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Seabird predation by great skuas *Stercorarius skua* – intra-specific competition for food?

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Competition for food is widely cited as an important cost of coloniality among birds and much of the evidence in support of this hypothesis comes from studies of colonial piscivorous seabirds. However, for generalist seabirds able to switch between different prey types, the role of food availability in relation to colony size is unclear. Here we investigate patterns of the consumption of seabird prey in relation to colony size in a generalist seabird, the great skua *Stercorarius skua*, in Shetland, UK. At the population level skuas feed mainly on sandeels *Ammodytes marinus* and fishery discards, but respond to declines in fish availability to facultatively prey on other seabirds. By comparing the consumption of seabirds among seven different sized colonies, including one colony with artificially reduced numbers of skuas (Fair Isle), we investigate whether consumption of seabird prey is influenced by skua population size, while simultaneously measuring seabird prey availability. Data from five years also enables us to investigate the influence of annual variation in environmental conditions on seabird consumption. Using measures of body condition and reproductive performance we investigate the consequences of living in different sized colonies, which may provide insight into ultimate costs of nesting at high population density. Skua diets varied among colonies and the proportion of seabird prey in the diet was inversely related to skua colony size, despite similar per capita numbers of seabirds across colonies. At the colony where their numbers were artificially suppressed, skuas consumed a greater proportion of seabirds per capita. Highly significant year effects in seabird predation were observed but the pattern among colonies remained consistent over time. Two measures of adult body condition (pectoral muscle index and mean corpuscular volume) revealed that adult great skuas were in poorer condition at the largest colony (Foula), but reproductive performance did not alter significantly among colonies. This study provides evidence that intra-specific competition among skuas may limit opportunities for obtaining seabird prey, which may be particularly important during periods of poor availability of sandeels and fishery discards, and has implications for assessing the impact of skuas on seabird populations.

Coloniality is a common feature among breeding birds and much research has focused on the evolution and function of group living (Rolland et al. 1998, Brown and Brown 1996, 2000). Colonial nesting seabirds are among the most striking examples of group living and their study has formed the basis of much theory, in particular the mechanisms underlying intra-specific variability in colony size (Lewis et al. 2001, Tella et al. 2001, Forero et al. 2002, Ainley et al. 2003, 2004). A wide range of fitness benefits to breeding in conspecific aggregations have been described and these appear to be driven largely by protection against predators (Serrano et al. 2005), the need to find a mate, or information transfer to improve foraging efficiency (Mikami 2006). Yet the considerable variation in colony size reveals that there must be some limits to the size of nesting aggregation seabirds can form. Early work suggested that seabird colonies were limited by nest sites (Alexander 1974), yet in most instances nesting sites are not restricted and instead it is now widely believed that competition for food limits colony size (Coulson 1983, Clode 1993, Moss et al. 2002). Indeed there is now a body of evidence that foraging costs are higher at large colonies compared with small colonies (Furness and Birkhead 1984, Lewis et al. 2001, Ainley et al. 2004) and that depletion of fish prey is negatively correlated with colony size (Birt et al. 1987, Forero et al. 2002, Ainley et al. 2003).

Skuas *Stercorarius* spp. and predatory gulls *Larus* spp. are colonial or semi-colonial and occur at a range of population aggregations in marine eco-systems (Mitchell et al. 2004). They are dietary generalists at the population level, feeding on human waste, shoaling fish and discards from fisheries, as well as on the chicks, eggs and adults of other seabirds (Oro et al. 1997, Votier et al. 2004a, b). The ability to switch between a wide range of foods may make these generalist seabirds less vulnerable to changes in the availability of marine resources and it is currently unclear whether competition at high population densities may restrict food availability in the same way as has been shown for piscivorous species.

The population of great skuas *Stercorarius skua* breeding in the UK has increased markedly over the last 100 years, and an abundance of forage fish (mainly sandeels *Ammodytes marinus*) and fishery discards, are implicated with this increase (Mitchell et al. 2004). Recent work from the Shetland Islands, UK, suggests that large great skua colonies are decreasing in size, while small colonies continue to grow (Mitchell et al. 2004). Given that there is still space for more nesting sites at most of the colonies, this pattern may be a result of differences in food availability mediated by competition. It is unlikely that skuas consume sufficient quantities of sandeels or discards to deplete these food resources (Garthe et al. 1996), although there is evidence that skuas compete for discards scavenged behind fishing boats (Hudson and Furness 1988). At some colonies a small proportion of skua pairs defend feeding territories and specialise as seabird predators (Votier et al. 2004a), yet at the population level skuas feed facultatively on other seabirds, particularly in response to changes in the availability of forage fish and fishery discards (Hamer et al. 1991, Votier et al. 2004c). Therefore access to seabirds for food may be important for buffering the effects of changes in the availability of fish prey and therefore play a role in population regulation. Different levels of competition for seabird prey may also have implications for conservation. Being subsidized by fishery discards, skuas may be able to suppress seabird prey populations because their numbers remain high even as avian prey densities decline. In the presence of intra-specific competition, the impact on prey populations may differ among colonies of different sizes.

Here we investigate the relationship between colony size and the consumption of seabird prey in great skuas breeding at seven very different sized colonies. We collected data on diet to test whether skuas consumed fewer seabirds at large colonies, where we predict competition to be highest, while correcting for potential differences in prey availability. Although skuas feeding on fish travel long distances to find them at sea, those feeding on other seabirds tend to forage around the coastline of their breeding colony (Votier et al. 2004a, 2006), which reduces the potentially confounding effects of inter-specific and inter-colony competition. The availability of sandeels and discards are a function of several factors including climate (Arnott and Ruxton 2002), and fisheries management policy (Stratoudakis et al. 1999), which vary over time and space. Data detailing availability of these prey are not available at the colony level, but by conducting this study over five years when fish availability will very likely fluctuate over time or space, or both, we are therefore able to gain insight into the variance in seabird consumption attributable to extrinsic environmental factors. In addition, one of the colonies (Fair Isle) has artificially low numbers of great skuas as a result of human persecution and disturbance (Mitchell et al. 2004). Competition has been artificially manipulated at this colony and we predict that skuas will consume more seabirds per capita.

