

High pathogenicity avian influenza (H5N1) in Northern Gannets (*Morus bassanus*): Global spread, clinical signs and demographic consequences

JUDE V. LANE,*¹ ID JANA W.E. JEGLINSKI,² ID STEPHANIE AVERY-GOMM,³ ID
 ELMAR BALLSTAEDT,⁴ ASHLEY C. BANYARD,⁵ ID TATSIANA BARYCHKA,³ ID IAN H. BROWN,⁵ ID
 BRIGITTE BRUGGER,⁶ ID TORI V. BURT,⁷ ID NOAH CAREEN,⁷ JOHAN H.F. CASTENSCHILD,⁸
 SIGNE CHRISTENSEN-DALSGAARD,⁹ ID SHANNON CLIFFORD,² SYDNEY M. COLLINS,⁷ ID
 EMMA CUNNINGHAM,¹⁰ JÓHANNIS DANIELSEN,¹¹ FRANCIS DAUNT,¹² ID KYLE J.N. D'ENTREMONT,⁷ ID
 PARKER DOIRON,⁷ STEVEN DUFFY,¹³ MATTHEW D. ENGLISH,¹³ MARCO FALCHIERI,⁵ JOLENE GIACINTI,³ ID
 BRITT GJERSET,¹⁴ SILJE GRANSTAD,¹⁴ DAVID GRÉMILLET,^{15,16} ID MAGELLA GUILLEMETTE,¹⁷
 GUNNAR T. HALLGRÍMSSON,¹⁸ KEITH C. HAMER,¹⁹ ID SJÚRÐUR HAMMER,^{20,21} ID KATHERINE HARRISON,²²
 JUSTIN D. HART,²³ CIARAN HATSELL,²⁴ RICHARD HUMPIDGE,²⁵ JOE JAMES,⁵ ID AUDREY JENKINSON,²²
 MARK JESSOPP,²⁶ ID MEGAN E.B. JONES,²⁷ STÉPHANE LAIR,²⁸ THOMAS LEWIS,⁵ ID
 ALEXANDRA A. MALINOWSKA,²⁹ ID ALY MCCLUSKIE,¹ GRETCHEN MCPHAIL,⁷ BØRGE MOE,⁹ ID
 WILLIAM A. MONTEVECCHI,⁷ ID GREG MORGAN,³⁰ CAROLINE NICHOL,³¹ CRAIG NISBET,²⁴
 BERGUR OLSEN,¹¹ JENNIFER PROVENCHER,³ ID PASCAL PROVOST,³² ALEX PURDIE,²³
 JEAN-FRANÇOIS RAIL,¹³ GREG ROBERTSON,³ ID YANNICK SEYER,¹⁷ ID MAGGIE SHEDDAN,³³
 CATHERINE SOOS,³ ID NIA STEPHENS,³⁰ HALLVARD STRØM,³⁴ ID VILHJÁLMUR SVANSSON,³⁵
 T. DAVID TIERNEY,³⁶ GLEN TYLER,³⁷ TOM WADE,³¹ SARAH WANLESS,¹² ID CHRISTOPHER R.E. WARD,¹³ ID
 SABINA I. WILHELM,¹³ ID SASKIA WISCHNEWSKI,¹ ID LUCY J. WRIGHT,¹ ID BERNIE ZONFRILLO,²
 JASON MATTHIOPOULOS² ID & STEPHEN C. VOTIER³⁸ ID

¹RSPB Centre for Conservation Science, Sandy, Bedfordshire, UK

²School of Biodiversity, One Health and Veterinary Medicine, University of Glasgow, Glasgow, UK

³Wildlife and Landscape Science Directorate, Science & Technology Branch, Environment and Climate Change Canada, Ottawa, Ontario, Canada

⁴Verein Jordsand zum Schutz der Seevögel und der Natur e. V., Ahrensburg, Germany

⁵Influenza and avian virology workgroup, Animal and Plant Health Agency, Weybridge, Addlestone, Surrey, UK

⁶Icelandic Food and Veterinary Authority, 800 Selfoss, Iceland

⁷Psychology Department, Memorial University of Newfoundland and Labrador, St. John's, Newfoundland and Labrador, Canada

⁸Aarhus University, Department of Ecoscience, Roskilde, Denmark

⁹Norwegian Institute for Nature Research (NINA), Trondheim, Norway

¹⁰Institute of Evolutionary Biology, School of Biology, Centre for Immunity, Infection and Evolution, University of Edinburgh, Edinburgh, UK

¹¹Seabird Ecology Department, Faroe Marine Research Institute, Tórshavn, Faroe Islands

¹²UK Centre for Ecology & Hydrology, Penicuik, UK

¹³Canadian Wildlife Service, Environment and Climate Change Canada, Ottawa, Ontario, Canada

¹⁴Norwegian Veterinary Institute, Ås, Norway

¹⁵CEFE, Univ Montpellier, CNRS, EPHE, IRD, Montpellier, France

¹⁶FitzPatrick Institute, DST/NRF Excellence Centre at the University of Cape Town, Rondebosch, South Africa

¹⁷Department of Biology, Chemistry and Geography, Université du Québec à Rimouski, Rimouski, Québec, Canada

¹⁸Department of Life and Environmental Sciences, University of Iceland, Reykjavik, Iceland

¹⁹School of Biology, University of Leeds, Leeds, UK

²⁰Faroese Environment Agency, Argir, Faroe Islands

²¹University of the Faroe Islands, Tórshavn, Faroe Islands

²²Department of Agriculture, Food and the Marine (DAFM), Dublin, Ireland

²³Alderney Wildlife Trust, Alderney, Channel Islands

²⁴National Trust for Scotland, Hermiston Quay, Edinburgh, UK

²⁵RSPB, Edinburgh, UK

²⁶*School of Biological, Earth & Environmental Sciences, University College Cork, Cork, Cork, Ireland*

²⁷*University of Prince Edward Island, Charlottetown, Prince Edward Island, Canada*

²⁸*Centre québécois sur la santé des animaux sauvages, Canadian Wildlife Health Cooperative, Faculté de médecine vétérinaire, Université de Montréal, St. Hyacinthe, Québec, Canada*

²⁹*RSPB Orkney, Stromness, UK*

³⁰*RSPB Ramsey Island, St Davids, Pembrokeshire, UK*

³¹*School of Geosciences, University of Edinburgh, Edinburgh, UK*

³²*Ligue pour la Protection des Oiseaux, Réserve Naturelle Nationale des Sept-Iles, Pleumeur Bodou, France*

³³*Scottish Seabird Centre, North Berwick, UK*

³⁴*Norwegian Polar Institute, Fram Centre, Tromsø, Norway*

³⁵*Institute for Experimental Pathology, Biomedical Center, University of Iceland, Keldur, Iceland*

³⁶*Science and Research Directorate, National Parks and Wildlife Service, Dublin-7, Ireland*

³⁷*NatureScot, Great Glen House, Inverness, UK*

³⁸*Lyell Centre, Institute for Life and Earth Sciences, Heriot-Watt University, Edinburgh, UK*

During 2021 and 2022 High Pathogenicity Avian Influenza (HPAI) killed thousands of wild birds across Europe and North America, suggesting a change in infection dynamics and a shift to new hosts, including seabirds. Northern Gannets *Morus bassanus* appeared to be especially severely impacted, but a detailed account of the data available is required to help understand how the HPAI virus (HPAIV) spread across the meta-population, and the ensuing demographic consequences. Accordingly, we analyse information on confirmed and suspected HPAIV outbreaks across most North Atlantic Gannet colonies and, for the largest colony (Bass Rock, UK), provide impacts on population size, breeding success, and preliminary results on apparent adult survival and serology. Unusually high numbers of dead Gannets were first noted at colonies in Iceland during April 2022. Outbreaks in May occurred in many Scottish colonies, followed by colonies in Canada, Germany and Norway. By the end of June, outbreaks had occurred in colonies in Canada and the English Channel. Outbreaks in 12 UK and Ireland colonies appeared to follow a clockwise pattern with the last infected colonies recorded in late August/September. Unusually high mortality was recorded at 40 colonies (75% of global total colonies). Dead birds testing positive for HPAIV H5N1 were associated with 58% of these colonies. At Bass Rock, the number of occupied nest-sites decreased by at least 71%, breeding success declined by c. 66% compared with the long-term UK mean and the resighting of marked individuals suggested that apparent adult survival between 2021 and 2022 could have been substantially lower than the preceding 10-year average. Serological investigation detected antibodies specific to H5 in apparently healthy birds, indicating that some Gannets recover from HPAIV infection. Further, most of these recovered birds had black irises, suggestive of a phenotypic indicator of previous infection. Untangling the impacts of HPAIV infection from other challenges faced by seabirds is key to establishing effective conservation strategies for threatened seabird populations as the likelihood of further epizootics increases, due to increasing habitat loss and the industrialization of poultry production.

Keywords: avian flu, disease, immunity, seabirds, virus outbreak.

*Corresponding author.
Email: jude.lane@rspb.org.uk
Twitter: [heyjoode](https://twitter.com/heyjoode)

The increasing frequency and severity of disease outbreaks linked with climate warming require improved methods for detecting and quantifying

impacts (Harvell *et al.* 2002). High pathogenicity avian influenza virus (HPAIV) H5Nx has negatively impacted wild and domestic bird populations globally for decades (Nuñez & Ross 2019). However, the current global panzootic of H5Nx has seen shifts in both the seasonality of outbreaks and the species affected (EFSA *et al.* 2023). H5Nx (A/goose/Guangdong/1/1996 (Gs/GD) H5N1) was first detected in 1996 on a domestic goose farm in Guangdong Province, China (Xu *et al.* 1999). This goose Guangdong lineage (Gs/Gd) has since caused significant outbreaks in a variety of bird populations and has also raised concerns about the potential zoonotic consequences for humans (Wan 2012, EFSA *et al.* 2023). Genetic reassortment has led to the emergence and evolution of multiple subtypes and genotypes of this group of high pathogenicity viruses on a global scale, potentially with different epidemiological properties, especially with respect to host range in wild birds (Monne *et al.* 2014, Falchieri *et al.* 2022). The mechanism of viral transmission is probably a combination of infected wild bird migration and the global domestic poultry trade or their products, although the mechanism of spread between colonies of seabirds may involve other types of movements (Blagodatski *et al.* 2021, Ramey *et al.* 2022).

