

# Profiting from prior information in Bayesian analyses of ecological data

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## Summary

1. Most ecological studies include prior information only implicitly, usually in their design or the discussion of results. In this study, two examples demonstrate that using Bayesian statistics to incorporate basic ecological principles and prior data can be very cost-effective for increasing confidence in ecological research.

2. The first example is based on examining the effects of an experimental manipulation of the habitat of mulgara *Dasycercus cristicauda*, a marsupial of inland Australia. The second example is based on observational mark–recapture data to estimate the annual survival of the European dipper *Cinclus cinclus*, a passerine in France.

3. In the mulgara example, the prior information obtained from an observational study increased confidence that there was an adverse effect of experimental habitat manipulation on the species. The results suggested that the capture rate of mulgara was reduced to approximately one-quarter by reduction of vegetation cover.

4. In the European dipper example, prior information based on the body mass of the species and estimates of annual survival of other European passerines was shown to be worth between 1 and 5 years of mark–recapture field data.

5. *Synthesis and applications.* Body mass can be used to predict annual survival of European passerines and other animals. Results of observational studies can provide prior information in experimental studies of impacts of habitat change. By using Bayesian methods, such prior information, if represented in a coherent and logical way, can be cost-effective for adding certainty to ecological studies.

*Key-words:* *Cinclus cinclus*, *Dasycercus cristicauda*, habitat manipulation, mark–recapture, Markov chain Monte Carlo, survival

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## Introduction

Ecology represents a substantial body of knowledge about how organisms are influenced by their biotic and abiotic environments. Yet most ecologists, while motivated by this background knowledge, rarely use it explicitly in their analyses and interpretation of data, with null hypothesis testing, which specifically ignores prior information, being the dominant approach to statistics in ecology (Anderson, Burnham & Thompson 2000; Fidler *et al.* 2004). Meta-analysis uses quantitative methods to synthesize the results of several analyses

(Gurevitch & Hedges 2001) but such analyses are not routinely conducted. Instead, the results of previous research are considered, usually qualitatively, in the discussion section of manuscripts.

Despite prior information being used only implicitly, knowledge derived from previous studies can be used explicitly and quantitatively by using Bayesian statistics. Bayesian analyses have four basic components: the prior distribution that reflects any prior belief in possible values of parameters; data; a model that relates the data to the parameters; and the posterior distribution that reflects the updated belief in the parameter values given the data and the model. The belief in the parameter values is expressed as a probability. The mathematical details of Bayesian methods can be found elsewhere (Gilks, Richardson & Spiegelhalter 1996; Hilborn & Mangel 1997). For the purposes of

this study, an important point is that the posterior distribution is essentially a weighted average of the prior and the data. Because the data and prior both influence the results of the analyses, they need to be treated with the same care and rigour.

There is a growing literature that applies Bayesian statistics in ecology. Most of these previous studies do not use prior information (Wade 2000; Link *et al.* 2002; McCarthy & Parris 2004) although there are exceptions (Crome, Thomas & Moore 1996; Wyckoff & Clark 2000; Ellison 2004; Martin *et al.* 2005). These exceptions illustrate that Bayesian methods can be used to represent and highlight agreement and disagreement in the face of accumulating data (Crome, Thomas & Moore 1996), use expert opinion in evaluating environmental impacts (Martin *et al.* 2005) and help overcome gaps in data (Wyckoff & Clark 2000). Ellison (2004) showed that prior information improved the precision of parameter estimates for a Poisson regression model (see also [http://harvardforest.fas.harvard.edu/personnel/web/aellison/publications/ellison\\_2004\\_winbugs.html](http://harvardforest.fas.harvard.edu/personnel/web/aellison/publications/ellison_2004_winbugs.html)). When prior information is not used, Bayesian analyses and likelihood-based frequentist analyses produce numerically equivalent results, although implementing many models in a Bayesian framework is often easier (Clark 2005).

There are many areas of ecology that might be able to benefit from the inclusion of prior information. For example, ecologists studying the population ecology of animals could use the knowledge that annual survival rates can be predicted from body mass, with larger species tending to be longer lived than smaller species (Peters 1983; Calder 1984; Savage *et al.* 2004). As another example, it may be useful to know a priori that modifying the habitat of a species is likely to affect its abundance to at least some extent (Caughley & Gunn 1996). Examples of these two general principles are analysed here to illustrate how prior information can assist with interpretation of data, both in observational and experimental studies.

