THE BREEDING ECOLOGY OF GREAT AND ARCTIC SKUAS ON HANDA ISLAND 2003

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SUMMARY

The breeding ecology of the expanding Great and Arctic skua colony on Handa Island, Sutherland was examined in 2003. Both populations were monitored through the entire breeding season to determine hatching, fledging and overall breeding success, and the effects of territory density and inter- and intra-specific interactions. Monitoring of chick diet and development, and territorial attendance by parents, were also initiated, and chicks were ringed. Skua territories now cover most of the interior of the island. In 2003 there were 202 Great skua breeding pairs (3% of the world population), and 33 Arctic skua breeding pairs. The Great skua population has doubled in the last 12 years; Arctic skua numbers have remained fairly stable, but territory density has increased. This year, both populations experienced a poor breeding season for differing reasons. Great skuas suffered a high rate of chick loss, probably due to predation by Great black-backed gulls and other Great skuas. Among the Arctic skuas, productivity was high, but many fledglings were predated by Great skuas within a few days of beginning to fly. These high levels of predation occurred in spite of the fact that food availability generally appeared to be good throughout the season. Other possible explanations for the losses are discussed, and topics for further research are highlighted.

CONTENTS

1. Introduction

Skuas are provocative birds. To some, they are magnificent 'seabirds of prey' of enormous charisma. To others, they are large annoying pests who offend with their aggression towards people and killing of other birds. To the biologist and conservationist, they are fascinating and important study subjects for a number of reasons, both theoretical and practical. For example, Arctic skuas *Stercorarius parasiticus* display a unique evolutionary adaptation in being able to acquire their food all the year round by stealing it from other birds in flight (kleptoparasitism), often at the end of a spectacular chase[1]. Arctic skuas also maintain an extreme variation in plumage colour, their underparts ranging from dark grey-brown to white, the function of which remains unexplained[2]. The role of the skua in the marine ecosystem, often as the top predator, is an important and sometimes controversial issue: they form large breeding colonies, often close to the colonies of other seabirds upon whom they prey or kleptoparasitise, and their impact on these populations is contentious[3,4]. Skuas' position at the top of the food chain also means they can be useful indicators of the health of the marine ecosystem as a whole[5]: they can be monitored in terms of their breeding performance[6], diet[7], foraging effort[8], survival rates[9], and even for levels of pollution in their bodies[10]. Finally, and perhaps most importantly, certain skua species, e.g. the Great skua *Catharacta skua*, are themselves classified as endangered[11].

Over the last four decades, Handa Island in north-west Scotland has become home to a dense breeding colony of Arctic skuas and Great skuas (also known as "bonxies", a Shetland word meaning 'dumpy, untidy women'). From a conservation perspective, it is an important site for all of the reasons outlined above. Firstly, over 200 pairs of Great skua breed annually, or approximately 3% of the world population of this endangered species. Secondly, these are the largest breeding populations of both skua species in the Outer Hebrides, where a huge and diverse array of seabirds come to breed each year, supported by the traditionally rich feeding grounds of this region of the North Sea. And thirdly, on Handa, the two skua species have formed predator-prey relationships with a nationally important community of seabirds, including the largest breeding populations in Britain and Ireland of both Common guillemots *Uria aalge* and Razorbills *Alca torda*[12].

The Handa Great skua colony has doubled in numbers since 1991, and the birds' territories now cover most of the interior of the island. The 36 Arctic skua pairs, with only a few exceptions, have been pushed into a densely clustered area in the east of the island, surrounded by breeding bonxies. Very little research has been carried out on these birds, and therefore there is a paucity of sound information on which to base assessments of the Handa skua colonies, their role in the Handa seabird community and impact on the other populations, and trends in the regional marine ecosystem.

The general aims of this study were to provide vital baseline data on the two skua populations in order to begin plugging the gaps in our knowledge, to provide a rigorous scientific foundation for sound assessment of skua ecology on Handa and related issues, both current and those which may arise in the future. It was also hoped that this year's results would highlight those questions which will need to be answered through further research.

Therefore this year I examined the breeding ecology of Great and Arctic skuas on Handa, looking at timing of breeding, breeding success, causes of breeding failure,

territory density, and interactions within and between the two skua species and with one close neighbour, the Great black-backed gull *Larus marinus*. The great majority of chicks which reached fledging were ringed, in collaboration with members of the Highland Ringing Group, in preparation for further long-term monitoring of adult survival rates. In addition, the monitoring of two further indicators of both local food availability and predator-prey interactions with the local seabird populations, was initated: of territorial attendance by parents of both skua species while rearing chicks, and of diet in the Great skua (in collaboration with L. Williams).

2. Handa Island

Handa Island comprises 363 hectares of Torridonian sandstone and lies 0.4km off the coast of Sutherland, at a latitude of 57°N (Grid reference NC 138480). There are areas of maritime heath, coastal grassland or machair, sand dunes, sandy and rocky beaches, and sea cliffs to over 100m. The quality and diversity of these coastal habitats, and the assemblage of breeding birds which they support, are considered nationally important. The whole island is a Site of Special Scientific Interest (SSSI) and, on the basis of the nationally and internationally important populations of breeding seabirds, a Special Protection Area[13]. These critical populations include approximately 30-40 pairs of Arctic skua (>1% of the EC population), 200+ pairs of Great skua (3%), 10,000 pairs of Black-legged kittiwake *Rissa tridactyla* (1%), 90,000 Common guillemot (>10%) and 15,000 Razorbill (>10%)[12,14,15]. Handa is the largest colony in Britain for both guillemots and razorbills, and the fourth largest kittiwake colony in Britain[11].

