

Bayesian meta-analysis of demographic parameters in three small, temperate passerines

Jarle Tufto, Bernt-Erik Sæther, Steinar Engen, Peter Arcese, Kurt Jerstad, Ole Wiggo Røstad and James N. M. Smith

Tufto, J., Sæther, B.-E., Engen, S., Arcese, P., Jerstad, K., Røstad, O. W. and Smith, J. N. M. 2000. Bayesian meta-analysis of demographic parameters in three small, temperate passerines. – *Oikos* 88: 273–281.

Accurate estimates of population parameters are vital for estimating extinction risk. Such parameters, however, are typically not available for threatened populations. We used a recently developed software tool based on Markov Chain Monte Carlo methods for carrying out Bayesian inference (the BUGS package) to estimate four demographic parameters; the intrinsic growth rate, the strength of density dependence, and the demographic and environmental variance, in three species of small temperate passerines from two sets of time series data taken from a dipper and a song sparrow population, and from previously obtained frequentist estimates of the same parameters in the great tit. By simultaneously modeling variation in these demographic parameters across species and using the resulting distributions as priors in the estimation for individual species, we improve the estimates for each individual species. This framework also allows us to make probabilistic statements about plausible parameter values for small passerines temperate birds in general which is often critically needed in management of species for which little or no data are available. We also discuss how our work relates to recently developed theory on dynamic stochastic population models, and finally note some important differences between frequentist and Bayesian methods.

J. Tufto and S. Engen, Dept of Mathematical Sciences, Lade Section, Norwegian Univ. of Science and Technology, N-7491 Trondheim, Norway (present address of JT: Inst. of Cell, Animal & Population Biology, Univ. of Edinburgh, Kings' Buildings, West Mains Road, Edinburgh, Scotland EH9 3JT [jarle.tufto@ed.ac.uk]). – B.-E. Sæther, Dept of Zoology, Norwegian Univ. of Science and Technology, N-7491 Trondheim, Norway. – P. Arcese, Dept of Wildlife Ecology, Univ. of Wisconsin, Madison, WI 53706, USA. – K. Jerstad, Aurebekk, N-4500 Mandal, Norway. – O. W. Røstad, Dept of Biology and Nature Management, Agricultural Univ. of Norway, P.O. Box 5014, N-1432 Ås, Norway. – J. N. M. Smith, Dept of Zoology, Centre for Biodiversity Research, Univ. of British Columbia, Vancouver, BC, Canada V6T 1Z4.

Stochastic population dynamic models have recently received increased attention among ecologists since the pioneering work of May (1973, 1974). One reason for this popularity is the need for quantitative assessment of risks in several areas of applied ecology. Both demographic and environmental stochasticity (see Engen et al. 1998) are likely to influence estimates of minimum size of viable populations of threatened or endangered species (Goodman 1987, Dennis et al. 1991, Lande

1993, Lande et al. 1998) and the population dynamical consequences of habitat fragmentation (Lande et al. 1998). Furthermore, consideration of stochastic fluctuations in the environment should strongly influence the choice of strategies for a sustainable harvest (Lande et al. 1997).

In order to apply stochastic models in decision-making, knowledge about plausible parameter values must be inferred from data using statistical methods. The

Accepted 7 May 1999

Copyright © OIKOS 2000

ISSN 0030-1299

Printed in Ireland – all rights reserved

classical frequentist school of statistics is based on the premise that probability only can be defined as the long run frequency of an outcome in repeated realizations of a 'random experiment'. According to the frequentist point of view, one is not allowed to make statements about the probability of different alternative hypotheses, because different hypotheses are not the outcomes of a random experiment. For a given model specifying the probability distribution of the data X , $P(X|\theta)$, a frequentist estimates the parameters of the model by constructing an estimator $\hat{\theta}$, being some function $\hat{\theta}=f(X)$ of the data. The relative performances of different estimators are then judged by their sampling distributions. No general principle, however, for constructing a 'best' estimator exists. Instead, one has to choose between a number of different criteria based on minimizing the bias or variance of the estimator, or one relies on asymptotic theory to justify the use of maximum-likelihood estimators.

Within the Bayesian school of thought, probability is defined very differently as a quantitative representation of the observer's degree of belief in different hypotheses (say, different parameter values) (see e.g. Jeffreys 1961), given the observer's present state of knowledge. Upon observing new data, these probabilities are updated according to the laws of probability, via Bayes theorem

$$P(\theta|X) \propto P(X|\theta)P(\theta), \quad (1)$$

resulting in a posterior probability distribution $P(\theta|X)$ for the parameter vector θ , given the observed data. This probability distribution is, in contrast to the frequentist sampling distribution of an estimator, straightforward to incorporate in decision analysis (see e.g. Berger 1985, Ellison 1996, Ludwig 1996, Taylor et al. 1996, Hilborn and Mangel 1997); once a utility function is chosen to represent one's preferences (or society's preferences), choosing the optimal action is a simple matter of determining which action has the highest expected utility. Carrying out Bayesian inference for complex realistic models of ecological processes is now also becoming feasible in practice (Best et al. 1996, Gilks et al. 1996a). A key advance is that numerical Markov Chain Monte Carlo simulations can be used to compute the posterior distribution. Modern statistical software such as the BUGS package makes this task relatively simple.

