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Foraging movements rather than migrations drive avian influenza (HPAIV H5N1) dynamics in Antarctic seabirds

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Abstract

Highly pathogenic avian influenza of subtype H5N1 (HPAIV H5N1) reached Antarctica in late 2023/2024 breeding season, but the host ecology and movement processes shaping its incursion and spread remain poorly resolved. We investigated these mechanisms by integrating viral genomics, multi-season serology, and seabird movement data at King George Island (Fildes Peninsula, South Shetland Islands), a likely gateway between South America and the Antarctic Peninsula. Across three breeding seasons (2022/23–2024/25), we collected swabs and blood serum from key scavenging and predatory seabirds (Brown skua, South Polar skua, Southern Giant petrel) and paired these data with light-level geolocator tracks (10–16 full annual tracks per species) and breeding-season GPS tracks (10–20 individuals per species). Phylogenetic analyses including three newly generated HPAIV H5N1 genomes from infected Brown skuas placed these viruses within the South Georgia–Antarctic lineage, consistent with introduction via South Georgia followed by onward spread within the region. Longitudinal serology revealed a rapid increase in cumulative exposure in scavenging species, with antibodies against influenza A virus' nucleoprotein and hemagglutinin subtype H5 rising to high levels by 2024/25 in Brown skuas (52.2%) and Southern Giant petrels (62.5%), but remaining markedly lower in South Polar skuas (12.5%), consistent with their more pelagic and less scavenging foraging behaviour. Tracking showed that migratory connectivity was greatest during the non-breeding period but contracted rapidly during colony return and early breeding. In contrast, network simulations parameterized by high-percentile breeding-season foraging distances indicated strong peninsula-wide connectivity and non-zero potential links toward South Georgia and other sub-Antarctic stepping-stones. Together, these results provide a mechanistic, host-based framework suggesting that HPAIV H5N1 likely reached Antarctica through the South Georgia pathway, but that its regional spread was shaped primarily by foraging ecology and breeding-season movement networks rather than by long-distance migration.

Introduction

The ongoing global outbreak of highly pathogenic avian influenza H5N1 (HPAIV H5N1), clade 2.3.4.4b, has developed into an unprecedented panzootic, causing extensive mortality in wild birds, massive outbreaks in poultry holdings, and spillover into multiple mammalian taxa across several continents (Pohlmann et al., 2023; Wille & Barr, 2022). After rapidly expanding through the Americas, the virus reached South America and subsequently the sub-Antarctic and Antarctic regions in early 2024, where outbreaks in seabirds and marine mammals demonstrated that even the remote Antarctic ecosystem is not insulated from global pathogen spread (Bennett-Laso et al., 2024; Clessin et al., 2025, 2026; Iervolino et al., 2025; Kuiken et al., 2026). These events have raised urgent questions about the impact of HPAIV H5N1 on Antarctic wildlife and the ecological pathways by which the virus is introduced into and potentially transmitted within seabird communities (Bestley et al., 2020; Rogers et al., 2020).

Seabirds are plausible hosts and connectors of HPAIV H5Nx spread because many species combine long-distance movements with seasonal aggregation at dense breeding colonies, where close contact, environmental contamination, and scavenging can facilitate transmission (Boulinier, 2023). Their role in

the current HPAIV H5Nx panzootic appears to have increased as outbreaks expanded from waterfowl-dominated systems into major mortality events in seabird colonies, including skuas, gulls, terns (e.g. Knief et al., 2024; Pohlmann et al., 2023), and dense seabird communities along the Pacific coast of South America (Kuiken et al., 2026). Yet exposure risk is unlikely to be uniform across seabirds. Species differ strongly in migratory strategy, colony association, diet, and habitat use, including the extent to which they scavenge on infected carcasses or move through terrestrial, coastal, and pelagic environments. These ecological differences may determine not only which species are most likely to become exposed, but also which species connect local outbreaks across colonies and regions.

In Antarctica, the movements relevant for viral incursion may differ from those driving regional transmission. Annual migration can link Antarctic breeding populations with distant regions such as South America, South Georgia, and, for some species, even the Northern Hemisphere. These broad-scale movements create opportunities for long-distance viral transport into the Antarctic system. Once birds have returned to their colonies, however, migratory connectivity contracts, while repeated breeding-season foraging movements, scavenging, and inter-colony movements may become more important for local amplification and onward spread (Boulinier, 2023). Distinguishing these mechanisms requires movement data across complementary spatial and temporal scales, combined with direct evidence of infection and prior exposure.

King George Island, the largest of the South Shetland Islands, provides a particularly informative setting to examine these processes. Situated at the northern edge of the Antarctic Peninsula region, it is a likely gateway for southward H5N1 spread from South America into Antarctica (Lisovski et al., 2024a). Our field campaigns spanned three consecutive breeding seasons, beginning before the first confirmed detection of H5N1 in Antarctica and continuing through its regional occurrence. We combined virological screening, viral genomics, multi-season serology, light-level geolocator tracking, and breeding-season GPS tracking of Brown Skuas, South Polar Skuas, and Southern Giant Petrels. We tested the hypothesis that Antarctic scavenging seabirds play epidemiological roles distinct from those of marine-feeding species such as penguins, and that these roles vary across spatial scales: annual migration may shape opportunities for long-distance incursion, whereas breeding-season foraging behaviour, scavenging, and local habitat use may determine exposure risk and regional transmission among colonies.

Results

Avian Influenza Virus (AIV) surveillance and virus phylogeny

All swabs collected in 2022/23 and 2023/24 from deceased or live birds were negative for IAV RNA. In 2024/25, we screened combined oropharyngeal and cloacal swabs from Brown Skuas (N = 41), South Polar Skuas (N = 26), Southern Giant Petrels (N = 20), Gentoo Penguins (N = 112), and Chinstrap Penguins (N = 2). IAV RNA was detected in two of the studied seabird species; Most RT-qPCR-positive samples originated from Brown Skuas found dead between 31 January and 12 February 2025 (N = 11),

with viral loads ranging from moderate to low (Ct 24.4–36.3). Ten of these individuals were confirmed as HPAIV H5N1-positive by subtype- and pathotype-specific RT-qPCR assays, while one additional Brown Skua carcass was confirmed as IAV subtype H5 but could not be fully subtyped. Among all samples collected from live birds without clinical signs of infection across the study period (N = 518), only one Southern Giant Petrel tested positive, with a low IAV RNA load (Ct 37.1) confirmed as subtype H5.

