Breeding skuas in Orkney: a 2010 census indicates density-dependent population change driven by both food supply and predation

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Abstract
Great Skuas *Stercorarius skua* and Arctic Skuas *S. parasiticus* were counted on their breeding grounds in Orkney during June 2010. Great Skua numbers had fallen by 23% overall since the previous census in 2000. However, the decline was not uniform across Orkney, the major colony on Hoy declining by 32% but with many smaller colonies actually increasing. Possible reasons for this difference are discussed. Arctic Skua numbers fell by 47% in the same time period and by 64% from their peak in 1992. We found evidence of intra-specific negative density dependence in trends of both skua species, suggesting that declines may have been driven by low food availability. In addition, we found a negative relationship between Arctic Skua trends between 2000 and 2010 and the numbers of Great Skuas present in each colony in 2000. These findings suggest that whilst scarcity of food may have contributed to Arctic Skua declines, predation by Great Skuas is likely to have played an additional role. Predation on Arctic Skuas, both adults and young, is also likely to be ultimately attributable to a scarcity of alternative fish prey for Great Skuas.

Introduction

The Arctic Skua *Stercorarius parasiticus* has a circumpolar breeding distribution at high latitudes, Scotland being at the southern edge of its breeding range; the Seabird 2000 census of 1998–2002 put its British population at 2,100 pairs out of a world population in the range of 85,000–340,000 (Furness & Ratcliffe 2004a). Great Skuas *S. skua* (hereafter 'Bonxies'), in contrast, have a very restricted breeding range in the northeast Atlantic with their population concentrated on Iceland, Shetland and Orkney. The British population at the time of the Seabird 2000 surveys was 9,600 pairs, 60% of the world population of just 16,000 pairs (Furness & Ratcliffe 2004b).

All-Orkney surveys of both skua species have been undertaken on five previous occasions. The first two of these, for the Operation Seafarer census in 1969–70 (Cramp *et al*. 1974) and in 1974–75 (Everett 1982), used the count unit of territorial pairs. In 1982, the colonies were counted again (Meek *et al*. 1985), using for the first time the 'apparently occupied territory' (AOT) methodology (Furness 1982). The 1982 counts were used as the basis for the Seabird Colony Register (SCR) census

Figure 1. Location of islands and key sites censused for skuas *Stercorarius* in Orkney during surveys in 2000 and 2010. Numbers refer to islands in Table 1a.

(Lloyd *et al*. 1991) and no additional complete survey was undertaken during the SCR years (1985–88) although Furness (1986) updated the 1982 data with estimates made in 1984. Further full surveys were undertaken in 1992 (Meek *et al*. 1994), and again in 2000 for the Seabird 2000 census (Mitchell *et al*. 2004).

Agricultural 'improvement' of moorland nesting habitat and increasing Bonxie numbers were identified as possible threats to Arctic Skua populations in Orkney and Shetland in the 1980s, as well as a reduction in the availability of sandeels *Ammodytes* sp., the main fish prey of other seabird species which Arctic Skuas kleptoparasitise (Meek *et al*. 1985; Lloyd *et al*. 1991). Habitat loss has since almost been eliminated in Orkney and is now considered an unimportant influence on Arctic Skua numbers and distribution. However, food shortage that impacted on various parameters of breeding performance, as well as adult survival, and competition for space with Bonxies and their predation of Arctic Skua fledglings were considered important factors in both island groups in the 1990s (Phillips *et al*. 1996; Furness & Ratcliffe 2004a; Davis *et al*. 2005; Dawson *et al*. 2011). By the time of the Seabird 2000 census, Arctic Skuas had declined in both Orkney and Shetland by 39% and 42% respectively since the SCR (Furness & Ratcliffe 2004a). Within Orkney, an even greater decrease at the largest colony, on Hoy, had been partly offset by some increases elsewhere, possibly due to recruits, and possibly even breeding adults emigrating from Hoy to other colonies, although there was no proof of this.

