

UNIVERSIDADE DE SÃO PAULO

Instituto de Ciências Matemáticas e de Computação

**BAYESIAN INFERENCE FOR THE
THETA-LOGISTIC POPULATION GROWTH
MODEL**

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Bayesian Inference for the Theta-Logistic Population Growth Model

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Abstract

In this paper, we introduce a Bayesian approach to identify a population growth model employing a discrete dynamic model based on

generalized logistic growth model known as theta-logistic model. The parameter estimates for these models are obtained using Monte Carlo Markov Chain (MCMC) methods and the appropriate model is identified using some information criteria for model selection. The identification method developed here can be applied to evaluate the asymmetric growth rate per capita, due to the consideration of a shape parameter (θ). In this way we use these discrimination methods to identify the model of best fit among the Logistic ($\theta = 1$), Gompertz ($\theta = 0$) or the Theta-logistic model ($\theta \neq 1$). The Bayesian approach introduced in this paper is applied to two real data sets: the population of American Black Bears (*Ursus americanus*) and the Brazilian Capybara (*Hydrochoerus hydrochaeris*).

Keywords:Theta-logistic growth model, Bayesian approach, Model selection criterion, MCMC methods, profile likelihood function function

1 Introduction

There are several reasons for modeling the growth of a population of a certain species. A growth model of a given population is an important instrument for the understanding of how environmental uncertainties affect growth as well as for the establishment of growth control policies, slaughter control, among many other factors. In addition, these models can be used to foresee populational behavior and to permit risk calculation of extinction or population explosion. From a stochastic point of view, they permit calculation of the probability of extinction or explosion or the time expected for the occurrence of these events. These populational characteristics are known as population viability indicators Boyce (1992), Ludwig (1996), Ludwig (1999), Hertzler (1997), Omlin and Reichechert (1999), Homes (2001).

In this work, we consider the Theta-logistic growth model equivalent to the Richards model described in Richards (1959) and Loibel et.al. (2006). The Theta-logistic growth model is a very general class of models proposed by Gilpin and Ayala (1973), Gilpin et al (1976) and throughly used to study different populations (see for example Saether et al., 1996, 2000, 2002a,b), Lande et al. (2003) and citations in Saether et al. (2005). This model also is known as generalized logistic model because this generalizes the usual Logistic model, the Gompertz model, among others (see Saether et al., 2005). The majority of the works encountered in the literature relies on one of the two particular cases mentioned above, due to the inference difficulties associated to the parameter estimation of the Theta-logistic non-linear model (see Dushoff, 2000).

Usually, a three parameter model such as Theta-logistic gives better fit for asymmetric growth rate per capita, since there is the presence of a shape parameter (θ), (see Sibly et. al., 2005; Keeling, 2000; Fitzhugh, 1974). The models with two parameters have a growth rate per capita that is symmetric around the mean level of the support capacity. However, this is not the case for populations of large mammals (e.g., see Fowler, 1981). The third parameter (θ) is very important because it reveals the survival strategy adopted by a population, which is fundamental when concerning several ecological and economic aspects. Saether et al. (2002c) used the Theta-logistic model to show that in long-survival species like the south polar skua, density dependence has the greatest influence on the dynamics of the population when the size of the population is close to carrying capacity. In contrast, in shorter-survival birds, the effect of density dependence is greater at lower relative densities.

One of the existing statistical problems when we use the Theta-logistic model adjusted for population data, is hypotheses testing about the parameter θ for the samples considered. If there is not enough evidence to reject the null hypothesis $H_0 : \theta = 1$ against the alternative hypothesis $H_1 : \theta \neq 1$, we can not reject the two parameter Logistic model ($\theta = 1$) in favor of the three parameter Theta-logistic model ($\theta \neq 1$); in the same way for $H_0 : \theta = 0$ corresponding to the Gompertz model.

Statistical tests are asymptotical in nature, and statistical tests based on asymptotic theory may not always be reliable for small sample size. Even when we reject the null hypothesis, the effect of the sample sizes should be taken into consideration. If the sample size is very small, then it is advisable to consider this effect as theoretically important. Therefore, if sample sizes are large enough, we can use these tests. Under the classical statistical framework, bootstrap methods Loibel et.al. (2006) are preferable, since they give an improvement in these estimates, and provide better performance of the likelihood methods in small samples.

In this paper we present a Bayesian approach to Theta-logistic model. The estimates of the parameters were obtained using Monte Carlo Markov Chain (MCMC) methods and the appropriate model is identified using information criterion for model selection. The Bayesian model is more appropriate than likelihood method when we are dealing with random samples of small size and we have same knowledge about the analyzed population. We also have many Bayesian criterion for model selection among the Logistic model ($\theta = 1$), Gompertz model ($\theta = 0$) or the Theta-logistic model ($\theta \neq 1$).

