# HIGHLY PATHOGENIC AVIAN INFLUENZA VIRUS RESULTED IN UNPRECEDENTED REPRODUCTIVE FAILURE AND MOVEMENT BEHAVIOUR BY NORTHERN GANNETS

NOAH G. CAREEN[1], SYDNEY M. COLLINS[2]*, KYLE J. N. D'ENTREMONT[2], JORDAN WIGHT[3], ISHRAQ RAHMAN[3], KATHRYN E. HARGAN[3], ANDREW S. LANG[3] & WILLIAM A. MONTEVECCHI[1]

[1]*Department of Psychology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada*
[2]*Cognitive and Behavioural Ecology Program, Departments of Psychology and Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada *(smcollins@mun.ca)*
[3]*Department of Biology, Memorial University of Newfoundland, St. John's, Newfoundland and Labrador, Canada*

*Received 25 May 2023, accepted 16 October 2023*

**ABSTRACT**

CAREEN, N.G., COLLINS, S.M., D'ENTREMONT, K.J.N., WIGHT, J., RAHMAN, I., HARGAN, K.E., LANG, A.S. & MONTEVECCHI, W.A. 2024. Highly pathogenic avian influenza resulted in unprecedented reproductive failure and movement behaviour by Northern Gannets. *Marine Ornithology* 52: 121–128.

In 2022, highly pathogenic avian influenza (HPAI) virus resulted in mass mortality throughout seabird colonies in the North Atlantic Ocean. While mortalities and transmission of the virus are being documented, other effects are less understood. We documented nest abandonment and unprecedented reproductive failure by Northern Gannets *Morus bassanus* at Cape St. Mary's, Newfoundland and Labrador, Canada, the species' southernmost colony. Reproductive success in 2022 was the lowest on record at 17%, which was likely a result of adults abandoning the nest and succumbing to avian influenza virus (AIV) infection. Following the AIV outbreak at Cape St. Mary's, we also documented extremely long foraging trips, including the second known instance of inter-colony movement by an adult Northern Gannet, who embarked on two trips to the gannet colony on Baccalieu Island. This inter-colony movement represents a possible means of viral transmission between colonies. The effects of HPAI may have been exacerbated as a result of heat stress during a marine heatwave, which coincided with the major outbreak at this colony. As this HPAI virus could continue to circulate in seabirds, ongoing monitoring of mortality and other indirect effects of AIV outbreaks are needed to inform future impacts.

**Key words:** *Morus bassanus*, reproductive success, ocean climate change, biotelemetry, tracking

## INTRODUCTION

During the 2022 boreal breeding season, there was a major outbreak of a highly pathogenic avian influenza (HPAI), caused by a subtype H5N1 viral strain (hereafter H5N1), throughout seabird colonies in the North Atlantic Ocean (Caliendo *et al.* 2022, Lane *et al.* 2023). Initial assessments suggested the mortality associated with the outbreak were profound (Camphuysen & Gear 2022), but the extent of the devastation remains to be determined as viral transmission continues at seabird colonies across the globe (as of the time of writing; CWHC 2023, EFSA *et al.* 2023, FAO 2023).

The outbreak of H5N1 has been especially devastating for Northern Gannets *Morus bassanus* (hereafter, gannets) in eastern Canada (Avery-Gomm *et al.* 2023) and throughout the North Atlantic Ocean (Camphuysen & Gear 2022, Lane *et al.* 2023). The little data available suggest that gannets are not frequent hosts of avian influenza viruses (AIVs, Lang *et al.* 2016). While mortalities have been well documented (Avery-Gomm *et al.* 2023, Lane *et al.* 2023), indirect effects of the outbreak are less understood and may contribute to long-term population effects. For example, the energetic cost of immune responses may lead to reduced reproductive success (Hanssen 2006), and individuals may abandon breeding sites if conditions are deemed unfavourable (Barrile *et al.* 2021). Here, we documented three novel observations at Cape St. Mary's, Newfoundland and Labrador (NL), Canada—the Northern Gannet's southernmost colony—that are likely indirect impacts of the HPAI outbreak.

First, we observed that parental attendance at the nest rapidly declined following the HPAI outbreak at Cape St. Mary's. Typically, parental attendance at the nest is continuous during incubation and early chick-rearing (Kirkham 1980). Parents do not leave the chick alone until about four weeks of age, after which chicks are attended by at least one parent about 85% of the time (Lewis *et al.* 2004). Extraordinary events, however, may result in reduced parental attendance or abandonment. One example of mass colony abandonment occurred at Cape St. Mary's in 2012, when at least 40% of chicks were abandoned for several days during a marine heatwave (Montevecchi *et al.* 2021).

Second, reproductive success at Cape St. Mary's was exceptionally low in 2022. Rapidly warming ocean climate is often a driving factor that influences seabird reproductive success and survival at colonies (Piatt *et al.* 2020, Montevecchi *et al.* 2021, d'Entremont *et al.* 2022b). Human disturbance of breeding sites (Allbrook & Quinn 2020), predation of adults and chicks (Montevecchi *et al.* 2019), and chemical pollution (Chapdelaine *et al.* 1987, Champoux *et al.* 2017) can also result in poor reproductive success among gannets. Recently, poor reproductive success was also noted at the gannet colony on Bass Rock in Scotland during the outbreak of HPAI at that colony (Lane *et al.* 2023).

Third, we observed atypical movement behaviour by breeding adults, which included inter-colony movements. Aside from additional observations of inter-colony movements in Europe during the 2022 HPAI outbreak (Jeglinski *et al.* 2024), there is minimal evidence outside of this viral outbreak for inter-colony movements by breeding adult Northern Gannets.

Here, we examine the occurrence of 1) nest abandonment by parental gannets, 2) especially low reproductive success, and 3) abnormal movement behaviour of parental gannets during the HPAI outbreak at Cape St. Mary's. We also outline the timing of the outbreak based on tests conducted on live and dead gannets at or near the colony. Finally, we discuss how heat stress due to a moderate marine heatwave that coincided with the HPAI outbreak may have contributed to the lower reproductive success than observed at other infected colonies.

