Bird Study

ISSN: (Print) (Online) Journal homepage: www.tandfonline.com/journals/tbis20

A case study of highly pathogenic avian influenza (HPAI) H5N1 at Bird Island, South Georgia: the first documented outbreak in the subantarctic region

Ashley Bennison, Stacey Adlard, Ashley C. Banyard, Freya Blockley, Marcia Blyth, Emma Browne, George Day, Michael J. Dunn, Marco Falchieri, Elaine Fitzcharles, Jaume Forcada, Jennifer Forster Davidson, Anthony Fox, Rosamund Hall, Elizabeth Holmes, Kevin Hughes, Joe James, Joshua Lynton-Jenkins, Steve Marshall, Dan McKenzie, Simon A. Morley, Scott M. Reid, Isabel Stubbs, Norman Ratcliffe & Richard A. Phillips

To cite this article: Ashley Bennison, Stacey Adlard, Ashley C. Banyard, Freya Blockley, Marcia Blyth, Emma Browne, George Day, Michael J. Dunn, Marco Falchieri, Elaine Fitzcharles, Jaume Forcada, Jennifer Forster Davidson, Anthony Fox, Rosamund Hall, Elizabeth Holmes, Kevin Hughes, Joe James, Joshua Lynton-Jenkins, Steve Marshall, Dan McKenzie, Simon A. Morley, Scott M. Reid, Isabel Stubbs, Norman Ratcliffe & Richard A. Phillips (26 Sep 2024): A case study of highly pathogenic avian influenza (HPAI) H5N1 at Bird Island, South Georgia: the first documented outbreak in the subantarctic region, Bird Study, DOI: 10.1080/00063657.2024.2396563

To link to this article: https://doi.org/10.1080/00063657.2024.2396563

Published online: 26 Sep 2024.

BIRD STUDY
https://doi.org/10.1080/00063657.2024.2396563

Birds Science People
BTO

OPEN ACCESS
Check for updates

A case study of highly pathogenic avian influenza (HPAI) H5N1 at Bird Island, South Georgia: the first documented outbreak in the subantarctic region

Ashley Bennison[a], Stacey Adlard[a], Ashley C. Banyard[b,c], Freya Blockley[a], Marcia Blyth[a], Emma Browne[a], George Day[a], Michael J. Dunn[a], Marco Falchieri[b], Elaine Fitzcharles[a], Jaume Forcada[a], Jennifer Forster Davidson[a], Anthony Fox[a], Rosamund Hall[a], Elizabeth Holmes[a], Kevin Hughes[a], Joe James[b,c], Joshua Lynton-Jenkins[b,c], Steve Marshall[a], Dan McKenzie[a], Simon A. Morley[a], Scott M. Reid[b], Isabel Stubbs[a], Norman Ratcliffe[a] and Richard A. Phillips[a]

[a]British Antarctic Survey, Natural Environment Research Council, Cambridge, UK; [b]Influenza and Avian Virology Team, Department of Virology, Animal and Plant Health Agency (APHA-Weybridge), Addlestone, UK; [c]WOAH/FAO International Reference Laboratory for Avian Influenza, Animal and Plant Health Agency (APHA-Weybridge), Addlestone, UK

ABSTRACT
Capsule: HPAI H5N1 was documented for the first time in the subantarctic region on Bird Island, South Georgia, resulting in the mortality of Brown Skuas *Stercorarius antarcticus*, Gentoo Penguins *Pygoscelis papua*, Snowy Albatrosses *Diomedea exulans*, and Antarctic Fur Seals *Arctocephalus gazella*.
Aims: The spread of the HPAI H5N1 subtype has had dramatic impacts on numerous populations of wild birds and mammals. We describe a case study that can inform the management of HPAI for conservation practitioners and researchers globally.
Methods: We documented the detection, monitoring, and impact of the first known outbreak of H5N1 HPAI in the subantarctic region, at Bird Island in South Georgia (−54.3582, −36.5112) during 2023–2024. Deaths from HPAI were first suspected in September 2023 and later confirmed by genetic analysis.
Results: In total, 77 Brown Skuas, 38 Gentoo penguins, and 58 Snowy Albatrosses were suspected to have died from HPAI infection, and HPAI was confirmed in 5 dead Antarctic Fur Seals. Total mortality was unknown for all species, as other individuals will have been scavenged before discovery, or died at sea.
Conclusion: This case study provides lessons for the management, risk, safety considerations, and ethical decisions regarding animal welfare that may help guide research and management responses to HPAI outbreaks elsewhere, particularly in remote areas or in species of conservation concern.

ARTICLE HISTORY
Received 17 May 2024
Accepted 8 August 2024

KEYWORDS
Highly pathogenic avian influenza; Antarctic; penguin; Albatross; Fur Seal; management

Highly pathogenic avian influenza (HPAI) viruses have had worldwide ecological impacts, particularly since the recent emergence and global spread of HPAI H5N1 subtype (Lewis *et al.* 2021, Caliendo *et al.* 2022). A shift in the infection dynamics of the virus (Falchieri *et al.* 2022, James *et al.* 2023, Lean *et al.* 2023) resulted in very high mortality among seabird populations across the Northern Hemisphere from 2021 onwards (Ramey *et al.* 2022, Lane *et al.* 2023, Pohlmann *et al.* 2023). HPAI reached South America by October 2022 and then spread widely throughout the continent, causing high mortality in seabirds and marine mammals (Leguia *et al.* 2023, Plaza *et al.* 2024). It is estimated that South American bird and mammal fatalities exceeded 597,000 and 20,179 individuals respectively (Banyard *et al.* 2023). A large proportion of the mortalities were recorded from Peru (557,140 seabirds and 10,458 marine mammals) and Chile (29,432 seabirds and 20,179 marine mammals), but deaths were recorded throughout the continent (Banyard *et al.* 2023). Until October 2023, HPAI had not been detected in Antarctica or the subantarctic region (Lisovski *et al.* 2023).

The islands of South Georgia hold globally important populations of birds and marine mammals (Martin *et al.* 2009, Trathan *et al.* 2012, Poncet *et al.* 2017, Foley *et al.* 2018, Forcada *et al.* 2023). Most of the intensive wildlife monitoring in the region is carried out at Bird Island (54°00′ S, 38°03′ W; Figure 1), which is a ∼4.5 km-long island at the north-west tip of South Georgia,

CONTACT Ashley Bennison ashben@bas.ac.uk
Supplemental data for this article can be accessed online at https://doi.org/10.1080/00063657.2024.2396563.

