

RESEARCH ARTICLE

Robustly estimating the demographic contribution of immigration: Simulation, sensitivity analysis and seals

Murray Christian^{1,2}  | W. Chris Oosthuizen²  | Marthán N. Bester¹  |
P. J. Nico de Bruyn¹ 

¹Department of Zoology and Entomology, Mammal Research Institute, University of Pretoria, Hatfield, South Africa

²Centre for Statistics in Ecology, the Environment and Conservation, Department of Statistical Sciences, University of Cape Town, Cape Town, South Africa

Correspondence

Murray Christian

Email: murraychristian@live.co.za

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Abstract

1. Identifying important demographic drivers of population dynamics is fundamental for understanding life-history evolution and implementing effective conservation measures. Integrated population models (IPMs) coupled with transient life table response experiments (tLTREs) allow ecologists to quantify the contributions of demographic parameters to observed population change. While IPMs can estimate parameters that are not estimable using any data source alone, for example, immigration, the estimated contribution of such parameters to population change is prone to bias. Currently, it is unclear when robust conclusions can be drawn from them.
2. We sought to understand the drivers of a rebounding southern elephant seal population on Marion Island using the IPM–tLTRE framework, applied to count and mark–recapture data on 9500 female seals over nearly 40 years. Given the uncertainty around IPM–tLTRE estimates of immigration, we also aimed to investigate the utility of simulation and sensitivity analyses as general tools for evaluating the robustness of conclusions obtained in this framework.
3. Using a Bayesian IPM and tLTRE analysis, we quantified the contributions of survival, immigration and population structure to population growth. We assessed the sensitivity of our estimates to choice of multivariate priors on immigration and other vital rates. To do so we make a novel application of Gaussian process priors, in comparison with commonly used shrinkage priors. Using simulation, we assessed our model's ability to estimate the demographic contribution of immigration under different levels of temporal variance in immigration.
4. The tLTRE analysis suggested that adult survival and immigration were the most important drivers of recent population growth. While the contribution of immigration was sensitive to prior choices, the estimate was consistently large. Furthermore, our simulation study validated the importance of immigration by showing that our estimate of its demographic contribution is unlikely to result as a biased overestimate.

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5. Our results highlight the connectivity between distant populations of southern elephant seals, illustrating that female dispersal can be important in regulating the abundance of local populations even when natal site fidelity is high. More generally, we demonstrate how robust ecological conclusions may be obtained about immigration from the IPM-tLTRE framework, by combining sensitivity analysis and simulation.

KEYWORDS

demographic contribution, Gaussian process, immigration, integrated population model, IPM, robust estimation, tLTRE, transient life-table response experiment

1 | INTRODUCTION

Understanding the drivers of population dynamics is a fundamental goal in ecology, and an important ingredient in efforts to mitigate current global declines in biodiversity. A better understanding of the demographic drivers (e.g. survival, reproduction, dispersal) of population growth allows us to predict how populations will change over time, to assess their vulnerability to environmental stressors and to develop effective conservation strategies (Koons et al., 2017). Moreover, identifying the demographic processes that shape population dynamics can generate insights into the evolution of life histories (Stearns, 1992). It is therefore essential that robust methods are available to quantify population growth rates and the demographic forces shaping them. The current state of the art consists of transient life table response experiments (tLTREs; Koons et al., 2016) coupled with integrated population models (IPMs; Besbeas et al., 2002; Schaub & Kéry, 2021). Together, these analyses leverage individual- and population-level data to potentially identify the most important drivers of observed population trends. However, several recent studies have shown that some IPM estimates are very sensitive to model misspecification (Plard et al., 2021; Riecke et al., 2019), while others obtained in the IPM-tLTRE framework may be systematically biased (Paquet et al., 2021). Thus, ecologists wishing to use these powerful methods face a dilemma. In most studies, no alternative methods of equal scope or rigour will be available, and yet, the reliability of certain IPM-tLTRE estimates may be doubtful, or difficult to gauge.

Integrated population models combine multiple data types in a single likelihood to estimate vital rates, population size and structure. They do this by modelling the state of the population as a latent process on which each data type depends through its own observation model. A major feature of IPMs is their ability to estimate 'additional' parameters (sensu Riecke et al., 2019) that are not identifiable from models of any one data type alone. A typical example is the estimation of immigration using mark-recapture, fecundity and population count data (Abadi et al., 2010). The mark-recapture and fecundity data inform rates of birth, death and emigration, allowing the IPM to extract the signal on immigration from the population count data.

The tLTREs we consider decompose the temporal variance in realised population growth rates into contributions due to each of the vital rates and population structure (see Koons et al., 2016 for two other types). These contributions take into account the temporal variance in each parameter, its covariance with other parameters and the sensitivity of the growth rate to changes in each parameter (Koons et al., 2016, 2017). In contrast to their predecessors, the various life table response experiments (LTREs; Caswell, 1989, 2010), they relax the assumptions that the population is in equilibrium or subject to stationary environmental variation—assumptions that are often inappropriate in a rapidly changing world. Whereas LTREs are possible using only vital rate estimates, tLTREs also require estimates of the population size and structure over time (Koons et al., 2016). Since few natural populations can be studied in sufficient detail to directly estimate all these quantities, IPMs will often be a prerequisite for tLTREs (Schaub & Kéry, 2021; Chapter 9.4).

While the estimation of additional parameters is a major potential benefit of IPMs, it is also one of their main challenges. Recent simulation studies show that biases in other model parameters readily propagate to the additional parameter (Plard et al., 2021; Riecke et al., 2019). Such biases may arise from a failure to account for individual heterogeneity, non-breeding adults and marker loss, among others. Even in the absence of bias affecting mean additional parameter estimates, their temporal variation may be difficult to estimate, creating problems for downstream tLTREs (Paquet et al., 2021). For example, when immigration is estimated as an additional parameter, these authors found that its tLTRE contribution was accurately estimated when the true contribution is moderate or large, but systematically overestimated when the true contribution is small. Here, we focus on immigration, but it is important to note that most of the methodological discussion applies to any additional parameter.

Integrated population models are typically fit in a Bayesian framework, where priors are specified as well as a likelihood. Because additional parameters are not directly informed by data, one expects their estimates to be sensitive to the prior structure used for them. While there is some work on prior specification for additional parameters (e.g. Schaub & Fletcher, 2015), there is still a need to better understand the use of multivariate priors in this

context. The multivariate priors we consider specify a distribution over the vector of annual values for a parameter in all years of the study; a common example is a year random effect (Kéry & Schaub, 2011, Chapter 4). Merely adopting a year random effect will draw annual estimates towards the overall mean, so these 'shrinkage' priors directly affect the temporal variance of parameters, and the sensitivity of tLTRE estimates to this choice should be carefully assessed. On the other hand, if additional parameter estimates are not regularised by any prior structure, their tLTRE contributions are severely overestimated, regardless of the size of the true contribution (Paquet et al., 2021).

