

# Ecologically realistic estimates of maximum population growth using informed Bayesian priors

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## Summary

1. Phenomenological density-feedback models estimate parameters such as carrying capacity ( $K$ ) and maximum population growth rate ( $r_m$ ) from time series of abundances. However, most series represent fluctuations around  $K$  without extending to low abundances and are thus uninformative about  $r_m$ .
2. We used informative prior distributions of maximum population growth rate,  $p(r_m)$ , to estimate Bayesian posterior distributions in Ricker and  $\theta$ -logistic models fitted to abundance series for 36 mammal species. We also used state-space models to account for observation errors.
3. We used two data sets of population growth rates from different mammal species with associated allometry (body mass) and demography (age at first reproduction) data to predict  $r_m$  prior distributions.
4. We assessed patterns of differences in posterior means ( $\bar{r}_m$ ) from models fitted with and without informative priors and used the deviance information criterion (DIC) to rank models for each species.
5. Differences in posterior  $\bar{r}_m$  from models with informative vs. vague priors co-varied with the prior mean ( $\hat{r}_m$ ) for Ricker models, but only posterior  $\bar{\theta}$  co-varied with prior  $\hat{r}_m$  in  $\theta$ -logistic models. Informative-prior Ricker models ranked higher than (81% of species), or equivalent to (all species), those with vague priors, which decreased to 70% ranking higher for state-space models. Prior information also improved the precision of  $\bar{r}_m$  by 13–45% depending on model and prior.
6. Posterior  $\bar{r}_m$  were highly sensitive to  $\hat{r}_m$  priors for  $\theta$ -logistic models (halving and doubling prior mean gave –56% and 95% changes in  $\bar{r}_m$ , respectively) and less sensitive for Ricker models (–25% and 35% changes in  $\bar{r}_m$ ).
7. Our results show that fitting density-feedback models without prior information gives biologically unrealistic  $\bar{r}_m$  estimates in most cases, even from simple Ricker models. However, sensitivity analysis shows that high  $r_m - \theta$  correlation in  $\theta$ -logistic models means the fit is largely determined by the prior, precluding the use of this model for most census data. Our findings are supported by applying models to simulated time series of abundance. Prior knowledge of species' life history can provide more ecologically realistic estimates (matching theoretical predictions) of regulatory dynamics even in the absence of detailed demographic data, thereby potentially improving predictions of extinction risk.

**Key-words:** density dependence, measurement error, population dynamics, Ricker, state-space, theta-logistic

## Introduction

Mathematical models of the dynamics of density feedback based on abundance time series, including the Ricker, Gompertz and  $\theta$ -logistic, give a functional form to the relationship between sequential population size estimates under the constraints of maximum growth rate and environmental carrying capacity. The estimated strength and type of density feedback arising from these phenomenological models influence projections of population viability and sustainable yield targets in planned conservation and management interventions, such as the proportional annual harvest that would lead to

extinction (Holmes *et al.* 2007; Hone, Duncan & Forsyth 2010). Estimates of the growth response of individual populations are obtained from fitting stochastic models of density feedback. However, these models fitted to abundance data often give biased (Lande *et al.* 2002; Freckleton *et al.* 2006), imprecise and ecologically unrealistic (Polansky *et al.* 2009; Clark *et al.* 2010) estimates of growth response parameters.

Bayesian statistical methods provide an explicit means of using prior knowledge to inform the estimation of the parameters of ecological models (Clark 2007; McCarthy 2007). Such information is incorporated into the estimation process by specifying prior distributions for model parameters which weight the likelihood function to generate posterior distributions and can improve the precision of the estimates (McCarthy & Masters 2005). As an example, allometric and

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demographic predictions of ecological rates can be used within a Bayesian setting as independent, *a priori* distributions. McCarthy, Citroen & McCall (2008) showed that estimated allometric scaling exponents for birds and mammals conform to theoretical predictions and used the corresponding estimates as Bayesian priors to refine estimates of survival rate.

In population dynamics, the stochastic Ricker model (Ricker 1975) predicts the population size  $N$  (or an index thereof) at time  $t$  as a function of the population size at the preceding time, the maximum rate of population increase  $r_m$  and the population carrying capacity  $K$ . Taking  $Y_t = \log(N_t)$ , the model is given as follows:

$$Y_t = Y_{t-1} + r_m(1 - (N_{t-1}/K)) + \varepsilon_{t-1} \quad \text{eqn 1}$$

where  $\varepsilon_{t-1}$  is the process (or environmental) variance (a Gaussian-distributed random variable with mean 0 and variance  $\sigma^2$ ). This model can be generalised to account for a nonlinear growth response to changes in population size by adding a shape parameter  $\theta$ :

$$Y_t = Y_{t-1} + r_m(1 - (N_{t-1}/K)^\theta) + \varepsilon_{t-1} \quad \text{eqn 2}$$

where the growth response, or return tendency, is then represented jointly by the product of  $r_m$  and  $\theta$  (Saether *et al.* 2008; Clark *et al.* 2010); setting  $\theta = 1$  gives the Ricker model (see Fig. 1a in Clark *et al.* 2010).

These models can be further generalised to account for sampling errors in the measurement of population size, which is likely to exist in most real-world monitoring situations and can bias parameter estimates (Shenk, White & Burnham 1998; Freckleton *et al.* 2006). State-space time-series models can incorporate both observation and process error (de Valpine & Hastings 2002; de Valpine 2003; Clark & Bjornstad 2004). Here, recorded population sizes are assumed to represent an unobserved 'true population state' plus random errors. Process error represents the stochastic model of temporal variation in the unobserved state variable. de Valpine & Hastings (2002) showed that state-space estimation in linear, Gaussian-distributed models accounting for process and observation error performed better in recovering the simulated parameters than models that ignored either process or observation error.

The state-space formulation of the Ricker model for log-transformed observed population size at time  $t$ ,  $\log(N_t) = Y_t$ , can be given as:

$$\begin{aligned} X_t &= X_{t-1} + r_m(1 - (e^{X_{t-1}}/K)) + \varepsilon_{t-1} \\ Y_t &= X_t + v_t \end{aligned} \quad \text{eqn 3}$$

where  $Y_t$  is equal to the unknown 'true' population state  $X_t$  plus random observation (i.e. measurement) error  $v_t$ , which can be, for example, Gaussian- or Poisson-distributed. The unknown population state  $X_t$  propagates through time via a Ricker model that depends on  $r_m$ ,  $K$  and random process (e.g. environmental) error  $\varepsilon_{t-1}$ , which is usually assumed to follow a Gaussian distribution with mean 0 and process variance  $\sigma^2$ . Calder *et al.* (2003) used Gibbs sampling to fit a Ricker state-space model (as a linear model on the raw abundance scale);

however, the Bayesian framework also allows nonlinear functional forms of density feedback (Wang 2007) and non-Gaussian probability density functions. State-space approaches have been used previously to model the dynamics of mammal populations (Zeng *et al.* 1998; Wang *et al.* 2006), including using Bayesian estimation (Clark & Bjornstad 2004). Bayesian fitting of these models requires specification of prior distributions for all model parameters, including the initial population state  $X_0$  (Calder *et al.* 2003).

