# Investigating high pathogenicity avian influenza virus incursions to remote islands: Detection of H5N1 on Gough Island in the South Atlantic Ocean

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## Abstract

Understanding the mechanisms underlying the emergence and spread of high pathogenicity avian

influenza virus (HPAIV) is critical for tracking its global dissemination, particularly via migratory

seabirds, given their role in transmission over long distances. Scavenging seabirds, such as skuas, may

act as both reservoirs and vectors, and have been linked to multiple outbreaks since 2021. Here, we

report the detection of HPAIV clade 2.3.4.4b H5N1 in three Tristan skua (*Stercorarius antarcticus*

*hamiltoni*) carcasses on Gough Island in the central South Atlantic Ocean. To investigate potential

incursion routes, we combined genomic analyses with year-round tracking data from global location

sensors. Although migratory movement patterns suggested southern Africa as the most obvious

pathway, the strain detected on Gough Island was more closely related to that found in South Georgia,

suggesting infection may have occurred during the pre-laying exodus when skuas disperse into frontal

waters south of the island. No further cases have been confirmed for Gough, but further systematic

monitoring is needed to understand the dynamics of virus infection. The detection of HPAIV H5N1 in

skuas on Gough Island highlights the importance of continued vigilance, coordinated surveillance,

and proactive biosecurity across the South Atlantic and Southern Ocean, alongside efforts to reduce

other pressures on globally important seabird populations to help strengthen their resilience.

**Keywords (5-8)** High pathogenicity avian influenza, Gough Island, Brown Skua, migration,

transmission, emerging

## Introduction

The ongoing expansion of high pathogenicity avian influenza virus (HPAIV) poses a major threat to

wildlife, livestock, and, through its zoonotic potential, human health. Since first emerging in poultry

in China in 1996, the A/goose/Guangdong/1/96 (GsGd)-lineage of HPAIV H5Nx has evolved to

spread efficiently among a broad range of bird species globally, causing mass mortality events in

unprecedented numbers [1-6]. Following its dissemination across Europe by migratory species, H5N1

reached North America via the trans-Atlantic flyway and, by October 2022, had expanding rapidly

throughout South America, with devastating impacts on both seabird and pinniped populations [7,8].

In the austral spring of 2023, HPAIV reached the sub-Antarctic islands and Antarctica, first detected

in brown skuas (*Stercorarius antarcticus*) on Bird Island, South Georgia [9]. Soon after, cases were

reported in southern fulmars (*Fulmarus glacialoides*) and black-browed albatrosses (*Thalassarche*

*melanophris*) in the Falkland Islands [9], and in multiple species across the Antarctic Peninsula [10].

Genetic analyses indicate that the detections in these regions were linked to strains originating in

South America, likely introduced via long-distance movements of scavenging seabirds such as skuas,

gulls, and giant petrels [9, 11]. In the following breeding season 2023/2024, the virus had spread

further east across the sub-Antarctic and into the southern Indian Ocean, causing significant die-offs

in wandering albatross (*Diomedea exulans*) chicks on Marion Island [12], before it was reported for

the Crozet and Kerguelen Archipelagos, where mass mortality events predominantly affected southern

elephant seals (*Mirounga leonina*) [11]. Genetic evidence suggests that the Crozet and Kerguelen

outbreaks incurred from independent introductions linked to South Georgia rather than from the

nearer southern African coast [11].

Gough Island in the central South Atlantic is situated approximately 3,600 km northeast of South

Georgia and 2,450 km northwest of Marion Island and considered one of the most important seabird

breeding sites globally [13]. Despite its small size (~65 km²), the island supports an estimated eight

million birds of at least 24 species, many of them endemic or near-endemic to the island or island

group of Tristan da Cunha, and several of global conservation concern, including the Critically

Endangered Tristan albatross (*Diomedea dabbenena*), MacGillivray's prion (*Pachyptila*

*macgillivrayi*), and Gough finch (*Rowettia goughensis*) [13-16]. Consequently, the potential for

arrival of HPAIV into this sensitive environment had remained a significant conservation concern. A

risk assessment in 2022 considered the likelihood of the emergence of HPAIV on Gough Island as

'low' [17]. However, the spread of the HPAIV epizootic into the southern hemisphere and its

continued expansion across the sub-Antarctic region immediately increased the risk of incursion and,

given the island's position along major migratory flyways and marine corridors, linking the Atlantic

and Southern Oceans [18], means Gough was vulnerable to viral introduction from multiple directions [18].

Evidence of antibodies against AIVs was first detected in 2009, when a serosurvey on Gough Island revealed exposure in brown skuas (*S. a. hamiltoni;* hereafter referred to as Tristan skua) and northern rockhopper penguins (*Eudyptes moseleyi*), demonstrating that the virus had previously reached the island and circulated among these species [19, 20]. Given their scavenging behaviour, skuas represent both key reservoirs and vectors for disease transmission, making the study of their movements critical for identifying introduction pathways [20, 21].