Figure 1. The location of Bird Island, in South Georgia, in relation to South America and the Antarctic Peninsula.

and is occupied year-round by a small team from the British Antarctic Survey (BAS). The long-term monitoring programmes that record breeding histories of individually-marked animals are focused on Snowy (formerly 'Wandering') Albatross *Diomedea exulans*, Grey-headed Albatross *Thalassarche chrysostoma*, Black-browed Albatross *Thalassarche melanophris*, Northern Giant Petrel *Macronectes halli*, Southern Giant Petrel *Macronectes giganteus*, Brown Skua *Stercorarius antarcticus*, Macaroni Penguin *Eudyptes chrysolophus*, Antarctic Fur Seal *Arctocephalus gazella*, and Leopard Seal *Hydrurga leptonyx*. There is also monitoring of the population trends and productivity of Gentoo Penguin *Pygoscelis papua*, Light-mantled Albatross *Phoebetria palpebrata*, White-chinned Petrel *Procellaria aequinoctialis*, and Southern Elephant Seal *Mirounga leonina*. Other seabirds, including several species of petrel, are abundant on the island. The first monitoring at Bird Island was in 1957, involving studies of Snowy Albatrosses and Antarctic Fur Seals, and the station has been occupied year-round since 1982. South Georgia is within the jurisdiction of the Government of South Georgia and the South Sandwich Islands (GSGSSI), which is a UK Overseas Territory, and all operations are conducted under permits issued by GSGSSI.

In September 2023, the first suspected case of HPAI in the Antarctic or subantarctic regions was recorded on Bird Island. The following is an account of the surveillance, impact, and management of the outbreak. Here, we document the results, including timelines, for species that were confirmed to have HPAI on Bird Island in the 2023–2024 austral summer season; deaths or behaviours where signs of HPAI were equivocal are not included.

Methods

Surveillance, monitoring, and recording

Planning for the expected arrival of HPAI began in early 2022, following outbreaks of the H5N1 clade in southern South America, with BAS and GSGSSI coordinating a response plan for its management, including observation and reporting protocols (GSGSSI 2022). Planning also involved discussions with the UK Animal and Plant Health Agency (APHA) to ensure that preparations were in place to enable controlled sample collection, testing, and risk assurance. This was consistent with guidelines on biosecurity, working with wildlife in the event of an outbreak and the monitoring of cases that were also developed by other bodies, including the mitigation strategy of the UK Government's Department for Environment, Food & Rural Affairs (DEFRA 2024), the Scientific Committee on Antarctic Research (SCAR 2024), Agreement on the Conservation of Albatrosses and Petrels (ACAP 2023), and the International Association of Antarctic Tour Operators (IAATO 2022). All dead or moribund birds seen on Bird Island were recorded from the austral summer of 2022–2023 onwards, but data from that season are not presented here as there were no suspicions of HPAI, nor any confirmed outbreaks elsewhere in the subantarctic or Antarctic regions (Lisovski *et al.* 2023).

Due to the widespread reporting of HPAI outbreaks in the Northern Hemisphere, descriptions were available of signs associated with the infection; these consisted primarily of neurological dysfunction, such as twitching, head spasms, lethargy, uncoordinated behaviour, or an inability to walk or fly (Cardona *et al.* 2009, Banyard *et al.* 2022). Following a decision by the Bird Island scientists that mortality was above the baseline, and there was evidence of clinical signs consistent with HPAI, all handling work ceased for the affected species apart from the taking of swabs for genetic analysis with an appropriate level of personal protective equipment (PPE) (see the 'Management' section for further details). In terms of response, it was considered important to distinguish levels of potential mortalities of wildlife from HPAI that were above baselines (i.e. the number of deaths from other causes in previous seasons). Any deaths that were spatially or temporally clustered, with an initial cluster of three dead individuals determined to be above normal, were considered to potentially indicate an HPAI outbreak. This would trigger discussions between scientists within BAS to assess the circumstances and any other signs. All information relating to suspected HPAI outbreaks was communicated to GSGSSI through standardized reporting forms, and GSGSSI communicated these to SCAR and other stakeholders.

Results

Timeline: birds

On 16 September 2023, a juvenile Southern Giant Petrel on Freshwater Beach, Bird Island (−54.0087, −38.0515) was observed that was unable to walk or fly, and displayed drooped wings and head. This bird died on the 17 September and was seen being scavenged by Brown Skuas and other giant petrels. This is suspected to be the start of the HPAI outbreak at South Georgia. Even though this was the first species affected, subsequent mortalities of Southern Giant Petrels at Bird Island remained low and did not exhibit any spatial clustering.

Brown Skuas were first observed showing signs consistent with HPAI on Freshwater Beach on 7 October 2023, including muscle twitching, lethargy and an inability to fly. The first recorded deaths were on 8 October (Figure 2) and the numbers rose exponentially until December. Deaths were recorded across the island, with the majority at the roosting aggregation (known as the 'club' site) on Freshwater Beach. As of 12 March 2024, a total of 77 Brown Skuas were found dead from suspected HPAI. Eleven of the Brown Skuas that died or were observed with symptoms had been ringed, of which two had been ringed as chicks and so were of known age (15 and 17 years), and the rest had been ringed as adults. Three birds that were observed as symptomatic were later observed breeding in the intensive study area for this species; two of these fledged one chick each and another failed at the chick stage.

Two Gentoo Penguins on Landing Beach, Bird Island (−54.0102, −38.0511) were observed between 7 and 10 October 2023 showing a lack of coordination, but bodies were not recovered and this could not be attributed directly to HPAI. Observed mortality of Gentoo Penguins was low for most of the breeding season and did not trigger the threshold for consideration as a possible HPAI outbreak due to the lack of spatial or temporal clustering. However, on 3 February 2024, 38 Gentoo Penguins were found dead at the Natural Arch (−54.0069, −38.0207) colony. All individuals had died within an estimated 24–48 h, and

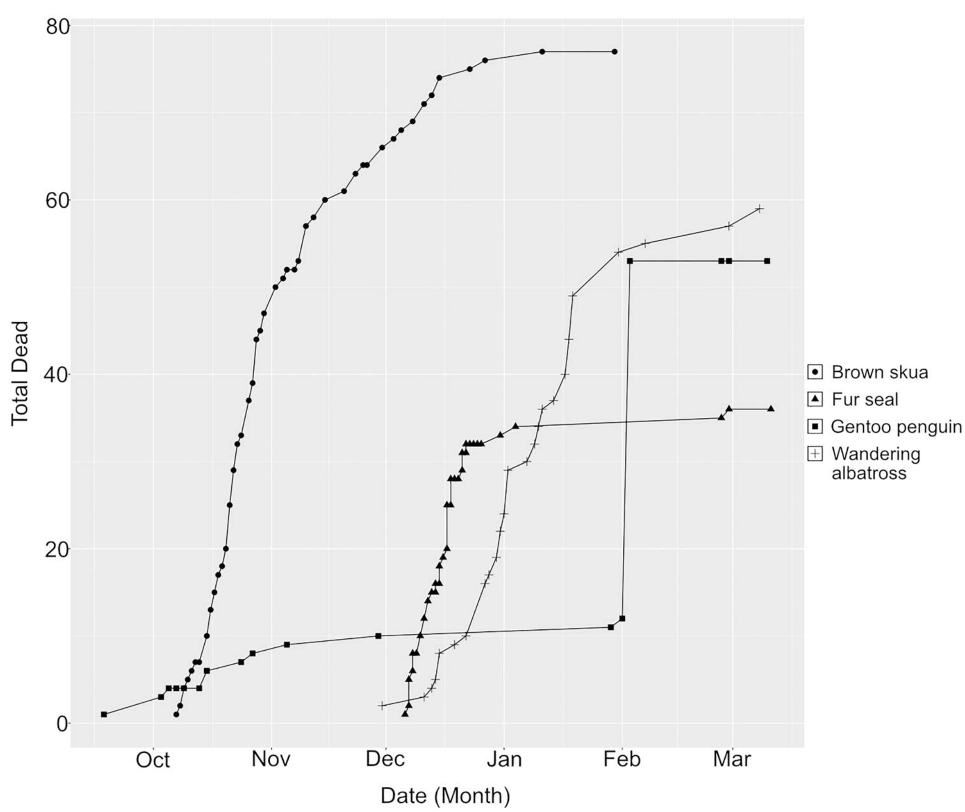

Figure 2. The progression of deaths in species affected by HPAI on Bird Island between 16 September 2023 and 12 March 2024. Mortalities of Brown Skuas, Gentoo Penguins and Snowy ('Wandering') Albatrosses were noted across the island, although some dead birds may have been missed. Antarctic Fur Seal mortalities were noted on three beaches and may not represent the trajectory of the outbreak across the whole island.

