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Coastal connectivity of marine predators over the Patagonian Shelf during the highly pathogenic avian influenza outbreak

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SUMMARY

"Animal movement and population connectivity are key areas of uncertainty in efforts to understand and predict the spread of infectious disease. The emergence of highly pathogenic avian influenza (HPAI) in South America poses a significant threat to globally significant populations of colonial breeding marine predators in the South Atlantic. Yet, there is a poor understanding of which species or migratory pathways may facilitate disease spread. Compiling one of the largest available animal tracking datasets in the South Atlantic, we examine connectivity and inter-population mixing for colonial breeding marine predators tagged at the Falkland Islands. We reveal extensive connectivity for three regionally dominant and gregarious species over the Patagonian Shelf. Black-browed albatrosses (BBA), South American fur seals (SAFS) and Magellanic penguins (MAG) used coastal waters along the Atlantic coast of South America (Argentina and Uruguay). These behaviours were recorded at or in close proximity to breeding colonies and haul-out areas with dense aggregations of marine predators. Transit times to and from the Falkland Islands to the continental coast ranged from 0.2–70 days, with 84% of animals making this transit within 4 days - a conservative estimate for HPAI infectious period. Our findings demonstrate BBA, SAFS and MAG connectivity between the Falkland Islands and mainland South America over an expansive spatial network and numerous pathways, which has implications for infectious disease persistence, transmission and spread. This information is vital in supporting HPAI disease surveillance, risk assessment and marine management efforts across the region."

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ECOGRAPHY

Research article

Coastal connectivity of marine predators over the Patagonian Shelf during the highly pathogenic avian influenza outbreak

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Animal movement and population connectivity are key areas of uncertainty in efforts to understand and predict the spread of infectious disease. The emergence of highly pathogenic avian influenza (HPAI) in South America poses a significant threat to globally significant populations of colonial breeding marine predators in the South Atlantic. Yet, there is a poor understanding of which species or migratory pathways may facilitate disease spread. Compiling one of the largest available animal tracking datasets in the South Atlantic, we examine connectivity and inter-population mixing for colonial breeding marine predators tagged at the Falkland Islands. We reveal extensive connectivity for three regionally dominant and gregarious species over the Patagonian Shelf. Black-browed albatrosses (BBA), South American fur seals (SAFS) and Magellanic penguins (MAG) used coastal waters along the Atlantic coast of South America (Argentina and Uruguay). These behaviours were recorded at or in close proximity to breeding colonies and haul-out areas with dense aggregations of marine predators. Transit times to and from the Falkland Islands to the continental coast ranged from 0.2–70 days, with 84% of animals making this transit within 4 days - a conservative estimate for HPAI infectious period. Our findings demonstrate BBA, SAFS and MAG connectivity between the Falkland Islands and mainland South America over an expansive spatial network and numerous pathways, which has implications for infectious disease persistence, transmission and spread. This information is vital in supporting HPAI disease surveillance, risk assessment and marine management efforts across the region.

Keywords: Animal movement, Avian influenza, connectivity, Falkland Islands, HPAI

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Introduction

Animal movement plays a fundamental role in shaping the ecological and evolutionary dynamics of wild populations (Morales et al. 2010, Sutherland et al. 2013). Spatial connectivity between populations is essential for maintaining genetic diversity and long-term population persistence and viability (Bowler and Benton 2005, Bicknell et al. 2012). However, animal movements can also facilitate the dispersal of pathogens they host via direct or indirect contact between infected and susceptible individuals, posing a significant threat to population health and conservation status (Altizer et al. 2011). Movement behaviours (i.e. foraging, prospecting, resting and transit) play different roles in disease spread (Boulinier et al. 2016), and characterising these dynamics is critical to understand how pathogens spread through spatial networks (Daversa et al. 2017).

Since 2021, a highly pathogenic avian influenza (HPAI) panzootic has had dramatic impacts on wild populations around the world, causing mass mortalities in numerous seabird and marine mammal populations (Falchieri et al. 2022, Klaassen and Wille 2023, Leguia et al. 2023, Lane et al. 2024). For instance, the virus has devastated several seabird populations in Europe (i.e. northern gannets *Morus bassanus* and great skuas *Stercocarius skua*), with evidence suggesting declines of up to 75% in certain populations (Tremlett et al. 2024). Driven by connectivity over vast spatial scales, HPAI is spreading at unprecedented rates (Boulinier 2023, Klaassen and Wille 2023, Jeglinski et al. 2024) and is beginning to impact geographically remote, high-latitude marine predator communities in the Southern Hemisphere, which have traditionally been insulated from periodic HPAI outbreaks affecting wild populations in Eurasia, Africa and North America (Dewar et al. 2023b). The virus first spread to the Pacific coast of South America (i.e. Peru and Colombia) in late 2022, facilitated by avian migratory pathways and connectivity with afflicted populations in North America. Following its introduction to South America, HPAI rapidly spread to seabird and pinniped communities distributed along the Pacific (Ecuador, Peru and Chile) coastline, spreading to the southern tip of the continent and around to populations distributed along the Atlantic (Argentina, Uruguay and Brazil) coast (Banyard et al. 2023, Plaza et al. 2024). HPAI reached South Georgia Island at the beginning of the seabird nesting period in October 2023, causing die-offs of southern elephant seals *Mirounga leonine*, Antarctic fur seals *Arctocephalus gazella*, and progressively impacting seabird populations including brown skuas *Stercorarius antarcticus* and wandering albatrosses *Diomedea exulans* (Banyard et al. 2023, British Antarctic Survey 2024). Despite large-scale concurrent outbreaks in coastal South America and further south, HPAI outbreaks in the Falkland Islands have been sporadic and unpredictable thus far, with multiple local infections identified beginning in late October 2023 (Banyard et al. 2023).

