

Geographic, ecological, and temporal patterns of seabird mortality during the 2022 HPAI H5N1 outbreak on the island of Newfoundland

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Abstract

Highly pathogenic avian influenza (HPAI) H5N1 caused mass mortality of wildlife across the North Atlantic in 2022. Following European outbreaks, the first North American case was detected on the island of Newfoundland, Canada in November 2021, before spreading throughout North America. During the following summer, Newfoundland and surrounding islands (NFLD) experienced one of the most significant mortalities in Canadian provinces, with seabirds being the most affected taxa. From surveys and citizen reports, we estimate that 13 517 mortalities that can be attributed to HPAI occurred in NFLD from April to September 2022. Most estimated mortalities were among Northern Gannets (*Morus bassanus* (Linnaeus, 1758)) (6596), Common Murres (*Uria aalge* (Pontoppidan, 1763)) (5992), Atlantic Puffins (*Fratercula arctica* (Linnaeus, 1758)) (282), and Black-legged Kittiwakes (*Rissa tridactyla* (Linnaeus, 1758)) (217). Mortality reports moved from west to east along the southern, then eastern NFLD coast, and peaked in July and August. We formulated exploratory hypotheses regarding traits that could contribute to infection and mortality. Species differences in mortality most strongly associated with inter-nest distance, breeding phenology, and at-sea overlap with allospecifics from other colonies. Unprecedented seabird mortality and ongoing transmission within the circulating avian influenza viruses highlight the need for continued monitoring and development of conservation strategies.

Key words: highly pathogenic avian influenza, pathogen transmission, seabird ecological traits, population monitoring, seabirds

Introduction

A wide range of birds and a number of mammalian species have been found to be infected with highly pathogenic avian influenza virus (HPAIV), though infection and mortality rates depend in part on differences in taxa- and species-specific traits (Alkie et al. 2023; European Food Safety Authority et al. 2023; Teitelbaum et al. 2023). One of the most impactful HPAI outbreaks began in 2020, when A/Goose/Guangdong/1/1996 (GsGD) clade 2.3.4.4b H5N1 virus caused several outbreaks in both domestic and wild bird populations across Western Europe (European Food Safety Authority et al. 2020). Spread of H5N1 into North America was first detected in a Great

Black-backed Gull (*Larus marinus* Linnaeus, 1758) in November 2021 in St. John's, Newfoundland and Labrador, and subsequently spread into poultry and other local wild bird populations (Caliendo et al. 2022). The virus was closely related to H5N1 circulating in northwestern Europe in spring 2021 (Caliendo et al. 2022) and represented the first incursion of HPAIV from Eurasia to Canada since 2014, with that virus last detected in Canada in 2015 (Pasick et al. 2015; Ramey et al. 2022). Widespread H5N1-linked mortality of Canadian seabirds subsequently occurred among Common Eiders (*Somateria mollissima dresseri* (Linnaeus, 1758)) in Québec, Canada in May 2022 and was immediately followed by observations

Table 1. Population sizes and global proportions of breeding seabirds on and surrounding the island of Newfoundland, Canada.

Species	Estimated number of breeding pairs	Approximate percent of global breeding population	Reference
Northern Gannet (<i>Morus bassanus</i> (Linnaeus, 1758))	29 050	6%	d'Entremont et al. (2022b) from S. Wilhelm unpubl. data
Common Murre (<i>Uria aalge</i> (Pontoppidan, 1763))	755 322	5%	Ainley et al. (2021)
Atlantic Puffin (<i>Fratercula arctica</i> (Linnaeus, 1758))	250 000–300 000	6%	Lowther et al. (2020)
Leach's Storm-Petrel (<i>Hydrobates leucorhous</i> (Vieillot, 1818))	2 500 000	30%	Pollet et al. (2021)
Black-legged Kittiwake (<i>Rissa tridactyla</i> (Linnaeus, 1758))	70 000	0.5%	Hatch et al. (2020)

of sick and dead Northern Gannets (*Morus bassanus* (Linnaeus, 1758)) on the shores of the Gulf of St. Lawrence (Avery-Gomm et al. 2024b). These initial outbreaks among colonial-nesting seabirds signalled the onset of extensive mass seabird mortality that occurred throughout eastern Canada from May to September 2022 (Giacinti et al. 2023; Avery-Gomm et al. 2024b).

The island of Newfoundland and adjacent islands (distinguished from the province of Newfoundland and Labrador, hereafter “NFLD”) were severely impacted by the HPAI outbreak and exhibited the second-highest number of mortalities among Canadian provinces, almost all of which were seabirds (Avery-Gomm et al. 2024b). It is vital to examine the species-specific impacts that occurred during the 2022 HPAI outbreak in NFLD to understand the local and global impacts, because NFLD hosts significant proportions of seabirds that breed in the North Atlantic Ocean (Table 1). The ecology, behaviour, and movement of seabirds that breed in NFLD have been studied extensively since the 1970s (e.g., Montevecchi and Tuck 1987), providing a compelling opportunity to explore the roles species- and colony-specific behaviour and ecology might play in possible transmission routes, incidence of infection, and subsequent mortality.

Examining the traits of species that incurred many mortalities during the outbreak could help identify those traits that make species more vulnerable to viral infection and mortality (van Dijk et al. 2018). Although the slope of the relationship between the number of infected individuals and number of individuals that subsequently die from infection is unknown and likely varies among species and regions, this relationship is inherently positive, so inferences about levels of infection can be made from incidences of mortality. As AIV transmission generally requires close contact between individuals or contact with contaminated environments (Ramey et al. 2020), we expect that species traits that increase the frequency and (or) duration of inter-individual contact, such as distance between nests, overlap of nesting and foraging ranges with con- and allospecifics, and diet, will be associated with increased incidences of infection and mortality.

