

A role for Bayesian inference in cetacean population assessment

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ABSTRACT

Decisions concerning the management and conservation of cetacean populations depend upon knowledge of population parameters, which generally must be estimated from sample data using statistical models. However, data from the cetacean populations are often sparse, and resultant parameter estimates can be uncertain and difficult to obtain. This review uses examples from published work to highlight the utility of the Bayesian statistical paradigm as a suitable estimation framework in these situations. By evaluating the probability of obtaining the available data, given a specified estimator model, for a whole prior distribution of possible parameter values, the Bayesian approach is capable of quantifying the uncertainty associated with parameter estimates. The potential also exists for reducing uncertainty by incorporating relevant information into the prior distributions used in the Bayesian estimation procedure. The paper describes how the use of graphical model specification and graphical output of parameter estimates can make Bayesian methods attractive for data analysis and explains the recent advances in computational methods that have made Bayesian techniques more available for providing useful estimates of cetacean population parameters.

KEYWORDS: STATISTICS; POPULATION ASSESSMENT; POPULATION PARAMETERS; MANAGEMENT; CONSERVATION

BACKGROUND

Scientific advice is essential when making decisions concerning the conservation and management of cetacean populations. These decisions often depend upon knowledge of population parameters, which generally are not directly observable but estimated from sample data using statistical models. The past two decades have seen major breakthroughs in the collection and analysis of such sample data, such as the application of mark-recapture type models to photo-identification data to produce estimates of population size (e.g. Hammond *et al.*, 1990), population trends (e.g. Whitehead *et al.*, 1997) and other demographic parameters (e.g. Olesiuk *et al.*, 1990; Wells and Scott, 1990; Slooten *et al.*, 1992; Brault and Caswell, 1993; Barlow and Clapham, 1997; Caswell *et al.*, 1999).

Despite the developments of successful field-based sampling techniques, however, the inherent difficulties of studying cetaceans often leaves biologists and managers with the problem of drawing inference from sparse data. For example, small sample sizes of photo-identification data often results in high uncertainty in abundance estimates (Hammond, 1987), and there is consequently limited power for directly detecting trends in population estimates (Gerrodette, 1987; Thompson *et al.*, In press). Furthermore, estimates of demographic parameters are limited to a minority of well-studied populations, as long-term studies are necessary to accurately estimate fecundity of long-lived cetaceans (Barlow, 1990), and a high rate of re-identification of individuals is necessary for precise estimates of survival (Buckland, 1990). In the majority of cases, information on population parameters is simply not available. Where data do exist, sample sizes are often small, and estimates are extremely uncertain. Consequently, if models are to be used to provide reliable management advice, explicit recognition of this uncertainty in parameter estimates is essential and indeed was inherent in the design of the International

Whaling Commission's Revised Management Procedure (e.g. Hilborn *et al.*, 1993).

This review highlights the utility of the Bayesian statistical paradigm as a suitable framework for producing useful estimates of cetacean population parameters under these circumstances. It is particularly aimed at introducing this approach to cetologists and managers not familiar with developments within the IWC Scientific Community. It begins by contrasting the Bayesian philosophy with the more widely used frequentist statistical approach, proceeds by describing the practical computational mechanisms for presenting parameter uncertainty in Bayesian posterior distributions, and then uses examples from the published literature to demonstrate the utility of these mechanisms. It also highlights the potential for using the Bayesian framework to reduce uncertainty by incorporating all relevant information directly into the estimation procedure. Finally, it suggests how Bayesian estimates of cetacean population parameters can be directly integrated into management decisions.

STATISTICAL PHILOSOPHIES

The commonest approach to parametric statistical inference is to use models for the data-generating mechanism to specify a likelihood function, which quantifies the probability of observing the data given the values of the model parameters. However, there are widely differing views as to how the likelihood function should be interpreted. Whilst many statisticians now take the pragmatic stance of moving between the philosophies outlined, this does not mean that the differences in philosophy have been removed.

