An assessment of integrated population models: bias, accuracy, and violation of the assumption of independence

Fitsum Abadi,[1,4] Olivier Gimenez,[2] Raphaël Arlettaz,[1,3] and Michael Schaub[1,3]

[1]*Institute of Ecology and Evolution, Division of Conservation Biology, University of Bern, Baltzerstrasse 6, CH-3012 Bern, Switzerland*
[2]*Centre d'Ecologie Fonctionnelle et Evolutive, UMR 5175, 1919 Route de Mende, 34293 Montpellier Cedex 5, France*
[3]*Swiss Ornithological Institute, CH-6024 Sempach, Switzerland*

Abstract. Understanding population dynamics requires accurate estimates of demographic rates. Integrated population models combine demographic and survey data into a single, comprehensive analysis and provide more coherent estimates of vital rates. Integrated population models rely on the assumption that different data sets are independent, which is frequently violated in practice. Moreover, the precision that can be gained using integrated modeling compared to conventional modeling is only known from empirical studies. The present study used simulation methods to assess how the violation of the assumption of independence affects the statistical properties of the parameter estimators. Further, the gains in precision and accuracy from the model were explored under varying sample sizes. For capture–recapture, population survey, and reproductive success, we generated independent and dependent data that were analyzed with integrated and conventional models. We found only a minimal impact of the violation of the assumption of independence on the parameter estimates. Furthermore, we observed an overall gain in precision and accuracy when all three data sets were analyzed simultaneously. This was particularly pronounced when the sample size was small. These findings contribute to clearing the way for the application of integrated population models in practice.

Key words: accuracy; Bayesian; capture–recapture; dependent data; independent data; individual-based model; Leslie matrix model; population survey data; reproductive success; state-space model.

Introduction

The dynamics of populations are essentially driven by the variation in the number of surviving and newly recruited individuals. To understand the demographic mechanisms that drive population trajectories, it is thus essential to accurately estimate vital rates. This is indeed crucial for effective species management and conservation (Williams et al. 2002, Norris 2004). As the study of the dynamics of wildlife populations usually requires detailed demographic data, researchers often collect different kinds of data such as capture–recapture, ring or tag recovery from dead animals, fecundity, and/or population-survey data. Traditionally, these data sets are analyzed individually while studying demographic processes. However, separate analyses will lead to more uncertainty and bias in the estimated demographic rates, in particular if sample size is small (Doak et al. 2005).

A promising, recently developed tool to analyze different sources of data simultaneously is *integrated population modeling* (Besbeas et al. 2002, 2003, Buckland et al. 2004, Thomas et al. 2005). The core of this model is a projection matrix parameterized with demographic parameters, which maps population sizes of different age or stage classes from one year to the next. Typically, part of the demographic information comes from capture–recapture type of data, while the information about population size is drawn from population surveys. Integrated population models have successfully been used to jointly analyze ring-recovery and population-survey data (Besbeas et al. 2002, Brooks et al. 2004), capture–recapture and population-survey data (Gauthier et al. 2007), capture–recapture, population-survey, and productivity data (Schaub et al. 2007) as well as estimates of abundance and data on incidental mortality in fisheries (Hoyle and Maunder 2004). Empirical studies have shown that integrated population models deliver demographic estimates with a higher precision than separate, conventional models (Besbeas et al. 2003). For estimating some parameters that are especially difficult to evaluate and cannot be retrieved from single analyses (e.g., fecundity from either capture–recapture or population-survey data), they even constitute the only feasible solution (Besbeas et al. 2002, Schaub et al. 2007). This is due to the fact that the information about all demographic processes is included in the population-survey data, and with the integrated model the entire information can be extracted. Eventually, it is the combination of different, independent information for a given parameter (e.g., survival probability determined through popula-

tion-survey and capture–recapture data) that leads to an increase in precision.

Although integrated population models are very appealing in principle, and potentially very useful, a thorough assessment of their accuracy for parameter estimation has never been performed. Moreover, the model relies on the critical assumption that the different data sets that are jointly analyzed are independent from each other. This assumption must be met because the joint likelihood of the model is calculated as the product of the likelihoods of the different data sets. It is currently little known whether the model performs well if this assumption is violated. Besbeas et al. (2009) combined ring-recovery and census data to test this assumption and concluded that the effect of dependency is a serious issue. In practice, however, it is often easier to obtain capture–recapture than ring-recovery data. It would thus be worth assessing the violation of the assumption in integrated models combining capture–recapture with other sources of demographic information such as data on population surveys and reproductive success.