If access to seabirds as food has consequences for demographics, negative feedback costs on at least some demographic parameters are expected. We used inter-annual measures of reproductive performance and intra-annual measures of adult body condition to investigate the consequences of nesting in different sized colonies. Theory predicts that intense competition at high breeding densities will lead to a negative correlation between colony size and reproductive performance (Gaston et al. 1983, Hunt et al. 1986), yet adults may increase their foraging effort to maintain high breeding success (Hamer et al. 1991). If this is the case then a measure of adult body condition may be more revealing in terms of the costs of nesting at high population density. We predict that more intense competition at large colonies may be expressed in terms of reduced annual fecundity, reduced adult body condition, or both.

Methods

Study sites

Work was conducted in Shetland, UK – an archipelago that holds 6,846 breeding pairs of great skuas (during 2000–2002), representing 71% of the UK and 60% of the world population (Mitchell et al. 2004) – in five years between 1996 and 2003. We studied seven well-spaced colonies: Foula (60°08′N, 2°05′W), Hermaness (60°50′N, 1°12′W), Fetlar (60°38′N, 0°54′W), Noss (60°08′N, 1°00′W), Bressay (60°11′N, 1°00′W), Fair Isle (59°32′N, 1°38′W) and Noness (60°42′N, 1°16′W; Fig. 1), which support different sized populations ranging from 19 to 2,293 breeding pairs (Table 1). The number of breeding pairs was estimated at each colony during 1998–2002 (Mitchell et al. 2004). As mentioned, great skua breeding numbers at Fair Isle have been substantially suppressed by an unquantified amount, either by killing or by exclusion from suitable nesting habitat. For this reason we exclude Fair Isle in analysing the relationship between skua colony size and seabird colony size, but retain it in analysis of diet composition and adult body condition.

Diet composition

The indigestible components of prey are regurgitated by great skuas as pellets and provide a convenient and accurate method for assessing diet composition (Votier et al. 2001, 2003). Pellets were collected from a random sample of breeding territories throughout the breeding season at all seven colonies over five years (1996, 1998, 1999, 2000 and 2003) during the incubation and chick-rearing period in June and July. These data were collected from virtually all breeding territories at small colonies and from a considerable sample of territories (50 to 120) at large colonies to provide a representative sample of the colony as a whole. Individual specialisation has been studied in detail at only two colonies (Foula in 1996, Hermaness during 1998–2000) and revealed that a small proportion of skuas feed almost exclusively on other birds. These skuas were characterised on the basis of 70% or more bird prey in the diet and typically defended a feeding territory within a seabird colony (Votier et al. 2004a). Data from these pairs were excluded from our analysis of cross colony comparisons since they are not representative of the colony as a whole, although study of this behaviour among colonies may prove interesting. The vast majority of pellets contained a single prey item and were assigned to the lowest possible taxon, then removed from the territory to prevent repeat counting on subsequent visits. Pellets of bird remains were identified to species or generic level on the basis of the colour and odour of feathers, as well as skulls and bones. Sagittal otoliths in fish pellets were used to identify species of fish prey (Votier et al. 2003). Although analysis of pellets may underestimate the presence of soft-bodied prey in the diet, by using the same sampling technique among colonies and years, any errors are likely to be uniform across sampling locations and dates.

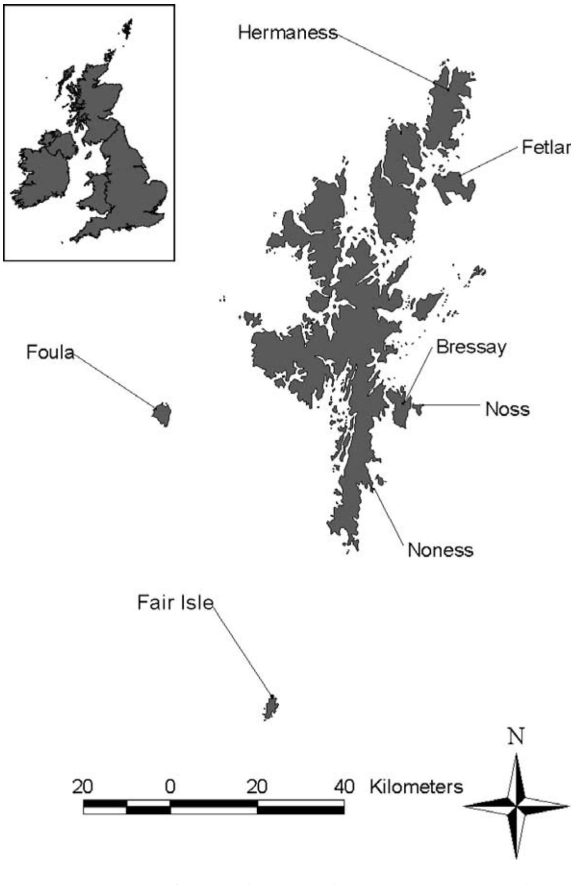

Fig. 1. Location of great skua breeding colonies in Shetland, UK, sampled in this study.