## METHODS

### Study site

The Cape St. Mary's Ecological Seabird Reserve (46.82°N, 054.21°W), located on the southwestern tip of the Avalon Peninsula on the island of Newfoundland, Canada (Fig. 1), is the southern limit of the Northern Gannet's breeding range (Mowbray 2020). Gannets nest along the mainland cliffs and on a large, isolated sea stack, known as Bird Rock (Fig. A1 in the Appendix, available online).

### Field methods

*Adult nest attendance and reproductive success*

Three study plots on the sea stack were used to monitor breeding gannets for nest attendance and reproductive success (Fig. A2). Our plots each consisted of 40–50 nests and were comparable in size and location to study plots used to calculate reproductive success in previous years at this colony (d'Entremont *et al.* 2022b). Photographs of each plot were taken throughout the breeding season to monitor adult nest attendance and chick survival. Long absences of adults were noted and assumed to result from infection and mortality due to the H5N1 virus (see corroborative methods below). Photos taken on 16 September 2022 were used to determine reproductive success (the proportion of chicks that remained in the nest). This date was chosen because it occurs at the end of the breeding season but before the typical fledging period, and it falls within the date range during which previous assessments of reproductive success have been conducted at this colony (d'Entremont *et al.* 2022b).

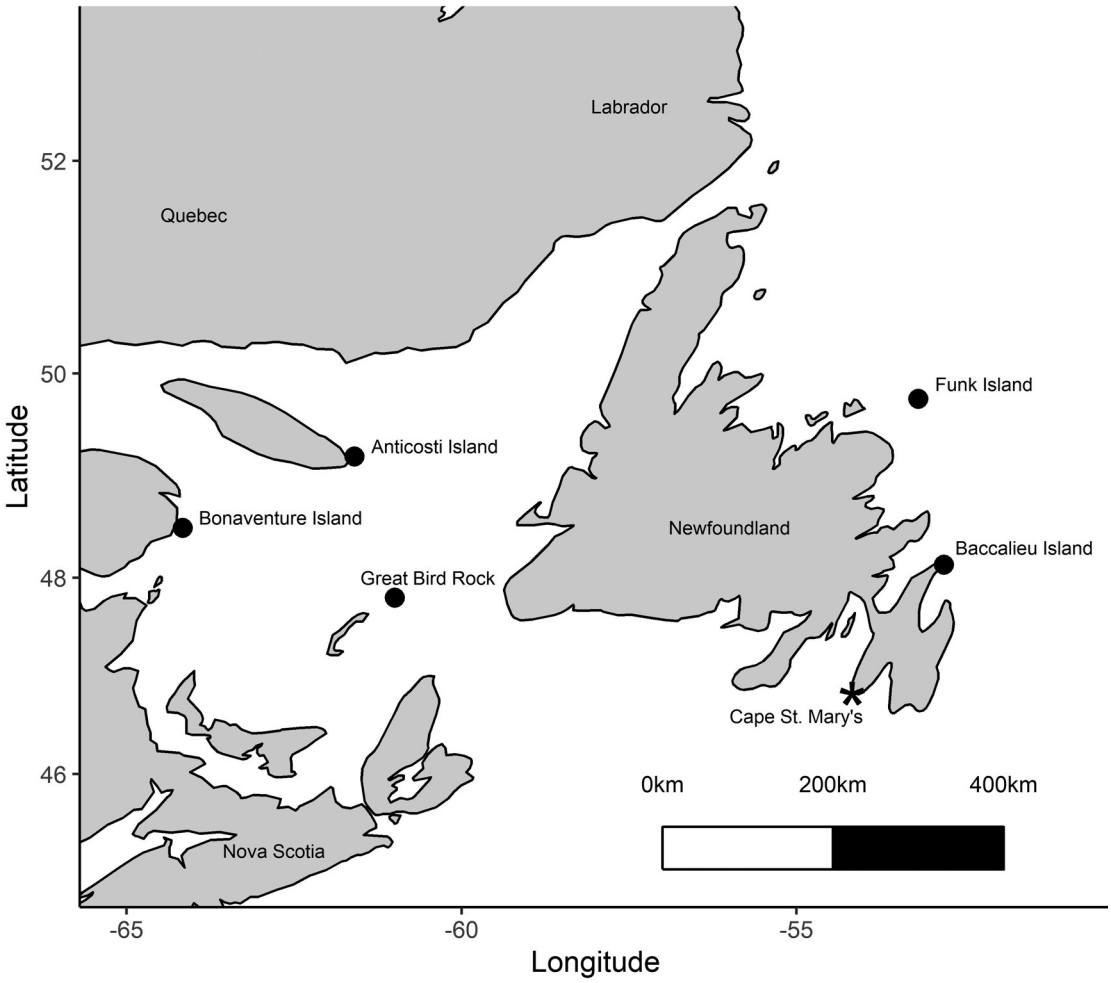


**Fig. 1.** The six Northern Gannet *Morus bassanus* colonies in North America. The study site at Cape St. Mary's on the island of Newfoundland in Canada is indicated by a star.

*Avian influenza virus testing*

Live and dead Northern Gannets were tested on or near the colony in July 2022. Oropharyngeal and cloacal swabs were collected from each individual, and these paired swabs were placed into a single vial of Multitrans viral transport media (Starplex Scientific; Toronto, Canada) and represent a single sample per individual. Samples were kept cool until delivered to the laboratory, then they were frozen at −80 °C. RNA was extracted from the swab samples using the QIAamp Viral RNA Mini Kit (Qiagen; Hilden, Germany) and tested for the presence of AIV using reverse-transcriptase PCR (Spackman 2020). Positive samples were then tested for the presence of the H5 subtype of the haemagglutinin (HA) gene (Spackman *et al.* 2002) present in the strain that circulated in North America in 2022.

*GPS deployments*

Four parental Northern Gannets from a nesting site on the mainland cliff were equipped with Ecotone URIA 300 LPS solar-powered GPS/time-depth recorder devices (13.5 g, 36×22×12.5 mm, < 0.5% of gannet body weight) on 02 July 2022. The GPS units were attached to the birds' innermost four rectrices, posterior to the uropygial gland, with Tesa® tape and cable ties. Birds were captured on the nest using an extendable noose pole, weighed with a 5-kg Pesola® scale, and banded with a Canadian Wildlife Service aluminum band on the right leg. Tags were programmed to record GPS locations every 15 minutes. An Ecotone base station with a directional antenna was deployed within the colony to facilitate remote downloading of GPS data each time a tagged bird returned to the colony. To conserve battery life, devices were set to record only when out of range of the base station (i.e., more than ~1 km away). All tagged birds had chicks that were approximately 2–3 weeks old when the devices were deployed.