Here, we sought to quantify the demographic drivers of population growth in a recovering southern elephant seal (*Mirounga leonina*) population at Marion Island in the southern Indian Ocean. Southern elephant seals are sexually dimorphic marine predators that exhibit high foraging and breeding site fidelity (McIntyre et al., 2017). Over the past seven decades, their southern Indian Ocean populations have experienced significant shifts in abundance (Laborie et al., 2023), but no studies have attempted retrospective analysis to assess the contribution of different vital rates and population structure to long-term variation in realised population growth. In relatively long-lived mammals such as elephant seals, life-history theory predicts that population growth will be more sensitive to factors affecting adult survival rather than changes in juvenile survival or birth rates (Gaillard et al., 1998). Due to elephant seals' extreme polygynous mating system, dispersal might be expected to be male-biased (but see Li & Kokko, 2019). Female elephant seals generally display high site fidelity, especially in the breeding season (Hofmeyr et al., 2012). However, encounters of foreign-tagged seals have highlighted a degree of inter-island female dispersal (Bester, 1988; Oosthuizen et al., 2011) and suggested that even low levels of female immigration can have important effects on population structure and growth rate of the small populations (McMahon et al., 2005). Thus, quantifying the contribution of female immigration is important to understand changes in observed population growth over the past decades.

We built a Bayesian IPM with nearly 40 years of mark-recapture, fecundity and population count data, then used the posterior estimates to calculate tLTRE contributions. Our IPM estimated immigration as an additional parameter, and we used two approaches to evaluate the robustness of its estimated tLTRE contribution. First, we followed the suggestion of Paquet et al. (2021) and fitted our IPM to simulated data with different levels of variation in immigration, comparing true and estimated contributions. Second, we compared the tLTRE estimates obtained using different multivariate priors on the vital rates and on immigration. In addition to the commonly used 'temporal random effect' structure, we explored Gaussian process priors as an alternative way to regularise our estimates in time. We discuss the ecological implications of our results and draw attention to the effects of regularisation and model fit in estimating the demographic contribution of immigration in the IPM-tLTRE framework.

2 | METHODS

2.1 | Study species and data collection

The southern elephant seal is a strongly sexually dimorphic, polygynous, capital-breeding marine predator. Adult seals spend most of their lives at sea, but haul out to breed during the austral spring and moult during summer. Female seals produce offspring from age 3, with the majority pupping for the first time aged 4 (Oosthuizen et al., 2021). On Marion Island, breeding females come ashore from mid-September to mid-October, forming aggregations of up to 70 individuals on isolated rocky beaches. They give birth to a single pup a few days after arriving and remain ashore for just over 3 weeks to suckle. At the end of this period, they wean their pup, mate and return to sea to forage.

Since 1983, almost every weaned pup at Marion Island has been marked with two tags on the inter-digital webbing of their hind flippers. Tag loss is known to occur in this study (Oosthuizen et al., 2010), and double-tagging allows us to account for it in our mark-recapture model. Surveys to resight tagged seals were conducted on all the island's beaches, weekly during the breeding season and every 10 days at other times of the year. All animal handling activities were approved by the Animal Ethics Committee of the Faculty of Veterinary Science, University of Pretoria (AUCC040827-022, AUCC040827-023, AUCC040827-024 and previous permits).

2.1.1 | Mark-recapture data

Here, we analysed individual-based demographic data from all 9500 female seals tagged between 1983 and 2020. From the raw resighting data, we defined robust design mark-recapture data following Oosthuizen et al. (2019). The robust design is made of primary periods, in our case years, between which the population is assumed open, and secondary periods within each year, between which the population is assumed closed (Pollock, 1982). The robust design sampling enables better estimation of breeding probabilities in our mark-recapture model (see below).

We defined three secondary periods as (i) the even weeks of the breeding season, (ii) the odd weeks of the breeding season and (iii) the rest of the year outside the breeding season. The breeding season is 8 weeks long, and female seals may arrive during any of the first 4 weeks. By partitioning these 8 weeks into even and odd weeks, every seal is available for resighting during both secondary periods of the breeding season, regardless of the week in which she arrives. Furthermore, all seals undertake an obligatory moult outside the breeding season.

These three secondary periods result in 15 observable states for each tagged seal in each year. A tagged seal may be resighted, or not, within each of these three periods, giving $2^3 = 8$ preliminary states. For the seven states in which at least one resighting occurred, the seal may have one or two tags, giving the $2 \cdot 7 + 1 = 15$ observable states per tagged seal per year. (We assumed that the number of

tags does not change between the three resighting periods in each year).

2.1.2 | Breeding count data

From 1986 to 2021, the number of breeding females was counted on 15 October every year. This date coincides with the peak number of breeding females, but seals that arrive very early or very late in the breeding season may be absent then (Kirkman et al., 2004; Oosthuizen et al., 2023). Therefore, these counts represent an index of abundance rather than true abundance.

2.1.3 | Fecundity data

Adult female southern elephant seals may skip breeding in some years (de Bruyn et al., 2011) and we estimate breeding probabilities in our mark-recapture model (see below). Those that do breed almost always give birth to a single pup, with twins accounting for less than 1% of births (McMahon & Hindell, 2003). Hence, we assume that all births produce a single pup, and fecundity is described by a single parameter, the probability of surviving from birth until weaning when the pups are tagged. Survival to weaning has been estimated in the Marion Island population (Pistorius et al., 2001), so we use these estimates to define an informative prior for it and do not model fecundity data directly (see Appendix 2.3).

2.2 | Integrated population model

We fitted three versions of our IPM that differed in the multivariate priors we placed on the vital rates and on immigration. Because immigration is estimated as an additional parameter, we allow our prior structures to differ between it and the other demographic parameters. Therefore, for convenience, we restrict the term 'vital rates' to include survival and breeding probabilities and exclude immigration. We considered temporal random effects ('RE') and Gaussian process ('GP') prior structures, with the precise formulation of these differing between the vital rates and immigration (see below). In what follows we refer to the three versions of the IPM as $IPM_{RE,RE}$, $IPM_{GP,RE}$ and $IPM_{GP,GP}$, where the first subscript denotes the prior on the vital rates and the second the prior on immigration (we do not consider $IPM_{RE,GP}$ due to poor model fit; see the discussion).

2.2.1 | Latent population model

Our IPM used a female-based, stage-structured model with a 'pre-breeding census' to describe the latent population dynamics. Here and elsewhere, 'breeding' refers to the birth of a pup, not conception. The population was divided into four age-specific pre-breeding classes ($Pb_{1,t}$, $Pb_{2,t}$, $Pb_{3,t}$, $Pb_{4,t}$) consisting of locally born

1- to 4-year-olds that had never bred, a breeding class (Br_t) of seals that give birth in the current year, and a non-breeding class (Nb_t) of seals that bred in the past but not in the present year. In addition, we defined an immigrant class (In_t) of foreign-born seals breeding for the first time on Marion Island in the present year. Although most foreign-born seals probably arrive at Marion as pre-breeders (Oosthuizen et al., 2011), our definition of the immigrant class implies that they contribute to In_t only if they breed on Marion for the first time in year t . A life-cycle diagram of our stage-structured population model is presented in Figure 1.

