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# Predation by great skuas at a large Shetland seabird colony

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## Summary

1. Skuas are top predators in marine ecosystems and may have detrimental effects on seabird communities they prey upon. However, predation rates are poorly understood and poorly quantified. Using a bio-energetics model we estimate seabird predation by great skuas, *Stercorarius skua*, at a large UK colony (Hermaness, Shetland). We investigate the influence of dietary specialization and fishery management on predation and explore the effect of experimental removal of specialist bird predators.

2. Great skuas at Hermaness required  $491.5 \times 10^6$  kJ and  $546.6 \times 10^6$  kJ of energy in each of two breeding seasons. Breeding skuas fell into one of two groups: a small proportion (5%) of specialist bird predators or the vast majority (95%) that fed opportunistically on birds or specialized on fishery discards. During 1999, great skuas consumed  $\approx 80\,000$  kg of fish, which increased to over 90 000 kg in 2001. About 13 000 seabirds were consumed by great skuas each year, with 26–29% being consumed by specialist bird predators.

3. Although it is difficult to assess, great skuas appear to be having a negative impact on seabird populations. Altering model inputs to test differing scenarios revealed that reductions in fishery discards would result in increased seabird predation rates. However, proposed changes in fishery management over the period of the study did not reduce discarding rates, which instead increased.

4. *Synthesis and applications.* The use of a bioenergetics model reveals that great skua predation may negatively affect seabird populations. Availability of fishery discards is an important factor influencing seabird predation rates, but predicting the effect of changes in fishery management may be difficult in the short term. Specialist bird predators consume large quantities of seabird prey, but this is less significant at the population level. Although experimental removal of specialist bird predators may reduce predation at a minimal loss of skuas, it is unclear whether conspecifics may replace them and retain high rates of predation.

*Key-words:* bioenergetics, discards, seabird conservation, *Stercorarius skua*.

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## Introduction

Predatory birds may act on prey populations in complex ways, depending upon the predators' foraging behaviour. In cases where predators are specialized, prey density may drive predator density (Nielsen 1999). The ability of generalist predators to sustain themselves on alternative food may result in predators driving prey

population density (Korpimäki 1994; Redpath & Thirgood 1999).

Predatory gulls *Larus* and skuas *Stercorarius* are dietary generalists, able to exploit a wide range of prey and food made available by human activities. In marine ecosystems their diets consist predominantly of small shoaling fish, larger fish stolen by kleptoparasitism or scavenged at fishing vessels, invertebrates, or bird eggs, chicks and adults (Phillips, Thompson & Hamer 1999; Oro 2003). Among the generalist population, some birds show individual specializations, including feeding almost exclusively on other birds (Spear 1993; Votier *et al.* 2004a).

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During periods of declining marine food availability, skuas and large gulls switch to feeding upon other birds (Oro 2003; Votier *et al.* 2004b). A combination of these factors, along with historically large populations, is increasing concern that large gulls and skuas may be adversely affecting seabird populations around the world, through competition for breeding sites (Quintana & Yorio 1998) and predation pressure (Phillips *et al.* 1999; Votier *et al.* 2004b).

The great skua, *Stercorarius skua* (Brünnich), breeds only in the north Atlantic with approximately 60% of the world's population nesting in the UK (Mitchell *et al.* 2004). The population has grown dramatically in the past 100 years, probably as a consequence of reduced persecution and an increase in the abundance of food in the form of fishery discards (Mitchell *et al.* 2004). In addition to fishery discards, UK great skuas feed on sandeels, *Ammodytes marinus* (Raitt), invertebrates and extensively on other seabirds (Phillips *et al.* 1997a; Votier *et al.* 2003). At St Kilda, Outer Hebrides, great skuas ( $\approx$  230 pairs) were estimated to consume 40 800 seabirds in a breeding season (Phillips *et al.* 1999). In Shetland, great skuas appear to feed more extensively on sandeels, but a decline in sandeel availability has resulted in an increased reliance on discards and seabird prey (Hamer, Furness & Caldow 1991). In certain parts of Shetland, dramatic declines in populations of black-legged kittiwakes, *Rissa tridactyla* (Linnaeus), are in part a result of predation by great skuas (Heubeck, Mellor & Harvey 1997; Oro & Furness 2002). Certain pairs of skuas develop specialized foraging behaviour, feeding almost exclusively on birds (Votier *et al.* 2004a). Proposals to cut quotas for several whitefish species in the North Sea and the introduction of square mesh (escape) panels in the top of cod ends are likely to result in a reduction in the quantity of fish discarded in the North Sea (Reeves & Furness 2002). This shortfall in discard availability may be met by great skuas increasing the amount of seabird prey they consume (Votier *et al.* 2004b).

In this study we use a bio-energetics model described by Phillips *et al.* (1999) for great skuas at St Kilda, to estimate the amount of prey consumed by great skuas attending the third largest colony in the UK, at Hermaness, Shetland. Using this model, together with sensitivity analysis and scenario testing, we: (1) quantify the impact of seabird predation by great skuas at Hermaness; (2) compare great skua predation rates in a period before (1999) and after (2001) changes in fishing policy (a reduction in quotas and change in net structure), expected to reduce the availability of discards; (3) test the generality of the St Kilda model to a different UK great skua colony; (4) use recent advances in understanding pellet production by great skuas to test how their estimation may influence model outputs; (5) investigate the role of individual foraging specialists at the population level; and (6) test what effect hypothetical removal of specialist bird predators might have for seabird conservation.

## Methods

### STUDY SITE

This study was conducted at Hermaness National Nature Reserve, Unst, Shetland (60°50'N, 0°52'W) during the breeding seasons of 1999 and 2001. Hermaness holds the third largest concentration of great skuas in Britain, with an estimated 659 pairs in 1999 and 726 pairs in 2001 (this study).

