

# Estimating immigration using a Bayesian integrated population model: choice of parametrization and priors

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**Abstract** Bayesian integrated population modelling provides a natural tool for estimating immigration into a single study population when we have indices of population size, mark–recapture data and fecundity data. We consider the choice of both the parametrization of immigration and its prior. Using a simulation study for a model that is typical of those used for short-live bird species, we assess the effect of specifying immigration in terms of the number of immigrants each year, as opposed to an immigration rate. We also assess the effect of the assumption of independence of the data sets, which is commonly required in such modelling. If immigration is occurring, our results suggest that parametrizing the model in terms of number of immigrants will provide a more precise estimate, compared to a parametrization involving an immigration rate, even if we wish to estimate the rate. If there is little or no immigration, use of a model parametrized in terms of an immigration rate can result in overestimation, whereas a model in which immigration is specified as a number offers the possibility to use priors that have a negative lower bound with the consequence that immigration is correctly estimated. Use of such a model appears to be robust to the assumption of

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independence being wrong, our results for independent and dependent data sets being remarkably similar in terms of the distribution, across all simulations, of the posterior means and standard deviations.

**Keywords** Bayesian model · Immigration · Integrated population model · Prior sensitivity · Source–sink dynamics

## 1 Introduction

Immigration is an important demographic process that has long been a neglected component of population modelling, even though it may have a strong impact on population dynamics (Ward 2005; Lampila et al. 2006; Grøtan et al. 2009; Schaub et al. 2010, 2012, 2013; Brown and Collopy 2013). An assessment of the amount of immigration into a population can help identify whether a local population is a sink (Pulliam 1988; Peery et al. 2006) and therefore how it might be managed.

One of the reasons immigration has been ignored in population modelling is that it is difficult to estimate directly. Immigrants can only be distinguished from “locals” if all the individuals within either group are marked, which is rarely feasible in practice (Møller 2002; Grøtan et al. 2009; O’Hara et al. 2009). If we have mark–recapture data from several sub-populations, immigration can in principle be measured by using a multi-state model to estimate the rate of movement between the sub-populations (Spendelov et al. 1995). However, it might be impossible to carry out fieldwork at all the sub-populations and such an approach could lead to underestimation of the amount of immigration. Immigration can also be estimated using a robust mark–recapture design (Nichols and Pollock 1990), as long as every individual matures exactly one sampling occasion (usually a year) after they are born. Even when this assumption is satisfied, a robust design might not be used in practice due to the extra sampling effort required, compared to a standard mark–recapture study. Peery et al. (2006) proposed estimating immigration indirectly by comparing the asymptotic population growth rate predicted by a population model with an estimate of the empirical growth rate, the latter being obtained from an analysis of the trend in annual estimates of population size or from the “temporal symmetry” mark–recapture model of Pradel (1996). The idea behind this approach is that the growth rate predicted by the population model does not allow for immigration, and will therefore tend to underestimate the true growth rate. Comparison of the two estimates will therefore provide an idea of the amount of immigration.

One of the most promising approaches to estimating immigration is the use of an integrated population model (Abadi et al. 2010b). Typically, integrated modelling involves simultaneous analysis of counts or indices of population size, mark–recapture data and data on fecundity (Besbeas et al. 2002; Buckland et al. 2007; Schaub and Abadi 2011; Kéry and Schaub 2012). This approach is closely related to that of Peery et al. (2006), but has the conceptual and practical advantage of allowing the amount of immigration to be directly specified in the population model. Abadi et al. (2010b) provide a summary of the advantages of the use of integrated population modelling to estimate immigration, but do not evaluate the performance of such a model.

There are several objectives in this paper. First, we wish to check that use of an integrated population model can lead to reliable estimates of the amount of immigration occurring in a population. Second, we consider the manner in which immigration is specified in an integrated population model. Unlike other demographic parameters, there is some choice as to how immigration is parametrized. It might be convenient to specify immigration as a rate, analogous to the definition of a survival probability (Cooch et al. 2001; Abadi et al. 2010b; Schaub et al. 2010, 2012). However, unlike in the case of survival, there is some arbitrariness in the choice of the denominator. For example, in many settings it might be natural to consider an immigration rate that is scaled by the size of the donor population(s). However, as this information is usually lacking, such a rate might be impossible to use. A common alternative is to scale by the size of the focal population, but this may not be the best way to represent the dynamics. As an alternative to use of an immigration rate, we might prefer to simply specify the number of immigrants (Nichols and Pollock 1990; Schaub et al. 2013). A disadvantage of this approach is that we can only hope to estimate the true number of immigrants when the detection probability associated with the population count is 1 (Kéry and Schaub 2012). Third, as we focus on use of a Bayesian integrated population model, we also consider the choice of prior for immigration. Finally, we assess the impact of an assumption commonly made in such models, that the data sets are independent (Abadi et al. 2010a). We use simulation to study all of the above issues, focussing on a situation that will be commonly encountered when modelling a short-lived bird species.

