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Short Communication

Effect of a previous high pathogenicity avian influenza (HPAIV) infection on the breeding success of Northern Gannets (*Morus bassanus*)

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Highly pathogenic avian influenza (HPAIV) caused widespread mortality and breeding failure among many wild, avian populations in Europe and North America in 2021–2023, but most populations exhibited a marked reduction in mortality in the year following an outbreak, suggesting that surviving individuals may have developed immunity. A critical mechanism for population resilience is whether individuals that have survived the disease show reduced breeding success because of the potential costs associated with recovery, notably elevated immune defence. We found that, at two UK colonies, the breeding success of Northern Gannets *Morus bassanus* with black eyes (an indicator of past exposure to HPAIV) was similar to those with normal blue eyes in the year following a severe disease outbreak, suggesting that population recovery may not be hampered by lower reproductive performance of recovered individuals compared to those that were unexposed. However, breeding success, irrespective of past exposure, was lower than the long-term average, suggesting potential carry-over effects on all individuals from the extensive disruption caused by the epidemic the previous year.

Keywords: bird flu, demography, disease, reproductive performance, seabird ecology.

The outbreak of highly pathogenic avian influenza (HPAIV) in 2021–2023 resulted in substantial declines in many wild bird populations in Europe and North America (Klaassen & Wille 2023). HPAIV H5N1 was first detected in UK seabirds in 2021 (Great Skua *Stercorarius skua*, Banyard *et al.* 2022), and subsequently spread to numerous other species in 2022 (Cunningham *et al.* 2022, Falchieri *et al.* 2022, Rijks *et al.* 2022, Avery-Gomm *et al.* 2024). The extent to which populations recover from the disease will in part depend on whether exposed individuals that have survived perform similarly to unexposed individuals in key subsequent demographic rates such as reproduction. A similar performance may not occur because there are fitness costs associated with maintaining immunity (Hasselquist & Nilsson 2012). Studies of effects on recovered individuals have focused on foraging and migration. However, the evidence is equivocal, with some studies finding that migratory behaviour was significantly affected and others recording that surviving individuals returned rapidly to typical foraging and migratory routines (Duriez *et al.* 2023, Teitelbaum *et al.* 2023a, 2023b). However, the longer-term effects of avian influenza on the demography of recovered individuals remain poorly understood.

The Northern Gannet *Morus bassanus* (hereafter Gannet) was one of the most severely affected species in 2022 (Camphuysen *et al.* 2023, Grémillet *et al.* 2023, Careen *et al.* 2024, Jeglinski *et al.* 2024, Lane *et al.* 2024). However, despite high levels of mortality and widespread breeding failure during the outbreak, some infected adults were found to have survived (Lane *et al.* 2024). Aberrant eye colour, with one or both eyes appearing black or mottled black rather than the typical pale blue, was reported at a number of colonies during or immediately after outbreaks and, of the individuals sampled on the Bass Rock that were carrying antibodies specific to HPAIV H5, 87.5% showed this phenotypic change in eye colour (Lane *et al.* 2024). As such, eye colour is an indicator of past exposure to the disease that can be used in the field to investigate whether previously diseased individuals have lower subsequent breeding success compared to unexposed individuals.

The aim of this study was to compare the reproductive performance of Gannets that had recovered from

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the disease with those that were less likely to have been exposed, using eye colour as an index of past exposure. We quantified reproductive performance in two ways: (a) breeding success and (b) laying date. Timing of breeding is closely linked to breeding success such that success declines with laying date, a relationship that has been demonstrated in a large number of bird populations including Gannets (Perrins 1970, Verhulst *et al.* 1995, Nelson 2002). We tested this question at two breeding colonies in the UK, the Bass Rock and Bempton Cliffs (Flamborough and Filey Coast SPA) in 2023, a year after severe HPAIV outbreaks and substantial mortality during 2022 (Harris *et al.* 2023, Wanless *et al.* 2023, Tremlett *et al.* 2024).