Hermaness is a special protection area (SPA) for breeding seabirds with approximately; 28 000 northern fulmars, *Fulmarus glacialis* (Linnaeus), 32 000 northern gannets, *Morus bassanus* (Linnaeus), 100 European shags, *Phalacrocorax aristotelis* (Linnaeus), 1600 black-legged kittiwakes, 15 000 common guillemots, *Uria aalge* (Pontoppidan), 1500 razorbills, *Alca torda* (Linnaeus), 30–80 000 Atlantic puffins, *Fratercula arctica* (Linnaeus), and small numbers of European storm petrels, *Hydrobates pelagicus* (Linnaeus) (Mitchell *et al.* 2004; Pennington *et al.* 2004).

### BIOLOGICAL PARAMETERS OF ENERGY REQUIREMENT MODEL

We estimated the energetic requirements of breeding adults, non-breeding adults and chicks throughout the period of colony attendance using life-history parameters (Table 1). A food assimilation efficiency of 0.76, calculated from captive great skuas fed sandeels and whiting, *Merlangius merlangus* (Linnaeus) (Hilton, Furness & Houston 2000), was used throughout.

To estimate the number of great skuas breeding at Hermaness in 1999 we used a value of 631 apparently occupied territories (AOTs) (Lewis 1997), increased by 4.5% to 659 on the basis of a change in skua breeding numbers from study plots mapped in detail over both years. A complete census in 2001 (this study) estimated 726 AOTs. Non-breeding birds attend the colony at specific 'club-sites' (Klomp & Furness 1992), where we made counts throughout the breeding season. These counts comprised the mean of eight visits to the three largest clubs plus 30 birds counted at one small club visited only once. Reproductive parameters (mean clutch size, mean brood size at 20 days and mean brood size at fledging) were obtained from a sample of 109 pairs in 1999 and 98 pairs in 2001.

Previous studies have revealed differences in the foraging strategies of great skuas breeding at Hermaness (Votier *et al.* 2004a). Regurgitated pellets revealed that the proportion of bird prey in the diet of breeding pairs formed a bimodal distribution, the majority of birds produced no, or very few, bird remains with a small number producing almost exclusively bird pellets. Furthermore, many specialist bird predators defended a feeding territory within a seabird colony. Based on this distinction we categorized pairs with either >70% of bird pellets in the diet or defending a feeding territory within a seabird colony as specialist bird predators (see

**Table 1.** Parameters used in bio-energetics model

	1999	2001	Source
Breeding pairs	659	726	This study
Non-breeding birds	110	112	This study
Pre-breeding period	30 days	30 days	Phillips <i>et al.</i> 1999
Incubation period	29 days	29 days	Furness 1978
Chick-rearing period	46.4 days	46.4 days	This study
Post-fledging period	18 days	18 days	Phillips <i>et al.</i> 1999
Adult BMR	538 kJ day <sup>-1</sup>	538 kJ day <sup>-1</sup>	Bryant & Furness 1995
Adult FMR:BMR ratio			
Fish specialists	3.6	3.7	This study (see Table 2)
Bird specialists	2.1	2.2	This study (see Table 2)
Mean clutch size	1.83	1.80	This study
Mean brood size at 20 days	1.2	1.12	This study
Mean breeding success	1.12	0.89	This study
Mean fresh egg mass	96 g	96 g	Furness 1978
Mean egg energy density	6.45 kJ g <sup>-1</sup>	6.45 kJ g <sup>-1</sup>	Meathrel & Ryder 1987; Meathrel, Ryder & Termaat 1987
Egg synthesis efficiency	0.75	0.75	Ricklefs 1974, 1983
Food assimilation efficiency	0.76	0.76	Hilton <i>et al.</i> 2000
Mean chick fledging mass	1170 g	1170 g	Phillips, Thompson & Hamer 1997b

**Table 2.** Daily field metabolic rate (FMR) of breeding adult great skuas calculated from time budget analysis of specific activities (Caldow 1988) during 1999 and 2001

Activity	FMR:BMR ratio	Percentage of time for bird-specialists		Percentage of time for fish-specialists	
		1999	2001	1999	2001
Resting/incubation	1.5	41.7	41.7	40.3	41.7
General	1.97	36.8	38.8	37.5	37.8
Gliding flight	3.1	20.8	17.6	5.5	2.6
Flapping flight	12.65	0.6	1.7	16.67	17.93
High speed flapping flight	26.7	0.1	0.2	0	0
Mean FMR:BMR ratio for daily maintenance and activity		2.1	2.2	3.6	3.7

Votier *et al.* 2004a for more details). The remainder of the population comprised a small number of birds feeding as generalists and many more feeding almost exclusively on fish. From hereon we combine these groups and refer to them as fish specialists.

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 calculated energy requirements of breeding adults in terms of field metabolic rate (FMR). Timed watches of a sample of breeding pairs (31 in 1999 and 19 in 2001) were conducted between 04:00 and 13:30 Greenwich Mean Time (GMT), which was assumed to be representative of the daily activity. Observations included both bird specialists (7 in 1999 and 4 in 2001) and fish specialists (24 in 1999 and 15 in 2001). We estimated the relative proportion of time spent performing four specific activities – resting, general (preening, walking, bathing, long-calling), gliding flight and flapping flight (Table 2). Specialist bird predators were observed foraging to estimate the proportion of time spent performing specific activities. To

estimate the proportion of time spent in flapping or gliding flight for great skuas foraging at sea, we assumed observations of birds attending a single inshore fishing vessel in 1999 were representative of behaviour at sea.

The estimated FMR:BMR ratios were lower for bird specialists than fish specialists, but consistent among years (Table 2). The values for fish specialists were similar to the 3.5 times BMR used by Phillips *et al.* (1999), which was the average estimated by Caldow (1988) for great skuas breeding on Foula, Shetland. Despite not incurring the costs of foraging for chicks, we make the assumption that non-breeders are probably less efficient foragers than breeders and therefore have similar energetic requirements (following Cairns *et al.* 1990; Phillips *et al.* 1999). Therefore activity costs for non-breeders were assumed to be similar to those for breeding birds, excluding the costs of clutch production and maintenance.

