**Performance of integrated population models across varying data landscapes**

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**Introduction**

Understanding the processes that control population dynamics in wild populations is a critical component of conservation and management but is frequently limited by missing demographic information, uncertainty, and temporally or spatially misaligned datasets (Schaub & Abadi 2011, Zipkin & Saunders 2017). Integrated population models (IPMs; Besbeas et al. 2002, Brooks et al. 2004) are an increasingly popular tool in ecology that can help overcome these limitations by combining disparate datasets in a single, unified analysis (Schaub & Abadi 2011). This approach can provide several advantages, such as improved precision (Schaub et al. 2007, Tavecchia 2009, Abadi et al. 2010) and the estimation of parameters that would otherwise be unidentifiable (Besbeas 2005, Schaub et al. 2007, Veran & Lebreton 2008), which is often the case for key demographic rates such as recruitment or immigration. These advances have practical benefits for resource managers that must make decisions based on limited available information. As IPMs become more widely used, however, it is critical that they are robustly evaluated.

Since the introduction of IPMs to wildlife ecology in the early 2000s and following the work of Besbeas and colleagues with passerines (Besbeas et al. 2002, 2005), the common approach has been to estimate parameters by combining mark-recapture and abundance data into a joint likelihood. Researchers have since expanded the use of IPMs to include a variety of taxa (e.g., bats *Rhinolophus ferrumequinum* (Schaub et al. 2007); Svalbard reindeer *Rangifer tarandus platyrhynchus* (Lee et al. 2015); Antarctic toothfish *Dissostichus mawsoni* (Mormede et al. 2019); wild boar *Sus scrofa* (Gamelon et al. 2019)). Applications have also been developed to estimate transition probabilities within multi-state and multi-site systems (McCrea et al. 2012), evaluate management efficacy and trade-offs (Cruz et al. 2018), and to estimate the effects of environmental processes and stochasticity on demography (Oppel et al. 2014, Woodworth et al. 2017). This proliferation of integrated population modeling has occurred despite a relatively poor understanding of how to assess goodness of fit for the joint likelihood. Additionally, the limitations of the IPM framework are still underexplored, particularly in situations where available data are sparse, of poor quality, or when data to inform specific parameters are entirely absent (i.e., most field studies may have count surveys, but not all have data informing both recruitment and survival).

Data simulation studies provide an avenue for robust evaluations of the IPM framework, but few such studies exist. Those that have used data simulation largely focus on (1) proof of concept (i.e., improved precision and reduced bias of parameter estimation) or (2) violation of assumptions within the subcomponent models (i.e., marker-induced bias or heterogeneity in survival) or the joint likelihood (i.e., dataset independence). In the former, IPMs generally have led to improved precision and unbiased estimates of parameters that would otherwise be unidentifiable using traditional approaches (McCrea et al. 2010, Chandler & Clark 2014, Schaub & Fletcher 2015, Bled et al. 2017, Ahrestani et al. 2017, Bowler et al. 2019), though not always depending on sample sizes, dominance of one dataset over another, or the likelihood structures (Ahrestani et al. 2017). In examining the effects of violating model assumptions on bias and precision, results have been mixed and again largely depend on sample sizes, effect sizes, parameterization, and the dominance of given datasets. In some cases, dependence across datasets resulted in biased estimates or at least overly optimistic estimates of uncertainty (Goodman et al. 2004, Besbeas et al. 2009) while in others, the effects on bias and precision were minimal (Abadi et al. 2010, Schaub & Fletcher 2015, Weegman et al. 2020). Riecke et al. (2019) found that estimates for previously unidentifiable parameters were highly sensitive to violations of mark-recapture model assumptions (i.e., marker-induced bias and survival heterogeneity).