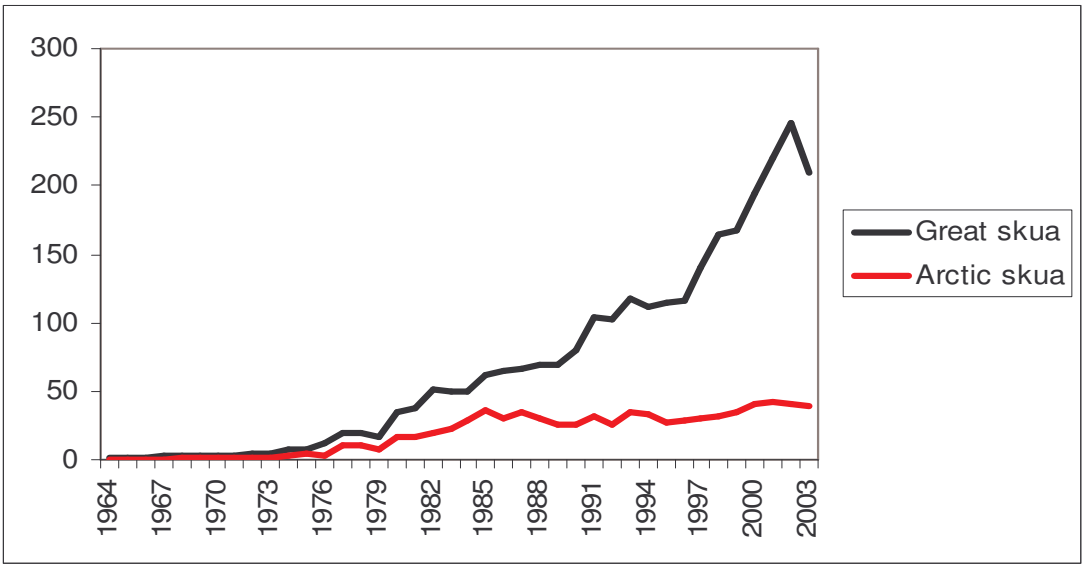
The island is owned by Dr. Jean Balfour. From 1961 until 1991, it was managed as a reserve by the Royal Society for the Protection of Birds (RSPB). Since that time, it has been managed in agreement with the landowner by the Scottish Wildlife Trust. From March until September each year, there are a warden and a succession of volunteers staying on the island, monitoring the wildlife and managing the visitors. Up to 6,000 visitors visit the island each year on day-trips, touring a path that takes in about two thirds of the island, including the main breeding cliffs.

3. Handa's colonisation by skuas

Until the 1960s, there were no skuas breeding on Handa. Then in 1964, a pair of Great skuas nested on the island for the first time[16]. This occurred in the context of a general pattern of dispersal and colonisation of new sites by bonxies in the course of the last century, from their British stronghold in the Shetland Isles[1]. Gradually they were joined by other breeding pairs, and by 1980 there were 34 apparently occupied territories (AOTs). Throughout the 1980s and 90s, the colony continued to grow steadily. By the summer of 2002 over half of the island's interior was occupied by bonxies, and the census had recorded 245 AOTs.

In 1968, the first pair of Arctic skuas nested, and until 1974, a solitary pair bred. Their numbers then began to increase slowly, and reached a total of 36 AOTs in 1985. Pushed by the increasing numbers of breeding Great skuas into a small concentration of territories around Bothy Loch, with only a handful of isolated territories elsewhere on the island, their numbers have remained fairly stable at around 30-35 AOTs up to the present day (fig. 1).

Fig. 1 Numbers of Great and Arctic skua AOTs on Handa Island, 1964-2003



4. Previous monitoring and research

Very little research has been carried out on the skuas of Handa, perhaps because until recently, their numbers were few, and their ecological impact on the island was considered insignificant. However, there are some data available from previous years, in particular the numbers of breeding pairs. As shown above, there are records of the early years of the Handa skua colonies, and from 1974, the various RSPB and SWT wardens of the island have charted their growth by counting the number of AOTs each year[13] (Appendix 1). In addition, in recent years, territories were mapped in 1995, 2000 and 2002 [14,17].

Table 1. Summary of results of productivity study by Applied Ornithology Unit, University of Glasgow, 1989-91[18,19,20]

	Number of nests monitored	Mean clutch size	Hatching success (%)	Fledging success (%)	Chicks fledged per nest
Great skua					
1989	68	1.84	88.0	77.3	1.25
1990	80	1.89	79.5	80.0	1.20
1991	89	1.93	82.6	80.3	1.28
3-year mean		**1.89**	**83.1**	**79.3**	**1.24**
Arctic skua					
1989	20	1.90	86.8	75.8	1.25
1990	21	1.95	80.5	75.8	1.19
1991	28	1.89	84.9	84.4	1.36
3-year mean		**1.91**	**84.1**	**79.3**	**1.28**

The only work on productivity (since each population began to exceed a handful of pairs in the late 1970s) took place from 1989-1991[18,19,20]. For each of these three years, Dr. R.W. Furness of The Applied Ornithology Unit of the Department of Zoology, University of Glasgow, was contracted to monitor the breeding success of all the seabirds on Handa. Table 1 summarises the results obtained by Dr. Furness and his colleagues from these years.

In addition, between 1989 and 1993 Dr. Furness oversaw the colour-ringing of a total of 57 adult bonxies breeding on the island. The apparent survival of these birds, based on the knowledge that most bonxies return faithfully to the same colony each year[21], continues to be monitored by Dr. Furness with the help of successive wardens of the island.

In 2000, I undertook a study on Handa into the relationship between plumage polymorphism in Arctic skuas and their kleptoparasitic feeding behaviour. By observing over 1500 attacks by Arctic skuas on other seabirds returning to the island with food for their chicks or mates, I discovered that the great majority of attacks (94%) were on guillemots, as might be expected given that they are by far the most numerous species on Handa. They were also seen attacking razorbills, puffins *Fratercula arctica*, kittiwakes, fulmars *Fulmarus glacialis*, and a peregrine *Falco peregrinus* carrying a guillemot chick. Overall, the Arctic skuas are successful in provoking their victim to drop their food on only one in every ten chases. I then tested two hypotheses that individual Arctic skuas' colouration might confer some advantage in attaining food. In fact, there were no detectable differences in the outcome of attacks under a variety of different circumstances by birds of different morphs, and the hypotheses were rejected[1].

5. Methods

This year's warden, Lizzie Williams, arrived on Handa at the end of March, began the mapping of Great skua territories on 11th May, and found the first nest containing eggs on 15th May. I arrived on the island on 26th May, and worked on the skuas until 15th August, whereafter the warden continued monitoring the late breeders until the end of August. Thus the entire breeding season of both skua species was observed from start to finish. Bad weather while birds were brooding eggs or small chicks prevented me from doing fieldwork on a total of 7 days, but I was nevertheless able to complete 64 days in the field.

To provide a rough picture of the colony, and for the purpose of testing the relative efficacy of censusing methods on Handa, all apparently occupied territories were mapped in May, following Walsh *et al.*[22]. This is the standard methodology which has been used by wardens and fieldworkers in recent years[14,17], which involves walking transects at 200m intervals, stopping regularly to thoroughly scan the surrounding areas, and recording all evidence of territorial skuas.