## 2 Methods

### 2.1 Population models

We consider three population models that differ only in the manner in which immigration is parametrized. We focus on females only and assume a pre-breeding census. We specify two age-classes: individuals that are 1-year old and those that are at least 2 years old, the number in these two classes in year  $t$  being  $N_t^1$  and  $N_t^{2+}$ , respectively. All immigrants are arbitrarily assumed to be 1 year old, so  $N_t^1 = N_t^I + N_t^R$ , where  $N_t^R$  is the number of 1-year olds in year  $t$  that were local newborns in year  $t-1$  (local recruits), and  $N_t^I$  is the number of immigrants that entered the population between years  $t-1$  and  $t$ . The total number of individuals in year  $t$  is  $N_t = N_t^1 + N_t^{2+} = N_t^R + N_t^I + N_t^{2+}$ . Model 1 is given by

$$\begin{aligned}
 N_{t+1}^R &\sim \text{Poisson} \left( f_t \phi_t^0 N_t \right) \\
 N_{t+1}^{2+} &\sim \text{Binomial} \left( N_t, \phi_t \right) \\
 N_{t+1}^I &\sim \text{Poisson} \left( \mu_{t+1}^I \right)
 \end{aligned}$$

where  $f_t$  is fecundity (mean number of females per reproductive female) in year  $t$ ,  $\phi_t^0$  is the probability of surviving from year  $t$  to  $t + 1$  in the first year of life,  $\phi_t$  is the probability of surviving from year  $t$  to  $t + 1$  for all other ages, and  $\mu_{t+1}^I$  is the expected

number of immigrants that enter the population between years  $t$  and  $t + 1$ . Model 2 differs from Model 1 in the equation for the number of immigrants, which is given by

$$N_{t+1}^I \sim \text{Poisson}(i_t N_t)$$

where  $i_t$  is an immigration rate given by  $i_t = E(N_{t+1}^I)/N_t$ , i.e. the expected number of immigrants that enter between years  $t$  and  $t + 1$  per individual in year  $t$ . Finally, Model 3 does not include immigration, i.e.  $N_{t+1}^I = 0$  for all  $t$ .

## 2.2 Simulation study

We carried out simulation of a 10-year study in the following three steps. First, using Model 1 with specified values for the demographic parameters in each year, we created a set of “life histories” for all individuals that were in the population at some stage during the study. For simplicity, when simulating the data in this way, we set  $N_t^I = \mu_t^I$ . Second, we selected individuals from the population for inclusion in the mark–recapture data, the productivity data and the population survey. We performed this second step in two ways, with the data sets being either independent or dependent. Third, we analysed the data using either Model 1, 2 or 3, and with different priors for  $\mu_t^I$  or  $i_t$ , as appropriate. We now describe the three steps in detail.

### 2.2.1 Life histories

Using Model 1 and an initial population size of 100 in each age group, we created the life history of each individual that was in the population during a 10-year period. For each year, we recorded the state of the individual (alive or dead, and age class if alive) and the number of offspring it produced, and added a specified number of immigrants. In order to reach an approximately stable age distribution, we ran the process for a total of 13 years and discarded the first 3 years. We used the following steps in year  $t$ , these steps being carried out in each year until the individual died or the study ended:

1. If the individual was at least 1 year old, we generated offspring by randomly generating a number from a Poisson distribution with mean  $f_t$ ;
2. We determined whether the individual survived to year  $t + 1$  by randomly generating a number from a Bernoulli distribution with parameter equal to  $\phi_t^0$  or  $\phi_t$ , according to their age;
3. If the individual survived, it moved to the next year and, if relevant, to the next age class.

We chose values for the parameters that are typical of those for a short-lived bird, such as a passerine. We set  $f_t = 2.6$  and  $\mu_t^I = 0, 35$  or  $60$  for all  $t$ . The survival probabilities depended on the number of immigrants as follows:

$$\begin{aligned} \phi_t^0 &= 0.20 & \phi_t &= 0.50 & \text{when } \mu_t^I &= 0 \\ \phi_t^0 &= 0.20 & \phi_t &= 0.42 & \text{when } \mu_t^I &= 35 \\ \phi_t^0 &= 0.15 & \phi_t &= 0.42 & \text{when } \mu_t^I &= 60 \end{aligned}$$

for all  $t$ . These choices were motivated by the desire to make the population growth rate similar in the three scenarios.

