Breeding ecology and diet of Great and Arctic skuas on Handa Island 2005

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Report of the Handa Island Skua Monitoring Programme 2005

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1. Summary

2005 saw the third full season of activities by the Handa Island skua monitoring programme. Productivity of the island's important great and Arctic skua populations continued to be monitored following standard methodologies, and chicks ringed with standard BTO and colour rings. This year's research put a greater focus on the diet of great skuas, through the analysis of regurgitated pellets.

The number of breeding great skuas on the entire island remained stable compared to the past 2 years, at 212 apparently occupied territories (AOTs). The Arctic skua population continued its decrease since 2001, with only 17 breeding and 4 non-breeding pairs.

Almost certainly in response to a period of very poor weather in late winter and early spring, many great skuas delayed the onset of breeding until conditions were more favourable, though mean lay-date of the colony was still roughly consistent with the previous two years.

In line with most other Scottish colonies, productivity among both skua species was extremely low this year. In the case of great skuas productivity dropped by over 90% to 0.07 chicks fledged per pair, while Arctic skua productivity halved to 0.6 chicks fledged per pair.

Egg predation in both species was higher than in the previous two years; however an extremely high level of chick loss in both species was the principal cause of the widespread breeding failure. Post-fledging mortality of Arctic skuas decreased, probably due to there being less great skuas on territory during the relevant two-week period than in previous years, though it was still estimated at a significant 40% of fledglings.

Diet among great skuas was broadly split between fish and seabirds, with club site skuas eating proportionally more birds than the breeding adults (62.7% vs 42.9% of single item pellets respectively).

Further analysis of the data presented here is ongoing, and together with results from the two previous years, will form the basis of a forthcoming publication. However, longer-term monitoring and research will be required to better understand the mechanisms underlying these results, and whether this bad year represents a mere 'blip', or is indicative of a genuine downward trend for Handa's skuas.

2. Methods

Trevor Jones conducted fieldwork between 12-21 June and 5-10 August; Claire Smith between 23 June and 23 August.

Methods for locating nests and monitoring productivity were consistent with those used in 2003 (Jones, 2003) and 2004 (Smith & Jones, 2004). This year the breeding ecology of 71 pairs of great skuas (bonxies) was monitored within the 2 study sites established in 2004; with 36 in site 1 and 35 in site 2 (Appendix 1).

The all island survey of bonxies was conducted on the 26th of June, following standard methodology outlined in Walsh *et al.* (1995). All Arctic skua AOTs and nests were mapped throughout June.

The bonxie pellet transect set up by Lizzie Williams in 2003 was extended in a north-easterly direction and this year passed through the territories of 17 breeding pairs (11 in study site 1, and 6 in study site 2.) A second transect was established passing through 8 territories in site 2 (Appendix 1). All 25 territories and the 2 club sites were cleared of pellets on the 25th June. Pellets were then collected from these territories and the 2 club sites every 7-10 days and categorised as sand-eel, other fish, auk (guillemot, razorbill or puffin), gull or fulmar. All other food items were identified as accurately as possible (see Appendix 3). Chicks from these pairs were weighed and the wing length (maximum chord length), bill and tarsus were measured 3 times during the linear growth period (13-34 days, Furness 1983), and metal and colour rings were fitted. Otoliths (fish 'ear' bones from which individual species can be identified) were removed from all pellets and used to identify fish species using the otolith collection at Glasgow University, with the assistance of Professor Bob Furness and an identification guide (Harkonen, 1986). Additional otoliths were identified by Dr Bernie Zonfrillo of Glasgow University.

All 17 breeding pairs of Arctic skuas were monitored. Chicks were weighed and measured at least twice (growth is linear; Phillips, 2001), and metal and colour rings fitted. Any chick regurgitates were noted from both species.

A methodology for monitoring and estimating post-fledging predation on Arctic skuas by Great skuas, first developed in 2003 (Jones, 2003) was again implemented and refined this year. Each Arctic skua territory was searched for carcasses during the fledging period by 2-4 observers walking parallel linear transects 5-10m apart (depending on the visibility afforded by the terrain), until the whole territory had been covered. Areas adjacent to territories where fledglings were seen practising to fly, were also searched following the same methodology. These searches were repeated every 5-7 days until all fledglings had either left their territory or been predated.