**Data analysis**

Data analyses were performed using R Statistical Software, version 4.2.2 (R Core Team 2022). Reproductive success for 2022 was compared to the annual mean reproductive success from 1977 to 2021 at Cape St. Mary's (d'Entremont *et al.* 2022b) using a one-proportion *z*-test.

Sea-surface temperature (SST) data were retrieved from NASA (2023). SST and adult presence on the nest were plotted in a time-series graph for comparison with the onset and progression of the H5N1 outbreak.

Analysis of GPS data was adapted from Collins *et al.* (2022) and d'Entremont *et al.* (2022a). Briefly, trips were classified manually by assessing distance from the colony and communication by the GPS tag indicating when birds were in range of the base station (6 km, ground-to-air detection). Distances from the Baccalieu Island and Cape St. Mary's colonies were calculated using the "sp" package in R (Bivand *et al.* 2013); when a bird was within 3 km of the Baccalieu Island colony, it was considered to be visiting that colony. Trip distance and duration were calculated for each trip. Behavioural classifications were computed using a three-state Hidden Markov Model (HMM) that assigns behaviours to each point based on the step length and turning angle between subsequent points (McClintock & Michelot 2018). HMMs require consistent time intervals between points (McClintock & Michelot 2018) but GPS devices occasionally failed to record a point, so points were interpolated at 15-minute intervals from the first recorded point. Following interpolation, complete trips were forced to start and end at the colony by adding a colony point 7.5 minutes (i.e., half the sampling interval) before/after the first/last points. Behaviours were classified using the package "momentuHMM" (McClintock & Michelot 2018). Three states were chosen to align with previous studies (Bennison *et al.* 2018, Collins *et al.* 2022, d'Entremont *et al.* 2022a) and because a three-state model fit better than a two-state model. The behaviours represented by each state (rest, transit, and area-restricted search) were assigned based on three criteria: the average step length of each state, the average turning angle of each state, and the timing of dives. Diving seldom occurred during the state characterised by short step lengths (mean 0.22 km) and turning angles close to zero radians; hence, this state is referred to as "rest". "Transit" was characterised by long step lengths (mean 7.71 km) and moderate turning angles. "Area-restricted search" was characterised by medium step lengths (mean 1.31 km) and wide turning angles (Fig. A3). Diving occurred during area-restricted searches and transits.

**Ethics statement**

This study was reviewed and approved by Environment and Climate Change Canada (ECCC) scientific permit 10332K and the NL Seabird and Ecological Reserves Advisory Committee. Collection of samples from birds was done under Protocol 20-05-AL from the Memorial University of Newfoundland (MUN) Institutional Animal Care Committee. Testing of samples was done under permit S-103 from the MUN Institutional Biosafety Committee.

**RESULTS**

**Adult presence and reproductive success**

Reproductive success averaged 17% ± 0.06% (95% confidence interval) across the three study plots (Table 1). This is the lowest recorded reproductive success at Cape St. Mary's (Fig. 2A), and it is significantly lower than the mean annual reproductive success at Cape St. Mary's (mean = 0.61 ± 0.08, $\chi^2$ = 128.76, *df* = 1, *P* < 0.0001; Fig. 2A).

Gannet presence on the nest was high (~100%) until 17 July 2022, at which point it declined rapidly. Complete nest abandonment was recorded on 30 September (Fig. 2B). The initiation of nest abandonment coincided with the detection of H5N1 in dead birds found near the colony (see next section) and with the onset of a marine heatwave (Fig. 2B, Fig. A4).

**TABLE 1**
**Northern Gannet *Morus bassanus* reproductive success in 2022 at Cape St. Mary's, Newfoundland and Labrador, Canada**

| Study plot | Number nests | Number chicks | Reproductive success (± 95% confidence interval) |
|---|---|---|---|
| Sea Stack East | 50 | 6 | 0.12 |
| Sea Stack West | 50 | 10 | 0.20 |
| Sea Stack Cliff | 40 | 8 | 0.20 |
| Total | 140 | 24 | 0.17 ± 0.06 |