Here, we describe the detection of HPAIV clade 2.3.4.4b H5N1 in three Tristan skuas from Gough Island from September 2024 and investigate potential incursion routes by using a combination of genetic analyses of the virus and year-round tracking data from global location sensors.

**Materials & Methods**

**Study site**

Gough Island (40°19′12″S 09°56′24″W) is part of the British Overseas Territory of St Helena, Ascension, and Tristan da Cunha in the central South Atlantic Ocean (Fig.1). Gough Island lies approximately 380 km south-southeast from the Tristan da Cunha archipelago, which consists of three main islands: Tristan da Cunha (96 km²), Inaccessible (14 km²), and Nightingale (4 km²), along with its satellite islets Middle (or Alex) and Stoltenhoff (both ~0.1 km²), all within 40 km of each other (Fig. 1). Gough is uninhabited except for a small year-round team of 7-9 people operating the research station. The station is re-supplied once a year in September/October by the South African research vessel *SA Agulhas II*. A field team of 2-3 biologists is on the island year-round as part of the island's long-term term monitoring and science programme, trained to provide surveillance for unusual avian mortality events.

**Tracking data**

Migrate Technology Intigeo-C330 geolocation tags (17 x 19 x 8 mm, 3.3 g) were deployed on 10 incubating adult Tristan skuas near the Gough Island research station in October-November 2017. The tags were attached to standard stainless steel SAFRING rings. Eight tags were retrieved during the following breeding season; the two other devices were not recovered.

Light-level data were processed in R version 4.4.1 using the *SGAT* package (v0.1.3) [22], implementing a Bayesian state-space model to estimate probable locations based on the timing of twilight transitions, while accounting for uncertainties in light detection and movement behaviour. Raw light data were pre-processed using the *BAStag* package (v0.1.3) [23] to identify twilight events (sunrise and sunset) based on light intensity thresholds. These twilight times were then manually reviewed and edited to correct for anomalies caused by shading, cloud cover, or behavioural factors e.g., incubation. The resultant data were used to infer two positions per day, corresponding to daily twilight transitions.

To quantify space use, we calculated kernel utilisation distributions (KUDs) using the *adehabitatHR* package (v0.4.22) [24]. *SGAT*-derived location estimates were projected onto an equal-area coordinate reference system to allow for unbiased spatial analysis. For each bird, 50% and 95% KUDs were calculated to represent core use areas and home ranges, respectively, across the pre-laying, breeding, and non-breeding periods. Location data during incubation in 2017 and 2018 were pooled for KUD analysis. To evaluate population-level space use, individual KUDs were averaged to assess spatial habitat use. Migration pathways between breeding and non-breeding areas were excluded from the KUD analysis and instead visualised using raw location data. For each individual, the onset of north-east migration away from the breeding colony and that of south-west return migration, was defined as the point at which the individual's distance from the colony increased or decreased continuously, without subsequent decreases/increases. The end point of each migration phase was defined as the point at which the distance from the colony stabilised, indicating arrival at a new residency area. All spatial operations were conducted using the *sp*, *sf*, and *raster* packages in R.

**Sample collection**

Swab samples from the brain, trachea, and cloaca of dead birds were collected, frozen at −20°C within one hour of collection, and shipped to the World Organisation for Animal Health/Food and Agriculture Organisation (WOAH/FAO) International Reference Laboratory for Avian Influenza at the Animal and Plant Health Agency (APHA) in Weybridge, UK, for diagnostic evaluation. Surveillance for suspicious wildlife mortality continued with special attention given to any spatial or temporal clustering of cases or unusual behaviours in wildlife.

**Molecular methods**

Total nucleic acid was extracted from all swab samples as described previously [25] and viral RNA was screened using four real-time reverse transcription polymerase chain reaction (rRT-PCR) assays including: i) a Matrix (M)-gene assay for generic influenza A virus detection [26], ii) a HPAIV H5 clade 2.3.4.4b specific assay for HA subtype and pathotyping [25], iii) an N1-subtype specific rRT-PCR to confirm the neuraminidase type [27], and iv) an avian paramyxovirus type-1 (APMV-1) large polymerase (L)-gene assay [28]. All rRT-PCRs were undertaken on the AriaMx qPCR System (Agilent, United Kingdom). Material from positive brain tissue swabs was used for virus isolation in 10-day-old specific pathogen-free (SPF) embryonated fowls' eggs according to internationally recognised methods (Codes and Manuals - WOAH - World Organisation for Animal Health).

**Viral Sequencing**

Whole-genome sequencing (WGS) was undertaken on brain tissue swabs. Extracted vRNA was converted to double-stranded cDNA and amplified using a one-step RT-PCR using SuperScript III One-Step RT-PCR kit (Thermo Fisher Scientific) as previously described [29]. PCR products were purified with Agencourt AMPure XP beads (Beckman Coultrer) prior to sequencing library preparation using the Native Barcoding Kit (Oxford Nanopore Technologies) and sequenced using a GridION Mk1 (Oxford Nanopore Technologies) according to manufacturer's instructions. Assembly of the influenza A viral genomes was performed using a custom in-house pipeline as previously described [9].