3. Results

3.1 Populations

The bonxie breeding population remained stable at 212 AOTs, at a density of 117 pairs per km^2. The Arctic skua breeding population has halved since 2001 with 17 breeding pairs and 4 AOTs; only 9 pairs bred in the traditional stronghold area, at a density of 135 pairs per km^2.

A second bonxie club site was established, either due to disturbance caused by attempted adult-trapping with a woosh net in 2004; immigration and recruitment; the increased growth of sorrel on the site; or the influence of adult birds joining the 'loafing' non-breeders after early failure of their breeding attempt. No birds were observed on the Arctic skua club site until the 18th July, suggesting that they may have been failed breeders, rather than non-breeders.

3.2 Breeding statistics

	Breeding pairs monitored	Mean laying date	Mean clutch size	Mean alpha egg volume	Hatching success (%)	Fledging success (%)	Chicks fledged per pair
Great skua	71	May 26±0.9 (51)	1.70±0.05 (71)	78.85 ±1.07 (41)	76.9 (71)	5.4 (71)	0.07 (71)
Study site 1	36	May 26± 1.7 (22)	1.67±0.07 (36)	79.8 ±1.94 (17)	66.7 (36)	0 (36)	0 (36)
Study site 2	35	May 26± 1.0 (29)	1.74±0.07 (35)	78.1 ±1.18 (22)	86.9 (35)	9.4 (35)	0.14 (35)
Arctic skua	17	June 8±1.2 (10)	1.76 ± 0.1(17)	43.71 ± 0.83 (12)	60 (17)	55.6 (17)	0.6 (17)

Table 1. Summary of breeding statistics for great and Arctic skuas on Handa Island, 2005. Sample sizes are in parentheses.

Bonxies laid alpha eggs between the 13th May and 17th June, and the mean lay-date of 26th May was remarkably consistent with 2003 (24th May) and 2004 (26th May). However, it is clear from fig. 1 that the pattern of laying was very different, with a much larger and later peak in laying. Although there will be some turnover in the individuals breeding, this will be very small in a long-lived seabird. Rather the 2005 temporal pattern is probably due to especially poor weather through the spring, causing many birds who usually lay early to wait until conditions were more favourable before laying.

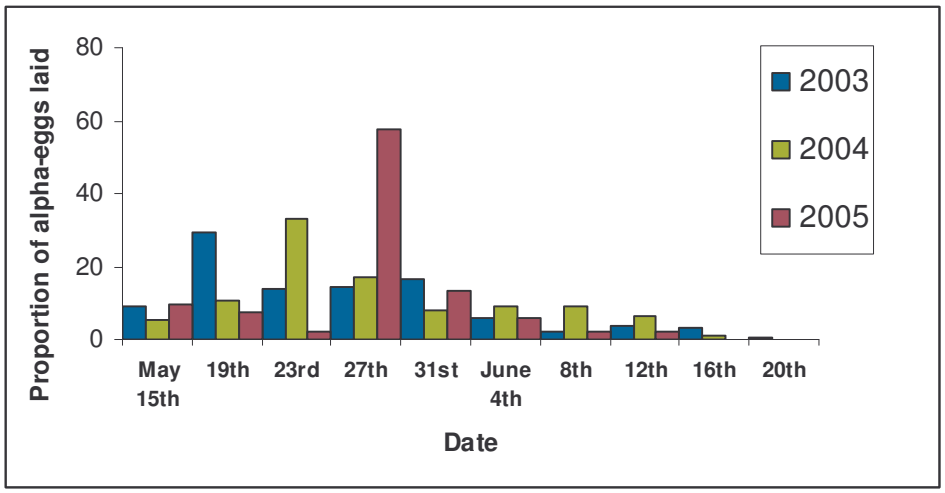

Figure 1. Bonxie lay-dates 2003-2005. Each bar represents eggs laid in successive 4-day periods, as proportion of total number of eggs laid that year.

Arctic skuas laid alpha eggs between the 2nd June and 14th June, therefore their mean lay-date was midway between that of the previous 2 years. It is not possible to identify a pattern in their lay-dates due to the small sample size. (As in previous years lay-dates were calculated by subtracting incubation time from hatch date, reducing the sample size this year due to the high level of egg predation.)

Hatching success was far higher in site 1 than site 2 and overall egg volume was higher than in 2004.

The 2005 season was typical of this year; all 36 pairs of bonxies in Site 1 failed by 20th July. Of the 4 productive pairs in Site 2, only 1 fledged 2 chicks. The majority of pairs failed when chicks were less than 10 days old (Table 2).