### 2.2.2 Generating the data sets

We considered two types of data collection. First, in order to obtain independent data sets, we generated three replicate populations and then sampled from the first population to obtain the fecundity data, from the second to obtain the mark–recapture data and from the third to obtain the population survey data. The second type involved randomly selecting individuals from a single generated population for inclusion in each data set. This meant that the data sets were dependent, as an individual could be included in more than one data set.

To create the mark–recapture data, for each individual, and for each year that the individual was alive, we randomly generated a number from a Bernoulli distribution, with parameter equal to the capture probability for that year, to determine whether the individual was captured or not. The probability of initial capture was set to 0.75 for newborns and 0.60 for all other individuals; the probability of recapture was set to 0.60. For both the fecundity data and the population survey data, we randomly generated a number from a Bernoulli distribution with parameter equal to 0.9 to determine whether an individual was included in the data set or not.

### 2.2.3 Data analysis

We analysed the data by assuming that the population model component corresponded to Model 1, 2, or 3. In addition, we made three simplifying assumptions. First, we assumed that the survival and fecundity parameters were constant. Second, we assumed that the recapture probability used in the model for the mark–recapture data and the observation variance used in the model for the population survey data were also constant. Third, we made the commonly-used assumption that the data sets were independent, leading to the overall likelihood being the product of the likelihoods for each data set. We now consider the form of each of these likelihoods (see also [Abadi et al. 2010b](#)).

### 2.2.4 Likelihood for the mark–recapture data

We summarized the mark–recapture data in a reduced m-array ([Burnham et al. 1987](#)), the  $(i, j)$ th element of this being  $m_{ij}$  ( $i = 1, 2, \dots, 9; j = i + 1, \dots, 11$ ). For  $j < 11$ ,  $m_{ij}$  is the number of individuals released in year  $i$  that were recaptured for the first time in year  $j$ ;  $m_{i,11}$  is the number of individuals released in year  $i$  that were never recaptured. The likelihood was given by

$$\prod_{i=1}^9 \prod_{j=i+1}^{10} \pi_{ij}^{m_{ij}} \left( 1 - \sum_{j=i+1}^{10} \pi_{ij} \right)$$

where  $\pi_{ij}$  is the probability that an individual released in year  $i$  is recaptured for the first time in year  $j$ . For an individual released as a newborn in year  $i$ , we have

$$\pi_{ij} = \phi^0 \phi^{j-i-1} p (1-p)^{j-i-1}$$

where  $p$  is the recapture probability in each year. For all other individuals released in year  $i$ , we have  $\pi_{ij} = \phi^{j-i} p (1-p)^{j-i-1}$ .

### 2.2.5 Likelihood for the population survey data

The overall likelihood for the population survey data is the product of the likelihood for the state process and that for the observation process (Besbeas et al. 2002; Valpine and Hastings 2002; Buckland et al. 2004). The state process was given by either Model 1, 2 or 3, together with the extra assumption that the fecundity and survival parameters were constant. The observation process was modeled by assuming that the annual count,  $y_t$ , is lognormal with constant variance  $\sigma^2$ . The likelihood for the observation process was therefore given by

$$(2\pi\sigma^2)^{-n/2} \prod_{t=1}^{10} y_t^{-1} \exp\left(-\frac{(z_t - \eta_t)^2}{2\sigma^2}\right)$$

where  $z_t = \log(y_t)$  and  $\eta_t = \log(N_t)$ .

### 2.2.6 Likelihood for fecundity data

The total number of newborn females observed in year  $t$  ( $B_t$ ) was modeled as  $B_t \sim \text{Poisson}(R_t f)$ , where  $f$  is the fecundity (assumed constant) and  $R_t$  is the number of broods monitored in year  $t$ . The overall likelihood was the product of the individual Poisson likelihood terms.

### 2.2.7 Priors

For Model 1, that estimates the number of immigrants, we used two different priors. The first one allows negative numbers of immigrants. Although negative numbers of immigrants are not possible from a biological perspective, we included this possibility in order to provide a useful diagnostic about whether there is immigration at all. Thus, we specified for each  $N_t^I$  the uniform distribution  $N_t^I \sim \text{Uniform}(-50, 100)$  as our first prior M1a. The use of the Poisson distribution was not possible here, as it is not defined for negative values. The second prior considered only positive values and thus we specified a uniform distribution for the expected number of immigrants as  $\mu_t^I \sim \text{Uniform}(0, 100)$ . This is our prior M1b.

For Model 2, that estimates the immigration rate, we also used two different priors. First, we used a vague prior that was truncated to avoid impossible negative and unreasonably large values, i.e.  $i_t \sim \text{Normal}(0, 1000)I(0, 5)$ . This is our prior M2a. Second, we used a gamma distribution that has much more support for small than for large values. Thus prior M2b is  $i_t \sim \text{Gamma}(1, 2)$ .