Energy required for clutch formation for each pair ( $E_{\text{clf}}$  in kJ) was derived from the equation:

$$E_{\text{clf}} = \text{Cls} \times M_{\text{egg}} \times \text{Cal}_{\text{egg}} \times (1/E_{\text{syn}}),$$

where Cls is mean clutch size,  $M_{\text{egg}}$  is mean fresh egg mass,  $\text{Cal}_{\text{egg}}$  is average energy density of larid eggs in kJ and  $E_{\text{syn}}$  is egg tissue synthesis efficiency (source references listed in Table 1).

There is increasing evidence that incubation is a costly part of any avian breeding attempt (Thomson, Furness & Monaghan 1998). No data exist for great skua metabolic rate during incubation, but using data from five species of seabird Tinbergen & Williams (2002) derived the equation  $\text{FMR}_{\text{INC}} = 3.48\text{BM}^{0.749}$ , where BM is adult seabird body mass. Since incubation duties are shared, we took the mean published body mass of male and female great skuas (Hamer 2001) as 1414 g, which provides an  $\text{FMR}_{\text{INC}}$  of  $796.65 \text{ kJ day}^{-1}$ , or  $1.48\text{BMR}$ . This value was so close to the value of  $1.5\text{BMR}$  for resting that the model retained this estimate.

Energy requirement of chicks from hatching to fledging was estimated from the equation  $\text{ME}_{\text{chicks}} = 35.15 \times M_{\text{C}}^{1.015}$ , where  $M_{\text{C}}$  is chick mass at hatching. 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).

A sensitivity analysis was performed on the energetics model, by increasing the values used to parameterize the model by 1% and also by introducing a range of likely extremes for all parameters. We also tested the effect of experimental removal of specialist bird predators on energetic requirements of the colony.

#### DIET COMPOSITION

The diet of breeding adults was estimated on the basis of pellets collected from marked skua territories (109 in 1999 and 98 in 2001) every 5–10 days from late May (incubation) to mid-August (fledging). Non-breeder club-sites were searched for pellets over the same time period. Pellets were identified to the lowest possible taxon using the categories in Votier *et al.* (2003) and were removed to prevent recounting. Pellets of bird prey were identified to species, based on feather colour and smell, or any hard parts (legs, skull or bill). It was difficult to identify the pellets of adult auks (Alcidae) to a species, therefore we assumed that Atlantic puffins and common guillemots (the only two species positively identified) occurred in similar proportions (but see Discussion). Otoliths in pellets of fish prey were identified using Härkönen (1986), and measured to the nearest mm.

The proportions of the three main prey types (whitefish, bird and 'other') in the diet of chicks were calculated 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 adult breeders.

Using transects to sample skua territories for pellets throughout Hermaness, we estimated that around 5% of the population were feeding primarily on birds. The 95% that fed mostly on fish, cast small numbers of

pellets containing bird remains. 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  $r_s = -0.47$ ,  $P < 0.001$ ,  $n = 71$ ), birds closer to a seabird colony having more bird in their diet. Therefore we estimated the whole colony diet based on two study areas, one adjacent to seabird colonies (making up 26% of the breeding population) and one in the centre of the colony and therefore away from seabird colonies (making up the remaining 69% of the population).

*Contra* Phillips *et al.* (1999) we did not assume one meal resulted in the production of one pellet. Pellet to meal ratios were obtained from Votier *et al.* (2001) and corrections applied accordingly. Pellets comprising passerines typically contained remains of a single bird so in this case we assumed one meal resulted in a single pellet.

#### PREY ENERGY CONTENT AND MEAL SIZE

From otoliths collected in pellets, 95% of the fish diet at Hermaness consisted of whitefish: haddock *Melanogrammus aeglefinus* (Linnaeus), whiting, blue whiting, *Micromesistius poutassou* (Risso), and Norway pout, *Trisopterus esmarkii* (Nilsson). Otolith sizes indicated that haddock, whiting and blue whiting were all large fish (often greater than 100 g) and while Norway pout were much smaller than this (mean of 23.6 g), pellets of this species contained several otoliths. We used the average meal size of 100 g proposed by Furness & Hislop (1981) and mean energy content of  $5.2 \text{ kJ g}^{-1}$  of fresh mass for gadoid fish (Hislop, Harris & Smith 1991).

There are various published values for the energetic composition of whole adult birds, but the value of  $10.9 \text{ kJ g}^{-1}$  used by Phillips *et al.* (1999) was used here. Because of the high proportion of indigestible material in birds we estimated that only around 65% of the fresh body mass was available as food.

Goose barnacle *Lepas* sp. energy content was calculated assuming 40 g meal size and  $1.9 \text{ kJ g}^{-1}$  calorific content (Phillips *et al.* 1999).

Rabbits *Oryctolagus cuniculus* (Linnaeus) have a mean calorific value of  $6.24 \text{ kJ g}^{-1}$  (derived from  $4.95 \text{ kCal/g}$  dry weight in Moors 1977) and we assumed a meal mass of 100 g. 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. A very small number of sheep, *Ovis aries* (Linnaeus), pellets were present in the diet of great skuas, and these were assumed to have a similar energetic value to rabbits.

Sotherland & Rahn (1987) estimated the calorie content of a typical avian egg as  $29 \text{ kJ g}^{-1}$  (dry weight). Eggs found in the diet of great skuas at Hermaness belonged mostly to kittiwakes and terns, therefore egg mass was assumed to be 50 g (Cramp & Simmons 1983), which corresponds to  $14.4 \text{ g}$  dry weight, and  $417.6 \text{ kJ}$  per egg.