some were not yet scavenged, being in good body condition with no evidence of injury. As of 12 March 2024, this remained the only high mortality event for Gentoo Penguins at Bird Island (Figure 2). No further deaths were recorded at Natural Arch, nor the other four colonies of Gentoo Penguins, or three colonies of Macaroni Penguins.

Snowy Albatross deaths were first reported as above the baseline on 30 November 2023, and increased steeply until a plateau was reached in January 2024. No Snowy Albatrosses were observed with neurological symptoms of HPAI, and all birds found dead were as singles rather than in groups (Table 1). There was no obvious spatial pattern to the deaths, which occurred across Bird Island. In total, 58 deaths of Snowy Albatrosses were recorded by 12 March 2024, which were thought likely to be the result of HPAI. The age range of birds found dead was 5–40 years old, with a mean of 20.3 (±10.5 years SD). Five birds were confirmed as females and 24 as males, which was significantly different from a 1:1 sex ratio ($\chi^2 = 12.45$, $P < 0.001$). Nine birds were thought to be current breeders, 23 appeared to be deferring breeders (birds that had bred previously but not in the current season, but see below) and 15 birds appeared to be pre-breeders (had never bred). However, nest checks were halted before all breeding birds on the island had been recorded, and so some of the presumed deferring or older pre-breeders may have been active breeders (see the 'Management' section for details of the decision-making process regarding the halting of nest checks). A census of all Snowy Albatross nests on Bird Island was conducted on 1 April 2024. Only 497 nests were still active out of an estimated 695 where an egg was initially laid; this failure rate of 28.5% is markedly higher than the mean of 19.8% (± SD of 2.9%) by the same date in the 2020/21 to 2022/23 breeding seasons.

There were 23 instances of colour-ringed birds (6 Brown Skuas and 17 Northern Giant Petrels) from the long-term study populations seen scavenging on carcasses suspected to have died from HPAI. None of these individuals were later observed with signs of HPAI.

Timeline: seals

Bird Island has a small breeding population of Southern Elephant Seals, with a mean annual total of four pups produced in 2013/14 to 2022/23. The 2023–2024 season was unusual in that an estimated 55 pups were born. Although there was a high mortality of Southern Elephant Seals in other parts of South Georgia during the HPAI outbreak, many of the pups at Bird Island had been weaned before the outbreak. One yearling on Freshwater Beach died on 1 December 2024 within 24 h of showing signs of HPAI, but no swabs were taken due to initial restrictions on collecting samples for safety reasons. No other Southern Elephant Seals were suspected have died from HPAI at Bird Island in 2023–2024.

Mortalities of Antarctic Fur Seal pups and territorial males have been observed frequently during the breeding season (October–March). The mortality levels are extremely variable, from 5% to 50% of pups, with variation driven mostly by starvation and density-dependent mortality due to being physically crushed by adult males defending territories (Doidge *et al.* 1984, Reid & Forcada 2005). Territorial males, which fight to hold territories while fasting during some of this period, are exposed to higher levels of physical stress and often die from injuries and infections (Baker & Doidge 1984). Data from the demographic study at Bird Island, which has been ongoing for over 40 years, indicate that mortality of all age classes and groups has been higher in years when food is scarce (Doidge *et al.* 1984, Forcada *et al.* 2008, Forcada & Hoffman 2014, Forcada *et al.* 2023).

The main challenge in assessing the impact of HPAI on the Antarctic Fur Seals at Bird Island was that there remains no agreed diagnostic for neurological signs of HPAI in seals that deviate conclusively from other causes of mortality. As such, deaths cannot be confirmed as HPAI without clinical tests. Fur seal pups showed symptoms including tremors, swaying, lack of coordination and seizures. However, many pups ordinarily die from crushing, the effects of which can be indistinguishable from HPAI signs. Similarly, dying territorial males show extreme levels of ataxia due to exhaustion, which was also difficult to distinguish from HPAI. Deaths of adults and sub-adults were recorded at Bird Island, but the levels of mortality did not depart from observations over the previous 40 years. The annual mortality rate of territorial males has been assessed since 1996 from a systematic count of corpses in streams surrounding breeding beaches. A total of 40 males were counted in January 2024 and, although elevated, this was no higher than in other recent years (49 in 2021 and 42 in 2019).

On 6 December 2023, the first death of an adult Antarctic Fur Seal with suspected HPAI was recorded. Numbers rapidly increased until early January 2024, when the rate of deaths decreased. This is when the breeding season ends and the density of seals on the beaches declines due to dispersal to the sea. Individual deaths of adult seals were recorded on Freshwater

Table 1. A summary of deaths recorded at Bird Island during the 2023–2024 austral summer breeding season that were considered to be associated with HPAI H5N1, and the number of samples confirmed by genetic testing, as of 12 March 2024.

Species	Total deaths considered HPAI	Date tested	Date confirmed	No. samples taken	No. samples confirmed
Brown Skua ***Stercorarius antarcticus***	77	8 Oct 2023	23 Oct 2023	4	4
Gentoo Penguin ***Pygoscelis papua***	38	4 Feb 2024	4 Mar 2024	6	6
Antarctic Fur Seal ***Arctocephalus gazella***	36	18 Jan 2024	9 Feb 2024	5	5
Snowy Albatross ***Diomedea exulans***	58	16 Dec 2023	9 Feb 2024	5	5

Beach and Landing Beach. Pup mortality rates were hard to assess during the breeding season due to their mobility and small size on crowded beaches.

A total of 36 observed seals deaths were recorded by field scientists, with animals showing signs that may have been HPAI but which could also be attributed to other causes of mortality. Counts of seal deaths were only undertaken on Freshwater Beach and Landing Beach. The 36 suspected HPAI-related deaths of Antarctic Fur Seals comprised 30 adult males, 3 adult females and 3 of sub-adults of unknown sex or age. Aside from these 36 seals that were assumed to have died due to HPAI, there were a further 5 deaths of adult males on Freshwater Beach and Landing Beach believed to have resulted from injuries sustained in fighting. One adult male on Landing Beach displayed neurological symptoms not thought to be from fighting (as there were no external injuries), including tremors and lack of coordination, but it recovered over several days before leaving the beach. Although not included in the summary statistics for deaths on Bird Island, 19 seal pups were observed displaying potential signs of HPAI, of which 13 were later confirmed dead. One of the pups showing such signs was observed being trampled upon by adult seals.