Low pathogenicity avian influenza virus (LPAIV) is widely circulating in wild aquatic birds; Anseriformes (waterfowl) and Charadriiformes (shorebirds) are known to act as reservoirs (Venkatesh *et al.* 2018); however, we know little about the recent emergence, spread and impact of HPAIV in aquatic birds, including seabirds (Burggraff *et al.* 2014, Falchieri *et al.* 2022, Boulinier 2023, Roberts *et al.* 2023). HPAIVs do not originate within wild bird populations but once they have spilled into wild populations, they are transmitted via infected saliva, nasal secretions and faeces; however, shedding methods differ between species and are not well understood (Arnal *et al.* 2014, Caliendo *et al.* 2020).

The winter of 2021/22 saw a record number of confirmed cases of HPAIV H5N1 in poultry, captive and wild birds across Europe (EFSA *et al.* 2023). HPAIV H5N1 was first detected in UK breeding seabirds in July 2021, when Great Skuas *Stercorarius skua* on Fair Isle, Scotland, tested positive (Banyard *et al.* 2022). The first case of H5N1 detected in North American seabirds was in a Great Black-backed Gull *Larus marinus* in

Newfoundland and Labrador, Canada, in November 2021, with phylogenetic analyses revealing that the virus was of the European H5N1 lineage (Caliendo *et al.* 2022). In early April 2022, Common Eider *Somateria mollissima* was the first seabird species to test positive for HPAIV in the UK that year, followed in late April by Great Skuas (Falchieri *et al.* 2022). Then followed an unprecedented epidemic in seabirds across the North Atlantic, with Northern Gannets *Morus bassanus* (hereafter Gannet), previously unknown to have been impacted by H5Nx, being severely impacted (Cunningham *et al.* 2022).

Gannets breed in 53 colonies of various sizes (< 10 to > 60 000 breeding pairs and non-breeding immatures) on sea cliffs, stacks and islands across both sides of the North Atlantic from Russia to northeastern North America (d'Entremont *et al.* 2022, Jeglinski *et al.* 2023). During the breeding season, Gannets are medium-range foragers, capable of travelling more than 1000 km to find food (Hamer *et al.* 2007), whereas immatures generally travel further and also prospect other colonies (Votier *et al.* 2011, 2017, Grecian *et al.* 2018). During the non-breeding period, Gannets are migratory with birds from Iceland and the eastern Atlantic occupying marine wintering grounds in UK waters and Iberia, with the majority wintering off the coast of West Africa (Veron & Lawlor 2009, Fort *et al.* 2012, Furness *et al.* 2018, Deakin *et al.* 2019). Birds from the western Atlantic primarily winter along the coasts of the eastern USA south to the Gulf of Mexico, although some also winter off the coast of West Africa (Fifield *et al.* 2014). Considering the oral-faecal spread of avian influenza viruses, opportunities for spread between Gannets are most likely at the colony, but may also occur at foraging grounds and wintering areas by asymptomatic birds or birds in the early stages of infection (Weber & Stilianakis 2007), although this is a topic on which little is known.

Globally, Gannets are classified as Least Concern by the International Union for Conservation of Nature (IUCN) due to their wide distribution and growing populations in Europe and North America (IUCN, BirdLife International 2023). The European population comprises 75–94% of the global population with 55.6% breeding in the UK (IUCN, BirdLife International 2023). The Bass Rock, Scotland (56°6'N, 2°36'W), is the world's largest Gannet colony with an estimated 75 259

apparently occupied sites in 2014 (Murray *et al.* 2015).

Understanding virus spread and infection outcome is essential to evaluate how the HPAIV outbreak impacted Gannets and other seabirds. Here, we provide the first comprehensive assessment of the spatio-temporal detection of HPAIV outbreaks at most Gannet colonies across their North Atlantic breeding range. Moreover, to better understand HPAIV transmission and immunity, and the potential for population recovery, we present detailed results from the largest gannetry at Bass Rock, Scotland. We quantify the influence of the 2022 HPAIV outbreak on adult survival and breeding success. Moreover, based on unusual observations of Gannets with dark (as opposed to the normal pale blue) irises in 2022, we test the hypothesis that this is related to exposure based on serology.

METHODS

Global context: HPAIV spread across the North Atlantic Gannet meta-population

To create an overview of the occurrence and spread of HPAIV across the Gannet meta-population (as defined by Jeglinski *et al.* 2023) we aimed to collate the first date of detection of unusually high Gannet mortalities for each Gannet colony. Direct observations of unusually high mortality or of its absence ($n = 1$) were available for 22 of the 53 colonies (see Supporting Online Information Table S1). Unusually high levels of mortality are hereby defined as levels exceeding normal observable Gannet mortality during the breeding season. Gannet mortality at the colony is very low in normal years, so relied on the expertise of fieldworkers, wardens and local observers familiar with the respective colonies. There were no direct observations available for colonies in Iceland, Norway and most of the Irish colonies, because of their remoteness and inaccessibility, but unusual numbers of dead Gannets (again defined as difference to the background of very low mortality in normal years) had been washing up on beaches in the vicinity of these colonies and had been reported to the relevant authorities or logged on specific apps for bird observation. We made use of these data by gathering information on dead Gannet sightings for 2022 reported to the Norwegian Species Observation System (<http://www.artsobservasjoner.no>), to the Icelandic Food and Veterinary Authority, and to the Department of Agriculture, Food and the Marine's Avian Check App (<https://aviancheck.apps.services.agriculture.gov.ie/>). Data were provided as number of carcasses, date of observation and geographical coordinates of observation, and we associated these observations with the nearest Gannet breeding colony.

We also collated information on positive HPAIV tests associated with Gannet colonies where available, based on carcasses sampled directly at colonies or in the vicinity, based on data from the national testing laboratories for the relevant countries.

We also collated information on positive HPAIV tests associated with Gannet colonies where available, based on carcasses sampled directly at colonies or in the vicinity, based on data from the national testing laboratories for the relevant countries.

Case study: Impact of HPAIV on the Bass Rock Gannet colony

Health and safety and biosecurity

Strict biosecurity and health and safety measures were followed to ensure the safety of birds and field workers. During handling, our personal protection equipment comprised coveralls, face masks, goggles, disposable aprons and gloves. Safe4 disinfectant was used for disinfecting equipment and footwear (see Supporting Online Information Appendix S1).

Impact of HPAIV on apparently occupied sites, breeding success, adult survival and immatures

Apparently occupied sites. To identify the number of sites occupied by live birds, a DJI Matrice 300 RTK uncrewed aircraft system fitted with a DJI-Zenmuse L1 LiDAR and photogrammetry sensor was flown over Bass Rock between 3:07 and 3:19 PM on 30 June to count live and dead birds. All flights were conducted from the southern tip of the island with a Real-Time-Kinematic (RTK) base station, in good light with light winds ($< 5 \text{ ms}^{-1}$) enabling a flight speed of 4 ms^{-1} , with image side-lap of 70% and end-lap of 80%. The resulting 102 images (captured with 0.001 s shutter speed and auto ISO) collected at an altitude of 100 m above ground level, were processed through Agisoft Metashape (Agisoft LLC, St Petersburg, Russia) to produce an orthomosaic of the Bass Rock with a ground sampling distance of approximately 3 cm (see Supporting Online Information, Appendix S2). The composite image was loaded into

DotDotGoose version 1.5.3 (DotDotGoose (amnh.org)) to allow manual counting of birds on the colony. White birds were presumed to be adults but could not be distinguished from 4- to 5-year-old immatures. Birds were considered dead based on spread wings or contorted body shape, or alive if their posture was apparently natural. Birds that could not be clearly categorized were classed as alive to avoid overestimating the at-colony mortality.

Immature Gannets, identified by their plumage, are predominantly found on the fringes of the Bass Rock colony alongside non-breeding adults. In recent years, club sites (areas containing non-breeding birds) on the Bass Rock have become smaller and dominated by non-breeding adults and older (4–5 years) immatures. Immature birds typically arrive at the colony later than breeding adults, but club sites are full by the end of June. Younger immature birds (2–3 years) typically arrive later in the summer, during July and August, and are predominately seen in flight around the colony or on the lower ledges of the colony just above sea height. A count of immature and non-breeding birds was not possible because the club sites were empty on the date of the survey.

Breeding success. We monitored 93 active nests in two study sites, during 14 visits between 15 June and 14 August 2022. Nests are located on all aspects of the Bass Rock, on ground varying from vertical to horizontal. The study sites were located on horizontal ground within the main colony on the south-facing aspect. The sites were established as study areas over 20 years ago for tagging and marking and resighting colour-ringed breeding adults (Hamer *et al.* 2000). Photographs of the study areas were taken on the first visit and active nests marked on the images to enable the outcome of each nest to be determined. All nests had an egg on the first visit, and those with a chick on 14 August were considered successful.

Adult survival. Visual searches for 370 colour-ringed breeding adults (marked within three study sites during 2010–21) took place weekly from 15 June until 30 July 2022 on a total of 12 days. Gannets are site faithful, and breeders will return annually to the same nest or within close proximity. Nest-sites of colour-ringed birds were repeatedly scanned from a distance of between c.

5 and 30 m, and the ring sequence of each bird was recorded during a total of c. 11 person-observation hours each day. Resighting of marked birds has taken place on the Bass Rock annually during July since 2011. We therefore constructed annual encounter histories (1 for present, 0 for absent) for each marked bird using resighting data from visits made in July 2011–22 to estimate apparent annual survival between 2011 and 2022. We used Cormack–Jolly–Seber models for the capture–mark–recapture analysis. The most suitable models for open populations do not distinguish between mortality and emigration and produce estimates of apparent survival that assume the probability of detection is equal (Lebreton *et al.* 1992). A goodness-of-fit test showed that a fully time-dependent (both survival (ϕ) and resighting (p) probabilities vary with time) Cormack–Jolly–Seber model did not fit the data well (goodness-of-fit: $\chi^2_{34} = 73.33$, $P < 0.01$) with evidence of trap dependence (TEST2.CT; $z = -6.1484$, two-sided test, $P < 0.01$) but no evidence for transience (TEST3.SR; $z = -1.9044$, two-sided test, $P = 0.056$). After accounting for trap-dependence, a variance inflation factor (\hat{c}) of 1.212 was estimated by U-CARE (Choquet *et al.* 2009). We set $\hat{c} = 1.212$ to account for the over-dispersion in the data and a two-stage Time Since Marking structure was applied to model resightings with the first year after marking was set to a constant probability but then allowed to vary with time.

Models were specified in MARK (Version 9.0, White & Burnham 1999) with the candidate model set ($n = 4$) built so that the survival and resighting probability parameters could vary with year (t) or remain constant over time (c).