In this paper, we briefly introduce the evaluation of models with Bayesian statistics, and then illustrate the use of prior information with two examples. The first is an experimental study conducted by Masters, Dickman & Crowther (2003) examining effects of spinifex removal on an Australian mammal. The second is an observational study in which the survival rate of a European passerine is estimated using mark-recapture methods (Marzolin 1988). Important contributions of this study are to demonstrate logical and repeatable approaches to constructing informative priors in ecology, the cost-effectiveness of using this prior information, and how the consistency of the data and prior can be evaluated.

### Comparing models and the deviance information criterion

Bayesian methods and frequentist methods differ in

how hypotheses are evaluated. In null hypothesis significance testing, researchers attempt to reject null hypotheses (Underwood 1997). In ecology, commonly used null hypotheses of no difference or no effect (nil nulls) are likely to be true only rarely (Johnson 1999; Anderson, Burnham & Thompson 2000). Because of this, various authors have recommended methods to evaluate different hypotheses by using data to assess their relative merits (Hilborn & Mangel 1997; Burnham & Anderson 2002). Such analyses are usually achieved by using information theoretic approaches and likelihood-based frequentist methods to select the best model (or set of models). The selection is based on assessing the trade-off between the fit and complexity of the models (Hilborn & Mangel 1997; Burnham & Anderson 2002), with the aim of finding the most parsimonious.

One of the difficulties of implementing information theoretic approaches in ecology is that we rarely have precise hypotheses to be evaluated. At best, expected values of most parameters can only be specified as probability distributions rather than as precise values. This may be why hypotheses of no effect or no difference are evaluated so frequently, because it is difficult to decide on any particular non-nil hypothesis. Likelihood-based methods require precise hypotheses that rarely exist in ecology. In contrast, Bayesian methods can accommodate imprecise hypotheses if they can be expressed probabilistically.

In Bayesian statistics, the relative parsimony of the models can be compared using the deviance information criterion (DIC; Spiegelhalter *et al.* 2002). DIC is a measure of the fit of the model to the data that is penalized for the model's complexity. The measure of fit is based on the likelihood of obtaining the observed data given the means of the posterior distribution of the parameters. Parameter values provide a better fit if they are more likely to have produced the observed data. The complexity of the model is measured by the effective number of estimated parameters. In Bayesian models, the effective number of estimated parameters and model complexity are reduced when informative prior distributions are used (Spiegelhalter *et al.* 2002). When this prior information does not reduce the fit of the model, the DIC value will improve.

Models with smaller DIC values represent more parsimonious descriptions of the data than models with larger DIC values. The relative parsimony of the models can be assessed by comparing the difference in the DIC values. The DIC is a Bayesian equivalent of Akaike's information criterion (AIC; Akaike 1973; Hilborn & Mangel 1997; Burnham & Anderson 2002) and the rules of thumb suggested by Burnham & Anderson (2002) for comparing models with AIC seem to apply for DIC (Spiegelhalter *et al.* 2002). Therefore, differences of less than 2 indicate that the two models are indistinguishable, differences of 4–7 that the poorer model has considerably less support, and differences of more than 10 that the poorer model has essentially no support (Burnham & Anderson 2002).

DIC values are easily calculated for Bayesian models using Markov chain Monte Carlo (MCMC) methods (Gilks, Richardson & Spiegelhalter 1996; Spiegelhalter *et al.* 2002; Spiegelhalter *et al.* 2003). MCMC works by randomly sampling parameter values of the specified model from their joint posterior distribution. A precise estimate of a posterior distribution can be obtained by taking numerous samples. It may be necessary to discard the first few thousand samples as a 'burn-in' because it can take some time before the MCMC algorithm begins to sample from the posterior distribution (the stationary distribution). Methods for ensuring that the samples have in fact been drawn from the posterior distribution are discussed elsewhere (Gilks, Richardson & Spiegelhalter 1996). Analyses in this study were conducted using the program WinBUGS (Spiegelhalter *et al.* 2003) with DIC values used to evaluate the different models. DIC values and posterior distributions were obtained from 100 000 samples after excluding the first 10 000 as a burn-in.