Availability of seabird prey

The same seven colonies also support large numbers of other breeding seabirds including: northern fulmar *Fulmarus glacialis*, northern gannet *Morus bassanus*, European shag *Phalacrocorax aristotelis*, black-legged kittiwake *Rissa tridactyla*, common tern *Sterna hirundo*, Arctic tern *S. paradisaea*, common guillemot *Uria aalge*, razorbill *Alca torda*, Atlantic puffin *Fratercula arctica*, and very small numbers of European storm-petrel *Hydrobates pelagicus* and Leach's storm-petrel *Oceanodroma leucorhoa*. The size of these birds' breeding populations are documented and their reproductive performance has also been studied (Table 2). Because skuas feed opportunistically on the chicks and eggs of other seabirds as well as adults, we estimated the number of young seabirds by multiplying respective population size by their respective reproductive performance (Table 2). We considered only species that are known to occur regularly in great skua diets (Votier et al. 2003, 2004a,b). This approach is unlikely to explain all of the variance in seabird predation by

Table 1. Population estimates and breeding success of great skuas from seven colonies in Shetland, UK. Population estimates are from Mitchell et al. 2004, except Hermaness in 2001, in Votier et al. 2004b. Breeding success data (number of young fledged per breeding attempt) were obtained from the Joint Nature Conservancy Council seabird monitoring programme (Mavor et al. 2002).

Colony	Population estimate	Breeding success												
Year	1999–2002	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001
Foula	2293	0.2	0.4	0.6	0.4	0.5	0.8	1	1	1	1	1.1	0.8	0.7
Hermaness	726	1.03	0.69	1.14	1.27	0.98	0.74	0.92	1.11	0.31	0.63	1.1	0.85	0.91
Fetlar	593	0.13	–	0.73	1.12	0.83	1.08	0.95	1.13	0.69	0.71	0.48	1.17	0.76
Noss	432	0.61	0.22	0.47	0.69	0.86	0.76	0.96	0.68	0.37	0.32	0.7	0.54	0.15
Bressay	275	–	–	–	–	–	–	–	–	–	–	–	–	–
Fair Isle	143	0.79	0.7	0.7	0.65	1.09	1.2	1.15	0.83	0.76	1	0.77	0.74	–
Noness	19	–	–	0.08	0.3	0.65	0.8	1.17	0.79	0.06	0.50	0.61	–	–

great skuas for a number of reasons: we are unable to calculate the numbers of non-breeders at each colony and some seabird species may be more vulnerable to predation than others. Although data to quantify these potentially confounding effects do not exist at present, we believe our approach is conservative as such effects would reduce our chances of finding a statistically significant relationship between seabird consumption and great skua colony size.

Skuas feed largely on seabirds that breed along the coastal fringes of colonies. Because the area of a surface increases faster than its perimeter, the coast at small colonies is a larger proportion than at large colonies. Therefore skuas nesting at small colonies will have greater accessibility to coastal areas, and therefore potentially seabird-prey, than skuas nesting at large colonies. To investigate the role that coastline length plays in per capita consumption of seabirds we measured the coastline length and area of each colony on a 1:500, 000 map using programme Scion Image Beta 4.03 (Appendix 1).

Reproductive performance

Great skua breeding success has been estimated annually at a number of colonies in Shetland by the Joint Nature Conservancy Council, using the ratio of chicks fledged to the number of breeding attempts (Mavor et al. 2002). We used these published estimates, available for all study colonies except Bressay, to investigate the effect of skua colony size on skua breeding success (Table 1).

Adult body condition

During June and July 2003 we trapped 100 adult great skuas on the nest, which were brooding either very small chicks or eggs close to hatching (and therefore at very similar stages of the breeding season), at four breeding colonies (49 at Foula, 16 at Hermaness, 15 at Fetlar and 20 at Fair Isle). Skuas were sampled from a broad cross-section of each colony to correct for possible effects of heterogeneity in individual quality.

Laying date is an indicator of individual quality in skuas (Catry et al. 1998) so we investigated its possible influence by including it as a covariate in all our analyses. Laying date was assessed in three ways: (1) direct observation, (2) measuring the flattened wing chord of chicks and comparing this with logistic growth curves of great skua chicks in Phillips et al. (1997) to calculate chick age, then back-calculate laying dates assuming a 30 day incubation period or (3) measuring egg length, breadth and weight to calculate egg density and hence laying date (Furness and Furness 1981).

Table 2. Breeding population estimates of seabirds at the same seven Shetland, UK, colonies as great skuas in Table 1. Breeding success data were obtained from the Joint Nature Conservancy Council seabird monitoring programme (Mavor et al. 2002), or Shetland Bird Reports 1985–2001 and, in all instances except Fair Isle, averaged for the whole of Shetland. Source data on breeding population estimates are listed for each site and year of survey in parenthesis. Northern gannets *Morus bassanus* were present at all sites but are not an important prey item for great skuas and very small numbers (<10) of European storm-petrels *Hydrobates pelagicus* and Leach's storm-petrels *Oceanodroma leucorhoa* breed at some sites but their numbers are not known. Dashes represent missing data.

