

REPRODUCTIVE CONSEQUENCES FOR GREAT SKUAS SPECIALIZING AS SEABIRD PREDATORS

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Abstract. Most of the Great Skuas (*Stercorarius skua*) breeding at Hermaness, Shetland, exhibit dietary specialization: a small proportion feed almost exclusively upon seabird prey, a small proportion feed as generalists, and most feed on fishery discards. We investigated the foraging dynamics, reproductive performance, and survival of Great Skuas that specialized in depredating other seabirds compared with those feeding predominantly on fish. Around half of the specialist bird predators defended combined breeding and feeding territories that included a section of seabird colony; the remainder of the predatory skuas foraged away from breeding territories. Specialist bird predators retained their feeding habit and, if present, feeding territory, across years. Time budgets revealed that specialist bird predators spent less time foraging than skuas feeding predominantly on fish. Results of radio-telemetry indicated that bird-specialist skuas have smaller home ranges than other birds. In a comparison of reproductive performance, specialist bird predators consistently hatched earlier among years. They also showed larger clutch volumes and improved chick condition, but these were subject to annual variations. Hatching success and fledging success for specialist bird predators and specialist fish predators were similar. Specialist bird predators showed similar annual survival compared with fish-feeders over the same period. Specializing as a bird predator may be limited to the best birds in the population, but their poorer than predicted breeding success reveals the need for further study into the relationship between diet and reproductive success in this species.

Key words: foraging behavior, Great Skua, reproductive performance, specialist predator, *Stercorarius skua*.

Consecuencias Reproductivas para Individuos de *Stercorarius skua* que se Especializan como Depredadores de Aves Marinas

Resumen. La mayoría de los individuos de *Stercorarius skua* que se reproducen en Hermaness, Shetland, presentan una especialización de la dieta: una proporción pequeña se alimenta casi exclusivamente de aves marinas, otra proporción pequeña generalista y la mayoría se alimenta de desechos de pesqueros. Se investigó la dinámica de forrajeo, el desempeño reproductivo y la supervivencia de individuos de *S. skua* que se especializan en la depredación de otras aves marinas comparándolo con otros que se alimentan predominantemente de pescado. Cerca de la mitad de los depredadores especialistas de aves defienden de manera combinada territorios para reproducción y para alimentación que incluyen una sección de la colonia: el resto de los individuos depredadores forrajean lejos de los territorios de reproducción. Los aves depredadores especialistas de aves mantienen sus hábitos alimenticios y, en caso de presentarse, el territorio para alimentación, a través de los años. Los presupuestos de tiempo revelaron que los depredadores especialistas de aves pasan menos tiempo forrajeando que los que se alimentan predominantemente de pescado. Los resultados de radio-telemetría indicaron que las aves especialistas tienen rangos de hogar menores que otras aves. En una comparación de desempeño reproductivo, los depredadores especialistas de aves presentaron fechas de eclosión más tempranas, las cuales se repitieron a través de los años. Así mismo, mostraron volúmenes de puesta más grandes y mejor condición de las crías, pero éstos estuvieron sujetos a variaciones anuales. El éxito de eclosión y el éxito de emplumamiento de los depredadores especialistas de aves y de los depredadores especialistas de pescado fueron similares. Los depredadores especialistas de aves mostraron una supervivencia anual similar a la de los que se alimentan de pescado.

durante el mismo periodo. La especialización como depredador de aves puede limitarse a las mejores aves de la población, pero el bajo éxito reproductivo encontrado, contrario a lo predicho, revela la necesidad de estudios adicionales sobre la relación entre la dieta y el éxito reproductivo en esta especie.

INTRODUCTION

One of the most important factors in any ecosystem is food availability. Many studies have demonstrated relationships between feeding conditions and aspects of avian reproduction, including lifetime reproductive success (Korpimäki 1992, Annett and Pierotti 1999), annual productivity (Annett and Pierotti 1989, Hamer et al. 1991, Bolton et al. 1992, Oro et al. 1995, Phillips et al. 1996) and adult survival (Oro and Furness 2002).

Within any population, some birds may be able to improve feeding opportunities (and therefore reproductive success) by altering their foraging behavior. Differences in foraging behavior can arise because (1) individual birds gain experience that makes them more efficient foragers (Greig et al. 1983), (2) birds with differing morphology may exploit novel foods (Grant and Grant 1996), or (3) birds may breed close to good foraging areas (Ens et al. 1995). Variations in foraging strategy at the population level may result in pronounced prey specializations at the individual level, and specializing when selecting prey to feed offspring may improve reproductive success (Golet et al. 2000).

Gulls (*Larus* spp.) and skuas (*Stercorarius* spp.) are generalist predators, but show pronounced feeding specializations at the individual level. Variations in reproductive performance have been described as a result of diet choice in these groups of birds. However, certain prey types do not yield the same advantages in all cases. For example Herring Gulls (*Larus argentatus*) specializing on intertidal invertebrates showed improved reproductive performance compared with specialist bird predators, garbage specialists, and generalists (Pierotti and Annett 1991). By contrast other studies have shown that where foragers specialized on bird prey, they exhibited higher reproductive rates and survival than generalist conspecifics (Trillmich 1978, Trivelpiece et al. 1980, Pietz 1987, Watanuki 1992, Spear 1993).

