74	6.5%	7	4.2%	1	4.6%	2	5.3%
	Total	1148		168		22		38	
1999	WF	559	58.5%	169	88.5%	7	100%	23	69.7%
	Bird	323	33.8%	15	7.9%	0	0.0	1	3.0%
	Other	73	7.6%	7	3.7%	0	0.0	9	27.3%
	Total	955		191		7		33	
2000	WF	751	52.1%	185	64.5%	19	79.2%	11	78.6%
	Bird	535	37.1%	74	25.8%	3	12.5%	0	0.0
	Other	155	10.8%	28	9.8%	2	8.3%	3	21.4%
	Total	1441		287		24		14	

ADULT DIET BASED ON PELLETS & REMAINS

Using data from 2000 only (Table 1) we found that the bulk of the prey consumed by adult great skuas at Hermaness and Noss was "whitefish" (predominantly gadids), making up over 52% of pellets and 65% of prey remains. "Bird" was the next most frequently recorded prey item making up 37% and 26% of pellets and prey remains respectively. "Mammals" made up between 8 & 9% for both pellets and remains, with the remaining prey items ("other") accounting for around 2.2% of pellets but not found as remains. Relative numbers of prey types were significantly different between pellets and remains ($\chi^2_3=21.77$, $p<0.001$). Pellets under-represented fish in the diet and over-represented bird in the diet compared with remains.

Variation in bird species consumption

Within the "bird" category many pellets and remains could be identified to a lowertaxon. Their composition is shown in Table 4. The effect of sampling technique (pellets or remains) on proportions of different bird prey estimated in the diet was significant ($\chi^2_3=19.69$, $p<0.001$). Pellets suggested a much greater proportions of auk, and much lower proportion of gull/tern and "other" in the diet than remains.

Table 4. Numbers of prey remains and regurgitated pellets of birds eaten by great skuas *Catharacta skua* on Shetland 1998-2000. 'Other' represent gannet *Morus bassanus*, great skuas and a single storm petrel *Hydrobates pelagicus*.

	Pellets Number		Remains Number	
Auk	83	51.2%	14	25.0%
Gull/tern	54	33.3%	31	55.4%
Fulmar	23	14.2%	6	10.7%
Other	2	1.2%	5	8.9%
Total	162		56	

Fish species

Using pellets collected during 2000 we were able to identify fish species to broad categories based on the use of bones and otoliths or vertebrae (Table 5). There was a statistically significant difference in the numbers of fish types determined by the two identification techniques (χ^2_2=88.3 $p<0.01$) - bones/otoliths grossly under-represent mackerel and over-represent gadid fish compared with vertebrae.

Table 5. Numbers of fish types identified from great skua *Catharacta skua* pellets collected during 2000 breeding season only, using two techniques -'Bones/otoliths' from Furness (1997) and 'vertebrae' from Watt *et al.* (1997).

	Bones/otoliths		**Vertebrae**	
Mackerel	0	0%	41	36.2%
Gadidae	200	96.6%	66	58.7%
Clupeidae/Ammodytidae	7	3.4%	6	5.3%
Total	207		113	

DIET BASED ON SPONTANEOUS REGURGITATES AND OBSERVED FEEDS

Estimates of diet, collected during 2000, using spontaneous regurgitates and observed feeds are presented separately for adult and young great skuas in Table 6.

Adult diet

Due to the small sample sizes of spontaneous regurgitates and observed feeds from adults, comparisons between these techniques were only possible by collapsing contingency tables into two dietary categories – "whitefish" and "other". Using Fisher's Exact tests we detected no difference in diet of adults (p=0.57) comparing between spontaneous regurgitates and observed feeds.

Comparing the diet of adults based on pellets, remains and spontaneous regurgitates & observed feeds combined we found that the estimates of the proportions of "whitefish" and "other" were significantly different between the three sampling techniques ($\chi^2_2=15.70$, $p<0.01$).

Chick diet

Comparing the estimates of chick diet using spontaneous regurgitates and observed feeds revealed no significant differences (Fisher' Exact p=0.53).

Do adult and chick diet differ?

The diet of adults and chicks could be compared using only data on spontaneous regurgitates and observed feeds. Chicks were fed relatively more whitefish than taken by adults and less "other" foods (Fisher's Exact (two-tailed) p=0.015).

Table 6. Estimates of diet composition of adult and young great skuas using spontaneous regurgitates and observed feeds collected during 2000.

	Spontaneous regurgitates				**Observed feeds**			
	Adult		Young	%	Adult	%	Young	%
WF	2	40%	9	100%	4	66.7%	15	83.3%
Bird	0	-	0	-	2	33.3%	1	5.6%
Mammal	0	-	0	-	0	-	1	5.6%
Invert	1	20%	0	-	0	-	0	-
Herring/mackerel	2	40%	0	-	0	-	1	5.6%
Total	5		9		6		18	

WATER-OFFLOADING

Comparing estimates of chick diet from water off-loading (Table 1) with spontaneous regurgitates and observed feeds (Table 6) showed that the differences were statistically significant ($\chi^2_2=6.5$, $p<0.05$). Water-offloading estimated a much higher proportion of "other" prey items, predominantly bird and herring/mackerel.

Discussion

COMPARISON OF ALL SAMPLING TECHNIQUES

Broad comparisons of the different sampling techniques reveal a high degree of agreement with one another. Therefore it seems that on a broad scale each sampling method provides a similar assessment of diet. The lack of a significant relationship between pellets and spontaneous regurgitates is at least in part due to the small sample sizes for this technique as the correlation coefficient is high. However, some foods may more readily be regurgitated than others.

Loglinear analysis revealed that the proportions of the three main prey types were not only influenced by year and sampling method, but this effect was interactive. Variation in the proportions of prey types among years is likely to effect bias resulting from sampling regimes differently. Several studies have reported that pellets/remains tend to over-estimate the presence of indigestible material in the diet (see Duffy & Jackson 1986 for a review). Also, when an individual bird is eaten it often results in the production of more than one pellet (Votier *et al.* in press). In years of high bird consumption, this difference is likely to be most obvious in data derived from pellets/remains compared to other methods.

The advantages, disadvantages and major bias of each method is summarised in Table 7, and discussed further below.

Table 7. Advantages and disadvantages of each method for studying great skua diet composition.

Method	**Advantages**	**Disadvantages**	**Major bias**
Pellets	Ease of collecting large sample sizes. Provides useful comparative data.	Several pellets may reflect a single meal.	Underestimates mackerel, herring and sandeel.
Prey remains	Ease of collecting large sample sizes. Provides useful comparative data.	Single carcass may be torn-apart and found in several territories.	Underestimates prey swallowed whole (mackerel, herring, sandeel and small chicks).
Spontaneous regurgitates	Can be collected as a by-product of ringing effort.	Rather random occurrence provides small sample sizes.	May over-represent easily egested prey.
Observed feeds	Can be collected during time budget studies.	Most time-consuming of five techniques.	Over-records easily identifiable prey.
Water offloading	Accuracy of sampling food in the stomach.	May stress birds; requires licence; labour intensive.	Period when chicks may be sampled is short.

SAMPLE SIZES

One reason for variability in the sample sizes for each of the techniques is the relative ease of collecting samples. Pellets have been widely used in dietary studies for great skuas (as well as other seabirds) mainly because they are cast in large numbers and are generally easy to sample and classify to prey type. Prey remains are also attractive as a dietary sampling technique because of the ease of collection and identification. Pellets out-number prey items because an individual bird meal will usually result in the production of more than one pellet (Votier*et al.* in press), and because many bird kills are eaten away from the breeding territory.

Water off-loading is time consuming and it seems likely that the procedure causes some stress in the young skuas. Sample sizes were reduced because a number of chicks produced only vegetation (unlikely to be an important food resource) and around 25% of the birds sampled produced completely clear flushes - presumably representing empty stomachs. Since the stage of digestion may affect different samples in different ways, the timing of feeds may alter results from water off-loading. Gales (1985) reported variable recovery rates of fish fed to little penguins *Eudyptula minor* depending on the size of the meal and time since ingestion. In general it was found that recovery rate was very high (80-100%) after four hours, moderate (40-90%) after eight hours, but generally zero by 16 hours.

The low number of spontaneous regurgitates was partly due to attempts to cause the minimal amount of disturbance when handling birds (longer handling time often prompts regurgitation). Also the timing, size, and composition of the previous meal may influence how readily young skuas regurgitate, and this was not standardised in this study. The very small sample of observed feeds was in part influenced by the low provisioning rate and difficulty in identifying prey items accurately, and a further 16 observed feeds were not identified.

It is relatively straightforward to obtain large samples of pellets and prey remains but the larger sample sizes do not automatically validate these sampling techniques above others. However, they do suggest that pellets and prey remains may provide the best index of relative importance of prey types among time periods or localities, rather than an absolute measure of prey taken.

SEASONAL EFFECTS

Several studies have shown that seabird diets vary across the breeding season (Spaans 1971, Bearhop *et al.* In Press), which may be related to changing nutritional requirements of offspring (Annett & Perrotti 1989) or simply prey availability. The evidence from this study suggests that great skua diet does also vary seasonally, but only in certain years. The changes in pellet composition during 1998 & 1999 were largely due to an increase in the proportion of bird pellets and a decrease in the proportion of whitefish pellets in the diet towards the end of the breeding season. A trend not observed during 2000. While these differences among years may reflect a change in foraging conditions, because pellets were not sampled late in the season, it is unsafe to make such comparisons. This underlines the importance of sampling diet across the whole of the breeding season.

ADULT DIET

Differences in the proportions of prey derived from pellets and remains probably reflect the way in which food is ingested. Direct comparisons of the two methods give equal weight to each sample collected. However a bird pellet may represent as little as a quarter of a dead bird, whereas remains account for a whole carcass. In contrast a single whitefish generally results in the production of one or less pellets (Votier *et al.* in press). Just after hatching, great skuas regularly bring back whole whitefish in the proventriculus which they carefully pick clean to feed to the small chicks and this is likely to produce proportionately higher numbers of whitefish remains compared with pellets.

Differences in proportions of bird species between regurgitated pellets and remains have been shown in brown skuas (Moncorps *et al.* 1998). In that study higher proportions of diving petrels (*Pelecanoides georgicus*) and rabbits (*Oryctolagus cuniculus*) in pellets compared with remains was attributed to these prey items being swallowed whole. Higher proportions of pellets contained auks whereas remains contained higher proportions of fulmars, gull/terns, skuas and shags. This probably reflects skuas' ability to swallow auk chicks whole instead of dealing with the carcass of the larger species.

Conventionally, pellets are identified on the basis of bone structure and otoliths (Furness 1997), however for species with less readily identifiable hard parts this method is less useful. Analysis of vertebrae sub-sampled from pellets revealed that mackerel is under-represented by conventional sampling techniques owing to their otoliths being small and easily digested (Härkönnen 1986) and indistinct bones – this is clear evidence that the use of otoliths and bones alone will produce biased estimates of great skua diet. A similar bias exists with herring, where otoliths do not survive digestion.

In summary while it seems that pellets and remains provide different estimates of diet which may, in part, depend upon whether prey is consumed away from the breeding territory and regurgitated as pellets or simply brought back to the nest as a carcass. Identification of fish species in pellets should utilise vertebrae as well as bones and otoliths.

CHICK DIET

Estimates of chick diet collected during 2000 using spontaneous regurgitates and observed feeds were similar but differed when using water-offloading (Tables 1 & 6). This difference was strongly influenced by the very low proportion of whitefish found in samples of flushed stomachs. A number of suggestions may explain the reasons for these differences. Very few observed feeds contained "other" food types (i.e. mainly non-whitefish species) which is probably due to the difficulty in identifying prey items fed to a skua chick through a telescope. A number of fish were noted being fed to chicks but they could not be classified to a specific category. Differences between water off-loading and spontaneous regurgitates are more surprising however. Water off-loading has been used successfully on a wide range of seabird species. Some workers have suggested that it does not result in recovery of entire stomach contents (Lishman 1985). However its efficacy has been successfully tested for jackass penguins *Speniscus demersus* (Wilson 1984) and three species of *Procellariiform* (Ryan & Jackson 1986). Assuming that this technique is obtaining a relatively high proportion of the stomach contents of young skuas would imply that results obtained from spontaneous regurgitates are not an accurate measure of the diet of great skua chicks. However a more detailed examination of the differences between the methods indicates that a proportionately higher number of samples in the 'other' category consisted of herring (*Clupea harengus)* & mackerel (*Scomber scombrus*). This may be partly explained by large numbers of mackerel boats observed offshore during one period of sampling which coincided with a high incidence of this prey in the stomachs of young skuas and spontaneous regurgitates by adults. The bulk of spontaneous regurgitates were collected earlier in the breeding season which did no coincide with the mackerel boats, sampling skuas at different stages of the season have bias diet estimates. However another difference between the two techniques is the complete absence of bird in spontaneous regurgitates which cannot be explained by any unusual event. We can only speculate that perhaps young skuas find bird meat is more difficult to regurgitate, or it may simply be a result of small sample sizes.

The reasons for differences in chick sampling regimes are not clear, but the difficulty of obtaining large sample sizes of spontaneous regurgitates and observed feeds is a considerable constraint. Water off-loading was generally performed on chicks that were at least 14 days old and from this time until fledging different birds were sampled almost daily. By contrast the rather random nature of spontaneous regurgitates makes it more difficult to identify short term trends in diet or collect data systematically according to an experimental design.

ADULT AND CHICK DIET

Differences in diet between adult and young skuas have been demonstrated in a number of previous studies (Furness & Hislop 1981, Hamer *et al.* 1991, Phillips *et al.* 1997a,b). In these studies, great skuas were found to preferentially feed their young with sandeels (*Ammodytes* sp) – when they were available. However when this energy rich food with low indigestible material is absent, larger fish are preferentially fed to young. Sandeels were rarely found in great skuas' diet at Hermaness and Noss in 1998-2000, where whitefish predominated. During the onset of hatching, skuas were regularly observed regurgitating whole fish carcasses before carefully feeding the young with pieces of this fish. This is presumably preferable to feed to small chicks than the Cephalopod and bird prey found in the regurgitates and observed feeds of adults.

Another possible reason for the difference in the diet of adult and young skuas is the sampling period (adults caught during incubation and chicks after hatching) since some seabirds switch diet to feed to their young on particular foods (Annett & Pierrotti 1989). However if this were the case it would be expected that other sampling methods would register a switch in diet at the onset of chick hatching, which was not the case.

This study reiterates that different sampling techniques provide slightly different estimates of diet composition. Pellets and remains are easy to collect in large numbers making them convenient and attractive as sampling techniques for dietary study. They are useful for comparing between different time periods or locations but due to biases the estimates of diet derived from them need to be carefully assessed. Feeding trials used to validate pellet production as well as integration with other techniques is advisable. Spontaneous regurgitates tend to be biased toward easily egested prey and due to their unpredictability in collection are probably not suitable for specific dietary studies. Because observed feeds require long periods of observation and offer poor levels of taxonomic identification they are probably only appropriate to researchers if information on foraging effort and territorial attendance is required. Because water offloading can be performed systematically and apparently provides a non-biased sample, it is the most appropriate method for assessing chick diet. However because of the stress it is likely to cause chicks, necessity of licenses and considerable effort required, this method is only applicable to specific diet studies and not to general dietary monitoring.

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Chapter four

Ecological correlates of dietary specialisation in great skuas *Catharacta skua*

Abstract

1. A small proportion of great skuas breeding at Hermaness, Shetland exhibit distinct dietary specialisation, feeding almost exclusively upon seabird prey.
2. In this study we investigate the foraging dynamics, reproductive performance and survival of these "bird-specialists" with "other" non-specialist birds, among and within years.
3. Around half of these "bird-specialists" defended feeding territories within a section of seabird colony, the remainder foraging away from breeding territories. "Bird-specialists" retained their feeding habit and, if present, territory, between years. Time-budgets revealed that "bird-specialists" with feeding territories spent less time foraging than "bird-specialists" without a feeding territory or skuas feeding predominantly on fish. Results of radio-tracking great skuas for the first time suggest that "bird-specialists" have smaller home ranges than "others".
4. In all years "bird-specialists" show similar productivity to "others", but earlier hatching dates (a good measure of quality in great skuas). While we do not know whether high quality skuas feed on seabirds or that feeding on seabirds advances laying date, hatching early is likely to provide a fitness benefit to "bird-specialists".
5. Non-specialist great skuas experienced a reduction in clutch volume and chick condition during 1999, compared with 1998 – presumably due to a reduction in food availability. "Bird-specialists" did not experience a similar decline in clutch volume and chick condition between years, and showed higher clutch volume and chick condition than "others" in 1999. In addition to changes in clutch volume and chick condition, adult non-specialists showed reduced annual survival, compared with "bird-specialists" over the same period. These results suggest that bird-specialists gain a considerable advantage in terms of chick condition and adult survival which may have implications for LRS.

6. Apparently high quality specialist great skuas may suggest that this trait is limited in the population which may have implications for seabird predation in Shetland.

Introduction

One of the most important factors determining reproductive performance in birds is the availability of food. A number of studies have shown that feeding conditions can have an effect on avian lifetime reproductive success (e.g. Korpimäki 1992; Annett & Pierotti 1999) as well as annual productivity (e.g. Annett & Pierotti 1989, Hamer, Furness & Caldow 1991, Bolton Houston & Monaghan 1992, Oro, Jover & Ruis 1995, Phillips, Furness & Caldow 1995).

Fluctuations in food availability may also affect reproductive strategies indirectly by altering foraging behaviour. Differences in foraging strategies can arise because individual birds gain experience that makes them more efficient foragers, or because they have access to high quality food resources unavailable to the rest of the population. For example, Ens, Weissing & Drent (1992) reported that oystercatchers *Haematopus ostralegus* with feeding areas which were not adjacent to their nest site had higher foraging demands than pairs with nests which were adjacent to their feeding area, and therefore showed reduced reproductive success. In a study by Grant & Grant (1996) hybrid offspring of two species of Darwin's finch (*Geospiza spp.*) showed a selective advantage following a change in food availability, which their intermediate bill morphology allowed them to exploit. Therefore a combination of individual behaviour and environmental conditions suggest that different foraging strategies are often acquired rather than heritable traits.

Individual variations in diet and foraging specialisations are pronounced in gulls *Larus* spp. and skuas *Catharacta* spp., with specialised members of the population showing higher reproductive rates and survival than generalist con-specifics (Trillmich 1978, Trivelpiece, Butler & Volkman. 1980, Pietz 1987, Watanuki 1992, Spear 1993). Great skuas *Catharacta skua* breeding in Shetland responded to a decline in the availability of sandeels *Ammodytes marinus* (a principal food source) by increasing their consumption of discarded fish from fishing boats (Furness & Hislop 1981) or by increasing the amount of bird prey in their diet (Hamer *et al.* 1991). Subsequently, sandeel availability recovered but the number of skuas taking seabirds in Shetland remained locally high (Furness 1997), causing concern in certain areas (Heubeck, Mellor & Harvey 1997). This suggests that skuas have continued to use feeding specialisations learned during the period of sandeel shortage. Since skuas switch to killing birds when prey fish are scarce, it might be anticipated that those feeding on fish (the predominant diet) would perform better than those feeding mainly on birds.

In this study we investigate the dietary and foraging strategies of great skuas at a large breeding colony in Shetland. We compare reproductive performance of pairs with differing diets, quantify the amount of time spent foraging and investigate foraging ranges using radio-telemetry. We explore the ecological correlates of observed dietary specialisations and briefly consider potential implications of skua predation on other seabird populations.

Methods

STUDY SITE

Great skuas were studied at Hermaness National Nature Reserve (60^0 50'N, 0^0 52'W) during the breeding seasons of 1998, 1999 and 2000. A complete survey of great skuas at Hermaness in 2000 estimated 748 apparently occupied territories (Rodger 2000), and the numbers in 1998 and 1999 were broadly similar. These birds breed adjacent to a large mixed colony of northern fulmars *Fulmarus glacialis*, northern gannets *Morus bassanus*, Atlantic puffins *Fratercula arctica*, common guillemots *Uria aalge*, razorbills *Alca torda* and black-legged kittiwakes *Rissa tridactyla*.

IDENTIFYING SPECIALISTS

Great skuas at Hermaness feed by a variety of methods; catching fish at sea, scavenging discarded fish behind trawlers, stealing fish from other seabirds (kleptoparasitism), picking goose-barnacles *Lepas* sp. off flotsam and jetsam, scavenging on dead seabirds, and killing seabirds at sea or at colonies (Furness & Hislop 1981, Furness 1987). Diet of adult skuas can be assessed from the contents of regurgitated pellets of indigestible material (Furness & Hislop 1981, Furness 1997).

To determine diet, pellets were collected every four to seven days from 91 marked breeding territories in 1998 and the same, plus a further 18 territories in 1999. Since great skuas aggressively defend breeding territories against conspecifics, pellets can be confidently assigned to a breeding pair. Pellets were classified using the prey categories in Furness (1997), and removed to prevent re-counting. Breeding pairs of skuas were assigned to a dietary class on the basis of the proportion of bird pellets in their territory (see results). This is aided by the fact that both members of great skua pairs tend to show the same food preference, with most foraging during the nesting period being performed by the male partner (Furness 1987). Only pairs from which we collected at least five pellets on three separate dates were assigned a dietary group.

In addition to pellet analysis, a number of pairs were recorded defending a section of a seabird colony from other conspecifics and larids, as described by Boulinier (1992). Presence or absence of these feeding territories was noted for all pairs.

BREEDING PARAMETERS

Breeding attempts of great skuas were monitored from late May (egg-laying and incubation) to fledging in late August in the same territories where pellets were collected. In these study territories, 45 adults were colour-ringed with a unique combination to facilitate individual recognition. Great skuas at Foula, Shetland show high site fidelity, being found at the same territory year after year (N. Ratcliffe unpublished data). At Hermaness, re-sightings of individuals with distinctive plumage features as well as colour-ringed birds at the same territory suggest similarly high fidelity. Nests were located and marked during the onset of egg-laying and visited every four to seven days until chicks fledged. On completion of clutches length and breadth of eggs were measured to 0.1mm using Vernier calipers. Egg volume (cm^3) was calculated as 0.0048 x length x breadth^2 (Coulson 1963). Where hatching date was not observed directly, it was calculated from wing length by reference to the logistic growth curve as described by Phillips, Thompson & Hamer (1997). Repeatability of hatch date and clutch volume was calculated for pairs that were known to breed together in both 1998 and 1999.

After hatching, chicks were fitted with a single monel BTO ring as soon as size allowed. On subsequent visits, chicks were weighed to the nearest 1 g, during the linear phase of growth (13-34 days, Furness 1983), and their maximum flattened wing chord was measured to the nearest 1 mm. To produce an estimate of condition we compared the weight of first hatched chicks during the linear growth phase, controlling for age. Only a single measurement was used per chick, but where chicks were measured repeatedly, data points were included to ensure a spread of ages. Territories were checked until chicks had fledged or had been lost.

FORAGING BEHAVIOUR

Time budgets

In 1999, 31 breeding pairs were studied during chick rearing to determine the length of time adults spent foraging. Watches were conducted from secluded locations approximately 200 m from the nests, where there was no apparent observer effect. Watches commenced between 0500 and 0600 BST, which usually preceded the first foraging trip of the day. Watches were conducted on four dates, with up to 11 pairs watched simultaneously. Territorial attendance was recorded every ten minutes to determine the length of absences from the breeding territory. Absences were classified as foraging time on the basis of courtship feeds or chick feeds immediately on return of the adult to the territory.

Radio-telemetry

During 1999, ten breeding adult great skuas were caught on the nest during incubation using dummy eggs and a radio-controlled trap. All birds were fitted with 10g Biotrack TW-3 single cell tags mounted on the central pair of tail feathers using cable ties (under licence from Scottish Natural Heritage). Subsequent checks revealed that three birds lost their transmitters within 24 hours of fitting. However the remaining birds appeared oblivious to their tags.

Signals were tracked at Hermaness from the highest two points above sea level (150m and 200m respectively) from which the study birds' nests were in line of sight. Three-element Yagi antennae were used to obtain directional compass bearings at 10-15 minute intervals throughout the day. Bearings were converted to six-figure grid references using the expression;

For x coordinates:

$$x_3 = \frac{(y_2 - y_1)\tan\theta_1 \tan\theta_2 + x_1 \tan\theta_2 - x_2 \tan\theta_1}{\tan\theta_2 - \tan\theta_1}$$

And y coordinates:

$$y_3 = y_1 + \frac{x_3 - x_1}{\tan\theta_1}$$

Where:

x_1 & x_2 = longitude in three figure grid reference of each receiving station

y_1 & y_2 = latitude in three figure grid reference of each receiving station

tan θ_1 tan θ_2 = angle in radians of strongest signal from respective receiving station

Test bearings used a fixed position transmitter placed at approximately 3km and 5km from the two receiving stations respectively. 95% of all test bearings were found to fall within a 1.2km^2 area centered on the transmitter location. Home ranges were estimated using the minimum convex polygon technique (MCP) (Redpath 1995). To test for possible effects of radio transmitters on the foraging performance of skuas, the mean foraging trip duration of five birds fitted with transmitters was compared with a further 28 control breeders without transmitters, studied simultaneously.

ADULT RETURN RATE

The presence of colour-ringed birds was checked carefully throughout the breeding season in 1998, 1999 & 2000. Since no birds marked in 1998 and not present in 1999 were seen again in 2000, we assumed that no birds were taking a year off from breeding. Since colour-ringed birds have never been shown to move to breed at other colonies (Klomp & Furness 1992, Catry *et al.* 1998) these return rates probably represent survival rates.

STATISTICAL ANALYSIS

The relationship between diet and productivity was investigated using two Generalised Linear Models (GLIM for Ecologists version 4) with binomial error distribution and logit-link function, where hatching and fledging success were dependent variables, diet a factor and hatching date as a covariate. Where there was evidence of over-dispersion, scaled deviance was altered and effect of parameters tested using analysis of deviance (Crawley 1998). Logit-linear modelling with binomial errors was also used to model adult return rate, with return rate as the dependent variable and diet as a two-level factor. For all models in GLIM, significance of effects were tested by comparing changes in deviance values using likelihood ratio tests (LRT).

Repeatability, the intra-class correlation coefficient, of clutch parameters and hatch date was calculated following Lessells & Boag (1987). Comparisons of chick weight used analysis of covariance (ANCOVA), with weight as the dependent variable, diet class as a factor and age as a covariate.

To investigate the effect of day and diet on mean length of foraging trip a General Linear Model (SPSS version 8.0) was run with foraging trip length as the dependent variable with individual, diet, and day as factors. Data were log transformed to produce equal variances and normal error distribution.