In this paper, we use these new tools to estimate several demographic parameters; the growth rate, the strength of density dependence, and the demographic and environmental variance, in three passerine species. As noted by Sæther et al. (1998), even when relatively long time series are available, the uncertainty of estimates of especially the environmental variance can still become quite large. Here we intro-

duce a Bayesian framework that allows prior knowledge that may be available to be incorporated in the analysis which improves the precision of the estimates. Such an approach may be particularly useful in the management of threatened or endangered species, where good long-term data are rarely available. The approach we use is to create a hierarchical model in which we model variation in the demographic parameters on the level of general small temperate passerines. We then let the resulting distribution simultaneously serve as the prior in the estimation of the demographic parameters on the level of individual species.

We use time series data from two species of birds; the dipper (*Cinclus cinclus*) and the song sparrow (*Melospiza melodia*), and in addition previous estimates (Sæther et al. 1998) of demographic parameters taken from a third passerine; the great tit (*Pares major*).

Study populations

The dipper is a 60-g temperate passerine living in close connection to running water. We studied the species in Lygnavassdraget in southern Norway (58°15'N 7°15'E) during a period of 20 yr (1978–1997). Each year the population was thoroughly censused and a large proportion of the breeding adults and their offspring were ringed. The conspicuous behaviour of the adults in the breeding season, especially in the mornings, and the relative restricted availability of suitable breeding sites suggest that the accuracy in the population estimates for this population is high. The population size fluctuated from a minimum of 54 pairs in 1982 to a maximum of 234 pairs in 1993, due to a combined effect of density dependence and stochastic variation in winter climate (Sæther et al. unpubl.).

The song sparrow was studied on Mandarte Island, British Columbia during the period 1975 to 1997. Mandarte island is a small (approximately 600 × 100 m) island situated in the Haro Strait, approximately 25 km from Victoria, British Columbia, Canada. All individuals on the island are individually recognized by a combination of a metal ring and 1–3 plastic colour rings. For further details, see Arcese et al. (1992). The time series of the dipper and song sparrow population sizes are shown in Fig. 1.

We also include results from an analysis of the fluctuations of the great tit population in Wytham Wood during a 31-yr-long period 1960–1990 (Sæther et al. 1998). A large proportion of the great tits in Wytham Wood breed in nest boxes and many individual birds are colour-ringed. For further description, see Sæther et al. (1998) and references therein.

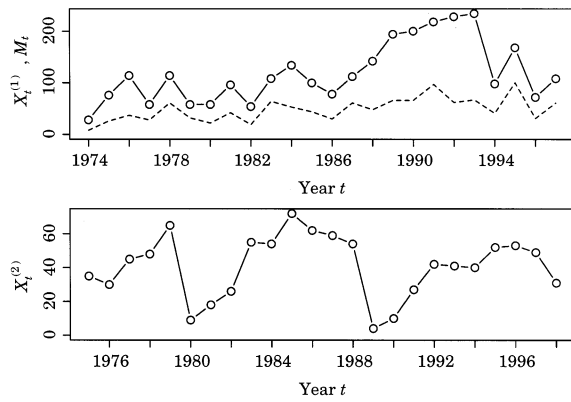


Fig. 1. Population sizes for the dipper and song sparrow populations, $X_t^{(1)}$ and $X_t^{(2)}$. The number of immigrants entering the dipper population is represented by the dotted line.

Directed acyclic graphs

Before describing the details of our model, we first introduce the concept of directed acyclic graphs (DAGs) (Spiegelhalter et al. 1996), which provide a convenient way of representing the qualitative relationship between the different quantities in a model (Fig. 2). Each of these quantities, whether it is a data observation, an unknown parameter, or a missing observation, is represented by a node in the DAG, and these nodes may be connected by directed links (arrows). Any node with an arrow emanating from it pointing to some particular node v is referred to as 'parent' of v , and 'descendants' of v are defined as those nodes on the

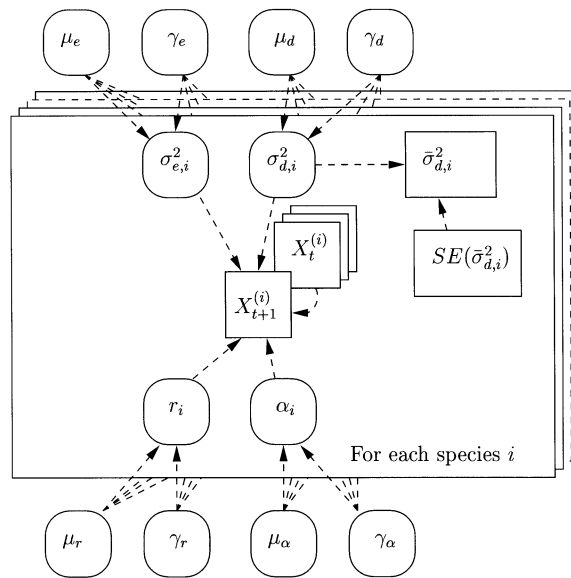


Fig. 2. Directed acyclic graph for the model. The arrows represent prior conditional dependence between nodes. Observed nodes are represented by square boxes and unknown quantities by rounded boxes.

directed path starting from v . The assumptions of the model are then specified by assigning conditional probability distributions, given parental nodes, to each node v . Prior probability distributions representing prior knowledge that may be available are assigned to those nodes in the graph without any parents. This defines the full joint probability distribution of all observed and unobserved quantities.