The Patagonian Shelf Large Marine Ecosystem (LME) spans the Atlantic coast of South America, encompassing the continental shelf areas adjacent to Uruguay, Argentina and the Falkland Islands. It is regarded as one of the most productive marine ecosystems in the world, supporting a diverse range of colonial breeding marine predators (i.e. pinnipeds, penguins and flying seabirds) (Croxall and Wood 2002, van der Grient et al. 2023). For these animals, the Falkland Islands are one of the most important breeding locations in the Patagonian Shelf LME (Baylis et al. 2019b, 2021). For example, the Falkland Islands are home to approximately 75% of the world's black-browed albatross *Thalassarche melanophris* population, 50% of the global South American fur seal *Arctocephalus australis* population, and globally significant populations of southern rockhopper *Eudyptes chrysocome*, gentoo *Pygoscelis papua* and Magellanic *Spheniscus magellanicus* penguins (Baylis et al. 2013a, b, 2019a, Wakefield et al. 2014).

HPAI is an emerging threat to these globally significant seabird and pinniped populations (Bennison et al. 2023, Falkland Islands Government 2024). Biological risk assessments seeking to identify spatial and temporal components of HPAI spread in the region have been hampered by a limited understanding of animal movement, specifically, population connectivity and migration pathways (Dewar et al. 2023a). Uncertainty about which candidate species or spatial networks act as vectors of disease spread can undermine predictive modelling efforts (Webster et al. 2017), ultimately affecting disease surveillance and the development of adaptive conservation and management strategies (Bestley et al. 2020, Murphy et al. 2021).

In this study, we compile an extensive multi-year telemetry dataset for regionally representative colonial marine predators over the Patagonian Shelf to assess land-associated population connectivity and networks for disease spread. Using data from numerous seabird and pinniped species tagged at the Falkland Islands with Platform Terminal Transmitters (PTT) and Global Positioning System (GPS) devices, we quantify residency in adjacent South American coastal waters (Argentina and Uruguay) and identify potential hotspots of connectivity between populations. Our findings can support HPAI risk assessments in the region and improve capacity to predict future threats posed by new infectious diseases, guiding surveillance efforts and population viability assessments.

Material and methods

In this study, we compiled GPS and PTT satellite telemetry datasets available for nine colonial breeding marine predators at the Falkland Islands. This included three pinniped species (South American fur seal; South American sea lion *Otaria flavescens* and southern elephant seal), four penguin species (Magellanic; gentoo; southern rockhopper and king *Aptenodytes patagonicus*) and two species of flying seabirds (black-browed albatross and sooty shearwater *Ardenna grisea*). While light-based geolocation (GLS) tracking data are also available for some penguin and flying seabird species, these data were excluded due to low spatial precision over regional scales (cf. the Supporting information for full details of compiled tracking data). Following visual inspection of tracking data from each of the nine species, only black-browed albatrosses (BBA), South American fur seals (SAFS) and Magellanic penguins (MAG) showed evidence of regional-ranging movements to coastal waters in South America. Therefore, we restricted the tracking dataset to these three species (Table 1). Animal handling and tag deployment procedures are available in source literature (Campioni et al. 2017, Baylis et al. 2019b, Riaz et al. 2023) and the Supporting information.