Great Skuas (*Stercorarius skua*) breeding in Shetland, Scotland, forage in a number of different ways including fishing for sandeels (*Ammodytes marinus*), stealing prey from other sea-

birds, scavenging for discards at fishing boats, and by direct predation on other seabirds (Phillips, Catry et al. 1997). There are marked differences in skua diets among different colonies (Phillips, Catry et al. 1997). At many of the large Great Skua colonies concern has been expressed over the predation pressure on other seabird species (Heubeck et al. 1997, Phillips et al. 1999), emphasizing the need for a better understanding of the relationship between diet choice, particularly bird prey, and breeding biology in this species.

Detailed studies from the largest Great Skua colony in Shetland, Foula, revealed sandeels (a high-lipid fish) to be the predominant prey item at the population level. During a period of low sandeel availability Great Skuas experienced reduced reproductive success and took a higher proportion of bird prey and fishery discards (Hamer et al. 1991, Ratcliffe et al. 1998). However, at another large colony, St. Kilda, Outer Hebrides, Great Skuas take few sandeels but a high proportion of bird prey and show levels of reproductive success comparable with Foula (Phillips, Catry et al. 1997). A further behavior has been recorded at Hermaness, Unst, where some skua pairs specialize as seabird predators (Andersson 1976; T. Boulinier, unpubl. data). There is currently no information on the breeding biology of Great Skuas that specialize as bird predators.

In this study we investigate the relationship between reproductive success and diet choice by Great Skuas in a single Shetland colony, with particular reference to specialist seabird predators. Despite evidence that not all larids selecting predominantly bird prey show improved reproductive performance and that some Great Skuas select seabird prey only when sandeels are scarce, we predicted that specialist bird predators would exhibit reproductive benefits compared to skuas selecting other prey. We made this prediction because (1) bird prey has a higher caloric content than fish, which may enable early reproduction and the production of larger eggs and heavier chicks; (2) skuas nesting adjacent to seabird colonies may spend less time foraging and increase nest attendance, and (3) specialist

seabird predators have persisted in the Great Skua population for a number of years.

METHODS

STUDY SITE

Great Skuas were studied at Hermaness National Nature Reserve (60°50'N, 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 (C. Rodger, unpubl. data), and the numbers in 1998 and 1999 were similar. These birds breed adjacent to a large mixed colony of 28 000 Northern Fulmars (*Fulmarus glacialis*), 32 000 Northern Gannets (*Morus bassanus*), 50 000 Atlantic Puffins (*Fratercula arctica*), 15 000 Common Murres (*Uria aalge*), 1500 Razorbills (*Alca torda*), and 1600 Black-legged Kittiwakes (*Rissa tridactyla*).

IDENTIFYING SPECIALISTS

Diet of adult skuas can be assessed from the contents of regurgitated pellets of indigestible material (Votier et al. 2001). First, all pellets were cleared from breeding territories at the start of the study. Sampling from 91 marked breeding territories in 1998 and these same territories, plus a further 18, in 1999, began shortly after egg laying and continued every 4–7 days until skua chicks fledged. 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 Votier et al. (2003), and removed to prevent recounting. Diet composition was estimated based on the percentage of identified prey remains. We placed pairs into one of three categories: specialist bird predators (70% or more seabird prey), specialist fish predators (70% or more fish prey) or generalists (seabirds, fish, mammals or invertebrates in any combination, none comprising 70% or more of the diet). We treated pairs as a single unit since both members of Great Skua pairs tend to show the same food preference, with males performing the majority of foraging during the nesting period (Catry and Furness 1999, Caldow and Furness 2000).

As an independent line of evidence of dietary preference, we recorded the presence or absence of a feeding territory within a seabird colony. Typically Great Skuas attended grassy slopes with large numbers of Atlantic Puffin nesting

burrows or a section of cliff immediately above mixed colonies of Black-legged Kittiwakes, Common Murres, and Razorbills. These territories were defended from other conspecifics and larids either by chasing or other aggressive territorial displays such as wing raising and “long calling” (Furness 1987). A sample of 32 breeding skuas were caught on the nest during incubation using dummy eggs and a radio-controlled trap (a standard method for this species) and were color banded with unique combinations to facilitate individual recognition. We observed whether feeding territories occurred within skua breeding territories.

FORAGING BEHAVIOR

Time budgets. During the chick-rearing period, 27 and 31 breeding pairs were studied during 1998 and 1999 respectively, 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 04:00 and 05:00 GMT, which usually preceded the first foraging trip of the day, and were continuous until at least one complete trip was observed for each pair monitored. Watches were conducted on four dates per year, with up to 11 pairs watched simultaneously by a single observer in 1998 and by two observers in 1999. Territorial attendance was recorded every 10 min, and durations of foraging trips were estimated by calculating the time between departure from territory and returning to feed a chick or the mate. Only one member of the pair was observed foraging at any one time.

Radio-telemetry. During 1999, seven breeding Great Skuas were fitted with 10-g Biotrack (Wareham, UK) TW-3 single-cell radio-transmitters mounted on the central pair of tail feathers using cable ties (under licence from Scottish Natural Heritage). To test for effects of radio-transmitters on the foraging performance of skuas, the mean foraging-trip duration of five birds fitted with transmitters was compared with 28 controls (breeders without transmitters) studied simultaneously. The other two birds yielded insufficient data for analysis.

Signals were tracked at Hermaness from the highest two points above sea level (150 and 200 m respectively) from which the study birds' nests were in line of sight. Three-element Yagi antennae were used to obtain compass bearings

at 10–15 min intervals throughout the day, and pairs of bearings were converted to six-figure grid references.

