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**Horswill, C ORCID: 0000-0002-1795-0753, Wood, Matt J ORCID: 0000-0003-0920-8396 and Manica, A (2022) Temporal change in the contribution of immigration to population growth in a wild seabird experiencing rapid population decline. *Ecography*, 2022. ART e05846. doi:10.1111/ecog.05846 (In Press)**

Official URL: <http://doi.org/10.1111/ecog.05846>  
DOI: <http://dx.doi.org/10.1111/ecog.05846>  
EPrint URI: <https://eprints.glos.ac.uk/id/eprint/11618>

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## Research

### Temporal change in the contribution of immigration to population growth in a wild seabird experiencing rapid population decline

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#### Ecography

2022: e05846

doi: 10.1111/ecog.05846

Subject Editor:

Jean-Michel Gaillard

Editor-in-Chief: Miguel Araújo

Accepted 29 August 2022



The source–sink paradigm predicts that populations in poorer-quality habitats ('sinks') persist due to continued immigration from more-productive areas ('sources'). However, this categorisation of populations assumes that habitat quality is fixed through time. Globally, we are in an era of wide-spread habitat degradation, and consequently there is a pressing need to examine dispersal dynamics in relation to local population change. We used an integrated population model to quantify immigration dynamics in a long-lived colonial seabird, the black-legged kittiwake *Rissa tridactyla*, that is classified as globally 'Vulnerable'. We then used a transient life table response experiment to evaluate the contribution of temporal variation in vital rates, immigration rates and population structure to realised population growth. Finally, we used a simulation analysis to examine the importance of immigration to population dynamics. We show that the contribution of immigration changed as the population declined. This study demonstrates that immigration is unlikely to maintain vulnerable sink populations indefinitely, emphasising the need for temporal analyses of dispersal to identify shifts that may have dramatic consequences for population viability.

Keywords: demography, dispersal, integrated population model, population dynamics, population viability, *Rissa tridactyla*

#### Introduction

To robustly predict how species and communities will respond to environmental change, we need to understand the mechanisms that stabilise meta-population dynamics (Kahilainen et al. 2018, Perry and Lee 2019). Meta-populations include individual subpopulations that vary in size, stability and dispersal-mediated connections (Thomas and Kunin 1999). There are several conceptual frameworks for describing the dynamics of spatially structured populations (Doncaster et al. 1997, Hanski 1999, Morris and Diffendorfer 2004), however, a dominant paradigm is the source–sink perspective (Pulliam 1988, Pulliam and Danielson 1991). Source populations are self-supporting,



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occupy higher quality habitats and produce surplus individuals that emigrate to sink populations. By contrast, sink populations occupy lower quality habitats and require an influx of individuals from source populations in order to persist (i.e. a rescue effect, Brown and Kodric-Brown 1977). However, this categorisation of populations as either sources or sinks assumes that habitat quality is constant through time. In reality, many species are experiencing wide-spread population decline due to habitat degradation (Newbold et al. 2015, Maxwell et al. 2016), and how this may influence local emigration or immigration dynamics, and in turn population viability, remains an open question.

Rigorous identification of source–sink dynamics requires detailed information on population-specific vital rates, as well as rates of movement among populations (Schaub et al. 2010). Although rates of reproduction and adult survival are often empirically estimable, measuring dispersal between populations remains complicated by the logistic requirements of data collection at several sites, with large samples needed at each site if rates of dispersal are low (MacDonald and Johnson 2001). Few datasets are available to investigate source–sink dynamics at this scale (Furrer and Pasinelli 2016), and, as a result, studies of source–sink systems are typically based on single populations and little or no movement data (Diffendorfer 1998).

Studies identifying wild populations as apparent sinks or sources typically compare the observed population trajectory to the theoretical one calculated from vital rates (Pulliam 1988, Runge et al. 2006). More recently, there is a growing body of literature using integrated population models (IPM) to conduct this analysis (Peery et al. 2006, Schaub et al. 2010, Weegman et al. 2016, Fay et al. 2019, Paquet et al. 2020). IPMs provide an analytical framework for combining demographic and count data with the benefit of obtaining more precise parameter estimates (Schaub and Abadi 2011) and imputing demographic parameters for which no direct data are available. For example, fecundity in Besbeas et al. (2002), age-specific survival in Horswill et al. (2016) and immigration in Abadi et al. (2010). However, to date, studies using this approach to quantify temporal change in emigration or immigration dynamics and their contribution to population dynamics as a population declines are lacking.

In this study, we use an IPM to quantify temporal changes in vital rates, immigration dynamics and population structure for a declining population of black-legged kittiwakes *Rissa tridactyla* (hereafter kittiwake). We then used a transient life table response experiment to evaluate the contribution of these changes to realised population growth, and a simulation analysis to examine the importance of immigration to population viability. Kittiwakes are long-lived colonial seabirds that are classified as globally ‘Vulnerable’ and have experienced marked population decline since the 1980s (BirdLife International 2022b). Furthermore, current rates of decline are estimated to be greater than 40% over three generations raising concerns over the impact of future threats from climate change and offshore renewable energy developments (Bradbury et al. 2014, Ruffino et al. 2020, BirdLife International 2022a). More

broadly, seabirds are one of the most threatened groups of birds in the world with almost half (47%) of all species demonstrating declining population trends (Croxall et al. 2012, BirdLife International 2018, 2022a). Consequently, there is a pressing need to identify sink populations and understand their resilience to continued population decline.

