The highly pathogenic H5N1 outbreak did not increase mortality rates of adult Atlantic Puffins (*Fratercula arctica*) in Newfoundland, Canada

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Running Head - HPAI H5N1 and Atlantic Puffin adult survival

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Introduction

Highly pathogenic avian influenza (HPAI) caused by the H5N1 subtype, clade 2.3.4.4b, has emerged as one of the most consequential wildlife health crises in recent decades (Xie *et al.* 2023, Peacock *et al.* 2025). Unlike earlier H5N1 strains that circulated primarily in poultry, this variant proved exceptionally well-adapted to wild birds: it achieved year-round circulation, infected a far broader range of species, and spread with unprecedented efficiency through wild bird communities (Klaassen & Wille 2023). Dispersing from its European epicentre along migratory flyways, the virus reached North America in late 2021, with the first confirmed detections on the continent occurring in Newfoundland and Labrador; in domestic poultry in November 2021 and in a Great Black-backed Gull (*Larus marinus*) in December of that year (Caliendo *et al.* 2022). High-density colonial seabirds proved among the most vulnerable taxa.

The most comprehensive assessment of the 2022 breeding-season outbreak in Newfoundland was carried out by McPhail *et al.* (2024), who documented an estimated 13,517 seabird mortalities attributed to HPAI between April and September, the second-highest provincial toll in Canada after Québec. Northern Gannets (*Morus bassanus*), Common Murres (*Uria aalge*), and Atlantic Puffins (*Fratercula arctica*) accounted for the largest share of casualties. For gannets, the impact was unambiguous: mass mortality events were confirmed at colonies across the Canadian range (Avery-Gomm *et al.* 2024), with severe losses among both adults and chicks (Lane *et al.* 2024, Careen *et al.* 2024). Common Murres were found dead in large numbers along coastlines and confirmed HPAI-positive, yet no mass mortality was documented at any of the 11 surveyed colonies (Avery-Gomm *et al.* 2024). Likewise, Atlantic Puffins showed no reported mass mortality events at colonies, but no systematic colony surveys were conducted during those years.

PCR-based surveillance confirmed widespread past HPAI H5N1 infection in Atlantic Puffins sampled in 2022 (Rahman *et al.* 2026), establishing that viral exposure had occurred even in the absence of observable mass mortality. Yet whether these infections translated into elevated adult mortality remained unknown. Here, we used capture-mark-recapture (CMR)

data from a colour-banded population of adult Atlantic Puffins to estimate apparent annual survival rates spanning the 2021–2022 and 2022–2023 intervals. We predicted that if the 2022 HPAI outbreak lead to measurably increased adult mortality, apparent survival rates to the colony in 2023 would be detectably lower than those observed in 2022.

Methods

Study species and study site

The Atlantic Puffin is a long-lived pelagic seabird of the family Alcidae, widely distributed across the North Atlantic (Lowther et al. 2020). Adults are highly philopatric, returning year after year to the same burrow, and generally begin breeding between four and six years of age (Harris 1983). With only one chick raised per breeding attempt and lifespans commonly exceeding 20 years, adult survival has not been consistently associated with population dynamics in this species (Miles et al. 2015), but seabird populations are highly sensitive to adult mortality in general (Cairns 1992).

Field data collection

We collected capture-recapture data for adult Atlantic Puffins at Great Island (47.1855°N, 52.8121°W) in the Witless Bay Ecological Reserve. The Atlantic Puffin colony in this reserve is the largest in North America, with an estimated 350,000 breeding pairs, and the second largest in the world after Vestmannaeyjar off the southern coast of Iceland (Hansen *et al.* 2011; Wilhelm *et al.*, 2015). A study plot of approximately 168 square metres (14 m × 12 m), encompassing an estimated maximum of 170 active burrows, was established as representative of the colony. To evaluate adult survival, we colour-banded 124 individuals across two breeding seasons (50 in 2021, 74 in 2022) and monitored their return in 2022 and 2023. Because Atlantic Puffins are prone to nest abandonment when disturbed during incubation (e.g., Carey 2009), adults were captured only after the chick had hatched. Individuals were extracted from their burrows by hand and carried to a banding station located a few metres away, where each bird was fitted with a unique combination of colour leg bands enabling individual identification in the field. Bands consisted of three Darvic plain colour bands custom-made by Avian ID (9.53 mm internal diameter × 7.93 mm height; colours: Black, White, Green, Grey, Red, Yellow, Dark Blue, and Light Blue) and a Canadian Wildlife Service stainless steel band with a unique identifier. In combination with procedures addressing other research questions (Morel *et al.* Under Review), handling time never exceeded seven minutes before birds were returned to their original burrows.