Serology and iris colour

Gannets have pale blue-grey irises, but from the first monitoring visits on 15 and 16 June, Gannets with completely black or mottled irises were observed (in some cases there was variation between the left and right eye, see Supporting Online Information Fig. S1). The dark and mottled eyes did not present like a dilated pupil, and we suspected this phenotype to be linked to a previous or current HPAIV infection.

During September 2022 we caught 19 apparently healthy adults and took c. 1 mL of blood from the tarsal vein (under licence from the UK Home Office; Project licence number

PEAE7342F). Sampling effort focused on catching equal numbers of birds with healthy blue-grey and abnormally black irises. Where possible, birds with chicks ($n = 8$) were caught preferentially to guarantee that they had been present throughout the HPAIV outbreak. Birds without chicks ($n = 11$) were caught if they appeared to be holding a territory; all birds with black irises fell into this second category as there were no birds with black irises and chicks. Birds were caught from seven distinct locations to minimize potential bias in virus exposure between clusters of nests.

We took external cloacal swabs from 18 of the 19 birds to test for any possible asymptomatic HPAIV infection. Blood and cloacal swabs were stored in a cool bag with ice blocks in the field, then stored at c. 4°C before being transported directly to the UK reference laboratory for avian influenza at the Animal and Plant Health Agency. Blood samples were tested for an indication of previous infection using a haemagglutination inhibition assay to detect antibodies to H5 avian influenza virus (clade 2.3.4.4b) using a viral antigen homologous to the outbreak virus. Birds that tested positive for H5 antibodies were presumed to have been infected with and recovered from H5N1 during the 2022 outbreak. Swabs were tested for influenza A virus nucleic acid following RNA extraction using a matrix (M) gene-specific real-time reverse-transcriptase polymerase chain reaction assay (Nagy *et al.* 2021) and an HPAIV-specific H5 polymerase chain reaction assay (James *et al.* 2022). Birds that tested positive for avian influenza virus were assumed to have a current H5N1 infection. Unless already ringed, birds were fitted with a metal British Trust for Ornithology ring and a blue plastic Darvic ring engraved with a unique alphanumeric code to allow future identification.

A Fisher's exact test was used to determine the associations between iris colour and exposure status. Statistical analyses were performed using R 4.1.1 (R Core Team 2016).

RESULTS

Global context: HPAIV spread across the North Atlantic Gannet meta-population

We gathered evidence of confirmed and suspected HPAI outbreaks at 41 of the 53 colonies.

Unusually large numbers of dead Gannets were detected at 40 of the 41 colonies during the breeding season; only one colony (Bjørnøya) was not affected, and 12 colonies were not monitored or associated with observations of dead Gannets (Fig. 1). Positive H5N1 samples were associated with 24 of the 41 sampled colonies (58%), either through direct sampling of dead Gannets from the colony or by proximity of dead Gannets to colonies. A small colony at Store Ulvøyholmen, Norway (330 apparently occupied nests in 2015, Barrett *et al.* 2017), was reported abandoned (Børge Moe, pers. comm.) and, as dead Gannets were reported close to the colony, this may have been due to HPAI. One Gannet sample from a bird found dead at Kjelmøya (Norway) tested positive for H5N5.

The first outbreaks to be detected occurred in the northeast Atlantic in Iceland (at Eldey, Brándur and Raudinupur during mid- to late April), followed by Shetland, Scotland (Noss and Hermaness in early May) then the Outer Hebrides, Scotland (St Kilda, 10 May). Subsequent outbreaks were then detected from early June in southern Norway (Runde, 8 June). The concurrent, southwards detection occurred along the east coast of the UK (e.g. Troup Head, mid-May, Bass Rock early June). By mid-June, HPAIV outbreaks were detected in northern Norway (Syltefjord, mid-June), the southern North Sea (Heligoland, mid-June), the Channel Islands (Les Etacs and Ortac, late June) and the southernmost colony Rouzic, France (early July). In July and early August, signs of HPAI were detected in northwest Norway, the Faroe Islands (Mykineshólmur) and in a clockwise progression around the UK, followed by Wales (Grassholm, mid-July) and then in Ireland (Clare Island, Lambay, Bull Rock, Little Skellig, Great Saltee, Ireland's Eye; mid- to late August, and early to mid-September, respectively). The northernmost colony Bjørnøya (52 apparently occupied nests in 2016, Barrett *et al.* 2017) appeared unaffected by HPAIV. No information was available for several remote colonies in the west and northwest of Scotland but unusually high mortality at Sule Skerry was detected after the breeding season in October (Harris & Wanless 2023).

The outbreaks in the northwest Atlantic meta-population appeared to develop in parallel to these in the northeast, with the earliest outbreaks detected between early and mid-May in the three colonies in the Gulf of St Lawrence (at Rochers

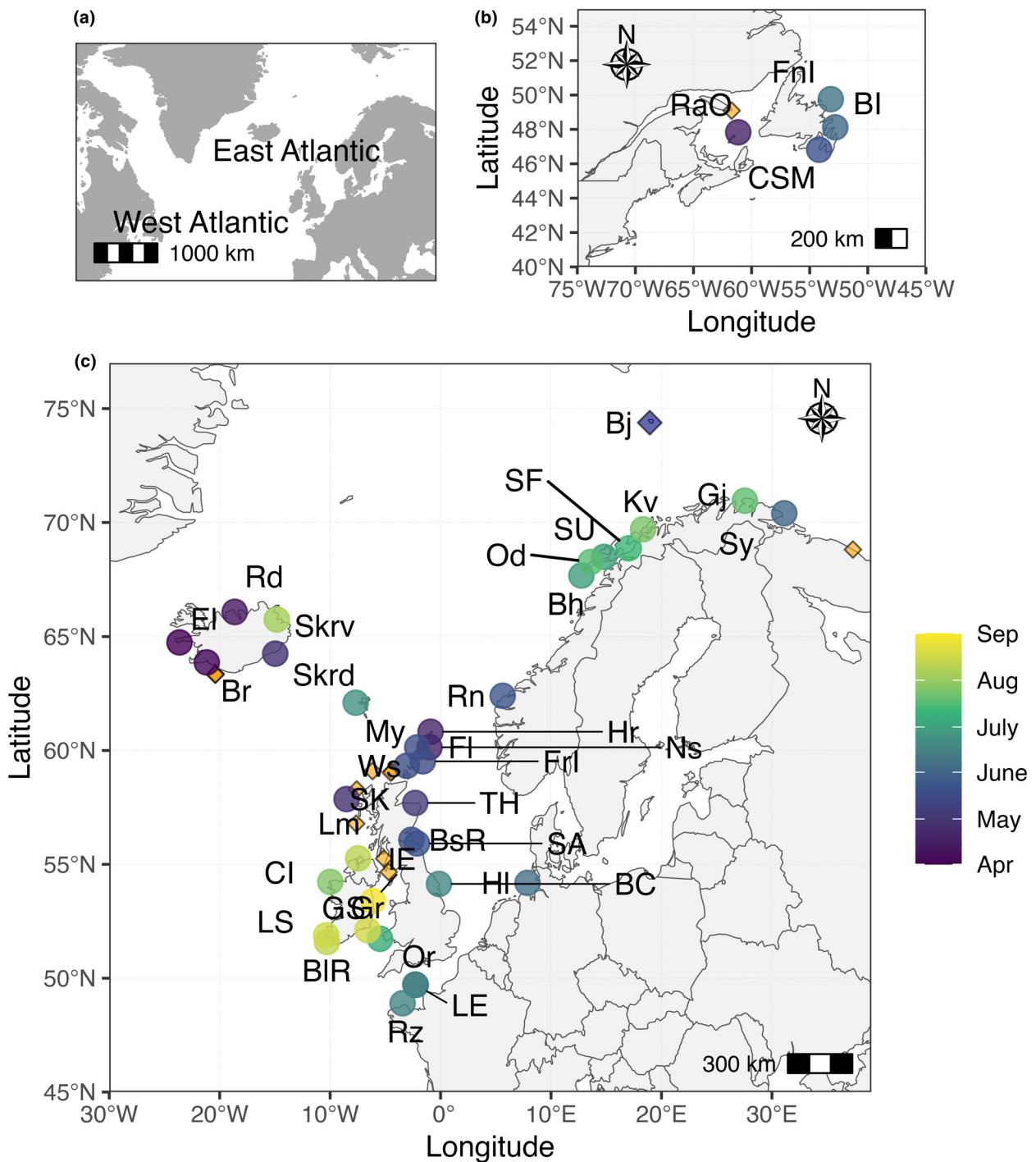


Figure 1. The timing of HPAIV outbreaks across the Gannet meta-population in 2022, based on the first date unusual mortalities in adults were observed. Affected colonies ($n = 40$) are indicated by circles, coloured by date. Colonies where information was unavailable ($n = 12$) are indicated by open diamonds. Letter combinations indicate colony name abbreviations (for full colony name see Supplementary Online Material, Table S1). (a) Geographical context; (b) colonies in the west Atlantic; (c) colonies in the east Atlantic. A filled diamond indicates Bjørnøya (Bj, Norway, the northernmost colony, H. Strøm pers. obs.) where no signs of HPAIV were observed. The Store Ulvøyholmen colony (SU) was found abandoned (confirmation received 29 June 2022 in litt.). No signs of HPAIV were detected in the colony Ailsa Craig (AC) between Northern Ireland and Scotland on 28 July 2022, but there was no visit later in the season when the surrounding colonies were affected.

aux Oiseaux, Magdalen Islands and Île Bonaventure) followed by the colonies in Newfoundland throughout June (Cape St Mary's, Baccalieu Island and Funk Island).

Case study: Impact of HPAIV on the Bass Rock Gannet colony

Unusually high Gannet mortality during incubation in early June 2022 was the first suggestion of an HPAIV outbreak at the Bass Rock and subsequent testing of four carcasses from 4 June proved positive for clade 2.3.4.4b HPAIV H5N1.

Impact of HPAIV on apparently occupied sites, breeding success, adult survival and immatures

Apparently occupied sites. A total of 21 227 live birds were counted on 30 June 2022. An additional 5035 birds were identified as dead, approximately 3.3% of the breeding population (assuming 150 518 breeding adults from 75 259 apparently occupied sites, Murray *et al.* 2015); however, many additional birds will have died at sea. The distribution of dead birds across the areas of the colony appeared uneven with clusters observed in flatter areas of the colony and below slopes. The club sites, traditionally full of non-breeding adults and older immature birds by the end of June, remained empty throughout the entirety of the 2022 breeding season – before, during and after the outbreak. Given the almost complete absence of immatures and non-breeders at the colony during June, it is highly likely that the majority of birds counted, both live and dead, would have been breeding adults.