3.3 Mortality factors

Stage	Cause	Arctic skuas	Great skuas	Site 1	Site 2
Egg stage	Addled	0	13.2	23.3	3.3
	Predated	38	8.3	8.3	8.2
	Died hatching	0	0.8*	1.6	0
	Squashed	0	1.0*	2.5	0
Chick stage	Total chick loss	44.4	94.6	100	90.6
	Chick loss 0-10 days	44.4	76.3	80	73.6
	Chick loss 10+ days	0	18.3	20	17
Post fledging	Predated	~40	-	-	-

*1 chick

Table 2. Chick mortality factors for great and Arctic skuas, expressed as percentages of all mortalities.

Great skuas

The proportion of eggs predated (8.3%) was higher than the previous two years (5.4% & 4.3% respectively, Jones, 2003; Smith & Jones, 2005), but consistent between study sites. One incidence of a bonxie successfully predating another bonxie's eggs was directly observed on 19th June by T. Jones, and an attempted predation by C. Smith on 13th July.

As in 2004 the incidence of addled eggs was higher in Site 1 than Site 2, presumably due to increased disturbance by Great black-backed gulls (*Larus marinus)* (as evidenced by shorter incubation times in focal pairs in 2004; Smith & Jones, 2005) However, incidence of addling was 7 times higher in Site 1 than Site 2 this year. This is unlikely to be due to eggs cooling whilst left unattended as both adults forage, because the eggs would probably be predated. It is more likely that increased disturbance due to number and proximity of Great black-backed gulls had a more serious effect this year in combination with the poor weather, high rainfall and resultant chilling of eggs. Alternatively, if birds had a problem obtaining food on migration and/or once on territory, a higher number of eggs may have been unfertilized or not formed properly due to 1 or both adults being in poor condition.

As last year, one bonxie chick was found squashed in the nest and another died hatching.

The majority of bonxie chick mortality occurred when chicks were less than 10 days old.

Outside of the study sites, two chicks were found to be developing abnormally and probably starved; these were both from pairs with two chicks.

For the first time, one great skua chick died subsequent to handling, apparently due to stress.

Arctic skuas

A drop of over 30% in hatching success compared to the previous 2 years was attributable entirely to egg predation (38% of eggs laid). Arctic skuas have a much lower tendency to egg addling than great skuas (Furness, 1987.)

Chick loss (44.4%) was far higher this year compared to previous years (with fledging success of 85.7 and 90.6% respectively.) All chicks that survived beyond 10 days fledged successfully.

Post-fledgling mortality was lower than 2003 (when the same method of estimation was used). This is probably attributable to fewer bonxies being on territory during Arctic fledging stage this year. However all 'successful' pairs of bonxies were within 300m of the Arctic stronghold and 2 outlying pairs of Artics were within 200m of 1 or more successful pairs of bonxies.

3.4 Chick growth

Growth of bonxie chicks does not follow a linear patter until they reach 13 days of age; due to the high rate of early failure, measurements were only obtained from 5 chicks and so no comparison can be made between chick growth in 2004 and 2005.

3.5 Diet

Bonxie diet

Food item	Breeders (n=431)	Club sites (n=861)
Fish total	49.7	28.9
Bird total	42.9	62.7
Other	7.4	8.4
Sand eel	4.9	0.3
Fish other	44.8	28.6
Auk	23	46
Gull	14.8	11.1
Fulmar	3.9	5.2
Storm Petrel	0.9	0
Great skua chick	0	0.3
Arctic skua chick	0.2	0
Egg	0.5	0
Rabbit	5.3	1.0
Crustacean	1.2	2.4
Goose barnacle	0.2	3.5
Miscellaneous	0.2	1.3

Table 3. Food items comprising single item pellets collected from territories of breeders and club-sites of non-breeders and loafing birds, expressed as percentages of total pellets collected. n=total number of pellets collected. Miscellaneous includes crowberry, fish eggcase and unidentified mollusc.

Breeders' diet was more evenly split between fish and bird items, whilst non-breeders' diet was bird-dominated. Breeders' diet contained a far higher proportion of sand-eel than non-breeders, and half the amount of auk.