**Phylogenetic Analysis**

To identify the genetic relatedness of Gough Island viruses to other reported strains, H5N1 HPAIV clade 2.3.4.4b sequences from Europe, Africa, Antarctica and South America available in the EpiFlu database between 1st January 2020 and 28th July 2025 were collated. To remove over-represented groups, the sequences were subset to cover 0.5% sequence divergence using PARNAS [30]. The remaining dataset was separated by segment and aligned using Mafft v7.525 [31] and manually trimmed to the open reading frame using Aliview v.2021 [32]. The trimmed alignments were used to infer maximum-likelihood (ML) phylogenetic trees using IQ-Tree v2.4.0 [33] with model finder, 1000 ultrafast bootstraps and SH-like approximate likelihood ratio test. Clade classification of Gough Island sequences was confirmed with GenoFLU-multi https://github.com/moncla-lab/GenoFLU-multi.

To produce a time scale phylogeny, all H5 HA sequences from South America and Antarctica were used alongside a subset of North American sequences to improve temporal signal. The dataset was aligned, trimmed, and an ML phylogenetic tree was inferred using the same approaches as described above. The HA ML phylogeny was then used to infer a time scaled phylogeny using TreeTime v0.11.4 [34]. Discrete trait analysis of transitions between locations was carried out using the mugration inference model in TreeTime with default settings.

**Results**

The first suspected HPAIV-related death of an adult Tristan skua was observed on Gough Island on 12 September 2024 at a club of 50-200 non-breeding skuas at the helipad near the research station. The following day, another skua at the same location exhibited clinical signs consistent with HPAIV, including drooping head and wings, lethargy, and an inability to walk or fly, and was found dead later the same day [35]. Two additional carcasses were discovered on 15 September. Swab samples were collected from three of the four carcasses on 20 September 2025 and the carcasses were buried afterwards. The fourth carcass had disappeared by the time of sampling and was presumed to have been scavenged by other skuas.

*Diagnostic evaluation of samples*

All three birds sampled on Gough Island tested positive for HPAIV H5N1 in oropharyngeal and brain

swabs but tested negative in cloacal swabs (Table 1). Brain samples indicated a high viral load with

HPH5 rRT-PCR values ranging from 19.5 - 23.8 Cts. Virus isolation was attempted on two of the

three brain samples and both yielded hemagglutinating virus.

Whole genome sequences (WGS) obtained from two samples confirmed the viruses belonged to HA

clade 2.3.4.4b, genotype B3.2, as previously detected in the Antarctic region (Fig. 2a) [9]. The two

WGS shared >99% identity across all genes. Phylogenetic analysis shows that these viruses are part of

monophyletic clade within the Antarctic Peninsula and sub-Antarctic region, including ancestral

viruses from South Georgia and their descendants in Crozet and Kerguelen (Figure 2). This suggests

an expansion of the introduction described by Banyard et al. [9], rather than a new incursion from

Africa. Analysis of the asymmetric transition rate matrix reveals notable patterns of viral movement

among key sub-Antarctic and South Atlantic islands (Figure 2b). South Georgia appears to be a

significant ancestral source, exhibiting outward transitions to Crozet, Kerguelen, Gough Island and

the Falkland Islands. Gough Island demonstrates moderate connectivity across the region, particularly

with Crozet and Kerguelen. However, transition rates from Gough Island to South Georgia and back

suggest less frequent bidirectional exchange. Overall, the data supports a model in which South

Georgia serves as a primary source, seeding transmission across the sub-Antarctic and South Atlantic

islands (Figure 2b).

*Ringing and tracking data*

Tracking durations ranged from 343 to 353 days (mean ± SD: 345 ± 3.3 days), yielding 687 ± 7.8

locations per individual (Fig. 3 and Fig. 4).

Following the breeding season, individuals departed the foraging grounds around Gough Island

between 12 January and 12 February 2018, *en route* to non-breeding foraging grounds off the coasts

of South Africa and Namibia. Arrival at these non-breeding areas occurred between 20 January and 25

February 2018, with the north-eastward migration taking 11.9 ± 4.9 days (range 4–17 days).

Individuals remained within the non-breeding wintering grounds for 141 ± 19.5 days (range 109–165

days). Departures from these areas occurred between 4 June and 15 July 2018, with arrival back at the

pre-laying foraging area near Gough Island occurring between 13 June and 1 August 2018. The south-

westward return migration took 13.8 ± 6.1 days (range 7–23 days).

Two of the three dead skuas sampled for HPAIV had been ringed on Gough Island in 2016 and 2017.

The individual ringed in 2017 (SAFRING 888666) was a known breeder on the island and had been

equipped with a GLS device (BH142) as part of the tracking study (Table 2, Figure 4d). In contrast,

the skua ringed in 2016 (SAFRING 888054) was caught as a non-breeder at the skua club near the

helipad.