Seabird species		Colony						
		Fair Isle[1]	Foula[2]	Hermaness[3]	Noss[4]	Fetlar[5]	Bressay[6]	Noness[7]
Northern fulmar *Fulmarus glacialis*	Breeding pairs	43 300 (1996)	21 000 (2000)	14 000 (1997)	5 000 (1998)	12 566 (1986)	6 200 (1999–00)	2000 (1999)
	Breeding success	0.42	0.42	0.42	0.42	0.42	0.42	0.42
	Young	18 186	8,820	5,880	2100	5278	2604	840
European shag *Phalacrocorax aristotelis*	Breeding pairs	550 (1998)	2500 (2000)	–	80 (2000)	128 (1986)	100 (2000)	150 (1999)
	Breeding success	1.29	1.29	–	1.29	1.29	1.29	1.29
	Young	710	3225	–	103	165	129	116
Black-legged kittiwake *Rissa tridactyla*	Breeding pairs	11 650 (1997)	1000 (2000)	800 (1999)	2500 (2000)	<100 (2002)	0	500 (1999)
	Breeding success	0.90[1]	0.47	0.47	0.47	0.47	–	0.47
	Young	10 485	470	752	1175	47	0	235
Arctic/Common tern *Sterna paradisea/hirundo*	Breeding pairs	1750 (1997)	850 (2000)	50 (2001)	200 (2000)	488 (2002)	250 (2000–02)	5 (1999)
	Breeding success	0.18	0.18	0.18	0.18	0.18	0.18	0.18
	Young	315	153	9	36	88	45	1
Common guillemot *Uria aalge*	Breeding pairs	19 650 (1999)	20 750 (2000)	7500 (2000)	23 000 (1996)	115 (1986)	250 (2000)	1000 (1999)
	Breeding success	0.71	0.71	0.71	0.71	0.71	0.71	0.71
	Young	13 952	14 733	5,325	16 330	82	178	710
Razorbill *Alca torda*	Breeding pairs	1650 (1998)	2100 (2000)	750 (2000)	1000 (1996)	66 (1986)	50 (2000)	85 (1999)
	Breeding success	0.68	0.68	0.68	0.68	0.68	0.68	0.68
	Young	1122	14280	510	680	45	34	58
Atlantic puffin *Fratercula arctica*	Breeding pairs	21 000 (1995)	22 500 (2000)	28 000 (1997)	1500 (2000)	2000 (1991)	100 (2000)	35 (1999)
	Breeding success	0.67	0.67	0.67	0.67	0.67	0.67	0.67
	Young	14070	15075	18760	1005	1340	67	23
	Total adults	199 000	141 000	102 000	67 000	30 725	14 000	8 000
	Total young	58 840	56 756	31 881	21 429	7 045	3,057	1,983
Total (nearest 1 000)		258 000	198 000	134 000	88 000	38 000	17 000	10 000

Population data from: [1]Fair Isle Bird Observatory Reports 1995–98, [2]Pennington et al. 2004, [3]Unpubl. data, Hermaness Reports to Scottish Natural Heritage: Goddard and Lewis (1996), Lewis (1997), King (1999), Rodger (2000), Duffield (2001), [4]Unpubl. data Noss Reports to Scottish Natural Heritage: Goddard and Lewis (1996), Upton and Brown (1998), Upton and Maher (2000), [5]M. Smith pers. comm., [6]P.V.Harvey pers comm., [7]M.Heubeck pers. comm.

All trapped birds were measured (maximum flattened wing-chord, total head and bill length, sternum length, tarsus length and body mass) and we also took a profile of the pectoral muscle using methods described in Bolton et al. (1991). Birds were sexed using molecular techniques developed by Griffiths et al. (1998).

We used the biometrics and pectoral muscle profiles to estimate two measures of body condition: body mass index (BMI) and pectoral muscle index (PMI), which provide indications of lipid and protein reserves respectively (Bolton et al. 1991, Kalmbach et al. 2004). The first factor extracted by a principal component analysis (PCA) on four body measurements (wing, sternum, head and bill, tarsus) was used as a measure of overall body size for males and females separately, which explained 56.1% and 40.4% of the variance respectively. Using the residuals of a regression for body mass on the body size PCA, expressed as a proportion of the predicted component mass, we calculated BMI. This provides an index primarily reflecting body lipid reserves (Zwarts et al. 1996), and we predict that skuas breeding at large colonies will exhibit lower indices reflecting reduced lipid reserves because of greater foraging costs. PMI provides an index reflecting body protein reserves and was calculated using the residuals of a breast muscle volume estimate (the cross sectional area 3cm under the highest point of the profile trace multiplied by the sternum length) to body size PCA regression (Bolton et al. 1991, Kalmbach et al. 2004, for more details). At large colonies PMI should be lower than at small colonies, if competition for protein-rich food (i.e. bird prey) is greater at high population densities.

A third measure of condition was estimated using Mean Corpuscular Volume (MCV). This haematological parameter is calculated from haematocrit and total red blood cell count to provide information on age and synthesis of red blood cells, which is related to individual quality, short-term stressful events, or both (Bearhop et al. 1999). Blood was taken from the tarsal vein (under license from the Home Office) with 22G 1.5" needles and drawn into Sarstedt Monovette tubes. Each tube contained 2.6ml of an anticoagulant, ethylene diamine tetra-acetic acid (EDTA), which was mixed well with the blood. Enough blood was also used to fill two 75 mm heparinised microhaematocrit capillaries. Blood samples were subject to standard haematological methods (Bearhop et al. 1999) within five hours of sampling. Serial dilutions (1: 200) of blood to formal citrate buffer were made and the solution introduced into an improved Neubauer haemocytometer. Using a light microscope we made four repeat counts of total erythrocytes. The microhaematocrit capillaries were spun at 10, 500 g for 10 min and packed cell volume measured to the nearest 0.1 mm using Vernier callipers. MCV was calculated as haematocrit/total erythrocyte count ($10^6/\mu L$) × 10 with high values associated with poor body condition or ill health (Bearhop et al. 1999).

Statistical analysis

We compared the number of breeding great skuas with the breeding seabird population at the same colony. To investigate whether such a relationship may also be a function of the size of the respective sites, we included the area (km^2) of each island/ headland (Appendix 1) in stepwise multiple regression models. The area excluded parts of each site that contained human habitation and were therefore unsuitable for breeding seabirds.