The nests of each breeding pair were then located. Like all birds, skuas are extremely mindful of not betraying the precise location of their nest, and while you are in view, will either circle their territory continually, or settle on a prominent rock or clump of heather up to 50m from the nest. Furthermore, they react to the actions of their neighbours, causing a 'domino effect' of birds leaving their nests as (and sometimes even before) you enter an area. The increased density of the breeding birds on Handa exacerbates this problem. In order to overcome their vigilance and cunning, two main tactics were adopted. The first was to approach the territory from a blind spot (e.g. from behind a hill), and then walk directly to the spot from which the sitting bird had flown up. Often, however, this was not possible because of the local topography. The second method, only employed on warm dry days, involved taking up a vantage point far enough from the territory (>100m), sitting motionless in the heather, and waiting. Invariably, the sitting bird will eventually give up and return to brood its eggs. This can take up to half an hour, and it is therefore helpful to choose vantage points which are in view of a number of territories, sketch their locations in relation to landmarks as they are revealed (using a compass), and then approach a number of nests in one go.

Each nest was given an individual code, with reference to the existing grid posts which physically divide the island into four-hectare quadrats. The nest was then marked with a 1m tall bamboo cane (placed 5m away), and its location recorded onto a Garmin 12 hand-held GPS.

Each territory containing a nest was subsequently visited every 5-10 days in the case of bonxies, and every 5-7 days in the case of Arctic skuas. On each visit, the following observations were recorded: time of day, number of eggs and/or chicks present, and number of adults present. (The resulting data on territorial attendance are not presented as they are meaningless *per se*, but will form the basis of an index for comparison with attendance rates in future years). The great majority of chicks were ringed with standard BTO metal rings, with the assistance of members of the Highland Ringing Group. In addition, a number of chicks of known age were regularly weighed and measured, and all indications of diet were recorded, either regurgitates or fresh food delivered by a parent. Visits to each territory continued until the offspring had "fledged",

or until it had been noted that the breeding pair had failed on three consecutive visits. In this study, a bonxie chick was recorded as "fledged" when it had reached 42 days. All the Arctic skua fledglings were observed within one or two days of beginning to fly.

Having returned repeatedly to the more difficult territories harbouring the most elusive chicks, I estimate that the outcomes of 98-100% of the Bonxie breeding territories were accurately recorded. In the case of the Arctic skuas, 100% of the breeding territories were known, but three nests were situated too close to the nest of a pair of Red-throated divers *Gavia stellata* to be continually monitored. Of these, the outcome of one nest (coincidentally, the only Arctic skua nest to contain three eggs) remained elusive, and was excluded from all analysis of breeding success.

6. Results

6.1 The breeding populations

The initial all-island transect survey conducted in May gave a total of 224 Great skua AOTs. However, the subsequent thorough locating and marking of nests revealed a total of 209 Great skua AOTs. The transect survey therefore overestimated the size of the colony by approximately 7%. Among the 209 confirmed AOTs, seven pairs appeared to not lay eggs, giving a total of 202 breeding pairs.

There were 36 Arctic skua AOTs; three of these pairs appeared to not lay eggs, giving a total of 33 breeding pairs.

Table 2. Summary of Great and Arctic skua breeding statistics on Handa Island, 2003 (means ± standard error, sample sizes in parentheses).

	Breeding pairs	**Density (pairs per km^2)**	**Mean laying date**	**Mean clutch size**	**Hatching success (%)**	**Fledging success (%)**	**Chicks fledged per pair**	**Post-fledging mortality (%)**
Great skua	202	132 (202)	May 24±0.69 (150)	1.80±0.04 (127)	79.9 (184)	45.5 (165)	0.59±0.05 (202)	~0 (120)
Arctic skua	33	138[a] (26)	June 3±1.04 (29)	1.89±0.08 (27)	81.0 (42)	85.7 (35)	1.22±0.10 (32)	50-60 (39)

[a]Excluding outlying territories (see Section 6.2)

6.2 Territory density

Over the entire colony, Great skua pairs bred at an average density of 132 territories per km^2.

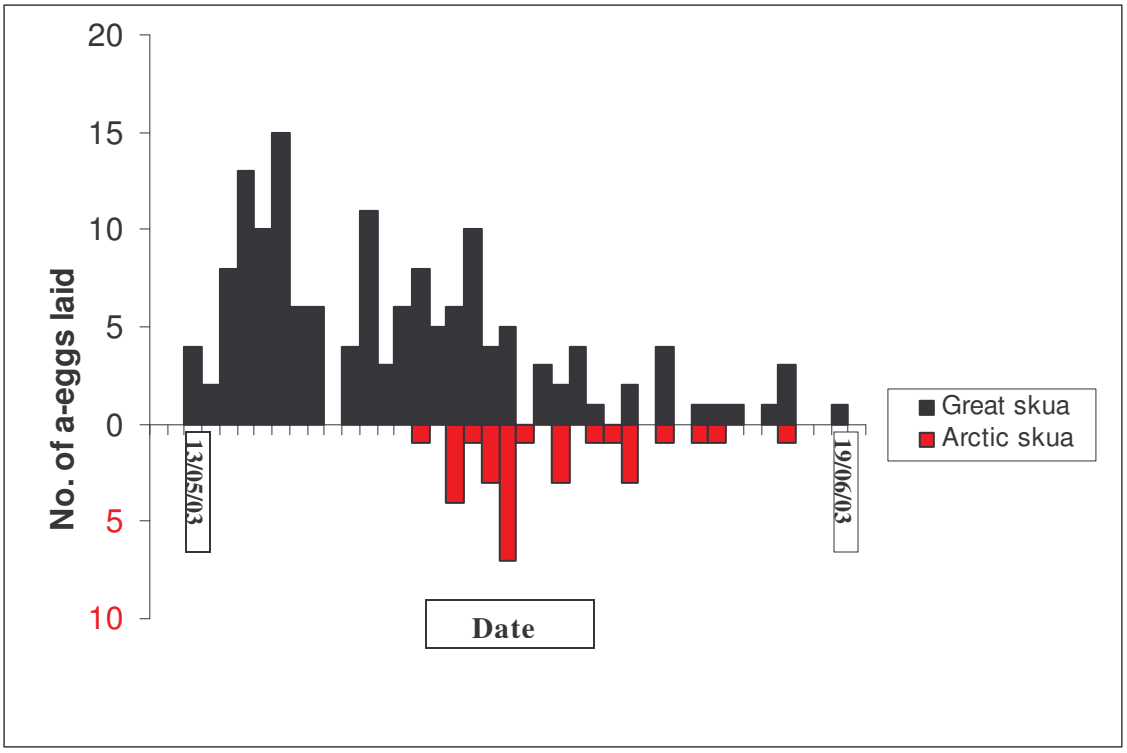
Among the Arctic skuas, 26 pairs bred in their stronghold in the east of the island, at a density of 138 territories per km^2. Ten other pairs held territories away from this stronghold in isolated positions surrounded by bonxie territories; including these pairs in the analysis gives a whole-colony density for Arctic skuas of 24 territories per km^2.

