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1 **Strong breeding colony fidelity in northern gannets following High Pathogenicity Avian**
2 **Influenza Virus (HPAIV) outbreak**

3

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29 Abstract:

30 High pathogenicity avian influenza virus (HPAIV) caused the worst seabird mass-mortalities in
31 Europe across 2021-2022. The northern gannet (*Morus bassanus*) was one of the worst
32 affected species, with tens of thousands of casualties in the northeast Atlantic between April-
33 September 2022. Disease outbreaks can modify the movement ecology of animals by
34 diminishing spatial consistency, thereby increasing the potential for disease transmission. To
35 detect potential changes in movement behaviour, we GPS-tracked breeding adults following
36 the initial HPAIV outbreak, at three of the largest northern gannet breeding colonies where
37 major mortality of adults and chicks occurred (Bass Rock, Scotland, UK; Grassholm, Wales,
38 UK; Rouzic, Brittany, France). We also gathered background epidemiological information and
39 northern gannet colony dynamics during the outbreak. Our data indicate that HPAIV killed at
40 least 50% of northern gannets, and suggest the presence of HPAIV H5N1 antibodies in
41 juveniles. GPS-tracked adult northern gannets remained faithful to their breeding sites
42 despite the HPAIV outbreak and did not prospect other breeding colonies. They performed
43 regular foraging trips at sea, similar to their behaviour before the outbreak. Comparison with
44 GPS-tracking data gathered in 2019, i.e. before the HPAIV outbreak, suggested lower foraging
45 effort in birds which survived HPAIV in 2022, potentially as a consequence of reduced intra-
46 and interspecific food competition. Breeding colony fidelity of surviving adult northern
47 gannets following HPAIV mass-mortalities indicates limited capacity for viral spread during
48 our study. This may contrast with the behaviour of adults during the initial disease outbreak,
49 and with that of younger individuals.

50

51 Keywords: Avian pathogens, Behavioural latency, Human/wildlife interaction, Movement
52 ecology, Seabird conservation, Viral transmission

53

54 Introduction

55 Avian influenza was first reported in farmed poultry in 1878 in Northern Italy (Perroncito,
56 1878). Outbreaks of the virus occurred worldwide in domestic fowl across the 20th century
57 (Swayne and Suarez, 2000). During this period, wild birds were also regularly affected
58 (Gauthier-Clerc et al., 2007). In 1996, a form of highly pathogenic avian influenza virus (HPAIV;
59 H5Nx clade 2.3.4.4) evolved in farmed poultry in Southern China. It subsequently spilled over
60 to wild birds, and occasionally to humans (Alexander and Brown, 2009). HPAIV has since
61 occurred in 61 countries and is endemic in poultry farms around the world. In 2021/2022, the
62 worst-ever HPAIV outbreak was recorded in poultry farms, especially in Europe (Wille and
63 Barr, 2022), resulting in the culling of an estimated 47.7 million birds (Authority et al., 2022).
64 These events deeply challenge intensive bird farming, as high-density housing conditions and
65 long-distance poultry transport lead to the spread of HPAIV (Kuiken and Cromie, 2022). Rapid
66 evolution in high-density, confined poultry farms also enhances the likelihood of mutations
67 leading to the emergence of HPAIV as the next human pandemic (Roberts Jr and Krilov, 2022).
68 Finally, HPAIV is now causing substantial mortalities to wild birds, including in species already
69 challenged by other human activities (Gamarra-Toledo et al., 2023).

70 This is the case for seabirds, which are currently the most endangered bird group apart from
71 parrots (Phillips et al., 2023). Half of the worldwide abundance of seabirds has been lost since
72 1970 (Grémillet et al., 2018), mainly because of breeding habitat loss, mortality caused by
73 fishing gear, invasive species (e.g. cats and rats), food competition with fisheries, direct and
74 indirect consequences of climate change, and pollution (Young and VanderWerf, 2023).
75 Pathogens can also have significant impacts on seabird populations, as demonstrated by the
76 effects of avian cholera (*Pasteurella multocida*) on Cape cormorants (*Phalacrocorax capensis*)
77 in South Africa (Crawford et al., 1992), and on common eiders (*Somateria mollissima*) in North
78 America (Iverson et al., 2016). While seabirds are common hosts of low pathogenicity avian
79 influenza viruses (LPAIV) (Lang et al., 2016), HPAIV had rarely been detected before the 2021-
80 2022 outbreak, except in Southern Africa where recurrent HPAIV outbreaks have affected
81 seabirds since 2016 (Molini et al., 2020). Now, for the first time, HPAIV is significantly affecting
82 European seabird populations, with the virus spreading to 12 species in the UK (Falchieri et
83 al., 2022). Tens of thousands of seabirds are thought to have been affected in the Northeast
84 Atlantic in 2022, with northern gannets (*Morus bassanus*; hereafter gannets) among the most

85 severely impacted species (Lane et al., 2023), together with great skuas (*Stercorarius skua*)
86 (Banyard et al., 2022) and sandwich terns (*Thalasseus sandvicensis*) (Rijks et al., 2022).
87 Gannets are an iconic species that attract conservation and media interest, in their own right,
88 but also as umbrella species for the marine environment. Despite living in some of the most
89 anthropogenically modified marine regions of the planet (e.g. the North Sea), gannet
90 populations consistently increased across their distribution zone in the northeast Atlantic
91 during the second half of the 20th century (Grandgeorge et al., 2008).

92 The present HPAIV panzootic highlights the urgent need for a better understanding of the
93 impact of such disease outbreaks on the movement ecology of affected species, both during
94 and following HPAIV outbreaks, and the associated consequences for disease transmission.
95 Seabirds such as gannets are organised as metapopulations where colonies are connected
96 through dispersal movements of pre-breeding birds (Jeglinski et al., 2022). In contrast,
97 breeding seabirds generally show very high fidelity to their colony and to their breeding site
98 (Hamer et al., 2001). As central place foragers, they travel large distances away from their
99 breeding colony to their foraging sites at sea, but many species show a marked degree of
100 repeatability in their individual movement and space use patterns (Guiry et al., 2022).
101 Gannets in particular have also been shown to forage in colony-specific non-overlapping areas
102 (Wakefield et al., 2013) suggesting a limited capacity for close contact (and thus potential
103 transmission routes) between breeders from different colonies.

104 However, dense seabird colonies also function as information centres (Evans et al., 2016)
105 where birds acquire public information from their conspecifics, such as the location of
106 potential food resources at sea (Courbin et al., 2020), or the quality of local breeding habitats
107 (Danchin et al., 1998). During the 2022 HPAIV outbreak, when many chicks and adult gannets
108 died at breeding colonies, surviving adult gannets were exposed to public information
109 signalling that they were breeding in a highly hazardous habitat. As an effect of such
110 disturbance, we might expect to see drastic changes in movement and space use patterns.
111 Indeed, recent work has shown that surviving adults gannets that had lost their chick and
112 partner drastically modified their movement patterns in May/June 2022, during the initial
113 phase and peak of the HPAIV outbreak on the Bass Rock (Jeglinski et al., 2023): Birds thereby
114 switched from exclusively commuting between their nest and foraging areas at sea, to visiting
115 other breeding colonies. Such changes in movement patterns increase the potential for

116 disease transmission, by increasing the likelihood of contact, be it on land or at sea, between
117 birds from different colonies (Boulinier, 2023; Boulinier et al., 2016).

