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1 **High pathogenicity avian influenza (H5N1) in Northern Gannets:** 2 **Global spread, clinical signs, and demographic consequences**

3

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93

94 **Conflict of Interest**

95 The authors confirm that they have no conflicts of interest.

96

97 **Abstract**

98 During 2021-22 High Pathogenicity Avian Influenza (HPAI) killed thousands of wild birds across Europe
99 and North America, suggesting a change in infection dynamics and a shift to new hosts, including
100 seabirds. Northern Gannets (*Morus bassanus*) appeared especially severely impacted, but limited
101 understanding of how the virus spread across the metapopulation, or the demographic consequences
102 of mass mortality limit our understanding of its severity. Accordingly, we collate information on HPAIV
103 outbreaks across most North Atlantic gannet colonies and for the largest colony (Bass Rock, UK),
104 provide impacts on population size, breeding success, adult survival, and preliminary results on
105 serology. Unusually high numbers of dead gannets were first noted in Iceland during April 2022.
106 Outbreaks in May occurred in many Scottish colonies, followed by colonies in Canada, Germany and
107 Norway. By the end of June, outbreaks had occurred in five Canadian colonies and in the Channel
108 Islands. Outbreaks in 12 UK and Ireland colonies appeared to follow a clockwise pattern with the last
109 infected colonies recorded in late August/September. Unusually high mortality was recorded at 40
110 colonies (75% of global total colonies). Dead birds testing positive for HPAIV H5N1 were associated
111 with 58% of these colonies. At Bass Rock, the number of occupied sites decreased by at least 71%,

112 breeding success declined by ~66% compared to the long-term UK mean and adult survival between
113 2021 and 2022 was 42% lower than the preceding 10-year average. Serological investigation detected
114 antibodies specific to H5 in apparently healthy birds indicating that some gannets recover from HPAIV
115 infection. Further, most of these recovered birds had black irises, suggestive of a phenotypic indicator
116 of previous infection. Untangling the impacts of HPAIV infection from other key pressures faced by
117 seabirds is key to establishing effective conservation strategies for threatened seabird populations,
118 HPAIV being a novel and pandemic threat.

119 **Key Words**

120 HPAIV; avian flu; virus outbreak; seabirds; immunity

121

122 **1. Background**

123 High Pathogenicity Avian Influenza Virus (HPAIV) H5Nx has negatively impacted wild and domestic
124 bird populations globally for decades (Nuñez and Ross. 2019). However, the current global panzootic
125 of H5Nx has seen shifts in both the seasonality of outbreaks and the species affected (EFSA, 2023).
126 H5Nx (A/goose/Guangdong/1/1996 (Gs/GD) H5N1) was first detected in 1996 on a domestic goose
127 farm in Guangdong Province, China (Xu et al. 1999). This goose Guangdong lineage (Gs/Gd) has since
128 caused significant outbreaks in a variety of bird populations and has also raised concerns about the
129 potential zoonotic consequences for humans (Wan 2012, EFSA 2023). Genetic reassortment has led
130 to the emergence and evolution of multiple subtypes and genotypes of this group of high
131 pathogenicity viruses on a global scale, potentially with different epidemiological properties,
132 especially with respect to host range in wild birds (Monne et al. 2014, Falchieri et al. 2022). The
133 mechanism of viral transmission is likely a combination of infected wild bird migration and the global
134 domestic poultry trade or their products (Blagodatski et al. 2021, Ramey et al. 2022).

135 Low Pathogenicity Avian Influenza Virus (LPAIV) is widely circulating in wild aquatic birds; *Anseriformes*
136 (waterfowl) and *Charadriiformes* (shorebirds) are known to act as reservoirs (Venkatesh et al. 2018)
137 however, we know little about the recent emergence, spread and impact of HPAIVs in aquatic birds,
138 including seabirds (Burggraaf et al. 2014, Falchieri et al. 2022, Boulinier. 2023, Roberts et al. 2023).
139 HPAIVs do not evolve within wild bird populations but once they have spilled into wild populations,
140 are transmitted via infected saliva, nasal secretion and faeces but shedding methods differ between
141 species and are not well understood (Arnal et al. 2014, Caliendo et al. 2020).

142 The winter of 2021/2022 saw a record number of confirmed cases of HPAIV H5N1 in poultry, captive
143 and wild birds across Europe (EFSA 2023). HPAIV H5N1 was first detected in UK breeding seabirds in
144 July 2021 when Great Skuas (*Stercorarius skua*) on Fair Isle, Scotland tested positive (Banyard et al.
145 2022). The first case of H5N1 detected in North American seabirds was a Great Black-backed Gull

146 (*Larus marinus*) in Newfoundland and Labrador, Canada in November 2021, with phylogenetic
147 analyses revealing the virus was of the European H5N1 lineage (Caliendo et al. 2022). In early April
148 2022, Common Eider (*Somateria mollissima*) was the first seabird species to test positive for HPAIV in
149 the UK that year, followed in late April by Great Skua (Falchieri et al. 2022). Then followed an
150 unprecedented epidemic in seabirds across the North Atlantic, with Northern Gannets (*Morus*
151 *bassanus*; hereafter gannet), previously unknown to have been impacted by H5Nx, being severely
152 impacted (Cunningham et al. 2022).

153 Gannets breed in 53 colonies of various sizes (<10 to >60,000 breeding pairs and non-breeding
154 immatures) on sea cliffs, stacks, and islands across both sides of the North Atlantic from Russia to
155 north-eastern North America (d'Entremont et al. 2022a, Jeglinski et al. 2023). During the breeding
156 season, gannets are medium-range foragers capable of travelling more than 1000 km to find food
157 (Hamer et al. 2007). Moreover, immature gannets travel greater distances than adults and prospect
158 other colonies (Votier et al. 2011, Votier et al. 2017, Grecian et al. 2018). During the non-breeding
159 period, gannets are migratory with birds from Iceland and the eastern Atlantic occupying marine
160 wintering grounds in UK waters, Iberia, with the majority wintering off the coast of West Africa (Veron
161 and Lawlor 2009, Fort et al. 2012, Furness et al. 2018, Deakin et al. 2019). Birds from the western
162 Atlantic primarily winter along the coasts of the eastern United States of America south to the Gulf of
163 Mexico, although some also winter off the coast of West Africa (Fifield et al. 2014). Considering the
164 oral-faecal spread of avian influenza viruses, opportunities for spread between gannets are most likely
165 at the colony but may also occur at foraging grounds and wintering areas by birds in the early stages
166 of infection (Weber and Stilianakis 2007).

167 Globally, gannets are classified as Least Concern by the International Union for Conservation of Nature
168 (IUCN) due to their wide distribution and growing populations in Europe and North America (IUCN
169 2023). The European population comprises 75-94% of the global population with 55.6% breeding in
170 the UK (IUCN, 2023). The Bass Rock, Scotland (56° 6' N, 2° 36' W) is the world's largest gannet colony
171 with an estimated 75,259 apparently occupied sites (AOSs) in 2014 (Murray et al. 2015).

172 Understanding virus spread and infection outcome is essential to fully understand how the HPAIV
173 outbreak impacted gannets and other seabirds. Here, we provide the first comprehensive assessment
174 of the spatio-temporal occurrence of HPAIV outbreaks at most gannet colonies across their North
175 Atlantic breeding range. Moreover, to better understand HPAIV transmission, immunity, and the
176 potential for population recovery, we present detailed results from the largest gannet colony at Bass
177 Rock, Scotland. We quantify how the 2022 HPAIV outbreak influenced adult survival and breeding
178 success and present a non-invasive method that has the potential to determine exposure status based
179 on iris colour.

180

181 2. Methods

182 a. Global context: HPAIV spread across the North Atlantic gannet metapopulation

183 We collated and mapped data on the timing of unusually high gannet mortalities (the earliest
184 observations notable to fieldworkers familiar with their sites) at existing colonies across the global
185 metapopulation as defined by Jeglinski et al. 2023. Colonies in Norway, Iceland and some Irish colonies
186 were not monitored directly, but instead we gathered information on dead gannet sightings reported
187 to the Norwegian Species Observation System (www.artsobservasjoner.no), the Icelandic Food and
188 Veterinary Authority and to the Department of Agriculture, Food and the Marine's (DAFM) Avian Check
189 App (<https://aviancheck.apps.services.agriculture.gov.ie/>), and we associated these observations with
190 the nearest gannet breeding colony. We also collated information on positive HPAIV tests associated
191 with gannet colonies, based on data from the national testing laboratories for the relevant countries.