On the one hand, the frequentist philosophy is to treat the parameter values as fixed but unknown and ascribe all of the randomness to the data. Parameters are estimated by

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maximising the likelihood, with confidence intervals being obtained by a mathematical consideration of what other data could have been drawn and finding functions of these data with the correct coverage probabilities. In complex situations where the mathematics are too difficult, simulated inference is used to actually generate new datasets, either by Monte Carlo simulation or by using bootstrap methods to resample from the data. For each new dataset, the entire method of parameter estimation must be repeated and the variability in the set of parameter estimates is taken as an indication of the uncertainty in the estimate from the original data (Efron and Tibshirani, 1993).

On the other hand, the Bayesian philosophy is to treat the data as fixed and the parameters as random. Bayesian methods evaluate the probability of obtaining the same fixed data for a whole range of possible parameter values, which is specified by a prior probability distribution (Appendix 1). This prior distribution encapsulates all information about the model parameters that is not present in the data used in the likelihood function, and therefore the combination of prior and likelihood should contain all available information about the parameters. The product of the prior distribution and the likelihood function can be thought of as a full probability model – a joint probability distribution for all observable and unobservable components of a model. Conditioning on the observed data, this model can therefore be used to calculate the joint conditional or ‘posterior’ probability distribution of all the unobserved parameters of interest. Inference about a given parameter, or functions of parameters, is performed by integrating out all other parameters to obtain the marginal posterior distribution of interest (Gelman *et al.*, 1995). This marginal posterior distribution has the intuitive appealing property of being a probability density function, with all the associated measures of uncertainty being readily presented.

PRACTICAL BAYESIAN INFERENCE

The potential to express information about model parameters as direct probabilistic statements renders the Bayesian approach particularly attractive for ecological applications (Ellison, 1996). However, the calculation of marginal posterior distributions for individual parameters requires multidimensional integration, with the dimension equal to the number of parameters being estimated, which can present practical difficulties in all but the simplest cases (Smith and Gelfand, 1992). As the number of parameters increases, marginal posterior distributions become increasingly difficult to calculate analytically, and in some cases impossible. The high dimensionality required for biologically meaningful models has thus limited the implementation of the Bayesian approach in ecological analyses until recently. However, methods are now available for estimating posterior probability distributions, specifically through two distinct Monte Carlo simulation approaches: (i) importance sampling; and (ii) Markov Chain methods (Smith, 1991).

In importance sampling, the posterior distribution of interest is approximated by a specified probability distribution known as an importance function. Using a Monte Carlo approach, random draws are then made from the importance function to produce a collection of possible values for the parameter to be estimated, along with their corresponding probabilities (Smith, 1991). Thus, the key to this approach is to find a suitable importance function, namely one that approximates the posterior distribution as

accurately as possible. One method by which this can be obtained is through the Sampling-Importance-Resampling algorithm, SIR (Rubin, 1988; Smith and Gelfand, 1992), in which the importance function comprises sampled values from the prior distribution weighted by their relative likelihoods. These sampled values are then resampled to produce a sample from the posterior, with the probability of sampling a particular value being determined by its likelihood (Appendix 2). This sampling-resampling approach provides essentially calculus-free use of Bayes’ Theorem, and has been advocated as allowing practitioners to perform ‘Bayesian statistics without tears’ (Smith and Gelfand, 1992).

The practical utility of SIR can be exemplified by its application in fisheries stock assessments (e.g. Hilborn and Walters, 1992; McAllister *et al.*, 1994; McAllister and Ianelli, 1997), and particularly by a Bayesian approach to trend analysis for a population of spectacled eiders (*Somateria fischeri*; Taylor *et al.*, 1996). The Bayesian SIR has also been employed in studies of cetaceans: Raftery *et al.* (1995) used the SIR as part of a Bayesian assessment of bowhead whale (*Balaena mysticetus*) catch quotas; Wade (In press) used the SIR to estimate parameter distributions in a Bayesian stock assessment of the gray whale (*Eschrichtius robustus*); and Wade (1999) demonstrated the utility of SIR for fitting population models to abundance data for spotted dolphins (*Stenella attenuata*). The graphical and easy-to-interpret probabilistic displays of parameter uncertainty that these studies present, along with the relative ease in which they were produced, presents a persuasive argument for the use of the Bayesian SIR in these types of ecological studies.