118 However, it is unclear if the behavioural responses to the initial HPAI outbreak found by
119 Jeglinski and colleagues (2023) translate to longer term and more permanent modifications
120 in movement ecology and space use of surviving gannets. For example, seabird mass-
121 mortalities are likely to reduce food competition for surviving individuals and may therefore
122 lead to modified foraging patterns and changes in at-sea distribution of gannets which are
123 relevant for the conservation management of the species. Short-term effects on movement,
124 such as the increase in adult prospecting frequency described above, could become a more
125 permanent feature. This would lead to increased connectivity between usually segregated
126 breeding colonies and thus have the potential to maintain enhanced disease transmission,
127 within gannet metapopulations and at the scale of multispecies seabird communities
128 (Boulinier et al., 2016). Finally, survivors could abandon their breeding colony permanently,
129 as shown in Cape cormorants or Double-crested cormorants (*Phalacrocorax auritus*) which
130 desert breeding colonies when exposed to avian cholera or Newcastle disease virus (Crawford
131 et al., 1992; Leighton et al., 2021). It is uncertain whether gannets display such longer-term
132 behavioural shifts, because they are known for their high fidelity to nesting (Nelson, 1966),
133 and foraging sites (Votier et al., 2017; Wakefield et al., 2015). Also, studies on closely-related
134 Cape gannets (*Morus capensis*) showed that, even when confronted with strongly degraded
135 environmental conditions, adult breeders kept the same breeding and foraging locations
136 (Grémillet et al., 2016; Pichegru et al., 2010).

137 Previous investigations showed that, in Indian yellow-nosed albatrosses (*Thalassarche*
138 *carteri*) exposed to avian cholera, failed breeders showed higher flexibility in habitat use
139 (Ponchon et al., 2021). Yet, to the best of our knowledge, no study has investigated seabird
140 movements following an HPAIV outbreak, and very few have done so in other birds (Gaidet
141 et al., 2010), generally because of the unpredictability of outbreaks and restrictions regarding
142 colony access in an HPAIV context. We used the rare opportunity to fill this critical knowledge
143 gap by collecting data in three of the largest gannet breeding colonies in the Northeast
144 Atlantic which all experienced very high levels of HPAIV-related chick and adult mortality in
145 2022; the Bass Rock in Scotland (UK), Grassholm in Wales (UK), and Rouzic in Brittany (France).
146 Bass Rock was, before the HPAIV outbreak, the largest northern gannet colony in the world,

147 with an estimated 75,259 breeding pairs (Murray et al., 2014). Taken together, the three
148 studied colonies totalled ca. 26% of the northern gannet world population (134,259 out of
149 525,694 pairs (Murray et al., 2015)).

150 Our primary objective was to better understand the effect of the HPAIV outbreak on breeding
151 gannet space use, since potential persistent behavioural shifts may maintain a high degree of
152 transmission potential in the metapopulation (Boulinier, 2023). Specifically, we tested the
153 hypothesis that gannets which survived the initial HPAIV outbreak modified their movement
154 patterns relative to their behaviour prior to the outbreak. We predicted (1) that surviving
155 birds would prospect for alternative breeding sites and (2) they also modified their foraging
156 patterns in response to the reduction of food competitors.

157 Our second objective was to provide background epidemiological information, and data on
158 gannet colony dynamics in our three study colonies during the outbreak. The HPAI outbreak
159 disrupted ecological data collection in seabird colonies in 2022. Consequently, there are very
160 limited ecological and epidemiological insights based on field data available, making it
161 paramount to share contextual information with the scientific community.

162

163 Methods

164 Gannets were primarily studied in May-October 2022 on Bass Rock, Scotland (56°04'N,
165 2°29'E), Grassholm, Wales (51°43'N, 05°28'W), and Rouzic, Brittany (48°54'N, 3°26'W).
166 Gannet spatial ecology was also compared between 2022 and 2019 (i.e. before the HPAIV
167 outbreak). Gannets breed between February and October, with peak hatching during the first
168 half of June. Time of hatching is influenced by latitude, with median hatching occurring on
169 average two weeks later on Bass Rock than on Grassholm and Rouzic (Wanless et al., 2008).
170 The chick-rearing phase lasts 11 to 12 weeks, with chicks fledging from late August to early
171 October. All personnel involved in field operations were equipped with full-body suits and
172 disposable gloves, face masks, goggles and caps. Biocides (Virkon® or SafeFour®) were used
173 between each manipulated bird to clean clothing, shoes and equipment.

174

175 Characterization of the HPAIV outbreak:

176 - Bass Rock:

177 On 4th June 2022, unusual numbers of dead and dying gannets were observed on Bass Rock
178 (Scottish Seabird Centre, pers. comm., see also Suppl. 1). Due to permit issues, gannets
179 equipped with GPS-GSM tags (see below) were not screened for HPAIV.

180 - Grassholm:

181 Following an unusually high number of dead gannets at the colony, HPAIV was confirmed
182 from Grassholm on 3rd August with no further access to site permitted for the rest of the
183 breeding season.

184 - Rouzic:

185 Mortality affecting adult gannets was first recorded on 1st July 2022 on the live camera
186 monitoring the Rouzic colony. Samples were subsequently collected from 31 live or dead
187 gannets in, and around the Rouzic colony between July and September 2022, for HPAIV
188 screening and characterization. We performed opportunistic necropsies on four adult birds
189 found dead on the colony, from which we collected tracheal and cloacal swabs and/or lung
190 and trachea samples. We also collected cloacal swabs, tracheal swabs and/or external wipes
191 impregnated with sterile distilled water (applied to the feathers and featherless areas of the
192 birds) from live individuals showing no HPAIV symptoms, including 15 adult birds equipped
193 with GPS-GSM loggers (see below), and 12 recently fledged juvenile birds captured at sea or
194 in the colony. We also collected plasma samples from seven of these juvenile birds. All
195 samples were stored at -20°C until laboratory analyses.

196 Samples were analysed using the protocols recommended by the French Ministry of
197 Agriculture and based on the recommendations provided by the OIE/FAO international
198 reference laboratory for avian influenza. Tissue and swab samples were screened for HPAIV
199 genetic material by real-time reverse transcription polymerase chain reaction (rRT-PCR)
200 targeting the M gene. To identify the subtype of the circulating virus, positive samples were
201 then typed using an rRT-PCR targeting either the H5 or H7 type of the haemagglutinin gene.
202 One sample testing positive for H5 was analysed for further characterization of the virus with
203 an RT-PCR discriminating HP H5 of the 2.3.4.4b clade, and an RT-PCR targeting the N1 type of
204 the neuraminidase gene. Samples testing negative for host genetic material were classified as
205 potential false negative (Zhang et al., 2020), likely due to the degradation of the samples, and

206 were excluded from the study. Plasma samples were screened for antibodies specifically
207 targeting H5N1, H5N3, H5N5 or H5N8 by haemagglutination inhibition (HI). Collected samples
208 and associated laboratory results are summarized in Table S2 (Suppl. 2).