These studies motivate further examination of the strengths and weaknesses of IPMs across a range of model structures and data landscapes, particularly when certain demographic rates are not directly informed by data or when a data source is sparse, biased, or highly uncertain. This type of analysis has been conducted for species distribution models in a few cases (Farr et al. 2020, Simmonds et al. 2020), but has not yet been rigorously explored for an IPM. Through a simulation analysis, we aim to gain insights about this statistical framework, particularly as applied to a passerine bird life history. We assume all model assumptions are met and compare parameter estimation for a traditional IPM with data informing abundance (count data), survival (mark-recapture data), and reproductive output (nest monitoring data) to situations when either of the latter two datasets are omitted. In each of these three cases, we also examine parameter estimation when juvenile survival varies and under situations with low detection to reflect a higher degree of uncertainty. In future iterations of this analysis, we plan to compare model performance in situations when datasets informing survival and reproduction are not only uncertain (low detection probability) but also sparse (reduced survey frequency), and the effects of having lower or variable adult survival and reproductive output.

Through this study, we will identify scenarios where IPMs may not lead to improved precision or return unbiased estimates of parameters that would otherwise be unidentifiable when certain datasets are excluded. In doing so, we will refine our understanding of the mechanisms underlying IPMs and can better identify when they may serve as a useful tool or might not be necessary or warrant the collection of additional data. Improving our understanding of the strengths and weaknesses of the IPM framework can provide helpful insights for the design and implementation of field survey programs that make efficient use of limited resources to inform management decisions. This is particularly important for efforts aimed at monitoring or recovering species that are deemed ecosystem indicators or depleted and in need of conservation intervention.

**Methods**

*Data simulation: life history*  
We simulated data for an avian species assuming life history stages and traits of a typical passerine. Our simulated hypothetical species has two age-classes: juveniles (individuals that hatched in the previous year) and adults (individuals in their second year of breeding and older). Each age class has a unique survival rate (, ) and adults produce new chicks at fecundity rate *f*, and those chicks survive to be juveniles at rate . Juveniles also breed, producing chicks at rate (Fig 1). We assume an annual breeding cycle, with females nesting once per year. The period from nest initiation to fledging is 30 days, regardless of clutch size. We assume that survival and fecundity are constant across years and individuals.

As is often the convention, we use a female-only model because we assume that the population dynamics of our species are driven largely by female abundance and demography. All demographic rates are assumed constant over a 10-year study period. The population is quite small, and the survey extends across the entire range, and we therefore assume no immigration or emigration.

Graphical user interface, application

Description automatically generated

Figure 1: Female only life-cycle diagram for the described species showing two age classes ( and ) with a single fecundity parameter (), and survival parameters for each age class (and ).

*Model framework and assumptions*

*Count model*  
We simulated data such that the population is surveyed annually in a 10-year pre-breeding census. Because count surveys are conducted three times per year in quick succession, we assume the population is closed between secondary sampling periods. We use an N-mixture model (Royle 2004) to estimate annual abundance from these repeated counts, where we assume no individual is double counted and that individual detections are independent and occur with equal probability. The underlying state process represents the stage-specific abundance at each occasion for juveniles, and is modeled as:

where the number of juveniles in the next year, , is estimated using a Poisson distribution with probability based on the sum of stage-specific individuals at time that survive () and reproduce ().

A binomial distribution is used to estimate the number of adults in the next year, based on the stage-specific survival and abundance in the previous occasion *t*:

The observation process model for the count data in each year is modeled using a binomial distribution:

with . The observed counts in each year, , are assumed to be binomially distributed with a sample size of and probability of detection . The probability of detection for the observation process, , of the count model is assumed constant across years and surveys. The survey detection probability was modeled on the probability scale using a uniform prior, .

The likelihood of the N-mixture abundance model is the product of the state and observation process models: .

*Nest success productivity model*

In this simulation, nests are monitored according to the procedures described in Martin and Geupel (1993), where adults are observed for behavioral clues that indicate nesting behavior and followed until a nest is found. After locating a nest, it is revisited every three days to check its status until it either fledges or fails. We assume no state uncertainty in our nest observations, that nests can be correctly aged when first found, and that monitored nests are independent and representative of the population. We assume the daily survival probability is uniform across nest stages (i.e., laying, incubating, nestlings). We estimate daily nest survival to obtain unbiased estimates for the probability of nest success (i.e., at least 1 chick fledges). We use a Poisson model to estimate the number of chicks fledged conditional on a nest being successful:

The fecundity rate, *f*, is derived from the rate at which chicks fledge,

where is the nest survival probability and we assume that the maximum nest age, the number of days the nest was active, is 30. The observation process for the daily nest surveys is modeled using a Bernoulli distribution, based on daily nest survival probabilities and the state of the nest during the previous survey occasion:

where is the status of nest at survey occasion , is the nest surivial probability, and is the state of nest at the previous survey occasion .