Bonxie numbers increased during the 1960s and 1970s probably due to the fact that sandeels, fisheries' discards and seabird prey all increased in the northwest North Sea during that period (Furness & Ratcliffe 2004b). From the mid 1980s, sandeel availability decreased, as did gadoid stocks, the latter leading to a decline in the amount of fish discarded from fishing boats. The increasing Bonxie population was therefore subjected to a much reduced food supply (Furness & Ratcliffe 2004b). In Shetland, this resulted in some years of increased non-breeding, reduced breeding success and, at least on Foula, reduced adult survival rates (Hamer *et al*. 1991; Catry *et al*. 1998; Ratcliffe *et al*. 2002). Despite this, the Seabird 2000 census recorded increases since the SCR of 10% in Orkney and 26%

in Shetland, although increases in Shetland were entirely at small or newly established colonies, the largest ones being stable or in slight decline, while in Orkney, the colony on Hoy had increased to become the second largest (after Foula) in Britain and Ireland (Furness & Ratcliffe 2004b).

Since 2000, breeding numbers and breeding performance of both skua species have been variable in both island groups, with a generally very poor season in 2004 (Mavor *et al*. 2005), and marked differences between colonies in other years (e.g. 2006; Mavor *et al*. 2008). In Orkney, observers familiar with the Bonxie colony on Hoy had commented for several years that it appeared to be declining with, for example, a 50% decrease between 2000 and 2006 in numbers in the RSPB reserve there, while away from monitored sites a general decrease in Arctic Skua numbers was suspected (Mavor *et al*. 2008). By 2010, another all-Orkney survey was clearly required in order to elucidate what was happening to the populations of both species, not least because Arctic Skua had been recently added to the Red List of Birds of Conservation Concern (Eaton *et al*. 2009).

Methodology

The Operation Seafarer surveys of 1969–70 concentrated on seabirds nesting on the coast and may well have missed a considerable proportion of Orkney's nesting skuas. The 1974–75 counts were of 'pairs holding territories' and therefore slightly different from the currently accepted counting unit, the apparently occupied territory (AOT). Counts from 1982 onwards have attempted to cover all suitable nesting habitat in Orkney and have used the AOT as the standardised unit, so should be directly comparable.

The 2010 methodology involved a single visit during June to all suitable skua breeding habitat, mapping AOTs, usually at a scale of 1:25,000, and calculating a population for each species for each island. For more intensive studies, three visits to each area of habitat are recommended but for a full survey of the whole archipelago, this was impractical. Surveys in previous years have also employed the single visit methodology.

In 2010, it was not possible to visit a small number of uninhabited islands that had in the past held small numbers of nesting skuas; details are given under 'Results'. All other skua colonies in the islands were visited. Hoy has been treated as one very extensive colony. Mainland, however, has several areas of suitable breeding habitat interrupted by extensive areas of agricultural land and these have been treated separately; the smaller islands are considered as individual colonies (Tables 1a, 1b). Whilst the objective of this study was simply to resurvey the skua colonies throughout Orkney, we did examine: i) whether the recent trends of both skua species exhibited intra-specific negative density dependence, suggesting that competition for food was driving population change, and ii) whether recent trends of Arctic Skuas showed inter-specific negative density dependence, suggesting declines were being driven by Bonxie predation of Arctic Skuas, adults and/or young. In the latter case, we also considered the interaction between these two effects, to determine if any effect of Bonxie numbers was greatest in situations of

greater food shortage. Since there were cases of both colony extinction and colony establishment between 2000 and 2010, the index of change we used was: Number of AOTs in 2010/(number of AOTs in 2000 + number of AOTs in 2010).

This returns a value between 0 (colony extinction) and 1 (colony establishment) where 0.5 represents no change in numbers. We used binomial errors General Linear Models to examine i) whether the change in Bonxie numbers at each colony between 2000 and 2010 was related to the number present in 2000, and ii) whether the change in Arctic Skua numbers at each colony during the same time period was related to the number of Bonxies present in 2000, the number of Arctic Skuas present in 2000 and the interaction between these two covariates. In 2000

Table 1a. The number of Great Skua *Stercorarius skua* and Arctic Skua *S. parasiticus* apparently occupied territories (AOT) recorded per island in each of the last four census counts in Orkney. n/c = no count. The % change between 2000 and 2010 is shown for islands where either or both species had counts of > 10 AOT in either year.