### Effects on mulgara of removing spinifex

Field-based experiments in ecology are often expensive and involve logistical hurdles that limit their sample size and therefore their statistical power. In such cases, prior information would be useful if it could contribute to the knowledge gained from the experiment. For example, an experimental manipulation of habitat was conducted by Masters, Dickman & Crowther (2003) in which vegetation cover of a site in arid inland Australia was reduced and the response of the mammal fauna monitored. In an observational study comparing recently burnt and long unburnt sites, Masters (1993) obtained higher capture rates of mulgara *Dasyurus cristicauda* Krefft on the long unburnt sites. The difference in capture rates was attributed to lower cover, particularly that of hard spinifex *Triodia basedowii* E. Pritzel in the more recently burnt sites. The ultimate motivation of the experiment was that a tourist resort was harvesting spinifex to use as mulch on garden beds. Given the results of the observational study, there was concern that the harvesting may have been reducing the abundance of the resident wildlife and an experiment was designed to evaluate whether this was the case.

Masters, Dickman & Crowther (2003) monitored five treatment and five control sites, once prior to the experimental manipulation and twice after. Using a frequentist analysis of variance (ANOVA), Masters, Dickman & Crowther (2003) did not detect a statistically significant reduction in the capture rate of mulgara in the experimental study, although the data were suggestive of an effect ( $P = 0.15$ ) and the observed difference appeared to be similar to that in the observational study. The power of the experiment was not evaluated at the time of the study, but turned out to be small (0.4, based on the variance and effect size obtained previously; Masters 1993). How might a Bayesian approach to this analysis help to clarify the available evidence?

### ALTERNATIVE MODELS AND PRIOR INFORMATION

A Bayesian analysis requires the specification of models that may explain the data that were observed in the experiment. One model that could be chosen is the same as the null hypothesis used by Masters, Dickman & Crowther (2003), that being of no effect of the experimental manipulation on the capture rate of mulgara (model A).

A second group of models is that the experiment causes a change in the capture rate of mulgara. There are at least two possible ways of specifying an effect of the experiment. The first of these is that the effect of the experiment on mulgara is the same as that recorded in the observational study (model B). The second model with an effect is that we have no prior information that would allow us to predict the magnitude or even direction of the experimental effect (model C). Model C is equivalent to the alternative model used by Masters, Dickman & Crowther (2003) in their null hypothesis test.

It is somewhat pessimistic to say we have no prior information given the observational data on the effect of spinifex removal. However, such a point of view could be justified. For example, we might be uncertain about the possible confounding role of pseudoreplication in the observational study (as with any unplanned fire, there was spatial structure in the arrangement of sites; Masters 1993). Alternatively, the observed reduction may have been caused by some other effect of the fire instead of the reduction in spinifex cover.

These three models (A, no effect; B, an effect consistent with the observational study; and C, some effect that cannot be predicted a priori) can be considered as three competing points of view. By using the results of the experiment, we hope to be able to help discriminate between them to determine which model or models are best supported by the data.

We used repeated-measures ANOVAs to analyse the experimental data, with the effect of the treatment being expressed in the interaction terms for time and treatment (Masters, Dickman & Crowther 2003). Essentially, this means that an effect of the treatment would be detected if the difference between sites in different treatments differed between time periods (particularly between the pre- and post-treatment time periods). Site was treated as a random factor (see Appendix S1 for the WinBUGS code) to account for the fact that the capture rate might vary randomly from site to site because of differences other than the spinifex cover.

To reflect a lack of prior information in model C, an uninformative prior for the effect of spinifex removal was specified by the using a normal distribution with a mean of zero and large standard deviation (1000) for the parameter that described the effect. The large standard deviation meant that the parameter can take any value (i.e. positive or negative effects of the experiment were permitted), with essentially no prior influence on the actual value.

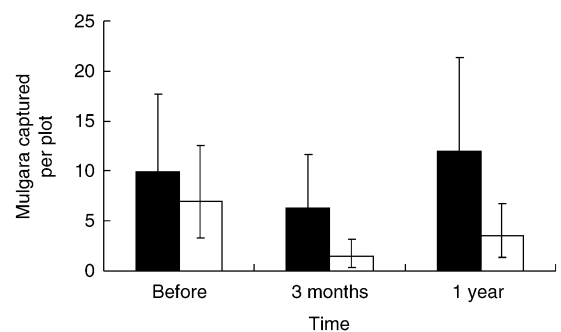
**Table 1.** The value of the deviance information criterion (DIC) for the three competing models used to describe the observed data in the experimental study of the effects of habitat manipulation on mulgara conducted by Masters, Dickman & Crowther (2003)