**Discussion**

The arrival of HPAIV H5N1 on Gough Island represents one of the most geographically isolated

detections to date, highlighting the interconnectivity of pelagic seabird populations and their role in

assisting global transmission in the current HPAIV H5N1 epizootic into some of the world's most

remote (and sensitive) ecosystems. Confirmation of HPAIV in Tristan Skuas on Gough prompted

suspicions that individuals had become infected by viruses originating from Africa due to the species'

extensive connectivity with southern African coastal habitats outside their breeding season [36]. The

GLS data analysed in this study corroborated this migratory pattern, demonstrating high temporal and

spatial consistency in the species' use of their wintering foraging grounds and suggesting that this

behaviour is likely representative of the wider Gough Island skua population.

Multiple outbreaks of clade 2.3.4.4b H5 HPAIV among seabird and Cape fur seal *(Arctocephalus*

*pusillus)* colonies in southern Africa [37-40] could have provided opportunities for transmission to

scavenging species such as skua. However, a phylogenetic analysis of global 2.3.4.4b H5 HA

sequences places the Gough Island viruses within a cluster of South American strains, distinct to the

ones reported for Africa. Further analysis identified the Gough strains as belonging to genotype B3.2,

previously detected in the Antarctic region [9]. While terrestrial aggregations such as breeding

colonies represent clear and obvious hotspots for virus transmission, at-sea connectivity may play an

equally critical role with overlapping foraging grounds and shared marine habitats increasing the

potential for interspecies contact, facilitating viral spread between geographically distant populations.

The Benguela upwelling region, stretching from Cape Agulhas in South Africa north to southwest

Angola, is one of the most productive marine ecosystems globally [41] and plays a vital role as a

migratory corridor and seasonal feeding area for numerous migratory species, breeding in the

Antarctic or sub-Antarctic (e.g. White-capped/Shy albatross (*T. cauta*) [36]; Indian yellow-nosed

albatrosses (*T. carteri*) and northern giant petrels (*Macronectes halli*) [42]; black-browed albatrosses

[43]. The frequency and likelihood of interspecies interactions at shared foraging grounds, whether

through direct or indirect contact, make these zones high-risk areas for the persistence and

transmission of infectious diseases. However, any spatial pattern needs to be considered in a temporal

context i.e., the timing of seasonal/migratory movements within and across species and how it

coincides with outbreaks. Based on tracking records for 2018, individuals completed their south-

westward migration in one to three weeks, arriving near Gough Island between 13 June and 1 August.

While the incubation period for HPAIV can vary considerably depending on species susceptibility and

viral genetic characteristics, it is unlikely symptoms would only present 2–4 months after infection

(assuming broadly similar migratory timing in 2024) and thus improbable that the skuas picked up the

virus during their winter migration.

It is therefore more plausible that the virus reached Gough via broader Southern or Atlantic Ocean

flyways, potentially during the species' pre-laying exodus period in August and September, when

Tristan skuas disperse into the frontal region south of the island. These nutrient-rich boundary waters

between the sub-tropical and Antarctic polar fronts are known to support large congregations of

pelagic seabirds and serve as foraging grounds for marine mammals [18, 44, 45]. Seabird species

breeding on Gough Island use both the Southern and Atlantic Ocean Flyways [45-47] which overlap

considerably between 30-60°S, linking Antarctic seabird populations to those on islands in the South

Atlantic [18]. For example, populations of southern elephant seals, brown skua, and black-browed

albatross on South Georgia have all been found to utilise waters near Gough Island [43, 48-50].

Ultimately the timing and location of transmission of HPAIV to the Tristan skuas in this study remains

unknown along with the uncertainty about whether in fact skuas introduced the virus to the island or

other avian species or seals, vagrants or breeding on Gough (45, 51-53]. However, scavenging species

are more likely than other seabird species to interact with carcasses, spend extended periods of time

sitting on the water, and come into close contact with other foraging individuals [35, 49, 54]. Such

behaviours increase the opportunities for viral transmission under conditions where environmental

dilution of virions would otherwise hinder infection, supporting the role of skuas and giant petrels as

the most likely vectors of AIV across the Southern Ocean [20]. Despite these unknowns, the detection

of HPAIV H5N1 originating from the Antarctic peninsula illustrates a novel pathway by which

influenza viruses from the Americas could also be introduced back into wild bird populations in Afro-

Eurasia. Therefore, understanding the spatial and temporal dynamics of at-sea dispersal and

interactions, especially in areas of high biodiversity and migratory fly- and swim-ways, is essential for

anticipating and mitigating future outbreaks.

Initial concerns that HPAIV detection could constitute the onset of a mass outbreak on Gough Island,

have not materialized; no further symptomatic birds or mortalities related to HPAIV have been

confirmed (aside from the suspicious death of a breeding female Tristan albatross in April 2025).

Although mass mortality has occurred in other skua populations as a result of HPAIV, notably in the

UK where great skua (*Stercorarius* skua) declined by 73% [4, 35], the apparent failure of the virus to

cause a large-scale outbreak on Gough may be due to several factors. Cloacal swabs taken during the

initial investigation returned negative results for AIV, suggesting minimal environmental shedding.