In this study, we use the most comprehensive data available on HPAI-linked mortality in seabirds in NFLD (Avery-Gomm et al. 2024b) to (1) document the overall seabird mortality in NFLD throughout the 2022 HPAI outbreak, (2) summarize the spatiotemporal trends of the mortality, and (3) assess species traits, which might have contributed to the seabird mortality patterns. Specifically, we report the total and species-specific number of seabird mortalities and de-

scribe the overall and species-specific spatiotemporal patterns of seabird mortality. We then summarize species’ traits that influence frequency of contact among individuals, and formulate exploratory hypotheses and predictions about trait-based species-specific incidences of infection. Finally, based on the assumption that incidence of infection and incidence of mortality are positively related, we qualitatively compare observed species-specific mortality to our exploratory predictions.

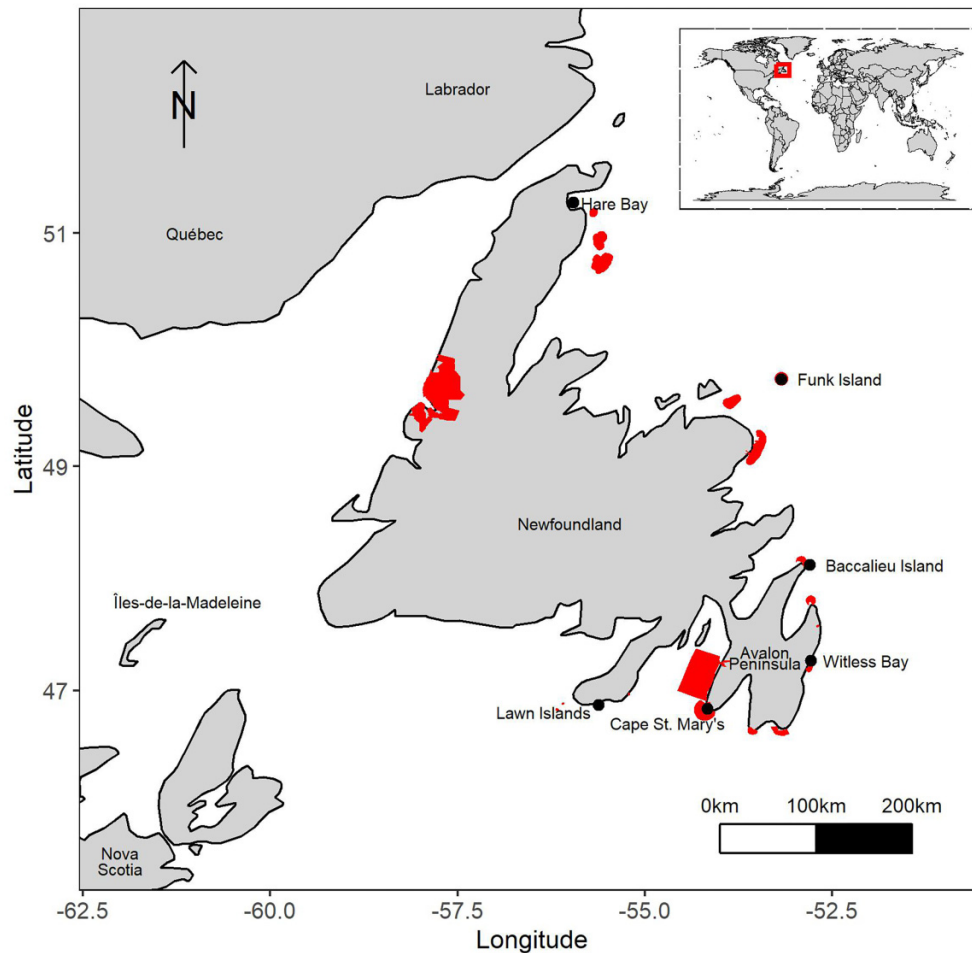
Materials and methods

Study area and data collection

We extracted reports of seabird mortalities (Fig. S1) in NFLD (Fig. 1) from a comprehensive dataset of wild bird mortalities in eastern Canada (Avery-Gomm et al. 2024b). Specifically, we utilized the results of the double count-corrected dataset that was recommended as the best estimate of HPAI-linked mortality for 1 April to 30 September (i.e., Scenario B, Avery-Gomm et al. 2024b, see below). Avery-Gomm et al. (2024b) provide a complete description of the data collation, processing, assumptions, and limitations. Briefly, data included wild bird mortality observations from federal, provincial, and Indigenous governments, the Canadian Wildlife Health Cooperative, universities, citizen science platforms, and the public. Observations on seabird colonies were obtained by government biologists and academic researchers with appropriate permits. The collated dataset included information on species, date, location (latitude and longitude), observer information, and total observed mortality. Avery-Gomm et al. (2024b) attributed reported mortalities to HPAI if a species tested positive for the HPAI clade 2.3.4.4b H5N1 virus in eastern Canada between 1 April and 30 September 2022 (i.e., from Giacinti et al. 2023). For records with less specific taxonomic identity (e.g., unknown gull), Avery-Gomm et al. (2024b) presumed HPAI to be the cause of mortality if more than 50% of that group of species tested positive for HPAIV. Avery-Gomm et al. (2024b) removed carcasses with an unknown taxonomic identity from the HPAI-linked dataset.

In the absence of beached bird surveys and organized marking and removal of sick and dead birds from the landscape during the 2022 HPAI outbreak, many observations of sick and dead wild birds were opportunistic and unstructured. Avery-Gomm et al. (2024b) present a scenario-based analysis to identify and remove observations of the same species reported two or more times within 1 km and 1 day to gen-

Fig. 1. Important bird areas for seabirds (red polygons) (Birds Canada n.d.) and Seabird Ecological Reserves (black points) on and near the island of Newfoundland, Canada, and surrounding islands (Environment and Climate Change Canada 2020). Land polygons were created using the maps package (Becker et al. 2023) in R (R Core Team 2023). The map projection is Mercator, and the coordinates are latitude and longitude.



erate the estimates they present in Scenario B (i.e., potentially double-counted records; Avery-Gomm et al. 2024b). Our dataset therefore represents estimated seabird mortalities from HPAI in NFLD during the study period (hereafter “mortalities”).