For many problems, however, especially high dimensional ones, it may be difficult or impossible to find an importance sampling density that is an acceptably accurate approximation of the posterior distribution (Carlin and Louis, 1996). In such cases, Markov Chain Monte Carlo (MCMC) methods provide an alternative approach, in which an approximate sample is drawn from the posterior distribution itself (Brooks, 1998). MCMC is essentially Monte Carlo integration using Markov Chains, in that the posterior sample is drawn by running a Markov Chain with the posterior serving as the chain’s stationary distribution (Appendix 3).

The MCMC method has enjoyed an enormous upsurge in interest and application over the last few years (Brooks, 1998). Much of this recent use can be attributed to the development of the computer software BUGS (‘Bayesian inference Using Gibbs Sampling’; Thomas *et al.*, 1992; Gilks *et al.*, 1994), which allows relatively straightforward implementation of the Gibbs sampling MCMC method (Gelfand and Smith, 1990; Smith and Roberts, 1993). Gibbs sampling is especially useful because it reduces the problem of dealing simultaneously with a large number of related unknown parameters and missing data into a much simpler problem of dealing with one unknown quantity at a time, estimating the posterior probabilities for this quantity conditional upon the current values of all other quantities and the relationship between them (Gilks *et al.*, 1994). The BUGS software provides a language for specifying the quantities involved in the model, processes this model structure and data to compile the sampling distributions required for MCMC, and then implements the sampling procedure. As such, BUGS is a computer-intensive statistical tool that allows practitioners to perform MCMC sampling with the minimum investment of programming and training time.

This utility has been further extended by a recently released version of the BUGS software for the Windows computing environment (WinBUGS; Spiegelhalter *et al.*, 1999). A notable feature of the WinBUGS package is that model structures can be specified using graphical models that express the relationship between variables, and sampling can actually be performed directly from these graphical model representations without the use of programming code. A graphical model is a tool to represent conditional independence assumptions. By providing simple representations of the conditional independence between model variables, graphical models can simplify the implementation of Gibbs sampling by alleviating the requirement to derive 'by hand' the full conditional distribution of each variable in the model (Speigelhalter *et al.*, 1996). In addition, graphical models are of immense value in ecological data analysis, by allowing the drawing of inferences from realistically complex models in a form that is readily communicable and understood (e.g. Best *et al.*, 1996; Speigelhalter *et al.*, 1996).

MCMC methods have been used infrequently in ecological applications to date. However, these methods are now being employed in fisheries stock assessments (Bjornstad *et al.*, 1999; Meyer and Millar, 1999a) and the utility of the BUGS software has recently been demonstrated in this context (Meyer and Millar, 1999b). As this software tool continues to become discovered by ecologists, it is likely that MCMC methods will see increasing use in drawing inference in these types of high dimensional, non-linear ecological problems. Furthermore, in the context of this review, MCMC may be of some value when assessing cetacean population dynamics using demographic models with several parameters, and when attempting to parameterise models using sparse or incomplete data.

USING PRIOR INFORMATION

In order to provide the posterior distribution for parameter estimates, the Bayesian method requires the specification of a prior distribution. Two types of prior distributions can be used in Bayesian analysis: non-informative and informative priors (Box and Tiao, 1973). To many attracted to the Bayesian inferential paradigm, but sceptical about the role of subjectivity in specifying priors, the idea of a non-informative prior distribution has proved highly seductive. Non-informative priors are seen as representing ignorance and 'letting the data speak for themselves', and are thus often regarded as synonymous with providing objective inference (Bernardo and Smith, 1994).

However, whilst non-informative priors allow the use of the Bayesian approach, methods that use this framework without fully exploiting the utility of prior specification of possible parameter values are not taking advantage of the full potential of the Bayesian approach. The use of informative priors can allow the efficient incorporation of diverse sources of pre-existing information into statistical procedures, with the potential for parameterising a model far more accurately than would otherwise be possible. This is aptly demonstrated by studies in which inference has only been possible due to the use of prior information. For example, Raftery *et al.* (1995) used a Bayesian approach to incorporate three different types of information into a model of bowhead whale population dynamics. The three types of information (recent census information, historic whaling records and biological information about birth and death rates) were combined into a joint prior (termed 'premodel') distribution, to be incorporated into this model-based

inference. Through the explicit combination of different types of prior information, Raftery *et al.* (1995) were able to yield full inference about population management questions¹.

