



Great Skuas and Northern Gannets on Foula, summer 2022

An unprecedented, H5N1 related massacre

Field report

Kees (C.J.) Camphuysen & Sheila C. Gear

NIOZ Royal Netherlands Institute for Sea Research



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Front cover: dying Great Skua (#503) on nest, 10 June 2022, North Harrier, Foula. The bird was still alive, but incapable of any other response than just the flickering of the eyes and an occasional small spasm of the body.

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Key words

Great Skua, *Stercorarius skua* , breeding numbers, status, mortality, avian influenza HPAIV H5N1 pandemic, reproductive performance, breeding success, population decline, future prospects

Northern Gannet *Morus bassanus*, Red-throated Diver *Gavia stellata*, Common Eider *Somateria mollissima*, Great Black-backed Gull *Larus marinus*, Herring Gull *Larus argentatus*, Arctic Skua *Stercorarius parasiticus*, Arctic Tern *Sterna paradisaea*

Front cover: dying Great Skua (#503) on nest, 10 June 2022, North Harrier, Foula. The bird was still alive, but incapable of any other response than just the flickering of the eyes and an occasional small spasm of the body.

Summary

- A highly pathogenic avian influenza virus (HPAIV) pandemic struck, more or less unexpectedly, and affected numerous species of seabirds all over the Northern Hemisphere in summer 2022. This field report was prepared to share details and results of ad hoc studies on the effects of the HPAIV pandemic on seabirds breeding on Foula (Shetland Islands) in summer 2022.
- The work reported here focused on two species that were clearly affected by the pandemic: Great Skuas *Stercorarius skua* and Northern Gannets *Morus bassanus*, but unusual mortality patterns were investigated for all non-passerines on the island.
- Direct contact with sick or dead birds was avoided as much as possible. Hands, tools, and anything that was close to dead birds was subsequently disinfected before re-use. Swab samples to detect infections with H5N1 were taken outdoors, with extensive personal protection in a team of two persons. Further measures and precautions were taken to avoid cross-contamination between breeding sites, between species, and between areas.
- Colony counts were conducted of apparently occupied territories (AOTs) of Great Skuas all over Foula in the first two weeks of June, and results were compared with the latest full census (2015).
- Mortality rates of Great Skuas were assessed based on systematic searches in breeding as well as in non-breeding habitats of this species, all over the island, May-July. All corpses were identified, photographed, the level of decomposition was categorized on a seven-point scale (Appendix 1), geographical positions and postures were recorded, legs were checked for (colour-)rings, the level and type of scavenging was documented, and the birds were marked (primaries cut in half on both wings) to avoid double counts.
- The colonies of Northern Gannets were photographed 15 May, 1 June, 23 June, and 31 July 2022 in order to detect changes in the attendance of breeding birds or any cases of mortality at the cliffs. The photos were studied by two independent observers, and changes in numbers of apparently occupied sites (AOSs) and apparently occupied nests (AONs) were assessed. Results were compared with the latest, full colony census (an aerial survey in August 2017).
- Dead gannets, any other dead seabirds and dead waterfowl were identified, described and recorded, just as the dead skuas, in order to find evidence for further spread of the virus, or to explain where infections could come from.
- The reproductive performance of Great Skuas was assessed on two study plots: the long-term study plot at Da Bitten (just to the north of Mill Loch), and a site between Ristie – Da Logat in the north of Foula. Da Bitten was studied in the usual way, but with observations at distance instead of hands-on (also no ringing was conducted). At Ristie, eggs were measured when found, but otherwise eggs, chicks, and nests remained untouched, while nests were monitored every third or fourth day, between early June and mid-July. The work was constantly critically evaluated by the observers, in search for potentially adverse impacts of their activities on the breeding birds.

Key results

- Searches on Foula, May-August, produced 1400 documented corpses of **Great Skuas**, of which 100 were (colour-) ringed earlier in life. The distribution was non-homogeneous, with clusters of corpses in relatively wet areas (lochs, burns, swamps), known clubs and bathing sites (Fig. 8).
- The mean age of ringed birds found dead was ~21 years for 87 individuals ringed at Foula itself and ~15 years for 13 individuals ringed elsewhere in Shetland and on Orkney.

- The mortality commenced in early May, peaked late May-early June, then slowed down, but picked up again later in the season (Fig. 10). Carcasses that were scavenged by other birds (conspecifics included) were most abundant at club sites and bathing places (Fig. 12).
- That the mortality of Great Skuas was caused by avian influenza is concluded on the basis of circumstantial evidence (scale of the impact, behaviour of the casualties, postures of carcasses) and the international context (tests conducted on birds found in neighbouring breeding colonies). All three Great Skuas that were sampled (in early July 2022) on Foula tested positive for HPAIV H5N1.
- A 57% decline in breeding numbers (AOTs) of Great Skuas at Foula was found, in comparison with census results obtained in 2015 (Table 5). Given ongoing mortality throughout the summer, this must be seen as a conservative estimate, and an order of magnitude of 60-70% decline in occupied territories is likely.
- Clutch size across 34 AONs monitored at Ristie – Da Logat amounted to 1.74 ± 0.45 eggs (Table 6). Camera traps revealed that provisioning rates were high (predominantly fish and rabbits), but pairs in which one of the partners became infected and died failed promptly. All observations suggest that breeding effort and performance were ‘normal’ until the virus struck. In early August, only two partially feathered chicks were detected and reproductive success must have been very low indeed, if not a complete failure.
- The breeding failure at the Da Bitten monitoring plot was complete, just as in 2021, and birds seemed to abandon the colony already in July.
- Searches on Foula produced 42 adult, dead, **Northern Gannets**, mostly on stacks and cliffs or afloat in the ocean (Table 9). Even though numerous casualties may have washed away quickly, the results suggest that the extra-mortality was fairly low compared to unpublished reports from other Scottish colonies.
- A study of photographic material taken on 1st June, 23rd June 2022 and 31st July, indicates a ~22% decline in AONs and a ~16% decline in AOSs over the summer (Table 10). This could be a genuine population decline, or, at least in part, the effect of early colony departures. A full survey will be required to assess the loss in breeding birds, but because the most recent census was in 2017 (with 20% fewer sites occupied), it will be hard to estimate the actual damage inflicted by HPAIV on Foula in 2022.
- Only few further HPAIV suspected cases of mortality were recorded, in Common Eider *Somateria mollissima* (1), Great Black-backed Gull *Larus marinus* (1), Herring Gull *L. argentatus* (>2), and perhaps in Arctic Terns *Sterna paradisaea* (4).
- There was no evidence for extra mortality (whether or not inflicted by HPAIV) in Red-throated Divers *Gavia stellata*, Arctic Skuas *Stercorarius parasiticus*, or any other seabirds on Foula.

Implications and considerations

- Studying the epidemiology and transmission of avian influenza viruses in (pelagic) seabirds is critical to understand how and where outbreaks that cause extensive mortalities in seabird colonies develop and spread. Remains of H5N1 infected migratory *waterbirds* are often found in the vicinity of (fresh) water reservoirs (wetlands). Transmission of HPAIV may occur in water, in the air (aerosols), through faeces, or through consumption of infected prey (predators, scavengers). In Great Skuas, their scavenging habits were hypothesised being a key factor in 2021, but the bushfire like spread of infections in 2022 all over Foula suggests that other factors played a major role.
- The rapid spread of infections over Foula has probably been facilitated by the habit of Great Skuas to bath and socialise (interact) at fresh water lochs and pools (bathing places and clubs). Bathing places are the only sites where close individual contacts occur frequently and all major pathways of infection could play a role: through accumulating virions in communally used water bodies, aerosols shed from the respiratory tract, from faeces, or indeed by scavenging.
- Studies to assess the presence, but in particular the persistence of infectious (H5N1) influenza viruses in Foula’s wetlands are now particularly urgent.

Introduction

Great Skuas *Stercorarius skua* on Foula had a poor breeding season in 2021, with many dead adults found in colonies (estimated 3-4 times as many as normal), the club sites mainly deserted and with only 41 AOTs on the productivity monitoring plot along Da West Burn (Mill Loch, Da Bitten, Da Lieug). By the time of the scheduled ringing visit, on 24th July 2021, most adults had left Foula and only one normal sized chick on the monitoring plot had survived, along with two downy chicks too small to ring. These chicks all disappeared the following week and productivity was assessed as 'zero'; an unprecedented event on Foula even though reproductive success had been extremely low in several recent years after a longer term decline (Gear 2022).

In fact, in Scotland, 'an emerging situation involving observational die-offs' of Great Skuas occurred in July 2021, escalating to a point where mass mortality events were seen across several islands off the Scottish mainland (Banyard *et al.* 2022). This prompted a disease investigation which subsequently detected highly pathogenic avian influenza virus (HPAIV) subtype H5N1 clade 2.3.4.4b as the cause of the mortalities. The first dead Great Skuas were reported in the end of June, HPAIV infections were first confirmed on 20 July, and the last individuals were found in autumn 2021. Affected areas were Hirta (St Kilda), the Flannan Isles, Orkney, and seven locations on Shetland (Fair Isle, Mainland, Papa Stour, Noss, Yell, Fetlar, Unst). H5N1 infections were detected in samples taken at St Kilda, the Flannans and on Fair Isle. The Great Skua mortality found at Foula in June-July 2021 was not mentioned by Banyard *et al.* (2022). Although none of the animals found on Foula in 2021 were sampled and tested, the mortality and breeding failures observed were still regarded within that same perspective (R.W. Furness & G. Tyler *in litt.*). Given the planned presence of the first author on Foula for at least six weeks in summer 2022, it was considered useful to conduct a census of apparently occupied territories (AOTs) on the island, to assess the impact of the mortality in 2021 on Foula's breeding population.

In May 2022, however, mass mortality events in seabirds occurred again around Scotland, involving more seabird species, and apparently affecting unprecedented numbers. When Great Skuas at Foula arrived from the wintering quarters in April, no signs of bird flu were detected initially. This changed dramatically in May, when many birds died, especially at clubs and favourite bathing places where larger numbers of individuals assembled (*pers. obs.* Sheila Gear). On 31st May, 330 dead Great Skuas had already been found during inspections of various clubs and around lochs. In Shetland as a whole, mortality of Northern Gannets *Morus bassanus* and Great Skuas was spreading rapidly in May. Seabirds sampled and tested from other breeding areas in Shetland were found positive for HPAIV H5N1 (*pers. comm.* Glen Tyler).

Given these unfortunate developments, immediate assessments of the damage inflicted by HPAIV infections on seabirds on Foula, notably for skuas and gannets, were felt as more urgent than just a census of Great Skua territories. The first author embarked on that task, thereby freeing time for the second author to conduct her long-term monitoring of seabird numbers and reproductive success on various study plots on Foula. Six main tasks were agreed upon:

- (1) Continuation of the long-term seabird monitoring (SG, Foula Ranger Service)
- (2) A full assessment of Great Skua mortality, based on repeated systematic searches of the entire island (CJC)
- (3) Assessments of other 'suspect' seabird mortality on Foula, notably among Northern Gannets (SG, CJC)
- (4) Tissue sampling (whole carcasses) of Great Skuas to test for HPAIV infections (CJC)
- (5) A full colony census of Great Skuas, and a comparison with 2007/2015 data (CJC)
- (6) A second study plot to study Great Skua breeding performance (CJC)

The first task, a continuation of long-term monitoring on the island working on various study plots, will not be reported in this report, except occasionally in reference to other work conducted in 2022. These data will be submitted to SOTEAG directly, as every year. This field report will focus on the extra work conducted on seabird mortality and apparent reproductive performance on Foula in 2022, with emphasis on the Great Skua, which was only possible because there was a second observer. Given the mass mortality that has occurred, work was conducted with the following priorities: (1) Assessing the damage, (2) Understanding infections → where and how, and (3) Timing and spatial trends in mortality patterns.

Species introductions

Great skuas breed on Iceland, the Faroe Islands, in Ireland, Scotland, Norway, at Jan Mayen and Bear Island, on Svalbard, and in NW Russia to Novaya Zemlya (IOC 2022). The World population is only around 16,000 apparently occupied territories (AOTs), of which 60% are in Scotland, concentrated in Shetland and Orkney (JNCC 2022). Note however, that several large colonies, such as in Iceland, but also in Scotland, have not been censused for years (Glen Tyler, Aevan Petersen *pers comm.*). Foula is still assumed to hold the largest population of Great skuas in the world, following a rapid growth in the last century that peaked at around 3200 pairs in 1977 (Furness 1983a, 1987). More recently, numbers of breeding pairs were found in decline, from 2500 AOTs in 1985-86 to 2174 AOTs in 1992, 2293 AOTs in 2000 (Furness & Ratcliffe 2004), 1657 AOTs in 2007 (NatureScot) and around 1800 AOTs in 2015 (Sheila Gear). Counts are done every seven years by Scottish Natural Heritage (SNH)/NatureScot, because Foula is a Site of Special Scientific Interest (SSSI). In Iceland, currently assumed to be the second most important breeding area for Great skuas, the most recent national census has been carried out in 1984-85, when the population was estimated to number around 5400 pairs (Lund-Hansen & Lange 1991). A repeated census is badly needed (Ævar Petersen *pers. comm.*). In summer 2022 on Foula, a corpse count of the entire island during May-July (SG, CJC) and an assessment of apparently occupied breeding territories (June) in almost all breeding areas were conducted (CJC), while the reproductive performance was studied in study plots at Da Bitten (SG) and near Ristie (CJC).

Northern Gannets colonised Foula in the 1970s, but first bred successfully on Foula in 1980 (Furness 1981). A recent aerial survey of Northern Gannets on Foula in August 2017 using photographs to assess breeding numbers resulted in approximately 1465 AOTs, of which 873 at Waster Hoevda, 275 at Da Scrodhurdins, 249 at the Kame, and 68 at Da Stab (Murray *et al.* 2021). Because much of the Foula coastline is unsuitable for nesting gannets, it is unlikely that the gannetry will ever become comparable in size to those on Noss or Hermaness. The gannetries on Foula are highly inaccessible and only partially visible from land. Photo's obtained from the major ledges during repeated visits (SG, CJC), and visual observations during one circumnavigation of the island by ship (SG) were used to obtain an idea of the rate of HPAIV infections and the damage inflicted within the colonies. As with all birds on the island, corpses were recorded and carefully documented whenever possible.

Methods

Continuation of the long-term seabird monitoring (SG, Foula Ranger Service)

Great Skua breeding success was monitored by Sheila Gear as part of her long-term monitoring programme on the study plot along Da West Burn, between Mill Loch, Da Bitten, and Da Lieug (~60°08.17'N, 02°03.67'W). It had been a very poor season in 2021, with only 41 AOTs established on the standard monitoring plot (Gear 2022). In 2022, only 24 AOTs could be found (42.5% decline) in which, as in all earlier years, clutch size was assessed (SG), followed by only few area visits to count dead birds (CJC). At a later date reproductive success (potential fledglings) could only be assessed by overlooking the area from the public road (SG). Data will be provided separately to SOTEAG for their annual report.

Assessment of Great Skua mortality, based on repeated systematic searches of the entire island (CJC)

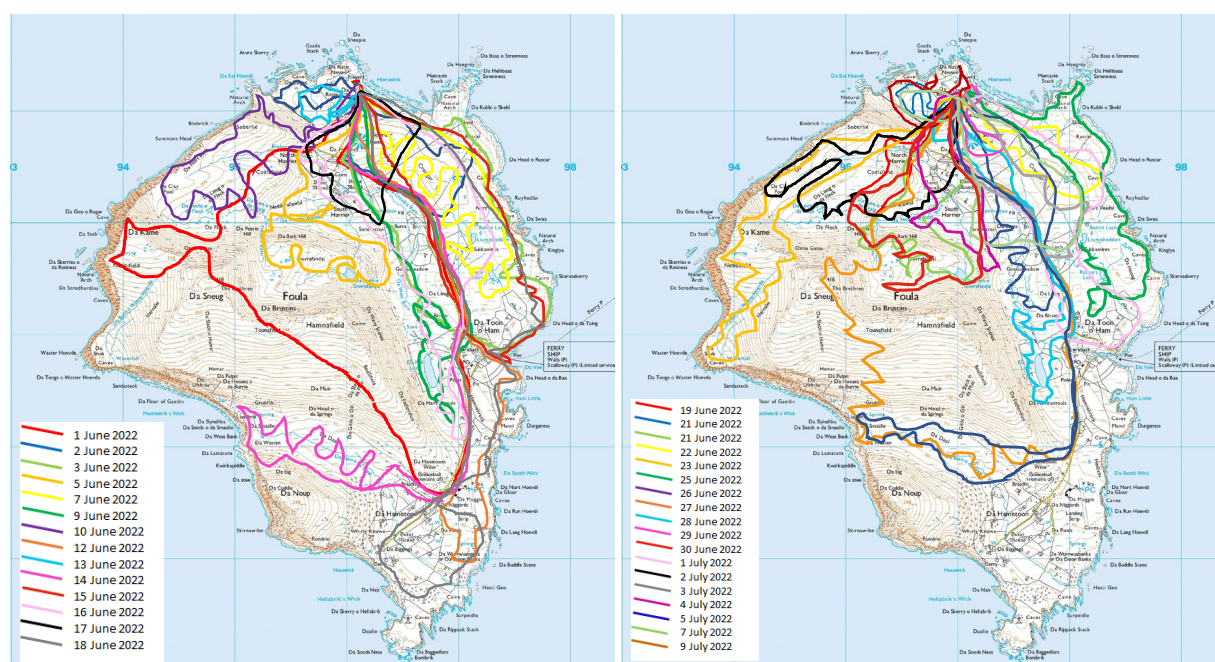


Fig. 1-2. CJC search effort on Foula, 1 June-9 July 2022. Routes are approximate transects (lines drawn by hand). Most areas were visited again in late July (SG), now also including the slopes of Da Noup and more of the area between Hamar and Da Sneug.

Foula was searched three times in full in June and July 2022, for the presence of carcasses of Great Skuas at the breeding grounds, on club sites and around bathing places (CJC; **Figs 1-2**). All corpses were identified, photographed, the level of decomposition was categorized, geographical positions and postures were recorded, legs were checked for (colour-)rings, the level and type of scavenging was documented, and the birds were marked (primaries cut in half on both wings) to avoid double counts. Geographical positions (latitude, longitude) were determined with a handheld Garmin Etrex 32x GPS and finds were subsequently mapped using Dmap for Windows 7.3b over a background map of the Ordnance Survey <https://i.pinimg.com/originals/e6/a5/b9/e6a5b9825e5fda231a52acca0781797.jpg>.

Categories of decomposition were judged by eye (see **Appendix 1**), ranging from:

- | | |
|------------------------------|---|
| (1) dying birds, | Incapacitated birds with typical AI spasms and incapable of flight or any other fleeing modus. Assumed dead, the next day after finding; living birds were not wing-marked. |
| (2) very fresh, | Rigor mortis stage, often still glossy eyes, good looking carcasses that evidently just died. Assumed 0-3 days dead. |
| (3) fresh, | Good looking carcasses, feathers bouncing and typically dry (when the carcass is on land), eyes dry out, very limited damaging insect activity visible, but attracting flies. Assumed 4-7 days dead. |
| (4) rather fresh, | Fairly good-looking carcasses, feathers still bouncing, eyes dry, insects became interested, often the first maggots to be seen. Assumed 8-14 days dead. |
| (5) rather old, | At least several weeks old carcasses, feather messy and or flattened, eyes deep dry, insects, slugs and mice usually have visibly done their work. Assumed 15-21 days dead. |
| (6) old, and | Decomposing carcasses, feathers loosening, often damaged and twisted, insects lost interest. Assumed 22-28 days dead. |
| (7) very old corpses. | Dried remains, old carcasses, often disintegrated, or dried and mummified. Assumed >one-month dead. |

The development of the pandemic could be timed and evaluated with hindsight, by subtracting the expected range of time (d) since dying (based on decomposition) from the date of finding each corpse. A descriptive manual is provided as an appendix of this report, which includes the expected time-windows for each state (**Appendix 1**). All photographic material is catalogued and has been stored for later, independent re-evaluations. Dying birds (incapable of flight and unable to move away when approached) were not wing-clipped for ethical reasons, but were included in the counts. While this imposed a slight risk of double counting when an area was revisited, written notes and descriptions were used to avoid that as much as possible. In practice, the risk of *overlooking* carcasses in the complex and very hilly terrain was much greater. Repeat visits invariably revealed the presence of corpses that must have been there during the earlier search effort. As a result, the area census provides an absolute minimum number of dead birds on Foula.

Prior to these systematic surveys, SG conducted counts at clubs and in surrounding marshlands at weekly intervals in May 2022, with emphasis on Da Daal, Mill Loch, Da Bitten, Rossie's Loch, Bottle Loch, Crougar, Bark Hill, Fleck Lochs, Ouvrafandal loch, Broos o Edlar, Tounafield, and Haamar. During some of these visits, carcasses were colour-marked with yellow or red paint, but not always. During the main survey (CJC), all carcasses were 're-counted', thereby 'ignoring' the initial results obtained in May, but the presence of red and yellow colour-marks were recorded, such that it would be possible to evaluate the overlap, and thereby the number of carcasses missed during these re-visits. In the second half of July, the area was again searched for corpses, and this included a more extensive search over some of the hill slopes surrounding Da Daal (Da Noup and Hamar to Da Sneug).

Assessments of other 'suspect' seabird mortality on Foula, notably among Northern Gannets (SG, CJC)

All other seabirds and waterbirds found dead were recorded and described, such that any possible significant outbreaks of disease could be documented, but also to find evidence for the scavenging habits of skuas: remains of their scavenged carcasses. With regard to the mortality of Northern Gannets, however, it should be realized that with mortality on the highly exposed breeding colony on the west coast, 'complete' counts of carcasses were impossible. Most dying birds would likely end up in the ocean and simply float away, given wind and currents, straight into the open Atlantic. Seawatches were a source of information for the presence or absence of dead birds in the water, combined with occasional finds of dead or dying birds on shore or even on land. Such data evidently underestimate any existing problems with gannets. Instead, colony photography was used to assess changes in densities of nesting birds (AONs and AOSs) on selected cliff sections between 1 June, 23 June, and 31 July (independent counts of the same material by CJC and Mike Harris; photos taken by SG and CJC).

Tissue sampling and swabs of Great Skuas to test for HPAIV infections (CJC)

Initial plans to collect at least three fresh carcasses of Great Skuas and send them for virologic analysis were cancelled by NatureScot. To compensate for the lack of evidence that HPAIV was the probable cause of the mass mortality in 2022, we carefully documented and filmed symptoms of sick and dying individuals and presented that to specialized virologists at the Erasmus University in Rotterdam. All film footage is catalogued and stored for later evaluations. In early July, NatureScot sent three sets of swab sticks to the island with the request to swab the buccal cavity and cloaca of three Great Skuas from various locations for HPAIV testing. The sampling was carried out instantly (CJC & Threes Schreurs), in the study plot at Ristie, in Nedderafandal and in Sukkamires, all on the northern quarter of Foula (**Table 1**), and the samples were returned by ferry to Walls and picked up by Glen Tyler (NatureScot).

Table 1. Metadata swab-samples Great Skuas Foula

<p>#999</p> <p>60° 08.627'N, 02° 04.405'W</p> <p>Initially found 04/07/2022</p> <p>Nedderafandal (South Harrier)</p> <p>Very fresh, rigor mortis, intact corpse</p> <p>Territorial area next to nest with dead chick</p>		<p>#1040</p> <p>60° 09.218'N, 02° 04.886'W</p> <p>Found 07/07/2022</p> <p>Ristie - Da Logat</p> <p>Fresh, intact corpse</p> <p>Territorial area, boggy, one of 34 local breeding pairs</p>	
<p>#1044</p> <p>60° 08.631'N, 02° 03.225'W</p> <p>Found 07/07/2022</p> <p>Sukkamires</p> <p>Fresh corpse, intact</p> <p>Territorial area, boggy</p>			

Colony census of Great Skuas, and a comparison with 2007 and 2015 census data (CJC)

The colony census was conducted primarily on the first visits of all breeding areas (first half of June), even though it was evident that mortality was high, and ongoing, such that breeding failures were common and numerous dead adults were found at nest sites (often with eggs and chicks under care) throughout June and early July. AOTs found could be compared to data provided from the 2007 survey, but these should be seen as indications of decline or a population change only: the future will have to show how big losses actually have been. AOT assessments were conducted according to guidelines provided by Walsh *et al.* (1995), using a) nest, eggs, or chicks; b) apparently incubating or brooding adults; c) adults distracting or alarm-calling; and d) pairs or single birds in potential breeding habitat, apparently attached to the area, as indicators of a breeding attempt or territorial occupancy.