	Great Skua				% change	Arctic Skua				% change
Island	**1982**	**1992**	**2000**	**2010**	**2000–10**	**1982**	**1992**	**2000**	**2010**	**2000–10**
1 North Ronaldsay	0	0	0	1		1	1	1	1	
2 Sanday	0	0	0	2		25	28	21	6	-71
3 Papa Westray	2	3	8	29	+262	96	151	64	44	-31
4 Holm of Papay	0	0	0	0		1	2	0	0	
5 Westray	6	12	15	19	+27	45	98	88	27	-69
6 Eday	4	9	16	37	+131	80	106	69	56	-19
7 Calf of Eday	4	3	10	n/c		22	14	7	n/c	
8 Faray (& Holm)	0	0	0	1		1	2	0	0	
9 Stronsay	8	15	22	26	+18	44	40	29	10	-66
10 Linga Holm	0	0	0	n/c		2	0	1	n/c	
11 Holm of Huip	0	0	0	n/c		0	1	0	n/c	
12 Auskerry	1	1	1	1		2	2	1	1	
13 Rousay	13	31	81	85	+5	96	137	115	37	-68
14 Egilsay	0	0	0	0		1	0	0	0	
15 Wyre	0	0	0	0		3	2	1	1	
16 Holm of Scockness	0	0	0	n/c		1	0	0	n/c	
17 Eynhallow	1	3	4	9		19	13	9	8	
18 Gairsay	3	2	2	7		38	31	29	17	-41
19 Sweyn Holm	0	0	0	n/c		1	1	1	n/c	
20 Shapinsay	n/c	1	2	1		n/c	10	6	2	
21 Helliar Holm	n/c	0	0	1		n/c	1	1	1	
22 Mainland	24	25	50	81	+62	64	79	120	79	-34
23 Copinsay	0	0	0	5		0	0	0	0	
24 Hoy & South Walls	1,573	1,900	1,973	1,346	-32	406	211	72	16	-78
25 Fara	6	7	5	13	+160	28	20	13	22	+69
26 Cava	n/c	1	1	2		n/c	1	0	1	
27 Flotta	0	2	9	29	+222	26	80	66	47	-29
28 Burray (Hunda)	0	2	1	1		2	3	2	2	
29 South Ronaldsay	2	2	5	7		7	8	3	2	
30 Swona	n/c	n/c	3	5		n/c	1	1	0	
31 Muckle Skerry	n/c	n/c	0	2		0	0	0	0	
Totals	1,647	2,019	2,209	1,710	-23	1,011	1,043	720	380	-47

Table 1b. The number of Great Skua *Stercorarius skua* and Arctic Skua *S. parasiticus* apparently occupied territories (AOT) in different areas of the Orkney Mainland in 2000 and 2010. n/c = no count. The % change between 2000 and 2010 is shown for counts of ≥ 10 AOT in either year. Data for 2000 are from original field maps and are two Great Skua and one Arctic Skua AOT fewer than the published totals in Table 1a.

	Great Skua		% change	Arctic Skua		% change
	2000	2010	2000–2010	2000	2010	2000–2010
West Mainland Moors SSSI	34	54	+59	77	39	-49
Stromness SAC	9	10	+11	35	33	-6
Brown Hill	0	0		0	2	
Hobbister	2	5		0	0	
Head of Work	n/c	1		n/c	1	
Head of Holland	n/c	2		n/c	1	
Rose Ness	1	1		1	0	
Mull Head	2	8		6	3	

the size of Great skua colonies varied by three orders of magnitude: one colony held almost 2,000 AOTs, whereas all other colonies held fewer than 90 AOTs. In considering the number of Bonxies present in 2000 as a covariate of change, we therefore took the natural logarithm of Bonxie numbers in 2000. Since some sites held zero Bonxies in 2000 a value of one was added to all values before log transformation. Logarithmic transformation resulted in better model fit, judged from the deviance values and visual inspection of plots of residuals against predicted values. All models were implemented in SAS® v. 9.1.