The aim of this paper is to make a thorough assessment of the performance of integrated population models using extensive simulations. To study parameter performance we considered the life history of a short-lived species and used three different classes of sample size for evaluating the behavior of this model with respect to variation in sample size. Generally, we expect a greater benefit of the integrated population model at small than at large sample sizes. We addressed the following three main issues considering different sample sizes.

First, we assessed the magnitude of the improvement in the estimates of demographic rate in the integrated population model compared to conventional, separate analyses. Second, we evaluated the accuracy of the demographic parameters for which no empirical data are available and that can thus solely be extracted from population-survey data. Third, we assessed the extent to which the violation of the assumption of data sets inter-independency affects the accuracy of the estimated parameters. In the strict sense of the term, this assumption of independence requires that the different data sets have no individuals in common, which could be achieved either by sampling individuals from different populations or by sampling different individuals from the same population. The former further requires that the dynamics of the different populations under scrutiny is identical. The latter can be difficult to achieve in practice, especially when data stem from small populations, as is often the case in conservation science; the likelihood of sampling the same individual several times would be high under these circumstances. Fulfilling these assumptions of the independence of data sets would thus be particularly challenging precisely when the benefits of integrated modeling would be expected to be greatest, i.e., in small and local populations for which a clear demographic diagnosis (e.g., population trend, viability analysis) is essential.

METHODS

We examined the performance of the integrated population model with simulations. We first created populations using age-structured individual-based population models. We simulated each individual separately in such a way that its complete life sequence was known. Second, we sampled from the population three different types of data (capture–recapture, productivity, population survey) under various degrees of independence and with different sample sizes. Third, we analyzed these data under two different kinds of integrated population models (all three types of data above vs. using only capture–recapture and population-survey data) and with separate analyses considering only capture–recapture data or only fecundity data. We repeated these steps 500 times. Next we describe each of the three steps in more detail.

Creation of the life history in the population and the data sets

To create the populations from which data were then sampled we considered the life history of a short-lived bird species such as the Hoopoe (*Upupa epops*; see Plate 1). We assumed geographic closure (no immigration or emigration), constant survival probabilities and fecundity, and a pre-breeding census. We further assumed two age classes (1 and 2+ years), with reproduction starting from age 1, and the simulation only included female animals. Fecundity (average number of females produced per female, f) was set at 2.6, juvenile survival (survival from birth until 1 yr old, ϕ_{juv}) at 0.2 and adult survival (annual survival after 1 yr of age, ϕ_{ad}) at 0.5. The expected number of individuals in the two age classes at time $t + 1$ is given by the product of the population vector (containing the number of individuals) in year t and the projection matrix (Caswell 2001, Buckland et al. 2007) as

$$E(\mathbf{N}_{t+1} \,|\, \mathbf{N}_t) = E\left(\begin{bmatrix} N_{1,t+1} \\ N_{2+,t+1} \end{bmatrix} \right) = \begin{bmatrix} f\phi_{juv} & f\phi_{juv} \\ \phi_{ad} & \phi_{ad} \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2+,t} \end{bmatrix} \tag{1}$$

where $N_{1,t}$ is the number of 1-yr-old individuals at time t and $N_{2+,t}$ is the number of individuals older than 1 yr at time t.

Using this population matrix model and an initial population size of 300 individuals per age group, we carried out the following steps to create the life history of each individual in the population for 10 years:

1) Select an individual from the initial population or from the produced offspring (juvenile) at time t.

2) If the individual is at least one year old, generate the number of offspring produced at time t by drawing a random number from a Poisson distribution with parameter equal to the fecundity (f). If an individual is a juvenile, move to step 3.

3) Determine whether the individual survives from year t to $t + 1$ by drawing a random number from a

Bernoulli distribution with parameter equal to the age-specific survival probability (ϕ_{juv} or ϕ_{ad}).

4) If the individual survives, it moves to the next time $t + 1$ and to the next age class if it is not yet in the oldest age class. Repeat steps 2 to 3 until it dies or until the end of the study period.

5) If the individual does not survive, pick the next individual and repeat steps 2 to 5.

Thus, for each year we stored information about the state of an individual (dead or, if alive, in which of the considered age classes it is) and the number of newborn it has produced. The population reaches a stable age distribution very quickly, but we discarded the first five years to avoid transition effects of the initial conditions. Examples of the life histories of three individuals, along with the stored information, are provided in Appendix A.