192

193 b. Case Study: Bass Rock

194 i. Health and safety and biosecurity

195 Strict biosecurity and health and safety measures were followed to ensure the safety of birds and field
196 workers. During handling our Personal Protection Equipment (PPE) comprised coveralls, face masks,
197 goggles, disposable aprons, and gloves. Safe4 disinfectant was used for disinfecting equipment and
198 footwear (see Supplementary Online Material S1).

199

200 ii. Impact of HPAIV on apparently occupied sites, breeding success and adult survival

201 *Apparently occupied sites* - A DJI Matrice 300 RTK unmanned aircraft system fitted with a DJI-Zenmuse
202 L1 LiDAR and photogrammetry sensor was flown over the Bass Rock between 15:07-15:19 on 30th June
203 to count live and dead birds. All flights were conducted from the southern tip of the island with a Real-
204 Time-Kinematic (RTK) base station, in good light with light winds (<5ms⁻¹) enabling a flight speed of 4
205 ms⁻¹, with image sidelap of 70% and endlap of 80%. The resulting 102 images (captured with 0.001 of
206 a second shutter speed and auto ISO) collected at an altitude of 100 m above ground level, were
207 processed through Agisoft Metashape (Agisoft LLC, St Petersburg, Russia) to produce an orthomosaic
208 of the Bass Rock with a ground sampling distance of approximately 3 cm (see Supplementary Online
209 Material S2). The composite image was loaded into DotDotGoose version 1.5.3 (DotDotGoose
210 amnh.org) to allow manual counting of birds on the colony. White birds were presumed to be adults
211 but could not be distinguished from 4-5-year-old immatures. Birds were considered dead based on
212 spread wings or contorted body shape, or alive if their posture was apparently natural or too indistinct
213 to see.

214 *Breeding success* - We monitored 93 active nests in two study sites, during 14 visits between 15th June
215 and 14th August 2022. All nests had an egg on the first visit, those with a chick on 14th August were
216 considered successful.

217 *Adult survival* - Visual searches for 370 colour-ringed adults (marked during 2010-2021) took place
218 weekly (total of 12 days) from 15th June until 30th July 2022. Nest sites of colour-ringed birds were
219 repeatedly scanned from a distance of between ~5-30m and the ring sequence of each bird recorded
220 during a total of ~11 person-observation hours each day.

221 We constructed annual encounter histories for each marked bird using resighting data from July 2022
222 and from visits made in July 2011-2021. A goodness-of-fit test (GOF) showed that a fully time-
223 dependent (both survival (ϕ) and resighting (p) probabilities vary with time) Cormack-Jolly-Seber (CJS)
224 model did not fit the data well (GOF: $\chi^2_{34} = 73.33$, $P = <0.01$) with evidence of trap dependence
225 (TEST2.CT; $z = -6.1484$, two-sided test, $p < 0.01$) but no evidence for transience (TEST3.SR; $z = -1.9044$,
226 two-sided test, $p = 0.056$). After accounting for trap-dependence a variance inflation factor (\hat{c}) of 1.212
227 was estimated by U-CARE (Choquet et al. 2009). Therefore we set $\hat{c} = 1.212$ to account for the over-
228 dispersion in the data and a two-stage TSM structure was applied to model re-sightings.

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

232

233 *III. Serology and iris colour*

234 During September 2022 we caught 19 apparently healthy chick-rearing adults and took ~1 ml of blood
235 from the tarsal vein (under licence from the UK Home Office; Project licence number PEAE7342F).
236 Sampling effort focused on catching equal numbers of birds with healthy and abnormally black irises,
237 seen for the first time during the outbreak. Birds were caught from seven distinct locations to minimise
238 potential bias in virus exposure between clusters of nests. Where possible, birds with chicks were
239 caught preferentially to guarantee that they had been present throughout the HPAIV outbreak. Birds
240 without chicks were caught if they appeared to be holding a territory.

241 We took external cloacal swabs from 18 of the 19 birds to test for any possible asymptomatic HPAI
242 infection. Blood and cloacal swabs were stored in a cool bag with ice blocks in the field, then stored
243 at ~4°C before being transported directly to the UK reference laboratory for avian influenza at the
244 Animal and Plant Health Agency (APHA). Blood samples were tested for an indication of previous
245 infection using an hemagglutination inhibition assay to detect antibodies to H5 avian influenza virus
246 (clade 2.3.4.4b) using a viral antigen homologous to the outbreak virus. Swabs were first tested for
247 influenza A virus nucleic acid following RNA extraction using a matrix (M) gene-specific real-time

248 reverse-transcriptase polymerase chain reaction (rRT-PCR) assay (Nagy et al. 2021) and a HPAIV
249 specific H5 PCR assay (James et al. 2022). Unless already ringed, birds were fitted with a metal British
250 Trust for Ornithology (BTO) ring and a blue plastic darvic ring engraved with a unique alphanumeric
251 code to allow future identification.

252 A Fisher's exact test was used to determine the associations between iris colour and exposure status.
253 Statistics were performed using R 4.1.1 (R Development Core Team 2007).

254

255 **3. Results**

256 a. Global Context: HPAIV spread across the North Atlantic gannet metapopulation

257 We gathered evidence of HPAI occurrence for 41 colonies. Unusually large numbers of dead gannets
258 were detected at 40 of 53 colonies during the breeding season, only one colony (Bjørnøya) was not
259 affected, and 12 colonies were not monitored (Figure 1). Positive H5N1 samples were associated with
260 24 of the 41 sampled colonies (58%), either through direct sampling of dead gannets from the colony
261 or by proximity of dead gannets to colonies. A small colony at Store Ulvøyholmen, Norway (330
262 Apparently Occupied Nests (AONs) in 2015, Barrett et al. 2017) was reported abandoned (Børge Moe,
263 pers comm) and, since dead gannets were reported close to the colony, this may have been due to
264 HPAI. One gannet sample from a bird found dead at Kjelmøya (Norway) tested positive for H5N5.
265 The earliest outbreaks occurred in the northeast Atlantic in Iceland (at Eldey, Brandur and Raudinupur
266 during 15th, 17th and 26th April), followed by Shetland, Scotland (Noss and Hermaness on 1st and 4th
267 May, respectively) then the Outer Hebrides, Scotland (St Kilda, 10th May). Subsequent outbreaks
268 appeared to occur from early June in southern Norway (Runde, 8th June). The concurrent, southwards
269 progression occurred along the east coast of the UK (e.g., Troup Head, 20th May, Bass Rock 4th June).
270 By mid-June, there were HPAIV outbreaks in northern Norway (Syltefjord, 16th June), the southern
271 North Sea (Heligoland, 21st June), the Channel Islands (Les Etacs and Ortac, 28th June) and the
272 southernmost colony Rouzic, France (1st July). In July and early August, signs of HPAI appeared in
273 northwest Norway, the Faroe Islands (Mykineshólmur, 7th July) and in a clockwise progression around
274 the UK, followed by Wales (Grassholm, 21st July) and then in Ireland (Clare Island, Lambay, Bull Rock,
275 Little Skellig, Great Saltee, Ireland's Eye; 10th, 25th, 26th, 31st August, 1st and 12th September
276 respectively). The northernmost colony Bjørnøya (52 AON in 2016, Barrett et al. 2017) appeared
277 unaffected by HPAIV. No information was available for several remote colonies in the west and
278 northwest of Scotland but unusually high mortality at Sule Skerry was detected after the breeding
279 season in October (Wanless and Harris, in press).

280 The outbreaks in the northwest Atlantic metapopulation developed in parallel to these in the
281 northeast, with the earliest outbreaks occurring between early and mid-May in the three colonies in

282 the Gulf of St. Lawrence (at Rochers aux Oiseaux, Magdalen Islands, 1st May and, Le Bonaventure, 20th
283 May) followed by the colonies in Newfoundland throughout June (Cape St. Mary's, 6th June, Baccalieu
284 Island, 17th June, and Funk Island, 24th June).

285

286 b. Case Study: Impact of HPAIV on Bass Rock

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

290 i. Impact of HPAIV on apparently occupied sites, breeding success and adult survival

291 *Apparently occupied sites* - A total of 21,227 live birds were counted on the 30th June 2022. An
292 additional 5,035 birds were identified as dead, approximately 3.3% of the breeding population
293 (assuming 150,518 breeding adults from 75,259 AOS, Murray et al. 2015), however, many additional
294 birds will have died at sea. Given the almost complete absence of immatures and non-breeders at the
295 colony during June, it is highly likely that the majority of birds counted, both live and dead, would have
296 been breeding adults.

