

RESEARCH ARTICLE

Evaluating the demographic impacts of the highly pathogenic avian influenza panzootic

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Handling Editor: Manvi Sharma**Abstract**

1. The spread of a new highly pathogenic avian influenza virus (HPAIV-H5N1) has, since 2021, triggered one of the most severe wildlife panzootic ever reported, with suspected population crashes in hundreds of bird and mammal species. However, to date no studies have evaluated the demographic mechanisms underlying these declines.
2. We used Integrated Population Modelling (IPM) along with Bayesian population forecasting and resilience analysis, to evaluate the impact of HPAIV-H5N1 on age-structured survival, productivity, stage-specific population dynamics and demographic resilience in a long-lived bird, the peregrine falcon (*Falco peregrinus*), in the Netherlands.
3. Our analyses revealed drastic declines in adult survival—the key driver of population dynamics in a long-lived species—in 2022 and 2023, coinciding with a ~25% decline in breeding pairs. This suggests a shift in HPAIV dynamics compared to previous epizootics, with recurrent outbreaks during consecutive seasons and years, resulting in potentially stronger population impacts.
4. Resilience analysis revealed that HPAIV outbreaks could cause long-lasting demographic impacts in the population. The breeding population could take a decade to recover to pre-panzootic levels and may ultimately stabilize at ~21% below its former size. Recovery could take longer if HPAIV outbreaks become more frequent in the future, which is likely under current epidemiological predictions.
5. *Synthesis and applications.* Our findings demonstrate that the HPAIV panzootic can cause rapid and long-lasting impacts on the dynamics of long-lived species. This raises major concerns for the conservation and long-term viability of the many severely affected long-lived species worldwide. As wildlife disease is predicted to become a leading cause of biodiversity loss, a global-scale conservation

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strategy is urgently needed, which includes improved management, surveillance and applied research efforts. Our combined use of IPMs, forecasts and resilience analyses also serves as a benchmark for evaluating the effects not only of zoonotics, but also of any other type of disturbance in wild populations.

KEYWORDS

avian influenza, capture-mark-recapture, demographic resilience, Integrated Population Modelling, long-lived species, peregrine falcon, population models, wildlife disease

1 | INTRODUCTION

Infectious wildlife diseases are among the leading causes of population declines and extinctions, and their frequency and geographic range are predicted to increase under global change (Daszak et al., 2000). A paradigmatic example is the highly pathogenic avian influenza virus (HPAIV). Over the past three decades, HPAIV has spilled over from poultry to wild birds (Shi et al., 2023). Since 2021, a particularly virulent H5N1 has caused the most widespread and persistent HPAIV panzootic ever recorded (Campagna et al., 2024; Klaassen & Wille, 2023; Lambertucci et al., 2025). For the first time ever, this panzootic has triggered high-mortality outbreaks in wild vertebrates across all continents except Oceania. The cumulative death toll may reach millions, with confirmed outbreaks in at least 406 bird and 51 mammal species in the wild by 2024 (Lambertucci et al., 2025; Plaza et al., 2024).

Of particular concern are HPAIV-H5N1 impacts on long-lived species, characterized by long life expectancy, delayed sexual maturity and reduced brood size. To sustain viable populations, these species typically rely on high survival probabilities that must be fairly stable over time, and they show only limited recovery ability to perturbations affecting their demography (Capdevila, Stott, et al., 2022a). Reports of mortality in long-lived species due to HPAIV-H5N1 between 2021 and 2024 have been unprecedentedly frequent and widespread (Klaassen & Wille, 2023; Lambertucci et al., 2025). However, most existing information is based on counts of animals reported dead (Günther et al., 2024; Rayment et al., 2025). This may result in an underestimation of the impact of the disease, as it is highly likely that an unknown proportion of deceased individuals in a population goes undetected. Instead, estimating survival using mark-recapture data provides estimates of survival unaffected by imperfect detection. This is fundamental for a mechanistic understanding of the demographic pathways underlying HPAIV-related population crashes. Intuitively, survival must have declined, but nothing is known about the magnitude of such a decline at the population level nor about its rate of change over time. Little is known about potential HPAIV-induced effects on other vital rates, about whether specific population stages may be more affected than others, and how all of this may affect the overall dynamics of populations and their likely trajectories in the future. As a result of these knowledge gaps, we currently lack the ability to design and implement effective conservation strategies, that is, those

that target the most affected population stages and most influential demographic parameters.

Likewise, the resilience of natural populations to periodic disturbances induced by HPAIV has apparently not been studied yet. Long-lived species typically show only a limited ability to recover from severe reductions of population size, and need long recovery times (Capdevila, Stott, et al., 2022a). Consequently, their populations may be at a higher risk for decline if epizootics occur repeatedly within a short time interval (Capdevila, Noviello, et al., 2022b). Furthermore, populations subject to repeated severe disturbances may stabilize below their carrying capacity, even after the disturbance ceases—a phenomenon known as population inertia (Koons et al., 2007). These mechanisms are rarely considered when studying the effects of severe disturbance in a population, yet they may be critical given the increasing frequency and intensity of global disturbances such as epizootics.

Here, we elucidate the precise demographic pathways and resilience responses of a long-lived species: the peregrine falcon *Falco peregrinus* in the Netherlands (Caliendo et al., 2024, 2025). The study area lies at the crossroads of Western Europe and Scandinavia, and is an area with a particularly high incidence of the HPAIV-H5N1 virus that is known to have caused severe casualties in several bird species (Caliendo et al., 2024). As peregrines feed almost exclusively on birds, it is a good model for studying the impact of HPAIV, as it potentially has a large exposure to the virus. In the Dutch peregrine population, steep declines, large recorded casualties and high HPAIV positivity in dead birds (~80%) suggest a strong impact of recurrent HPAIV outbreaks (Caliendo et al., 2024, 2025). Similar declines have been reported in some other northern European populations, especially in the Nordic region (Järås, 2023).