Trenkel *et al.* (2000) further demonstrate the utility of empirically-based informative priors, in this case when producing red deer (*Cervus elaphus*) population management models. They demonstrate how information on demographic processes, obtained from closely studied deer populations, can be used to parameterise a management model for a less studied population. This was only possible through the adoption of a Bayesian framework. The demographic data from the well studied populations were used in the specification of prior distributions for a population dynamics model, which also incorporated count and cull data from the less studied population, which was of interest to managers. This pioneering approach is of immense value for modelling the dynamics of wildlife populations, where much of the parameter uncertainty often originates because it is not possible to parameterise the population model using data from the study population alone. This is a common situation when trying to use demographic models to estimate cetacean population growth rates (Barlow, 1991) and population viability (Thompson, *et al.*, In press). As such, the type of approach presented by Trenkel *et al.* (2000) has great potential for parameterising models for cetacean populations, for which only limited data exist.

The ability of Bayesian analyses to combine data from more than one population has also been exploited by Taylor *et al.* (1996). When fitting a population model to a time series of abundance data for spectacled eiders, they used data from common eider populations to parameterise environmental stochasticity. It is widely recognised that, when fitting a population model to abundance data, it is generally impossible to distinguish between environmental variance and sampling error from the abundance data alone (Hilborn and Walters, 1992). This has often led researchers to ignore one or the other. However, by incorporating information on the natural variation in common eider population size into their analysis, Taylor *et al.* (1996) were able to estimate the relative magnitude of both the environmental and sampling variation in spectacled eider population trends. Admittedly, using common eider data to parameterise environmental variance is not ideal, but is preferable to ignoring the role of environmental stochasticity in population growth (Taylor *et al.*, 1996).

This type of approach is likely to be particularly valuable for assessing cetacean population trends, as cetacean population estimates are typically subject to large sampling variance (Hammond, 1987). Using conventional approaches, which do not provide the facility for incorporating relevant pre-existing data, it is not possible to detect real trends beyond this sampling variance. Perhaps a Bayesian approach of using prior information on real abundance variation from those few accurately enumerated populations will allow some useful, albeit uncertain, inference to be drawn from time series of uncertain abundance estimates from other populations.

¹ It is important here to refer to the potential problem of Borel's Paradox as arose in the 'Bayesian Synthesis' approach used to assess bowhead whales (e.g. see Givens *et al.*, 1995; Raftery *et al.*, 1995; Wolpert, 1995; Schweder and Hjørt, 1996). Put simply, under certain cases, post-model distributions are not unique and depend on the particular functional form of parameters used in the model (see discussion in e.g. Givens and Bravington, 1996; Punt and Butterworth, 1997; 1999).

The procedure of specifying a prior distribution for the parameter to be estimated therefore allows Bayesian approaches to borrow strength from data on other populations. Using a similar approach, a Bayesian framework can also be used for a more efficient analysis of temporally structured data, by borrowing strength from previous estimates of the same population. Consider, for example, a population for which it is required to estimate population size in each of a series of consecutive years. Conventionally this estimation would proceed independently for each year in turn. However, under the Bayesian paradigm each year's data can be seen as an accumulation of further evidence which can be used to update beliefs generated through the analysis of previously available data. Since Bayesian inference is an iterative process, the posterior probability obtained by one analysis can be used as the prior probability distribution for a new analysis (Bernardo and Smith, 1994).

The practical implementation of this kind of updating procedure is again exemplified by Trenkel *et al.* (2000) in their Bayesian approach to constructing a red deer population dynamics model. Because their model was based on temporally structured annual count and cull data, they implemented a procedure that allowed model parameters to change over time as more years of data were used in the estimation. In order to achieve this, a sequential approach to importance sampling was used, known as the Bayesian Filter (Gordon *et al.*, 1993). In the Bayesian Filter, a sample from the posterior distribution at one time interval is obtained, just as in the SIR, via a weighted bootstrap, where the weights for each simulation realisation are given by the re-scaled likelihood values. The posterior sample then serves to create the sample from the prior distribution for the next time interval (Trenkel *et al.*, 2000).