METHODS

Timing of breeding and breeding success

Fieldwork was carried out during the 2023 breeding season at Bass Rock, Scotland (56.08°N, 2.62°W) and Bempton Cliffs, England (54.13°N, 0.17°W). Apparently occupied nests (AONs, i.e. suitable nesting sites occupied by one or two adult Gannets where some nest material is present, Walsh *et al.* 1995) were monitored at Bass Rock ($n = 45$) and Bempton ($n = 608$) within study plots (Bass Rock; $n = 1$, Bempton Cliffs; $n = 16$, range 9–60 AONs per study plot).

Monitoring of the Bass Rock study plot was undertaken using a remote webcam managed by the Scottish Seabird Centre (SSC). Observations were made for an hour, three to four times each week (total number of observation sessions = 69) between 20 April and 14 September. Each observation session took place at *ca.* 05:45 GMT, using remote camera controls via TeamViewer (TeamViewer GmbH, n.d.). Monitoring of the Bempton Cliffs study plots was undertaken every 3–10 days between April and October. Observations were made by fieldworkers using binoculars or telescopes (total number of checks = 443). Photographs of the Bempton study plots were taken during the first visit and AONs numbered so that the breeding status of each nest could be recorded throughout the season (Walsh *et al.* 1995).

During each observation session, we recorded the presence of an incubating or brooding adult, or if visible the presence of an egg or chick (Walsh *et al.* 1995). For each AON, breeding success was classified as successful (1) or unsuccessful (0). Successful fledging was assumed at AONs where a chick reached an age of at least 12 weeks, the typical fledging age of Gannets (Walsh *et al.* 1995, Nelson 2002). The zoom function of the Bass Rock camera, and the greater frequency of observation sessions, allowed the timing of breeding to be recorded reliably ('laying date' was the first date an egg was observed).

The Bass Rock camera stopped working on 28 July, and thereafter was only operational on 17 August and from 14 September. Overall, 25 out of 26 AONs that were active on 28 July were still active on 17 August. The chick at the remaining site was too young to have fledged prior to 17 August, so the breeding attempt was classed as unsuccessful. All chicks present on 17 August but absent on 14 September ($n = 16$) would have reached the age of 12 weeks between checks, so were classed as successful. This assumption was justified because mortality of large chicks in the absence of disease, as was the case in 2023, is rare in Gannets (Nelson 1978). For the remaining nine chicks present on 14 September, monitoring was continued until after fledging.

Eye colour

During monitoring sessions, efforts were made to observe the eye colours of the adult(s) present at each AON. Eye colour was recorded as 'black' if the iris of one or both eyes appeared >5% black, and 'blue' if the eye(s) appeared typical pale blue in colour. No distinction was made between birds with one or two black eyes because both phenotypes are indicative of past exposure to the disease (Lane *et al.* 2024). For almost all nests, it was not possible to identify individual birds, since only a very few were marked with colour rings at Bempton and none at Bass Rock. As such, we were unable to determine whether the eye colour of both birds from each AON had been recorded. However, given the large number of monitoring sessions undertaken at each plot at both sites, it is unlikely that an individual would have gone unobserved. At Bass Rock, the eye colour of both members of 14 pairs was checked when they were together at the AON. In five of these pairs, one bird had at least one black eye, and the other had two blue eyes. In the other nine pairs, both birds had two blue eyes. At all remaining AONs where a black-eyed bird was recorded it was not possible to determine whether just one or both birds had a black eye. Thus, each AON was classed as 'black' if at least one observation was made of an adult with a black eye or 'blue' if all observations of eyes appeared normal.