For three Brown Skua samples, whole-genome sequencing yielded complete coding sequences for all eight viral segments (Fig. 1a; sample IDs 2025AI02076, 2025AI02033, and 2025AI02064). Phylogenetic analyses of concatenated coding sequences from South American, sub-Antarctic, and Antarctic HPAIV H5N1 viruses (2023-02-20 to 2024-12-26) placed the King George Island sequences within Goose/Guangdong-like clade 2.3.4.4b genotype B3.2 viruses circulating in the sub-Antarctic and Antarctic region. The new sequences from Brown Skua formed part of a cluster of HPAIV H5N1 viruses detected in early 2025 that originated from South Georgia viruses sampled in late 2024, supporting a South Georgia–Antarctic lineage. The generated sequences share a deletion in the stalk region of the neuraminidase (NA) segment that has previously been described (Xu et al., 2025), and clustered with other skua-derived viruses; however, whether this reflects a genuine host-associated transmission pattern or sampling bias from passive mortality-based surveillance remains unresolved.

Serological evidence of prior exposure

Across three breeding seasons (2022/23–2024/25), antibody screening revealed distinct temporal dynamics among the focal seabird species (Fig. 2). In Brown Skuas and Southern Giant Petrels, the seroprevalence of antibodies against the IAV nucleoprotein (NP) ranged from moderate to high and increased over time, while subtype H5-specific antibodies rose markedly across seasons. In contrast, South Polar Skuas and penguins showed consistently lower seroprevalences. In Brown Skuas, NP-specific seroprevalence remained high across seasons (53–78%), while the H5-specific seroprevalence increased from 6% in 2022/23 to 39% in 2023/24 and to 52% in 2024/25 (N = 32, 26, 23). The sharp increase between 2022/23 and 2023/24 coincided with the first large-scale HPAI H5 mortality events reported along the east coast of Argentina in 2023, a major non-breeding foraging area for Brown Skuas. Notably, low-level H5 seroprevalence (6%) was present in 2022/23, prior to documented virus detection on King George Island. Southern Giant Petrels exhibited a delayed but pronounced increase in IAV/H5 seroprevalence. NP antibody prevalences remained low in 2022/23 and 2023/24 (13% and 3%, respectively) but rose sharply to 88% in 2024/25, while H5 seroprevalence increased from 0% in the first two seasons to 63% in 2024/25 (N = 15, 32, 16). The timing of these increases corresponded with mortality events attributed to HPAIV H5 on the northern Antarctic Peninsula in 2024 and 2024/25, an area frequently used by Southern Giant Petrels outside the breeding period. South Polar Skuas showed lower overall seroprevalences across seasons, with NP-antibody prevalence ranging from 5–29% and H5-antibody prevalence from 0–13% (N = 30, 37, 24). The modest increase to 13% H5 seropositivity in 2024/25 coincided with documented HPAIV H5 circulation in South Polar Skuas on the Antarctic Peninsula, including the die-off reported from Beak Island (Iervolino et al., 2026). The low-level

seroprevalence in 2022/23 (3%) preceded confirmed virus detection in Antarctica and may reflect exposure outside the region during the non-breeding period. In contrast, penguins showed low and declining NP-seroprevalences over the study period (19% to 1%; N = 67, 46, 101), and H5-specific antibodies were rare (0–2%). Together, these patterns indicate rapidly increasing exposure to H5-viruses in scavenging seabirds over consecutive seasons, while more marine-associated species showed substantially lower sero-prevalences.

Migratory movements

Light-level geolocator tracks revealed pronounced interspecific differences in migratory connectivity from King George Island (Fig. 3a). South Polar Skuas travelled farthest, with individuals using both Pacific and Atlantic sectors and migrating to the Northern Hemisphere. Brown Skuas remained within the Southwest Atlantic, concentrating their at-sea movements in oceanic and shelf waters east of Argentina and southern Brazil. Southern Giant Petrels showed the most restricted non-breeding distribution, making only brief excursions to waters east of Argentina while otherwise remaining within Antarctic and sub-Antarctic waters. Across taxa, individuals remained predominantly pelagic, and only a small proportion of reconstructed locations occurred within 50 km of shorelines (South Polar Skua: 1.8%, Brown Skua: 3.9%, Southern Giant Petrel: 11.5% of locations).

Distance to the breeding colony varied markedly over the annual cycle (Fig. 3b). During the non-breeding period, South Polar Skuas moved farthest from the colony, reaching a peak mean ± SD distance of 13,989 ± 1,681 km. Brown Skuas and Southern Giant Petrels remained closer on average, reaching peak distances of 3,635 ± 1,548 km and 1,947 ± 914 km, respectively. Across all three species, broad-scale migratory connectivity contracted rapidly during colony return and early breeding (October–November), when individuals moved back into Antarctic waters and remained comparatively close to their breeding sites.

Foraging trips and network simulation

Breeding-season movement distances differed most strongly in the upper tails of the species-specific distributions (Fig. 4a). While typical foraging radii were broadly similar between the two skua species, extensive movements were more frequent in Brown Skuas and Southern Giant Petrels than in South Polar Skuas. Individual time-weighted 99th-percentile distances exceeded approximately 900 km in Brown Skuas and 1,100 km in Southern Giant Petrels, indicating that these species occasionally ranged far enough from their breeding colonies to connect distant sites within the Antarctic Peninsula region.

The species also differed in their use of marine versus terrestrial or coastal habitats during breeding. South Polar Skuas foraged predominantly in marine habitats, with 89.4% of potential foraging locations classified as marine. Brown Skuas showed the lowest marine habitat use (30.2%), indicating much greater use of terrestrial and coastal environments, while Southern Giant Petrels were intermediate

(74.3%; Fig. 4b). These differences suggest that Brown Skuas, and to a lesser extent Southern Giant Petrels, are the species most likely to encounter colony- or shoreline-associated sources of exposure during the breeding season.

We used empirical GPS-derived foraging distances to simulate potential connectivity among colony clusters across the Antarctic Peninsula region and adjacent sub-Antarctic islands. The resulting network indicated the sites across the Antarctic Peninsula to be tightly connected (mean ± SD connectivity probability: 0.19 ± 0.26), with weaker but non-zero potential links even extending toward South Georgia (0.06 ± 0.008; Fig. 5). When breaking down the network for specific species, Southern Giant Petrels (0.24 ± 0.33) and Brown Skuas (0.19 ± 0.12) appear to contribute most strongly to this regional connectivity, whereas South Polar Skuas contributed least (0.07 ± 0.19).

Discussion

Our results suggest that the emergence and spread of HPAIV H5N1 clade 2.3.4.4b in Antarctic seabirds cannot be explained by migration distance alone. Instead, they point to a two-stage process in which broad-scale movement networks facilitate viral incursion into the wider Antarctic region, while breeding-season foraging ecology shapes exposure risk and onward spread among local and regional colonies. Phylogenetic analyses indicated that viruses detected on King George Island clustered within the South Georgia–Antarctic lineage, consistent with a regional introduction through South Georgia during the first year of incursion (Clessin et al., 2026). At the same time, serology and movement data showed marked ecological differences among host species. Brown Skuas and Southern Giant Petrels exhibited substantially higher cumulative H5 exposure than South Polar Skuas despite the latter showing the broadest migratory connectivity. Together, these patterns suggest that scavenging behaviour, terrestrial and near-shore habitat use and breeding-season connectivity were more important for exposure and transmission than migration distance itself.