Predicting  $r_m$  and  $K$  from the  $\theta$ -logistic model, however, gives biased and imprecise estimates because of the inherent trade-off between  $r_m$  and  $\theta$  (Polansky *et al.* 2009; Clark *et al.* 2010), particularly where population abundance fluctuates around  $K$  and thus contains little information about the true value of  $r_m$ . Hence, one option is to 'fix' the  $r_m$  parameter (Saether, Engen & Matthysen 2002) to reduce the negative correlation between  $r_m$  and  $\theta$  which, without some independent knowledge of at least one, tends to make estimates of both parameters ecologically meaningless (Clark *et al.* 2010). The  $r_m$  parameter represents the capacity of a population to grow under conditions where resources are not limiting and competition is negligible (Sibly & Hone 2002; Savage *et al.* 2004a), such that survival and reproduction are maximal. Thus, it can be estimated directly from demographic data using population matrix models parameterised with maximum vital rates (Caswell 2001), or observed abundance counts from populations at low abundance and where survival and reproduction are maximal using the Lotka–Euler equation (Kot 2001). When detailed demographic data are unavailable, a simplified, two-stage version of Cole's equation (Cole 1954) using annual fecundity, age at first reproduction and reproductive life span (and assuming survival probability = 1) can also be used to estimate  $r_m$ , although this approach can overestimate it (Fagan, Lynch & Noon 2010).

Theoretical relationships between a species' life history and rates of population growth can also be used to estimate  $r_m$ . There are several examples where allometric relationships to predict  $r_m$  have been fitted to data sets on mammals and other taxa (Fenchel 1974; Caughley & Krebs 1983; Hennemann 1983; Thompson 1987; Sinclair 1996; McCallum, Kikkawa & Catterall 2000; Duncan, Forsyth & Hone 2007). These theoretical relationships provide the basis for the allometry of interspecific variation in  $r_m$  (Savage *et al.* 2004b), although phylogenetic differences should ideally be incorporated into predictive models (Duncan, Forsyth & Hone 2007). Hone, Duncan & Forsyth (2010) showed for mammals that Cole's equation accurately predicts field-based estimates of  $r_m$ ; estimated from age at first reproduction ( $\alpha$ ),  $r_m$  estimates match theoretical predictions (slope = -1) of the  $(\log_{10} - \log_{10}) r_m - \alpha$  relationship. The theoretical slope of -1 is derived from a rearrangement of the simplified Cole's equation where survival in all age classes is fixed at 1 (Duncan, Forsyth & Hone 2007). Hone, Duncan & Forsyth (2010) recommend using predictions of  $r_m$  from  $\alpha$  over those estimated from allometric relationships based on body mass because the former is independent of phylogeny (Duncan, Forsyth & Hone 2007).

We used two data sets of population growth rates with associated allometry (body mass; 44 species) and demography (age at first reproduction; 64 species) variables to develop predictive models of maximum population growth. To assess the usefulness of this prior information, we used these independent prior distributions for  $r_m$  in a Bayesian framework to estimate posterior distributions of the parameters in the Ricker and  $\theta$ -logistic models fitted to population time series for 36 mammal species. While Bayesian state-space models that account for observation error in the abundance counts have been used previously to investigate the dynamics of mammal populations, ours is the first to incorporate independent prior information about maximum population growth (including uncertainty) into the estimation of density-feedback model parameters. We hypothesised that accurate prior information would give rise to more biologically realistic estimates of maximum population growth for both models, so we compared posterior estimates from informative prior models with those from uninformative (vague) prior models. Additionally, we simulated abundance series from Ricker and  $\theta$ -logistic models with known parameter values and refitted models to these data to assess the characteristics of time series that resulted in biased estimates of  $r_m$ .

We also hypothesised that posterior estimates of  $r_m$  would be sensitive to incorrect (i.e. unrealistic) prior information and were interested in how much the priors affected posteriors for each model. For example, we expected the prior to dominate the posterior for the  $\theta$ -logistic model based on previous research showing high correlation between the  $r_m$  and  $\theta$  estimates and the generally flat likelihood for this model (Polansky *et al.* 2009; Clark *et al.* 2010). Therefore, we assessed relative changes in posterior means from specifying incorrect relative to correct priors as a measure of how much (or little) information was contained in the data about the  $r_m$  parameter.

## Materials and methods

### DERIVATION OF INDEPENDENT PRIOR INFORMATION ON $R_M$

We used estimates of  $r_m$  and body mass (kg) for 44 mammal species from 13 taxonomic orders reported in Hennemann (1983) to develop an allometric scaling model to predict  $r_m$  from body mass. The  $r_m$  estimates used by Hennemann (1983) were calculated using the Cole's equation (Cole 1954). We fitted a linear mixed-effects model to predict  $\log_{10}(r_m)$  from  $\log_{10}(\text{mass})$  and included a random effect for taxonomic order, to account for possible intercept differences associated with phylogeny (Blackburn & Duncan 2001; Duncan, Forsyth & Hone 2007). There was high correlation between observed and predicted  $r_m$  values from this model ( $\rho = 0.79$ ; model residual diagnostics are provided in Data S1 and S2).

We compared the predicted mean of the prior distribution, hereafter denoted  $\hat{r}_m$ , from the model above with those from an allometry model (derived using the estimation approach outlined above) based on  $r_m$  estimates calculated by Pereira & Daily (2006; as recommended by Fagan, Lynch & Noon 2010). The  $\hat{r}_m$  predictions from models that used  $r_m$  calculated with the Cole's equation were higher than those from models using the Pereira & Daily (2006) method; however, the

differences were well within the 95% prediction intervals of  $\hat{r}_m$ , so no bias in posterior parameter estimates was expected (see Fig. S1). Therefore, given the restricted geographical range of the species used to derive the Pereira & Daily (2006)  $r_m$  estimates, we instead used those estimates from Hennemann (1983) as outlined above to ensure more generalised predictions.

Following the recommendation of Hone, Duncan & Forsyth (2010) regarding the preferred use of  $\hat{r}_m$  predictions from age at first reproduction over those estimated from allometric relationships, we also used 98 recorded values of  $r_m$  and the age at first reproduction ( $x$ ; in years) from 64 mammal species from 10 taxonomic orders, as reported in Duncan, Forsyth & Hone (2007), to develop a model to predict  $\hat{r}_m$  from  $x$ . The  $r_m$  values were, in this method, estimated from observed counts by modelling the trend in  $\log_{10}$  abundance (Eberhardt, Simmons & Press 1992). We fitted a linear mixed-effects model to predict  $\log_{10}(\hat{r}_m)$  from  $\log_{10}(x)$  and included a random intercept effect for taxonomic order to account for phylogenetic differences (Duncan, Forsyth & Hone 2007; although these turned out to be small, see Results). Some species had multiple field estimates of  $r_m$ , so we also included a random intercept effect in the model to account for among-species differences. There was high correlation between observed and predicted  $r_m$  values from this model ( $\rho = 0.99$ ; model residual diagnostics are provided in Data S1 and S2).