209

210 GPS tracking:

211 Gannets were tracked (1) ~ 2 months following the first signs of an HPAIV outbreak in each
212 respective colony in 2022. This period, spanning mid-August to early October 2022,
213 corresponded to the late chick-rearing phase. This information was compared with (2) GPS
214 tracking data collected in 2019, a normal year prior to the occurrence of HPAIV in gannets.
215 For logistical reasons, this second data set was collected during June-July 2019, a period
216 corresponding to early chick-rearing. Since gannet foraging effort may differ between early
217 and late chick-rearing this comparison requires some caution. Notably, because chick energy
218 requirements double between early and late chick-rearing (Montevocchi et al., 1984), and
219 because food resources may become depleted around seabird colonies at the end of the
220 breeding season (Weber et al., 2021), adult gannet foraging effort should increase between
221 early and late chick-rearing.

222 (1) To study gannet movement ecology following the initial HPAIV outbreak, we deployed
223 GPS-GSM tags on breeding adults which showed no HPAIV symptoms on the Bass Rock (10
224 birds between 11th - 13th August 2022) and on Rouzic (15 birds between 23rd - 26th August
225 2022). GPS-GSM tags were pre-programmed to send data to a server using the 2G mobile-
226 phone network so that data can be transmitted from anywhere within 2G coverage and
227 accessed by the user in near-real-time. At Grassholm, 11 birds had been fitted with remotely-
228 downloadable tags that send data via a UHF link to a base station deployed at the breeding
229 colony, in May 2022, prior to the HPAIV outbreak. Some of these tags were still functional
230 across August-September 2022.

231 For all GPS deployments, adults rearing chicks (2 to 8 weeks old) were caught at the nest and
232 handled so as to minimize stress: the procedure lasted < 10 min and birds were kept in the
233 shade. Tags were attached with Tesa® tape to the three central tail feathers. For Bass Rock
234 gannets, we used nanofix tags (Pathtrack Ltd., solar powered, mass 18 g, 0.7% of bird body
235 mass, dimensions 56x28x15mm plus ~40 mm external whip antenna). For Grassholm gannets,

236 we used axy-trek remote tags (Technosmart solar powered, mass 15 g, < 0.5% of bird body
237 mass, dimensions 52x25x15 mm). For Rouzic gannets, we used OrniTrack-9 tags (Ornitela,
238 solar powered, mass 9 g, 0.3% of bird body mass, dimensions 37x19x12 mm, plus ~10 cm
239 external whip antenna). All tags recorded a GPS position every 15 to 60 min, depending on
240 battery voltage. We planned for tags to fall off once birds were starting to moult their tail
241 feathers - previous deployments lasted up to 3 - 5 months (J. Jeglinski, D. Grémillet,
242 unpublished data). At all three colonies we weighed gannets to the nearest 10 g. All birds
243 were ringed with a metal ring and plastic ring with a unique alphanumeric combination. Once
244 released, most birds returned immediately to their nests. We monitored chicks until the
245 captured parent had returned, generally immediately, at the latest within 1 h after capture.

246 (2) We studied the movements of breeding adult gannet before the HPAIV outbreak, during
247 early chick-rearing in June-July 2019. We used the same methodology as above, yet slightly
248 different GPS recorders. On Bass Rock, 22 gannets were fitted with i-gotU GT600 tags (Mobile
249 Action Technology, mass 30g, 1% of body mass, dimensions 47 × 30 × 20 mm, set to record
250 GPS position every 1 min). On Grassholm 7 gannets were fitted with i-gotU GT120 tags
251 (Mobile Action Technology, mass 18g, 0.7% of body mass, dimensions 47 × 30 × 20 mm, set
252 to record GPS position every 1 min). On Rouzic, 14 gannets were fitted with CatTraQ™ tags
253 (Catnip Technologies, mass 20g, 0.8% of bird body mass, dimensions 47 × 30 × 13 mm, set to
254 record GPS position every 1 min).

255 GPS Data processing:

256 Data were analyzed using R version 4.1.2. Data from Rouzic, which are stored in the Movebank
257 database, were imported with the *move* R package (Kranstauber et al., 2022) while data from
258 Bass Rock and Grassholm were imported from csv files.

259 For all tracking data recorded in 2022 and 2019 (Tab. 1), at-sea trips were discriminated from
260 periods in the colony when the birds were > 1 km away from the colony for > 1 h. GPS
261 recordings which were interrupted for > 10 hours were excluded. At-sea locations were
262 linearly interpolated with a 15 min time resolution using the *pastecs* package (Grosjean et al.,
263 2018). Trip data were checked for prospecting visits to other gannet colonies, which we
264 defined as two or more consecutive locations in any other gannet known colony.

265 We calculated trip characteristics for the 2019 and 2022 data sets (maximal distance to the
266 colony, total trip duration and total distance travelled), as well as the time spent in the colony
267 between at-sea trips, and presented these averaged for each individual and then averaged by
268 colony in Table 1. Further, we fitted linear mixed models on each colony separately to test
269 whether log-transformed trips characteristics and colony attendance changed significantly
270 between 2022 and 2019.

271 To test our hypotheses, we were specifically interested in temporal dynamics of foraging
272 patterns following the HPAIV outbreak. Hence, for the 2022 data set, we fitted linear mixed
273 models separately for each colony using the respective trip characteristics for each bird as
274 response variables to test whether log-transformed trip characteristics and time spent in the
275 colony between at-sea trips changed significantly over time (converted as day since 10th
276 August 2022, first day of the study period). Bird ID was included as a random effect.

277 Inferring at-sea behavioural states:

278 To test for temporal dynamics in behavioural patterns across the 2022 data set, we also fitted
279 a 3-state hidden Markov model (HMM) to the at-sea interpolated location data from all three
280 colonies combined, using the *moveHMM* package (Michélot et al., 2016). The states can be
281 interpreted to reflect three different activities at sea: (1) resting, characterised by a small step
282 length and low turning angle, (2) travelling, characterised by a long step length and low
283 turning angle and (3) foraging, characterised by an intermediate step length and a large
284 turning angle. A set of different initial parameter values was used to ensure that the global
285 maximum log-likelihood had been reached. The Viterbi algorithm was used to classify the
286 most likely behaviour at each location and proportions of each activity occurring during one
287 at-sea trip were calculated, averaged by individual and then, by colony. We then fitted logistic
288 regressions to the proportions of each activity during a trip for each bird as response variables
289 using the *glmmTMB* package (Brooks et al., 2017), accounting for zero-inflated data, to test
290 whether activity proportions changed over time (converted as day since 10th August 2022,
291 first day of the study period). Bird ID was included as a random effect.