**Table 3.** Energetic requirements of great skuas at Hermaness during 1999 and 2001

	1999			2001		
	Individual/pair		Whole colony	Individual/pair		Whole colony
	Daily	Whole season	Daily	Daily	Whole season	Daily
<b>Breeding adults</b>						
Maintenance and activity						
Fish specialist	2548 kJ bird <sup>-1</sup>	314.5 × 10 <sup>3</sup> kJ bird <sup>-1</sup>	3190.0 × 10 <sup>3</sup> kJ	2619 kJ bird <sup>-1</sup>	323.2 × 10 <sup>3</sup> kJ	3614.5 × 10 <sup>3</sup> kJ day <sup>-1</sup>
Bird specialist	1487 kJ bird <sup>-1</sup>	183.5 × 10 <sup>3</sup> kJ bird <sup>-1</sup>	98.1 × 10 <sup>3</sup> kJ	1557 kJ bird <sup>-1</sup>	189.7 × 10 <sup>3</sup> kJ	112.1 × 10 <sup>3</sup> kJ day <sup>-1</sup>
Cost of egg production	–	1988 kJ pair <sup>-1</sup>	–	–	1955 kJ pair <sup>-1</sup>	–
Fish specialist	–	1988 kJ pair <sup>-1</sup>	–	–	1955 kJ pair <sup>-1</sup>	–
Bird specialist	–	1988 kJ pair <sup>-1</sup>	–	–	1955 kJ pair <sup>-1</sup>	–
<b>Non-breeding adults</b>						
Maintenance and activity	2548 kJ bird <sup>-1</sup>	314.5 × 10 <sup>3</sup> kJ bird <sup>-1</sup>	280.2 × 10 <sup>3</sup> kJ	2619 kJ bird <sup>-1</sup>	323.2 × 10 <sup>3</sup> kJ	293.4 × 10 <sup>3</sup> kJ day <sup>-1</sup>
<b>Chicks</b>						
Hatching to fledging	–	45.7 × 10 <sup>3</sup> kJ	–	–	45.7 × 10 <sup>3</sup> kJ	–
Fish specialist	–	45.7 × 10 <sup>3</sup> kJ	–	–	45.7 × 10 <sup>3</sup> kJ	–
Bird specialist	–	45.7 × 10 <sup>3</sup> kJ	–	–	45.7 × 10 <sup>3</sup> kJ	–
Fledging to departure	1025 kJ fledgling <sup>-1</sup>	18.5 × 10 <sup>3</sup> kJ fledgling <sup>-1</sup>	718.6 × 10 <sup>6</sup> kJ	1025 kJ fledgling <sup>-1</sup>	18.5 × 10 <sup>3</sup> kJ fledgling <sup>-1</sup>	629.5 × 10 <sup>3</sup> kJ
Fish specialist	1025 kJ fledgling <sup>-1</sup>	18.5 × 10 <sup>3</sup> kJ fledgling <sup>-1</sup>	37.9 × 10 <sup>3</sup> kJ	1025 kJ fledgling <sup>-1</sup>	18.5 × 10 <sup>3</sup> kJ fledgling <sup>-1</sup>	32.8 × 10 <sup>3</sup> kJ
Bird specialist	–	–	–	–	–	–
<b>Total colony energy</b>			<b>491.5 × 10<sup>6</sup> kJ</b>			<b>546.6 × 10<sup>6</sup> kJ</b>

## PREY CONSUMPTION MODEL

### Mass of all prey consumed

The relative energetic contribution of different prey types was estimated from mass and calorific content of meals and the proportion of these meals in the diet of adult breeders, non-breeders and chicks. Knowing the energy requirements for adult maintenance and activity, egg production and chick development, we calculated the proportion of the energy requirements provided by each prey type. From prey calorific densities we back-calculated the weight of each prey type consumed.

### Numbers of birds consumed

Using known body weights of birds (Snow & Perrins 1998) and assuming 35% of each carcass is indigestible, we estimate numbers of seabirds consumed by great skuas. The weight of guillemot chicks was taken as the mean of three published fledging weights, and since adult auks could not be readily identified on the basis of pellets, we adopted an intermediate weight between Atlantic puffin and common guillemot to represent adult auks. As young great skuas are susceptible to cannibalism when they become mobile at around 25 days old, a mean weight at this age of 800 g was adopted. Pellets containing remains of passerines were often difficult to assign to species, however, virtually all those identified contained remains of common starlings, *Sturnus vulgaris* (Linnaeus), and therefore we used published weights of this species in the model.

## SENSITIVITY ANALYSIS FOR PREY CONSUMPTION MODEL AND SCENARIO TESTING

Performance of the prey consumption model was tested by increasing input values by 1% and by introducing 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 altered the model to investigate two scenarios: the effect of a reduction in fishery discards and experimental removal of specialist bird predators.

## Results

### BIOENERGETICS MODEL

The total energy requirement for the great skua colony at Hermaness, including breeding adults, non-breeding adults and chicks, was 491.5 × 10<sup>6</sup> kJ in 1999 and this value increased by 11.2% to 546.6 × 10<sup>6</sup> kJ during 2001 (Table 3).