Genetic testing

A detailed account of the genetic testing for HPAI can be found in Bennison *et al.* (2023). In brief, birds suspected to have died from HPAI were sampled using oropharyngeal and cloacal swabs. Antarctic Fur Seals were swabbed orally, nasally, and anally, and brain samples were also taken. Samples were stored in a refrigerator before transportation to the UK's International Reference Laboratory for avian influenza, swine influenza and Newcastle disease virus at the Animal and Plant Health Agency (APHA), at Weybridge, for testing. An animal was considered to have been infected with HPAI if any of the samples tested positive using United Kingdom Accreditation Service (UKAS) accredited front line diagnostic assays, as described previously (Byrne *et al.* 2023). Swabs from Brown Skuas, Gentoo Penguins, Antarctic Fur Seals, and Snowy Albatrosses all tested positive for HPAI H5 and N1-specific rRT-PCR assays (Table 1).

Management

A phased response to an HPAI outbreak was agreed by BAS and GSGSSI during the drafting of the revised GSGSSI biosecurity handbook in early 2022 (GSGSSI 2022). Sites were closed where HPAI was suspected from the pattern of observed mortality or symptoms in wildlife, and handling activities were paused for that species, pending a periodic review based on further evidence of mortality and its causes. All researchers were required to wear one of two levels of PPE for different tasks. Level 1 PPE consisted of oilskins or a lighter, wipeable protective barrier, eye protection, a surgical face mask, and good hand hygiene. Level-2 PPE consisted of a Tyvek suit, FFP2 or FFP3 face mask, eye protection and double-gloved hands. Level-1 PPE was required for all animal handling or working in proximity (<5 m) of animals within an area where HPAI was known or suspected. Level-2 PPE was required for swabbing for genetic testing. Biosecurity protocols were designed to ensure both the protection of researchers and to minimize spread between individual birds and colonies. Upon leaving a colony or having handled a bird, fieldworkers were required to wash down outer layers with a disinfectant and maintain good hand hygiene.

Most carcasses were scavenged prior to discovery by fieldworkers. There was concern that moving carcasses would aid the spread of disease and, given that there was no facility for incineration of carcasses, nor storage for later disposal, carcasses were left in situ. Restarting research after the outbreak required two steps: (1) a human health and safety assessment and (2) a cost–benefit analysis of the potential risk of handling birds versus interruption of long-term datasets.

The risk of infection by H5N1 via transfer from animals to humans is low (UKHSA 2024a). However, concern was expressed about the risk of exposure to humans in a remote location if the virus mutated. To address this, a corporate risk management contingency plan was established by BAS and GSGSSI that detailed a five-phase response. Each phase described the actions to be put into place for a station or science activity depending upon the HPAI situation. Specific local risk assessments were developed before the start of the outbreak and updated throughout the season as the situation evolved and new information on the virus was obtained through swabbing.

Before entering a new phase, risk assessments were utilized as a tool to re-determine the hazards and risks, and to re-evaluate the controls required; this involved an escalation from Phases 0 to 4 with intermediate steps between them. Phase 0 was defined as no suspicion of HPAI on any bases, but an increased awareness and vigilance for signs of an outbreak. Phase 1 was to be declared when HPAI was detected in Antarctic gateways (travel hubs used for movement into and out of Antarctic stations, namely The Falkland Islands, and Punta Arenas in Chile), with restricted travelling for staff visiting bird colonies in these gateways. Phase 2 was to be declared when local monitoring on stations found an increase in bird mortality that suggested a potential HPAI outbreak. At this point, all works would be paused until testing could confirm the presence of HPAI. Phase 3 resulted from confirmation of the presence of HPAI on-site, and only approved activities deemed essential for science and operations were to be undertaken. Samples were to be collected (wearing appropriate PPE) for genetic testing, and local seal populations to be monitored closely for signs of disease. During this phase, exclusion zones may be established and disinfection areas to be established at affected bases. Phase 4 was declared when presented with suspected evidence of HPAI in local seal populations. At this point, all interactions with seals would be halted and specialist advice would be sought to reassess the risk. During Phase 4, the BAS Major Incident System would be initiated due to the increased risk of infection to personnel.

Before moving between phases, discussion was held with relevant stakeholders from the BAS Cambridge Avian Response Team, scientists, and animal experts. At Phase 3, the BAS Major Incident Teams were alerted, and from Phase 4 the major incident response teams (named Bronze, Silver, and Gold) of the BAS Major Incident Plan were initiated, which involved weekly meetings to discuss latest updates and safety concerns.

Training was provided on the use of Level 2 PPE to staff prior to deployment to Bird Island. All material connected to PPE and swabbing was disposed of as biological waste. Staff were tested for a good fit of FFP 2 or FFP 3 disposable face masks, and the importance of good hand hygiene was emphasized, as ingestion and inhalation are the two main routes of exposure for humans. Antiviral medication was provided to stations at the start of the 2023–2024 season, and its administration to patients with possible symptoms of HPAI was to be under strict protocols overseen by the BAS Medical Unit, following UK government advice (UKHSA 2024b). Detergent selected for the cleaning of reusable PPE and equipment for sampling met the criteria required to deactivate the H5N1 virus.

When the mortality of Snowy Albatrosses had returned to baseline levels, the BAS Animal Welfare and Ethical Review Body (AWERB) considered an application to restart minimally invasive science. The timing was important because it was just before the start of the hatching period. In the 3 weeks after hatching, during the brood guarding period, the foraging trip durations are shorter and the change over of adults at the nest is therefore more frequent. As such, the resuming of monitoring would allow the resighting of ringed individuals and reduce the loss of integrity of the long-term demographic datasets. The BAS AWERB decided that a single check of the ring of each individual adult was low risk, if there were no symptoms of HPAI, and so these checks were acceptable, given the alterative was a major loss of information that would be used for conservation efforts. A flow chart (Figure 3) that detailed the actions and decisions taken before a bird was approached was a crucial component of the documentation that led to this conclusion.

The decision of the BAS AWERB was communicated to GSGSSI, who approved the restarting of monitoring activities. The removal of tracking devices (geolocators) that had been deployed previously was approved on animal welfare grounds, but not new deployments. A small subset of the albatross population was approached initially (~80 individuals), which were checked from a distance during the following week to ensure there was no above-baseline mortality. As there was no evidence of an impact of the research activities, monitoring was expanded to include the other nests on Bird Island. The same decision process was applied to the monitored nests of other species where fieldwork had been paused.

