Estimating the strength of density dependence in the presence of observation errors using integrated population models

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ABSTRACT

Assessing the strength of density dependence is crucial for understanding population dynamics, but its estimation is difficult. Because estimates of population size and demographic parameters usually include errors due to imperfect detection, estimations of the strength of density dependence will be biased if obtained with conventional methods and lack statistical power to detect density dependence. We propose a Bayesian integrated population model to study density dependence. The model allows assessing the effect of density both on the population growth rate as well as the demographic parameters while accounting for imperfect detection. We studied the performance of this model using simulation and illustrate its use with data on red-backed shrikes *Lanius collurio*. Our simulation results showed that the strength of density dependence is identifiable and it was estimated with higher precision using the integrated population model than the conventional regression model. As expected, the conventional regression model tended to overestimate density dependence at the population level whereas underestimates at the demographic level, but the bias was small. The analysis of the red-backed shrike data revealed negative density dependence at the population level most likely mediated by a density-dependent decline in adult survival. This work highlights the potential of integrated population models in assessing density dependence and its practical application in population studies.

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1. Introduction

Factors regulating population size are broadly classified into density-independent (stochastic) and density-dependent (deterministic) factors (Williams et al., 2002). To better understand how populations are regulated, the effect of density on different age or stage classes should be quantified. Knowledge of density dependence is also crucial in practical applications such as conservation or harvest regulations (Hanski et al., 1996; Sinclair and Pech, 1996; Drake, 2005). Many studies have used long-term time series data to estimate the strength of density dependence (Dennis and Taper, 1994; Lande et al., 2003). The main principle is to study whether there is a negative relationship between population growth rate and population size. An important limitation of this approach is that it requires a population census, i.e., a complete enumeration without errors in the counts. If an observation error is present and not accounted for, it inflates the type I error and misleadingly indicates the presence of density dependence (Shenk et al., 1998; Freckleton et al., 2006; Knape, 2008; Lebreton, 2009). More recently, state-space models have been used to reduce or remove bias in parameters or functional forms of density relationships resulting from observation error (de Valpine and Hastings, 2002; Jamieson and Brooks, 2004; Dennis et al., 2006). However, estimates are unbiased only if the observation error is relatively small (Knape, 2008). A further limitation is that the analysis of population counts only reveals the effect of density at the population level and, consequently, the demographic mechanisms causing density dependence remain unknown.

Some studies have used long-term data to assess the impact of density on demographic parameters by regressing estimates of demographic parameters on population counts (Coulson et al.,

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2000; Sæther et al., 2000; Barker et al., 2002; Paradis et al., 2002; Barbraud and Weimerskrich, 2003; Tavecchia et al., 2007). To get unbiased estimates of the strength of density dependence this approach requires estimates of demographic rates and population counts that are not subject to observation errors. If there are observation errors (either on the demographic rates and/or on the population counts), the test for density dependence will suffer from a lack of statistical power (Lebreton, 2009). Recently, Schofield et al. (2009) applied the Jolly–Seber model to mark-recapture data to estimate the strength of density dependence on survival. Using this model, estimates of survival and of population sizes are obtained while accounting for imperfect detection, and thus the power to detect density dependence is maximized.

Despite the development of different methods for studying density dependence, there are currently no approaches to assess the effect of density on all demographic parameters simultaneously while accounting for observation error. This is a drawback because the full demographic mechanisms of density-dependent population regulation cannot rigorously be studied.

Here we propose the use of a Bayesian integrated population model to study density dependence in a coherent fashion. Integrated population models combine different sources of demographic data into a single model and provide estimates of all demographic parameters and population size with improved precision and that are free of observation error (Besbeas et al., 2002; Brooks et al., 2004; Schaub et al., 2007; Abadi et al., 2010a; Kéry and Schaub, 2012). Parameters that are unidentifiable from a single source can be estimated with these models [e.g. fecundity (Besbeas et al., 2002); immigration rate (Abadi et al., 2010b; Schaub et al., 2012)]. These models also are very appealing and powerful when the sample size is small (Abadi et al., 2010a). A review on integrated population models is provided in Schaub and Abadi (2011).

The model we propose for studying density dependence potentially has several advantages. Firstly, because integrated population models involve the use of state-space models for the population counts, it is possible to assess density dependence based on estimates of population indices corrected for random observation errors rather than on the population counts including errors, which avoids the confounding effect of observation errors. Secondly, because demographic parameters (e.g. age-specific survival, fecundity) are estimated, it allows a test of density dependence for them, and thus the demographic mechanisms of density-dependent population regulation can be identified. It also allows assessing density dependence at the population level using the derived population growth rate. Thirdly, combined analysis of demographic data results in improved precision of estimates, which is expected to increase the statistical power to detect density dependence.

We conducted simulations to examine the performance of integrated population model in estimating the strength of density dependence under different magnitudes of observation error. We illustrate the method using a data set on a population of red-backed shrikes *L. collurio*. Previous studies have shown that the studied shrike population is regulated by density at the level of the population (Pasinelli et al., 2011), but that neither survival nor fecundity was a function of local density (Schaub et al., 2011). The latter study was performed with conventional methods (i.e., models that ignore observation error in population counts) which are expected to have lower power than the integrated analysis. Here, our objective was to evaluate whether density dependence at the level of the demographic rates could be estimable using the newly proposed model.

2. Methods

We first present the integrated population model to estimate the strength of density dependence. We then briefly describe the

simulation procedure and the case study, and how the model is implemented in the Bayesian framework. We were motivated by a short-lived bird species from which we sampled capture–recapture and reproductive success data, as well as annual population counts.