### TIME SERIES OF MAMMAL ABUNDANCE

To assess the effect of incorporating prior knowledge of  $r_m$  determined from the models described previously, we fitted Ricker and  $\theta$ -logistic models to the abundance time series of 36 mammal species extracted from a set of 99 high-quality series identified in Clark *et al.* (2010), which were in turn a subset of 1198 time series (all taxa) used in Brook & Bradshaw (2006). The 36 mammal species represented the orders rodentia, carnivora, lagomorpha, artiodactyla and sirenina, and ranged between 0.02 and 750 kg in body mass and 0.33 to 5 years for age at first reproduction (see Table S1). The filtering criteria retained series with >18 transitions and excluded those with long series of low counts and those which included duplicate series from multiple species in the same study (Clark *et al.* 2010). We also excluded abundance values outside a 10-fold range of abundance and those series with many missing values (Clark *et al.* 2010).

We used the models described previously to predict  $r_m$  from the mean body mass and age at first reproduction of the 36 mammal species. We calculated prediction variance by accounting for both between-order and residual sources of variation for the allometry case and also incorporated the sum of the variance among taxa and among species for the demography case. We used the mean and variance of the allometry and demography predictions for each species to parameterise Gaussian prior distributions for  $r_m$ ,  $p(r_m)$ , in Bayesian formulations of the Ricker and  $\theta$ -logistic models.

### ESTIMATING MODEL PARAMETERS USING VAGUE AND INFORMATIVE PRIORS

We fitted the Ricker and  $\theta$ -logistic models under a Bayesian framework using Markov chain Monte Carlo (MCMC) simulation. We first modelled the log population abundance  $Y_t = \log(N_t)$  using process error-only Ricker and  $\theta$ -logistic models that assumed the process variance ( $\varepsilon$ ) was Gaussian-distributed with mean 0 and variance  $\sigma^2$  (eqns 1 and 2). We also fitted hierarchical state-space Ricker (SS-Ricker) and  $\theta$ -logistic (SS- $\theta$ -logistic) models that assumed the same process variance ( $\varepsilon$ ) as above for the underlying 'true' population state  $X_t$  (eqn 3). Observation

errors were modelled as a log-Gaussian distribution and hence Gaussian on the log scale (eqn 3). A small number (< 2%) of missing observations in some time series were imputed using linear interpolation (values before and after the missing value are joined linearly).

We fitted the Ricker and  $\theta$ -logistic models, and the state-space SS-Ricker and SS- $\theta$ -logistic models, to each species. For model fitting, we ran each MCMC chain for 100 000 iterations with an initial burn-in of 2000 iterations and thinned chains by retaining parameter values from every 10th iteration to reduce the influence of any autocorrelation. We used the resulting 9800 values of each model parameter to generate posterior distributions. In an attempt to minimise the time to convergence of the MCMC chains, we set initial parameter values using the maximum likelihood estimates from the Ricker model (an initial  $\theta = 1$  was used for the  $\theta$ -logistic model). We ran two chains with different initial values (i.e. perturbed maximum likelihood estimate values) to ensure adequate mixing and that posterior distributions were independent of starting values (results not shown). We assessed convergence to a stationary distribution using Geweke scores (Geweke 1992) and by visual inspection of the traces retained (after burn-in and thinning) for each model parameter to ensure adequate mixing. We summarised posterior distributions of the unknown parameters by their means and standard deviations; the mean of the posterior distribution is hereafter denoted  $\bar{r}_m$ .

We fitted Bayesian models using the adaptive random walk Metropolis-Hastings algorithm (Metropolis *et al.* 1953; Hastings 1970) for MCMC sampling as implemented in PyMC 2.1 (Patil, Huard & Fonnesbeck 2010; <http://pypi.python.org/pypi/pymc>). In this implementation, new parameter values are proposed according to a random walk at each iteration of the algorithm, and the scale of the proposal distribution is adapted according to the recent acceptance probability for each parameter. We used an adaptive Metropolis step method that block updated variables using a multivariate Gaussian covariance matrix to sample jointly the  $r_m$  and  $\theta$  parameters of the  $\theta$ -logistic models; this approach accounted for the correlation between these parameters in model fitting. Our approach is an implementation of the adaptive algorithms proposed by Wang (2007). We also used the adaptive Metropolis algorithm to sample the correlated 'population state' variables in the state-space models. We summarised sampling chains and did all other analyses using R-2.12.1 (R Core Development Team 2011; [www.r-project.org](http://www.r-project.org)). Example code for fitting the Ricker state-space model in PyMC and OPENBUGS is provided in the Data S2.

We specified uninformative uniform prior estimates for the  $r_m$ ,  $\theta$  and  $K$  parameters, although these were better described as weakly informative or 'vague' priors because they had a lower bound of zero, and the upper limit for the prior on  $K$  was set as the maximum observed  $N_t$  in the time series. We arbitrarily set the upper limit of the  $r_m$  and  $\theta$  uniform priors to 20, although exploratory analyses showed posterior  $\bar{r}_m$  were insensitive to variation of this upper bound over a wide range (results not shown).

We specified an informative prior distribution  $p(r_m)$  for each species using a Gaussian distribution with mean equal to the allometric or demographic prediction of  $\hat{r}_m$  and the precision of the distribution equal to the inverse of the  $\hat{r}_m$  prediction variance described previously. We compared two prior distributions for the observation and process standard deviation parameters: (i) an uninformative uniform prior (0, 10) as suggested for variance components by Gelman (2006) and (ii) an uninformative inverse gamma prior ( $a = 0.001$ ,  $b = 0.001$ ). The estimated process standard deviation was insensitive to the choice of prior, so we present only results based on the inverse gamma prior.

We used the deviance information criterion (DIC; Spiegelhalter *et al.* 2002) to compare the bias-corrected explanatory power of models

fitted using MCMC. Specifically, we used DIC to compare models using vague priors with those based on informative priors, and between models using different informative priors, to assess whether prior information improved model fit or which prior prediction was more consistent with the data. Informative prior distributions reduce the effective number of parameters and model complexity (Spiegelhalter *et al.* 2002) such that DIC will be lower if prior distributions do not reduce model fit (McCarthy & Masters 2005). We assessed the DIC assumption of multivariate normality of the joint posterior distribution of the unknown parameters (Spiegelhalter *et al.* 2002) by visual inspection of the bivariate posterior densities of the parameter MCMC traces (see Figs S22–S24).