297 *Breeding success* - Monitored nests declined from 93 to 23 (75% decline) between 15th June and 14th
298 August. However, empty nest sites on the 15th June indicated nests had already failed prior to the start
299 of monitoring (Figure 2). The majority of the 93 nests had failed by the beginning of July with nest
300 abandonment leaving gaps within the colony (Figures 2 and 3). An index of breeding success was
301 estimated as 0.247 based on the presence of 23 large, apparently healthy chicks in the study areas on
302 the 14th August. Clinical signs of viral infection, seizures, and lethargy were observed in a small number
303 of chicks (aged 2+ weeks) outside of our study areas, but since they were not monitored their fate is
304 unknown.

305 *Adult survival* - The top model showed strong support for survival probability varying with time and
306 for re-sightings to vary with time following the first year after marking (Table 1). Adult survival
307 between 2021 and 2022 was 0.455 (95% CI: 0.153 – 0.794) compared with an average annual survival
308 of 0.940 (SD 0.035) between 2011 and 2021. The resighting probability during 2022 was 0.615 (95%
309 CI: 0.144 – 0.938) compared with an average of 0.839 (SD: 0.066) between 2011 and 2021.

310 Seven colour-ringed birds were found dead during June and July 2022 on the North Sea coasts of the
311 UK, Sweden and Denmark, and eight were found dead on the colony in October, compared with 3
312 dead recoveries between 2015 and 2021.

313 *II. Serology and iris colour*

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

317 Black irises – instead of the usual pale blue – were first noted on 15-16th June 2022. Iris colour varied
318 from completely black to mottled and with some variation between eyes and did not present like a
319 dilated pupil (Figure 4). The likelihood of testing positive for HPAIV H5 antibodies was higher in birds
320 with black irises (77.7%) compared to birds with normally coloured eyes (12.5%; Fisher’s exact test; p
321 <0.05). The hemagglutinin (HA) binding antibody levels in serum samples, as detected by a
322 Haemagglutination Inhibition (HAI) titre, were 1/16 ($n = 3$) and 1/32 ($n = 5$, including the sample from
323 the bird with healthy irises) (Table 2 and Supplementary Online Material, Table S2).

324

325 **4. Discussion**

326 *a. Global Context: HPAIV spread across the North Atlantic gannet metapopulation*

327 During summer 2022 HPAIV H5N1 was recorded for the first time in gannets, causing mortality on an
328 unprecedented scale across their entire Atlantic breeding range. Positive tests from 58% of monitored
329 colonies mean it is likely that unusually high mortality in the 16 untested colonies in 2022 was due to
330 HPAI. Of the 41 colonies monitored, only one was confirmed to have been unimpacted/unaffected.
331 Strong evidence of an HPAIV outbreak at a colony unmonitored during the breeding season, Sule
332 Skerry, northern Scotland (Harris and Wanless in press) suggests it is likely some of the 12 remote
333 unmonitored colonies were also affected.

334 All positive samples collated across the northeast and northwest Atlantic metapopulations were
335 subtype H5N1 apart from a single gannet sample testing positive for subtype H5N5 from the Sør-
336 Varanger municipality in Troms and Finnmark county, Norway. In Norway, Subtype H5N5 has also
337 been detected in 30 birds from different species, including White-tailed Eagles, gulls (*Laridae*), Great
338 Skuas and corvids (*Corvidae*) (S. Granstad, personal communication, March 26, 2023).

339 Although a thorough estimation of gannet mortality during the 2022 HPAIV outbreak is beyond the
340 scope of the paper, we document the spread of the HPAIV outbreak and provide details on impacts at
341 the largest gannet colony. Following the first confirmed cases in Iceland during April 2022, HPAIV was
342 detected almost simultaneously across the northeast and northwest Atlantic metapopulations. HPAIV
343 outbreaks, confirmed and inferred from dead untested birds, occurred in at least 75% of all 53 known
344 gannet colonies. While gannets are a well-studied species, we note that sampling effort was not
345 standardised among colonies (e.g. uncertainty in data from northern Norway, Iceland and some of the

346 Irish colonies is largely due to the use of passive surveillance data rather than direct colony
347 monitoring), but we have no reason to believe this leads to an inaccurate representation of the timing
348 of HPAIV outbreaks.

349 b. Possible mechanism of HPAIV transmission between gannet colonies

350 The scale and speed at which HPAIV spread through the gannet metapopulation was dramatic, but
351 the mechanism of transmission and the subsequent spread between colonies is unclear. A possible
352 source may have been infectious gannets returning from their wintering areas. During the spring
353 migration, gannets in the eastern North Atlantic frequently perform a clockwise loop around the UK,
354 with Icelandic breeders arriving earlier than those breeding on the Bass Rock (Furness et al. 2018).
355 However, gannets from different colonies overlap to some degree in the wintering areas (Fort et al.
356 2012; Furness et al. 2018), making the sequential nature of the spread less likely due to differences in
357 migratory timing. Yet an unprecedented stranding of dead adult gannets on the Dutch coast prior to
358 the start of the breeding season in April 2022 potentially indicates HPAIV exposure over the previous
359 winter although none of these birds were tested (Camphuysen et al. 2023).

360 The timing of outbreaks on each side of the Atlantic and throughout the northeast metapopulation,
361 might point towards HPAIV transmission via other infected seabirds. Great Skuas (Grecian et al. 2016)
362 were severely affected by HPAIV H5N1 in Scotland in 2021 (Banyard et al. 2022) and again in 2022
363 (Camphuysen et al. 2022, Falchieri et al. 2022). Great Skua breed in close proximity to gannets in
364 Iceland, the Faroes and northern Scotland (Birdlife International, 2023) and overlap with the winter
365 range of gannets from both sides of the North Atlantic (Magnusdottir et al. 2012, Fifield et al. 2014).
366 Great Skua regularly kleptoparasitise gannets (Anderson 1976) which in addition to transmission via
367 faeces and respiratory secretions could explain the spread across taxa. Brown Skuas (*Stercorarius*
368 *antarcticus*) are likely vectors of avian cholera on Amsterdam Island, Indian Ocean (Gamble et al. 2019)
369 and we speculate a similar role for Great Skuas triggering the HPAIV outbreak in gannets in 2022. Yet
370 this does not explain the subsequent spread through the gannet metapopulation, and questions
371 remain about why spill-over into gannets may or may not have occurred during the 2021 outbreak
372 among skuas. Similarly, waterfowl and gull species have been found to play an important role in
373 intercontinental transmission of LP and HPAIVs via Iceland, the link between the East Atlantic and
374 North American Atlantic Flyways (Duesk et al. 2014). Gulls are known to frequent seabird colonies to
375 opportunistically prey on eggs and chicks (Donehower et al. 2007, pers obs) and may therefore have
376 played a role in virus spread.

377 The subsequent clockwise spread around the UK seems unlikely to be linked to centrally-placed adults
378 foraging at sea, based on current evidence. During chick-rearing, gannets have colony-specific foraging
379 ranges with limited overlap (Wakefield et al. 2013) and tend to have individual specific foraging

380 grounds (Wakefield et al. 2015, Votier et al. 2017). However, the HPAIV outbreak may have altered
381 their movement behaviour leading to an increased inter-colony contact (Jeglinski et al. in prep;
382 d'Entremont and Montevecchi unpubl. data). Immature gannets are another possible route for
383 spreading the virus while prospecting among colonies (Votier et al. 2011). They also have larger
384 foraging ranges than breeders (Votier et al. 2017, Grecian et al. 2018), and therefore a greater chance
385 of inter-colony overlap. Nevertheless, immature gannets tend to return to the colony much later than
386 adults, being scarce during April-May and only appearing in large numbers during June/July (Wanless
387 1983, Nelson 2002), so were unlikely to have played a role during outbreaks during April and May,
388 though they may have played a role during outbreaks later in the breeding season (Figure 1). More
389 research into virus incubation and length of infectious period in addition to possible transmission
390 pathways between species that overlap in their wintering, migratory and breeding areas is paramount
391 (Hill et al. 2022).

392 c. Case Study: Impact on Bass Rock Gannet Colony

393 Drone footage on 30th June recorded 5,035 dead individuals that represented ~3% of breeding adult
394 gannets on Bass Rock. This is likely an underestimate as it excludes decomposed birds or those that
395 died at sea and does not account for the colony growth since 2014 (Murray et al. 2017). This figure
396 compares with an estimated 7% mortality at Mykineshólmur, Faores (unpublished) and 6% at Sule
397 Skerry, Scotland (Harris and Wanless, in press), both from aerial counts although the Sule Skerry count
398 was performed at the end of the breeding season. Drone counts in late June indicate that the colony
399 was ~71% smaller than during the last full colony count in 2014 (Murray et al. 2015). However, the
400 colony had grown since 2014 (Murray 2017) so again, this is almost certainly an underestimate, though
401 note that different methodologies and counting units make a direct comparison difficult.