Model	DIC
A No effect	62.8
B Effect consistent with observational study	58.0
C Uncertain effect	61.8

For the model with an effect consistent with the observational study (model B), the prior distribution was taken from the posterior distribution of the effect of spinifex removal in the observational study. This was obtained by analysing the observational data of Masters (1993) in the same manner as the experiment (i.e. the data on capture rate were  $\ln(x + 1)$  transformed before conducting a repeated-measures ANOVA that included the effect of sites as a random factor). The difference in the log-transformed capture rate between the sites with different spinifex cover in the observational study (i.e. between those sites recently burnt and those long unburnt) was estimated (see Appendix S1 for the WinBUGS code). The mean difference was a reduction of 0.74 in the more recently burnt area, with the standard deviation of the estimate being 0.23. A normal distribution with this mean and standard deviation was used as the informative prior in model B. For model A (no effect of the experiment) the parameters that specified the reduction in the capture rate of mulgara because of habitat manipulation were set to zero.

#### MODEL EVALUATION

The model in which the observed effect of the experiment was consistent with the observational data (model B) had the lowest DIC value (Table 1), suggesting that this model was the best explanation of the data. The next best model was one of an uncertain effect (model C), and the difference in the DIC value (*c.* 3.8) suggested that it had considerably less support than model B. The difference in the DIC values for the two inferior models was approximately 1, suggesting that they were largely indistinguishable. If the prior information was ignored, we would be unable to discriminate reliably between the hypothesis of no effect (model A) and the alternative of an effect (model C), with only weak evidence in favour of the latter. This is similar to the conclusion of Masters, Dickman & Crowther (2003), where the *P*-value was 0.15. However, by using the observational data and finding that the experimental results were consistent with those data, the ability of the experiment to determine whether there was an effect was increased. By considering both the observational and experimental studies, we can be reasonably sure that harvesting of spinifex reduces the capture rate of mulgara.



**Fig. 1.** Posterior distribution of the mean number of mulgara captures in treatment (open columns) and control (filled columns) plots, assuming an informative prior derived from the study of Masters (1993). Samples were taken before the treatment, and both 3 months and 1 year after the treatment. The columns give the means of the posterior distributions and the bars are the 95% Bayesian confidence intervals (credible intervals).

The estimated effect of the removal of spinifex cover, taking into account the prior information from the observational study, was that the capture rate of mulgara was reduced by approximately 0.75 in both time periods when using  $\ln(x + 1)$ -transformed data (0.78 in the first and 0.74 in the second). With back-transformed results, the posterior distribution implied that the removal of spinifex reduced the capture rate of mulgara to approximately one-quarter of the original rate (Fig. 1). The 95% Bayesian confidence intervals (credible intervals) were approximately half as wide as the frequentist confidence intervals obtained by Master, Dickman & Crowther (2003). The standard deviation of the posterior distribution for the effect in both time periods was 0.20. This standard deviation was only slightly less than that of the prior (0.23), which indicated that the prior had a large influence on the estimated effect of vegetation removal in the experiment. When using uninformative priors, the standard deviation for the experimental effect was 0.51. Therefore, conclusions about the effects of spinifex removal had only been clarified to a small extent by the experiment. The observational data provided the most compelling evidence, with the experimental data being consistent with this prior evidence. This approach encourages precautionary management and helps to avoid the misinterpretation that *P*-values greater than 0.05 provide evidence in favour of the null hypothesis (no effect).

#### Annual survival of European dippers

Mark–recapture analysis provides estimates of annual survival in the case where there is imperfect detection of individually marked animals (Lebreton *et al.* 1992). For this study, we analysed data from a 7-year study (Marzolin 1988) of female European dipper *Cinclus cinclus* Linnaeus, a passerine bird specialized to an aquatic lifestyle. This data set is one of the classics in mark–recapture analysis (Lebreton *et al.* 1992). We fitted a model in which survival and resighting rates did not



vary from year to year. Models in which the survival and resighting rate vary annually could be fitted and compared with the simpler model (Lebreton *et al.* 1992) but we used the simpler model only for illustrative purposes. The influence of prior information would be even more pronounced with the more complex models because the estimated mean survival rate is less certain when more parameters are estimated. The code for analysing the mark–recapture data is provided in Appendix S1.