## Methods

### Study species

This study uses long-term population and demographic data collected from kittiwakes breeding on Skomer Island, Wales, UK (51.74°N, 5.30°W). Kittiwakes are a pelagic seabird that reproduce once per year during the boreal summer. More than 50% of the global population breed in Europe (including Greenland) and breeding colonies are located along the Atlantic coast from the high Arctic (80°N) to mid-temperate latitudes (40–45°N) (BirdLife International 2022b). During the breeding season, kittiwakes forage under central place constraint, such that foraging trips are limited by the distance they can travel from their colony (11.9 km, IQR 4.2–30.9; Wakefield et al. 2017). Outside of the breeding season, kittiwakes from different breeding colonies in the North Atlantic predominantly share wintering grounds in the West Atlantic, between Newfoundland and the Mid-Atlantic Ridge (Frederiksen et al. 2012).

Mark–recapture data were collected between 1978 and 2018 from 604 kittiwakes marked as breeding adults with colour rings. Birds were marked and re-sighted during the summer breeding season, such that the re-sighting interval was 1 year. Repeated checks were made during the breeding season to record all colour ringed birds. Although intermittent breeding is reported in kittiwakes, whereby approximately 90% of birds breed annually, non-breeders still return to the colony and are equally available for recapture (Cam et al. 1998). Fecundity was monitored annually from 1989 to 2018 within three subplots on Skomer Island. Each plot was checked regularly from the onset of egg laying in late May until the completion of fledging in early August. Fecundity rates represent the proportion of nests that produce a successful fledgling each year. Although kittiwakes can produce a clutch of three eggs, annual rates of fecundity on Skomer Island are consistently below two chicks per nest. Finally, to estimate the size of the breeding population, full-island censuses of apparently occupied nests were conducted annually between 1989 and 2018. Counts were completed in good visibility during the incubation period of the breeding season which occurs between late May and mid-June. All observations were conducted from permanent vantage points using binoculars or a telescope following international guidelines for seabird monitoring (Walsh et al. 1995).

### Integrated population model (IPM)

We constructed an integrated population model (IPM) to make inference on the population dynamics of kittiwakes

breeding on Skomer Island. The IPM consisted of a structured population model parameterised using three interlinked components describing the likelihood of the mark–recapture, fecundity and breeding population count data (Fig. 1). Using this framework, we were able to solve for annual rates of immigration based on the difference between the observed population size and the theoretical population trajectory calculated from the imputed vital rates (i.e. survival and fecundity) (Abadi et al. 2010, Schaub and Fletcher 2015, Fig. 1–2).

The structured population model was based on a pre-breeding census (Caswell 2001). The mark–recapture data did not include information on sexes and therefore we assumed an even sex ratio and modelled females only. Previous studies have shown that kittiwakes first breed between three and five years old (Porter and Coulson 1987, Cam et al. 2002). We included this structure by assuming that 25% of 3 year olds, 75% of 4 year olds and all birds 5 years or older are breeders (Frederiksen et al. 2004). In Eq. 1, the value  $b$  describes the proportion of individuals that move between the pre-breeding age classes annually;  $b = 0.25$  (Fig. 2).

$$\begin{aligned}
 N_{1,t+1} &\sim \text{Bin}(f_t * \phi_{j,t}, N_{4,t}) \\
 N_{2,t+1} &\sim \text{Bin}(\phi_{j,t}, N_{1,t}) \\
 N_{3,t+1} &\sim \text{Bin}(\phi_{a,t}, ((1-b) * N_{2,t} + b * N_{3,t})) \\
 N_{4,t+1} &\sim \text{Bin}(\phi_{a,t}, (b * N_{2,t} + (1-b) * N_{3,t} + N_{4,t} + N_{im,t}))
 \end{aligned}
 \tag{1}$$

Here,  $N_{n,t}$  is the population size of  $n$  classes in year  $t$  (for  $1 \leq n \leq 4$ ) each modelled with binomial demographic stochasticity. The proportion of nests that produce a successful

fledgling ( $f$ ) and the probability of surviving to age one year ( $\phi_{j,t}$ ) were combined to estimate survival across the juvenile age class (0–1 years):  $f_j \phi_{j,t}$ . Following previous studies on kittiwake rates of survival (Link et al. 2002, Cam et al. 2005), we allowed birds to survive the immature age class (1–2 years,  $N_{2,t}$ ) with a probability equivalent to juveniles ( $\phi_{j,t}$ ) and the pre-breeding class ( $N_{3,t}$ ) with a probability equivalent to breeding adults ( $\phi_{a,t}$ ) (Fig. 2). All survival probabilities are apparent survival from year  $t - 1$  to  $t$ . Data on fecundity in year  $t$  ( $f$ ) were included at 50% to reflect the assumption of an even sex ratio. Immigrant birds ( $N_{im,t}$ ) entered the breeding age class to reflect birds recruiting into the breeding population, as opposed to prospecting (Cadiou et al. 1994). We also assumed that individuals breed every year. Details describing the specification of the initial population structure are given in the Supporting information.