Additionally, while one carcass was presumed scavenged, the remaining three were buried following

sampling, preventing further scavenging. Furthermore, while Gough hosts large populations of

seabird species, many of these species nest at low densities (e.g., Tristan albatross) or in burrows, such

as petrels and prions [13], reducing opportunities for direct contact and environmental transmission. A

serological study in 2009 demonstrated some seropositivity against influenza in northern rockhopper

penguins and brown skua on Gough [19, 20], however, how far pre-existing immunity against

influenzas could have influenced transmission dynamics in this outbreak remains unknown.

While there have been no further mortalities attributed to HPAIV on Gough Island or in the neighbouring Tristan da Cunha Archipelago, the impact of HPAIV in the region could be substantially underestimated. Large parts of these remote islands are inaccessible, limiting timely monitoring to detect carcasses or individuals exhibiting clinical signs. While there has been consistent presence of a field team of biologists on Gough year-round since 2008, there is less systematic surveillance at the Tristan da Cunha Archipelago. In February 2024, the island's fishery observer reported a dead skua floating at sea off Nightingale Island, but no further unusual mortality of skuas (or other seabirds) was observed on Nightingale and Inaccessible islands when visited in March and September 2024, respectively (PGR pers. obs.). Therefore, the absence of confirmed cases should not be taken as evidence of the absence of the disease. The foraging behaviour of Tristan skuas during the breeding season could increase the risk for both intra- and interspecific transmission among susceptible seabird taxa, contributing to the spread of the virus, locally and regionally. Other scavenging species such as southern (*M. giganteus,* resident) and northern giant petrels (vagrants) are also frequent visitors to the Tristan da Cunha Archipelago, where they depredate northern rockhopper penguins and generally scavenge on carcasses [55]. If HPAIV were to reach the Tristan archipelago, it would heighten the threats faced by already vulnerable populations endemic to the islands.

Only few mitigating activities are available to prevent the movements of migratory birds, especially over large distances, and as such, avoidance of incursions of diseases like that described here is seemingly not possible. Understanding the spatiotemporal dynamics of seabird movements -in particular scavenging seabirds- disease ecology, and host-pathogen interactions is essential for mitigating the impact of HPAIV and other emerging disease threats, particularly in high-risk and ecologically sensitive areas [56]. This emphasises the need for continued vigilance, proactive biosecurity measures, as well as an integrated research framework linking surveillance efforts across the South Atlantic and Southern Oceans to design and implement adaptive disease management strategies. Finally, it is a stark reminder of the vulnerability of remote ecosystems to infectious diseases and for the need to alleviate already persisting pressures on globally important seabird

populations including habitat degradation and disturbance, invasive species, and climate-driven

stressors to strengthen their resilience.

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**Declaration of interest statement**

The authors declare that they do not have any competing interests to disclose.

**References**

[1] Caliendo V, Lewis NS, Pohlmann A, et al. Transatlantic spread of highly pathogenic avian

influenza H5N1 by wild birds from Europe to North America in 2021. Sci Rep. 2022;12(1):11729.

doi:10.1038/s41598-022-13447-z

[2] Falchieri M, Reid SM, Ross CS et al. Shift in HPAI infection dynamics causes significant losses in

seabird populations across Great Britain. Veterinary Record. 2022;191(7):294-6.

[3] Lane JV, Jeglinski JW, Avery-Gomm S, et al. High pathogenicity avian influenza (H5N1) in

Northern Gannets (*Morus bassanus*): Global spread, clinical signs and demographic consequences.

Ibis. 2024;166(2):633-50. doi:10.1111/ibi.13275

[4] Tremlett CJ, Cleasby IR, Bolton et al. Declines in UK breeding populations of seabird species of

conservation concern following the outbreak of high pathogenicity avian influenza (HPAI) in 2021–

2022. Bird Study. 2024;71(4):293-310. doi:10.1080/00063657.2024.2438641

[5] Kuiken T, Vanstreels RE, Banyard A, et al. Emergence, spread, and impact of high-pathogenicity

avian influenza H5 in wild birds and mammals of South America and Antarctica. Conserv Biol.

2025;e70052. doi:10.1111/cobi.70052

[6] Pardo-Roa C, Nelson MI, Ariyama N, et al. Cross-species and mammal-to-mammal transmission

of clade 2.3. 4.4 b highly pathogenic avian influenza A/H5N1 with PB2 adaptations. Nat Commun.