The model's vital rates consisted of time-varying, annual survival probabilities, and conditional probabilities that a seal in a particular state in 1 year will breed the following year, given survival. We defined survival probabilities for weaned pups ($s_{0,t}$), pre-breeders and non-breeders ($s_{N,t}$), and breeders ($s_{B,t}$), and conditional breeding probabilities for 2- ($f_{3,t}$) and 3- ($f_{4,t}$) year-old pre-breeders, non-breeders (nb_t) and breeders (bb_t). We also defined $s_{W,t}$ as the probability of survival from birth in year t until weaning. As usual, we use the term 'survival' for 'apparent survival', namely, the event that a seal survives and does not permanently emigrate from the population.

Following Schaub and Fletcher (2015), we parametrised immigration as a number rather than a rate, as it is then independent of estimates of the population size. Immigration rate ω_t is then a derived parameter, defined as the number of immigrants in year $t + 1$ per seal in year t :

$$\omega_t = \frac{In_{t+1}}{Pb_{1,t} + Pb_{2,t} + Pb_{3,t} + Pb_{4,t} + Br_t + Nb_t + In_t}$$

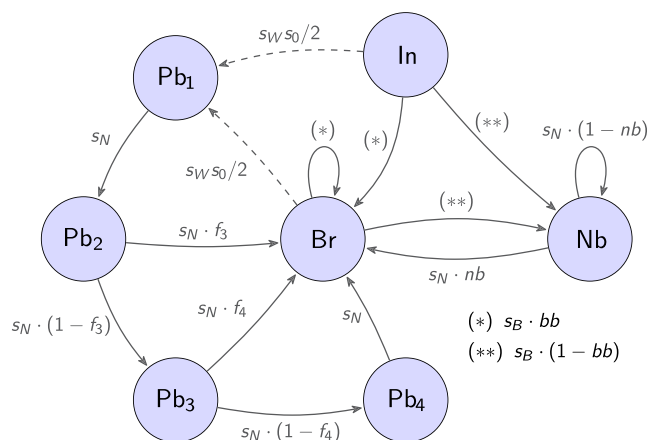


FIGURE 1 A life-cycle diagram for the female-based population model with a 'pre-breeding census'. Nodes represent stage classes for pre-breeders (Pb_{age}) age 1–4, breeders (Br), non-breeders (Nb) and new immigrant breeders (In). Solid lines represent survival and state transitions, and dashed lines represent birth and survival of the single pup to age one. The stage-specific survival probabilities are for survival from birth to weaning (s_W), from weaning to age one (s_0) and annual survival for pre-breeders and non-breeders (s_N), and breeders and immigrants (s_B). f_3, f_4 are probabilities of first breeding age 3–4, and nb, bb are the breeding probabilities of non-breeders, and breeders and immigrants, respectively. The factor of $1/2$ on the dashed lines reflects an assumption of equal sex ratio at birth.

We incorporated demographic stochasticity by using binomial distributions for non-immigrant population stage sizes at time $t + 1$, given the population and vital rates at time t (see [Appendix 2.1](#) for full details). With a slight abuse of notation, our population model can be written as a matrix population model:

$$\begin{pmatrix} Pb_1 \\ Pb_2 \\ Pb_3 \\ Pb_4 \\ Br \\ Nb \\ In \end{pmatrix}_{t+1} = \begin{pmatrix} 0 & 0 & 0 & 0 & \frac{1}{2}s_Ws_0 & 0 \\ s_N & 0 & 0 & 0 & 0 & 0 \\ 0 & s_N(1-f_3) & 0 & 0 & 0 & 0 \\ 0 & 0 & s_N(1-f_4) & 0 & 0 & 0 \\ 0 & s_Nf_3 & s_Nf_4 & s_N & s_Bbb & s_Nnb \\ 0 & 0 & 0 & 0 & s_B(1-bb) & s_N(1-nb) \\ \omega & \omega & \omega & \omega & \omega & \omega \end{pmatrix} \begin{pmatrix} \frac{1}{2}s_Ws_0 \\ 0 \\ 0 \\ 0 \\ s_Bbb \\ s_B(1-bb) \\ \omega \end{pmatrix}_t \begin{pmatrix} Pb_1 \\ Pb_2 \\ Pb_3 \\ Pb_4 \\ Br \\ Nb \\ In \end{pmatrix}_t. \quad (1)$$

More precisely, this describes the conditional expectation of the variables on the left side of the equation, given those on the right side (Buckland et al., 2007). Our priors on the stage class sizes in the initial year are described in [Appendix 2.2](#).

The population model makes several simplifying assumptions. First, because very few immigrants are tagged, it assumes that new immigrant breeders share survival and breeding probabilities with locally born breeders. Second, it assumes that 4-year-old pre-breeders that survive to the following year necessarily breed; only 2% of tagged seals were observed to live at least 5 years without being observed breeding by their fifth year. Third, the model assumes that there is no heterogeneity in survival or breeding probabilities beyond that captured by our stage classes.

2.2.2 | Multievent mark-recapture model

Multievent models generalise multistate mark-recapture models by allowing uncertainty in the assignment of state upon capture (Pradel, 2005). Non-breeding seals do not attend the breeding aggregations (de Bruyn et al., 2011) but may still be resighted during the moult. However, undetected breeders can generate the same capture history, so adult seals that are not observed in the breeding season cannot be assigned a breeding state with certainty. Although it is possible to incorporate non-breeders as an unobservable state in a multistate model, this requires further assumptions, for example, that breeders and non-breeders share survival and breeding probabilities (Kendall & Nichols, 2002). The model of Oosthuizen et al. (2019) incorporates non-breeders without requiring this common demography assumption, and their results suggest that vital rates may differ between breeders and non-breeders on Marion Island. Therefore, we use their multievent model instead of a multistate model.

Multievent models characterise each individual using a hidden Markov model, with their observed capture history arising from a (partially) hidden process representing their biological state through time. Our 'hidden' states are defined to be the pre-breeding, breeding and non-breeding states described above for our population

model, as well as a zero-year-old state in which all seals are tagged. To account for tag loss, we include tag number (one or two) as part of a seal's state. Lastly, we also include an absorbing 'dead' state to which a seal transitions if it dies, permanently emigrates from the population, or loses all tags.

Each seal transitions between these states according to our stage-dependent survival ($s_{0,t}, s_{N,t}, s_{B,t}$) and breeding probabilities ($f_{3,t}, f_{4,t}, nb_t, bb_t$), as well as τ , the probability of losing one tag. We model τ as constant in time, but allow it to vary according to the tag location on the inner or outer inter-digital webbing, as this is known to affect rates of tag loss (Oosthuizen et al., 2010). Our model assumes that at most one tag can be lost annually, and that tag loss events are independent of each other (given tag location). These assumptions are likely to be violated (Schwarz et al., 2012); therefore, although our model corrects estimates of survival for tag loss, a small bias may persist.