We made test bearings for fixed-position transmitters placed at 3 and 5 km from the two receiving stations, and 95% of all test bearings were found to fall within a 1.2-km² area centered on the transmitter location. Home ranges were estimated using the minimum convex polygon technique (Redpath 1995).

BREEDING PARAMETERS

Breeding attempts of Great Skuas were monitored from late May (egg laying and incubation) to fledging in late August. Great Skuas at Foula, Shetland, show high site fidelity (Catry, Phillips et al. 1998). At Hermaness, resightings of individuals with distinctive plumage features as well as color-banded birds at the same territory suggest similarly high fidelity. Nests were located and marked during the onset of egg laying and visited every 4–7 days throughout the breeding attempt. Upon clutch completion, the length and breadth of eggs were measured to 0.1 mm using Vernier calipers. Internal egg volume (cm³) was calculated as 0.00048 (shape constant K_v for Black-legged Kittiwake eggs) \times length \times breadth² (Coulson 1963). Although K_v has not been calculated directly for Great Skuas, Hoyt (1979) found variations in this constant to be almost as great within a species as among species; therefore we considered this value to be appropriate. Where hatching date was not observed directly, it was calculated from the chicks' maximum flattened wing chord (measured to the nearest 1 mm) by reference to the logistic growth curve described by Phillips, Thompson, and Hamer (1997). Repeatabilities of hatch date and clutch volume were calculated for pairs that were known to breed together in both 1998 and 1999.

After hatching, chicks were fitted with a single monel British Trust for Ornithology band as soon as foot size was adequate to prevent band loss. 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. Territories were checked until chicks either fledged, died, or were depredated.

ADULT RETURN RATE

The presence of color-banded birds was checked carefully throughout the breeding season in

1998, 1999, and 2000. None of the birds marked in 1998 and resighted in 2000 were missing in 1999, and so resighting likelihoods were treated as one. No color-banded adult Great Skuas have moved to breed at other studied colonies (Klomp and Furness 1992, Catry, Phillips et al. 1998). Permanent emigration is apparently negligible, and so these return rates probably represent true survival rates.

STATISTICAL ANALYSIS

To test whether bird pellets were found randomly among skua territories, we compared the observed frequencies with a Poisson distribution using a *G*-test. The relationship between diet and reproductive output was investigated using generalized linear models (Crawley 1996) with binomial error distribution and logit-link function, in which clutch size, hatching success, and fledging success were response variables with diet and year as factors. Because not all of the nests were found on the day of clutch initiation, productivity may have been biased owing to clutches being lost prior to discovery (Mayfield 1975). By modeling daily nest survival expressed as a proportion of exposure days, variance attributable to observation period was removed. Where there was evidence of overdispersion, scaled deviance was altered and effect of parameters tested using analysis of deviance (Crawley 1996). Logit-linear models with binomial errors were used to investigate 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 was tested by comparing changes in deviance values using likelihood-ratio tests.

The effects of year and diet on hatching date and clutch volume were modeled using two-way ANOVA. Repeatability, the intraclass correlation coefficient of clutch volume and hatch date, was calculated following Lessells and Boag (1987). An index of chick body condition was calculated by taking the residuals from the regression of chick age against weight, during the linear phase of growth. Only one measurement was used per chick. We compared these indices among years and dietary groups using two-way ANOVA.

To investigate the effect of day and diet on mean length of foraging trip a general linear model (Norusis 1998) was run with foraging-trip length as the dependent variable with individual,

TABLE 1. Diet composition (%) of Great Skuas breeding at Hermaness, Unst, UK, based on analysis of regurgitated pellets. Values are percent of identified prey remains in each pellet.

Diet component	1998	1999	Total
<i>n</i>	1003	889	1892
Whitefish ^a	54	58	56
Bird ^b	45	35	41
Mammal ^c	<1	2	1
Herring/mackerel ^d	<1	2	1
Goose barnacle ^e	<1	1	<1

^a Cod (*Gadus morhua*), haddock (*Melanogrammus aeglefinus*), whiting (*Merlangius merlangus*), blue whiting (*Micromesistius poutassou*), Norway pout (*Trisopterus esmarkii*), redfish (*Sebastes marinus*), and long rough dab (*Hippoglossoides platessoides*).

^b Northern Fulmar (*Fulmarus glacialis*), European Shag (*Phalacrocorax aristotelis*), Great Skua chick, Black-legged Kittiwake (*Rissa tridactyla*), Common Murre (*Uria aalge*), Atlantic Puffin (*Fratercula arctica*), unidentified gull/tern, unidentified passerine, and unidentified bird.

^c Rabbit (*Oryctolagus cuniculus*) and sheep (*Ovis aries*).

^d *Clupea harengus* and *Scomber scombrus*.

^e *Lepas* sp.

diet, and day as factors. Data were log transformed to produce equal variances and normal error distribution. Independent sample *t*-tests were two-tailed. Alpha level of significance for all tests was 0.05. Means are reported \pm SE.

RESULTS

FORAGING BEHAVIOR AND DIETS

We collected 1003 pellets in 1998 and 889 in 1999. Overall, the diet comprised mostly whitefish (56%; particularly gadoids and flatfish) or bird (41%), with small proportions of mammal, herring (*Clupea harengus*), mackerel (*Scomber scombrus*), and goose barnacle (*Lepas* sp.; Table 1). From each study pair we obtained 5–55 pellets in 1998 (mean = 17.8 ± 1.6 , $n = 55$ breeding pairs) and 5–65 pellets in 1999 (mean = 12.5 ± 1.2 , $n = 72$ breeding pairs).