To obtain completely independent samples, we randomly selected individuals in such a way that none of them appeared in common in any of the three data types. To create highly dependent samples, we selected a random sample of individuals at the beginning and created samples for the three different data types using only these individuals. To create three levels of sample size the number of randomly selected individuals was varied (small = 200 individuals; medium = 1000 individuals; large = 2000 individuals). Sample size may differ between iterations, because not all individuals that were initially considered were marked or surveyed. We stored the sample size for each iteration and also the number of identical individuals that are selected in the three different data sets.

Capture–recapture data.—We created individual capture–recapture histories using the individuals that were subject to capture–recapture sampling. For each year and when a specific individual was alive, we determined by a Bernoulli random number, with parameter equal to the capture probability, whether or not the individual was captured. The probability of initial capture was set at 0.76 for juveniles and 0.60 for adults, and the probability of recapture was set at 0.60.

Reproductive-success data.—We created reproductive-success data using the individuals that were subject to sampling for this data type. For each year when an individual was reproducing, we generated a random number from a Bernoulli distribution with probability equal to 0.9 to determine whether its reproductive success was recorded.

Population-survey data.—We created population-survey data using the individuals that were subject to sampling of this data type. For each breeder and year we generated a random number from a Bernoulli distribution with probability equal to 0.9 and determined whether it was included in the count. We then stored the number of detected breeders in each year.

Data analysis

We performed three different analyses for the sampled data. First, we analyzed all data types simultaneously using an integrated population model (IPM3); second, we analyzed only the capture–recapture and the population-survey data simultaneously in another integrated population model (IPM2); and third, we analyzed the capture–recapture data and fecundity data separately with a Cormack-Jolly-Seber (CJS) model and a Poisson regression model, respectively. We first describe the likelihood of each single data set and then show how the integrated likelihoods are created.

Likelihood for the capture–recapture (CR) data.—We summarized the capture–recapture data in matrix $m_{t_1 t_2}$, $t_1 = 1, 2, \ldots, T - 1$, $t_2 = t_1 + 1, \ldots, T + 1$, where $m_{t_1 t_2}$ denotes the number of individuals released at time t_1 and subsequently recaptured for the first time at time t_2 for $t_2 \leq T$, $m_{t_1, T+1}$ denotes the number of individuals never recaptured after being released in year t_1, and T denotes the number of capture occasions (m-array; Burnham et al. 1987). Then, each row of the data matrix is of a multinomial form and the likelihood (L) can be calculated as

$$L_{CR}(\mathbf{m} \mid \phi_{juv}, \phi_{ad}, p) \propto \prod_{t_1=1}^{T-1} \prod_{t_2=t_1+1}^{T} \pi_{t_1 t_2}^{m_{t_1 t_2}} \prod_{t_1=1}^{T-1} \chi_{t_1}^{(R_{t_1} - \Sigma_{t_2=t_1+1}^{T} m_{t_1 t_2})}$$

(2)

where R_{t_1} denotes the number of animals released in year t_1 and $\chi_{t_1} = 1 - \Sigma_{t_2=t_1+1}^{T}\pi_{t_1 t_2}$; $\pi_{t_1 t_2}$ denotes the cell probability of $m_{t_1 t_2}$, which is a function of survival and recapture probabilities. We defined $\pi_{t_1 t_2}$ as follows:

$$\pi_{t_1 t_2} = \begin{cases} \phi_{juv} p \left(\phi_{ad}(1-p)\right)^{(t_2 - t_1 - 1)} \\ \quad \text{for individuals released as juveniles} \\ \phi_{ad} p \left(\phi_{ad}(1-p)\right)^{(t_2 - t_1 - 1)} \\ \quad \text{for individuals released as 1 yr old or 2 yr+} \end{cases}$$

(3)

where $t_1 = 1, \ldots, T - 1$; $t_2 = t_1 + 1, \ldots, T$; and p is recapture probability. This is the well-known Cormack-Jolly-Seber model (see Lebreton et al. 1992).

Likelihood for the population-survey (PS) data.—We used a state-space model to describe the population-survey data (Besbeas et al. 2002, de Valpine and Hastings 2002, Buckland et al. 2004). The state process models the true, but unknown population trajectory under the population matrix model defined by Eq. 1, and the observation process links the observed population counts to the true population sizes assuming an observation error.