Mixed pellets

Of a total of 1292 pellets collected 111 (8.6%) were mixed (i.e. contained 2 or more different food items); these are not included here as pellets are not always equally split between food items and otoliths remaining in the bird's crop from a previous meal may then be regurgitated with a later bird pellet. However, food items found in these pellets have been included in the food item list (Appendix 3).

From identification of otoliths removed from pellets, for breeding pairs 75.8% were Norway Pout (*Trisopterus esmarkii*), 15.4% Whiting (*Merlangius merlangus*), 4% Poor Cod (*Trisopterus minutus*) and 2.6% Haddock (*Melanogrammus aeglefinus*). Otoliths of a further 12 species were found (Appendix 3). It was not possible to compare the diets of pairs from sites 1 and 2 as the early failure of the majority of pairs meant that only one sample of pellets was obtained from many pairs, particularly in site 1.

Otoliths from non-breeders' pellets comprised 59.2% Norway Pout, 31.1% Whiting, 1.3% Poor Cod and 4.8% Haddock, the remainder being from a further 6 species.

Arctic skua diet

Arctic skuas only produce very small pellets if at all, due to the nature of the food they eat (having been partially digested), and due to the smaller size of the birds. They were observed however taking more food on territory than had been observed in previous years, notably meadow pipits (*Anthus pratensis*), snipe (*Gallinago gallinago*), rock doves (C*olumba livia*) and wood pigeons (*C. palumbus*). Cuttlefish (*Sepia officinalis*) 'bones' were also discovered on 2 separate territories.

Chick regurgitations

Of 7 regurgitations by bonxie chicks, all were fish with 1 chick regurgitating rabbit. Two regurgitations by Arctic skua chicks were observed, by separate chicks, of whitefish and sand-eel.

3.6 Attendance

Great skua chicks were observed being left unattended on more occasions than previous years. Two known pairs (identified by individual markings) were observed leaving their chicks unattended (in the final 2 weeks of chick stage) this year when they had not been observed doing so in 2004.

Arctic skuas

One pair of Arctic skuas, breeding on the edge of the stronghold, consistently left their chicks unattended, they lost 1 chick and fledged 1 chick.

There appeared to be a breakdown of cooperative defence by Arctic skuas this year and no defensive chases of bonxies by trios were observed all season. Arctic skuas rely upon cooperative defence against chick predation by larger bonxies; loss of this defensive mechanism is the likely cause of the higher level of chick loss this year.

4. Ringing

Over the whole island only 22 bonxie chicks were ringed compared to 117 in 2004. Two un-ringed fledglings were seen, but it is estimated that bonxies only got a maximum of 30 fledglings off the island. Due to early failure of the majority of study site pairs, searching and ringing of chicks over the rest of the island began earlier than last year and it is unlikely that many chicks were missed.

Figure 2. Arctic skua chick fitted with standard BTO ring and colour-ring.

Four colour-ringed birds (ringed in 1989-91 by Professor. Bob Furness) were seen on the island this year, of which at least three were still breeding in 2005. (A fourth was seen bathing on Swaabie Loch.)

No birds colour-ringed as chicks were observed on Handa in 2005; this is not unsurprising as Great skuas do not start to breed until they are at least 4 years old and juveniles have not been observed returning to their natal colonies in their first year at other sites (Furness, 1987).

19 Bonxies and 2 adult Arctic skuas were seen wearing BTO metal rings this year. Some of these birds were probably ringed as chicks at other colonies and then emigrated to Handa. However, an unknown number of chicks were ringed under the supervision of Professor Bob Furness during his monitoring of Handa skuas between 1989-1991. The BTO ring number of 1 adult, pale phase Arctic skua was read using binoculars. It was ringed by Professor Bob Furness on the 24th June 1989 as a chick on Handa, making it 16 years old and meaning that it has been breeding for at least 12 years. (Based on mean breeding age of 4.4 years, with light phase birds such as this one more likely to recruit at 3 years; Phillips, 2001.) It produced 2 chicks this year, although unfortunately one was predated post-fledging by a neighbouring bonxie.

5. Arctic skua colour phases

Figure 3. Partially albino Arctic skua chick.

A partially albino chick (fig. 3), the first on record for Handa, hatched on the 5th of July to a dark and intermediate pair. It had a normally pigmented sibling but 1 of the adults alos exhibited partial albinism with white spots on its carpels. Albinism occurs regularly in birds from the North Atlantic Islands and can be as high as 2% in some populations (Olsen & Larsen, 1997), but figures for partial albinism in Scottish populations are unknown. Unfortunately the chick was predated when less than 5 days old, perhaps due to its conspicuousness.