292

293 Results:

294 Gannet colony dynamics:

295 The impact of HPAIV on the Bass Rock was extremely high, with thousands of dead gannets
296 recorded in the colony and washed up on the surrounding beaches. A drone survey on 30th
297 June 2022 counted 21,277 gannets (Lane et al., 2023), whereas a previous census counted
298 75,259 apparently occupied sites (AOS) in 2014 (Murray et al., 2015). Although the two counts
299 use different count units, they indicate a substantial decline in numbers of around 70% during
300 the 2022 HPAIV outbreak (Lane et al., 2023). Direct observations on Bass Rock also indicated
301 that at least 75% of active nests disappeared during the 2022 breeding season (Lane et al.,
302 2023). On Grassholm, adult and chick mortality were extremely high with many thousands of
303 birds dead on the colony and in the surrounding waters. On Rouzic, aerial pictures of the
304 colony revealed that AOS numbers declined from 18,839 on 17/05/2022, to 8,625 on
305 28/08/2022 (54% decline during the breeding season). Observations via the live camera
306 installed on the breeding colony estimated that >90% of chicks died during the same period
307 (Suppl. 1). More detailed, weekly counts performed between 11/07/2022 and 30/09/2022 on
308 five sections of the colony containing 40-102 AOS, suggested that between 58-87% of
309 breeding adults, and between 67-94% of the chicks died (see Suppl. 4).

310

311 Characterization of the HPAIV outbreak

312 - Bass Rock:

313 Samples collected on the 4th June 2022 from dead gannets and analysed by the Animal and
314 Plant Health Agency (APHA), UK, confirmed an outbreak of HPAIV H5N1 (Scottish Seabird
315 Centre, pers. comm.).

316 - Grassholm:

317 Following unusual gannet mortality in late July, four birds found dead on 21st July 2022 were
318 confirmed as positive for HPAIV H5N1 by APHA.

319 - Rouzic:

320 The first necropsy samples collected from a dead adult found on the colony on 11th July 2022
321 tested positive for HPAIV. Laboratory analyses conducted on samples collected from a bird

322 found dead on the colony on 30th September 2022 confirmed the circulation of HPAIV H5N1
323 clade 2.3.4.4b in the colony. HPAIV H5 was also detected in live birds: 1/9 cloacal swabs from
324 adults subsequently equipped with GPS, and 2/7 external wipes from juveniles (recently
325 fledged and captured on land/at sea) tested positive for HPAIV H5. All the cloacal and tracheal
326 swabs collected from these juveniles, as well as from 5 other juveniles were classified as
327 negative or inconclusive, suggesting varying detection probabilities across sample types (see
328 Suppl. 2). Antibodies against H5N1 were detected in 4/7 juveniles (including the 2 with RT-
329 PCR-positive external swipes). These individuals also tested positive for antibodies against
330 H5N5 and H5N8, and to a lesser degree, for antibodies against H5N3, although higher titers
331 were systematically observed for H5N1 (Suppl. 2), suggesting cross-reactions with other
332 serotypes. None of the samples tested positive for HPAIV H7.

333

334 Movement ecology:

335 All 10 GPS tags deployed on Bass Rock gannets in 2022 sent GPS positions. On Grassholm, 5
336 out of the 11 tags which had been deployed in May 2022 provided data during the study
337 period (see Table 1 for details). Of the 15 tags deployed on Rouzic, 14 provided data; 13 of
338 the 15 remained in the English Channel. One gannet, sampled at tag deployment, tested
339 positive to HPAIV and never provided GPS positions, and another (tested negative at tag
340 deployment) initiated migration after being equipped, moving toward West Africa without
341 touching land until the tag stopped sending data on 16th November 2022 (Table 1). Average
342 gannet body mass was 3230 ± 298 g (Bass Rock), 3004 ± 325 g (Grassholm), and 2920 ± 240 g
343 (Rouzic), values which were similar to those in previous years (Le Bot et al., 2019).

344 While alive, none of the gannets tagged in 2022 came ashore anywhere outside of their
345 respective breeding colonies during the GPS data transmission period. Overall, gannets from
346 Bass Rock, Grassholm and Rouzic did not change their space use across the 4-8 week 2022
347 study period, and foraged consistently in the same areas (Fig. 1 & 2). Birds from Rouzic did
348 not change their at-sea trip characteristics during the 2022 study period (similar duration,
349 maximal distance to the colony and total distance travelled; Table 2; Fig. S3a-c), but they
350 slightly decreased the time spent at the colony between at-sea trips (Table 2; Fig. S3d). Among
351 them, one individual was found dead on a beach on the island of Guernsey (82 km Northeast

352 of Rouzic), 14 days after being equipped. This individual was not tested for HPAIV when found
353 dead, and its behaviour for the time period during which we received GPS data did not differ
354 from that of other Rouzic birds we tracked. During the 2022 study period, birds nesting on
355 Bass Rock spent the same amount of time attending their colony but increased the duration
356 of their at-sea trips marginally, travelling slightly further and being absent from the colony for
357 slightly longer (Table 2; Fig. S3). During the same period, birds from Grassholm did not change
358 any trip characteristics nor their nest attendance patterns. Considering their activity budgets
359 during trips, birds maintained the same proportions of time spent foraging, flying and resting
360 on the water, regardless of their colony (Table 2; Fig. 3). For the 3 colonies, compared to early
361 chick-rearing in 2019, at-sea trips in 2022 were 47-58% shorter in maximal distance and total
362 distance travelled and 10-53% shorter in duration (Table 1; S3). Overall, foraging effort as
363 conveyed through foraging trip indicators was significantly lower in 2022 compared to 2019,
364 except for foraging trip duration in Rouzic gannets (Fig. 4; Table S3).

365

366 **Table 1.** Details of the GPS tracking data set for gannets nesting on Rouzic, Grassholm and
 367 Bass Rock in 2022 and 2019. Results are shown as mean \pm SE

368

| | Bass Rock | Grassholm | Rouzic | Bass Rock | Grassholm | Rouzic |
|--|------------|------------|------------|---------------|---------------|---------------|
| | 2022 | | | 2019 | | |
| Total nb of equipped individuals | 10 | 12 | 15 | 22 | 7 | 14 |
| Nb of individuals retained | 10 | 5 | 13 | 22 | 7 | 14 |
| Total nb of foraging trips | 310 | 53 | 257 | 66 | 11 | 27 |
| Average nb of foraging trips per individual | 31 \pm 4 | 10 \pm 5 | 20 \pm 3 | 3.0 \pm 0.3 | 1.5 \pm 0.3 | 1.9 \pm 0.3 |
| Total Nb of periods on the colony | 49 | 31 | 36 | 6 | 0 | 7 |
| Average nb of periods on the colony | 30 \pm 4 | 12 \pm 5 | 18 \pm 2 | 1.8 \pm 0.3 | - | 2.9 \pm 0.3 |