2.1. Modelling density dependence in the integrated population model

Integrated population models first require the formulation of the likelihood for the available demographic data sets. Detailed discussion of this likelihood formulation is provided in Abadi et al. (2010a). In summary, we used the standard Cormack–Jolly–Seber model (CJS; Lebreton et al., 1992) for the capture–recapture data. We assumed the number of individual encounter histories summarized in the m-array (m, Burnham et al., 1987) follows a multinomial distribution with parameters that are functions of time- and age-specific apparent survival ($\phi_{ju,t}$, $\phi_{ad,t}$) and recapture probabilities (p_t) where $\phi_{ju,t}$ denotes the probability that a newborn individual survives and becomes a yearling (1 year old) from year t to $t+1$ and $\phi_{ad,t}$ denotes the survival probability of yearlings and adults (older than 1 year) from t to $t+1$. We denote the likelihood for this model by $L_{cr}(m|\phi_{jv}, \phi_{ad}, \mathbf{p})$. For the data on reproductive output, we assumed that the annual number of offspring produced per female (J_t) is Poisson distributed whose parameter is the product of annual fecundity (f_t) and the annual number of females recorded to produce young (R_t). Fecundity (i.e. the number of newborns per adult females) of both yearlings and adults is assumed to be the same. The likelihood for this model is denoted by $L_{rp}(\mathbf{J}, \mathbf{R}|f)$.

To describe the population counts we use a state-space model, which consists of a process and an observation model (Besbeas et al., 2002; Abadi et al., 2010a). The process model describes the evolution of the underlying population sizes over time, thus it determines the link between the demographic rates and population size. Let $N_{1,t}$ denote the number of 1 year old individuals in year t, $N_{2+,t}$ denote the number of individuals older than 1 year in year t, and $N_t = N_{1,t} + N_{2+,t}$, denote the total population size in year t. We assume that $N_{1,t+1}$ is generated by a Poisson process with rate parameter based on the product of fecundity, juvenile survival and total population size in year t. The sex ratio of newborn is assumed to be even and therefore we divide f by 2, and thus,

$$N_{1,t+1} \sim Po\left(N_t\left(\frac{f_t}{2}\right)\phi_{jv,t}\right) \tag{1}$$

We further assume that $N_{2+,t+1}$ is generated by a binomial process as

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

The observation model links the population counts (i.e. the number of detected and counted female breeders, denoted by y_t) to the latent total population sizes (N_t). We then assume

$$y_t \sim N(N_t, \sigma_y^2) \tag{3}$$

where the variance σ_y^2 quantifies the observation error. The likelihood for the state-space model is given by the product of the likelihood of the process and observation models, $L_{sy}(\mathbf{N}|\phi_{jv}, \phi_{ad}, f) \times L_{ob}(y|\mathbf{N}, \sigma_y^2)$. The likelihood of the integrated population model is then obtained as the product of the likelihoods of all three data sources under the assumption of independence as

$$L_{joint}(m, J, R, y|\phi_{jv}, \phi_{ad}, f, \mathbf{p}, \mathbf{N}, \sigma_y^2) = L_{cr}(m|\phi_{jv}, \phi_{ad}, \mathbf{p}) \times L_{rp}(J, R|f)$$
$$\times L_{ob}(y|\mathbf{N}, \sigma_y^2) \times L_{sy}(\mathbf{N}|\phi_{jv}, \phi_{ad}, f) \tag{4}$$

A simulation study by Abadi et al. (2010a) that combined and analyzed completely dependent data of capture–recapture, population counts, and reproductive success showed that the violation

of the independence assumption only had a negligible effect on the precision of parameter estimates. We assume that this is true also in the present study.

All demographic parameters and population sizes appear in the likelihood of the integrated models as shown in Eq. (4). This allows the possibility to model density dependence of the demographic rates within a single model. We modelled the effect of density on both survival probabilities and fecundity as follows.

$$\log it(\phi_{jv,t}) = \beta_0 + \beta_1 N_t^* + \varepsilon_{\phi_{jv,t}} \quad \varepsilon_{\phi_{jv,t}} \sim N(0, \sigma_{\phi_{jv}}^2) \tag{5}$$

$$\log it(\phi_{ad,t}) = \beta_2 + \beta_3 N_t^* + \varepsilon_{\phi_{ad,t}} \quad \varepsilon_{\phi_{ad,t}} \sim N(0, \sigma_{\phi_{ad}}^2) \tag{6}$$

$$\log(f_t) = \beta_4 + \beta_5 N_t^* + \varepsilon_{f_t} \quad \varepsilon_{f_t} \sim N(0, \sigma_f^2) \tag{7}$$

where N_t^* is the standardized population size (i.e., $N_t^* = (N_t - mean(N_t))/sd(N_t)$, $N_t = N_{1,t} + N_{2+,t}$ is the population size in year t, and the σ^2 are the temporal variances of the demographic parameters. The slope coefficients (β_1, β_3, β_5) estimate the strength of density dependence on juvenile survival, adult survival and fecundity, respectively. For the recapture probability, which is a nuisance parameter, we assumed a random year effect, thus $\log it(p_t) = \alpha + \varepsilon_{p_t}$ with $\varepsilon_{p_t} \sim N(0, \sigma_p^2)$ where σ_p^2 is the temporal variability of recapture. The goal is to estimate the regression coefficients (α, $\boldsymbol{\beta}$) and the magnitude of temporal variances ($\boldsymbol{\sigma}^2$).

We also estimated the strength of density dependence on the population growth rate (i.e. at the level of the population). This was done by first calculating the population growth rate ($\lambda_t = N_{t+1}/N_t$), and then regressing the growth rate on population size as

$$\log(\lambda_t) = \beta_6 + \beta_7 N_t^* + \varepsilon_{\lambda_t} \quad \varepsilon_{\lambda_t} \sim N(0, \sigma_\lambda^2) \tag{8}$$

We calculated this regression outside the integrated population model, because we did not want to induce any constraints on the density dependence at the population level, since density dependence at the population level is always the result of density-dependent variation of demographic rates.