Results

IDENTIFYING SPECIALISTS

To test if bird pellets were found randomly among skua territories, we compared the observed frequencies with a Poisson distribution. Using a G-test we found that the observed distribution of bird pellets was significantly different from an expected distribution based on a Poisson distribution in 1998 (G_{10}=117.5, $p<0.01$) and 1999 (G_{10}=367.9, $p<0.01$). The non-random distribution of pellets among territories suggests some degree of dietary specialisation among great skuas at Hermaness. An approximately bi-modal distribution suggested that skuas were either feeding largely on fish or largely on birds with "fish feeders" greatly outnumbering "bird feeders" (Fig. 1). Since the trough between the two peaks was at 60% of bird pellets, this was taken as the threshold for our definition of a "bird-specialist". Skuas with less than 60% of their pellets containing bird remains are hereafter referred to as "others".

From the original sample of skua pairs, several were excluded from analysis because of insufficient pellet data to award them a dietary category. Therefore 55 pairs of skuas were included for study of diet and breeding parameters during 1998 with 75 in 1999. In 1998, ten (18.2%) were classified as "bird-specialists" and 45 (81.8%) as "others", with eleven (14.7%) "bird-specialists" and 64 (85.3%) "others" in 1999. Of the "bird-specialists" five were observed defending feeding territories in 1998, with six in 1999.

Re-sighting of colour-ringed birds and uniquely marked individuals at the same territories suggest that individuals retain the same breeding territories among years. Comparison of dietary data from mapped territories revealed that skuas breeding at the same territories retained similar feeding preferences from 1998 to 1999. All skuas observed defending a feeding territory defended a similar section of sea cliff in each of the two years.

BREEDING PARAMETERS

Productivity & hatch date

Because hatching date was included as a covariate in analysis of breeding productivity, where this data was not collected (as a result of complete brood losses) skua pairs were excluded from analysis. A GLM revealed that in 1998 there was no significant effect of diet on hatching success (LRT; $\chi^2_1=3.21$, NS) or fledging success (LRT; $\chi^2_1=1.33$, NS) (Table 1). In the same year, hatching date had no effect on hatching success (LRT; $\chi^2_1=3.80$, NS), but a significant effect on fledging success (LRT; $\chi^2_1=4.93$, $p<0.05$). Hatching success and fledging success were not significantly effected by diet during 1999 (LRT; $\chi^2_1=1.51$, NS & LRT; $\chi^2_1=0.05$, NS, respectively). While there was no effect of hatching date on hatching success (LRT; $\chi^2_1=1.42$, NS) or fledging success (LRT; $\chi^2_1=0.30$, NS) in 1999, there was a significant interactive effect of diet and hatching date on hatching success (LRT; $\chi^2_1=4.86$, $p<0.05$).

Comparing the date on which the first egg was hatched revealed that "bird-specialists" had significantly earlier hatching dates than "others" in both 1998 ($t_{38}=3.093$, $p=0.004$) and 1999 ($t_{54}=4.308$, $p<0.001$) (Table 2). There was a linear relationship across all pairs between the proportion of bird pellets in the diet and hatching date (Fig. 2).

Hatch date was repeatable between 1998 and 1999 ($r=0.72$, $F_{13,14}=6.16$, $p=0.001$), showing that individual birds exhibited similar reproductive phenology among years.

Clutch volume

There was an effect of year and dietary class on the total volume of two egg clutches laid by great skuas, but with no significant interaction (Table 3; two-way ANOVA, year effect, $F_{1,98}=5.042$, $p=0.027$; diet effect, $F_{1,98}=4.172$, $p=0.044$; interaction, $F_{1,97}=0.445$, NS). Clutch volumes were larger in 1998 than 1999 and larger for "bird-specialists" than "others" (Table 3).

Clutch volume for individual birds showed low repeatability between 1998 and 1999 (r=0.33, $F_{10,11}$=1.929, NS).

Chick weight

In 1998 there was no difference in the weight of chicks, controlling for age, between "bird-specialists" and "others" (ANCOVA: interaction, $F_{1,37}$=0.401; diet effect, $F_{1,38}$=0.828, NS). However, in 1999 chicks of "bird-specialists" were significantly heavier for a given age than chicks of "others" (ANCOVA: interaction, $F_{1,54}$=0.659, NS; diet effect, $F_{1,55}$=5.419, p=0.024; Fig. 3).

Comparing between 1998 and 1999 revealed that the weight of "bird-specialists" chicks, controlling for age, were similar in both years (ANCOVA: interaction, $F_{1,7}$=0.252, NS; year effect, $F_{1,8}$=0.701, NS). In contrast, chicks of "others" were significantly heavier in 1998 than in 1999 (Fig. 4; ANCOVA: interaction, $F_{1,84}$=0.155, NS; year effect, $F_{1,85}$=5.119, p=0.026).

FORAGING BEHAVIOUR

Adult time budgets

A GLM showed that there was no effect of day or individual on foraging trip length but the effect of diet was significant ($F_{3,89}$=5.11, p=0.03). There were no significant interactions. Scheffé-ranges tests indicated that birds with a feeding territory had a significantly shorter mean foraging trip duration than either "non-territory holding bird-specialists" or "others". "Non-territory holding bird specialists" had longer foraging trips than "other" pairs but this difference was not statistically significant (Table 4).

Because skuas often performed more than one foraging trip per day, the total time spent foraging was also compared for the three groups. A GLM revealed that diet had a significant effect on the total amount of time spent foraging ($F_{2,53}$=6.50, p=0.003), but there was no effect of day and there was no interaction between day and diet. Scheffé-ranges tests showed that skuas with a feeding territory spent significantly less time foraging per day than the two other groups. "Non-territory holding bird specialists" and "others" spent similar amounts of time foraging per day (Table 4).

Radio-tracking adults

An independent sample t-test showed no significant difference between skuas with transmitters and those without transmitters in mean duration of foraging trip (t=0.44,df=31, p=0.97). Therefore we assumed that skuas with radio-transmitters were behaving normally.

Of the skuas tracked only five provided sufficient detail for analysis. The mean minimum convex polygon home range sizes of skuas are shown in Table 5. Due to the small sample sizes of radio-tracked skuas it was not possible to perform any statistical tests on the data. However, indications were that skuas feeding on fish were travelling large distances compared with those skuas feeding on birds. Calculated home ranges are shown in Figure 5.

ADULT RETURN RATE

Of the 45 adults individually colour-marked, we only obtained sufficient dietary data to award 32 a dietary classification. Using GLIM we found that the number of colour-marked adults returning to breed in 1999 after being marked in 1998 was similar for "bird-specialists" and "others" (LRT; χ^2_1=0.04, NS) (Table 6). However, the number of "bird-specialists" returning to breed in 2000 was significantly greater than the number of "others" (LRT; χ^2_1=4.49, p<0.05) (Table 6).

Table 1. Breeding success (number of eggs hatched or young fledged from per breeding) of great skuas classified as "bird specialists" and "other" in 1998 and 1999. 95% confidence intervals and sample sizes in parentheses.

Year	Breeding parameter	Bird specialist	Other
1998	Hatching success	1.50 (0.71-0.92) (n=6)	1.68 (0.78-0.96) (n=34)
1998	Fledging success	0.83 (0.44-0.77) (n=6)	1.23 (0.61-0.90) (n=34)
1999	Hatching success	1.55 (0.72-0.89) (n=11)	1.64 (0.75-0.93) (n=45)
1999	Fledging success	1.27 (0.57-0.78) (n=11)	1.38 (0.60-0.84) (n=45)

Table 2. Great skua hatching date in two years for "bird-specialist" and "other" ± 1 SD; n in parenthesis.

	1998 Mean ±SD	1999 Mean ±SD
Bird specialist	14.0 ± 5.62 (6)	13.5 ± 10.1 (11)
Other	23.9 ± 7.45 (34)	24.2 ± 6.59 (45)

Table 3. Total clutch volumes from bird specialist and other great skuas sampled during 1998 & 99. Sample sizes differ from data including hatching date since only two-egg clutches were included and for some nests hatching date was not determined.

	1998	1999
Bird-specialist (cm^3)	170.2 ± 9.8 (9)	168.7 ± 4.33 (8)
Other (cm^3)	166.4 ± 9.07 (37)	161.2 ± 1.17 (47)

Table 4. Mean foraging trip duration and total spent foraging per day for breeding great skuas. Values are presented in minutes with standard errors and number of individuals in parentheses.

Foraging strategy	Mean foraging trip duration (mins)	Total time spent foraging per day (mins)
Bird specialists with feeding territory	62.3 ± 9.91 (3)	115.1 ± 25.8 (3)
Bird specialists without feeding territory	234.4 ± 51.7 (4)	302.5 ± 10.3 (4)
Other	197.0 ± 17.1 (24)	293.6 ± 16.7 (24)

Table 5. Minimum convex polygon (MCP) areas in km^2 for breeding great skuas according to diet. Mean home range is presented followed by ±1 SE; the number of individuals are in parentheses and the range of values given below.

Dietary category	MCP home range
Fish feeder	17.38 ± 4.92 (1)
	9.33 – 26.30
Bird specialist (no feeding territory)	4.66 ± 2.03 (1)
	0.91-8.51
Bird specialist (with feeding territory)	0.95 ± 0.37 (3)
	0.04 – 2.55

Table 6. Survival estimates of adult great skuas among years for different dietary classes. Because of binomial variance bounded around 0 and 1 standard errors are asymmetrical.

Years	Bird-specialists	Other
1998 to 1999	0.89 (0.73-0.96) (n=9)	0.86 (0.67-0.95) (n=7)
1999 to 2000	1.00 (0) (n=15)	0.80 (0.68-0.88) (n=15)

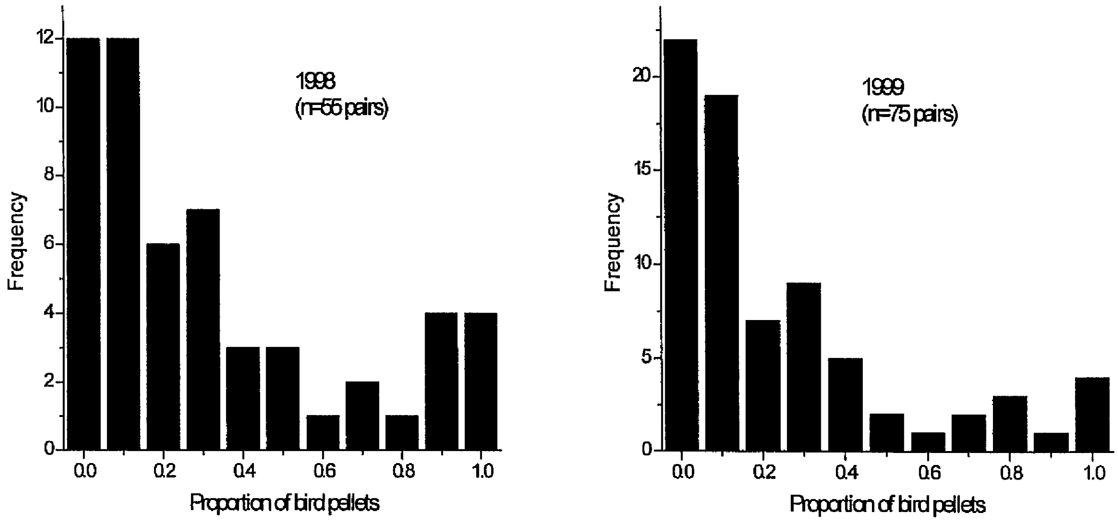

Figure 1. Frequency distribution of great skua breeding pairs with differing proportions of bird pellets collected from territories during 1998 and 1999.

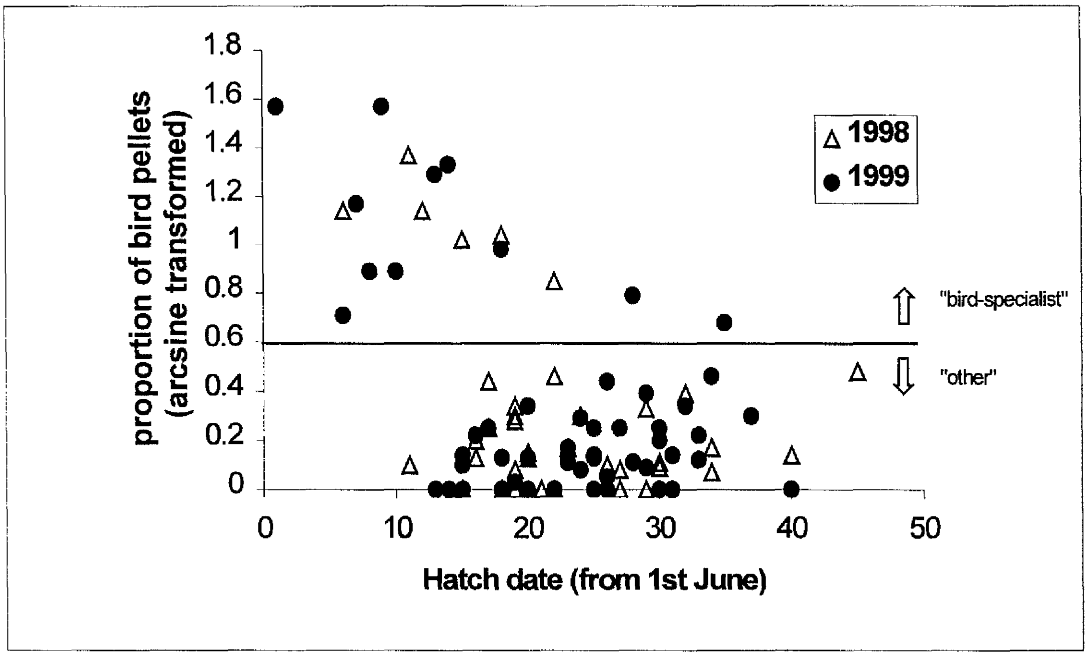

Figure 2. Relationship between hatching date and the proportion of bird pellets in the diet of great skuas. Horizontal line represents division between classification as a "bird-specialist" or "other". Great skuas hatching early have a higher proportion of bird remains in their pellets.

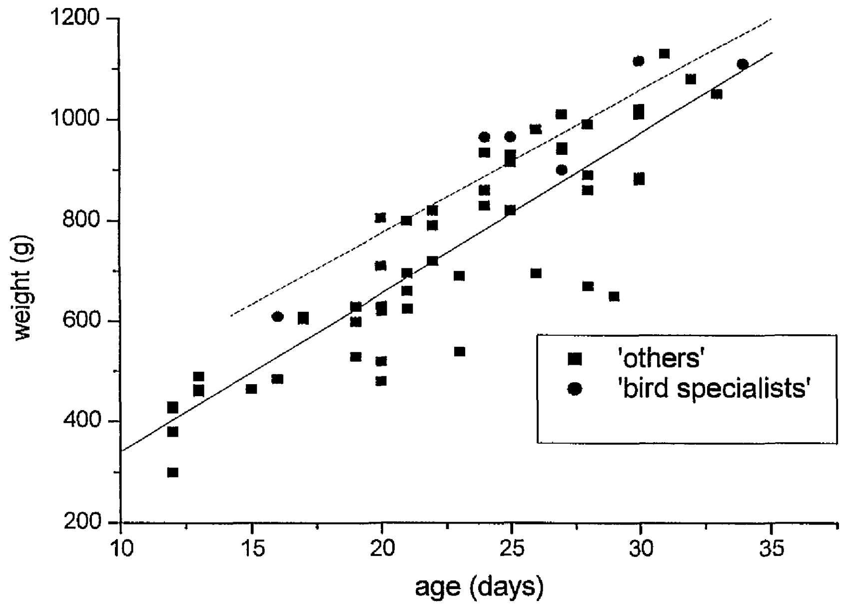

Figure 3. Body mass versus age in great skua chicks during the linear phase of growth in 1999. The young of "bird-specialist" pairs show significantly higher weights for a given age than the young of "others" (see text for classification of dietary classes).

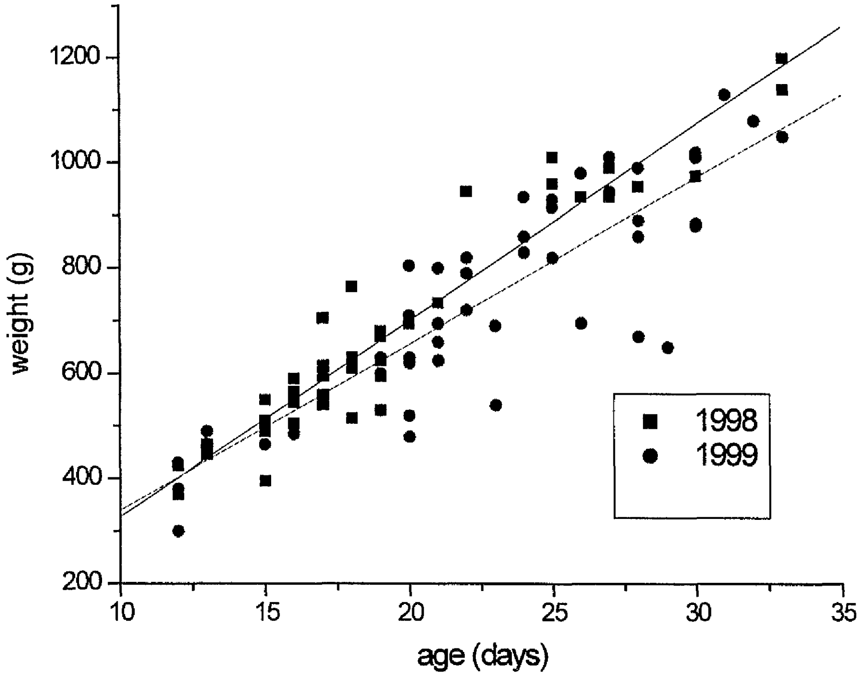

Figure 4. Body mass regressed against age for chicks of "other" great skuas during the linear growth phase. Chicks were heavier for a given wing length in 1998 than in 1999.

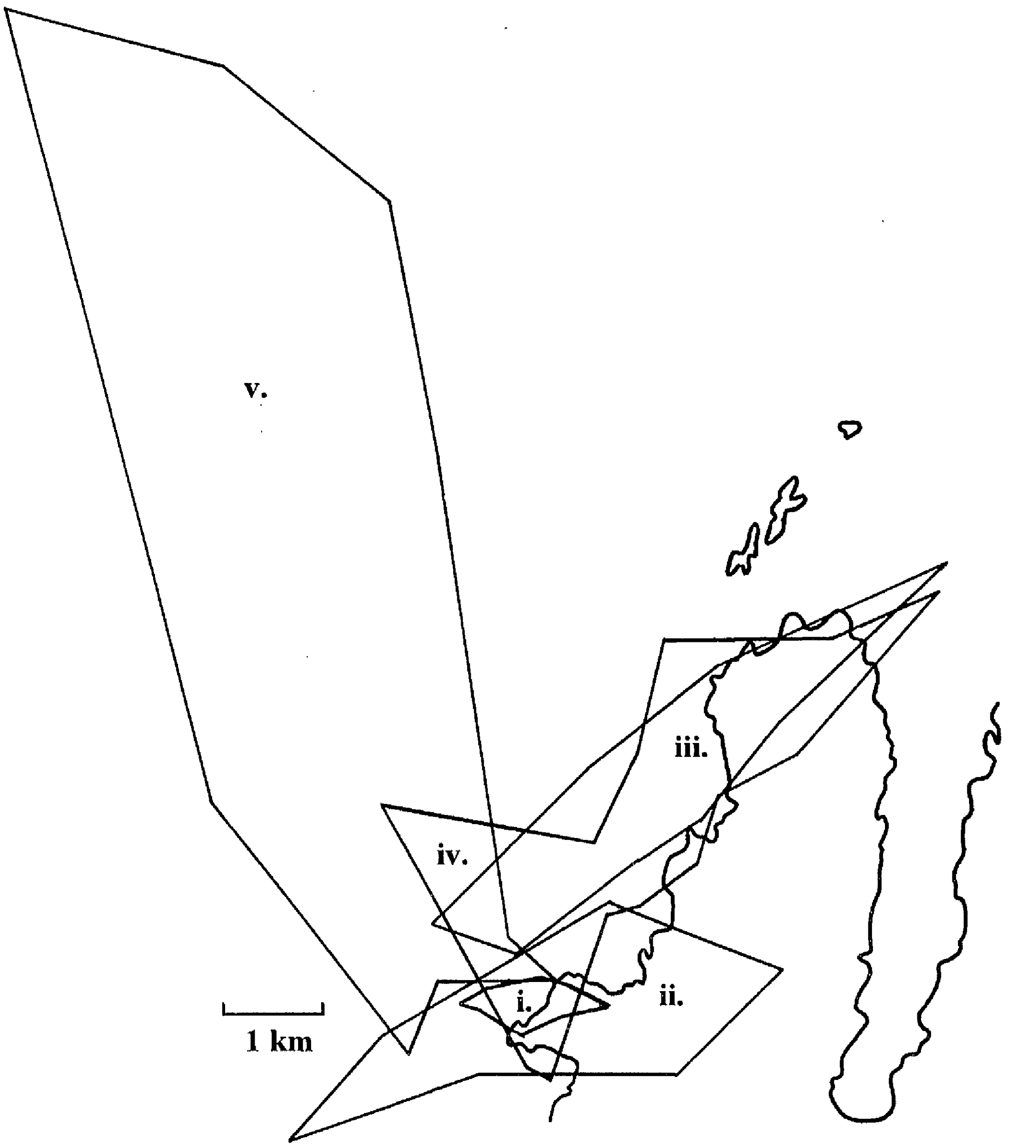

Figure 5. Home ranges of great skua. Each area represents foraging range for an individual bird. Numbers within ranges refer to dietary classification; **i** - **iii** are territory holding bird specialists; **iv** is a bird-specialist without a feeding territory & **v** showed predominantly fish in its' diet.

Discussion

DIETARY SPECIALISATION

Differences in pellet composition between pairs of great skuas breeding at Hermaness clearly indicate dietary specialisation, with a small proportion of skuas feeding predominantly on birds while most skuas fed mainly on fish. Data from radio telemetry showed that skuas producing mainly bird pellets were foraging predominantly around coastal seabird colonies, whereas a single skua producing mainly fish pellets foraged further out to sea at fishing trawling grounds. Several other species of skua and large gulls show similar specialisations (Trivelpiece *et al.* 1980, Pietz 1987, Watanuki 1992, Spear 1993) although in most cases these specialists were defined as such because they defended a feeding territory within a seabird colony. However at Hermaness less than half of the bird specialists held a feeding territory. Where skuas did defend feeding territories, males performed the bulk of the defence behaviour, females spending the majority of their time attending the nest, or on several occasions were observed expelling conspecifics while the male killed adult seabird prey (S.Votier, unpublished data). Observations of known individuals revealed that pairs retained similar feeding strategies and "bird-specialists" retained feeding territories, from year to year.

The proportion of bird specialists within our sample of pairs at Hermaness was relatively high (around 22% in 1998 and 15% in 1999). The proportion at Hermaness as a whole was much lower than this. Initial searches for bird specialists revealed them to be scarce and so we included as many bird specialist pairs in our study sample as we could find. In 2000, a random sample of 100 great skua territories revealed only four with a higher proportion of bird than fish pellets (S.Votier, unpublished data). From this we estimated that less than five percent of the great skuas breeding at Hermaness were bird specialists.

BETWEEN YEAR DIFFERENCES

In this study clutch volumes were larger in 1998 compared with 1999 and larger in "bird-specialist" skuas compared with "other" skuas. Because an increase in clutch volume may result in improved survival and growth of chicks (Furness 1983, Bolton 1991), one might expect great skuas to increase egg volume where sufficient nutrient reserves allowed. During years of increased food abundance great skuas at Foula, Shetland showed increased clutch volume (Ratcliffe, Furness & Hamer 1998) and only during years of reduced food supply did experimentally fed lesser black-backed gulls *Larus fuscus* show an increase in egg size compared with control birds (Bolton *et al.* 1992). While we do not have measures of natural food availability for great skuas at Hermaness, the reduction in clutch volume of non-specialist skuas in 1999 compared with 1998 infers that these birds were finding it difficult to find food during 1999. By contrast the similar sizes of clutches laid by "bird-specialists" in 1998 & 1999 probably reflects the relative abundance of bird prey in both years.

In 1999 chicks of non-bird-specialists were heavier than chicks of "bird-specialists", although the two groups showed similar chick weights in 1998. Heavier chicks at fledging have a higher probability of survival (e.g. Sagar & Horning 1998) therefore "bird-specialists" are likely to gain a fitness benefit over and above those skuas which do not feed predominantly on birds.

Since larger eggs generally result in the production of larger chicks (Furness 1983, Bolton 1991, Bolton *et al.* 1992), the decrease in chick weight of non bird-specialists shown during 1999 may be an artifact of smaller clutch volumes. Alternatively both may have been affected by poor conditions with insufficient food to lay large eggs or raise large chicks. Without conducting manipulation experiments it was not possible to separate these effects.

But what are the implications of improved clutch volume for "bird-specialist" great skuas in certain years? While large eggs may improve hatching success, chick growth and survival (Williams 1994), in this study we found no differences between skuas with different clutch volumes in terms of chick survival. However Bolton (1991) showed that parental quality was a more important determinant of successful chick rearing than egg size, so clutch volume alone may not influence productivity. Furthermore, Catry & Furness (1997) found no relationship between clutch characteristics and measures of adult quality in greatskuas in three different breeding seasons. In another study on great skuas, Ratcliffe, Furness & Hamer (1998) demonstrated that clutch volume was affected by male age, and went on to suggest that male foraging skills during courtship feeding influenced this trend. Therefore the improved clutch volume shown by "bird-specialist" greatskuas may simply reflect good feeding conditions or efficient foraging performance.

There was a small but significant difference in the return rates of great skuas between 1999 and 2000 – a higher proportion of "bird-specialists" returned to breed compared with "others". While most predictions of life-history theory predict that long-lived birds do not trade their own survival in favour of their offspring (Lindén & Møller 1989) in two species of larids accidental or experimental reduction of breeding effort resulted in increased chances of adult survival (Pugesek & Diem 1990, Golet, Irons & Estes 1998). The smaller clutches and lighter chicks of skuas feeding mainly on fish in 1998 compared with 1999 may suggest a that adult condition was compromised sufficiently to effect over-winter mortality or prompt a deferral in breeding. Kittiwakes respond to a reduction of favoured food supply by either increasing foraging effort (Hamer *et al.* 1993) or by switching prey (Suryan, Irons & Benson 2000). Since skuas showed similar diets between years, it seems likely that non-specialists increased their foraging effort, beyond a level which was sustainable.

