The demographic role and drivers of crash mortality in nesting seabirds

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Submitted to Swansea University in fulfilment of the requirements for the Degree of MRes - *Ecosystems and Biodiversity*

December 2025

Abstract

Recent research suggests that animals adjust their space-use to minimise their chance of accidents, such as slips or collisions. The consequences of such accidents should be particularly severe in flying animals, but examples of collisions in natural scenarios remain rare. Regular crashes have been documented in a population of northern gannets breeding on Ailsa Craig. In this study I use a dataset of crashes recorded each month over three consecutive years, along with reanalysis data, to investigate the environmental drivers of gannet crashes and assess their demographic consequences. I combined statistical and demographic approaches to address three questions: (1) can environmental factors predict crash events, (2) what are the consequences of crash mortality for population growth rates, and (3) how might shifting wind regimes influence long-term population trajectories? Quasibinomial generalized linear models were used to test environmental predictors of crash events, while matrix population models were used to project population dynamics. Outputs from statistical models were integrated into matrix population models by adjusting adult survival transitions. Wind direction emerged as the sole significant predictor of crashes, with the probability of crashes increasing in north-westerly winds and decreasing with south-easterlies. Crash mortality accounted for 5.4% of annual adult mortality. Removing this mortality led to increases in projected population sizes of 11.3% and 23.9% over 25 and 50 years, respectively. Incorporating wind-driven crash probabilities into demographic models revealed the full envelope of population responses that would be possible under changing wind regimes. These findings identify accident mortality as a novel, demographic, non-anthropogenic pressure in a long-lived seabird. Shifting wind regimes may influence seabird populations by altering habitat suitability and modifying the landscape of risk around colonies, thereby broadening our understanding of how environmental variability shapes avian population dynamics.

Keywords: seabird demography, landscape of risk, matrix population models, wind regimes

University declarations and statements

This work has not previously been accepted in substance for any degree and is not being concurrently submitted in candidature for any degree.

Signed: [redacted]

Date: 23/09/25

This thesis is the result of my own investigations, except where otherwise stated. Other sources are acknowledged by footnotes giving explicit references. bibliography is appended.

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I hereby give consent for my thesis, if accepted, to be available for electronic sharing.

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The University's ethical procedures have been followed and, where appropriate, that ethical approval has been granted.

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Statement of contributions

Contribution	Persons involved
Conceptualisation	ES, JB, SB
Data curation	ES, JB, SB, SW
Formal analysis	ES, JB, SB
Investigation	SB
Methodology	ES, JB, SB
Project administration	ES, JB, SB
Resources	ES, JB
Supervision	ES, JB
Validation	ES, JB, JS, SW
Visualisation	SB
Writing – original draft preparation	SB
Writing – review and editing	ES, JB, SB

ES – Professor Emily Shepard

JB – Professor Jim Bull

JS – Dr Janine Schoombie

SB – Stefan Barnett

SW – Professor Sarah Wanless

Statement of Expenditure

Category	Description	Item	Cost (£)
Reference material	Book	The Gannet, Bryan Nelson	54.00
Total			54.00

Contents

Abbreviations

BTO – British trust for ornithology

GHA – Grey-headed albatross

HPAI – Highly pathogenic avian influenza

MPMs – Matrix population models

SMP – Seabird monitoring program

GLM – Generalized linear model

Acknowledgements

I feel extremely lucky to have had the opportunity to work with my supervisors, Professor Jim Bull and Professor Emily Shepard. I am especially grateful for their constant support, guidance, and for always finding the time to answer my questions. Their insight and encouragement have not only shaped this project but have also inspired me as a researcher.

I would also like to thank Professor Sarah Wanless and Dr Janine Schoombie for their support and guidance throughout this project.

Finally, I would like to thank the SpacePop group and the SLAM lab for creating such a friendly and supportive environment. The discussions and feedback made this project a far more enjoyable and enriching experience.

Introduction

Risk is a well-established currency in ecology, with the risk of predation impacting animal physiology (Sheriff and Thaler 2014), decisions (Hebblewhite and Merrill 2007) and space-use (Dellinger et al. 2019). Accidents represent another source of risk, defined as a momentary loss of control that can result in injury or mortality. Such accidents may increase an animal's vulnerability to predation, and some species actively modify their behaviour to avoid them. For example, in Yellowstone national park, elk (*Cervus canadensis*) avoid terrain features that could hinder escape from predators, such as wood piles and steep gullies, which pose a higher risk of accidents (Ripple and Beschta 2003). In less commonly studied scenarios, risk can also cause mortality in the absence of predation. For example, wild antechinus (*Antechinus mysticus*) modulate their speed whilst foraging to avoid accidents (Wheatley et al. 2018). Wheatley et al. (2021), have developed a framework for how this could affect animal ecology, but examples of fatal accidents in absence of predation remain rare.

Flying species should be at risk from accidents, particularly when operating close to ground. Flight control in a variety of scenarios from migration, foraging and predator evasion is clearly important for most avian species (Alerstam 1991; Hedenström and Rosén 2001; Pelletier et al. 2007). Flight is fast, typically between 5 and 20 m/s (Hedenström 2002; Tobalske et al. 2003), making even split second losses of flight control potentially catastrophic especially when operating close to solid surfaces. Environmental factors, such as gusts, represent a particular threat when flying close to solid surfaces, because a momentary loss of flight control could lead to an increased chance of collision and hence injury and even death (Schoombie et al. 2023; Shepard et al. 2016). Additionally, landings and take-offs can be some of the riskiest behaviours and occur closest to the ground. Drawing a parallel from aviation, a review by Boeing showed that 61% of fatal aircraft accidents occur during take-off or landing (Boeing Company 2017). Animals must therefore control their deceleration forces at the point of touchdown (KleinHeerenbrink et al. 2022). This explains why animals use headwinds to reduce their groundspeed when they come into land. It is also thought to explain why auks make multiple landing attempts in challenging condition (Shepard et al.

2019). However, mortality or injury caused by accidents in avian species is tricky to quantify and has rarely been studied.

Two studies suggest that accidents can cause substantial and repeated mortality in a population of wild flying species. In a colony of grey-headed albatross (*Thalassarche chrysostoma*) (GHA), Schoombie et al. (2023) found an average of >100 carcasses a year for almost 4 years, with many showing signs of injury consistent with collisions. Carcasses were concentrated in an area close to the breeding ridge where a down-draft occurs in the dominant wind direction, however, the study did not test whether crash frequency was predicted by wind speed or direction. Wanless (1979), also presented evidence of regular fatalities from crashes in northern gannets (*Morus bassanus*) (hereafter, “gannets”) breeding on Ailsa Craig in Scotland. This dataset provides the opportunity to examine both the environmental drivers of crashes and their demographic consequences.

Gannet are large, long-lived seabirds that breed on islands across the North Atlantic, ranging from northern France and the British Isles to Iceland and eastern Canada (Birdlife International 2018; Maestri et al. 2017). Gannet breeding occurs during the boreal summer, though birds generally arrive from February and may remain until November. The exact timing varies among colonies with Ailsa Craig birds typically arriving in February and departing by mid-October (Nelson 2010). Gannets have a wingspan around 1.8m with a high aspect ratio, making them vulnerable to turbulent eddies and fine scale wind perturbations (Birdlife International 2018; Thorne et al. 2023). They typically reach sexual maturity at four to five years of age, after which they exhibit high adult survival (Wanless et al. 2006; Wood et al. 2021; Wooller et al. 1992). Juveniles usually remain at sea during their early life stages, returning to colonies only as they approach recruitment age (Wanless et al. 2006; Wooller et al. 1992). Survival increases steadily with age, from 0.420 in the second year to 0.910 by the fourth, approaching adult levels (Wanless et al. 2006). These high survival rates support extended lifespans, with some individuals reaching at least 37 years, based on long-term ringing data (British Trust for Ornithology, 2010). Like all long-lived organisms, gannets are projected to be particularly sensitive to changes in adult mortality.

This study used data from Ailsa Craig, a small island in the outer Firth of Clyde approximately 10 miles off the coast of Ayrshire, Scotland (55.254° N, 5.121° W) (figure 1). The island is home a breeding colony of gannets containing approximately 15% of Scottish gannets (BirdLife International 2025). Although the colony is not the largest or most well studied, its topography lends itself to recording gannet crashes below the colony, which is distributed along the west-facing slopes (no gannets nest on the eastern side of the island, figure 1). Most nests are found on steep cliffs above talus slopes. In the 1970s, carcasses were observed at the base of the colonies with injuries such as, broken wings, beaks and necks consistent with uncontrolled collisions with the ground. Systematic counts of gannet carcasses on these talus slopes were undertaken. It was found that most of these carcasses were adults (Wanless 1979). The availability of reanalysis models, which can estimate conditions in the past as well as forecasting conditions in the future, enabled me to explore the environmental drivers behind this crash-induced mortality. As carcasses were mainly adults (343 out of 367), I hypothesised that these adult crashes may have a tangible impact on the population.

The drivers of crashes at Ailsa Craig have yet to be investigated. I hypothesised that this could be related to environmental conditions, including wind, as large seabirds appear to be clumsy when landing in low wind speeds, with records of albatrosses sustaining fatal injuries when landing in low winds (Cone 1964). It is also possible that the likelihood of collisions could increase in conditions with poor visibility i.e. in sea fog, which has been linked to grounding in shearwater (Syposz et al. 2018). The risk of crashes could also vary with the number of landings, which changes through the season with chick-provisioning routines (Harding et al. 2007; Rishworth and Pistorius 2015). Alternatively, the probability of birds crashing could be influenced by biological factors, such as the effect of crowding at the colony (Schippers et al. 2011).

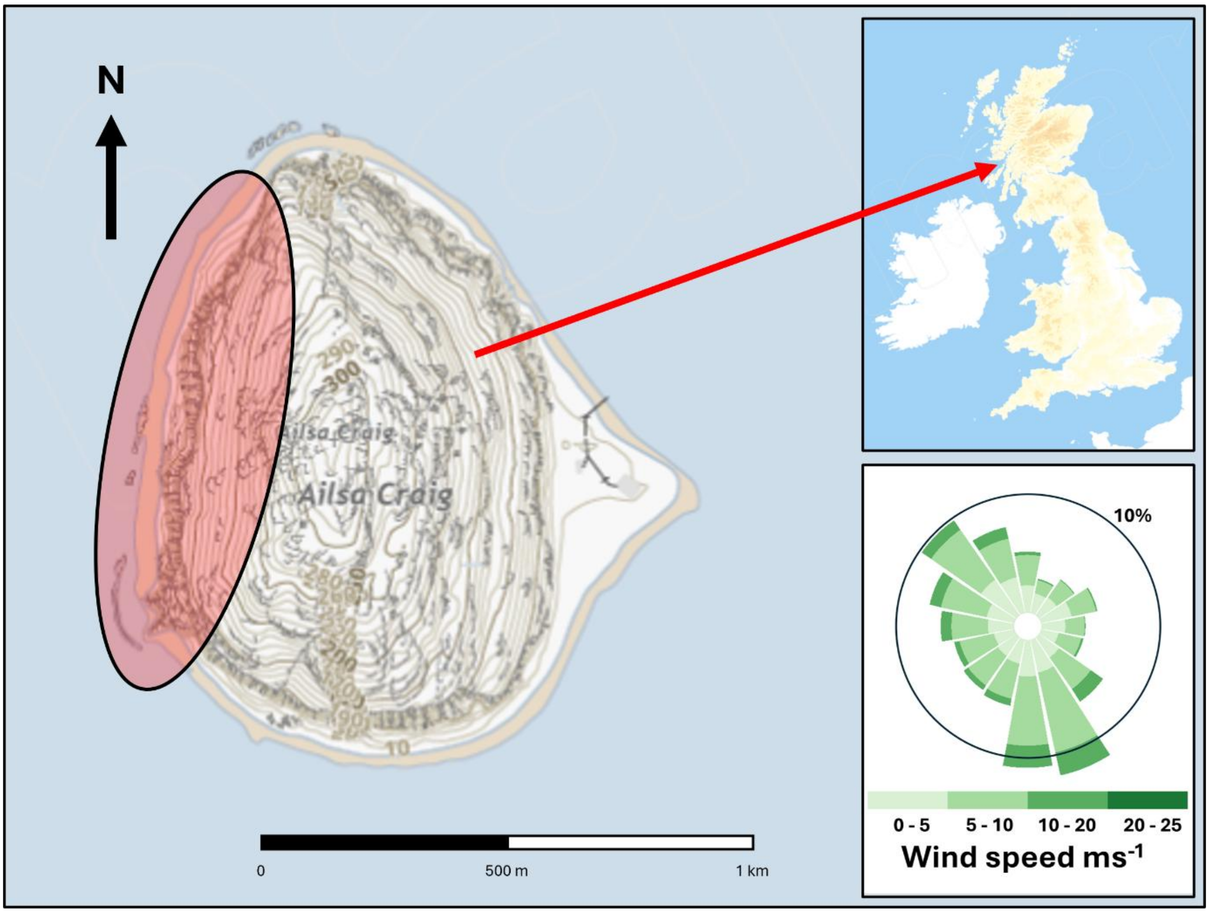


Figure 1. *Map of Ailsa Craig, outer Firth of Clyde, Ayrshire, Scotland (55.254° N, 5.121° W). Gannet colonies on Ailsa Craig all fall within the area highlighted in red on the west coast of the island. All carcasses were collected beneath these cliffs* (Wanless 1979). *Inset (top right), map of the UK with a red arrow showing Ailsa Craigs location. Additional inset (bottom right), containing a wind rose gained from ERA5 reanalysis data (see methods) showing two prevailing wind directions. Each petal represents the frequency of winds blowing from each compass direction, with colour intensity indicating wind speed categories. Data visualisation created using the openair package in R (Carslaw and Ropkins 2012).*

In this study, I investigated whether environmental factors influence individual crash risk in gannets at Ailsa Craig and whether this, in turn, could impact population growth rates, both under current and future environmental conditions. This was addressed through three objectives, (1) investigate whether crash events in northern gannets could be predicted by environmental factors at Ailsa Craig, using statistical models to assess the role of wind direction and magnitude and the frequency of foggy conditions. Then, to (2) quantify the impact of crash mortality on the population growth rate of gannets at Ailsa Craig. As gannets are long-lived species with extremely high adult survival, I predicted that even a small number of adult crashes could have a significant effect on the population (Maestri et al. 2017; Spencer and Janzen 2010). I examined the demographic effects of crashes on the Ailsa Craig gannet population with matrix population models (MPMs), a common ecological tool that projects population trajectories from stage-specific survival transitions to estimate exponential growth rates (Logofet 2002). Finally, (3) integrating outputs from the statistical models with the MPMs, I explored how shifts in prevailing wind direction could influence gannet population trajectories. The outcomes of these objectives provide insight into the relationship between the environment and crash risk; how crash risk might be influencing population demographics and how wind direction impacts population trajectories.

Methods

Carcass data

Carcass data from Ailsa Craig were sourced from Wanless (1979), based on monthly surveys conducted between February and October from 1974 to 1976. Surveys were conducted along the talus slopes that lie underneath many of the of the breeding cliffs on the south-western side of the island (Wanless 1979) (table 1; figure 1). Carcasses were aged as adult or juvenile based on plumage. Most showed signs of traumatic injury, such as broken wings, necks, or beaks, as well as internal haemorrhaging suggesting collision as the cause of death. Carcass numbers were used in objective 1, where they were modelled in relation to environmental conditions and objective 2, where they were used to assess the demographic consequences of removing crash-based mortality.

Table 1. *Carcass count data used in MPMs to adjust transition probabilities as well as statistical models. Collected at the base of Ailsa craig (Wanless 1979).*

Year	Age Class	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Totals
1974	**Ad.**	0	14	9	7	16	26	23	13	0	108
	Imm.	0	0	0	0	0	2	2	1	0	5
1975	**Ad.**	0	5	22	17	20	28	21	19	0	132
	Imm.	0	0	1	0	7	4	1	2	0	15
1976	**Ad.**	9	10	17	13	14	18	25	20	1	127
	Imm.	0	0	0	0	2	1	1	0	0	4
Totals	**Ad.**	9	29	48	37	50	72	69	52	1	367
	Imm.	0	0	1	0	9	7	4	3	0	24

Statistical modelling of crash probability

To evaluate if environmental conditions were impacting gannet crashes at Ailsa Craig (objective 1), I obtained wind estimates from ERA5, a weather reanalysis tool that allows both forecasting and back-casting of wind conditions. Wind data were extracted for a 0.25° × 0.25° grid cell centred on the breeding colony (55.254° N, 5.121° W) (Hersbach et al. 2023). As carcass counts were conducted monthly, I aggregated wind speed and direction data to monthly proportions, capturing the percentage of time wind fell into each category per month. I also included the number of days with sea fog. Finally, I took monthly total number of gannets at Ailsa Craig from Wanless (1979).