**Table 4.** Sensitivity analysis for energetic requirements

Parameter	% change following 1% increase		Range of parameter extremes (%)	% change following parameter extremes	
	1999	2001		1999	2001
Breeding population	0.93	0.93	±10	±9.30	±9.34
Number of bird specialists	-0.36	-0.36	+25, removal	-0.45, -2.92	-0.45, -2.92
Non-breeding population	0.07	0.07	±50	±3.61	±3.39
Pre-breeding period	0.22	0.23	±50	±11.19	±11.27
Incubation period	0.22	0.23	±10	±2.16	±2.18
Chick rearing period	0.34	0.35	±10	±3.46	±3.49
Post-fledging period	0.13	0.14	±50	±6.72	±6.76
Adult BMR	0.85	0.86	±10	±8.48	±8.60
FMR: BMR fish specialist	0.82	0.81	±15	±12.35	±12.50
FMR: BMR bird specialist	0.03	0.03	±15	±0.38	±0.39
FMR: BMR non-breeders	0.07	0.07	±15	±1.08	±1.01
Clutch size	<0.01	<0.01	±10	±0.02	±0.02
Fresh egg mass	<0.01	<0.01	±10	±0.02	±0.02
Egg energy density	<0.01	<0.01	±10	±0.02	±0.02
Egg synthesis efficiency	<0.01	<0.01	±10	±0.02	±0.02
Food assimilation efficiency	-0.82	-0.83	±8	-7.16, +6.10	-6.17, +7.25
Brood size at 20 days	0.08	0.07	±10	±0.76	±0.70
Brood size at fledging	0.08	0.07	±10	±0.77	±0.71
Chick mass at fledging	0.07	0.07	±10	±0.77	±0.71
Energy for chick development	<0.01	<0.01	±10	±0.03	±0.02

Following changes in parameter estimates, sensitivity analysis for the energetic requirements showed very similar patterns between years (Table 4). The three parameters causing the greatest change are size of the breeding population, adult BMR and food assimilation efficiency. A 1% change in these parameters altered the output by almost 1%, revealing the need for accuracy in these estimates. Altering numbers of specialist bird predators had a minor influence on the bioenergetics model (Table 4).

#### PREY CONSUMPTION MODEL

##### *Mass of all prey consumed*

Using estimates of the total energy requirement of breeders, non-breeders and chicks (Table 3) along with the relative contribution of each prey type (Table 5) we calculated the amount of each prey required (Table 6), according to breeding status, dietary preference and year. The majority of prey consumed was fish, 80 000 kg in 1999, and despite predicted declines in discard rates this amount increased to over 90 000 kg in 2001 (87.7% and 89.5% of the total by mass, respectively). The second most abundant prey item was bird (7610 kg in 1999 and 7460 kg in 2001). It was estimated that 2900 kg mammal prey was consumed in 1999 and 3000 kg in 2001. The 650 kg of goose barnacles estimated to be consumed in 1999 contrasted markedly with 2001 when only 161 kg were consumed.

Adult breeders, excluding bird specialist pairs, consumed the bulk of the prey (90% in 1999 and 91% in 2001). Bird specialist breeders accounted for a small

proportion of the prey mass consumed (2.4% and 2.5% in 1999 and 2001, respectively), with non-breeders requiring relatively more food in each of the two years (7.2% and 6.7%, respectively).

Fish specialists consumed the vast majority of the fish (92.8% in 1999 and 92.4% in 2001). Fish specialists also accounted for the majority of the birds eaten in both years (69.8% and 72.1%, respectively). Although constituting only 5% of the population, bird specialists consumed 23.8% of the total mass of birds in 1999 and 22% in 2001, with non-breeders accounting for around 6% of the birds in both years. Fish specialists ate most of the mammals with little annual variation, and non-breeders consumed 12% in 1999 and 9.8% in 2001. Non-breeders fed extensively on goose barnacles, accounting for 37.7% consumed in 1999 and nearly 50% in 2001.

##### *Numbers of birds consumed*

During the 1999 and 2001 breeding seasons, we estimated great skuas consumed in excess of 12 500 and 13 000 birds, respectively (Table 7; Fig. 1). In both years the predominant prey was adult auks, although the estimate of 7837 consumed in 1999 decreased by 9% to 7125 in 2001. Northern fulmar was the next most commonly eaten seabird with approximately 3000 being eaten in both years. Almost 1000 auk chicks were eaten in 1999 and this estimate almost doubled in 2001. Passerine birds also increased between 1999 and 2001 from 205 to nearly 1000 birds, predominantly common starlings. The number of black-legged kittiwakes that were consumed declined from over 400 in 1999 to fewer than 300 in 2001. Three species consumed in 2001 (215

**Table 5.** Prey types in the diet of great skua at Hermanes during 1999 and 2001. Presented here are raw frequencies, frequencies following conversion for meal to pellet ratios (Votier *et al.* 2001) and the relative energetic contribution of each prey type (see Methods). The diet composition of adults and chicks are combined in this table

	1999									2001											
	Adult breeders and chicks combined									Adult breeders and chicks combined											
	Bird specialists			Fish specialists			Non-breeders			Bird specialists			Fish specialists			Non-breeders					
	Calorific content (kJ g <sup>-1</sup> )	Wet meal mass (g)	Meal energy content (kJ)	% all meals	% corrected	% energy	% all meals	% corrected	% energy	% all meals	% corrected	% energy	% all meals	% corrected	% energy	% all meals	% corrected	% energy	% all meals	% corrected	% energy
Auk sp. (adult)	10.9	100	1090	52.9	53.4	61.5	5.9	3.7	7.2	4.6	2.8	5.9	39.5	34.9	44.9	6.2	3.8	7.5	2.5	1.5	3.1
Northern fulmar (adult & chicks)	10.9	100	1090	20.3	12.2	14.1	7.1	2.6	5.1	4.6	1.7	3.5	14	7.4	9.5	6.9	2.5	4.9	6.5	2.3	4.8
Fish	5.2	100	520	12	21.1	11.6	82.5	89.1	84	76.8	81.2	82.5	26.1	40.4	24.8	83.4	90.4	84.2	82.7	87.6	85.2
Black-legged kittiwake (adult & chicks)	10.9	100	1090	9.1	5.5	6.3	0	0	0	0.7	0.2	0.5	2.6	1.4	1.8	0.3	0.1	0.2	0	0	0
Auk sp. (chick)	10.9	100	1090	2.6	2.6	3	0.1	0.1	0.2	0	0	0	14	12.4	15.9	0.2	0.1	0.2	0.6	0.4	0.8
Mammal	6.24	100	624	1.7	3	1.9	2.1	2.3	2.6	4.8	5.1	6.2	0	0	0	1.6	1.7	1.9	4	4.3	5
Goose barnacle	1.9	40	76	0.6	1	0.1	1.4	1.5	0.2	8.5	9	1.3	0	0	0	0.5	0.6	0.1	2.8	3	0.4
Passerine	10.9	100	1090	0.6	1	1.1	0	0	0	0	0	0	0.6	1	1.3	0.2	0.2	0.4	0	0	0
Great skua (chick)	10.9	100	1090	0.4	0.3	0.3	0.3	0.1	0.2	0	0	0	0	0	0	0.2	0.1	0.1	0	0	0
Eggs	29	14.4*	417.6	0	0	0	0.6	0.6	0.5	0	0	0	1.2	1.9	0.9	0.4	0.5	0.3	0.9	1	0.8
European shag (adult)	10.9	100	1090	0	0	0	0	0	0	0	0	0	0	0	0	0.2	<0.1	0.1	0	0	0
European storm petrel (adult)	10.9	100	1090	0	0	0	0	0	0	0	0	0	0.6	0.2	0.3	0	0	0	0	0	0
Northern gannet (adult)	10.9	100	1090	0	0	0	0	0	0	0	0	0	1.3	0.5	0.6	0	0	0	0	0	0
<i>n</i> = diet samples	–	–	–	264	–	–	728	–	–	457	–	–	249	–	–	949	–	–	323	–	–