In Bayesian statistics, prior distributions can be used to summarise our understanding of how the world works to obtain meaningful inference from small and fragmented datasets (Hobbs and Hooten 2015). Like many seabirds, kittiwakes are largely unobservable during the first years of life, and population-specific estimates of juvenile survival rates are limited (Horswill and Robinson 2015). Similar to other species of seabird (Horswill et al. 2014), previous studies on age-specific survival in kittiwakes report that probabilities are similar during the first two years following fledging and vary additively with time across age-classes (Link et al. 2002, Cam et al. 2005, Aubry et al. 2009, Desprez et al. 2011). We incorporated this structure by assuming identical rates of survival during the juvenile and immature years and assigning the intercept (i.e. mean) value on the observed scale from a beta prior distribution to limit inference between zero and

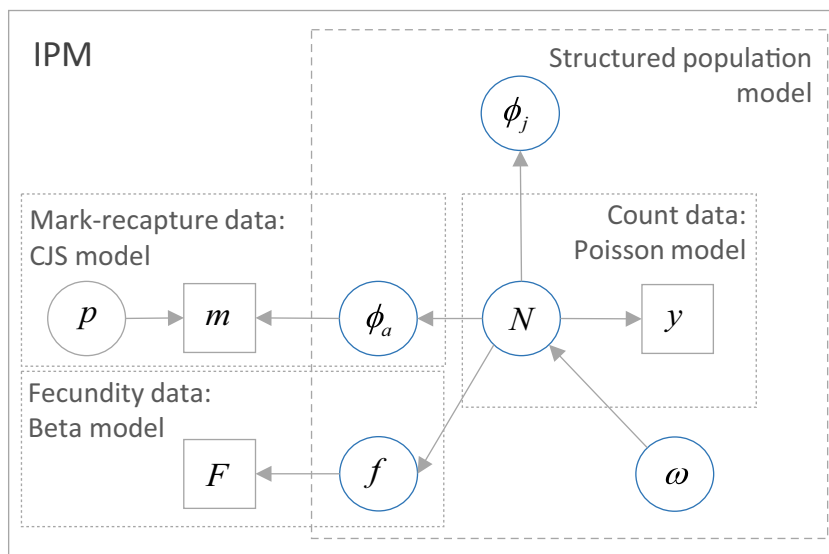


Figure 1. Graphical representation of the integrated population model (IPM) used to estimate demographic parameters of kittiwakes breeding on Skomer Island. Small grey squares represent data sources;  $m$  mark–recapture,  $F$  fecundity,  $y$  breeding population counts. Small circles represent the parameters (blue denotes target parameters);  $\phi_j$  juvenile survival probability,  $\phi_a$  adult survival probability,  $f$  fecundity probability,  $\omega$  immigration,  $N$  structured population,  $p$  recapture probability. Large dotted squares show the individual likelihood components, large dashed square the structured population model and large solid square the joint likelihood IPM. Arrows show the flow of information.

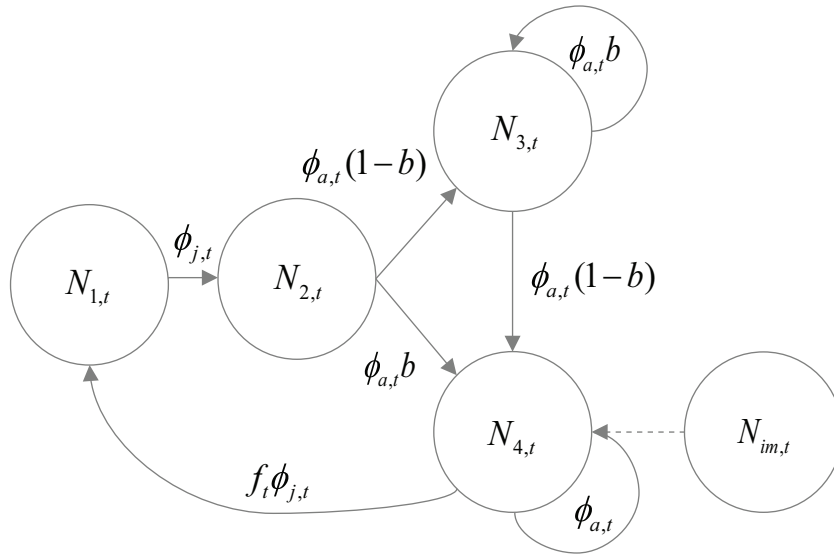


Figure 2. Lifetime cycle graph representing the state process equations (Eq. 1) describing kittiwake population dynamics at Skomer Island. Birds reach age 1 year ( $N_{1,t}$ ) with probability  $f_t\phi_{j,t}$ , and age 2 years ( $N_{2,t}$ ) with probability  $\phi_{j,t}$ . At age two, 75% ( $1 - b$ ) of individuals move to the third (pre-breeding) class ( $N_{3,t}$ ) and 25% ( $b$ ) of individuals enter the breeding class ( $N_{4,t}$ ). From the third class, 25% ( $b$ ) of individuals remain as pre-breeders and 75% ( $1 - b$ ) become breeders ( $N_{4,t}$ ). From age two, individuals have a survival probability equivalent to that of adults ( $\phi_{a,t}$ ). Immigrating birds ( $N_{im,t}$ ) enter the breeding class (dashed arrow).

one. Following reported estimates of juvenile and immature rates of kittiwake survival, we set the mean of this prior distribution at 0.6 (Link et al. 2002, Cam et al. 2005) and assigned a large variance to allow some flexibility during model fitting (see Supporting information for the prior and posterior distributions of this parameter).

To incorporate additive temporal variation in age-specific survival, we applied environmental stochasticity to the juvenile age class on the logit scale using the value imputed from the mark–recapture data for adults ( $\varepsilon_{\phi,t}$ , Eq. 2). Variation on the logit scale is reduced on the observed scale at the bounds (i.e. zero and one). Therefore, although annual fluctuations in survival will occur synchronously across age classes, the magnitude of these fluctuations will vary depending on the age-specific intercept (i.e. mean) value. Here, age-classes with a high mean value, such as adults, will have lower annual variation on the observed scale, than age classes with a mean value closer to 0.5, such as juveniles. The influence of assumptions regarding age of first breeding, breeding propensity and age-specific survival rates were tested and found to either 1) not qualitatively affect the results, or 2) substantially reduce model fit (Supporting information).