All data processing and analyses were performed using R statistical software (www.r-project.org). Raw location data for the three species were assembled, plotted and visually inspected. Data were then subjected to quality-control checks adapted from the framework provided in Ropert-Coudert (2020). Near-duplicate location estimates were removed (locations occurring within 2 minutes for PTT data and 10 seconds for GPS data). We also removed locations implying unrealistic travel speeds within movement trajectories (exceeding 4 m s^{-1} for SAFS, 10 m s^{-1} for MAG and 20 m s^{-1} for BBA). With the quality-controlled data for the three species, we fitted a random walk state-space model (SSM) using the 'aniMotum' package (Jonsen et al. 2023). This approach provides location estimates at regularised time-steps along movement trajectories, while also accounting for observation errors in tracking data (Jonsen et al. 2023). All PTT data for SAFS and MAG were regularised at 1 hour time steps, while GPS data for SAFS and BBA were regularised at 15-min and 10-min time steps, respectively. The programming of these species- and device-specific time-steps within the movement model were chosen based on visual and comparative assessment of predicted location estimates with the raw location fixes for each individual (Riaz et al. 2021, 2023). The final SSM dataset contained location information for 460 individuals, which comprised of 341 BBA (all adults), 74 SAFS (19 adult males, 35 adult females, 20 pups) and 45 MAG (40 adults, 5 fledglings) (Table 1). Tracking data was available throughout most of the annual cycle for SAFS, while BBA and MAG tracking data were restricted to the summer breeding and pre-moult period (Supporting information).

To quantify movement along predicted location estimates and assess where individuals spend disproportionally more or less time, we also fitted a time-varying move persistence (γ_t) model to SSM location data (Jonsen et al. 2023). This indexed changes in movement behaviour as a continuous variable (ranging from 0–1) based on autocorrelation in both speed and direction (Jonsen et al. 2023). Relatively low γ_t values are indicative of residency (low speed and directionality) in movement trajectories, typically encompassing rest or more stationary foraging behaviours. Conversely, relatively high values represent more directed movements (high travel speeds and linear directionality), and encompass transit and larger-scale searching movements (Jonsen et al. 2019, Riaz et al. 2021, Grecian et al. 2022). For each individual, values were normalised, rescaling all estimates to span the full range (0 through to 1). This approach offers a more detailed and nuanced quantification of changes in behaviour along movement trajectories, and enables comparison between species which move over different spatiotemporal scales (Jonsen et al. 2023).

With the processed movement dataset for BBA, SAFS and MAG, we quantified the degree of connectivity between the Falkland Islands and adjacent South American coastal habitats. As colonial breeding and central-place marine predators, dense aggregations of seabirds and pinnipeds predictably occur in coastal regions (Miloslavich et al. 2011). The Atlantic coast of South America is home to three pinniped and 18 seabird species which live and breed (> 300 colonies) in high densities, and additionally, hosts many other migratory species which use the habitat as a staging area for travel to more distant foraging/breeding sites (i.e. sub-Antarctic and Antarctic regions) (Miloslavich et al. 2011). The frequency and likelihood of wildlife exchange (direct and proximate interactions) within these areas make them high-risk for disease persistence and transmission between populations/colonies. To date, numerous HPAI outbreaks among colonial seabird and pinniped populations (i.e. sea lions,

Table 1. Summary of satellite telemetry data and tracking efforts for the three colonial breeding marine predators at the Falkland Islands. Some BBA and MAG individuals were tracked over multiple life history stages (i.e. incubation/chick-rearing and chick-rearing/moult). The total number of location estimates after state-space model (SSM) data processing are also provided. See the Supporting information for details of the number and proportion of colonies tracked.

Species	Demographic	Breeding stage	No. individuals and device type	Date range	SSM location estimates	Data source
South American fur seal (SAFS)	adult male	non-breeding	19 (PTT)	2023	32 579	this study
	adult female	lactation	35 (18 GPS and 17 PTT)	2018–2019	24 125 GPS 24 362 PTT	Baylis et al. 2019b, Riaz et al. 2023, this study
	pup	initial dispersal	20 (PTT)	2022–2023	43 072	this study
Black-browed albatross (BBA)	adult	incubation/ chick-rearing	341 (GPS)	2008–2022	347 265	Campioni et al. 2017, Baylis et al. 2019b, this study
Magellanic penguin (MAG)	adult	chick-rearing/ pre-moult	40 (PTT)	2014–2016	59 568	Baylis et al. 2019b, this study
	fledgling	initial dispersal	5 (PTT)	2015	4133	Tierney unpubl. data, this study

elephant seals, gulls *Larus* spp. and terns *Sterna* spp.) have been recorded along the Atlantic coastline (for example – refer to the Supporting information in Rimondi et al. (2024) and Fig. 1 in Plaza et al. (2024)). While at-sea connectivity, such as species overlap and exchange in foraging grounds, may also play a role in HPAI spread, the regional scope of our dataset (i.e. limited to Falkland Islands data) did not support these analyses.

To quantify coastal connectivity, we calculated the proportion of time each tracked individual spent in connection with the South American coastline. This was defined as any animal location recorded between land and the limit of the territorial sea maritime boundary (12 nautical miles from baseline, ~ 25 km). This spatial delineation was chosen primarily because it was considered to be a reasonable measure of distance to land where high densities and aggregations of colonial breeding marine predators are likely to occur. As an additional justification, the boundary is also relevant to national marine conservation and management efforts (Kraska et al. 2015). To understand the temporal components of connectivity, we also calculated the time taken for individual animals to travel between the coastal habitats of the Falkland Islands and South America.