\*Dry meal mass.

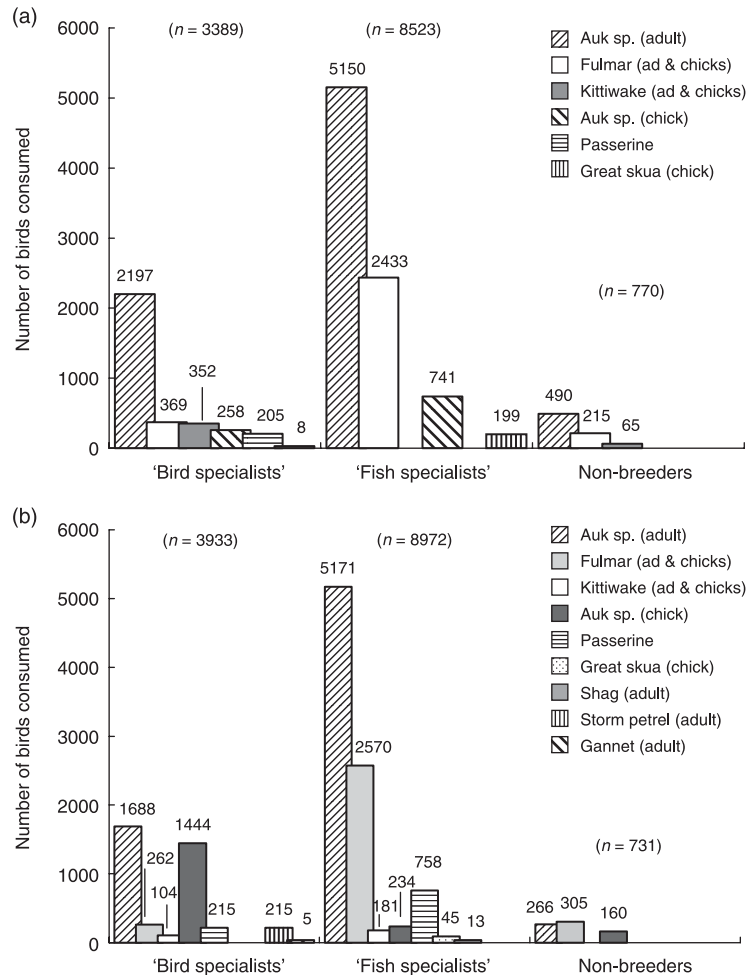
**Table 6.** Total mass of prey consumed by breeding and non-breeding great skuas at Hermanes in 1999 and 2001

	1999				2001				Change from 1999 to 2001	% change
	Bird specialists	Fish specialists	Non-breeders	Total	Bird specialists	Fish specialists	Non-breeders	Total		
Auk sp. (adult)	1290.5	3 025.8	288	4 604.4	991.7	3 037.9	156.3	4 185.9	-418.5	-9.1%
Fish	296.1	74 136.6	5489.3	79 922.1	882.7	83 953.7	5933.2	90 769.6	+10 847.8	+13.6%
Northern fulmar (adult & chicks)	295.1	1 946.3	171.8	2 413.2	209.7	2 056.1	244.2	2 510	+96.8	+4.0%
Black-legged kittiwake (adult & chicks)	131.9	0	24.5	156.5	38.9	68.0	0	106.9	-49.6	-31.7%
Auk sp. (chick)	63.0	180.9	0	243.8	352.2	57.1	39.1	448.4	+204.6	+83.9%
Mammal	52.7	2 480.6	344.1	2 877.3	0	2 673.7	288.9	2 962.6	+85.3	+3.0%
Passerine sp.	27.0	0	0	27.0	28.4	100.0	0	128.4	+101.4	+375.6%
Goose barnacle	7.0	395.8	243.9	646.8	0	81.3	80	161.3	-485.5	-75.1%
Great skua (chick)	6.4	159.5	0	165.9	0	36.4	0	36.4	-129.5	-78.1%
Eggs	0	96.7	0	96.7	4.4	87.1	9.6	101.1	+4.4	+4.6%
European shag (adult)	0	0	0	0	0	25.0	0	25.0	+25.0	–
European storm petrel (adult)	0	0	0	0	5.4	0	0	5.4	+5.4	–
Northern gannet (adult)	0	0	0	0	14.2	0	0	14.2	+14.2	–
<b>Total</b>	<b>2169.9</b>	<b>82 422.2</b>	<b>6561.7</b>	<b>91 153.7</b>	<b>2527.7</b>	<b>92 176.3</b>	<b>6751.2</b>	<b>101 455.2</b>	<b>+10 301.5</b>	<b>+11.3%</b>