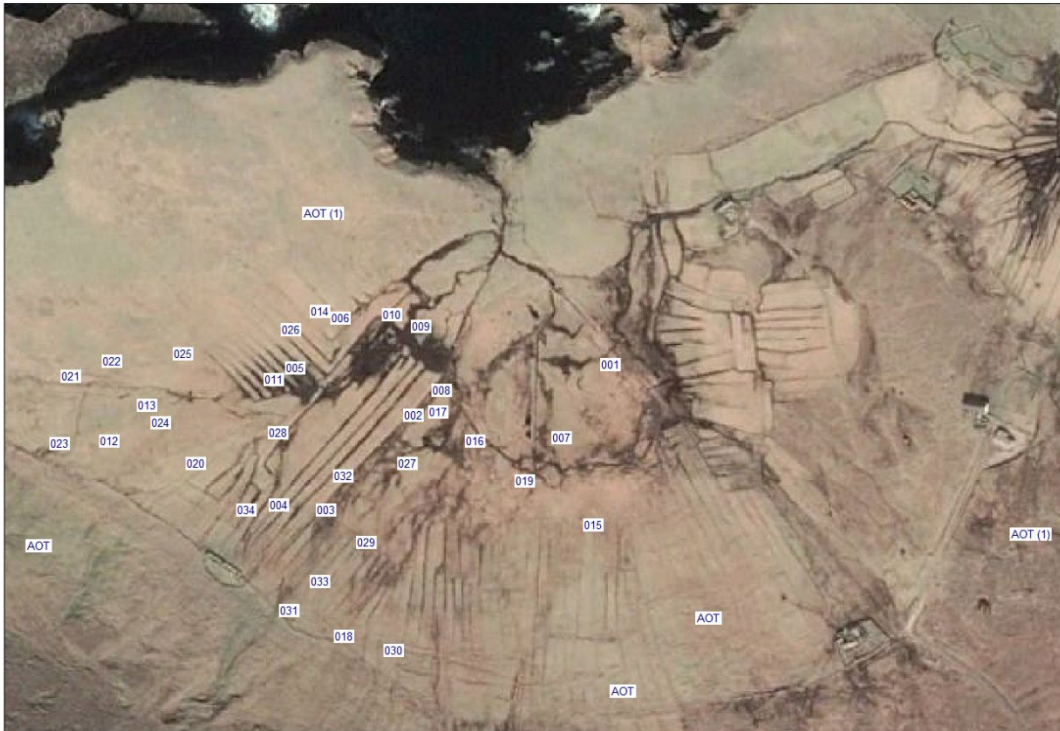


Fig. 4. Monitoring plot of Great Skua breeding success, Ristie – Da Logat – Soberlie area (N Foula)

A second study plot to study Great Skua breeding performance (CJC)

Although Great Skua breeding success was monitored by Sheila Gear as part of her long-term monitoring programme on the study plot along Da West Burn, between Mill Loch, Da Bitten, and Da Lieug (~60°08.17'N, 02°03.67'W), the opportunity was taken to open up an additional monitoring plot, and to study active nests between the Soberlie hill slope, Da Logat and Da Ristie (~60°09.26'N, 02°04.84'W).

Nests with eggs or chicks were marked with small, numbered wooden sticks after 6 June. In total, 34 nests were found, but at least another 3 territorial pairs and 3 single territorial birds occurred within that general (low-lying) area (Σ 34 AON, 6 AOT; **Fig. 4**). When found, eggs were measured (maximum length and breadth to 0.1mm, plus assessments of peculiar shapes or colours of the eggs), but only after thorough disinfection of hands and instruments. Marked nests were checked at three- to four-day intervals while keeping a few meters distance, thereby avoiding any further direct (physical) contact with chicks or eggs, to further minimize the risk of cross-contamination with the avian influenza virus between sites.

A Bushnell DS-4K camera trap was deployed to monitor parental care, behaviour and provisioning routines at nests with hatchlings and/or hatching eggs. Aggression of parents was measured while entering territories in the incubation phase, and around hatching, and in later stages of chick care using the 5-point scale suggested by Furness (1987). Furness (1977) considered the aggression scores to be very consistent from day to day, and used the median score obtained from multiple visits study nests over 20 days of incubation to the level of aggression of each breeding pair. Laying dates were assessed on the basis of back-calculation, by subtraction of an assumed incubation period of 29 days from the day of hatching (Furness 1977). As a result, for predated clutches the exact laying date remained unknown.

Handling the avian influenza virus

Dead birds from Foula were not tested for HPAIV until late July 2022, and it was circumstantial evidence and an international context which made infections with avian influenza the likely prime cause of the excessive mortality amongst Great Skuas (late summer 2021 and summer 2022) and Northern Gannets (summer 2022) on Foula. Under the assumption that large numbers of seabirds were dying of avian influenza HPAI, before any tests were done, serious precautions were taken from the very start of the field work by the observers themselves, in May 2022. These precautions were meant to enhance personal health and safety, to reduce the risk of cross-contaminations within and between taxa, and within and between areas on the island. The steps taken immediately and on a voluntary (common sense) basis agreed with subsequently issued UK Government guidance, such as to leave dead birds in situ rather than collecting them for incineration, and to avoid or strictly minimise direct physical contact with dead animals whenever possible. Also, later guidance from BTO was followed that no (seabird) ringing should be carried out (BTO guidance was issued on 17 June 2022), but not only that, the handling of eggs, chicks and mature birds was entirely stopped when that guidance was issued¹.

Personal safety – direct contact with sick or dead birds was avoided as much as possible. To mark corpses, a pair of scissors was used that was only handled from the same pocket and that was frequently disinfected (**Fig. 5**). Rings were removed with circlip pliers, again without touching the birds with hands or otherwise (using small plastic bags or rubber gloves to handle and temporarily store the rings). Hands, tools, pockets, and anything that was close to the bird was subsequently disinfected before storage and re-use. Swab samples were taken out in the open, with proper personal protection (gloves, medical mouth mask, disinfectants) in a team of two, again minimising direct contact with the swabbed birds. Rings were disinfected in boiling water after a thorough exposure to disinfectant. By giving a special class (CJC), Foula children were pointed at the risks of touching or approaching sick and dying skuas and were advised to not use Mill Loch in 2022, as a water-play ground, given the huge number of dead Great Skuas present along the edge of the lake, in the water, and around their playing instruments (small boats) (**Fig. 6**).

Avoidance of cross-contamination (other birds, other areas) – The entire island was affected by the pandemic, but casualties of Great Skuas were relatively rare in the more cultivated areas around Ham, Da Hametoon, along the east coast, and around the airstrip where most Arctic Skuas are nesting. These areas were therefore visited in different clothes and with different footwear by the key fieldworkers (SG, CJC) than the (known) affected breeding grounds, and marshes where most casualties occurred and where searches were conducted. Clothes, footwear, and luggage were thoroughly disinfected, washed warm, or discarded when the island was left on 11 July 2022 (CJC).

In the Ristie Da Logat study plot, eggs were handled and measured only once (when found), and only after thorough disinfection (hands and instruments). Subsequent nest controls were conducted only from a distance, or by deploying camera traps to monitor parental care and chick provisioning near a small number of nests. Neither

¹ Exact wording of BTO advice, issued 17 June 2022: At a meeting on 16 June 2022, on the basis of expert advice and monitoring data, the Avian Flu Coordination Team at NatureScot made the decision to suspend all ringing research activities within seabird colonies for the remainder of this breeding season, effective immediately; this extends to any ringing activity focused on non-seabird species within seabird colonies. This decision was based both on the risk of onward transmission from infected colonies to other locations, but also on the need to minimise any additional stress experienced by potentially infected birds. Given this position, BTO has taken the decision to suspend ringing activities relating to seabirds at all other sites in Scotland until further notice.

chicks nor adults were handled, no birds were ringed. Sick individuals with clear HPAIV signs (spasms, unable to make controlled movements, unable to fly, or completely docile) were only observed from a distance, filmed and photographed, and never handled. Corpses were dealt with as elsewhere on the island, and were not removed, so that the conditions would be similar as in other parts of the breeding colonies on Foula. At the study plot, careful observations were conducted as critical attempts to detect any detrimental effects of the field monitoring activities (e.g. frequency of new casualties, and locations of casualties relative to the key working areas). In case of doubt, field work was discontinued and more distance was kept. There were no nest visits after hatching, except when the camera traps were deployed for a few days, but otherwise only observations at distance.

The well-being of especially Red-throated Divers *Gavia stellata*, Red-necked Phalaropes *Phalaropus lobatus*, Arctic Terns *Sterna paradisaea*, and Arctic Skuas *Stercorarius parasiticus* was carefully monitored, because either contamination with virus-infested waters was likely (divers and skuas), or because chases by Great Skuas could occur as a result of which for example the terns (heavily affected elsewhere in Europe) could become infected with virus. Distance was kept to all these birds to avoid disturbance, but from some small lochs with breeding divers the floating corpses of Great Skuas were removed to minimize further contacts between the two species (2x). Both divers that were approached for that purpose hatched chicks. None of the species mentioned here showed signs of infections.



Fig. 5. Marking dead Great Skua (wing clipping) with minimal risk of unwanted physical contact.



Fig. 6. Corpses of dead Great Skuas in wet areas on Foula. Top: Numerous dead Great Skuas mixed with bathing individuals at the southern edge of Mill Loch, in good weather a popular playground of the children on Foula. Bottom: Direct contact between livestock and dead skuas near Ristie (N Foula).

Results (1) Great Skua mortality on Foula, summer 2022

Arrival of the skuas, start and development of a pandemic, April – May 2022

Great Skuas returned to Foula in April 2022, and initially there were no signs of avian influenza when the birds reoccupied their territories (SG, 24 April 2022). Given the breeding results and excess mortality witnessed in 2021, however, observers on the island were alert. During the first week of May, the first three corpses of Great Skuas were found, but rather few areas were visited at that time (SG, **Table 2**). However, dedicated searches in the second week of May in club areas and some breeding habitats (e.g. Da Bitten) showed that the Great Skuas were in trouble, given that 84 corpses were found, with particularly large numbers at club areas in The Daal, in Nedderafandal (Bark Hill) and around Da Fleck Lochs. Mortality accelerated in the second half of May, with another 100 dead birds in The Daal, high numbers around Mill Loch (the major club site near the human settlements, also a favourite playing ground of children living on Foula) and at the lochs at higher altitudes (Fleck and Ouvrafandal). With nearly 350 recorded dead birds within one month, coupled with behavioural signs (see below) suggesting that the mortality was caused by avian influenza, it became obvious that this event required a more systematic approach to assess the damage. Some of the birds found in May in The Daal and Da Bitten were sprayed with paint (red or yellow) to avoid double counting, but corpses were typically not touched and therefore not marked.

Table 2. Great Skuas found dead at major club sites and some breeding areas on Foula, May 2022. Observations Sheila Gear (Foula Rangers). 0 = none found, - = not searched.

Site	1 st week May	2 nd week May	3 rd week May	4 th week May
The Daal	-	36	56	47
Mill Loch	1	7	48	0*)
Da Bitten	1	2	9	19
Rossie's Loch	-	9	0	-
Bottle Loch	-	0	2	-
Crougar	1	0	11	-
Bark Hill	-	12	10	-
Fleck Lochs	-	11	29	-
Ouvrafandal Loch	-	6	31	-
Broos o Edlar	-	0	-	-
Tounafield	-	0	-	-
Haamar	-	1	-	-
Totals	3	84	196	66

*) none found, but corpses may be blown under overhanging east bank

June – July 2022

From 1 June, long walks were conducted covering the entire island, covering clubs as well as breeding grounds, to locate, pinpoint (geographical location), describe, and mark (clipping primaries) dead and dying Great Skuas (see Methods; CJC). It was decided to collect complete data, thereby recounting (i.e. including) corpses that had been spray-marked the month before (during this census, 62 colour-marked birds were found in The Daal, 35 in Da

Bitten) in an attempt to assess the timing and trends in mortality all over the island. Search areas and numbers of unmarked corpses found (*n*) are listed below (see also **Figs 1-2** for routes):

- 1 June 2022 Codlafield, Da Fleck, Da Height-Blobers Burn, Hamnafield-Da Muir, Nebbifield, Tounafield (52)
- 2 June 2022 Crougar, Freyers-Da Logat, Ruscar, Skiordar-Stremess (50)
- 3 June 2022 Da Heoag, Nort Veedal, Ruscar, Sandvatten-Da Bitten (53)
- 4 June 2022 Freyers-Da Logat, Ruscar (3)
- 5 June 2022 Gossameadow-Loch Ouvrefandal, Loch Ouvrefandal, Mucklegrind, Nedderafandal-Sandvatten, Ouvrefandal, Sandvatten-Gossameadow (121)
- 6 June 2022 Freyers-Da Logat (12)
- 7 June 2022 Arctic Skua territories (approx loc), Crougar, Da Heoag, Da Sukkamires, Da Sukkamires-Rossie's Loch, Skiordar-Stremess (76)
- 8 June 2022 Crougar, Freyers-Da Logat (10)
- 9 June 2022 Crougar, Da Crookit Burn, Da Mill Loch, Gossameadow-Da Bitten, Ham, Sandvatten-Gossameadow (80)
- 10 June 2022 Blobers Burn-Soberlie, Da Clay Pool-Fleck-Codlafield, Da Heights, Freyers-Da Logat, North Harrier (52)
- 11 June 2022 Freyers-Da Logat (2)
- 12 June 2022 Da Lieug, Da Loch, Da Wurrwusbanks (S of airstrip), Freyers-Da Logat (5)
- 13 June 2022 Freyers-Da Logat (1)
- 14 June 2022 Hamnastouis, Smallie, The Daal, The Daal club area, The Kirk, The Noup (187)
- 15 June 2022 Crougar, Freyers-Da Logat (4)
- 16 June 2022 Crougar, Da Hamnastouis, Da Sukkamires, Gossameadow-Da Bitten, Mill Loch, Nedderafandal-Sandvatten, South Harrier (35)
- 17 June 2022 Crougar, Sandvatten-Gossameadow (5)
- 18 June 2022 Cemetery Hametoon, Crougar (2)
- 19 June 2022 Blobers Burn-Soberlie, Codlafield (13)
- 21 June 2022 Bark Hill, Loch Ouvrefandal, Nedderafandal-Sandvatten, Ouvrefandal (35)
- 22 June 2022 Crougar, Freyers-Da Logat, Ruscar (10)
- 23 June 2022 Blobers Burn-Soberlie, Da Kame, Da Lieug o da Fleck, Nebbifield-Harnalie, Soberlie Hill-Da Nort Bank (41)
- 25 June 2022 Da Heoag, Da Sukkamires-Rossie's Loch, Da Toon Ham, Rossie's Loch, Stremness (19)
- 26 June 2022 Crougar, Da Bitten, Da Burns (14)
- 27 June 2022 Brustins, Hametown Wilse-Tounafield, Mucklegrind, The Brethren, The Daal, Tounafield, Yelpers Burn (29)
- 28 June 2022 Da Bitten, Da Mill Loch, Ristie-Da Logat (11)
- 29 June 2022 Crougar (1)
- 1 July 2022 Da Sukkamires (3)
- 2 July 2022 Da Fleck, Netherfandal, Ristie-Da Logat, Soberlie Hill-Da Nort Bank (35)
- 3 July 2022 Crougar, Da Loch, Da Sukkamires, Freyers-Da Logat, Netherfandal (19)
- 4 July 2022 Bark Hill club, Netherfandal, Freyers-Da Logat, Netherfandal, Sandvatten-Gossameadow (26)
- 5 July 2022 Da Heights, Da Loch, The Daal (33)
- 7 July 2022 Crougar, Gossameadow-Da Bitten, Netherfandal, Ristie-Da Logat, Sukkamires 6
- 8 July 2022 Ristie-Da Logat (1)
- 9 July 2022 Da Bark Hill, Da Fleck, Freyers, Loch Ouvrafandal, Ouvrafandal, Sandvatten, Nedderafandal (37)
- 10 July 2022 Da Heoag (4)

Further searches were conducted in the second half of July (SG; routes not mapped)

- 16 July 2022 Mill Loch to North end Myres (30)
- 17 July 2022 Bitten, Bark Hill to Burn Ouvrafandal (27)
- 18 July 2022 Logat and Soberlie crofts (6)
- 21 July 2022 Yockle, Gillick o Gill, Muir, Boddlifield (19)
- 22 July 2022 Hamar, back of Tounafield (26)
- 23 July 2022 Heights to Rossies Loch (27)
- 24 July 2022 SE coast (4)
- 26 July 2022 Noup (41)
- 29 July 2022 Soberlie, Fleck, Ouvrafandal (38)
- 30 July 2022 Burns, Nedderafandal, Bark Hill, Codlifield (34)
- 31 July 2022 Kame, Nebbifield, Waster Hoevda, Harnali (20)

A total of 1400 different corpses of great skuas were found during these searches, of which 100 individuals were (colour-) ringed earlier in life. The distribution was non-homogeneous, with clusters of corpses in relatively wet areas (lochs, burns, swamps), many of them known as clubs or bathing sites (**Fig. 8**). The terrain all over Foula is such that corpses were very easily missed, so that the result must be seen as a conservative figure of the number

of Great Skuas lying dead on the island, let alone the number that died in total. Steep slopes were, by the very nature of that terrain, not covered in full during searches, but the densities of dead skuas were much lower in these parts of the breeding colonies, such that the overall distribution can be seen as a good representation of spatial patterns in densities of dead Great Skuas on the island. Some of these slopes were covered in late July, yielding several dozens of often rather old carcasses. See **Appendix 3** for monthly distribution patterns.

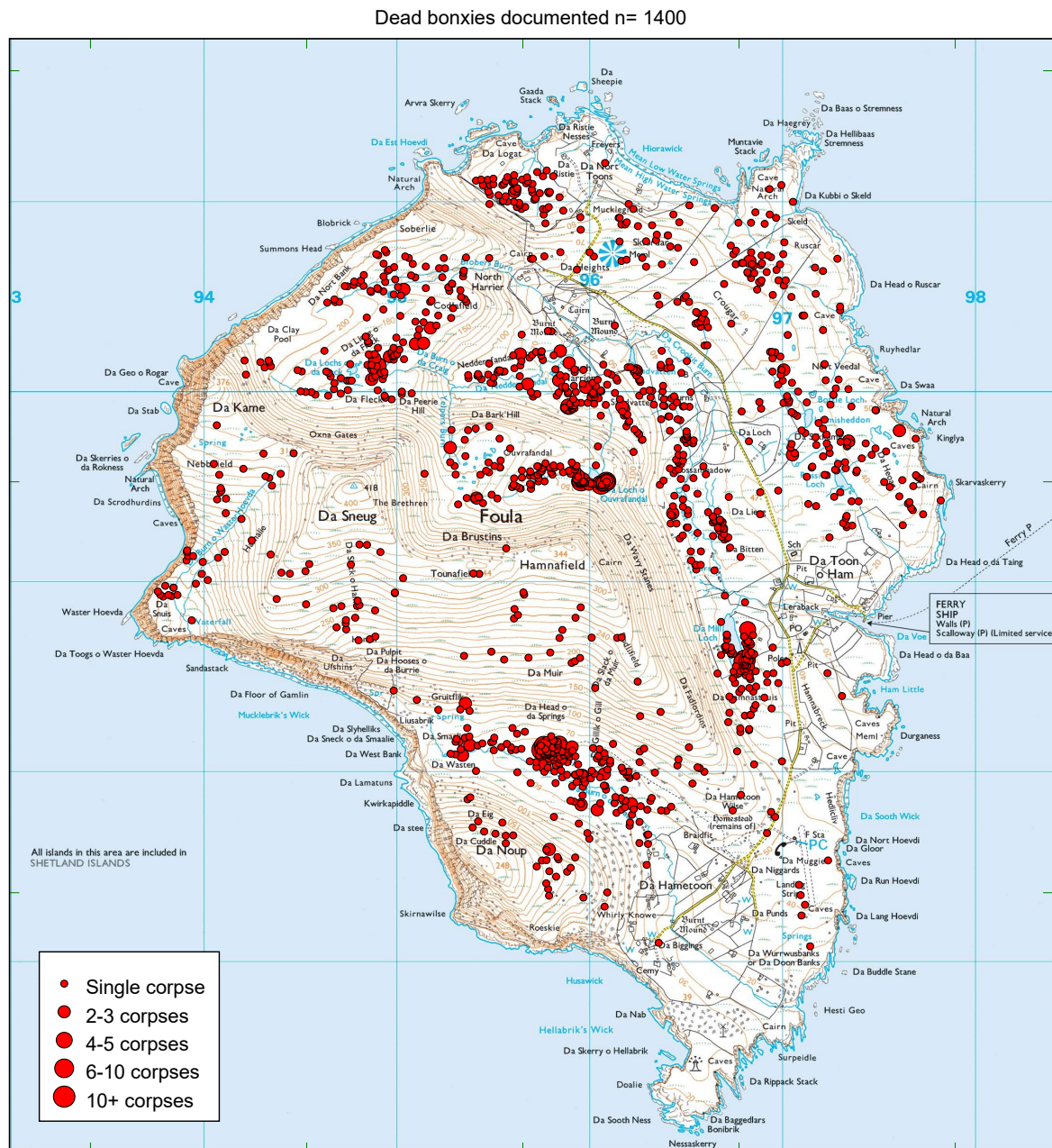


Fig. 8. Dead Great Skuas found on Foula, summer 2022 ($n = 1400$). Background map of Ordnance Survey <https://i.pinimg.com/originals/e6/a5/b9/e6a5b9825e5fda231a52accba0781797.jpg>

Ringed individuals were not evenly distributed over the area either, when compared to the distribution pattern of all dead birds, and the distribution pattern reflects distinct patterns in ringing effort (R.W. Furness *pers. comm.*). While 7.1% were ringed overall ($n = 1400$), relatively high proportions occurred at the clubs of Bark Hill in Nedderafandal (12.2%, $n = 123$), in Da Bitten-Gossameadow (12.7%, $n = 118$), in unassigned areas the northern half of the island (Soberlie Hill and Da Nort Bank to Da Height, Crougar, Sandvatten towards Da Heaog and south

towards Da Toon o Ham, 11.2%, $n= 268$), and around Rossie's and Bottle Lochs (9.7%, $n= 93$). Rather low numbers of rings were found in the Ristie-Da Logat study plot (4.7%, $n= 64$), in Ouvrafandal (4.1%, $n= 123$) and particularly at The Noup (2.6%, $n= 38$) and in The Daal (1.8%, $n= 278$); **Table 3, Fig. 9**). Ringed birds originated from Foula (87%), Fair Isle (7%), Fitful Head (3%), Hermaness (2%; all Shetland) and Westray (1%, Orkney; $n= 100$). Birds from Foula were usually ringed as chicks (84%, between 1986 and 2012), the rest as immatures (2%, 2001), and adults (14%, 2003-2010; $n= 87$). Mean age of Great Skuas ringed on Foula was 20.7 ± 5.3 years, range 10-36 years, $n= 87$).²

In earlier years, 'foreign' ringed Great Skuas (ringed away from Foula) were rare, if not completely unknown on the island (R.W. Furness *pers. comm.*). Dead Great Skuas that were ringed outside Foula were mostly found in southerly areas (south of Ouvrafandal), areas where rings were overall rather uncommon (**Fig. 9**). All these birds had been ringed as chick, and had a mean age of 15.3 ± 7.9 years, range 6-28 years, $n= 13$ when found.

Table 3. Frequency of occurrence (%) of dead Great Skuas carrying metal rings in various search areas on Foula.

	Latitude	skuas found	ringed	Foula	elsewhere
Ristie-Da Logat	60.154°N	64	4.7%	3	
unassigned northern half	60.147°N	268	11.2%	29	1
Fleck Lochs	60.146°N	88	6.8%	5	1
Bark Hill/Nedderafandal	60.145°N	123	12.2%	14	1
Rossies-Bottle Loch	60.142°N	93	9.7%	8	1
Da Bitten/Gossameadow	60.140°N	118	12.7%	14	1
Ouvrafandal	60.140°N	123	4.1%	3	2
Mill Loch	60.131°N	105	6.7%	6	1
unassigned southern half	60.131°N	102	3.9%	2	2
The Daal	60.127°N	278	1.8%	3	2
The Noup	60.122°N	38	2.6%		1
		1400	7.1%	87	13

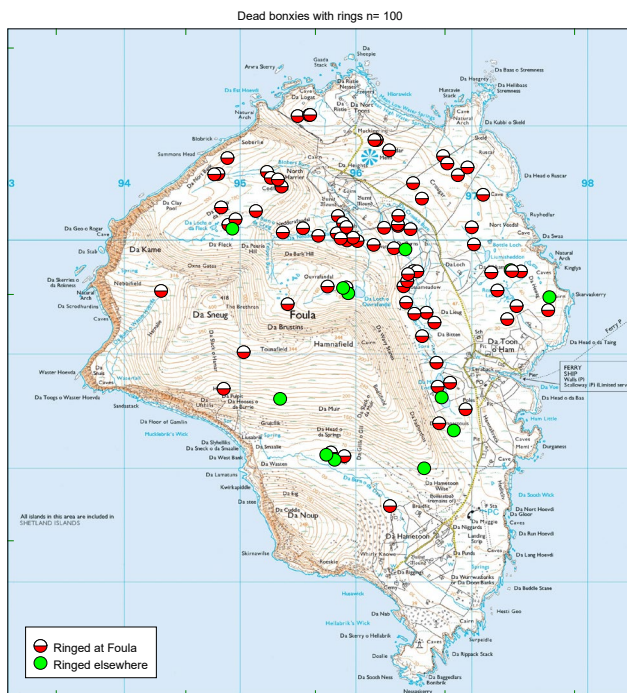


Fig. 9. Dead Great Skuas carrying metal rings, found on Foula, summer 2022 ($n= 100$).

² Adding 6 years to birds ringed as adults and 2 years for skuas ringed as immatures.