Residual (or restricted) maximum likelihood (REML) techniques were used to assess factors influencing the consumption of seabirds by great skuas. We used $\log_e$ skua colony size, the ratio of colony coastline to colony area and year as explanatory variables in a generalised linear mixed model with binomial error distribution and logit-link function. The number of regurgitated pellets containing bird remains was the response variable and the total number of regurgitated pellets included as a binomial denominator. We controlled for repeated measures at the same colonies by including colony as a random effect. All likely explanatory variables were included in a maximal regression model and each term was dropped sequentially until only terms which significantly affected power were retained. Wald statistics (distributed approximately as χ^2) were used to estimate the significance of terms fitted last in the models.

The estimates of great skua breeding success are expressed as the number of chicks fledged per breeding attempt, averaged over a sub-sample of skuas from each colony. Because we do not have the raw data this is based upon, we treated this success as a continuous variable with an upper limit of two (great skuas lay a maximum of two eggs), the distributions of these data not departing significantly from normal (Kolmogorov-Smirnov $Z = 0.801$, $P = 0.542$) and the variances being equal (Levene's Statistic $= 1.20$, $P = 0.305$). We used this as the response variable in a linear mixed model with $\log_e$ great skua colony size, the ratio of colony coastline to colony area and year as fixed explanatory variables, with colony as a random effect.

General linear models were used to investigate the effect of colony size on adult body condition. Although it would have been preferable to use colony size as a continuous explanatory variable, for logistic reasons we only had samples from four skua colonies and we therefore included colony as a four-level factor. Body condition measure (BMI, PMI or MCV) was used as the response variable with laying date as a covariate.

Post-hoc least significant difference (LSD) tests were used to identify factors influencing statistically significant models.

Analyses were performed using Genstat 8 release 8.1 (Genstat 8 committee 2005). All tests were two-tailed, significance was set at $\alpha = 0.05$ for acceptance of null hypotheses and all data met requirements of homoscedasticity.

Results

Prey composition

Great skua diets assessed from regurgitated pellets of indigestible material were dominated by fish and bird prey, with very small amounts of mammalian and invertebrate prey (Table 3).

Skua colony size, seabird colony size and prey consumption

Excluding the artificially small number of great skuas at Fair Isle, the size of skua colonies (Table 1) were positively correlated with the ($\log_e$) number of seabirds at the same sites (Table 2; stepwise multiple regression: $F_{1,5} = 11.81$, $P = 0.026$, slope $= 0.637$, SE ± 0.185; Fig. 2), and this relationship was independent from the area of each island/headland studied (stepwise multiple regression: $F_{1,4} = 2.06$, $P = 0.225$, slope $= 0.117$, SE ± 0.081).

Table 3. Prey composition (%) based on pellets of indigestible material regurgitated by great skuas breeding at seven colonies in Shetland, UK, over five years.

	Fish[a] (excl. sandeel)	Bird[b]	Sandeel	Mammal[c]	Other[d]	n
			1996			
Foula	61.7	15.0	20.8	0	2.5	433
Hermaness	75.1	19.7	0	2.1	3.1	711
Bressay	61.3	24	0	1.1	13.7	271
Fetlar	71.5	18.2	1.8	8.5	0	165
Noss	72.1	14.4	7.1	0.3	6.2	1152
Fair Isle	46.5	47.2	0	0.3	6	604
Noness	72.2	24.8	0.5	0.2	2.3	436
			1998			
Foula	75.5	19.1	4.4	1	0	204
Hermaness	52.9	46	0	0.8	0.3	987
Noss	23.7	60.9	3.8	11.5	0	156
Noness	35.5	63.7	0	0.9	0	547
			1999			
Foula	64.6	17.1	11.1	3.8	3.4	799
Hermaness	60.1	36.2	0.2	2.1	1.5	961
Noness	46.5	51.2	0.9	0.5	1	213
			2000			
Hermaness	58.2	36.9	0.2	3.3	1.5	1030
Noss	36.5	38.7	0.6	23.4	0.8	359
Noness	49.1	46.6	0	4.3	0	116
			2003			
Foula	84.8	9.5	4.3	0.5	1.0	210
Hermaness	88.8	11.1	0	0	0	27
Fetlar	77.5	20	0	0	2.5	40
Fair Isle	36	57.3	0	6.7	0	75

[a] Herring *Clupea harengus*, sprat *Sprattus sprattus*, cod *Gadus morhua*, haddock *Melanogrammus aeglefinus*, whiting *Merlangius merlangus*, blue whiting *Micromesistius poutassou*, Norway pout *Trisopterus esmarkii*, redfish *Sebastes marinus*, long rough dab *Hippoglossoides platessoides* and mackerel *Scomber scombrus*.

[b] Northern fulmar, European storm-petrel, European shag, great skua chick, black-legged kittiwake, common guillemot, Atlantic puffin, unidentified gull/tern, unidentified passerine, and unidentified bird.

[c] Rabbit *Oryctolagus cuniculus* and sheep *Ovis aries*.

[d] Goose barnacle *Lepas* sp. and squid spp.

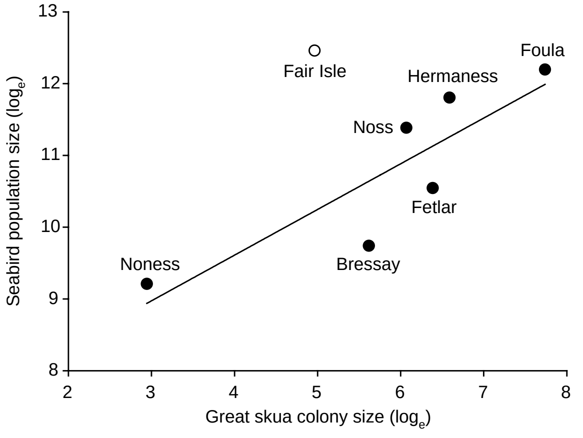

Fig. 2. Relationship between ($\log_e$) great skua colony size and the ($\log_e$) size of seabird population breeding at the same sites. The number of great skuas breeding at Fair Isle is known to be negatively biased through direct and indirect competition with man, and is therefore excluded from statistical analysis, but is included here for completeness.