Of 42 adult Arctic skuas either breeding or holding territory on Handa this year 25 were dark phase, 10 light phase, 4 intermediate phase (figure 2) and the colour phase of 3 remaining birds was unknown (Due to both individuals never being observed on territory simultaneously.) This is consistent with the theory that dark phenotypes are favoured at the southern end of the species' breeding range (Phillips, 2001.)

This year the probable phase of arctic chicks was determined based on plumage description in Olsen & Larssen (1997). Normally pigmented chicks are identical when downy and their phase can only be determined when they are at least 3 weeks old with the majority of their plumage; therefore chick phases were only determined for chicks that reached fledging age.

Table 4. Phases of fledged Arctic skua chicks, 2005.

Adult phases	Chick phases
Dark/Dark	Dark
Dark/Dark	Dark
Dark/Dark	Dark
Dark/Intermediate	Dark, Dark
Light/Intermediate	Light, Light
Light/Dark	Dark, Dark
Light/Dark	Dark
Light/Light	Light
Light/Light	Light

6. Discussion

2005 was the first 'bad year' for Handa's skuas. Bonxie productivity was 90% lower than in 2004, and Arctic skua productivity halved. However, this is consistent with the general pattern for Scottish seabirds this year. One bad year is unlikely to have a detrimental effect on the population of long-lived seabirds such as skuas, but makes productivity and dietary monitoring all the more important.

Poor productivity in both species was attributable to increased losses at both chick and egg stage. The majority of bonxie chick loss across both study sites occurred when chicks were less than 10 days old. Bonxie chicks are more vocal and therefore more conspicuous to predators (neighbouring bonxies and great black-backed gulls) the younger they are. During years of poor food supply at other colonies, both parents were observed to leave the territory to forage in order to maximize chick feeding and growth (Hamer *et al*.,1991), leaving chicks unattended more often and increasing the risk of predation.

In the context of the widespread poor breeding season across Scotland there are two main possible causes: either a lack of food, or problems obtaining food. A lack of food and in particular sandeels, which are necessary for chick growth in many seabird species, may be caused by either a depletion or movement of food sources/currents. Stocks of some fish within the Minch are currently monitored as part of a much larger area stretching into the north-east Atlantic by the International Council for Exploration of the Sea. The status of sand-eel stock in this area is unknown (www.ices.dk).

Alternatively birds may have had a problem obtaining food resulting from being in bad condition due to poor weather on Handa. The large proportion of addled eggs in site 1 suggests that inclement weather may have had a detrimental effect at least on this stage of breeding, reducing hatching success through egg chilling. The delay in breeding of some pairs suggests that bonxies were waiting for conditions (either food availability or weather) to improve. It cannot be concluded which of these factors resulted in reduced productivity this year.

The reason for the increase in bonxie egg volume is unknown; in fact egg volume has been found to increase slightly with improved food supply (e.g. Ratcliffe, et al, 1998).

Unfortunately due to the extremely high failure rate it was not possible to compare chick growth rates between study sites or pairs with different dietary specializations.

Bonxie diet

Whiting and Norway Pout, the 2 most dominant fish species in bonxie diet, are most commonly found at depth ranges of 10-200m (Cohen *et al.*, 1990). Bonxies are surface divers and are unable to catch these species. Both species are a common discard from mixed demersal fisheries. The most important finding from this year's dietary study is that Handa's bonxies are similar to Shetland (Furness & Hislop, 1981; Hamer *et a*l.,

1991) and St Kilda (e.g. Bearhop *et al*., 2001) populations in feeding on fisheries' discards. The predominance of Norway Pout over Whiting in bonxie diet reflects the sizes of these fish with the former weighing 150g compared to 1.5-3kg. (Cohen *et al*, 1990).

For non-breeders the relative importance of fish and bird in the diet is similar to that found in St Kilda birds during a dietary study between 1994-1996 (Phillips *et al*, 1997). However, the proportion of fish in the diet of Handa's breeding pairs was over double that found in the St. Kilda study. Unsurprisingly, given the size of the Handa populations, auk species have been the dominant bird prey type in the diet of breeders and non-breeders for the past 3 years. The low-level of sand-eel in diet is not unexpected, as their very small otoliths break down quickly and may be missed in pellets. The proportion of sand-eel in the diet in 2005 is consistent with 2003. It is also over 10 times greater than that found in the St Kilda study. Non-breeders' diet may be more bird dominated for 2 reasons, either that foraging for fish is less important as these birds do not have chicks to feed, or due to sampling differences due to high failure rate. These results should be treated with caution as non-breeders' diet was recorded throughout the season, whereas many breeding pairs failed before the peak time for chicks of cliff birds, meaning that bird was a smaller component of their diet as they had left territory by then.