402 Around one quarter of nests with an egg on 15th June still had a chick in late August, which is much
403 lower than the mean UK gannet breeding success during 1961–2018 (mean \pm standard deviation) 0.72
404 ± 0.12 (Jeglinski et al. 2023). There are methodological differences in approach, but the comparison
405 provides a further indication of the severe impact of the virus. The primary cause of breeding failure
406 appeared to be nest abandonment, either when adults did not return from foraging trips or died at
407 the nest.

408 Adult survival was approximately 42% lower than the average of 0.940 (SD 0.035) between 2011 and
409 2021. The reduction in the number of re-sighted colour-ringed birds indicates that a large proportion
410 of adults have died, but a full assessment of the impact on adult survival will have to wait until 2023
411 when visual searches will be made for returning birds. Similar to most seabirds, gannets are a long-
412 lived species making their populations particularly sensitive to changes in adult survival therefore the

413 consequences of a significant reduction in adult survival could be considerable (Croxall & Rothbury,
414 1991).

415 Despite a modest sample size, our study suggests that gannets infected with HPAIV H5N1 can survive,
416 with important implications for the long-term consequence of the virus impact. We also found that
417 black iris coloration in otherwise apparently healthy gannets is a likely indicator of prior infection. One
418 seropositive bird had healthy irises, but this may be related to a different subtype of HPAIV or LPAIV
419 (Wilson et al. 2013), to waning antibody levels following prior infection, or may suggest that not all
420 infected birds develop black irises. We suggest the two birds with black irises that tested negative for
421 antibodies had previously been infected but had already lost the antibodies, however further
422 investigation is needed to inform on antibody persistence. Black eyes have been reported in gannets
423 once before, but the reason is unknown (J. Swales pers comm., Balfour 1922). During the HPAIV
424 outbreak in 2022, gannets with black irises were also reported from colonies in the UK (Bempton Cliffs,
425 Grassholm and Ortac), France (Rouzic), Germany (Heligoland) and Canada (île Bonaventure). In early
426 spring 2023, gannets with black irises were observed at the Bempton Cliffs, Bass Rock, Troup Head,
427 Rouzic and Les Etacs colonies, suggesting the potential for a longer-lasting or even permanent
428 modification of the iris.

429

430 **5. Recommendations**

431 Future research should quantify changes in demography (i.e. population size, adult survival and
432 breeding success) of gannets and other impacted seabirds while also assessing whether previously
433 infected birds have developed immunity in order to model disease progression and long-term impacts
434 of HPAIV (Hill et al. 2019). Additionally, assessments of infection and mortality rates in different age
435 classes, and of how previous infection might influence fertility or the outcome of a second infection
436 are also needed (Wilson et al. 2013). Juvenile gannets have been found to carry antibodies to HPAIV
437 (Grémillet et al. in prep) but it is unknown whether these were maternally derived or produced in
438 response to infection (DeVriese et al. 2010).

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

446 If sampling for live virus, we recommend cloacal swabs be taken in conjunction with oropharyngeal
447 swabs (Suarez et al. 2000, van den Brand et al. 2018) because of possible differences in virus genotype
448 detectability (Slomka et al, in prep). Primary flight feathers can also be used as a diagnostic indication
449 of systemic viral infection as infectious virus can be detected in these samples (Nuradji et al. 2015).
450 The 2022 HPAIV H5N1 outbreak has provided another significant stressor to those already faced by
451 our rapidly declining seabird populations (Dias et al. 2019, Careen et al. 2023) - quantifying and
452 perhaps even mitigating its impact is therefore crucial if we hope to see a healthy seabird assemblage
453 across the world's oceans.

454 **6. References**

- 455 Andersson, M. 1976. Predation and kleptoparasitism by skuas in a Shetland seabird colony. *Ibis*.
456 **118**(2), 208-217. <https://doi.org/10.1111/j.1474-919X.1976.tb03066.x>
- 457 Arnal, A. Marion Vittecoq, M., Pearce-Duvel, J., Gauthier-Clerc, M., Boulinier, T & Jourdain, E. 2014.
458 Laridae: A neglected reservoir that could play a major role in avian influenza virus epidemiological
459 dynamics. *Critical Reviews in Microbiology*. **41**(4). [10.3109/1040841X.2013.870967](https://doi.org/10.3109/1040841X.2013.870967)
- 460 Balfour, H. 1922. Varieties of the common gannet. *British Birds*.
461 https://britishbirds.co.uk/sites/default/files/V15_N04_P082-084_A019.pdf
- 462 Banyard, A. C., Lean, F. Z. X., Robinson, C., Howie, F., Tyler, G., Nisbet, C., Seekings, J., Mirisr, S.,
463 Whittard, E., Ashpitel, H. F., Bas, M., Byrne, A. M. P., Lewis, T., James, J., Stephan, L., Lewis, N. S.,
464 Brown, I. H., Hansen, R. D. E. & Reid, S. M. 2022. Detection of Highly Pathogenic avian influenza virus
465 H5N1 clade 2.3. 4.4 b in Great Skuas: a species of conservation concern in Great Britain. *Viruses*. **14**:
466 212.
- 467 Barrett, R.J., Strøm, H. & Melnikov, M. 2017. On the polar edge: the status of the northern gannet
468 (*Morus bassanus*) in the Barents Sea in 2015-16. *Polar Res*. 36:1, DOI:
469 [10.1080/17518369.2017.1390384](https://doi.org/10.1080/17518369.2017.1390384)
- 470 Blagodatski, A.; Trutneva, K.; Glazova, O.; Mityaeva, O.; Shevkova, L.; Kegeles, E.; Onyanov, N.; Fede,
471 K.; Maznina, A.; Khavina, E., Yeo, S-J., Park, H. & Volchkov, P. 2021. Avian Influenza in wild birds and
472 poultry: Dissemination pathways, monitoring methods, and virus ecology. *Pathogens*. **10**: 630.
473 <https://doi.org/10.3390/pathogens10050630>
- 474 Boulinier, T. 2023. Avian influenza spread and seabird movements between colonies. *Trends Ecol*
475 *Evol*. **23**:S0169-5347(23)00031-9. doi: 10.1016/j.tree.2023.02.002.
- 476 Burggraff, S., Kapala, A.J., Bingham, J., Lowther, S., Selleck, P, Kimpton, W. & Bean, A.G.D. 2014.
477 H5N1 infection causes rapid mortality and high cytokine levels in chickens compared to ducks. *Virus*
478 *Res*. **185**: 23-31. doi: 10.1016/j.viruses.2014.03.012
- 479 Caliendo, V., Leijten, L., Begeman, L., Poen, M.J., Fouchier, R.A.M., Beerens, N., Kuiken, T. 2020.
480 Enterotropism of Highly Pathogenic avian influenza virus H5N8 from the 2016/2017 epidemic in
481 some wild bird species. *Vet Res*. **51**(1):117. doi: 10.1186/s13567-020-00841-6.