All observations were conducted by experienced observers familiar with individual variation in black pigmentation including very subtle markings, and the influence of light conditions, and they only assigned eye colour when confident in their assessment. Unfortunately, it was not possible to verify these observations, for example by a randomized trial of repeated observations by a different observer, or via an independent method. However, at Bempton Cliffs, we recorded the number of times eye colour was seen in a sample of AONs ($n = 169$). At 40% of nests classed as black-eyed,

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this eye colour was recorded on at least two occasions, providing some reassurance that eye colour could be assigned repeatedly, given that the limited data from Bass Rock suggest that black-eye/black-eye pairs were uncommon. Furthermore, Lane *et al.* (2024) independently verified eye colour in 19 individuals, whereby eye colour in the hand matched that recorded in the field in all cases. Although field methods in Lane *et al.* (2024) were not identical to those undertaken in this study, they provide further reassurance that eye colour can be accurately recorded in the field.

Statistical analysis

A generalized linear mixed model (GLMM with a binomial error distribution) was performed on the breeding success of Gannets (unsuccessful: 0; successful: 1), in relation to eye colour (black or blue) and study colony (Bass Rock or Bempton Cliffs), with study plot fitted as a random effect to examine any variation attributed to study plot effects as follows:

$$y_{ij} \sim Binomial\left(m_{ij}, p_{ij}\right)$$

$$p_{ij} = logit^{-1}\left(\beta_0 + \beta_1 \times eye\ colour_i + \beta_2 \times study\ colony_i + study\ plot_j\right)$$

$$Study\ plot_j \sim N\left(0, \sigma^2_{study\ plot}\right)$$

where y_{ij} is the number of 'successes' in m_{ij} trials for the ith individual at the jth study plot (for binary data m_{ij} is 1.0), p_{ij} is the underlying probability of success for the ith individual at the jth study plot, β_0 is the model intercept, β_1 and β_2 are regression coefficients for eye colour and study colony on the logit link-scale, and $study\ plot_j$ represents a random effect for study plot that is normally distributed with a mean of 0 and a variance of $\sigma^2_{study\ plot}$.

All statistical analyses were performed using R version 4.4.0 (R Core Team 2024). The GLMM was undertaken in the package lme4 v 1.1–35.3 (Bates *et al.* 2015) and the intraclass correlation coefficient (ICC) for the random effect was calculated using performance v 0.12.0 (Lüdecke *et al.* 2021). All plots were produced using the package ggplot2 v 3.5.1 (Wickham 2016).

A key assumption in our main analysis is that eye colour represented a perfect indicator of HPAI exposure. However, there is uncertainty associated with the eye colour indicator, since Lane *et al.* (2024) found that 7/9 black-eyed and 1/8 blue-eyed individuals tested positive for HPAI H5 antibodies. Additionally, there is potential for misclassification of eye colour in the field, where observers might mistakenly identify black-eyed individuals as having blue eyes.

In case–control studies such exposure misclassification can bias subsequent estimates of odds ratios, obscuring the true relationship between disease exposure and outcomes (Jurek *et al.* 2005) – in this case breeding success. Statistical methods can account for this bias using prior information on the sensitivity and specificity of the exposure indicator (Greenland 2005). Sensitivity is the proportion of exposed subjects that are correctly classified as exposed (i.e. true positive), and the specificity is the proportion of non-exposed subjects that are correctly classified as non-exposed (i.e. true negative).

Here, we conducted a Bayesian sensitivity analysis to assess how comparisons of breeding success between blue-eyed and black-eyed individuals were influenced by the diagnostic performance (sensitivity and specificity) of eye colour as an indicator of HPAI exposure. We used the BayesSenMC package (Yang *et al.* 2021), which includes a Bayesian framework to calculate misclassification-corrected odds ratios and requires that users input suitable values for test sensitivity and specificity. Based on data from Lane *et al.* (2024), we estimated the sensitivity of our test (Number of True Positives/(Number of True Positives + Number of False Negatives)) as: $7/(7+1) = 0.875$ and the specificity of our test (Number of True Negatives/(Number of True Negatives + Number of False Positives)) as: $7/(7+2) = 0.77$. However, given the presence of black eyes we may be willing to assume that such individuals must have been exposed to HPAI despite not detecting antibodies in 2/9 black-eyed individuals. In this case these two apparent false positives would be considered true positives, and so we also calculated corrected odds ratios assuming this was the case, which meant the sensitivity and specificity of our test were 0.9 and 1.0 respectively.