Results

As noted above, a number of small, uninhabited islands could not be visited in 2010. These included Linga Holm, Holm of Huip, Holm of Scockness and Sweyn Holm all of which have held only single pairs of Arctic Skuas in the past. However, rather more importantly, the Calf of Eday was not reached; in 2000 this island held ten Bonxie AOTs and seven Arctic Skua AOTs. All other breeding areas were visited and counts of AOTs are shown in Table 1a.

For Bonxie, the Orkney total was 1,710 AOTs, a decline of 23% since the peak count of 2,209 AOTs during Seabird 2000 (Table 1a). The large colony on Hoy had declined to a greater extent than other, much smaller colonies, decreasing by 32% from 1,973 to 1,346 AOTs. In absolute terms, 627 AOTs were lost from Hoy but 129 gained elsewhere; 498 AOTs have therefore been lost from Orkney in the past decade. This represents some 5% of the British or 3% of the World population. Whilst the total number of Bonxies breeding in Orkney declined, breeding occurred for the first time in 2010 at six new locations (Table 1a). It was not surprising therefore that we found a significant relationship between the natural logarithm of colony size in 2000 and population trend between 2000 and 2010 ($\chi^2 = 105.30$, df = 1, $P < 0.0001$; Figure 2), since the six new colonies represent cases of maximum possible growth (index = 1) from the lowest possible base (0). However we also found negative density dependence among the 21 colonies that existed in 2000 ($\chi^2 = 92.32$, df = 1, $P < 0.0001$; Figure 2), suggesting the population trend of Bonxies was influenced by local competition for food.

Only 380 Arctic Skua AOTs could be located in 2010 (Table 1a), a 47% decline since Seabird 2000 and a 64% decline since the peak of 1,043 AOTs in 1992. The decline has been seen throughout Orkney but has been at its most severe on Hoy where, in 1982, there were 406 AOTs but only 16 in 2010, a 96% decrease. However, the possibility should be borne in mind that 2010 was a year in which many Arctic Skuas may have simply not attempted to breed, a phenomenon known elsewhere in its range (Mavor *et al*. 2005).

There were sufficient data from 25 colonies to examine the effect of Arctic Skua and Bonxie numbers in 2000 on Arctic Skua trends between 2000 and 2010. Univariate analyses indicated that changes in Arctic Skua numbers were very strongly related to numbers of both species in 2000 (Figures 3 & 4), with a marginally stronger association with numbers of Bonxies (log transformed) than Arctic Skuas ($\chi^2 = 22.47$, df = 1, $P < 0.0001$ and $\chi^2 = 17.73$, df = 1, $P < 0.0001$ respectively). However, there was a very high degree of correlation between numbers of Bonxies and Arctic Skuas across colonies in 2000 ($R^2 = 0.61$), so to examine whether there were both inter- and intra-specific effects on Arctic Skua declines we used a Type 3 multivariate analysis to determine the significance of the relationships (i.e. controlling for the effect of the other species). We found that there was still a significant effect of log transformed Bonxie numbers in 2000 when controlling for the effect of Arctic Skua numbers in 2000 ($\chi^2 = 7.91$, df = 1, $P = 0.005$), whereas the reverse was not the case: the relationship between size of Arctic Skua colonies in 2000 and the extent of their subsequent declines was marginally non-significant ($\chi^2 = 3.18$, df = 1, $P = 0.07$), once the relationship with Bonxie numbers was included in the model.

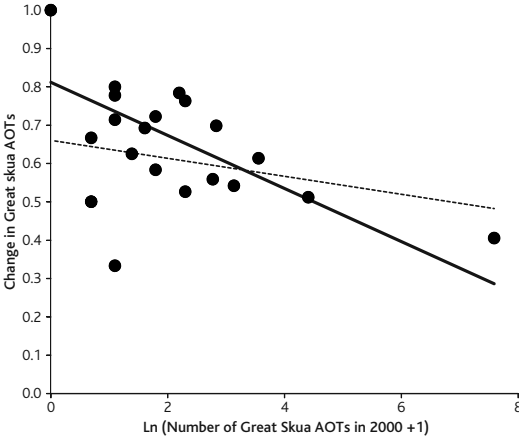

Figure 2. Change in size of Great Skua *Stercorarius skua* colonies in Orkney between 2000 and 2010 in relation to their size in 2000. Change in colony size is computed as the number of AOTs in 2010/(the number of AOTs in 2000 + the number of AOTs in 2010). Note the use of a log scale for Great Skua AOTs in 2000. Solid line shows linear regression including the six cases of colony formation ($x = 0.0$, $y = 1.0$). Dashed line shows linear regression excluding these cases.