## SIMULATIONS TO DEMONSTRATE EFFECTS OF USING INFORMATIVE PRIORS

To assess further the influence of prior information about  $r_m$  on model parameter estimates, we simulated abundance time series using the Ricker model with known  $r_m$  values and log-Gaussian errors. We simulated 30 time series of length 25 with each combination of low (0.2) and high (1.5)  $r_m$  and low (0.05) or high (0.3) standard deviation of log abundance. The standard deviation values represent low and high variation observed for the real abundance series used above. In all cases, we set  $K = 100$ .

Similarly, we simulated abundance series under the  $\theta$ -logistic model (again, with log-Gaussian errors) using all four combinations of  $r_m = 0.2$  or 1.5 (consistent with the Ricker model simulations) and  $\theta = 0.5, 1.5$  (corresponding to species with low and high threshold-density feedback responses, respectively). We simulated data for these  $r_m - \theta$  combinations under either low (0.05) or high (0.3) standard deviation of log abundances as above.

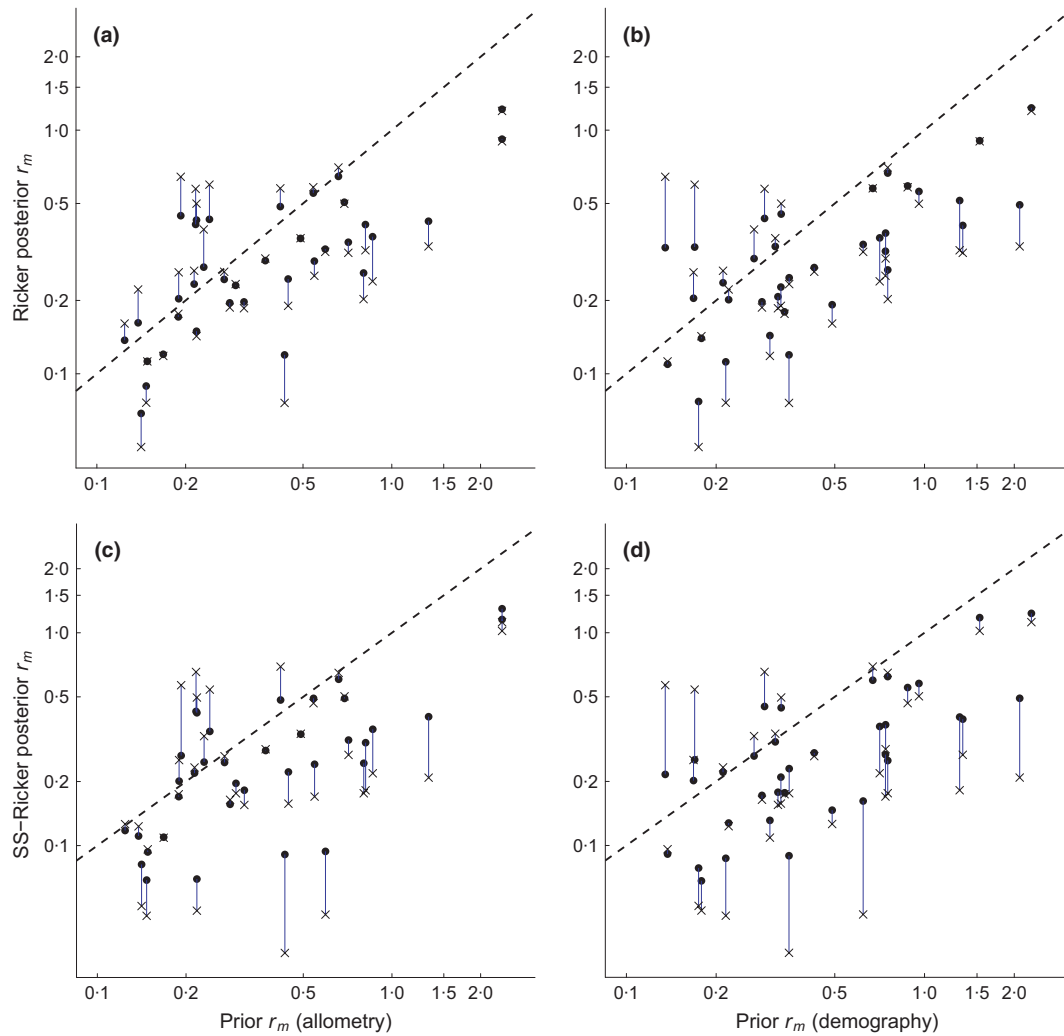
We then refitted the Ricker and  $\theta$ -logistic model assuming log-Gaussian errors to each time series generated under the same model specifying either vague or informative priors for the  $r_m$  parameter. We used a uniform distribution (over the interval 0–20) for the vague prior. We used a Gaussian informative prior with mean equal to the generating value of  $r_m$  in the simulations and standard deviation equal to 10% of the generating value.

To examine the influence of assuming an incorrect form for the probability density of the modelled errors, we also simulated 30 abundance time series from the Ricker model with errors drawn from the negative binomial distribution for each combination of low (0.2) and high (1.5)  $r_m$  and low (10) and high (50)  $k$  (lower  $k$  represents greater overdispersion). For the abundance series simulated from the negative binomial distribution, we refitted Ricker models assuming the same error distribution and models assuming log-Gaussian errors and compared the results of using vague and informative priors to the estimated  $r_m$  values. The main simulation results are presented as Data S1 and S2.

## Results

### INFORMATIVE PRIORS BASED ON ALLOMETRY AND DEMOGRAPHY

Differences in posterior  $\bar{r}_m$  from using an informative vs. a vague prior depended on the value of the prior  $\hat{r}_m$  itself (Fig. 1, Table 1a). For the Ricker model, larger  $\hat{r}_m$  priors increased posterior  $\bar{r}_m$  relative to a model using vague priors, whereas low  $\hat{r}_m$  priors decreased the posterior  $\bar{r}_m$  (Fig. 1a,b; Table 1a), and these results are supported by simulations



**Fig. 1.** Scatter plots of informed prior estimates of maximum population growth rate (prior  $r_m$ ) and model-estimated posterior  $\bar{r}_m$  (posterior  $r_m$ ) for 36 mammal species (filled circles; a–b Ricker model, c–d SS-Ricker state-space model). Informative prior distributions  $p(r_m)$  were predicted from independently derived relationships with body mass (allometry; a and c) and age at first reproduction (demography; b and d). The dashed line indicates a 1 : 1 relationship between the prior and posterior  $\bar{r}_m$ . Vertical lines show the change in  $\bar{r}_m$  estimated from a model with an uninformative (vague) prior (x) to  $\bar{r}_m$  estimated using an informed prior (filled circles). Due to some equal prior values of  $\hat{r}_m$  predicted from demography data, filled circles in the right column of plots were jittered a small amount in the x-space to aid visualisation.