This elegant and straightforward approach of using new data to update previous beliefs presents considerable potential for the analysis of temporally structured data on cetacean populations. It will have particular utility for assessing trends in populations which change little between years, and as such offers considerable potential for the analysis of mark-recapture data from cetacean populations, where variances in population estimates are generally large relative to actual changes in the population size (Hammond, 1987). Mark-recapture methods are carried out over time, so the procedure of updating a posterior distribution over time is appealing (Pollock, 1991) and innovative Bayesian approaches to mark-recapture modelling have already been developed (Casteldine, 1981; Gazey and Staley, 1986; Smith, 1988; 1991; George and Robert, 1992). However, these models still approach mark-recapture estimation as a separate problem for each estimation period, and it may be that sequential Bayesian approaches to mark-recapture modelling are capable of exploiting previous estimates to reduce estimate precision and increase the potential to detect trends. If they are successful, then such approaches will represent a significant advancement in the study of cetacean population trends from uncertain mark-recapture data.

APPLIED BAYESIAN INFERENCE

This review has advocated the Bayesian paradigm as a powerful method for combining multiple sources of data into a single inferential framework, whilst at the same time fully incorporating uncertainty into the resulting inference. These facilities alone present a persuasive argument for the use of Bayesian approaches in ecological data analysis and the particular potential for their use in assessing cetacean

population dynamics is clear. However, a further benefit of Bayesian inference is that the resultant posterior distribution for parameter estimates can be used to lead quickly and naturally to estimates of applied interest, which will themselves explicitly account for all sources of uncertainty. For example, Taylor *et al.* (1996) demonstrated the utility of incorporating Bayesian posterior inference into a population viability analysis (PVA) for a threatened spectacled eider population. By performing a Bayesian analysis of population trends, they were then able to directly incorporate the entire posterior distribution for the population growth rate into stochastic projections of future population size, thus fully accounting for data uncertainty when estimating extinction parameters. Previous PVA calculations have been criticised for not accounting for uncertainty due to parameter estimation (Taylor, 1995). Furthermore, the need to consider uncertainty about crucial parameters when estimating extinction parameters was aptly demonstrated by Ludwig (1996), who showed that methods based upon point estimates, that do not incorporate parameter uncertainty, can grossly underestimate the risk of extinction. As such, the PVA performed by Taylor *et al.* (1996), which does account for parameter uncertainty within its estimates of extinction rates, represents a major advance over previous PVA attempts. However, this Bayesian approach of fully representing scientific uncertainty can actually present further problems to decision-makers, as it now precludes the use of simple patterns of decision-making that are appropriate for predictable systems. Instead, some form of decision-making that can take explicit account of uncertainty is required (Ludwig, 1999).

One of the most notable advantages of Bayesian posterior inference in ecological analysis is that it does provide the potential for incorporating scientific uncertainty directly into management decision processes. For example, McAllister *et al.* (1994) used the entire posterior output distribution from a Bayesian fisheries stock assessment to make accompanying estimates of biological and economic risks of alternative harvesting policies, whilst explicitly accounting for uncertainty about stock size. In this study, the probabilities of each possible current stock size were obtained from the output posterior distribution of the Bayesian stock assessment. For each possible stock size, the consequences of each alternative management action were then evaluated, and summarised by a performance index (total catch). This performance index was then weighted by the probability of each stock size to provide the expected values for each performance index for each candidate management action (McAllister *et al.*, 1994). The conceptually straightforward and easily interpretable approach adopted in this example demonstrates why Bayesian approaches are increasingly being used to provide scientific advice in fisheries management (e.g. Thompson, 1992; Hilborn *et al.*, 1994; McAllister *et al.*, 1994; Walters and Punt, 1994). A Bayesian approach is being used in the development of a management procedure for aboriginal subsistence whaling by the IWC Scientific Committee (e.g. see IWC, 1997; 1998; 1999).

CONCLUDING REMARKS

This review has highlighted a number of ways in which the Bayesian approach can provide a formal framework for including scientific uncertainty into management decisions concerning cetacean populations. Uncertainty is fundamental to all scientific activities, and therefore its inclusion in the decision-making process is not simply