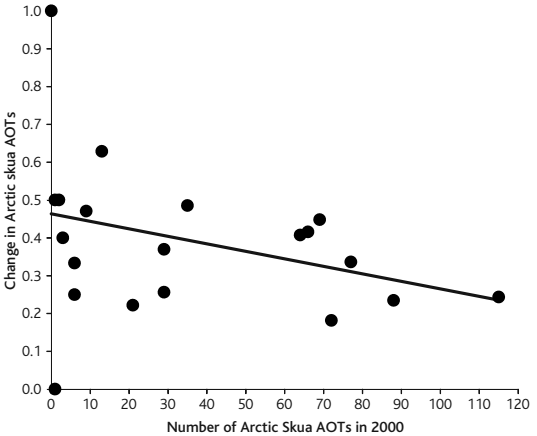

Figure 3. Change in size of Arctic Skua *Stercorarius parasiticus* colonies in Orkney between 2000 and 2010 in relation to their size in 2000. Change in colony size is computed as in Figure 2.

The pattern of Arctic Skua declines in Orkney is potentially heavily driven by the colony at Hoy which held 89% of Orkney's Bonxies in 2000. We therefore also considered inter- and intra-specific effects for all colonies except Hoy. In contrast to the results above, we found stronger univariate effects of Arctic Skuas than Bonxies on Arctic Skua declines (χ^2 = 15.91, df = 1, P < 0.0001 and χ^2 = 9.70, df = 1, P < 0.002 respectively). This was supported by multivariate modelling to control for the effect of the other species: for colonies away from Hoy, Arctic Skua declines were significantly related to Arctic Skua numbers in 2000 (χ^2 = 6.36, df = 1, P = 0.01), but not to Bonxie numbers (χ^2 = 0.15, df = 1, P = 0.69). Taken together, these analyses indicate that at the scale of the entire archipelago, Arctic Skua declines are being primarily driven by negative interaction with Bonxies, rather than intra-specific effects. However, this pattern is dominated by the Hoy colony, where Bonxie numbers are extremely high. Away from Hoy, patterns of Arctic Skua declines are more closely related to intra-specific effects.

Discussion

The overall decline of Bonxies over the past decade in Orkney has been accompanied by a marked redistribution of the breeding population. Many of the outlying, smaller Bonxie colonies have increased and six new locations have been colonised (Table 1a).

Seabirds nesting in the northern isles of Scotland have been experiencing food shortages for the last 20 years as a result of a lack of Lesser Sandeels *Ammodytes marinus*. Food shortage has been shown to have a very large impact on seabird breeding performance elsewhere in the North Sea (Frederiksen *et al*. 2006; Heath *et al*. 2009). Although there is good evidence for a large role of climate-induced oceanographic change in reducing the abundance and species composition of the zooplankton on which sandeels feed (Arnott & Ruxton 2002; Frederiksen *et al*. 2006; van Deurs *et al*. 2009), there is also evidence of top-down effects (fisheries, predation) in determining sandeel abundance (Frederiksen *et al*. 2007) and seabird breeding performance (Frederiksen *et al*. 2004, 2008) in the North Sea.

Here we have found evidence that population change of both Bonxies and Arctic Skuas in Orkney has been influenced by density dependent processes, suggesting that competition for food at a local (colony) level has been a driver of population change. Amongst Bonxies, this has been expressed as a redistribution away from the main stronghold of Hoy, with the establishment of new colonies and increase in size of existing smaller ones elsewhere.