The observed distribution of bird pellets across Great Skua territories was significantly different from an expected Poisson distribution in 1998 ($G_{adj,10} = 117.5$, $P < 0.01$) and 1999 ($G_{adj,10} = 367.9$, $P < 0.01$). Using a minimum of seven separate daily records from each pair, we assigned each pair to a dietary category. In 1998, 10 pairs (20%) were classified as specialist bird predators, 34 pairs (68%) as specialist

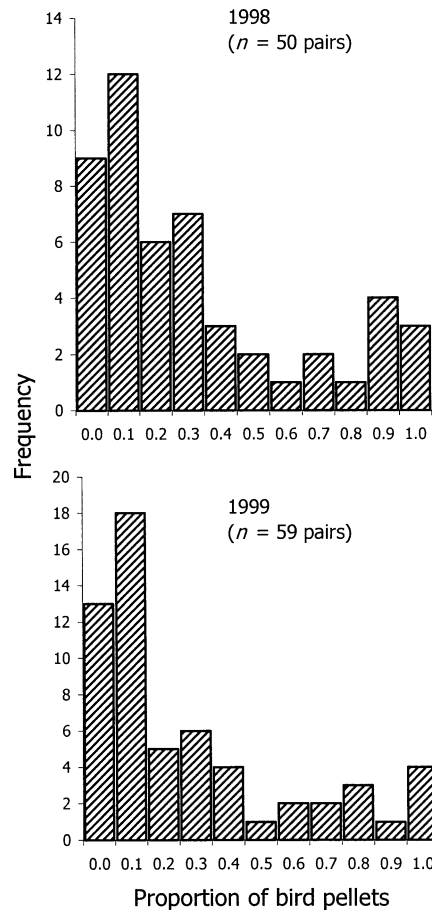


FIGURE 1. Dietary specialization in Great Skua pairs breeding at Hermaness, Unst, UK, as identified by pellet analysis. Pairs with more than 70% bird remains in pellets were considered specialist bird predators.

fish predators, and 6 pairs (12%) as generalists (Fig. 1). In 1999 there were 10 pairs (17%) of specialist bird predators, 42 pairs (71%) of specialist fish predators, and 7 pairs (12%) of generalists (Fig. 1). The proportion of each dietary class was consistent among years ($G_{adj,2} = 0.4$, $P = 0.83$). Because of the small number of generalists we did not consider these further in our analysis. Pellets were collected between the first week of June (incubation) and the last week of July (chick growth and fledging). To investigate for possible diet switching, data were grouped on a nest-by-nest basis according to reproductive stage of each pair. The proportions of the three main diet items were similar over each of the reproductive stages for specialist bird predators

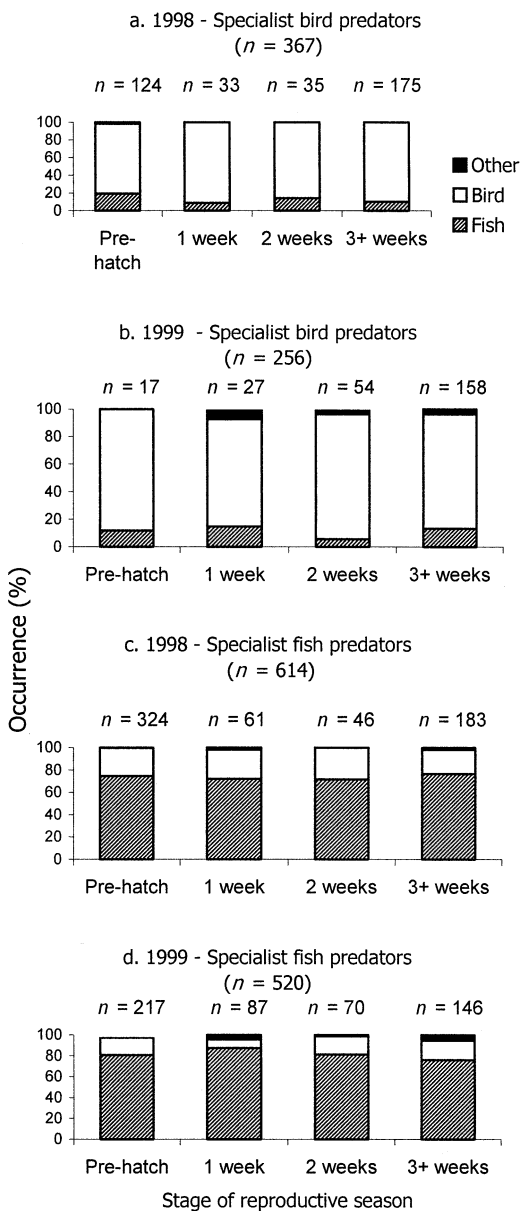


FIGURE 2. Diet composition of Great Skuas, determined from pellet analysis, for two dietary groups (specialist bird predators and specialist fish predators) during 1998 and 1999. Data are grouped according to the reproductive stage of each pair. "Other" includes remains of mammals and goose barnacles.

in 1998 ($G_{adj,6} = 8.1$, $P = 0.45$) and 1999 ($G_{adj,6} = 3.4$, $P = 0.75$; Fig. 2). Skuas feeding primarily on fish demonstrated a similar pattern with no seasonal change in pellet proportions in 1998 ($G_{adj,6} = 3.3$, $P = 0.76$) but there was a signifi-

cant difference in 1999 ($G_{adj,6} = 16.2$, $P < 0.025$; Fig. 2). Despite the temporal variation in diet composition in 1999, we found no evidence of systematic prey switching at the onset of hatching as exhibited in some other large generalist seabirds (Annett and Pierotti 1989). Therefore we are confident that seasonal patterns of diet switching did not alter our assignment of pairs into dietary groups.