| | | | | | | |
|--|-------------------------------|-------------------------------|----------------------------|---------------------------|-------------------------------|----------------------------|
| per individual | | | | | | |
| Tracking period | 11/08/2022 - 12/10/2022 | 10/08/2022 - 18/09/2022 | 24/08/2022 – 28/09/2022 | 23/06/2019 - 30/07/019 | 15/07/2019 - 17/07/2019 | 21/06/2019 – 28/06/2019 |
| Average tracking duration per individual (days) | 44.2 ± 5.1 | 13.8 ± 5.8 | 22.0 ± 2.4 | 4.8 ± 0.5 | 1.6 ± 0.4 | 4.2 ± 0.5 |
| Maximal distance to the colony (km) | 98 ± 8 | 65 ± 8 | 62 ± 4 | 186 ± 25 | 147 ± 18 | 127 ± 12 |
| Total distance travelled per trip (km) | 254 ± 21 | 191 ± 28 | 171 ± 11 | 450 ± 60 | 450 ± 78 | 328 ± 35 |
| Trip duration (h) | 19 ± 2 | 16 ± 4 | 18 ± 1 | 27 ± 3 | 34 ± 8 | 20 ± 2 |
| Time spent resting during a trip (%) | 21.7 ± 10 | 23.4 ± 3.2 | 42.4 ± 1.5 | - | - | - |
| Time spent | 54.4 ± 1.2 | 55.7 ± 2.9 | 36.9 ± 1.2 | - | - | - |

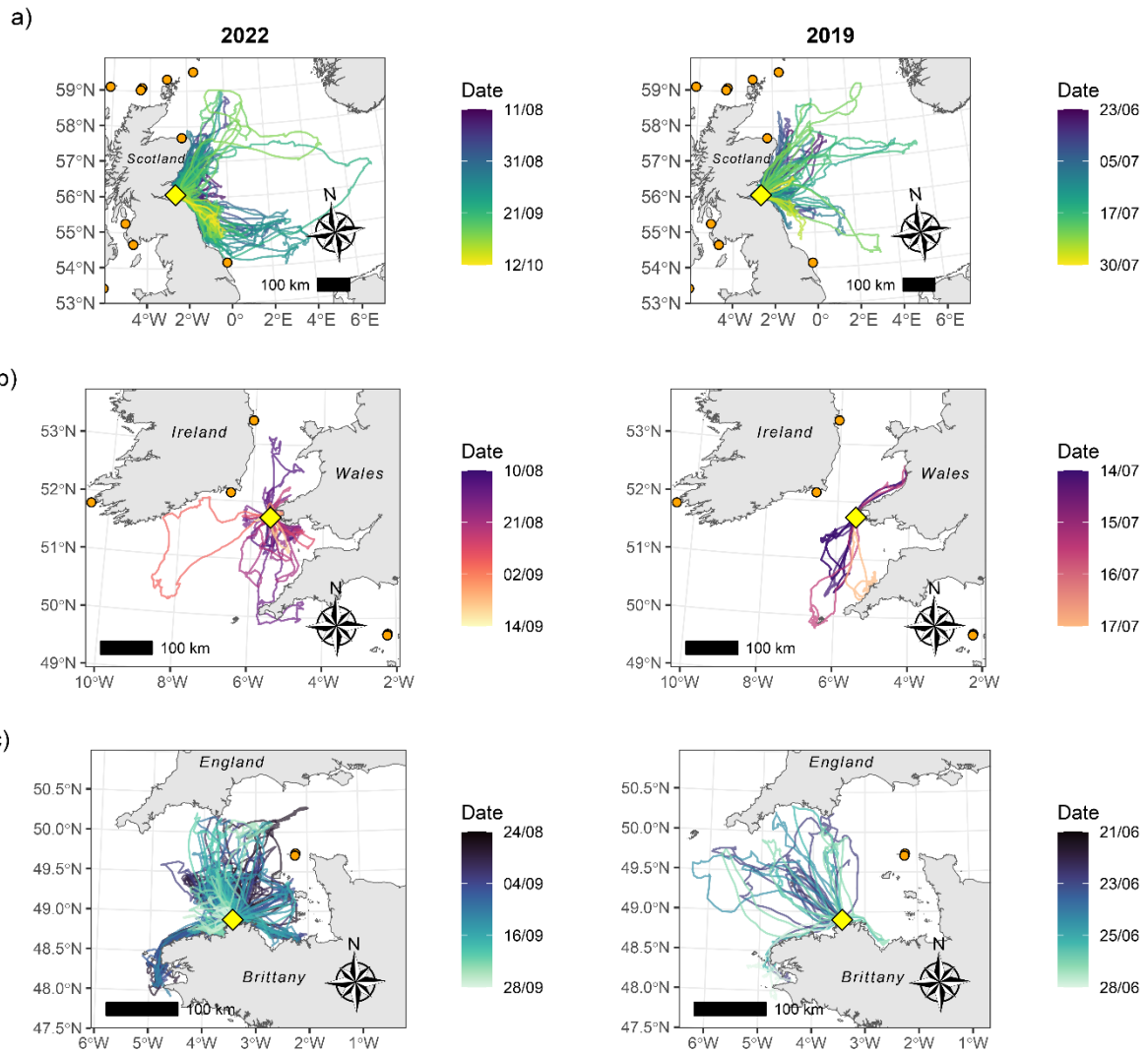
| | | | | | | |
|--|------------|------------|------------|--------|---|--------|
| foraging during a trip (%) | | | | | | |
| Time spent flying during a trip (%) | 23.9 ± 0.8 | 20.9 ± 2.2 | 20.7 ± 0.9 | - | - | - |
| Time at the colony between at-sea trips (h) | 16 ± 1 | 18 ± 2 | 11 ± 1 | 26 ± 2 | - | 22 ± 2 |

370 **Table 2.** Results from the models testing the effects of time for the 2022 data set, on gannet trip characteristics and nest attendance (linear
371 mixed models) and proportion of time spent in the 3 inferred behavioural states (logistic regressions). Individual identity is included as a
372 random effect. Significant results ($p < 0.05$) are in bold.