REML models revealed that a significant amount of the variation in bird prey consumption by great skuas was explained by the number of conspecifics (Table 4) – at large colonies skuas fed less on other seabirds than at small colonies (Fig. 3). The ratio of coastline length to colony size also positively influenced the proportion of birds consumed by skuas – where the coast is a smaller proportion of the colony bird consumption decreases (Table 4). Year had a highly significant effect on seabird consumption (Table 4, Fig. 3) but with no significant interactions the relative numbers of seabirds consumed at each colony remained similar among years. Models excluding Fair Isle revealed skua colony still explained a considerable amount of the variance in bird consumption (Table 4). We interpret the very high proportion of seabird prey in the diet of skuas at Fair Isle as a result of the artificially low numbers of conspecifics at this colony (Fig. 3).

Reproductive performance

Over the period 1989–2001 inclusive, there was no significant relationship between great skua breeding success and either $\log_e$ skua colony size (REML: Wald $= 3.23$, df $= 1$, $P = 0.071$) nor the ratio of coastline length to colony size (REML: Wald $= 1.49$, df $= 1$, $P = 0.221$). However there was marked and highly significant inter-annual variation in breeding success (Wald $= 30.25$, df $= 11$, $P = 0.017$, average estimate $= -0.250$, SE ± 0.124). All first-order interactions were not significant.

Adult body condition

Adult body condition measures are shown in Table 5. MCV was significantly influenced by colony and sex (GLM: colony effect, $F_{3,94} = 5.144$, $P = 0.003$; sex effect, $F_{1,94} = 6.00$, $P = 0.016$: Fig. 4a) but not laying date ($F_{1,94} = 0.121$, $P = 0.729$), with no significant interactions. PMI was also significantly different among colonies (colony effect, $F_{3,97} = 4.216$, $P = 0.008$: Fig. 4b), but was not influenced by sex or laying date (sex effect, $F_{1,97} = 0.189$, $P = 0.665$; laying date effect, $F_{1,97} = 0.421$, $P = 0.518$), with no significant interactions. Post-hoc (LSD) tests revealed these differences were the result of higher values of MCV (indicating poorer condition) and lower PMI (indicating lower protein reserves) at the largest colony, Foula, and that females had higher MCV values compared with males.

There was no significant differences in BMI as a result of sex, laying date or colony (sex effect, $F_{1,97} = 0.019$, $P = 0.892$; laying date effect, $F_{1,97} = 1.395$, $P = 0.241$, colony effect, $F_{3,97} = 2.653$, $P = 0.053$). There were no significant interactions. Female BMI values were very low at Foula, but males were in better condition than at either Hermaness or Fetlar (Table 5).

Table 4. Model outputs (from residual maximum likelihood generalized linear mixed models) investigating factors influencing the proportion of seabird prey in the diet of breeding great skuas over five years. All two-way interactions were non-significant.

	Model term	Wald	df	Wald/df	P	Parameter estimate (β)	SE
All colonies	Constant					−1.165	0.192
	Skua colony size ($\log_e$)	8.84	1	8.84	0.003	−0.557	0.187
	Year	14.68	4	3.67	0.005	0.6021	0.490
	Coast/area ratio	4.16	1	4.16	0.041	−0.371	0.182
Excl. Fair Isle	Constant						
	Skua colony size ($\log_e$)	6.01	1	6.01	0.014	−0.176	0.072
	Year	23.33	4	5.83	<0.001	0.575	0.530
	Coast/area ratio	0.70	1	0.70	0.402	−0.167	0.199

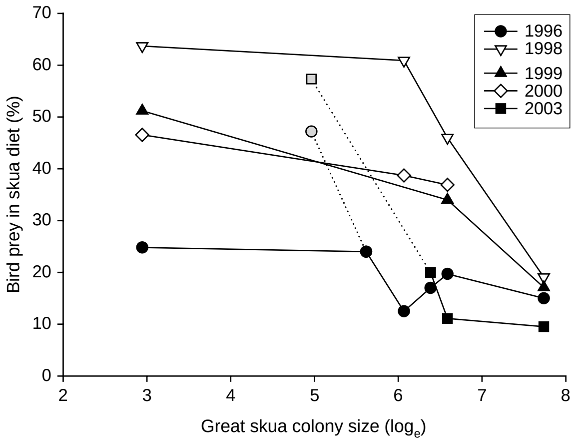

Fig. 3. Consumption of seabird prey by great skuas is negatively correlated with the number of con-specifics and reveals marked inter-annual variation. Years are labelled with different symbols. Note that great skuas on Fair Isle (shaded and with dashed lines) consumed a particularly large proportion of seabirds. This site has artificially low numbers of skuas and therefore this pattern fits with density-dependent food competition theory.