Breeding success. Monitored nests declined from 93 to 23 (75% decline) between 15 June and 14 August. However, empty nest-sites on 15 June indicated that nests had already failed before the start of monitoring (Fig. 2). The majority of the 93 nests had failed by the beginning of July with nest abandonment leaving gaps within the colony (Fig. 2; Fig. S2). An index of breeding success was estimated as 0.247 based on the presence of 23 large, apparently healthy chicks in the study areas on 14 August. Clinical signs of viral infection, seizures and lethargy were observed in a small number of chicks (aged 2+ weeks) outside our study areas, but as they were not monitored their fate is unknown.

Adult survival. The top model showed strong support for survival probability varying with time and for re-sightings to vary with time following the first year after marking (Table 1). Apparent adult survival between 2021 and 2022 was 0.455 (95% confidence interval (CI) 0.153–0.794) compared with an average apparent annual survival of 0.940 (95% CI 0.771–0.993) between 2011 and 2021. The resighting probability during 2022 was 0.615 (95% CI 0.144–0.938) compared with an average of 0.839 (95% CI 0.626–0.973) between 2011 and 2021.

Fourteen dead recoveries of colour-ringed birds from Bass Rock were recorded during 2022; seven were found during June and July 2022 on the North Sea coasts of the UK, Sweden and Denmark, and eight were found dead on the colony in October. Between 2015 and 2021 three dead recoveries of colour-ringed birds were recorded.

Serology and iris colour

All 18 birds tested negative for viral nucleic acid from cloacal swabs, indicating that they were not currently infected. Of the 19 blood samples, two were insufficient for testing and eight tested positive for H5 antibodies, indicating a previous infection.

The likelihood of testing positive for HPAIV H5 antibodies was higher in birds with black irises (77.7%) compared with birds with normally coloured eyes (12.5%; Fisher's exact test; $P < 0.05$). The haemagglutinin binding antibody levels in serum samples, assessed by a haemagglutination inhibition test, were 1/16 ($n = 3$) and 1/32 ($n = 5$, including the sample from the bird with healthy irises; Table 2; Table S2).

DISCUSSION

We provide the first comprehensive account of the spatio-temporal detection of HPAIV outbreaks in Gannets at 75% of global breeding colonies. At the world's largest gannetry, Bass Rock, the impact was severe with a conservative estimate of c. 3% breeding adults dead at the colony, and annual survival and breeding success both substantially lower than would be expected compared with long-term averages. However, in addition we also found evidence from serological testing that Gannets can recover from infection with H5N1 and that a change in eye colour from pale blue to black is a likely phenotypic indicator of a previous infection.

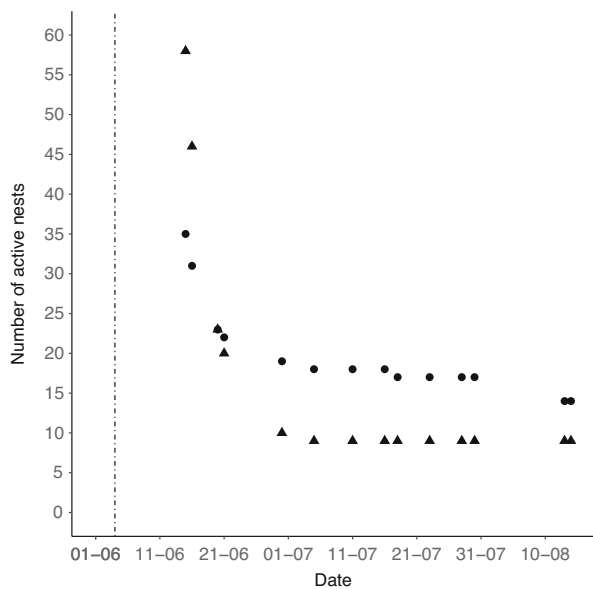


Figure 2. The number of active nests within two study areas on Bass Rock; area 1 as circles, area 2 as triangles. Dotted vertical line indicates 4 June, the date carcasses were collected for testing by the Animal Plant Health Agency.

Global context: HPAIV spread across the North Atlantic Gannet meta-population

During summer 2022, HPAIV H5N1 was recorded for the first time in Gannets, causing mortality on an unprecedented scale across their entire Atlantic breeding range. Positive tests from 58% of monitored colonies mean it is likely that unusually high mortality in the 16 untested colonies in 2022 was due to HPAI. Of the 41 colonies associated with unusually high levels of Gannet mortality, only one, Bjørnøya, the most northerly colony in the meta-population, was confirmed to

Table 2. Serological results from 17 adult Gannets from Bass Rock tested for H5 antigen.

Iris condition	HPAIV H5 antibody status	
	Positive	Negative
Black	7	2
Healthy	1	7

have been unimpacted/unaffected. In addition, strong evidence of an HPAIV outbreak at a colony unmonitored during the breeding season, Sule Skerry, northern Scotland (Harris & Wanless 2023), suggests that it is likely some of the 12 colonies where information is lacking were also affected. The data on first detection of unusual Gannet mortalities probably associated with HPAIV that we present here vary in spatial and temporal precision because of the inherent differences in observation methods between different data sources. Although Gannets are a well-studied species, we note that sampling effort was not standardized among colonies (e.g. uncertainty in data from northern Norway, Iceland and some of the Irish colonies is largely the result of the use of passive surveillance data rather than direct colony monitoring), but given the scale of the mortality (e.g. reported here for the Bass Rock colony) an outbreak would probably be obvious with only low-intensity monitoring. Despite the acknowledged uncertainty, the data that we present here represent the best data available at the time of writing and they allow us to document the probable temporal progression of HPAIV spread throughout the global distribution of the Gannet. Following the first confirmed cases in Iceland during April 2022, HPAIV was detected almost simultaneously across the northeast and northwest Atlantic meta-populations. HPAIV outbreaks, confirmed and

Table 1. Candidate model set for estimating annual survival of Northern Gannets from Bass Rock between 2010 and 2022. Inflation factor (\hat{c}) = 1.212.

Model	QAICc	Δ QAICc	AICc weights	Model likelihood	Num. Par.	QDeviance
$\varphi(t) p(c/t)$	2031.27	0.00	0.912	1.000	24	377.31
$\varphi(c) p(c/t)$	2036.85	5.58	0.056	0.061	13	405.39
$\varphi(t) p(c/c)$	2037.94	6.67	0.032	0.036	14	404.45
$\varphi(c) p(c/c)$	2225.89	194.62	0.000	0.000	3	614.63

Effects fitted to apparent survival (φ) and resighting probabilities (p) (t , time dependent; c , time constant). AICc, Akaike Information Criterion for small samples; Δ AICc, difference in AICc between model in question and best model; Num. Par., number of parameters.

inferred from dead untested birds, occurred in at least 75% of all 53 known Gannet colonies. A thorough estimation of Gannet mortality during the 2022 HPAIV outbreak is beyond the scope of this paper, but would be a highly valuable future contribution to better understand the impact of the 2022 HPAIV outbreak on Gannet colony and meta-population recovery.

All positive samples collated across the north-east and northwest Atlantic meta-populations were subtype H5N1 apart from a single Gannet sample testing positive for subtype H5N5 from the Sør-Varanger municipality in Troms and Finnmark county, Norway. In Norway, subtype H5N5 has also been detected in 30 birds from different species, including White-tailed Eagles *Haliaeetus albicilla*, gulls (Laridae), Great Skuas and corvids (Corvidae; S. Granstad pers. comm., 26 March 2023).

Possible mechanism of HPAIV transmission between Gannet colonies

The scale and speed at which HPAIV spread through the Gannet meta-population was dramatic, but the mechanism of transmission and the subsequent spread between colonies is unclear. A possible source may have been infectious Gannets returning from their wintering areas. During the spring migration, Gannets in the eastern North Atlantic frequently perform a clockwise loop around the UK, with Icelandic breeders arriving earlier than those breeding on the Bass Rock (Furness *et al.* 2018). However, Gannets from different colonies show some overlap in the wintering areas (Fort *et al.* 2012, Furness *et al.* 2018), making the sequential nature of the spread less likely to be due to differences in migratory timing. Conversely, the unprecedented stranding of dead adult Gannets on the Dutch coast during April 2022 may be attributable to HPAIV (although none of these birds were tested; Camphuysen *et al.* 2023). The possibility exists therefore that the disease arrived earlier in the northeast Atlantic than colony data suggest.

The timing of outbreaks on each side of the Atlantic and throughout the northeast meta-population might point towards HPAIV transmission via other infected seabirds. Great Skuas were severely affected by HPAIV H5N1 in Scotland in 2021 (Banyard *et al.* 2022) and again in 2022 (Camphuysen *et al.* 2022, Falchieri *et al.* 2022).

Great Skuas breed near Gannets in Iceland, the Faroes and northern Scotland (Birdlife International 2023) and these species overlap in winter from both sides of the North Atlantic (Magnusdottir *et al.* 2012, Fifield *et al.* 2014, Grecian *et al.* 2016). Great Skuas kleptoparasitize Gannets (Andersson 1976) and they feed together behind trawlers, which might explain cross-taxon spread. Brown Skuas *Stercorarius antarcticus* are probably vectors of avian cholera on Amsterdam Island, Indian Ocean (Gamble *et al.* 2019), and we speculate a similar role for Great Skuas triggering the HPAIV outbreak in Gannets in 2022. Yet this does not explain the subsequent spread through the Gannet meta-population, and questions remain about why spill-over into Gannets may or may not have occurred during the 2021 outbreak among skuas. Similarly, waterfowl and gull species have been found to play an important role in intercontinental transmission of both LPAIV and HPAIV via Iceland, the link between the East Atlantic and North American Atlantic Flyways (Dusek *et al.* 2014). Gulls are known to frequent seabird colonies to opportunistically prey on eggs and chicks (Donehower *et al.* 2007, pers. obs.) and may therefore have played a role in virus spread.

The subsequent clockwise spread around the UK seems unlikely to be linked to centrally placed adults foraging at sea, based on current evidence. During chick-rearing, Gannets have colony-specific foraging ranges with limited overlap (Wakefield *et al.* 2013) and tend to have individual specific foraging grounds (Wakefield *et al.* 2015, Votier *et al.* 2017). However, the HPAIV outbreak may have altered their movement behaviour, leading to increased inter-colony contact (Jeglinski *et al.* In Review; d'Entremont & Montevicchi unpubl. data). Immature Gannets are another possible route for spreading the virus while prospecting among colonies (Votier *et al.* 2011). They also have larger foraging ranges than breeders (Votier *et al.* 2017, Grecian *et al.* 2018), and therefore a greater chance of inter-colony overlap. Nevertheless, immature Gannets tend to return to the colony much later than adults, being scarce during April/May and only appearing in large numbers during June/July (Wanless 1983, Nelson 2002), so were unlikely to have played a role during outbreaks during April and May, although they may have played a role during outbreaks later in the breeding season (Fig. 1).