373

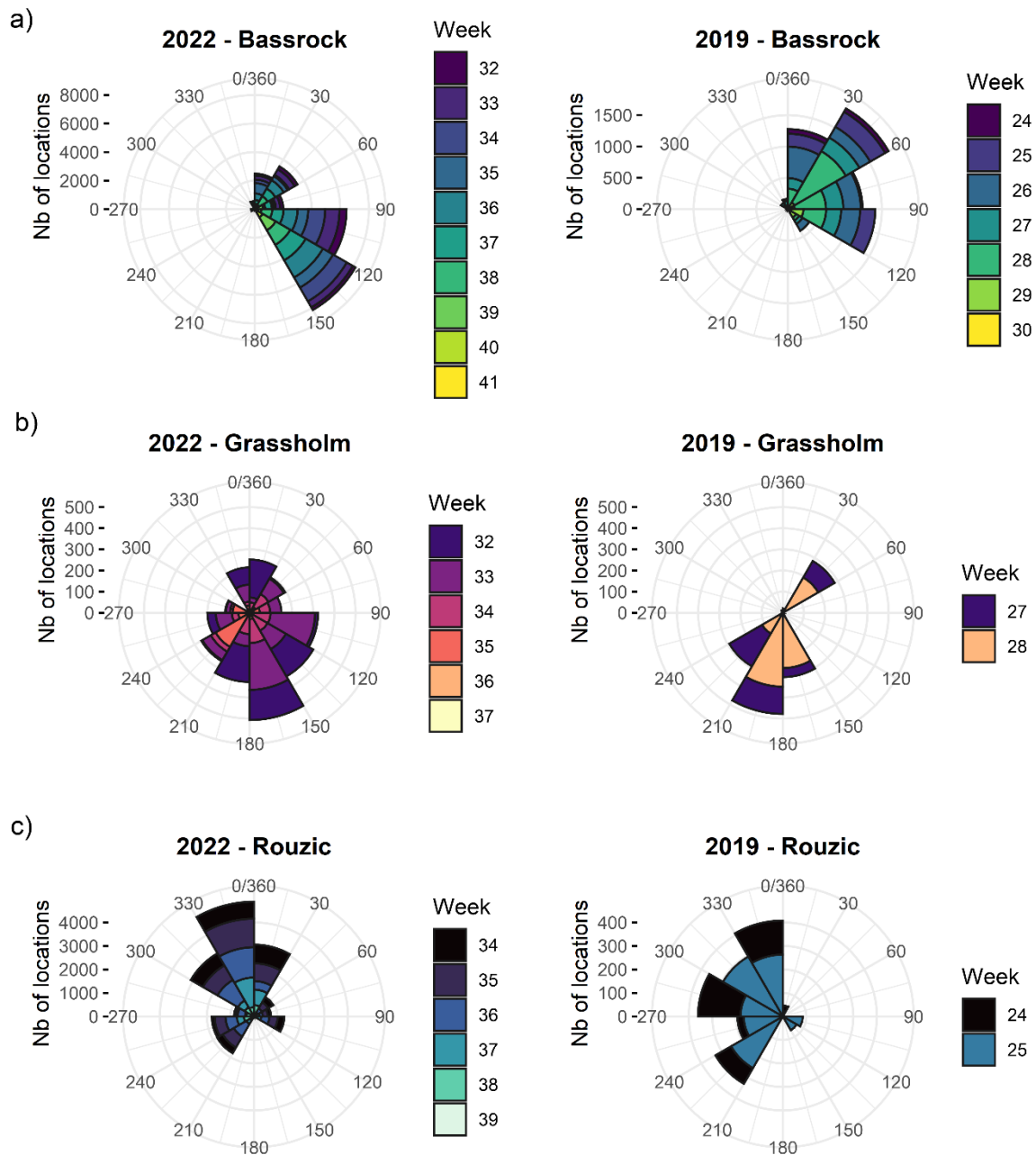
| Linear mixed models | Bass Rock | | | | Grassholm | | | | Rouzig | | | |
|--|--------------------------|------------|-------------|--------------|--------------------|----|---------|-------------|--|------------|--------------|--------------|
| | Estimate ± SE | df | t-value | p- value | Estimate ± SE | df | t-value | p- value | Estimate ± SE | df | t-value | p-value |
| Maximal distance | 0.009 ± 0.005 | 299 | 2.03 | 0.043 | -0.012 ± 0.014 | 44 | -0.85 | 0.40 | -0.003 ± 0.006 | 243 | -0.53 | 0.60 |
| Total distance travelled | 0.011 ± 0.005 | 299 | 2.34 | 0.02 | -0.017 ± 0.016 | 44 | -1.07 | 0.29 | 1.8e10 ⁻⁵ ± 6.0e10 ⁻³ | 243 | 0.003 | 0.99 |
| Trip duration | 0.013 ± 0.004 | 299 | 3.29 | 0.001 | -0.014 ± 0.019 | 44 | -0.74 | 0.46 | 0.011 ± 0.006 | 243 | 1.73 | 0.09 |
| Time at the colony between at-sea trips | -0.003 ± 0.003 | 288 | -0.77 | 0.45 | -0.011 ± 0.0010 | 56 | -1.13 | 0.26 | -0.015 ± 0.007 | 220 | -2.09 | 0.038 |
| Logistic regressions | Bass Rock | | | | Grassholm | | | | Rouzig | | | |
| | Estimate ± SE | df | z-value | p- value | Estimate ± SE | df | z-value | p- value | Estimate ± SE | df | z-value | p-value |
| Proportion of a trip spent resting | 0.0053 ± 0.0086 | 307 | 0.63 | 0.53 | -0.05 ± 0.05 | 47 | -1.18 | 0.24 | 0.018 ± 0.014 | 253 | 1.24 | 0.21 384 |
| Proportion of a trip spent foraging | -0.0017 ± 0.007 | 307 | -0.24 | 0.81 | 0.037 ± 0.034 | 47 | 1.05 | 0.29 | -0.014 ± 0.015 | 254 | -0.91 | 0.36 |
| Proportion of a trip spent flying | -0.0028 ± 0.008 | 307 | -0.33 | 0.74 | -0.0021 ± 0.040 | 47 | -0.05 | 0.96 | -0.008 ± 0.018 | 254 | -0.43 | 0.67 387 |

388



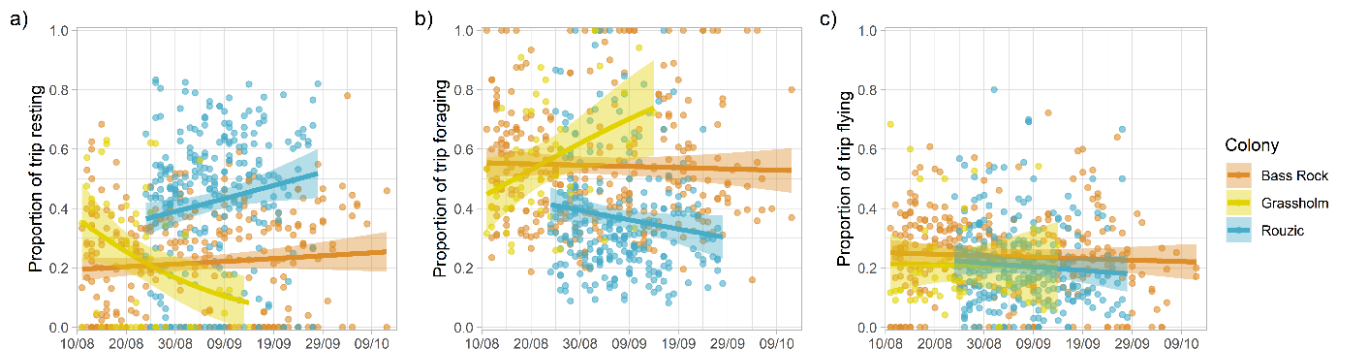
390

391 **Figure 1.** Tracks of gannets nesting in 2022 (left) and 2019 (right) on (a) Bass Rock, Scotland,
 392 (b) Grassholm, Wales and (c) Rouzic, Brittany, (yellow diamonds). Orange circles represent
 393 neighbouring gannet colonies to the respective study colonies. Gradual changes in colour
 394 represent time in days since start of GPS tracking.