- 482 Caliendo, V., Lewis, N.S., Pohlmann, A., Baillie, S.R., Banyard, A.C., Beer, M., Brown, I.H., Fouchier,
483 R.A.M., Hansen, R.D.E., Lameris, T.K., Lang, A.S., Laurendeau, S., Lung, O., Robertson, G., van der
484 Jeugd, H., Alkie, T.N., Thorup, K., van Toor, M.L., Waldenström, J., Yason, C., Kuiken, T. & Berhane, Y.
485 2022. Transatlantic spread of Highly Pathogenic avian influenza H5N1 by wild birds from Europe to
486 North America in 2021. *Sci Rep.* **11**;12(1):11729. doi: 10.1038/s41598-022-13447-z. PMID: 35821511;
487 PMCID: PMC9276711.
- 488 Camphuysen, K., Kelder, L., Zuhorn, C. & Fouchier, R. 2023. Avian influenza panzootic leads to mass
489 strandings of Northern Gannets *Morus bassanus* in the Netherlands, April-October 2022. *Limosa* (in
490 press).
- 491 Camphuysen, C.J. Gear, S.C. & Furness, R.W. 2022. Avian influenza leads to mass mortality of adult
492 Great Skuas in Foula in summer 2022. *Scottish Birds.* **42**(4), 312-323.
- 493 Careen, N., d'Entremont, K., Mooney, C., Montevecchi, W. 2023. Avian influenza (H5N1) and a
494 marine heatwave spell reproductive disaster for Northern Gannets at their southernmost colony.
495 Poster, Pacific Seabird Group Annual Meeting (San Diego, 15-17 February).
- 496 Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M. & Pradel, R. 2009. U-CARE: utilities for
497 performing goodness of fit tests and manipulating Capture– Recapture data. *Ecography.* **32**, 1071–
498 1074. <https://doi.org/10.1111/j.1600-0587.2009.05968.x>.
- 499 Croxall, J.P. & Rothery, P. 1991. Population regulation of seabirds: implications of their demography
500 for conservation. p272-296 in Perrins, C.M., Lebreton, J-D. & Hiron, G.J.M. editors *Bird population*
501 *Studies: relevance to conservation and management*. Oxford University Press, Oxford, England.
- 502 Cunningham, E.J.A, Gamble, A., Hart, T., Humphreys, E.M., Philip, E., Tyler, G. & Wood, M.J. 2022.
503 The incursion of Highly Pathogenic Avian Influenza (HPAI) into North Atlantic seabird populations: An
504 interim report from the 15th International Seabird Group conference. Report on HPAI in North
505 Atlantic seabirds. *Seabird.* **34**.
- 506 Deakin, Z., Hamer, K.C., Sherley, R.B., Bearhop, S., Bodey, T.W., Clark, B.L., Grecian, W.J., Gummery,
507 M., Lane, J., Morgan, G., Morgan, L., Phillips, R.A., Wakefield, E.D & Votier, S.C. 2019. Sex differences
508 in migration and demography of a wide-ranging seabird, the northern gannet. *Mar Ecol Prog Ser.*
509 **622**: 191–201. doi.org/10.3354/meps12986
- 510 d'Entremont, K.J.N., Guzzwell, L.M., Wilhelm, S.I., Friesen, V.L., Davoren, G.K., Walsh, C.J. &
511 Montevecchi, W.A. 2022a. Northern Gannets (*Morus bassanus*) breeding at their southern limit
512 struggle with prey shortages as a result of warming waters, *ICES J Mar Sci.* **79** (1), 50–60.
513 <https://doi.org/10.1093/icesjms/fsab240>
- 514 DeVriese, J., Steensels, M. Palya, Gardin, Y., Moore Dorsey, K., Lambrecht, B., Van Borm, S. & van
515 den Berg, T. 2010. Passive protection afforded by maternally-derived antibodies in chickens and the
516 antibodies' interference with the protection elicited by avian influenza–inactivated vaccines in
517 progeny. *Avian Dis.* **54**(s1), 246-252. <https://doi.org/10.1637/8908-043009-Reg.1>

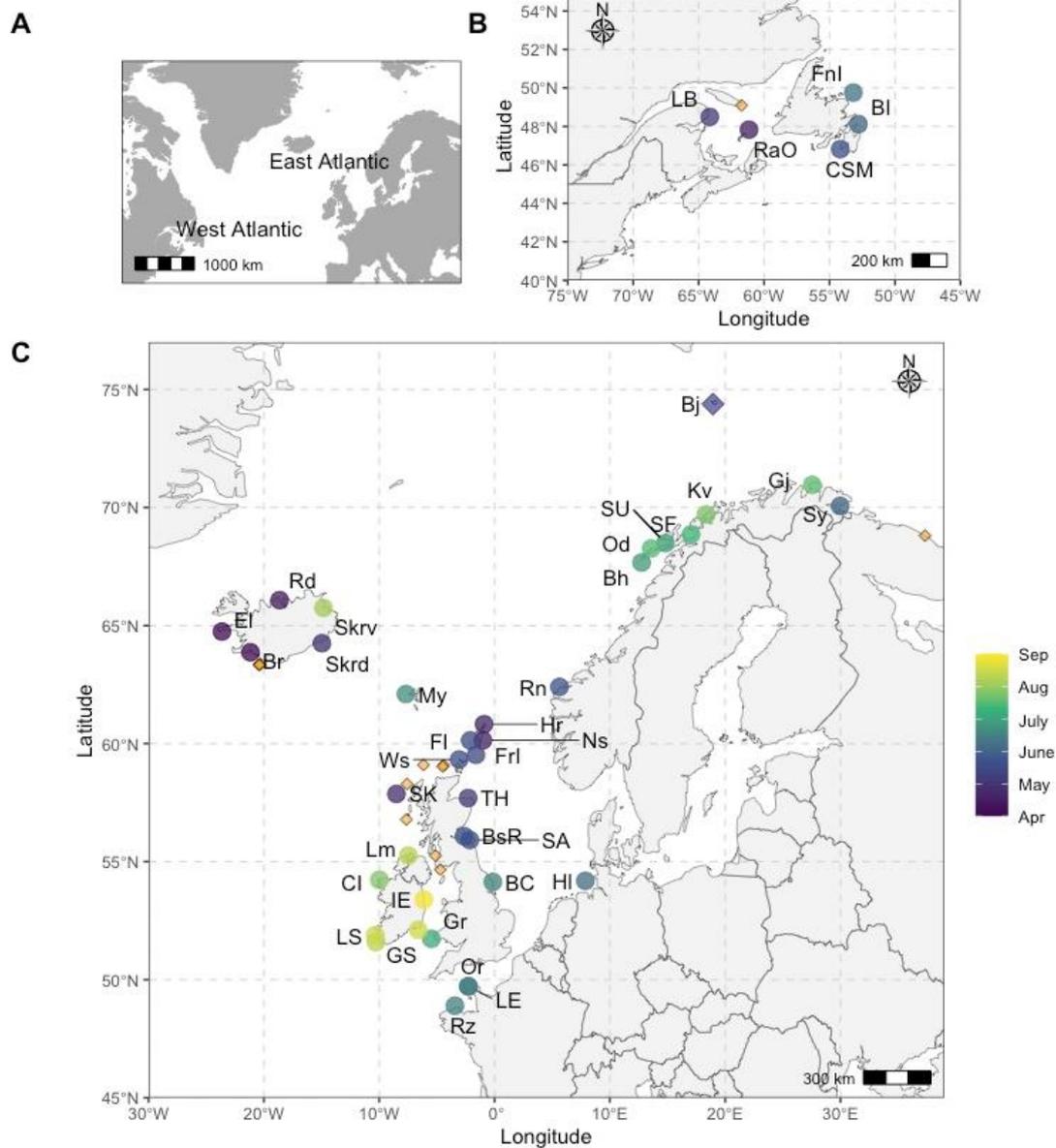
- 518 Dias, M.P., Martin, R., Pearmain, E.J., Burfield, I.J., Small, C., Phillips, R.A., Yates, O., Lascelles, B.,
519 Garcia Borboroglu, P. & Croxall, J.P. 2019. Threats to seabirds: A global assessment. *Biol Conserv.*
520 **237**: 525-537. <https://doi.org/10.1016/j.biocon.2019.06.033>.
- 521 Donehower, C.E., Bird, D.M., Hall, C.S. & Kress, S.W. 2007. Effects of gull predation and predator
522 control on tern nesting success at Eastern Egg Rock, Maine. *Waterbirds*. **30**(1):29-39.
- 523 Dusek, R.J., Hallgrimsson, G.T., IP, H.S., Jónsson, J.E., Sreevatsan, S., Nashold, S.W. 2014. North
524 Atlantic migratory bird flyways provide routes for intercontinental movement of avian influenza
525 viruses. *PLoS ONE*. **9**(3): e92075. <https://doi.org/10.1371/journal.pone.0092075>
- 526 EFSA (European Food Safety Authority), ECDC (European Centre for Disease Prevention and Control),
527 EURL (European Reference Laboratory for Avian Influenza), Adlhoch, C., Fusaro, A., Gonzales, J.L.,
528 Kuiken, T., Marangon, S., Niqueux, É., Staubach, C., Terregino, C., Aznar, I., Muñoz Guajardo, I. &
529 Baldinelli, F. 2023. Scientific report: Avian influenza overview September–December 2022. *EFSA*
530 *Journal*. **21**(1):7786. <https://doi.org/10.2903/j.efsa.2023.7786>
- 531 Falchieri, M., Reid, S.M., Ross, C.S., James, J., Byrne, A.M.P., Zamfir, M., Brown, I.H., Banyard, A.C.,
532 Tyler, G., Philip, E. & Miles, W. 2022. Shift in HPAI infection dynamics causes significant losses in
533 seabird populations across Great Britain. *Vet Rec*. **191**: 294-296. <https://doi.org/10.1002/vetr.2311>
- 534 Fifield, D.A., Montevecchi, W.A., Garthe, S., Robertson, G.J., Kuetzki, U. & Rail, J-F. 2014. Migratory
535 tactics and wintering areas of Northern gannets (*Morus bassanus*) breeding in North America.
536 *Ornithol Monographs*. **79**: 1-63. <https://doi.org/10.1642/aoum.79-1>
- 537 Fort, J., Pettex, E., Tremblay, Y., Lorentsen, S.-H., Garthe, S., Votier, S., Pons, J.B., Siorat, F., Furness,
538 R.W., Grecian, W.J., Bearhop, S., Montevecchi, W.A., Gremillet, D. 2012. Meta-population evidence
539 of oriented chain migration in northern gannets (*Morus bassanus*). *Front Ecol Environ*. **10**(5): 237-
540 242. <https://doi.org/10.1890/110194>
- 541 Furness, R.W., Hallgrimsson, G.T., Montevecchi, W.A., Fifield, D., Kubetzki, U., Mendel, B. & Garthe,
542 S. 2018. Adult Gannet migrations frequently loop clockwise around Britain and Ireland. *Ringing and*
543 *Migration*. 1–9. <https://doi.org/10.1080/03078698.2018.1472971>.
- 544 Gamble, A., Bazire, R., Delord, K., Barbraud, C., Jaeger, A., Gantelet, H., Thibault, E., Lebarbenchon,
545 C., Lagadec, E., Tortosa, P., Weimerskirch, H., Thiebot, J-B., Garnier, R., Tornos, J. & Boulinier, T.
546 2019. Predator and scavenger movements among and within endangered seabird colonies:
547 Opportunities for pathogen spread. *J Appl Ecol*. **57**(2), 367-378. <https://doi.org/10.1111/1365-2664.13531>
- 549 Grecian, W.J., Lane, J.V., Michelot, T., Wade, H.M. & Hamer, K.C. 2018. Understanding the ontogeny
550 of foraging behaviour: insights from combining marine predator bio-logging with satellite-derived
551 oceanography in hidden Markov models. *Royal Society Interface*. **15**: 20180084.
552 <https://doi.org/10.1098/rsif.2018.0084>
- 553 Grecian, J.W., Witt, M.J. Attrill, M.J., Bearhop, S., Becker, P.H., Egevang, C., Furness, R.W., Godley,
554 B.J., González-Solís, J., Gremillet, D., Kopp, M., Lescroël, Amélie., Matthiopoulos, J., Patrick, S.C.,
555 Peter, H-U., Phillips, R.A., Stenhouse, I.J. & Votier, S.C. 2016. Seabird diversity hotspot linked to