For Model 3, there is no prior needed, as each  $\mu_t^I$  is set to zero. In all three models, we used a uniform distribution between 0 and 1 as the prior for each of the survival and

recapture parameters. For the standard deviation of the observation error, we used a uniform distribution between 0 and 10. For both  $N_1^1$  and  $N_1^{2+}$  we used a uniform prior between 0 and 300. Finally, for  $f$  we used a truncated-lognormal with the untruncated distribution having mean 0 and variance 5 on the log-scale, the truncation ensuring that the final value was between  $-3$  and  $+3$  on the log-scale. Note that immigration rate is a derived parameter in Model 1, while the number of immigrants is a derived parameter in Model 2.

We assessed the sensitivity of our results by carrying out further analyses in which we used the following alternative priors:

$$N_t^I \sim \text{Uniform}(-100, 100), i_t \sim \text{Uniform}(0, 5) \text{ and } f \sim \text{Uniform}(0, 10).$$

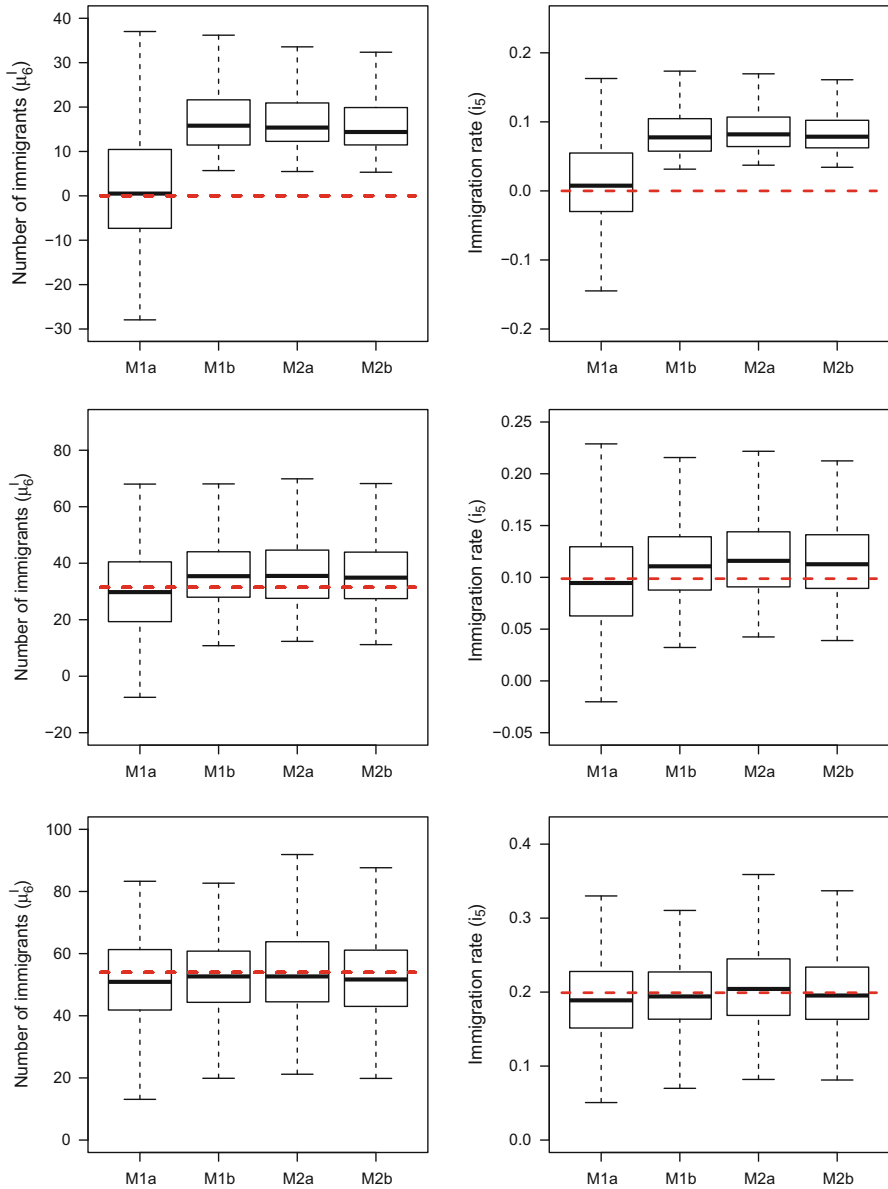
### 2.2.8 Computational details

For each simulation run, we ran two Markov chain Monte Carlo (MCMC) chains (Gilks et al. 1996) for 10,000 iterations. We discarded the first 5,000 iterations and retained every 5th iteration of the remainder. We summarised each posterior distribution by its mean and standard deviation. If the  $\hat{R}$  value (Brooks and Gelman 1998) for a parameter of interest was  $> 1.03$ , implying lack of convergence, we did not record any summaries for that posterior. We used as many simulations as were required in order to obtain a total of 500 summaries for each parameter of interest. The data were generated using R 2.9.1 (R Development Core Team 2009) and the analyses were performed in WinBUGS (Lunn et al. 2000) using the R2WinBUGS package (Sturtz et al. 2005).