WITHIN YEAR DIFFERENCES

Trivelpiece *et al.* (1980), Pietz (1987) and Spear (1993) showed that specialist skuas and gulls had higher breeding success than non-specialists did. However, there were no comparable differences in the breeding success of "bird-specialist" and "other" great skuas in our study. In previous studies, specialists defended a feeding territory within a seabird colony and they gained an advantage by using less energy in foraging and were also able to spend more time in nest defence. Similarly Chudzik, Graham & Morris (1994) showed that in a comparison between ring-billed *L. delarwarensis* and herring gulls *L. argentatus,* ring-billed gulls showed higher reproductive output because they spent less time foraging and more time in nest defence. Only those great skuas at Hermaness which defended a feeding territory (less than half of the bird-specialists) showed reduced foraging effort, therefore only this small proportion of the population showed reduced energy expenditure and were able to spend more time defending their young.

High quality birds often lay eggs early and are more efficient foragers (Coulson & Porter 1985, Spear & Nur 1994). Catry *et al.* (1998) showed that adult great skuas which lay earlier in the season have a greater probability of over-winter survival and early hatched chicks have increased body condition and greater probability of survival to their first year. The earlier hatching date of bird-specialist great skuas may suggest that they are high quality members of the population. An advancement in laying (and therefore hatching) date is also associated with improved food supply in larids and skuas (Spaans 1971, Ratcliffe, Furness & Hamer 1998). One advantage of feeding primarily on birds may be that bird prey has a higher energy content than fish. Phillips *et al.* (1999) calculated the mean energy content of a typical great skua meal of bird to be more than double that of a similar sized meal of fish. Therefore it is unclear whether bird-specialists have earlier hatching dates because of access to an energy rich food source, because high quality birds lay earlier and out-compete others for feeding territories or because there is a genetic component connected with the learning of a highly adaptive foraging technique.

Other studies have shown that during periods of poor food supply, non-specialist skuas and gulls show reduced reproductive output (Trivelpiece *et al.* 1980, Pietz 1980, Spear 1993). While we found no similar effect on productivity (in terms of young hatched and fledged), in certain years bird-specialists were able to lay larger clutches, rear heavier chicks, either decrease the proportion of years off from breeding or increase adult survival. These annual variations in reproductive success may have important implications for LRS. Earlier hatch dates may also confer an advantage to bird-specialists independent of annual fluctuations in non-bird food availability.

CONSERVATION IMPLICATIONS

Although the great skua population is healthy and increasing around the UK, this species is globally scarce (Lloyd, Tasker & Partridge 1991) and therefore potentially of conservation concern. Concerns about the impact of great skuas on the population of other seabirds also need to be carefully considered. The bulk of the fish eaten by great skuas at Hermaness consists of demersal species (S.Votier unpublished data) which are unlikely to be caught at sea and most likely scavenged behind fishing boats (e.g. Furness & Hislop 1981, Hamer, Furness & Caldow 1991). Current EU proposals to reduce the amount of fish discarded in European waters is likely to reduce feeding opportunities for skuas which rely on this food resource. Results from this study suggest that skuas feeding predominantly on fish appear to show reduced reproductive output, particularly in certain years, compared with skuas that specialise in feeding upon other birds. Since "bird-specialists" only appear to represent a small proportion of the great skua population at Hermaness (this study), as well as other Shetland colonies (Furness 1997), the majority of the great skua population could experience reduced reproductive output, reduced adult survival and a reduction in overall fitness. Alternatively seabird prey may become increasingly important in the diet of great skuas as the availability of discard diminishes. As is the case with a number of other studies, "bird-specialist" pairs appear to be high quality individuals, suggesting that this method of feeding will be maintained within the population. The heritability of foraging technique is beyond the scope of this study, but a foraging preference could be passed to offspring through vertical transmission of an acquired trait by learning (Feldman & Laland 1996). Any potential management policy that advocated the removal of bird specialists may reduce seabird predation with little change in the numbers of great skuas, although these birds may represent the highest quality component of the genetic population. Also, because feeding on birds appears to be advantageous, territories may quickly be re-occupied with little change in the impact of predation. An alternative scenario is that removal of specialists may cause predation to increase as skuas defending feeding territories aggressively expel other skuas and gulls. Experimental removal of these bird-specialists is one potential way of addressing this controversial problem.

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Chapter five.

Prey consumption by great skuas *Catharacta skua* at Hermaness, a bioenergetics approach

Abstract

Hermaness National Nature Reserve holds the third largest colony of great skuas *Catharacta skua* in the UK, as well as internationally important numbers of other seabirds. Around five % of great skuas at Hermaness specialise in feeding upon seabirds, while the remainder of the population rely heavily on discarded gadoid whitefish, taking seabirds more opportunistically. Concern about the numbers of seabirds currently being taken, as well as the effect that a reduction in discarding may have highlights the need to quantify great skua predation at Hermaness. In this study we use a bioenergetics model to estimate the amount of prey consumed in a single breeding season, with particular reference to the numbers of seabirds eaten.

The great skua population at Hermaness was estimated to require 428.9 x 10^6 kJ during 1999. 80% of the energy demanded was required by breeding adults with less than 5% being required by breeding adult bird-specialists.

Combining data on energy requirements and prey composition we estimate that great skuas at Hermaness feed on 69.3 tonnes of fish, 6.9 tonnes of seabirds, 2.5 tonnes of rabbit *Oryctolagus cuniculus* and 0.6 tonnes of goose barnacles *Lepas sp.*

The number of seabirds estimated to have been consumed by great skuas was over 11,000, the majority being auks (Alcidae) (71%). While bird-specialists made up only 5% of the population they consumed 30% of the seabirds.

While the number of seabirds being taken by great skuas is large, the impact on populations is not clear. Despite the large numbers consumed, the impact by great skuas is much less severe than has been reported at other smaller skua colonies. Declines in discarded whitefish may result in an increase in seabird predation, but to an unknown extent.

Introduction

Predatory birds may act on prey populations in a number of complex ways, depending upon predators response to prey density. In cases where predator populations are resident and specialised, prey density may drive predator density (Nielsen 1999). For more generalist or nomadic predators, the ability to exploit a range of prey or follow fluctuations in favoured prey, may cause predators to affect prey population densities (Korpimäki & Norrdahl 1991, Cresswell & Whitfield 1994, Korpimäki 1994, Redpath & Thirgood 1999). Since predatory *Larus* gulls and *Catharacta* skuas show strong site fidelity and a broad dietary range which includes other seabirds (Furness 1979, Spear 1984, Yorio & Quintana 1997), they may be expected to affect seabird populations.

Gulls and skuas are widely recognised as important predators of other seabirds (Harris 1980, Russel & Montevecchi 1986, Yorio & Quintana 1997). A number of studies have addressed the level of impact of these groups of birds (Furness 1981, Phillips, Thompson & Hamer 1999, Watanuki 1986), but because of the complex interactions between fish and seabird prey as well as inter-colony variations in diet (Phillips, Thompson & Hamer 1997b) findings of different studies are often very site specific.

The great skua *Catharacta skua* breeds only in the north Atlantic with approximately 60% of the population nesting in Britain. The population has grown dramatically in the past 100 years, probably through reduced persecution and the availability of waste associated with commercial fisheries (Furness 1987, Lloyd, Tasker & Partridge 1991). While the dietary flexibility of great skuas is key to their success it has also become a matter for conservation concern.

Changes in the breeding distribution and numbers of black-legged kittiwakes *Rissa tridactyla* along the coast of Unst, Shetland are believed to have been influenced by predation pressure from great skuas (Heubeck & Mellor 1994, Heubeck, Mellor & Harvey 1997). Since discarded fish appear to be important in the diet of great skuas (Furness & Hislop 1981, Hamer Furness & Caldow 1991, Phillips *et al.* 1997b) current EU proposals to reduce the amount of discards, may further limit the availability of this resource which has been declining as stocks have fallen. Since a reduction in sandeel *Ammodytes marinus* availability during the 1980s corresponded with an increase in the amount of bird meat in the diet of great skuas at Foula, Shetland (Hamer *et al.* 1991), a similar response might be predicted by great skuas feeding on discards as that food supply declines. Therefore it is prudent to quantify the impact of great skuas on seabird numbers in Shetland.

In this study we use a bioenergetics model developed by Phillips *et al.* (1999) to estimate the amount of prey and in particular the numbers of seabirds consumed by great skuas at Hermaness during the 1999 breeding season. Combining these estimates and counts of seabirds breeding at Hermaness, we assess their current impact. Using sensitivity analysis we investigate how changes in the availability of discarded fish may influence consumption of different prey types, in particular other seabirds. We also discuss the role of bird-specialists in the population with particular attention to the number of birds that these members of the population consume.

Methods

This model uses metabolic rates and energetic requirements to calculate energy demands of breeding and non-breeding adult as well as young great skuas. Data gathered on diet and published values of calorific densities of prey enable an estimation of the amount of each prey type consumed. Our methods are taken directly from the model developed by Phillips *et al.* (1999), who calculated the impact of great skuas on seabird populations breeding at St. Kilda.

STUDY SITE

Unst holds the third largest concentration of great skuas in Britain with 1,567 apparently occupied territories (AOTs) in 1992 (Sears *et al.* 1992). Over half (854 AOTs) of these birds breed at Hermaness National Nature Reserve (60° 50’ N, 0° 52’ W). Hermaness is also home to internationally important numbers of other breeding seabirds including ≈28,000 northern fulmars *Fulmarus glacialis*, ≈32,000 northern gannets *Morus bassanus*, ≈1600 black-legged kittiwakes *Rissa tridactyla*, ≈15,000 guillemots *Uria aalge*, ≈1500 razorbills *Alca torda* and 30-80,000 atlantic puffins *Fratercula arctica* (Lewis 1997, Stenning 1998, King 1999, Rodger 2000).

A census of breeding great skuas at Hermaness by Scottish Natural Heritage during 1997 revealed 631 apparently occupied territories (AOTs) (Lewis 1997). Using mapped skua territories we compared the numbers estimated in 1997 with the numbers we found in the same sections of the colony during 1999. Our estimates suggested a 4.5% increase between the two years, therefore we estimated 659 AOTs during 1999. To determine productivity, breeding duration and diet, we followed a sample of 109 pairs throughout the breeding season.

Since non-breeding skuas gather at specific club-sites (Furness 1987), we were able to obtain an estimate of the non-breeding population and sample the diet of non-breeders. The number of great skuas using the three major club-sites at Hermaness were counted every five to ten days throughout the breeding season. The number of birds present producing a mean of 90 birds (SD±17.8). A fourth club-site was only visited on one date and produced a count of 20 birds. Our estimate of the non-breeding population was therefore taken as 110 birds.

DIET COMPOSITION

Because skuas at Hermaness show dietary specialisation (S. Votier *unpublished data*) it was not appropriate to sample diet at random. It was estimated that around 5% of the population specialise in feeding almost exclusively upon seabird prey. For the remainder of the population there was a relationship between the proportion of bird prey in the diet and distance to the nearest seabird colony (Spearman's Rank-order correlation r_s=-0.473, $p<0.001$, n=71) – birds closer to a seabird colony having more bird in their diet. To correct for these differences we sampled diet from different areas of the colony using a stratified approach. All the skuas breeding in two study areas (comprising 35 and 28 skua territories) were sampled adjacent to the extensive seabird colonies on the western coast of Hermaness. Apportioning similar sized areas adjacent to seabird colonies along the whole coast of Hermaness we estimated 171 pairs (26% of the Hermaness population) had diets in the same proportion as the two study plots. The remaining 69% of the skuas at Hermaness had their diet estimated on the basis of 32 pairs sampled from the central/eastern fringe of the colony, away from any sizeable seabird colonies.

The diet of breeding adults was estimated on the basis of pellets collected from marked skua territories every five to ten days from late May (incubation) to mid August (fledging). Pellets were identified following Furness (1997) and removed. Pellets of bird prey were identified to species, based on feather colour and smell or any hard parts (legs or bill). A small number of passerines were found in the pellets of skuas (n=3), but the rather random nature of their occurrence suggests that they are unimportant to the skuas, and were excluded from analysis. Because chicks do not produce pellets (Furness 1987), we estimated the proportion of the three main prey types (whitefish, bird and 'other') in the diet of chicks using regurgitates produced during handling or from observing adults feeding chicks. The relative proportions of bird species were assumed to be the same as those found in pellets of adults.

Because no data were available on the diet of skuas prior to incubation, we had to consider the problem of any potential prey switching. The proportion of the main prey types did not differ through the period from incubation to fledging for bird-specialists (χ^2_7=11.2, NS) or other skuas breeding away from seabird colonies (χ^2_7=4.32, NS). However, non-specialists breeding adjacent to seabird colonies showed a seasonal change in diet (χ^2_7=19.5, $p<0.01$), by switching to taking more seabirds and eggs late in the season. Therefore diet composition prior to incubation for this group was assessed excluding the period of switching.

Pellets were collected from club-sites every five to ten days from late May to mid August to assess the diet of non-breeding birds. The proportion of the three main prey types was not the same throughout the sampling period (χ^2_6=29.5, p<0.01), showing an increase of 'other' prey towards the end of the breeding season. Because of this change in prey composition, diet for the remainder of the breeding season was assumed to be the same as for the period of this switch.

Captive skuas fed a large fish produce a single pellet, but the meal to pellet ratio is smaller for skuas fed bird carcasses (Votier *et al. in press*). Using data from Table 2 in that study, we made a correction to the number of pellets for each fulmar/gull/tern (1 meal = 2.94 pellets), auk (1 meal =1.75 pellets) and great skua chick (1 meal = 2.75 pellets). This differed from the approach by Phillips *et al.* (1999), they assumed one meal resulted in the production of a single pellet. The effect of meal to pellet ratios on prey consumption estimates are tested in sensitivity analysis (see Discussion).

ENERGETIC DEMANDS

Using published values of basal metabolic rate (BMR) (Bryant & Furness 1995) and estimates for the cost of performing specific activities as multiples of BMR (Caldow 1988), we were able to calculate energy requirements of breeding adults in terms of field metabolic rate (FMR). Timed watches of 31 birds (7 bird-specialists and 24 non bird-specialists) determined the relative proportion of time performing four specific activities – resting, general (preening, walking, bathing, long-calling), gliding flight and flapping flight (Table 1). The values of FMR calculated in this study are very similar to those calculated by Caldow (1988) and subsequently used by Phillips *et al.* (1999), but see discussion for differences. Excluding the costs of clutch production, maintenance and activity costs for non-breeders was assumed to be similar as those for breeding birds. Despite not incurring the costs of foraging for chicks, non-breeders are probably less efficient foragers than breeders and therefore have similar energetic requirements (following Gaston 1985, Cairns *et al.* 1990, Phillips *et al.* 1999). For all energy requirements, including the cost of egg production, food assimilation efficiency was assumed to be 0.76. This value was that applied by Phillips *et al.* (1999) based on a value obtained from controlled feeding trials of captive great skuas fed on a diet of whiting *Merlangius merlangus*.

The cost of producing a clutch, energy demands of chicks from hatching to fledging and energy requirements of fledglings prior to leaving the colony, were calculated following Phillips *et al.* (1999). Energy required for clutch formation for each pair was derived from the equation:

$$E_{pair} = Cls \times M_{egg} \times Cal_{egg} \times (1/E_{syn})$$

Where:

Cls = mean clutch size	(This study)
M_{egg} = mean fresh egg mass (g)	Furness 1978
Cal_{egg} = average calorific value of gull egg (kJ)	Meathrel & Ryder (1987), Meathrel, Ryder & Termaat (1987)
E_{syn} = egg tissue synthesis efficiency	Ricklefs (1974, 1983)

Energy requirements of chicks from hatching to fledging was estimated from the equation:

$$ME_{chicks} = 35.15 \times M_c^{1.015}$$

Where:

M_C = chick mass at hatching in grammes	Drent, Klaassen & Zwaan (1992)

Energy demands of each chick for the short period following fledging and prior to departure from the colony was calculated using the daily energy requirement of chicks at fledging vs. fledging mass (Drent, Klaassen & Zwaan 1992).

The duration of the breeding season was calculated as 106.4 days, based on 13 days pre-breeding period (Phillips *et al.* 1999), 29 days incubation (Furness 1978), 46.4 days chick rearing (this study) and 18 days post-fledging period (Phillips *et al.* 1999). Non-breeders are present at the colony for a similar period, although because of a high turn over of individuals, this may not represent the same individuals (Klomp & Furness 1992).

SENSITIVITY ANALYSIS FOR ENERGETIC REQUIREMENTS

To investigate the importance of changes in inputs to the model, we increased input parameters by 1% (following Furness 1978 & Phillips *et al.* 1999) and also by including a range of likely extremes (following Diamond, Gaston & Brown 1993 & Phillips *et al.* 1999). For energy requirements of the whole population we used the approach and range of values used by Phillips *et al.* (1999).

PREY ENERGY CONTENT & MEAL SIZE

From otoliths collected in pellets, 95% of the fish diet at Hermaness consisted of haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*) blue whiting *(Micromesitius poutassou*) and Norway pout (*Trisopterus esmarkii*). As found at St Kilda by Phillips *et al.* (1999), the size of the otoliths indicated that haddock, whiting and blue whiting were all large fish (greater than 100g) and while Norway pout were much smaller than this (mean of 23.6g), pellets of this species generally contained between five and ten otoliths. Therefore we used the average meal size of 100g as first proposed by Furness & Hislop (1981). Mean energy content of 5.2 kJ g^{-1} of fresh mass for gadoid fish (Hislop, Harris & Smith 1991) was applied throughout. A small proportion of herring *Clupea harengus* and mackerel *Scomber scombrus* were also present in the diet and recent studies (Votier *et al.* 2001) suggest that pellets underestimate the proportion of these species in the diet of great skuas. Mature Clupeids and scombrids have a high energy content but because seabirds are only able to exploit small, not fully mature, fish these have similar energetic content values to gadids

(Hislop *et al.* 1991). Therefore we applied a common value for fish energy content throughout.

We followed the approach adopted by Phillips *et al.* (1999) in assuming that the calorific value of birds was 10.9 kJ g^{-1}. Because of the high proportion of indigestible material in birds (plumage, bones and bare parts - bill, legs and feet) Phillips *et al.* (1999) assessed that only around 65% of the fresh body mass was available as food. The same correction was applied in this study.

For the energetic content of goose barnacle we used the same values for meal size (35g) and calorific content (1.9 kJ g^{-1}) as Phillips *et al.* (1999).

Rabbits (*Oryctolagus cuniculus*) have a mean calorific value of 6.24 kJg^{-1} (derived from 4.95 Kcal g^{-1} dry weight in Moors 1987) and we assume the universal meal mass of 100g. While rabbits undoubtedly have a high proportion of indigestible material, we are not concerned with the numbers consumed and therefore present only the calorific content per meal.

Sotherland & Rahn (1987) estimate the calorie content of a typical avian egg as 29 kJ g^{-1} multiplied by the dry weight of the egg. Eggs found in the diet of great skuas belonged mostly to kittiwakes and terns, therefore egg mass was assumed to be 50g (Cramp & Simmons 1983), which corresponds to 14.4g dry weight. Therefore energetic value of a single egg was 417.6 kJ g^{-1}.

PREY CONSUMED

From the proportion of meals of each prey type and the calorific content of these meals, it is possible to calculate the proportion of energy derived from each prey type for adult and young skuas (Table 3). Since we also know the energy requirements for maintenance and development (Table 2) it is possible to calculate the energy provided by each of the main prey types. On the basis of calorific values of prey it is then possible to back-calculate the weight of each prey consumed. With known body weights of seabirds and assuming 35% of each carcass is indigestible, it is possible to estimate the numbers of seabirds consumed.

For weights of seabirds we used values published in Cramp & Simmons (1977, 83). The weight of guillemot chicks was taken as the mean of three published fledging weights in Cramp & Simmons (1983). As young skuas are mostly predated as they become mobile at around 25 days old, the mean weight at this age was ≈800g (S.Votier *unpublished data*).

SENSITIVITY ANALYSIS FOR PREY CONSUMPTION MODEL

As with sensitivity tests for energy requirements, inputs to the prey consumption model were initially increased by 1% and also a range of likely extremes. This approach closely followed Phillips *et al.* (1999) who found published values of prey calorific densities to be ±25%, upper and lower limits for mean meal mass of birds and fish to be ±30% and a broader range for mean meal mass of goose barnacles (±50%). Variations in the proportion of different prey taken were set at ±50% because of the problems of using pellets to assess great skua diet (see Discussion). We also investigate the effect on prey consumption that a ±10% change in the proportion of bird-specialists would have.

Results

ENERGY REQUIREMENTS

Energy requirements for breeding adult and young of bird-specialists and non-specialists as well as non-breeders are shown in Table 2. Over 80% of the energy demands of the whole colony were required for maintenance and activity of breeding adults, with less than 5% of this value being required by adult bird-specialist skuas. The next largest energy requirement was by chicks (11.5%) with the remaining amount (< 8%) going to non-breeding adults.

SENSITIVITY ANALYSIS OF ENERGETIC REQUIREMENTS

The effect on the energy requirements of the colony following adjustments to input parameters are presented in Table 6. These show that the parameters most effected by a 1% increase are the size of the breeding population, BMR (and therefore also the FMR:BMR ratio) and food assimilation efficiency. Other parameters showed relatively minor changes after a 1% change. However because of the broad range of extremes for estimates of the non-breeding population, pre-breeding period and post-fledging period, all of these parameters affected model outputs considerably.

PREY CONSUMPTION

By combining data on prey composition in the diet and energy content of meals (Table 3) we were able to estimate the mass of prey consumed by skuas during 1999 at Hermaness (Table 4). The bulk of prey consumed was fish (69.3 tonnes), followed by birds (6.9 tonnes) with smaller but substantial amounts of rabbit (2.5 tonnes) and goose barnacle (0.6 tonnes) also consumed. A further 0.08 tonnes of eggs were also estimated to have been eaten.

SEABIRD CONSUMPTION

The numbers of seabirds estimated to have been consumed by great skuas at Hermaness during 1999 is shown in Table 5. In all, just over 11,000 seabirds were consumed, the bulk of these being adult and young auks (71%) with large numbers of fulmars (23%) and the remainder consisting of kittiwakes (4%) and cannibalised great skua chicks (2%).

The majority of seabirds were consumed by non bird-specialist skuas (64%). However, while bird-specialists only consisted of 5% of the population, they consumed 30% of the bird prey. Non-breeders only consumed around 6% of bird prey at Hermaness.

SENSITIVITY ANALYSIS OF PREY CONSUMPTION MODEL

The effect of altering input parameters on the prey consumption model are shown in Appendices I-IV. In summary, changes in the calorie content of fish and bird have a considerable effect on the estimated amounts of all prey consumed, whereas the calorie content of goose-barnacle, rabbit and eggs have very little effect. The effect of reducing meal mass on parameter outputs for the main prey types are similar to the effect of calorie content, but reduced.

Parameters that resulted in at least a 5% change to the estimated numbers of birds consumed (and therefore most important to the question being addressed by this study) are presented in Table 7. The percentage of carcass utilisation had a considerable effect on the estimated numbers of seabirds consumed – a 25% decrease resulted in an estimated increase in prey consumption by a third. The meal to pellet ratio also considerably effected the estimated numbers of birds eaten, using a ratio of one meal to one pellet produced an increase of 60% for adult breeders, 10% for chicks and 95% for non-breeders.

Table 1. Daily field metabolic rate of breeding adult great skuas calculated from time budget analysis. The energy cost of specific activities are from Caldow (1988).

Activity	FMR:BMR ratio	Percentage of time for bird-specialists	Percentage of time for non-specialists
Resting	1.5	41.7	40.3
General	1.97	36.8	37.5
Gliding flight	3.1	20.8	5.5
Flapping flight	12.65	0.7	16.67
Mean FMR:BMR ratio		2.1	3.6

Table 2. Energy requirements of all great skuas at Hermaness. Note that for all energy requirements a value for food assimilation efficiency (0.76) was applied (see text for calculation of other values).

	Individual/pair		Whole colony	
	Daily	Whole season	Daily	Breeding season
Breeding adults				
Maintenance and activity				
Non bird-specialist	2548 kJ	271.1 x 10^3 kJ	3.15 x 10^6 kJ	336.5 x 10^6 kJ
Bird-specialist	1487 kJ	158.2 x 10^3 kJ	118.7 x 10^3 kJ	12.7 x 10^6 kJ
Cost of egg production				
Non bird-specialist	-	1470 kJ pair^{-1}	-	909.7 x 10^3kJ
Bird-specialist	-	1470 kJ pair^{-1}	-	58.8 x 10^3 kJ
Non-breeding adults				
Maintenance and activity	2548 kJ	271.1 x 10^3 kJ	331 x 10^3 kJ	29.8 x 10^6 kJ
Chicks				
Hatching to fledging				
Non bird-specialist	-	45.7 x 10^3 kJ	-	34.0 x 10^6kJ
Bird-specialist	-	45.7 x 10^3 kJ	-	2.19 x 10^6kJ
Fledging to departure				
Non bird-specialists	-	18.5 x 10^3 kJ	-	12.8 x 10^6 kJ
Bird-specialist	-	18.5 x 10^3 kJ	-	827 x 10^3 kJ
Total colony energy	-	-	-	428.9 x 10^6 kJ

Table 3. Energy content of main prey types and percentage contribution to the diet of breeding adult, young and non-breeding great skuas. For definition of bird-specialists see main text.

				Adult breeders				Chicks				Non-breeders	
				Bird-specialists		Other		Bird-specialists		Other			
	Energy content (kJ g^{-1})	Prey meal mass (g)	Prey energy content (kJ)	% in diet	% energy	% in diet	% energy	% in diet	% energy	% in diet	% energy	% in diet	% energy
Fish	5.2	100	520	16.2	8.7	88.5	83.1	33.8	19.6	100	100	81.2	82.5
Auk	10.9	100	1090	56.5	63.9	3.9	7.6	47.8	58.0	0	0	2.8	5.9
Guillemot (chick)	10.9	100	1090	2.8	3.2	0.1	0.2	2.1	2.6	0	0	0	0
Kittiwake	10.9	100	1090	5.7	6.5	0	0	5.1	6.1	0	0	0.2	0.5
Fulmar	10.9	100	1090	12.9	14.6	2.7	5.4	11.0	13.3	0	0	1.7	3.5
Great skua (chick)	10.9	100	1090	0.3	0.3	0.1	0.3	0.2	0.3	0	0	0	0
Egg	29	50	417.6	0	0	0.6	0.5	0	0	0	0	0	0
G/B	1.9	40	76	1.4	0.1	1.6	0.2	0	0	0	0	9.0	1.3
Rabbit	6.24	100	624	4.2	2.7	2.4	2.7	0	0	0	0	5.1	6.2

Table 4. Results of prey consumption model at Hermaness during 1999, for all main prey types.