Arctic skua diet

Colonially breeding Arctic skuas are true kleptoparasites, relying on stealing food (predominantly sand-eels) from other birds to a much greater extent than bonxies (Phillips, 2001). The regular occurrence of hunting prey on territory this year (e.g. snipe) is indicative of a problem obtaining food by normal means; due to their being less food and/or less active bird hosts. The two cuttlebones found on territories were probably obtained as discarded bycatch as they are found on the seabed (Wilson, 1999.)

Arctic skua population decline

Arctic skua numbers appear to be decreasing having declined in successive years from their peak of 42 AOTs in 2001 (Jones, 2003), to 17 AOTs in 2005. Mean breeding age of Arctic skuas is 4.4 years (Phillips, 2001) meaning that some birds hatched during 2001 may still not be breeding yet. However, the lack of a definite club-site this year may suggest that new breeders are recruiting to other, larger populations, a behaviour which is not unusual in colonially breeding birds.

Given the consistently high recorded levels of post-fledging predation on Arctic skuas by bonxies over the last three years, it seems unlikely that this decline will be reversed in the coming years.

Recommendations for 2006

1) Continuation of the **skua monitoring programme**: see Appendix 4

2) In light of the poor breeding season in 2005, apparently due to food shortage, it is important to monitor whether Handa's internationally important seabird populations (especially guillemot and razorbill) are also affected; therefore, to supplement the warden's existing monitoring duties, we recommend the **recruitment of a volunteer** to make observations on the cliff-breeding species of Handa, recording food items (i.e. fish species) delivered to chicks by parents; to be trained on arrival by skua team.

3) In light of the decline in the breeding Arctic skua population on Handa (50% decline since 2001): **low-level monitoring of Arctic skua productivity only**; no other activities that have potential either to cause disturbance or reveal location of eggs or chicks to predators.