Each year a tagged seal may be observed during the two secondary periods of the breeding season, and outside the breeding season, resulting in one of the 15 observation states defined above in the section 'Mark-recapture data'. The conditional distributions of the observation states given the hidden state are defined in terms of four time-varying detection probabilities. These are the probability of detecting a breeder in the even ($p_{Be,t}$) and odd ($p_{Bu,t}$) weeks of the breeding season, and the probability of detecting breeders ($q_{B,t}$), and pre-breeders and non-breeders ($q_{N,t}$), outside the breeding season. For the full specification of transition and emission matrices for the multievent model, see [Appendix 1.1](#).

2.2.3 | Breeding count model

We modelled the breeding counts as

$$\text{count}_t \sim \text{Normal}(Br_t + In_t, \sigma_c = 10).$$

Due to the ease of counting seals on Marion Island, it is highly unlikely that the counts differ from the true number present on 15 October by more than 20; setting the count standard deviation σ_c to 10 encodes this prior information in our model. This treatment relies on the interpretation of σ_c as the standard deviation of the count errors alone, and not as the residual standard deviation for the entire IPM (cf. Schaub & Kéry, 2021, chapters 5.5.2, 6.6.5 and elsewhere). Indeed, we do not have strong prior beliefs about residual variance in the IPM as a whole and would certainly not feel justified in setting a value for it.

We offer results and discussion to support our interpretation of σ_c in [Appendix 7](#). In addition, to show that this choice has little effect on our results, we fit two different versions of $IPM_{GP,RE}$ in which we estimate σ_c under an informative and a vague prior (see [Appendix 2.6](#)).

As noted above, early- and late-arriving females are not present for the 15 October counts. Therefore, the 'true' number of seals estimated by these counts is some (high) proportion of the season's total number of breeding females. There is no evidence to suggest that the proportion missed has changed systematically over the course of the study so, although our population estimates are a slight underestimate, our population growth rate estimates should be unbiased (Schaub & Kéry, 2021; Chapter 4.3.2).

2.2.4 | Priors on vital rates

Here, we use 'vital rates' as shorthand for all the survival and conditional breeding probabilities except for survival to weaning, as the latter is incorporated with an informative prior rather than estimated from data in our study. We let v_t denote a generic vital rate in year t , and use boldface for vectors of time-varying quantities over the study period, for example, $\mathbf{v} = (v_1, \dots, v_T)$.

We fitted the multievent model with two multivariate priors on each of the vital rates. First, we used a 'random effects' (RE) structure with a temporal random effect on the logit scale:

$$\text{logit}(v_t) \sim \text{Normal}(\mu_v, \sigma_v) \text{ for all } t.$$

Second, we used a Gaussian process (GP; Rasmussen & Williams, 2006) structure inspired by Vehtari (2023), in which we placed GP priors on the mean and (log) standard deviation of the logit-normal distributions on each vital rate:

$$\begin{aligned} \text{logit}(v_t) &\sim \text{Normal}(\mu_{v,t}, \sigma_{v,t}) \text{ for all } t, \\ \boldsymbol{\mu}_v &= (\mu_{v,1}, \dots, \mu_{v,T}) \sim \text{Multivariate Normal}(\mathbf{0}, \mathbf{K}_{\boldsymbol{\mu}_v}), \\ \log(\boldsymbol{\sigma}_v) &= (\log(\sigma_{v,1}), \dots, \log(\sigma_{v,T})) \sim \text{Multivariate Normal}(\mathbf{0}, \mathbf{K}_{\log(\boldsymbol{\sigma}_v)}). \end{aligned}$$

Both the RE and GP priors have the desirable property of regularising the estimates of v_t in time. The RE priors shrink the estimates towards the overall mean (Kéry & Schaub, 2011, Chapter 4), providing 'global' regularisation in the sense that information is shared between estimates in all years. In contrast, the more flexible GP priors provide 'local' regularisation in which information is only shared between 'nearby' years, and the scale at which this partial pooling occurs is learnt from the data (McElreath, 2020; Chapter 14.5).

[Appendix 1.2](#) contains the specification of hyperprior distributions and describes the exponentiated quadratic kernels defining the covariance matrices of each GP.

2.2.5 | Priors on immigration

The estimated tLTRE contribution of immigration is unreliable without some form of regularisation (Paquet et al., 2021). We

considered two multivariate priors on the number of immigrants, which achieve this regularisation in different ways. First, we used a Poisson-Lognormal prior for the number of immigrants each year:

$$\begin{aligned} \ln_t &\sim \text{Poisson}(\Lambda_t) \text{ for all } t, \\ \Lambda_t &\sim \text{Lognormal}(\mu_{\log(\Lambda)}, \sigma_{\log(\Lambda)}). \end{aligned}$$

This is analogous to a temporal random effect. Second, we used a Gaussian process prior (on the log scale):

$$\log(\ln) \sim \text{Multivariate Normal}(\boldsymbol{\mu}_{\log(\ln)}, \mathbf{K}_{\log(\ln)}),$$

where $\boldsymbol{\mu}_{\log(\ln)}$ is constant with value $\mu_{\log(\ln)}$ and the covariance matrix $\mathbf{K}_{\log(\ln)}$ is determined by an exponentiated quadratic kernel.

[Appendix 2.4](#) contains the specification of hyperprior distributions for the Poisson-Lognormal and Gaussian process priors.

2.2.6 | Goodness-of-fit

We used posterior predictive checks to assess the fit of our multievent models and IPMs (Conn et al., 2018). Currently, there is no test for the overall goodness-of-fit of IPMs (Schaub & Kéry, 2021; Chapter 7), and model checking practices are underdeveloped for multievent models (Pradel, 2005). See [Appendix 3](#) for details.

2.2.7 | Implementation

We fitted our IPM in Stan (Carpenter et al., 2017), using cmdstanr to interface from R (R Core Team, 2022), where we performed all other analyses. For all models, we ran four chains with 1000 warmup and 1000 sampling iterations each, and checked that all parameters had split- \hat{R} statistic less than 1.01 (Vehtari et al., 2021), large effective sample sizes and that divergent transitions after warmup were absent or rare (Monnahan et al., 2017). For further details of our implementation, including marginalisation of discrete latent states, approximations to Binomial and Poisson distributions, reduced data representations (Turek et al., 2016), and 'cheap', approximate Gaussian processes, see [Appendix 6](#).

2.3 | Transient life table response experiment

We conducted a tLTRE with the posterior samples of our fitted $IPM_{GP,RE}$ (Koons et al., 2016, 2017). Although seals were tagged from 1983, we restricted our tLTRE to the period 1990–2021. As all seals are tagged as pups, it takes several years for some stage classes to contain marked individuals, and hence for some class-specific vital rates to be informed by data (e.g. *nb*, non-breeders' breeding probability). To see how well the vital rates are informed by the data alone (without the influence of multivariate priors that share information between years), we fitted a 'fixed effects' version of the multievent model with independent Uniform(0, 1) priors on all

vital rates. Using it, we judged that the vital rates were only reliably estimated from 1990 (see Appendix 1.3, Figure S2).