Statistical models were constructed and visualised using R v4.4.1 (R Core Team 2024). I used the packages ggplot2 and visreg (Breheny and Burchett 2017) for visualising results. The response variable was binary, with 0 indicating a bird that did not crash and 1 indicating a bird that did. Accordingly, binomial GLMs were initially applied. Post-hoc diagnostic tests revealed evidence of overdispersion in the data. Therefore, final models used a quasibinomial error distribution. To normalise crashes by colony size, I calculated a monthly crash probability as the number of crashes divided by the number of birds at the colony.

I excluded October from the statistical analysis as while surveys were conducted from February to October, October bird counts were consistently low, with a mean of 5,200 across all years (figure S2) (Wanless 1979). Additionally, gannets may be completely gone from colonies by early to mid October depending on the year (Nelson 2010). Whilst the use of crashes per bird at the colony adjusts for low bird counts, including months when birds leave the colony early would introduce error in the model as the proportion of wind speeds and direction is estimated per month.

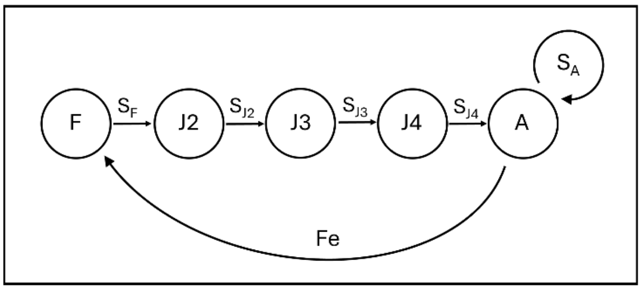
I conducted preliminary analyses to examine whether wind speed influenced crash mortality. To address the mismatch between monthly carcass counts and hourly wind estimates I grouped hourly wind speeds into five categories (0–2, 2–4, 4–6, 6–8, and >8 m s^{-1}), providing the number of hours each month that fell within each wind class. These categories were included as predictors in models of monthly crash probability, but wind speed was not statistically significant. Based on this result, I focussed only on the two extremes of wind conditions in subsequent analysis, calm (<2 ms^{-1}) and high (>8 ms^{-1}). This tested for potential effects of unusually low or high wind speeds on crash probability.

Initially, I classified wind direction into eight ordinal compass directions (N, NE, E, SE, S, SW, W, NW). I tested the proportion of observations in each direction within a given month in relation to crash probability. North westerly and south easterly winds emerged as the most influential directions. These were also the modal wind directions during the study period (figure 1). Following this, I categorised wind direction into two broad directional bins in the final analysis: northwest (NW) and southeast (SE) the mid point of each bin, each encompassing 180°. I ruled out collinearity with wind direction, fog, bird count and wind speed, by testing them against each other using the ggpairs in the GGally package (Schloerke et al. 2025).

Northern gannet matrix population model construction

Northern gannets are long-lived seabirds that typically recruit in their fifth summer. I therefore divided their life cycle into five stages: Fledgling (1st year), juvenile 2nd year, juvenile 3rd year, juvenile 4th year, and adult. I incorporated this age-structured framework into MPMs (Figure 2). I constructed and visualised all MPMs in R v4.4.1 (R Core Team 2024). I used the tidyr (Wickham, Vaughan, et al. 2025) and dplyr (Wickham, François, et al. 2025) packages for matrix construction, while popbio (Stubben and Milligan 2007) and ggplot2 (Wickham 2016) were used for time series visualisation.

(a)



(b)

$$X=\left(\begin{array}{cccccc} & \mathbf{F} & \mathbf{J2} & \mathbf{J3} & \mathbf{J4} & \mathbf{A} \\ \mathbf{F} & 0 & 0 & 0 & 0 & Fe \\ \mathbf{J2} & S_F & 0 & 0 & 0 & 0 \\ \mathbf{J3} & 0 & S_{J2} & 0 & 0 & 0 \\ \mathbf{J4} & 0 & 0 & S_{J3} & 0 & 0 \\ \mathbf{A} & 0 & 0 & 0 & S_{J4} & S_A \end{array}\right)$$

Figure 2. *(a) A simplified diagram of the six stage Leslie style matrix population model (MPM) used where, F = fledgling, J2-J4 = juvenile in their 2nd to 4th year respectively and A = adult. Arrows pointing right indicate a life stage transition.* S_C *= chick survival probability,* S_F *= fledgling survival probability,* $S_{J2} – S_{J4}$ *= 2nd to 4th year juvenile survival probability and* S_A *= adult survival probability. Fe = adult fecundity. (b) Generic MPM matrix (X) with transition probabilities (S) of fledglings (F), Juveniles 2-4 (J2-4) and adults (A). Fecundity is represented as Fe in the top right of the matrix.*

I obtained life stage transition rates for gannets from Wanless et al. (2006), who estimated them using ring recovery data, analysed with multinomial stochastic models (White and Burnham 1999). The dataset included recoveries from 44,582 chicks ringed between 1959 and 2002 across 10 of the 19 UK gannet colonies and 1,445 adult gannets ringed at three major colonies. Bass Rock, the UK's largest gannet colony, showed significantly different transition rates compared to all other colonies and was therefore treated separately. Since the present analysis focuses on Ailsa Craig, I took transition rates from the 'other colonies' category, of which Ailsa Craig made up the greatest proportion (Table 2).

Table 2. *Survival probabilities and 95 % confidence intervals calculated by Wanless et al. (2006) for northern gannets in the UK between 1959 and 2002.*

Age class	All colonies	Bass Rock	Other colonies
1st year	0.424 (0.410–0.439)	0.542 (0.516–0.567)	0.420 (0.394–0.445)
2nd year	0.829 (0.821–0.836)	0.779 (0.765–0.793)	0.852 (0.842–0.861)
3rd year	0.891 (0.886–0.896)	0.859 (0.848–0.869)	0.908 (0.901–0.915)
4th year	0.895 (0.889–0.900)	0.863 (0.852–0.874)	0.910 (0.903–0.917)
Adult	0.919 (0.915–0.922)	0.916 (0.910–0.922)	0.922 (0.916-0.927)

Fecundity refers to the reproductive output of individuals or populations, often measured as the number of offspring produced per individual (Bradshaw and McMahon 2008). In this analysis, I defined fecundity as the transition from adult to fledgling, representing the successful production of a fledgling by a breeding female. Gannet hatching success was estimated at 0.817 based on Wanless et al. (2006). I followed the MPM convention of halving this value to reflect only the female contribution, as gannets lay a single egg per breeding season and show no sex bias (Birdlife International 2018). I used the resulting fecundity value of 0.4085 as the adult-to-chick transition term in the MPMs. I later multiplied with the chick to fledgling transition probability. Although some individuals may breed before their fifth year (Nelson 1966), no quantitative estimates of early fecundity were available. Furthermore, sensitivity analyses indicated that including low-probability early breeding transitions had negligible effects on overall population growth. These transitions were therefore excluded from adjustment in the MPMs.

I took the probability of a chick successfully fledging as 0.737, based on estimates from Wanless and Harris (2003) and consistent with Wanless et al. (2006). I then multiplied this value with fecundity to give an accurate representation of the probability of a female gannet producing a successful fledgling. Although this transition occurs over several months within the breeding season, I treated it as a discrete annual stage to maintain consistency with the age-structured MPM framework. This simplification captures key biological timing, while allowing for integration of crash mortality in the MPM framework, and ultimately enabling me to adjust the fecundity in response to environmental conditions.

Census data

To test how similar MPM projections were to the actual population trajectory at Ailsa Craig, I obtained census data from the seabird monitoring program (SMP) and British trust for ornithology (BTO) for the period 1970 – 2023. Surveys were conducted yearly from 1970 – 1985 and then around once every 10 years from 1985 - present (BTO 2024). I fitted a negative binomial model to these data to obtain an estimated growth rate.

Incorporating crash-induced mortality into matrix population models

To test hypotheses on the role of crashes in gannet population dynamics, I used MPMs. MPM transitions can be adjusted to reflect environmental pressures when carcasses or affected individuals are counted and accurately aged, allowing the proportion of mortality attributable to a given pressure to be quantified and incorporated into the model (Romanov and Masterov 2020). In this study, I used carcass count data from Wanless (1979) to estimate crash-related mortality, with adjustments applied to adult and chick-to-fledgling survival transitions. This created a hypothetical 'no-crash' scenario by calculating the proportion of annual mortality represented by crashed carcasses and removing this proportion from the relevant survival transitions. To investigate the environmental drivers of crash probability, I used quasibinomial models, and I integrated outputs showing significant effects into MPMs by adjusting transition rates according to the fitted relationships. This approach allowed me to evaluate both the direct demographic impact of crashes and the potential influence of shifting environmental drivers on crash-related mortality.

Wanless (1979), reported that most carcasses found at the base of the colony were adults. Across the three-year study period, only 24 out of 367 carcasses were classified as immature, averaging just eight individuals per year. Moreover, immature birds could not be reliably assigned to specific life stages (i.e. fledgling through fourth-year juvenile) due to uncertainty in gannet plumage and ageing. Given the low frequency of immature carcasses and the disproportionate influence of adult survival on population growth in long-lived species (Maestri et al. 2017; Romanov and Masterov 2020; Spencer and Janzen 2010), a pattern supported by sensitivity analyses, I did not adjust the juvenile survival transitions.

I adjusted the chick-to-fledgling transition under the assumption that if one parent died, the chick would fail. I then used this to adjust the adult to chick transition (0.4085) by multiplying them together. Northern gannets exhibit obligate biparental care, with both adults required for successful incubation, provisioning, and chick protection throughout the breeding season (Wojczulanis-Jakubas et al. 2018). The loss of a single parent typically results in nest failure due to starvation or exposure (Botha and Pistorius 2018). Because the timing of crashes relative to the breeding period could not be determined, and parent specific crash rates were unavailable, I assumed the full 5.4% annual crash mortality affected chick rearing.

Incorporating stochastic variability into matrix population model projections

To improve the robustness of MPM projections, I incorporated stochastic variance into both the survey population and ‘no crash’ scenarios. I used Beta distributions to simulate variability as survival probabilities are bounded between 0 and 1. For the survey population projection, I used confidence intervals for gannet survival rates reported in Wanless et al. (Wanless et al. 2006) to derive shape parameters for a beta distribution using beta distribution equation (Johnson et al. 1995). Then, I used these parameters to simulate 1000 iterations of survival transitions in R studio, generating confidence ribbons around the survey population trajectory.

For the population projection under the ‘no crash’ scenario, I calculated confidence intervals from mean carcass counts reported over three years (Wanless 1979). I converted these to shape parameters for a beta distribution using the equations for beta distribution. I used simulated values to increase chick and adult survival 1000 times, with each combination run through the MPMs.

Integrating wind-driven crash risk into matrix population models

Wind was the main predictor of crash rate (see Results). I integrated coefficients from the quasibinomial GLM with the MPMs to investigate how different wind conditions could influence population growth rates. I calculated the probability of crashing for a range of NW:SE wind proportions, using the equation for the GLM. I compounded monthly crash probabilities across the 8 months when gannets were present at the colony to obtain yearly probabilities. I calculated this as one minus the probability of no crash occurring raised to the eighth power. I aligned these values with the mean NW:SE wind proportion between 1974 and 2024, the annual survival estimate (0.922) was at a NW:SE wind proportion of 0.56. A complete equation for this calculation is shown in Equation 1. This produced wind adjusted annual survival rates, centred around the observed survival and mean wind direction proportion, which I used to modify transition probabilities in the MPMs (Table S1).

$$s_{\mathrm{adj}}(NW) = s_{\mathrm{base}} \cdot \frac{\left(1 - \frac{e^{\beta_0 + \beta_1 NW}}{1 + e^{\beta_0 + \beta_1 NW}}\right)^8}{\left(1 - \frac{e^{\beta_0 + \beta_1 NW_{ref}}}{1 + e^{\beta_0 + \beta_1 NW_{ref}}}\right)^8}$$

Equation 1. *formula used to adjust chick fledging transition probability where:* $s_{adj}(NW)$*= wind-adjusted annual adult survival at wind proportion NW,* s_{base} *= survey population annual adult survival (fixed at 0.922 when NW = 0.56),* β_0 *and* β_1*= intercept and slope from the quasibinomial generalised linear model,* NW *= proportions of wind from the 180° NW direction,* NW_{ref} *= the mean NW proportion since 1974 (0.56) and* $(1 - p_{\mathrm{crash}})^8$*= the annual survival across 8 breeding months, where* p_{crash} *is crash probability.*

To adjust chick fledging probability, I assumed that chicks only survive to fledge if both parents survive the breeding season (Nelson 1966). For each year, I calculated the probability that both parents survive as the square of adult annual survival (s^2). As before, I rescaled this survival probability relative to the mean NW:SE wind proportion between 1974 and 2024 (0.56). I used the relative scaling factor to adjust the survey population fledging probability from the unmodified MPMs ($p_{\text{fledge, base}} = 0.737$), which yielded an adjusted fledging transition probability that incorporates wind-driven parental crashes. A complete equation for this calculation is shown in Equation 2 (Table S2).

$$f_{adj}(NW) = p_{fledge,base}\left(\frac{s_{adult}(NW)}{s_{adult}\left(NW_{ref}\right)}\right)^2$$

Equation 2. *formula used to adjust chick fledging transition probability. Where:* $f_{adj}(NW)$ *= adjusted chick fledging transition at wind condition NW,* $p_{fledge,\ base}$ *= Survey population fledging probability from the unmodified MPMs (0.737),* $s_{adult}(NW)$ *= adult annual survival under wind condition NW (from quasibinomial generalised linear model) and* NW_{ref} *= adult annual survival at the reference NW proportion (0.56). The exponent 2 reflects the assumption that both parents must survive.*

Analysis of wind regimes at Ailsa Craig

To assess long-term wind trends at the gannet colony on Ailsa Craig, I obtained historical ERA5 reanalysis data spanning 1974 to 2025. I derived hourly wind speed and direction from the zonal (u) and meridional (v) wind components provided by the ERA5 global dataset at the colony's geographic coordinates (Hersbach et al. 2023). As before, I categorised wind direction into two broad directional bins, northwest (NW) and southeast (SE), each encompassing 180°. I used linear models to test for temporal trends in the proportion of wind originating from each direction over the study period. Additionally, I assessed interannual variation in wind direction proportions using one-way ANOVA followed by post-hoc Tukey tests,

Results

Effects of crash mortality on population growth rates

I constructed survey population MPMs using data from Wanless (1979), shown in table 1. Results from the survey population MPMs indicate that the gannet population on Ailsa Craig was experiencing steady growth, with a dominant eigenvalue (λ) estimated at 1.008 (Figure 3). I used census data from Ailsa Craig to calculate an estimated 'true' population growth rate (λ) from a negative binomial GLM. This was calculated as 1.020 (1.015-1.025 95% CIs) (Figure 3).

I modelled a 'no crash' scenario where adult and chick-to-fledgling (fecundity) survival transitions were modified. Adult Crashes at the base of the colony accounted for an estimated 5.4% of annual adult mortality. I used this to adjust the adult survival transition, increasing it from 0.922 to 0.926. I used this value to adjust the chick-to-fledgling transition from 0.737 to 0.752 (Table 3).This carried through to change fecundity from 0.301 to 0.307.