6.3 Laying dates

The first Great skuas laid their first egg (a-egg) on 13th May, and by 31st May, 84.0% of breeding pairs were brooding eggs. A minority of birds continued to lay up to 19th June (fig. 2). Mean laying date was May 24±0.69 (n=150).

The Arctic skuas have a more compact breeding season. The first birds laid on 26th May, and 58.6% of breeding birds were on eggs within a week of this date. However, there was a tail of later breeders, and the last bird laid on 16th June. As a result, mean laying date was June 3±1.04 (n=29).

Fig. 2. Timing of laying of a-egg by Great and Arctic skuas on Handa Island, 2003.



6.4 Clutch size

The following results consider only clutches recorded within one week (Arctic skuas) to ten days (Great skuas) of laying, to reduce bias caused by loss of eggs.

Among Great skuas, 78.7% of breeding females laid two eggs, 20.5% of breeding females laid one egg, and 0.8% (one bird) laid three eggs. Mean clutch size was 1.80±0.04 eggs (n=127).

Similarly, among Arctic skuas 78.3% of breeding females laid two eggs, 18.0% of breeding females laid one egg, and 3.7% (one bird) laid three eggs. Mean clutch size was 1.89±0.08 eggs (n=27).

6.5 Hatching and fledging success

Hatching success is expressed as the percentage of eggs laid that hatched out successfully. Fledging success is the percentage of hatchlings that fledged (i.e. reached 42 days old). In all cases, the samples used for analysis contain only those eggs and chicks whose fortunes were individually followed from start to finish.

Among the Great skuas, hatching success was 79.9% (n=184), while fledging success was much lower at 45.5% (n=165).

The Arctic skuas achieved hatching success of 81.0% (n=42), and fledging success of 85.7% (n=35).

6.6 Productivity/breeding success

As with other skua studies, productivity is expressed here as the mean number of chicks successfully fledged per breeding pair. Breeding success is an expression of the proportion of eggs laid which result in fledglings (with ‘eggs laid’ being calculated by multiplying the number of breeding pairs by the mean clutch size).

The Great skua colony of 202 breeding pairs produced a total of 120 fledglings, therefore productivity was 0.59±0.05 chicks per pair (breeding success 33.0%).

In the Arctic skua colony, 32 breeding pairs produced a total of 39 fledglings, therefore productivity was 1.22±0.10 chicks per pair (breeding success 64.5%)

6.7 Mortality factors: Great skuas

Great skuas suffered egg mortality of 20.1% (n=184), and then lost 54.5% (n=165) of their chicks. Table 3 indicates the reasons for these heavy losses. At the egg stage, the greatest contributing factor was the failure of eggs to hatch (13.6% of eggs laid). There was also some predation of eggs, and the rate given (5.4% of eggs laid) may be an underestimate, as predation of eggs within a few days of their being laid may have gone unrecorded if the parents then abandoned that nest site. However, skuas will often re-lay if they lose eggs early in the season[1], so in terms of the effect on productivity of the population, this potential bias should be insignificant.

Table 3. Causes of Great skua egg and chick mortality on Handa Island, 2003

	Mortality Factor	Number	Percentage
Egg stage (n=184)	Eggs predated	10	5.4% of eggs laid
	Eggs not hatching	25	13.6% of eggs laid
	Died hatching	2	1.1% of eggs laid
Chick stage (n=165)	Cause unknown	1	0.6% of chicks hatched
	Chicks ill/starved	5	3.0% of chicks hatched
	Chicks predated	84	50.9% of chicks hatched

At the chick stage, mortality was high (54.5% of chicks hatched), and the predation of chicks was clearly the major factor (93% of chicks lost).

To determine the age at which most chicks were predated, I considered 95 chicks that were seen at age 7-10 days, whose progress was successfully monitored every 5-7 days thereafter, up to "fledging". 74 of these chicks survived to 42 days, and only two had died of illness or starvation, giving a rate of chick predation of 22.1% between these ages. This indicates that of all the chicks that were predated, 73% were lost within the first 7-10 days after hatching, compared with 27% of all chicks lost to predation being taken after this age.

6.8 Post-fledging mortality: Arctic skuas

Arctic skua fledglings suffered significant mortality on or close to their natal territory in the first week after fledging, due to predation by Great skua adults. Two kills were observed, as well as a number of attacks which failed, usually as a result of vigorous aerial defence of the fledgling by its parents and other adult Arctic skuas. Out of the 39 chicks fledged by the whole colony, 13 carcasses (33.3% of fledglings) had been recovered by 15th August. Based on observations of those fledglings which were still present up to two weeks after fledging, and fledglings which were apparently missing, I estimate that 50-60% of the colony's fledglings were killed by Great skuas during their first few days of flying.

There was no evidence of any mortality of Great skua fledglings while they were still on Handa.

6.9 Ringing

106 Great skua and 27 Arctic skua pulli were ringed in 2003 with standard BTO metal rings by myself, Andrew Ramsay and Justin Grant of the Highland Ringing Group.

6.10 Colour-ringed birds

Of the 57 Great skuas given colour rings on Handa by Dr. Furness between 1989 and 1993 (see section 4, above), 9 birds were still breeding on the island this year: 5 from 1989, 2 from 1992, and 2 from 1993.

6.11 Non-breeding birds

At the breeding colonies of Great and Arctic skuas, non-breeding birds congregate in specific places, called 'club sites'[1]. On Handa, there are two Great skua and one Arctic skua club sites. However, one of the Great skua club sites (Hill Loch) is also used by breeding birds for the purposes of washing, and it is impossible to distinguish these birds from the non-breeders. However, as most breeding Great skuas return to their territory in the evening[1], it is likely that the birds attending the club at this time are the true non-breeders. The number of birds attending all of these sites was regularly recorded throughout the season.

At the Hill Loch site, up to 90 Great skuas were in attendance during the day throughout the season. Considering only those counts made after 1900 hours, the maximum number of birds recorded was 28, in both May and June. At the other Great skua club site, the maximum recorded count was 18 birds, on the 16th of July.

Attendance at the Arctic skua club site ranged from zero to a maximum of 7 birds in July.

6.12 Human sabotage

On 7th July, an Arctic skua nest 10m from the boardwalk was found sabotaged, presumably by a visitor to the island. Both eggs had been pierced by a narrow object, probably a pen.