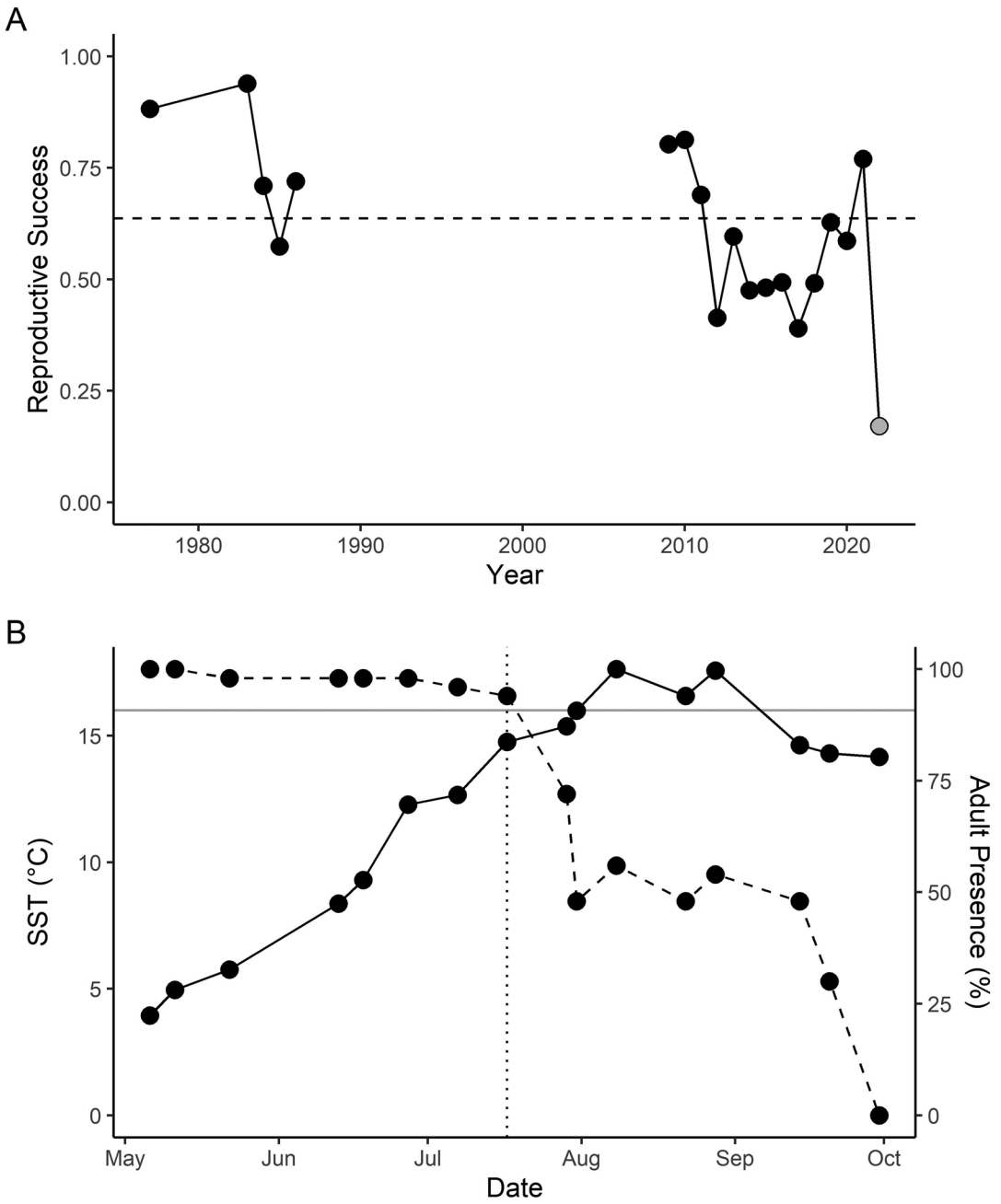


**Fig. 2.** A) Historic reproductive success (solid black line) and average reproductive success (0.61 ± 0.08; horizontal dashed line) of Northern Gannets *Morus bassanus* at Cape St. Mary's, Newfoundland and Labrador, Canada from 1977 to 2022. The lowest recorded reproductive success for this colony is in 2022 (in grey). B) Adult gannet presence at the nest (dashed black line), daily sea-surface temperature (SST, solid black line), critical SST (i.e., temperature above which conditions for Atlantic mackerel *Scomber scombrus* and capelin *Mallotus villosus* are unfavourable, grey horizontal line), and the onset of the H5N1 outbreak (dotted vertical line) at Cape St. Mary's during the 2022 breeding season.

**Avian influenza**

All live adults sampled from the colony on 02 July 2022 were negative (Table 2). Nearly all of the dead adults found near the breeding colony at Point Lance beach (7.3 km east of colony) on 17 July tested positive for H5 AIV (Table 2), indicating that an outbreak was ongoing. From the weekly photos taken at the colony, a few corpses first appeared around 17 July (Fig. A5). Around 08 August, many corpses (> 10) could be seen on the cliffs (Fig. A5). Positive tests and observations of dead adults at the colony indicated that an outbreak of H5 AIV began on approximately 17 July at Cape St. Mary's.

**Inter-colony and extreme movement**

On 07 August 2022, a GPS-tagged parental Northern Gannet visited the nearest gannet colony at Baccalieu Island, NL, (~50–60 km further north than previously recorded foraging trips from Cape St. Mary's) for approximately 75 minutes before beginning its return

**TABLE 2**
**Dates and counts of swabs for highly pathogenic avian influenza virus testing in Northern Gannets *Morus bassanus* at Cape St. Mary's, Newfoundland and Labrador, Canada and the surrounding areas in 2022**

| Date | Status, age | Location | Number of birds | Number of positive tests |
|---|---|---|---|---|
| 02 July | Live, breeding adults | Mainland cliffs of Cape St. Mary's | 15 | 0 |
| 17 July | Dead, adults | Point Lance Beach (7.3 km from Cape St. Mary's colony) | 11 | 9 |

trip to Cape St. Mary's (Fig. 3A). The same individual made a second trip to the Baccalieu colony for approximately 60 minutes on 02 September. The HMM revealed that the individual engaged in area-restricted searches within 3 km of Baccalieu Island and performed dives within 50 km of the island.

A second individual undertook a 14-day foraging trip and an 18-day foraging trip on 23 July and 12 August, respectively (Fig. 3B). These trips were extreme relative to the median trip duration of 12.65 hours for gannets tracked in 2022.

## DISCUSSION

The 2022 reproductive success at the Cape St. Mary's Ecological Seabird Reserve was 17%, which is the lowest at this colony since records began in the 1970s (Fig. 2A; d'Entremont *et al.* 2022b). This reproductive failure is concerning, as it is much lower than the average reproductive success of Northern Gannets (Mowbray 2020). In some cases, it was lower than values recorded at highly disturbed breeding sites (Allbrook & Quinn 2020), at sites contaminated with pollutants that cause eggshell thinning (Chapdelaine *et al.* 1987), during prey shortages (d'Entremont *et al.* 2022b), and during marine heatwaves (Montevecchi *et al.* 2021). Reproductive failure at Cape St. Mary's in 2022 was likely due to the catastrophic effects of the HPAI outbreak. Reproductive failure associated with the ongoing HPAI panzootic was also observed at other colonies. For example, at Scotland's Bass Rock, the world's largest colony of Northern Gannets, reproductive success in 2022 was around 25% (Lane *et al.* 2023). The average reproductive success across all monitored years at colonies across the United Kingdom (72% ± 12%; Jeglinski *et al.* 2023) is comparable to that at Cape St. Mary's, emphasizing the severity of the HPAI impacts at these colonies. The low reproductive success likely resulted from nest abandonment by parental gannets, or possibly from chicks dying of AIV infection (Falchieri *et al.* 2022, Lane *et al.* 2023).