**Table 1.** (a) Correlation between  $\hat{r}_m$  prior and difference between posteriors using vague and informative priors, and (b) per cent change in precision (CV, coefficient of variation) of posterior  $\bar{r}_m$  from using vague vs. informative priors for each model and type of prior. 95% confidence intervals are in parentheses

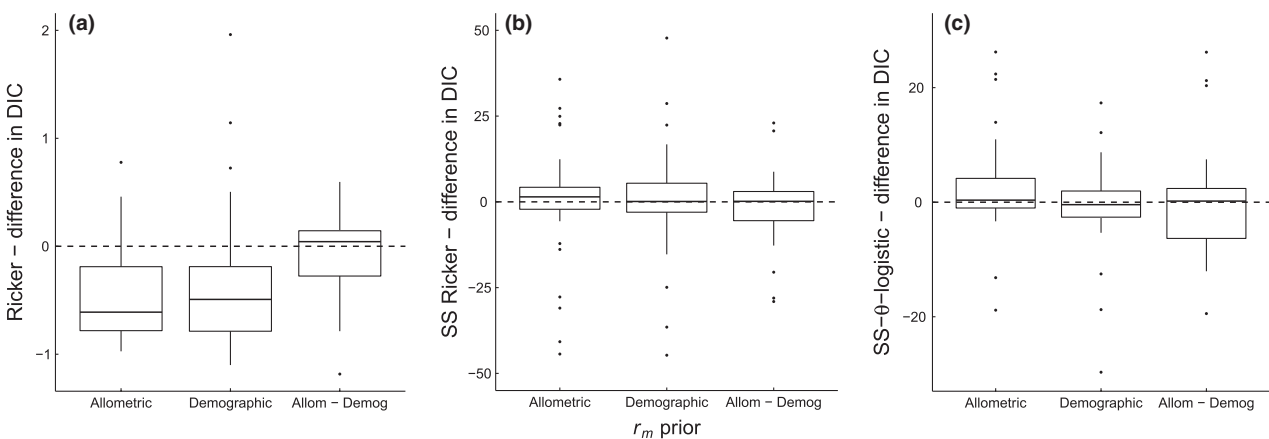
Parameter	Model	Prior type	(a) Correlation	(b) % difference in CV
$\bar{r}_m$	Ricker	Allometry	0.47 (0.17, 0.69)	12.9 (6.1, 19.8)
		Demography	0.62 (0.37, 0.79)	18.4 (9.6, 27.2)
	SS-Ricker	Allometry	0.55 (0.27, 0.75)	20.4 (12.7, 28.1)
		Demography	0.70 (0.48, 0.84)	26.1 (18.2, 34.0)
$\bar{\theta}$	$\theta$ -Logistic	Allometry	−0.24 (−0.52, 0.10)	31.4 (23.1, 39.7)
		Demography	−0.06 (−0.38, 0.27)	37.2 (29.8, 44.6)
	SS- $\theta$ -Logistic	Allometry	−0.01 (−0.34, 0.32)	44.0 (37.6, 50.5)
		Demography	0.18 (−0.15, 0.48)	45.1 (39.3, 50.9)
$\bar{\theta}$	$\theta$ -Logistic	Allometry	−0.42 (−0.66, −0.10)	27.8 (22.4, 33.2)
		Demography	−0.43 (−0.67, −0.12)	28.3 (21.6, 35.0)
	SS- $\theta$ -Logistic	Allometry	−0.31 (−0.58, 0.02)	23.4 (13.4, 33.3)
		Demography	−0.35 (−0.61, −0.03)	16.3 (4.9, 27.6)

(Fig. S4). A similar pattern was evident for posterior estimates from the SS-Ricker model (Fig. 1b,c; Table 1a). These results were consistent for both allometric and demographic predictions of  $\hat{r}_m$ . Under Bayes' rule, the joint posterior is proportional to the product of the prior and the likelihood. We compared the difference in  $\bar{r}_m$  from using an informative vs. a vague prior with the difference between the prior  $\hat{r}_m$  and the posterior  $\bar{r}_m$  from a model with vague priors. The difference in  $\bar{r}_m$  due to the alternative methods of generating priors was generally much smaller than the difference between the prior  $\hat{r}_m$  and the vague prior  $\bar{r}_m$  and was not correlated with the  $\hat{r}_m$  prior used, indicating that the prior was not dominating the modelled data (Fig. S16).

Both allometry and demography priors provided more parsimonious fit to the data for the Ricker model (81% of species; Fig. 2a), although the improvement was not substantial, given the DIC difference was within two units (i.e. the models were statistically indistinguishable). Simulations showed that informative-prior Ricker models were always ranked highest for abundance series with high standard deviation, but not for series with low standard deviation (Fig. S5), independent of the size of generating  $r_m$ . Neither the allometry- nor demography-based prior provided a consistently better fit across species (allometry was better in 47% of species; Fig. 2a). Differences in DIC between models with and without informative  $r_m$  priors were distributed around zero for the SS-Ricker models (Fig. 2b); the model using an informative prior gave a better or similar fit for 72% (allometry) and 70% (demography) of species. Generally, models using the demographic predictions of  $\hat{r}_m$  (and variance) as prior information gave an equivalent or better fit than those using the allometric predictions (64% of species; Fig. 2b). With the exception of the consistently lower DIC for informative-prior Ricker models relative to vague prior models, there were no obvious trends in DIC differences associated with the value of the prior (Fig. S14) for the other

models. For all species, the state-space models, which accounted for observation errors in the abundance counts, had higher support from the data (based on DIC) than single error-term models (Tables S2–S37). This indicates evidence for substantive variation associated with measurement errors in the abundance counts or poor model fit when these errors are ignored.

In general, the  $\theta$ -logistic model, when specified with vague priors, did not converge to a stable solution, due mainly to the previously noted high correlation between the  $r_m$  and  $\theta$  parameters (Clark *et al.* 2010). Therefore, comparing  $\theta$ -logistic parameter estimates from vague prior models with those using informative priors was not meaningful. In contrast, SS- $\theta$ -logistic models fitted to the data with only vague priors did converge. In these cases, the informative prior information did not consistently result in a better model (based on DIC), but the fit of models for 36% (allometry prior) and 53% (demography) of species was better than the vague prior models (Fig. 2c). Also, neither type of prior (i.e. allometry vs. demography) was consistently better than the other (demography prior better in 56% of species). The equivocal results for model improvement from using prior information in the SS- $\theta$ -logistic models might have been due in part to skewness in the marginal distributions of the  $r_m$  and  $\theta$  posteriors from the vague prior model fits (see Figs S22–S24), which violates the assumption of DIC that the joint posterior distribution be multivariate normal (Spiegelhalter *et al.* 2002), although this suggestion requires further examination. Under simulation, we showed that including informative priors increased precision of posterior  $r_m$  and (i) increased positive bias, but did not change the precision of posterior  $\theta$  when  $r_m$  was low, and (ii) negatively biased, but increased the precision of posterior  $\theta$  when  $r_m$  was high (Figs S6–S9). Despite this, the DIC consistently supported the vague prior models for both low- and high-