More research into virus incubation and length of infectious period in addition to possible transmission pathways between species that overlap in their wintering, migratory and breeding areas is paramount (Hill *et al.* 2022).

Case study: Impact of HPAIV on the Bass Rock Gannet colony

A routine visit to the Bass Rock on 28 May 2022 indicated nothing untoward at the colony, yet fresh dead Gannets found on the beaches closest to the Bass Rock on 30 May prompted a visit on 4 June, during which unusual levels of mortality and sick birds were seen. Increasing numbers of dead and sick birds were seen throughout June, and July saw a reduction in sick and dying birds and an increase in birds seemingly returning to previously occupied sites; we estimate that the disease had passed through the colony by 23 July. Footage from the uncrewed aircraft system on 30 June recorded 5035 dead individuals at the colony, which represented c. 3% of breeding adult Gannets on Bass Rock. Our conservative count means that this is likely to be an underestimate of the total number of adults that died because some dead birds may have been counted as alive, it excludes decomposed birds or those that died at sea (Himes Boor & Ford 2019), and it does not account for the colony growth since 2014 (Murray 2017). This figure compares with an estimated (from ring recovery data) 3500–4300 dead adult birds from the Alderney colonies (Atkinson unpublished) and 3100 dead Gannets (< 4% of birds) from the two largest Irish colonies detected in aerial surveys (Paradell *et al.* 2023). In addition, 7% mortality was estimated at Mykineshólmur, Faroe Islands (unpublished), and 6% at Sule Skerry, Scotland (Harris & Wanless 2023), both from aerial counts, although the Sule Skerry count was performed at the end of the breeding season. Variation in mortality rates could be linked to the timing of the outbreak in relation to the stage of the breeding season, with mortality rates higher at colonies affected earlier in the season when colony attendance is higher (Paradell *et al.* 2023). Evidence from other colonial seabirds badly affected in 2022, particularly Great Skuas and Sandwich Terns *Thalasseus sandvicensis*, indicates that outbreak timing had an impact on the severity with higher numbers of dead adults found in the colony when the outbreak occurred

earlier in the season (Camphuysen *et al.* 2022, Knief *et al.* 2023).

Uncrewed aircraft system counts in late June indicated that the colony was c. 71% smaller than during the last full colony count in 2014 (Murray *et al.* 2015). However, the colony had grown since 2014 (Murray 2017) so again, this is almost certainly an underestimate, although the different methodologies and counting units make a direct comparison difficult.

The almost complete absence of immature birds at club sites throughout the breeding season was striking and the reason for this is unknown. The mass stranding of Gannets along the Dutch North Sea coast during April and May 2022 was predominately made up of adult birds, though in May, a notable increase in the proportion of birds with immature plumage compared with the long-term average was recorded (Camphuysen *et al.* 2023), perhaps indicating that non-breeding adults and immature birds had been disproportionately affected at sea while on their return migration. However, these birds were never tested and the lack of data on both live and dead immature birds at both the Bass Rock and across the meta-population means the impact of HPAI on immature birds is difficult to assess.

Around one-quarter of nests with an egg on 15 June still had a chick in late August, which is much lower than the mean UK Gannet breeding success during 1961–2018 (mean \pm standard deviation 0.72 ± 0.12 ; Jeglinski *et al.* 2023). There are methodological differences in approach, but the comparison provides a further indication of the severe impact of the virus. The primary cause of breeding failure appeared to be nest abandonment, either when adults did not return from foraging trips or died at the nest.

Apparent adult survival in 2021/22 was 0.455, substantially lower than the average of 0.940 (95% CI 0.771–0.993) between 2011 and 2021. Notwithstanding the inflated uncertainty in the 2022 survival estimate, the reduction in the number of re-sighted colour-ringed birds, in association with the unusually high number of dead recoveries, indicates that a large proportion of adults failed to return to the colony in 2022 as a result of mortality or disturbance; however, a full assessment of the impact on adult survival will have to wait until 2023 when visual searches will be made for returning birds. Similar to most seabirds, Gannets are a long-lived species, making their populations

particularly sensitive to changes in adult survival, so the consequences of a significant reduction in adult survival could be considerable (Croxall & Rothery 1991). The distribution of dead birds across the colony suggests an influence of topography on virus spread, with flatter areas appearing to contain higher numbers of carcasses. However, it is not known how many of these birds were from other areas of the colony; sick birds nesting on steeper ground are likely to have fallen straight into the sea and gone undetected in the count.

Despite a modest sample size, our study suggests that Gannets infected with HPAIV H5N1 can survive, with important implications for the long-term consequences of the virus. We also found that black iris coloration in otherwise apparently healthy Gannets was a probable indicator of previous infection. One seropositive bird had healthy irises, but this may be related to a different subtype of HPAIV or LPAIV (Wilson *et al.* 2013), to waning antibody levels following previous infection, or may suggest that not all infected birds develop black irises. We suggest that the two birds with black irises that tested negative for antibodies had previously been infected but had already lost the antibodies; however, further investigation is needed to inform on antibody persistence. That no birds with black eyes were seen to have chicks at the time of sampling in September when chicks would be expected to be close to fledging was an interesting observation, and we suggest that this indicates infected birds abandoned their nesting attempts when infected but subsequently returned when recovered to maintain their territory.

Changes in iris colour in birds is not abnormal, with age being the most commonly identifiable factor (Corbett *et al.* 2023), which does occur in Gannets; juvenile Gannet eyes change from either dark blue-grey or dark brown to pale blue-grey by adulthood (J.V. Lane and M. Sheddán pers. obs.). Evidence of changes in colour and eye condition related to disease is limited, but cloudy eyes have been observed in Herring Gulls *Larus argentatus* and ducks experimentally infected with HPAIV (Brown *et al.* 2008, Yamamoto *et al.* 2016). Changes in human eye colour in association with disease have also been documented (Soydan & Kaymaz 2023). Our study is the first we are aware of to document changes to the iris colour of wild seabirds previously infected with HPAIV but a post-mortem examination will be required to determine the mechanism.

If black eyes can be used as a non-invasive diagnostic method for monitoring recovered and now immune individuals, this has important implications for population modelling through establishing potential impacts of the virus on fecundity and longer-term survival.

Black eyes have been reported in Gannets once before, but the reason is unknown (J. Swales pers. comm., Balfour 1922). During the HPAIV outbreak in 2022, Gannets with black irises were also reported from colonies in the UK (Bempton Cliffs, Grassholm and Ortac), France (Rouzig), Germany (Heligoland) and Canada (Île Bonaventure). In early spring 2023, Gannets with black irises were observed at the Bempton Cliffs, Bass Rock, Troup Head, Rouzig and Les Etacs colonies, suggesting the potential for a longer-lasting or even permanent modification of the iris.

Study challenges

The outbreak of HPAIV H5N1 across North Atlantic seabird colonies during 2022 was unprecedented and presented challenges for even the most experienced field teams to deliver the detailed studies warranted for such a novel and serious threat to seabird populations. Our work presents evidence of the temporal detection of the virus across the Gannet meta-population and how the largest, and one of the best studied, colonies was impacted. There is still considerable work to be done to understand the full impacts across the meta-population and we intend for the work presented here to contribute to our understanding while acknowledging its limitations and highlighting knowledge gaps.

CONCLUSION

Future research should quantify changes in demography (i.e. population size, adult survival and breeding success) of Gannets and other impacted seabirds while also assessing space-use during breeding and non-breeding seasons and whether previously infected birds have developed immunity in order to model disease progression and long-term impacts of HPAIV (Cunningham *et al.* 2022, Hill *et al.* 2022, Pearce-Higgins *et al.* 2023). Additionally, assessments of infection and mortality rates in different age classes, and of how previous infection might influence fertility or the outcome of a second infection are also needed (Wilson *et al.* 2013). Juvenile

Gannets have been found to carry antibodies to HPAIV (Grémillet *et al.* 2023) but it is unknown whether these were maternally derived or produced in response to infection (DeVriese *et al.* 2010).

Black irises may provide a useful non-invasive diagnostic tool, but more work is required to better understand its efficacy, if it applies to any other species, and whether there are any potential costs in terms of vision. Ophthalmology examinations or histopathology examinations are also required to determine what is causing the black coloration. It is also desirable to better understand the circulation of LPAIVs and previous exposure to antigenically related HPAIV sub-types in seabird populations to better understand potential cross-protective immunity, as well as the potential for compensatory recruitment to offset mortality (Votier *et al.* 2008, Jeglinski *et al.* 2023).

If sampling for live virus, we recommend cloacal swabs be taken in conjunction with oropharyngeal swabs (van den Brand *et al.* 2018, Suarez *et al.* 2000) because of possible differences in virus genotype detectability (Slomka *et al.* 2023). Primary flight feathers can also be used as a diagnostic indication of systemic viral infection as infectious virus can be detected in these samples (Nuradji *et al.* 2015).

The 2022 HPAIV H5N1 outbreak has provided another significant stressor to those already faced by our rapidly declining seabird populations (Dias *et al.* 2019, Careen *et al.* 2023) – quantifying and perhaps even mitigating its impact is therefore crucial if we hope to see a healthy seabird assemblage across the world's oceans.

We thank Sir Hew Hamilton-Dalrymple and the Scottish Seabird Centre, North Berwick for support and access to Bass Rock, and Jack Dale and John McCarter for logistical support. We thank Esbern í Eyðanstovu for making the observations of Mykineshólmur available to us. We thank Armel Deniau, Grgoire Delavaud, Aurlien Prudor, Timothe Poupart and Gauthier Poiriez for support with data collection at Rouzic. We thank Andrew Lang, Kathryn Hargan (Memorial University of Newfoundland and Labrador, Canada), Pauline Martigny (Université du Québec à Rimouski) and Ishraq Rahman and Jordan Wright (Memorial University of Newfoundland) for field and laboratory support. We also thank Ruedi Nager, Matt Wood and two anonymous referees for very helpful comments that helped to improve a previous version of the manuscript. Permission to undertake work on the Bass Rock during the HPAIV outbreak was granted by NatureScot. Birds were ringed and swabbed with permits

and approval from the British Trust for Ornithology. Blood sampling was carried out under licence from the UK Home Office; Project licence number PEAE7342F and Personal licence number IF2464041.