#### ALTERNATIVE MODELS AND PRIOR INFORMATION

In the case of the European dipper model, there was no particular hypothesis about the annual survival rate being tested. This is an example of parameter estimation rather than evaluation of competing hypotheses. Therefore, to evaluate the influence of prior information, a model using an uninformative prior was simply compared with a model using an informative prior.

The informative prior distribution was based on knowledge that species with similar body masses tend to have similar survival rates. Therefore, an informative prior for the survival rate of the European dipper could be constructed by using a regression of survival of other European passerines vs. body mass. We constructed such a regression by using data provided in the appendix of Johnston *et al.* (1997) for annual survival and Dunning (1993) for body masses. Only survival estimates in Johnston *et al.* (1997) that included standard errors were included in the analysis because the reliability of the others could not be ascertained. Additionally, the estimate of annual survival of European dippers provided in Johnston *et al.* (1997) was excluded from construction of the prior because it was derived from the same data used in the current study.

Multiple studies of annual survival were available for some species. We included these studies by including each as a random effect nested within each species. Similarly, the species effect was treated as a random variable. Therefore, the total variance around the regression line of annual survival on body mass included variation as a result of species, variation among studies, and variation within studies. This latter source of variation was estimated by the standard error of the estimate provided in Johnston *et al.* (1997). Normal distributions were assumed for the random effects and body mass was log-transformed to improve linearity of the relationship.

The prior for the annual survival of European dippers was constructed by predicting annual survival for a bird of the appropriate body mass (59.8 g) and accounting for the fact that species and study effects were random (see Appendix S1 for the WinBUGS code). This led to a prior distribution with a mean of 0.57 and a standard deviation of 0.075. An alternative model with an uninformative prior (survival rate uniform between 0 and 1) was also considered.

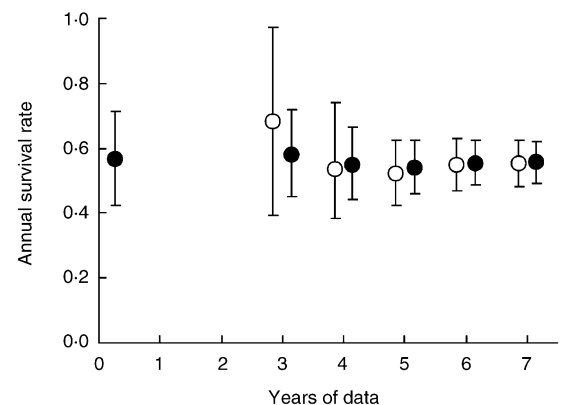
To examine more fully how prior information can assist parameter estimation, the annual survival rate of

European dippers was estimated for the full 7 years of the study and also when the final 1–4 years of data were deleted. This allowed the effect of the prior to be evaluated for different sample sizes (3–7 years of data). A minimum of 3 years of data is required to estimate parameters for a mark–recapture study when prior information is ignored, so smaller sample sizes were not considered.

#### MODEL EVALUATION

Using 7 years of data, the difference in the DIC values (0.4) suggested that the model based on the uninformative prior (DIC = 344.3) and the model with the informative prior (DIC = 343.9) were indistinguishable. Indeed, the posterior distributions for annual survival were very similar whether the uninformative (mean = 0.554, SD = 0.036) or informative (mean = 0.556, SD = 0.032) prior was used. This occurred because both priors were consistent with the data, and the data had an overwhelmingly large influence on the posterior distribution.

However, the benefit of using the prior information was clear when examining changes in the parameter estimates with the addition of each year of data (Fig. 2). If only 3 years of data were available, the 95% Bayesian confidence interval when prior information was ignored had a width of 0.58. This was double that obtained when prior information was used (0.29), illustrating the increased precision provided by the prior. If prior information was ignored, 5 years of data collection would be required to obtain a more precise estimate than the one based on body mass alone (Fig. 2). Therefore, at the start of the mark–recapture study, the information on body mass was equivalent to 4–5 years of field data. The width of the Bayesian confidence interval was 0.138 after 6 years when using prior information and 0.139 after 7 years without prior information. By the end of the 7-year study, the improvement in



**Fig. 2.** Posterior distributions of the annual survival rate of female European dippers. The results based on an uninformative prior (open circles) are compared with those in which body mass is used to establish an informative prior (closed circles). Circles are the means of the posterior distributions and the bars represent 95% Bayesian confidence intervals (credible intervals).

precision by using the prior information was equivalent to adding 1 year of data in the mark–recapture analysis. Thus, using prior information derived from body mass is a very inexpensive way of adding precision to the study relative to conducting further data collection. In this example, the prior information was worth between 1 and 5 years of field data.