## 3 Results

The results for the posterior means and standard deviations of the number of immigrants ( $\mu_t^I$ ) and the immigration rate ( $i_t$ ) did not vary much with  $t$ , so we arbitrarily focus on  $t = 6$  (i.e.  $\mu_6^I$  and  $i_5 = E(N_6^I)/N_5$ ). Figure 1 provides a summary of the distribution of the posterior mean of  $\mu_6^I$  and  $i_5$  for each level of the true number of immigrants (0, 35 or 60) for independent data sets. As mentioned in the Introduction, we cannot hope to estimate the true number of immigrants when the detection probability associated with the population counts is  $< 1$ . As the detection probability used in the simulations was 0.9 in each year, we therefore compare the posterior mean with the “true index” of the number of immigrants, given by  $0.9\mu_6^I$  (0, 31.5 and 54 individuals for the three immigration scenarios, respectively). By contrast, it is possible to estimate the true immigration rate, as the detection probability associated with the population counts is constant, and the immigration rate involves a ratio of population sizes. When there is no immigration, M1b, M2a and M2b all lead to overestimation of  $\mu_6^I$  and  $i_5$ , while M1a has posterior means for  $\mu_6^I$  and  $i_5$  that are approximately unbiased but also more variable. When there is immigration, the differences between the methods are less clear-cut for both the number and the rate. The results for the dependent data sets are very similar (Appendix 1, Fig. S1).

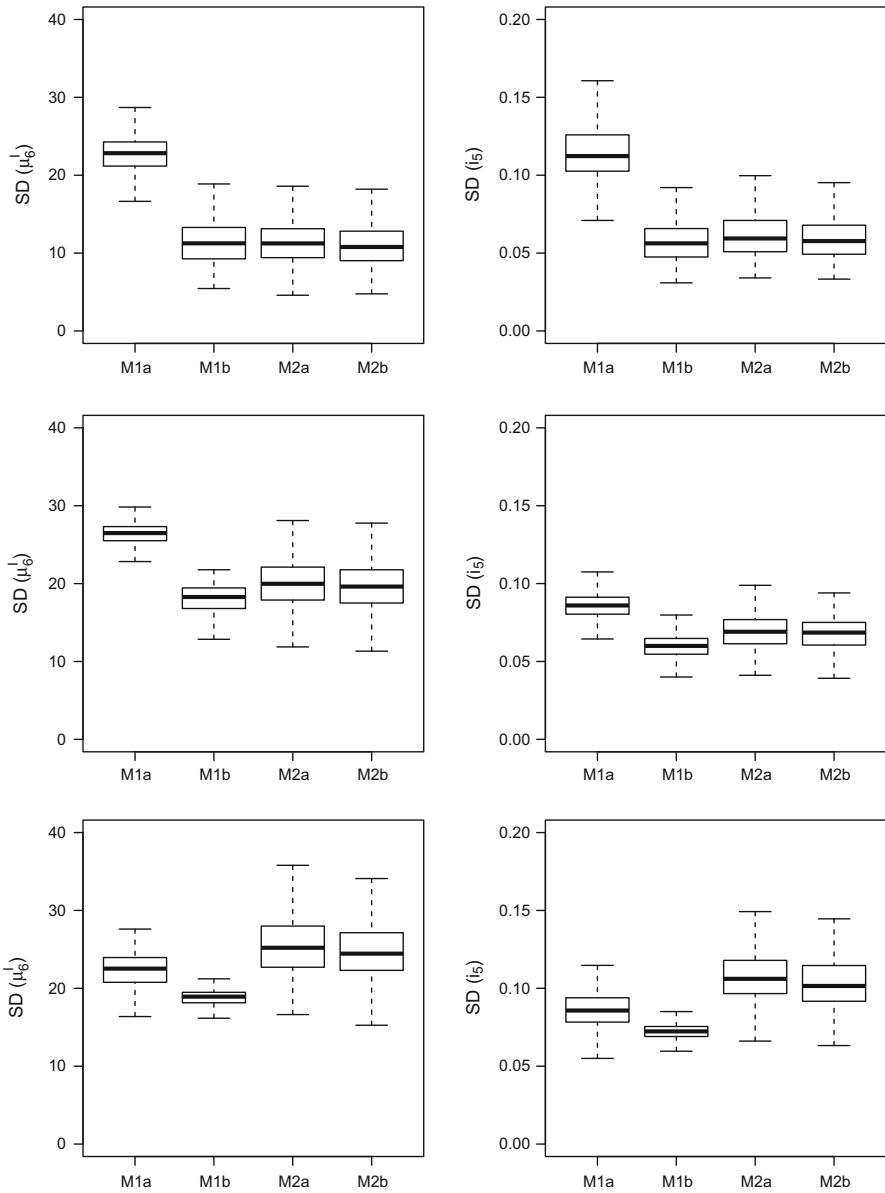
Figure 2 shows the corresponding summary for the posterior standard deviation of  $\mu_6^I$  and of  $i_5$ . Use of M1a leads to a higher posterior standard deviation for both