We also estimated the strength of density dependence, ignoring the observation error, by regressing demographic rates estimated with single data analysis (i.e. survival probabilities from capture–recapture data estimated with the CJS model and fecundity estimated from data on reproductive success with a Poisson regression model) on standardized population counts. The relationships between demographic parameters and population counts were similar with Eqs. (5)–(8), but here we used the population counts y_t^* rather than N_t^* and the population growth rate was calculated as $\lambda_{obs,t} = y_{t+1}/y_t$ and modelled as a function of y_t^*.

2.2. Simulation study

2.2.1. Individual-based simulation of the data

The way we conducted simulations is analogous to that described in Abadi et al. (2010a). It consists of creating a population by simulating fates of individuals, sampling demographic data from this population, and analysing these data with the developed integrated population model. These steps are repeated several times and point estimates stored, serving the base to evaluate the performance of the model.

To create the population, we mimic a short-lived bird species and the development of the population sizes from one year to another is described by Eqs. (1) and (2). We specified the relationship between demographic parameters and the actual population size in year t as

$$\log it(\phi_{jv,t}) = 0 - 0.05 N_t + \varepsilon_{\phi j v_t} \quad \varepsilon_{\phi j v_t} \sim N(0, (0.15)^2) \tag{9}$$

$$\log it(\phi_{ad,t}) = 1.735 - 0.02 N_t + \varepsilon_{\phi ad_t} \quad \varepsilon_{\phi ad_t} \sim N(0, (0.20)^2) \tag{10}$$

$$\log(f_t) = 1.386 - 0.01 N_t + \varepsilon_{f_t} \quad \varepsilon_{f_t} \sim N(0, (0.10)^2) \tag{11}$$

The simulation parameters in Eqs. (9)–(11) were chosen in such a way that they result in reasonable demographic rates for a short lived bird species at the population size of about 50.

Next, we created the life history of individuals in the population for 20 years. To start the creation of the population, we set the initial population size at 40 individuals. We then specified the actual probabilities of survival and fecundity applying Eqs. (9)–(11) under consideration of the actual population size. For each individual alive in the population it was then simulated whether it survived for another year, how many juveniles it produced, and how many of the juveniles survived. The sum of the number of yearlings and surviving adults gives then the population size in the following year, and we specified the demographic rates for this following year. This was repeated for 20 years. Information about the state of an individual (dead, alive, in which age group it is given alive) and the number of offspring it has produced were stored. To avoid transition effects of the initial conditions we only used the last 10 years of the simulated data sets.

Once we created the population, the next step was to sample individuals for the different studies. We independently selected 1000 individuals at random from the population to be available for capture–recapture and reproductive success data sampling. To create the capture–recapture histories and reproductive success data based on individuals subject to each study, we set the initial capture probability at 0.90 and 0.50 for juveniles and adults (1 year and older), respectively, and the recapture probability at 0.50. The probability to detect and record reproductive success was set at 0.90. All these capture/recapture and detection probabilities were assumed to be constant across time. To create the population counts in each year, we used a binomial distribution with parameters actual population size in the given year (N_t) and detection probability (P_s). The detection probability was assumed to be constant over time. We considered two scenarios, one with detection probabilities of female breeders of 0.50, and one with 0.90. The lower detection probability corresponds to a large observation error in the population counts. This is because the variance of binomial sampling (i.e. $NP_s(1 - P_s)$) is largest with $P_s = 0.50$. Our sampling procedures did not result in completely independent data sets as some individuals that were involved in either capture–recapture or reproductive success data sampling also had a chance to be included in the population counts. We simulated 500 data sets and analyzed them using the proposed integrated population models and conventional models. We then assessed the identifiability of the density-dependence parameters by comparing the posterior means obtained from the integrated as well as conventional models with their corresponding prior distributions (Gimenez et al., 2009). We also assessed the precision of the estimates of density dependence at varying levels of observation error in population counts.