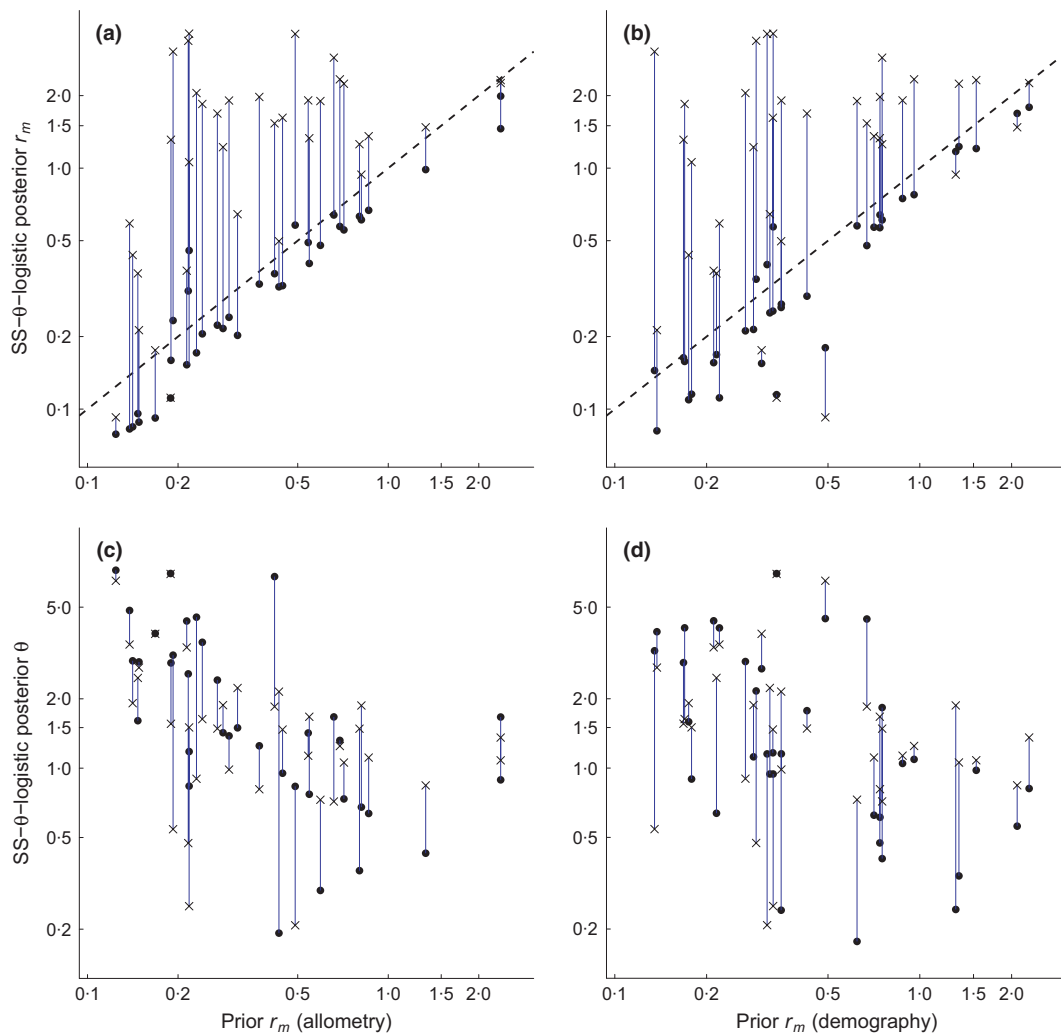
**Fig. 2.** Box plots of the distribution of differences in the deviance information criterion (DIC) between models using informative vs. uninformative (vague) prior distributions for  $r_m$  in the Ricker (a and b) and  $\theta$ -logistic (c) models. Plots b and c show results from Gaussian state-space (SS) models. Informative prior distributions  $p(r_m)$  were predicted from independently derived relationships with body mass (allometry) and age at first reproduction (demography), and DIC differences between models using these different prior predictions are also shown ('Allom-Demog'). Negative DIC differences indicate that the model using prior information gave a more parsimonious fit (except for the 'Allom-Demog' comparison where negative DIC indicated the demographic prior information gave a better fit). Horizontal dashed line indicates zero DIC difference (i.e. no net benefit of using an informative prior).

variance series, although the differences were much smaller for the high-variance case (Fig. S10).

In contrast to the Ricker model, differences in  $\bar{r}_m$  from using either allometry or demography priors in the  $\theta$ -logistic model were large and negative and were independent of the value of the prior for the SS- $\theta$ -logistic models (Fig. 3a,b; Table 1a). That is, the  $\theta$ -logistic model consistently overestimated  $\bar{r}_m$  relative to prior knowledge. The influence of the priors was also evident in the negative correlation between the  $\hat{r}_m$  prior and differences in posterior  $\bar{\theta}$  from using informative  $\hat{r}_m$  priors (Fig. 3; Table 1a; Fig. S17). Smaller  $\hat{r}_m$  priors tended to result in increases in  $\bar{\theta}$  (highest rate of density feedback occurs at relatively high population size), while larger priors were associated with decreases in  $\bar{\theta}$  (highest density feedback occurs at low population size; Fig. 3c, d; Table 1a).

#### CHANGES IN PRECISION OF $\bar{r}_m$

Informative prior information on  $r_m$  for the 36 mammal species we examined improved the precision of posterior  $\bar{r}_m$  by 13–18% for the Ricker model and by 20–26% for the SS-Ricker models (Table 1b; Fig. S3). Improvements in precision of  $\bar{r}_m$  from using demography priors were more marked than those using allometry priors for all models (Table 1b); precision was higher for 86% of species using the allometry prior and 89% of species using the demography prior. In addition to differences in  $\bar{\theta}$  in response to  $\hat{r}_m$  priors, the precision of  $\bar{\theta}$  also increased by 16–28% (Table 1b; Figs S8–S9). The coefficient of variation for  $\bar{r}_m$  was higher when estimated using the  $\theta$ -logistic model relative to the Ricker, indicating again the effect of the  $r_m - \theta$  correlation.



**Fig. 3.** Scatter plots of informed prior estimates of maximum population growth rate (prior  $r_m$ ) and model-estimated posterior  $\bar{r}_m$  (a–b) and posterior  $\bar{\theta}$  (c–d) for 36 mammal species (filled circles) using the SS- $\theta$ -logistic state-space model. Informative  $r_m$  priors were predicted from independently derived relationships with body mass (allometry) and age at first reproduction (demography). The dashed line indicates a 1 : 1 relationship between the  $\hat{r}_m$  prior and posterior  $\bar{r}_m$ . Vertical lines show the change in posterior ( $\bar{r}_m$  in a–b,  $\bar{\theta}$  in c–d) estimates from a model with an uninformative (vague) prior ( $\times$ ) to posteriors estimated using an informed prior (filled circles). Due to some equal prior values of  $r_m$  predicted from demography data, filled circles in the b and d were jittered a small amount in the  $x$ -space to aid visualisation. Posterior  $\bar{\theta}$  from models using informative priors  $p(r_m)$  were negatively related to the informative mean prior  $\hat{r}_m$ ; lower prior  $\hat{r}_m$  lead to increased posterior  $\bar{\theta}$ , whereas higher prior  $\hat{r}_m$  lead to decreased posterior  $\bar{\theta}$ .