	Mass of prey (kg) consumed by:					
	Bird specialists	Bird specialist (chicks)	Others	Others (chicks)	Non-breeders	Total
Fish	213	114	55,271	8991	4733	69,332
Bird	1582	343	4533	0	418	6876
Rabbit	55	0	2102	0	297	2454
Goose barnacle	7	0	337	0	210	554
Egg	0	0	82	0	0	82

Table 5. Estimated number of birds eaten by great skuas at Hermaness during 1999

	Total numbers consumed by					
	Bird specialists	Bird specialist (chicks)	Others	Others (chicks)	Non-breeders	Total
Puffin	1945	421	4394	0	423	7183
Guillemot chicks	232	45	627	0	0	904
Kittiwake	309	70	0	0	56	435
Fulmar	326	71	2079	0	185	2661
Great skua chicks	7	2	169	0	0	178
Total	2819	607	7269	0	664	11,359

Table 6. Sensitivity tests for energy demands of adult skuas

Parameter	Change for 1% increase (%)	Range of likely extremes (see text for explanation) (%)	Change in output after extremes (%)
Breeding population	0.92	±10	±9.21
Proportion population which are bird-specialists	<0.001	±10	0
Non-breeding population	0.06	-50 +120	-4.14 +1.66
Pre-breeding period	0.22	±50	±11.22
Incubation period	0.22	±10	±2.17
Chick-rearing period	0.34	±10	±3.47
Post-fledging period	0.13	±50	±6.73
Adult BMR	0.84	±10	±8.43
FMR:BMR ratio non-specialists	0.84	±15	±12.60
FMR:BMR ratio bird-specialists	<0.001	±15	0
FMR:BMR ratio non-breeders	0.08	±15	±1.24
Clutch size	<0.001	±10	±0.02
Fresh egg mass	<0.001	±10	±0.02
Egg energy density	<0.001	±10	±0.02
Egg synthesis efficiency	<0.001	±10	±0.02
Food assimilation efficiency	0.84	±8	-6.22 +7.31
Brood size at 20 days	0.07	±10	±0.73
Brood size at fledging	<0.001	±10	±0.02
Chick mass at fledging	0.07	±10	±0.74
Energy demands for chick development	<0.001	±20	±0.03

Table 7. Outputs for sensitivity analysis influencing the number of birds consumed.

	% Change in estimated number of birds eaten		
Input parameter	Adult breeders	Chicks	Non-breeders
Fish calorific content			
+1%	-0.62	-0.20	-0.82
+25%	-13.08	-4.68	-17.10
-25%	+19.75	+5.16	+26.00
Bird calorific content			
+1%	+0.66	-0.78	-0.10
+25%	+16.01	-16.73	-2.42
-25%	-17.32	+25.15	+2.54
Fish meal mass			
+1%	-0.62	-0.20	-0.82
+30%	-15.19	-5.56	-19.85
-30%	+24.99	+6.25	+32.91
Bird meal mass			
+1%	+0.66	+0.19	+0.90
+30%	+19.07	+4.74	+22.73
-30%	-20.98	-7.76	-32.91
% carcass utilisation			
+1%	-0.99	-0.99	-0.99
+25%	-20.00	-20.00	-20.00
-25%	+33.33	+33.33	+33.33
Meal:pellet ratio			
1:1 (following Phillips et al. 1997)	+62.09	+10.41	+94.73
Proportion of bird-specialists			
+10%	+3.11	+8.08	-
-10%	-1.77	-11.57	-

Discussion

Bioenergetics models are only likely to provide broad estimates of prey consumption and the results may be subject to a number of biases. From the sensitivity analysis it was found that the parameters which had the greatest effect on energy demand was the FMR:BMR ratios for breeding adults. These values have been the source of considerable uncertainty in other similar studies (i.e. Furness 1978, Cairns *et al.* 1990, Adams *et al.* 1991, Phillips *et al.* 1999) but are very similar to those published for other seabirds (Gabrielsen *et al.* 1987, Bryant & Furness 1995) and are certainly comparable with those used by Phillips *et al.* (1999). While differences in the energy requirements of specialist and non-specialist skuas have not, to our knowledge, been accurately calculated previously, specialist gulls and skuas with improved reproductive output was thought to have been contributed, in part, by spending less time foraging (Tivelpiece & Volkman 1982, Pietz 1987, Spears 1994).

Estimates of the costs of egg production are typically based on indirect calculations of egg energy content and egg synthesis efficiency (i.e. Ricklefs 1974, Rahn *et al.* 1985, Phillips *et al.* 1999). These estimates tend to provide a wide range of values from 13-41% of BMR in passerines, 29% in hawks & owls, 82-128% in shorebirds and over 200% in waterfowl (Carey 1996). The costs of egg production in this study of 1470 kJ pair^{-1} accord to 208% of BMR (including assimilation efficiency of 0.76), which is in keeping with the high estimates for non-passerines listed above. However Monaghan & Nager (1997) provide a review of evidence that typical estimates of the cost of egg production may be underestimates as these models do not take into account the costs of finding and manufacturing materials for egg production and apply conservative estimates of biosynthesis efficiency. Indeed, Ward (1996) measured daily energy expenditure of barn swallows *Hirundo rustica* during egg formation as 370% of BMR, but conversely this value was not different from that calculated during chick rearing. But in contrast Nilsson & Råhberg (2001), who calculated the actual biosynthetic costs of producing an egg in great tits, found it to be 27% of BMR, which is relatively low compared to published values for passerines

BMR). In short, while the estimates of the costs of egg production used in this bioenergetics model may have error associated with them, conflicting evidence suggests that until specific studies measure these costs in great skuas directly, we stuck with these best estimates.

Because great skuas show bi-parental care with males provisioning females during incubation (Furness 1987) the demands of re-heating eggs following cooling are slight and therefore our model estimates assumed no extra costs to incubation. However in other species with bi-parental care, energy expenditure of females during incubation may be 20-30% higher than for non-incubating females (Williams 1996). Typically costs of incubation in seabirds are 120% of BMR (Williams 1996), which is lower than the FMR values used in our study, but given the uncertain increased energy demands incurred by the foraging male these estimates may prove reasonably accurate.

The size of the breeding population had a considerable effect on the energy demand of the whole colony. Great skuas are a difficult species to census accurately, particularly at areas where topography prevents counting from a series of high vantage points, as is the case at Hermaness. However, the similarity between the distribution of AOTs mapped in 1997 and those mapped in areas intensively studied as part of the research, suggests a fairly accurate estimate of the breeding population at Hermaness.

Errors in estimating the non-breeding population of skuas at Hermaness are unlikely to dramatically alter the model outputs, but deserve consideration. Counts of non-breeding birds used in this study are lower than those previously made at Hermaness (SNH Reports 1987-92), possibly because previous counts were made at night when numbers are greatest (Klomp & Furness 1990). However given that factors such as food availability and recruitment rates to the colony may effect counts of non-breeding birds (Klomp & Furness 1990), it may be that numbers have declined.

While changes in the values for food assimilation efficiency have a considerable effect on model outputs, because they were calculated specifically for great skuas, we are confident that this parameter is accurate.

PREY CONSUMPTION ESTIMATES

Assessing diets in the manner used in this study are known to be subject to error (Duffy & Jackson 1986). Variations in the composition of prey can have serious effects on the estimates of prey consumed as predicted by this model. Phillips *et al.* (1999) assumed that one pellet was equivalent to one meal, however captive trials suggest that skuas produce several pellets per meal (Votier *et al.* 2001). Relaxing the model to assume that one pellet was equal to one meal dramatically increased the estimated numbers of seabirds eaten by skuas. But we concede that using captive birds to compare with a natural system may be problematic. Captive skuas could be less efficient at dealing with bird prey and therefore may ingest a higher proportion of indigestible material. Also the meals fed to captive skuas were not all 100g as assumed in this study. However because captive birds had plenty of time to feed upon a carcass, without the threat of kleptoparasitism, it is likely that they were able to carefully pick at the carcass and therefore actually ingest a smaller proportion of indigestible material than wild birds. While the exact number of pellets produced by wild skuas is unknown, our evidence suggests that a ratio of one meal to one pellet is inaccurate.

STRATIFIED SAMPLING

There is compelling evidence that great skuas breeding at Hermaness show dietary specialisation with bird-specialists being more abundant adjacent to coastal seabird colonies. Therefore sampling diet at random from this site may have provided a biased estimate of the overall diet composition. To correct for this possible bias we adopted stratified sampling technique, incorporating the numbers of skua pairs that specialised in feeding predominantly on birds. The estimation of the proportion of bird-specialists in the population therefore has implications for the impact of skuas on seabirds at Hermaness. Spears (1994) reports that the in a colony of 25,000 western gulls *Larus occidentalis* the percentage which specialised in feeding on birds was 1.1%, which compares with 5% of bird-specialists estimated in this study. However we have data suggesting that the proportion of bird-specialists may vary with colony size, and also that the percentages were similar at selected study plots in three consecutive years (Chapter 6). Therefore we are confident that our estimate of bird-specialists is accurate.

EFFECT ON SEABIRD POPULATIONS

Since Phillips *et al.* (1999) calculated that 229 pairs of great skuas breeding at St Kilda consumed 40,800 seabirds in 1996, we may have predicted that the much larger skua colony at Hermaness would consume even more seabirds. However despite using the same model, differences in diet composition as well as the use of different pellet to meal ratios, meant we calculated that great skuas at Hermaness only consumed just over 11,000 seabirds (Table 5). Therefore the impact by great skuas was much less than at St Kilda.

Auks are the most abundant bird prey in the diet of great skuas and are also the most abundant seabirds at Hermaness. While the pellets of adult auks could not confidently be identified to species, the large number of remains and observed attacks on Atlantic puffins suggest that this species made up the bulk of those birds taken, and our model was calculated accordingly. Most Atlantic puffins taken appear to be adults with no chick remains or pellets discovered. Given that young puffins rarely stray from the safety of deep nesting burrows and fledge at night (Harris 1984) this is not surprising. Adult puffins were either taken in flight or, by skuas defending a feeding territory, caught attending the breeding colony. Assuming that most of the estimated 7183 auks taken by all skuas were adult puffins, what is the impact of this predation? The mean number of puffin pairs estimated at Hermaness in 1997 was 28,300 (range 14,100 to 42,200 pairs) (Lewis 1997). Great black-backed gulls feeding on puffins at St Kilda took a high proportion of immature birds, but gulls with territories in puffin areas took few immatures (Harris 1980). Therefore we might expect that the bird-specialist great skuas were taking predominantly breeding adult puffins, and other skuas a higher proportion of adult birds not yet breeding. We calculated that bird-specialists consumed 2366 puffins (Table 5) which accounts for ≈ 6-17% of the breeding population. The remainder of the skua population consumed 4817 puffins (Table 5) which represents a higher proportion of the puffin population (≈11-34%), but given that these birds may be taking predominantly immatures, the impact on the population is probably much less severe than this. Further work is required to determine the size of the non-breeding population of puffins.

The large numbers of Northen fulmars estimated to be consumed reflects their abundance (≈30,000 birds) at the colony. Their presence in the diet of all skuas around Hermaness reflects their ubiquitous nature. Compared with the densely packed colonies of auks and black-legged kittiwakes, northern fulmars nest widely dispersed throughout the coastline at Hermaness. It seems likely that because of their large size and their habitat of ejecting foul-smelling oil in response to predators, great skuas may find it difficult to kill adult fulmars and the bulk of birds eaten may be represented by young. With productivity estimated at 0.56 young fledged per nesting attempt and 13,956 apparently occupied sites (AOS), 7815 young were produced. Therefore it is unlikely that the estimated 2,661 fulmars consumed by great skuas at Hermaness are likely to have a serious effect on the population.

It is conspicuous that the vast majority of black-legged kittiwakes are taken by bird-specialists. Heubeck, *et al.* (1997) report that black-legged kittiwakes at Shetland colonies have moved from exposed coastlines to areas of enclosed cliffs and even caves, possibly in response to predation pressure. Black-legged kittiwakes nesting on exposed cliffs appear to be at high risk from predation and perhaps only skuas adapted to bird predation are able to gain access to birds now nesting in coastal inlets or caves. Unfortunately the proportion of young to adult kittiwakes is not known, but observations suggest that both are taken by great skuas. Of the 788 breeding attempts by kittiwakes at Hermaness during 1999, and assuming a productivity of 0.74 chicks fledged per pair (average Shetland productivity: Upton, Pickerel & Heubeck 1999) a total of 2159 kittiwakes were available for predation. Therefore ≈20% of all kittiwakes at Hermaness were predated.

Because sick or weak birds are more likely to be taken by predators (Temple 1987, Møller & Nielsen 1997), is it possible that predation by great skuas is actually likely to remove low quality members from the population and have little effect on population dynamics? Temple (1987) showed that while predators are more likely to take sub-standard prey, the proportion of this prey depends upon the ease of capture. If prey are relatively easy to catch then sub-standard prey are just as likely to be caught as 'normal' members of the population. But for prey which are difficult to catch, sub-standard members of the population are more likely to be caught. Therefore fast flying powerful seabirds like auks, which are difficult for skuas to catch, may not only be less likely to be predated overall but also be more likely to lose less fit members of the population. By comparison smaller and slower flying species like black-legged kittiwakes may be more easier to catch and so could not only suffer from high predation pressure, but may lose many high quality individuals. The corollary of this effect may explain the declines in the black-legged kittiwake more fully.

FUTURE CHANGES

A reduction in the amount of fish in the diet of great skuas is most likely to be compensated by an increase in either of the other main prey; birds, goose-barnacles or rabbits. The extent of any switching is impossible to predict, but given that currently$\approx$ 9% of the mass of prey consumed consists of bird prey, compared with $\approx$ 4% of rabbits and goose-barnacles, bird prey is the most likely food to replace fish. The dietary specialisation exhibited by great skuas at Hermaness may have implications for seabird predation. Since these birds take a high proportion of seabirds (30%) compared with their numbers (5% of the population at Hermaness), any increase in their number may increase bird predation disproportionately to any population increase. However work suggests that these may be high quality individuals (S.Votier *unpublished data*) and so the number of bird-specialists may be limited. But until more is understood about what regulates the numbers of bird-specialist great skuas, the future is uncertain. Also because of the complex nature of fish populations and the possibility that reduced fishing pressure may allow some fish stocks to recover, only continued monitoring of skua foraging behaviour and diet, as well as population dynamics of other seabirds will reveal such effects.

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Chapter 5, Appendix I. Sensitivity analysis of prey consumption model for all adult breeders.

Model parameter	% change weight of fish consumed	% change to number of birds consumed	% change weight of goose barnacle consumed	% change weight of rabbit consumed	% change weight of eggs consumed
Fish calorie content					
+1%	-0.14	-0.62	-0.83	-0.84	-0.86
+25%	+3.00	-13.08	-17.16	-17.48	-17.904
-25%	-4.58	+19.75	+26.41	+27.20	+27.88
Bird calorie content					
+1%	-0.10	+0.66	-0.12	-0.19	-0.07
+25%	-2.32	+16.01	-2.94	-2.19	-1.75
-25%	+2.50	-17.32	+3.35	+2.53	+1.83
Goose-barnacle calorie content					
+1%	0	0	+1.00	0	0
+25%	-0.05	-0.05	+24.94	-0.04	-0.05
-25%	+0.05	+0.05	-24.96	+0.04	+0.05
Rabbit calorie content					
+1%	-0.04	-0.03	-0.04	+0.95	-0.05
+25%	-0.98	-0.74	-0.87	+23.59	-1.15
-25%	+1.00	+0.75	+0.89	-24.13	+1.17
Egg calorie content					
+1%	0	0	0	0	+0.99
+25%	-0.18	-0.10	-0.16	-0.20	+24.74
-25%	+0.18	+0.10	+0.16	+0.20	-24.84
Fish meal mass					
+1%	+0.14	-0.62	-0.83	-0.84	-0.86
+30%	+3.49	-15.19	-19.90	-20.260	-20.73
-30%	-5.81	+24.99	+33.50	+34.57	+24.12
Bird meal mass					
+1%	-0.10	+0.66	-0.12	-0.09	-0.07
+30%	-2.77	+19.07	-3.49	-2.60	-2.09
-30%	+3.03	-20.98	+4.08	+3.10	+2.200
G/B meal mass					
+1%	0	0	+1.00	0	0
+50%	-0.09	-0.09	+49.85	-0.09	-0.09
-25%	+0.05	+0.05	-24.96	+0.04	+0.04
Rabbit meal mass					
+1%	-0.04	-0.03	-0.04	+0.95	-0.05
+30%	-1.18	-0.89	-1.04	+28.25	-1.37
-30%	+1.21	+0.91	+1.07	-29.03	+0.30
Egg meal mass					
+1%	0	0	-0.01	-0.01	+1.00
+30%	-0.24	-0.13	-0.21	-0.27	+32.966
-30%	+0.24	+0.13	+0.21	+0.27	-33.15
% Carcass used					
+1%	0	-0.99	0	0	0
+25%	0	-20.00	0	0	0
-50%	0	+33.33	0	0	0
Meal:pellet ratio	-9.98	+62.09	-12.10	-8.77	-7.66
Proportion of bird-specialists					
+10%	+0.20	+3.11	+0.45	+0.32	+0.05
-10%	+0.63	-1.77	+0.75	-0.03	+0.21

Chapter 5, Appendix II. Sensitivity analysis of prey consumption model for all adult breeders, showing percentage change in estimates of different prey consumed.

	Fish	G/B	Rabbit	Total birds	Auk	Auk chick	Kittiwake	Fulmar	Skua chick	Egg
Proportion fish										
+1%	+0.14	-0.83	-0.84	-0.62	-0.60	-0.66	-0.09	-0.72	-0.82	-0.86
+50%	+5.13	-29.22	-29.672	-22.44	-21.72	-23.39	-4.18	-25.90	-29.06	-30.36
-50%	-12.50	+72.37	+75.42	+53.44	+51.40	+58.37	+4.56	+62.05	+73.00	+77.37
Proportion G/B										
+1%	0	+1.0	0	0	0	0	0	0	0	0
+50%	-0.08	+48.85	-0.08	-0.09	-0.09	-0.07	-0.06	-0.10	-0.09	-0.09
-50%	+0.08	-49.95	+0.08	+0.09	+0.09	+0.07	+0.06	+0.10	+0.09	+0.09
Proportion rabbit										
+1%	-0.04	-0.04	+0.96	-0.03	-0.03	-0.04	-0.03	-0.03	-0.04	-0.05
+50%	-1.94	-1.72	+46.66	-1.46	-1.43	-2.12	-1.34	-1.31	-2.00	-2.26
-50%	+2.03	+1.80	-48.83	+1.52	+1.48	+2.22	+1.38	+1.36	+2.10	+2.38
Proportion Auk										
+1%	-0.06	-0.07	-0.06	+0.40	+0.75	-0.20	-0.63	-0.15	-0.07	-0.04
+50%	-2.66	-3.41	-2.60	+19.20	+35.30	-7.83	-24.21	-6.49	-3.29	-2.00
-50%	+2.93	+4.14	+3.29	-21.05	-41.50	+9.71	+46.94	+9.88	+4.36	+2.11
Proportion Auk chick										
+1%	0	0	-0.01	+0.07	-0.01	+1.00	-0.03	-0.01	0	0
+50%	-0.17	-0.17	-0.24	+3.73	-0.55	+49.12	-1.56	-0.29	-0.23	-0.21
-50%	+0.17	+0.17	+0.24	-3.76	+0.57	-49.70	+1.61	+0.29	+0.24	+0.21
Proportion Kittiwake										
+1%	0	0	0	+0.01	-0.02	-0.02	+0.93	-0.01	0	0
+50%	-0.01	-0.07	-0.07	+0.61	-0.96	-0.85	+45.29	-0.43	-0.13	0
-50%	+0.01	+0.07	+0.08	-0.65	+1.02	+0.91	-48.32	+0.43	+0.14	0
Proportion Fulmar										
+1%	-0.03	-0.04	-0.03	+0.16	-0.08	-0.05	-0.15	+0.93	-0.04	-0.02
+50%	-1.68	-2.10	-1.31	+7.96	-3.76	-2.51	-6.80	+45.13	-1.72	-1.15
-50%	+1.77	+2.25	+1.39	-8.36	+4.21	+2.82	+7.87	-48.23	+1.84	+1.19
Proportion skua chick										
+1%	0	0	0	+0.01	0	0	0	0	+0.99	0
+50%	-0.13	-0.12	-0.14	+0.66	-0.13	-0.14	-0.14	-0.12	+49.80	-0.14
-50%	+0.13	+0.12	+0.14	-0.66	+0.13	+0.14	+0.14	+0.12	-49.93	+0.14
Proportion egg										
+1%	-0.01	-0.01	0	0	0	-0.01	0	0	-0.01	+0.99
+50%	-0.36	-0.30	-0.41	-0.20	-0.18	-0.35	0	-0.20	-0.36	+49.37
-50%	+0.36	+0.30	+0.41	+0.20	+0.19	+0.35	0	+0.20	+0.36	-49.79
Proportion of bird specialists										
+10%	+0.20	+0.45	+0.32	+3.11	+3.39	+2.79	+10.3	+1.7	+0.54	+0.05
-10%	+0.63	+0.75	-0.03	-1.77	-2.02	-2.61	-9.66	-0.07	-0.12	+0.21

Chapter 5, Appendix III. Sensitivity analysis of prey consumption model for all chicks.

Model parameter	% change weight of fish consumed	% change to number of birds consumed	% change weight of goose barnacle consumed	% change weight of rabbit consumed	% change weight of eggs consumed
Fish calorie content					
+1%	-0.98	-0.20	-	-	-
+25%	-19.80	-4.68	-	-	-
-25%	+32.97	+5.16	-	-	-
Bird calorie content					
+1%	-0.01	-0.78	-	-	-
+25%	-0.21	-16.73	-	-	-
-25%	+0.32	+25.15	-	-	-
Goose-barnacle calorie content					
+1%	-	-	-	-	-
+25%	-	-	-	-	-
-25%	-	-	-	-	-
Rabbit calorie content					
+1%	-	-	-	-	-
+25%	-	-	-	-	-
-25%	-	-	-	-	-
Egg calorie content					
+1%	-	-	-	-	-
+25%	-	-	-	-	-
-25%	-	-	-	-	-
Fish meal mass					
+1%	+0.01	-0.20	-	-	-
+30%	+0.29	-5.56	-	-	-
-30%	-0.33	+6.25	-	-	-
Bird meal mass					
+1%	-0.01	+0.19	-	-	-
+30%	-0.25	+4.74	-	-	-
-30%	+0.40	-7.76	-	-	-
G/B meal mass					
+1%	-	-	-	-	-
+50%	-	-	-	-	-
-25%	-	-	-	-	-
Rabbit meal mass					
+1%	-	-	-	-	-
+30%	-	-	-	-	-
-30%	-	-	-	-	-
Egg meal mass					
+1%	-	-	-	-	-
+30%	-	-	-	-	-
-30%	-	-	-	-	-
% Carcass used					
+1%	0	-0.99	-	-	-
+25%	0	-20	-	-	-
-50%	0	+33.33	-	-	-
Meal:pellet ratio					
1:1	+0.58	+10.41			
Proportion of bird-specialists					
+10%	-0.54	+8.08			
-10%	+0.49	-11.57	-	-	-

Chapter 5, Appendix IV. Sensitivity analysis of prey consumption model for all chicks, showing percentage change in estimates of different prey consumed.

	Fish	G/B	Rabbit	Total birds	Auk	Auk chick	Kittiwake	Fulmar	Skua chick	Egg
Proportion fish										
+1%	+0.01	-	-	-0.20	-0.20	-0.20	-0.20	-0.20	-0.20	-
+50%	+0.47	-	-	-8.93	-8.93	-8.93	-8.93	-8.93	-8.93	-
-50%	-0.57	-	-	+10.88	+10.88	+10.88	+10.88	+10.88	+10.88	-
Proportion G/B										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%	-	-	-	-	-	-	-	-	-	-
Proportion rabbit										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%	-	-	-	-	-	-	-	-	-	-
Proportion Auk										
+1%	0	-	-	+0.11	+0.42	-0.58	-0.58	-0.58	-0.58	-
+50%	-0.29	-	-	+4.33	+16.27	-22.45	-22.45	-22.45	-22.45	-
-50%	+0.52	-	-	-7.87	-29.56	+40.87	+40.87	+40.87	+40.87	-
Proportion Auk chick										
+1%	0	-	-	+0.05	-0.03	+0.97	-0.03	-0.03	-0.03	-
+50%	-0.02	-	-	+2.37	-1.27	+48.10	-1.27	-1.27	-1.27	-
-50%	+0.02	-	-	-2.44	+1.30	-49.35	+1.30	+1.30	+1.30	-
Proportion Kittiwake										
+1%	0	-	-	+0.05	-0.06	-0.06	+0.94	-0.06	-0.06	-
+50%	-0.04	-	-	+2.59	-2.98	-2.98	+45.53	-2.98	-2.98	-
-50%	+0.04	-	-	-2.75	+3.17	+3.17	-48.41	+3.17	+3.17	-
Proportion Fulmar										
+1%	0	-	-	-0.02	-0.13	-0.13	-0.13	+0.87	-0.13	-
+50%	-0.08	-	-	-0.78	-6.26	-6.26	-6.26	+40.62	-6.26	-
-50%	+0.09	-	-	+0.88	+7.154	+7.154	+7.154	-46.43	+7.15	-
Proportion skua chick										
+1%	0	-	-	0	0	0	0	0	1.00	-
+50%	0	-	-	-0.02	-0.14	-0.22	-0.22	-0.22	49.78	-
-50%	0	-	-	+0.02	+0.14	+0.22	+0.22	+0.22	-49.93	-
Proportion egg										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%	-	-	-	-	-	-	-	-	-	-
Proportion of bird-specialists										
+10%	-0.54	-	-	+8.08	+8.08	+8.08	+8.08	+8.08	+8.08	+8.08
-10%	+0.49	-	-	-11.57	-11.57	-11.57	-11.57	-11.57	-11.57	-11.57

Chpater 5, Appendix V. Sensitivity analysis of prey consumption model for all non-breeders.