- 556 ocean productivity in the Canary Current Large Marine Ecosystem. *Biol. Lett.* **12**(8).
557 <https://doi.org/10.1098/rsbl.2016.0024>
- 558 Grémillet, D., et al. in prep
- 559 Hamer, K.C., Humphreys, E.M., Garthe, S., Hennicke, J., Peters, G., Grémillet, D., Phillips, R.A., Harris,
560 M.P. & Wanless, S. 2007. Annual variation in diets, feeding locations and foraging behaviour of
561 gannets in the North Sea: flexibility, consistency and constraint. *Mar Ecol Prog Ser.* **338**. 295-305.
- 562 Harris, M.P. & Wanless, S. A major mortality of Gannets due to a probable outbreak of High
563 Pathogenicity Avian Influenza on Sule Skerry in 2022. (in press *Scottish Birds*).
- 564 Hill, N.J., Bishop, M.A., Trovão, N.S., Ineson, K.M., Schaefer, A.L., Puryear, W.B., et al. 2022.
565 Ecological divergence of wild birds drives avian influenza spillover and global spread. *PLoS Pathog.*
566 **18**(5): e1010062. <https://doi.org/10.1371/journal.ppat.1010062>
- 567 IUCN. BirdLife International. 2023. Species factsheet: *Catharacta skua*. Downloaded from
568 <http://www.birdlife.org> on 23/02/2023.
- 569 IUCN. BirdLife International. 2023. Species factsheet: *Morus bassanus*. Downloaded from
570 <http://www.birdlife.org> on 20/03/2023.
- 571 James, J., Seekings, A.H., Skinner, P., Purchase, K., Mahmood, S., Brown, I.H., Hansen, R.D.E.,
572 Banyard, A.C. & Reid, S.M. 2022. Rapid and sensitive detection of high pathogenicity Eurasian clade
573 2.3.4.4b avian influenza viruses in wild birds and poultry. *J Virol Methods.* **301**:114454. doi:
574 [10.1016/j.jviromet.2022.114454](https://doi.org/10.1016/j.jviromet.2022.114454).
- 575 Jeglinski, J.W.E., Wanless, S., Murray, S., Barrett, R.T., Gardarsson, A., Harris, M.P., Dierschke, J.,
576 Strøm, H., Lorentsen, S-V. & Matthiopoulos, J. 2023. Metapopulation regulation acts at multiple
577 spatial scales: Insights from a century of seabird colony census data. *Ecological Monographs.*
578 <https://doi.org/10.1002/ecm.1569>
- 579 Magnúsdóttir, E., Leat, E.H.K., Bourgeon, S., Strøm, H., Petersen, A., Phillips, R.A., Hanssen, S.A.,
580 Bustnes, J.O., Hersteinsson, P. & Furness, R.W. 2012. Wintering areas of great skuas *Stercorarius*
581 *skua* breeding in Scotland, Iceland and Norway. *Bird Study.* **59**:1–9.
- 582 Monne, I., Fusaro, A., Nelson, M.I., Bonfanti, L., Mulatti, P., Hughes, J., Murcia, P.R., Schivo, A.,
583 Valastro, V., Moreno, A., Holmes, E.C. & Cattoli, G. 2014. Emergence of a highly pathogenic avian
584 influenza virus from a low-pathogenic progenitor. *J Virol.* **88**(8):4375-88. doi: [10.1128/JVI.03181-13](https://doi.org/10.1128/JVI.03181-13).
- 585 Murray, S., Harris, M.P. & Wanless, S., 2015. The status of the gannet in Scotland in 2013- 14.
586 *Scottish Birds.* **35**: 3–18.
- 587 Murray, S. 2017. Gannets and tree mallow – change on the Bass Rock, 2009-17. *Scottish Birds.*
588 **37**(4):346-347.
- 589 Nagy A, Černíková L, Kunteová K, Dirbáková Z, Thomas SS, Slomka MJ, et al. 2021. A universal RT-
590 qPCR assay for “One Health” detection of influenza A viruses. *PLoS ONE* **16**(1): e0244669.
591 <https://doi.org/10.1371/journal.pone.0244669>