Data analysis

Analyses were conducted using R Statistical Software version 4.3.2 (R Core Team 2023). The sum total mortalities were calculated for each day and month of the outbreak, and each reported species. We created daily and monthly maps of the spatial and temporal patterns of mortality around NFLD. Total daily mortalities were plotted in a time-series graph to determine the period of peak mortality. To further examine spatial and temporal interactions, we plotted the daily sum of mortalities for northern and southern areas of NFLD in relation to the breeding phenology of the four most impacted species. Northern regions were defined as any location north of 48.1°N latitude (the most northerly point of the Avalon Peninsula, Fig. 1).

Trait exploration

We created a table of seabird ecological traits that influence the frequency and (or) duration of contact among individuals or with contaminated environments during the breeding season (Table 2). Specifically, we considered traits that influence the frequency and (or) duration of inter-individual contact among con- and allospecifics from the same and different colonies: (1) at the colony (inter-nest distance, inter-individual interaction via resting/roosting on land outside of the nest site, overlap of nesting habitat among allospecifics), (2) at sea (overlap of at-sea foraging and rafting ranges), and (3) throughout the breeding season (diet, timing of breeding and presence at the colony). Species trait information was extracted from global primary and secondary literature, and supplemented with NFLD-specific literature when available (Table S1).

Based on the information collated in Table S1, we qualitatively classified the frequency and (or) duration of inter-individual contact based on each trait for each of the four species with the highest mortalities as one of (1) *often*—inter-individual contact occurs due to the trait regularly through-

Table 2. Seabird ecological traits that influence the frequency and (or) duration of interaction with other seabirds, predictions regarding how these traits will influence exposure and transmission from a virus (Vulnerability column), species-specific traits (see Table S1; NOGA = Northern Gannets *Morus bassanus* (Linnaeus, 1758), COMU = Common Murre *Uria aalge* (Pontoppidan, 1763), ATPU = Atlantic Puffin *Fratercula arctica* (Linnaeus, 1758), BLKI = Black-legged Kittiwake *Rissa tridactyla* (Linnaeus, 1758)), exploratory predictions for observed mortality if the associated trait is the key factor determining infection rates, and a comparison of each prediction with the observed species-specific mortality.

Trait	Vulnerability	NOGA	COMU	ATPU	BLKI	Prediction	Result
Inter-nest distance	Species with a small inter-nest distance will likely make direct contact with conspecifics or contaminated feces more frequently or for longer	Often	Often	Rarely	Sometimes	NOGA = COMU > BLKI > ATPU	Mostly supported
Overlap of nesting habitat	Species that share nesting habitat with allospecifics will likely make direct contact with allospecifics or contaminated feces more frequently and (or) for longer	Often	Often	Rarely	Often	NOGA = COMU = BLKI > ATPU	Partially supported
Roosting/resting with conspecifics	Species which roost/rest together outside of the nest at the colony (on land) will likely make direct contact with conspecifics or contaminated feces more frequently and (or) for longer	Often	Often	Often	Often	NOGA = COMU = ATPU = BLKI	Not supported
Roosting/resting with allospecifics	Species which roost/rest with allospecifics outside of the nest at the colony (on land) will likely make direct contact with allospecifics or contaminated feces more frequently and (or) for longer	Rarely	Often	Often	Often	COMU = ATPU = BLKI > NOGA	Not supported
Breeding phenology and timing of parental nest attendance	Breeding phenology varies among species and colonies; adult attendance at the nest is much higher during egg incubation and brooding than chick-rearing and post-fledging, so birds that were present at the nest during an outbreak are more likely to make contact with infected individuals or environments	Often	Sometimes	Rarely	Sometimes	NOGA > COMU = BLKI > ATPU	Mostly supported
Foraging/rafting/resting with conspecifics from the same colony	Species that forage, raft, or rest with conspecifics at sea will likely make direct contact with conspecifics or contaminated environments (i.e., seawater) more frequently and (or) for longer	Often	Often	Often	Often	NOGA = COMU = ATPU = BLKI	Not supported
Foraging/rafting/resting with allospecifics from the same colony	Species that forage, raft, or rest with allospecifics at sea will likely make contact with allospecifics or contaminated environments more frequently and (or) for longer	Sometimes	Often	Often	Often	COMU = ATPU = BLKI > NOGA	Not supported
Foraging/rafting/resting with conspecifics from different colonies	Species that forage, raft, or rest with conspecifics at sea will likely make contact with conspecifics or contaminated environments more frequently and (or) for longer	Rarely	Sometimes	Rarely	Sometimes	COMU = BLKI > NOGA = ATPU	Partially supported
Foraging/rafting/resting with allospecifics from different colonies	Species that forage, raft, or rest with allospecifics at sea will likely make contact with allospecifics or contaminated environments more frequently and (or) for longer	Often	Sometimes	Rarely	Sometimes	NOGA > COMU = BLKI > ATPU	Mostly supported
Diet	Species that feed on other birds may contract the virus through ingestion of infected tissue; species that feed exclusively on fish, which are less likely to carry HPAI than birds, are less likely to contract the virus from ingestion of prey	Rarely	Rarely	Rarely	Rarely	Low for all	Not supported

out the breeding season; (2) *sometimes*—inter-individual contact does not always but can occur due to the trait throughout the breeding season, or inter-individual contact occurs regularly due to the trait at specific times of the breeding season (e.g., incubation but not chick-rearing); (3) *rarely*—inter-individual contact due to the trait is highly unlikely or does not occur. Each of the four target species received a classification of rarely for diet, so this trait was excluded from further analyses. For the remaining traits, we ranked the four species in order of the frequency/duration of inter-individual contact predicted by each trait (often = 1, sometimes = 2, rarely = 3). Based on the assumption that greater inter-individual contact will lead to greater viral spread (Ramey et al. 2020; Boulinier 2023), we compared the predicted ratings to the rank order of the four species with the most mortalities (Northern Gannet = 1; Common Murre (*Uria aalge* (Pontoppidan, 1763)) = 2; Atlantic Puffin (*Fratercula arctica* (Linnaeus, 1758)), and Black-legged Kittiwake (*Rissa tridactyla* (Linnaeus, 1758)) = 3, see Results). We determined the absolute difference in predicted versus observed rank for each species for each trait and calculated the sum of absolute rank differences for each trait. Traits with a score of 3 or 4 were considered a partial or weak contributor (“Partially supported” in Table 2), and traits with a score of 2 or less were implicated (“Mostly supported” in Table 2) in the spread of HPAI in NFLD.