AUTHOR CONTRIBUTIONS

Jude V. Lane: Conceptualization; data curation; formal analysis; investigation; project administration; writing – original draft; writing – review and editing; visualization; funding acquisition; methodology. **Jana W.E. Jeglinski:** Conceptualization; data curation; investigation; methodology; project administration; writing – original draft; writing – review and editing; visualization. **Stephanie Avery-Gomm:** Investigation; writing – review and editing. **Elmar Ballstaedt:** Investigation; writing – review and editing. **Ashley C. Banyard:** Funding acquisition; investigation; writing – original draft; writing – review and editing. **Tatsiana Barychka:** Investigation; writing – review and editing. **Ian H. Brown:** Funding acquisition; writing – original draft; writing – review and editing; investigation. **Brigitte Brugger:** Investigation; writing – review and editing. **Tori V. Burt:** Investigation; writing – review and editing. **Noah Careen:** Investigation; writing – review and editing. **Johan H.F. Castenschild:** Investigation; writing – review and editing. **Signe Christensen-Dalsgaard:** Investigation; writing – review and editing. **Shannon Clifford:** Writing – original draft; writing – review and editing; investigation. **Sydney M. Collins:** Investigation; writing – review and editing. **Emma Cunningham:** Funding acquisition; project administration; resources; writing – original draft; writing – review and editing. **Jóhannis Danielsen:** Investigation; writing – review and editing. **Francis Daunt:** Project administration; writing – original draft; writing – review and editing. **Kyle J.N. d'Entremont:** Investigation; writing – review and editing. **Parker Doiron:** Investigation; writing – review and editing. **Steven Duffy:** Investigation; writing – review and editing. **Matthew D. English:** Investigation; writing – review and editing. **Marco Falchieri:** Investigation; writing – review and editing. **Jolene Giacinti:** Investigation; writing – review and editing. **Britt Gjerset:** Investigation; writing – review and editing. **Silje Granstad:** Investigation; writing – review and editing. **David Grémillet:** Investigation; writing – review and editing. **Magella Guillemette:** Investigation; writing – review and editing. **Gunnar T. Hallgrímsson:** Investigation; writing – review and editing. **Keith C. Hamer:** Writing – original draft; writing – review and editing. **Sjúrður**

Hammer: Investigation; writing – review and editing. **Katherine Harrison:** Investigation; writing – review and editing. **Justin D. Hart:** Investigation; writing – review and editing. **Ciaran Hatsell:** Investigation; writing – review and editing. **Richard Humpidge:** Investigation; writing – review and editing. **Joe James:** Investigation; writing – review and editing. **Audrey Jenkinson:** Investigation; writing – review and editing. **Mark Jessopp:** Investigation; writing – review and editing. **Megan E.B. Jones:** Investigation; writing – review and editing. **Stéphane Lair:** Investigation; writing – review and editing. **Thomas Lewis:** Formal analysis; investigation; methodology; writing – review and editing; writing – original draft. **Alexandra A. Malinowska:** Investigation; writing – review and editing. **Aly McCluskie:** Funding acquisition; writing – review and editing; project administration. **Gretchen McPhail:** Investigation; writing – review and editing. **Børge Moe:** Investigation; writing – review and editing. **William A. Montevecchi:** Investigation; writing – review and editing. **Greg Morgan:** Investigation; writing – review and editing. **Caroline Nichol:** Investigation; writing – review and editing; methodology; resources; writing – original draft. **Craig Nisbet:** Investigation; writing – review and editing. **Bergur Olsen:** Investigation; writing – review and editing. **Jennifer Provencher:** Investigation; writing – review and editing. **Pascal Provost:** Investigation; writing – review and editing. **Alex Purdie:** Investigation; writing – review and editing. **Jean-François Rail:** Investigation; writing – review and editing. **Greg Robertson:** Investigation; writing – review and editing. **Yannick Seyer:** Investigation; writing – review and editing. **Maggie Sheddan:** Investigation; writing – original draft; writing – review and editing. **Catherine Soos:** Investigation; writing – review and editing. **Nia Stephens:** Investigation; writing – review and editing. **Hallvard Strøm:** Investigation; writing – review and editing. **Vilhjalmur Svansson:** Investigation; writing – review and editing. **T. David Tierney:** Investigation; writing – review and editing. **Glen Tyler:** Investigation; writing – original draft; writing – review and editing. **Tom Wade:** Investigation; methodology; resources; writing – original draft; writing – review and editing. **Sarah Wanless:** Writing – review and editing; writing – original draft. **Christopher R.E. Ward:** Investigation; writing – review and editing. **Sabina Wilhelm:** Investigation; writing – review and editing. **Saskia Wischniewski:** Investigation; writing – review and editing. **Lucy J. Wright:** Project administration; supervision; writing – original draft; writing – review

and editing. **Bernie Zonfrillo:** Investigation; writing – review and editing. **Jason Matthiopoulos:** Formal analysis; funding acquisition; investigation; writing – original draft; writing – review and editing; methodology. **Stephen C. Votier:** Conceptualization; funding acquisition; investigation; writing – original draft; writing – review and editing; project administration; methodology.

FUNDING

This work was funded by the Forth and Tay Offshore Wind Farm Developers; Neart na Gaoithe Offshore Wind Ltd, Seagreen Wind Energy Ltd and SSE Renewables, the Animal Plant Health Agency, and the UK Department for Business, Energy and Industrial Strategy Offshore Energy Strategic Environmental Assessment BEIS OESEA programme, as well as an NERC Urgency Grant NE/X013502/1 and Natural Sciences and Engineering Research Council of Canada (NSERCC) and Fisheries and Oceans Canada. ACB, JJ, TL and IHB were part supported by the Biotechnology and Biological Sciences Research Council (BBSRC) and Department for Environment, Food and Rural Affairs (Defra, UK) research initiative ‘FluMAP’ (grant number BB/X006204/1). Funding was also provided by Defra and the Devolved Administrations of Scotland and Wales, through grants SE2213 and SV3006. Unmanned aerial vehicle data collection was undertaken by the University of Edinburgh’s Airborne Research and Innovation facility (ARI), the NERC Field Spectroscopy Facility (FSF) and Scotland’s Rural College (SRUC), in partnership with the Scottish Seabird Centre. Data collection in Norway including Svalbard was funded by SEAPOP (www.seapop.no, grant number 192141).

ETHICAL NOTE

None.

CONFLICT OF INTEREST

The authors confirm that they have no conflicts of interest

Data Availability Statement

The data that support the findings of this study are available in the supplementary material of this article.

REFERENCES

- Andersson, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. *Ibis* **118**: 208–217.
- Arnal, A.M., Vittecoq, M., Pearce-Duvel, J., Gauthier-Clerc, M., Boulinier, T. & Jourdain, E. 2014. Laridae: A neglected reservoir that could play a major role in avian influenza virus epidemiological dynamics. *Crit. Rev. Microbiol.* **41**: 508–519.
- Balfour, H. 1922. Varieties of the common gannet. *Br. Birds* **15**: 82–84. https://britishbirds.co.uk/sites/default/files/V15_N04_P082-084_A019.pdf
- Banyard, A.C., Lean, F.Z.X., Robinson, C., Howie, F., Tyler, G., Nisbet, C., Seekings, J., Mirisr, S., Whittard, E., Ashpitel, H.F., Bas, M., Byrne, A.M.P., Lewis, T., James, J., Stephan, L., Lewis, N.S., Brown, I.H., Hansen, R.D.E. & Reid, S.M. 2022. Detection of highly pathogenic avian influenza virus H5N1 clade 2.3. 4.4 b in great skuas: A species of conservation concern in Great Britain. *Viruses* **14**: 212.
- Barrett, R.J., Strøm, H. & Melnikov, M. 2017. On the polar edge: The status of the northern gannet (*Morus bassanus*) in the Barents Sea in 2015–16. *Polar Res.* **36**: 1390384.
- Blagodatski, A., Trutneva, K., Glazova, O., Mityaeva, O., Shevkova, L., Kegeles, E., Onyanov, N., Fede, K., Maznina, A., Khavina, E., Yeo, S.-J., Park, H. & Volchkov, P. 2021. Avian influenza in wild birds and poultry: Dissemination pathways, monitoring methods, and virus ecology. *Pathogens* **10**: 630.
- Boulinier, T. 2023. Avian influenza spread and seabird movements between colonies. *Trends Ecol. Evol.* **38**: 391–395.
- van den Brand, J.M.A., Verhagen, J.H., Veldhuis Kroeze, E.J.B., van de Bildt, M.W.G., Bodewes, R., Herfst, S., Richard, M., Lexmond, P., Bestebroer, T.M., Fouchier, R.A.M. & Kuiken, T. 2018. Wild ducks excrete highly pathogenic avian influenza virus H5N8 (2014–2015) without clinical or pathological evidence of disease. *Emerg. Microbes Infect.* **7**: 1–10.
- Brown, J.D., Stallknecht, D.E. & Swayne, D.E. 2008. Experimental infections of herring gulls (*Larus argentatus*) with H5N1 highly pathogenic avian influenza viruses by intranasal inoculation of virus and ingestion of virus-infected chicken meat. *Avian Pathol.* **37**: 393–397.
- Burggraaf, S., Kapala, A.J., Bingham, J., Lowther, S., Selleck, P., Kimpton, W. & Bean, A.G.D. 2014. H5N1 infection causes rapid mortality and high cytokine levels in chickens compared to ducks. *Virus Res.* **185**: 23–31.
- Caliendo, V., Leijten, L., Begeman, L., Poen, M.J., Fouchier, R.A.M., Beerens, N. & Kuiken, T. 2020. Enterotropism of highly pathogenic avian influenza virus H5N8 from the 2016/2017 epidemic in some wild bird species. *Vet. Res.* **51**: 117.
- Caliendo, V., Lewis, N.S., Pohlmann, A., Baillie, S.R., Banyard, A.C., Beer, M., Brown, I.H., Fouchier, R.A.M., Hansen, R.D.E., Lameris, T.K., Lang, A.S., Laurendeau, S., Lung, O., Robertson, G., van der Jeugd, H., Alkie, T.N., Thorup, K., van Toor, M.L., Waldenström, J., Yason, C., Kuiken, T. & Berhane, Y. 2022. Transatlantic spread of highly pathogenic avian influenza H5N1 by wild birds from Europe to North America in 2021. *Sci. Rep.* **12**: 11729.
- Camphuysen, C.J., Gear, S.C. & Furness, R.W. 2022. Avian influenza leads to mass mortality of adult great skuas in Foula in summer 2022. *Scot. Birds.* **42**: 312–323.
- Camphuysen, K., Kelder, L., Zuhorn, C. & Fouchier, R. 2023. Avian influenza panzootic leads to mass strandings of northern gannets *Morus bassanus* in The Netherlands, April–October 2022. *Limosa* **95**: 49–59.
- Careen, N., d'Entremont, K., Mooney, C. & Montevecchi, W. 2023. Avian Influenza (H5N1) and a Marine Heatwave Spell Reproductive Disaster for Northern Gannets at their Southernmost Colony. Poster, Pacific Seabird Group Annual Meeting (San Diego, 15–17 February).
- Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M. & Pradel, R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating capture–recapture data. *Ecography* **32**: 1071–1074.
- Corbett, E.C., Brumfield, R.T. & Faircloth, B.C. 2023. Bird eye color: A rainbow of variation, a spectrum of explanations. Available at: <https://ecoevorxiv.org/repository/view/3682/> (accessed 13 July 2023).
- Croxall, J.P. & Rothery, P. 1991. Population regulation of seabirds: Implications of their demography for conservation. In Perrins, C.M., Lebreton, J.-D. & Hiron, G.J.M. (eds) *Bird Population Studies: Relevance to Conservation and Management*. 272–296. Oxford: Oxford University Press.
- Cunningham, E.J.A., Gamble, A., Hart, T., Humphreys, E.M., Philip, E., Tyler, G. & Wood, M.J. 2022. The incursion of highly pathogenic avian influenza (HPAI) into North Atlantic seabird populations: An interim report from the 15th international seabird group conference. Report on HPAI in North Atlantic seabirds. Seabird, 34.
- Deakin, Z., Hamer, K.C., Sherley, R.B., Bearhop, S., Bodey, T.W., Clark, B.L., Grecian, W.J., Gummery, M., Lane, J., Morgan, G., Morgan, L., Phillips, R.A., Wakefield, E.D. & Votier, S.C. 2019. Sex differences in migration and demography of a wide-ranging seabird, the northern gannet. *Mar. Ecol. Prog. Ser.* **622**: 191–201.
- d'Entremont, K.J.N., Guzzwell, L.M., Wilhelm, S.I., Friesen, V.L., Davoren, G.K., Walsh, C.J. & Montevecchi, W.A. 2022. Northern gannets (*Morus bassanus*) breeding at their southern limit struggle with prey shortages as a result of warming waters. *ICES J Mar. Sci.* **79**: 50–60.
- DeVriese, J., Steensels, M.P., Gardin, Y., Moore Dorsey, K., Lambrecht, B., Van Borm, S. & van den Berg, T. 2010. Passive protection afforded by maternally-derived antibodies in chickens and the antibodies' interference with the protection elicited by avian influenza-inactivated vaccines in progeny. *Avian Dis.* **54**(s1): 246–252.
- Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B., Garcia Borboroglu, P. & Croxall, J.P. 2019. Threats to seabirds: A global assessment. *Biol. Conserv.* **237**: 525–537.
- Donehower, C.E., Bird, D.M., Hall, C.S. & Kress, S.W. 2007. Effects of gull predation and predator control on tern nesting success at eastern egg rock, Maine. *Waterbirds* **30**: 29–39.
- Dusek, R.J., Hallgrímsson, G.T., IP, H.S., Jónsson, J.E., Sreevatsan, S. & Nashold, S.W. 2014. North Atlantic migratory bird flyways provide routes for intercontinental movement of avian influenza viruses. *PLoS One* **9**: e92075.
- EFSA (European Food Safety Authority), ECDC (European Centre for Disease Prevention and Control), EURL (European Reference Laboratory for Avian Influenza), Adlhoch, C., Fusaro, A., Gonzales, J.L., Kuiken, T.,