The likelihood of the nest success productivity model is .

*Mark-resight model*  
In this simulation study, juveniles and adults are marked just prior to the end of the breeding season with a unique combination of colored leg bands such that they can be individually identified over the course of their lives. Marked individuals are resighted during marking efforts and opportunistically throughout the breeding season. To estimate stage-specific survival based on the individual encounter histories, we use a Cormack-Jolly-Seber (Lebreton et al. 1992) model where we assume that marks are not lost or misread and that each marked individual has independent and identical survival and detection probabilities across occasions. The ecological state process *z* describes the probability that individual *i* at time *t* is alive or dead, namely:

where the state at time *t* is modeled with a Bernoulli distribution based on the state at the previous occasion and adult survival probability . Similarly, the observation process model

describes capture history observations, *CH,* using a Bernoulli distribution based on the state of the individual in the current occasion and detection probability . Mean survival and detection probabilities are modeled on the probability scale using uniform priors, and , respectively. The likelihood of the mark-resight model estimating the adult survival probability:

Diagram

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Figure 2: Overview of survey design with respect to breeding phenology.

*Integrated population model*  
To estimate abundance of the overall population at each time *t*, we combined the parameter estimates from the productivity and mark-resight models with the stage-specific abundance estimated using the N-mixture model in a stochastic Leslie population matrix model.

The joint likelihood for the integrated population model is the product of the likelihoods for the three subcomponent models:

In instances when one dataset is removed, we used uninformative priors in place of the data to estimate each of the relevant parameters.

*Simulation scenarios*  
We developed three versions of an IPM: 1) a ‘full’ IPM that incorporates all three datasets (counts, productivity, mark-resight); 2) an IPM with the counts and productivity datasets only (excludes mark-resight data); and, 3) an IPM with the counts and mark-resight datasets only (excludes productivity data) (Figure 3). There are numerous scenarios we could run to vary detection and survival probabilities for each IPM version and test our objectives. We opted to run a select number of scenarios to provide preliminary findings to inform future work. For each version of the IPM, we ran 5 scenarios for a total of 15 scenarios (Table 1). Within each scenario, we varied the following parameters: mark-resight probability (0.3, 0.5, 0.8), count detection probability (0.3, 0.5, 0.85), and juvenile survival (0.3, 0.4, 0.5). The remaining parameters were kept constant for all scenarios: daily nest survival (0.975), mean clutch size (2.5), max nest age (30), initial age distribution (1000 juveniles, 1000 adults), and adult survival (0.77). For demographic parameters, we chose to vary juvenile survival because it is a hidden parameter, and these various values result in 5% annual decline, a stable population size, and 5% annual growth, respectively.

|  |  |  |  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
|  | Model type | | | | | | | |  |  |
|  | Full IPM | | | Abundance + Productivity | | Abundance + Survival | | |  |  |
| Scenario  number | (0.85, 0.5, 0.3) | (0.8, 0.5, 0.3) | (0.5, 0.4, 0.3) | (0.85, 0.5, 0.3) | (0.5, 0.4, 0.3) | (0.85, 0.5, 0.3) | (0.8, 0.5, 0.3) | (0.5, 0.4, 0.3) |  |  |
| 1 | 6 | 11 |  |  |  |  |  |  |  |  |  | Legend |
| 2 | 7 | 12 |  |  |  |  |  |  |  |  |  | High |
| 3 | 8 | 13 |  |  |  |  |  |  |  |  |  | Medium |
| 4 | 9 | 14 |  |  |  |  |  |  |  |  |  | Low |
| 5 | 10 | 15 |  |  |  |  |  |  |  |  |  |  |

Table 1: Schematic of parameters varied across simulations.