We specified annual immigration in terms of the number of individuals ( $N_{im,t}$ , Eq. 1) entering the breeding age class ( $N_{4,t}$ , Eq. 1) each year using a gamma random effect. We imputed immigration as individuals, rather than a rate, to obtain more precise parameter estimates (Schaub and Fletcher 2015). We set the mean of the gamma distribution to 100 and assigned the standard deviation from a uniform prior distribution bound between 0.001 and 5000. We selected a gamma distribution to impute immigration, as opposed to a Poisson, to allow the mean and variance

terms to differ. This is similar to parameterising this prior distribution using a Poisson regression model with a log link function (Paquet et al. 2021). However, using a Poisson model reduced model fit and convergence (Supporting information).

To estimate rates of kittiwake apparent adult survival from the mark–recapture data, we used a state-space formulation of the Cormack–Jolly–Seber (CJS) model (Gimenez et al. 2007, Fig. 1). Here, we used the state process to impute individual ( $i$ ) survival events ( $\phi_{i,t}$ ) and the observation process to impute individual recapture events ( $p_{i,t}$ ). Both processes were modelled using Bernoulli distributions with a logit link function (Eq. 2):

$$\begin{aligned} \text{logit}(\phi_{i,a,t}) &\sim \text{Bern}(\alpha_0 + \varepsilon_{\phi,t}) \\ \text{logit}(p_{i,t}) &\sim \text{Bern}(\delta_k + \varepsilon_{p,t}) \end{aligned} \tag{2}$$

Initial goodness-of-fit testing conducted in Program MARK (v.9.x) (White and Burnham 1999) using the RELEASE program (Burnham et al. 1987) identified trap-dependence (i.e. capture heterogeneity) in the data (Supporting information). Consequently, we incorporated this structure (i.e. trap-dependent recapture rates) in the CJS model. In Eq. 2,  $\alpha_0$  and  $\delta_k$  are the intercept terms for adult survival and recapture probabilities, respectively, and recapture is modelled as a function of whether or not an individual was captured in the preceding year ( $\delta_1 = \text{yes}$ ,  $\delta_2 = \text{no}$ ) (Kéry and Schaub 2012). We also included a random effect term ( $\varepsilon_{\cdot,t}$ ) in each function to represent annual environmental stochasticity for survival and variation in sampling effort for recapture.

For the likelihood component describing the fecundity data we used a beta state-space formulation (Fig. 1). Here, we imputed annual fecundity ( $f_t$ ) as the state process and used a beta observation process to link the observed rates of fecundity to the imputed values. In the state process, we assumed an even sex ratio and modelled fecundity as 50% of the true fecundity (i.e. only females):

$$\text{logit}(f_t) = \beta_0 + \beta_1 t + \varepsilon_{f,t} \quad (3)$$

Here,  $\beta_0$  is the intercept term and  $\beta_1$  is a fixed effect with time ( $t$ ) that accounts for the long-term directional trend in this vital rate on Skomer Island (Horswill et al. 2022a). Finally,  $\varepsilon_{f,t}$  is a random effect term representing annual environmental stochasticity in fecundity. To define the shape of the beta observation process, we used the imputed values (Eq. 3) to set an annual mean and a published measure of sampling variability to set a constant variance (i.e.  $3 \times 10^{-3}$ , Frederiksen et al. 2004, Supporting information provides further details and example distribution reflecting the beta observation process).

To describe the likelihood of the breeding population count data we used a Poisson state-space model (Fig. 1). Here, we included the imputation of the annual structured population (Eq. 1) as the state process and used a Poisson observation process to link the observed annual counts of breeding pairs ( $y_t$ ) to the imputed values (i.e.  $y_t \sim \text{Poisson}(N_{4,t})$ , see Supporting information for example distributions reflecting the Poisson observation process).

We fitted the IPM using a Bayesian approach in JAGS (v. 4.3.0) (Plummer 2003) via the 'jagsUI' library (v. 1.5.1) (Kellner 2019) for program R (v. 4.0.2) (<www.r-project.org>). We specified the prior distributions using biologically driven bounds (see Supporting information for details on the prior distributions). Model fitting involved running three Monte Carlo Markov chains (MCMC) for  $5 \times 10^5$  iterations and retaining every 100th step to minimise autocorrelation in the MCMC sampling. To confirm convergence of the chains we used the Brooks–Gelman–Rubin diagnostic tool (all values  $\hat{r} \leq 1.01$ ) and the effective sample size of the MCMC chains for each parameter. Trace plots of the MCMC chains for imputed vital rates and parameters are provided in the Supporting information. We removed the first  $5 \times 10^5$  MCMC draws as burn-in, and visually checked that convergence of the MCMC chains had occurred before this cut off. Global goodness-of-fit tests do not exist for IPMs. Therefore, we verified goodness of fit separately for each likelihood component and by simulating the population trajectory from the joint posterior distribution of the IPM without the count data (see Supporting information for details and results).