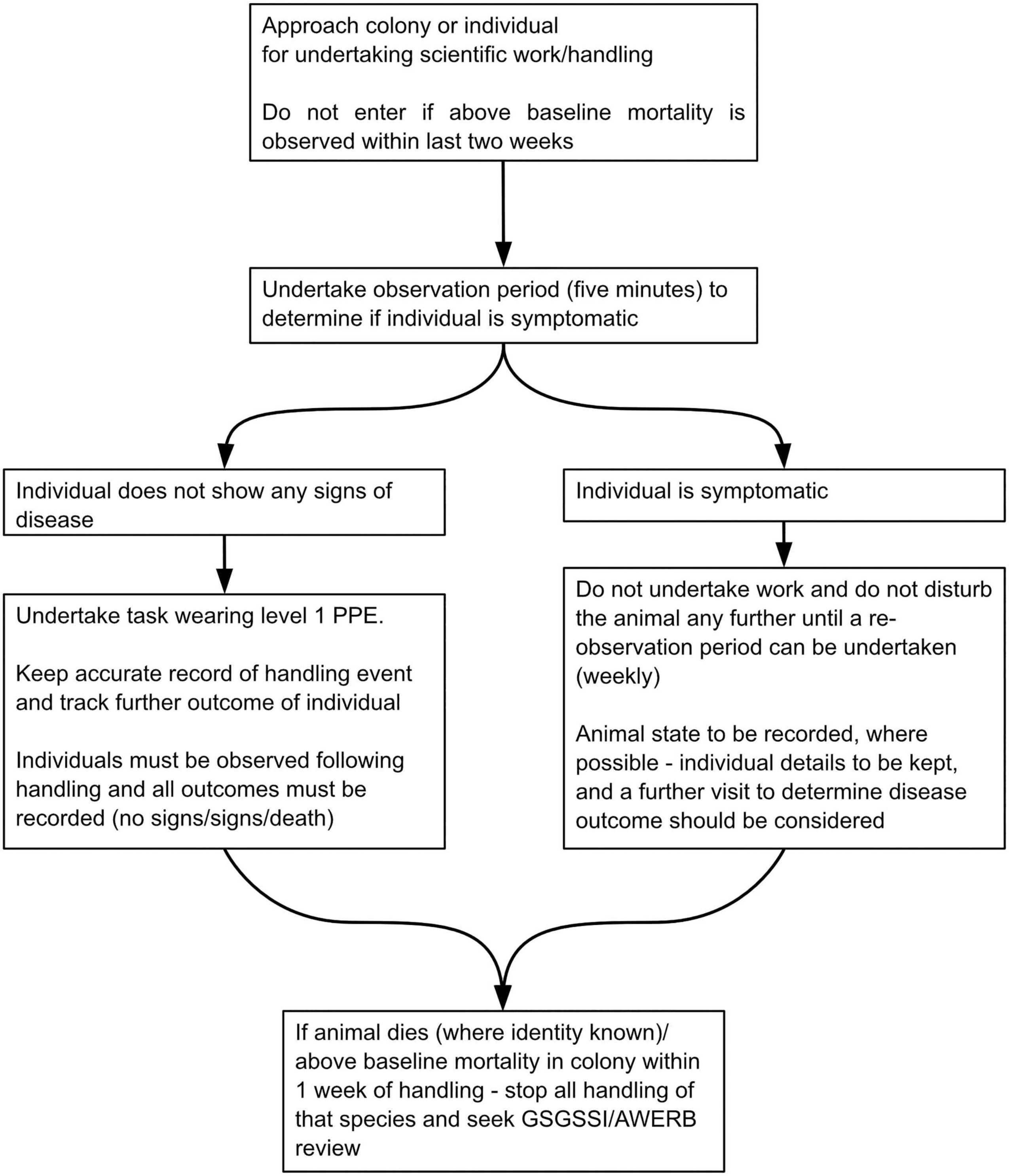

Figure 3. The decision flowchart for restarting research work on affected species at Bird Island. This was to ensure that birds were not at risk of elevated levels of stress should they be affected by HPAI. Nests were revisited 1 week after handling of the animal to check for any impact.

Discussion

In total, four species tested positive for HPAI at Bird Island in the austral summer of 2023–2024: Brown Skua, Gentoo Penguin, Snowy Albatross, and Antarctic Fur Seal. These cases represented the first known infections of HPAI in the Antarctic and subantarctic regions. A total of 173 birds were considered to have died from HPAI on Bird Island.

The total mortality among Antarctic Fur Seals was unknown. Three of the four species displayed a rapid initial increase in mortality associated with the HPAI outbreak, but deaths reached a plateau in the second half of the summer. The exception was the Gentoo Penguin, where the mortality rate was low until a single, large mortality event was reported, after which no further cases were observed (Figure 2). The symptoms of HPAI are not well documented in albatrosses and penguins, and even less so in mammals like the Antarctic Fur Seal. However, positive genetic tests confirmed the presence of disease in these species (Table 1) and so this case study provides key contextual cues for assessing the future presence of HPAI elsewhere.

Great Skuas *Stercorarius skua*, in particular, have been greatly impacted by HPAI outbreaks in the Northern Hemisphere (Banyard *et al.* 2022, Camphuysen *et al.* 2022). Like other skuas, the Brown Skuas at Bird Island are generalist predator-scavengers that feed primarily on seal carrion in the early part of the summer season, before switching to predation of seabird prey (Phillips *et al.* 2004). HPAI is spread by scavengers, such as skuas, particularly in high-density seabird communities (Banyard *et al.* 2022). The Brown Skua was the first species to be affected during the outbreak at South Georgia, with a rapid trajectory to 77 deaths in total on Bird Island. Many of these skuas were unringed individuals, and so their age and breeding status were unknown. Three individuals that displayed HPAI symptoms were later found in apparently good health and breeding in the study area. Two of the three birds then successfully fledged chicks, indicating that subsequent effects of HPAI infection can be mild or absent if the individual recovers.

Following mass mortalities of penguins in South America, there was particular concern about the susceptibility of penguins to HPAI in Antarctic and subantarctic regions (Dewar *et al.* 2022, Bennison *et al.* 2023). Transmission and mortality rates were expected to be substantial, given the high nest densities in penguin colonies. However, the trajectory of the disease and its impact at Bird Island was not as severe as expected; there was a single mass mortality event affecting only 38 Gentoo Penguins of the 736 pairs at the Natural Arch colony on Bird Island in the 2023–2024 season. The low mortality rate among Gentoo Penguins, and the absence of any above-baseline mortality in Macaroni Penguins, indicated that these species were not necessarily at elevated risk from HPAI. It is unknown whether that outcome was due to low levels of infection or because the infection was not detectable, and there is the potential for outbreaks to be severe in future seasons. Furthermore, population-level immunity to avian influenza viruses is unknown in these species and might vary among colonies.

Snowy Albatrosses do not nest at high densities, from which it might be inferred that they are at low risk from HPAI, but this was not borne out from the evidence at Bird Island. Like the Brown Skuas, and skuas elsewhere, HPAI may have spread in Bird Island's Snowy Albatrosses through ingestion of carrion. Several albatross chicks that hatched in the previous season (April 2023) were found dead early in the 2023–2024 austral summer, having choked as they regurgitated boluses containing Antarctic Fur Seal fur. Although carrion has not been recorded in the diet of Snowy Albatrosses at South Georgia, it can be an important component elsewhere that includes seals (Cherel & Klages 1998, Xavier *et al.* 2003, Pereira *et al.* 2018). Snowy Albatrosses do not feed on land, and so it is possible that they contracted HPAI by scavenging the floating carcasses of infected Antarctic Fur Seals at sea, the number of which would have increased around the same time as increased mortality was observed in the albatrosses.