Resighting was conducted by two trained observers from a hide with an unobstructed view of the study plot. In 2022, over 85 hours of scan sampling were distributed among 34 sessions from 20 July to 9 August; in 2023, 210 hours of scan sampling were distributed among 53 sessions from 6 June to 7 August. When many birds were present, observers scanned the slope systematically from top to bottom and right to left; when few birds were visible, observers focused on and followed specific groups. Every observation session, an event was logged each time a new colour-banded individual was detected.

Analyses

Traditional CMR approaches involve marking individuals and recording their detection, or non-detection, at subsequent sampling occasions (Lebreton *et al.* 1992). This framework yields an estimate of detection probability: the probability that a known-alive individual is observed during a given sampling session. Accounting for detection probability then allows estimation of apparent survival. A key constraint, however, is that detection probability conflates two processes: the probability of being detected given presence, and the probability of being present in the sampling area in the first place. When temporary emigration, the transient absence of an individual from the sampling area, goes unaccounted for, apparent survival estimates may be biased low (Pollock 1982, Riecke *et al.* 2022). This bias is compounded when the number of sampling occasions is small, as absent individuals have limited opportunity to return and be detected.

Several approaches address this issue. Among the earliest is the robust design (Pollock 1982), in which multiple short sampling windows are nested within each primary occasion and the population can be assumed closed within those windows. When individual detection effort is intensive, such as repeated daily records, the robust design can be extended to treat detection as a continuous count: the number of times each individual was sighted during the occasion (Riecke *et al.* 2022). Under this framework, unseen individuals are treated as a mixture of those present but undetected by chance, and those genuinely absent from the sampling area. This distribution is modelled as a zero-inflated Poisson process, with the binary component capturing the probability of being available for detection (Riecke *et al.* 2022).

We implemented the state-space formulation of the Cormack-Jolly-Seber (CJS) model, in which the observed detection state (detected or not) informs the underlying true state (alive or dead, z) at each sampling occasion (Kéry & Schaub 2011). The model was

extended to include a second latent state variable (a), representing the probability of being available for detection during each occasion (Riecke *et al.* 2022). Estimated parameters are: apparent survival (ϕ, modelled with a Beta distribution), the probability of transitioning between available and unavailable states (γ, Beta distribution), and the mean number of detections per occasion conditional on being available (ε, Poisson distribution). As in standard CMR models, these parameters can be allowed to vary over time or with covariates; γ can additionally be modelled as a Markovian process in which the previous availability state influences subsequent state transition probabilities. A further advantage of the state-space formulation is the ease with which additional parameters can be incorporated. Because individuals vary in detection probability — due to differences in behaviour, visibility, or distance from observation posts — we added an individual-level random effect (h), modelled as a gamma distribution with equal shape and rate parameters (θ, giving a mean of 1). Lower values of θ produce greater overdispersion in individual detection counts.

Models were fitted using the jagsUI package (Kellner 2015) in R v4.3.1 (R Core Team 2026), interfacing with JAGS (Plummer 2003). Following Riecke *et al.* (2022), three MCMC chains were run with a thinning rate of 10, a burn-in of 10,000 samples, and 50,000 post-burn-in iterations per chain. Priors also followed Riecke *et al.* (2022): flat Beta(1,1) distributions for all probability parameters (ϕ and γ), a Uniform(0, 250) prior for θ, and a Gamma(1, 0.1) prior for ε. We compared models with different parameterisations of ϕ, γ, and θ using the Deviance Information Criterion (DIC; Spiegelhalter et al 2014), selecting the model with the lowest value. Given the small number of sampling occasions (three years), we fitted a targeted set of candidate models to test whether ϕ and θ varied across the two intervals, and whether γ followed a Markovian process in which prior availability state influenced subsequent transition probabilities. We constrained ε to vary across years, as not doing so confounded annual variation in detection frequency with the individual heterogeneity captured by θ. All estimates are reported as means (SD, 95% credible interval) from the posterior distribution.

Results

All models converged readily within 50,000 iterations, with well-mixed chains, $\hat{R}$ values well below 1.1, and high effective sample sizes. The best-supported model included constant ϕ and θ across years, and a single γ parameter, indicating that the probability of transitioning between availability states was independent of the prior state (Table 1). Both annual apparent

survival and availability for detection were high and did not detectably vary between intervals: ϕ = 0.97 (SD = 0.02, 95% Credible Interval - CI: 0.93–0.99) and availability = 0.96 (SD = 0.02, 95% CI: 0.91–0.99), respectively. As expected given the substantially greater sampling effort in 2023, the mean number of sightings per individual (ε) was higher in 2023 (11.0, SD = 0.7, 95 % CI: 9.8–11.5) than in 2022 (5.1, SD = 0.5, 95 % CI: 4.2–6.3). The individual heterogeneity parameter θ was estimated at 3.0 (SD = 0.5, 95 % CI: 2.1–4.2), reflecting substantial variation among individuals in detection frequency; this corresponds to detection rates ranging from approximately 0.20× to 2.5× the mean at the 2.5th and 97.5th percentiles.