The corpses found varied in decomposition rate from very old (14.9%), old (19.4%), rather old (22.4%), rather fresh (24.2%), fresh (13.3%), to very fresh (3.1%), or dying (2.7%; $n = 1400$). Using the rate of decomposition relative to the date of finding, the overall timing of the mortality was reconstructed (**Fig. 10**). The data suggest that the mortality accelerated in late May and early June, then slowed down, but picked up again later in the season. The results would indicate that around 41-57% of all Great Skuas found had died already in May, prior to hatching, and around 10-15% in July during chick care. Peak mortalities occurred relatively early in four areas: Da Fleck lochs, Mill Loch, Rossie's and Bottle lochs, and in The Daal, all major club and bathing sites of Great Skuas, but the mortality must have spread as a bushfire over Foula, almost immediately after the first signals of infections, given overall minor differences in apparent timing between areas.

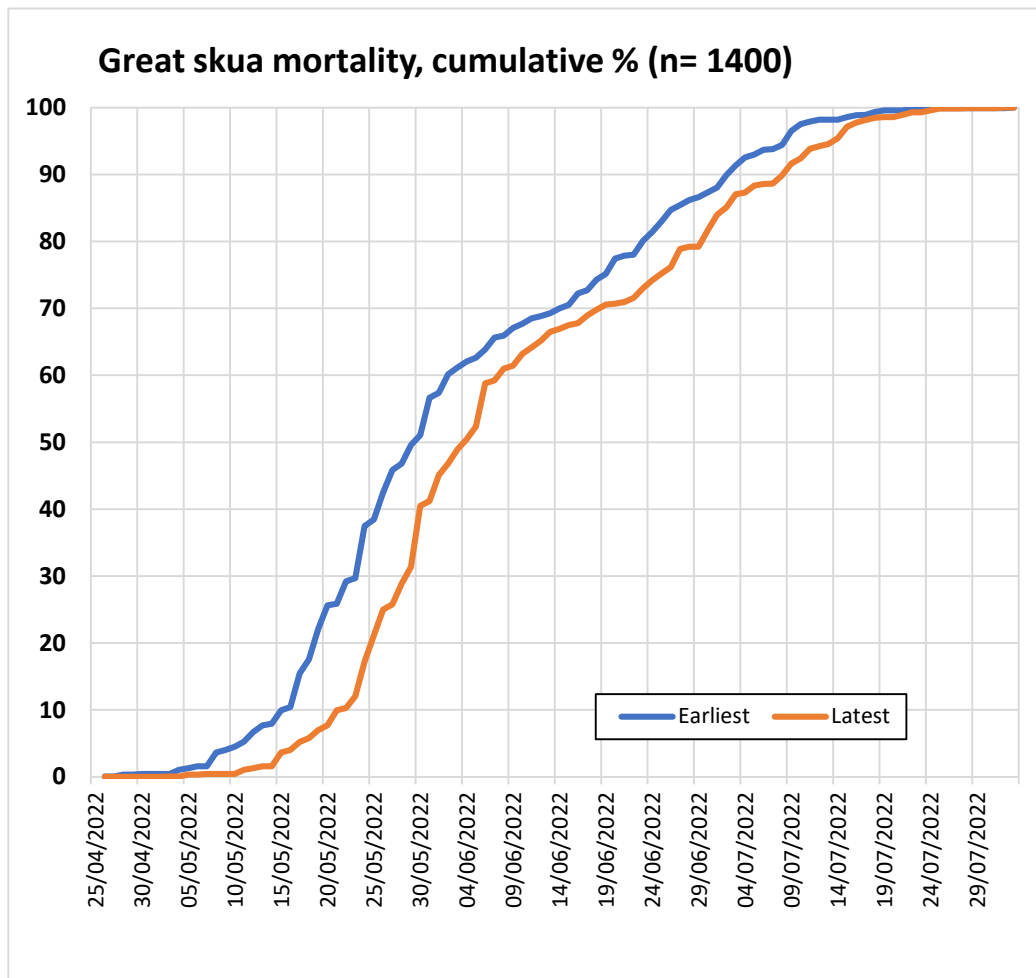


Fig. 10. Expected timing of Great Skua mortality ($n = 1400$, cumulative trend) based on corpses found all over Foula, 1 June – 1 August 2022, based on the condition of the corpses when found (see Methods, see Appendix 1).

The disintegration of carcasses started fairly soon, but at first as a result of insects entering the corpse, usually via the cloaca (**Appendix 2**). Insects entered the bodies usually via the cloaca, the beak or the eyes, consuming the corpses from the inside out. Several mice were seen to scavenge on the carcasses, damaging feathers and skin, but usually from below (under the corpse), not from above, leading to a great mess in contour feathers.

Evidence for scavenging activities of birds emerged in some rather fresh birds, still only rarely, but increased markedly in older corpses (pecking wounds to open up the body, flesh, intestines or other organs eaten, usually up to the bare bone; **Appendix 2**). Overall, at most 12% of the corpses found had signs of scavenging activities, likely or possibly inflicted by birds. (Very) fresh corpses rarely showed evidence of scavenging by conspecifics or other birds, meaning they would typically remain untouched for at least a week or so (**Fig. 11**).

Great Skuas scavenging on conspecifics were rarely seen in action. SG observed Great Skuas at the Daal club attacking obviously ill birds several times during May. In June and July, evidently sick birds that could still fly, entering territories of other skuas and were typically vigorously attacked. One Great Skua was seen eating a fresh corpse on 11th May. As the season progressed they mainly seemed to ignore dead and dying birds.

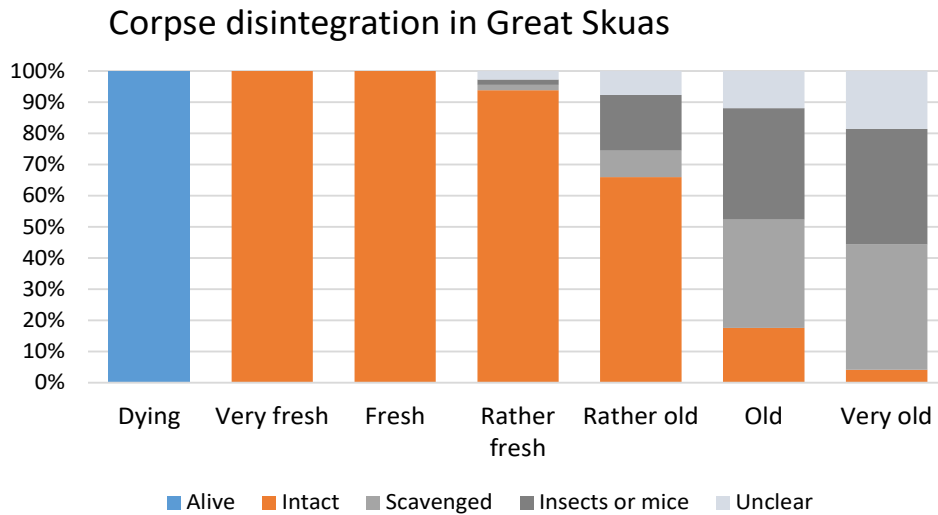


Fig. 11. Corpse disintegration as a result of scavenging by other birds, or by mice or insects, of Great Skuas ($n= 1087$, %) based on corpses found all over Foula, 1 June – 10 July 2022.

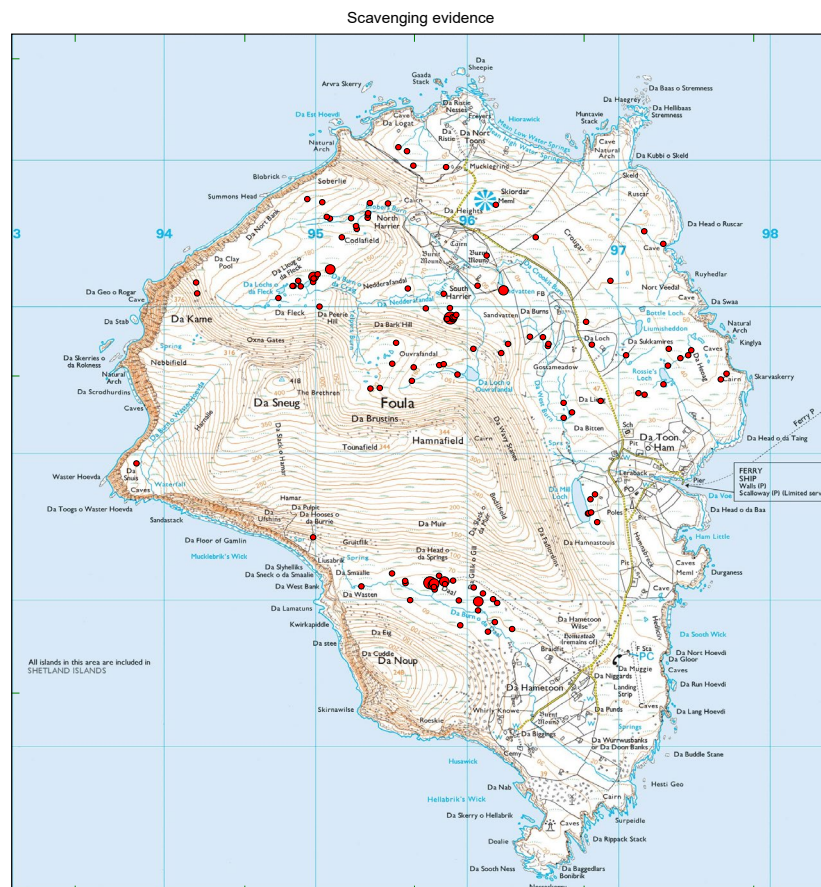


Fig. 12. Corpse disintegration of Great Skuas as a result of likely scavenging by conspecifics or other birds ($n= 133$) based on descriptions made of corpses found all over Foula, 1 June – 10 July 2022.

Carcasses of which it was believed that they were scavenged by other birds (conspecifics included) had a peculiar distribution, with notable clusters at wet or damp areas around or at club sites and bathing places: Bark Hill/Nedderafandal (14%), Da Bitten-Sandvatten (10%), Fleck Lochs – Soberlie (14%), The Daal (26%), and smaller frequencies around Rossie’s -Bottle lochs (8%), Ouvrafandal (6%), Mill Loch (5%), and Ristie - Da Logat (3%; $n= 133$, Fig. 12).

Behavioural signs suggesting H5N1 infections in seabirds

Dying Great Skuas typically stumbled around when disturbed, walked in circles or without any co-ordination, tripped over their own feet, rolled over, crashed down soon after taking wing, and could be motionless with a head drooping down or swinging about. When they finally collapsed on their breast, such birds often had their head turned backwards over ‘the shoulders’ (Fig. 13), or with the bill pointing upright, as silent witnesses of final spasms. We considered these behavioural aspects and postures being further evidence that the birds suffered from avian influenza. ‘Postures’ of dead Great Skuas were recorded during the surveys between 1 June and 10 July 2022. Normally, when dead adults were found, they lie face down, often with one or both wings outstretched. SG did not recall seeing fresh adult corpses before, lying on their backs with their legs in the air. Of 479 corpses in which the ‘position’ of the bird was thought to be representative for the posture in which the bird had died (very fresh to rather fresh corpses only), 43.0% were laying on their back, 57.0% face down on their belly (Table 4). With hindsight, one could probably argue that corpses that were found afloat in water were unintentionally ‘downgraded’ regarding their expected date of dying, relative to corpses high and dry on land. Fortunately, that category is relatively small (68 individuals; Table 4).



Fig. 13. Some typical postures of Great Skuas found dead with ‘frozen spasms’ and heads swung over shoulders (Appendix 6).

Table 4. Postures of Great Skuas found dead, 1 June – 10 July 2022.

	Sitting	On back	On belly	Sideways	Afloat	Unclear
Dying	33					
Very fresh		12	31	1		
Fresh		74	89	1		2
Rather fresh		120	153	2	8	9
Rather old		87	116	6	25	28
Old		31	51	4	30	77
Very old		5	14		5	73
		206	273	14	68	189

Test results, July 2022

The three Great Skuas tested, using swab samples taken from cloaca and buccal cavities on each (fresh) bird, were all found positive for H5N1 (Glen Tyler, NatureScot *pers. comm.*).

Results (2) Great Skuas breeding at Foula in 2022

Estimates of the number of apparently occupied territories (AOTs) of Great Skuas on Foula slowly declined from an all-time high of 3180 in 1977 to 2670 in 1980 (Furness 1983a), and this decline continued from around 2500 AOTs in the late 1980s, to 2300 AOTs around the turn of the century and 1657 and 1846 AOTs respectively during the most recent censuses in 2007 and 2015 (JNCC, Seabird Monitoring Programme database). The 20 study plots used for the 2007 census (A-W) plus the results obtained in that year are shown in **Fig. 14**. In 2022, during the first few weeks of June, all sectors were visited and most were sufficiently covered under good conditions to produce a more or less reliable count. Most problematic were sectors T, U, and V because the weather was appalling during the first visit (14 June 2022; fog, drizzle, low cloud and strong gusts of wind), while the second and third visits (27 June and 5 July 2022) were in fact too late in the season to produce comparable and meaningful results.

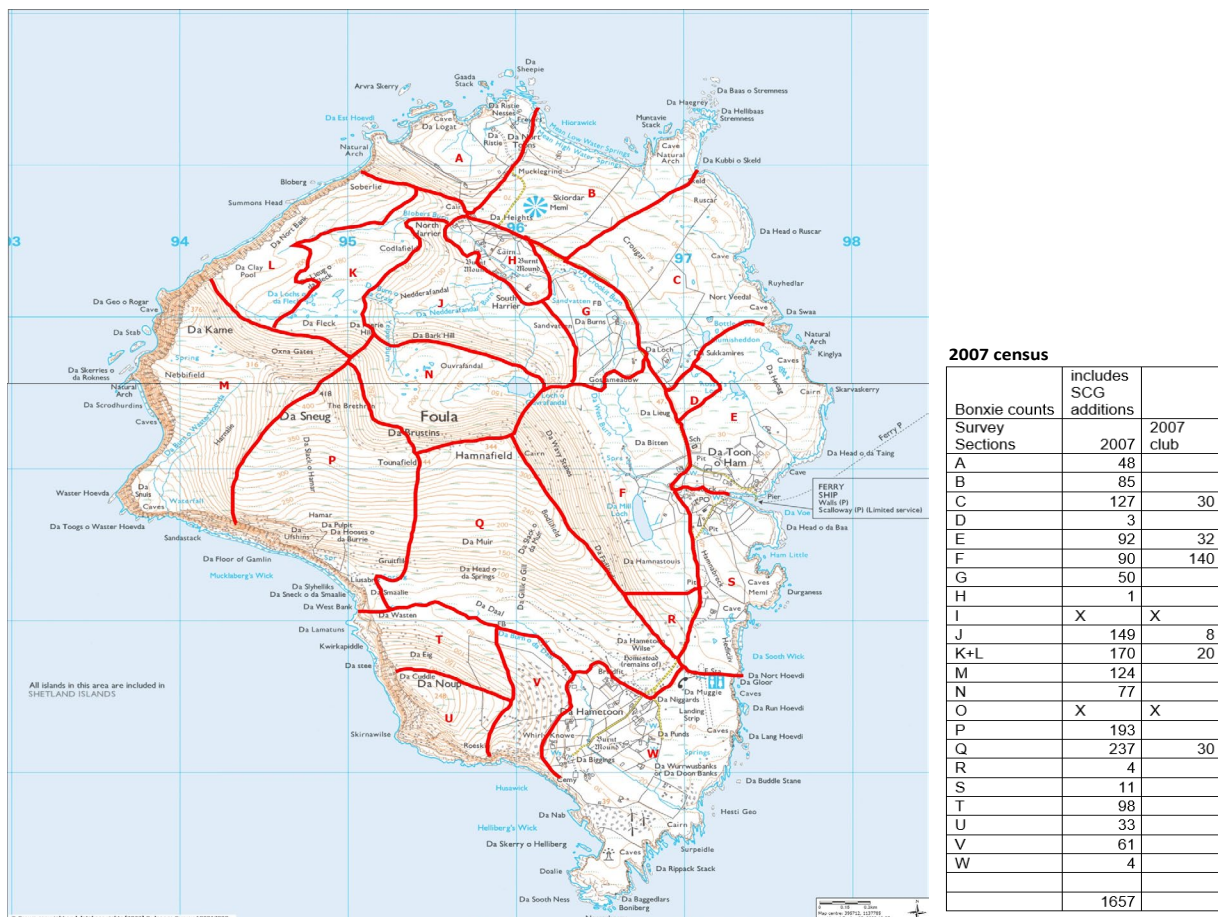


Fig. 14. Sectors A-W used for colony censuses in 2007 and 2015 (Glen Tyler, NatureScot, *pers. comm.*) and the number of AOTs recorded in 2007 plus the number of Great Skuas reported at club sites. The letters I and O have not been used and sectors K and L are usually combined.

The results of area censuses in 2022 are summarised in **Table 5**, in comparison with data collected in 2007 and 2015 respectively. Substantial declines in breeding numbers (or AOTs) were found in all areas, but most particularly in sectors **M**, **P**, and **Q** (69-82% decline in comparison with the 2015 census), where especially at higher altitudes rather few territorial skuas were found. Suggestions for strong declines at The Noup cannot be accepted, given poor conditions during the 2022 survey and rather late subsequent area visits. A 15% increase was found in sector **A**, despite serious mortality in May. Mortality largely stopped in that area in June and July. The rather modest decline (36%) in the areas between Gossameadow and Da Hamnastouis (**F**, including the Da Bitten study plot) may be misleading, because mortality was ongoing in June and the area went remarkable silent during chick care (CJC & SG *independent pers. obs.*), suggesting either large scale early departures, or a much stronger decline in surviving adults than is indicated by the count presented here. Further relatively modest declines occurred in Ouvrafandal (**N**, 38% relative to 2007, but only 6% relative to 2015) where later visits revealed rather little nesting activity in comparison with the first round, as in sector **F**. The rather large sector between The Kame, Da Fleck, Da Nort Bank and Soberlie (**K-L**, 40%) remained relatively well-populated into July with fairly aggressive breeding birds and rather many visible and developing chicks all over.

Some observed changes, such as a relatively strong reduction in breeding numbers at higher altitudes, may have been ongoing for a longer period (SG). In 2000 in sector **M**, SG along with Scottish Natural Heritage (SNH) counted 243 AOTs, included Harnalie and The Sneug up to the top. In later years, it was found that the colony moved downhill, until they covered almost all the low ground, while numbers breeding high up decreased together with numbers using the high clubs (just down from the top of the Noup, the Sneug and just south east down the ridge from the top of Hamnafield), until these were no longer in use. Alternative new clubs broke out lower down. The early count in 2022 would suggest that Great Skuas at Foula in the laying phase had declined by at least 53% in comparison with 2007, by around 58% compared with the results collected in 2105 (**Table 5**). Further mortality occurred later in the breeding season such that an even stronger decline is more than likely.

Table 5. Territorial Great Skuas on Foula (AOTs) in early June 2022, in comparison with surveys in 2007 and 2015 (see **Fig. 13**). The 2015 data are read from handwritten notes on maps provided by SG. %^{change} is the difference between 2015 and 2022.

Sector		2007	2015	2022	% ^{change}	Notes 2022
A	Ristie – Da Logat	48	39	45	+15%	
B	Da Height - Stremness	85	117	49	-58%	
C	Crougar – Ruscar	127	137	70	-49%	
D	E of Da Lieug	3	6	3		
E	Ham – Da Heoag	92	114	50	-56%	
F	Gossameadow – Da Hamnastouis	90	86	55	-36%	Rapid decline in June
G	Sandvatten - Gossameadow	50	45	28	-38%	
H	North – South Harrier	1	3	0		
J	Da Nedderafandal	149	211	83	-61%	Rapid decline in June
K+L	Fleck lochs – Soberlie	170	149	91	-39%	Quite busy into July, fledglings in July
M	Nebifield, Waster Hoevda and Harnalie	124	128	36	-72%	Max 42, more likely 36!
N	Ouvrafandal	77	51	48	-6%	Quite busy into July
P	Da Sneug, Tounafield – Ufshins	193	217	68	>-69%	Poor data lower slope, low densities upper slopes
Q	Hamnafield – Da Daal	237	317	75	-76%	First visit rather late, much less than 2007
R	Kirk area	4	0	3		
S	Hamnabreck	11	20	1	-95%	Some more birds hanging around, but not clearly attached
T	N flank Da Noup	98	64	35	-45%	Poor weather during first visit
U	Da Noup	33	18	n.d.	n.d.	In clouds during first visit
V	E flank Da Noup	61	96	37	-61%	Poor weather during first visit
W	Da Hametoon – South Ness	4	2	1		One of which HPAIV
Totals		1657	1820	778	57%*	*) excluding sector U

Results (3) breeding performance and mortality of Great Skuas in study plots



Fig. 15. Great Skua alighting at nest 001 in the monitoring plot Da Ristie – Da Logat (N Foula), 10 June 2022 (12:58) (note faulty camera date settings). The nest was occupied by a solitary bird when found and it failed during incubation.

Great Skuas breeding at Ristie – Da Logat

The study plot at Ristie – Da Logat was chosen as a second location to monitor the breeding success of Great Skuas (N Foula). The area is also sufficiently ‘distant’ from the long-term monitoring plot at Da Bitten (E Foula) to provide truly complimentary data. The shallow area turned out to be a rather high-density colony area on extremely wet soil, where at least some breeding birds seemed to use local fresh water resources to bath and preen, often even within their own territories, rather than to fly towards the larger bathing places elsewhere on the island. The area is part of subregion A of the NatureScot Great Skua census (**Fig. 14**), where 48 AOTs occurred in 2007 and 39 in 2015 (Glen Tyler & Sheila Gear *pers. comm.*; **Table 5**). The breeding population of the area during the first two weeks of June was estimated to number at least 45 AOTs, 34 of which were active nests within the chosen study plot. Note that this assessment was made *after* ~80% of the Great Skuas actually found dead within the area had already died, given the level of decomposition of the carcasses (43-48 individuals; see below). If these were all local, prospecting birds, subregion A may have originally numbered at least 57 pairs in 2022, or considerably more birds than in either in 2007 or 2015. Between 10 and 15 birds died during the nest monitoring itself, which included one partner of active pairs as well as complete pairs. Self-chosen access restrictions (to minimise the risk of cross-

contaminations of the virus) made it difficult to locate pairs in which one or both partners had surely died. Observations and information collected with camera traps suggested that around 8-10 nesting attempts on the study plot failed with the strong suspicion that one or both partners had died, which would compare well with the additional number of birds found dead in the area since the monitoring started. After 10 July, at least one further adult was found dead in the area (SG).

Skua mortality at monitoring plots Ristie – Da Logat and Da Bitten, May-July 2022

As part of the monitoring programme, Ristie was visited and surveyed for the first time on 2 June 2022, when 19 corpses of Great Skuas were found and marked. Excluding various ‘accidental’ finds during nest controls or other area visits (including older corpses that were clearly missed during the first visit), further searches revealed 12 corpses on 6 June and 9 corpses on 8 June until a total of 58 dead Great Skuas was established at 10 July 2022. Carcasses were evenly spread over the study area, but exclusively in areas where also active nests were located (**Fig. 16**). Reconstructing the mortality based on the condition of the corpses found, shows that the mortality commenced probably in late April or early May (assuming the oldest of corpses were around one month old), surged in the second half of May, and then declined markedly (**Fig. 17**). Six more birds were found 18 July 2022 (not included in **Fig. 17**): 1 dying, 3 fresh, 2 rather fresh (SG).

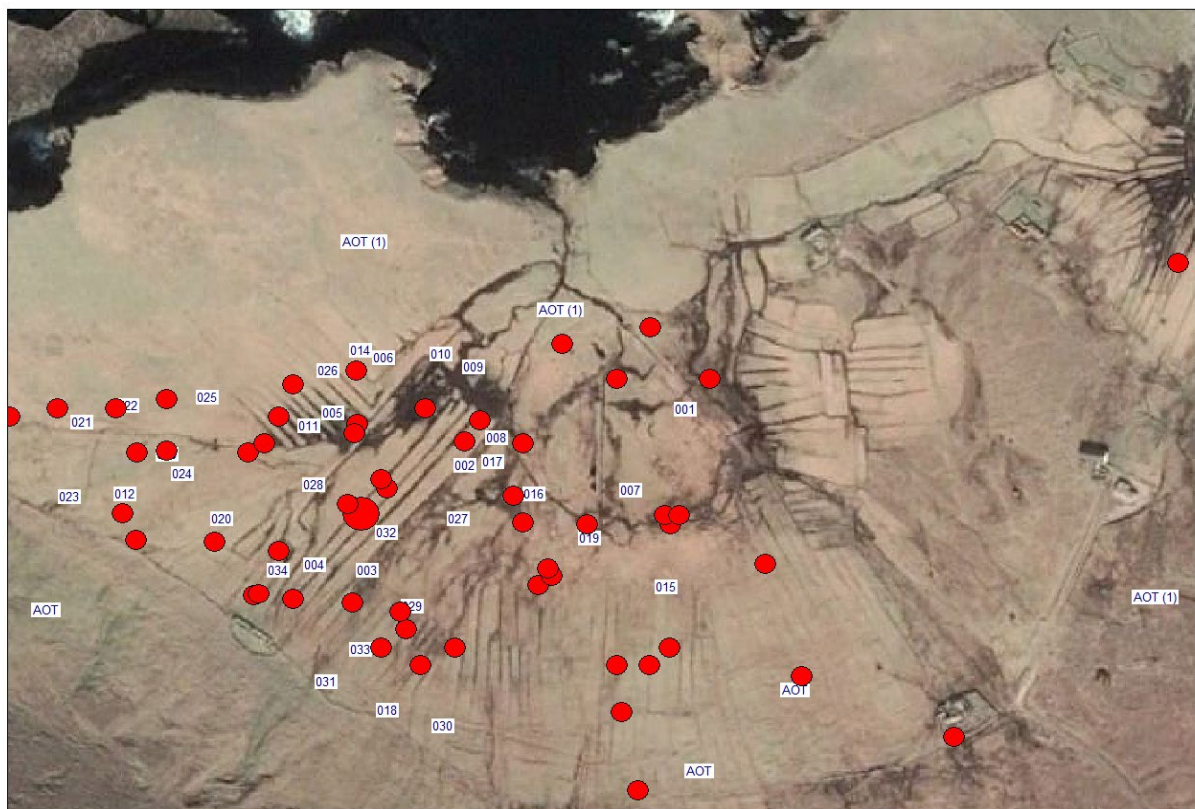


Fig. 16. Dead Great Skuas ($n=58$) found in the monitoring plot Da Ristie – Da Logat – Soberlie (N Foula), June-July 2022, relative to marked active nests ($n=34$ AONs) and apparently occupied sites without nests containing eggs ($n=6$ AOTs) in that same period. The three most northerly AOTs were occupied by solitary birds. Note that AOTs were all at the periphery of the main breeding concentration, but additional AOTs in the high-density nesting area would most likely be overlooked.