Most abandoned nests were likely due to adults succumbing to HPAI (Lane *et al.* 2023). Northern Gannets are not known to be regular hosts of AIV (Lang *et al.* 2016), and adult blood collected from before the 2022 outbreak lacked detectable antibodies against this virus (Lang *et al.* unpubl. Data). Northern Gannets are possibly more likely to succumb to HPAI due to a lack of pre-existing immunity, and they were the species most impacted by the HPAI panzootic in 2022 (Avery-Gomm *et al.* 2023, Lane *et al.* 2023). At Bass Rock, an estimated 71% of the colony abandoned or died (Lane *et al.* 2023). Across Canada, reported mortality of Northern Gannets accounted for 11% of the Canadian breeding population (Avery-Gomm *et al.* 2023). Given that so many adults were lost, it is not surprising that reproductive success was drastically reduced. Even if adults survived, they may have aborted nesting due to the high energetic cost of the immune response (Hanssen 2006, Hammouda *et al.* 2014) or to the increased effort to obtain food for chicks during the marine heatwave (Montevecchi *et al.* 2021, d'Entremont *et al.* 2022b).

At Cape St. Mary's, a "moderate" marine heatwave, as classified by Schlegel (2020), coincided with the onset of the 2022 AIV outbreak at the colony (Fig. 2B). The coincident occurrence of a marine heatwave may have exacerbated the stress experienced from HPAI, which may in turn explain the lower reproductive success experienced at Cape St. Mary's compared to Bass Rock, despite the greater estimated population loss at Bass Rock (Lane *et al.* 2023). There was no marine heatwave occurring within the foraging range of the Bass Rock colony at the time of the HPAI outbreak (Schlegel 2020, Lane *et al.* 2023, Jeglinski *et al.* 2024). Marine heatwaves have had significant impacts on seabird reproductive success (Newell *et al.* 2015, Piatt *et al.* 2020, Montevecchi *et al.* 2021). High SST can cause prey shortages that result in reduced reproductive success for Northern Gannets (d'Entremont *et al.* 2022b). The 2012 Northwest Atlantic marine heatwave event, which was classified as "strong" by Schlegel (2020), was stronger than the 2022 event and led to very poor reproductive success (41%) at Cape St. Mary's (Montevecchi *et al.* 2021, d'Entremont *et al.* 2022b). This contrasted with the 70% to 90% reproductive success that is typical across colonies and years (Mowbray 2020), yet it was considerably higher than the reproductive success of 2022. Heat stress can cause birds to be more susceptible to viral infection through depression of the immune response (Liew *et al.* 2003, Shini *et al.* 2010, Pawar *et al.* 2016). Therefore, the HPAI outbreak that coincided with the marine heatwave may explain the especially low reproductive success observed at Cape St. Mary's.

Abnormal foraging trips were also associated with the HPAI outbreak. We observed extreme trips by two parental gannets, one involving inter-colony movement (Fig. 2). During the three previous years of tracking gannets with GPS devices at this same nesting site (2019 to 2021, $n_{trips}$ = 719, $n_{birds}$ = 25; d'Entremont *et al.* 2022a), no other extreme trips (i.e., trips greater than four days in length) or inter-colony movements were recorded by breeding gannets. Inter-colony movements by non-breeding gannets have been documented during both the breeding season and migration (Votier *et al.* 2011, Bicknell *et al.* 2014), and movements between colonies by adult Cape Gannets *Morus capensis* have been observed, though occurrences are rare (Distiller *et al.* 2012). Only one other occurrence of inter-colony movement by a breeding Northern Gannet has been reported, and this occurrence was also coincident with an HPAI outbreak at its colony in the eastern Atlantic Ocean (Jeglinski *et al.* 2024). Inter-colony movement by breeding adults may be a response to excessive stress and poor breeding conditions, such as loss of a chick at the native colony.

Reproductive success at Cape St. Mary's has decreased over the past decade as a result of high SST reducing prey availability (d'Entremont *et al.* 2022b). Further, adult gannets and chicks nesting at our study site were preyed on by Eastern Coyotes *Canis latrans* in 2016, 2018, and 2021 (Montevecchi *et al.* 2019, d'Entremont & Montevecchi 2022). Coyotes are a new predator at this colony, having first arrived on the island of Newfoundland in 1985 (Blake 2006); they were first observed at Cape St. Mary's in 2010 (Montevecchi *et al.* 2019). The combined influences of