We analysed population dynamics using Integrated Population Models (IPMs), a statistical framework that allows the integration of multiple data streams to jointly estimate demographic parameters (Besbeas et al., 2002; Schaub & Kéry, 2022). Our analyses yield annual estimates of age-specific survival probabilities, productivity, immigration rate and age- and stage-specific population sizes. First, we evaluate and compare annual fluctuations in parameter estimates before (1993–2020) and during (2021–2024) the HPAIV panzootic. Then, we use Bayesian population forecasting to assess two key components of population resilience: recovery time and population inertia (Figure 1; Capdevila et al., 2020). Our findings aim to inform conservation strategies that prioritize the most sensitive demographic parameters and life

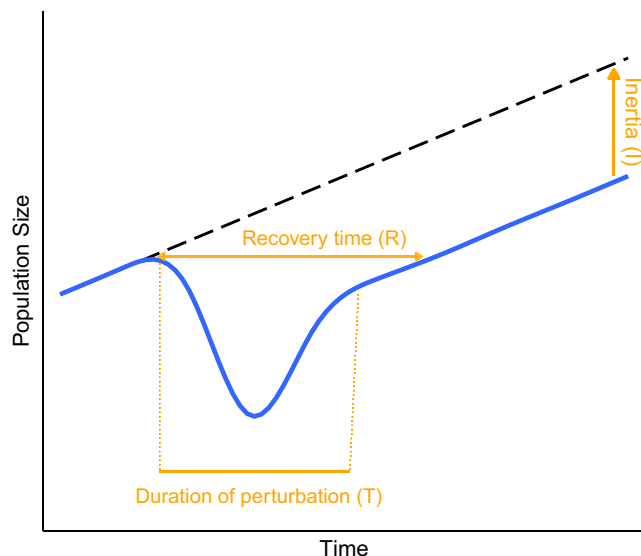


FIGURE 1 Schematic showing recovery time, disturbance duration and inertia in a hypothetical population affected by a disturbance. The thick blue line represents the trajectory of a population affected by a disturbance event. The dashed black line represents the size trajectory of the same population not affected by the disturbance.

stages to HPAIV in this and other long-lived species affected. In addition, we suggest that the accurate demographic accounting yielded by an IPM may become the benchmark approach for gauging the effects on a population of a zoonotic or indeed of any other impact.

2 | METHODS

2.1 | Study species and area

The peregrine falcon is a medium-sized territorial raptor found on all continents except Antarctica (Ratcliffe, 1993). In Europe, it nests primarily on cliffs or tall buildings, while in our Dutch study area, nesting is almost exclusively on buildings or transmission line pylons equipped with nest-boxes (van Geneijgen, 2014). Peregrines lay three to four eggs in March that hatch after 30 days. Fledging occurs around 42 days post-hatch, typically in May or early June (van Meerendonk, 2023). As in many territorial species, young peregrines are nomadic and (for Western European birds) typically spend their first winter in the Western Mediterranean (Ratcliffe, 1993). They generally begin breeding at 2 years old (Kauffman et al., 2004).

Our study covered the entire Netherlands, characterized by lowlands, coasts and urban-farmland mosaics. During the 'pesticide crash' in the 1960s (Kéry et al., 2025; Ratcliffe, 1993), peregrines became extinct in the Netherlands until recolonization began in 1990 (van Geneijgen, 2014). Since then, the number of breeding pairs has steadily increased up to ~225 in 2021, before dropping to ~163 until 2024 (Sovon, 2024). This decline coincided with HPAIV outbreaks (Caliendo et al., 2024, 2025). Raptors, including peregrines, are likely infected via ingestion of infected prey. In the Netherlands,

peregrines may be affected by feeding on seabirds, waders and ducks, which are very abundant prey with high HPAIV prevalences (Caliendo et al., 2025; Günther et al., 2024).

2.2 | Data acquisition and field methods

In our models, we used data from mark-resighting schemes, counts of breeding pairs and productivity surveys. Since 1993, peregrines have been intensively monitored with a ringing and resighting scheme coordinated by Werkgroep Slechtvalk Nederland (WSN) and the Dutch Ringing Scheme (Vogeltrekstation). The ringing permits for the whole study period were issued by the Vogeltrekstation. A total of 2881 birds have been ringed—2807 as chicks and 74 as subadults or adults. Most birds were ringed with both alphanumeric colour and metal rings ($n=2795$), while 86 birds were ringed with metal rings only. Resightings of breeders were made during nest visits, while nonbreeder resightings occurred throughout the country. In total, 10.1% of ringed birds were resighted alive. In addition, ringed birds found dead were recorded in the Netherlands and abroad. Up to 15.2% of all ringed birds were recovered dead. Birds with metal rings only could not be resighted alive, because their code was too small to be read from a distance, but they could be recovered dead.

Breeding pair counts (C_t) were carried out by the Sovon-Dutch Center for Field Ornithology between March and June 2010–2024. This comprised repeated visits to all known territories occupied in previous years and to potential new nesting areas in search for colonizing pairs. The resulting counts were taken as a measure of the Dutch breeding population size.

Breeding surveys were performed by the WSN in the southern half of the Netherlands, which hosts about 70 breeding territories, between 2010 and 2024. These included repeated visits late in the breeding season to count the number of chicks in every monitored nest. The surveys encompassed a minimum of 8 occupied territories in 2010 and a maximum of 44 in 2021. Table S1 (see Supporting Information) provides the yearly counts of breeding pairs, the numbers of territories surveyed for reproduction and the fledglings counted.