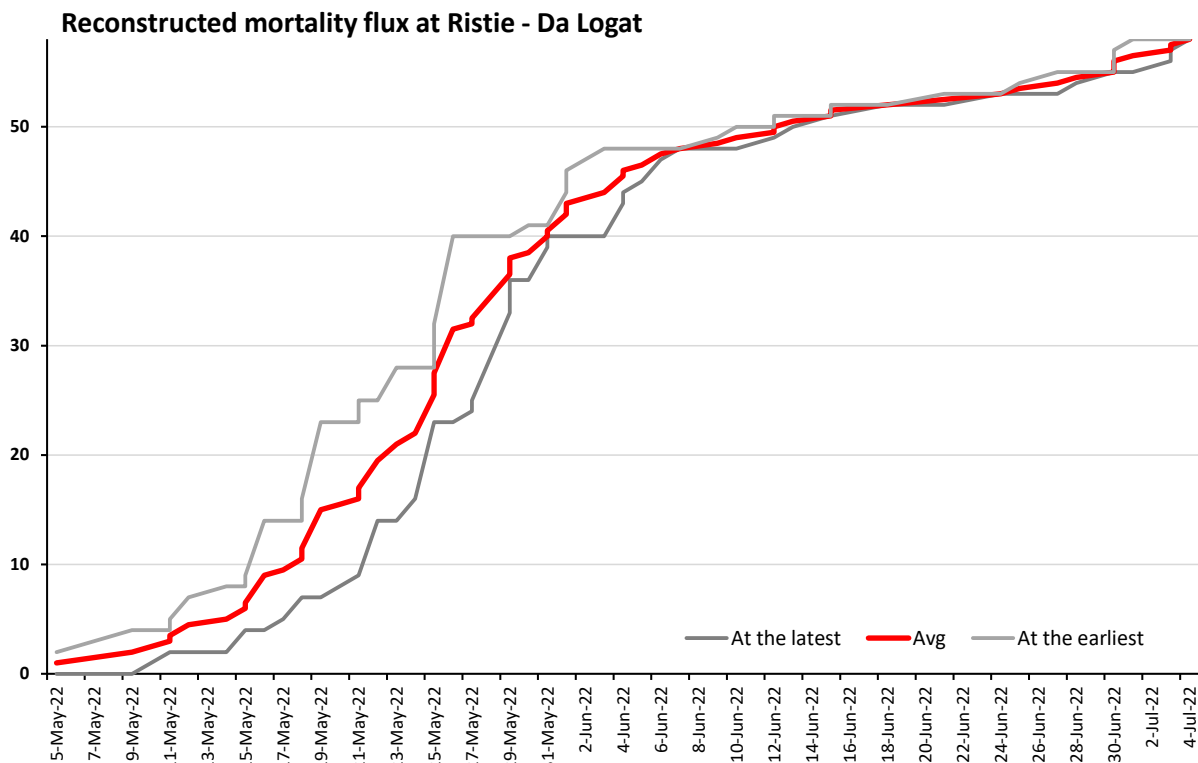


Fig. 17. Expected timing of Great Skuas mortality ($n= 58$, cumulative numbers) based on corpses found in the monitoring plot Da Ristie – Da Logat – Soberlie (N Foula) in the period 1 June – 10 July 2022, based on the condition of corpses when found.

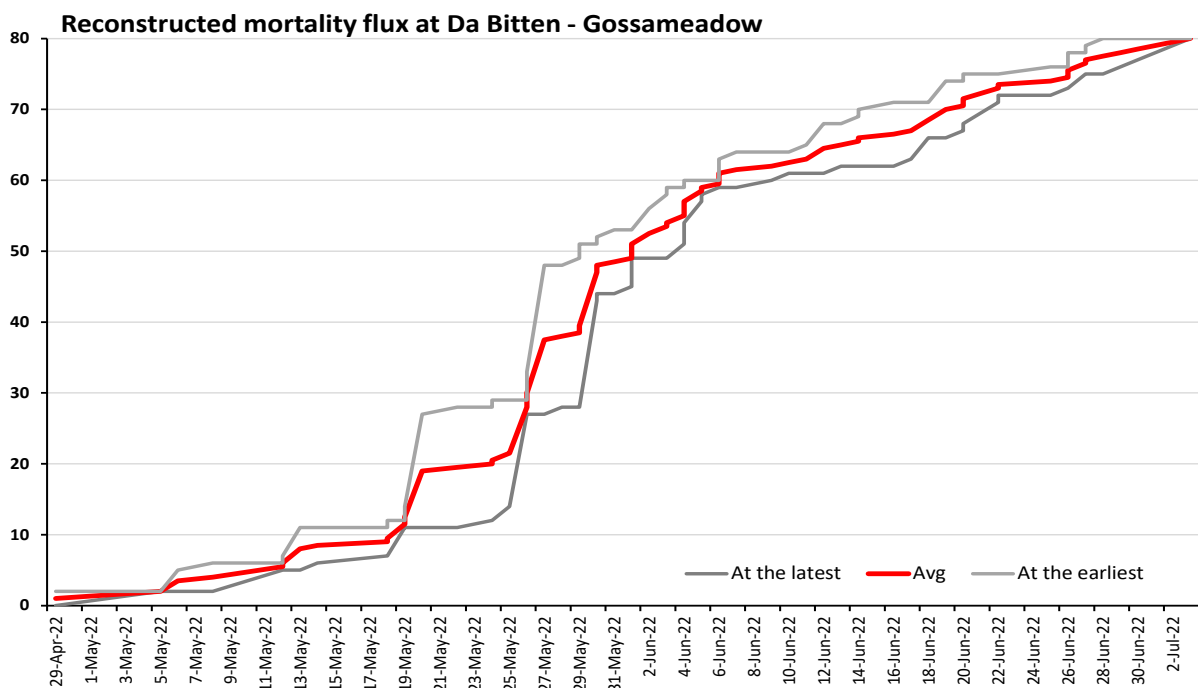


Fig. 18. Expected timing of Great Skuas mortality ($n= 80$, cumulative numbers) found in the long-term monitoring plot Da Bitten - Sandvatten (see Fig. 19) 1 June – 10 July 2022, based on the condition of the corpses when found.

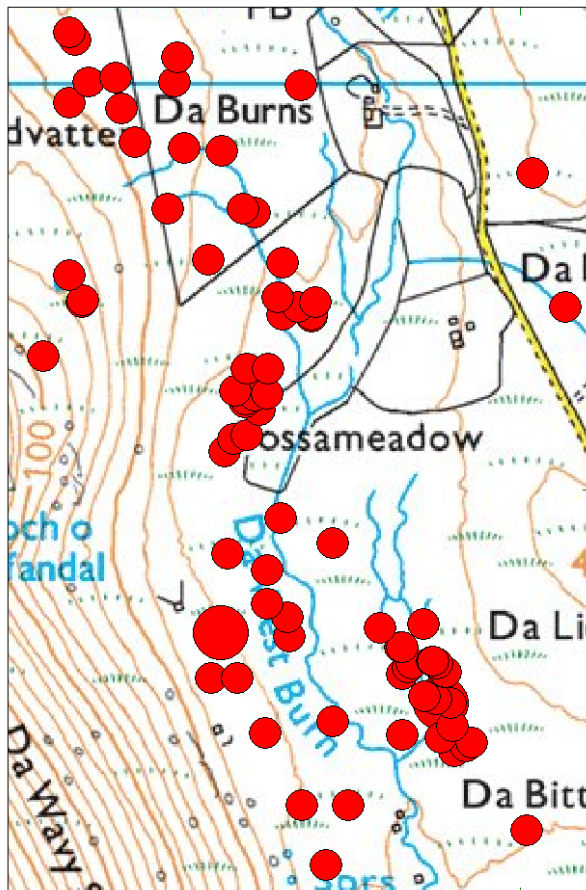


Fig. 19. Dead Great Skuas ($n=80$) found in the monitoring area Da Bitten – Gossameadow – Sandvatten (E Foula) during systematic searches 3-June – 10 July 2022.

Based on area searches and corpses examinations conducted between 3 and 12 June 2022 in the monitoring area around Da Bitten (Da West Burn area from Gossameadow to just north of Mill Loch), mortality of Great Skuas again commenced in late April, and showed a strong surge after mid-May, to gradually, but continuously increase further throughout June (**Fig. 18**). Precise nest locations for this study area are unknown, but the corpses were found in discrete clusters, not widespread (**Fig. 19**).

Reproductive performance of Great Skuas at Ristie – Da Logat

Clutch size across 34 AONs amounted to 1.74 ± 0.45 eggs (or 1.59 ± 0.64 , if three non-laying pairs with well-established AOTs are included; **Table 6**). One nest contained a dwarf egg (45.2×34.8 mm), two clutches contained two bright blue eggs, one nest of which with slight eggshell deformations (shape, calcium) in both eggs. All other eggs were seemingly normal. Five eggs (in three nests) were damaged or leaking when found, and only one of these could be measured. One nest contained small hatchlings when found. Excluding the dwarf egg, the **size of the eggs** that could be measured amounted to $70.5 \pm 3.4 \times 48.8 \pm 1.5$ mm ($n = 49$), which included the blue, slightly malformed eggs, which were the smallest of all eggs found (63.4×47.1 and 63.2×46.5 mm; **Fig. 20**). Considering the first hatchlings at Ristie (well dried chicks observed 8 June 2022), **laying commenced** around 8 May 2022, but continued at least until 10 June 2022. The timing of first egg-laying compares well with that on the long-term monitoring plot in Da Bitten, where the first hatchling was observed on 4 June 2022, suggesting a laying date of ~6 May 2022 (SG).

Table 6. Hatching success at monitoring plot Ristie – Da Logat in 34 nests marked 4 June – 4 July 2022. Shown are nest number, marking date, calculated laying date (hatching date minus 29d), clutch size, egg size (LxB^{mm}), egg volume (cc), and outcome of the attempt. Dwarf egg in red, blue eggs in blue. Eggs were not sequenced.

Nest	Marked	Laying date	Clutch	Egg1		Egg2		Vol 1	Vol 2	Fate of the eggs		
001	04-06-22	n.d.	2	68.3	x	47.9	67.0	x	48.5	75.2	75.6	Predated
002	04-06-22	23-05-2022	2	75.6	x	49.1	71.7	x	49.8	87.5	85.4	One rolled out, 1 egg hatched
003	04-06-22	n.d.	2	73.0	x	48.8	68.6	x	48.2	83.4	76.5	Predated
004	04-06-22	25-05-2022	2	68.1	x	48.9	69.5	x	48.8	78.2	79.4	Hatched
005	04-06-22	04-06-2022	2	68.7	x	46.7	68.0	x	50.1	71.9	81.9	Hatched
006	04-06-22	18-05-2022	1	76.2	x	47.9			83.9			Hatched
007	06-06-22	20-05-2022	1	67.1	x	48.2			74.8			Hatched
008	06-06-22	n.d.	2									Eggs predated prior to marking
009	06-06-22	n.d.	1	73.7	x	51.4			93.5			Egg predated prior to marking
010	06-06-22	13-05-2022	2	75.6	x	50.2	70.5	x	50.2	91.4	85.3	Hatched
011	06-06-22	n.d.	1	67.2	x	50.4			81.9			Predated
012	06-06-22	25-05-2022	2	70.2	x	51.6	72.4	x	51.2	89.7	91.1	Hatched
013	06-06-22	n.d.	2									Dead, damaged eggs when marked
014	06-06-22	n.d.	1	69.3	x	50.6			85.2			Pecked empty (predated)
015	11-06-22	22-05-2022	2	69.0	x	46.5	68.8	x	47.7	71.6	75.1	1 egg hatched , 1 egg self-predated
016	08-06-22	08-05-2022	2	pullus		pullus						Hatched
017	08-06-22	17-05-2022	2	69.2	x	48.8	70.9	x	48.1	79.1	78.7	Hatched
018	11-06-22	n.d.	2	67.0	x	48.6	68.1	x	48.1	76.0	75.6	Predated
019	02-06-22	n.d.	1	45.2	x	34.8			26.3			Dwarf egg, predated
020	11-06-22	n.d.	2	63.4	x	47.1	63.2	x	46.5	67.5	65.6	Infertile
021	13-06-22	18-05-2022	2	71.0	x	49.7	71.2	x	48.4	84.2	80.1	1 died hatching, 1 infertile egg
022	13-06-22	18-05-2022	2	71.3	x	48.5	73.8	x	49.3	80.5	86.1	Hatched
023	13-06-22	19-05-2022	2	68.9	x	50.3	70.0	x	51.7	83.7	89.8	Hatched
024	13-06-22	10-06-2022	2	75.1	x	48.2	71.7	x	47.3	83.7	77.0	Hatched
025	13-06-22	04-06-2022	2	72.8	x	49.6	69.4	x	48.0	86.0	76.8	Hatched
026	13-06-22	n.d.	1	73.8	x	46.9			77.9			Predated
027	13-06-22	n.d.	1	67.0	x	49.4			78.5			Predated
028	13-06-22	20-05-2022	2	76.1	x	47.0	74.3	x	44.5	80.7	70.6	Hatched
029	13-06-22	07-06-2022	2	75.2	x	47.8	71.2	x	48.8	82.5	81.4	Hatched
030	13-06-22	31-05-2022	2	66.7	x	49.3	64.0	x	47.5	77.8	69.3	Hatched
031	21-06-22	04-06-2022	2	72.2	x	50.2	68.3	x	50.5	87.3	83.6	Hatched
032	22-06-22	n.d.	1	pullus								Hatched
033	26-06-22	~16-06-2022	2	77.7	x	48.8	74.5	x	49.2	88.8	86.6	(Still incubated 10 July 2022)*
034	04-07-22	07-06-2022	2	pullus		pullus						Hatched
First confirmed laying	08-05-2022		1.74	clutch size per nest				62.9	%	1.09	hatchlings per nest	
Last confirmed laying	~16-06-2022		0.45	±SD				hatched		0.91	±SD	
			34	n						33	n	

*) one chick of a few days old seen on 18 July 2022 (SG).

Table 7. Egg size^{mm} and volume^{cc} (average ± SD, range, n) at monitoring plot Ristie – Da Logat in 34 nests marked 4 June – 4 July 2022. Egg volume as kLW², with k= 0.00048, following Furness (1977). Dwarf egg excluded.

	Length		Width		Volume	
Average size	70.5	x	48.8	mm	80.7	cc
SD	3.4		1.5	mm	6.4	cc
Min	63.2		44.5	mm	65.6	cc
Max	77.7		51.7	mm	93.5	cc
n=	49		49		49	



Fig. 20. Bright blue eggs in nest 020 with slight eggshell deformations (note the rough calcium formation running diagonally over the egg on the left, and the curved tip of the egg on the right). Both eggs failed to hatch. Of 134 eggs checked on Foula, 7 were ‘blue eggs’ (5.2%). With four blue eggs on the Ristie – Da Logat study plot, the frequency was just above average (6.8%). Only one of these eggs hatched, but the chick died half-way. The single egg clutch with a dwarf egg (found on 8 June, nest 019) was predated two weeks after being found.

Camera trap observations

Six nests were followed with camera traps around hatching (**Fig. 21**): nest **016** (9-10 June), nest **001** (10-11 June), nest **010** (11-16 June), nest **023** (18-22 June), nest **015** (22-24 June), and nest **004** (24-26 June 2022). The camera traps revealed single parents on two occasions (001 and 016), but bi-parental care in the other four nests.



Fig. 21. Confirmed pair of Great Skuas at nest 004 in the monitoring plot Da Ristie – Da Logat (N Foula), 24 June 2022, with a young chick under care and an incubated, pipping egg that would hatch the next day.



Fig. 22. The first hatchlings, **nest 016**, at Da Ristie, N Foula. Upper frame 9 June 2022 (11:00), lower frame 9 June 2022 (14:45), after the smaller chick had died in the nest (camera trap exposures).



Fig. 23. Intruder attack and nest defence by solitary female, **nest 016**, at Da Ristie, N Foula, 9 June 2022 (22:50).

Nest 016 → camera deployed 9 June 2022 08:33, retrieved 10 June 2022 08:14 (1112 photos). Two small chicks found on nest when marked 8 June 2022, guesstimated laying date first egg 8 May 2022, aerial defence of the single parent very weak (2), one surviving chick when the camera trap was removed, but no chick nor a parent bird seen during subsequent area visits on 11 and 15 June 2022 (examples **Fig. 22-23**).

Camera trap confirmed the absence of a partner; female bird engaged in chick care alone, thereby conducting repeated short foraging trips over a 24h period of camera surveillance. One-night attack/nest defence at 22:50h was the only evidence of a second bird in the neighbourhood of the nest (**Fig. 23**). The camera trap provided reliable presence-absence data for 21 hours and 12 minutes covering 9-10 June 2022 (09:09 – 08:14), during which 20 absences of the care taking female individual were recorded: 5 hours and 35 minutes of absence, average 'trip' duration 16 ± 17 minutes (range 2 minutes – 1 hour and 22 minutes, $n=20$ absences), or 73.7% nest attendance. The smaller chick died five hours after camera deployment and was not seen to receive any food, despite evidence of chick provisioning for its sibling, shortly earlier, after the longest recorded trip or absence. Five chick provisioning bouts were recorded with certainty, with preceding trip durations 27 ± 31 minutes in length (range 5 minutes – 1 hour and 22 minutes, $n=5$ trips). Small fish prey was delivered once after a 9-minute absence. Standard nest controls: 9 June 2 chicks (one died, seen on camera), 10 June 1 chick, 11 June no chicks and no adult during nest control, no adult in the vicinity of the nest during subsequent controls (15 and 18 June). Bird either died or abandoned the site (no signs of illness seen).



Fig. 24a Solitary parent at **nest 001** at Da Ristie, 10 June 2022, overlooking the clutch, 60.15470°N, 02.07743°W.



Fig. 24b Dead Great Skua **#808**, found as a fresh bird 22 June 2022, 60.15383°N, 02.07662°W.

Nest 001 → camera deployed 10 June 2022 08:18 - 21:23, 2012 photos obtained. Two egg clutch marked 4 June 2022, assumed being 'incubated' during subsequent nest controls (6-18 June 2022), always with a single bird attending during nest controls; bird was typically alarmed at great distances, performing mild swooping behaviour without physical contact of a territory intruder.

Over 2000 photos of the exact same incubating bird over a 13-hour period, with seven brief breaks of a duration of 3-7 minutes only. No partner visits and no intruder attacks witnessed (single short disturbance recorded, no clear cause). The many photos are considered being sufficient evidence of single parent care and almost continuous incubation. Field observations confirmed this; the same bird was simply 'always' there. The single adult bird was suddenly gone and the nest appeared to have been plundered on 19 June 2022. The site was apparently abandoned straight away, but a fresh corpse found nearby on 22 June 2022 (**#808**) was almost certainly that same adult individual (identical plumage, same neck and mantel streaks **Fig. 24**), suggesting a HPAIV strike.



Fig. 25. Confirmed pair of Great Skuas at **nest 010** in the monitoring plot Da Ristie – Da Logat (N Foula), 14 June 2022 (04:32) (note faulty camera date settings), with two small chicks under care. Camera deployed 11-16 June 2022 (5994 photo's), 2 egg clutch marked 6 June 2022, first hatchling 11 June 2022, expected laying date first egg 13 May 2022, aerial defence of pair 3-4 during nest visits, at least one large chick on site during final nest visit 10 Jul 2022; no record of nest site or chick on 18 July (SG). Camera trap confirmed bi-parental care and fish prey during early chick-care.



Fig. 26. Confirmed pair of Great Skuas at **nest 023** in the monitoring plot Da Ristie – Da Logat (N Foula), 18 June 2022 (12:47), with one small chick and an incubated egg under care. Camera deployed 18-22 June 2022 (4399 photo's), 2 egg clutch marked 13 June 2022, first hatchling 18 June 2022, expected laying date first egg 19 May 2022, aerial defence of pair 3 during nest visits, at least one large chick site during final nest visit 4 Jul 2022; no record of nest site or chick on 18 July (SG). Camera trap confirms bi-parental care and frequent feeding bouts of mostly mammalian (rabbit) and some avian (unidentified) prey.



Fig. 27. Confirmed pair of Great Skuas at **nest 015** in the monitoring plot Da Ristie – Da Logat (N Foula), 22 June 2022 (12:35), with one small chick and an incubated egg under care. Camera deployed 22-24 June 2022 (3651 photo's), 2 egg clutch marked 11 June 2022, first hatchling 21 June 2022, expected laying date first egg 22 May 2022, increasingly aggressive birds, aerial defence of pair increased from 3 to 4 during nest visits on later dates, violently defending offspring (not seen) during final nest visit 4 Jul 2022; no record of nest site or chick on 18 July (SG).



Fig. 28. Confirmed pair of Great Skuas at **nest 004** in the monitoring plot Da Ristie – Da Logat (N Foula), 25 June 2022 (13:20), with two small chicks under care. Camera deployed 24-26 June 2022 (6536 photo's), 2 egg clutch marked 4 June 2022, first hatchling 24 June 2022, expected laying date first egg 25 May 2022, weak aerial defence of pair, usually 2-3 during nest visits, but evidently defending offspring (not seen) during final nest visit 4 Jul 2022; no record of nest site or chick on 18 July (SG)

Breeding success of Great Skuas at the Ristie – Da Logat monitoring plot

Two only partially feathered small chicks were detected on 3 August, one near nest 029, and another fairly nearby at ‘ Da Logit’-house, a ruined site nearby. The remains of an almost fledged chick were found near nest 006. Two dead fledglings were found on 24 August, one almost intact corpse, drowned near nest 025 and the scavenged remains of another fledgling near Logit house. The sightings show that at least some chicks have reached the fledgling stage, but whether or not some juveniles managed to survive and actually leave Foula from this plot is not clear. If anything, reproductive success must have been very low indeed, if not a complete failure.



Near fledgling nest 006, 3 August 2022 (SG)



Fledgling Logit house, 24 August 2022 (SG)

Breeding success of Great Skuas at the Da Bitten monitoring plot

During an area visit on 29 July, there were no signs of any surviving chicks and only two adults were there, vaguely flying around (SG). The Da Bitten monitoring area, like some other major breeding areas on Foula, had gone remarkably quiet in late June and early July. Mortality had been considerable in 2022 in the area between Da Mill Loch and Gossameadow (see above), and was also ongoing throughout July given the results of searches throughout the summer (e.g. **Fig. 18**), but that activities of breeding birds on these grounds were so much reduced was thought to relate at least in part to an early departure of the remaining breeding birds. Other, busier, parts on Foula all had easily visible chicks in the terrain, including some fledglings, evidently keeping at least part of the resident skua population in check.

Visits late August confirmed that again a full breeding failure must have occurred at Da Bitten, and only a single adult bird was seen on 24 August (SG). At that time, there were still small numbers of Great Skuas on Foula, but none of the (human) residents has seen any fledglings anywhere in the parts of Foula they could normally oversee.

Results (4) HPAIV related or other mortality of other waterbirds on Foula

During systematic searches, all over Foula, all corpses of birds and mammals were recorded and at least briefly studied to try and understand the cause of death, or to try and pinpoint anything that could be considered ‘out of the ordinary’ in relation to the overall pandemic (Table 8). None of the birds found were sampled and tested, so any suspected relationship with avian influenza (or the contrary) is speculative. Bottom line is, there is nothing unusual about dead birds in nature. Hence, signals looked out for were: abnormal numbers, abnormal dying behaviour, resulting in abnormal postures (fresh birds only), abnormal locations, abnormal species, and the likely role the dead birds might have played for scavengers (such as Great Skuas or large gulls) or hunters (raptors, Great Skuas, Great Black-backed Gulls).

Table 8. Large birds found dead, all over Foula, summer 2022 (chicks excluded). See also Appendix 4.