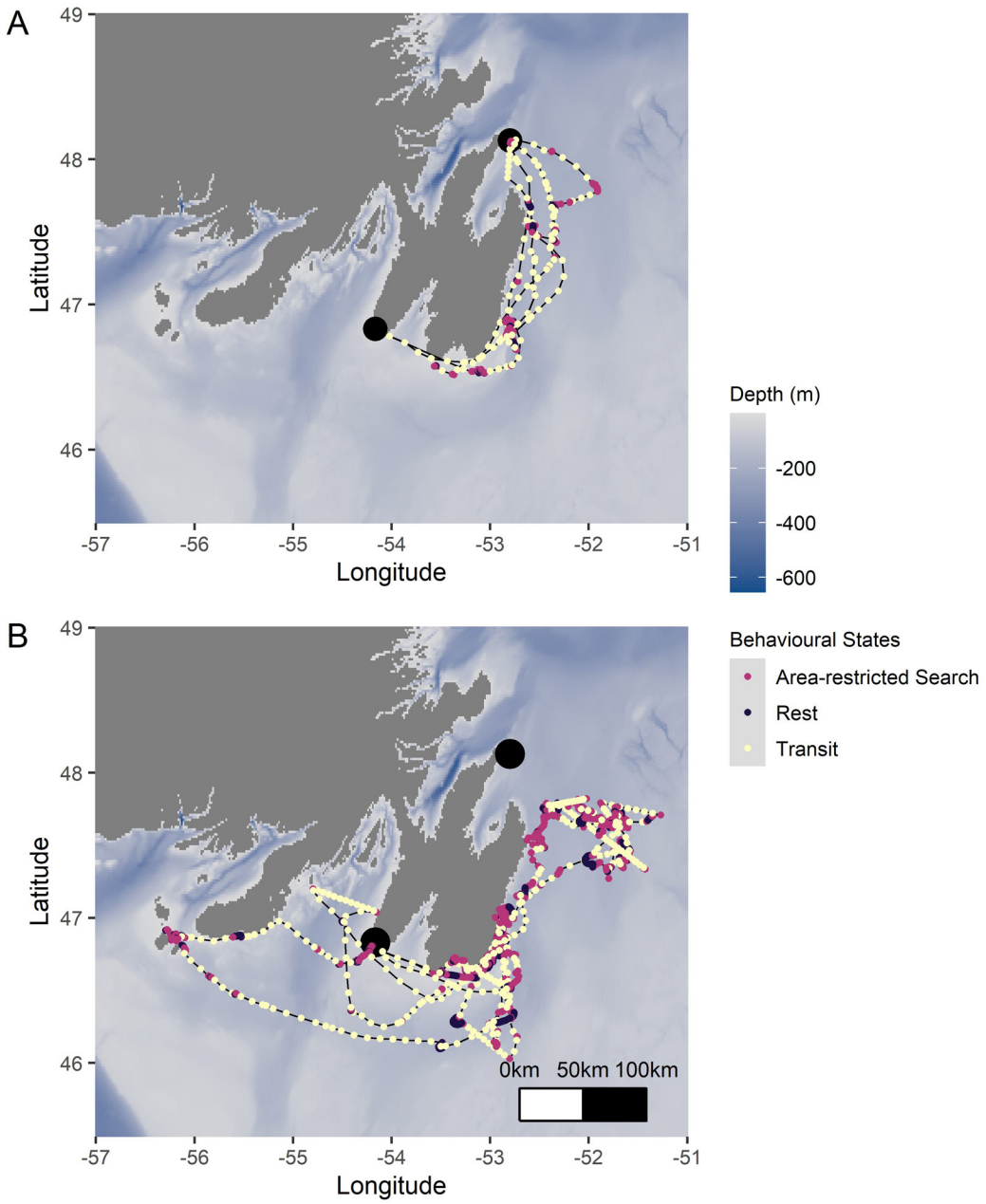


**Fig. 3.** A) Inter-colony and B) extreme foraging trips of parental Northern Gannets from Cape St. Mary's, Newfoundland and Labrador, Canada. The large black dots represent the Cape St. Mary's (south) and Baccalieu Island (north) colonies.

disease, prey shortages associated with increased SST, and coyote predation could have led to inter-colony movements by an adult prospecting for a safer and more productive breeding site. Inter-colony movements may also serve as a route by which AIV is spread between locations.

While low-pathogenic AIV circulation follows a yearly pattern in most migratory flyways (Kent *et al.* 2022), it remains to be seen how the introduction of the HPAI H5N1 into North American seabirds will change these dynamics. Susceptibility to the virus may increase during heat stress (Liew *et al.* 2003, Shini *et al.* 2010, Pawar *et al.* 2016), so continued increasing global and ocean temperatures could exacerbate circumstances if the virus continues to circulate in seabirds. Early reports from the 2023 breeding season show that Northern Gannets appear to be relatively unaffected by HPAI (BBC News 2023, CFIA NEOC GIS Services 2023). Given that H5N1 transmission is predicted to continue (Ramey *et al.* 2022) and that the frequency and intensity of marine heatwaves are predicted to increase (Oliver *et al.* 2019), the effects of viral outbreaks, along with the impacts from heat stress on mortality and reproductive success, warrant continued monitoring and investigation.

## ACKNOWLEDGMENTS

This paper was developed from the Undergraduate Honours thesis of NGC. We thank the staff at Cape St. Mary's Ecological Seabird Reserve for help with data collection and the NL Natural Areas Program for permitting. Special thanks to Chris Mooney, who

photographed the colony on a weekly basis throughout the breeding season and assisted with both GPS deployments and AIV sampling. We thank Parker Doiron and Mohammad Fahmy for assisting with HPAI sample collections and GPS deployments.

Research was supported by grants to WAM from Fisheries and Oceans Canada, Natural Sciences and Engineering Research Council of Canada (NSERC), and MUN. JW and IR were supported by funding from the School of Graduate Studies at MUN. JW was also supported by funding from the NSERC - Canadian Lake Pulse Network (NETGP 479720) and an NSERC Alexander Graham Bell Canada Graduate Doctoral Scholarship. We thank ECCC for providing materials and reagents to perform the AIV sampling and testing. Two anonymous reviewers provided valuable comments on our paper, and their efforts are much appreciated.

## REFERENCES

ALLBROOK, D.L. & QUINN, J.L. 2020. The effectiveness of regulatory signs in controlling human behaviour and Northern Gannet (*Morus bassanus*) disturbance during breeding: An experimental test. *Journal for Nature Conservation* 58: 125915. doi:10.1016/j.jnc.2020.125915

AVERY-GOMM, S., BARYCHKA, T., ENGLISH, M., ET AL. 2023. *A comprehensive summary of wild bird mortalities in eastern Canada during the 2022 Highly Pathogenic Avian Influenza (HPAI) outbreak*. Poster presented at the 71st Annual International Conference of the Wildlife Disease Association, 29 July–04 August, Athens, USA.

BARRILE, G.M., WALTERS, A., WEBSTER, M. & CHALFOUN, A.D. 2021. Informed breeding dispersal following stochastic changes to patch quality in a pond-breeding amphibian. *Journal of Animal Ecology* 90: 1878–1890. doi:10.1111/1365-2656.13503

BBC (BRITISH BROADCASTING CORPORATION) NEWS. 2023. *Bass Rock's gannet colony "recovering" after avian flu.* London, UK: BBC News. [Accessed at https://www.bbc.com/news/uk-scotland-edinburgh-east-fife-66120122 on 30 August 2023.]

BENNISON, A., BEARHOP, S., BODEY, T.W., ET AL. 2018. Search and foraging behaviors from movement data: A comparison of methods. *Ecology and Evolution* 8: 13–24. doi:10.1002/ece3.3593

BICKNELL, A.W.J., KNIGHT, M.E., BILTON, D.T., ET AL. 2014. Intercolony movement of pre-breeding seabirds over oceanic scales: Implications of cryptic age-classes for conservation and metapopulation dynamics. *Diversity and Distributions* 20: 160–168.