2.3. Case study

We used 26 years of demographic data (capture–recapture data and data on reproductive success) as well as population counts of red-backed shrikes collected from 1981 to 2006 in southwestern Germany near Göppingen (48°39′N, 9°47′E) to illustrate the method. The red-backed shrike is a medium-sized ($\sim$30 g) migratory passerine living in agricultural landscapes during the breeding season (Glutz von Blotzheim and Bauer, 1993). Detailed descriptions of the study and data are provided in Schaub et al. (2011). The population size varied between 35 and 71 breeding pairs during the study period and we monitored the fate of 1154 broods. 513 adult females and 1799 fledged females were colour ringed, of which 126 and 63, respectively, were resighted at least once in a later year in the study area. The goal was to estimate the strength of density dependence at the population level and of the demographic rates of females to assess (1) whether the population
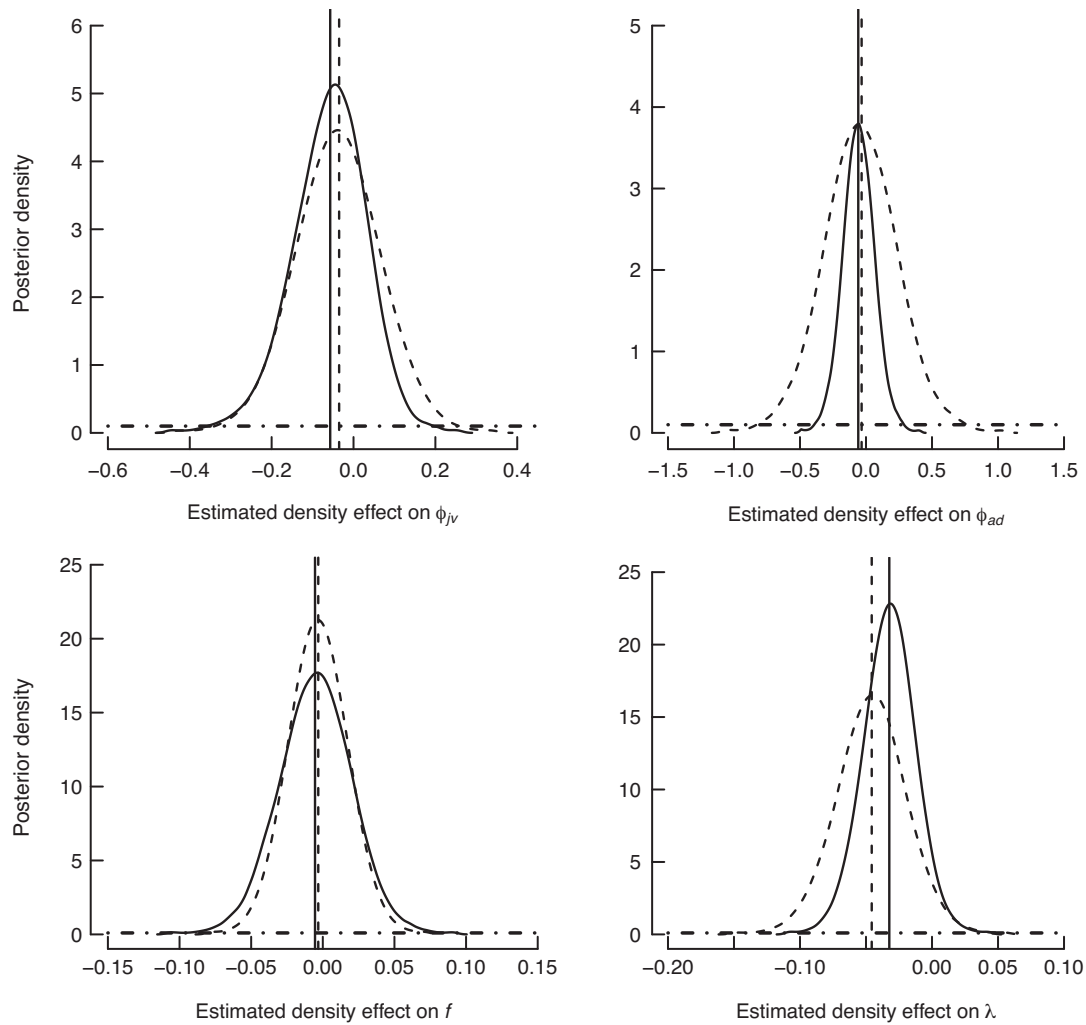
Fig. 1. Density plots of 500 estimated posterior means of strength of density dependence on juvenile survival (ϕ_{jv}, i.e. β_1), adult survival (ϕ_{ad}, i.e. β_3), fecundity (f, i.e. β_5) and population growth rate (λ, i.e. β_7) obtained from integrated population model (solid line), and from single data analysis ignoring observation error (dashed line) when the observation error for population count data was large (probability to detect female breeders = 0.50). Vertical lines are the means of the estimated posterior means of the strength of density dependence over 500 simulations. Dotdash lines are prior densities of the $\boldsymbol{\beta}$.

is regulated by density, and (2) if so, through which demographic mechanisms.

Because the studied red-backed shrike population is geographically open, we had to extend the integrated population model to include immigration (Abadi et al., 2010b). Therefore, we modified the state-space model (Eqs. (1)–(3)) as follows: the number of 1 year old individuals $N_{1,t+1}$ followed a Poisson process with

$$N_{1,t+1} \sim Po\left(N_t \left(\frac{f_t}{2}\right) \phi_{jv,t}\right) \tag{12}$$

The number of immigrants $N_{im,t+1}$ was modelled with a Poisson distribution as

$$N_{im,t+1} \sim Po(N_t \omega_t) \tag{13}$$

where the immigration rate ω_t is defined as the number of female immigrants of age 1 year or older in year $t+1$ per breeding females in the previous year N_t.

The number of at least 2 years old surviving individuals followed a binomial process with

$$N_{ad,t+1} \sim Bin(N_t, \phi_{ad,t}) \tag{14}$$

and the total number of individuals in year t is given by $N_t = N_{1,t} + N_{ad,t} + N_{im,t}$.

For the observation equation, we assumed a normal distribution, hence y_t, the annual number of counted breeding females in year t, distributed as a $N(N_t, \sigma_y^2)$.

To estimate the strength of density dependence on the demographic parameters as well as the population growth rate, we fitted the models specified in Eqs. (5)–(8). We also modelled immigration rate with a random year parameter, but did not impose density dependence on it for identifiability reasons. Further, the recapture probability ($\boldsymbol{p}$) was modelled time dependent where time was treated as random. A model without density dependence (i.e. $\beta_1 = \beta_3 = \beta_5 = 0$ in Eqs. (5)–(7)) was also fitted to get unconstrained annual estimates of the demographic parameters. To assess the identifiability of the density-dependence parameters we performed a prior sensitivity analysis.