Euring	Species	Scientific name	Number found dead
220	Northern Fulmar	<i>Fulmarus glacialis</i>	3
710	Northern Gannet	<i>Morus bassanus</i>	42
809	cormorant	<i>Phalacrocorax spec.</i>	1
1611	Greylag Goose	<i>Anser anser</i>	3
2060	Common Eider	<i>Somateria mollissima</i>	3
5380	Whimbrel	<i>Numenius phaeopus</i>	1
5690	Great Skua	<i>Stercorarius skua</i>	1400
5920	Herring Gull	<i>Larus argentatus</i>	5
6000	Great Black-backed Gull	<i>Larus marinus</i>	3
6160	Arctic Tern	<i>Sterna paradisaea</i>	5
15720	Common Raven	<i>Corvus corax</i>	1

Table 9. Northern Gannets found dead, all over Foula, summer 2022.

Da Snuis / Waster Hoevda	1	6	2022	8	ad	colony and club
Da Kame	1	6	2022	4	ad	colony and club
Waster Hoevda	23	6	2022	12	ad	colony and club
Da Kame	23	6	2022	3	ad	colony and club
Da Est Hoevdi	2	6	2022	2	ad	colony and club
Nebbifield	23	6	2022	1	ad	inland
Blobers Burn, Da Noort Bank	2	7	2022	1	ad	inland
Da Logat	6	6	2022	2	ad	coastal / at sea
Hiorawick	6	6	2022	1	ad	coastal / at sea
	7	6	2022	4	ad	coastal / at sea
	1	7	2022	1	ad	coastal / at sea
Stremness	3	6	2022	1	ad	coastal / at sea
	24	6	2022	1	(unaged)	coastal / at sea
	10	7	2022	1	ad	coastal / at sea

Northern Gannet population trends

The gannetry of Foula, situated on steep cliffs on the west coast, was visited, observed and photographed on 15th May, on the 1st June, 23rd June and 31st July (SG & CJC), in order to assess whether virus-suspect mortality occurred on the breeding cliffs or clubs of Northern Gannets, as elsewhere in the North Atlantic. Dead gannets were indeed

seen during all colony visits, on ledges, stacks and in the sea, but also floating by or onshore in Hiorawick and at Stremness, but numbers remained relatively small (**Table 9**). One dead bird was found inland at Nebbifield, and a sick bird was found in Blobers Burn near da Noort Bank (dead the next day), and this individual had clear behavioural signs of a virus infection (disorientation, spasms). All aged Gannets found dead were fully mature, while both at sea (foraging birds) and in the colony (prospectors) immatures were common (around 10-15% of all birds).

The gannetry at Foula, is only in part visible from land, and a direct comparison with the results from the most recent colony census (which was an aerial survey; Murray *et al.* 2021) is therefore compromised. The visible part of the colony, however, is large enough to get an idea of a major change in numbers, in comparison with that most recent aerial survey in 2017, or if a significant drop in colony attendance occurred through in 2022. Unfortunately, the photographic material obtained on 15 May was just not sharp enough to be of use (**Fig. 29**).



Fig. 29. Foula gannetry at Waster Hoevda and Da Scrodhurdins, seen from Nebbifield, 15 May 2022 (Sheila Gear)

Seven sectors (A-G) were selected from the photographic material collected in May and June from land (**Fig. 30-31**), three further sectors (H-K) were identified using the aerial survey in 2017 (**Fig. 32-33**). With hindsight, one of these (H) appeared to be a club site, for no confirmed nests could be detected during careful inspections of the photos from the land counts. More detailed photos were available and used than shown here, to get the counts as accurate as possible. One observer followed a conservative strategy (counting Apparently Occupied Nests, AONs, CJC), the other followed the earlier routine, also used in 2017, and assessed Apparently Occupied Sites (AOSs, Mike Harris), where regular spacing plays a considerable part. The latter count could be compared with similar sections available from the 2017 survey. The results are summarised in **Table 10**. As with all material, the photos are available for revisits or future inspections.



Fig. 30. Foula gannetry at Waster Hoevda 15 May 2022, 1 June 2022, and 23 June 2022 (Sheila Gear & Kees Camphuysen)

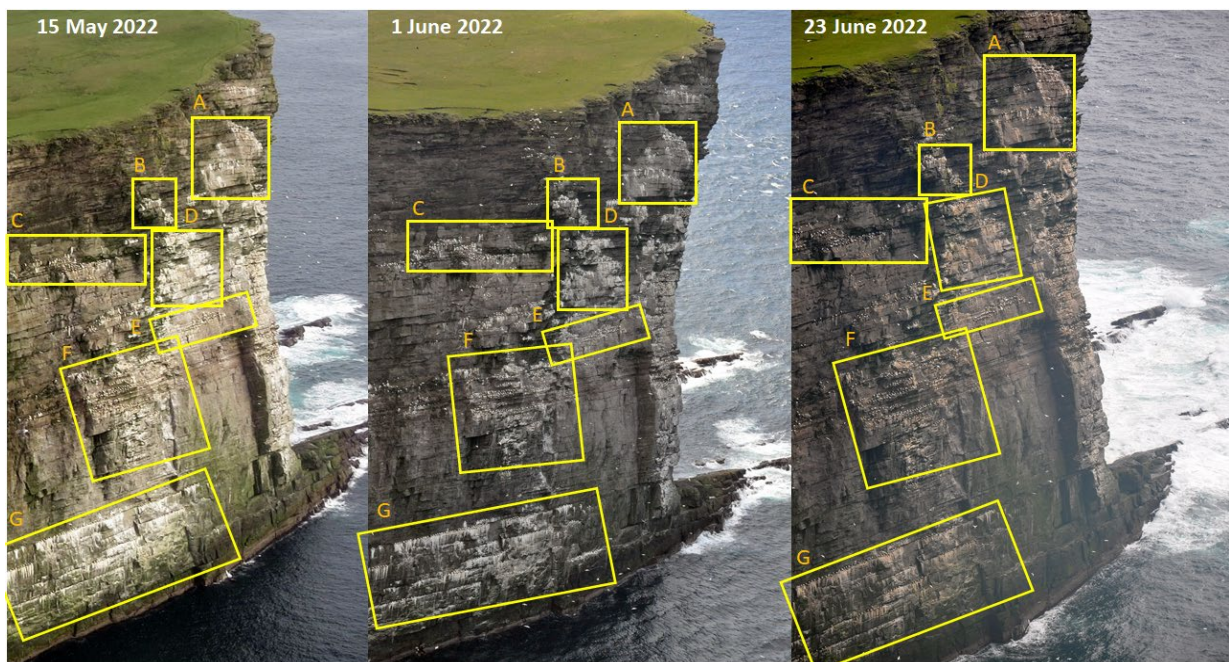


Fig. 31. Sector-by-sector comparisons based on photos taken from land

Sector A could not be identified with certainty in photos taken in August 2017, but overall, numbers were ~20% higher in 2022 than in 2017 (AOSs; **Table 10**). The photos taken 15 May 2022 are insufficiently clear for several sectors, and were therefore left out of consideration. A comparison of photographic material taken on 1st June, 23rd June 2022 and 31st July, for all (sub-)sectors covered with suitable material, indicates a ~22% decline in AONs and a ~16% decline in AOSs over the summer (**Table 10**). The results suggest a population decline, but it could also have been, at least in part, early colony departures. A full survey will be required to collect adequate material, but since the latest photographic census was in 2017 (with 20% fewer sites occupied, given counts on selected ledges in 2022), it will be difficult to assess the damage inflicted by HPAIV in 2022.



Fig. 32. Foula gannetry at Waster Hoevda during aerial survey 25 August 2017 and from land 23 June 2022 (courtesy Mike Harris & Kees Camphuysen). Note only partial overlap (central part of left image)

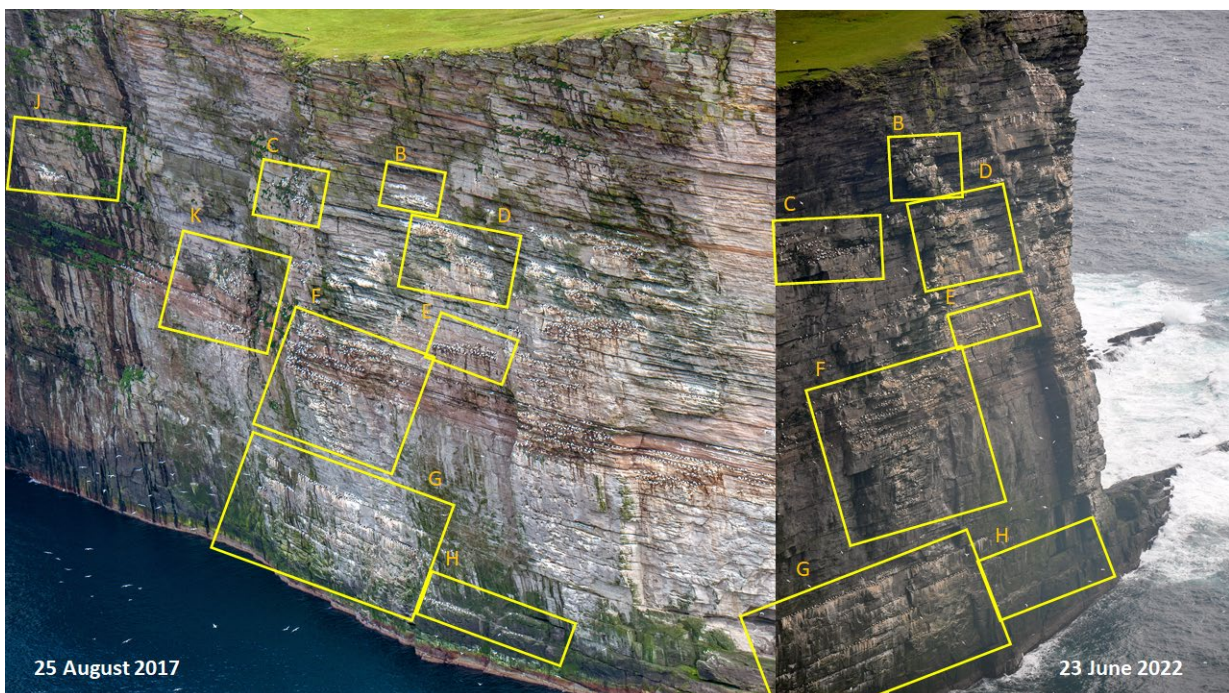


Fig. 33. Sector-by-sector comparisons based on photos taken from the air in 2017 (left) and from land in 2022 (right).

HPAIV suspect mortality in large gulls *Laridae*

Similar observations were conducted on the (very small) colonies of breeding large gulls, mostly situated on the east coast of Foula. Great Black-backed Gulls *Larus marinus* formed territorial pairs at Gaada Stack, Stremness, Da Swaa, and Da Smaallie, nesting birds could be observed only at Stremness and Da Swaa. Of the latter pair, the male died in spasms (apparently infected from HPAIV) next to the nest and the attempt failed. Great Black-backed Gulls attended Great Skuas bathing pools at Da Loch o da Fleck and in Da Mill Loch. On that last site one adult bird

was found dead among the Great Skuas. A final dead bird was a very old 2cy bird at Da Head o Ruscar (probably died in its first year in 2021).

Herring Gulls *Larus argentatus* formed a small colony at Da Swaa (6 AON), where up to 18 adults could be seen together. Three adults died during incubation, and the postures of the casualties were suggestive for HPAIV infections. Two pairs hatched at least 2 young each (survival until near-fledging has been observed). In flocks of non-breeding Herring Gulls at Da Doon Banks (up to 30 birds), no unusual mortality has been observed. A single, long dead 2cy individual was found in West Burn.



Fig. 34. HPAIV suspect casualties at the small gull colony Da Swaa: adult Great Black-backed Gull (top) and one of the adult Herring Gulls (bottom), 4 June 2022.

Table 10. Numbers of Northern Gannets on suitable ledges in sectors outlined in **Figs. 30-33**, August 2017 (aerial survey) and summer 2022 (1 June, 23 June, and 31 July) based on photographs. Left: assessment of AONs (CJC), centre: assessment of AOSs (Mike Harris), and right: assessment of AOSs in similar sections available from the aerial survey in 2017 relative to the 2022 census (MH). The bottom line reports the change (%) between subsequent counts. Sectors A and G were only partially photographed on 31 July, and the totals reflect only the sections that overlapped between each of the three datasets, used also to assess the percentage change.

	01-Jun AON	23-Jun AON	31-Jul AON	01-Jun AOS	23-Jun AOS	31-Jul AOS	2017 AOS	2022 AOS
A	102	97		127	131			
A^{lower}	58	57	53	72	76	67		
B	27	21	19	27	30	25	9	12
C	63	41	43	84	62	72	9	23
D	64	62	57	73	68	74	32	52
E	58	64	60	65	65	64	38	45
F	219	210	178	303	255	256	214	214
G	130	112		159	132		86	98
G^{partial}	103	89	71	143	132	98		
H	0	0	0	21	0	18	14	28
J	18	19	14	31	27	22	20	22
K	106	98	66	139	110	105	76	105
Totals	716	661	561	937	825	783	498	599
Trend	0	-7.7%	-15.1%	0	-12.0%	-5.1%	0	+20.3%

Other seabirds found dead

Dead Northern Fulmars *Fulmarus glacialis* were found in Hiorawick (beach cast) and at the Great Skua breeding grounds Sandvatten – Gossameadow (prey remains, pairs of wings connected by breast bone). A very old corpse of a Shag or Cormorant *Phalacrocorax* sp. was found at Da Mill Loch. One dead Arctic Tern *Sterna paradisaea* was found in Da Daal (prey remains), four fairly fresh and intact corpses were found in the colony area next to the airstrip. Cause of death unknown, HPAIV cannot be excluded. One Arctic Skua was killed from a collision with an aircraft on the airstrip.

Ducks and geese found dead

Grey-lag Geese *Anser anser* were seen throughout the summer, mostly around Stremness and Ruyhedlar (up to 52 individuals, for a long time together with two Bean Geese *Anser fabalis*). Nesting of Grey-lag Geese was confirmed at Stremness. One old corpse of a Grey-lag Goose was found at Hiorawick, another, fresher and scavenged corpse was found at Stremness. On 10th July, a sick adult Grey-lag Goose, stumbling and incapable of flight (also because of primary moult), was encountered at Ruscar. If there had not been an avian influenza pandemic, this case would normally not have attracted any attention. Cause of illness unknown.

Common Eiders *Somateria mollissima* were regular 'inland' breeders of which flocks of non-breeders (of very different size, age-composition and sexratio) could be seen along the east and north coast of Foula (most between Ham Little, Ham Voe, Stremness, Hiorawick, and Gaada Stack). Small flocks, up to 26 individuals, were seen frequently. Adult females and small ducklings were seen after 12 June, in Ham Voe, at Ruscar, in Hiorawick and around Gaada Stack. (max litter 5 ducklings) One very fresh drake floating in Ham Voe harbour 31st May 2022 looked suspect, but otherwise, no (fresh) mortality of Common Eiders occurred. A very old corpse of an immature male was found at Da Head o da Taing, another very old carcass was found near Ristie.

No further dead ducks or geese were found. Further sightings of Anatidae were three Mallards *Anas platyrhynchos* at Ham Voe, a flock of six Mallards at Mill Loch (later a pair, same?), a male in Da Burns. Two male Tufted Ducks *Aythya fuligula* were seen in a pool at Da Fleck in July. In early June, a pair of Red-breasted Mergansers *Mergus serrator* stayed a few days at Stremness.

Other birds found dead

Nothing unusual was found in terms of observed mortality patterns. One long dead Raven *Corvus corax* at Nebbifield, one dead Whimbrel *Numenius phaeopus* at South Harrier – Da Crookit Burn.

Discussion

Emerging H5Nx lineages of the avian influenza virus (AIV) with genomic reassortments have posed a continuous threat to animals and human beings in recent decades (Sonnberg *et al.* 2013, Xiao *et al.* 2021). H5N1, that arose in the early 1990s in Southern China, became established in aquatic poultry as a stable reservoir and has now been endemic in poultry in southeast Asia for decades (Chen *et al.* 2005). Recent outbreaks of H5N1 in humans in numerous countries throughout Asia, Africa and Europe, however, raised concerns that a new influenza pandemic affecting more than ‘just birds’ may occur in the near future (Kaplan & Webby 2013), and the cumulative number of confirmed human cases meanwhile stands at 865 infections leading to 456 deaths (WHO 2022^{June 2022}).

Initially, it was considered likely that wild birds, notably waterfowl, became dead-end hosts of virus acquired from poultry. There was no evidence that the virus was transmitted within wild bird populations or that migratory birds carried the virus any further (Chen *et al.* 2005). On 30 April 2005, however, an outbreak was detected in Bar-headed Geese *Anser indicus*, and over 1500 of these migratory wild birds died as a result of H5N1 bird flu at the Qinghai Lake nature reserve in western China (Chen *et al.* 2005). This was the first reported instance of a highly pathogenic strain of avian influenza causing mass die-offs in wild birds, and it was considered ‘a worrying development [that] could help spread this dangerous virus beyond its stronghold in southeast Asia’. The rest is history. In Europe, distinct episodes of outbreaks of highly pathogenic avian influenza virus of subtype H5N1 (HPAIV H5N1) in wild birds occurred in early 2006 (Globig *et al.* 2009), and further outbreaks occurred almost annually ever since. Migratory wild birds have been implicated in the long-range spread of HPAIV H5N1 from Asia to Europe and Africa, where high local densities of wild birds apparently sparked clinically detectable outbreaks. In winter 2014/15, the U.S. Department of Agriculture received reports of birds infected with Asian-origin, highly pathogenic avian influenza A (H5N2, H5N8, and H5N1) viruses, and these represented the first reported infections with these viruses in wild or domestic birds in the New World (Jhung & Nelson 2015).

HPAI viruses of the original lineage, predominantly H5N1 and H5N8, have continued to circulate in Asia, Africa and Europe following the resurgence of extensive outbreaks since 2013-6 and October 2021. The epizootic at that time in Europe, caused by viruses of the 2.3.4.4b clade, was considered unprecedented. This lineage can be considered particularly ‘fit’, and unusually, there were detections of these viruses in the summer in wild birds (as well as poultry) in Europe, indicating continued circulation of virus in wild birds (STFAIWB 2022). H5N8 is still responsible for infections in Asia, but H5N1 has now almost completely replaced this subtype in Africa and Eurasia. The ecology of highly pathogenic avian influenza H5N1 has significantly changed from sporadic outbreaks in terrestrial poultry to persistent circulation in wild birds, all over the Northern Hemisphere (Sonnberg *et al.* 2013, STFAIWB 2022).

In virtually all earlier reported outbreaks, migratory fresh waterfowl such as wild geese and ducks were involved (Anseriformes), but over the years, infections were detected in an increasingly wide range of species including wildfowl, waders, skuas, gulls, terns, cranes, grebes, herons, pelicans, gamebirds, corvids and raptors (diurnal and nocturnal), in addition to sporadic cases in mammals such as Red Fox *Vulpes vulpes*, Eurasian Otter *Lutra lutra* and Harbour Seal *Phoca vitulina* and Grey Seal *Halichoerus grypus*, indicating the potential for multiple and complex negative ecological impacts (Kaplan & Webby 2013, Huang *et al.* 2014, Wille *et al.* 2014, Lang *et al.* 2016, STFAIWB 2022). Still, the role of seabirds, an abundant, diverse, and globally distributed group of birds, in the perpetuation and transmission of IAVs remained less clear and the massacres that were witnessed in 2022 all over the North Atlantic, both in the Old and in the New World, took most seabird ecologists completely by surprise.

Remains of H5N1 infected migratory birds are often found in the vicinity of (fresh) water sources, or wetlands, along migratory flyways (Kaplan & Webby 2013). It has therefore been hypothesized that the feeding behaviour of waterfowl determines the prevalence of influenza virus infections, whether these are low or highly pathogenic viruses. Dabbling ducks and geese are especially vulnerable, because they forage on food floating on the surface of water where avian influenza virions accumulate (Kaplan & Webby 2013). In Anseriformes, the primary site of influenza virus replication is the intestine (shedding of virus upon defecation; Webster *et al.* 1978). The HPAI H5N1 viruses are somewhat of an exception because they can replicate in and be shed from the respiratory tract of infected birds (Kaplan & Webby 2013). Raptors and scavengers are highly susceptible to H5N1 infection, and molecular characterisation of the raptor-isolated viruses showed that these were closely related to chicken strains circulating in domestic poultry, probably following predation or scavenging on infected poultry carcasses (Van Borm *et al.* 2005, Marinova-Petkova *et al.* 2012). A short search in the availability literature shows that the following forms of transmission of HPAIV occur:

- in water (especially at the surface),
- in the air (aerosols),
- through faeces, and
- as a result of the consumption of infected prey or carrion (predator, scavengers).

The *history* of highly pathogenic avian influenza infections in wild birds for a long time suggested that fresh water reservoirs played a key role. LPAIV infections are known for longer in seabirds, but the contacts with highly pathogenic strains are from a considerably more recent date. Studying both the epidemiology and transmission of avian influenza viruses in wild birds, now also in (pelagic) seabirds is critical to help understand how and where outbreaks that cause extensive mortalities in the marine environment develop and spread, and how the 2022 pandemic could develop so quickly and on such a grand scale.

Key characteristics of seabird population dynamics vary considerably, and this includes the condition the various species live in and the associated risks to become infected by conspecifics. Some seabirds live in crowded colonies numbering up too many thousands of individuals in small areas, either on steep cliffs, remote stacks (e.g. fulmars, gannets, gulls, auks), or flat ground (e.g. terns), other species are burrow nesters (e.g. puffins, shearwaters, storm-petrels), or occupy widely spaced territories on more inland breeding grounds (e.g. skuas, gulls). Understanding the dynamics of pathogens in dense populations and the way in which most infections occur as in seabird colonies, is crucial (O'Regan *et al.* 2008). Long-term dynamics of avian influenza H5N1 virus in seabird colonies, with no existing herd immunity, has been investigated using sophisticated mathematical techniques, but accurate field data are essential to feed and validate such models.

At the start of the breeding season 2022, it appeared that several seabirds on Shetland had severe problems. 'Gannet soup' was reported (Noss, Shetland), thereby describing the incredible number of dead gannets bobbing around in the sea under the cliff face of a major colony. 'Great Skua soup' may have been the most adequate description of what was encountered in various lochs (bathing places) on Foula, but what was encountered in the colonies themselves on the island was equally grim. The fact that so many different seabird species (including gannets, cormorants, skuas, gulls, terns and auks) fell victim to the pandemic for the first time and all over Scotland (Philips 2022), but also elsewhere in Europe, Canada and the USA in 2022, often with devastating effects, made detailed investigations on the pathways of infections and the scale of the impact highly important. This report documents the observations on a heavily impacted, major breeding site for seabirds in the Shetland Islands, on Foula, in the hope that the data may contribute to a deeper understanding of infection risks, virus spread and effects on the population level.

Great Skua mortality

Shortly after their arrival on the breeding grounds, unusual mortality of Great Skuas was reported from Foula (SG) and from several other colonies around the islands (Glen Tyler *pers. comm.*). Overseeing data collected in summer 2022, the mortality rate of Great Skuas on Foula was clearly unprecedented, even given that significant extra mortality had occurred in 2021, presumably also as a result of avian influenza (Banyard *et al.* 2022). Despite the earlier outbreak in June-July 2021, there was no evidence, whatsoever, for existing herd immunity. The observed death toll and population decline documented in summer 2022 is such that long-lived seabirds as these will need many years to rebuild the population to the recent original, now historical, levels (\pm 1500-1800 pairs). That the extra mortality was caused by avian influenza (H5N1) is beyond dispute, even though only three birds were sampled and shown to be 'positive', given the highly characteristic behaviour of affected individuals, which in turn lead to characteristic postures of (fresh) dead birds. It is also important to realise that virtually all Great Skua colonies in the NE Atlantic, for as far as they were visited by critical observers, were at least somehow affected by the pandemic.

Since HPAIV related mortality in seabird colonies such as these was new, and because significant adult mortality would have devastating effects on populations such as these (see life history implications below), we studied what we considered to be the most urgent aspects:

- assess the damage (scale, impact and age composition),
- try and understand the process of infections (where and how, spread, source),
- understand the timing and spatial trends of the pandemic,
- examine the effect on reproductive performance.

In order to understand where, how and when birds probably got infected, whether the virus had similar effects in birds of different age groups or sexes, and how the virus spread, more data were required than simple before-and-after presence/absence counts (such as an AOT census). Given that there would be only one opportunity for research (as a result of ongoing processes throughout a typical breeding season), decisions had to be made on the spot, often just using common sense, while relying on earlier experiences when studying seabird mortality and breeding biology. Hence, protocols used were based on earlier work, whether or not they had to be adjusted to fit the occasion. Also, we felt that long-term monitoring (largely SG) had to continue whenever possible, to collect comparable data with earlier seasons, for as long as this work was considered safe for both the birds and the observers. The second observer (CJC) was thereby freed to do most of the additional research required to address the above issues, that had suddenly emerged as a result of the pandemic.

The key findings of our observations, all discussed below, are:

- Great skuas arrived in apparently normal condition and were seemingly healthy when they arrived, occupied territories all over Foula, commenced breeding, laid 'normal' clutches and eggs, with 'normal' hatching rates.
- Soon after the spring arrival, the first mortality was observed, at first mostly at clubs, but soon over the entire island.
- Mortality peaked in the second half of May, with a second wave in July
- Great Skuas birds hit by the virus were easy to recognise: no sense of direction, stumbling, unable to fly or crashing down almost immediately, spasms in head movements, collapse.