desirable, but essential. As Ludwig *et al.* (1993) illustrated, ignoring ecological uncertainty has led repeatedly to environmental catastrophes. Nonetheless, the lack of quantifiable uncertainty has often been used by ecologists to justify their lack of involvement in decision-making processes, and by some decision analysts as a vehicle to avoid using scientific information in the process (Ellison, 1996). However, the application of Bayesian approaches now provides ecologists with a powerful and formal tool for presenting the kind of complex and uncertain advice that pertains to most conservation and management decisions (Doak and Mills, 1994; Ludwig, 1999). This improved integration between scientific estimates and management decisions has already been demonstrated in the management of unpredictable fisheries (e.g. Hilborn and Walters, 1992; Punt and Hilborn, 1997). Bayesian approaches have become widely used in this fisheries context, due to a need for scientists to use uncertain data as a basis for advice to fisheries managers, and to the intense international scrutiny that requires the most rigorous statistical analysis be used. Similar requirements should see the increasing use of Bayesian inference in both the scientific study and management of cetacean populations in the future.

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Appendix 1

BAYES' THEOREM

Bayes' theorem (Bayes, 1763) can be stated as follows:
where'

$$p(y|x) = l(x|y)p(y) / \int l(x|y)p(y)dy$$

$l(x|y)$ is the likelihood of obtaining data x given parameter value y ;
 $p(y)$ is prior probability distribution for the parameter y ;

$p(y|x)$ is posterior probability distribution for the parameter y given the data x .

This theorem therefore states that the posterior probability of a parameter y given the data x is proportional to the product of the likelihood of the data given specified values for the parameter and the prior probability for the parameter. The denominator of the above equation is the expected value of the likelihood function, which acts as a scaling constant to normalise the integral of the area under the posterior probability distribution.

Appendix 2

THE SIR ALGORITHM

Sampling-Importance-Resampling (SIR) (Rubin, 1988; Smith and Gelfand, 1992) is a simple and versatile method of generating posterior probability distributions through importance sampling (Smith, 1991). The approach involves parameter values being randomly selected from the prior distribution to form a sample set y_i . Using the likelihood function, the likelihood of the data x given a particular y_i is calculated and stored. This is repeated, generating n y_i 's with associated likelihoods. This serves to create an importance function, with the possible parameter values forming a

discrete distribution with mass being placed according to relative likelihoods. These n y_i 's are then re-sampled m times with replacement, with probability equal to weight q_i , where:

$$q_i = l(x|y_i) / \sum l(x|y_i)$$

This re-sampling procedure serves to approximate a random sample from the joint posterior distribution.

Appendix 3

MARKOV CHAIN MONTE CARLO SIMULATION

Suppose we generate a sequence of random variables $\{X_0, X_1, X_2, \dots\}$, such that at each time $t \geq 0$ the next state X_{t+1} is sampled from a distribution $P(X_{t+1}|X_t)$ which depends only on the current state of the chain, X_t , not on any further previous history. This sequence is called a *Markov chain*. As it progresses, a chain will gradually forget its starting state (X_0) and the distribution of any X_t given X_0 will eventually converge to a unique *stationary distribution*, which does not depend on t or X_0 . Thus, as t increases, the sampled points $\{X_t\}$ will look increasingly like dependent samples from this stationary distribution, and after a sufficiently large number of iterations the sample points will reasonably approximate this distribution (Gilks *et al.*, 1996).

The problem of constructing a Markov chain so that its stationary distribution is precisely the distribution of interest (in this case the posterior distribution) is the focus of *Markov Chain Monte Carlo* (MCMC) methods. To date, most statistical applications have used an MCMC approach known as the Gibbs sampler (Gelfand and Smith, 1990; Smith and Roberts, 1993; Gilks *et al.*, 1996). The Gibbs sampler is a special case of a general method known as the

Metropolis-Hastings algorithm (Hastings, 1970), which provides the basis for MCMC methods. These methods begin by selecting an initial value for each parameter. The prior probability and likelihood of that value can be calculated from the specified model for inference, and Bayes theorem can be used to calculate the value's posterior probability. A new parameter value is then randomly drawn, and its posterior probability is calculated. If this probability is higher than that of the previous value then the Markov chain proceeds; if it is lower than the previous value, then the chain proceeds with probability equal to the posterior probability of the new value divided by the old value's posterior probability. This iterative step is repeated with further random draws of new parameter values. Because the chain's progression is determined by the relative posterior probabilities of sampled values, the chain will gradually converge towards the region of the parameter space with greatest probability, and the parameter values comprising the chain will then provide a random sample from the posterior distribution for the parameter of interest.