2.4. Bayesian analysis of the model

All the models were fitted within the Bayesian framework, specifying non-informative priors for the parameters. Specifically, we assigned a Normal distribution truncated between −5 and 5 ($N(0,100)I(-5,5)$) for the regression coefficients (α and $\boldsymbol{\beta}$). A Normal distribution truncated to positive values ($N(30,100)I(0,)$) was assigned for age-specific initial population sizes, and a
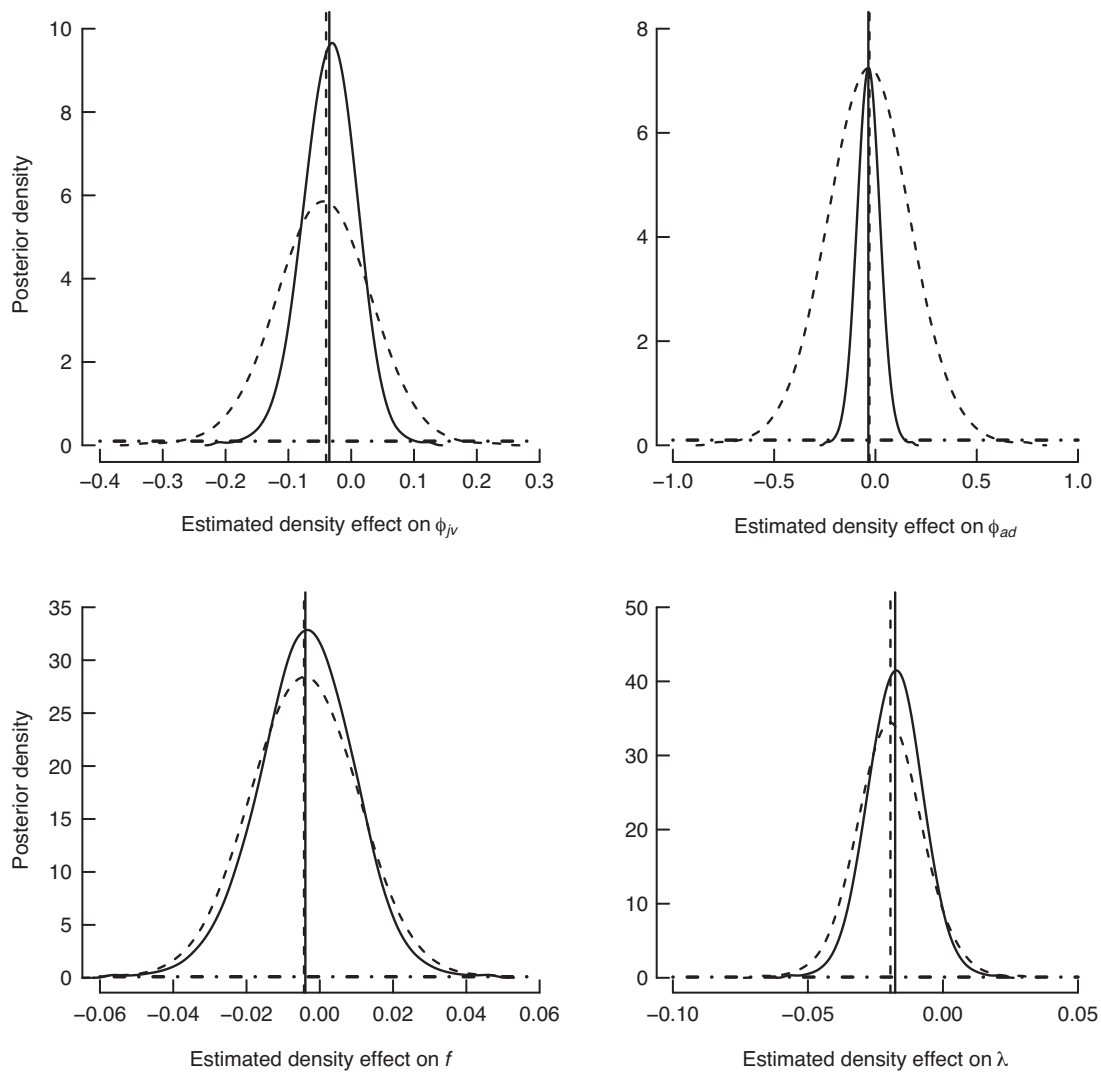
Fig. 2. Density plots of 500 estimated posterior means of strength of density dependence on juvenile survival (ϕ_{jv}, i.e. β_1), adult survival (ϕ_{ad}, i.e. β_3), fecundity (f, i.e. β_5) and population growth rate (λ, i.e. β_7) obtained from integrated population models (solid line), and from single data analysis ignoring observation error (dashed line) when the observation error for population count data was small (probability to detect female breeders = 0.90). Vertical lines are the means of the estimated posterior means of the strength of density-dependence over 500 simulations. Dotdash lines are prior densities of the $\boldsymbol{\beta}$.

uniform (U(0,10)) distribution for the temporal standard deviations of demographic parameters. To assess convergence for the simulated data sets, we randomly chose a single simulated data set and ran three chains, each with different initial values, of 20,000 iterations with a burn-in of 15,000 iterations. The $\hat{R}$ (Brooks and Gelman, 1998) values were less than 1.1 for all parameters, suggesting convergence. We then ran a single chain of 30,000 MCMC iterations with a burn-in of 20,000 thinning every 10th observation to compute the posterior summary statistics for all 500 simulations. For the case study, in addition to the non-informative priors for the density-dependence parameters defined above, we used three priors that are fairly informative (N(0,1), N(0.1,1), and N(−0.1,1)) to assess the sensitivity of the posterior estimates. Convergence was achieved after running three chains of 20,000 iterations with a burn-in of 10,000 (all the $\hat{R}$ values <1.02). We then ran a single chain of length 100,000, discarded the first 50,000 as burn-in and thinned every 10th observation. The MC errors for all parameters were less than 5% of the corresponding posterior standard deviations, indicating the accuracy of the posterior estimates for each parameter. We used the R software version 2.9.1 (R Development Core Team, 2008) to simulate the data and the analyses were done using the WinBUGS software calling it from R through the

package R2WinBUGS (Sturtz et al., 2005). The R and WinBUGS codes to analyze the red-backed shrike data are provided in the electronic supplement (Appendix B).