To identify areas where and when individuals were likely to be resident in coastal South America, we used the continuous behavioural index of persistence (γ_t) in movement trajectories. The γ_t parameter is traditionally used to quantify behavioural states at-sea, with low γ_t assumed to represent area-restricted search (ARS) foraging behaviours (Jonsen et al. 2019, Grecian et al. 2022, Shuert et al. 2022). However, areas of low γ_t may also represent resting or haul-out (i.e. land-based resting for pinnipeds) behaviours (Riaz et al. 2021, Thums et al. 2022, Oosthuizen et al. 2022). We defined land-associated residency behaviours as any location either over land or within 1 km of land where normalised γ_t values were < 0.5. Our approach summarising γ_t into a binary measure was considered pragmatic to calculate discrete land-associated behavioural states (Thums et al. 2022). Finally, the individual tracks reaching the coast were inspected for evidence of haul-out or roosting behaviour (Kralj et al. 2023). To assess evidence of intra-specific and inter-colony interactions across the Patagonian Shelf LME, spatial information of all known BBA, SAFS and MAG breeding and haul-out sites in the region were collated from published sources (Supporting information) (Crespo et al. 2015, Phillips et al. 2016, Franco-Trecu 2017, Dodino et al. 2022, Garcia-Borboroglu et al. 2022, Millones et al. 2022, Raya Rey et al. 2022).

Results

Black-browed albatrosses, SAFS and MAG were distributed in close connection with South American breeding/haul-out sites, where conspecifics and other colonial marine predators

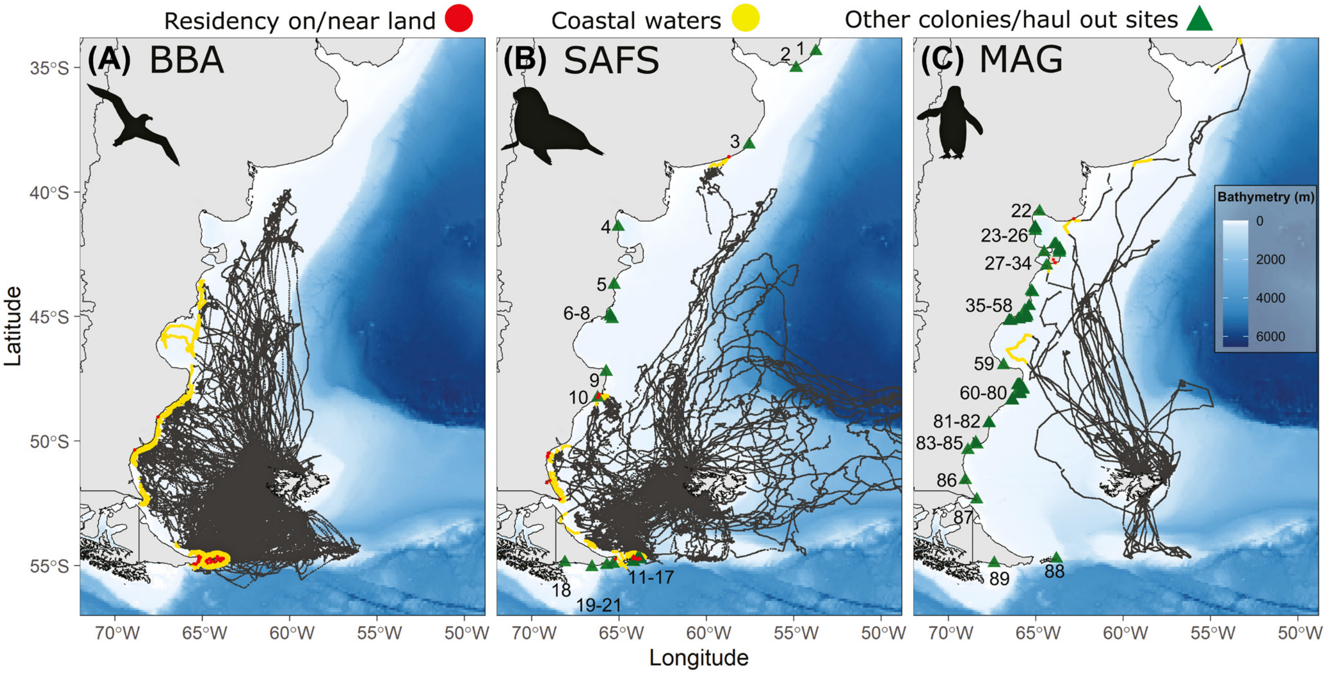

Figure 1. State-space model (SSM) location estimates for BBA (n = 341), SAFS (n = 74) and MAG (n = 45) individuals tracked at the Falkland Islands . Dark grey points represent all SSM locations estimates outside the coastal waters of Argentina and Uruguay, delineated as the boundary between land and the limit of the territorial sea (12 nautical miles from baseline). Yellow points indicate all location estimates within this coastal boundary, while red points illustrate residency on/near land. Green triangles (and associated numbers) summarise other known breeding or haul-out sites across the southern Patagonian Shelf region for these three species (Supporting information). Bathymetric gradients displayed were created using the 'ggOceanMaps' package (Vihtakari 2022).