There was also a clear bias towards mortality of male Snowy Albatrosses (83% of the 29 birds of known sex), but not towards any particular age class. Studies of previous avian influenza infections in other species have found sex-specific infection rates (Ip *et al.* 2008, Valdebenito *et al.* 2021). A higher mortality rate for male Snowy Albatrosses may reflect higher rates of carrion ingestion, as there have been sex differences in dietary components in other years (Xavier *et al.* 2004, Xavier & Croxall 2005, Pereira *et al.* 2018). Alternatively, males may have been more likely to die on land, as they spend around 10 times as much time ashore as the females during the pre-laying period (Tickell 1968). The breeding failure rate of Snowy Albatrosses between egg-laying and the 1 April 2024 census at Bird Island was markedly higher than in the preceding 3 years. This suggested that, although many albatross deaths were seen on the island, more birds may have died from HPAI at sea. It is only with future monitoring and analysis of the long-term resighting data for Snowy Albatrosses and Brown Skuas will it become clear how many died from HPAI.

Antarctic Fur Seals have experienced major population changes over the last 250 years. Unregulated hunting caused mass declines in populations before a fast-growth recovery (Bonner 1968). However, the species is now declining again at South Georgia (Forcada *et al.* 2023). Seals arrive at

Bird Island in October, and the numbers of males increase as they defend territories with access to females for breeding. Seal beaches are often very densely populated, and at the height of the breeding season they may contain thousands of adult males, females and newly born pups, all in close proximity, which creates a high risk of contagion. Following the breeding season, most male seals depart from the island, whereas females and pups remain until they have moulted and weaned in March–April (Bonner 1968). Seal mortality is often high but variable between years (Forcada *et al.* 2023), and so the true impact of HPAI is unknown; it is likely that many deaths from HPAI were undetected. Further research will be required in the long term to confirm the clinical signs of infection in Antarctic Fur Seals and to put a thorough testing regime in place.

Although HPAI was confirmed in four species at Bird Island, there were suspicions that it may have been present in several others in the 2023–2024 season. Fieldwork in colonies of Black-browed and Grey-headed Albatrosses was stopped in November 2023 because small numbers of individuals were observed to be lethargic and displayed wing-droop. No deaths were observed, but handling ceased until further investigations could take place. As live swabbing was not permitted, guano samples were taken from individuals showing symptoms and sent to the UK for testing; none of these tested positive. In January 2024, 15 Northern Giant Petrel chicks were observed with neurological symptoms that would normally be associated with HPAI, including an inability to walk, lethargy and wing droop, and showed arrested development in wing growth. Seven of these chicks subsequently died and two of them were swabbed but with negative results. One chick outside of the study area was also observed with malformed wings. No indications of HPAI were noted in the other species on the island, suggesting that they may have some natural immunity, did not show obvious symptoms, or infected animals died unobserved at sea.

Many ducks and waterfowl have been impacted in the current global H5N1 outbreak (Gaide *et al.* 2022, James *et al.* 2023, Spackman *et al.* 2023). However, there were no confirmed cases of HPAI in the South Georgia Pintail *Anas georgica georgica* at Bird Island, or more widely on South Georgia.

There are long-term monitoring programmes of predators at Bird Island that require the presence of researchers throughout the year, given inter-specific differences in phenology. That Bird Island was the first place to document the outbreak of HPAI is perhaps unsurprising, given its proximity to South America and the intensity of monitoring in comparison to uninhabited islands in the South Atlantic. However, it is only through the vigilance of field researchers that we were able to document in such detail the outbreak in real time. In preparation for an outbreak of HPAI, teams on the island were briefed and made familiar with the clinical signs to expect in animals (or were already familiar). The reactions of team members then made sure that the process was documented fully and clinical signs were confirmed in many species, including the Antarctic Fur Seals for which the clinical signs were uncertain. By allowing open communications regarding observations between the team, all stakeholders were made aware of potential new cases as they arose. During the observation period, researchers were also asked to collect pictures and video of symptomatic animals for a comprehensive library of symptoms in previously undocumented species. These will be made available to teams at other research stations to allow for quick responses to HPAI outbreaks.

Bird Island is an isolated field site, which presented difficulties with logistics and testing of suspected HPAI cases. Bird Island receives two main ship calls per year from the *RSS Sir David Attenborough* with support from the *MV Pharos SG,* the fisheries patrol vessel for GSGSSI. This required that PPE and equipment was purchased and shipped to the island at least six months before any potential use. Preparations began in early 2023 for the arrival of HPAI and the site was supplied with PPE, disinfectants and all required equipment to continue monitoring work during any potential outbreak.

Once an outbreak was suspected it was important to ensure the quick transit of samples from Bird Island via the Falkland Islands to the National Reference Laboratory at APHA for accredited testing. This required coordination of teams from BAS, GSGSSI, Falklands Islands Government and APHA to ensure the correct licenses, permits and transport arrangements could be put in place. The swabs collected at Bird Island could then be tested in as little as 15 days, although ship movements meant that the average time was 30.0 ± 17.5 days. During the interim periods between taking samples and test results, cases were treated as positive and the appropriate management responses were taken to halt work with affected species.

Due to the nature of working in isolated field sites it was not always possible to effectively sample seals. Although bird sampling may be undertaken in Level 2 PPE, the sampling of mammals such as seals requires enhanced respirator protection, including a powered respirator hood (PARP) and equipment for sampling of the brain

(Floyd *et al.* 2021), which needs specialized training. Although a scientist with this training travelled to South Georgia in December 2023, poor weather conditions prevented them from landing at Bird Island and so the sampling of seals was not undertaken until January.

The pause in research activities due to the outbreak, and the phased restart, involved complex discussions between experts and stakeholders: scientists, institutions, regulators (government), human health and animal welfare experts. Human and animal welfare priorities were at the forefront of all decisions. For threatened populations of animals there are, however, direct trade-offs between reducing the impacts of animal handling and the interruption of long-term research that is essential for developing effective conservation policies. The trajectory of HPAI outbreaks in the Northern Hemisphere makes it clear that this disease will be present for years to come, and so it requires carefully considered approaches that allow essential research to continue.

The outbreak of HPAI at Bird Island represents the first major outbreak to be recorded on a subantarctic island and was also the first known exposure for multiple Antarctic species. Many questions have been raised through the response process, but our case study provides valuable lessons for the management of HPAI elsewhere in the subantarctic and Antarctic regions. It will likely be years before the true impact of HPAI at South Georgia is understood, and it is important to continue monitoring the spread and development of the disease for future conservation efforts.

Acknowledgements

The paper is a contribution to the Ecosystems component of the British Antarctic Survey Polar Science for Planet Earth Programme, funded by NERC, and the 'Human Impacts and Sustainability' research theme of the Scientific Committee on Antarctic Research (SCAR) Scientific Research Programme 'Integrated Science to Inform Antarctic and Southern Ocean Conservation' (Ant-ICON). We would like to thank the Government of South Georgia and the South Sandwich Islands for their help with logistics, planning, and sample collection.

Disclosure statement

No potential conflict of interest was reported by the author(s).

Funding

ACB, JLJ, JJ, SR and MF were supported through UK Department for the Environment, Food and Rural Affairs (Defra) and the devolved Scottish and Welsh governments funding under grants SV3006 and SV3400.