- Marangon, S., Niqueux, É., Staubach, C., Terregino, C., Aznar, I., Muñoz Guajardo, I. & Baldinelli, F. 2023. Scientific report: Avian influenza overview September–December 2022. *EFSA J.* **21**: 7786.
- Falchieri, M., Reid, S.M., Ross, C.S., James, J., Byrne, A.M.P., Zamfir, M., Brown, I.H., Banyard, A.C., Tyler, G., Philip, E. & Miles, W. 2022. Shift in HPAI infection dynamics causes significant losses in seabird populations across Great Britain. *Vet. Rec.* **191**: 294–296.
- Fifield, D.A., Montevecchi, W.A., Garthe, S., Robertson, G.J., Kuetzki, U. & Rail, J.-F. 2014. Migratory tactics and wintering areas of northern gannets (*Morus bassanus*) breeding in North America. *Ornithol. Monogr.* **79**: 1–63.
- Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J.B., Siorat, F., Furness, R.W., Grecian, W.J., Bearhop, S., Montevecchi, W.A. & Grémillet, D. 2012. Meta-population evidence of oriented chain migration in northern gannets (*Morus bassanus*). *Front. Ecol. Environ.* **10**: 237–242.
- Furness, R.W., Hallgrímsson, G.T., Montevecchi, W.A., Fifield, D., Kubetzki, U., Mendel, B. & Garthe, S. 2018. Adult gannet migrations frequently loop clockwise around Britain and Ireland. *Ringing Migr.* **33**: 1–9.
- Gamble, A., Bazire, R., Delord, K., Barbraud, C., Jaeger, A., Gantelet, H., Thibault, E., Lebarbenchon, C., Lagadec, E., Tortosa, P., Weimerskirch, H., Thiebot, J.-B., Garnier, R., Tornos, J. & Boulinier, T. 2019. Predator and scavenger movements among and within endangered seabird colonies: Opportunities for pathogen spread. *J. Appl. Ecol.* **57**: 367–378.
- Grecian, J.W., Witt, M.J., Attrill, M.J., Bearhop, S., Becker, P.H., Egevang, C., Furness, R.W., Godley, B.J., González-Solis, J., Grémillet, D., Kopp, M., Lescroël, A., Matthiopoulos, J., Patrick, S.C., Peter, H.-U., Phillips, R.A., Stenhouse, I.J. & Votier, S.C. 2016. Seabird diversity hotspot linked to ocean productivity in the canary current large marine ecosystem. *Biol. Lett.* **12**: 20160024.
- Grecian, W.J., Lane, J.V., Michelot, T., Wade, H.M. & Hamer, K.C. 2018. Understanding the ontogeny of foraging behaviour: Insights from combining marine predator biology with satellite-derived oceanography in hidden Markov models. *R. Soc. Interface.* **15**: 20180084.
- Grémillet, D., Ponchon, A., Provost, P., Gamble, A., Abed-Zaharh, M., Bernard, A., Courbin, N., Delavaud, G., Deniau, A., Fort, J., Hamer, K.C., Jeavons, R., Lane, J.V., Langley, L., Matthiopoulos, J., Poupart, T., Prudor, A., Stephens, N., Trevail, A., Wanless, S., Votier, S.C. & Jeglinski, J.W.E. 2023. Strong breeding colony fidelity in northern gannets following high pathogenicity avian influenza virus (HPAIV) outbreak. *Biol. Conserv.* **286**: 110269.
- Hamer, K.C., Phillips, R.A., Wanless, S., Harris, M.P. & Wood, A.G. 2000. Foraging ranges, diets and feeding locations of gannet *Morus bassanus* in the North Sea: Evidence from satellite telemetry. *Mar. Ecol. Prog. Ser.* **200**: 257–264.
- Hamer, K.C., Humphreys, E.M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R.A., Harris, M.P. & Wanless, S. 2007. Annual variation in diets, feeding locations and foraging behaviour of gannets in the North Sea: Flexibility, consistency and constraint. *Mar. Ecol. Prog. Ser.* **338**: 295–305.
- Harris, M.P. & Wanless, S. 2023. A major mortality of gannets due to a probable outbreak of high pathogenicity avian influenza on Sule skerry in 2022. *Scot. Bird.* **43**: 228–231.
- Harvell, C.D., Mitchell, C.E., Ward, J.R., Altizer, S., Dobson, A.P., Ostfeld, R.S. & Samuel, M.D. 2002. Climate warming and disease risks for terrestrial and marine biota. *Science* **296**: 2158–2162.
- Hill, N.J., Bishop, M.A., Trovão, N.S., Ineson, K.M., Schaefer, A.L., Puryear, W.B., Zhou, K., Foss, A.D., Clark, D.E., MacKenzie, K.G., Gass, J.D., Borkenhagen, L.K., Hall, J.S. & Runstadler, J.A. 2022. Ecological divergence of wild birds drives avian influenza spillover and global spread. *PLoS Pathog.* **18**: e1010062.
- Himes Boor, G.K. & Ford, R.G. 2019. Using a mark–recapture model to estimate beaching probability of seabirds killed in nearshore waters during the Deepwater horizon oil spill. *Environ. Monit. Assess.* **191**: 813.
- IUCN, BirdLife International. 2023. *Species factsheet: Morus bassanus*. Downloaded from <http://www.birdlife.org> (accessed 20 March 2023).
- James, J., Seekings, A.H., Skinner, P., Purchase, K., Mahmood, S., Brown, I.H., Hansen, R.D.E., Banyard, A.C. & Reid, S.M. 2022. Rapid and sensitive detection of high pathogenicity Eurasian clade 2.3.4.4b avian influenza viruses in wild birds and poultry. *J. Virol. Methods* **301**: 114454.
- Jeglinski, J.W.E., Lane, J.V., Votier, S.C., Furness, R.W., Hamer, K.C., McCafferty, D., Nager, R.G., Sheddan, M., Wanless, S. & Matthiopoulos, J. In Review. HPAIV outbreak triggers enhanced colony connectivity in a seabird metapopulation. *Sci. Rep.*
- Jeglinski, J.W.E., Wanless, S., Murray, S., Barrett, R.T., Gardarsson, A., Harris, M.P., Dierschke, J., Strøm, H., Lorentsen, S.-V. & Matthiopoulos, J. 2023. Metapopulation regulation acts at multiple spatial scales: Insights from a century of seabird colony census data. *Ecol. Monogr.* **93**: e1569.
- Knief, U., Bregnballe, T., Alfari, I., Ballmann, M., Brennikmeijer, A., Bzoma, S., Chabrolle, A., Dimlich, J., Engel, E., Fijn, R., Fischer, K., Hälterlein, B., Haupt, M., Hennig, V., Herrmann, C., in 't Veld, R., Kirchhoff, E., Kristersson, M., Kühn, S., Larsson, K., Larsson, R., Lawton, R., Leopold, M., Lilipaly, S., Lock, L., Marty, R., Matheve, H., Meissner, W., Morisson, P., Newton, S., Olofsson, P., Packmor, F., Pedersen, K.T., Redfern, C., Scarton, F., Schenk, F., Scher, O., Serra, L., Smith, L., Smith, W., Sterup, J., Stienen, E., Strassner, V., Valle, R.G., van Bemmelen, R.S.A., Veer, J., Vervaeke, M., Weston, E., Wojcieszek, M. & Courtens, W. 2023. Highly pathogenic avian influenza causes mass mortality in Sandwich tern (*Thalasseus sandvicensis*) breeding colonies across northwestern Europe. *bioRxiv* 2023.05.12.540367 <https://doi.org/10.1101/2023.05.12.540367>
- Lebreton, J.-D., Burnham, K.P., Clobert, J. & Anderson, D.R. 1992. Modeling survival and testing biological hypotheses using marked animals: A unified approach with case studies. *Ecol. Monogr.* **62**: 67–118.
- Magnusdottir, E., Leat, E.H.K., Bourgeon, S., Strøm, H., Petersen, A., Phillips, R.A., Hanssen, S.A., Bustnes, J.O., Hersteinsson, P. & Furness, R.W. 2012. Wintering areas of great skuas *Stercorarius skua* breeding in Scotland, Iceland and Norway. *Bird Study* **59**: 1–9.