- 592 Nelson, B. 2002. The Atlantic Gannet. Poyser Monographs.
- 593 Nuñez, I.A. & Ross, T.M. 2019. A review of H5Nx avian influenza viruses. *Ther Adv Vaccines*
594 *Immunother.* **7**:2515135518821625. doi: 10.1177/2515135518821625.
- 595 Nuradji, H., Bingham, J., Lowther, S., Wibawa, H., Colling, A., Thanh Long, N & Meers, J. 2015. A
596 comparative evaluation of feathers, oropharyngeal swabs, and cloacal swabs for the detection of
597 H5N1 highly pathogenic avian influenza infection in experimentally infected chicks and ducks. *J Vet*
598 *Diagn Investig.* **27**:704-715. doi:10.1177/1040638715611443
- 599 Ramey, A.M., Hill, N.J., DeLiberto, T.J., Gibbs, S.E.J., Hopkins, C., Lang, A.S., Poulson, R.L., Prosser,
600 D.J., Sleeman, J.M., Stallknecht, D.E. & Wan, X. 2022. Highly Pathogenic avian influenza is an
601 emerging disease threat to wild birds in North America. *J Wildlife Manage.* **86**(2), e22171.
602 <https://doi.org/10.1002/jwmg.22171>
- 603 Roberts, L.C., Abolnik, C., Waller, L.J., Shaw, K., Ludynia, K., Robers, D.G., Kock, A.A., Makhado, A.B.,
604 Snyman, A. & Abernethy, D. 2023. Descriptive epidemiology of and response to the High
605 Pathogenicity Avian Influenza (H5N8) epidemic in South African coastal seabirds. *Transbound Emerg*
606 *Dis.* **2023**:2708458. doi.org/10.1155/2023/2708458 Slomka et al. in prep
- 607 van den Brand, J.M.A., Verhagen, J.H., Veldhuis Kroeze, E.J.B., van de Bildt, M.W.G., Bodewes, R.,
608 Herfst, S., Richard, M., Lexmond, P., Bestebroer, T.M., Fouchier, R.A.M. & Kuiken, T. 2018. Wild
609 ducks excrete Highly Pathogenic avian influenza virus H5N8 (2014–2015) without clinical or
610 pathological evidence of disease. *Emerg Microbes Infect.* **7**(1): 1-10. doi:10.1038/s41426-018-0070-9
- 611 Venkatesh, D., Poen, M.J., Bestebroer, T.M., Scheuer, R.D., Vuong, O., Chkhaidze, M., Machabishvili,
612 A., Mamuchadze, J., Ninua, L., Fedorova, N.B., Halpin, R.A., Lin, X., Ransier, A., Stockwell, T.B.,
613 Wentworth, D.E., Kriti, D., Dutta, J., van Bakel, H., Puranik, A., Slomka, M.J., Essen, S., Brown, I.H.,
614 Fouchier, R.A.M. & Lewis, N.S. 2018. Avian Influenza Viruses in Wild Birds: Virus Evolution in a
615 Multihost Ecosystem. *J Virol.* **92**(15): e00433-18. doi: 10.1128/JVI.00433-18
- 616 Veron, P.K. & Lawlor, M.P. 2009. The dispersal and migration of the Northern Gannet *Morus*
617 *bassanus* from Channel Islands breeding colonies. *Seabird.* **22**, 37-47.
- 618 Votier, S.C., Birkhead, T.R., Oro, D., Trinder, M., Grantham, M.J., Clark, J.A., McCleery, R.H.
619 & Hatchwell, B.J. 2008. Recruitment and survival of immature seabirds in relation to oil spills and
620 climate variability. *J Anim Ecol.* **77**(5): 974-983.
- 621 Votier, S.C., Fayet, A.L., Bearhop, S., Bodey, T.W. and others. 2017. Effects of age and reproductive
622 status on individual foraging site fidelity in a long-lived marine predator. *Proc Biol Sci.* **284**: 1859
- 623 Votier, S. C., Grecian, W. J., Patrick, S., & Newton, J. 2011. Inter-colony movements, at-sea behaviour
624 and foraging in an immature seabird: results from GPS-PPT tracking, radio-tracking and stable
625 isotope analysis. *Mar Biol.* **158**: 355-362.
- 626 Wakefield, E.D., Cleasby, I.R., Bearhop, S., Bodey, T.W., Davies, R.D., Miller, P.I., Newton, J., Votier,
627 S.C., & Hamer, K.C. 2015. Long-term individual foraging site fidelity--why some gannets don't change
628 their spots. *Ecology.* **96**(11), 3058-74. doi: 10.1890/14-1300.1.

- 629 Wakefield, E.D., Bodey, T.W., Bearhop, S., Blackburn, J., Colhoun, K., Davies, R., Dwyer, R.G., Green,
630 J.A., Gremillet, D., Jackson, A., Jessopp, M., Kane, A., Langston, R., Lescroel, A., Murray, S., Le Nuz,
631 M., Patrick, S., Peron, C., Soeanes, L., Wanless, S., Votier, S. & Hamer, K.C. 2013. Space partitioning
632 without territoriality in gannets. *Science*. **341**, 68-70. 10.1126/science.1236077
- 633 Wan, X.F. 2012. Lessons from emergence of A/goose/Guangdong/1996-like H5N1 highly pathogenic
634 avian influenza viruses and recent influenza surveillance efforts in southern China. *Zoonoses Public*
635 *Hlth*. **59**, Suppl 2(0 2):32-42. doi: 10.1111/j.1863-2378.2012.01497.x.
- 636 Wanless, S. 1983. Seasonal variation in the numbers and condition of gannets *Sula bassana* dying on
637 Ailsa Craig. *Bird Study*. **30**: 102-108.
- 638 Weber, T.P. & Stilianakis, N.I. 2007. Ecologic immunology of avian influenza (H5N1) in migratory
639 birds. *Emerg Infect Dis*. **13**(8): 1139-43. doi: 10.3201/eid1308.070319
- 640 Wilson, H.M., Hall, J.S., Flint, P.L., Franson, J.C., Ely, C.R., Schmutz, J.A. & Samuel, M.D. 2013. High
641 seroprevalence of antibodies to avian influenza viruses among wild waterfowl in Alaska: Implications
642 for surveillance. *PLoS ONE*. **8**(3): e58308. <https://doi.org/10.1371/journal.pone.0058308>
- 643 Xu, X., Subbarao, K., Cox, N. J. & Guo, Y. 1999. Genetic characterization of the pathogenic influenza
644 A/Goose/Guangdong/1/96 (H5N1) virus: similarity of its hemagglutinin gene to those of H5N1
645 viruses from the 1997 outbreaks in Hong Kong. *Virology*. **261**: 15–19.
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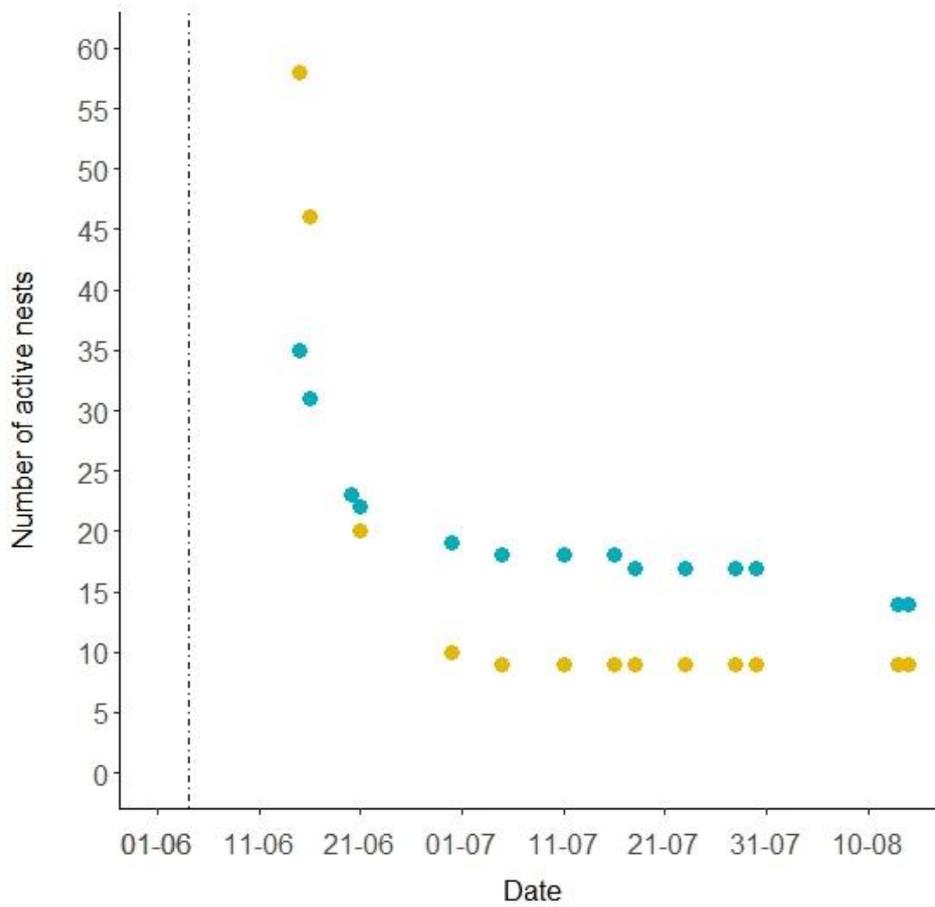
664 **Figures**



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666 **Figure 1:** The timing of HPAIV outbreaks across the gannet metapopulation in 2022, based on the
667 first date unusual mortalities in adults were observed. Affected colonies (n = 40) are indicated by
668 circles, coloured by date. Colonies where information is unavailable (n=12) are indicated by orange
669 diamonds. Letter combinations indicate colony name abbreviations, for full colony name see
670 Supplementary Online Material, Table S1). A) Geographical context. B) Colonies in the West Atlantic.
671 C) Colonies in the East Atlantic. A navy-coloured diamond indicates Bjørnøya (Bj, Norway, the
672 northernmost colony, H Strøm pers. obs.) where no signs of HPAIV were observed. The Store
673 Ulvøyholmen colony (SU) was found abandoned (confirmation received 29th June 2022 in litt.) No
674 signs of HPAIV were detected in the colony Ailsa Craig (AC) between Northern Ireland and Scotland
675 on the 28th July 2022, but there was no visit later in the season when the surrounding colonies were
676 affected.