Five Great Skua pairs defended feeding territories within a section of seabird colony during 1998, with the same five and an additional pair in 1999. None of the other skua pairs were observed holding feeding territories. Feeding territories contained a similar section of sea cliff in each year and males performed the bulk of the defense, females spending the majority of their time attending the nest. However, on several occasions females were observed expelling conspecifics while the male killed adult seabird prey.

Resighting of color-banded birds at the same territories across years showed that individuals retained the same breeding localities. Comparison of dietary data within mapped territories among years revealed that for all territories observed in both years, the feeding preferences were retained from 1998 to 1999.

ADULT FORAGING BEHAVIOR

Foraging effort. Comparing the mean foraging-trip duration between specialist bird predators and specialist fish predators for years 1998 and 1999 revealed significant differences (two-way ANOVA; year effect, $F_{1,63} = 100.4$, $P < 0.001$; diet effect, $F_{1,63} = 16.5$, $P < 0.001$) with no interaction ($F_{1,62} = 1.3$, $P = 0.26$). All skuas spent less time foraging in 1998 compared with 1999, and although specialist bird predators spent three times longer foraging in 1999 than in 1998 (185 ± 39 min, $n = 7$, vs. 67 ± 20 min, $n = 3$, respectively), they still spent less time foraging than skuas feeding on fish (297 ± 15 min, $n = 25$, vs. 124 ± 9 min, $n = 31$, respectively).

Radio-telemetry. Skuas fitted with radio-transmitters had similar foraging-trip lengths compared with control birds ($t_{31} = 0.4$, $P = 0.97$), suggesting that skuas with radio-transmitters were behaving normally. Three specialist bird predators with feeding territories had smaller minimum-convex-polygon home ranges (mean = 1.0 ± 0.4 km²) compared with a bird predator

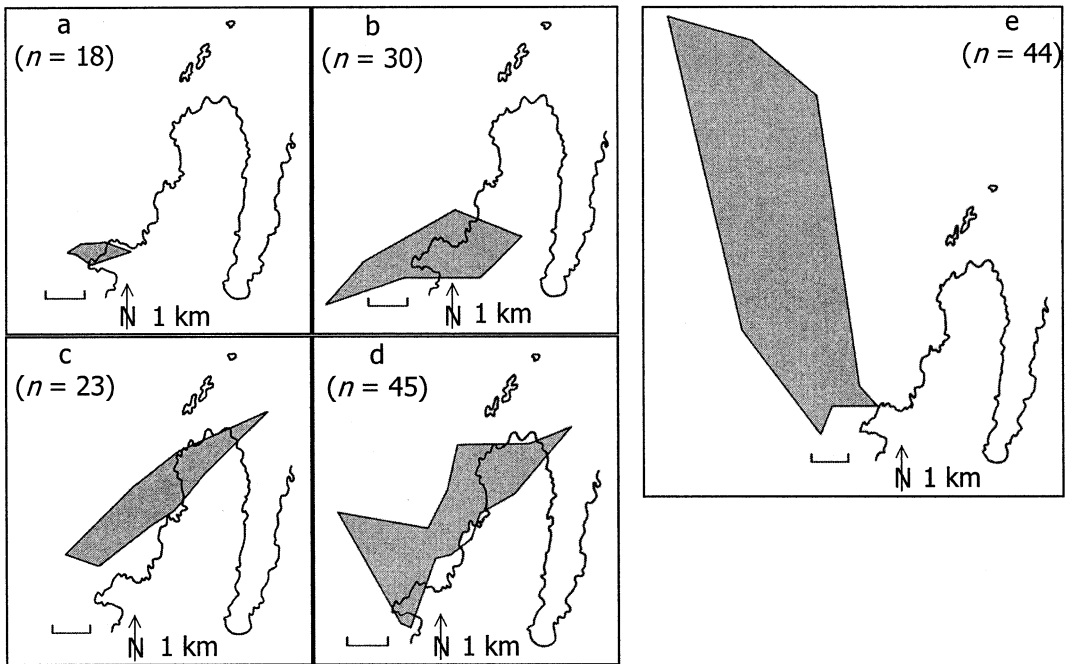


FIGURE 3. Home ranges of five breeding Great Skuas based on radio-telemetry over 5 days in 1999. Each shaded polygon represents foraging range for an individual bird. (a)–(c): territory-holding specialist bird predators; (d): a specialist bird predator without a feeding territory; (e): a specialist fish predator. Sample sizes are number of radio-telemetry locations.

that did not defend a feeding territory (mean = 4.7 ± 2.0 km²; Fig. 3). However, one skua feeding exclusively on fish had a much larger home range (mean = 17.4 ± 4.9 km²).

BREEDING PARAMETERS

Hatching date. There was a statistically significant difference between hatching dates of specialist bird predators and specialist fish predators in both 1998 and 1999, but with no difference between years and no interaction (Fig. 4; two-way ANOVA, diet effect, $F_{1,74} = 38.4$, $P < 0.001$; year effect, $F_{1,74} = 0.4$, $P = 0.85$; interaction, $F_{1,73} = 0.9$, $P = 0.36$). Specialist bird predators hatched chicks earlier in both 1998 and 1999 (Fig. 4). Hatching date was repeatable between 1998 and 1999 ($r = 0.72$, $F_{13,14} = 6.2$, $P = 0.001$).