7 Discussion

7.1 *Comparisons with other studies*

Table 4 shows how the current breeding statistics of Handa's bonxies compare with results from the Handa colony 12 years ago, and from two other colonies. The St. Kilda colony is of interest because its history mirrors that of the Handa colony. The first bonxies arrived and began breeding there in the 1960s, and the population subsequently expanded, at first slowly, and then more rapidly[26]. By 1996, when the study referred to here was carried out, there were 229 Great skua AOTs on St. Kilda. I have also selected for comparison the results from the classic Foula study of the mid-1970s because they are derived from the largest number of skua nests ever studied. At this time (unlike in recent years), though the composition of the diet may well have been different, the Foula population shared with the Handa population of 2003 a fairly consistent food supply throughout the breeding season.

Mean clutch size was relatively low on Handa this year, compared to the other studies. Although the sample included only those clutches which were recorded within ten days of being laid, it is possible that this low result is due to a number of eggs having been lost to predators within a few days of being laid.

Great skua hatching success on Handa has not changed significantly since 1991, and is comparable to results from other colonies.

Table 4. Comparison of key breeding statistics between the Great skua colony of Handa 2003, and other studies.

	Handa 2003 (n=127-202)	Handa 1989-91[18,19,20] (n=68-89)	St. Kilda 1996[23,24] (n=184-197)	Foula 1975-6[25] (n=881)
Mean clutch Size	**1.80**	1.89	1.85	1.90
Hatching success (%)	**79.9**	83.1	69.4	70.0
Fledging success (%)	**45.5**	79.3	70.1	93.2
Chicks fledged per pair	**0.59**	1.24[a]	0.92[b]	1.24

[a] Chicks "fledged or nearly fledged"[18]
[b] Value converted to estimate survival to 40 days

In contrast, fledging success (proportion of chicks hatched that survive to fledging) has fallen on Handa from 79% in 1989-91 to 45% in 2003. This figure is also much lower than fledging rates on either St. Kilda or Foula. As a consequence of this high rate of failure to rear chicks, overall productivity is also low in comparison to the

other studies. Indeed, the Handa 2003 mean of 0.59 chicks fledged per breeding pair is lower than any other figure published for a Great skua colony of more than 50 pairs[1].

In summary, Table 4 clearly shows that bonxies on Handa had a relatively poor breeding season, and that loss of chicks was the overriding factor.

In Table 5, the current breeding statistics for Arctic skuas on Handa are compared with the colony 12 years ago, and with a study on Foula from approximately ten years ago. The values given in the table are from 1994 (which are very similar to results from 1992 and 1993), with the exception of the post-fledging mortality value, which is a mean from 1992-93[6].

Clutch size, fledging and hatching success and overall productivity all compare well with both the situation on Handa in the early 1990s, and with the much larger study population on Foula.

There are no data available for post-fledging mortality on Handa prior to 2003. The current rate of loss of fledglings within their first week of flying on Handa is three times greater than it was on Foula in 1992 and 1993.

Table 5. Comparison of key breeding statistics between the Arctic skua colony of Handa 2003, and other studies.

	Handa 2003 (n=27-42)	Handa 1989-91[18,19,20] (n=20-28)	Foula 1992-4[6] (n=130-277)
Mean clutch Size	**1.89**	1.91	1.93
Hatching success (%)	**81.0**	84.1	77.7
Fledging success (%)	**85.7**	79.3	87.0 [b]
Chicks fledged per pair	**1.22**	1.28	0.90
Post-fledging mortality (estimate)	**50-60%**	-	19.3%

[b]Chick survival to one week

7.2 Why is bonxie fledging success so low?

The productivity of the Great skua colony on Handa has declined dramatically over the last 12 years, from a mean of 1.24 chicks fledged per breeding pair in 1989-1991, to 0.59 fledglings per pair in 2003. How do we explain this? If we compare the breeding statistics from these years, we find that hatching success has fallen only slightly from 83.1% to 79.9%, and the major difference is clearly in mean fledging success, which has fallen from 79.3% to 45.5%.

The results show 93% of this substantial loss of chicks is attributable to predation (Table 3). The first question to ask is: who is taking these bonxie chicks? Unfortunately, we have no direct observational evidence of kills, and must therefore consider each of the suspects in turn. The only possible non-avian predator of bonxie chicks present on Handa is the Eurasian otter *Lutra lutra* (Brown rats *Rattus norvegicus* were eradicated in 1997). Though there are a pair of otters breeding on Handa (L. Williams, pers. comm.), they rarely visit the interior of the island – most probably because of the reaction they would receive from the territorial bonxies! – and can probably therefore be discounted as a major factor.

Fig. 3 Bonxie chick (1 day old) and egg

Thus the bonxie chicks are being taken by one of Handa's larger avian predators: the Arctic skua, the Great skua, or the Great black-backed gull. On Foula in Shetland, Arctic skuas have been observed hunting bonxie chicks during only one of the last 30 breeding seasons, and this was considered an extremely risky strategy employed as a "last resort" during a period of crisis in terms of their usual food sources[27]. In 2003 on Handa, Arctic skuas had a productive breeding season, there was always at least one parent on territory throughout the season, and no starving chicks were recorded, indicating that food availability was good for them this year. Moreover, I observed that whenever Arctic skuas flew through a bonxie territory, the adult bonxies on territory never responded, suggesting they do not consider the Arctic skua a threat. Therefore I very much doubt that Arctic skua adults take any bonxie chicks on Handa.

Breeding bonxie adults are known to predate bonxie chicks from neighbouring territories on Foula[1]. Aside from the Foula studies, there is little detailed information on causes of chick loss in the Great skua, so it is impossible to know in how many populations, and under what circumstances, this behaviour occurs. Is it occurring on Handa? I think that it is likely. It is commonplace to observe aggressive displays, chases - and occasionally fights - between bonxies caused by intrusions into another's territory (although there are reasons for territorial intrusions among bonxies that do not involve chick predation[28]). I have also seen intruding adult bonxies cruising overhead and visually

scanning the moorland below. The fact that predation of conspecifics was detected at the Foula colony during the 1970s, when availability of that population's major food sources (sandeels and discards from trawlers) was adequate, shows that it is not a behaviour found only in populations struggling for food.