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679 **Figure 2:** The number of active nests within two study areas on Bass Rock; area 1 in blue, area 2 in
680 yellow. Dotted vertical line indicates 4th June, the date carcasses were collected for testing by the
681 Animal Plant Health Agency (APHA).

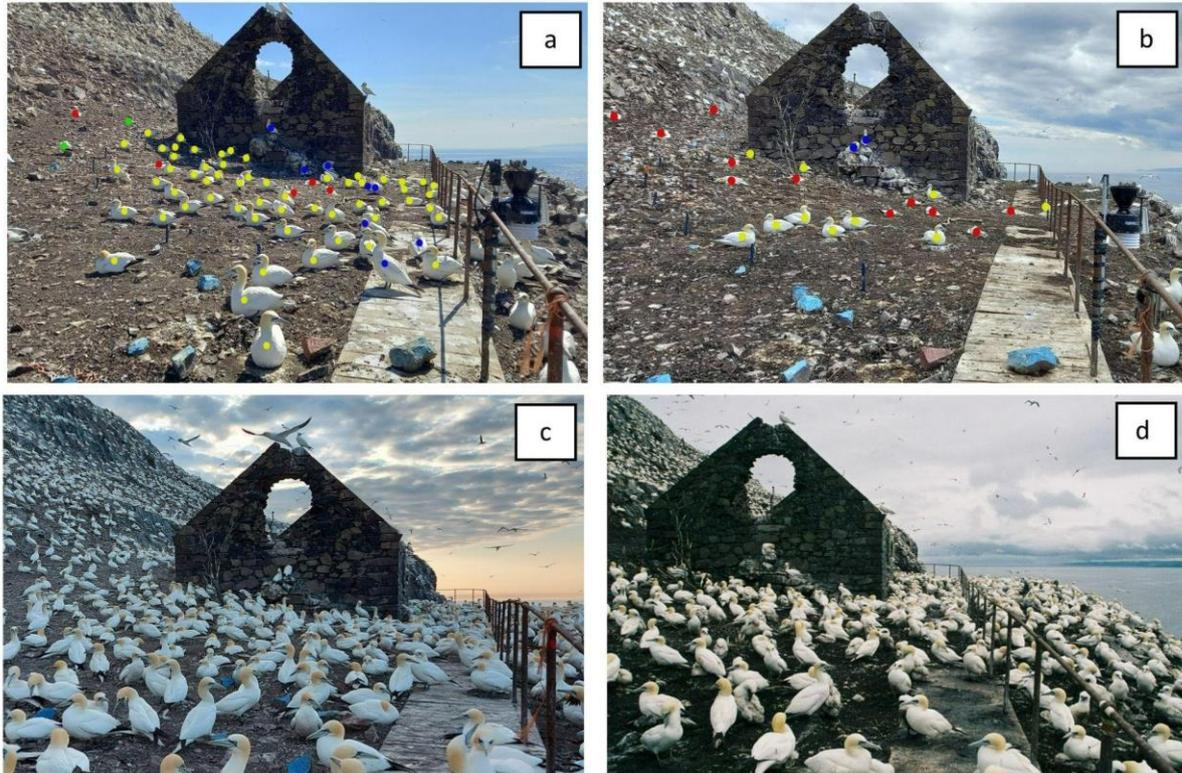
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688 **Figure 3.** Nest failures, apparent from gaps between birds, and dead birds in study area 2 of the Bass
689 Rock on **(a)** 15th June and **(b)** 30th June, **(c and d)** study area on 29th April 2022 and 23rd July 2020
690 showing typical nest spacings and densities for the respective time of year; **(c)** pre-laying and **(d)**
691 mid-chick rearing. Coloured dots in **(a)** and **(b)** indicate the status of the bird; red - dead, green -
692 visibly sick, yellow - active nest with healthy adults, dark blue - non-breeding healthy adults, light
693 blue painted rocks delineate a path.

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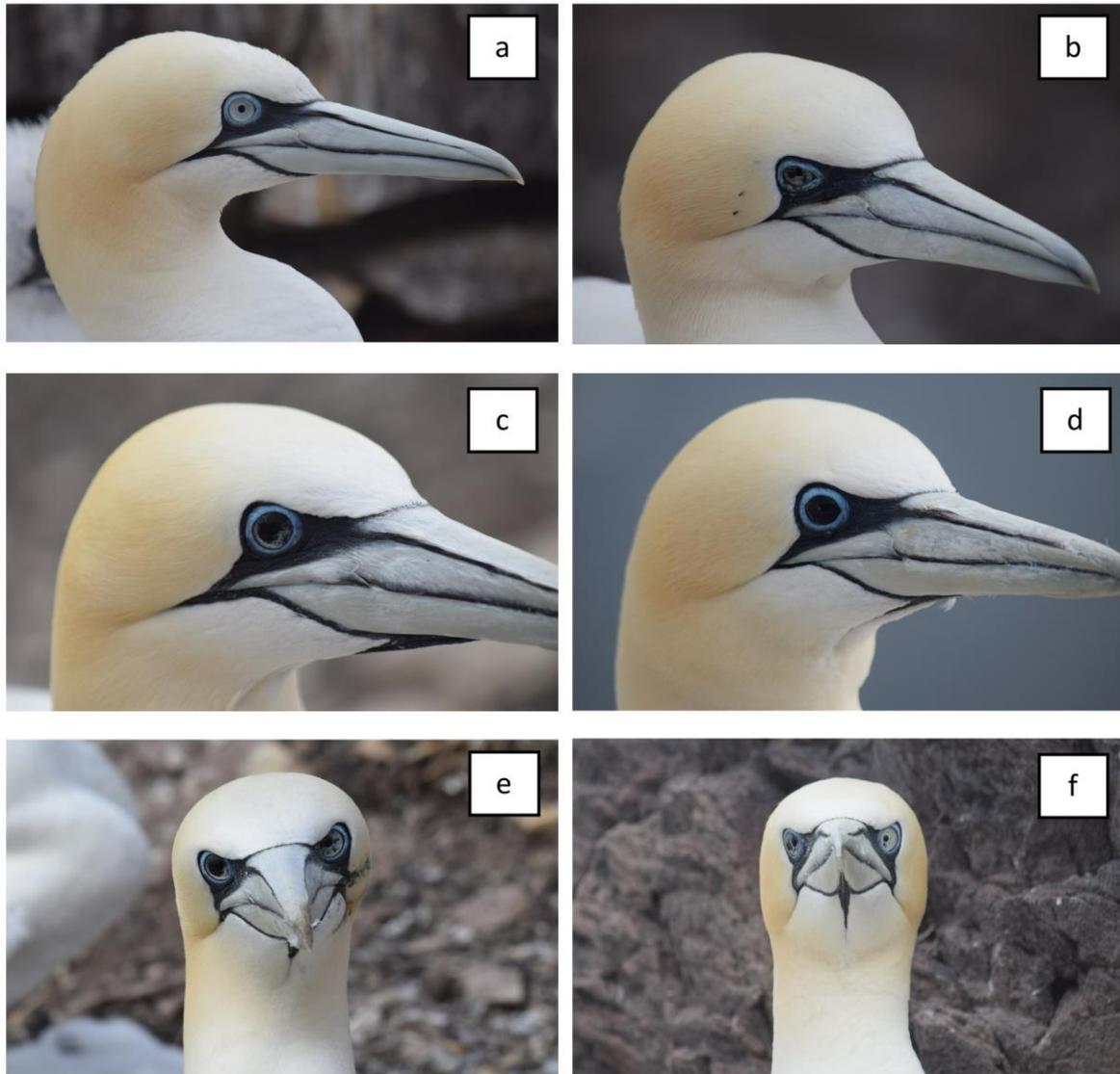
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Figure 4. Gannets on the Bass Rock colony in 2022 with black flecking in their irises. The condition was variable between individuals from **a)** healthy, **b** and **c)** increasing degrees of black flecks in the iris **d)** completely black iris, and asymmetrical irises affected to **e)** greater and **f)** lesser extents. No pattern was detected in the asymmetry of black irises.

718 **Tables**

719 **Table 1.** Candidate model set for estimating annual survival of northern gannets from Bass Rock
720 between 2010 and 2022. Inflation factor (\hat{c}) = 1.212. Effects fitted to apparent survival (φ) and
721 resighting probabilities (p) (t : time dependent; c : time constant). AICc: Akaike Information Criterion
722 for small samples. Δ AICc: difference in AICc between model in question and best model. Num. Par.:
723 number of parameters.

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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

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744 **Table 2.** Serological results from 17 adult gannets from Bass Rock tested for H5 antigen.

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

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