2.3 | Analysis of population dynamics with an Integrated Population Model

We estimated demographic parameters and population dynamics by jointly analysing the mark-resight-recovery (1993–2024), population count (2010–2024) and productivity data (2010–2024) in an IPM (Besbeas et al., 2002; Schaub & Kéry, 2022). The core of the IPM is a state-space model whose state-process model corresponds to a stochastic, stage-structured population model that reflects the species life cycle and an observation model that links the observed with the estimated number of breeding pairs. The demographic rates that drive population change are additionally informed by the productivity and the mark-resight-recovery data. Our stage-structured population model was female-based, assumed an even sex ratio and

was constructed according to a pre-breeding 'census'. We defined population stages considering a combination of age (1-year-old, 2-year-old, 3-year-old, 4-year-old and 5-year-old and older individuals) and breeding status (breeder vs. nonbreeder), plus an immigrant stage. We assumed all 1-year-olds ('juveniles') are nonbreeders. We also assumed that recruitment occurs at ages 2, 3 or 4 according to probabilities that we estimated in the models, is irreversible and that all individuals aged 5 and older were breeders. The stage-specific expected numbers of individuals alive in each year were given by the numbers in the preceding year and the year-specific demographic rates. This resulted in nine different population stages (Equation 1; see also life-cycle graph in Figure S1). We accommodated demographic stochasticity in the model by using Poisson distributions in 1-year-old nonbreeders ('juveniles') and immigrants, and binomial distributions for the remaining population stages (Schaub & Kéry, 2022).

$$\begin{aligned}
 N_{1,t+1} &\sim \text{Poisson}\left(N_{B,t} * S_{1,t} * \frac{\rho_t}{2}\right), \\
 N_{2,t+1} &\sim \text{Binomial}(S_{2,t} * \gamma_2, N_{1,t}), \\
 N_{3,t+1} &\sim \text{Binomial}(S_{2,t} * (1 - \gamma_2), N_{1,t}), \\
 N_{4,t+1} &\sim \text{Binomial}(S_{3,t} * \gamma_3, N_{3,t}), \\
 N_{5,t+1} &\sim \text{Binomial}(S_{3,t} * (1 - \gamma_3), N_{3,t}), \\
 N_{6,t+1} &\sim \text{Binomial}(S_{3,t} * \gamma_3, N_{5,t}), \\
 N_{7,t+1} &\sim \text{Binomial}(S_{3,t} * (1 - \gamma_3), N_{5,t}), \\
 N_{8,t+1} &\sim \text{Binomial}(S_{3,t}, N_{B,t} + N_{7,t}) \\
 N_{9,t+1} &\sim \text{Poisson}(\omega_t)
 \end{aligned} \quad (1)$$

In Equation (1), N are the stage-specific population sizes, with the first subscript denoting stage class and the second one the year (see Table 1 for definitions). Symbols ρ , γ , S and ω stand for productivity, recruitment, survival probabilities and for the expected number of immigrants, respectively. Numeric subscripts in γ and S indicate stage classes. The number of breeders N_B is defined as the sum of the number of all stages that reproduce at time t :

TABLE 1 Definition of the symbols for the stage-specific population sizes used in the Integrated Population Model.

Symbol	Definition
$N_{1,t}$	Locally born, 1-year-old nonbreeders at year t
$N_{2,t}$	Locally born, 2-year-old first-time breeders at year t
$N_{3,t}$	Locally born 2-year-old nonbreeders at year t
$N_{4,t}$	Locally born 3-year-old first-time breeders at year t
$N_{5,t}$	Locally born 3-year-old nonbreeders at year t
$N_{6,t}$	Locally born 4-year-old first-time breeders at year t
$N_{7,t}$	Locally born 4-year-old nonbreeders at year t
$N_{8,t}$	Experienced breeders at year t
$N_{9,t}$	Immigrant first-time breeders at year t

$$N_{B,t} = N_{2,t} + N_{4,t} + N_{6,t} + N_{8,t} + N_{9,t} \quad (2)$$

All demographic parameters were estimated with full annual random variation except for recruitment, which was estimated as constant over time, given the limited sample size and the general difficulty with which this parameter can be estimated (Schaub & Kéry, 2022).

Immigrants were defined as the yearly number of first-time breeders that were not locally born. These were estimated as a hidden parameter, using the indirect information contained in the different data sources used in the model (Schaub & Kéry, 2022).

We related $N_{B,t}$ to the yearly breeder counts C_t using a Poisson distribution as a way of accommodating some counting error, but which also functions as a residual error of the model (Schaub & Kéry, 2022).

$$C_t \sim \text{Poisson}(N_{B,t}) \quad (3)$$

As a derived latent quantity, we calculated the annual number of floaters as the number of sexually mature nonbreeders; that is, the number of all nonbreeders that are 2 years old or older.

$$N_{\text{float}_t} = N_{3,t} + N_{5,t} + N_{7,t} \quad (4)$$

Floaters typically act as a pool of individuals that replace dead breeders in territories, thus contributing to the stability of breeder populations by functioning as a buffer (Penteriani et al., 2011).