Diagram

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Figure 3: Directed acyclic graph (DAG) for full IPM (top); DAG for counts + productivity model (center); DAG for counts + survival model (bottom).

*Estimation and diagnostics*  
We ran models in NIMBLE using program R (NIMBLE 2020). We ran 45,000 iterations with the first 35,000 as a burn-in. We thinned samples to reduce autocorrelation and retained every 10th sample, for a total of 1,000 samples. Model convergence was assessed visually using traceplots and a Brooks-Gelman-Rubin statistic (Rhat) <1.1. Some parameters did not converge in some simulations. In future work, we should run these simulations longer. We examined model performance using relative bias and root mean square error (RMSE).

**Results**

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Figure 4: Posterior medians of parameters estimated in each scenario. Red dots represent the true parameter value.

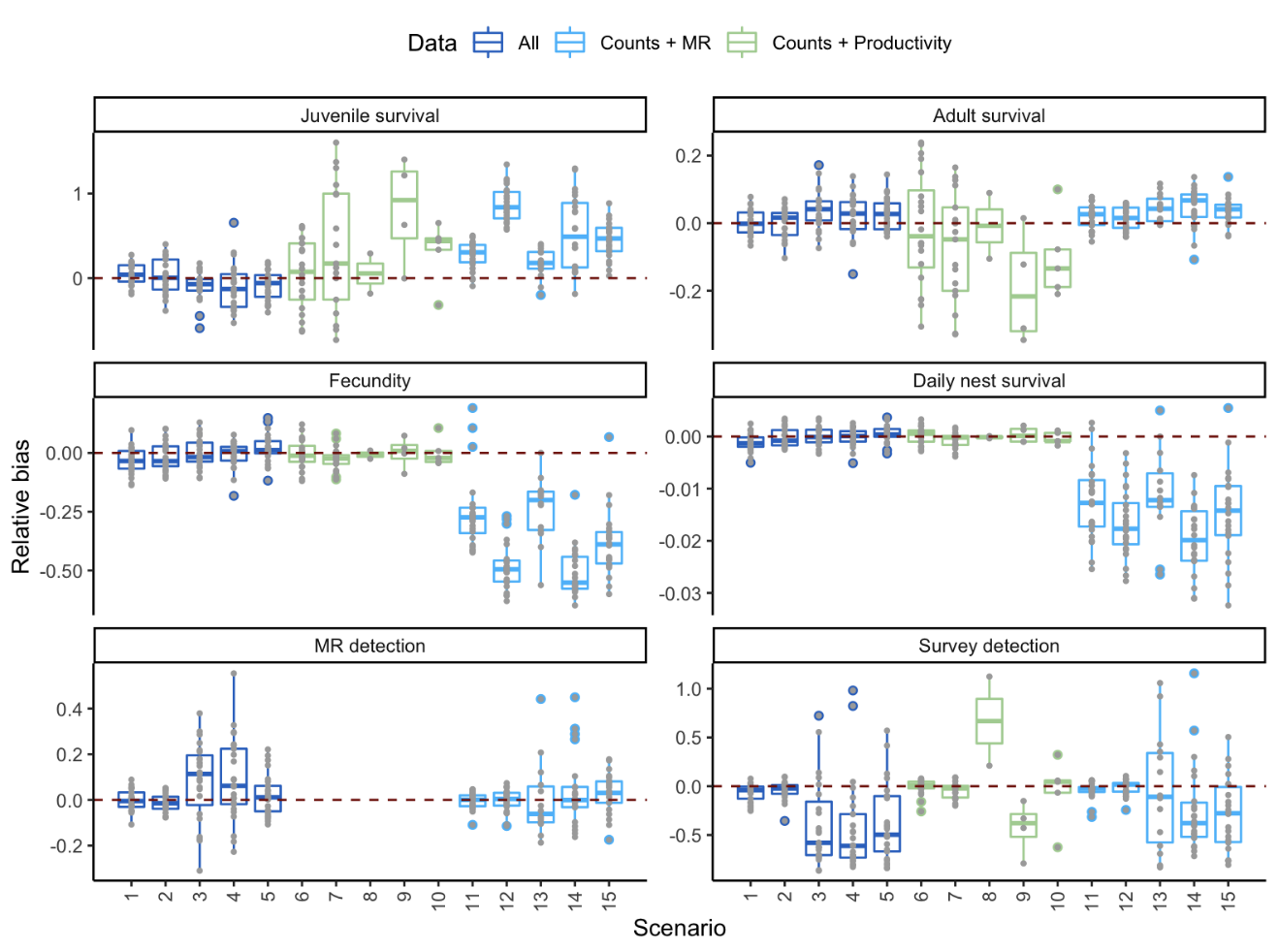


Figure 5: Relative bias of parameter estimates. Dotted lines at 0 indicate unbiased estimates.

| Model type | Scenario |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Full IPM | 1 | 0.07 | 0.03 | 0.04 | 0 | 0.09 | 0.04 |
| Full IPM | 2 | 0.06 | 0.03 | 0.04 | 0 | 0.09 | 0.03 |
| Full IPM | 3 | 0.1 | 0.05 | 0.04 | 0 | 0.17 | 0.06 |
| Full IPM | 4 | 0.09 | 0.05 | 0.03 | 0 | 0.19 | 0.06 |
| Full IPM | 5 | 0.08 | 0.04 | 0.04 | 0 | 0.27 | 0.05 |
| Counts + Productivity | 6 | 0.2 | 0.13 | 0.04 | 0 | 0.07 |  |
| Counts + Productivity | 7 | 0.24 | 0.13 | 0.03 | 0 | 0.08 |  |
| Counts + Productivity | 8 | 0.12 | 0.08 | 0.01 | 0 | 0.24 |  |
| Counts + Productivity | 9 | 0.29 | 0.19 | 0.03 | 0 | 0.15 |  |
| Counts + Productivity | 10 | 0.18 | 0.12 | 0.03 | 0 | 0.16 |  |
| Counts + MR | 11 | 0.16 | 0.03 | 0.17 | 0.01 | 0.08 | 0.03 |
| Counts + MR | 12 | 0.27 | 0.03 | 0.29 | 0.02 | 0.07 | 0.04 |
| Counts + MR | 13 | 0.12 | 0.05 | 0.16 | 0.01 | 0.18 | 0.05 |
| Counts + MR | 14 | 0.21 | 0.06 | 0.3 | 0.02 | 0.15 | 0.05 |
| Counts + MR | 15 | 0.2 | 0.04 | 0.24 | 0.02 | 0.23 | 0.05 |

Table 2: Root mean squared error (RMSE) for parameter estimates. Greener colors indicate lower error, redder colors indicate higher error.