3. Results

3.1. Simulation study

Our simulation study clearly showed that the strength of density dependence in the demographic rates as well as in the population growth rate was identifiable with the integrated population model regardless of the magnitudes of observation error we considered, indicated by smooth posterior densities with a clear peak (Figs. 1 and 2). If the parameters were not identifiable, we would have expected a posterior density similar to the specified prior distribution (Gimenez et al., 2009). The widths of the posterior densities resulting from the integrated population model were narrower when the observation error was small compared to when it was large. This indicates that the precision of the density-dependence estimator declined with increasing observation error of the population counts. In general, the strength of density dependence was estimated with more precision at the population level
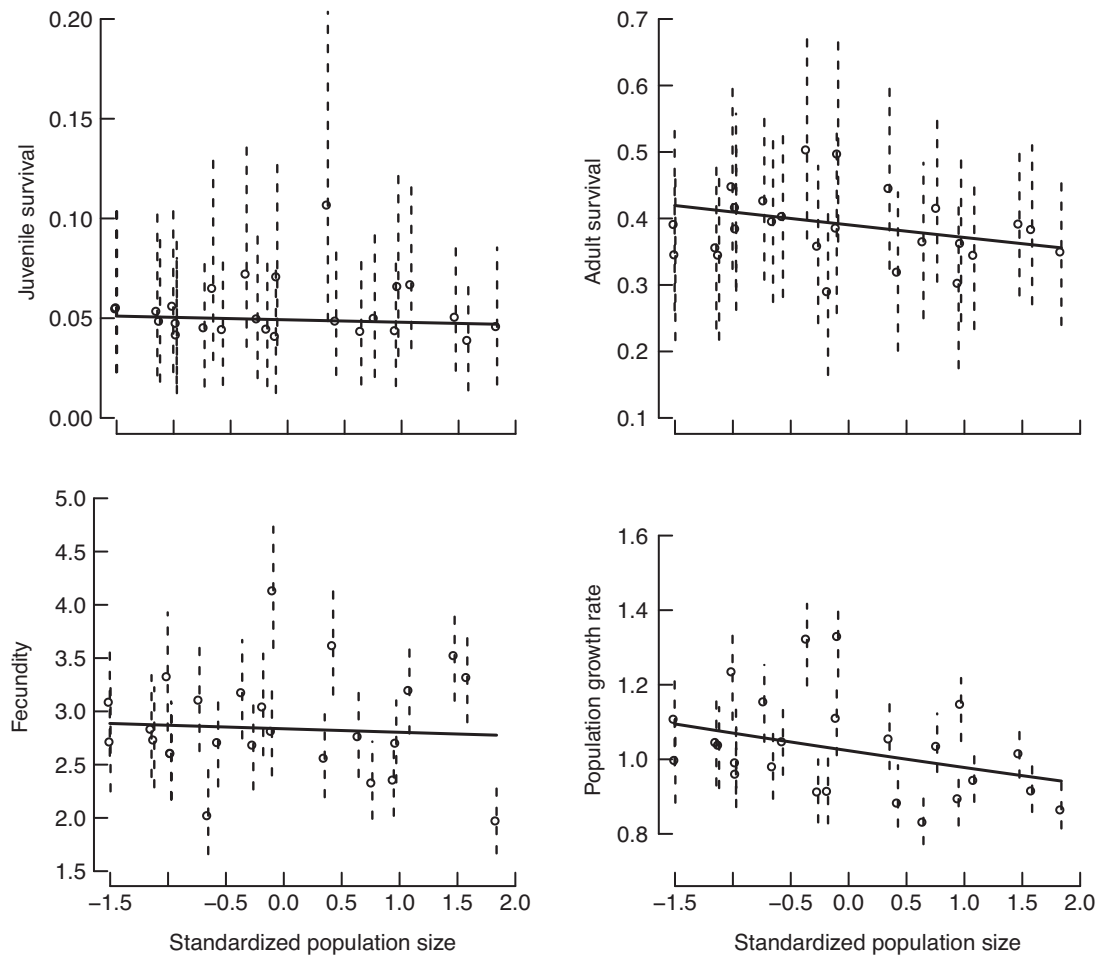
Fig. 3. Annual variation in demographic rates and population growth rate against standardized population size in the studied red-backed shrike population. Posterior means (open circles) with 95% credible intervals (vertical dashed line) obtained from an integrated population model without density dependence, along with the estimated linear relationship between demographic parameters as well as population growth rate and standardized population size obtained from an integrated population model with density dependence (solid line).

than at the demographic level, indicated by a narrow width of the posterior densities (Figs. 1 and 2).

Estimates of the strength of density dependence obtained from the integrated population model were generally more precise compared to that of the regression analysis. This was particularly evident for adult survival (Figs. 1 and 2). As expected, the estimates of strength of density dependence in the demographic parameters were slightly shifted towards zero when the observation error was large and not accounted for. However, this effect was not very strong. The model ignoring the observation error yielded stronger and slightly less precise estimates of density dependence at the population level in comparison to the integrated population model (Figs. 1 and 2). Our simulation results also showed both the integrated population and conventional models yielded only a small bias of the estimated strength of density dependence within the range between −0.038 and 0.015.

3.2. Case study

Since there is no established goodness-of-fit test of the integrated population model available, we tested the goodness-of-fit just for the capture–recapture model using contingency tables (Pradel et al., 2005) via program U-CARE (Choquet et al., 2009): there was no sign of lack of fit ($\chi^2_{59} = 42.75$, $P = 0.94$). Based on the integrated population model without imposing density dependence, the annual estimates of age-specific survival, fecundity