Results

Spatiotemporal and species-specific patterns of mortality

Overall, an estimated 13 517 seabirds died from HPAI in NFLD between 3 April and 20 September 2022. Species with the highest mortalities were, in decreasing order: Northern Gannets (6596 individuals), Common Murres (5992 individuals), Atlantic Puffins (282 individuals), and Black-legged Kittiwakes (217 individuals) (Fig. S1). Razorbills (*Alca torda* Linnaeus, 1758) (79 individuals) and gulls also incurred many mortalities—60 Herring Gulls (*Larus argentatus* Pontoppidan, 1763), 31 Great Black-backed Gulls, 2 Ring-billed Gulls (*Larus delawarensis* Ord, 1815), and 137 unidentified gulls (Fig. S1). There were no mortalities of Leach’s Storm-Petrels (*Hydrobates leucorhous* (Vieillot, 1818)), despite their high regional abundance (Pollet et al. 2021).

Mortalities in NFLD began on the west coast in April to June, followed by reports further to the east along the south coast in July, then in the north along the northeast coast in August before tapering off in September (Figs. 2 and S2 (Supplementary material B)). The first eight observations of dead seabirds (mostly Common Murres along the west coast) during the study period were made in April 2022 (Figs. 2 and S3). In May 2022, 14 seabird carcasses, primarily Northern Gannets, appeared on the west coast (Figs. 2 and S4), while in June, 14 dead Northern Gannets were observed along the west coast and four were on the Avalon Peninsula (Figs. 2 and S4). The highest estimated number of mortalities occurred in July (5441 total), with overall peaks for Common Murres and Black-legged Kittiwake mortalities in mid-July (Fig. S5). July mortalities overall and for Northern Gannets, Common Mur-

res, and Atlantic Puffins were concentrated along the south-east coast on the southern regions of the Burin and Avalon Peninsulas (Figs. 2–4, and S3, S4, and S6). Black-legged Kittiwake mortalities were almost exclusively reported on the Avalon Peninsula (Figs. 4 and S7). The estimated number of mortalities continued to be high in August (3555), with overall mortalities of Northern Gannets and Atlantic Puffins peaking in early August (Fig. S5). The estimated number of mortalities was also high in September (4481, Fig. 3) and was concentrated on the east coast (Fig. 2). Most mortalities detected in September were identified through population surveys conducted by the Canadian Wildlife Service based on aerial photographs at the three Northern Gannet colonies in NFLD (3158 Northern Gannets at Funk Island, 1136 at Cape St. Mary’s, and 20 at Baccalieu Island). Although these carcasses were observed and reported in September, many likely died between early August and mid-September and persisted, as aerial surveys during late July recorded only 527 total carcasses across the three colonies (see Data S3 of Avery-Gomm et al. 2024a). Excluding the September Northern Gannet colony surveys, the mortality of all other seabird species decreased throughout September (Figs. 3 and S3–S7).

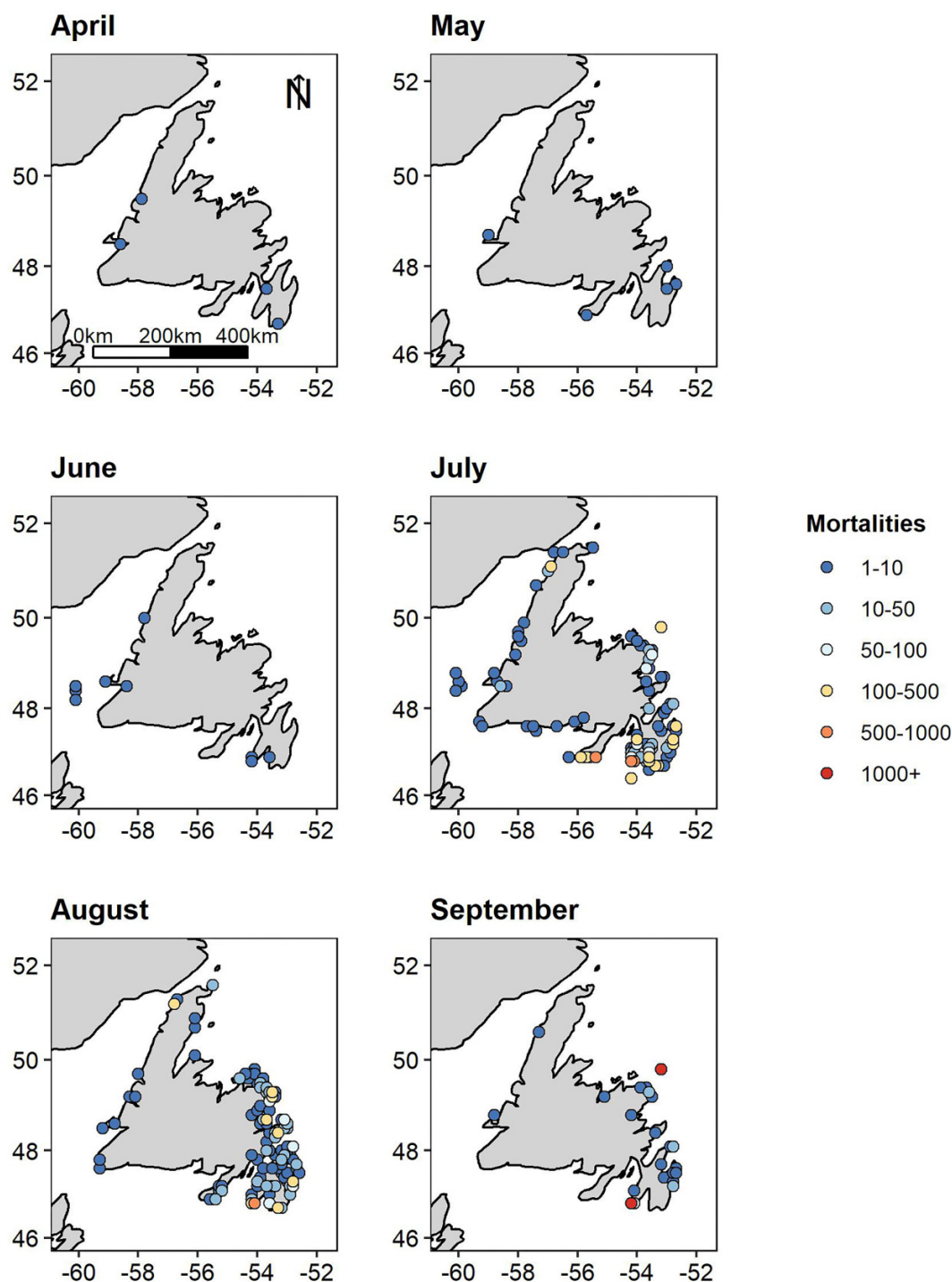
Mortality predicted by seabird ecological traits