The phylogenetic placement of the King George Island viruses supports a distinction between regional incursion and subsequent local or regional spread. The newly generated Brown Skua genomes and viruses detected elsewhere on the Antarctic Peninsula in 2024/25 grouped within the South Georgia–Antarctic lineage. This pattern is consistent with H5N1 entering the Antarctic Peninsula region through South Georgia and subsequently spreading within a broader sub-Antarctic–Antarctic host network. The close relationship among these viruses may be further supported by the shared deletion in the neuraminidase stalk region (Xu et al., 2025). Long-distance migration provides a plausible mechanism for such introductions. South Polar Skuas, Brown Skuas, and Southern Giant Petrels all connected King George Island to distant marine regions during the non-breeding period, with South Polar Skuas ranging across ocean basins and into the Northern Hemisphere. Similar migratory movements have previously been implicated in long-distance transport of avian influenza viruses in other systems (Caliendo et al., 2022; Tian et al., 2015; Yang et al., 2024). However, viral phylogeny alone cannot identify the host species responsible for spatial spread. Availability of sequence data remains strongly shaped by mortality-based surveillance, which is biased to accessible areas and conspicuous mortality events. Brown Skuas should

therefore not be interpreted as exclusive vectors, but as visible and plausible participants in a broader multi-host system involving multiple scavenging seabirds (Kuiken et al., 2026).

While migration may explain how H5N1 reached the Antarctic region, serology and local/regional movement better explained exposure and seasonal maintenance patterns. Brown Skuas and Southern Giant Petrels showed strong increases in H5-specific antibodies across the study period, whereas South Polar Skuas and sympatric penguins showed consistently lower serological signals. Because antibodies indicate previous infection and survival, these results reveal substantial sublethal exposure that would remain undetected by passive mortality surveillance alone. Similar discrepancies between mortality, active infection, and antibody prevalence have been reported in other seabird systems affected by HPAIV H5N1 (Greco et al., 2025). The low H5 antibody prevalence in penguins further suggests that exposure was not simply determined by co-occurrence within the same ecosystem, but instead depended on species-specific ecology, contact structure, susceptibility (i.e. some species require a higher number of virus particles to become infected than other species), and transmission pathways. It is also likely that a scavenging bird feeding on an infected carcass is exposed to a much higher virus dose than a non-scavenging bird (e.g. Penguin species) that may only be exposed to a virus-contaminated environment.

Ecological differences among species provide a likely explanation of these contrasting exposure patterns. During the breeding season, broad-scale migratory connectivity contracted rapidly, but local and regional foraging movements continued to create opportunities for connectivity among colonies. Brown Skuas and especially Southern Giant Petrels occasionally ranged far enough to connect colony clusters across the Antarctic Peninsula region, and connectivity simulations further indicated weaker but non-zero links toward South Georgia. Tracking studies from South Georgia similarly show that breeding albatrosses and petrels can move extensively across the Scotia Sea and into Antarctic and South American-associated marine regions (González-Solís et al., 2000; Phillips et al., 2008; Wakefield et al., 2025). At the same time, Brown Skuas and Southern Giant Petrels used terrestrial and nearshore habitats more frequently than South Polar Skuas and engaged more heavily in scavenging behaviour. These are precisely the ecological settings in which birds are likely to encounter infected carcasses, contaminated substrates, or other exposed scavengers (Boulinier, 2023). Breeding-season foraging movements therefore likely acted not merely as local colony movements, but as mechanisms linking colony-associated, coastal, and marine transmission environments (Lamb et al., 2023).

The timing of mortality events further suggests that regional incursion, colony-level amplification, and visible disease outcomes were temporally decoupled. HPAIV H5N1 did not become apparent on King George Island during the period of maximum broad-scale migratory connectivity, but later in the breeding season, when local and regional movements were shaped by breeding constraints. During incubation, adults are tied strongly to nest attendance, whereas chick rearing can increase the frequency, duration, or variability of foraging trips as parents meet the energetic demands of growing chicks (Ropert-Coudert et al., 2004; Weimerskirch, 1998; Weimerskirch et al., 2003). Failed breeders and non-breeders may contribute additional connectivity because they are less constrained by nest duties and can range more widely or visit multiple colonies (Lamb et al., 2023; Ponchon et al., 2015). Additionally, in cold Antarctic

environments, carcasses, contaminated substrates, or scavenging sites may remain infectious for extended periods and provide sources of exposure beyond the initial introduction (Ramey et al., 2020; Yamamoto et al., 2017). Together, these processes could generate delayed or secondary waves of transmission during the breeding season, explaining why mortality events may peak after the period when migratory return would have provided the strongest opportunity for long-distance incursion.

The three focal species appear to occupy functionally distinct positions within the Antarctic H5N1 host-virus system. South Polar Skuas create broad-scale migratory connectivity and therefore potential opportunities for long-distance encounter or transport, but their lower H5 seroprevalence and more pelagic breeding-season habitat use suggest lower exposure to colony-associated sources. Brown Skuas showed high exposure, frequent use of terrestrial and coastal habitats, and strong potential to connect local colony environments, making them likely sentinels and plausible regional connectors (see also Wille et al., 2026). Southern Giant Petrels showed similarly high H5 exposure and extensive upper-tail foraging movements, suggesting that they may connect scavenging opportunities and colony systems across broader regional scales. Rather than representing isolated vectors, these species appear to function as complementary components of a broader multi-host transmission network in which movement, habitat use, and scavenging ecology jointly structure exposure and connectivity (Kuiken et al., 2026).

Several limitations are inherent to linking pathogen dynamics with wildlife movement data. Serology provides evidence of prior exposure but cannot identify the exact timing or location of infection, while movement tracks reveal plausible pathways of contact and connectivity rather than transmission events themselves (Dunning et al., 2025). Likewise, available sequence data are shaped by passive surveillance and uneven sampling effort, which is biased toward accessible areas and conspicuous mortality events. Furthermore, our focal species represent only part of the Antarctic host community, and unsampled species may contribute to viral maintenance, amplification, or spread. Nevertheless, the convergence of phylogenetic evidence, multi-season serology, and movement data supports a consistent interpretation: HPAIV H5N1 dynamics in Antarctic seabirds is structured not simply by how far birds migrate, but by how breeding-season movements intersect with scavenging behaviour and colony-associated exposure environments.

Our findings have important implications for disease surveillance and animal conservation in Antarctica. If H5N1 exposure is primarily shaped by scavenging ecology and breeding-season connectivity, surveillance strategies should not rely solely on mortality reports, which capture only the most visible part of viral circulation. Instead, monitoring efforts should prioritise scavenging species, terrestrial and nearshore colony environments, and periods when local and regional movements are most likely to connect colonies. This is particularly important in those Antarctic regions where H5N1 has not yet been detected, or where apparent absence may simply reflect limited surveillance intensity rather than true absence. More broadly, Antarctic seabirds are sentinels of ecological change, and shifts in their infection dynamics may provide early warning of broader disruption in rapidly changing polar ecosystems (Hazen et al., 2019). Integrating virology, serology, and movement ecology will therefore be essential for

detecting hidden circulation, anticipating future outbreaks, assessing population-level consequences, and informing conservation strategies.