**Table 7.** Change in number of birds consumed at Hermaness between 1999 and 2001

	1999	2001	Change from 1999 to 2001	% change
Auk sp. (adult)	7 837	7 125	-712	-9.1%
Northern fulmar (adult & chicks)	3 017	3 137	+120	+4.0%
Black-legged kittiwake (adult & chicks)	417	285	-132	-31.7%
Auk sp. (chick)	999	1 838	+839	+84.0%
Passerine sp.	205	973	+768	+374.6%
Great skua (chick)	207	45	-162	-78.3%
European shag (adult)	0	13	+13	-
European storm petrel (adult)	0	215	+215	-
Northern gannet (adult)	0	5	+5	-
<b>Total birds</b>	<b>12 682</b>	<b>13 636</b>	<b>+954</b>	<b>+7.5%</b>



**Fig. 1.** Estimated number of birds consumed by great skuas at Hermaness in (a) 1999 and (b) 2001 separated into foraging behaviour (breeders) and non-breeders. For each sub-group the total number of bird prey are shown in parentheses and columns show numbers sub-divided into the lowest identifiable taxon.

European storm petrels, 13 European shags and 3 northern gannets) were not present in the diet during 1999.

Published estimates of the breeding population of seabirds at Hermaness, including estimates of the non-breeding population (based on life table calculations, Appendix 2; see Supplementary material) are presented in relation to the number of each species consumed by great skuas in Table 8.

*Change in prey consumption model by varying input parameters*

The effects of altering input parameters on the prey consumption model are shown in Appendix 1 (see Supplementary material). The sensitivity analysis is consistent between years. In summary, changes in the calorie content of fish and bird have a considerable

**Table 8.** Estimated seabird populations at Hermaness and proportion eaten by great skuas. Non-breeding population calculated from life tables in Appendix 2 (see Supplementary material)

Species	Population estimate of breeding seabirds at Hermaness				Annual percentage of seabirds consumed by great skuas		
	Breeders	Non-breeders	Total	Chicks	Grand total	1999	2001
	Adults						
Common guillemot/razorbill/Atlantic puffin combined	78 521	18 590	97 111	20 183	117 294	7.5% (all birds) 8.1% (adults) 5.0% (chicks)	7.6% (all birds) 7.3% (adults) 9.1% (chicks)
Northern gannet	32 772	12 637	45 409	10 979	56 388	0	<0.01% (all birds)
Northern fulmar	27 912	15 678	43 590	6 001	49 591	6.1% (all birds)	6.3% (all birds)
Black-legged kittiwake	1 846	40	1 886	198	2084	20.0% (all birds)	13.7% (all birds)
Great skua	659 (1999) 726 (2001)	—	—	738 (1999) 646 (2001)	—	28.0% (chicks)	7.0% (chicks)
European storm petrel	Unknown	—	—	—	—	—	—
European shag	Unknown	—	—	—	—	—	—

effect on the estimated amounts of all prey consumed, whereas the calorie content of goose barnacle, rabbit and eggs have very little effect. The effects of reducing estimated meal mass on parameter outputs for the main prey types are similar to the effect of calorie content, but smaller.

Altering the amount of fish in skua diets has a profound impact on the number of seabirds consumed. A 50% decrease in the proportion of fish in the diet resulted in more than a 50% increase in bird predation estimates for adult breeders and over 70% for non-breeders. More significantly, the effect of relaxing the model to assume a meal to pellet ratio of 1:1 alters the estimated number of birds consumed by between 10–23% for chicks and 57–100% for adults. The model reveals that calorific content, meal mass and percentage of bird carcass utilization also had a marked effect on prey consumption estimates. A scenario where all specialist bird predators were removed from the population reduced the estimated number of birds consumed by 25–28%.

## Discussion

This study further illustrates that great skuas consume substantial numbers of seabirds, at levels that currently appear to be unsustainable for prey populations. Furthermore, the availability of fishery discards is an important determinant of seabird predation rates, as evidenced by altering model input parameters of fish consumption. However, predation rates showed little annual variation despite changes in fishing policy over this period. Predation rates differed between St Kilda and Hermaness; although the number of birds consumed at St Kilda were very much larger, for some species they were relatively greater at Hermaness. One possible management strategy is the removal of specialist bird predators (Bosch *et al.* 2000; Guillemette & Brousseau 2001), although the very much larger population that are fish specialists but also opportunistic seabird predators consume the bulk of the seabird prey.

## MODEL PERFORMANCE

Bioenergetics models may be subject to a number of biases. Sensitivity analysis indicated the parameter with the greatest effect on energy demand was the FMR:BMR ratio for breeding adults. FMR:BMR ratios for seabirds are the source of some uncertainty (Adams *et al.* 1991; Phillips *et al.* 1999). Despite this, the values published for most seabirds are multiples of between 3 and 4 (Bryant & Furness 1995; Ellis & Gabrielsen 2002). Data on activity budgets for skuas feeding at fishing boats were limited to a single day, therefore because variations in wind speed or discarding practices may influence FMR:BMR ratios considerably (Furness & Bryant 1996; Ellis & Gabrielsen 2002), we should view these values with caution. Moreover, although other studies have found that bird specialists spend less time foraging

compared with conspecifics (Pietz 1987; Spear 1993) their energy expenditure has not been quantified. Future detailed study of great skua foraging activities would be valuable, particularly in light of possible future changes to fishery management or changes in the number of specialist bird predators.

Estimates of the breeding population and food assimilation efficiency both had marked effects on model outputs (Table 4). Future studies should ensure accurate collection of population estimates as well as more extensive data on assimilation efficiency to ensure model outputs are robust.