congregate (Fig. 1). For these three species, transit times to and from the Falklands Islands – South American coast took up to 70 days for some individuals, although the vast majority (84%) made this trip within four days. Notably, individuals of BBA, SAFS, and MAG that migrated to coastal South America also made return trips to the Falkland Islands. While the number of individuals transiting between coastal waters is influenced by the coverage of the tracking data (Supporting information, Table 1), we found connectivity occurred throughout the annual cycle (Fig. 2).

Black-browed albatrosses displayed a high degree of connectivity (32% of individuals) extending along the east coast of Argentina from Staten Island to Peninsula Valdes (approximately −55° to −44°S) (Fig. 1). These individuals spent an average of 13.6% of their trips (36.7 hours) in Argentine coastal waters (means and 95% CI provided in Table 2). Connectivity was particularly pronounced in waters surrounding Staten Island, which hosted 88 BBA individuals (81% of all individuals exhibiting connectivity). Most individuals performed several foraging trips between the Falkland Islands and South America, with transit times lasting < 5 days in duration (Fig. 2). Staten Island was also an important area of residency for 25 (28%) of these individuals. While we did not find any evidence of BBA roosting on land in South America, individuals displayed nearshore rafting. Two BBA individuals also recorded these behaviours slightly further north along the Argentine coast (−52° to −49°S) (Fig. 1). The mean duration individuals spent in nearshore residency was 0.8 hours (0.4% of trips), although this lasted up to 5 hours for some individuals in Argentina (Table 2).

Of all SAFS individuals tracked, 17 (23%) were recorded in coastal Argentine waters (Fig. 1 and 2). These 17 individuals comprised of all demographic groups examined (males, females and pups) (Supporting information). The mean proportion of time spent in Argentine coastal waters was 22% (366 hours) (Table 2). Locations in Argentine coastal waters were primarily concentrated (n = 14 individuals) around the breeding/haul-out sites at Staten Island (Fig. 1 icon 11–17, Supporting information), but also extended northwards along the coastline to the SAFS haul-out at Islote del Cabo (Fig. 1 icon 10, Supporting information). Inbound/return migrations from South America to the Falkland Islands were recorded for both breeding females and non-breeding males, and generally took between 2–5 days (Fig. 2). Most of the SAFS recorded in this region of southern Argentina also hauled-out on land (n = 12), with 10 males hauling out on Staten Island (in multiple locations), one male hauling out at Islote del Cabo and one pup hauling out at multiple locations between these sites (−54° to −51°S) (Fig. 1, Supporting information). One male was also recorded resting in northern Argentinian waters, near the haul-out site at Mar Del Plata (Fig. 1 icon 3, Supporting information). On average, haul-out periods lasted 74 h in duration, although one male was hauled-out for over 13 days on Staten Island (Table 2).

For MAG, five individuals (three fledglings and two adults; 11% of all individuals) were recorded in close proximity to South America (Fig. 1). On average, these individuals spent 13% (104 h) of their trip in these coastal areas (Table 2). All five MAG individuals were recorded nearby to other MAG breeding sites (Fig. 1 icons 22–80, Supporting information) in coastal regions of Argentina, and two individuals ventured into more northern waters located in Argentina and Uruguay. Two individuals were recorded resting on land in northern Argentina, with one at Peninsula Valdes for over one day in duration (Fig. 1 icons 27–34, Supporting information). One MAG adult returned from coastal Argentine waters to the Falklands Islands in ~ 6 days (Fig. 2).

Discussion

This study is the first to quantitatively assess spatiotemporal connectivity of colonial marine predators over the Patagonian Shelf. By compiling the largest dataset available for marine predators tagged at the Falkland Islands to date, we reveal a high degree of coastal connectivity and evidence for interpopulation mixing for BBA, SAFS and MAG – three highly abundant and gregarious colonial marine predators within the Patagonian Shelf LME. Our findings improve understanding of the candidate species and spatial networks which may facilitate the spread of HPAI and other infectious diseases from South America. This study represents an important first step in developing evidence-based disease risk assessments capable of evaluating geographic vulnerabilities and predicting disease spread across space and time in wildlife populations.