Assuming that the proportion of infected individuals that died from the virus was similar among species, the rank order of the four species with the highest number of mortalities most closely aligned with the rank order predicted by conspecific inter-nest distance, at-sea overlap with allospecifics from different colonies, and breeding phenology and adult nest attendance (Table 2). The observed rank order partially aligned with the rank order predicted by overlap of nesting habitat with allospecifics, and interactions with conspecifics from different colonies at sea (Table 2). The observed rank order did not align with the rank order predicted by interaction at the colony outside of the nest site with con- or allospecifics, and interaction at sea with con- or allospecifics (Table 2). Northern Gannets, Common Murres, Atlantic Puffins, and Black-legged Kittiwakes are piscivorous (Table S1), so diet was also unlikely to play a key role in viral transmission among these species.

Discussion

During the 2022 HPAI H5N1 panzootic, 13 517 seabirds were estimated to have died from HPAI in NFLD, with Northern Gannets comprising nearly half of the total (Fig. S1). Both within NFLD and throughout their breeding range, Northern Gannets experienced substantial impacts from the HPAI H5N1 panzootic (Lane et al. 2023). Northern Gannets began washing ashore on the west coast of NFLD in May–June 2022, and drift modelling suggests that these birds likely originated from the Rochers aux Oiseaux colony in the Îles-de-la-Madeleine in the province of Québec (Avery-Gomm et al. unpub. data). After these first mortality reports, seabird mortalities were observed with increasing frequency along the southern NFLD coast in July, then along the east and northeast coasts in August. Northern Gannets may, therefore, have acted as a vector for the transmission of H5N1 to and among

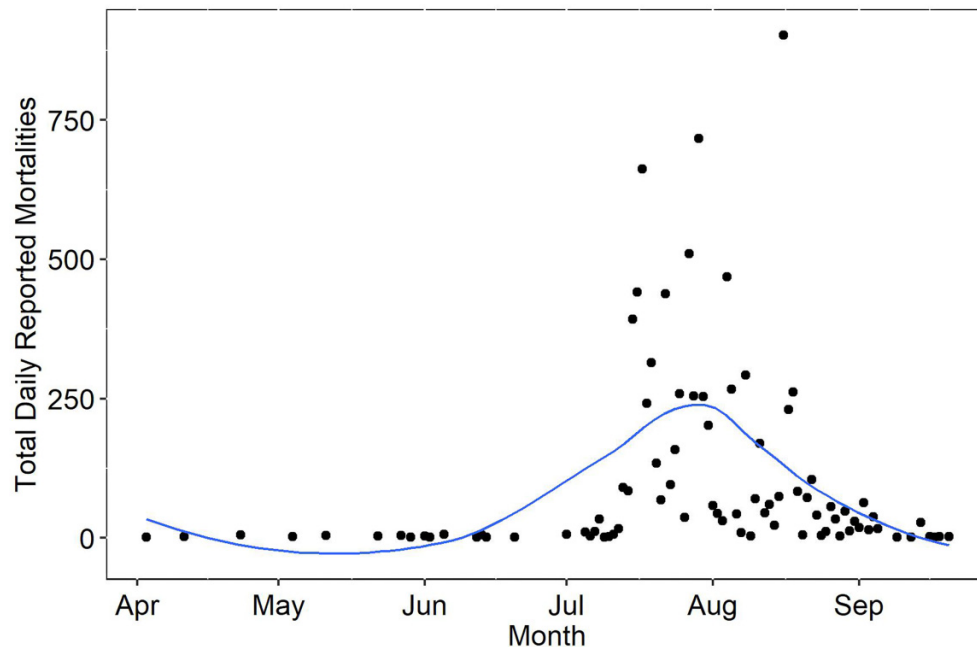
Fig. 2. Spatial distribution of estimated seabird mortalities on and near the island of Newfoundland, Canada, and surrounding islands, in April through September 2022. Refer to Fig. S2 (Supplementary material B) for a video illustrating the spatiotemporal distribution of estimated mortalities. Refer to Figs. S3, S4, S6, and S7 for species-specific figures for Common Murre (*Uria aalge* (Pontoppidan, 1763)), Northern Gannet (*Morus bassanus* (Linnaeus, 1758)), Black-legged Kittiwake (*Rissa tridactyla* (Linnaeus, 1758)), and Atlantic Puffin (*Fratercula arctica* (Linnaeus, 1758)). Land polygons were created using the maps package (Becker et al. 2023) in R (R Core Team 2023). The map projection is Mercator, and the coordinates are latitude and longitude.