Materials and Methods

Sample collection

Fieldwork was conducted on King George Island, South Shetland Islands, Antarctica, primarily on the Fildes Peninsula and Ardley Island, ice-free coastal areas hosting breeding populations of multiple seabird species and forming part of a key biogeographic gateway between South America and the Antarctic Peninsula. Across three consecutive austral breeding seasons (2022/23, 2023/24, and 2024/25), we collected blood and swab samples from clinically healthy seabirds. In addition, swab samples were collected from dead birds found in the field. Individuals were captured by hand or using standard noose-based techniques at nests or in their immediate vicinity. Sampling targeted live Brown Skuas (*Stercorarius antarcticus*), South Polar Skuas (*Stercorarius maccormicki*), and Southern Giant Petrels (*Macronectes giganteus*) throughout the study area, and, to provide broader context, also included the three penguin species breeding locally (Adelie penguin *Pygoscelis adelie*, Gentoo penguin *Pygoscelis papua*, Chinstrap penguin *Pygoscelis antarcticus*). For live birds, blood samples from the brachial vein (50-200 µl) were collected for serological analyses and oropharyngeal and cloacal swabs (pooled) for molecular screening. Blood samples were collected in Sarstedt Microvettes (Microvette® 200 Serum CAT) stored cool and centrifuged within 15 hours. Separated blood cells and serum samples were kept frozen until further analyses. Swab samples were stored in PrimeStore MTM or Nucleoprotect VET (Macherey-Nagel, Germany) reagent and kept cool (<5 degrees) until further analyses. Sampling effort varied between species and seasons depending on colony accessibility, breeding phenology, and field logistics. An overview of seasonal sample sizes and sample type is provided in Table 1, more details (sample size per species is provided in Supplementary Table 1).

Movement data collection

To quantify migratory connectivity and breeding-season space use, we deployed archival light-level geolocators (C330 2.5 g, Migrate Technology Ltd.) and high-resolution GPS loggers or ARGOS satellite transmitters (PinPoint GPS Argos Solar L 16g, Lotek; and YAWL 11.4 g, Druid Technology) on a subset of adult Brown Skuas, South Polar Skuas, and Southern Giant Petrels. All tracked flying seabirds were individually marked with metal leg bands, either already present from previous years or newly fitted using uniquely engraved bands issued by the Vogelwarte Hiddensee, Germany. Geolocators were attached to these metal bands and retrieved, where possible, during the following breeding season. Device masses, including attachment material, remained below the commonly applied 3% body-mass guideline for seabird biologging (0.005 - 0.3 % for the light-level geolocators, and 0.025 - 1.33 % across species/device types), a threshold above which negative effects on foraging performance and breeding parameters become more likely in petrels and other seabirds (Phillips et al., 2003). GPS and ARGOS

devices were attached either by harness with a weak-link release (n = 6) or, in all remaining cases, externally to the back feathers using adhesive tape (Wilson & Wilson, 1989). While tracking-device effects can never be fully excluded, keeping tag loads low and using short-term external attachments reduces the likelihood of substantial behavioural impacts (Geen et al., 2019). Penguins were not banded. Detailed deployment procedures, attachment methods, deployment durations, and species-specific sample sizes are provided in Supplementary Material S2.

Table 1. *Total seasonal sampling effort and tracking deployments on King George Island, South Shetland Islands, Antarctica, across the 2022/23, 2023/24, and 2024/25 breeding seasons. Counts summarize all sampled focal seabird species and sympatric penguins combined. Live and dead birds sampled refer to individuals from which biological material was collected. Serum samples were used for serological analyses, swab samples for virological screening, and GPS and GLS columns indicate the number of tracking devices deployed and retrieved.*

Season	Live birds sampled	Dead birds sampled	Serum samples	Swab samples	GPS/Argos deployed	GLS deployed / retrieved
2022/23	153	0	142	153	0	0
2023/24	180	1	133	165	33	90/0
2024/25	185	25	163	208	28	0/38

Laboratory analyses

Extraction of nucleic acids and RT-qPCR screenings**:** Swab samples were stored in inactivation buffer that preserves nucleic acids immediately after retrieval (2022/23: Fischer Scientific RNAlater; 2023/24: Primestore MTM, Longhorn Diagnostics; 2024/25: Nucleoprotect VET, Macherey-Nagel). The analyses of the swab samples collected in season 2024/25 followed the description of the Primestore MTM-swab samples described in Lisovski et al. (2024b), and included RNA extraction and initial RT-qPCR screening that targets the matrix (M) protein gene of Alphainfluenzavirus influenzae. Positive samples were screened for the presence of the hemagglutinin (HA) 5 subtype and neuraminidase (NA) 1 subtype. In addition, an RT-qPCR, specific for the HA cleavage site of HPAIV H5 of clade 2.3.4.4b, was used to pathotype H5-positive samples (Hassan et al., 2022).

Whole-genome sequencing and sequence analyses: We followed the nanopore sequencing workflow initially described by King et al., (2020) with modifications on updated primer pairs and sequencing platform as applied by Halwe et al., (2025). Briefly, viral RNA was reverse-transcribed and amplified with influenza A–specific primers targeting conserved segment ends. Amplicons were purified and ~200 ng cDNA served as input applying the Rapid Barcoding Kit (SQK-RBK114, Oxford Nanopore Technologies, Oxford, UK) on a PromethION P2 Solo platform. High-accuracy basecalling (Dorado v7.9.8) was followed by demultiplexing, quality control, and trimming of low-quality and short reads. Data were subsequently

analyzed in Geneious Prime. Consensus sequences were generated via iterative mapping using Minimap2 (v2.24; Li, 2021) against curated reference genomes, followed by manual polishing and annotation. For three samples with Cq values between 23.7-24 in the initial RT-qPCR complete coding sequences were obtained. Generated sequence data have been deposited in Genbank and are publicly available under accession PZ386673 - PZ386696. Additional sequences used in this analysis were obtained from the EpiFlu™ database and are available as EPI_SET_260511vo under https://doi.org/10.55876/gis8.260511vo. Time-scaled phylogenies were reconstructed with the BEAST X (v10.5.0) software package (Baele et al., 2025) using a GTR GAMMA substitution model, as an uncorrelated relaxed clock with a lognormal distribution and coalescent constant population tree models. Phylogeographic calculations were inferred using Bayesian continuous trait models with sampling coordinates, depending on metadata provided with sequences using a Bayesian coalescent model. Maximum clade credibility trees with 10% post- burn-in posterior were generated with TreeAnnotator (v1.10.4) with node support robustness evaluated by posterior probabilities and 95% HPD intervals. The spatio-temporal diffusion models were analyzed and visualized using Spread (v.1.0.7).