Table 3. *Summary of transition probabilities used in matrix population models (MPMs) for gannets at Ailsa Craig. Including adjusted transitions based on carcass counts found at Ailsa Craig between 1994 and 1996 (Wanless 1979).*

Transition	Transition Probabilities	
	Survey population	'No Crash' Scenario
Fledgling – Y2 Juvenile	0.420	0.420
Y2 Juvenile – Y3 Juvenile	0.852	0.852
Y3 Juvenile – Y4 Juvenile	0.908	0.908
Y4 Juvenile – Adult	0.910	0.910
Adult	0.922	0.926
Fecundity	0.301	0.307

The modified 'no crash' MPMs indicated that, over a 50-year projection period, the elimination of crash mortality is associated with a 25.6% increase in adult population at Ailsa Craig, corresponding to an increase from 41,272 to 51,855 adult birds (Table 4;

Figure 3). The reduction in adult mortality contributed most strongly to the observed population growth, as also shown in the sensitivity and elasticity analysis of the original model. Decreases in chick-to-fledgling mortality had a more limited demographic effect, resulting in a 6.7% increase or around 2,800 additional adult gannets (Table 4; Figure S1).

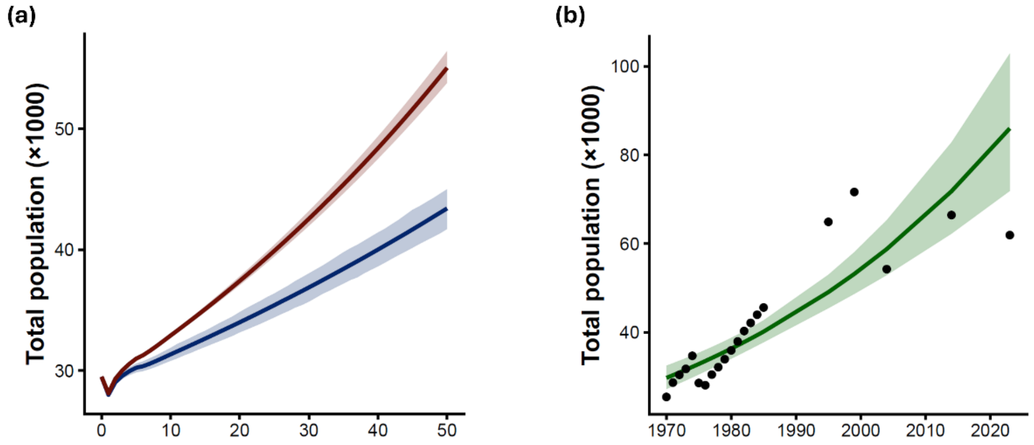


Figure 3. *(a) Demographic predictions of the Ailsa Craig gannet population for scenarios with crash mortality (survey population), (blue) and without crash mortality (red). Lines include stochastic variation calculated from beta distribution of survival estimate confidence intervals (blue) and carcass count means (red). (b) Plot of actual population trend at Ailsa Craig according to census data from the seabird monitoring program (SMP) (BTO 2024). Fitted model and green confidence ribbon represents a negative binomial model fitted to the data. Outputs from this model were used to calculate a population growth rate (λ) 1.020 (1.015-1.025 95% CIs).*

Table 4. *Predicted population growth rates for scenarios where adult crashes were included (survey population), only affected chicks (chick rearing crashes removed), only affected adults (adult crashes removed) and were excluded entirely (All crashes removed). The dominant eigen values are given for each scenario, as well as the percentage changes from the survey population scenario over 10, 25 and 50 years.*

Scenario	**Lambda (λ)**	**Percentage change (%)**		
		10 Years	25 Years	50 Years
Survey population	1.008	0	0	0
Chick rearing crashes removed	1.009	1.31	3.30	6.72
Adult crashes removed	1.011	3.35	8.58	17.91
All crashes removed	1.012	4.67	12.10	25.64

Adult survival emerged as the most influential demographic rate. It had the highest sensitivity value (0.71), indicating that small absolute changes in survival would strongly affect population growth. It also had the highest elasticity (0.63), meaning that proportional changes in adult survival would have the greatest relative impact on λ. In contrast, adult fecundity had a lower sensitivity (0.19), suggesting smaller absolute influence, and a low elasticity (0.07). All other transitions had sensitivity values lower than that of adult fecundity, and elasticities of 0.07 (Figure 4).

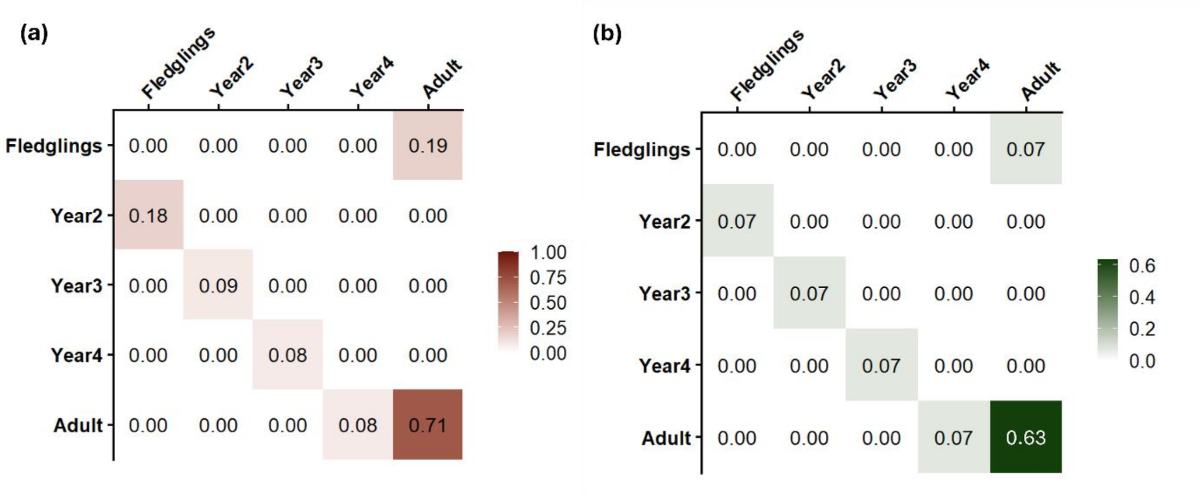


***Figure 4**. Sensitivity (a) and elasticity (b) results from a matrix population model (MPM) growth rate to perturbations based on survival transitions in northern gannets at Ailsa Craig. Darker colours in both figures indicate greater values.*

Environmental drivers of crash mortality at Ailsa Craig

ERA5 reanalysis data revealed two modal wind directions at Ailsa Craig (Figure 1), with frequent winds from both NW and SE. When testing these directions against crash probability, the model revealed that gannet crash rates increased with the proportion of NW winds (Log odds = 1.62, SE = 0.57, z = 2.87, p = 0.009, binomial GLM), suggesting that wind direction plays a key role in mortality at the colony. McFadden's pseudo-R^2 indicated that approximately 17.1% of the variation in carcass rates was explained by the model. Month was also a significant predictor of crash probability. However, the effect size was extremely low (Table 5). For this reason, the effect of wind direction on crash probability was the main focus.

Table 5. *Results from independent generalized linear models (GLMs) with quasibinomial error families where crash probability was tested against environmental factors. Only month and wind direction emerged as significant results. Despite being significant, month had a very low effect size.*

Model	Log odds	Standard estimate	z	p
Month	0.12	0.04	1.49	0.002*
Bird count	<0.01	<0.01	1.88	0.073
Fog days	0.05	0.03	1.81	0.084
Calm	1.80	1.64	1.09	0.286
High winds	-0.94	0.66	-1.41	0.172
Wind direction	1.62	0.57	2.87	0.009*

Pairwise correlation plots (Figure S3) revealed a moderate positive correlation between bird count and month (r = 0.53), indicating higher bird presence during peak breeding months. Bird count was also positively associated with calm wind conditions and negatively with high winds. A strong negative correlation between calm and high wind conditions (r = -0.83) reflects their opposing distributions. Foggy days were uncorrelated with other variables, except for a weak association with calm conditions. NW wind proportion showed weak positive correlations with both month and bird count, indicating some seasonal trend but not enough to suggest problematic collinearity. Overall, I found little evidence to suggest that any other factors should be included when testing NW wind proportion against crash probability.

Temporal patterns of NW winds at Ailsa Craig

I used ERA5 data to assess whether and how the monthly proportion of NW winds have changed between 1974 and 2022 (Figure 5). The years I used in my analyses (1974 to 1976) exhibited a slightly lower average NW wind proportion compared to the mean for the subsequent years. Across the 48-year period, the proportion of NW winds per year ranged from 0.484 - 0.653 (mean of 0.564). This translates into predicted crash rates of

0.62% - 0.79% across a breeding season, using the coefficients from the quasibinomial GLM.

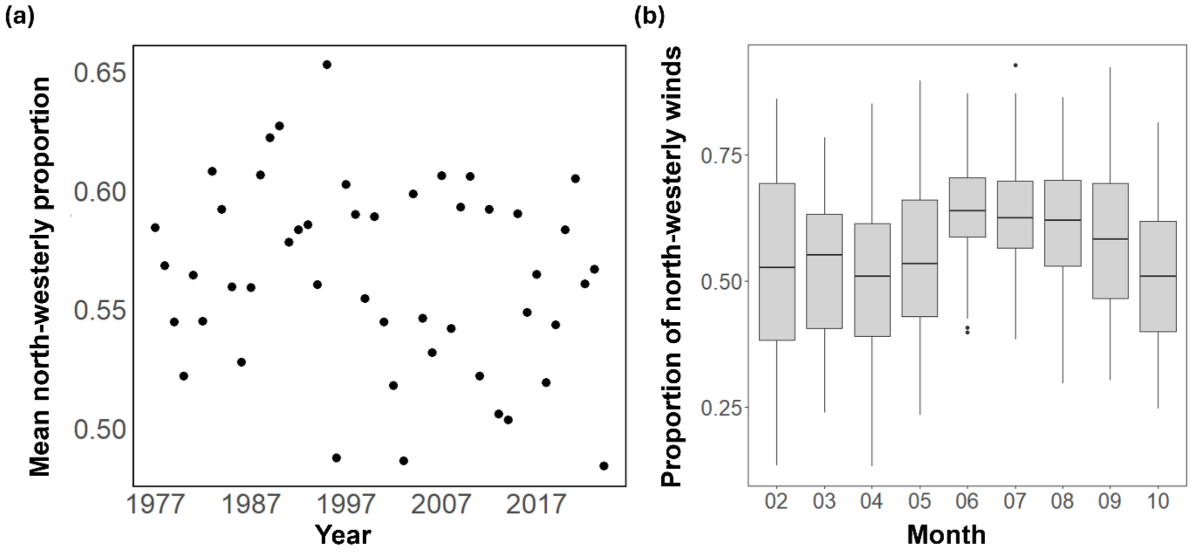


Figure 5. *(a) Annual mean proportion of north-westerly (NW) winds at Ailsa Craig from 1977 to 2024, based on ERA5 wind reanalysis data. Each point represents the average NW wind proportion from February to October for a given year. No significant temporal trend was detected (SE = -0.001, p = 0.168). (b) Monthly variation in the proportion of NW winds across all years (February to October). NW winds were most frequent in June and July, while October had the lowest NW wind proportions. Boxes show interquartile ranges (IQR) with medians. Whiskers represent an additional 1.5× IQR. Further outliers are shown as individual points.*

A linear regression revealed no significant linear trend in NW wind proportion over time (SE = -0.001, p = 0.168, linear regression). However, ANOVA revealed a significant effect of month on the proportion of NW winds throughout the year (F = 5.395, df = 8, 423, $p < 0.001$), indicating a seasonal pattern in wind directionality. Post-hoc Tukey tests showed that NW wind proportions were significantly higher in June and July than in February (mean differences = 0.114 and 0.109; p = 0.008 and 0.013, respectively). October had the lowest NW wind proportions, significantly lower than June and July (mean differences = -0.119 and -0.114; p = 0.004 and 0.007, respectively). While February’s

NW proportion did not differ significantly from many months, it exhibited the highest interannual variability.

Demographic consequences of shifting wind regimes

Integrating the output of the quasibinomial GLM with the MPMs demonstrated how increasing the proportion of NW winds would have a negative impact on gannet population size at Ailsa Craig. In a theoretical scenario where all winds are NW, and all other factors, including colony location, remain the same, the population is projected to show a 21.50% reduction compared to the current wind scenario (0.564 proportion NW winds). Conversely, if all winds shifted to SE, the population is expected to increase by 14.91% compared to survey population. Together, these scenarios illustrate the possible envelope of population outcomes under future wind regime shifts (Figure 6; Table 6).

Table 6. *Demographic predictions for 7 different wind scenarios where the proportion of north-westerly winds are fixed at levels from 0.0 to 1.0, Estimates include the percentage change in population compared to the average wind proportion during the study period (1973 to 1976), and each scenario's dominant eigen value (λ).*

NW wind proportion scenario	**Lambda (λ)**	**Percentage change (%)**		
		10 Years	25 Years	50 Years
0.0	1.011	2.82	7.20	14.91
0.2	1.010	2.08	5.29	10.85
0.4	1.009	1.07	2.69	5.46
0.56 (survey population)	1.008	0.00	0.00	0.00
0.6	1.008	-0.38	-0.78	-1.56
0.8	1.006	-2.19	-5.38	-10.47
1.0	1.003	-4.72	-11.40	-21.50

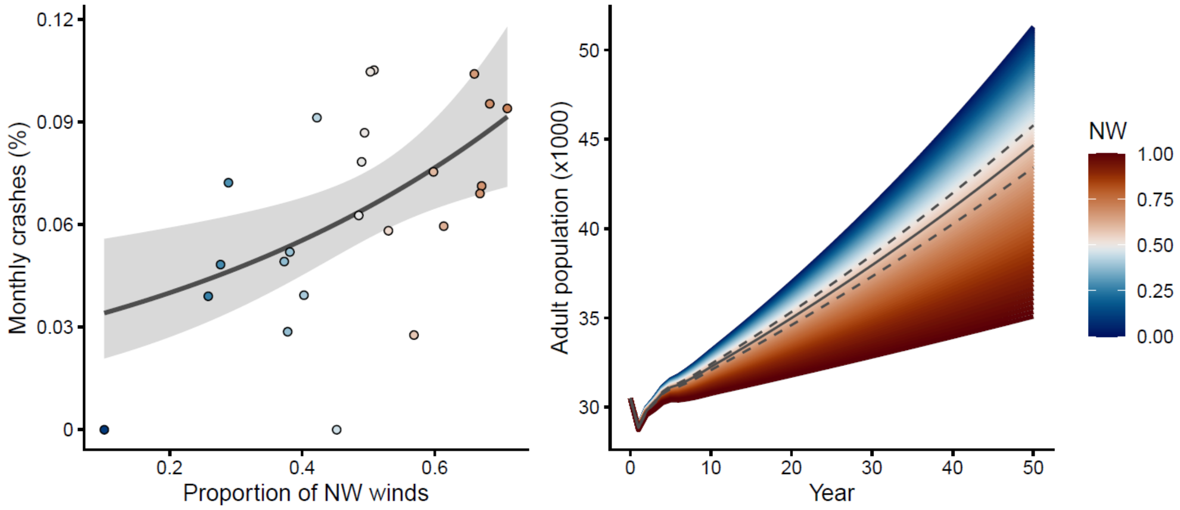


Figure 6. *(a) The monthly crash probability, calculated from gannet carcass and bird count data (Wanless 1979), as a function of the proportion of north westerly (NW) winds. The fitted line represents a generalized linear model (GLM) with a quasibinomial error structure, including 95% confidence intervals. Points are coloured by their NW:SE wind proportion with red showing higher proportion and blue a lower proportion. (b) Matrix population model (MPM) projections over 50 years under hypothetical NW:SE wind proportions: Colour gradient represents the proportion of NW:SE winds with red showing more NW and blue more SE. Dotted lines show the 95% prediction interval of wind conditions over the past 50 years at Ailsa Craig. The model incorporates survival adjustments derived from the GLM in panel (a), simulating the demographic consequences of shifts in prevailing wind direction.*

Discussion

Adult gannets exhibit high annual survival rates (0.922) and are long-lived, making their populations particularly sensitive to perturbations in adult survival (Spencer and Janzen 2010; Wanless et al. 2006). In recent years, anthropogenic sources of mortality in adult gannets have become increasingly well documented, including fisheries bycatch (Araújo et al. 2022; Calado et al. 2021), collisions with wind turbines (Peschko et al. 2021; Pollock et al. 2021), and, most notably, outbreaks of highly pathogenic avian influenza (HPAI) (Giralt Paradell et al. 2023; Lane et al. 2024). By contrast, non-anthropogenic pressures remain difficult to quantify, particularly given the species' pelagic lifestyle. Here, I investigate a novel, non-anthropogenic pressure affecting adult gannets at the Ailsa Craig colony: wind-driven crashes at the base of the breeding cliffs. I show that these crashes substantially impact the local population, potentially reducing adult numbers by up to 21.5% over a 50-year period. Furthermore, I demonstrate that crash frequency is linked to wind direction, with higher proportions of north-westerly winds associated with increased mortality. To my knowledge, this is the first study to demonstrate that crashes at the breeding colony could have a measurable demographic impact in a long-lived seabird species.