In this study, we show Falkland Island populations of BBA, SAFS and MAG have extensive connectivity with adjacent South American coastal habitats. All species used nearshore habitats along the coast of Argentina, with MAG also migrating further north over the Patagonian Shelf into Uruguayan waters in late autumn (May). Both SAFS and MAG have an extensive and highly abundant distribution along the Atlantic coast of South America from Argentina to Uruguay (Schiavini et al. 2005, Stokes et al. 2014, Crespo et al. 2015, Franco-Trecu 2015), with over 80 breeding and haul-out locations (Fig. 1). While there are no known BBA breeding colonies in Argentina (Phillips et al. 2016), albatrosses tracked at colonies in the South Atlantic regularly use these productive coastal waters for foraging and prospecting (Croxall and Wood 2002, Clay et al. 2019). Our study provides evidence that BBA, SAFS and MAG from the Falkland Islands likely interact with conspecifics in South America, particularly in densely populated terrestrial (breeding colonies/haul-out sites) and nearshore environments. Furthermore, all species were capable of transiting between South America and the Falkland Islands within 4–7 days, an estimate of HPAI infectious period according to experimental studies conducted on multiple gull species (Brown et al. 2008, Ramis et al. 2014). This demonstrates a substantial risk of HPAI and other pathogens spreading from South America to colonial breeding marine predator populations at the Falkland Islands (or vice versa), confirmed by multiple case detections in BBA (Falkland Islands Government 2024). While the first case

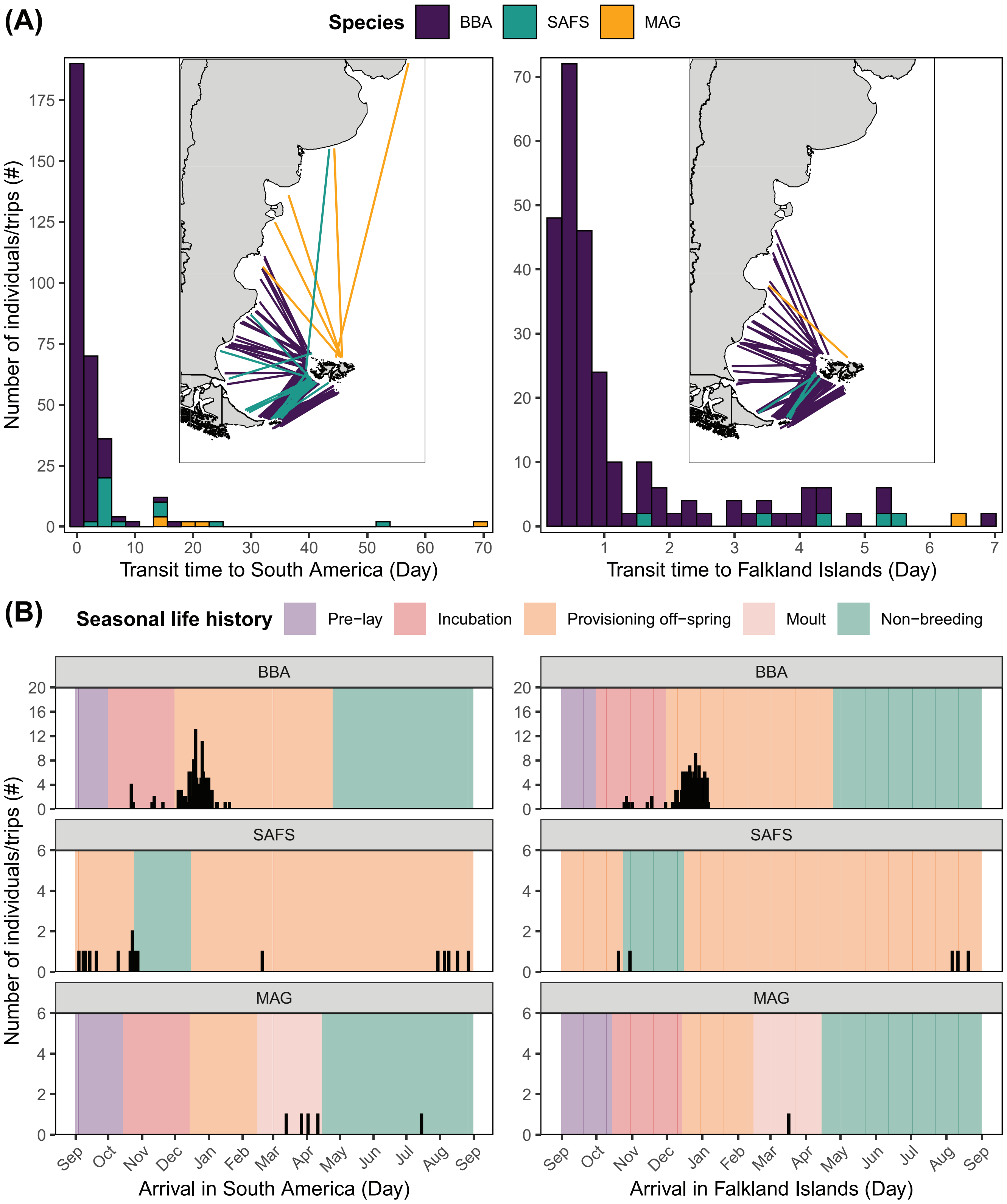

Figure 2. Transit time to (A) and seasonal arrival in (B) South America from the Falkland Islands during outbound migrations; and the Falkland Islands from South America during inbound migrations. Travel times are calculated based on the last and the first location recorded in coastal waters.