Discussion

Consumption of seabird prey

Our data provides evidence that prey consumption by great skuas varied with colony size and importantly that the proportion of seabirds consumed was negatively correlated with the number of con-specifics (Fig. 3). While the ratio of coast length to colony area had a significant effect on seabird consumption by skuas (Table 4), this explained less of the variance than the number of con-specifics, and the relationship was not apparent when one colony with artificially reduced numbers of skuas (Fair Isle) was excluded from the analysis (Table 4). Moreover, the ratio of skuas to seabirds is relatively consistent across colonies (with the exception of Fair Isle; Fig. 2), so that the negative relationship is not a function of fewer seabirds at large skuas colonies. One interpretation of these results is that large seabird colonies are associated with high fish availability and therefore at these sites skuas eat fewer seabirds. However given the evidence from other studies that piscivorous species may reduce fish availability by depletion or interference competition (Lewis et al. 2001, Ainley et al. 2004), it is more likely that skuas at large colonies would have reduced access to fish and therefore rely more heavily on seabirds for food. Further, if this were the case we would expect skuas to consume proportionately more fish and fewer seabirds at the largest colony with artificially reduced numbers of skuas (Fair Isle), but this is not the case. Therefore we believe the most parsimonious explanation of our results is that per capita access to seabirds is lower at large colonies than at small colonies.

A number of studies have already provided evidence that large colonies may deplete food or feeding opportunities (Furness and Birkhead 1984, Lewis et al. 2001, Forero et al. 2002, Ainley et al. 2004), yet this study is one of the first to provide similar evidence for a polyphagous species. Evidence that consumption of seabirds is limited at large conspecific densities was further corroborated by the finding that the proportion of seabirds consumed by skuas was higher than the annual mean at one colony (Fair Isle) where the number of great skuas has been artificially suppressed (Fig. 3).

The numbers of skuas and other seabirds at the colonies studied here remained relatively stable over time but despite this, the proportion of seabirds consumed varied significantly among years (Table 4, Fig. 3). We believe these differences reflect changes in the availability of alternative prey (mainly forage fish such as sandeels and fishery discards; Votier et al. 2004c). Despite annual variations in predation rates, the influence of colony size on seabird consumption remained remarkably consistent over time (Fig. 3), with no significant interactions (Table 4).

One way in which an increase in great skua density might decrease per capita seabird prey availability is via interference competition. Skuas regularly fight over

Table 5. Descriptive statistics for adult body condition measures of breeding male and female great skuas sampled at four different sized colonies during 2003 (mean ± SE, sample size in parenthesis). See main text for details of the body condition measures.

Condition measure	Sex	Colony			
		Foula	Hermaness	Fetlar	Fair Isle
Mean corpuscular volume (MCV)	Male	194.17 ± 18.32 (12)	189.55 ± 19.57 (4)	183.40 ± 24.74 (4)	187.18 ± 18.15 (6)
	Female	211.73 ± 21.62 (31)	191.86 ± 17.54 (12)	187.74 ± 18.95 (11)	195.39 ± 17.54 (14)
Pectoral muscle index (PMI)	Male	−0.26 ± 0.28 (17)	0.66 ± 0.19 (4)	0.27 ± 0.57 (3)	0.16 ± 0.22 (6)
	Female	−0.39 ± 0.15 (31)	0.38 ± 0.30 (12)	0.25 ± 0.31 (11)	0.36 ± 0.29 (13)
Body mass index (BMI)	Male	0.017 ± 0.021 (17)	−0.0037 ± 0.025 (4)	−0.0075 ± 0.036 (3)	0.017 ± 0.021 (6)
	Female	−0.74 ± 4.62 (32)	0.011 ± 0.023 (12)	0.004 ± 0.026 (11)	0.009 ± 0.013 (13)

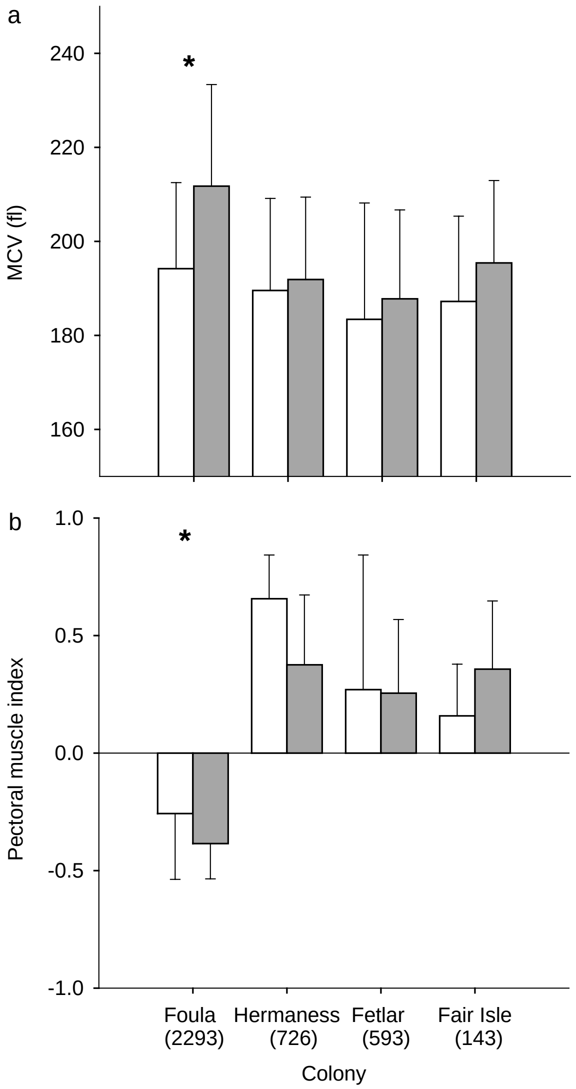

Fig. 4. High breeding density negatively influences the body condition of breeding adult great skuas. Adults were in poorer condition at the largest colony (Foula) as measured using (a) MCV (*, colony effect, $F_{3,94} = 5.144$, $P = 0.003$) and (b) pectoral muscle index (PMI) (*, colony effect, $F_{3,97} = 4.216$, $P = 0.008$). Open bars represent values for males, shaded bars for females and error bars are ± SE. Values beneath each colony name indicate number of breeding pairs. Low PMI values generally reflect depleted protein stores and elevated MCV values indicate reduced body condition, poorer quality, or both. Data were collected during the same breeding season (2003).