Serology: All serum samples have undergone heat inactivation according to IATA regulations before shipment. The ID Screen® Influenza A Antibody Competition Multi-species and ID Screen® Influenza H5 Antibody Competition 3.0 Multi-species (Innovative Diagnostics, Grabels, France) were applied according to the manufacturer's instructions in a two-step approach to detect NP-specific and then, in the NP antibody-positive samples, to test for H5-specific antibodies.

Movement analyses

Light-level geolocation data**:** Light-level and temperature recordings from archival geolocators were downloaded and processed using a twilight-threshold workflow and Bayesian track estimation implemented in the R package SGAT (Wotherspoon et al., 2013). Raw light files were imported and twilight events were annotated using TwGeos (Lisovski et al., 2015). A known-location calibration at the breeding colony on Fildes Peninsula (58.96° W, 62.18° S) was used to estimate the effective solar zenith angle for each tag. Initial position estimates were obtained from threshold-based geolocation and used to initialize Bayesian track estimation, with the first and last part of each track constrained to the colony location to anchor the reconstruction. We then fit an SGAT threshold model, following recommended practices for threshold based geolocation (Lisovski et al., 2020), with a Modified Gamma/Gamma twilight likelihood (shape/scale parameters $\alpha = (2, 0.15)$, $\beta = (1, 0.10)$), and combined this with a sea-surface temperatures (SST) informed spatial likelihood: per-twilight SSTs inferred from the tag's temperature series within ±8 h were matched to environmental SST layer (NCEP-NCAR Reanalysis 1 data provided by the NOAA PSL, Boulder, Colorado, USA (Kalnay et al., 1996)). Proposals were multivariate normal, initially $\Sigma = \mathrm{diag}(0.005, 0.005)$, then tuned using chain covariance ($s = 0.25$). The MCMC was run in stages (tuning) followed by a main run of 2,000 iterations, retaining posterior daily locations. We summarized tracks as median daily positions with 95% credible intervals.

GPS/Argos tracking data**:** GPS/Argos tracks from breeding Brown Skuas, South Polar Skuas, and Southern Giant Petrels were recorded at variable sampling intervals, nominally every 10 min, with higher fix frequency when movement and battery status allowed. Raw tracking data were standardized and projected to a custom equidistant conic projection (+proj=eqdc +lat_1=-80 +lat_2=0 +lon_0=-57) to allow distance-based analyses. For each individual, the nest location was estimated as the centroid of the densest cluster of locations around the deployment site. Distances between each GPS fix and the corresponding nest were then calculated in kilometres.

To delineate foraging trips, locations within a species- and deployment-specific threshold distance from the nest (500 m) were classified as nest attendance, and consecutive fixes beyond this threshold were grouped into trips. A new trip was defined when an individual departed from the nest area and subsequently returned. Trips with fewer than four locations or without a clear outbound and return phase were excluded from further analyses. The resulting dataset consisted of timestamped GPS locations linked to nest distance, trip identity, and individual metadata, and formed the basis for analyses of breeding-season foraging distance, habitat use, and colony connectivity.

Global migratory connectivity**:** Global migratory connectivity was quantified from annual light-level geolocator tracks reconstructed for Brown Skuas, South Polar Skuas, and Southern Giant Petrels breeding on King George Island. For each species, posterior daily locations were used to visualize broad migratory routes and to describe seasonal changes in spatial connectivity relative to the breeding colony. Specifically, we calculated the geodesic distance between each daily position and the breeding site on King George Island and summarized these distances through time to quantify colony connectivity across the annual cycle. This allowed direct comparison among species in the timing and extent of migratory displacement.

To identify periods and regions where tracked birds were most likely to overlap with coastal or terrestrial bird communities outside Antarctica, we additionally calculated the minimum distance of each reconstructed location to the nearest shoreline. Locations within 50 km (within the estimated accuracy of light-level geolocation (Lisovski et al., 2012; Phillips et al., 2004) of the shoreline were classified as potential contact points with terrestrial or nearshore ecosystems. This metric was used as a conservative proxy for opportunities for ecological contact beyond pelagic habitat use. To assess when potential ecological contact with terrestrial systems was most likely, we summarized the number of geolocator positions within 50 km of the shoreline over time for each species, providing a temporal index of possible land-associated overlap prior to return to Antarctica.

Local connectivity**:** Local connectivity during the breeding season was quantified from GPS tracks of Brown Skuas, South Polar Skuas, and Southern Giant Petrels breeding on King George Island. For each individual, distances between GPS fixes and the estimated nest location were calculated after projection to an equidistant coordinate system, and only locations associated with foraging behaviour were retained for subsequent analyses (low-movement foraging: speeds < 0.5 km/h between two fixes). To summarize the upper spatial extent of breeding-season movements while accounting for unequal fix

intervals, we calculated an individual time-weighted 99th percentile of distance to the nest. This metric was used as a robust estimate of maximum routine foraging range that captures extensive movements while reducing sensitivity to isolated outlier locations.

To translate observed foraging movements into a broader spatial estimate of regional connectivity, we constructed a network of potential breeding nodes across the Antarctic Peninsula and adjacent sub-Antarctic islands and evaluated whether empirically observed foraging distances could span the distance between nodes (clustered colonies). Connectivity between nodes was weighted by the probability that an individual's observed time-weighted 99th percentile foraging distance equaled or exceeded the geographic distance separating two nodes. This produced a probabilistic connectivity network in which stronger edges indicate a greater likelihood that breeding-season movements could connect colony areas within the region, including potential links extending beyond the Antarctic Peninsula toward South Georgia.

Feeding habitat use**:** To characterize potential differences in exposure-related foraging ecology during breeding, GPS locations classified as foraging were assigned to either marine or terrestrial/coastal habitat based on their spatial position relative to land. For each individual, we calculated the proportion of low-movement foraging locations in each habitat class and summarized these proportions at the species level. This metric provides a simple spatial proxy for likely foraging environment and potential contact context, rather than a direct measure of diet.

Declarations

Data, Materials, and Software Availability

Table with sampling information, laboratory results, as well as tracking device deployment upload as supplement for review. All data and code will aslo be uploaded to a repository (Zenodo) during the reviewing process. Raw GLS data and estimated locations as well as GPS locations will be uploaded to Movebank.org.