The other possibility is that Great black-backed gulls (GBBs) are predating bonxie chicks. On Handa, there is some strong circumstantial evidence to support this notion, and even to suggest they may currently be having a significant impact on the productivity of the bonxie colony. In 2003, 38 GBB pairs successfully reared between one and three chicks, and were therefore present on their territories for the entire duration of the breeding season of all but a very few (late breeding) bonxies. The majority of the GBB territories were on the moorland in the midst of the bonxie colony (fig. 4). Many GBB-bonxie interactions were observed throughout the season, usually between neighbouring birds, and always aggressive in nature. The most common interaction involved a GBB attacking a bonxie, and in every case it was the larger gull who came out on top. Preliminary analysis suggests that proximity of a bonxie nest to GBB nests has a negative effect on the number of chicks fledged by the bonxie pair. This effect appears to be stronger where there are more than one GBB nests in the local area. Each of the 2 shaded areas in fig. 4 contained 63 bonxie nests of known outcome. The south-western shaded area also contained 20 GBB nests, and every bonxie nest was within 150m of one of these GBB

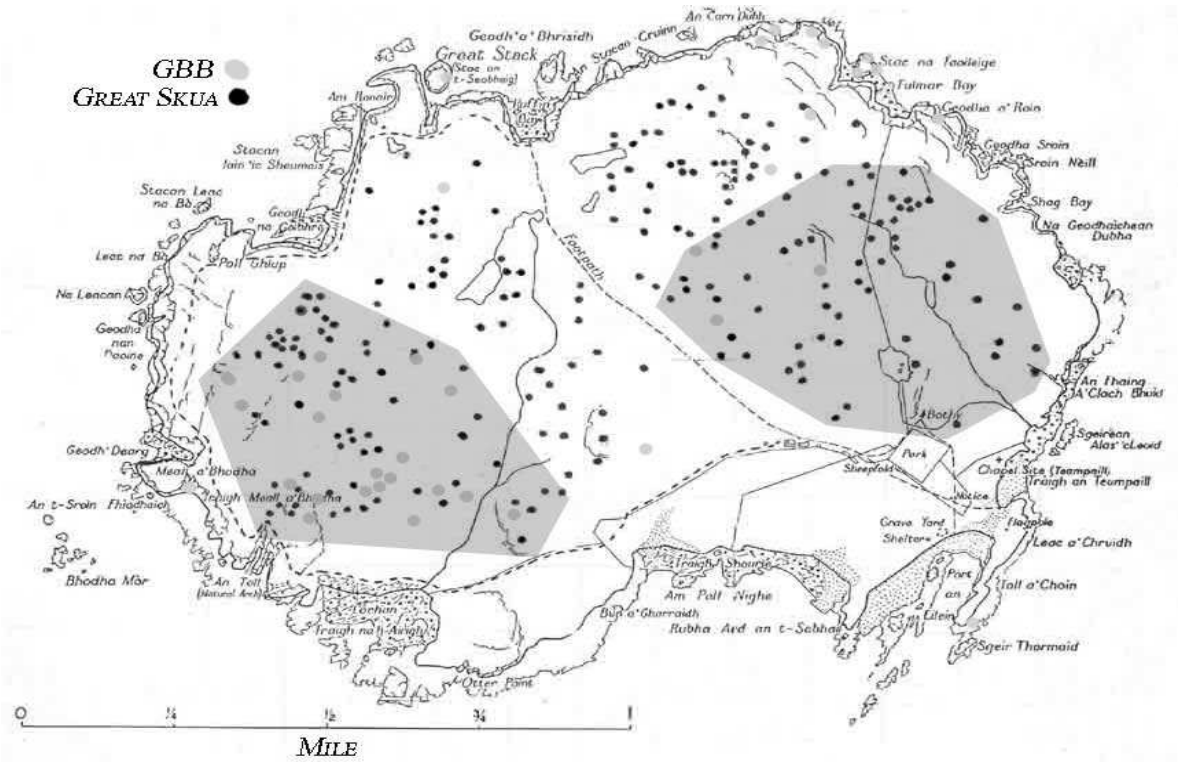


Fig.4 Great skua and Great-black backed gull (GBB) nests on Handa Island, 2003.

nests. Productivity among these bonxies averaged 0.33 chicks fledged per pair (range 0-2), which is significantly lower than the mean of 0.59 chicks for the colony as a whole (one-tailed test: $t=3.28$, d.f.=136, $p<0.001$). In contrast, in the eastern shaded area of the island, there were only 3 GBB nests. In this area bonxie productivity averaged 0.79 chicks per pair (range 0-2), which is significantly higher than the mean for the whole colony (one-tailed test: $t=1.95$, d.f.=98, $p<0.05$).

While there is a high incidence of breeding failure wherever bonxies have nested close to a GBB nest, there are also a number of cases of failure which are not close to a GBB nest, and cannot therefore necessarily be attributed to the gulls. It therefore appears likely that predation of chicks both by GBBs, and by other bonxies, accounts for the high rate of chick mortality on Handa.

It is interesting to note that the number of GBBs breeding on Handa has not been rising, but has steadily fallen from an average of 61 breeding pairs in the 1970s (range 48-75), to an average of 31 breeding pairs from 1994-2003 (range 26-38). In 1989, when bonxie productivity was measured at a mean of 1.25 fledglings per nest, there were 62 GBB pairs on the island, compared to 38 GBB pairs in 2003 when bonxie productivity was only 0.59 fledglings per nest.

Could the increased predation of bonxie chicks recorded in 2003 therefore be related to the increase in territory density over the last ten years as the colony has doubled in numbers? Evidence from elsewhere does not appear to support this hypothesis. The current density of 132 territories per km^2 on Handa is towards the lower end of the range of densities recorded on Foula (120-4000 territories per km^2), yet the rate of predation of bonxie chicks by conspecifics there is much lower than on Handa[1]. It therefore seems unlikely that territory density is an important factor in the relatively high rate of chick loss on Handa.

Though fledging success on St. Kilda (70.1%) is higher than on Handa (45.5%), it is still lower than that recorded on Foula (93.2%) when all three colonies were experiencing good food availability. Given the recent parallel histories of the Handa and St. Kilda colonies, one characteristic that we might expect them to share would be a young population of breeders, relative to the long established Foula colony. Furness[1] has shown that older, more experienced breeders are more successful in rearing chicks than younger, less experienced birds. It should be noted that it was extremely rare on Handa this year to find a bonxie territory which was not attended by one or both adults. Nevertheless, with predation pressure very high on Handa, a lack of experience among a number of young individuals in protecting their offspring against other bonxies and GBBs, may be an important factor in the overall breeding failure of the colony.

Bonxie chicks are more vocal and conspicuous, and therefore more vulnerable to predation in the first few days of their lives[1]. On Handa, 73% of chicks lost were predated in the first week to ten days of their lives, and perhaps most of these were lost within a few hours of hatching, when they can be especially noisy. However, a relatively high proportion of older chicks were also taken (13.7% of all chicks hatched), whereas only 5.4 % of all eggs laid were predated. It is a mystery why predation of chicks should be so high, and predation of eggs relatively low. Perhaps this is partly due to a strategy or preference by predators in favour of chicks over eggs. Alternatively, predation pressure on bonxie chicks may increase at different times because of the increased demand for

food from the predators' own growing chicks, or because of changes through the season in the availability of other food sources.