2025;16(1):2232. doi:10.1038/s41467-025-57338-z

[7] Leguia M, Garcia-Glaessner A, Muñoz-Saavedra B, et al. Highly pathogenic avian influenza A

(H5N1) in marine mammals and seabirds in Peru. Nat Commun. 2023;14(1):5489.

doi:10.1038/s41467-023-41182-0

[8] Gamarra-Toledo V, Plaza PI, Angulo F, et al. Highly pathogenic avian influenza (HPAI) strongly

impacts wild birds in Peru. Biol Conserv. 2023;286:110272. doi:10.1016/j.biocon.2023.110272

[9] Banyard AC, Bennison A, Byrne AM, et al. Detection and spread of high pathogenicity avian

influenza virus H5N1 in the Antarctic Region. Nat Commun. 2024;15(1):7433. doi:10.1038/s41467-

024-51490-8

[10] León F, Ulloa-Contreras C, Pizarro EJ, et al. Skuas mortalities linked to positives HPAIV A/H5

beyond Polar Antarctic Circle. bioRxiv. 2025;1. doi:10.1101/2025.03.02.640960

[11] Clessin A, Briand FX, Tornos J, et al. Mass mortality events in the sub-Antarctic Indian Ocean

caused by long-distance circumpolar spread of highly pathogenic avian influenza H5N1 clade 2.3. 4.4

b. 2025. BioRxiv;2025-02. doi:10.1101/2025.02.25.640068

[12] Ryan PG, Gill R, Roberts L, Stephen V. Avian flu reaches Marion Island. African Birdlife.

2025;13(5):14-15.

[13] Caravaggi A, Cuthbert RJ, Ryan PG, et al. The impacts of introduced House Mice on the

breeding success of nesting seabirds on Gough Island. Ibis. 2019;161(3):648-61.

doi:10.1111/ibi.12664

[14] Oppel S, Clark BL, Risi MM, et al. Cryptic population decrease due to invasive species predation

in a long-lived seabird supports need for eradication. J Appl Ecol. 2022;59(8):2059-70.

doi:10.1111/1365-2664.14218

[15] Jones CW, Risi MM, Osborne AM, et al. Mouse eradication is required to prevent local

extinction of an endangered seabird on an oceanic island. Anim Conserv. 2021;24(4):637-45.

doi:10.1111/acv.12670

[16] BirdLife International. *Rowettia goughensis*. *The IUCN Red List of Threatened Species* 2024:

e.T22723149A252044473. 2024 [cited on 07 August 2025]. doi:10.2305/IUCN.UK.2024-

2.RLTS.T22723149A252044473.en

[17] Dewar ML, Vanstreels RET, Boulinier T, et al. Biological Risk Assessment of Highly Pathogenic

Avian Influenza in the Southern Ocean. Scientific Committee on Antarctic Research. Cambridge UK.

SCAR Antarctic Wildlife Health Network. 2023.

[18] Morten JM, Carneiro AP, Beal M, et al. Global Marine Flyways Identified for Long-Distance

Migrating Seabirds From Tracking Data. Glob Ecol Biogeogr. 2025;34(2):e70004. doi:

10.1111/geb.70004

[19] Abad, F.X., N.Busquets, A.Sanchez, et al. Serological and virological surveys of the influenza A

viruses in Antarctic and sub-Antarctic penguins. Antarct. Sci. 2013;25:339-344.

doi:10.1017/S0954102012001228

[20] Gittins O, Grau-Roma L, Valle R, et al. Serological and molecular surveys of influenza A viruses

in Antarctic and sub-Antarctic wild birds. Antarct Sci. 2020;32(1):15-20.

doi:10.1017/s0954102019000464

[21] Gamble A, Bazire R, Delord K, et al. Predator and scavenger movements among and within

endangered seabird colonies: Opportunities for pathogen spread. J Appl Ecol. 2020;57(2):367-78.

doi:10.1111/1365-2664.13531

[22] Sumner MD, Wotherspoon SJ, Hindell MA. Bayesian estimation of animal movement from

archival and satellite tags. PLoS One. 2009.13;4(10):e7324. doi:10.1371/journal.pone.0007324

[23] Colchero F, Jones OR, Rebke M. BaSTA: an R package for Bayesian estimation of age-specific

survival from incomplete mark–recapture/recovery data with covariates. Methods Ecol Evol.

2012;3(3):466-470. doi: 10.1111/j.2041-210x.2012.00186.x

[24] Calenge C. Home range estimation in R: the adehabitatHR package. Office national de la classe

et de la faune sauvage: Saint Benoist, Auffargis, France. 2011.

[25] James J, Seekings AH, Skinner P, et al. Rapid and sensitive detection of high pathogenicity

Eurasian clade 2.3. 4.4 b avian influenza viruses in wild birds and poultry. J Virol Methods.

2022;301:114454. doi: 10.1016/j.jviromet.2022.114454

[26] Nagy A, Černíková L, Kunteová K, et al. A universal RT-qPCR assay for "One Health" detection

of influenza A viruses. PloS one. 2021;16(1):e0244669. doi:10.1371/journal.pone.0244669

[27] Payungporn S, Chutinimitkul S, Chaisingh A, et al. Single step multiplex real-time RT-PCR for

H5N1 influenza A virus detection. J Virol Methods. 2006;131(2):143-7.

doi:10.1016/j.jviromet.2005.08.004

[28] Sutton DA, Allen DP, Fuller CM, et al. Development of an avian avulavirus 1 (AAvV-1) L-gene

real-time RT-PCR assay using minor groove binding probes for application as a routine diagnostic

tool. J Virol Methods. 2019;265:9-14. doi:10.1016/j.jviromet.2018.12.001

[29] Slomka MJ, Reid SM, Byrne AM, et al. Efficient and informative laboratory testing for rapid

confirmation of H5N1 (Clade 2.3. 4.4) high-pathogenicity avian influenza outbreaks in the United