**Fig. 1** Boxplots showing the distribution over 500 simulations of the posterior mean for the number of immigrants ( $\mu_6^I$ , left column) and the immigration rate ( $i_5$ , right column) for each choice of parametrization and prior, when the true number of immigrants is 0 (top row), 35 (middle row) or 60 (bottom row) and the data sets are independent. The dashed red lines show the true index of the number of immigrants (left column) and the true immigration rate (right column)

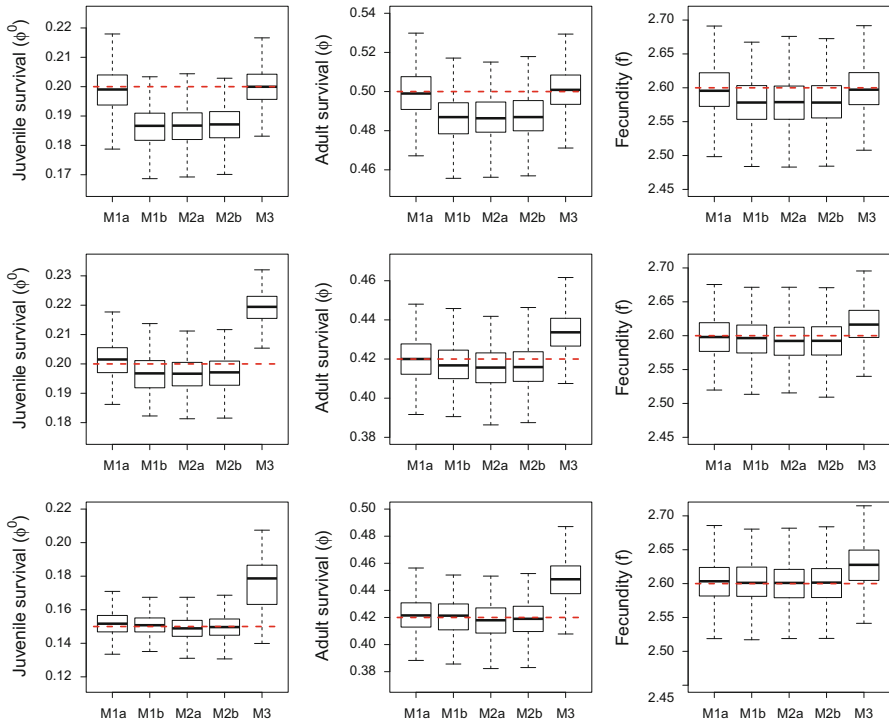
parameters, reflecting the greater uncertainty induced by a prior which allows the number of immigrants to be negative. This effect reduces as the amount of immigration increases, as would be expected. When there is no immigration, the other three methods





**Fig. 2** Boxplots showing the distribution over 500 simulations of the posterior standard deviations for the number of immigrants ( $\mu_6^I$ , left column) and immigration rate ( $i_5$ , right column) for each choice of parametrization and prior, when the true number of immigrants is 0 (top row), 35 (middle row) or 60 (bottom row) and the data sets are independent