### Transient life table response experiment (LTRE) analysis

We used a transient life table response experiment (LTRE) analysis to examine the retrospective contribution of survival, fecundity, immigration and population structure to changes

in the realised population growth rate between successive years (Koons et al. 2016, 2017). Here, we calculated the difference in the realised population growth rate ( $\lambda_t$ ) between years  $t$  and  $t+1$  as:

$$\Delta\lambda_t = \sum_i (\theta_{i,t+1} - \theta_{i,t}) \frac{\partial \lambda_t}{\partial \theta_{i,t}} \bigg|_{\bar{\theta}_i} \quad (4)$$

Here,  $\theta$  is a vector containing the full posterior distribution for survival probability, fecundity probability, immigration probability and population structure, and  $\frac{\partial \lambda_t}{\partial \theta_{i,t}} \bigg|_{\bar{\theta}_i}$

are the growth rate sensitivities calculated as the first derivative of the realised growth rate with respect to all elements in  $\theta$  evaluated at the mean values between successive years (Koons et al. 2016). To validate this analysis, we checked that the sum of the estimated annual contributions from survival, fecundity, immigration and population structure to population growth were approximately identical to the annual difference in rates of population growth estimated directly by the IPM (Spearman correlation coefficient = 0.96, Supporting information). The LTRE analysis was conducted in program R (v. 4.0.2) (<www.r-project.org>).

### Influence of immigration on population size

We used a simulation analysis based on the modelled vital rates without immigration to examine the importance of immigration to population viability. Inspection of the breeding population count data showed that population decline over the study period did not occur at a constant rate but in two step changes with three periods of relative stability (Fig. 3). To objectively identify the start and end points of these phases, we used a multiple changepoint algorithm with a nonparametric cost function implemented using the statistical package 'changepoint.np' (ver. 1.0.2) (Haynes and Killick 2020) in program R (ver. 4.0.2) (<www.r-project.org>). To obtain measures of uncertainty in the change points, we applied the multiple changepoint analysis to 500 timeseries of population counts ( $N_{4,t}$ ) randomly selected from the full posterior distribution of this parameter (Fig. 3). We used the modified Bayesian information criterion (MBIC) penalty when fitting the changepoint analysis, however the results were unchanged by replacing this penalty with the Schwarz information criterion (SIC) or Bayesian information criterion (BIC).

We built discrete population projection models for each phase of the population trajectory. The structure of these models followed the structure of the IPM (Eq. 1) without immigration. We examined the three phases of the population trajectory in isolation to prevent deficit individuals generated during the previous phase from biasing the starting population size. The three time periods were initiated with a stable age distribution based on the number of breeding

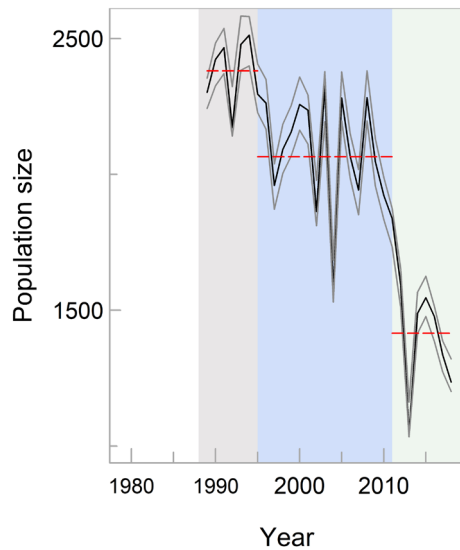


Figure 3. The population of black-legged kittiwakes on Skomer Island declined rapidly in two step changes and three phases of relative stability. During the first phase (grey polygon; 1989–1995) the mean population size was 2378 (shown by red dashed line). During the second phase (blue polygon; 1995–2012) the mean population size was 2068 (shown by red dashed line), and during the third phase (green polygon; 2012–2018) the mean population size was 1390 (shown by red dashed line). Observed population count data are shown as a black line with 95% credible intervals from the IPM as grey lines.

females observed in that year. We ran each model for 5000 iterations, each parameterised with a time-series of vital rates randomly selected from the complete joint posterior distribution of the IPM. By randomly selecting values from the complete joint posterior distribution, we were able to propagate correlated parameter uncertainty through to the population projections (Horswill et al. 2021). We also repeated this analysis by altering the change points in the population trajectory by  $\pm 1$  year to account for uncertainty estimated in the multiple changepoint analysis.

## Results

### Demography

All values reported are median posterior values imputed by the IPM. The intercept (i.e. mean) value for adult kittiwake survival on Skomer Island was 0.88 (95% CRI: 0.85–0.90). In addition, the standard deviation of temporal variation in adult survival was 0.65 (95% CRI: 0.48–0.90, Fig. 4A). The intercept (i.e. mean) value for recapture rates was higher for individuals seen in the previous year (0.88, 95% CRI: 0.85–0.91), than individuals not seen in the previous year (0.29, 95% CRI: 0.23–0.35). In addition, the standard deviation of temporal variation in recapture was 0.63 (95% CRI: 0.46–0.85). The intercept (i.e. mean) value for juvenile kittiwake survival was 0.18 (95% CRI: 0.03–0.38, Fig. 4B). Fecundity declined at a constant rate over the study period from 0.75

(95% CRI: 0.55–0.94) in 1989 to 0.62 (95% CRI: 0.43–0.82) in 2018 (slope =  $-0.02$ , 95% CRI:  $-0.04$ ,  $-1.07 \times 10^{-4}$ , Fig. 4D). In addition, the standard deviation of temporal variation in fecundity was 0.41 (95% CRI: 0.27–0.60). Rates of immigration were highly variable between years (range: 0–0.57, Fig. 4E), and the standard deviation of the random effect term assigning immigration of individuals was 203.23 (95% CRI: 146.86–300.42). Median posterior values and 95% credible intervals are provided for all parameters in the Supporting information.

### Transient life table response experiment (LTRE) analysis

Immigration was the dominant driver of population dynamics over the study period and its contribution was greatest during the second phase of the population trajectory when high variation in realised population growth also occurred (Fig. 5A–B, Supporting information). These results were unchanged by altering model assumptions (Supporting information).