We describe the population trajectory (state process) using Poisson (Po) and binomial (Bin) distributions as

$$N_{1,t+1} \sim \text{Po}\left((N_{1,t} + N_{2+,t})f\phi_{juv}\right)$$

(4)

and

$$N_{2+,t+1} \sim \text{Bin}(N_{1,t} + N_{2+,t}, \phi_{ad}).$$

(5)

The likelihood of the state process is a product over

TABLE 1. The average number of unique individuals involved in data sampling, for different sample sizes and independence.

Sample size	Type of data	Independent			Dependent		
		CR	RS	PS	CR	RS	PS
Small (200 ind.)	CR	23	⋯	⋯	23	22	22
	RS	⋯	30	⋯	⋯	30	29
	PS	⋯	⋯	31	⋯	⋯	30
Medium (1000 ind.)	CR	156	⋯	⋯	155	147	147
	RS	⋯	202	⋯	⋯	204	192
	PS	⋯	⋯	203	⋯	⋯	204
Large (2000 ind.)	CR	310	⋯	⋯	309	293	293
	RS	⋯	407	⋯	⋯	406	382
	PS	⋯	⋯	407	⋯	⋯	405

Notes: The three data types are: CR, capture–recapture; RS, reproductive success; and PS, population survey. The number in the diagonal shows the sample size of the corresponding data type; the off-diagonals contain the numbers of adults included in two data types.

Poisson and binomial densities and denoted by $L_{SY}(\mathbf{N} | f, \phi_{juv}, \phi_{ad})$, where $\mathbf{N} = (\mathbf{N}_1, \mathbf{N}_2)'$ is a vector of the true population sizes.

The observation process expresses the population indices actually observed at time t (y_t) conditional on the state process. Here, the observation equation is given as $y_t = (1, 1) \times (N_{1,t}, N_{2+,t})' + \eta_t$. The term η_t accounts for the observation error and we assume that $\eta_t \sim \mathcal{N}(0, \sigma_y^2)$. The variance ($\sigma_y^2$) was small enough to ensure that negative values for the number of animals (y_t) were not sampled. Thus, the likelihood of the observation process, denoted by $L_{OB}(\mathbf{y} | \mathbf{N}, \sigma_y^2)$, is a product over normal densities.

Then, the corresponding likelihood of the population-survey data is given by

$$L_{PS}(\mathbf{y} | \mathbf{N}, \phi_{juv}, \phi_{ad}, f, \sigma_y^2)$$
$$= L_{OB}(\mathbf{y} | \mathbf{N}, \sigma_y^2) \times L_{SY}(\mathbf{N} | \phi_{juv}, \phi_{ad}, f). \quad (6)$$

Likelihood for reproductive-success (RS) data.—We assumed that the number of newborn females in year t (J_t) follow a Poisson distribution with parameter written as a function of the number of reproducing females (N_t) and the fecundity (f), hence, $J_t \sim Po(N_t f)$. Thus, the likelihood is a product over Poisson densities and denoted as $L_{RS}(\mathbf{J} | f)$.

Likelihoods of the integrated models.—Assuming the different data types are independent, the joint likelihood of the integrated models is constructed as a product of the single data likelihoods (Besbeas et al. 2002, 2003, Brooks et al. 2004). That is, for IMP3 it is

$$L_{IPM3}(\mathbf{m}, \mathbf{y}, \mathbf{J} | \phi_{juv}, \phi_{ad}, p, f, \mathbf{N}, \sigma_y^2) = L_{CR}(\mathbf{m} | \phi_{juv}, \phi_{ad}, p)$$
$$\times L_{PS}(\mathbf{y} | \phi_{juv}, \phi_{ad}, f, \mathbf{N}, \sigma_y^2) \times L_{RS}(\mathbf{J} | f) \quad (7)$$

and for IPM2 it is

$$L_{IPM2}(\mathbf{m}, \mathbf{y} | \phi_{juv}, \phi_{ad}, p, f, \mathbf{N}, \sigma_y^2) = L_{CR}(\mathbf{m} | \phi_{juv}, \phi_{ad}, p)$$
$$\times L_{PS}(\mathbf{y} | \phi_{juv}, \phi_{ad}, p, f, \mathbf{N}, \sigma_y^2). \quad (8)$$

All models were fitted within the Bayesian framework, specifying non-informative priors for all model parameters. Specifically, we used the beta distribution, $\beta(1, 1)$, for the survival and recapture parameters, an inverse gamma with parameters 0.0001 and 0.0001 for the variance (σ_y^2), a normal distribution with mean 100 and variance 10^4 truncated to positive values for age-specific population sizes, and a uniform distribution between 0 and 10 for the fecundity parameter. We first run three Markov-chain Monte Carlo (MCMC) chains (Gilks et al. 1996) in parallel for 10 000 iterations, discarding the first 3000 iterations. The $\hat{R}$ values of all parameters were less than 1.01, suggesting that convergence had been reached (Brooks and Gelman 1998). We then run 100 000 iterations with the first 30 000 as burn-in and thinned so that every 70th observation was retained.