2.4 | Submodel for productivity (ρ)

We used brood size, the number of chicks aged 2 weeks or older per breeding pair, as an estimate of productivity. We modelled the annual count of fledglings (J_t) as a Poisson random variable with an expectation given by the product of the annual number of pairs monitored (M_t) and productivity rate ρ_t (Schaub & Kéry, 2022).

$$J_t \sim \text{Poisson}(M_t * \rho_t) \quad (5)$$

2.5 | Submodel for survival (S) and recruitment (γ)

We jointly modelled live-encounter and dead-recovery data using a multistate capture-mark-recapture (CMR) model to estimate survival and recruitment, live resighting and dead-recovery probabilities (Burnham, 1993). We considered live resightings from within the Netherlands from February to September each year and dead recoveries from anywhere and all-year-long, with the annual divide at the start of the ringing season (April 26). The inclusion of recoveries from beyond the Netherlands allowed us to estimate true survival, unaffected by emigration (Burnham, 1993). Additionally, our dataset

provided information about the breeding status (seen as a breeder vs. seen as a nonbreeder), and the age of the individual at ringing. This information allowed us to model survival, recruitment and live resighting probabilities by stage class.

Multistate models consist of a state process, which defines the relationship between the state of an individual between years t and $t + 1$, and an observation process, which relates the observation at occasion t to the state of an individual at time t . We defined six different observation states that depended on whether the individuals were alive or dead, breeders or nonbreeders, and were carrying an alphanumeric colour ring or a metal ring only (see [Figures S2 and S3](#) in the Supporting Information).

We defined three age classes in survival based on the peregrine life-history: 1-year-olds (juveniles, S_1), 2-year-olds (subadults, S_2) and individuals aged 3 and older (adults, S_3) (Faccio, 2013). For recruitment probabilities, we defined two stage classes: one for subadults (γ_2), and another for 3 and 4-year-olds (γ_3).

Annual resighting probabilities of live ringed birds (p) were structured into age classes to capture the likely heterogeneity in this parameter over the life of an individual. After evaluating different age structures using goodness-of-fit tests (GoF, see [Supporting Information](#)), we retained a structure with three age classes: one for juveniles (p_1), a second for individuals aged 2 to 4 (p_2), and a third for individuals aged 5 and older. The probability of finding and reporting a recently dead ringed individual (recovery probability, r), on the logit scale, was assumed to be unrelated to age, but was modelled with a linear regression on the year to accommodate likely gradual changes in recovery efforts over time.

We formulated our multistate model with a marginalized likelihood of the state-space formulation. This equivalent likelihood provides a considerable speed gain compared to the standard state-space formulation (Schaub & Badia-Boher, 2025).

2.6 | Population projections 10 years into the future

To gauge the longer-term impact of HPAIV, we projected the population under two scenarios and calculated key metrics of population resilience (Capdevila et al., 2020). In both scenarios, we simulated future population dynamics until 2034 using the temporal random-effects means and variances of all demographic parameters, as estimated from the respective IPM fits. We also accounted for parameter uncertainty, as well as demographic and environmental stochasticity in these predictions (Schaub & Kéry, 2022). In the first scenario, the IPM was fitted with all the available data (until 2024), that is, including the demographic effects of the HPAIV outbreaks (2021–2023). We then projected population trajectories to 2034. In the second scenario, we refitted the IPM using only the pre-outbreak data (until 2020) to provide parameter estimates representing population dynamics unaffected by HPAIV. Using these parameters, we projected the population again to 2034. The comparison between both scenarios allows an evaluation of key properties of a

disturbance of population dynamics, that is, of population resilience (Capdevila et al., 2020; [Figure 1](#)). First, we evaluated recovery time, that is, the number of years required for the breeder population to again reach its size from 2021 (which was the maximum population size ever achieved, right before the most intense HPAIV outbreaks were recorded; Caliendo et al., 2025). Second, we assessed the difference between the projected breeder population size in the absence of the HPAIV outbreak (Scenario 2) and that including the outbreak years (Scenario 1) once stable growth was reached in both (i.e. 2030). This metric informs about the effect on long-term population size caused by a disturbance or population inertia (Koons et al., 2007).

2.7 | Statistical inference and model fitting

All models were fitted using Bayesian MCMC in JAGS (Plummer, 2003), via R 4.4.2 and the package 'jagsUI' (Kellner, 2024). We ran four chains of 80,000 iterations with the first 40,000 discarded as burn-in and the remainder thinned by 1 in 40. Convergence was confirmed visually by traceplots and by the Brooks-Gelman Rubin statistic ($R_{hat} < 1.02$).

Based on posterior predictive checks (Schaub & Kéry, 2022), model fit was adequate, with Bayesian p -values of 0.59 for the count model and 0.39 for the productivity model. The CMR model also fit well (see [Supporting Information](#)). We report all estimates as posterior means and 95% credible intervals (CRI) in parentheses.

3 | RESULTS

Mean annual adult survival before the HPAIV panzootic (1994–2020) varied between 0.73 and 0.86 ([Figure 2](#)). During the panzootic period, it dropped to 0.72 (0.65–0.80) and 0.57 (0.47–0.66) in 2021 and 2022, respectively, before recovering to 0.70 (0.59–0.80) and 0.79 (0.67–0.88) in 2023 and 2024. Mean pre-panzootic survival of subadults varied between 0.58 and 0.75. During the panzootic, it declined from 0.72 (0.55–0.87) in 2021 to 0.44 (0.16–0.70) in 2022 and 0.56 (0.36–0.75) in 2023 and then recovered to 0.73 (0.52–0.92) in 2024. Juvenile survival showed little annual variation only and fluctuated between 0.30 and 0.35 in the pre-panzootic years, with similar values during panzootic years.

Mean annual productivity rates before the HPAIV panzootic (2010–2020) varied between 1.9 and 2.2 ([Figure 2](#) and [Figure S4](#)). During the panzootic period, the rates were similar, oscillating between a minimum of 1.90 (1.56–2.17) in 2021 and a maximum of 2.15 (1.89–2.61) in 2023.