Additionally, we also considered potential field misclassification, where black-eyed individuals might be wrongly identified as having blue eyes by observers. This would inflate the number of false negatives observed, lowering test sensitivity. With no data on misclassification rates of eye colour by field observers, we calculated corrected odds ratios under assumed sensitivities of 0.6, 0.7 and 0.8, paired with specificities of either 0.77 or 1.0. Using these scenarios, we compared observed and corrected odds ratios for breeding success (unsuccessful: 0; successful: 1) between black- and blue-eyed Gannets. More details on this approach and its formulation in BayesSenMC can be found in Appendix S1.

RESULTS

Frequency of black eyes

Black eyes were recorded in 9.6% of monitored AONs (63/653; Bass Rock: 13.3%, 6/45 AONs; Bempton Cliffs: 9.4%, 57/608 AONs).

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Timing of breeding

The first egg was observed on the Bass Rock on 26 April. The mean lay date was 9 May ±11 days (median lay date 3 May). The mean (± SD) lay date for black and blue AONs was 4 May ±7 days and 9 May ±11 days, respectively. The median lay date was 3 May for both black and blue AONs.

Breeding success

There was no difference in breeding success (average chicks fledged per AON) between Bass Rock (mean ± sd, 0.56 ± 0.50) and Bempton Cliffs (0.62 ± 0.49) (Table 1, estimate = 0.25; $z = 0.66$; $P = 0.51$). Similarly, there was no difference in the breeding success of AONs that had birds with black eyes (0.64 ± 0.49, $n = 63$) and AONs that had birds with blue eyes (0.61 ± 0.49, $n = 590$; Fig. 1; Table 1, estimate −0.06; $z = -0.21$; $P = 0.830$). The ICC for the random effect plot was 0.013, highlighting that the plot-level differences accounted for only 1.3% of the total variability in breeding success (Fig. 2).

We found little evidence that breeding success differed between black-eyed and blue-eyed individuals, based on either observed or misclassification-corrected odds ratios (ORs). When pooling data from both colonies, the observed OR was 1.11 (95% credible interval (CRI): 0.66–1.91). Colony-specific estimates were as follows: at Bass Rock, the observed OR was 0.86 (95% CRI: 0.25–3.05), whereas at Bempton, the observed OR was 1.16 (95% CRI: 0.68–2.06). Misclassification-corrected ORs were associated with greater uncertainty, reflected in wider 95% CRIs, particularly when assuming a specificity of 0.77 – the lower of the two specificity values we considered (Table S3). These results support our main finding that there was no observable difference in breeding success between Gannets with blue or black eyes.

Table 1. Estimates, standard errors (se), *z* values, *P* values, variance components and standard deviations (sd) from the GLMM with binomial distribution testing the effect of eye colour and colony on the probability of breeding success of Northern Gannets at the Bass Rock and Bempton Cliffs in 2023, the year following the major HPAIV outbreak. The intercept corresponds to the centred value for AONs for each effect.

Fixed effects	Estimate	se	*z* value	*P*
(intercept)	0.278	0.443		
Eye colour	−0.062	0.288	−0.214	0.830
Colony	0.252	0.380	0.662	0.508

Random effects	Variance component	sd	
Variance of plot	0.043	0.209	No. of AONs: 653; No. of plots: 17

63/653 nests had black eyes.