We simulated 500 repetitions and calculated relative bias, precision (standard error), and accuracy (mean-square error) for all demographic parameters. The data were generated with R 2.6.1 (R Development Core Team 2005) and the analyses were performed in Win-BUGS (Lunn et al. 2000) using the R2WinBUGS package (Sturtz et al. 2005). All source code files and their descriptions for the analyses are provided in the electronic Supplement.

RESULTS

The average sample sizes across the 500 simulations for the independent and the dependent data are provided in Table 1. Between 72% and 94% of all individuals occurred in two or three data sets in the dependent data, indicating strong data dependency.

Integrated vs. independent analyses

Generally, integrated population models provided slightly more precise, less biased, and more accurate parameter estimates compared to the separate analyses (Fig. 1; Table B1 in Appendix B). As expected, the increase in precision and accuracy was more pronounced at small sample size. With medium or large sample sizes, the difference became minute. The increase in precision
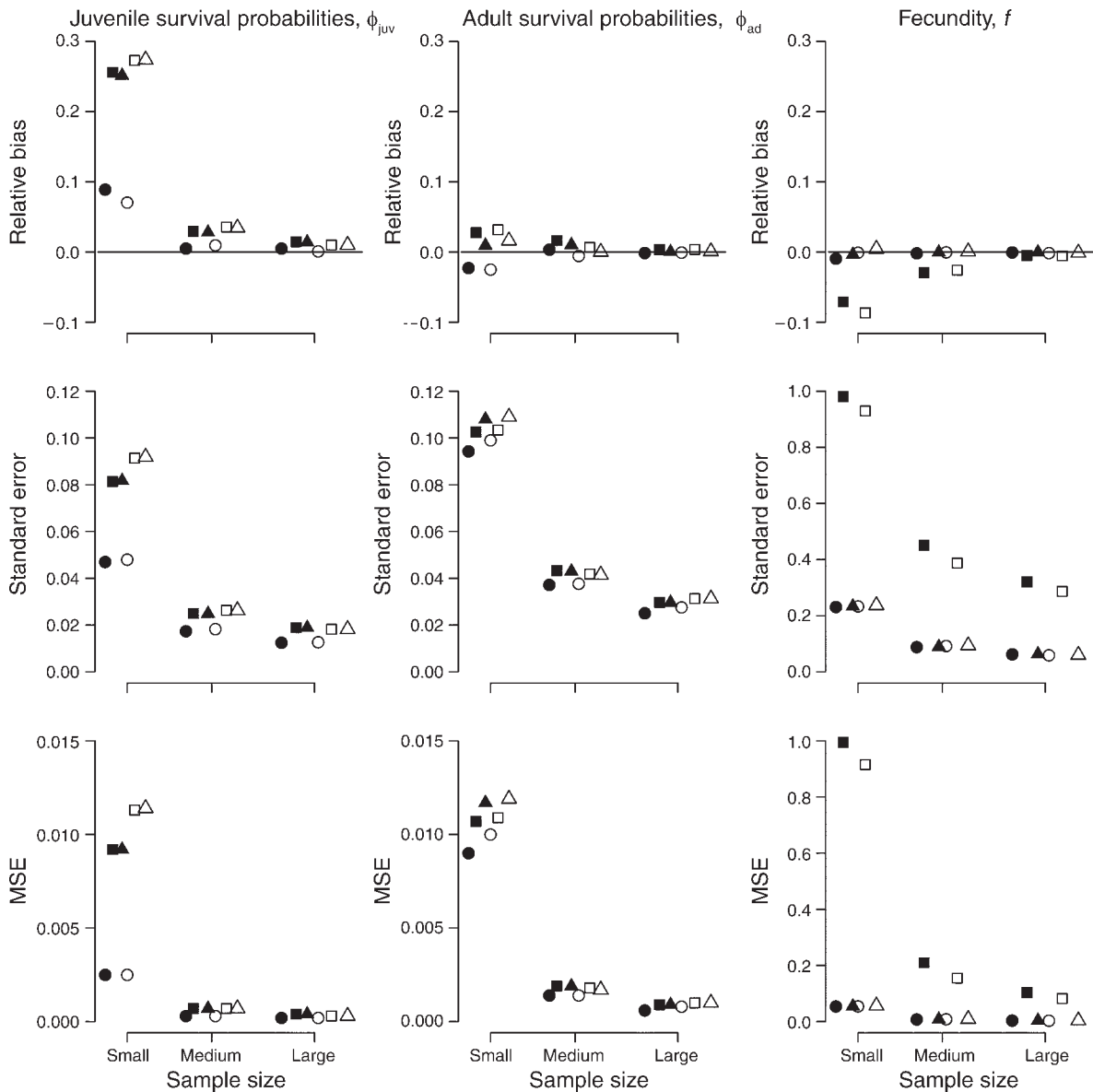
FIG. 1. Relative bias, standard error (precision), and mean-square error (MSE, accuracy) of juvenile and adult survival probabilities, and of fecundity, all as a function of sample size, estimated with different analyses. Estimates obtained with the integrated analyses are shown as circles (three data sets) and as squares (two data sets); estimates obtained with separate analyses are shown with triangles. Closed symbols represent independent data; open symbols represent dependent data.