The estimated number of breeding pairs more than doubled from 2010 to the beginning of the panzootic, reaching 222 (200–246) in 2021. This was followed by a 25% (13%–35%) crash in just 2 years, reaching a minimum of 169 (150–188) pairs in 2023, with 172 (151–195) in 2024, that is, hardly any improvement ([Figure 3](#) and [Figure S4](#)). The number of juvenile females increased over time

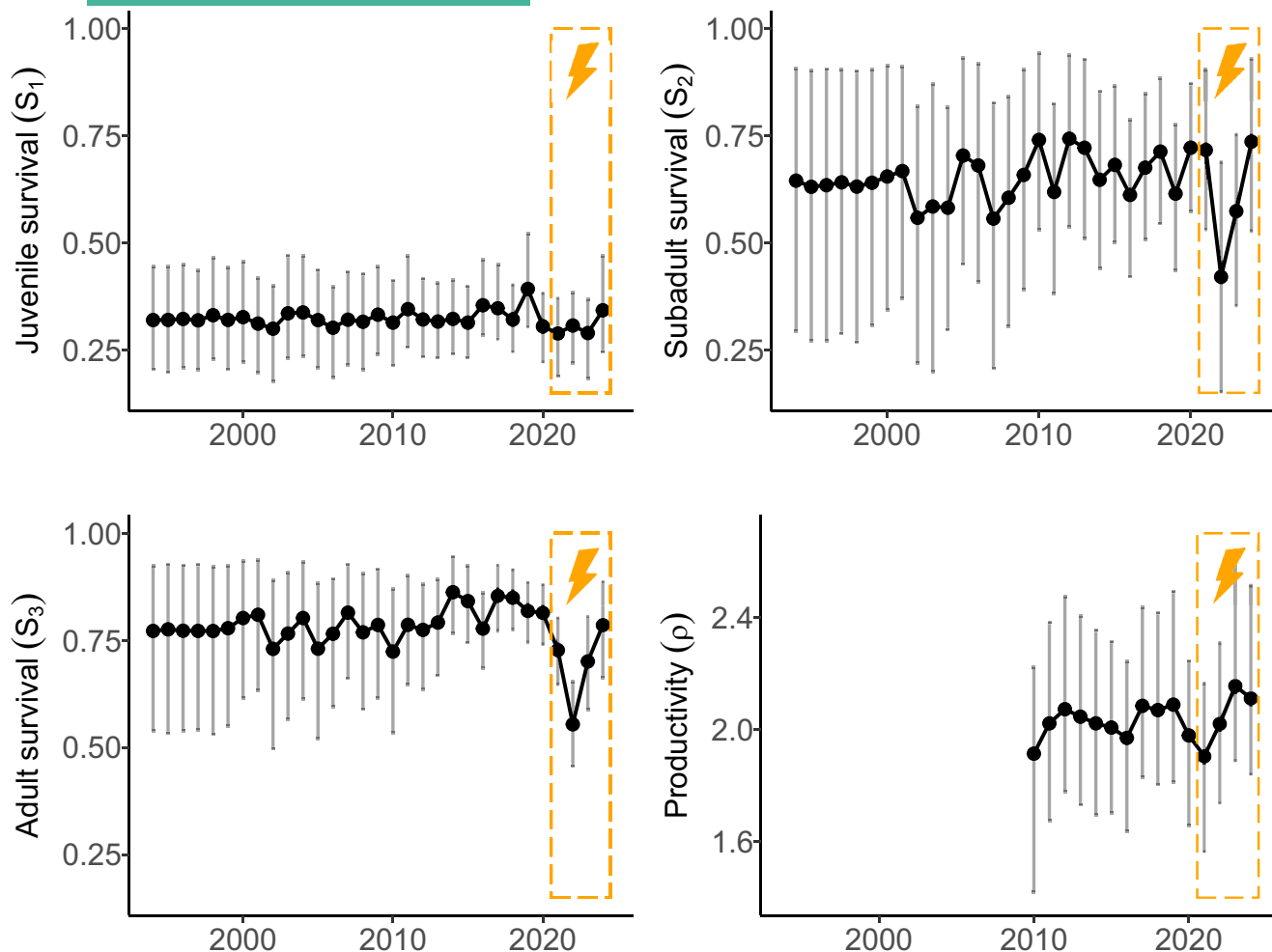


FIGURE 2 Stage-specific survival and productivity estimates over the years. Points indicate means and whiskers indicate 95% credible intervals. The dashed rectangle with the lightning symbol encompasses the years where highly pathogenic avian influenza virus (HPAI)-H5N1 outbreaks were reported in the study population.

reaching a maximum of 77 (53–113) in 2019 and declined by 30% (18%–66%) during the panzootic period. Similarly, floaters reached a maximum of 24 females (12–40) in 2020 and declined by 40% (37%–76%) thereafter. The number of immigrant females was relatively constant over time, oscillating between 8 and 12 individuals on average. However, in 2022, coinciding with the decline in the breeding population, it grew to 20 (2–80).

Recruitment probability was estimated at 0.67 (0–55–0.77) for 2-year-olds and 0.62 (0.40–0.81) for 3 and 4-year-olds (Figure S5). Resighting and recovery probabilities are presented in the Supporting Information and Figures S6 and S7 therein.

Fitting the model to the full data set (i.e. including the panzootic years), 10-year projections suggested a steady increase in the number of breeding pairs over the years, reaching 249 (109–482) pairs by 2034. Fitting the model instead to the reduced data set only (i.e. without the years of the HPAIV outbreaks), the number of breeding pairs was estimated at 216 (175–269) in 2020, 238 (167–332) in 2024 and 294 (168–508) in 2034. The estimated recovery time to the highest number of breeding pairs (2021) was 9 years on average (2031; Figure 4), although with a large uncertainty. There was a

probability of 23% that the 2021 numbers would not be recovered before 2034, of 57% that recovery was achieved before 2029 and of 20% that recovery was attained between 2030 and 2034. Inertia estimates indicated that by 2030 the breeding population will have lost 21% of its size, that is, 55 breeding pairs (Figure 4), although the uncertainty was again large (–127 to +235 pairs).