NFLD seabirds (Careen et al. 2024; Jeglinski et al. 2024). Alternatively, Northern Gannets may have acted as early indicators of ongoing viral outbreak due to their conspicuousness and the heavy impact they suffered.

The susceptibility of Northern Gannets and other seabirds in NFLD to infection from HPAI may be partially related to their ecological traits (Tables 2 and S1). We found that traits that influence the frequency of inter-individual contact

Fig. 3. Sum of estimated daily mortalities from 1 April to 30 September 2022 of seabirds on and near the island of Newfoundland, Canada, during an HPAI outbreak. The blue line is the LOESS (locally weighted smoothing) line of smoothing. Note that three aerial surveys of Northern Gannet colonies conducted on 8, 14, and 15 September 2022 (Cape St. Mary's and Funk Island, respectively) were omitted from this figure, as these surveys were conducted late in the season and these dates are unlikely to be representative of the dates the surveyed birds died based on carcasses detected during July aerial surveys and on varied stages of decomposition observed in the survey photos.



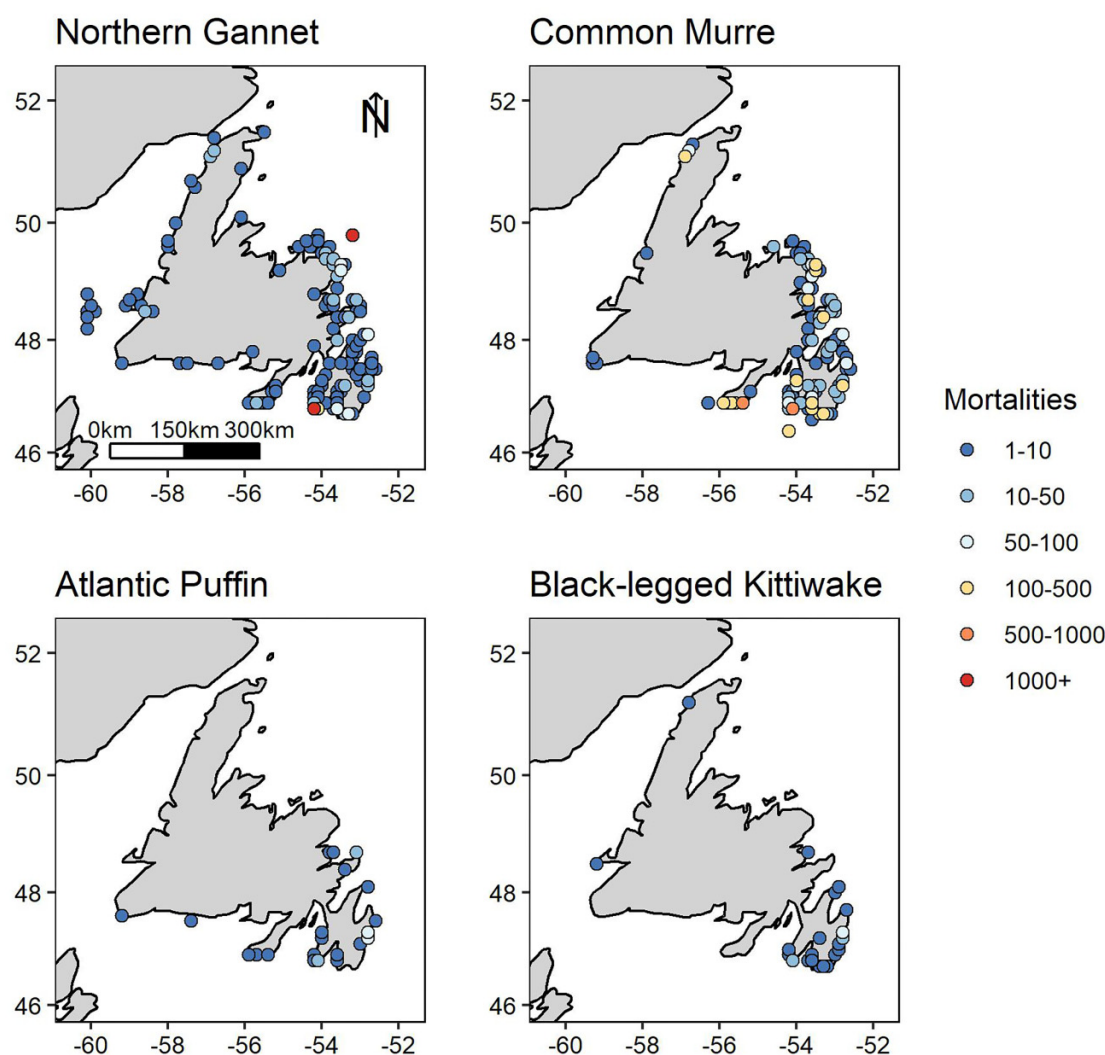
among conspecifics at the colony may be associated with the observed species-specific mortality (Table 2). Common Murres often breed shoulder-to-shoulder, and Northern Gannets nest in close proximity that allows contact between neighbouring pairs (Nelson 1978; Falchieri et al. 2022), creating favourable conditions for viral transmission directly from other infected birds, carcasses, aerosols, and environmental (fecal or water) contamination (Fig. S8) (Webster et al. 1992; Boulinier 2023). Black-legged Kittiwakes nest more sparsely, and Atlantic Puffins nest in burrows, which separate them from other birds (Rodway et al. 2003; Hatch et al. 2020; Zabala Belenguer 2023), limiting inter-individual contact at the nest.