- Breeding Great Skuas ‘caught in the act’ by the virus, at least in the egg- or chick phase, typically collapsed on the breeding grounds, usually near or even at the nest, thereby contributing to the observed shift in corpse distribution away from clubs and bathing places, later in the breeding season.
- Breeding attempts in which only one of the partners died invariably failed.
- Fresh corpses often seemed to be frozen images of the final spasms and collapse, quite distinctly different from fresh dead birds found under other conditions from other causes.
- The age of great skuas carrying rings could suggest that most casualties were not only adults, but also adults of relatively high age.
- There were only very few corpses of waterfowl on Foula (ducks and geese), birds that had died in winter or spring 2022, which could have contributed to the outbreak of HPAIV, thought to be an issue beforehand because Great Skuas have scavenging habits.
- Corpses of Great Skuas were often not cannibalised, or only with a considerable delay. Most cannibalised corpses were found on clubs, and these are the only areas where cannibalism has (rarely!) been observed.
- Great Skuas were seen scavenging (in flocks) on Northern Gannets floating in the ocean, but such sightings were rare.
- Most territories on Foula were abandoned in late July, when relatively few birds were seen on clubs, roosts or bathing places, suggesting that birds had either died or left the island en masse.
- An area census in early June suggests that a decline in breeding densities of at least 65% had occurred, in comparison with counts in 2007 and 2015.
- The presence of several hundreds of adults in the second half of July and sightings of developing chicks (at distance only) suggested that breeding success (fledging rates), has been (very) low.

Arrival of Great Skuas in April and May –Observations on important Great Skua (pelagic) wintering grounds off NW Africa in February 2022 had not resulted in anything unusual, except that “*in comparison with earlier winter surveys, rather many Great Skuas were observed*” (Camphuysen *et al.* 2022). Based on systematic, ship-based surveys conducted between Nouadhibou (Northern Mauritania) and the border with Senegal, ~10,000 Great Skuas occurred in Mauritanian waters at that time (order of magnitude: ~30% of the world population). The Great Skuas at sea typically operated in pairs or duos, and virtually all birds seen were adults. The birds were strongly attracted to fishing vessels and operated usually at the periphery of associated flocks of scavenging seabirds, looking for targets to steal food from.

In two months that followed, the birds travelled north towards their breeding grounds along the coast of SW and W Europe. Nowhere along this route has anything unusual been reported, such as more frequent strandings of dead birds, but it is important to realise that the more exposed coasts and beaches along this Atlantic flyway are not regularly visited by people to search for dead birds. Great Skuas arrived in ‘good condition’ on Foula in spring, and swiftly occupied territories all over the island to commence breeding as in ‘normal’ seasons. Obviously, nobody weighed them or felt their breastbone when they arrived, but from observations at distance, the birds appeared healthy when they arrived (SG). The first dead birds on Foula were found in early May 2022, at bathing places and club sites (**Table 2**). That the mortality of Great Skuas on Foula actually *started* at these sites was a suggestion based on field observations, but these may have been misleading, simply because widely dispersed corpses on territorial grounds would not immediately have left an impression on the very few observers on the island. Yet, the reconstruction of the development and chronology of the pandemic based on systematic searches combined with observations of corpse disintegration apparently confirmed that early suggestion.

In the southern North Sea, where beached bird survey schemes are well established, the number of dead Great Skuas in spring 2022 was very low (normal), but a distinct and highly unusual peak in strandings of Northern Gannets occurred in April (Camphuysen 2022). This stranding, which comprised primarily fully mature birds in ‘good’ condition (fat) has unfortunately not been studied in any detail at the time. Strandings frequencies in April 2022 in The Netherlands, however, were 12x background levels, calculated over the past 45 years (Dutch Seabird Group, beached bird survey database 1976-2020; 0.04 ± 0.04 dead gannets km^{-1} searched; **Fig. 35**). That this stranding was not investigated in any detail, or that no birds were collected for HPAIV tests, had much to do with the ‘all time high’ for April documented just one year earlier, in April 2021, when 7x background densities were recorded. We now know about the H5N1 pandemic that occurred on seabird breeding colonies in summer 2022, and the higher than normal numbers of dead gannets found in April may have been a first sign. So, when Great Skuas travelled towards their breeding grounds in April, they must have encountered unusual numbers of dead Northern Gannets floating at sea, perhaps not in the Atlantic Ocean, but certainly within the North Sea. If those gannets had already been infected with avian influenza (causing unusual mortality rates) in April, this could explain how Great Skuas (as scavengers) have picked up the virus on their way to their own colonies.

After a dip in gannet strandings in The Netherlands in May 2022 (which is after the peak of normal spring migration in that region), the North Sea became literally flooded with dead (adult) Northern Gannets leading to numerous reports by yachtsmen and the general public, around the North Sea. In June. A new peak in strandings in July in the Southern Bight, indicated that (infected) gannets were leaving their breeding grounds early, and died in part while under way.

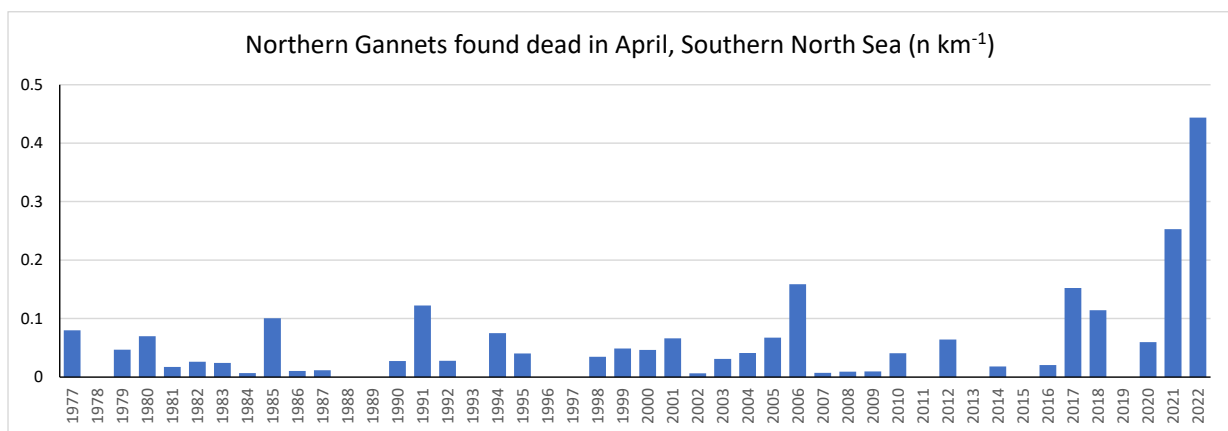


Fig. 35. Long-term strandings data of Northern Gannets in April in the Southern North Sea, based on systematic beached bird surveys in The Netherlands (calculated from data published in Camphuysen 2022).

Chronology of the kill – Mortality of Great Skuas on Foula accelerated and peaked in May, but slowed down in the months that followed, perhaps with a second wave in late June/early July. This conclusion is based on the careful assessment of the condition (level of decomposition) of the corpses when found (**Appendix 1**). It should be realised that for older corpses, this assessment is probably increasingly inaccurate, because corpse decomposition follows a trajectory that is relatively quick at first (the effect of microbes, insects and scavenging animals, the trajectories of rotting meat), but reaches a stage of seeming ‘standstill’ (mummification) when carcasses are several weeks old (Janzen 1977, Bijlsma 2001, Mondor *et al.* 2012). Water could accelerate the process such that corpses in water were more likely misjudged during visual inspections (considered older) than corpses on dry land. Old and very old

corpses were found throughout our searches on Foula, well into July, simply because corpses were notoriously difficult to find. With the fixed 'ages' of carcasses based on standardised categories, the later discoveries of older corpses may have influenced the calculated timeline such that the mortality overall may have peaked earlier and more strongly than suggested in **Fig. 10**. Very old carcasses found in July were assigned to June for their likely day of death, but at least some of these very old bodies may in fact have died in May. That the curve is a typical sigmoid curve is no surprise, given that the mortality was so widespread and significant at first. Just the lack of new birds being 'available and around' to get infected and die on the island later in the season, made the mortality curve reach a plateau. We should read the graph therefore as a gradual, slow start, followed by a very rapid and dramatic peak in disease and mortality all over Foula, as if a dry bush was set on fire. That the spread of the mortality was so rapid and widespread from the very start are the key points to take home. There is no evidence for a single point of infection leading to a gradual spread all over the island.

HPAIV as a mortality factor in Great Skuas on Foula - There is nothing strange about dead birds in nature and there is an endless list of natural and unnatural factors that could contribute to mass mortality, even on breeding grounds. Three key aspects made the 2022 mass mortality of Great Skuas suspect:

- (1) exceptionally high levels of mortality under adult individuals,
- (2) active breeding birds 'caught in the act', and
- (3) highly specific behaviour of affected birds shortly before death, leading to quite particular postures of freshly dead individuals.

The uncontrolled behaviour of dying birds, with their heads swinging up and down, apparent difficulties to properly see or orientate, walking circles and tripping all the time, was characteristic for skuas that were observed in their final stages of life. Identical behaviour is well known from affected waterfowl (Anseriformes) in earlier outbreaks around Europe, and was seen in Northern Gannets and other birds affected by avian influenza. Fresh corpses often seemed to be frozen images of the final spasms and collapse, quite distinctly different from fresh dead birds found under other conditions from other causes. Examples of the movements of HPAIV infected birds are shown on videos listed here

<https://www.youtube.com/watch?v=WIVL7oYJSM> (Great Skua, Foula, CJC)

<https://www.youtube.com/watch?v=3dth-KOcgGs> (Great Skua, Foula, CJC)

<https://www.youtube.com/watch?v=h7wGdFV41O0> (Great Skua, Foula, CJC)

<https://www.youtube.com/watch?v=Gkuy8SxPeqk> (Great Skua, Foula, CJC)

<https://www.youtube.com/watch?v=YXmp3phAqY8> (Northern Gannet, Lyme Bay, Tanya Langman)

<https://www.youtube.com/watch?v=YR7OwT-y1x0> (Northern Gannet, Foula, CJC)

<https://kvf.fo/netvarp/sv/2022/08/05/deyd-sula-i-hopatali> (Northern Gannet colony, Faeroe Islands, Johan Henrik Funder)

<https://www.youtube.com/watch?v=Htd8HQ28QwA> (Common Eider, Nunavut)

<https://www.youtube.com/watch?v=pbC-0yRm3yg> (Canada Goose, NF Fish and Game)

<https://www.youtube.com/watch?v=byV2DTTuCTS> (Grey-lag Goose pullus, Leon Kelder)

Only three birds collected on Foula have been tested for avian influenza and all three tested positive for H5N1. This was by no means a surprise, even though it was so far 'just' circumstantial evidence and an international context which made infections with avian influenza the likely prime cause of the excessive mortality amongst Great Skuas on Foula (Banyard *et al.* 2022, and test results on collected seabirds obtained during the 2022 pandemic around Scotland from summary reports compiled by NatureScot, Philip 2022).

Age of the casualties - Sonnberg *et al.* (2013) observed, based on a fair number of sources, that “In wild waterfowl, the highest attack rates of LPAI have been found in immunologically naïve juvenile (1st season) birds, presumably due to herd immunity of adult birds”. There is no evidence for this, whatsoever, in the Great Skuas found on Foula. For a start, one-year old birds rarely visit their native colonies, so any immatures around would be several years old already (Furness 2015). The Foula population itself did not produce any offspring in 2021, and if some fledglings have escaped attention they must have been very rare (Gear 2022). Breeding success as a whole has been very low in recent years on this island (**Table 11**), so the population at large must have been ageing. That the mean age of 87 dead Great Skuas found on Foula in summer 2022 was 20.7 ± 5.3 (10-36 years) is a suggestive, but in fact less informative statistic. Ringing effort has declined massively over the years, which is only in part (during recent decades) the result of a decline in reproductive success (**Table 11**). The oldest recovered Great Skua was ringed as a chick on Foula in 1986. A future analysis will have to demonstrate whether (older) adult birds were more likely to be involved and die than relatively young (breeding) individuals, or that there is no evidence for that suggestion.

Table 11. Estimated reproductive success of Great Skuas on Foula (summary from Furness *in litt.*).

Interval	Fledglings nest ⁻¹	S.D.	Chicks ringed
1970-1979	1.13	± 0.12	17926
1980-1989	0.77	± 0.34	9760
1990-1999	0.80	± 0.30	5799
2000-2009	0.60	± 0.37	2383
2010-2020	0.18	± 0.08	325

Source of the infection and subsequent spread on Foula - The scavenging and predatory habits of Great Skuas were immediately highlighted during the earlier outbreak of H5N1 in Scottish populations (Banyard *et al.* 2022). Perhaps for good reasons, but in fact as a hypothesis and without particular investigations that could confirm or reject the suggestion. In 2022, the pandemic spread in no time over numerous seabird species with very different attributes, foraging habits and ecologies, and with relatively few scavenging birds among them (Philip 2022). So how did the virus spread, and how did it ignite into these populations in the first place? One thing is for sure, there was no herd immunity detectable in species like Great Skuas, Northern Gannets and Sandwich Terns *Sterna sandvicensis* in Europe in 2022.

As a scavenger or predator, a direct connection between Great Skuas and chicken strains, circulating in domestic poultry (as found in terrestrial raptors), is very, very unlikely indeed. For a predator like the Great Skua, there must have been another, intermediate host, either (fresh) waterfowl or some seabird. On Foula, carcasses of geese and ducks in 2022 were rarely encountered, and the island is essentially unsuitable as a stop-over for large numbers of migratory waterfowl, except perhaps in autumn³. One or two infected waterbird corpses, if they were infected at all, would never have caused a spread of infections as we found. And if an occasional infected carcass ignited the pandemic in the first place, the spread could only be so fast and widespread if the virus was highly contagious and easily exchanged between conspecifics. Cannibalism occurred, but it may not have been key

³ In the autumn particularly, large numbers of geese may pass through Foula, mainly Pink-footed Geese *Anser brachyrhynchus*, sometimes thousands. Some flocks go straight through on their way south, others stay a while to rest and sometimes feed around the same small boggy pools that the Great Skuas use. Other species of geese come through in spring and autumn though are more inclined to feed on the croftland and maritime grassland. Whooper Swans *Cygnus cygnus* stop off, mainly on the Mill Loch and Luimishidden, in spring and autumn. Flocks of various ducks overwinter but in small flocks, only 20 - 30, mostly Teal *Anas crecca*, Wigeon *Mareca penelope* and Mallard *Anas platyrhynchus*. SG was not aware of any more geese and ducks than usual occurring in winter 2021/22.

in this debate. Fresh corpses of Great Skuas that died remained untouched for days to weeks and scavenging Great Skuas were in fact rarely seen to feed on conspecifics. Also, infected carcasses of Great Skuas must have picked up the virus somewhere else, in that case. Great Skuas are seabirds that fish, follow fishing vessels, kleptoparasite seabirds, and scavenge dead floating carcasses at sea. One particular source thereby springs to mind: dead, HPAIV infected Northern Gannets, which were around in large numbers in the North Sea in April 2022. Scavenging Great Skuas accumulating around floating Northern Gannets have been seen around Foula, but sightings were few and far apart. A link with gannets, however, would be an excellent explanation for the flyway-wide outbreak, with widely spaced breeding colonies on isolated islands included.

So far the scavengers hypothesis. Either each and every infected Great Skua must have been scavenging on gannets at sea, or there must have been conspecific transmission on the breeding grounds explaining the bushfire like spread in the colony. If so, where could that occur. (Fresh) water basins, aerosols, and faeces are issues to consider. Great Skuas are territorial, on average breeding tens of metres apart. They do not accept intruders within their territories; conspecifics are a threat and therefore driven away immediately. Close (physical) contact between non-pair members is therefore limited and truly high densities do not occur. Furness (1977) reported that in established breeding pairs, almost every trip away from the territory is a foraging trip (hence, a trip to the ocean). *“The only other activity in which breeding adults may be indulging is bathing or drinking in freshwater pools.”* On Foula there are about 12-13 clubs that are regularly used by Great Skuas to preen feathers and rest, 7-8 of which have important nearby bathing places (Fleck, Nedderafandal, Ouvrafandal, Mill Loch, Bottle club, Rossies club, and Daal club (Klomp & Furness 1992)). Important bathing places, with occasionally up to around 100 individuals bathing in large flocks, are Mill Loch and Ouvrafandal Loch, but large numbers of skuas can be seen to hang around in Da Daal, a wetland with numerous smaller pools and marshes. It is at these clubs that skuas approach each other to socialise, where they preen, bath, swim and drink, thereby communally using freshwater pools and small lakes. It may be at such sites that shed viruses via the air, the water, or the faeces can infect other individuals (**Fig. 6**). It is there that most scavenged corpses of skuas were found (**Fig. 12**).

Influenza viruses deposited into the environment by wild birds may lead to further infections and mortality events (Ramey *et al.* 2022). Fresh water reservoirs, such as bathing places for skuas on islands like Foula, may therefore represent an important medium in which infectious influenza viruses may reside outside of a biotic reservoir. There is very little information regarding the persistence of infectious influenza viruses in the field at ambient temperatures, for example in wetlands. In a study conducted in Alaska, some influenza A viruses remained viable for more than one year (Ramey *et al.* 2022). Water-borne transmissions were the main determinants of disease dynamics and observed prevalence levels in the Camargue area (France), which further highlights the importance of the persistence of viral particles in water to infect wild birds (Roche *et al.* 2009).

In the heydays of Great Skuas on Foula, a large proportion of the skuas at club sites were non-breeders (identified by their colour ring combinations). In the late 1980s, 3000-4000 non-breeding Great Skuas were estimated to frequent Foula (Klomp & Furness 1992). Both the number of breeders and the peak number of non-breeders have declined markedly between 1977 and the late 1980s; the number of non-breeders by 80%, breeders by 22%. With breeding success at that time only 25% of the ‘original’ (earlier) average, it was predicted that the dramatic reduction in numbers of non-breeders would be followed by a rapid decline in recruitment, and a further and much faster drop in breeding numbers. In the 1990s, following these well-predicted declines, mean reproductive success was still around 4x *current* levels (2010-2020), which would mean that the pool of non-breeders must be very small nowadays. This might explain why clubs in 2022 were visited by relatively small

numbers of birds, probably all breeding adults, and that numbers at clubs and bathing places declined even further when the breeding season progressed.

Some Great Skuas breed in areas where they have access to drinking/bathing freshwater within their territories and these might have lower infection risk than for example skuas breeding on dry ground and steep slopes, that must participate in communal bathing at bathing sites. The birds at the study plot at Ristie – Da Logat, for example, may have been less likely to attend bathing sites elsewhere on the island, because they have plenty freshwater within their territory or in the immediate surroundings of their nesting place. If infection from communal bathing is a major pathway of infection in Great Skuas, then pairs that do not or rarely join those flocks in lochs and pools might be at less risk of infection. Of the colony sectors used for recent censuses (**Fig. 14**), it could be said that sectors A, E, G, J, K/L, N, and Q are in relatively soggy breeding grounds and marshlands with numerous pools, F is a mix of damp ground territories and steep slope habitat, with a major bathing place in the centre, and B, C, M, P, T, U, and V are relatively dry, while H, D, R, S, and W have only very small breeding populations. If the census in early June represents the rate of decline in each of the chosen sectors (**Table 5**), it is at least interesting to note that the decline was indeed stronger in six ‘dry’ sectors, that may have relied more heavily on communal bathing places ($-59 \pm 11\%$, $n=6$), than in six ‘wet’ sectors ($-37 \pm 32\%$, $n=7$), where most breeders have immediate access to fresh water. The variability between areas was high, however, and more detailed information on the use versus neglect of communal bathing places is required to come to firmer conclusions.

In conclusion, the rapid spread of infections over the entire island has probably been facilitated by the habits of Great Skuas to bath and socialise (interact) at fresh water lochs and pools (bathing places and clubs). Whether or not only few, or perhaps even quite many birds were infected as a result of their feeding habits as scavengers is thereby irrelevant; the dramatic spread over the island must have been caused by frequent, more or less close (physical) contacts between conspecifics away from the breeding territories. Bathing places are the only sites where such contacts might occur regularly and in fact all major pathways of infection could play a role: through accumulating virions in communally used water bodies (e.g. virus shed upon defecation, or from carcasses in water), virus in the air (aerosols shed from the respiratory tract of socializing birds), or indeed by scavenging (cannibalism, scavenging on dead conspecifics mainly on clubs, as shown in **Fig. 12**). The fact that the wetlands used by skuas on Foula were also used by larger numbers of waterfowl (notably geese) on autumn migration (see footnote page 42), is a further issue of concern, making studies to assess the presence, but certainly also the persistence of infectious (H5N1) influenza viruses in Foula’s wetlands particularly urgent.

Northern Gannet mortality

Northern Gannets on Foula must have been affected by the pandemic, given an unusually large number of dead, adults seen on ledges and cliffs, afloat in the sea or dying and dead on land. None of the birds were tested, however, so the evidence is entirely circumstantial. As in most other areas in Europe, it was primarily fully mature gannets that died and were found on Foula. Immatures (plumage stages 2-5) were ‘common’ at sea (seawatching results, CJC) and on clubs at the colony (CJC), but immatures were seemingly unaffected by the pandemic.

Photographs of breeding ledges of Northern Gannets on Foula, taken in summer 2022, indicate a slow but fairly consistent decline in apparently occupied nests and sites between the 1st June and 31st July (**Table 10**), which could be a mix of breeding failures and associated colony departures and the extra mortality that has occurred. The effects of the 2022 H5N1 pandemic, on colonies such as the Bass Rock, Hermaness or Noss, for as far as the earliest, partly unconfirmed information is considered (e.g. Amos 2022, Philips 2022, Tiwari 2022), were

far more dramatic than those on Foula. Unfortunately, the gannetries on Foula are censused only very occasionally. Our results suggest that ~20% higher numbers of gannets were nesting in 2022 on Foula than during the last (aerial) survey conducted in August 2017 (Murray *et al.* 2021). It was suggested, at the time, that numbers on Foula were increasing at a far slower rate than on Fair Isle, perhaps because much of the Foula coastline is unsuitable for nesting gannets. The decline that has occurred in 2022, as a result of H5N1 related extra-mortality of mature Northern Gannets on Foula, will be difficult to quantify with such a low census frequency.

How Northern Gannets have picked up the H5N1 virus is nothing less than a mystery. Transmission between individuals on cliff and stack colonies is easy to understand (high densities, faecal transmissions, aerosols), but where the first birds have picked up the virus is unclear and all evidence points at (numerous) birds affected by the virus *before* they had even reached the colonies, and under their normal 'winter conditions' it is very difficult to understand where and how they could become infected and if and how they could infect each other. Obviously, more needs to be done to understand the ecology of the virus infection and which factors affect transmission risk in pelagic, in this case entirely piscivorous seabirds in a salt water environment.

Mortality of other seabirds

Large gulls on Foula were apparently affected by the H5N1 pandemic, but again, the evidence is no more than circumstantial (postures, behaviour, international context). The breeding populations of Great Black-backed Gulls and Herring Gulls on the island are very small, and even a few extra deaths 'count' with such low numbers.

H5N1 pandemic affecting Great Skuas and Northern Gannets elsewhere in Europe

An early report from Iceland (30 June 2022), on 109 seabirds collected by the general public that were tested (11 species), 21% tested positive. Northern Gannets predominated, for Great Skuas the information was incomplete (Ævar Petersen *in litt*). Northern Gannets and Great Skuas were affected by HPAIV on the Faeroe Islands, so much so that even the annual cull for (young) gannets was called off (Sjúrdur Hammer *in litt.*). Even Great Skuas on Svalbard were impacted (Borge Moe, via Rob van Bemmelen *in litt.*). The Norwegian Veterinary Institute detected highly pathogenic avian influenza virus (HPAI, avian influenza) from five Great Skuas that were found dead on Hermansenøya in Svalbard in July. Two different virus variants were detected, H5N5 and H5N1. Bird flu had previously been detected in the Glaucous Gull *Larus hyperboreus* (H5N5) in Svalbard, and in several Northern Gannets, gulls and White-tailed Eagles *Haliaeetus albicilla* along the coast of mainland Norway.

Great Skua reproductive success

Despite frequent (every third to fourth day) and thorough searches of a relatively small breeding area, some nests were found when the chick(s) had already hatched. Also, in line with Furness (1977), clutches that disappeared shortly after laying may have been missed in which case replacement clutches could have been mistaken for first clutches. The self-imposed restrictions to visit the colony as briefly as possible and to observe at a distance whenever that seemed appropriate to avoid cross-contaminations of the virus, made the collection of more comprehensive data virtually impossible, however. Given the time span between the earliest and latest calculated laying dates at Ristie – Da Logat (nest **010** 13 May, nest **033** around 16 June; **Table 6**), replacement clutches may indeed have occurred. The few birds that were territorial, but seemingly didn't nest, may have been individuals

that had lost their eggs for example in May, but went unnoticed given the late first area visit (early June) relative to the start of laying. The fact that more 'active nests' and territorial pairs were found than expected, given area censuses in 2007 and 2015, suggests that very few returning pairs may have been missed completely (Table 5).

A clutch size of 1.74 ± 0.45 eggs per nest ($n=34$), and a hatching success of 1.09 ± 0.91 chicks per nest ($n=33$) is marginally lower than that reported by Furness (1977) for birds with known breeding experience in the mid-1970s, when the population was 'booming'. The average egg volume found, 80.7 ± 6.4 cc (65.6 - 93.5 cc), was ca. 7.5% lower than expected on data collected on Foula in that same period (~ 87.3 cc; Furness 1977). One third (29%) of the nests were plundered prior to hatching, and on several occasions, this had to do with the health condition and subsequent death of the attending birds (pairs halved, or both parents died). Yet, that around one third of all nests was predated is not too far from the 25% of clutches lost before hatching (with only some of them replaced) as reported by Furness (1977).