4 | DISCUSSION

The recent spread of HPAIV-H5N1 (2021–2024) has caused one of the most severe wildlife diseases ever reported, but to date no demographic analyses have evaluated its effects on the dynamics of wild populations. Our results suggest that the effects of HPAIV-H5N1 outbreaks in the Dutch peregrine falcon population have been severe, with a sharp decline in adult survival and all population stages during consecutive panzootic years. Furthermore, resilience analyses predict that the population may take a decade to recover, which is concerning given the likely increase in the recurrence of HPAIV outbreaks in future years. Our findings illustrate the

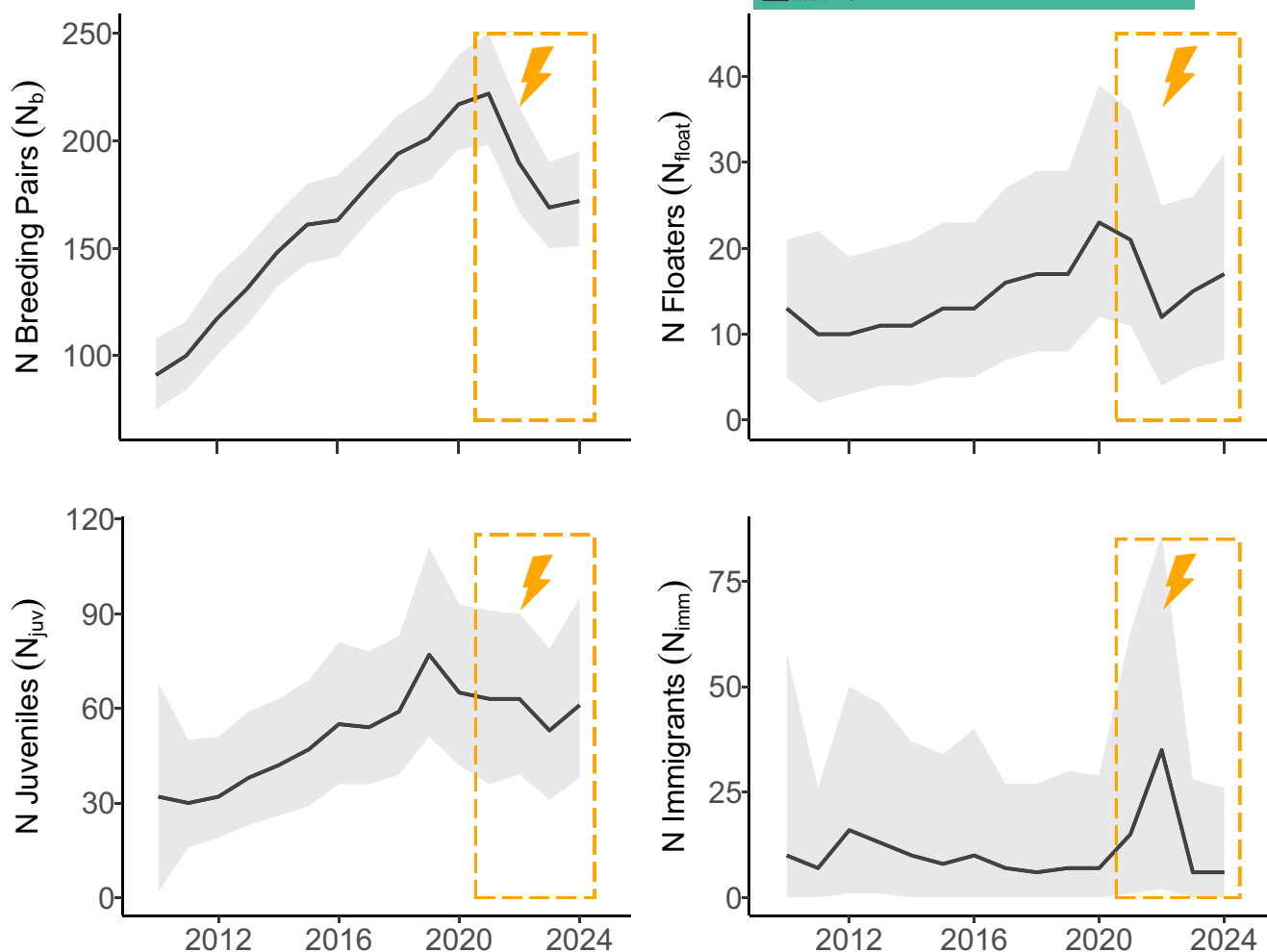


FIGURE 3 Stage-specific population sizes over the years. Thick lines indicate mean values, and grey shaded areas indicate 95% credible intervals. The dashed rectangle with the lightning symbol encompasses the years where highly pathogenic avian influenza virus (HPAI)-H5N1 outbreaks were reported in the study population.

potentially larger population impacts caused by the new HPAIV virus and call for a global-scale conservation response.