and population growth rate tended to decline with increasing population size in red-backed shrikes (Fig. 3), suggesting density dependence in these demographic parameters and at the population level. We then explicitly estimated the strength of density dependence in the demographic parameters and in the population growth rate using the integrated population model. The estimated linear relationships between demographic rates as well as population growth rate (on the transformed scale) and population size are shown in Fig. 3. Our analyses revealed that the mean annual juvenile and adult survival probabilities of red-backed shrikes females were 0.05 (sd = 0.01) and 0.39 (sd = 0.02), respectively. Mean fecundity was 2.84 (sd = 0.13) and the mean immigration rate was estimated to be 0.55 (sd = 0.04). The posterior distributions of the strength of density dependence were wide for juvenile and adult survival, and more peaked for fecundity and population growth. As expected, the posterior means of the strengths of density dependence were negative in all parameters (Fig. 4). The posterior probability that the estimated effect of density were negative was high for population growth (0.96), followed by adult survival (0.79), fecundity (0.60), and juvenile survival (0.56). Thus, there was clear evidence of a density-dependent population regulation at the level of the population that was more likely due to adult survival, than due to juvenile survival or fecundity. The prior sensitivity analysis showed that the posteriors of the density-dependence parameters were nearly identical under different priors (non-informative and informative, Fig. A.1, Appendix A). Hence, posterior estimates
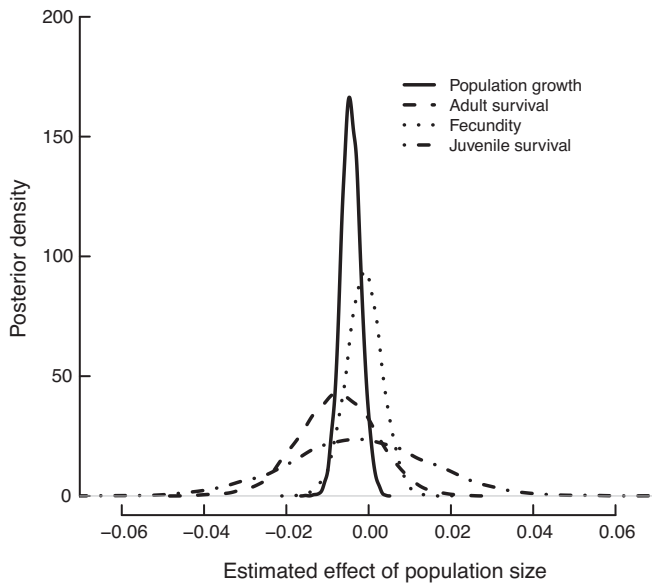
Fig. 4. Posterior distributions of the estimated strength of density dependence on female juvenile survival (dotdash line), female adult survival (dashed line), fecundity (dotted line) and population growth rate (solid line) in studied red-backed shrike population. Non-informative priors (N(0,100)I(−5,5)) were used for the density (population size) effect parameters.

were little sensitive to the choice of priors and dominated by the data.

4. Discussion

Density dependence is an important ecological concept and understanding how it operates is crucial in conservation, harvesting and for accurate demographic projections (Sinclair and Pech, 1996; Lande et al., 2003). In this paper we provide a framework for studying density dependence using a Bayesian integrated population model. A key advantage of this unifying framework is that it allows estimating the strength of density dependence both at the demographic and population level while accounting for observation error and, consequently, the demographic mechanism causing density-dependent population regulation can be identified. In contrast, most existing techniques for testing density dependence rely on time series data and do not account for observation error, or focus either on the effect of density on population growth rate or on a single demographic parameter only.

Using simulations, we showed that integrated population models provide estimates of the effect of population size on demographic parameters as well as on population growth rate with good precision. The parameters estimating the strength of density dependence were identifiable with our model regardless of the magnitudes of observation error we considered. As expected, the estimates were slightly more precise when the observation error was small than large. Our simulation study also highlight that ignoring observation error had differential impact on the estimators of the strength of density dependence at the population than at the demographic level. The conventional regression model tended to estimate stronger density dependence at the population than at the demographic level. These results are in agreement with previous findings (e.g. Shenk et al., 1998; Freckleton et al., 2006; Lebreton, 2009). Interestingly, our simulation study showed that the conventional regression model provided nearly the same point estimates of the strength of density dependence at the demographic level as the integrated population model regardless of the magnitude of the observation error. Both models estimated the strength of density

dependence with small bias only. This suggested that the conventional regression model to estimate density dependence was robust, and the main advantage of the integrated population model was increased power to detect effects.

We also illustrated the application of the method using demographic data from a geographically open red-backed shrike population. We found strong support of density dependence for the population growth rate. Of the considered demographic parameters, only adult survival was likely to be regulated by density dependence, while juvenile survival and fecundity were hardly impacted by breeding density. Our prior sensitivity analysis showed the posterior distributions of the strength of density dependence were highly dominated by the data and little sensitive to the choice of the priors. This was a further indication that the strength of density dependence was an identifiable parameter in the integrated population model. Using the same data analyzed with regression analyses with population counts uncorrected for observation error, Schaub et al. (2011) did not find support of density dependence for survival and fecundity. With the application of the integrated population model the power to detect density dependence increases (see simulations), which is the reason why we now found support of density dependence operating on adult survival. One may wonder how there can be strong density dependence for population growth and only relatively weak density dependence for the demographic rates. First, even if density dependence for the demographic rates is weak, all demographic rates work jointly, and thus the effect at the population level magnifies. Second, the red-backed shrike population is geographically open, and immigration is substantial (mean (sd): 0.55 (0.04)). It is well possible that immigration is regulated by density, i.e., few individuals immigrate in years where the number of survivors and local recruits is high, and vice versa. Yet, immigration is a parameter in our integrated population model that is estimated without having observed data (Abadi et al., 2010b) and a simulation study needs to be done to assess whether the strength of density dependence for parameter for which no explicit data are available, can be estimated. To evaluate for which demographic parameter density dependence is important, we computed the probability that the strength of density dependence is negative and use this as a testing criterion. Alternatively, one could also apply model selection for the same purpose. The set of models could then include models that impose density dependence in some demographic parameters only. Yet, model selection in Bayesian hierarchical models is not an easy task (Link and Barker, 2004; Millar, 2009).

In our simulation as well as in the case study we expressed density in terms of population size. Since the study area associated with the red-backed shrike population remained the same over time, the use of population size as a measure of density was justified. However, it is important to note that the influence of density on biological processes can be overlooked due to an inappropriate measure of density (Barker et al., 2002; Williams et al., 2002). Moreover, the main driving force for density dependence is often competition for resources and not space. Ideally, one would therefore model the strength of density dependence not with population size, but with the available resources per individual. Our model could be extended in this way if an estimate of resource availability could be obtained.