Clutch size. Specialist bird predators had similar frequencies of one-egg clutches as specialist fish predators (1998: 13%, $n = 8$, vs. 14%, $n = 34$, respectively; 1999: 0%, $n = 9$, vs. 17%, $n = 42$; likelihood-ratio tests; $\chi^2_1 = 0.7$, $P = 0.37$). There was no significant effect of year on clutch size ($\chi^2_1 = 0.0$, $P = 0.98$) and no signif-

icant interaction between year and diet ($\chi^2_1 = 0.4$, $P = 0.50$).

Clutch volume. Total clutch volumes were significantly larger in specialist bird predators than fish predators (Fig. 5; two-way ANOVA, diet effect, $F_{1,70} = 5.3$, $P = 0.03$). There was no significant year effect ($F_{1,70} = 3.3$, $P = 0.07$) or interaction ($F_{1,69} = 0.4$, $P = 0.54$), although eggs tended to be larger in 1998. Diet and year affected egg volumes differently depending upon laying sequence. A-eggs (first-laid) were larger in specialist bird predators, but did not differ between years (Fig. 5; diet effect, $F_{1,70} = 6.4$, $P = 0.01$; year effect, $F_{1,70} = 2.6$, $P = 0.10$; interaction, $F_{1,70} = 1.8$, $P = 0.19$). B-eggs (second-laid) were also larger for specialist bird predators than fish specialists, but were larger in 1998 than 1999 (Fig. 5; year effect, $F_{1,70} = 6.6$, $P = 0.01$; diet effect, $F_{1,70} = 4.2$, $P = 0.05$; interaction, $F_{1,69} = 0.3$, $P = 0.64$). Total clutch volume for individual birds showed low repeatability between 1998 and 1999 ($r = 0.33$, $F_{10,11} = 1.9$, $P = 0.35$).

Productivity. Analysis of hatching success, corrected for the number of exposure days, re-

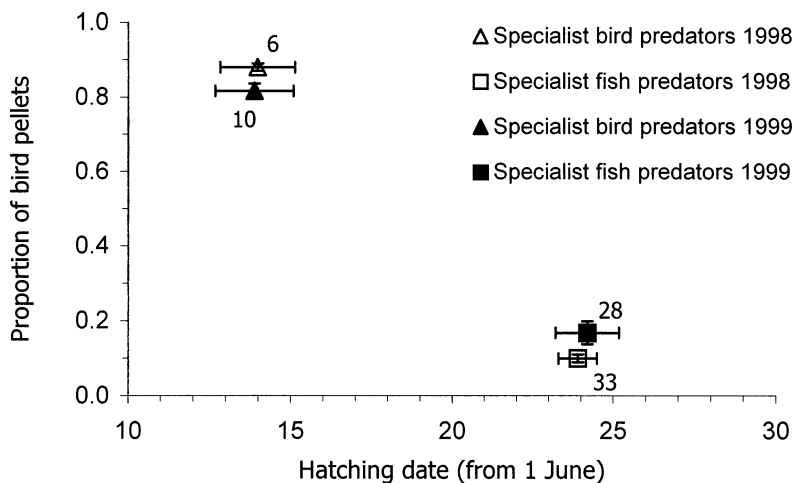


FIGURE 4. Mean \pm SE hatching date and proportion of bird pellets in the diet of Great Skua pairs classified as specialist bird predators and specialist fish predators. Numbers adjacent to each plot represent the number of pairs in each dietary group.

vealed no significant differences between specialist bird predators and specialist fish predators (Table 2; likelihood-ratio tests; $\chi^2_1 = 0.9$, $P = 0.31$) or between 1998 and 1999 ($\chi^2_1 = 3.7$, $P = 0.06$), with no interaction ($\chi^2_1 = 0.9$, $P = 0.38$). Fledging success, corrected for exposure days, was similar for specialist bird predators and specialist fish predators ($\chi^2_1 = 0.1$, $P = 0.75$), with no difference between years ($\chi^2_1 = 2.6$, $P = 0.10$) and no interaction ($\chi^2_1 = 0.1$, $P = 0.75$; Table 2). Of the banded chicks lost, 50% ($n = 10$) and 60% ($n = 5$) were found picked clean in other skua territories, in 1998 and 1999 respectively. This reveals that predation was almost invariably by conspecifics.

Chick condition. The condition of chicks reared by specialist bird predators was significantly higher than condition of chicks reared by skuas feeding predominantly upon fish (Fig. 6; two-way ANOVA, diet effect, $F_{1,70} = 4.1$, $P = 0.05$); there was also an effect of year ($F_{1,70} = 4.4$, $P = 0.04$) and no interaction between year and diet ($F_{1,69} = 2.1$, $P = 0.15$).

ADULT RETURN RATE

The number of color-marked adults returning to breed in consecutive years was similar for specialist bird predators and specialist fish predators (Table 3; likelihood-ratio tests; $\chi^2_1 = 2.5$, $P = 0.13$). Return rates were similar in 1999 compared with 2000 ($\chi^2_1 = 2.0$, $P = 0.18$), and there

was no interaction with diet ($\chi^2_1 = 0.1$, $P = 0.75$).