The large drop in adult survival that we found during the HPAIV panzootic is uncommon in long-lived species. In these species, there is strong selection towards high and stable adult survival over time even in the case of disturbances, given the large sensitivity of population growth rates to this parameter (i.e. 'demographic buffering', Hilde et al., 2020). As a result, declines of this magnitude often have catastrophic effects on population size, such as the quick decline in the number of breeders that we estimated over barely 2 years. Hence, understanding whether adult survival has been affected generally in other long-lived species affected by HPAIV is fundamental to assess the impact magnitude of the panzootic on populations. To date, we found only a single study estimating survival, which was in colonies of northern gannets *Morus bassanus* (Lane et al., 2024). The study reported a drop in adult survival of a similar magnitude to the one we found. Besides, many monitoring schemes of affected long-lived species have reported sharp declines in breeder numbers (e.g. Avery-Gomm et al., 2024; Falchieri et al., 2022). Although no demographic studies have been performed, the steepness of these

declines and the large numbers of dead adults found in many populations affected (e.g. Günther et al., 2024; Rayment et al., 2025) suggest that a decline in adult survival was the main cause.

The strongest reductions in survival and breeder population size in 2022 and 2023 matched the strongest outbreaks in late winter and early spring of the same years in the Netherlands (Caliendo et al., 2024, 2025). The fact that the HPAIV-H5N1 outbreaks affected the population during consecutive years constitutes a different trend from previous HPAIV epizootics, which only generated outbreaks within single years (Kleyheeg et al., 2017). Seemingly, another new particularity of HPAIV-H5N1 is that outbreaks can extend through all seasons in many species, whilst former epizootics were limited to winters (Caliendo et al., 2025; Pohlmann et al., 2022). This epidemiological change may have considerable repercussions on population dynamics, as spring outbreaks overlap with the breeding season in many species. Energy expenditure is particularly high during breeding, which could result in higher individual vulnerability to disease, and ultimately, stronger population-level impacts (Drent & Daan, 1980). In this respect, the highest adult and subadult mortalities in the study population were reported already in the breeding

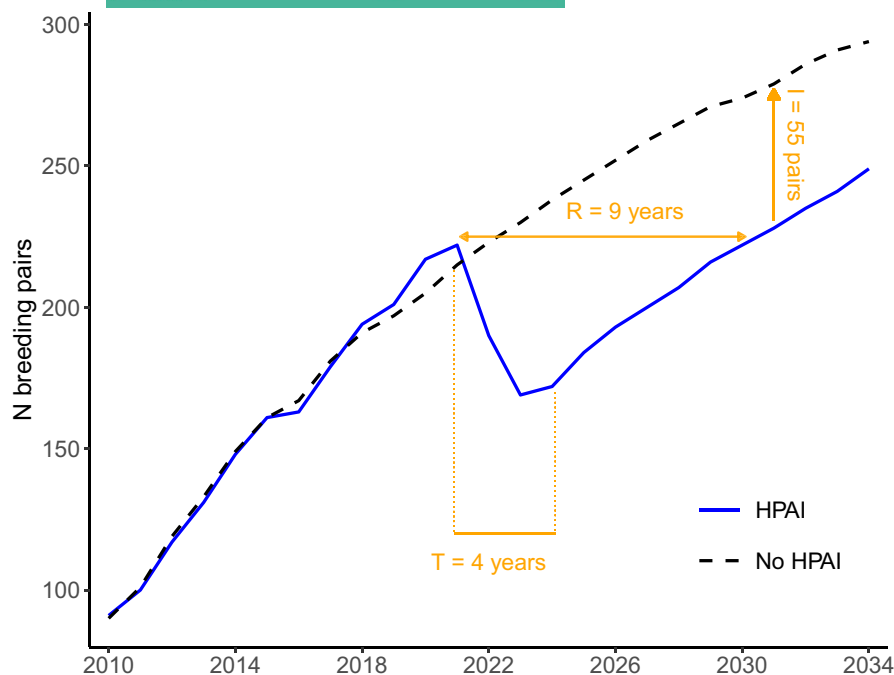


FIGURE 4 Mean numbers of breeding pairs over the years in models including years with highly pathogenic avian influenza virus (HPAI)-H5N1 outbreaks (2010–2024) and not including them (2010–2020), plus projections until 2034. The annotated values refer to the duration of the HPAIV perturbation (T), the median recovery time (R) and median inertia (I).

season (March 2022–2023), along with 93% of all sampled dead peregrines tested positive for HPAIV ($n=15$, Caliendo et al., 2025). Instead, previous winter-only outbreaks (e.g. in 2016–2017 or an outbreak in late 2020) did not coincide with noticeable declines in survival nor in the number of breeding pairs.

The combination of increased outbreak recurrence and potentially larger effects on breeder survival may be a dangerous combination for population viability. The repeated, sudden removal of large numbers of breeders may progressively slow down recovery times (Capdevila, Noviello, et al., 2022b). Juveniles must survive several years to reach the age of first breeding and consequently the replacement of dead breeders may take several years. In addition, the drastic decline in the number of breeders in our study population also resulted in lower numbers of fledglings in subsequent years. Given these cascading effects, our projections showed that it would take about a decade for the breeding population to recover to its former size. Importantly, recovery times could be considerably longer in other affected, long-lived species with lower productivity and a later age of first breeding (e.g. condors, albatrosses, Kozlov, 2023; Kuiken et al., 2025). Besides this, our model did not account for any demographic trade-offs (e.g. between survival and reproduction), although such relationships may modify recovery times under disease-driven mortality (Jaggi et al., 2024).

Our estimated reductions in survival and breeding pair numbers were accompanied by a decline of the size of the floater population, which typically acts as a buffer for the breeder population (Penteriani et al., 2011). Instead, our results suggest that an increase in the number of immigrants from other populations actually buffered the breeding population to some degree. These immigrant recruits likely originated from populations where HPAIV impacts have apparently been lower, according to field observations (e.g. Belgium and southwestern Germany, Didier Vangeluwe and Frank Rau, pers.

comm.). This may be due to a lower prevalence of HPAIV, or because peregrines depend less on seabirds as a food source and are therefore less exposed to the virus. The contributions from these healthier populations probably prevented an even more drastic decline in the Dutch breeding population.