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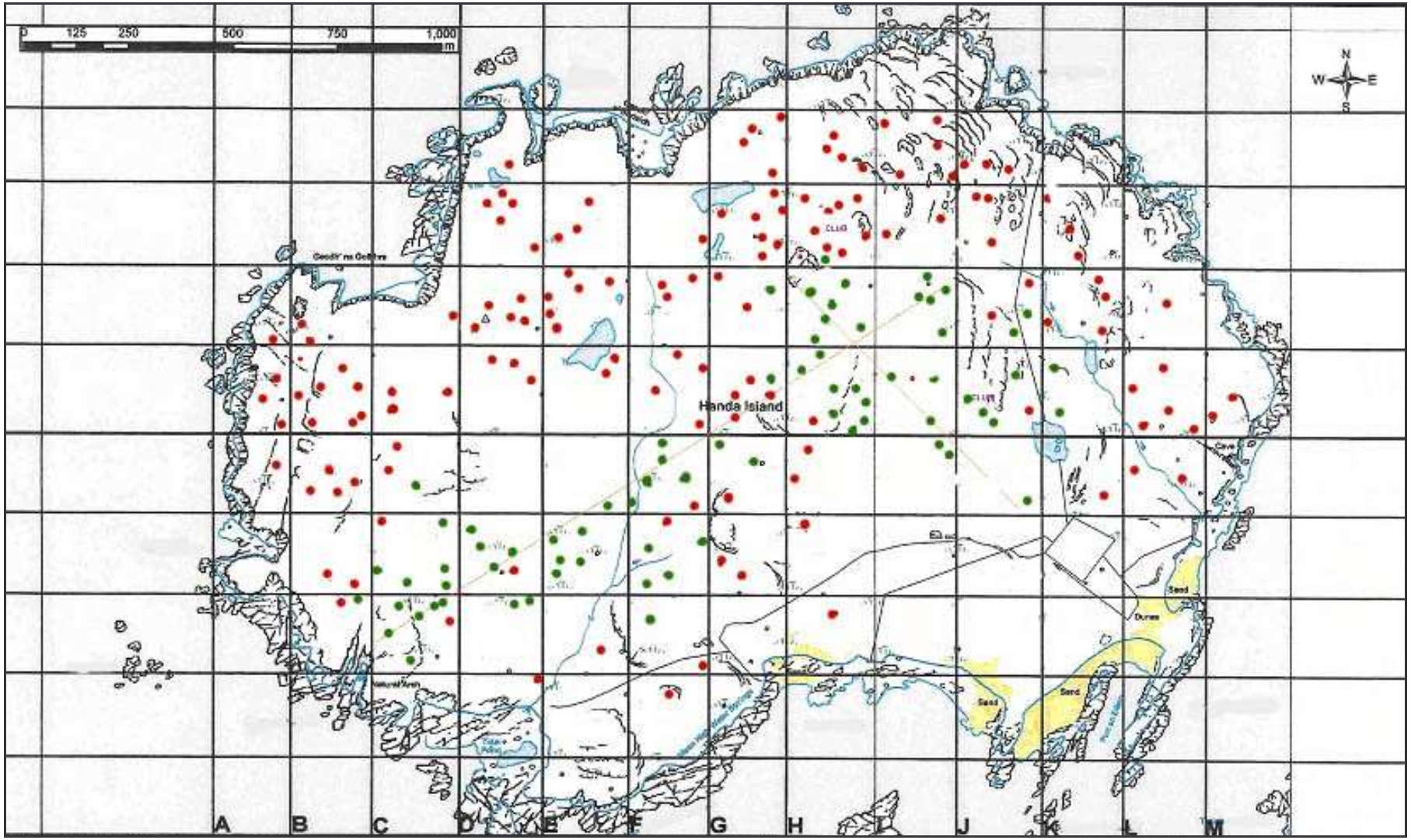
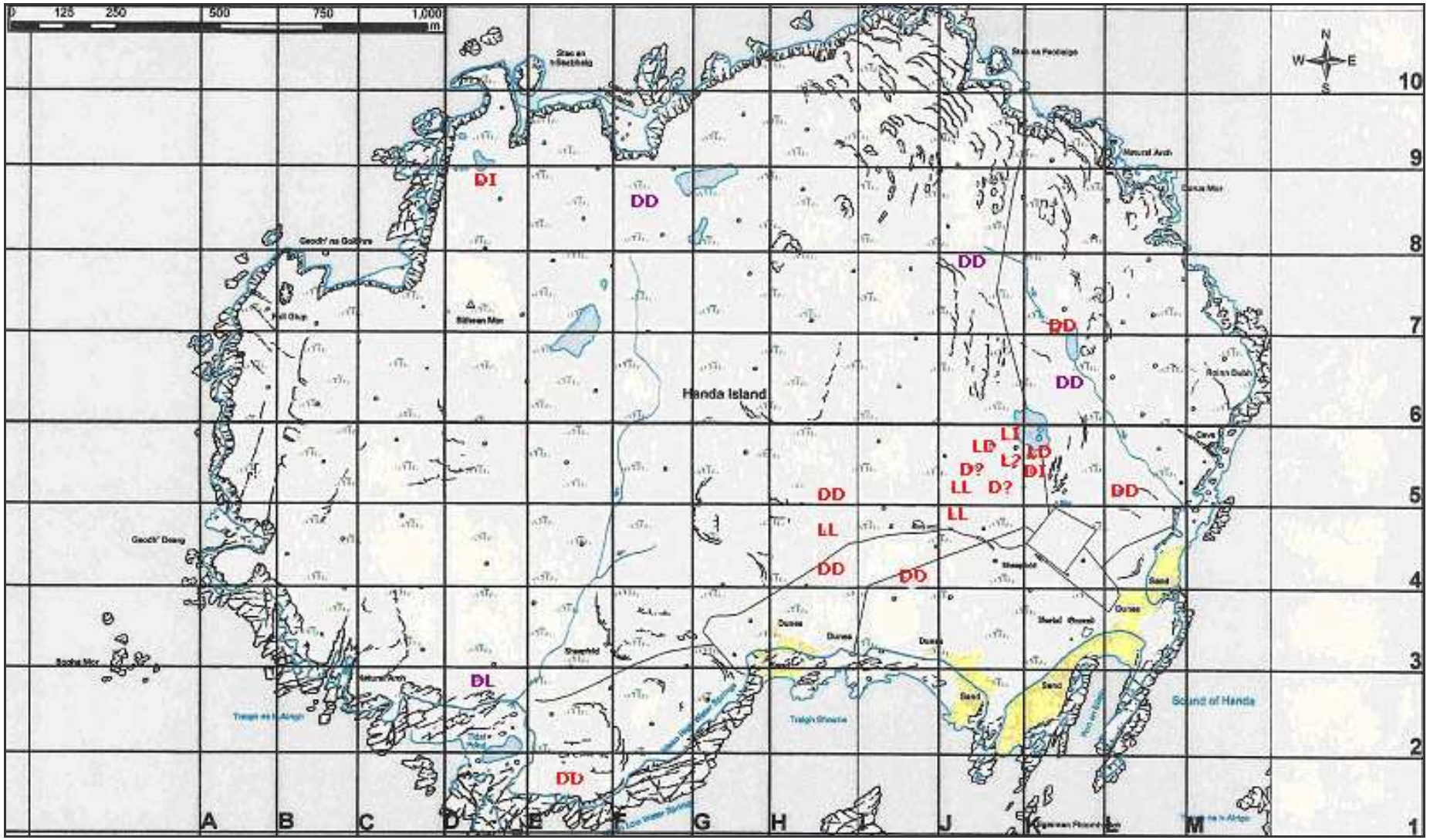
Appendix 1. Map of bonxie AOTs, study sites nests, club-sites and pellet transects.