and accuracy, and the decrease in bias differed among demographic parameters. The benefit of the integrated analysis was slightly higher for juvenile survival than for adult survival, while for reproductive success the precision and accuracy of the integrated analysis, which used the three data sets, was virtually similar to that of the separate analysis.

Differences between integrated analyses

The performance of the two integrated population models differed only slightly for the estimated survival probabilities for which explicit data were available (Fig.

1; Table B1 in Appendix B). Still, the integrated population model that used all three types of data (IPM3) provided slightly less biased, more precise, and more accurate survival estimates than the model that used only two types of data (IPM2). The difference was slightly larger when sample size was small compared to when sample size was large. For fecundity, the difference between the two integrated population models was much more important: fecundity estimated with the integrated population model that used no explicit data for fecundity (IPM2) was clearly more biased, less precise, and less accurate compared to the estimates

PLATE 1. The evaluated integrated population model is useful to study the dynamics of populations of short-lived species, such as Hoopoes (*Upupa epops*). Photo credit: R. Arlettaz.

coming from the integrated population model that used explicit data on fecundity. As for the other parameters, this strongly depended on sample size. If sample size was medium or large, then the performances of the two models were not very different.

Assumption of independence

Bias, precision, and accuracy of the parameter estimates originating from the independent and the dependent data were nearly the same, regardless of sample size (Fig. 1; Table B1 in Appendix B). Accuracy for the independent data tended to be slightly higher than for the dependent data in the case of small sample size and almost the same with large sample size, indicating that the violation of the assumption of independence does not have a strong impact on the performance of the estimators.

DISCUSSION

Using extensive simulations, we show that integrated population models performed better than separate analyses as the parameter estimates were more accurate and because integrated population models allow estimating parameters for which no explicit data were collected (Besbeas et al. 2005). Moreover, the violation of the assumption of independence had only minor consequences on the precision and accuracy of the parameter estimates. These are very encouraging results for the practical application of integrated population models (IPMs).

Empirical studies have stressed that the main advantages of integrated compared to separate analyses are that parameter precision is increased and that they provide estimates for parameters that cannot be estimated when using each data set in isolation. Our simulation study shows that integrated analyses provide more precise parameter estimates, but that the difference compared to separate analyses is slight only, even if sample size is low. These results are in agreement with the empirical findings of Besbeas et al. (2002) and Brooks et al. (2004). In their work, estimated precision of survival was slightly increased when coming from an integrated analysis (ring-recovery and census data) compared to when coming from a separate ring-recovery model. The reason for this only slight increase of precision is that most information about survival and fecundity comes from the capture–recapture and reproductive-success data, respectively. Borysiewicz et al. (2009) demonstrated that the improvement in precision is much more pronounced for multi-site compared to single-site integrated population models. This suggests that the integration of additional information has an effect on parameter accuracy, when the content of information in the original data source is low. We expect therefore that the benefit is largest when complicated models with many parameters, as needed in ecological studies, are used. Increased precision of parameter estimates can be of importance if temporal patterns in the parameter estimates will be evaluated, because the power to detect patterns is enhanced. However, given the small increase in precision restricted basically to small data sets, it appeared that the gain of precision was an advantage of practical relevance only when data sets are small. Still, it is exactly in such small data sets, for instance stemming from localized and small populations of conservation concern, that we would be most likely to want to apply an integrated analysis.