- Monne, I., Fusaro, A., Nelson, M.I., Bonfanti, L., Mulatti, P., Hughes, J., Murcia, P.R., Schivo, A., Valastro, V., Moreno, A., Holmes, E.C. & Cattoli, G. 2014. Emergence of a highly pathogenic avian influenza virus from a low-pathogenic progenitor. *J. Virol.* **88**: 4375–4388.
- Murray, S. 2017. Gannets and tree mallow – Change on the bass rock, 2009–17. *Scott. Birds* **37**: 346–347.
- Murray, S., Harris, M.P. & Wanless, S. 2015. The status of the gannet in Scotland in 2013–14. *Scott. Birds* **35**: 3–18.
- Nagy, A., Černíková, L., Kunteová, K., Dirbáková, Z., Thomas, S.S., Slomka, M.J., Dán, Á., Varga, T., Máté, M., Jirincová, H. & Brown, I.H. 2021. A universal RT-qPCR assay for “one health” detection of influenza A viruses. *PLoS One* **16**: e0244669.
- Nelson, B. 2002. *The Atlantic Gannet. Poyser Monographs*. London: Bloomsbury Publishing.
- Núñez, I.A. & Ross, T.M. 2019. A review of H5Nx avian influenza viruses. *Ther. Adv. Vaccines Immunother.* **7**: 2515135518821625.
- Nuradji, H., Bingham, J., Lowther, S., Wibawa, H., Colling, A., Thanh Long, N. & Meers, J. 2015. A comparative evaluation of feathers, oropharyngeal swabs, and cloacal swabs for the detection of H5N1 highly pathogenic avian influenza infection in experimentally infected chicks and ducks. *J. Vet. Diagn. Invest.* **27**: 704–715.
- Paradell, O.G., Goh, T., Popov, D., Rogan, E. & Jessop, M. 2023. Estimated mortality of the highly pathogenic avian influenza pandemic on northern gannets (*Morus bassanus*) in Southwest Ireland. *Biol. Lett.* **19**: 20230090.
- Pearce-Higgins, J.W., Humphreys, E.M., Burton, N.H.K., Atkinson, P.W., Pollock, C., Clewley, G.D., Johnston, D.T., O’Hanlon, N.J., Balmer, D.E., Frost, T.M., Harris, S.J. & Baker, H. 2023. *Highly pathogenic avian influenza in wild birds in the United Kingdom in 2022: Impacts, planning for future outbreaks, and conservation and research priorities. Research Report no. 752*. Thetford: British Trust for Ornithology.
- Ramey, A.M., Hill, N.J., DeLiberto, T.J., Gibbs, S.E.J., Hopkins, C., Lang, A.S., Poulson, R.L., Prosser, D.J., Sleeman, J.M., Stalknecht, D.E. & Wan, X. 2022. Highly pathogenic avian influenza is an emerging disease threat to wild birds in North America. *J. Wildl. Manage.* **86**: e22171.
- R Core Team. 2016. *R: A Language and Environment for Statistical Computing*. Vienna: R Foundation for Statistical Computing. <https://www.R-project.org/>
- Roberts, L.C., Abolnik, C., Waller, L.J., Shaw, K., Ludynia, K., Robers, D.G., Kock, A.A., Makhado, A.B., Snyman, A. & Abernethy, D. 2023. Descriptive epidemiology of and response to the high pathogenicity avian Influenza (H5N8) epidemic in south African coastal seabirds. *Transbound. Emerg. Dis.* **2023**: 2708458.
- Slomka, M.J., Reid, S.M., Byrne, A.M.P., Coward, V.J., Seekings, J., Cooper, J.L., Peers-Dent, J., Agyeman-Dua, E., de Silva, D., Hansen, R.D.E., Banyard, A.C. & Brown, I.H. 2023. Efficient and informative laboratory testing for rapid confirmation of H5N1 (Clade 2.3.4.4) high-pathogenicity avian influenza outbreaks in the United Kingdom. *Viruses* **15**: 1344. <https://doi.org/10.3390/v15061344>
- Soydan, A. & Kaymaz, A. 2023. Bilateral acute depigmentation of the iris determined in two cases after COVID-19 infection. *Indian J. Ophthalmol.* **71**: 1030–1032.
- Suarez, D.L., Pantin-Jackwood, M.J., Swayne, D.E., Lee, S.A., DeBlois, S.M. & Spackman, E. 2020. Lack of susceptibility to SARS-CoV-2 and MERS-CoV in poultry. *Emerg Infect Dis.* **26**: 3074–3076. <https://doi.org/10.3201/eid2612.202989>
- Venkatesh, D., Poen, M.J., Bestebroer, T.M., Scheuer, R.D., Vuong, O., Chkhaidze, M., Machabishvili, A., Mamuchadze, J., Ninua, L., Fedorova, N.B., Halpin, R.A., Lin, X., Ransier, A., Stockwell, T.B., Wentworth, D.E., Kriti, S.C., Dutta, J., van Bakel, H., Puranik, A., Slomka, M.J., Essen, S., Brown, I.H., Fouchier, R.A.M. & Lewis, N.S. 2018. Avian influenza viruses in wild birds: Virus evolution in a multihost ecosystem. *J. Virol.* **92**: e00433–18.
- Veron, P.K. & Lawlor, M.P. 2009. The dissal and migration of the northern gannet *Morus bassanus* from Channel Islands breeding colonies. *Seabird* **22**: 37–47.
- Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H. & Hatchwell, B.J. 2008. Recruitment and survival of immature seabirds in relation to oil spills and climate variability. *J. Anim. Ecol.* **77**: 974–983.
- 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. *Mar. Biol.* **158**: 355–362.
- Votier, S.C., Fayet, A.L., Bearhop, S., Bodey, T.W., Clark, B.L., Grecian, J., Guilford, T., Hamer, K.C., Jeglinski, J.W.E., Morgan, G., Wakefield, E. & Patrick, S.C. 2017. Effects of age and reproductive status on individual foraging site fidelity in a long-lived marine predator. *Proc. Biol. Sci.* **284**: 1859.
- Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green, J.A., Gré millet, D., Jackson, A., Jessopp, M., Kane, A., Langston, R., Lescroel, A., Murray, S., Le Nuz, M., Patrick, S., Peron, C., Soeanes, L., Wanless, S., Votier, S. & Hamer, K.C. 2013. Space partitioning without territoriality in gannets. *Science* **341**: 68–70.
- Wakefield, E.D., Cleasby, I.R., Bearhop, S., Bodey, T.W., Davies, R.D., Miller, P.I., Newton, J., Votier, S.C. & Hamer, K.C. 2015. Long-term individual foraging site fidelity—why some gannets don’t change their spots. *Ecology* **96**: 3058–s.
- Wan, X.F. 2012. Lessons from emergence of a/goose/Guangdong/1996-like H5N1 highly pathogenic avian influenza viruses and recent influenza surveillance efforts in southern China. *Zoonoses Public Health* **59**(Suppl 2): 32–42.
- Wanless, S. 1983. Seasonal variation in the numbers and condition of gannets *Sula bassana* dying on Ailsa Craig. *Bird Study* **30**: 102–108.
- Weber, T.P. & Stilianakis, N.I. 2007. Ecologic immunology of avian influenza (H5N1) in migratory birds. *Emerg. Infect. Dis.* **13**: 1139–1143.
- White, G.C. & Burnham, K.P. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* **46**(Sup 001): 120–138. <https://doi.org/10.1080/00063659909477239>
- Wilson, H.M., Hall, J.S., Flint, P.L., Franson, J.C., Ely, C.R., Schmutz, J.A. & Samuel, M.D. 2013. High seroprevalence of antibodies to avian influenza viruses among wild waterfowl in Alaska: Implications for surveillance. *PLoS One* **8**: e58308.

Xu, X., Subbarao, K., Cox, N.J. & Guo, Y. 1999. Genetic characterization of the pathogenic influenza a/goose/Guangdong/1/96 (H5N1) virus: Similarity of its hemagglutinin gene to those of H5N1 viruses from the 1997 outbreaks in Hong Kong. *Virology* **261**: 15–19.

Yamamoto, Y., Nakamura, K., Yamada, M. & Mase, M. 2016. Corneal opacity in domestic ducks experimentally infected with H5N1 highly pathogenic avian influenza virus. *Vet. Pathol.* **53**: 65–76.

Received 3 April 2023;
Revision 20 July 2023;
revision accepted 12 September 2023.
Associate Editor: Matt Wood.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

Appendix S1. Health and Safety, and Biosecurity Protocols – working on Bass Rock.

Appendix S2. Collection of Uncrewed Aircraft System data – detailed methodology.

Figure S1. Images of Gannets on the Bass Rock colony in 2022 with black flecking in their irises.

Figure S2. Images of nest failures, apparent from gaps between birds, and dead birds in study area 2 of the Bass Rock and comparison photos of the same area from before the outbreak in 2022 and in 2021.

Table S1. Names, abbreviations and the first date when unusually high mortality in adult Gannets was detected at colonies across the meta-population.

Table S2. Serology results for H5 antibodies and iris colour of 17 Gannets on Bass Rock in September 2022.