Neither chick growth nor fledging rates could be measured for various reasons, but later visits to the area (SG) indicated that there continued to be chicks under care later in July, developing feathers. Observations just after hatching (using camera traps) showed that hatchlings were generally well-provisioned by pairs that managed to stay clear of the avian influenza virus, or that were perhaps immune. Pairs of which one partner died failed without exceptions. Complete pairs spent considerable amounts of time together on territory, with very few disturbances (from other birds, grazing mammals, or human visitors alike). Prey fed to chicks was mostly fish, occasionally rabbits, but very rarely birds (except some cases in which conspecific chicks were taken). Until 10th July, which is when guillemots were leaving the ledges, but when juvenile kittiwakes were still at their nests, there were no signs that any seabird was brought ashore to provision the chicks. Some chicks were found in early (3) August, but by late (24) August only the feathered remains of near-fledglings were found (SG). If the plot managed to fledge any chicks is not completely clear, but breeding success must have been very low indeed.

As in 2021, there is no evidence that any chicks have fledged from the Da Bitten long-term monitoring plot in summer 2022 (SG). In fact, no fledglings have been detected anywhere, on parts of Foula overseen by residents (status 24 August 2022), suggesting that the breeding failure on Foula may have been virtually complete.

Possible long-term implications of the pandemic for Great Skuas

Life history theory suggests that animals should balance their current investment in young against their chances to reproduce in the future (Stearns 1992, Erikstad *et al.* 1998, Saether *et al.* 2004). One fundamental prediction is that long-lived species, such as Great Skuas and many other seabirds, have evolved a fixed level of investment in young in order to maximize their own adult survival. During poor breeding conditions, maximum fitness is achieved either by not breeding at all, or by abandoning the brood. Food limitation is generally thought to underlie much of the variation in life history traits of birds (Martin 1987, 1995, Pons & Migot 1995). Long-lived animals tend to be particularly vulnerable to excessive mortality and a rapid, strong population collapse, after which recovery may take decades (Muscik 1999).

Great Skuas may first breed when somewhere between four and over 11 years old. Modal and median age of first breeding of Great Skuas at Foula is, or was, seven years, but with considerable individual variation (Furness 2015). In long-lived organisms, effort towards reproduction will increase with age, and research from oviparous vertebrates largely supports this prediction (Paitz *et al.* 2007). When food supplies around Foula

deteriorated (thereby reducing adult survival and breeding success resulting in a population decline), the age of first breeding increased, implying a density-dependent age of recruitment. Clutch volume increased with age up to 14 years and decreased with age above this (Furness 1983b, Hamer & Furness 1991). Clutch size and (a-)egg volume increased with breeding experience but hatching rates were not affected. Improvements in clutch size were associated with breeding experience rather than with the age of the birds, thereby providing support for the maturation hypothesis (Ratcliffe *et al.* 1998). There was no relationship between age and territorial attendance during incubation, but time spent foraging to provide food for chicks and aggression increased with age, which is seen as evidence of an increase in reproductive effort in older individuals (Hamer & Furness 1991). Older, more experienced birds may have expended greater reproductive effort simply because they had learned to do so without incurring higher mortality or lower future breeding success.

The Great Skua population on Foula has almost halved since the late 1970s (3180 pairs in 1977, 2293 pairs in 2000, 1846 pairs in 2015), which was a fairly gradual process and the result of a significant decline in reproductive success: 1.1 ± 0.1 fledglings nest⁻¹ in 1970-79, 0.8 ± 0.3 fledglings nest⁻¹ in 1980-89, 0.8 ± 0.3 fledglings nest⁻¹ in 1990-99, 0.6 ± 0.4 fledglings nest⁻¹ in 2000-09 (R.W. Furness *in litt.*). Their breeding success was extremely low in most recent years (Da Bitten study plot 2010-21 0.16 ± 0.1 fledglings nest⁻¹; Gear 2022). Still, it was one of the more successful seabirds in comparison with numerous other species, three of which even went locally extinct on Foula (Heubeck *et al.* 1999, Church *et al.* 2018, Owen *et al.* 2018). The Great Skua census of apparently occupied breeding territories in 2022 was conducted in early June, immediately after peak mortality had occurred, but with continuing infections and kills of adult breeders in two further months. The almost 60% decline, therefore, is probably overly optimistic, and the actual drop in numbers is likely at least 70%, over a single breeding season, affecting almost exclusively adult individuals. A sudden ~70% decline in just one year, following a gradual ~42% decline in breeding numbers over four decades. The long-term decline is the result of deteriorating environmental conditions, affecting so many other seabirds at the same time, the short-term decline is the result of a novel pathogen, affecting some species so much more than others.

It is possible that many breeding birds abandoned the colonies and left, which could explain the dramatic drop in Apparently Occupied Territories (AOTs) that was detected in early June 2022 in comparison with the most recent census in 2015: after all, “animals should balance their current investment in young against their chances to reproduce in the future”, and “during poor breeding conditions, maximum fitness is achieved either by not breeding at all, or by abandoning the brood”. However, 1400 dead Great Skuas were found on the island, while countless others (still on the island and dead) were missed, given difficulties to oversee the landscape and despite thorough and repeated searches all over the island. That is a very large number of dead birds indeed, and strong evidence that most birds did not leave the island, but died. Breeding conditions were not poor; certainly not poor enough to forego breeding, and breeding is what the Great Skuas did according to our studies at Da Bitten and Ristie – Da Logat (plus observations elsewhere on the island). They bred for as long as the birds remained unaffected by the virus, and (many) birds continued with their breeding attempts, even when they were fatally ill (see the image on the front cover as a prime example). Hence, vulnerable to excessive mortality as they are, as long-lived, slowly reproducing seabirds, the recovery of the present population collapse will take decades (*cf.* Muscik 1999).

Seemingly unaffected species

The well-being of other seabirds, so far unaffected by the pandemic, was a continuous concern during our field work in 2022. Working protocols were adjusted, such that cross-contamination between areas and species was

avoided as much as possible. We were particularly concerned about the small (remaining) populations of breeding Arctic Skuas, Arctic Terns and Red-throated Divers on Foula, all of which breed on the island itself rather than on the cliffs, and none of which could stay completely clear of close contact with the omnipresent and evidently affected Great Skuas on the island. We found no problems, except some unexplained dead terns in the colony near the airstrip. Divers were present in virtually all lochs and pools, and if virions accumulated in water bodies communally used by Great Skuas (e.g. virus shed upon defecation, or from carcasses in water), they must have been in contact, but were either not infected, or did not develop a detectable illness. Arctic Skuas tend to use their own ponds for bathing, rather than to join Great Skuas at preferred bathing places. This might explain why Arctic Skuas remained (seemingly) unaffected, but this conclusion is in fact highly speculative and the observation underpins again that more needs to be done to understand the ecology of the virus infection and which factors affect transmission risk.

Conclusions

The extra mortality, inflicted by the H5N1 pandemic on Great Skuas breeding on Foula, may lead to a 60-70% decline in breeding numbers, following a gradual 40% decline in numbers and poor reproductive success over four decades as a result of deteriorating environmental conditions. Only very small numbers now remain of what has been the largest colony of Great Skuas in the world.

The extra mortality, inflicted by the H5N1 pandemic on Northern Gannets breeding on Foula, was fairly small and nesting densities declined by approximately 20% over two months, following a steady, slow, but long-term increase in breeding numbers, following the colonisation of Foula in the late 1970s.

Great Skuas may have picked up the virus while scavenging at sea on dead (infected) Northern Gannets, but that the virus spread so rapidly all over the island and affecting so many individuals in such a short time span must have been caused by their sensitivity to the virus (conspecific infections), and most infections may have taken place at communal bathing places and clubs where the birds socialise.

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References

- Amos I. 2022. Devastating scenes as avian flu causes massive seabird deaths across Scottish islands. The Scotsman 5 June 2022 <https://www.scotsman.com/news/environment/devastating-scenes-as-avian-flu-causes-massive-seabird-deaths-across-scottish-islands-3719027>.
- Anon. 2022. Fugleinfluensa påvist hjå storjo på Svalbard. Norwegian Veterinary Institute News 12 July 2022. <https://www.vetinst.no/nyheter/fugleinfluensa-pavist-hja-storjo-pa-svalbard>.
- Banyard A.C., F.Z.X. Lean, C. Robinson, F. Howie, G. Tyler, C. Nisbet, J. Seekings, S. Meyer, E. Whittard, H.F. Ashpitel, M. Bas, A.M.P. Byrne, T. Lewis, J. James, L. Stephan, N.S. Lewis, I.H. Brown, R.D.E. Hansen & S.M. Reid 2022. Detection of highly pathogenic avian influenza virus H5N1 clade 2.3.4.4b in Great Skuas: a species of conservation concern in Great Britain. *Viruses* 14: 212. <https://doi.org/10.3390/v14020212>.
- Berry R.J. & B.J.K. Tricker 1969. Competition and extinction: the mice of Foula, with notes on those of Fair Isle and St Kilda. *J. Zool.* 158: 247-265.
- Bijlsma R.G. 2001. All that remains: bij de dood van een reekalf. *Zoogdier* 12(4): 14-16.
- Borm S. van, I. Thomas, G. Hanquet, B. Lambrecht, M. Boschmans, G. Dupont, M. Decaestecker, R. Snacken & T. van den Berg 2005. Highly pathogenic H5N1 influenza virus in smuggled Thai eagles, Belgium. *Emerg. Infect. Dis.* 11: 702–705.
- Camphuysen C.J. 2022. Beached bird surveys in The Netherlands, autumn 2021 and winter 2021/22. NIOZ Report, RWS Centrale Informatievoorziening BM 22.xx, Aug 2022. Royal Netherlands Institute for Sea Research, Texel.
- Camphuysen C.J., T.A.W. Schreurs & A. Samba Bilal 2022. Ship-based seabird and marine mammal surveys off Mauritania, 17 February - 1 March 2022. Royal Netherlands Institute for Sea Research (NIOZ), Den Burg, Texel and the Institut Mauritanien de Recherche Océanographique et des Pêche (IMROP), Nouadhibou.
- Chen H., G.J.D. Smith, S.Y. Zhang, K. Qin, J. Wang, K.S. Li, R.G. Webster, J.S.M. Peiris & Y. Guan 2005. H5N1 virus outbreak in migratory waterfowl - A worrying development could help to spread this dangerous virus beyond its stronghold in southeast Asia. *Nature* 436: 191-192.
- Church G.E., R.W. Furness, G. Tyler, L. Gilbert & S.C. Votier 2018. Change in the North Sea ecosystem from the 1970s to the 2010s: great skua diets reflect changing forage fish, seabirds, and fisheries. *ICES J. Mar. Sc.* 76: 925-937.
- Erikstad K.E., Fauchald P., Tveraa T. & Steen H. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology* 79: 1781-1788.

- Furness R.W. 1977. Studies on the breeding biology and population dynamics of the great skua (*Catharacta skua* Brünnich). Ph.D.-thesis, Durham University.
- Furness R.W. 1981. Colonisation of Foula by Gannets. *Scott. Birds* 11: 211-213.
- Furness R.W. 1983a. Foula, Shetland vol. 4, The Birds of Foula. Brathay Centre Expl. Field Stud., Old Brathay.
- Furness R.W. 1983b. Variations in size and growth of Great skua *Catharacta skua* chicks in relation to adult age, hatching date, egg volume, brood size and hatching sequence. *J. Zool., Lond.* 199: 101-116.
- Furness R.W. 1987. The Skuas. T. & A.D. Poyser, Calton.
- Furness R.W. 2015. Density dependence in seabirds: Great Skuas *Stercorarius skua* start to breed at a younger age when conditions are better. *Ringling & Migr.* 30: 43-50.
- Furness R.W. & N. Ratcliffe 2004. Great Skua *Stercorarius skua*. In: Mitchell P.I., S.F. Newton, N. Ratcliffe & T.E. Dunn (eds) *Seabird populations in Britain and Ireland: 173-186*. T. & A.D. Poyser, London.
- Furness R.W. 1987. The Skuas. T. & A.D. Poyser, Calton.
- Gear S. 2022. Appendix 1. Seabird monitoring on Foula in 2021. In: Miles W. & M. Mellor 2022. SOTEAG Ornithological monitoring programme - 2021 report: 42-44. Report to the Shetland Oil Terminal Environmental Advisory Group, Univ. St Andrews.
- Globig A., C. Staubach, M. Beer, U. Köppen, W. Fiedler, M. Nieburg, H. Wilking, E. Starick, J.P. Teifke, O. Werner, F. Unger, C. Grund, C. Wolf, H. Roost, F. Feldhusen, F.J. Conraths, T.C. Mettenleiter & T.C. Harder 2009. Epidemiological and ornithological aspects of outbreaks of highly pathogenic avian influenza virus H5N1 of Asian lineage in wild birds in Germany, 2006 and 2007. *Transb. Emerg. Dis.* 56: 57-72
- Hamer K.C. & Furness R.W. 1991. Age-specific breeding performance and reproductive effort in great skuas *Catharacta skua*. *J. Anim. Ecol.* 60: 693-704.
- Heubeck M., R.M. Mellor, P.V. Harvey, A.R. Mainwood & R. Riddington 1999. Estimating the population size and rate of decline of Kittiwakes *Rissa tridactyla* breeding in Shetland, 1981-97. *Bird Study* 46: 48-61.
- Huang Y., G.J. Robertson, D. Ojkic, H. Whitney & A.S. Lang 2014. Diverse inter-continental and host lineage reassortant avian influenza A viruses in pelagic seabirds. *Infection, Genetics and Evolution* 22: 103-111.
- IOC 2022. World Bird List Data Sets version 12.0 (<https://doi.org/10.14344/IOC.ML.12.0>).
- Janzen D. H. 1977. Why fruits rot, seeds mold, and meat spoils. *Am. Nat.* 111: 691-713.
- JNCC 2022. Great skua (*Stercorarius skua*). SMP Report 1986–2019, Joint Nature Conservation Committee, Peterborough. <https://jncc.gov.uk/our-work/great-skua-stercorarius-skua/> Accessed 29 June 2022.
- Jhung M.A. & D.I. Nelson 2015. Outbreaks of Avian Influenza A (H5N2), (H5N8), and (H5N1) Among Birds - United States, December 2014-January 2015. *Morbidity and Mortality Weekly Reports* 64(4): 111.
- Kaplan B.S. & R.J. Webby 2013. The avian and mammalian host range of highly pathogenic avian H5N1 influenza. *Virus Res.* 178: 3-11.
- Klomp N.I. & R.W. Furness 1992. Non-breeders as a buffer against environmental stress: declines in numbers of Great Skuas on Foula, Shetland, and prediction of future recruitment. *J. Appl. Ecol.* 29: 341-348.
- Lang A.S., C. Lebarbenchon, A.M. Ramey, G.J. Robertson & J. Waldenström 2016. Assessing the role of seabirds in the ecology of influenza A viruses. *Avian Dis.* 60 (1s): 378-386.
- Lund-Hansen L.C. & P. Lange 1991. The numbers and distribution of the Great Skua *Stercorarius skua* breeding in Iceland 1984-1985. *Acta Nat. Isl.* 34: 1-16.

- Marinova-Petkova A., G. Georgiev, P. Seiler, D. Darnell, J. Franks, S. Krauss, R.J. Webby & R.G. Webster 2012. Spread of influenza virus A (H5N1) clade 2.3.2.1 to Bulgaria in common buzzards. *Emerg. Infect. Dis.* 18: 1596–1602.
- Martin T.E. 1987. Food as a limit on breeding birds: a life-history perspective. *Ann. Rev. Ecol. Syst.* 18: 453-487.
- Martin T.E. 1995. Avian life-history evolution in relation to nest sites, nest predation, and food. *Ecol. Monogr.* 65: 101-127.
- Mondor E.B., M.N. Tremblay, J.K. Tomberlin, E.M. Benbow, A.M. Tarone & T.L. Crippen 2012. The ecology of carrion decomposition. *Nature Education Knowledge* 3(10): 21.
- Murray S., W.T.S. Miles, D. Parnaby, D. Cowlet & M.P. Harris 2021. First aerial surveys of Gannets on Fair Isle and Foula, Shetland, in 2017. *Scottish Birds* 41: 195-201.
- Muscik J.A. 1999. Ecology and Conservation of Long-Lived Marine Animals. *American Fisheries Society Symposium* 23: 1-10.
- O'Regan S.M., T.C. Kelly, A. Korobeinikov, M.J.A. O'Callaghan & A.V. Pokrovskii 2008. Qualitative and numerical investigations of the impact of a novel pathogen on a seabird colony. *Journal of Physics: Conference Series* 138 (2008) 012018 doi:10.1088/1742-6596/138/1/012018.
- Owen E., O. Prince, C. Cachia-Zammit, R. Cartwright, T. Coledale, S. Elliott, S. Haddon, G.K. Longmoor, J. Swale, F. West & R. Hughes 2018. Counts of Puffins in Shetland suggest an apparent decline in numbers. *Scottish Birds* 38: 223-231.
- Paitz R.T., H.K. Harms, R.M. Bowden & F.J. Janzen 2007. Experience pays: offspring survival increases with female age. *Biol. Lett.* 3: 44-46.
- Philip E. 2022. Seabird HPAI outbreak surveillance - NatureScot weekly update. Weekly unpublished reports, June, July, August 2022 [in series], NatureScot, Aviemore.
- Pons J-M. & Migot P. 1995. Life-history strategy of the herring gull: changes in survival and fecundity in a population subjected to various feeding conditions. *J. Anim. Ecol.* 64: 592-599.
- Ramey A.M., A.B. Reeves, B.J. Lagassé, V. Patil, L.E. Hubbard, D.W. Kolpin, R.B. McCleskey, D.A. Repert, D.E. Stallknecht & R.L. Poulson 2022. Evidence for interannual persistence of infectious influenza A viruses in Alaska wetlands. *Sc. Tot. Env.* 803 (2022) 150078.
- Ratcliffe N., R.W. Furness & N.I. Klomp 1998. Influences of breeding experience on the reproductive performance of Great Skuas *Catharacta skua*. *J. Avian Biol.* 29: 293-298.
- Roche B., C. Lebarbenchon, M. Gauthier-Clerc, C-M Chang, F. Thomas, F. Renaud, S. van der Werf & J-F. Guégan 2009. Water-borne transmission drives avian influenza dynamics in wild birds: The case of the 2005-2006 epidemics in the Camargue area. *Inf., Gen. & Evol.* 9: 800-805.
- Sæther B-E., S. Engen, A.P. Moller, H. Weimerskirch, M.E. Visser, W. Fiedler, E. Matthysen, M.M. Lambrechts, A. Badyaev, P.H. Becker, J.E. Brommer, D. Bukacinski, M. Bukacinska, H. Christensen, J. Dickinson, C. du Feu, F.R. Gehlbach, D. Heg, H. Hötker, J. Merilä, J. Tottrup Nielsen, W. Rendell, R.J. Robertson, D.L. Thomson, J. Török & P. van Hecke 2004. Life-history variation predicts the effects of demographic stochasticity on avian population dynamics. *Am. Nat.* 164: 793-802.
- Scientific Task Force on Avian Influenza and Wild Birds (STFAIWB) 2022. H5N1 Highly Pathogenic Avian Influenza in poultry and wild birds: Winter of 2021/2022 with focus on mass mortality of wild birds in UK and Israel. https://www.cms.int/sites/default/files/uploads/avian_influenza_0.pdf.

- Sonnberg S., R.J. Webby & R.G. Webster 2013. Natural history of highly pathogenic avian influenza H5N1. *Virus Res.* 178: 63-77.
- Stearns S.C. 1992. *The evolution of life histories.* Oxford Univ. Press, Oxford.
- Tiwari V. 2022. 'Significant drop' in gannets on Bass Rock amid avian flu outbreak <https://news.stv.tv/east-central/significant-drop-in-seabird-numbers-on-bass-rock-amid-avian-flu-outbreak-says-scottish-seabird-centre>.
- Walsh P.M., Halley D.J., Harris M.P., Nevo A. del, Sim I.M.W. & Tasker M.L. 1995. *Seabird monitoring handbook for Britain and Ireland.* Joint Nature Conservation Committee / RSPB / ITE / Seabird Group, Peterborough.
- Webster R.G., M Yakhno, V.S. Hinshaw, W.J. Bean & K.G.Murti 1978. Intestinal influenza: replication and characterization of influenza viruses in ducks. *Virology* 84: 268-278.
- Wille M., Y. Huang, G.J. Robertson, P. Ryan, S.I. Wilhelm, D. Fifield, A.L. Bond, A. Granter, H. Munro, R. Buxton, I.L. Jones, M.G. Fitzsimmons, C. Burke, L. McFarlane Tranquilla, M. Rector, L. Takahashi, A.-L. Kouwenberg, A. Storey, C. Walsh, A. Hedd, W.A. Montevicchi, J.A. Runstadler, D. Ojkic, H. Whitney & A.S. Lang 2014. Evaluation of seabirds in Newfoundland and Labrador, Canada, as hosts of influenza A viruses. *J. Wildl. Dis.* 50: 98-103.
- World Health Organization 2022. Cumulative number of confirmed human cases for avian influenza A(H5N1) reported to WHO, 2003-2022. www.who.int/publications/2022_june_tableh5n1.pdf.

Appendix 1. Condition of birds found (7-point scale)



Very old → dried remains, at least a month old carcasses, often disintegrated and mummified (>28d old).



Old → several weeks to more than a month or so old; feathers loosening, carcasses often damaged, twisted, insects loose interest (22-28d old).



Rather old → several weeks old, feathers messy, flattened, eyes deep dry, insects and mice are doing their work or have done so (15-21d old).



Rather fresh → a week, or just over a week, feathers still bouncing and in good condition, eyes dry, insects become interested, first maggots (cloaca!) (8-14d old).



Fresh → several days old at most (eyes initially not really dry), feathers bouncing and dry (3-7 d old).

Very fresh → rigor mortis, died that same day or 1-2 days earlier at most (0-2d old).



Dying → Dizzy, spasms, falling over their own legs, unable to fly or properly respond (assumed to die the next day, or -1 d old).

Appendix 2. Scavengers and Great Skua corpses



Assumed avian scavenger – flank and belly pecked open, and organs intestines consumed until the bare bone (note ribs).



Assumed avian scavenger – breast and belly pecked open, and organs, intestines and breast muscles consumed until the bare bone (note sternum).



Assumed non-avian scavenger – no evidence for an opening of the body, but major insect intrusions and messy feathers perhaps as a result of feeding mice.



Assumed non-avian scavenger - no evidence for an opening of the body, even though rump feathers all removed until the bare bone (note synsacrum), perhaps by mice, also major insect intrusions.