Results from MPMs indicate that the Ailsa Craig gannet population was experiencing modest growth ($\lambda = 1.008$, prior to the recent HPAI outbreak), aligning with species-wide trends reported by the IUCN Red List, where northern gannets are currently classified as Least Concern (Birdlife International 2018). SMP census data from Ailsa Craig shows the growth rate to be slightly higher than my MPM estimates, at 1.020 (1.015 – 1.025) (BTO 2024). This elevated growth rate is likely due to changes in habitat suitability for gannets at Ailsa Craig. Quarrying operations were all but ceased in the mid 1900s on the island, reducing the amount of human disturbance (Harrison et al. 1987). Furthermore, Ailsa Craig was declared rat free in the 1990s (Zonfrillo 2001). Both factors may have allowed non-breeding adults and juveniles to establish nest sites in new areas across the island and facilitated greater nesting density (Anderson and Keith 1980). Regardless of the causes of the measured population growth at Ailsa Craig, it is similar to the MPM projected growth rate over the past 50 years.

Environmental drivers of crash-risk were assessed. The monthly crash rate was not predicted by the number of foggy days, suggesting that crashes were not caused by sensory impairment that affected the bird’s ability to judge the distance to the ground. Against my expectations, neither was wind speed important. Auks have been previously shown to abort landing attempts in high winds and it was hypothesised that high winds produced strong gusts near cliffs, which are challenging for birds to respond to (Shepard et al. 2019). A similar response might be expected in gannets, with high winds potentially disrupting landings as seen in auks. However, in gannets at Ailsa Craig, there was no link between wind speed and crashes, suggesting this was not the mechanism. Low winds could also pose challenges. In aviation, headwinds allow aircraft to maintain airspeed whilst decreasing their ground speed allowing for more controlled landings (Hastings and Kelley 1979). Birds may utilise headwinds in similar ways (Gremillet unpublished data; KleinHeerenbrink et al. 2022). Therefore, calm winds could reflect more risky landing conditions. Moreover, gannets may utilise wind-driven updrafts near their landing sites to control the final phase of the landing. Again, resulting in higher risk when conditions are calm. However, again calm winds were not a predictor of crashes and wind direction emerged as the only significant predictor of crashes.

The low-resolution wind data compared to the crash data means wind speed cannot be completely ruled out as a driver. Nonetheless, the models indicate that the primary driver was direction, rather than speed. This may influence landing capacity in other ways such as through turbulence levels at the nesting cliffs (Shepard 2025; Thorne et al. 2023). In NW winds, wind would be blowing directly onto the breeding cliffs resulting in orographic blocking that could result in wind being accelerated over the top of the cliff whilst being directed downwards in the middle and lower regions of the cliff, leading to a complex flow field directly at the colony. By contrast, SE winds may flow either side of the island resulting in predictable flow fields (Lempidakis et al. 2022). The turbulent flow field caused by NW wind could well be problematic for maintaining flight control. This is critical when birds are operating close to ground, as a loss of flight control is likely to lead to a fatal collision. A similar phenomena has been described in a colony of GHA where carcasses, found with evidence of injuries sustained through crashing, are concentrated in a region below a slope with a turbulent flow field with a downdraft (Schoombie et al. 2023).

Results show that removing crash-related mortality increases the population growth rate from λ = 1.008 to λ = 1.013 at the Ailsa Craig colony. While this change may appear small on an annual basis, it translates to a 25.6% increase in adult abundance over a 50-year period (Table 4). Crash-related mortality accounts for approximately 5.4% of annual adult mortality, which is comparable to losses from fisheries bycatch (Le Bot et al. 2019) and far greater than those caused by an extreme weather year that lead to prey shortages in the southern breeding range of the gannet. These events were caused by a marine heatwave and led to mass breeding failure at colonies in the western Atlantic (Montevecchi et al. 2021). Therefore, while levels of mortality do not approach those associated with recent HPAI outbreaks, chronic crash-related mortality may still impose significant long-term demographic pressure on gannet populations (Camphuysen and Gear 2022; Lane et al. 2024). Gannet populations are relatively stable (Birdlife International 2018), but seabirds are some of the most endangered taxa and a 0.004 difference in population growth rate could be the difference between a stable and a declining population in many species (Croxall et al. 2012).

The demographic consequences of crash mortality in GHAs may be particularly significant. Schoombie et al. (2023) estimated that crashes at the ridge colony on Marion Island accounted for 11% of annual adult mortality. This is notable given that natural adult survival in GHA (0.951) (Converse et al. 2009) is higher than in northern gannets (0.922) (Wanless et al. 2006). This suggests that even modest additional mortality could have disproportionate demographic effects. Furthermore, natural crash mortality may not be as apparent in the GHA, as anthropogenic mortality in the form of fisheries bycatch is far higher (Baker et al. 2007; Bentley et al. 2021; Frankish et al. 2021). In both cases, crash events primarily affect adults rather than juveniles. At Ailsa Craig, 343 of 367 gannet carcasses recovered were adults, representing 5.4% of annual adult mortality, while in GHA, crashes accounted for 11% of adult mortality. My sensitivity analysis (Figure 4) shows that adult survival is the most elastic transition in the gannet life cycle, meaning that even modest reductions in adult survival cause disproportionate declines in population growth. This sensitivity is likely even greater in GHA, which have higher baseline adult survival. Taken together, the documented losses in both species indicate that crash mortality represents a meaningful demographic pressure across long-lived seabirds.

Model projections indicate that while a complete shift to NW wind is unlikely at Ailsa Craig, such a scenario would reduce the population by 21.5% over 50 years. Weather trend analysis from Ailsa Craig show that the yearly proportion of NW winds has been between 48% and 65% with no apparent trend. Prevailing westerlies have long been a feature of the north eastern Atlantic (Trigo et al. 2008). Despite little change in wind patterns at Ailsa Craig since 1974, sea surface temperatures may be driving changes in wind regimes in the north Atlantic, leading to a decrease in weakened westerly winds. Although trends are tricky to predict, evidence suggests that the north Atlantic wind regimes could change (Robson et al. 2018; 2016). Other shifts in wind regimes can be seen in other regions such as the southern sea where westerlies are drifting southwards (Goyal et al. 2021). Regardless of trend, changes in wind regimes may change the levels of risk, not only for gannets at Ailsa Craig, but also for seabirds at colonies around the globe.

Although competition at the start of the breeding season can relegate less successful individuals to riskier peripheral sites (Kokko et al. 2004), strong site fidelity limits the capacity of most breeders to track shifting risk landscapes over time. Many seabirds, including gannets, show extreme nest-site fidelity, often returning to the same nest within the same colony for their entire lives (Coulson 2002; Nelson 1966; 2010). Birds typically only vacate a site following their own or their partner’s death, allowing new or non-breeders to move in (Bourgeois et al. 2014; Sapoznikow and Quintana 2008). This fidelity constrains flexibility. Meaning if wind conditions change and render certain nest sites riskier, as I have shown at Ailsa Craig under increased NW winds, gannets are unlikely to shift to safer locations. The consequences could include increased energetic costs during landings, or in rarer cases, mortality. Thus, perturbations in wind regimes occurring within the lifespan of individual gannets may not only generate demographic effects at the population level but also reshape how birds perceive and use their nesting landscapes.

Landscapes of fear or risk shaped by wind may influence how seabirds use colony sites. Ailsa Craig is an unusual, though not unique (Schoombie et al. 2023), example of a seabird colony where vertical cliffs do not drop directly into the sea. Here, collisions with land are far more likely to result in serious injury or death. At other colonies, however, a loss of flight control may instead lead to uncontrolled landings on the sea. Even in the best case, such crashes increase the energetic cost of foraging trips and in worse cases may still result in injury or death (Lewis et al. 2015; Shepard et al. 2019). Importantly, only fatal crashes onto land are likely to be detected, while fatal crashes at sea or non-fatal crashes almost certainly go unnoticed. From the landscape of fear literature, we know that even small increases in mortality risk can strongly influence animal behaviour and ecology (Gallagher et al. 2017; Laundre et al. 2010). Building on this, Wheatley et al. (2021) introduced the concept of risk and accident landscapes. For gannets at Ailsa Craig and great-headed albatrosses at Marion Island, such landscapes may arise around colonies where nest sites carry a higher risk of crash-induced mortality, affecting individual landing decisions (Gremillet unpublished data) and potentially breeding site selection. More broadly, wind-driven risk landscapes may also exist at colonies where cliffs drop directly into the sea, with the energetic and survival costs of crashes shaping how seabirds use these environments.

In summary, these findings identify wind-induced crashes as a substantial and previously overlooked source of adult mortality in northern gannets, a long-lived species whose population dynamics are highly sensitive to changes in adult survival. The MPMs suggest that this subtle, chronic, environmental pressure may play a key role in the population trajectory of the species at Ailsa Craig and potentially other colonies. Understanding how wind impacts seabirds is increasingly important as climate change continues to alter wind regimes globally (Pryor et al. 2012). The role of wind speed is generally well-understood through its impact on flight speed, flight costs and prey availability (Lewis et al. 2015; Pennycuick et al. 2013; Shepard et al. 2019), but much less is known about the importance of wind direction. The results of this study demonstrate that wind direction can influence the risk of mortality at the colony, suggesting a novel mechanism and potential pressure if the prevailing wind directions were to shift as a result of climate change. While this study used data collected at Aisla Craig, risks relating to flight control should act as a selective pressure affecting seabirds more generally (KleinHeerenbrink et al. 2022; Lempidakis et al. 2022; Shepard et al. 2019), particularly given the mounting evidence of crash-related mortality across seabird species (Cone 1964; Schoombie et al. 2023). The risks of crashing may therefore already be shaping the spatial structure, survival, and evolutionary trajectories of cliff-nesting species in ways that remain largely undocumented.

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Supplementary material

Additional matrix population model projections

Survival transition adjustments, based on carcass data from Wanless (1979), were made to both the adult transition and the chick-to-fledgling transition. MPMs were constructed with only adult transition changes and only chick-to-fledgling transition changes. Adult adjustments had the greatest impact on the MPMs lambda value (figure S1).

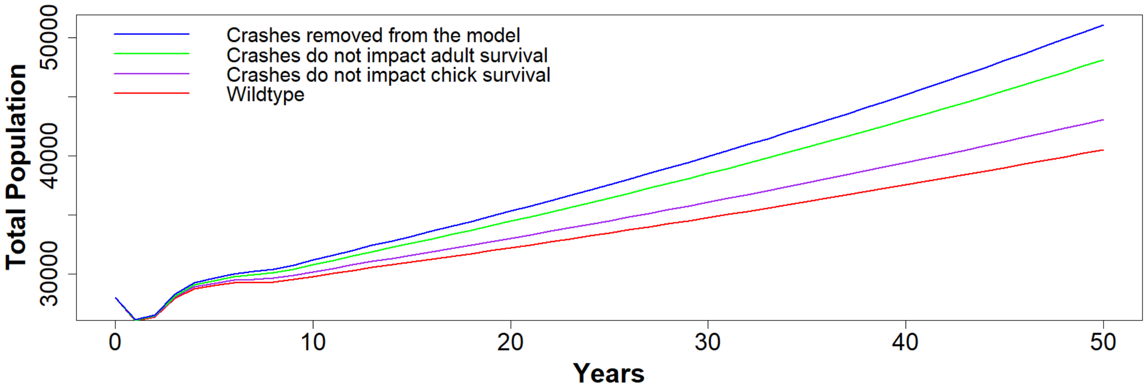

Figure S1. *Projected population trajectories for the Ailsa Craig gannet colony under four demographic scenarios: the survey population model including crash-related mortality (red), crash mortality removed during chick-rearing only (purple), crash mortality removed from adult survival only (green), and all crash mortality removed (blue). These projections highlight the dominant influence of adult survival on long-term population dynamics, consistent with sensitivity analyses showing that changes to adult survival transitions have the greatest effect on population growth rate.*

Preparing data for statistical analysis

Whilst preparing the crash data for statistical analysis, it was decided to remove October. Bird counts during October were consistently low, fewer than 10,000 individuals, with a mean of 5,200 across all years, reflecting the end of the breeding season (figure S2) (Wanless 1979). Additionally, the changeable nature of the end of the gannet breeding season means gannets may be completely gone from colonies by early to mid October depending on the year (Nelson 1966). Whilst statistical models used crashes per bird at the colony adjusts for low bird counts, it does not account for birds all leaving to colony early in the month. Wind proportion, by contrast, use data from the whole month leaving uncertainty whether wind conditions were even able to impact gannets at the colony. Therefore, October was excluded from the statistical analysis to ensure more robust and interpretable model.

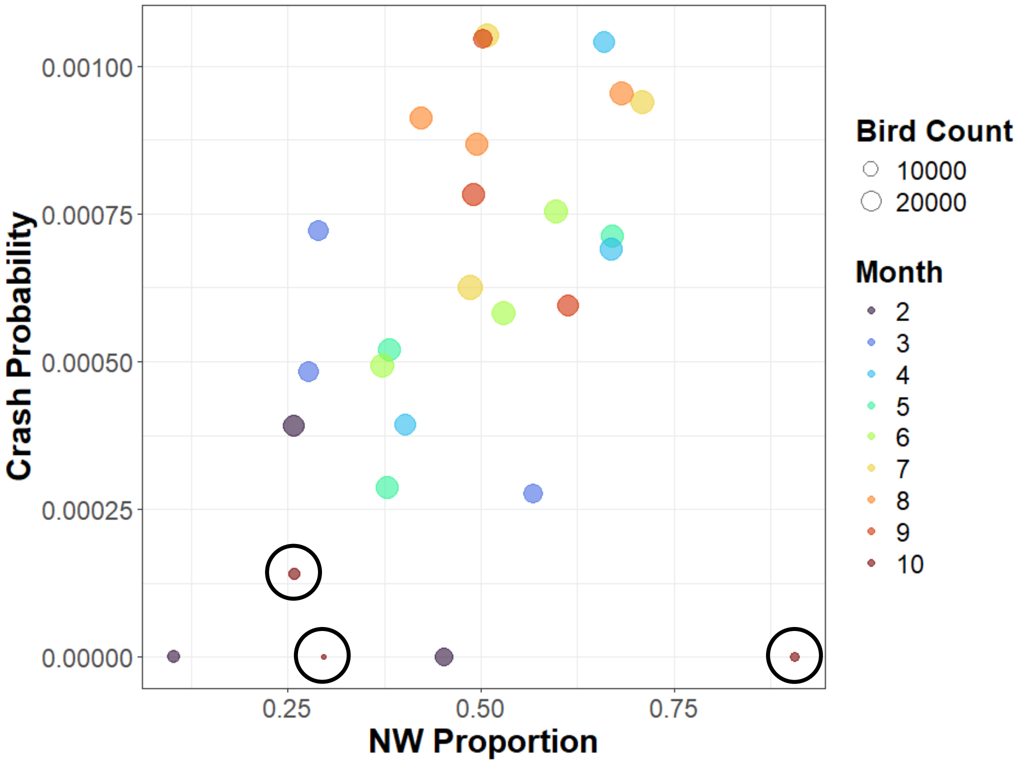

Figure S2. *Monthly crash probability plotted against wind proportion (NW:SE) With points coloured by month with proportional sizes depending on the number of birds at the colony in that month and year. October points are circled*.

Correlation testing of environmental factors

To evaluate if there was confounding in the environmental data, pairwise corelation tests were done for a range of environmental factors. The results from these tests are shown in figure S3.