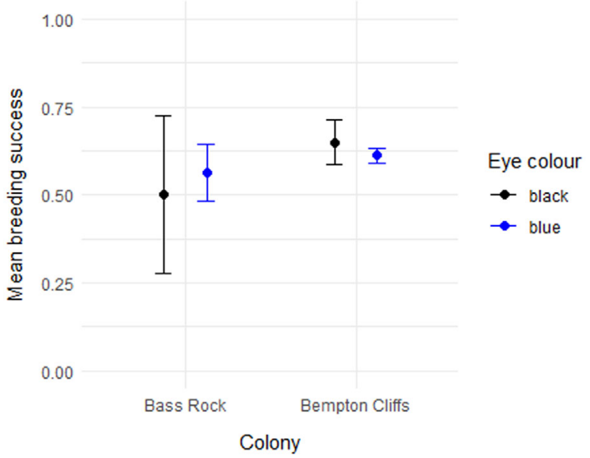

Figure 1. Mean (± standard error) breeding success (chicks fledged per AON) by eye colour in Northern Gannets ($n = 653$ AONs) breeding at the Bass Rock and Bempton Cliffs in 2023, the year following the major HPAIV outbreak (blue: blue eyes; black: black eyes).

DISCUSSION

Our finding that the breeding performance of black-eyed Gannets – indicating that they had been exposed and recovered from HPAIV within the previous 12 months – apparently did not differ from blue-eyed Gannets is potentially encouraging when considering the population's capacity to recover from the outbreak. However, overall breeding success in 2023 was considerably lower than the long-term average (Bass Rock: 0.56 in 2023 vs mean of 0.78 between 1961 and 1963 and range 0.73–0.85 for 13 years, 1961–77 (Nelson 2002); Bempton Cliffs: 0.62 in 2023 vs mean of 0.81 between 2009 and 2021 (Butcher *et al.* 2023)). This breeding performance equates to an approximate doubling of breeding failure rate, measured as 46% and 38% for Bass Rock and Bempton Cliffs compared to historical averages of 22% and 19%, respectively. We excluded the 2022 breeding season in this comparison, where breeding failure was widespread, linked to mortality or temporary abandonment of breeding adults during the epidemic (Jeglinski *et al.* 2024, Lane *et al.* 2024). The epidemic could have resulted in lower than average breeding success the following year for several reasons: (1) a higher proportion of widowed individuals than usual, leading to new pairings that typically have lower

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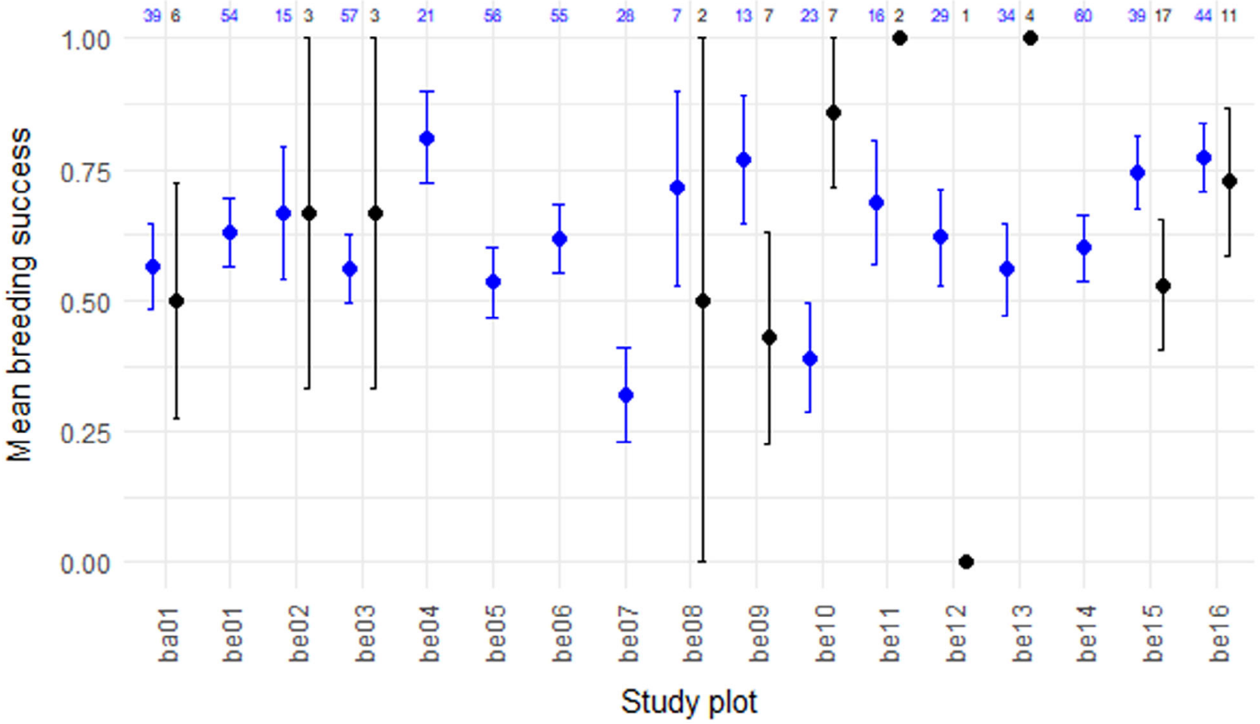