Discussion

Using a rigorous CMR framework, we found no evidence that the 2022 HPAI H5N1 outbreak increased adult mortality in Atlantic Puffins at Witless Bay Ecological Reserve. Annual apparent survival was high and constant across both intervals examined (ϕ = 0.97), providing the first mark-based estimate of adult survival in this species through the panzootic. This result stands in contrast to assessments based on carcass counts and colony surveys, which attributed 282 Atlantic Puffin deaths to HPAI on the island of Newfoundland in 2022 (McPhail *et al.* 2024). Carcass-based mortality estimates are subject to well-documented detection biases: seabirds dying at sea rarely strand on shore, decomposition and oceanographic dispersal further reduce recovery probability, and the absence of pre-outbreak baseline counts complicates attribution. Our data suggest that, at Witless Bay at least, these carcass detections did not reflect measurable population-level mortality in the adult breeding cohort.

The contrast between the impact of HPAI H5N1 on Atlantic Puffins and Northern Gannets is clear. Gannets suffered confirmed mass mortality and near-complete reproductive failure across Newfoundland and the broader North Atlantic in 2022 (Lane *et al.* 2024, Careen *et al.* 2024), Puffins did not. Differences in nesting ecology is certainly a possible reason why this was the case. Gannets have open-nests and breed at extreme densities (Mowbray 2020), conditions that facilitate rapid within-colony contact and efficient virus transmission. Atlantic Puffins, by contrast, nest in individual burrows distributed across the colony (Lowther *et al.* 2020); while foraging aggregations bring birds from across the colony into close contact, burrow nesting may reduce direct transmission rates at the breeding site itself. Consistent with this, serological studies of co-occurring seabird assemblages in European colonies show that auk species — including puffins — display intermediate levels

of prior AIV exposure relative to surface-nesting gulls and kittiwakes (Greco *et al.* 2025). At the Isle of May, Scotland, approximately one-third of apparently healthy Atlantic Puffins sampled in 2023 showed antibodies indicative of prior AIV infection, suggesting that a substantial fraction of birds had survived HPAI exposure without apparent demographic consequence (Greco *et al.* 2025). This pattern broadly parallels the picture in Newfoundland, where PCR surveillance confirmed past H5N1 infection in puffins at Gull Island in 2022 (Rahman *et al.* 2026); widespread evidence of exposure, but without the lethal outcomes documented in gannets.

Several caveats apply. Our study plot is a small, defined area within one of the largest puffin colonies in the world. While we assumed that it is representative of the population, broader geographical coverage would be favourable albeit logistically very challenging. The three-year study window provides limited statistical power to detect subtle or transient changes in survival, even though the best-supported model showed no temporal variation in ϕ. Furthermore, our analysis addresses adult mortality only; sublethal effects of HPAI, including impaired body condition, reduced breeding success, or elevated chick mortality, could influence population dynamics independently of adult survival and warrant dedicated investigation. Anecdotally, the chick productivity in Witless Bay Ecological Reserve has been very low since 2022 (pers. observ.).

Our results offer a cautiously optimistic picture of adult survival in Atlantic Puffins through the 2022 outbreak at Witless Bay. However, ongoing HPAI H5N1 circulation across the North Atlantic, and the prospect of renewed introductions from European and Arctic breeding populations, means that the threat to this Vulnerable species (in North America) has not passed. Carcass-based reporting, while essential for detecting outbreak events, is an imperfect tool for quantifying demographic impact in seabirds with predominantly at-sea mortality (Harvey *et al.* 2026). Long-term CMR programmes at key Atlantic Puffin colonies across the western North Atlantic represent the most rigorous means of detecting future changes in adult survival and providing the demographic data needed for evidence-based population management.

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Table 1. Capture-Mark-Recapture model selection results for Atlantic Puffins marked in Newfoundland, Canada from 2021-2023. Modeled parameters included apparent survival (ϕ, constant or annual variation (*time*)), the probability of transitioning between available and unavailable states (γ, Markovian or independent), and an individual-level random effect, modelled as a gamma distribution with equal shape and rate parameters (θ, constant or annual variation (*time*)). The mean number of detections per occasion conditional on being available (ε) was constrained to be different across the 2 years. DIC values for all candidate models differing in parameterisations of ϕ, γ, and θ. Best-supported model shown in bold (lowest DIC).

ϕ	γ	θ	**DIC**	**deviance**
·	Markovian	·	1023.44	817.52
·	**·**	**·**	**1022.45**	**817.13**
·	Markovian	time	1031.03	818.63
time	Markovian	time	1033.68	820.15