In our study, the use of IPMs enabled the joint modelling of three key aspects of population dynamics within a unified framework: (1) the retrospective impact of a disease-induced perturbation on demographic parameters and population stages, (2) the likely future response of the population and (3) key metrics of demographic resilience. These components are rarely assessed together, and our approach thus offers a valuable and broadly applicable framework for comprehensively evaluating the effects of perturbations. Importantly, we estimated resilience metrics within the IPM by comparing future scenarios with and without the impact of HPAIV, aligning with the conceptual framework outlined by Capdevila et al. (2020). This approach contrasts with most resilience studies, which typically derive resilience metrics from population projection matrices (PPMs; Capdevila, Noviello, et al., 2022b; Capdevila, Stott, et al., 2022a; Stott et al., 2011). In these studies, resilience estimates are hardly ever presented with their associated uncertainties, probably because these are not easy to calculate from PPMs. Instead, a notable advantage of using IPMs is that the propagation of uncertainty into the resilience estimates is straightforward. Importantly, as resilience metrics are always based on projections, their uncertainties will be inherently large, a pattern also evident in our results. Here, we focused our discussion on the means of the metrics, to adhere to standard practices in resilience studies.

The effect of HPAIV-H5N1 on juvenile survival and productivity was mild, if anything. The lack of HPAIV effects on productivity agrees with findings in other birds of prey in central and

northern Europe, where this parameter was hardly affected (Günther et al., 2024). However, strong drops in productivity were found in other animal groups, suggesting that productivity effects might be taxon- or case-specific (Campagna et al., 2024; Duriez et al., 2023). In our study population, Caliendo et al. (2025) found no trace of HPAIV in unhatched eggs during the breeding season, suggesting that pre-hatching HPAIV infection was unlikely. In another study, Günther et al. (2024) reported low HPAIV prevalence in white-tailed sea eagle nestlings (*Haliaeetus albicilla*) in Germany despite high exposure of adults, a pattern possibly explained by the transfer of maternal antibodies to nestlings. This hypothesis could also explain the mild to non-existent decline in juvenile survival throughout the outbreak. Another nonexclusive explanation relates to movement ecology: as in many raptors, young peregrines often disperse hundreds of kilometres from their birthplace, which may have reduced their exposure to the virus by moving them away from the Netherlands during the outbreaks (Newton, 1979).

Interestingly, in former epizootics, HPAIV systematically showed lower virulence in adults than in juveniles (Günther et al., 2024; Hill et al., 2016). This was attributed to the acquisition of an immune response in adults that survived previous outbreaks. Our more severe mortality estimates in adults, together with growing reports of dead adults found in other studies, suggest a lack of pre-existing protective immunity during panzootic years (Günther et al., 2024; Rayment et al., 2025). Encouragingly, our results also indicate that subadult and adult survival in Dutch peregrines both recovered to pre-panzootic levels in 2024, suggesting that the population may have developed some degree of immunity, although antibody data are lacking to confirm this. The limited evidence available supports this hypothesis, as Günther et al. (2024) reported rising antibody levels in white-tailed sea eagles in Germany following successive outbreaks. Nevertheless, further epidemiological and demographic studies are required to ascertain whether virus resistance is indeed increasing across affected populations, and to assess how long such protection may persist.

Crucially, this will not be the last panzootic we witness. Under ongoing global change, both the spread and the impact of infectious diseases are increasing, accentuating the role of disease as a major driver of biodiversity loss. This may pose yet another challenge to the conservation of long-lived birds and mammals, which are already threatened by a number of anthropogenic factors (Rowe, 2008). In this context, a global-scale response is required. Diseases are rarely integrated into species conservation plans, despite their growing impact. Wildlife surveillance schemes should incorporate systematic testing and sequencing to anticipate outbreaks and detect mutations, especially in species previously affected by diseases. Applied demographic research should evaluate how disease impacts differ across population stages and age classes—this would help predicting demographic impacts and targeting the most affected stages with management action (e.g. Benhaïem et al., 2018). Further efforts in applied research should prioritize building a base of evidence to identify effective management strategies and promote their implementation. For example, recent studies suggest that the removal of

carcasses during HPAIV outbreaks was beneficial to limit the spread of the virus to other wild animals, pets and ultimately to humans (Campagna et al., 2024; Rijks et al., 2022). Lastly, we should not dismiss that global change is increasing the spillover of wildlife disease to humans. Therefore, anticipating and mitigating the effects of wildlife disease should not only be seen as a measure to protect biodiversity, but also to safeguard human societies.

AUTHOR CONTRIBUTIONS

Jaume A. Badia-Boher, Marc Kéry, Michael Schaub, Peter van Geneijgen and Martin Mollet conceived the main ideas of the study. Peter van Geneijgen, Martin Mollet and Henk P. van der Jeugd designed and performed field work and arranged the data. Jaume A. Badia-Boher performed the statistical analyses with support from Marc Kéry and Michael Schaub. Jaume A. Badia-Boher took the lead in writing the manuscript. Valentina Caliendo contributed towards introducing and discussing the epidemiological implications of the work. All authors provided critical feedback during manuscript elaboration and rounds of revision.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflict of interest.

DATA AVAILABILITY STATEMENT

The data and code that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.17571734> (Badia-Boher et al., 2025).

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SUPPORTING INFORMATION

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

Table S1. Yearly counts of breeding pairs, number of breeding pairs where reproduction was surveyed, and number of fledglings counted in surveyed pairs.

Figure S1. Diagram of the Peregrine falcon life cycle as modelled in the state-space population dynamics submodel of the Integrated Population Model.

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