DISCUSSION

DIET AND FORAGING BEHAVIOR

Elsewhere in Shetland, sandeels form an important component of Great Skua diets (Phillips, Catry et al. 1997), but were absent from the diet samples in this and other recent studies at Hermaness (RWF, unpubl. data). Specialist fish predators fed on demersal species, which they are unable to catch for themselves but are discarded in large quantities by commercial fisheries (Furness and Hislop 1981). It would be useful in future studies to compare the performance of Great Skuas feeding on lipid-rich sandeels and those feeding on birds or other fish. During years of low sandeel abundance, there is evidence of poor breeding performance in Great Skuas (Hamer et al. 1991).

Typically, skuas and large gulls that specialize in feeding on birds defend a feeding territory within a seabird colony (Trivelpiece et al. 1980, Pietz 1987, Watanuki 1992, Spear 1993), whereas we observed feeding territories in fewer than half of the specialist bird predators at Hermaness. However, because many seabirds nest at the foot of inaccessible sea cliffs, we may have overlooked skuas foraging in these areas. Observations of known individuals revealed that pairs retained similar feeding strategies and the

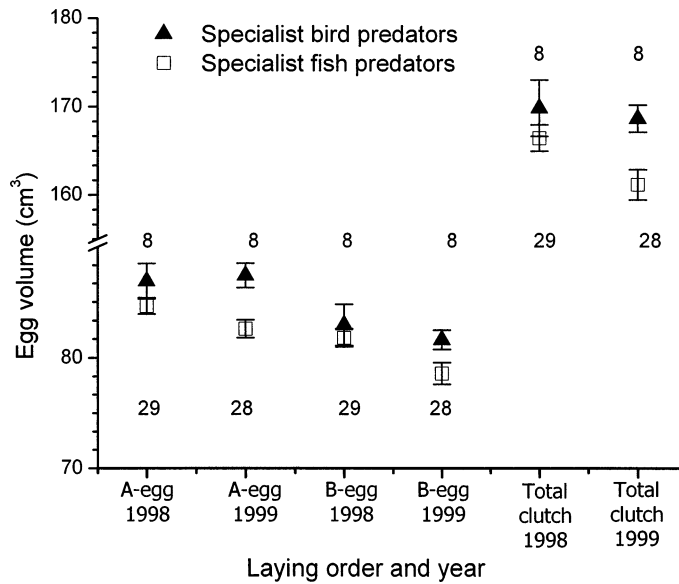


FIGURE 5. Mean \pm SE egg volumes in relation to laying order and for total clutches of Great Skua pairs specializing as bird predators or as fish predators. Numbers adjacent to each plot represent sample sizes. A-eggs are first-laid; B-eggs are second-laid.

same feeding territories from year to year. Similarly, Young (1972) found that the territories of South Polar Skuas (*Stercorarius maccormicki*) within penguin colonies remained constant over years, even after the experimental removal of skua pairs.

The proportion of specialist bird predators within our sample of Great Skua pairs at Hermaness (20% in 1998 and 16% in 1999) was greater than at the colony as a whole. Bird predators are scarce and so we included as many as we could find in the whole colony in our study sample. In 2000, we randomly sampled 100 Great Skua territories on a single date in the middle of the breeding season, which revealed only four territories with a higher proportion of

bird than fish pellets, and only two of these territories containing 70% or more bird in the diet (Votier 2001). From this we estimated that 2–5% of the Great Skuas breeding at Hermaness were specialist bird predators. In a colony of Western Gulls (*Larus occidentalis*) in California, Spear (1993) found only 1% (269) of the 25 000 breeding birds depredating predominantly other bird species, although this number covaried with the number of potential seabird prey.

By accessing seabird colonies, specialist bird predators are able to spend less time foraging than skuas feeding predominantly on fish. Shorter foraging bouts result in high nest-attendance rates, reflecting efficient foragers or good foraging conditions (Catry and Furness 1999, Cal-

TABLE 2. Breeding success (mean and 95% CI) of Great Skuas classified as specialist bird predators or specialist fish predators in 1998 and 1999. Success was calculated as the percentage of nests that hatched eggs or fledged young.

Year	Variable	Major diet component					
		Birds			Fish		
		n	Mean	95% CI	n	Mean	95% CI
1998	Hatching success (%)	6	100	100–100	28	92	87–96
	Fledging success (%)	6	68	49–82	28	72	63–79
1999	Hatching success (%)	10	100	100–100	33	99	91–100
	Fledging success (%)	10	85	73–92	33	87	78–92

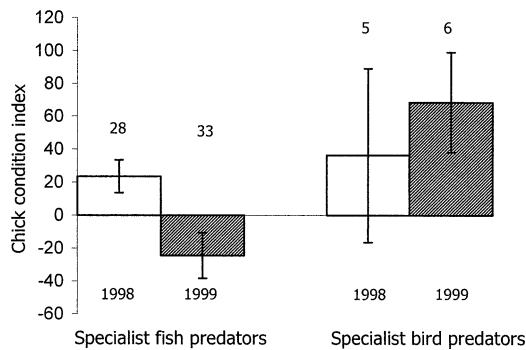


FIGURE 6. Mean \pm SE body condition indices for Great Skua chicks classified as specialist bird predators and specialist fish predators in 1998 and 1999. The index was calculated as the residuals from a regression of chick age against body weight of first-hatched chicks during the linear growth phase.

dow and Furness 2000). Despite this, all skuas, regardless of dietary preference, spent very much more time foraging in 1999 compared with 1998. Increased foraging effort may reflect poor food availability or poor environmental conditions (Hamer et al. 1993, Uttley et al. 1994, Davoren 2000). The weather was generally poor during the summer of 1999, characterized by high rainfall and persistent, coastal fog, which may have contributed to increased foraging costs for Great Skuas, as well as the seabirds that skuas preyed upon. Evidence of a reduction in productivity by Northern Fulmars, an important prey species for Great Skuas, between 1998 and 1999 (0.56 compared with 0.43 chicks fledged per nest; R. King, unpubl. data) supports the hypothesis that environmental factors were poor in 1999. Therefore environmental conditions likely affected the behavior of skuas specializing on bird prey directly by influencing foraging conditions, and indirectly by reducing prey items (i.e., seabird chicks).