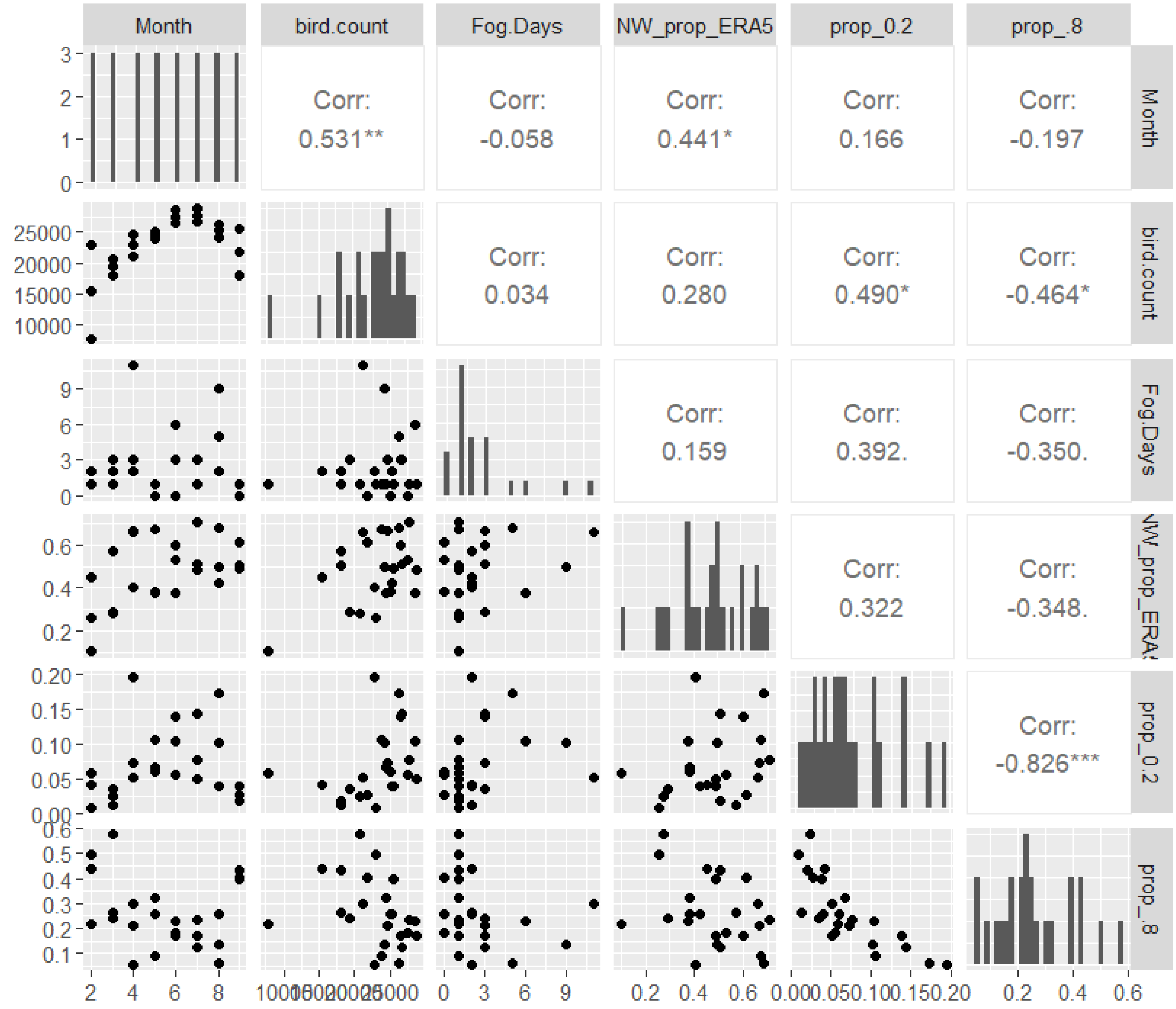

Figure S3. *Correlation plot testing for correlation between environmental factors at Ailsa Craig.*

Adjusting survival transitions

Table S1. *Stepwise process of adjusting adult survival probability using the outputs of a quasibinomial generalized linear model (GLM) on ERA5 data, which predicts the effect of wind direction on carcass count at Ailsa Craig.*

NW proportion	Crash probability	Yearly survival	Relative survival	Adjusted yearly survival
0.0	0.00031	0.99718	1.00292	0.92469
0.2	0.00042	0.99626	1.00199	0.92383
0.4	0.00055	0.99504	1.00076	0.92270
0.5	0.00064	0.99428	1.00000	0.92200
0.6	0.00073	0.99341	0.99913	0.92119
0.8	0.00097	0.99126	0.99696	0.91920
1.0	0.00129	0.99841	0.99410	0.91656

Table S2. *Stepwise process of adjusting chick survival probability using the outputs of a quasibinomial generalized linear model (GLM) on ERA5 data that predicts the effect of wind direction on carcass count at Ailsa Craig.*

NW proportion	Probability at least one parent crashes	Change in fledgling survival	Relative fledgling survival	Adjusted yearly survival
0.0	0.00563	0.99437	1.00584	0.74131
0.2	0.00747	0.99253	1.00398	0.73994
0.4	0.00990	0.99010	1.00152	0.73812
0.5	0.01140	0.98860	1.00000	0.73700
0.6	0.01313	0.98687	0.99825	0.73571
0.8	0.01740	0.98260	0.99393	0.73253
1.0	0.02304	0.97696	0.99823	0.72832