**Table 2.** Sensitivity analysis results

Parameter	Model	Prior type	Prior	Proportional difference
$\bar{r}_m$	Ricker	Allometry	Half	0.78 (0.76, 0.81)
			Double	1.18 (1.15, 1.21)
		Demography	Half	0.77 (0.73, 0.81)
			Double	1.19 (1.16, 1.23)
	SS-Ricker	Allometry	Half	0.76 (0.72, 0.79)
			Double	1.33 (1.21, 1.46)
		Demography	Half	0.74 (0.71, 0.78)
			Double	1.38 (1.18, 1.61)
	$\theta$ -Logistic	Allometry	Half	0.60 (0.56, 0.63)
			Double	1.74 (1.64, 1.84)
		Demography	Half	0.58 (0.55, 0.62)
			Double	1.83 (1.76, 1.90)
SS- $\theta$ -Logistic	Allometry	Half	0.58 (0.54, 0.62)	
		Double	1.87 (1.75, 2.00)	
	Demography	Half	0.55 (0.52, 0.58)	
		Double	1.98 (1.87, 2.10)	
$\bar{\theta}$	$\theta$ -Logistic	Allometry	Half	1.50 (1.40, 1.60)
			Double	0.61 (0.58, 0.66)
		Demography	Half	1.56 (1.46, 1.67)
			Double	0.57 (0.53, 0.61)
	SS- $\theta$ -Logistic	Allometry	Half	1.55 (1.38, 1.73)
			Double	0.56 (0.48, 0.66)
		Demography	Half	1.68 (1.47, 1.92)
			Double	0.55 (0.47, 0.65)

Proportional differences in  $\bar{r}_m$  and  $\bar{\theta}$  estimates after halving and doubling the prior  $\hat{r}_m$  relative to estimates using the correct informative prior (from allometric or demographic predictions) for each model and type of prior. Proportional differences indicate the sensitivity of the posterior estimates to the prior; differences > 1 indicate the prior increased the posterior relative to estimates using the known informative prior, and differences < 1 indicate the prior decreased the posterior. 95% confidence intervals of the proportional differences in parameter estimates resulting from using informative priors are in parentheses.

The prior estimates of  $\hat{r}_m$  predicted from allometry and demography were, on average, less precise than the  $\bar{r}_m$  from the Ricker and SS-Ricker models based on vague priors (Table S38). However, the precisions of posterior  $\bar{r}_m$  from using informative priors were higher than from vague prior models. In contrast, the priors were more precise than the posterior  $\bar{r}_m$  estimates from the SS- $\theta$ -logistic fitted with vague priors (i.e. negative difference in precision; Table S38). For this model, using priors improved the precision of posterior  $\bar{r}_m$ , resulting in approximately equal precision to that of the prior (Table S38).

SENSITIVITY ANALYSIS OF  $\bar{r}_m$  TO THE PRIOR

To assess the sensitivity of  $\bar{r}_m$  to the values of the allometric and demographic priors used, we arbitrarily refitted all informative-prior models using mean  $\hat{r}_m$  priors both half the value of the original prior and double the value of the original prior. We then used these ‘deflated’ and ‘inflated’ priors to assess the bias in  $\bar{r}_m$  from using an incorrect prior for each species (the variance of the prior for each species was held constant in all cases). For the Ricker model and using either an allometry or

demography prior, halving the prior  $\hat{r}_m$  decreased posterior  $\bar{r}_m$  by about 22%, whereas doubling the prior increased posterior  $\bar{r}_m$  by about 18% (Table 2; Figs S18 and S19). The effects were slightly larger for the SS-Ricker model where halving the prior decreased  $\bar{r}_m$  by about 25% and doubling the prior increased  $\bar{r}_m$  by 35% on average (Table 2; Figs S18 and S19).

The  $\bar{r}_m$  estimate from the  $\theta$ -logistic model was substantially more sensitive to the magnitude of the prior than for the Ricker model. Using the  $\theta$ -logistic model, halving the prior decreased  $\bar{r}_m$  by about 41% and doubling the prior increased  $\bar{r}_m$  by 79%, whereas for the SS- $\theta$ -logistic model halving the prior decreased  $\bar{r}_m$  by about 56% and doubling the prior increased  $\bar{r}_m$  by 93% (Table 2; Figs S20 and S21). Thus, for the  $\theta$ -logistic models, halving or doubling the prior nearly halves or doubles posterior  $\bar{r}_m$ , such that the posteriors are almost completely determined by the prior itself. Given the relatively large prediction variance associated with our informative priors (see Table S1), these results show there is little information about  $r_m$  in the data when fitting a  $\theta$ -logistic model. Also, there is an inverse relationship between the factor differences in posterior  $\bar{r}_m$  and the factor differences in posterior  $\bar{\theta}$ , with halving and doubling the  $\hat{r}_m$  prior resulting in c. 55% increases and 40% decreases in posterior  $\bar{\theta}$ , respectively.

Discussion

The two approaches we used to predict  $\hat{r}_m$  – from allometry and demographic rates – both provided informative priors that generally improved model fit and increased the precision of  $\bar{r}_m$  for the Ricker model. For the  $\theta$ -logistic model,  $\bar{r}_m$  were generally overestimated in the absence of prior information; however, sensitivity analysis showed that  $\bar{r}_m$  was almost entirely determined by the prior. The high  $r_m - \theta$  correlation (Saether *et al.* 2008; Polansky *et al.* 2009; Clark *et al.* 2010) means that the prior also constrains  $\bar{\theta}$ . These results suggest that, where available, prior knowledge of the estimated maximum rate of population increase should be incorporated into density-feedback models, but that their effects on posterior estimates should be carefully assessed (especially for full  $\theta$ -logistic predictions). For census data that are uninformative about  $r_m$  (e.g. where population sizes in a time series do not extend to low numbers relative to  $K$ ), there are many possible combinations of Ricker model parameters that will fit the time series almost equally well, and the  $r_m - \theta$  correlation makes this problem much worse for the  $\theta$ -logistic model. We have shown that independent prior distributions informed by demographic data can provide estimates of  $\bar{r}_m$  from phenomenological models that are consistent with life-history expectations, a result aligned with previous studies in fisheries (Myers, Bowen & Barrowman 1999; McAllister, Pikitch & Babcock 2001). In contrast to simply (and arbitrarily) fixing the value of  $r_m$  in the fitted model (Saether *et al.* 2008) to constrain the estimates of other model parameters (e.g.  $K$  and  $\theta$ ) based on the mean prior  $\hat{r}_m$ , Bayesian priors are preferable because they incorporate uncertainty in the prior information explicitly and directly into the analysis, and the resulting posterior distributions provide estimates of precision. Simple parameter fixing cannot achieve this.