### Influence of immigration on population size

The multiple changepoint analysis revealed that the population declined in two step changes between 1989 and 2018. The first step change occurred in 1995 ( $\pm 1.19$  years) and the second step change occurred in 2011 ( $\pm 0.74$  years) (Fig. 3). We used these divisions to examine the importance of immigration for maintaining population dynamics during each phase. Comparing the observed population count data to the simulated dynamics based on modelled vital rates without immigration confirmed that the population of kittiwakes at Skomer Island acted as a sink during the study period and was heavily reliant on immigration (Fig. 6). In agreement with the transient LTRE, immigration was most important during the second phase of the population trajectory for maintaining the observed dynamics (Fig. 5–6). Furthermore, these results were unchanged by altering model assumptions (Supporting information), or by accounting for uncertainty in the position of the changepoints in the population trajectory ( $\pm 1$  year, Supporting information).

## Discussion

The persistence of sink populations depends on a continued supply of immigrating individuals (Brown and Kodric-Brown 1977). However, it is unknown how the contribution of immigration to population dynamics may change as a sink population declines due to local changes in habitat quality. We used an integrated population model (IPM) to examine immigration dynamics in a declining population of kittiwakes over 30 years. We then used a transient life table response experiment to examine the contribution of changes in vital rates, immigration and population structure to realised population growth. Finally, we used a simulation analysis to investigate the importance of immigration to population viability.

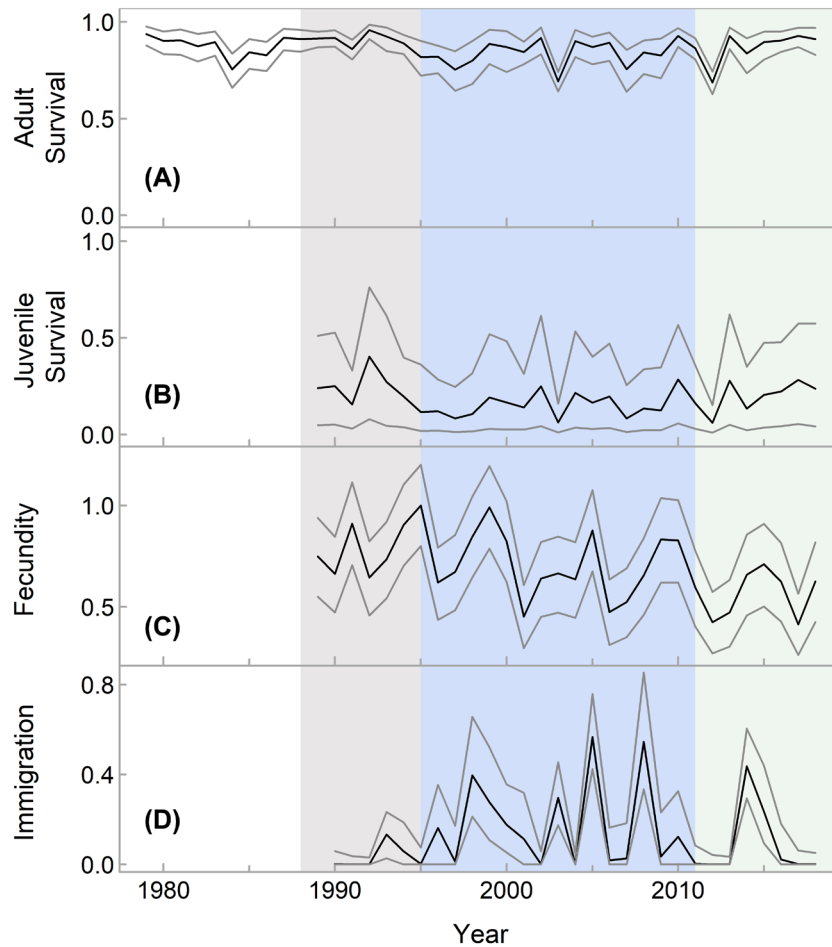


Figure 4. Demographic rates of black-legged kittiwakes breeding on Skomer Island across the three phases of the population trajectory: phase 1 – grey, phase 2 – blue, phase 3 – green (Fig. 3). (A) Rates of adult survival (i.e. birds older than 2 years of age). (B) Rates of juvenile survival (i.e. birds from 0 to 1 and 1 to 2 years of age). (C) Rates of fecundity (male and female chicks, i.e. 100% fecundity) declined over the study period. (D) Rate of immigration were consistently higher during the second phase of the population trajectory. In all panels, posterior median values from the IPM are shown as black lines and 95% credible intervals as grey lines.

It was not possible to recreate the observed population trajectory for kittiwakes at Skomer Island with only philopatric recruitment, indicating that immigration played an important role in generating the observed dynamics. However, the contribution of immigration to population growth changed over the study period. The observed changes in rates of immigration and its contribution to population growth may reflect the changing attractiveness of the breeding colony as the population declined. Here, immigration potentially increased during the second phase of the population trajectory as good nesting sites became available (Porter and Coulson 1987), but decreased during the third phase once local rates of fecundity reached a critical threshold indicating degeneration of the wider habitat (Frederiksen et al. 2004).