FITNESS COMPONENTS OF SPECIALIST BIRD PREDATION

Great Skuas selecting bird prey showed improvements in some reproductive parameters compared to those feeding largely on fish, by

breeding earlier, laying larger first eggs, and producing heavier chicks. However, despite spending less time foraging and therefore spending more time on territory, specialist bird predators showed slightly lower fledging rates. We predicted that specialist bird predators would show improved reproductive performance because of higher caloric content of bird prey (10.9 kJ g^{-1}) compared with fish prey (5.2 kJ g^{-1} ; Phillips et al. 1999), and reduced foraging costs of exploiting a nearby food resource.

Early hatching in birds is associated with phenotypic quality or improved foraging conditions (Spaans 1971, Coulson and Porter 1985, Spear and Nur 1994, Ratcliffe et al. 1998, Gill et al. 2002). Hatching date in Great Skuas at Hermaness was highly repeatable among years, despite annual variations in environmental conditions (as evidenced by increased foraging effort). Catry, Ratcliffe, and Furness (1998) revealed that early laying is a good indicator of individual quality in Great Skuas; therefore by laying on average 10–11 days earlier than skuas feeding on fish, specialist bird predators may be considered high-quality individuals.

A number of studies have shown a relationship between good food supply and increased

TABLE 3. Survival estimates of adult Great Skuas between study years and groups. Because of binomial variance bounded around 0 and 1, confidence intervals are asymmetrical.

	1998 to 1999			1999 to 2000		
	n	Estimate	95% CI	n	Estimate	95% CI
Specialist bird predators	9	0.89	0.73–0.96	15	1.00	1.00–1.00
Specialist fish predators	7	0.86	0.67–0.95	15	0.80	0.68–0.88

clutch volume (Bolton et al. 1992, Ratcliffe et al. 1998). The volume of total clutches was larger for skuas feeding on birds compared with those feeding on fish, and total clutch volumes were also larger in 1998 compared with 1999. This supports the view that egg size is sensitive to nutritional content of prey or annual fluctuations in prey availability (Gill et al. 2002). Larger eggs result in the production of larger and heavier chicks, which may have an advantage in terms of survival, particularly during the early stages of growth (Furness 1983).

Breeding success (hatching success and fledging success) is directly related to fitness and is also very sensitive to feeding conditions in seabirds (Gill et al. 2002). Despite predictions that feeding upon energy-rich bird prey will lead to fitness benefits, chicks of skuas feeding on birds did not have higher survival to fledging than chicks fed predominantly fish. The relationship with prey energy content may be confounded by nutritional composition of prey, however. Herring Gulls specializing in feeding on mussels (*Mytilus* sp.) gain reproductive benefits over conspecifics, not because of shorter foraging times or improved energy content but because mussels contain nutrients essential for avian development (Pierotti and Annett 1991). Further, a diet consisting of bird meat resulted in poor skeletal development in Western Gull chicks (Pierotti and Annett 2001), suggesting that bird prey may be a poor option for chicks. However, a number of skua chicks in this study were lost through predation, not growth deficiencies, and there is evidence from other studies that skuas feeding upon seabird prey show high breeding success compared with those feeding on fish (Trivelpiece et al. 1980, Trillmich 1978). Therefore we are unable to easily explain these results, which highlights the need for further study into the relationship between breeding success and diet choice in this species.

Although chicks reared by bird predators showed improved body condition compared with those raised by fish predators, this apparently has little consequence for fitness in this study since they exhibited similar or lower rates of survival at least to fledging.

CONSERVATION IMPLICATIONS

Although the Great Skua population is healthy and increasing around the United Kingdom, this species is globally scarce (Lloyd et al. 1991).

Concerns about the impact of Great Skuas on the population of other seabirds also need to be considered. The bulk of the fish eaten by Great Skuas at Hermaness consists of demersal species most likely to be scavenged from commercial fishing boats (e.g., Furness and Hislop 1981, Hammer et al. 1991). Current European Union proposals to reduce the amount of fish discarded in European waters are likely to reduce feeding opportunities for skuas that rely on this food resource. Therefore, seabird prey may become increasingly important in the diet of Great Skuas as the availability of discards diminishes (Votier et al. 2004). During periods of reduced oceanic food supply in California, seabird predation increased as the feeding territories of specialist Western Gulls were swamped (Spear 1993).

The specialist foraging preference could be passed to offspring through learning (Feldman and Laland 1996), as has been demonstrated in diet choice by gulls (Annett and Pierotti 1999). Alternatively other factors like the numbers of potential seabird prey, density-dependent competition (particularly inability of subordinate or low-quality skuas to defend kills against other skuas) or linearity of seabird cliffs may limit the numbers of specialist bird predators.

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