R Code

```
######################################################################################
### The role and drivers of crash mortality on nesting seabird population dynamics ###
######################################################################################

# Load required libraries for population modelling and plotting
library(dplyr)
library(ggplot2)
library(scales)
library(popbio)
library(tidyr)
library(readr)
library(MASS)
library(scales)
library(brms)
library(GGally)
library(visreg)
library(viridis)
library(knitr)
library(scico)




########################################
### MPM parameters for all scenarios ###
########################################

# Define stage names corresponding to life stages of the northern gannet
```

```
stageNames <- c("Fledglings", "Year2", "Year3", "Year4", "Adult")

# Initial population vector
initial_abundance <- matrix(c(6000, 2500, 3000, 7000, 7000))
rownames(initial_abundance) <- stageNames
colnames(initial_abundance) <- "Abundance"


###########################
### Observed gannet MPM ###
###########################

# Define the age-based matrix population model (MPM) for wild-type gannets
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_WT_MPM <- matrix(c(
  0,    0,     0,     0,     0.301,   # Fecundity
  0.420, 0,     0,     0,     0,      # Fledgling -> Year2
  0,    0.852,  0,     0,     0,      # Year2 -> Year3
  0,    0,     0.908,  0,     0,      # Year3 -> Year4
  0,    0,     0,     0.910,  0.922    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF <- tibble(
  x = rep(1:5, each = 5),
  y = rep(5:1, times = 5),
  z = as.vector(GANNE_WT_MPM)
)

# Calculate asymptotic population growth rate (lambda)
```

```
Lambda <- lambda(GANNE_WT_MPM)
Lambda  # Print the result

# Project population one time step into the future
N1 <- GANNE_WT_MPM %*% initial_abundance
N1

# Project the population over 50 years
years <- 50
N.projections <- matrix(0, nrow = 5, ncol = years + 1)
N.projections[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years) {
  N.projections[, i + 1] <- GANNE_WT_MPM %*% N.projections[, i]}

# Plot population size by stage over time (stable stage structure)

#matplot(0:years, t(N.projections), type = "l", ylim = c(0,50000),
#lty = 1:5, col = 1, ylab = "Number of individuals (WT)",
#xlab = "Year", main = "Stage change in wild-type population")
#legend("topleft", legend = stageNames, lty = 1:5, col = 1, bty = "n")

# Calculate the total population size over time
total_population <- colSums(N.projections)


####################################################################
### Sensitivity and elasticity analysis for observed population ###
####################################################################
```

```
#the stable stage distribution
SSDWT <- stable.stage(GANNE_WT_MPM)
SSDWT

#calculating sensitivity and elasticity of the elements in your matrix
sensWT <- sensitivity(GANNE_WT_MPM, zero = T)
elasWT <- elasticity(GANNE_WT_MPM)

#arranging the sensitivity dataframe
sensDFWT <- tibble(x = rep( 1:5, each = ncol(sensWT) ),
          y = rep( 5:1, times = nrow(sensWT) ) ,
          z = as.vector(sensWT), label = dplyr::if_else(is.na(z), "", sprintf("%1.2f", z)) )

# Figures4a and b
x11()
sensPlotWT <- sensDFWT %>%
 ggplot(aes(x = x, y = y, fill = z)) +
 geom_tile() +
 geom_text(aes(
  label = label,
  color = abs(z) < 0.3
 ), size = 6) +
 coord_fixed(expand = FALSE) +
 scale_color_manual(
  values = c("black", "black"),
  guide = "none"
 ) +
 scale_fill_gradient(
  low = "white", high = "red", name = "Sensitivity"
 ) +
 scale_x_continuous(breaks = 1:5, labels = stageNames, position = "top") +
 scale_y_continuous(breaks = 1:5, labels = rev(stageNames)) +
```

```
 labs(x = NULL, y = NULL) +
 theme(
  panel.border = element_rect(color = NA, fill = NA),
  legend.position = "none",
  plot.margin = unit(c(1, 2, 1, 1), "cm"),
  axis.text.x = element_text(size = 28, colour = "black", face = "bold", angle = 45,
hjust = 0, vjust = 0),
  axis.text.y = element_text(size = 28, colour = "black", face = "bold"),,  # ← Bigger
axis text
  axis.title = element_text(size = 28, colour = "black", face = "bold"),
  plot.title = element_text(size = 25, colour = "black", face = "bold"),
  strip.text = element_text(size = 25, colour = "black", face = "bold")
 )



sensPlotWT



#Elasticity plot

#create a plot for the elasticity results
#elasDFWT <- tibble(x = rep( 1:5 each = ncol(elasWT) ),
#              y = rep( 5:1, times = nrow(elasWT) ),
#              z = as.vector(elasWT), label = dplyr::if_else(is.na(z), "", sprintf("%1.2f", z)) )

#x11()
#elasPlotWT <- elasDFWT %>%
#  ggplot(aes(x = x, y = y, fill = z)) +
#  geom_tile() +
#  geom_text(aes(
```

```
#   label = label,
#   color = abs(z) < 0.14
#  ), size = 6) +
#  coord_fixed(expand = FALSE) +
#  scale_color_manual(
#   values = c("white", "black"),
#   guide = "none"
#  ) +
#  scale_fill_gradient(
#   low = "white", high = "purple4", name = "Elasticity"
#  ) +
#  scale_x_continuous(breaks = 1:6, labels = stageNames, position = "top") +
#  scale_y_continuous(breaks = 1:6, labels = rev(stageNames)) +
#  labs(x = NULL, y = NULL) +
#  theme(
#   panel.border = element_rect(color = NA, fill = NA),
#   legend.position = "none",
#   plot.margin = unit(c(1, 2, 1, 1), "cm"),
#   axis.text.x = element_text(size = 28, colour = "black", face = "bold", angle = 45, hjust = 0, vjust = 0),
#   axis.text.y = element_text(size = 28, colour = "black", face = "bold"),,  # ← Bigger axis text
#   axis.title = element_text(size = 28, colour = "black", face = "bold"),
#   plot.title = element_text(size = 25, colour = "black", face = "bold"),
#   strip.text = element_text(size = 25, colour = "black", face = "bold")
#  )

#elasPlotWT
```

```
########################################
### Calculate 'no crash' transitions ###
########################################

########################
### Adult transition ###
########################

N_Crash = 122 #Mean number of crashes from Wanless (1979)
N_total = 27499 # Mean number of peak birds at Ailsa Craig between 1974-1976 Wanless (1979)
Ob_Mort = 0.078 # Observed adult mortality (Wanless et al., 2006)
Ob_Sur = 0.922 # Observed adult mortality



P_Mort <- N_Crash/N_total # Mortality explained by crashes

NC_Sur <- Ob_Sur + P_Mort # No crash Survival

Per_mort <- (P_Mort/Ob_Mort) #percentage of mortality explained by crashes

############################
### Fledgling transition ###
############################

Ob_SurF <- 0.737 # Observed fledgling survival (Wanless et al., 2002)
Ob_MortF <- 0.263 # Observed Fledgling mortality

Delta_MortF <- Ob_MortF*Per_mort # Change in mortality

NC_SurF <- Ob_SurF + Delta_MortF # New fledgling transition in no crash scenario
```

```
##################################
### Crashes removed gannet MPM ###
##################################

# This scenario removes the crash effects by assuming higher adult survival and chick rearing.
# Represents the demographic trajectory in a hypothetical scenario where crashes do not happen.

# Define the stage-based MPM for a no crash gannet population
# Matrix is ordered by age class (rows = to, columns = from)

#####################################################
### Calculating the no-crash survival transitions ###
#####################################################

Fe <- 0.4085

Fe_SurNC <- Fe*NC_SurF

Fe_Ob <- 0.737*Fe



GANNE_Nocrash_MPM <- matrix(c(
 0,    0,     0,     0,     Fe_SurNC,  # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  NC_Sur    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))
```

```
# Convert matrix to data frame for visual inspection
matrixDFNC <- tibble(x = rep( 1:5, each = ncol(GANNE_Nocrash_MPM) ),
            y = rep( 5:1, times = nrow(GANNE_Nocrash_MPM) ) ,
            z = as.vector(GANNE_Nocrash_MPM) )

# Calculate asymptotic population growth rate (lambda)
LambdaNC <-lambda(GANNE_Nocrash_MPM)
LambdaNC

# Project population one time step into the future
N1NC <- GANNE_Nocrash_MPM %*% initial_abundance
N1NC

# Project the population over 50 years
yearsNC <- 50
N.projectionsNC <- matrix(0, nrow = nrow(GANNE_Nocrash_MPM), ncol = yearsNC + 1)
N.projectionsNC[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:yearsNC)
{N.projectionsNC[, i + 1]<-GANNE_Nocrash_MPM %*% N.projectionsNC[,i]}
N.projectionsNC

# Plot population size by stage over time
#matplot(0:yearsNC, t(N.projectionsNC), type = "l", ylim = c(0,50000), lty = 1:5, col = 1, ylab = "N", xlab = "Years", main = "Population stage change when crashes are removed from the matrix")
#legend("topleft", legend = c(stageNames), lty = 1:5, col = 1, bty = "n")

# Calculate total population size over time
```

```r
total_populationNC <- colSums(N.projectionsNC)


##########################################################
### Crashes removed only from chick rearing gannet MPM ###
##########################################################

# This scenario removes the crash effects from the chick rearing stage only.
# Working on the assumption that if one parent dies the chick will fail.
# Represents the demographic trajectory in a hypothetical scenario where crashes do not happen to parents that were chick provisioning.

# Define the age-based MPM for a no crash gannet population
# Matrix is ordered by stage class (rows = to, columns = from)
GANNE_Chickrear_MPM <- matrix(c(
  0,    0,     0,     0,     Fe_SurNC,  # Fecundity
  0.420, 0,     0,     0,     0,      # Fledgling -> Year2
  0,    0.852,  0,     0,     0,      # Year2 -> Year3
  0,    0,     0.908,  0,     0,      # Year3 -> Year4
  0,    0,     0,     0.910,  Ob_Sur    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDFCR <- tibble(x = rep( 1:5, each = ncol(GANNE_Chickrear_MPM) ),
           y = rep( 5:1, times = nrow(GANNE_Chickrear_MPM) ) ,
           z = as.vector(GANNE_Chickrear_MPM) )

# Calculate asymptotic population growth rate (lambda)
LambdaCR <-lambda(GANNE_Chickrear_MPM)
LambdaCR
```

```
# Project population one time step into the future
N1CR <- GANNE_Chickrear_MPM %*% initial_abundance
N1CR

# Project the population over 50 years
yearsCR <- 50
N.projectionsCR <- matrix(0, nrow = nrow(GANNE_Chickrear_MPM), ncol = yearsCR
+ 1)
N.projectionsCR[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:yearsCR)
{N.projectionsCR[, i + 1]<-GANNE_Chickrear_MPM %*% N.projectionsCR[,i]}
N.projectionsCR

# Plot population size by stage over time
#matplot(0:yearsCR, t(N.projectionsCR), type = "l", ylim = c(0,50000), lty = 1:6, col =
1, ylab = "N", xlab = "Years", main = "Population stage change when crashes are
removed from chick rearing")
#legend("topleft", legend = c(stageNames), lty = 1:6, col = 1, bty = "n")

# Calculate total population size over time
total_populationCR <- colSums(N.projectionsCR)

####################################################
### Crashes removed only from adult survival MPM ###
####################################################

# This scenario removes the crash effects from the adult survival stage only.
# Represents the demographic trajectory in a hypothetical scenario where crashes
do not affect this transition
```

```
# Define the age-based MPM for a no crash gannet population
# Matrix is ordered by stage class (rows = to, columns = from)
GANNE_Survival_MPM <- matrix(c(
 0,    0,     0,     0,     Fe_Ob,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  NC_Sur    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDFS <- tibble(x = rep( 1:5, each = ncol(GANNE_Survival_MPM) ),
             y = rep( 5:1, times = nrow(GANNE_Survival_MPM) ) ,
             z = as.vector(GANNE_Survival_MPM) )

# Calculate asymptotic population growth rate (lambda)
LambdaS <-lambda(GANNE_Survival_MPM)
LambdaS

# Project population one time step into the future
N1S <- GANNE_Survival_MPM %*% initial_abundance
N1S

# Project the population over 50 years
yearsS <- 50
N.projectionsS <- matrix(0, nrow = nrow(GANNE_Survival_MPM), ncol = yearsS + 1)
N.projectionsS[,1] <- initial_abundance

# Loop through each year to update the population vector
```

```
for (i in 1:yearsS)
{N.projectionsS[, i + 1]<-GANNE_Survival_MPM %*% N.projectionsS[,i]}
N.projectionsS

# Plot population size by stage over time
#matplot(0:yearsS, t(N.projectionsS), type = "l", ylim = c(0,50000), lty = 1:6, col = 1, ylab = "N", xlab = "Years", main = "Population stage change when crashes are removed from Survival")
#legend("topleft", legend = c(stageNames), lty = 1:6, col = 1, bty = "n")

# Calculate total population size over time
total_populationS <- colSums(N.projectionsS)



################################################
### Combined Plot: all scenario trajectories ###
################################################

# This plot visualises the total population trajectories under four key scenarios:
# - Wildtype (from Wanless et al., 2006)
# - No crash (hypothetical optimal case)
# - Chick-rearing crash only (affecting chick rearing)
# - Survival crash only (affecting adult survival)
# The y-axis is zoomed to focus on differences over a more relevant population range.
# Figure S1 in supplementary material

plot(0:years, total_population, type = "l", ylim = c(27000, 51000),
    col = "red", lwd = 2, ylab = "Total Population", xlab = "Years",
    main = "Total Population Across Scenarios")

# Add lines for each alternative scenario
```

```
lines(0:years, total_populationCR, col = "purple", lwd = 2)  # Chick-rearing crash
lines(0:years, total_populationS, col = "green", lwd = 2)    # Survival crash
lines(0:years, total_populationNC, col = "blue", lwd = 2)    # No crash

# Annotated legend
legend("topleft",
      legend = c("Crashes removed from the model",
              "Crashes do not impact adult survival",
              "Crashes do not impact chick survival",
              "Wildtype"),
      col = c("blue", "green", "purple", "red"), lwd = 2, bty = "n")



par(mar = c(6.5, 6.5, 4, 2))

plot(0:years, total_population, type = "l",
    ylim = c(27000, 51000),
    col = "red", lwd = 2,
    ylab = "Total Population",
    xlab = "Years",
    main = "Total Population Across Scenarios",
    cex.lab = 2,
    font.lab = 2.5,
    cex.axis = 1.8)

# Add lines for each alternative scenario
lines(0:years, total_populationCR, col = "purple", lwd = 2)  # Chick-rearing crash
lines(0:years, total_populationS, col = "green", lwd = 2)    # Survival crash
lines(0:years, total_populationNC, col = "blue", lwd = 2)    # No crash

# Annotated legend
```

```
legend("topleft",
    legend = c("Crashes removed from the model",
           "Crashes do not impact adult survival",
           "Crashes do not impact chick survival",
           "Wildtype"),
    col = c("blue", "green", "purple", "red"),
    lwd = 2,
    bty = "n",
    cex = 1.5)  # Match legend font size



########################################
### Lambda-Based Growth Projections ###
########################################

# This section uses the deterministic growth rate (lambda) from each model to
# estimate long-term exponential population trajectories over 50 years.
# Lambda values are derived from dominant eigenvalues of the MPMs.

# Define the projection time horizon and initial population
years <- 0:50
N0 <- 27499  # Hypothetical starting population

# Store lambda values for each scenario (previously calculated)
lambda_vec <- c(
 WildType    = Lambda,
 NoCrash     = LambdaNC,
 ChickRearing = LambdaCR,
 Survival    = LambdaS
)

# Apply exponential growth formula for each scenario:
```

```
# N_t = N0 * lambda^t
population_growth <- sapply(lambda_vec, function(lambda) N0 * lambda^years)

# Create a tidy data frame for plotting and comparison
population_comparison <- data.frame(Year = years, population_growth)

# Results
View(population_comparison)

# Works to here
#################################################################
### Percentage difference relative to observed: lambda-based ###
#################################################################

# This analysis quantifies the relative difference in population size
# from the observed trajectory for each alternate scenario.
# Results expressed as percentage deviation over time.
# Table 4 in main text

percent_diff_comp <- data.frame(
  Year = population_comparison $Year,
  NoCrash = 100 * (population_comparison $NoCrash -
population_comparison$WildType) / population_comparison$WildType,
  ChickRearing = 100 * (population_comparison$ChickRearing -
population_comparison$WildType) / population_comparison$WildType,
  Survival = 100 * (population_comparison$Survival -
population_comparison$WildType) / population_comparison$WildType
)

# View table of relative differences
View(percent_diff_comp)
```

```
#################################
### Stochastic variance plots ###
#################################



###############################
### Survival parameters ###
###############################

survival_data <- data.frame(
 Stage = c("1st", "2nd", "3rd", "4th", "Adult"),
 Mean = c(0.420, 0.852, 0.908, 0.910, 0.922),
 LowerCI = c(0.394, 0.842, 0.901, 0.903, 0.916),
 UpperCI = c(0.445, 0.861, 0.915, 0.917, 0.927)
)

estimate_beta_params <- function(mean, lower_ci, upper_ci, ci_level = 0.95) {
 lower_q <- (1 - ci_level) / 2
 upper_q <- 1 - lower_q

 cost_fn <- function(params) {
  alpha <- params[1]; beta <- params[2]
  q_lower <- qbeta(lower_q, alpha, beta)
  q_upper <- qbeta(upper_q, alpha, beta)
  mean_est <- alpha / (alpha + beta)
  (q_lower - lower_ci)^2 + (q_upper - upper_ci)^2 + (mean_est - mean)^2
 }

 var_guess <- ((upper_ci - lower_ci) / 4)^2
 tmp <- mean * (1 - mean) / var_guess - 1
 alpha_start <- mean * tmp
```

```
 beta_start  <- (1 - mean) * tmp

 opt <- optim(c(alpha_start, beta_start), cost_fn,
          method = "L-BFGS-B", lower = c(0.01, 0.01))

 list(alpha = opt$par[1], beta = opt$par[2])
}

beta_params <- survival_data %>%
 rowwise() %>%
 mutate(params = list(estimate_beta_params(Mean, LowerCI, UpperCI))) %>%
 unnest_wider(params)

alpha_vals <- beta_params$alpha
beta_vals  <- beta_params$beta

##############################
### Baseline projection ###
##############################

initial_abundance <- c(6000, 2500, 3000, 7000, 7000)
years <- 50
n_sim <- 1000

total_pops <- matrix(NA, nrow = n_sim, ncol = years + 1)
lambda_vals <- numeric(n_sim)

set.seed(42)

for (sim in 1:n_sim) {
 N <- matrix(0, nrow = 5, ncol = years + 1)
 N[,1] <- initial_abundance
```

```
 for (t in 1:years) {

   surv <- rbeta(5, alpha_vals, beta_vals)

   A <- matrix(0, 5, 5)
   A[1,5] <- Fe_Ob
   A[2,1] <- surv[1]
   A[3,2] <- surv[2]
   A[4,3] <- surv[3]
   A[5,4] <- surv[4]
   A[5,5] <- surv[5]

   N[,t+1] <- A %*% N[,t]
 }

 total_pops[sim,] <- colSums(N)
}

mean_pop <- colMeans(total_pops)
ci_lower <- apply(total_pops, 2, quantile, probs = 0.025)
ci_upper <- apply(total_pops, 2, quantile, probs = 0.975)

df_plot <- data.frame(
 Year   = 0:years,
 WT_mean = mean_pop,
 WT_lwr  = ci_lower,
 WT_upr  = ci_upper
)

##############################################
### Crash-removed stochastic projection ###
```

```
##############################################

# Crash parameters
baseline_survival <- 0.922
baseline_chick_surv <- 0.737
adult_deaths_per_year <- 27499 * (1 - baseline_survival)

alpha <- 367
beta  <- 5832

n_iter <- 1000
prop_draws <- rbeta(n_iter, alpha, beta)

survival_draws <- baseline_survival + prop_draws * (1 - baseline_survival)
chick_surv_draws <- baseline_chick_surv + prop_draws * (1 - baseline_chick_surv)

A_base <- GANNE_WT_MPM
N0 <- initial_abundance
T_max <- 50

pop_traj <- matrix(NA, nrow = n_iter, ncol = T_max + 1)

for (i in 1:n_iter) {

  A <- A_base
  A[1,5] <- 0.4085 * chick_surv_draws[i]
  A[5,5] <- survival_draws[i]

  N <- N0
  pop_sizes <- numeric(T_max + 1)
  pop_sizes[1] <- sum(N0)   # TRUE T0 alignment
```

```
 for (t in 1:T_max) {
  N <- A %*% N
  pop_sizes[t+1] <- sum(N)
 }

 pop_traj[i,] <- pop_sizes
}

median_pop <- apply(pop_traj, 2, median)
lower_pop  <- apply(pop_traj, 2, quantile, probs = 0.025)
upper_pop  <- apply(pop_traj, 2, quantile, probs = 0.975)

df_crash <- data.frame(
 Year    = 0:T_max,
 CR_mean = median_pop,
 CR_lwr  = lower_pop,
 CR_upr  = upper_pop
)

################################
### Final combined plot ####
################################

col_wt <- scico(1, palette = "vik", begin = 0.05)
col_cr <- scico(1, palette = "vik", begin = 0.95)

g <- ggplot() +

 geom_ribbon(data = df_plot,
       aes(x = Year, ymin = WT_lwr, ymax = WT_upr),
       fill = alpha(col_wt, 0.25)) +
 geom_line(data = df_plot,
```

```
         aes(x = Year, y = WT_mean),
         colour = col_wt, linewidth = 1.4) +

  geom_ribbon(data = df_crash,
          aes(x = Year, ymin = CR_lwr, ymax = CR_upr),
          fill = alpha(col_cr, 0.25)) +
  geom_line(data = df_crash,
         aes(x = Year, y = CR_mean),
         colour = col_cr, linewidth = 1.4) +

  labs(x = "Year",
     y = "Total population",
     title = "Baseline vs Crashes-Removed Population Projection") +

  theme_classic(base_size = 16) +
  theme(
   aspect.ratio = 1,
   plot.title = element_text(size = 20, face = "bold"),
   axis.title  = element_text(size = 18, face = "bold")
  )

################################
### Export PDF ###
################################

#desktop_path <- file.path(Sys.getenv("USERPROFILE"), "Desktop")

#pdf(file.path(desktop_path, "Baseline_vs_CrashesRemoved.pdf"),
#    width = 7, height = 5)

#print(g)
#dev.off()
```

```
###############################
### SMP census data analysis ###
###############################

# Data aquired from the SMP was used to compare MPM projections to real life
# population trends
# Figure 4b in main text

setwd("C:/Users/Stefa/Desktop/Uni/MRes/Project/Gannets/Gannet write up/Figure edits")

# Load census data from SMP
GanCount <- read_csv("Seabird monitoring program Gannet counts.csv")
View(GanCount)

# Negative binomial model
M1Cen <- glm.nb(Total.birds ~ Year, data = GanCount)
summary(M1Cen)

# find the r value
r <- coef(M1Cen)["Year"]
se_r <- summary(M1Cen)$coefficients["Year", "Std. Error"]

# 95% CI for r
r_CI <- c(r - 1.96*se_r, r + 1.96*se_r)

# Convert to lambda
lambda <- exp(r)
lambda_CI <- exp(r_CI)
```

```
# calculate 95% CIs
cat("Growth rate (r):", r, "\n")
cat("95% CI for r:", r_CI, "\n\n")

cat("Estimated finite growth rate (lambda):", lambda, "\n")
cat("95% CI for lambda:", lambda_CI, "\n")

#Get predictions
pred <- predict(M1Cen, type = "link", se.fit = TRUE)

# Convert from link (log) scale to response scale
GanCount$fit <- exp(pred$fit)
GanCount$lwr <- exp(pred$fit - 1.96 * pred$se.fit)
GanCount$upr <- exp(pred$fit + 1.96 * pred$se.fit)

ggplot(GanCount, aes(x = Year, y = Total.birds)) +
 geom_point(size = 3, color = "black") +
 geom_line(aes(y = fit), color = "darkgreen", size = 1) +
 geom_ribbon(aes(ymin = lwr, ymax = upr), alpha = 0.2, fill = "darkgreen") +
 labs(x = "Year", y = "Total number of birds") +
 scale_y_continuous(labels = label_number(big.mark = "")) +
 theme_minimal(base_size = 14) +
 theme(
  axis.title = element_text(size = 20, face = "bold"),
  axis.text = element_text(size = 16, color = "black"),
  axis.text.y = element_text(angle = 90, hjust = 0.5, color = "black"),
  axis.ticks = element_line(color = "black"),   # ensure ticks are drawn
  plot.title = element_text(size = 20, face = "bold", hjust = 0.5),
  panel.grid = element_blank(),
  panel.border = element_rect(color = "black", fill = NA, linewidth = 1)
 )
```

```
# New cleaner plot
CensP <- ggplot() +

 ## Confidence ribbon FIRST
 geom_ribbon(
  data = GanCount,
  aes(x = Year, ymin = lwr / 1000, ymax = upr / 1000),
  fill = alpha(col_cen, 0.25)
 ) +

 ## Fitted mean line
 geom_line(
  data = GanCount,
  aes(x = Year, y = fit / 1000),
  colour = col_cen,
  linewidth = 1.4
 ) +

 ## Observed points (kept subtle)
 geom_point(
  data = GanCount,
  aes(x = Year, y = Total.birds / 1000),
  size = 2,
  colour = "black"
 ) +

 scale_y_continuous(
  labels = label_number(accuracy = 1)
 ) +

 labs(
  x = "Year",
```

```
   y = "Total population (×1000)",
   title = "Northern gannet census population trend"
 ) +

 theme_classic(base_size = 16) +
 theme(
   aspect.ratio = 1,
   plot.title = element_text(size = 20, face = "bold"),
   axis.title = element_text(size = 18, face = "bold")
 )

CensP


################################################################################
### Statistical analysis of environmental impacts on crashes at Ailsa Craig ###
################################################################################



setwd("C:/Users/Stefa/Desktop/Uni/MRes/Project/Gannets/Gannet wind stats/Stats data")

# Read data
data <- read.csv("GannetWindMasterERA5.csv")

# Look at data structure
str(data)
View(data)

# Plot data
```

```
# Figure S2 in suplementry material

ggplot(data, aes(x = NW_prop_ERA5, y = carcasses / bird.count)) +
 geom_point(
  aes(size = bird.count, col = factor(Month), fill = factor(Month)),
  pch = 21, alpha = 0.6
 ) +
 scale_color_viridis_d(option = "H") +
 scale_fill_viridis_d(option = "H") +
 labs(
  x = "NW Proportion",
  y = "Crash Probability",
  size = "Bird Count",
  col = "Month",
  fill = "Month"
 ) +
 theme_bw() +
 theme(
  aspect.ratio = 1,
  axis.title = element_text(size = 18, face = "bold"),
  axis.text = element_text(size = 14),
  legend.title = element_text(size = 16, face = "bold"),
  legend.text = element_text(size = 14),
  plot.title = element_text(size = 18, face = "bold", hjust = 0.5)
 )

# It was decided to remove october

#####################
### Remove October ###
#####################
```

```
data <- data[data$Month != 10,]

# Pairwise correlation plots to look at multicolinearity between environmental
variables

g0 <- ggpairs( data[, c(2, 7, 9, 15, 21, 25)], upper = list( continuous = wrap("cor",
method = "spearman") ), diag = list( continuous = wrap("barDiag") ) )
g0

# Little to no colinearity in the important variables

#########################################################
### Testing environmental factors in independent GLMs ###
#########################################################


# Load data
data <- read.csv("GannetWindMasterERA5.csv")
Fogdata <- read.csv("Monthly_fog_day_stats.csv")

# Remove Month 10 from main data
data <- data %>% filter(Month != 10)

# Ensure Year and Month in main data are integers
data <- data %>% mutate(
  Year = as.integer(Year),
  Month = as.integer(Month)
)

# Convert DD/MM/YYYY and extract Year + Month
Fogdata <- Fogdata %>%
  mutate(
```

```
    Date = as.Date(Date, format = "%d/%m/%Y"),   # <-- important part
    Year = year(Date),
    Month = month(Date)
  ) %>%
  dplyr::select(Year, Month, Fog.days..Machrihanish., Fog.days..Prestwick.)

# Join fog data into main dataset
data_merged <- data %>%
  left_join(Fogdata, by = c("Year", "Month"))

#View(data_merged)



##########################################################
### Testing environmental factors in independent GLMs ###
##########################################################

# Table 5 in main text

mM <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ Month, family =
quasibinomial, data = data_merged )