*Full model*

Fitting the ‘full’ IPM model, including all simulated data types (counts, productivity, and mark-resight), generally produced parameter estimates close to the true value. The median model parameter estimates for , , , , and across the 25 simulated data sets and under scenarios 1 – 5 resulted in estimates where the true parameter values were contained within of the estimates. The model parameter estimates for the survey detection probability, , were returned under scenarios where was (i.e., scenarios 1 and 2), but with greater uncertainty in the model estimates for scenarios 3, 4, 5 where the true value of was or (Figure 4). Relative bias under scenarios was generally low (less than ), with the exception of , with high bias resulting in the low detection scenarios 3, 4, 5 where the model was not able to recover this parameter (Figure 5). RMSE for the full model was also generally low (less than ), with the exception of and . The RMSE for was high for scenario 3 and the RMSE for was high for scenarios 3, 4, 5 (Table 2).

*Counts + Productivity*

The IPM fit with data only from count and productivity datasets (excluding mark-resight) provided median estimates of and that were close to truth under all scenarios (6-10). The median estimates for and showed high variation in the model estimates for all scenarios and were unable to capture the true parameter values for scenarios 9 and 10 for both parameters. The survey detection probability estimates for scenarios 6, 7, and 10 resulted in medians covering the true parameter estimates, but under scenarios 8 and 9, the model estimates over and underestimated the true parameter value, respectively (Figure 4). The relative bias for under scenarios 7, 9, and 10 was high (greater than ), the relative bias for under scenario 9 was also high. The relative bias for was high under scenarios 8 and 9 (Figure 5). The RMSE for and under scenarios 6-10 was close to 0. The RMSE for was high (greater than 0.1) for all scenarios (6-10), the RMSE for was high for scenarios 6, 7, 9, and 10. The RMSE for was high for scenarios 8, 9, and 10 (Table 2).