The direction of the effect of informative priors on posterior  $\bar{r}_m$  from Ricker models were consistent with that expected under the 'slow-fast' life-history gradient that scales with body size. That is, lower  $\bar{r}_m$  are predicted for larger, slower-breeding species. Such predictions have been used to justify the application of the nonlinear  $\theta$ -logistic model (Gilpin & Ayala 1973) for explaining density feedbacks; organisms with slower life histories should be unaffected by density feedbacks below some threshold abundance and beyond which they become influential, whereas faster species should respond quickly to small increases in competition through increased abundance, with relatively less influence as carrying capacity is approached or exceeded. Our results showed that  $\bar{r}_m$  from the Ricker model without informative priors were underestimated for species with higher prior  $\hat{r}_m$  and overestimated for species with lower prior  $\hat{r}_m$ . Thus, the direction of change in  $\bar{r}_m$  from using prior information was consistent with expectations from life-history theory.

Models fitted to data that are uninformative about  $r_m$  also produce highly imprecise parameter estimates (Clark *et al.* 2010). Despite the high variance associated with the  $\hat{r}_m$  priors used in this study, the prior information substantially improved the precision and ecological realism (in terms of agreement with theory) of parameter estimates. More precise prior information, relative to the amount of information in the data about a parameter, will have a greater contribution to the posterior estimate of any parameter (McCarthy & Masters 2005). The allometric and demographic  $\hat{r}_m$  priors we used were predictions from mixed-effects models for new species where only the body mass or age at first reproduction was assumed known. Thus, the prediction variances incorporated uncertainties arising from both parameter estimation and stochastic variation associated with the random terms in the model. For allometric  $\hat{r}_m$  predictions, between-order and residual between-species variation were the random effects contributing to the variance of predictions. Because we had multiple field-based values of  $r_m$  from the same species used to predict  $\hat{r}_m$  from age at first reproduction (Duncan, Forsyth & Hone 2007), predictions from that model included an additional component of within-species variation (Hone, Duncan & Forsyth 2010). Consequently, prediction intervals around these  $\hat{r}_m$  priors were large, and so caution is recommended for their use in management decision making (Hone, Duncan & Forsyth 2010). We expect further improvements in the precision (and therefore accuracy) of  $\bar{r}_m$  from the Ricker and  $\theta$ -logistic models if more precise and unbiased prior information is available for a particular species (e.g. from field-based abundance counts of one [or many] recovering population[s] with unlimited resources, or from detailed, independent demographic data for life-table analysis). This improved precision is important for parameterising population and management models of wildlife dynamics (Hone, Duncan & Forsyth 2010). For example, application of harvest rate strategies, including the potential biological removal (Wade 1998) and potential take level (Runge *et al.* 2009), are improved by accurate  $r_m$  estimates and greater precision facilitates risk analysis of such strategies.

The  $\theta$ -logistic model estimates of  $\bar{r}_m$  were generally high and inconsistent with prior understanding of the mammal species' life histories. The high sampling covariance between  $r_m$  and  $\theta$  thus resulted in an underestimation of  $\bar{\theta}$ , particularly for species with lower prior  $\hat{r}_m$ . Saether *et al.* (2008) have noted that such underestimation might explain the predominance of lower  $\theta$  values reported controversially (Doncaster 2006; Ross 2006) by Sibly *et al.* (2005). Our study shows that prior information about a species' maximal rate of growth can help prevent such underestimation by breaking down the sampling covariance between these parameters. Bayes' rule could also be used to incorporate prior information, or reasonable assumptions, about population dynamics for other model parameters such as the carrying capacity,  $k$ , based on the life histories of conspecifics and/or congeners. Further, theory predicts that ecological carrying capacity should also scale with metabolic rate and resource supply (Savage *et al.* 2004b), so it might be possible to derive informative priors for  $K$  using such predictions. However, such an approach could be problematic in the absence of further information about the study population because local and environmental conditions will influence  $K$  and vary over time. Developing more flexible models that relax the constant  $K$  assumption and incorporate time-varying  $K$  dynamics could prove to be more fruitful than incorporating theoretical prior predictions of a constant  $K$ .

Using a sensitivity analysis, we showed that  $\bar{r}_m$  and  $\bar{\theta}$  are highly dependent on the prior  $\hat{r}_m$  in  $\theta$ -logistic models, but  $\bar{r}_m$  is much less sensitive to the prior for Ricker models. Thus, fitting the  $\theta$ -logistic model without prior information will give biologically unrealistic  $\bar{r}_m$  estimates in most cases and that, while using prior knowledge can be useful, the high  $r_m - \theta$  correlation means the fit is largely determined by the prior and that accurate prior information is necessary even for the Ricker model. Our simulation results show that even when armed with accurate priors, the correlation between  $r_m$  and  $\theta$  constrains the  $\theta$ -logistic model such that models incorporating priors can receive lower support than vague prior models. However, the priors will improve estimates from Ricker models, particularly for abundance series with higher variance.

Given the relatively large prediction variance associated with our informative priors, there is little information about  $r_m$  in the data when fitting a  $\theta$ -logistic model, a result expected based on previous studies showing the predominance of flat likelihoods with this model for most available time series (Polansky *et al.* 2009; Clark *et al.* 2010). The hierarchical SS-Ricker and SS- $\theta$ -logistic models accounted for often-ignored measurement errors in the abundance counts and generally gave a better fit to the data. In our study, the state-space Ricker model does not offer any substantial improvement over the process error-only Ricker model in evaluating the effect of using prior information. However, without additional information about the magnitude of observation errors, it is difficult to determine the relative contribution of environmental and observation errors to total error, highlighting the importance of repeated sampling of ecological count data to quantify observation errors. A proper treatment of this distinc-

tion is beyond the scope of this manuscript, but the issue of parameter identification (e.g. separate estimation of variance components) in Bayesian hierarchical models requires further investigation.

## CONCLUSIONS

Most stochastic census data do not cover enough of the range of possible population abundances to allow precise parameter estimation for density-feedback models (Clark *et al.* 2010). Informative prior distributions of some model parameters can potentially alleviate this problem by reducing bias and improving precision for Ricker-type models. However, the high  $r_m - \theta$  correlation and flat likelihoods observed using the  $\theta$ -logistic model for most ecological time-series data confirm that this model should not be used in most cases. We therefore recommend incorporating prior information on  $r_m$  into Ricker models of density feedbacks, but emphasise the importance of using sensitivity analysis to assess the effect of the prior on parameter estimates.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

**Data S1.** Ecologically realistic estimates of maximum population growth using informed Bayesian priors.

**Data S2.** Example code for fitting the Ricker state-space model using the Python module `pymc` (<http://pypi.python.org/pypi/pymc>) and `OPENBUGS` (<http://www.openbugs.info/w/>).

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