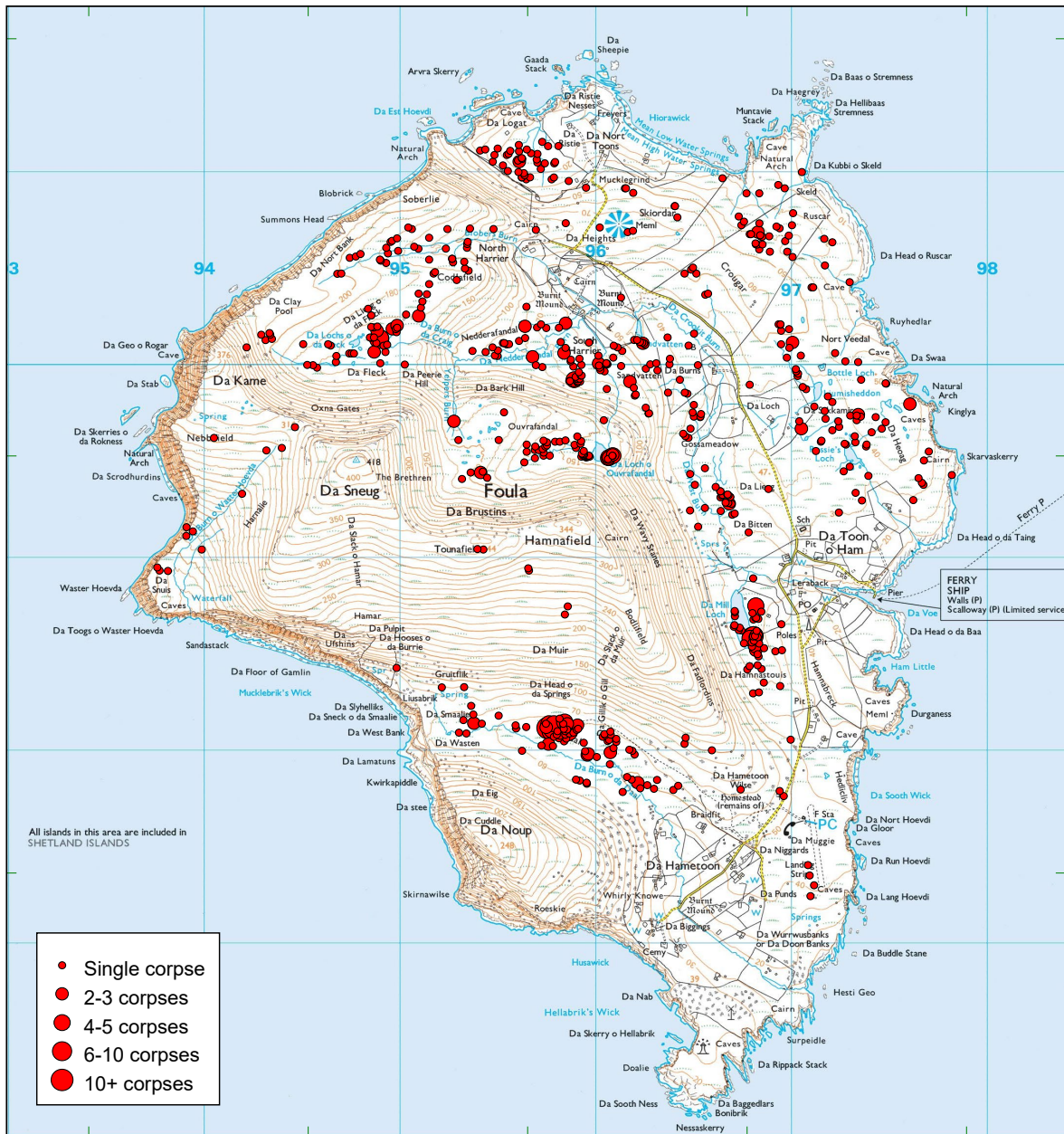
Insect intrusions – access via cloaca leading to massive maggot concentrations within days



Insect intrusions – access via cloaca leading to massive maggot concentrations within days

Appendix 3. Spatial pattern Great Skua corpses, May, Jun, and July 2022 ($n= 1400$)

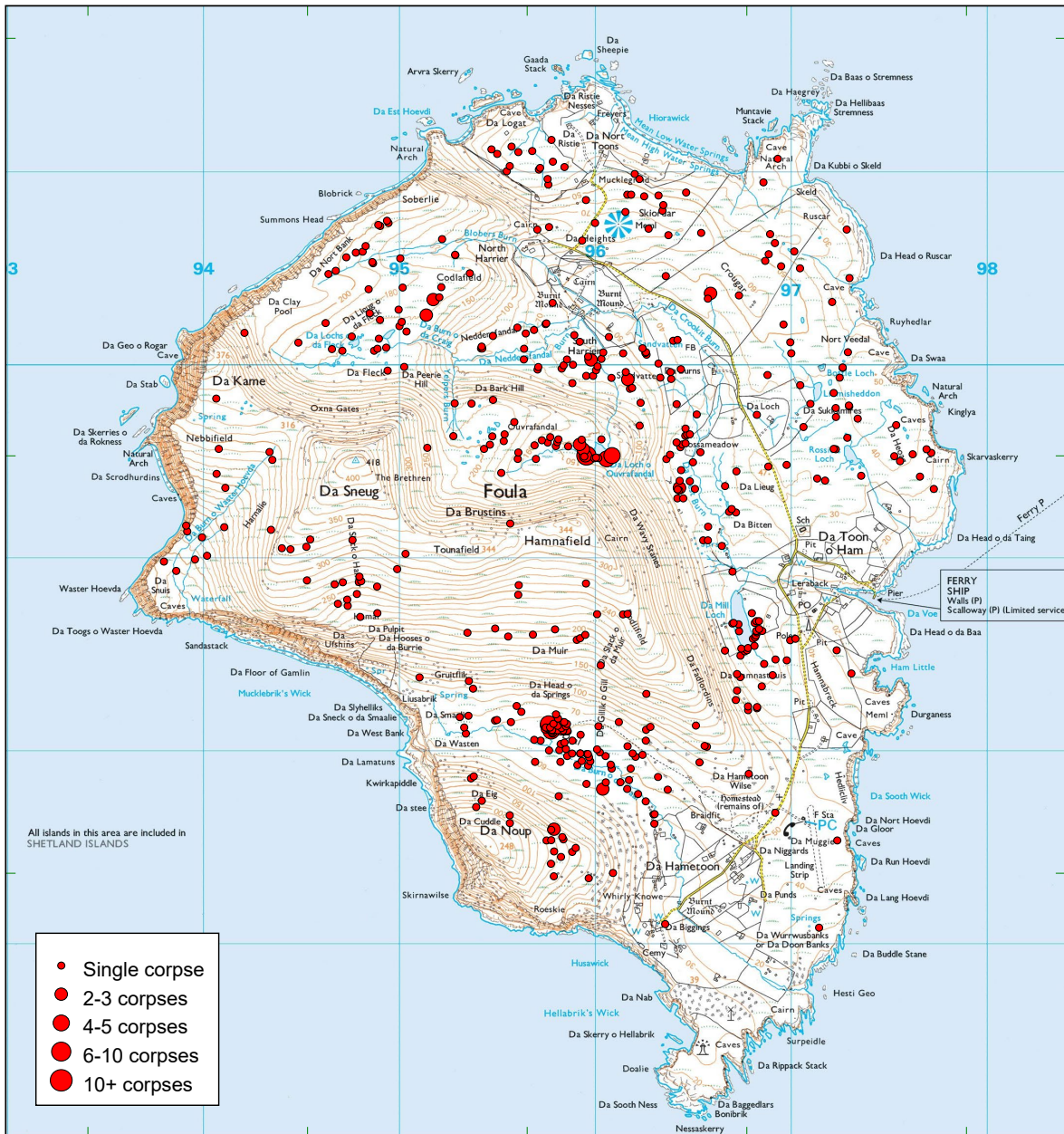
Bonxies that probably died in May ($n= 710$)



Appendix Fig. 8a. Great Skuas found on Foula that probably died in May 2022 ($n = 710$).

Background map of Ordnance Survey <https://i.pinimg.com/originals/e6/a5/b9/e6a5b9825e5fda231a52accba0781797.jpg>

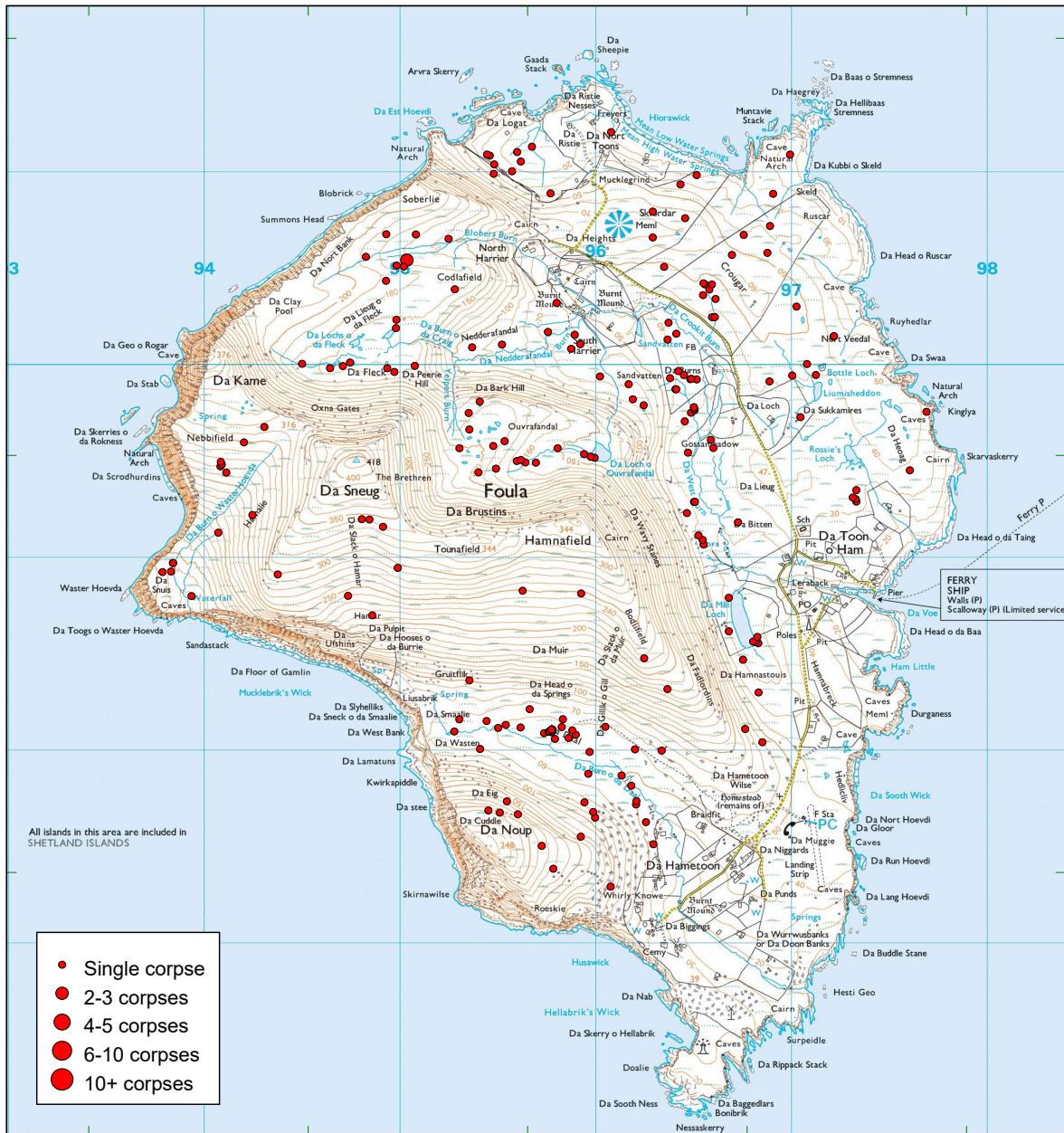
Bonxies that probably died in June (n= 494)



Appendix Fig. 8b. Great Skuas found on Foula that probably died in June 2022 (n = 494).

Background map of Ordnance Survey <https://i.pinimg.com/originals/e6/a5/b9/e6a5b9825e5fda231a52accba0781797.jpg>

Bonxies that probably died in July (n = 196)



Appendix Fig. 8c. Great Skuas found on Foula that probably died in July 2022 (n = 196).

Background map of Ordnance Survey <https://i.pinimg.com/originals/e6/a5/b9/e6a5b9825e5fda231a52accba0781797.jpg>

Appendix 4. Birds and mammals observed on Foula (CJC only), 31 May – 11 July 2022, numbers of carcasses recorded (Great Skuas including further searches by SG in July), and likelihood of HPAIV infections as primary cause.

Species		Observations	Found dead	HPAIV suspicions
Red-throated Diver	<i>Gavia stellata</i>	(BB)		
Great Northern Diver	<i>Gavia immer</i>	1		
White-billed Diver	<i>Gavia adamsii</i>	1		
Northern Fulmar	<i>Fulmarus glacialis</i>	(BB)	3	
Manx Shearwater	<i>Puffinus puffinus</i>	1		
European Storm-petrel	<i>Hydrobates pelagicus</i>	1		
Northern Gannet	<i>Morus bassanus</i>	(BB)	41	HPAIV
European Shag	<i>Phalacrocorax aristotelis</i>	(BB)		
cormorant	<i>Phalacrocorax spec.</i>	1	1	
Grey Heron	<i>Ardea cinerea</i>	2x		
Bean Goose	<i>Anser fabalis</i>	4x2		
Greylag Goose	<i>Anser anser</i>	(BB)	2	
Mallard	<i>Anas platyrhynchos</i>	(B)		
Tufted Duck	<i>Aythya fuligula</i>	2		
Common Eider	<i>Somateria mollissima</i>	(BB)	3	
Red-breasted Merganser	<i>Mergus serrator</i>	4		
Common Kestrel	<i>Falco tinnunculus</i>	1		
Common Quail	<i>Coturnix coturnix</i>	1		
Eurasian Oystercatcher	<i>Haematopus ostralegus</i>	(BB)		
Ringed Plover	<i>Charadrius hiaticula</i>	(BB)		
European Golden Plover	<i>Pluvialis apricaria</i>	(BB)		
Northern Lapwing	<i>Vanellus vanellus</i>	(BB)		
Dunlin	<i>Calidris alpina</i>	(BB)		
Snipe	<i>Gallinago gallinago</i>	(BB)		
Whimbrel	<i>Numenius phaeopus</i>	7	1	
Eurasian Curlew	<i>Numenius arquata</i>	(BB)		
Common Redshank	<i>Tringa totanus</i>	(BB)		
Ruddy Turnstone	<i>Arenaria interpres</i>	(B)		
Red-necked Phalarope	<i>Phalaropus lobatus</i>	(B)		
Arctic Skua	<i>Stercorarius parasiticus</i>	(BB)	1	
Great Skua	<i>Stercorarius skua</i>	(BB)	1400	HPAIV
Mew Gull	<i>Larus canus</i>	(BB)		
Herring Gull	<i>Larus argentatus</i>	(BB)	5	4x HPAIV
Great Black-backed Gull	<i>Larus marinus</i>	(BB)	3	2x HPAIV
Black-legged Kittiwake	<i>Rissa tridactyla</i>	(BB)		
Arctic Tern	<i>Sterna paradisaea</i>	(BB)	5	4x HPAIV?
Common Guillemot	<i>Uria aalge</i>	(BB)		
Razorbill	<i>Alca torda</i>	(BB)		
Black Guillemot	<i>Cephus grylle</i>	(BB)		
Atlantic Puffin	<i>Fratercula arctica</i>	(BB)		
Rock Pigeon	<i>Columba livia</i>	(BB)		
domestic pigeon	<i>Columba 'domestica'</i>	(BB)		
Common Wood Pigeon	<i>Columba palumbus</i>	2		
Eurasian Collared Dove	<i>Streptopelia decaocto</i>	5		

Species		Observations	Found dead	HPAIV suspicions
Sky Lark	<i>Alauda arvensis</i>	(BB)		
Barn Swallow	<i>Hirundo rustica</i>	(BB)		
House Martin	<i>Delichon urbica</i>	3		
Meadow Pipit	<i>Anthus pratensis</i>	(BB)		
Rock Pipit	<i>Anthus spinoletta petrosus</i>	(BB)		
Winter Wren	<i>Troglodytes troglodytes</i>	(BB)		
Northern Wheatear	<i>Oenanthe oenanthe</i>	(BB)		
Common Blackbird	<i>Turdus merula</i>	(BB)		
Common Chiffchaff	<i>Phylloscopus collybita</i>	3		
Carrion Crow	<i>Corvus corone corone</i>	2x1 ¹		
Hooded Crow	<i>Corvus corone cornix</i>	18 ¹		
Common Raven	<i>Corvus corax</i>	(B)	1	
Common Starling	<i>Sturnus vulgaris</i>	(BB)		
House Sparrow	<i>Passer domesticus</i>	(BB)		
Twite	<i>Carduelis flavirostris</i>	(B)		
Minke Whale	<i>Balaenoptera acutorostrata</i>	2		
Killer Whale	<i>Orcinus orca</i>	5		
Risso's Dolphin	<i>Grampus griseus</i>	4		
Grey Seal	<i>Halichoerus grypus</i>	65 ¹		
Common Seal	<i>Phoca vitulina</i>	106 ¹		
Hedgehog	<i>Erinaceus europaeus</i>	1	1	
Rabbit	<i>Oryctolagus cuniculus</i>	(BB)	++	
Foula Field Vole	<i>Apodemus sylvaticus thuleo</i>	(BB)		

¹) Frequent counts of the same animals

BB = breeding confirmed, or firmly established AOT observed

B = breeding likely, not confirmed

++ = very abundant

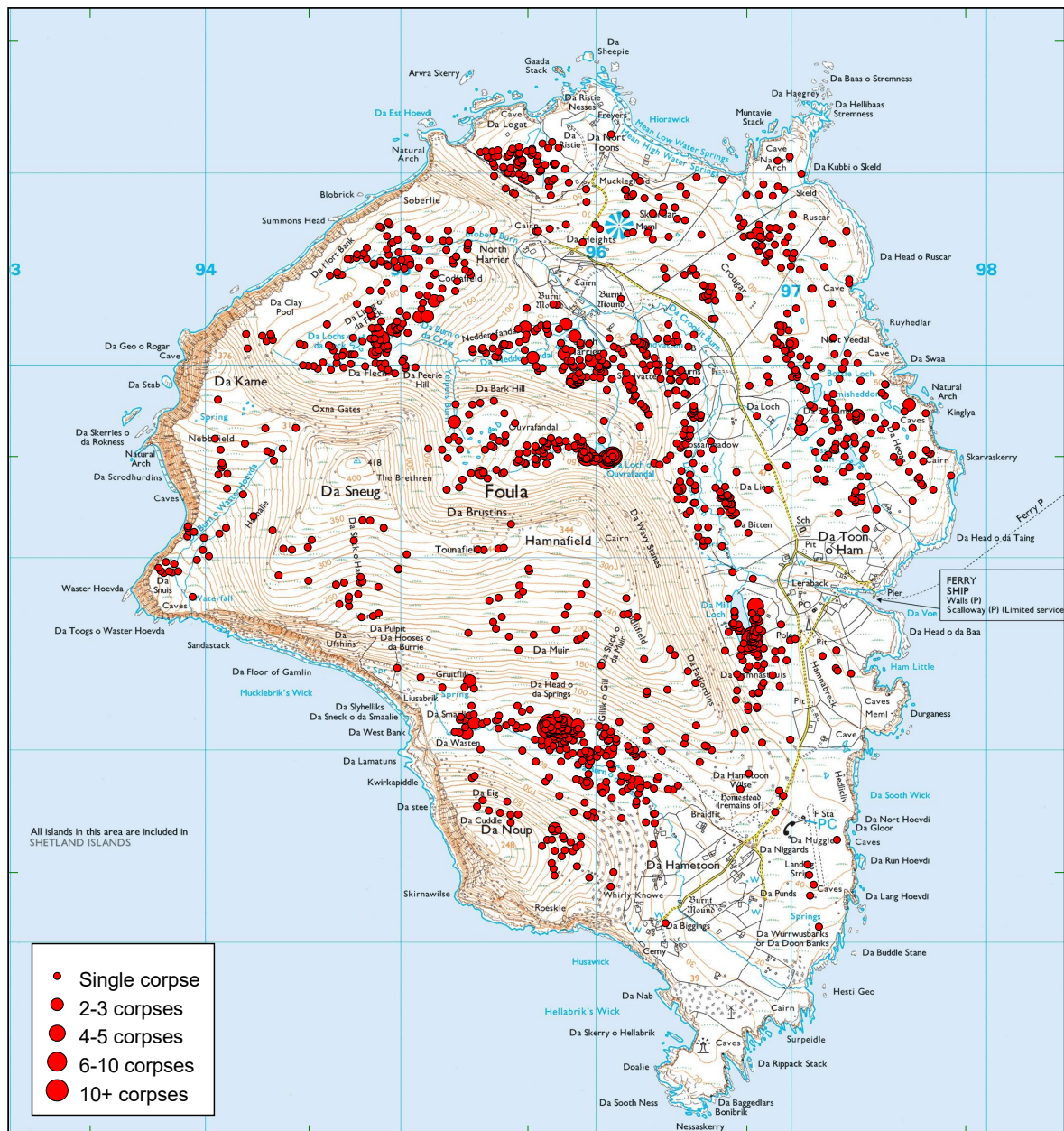
HPAIV = suspected avian influenza as primary cause of death

HPAIV? = possibly, only given (inter-) national context

Appendix 5. Post script – further finds of dead Great Skuas in August and September 2022 on Foula and evidence for poor reproductive success.

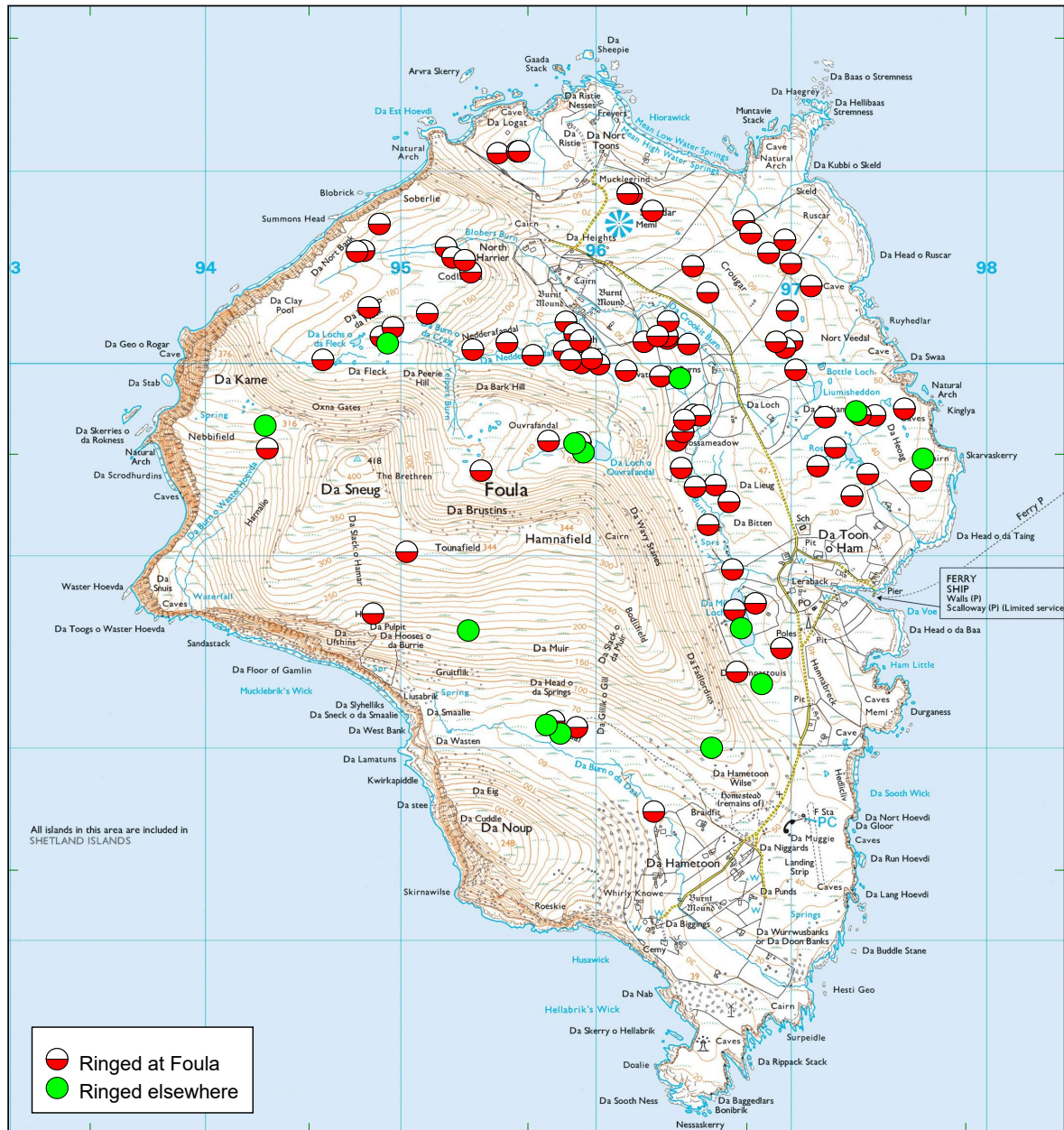
Further field surveys in August and September 2022 on Foula (SG) produced another 101 dead Great Skuas, most of which were found as very old carcasses, so these must have been missed during earlier searches. Of these, 9 individuals were ringed, 8 on Foula, and 1 (probably) at Fair Isle. Searches included Ridge of Hamnafield, Hamnabrek (20 Aug, 11 birds), North Toons (24 Aug, 4), Rossies Loch, Gaads, Luimishidden, and Bottle Loch (7 Sep, 19 of which 3 ringed), Crougar, Ruscar and Sandvatten (8 Sep, 16, 5 ringed), Fleck and Ouvrafandal (10 Sep, 26, 1 ringed), Da Noup (11 Sep, 15), and Tounafield, Veedal (12 Sep, 10). The grand total of Great Skuas found on Foula in summer 2022 (May-September) arrived thereby at 1501 individuals (**Fig. 8d**), of which 109 individuals were ringed earlier in life (**Fig. 9a**).

All dead Great Skuas Found, May-September (n= 1501)



Appendix Fig. 8d. Great Skuas found on Foula May- September 2022 ($n = 1501$).

Dead bonxies with rings n = 109



Appendix Fig. 9a. Great Skuas carrying metal rings found on Foula, summer 2022 (n = 109).

Breeding success of Great Skuas on Foula, summer 2022

Following up on late August visits to monitoring plots at Ristie – Da Logat and Da Bitten on 24 August, further observations were conducted on Foula in late August and the first 10 days of September (SG). One single successful fledgling was detected, just north of the top of Codlifield, flying quite well and being protected by a swooping adult. Around that time, there were still about 150 adults territorial, mainly soaring around and sometimes following the observer. The August-September observations confirmed that at least some chicks have reached the fledgling stage, but with very few juveniles managing to survive and actually fledge from Foula. Reproductive success must have been very low indeed, if not a complete failure.

Appendix 6. Typical postures of dead and dying Great Skuas, indicative for avian influenza infections, Foula summer 2022.



Severe hyperextension and spasticity in head and neck (opisthotonos), leading to typical postures of Great Skuas found dead, with heads swung over shoulders or bills pointing upright, as ‘frozen spasms’ (Kees Camphuysen).



Severe hyperextension and spasticity in head and neck (opisthotonos), leading to typical postures of Great Skuas found dead, with heads swung over shoulders or bills pointing upright, as 'frozen spasms' (Kees Camphuysen).

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