Fecundity declined over the study period and was lowest during the final phase of the population trajectory. Adverse environmental conditions are linked to increased dispersal in other species of seabird (Oro et al. 2004, Fernández-Chacón et al. 2013, Payo-Payo et al. 2018), and experimental studies have shown that failed breeding attempts in kittiwakes

precede increased prospecting of alternative breeding colonies (Ponchon et al. 2015). Low nesting densities have also been linked to depensatory control of fecundity in kittiwakes (Horswill et al. 2017), where the proposed mechanism is less efficient nest defence and increased predation (Porter 1990, Falk and Møller 1997). Depensatory mechanisms have been attributed to accelerated population decline and collapse in other species (Lande et al. 1994). Our results suggest that once declining sink populations reach a critical size, social cues that influence attractiveness to new recruits, such as colony-wide breeding success (Boulinier et al. 2008), may decrease rates of immigration potentially destabilising population dynamics.

We show that without immigration, the population of kittiwakes breeding on Skomer Island would be close to extinction. This result highlights the inflated vulnerability experienced by sink populations, whereby a decrease in rates of immigration accelerates population decline. Kittiwakes are declining throughout their range (BirdLife International 2022b), and therefore, understanding how changing immigration dynamics are likely to influence sink populations is



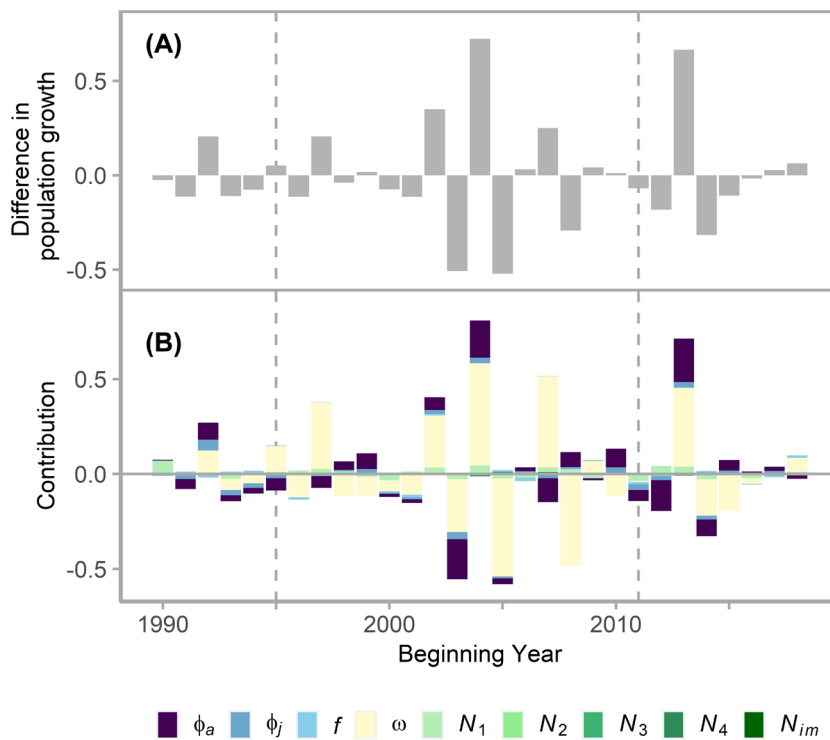


Figure 5. The transient life-table response experiment demonstrated that (A) changes in the realised population growth rate of kittiwakes breeding on Skomer Island estimated from the IPM could be (B) best explained by changes in immigration ( $\omega$ ) and adult survival ( $\phi_a$ ). Changes in juvenile ( $\phi_j$ ) survival rates and the population structure ( $N_1$ -1 year old birds,  $N_2$ -2 year old birds,  $N_3$ -pre-breeding birds age 3 years,  $N_4$ -breeding birds age 3+ years,  $N_{im}$  - immigrating breeders) had hardly any impact. Step declines in the population trajectory (Fig. 3) shown as dashed vertical lines. All contributions with 95% credible intervals are provided in the Supporting information.

central to predicting future meta-population resilience and identifying sites to protect for long-term species viability.

In this study, we use an IPM to impute the annual immigration dynamics of a declining seabird population. In the IPM, immigration is imputed using a hidden (or latent) parameter that is not directly informed by data but imputed based on the difference between the observed population growth rate and the theoretical growth rate calculated from vital rates. Hidden parameters can soak up inconsistencies from other parts of the model, for example from unmodelled heterogeneity of survival probabilities (Riecke et al. 2019) or non-random temporal variation in other demographic parameters (Paquet et al. 2019). Importantly, we did not identify significant levels of survival heterogeneity in the mark-recapture dataset (Supporting information). However, estimates of hidden parameters should still be interpreted with care (Schaub and Kéry 2021).

The inclusion of more than one hidden demographic parameter in an IPM can generate identifiability issues because they are both solving for the difference between the observed and theoretical population growth rates (Schaub and Kéry 2021). In our IPM, annual immigration and the intercept (i.e. mean) value for juvenile survival are both imputed using hidden parameters. However, whilst inference of immigration was highly flexible, we used scientific knowledge on the demography of kittiwakes to specify biologically driven constraints on the inference of juvenile survival (Link et al. 2002,

Cam et al. 2005, Aubry et al. 2009, Desprez et al. 2011, Supporting information). The median posterior value for mean juvenile survival (0.18, 95% CRI 0.03, 0.38) was considerably lower than the published estimate for juvenile kittiwakes breeding in France (0.6, Link et al. 2002, Cam et al. 2005). However, whilst loosening and tightening constraints on the prior distribution assigning mean juvenile survival allowed the posterior value to differ (Supporting information), the imputed number of annual immigrants remained qualitatively similar (Supporting information). This result most likely reflects the low demographic impact (i.e. elasticity) associated with juvenile rates of survival in long-lived species (Gaillard et al. 2000), such as seabirds. It also highlights that the values of juvenile survival reported here should not be used to describe the demography of kittiwakes breeding on Skomer Island or the UK more broadly.