Kingdom. Viruses. 2023;15(6):1344. doi:10.3390/v15061344

[30] Markin A, Wagle S, Grover S, Vet al. PARNAS: objectively selecting the most representative

taxa on a phylogeny. Syst Biol. 2023;72(5):1052-63. doi:10.1093/sysbio/syad028

[31] Katoh K, Standley DM. MAFFT multiple sequence alignment software version 7: improvements

in performance and usability. Mol Biol Evol. 2013;30(4): 772-780. doi:10.1093/molbev/mst010

[32] Larsson A. AliView: a fast and lightweight alignment viewer and editor for large

datasets. Bioinformatics 30.22. 2014:3276-3278. doi:10.1093/bioinformatics/btu531

[33] Minh BQ, Schmidt HA, Chernomor O, et al. IQ-TREE 2: new models and efficient methods for

phylogenetic inference in the genomic era. Mol Biol Evol 2020;37(5):1530-1534.

doi:10.1093/molbev/msaa015

[34] Sagulenko P, Puller V, Neher RA. TreeTime: Maximum-likelihood phylodynamic analysis. Virus

Evol. 2018;4(1):vex042. doi:10.1093/ve/vex042

[35] Banyard AC, Lean FZ, Robinson C, et al. 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.

2022;14(2):212. doi:10.3390/v14020212

[36] Carneiro APB, Dias MP, Clark BL, et al. The BirdLife Seabird Tracking Database: 20 years of

collaboration for marine conservation. Biol Conserv. 2024:299;110813.

doi:10.1016/j.biocon.2024.110813

[37] Abolnik C, Phiri T, Peyrot B, et al. The molecular epidemiology of clade 2.3.4.4B H5N1 high

pathogenicity avian influenza in Southern Africa, 2021–2022. Viruses. 2023;15(6):1383.

doi:10.3390/v15061383

[38] Abolnik C, Roberts LC, Strydom C, et al. Outbreaks of H5N1 High Pathogenicity Avian

Influenza in South Africa in 2023 Were Caused by Two Distinct Sub-Genotypes of Clade 2.3. 4.4 b

Viruses. Viruses. 2024;16(6):896. doi:10.3390/v16060896

[39] Roberts LC, Abolnik C, Waller LJ, et al. Descriptive epidemiology of and response to the high

pathogenicity avian influenza (H5N8) epidemic in South African coastal seabirds, 2018. Transbound

Emerg Dis. 2023;2023(1):2708458. doi:10.1155/2023/2708458

[40] World Organisation for Animal Health (WOAH), 2025. WAHIS Event 5034 Influenza A viruses

of high pathogenicity (Inf. with) (non-poultry including wild birds) (2017-).

https://wahis.woah.org/#/in-event/5034/dashboard

[41] Hutchings L, Van der Lingen CD, Shannon LJ, et al. The Benguela Current: An ecosystem of

four components. Prog in Oceanogr. 2009;83(1-4):15-32. doi:10.1016/j.pocean.2009.07.046

[42] Reisinger RR, Raymond B, Hindell MA, et al. Habitat modelling of tracking data from multiple

marine predators identifies important areas in the Southern Indian Ocean. Divers Distrib.

2018;24(4):535-50. doi:10.1111/ddi.12702

[43] Phillips RA, Silk JR, Croxall JP, et al. Summer distribution and migration of nonbreeding

albatrosses: individual consistencies and implications for conservation. Ecology. 2005;86(9):2386-96.

doi:10.1890/04-1885

[44] Bost CA, Cotté C, Bailleul F, et al.  The importance of oceanographic fronts to marine birds and

mammals of the southern oceans. J Mar Syst. 2009;78(3):363-376. doi:10.1016/j.jmarsys.2008.11.022

[45] Dias MP, Oppel S, Bond AL, et al. Using globally threatened pelagic birds to identify priority

sites for marine conservation in the South Atlantic Ocean. Biol Conserv. 2017;211:76-84.

doi:10.1016/j.biocon.2017.05.009

[46] Schoombie S, Dilley BJ, Davies D, et al. The foraging range of Great Shearwaters (*Ardenna*

*gravis*) breeding on Gough Island. Polar Biol. 2018;41(12):2451-8. doi:10.1007/s00300-018-2381-7

[47] Green CP, Green DB, Ratcliffe N, et al. Potential for redistribution of post-moult habitat for

Eudyptes penguins in the Southern Ocean under future climate conditions. Glob Chang Biol.