Model parameter	% change weight of fish consumed	% change to number of birds consumed	% change weight of goose barnacle consumed	% change weight of rabbit consumed	% change weight of eggs consumed
Fish calorie content					
+1%	-0.82	-0.82	-0.82	-0.82	-
+25%	-17.10	-17.10	-17.10	-17.10	-
-25%	+26.00	+26.00	+26.00	+26.00	-
Bird calorie content					
+1%	-0.10	-0.10	-0.10	-0.10	-
+25%	-2.42	-2.42	-2.42	-2.42	-
-25%	+2.54	+2.54	+2.54	+2.54	-
Goose-barnacle calorie content					
+1%	-0.01	-0.01	-0.01	-0.01	-
+25%	-0.30	-0.30	-0.30	-0.30	-
-25%	+0.30	+0.30	+0.30	+0.30	-
Rabbit calorie content					
+1%	-0.06	-0.06	-0.06	-0.06	-
+25%	-1.36	-1.36	-1.36	-1.36	-
-25%	0	0	0	+33.33	-
Egg calorie content					
+1%	-	-	-	-	-
+25%	-	-	-	-	-
-25%	-	-	-	-	-
Fish meal mass					
+1%	+0.17	-0.82	-0.82	-0.82	-
+30%	+4.20	-19.85	-19.85	-19.85	-
-30%	-6.60	+32.91	+32.91	+32.91	-
Bird meal mass					
+1%	-0.10	+0.90	-0.10	-0.10	-
+30%	-2.89	+22.73	-2.89	-2.89	-
-30%	+3.07	-32.91	+3.07	+3.07	-
G/B meal mass					
+1%	-0.01	-0.01	0.99	-0.01	-
+50%	-0.67	-0.67	49.11	-0.67	-
-25%	+0.34	+0.34	-24.78	+0.34	-
Rabbit meal mass					
+1%	-0.06	-0.06	-0.06	+0.94	-
+30%	-1.83	-1.83	-1.83	+27.62	-
-30%	+1.90	+1.90	+1.90	-28.67	-
Egg meal mass					
+1%	-	-	-	-	-
+30%	-	-	-	-	-
-30%	-	-	-	-	-
% Carcass used					
+1%	0	-0.99	0	0	-
+25%	0	-20.00	0	0	-
-50%	0	+33.33	0	0	-
Meal:pellet ratio					
1:1	-10.92	+94.73	-10.92	-10.92	-

Chapter 5, Appendix VI. Sensitivity analysis of prey consumption model for all non-breeders, showing percentage change in estimates of different prey consumed.

	Fish	G/B	Rabbit	Total birds	Auk	Auk chick	Kittiwake	Fulmar	Skua chick	Egg
Proportion fish										
+1%	+0.17	-0.82	-0.82	-0.82	-0.82	-	-0.82	-0.82	-	-
+50%	+6.18	-29.21	-29.21	-29.21	-29.21	-	-29.21	-29.21	-	-
-50%	-14.87	+70.26	+70.26	+70.26	+70.26	-	+70.26	+70.26	-	-
Proportion G/B										
+1%	-0.01	+0.99	-0.01	-0.01	-0.01	-	-0.01	-0.01	-	-
+50%	-0.67	+49.11	-0.67	-0.67	-0.67	-	-0.67	-0.67	-	-
-50%	+0.67	-49.70	+0.67	+0.67	+0.67	-	+0.67	+0.67	-	-
Proportion rabbit										
+1%	-0.06	-0.06	+0.94	-0.06	-0.06	-	-0.06	-0.06	-	-
+50%	-3.01	-3.01	+45.96	-3.01	-3.01	-	-3.01	-3.01	-	-
-50%	+3.20	+3.20	-48.58	+3.20	+3.20	-	+3.20	+3.20	-	-
Proportion Auk										
+1%	-0.06	-0.06	-0.06	+0.58	+0.94	-	-0.06	-0.06	-	-
+50%	-2.87	-2.87	-2.87	+28.04	+45.40	-	-2.87	-2.87	-	-
-50%	+3.04	+3.04	+3.04	-29.74	-48.48	-	+3.04	+3.04	-	-
Proportion Auk chick										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%	-	-	-	-	-	-	-	-	-	-
Proportion Kittiwake										
+1%	-0.01	-0.01	-0.01	+0.08	-0.01	-	+0.99	-0.01	-	-
+50%	-0.25	-0.25	-0.25	+4.00	-0.25	-	+49.62	-0.25	-	-
-50%	+0.26	+0.26	+0.26	-4.00	+0.25	-	-49.87	+0.25	-	-
Proportion Fulmar										
+1%	-0.04	-0.04	-0.04	+0.24	-0.04	-	-0.04	+0.96	-	-
+50%	-1.73	-1.73	-1.73	+11.97	-1.72	-	-1.73	+47.41	-	-
-50%	+1.73	+1.73	+1.73	-12.40	+1.79	-	+1.73	-49.10	-	-
Proportion skua chick										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%	-	-	-	-	-	-	-	-	-	-
Proportion egg										
+1%	-	-	-	-	-	-	-	-	-	-
+50%	-	-	-	-	-	-	-	-	-	-
-50%										

Chapter six

The effect of colony and year on great skua *Catharacta skua* diets

Abstract

In light of likely changes in food availability and concern about the effect that this might have on great skuas preying on other seabird species, we compare the diet of great skuas at two Shetland colonies in three different years. We also compare the proportion of bird-specialists among three years and among three colonies. While the main component of great skua diet is variable both within colonies and among years, clear trends in a switch away from discarded fish species has not been observed. Similarly while fish species vary among years and between colonies, there are no clear trends in a switch to larger discards. The species of bird prey in the diet varied between bird-specialists and non-specialists, between colonies and among years. A decrease in the proportion of black-legged kittiwakes *Rissa tridactyla* in the diet was compensated for by an increase in either auks (Alcidae) or northern fulmars *Fulmaris glacialis*. Among three different years there was no difference in the proportion of bird-specialist pairs at study plots. The proportion of bird-specialist pairs appeared to be related to the size of the great skua colony.

Introduction

The population of great skuas *Catharacta skua* breeding in the British Isles has increased dramatically over the last century. From a few dozen pairs around 1900 (Furness 1987), the population has grown to around 8000 pairs (del Hoyo, Elliot & Sargatal 1996) representing 60% of the species' population (Lloyd, Tasker & Partridge 1991, Sears *et al.* 1995). Over 90% of these breed in Shetland & Orkney. Cessation of persecution, an abundance of sandeels *Ammodytes marinus* and availability of discards have all been attributed as causes of this species' increase in Shetland & Orkney (Furness & Hislop 1981, Furness 1987, Lloyd *et al.* 1991).

During the 1980s, a reduction in sandeel abundance (Wight & Bailey 1993) and a low recruitment of haddock *Melanogrammus aeglefinus,* resulting in fewer discards (Reeves & Furness 2000) coincided with a slowing of population growth (Furness 1987, Sears *et al.* 1995) and a decline in chick growth rates and productivity (Hamer, Furness & Caldow 1991). At the same time the proportion of bird meat in the diet of skuas increased (Hamer *et al.* 1991) and at some Shetland seabird colonies predation by great skuas was severe (Heubeck, Mellor & Harvey 1997). With continued declines in the stocks of predatory fish like mackerel *Scomber scombrus* and herring *Clupea harengus* stocks, and the need to reduce discards, it is likely that the availability of this resource will decrease further, and this may have implications for skuas as well as other seabird populations in Shetland and Orkney.

Catharacta skuas at different colonies show a broad range of foods and foraging strategies in the Northern (Furness 1987 Phillips *et al.* 1997 a,b) as well as the Southern hemisphere (reviewed by Rheinhardt *et al.* 2000). The role of great skuas as seabird predators, especially in light of current changes to discarding practices, may be variable at different colonies. Great skuas at St Kilda feed almost exclusively on seabirds, compared with great skuas at Foula, which feed extensively on sandeels and discarded whitefish (Phillips *et al.* 1997a). In addition, annual variation in diet reflect changes in prey availability and have identified dietary switching by great skuas in the past (Hamer *et al.* 1991). Therefore the dynamics of the relationship between great skuas and their prey may vary among colonies as well as among years. In this study we investigate differences in diet among three different sized great skua colonies in Shetland, with particular reference to skuas which specialise as bird predators. We investigate how their diets vary across three years, how this effects a measure of reproductive performance, and discuss the potential effect that further reductions in discarded fish may have upon skuas and their potential prey species.

Methods

Data on diet and breeding performance were gathered from Hermaness National Nature Reserve (NNR) (60° 50' N, 1° 12' W) during 1998, 1999 & 2000, and from Noness (59° 58' N, 1° 12' W) during 1999. Data only on diet were gathered from Noness in 1998 & 2000 and Noss NNR (60° 08' N, 1° 00' W) during 2000. Hermaness has the third largest great skua colony in the UK with around 650 pairs (Lewis 1997). Noss is also an important great skua colony with 414 pairs (Upton & Brown 1998) whereas Noness supports only 15-20 pairs (this study).

DIET SAMPLING

Pellets were collected from marked breeding territories every 5-10 days throughout the incubation and chick-rearing period. Prey remains in pellets were identified to the lowest possible taxon and pellets were then destroyed to prevent repeat observation. Bird pellets were identified based on feather colour/odour and bare parts (legs/feet, bill/skull), unidentified bird pellets were assumed to occur in the same proportion as those positively identified. Sagittal otoliths were stored dry for species identification and measured to estimate fish length (Härkönen 1986).

Territories with 60% or more of the pellets containing bird remains were classified as bird-specialists (Chapter 4). Some of the bird-specialists also held a feeding territory adjacent to a seabird colony. Skua pairs with less than 60% of bird in their pellets were classified as non bird-specialists, hereafter referred to as non-specialists.

OVERALL DIET

Colony and year effects

Overall diet composition was estimated for breeding non-specialist skuas at Hermaness and Noness during 1998, 1999 & 2000. We investigated the effect of year and colony on the composition of the main prey types, as well as fish species separately. Any inter-colony and annual variation in the size of fish prey consumed, were also considered. We also compared bird species in the diet of bird-specialists and non-specialists, among years and between colonies.

PROPORTION OF BIRD-SPECIALISTS

Annual variation

At Hermaness we compared the proportion of bird-specialists in the same study among years. All skuas breeding at Noness were monitored with the ratio of bird-specialists noted. Annual variation in the proportion of bird-specialists was not monitored at Noss.

Inter-colony variation

During 2000 we estimated the proportion of bird-specialists at Noness, Noss and Hermaness. Because of the small breeding population at Noness, it was possible to sample all territories. Because of the large number of the great skuas at Hermaness and Noss, we took a sample of the two colonies. Walking four transects at each colony we sampled pellets from each breeding territory encountered (100 at Hermaness & 61 at Noss). We investigated the relationship between the proportion of bird specialists and colony size. Using published estimates, we also investigated the relationship between the number of five main seabird species preyed upon by great skuas (see Table 1) and the proportion of bird-specialists.

REPRODUCTIVE PERFORMANCE

From the same territories as pellets were sampled at Hermaness and Noness, breeding attempts were monitored from incubation through to fledging. Nests were visited every 5-10 days and the fate of eggs (losses or hatching) and young (losses or fledging) recorded.

STATISTICAL ANALYSIS

To investigate the effects of year and colony, as well as dietary group (bird-specialist or other) on the ratio of prey types we used logit loglinear analysis (Norušis 1999) with prey category as the dependent variable and year, colony and dietary group as factors. We compared the deviance values of fitted models using likelihood ratio tests. The relationship between diet, year and colony on reproductive success was investigated using Generalised Linear Models (GLIM for Ecologists version 4) with binomial error distribution and logit-link function. As with the logit loglinear analysis, likelihood ratio tests were used to compare deviances. Analysis of the relationship between the size of gaddid fish and year/colony was performed using two-way analysis of variance (ANOVA). For data that did not meet the assumptions of normality and homoscedasticity for parametric ANOVA, values were ranked and analysed using non-parametric two-way ANOVA (Zar 1984). For all tests alpha level of significance was set at 0.05.

Results

OVERALL DIET

Main prey types of non bird-specialists

The proportions of the main prey consumed by non-specialists are shown in Table 2. Using logit loglinear analysis in multi-dimensional contingency tables we tested the null hypothesis that the proportion of the three main prey types found in the diet of non bird-specialist skuas were mutually independent of year and colony. After removing the highest order interaction (between year and colony), the model was not a significantly poorer fit than the full model

(χ^2_4=8.99, p=0.06, NS). Therefore we accept the null hypothesis and assume there are no interactive effects of year and colony on prey composition.

By far the most important prey of non-specialists was whitefish (predominantly gadoids), although the average in all years was lower at Noness (55.4%) compared with Hermaness (74.8%). Non-specialists at Noness overall had a much higher percentage of bird pellets (35.4%) than non-specialists at Hermaness (20.3%). The proportions of goose barnacle *Lepas sp.*, rabbit/sheep & herring *Clupea harengus* /sandeel prey items were highly variable, suggesting that these foods were taken only opportunistically.

Fish species composition

The proportions of each whitefish species, identified from otoliths, was the same for bird-specialists and non-specialists during 1998 at Hermaness (χ^2_4=7.2, NS) and at Noness (χ^2_2=0.2, NS). Therefore data on fish species were pooled for bird-specialist and non-specialist skuas.

There was considerable variation in the ratio of fish species among years and between colonies (Table 3). Blue whiting *Micromesistus poutassou* made up a high proportion of the fish in pellets at Hermaness (12-39%), but was virtually unrecorded at Noness (maximum 1.1% in 1999). Similarly, Norway pout *Trisopterus esmarkii* was abundant at Hermaness (39-56%) but is less important in the diet at Noness (16-18%). By contrast, whiting *Merlangius merlangus* made up a higher proportion of the fish at Noness (39 % & 62% in 1998 & 1999 respectively) compared with Hermaness (peak of 10% in 1999). Haddock *Melanogrammus aeglefinus* showed the most variation in occurrence - at Hermaness between 10 & 21% of the identified otoliths were haddock and Noness showed a decrease between 1998 & 1999, from 42% to 18%. Redfish *Sebastes marinus*, long rough dab *Hippoglossoides platessoides* and cod *Gadus morhua* were all present in only very small numbers at either colony. Using logit loglinear analysis in multi-dimensional contingency tables we tested the null hypothesis that the proportion of the four main fish species found in the diet of skuas were mutually independent of year and colony. After removing the highest order interaction (between year and colony), we found that the model was not a significantly poorer fit (χ^2_6=1.83, p=0.93). Year and colony therefore had no interactive effects on the species of fish consumed.

Fish size

Fish sizes calculated from otoliths following Härkönen (1986) are shown in Table 4. There was a significant effect of year on the length of haddock (Two-way ANOVA: $F_{2,262}$=61.218, p<0.001), with no effect of colony ($F_{1,262}$=3.37, NS) and no significant interaction ($F_{1,261}$=0.385, NS). Scheffé tests revealed that haddock were smaller in 2000 than in both 1998 & 1999. The length of Norway pout was significantly effected by year (Non-parametric ANOVA: χ^2_2=8.95, p<0.05) with fish being larger in 2000 than in 1998 & 1999. There was no effect of year (Non-parametric ANOVA: χ^2_2=3.58, NS) or colony (χ^2_2=3.58, NS) on the length of whiting taken by great skuas.

There was no effect of year (one-way ANOVA: $F_{2,204}$=0.313, NS) on the length of blue whiting in the diet of great skuas at Hermaness.

Bird species consumed by bird-specialists and non-specialists

There were marked differences in species of bird prey found in pellets among year, colony and dietary group (Table 5). Analysis using multi-dimensional contingency tables removing the three-way interaction between diet, year and colony, resulted in a significantly poorer fit than the fully saturated model (χ^2_4=15.56, p=0.004). Therefore the proportion of the different bird species differed among diet groups and colonies, and these differences were not uniform among years.

Bird-specialist great skuas at Hermaness fed extensively on auks in all years and while they relied heavily on gull/terns (almost exclusively black-legged kittiwakes *Rissa tridactyla*), the proportion decreased from 22% in 1998 to 5.5% in 2000. By contrast bird-specialists at Noness fed more on gull/terns (again mostly black-legged kittiwakes) but also showed a similar decline in numbers from 1998 (48%) to 2000 (18%). Non-specialist great skuas at Hermaness tended to take many northern fulmars but very few gull/terns, instead eating more 'other' prey (mainly great skua chicks). Compared with Hermaness, non-specialists at Noness fed much more on black-legged kittiwakes, but as with specialist birds this species became more scarce in the diet from 1998 (54%) to 2000 (25%). Much of this reduction was replaced by an increase in the proportion of northern fulmar in the diet (20% in 1998 compared with 50% in 2000).

PROPORTION OF BIRD-SPECIALISTS

Inter-colony variation

During 2000 the proportion of bird-specialist breeding pairs was 4% of 100 pairs sampled throughout the Hermaness colony, 19% at Noss and 47% at Noness. The difference between the three colonies was significant (χ^2_2=24.6, p<0.01). The proportion of bird-specialists appeared to be negatively correlated with the size of the great skua population (Fig. 1) as well as the number of potential seabird prey (Fig. 2, Table 1).

Annual variation

To investigate possible differences in the number of bird-specialists during 1998, 1999 and 2000 we compared the proportions the same selected study plots at Hermaness and the whole of the Noness. The differences were not statistically significant at Hermaness (χ^2_2=4.2, NS) or at Noness (χ^2_2=0.7, NS) (Table 6).

REPRODUCTIVE PERFORMANCE

Analysis in GLM showed that hatching success (proportion of nests which produced a chick) was not significantly effected by year (χ^2_1=0.35, NS), dietary group (χ^2_1=0.25, NS) or colony (χ^2_1=0.37, NS) (Table 7). Similarly breeding success (the proportion of nests that fledged a chick or chicks) was not significantly different among years (χ^2_1=0.95, NS), between dietary group (χ^2_1=3.11, NS) or between colonies (χ^2_1=0.20, NS) (Table 7).

Table 1. Numbers of breeding seabirds of the main prey species of seabirds potentially available to great skuas at three Shetland study colonies.

Species	Number of individuals		
	Hermaness	Noss	Noness
Northern fulmar *Fulmarus glacialis*	28,000(2)	10,000(3)	4000(7)
Black-legged Kittiwake *Rissa tridactyla*	1600(4)	5000(6)	1000(7)
Common Guillemot *Uria aalge*	15,000(5)	46,000(1)	2000(7)
Razorbill *Alca torda*	1500(5)	2000(1)	170(7)
Atlantic Puffin *Fratercula arctica*	56,000(2)	3000(6)	70(7)
Total (nearest 1000)	102,000	66,000	7000

Sources: (1) Goddard & Lewis (1996); (2) Lewis (1997); (3) Upton & Brown (1998); (4) King (1999); (5) Rodger (2000); (6) Upton & Maher (2000) (7) M. Heubeck (pers com).

Table 2. Proportion of main prey types in pellets of non-specialist great skuas breeding at Hermaness and Noness.

	Hermaness						Noness					
	1998		1999		2000		1998		1999		2000	
Whitefish	463	74.9%	538	77.9%	351	70.6%	67	49.6%	77	55.8%	50	64.9
Bird (incl. egg)	145	23.5%	110	15.9%	111	22.3%	50	37%	52	37.7%	22	28.6
Goose-barnacle*	1	0.2%	11	1.6%	12	2.4%	0	-	3	2.2%	0	-
Rabbit/sheep*	7	1.1%	15	2.2%	18	3.6%	1	0.7%	1	0.7%	5	6.55
Herring/sandeel*	2	0.3%	17	2.5%	5	1%	17	12.6%	5	3.6%	0	-
Total	618		691		497		135		138		77	

*Goose barnacle, rabit/sheep and herring/sandeel were included as 'other' in logit loglinear analysis.

Table 3. Proportions of different fish species found in whitefish pellets of breeding great skuas at Hermaness and Noss.

	Hermaness						Noness				
	1998		1999		2000		1998		1999		20
Whiting	24	6.3%	25	9.8%	20	9.2%	119	38.6%	55	61.8%	No d
Haddock	54	14.1%	25	9.8%	46	21.1%	130	42.2%	16	18%	
Norway Pout	150	39.2%	105	41.3%	123	56.4%	55	17.9%	14	15.7%	
Blue Whiting	149	38.9%	91	35.8%	26	11.9%	0	-	1	1.1%	
Redfish	2	0.5%	3	1.2%	3	1.4%	2	0.6%	1	1.1%	
Long rough dab	2	0.5%	5	2%	0	-	0	-	0	-	
Cod	2	0.5%	0	-	0	-	2	0.6%	0	-	
Total	383		254		218		308		89		

Table 4. Fish lengths (mean ± SD) derived from measurement of otolith length based on equations in Härkönen (1986) in pellets of breeding great skuas.

Fish	Year	Hermaness (mm)	Noness (mm)
Blue whiting	1998	274.5 ± 42.0 (90)	-
	1999	272.7 ± 45.2 (91)	-
	2000	280.4 ± 44.2 (26)	-
Haddock	1998	266.2 ± 42.5 (54)	278.0 ± 36.9 (130)
	1999	278.7 ± 41.5 (23)	281.8 ± 25.2 (15)
	2000	191.5 ± 35.6 (44)	-
Norway pout	1998	169.9 ± 26.8 (150)	168.3 ± 13.2 (55)
	1999	157.4 ± 35.9 (104)	169.0 ± 34.2 (15)
	2000	265.8 ± 41.9 (20)	-
Whiting	1998	264.7 ± 83.5 (23)	292.6 ± 38.4 (119)
	1999	280.3 ± 52.2 (24)	291.6 ± 40.2 (54)
	2000	265.8 ± 41.9 (20)	-

Table 3. Proportions of bird species found in pellets of great skuas breeding at Hermaness and Noness during 1998, 1999 & 2000. Data are grouped into 'bird-specialists' and 'non bird-specialists' (non-specialists in the table) – see main text for description of these differences.

	Hermaness												Noness											
	1998				1999				2000				1998				1999				2000			
Pellet type	Bird-specialist		Non-specialist		Bird-specialist		Non-specialist		Bird-specialist		Non-specialist		Bird-specialist		Non-specialist		Bird-specialist		Non-specialist		Bird-specialist		Non-specialist	
Auk	184	59.7%	24	19.8%	148	63.2%	45	48.9%	183	76.9%	52	47.3%	70	35.4%	12	26.1%	17	28.3%	6	18.2%	14	41.2%	5	25%
Kittiwake	67	21.8%	16	13.2%	21	9%	1	1.1%	13	5.5%	0	-	95	48%	25	54.3%	36	60%	13	39.4%	6	17.6%	5	25%
Fulmar	57	18.5%	76	62.8%	64	27.4%	41	44.6%	42	17.6%	46	41.8%	33	16.6%	9	19.6%	7	11.7%	14	42.4%	14	41.2%	10	50%
Other*	0	-	5	4.1%	1	0.4%	5	5.4%	0	-	12	10.9%	0	-	0	-	0	-	0	-	0	-	0	-
Total	308		121		234		92		238		110		198		46		60		33		34		20	

*Other prey comprised of four unidentified passerines, single unidentified storm-petrel *Hydrobatidae*, single shag *Phalacrocorax aristotelis* and several great skua chicks.

Table 6. The number of bird-specialist great skuas at selected study plots at Hermaness, and the whole Noness colony.

	Hermaness			Noness		
	1998	1999	2000	1998	1999	2000
Bird-specialists	37.5%	17.8%	25%	38.5%	31.2%	46.75 %
Non-specialists	62.5%	82.2%	75%	61.5%	68.8%	53.3%
Total	32	56	68	13	16	15

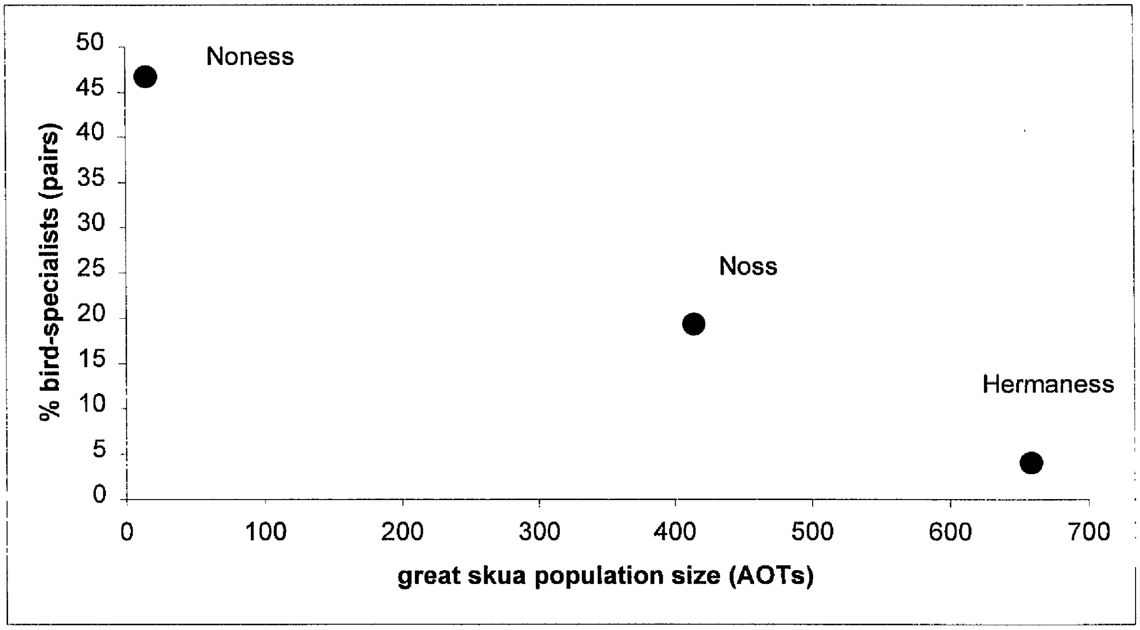

Figure 1. Proportion of bird-specialist great skuas at three different sized great skua colonies in Shetland.