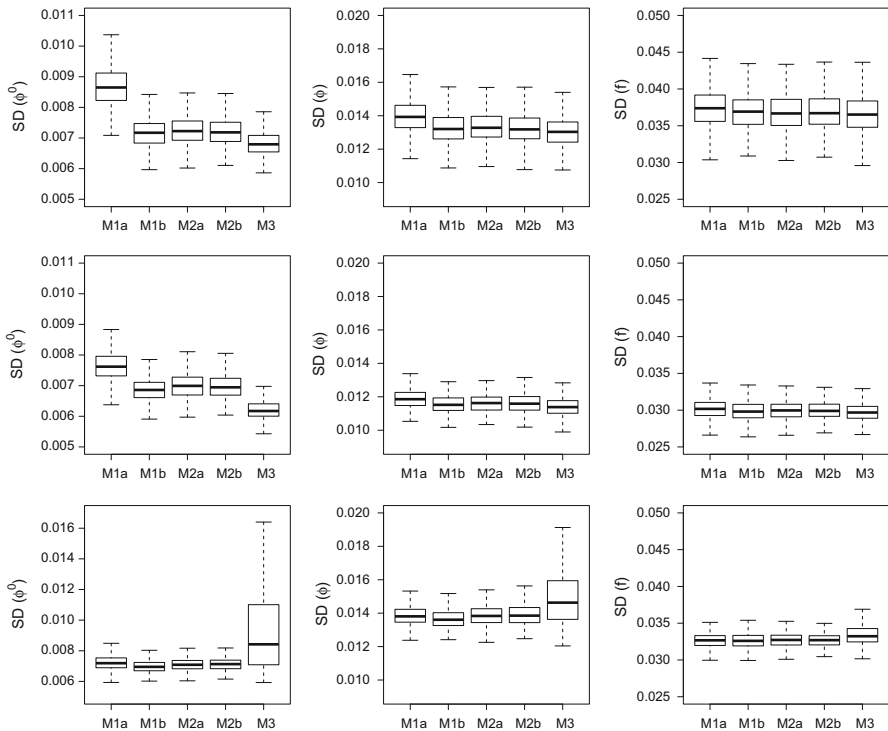
are almost identical. When there is immigration, M1b has the lowest posterior standard deviations for  $\mu_6^I$  and  $i_5$ , and these standard deviations are also less variable. Again the results for the dependent data sets very similar (Appendix 1, Fig. S2).



**Fig. 3** Boxplots showing the distribution over all simulations of the posterior mean for juvenile survival ( $\phi^0$ ), adult survival ( $\phi$ ) and fecundity ( $f$ ) for each choice of parametrization and prior, when the true number of immigrants is 0 (top row), 35 (middle row) or 60 (bottom row) and the data sets are independent. M3 corresponds to use of Model 3 in which there is assumed to be no immigration. The dashed red lines show the values of the simulating parameters

Overall, use of M1b is preferable to M2a or M2b when estimating  $\mu_t^I$  or  $i_t$  because immigration is estimated slightly more precisely. The choice between M1a and M1b comes down to one of bias versus variability and uncertainty, and depends on the amount of immigration. When there is no immigration, use of M1b can naturally lead to a posterior mean that is biased, while use of M1a leads to a more variable posterior mean and a higher posterior standard deviation.

Figure 3 provides a summary of the distribution of the posterior mean for  $\phi^0$ ,  $\phi$  and  $f$ , again for each level of the true number of immigrants and for independent data sets. As might be expected, use of Model 3, which assumes no immigration, leads to overestimation of all three parameters when there is immigration. When there is no immigration, M1b, M2a and M2b underestimate survival and fecundity in order to offset their overestimation of immigration, while M1a leads to an estimate that is approximately unbiased. When there is immigration, the differences between the methods are again less clear-cut. Figure 4 shows the summary for the corresponding posterior standard deviations. When there is no immigration, M1a has the highest posterior standard deviation, particularly for  $\phi^0$ , M3 has the lowest posterior standard deviation, and the other three methods are almost identical. When there is immigration,



**Fig. 4** Boxplots showing the distribution over all simulations of the posterior standard deviation for juvenile survival ( $\phi^0$ ), adult survival ( $\phi$ ) and fecundity ( $f$ ) for each choice of parametrization and prior, when the true number of immigrants is 0 (top row), 35 (middle row) or 60 (bottom row) and the data sets are independent. M3 corresponds to use of Model 3 in which there is assumed to be no immigration

M1b, M2a and M2b are again almost identical across all three parameters. For the highest level of immigration, M3 clearly performs worst, as would be expected. Results for the dependent data sets are very similar (Appendix 1, Figs. S3 and S4). The prior-sensitivity analysis shows that the results are not greatly influenced by the choice of prior (Appendix 2, Figs. S5-S7).

Overall, there is little to choose between M1b, M2a and M2b in terms of estimating  $\phi^0$ ,  $\phi$  and  $f$ . The choice between these methods and M1a comes down to one of bias versus uncertainty. Regardless of the amount of immigration, for all three parameters M1a provides a posterior mean that is approximately unbiased, whereas M1b, M2a and M2b provide a posterior mean that is negatively biased when there is little or no immigration. Conversely, M1a has a higher posterior standard deviation than M1b, M2a and M2b, especially when there is little or no immigration.