2023;29(3):648-67. doi:10.1111/gcb.16500

[48] Reisinger RR, Bester MN. Long distance breeding dispersal of a southern elephant seal. Polar

Biol. 2010;33(9):1289-91. doi:10.1007/s00300-010-0830-z

[49] Carneiro AP, Manica A, Clay TA, et al. Consistency in migration strategies and habitat

preferences of brown skuas over two winters, a decade apart. Mar Ecol Prog Ser. 2016;553:267-81.

doi:10.3354/meps11781

[50] Hindell MA, McMahon CR, Bester MN, et al. Circumpolar habitat use in the southern elephant

seal: implications for foraging success and population trajectories. Ecosphere. 2016;7(5):e01213.

doi:10.1002/ecs2.1213

[51] Bester MN, Wege M, De Bryn, et al. Ranging and fiving behaviour of Subantarctic fur seals from

the Tristan da Cunha Islands, South Atlantic. Tristan da Cunha Islands Seal Research Report (2009 –

2019). 2019

[52] Ryan PG, Dilley BJ, Risi MM, et al. Three new seabird species recorded at Tristan da Cunha

archipelago. Seabird. 2019;32:122-5. doi:10.61350/sbj.32.122

[53] Bester MN, Somers MJ. Monitoring of vagrant seals on mid-oceanic islands of the South Atlantic

Ocean. Polar Biology. 2025;48(3):79. doi:10.1007/s00300-025-03397-3

[54] Sinclair JC. Subantarctic Skua *Catharacta antarctica* predation techniques on land and at

sea. Mar Ornithol. 1980;8:3-6. doi:10.5038/2074-1235.8.1.27

[55] Ryan PG, Sommer E, Breytenbach E. Giant petrels *Macronectes* hunting northern rockhopper

penguins *Eudyptes moseleyi* at sea. Ardea. 2008;96(1):129-34. doi:10.5253/078.096.0116

[56] Sacristán C, Ewbank AC, Ibáñez Porras P, et al. Novel epidemiologic features of high

pathogenicity avian influenza virus A H5N1 2.3. 3.4 b panzootic: a review. Transbound Emerg Dis.

2024;2024(1):5322378. doi:10.1155/2024/5322378

**Tables**

**Table 1:** RT-PCR results, virus isolation and viral whole genome sequencing on samples collected from three Tristan skuas (*Stercorarius antarcticus*

*hamiltoni*) on Gough Island on the 20th September 2024.

| Bird number | Sample Type (Swab) | M Gene RT-PCR | H5HP RT-PCR | N1 RT-PCR | Interpretation | Strain | GISAID Accession number | Isolate |
|---|---|---|---|---|---|---|---|---|
| 1 | Tracheal | **Positive** | **Positive** | **Positive** | H5N1 HPAIV | A/Brown_Skua/Gough_Island/047354/2024_\|H5N1\|_2024-09-20 | EPI_ISL_201 51596 | **Yes** |
| | Cloacal | Negative | Negative | Negative | | | | |
| | Brain | **Positive** | **Positive** | **Positive** | | | | |
| 2 | Tracheal | **Positive** | **Positive** | **Positive** | H5N1 HPAIV | A/Brown_Skua/Gough_Island/047355/2024_\|H5N1\|_2024-09-20 | EPI_ISL_201 51597 | NA |
| | Cloacal | Negative | Negative | Negative | | | | |
| | Brain | **Positive** | **Positive** | **Positive** | | | | |
| 3 | Tracheal | **Positive** | **Positive** | **Positive** | H5N1 HPAIV | A/Brown_Skua/Gough_Island/ 050656/2024_\|H5N1\|_2024-09-20_EP1 | NA | **Yes** |
| | Cloacal | Negative | Negative | Negative | | | | |
| | Brain | **Positive** | **Positive** | **Positive** | | | | |

## Figures

### Figure 1

### Figure 2

Figure 3

Figure 4  a-d

**Figure Captions**

**Figure 1.** a) Map indicating the location for Gough Island in the context of locations with ongoing HPAIV H5N1 outbreaks reported to WAHIS (red dots), b) Gough Island with the research station located in the southeast of the island and the island helipad's (yellow diamond), c) view of research station and helipad, d) Tristan skua (*Stercorarius antarcticus hamiltoni*).

**Figure 2.** a) Maximum-likelihood tree of HA-gene including the two Gough Island sequences identified from this study and 944 HA-gene sequences from Antarctica, South and North America previously identified as 2.3.4.4b. Sequences from South America coloured according to country, all sequences from North America in black, b) a source-sink heat map of transmission rate estimates between geographic regions.

**Figure 3.** Time series showing the distance from the colony of GLS-tracked Tristan skuas (8) during the 2017/18 and 2018/19 breeding seasons, across key stages of the breeding cycle.

**Figure 4.** Kernel utilisation distributions (KUDs) representing home-range (95% UD) and core (50% UD) foraging areas of all tracked individuals during the a) pre-laying exodus, b) breeding, and c) non-breeding periods, overlaid on major frontal features from the 2017/18 and 2018/19 breeding seasons. Dashed lines indicate individual migration routes from the Gough Island region to non-breeding foraging grounds on the South African and Namibian continental shelves, and their return paths. The solid line represents the movement of one individual (GLS tag: BH142) that tested positive for HPAIV in 2024.