From this it follows that the distribution of all unknown quantities conditioned on the observed data can then be derived using Bayes theorem (1) (Spiegelhalter et al. 1996). This distribution, the posterior, can usually not be obtained analytically but can be computed using Markov Chain Monte Carlo methods, for instance, Gibbs sampling. This algorithm (which is the method used internally by the BUGS package) proceeds by repeatedly simulating new values from the distribution of each unobserved node in the graph (represented by round boxes), conditioned on the current state of neighbouring nodes. Data nodes (represented by square boxes in the graph) are held constant throughout the entire simulation. The resulting multivariate Markov Chain can be shown to have the desired posterior distribution as its stationary distribution (for further details, see e.g. Gilks et al. 1996b). Thus, by running this algorithm for a sufficient number of iterations, the posterior distribution of any quantity in the model can be computed with the desired accuracy.

The model

Population dynamic models for dippers and song sparrows

The DAG for the whole model is given in Fig. 2. First we consider the submodel defining the population dynamics of the dipper and song sparrow population for which complete census data are available. These data (for species $i = 1$ and $i = 2$) consist of counts of the number of individuals $X_t^{(i)}$ over periods of 20 and 24 yr (see Fig. 1), respectively. In addition, counts of the number of immigrants M_t that are new in the population in year t are available for the dipper population.

The assumption we make, for the dipper population $i = 1$, is that the change in the log of the population size $X_t^{(1)}$, excluding new immigrants, conditional on the state of the population at time t , is distributed as

$$\log\left(\frac{X_{t+1}^{(1)} - M_{t+1}}{X_t^{(1)}}\right) \sim N\left(r_1 - \alpha_1 X_t^{(1)}, \sigma_{e,1}^2 + \frac{1}{X_t^{(1)}} \sigma_{d,1}^2\right), \quad (2)$$

and similarly, for the song sparrow population,

$$\log\left(\frac{X_{t+1}^{(2)}}{X_t^{(2)}}\right) \sim N\left(r_2 - \alpha_2 X_t^{(2)}, \sigma_{e,2}^2 + \frac{1}{X_t^{(2)}} \sigma_{d,2}^2\right). \quad (3)$$

This corresponds to the assumption often made in the literature (e.g. Lande 1993) that the total variance of the change in population size is equal to $\sigma_{e,i}^2 X_t^{(i)2} + \sigma_{d,i}^2 X_t^{(i)}$. This will generally be true if the demographic and environmental variances are density independent, and if there is no demographic covariance, as defined by Engen et al. (1998).

Model assumptions (2) and (3) are represented by a directed link from $X_t^{(i)}$ to $X_{t+1}^{(i)}$ in Fig. 2 and directed links, to each node $X_t^{(i)}$ from the nodes $\sigma_{e,i}^2$, $\sigma_{d,i}^2$, r_i , and α_i representing the environmental and demographic variance, the growth rate, and the strength of density dependence in species i .

In addition, data on the reproductive success of subsets of individual females in the populations each year t are available. As noted by Sæther et al. (1998), this allows much more precise estimation of the demographic variance, defined by Engen et al. (1998) as the variance in reproductive contribution $R_{t,j}$ to the next generation among individuals $j = 1, 2, \dots, X_t$. For simplicity, in order to avoid complicated parametric modeling of under-dispersed data, we will not carry out a fully Bayesian analysis of the individually based data here, but only incorporate the information in these data provided by a frequentist estimate of $\sigma_{d,i}^2$. Following Sæther et al. (1998), we use the mean $\bar{\sigma}_{d,i}^2$ of sample variances of $R_{t,j}$ within each year and compute the standard error $SE(\bar{\sigma}_{d,i}^2)$ of this estimator from the variance between years. To incorporate this information in the overall inference we assume that the log of the estimate, given the true unknown demographic variance, follows a normal distribution

$$\log \bar{\sigma}_{d,i}^2 \sim N(\log \sigma_{d,i}^2, \text{Var}(\log \bar{\sigma}_{d,i}^2)). \quad (4)$$

In fact, the distribution of the estimator given the true parameter value is, apart from the exact distributional form of the estimator, exactly what we know from the frequentist analysis. Because it is the estimate $\bar{\sigma}_{d,i}^2$ and its standard error which is known, assumption (4) is represented by two additionally observed, hence rectangular nodes in Fig. 2.