Figure 2. Mean (± standard error) breeding success (chicks fledged per AON) by monitoring plot (Bass Rock; ba01, Bempton Cliffs; be01–be16), with respect to eye colour (blue: blue eyes; black: black eyes) in Northern Gannets in 2023, the year following the major HPAIV outbreak.

breeding success than faithful pairs (Black & Hulme 1996); (2) increased recruitment of young, inexperienced birds that may not have been breeding in 2022 and might therefore have been less likely to have succumbed to the disease – a lower average age may reduce population breeding success since young, inexperienced individuals are generally less successful (Nelson 2002); and (3) the greatly reduced nest density associated with the population decline (Harris *et al.* 2023), since Nelson (2002) suggested that dense nesting enhanced breeding success via social stimulation or reduced risk of egg or chick predation. As such, the downstream effects of an epidemic on subsequent breeding success may not operate via reduced performance of recovered individuals, but on processes that affect all individuals, irrespective of past disease exposure. However, it is also possible that the lower success was unrelated to the epidemic the previous year. The study region experienced an extreme heatwave in 2023 (ECMWF 2023) which could have resulted in reduced prey quality and/or increased consumption rates of fish competitors (the so-called 'ectothermic vice'; Piatt *et al.* 2020), with negative consequences for Gannet productivity. Data from additional years across a range of environmental conditions would therefore be useful in establishing the long-term recovery potential of populations that have experienced an outbreak of HPAIV.

A number of studies have shown that if the cost of maintenance of immune defence is sufficiently high, it may detrimentally affect reproductive success (Hasselquist & Nilsson 2012, and references therein), but that the immunity wanes over time (Fereidouni *et al.* 2010, Samuel *et al.* 2015, Wight *et al.* 2024). However, the costs and persistence of immunity to HPAIV are not known in our study populations, making it challenging to establish if black-eyed birds apparently showed similar breeding success to unexposed individuals because immune defence was not sufficiently costly to have fitness consequences or if immunity and associated costs had waned since exposure. Alternatively, fewer exposed individuals may reach the condition threshold for breeding because of the costs of immunity. Those that do might be in similar average condition to unexposed birds that similarly met this threshold to breed, resulting in a similar breeding success. Thus, exposure may instead influence the likelihood of breeding, if a larger proportion of individuals fail to meet the threshold than unexposed birds. However, we did not have data on breeding likelihood to investigate this.