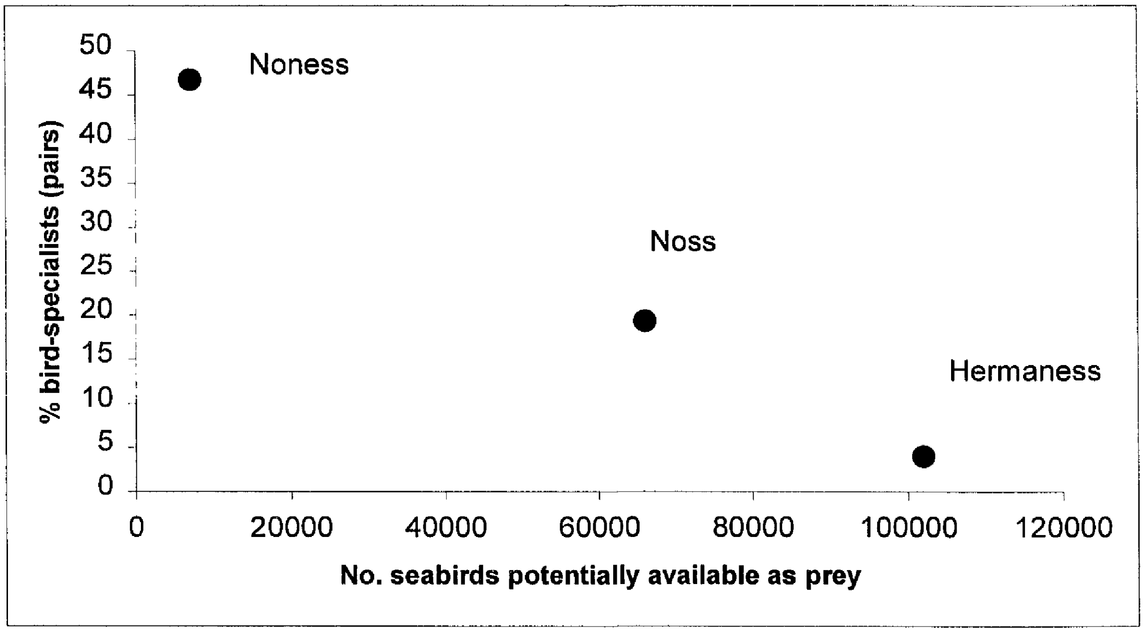

Figure 2. Proportion of bird-specialist great skuas at three Shetland seabird colonies relative to numbers of seabird prey potentially available. See Table 1 for details of potential seabird prey.

Table 7. Hatching success (proportion of nests where one or more eggs hatched) and breeding success (proportion of nests where one or more chicks survived to near fledging stage) of great skuas at Hermaness and Noness, in three breeding seasons. Data for specialist and non-specialist skuas presented separately. Range of standard errors (asymmetrical because of binomial error distribution) are in parentheses.

Year	Colony	Breeding parameter	Bird-specialists [*n*]	Non-specialists [*n*]
1998	Hermaness	Hatching success	0.91 (0.82-0.95) [8]	0.93 (0.88-0.96) [34]
		Fledging success	0.52 (0.42-0.63) [8]	0.70 (0.62-0.77) [34]
1999	Hermaness	Hatching success	0.92 (0.87-0.96) [8]	0.94 (0.88-0.97) [55]
		Fledging success	0.73 (0.64-0.73) [8]	0.85 (0.78-0.90) [55]
1999	Noness	Hatching success	0.83 (0.72-0.90) [5]	0.87 (0.72-0.94) [11]
		Fledging success	0.74 (0.62-0.84) [5]	0.57 (0.47-0.70) [11]
2000	Hermaness	Hatching success	0.88 (0.79-0.93) [14]	0.91 (0.82-0.95) [35]
		Fledging success	0.65 (0.55-0.73) [14]	0.79 (0.71-0.86) [35]

Discussion

NON-SPECIALISTS

While the prey of non-specialist skuas varied among years, there were no obvious trends in any of the main prey items. Most of the fish in the diet of great skuas in this study are demersal or meso-pelagic and therefore only available to great skuas by the actions of commercial fisheries (Furness & Hislop 1981, Hamer *et al.* 1991, Phillips *et al.* 1997). A need to reduce fishing impact on whitefish stocks, a desire to reduce discarding and long-term declines in the stock of many fished species are likely to reduce the amount of fish available to great skuas scavenging at trawlers (Furness 1992). However, our data suggest that despite variability among colony and year, there has been no large-scale switch from discarded whitefish to other prey. Garthe, Camphuysen & Furness (1996) show that discards and offal produced as a by-product of commercial fisheries in the North Sea during the early 1990s could support up to 21,000 great skuas. Given that the British breeding population is approximately 16,000 breeding individuals (Lloyd, Tasker & Partridge 1991) and that there are also several thousand non-breeders, only small reductions in discarding would lead to this food supply being insufficient to meet the needs of North Sea great skuas.

Great skuas have difficulty handling large discarded fish (Hudson & Furness 1988) and the increase in size of discards eaten by skuas at Foula between 1976 and 1996 (Furness 1997) suggests that birds are currently taking less favourable discards. However in out study, while the size of Norway pout increased in 2000, the size of haddock decreased, despite this species showing declines in landings and therefore discards (Fig. 3) (Anonymous 2000, Reeves & Furness 2000). The availability of fish scavenged behind trawlers is likely to be complex and not necessarily correlated with published values of discarding estimates (Reeves *et al.* 1992). Factors such as recruitment rates, localised movement of shoals and fluctuations in the population of fish species not commercially fished could all ameliorate the effect of reduced discards.

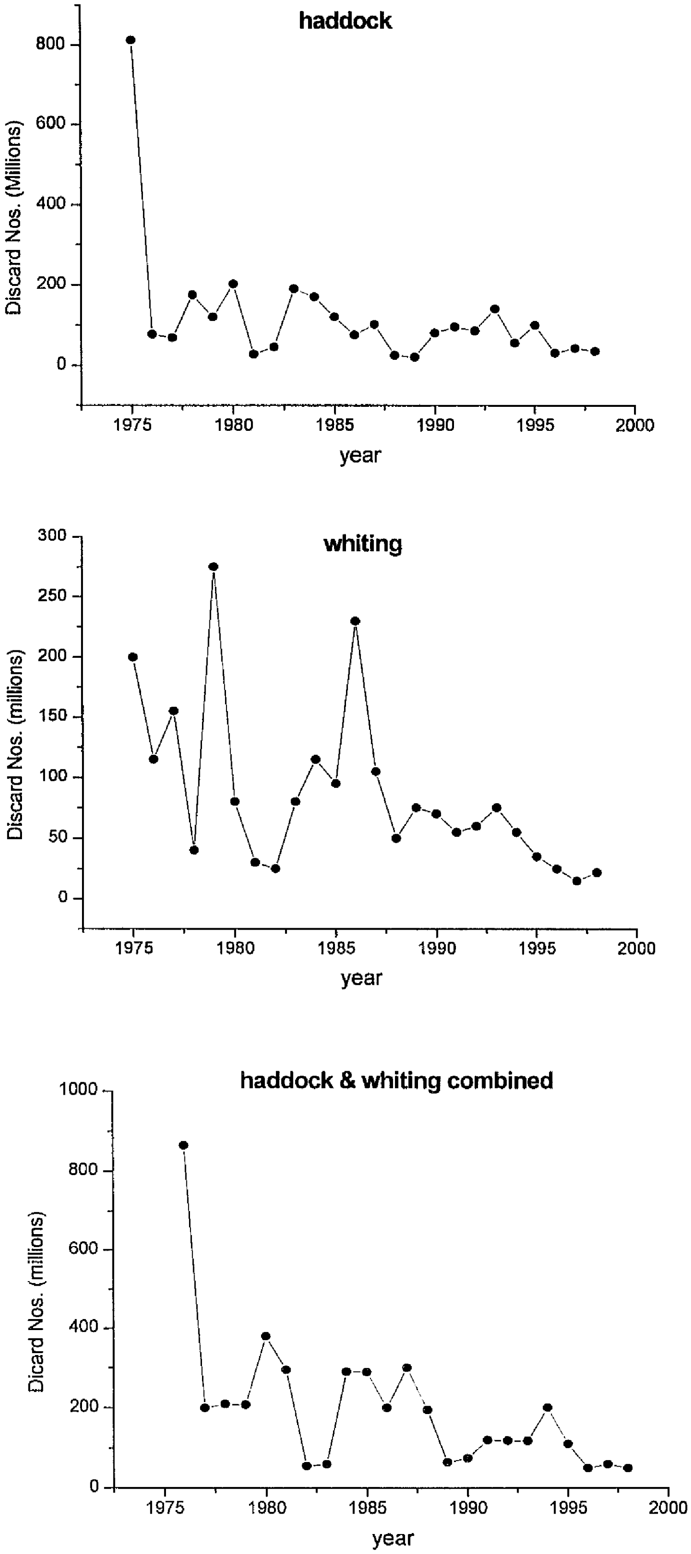

Figure 3. Numbers of haddock *Melanogrammus aeglefinus* and whiting *Merlangius merlangus* combined, < 26cm discarded by North Sea fisheries 1975-1998 (from: Reeves & Furness 2000).

BIRD SPECIES CONSUMED

Differences in the type of seabird prey present in the diet of great skuas not only varied among bird-specialists and non-specialists but also between Noness and Hermaness and among 1998, 1999 & 2000. These differences were also interactive. Specialising in taking seabirds by great skuas has been reported at a number of Shetland colonies, and these specialists often concentrate on a single species (Boulinier 1992, Heubeck *et al.* 1997, Furness 1997). Therefore, our results support these findings that bird-specialists are likely to differ from more opportunistic non-specialists and vary between colonies. However the interactive effect of year is more puzzling. Other research suggest that bird-specialist great skuas retain the same feeding territories and habits among years (S. Votier *unpublished data*). Given that most of the changes in seabird diet have been driven by a reduction in the amount of black-legged kittiwakes in the diet, localised declines in these species (Heubeck *et al.* 1997) may be forcing bird-specialists to seek alternative prey like auks and northern fulmars. While non-specialists showed a lower proportion of black-legged kittiwakes in the diet than bird-specialists, this proportion of this species still reduced over time. These results suggest that great skuas were feeding on a higher proportion of fulmars and auks at the end compared with the beginning of this study. If this trend continues these species may be most at risk from skua predation pressure.

PROPORTION OF BIRD-SPECIALISTS

Differences in the proportion of bird-specialists appear to be distinct in the three colonies studied here – smaller colonies have a higher proportion of great skuas that specialise in feeding extensively on seabirds. At Hermaness and Noness, at least, the number of bird-specialists appears relatively stable among years. Spear (1993) reported that in a large colony of 25,000 western gulls *Larus occidentalis* the proportion of bird-specialists was around 1.1%, such a low level of specialisation suggests, as in our study, some type of a density dependent effect. The reasons for these differences are not clear, but a number of theories can be postulated. Seabird colonies may only have a finite number of naive seabirds which skuas are able to feed upon. However, if this were the case then the ratio of bird-specialists would be related to the abundance of seabirds. Given that the ratio of bird-specialists to prey species is much higher at small colonies then availability of seabird prey does not appear to be limiting. Alternatively, small colonies may consist of birds forced to move out of large colonies to sites with less favourable feeding conditions. Assuming great skua distribution has been driven by the availability of fish prey, the most important food at Shetland colonies, (Furness & Hislop 1981, Hamer *et al.* 1991, Phillips *et al.* 1997 a,b) it is possible that small colonies may only be maintained if skuas can effectively exploit other prey like seabirds.

Due to the linearity of seabird cliffs, only skuas nesting along the edge are able to regularly exploit seabird prey and indeed many bird-specialists are found adjacent to seabird colonies (S. Votier *unpublished data*). However, because seabird cliffs are complex three-dimensional communities and not linear features, the situation may be less simple than this. Evidence from Hermaness suggests that some specialist birds breeding away from seabird colonies are able to 'leap-frog' coastal nesting pairs to exploit seabird colonies.

A final hypothesis may be that since skuas are generally inefficient at killing bird prey (personal observations) the risk of kleptoparasitism is high. At large colonies high levels of intra-specific competition may reduce the effectiveness of feeding upon bird prey. Phillips *et al.* (1997) propose that the lower level of bird consumption at a large skua colony (Foula) compared with a smaller colony (St Kilda) is influenced by intra-specific competition.

While factors influencing an apparent density-dependent effect are not clear, this difference may have implications for seabird conservation. In a study of a closed system where south polar skuas *C. maccormicki* feed exclusively on Antarctic petrels *Thalossica antarctica*, Brooke, Keith & Røv (1999) show that the population of skuas was limited by the number of petrels, and therefore petrels have not swamped the skua population. In this study the ratio of skuas to petrels was approximately 1:1000, which compares with ratios of bird-specialists to prey species of 1:4000 at Hermaness, 1:3500 at Noss and 1:1000 at Noness. It seems likely that both Hermaness and Noss could potentially support many more bird-specialists than they currently do. However, if the number of skuas preying exclusively on seabirds increased, seabird populations would suffer increased predation, which may not be sustainable.

REPRODUCTIVE SUCCESS

Phillips *et al.* (1997) found that great skuas breeding on St Kilda which fed predominantly on birds, produced larger clutches, hatched fewer eggs but produced similar numbers of fledglings compared with skuas which fed predominantly on fish at Foula. In this study there was no difference in the reproductive performance of skuas breeding at different colonies, either among years or among dietary groups. While hatching and reproductive success are not particularly sensitive to changes in food availability (Monaghan 1996), variations in diet among year and colony would not appear to have been large enough in the study years to have had detectable effects on great skua breeding success. More sensitive measures of reproductive performance (hatching date/clutch volume/chick condition) or foraging effort may reveal how these variations in diet affect great skuas.

Broad differences in diet composition and dietary specialisation among colonies and years demonstrate that the continued monitoring of great skua diets is desirable. These results also show that it would be inappropriate to apply the findings of studies into predation by great skuas from a single colony to other colonies in Shetland.

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Chapter seven

General discussion

While each chapter of this thesis has been written as a separate piece of work in its own right, they may be integrated to provide a better understanding of great skua foraging behaviour in Shetland. In this discussion I aim to draw together the main points addressed by each chapter to provide a broader context of the role of great skuas in the Shetland seabird community including interaction with fisheries. In **Chapters 2 & 3** I investigated dietary sampling methods to enable more accurate estimates of great skuas food intake. A correlative study in **Chapter 4** provided an insight into the ecology of dietary specialisation in great skuas. Integrating information on dietary studies and dietary specialisation into a bioenergetics model in **Chapter 5**, the numbers of seabirds consumed by great skuas at Hermaness in 1999 were estimated. Data on diet and dietary specialisation in **Chapter 6** reveal that there are considerable differences among colonies and among years, highlighting the need to monitor predation effects on a local scale.

Much of this work is written from the perspective of great skua ecology, since the demography of Shetland's seabirds in relation to great skuas is essentially beyond the scope of this study. Given the complex factors affecting regulation of seabird populations (Furness & Monaghan 1987), even a complete understanding of great skua foraging ecology and predation is unlikely to explain all changes that may be experienced in the demography of Shetlands' seabirds. Because the severity of any effect on seabird populations by great skuas could potentially be mitigated by independent factors, an integrated approach to assessing great skua predation and seabird population dynamics might be most appropriate in the future. In particular it would be inappropriate to assume that prey seabird numbers would decrease in proportion to the numbers eaten by great skuas. Not only may great skuas be killing some non-breeders rather than breeders, but there may also be increases in recruitment into the breeding populations that can offset impacts of increased mortality (i.e. Klomp & Furness 1992).

Diet studies

Diet plays a fundamental role in the study of seabird ecology, and therefore accurate assessment of this was seen as essential to this study. The diets of many seabird species have been studied in some detail (see Duffy & Jackson 1986 for review), with some work focusing on *Catharacta* skuas in the southern oceans (see Rheinhardt *et al.* 2000 for review). Moreover there is a large body of work on great skuas, using a range of dietary assessment techniques (i.e. Furness & Hislop 1981, Hamer *et al.* 1991, Phillips *et al.* 1997). Despite this few studies have dealt with the validity of these methods for this species (but see Bearhop*et al.* **Appendix I**). Our data suggest that while a range of sampling techniques do provide data that permit comparisons between years or between sites (**Chapter 3**), each of five methods employed (pellets, prey remains, spontaneous regurgitates, observed feeds and water-offloading) have biases which should be borne in mind when monitoring great skua diet. It is straightforward to collect large samples of pellets over a broad time scale and they provide a convenient dietary sampling technique, suitable for qualitative and comparative study. However the results of a captive feeding trial (**Chapter 2**) suggest that skuas produce several pellets per meal when feeding on birds which makes the use of pellets as a quantitative measure of diet problematic. However, using correction factors from these types of captive trials provides more accurate estimates. Since captive skuas may not produce pellets in the same way as wild skuas, only studies involving wild birds is likely to fully elucidate exactly how many pellets great skuas produce when feeding on bird prey. Integrating conventional diet studies with novel techniques like stable isotope analysis may provide more accuracy (Bearhop *et al.* **Appendix I**), especially given that many potential applications of these methods in animal ecology are relatively new.

Dietary specialisation

Pronounced dietary specialisation as shown by great skuas at the three Shetland colonies studied in this thesis, have similarly been described in a number of other *Catharacta* skuas and large Larids (Trillmich 1978, Trivelpiece, Butler & Volkman 1980, Pietz 1987, Watanuki 1992, Spear 1993). Because the number of seabirds taken by bird-specialists is high, in relation to their abundance in the population, we studied aspects of their breeding and foraging ecology in **Chapter 4**. Our results showed that bird-specialisation appears to have fitness benefits. While bird-specialists did not show improved reproductive success compared with other members of the population, they did have earlier hatching dates and, in certain years, improved clutch volume and chick condition. In other similar studies researchers found that specialist gulls and skuas had increased reproductive success compared with other members of the population (Trillmich 1978, Trivelpiece, Butler & Volkman 1980, Pietz 1987, Watanuki 1992, Spear 1993). Is it possible that our measures of breeding success were not powerful enough to detect these types of difference? Because some nests in this study were not found immediately after laying, hatching success may have been biased by nests which failed prior to discovery (Mayfield 1975), it is possible to estimate a daily nest survival for the incubation or chick rearing period. However while this is a more powerful measure of breeding success, the early hatching dates, and therefore shorter nest exposure period for bird-specialists, downwardly biased the estimates of nest survival for this whole treatment group. The generally high level of hatching and fledging success of great skuas at Hermaness may simply suggest that in most years these crude measures of productivity are too insensitive to reveal differences in hatching or fledging success between dietary groups. Evidence that differences in clutch volume and chick condition between bird-specialists and others was only apparent in certain years, might suggest that only during periods of extreme hardship will statistically significant differences in reproductive success be demonstrated. Instead further research avenues could be directed on understanding heritability of this feeding trait as well as factors which regulate their numbers. Selective removal experiments of bird-specialists may provide answers to some of these questions, as well as testing possible control measures (see **Removal experiments**).

Regulation of seabird populations

The regulation of seabird populations has long been the matter of debate among biologists (e.g. Ashmole 1963, 1971; Lack 1954, 1966; Birkhead & Furness 1985; Furness & Monaghan 1987; Croxall & Rothery 1991; Lewis *et al.* 2001). Despite this interest, much of the current evidence is still somewhat circumstantial or correlative. Also because seabirds spend much of their lives at sea and typically show *K*-selected reproductive strategies, being long-lived with delayed maturity and low rates of reproduction, it can be difficult to obtain appropriate data to monitor population trends accurately. Catastrophic density-independent events like El Nino Southern Ocean Oscillations can have a widespread affect on seabird populations (Schreiber & Schreiber 1984) but these may also operate together with other regulatory factors such as food and space, to an unknown extent (Croxall & Rothery 1991). Density-dependent effects like predation, parasitism, breeding space and perhaps most importantly food (reviewed in Croxall & Rothery 1991), also have profound and often interactive effects on seabird populations. Selecting an appropriate monitoring programme to investigate the effect of great skua predation on other seabirds would require a carefully collected long-term data set and is beyond the scope of this study. However it may be worth briefly considering some of the factors most likely to be relevant to such a study.

Typically indices such as reproductive success, juvenile and adult survival can be used to provide information on seabird demography. It is relatively easy to collect data on breeding success but work has shown that seabirds are able to buffer the effects of changes in environmental conditions to some degree therefore masking trends in demography (e.g. Cairns 1987). Adult survival can provide data more suited to monitoring seabird demography compared with reproductive success but has a number of potential problems associated. Firstly, studies of adult and juvenile survival require the establishment and collection of long-term data sets, with birds marked and re-sighted annually. As well as these practical problems, other factors such as deferred maturity, deferred breeding attempts as well as philopatry may confound data sets a invalidate assumptions of survival models. Also because some seabirds show variations in reproductive strategy, different components of the breeding cycle may provide rather different information on the health of the population. The health of a seabird population with extreme *K*-selected strategies (like Procellariforms) are likely to be most sensitive to changes in adult mortality rather than breeding performance, whereas the population of more *r*-selected species (like gulls & terns) are likely to be better described by reproductive performance (Croxall & Rothery 1991). With these considerations in mind the affect of great skua predation upon seabird populations was beyond the scope of this study, however we may speculate to what extent these processes may be occurring and offer advice for future avenues of research.

The evidence that great skuas are having an impact on seabird populations in Shetland is generally circumstantial (Heubeck & Mellor 1994, Heubeck, Harvey & Mellor 1997). At many Shetland colonies predation by great skuas is most conspicuous on black-legged kittiwakes *Rissa tridactyla*, terns Sternidae, and Atlantic puffins *Fratercula arctica*, all species 'popular' in the public eye. In addition to this, because great skuas aggressively defend nest sites (often striking an intruder to the territory), kill or scavenge lambs and are locally abundant, they have become unpopular in Shetland and Orkney, with many members of the public and birdwatchers alike (Heubeck 1996, Harvey 1997). With this background it is reasonable to speculate that the impact of predation by great skuas has either been over-emphasised or somewhat sensationalised by the media. Despite this background, the decline in black-legged kittiwake numbers reported at a number of Shetland colonies are at least in part a result of great skua predation (Heubeck & Mellor 1994, Heubeck, Harvey & Mellor 1997). And while the numbers of seabirds calculated to be consumed by great skuas at St Kilda by Phillips *et al.* (1997) are greater than if our estimates of pellet production from captive skuas were employed (**Chapter 2**), these skuas are clearly taking a large number of seabirds. The results of our bioenergetics model in **Chapter 5** show that great skuas at Hermaness were taking relatively large numbers of seabirds during 1999. The decline in the population of black-legged kittiwakes at several Shetland colonies has been reflected in an annual decrease in the proportion of this species in the diet of great skuas at both Hermaness and Noss (**Chapter 6**). Also changes in the distribution of black-legged kittiwake colonies to more protected caves (Heubeck *et al.* 1997) suggests that the impact of great skuas on this species may have reached a peak. Since the bulk of seabirds taken by great skuas now appears to be auks, there is clearly a need for continued monitoring of their populations. In addition, given the unknown quantity of non-breeding auks involved, using simple models of adult and juvenile survival rates, this important information could help to assess the possible extent of impact of great skua predation more accurately. The trend for great skuas to take an increasing proportion of northern fulmars *Fulmaris glacialis* (**Chapter 6**) is unexpected and interesting given recent suggestions that the Shetland population of northern fulmars has started to decline at least at some of the larger colonies.

Removal experiments

Despite the protection afforded to great skuas, selective control measures have been proposed (Harvey 1996). Setting aside the ethical question of controlling a globally scarce species that we hold in trust, it is worthwhile to consider the effectiveness and implications of particular control measures. Culling of 35,000 herring gulls *Larus argentatus* on the Isle of May reduced the breeding population from ≈30,000 pairs to ≈6,000 pairs, and in addition the measures caused sufficient disturbance to deter new recruits from breeding (Duncan 1978). An alternative to culling on the Isle of May was the repeated destruction of the clutches of herring and lesser black-backed gulls *L. fuscus*. This reduced the numbers of herring gulls, but because of their higher survival rates and low level of philopatry, this was less effective at reducing numbers of lesser black-backed gulls (Wanless *et al.* 1996). Politically, a large-scale cull of great skuas would be unacceptable, but because great skuas are extremely site faithful among years (Klomp & Furness 1992, Catry *et al.* 1998), the method of clutch removal described by Wanless *et al.* (1996) might prove successful. However such control programmes may lead to increased rates of emigration and thus stimulate rates of growth at nearby smaller colonies.

If control measures were considered desirable, selective removal of bird-specialists may be the most effective and appropriate method of reducing impact. Guillemette &

Brousseau (2001) showed that culling herring gulls reduced the predation rate on common terns *Sterna hirundo*, but following recruitment, predation was high again the following year. In the same study, selective removal of bird-specialists resulted in a reduction in predation rate, although this was offset somewhat by other specialist pairs increasing their predation rate. In the year following a cull, bird-specialist territories were re-occupied, suggesting that selective culling may only be appropriate if repeated annually. Evidence that the great skuas specialising in bird predation may be restricted to the best quality birds and limited by density-dependent processes suggests that selective removal of bird-specialist great skuas may reduce predation rates at Shetland colonies, especially if this were repeated annually.

Conclusions

At present the numbers of great skuas taking seabirds is high and therefore likely has an impact on other seabird populations. However estimates of the amount of prey consumed are variable and some factors such as non-breeding population are poorly known, meaning that the actual impact on seabird numbers is still difficult to quantify. Study of great skuas that specialise in feeding exclusively on seabirds shows that they probably present the greatest threat to seabird populations. In the three years of this study the component of great skuas' diet comprising of discarded fish has shown little change. Only time will tell how reduced availability of discards will effect great skuas as well as other seabird populations, but it seems to be highly likely that further reductions in discarding will increase great skua predation on seabirds. In this study I highlight the need for continued monitoring of seabird populations, their reproductive performance and diets particularly over the next decade as likely changes in fish stocks and discards have an impact.

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ANNUAL VARIATION IN GREAT SKUA DIETS: THE CHANGING IMPORTANCE OF COMMERCIAL FISHERIES AND PREDATION ON SEABIRDS REVEALED BY COMBINING DIETARY ANALYSES.

Running Head: Annual variation in skua diets

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Abstract. This study combines conventional dietary assessment with stable isotope techniques which enabled a more accurate picture of Great Skua diet to be obtained. Stable carbon and nitrogen isotope ratios in feathers of Great Skua chicks collected over three years were analysed in conjunction with pellet and regurgitate collections. A significant drop in trophic status was detected in 1997, which likely resulted from an increase herring and mackerel in the diet. These items were almost certainly obtained from a commercial trawler, as evidenced by the significant drop in territorial attendance during the ship's absence. δ^{13}C values of feathers were significantly different among years and part of this may have been related to a period of enhanced primary production during 1996. A combined approach, such as the one described here is likely to become increasingly important in elucidating the diets of polyphagous birds.