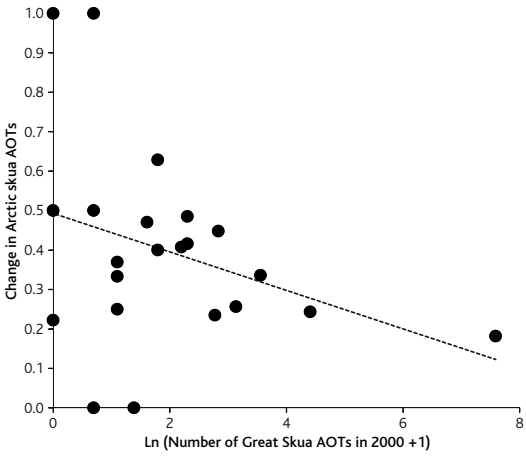

Figure 4. Change in size of Arctic Skua *Stercorarius parasiticus* colonies in Orkney between 2000 and 2010 in relation to numbers of Great Skuas *S. skua* at the same colony in 2000. Change in colony size and number of Great Skua AOTs are computed as in Figure 2.

In periods of severe food shortage, when neither sandeels nor fisheries discards are readily accessible, it is known that Bonxies turn to other seabirds as prey and will also become cannibalistic and prey on the chicks in neighbouring Bonxie territories (Hamer *et al*. 1991). Density-dependent competition for food may result in reduced territory attendance (Hamer *et al*. 1991) and thus facilitate cannibalism. It is probable that such cannibalism is more prevalent in high density nesting areas than in lower density ones (R. W. Furness pers. comm.).

The mechanism of population redistribution remains unclear. Great Skuas are known to be highly site faithful (Furness 1987; Hamer *et al*. 1991; Klomp & Furness 1992), and it seems unlikely that established breeders on Hoy would abandon the colony to relocate elsewhere. The scale of the decline on Hoy (3.75% per annum since the census in 2000) could be accounted for by low breeding success, or dispersal of recruits raised on Hoy to other colonies, without the need to invoke emigration of established breeders or reduced adult survival.

Arctic Skuas have been declining in Orkney for some time and at least since the mid 1990s. This has undoubtedly been, at least in part, the result of food shortages. The main seabird species targeted in Orkney by the kleptoparasitic Arctic Skuas are Arctic Tern *Sterna paradisaea* and Black-legged Kittiwake *Rissa tridactyla*, two seabird species that have undergone among the most severe declines in Orkney in recent years (Mavor *et al*. 2008; Williams 2010, 2011). Whilst the high correlation between numbers of Arctic Skuas and Bonxies across colonies made it difficult to disentangle inter- and intra-specific drivers of decline, away from Hoy we found a negative relationship between Arctic Skua numbers in 2000 and subsequent colony trends, suggesting that competition for food resources among breeding pairs was linked to the rate of population decline at a colony level. Analysis of the entire dataset, including Hoy, suggested that the strongest driver of Arctic Skua colony trend was the number of Bonxies present in 2000. Arctic Skuas and Bonxies often nest in close proximity and Arctic Skuas breeding in large Bonxie colonies showed larger declines than those nesting in smaller Bonxie colonies. In the light of observed predation of Arctic Skua adults and young by Bonxies, this behaviour presents the most likely mechanism to explain the observed relationship rather than competition for food or nesting territory. As long ago as the early 1990s, the Arctic Skua colony on Hoy was undergoing a major decline at a time when most other colonies in Orkney were at least stable or increasing quite markedly (Table 1a). Much of the Hoy decline was believed to be due to predation pressure by Bonxies on Arctic Skuas operating mainly late in the breeding season when newly fledged Arctic Skuas are easy prey for the larger species (pers. obs.). It is perhaps significant that the Flotta Arctic Skua colony, that closest to Hoy, was the colony that grew faster than any other between 1982 and 1992, presumably as Arctic Skuas from Hoy sought a safer breeding refuge.

Now that the current population status of both the skua species in Orkney has been clearly established, it would be extremely valuable for the current position in Shetland to be elucidated. We recommend that a survey of Shetland's skuas is undertaken at the earliest opportunity.

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