We defined the total population size, Tot_t , as the sum of all stage-class sizes:

$$Tot_t = Pb_{1,t} + Pb_{2,t} + Pb_{3,t} + Pb_{4,t} + Br_t + Nb_t + In_t.$$

According to our population model (Equation 1), the realised population growth rate from year t to $t + 1$ is given by

$$\lambda_t = (0.5s_{W,t}s_{0,t} + s_{B,t})(p_{Br,t} + p_{In,t}) + s_{N,t}(p_{Nb,t} + p_{Pb,t}) + \omega_t.$$

Here, the variables p_{Br} , p_{Nb} , p_{In} and p_{Pb} represent the proportion of the total population made of breeders, non-breeders, new immigrant breeders and pre-breeders (of any age), respectively. Note that the breeding probabilities f_3 , f_4 , bb and nb do not appear in the expression, because the total population size (hence realised growth rate) is unaffected by the stage class to which an individual transitions, as long as she survives. Lastly, to simplify the treatment of growth rate sensitivities to population structure (see Appendix 4.1 for more details), we reparameterise our expression for λ_t in terms of p_{Nb} and p_{Pb} alone:

$$\lambda_t = (0.5s_{W,t}s_{0,t} + s_{B,t})(1 - p_{Nb,t} - p_{Pb,t}) + s_{N,t}(p_{Nb,t} + p_{Pb,t}) + \omega_t.$$

2.4 | Simulations

To assess our model's ability to accurately estimate the demographic contribution of immigration, we conducted a simulation study following the recommendation of Paquet et al. (2021). We simulated data from $IPM_{GP,RE}$ under three levels of temporal variation in immigration, then fitted $IPM_{GP,RE}$ to each simulated data set and compared the estimated tLTRE contributions to truth. For each simulation, we set all parameters equal to a random draw from the joint posterior of $IPM_{GP,RE}$ fit to real data. The only exception was $\sigma_{\log(\Lambda)}$, the standard deviation of the Poisson-Lognormal model for the number of immigrants. Under the 'medium' and 'high' levels of variation in immigration, we set $\sigma_{\log(\Lambda)} = 0.2$ and $\sigma_{\log(\Lambda)} = 0.4$, respectively. Under the 'low' level of variation, we set the number of immigrants to be constant over time.

Repeatedly fitting the IPM is computationally expensive, so we used an approximate, iterative procedure when fitting simulated data; see Appendix 5 for details.

3 | RESULTS

3.1 | Realised growth rate and tLTRE contributions

The realised population growth rate fluctuated appreciably over the period 1990–2021, but exceeded one for most of the last third of this period (Figure 2a). This is consistent with our count data and general impression of a population that is growing rapidly in recent years (Figure 2b). The tLTRE analysis suggests that breeder survival (s_B) and immigration (ω) were the two most important drivers of this

growth (Figure 2c), although there is substantial uncertainty in the latter estimate (as is typical for additional parameters; Schaub & Kéry, 2021). These primary tLTRE contributions can be explained by the relatively large sensitivities of breeder survival and immigration, in conjunction with substantial temporal variation. Indeed, the annual number of immigrants fluctuated strongly over the study period, roughly trebling its minimum at its maximum and increasing sharply in recent years (Figure 2d). Breeder survival also showed a marked increase of ~ 10 percentage points over the second half of the study period (Figure 2e).

Secondary tLTRE contributions were made by pre- and non-breeder survival (s_N), and the non-breeder proportion of total population (p_{Nb}). Although survival from weaning to age one (s_0) varied more than the other survival probabilities (Figure 2e), its low sensitivity resulted in a smaller tLTRE contribution. Lastly, the contribution of the pre-breeder proportion of total population (p_{Pb}) was negligible.

3.2 | Prior sensitivity of immigration

Our choice of priors on immigration and the vital rates had a substantial effect on the estimates of annual immigration and its demographic contribution. The annual estimates of immigration from models $IPM_{GP,RE}$ and $IPM_{GP,GP}$ showed similar trends, such as low immigration in the mid-1990s and a sharp increase after 2015 (Figure 3b). However, the GP prior on immigration resulted in smaller credible intervals and smoother estimates without strong outliers (e.g. $IPM_{GP,RE}$'s large estimate in 2001). The tLTRE estimates reflected this reduction in the temporal variance of immigration, with a smaller contribution from $IPM_{GP,GP}$ than $IPM_{GP,RE}$ (Figure 3a). The largest tLTRE estimate of immigration was produced by $IPM_{RE,RE}$ with 'random effects' priors on the vital rates and immigration.

3.3 | Priors on the vital rates and goodness-of-fit for the multievent model

We found that our multievent model with random effects priors on the vital rates failed to capture the number of detected breeders in the data (Figure 4a). Comparing the estimates of breeder survival from this model to models with Gaussian process priors (Figure 4c cf. 4d), or fixed effects priors (Appendix 1.3, Figure S2), it appears that breeder survival was overestimated in the early years of the study, due to the 'global' sharing of information from the random effects structure. As a result of this, the annual number of detected breeders between 1986 and 1995 was consistently lower in the real data than in most posterior replicate data sets (Figure 4a). When using the more flexible GP prior this lack of fit was corrected (Figure 4b), as the estimates for breeder survival could respond to apparent, subtle trends and the uncertainty in these estimates could respond to scarcer information in the study's early years (Figure 4d).