The entire structure defined by eqs (2) to (4) is repeated for species $i = 1$ and $i = 2$, and this is indicated by the repeated large rectangles in the DAG (Fig. 2).

Submodel for variation between species

Having defined the distribution of the observed time series data and incorporated estimates of the demographic variances, conditional on the unknown demographic parameters characterizing each species, we next turn to defining the submodel specifying how these parameters vary between species. The approach we take is to create a hierarchical model involving additional unknown parameters to be inferred from the data

(Berger 1985: 107). These additional parameters are often referred to as hyper-parameters as they only determine the distribution of the other basic parameters in the model and not the distribution of the data directly.

We first need to keep in mind that the demographic and environmental variances only can take positive values, whereas there are no constraints on the growth rate and the strength of density dependence. This suggests that it is reasonable to work with the log of the demographic and environmental variances and let, for each species $i = 1, 2, \dots, 4$,

$$\log(\sigma_{d,i}^2) \sim N(\mu_d, \gamma_d^2), \quad (5)$$

and

$$\log(\sigma_{e,i}^2) \sim N(\mu_e, \gamma_e^2). \quad (6)$$

The submodels for species $i = 3$ and $i = 4$ follows in the next subsections. Here μ_d and μ_e are unknown hyper-parameters being the mean of the log of the demographic and environmental variances, respectively, within the passerine order, and γ_d^2 and γ_e^2 are the variances (on the log scale) of the demographic and environmental variance among species.

In addition we assume that the growth rates r_i and the coefficients α_i , the strength of density dependence, are distributed as

$$r_i \sim N(\mu_r, \gamma_r^2), \quad (7)$$

and

$$\alpha_i \sim N(\mu_\alpha, \gamma_\alpha^2). \quad (8)$$

Assumptions (5) to (8) are represented by additional parental nodes in the DAG for the model (Fig. 2).

Priors for the hyper-parameters

To fully specify our model we need to choose priors for the remaining nodes in the graph. These hyper-parameters, the μ 's and γ 's, are location and scale parameters (see e.g. Berger 1985: 83–85), respectively, in the submodels for log of the environmental and demographic variances, and in the submodel for r_i and α_i characterizing each individual species. One non-informative choice of prior for each μ is to assign a uniform density to μ on the whole real line, and density proportional to $1/\gamma$ for $\gamma > 0$ (Berger 1985: 83–85). Such priors are improper, that is, the total probability is infinite. For technical reasons, the BUGS package only allows the use of proper prior distributions. However, because very wide-tailed diffuse priors can be used, the distribution will essentially be approximately non-informative

over the parameter range permitted by the data as long as the data are not too sparse. Care is needed, however, in cases where little data are available and the posterior would be improper had an improper non-informative prior been used. This, however, appeared not to be the case in the present study.

The priors we use in the analysis are as follows

$$\mu_d \sim N(0, 100^2) \quad 1/\gamma_d^2 \sim \Gamma(0.00001, 0.00001), \quad (9)$$

$$\mu_e \sim N(0, 100^2) \quad 1/\gamma_e^2 \sim \Gamma(0.00001, 0.00001), \quad (10)$$

$$\mu_r \sim N(0, 100^2) \quad 1/\gamma_r^2 \sim \Gamma(0.00001, 0.00001), \quad (11)$$

$$\mu_\alpha \sim N(0, 100^2) \quad 1/\gamma_\alpha^2 \sim \Gamma(0.00001, 0.00001). \quad (12)$$

It can be noted that, for example, assumption (12) states that our degree of belief, a priori, in the hypotheses of negative and positive density dependence is equal.

Incorporation of great tit estimates

The third population we incorporate in the analysis is the great tit population in Wytham Wood, UK, for which a time series similar in form is available. Sæther et al. (1998) obtained frequentist estimates (with the uncertainty estimated by bootstrapping) of the environmental variance, $\hat{\sigma}_e^2 = 0.063 \pm 0.018$, of the growth rate, $\hat{r} = 4.4 \pm 1.0$, and of the strength of density dependence $\hat{\alpha} = \hat{r}/\hat{K} = 0.023 \pm 0.005$. To also incorporate the dependences in these estimates (which can be estimated from the bootstrap replicates), we assume that estimate of the growth rate, the strength of density dependence, and the environmental variance, follow (a priori) a multivariate normal distribution

$$\begin{bmatrix} \hat{r} \\ \hat{\alpha} \\ \log \sigma_e^2 \end{bmatrix} \sim MVN \left(\begin{bmatrix} r_3 \\ \alpha_3 \\ \log \sigma_{e,3}^2 \end{bmatrix}, \mathbf{C} \right), \quad (13)$$

where \mathbf{C} is the covariance matrix of the estimates, estimated from the bootstrap replicates. In addition we assume that Sæther et al.'s (1998) estimate of the demographic variance, $\hat{\sigma}_d^2 = 0.56 \pm 0.042$, based on another set of (individually based) data, is (independently) distributed as

$$\log \hat{\sigma}_d^2 \sim N(\log \sigma_{d,3}^2, \text{Var}(\log \hat{\sigma}_d^2)). \quad (14)$$

Incorporating the above estimates in this way, not only gives us new, improved Bayesian estimates of the great tit parameters (represented by the posterior for those quantities), with prior information coming from the other species taken into account, but also improves the

estimates of the hyperparameters, thereby indirectly improving the estimates of the demographic parameters for the dipper and song sparrow populations. (The nodes corresponding to eqs (13) to (14) are not shown in Fig. 2.)