summary(mM)

mCount <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ bird.count, family =
quasibinomial, data = data_merged )
summary(mCount)
```

```
m0.2 <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ prop_0.2, family = quasibinomial, data = data_merged )
summary(m0.2)

m0.8 <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ prop_.8, family = quasibinomial, data = data_merged )
summary(m0.8)

# Now a linear relationship
mDir <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ NW_prop_ERA5, family = quasibinomial, data = data_merged )
summary(mDir)

mFogPrest <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ Fog.days..Prestwick., family = quasibinomial, data = data_merged )
summary(mFogPrest)

mFogMach <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ Fog.days..Machrihanish., family = quasibinomial, data = data_merged )
summary(mFogMach)



# Both month and NW proportion of wind are significant
# Month has a far smaller standard estimate and they have weak colinearity suggesting some seasonal structure
# but not enough to include.

###########################################################
### Testing wind direction and finding best model fit ###
###########################################################
```

```
# Modelling wind proportion against crash probability with a polynomial
relationship
mDirPoly <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ poly(NW_prop_ERA5,
2), family = binomial, data = data )
summary(mDirPoly)

# Now a linear relationship
mDir <- glm( cbind( carcasses, (bird.count - carcasses) ) ~ NW_prop_ERA5, family =
binomial, data = data )
summary(mDir)

# Can't use AIC to test which model is better fitting
# Instead we used psudeo R squared values



1 - (mDir$deviance / mDir$null.deviance)

1 - (mDirPoly$deviance / mDirPoly$null.deviance)

# Polynomial GLM has greater R squared but only by <2%
# According to Burnham & Anderson this is not significant and therefore we
# go with the simpler model.



######################
### Plot the model ###
######################

# Figure 6a in main text

visreg(mDir, scale = "response", rug = FALSE, gg = TRUE) +
```

```
 geom_point(data = data, aes(x = NW_prop_ERA5, y = Crash.ratio)) +
 scale_y_continuous(limits = c(0, 0.00125)) +
 labs(x = "Proportion of NW winds", y = "Crash probability") +
 theme_bw() +
 theme(
  axis.title = element_text(size = 24, face = "bold"),
  axis.text = element_text(size = 20),
  panel.grid = element_blank()
 )



####################################################################
### Using the quasibinomial GLM to adjust survival probabilities ###
####################################################################

# Using the coefficients to adjust adult and fledgling transitions

#################################
### Adult survival transition ###
#################################

# Coefficients from the binomial GLM linking crash risk to NW wind proportion
intercept <- -8.1477
slope <- 1.6245

# Baseline adult survival from matrix population model (at NW_prop = 0.5)
s_base <- 0.922

# Define a range of NW wind proportions for scenario testing (0.5 included as
reference)
NW_values <- c(0, 0.2, 0.4, 0.56, 0.6, 0.8, 1.0)
```

```
# Calculate the linear predictor from the GLM (logit-scale)
eta <- intercept + slope * NW_values

# Convert logit-scale estimates to crash probabilities using the inverse logit
transformation
crash_probs <- exp(eta) / (1 + exp(eta))

# Monthly survival is 1 minus the crash probability
s_month <- 1 - crash_probs

# Convert to annual survival assuming crash risk applies over 8 months of the year
(based on gannet breeding season)
s_year <- s_month^8

# Extract annual survival at NW_prop = 0.56 to use as reference point
s_year_at_0.56 <- s_year[NW_values == 0.56]

# Calculate survival relative to the 0.5 NW:SE wind ratio (i.e., mean condition)
relative_survival <- s_year / s_year_at_0.56

# Adjust baseline annual survival using relative survival across wind scenarios
adjusted_survival <- s_base * relative_survival

# Combine results into a summary table for interpretation and export
results <- data.frame(
  NW_prop = NW_values,
  Crash_Prob = round(crash_probs, 5),
  Monthly_Survival = round(s_month, 5),
  Yearly_Survival_CrashOnly = round(s_year, 5),
  Relative_Survival = round(relative_survival, 5),
  Adjusted_Yearly_Survival = round(adjusted_survival, 5)
```

```
)

# Print the table
print(results)


# Annual survival declines with increasing NW wind frequency,
# consistent with GLM-predicted crash risk. Adjusted values can now be used in MPMs.


##################################
### Chick fledging transition ###
##################################

# Baseline fledging probability from matrix population model (no crash adjustment)
p_fledge_base <- 0.737

# Estimate the probability that at least one parent crashes (assuming independence)
p_at_least_one_crash <- 1 - s_year^2

# Fledging survival due to wind alone: chick survives only if both parents survive
fledge_survival_only <- 1 - p_at_least_one_crash

# Extract fledging survival at NW_prop = 0.56 to use as reference point
fledge_survival_at_0.56 <- fledge_survival_only[NW_values == 0.56]

# Calculate relative fledging survival compared to baseline condition
relative_fledge_survival <- fledge_survival_only / fledge_survival_at_0.56

# Adjust baseline fledging probability using relative values
```

```
adjusted_fledge <- p_fledge_base * relative_fledge_survival

# Summarise all values in a table for interpretation and plotting
fledging_table <- data.frame(
 NW_prop = NW_values,
 At_Least_One_Parent_Crashes = round(p_at_least_one_crash, 5),
 Fledge_Survival_Only = round(fledge_survival_only, 5),
 Relative_Fledge_Survival = round(relative_fledge_survival, 5),
 Adjusted_Fledge_Prob = round(adjusted_fledge, 5),
 Adjusted_fecundity = round(adjusted_fledge*0.4085, 5)
)

# Print table for review
print(fledging_table)



########################################
### MPM parameters for all scenarios ###
########################################

# Define stage names corresponding to life stages of the northern gannet
stageNames <- c("Chick", "Year2", "Year3", "Year4", "Adult")

# Initial population vector
initial_abundance <- matrix( c(6000, 2500, 3000, 7000, 7000) )
rownames(initial_abundance)  <- stageNames
colnames(initial_abundance) <- "Abundance"



################################
### 95% prediction intervals ###
################################
```

```
# bounds + reference
NW_vals <- c(0.4862815, 0.56, 0.6260113)
names(NW_vals) <- c("NW_lo","NW_ref","NW_hi")

invlogit <- function(x) exp(x) / (1 + exp(x))

calc_row <- function(NW){
 eta <- intercept + slope * NW
 crash <- invlogit(eta)           # monthly crash prob
 s_month <- 1 - crash
 s_year <- s_month^8              # annual survival from crash-only
 list(NW = NW, eta = eta, crash = crash, s_month = s_month, s_year = s_year)
}

rows <- lapply(NW_vals, calc_row)
df <- do.call(rbind, lapply(rows, function(x) {
 data.frame(NW = x$NW, eta = x$eta, crash = x$crash,
      monthly_surv = x$s_month, annual_surv = x$s_year)
}))

# reference annual survival
s_year_ref <- df["NW_ref","annual_surv"]

# adjusted adult survival (relative to reference)
df$relative_surv <- df$annual_surv / as.numeric(s_year_ref)
df$adjusted_adult_surv <- s_base * df$relative_surv

# chick effects: both parents survive => chick_surv = s_year^2
df$chick_surv_only <- df$annual_surv^2
df$relative_chick_surv <- df$chick_surv_only / (as.numeric(s_year_ref)^2)
df$adjusted_fledge_prob <- p_fledge_base * df$relative_chick_surv
```

```
df$adjusted_fecundity <- df$adjusted_fledge_prob*0.4085

# format and print
options(digits = 8)
print(df)

###################################################
### Observed Gannet MPM (0.56 NW:SE proportion) ###
###################################################

# Define the age-based matrix population model (MPM) for observed gannet population
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_WT_MPM <- matrix(c(
  0,    0,     0,     0,     0.30106,   # Fecundity
  0.420, 0,     0,     0,     0,      # Fledgling -> Year2
  0,    0.852,  0,     0,     0,      # Year2 -> Year3
  0,    0,     0.908,  0,     0,      # Year3 -> Year4
  0,    0,     0,     0.910,  0.922    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF <- tibble(
  x = rep(1:5, each = 5),
  y = rep(5:1, times = 5),
  z = as.vector(GANNE_WT_MPM)
)

# Calculate asymptotic population growth rate (lambda)
Lambda <- lambda(GANNE_WT_MPM)
```

```
Lambda  # Print the result

# Project population one time step into the future
N1 <- GANNE_WT_MPM %*% initial_abundance
N1

# Project the population over 50 years
years <- 50
N.projections <- matrix(0, nrow = 5, ncol = years + 1)
N.projections[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years) {
 N.projections[, i + 1] <- GANNE_WT_MPM %*% N.projections[, i]}

# Calculate total population over time
total_population <- colSums(N.projections)



########################################
## Gannet MPM 0.0 NW:SE proportion ###
########################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_0_MPM <- matrix(c(
 0,    0,     0,     0,     0.30314,   # Fecundity
 0.420, 0,     0,     0,     0,     # Fledgling -> Year2
 0,    0.852,  0,     0,     0,     # Year2 -> Year3
 0,    0,     0.908,  0,     0,     # Year3 -> Year4
 0,    0,     0,     0.910,  0.92517    # Year4 -> Adult
```

```
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF0 <- tibble(x = rep( 1:5, each = ncol(GANNE_0_MPM) ),
            y = rep( 5:1, times = nrow(GANNE_0_MPM) ) ,
            z = as.vector(GANNE_0_MPM) )

# Calculate asymptotic population growth rate (lambda)
Lambda0 <-lambda(GANNE_0_MPM)
Lambda0

# Project population one time step into the future
N10 <- GANNE_0_MPM %*% initial_abundance
N10

# Loop through each year to update the population vector
years0 <- 50
N.projections0 <- matrix(0, nrow = nrow(GANNE_0_MPM), ncol = years + 1)
N.projections0[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years0)
{N.projections0[, i + 1]<-GANNE_0_MPM %*% N.projections0[,i]}
N.projections0

# Calculate total population over time
total_population0 <- colSums(N.projections0)


########################################
```

```
## Gannet MPM 0.2 NW:SE proportion ###
########################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_0.2_MPM <- matrix(c(
 0,    0,     0,     0,     0.30260,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  0.92435    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF0.2 <- tibble(x = rep( 1:5, each = ncol(GANNE_0.2_MPM) ),
             y = rep( 5:1, times = nrow(GANNE_0.2_MPM) ) ,
             z = as.vector(GANNE_0.2_MPM) )

# Calculate asymptotic population growth rate (lambda)
Lambda0.2 <-lambda(GANNE_0.2_MPM)
Lambda0.2

# Project population one time step into the future
N10.2 <- GANNE_0.2_MPM %*% initial_abundance
N10.2

# Project the population over 50 years
years0.2 <- 50
N.projections0.2 <- matrix(0, nrow = nrow(GANNE_0.2_MPM), ncol = years + 1)
```

```
N.projections0.2[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years0.2)
{N.projections0.2[, i + 1]<-GANNE_0.2_MPM %*% N.projections0.2[,i]}
N.projections0.2

# Calculate total population over time
total_population0.2 <- colSums(N.projections0.2)



########################################
## Gannet MPM 0.4 NW:SE proportion ###
########################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_0.4_MPM <- matrix(c(
 0,    0,     0,     0,     0.30186,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  0.92321    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF0.4 <- tibble(x = rep( 1:5, each = ncol(GANNE_0.4_MPM) ),
            y = rep( 5:1, times = nrow(GANNE_0.4_MPM) ) ,
            z = as.vector(GANNE_0.4_MPM) )
```

```
# Calculate asymptotic population growth rate (lambda)
Lambda0.4 <-lambda(GANNE_0.4_MPM)
Lambda0.4

# Project population one time step into the future
N10.4 <- GANNE_0.4_MPM %*% initial_abundance
N10.4

# Project the population over 50 years
years0.4 <- 50
N.projections0.4 <- matrix(0, nrow = nrow(GANNE_0.4_MPM), ncol = years + 1)
N.projections0.4[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years0.4)
{N.projections0.4[, i + 1]<-GANNE_0.4_MPM %*% N.projections0.4[,i]}
N.projections0.4

# Calculate total population over time
total_population0.4 <- colSums(N.projections0.4)



########################################
## Gannet MPM 0.6 NW:SE proportion ###
########################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_0.6_MPM <- matrix(c(
 0,    0,     0,     0,     0.30083,   # Fecundity
```

```
 0.420, 0,    0,    0,    0,    # Fledgling -> Year2
 0,    0.852, 0,    0,    0,    # Year2 -> Year3
 0,    0,    0.908, 0,    0,    # Year3 -> Year4
 0,    0,    0,    0.910, 0.92164   # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF0.6 <- tibble(x = rep( 1:5, each = ncol(GANNE_0.6_MPM) ),
             y = rep( 5:1, times = nrow(GANNE_0.6_MPM) ) ,
             z = as.vector(GANNE_0.6_MPM) )

# Calculate asymptotic population growth rate (lambda)
Lambda0.6 <-lambda(GANNE_0.6_MPM)
Lambda0.6

# Project population one time step into the future
N10.6 <- GANNE_0.6_MPM %*% initial_abundance
N10.6

# Project the population over 50 years
years0.6 <- 50
N.projections0.6 <- matrix(0, nrow = nrow(GANNE_0.6_MPM), ncol = years + 1)
N.projections0.6[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years0.6)
{N.projections0.6[, i + 1]<-GANNE_0.6_MPM %*% N.projections0.6[,i]}
N.projections0.6

# Calculate total population over time
```

```
total_population0.6 <- colSums(N.projections0.6)


######################################
## Gannet MPM 0.8 NW:SE proportion ###
######################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_0.8_MPM <- matrix(c(
 0,    0,     0,     0,     0.29942,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  0.91948    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDF0.8 <- tibble(x = rep( 1:5, each = ncol(GANNE_0.8_MPM) ),
            y = rep( 5:1, times = nrow(GANNE_0.8_MPM) ) ,
            z = as.vector(GANNE_0.8_MPM) )

# Calculate asymptotic population growth rate (lambda)
Lambda0.8 <-lambda(GANNE_0.8_MPM)
Lambda0.8

# Project population one time step into the future
N10.8 <- GANNE_0.8_MPM %*% initial_abundance
N10.8
```

```
# Project the population over 50 years
years0.8 <- 50
N.projections0.8 <- matrix(0, nrow = nrow(GANNE_0.8_MPM), ncol = years + 1)
N.projections0.8[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years0.8)
{N.projections0.8[, i + 1]<-GANNE_0.8_MPM %*% N.projections0.8[,i]}
N.projections0.8

# Calculate total population over time
total_population0.8 <- colSums(N.projections0.8)


########################################
## Gannet MPM 1.0 NW:SE proportion ###
########################################

# Define the age-based matrix population model with adjustments based on
# NW:SE proportion
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_1.0_MPM <- matrix(c(
 0,    0,     0,     0,     0.29748,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  0.91649    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))
```

```
# Convert matrix to data frame for visual inspection
matrixDF1.0 <- tibble(x = rep( 1:5, each = ncol(GANNE_1.0_MPM) ),
          y = rep( 5:1, times = nrow(GANNE_1.0_MPM) ) ,
          z = as.vector(GANNE_1.0_MPM) )

# Calculate asymptotic population growth rate (lambda)
Lambda1.0 <-lambda(GANNE_1.0_MPM)
Lambda1.0

# Project population one time step into the future
N11.0 <- GANNE_1.0_MPM %*% initial_abundance
N11.0

# Project the population over 50 years
years1.0 <- 50
N.projections1.0 <- matrix(0, nrow = nrow(GANNE_1.0_MPM), ncol = years + 1)
N.projections1.0[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years1.0)
{N.projections1.0[, i + 1]<-GANNE_1.0_MPM %*% N.projections1.0[,i]}
N.projections1.0

# Calculate total population over time
total_population1.0 <- colSums(N.projections1.0)

####################################
### NW 95% prediction intervals ###
####################################

###################################
### Upper prediction intervals ###
```

```
##################################

# Define the age-based matrix population model at High 95% prediction interval
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_HiPred_MPM <- matrix(c(
 0,    0,     0,     0,     0.30067,   # Fecundity
 0.420, 0,     0,     0,     0,      # Fledgling -> Year2
 0,    0.852,  0,     0,     0,      # Year2 -> Year3
 0,    0,     0.908,  0,     0,      # Year3 -> Year4
 0,    0,     0,     0.910,  0.92140    # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))

# Convert matrix to data frame for visual inspection
matrixDFHi <- tibble(
 x = rep(1:5, each = 5),
 y = rep(5:1, times = 5),
 z = as.vector(GANNE_HiPred_MPM)
)

# Calculate asymptotic population growth rate (lambda)
LambdaHi <- lambda(GANNE_HiPred_MPM)
LambdaHi  # Print the result

# Project population one time step into the future
N1Hi <- GANNE_HiPred_MPM %*% initial_abundance
N1Hi

# Project the population over 50 years
years <- 50
N.projectionsHi <- matrix(0, nrow = 5, ncol = years + 1)
```

```
N.projectionsHi[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years) {
  N.projectionsHi[, i + 1] <- GANNE_HiPred_MPM %*% N.projectionsHi[, i]}

# Calculate total population over time
total_populationHi <- colSums(N.projectionsHi)

####################################
### Lower prediction intervals ###
####################################

# Define the age-based matrix population model (MPM) for wild-type gannets
# Matrix is ordered by age class (rows = to, columns = from)
GANNE_LoPred_MPM <- matrix(c(
  0,    0,     0,     0,     0.30146,  # Fecundity
  0.420, 0,     0,     0,     0,     # Fledgling -> Year2
  0,    0.852,  0,     0,     0,     # Year2 -> Year3
  0,    0,     0.908,  0,     0,     # Year3 -> Year4
  0,    0,     0,     0.910,  0.92260   # Year4 -> Adult
),
nrow = 5, byrow = TRUE,
dimnames = list(stageNames, stageNames))
# Convert matrix to data frame for visual inspection
matrixDFLo <- tibble(
  x = rep(1:5, each = 5),
  y = rep(5:1, times = 5),
  z = as.vector(GANNE_LoPred_MPM)
)

# Calculate asymptotic population growth rate (lambda)
```

```
LambdaLo <- lambda(GANNE_LoPred_MPM)
LambdaLo  # Print the result

# Project population one time step into the future
N1Lo <- GANNE_LoPred_MPM %*% initial_abundance
N1Lo

# Project the population over 50 years
years <- 50
N.projectionsLo <- matrix(0, nrow = 5, ncol = years + 1)
N.projectionsLo[,1] <- initial_abundance

# Loop through each year to update the population vector
for (i in 1:years) {
  N.projectionsLo[, i + 1] <- GANNE_LoPred_MPM %*% N.projectionsLo[, i]}

# Calculate total population over time
total_populationLo <- colSums(N.projectionsLo)

#####################################################
### Combined plot: all wind scenario trajectories ###
#####################################################
#########################
### GLM COEFFICIENTS  ###
#########################

intercept <- -8.1477
slope     <- 1.6245

# Baseline adult annual survival from MPM
s_base <- 0.922
```

```
# Baseline fledging probability from MPM
p_fledge_base <- 0.737

####################
### ANCHOR POINTS ###
####################

NW_anchor <- c(0, 0.2, 0.4, 0.56, 0.6, 0.8, 1.0)

eta_anchor <- intercept + slope * NW_anchor
crash_anchor <- exp(eta_anchor) / (1 + exp(eta_anchor))
s_month_anchor <- 1 - crash_anchor
s_year_anchor <- s_month_anchor^8    # 8 months crash exposure

# Chick survival via both parents surviving
p_atleast_anchor <- 1 - s_year_anchor^2
fledge_surv_anchor <- 1 - p_atleast_anchor

# Reference point at 0.56 NW
idx_ref <- which(NW_anchor == 0.56)

relative_fledge_anchor <- fledge_surv_anchor / fledge_surv_anchor[idx_ref]
adj_fledge_anchor <- p_fledge_base * relative_fledge_anchor
adj_fec_anchor <- adj_fledge_anchor * 0.4085



##########################################
### CONTINUOUS WIND GRID FOR PROJECTIONS ###
##########################################

NW_values <- seq(0, 1, length.out = 101)
```

```
# Interpolate fledging + fecundity to full grid
adj_fledge_cont <- approx(NW_anchor, adj_fledge_anchor, xout = NW_values)$y
adj_fec_cont    <- approx(NW_anchor, adj_fec_anchor,   xout = NW_values)$y



################################################
### ADULT SURVIVAL ADJUSTMENT FOR FULL GRID  ###
################################################

eta <- intercept + slope * NW_values
crash_probs <- exp(eta) / (1 + exp(eta))
s_month <- 1 - crash_probs
s_year  <- s_month^8

# Relative to NW=0.56 reference
i56 <- which.min(abs(NW_values - 0.56))
relative_survival <- s_year / s_year[i56]

adjusted_survival <- s_base * relative_survival



######################################
### ADJUSTED PARAMETERS IN TABLES   ###
######################################

results <- tibble(
  NW_prop = NW_values,
  Crash_Prob = crash_probs,
  Adjusted_Adult_Survival = adjusted_survival
)

fledging_table <- tibble(
```

```
  NW_prop = NW_values,
  Adjusted_Fledge_Prob = adj_fledge_cont,
  Adjusted_fecundity   = adj_fec_cont
)


#######################################
### BUILD MPM + PROJECT POPULATION ###
#######################################

stageNames <- c("Fledglings", "Year2", "Year3", "Year4", "Adult")

initial_abundance <- c(5000, 3500, 3000, 7000, 12000)
names(initial_abundance) <- stageNames

Lambda <- rep(NA, length(NW_values))
years <- 50
total_population <- array(NA, dim = c(length(NW_values), years+1))



for (i in seq_along(NW_values)) {

  fec_i <- adj_fec_cont[i]
  surv_adult_i <- adjusted_survival[i]

  MPM <- matrix(
    c(
      0,     0,     0,     0,     fec_i,       # fecundity (wind-adjusted)
      0.420,  0,     0,     0,     0,          # Fledgling -> Year2
      0,     0.852,  0,     0,     0,          # Year2 -> Year3
      0,     0,     0.908,  0,     0,          # Year3 -> Year4
      0,     0,     0,     0.910,  surv_adult_i  # Year4 -> Adult; Adult survival
```

```
  ),
  nrow = 5, byrow = TRUE,
  dimnames = list(stageNames, stageNames)
 )

 Lambda[i] <- lambda(MPM)

 Nproj <- matrix(0, nrow = 5, ncol = years + 1)
 Nproj[,1] <- initial_abundance

 for (t in 1:years) {
  Nproj[, t+1] <- MPM %*% Nproj[, t]
 }

 total_population[i, ] <- colSums(Nproj)
}


################################
### PREPARE OUTPUT FOR PLOT  ###
################################

trajectoryDF <- tibble(
 Year = rep(0:years, each = length(NW_values)),
 NW   = rep(NW_values, times = years+1),
 N    = c(total_population)
)


######################################
###  DEFINE REFERENCE BANDS plot ###
######################################
```

```
trajectoryDF2 <- list(
  mean = trajectoryDF %>% filter(NW == 0.56),
  lwr  = trajectoryDF %>% filter(NW == 0.49),
  upr  = trajectoryDF %>% filter(NW == 0.63)
)


g4 <- trajectoryDF %>%
  ggplot( aes(x = Year, y = N/1000, group = NW, col = NW) ) +
  geom_line(linewidth = 1) +
  geom_line( inherit.aes = F, data = trajectoryDF2$mean, aes(x = Year, y = N/1000, group = NW), col = "grey30" ) +
  geom_line( inherit.aes = F, data = trajectoryDF2$lwr, aes(x = Year, y = N/1000, group = NW), col = "grey30", linetype = "dashed" ) +
  geom_line( inherit.aes = F, data = trajectoryDF2$upr, aes(x = Year, y = N/1000, group = NW), col = "grey30", linetype = "dashed" ) +
  scico::scale_colour_scico(palette = "vik") +
  theme_classic() +
  theme(aspect.ratio = 1) +
  labs( y = "Adult population (x1000)" )




pdf("C:/Users/Stefa/Desktop/Wind_adjusted_time_plot.pdf", height = 4, width = 8)

(g3 + g4)

dev.off()
```

```
#################################
### Population numbers change ###
#################################

#Define time horizon and starting population size

years <- 0:50              # 51-year projection

N0 <- 30000                # Initial population size

# Store lambda values (population growth rates) in a named vector
lambda_vec <- c(WildType = Lambda,
        "0.0"   = Lambda0,
        "0.2"   = Lambda0.2,
        "0.4"   = Lambda0.4,
        "0.6"   = Lambda0.6,
        "0.8"   = Lambda0.8,
        "1.0"   = Lambda1.0)

# Project population growth over time for each lambda
population_growth <- sapply(lambda_vec, function(lambda) N0 * lambda^years)

# Convert to a data frame and include the year column
population_df <- data.frame(Year = years, population_growth)

# Check structure of population projections
View(population_df)


########################################
###Percentage difference calculations###
########################################
```

```
# Table 6 in main text

# Create an empty data frame to store percentage differences
percent_diff_df <- data.frame(Year = population_df$Year)

# Calculate % difference from WildType for each lambda scenario
for (lambda_name in names(lambda_vec)) {
  if (lambda_name != "WildType") {
    colname <- paste0("X", lambda_name)  # Column name in population_df
    percent_diff_df[[lambda_name]] <-
      100 * (population_df[[colname]] - population_df$WildType) /
population_df$WildType
  }
}

# Preview percentage differences
View(percent_diff_df)

##################################################
### Analysis of weather trends at Ailsa Craig ###
##################################################

# Set working directory to access ERA5 wind data
setwd("C:/Users/Stefa/Desktop/Uni/MRes/Project/Gannets/ERA5 data")

# Load required libraries



# Import ERA5 monthly wind data
data <- read.csv("1977to2024ERA5data .csv", stringsAsFactors = FALSE)
```

```
# Inspect summary statistics of the dataset
summary(data)

# Extract the year from the 'year_month' column (format assumed to be "YYYY-MM")
data$year <- substr(data$year_month, 1, 4)

# Calculate the mean proportion of NW wind direction per year
yearly_NW <- data %>%
 group_by(year) %>%
 summarise(mean_prop_NW = mean(prop_NW, na.rm = TRUE))

# Convert 'year' to numeric for plotting and modelling
yearly_NW <- yearly_NW %>%
 mutate(year = as.numeric(as.character(year)))

# Plot yearly mean NW wind proportion over time

ggplot(yearly_NW, aes(x = year, y = mean_prop_NW)) +
 geom_point(color = "black", size = 3) +            # Plot data points
 labs(
  x = "Year",
  y = "Mean NW Proportion"
 ) +
 scale_x_continuous(breaks = seq(min(yearly_NW$year),
                                 max(yearly_NW$year), by = 10)) +  # Breaks per decade
 theme_minimal() +
 theme(
  axis.title = element_text(size = 24),
  axis.text = element_text(size = 22),
  axis.line = element_line(color = "black"),
  plot.title = element_blank(),
```

```
  panel.grid = element_blank(),
  panel.border = element_rect(color = "black", fill = NA, linewidth = 1)
 )

# Fit a linear regression model to test for temporal trends
model <- lm(mean_prop_NW ~ year, data = yearly_NW)

# Display model summary (no significant effect here)
summary(model)

# Check structure of summarised dataset
summary(yearly_NW)

# 95% predcition intervals (PIs)
# Empirical 95% interval of annual NW proportions
quantile(yearly_NW$mean_prop_NW, probs = c(0.025, 0.975), na.rm = TRUE)
```