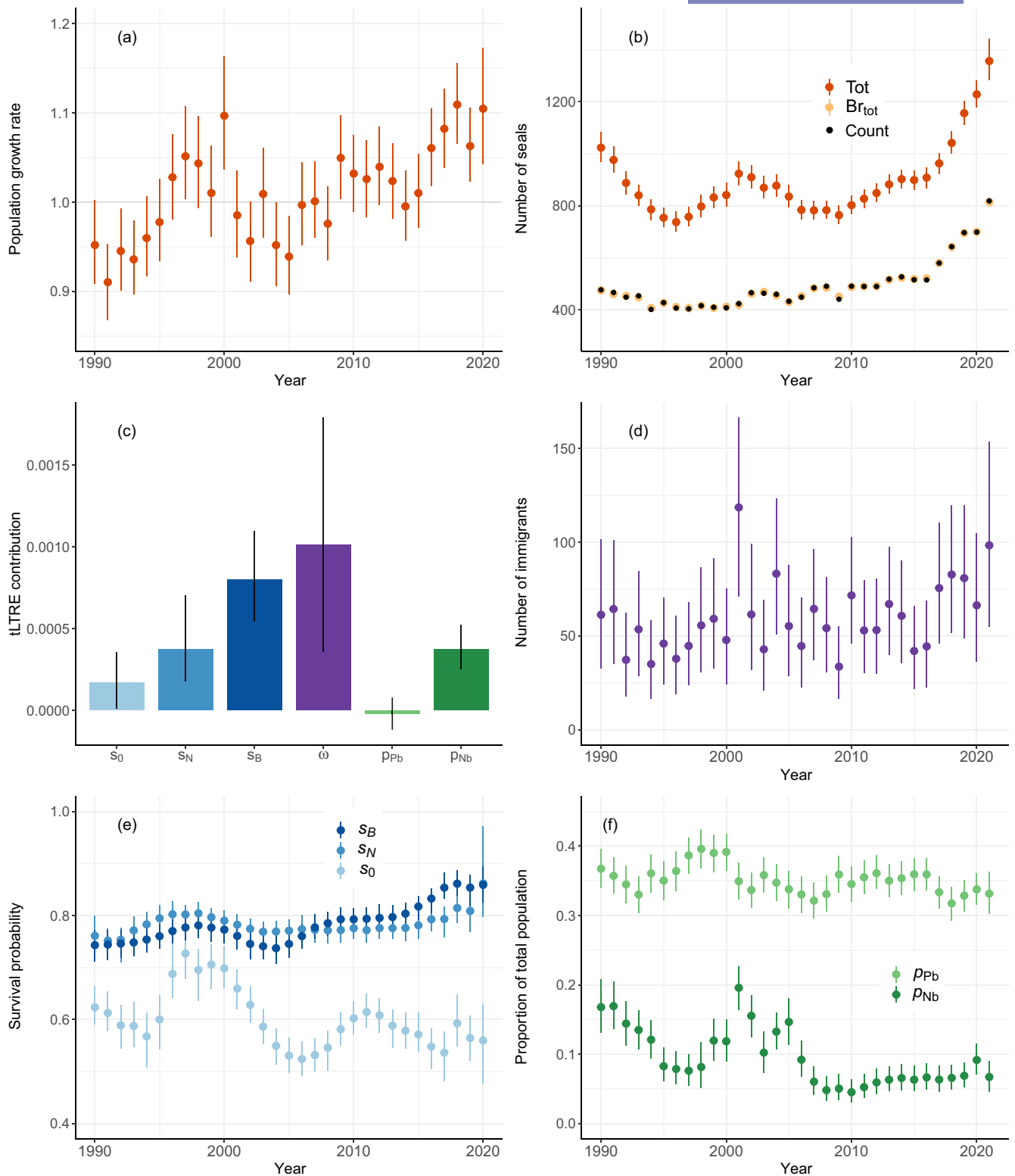


FIGURE 2 Estimates from IPM_{GP,RE} and the tLRE analysis for the period 1990–2021, showing posterior medians and 90% credible intervals. (a) Realised population growth rate; (b) total population size and the total number of locally born and new immigrant breeders ($Br_{tot} = Br + In$). The black dots show the 15 October breeding counts. The small credible intervals for Br_{tot} are not visible at this scale. (c) tLRE contributions of survival from weaning to age 1 (s_0), pre-breeder and non-breeder survival (s_N), breeder survival (s_B), immigration rate (ω) and the proportion of total population comprised of pre-breeder of any age (p_{pb}) and non-breeders (p_{Nb}). (d–f) Annual estimates for each of the variables in the tLRE analysis.

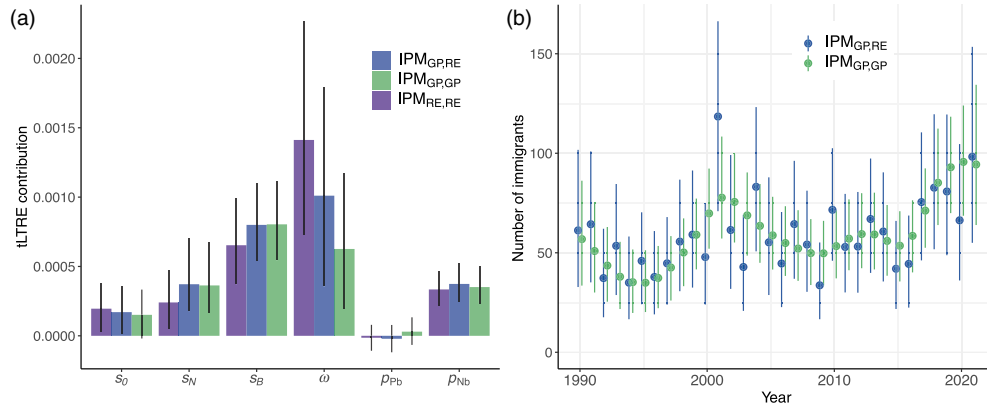


FIGURE 3 Sensitivity of tLRE contributions (a) and annual estimates of immigration (b) to multivariate priors placed on the vital rates and immigration. The IPM subscripts indicate whether a ‘random effect’ (RE) or Gaussian process (GP) prior structure was used for the vital rates (first subscript) and for immigration (second subscript). Annual estimates for $IPM_{RE,RE}$ are not shown in (b) as they are qualitatively similar to those of $IPM_{GP,RE}$ with which it shares a prior on immigration (see Appendix 2.5, Figure S8 for all three).

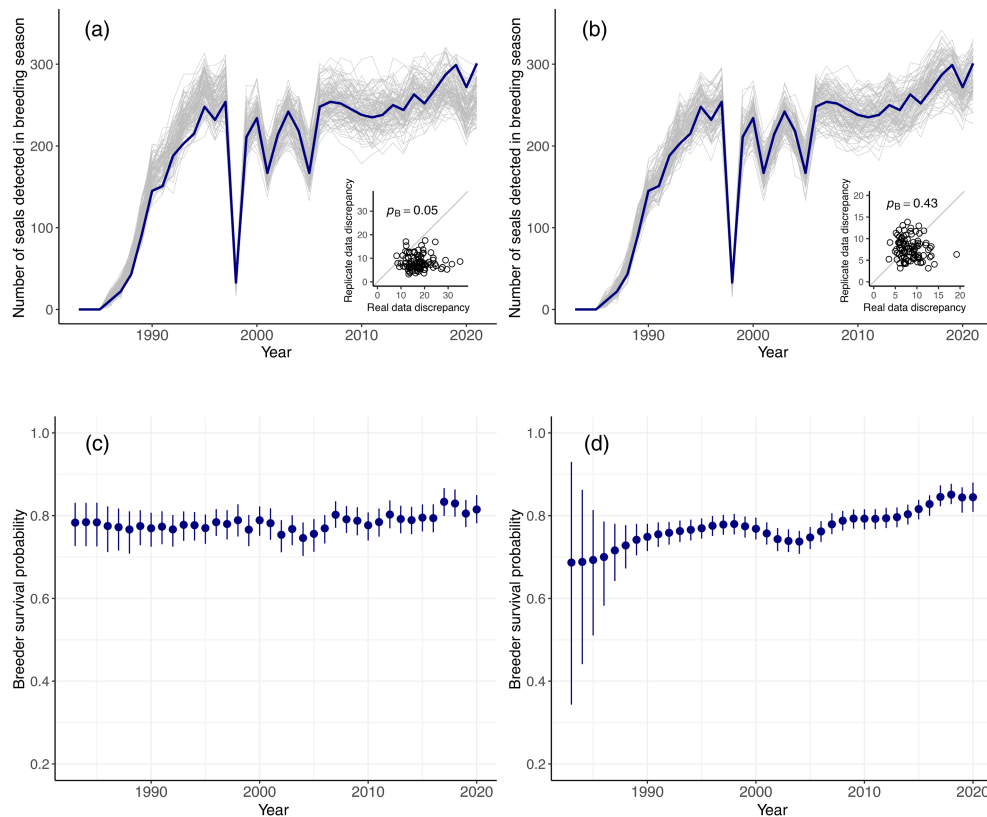


FIGURE 4 Posterior predictive checks of breeder detections (top row), and breeder survival estimates (bottom row), for multievent models with random effects (RE) or Gaussian process (GP) priors. (a) The observed number of seals detected during the breeding season each year (in dark blue) and 100 posterior replicates (in grey) under RE priors. The inset shows the Bayesian p -value for a Freeman–Tukey discrepancy measure of expected and observed breeders over all years (see Appendix 3.1 for details). (b) As for (a), but for the multievent model with GP priors on vital rates. The number of detections is low in the first few years as few tagged seals have entered the breeding population. One year (1998) had anomalously low detections due to fieldwork constraints. (c, d) Annual estimates of breeder survival for the multievent model with RE (c) and GP (d) vital rate priors.