395

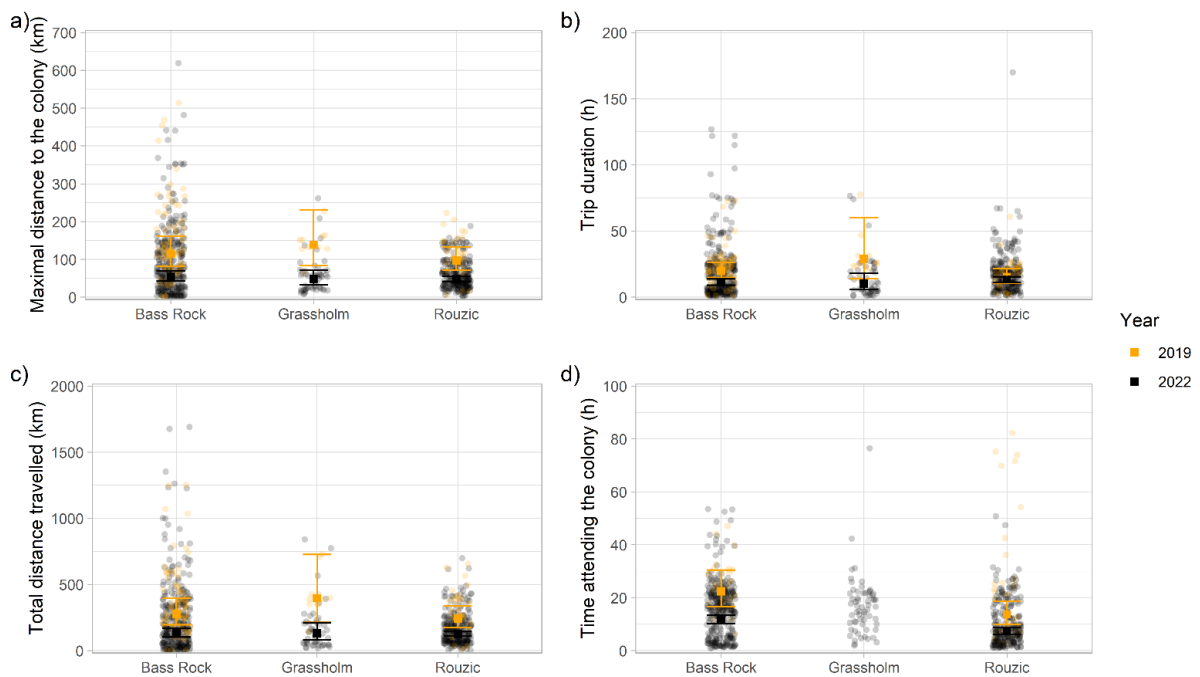
396 **Figure 2.** Rose diagrams illustrating the bearings in 30 degree bins of at-sea locations relative
 397 to the nesting colony of gannets nesting in 2022 (left) and 2019 (right) on (a) Bass Rock,
 398 Scotland, (b) Grassholm, Wales and (c) Rouzic, Brittany. The centre of each rose diagram
 399 represents the colony location, the length of each wedge represents the number of locations
 400 recorded in that direction over time, in coloured weekly bins.



401

402 **Figure 3.** Proportion of inferred behavioural states [(a) resting, (b) foraging, (c) flying] during
 403 at-sea trips of gannets nesting on Bass Rock (orange), Grassholm (yellow) and Rouzic (cyan),
 404 according to dates from August to October 2022. The dots represent raw data and the line
 405 and shadow, predicted average slope \pm 95% confidence interval.

406



407

408 **Figure 4.** Predicted means \pm 95% confidence interval of trip characteristics and nest
 409 attendance of gannets nesting on Bass Rock, Grassholm and Rouzic in 2022 (black) and 2019
 410 (orange). Note that nest attendance values were unavailable for Grassholm in 2019.

411

412

413 Discussion

414 - Epidemiology

415 Our analyses confirmed that gannets contracted HPAIV, and other investigations also pointed
416 to HPAIV as the cause of 2022 seabird mass mortalities in western Europe (Falchieri et al.,
417 2022; Lane et al., 2023). More specifically, we identified H5N1 (clade 2.3.4.4b) in Rouzic birds.
418 This contrasts with recent HPAIV outbreaks in southern African seabirds (Molini et al., 2020),
419 which were caused by H5N8 (clade 2.3.4.4b). Our study adds to the evidence that HPAIV has
420 become established in seabirds, and will probably recurrently re-emerge, as observed in
421 southern Africa (Molini et al., 2020). We also found that some juvenile gannets had H5N1
422 antibodies, but no live virus (Suppl. 2). This is in line with recent investigations (Caliendo et al.,
423 2022) suggesting that birds that survived HPAIV develop an immune response, which could
424 protect against future infections. Further longitudinal monitoring will nonetheless be
425 necessary to fully test this hypothesis. Those studies will also clarify the factors leading to intra
426 and interspecific heterogeneity in avian responses to HPAIV (Keawcharoen et al., 2008), which
427 are key to our understanding of the potential role of different species as HPAIV maintenance
428 host or spreaders (Huang et al., 2019).

429 Only one of the 15 birds equipped with GPS on Rouzic tested HPAIV positive using swab
430 samples (Suppl. 2), and gannets fitted with GPS on Bass Rock and Grassholm could not be
431 tested. Thus, the epidemiological status of most tracked gannets was not known. Ideally, swab
432 and plasma samples should have been collected in all birds. Yet, even in the presence of both
433 sample types, some uncertainty would remain. Notably, a positive plasma sample could reflect
434 a former, rather than an ongoing infection, and such samples are not adequate to infer
435 whether a bird is a HPAIV carrier and potential spreader at the time of the blood sample
436 (Gilbert et al., 2013). Indeed, experimentally infected birds stop excreting the virus after a
437 week or less (van den Brand et al., 2018). Swab samples are therefore theoretically adequate
438 during this brief excretion period, but half of those for gannets equipped with GPS on Rouzic
439 were inconclusive. External wipes were useful indicators of virus circulation in the colony, but
440 cannot be used with confidence for individual infection status considering the risk of
441 environmental contamination. Overall, we may therefore conclude that HPAIV was extremely
442 widespread and circulating at all three gannet colonies given observational data on the degree
443 of mortality, and that an unknown proportion of GPS-tracked birds could have been

444 symptomatic or asymptomatic carrier of the virus. This knowledge gap clearly calls for further
445 epidemiological studies during future seabird breeding seasons.

446 - Movement ecology

447 Contrary to our first prediction, we did not detect any change in breeding colony fidelity in the
448 context of HPAIV outbreaks that started approximately two months previous to data
449 collection. In contrast to the study performed by Jeglinski and colleagues (2023) during the
450 initial HPAIV outbreak, none of the gannets we tracked came ashore outside of their
451 respective breeding colonies while alive. We also found that GPS-tracked gannets did not
452 significantly modify their foraging patterns across the study period (Table 2; Fig. 1-4). Since
453 our visits to gannet breeding colonies were extremely limited due to the restrictions in place,
454 we could not monitor the survival of the chicks of the GPS-tracked gannets. Some birds may
455 have lost their chicks during the study period. Yet, all tracked birds continued to regularly
456 commute between at-sea feeding sites and their respective colonies, and none of them rested
457 on the mainland or on other islands in-between trips.