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Figures

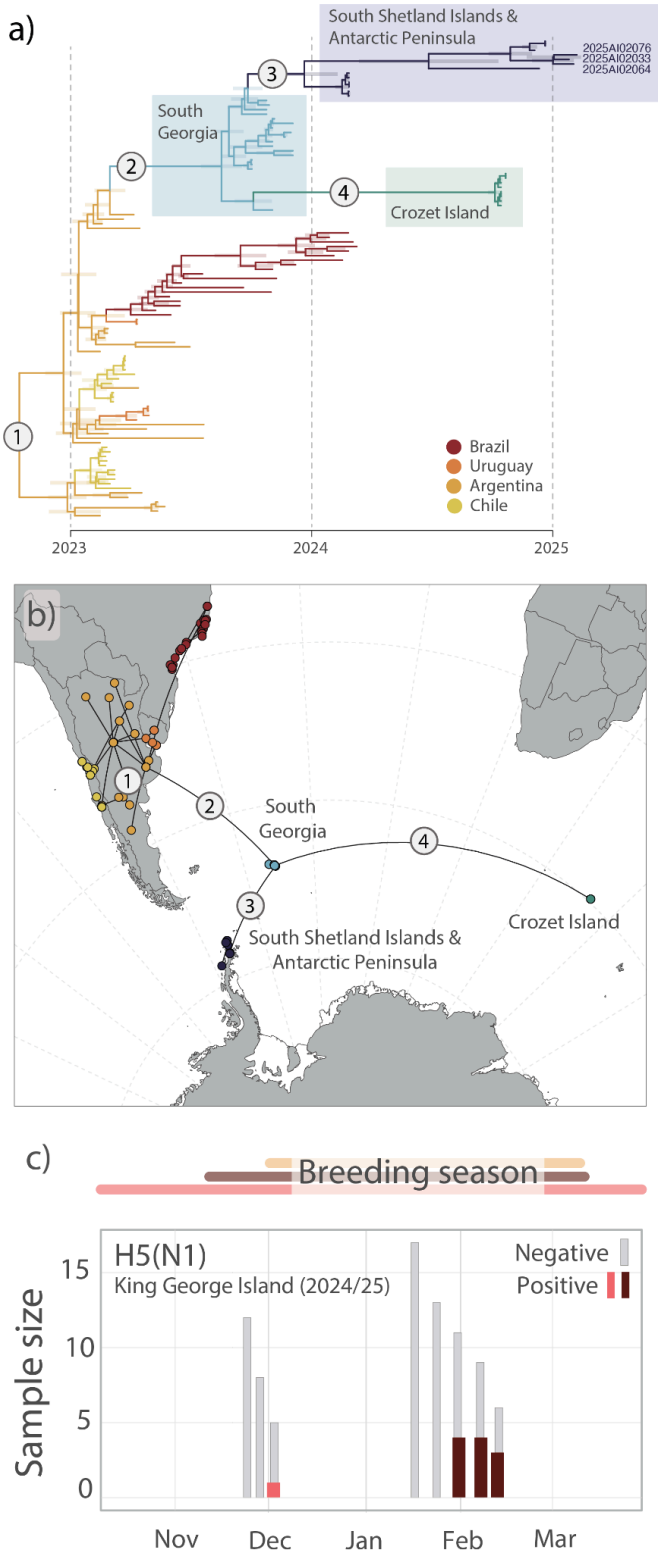


Figure 1

(a) Maximum clade credibility tree of high pathogenicity avian influenza viruses (HPAIV) of subtype H5N1 depicting the evolvement of major geographic clusters from a subset of South American viruses (Chile, Argentina, Uruguay, and Brazil [yellow to red coloring]) into sub-Antarctic (South Georgia [blue], Crozet Island [green]) and Antarctic regions (South Shetland Islands, Antarctic Peninsula [purple]). Analyses are based on concatenated coding full-length sequences of H5N1 segments, 2023 and 2025. The three sequences from

Brown Skuas breeding on King George Island, South Shetland Islands (late breeding season 2025), are highlighted within the South Shetland Islands & Antarctic Peninsula clade (purple). (b) Phylogeographic distribution and inferred movement pathway of HPAIV H5N1 lineages, illustrating the likely eastward progression of the virus from South America (1) through South Georgia (2) to the Antarctic Peninsula (3) and further east to the sub-Antarctic islands (4). (b) Geographic distribution and inferred movement pathway of H5N1 lineages, illustrating the likely eastward progression of the virus from South America (1) through South Georgia (2) to the Antarctic Peninsula (3) and further east to the sub-Antarctic islands (4). (c) Number of RT-qPCR screenings specific for subtype H5 tests performed on King George Island between December 2024 and February 2025, with bars indicating negative (grey) and positive (red) results for South Polar Skuas (yellow, no positives), Brown Skuas (brown) and Southern Giant Petrels (rosa).