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Although the physiological mechanisms responsible for the eye pigment change remain unknown, it is possible that eye colour has a direct impact on fitness, for example through the loss of visual acuity. However, individuals were presumably exposed to the disease during the main outbreak 12 months previously. As such, they survived a full winter post-disease, when environmental conditions are typically more severe than in the breeding season, and subsequently attained breeding condition the following spring. It seems unlikely that individuals would have survived and bred without fully functioning vision. Another possibility is that the change in eye colour alters attractiveness or communication between mates (Corbett *et al.* 2024). Further studies are therefore needed to establish what structural changes to the eye occurred, and whether these changes are temporary or permanent. Importantly, the potential lack of an effect of eye colour per se on performance does not detract from the main objective of the study, since eye colour is a strong indicator of past HPAIV exposure and, therefore, the potential costs to recovered birds.

It is possible that our results were affected by inaccuracies in eye colour assignment, in particular the under-recording of black eyes since it is unlikely that an observer would misclassify a blue-eyed bird as black-eyed. A further source of error in our analysis is the link between immune status and eye colour. Work undertaken late in the 2022 breeding season showed that 22.2% of those with black eyes did not have antibodies to HPAIV H5, and 12.5% of those with normal eyes did have antibodies to HPAIV H5 (Lane *et al.* 2024), so eye colour was not a perfect indicator of disease exposure at the time. We accounted for observation error and mismatch between eye colour and immune status in a Bayesian sensitivity analysis that compared observed and misclassification-corrected ORs and found increased uncertainty, but no evidence for an effect of eye colour on breeding success, supporting conclusions from our main analysis. However, it would be of value to establish ways to independently verify field observations beyond what was achieved in a limited sample size at a single locality in Lane *et al.* (2024), in order to increase confidence that observation error is minimized. Furthermore, it would be beneficial to build on the work of Lane *et al.* (2024) with additional studies linking eye colour and antibody status in a larger sample of birds across multiple colonies. This would help confirm the representativeness of their findings and improve our understanding of the sensitivity and specificity of different measures of HPAI exposure. A further limitation of our study is it is unclear what proportion of nests classed as black-eyed comprised one or two mates with that phenotype. However, given that there was no tendency for breeding success to differ between groups, even after accounting for uncertainty in eye colour as an indicator or past exposure, we believe our results are robust to any loss of statistical power arising from these factors.

A similar breeding success in exposed and unexposed individuals, as we found in our study, is an encouraging result since it suggests that population recovery will not be hampered by downstream negative fitness consequences of previously exposed individuals. However, recovery may be constrained if average breeding success across the whole population is depressed. We found this to be the case in our study, potentially as a carry-over effect from the huge colony-wide disruption caused by the epidemic the previous year. Our study suggests that the potential for population recovery following an HPAIV epidemic is hard to predict, but may not occur at the pace desired to fulfil conservation objectives. However, further studies are needed on the precise mechanisms underpinning post-epidemic fitness, undertaken on a broad range of species that differ in ecology and levels of exposure, in order to understand the rate at which hosts recover from disease outbreaks. In that vein, we strongly recommend field ornithologists collect iris pigmentation data and associated demographic information wherever possible in species that show aberrant eye colour in association with disease exposure.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHOR CONTRIBUTIONS

Sue Lewis: Conceptualization; investigation; writing – original draft; methodology; visualization; writing – review and editing; formal analysis; data curation. **Emily Burton:** Conceptualization; resources. **James Butcher:** Methodology; writing – review and editing; data curation; resources. **Ian Cleasby:** Writing – review and editing; formal analysis; resources; methodology. **Amy King:** Methodology; data curation; writing – review and editing; resources. **Emma Marriott:** Methodology; resources. **Dave O'Hara:** Writing – review and editing; methodology; data curation; resources. **Maggie Sheddan:** Methodology. **Mal Watson:** Resources; software. **Saskia Wischnewski:** Resources; methodology; data curation; writing – review and editing. **Lucy Wright:** Resources;

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writing – review and editing; methodology; data curation. **Sarah Wanless:** Writing – review and editing. **Jude V. Lane:** Conceptualization; writing – review and editing.

ETHICAL NOTE

None.

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DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available from the corresponding author upon reasonable request.

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SUPPORTING INFORMATION

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

Appendix S1. Accounting for misclassification.

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