BIVAND, R.S., PEBESMA, E. & GÓMEZ-RUBIO, V. 2013. *Applied Spatial Data Analysis with R, 2nd Edition.* New York, USA: Springer.

BLAKE, J. 2006. *Coyotes in Insular Newfoundland: Current Knowledge and Management of the Island's Newest Mammalian Predator*. St. John's, Canada: Newfoundland and Labrador Department of Environment and Conservation, Wildlife Division.

CALIENDO, V., LEWIS, N.S., POHLMANN, A., ET AL. 2022. Transatlantic spread of highly pathogenic avian influenza H5N1 by wild birds from Europe to North America in 2021. *Scientific Reports* 12: 11729. doi:10.1038/s41598-022-13447-z

CAMPHUYSEN, K. & GEAR, S. 2022. *Great Skuas and Northern Gannets on Foula, summer 2022 - an unprecedented, H5N1 related massacre*. Dataset. Texel, The Netherlands: Nederlands Instituut voor Onderzoek der Zee (NIOZ, Royal Netherlands Institute for Sea Research). doi:10.25850/nioz/7b.b.gd

CFIA NEOC GIS SERVICES (CANADIAN FOOD INSPECTION AGENCY, NATIONAL EMERGENCY OPERATIONS CENTER, GEOGRAPHIC INFORMATION SYSTEM SERVICES). 2023. *High Pathogenicity Avian Influenza in Wildlife*. Ottawa, Canada: CFIA. [Accessed at https://cfia-ncr.maps.arcgis.com/apps/dashboards/89c779e98cdf492c899df23e1c38fdbc on 30 August 2023.]

CHAMPOUX, L., RAIL, J.-F. & LAVOIE, R.A. 2017. Polychlorinated dibenzo-*p*-dioxins, dibenzofurans, and flame retardants in Northern Gannet (*Morus bassanus*) eggs from Bonaventure Island, Gulf of St. Lawrence, 1994–2014. *Environmental Pollution* 222: 600–608. doi:10.1016/j.envpol.2016.09.055

CHAPDELAINE, G., LAPORTE, P. & NETTLESHIP, D.N. 1987. Population, productivity and DDT contamination trends of Northern Gannets (*Sula bassanus*) at Bonaventure Island, Quebec, 1967–1984. *Canadian Journal of Zoology* 65: 2922–2926. doi:10.1139/z87-443

COLLINS, S.M., HEDD, A., FIFIELD, D.A., WILSON, D.R. & MONTEVECCHI, W.A. 2022. Foraging paths of breeding Leach's Storm-Petrels in relation to offshore oil platforms, breeding stage, and year. *Frontiers in Marine Science* 9: 816659. doi:10.3389/fmars.2022.816659

CWHC (CANADIAN WILDLIFE HEALTH COOPERATIVE). 2023. *Inter-agency wild bird avian influenza survey update: A report of samples collected and tested as of April 10, 2023*. Saskatoon, Canada: CWHC.

DISTILLER, G., ALTWEGG, R., CRAWFORD, R.J.M., KLAGES, N.T.W. & BARHAM, B. 2012. Factors affecting adult survival and inter-colony movement at the three South African colonies of Cape Gannet. *Marine Ecology Progress Series* 461: 245–255. doi:10.3354/meps09807

D'ENTREMONT, K.J.N., DAVOREN, G.K., WALSH, C.J., WILHELM, S.I. & MONTEVECCHI, W.A. 2022a. Intra- and inter-annual shifts in foraging tactics by parental Northern Gannets *Morus bassanus* indicate changing prey fields. *Marine Ecology Progress Series* 698: 155–170. doi:10.3354/meps14164

D'ENTREMONT, K.J.N., GUZZWELL, L.M., WILHELM, S.I., ET AL. 2022b. Northern Gannets (*Morus bassanus*) breeding at their southern limit struggle with prey shortages as a result of warming waters. *ICES Journal of Marine Science* 79: 50–60. doi:10.1093/icesjms/fsab240

D'ENTREMONT, K.J.N. & MONTEVECCHI, W.A. 2022. Nocturnal flight activity by Northern Gannets *Morus bassanus* in response to predator disturbance. *Marine Ornithology* 50: 159–163.

EFSA (EUROPEAN FOOD SAFETY AUTHORITY), EUROPEAN CENTRE FOR DISEASE PREVENTION AND CONTROL, EUROPEAN UNION REFERENCE LABORATORY FOR AVIAN INFLUENZA, ET AL. 2023. Scientific report: Avian influenza overview March–April 2023. *EFSA Journal* 21: 8039. doi:10.2903/j.efsa.2023.8039

FALCHIERI, M., REID, S.M., ROSS, C.S., ET AL. 2022. Shift in HPAI infection dynamics causes significant losses in seabird populations across Great Britain. *Veterinary Record* 191: 271–316. doi:10.1002/vetr.2311

FAO (FOOD AND AGRICULTURE ORGANIZATION OF THE UNITED NATIONS). 2023. *Global AIV with Zoonotic Potential.* Animal Health. Rome, Italy: FAO. [Accessed at https://www.fao.org/animal-health/situation-updates/global-aiv-with-zoonotic-potential/en on 27 July 2023.]

HAMMOUDA, A., PEARCE-DUVET, J., BOULINIER, T. & SELMI, S. 2014. Egg sampling as a possible alternative to blood sampling when monitoring the exposure of Yellow-legged Gulls (*Larus michahellis*) to avian influenza viruses. *Avian Pathology* 43: 547–551. doi:10.1080/03079457.2014.972340

HANSSEN, S.A. 2006. Costs of an immune challenge and terminal investment in a long-lived bird. *Ecology* 87: 2440–2446. doi:10.1890/0012-9658(2006)87[2440:COAICA]2.0.CO;2

JEGLINSKI, J., LANE, J., VOTIER, S., ET AL. 2024. HPAIV outbreak triggers short-term colony connectivity in a seabird metapopulation. *Scientific Reports* 41: 3126. doi:10.1038/s41598-024-53550-x

JEGLINSKI, J.W.E., WANLESS, S., MURRAY, S., ET AL. 2023. Metapopulation regulation acts at multiple spatial scales: Insights from a century of seabird colony census data. *Ecological Monographs* 93: e1569. doi:10.1002/ecm.1569

KENT, C.M., RAMEY, A.M., ACKERMAN, J.T., ET AL. 2022. Spatiotemporal changes in influenza A virus prevalence among wild waterfowl inhabiting the continental United States throughout the annual cycle. *Scientific Reports* 12: 13083. doi:10.1038/s41598-022-17396-5

KIRKHAM, I.R. 1980. *Chick development and parental care in the Northern Gannet.* MSc thesis. St. John's, Canada: Memorial University of Newfoundland.