By contrast, the possibility of being able to estimate additional demographic parameters is an important advantage of integrated compared to separate analyses (e.g., Besbeas et al. 2003, Schaub et al. 2007). Using an integrated analysis, our simulations showed that fecundity could be accurately estimated even if only capture–recapture data and population-survey data are available. Accuracy very strongly increased with sample size. If the sample size was medium, the accuracy of the fecundity estimate was almost similar to that from separate analyses, regardless of whether data on fecundity were available. For demographic monitoring with limited

financial resources our result suggests that sampling data on fecundity is not necessary provided that sample size of the other data is large enough. Using the simulations as performed in this paper allows one to identify the necessary sample size of different sources of data to find the most efficient monitoring strategy for the desired precision of parameter estimates.

It is currently not known whether other combinations of available information still allow estimating all relevant demographic parameters. For example, one might envision constructing an integrated population model when only population-survey data and data on fecundity are available. However, because in that case no explicit data are available for two parameters (juvenile and adult survival), there may be more problems to get accurate estimates. Future studies might investigate the minimal data required to estimate demographic processes.

The violation of the assumption of independence does not appear to have strong effects on the parameter estimates. This was true despite the fact that the degree of dependence in our data was strong, with the majority of individuals appearing in all three or two data sets, and even if the sample size was low. This result is very important for the practical application of integrated population models, since in most cases individuals appear in several data sets. This means that samples from the same population can be used, and hence it is less important to sample from different populations and to assume that their dynamics are the same. In this study, we specified high detection probabilities and this led to a strong dependency in the data. Had we specified lower detection probabilities, the degree of dependency would have been lower and hence less subject to the violation of the assumption of independence. A likely reason why the violation of the independence assumption did not had a strong impact on parameter accuracy is that most of the information about survival and fecundity originates from capture–recapture and fecundity data, respectively, and only little information about these parameters is taken from the survey data (Besbeas et al. 2009). Besbeas et al. (2009) showed that the accuracy of the parameter estimates decreased when there was a dependency between ring-recovery and census data. Unlike capture–recapture data, ring-recovery data do not dominate survey data to provide information about common parameters, and in this case the violation of the independence assumption has a stronger impact on parameter accuracy. It is possible to envision another, more extreme level of dependence. In our study we assumed that the different data sets were obtained independently from each other, but that individuals could be present in different data sets. One might consider that exactly the same data are exploited two or several times. For example, instead of conducting a separate population survey, the number of captured individuals derived from the capture–recapture data might be used as an index of population size. Although

we have not studied this kind of dependence, we expect that in this case the consequences in terms of parameter performance would be serious.

We used a relatively simple model in our simulations, since one of the main goals was the assessment of the violation-of-independence assumption and not the performance of differently complicated models. Moreover, the life history that we used and the type of data that we simulated reflect a frequent situation, at least in ornithological studies. However, since integrated population modeling is a very general and flexible framework, many more different scenarios could be envisioned (e.g., life history with delayed maturity, inclusion of density dependence) and simulated, and we here discuss some possible extensions. A frequent situation is time dependence in demographic parameters. We have conducted a few simulations in this regard, and our preliminary findings indicate that the violation of the assumption of independence was not a serious concern in estimating time-dependent demographic parameters. In our study all individuals are assumed to have the same vital rates, but in reality vital rates differ individually. If individual variation is strong and not accounted for in the integrated analysis, we expect a greater effect of data dependence on the precision of the parameter estimates. Finally, capture–recapture data could be used to estimate population size (Schwarz and Seber 1999). It would thus be possible to use information about population size not only from the population surveys, but also from the capture–recapture data. In that case we would expect a greater effect of data dependence on the parameter estimates, because more common information stemming from two data sets are treated as independent.

To sum up, the findings of this study provide support for the use of integrated population models even if the assumption of independence is violated. Integrated population models give slightly more precise parameter estimates and allow estimating demographic parameters for which no specific data have been sampled. These properties are indeed important in assessing the status of wildlife populations and in identifying factors that affect their demography. We therefore expect that integrated population models will become frequently used in future.