In summary, fledging success among bonxies on Handa is currently low because of high levels of predation by Great black-backed gulls, and probably also by neighbouring bonxies. If, as seems likely, this is a relatively young breeding population, loss of chicks may be exacerbated by the inexperience of many parents in the arts of deterring and repelling predators.

7.3 *The effects of bonxies on Arctic skuas on Handa*

(a) (b)

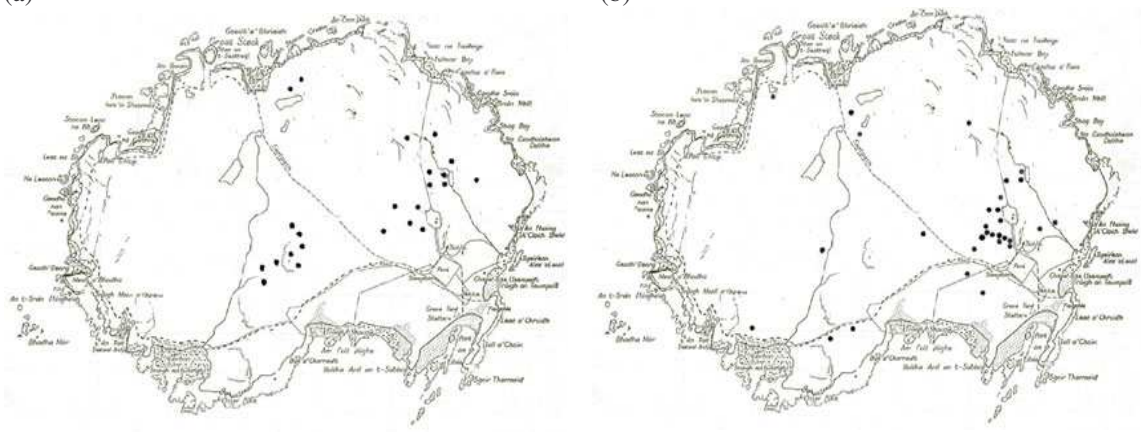


Fig. 5 Arctic skua AOTs on Handa Island in (a) 1983 and (b) 2003.

It is unusual in nature to find two closely related predatory species breeding colonially, and in close proximity to each other. For the smaller of the two species in particular, competition for resources and inter-specific interactions can bring a number of potential disadvantages which may have a serious impact on the population. So what effects do the more numerous Great skuas on Handa have on their smaller cousins, the Arctic skuas?

A study of the Arctic skuas' feeding behaviour on Handa in 2000 suggests that they do not compete with bonxies for food[2]. Arctic skuas were observed attacking other seabirds on over 1500 occasions, and only once (in the highly uncommon instance of Arctic skuas chasing a peregrine) was any intervention by a bonxie witnessed. Moreover, bonxies have never been observed stealing food from an Arctic skua, reinforcing this perception of niche separation.

On Handa, there is currently no evidence of predation of Arctic skua adults by bonxies. In 2003, all of the 78 adult Arctic skuas holding territory through the incubating and chick-rearing periods survived these two months, and no attacks on adults have been witnessed or reported either this year, or in recent years.

Fig. 5 illustrates how the distribution of Arctic skua territories on Handa has changed over the last 20 years. It appears that the Arctic skuas have been pushed into their current stronghold area around Bothy Loch, as the bonxie colony has expanded, and the Arctics are now breeding at a higher density as a result. It is possible that the presence

of breeding bonxies may limit expansion of the Arctic skua colony. However, the increase in Arctic skua territory density has not had a significant effect on productivity, which has only changed from 1.28 to 1.22 chicks fledged per pair since 1991. Eggs and chicks are either successfully defended, or are not a preferred food source of bonxies. Up to the point of fledging, the Arctic skua population of Handa are very successful breeders.

However, bonxies predate 50-60% of all Arctic skua fledglings while they are still on the island. This is high compared to Foula, where fledgling mortality has been recorded or estimated annually over the last half-century. In 1992 and 1993, a systematic study discovered that 19.3% of all Arctic skua fledglings were killed by bonxies[29]; in the 36 years prior to that study, the proportion killed fluctuated a lot but never exceeded 43%[1].

The same study of 1992-3 on Foula compared the breeding performance of Arctic skuas in high- and low-density areas. It showed that in higher density areas, Arctic skuas achieved greater short-term post-fledging survival than in the low-density areas, and this was attributed to the success of a united front of many adult Arctic skuas in being able to repel the attacks of the bonxies. On Handa, in the dense Arctic skuas' stronghold, this tactic was regularly adopted by the Arctic skua parents in defence of the fledglings, and it sometimes worked. However, the bonxies were often persistent and kills of fledglings were observed here, even in the course of the melée that is created when a bonxie is being attacked and pursued by up to eight adult Arctic skuas.

Thus the bonxies of Handa may be limiting the space which the Arctic skua breeding population may otherwise expand into, and may have increased the nesting density of the Arctic skuas, but they are not having a significant impact on their productivity. The main effect of bonxies on their smaller neighbours is through their predation of fledglings, though the reasons that this should occur at such a high level are unclear.

7.4 Potential effects of skuas on Handa's other seabird populations

Over the last ten years, the Great skua population of Handa has increased at an average rate of 6.52% per annum, to the current level of 209 pairs holding territory. In addition, the numbers of non-breeding birds attending the two club sites fluctuate, with recorded maximums at each site this year of 28 and 18 birds. Therefore approximately 450 bonxies are feeding on Handa, and from the skies and waters surrounding the island, from April/May until August/September, during which time 200,000+ individuals of other seabird species (guillemots, razorbills, puffins, kittiwakes, shags and fulmars) are also breeding on the island. The effect that Handa's bonxies may have on these important populations is currently open to speculation.

Great skuas, as a species, have a very broad diet which may include invertebrates, fish, eggs, birds, carrion and even plant material[1]. Some individuals are known to favour certain food items; thus a colony may include individual 'auk specialists' or 'crab specialists'. And there is also known to be great variation in diet between populations. In the 1990s studies were carried out on the diets of two different colonies by collecting the birds' pellets (each pellet is assumed to contain the remains of one meal). On St. Kilda, it was found that

44 to 65% of Great skuas' pellets contained seabirds, compared with only 4 to 12% of pellets collected on Foula[23].

Great skuas in particular are sometimes vilified by the public for their killing of other seabirds, and blamed for perceived declines in populations of their prey. Biologists at some sites have also expressed concern at the impact of bonxies[3]. On St. Kilda, a recent bioenergetics model estimated that the bonxie population there is consuming 40, 800 seabirds each year[30]. While certain parameters used in the model make it likely that the model overestimated the consumption of birds[7], the prediction is nevertheless cause for concern.