*Keywords: Pellets, Stable Isotopes, Regurgitates, Seabirds, Fisheries, Deitary analyse*s

INTRODUCTION

More than half of the entire breeding population of Great Skuas (*Catharacta skua*) nest in Scotland and the number of breeding pairs has more than doubled to around 7,900 since the early 1970s (Lloyd et al. 1991). One reason for this increase seems to be changes in fishing practices (Furness 1987) with discards from commercial fishing activities forming an important part of the diet (Furness and Hislop, 1981; Hamer et al. 1991). However, seabirds, pelagic fish such as sandeels (*Ammodytes* spp.) and herring (*Clupea harengus*), and goose barnacles (*Lepas* spp.) are also commonly taken (Furness and Hislop 1981, Phillips et al. 1997). During the decline in sandeel availability in the 1980s, the numbers of seabirds eaten by Great Skuas in Shetland increased markedly (Hamer et al. 1991). Concern has grown over the possible impact that predation by Great Skuas may be having on other seabird populations (Furness 1997, Heubeck et al. 1997, Phillips et al. 1999a). Likely future reductions in European fishing effort, with its associated decline in discard availability (Furness 1997), and continued growth in Great Skua numbers at some sites (Phillips et al.1999b), may lead to increased predation by skuas on other seabirds.

Until recently, analyses of Great Skua diets have relied almost exclusively on conventional techniques such as direct observation and collection of pellets (regurgitated hard indigestible remains of prey), regurgitates (regurgitated whole prey items) or stomach contents (Furness and Hislop 1981, Furness 1997). However, there are acknowledged drawbacks to these approaches (Duffy and Jackson 1986). Analyses of pellets tend to overestimate the importance of prey with hard body parts in comparison with soft-bodied prey items and certain prey types are more likely to produced in regurgitates than others (Duffy and Jackson 1986; Hobson et al. 1994). Furthermore, sampling must take place over an extended period, otherwise short-term fluctuations in diet may obscure longer-term patterns.

Analyses of stable carbon and nitrogen isotope ratios in consumer tissues do not suffer from these biases and are a powerful dietary assessment technique, particularly when used in conjunction with conventional methods (Hobson et al. 1994, Schmutz and Hobson 1998). This approach is now well established (Michener and Schell 1994). It has been widely demonstrated that the ratio of stable nitrogen isotopes in consumer proteins ($^{15}N/^{14}N$, expressed as $\delta^{15}N$) yields information on trophic position, exhibiting a stepwise enrichment of between 3 and 5‰ at each trophic level (e.g. DeNiro and Epstein 1981, Hobson and Welch 1992, Bearhop et al. 1999). The ratio of stable carbon isotopes ($^{13}C/^{12}C$, $\delta^{13}C$) can be used to assess the relative importance of different carbon pools to a consumer, such as marine versus fresh water, or inshore versus pelagic feeding habits (Chisholm et al. 1982, Hobson et al. 1994, Bearhop et al. 1999).

A further advantage of stable isotope analyses is that, depending on the turnover rate of the tissue chosen, dietary information spanning different temporal scales can be obtained (Hobson and Clark, 1992). For example, it has been demonstrated that isotopic signatures in feathers provide information on diet at the time of feather growth (Hobson and Clark, 1992). Thus, the feathers of chicks can provide dietary information integrated over the period during which the feathers were growing. Although chicks do not produce pellets their diet is broadly similar to adults (S. Votier unpubl. Data). Therefore the pellets produced by adults and the isotope signatures of chick feathers should reflect similar dietary intake.

Several studies using pellet analyses of Great Skua diet have shown marked annual changes in the relative occurrence of different prey types (Hamer et al. 1991, Phillips et al. 1997). These dietary shifts generally resulted from changes in prey abundance and commercial fishery activities. However, given the biases associated with conventional techniques, it is possible that under certain conditions only large scale changes in diet would be distinguished using these methods and more subtle changes would be left undetected. This is particularly likely for soft-bodied prey items or fish with small or delicate otoliths such as mackerel (*Scomber scombrus*) and herring (Jobling, and Breiby 1986).

We investigated the diet of breeding Great Skuas over a three-year period at the St Kilda archipelago, UK. Given the nature of the fishery operating in the waters around the islands, we predicted that herring and mackerel should feature more heavily in the diet of skuas when trawlers were present. We also predicted that pellets would be less likely to detect such changes than regurgitates or stable isotope analyses. Pellet and regurgitate data can sometimes produce equivocal results in terms of the relative importance of particular types. By adding the dimension of stable isotope analyses we hoped to resolve some of the uncertainties. Using this integrated approach, we provide evidence for annual variation in diet composition. Our results have important implications for studies estimating the impact of Great Skuas on their prey, particularly in light of recent concerns that predation may have resulted in the local decline of some seabird populations (Furness 1997, Heubeck et al 1997).

METHODS

SAMPLE COLLECTION AND PREPARATION

Body feathers (8-10 per individual) were sampled from 4-6 week old Great Skua chicks at Hirta, St Kilda archipelago (57° 49'N, 08° 05'W) in the summers of 1995, 1996 and 1997, and stored in sealed plastic bags.

Pellet collections were made at least once every 10 days from breeding territories in 1996 and 1997, following the methods described by Furness and Hislop (1981). Additionally, prey samples in the form of regurgitates were collected from adults (mostly from birds nest trapped during late incubation and early chick rearing) and chicks. Regurgitates from 1997 were stored frozen in sealed plastic bags in preparation for isotope analyses. In 1996 and 1997 pellet collections were made during most of the breeding season. In 1995 St Kilda was visited for only two weeks during chick rearing. Pellets from that year include those collected during this period plus some ad hoc collections by the warden earlier in the season. No regurgitates were sampled in 1995. Pellets were assigned to one of five categories: bird (mostly Hydrobatidae, Alcidae and Procellaridae), herring or mackerel, whitefish (all fish excl. mackerel and herring, mostly Gadidae), goose barnacle (*Lepas* spp.), and other (which included squid, sheep, rabbit, and crustacea). Temporal distribution of the three most common types of pellet (bird, whitefish, and goose barnacle) in 1996 and 1997 was recorded on a weekly basis, with week one being three weeks prior to median hatching date.

ISOTOPIC ANALYSES

Isotopic analyses, including cleaning, drying and powdering of feathers and regurgitate soft tissue samples, followed the methods described by Bearhop et al.

(2000). Lipids were extracted from the soft tissue of regurgitated prey items using a Soxhlet apparatus with refluxing solvent (1:1 mix of methanol and petroleum ether). Precision and accuracy for $\delta^{13}C$ measurements was $\leq 0.2‰$, and $\leq 0.4‰$ for $\delta^{15}N$.

ATTENDANCE

In most seabirds, time spent away from the colony can be taken as an index of foraging effort and this has been shown to be the case for Great Skuas in Shetland, UK (Furness and Hislop 1981, Caldow and Furness 2000). On St Kilda in 1997, we recorded the number of adults present at a minimum of 30 randomly selected territories every one to two days and a mean was calculated. Attendance data were only recorded between 09:00 and 13:00 (BST) to control for diurnal variation in foraging effort. These data were compared to those collected in 1996 (data already presented in Phillips et al. 1997). During 1997, a large factory trawler was operating in the waters close to St Kilda and periodically processing fish within 2km of the colony. Adult attendance data collected in 1997 during the period when the trawler was present were compared to attendance while the boat was absent. On most days visibility was good with the mainland (50 miles distant) regularly discernable. Trawler presence or absence was assessed visually and subsequently confirmed by the ship's operators (A. Sinclair pers comm.). It is unlikely that other trawlers could have been operating near the colony without being noticed and no trawlers were noted close to the colony during the 1996 and 1995 collections.

STATISTICAL ANALYSES

Differences among isotopic values of feathers and dietary samples were tested using Multivariate Analyses of Variance (MANOVA). In these models, $\delta^{15}N$ and $\delta^{13}C$ values of tissues were the dependent variables and year or dietary category were factors. In all cases, Scheffé tests were used to indicate groups that differed significantly. χ^2-tests and Fisher exact tests were used to check for among year differences in diet assessed via conventional means. The effects of time of season and year on the proportion of bird pellets were investigated using a Generalised Linear Model (GLM) with binomial error distribution and logit link function, which was run with an adjustment for overdispersion (Crawley 1993, GLIM version 4.0). Since attendance is known to decline as the breeding season progresses, the effect of trawler presence was also tested using a GLM (in this case with a normal error distribution) with date (expressed in days after the 30th May) as a covariate and trawler presence or absence as a factor. Unless stated otherwise, values presented are means ±1SD. In all cases a significance level of P<0.05 was used.

RESULTS

Isotope signatures of Great Skua chick body feather samples differed significantly among the three years (Fig. 1). Mean δ^{15}N values in 1997 (11.5 ± 0.5‰) were significantly lower than those collected in 1995 (12.6 ± 0.6‰) and 1996 (12.7 ± 0.6‰. ANOVA: $F_{2,77}$=36.5, P<0.001). δ^{15}N values in these two earlier years did not differ significantly. The mean δ^{13}C values of feathers from all years differed significantly from one another (1995 = -16.1 ± 0.5‰, 1996 = -15.3 ± 0.3‰, 1997 = -16.5 ± 0.4‰. ANOVA: $F_{2,77}$=67.1, P<0.001). Among the main dietary categories (goose barnacle not included since n=1), there was also some significant isotopic segregation. The δ^{15}N values of herring/mackerel regurgitates (n=9) differed from those of bird (n=5) and white fish (n=5) the latter two not differing significantly (ANOVA: $F_{2,16}$ = 7.3, P=0.005). A similar pattern was detected for δ^{13}C (ANOVA: $F_{2,16}$ = 9.5, P=0.002).

In the case of pellets herring/mackerel and 'other' dietary categories were combined to reduce the number of expected counts < 5. A χ^2-test indicated that sampled diet differed from expected distributions of pellets (χ^2_6 = 63.7, P<0.001), with more bird and less whitefish than expected in 1996 (Figure 2). Pellet data from 1995 were similar to those from 1997 (χ^2_3 = 6.1, P= 0.19.). Small sample sizes meant it was not possible to test for differences in the representation of herring and mackerel in pellets among years.

There were no detectable annual differences in the composition of chick regurgitates. A χ^2-test using all chick regurgitate data (Fig 2b) was not significant (χ^2_2 = 4.3, P=0.12), however the number of expected counts less than five was high (two out of six). There was no significant difference in the occurrence of mackerel and herring in chick regurgitates between the two years (Fisher exact test, p=0.09, whitefish and bird categories combined)

Most regurgitates produced by adults were of whitefish (Fig.2c). As with chicks, there was no significant difference in the occurrence of mackerel and herring in adult regurgitates between the two years (Fisher exact test, p=0.21, whitefish and bird categories combined).

The percentage of bird pellets at St Kilda in 1997 increased as the season progressed, while the occurrence of fish remained relatively constant and goose barnacle declined over the same period (Fig.3). A GLM (binomial errors) indicated that the increase in bird as the season progressed was significant and consistent across years (time of season effect, $F_{1,15} = 13.9$, $P<0.01$. year effect, $F_{1,15} = 0.1$, $P>>0.05$. season/year interaction, $F_{1,15} = 0.02$, $P>>0.05$).

In 1997, attendance declined significantly as the season progressed (GLM with normal errors, $F_{1,32} = 7.5$, $P=0.01$, *adjusted* $r^2 = 0.8$, *slope*=0.01) but this was strongly influenced by the presence of the factory trawler. Attendance was significantly lower when the vessel was not operating in St Kilda waters (GLM, $F_{1,32} = 68.6$, $P<0.001$, 1.8 ± 0.1 birds [trawler present], 1.4 ± 0.1 birds [trawler absent]). Median attendance in 1996 (median, 95%CI = 1.85, 1.79-1.9 birds, n = 29 days) was not significantly different from 1997 (median, 95%CI = 1.75, 1.69-1.85 birds, n = 36 days. Mann Whitney U test: $U = 638$, $P > 0.05$).

DISCUSSION

The significant decrease in $\delta^{15}N$ signatures of chick feathers collected in 1997 (Fig 1) suggests that there was an increase in occurrence of lower trophic status prey in the diets of these birds in that year. Other studies report fractionations of around 3 – 5 ‰ (e.g. DeNiro and Epstein 1981, Hobson and Welch 1992, Bearhop et al. 1999) for $\delta^{15}N$ between consumer tissues and their diets. In this study the differences between feather $\delta^{15}N$ signatures and those of the main dietary items, as indicated by conventional analyses (birds and whitefish), are much smaller. This suggests that lower trophic status prey comprise a larger part of Great Skua diet than would be predicted pellet collections alone.

Much of the evidence for the drop in trophic status points to an increase in the consumption of herring and mackerel in 1997. These fish species tend to consume prey of lower trophic status than do whitefish and seabirds (Whitehead 1984, Moller-Buchner et al. 1984, Furness 1997) and this is evidenced by the significantly lower $\delta^{15}N$ value of this group (Fig 1). Although not statistically significant, probably because of the small sample sizes, the increased occurrence of herring and mackerel in regurgitates collected in 1997 compared to 1996 supports the idea that the importance of this dietary category changed between the two years (Figs 2b and 2c). In addition, the significant decline in Great Skua attendance during the absence of a large fish-processing trawler suggests that the birds were utilizing discards from this vessel either directly or via kleptoparasitism of other species such as Northern Gannets (*Morus bassanus*). Large numbers of seabirds were observed feeding around this trawler which was landing between 50 and 100 tonnes of fish per haul, the bulk of which were herring and mackerel (A. Sinclair pers comm.). The implications of long-term drops in territorial attendance in Great Skuas were first noted during the Shetland sandeel crisis. During this period, low sandeel availability correlated with longer foraging trips, low territorial attendance, and low breeding success (Hamer et al. 1991). More importantly, the age structure of the breeding population changed with 28% of adults failing to return to breed and large numbers of immature birds recruiting into the colony (Hamer at al. 1991)

Despite the small sample size, it could be argued that an increase in goose barnacle consumption (Fig. 1), during 1997 could have produced the drop in $\delta^{15}N$ values in the feathers of Great Skua chicks. In fact, goose barnacle pellets are particularly conspicuous because of the hard calcareous plates and unlikely to be under-represented in pellet collections. Since there was no significant change in the numbers of goose barnacle pellets across the three-year study period (Fig 2a), it is unlikely that any significant change in their consumption occurred.

Annual differences among pellet data are likely a product of variation in the timing of pellet collections and a seasonal increase in the importance of birds in the diet (Fig 3). Compared with 1997, pellet collection in 1996 began when chicks on average were two weeks older and finished two weeks later than in 1997. It should be noted that isotope signatures of chick feathers represent the same period each year. A GLM indicated a significant seasonal increase in the amount of bird consumed, and that there was no year effect once the seasonal trend had been accounted for. Seasonal changes in the proportion of bird in the diet of Great Skuas are probably in response to the fledging of auks and increases in the numbers of non-breeding storm petrels (*Oceanodroma leucorhoa* and *Hydrobates pelagicus*) and Manx shearwaters (*Puffinus puffinus*) attending the colony.

Other discrepancies in conventional assessment techniques lead to variation in the apparent importance of different prey in the diet. One is related to the time of day when samples are collected. Storm petrels, which are the most common seabirds in Great Skua diet at St Kilda (Phillips et al. 1997), and shearwaters tend not to be seen in the waters close to St Kilda during daylight hours (Leaper et al. 1988). The difficulty of locating and capturing such mobile prey items makes it likely that the skuas catch petrels while they attend the colony during darkness or early dawn. This is supported by the presence of large numbers of Manx shearwater carcasses on the slopes where many of the shearwaters nest (Manx shearwaters are much larger than the two storm petrel species and are therefore not swallowed whole). Pellets produced on territories after consumption of these petrels can be easily detected several days later. By comparison, any item consumed during the hours of darkness would have been in the digestive tract for a considerable period less likely to be found in regurgitates, since it would be rare for these to be obtained from a Great Skua adult or chick until at least 5 hours after dawn. . This factor may therefore explain some of the disparity between pellets and regurgitates in their respective estimates of bird consumption.

There were significant differences among $\delta^{13}C$ signatures of chick feathers among the three years (Fig1, Table 1). Some of this variation is likely to be a consequence of trophic enrichment, as $\delta^{13}C$ values increase by about 1‰ on average at each trophic level (Rau et al. 1983, Fry and Sherr 1984, Hobson and Welch 1992). The difference between 1995 and 1997 $\delta^{13}C$ values (0.4‰) is consistent with the difference of $\delta^{15}N$ measurements (1‰). However, in 1996 $\delta^{13}C$ signatures in chick feathers were 0.8‰ lower than in 1995 (Fig 1, Table 1) and there are several possible explanations for this. The change could be a result of increased intake of prey with low $\delta^{13}C$ values, but since there was no difference in $\delta^{15}N$ between these two years, this seems unlikely. It has been demonstrated that the carbon isotope signatures of inshore foraging seabirds are enriched in ^{13}C when compared to those foraging offshore (Hobson et al. 1994). Conceivably, Great Skuas may simply have been foraging closer to the colony in 1996. If this were the case then lower adult attendance would be anticipated in other years and this was not recorded (see Results). A final possibility may be that there were changes in the carbon pool at the food web base in 1996. Isotopic enrichment may occur in phytoplankton and organic matter during periods of primary production due to increased carbon demand (Deuser et al. 1968, Rau et al. 1992, Pancost et al. 1997). Continuous plankton recorder surveys for the waters to the north of St Kilda indicate that primary production in 1996 was considerably higher than in 1995 or 1997 (Sir Alister Hardy Foundation for Ocean Science pers. comm.) and this could have resulted in the elevated $\delta^{13}C$ signatures observed in chick feathers grown in 1996.

It follows from this that the drop in $\delta^{15}N$ signatures of feathers during 1997 might also be interpreted as a change in oceanographic conditions. For example upwelling nitrate from deep oxygen depleted water can elevate $\delta^{15}N$ values of marine organisms (Michener and Schell 1994). A weakening of any upwelling in the waters around St Kilda during 1997 could conceivably have produced the drop in $\delta^{15}N$ values. However, if this phenomenon did explain the drop in $\delta^{15}N$ during 1997 we would not necessarily expect the corresponding fall in $\delta^{13}C$ (discussed in previous paragraph), because nitrogen and carbon isotope signatures are effectively uncoupled at the nutrient level. Moreover, all of the other evidence points to a real change in trophic status during this year rather than a change in the $\delta^{15}N$ signatures of nutrients.

It is clear from the results of this study that, when combined with conventional dietary analyses, stable isotopes can provide useful additional information. A combined approach to dietary assessment is likely to become increasingly important when assessing the diets of species where control or conservation is an issue. In particular, the integrated approach adopted here provided strong evidence that herring and mackerel were considerably more important in some years than would have otherwise been suggested. In general, the reliance of Great Skuas on these fish discards (which are rarely found in pellets) may be greater than currently realised. With respect to potential future reductions in fishing effort and reductions in the availability of discard fish, the predicted impacts of Great Skuas on other seabird populations may have to be re-assessed.

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Figure Legends.

FIGURE 1. Stable carbon and nitrogen isotopic compositions of Great Skua chick feathers collected at St Kilda in 1995, 1996 and 1997, and those of the main Great Skua dietary categories collected in 1997(error bars = ± 1 SD).

FIGURE 2. Percentage composition of the main prey categories in the diet of Great Skuas assessed via conventional techniques.

FIGURE 3. Temporal changes in the occurrence of the three main dietary categories in the pellets produced by Great Skuas at St Kilda in 1996 and 1997. Week 1 begins three weeks prior to median date of hatching.

Fig 1

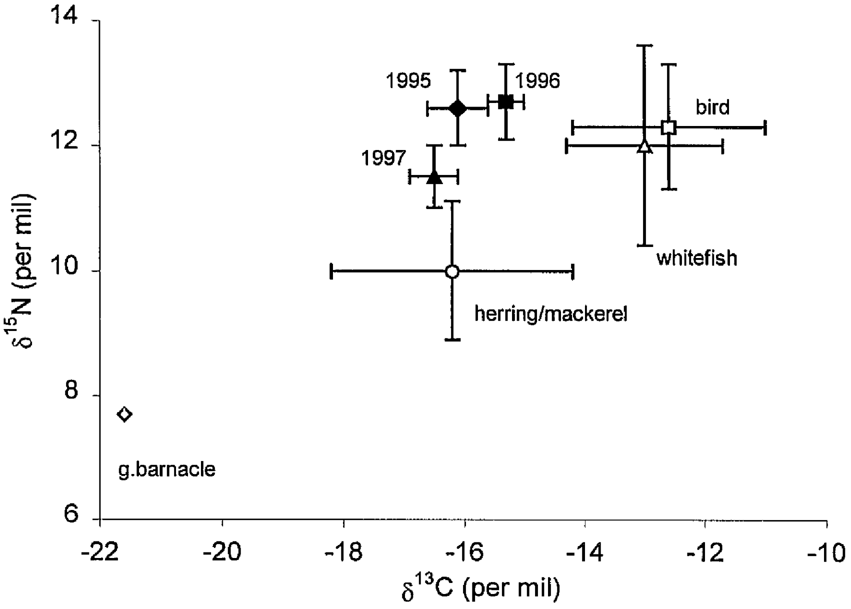

14
12
10
8
6
$\delta^{15}N$ (per mil)
-22
-20
-18
-16
-14
-12
-10
$\delta^{13}C$ (per mil)
1995
1996
1997
bird
whitefish
herring/mackerel
g.barnacle

Fig 2

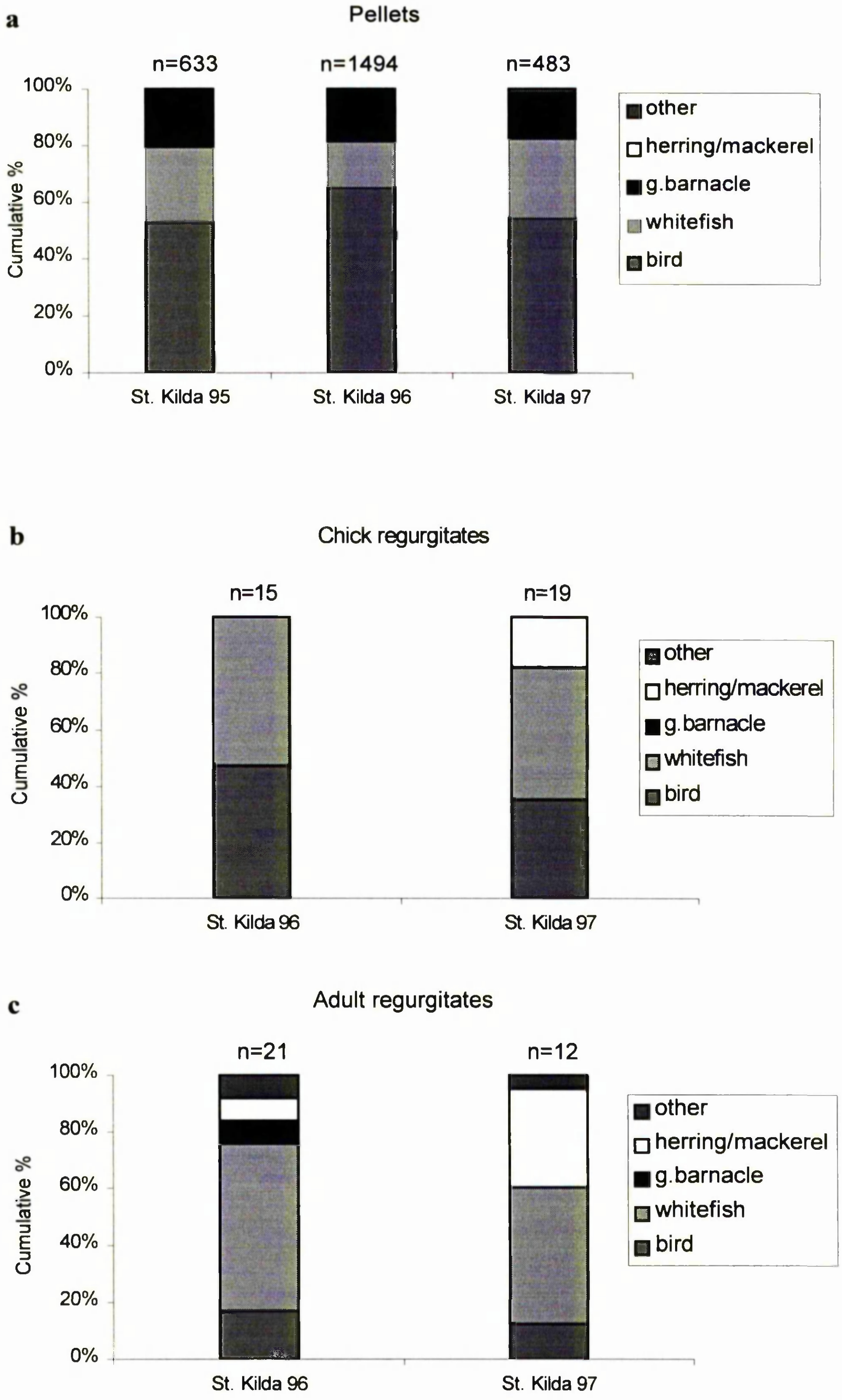
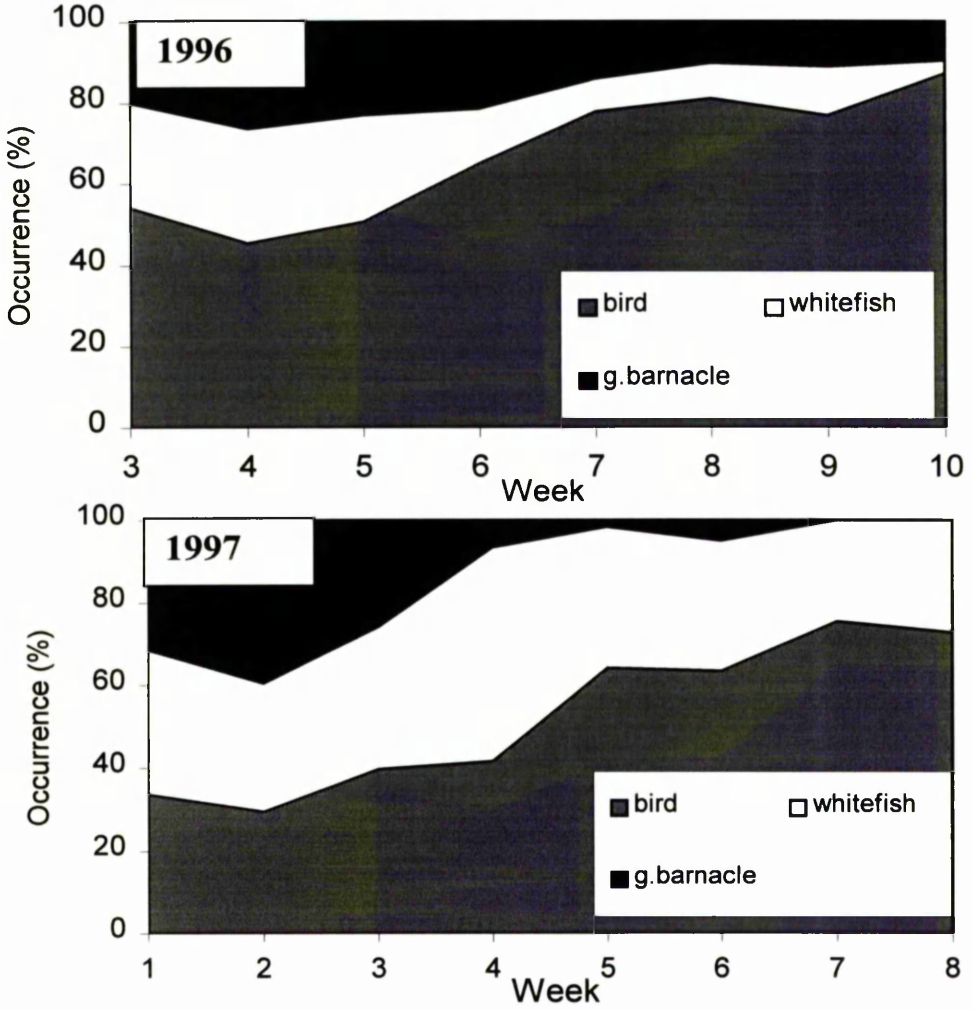

a
Pellets
n=633
n=1494
n=483
100%
80%
60%
40%
20%
0%
Cumulative %
St. Kilda 95
St. Kilda 96
St. Kilda 97
other
herring/mackerel
g.barnacle
whitefish
bird
b
Chick regurgitates
n=15
n=19
100%
80%
60%
40%
20%
0%
Cumulative %
St. Kilda 96
St. Kilda 97
other
herring/mackerel
g.barnacle
whitefish
bird
c
Adult regurgitates
n=21
n=12
100%
80%
60%
40%
20%
0%
Cumulative %
St. Kilda 96
St. Kilda 97
other
herring/mackerel
g.barnacle
whitefish
bird

Fig 3.