## Discussion

The two examples used in this study illustrate that the use of prior information can help to increase the confidence in conclusions drawn from ecological studies. In the case of the mulgara, the fact that the experimental effects of spinifex removal were entirely consistent with the previous observational study meant that we could be more confident that harvesting of spinifex does in fact reduce the abundance of mulgara. In the case of the European dipper, the precision of the estimate of the annual survival rate was increased noticeably by using prior information from other bird species. The regression used in this study could be used to construct informative priors for any European passerine, and similar methods could be used to construct priors for other taxa and birds in other parts of the world.

In Bayesian analyses, the prior information and the data both influence the results. The contribution of the prior and the data to the posterior distribution depends on their relative precision, with the more precise of the two having the greatest effect. Because the prior and data both contribute to a Bayesian analysis, the prior needs to be constructed with the same care and logic as required when collecting data, if the results are to be acceptable to the scientific community rather than simply reflecting a single person's belief (Dennis 1996). We have achieved this care and logic by using formal and repeatable methods for constructing the priors.

The value of the prior can be expressed in terms of the equivalent sample size ( $n$ ), with the prior information in the European dipper example being equivalent to between 1 and 5 years of data. In the mulgara example, the standard deviation of the informative prior for the effect of the experiment (0.23) is approximately half that obtained when using only the data from the five pairs of sites (0.51). Therefore, the prior is worth approximately 20 ( $52^2$ ) extra sites because the standard deviation of an estimate is approximately proportional to  $1/\sqrt{n}$ . Given costs associated with collecting field data and the need for obtaining results quickly in applied ecology problems, these savings in time and money that are provided by prior information are likely to be substantial.

Given the importance of the prior, an obvious question is what if a misleading prior was used in a Bayesian analysis? If the prior is inconsistent with the data, then the fit of the model will be reduced and the DIC value will be inflated. For example, assume that, by some strange turn of events, the observational study of mulgara had suggested that the capture rate was actually

increased by removal of spinifex, with the estimated effect having the same level of precision. In this case, the model with the uninformative prior would have generated a DIC value of 71.4 for the experimental study, which is substantially greater ( $> 8$  DIC units) than that for the model with no effect and the model with an uncertain effect (Table 1). Therefore, we would have concluded that the model of no effect or some other effect would have been better descriptions of the data than the model with the misleading prior. The conclusion would have been that the observational data were inconsistent with the experimental data. Fortunately, for the sake of consistency, this was not the case.

The possible effect of a misleading prior in the mark–recapture analysis can also be considered. Let us assume that a prior for the survival rate had the same standard deviation as obtained from the regression (0.075) but with a mean of 0.75 (instead of 0.57). This might arise, for example, if data from Australian passerines had been used, which tend to have higher survival rates than their northern hemisphere counterparts (Rowley & Russell 1991; Yom-Tov, McCleery & Purchase 1992). The DIC for this prior is 345.1, which is only marginally greater (0.8) than the model with an uninformative prior. We would conclude that it is difficult to be sure if the predictions of the model with the uninformative prior are better than the model with the informative prior. This is because the prior is relatively vague and somewhat consistent with the data, which means the DIC values are dominated by the data. However, even in this case, we would not be led too far astray. Because the data have an overwhelmingly large influence on the posterior estimate of annual survival, the posteriors derived from the two models are quite similar (mean of 0.59 vs. 0.55).

An alternative prior distribution for the annual survival rate of the European dipper could have been established by assuming that the instantaneous mortality rate scales as a power function of body mass with an exponent of  $-0.25$  (Savage *et al.* 2004). A regression of survival on body mass could be conducted using this specific assumption to develop a different prior. However, it would have yielded only a slightly different result; the prior distribution under this assumption would have the same mean (0.57) and a slightly smaller standard deviation (0.066, analysis not shown) as used in the current study. However, with further refinement and testing of allometric relationships, they are likely to be very useful in helping determine prior distributions for life-history traits.