#### 4 Discussion

Integrated population modelling is likely to become an increasingly important tool for assessing population dynamics (Schaub and Abadi 2011). If immigration occurs and is not included in a population model, the estimated demographic parameters are biased

and inference is unreliable (Fig. 3). If immigration is to be included in such modelling, it will be important to determine which parametrization of immigration is most suitable. Our simulation study shows that this choice is important when immigration is low, but becomes less critical as immigration increases. Overall, we recommend use of a model in which immigration is specified in terms of the number of immigrants arriving each year, as opposed to an immigration rate, because of its higher precision and because it allows the evaluation whether immigration is occurring at all. This recommendation applies even when we wish to estimate the immigration rate itself, as direct estimation is less reliable than deriving it from the ratio of the estimates of the number of immigrants and the population size in the previous year.

We included an assessment of the assumption of independence that is often used in integrated population modelling. The results for the independent and dependent data sets were very similar, despite the degree of dependence being quite high (the inclusion probabilities being 0.75 for the mark–recapture data and 0.90 for the population survey and fecundity data). This suggests that modelling immigration in this way is robust to the assumption of independence of data sets. [Abadi et al. \(2010a\)](#) reached the same conclusion for population models that do not allow for immigration. It would be of interest to assess the effect of this assumption on other aspects of the analysis, such as coverage rates of credible intervals.

This first assessment of the estimation of immigration using integrated population models shows that immigration can be estimated without bias, but the precision is typically quite low. Low precision is expected for parameters in integrated population models for which no explicit data have been collected, as the information about these parameters only originates from the population counts. For example, a decline of the precision of estimates of fecundity from integrated population models with and without data on fecundity was found in another simulation study ([Abadi et al. 2010a](#)). Our finding that immigration is estimated without bias with integrated population models (provided the correct specification and prior are chosen) is based on the assumption that the model structure is specified correctly for all parameters. Since information about immigration is low, we particularly expect bias in this parameter when the model structure is not appropriate (e.g. specifying survival as constant although it is increasing in the course of the study). Further studies will have to show how robust the estimates of immigration are to violations of the model assumptions.

An integrated population model will typically involve a state-space model for the population count data. False negative (individuals not detected) and false positive (double counting) errors are accounted for by use of the observation variance  $\sigma^2$ . Typically false negative errors are more common than false positive errors, leading to the detection probability being  $< 1$ . In this case, as long as there is no pattern in the detection probability across time, use of a state-space model can lead to an unbiased estimate of a population index, rather than the true population size ([Kéry and Schaub 2012](#)). Likewise, our results for Model 1 suggest that, with an appropriate choice of prior and a constant detection probability, we can obtain an unbiased estimate of an index of immigration. Such an index can be of use when we are interested in *relative* effects, such as assessing the relative contribution of immigration to population growth. As with total population size, if we wish to estimate the true number of immigrants using such a model, we need a sampling protocol that allows estimation of the detection

probability. Estimation of an immigration rate is not affected in this way, as long as the detection probability is constant. We would expect these results to hold even when the detection probability varies over time, as long as it does so randomly.

Abadi et al. (2010b) showed how integrated population modelling could be used to estimate immigration for a little owl (*Athene noctua*) population in Southern Germany. They parametrized the model in terms of immigration rate, and assessed whether this rate exhibited a trend over time and/or was influenced by the density of a prey species (*Microtus arvalis*). Modelling the impact of environmental factors on immigration is also possible if the model is specified by the number of immigrants, but care is needed when interpreting the results. For example, if food availability is driving immigration, as appears to be the case in the little owl example (Abadi et al. 2010b), the number of immigrants in a year with good food availability may be lower than the number in a year with bad food availability, simply because the size of the donor population may have been lower in the former case. Although we generally recommend to parametrize immigration as a number, it can be preferable to parametrize it as a rate for specific research questions.

Our simulation study is necessarily limited in several respects. First, for simplicity, we have considered a model that is typical of that used for a short-lived bird species, with all individuals maturing at age two. We would expect our results to be similar to those for a species with delayed age at maturation, provided that immigration is restricted to one age class. Second, again for simplicity, we have arbitrarily set the demographic rates and the number of immigrants arriving each year to be constant. Again, we would expect to obtain qualitatively similar results when there is inter-annual variation in the demographic rates or in the number of immigrants.

In summary, our simulation study suggests that the amount of immigration into a population can be estimated reliably using an integrated population model even when not all individuals in the focal and donor populations are individually marked. The absence of immigration, however, is more difficult to deal with, and our simulation has shown that specifying a prior for the number of immigrants that includes negative values is a promising approach. Since immigration can be an important driver of population dynamics, and is often neglected, the use of integrated population modelling in this setting is likely to enhance our understanding of population dynamics.

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