Literature Cited

Besbeas, P., R. S. Borysiewicz, and B. J. T. Morgan. 2009. Completing the ecological jigsaw. Pages 513–539 *in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Environmental and Ecological Statistics. Volume 3. Springer-Verlag, New York, New York, USA.

Reports

Reports

Besbeas, P., S. N. Freeman, and B. J. T. Morgan. 2005. The potential of integrated population modelling. Australian and New Zealand Journal of Statistics 47:35–48.

Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark–recapture–recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547.

Besbeas, P., J. D. Lebreton, and B. J. T. Morgan. 2003. The efficient integration of abundance and demographic data. Applied Statistics 52:95–102.

Borysiewicz, R. S., B. J. T. Morgan, V. Hénaux, T. Bregnballe, J. D. Lebreton, and O. Gimenez. 2009. An integrated anlaysis of multisite recruitment, mark–recapture–recovery and multisite census data. Pages 579–591 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Environmental and Ecological Statistics. Volume 3. Springer-Verlag, New York, New York, USA.

Brooks, S. P., and A. Gelman. 1998. General methods for monitoring convergence of iterative simulation. Journal of Computational and Graphical Statistics 7:434–455.

Brooks, S. P., R. King, and B. J. T. Morgan. 2004. A Bayesian approach to combining animal abundance and demographic data. Animal Biodiversity and Conservation 27:515–529.

Buckland, S. T., K. B. Newman, C. Fernandez, L. Thomas, and J. Harwood. 2007. Embedding populaton dynamics models in reference. Statistical Science 22:44–58.

Buckland, S. T., K. B. Newman, L. Thomas, and N. B. Koesters. 2004. State-space models for the dynamics of wild animal populations. Ecological Modelling 171:157–175.

Burnham, K. P., D. R. Anderson, G. C. White, C. Brownie, and K. H. Pollock. 1987. Design and Analysis methods for fish survival experiments based on release–recapture. American Fisheries Society Monograph 5. American Fisheries Society, Bethesda, Maryland, USA.

Caswell, H. 2001. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.

de Valpine, P., and A. Hastings. 2002. Fitting population models incorporating process noise and observation error. Ecological Monographs 72:57–76.

Doak, D. F., K. Gross, and W. F. Morris. 2005. Understanding and predicting the effects of sparse data on demographic analyses. Ecology 86:1154–1163.

Gauthier, G., P. Besbeas, J. D. Lebreton, and B. J. T. Morgan. 2007. Population growth in Snow Geese: a modeling approach integrating demographic and survey information. Ecology 88:1420–1429.

Gilks, W. R., S. Richardson, and D. J. Spiegelhalter. 1996. Markov chain Monte Carlo in practice. First edition. Chapman and Hall, New York, New York, USA.

Hoyle, S. D., and M. N. Maunder. 2004. A Bayesian integrated population dynamics model to analyze data for protected species. Animal Biodiversity and Conservation 27:247–266.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modelling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

Lunn, D. J., A. Thomas, N. Best, and D. Spiegelhalter. 2000. WinBUGS—a Bayesian modelling framework: concepts, structure, and extensibility. Statistics and Computing 10: 325–337.

Norris, K. 2004. Managing threatened species: the ecological toolbox, evolutionary theory and declining-population paradigm. Journal of Applied Ecology 41:413–426.

R Development Core Team. 2005. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schaub, M., O. Gimenez, A. Sierro, and R. Arlettaz. 2007. Use of integrated modeling to enhance estimates of population dynamics obtained from limited data. Conservation Biology 21:945–955.

Schwarz, C. J., and G. A. F. Seber. 1999. Estimating animal abundance: review III. Statistical Science 14:427–456.

Sturtz, S., U. Ligges, and A. Gelman. 2005. R2WinBUGS: a package for running WinBUGS from R. Journal of Statistical Software 12:1–16.

Thomas, L., S. T. Buckland, K. B. Newman, and J. Harwood. 2005. A unified framework for modelling wildlife population dynamics. Australian and New Zealand Journal of Statistics 47:19–34.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press, San Diego, California, USA.

APPENDIX A

A figure illustrating the life histories of individuals in the population (*Ecological Archives* E091-001-A1).

APPENDIX B

Detailed summary of the relative bias, standard error, and mean-square error of the integrated and conventional analyses (*Ecological Archives* E091-001-A2).

SUPPLEMENT

The R and WinBUGS codes used in the paper (*Ecological Archives* E091-001-S1).