food items, and this is particularly so with conspicuous prey which cannot be easily swallowed, like a seabird chick for instance. As the number of skuas increases aggressive interactions are likely to increase and therefore reduce the opportunity or profitability of feeding on seabirds. The same scenario has been proposed as a proximate factor limiting south Polar skuas' *S. maccormicki* access to Antarctic petrels *Thalassoica antarctica* (Brooke et al. 1999). The geometry of the colony may also play a role in regulating skuas' access to seabirds; the ratio of coast length to colony area also had a significant effect on the consumption of seabird prey (although this effect was not apparent when Fair Isle was excluded from the analysis). However, colony geometry and interference may not be mutually exclusive - relatively shorter coastlines may result in more skuas forced to forage in the same area and thereby experience more intense competition.

Evidence of individual specialisation has been described from two colonies in this study (Foula in 1996, Bearhop et al. 2000; Hermaness during 1998–2001, Votier et al. 2004a), as well as for south polar skuas among colonies of Adélie penguins *Pygoscelis adeliae* in the Antarctic (Young 1994). However, the vast majority of skuas sampled here showed no evidence of this type of behaviour, and appeared to be facultative seabird predators (as evidenced by the high levels of annual variation in seabird consumption). Although specialist predators consume significant quantities of seabirds, they account for less than half of the numbers consumed by the population as a whole (Votier et al. 2004b). We know of no study investigating the relationship between colony size and dietary specialisation, but great skuas provide a suitable model for such research.

Early work in the Arctic (reviewed by Tuck 1960) showed that populations of predatory gulls may be regulated by the numbers of potential seabird prey - as evidenced by the 'very consistent' ratio between the number of Brünnich's guillemots *U. lomvia* and glaucous gulls *Larus hyperboreus* (which feed at guillemot colonies). We are uncertain whether the numbers of seabird prey at Shetland colonies play a direct role in great skua population regulation, but it is interesting to note the weak correlation between seabird numbers and skua numbers at the colonies studied here (excluding Fair Isle; Fig. 2).

Effects of colony size on performance

At the largest colony (Foula) we found that, for two separate indices, adult great skuas were in poorer condition than at three smaller colonies (Fig. 4). One interpretation of this finding is that intense competition for seabirds among skuas breeding at large colonies prevents them from buffering the effect of variations in the availability of fish prey. Low pectoral muscle indices indicate depleted body reserves of protein (Bolton et al. 1991), which may be the result of increased foraging costs (skuas feeding almost exclusively on other birds spend less time foraging than those feeding on fish;

Votier et al. 2004a), increased interference competition with conspecifics, or the result of consuming lower quantities of highly calorific bird meat (which has more than double the energy content of the other main prey item, fish; Votier et al. 2004b). However, increased competition for fish at larger colonies may also produce a similar pattern, the result of which may manifest as an increase in foraging range (Lewis et al. 2001) or increased competition at fishing boats discarding fish (Hudson and Furness 1988).

Elevated values of MCV may be related to poor individual quality, the effect of a period of stress, or both (Bearhop et al. 1999). While MCV has been shown to correlate with some measures of quality in great skuas (fledging success and hatching date; Bearhop et al. 1999) we have no other evidence to suggest that great skuas breeding at small colonies were phenotypically superior to those breeding at large colonies. Although there were clear effects on MCV and PMI, the results from the BMI data were equivocal. Adult female great skuas were in a poorer condition at Foula compared with the other colonies (Table 5), but the difference was outside the 5% alpha level of significance.

Despite 13 years of data, we found no relationship between colony size and reproductive performance in great skuas. However, breeding success may provide an unreliable fitness currency since adult skuas may buffer costs by increasing foraging effort or prey-switching to maintain stable breeding success (Hamer et al. 1991) – this situation is consistent with the reduction in adult body condition found at the largest colony.

Although we provide some evidence that adult body condition is poorer at the largest skua colony, we cannot establish whether this is a direct result of reduced access to seabird prey, or other costs associated with nesting at high population density. It remains the case however that at large colonies access to an important resource is limited. Detailed research investigating the role of alternate food availability in intrinsic density dependent population regulation of polyphagous seabirds would be most illuminating, but given the complexities involved it is unlikely to be easily achieved.

Finally, conspecific competition for seabird prey may interact with changes in the marine environment to shape seabird communities. Reductions in fishery discarding rates and sandeel availability in the north Atlantic may lead to an increase in predation by great skuas on other seabirds (Votier et al. 2004c). It is unclear whether this may result in higher predation rates at large skua colonies, or whether skuas may switch to breed at smaller colonies where competition is less intense – but results from this study suggest that predation rates will differ among different sized skua colonies. Nevertheless, either scenario will likely influence not only great skua population dynamics but also the dynamics of other internationally important seabird populations in the north Atlantic.

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Appendix 1. Details of seabird colony sizes sampled in this study. All measurements exclude areas of the respective sites where there is human habitation, which is unsuitable for any species of breeding seabird and are based on the map in Fig. 1, measured using Scion Image *http://www.scioncorp.com/pages/download_now.htm*.

Colony name	Colony area (km^2)	Coastline length (km)	Coast/area
Foula	13.57	19.06	1.405
Hermaness	14.38	15.02	1.045
Fetlar	23.09	42.81	1.854
Noss	3.86	8.72	2.259
Bressay	16.43	18.37	1.118
Fair Isle	9.06	16.25	1.794
Noness	1.75	9.2	5.257