Table 2. Summary of the proportion (%) and amount (hours) of time each species (BBA, SAFS and MAG) spent in South American coastal waters and in resident behaviours on/near land. Mean (95% confidence intervals [CI]) and range values are provided, calculated across individuals which recorded connectivity with South America.

	Coastal waters		Residency on/near land	
	Mean (95% CI)	Range	Mean (95% CI)	Range
	BBA (n = 109)		**BBA (n = 27)**	
Proportion of time (%)	13.6 (10.9 – 16.3)	0.1 – 67.8	0.4 (0.1 – 0.8)	0.03 – 5.4
Total time (h)	36.7 (27.3 – 46.0)	0.2 – 298.9	0.8 (0.4 – 1.2)	0.2 – 5.0
	SAFS (n = 17)		**SAFS (n = 13)**	
Proportion of time (%)	21.6 (12.9 – 30.2)	3.7 – 67.8	4.1 (1.1 – 7.1)	0.4 – 17.2
Total time (h)	365.9 (182.7 – 550.5)	26.0 – 1268.3	74.0 (18.2 – 129.9)	6.0 – 321.9
	MAG (n = 5)		**MAG (n = 2)**	
Proportion of time (%)	12.9 (0.2 – 25.7)	1.6 – 28.1	2.9 (0.1 – 37.5)	0.2 – 5.6
Total time (h)	104.1 (0.1 – 214.0)	29.0 – 241.8	14.5 (0.1 – 185.7)	1.0 – 27.9

of HPAI detected at the Falkland Islands was in a migratory southern fulmar *Fulmarus glacialoides* in October 2023 (Bennison et al. 2023), outbreaks have since been recorded for several seabird species, including BBA. With their extensive and rapid coastal connectivity, our results indicate breeding BBA could play an important role in disease transmission or spread, despite not visiting colonies in South America (or spending time on land). For example, transmission could occur at-sea in areas of high inter-species mixing or from scavenging dead infected animals. To gain a more complete understanding of pathogen spread throughout the South Atlantic which incorporates these at-sea components of disease transmission, dedicated and collaborative research efforts are required to increase the regional and temporal coverage of available tracking data.

The tracking data compiled by this study indicates an expansive spatial network and numerous pathways for HPAI to spread from the Atlantic coast of South America to the Falkland Islands. In particular, as HPAI spreads southwards, Staten Island in southern Argentina may serve as a hotspot for disease transmission. Both BBA and SAFS from the Falkland Islands spent substantial amounts of time in close connection with Staten Island, recording resident behaviours on/near land. Numerous individuals recorded repeated foraging trips to/from Staten Island. There are several SAFS breeding/haul-out sites at Staten Island (Crespo et al. 2015). The area is also an important foraging habitat for albatrosses and a range of other seabird species (i.e. penguins and flying seabirds) (Yorio et al. 2001, Croxall and Wood 2002, Pütz et al. 2006, Finger et al. 2023). Should HPAI reach Staten Island, inter-population mixing may increase the risk of exposure to infected individuals, heightening the risk of rapid disease spread within BBA and SAFS across large spatial scales, and potential disease spillover with other migratory seabird species (Dewar et al. 2023a, Leguia et al. 2023, Uhart et al. 2024). This could accelerate widespread HPAI outbreak to the Falkland Islands marine predator community, and may also serve as a reservoir for HPAI spread into sub-Antarctic and Antarctic regions.

Understanding the temporal components of pathogen spread is also critical for effective disease surveillance. The dataset used in this study compiled BBA, SAFS and MAG movement information across different seasons and life history stages. Our findings demonstrate the risk of HPAI and pathogen spread to the Falkland Islands via these regional-ranging species is present throughout much of the year. It is particularly important to highlight breeding BBA and female lactating SAFS both showed evidence of connectivity with South America. During these periods, BBA and SAFS individuals conducted relatively short and frequent foraging trips to southern Argentina, regularly returning to colonies to incubate eggs or provision offspring. The spread of HPAI or other diseases to BBA or SAFS at the Falkland Islands during these critical life history stages, when there are large aggregations of conspecifics at colonies, may increase the likelihood of transmission (Lane et al. 2024). Given the globally significant populations of these species in the Falkland Islands, mass adult mortalities during the breeding period would have unprecedented conservation implications. Furthermore, high densities of seabirds and pinnipeds at the peak of the breeding season, including many likely immunologically naïve offspring, represent a fertile ground for the virus to transmit and persist locally within the marine predator community (Jeong et al. 2019). This is particularly relevant in light of recent findings suggesting HPAI outbreaks can amplify localised movement and connectivity between seabird colonies, facilitating viral spread and persistence among metapopulations (Jeglinski et al. 2024).