Predictions for an unspecified passerine

In the Gibbs sampling algorithm, unobserved data nodes and parameter nodes for which we have no data (that is, nodes with no descendants) need no special treatment; the only difference is that the conditional distribution used when updating these nodes depends on their parents only.

We have already introduced one set of such nodes, through eqs (5) to (8) in the overall model, corresponding to the demographic and environmental variance, the growth rate and strength of density dependence for a fourth species $i = 4$. The posterior for these quantities will represent our state of knowledge (the predictive density) for passerine species (similar to the ones included in the analysis) for which no data are available. The resulting structure is not shown in Fig. 2 but only indicated by the fourth layer in the DAG.

Eqs (2) to (14) fully specify our model. The corresponding implementation in the BUGS language (using a slightly different parameterization) is available at <http://www.math.ntnu.no/~jarlet/meta.bug>

Results

We ran 100000 iterations of the above model in BUGS, after a 'burn-in' of 10000 iterations, and used every 10th sample giving us 10000 (dependent) realizations from the posterior. Smoothed posterior marginal distributions for the demographic parameter for species $i = 1, 2, \dots, 4$ are shown in Fig. 3 and summarized in Table 1.

Several points can be noticed. In general, there is large variation in the estimates between species. Consequently, and because we only have three different species, there is a large amount of uncertainty in the hyper-parameters. The predictive densities (the posteriors) for the demographic parameters of species $i = 4$, are essentially mixtures of normal distributions, and therefore become very wide-tailed and leptokurtic. The 95% credible set (analogous to standard frequentist confidence interval) for e.g. $\sigma_{e,4}^2$ ranges from 0.0014 to 22.3 (Table 1). This interval includes unbelievably large environmental variances, but this is not that surprising given our non-informative choice of priors for μ_e and γ_e . Similarly, as a result of the extreme skew in the predictive density for species $i = 4$, the posterior means become very implausible. The posterior medians, however, for $\sigma_{e,4}^2$ and $\sigma_{d,4}^2$ are more reasonable and equal to 0.18 and 0.77, respectively.

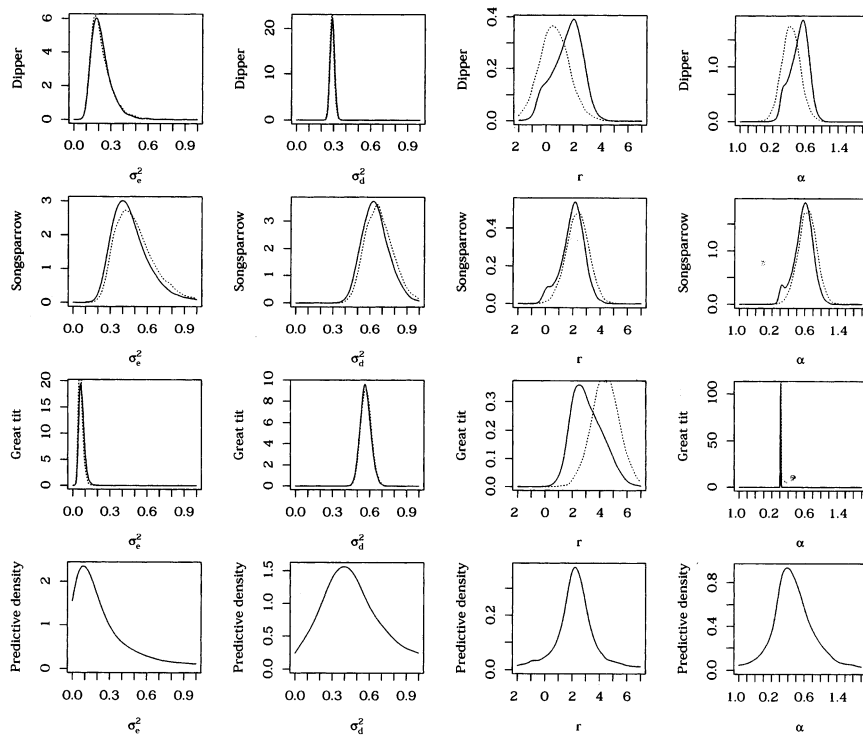


Fig. 3. Posterior marginal distributions for the demographic parameter of each species in the model smoothed with kernel density estimates (solid lines). Posterior distributions in the alternative model with non-informative priors on the demographic parameters of each individual species are indicated by dotted lines.