LANE, J.V., JEGLINSKI, J.W.E., AVERY-GOMM, S., ET AL. 2023. High pathogenicity avian influenza (H5N1) in Northern Gannets (*Morus bassanus*): Global spread, clinical signs, and demographic consequences. *Ibis* Advance publication online. doi:10.1111/ibi.13275

LANG, A.S., LEBARBENCHON, C., RAMEY, A.M., ROBERTSON, G.J., WALDENSTRÖM, J. & WILLE, M. 2016. Assessing the role of seabirds in the ecology of Influenza A Viruses. *Avian Diseases* 60: 378–386. doi:10.1637/11135-050815-RegR

LEWIS, S., HAMER, K.C., MONEY, L., GRIFFITHS, R., WANLESS, S. & SHERRATT, T.N. 2004. Brood neglect and contingent foraging behavior in a pelagic seabird. *Behavioral Ecology and Sociobiology* 56: 81–88. doi:10.1007/s00265-004-0762-0

LIEW, P.K., ZULKIFLI, I., HAIR-BEJO, M., OMAR, A.R. & ISRAF, D.A. 2003. Effects of early age feed restriction and heat conditioning on heat shock protein 70 expression, resistance to infectious bursal disease, and growth in male broiler chickens subjected to heat stress. *Poultry Science* 82: 1879–1885. doi:10.1093/ps/82.12.1879

MCCLINTOCK, B.T. & MICHELOT, T. 2018. momentuHMM: R package for generalized hidden Markov models of animal movement. *Methods in Ecology and Evolution* 9: 1518–1530. doi:10.1111/2041-210X.12995

MONTEVECCHI, W., POWER, K., WHITE, E., ET AL. 2019. Eastern coyote *Canis latrans* predation on adult and pre-fledgling Northern Gannets *Morus bassanus* nesting on mainland cliffs at Cape St. Mary's, Newfoundland, Canada. *Marine Ornithology* 47: 39–42.

MONTEVECCHI, W.A., REGULAR, P.M., RAIL, J.-F., ET AL. 2021. Ocean heat wave induces breeding failure at the southern breeding limit of the Northern Gannet *Morus bassanus. Marine Ornithology* 49: 71–78.

MOWBRAY, T.B. 2020. Northern Gannet (*Morus bassanus*), version 1.0. In: BILLERMAN, S.M. (Ed.) *Birds of the World*. Ithaca, USA: Cornell Lab of Ornithology

NASA (NATIONAL AERONAUTICS AND SPACE ADMINISTRATION). 2023. *Multi-scale Ultra-high Resolution (MUR) SST Analysis fv04.1, Global, 0.01°, 2002–present, Daily.* Dataset MUR-JPL-L4-GLOB-v4.1. Washington, USA: NASA Jet Propulsion Laboratory. [Accessed at https://coastwatch.pfeg.noaa.gov/erddap/griddap/jplMURSST41.html on 14 Mar 2023.]

NEWELL, M., WANLESS, S., HARRIS, M.P. & DAUNT, F. 2015. Effects of an extreme weather event on seabird breeding success at a North Sea colony. *Marine Ecology Progress Series* 532: 257–268. doi:10.3354/meps11329

OLIVER, E.C.J., BURROWS, M.T., DONAT, M.G., ET AL. 2019. Projected marine heatwaves in the 21st century and the potential for ecological impact. *Frontiers in Marine Science* 6: 734.

PAWAR, S.S., BASAVARAJ, S., DHANSING, L.V., ET AL. 2016. Assessing and mitigating the impact of heat stress in poultry. *Advances in Animal and Veterinary Sciences* 4: 332–341. doi:10.14737/journal.aavs/2016/4.6.332.341

PIATT, J.F., PARRISH, J.K., RENNER, H.M., ET AL. 2020. Extreme mortality and reproductive failure of Common Murres resulting from the northeast Pacific marine heatwave of 2014–2016. *PLoS One* 15: e0226087. doi:10.1371/journal.pone.0226087

R CORE TEAM. 2022. *R: A language and environment for statistical computing*. Vienna, Austria: The R Foundation for Statistical Computing.

RAMEY, A.M., HILL, N.J., DELIBERTO, T.J., ET AL. 2022. Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America. *The Journal of Wildlife Management* 88: e22171. doi:10.1002/jwmg.22171

SCHLEGEL, R.W. 2020. *Marine Heatwave Tracker, version v1.0.1.* Meyrin, Switzerland: European Organization for Nuclear Research. doi:10.5281/ZENODO.3787872

SHINI, S., HUFF, G.R., SHINI, A. & KAISER, P. 2010. Understanding stress-induced immunosuppression: Exploration of cytokine and chemokine gene profiles in chicken peripheral leukocytes. *Poultry Science* 89: 841–851. doi:10.3382/ps.2009-00483

SPACKMAN, E. (Ed.). 2020. *Animal Influenza Virus: Methods and Protocols, 3rd Edition.* New York, USA: Humana New York. doi:10.1007/978-1-0716-0346-8

SPACKMAN, E., SENNE, D.A., MYERS, T.J., ET AL. 2002. Development of a real-time reverse transcriptase PCR assay for type A influenza virus and the avian H5 and H7 hemagglutinin subtypes. *Journal of Clinical Microbiology* 40: 3256–3260. doi:10.1128/jcm.40.9.3256-3260.2002

VOTIER, S.C., GRECIAN, W.J., PATRICK, S. & NEWTON, J. 2011. Inter-colony movements, at-sea behaviour and foraging in an immature seabird: Results from GPS-PPT tracking, radio-tracking and stable isotope analysis. *Marine Biology* 158: 355–362. doi:10.1007/s00227-010-1563-9