The spatial pattern and chronology of HPAI spread in the region has been contrary to initial predictions. Given the Falkland Islands' relatively close proximity to South America, the virus' prior incursion into more distant regions south of the polar front has confounded biological risk assessments and underscored the complexity of animal movement and population connectivity as mechanisms of disease spread (Dewar et al. 2023a). Surprisingly, the Falkland Islands were seemingly buffered from the initial spread of HPAI in the region. For example, HPAI-related mass mortality events in sea lion and elephant seal populations in South America (occurring between January–October 2023) (Banyard et al. 2023, Ulloa et al. 2023, Campagna et al. 2024, Plaza et al. 2024) did not directly trigger outbreaks in the Falkland Islands, at least during the 2023/24 breeding season. While there is some evidence indicating spatial connectivity between

Argentina and the Falkland Islands for these particular species (Baylis et al. 2017, Hindell et al. 2020, Campagna et al. 2021), it is possible the seasonal timing of migratory movements across the Patagonian Shelf did not coincide with ongoing outbreaks in South America, limiting/delaying the regional spread of pathogens. Alternatively, transit times between South American and Falkland Islands coastal waters may exceed the period individuals remain infectious or limit infectious individuals' ability to successfully make the crossing. However, with numerous HPAI strains now circulating among seabird and pinniped species in South America (Bennison et al. 2023, Leguia et al. 2023, Ulloa et al. 2023, Uhart et al. 2024), spillover into other more mobile regional-ranging marine predators – such as BBA, SAFS and MAG, poses a significant threat.

Finally, it is important to note the movements of other highly mobile species or specific demographics not examined in this study may also play a significant role in HPAI spread in the region. Our compiled dataset did not include non-breeding individual BBA or MAG, which likely exhibit different behaviours and distributions than breeding individuals (Phillips et al. 2005, Copello et al. 2013, Campioni et al. 2017, Ponchon et al. 2019, Barrionuevo et al. 2023). Collection and analyses of these data may improve understanding of pathogen spread across seasons and between colonies (Boulinier 2023). Additionally, our dataset did not contain tracking information for several scavenging seabird species, such as southern giant petrels *Macronectes giganteus*, brown skuas, kelp gulls *Larus dominicanus* and snowy sheathbills *Chionis albus*, which can feed on the carcasses of infected individuals and rapidly move over large distances (Phillips et al. 2007, de Souza Petersen et al. 2017, Gamble et al. 2020, Bennison et al. 2023, Dewar et al. 2023a). The movements of these highly mobile and scavenging seabirds from the Patagonian Shelf LME are thought to be responsible for HPAI outbreaks in the sub-Antarctic and Antarctic region, where dense and globally significant breeding populations of many seabird and pinniped species are located (Banyard et al. 2023, Bennison et al. 2023). Indeed, recent HPAI outbreaks recorded in breeding gentoo penguins at the Falkland Islands indicate the virus is now transmitting locally, which suggests disease spillover from closely associated more mobile species (e.g. scavengers and predators, such as brown skuas) (Falkland Islands Government 2024). With the increasing prevalence of HPAI cases in the region, its variable spread and its long-term persistence in wild populations (based on epidemiology in the northern hemisphere) (Banyard et al. 2023), further research into animal movement and connectivity are urgently needed to inform ongoing disease surveillance and monitoring efforts.

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Author contributions

Javed Riaz: Conceptualization (equal); Formal analysis (lead); Investigation (lead); Resources (supporting); Writing – original draft (lead); Writing – review and editing (lead). **Rachael A. Orben**: Formal analysis (supporting); Investigation (supporting); Resources (supporting); Writing – original draft (supporting); Writing – review and editing (supporting). **Amandine Gamble**: Writing – original draft (supporting); Writing – review and editing (supporting). **Paulo Catry**: Resources (supporting); Writing – review and editing (supporting). **José P. Granadeiro**: Resources (supporting); Writing – review and editing (supporting). **Letizia Campioni**: Resources (supporting); Writing – review and editing (supporting). **Megan Tierney**: Resources (supporting). **Alastair M. M. Baylis**: Conceptualization (equal); Resources (lead); Writing – original draft (supporting); Writing – review and editing (supporting)

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Data availability statement

All R code and move persistence data are publicly available from the South Atlantic Environmental Research Institute data portal (http://dataportal.saeri.org/dataset/connectivity-of-marine-predators-over-the-patagonian-shelf-during-the-hpai). Access to raw tracking data can be requested and granted following account registration with this data repository.

Supporting information

The Supporting information associated with this article is available with the online version.

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