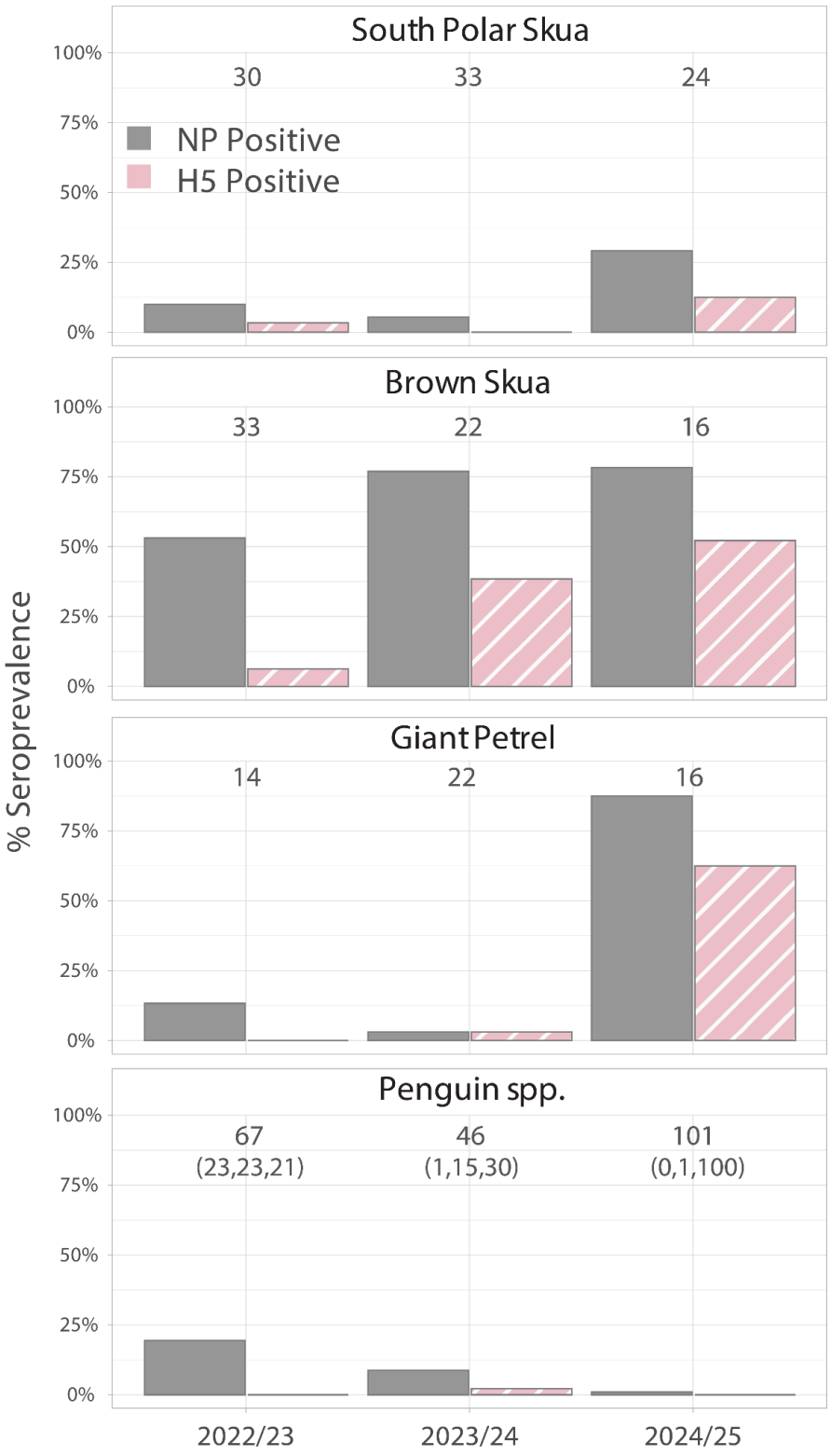


Figure 2

Seroprevalence of influenza A virus antibodies across three breeding seasons. Bars show the percentage of sampled individuals testing seropositive for antibodies against influenza A virus' nucleoprotein antibodies (NP; grey) and those specific for subtype H5-specific antibodies (H5; red) in apparently healthy South Polar Skua, Brown Skua, and Southern Giant Petrel (upper three panels), and in penguins (lower panel) during the

2022/23, 2023/24, and 2024/25 breeding seasons. Sample sizes (n) are given in each panel; for penguins, values in brackets indicate the species-specific sample sizes (Adélie, Chinstrap, Gentoo).

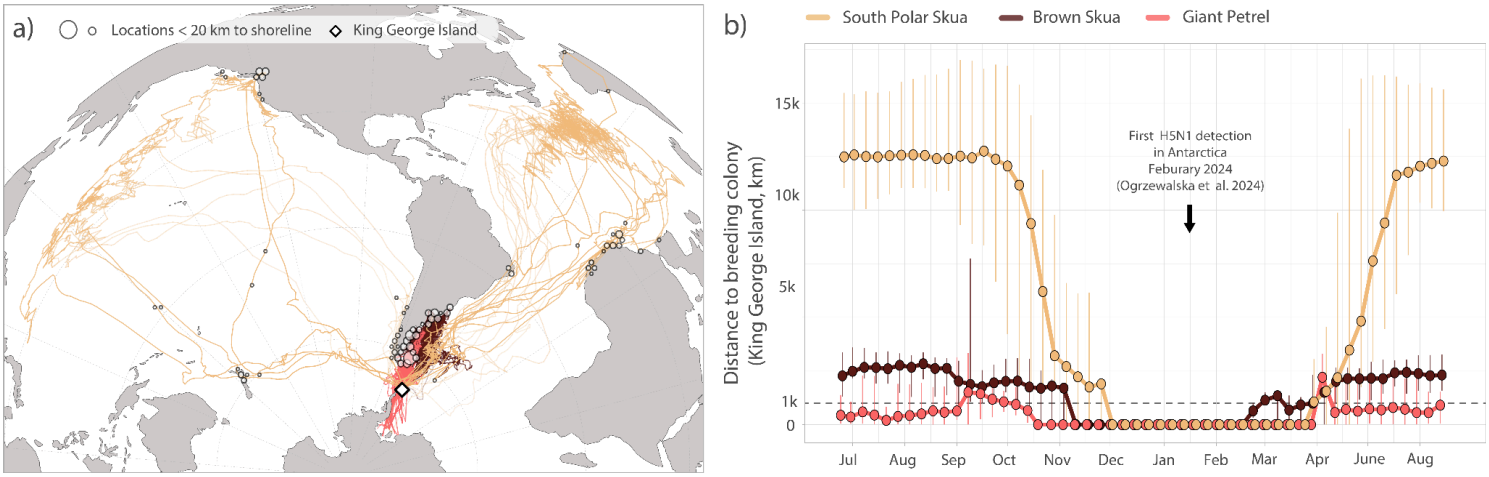


Figure 3

(a) Migratory routes of South Polar Skuas, Brown Skuas, and Southern Giant Petrels equipped with light-level geolocators at breeding colonies on King George Island, South Shetland Islands, Antarctica (diamond). Lines show individual tracks, with white circles (size corresponds to number of individuals) marking positions within 50 km of the shoreline, indicating potential contact with coastal and terrestrial bird communities along the migratory flyways. (b) Mean distance (± SD) of tracked individuals from their breeding colony over time, illustrating species-specific migratory connectivity and the seasonal timing of movements. The arrow marks the first recorded detection of highly pathogenic avian influenza (H5N1) in Antarctica (Ogrzewalska et al., 2024).