Breeding phenology likely interacted with inter-nest distance. Northern Gannets remain at the nest nearly continuously during incubation and chick brooding, which is when outbreaks first occurred at gannet colonies (Lewis et al. 2004; Mowbray 2020). Additionally, adult attendance remains high throughout the chick-rearing period, which is when gannet mortality peaked (Lewis et al. 2004; Mowbray 2020). At Cape St. Mary's, adult attendance was nearly 100% until the HPAI outbreak occurred, at which point attendance diminished rapidly due to parental abandonment and death of adults and chicks (Careen et al. 2024). Contrastingly, Common Murres, Atlantic Puffins, and Black-legged Kittiwakes would have been rearing chicks at or nearing fledging age when outbreaks occurred (Table S1, Fig. S9), which may partially account for their lower observed mortality. Nest attendance decreases during chick-rearing for these species (Mahoney 1979; Hatch et al. 2020; Ainley et al. 2021; Wilson 2023; Zabala Be-

lenguer 2023), so adults may have avoided infection if their chicks fledged prior to the outbreak, or they may have died at sea where their carcasses would not have been observed and reported.

We also found that species differences in the frequency and (or) duration of interaction with allospecifics from different colonies associated with the observed mortality (Tables 2 and S1). This might imply that the potential to contract and spread the virus among colonies and species was important in determining which species contracted the virus. At foraging hotspots, hundreds or thousands of seabirds, including Northern Gannets, Common Murres, Atlantic Puffins, and Black-legged Kittiwakes, compete for forage fish and raft in close proximity on the water (Wanless et al. 1990; Carter et al. 2016; Gulka et al. 2020; Petalas et al. 2021; d'Entremont et al. 2022a), creating opportunities for inter-individual contact or contact with viruses shed into the water. Northern Gannets have the longest foraging range of the four target species (d'Entremont et al. 2022a; Table S1), and therefore could have acted as inter-colony vectors. Northern Gannets from Cape St. Mary's often forage in Witless Bay (d'Entremont et al. 2022a), overlapping with Atlantic Puffins, Common Murres, and Black-legged Kittiwakes breeding at and foraging near those colonies. In rare instances, Northern Gannets have also been observed visiting other colonies (Careen et al. 2024; Jeglinski et al. 2024). Inter-colony movements by a gannet breeding at Cape St. Mary's to Baccalieu Island were tracked during the 2022 HPAI outbreak (Careen et al. 2024). The outbreak at Cape St. Mary's occurred before the one at Baccalieu

Fig. 4. Spatial distribution of estimated mortalities among Northern Gannets (*Morus bassanus* (Linnaeus, 1758)), Common Murres (*Uria aalge* (Pontoppidan, 1763)), Black-legged Kittiwakes (*Rissa tridactyla* (Linnaeus, 1758)), and Atlantic Puffins (*Fratercula arctica* (Linnaeus, 1758)) on and near the island of Newfoundland, Canada, from May to September 2022. Land polygons were created using the maps package (Becker et al. 2023) in R (R Core Team 2023). The map projection is Mercator, and the coordinates are latitude and longitude.



Island (Fig. S2, Supplementary material B), and such inter-colony movement may have facilitated the viral spread to Bacalieu and other colonies. Inter-colony movements by Northern Gannets were also implicated in viral spread between colonies in Scotland during the European HPAI H5N1 outbreak (Jeglinski et al. 2024).

The overlap of nesting habitat with allospecifics and interaction at sea with conspecifics from different colonies was partially associated with the observed mortalities (Table 2). Black-legged Kittiwakes, Northern Gannets, and Common Murres nest next to or above one another on cliffs at colony perimeters and often make direct contact with one another or with seabird feces (Fig. S10), which might result in inter-species viral transmission within a colony (Webster et al. 1992). In specific regions, the foraging ranges of Common Murres and Black-legged Kittiwakes can overlap with those from small adjacent colonies (e.g., Gulka et al. 2020), so trans-

mission among adjacent colonies could occur from at-sea interactions. However, interactions at sea and outside the nest site will, in general, occur less frequently than interactions among nest neighbours. Common Murres, for example, make nearly continuous contact with neighbours while at the nest site (Ainley et al. 2021), but do not continuously make contact on the water while rafting or foraging (e.g., King 2018). Although defecation into water can be a source of contamination, contaminated feces in the ocean will quickly become more dilute than feces on land. This may explain why roosting and resting with con- and allospecifics, and foraging and resting at sea with con- and allospecifics from the same colony, did not predict the observed mortality (Table 2). Inter-nest distance, and importantly, the overlap of high parental nest attendance with the timing of the outbreak, were likely the most important factors determining viral spread within colonies.

Diet was not associated with transmission among the four species, which incurred the most mortality. Northern Gannets, Common Murres, Black-legged Kittiwakes, and Atlantic Puffins feed almost exclusively on fish and marine crustaceans (Hatch et al. 2020; Lowther et al. 2020; Mowbray 2020; Ainley et al. 2021), species not known to be infected by AIVs. On the other hand, *Larus* gulls (e.g., Great Black-backed Gulls, Herring Gulls, and Ring-billed Gulls) are omnivores that commonly prey on other birds or scavenge carcasses (Good 2020; Weseloh et al. 2020). Many dead gulls presumed to be infected with HPAIV were reported in NFLD between April and September 2022, and these gulls may have become infected by consuming infected carcasses (Brown et al. 2008).