#### PREY CONSUMPTION ESTIMATES

Assessing diets in the manner used in this study is known to be subject to error (Votier *et al.* 2003), which can have serious effects on the prey consumption estimates predicted by this model. Phillips *et al.* (1999) followed Furness & Hislop (1981) in assuming one pellet was equivalent to one meal, in the absence of any data to the contrary. However, captive trials suggest that skuas can 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. While we acknowledge that using captive birds as a model may not represent the natural situation, we believe this to be a better estimate than a simple 1:1 meal to pellet ratio since different prey clearly have different amounts of indigestible material.

#### EFFECT OF PREDATION ON SEABIRD POPULATIONS

Although the numbers of seabirds consumed at Hermaness are substantial, the effect on different species varies considerably. The percentage of the black-legged kittiwake population consumed annually was particularly high (Table 8). Other studies have shown that great skuas negatively effect kittiwake survival (Oro & Furness 2002) and have caused localized extinctions (Heubeck *et al.* 1997). Our model supports the evidence that black-legged kittiwakes are particularly vulnerable to predation by great skuas.

In terms of total numbers, auks are the most abundant seabird prey in the diet of great skuas at Hermaness. Pellets containing remains of adult auks could not always be identified to species, but the majority did consist of fully grown Atlantic puffins. Pellets containing the remains of auk chicks were from guillemots or razorbills; no puffin chicks were recorded. Therefore by feeding on adult puffins, it is possible that the level of predation pressure exerted by great skuas is much more severe than on the other two species of auk. Given that the annual adult survival of puffins is  $\approx 90\%$  (Harris 1984), predation by great skuas could represent a significant proportion of this mortality, although it is not possible to estimate the number of non-breeders included in this total.

The estimated number of northern fulmars killed each year represents around 6% of the local population. Although it is difficult to distinguish between the pellets of adult and young fulmars, since fulmar pellets were collected throughout the breeding season and before chicks fledge, probably a large proportion of the birds killed were adults. Skua predation is likely to have an impact on the breeding population of this species. Given recent evidence that fulmars are declining significantly at several Shetland colonies (Pennington *et al.* 2004), this may in part be due to great skua predation.

#### EFFECT OF ANNUAL VARIATION IN FISHERY POLICY

Our model suggests that a 50% reduction in the proportion of fish in the diet will increase the number of seabirds consumed by over 50% for adult breeders and over 70% for non-breeders (Table 8). This would result in an additional  $\approx 6500$  birds being consumed annually and demonstrates the importance of fishery discards in this system. However, despite changes in fishery policy implemented on 1 January 2001, great skuas did not exhibit a switch to consuming more seabird prey from 1999 to 2001. The reductions in overall fishing effort and the introduction of technical measures to reduce bycatch after 2000 were expected to reduce discards, but an exceptional recruitment of haddock in the north-west North Sea during 2001 (more than double the mean discarded over the period 1986–2001; Votier *et al.* 2004b) buffered this effect. This highlights the complex interaction between commercial fisheries and seabird communities that utilize them.

#### APPLICATION OF MODELS TO DIFFERENT COLONIES

Despite having a larger colony of predators and a smaller colony of potential seabird prey, great skuas at Hermaness consumed far fewer birds than at St Kilda (Phillips *et al.* 1999). However, comparing the percentage of the local population of seabirds consumed between the two colonies reveals a different picture. Phillips *et al.* (1999) estimated the proportion of seabirds consumed by great skuas as 2.0% for northern fulmars, 15.5% for black-legged kittiwakes and 0.9% for Atlantic puffins, compared with values of 6.1–6.3%, 13.7–20.0% and  $< 7.5\%$  for Hermaness, respectively. Therefore in relative terms, predation pressure by great skuas at Hermaness appears greater than at St Kilda, owing to the smaller seabird numbers at Hermaness.

Skuas and gulls exhibit marked differences in diet choice among colonies (Pietz 1987; Spear 1993), as has already been established between Shetland and St Kilda (Phillips *et al.* 1997a). However, these differences have not, to our knowledge, been presented as estimates of relative prey consumption. When presented in this way it becomes all the more clear that it is not appropriate

to extrapolate conclusions about predator–prey interactions from differing parts of great skuas' range.

#### ROLE OF SPECIALIST BIRD PREDATORS

It was estimated that specialist bird predators constituted 5% of the breeding population and accounted for nearly 30% of the total birds consumed each year. Although the majority of bird prey was consumed opportunistically, the foraging behaviour of individual specialists may have implications at the population level. During 1999 all of the predated black-legged kittiwakes were taken by bird specialists. Among the much reduced kittiwake population at Hermaness, the remaining pairs nest in caves or enclosed cliffs, where great skuas cannot easily forage (Heubeck *et al.* 1997). The relatively high predation rate by specialist bird predators on this species may be explained by their ability to depredate these less accessible birds. Great skuas defending a feeding territory within puffin colonies at Hermaness may also be having a more severe impact than other members of the population. Harris (1984) found that great black-backed gulls, *Larus marinus* (Linnaeus), nesting within puffin colonies on St Kilda took a higher proportion of older (breeding) birds than those elsewhere, thereby having a more significant impact on puffin population trends.

One management strategy, although controversial, is the removal of specialist bird predators. Removal of all of the bird specialist predators would reduce the number of birds consumed by between 25 and 28%. Therefore our model predicts a substantial reduction in predation rates by removing only 5% of the population, which would be more effective than random removal of skuas in the population. However, this calculation assumes that after this change, other skuas retain the same feeding preferences. Because specialist bird predators defend feeding territories, it is unknown whether their removal may result in conspecifics swamping seabird colonies, or whether fish specialists may occupy vacated territories and switch to feed on seabirds themselves. Only experimental study would elucidate these responses.

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