*Counts + Mark-resight*

The IPM fit with data only from count and mark-resight datasets (excluding productivity data) resulted in median estimates of and that were close to truth for scenarios 11-15. The model excluding the productivity data resulted in medians that underestimated , , and under all scenarios. The model was able to capture the true value of under scenarios 11, 12, 13, and 15 (Figure 4). The relative bias and RMSE for and were high. Whereas the relative bias and RMSE for all other parameters in scenarios 11-15 was low (less than |0.1|; Figure 5).

**Discussion**

This simulation analysis aims to explore the benefits and weaknesses of data integration for population models across varying levels of data quality (degree of uncertainty) and quantity (sample size, number of available datasets) for a typical passerine bird species. One of the main goals of the study was to identify circumstances where developing IPMs is worth the potential additional resources needed for data collection. Similarly, we aimed to explore situations when this type of data integration framework could facilitate the estimation of parameters not directly informed by available data. Our initial results reaffirm the benefits of data integration for avian population modeling and highlight avenues of future investigation.

In our example of a typical passerine life history, the full IPM was the only data landscape in which all but one of the parameters were successfully returned with relatively little to no bias. In this case, we can also see the importance of integrating all three datasets for the estimation of juvenile survival, which is not directly informed by any of the datasets. Even in the full IPM, however, we do see increased bias and decreased accuracy (as measured by higher RMSE) in survival (particularly juvenile) at low detection rates that is not improved when the survival rate is higher. This suggests that detection probability is a strong determinant in parameter uncertainty. An important future scenario to examine under this full data landscape is whether that uncertainty could be overcome by increasing sample sizes and/or survey frequency.

When examining model performance across the other reduced data landscapes, similar patterns arose when removing either mark-resight or productivity datasets. With only two datasets, bias increased and accuracy was reduced only for parameters directly informed by the dataset that was omitted, and this deterioration in model performance was much greater than from decreased detection probability in the full IPM. This pattern, if explored further, will start to reveal some of the trade-offs that are most interesting to more fully investigate using this framework. Specifically, it will be helpful to examine to what extent sample size would have to increase and uncertainty would have to decrease in order to estimate the implicit parameters with a similar degree of accuracy and precision as with the IPM. And, when aiming to improve data quality and quantity, whether it can be accomplished more readily by increasing sample sizes and/or detection probability in mark-resight data versus productivity data. In other words, for our passerine, if, when, and to what extent does one dataset dominate another in terms of estimating abundance?

With the progression of these analyses, our aim is to additionally understand how some of these trade-offs within an IPM framework might vary for other life histories (e.g., additional life stages) and survey features. Here we assume that all datasets are independent and that mark-recapture model assumptions hold, but it would be possible to explore violations of any of these. We are also interested in examining the ability of our IPM to detect a trend in demographic rates or abundance across the three data landscapes or in the face of unmodeled heterogeneity.

Most research applications using an IPM framework cite the benefits of improved parameter estimation, including reduced bias and the ability to estimate implicit parameters, though not all authors can or choose to confirm this through data simulation or compare their IPM estimates with those from traditional modeling frameworks. It is likely that the benefits of IPMs are fairly variable and context-specific, meaning that the degree to which IPMs improve parameter estimation depend on life history, model assumptions, sample sizes, parameter uncertainty, and likelihood structure. This type of study can enhance our understanding of IPM performance when datasets may be sparse, biased, or both. Depending on the goal of a given monitoring or conservation and management program, it can be helpful to understand how biases in existing data affect our ability to produce accurate estimates of abundance and trends, and how it might or might not be possible to overcome sparseness or bias by collecting additional data. This information can be key to designing and implementing monitoring surveys for avian populations.

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