Leach's Storm-Petrels, the most abundant procellariiform in the North Atlantic and the most abundant breeding seabird in eastern Canada (Pollet et al. 2021), were seemingly unaffected by HPAI H5N1 in 2022. Although hundreds of live and dead Leach's Storm-Petrels were sampled during the 2022 viral outbreak, none were AIV-positive (Avery-Gomm et al. 2024b; J. Wight, unpub. data). Storm-petrels are attracted to anthropogenic light, which is a major source of mortality for this species, and their carcasses are commonly observed around brightly lit industrial sites (Wilhelm et al. 2021; Burt et al. 2023, 2024). Alternate causes of mortality like this emphasize the importance of viral testing to confirm the presence of virus during disease outbreaks. Storm-petrel ecology may partially explain their seeming lack of infection. They forage hundreds of kilometres offshore beyond the foraging ranges of gannets, auks, and gulls that breed in NFLD, and are unlikely to contact infected allospecific birds at sea (Ronconi et al. 2022), or are unlikely to wash up on shore if death at sea occurs. They also nest in burrows, which generally restrict contact with conspecifics, and are nocturnal (Pollet et al. 2021), so they are less likely to contact allospecific birds at the colony. On the other hand, storm-petrels in NFLD breed in extremely large colonies of hundreds of thousands to millions of birds (Pollet et al. 2021), and contact among conspecifics does occur, as they occasionally collide in the air (Williamson 1945), enter neighbouring burrows (Pollet et al. 2021), or contact feces at the colony. There is also some foraging range overlap among NFLD colonies (Hedd et al. 2018) and inter-individual foraging range overlap within a colony (Collins et al. 2022). Other procellariiformes that breed in very low numbers in NFLD, (i.e., Northern Fulmars *Fulmarus glacialis* (Linnaeus, 1761); Mallory et al. 2020) and others that do not breed in NFLD but are common in coastal waters (e.g., Great Shearwaters *Ardenna gravis* (O'Reilly, 1818); Carvalho and Davoren 2019), were among the reported mortalities (Fig. S1) and positive for HPAIV (Giacinti et al. 2023). Shearwaters form rafts of dozens to hundreds of individuals near shore (Rowan 1952; Brooke 1988) and could have been exposed to the virus through contact with infected con- and allospecifics. Notably, shearwaters are transequatorial migrants (Schoombie et al. 2018) and can travel many hundreds of kilometers per day, with the potential to carry HPAIV across large geographic areas.

Our results should be viewed as conservative mortality estimates as it is impossible to account for every bird that died from infection by HPAIV. First, birds that die at sea

and do not reach shore are essentially not detected and can thereby grossly reduce mortality estimates (Wiese and Robertson 2004; Munilla et al. 2011). Second, limitations and biases of citizen science, including biases of search effort in areas with high human populations (e.g., Burt et al. 2023) and temporal biases during the summer when participation in outdoor activities is high, influence spatiotemporal patterns of observed mortality reports. Third, previous exposure to AIVs and immunity from prior infection also play a role in the likelihood of infection and mortality from HPAI. A wide range of AIV subtypes have been identified in seabirds, with significantly varied distributions and prevalences across regions, particularly for Common Murres (Wille et al. 2014; Lang et al. 2016) and gulls (Wille et al. 2011; Huang et al. 2014; Benkaroun et al. 2016), with previous exposure and pre-existing immunity playing an important role on their outcomes from HPAI H5N1 infection (Tarasiuk et al. 2022). Prior to the 2022 outbreak, Atlantic Puffins, Northern Gannets, and Black-legged Kittiwakes were infrequent hosts of AIVs (Wille et al. 2014; Lang et al. 2016). Additional deaths of chicks likely occurred following parental death and abandonment. Indeed, reproductive success at Cape St. Mary's in 2022 was the lowest recorded (Careen et al. 2024). Although our dataset might contain individuals that died of natural causes, this is likely a small proportion of the dataset due to the magnitude of the outbreak and the high annual survival that is characteristic of seabirds (e.g., Sandvik et al. 2005; Dobson and Jouventin 2010). As a coarse frame of reference, summer (April–September) beached bird surveys conducted from 1984 to 2006 in southeastern Newfoundland, including beaches where dead birds were observed in 2022, yielded a total of 3767 dead birds, thereby averaging 164 birds/year (Wilhelm et al. 2009), which is orders of magnitude lower than the observed 2022 mortality.

To account for these missing data is a complicated exercise, though efforts attempt to bridge this knowledge gap. For example, standardized beached bird surveys and systematic surveys on and closely surrounding seabird colonies are useful to detect mass mortality events and to obtain reliable information on species composition as well as age and sex (e.g., Piatt et al. 2020). With appropriate correction factors, beached bird surveys can quantify, to some extent, mortalities associated with various threats, but cannot estimate population-level impact, as more research is needed to account for species-specific carcass losses at sea (Jones et al. 2023; Avery-Gomm et al. unpub. data). Experimental studies of releases of marked birds and decoys at sea coupled with systematic beach surveys can help indicate the proportion of birds that die at sea, which are found on beaches. Expansion or inflation factors based on studies like these have been used to account for losses of murres in the Pacific and Atlantic Oceans (e.g., Wiese 2002; Wiese and Robertson 2004; Piatt et al. 2020). As well, standardized surveys conducted following an outbreak can estimate actual population losses (Cunningham et al. 2022). Targeted research efforts, however, have geographic and temporal limitations. Encouraging the public to report out-of-the-ordinary occurrences regarding seabirds enables monitoring over a much larger geographic and temporal scale than is achievable through research surveys (Burt et al. 2023). Edu-

cating the public about species identification and behaviour will also enhance the utility and accuracy of citizen science reporting.

As HPAIVs continue to circulate in wild bird populations around the globe with possible reinfection of these seabird species and populations, it will be highly informative to assess the behavioural ecology and vital rates (reproductive success, recruitment, survival) of the surviving birds to assess longer term effects beyond immediate mortality. Using behavioural ecology to understand species' risks and the possible routes of viral transmission can aid government wildlife and health agencies in assessing risk and potential population-level impacts from future HPAI panzootic events affecting wild birds.

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Data availability

Data analyzed in this study (Data S1) were obtained from [Avery-Gomm et al. \(2024a\)](#). The mortality dataset, colony survey information, and code to reproduce the double count scenario analysis ([Avery-Gomm et al. 2024a](#)) are published on FigShare: <https://doi.org/10.6084/m9.figshare.24856869.v2>.

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Competing interests

The authors declare there are no competing interests.

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Supplementary material

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