Nevertheless, the distributions for the demographic parameters of species $i=4$ are far from being flat. Thus, modeling variation in the parameters between species does bring prior information into the estimation of the demographic parameters of each of the individual species $i=1$ to $i=3$. To illustrate this better, we changed the model and used approximately non-informative (very wide-tailed) priors directly on the demographic parameters instead of eqs (5) to (8). The posterior distributions obtained using this alternative non-hierarchical model are indicated by the dotted lines in Fig. 3. As indicated by the difference between the solid and dotted lines, the effect of modeling variation between species is in general that the posterior estimates are improved and slightly shifted towards the mean among species. As expected, this effect is especially pronounced for those parameters for which the data provide little information, e.g., for the estimate of the growth rate of the dipper and great tit populations, r_1 and r_3 .

In Bayesian statistics, testing some hypothesis H_0 against some alternative H_1 , say $\mu \leq 0$ against $\mu > 0$, is a simple matter of computing the posterior probabilities of H_0 and H_1 , that is $P(\mu \leq 0 | X_1, \dots, X_n)$ and $P(\mu > 0 | X_1, \dots, X_n)$, for the given choice of prior, which in practice, having simulated 10000 realizations from the posterior distributions, can be estimated from the number of positive μ 's in the Markov Chain out of the total number of sampled values.

Some special hypotheses of this form are of interest. We have, for example, assumed that the prior probabilities of positive and negative intrinsic growth rates both equal $1/2$, and similarly, that the prior probabilities of negative and positive density dependence are equal. The corresponding posterior probabilities of these hypotheses are shown in Table 2.

Discussion

Using an approach based on Markov Chain Monte Carlo simulation we have shown how to carry out Bayesian inference for a model involving simultaneous analysis of populations time series, taken from several species, and variation between these species in the demographic parameters characterizing the dynamics of each individual population. Because the overall approach should be conceptually easy to understand, and because implementation in the BUGS language (consisting of only about 50 lines of code) also is reasonably straightforward, we believe that this type of approach, as the necessary software tools are further developed, should be taken up widely by ecologists.

As already noted, the result of a Bayesian analysis consists of a probability distribution specifying the joint distribution of the various unknown parameters in the model, missing data, and predictions for future unknown quantities. It must be remembered that these quantities (the different nodes in the DAG) are random

Table 1. Posterior means and 95% credible sets (in parentheses) for the demographic parameters characterizing individual species.

<i>i</i>	Species	r_i	α_i	$\sigma_{e,i}^2$	$\sigma_{d,i}^2$
1	Dipper	1.55 (-0.56, 3.36)	0.44 (0.01, 0.82)	0.24 (0.11, 0.43)	0.29 (0.26, 0.33)
2	Song sparrow	2.00 (0.11, 3.48)	0.56 (0.03, 0.97)	0.47 (0.25, 0.87)	0.65 (0.46, 0.88)
3	Great tit	3.12 (1.32, 5.50)	0.016 (0.006, 0.028)	0.07 (0.04, 0.13)	0.57 (0.49, 0.66)
4	'General passerine'	2.20 (-3.59, 8.36)	0.35 (-1.04, 2.01)	2.8×10^{27} (0.001, 22.3)	1.8×10^8 (0.06, 4.25)

variables, not in the classical objective sense (which views randomness as an intrinsic property of the process under study); these quantities are only random (or uncertain) to us as the observer, given our present state of knowledge.

One obvious advantage of the Bayesian approach is that estimates of the parameters characterizing each individual species can be improved by including more general ecological knowledge coming from other related species. Furthermore, the posterior obtained in one study can be used as prior input in other studies and as input in decision analyses (Hilborn and Mangel 1997). If a prior consistent with the mean present rate of extinction across species is chosen, results of Bayesian analysis are also more easily incorporated in viability analysis because it allows simple direct statements to be made about the probability of extinction, including both parameter uncertainty and process noise, reflecting our present state of knowledge about the species in question. In contrast, within a frequentist framework, mixing the two forms of uncertainty is much more dangerous, because process noise and estimation error are fundamentally different, and because no mechanism for incorporating prior knowledge is available. One option is to present the results as a confidence interval for the probability of extinction (Tufto et al. 1999). This, however, makes statements about extinction doubly probabilistic and more awkward to interpret.

The approach taken here can be seen as an extension of the theory of stochastic abundance models, initiated by the work of Fisher et al. (1943), in which parameters characterizing each individual species are treated as if coming from a common distribution. Engen and Lande (1996a, b) among others generalized this work to also include dynamic abundance models in which the abundances of each individual species are modeled as correlated diffusion processes with growth rates r normally distributed among species. An approach similar to the one used here could possibly be used to estimate several of the parameters of, e.g., Engen and Lande's (1996b) dynamic abundance model, also in cases where several different forms of data are involved.