The predictions of ecological theories and models are rarely precise. These predictions cannot be assessed with frequentist methods without ignoring the uncertainty associated with them. Null hypothesis tests are limited to assessment of point or one-sided predictions. Likelihood-based methods are also limited to assessment of point hypotheses. For example, a model with a specified value for a parameter can be analysed and compared with a model in which the parameter is free

to vary, but it is not possible to evaluate models that have imprecise predictions for parameters. Bayesian statistics can evaluate such probabilistic predictions, making them particularly useful in ecology where predictions can rarely be made with complete certainty.

Linacre *et al.* (2004) advocated using actuarial methods to include prior information in risk assessments for conservation biology. These methods have arisen in the field of economics and are based on various approximations (e.g. linearity). The example used in their study involved estimation of the survival rate of an owl using data from other owl species. Such an analysis is somewhat similar to that for the European dipper. However, the example in our study demonstrates that a conventional Bayesian analysis can accommodate the 'collateral' data available from other species while accounting for the ecological principle that, on average, the survival rate of animal species increases with body mass. By using MCMC methods, it is possible to include arbitrarily complex statistical models in the Bayesian analysis rather than relying on linear approximations.

The main quantitative method of synthesis using frequentist statistics is meta-analysis. One of the main methods of meta-analysis, based on the estimation of effect size, constructs an estimate and standard error from weighted averages of the individual study. The weights used are equal to the inverse of the standard error squared (Gurevitch & Hedges 2001), making the method numerically identical to calculation of the Bayesian posterior distribution based on data and a prior that both have normal distributions. Therefore, both Bayesian methods that use information from previous studies and formal methods of meta-analysis in a frequentist framework will tend to produce parameter estimates that are numerically equivalent. The main advantage of Bayesian methods over conventional meta-analysis is that there is no need to rely on normal approximations, with it being possible to consider almost any statistical model.

Some of the problems encountered when using meta-analysis (Gurevitch & Hedges 2001) will also cause difficulties when constructing priors for Bayesian analyses. The most important problems are likely to be that the published literature may be a biased sample of all possible results (the 'file drawer problem') and that effect sizes and measures of precision often remain unreported in ecological studies (Anderson, Burnham & Thompson 2000; Gurevitch & Hedges 2001; Fidler *et al.* 2004). These problems can at least be partially overcome by authors and editors placing a greater emphasis on reporting effect sizes that are accompanied by appropriate measures of precision (Fidler *et al.* 2004).

The use of prior information is one of the most controversial aspects of Bayesian statistics, especially when the prior distribution reflects subjective belief (Dennis 1996). Dennis (1996) expresses concern that science should aim to reduce subjectivity rather than propagating its influence throughout an analysis of data. In

this study, we show that prior information in ecology can be used without undue reliance on subjective judgement. Nevertheless, subjective treatments of prior information remain useful for characterizing agreement and disagreement among different parties and determining how data can be used to resolve differences (Crome, Thomas & Moore 1996; Martin *et al.* 2005). Further, by using measures such as DIC, it is possible to evaluate how well different priors correspond to the data, thereby providing an objective measure of their reliability.

There are numerous papers and books that describe the 'pros and cons' of using Bayesian and other statistical methods in ecology (Dennis 1996; Wade 2000; Burnham & Anderson 2002; Ellison 2004; Stephens *et al.* 2005). It is not our intention to expand on these discussions in detail, but to show how prior information can be used in ecology. In this spirit we agree with Dennis (1996) who, in cautioning against the use of Bayesian methods, advocated that science should aim to reduce the influence of subjectivity. We suggest that by using as much care and logic in the construction of priors as is used to collect the data, and by evaluating the consistency of the data and prior, Bayesian statistics can be used to help reduce uncertainty in ecology.

Applied ecologists often have prior information at their disposal when predicting impacts or determining parameters for ecological models. In this study, we have shown that body mass can be used to make useful predictions of annual survival of European passerines. This parameter and others relevant to population dynamics of vertebrates are important for models that are used to predict extinction risk and effects of management. Our study also shows that results of observational studies can provide useful prior information for experiments that assess impacts of changes in habitats. By using Bayesian methods, prior information, if represented in a transparent, coherent and logical way, can be cost-effective for adding certainty to ecological studies.

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## Supplementary material

The following supplementary material is available for this article online.

**Appendix S1.** The WinBUGS code for the models used in this study. The code and data (the latter are not shown to save space) are available at <http://www.nceas.ucsb.edu/~mccarthy/research.html>.