The issue is a complicated one. Under 'natural' circumstances the fate of a predator population is closely tied to the fate of its prey populations, which may fluctuate but will never be destroyed by its predators. Bonxies are currently dynamically altering their breeding sites, and preying on different animals in different places. Food supply is also highly variable in some areas of the North Sea. The preliminary results of a study initiated this year suggest that the diet of Great skuas on Handa may be closer in composition to the population of St. Kilda than Foula (L. Williams, pers. comm.). However, diet within a single population can also vary between years[31]. In order to understand the effects of Handa's colony of Great skuas on its other breeding populations, it is important that bonxie diet continues to be monitored and analysed in subsequent years.

7.5 Handa's skuas as environmental indicators

Great and Arctic skuas' trophic status makes them excellent candidates for indicating trends in the marine ecosystem[5]. They are sensitive to changes in their food supply, and in particular studies of skua populations can yield important indications of declines and recoveries of fish stocks. Skuas can also be good indicators of pollutants which accumulate at the higher trophic levels of the marine food web, such as mercury.

In the waters around Shetland, the traditional British stronghold for Great skuas, a crash in the sandeel *Ammodytes marinus* population in recent years continues to have a serious impact on many seabird populations, contributing to high levels of breeding failure[27]. It is possible that in the future areas more recently colonised, including North-west Scotland and St. Kilda, may become more significant to the future of Great and Arctic skuas in Britain, adding to their already critical importance for other seabirds. The Handa skua populations, reliant as they are on the seas of the Outer Hebrides, provide a good opportunity for monitoring environmental changes in this rich marine ecosystem.

Conclusions

The relatively recent arrival of the two skua species, and the expansion of their populations to present levels, has undoubtedly had a significant impact on the character of Handa. The noisy territorial displays of the bonxies, and spectacular aerial dogfights of the Arctics, now rank among the highlights of the reserve for many of its visitors. Between them, the skuas' territories now cover over 90% of the interior of the island, and only the dunes and machair in the south-east corner of the island remain uncolonised. The skuas have now taken up residence on nearly all of the suitable breeding habitat available to them on Handa. Still, there are areas where territory density is relatively low, especially in the east of the island, and there is therefore room for further increases in the numbers of breeding birds.

However, future levels of recruitment remain to be seen, since neither population is currently very productive. Arctic skuas are probably spatially restricted by the larger Great skuas which are now defending territories all around, and even in the midst of, their small colony. And although the Arctic skuas' colonial strategy appears to serve them well through the incubation of eggs and the rearing of chicks – suffering minimal losses at these stages – fledglings are being severely predated before leaving the island, suffering losses to Great skuas of up to 60%.

Proportionally, in terms of getting fledglings away, Great skuas are faring just as poorly. Productivity has fallen dramatically since the last time it was measured – when the population was less than half the size it is today – at the beginning of the 1990s. The main reason for this is not post-fledging mortality, but a failure by the breeding adults to protect their younger chicks from predators, namely Great black-backed gulls and other bonxies. This phenomenon may be a function of an expanding population skewed towards younger and relatively inexperienced breeders, though this is difficult to prove.

These conclusions must carry the caveat that they are based primarily on the results from only one breeding season. The intensive work carried out this year provides a snapshot in time of the breeding ecology of a dynamic and changing population, within a dynamic and changing ecosystem. Further work in years to come will hopefully determine whether these results reflect a short-term situation, or are indicative of longer-term trends.

This year's low rates of breeding success occurred in the context of sufficient food supply throughout the breeding season. Among both species of skua, the development of the great majority of chicks to fledging was normal, and indicative of a regular delivery of meals by their parents. Overall, a relatively low degree of foraging effort was required, as reflected in the constant attendance on territory of at least one adult throughout the season. The continued monitoring of the diet of Great skuas will reveal more on what adults are feeding to their chicks, as well as informing us of the impact they are having on Handa's other seabird populations.

This is an exciting and fascinating period in the ecological history of Handa, and the skuas are now a significant component of this ecosystem. In common with all the other seabird populations of Handa, with whom they are interdependent, the future of the Great and Arctic skua colonies cannot be taken for granted, and we must continue careful monitoring in order to have a chance of detecting and understanding population declines. There are many factors to consider. Habitat availability, the effects of territory density on

breeding, the predation of chicks and fledglings, and food supply are all likely to interact to determine the extent and success of Handa's skua populations in years to come.

9. Recommendations

1. In the light of the destruction in 2003 of Arctic skua eggs close to the boardwalk, volunteers should continue to be encouraged to patrol the path in the afternoon, throughout June and July, whenever time allows.
2. The annual monitoring of Great skua diet by the collection of pellets every ten days along one fixed transect line, and at one bonxie club site, is strongly recommended. This constitutes four to five hours of work every ten days, and could perhaps be included in the warden's work programme, to be assisted by the long-term volunteers.
3. To assist with the long-term monitoring of adult survival rates, an important variable affecting the skua colonies, a few hours each month could be spent by the warden searching the colony for colour-ringed birds.
4. Priorities for future research (Great and Arctic skuas): annual ringing of chicks; colour-ringing of more adult birds; continued monitoring of productivity and chick growth; spot-checks on territorial attendance; monitoring of contamination levels of mercury and other heavy metals.

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Photo credits

Front page, Great skuas: D. Mower
Front page, Arctic skua: D. Mower
P. 15, Bonxie chick and egg: B. Ramsay

APPENDIX. GREAT SKUA AND ARCTIC SKUA AOTs 1964-2003

YEAR	Great skua AOTs	Arctic skua AOTs	YEAR	Great skua AOTs	Arctic skua AOTs
1964	1*	0	1984	50	28
1965	1*	0	1985	62	36
1966	2*	0	1986	65	30
1967	3*	0	1987	66	34
1968	3*	1*	1988	69	30
1969	3*	1*	1989	69*	25*
1970	3*	1*	1990	80*	25*
1971	3*	1*	1991	104*	31*
1972	4*	1*	1992	103	26
1973	5*	1*	1993	117	34
1974	7*	3*	1994	112	33
1975	8*	5	1995	115	27
1976	12*	3*	1996	116	29
1977	20*	11	1997	-	30
1978	20	10	1998	165	32
1979	16	8	1999	168	35
1980	34	16	2000	195	40
1981	37	16	2001	-	42
1982	52	19	2002	245	41
1983	50	22	2003	209	36

* Pairs proved to be breeding

Sources:

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This study.