It is important to emphasize that the difference between frequentist and Bayesian analysis is not only of theoretical interest, but that these two methods in general produce different results as they are based on entirely different underlying principles. It is clear that a similar form of analysis to the one presented here

within a frequentist framework would involve large difficulties. In order to make frequentist methods produce sensible results, many of the 24 parameters of our model which to a frequentist would be regarded as nuisance parameters, would have to be eliminated from the model, for example by conditioning on sufficient statistics for the nuisance parameters (Cox and Hinkley 1974). Finding such sufficient statistics is seldom possible, however, except for very simple models. Therefore, in most cases, frequentists usually compute the sampling distribution of the estimators based on the full sample space of the model. For example, in discussing how to bootstrap from a simple first order autoregressive model, Efron and Tibshirani (1993) suggest computing new bootstrap replicates of the estimators based on new simulated realizations of the entire time series. For short time series, we have found this method to give larger frequentist standard errors than the posterior standard deviations obtained using Bayesian methods with non-informative priors.

Most Bayesians would argue that the above form of comparison between frequentist and Bayesian methods is the one which is most relevant. It can also be noted that Bayesian parameter estimates, if judged by frequentist criteria, typically will have about the same performance as estimators derived using standard frequentist principles. In fact, if a uniform prior is used, then the maximum likelihood estimate and the posterior mode will coincide and their performance will be equal in the frequentist sense. In more complicated cases, this form of comparison can easily be done using stochastic simulations.

Even though modeling variation in the demographic parameters between species offers several advantages, our model at this point remains simplistic. In assuming independence in the variation of the demographic parameters between species we are clearly making a

Table 2. Posterior probabilities of the hypotheses of positive density dependences and growth rates for each species.

<i>i</i>	Species	Posterior probabilities	
		$r_i > 0$	$\alpha_i > 0$
1	Dipper	0.90	0.98
2	Song sparrow	0.98	0.99
3	Great tit	1.00	0.99
4	'General passerine'	0.90	0.77

strong assumption, and it would be interesting to build a more sophisticated model in which additional parameters quantifying the covariance between, say the r_i and $\sigma_{e,i}^2$ are introduced. This would also make the joint between-species distribution much more 'informative' which would further improve the estimates of the demographic parameters for each individual species. However, as we so far only have information from three species, it is unlikely that we would obtain separate estimates of such additional parameters.

It is also clear that we are being somewhat naive in assigning flat priors to μ_r and μ_x , the mean growth rate and mean strength of density dependence among species. Most populations in nature persist for a long time during which their growth rate and density dependence obviously are positive. When some of these parameters change as a result of slow, permanent changes in the environment, this typically quickly leads to extinction. As the long-persisting populations will be over-represented in our sampling, we could possibly have incorporated this in our prior distribution for μ_r and μ_x . However, considering that human activities are now causing mass extinctions in nature (May 1973, 1994), it seems safer to permit the possibility that most species in fact may be at the risk of extinction through the use of more non-informative priors for the hyper-parameters. In doing so, we are admittedly introducing an element of subjectivity, which may seem like an undesirable feature of the Bayesian analysis in general.

A misunderstanding of Bayesian methods, sometimes made by frequentists (e.g. Dennis 1996), is that non-informative priors necessarily have to be uniform. Noting that the corresponding prior, for different parameterizations of the model, will not be uniform, some frequentists then argue that the concept of a prior distribution has to be abandoned all together, since 'ignorance' is not preserved under reparameterization of the model. It is often the case, however, that non-informative priors, following from certain principles, are not uniform. One example is the diffuse priors (in effect being equivalent to scale priors) used here for some of the hyperparameters (eqs (10)–(12)). In other cases, in which no principle for deriving a non-informative prior is available, the prior will necessarily be arbitrary. An important finding, however, is that any method of inference, to satisfy certain sensible axioms defining rationality (see e.g. Ferguson 1967, Berger 1985), must correspond to Bayesian analysis and thus must involve a prior. Taken together, this suggests that 'objectivity' in fact is best sought through Bayesian analysis, since this framework forces prior subjective input to be stated explicitly.

Dennis (1996) objects to the idea that environmental decisions are best made within a Bayesian framework (Wolfson et al. 1996) and argues that the regulator instead should take 'responsibility, clearly admit that information is inadequate, institute an interim, cautious

policy until better data become available'. Dennis gives no advice, however, as to how this 'cautious policy' is to be determined. At this point, Dennis seems to suggest that verbal, non-quantitative arguments are preferable to Bayesian decision analysis in which all subjective input is stated explicitly and can be criticized by all parties. In sciences such as ecology, conclusive evidence which eliminates all uncertainties may never become available, but decisions still have to be made.

It is true, however, that many difficult problems relating to objectivity and non-informative priors for more complex models remain unsolved. Also, better computational numerical methods need to be developed. Nonetheless, as shown here, in some non-standard situations, Bayesian analysis can be easier to carry out than frequentist analysis for the same problem, and the use of Bayesian methods should therefore be encouraged.

Acknowledgements – We are indebted to the developers of BUGS, CODA, and R (a package similar to S-plus) for making these software packages freely available and the Norwegian Research Council and the Norwegian Directorate for Nature Management for financing this study.