3.4 | Simulations

When fit to simulated data, our IPM overestimated the contribution of immigration when the true contribution was small, slightly underestimated it when truth was moderate and

substantially underestimated it when truth was large (Figure 5a). The coverage of posterior credible intervals was very poor when the number of immigrants was constant over time (50% intervals had 2% coverage, 90% intervals had 45% coverage), improved for the medium level of immigration (50% CrI: 62%, 90% CrI: 93%),

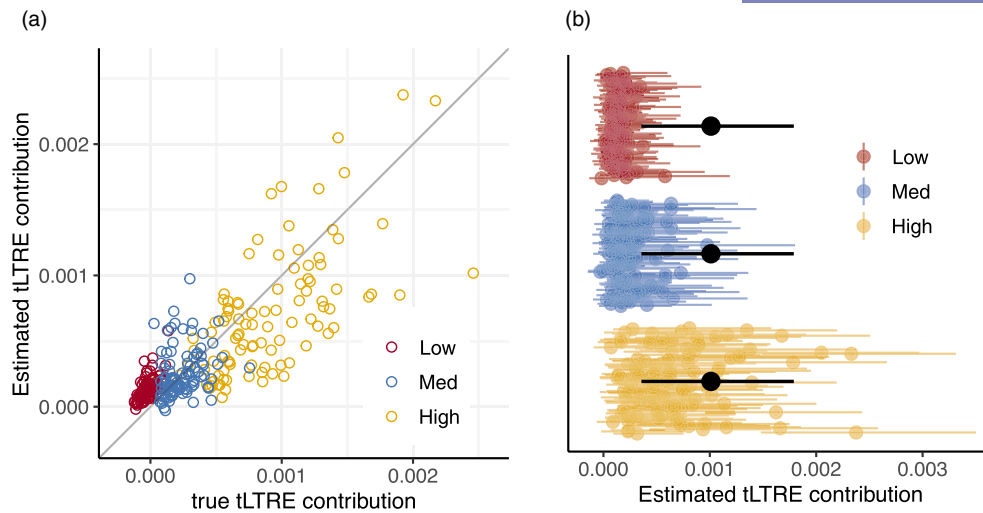


FIGURE 5 Transient life table response experiment (tLTRE) contributions of immigration for simulations in which $IPM_{GP,RE}$ is fit to data generated from the model, with low, medium or high levels of temporal variation in immigration. One hundred replicates were simulated under each level of immigration. (a) True versus estimated (posterior median) contributions for each simulation. (b) Posterior medians and 90% credible intervals for the tLTRE contribution of immigration in each of the simulations, with the real data estimate overlaid in black.

but declined again under the high level of variation in immigration (50% CrI: 42%, 90% CrI: 81%).

In comparison with the posteriors obtained from simulated data, our estimate of the contribution of immigration is consistent with those obtained under medium or high temporal variation in immigration (Figure 5b). Since the model did not overestimate the contribution of immigration when temporal variance in immigration was medium or high, we conclude that our estimated contribution of immigration is not an overestimate.

4 | DISCUSSION

We used more than 30 years of mark–recapture and population count data to estimate the demographic contribution of population structure, female immigration and annual survival to population growth in southern elephant seals. Our IPM–tLTRE analysis suggests that increased adult survival and immigration are responsible for reversing the long-term population decrease of the Marion Island population. Adult survival strongly influences the lifetime reproductive success of long-lived iteroparous species (Gaillard et al., 1998), including southern elephant seals (Oosthuizen et al., 2018). On the other hand, little is known about the importance of immigration for the population dynamics of elephant seals, reflecting the general difficulty of quantifying immigration in wild animal populations.

In recent years, IPMs have become the go-to method for estimating immigration when direct data on movement from source populations is unavailable (Millon et al., 2019). Coupling these models with retrospective population analyses offers ecologists the long-sought possibility of quantifying immigration and the demographic role it plays in local population dynamics. One of our primary aims was to understand the role of immigration in the recovery of Marion Island's

elephant seals over the last few decades. Previous work showed that a large proportion of breeding females could have been born elsewhere (Oosthuizen et al., 2012), suggesting that immigration might be important in driving population growth. However, recent theoretical work has shown that the IPM–tLTRE framework systematically overestimates the demographic contribution of immigration when the true contribution is small (see Figure 5a and Paquet et al., 2021). This is an issue of fundamental importance, but one which has not been adequately addressed in the literature; for example, it is not discussed in the recent monograph on IPMs (Schaub & Kéry, 2021).

To guard against erroneous inference about immigration, it is critically important to assess the goodness-of-fit of one's IPM. While all inference relies on a model that fits, immigration is particularly sensitive to model misspecification because it is not directly informed by data in an IPM (Plard et al., 2021; Riecke et al., 2019; Schaub & Kéry, 2021, Chapter 7). For the same reason, we expect that immigration and its demographic contribution will always be sensitive to the priors placed on it, as we found here (Figure 3). This is especially true of multivariate priors and the demographic contribution of immigration, because such priors directly influence temporal variance through shrinkage or smoothing. Furthermore, because immigration is a latent variable, we think it unlikely that one choice of prior could be preferred over another through goodness-of-fit or model selection. We therefore consider prior sensitivity analysis to be essential for obtaining robust conclusions about immigration.

Another way to guard against erroneously overestimating the importance of immigration is to 'calibrate' the estimates from one's own model using simulation (Paquet et al., 2021). Fortunately, the bulk of our real data estimates from $IPM_{GP,RE}$ exceed the range of estimates from simulated data with small true contributions (Figure 5b). Furthermore, our IPM underestimated medium and

large true contributions (Figure 5a). Taken together, this suggests that we have not overestimated the demographic contribution of immigration and may even have underestimated it. Therefore, although substantial uncertainty remains over our quantitative estimate of the contribution of immigration, at least partly due to prior sensitivity, we are confident of the ecological conclusion that immigration has played an important role in this population's recovery.