Appendix 2. Map of Arctic skua breeding pairs and AOTs



L Light phase adult
D Dark phase adult
I Intermediate phase adult
? Colour phase unknown

Breeding pair
AOT

Appendix 3. Food items consumed by great skuas in 2005

Food item		
Plant material	Crowberry(*Empetrum nigrum*)	
Marine Invertebrates	Crustacea - species not determined	
	Mussel (*Mytilus edulis*)	
	Goose-barnacle (*Lepas* sp.)	
	Edible Sea urchin (*Echinus esculentus)*	
	Violet Ground beetle (*Carabus violaceus*)	
Eggs	Great skua (*Catharacta skua*)	
	Guillemot (*Uria aalge*)	
	Unidentified bird egg	
Fish	Conger eel (*Conger conger*)	
	Sand-eel (*Ammodytes* sp.)	
	Norway Pout (*Trisopterus eskmarkii*)	
	Whiting (*Merlangius merlangus*)	
	Blue whiting (*Micromesistius poutassou*)	
	Poor Cod (*Trisopterus minutus*)	
	Bib (*Trisopterus luscus*)	
	Sea scorpion (*Taurulus bubalis*)	
	Haddock (*Melanogrammus aeglefinus*)	
	Saithe (*Pollachius virens*)	
	Plaice (*Pleuronectes platessa*)	
	Horse Mackerel (*Trachurus trachurus*)	
	Herring (*Clupea harengus*)	
	Dab (*Limanda limanda*)	
	Pollock (*Pollachius pollachius*)	
	Witch (*Glyptocephalus cynoglossus*)	
Amphibian	Common toad (*Bufo bufo*)	
Birds	Guillemot (*Uria aalge*)	
	Razorbill (*Alca torda*)	
	Puffin (*Fratercula arctica*)	
	Kittiwake (*Rissa tridactyla*)	
	Fulmar (*Fulmaris glacialis*)	
	Storm Petrel (*Hydrobates pelagicus*)	
	Great skua (*Catharacta skua*)	Chick
	Great skua (*Catharacta skua*)	Fledgling
	Arctic skua (*Stercorarius parasiticus*)	Fledgling
	Greater black-backed gull (*Larus marinus*)	Fledgling
Mammal	Rabbit (*Oryctolagus cuniculus*)	

Appendix 4.

Skua Monitoring Programme : Aims for 2006

1. All-island census of great and Arctic skuas.

2. Productivity monitoring of great skuas within two established study sites.

3. All-island productivity monitoring of Arctic skuas.

4. Monitoring of post-fledging mortality in Arctic skuas.

5. Monitoring of great skua chick growth.

6. Due to the early failure of focal pairs, continue great skua dietary study – via pellet collection along transects; analysis to involve correlation with chick growth.

7. Increased effort in trapping and colour-ringing of adult great skuas within study sites, and in reading BTO rings of adult skuas across whole island.

8. Train and supervise volunteer undertaking feeding observations on cliff-breeding species.