ORCID

George Day http://orcid.org/0000-0003-2449-2997
Jaume Forcada http://orcid.org/0000-0002-2115-0150
Simon A. Morley http://orcid.org/0000-0002-7761-660X

References

ACAP. 2023. Guidelines for working with albatrosses and petrels during the high pathogenicity avian influenza (HPAI) H5N1 panzootic. https://www.acap.aq/resources/acap-conservation-guidelines/4084-guidelines-for-working-with-albatrosses-and-petrels-during-h5n1-avian-influenza-outbreak/file. Accessed 15 July 2024.

Baker, J.R. & Doidge, D.W. 1984. Pathology of the Antarctic Fur-Seal (Arctocephalus-Gazella) in South Georgia. *Br. Vet. J.* **140:** 210–219.

Banyard, A.C., Begeman, L., Black, J., Breed, A., Dewar, M. & Fijn, R. 2023. Continued expansion of high pathogenicity avian influenza H5 in wildlife in South America and incursions in to the Antarctic Region. *OFFLU statement*, 21st December 2023.

Banyard, A.C., Lean, F.Z., Robinson, C., Howie, F., Tyler, G., Nisbet, C., Seekings, J., Meyer, S., Whittard, E. & Ashpitel, H.F. 2022. Detection of highly pathogenic avian influenza Virus H5n1 Clade 2.3. 4.4 B in Great Skuas: a species of conservation concern in Great Britain. *Viruses* **14:** 212.

Bennison, A., Byrne, A.M.P., Reid, S.M., Lynton-Jenkins, J.G., Mollett, B., Sliva, D.D., Peers-Dent, J., Finlayson, K., Hall, R., Blockley, F., Blyth, M., Falchieri, M., Fowler, Z., Fitzcharles, E.M., Brown, I.H., James, J. & Banyard, A.C. 2023. Detection and spread of high pathogenicity avian influenza virus H5n1 in the Antarctic Region. *bioRxiv*: 2023.11.23.568045.

Bonner, W.N. 1968. The Fur Seal of South Georgia. *British Antarctic Survey Scientific Reports* **56**, British Antarctic Survey, Cambridge.

Byrne, A.M., James, J., Mollett, B.C., Meyer, S.M., Lewis, T., Czepiel, M., Seekings, A.H., Mahmood, S., Thomas, S.S. & Ross, C.S. 2023. Investigating the genetic diversity of H5 avian influenza viruses in the United Kingdom from 2020–2022. *Microbiol. Spectr.* **11:** e04776–22.

Caliendo, V., Lewis, N., Pohlmann, A., Baillie, S., Banyard, A., Beer, M., Brown, I., Fouchier, R., Hansen, R. & Lameris, T. 2022. Transatlantic spread of highly pathogenic avian influenza H5n1 by wild birds from Europe to North America in 2021. *Sci. Rep.* **12:** 11729.

Camphuysen, C., Gear, S. & Furness, R. 2022. Avian influenza leads to mass mortality of adult Great Skuas in Foula in summer 2022. *Scott. Birds* **42:** 312–323.

Cardona, C.J., Xing, Z., Sandrock, C.E. & Davis, C.E. 2009. Avian influenza in birds and mammals. *Comp. Immunol. Microbiol. Infect. Dis.* **32:** 255–273.

Cherel, Y. & Klages, N. 1998. A review of the food of albatrosses. In Robertson, G. & Gales, R. (ed) *Albatross Biology and Conservation*, 113–136. Surrey Beatty & Sons, Chipping Norton.

Defra. 2024. Mitigation strategy for avian influenza in wild birds in England and Wales. Updated 18 March 2024. https://www.gov.uk/government/publications/mitigation-strategy-for-avian-influenza-in-wild-birds-in-england-and-wales. Accessed 15 July 2024.

Dewar, M., Wille, M., Gamble, A., Vanstreels, R., Boulinier, T., Smith, A., Varsani, A., Ratcliffe, N., Black, J. & Lynnes, A. 2022. The risk of avian influenza in the Southern Ocean: a practical guide. EcoevoRxiv.10.32942.osf-io.8jrbu.

Doidge, D.W., Croxall, J.P. & Baker, J.R. 1984. Density-dependent pup mortality in the Antarctic Fur-Seal *Arctocephalus gazella* at South Georgia. *J. Zool.* **202:** 449–460.

Falchieri, M., Reid, S.M., Ross, C.S., James, J., Byrne, A.M., Zamfir, M., Brown, I.H., Banyard, A.C., Tyler, G. & Philip, E. 2022. Shift in HPAI infection dynamics causes significant losses in seabird populations across Great Britain. *Vet. Record* **191:** 294–296.

Floyd, T., Banyard, A.C., Lean, F.Z., Byrne, A.M., Fullick, E., Whittard, E., Mollett, B.C., Bexton, S., Swinson, V. & Macrelli, M. 2021. Encephalitis and death in wild mammals at a rehabilitation center after infection with highly pathogenic avian influenza a (H5N8) virus, United Kingdom. *Emerg. Infect. Dis.* **27:** 2856.

Foley, C., Hart, T. & Lynch, H. 2018. King Penguin populations increase on South Georgia but explanations remain elusive. *Polar Biol.* **41:** 1111–1122.

Forcada, J. & Hoffman, J.I. 2014. Climate change selects for heterozygosity in a declining Fur Seal population. *Nature* **511:** 462–465.

Forcada, J., Hoffman, J.I., Gimenez, O., Staniland, I.J., Bucktrout, P. & Wood, A.G. 2023. Ninety years of change, from commercial extinction to recovery, range expansion and decline for Antarctic Fur Seals at South Georgia. *Glb. Chg. Bio.* **29:** 6867–6887.

Forcada, J., Trathan, P.N. & Murphy, E.J. 2008. Life history buffering in Antarctic mammals and birds against changing patterns of climate and environmental variation. *Glb. Chg. Bio.* **14:** 2473–2488.

Gaide, N., Lucas, M.-N., Delpont, M., Croville, G., Bouwman, K.M., Papanikolaou, A., Van Der Woude, R., Gagarinov, I.A., Boons, G.-J. & De Vries, R.P. 2022. Pathobiology of highly pathogenic H5 avian influenza viruses in naturally infected Galliformes and Anseriformes in France during winter 2015–2016. *Vet. Res.* **53:** 11.

GSGSSI. 2022. Environment documents. https://gov.gs/documents_environment/. Accessed 15 July 2024.

IAATO. 2022. IAATO 2022-23 biosecurity protocols regarding Avian Influenza. https://iaato.org/iaato-2022-23-biosecurity-protocols-regarding-avian-influenza/. Accessed 15 July 2024.

Ip, H.S., Flint, P.L., Franson, J.C., Dusek, R.J., Derksen, D.V., Gill, R.E., Ely, C.R., Pearce, J.M., Lanctot, R.B. & Matsuoka, S.M. 2008. Prevalence of influenza a viruses in wild migratory birds in Alaska: patterns of variation in detection at a crossroads of intercontinental flyways. *Virol. J.* **5:** 1–10.