Elephant seal breeding populations within the Indian sector of the Southern Ocean are likely the main source of immigrant seals to Marion Island. Movement between Marion Island, Prince Edward Island and the Crozet archipelago is common (Oosthuizen et al., 2009, 2011) but these source populations (particularly Prince Edward Island; Bester & Hofmeyr, 2005) are relatively small (about 4000 breeding females at Crozet; Laborie et al., 2023). Although more distant, the large populations of elephant seals at Heard Island and the Kerguelen Archipelago (about 100,000 breeding females; Laborie et al., 2023) probably also contribute immigrant seals to Marion Island (Bester, 1988; Oosthuizen et al., 2011). Both the Kerguelen and Crozet populations have increased since the 1990s (at 1.6% and 5.1% per annum, respectively; Laborie et al., 2023) and this could explain the increasing trend in immigrant seals estimated in our IPM. The general pattern of population increase may be linked to increased survival (but this is difficult to know as survival can only be estimated at Marion Island) and large-scale changes in productivity within the southern Indian Ocean in recent decades.

4.1 | Regularising immigration

To the extent that it can be resolved, we view the problem of accurately estimating the demographic contribution of immigration as a regularisation problem (assuming, crucially, that the IPM fits the data). Regularisation refers to a suite of techniques that constrain model estimates through the use of penalised likelihoods (in frequentist inference) or regularising priors (in Bayesian inference; Hobbs & Hooten, 2015; McElreath, 2020). Since immigration is not directly informed by data, it offers the IPM an almost unconstrained variable with which to fit the data (and its noise), and this makes regularisation a sensible strategy. Furthermore, Paquet et al. (2021) showed that an IPM without any regularising prior on immigration (their $IPM_{NoConst}$) dramatically overestimated the demographic contribution of immigration, while estimates from an IPM with regularising 'shrinkage' priors (their IPM_{Pois}) were unbiased when the true contribution was moderate or large. Therefore, we consider regularisation to be essential for estimating the demographic contribution of immigration as accurately as possible.

Granting this, the problem becomes one of choosing an appropriate regularising prior. The natural candidates are multivariate priors that share information between the annual estimates of immigration. To date, most (if not all) IPMs that have used a multivariate prior on immigration have opted for a Poisson-Lognormal prior

or similar temporal random effect (Paquet et al., 2021). These priors share information between annual estimates but do not take into account time-series structure. For example, the annual estimates of immigration in 1990 and 2019 are given equal weight in informing the estimate in 2020. In contrast, our Gaussian process prior exploits the time-series structure in the problem by inducing correlations between annual estimates in nearby years. These correlations decay with increasing time between years, so the 2019 estimate is much more informative of the 2020 estimate than is the 1990 estimate.

Our results suggest that Gaussian process priors on immigration have potentially useful properties for estimating the demographic contribution of immigration. In comparison with the Poisson-Lognormal prior, the GP prior provides smoother annual estimates with smaller standard errors (Figure 3b). This translates into reduced temporal variance in the posterior samples of immigration, and results in a smaller estimate of its demographic contribution (Figure 3a). If immigration is absorbing residual variation in the IPM (as it is expected to; Paquet et al., 2021), this behaviour may help to 'push' that variation into other variables in the model where it is less detrimental to the tLRE estimates. At the same time, the GP prior was flexible enough to capture apparent trends that contribute to temporal variance in immigration (e.g. the post 2015 increase in immigration; Figure 3b). These properties suggest that GP priors may be capable of providing more accurate estimates of the demographic contribution of immigration, but more work is required to formally assess if and when this is the case.

4.2 | Sensitivity of immigration to vital rate priors

Perhaps surprisingly, the contribution of immigration was also sensitive to the prior structure on the vital rates ($IPM_{RE,RE}$ cf. $IPM_{GP,RE}$). This occurred even though we have strong mark-recapture data, with hundreds of marked pups and breeders annually, and high detection probabilities (Appendix 1.3, Figure 4). Our interpretation of this result is that the effect of vital rate priors on the contribution of immigration was mediated through goodness-of-fit. The more flexible GP priors on the vital rates improved the model fit in at least one important respect (Figure 4a,b). The improved fit of $IPM_{GP,RE}$ is probably responsible for its smaller tLRE contribution relative to $IPM_{RE,RE}$, because a lack of fit should increase residual variation, which is probably absorbed by immigration, inflating its temporal variance (Paquet et al., 2021).

One could reasonably ask why we have considered $IPM_{RE,RE}$, when its component multievent model fails an important goodness-of-fit test (Figure 4a). We did so because it illustrates that the degree of fit of an IPM may have a non-negligible effect on the downstream tLRE estimate of immigration. In our case, we could detect (one kind of) lack of fit with a simple posterior predictive check, but this may not always be easy. Indeed, Bayesian p-values are known to be 'conservative' (they do not indicate

true lack of fit as often as they should; Conn et al., 2018), and goodness-of-fit tests for multievent models and IPMs are both underdeveloped at present. Therefore, it is conceivable that different IPMs could all have passable fit in terms of the tests applied, but substantially different estimates of the demographic contribution of immigration.

5 | CONCLUSIONS

Dispersal significantly influences ecological and evolutionary patterns by directly affecting processes such as gene flow, population size and species viability. Yet, because immigration can be challenging to estimate, it is often disregarded as a demographic process that affects the population dynamics of colonially breeding marine predators. Female elephant seals generally have high site fidelity (Hofmeyr et al., 2012) and male-biased dispersal would not be unusual in this extremely polygynous species. However, our results suggest that female dispersal and connectivity between distant populations, along with adult survival, were the main drivers responsible for the rebound of the Marion Island population.

This study is one of a growing number of studies that have used the IPM-tLRE framework and found immigration to be one of the most important drivers of population dynamics (Millon et al., 2019; Paquet et al., 2021). Given the potential biases inherent in this procedure (Paquet et al., 2021) and the sensitivity to prior choices, it is probably wise to interpret the contribution of immigration as 'immigration plus noise' in many circumstances (Paquet et al., 2021). Of course, what we want to estimate is immigration, and regularising priors could be a useful tool to reduce the noise in these estimates. Gaussian processes are often used to model time series (e.g. Gelman et al., 2013, Chapter 21; Vehtari, 2023), but have, to our knowledge, not been used in the context of IPMs before (e.g. Schaub & Kéry, 2021). Our results suggest promise for regularisation, but further investigation is required so that a regularising prior can be chosen in a principled way.

AUTHOR CONTRIBUTIONS

Murray Christian and W. Chris Oosthuizen conceived the ideas and designed methodology; W. Chris Oosthuizen, Marthán N. Bester and P. J. Nico de Bruyn collected and curated the data; Murray Christian analysed the data and led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest.

DATA AVAILABILITY STATEMENT

All data and code are available from <https://doi.org/10.5281/zenodo.10512980> (Christian et al., 2024) and https://github.com/MurrayChr/ses_ipm.

ORCID

Murray Christian  <https://orcid.org/0000-0001-8998-1367>

W. Chris Oosthuizen  <https://orcid.org/0000-0003-2905-6297>

Marthán N. Bester  <https://orcid.org/0000-0002-2265-764X>

P. J. Nico de Bruyn  <https://orcid.org/0000-0002-9114-9569>

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SUPPORTING INFORMATION

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

Appendix 1. Multievent model.

Appendix 2. Population model.

Appendix 3. Goodness-of-fit.

Appendix 4. tLTRE analysis.

Appendix 5. Simulations.

Appendix 6. Stan implementation.

Appendix 7. Interpretation of count standard deviation.

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