References

- Arcese, P., Smith, J. N. M., Hochachka, W. M., Rogers, C. M. and Ludwig, D. 1992. Stability, regulation, and the determination of abundance in an insular song sparrow population. – *Ecology* 73: 805–822.
- Berger, J. O. 1985. Statistical decision theory and Bayesian analysis. – Springer-Verlag, New York.
- Best, N. G., Spiegelhalter, D. J., Thomas, A. and Brayne, C. E. G. 1996. Bayesian analysis of realistically complex models. – *J. R. Statist. Soc. A* 159: 323–342.
- Cox, D. and Hinkley, D. 1974. Theoretical statistics. – Chapman & Hall, London.
- Dennis, B. 1996. Discussion: should ecologists become Bayesians? – *Ecol. Appl.* 6: 1095–1103.
- Dennis, B., Munholland, P. and Scott, J. M. 1991. Estimation of growth and extinction parameters for endangered species. – *Ecol. Monogr.* 61: 115–123.
- Efron, B. and Tibshirani, R. J. 1993. An introduction to the bootstrap. – Chapman & Hall, London.
- Ellison, A. M. 1996. An introduction to Bayesian inference for ecological research and environmental decision making. – *Ecol. Appl.* 6: 1036–1046.
- Engen, S. and Lande, R. 1996a. Population dynamic models generating species abundance distributions of the gamma type. – *J. Theor. Biol.* 178: 325–331.
- Engen, S. and Lande, R. 1996b. Population dynamic models generating the lognormal species abundance distribution. – *Math. Biosci.* 132: 169–183.
- Engen, S., Bakke, Ø. and Islam, A. 1998. Demographic and environmental stochasticity – concepts and definitions. – *Biometrics* 54: 840–846.
- Ferguson, T. S. 1967. Mathematical statistics – A decision theoretic approach – Academic Press, New York.
- Fisher, R. A., Corbet, A. S. and Williams, C. B. 1943. The relation between the number of species and the number of individuals in a random sample of an animal population. – *J. Anim. Ecol.* 12: 42–58.
- Gilks, W., Richardson, S. and Spiegelhalter, D. (eds) 1996a. Markov chain Monte Carlo in practice. – Chapman & Hall, London.

- Gilks, W., Richardson, S. and Spiegelhalter, D. J. 1996b. Introducing Markov chain Monte Carlo. – In: Gilks, W., Richardson, S. and Spiegelhalter, D. J. (eds), Markov chain Monte Carlo in practice. Chapman & Hall, London, pp. 1–20.
- Goodman, D. 1987. The demography of chance extinction. – In: Soulé, M. E. (ed.), Viable populations for conservation. Cambridge Univ. Press, New York, pp. 11–34.
- Hilborn, R. and Mangel, M. 1997. The ecological detective. – Princeton Univ. Press, London.
- Jeffreys, H. 1961. Theory of probability. – Oxford Univ. Press, London.
- Lande, R. 1993. Risk of population extinction from demographic and environmental stochasticity and random catastrophes. – *Am. Nat.* 142: 911–927.
- Lande, R., Sæther, B.-E. and Engen, S. 1997. Threshold harvesting for sustainability of fluctuating resources. – *Ecology* 78: 1341–1350.
- Lande, R., Engen, S. and Sæther, B.-E. 1998. Extinction times in finite metapopulation models with stochastic local dynamics. – *Oikos* 83: 383–398.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. – *Ecol. Appl.* 6: 1067–1076.
- May, R. M. 1973. Stability in randomly fluctuating versus deterministic environments. – *Am. Nat.* 107: 621–650.
- May R. M. 1974. Complexity and stability in model ecosystems. – Princeton Univ. Press, Princeton, NJ.
- May, R. M. 1994. The economics of extinction. – *Nature* 372: 42–43.
- Sæther, B.-E., Engen, S., Islam, A., McCleery, R. and Perrins, C. 1998. Environmental stochasticity and extinction risk in a population of a small songbird, the great tit. – *Am. Nat.* 155: 441–450.
- Spiegelhalter, D. J., Best, N., Gilks, W. and Inskip, H. 1996. Hepatitis b: a case study in MCMC methods. – In: Gilks, W., Richardson, S. and Spiegelhalter, D. J. (eds), Markov chain Monte Carlo in practice. Chapman & Hall, London, pp. 21–44.
- Taylor, B. L., Wade, P. R., Stein, R. A. and Cochrane, J. F. 1996. A Bayesian approach to classification criteria for spectacled eiders. – *Ecol. Appl.* 6: 1077–1089.
- Tufto, J., Sæther, B.-E., Engen, S., Swenson, J. E. and Sandegren, F. 1999. Harvesting strategies for conserving minimum viable populations based on World Conservation Union criteria: brown bears in Norway. – *Proc. R. Soc. B* 266: 961–967.
- Wolfson, L., Kadane, J. B. and Small, M. J. 1996. Bayesian environmental policy decisions: two case studies. – *Ecol. Appl.* 6: 1056–1066.