1996
100
80
60
40
20
0
Occurrence (%)
3
4
5
6
7
8
9
10
Week
▨ bird
☐ whitefish
■ g.barnacle
1997
100
80
60
40
20
0
Occurrence (%)
1
2
3
4
5
6
7
8
Week
▨ bird
☐ whitefish
■ g.barnacle

Stable isotopes identify winter foraging habitat of Kirtland's warbler

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Conservation biologists increasingly appreciate that the wintering and breeding biology of threatened species are inextricably linked, sometimes in complex ways. For example the effects of habitat removal in the wintering range can be dependent on the degree of density dependence in the breeding range *(1)* and habitat selection in wintering grounds may affect timing of spring migration, and hence breeding prospects *(2)*. Thus, effective species conservation programs, particularly those dealing with migrants, need to deal with habitat requirements throughout the annual cycle.

However, the non-breeding ecology of many migratory bird species has hitherto proved intractable to study. They are frequently dispersed over large tracts of often inhospitable terrain, lack a definable 'central-place' and behave cryptically. This is a particular problem for rare species - which are often those of highest conservation concern – because encounter rates are too low to allow meaningful research to be conducted. For many threatened migratory birds such as the aquatic warbler (*Acrocephalus paludicola*), even the geographic range of non-breeders is not known *(3)*. However, the novel technique of tissue stable isotope analysis potentially permits new answers to old questions. Here we report on an attempt, using stable isotopes, to elucidate the winter habitat selection of one of the world's rarest birds – Kirtland's warbler (*Dendroica kirtlandii*).

To date the conservation program for the globally vulnerable (4) Kirtland's warbler, has focused almost exclusively on its breeding areas in the northern part of the lower peninsula in Michigan, USA *(5,7)*. During the breeding season it is an extreme habitat specialist, relying exclusively on fire-dependent, early successional jack pine (*Pinus banksiana*) forest *(5,7)*. Conservation measures have included increasing the amount of suitable jack pine forest and control of the brood parasitic brown-headed cowbird (*Molothrus ater*) *(5,7)*. This program has been extremely expensive, but hitherto successful, and the population has recovered from 201 singing males in 1971 to around 903 in 2000 *(5,4)*. However Kirtland's warblers spend between seven and eight months of the year on their wintering grounds in the Bahama Archipelago *(6)* and surprisingly little is known about their habitat requirements during this time.

The winter habitat of the species has been neglected as a conservation concern, since the dry scrub habitat it was thought to favour was extensive in the archipelago, and not under threat *(7,8)*. However, recent work has suggested that Caribbean pine (*Pinus caribaea*) woodland may be the key habitat for Kirtland's warbler during winter *(9)*. This has important implications for the species since Caribbean pine is an even more restricted habitat than jack pine *(9)* and is under threat from development and logging interests. It is therefore crucial to the continuing success of the conservation program that the issue of winter habitat use be resolved.

The rarity of Kirtland's warbler and its elusiveness in the wintering areas means that direct observations of the species during the last 150 years have occurred at an average of little over one per year *(10)*, and attempts to make dedicated studies of wintering ecology have failed *(11)*. We attempted to avoid this difficulty by using stable isotope analysis of winter-grown Kirtland's warbler feathers to determine habitat selection.

The method relies on the fact that environmental stable isotope signatures are reflected in the tissues of organisms in a predictable manner *(12)*. These signatures vary among habitats. For example the ratio of ^{13}C to ^{12}C ($\delta^{13}C$) can be used to discriminate between habitats containing different proportions of C3, C4 and CAM plants *(13,14)* and recent work has used these and other isotope ratios, to determine habitat selection in birds, mammals, fish and insects *(12)*.

Since stable isotope signatures of a consumer's tissues reflect those of its diet at time of synthesis *(14)*, tissues that are metabolically inert after formation, such as feathers, will preserve an unchanging isotopic record of the habitat in which they were grown *(15-17)*. Kirtland's warblers undergo a partial moult in the wintering areas *(6)*, and hence any feathers grown at this time will contain an isotopic record of the wintering habitat in which they were grown. Small numbers of Kirtland's warblers are caught on the well-known breeding grounds in Michigan each year as part of the ongoing recovery programme. Thus, it is possible to access winter habitat information by sampling the appropriate feathers from Kirtland's warblers trapped on the breeding grounds and analysing their stable isotope ratios. This obviates the need to find and catch Kirtland's warblers in the wintering areas.

In order to determine which wintering habitat the Kirtland's warbler feathers match, we first needed to determine the isotopic signature of each of the main habitat types in the Bahama archipelago, and establish whether these signatures are sufficiently different to allow clear separation of the habitats. In order to do this, we sampled vegetation, arthropods and the feathers of resident birds as proxies for Kirtland's warbler in the three main habitats: xerophytic scrub, Caribbean pine woodland, and mangroves (Table 1). The selected proxy bird species occupied similar niches to Kirtland's warbler, being small, predominantly insectivorous and arboreal *(6)*.

Analyses of carbon isotope ratios *(18)* suggest that there are consistent differences among habitats but very little difference between the two islands visited (Fig. 1). However, the ability to discriminate between habitats among organisms occupying higher trophic levels is likely to be reduced due to fractionation of carbon isotopes and higher levels of omnivory *(13, 19)*. We controlled for trophic effects in feather samples by regressing $\delta^{13}C$ upon $\delta^{15}N$ ($R_{1,72}$=0.3, p=0.019), and used the residual $\delta^{13}C$ values as isotopic habitat markers. $\delta^{15}N$ fractionates to a far greater degree than $\delta^{13}C$ at each trophic level and is a reliable trophic marker *(13, 17)*. These residual values were then used as the dependent variable in a General Factorial Model, with species, habitat and island as factors, in order to determine whether there were significant between-habitat differences in carbon isotope signature (Fig. 2). This model indicated significant isotopic segregation between all habitats ($F_{2,61}$=5.27, p=0.008. Post hoc, Scheffé tests $p \leq 0.002$) and significant differences among species ($F_{10,61}$ =5.11, p<0.001), with no island effect. Since species and habitat confound one another to a certain degree (Table 1, only one species was caught in more than one habitat), it could be argued that the habitat effect is simply an artefact of this. However, two lines of evidence suggest that habitat is the major effect and is independent of the species effect. If 'species' were driving the difference among habitats then we would expect habitats represented by more species to have greater variability in residual $\delta^{13}C$, and this is not the case (Pine: n=8 species, SD= 0.65. Coppice: n=2 species, SD 0.57. Mangrove: n=3 species, SD 1.48). Moreover, the residual $\delta^{13}C$ values for thick-billed vireos (the only species caught in all three habitats, Table 1) show a similar pattern to the overall sample and were significantly higher in coppice than in pine (Fig.3, t_{23}=3.19, p=0.004).. Thus, there does appear to be consistent isotopic segregation between habitats (Figs 1-3) with respect to $\delta^{13}C$, and the ability to detect these differences are enhanced if trophic effects are held constant.

Although only three Kirtland's warblers were trapped during the 2000 breeding season, the nape feathers from these birds showed extremely low inter-individual variation in their residual carbon isotope ratios (SD=0.05, Fig.4). Intra-individual variation among nape feathers was also small with SDs for $\delta^{13}C$ ranging from 0.2-0.34 and $\delta^{15}N$ 0.1-1.0 (3 samples analysed for each individual). For all habitats (pine, coppice, mangrove) the values of residual $\delta^{13}C$ in bird feathers do not deviate significantly from a normal distribution (Kolmogorov-Smirnov test, $P>0.85$). We therefore determined the probability that the Kirtland's warblers belong to either the pine or the coppice populations.

We find that the isotope signatures of the three Kirtland's warblers lie 0.9-1.0 standard deviations below the mean value for coppice-dwelling birds. By contrast, the Kirtland's warbler isotope signatures lie within 0.04-0.19 standard deviations of the mean for pine-dwelling populations. These values allow us to reject the idea that all three Kirtland's warblers are drawn from a coppice-dwelling population ($P=0.046$, two-tailed), but are consistent with the hypothesis that all three birds are drawn from a pine-dwelling population ($P=0.9$).

If one assumes that the Kirtland's warbler values are drawn from a normal distribution, then a t-test indicates that they have a mean residual $\delta^{13}C$ value significantly different from that of the coppice-dwelling birds ($t_{17.2} = 3.69$, $P=0.002$), but not significantly different from that of pine-dwellers ($t_{46.5} = 0.85$, $P=0.40$). A Mann-Whitney test shows that residual $\delta^{13}C$ of Kirtland's warblers tend to be lower ranked than coppice-dwellers ($U = 9$, $P=0.081$), but are not different from pine-dwellers ($U = 66$, $P=0.77$).

Our results show that by using residual carbon isotope ratios it is possible to identify differences between Caribbean pine and coppice habitat use among insectivorous birds. Moreover, this difference is apparent in the same species living in different habitats (Fig. 3). The results provide compelling evidence that Caribbean pine forests in the Bahamas, which have come under renewed pressure from logging activity this year, are an important wintering habitat for one of the world's most endangered bird species. These results support the contention of Haney et al. *(9)*, whose suggestion was based on analysis of anecdotal records from a variety of sources, and acoustic surveys. The use of stable isotope analysis is objective, and avoids the biases inherent in these sampling methods; indeed a second analysis of the same set of anecdotal reports produced the opposite conclusion, that Kirtland's warblers are mainly found in dry scrub *(8)*.

Given that there are apparently suitable areas of breeding habitat in Michigan that remain unoccupied *(20)* it seems possible that winter habitat availability is a population limiting factor, *(9)*. Kirtland's warblers have been recorded in dry scrub habitats of the Bahamas *(8,9)*, and our findings do not rule out the possibility that this is an important habitat for some sections of the population. All the birds in our sample were males, and it may be the case that sub-dominant individuals (probably females and immatures) are excluded from the optimal habitats, resulting in some birds occupying other areas. This effect has been described in wintering American redstarts (*Setophaga ruticilla*), *(2)*.

Clearly there is great potential to investigate major questions concerning the ranges, migration routes, habitat use and diet of threatened migrants using stable isotopes. In particular, the use of more abundant species as proxies for the rare taxa of interest, as presented in this study, holds considerable promise. Moreover this sort of approach can provide rapid and relatively cheap solutions to conservation problems that could not easily be answered in any other way.

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18. During April 2000 random vegetation samples were collected from each habitat visited on each of the two islands visited (Andros and Abaco in the northen Bahamas). All samples from a habitat type within an island were combined, dried and homogenized in a freezer mill. Arthropod samples were collected using sweep nets, for each sampling site the animlas were sorted into Orders and prepared in the same manner as vegetation samples. Feather samples were clipped from birds trapped in mist nets. In the case of proxies, a random sample of body feathers was collected. With Kirtland's warblers, nape feathers (re-grown on the wintering grounds during the pre-nuptial moult) were clipped from three individuals trapped in Michigan in summer 2000. Feather samples were washed in 0.25M NaOH and then rinsed in distilled H_2O prior to analysis. About 0.5mg of each sample was analysed by continuous flow isotope ratio mass spectrometry (CF-IRMS) using a Finnigan Tracer Mat IRMS coupled to a Carlo Erba C/N/S analyser. Isotope ratios are expressed in ‰ relative to international standards (*13*). Internal standards were run for every 6 samples. Analytical precision for $\delta^{13}C$ and $\delta^{15}N$ was 0.2‰.

19. Carbon and nitrogen isotopes undergo significant fractionation during enzymatic processes such as digestion and assimilation (in this instance the fractionation refers to an enrichment of the heavier isotope). At each trophic level the fractionation factor for $\delta^{13}C$ is typically 1-2‰ and for $\delta^{15}N$ is 3-5‰ *(13,14,17)*. This means that at higher trophic levels and in groups of animals feeding at multiple trophic levels some of the variability in $\delta^{13}C$ is attributable to this fractionation effect, rather than to habitat differences.

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Table 1. Species captured in the three habitat types and sample sizes

	Pine	Coppice	Mangrove
Species	*Pinus caribbaea*, with understory (e.g. *Metopium toxiferum*, *Lantana* spp., *Byrsonima lucida, Serenoa repens*)	Broadleaf evergreen shrub, with a number of species from families where C4 and CAM metabolism has been recorded (e.g. *Erithalis* spp., *Gymnanthes lucida, Savia bahamensis* etc.)	*Rhizophora* spp.
Cuban Pewee *Contopus caribaeus*	5	0	0
La Sagra's Flycatcher *Myriarchus sagrae*	4	0	0
Blue-gray Gnatcatcher *Polioptila caerulea*	6	0	0
Red-legged Thrush *Turdus plumbeus*	3	0	0
Bahama Mockingbird *Mimus gundlachii*	0	1	0
Thick-billed Vireo *Vireo crassirostris*	8	16	2
Yellow warbler *Dendroica petecia*	0	0	3
Yellow-throated Warbler *Dendroica dominica*	3	0	0
Pine Warbler *Dendroica pinus*	6	0	0
Bahama Yellowthroat *Geothlypis rostrata*	14	0	0
Red-winged Blackbird *Agelaius phoeniceus*	0	0	3
Totals	49	17	8

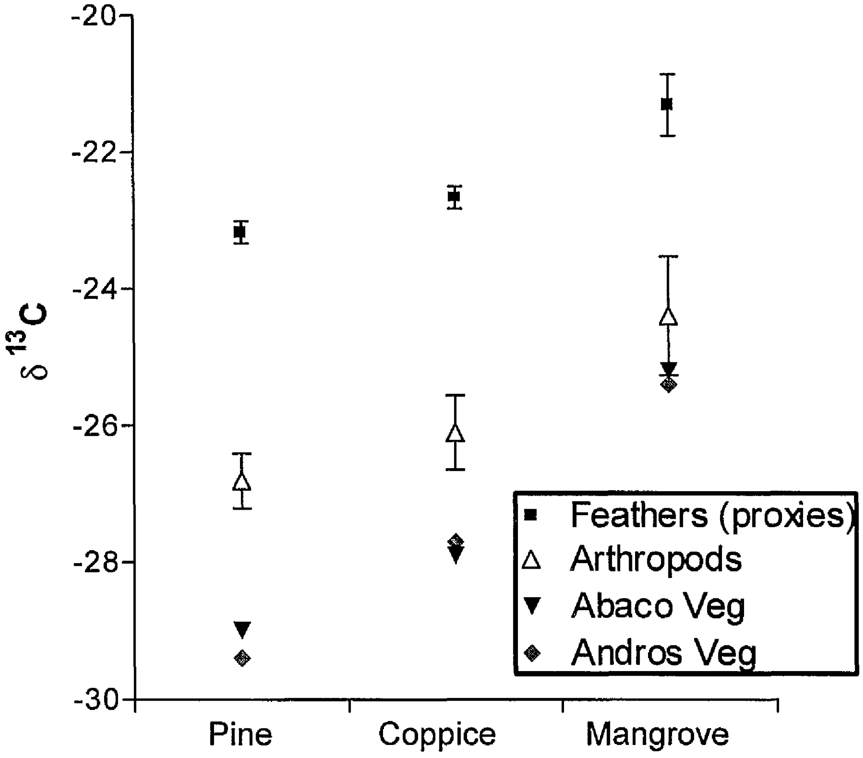
Figure 1. Actual $\delta^{13}C$ values for combined vegetation samples, and mean $\delta^{13}C$ values for arthropods and feathers collected from the three habitat categories in the Bahamas (error bars = ± 95% CIs). Abaco Veg = combined vegetation samples collected on the island of Great Abaco, Andros Veg = combined vegetation samples collected on the island of North Andros.

Figure 2. Residual $\delta^{13}C$ values in feathers of proxy bird species caught in the three habitat types (± 95 % CIs)

Figure 3. Residual $\delta^{13}C$ values in feathers of thick-billed vireos caught in pine and coppice (± 95 % CIs)

Figure 4. Residual carbon isotope ratios of Kirtland's warbler nape feathers, in comparison with those of proxy species from the three different habitats (± 95% CIs).

Fig.1



-20
-22
-24
-26
-28
-30
$\delta^{13}C$
Pine
Coppice
Mangrove
■ Feathers (proxies)
△ Arthropods
▼ Abaco Veg
◆ Andros Veg

Fig.2

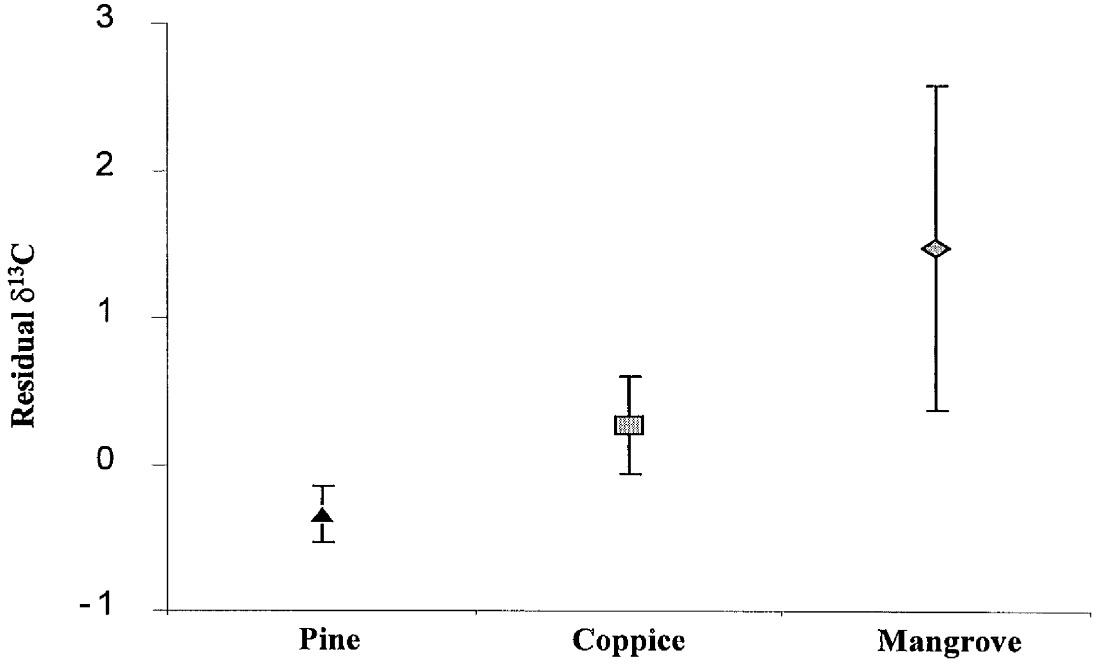


Fig.3

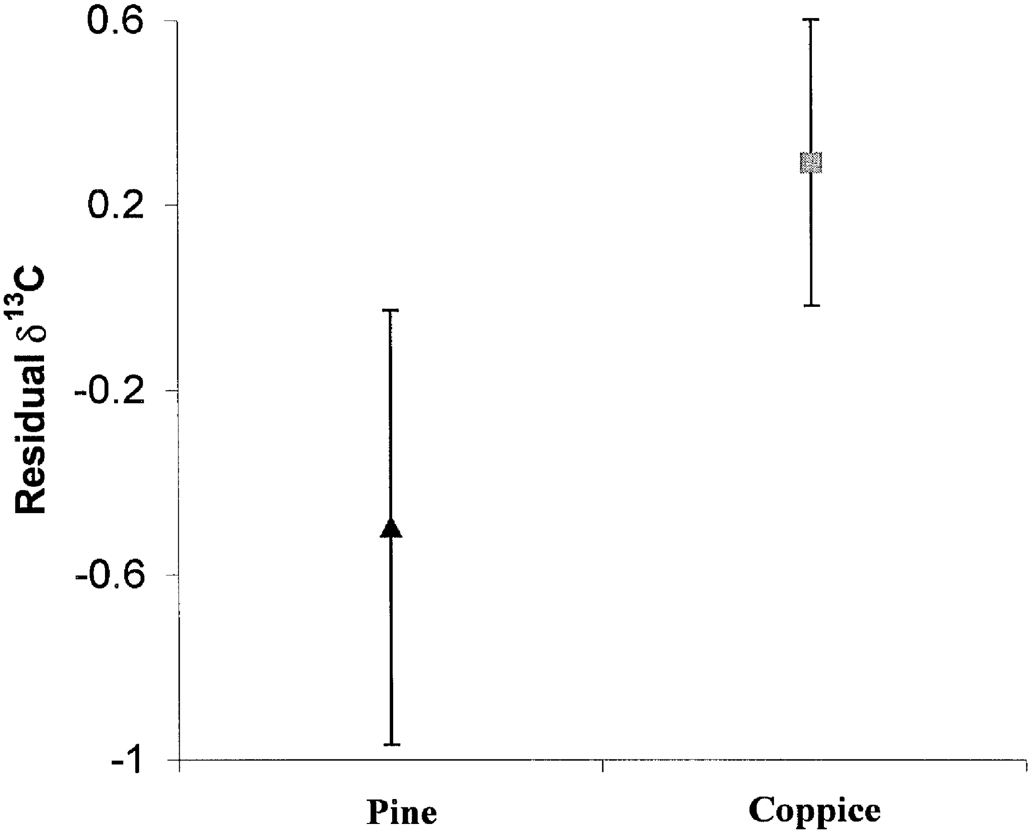
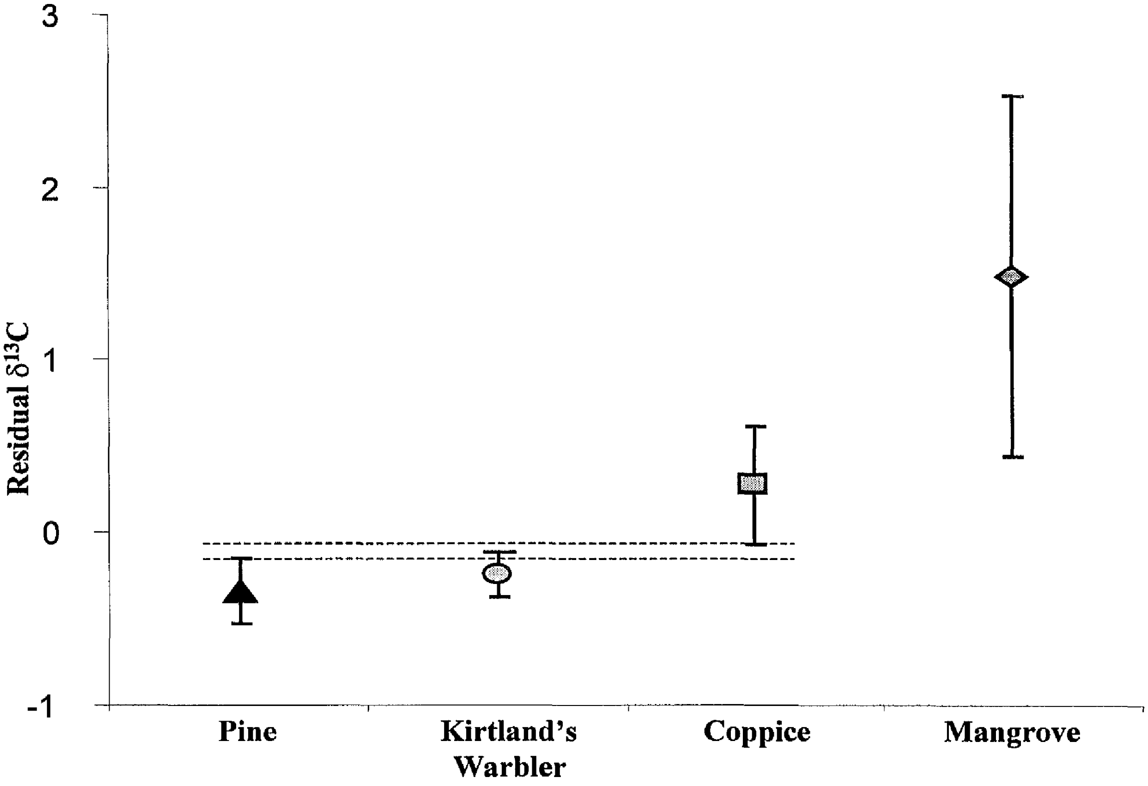


Fig.4


3
2
1
0
-1
Residual $\delta^{13}C$
Pine
Kirtland's Warbler
Coppice
Mangrove