James, J., Billington, E., Warren, C.J., De Sliva, D., Di Genova, C., Airey, M., Meyer, S.M., Lewis, T., Peers-Dent, J. & Thomas, S.S. 2023. Clade 2.3. 4.4 B H5N1 high pathogenicity avian influenza virus (HPAIv) from the 2021/22 epizootic is highly duck adapted and poorly adapted to chickens. *J. Gen. Virol.* **104:** 001852.

Lane, J.V., Jeglinski, J.W., Avery-Gomm, S., Ballstaedt, E., Banyard, A.C., Barychka, T., Brown, I., Brugger, B., Burt, T.V. & Careen, N. 2023. High pathogenicity avian influenza (H5N1) in Northern Gannets: global spread, clinical signs, and demographic consequences. *bioRxiv* 2023.05. 01.538918.

Lean, F.Z., Falchieri, M., Furman, N., Tyler, G., Robinson, C., Holmes, P., Reid, S.M., Banyard, A.C., Brown, I.H. & Man, C. 2023. Highly pathogenic avian influenza virus H5N1 infection in skuas and gulls in the United Kingdom, 2022. *Vet. Pathol.*, **61:** 03009858231217224.

Leguia, M., Garcia-Glaessner, A., Muñoz-Saavedra, B., Juarez, D., Barrera, P., Calvo-Mac, C., Jara, J., Silva, W., Ploog, K. & Amaro, L. 2023. Highly pathogenic avian influenza a (H5N1) in marine mammals and seabirds in Peru. *Nat. Commun.* **14:** 5489.

Lewis, N.S., Banyard, A.C., Whittard, E., Karibayev, T., Al Kafagi, T., Chvala, I., Byrne, A., Meruyert, S., King, J. & Harder, T. 2021. Emergence and spread of novel H5N8, H5N5 and H5N1 clade 2.3. 4.4 highly pathogenic avian influenza in 2020. *Emerg. Microbes. Infect.* **10:** 148–151.

Lisovski, S., Gunther, A., Dewar, M., Anley, D., Arce, R., Ballard, G., Belliure, J., Boulinier, T., Bennison, A. & Cary, C. 2023. No evidence for highly pathogenic avian influenza virus H5N1 (Clade 2.3. 4.4 B) in the Antarctic Region during the austral summer 2022/23. *bioRxiv* 2023.10. 24.563692.

Martin, A., Poncet, S., Barbraud, C., Foster, E., Fretwell, P. & Rothery, P. 2009. The white-chinned petrel (*Procellaria aequinoctialis*) on South Georgia: population size, distribution and global significance. *Polar Biol.* **32:** 655–661.

Pereira, J.M., Paiva, V.H., Phillips, R.A. & Xavier, J.C. 2018. The devil is in the detail: small-scale sexual segregation despite large-scale spatial overlap in the Wandering Albatross. *Mar. Biol.* **165:** 1–16.

Phillips, R., Phalan, B. & Forster, I. 2004. Diet and long-term changes in population size and productivity of Brown Skuas *Catharacta antarctica lonnbergi* at Bird Island, South Georgia. *Polar Biol.* **27:** 555–561.

Plaza, P.I., Gamarra-Toledo, V., Euguí, J.R., Rosciano, N. & Lambertucci, S.A. 2024. Pacific and Atlantic Sea Lion mortality caused by highly pathogenic avian influenza a (H5N1) in South America. *Travel Med. Infect. Dis.* **59:** 102712.

Pohlmann, A., Stejskal, O., King, J., Bouwhuis, S., Packmor, F., Ballstaedt, E., Hälterlein, B., Hennig, V., Stacker, L. & Graaf, A. 2023. Mass mortality among colony-breeding seabirds in the German Wadden Sea in 2022 due to distinct genotypes of HPAIv H5N1 Clade 2.3. 4.4 B. *J. Gen. Virol.* **104:** 001834.

Poncet, S., Wolfaardt, A.C., Black, A., Browning, S., Lawton, K., Lee, J., Passfield, K., Strange, G. & Phillips, R.A. 2017. Recent trends in numbers of Wandering (*Diomedea exulans*), Black-browed (*Thalassarche melanophris*) and Grey-Headed (*T. chrysostoma*) Albatrosses breeding at South Georgia. *Polar Biol.* **40:** 1347–1358.

Ramey, A.M., Hill, N.J., Deliberto, T.J., Gibbs, S.E., Camille Hopkins, M., Lang, A.S., Poulson, R.L., Prosser, D.J., Sleeman, J.M. & Stallknecht, D.E. 2022. Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America. *J. Wildl. Manage.* **86:** e22171.

Reid, K. & Forcada, J. 2005. Causes of offspring mortality in the Antarctic Fur Seal, *Arctocephalus gazella*: the interaction of density dependence and ecosystem variability. *Can. J. Zool.* **83:** 604–609.

SCAR. 2024. Sub-Antarctic and Antarctic highly pathogenic avian influenza H5N1 monitoring project. https://scar.org/library-data/avian-flu. Accessed 15 July 2024.

Spackman, E., Pantin-Jackwood, M.J., Lee, S.A. & Prosser, D. 2023. The pathogenesis of a 2022 North American highly pathogenic clade 2.3. 4.4 B H5N1 avian influenza virus in Mallards (*Anas platyrhynchos*). *Avian Pathol.* **52:** 219–228.

Tickell, W.L.N. 1968. The biology of the Great Albatrosses, *Diomedea exulans and Diomedea epomophora*. *Antarctic Bird Studies* **12:** 1–56.

Trathan, P., Ratcliffe, N. & Masden, E. 2012. Ecological drivers of change at South Georgia: the Krill surplus, or climate variability. *Ecography* **35:** 983–993.

UKHSA. 2024a. UKHSA update on avian influenza. Updated 14 July 2023. https://www.gov.uk/government/news/ukhsa-update-on-avian-influenza#full-publication-update-history. Accessed 15 July 2024.

UKHSA. 2024b. Investigation and initial clinical management of possible human cases of avian influenza with potential to cause severe human disease. Updated 28 February 2024. https://www.gov.uk/government/publications/avian-influenza-guidance-and-algorithms-for-managing-human-cases/investigation-and-initial-clinical-management-of-possible-human-cases-of-avian-influenza-with-potential-to-cause-severe-human-disease. Accessed 15 July 2024.

Valdebenito, J.O., Halimubieke, N., Lendvai, ÁZ, Figuerola, J., Eichhorn, G. & Székely, T. 2021. Seasonal variation in sex-specific immunity in wild birds. *Sci. Rep.* **11:** 1349.

Xavier, J., Croxall, J., Trathan, P. & Wood, A. 2003. Feeding strategies and diets of breeding Grey-Headed and Wandering Albatrosses at South Georgia. *Mar. Biol.* **143:** 221–232.

Xavier, J., Trathan, P., Croxall, J., Wood, A., Podesta, G. & Rodhouse, P. 2004. Foraging ecology and interactions with fisheries of Wandering Albatrosses (*Diomedea exulans*) breeding at South Georgia. *Fish. Oceanogr.* **13:** 324–344.

Xavier, J.C. & Croxall, J.P. 2005. Sexual differences in foraging behaviour and diets: a case study of Wandering Albatrosses. In Ruckstuhl, K. & Neuhaus, P. (ed) *Sexual Segregation in Vertebrates*, 74–91. Cambridge University Press, Cambridge.