The goals of our simulation were mainly on the assessment of the identifiability of the estimates of strength of density dependence and on the evaluation of the effect of observation error. We specified a short study period (i.e., 10 years), thus conditions where the estimation of density dependence were difficult. Yet, the model was able to estimate density dependence with good precision in this set up. We could further examine the performance of the model in different directions. For instance, we could set up a simulation varying the strength of density dependence and also the length of

the study period. The ability to detect density dependence usually increases with long time series data (Brook and Bradshaw, 2006) and a large change in density. In our simulation study, we focused on the common kind of observation error (i.e. non-detection or false-negative error). One might further evaluate the performance of the model considering other kinds of observation error such as false-positive errors occur.

The integrated population model is very flexible to include different shapes of density-dependence. Here we used the density-dependence model of the Ricker type for population growth rate (Dennis and Taper, 1994), but specifying other density-dependence models which are discussed in the literature (Dennis and Taper, 1994; Jamieson and Brooks, 2004) is straightforward. Moreover, some studies have shown that the effect can be non-linear in the parameters (Paradis et al., 1998; Sæther and Engen, 2002; Tavecchia et al., 2007). The integrated population model could also be extended to assess non-linear density dependence, for instance by using penalized splines (Gimenez et al., 2006) or thresholds (Besbeas and Morgan, 2011). In the present study, we looked at the direct effect of density but it is possible that density dependence can affect demographic parameters and population growth rate with time lag (Paradis et al., 2002). Our model can easily be extended to study delayed density dependence.

Overall, our model provides an improved statistical tool over current methods for estimating density dependence. We believe it has great potential in conservation, management and ecology.
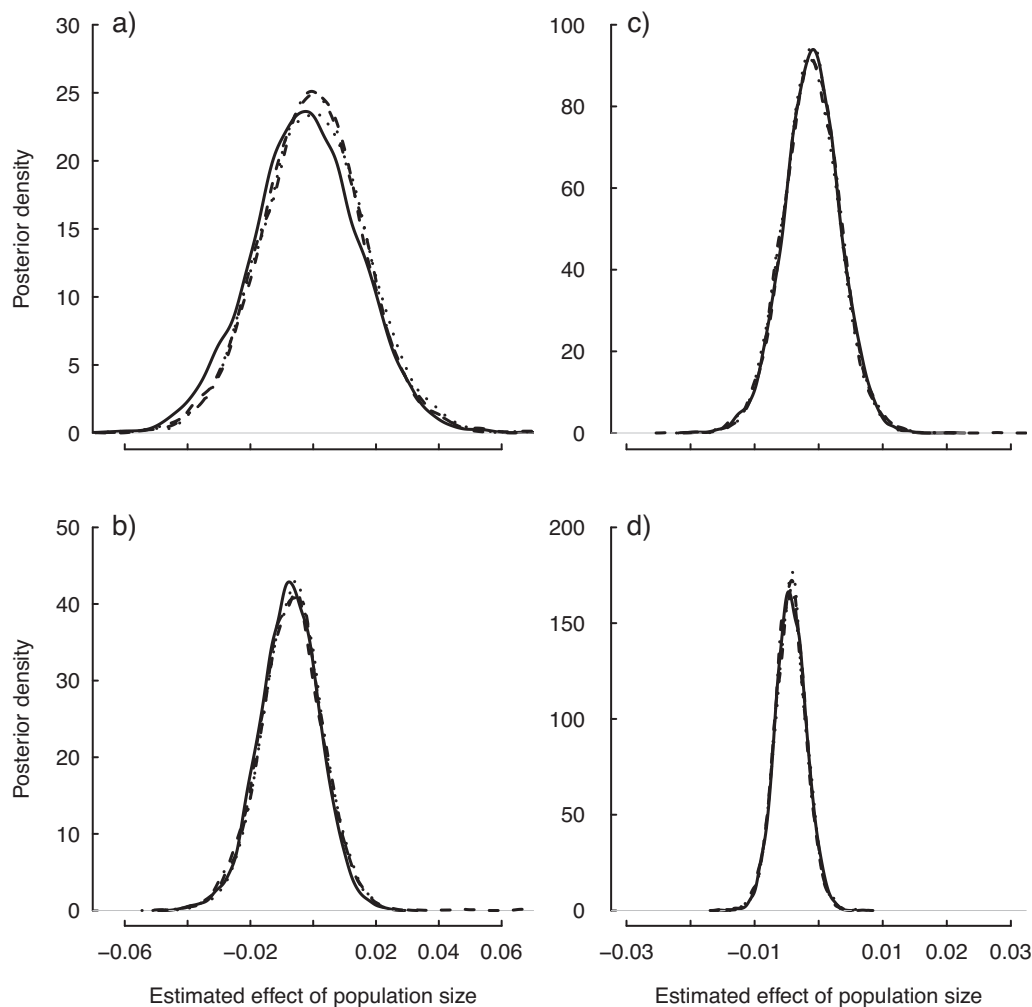
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Appendix A. Prior sensitivity analysis

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at http://dx.doi.org/10.1016/j.ecolmodel.2012.05.007.

Fig. A.1. Posterior distributions of the estimated strength of density dependence on female juvenile survival (panel a), female adult survival (panel b), fecundity (panel c), and population growth rate (panel d) in studied red-backed shrike population under different priors: A $N(0,100)I(-5,5)$ (solid line), a $N(0,1)$ (dotted line), a $N(0.1,1)$ (dashed line) and a $N(-0.1,1)$ (dotdash line) priors were used for the density effect parameters. Note that the overlap of posterior densities suggested the posterior estimates were little sensitive to the choice of priors.

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