458 Further, gannet foraging effort seemed lower than during the 2019 breeding season (hence
459 before HPAIV) at our three study sites (Grémillet et al., 2006; Hamer et al., 2007; Patrick et al.,
460 2014) (Fig. 1, 2 and 4, Table S3). Therefore, in accordance with our second prediction, gannets
461 surviving HPAIV may have benefited from reduced food competition following the death of
462 adults and chicks. Nevertheless, these results have to be taken with caution since, as
463 mentioned in the methods section, the 2022 GPS tracking sessions occurred during late chick-
464 rearing, whereas the 2019 tracking data were collected during early chick-rearing.

465 Our results are coherent with high breeding and foraging site fidelity in colonial seabirds
466 (Danckwerts et al., 2021), and contrary to the idea that gannets that have witnessed and
467 survived mass mortality at their breeding colony modify their movement patterns as a
468 consequence of the disease outbreak and maintain these changes several months after the
469 event. Thus, it appears that longer-term enhanced HPAIV transmission throughout the
470 metapopulation and potentially throughout the co-existing seabird populations is unlikely for
471 adult breeding gannets. This is an essential piece of information that contributes to a better
472 understanding of HPAIV transmission dynamics, since wild birds carrying HPAIV are

473 recurrently presented as virus spreaders to farm poultry (Global Consortium for H5N8 and
474 Related Influenza Viruses, 2016).

475 However, the data we presented here are collected following the initial disease outbreak to
476 study long-term behavioural responses, and they are only representative of the adult breeding
477 age class. Other age classes may differ in their propensity to act as a vector for HPAIV. Notably,
478 immature gannets have been shown to perform visits to other breeding colonies throughout
479 the breeding season (Votier et al., 2011) and thus likely regularly move between colonies.
480 These prospecting movements would appear to require limited time/energy investment: For
481 gannets from Bass Rock, the closest alternative colony is Troup Head on the Scottish mainland
482 (ca. 210 km), for Grassholm it is Great Saltee in Ireland (ca. 90 km), and for Rouzic it is Ortac
483 in the British Channel Islands (ca. 130 km) (Fig.1). Reaching these neighbouring colonies would
484 take 3.2 hrs (Bass Rock), 1.4 hrs (Grassholm), or 2 hrs (Rouzic), assuming a $65 \text{ km}\cdot\text{h}^{-1}$ travelling
485 speed (Grémillet et al., 2004). Forthcoming studies will clarify the respective potential of
486 juvenile and immature gannets to act as vectors in HPAIV transmission. Also, even if rated as
487 rare (Boulinier et al., 2016), at-sea HPAIV transmission may occur within, and between seabird
488 species. This might be facilitated by aggregations at natural foraging sites or whilst feeding on
489 fishery wastes behind trawlers, or through kleptoparasitism and scavenging (Wille et al.,
490 2016). Studying interspecific fine scale space-use overlap at sea is therefore a high priority for
491 future monitoring and evaluation of disease transmission scenarios (Boulinier, 2023).

492

493 - Outlook

494 It remains unclear how gannets contracted HPAIV, since they were either at sea, or at their
495 breeding colony during the outbreak. Larids (*Larus sp.*) or great skuas that klepto-parasitise
496 gannets might be potential vectors since they use similar terrestrial and marine habitats
497 (Falchieri et al., 2022), but further analyses will be necessary to test these hypotheses. HPAIV
498 first affected gannets in Iceland, Québec and Scotland (from early April 2022), and
499 subsequently arrived in Brittany (from early July 2022)(Lane et al., 2023). Hence, it is possible
500 that immature gannets moving between these colonies may have spread the virus, but this
501 pathway is still hypothetical. Equally unknown are HPAIV dynamics during gannet migration,
502 which started in September-October 2022. These inter-breeding movements took gannets

503 from the British Isles and Brittany to the Mediterranean or West Africa (Fort et al., 2012). Off
504 Africa, gannets met with some of their North American conspecifics, as well as with a vast
505 community of North Atlantic seabirds spending the winter in tropical waters (Grecian et al.,
506 2016). In February 2023, surviving gannets returned from migration and started breeding
507 again. Further investigations are now required, notably to clarify HPAIV impacts on gannet
508 movement ecology and population dynamics across age classes, and multiple years.

509 Our study is a key example of the common fate of wildlife and humanity facing global changes
510 (Díaz et al., 2019). Gannets are affected by the direct and indirect consequences of climate
511 change (heat waves and storms, changes in the distribution and abundance of marine
512 resources), by pollution (e.g. mercury in fish affecting seabird and human health), and by
513 uncontrolled fishing operations which threaten food security for seabird and human
514 populations alike (Grémillet et al., 2020). In addition, the current HPAIV outbreak
515 demonstrates that the anthropogenic environmental crisis enhances the potential for
516 emerging infectious disease, contaminating wild animals and humans (Carlson et al., 2022;
517 Kuiken and Cromie, 2022). Indeed, current industrial farming practices are responsible for the
518 emergence and the spread of HPAIV in poultry and subsequently in wild birds, potentially also
519 in humans (Yamaji et al., 2020).

520

521 Author contributions: DG, PP and SCV designed the study, with advice from SW and JJ. DG, PP,
522 APr, TP, JJ, SCV, JM, AB, JF, NC, RJ, LL, AT, NS and JL were leading the field studies including
523 funding acquisition, permit acquisition and field data collection. APo, PP, MA-Z, AG, NC and
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537 Ethics: All procedures followed the *guidelines for the treatment of animals in behavioural*
538 *research and teaching* of the *Association for the Study of Animal Behaviour*. Bass Rock:
539 fieldwork was performed in partnership with the Scottish Seabird Centre with permission of
540 the landowner of the Bass Rock, Sir Hew Dalrymple, and under a special method endorsement
541 and ringing permit of the British Trust for Ornithology BTO to Jana Jeglinski. Colour ringing was
542 performed under a permit to Jude Lane from the BTO. We conducted our fieldwork under an
543 exemption to the general ringing ban in seabird colonies granted by NatureScot which
544 permitted us to capture and tag gannets during the HPAIV outbreak. All fieldwork was
545 performed with the required risks assessments and ethical approval in place. Grassholm: All
546 research was carried out under licence (RSPB, Natural Resources Wales (#S091127-1), British
547 Trust for Ornithology (BTO: A4257), the BTO Special Methods Panel and the UK Home Office
548 (30/3065). Rouzic: fieldwork operated under the Programme Personnel de baguage n°536
549 CRBPO/MNHN validation 2020-2024.

550

551 Data availability: Data are available on the following archives:
552 https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2296851236 ;
553 <https://datadryad.org/stash/share/MmNkFWcQV79wnYDMQ8VTav-jRmHBUomyRohKVoAsNvE> and
554 https://www.movebank.org/cms/webapp?gwt_fragment=page=studies,path=study2658117564. All
555 statistical analyses can be found on the GitHub repository
556 (<https://github.com/auponchon/NorthernGannets2022>).

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