Ethics Approval

Swansea University
Prifysgol Abertawe

Approval Date: 04/06/2025

Research Ethics Approval Number: 1 2025 13592 12997

Thank you for completing a research ethics application for ethical approval and submitting the required documentation via the online platform.

Project Title	The role of wind-induced crash mortality on nesting seabird population dynamics
Applicant name	MR STEFAN BARNETT
Submitted by	MR STEFAN BARNETT /
Full application form link	https://swansea.forms.ethicalreviewmanager.com/Project/Index/16061

The Science and Engineering ethics committee has approved the ethics application, subject to the conditions outlined below:

Approval conditions

1. The approval is based on the information given within the application and the work will be conducted in line with this. It is the responsibility of the applicant to ensure all relevant external and internal regulations, policies, and legislations are met.
2. This project may be subject to periodic review by the committee. The approval may be suspended or revoked at any time if there has been a breach of conditions.
3. Any substantial amendments to the approved proposal will be submitted to the ethics committee prior to implementing any such changes.

Specific conditions in respect of this application:

The application has been classified as Low Risk to the University.

No additional conditions.

Statement of compliance

The Committee is constituted in accordance with the Governance Arrangements for Research Ethics Committees. It complies with the guidelines of UKRI and the concordat to support Research Integrity.

Science and Engineering Research and Ethics Chair

Swansea University.

If you have any queries regarding this notification, then please contact your research ethics administrator for the faculty.

- For Science and Engineering contact FSE-Ethics@swansea.ac.uk
- For Medicine, Health and Life Science contact FMHLS-Ethics@swansea.ac.uk
- For Humanities and Social Sciences contact FHSS-Ethics@swansea.ac.uk

Swansea University
Prifysgol Abertawe

HEALTH & SAFETY
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Risk Assessment

The demographic role and drivers of crash mortality in nesting seabirds - MRes project

College/PSU	Swansea university biosciences	Assessment Date	23/03/25
Location	SLAM lab/home desk	Assessor	Stefan Barnett
Activity	Desk based project	Review Date (if applicable)	n/a
Associated documents	•	•	

Part 1: Risk Assessment

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
Prolonged computer use (eye strain, repetitive strain injury, posture issues)	Stefan Barnett	Eye strain, headaches, musculoskeletal problems	Taking regular breaks, using ergonomic chair/desk, adjusting monitor height	No	n/a	n/a	n/a
Stress and workload management	Stefan Barnett	Anxiety, reduced wellbeing, burnout	Structured timetable, supervisor meetings, breaks	Access university wellbeing services if needed	Stefan Barnett	As needed	No

What are the hazards?	Who might be harmed?	How could they be harmed?	What are you already doing?	Do you need to do anything else to manage this risk?	Action by whom?	Action by when?	Done Yes/No
Electrical hazards from equipment	Stefan Barnett	Electric shock, equipment damage	Using PAT-tested university equipment, safe cabling	Report faulty equipment immediately	Stefan Barnett	As needed	Yes
Data loss or corruption	Stefan Barnett	Loss of research progress, delays in submission	Backing up work to university servers/external hard drive	Ensure regular automatic backups are set up	Stefan Barnett	Immediately	Yes

Part 2: Actions arising from risk assessment

Actions	Lead	Target Date	Done Yes/No
Set up regular data backups	Stefan Barnett	Immediately	Yes
Schedule work breaks	Stefan Barnett	Ongoing	Yes
Access university wellbeing services	Stefan Barnett	As needed	No
Report faulty electrical equipment as needed	Stefan Barnett	As needed	No