We assigned annual values of immigration using a random effect where a large standard deviation was estimated during model fitting. IPMs provide good estimates of temporal variation in immigration when this process varies substantially, although distinguishing between an accurate estimation from data with high temporal variation in immigration and an overestimation from data with low temporal variation is not consistently reliable (Paquet et al. 2021). The population size of kittiwakes on Skomer Island fluctuates greatly between years. The IPM indicates that this is predominantly driven by temporal variation in apparent adult survival and

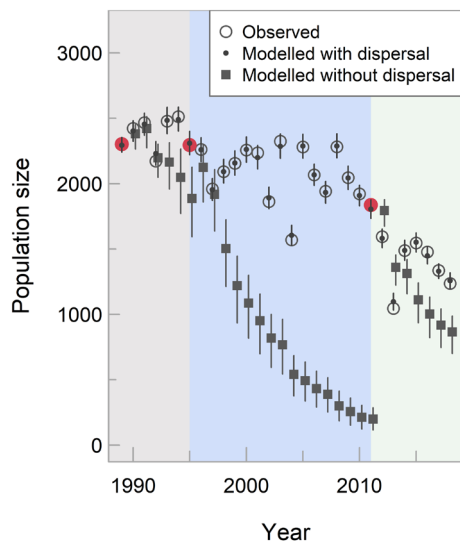


Figure 6. Observed population size (open circles) and modelled posterior median values estimated with immigration (black filled circles, with 95% credible intervals) for kittiwakes breeding on Skomer Island, 1989–2018. Population projections based on rates of survival and fecundity without immigration (with 95% credible intervals, offset filled squares) for each phase of the population trajectory. Starting values for each population projection shown as red circle. When immigration was included, the observed and modelled population sizes matched (i.e. open circles and filled circles overlapped); however, when immigration was not included deficit individuals were generated in all phases, albeit to a considerably greater extent during the second phase (blue polygon).

immigration. An alternative explanation is that it reflects unaccounted variation in breeding propensity. However, previous studies report that breeding propensity in kittiwakes is relatively stable through time and that, importantly, non-breeding individuals still return to the colony and, therefore, are equally available as breeding individuals for recapture and censusing (Cam et al. 1998). Understanding the processes driving large annual declines in kittiwake population size is therefore a key priority for future work.

By fitting the IPM using a Bayesian state-space framework, we incorporated observation models to account for uncertainty in fecundity, adult survival and population count estimates. In addition, we incorporated a temporal trend in fecundity with a vague prior distribution on the coefficient term to allow observed changes in this demographic process to be explicitly included and estimated during model fitting. Rates of adult survival did not show a directional trend over the study period; however, we cannot be certain that mean rates of juvenile survival or age of first breeding remained constant. Relaxing the biologically driven constraints on juvenile survival to generate large credible intervals on annual estimates did not qualitatively alter the results (Supporting information). In addition, a density-dependent decrease in the age of first breeding over the study period (Porter and Coulson 1987) would not generate the results observed because philopatric individuals can start breeding a year

earlier, such that less, not more, immigrants would be needed to stabilise dynamics as the population declined.

This study indicates that immigration into wild populations can change in relation to local population dynamics. We show that increased rates of immigration may compensate for local shortages in recruitment, however this buffering is unlikely to maintain population dynamics indefinitely. For example, continued decline in population size and breeding density may alter the attractiveness of a colony, decreasing rates of immigration and accelerating rates of population decline. More broadly, our results highlight the importance of considering the changing contribution of dispersal dynamics as populations decline to identify shifts that may lead to sudden changes in population viability.

**Acknowledgements** – We thank Professor Chris Perrins for starting and maintaining the long-term monitoring of kittiwakes on Skomer Island, as well as all fieldworkers who have supported data collection. We also thank David Koons and Michael Schaub for discussions regarding transient life table response experiences, as well as Jean-Michel Gaillard and three anonymous reviewers for providing comments during the review process.

**Funding** – This work was supported by funding from Research England to CH, and the UK Joint Nature Conservation Committee (DEFRA) and the Wildlife Trust of South and West Wales to MJW.

**Ethics statement** – Attachment of leg rings to birds for mark–recapture analysis is conducted by individuals certified with BTO ringing permits. All monitoring of kittiwakes on Skomer Island is evaluated and approved by the Wildlife Trust of South and West Wales.

## Author contributions

**Cat Horswill:** Conceptualization (lead); Data curation (supporting); Formal analysis (lead); Funding acquisition (equal); Investigation (lead); Methodology (lead); Project administration (lead); Resources (equal); Software (lead); Supervision (equal); Validation (lead); Visualization (lead); Writing – original draft (lead); Writing – review and editing (equal). **Matt J. Wood:** Data curation (lead); Funding acquisition (equal); Writing – original draft (supporting); Writing – review and editing (equal). **Andrea Manica:** Conceptualization (supporting); Formal analysis (supporting); Methodology (supporting); Writing – review and editing (equal).

## Transparent peer review

The peer review history for this article is available at <<https://publons.com/publon/10.1111/ecog.05846>>.

## Data availability statement

Data used in this study are available from the University of Gloucestershire Repository: <<https://doi.org/10.46289/C5DAC648>>. Code used to run the analyses are available from the Dryad Digital Repository: <<https://doi.org/10.5061/dryad.q83bk3jmj>> (Horswill et al. 2022b).

## Supporting information

The Supporting information associated with this article is available with the online version.

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