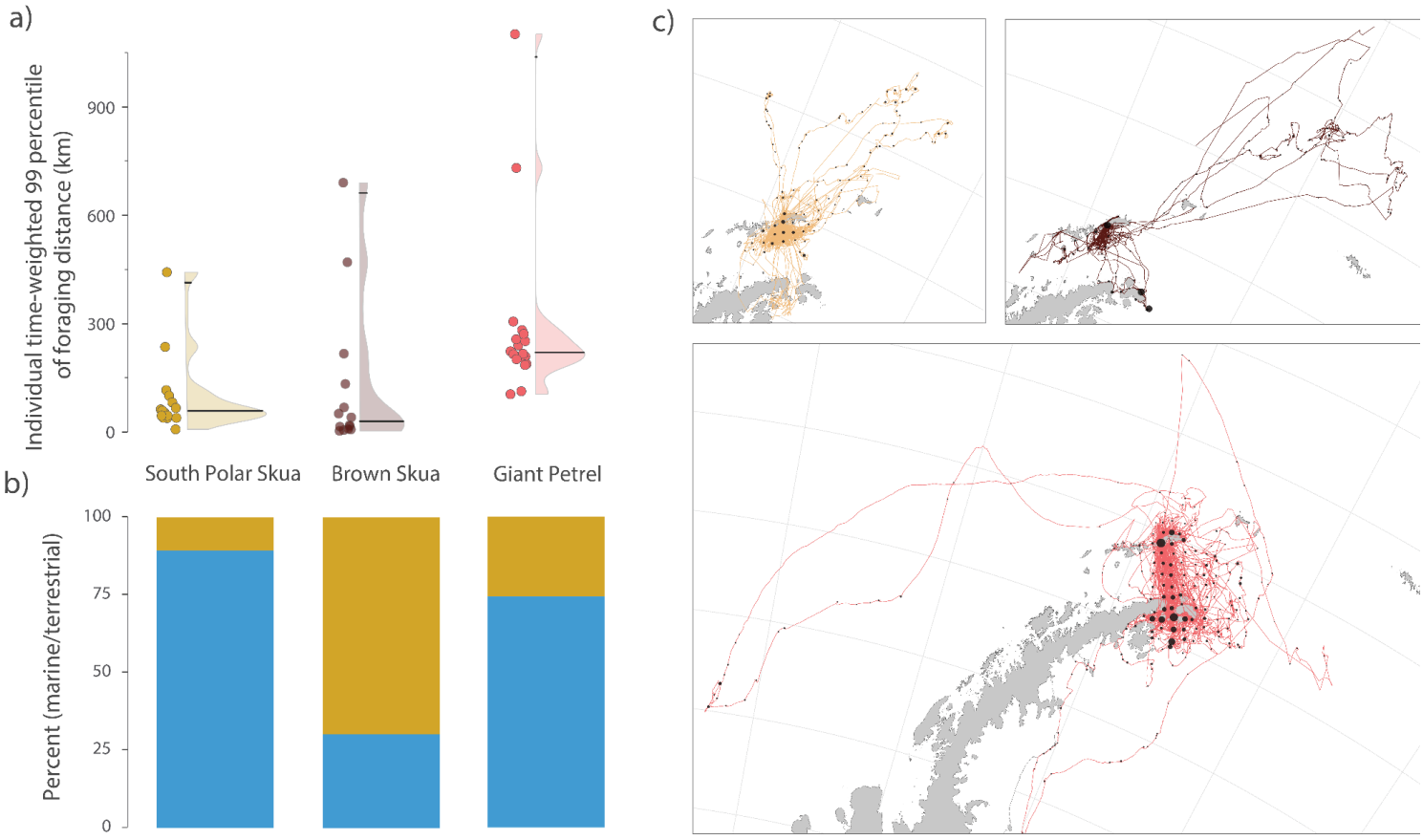


Figure 4

Foraging distances, foraging environment, and foraging tracks. (a) Individual time-weighted 99th percentile distance to the breeding colony (km) for South Polar Skuas, Brown Skuas, and Southern Giant Petrels; points are individuals and violins show the species-level distribution. (b) Proportion potential foraging locations classified as marine vs. terrestrial, indicating the expected foraging environment. (c) Individual GPS/Argos tracks South Polar Skuas, Brown Skuas, and Southern Giant Petrels (same spatial scale), with clustered foraging locations derived from consecutive slow-movement fixes (points scaled by foraging fixes within a grid-cell of 25 km).

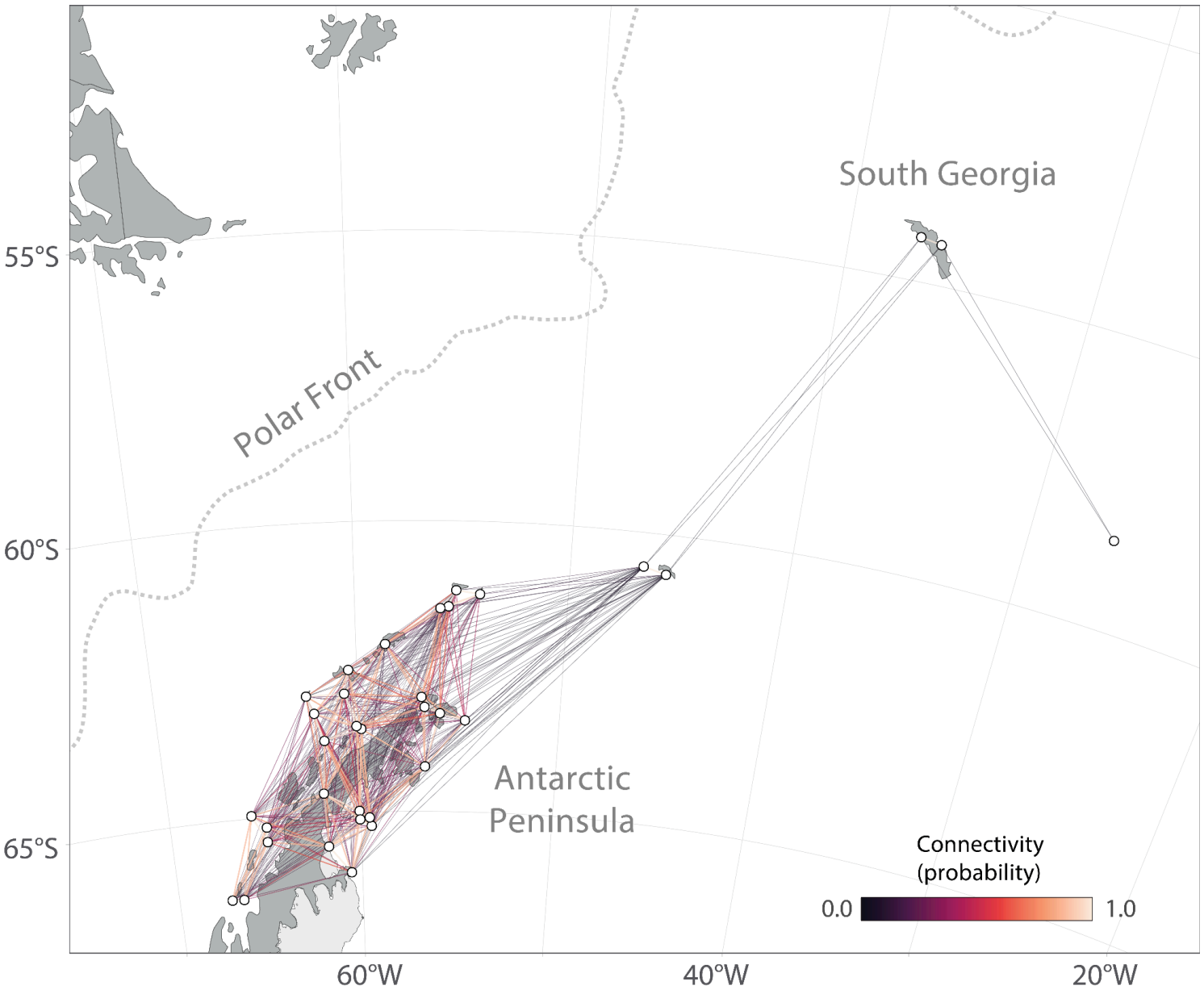


Figure 5

Simulated spatial connectivity among potential breeding colonies (clusters of ice-free areas) across the Antarctic Peninsula and surrounding islands south of the Polar Front; link colour indicates connectivity probability (0–1) based on repeated simulations using species- and individual specific foraging-distance distributions.

Supplementary Files

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- SupportingInformation.docx