The paper is organized as follows: in Section 2, we introduce the stochastic Theta-logistic model. In Section 3, we introduce a likelihood analysis for the Theta-logistic model. In Section 4, we introduce a Bayesian analysis for

the Theta-logistic model. In Section 5, usual criteria of model selection are presented. In Section 6, we introduce two case studies. A first numerical illustration considering real data representing the population of the common named American Black Bears, (species name: *Ursus americanus*) living in Manitoba, Canada, in the period of 1919 to 1981. The second numerical illustration considering real data from the Brazilian Capybara (species name: *Hydrochoerus hydrochaeris*) living in Atibaia river, near to Piracicaba city, in the State of São Paulo in the period of July, 1998 to July, 2002. Finally, in Section 7, we present a discussion of the obtained results and some conclusions

2 The Theta-logistic Model

In this paper, we are considering a stochastic version of the Theta-logistic population growth model by adding to the rate of the growth model a stochastic process that represents the random environmental effects. The considered Theta-logistic model is given by

$$N_{t+1} = N_t \exp \left\{ \rho \left(1 - \frac{N_t^\theta}{K^\theta} \right) + \epsilon_t \right\}, \quad (1)$$

where N_t and N_{t+1} are the numbers of individuals of the population in the instants t and $t + 1$ respectively, ρ is the the population's intrinsic growth rate, K is the carrying capacity, θ is the growth curve shape parameter. Let us assume that the process ϵ_t , $t = 1, 2, \dots$ are independent and identically distributed following a continuous Normal distribution $N(0, \tau^{-1})$ (where we are denoting $\sigma^2 = 1/\tau$) that represents the random environment effects.

The model (1) and the independence assumption of the process ϵ_t typically describes a Markovian model (see Kumar and Varaiya (1986)). The probability distribution function of the population levels, at each point in time, is influenced by current but not previous population levels. Considerable work has been done under the Markovian assumption. A non-Markovian model is introduced in Williams (2007).

2.1 The θ parameter

The third parameter θ makes the model more flexible, which facilitates the use of the same model in populations that have a distinct growth rate; as special case, for small-sized animals such as insects, this strategy will result in a fast growth rate, and in large-sized animals such as big mammals, it will result in a slow growth rate. This parameter allows that the same model can be used in populations with different growth rate, as it can be seen in the

Figure 1.

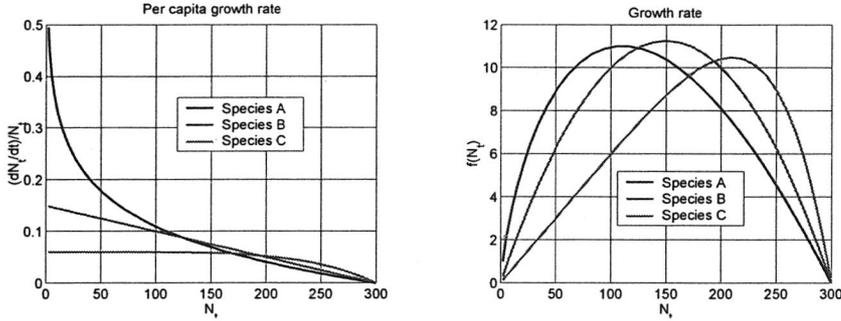


Figure 1. A comparison of three different growth survival strategies

Confidence Interval estimates for the population parameters estimates are asymptotic, and often the sample sizes are not that large; this is one of the reasons why we are proposing in this paper, a Bayesian approach for the Theta-logistic model (1), considering an informative prior probability density function to represent the “degree of belief” of information, about the parameter θ for different populations.

3 The classical approach

Considering a population size time series N_t , let us write the growth rate $y_{t+1} = \ln(N_{t+1}/N_t) \approx (N_{t+1} - N_t)/N_t$. We can write the model (1) as a power-linear model

$$y_{t+1} = \rho \left(1 - \frac{N_t^\theta}{K^\theta} \right) + \epsilon_t. \quad (2)$$

Using the parametrization $\rho = \alpha_0$ and $K^\theta = -\alpha_0/\alpha_1$ and assuming that each ϵ_t follows a continuous Normal distribution $N(0, \tau^{-1})$, the conditional probability density function for the random variable y_{t+1} given N_t , can be written as

$$p(y_{t+1}|N_t) \propto \tau^{\frac{1}{2}} \exp \left\{ -\frac{\tau}{2} (y_{t+1} - \alpha_0 - \alpha_1 N_t^\theta)^2 \right\}. \quad (3)$$

Thus, we can write the conditional probability density function of the random variable N_{t+1} given N_t , as:

$$P(N_{t+1}|N_t) = P(y_{t+1}|N_t) \left| \frac{dy_{t+1}}{dN_{t+1}} \right| \quad (4)$$

considering the relationship $y_{t+1} = \ln(N_{t+1}/N_t)$, the equation (4) is given as:

$$P(N_{t+1}|N_t) \propto \frac{\tau^{\frac{1}{2}}}{N_{t+1}} \exp \left\{ -\frac{\tau}{2} \left(y_{t+1} - \alpha_0 - \alpha_1 N_t^\theta \right)^2 \right\} \quad (5)$$

The classical approach (likelihood methods) has to support their inferences based only on the observations recorded. The maximum likelihood estimates (MLE) of the parameters $\alpha = (\alpha_0, \alpha_1)'$, τ and θ of the Theta-logistic model (1) are based only on the observations $\mathbf{N} = \{N_1, N_2, \dots, N_m\}$. In order to formulate the identifiability of the Theta-logistic model, it is necessary to know the joint distribution for $\mathbf{N} = \{N_1, N_2, \dots, N_m\}$. Under the Markovian assumption, the likelihood function can be written as:

$$L(\alpha, \tau, \theta | \mathbf{N}) = \left(\prod_{k=2}^m P(N_k | N_{k-1}) \right) P(N_1) \quad (6)$$

The partial likelihood introduced by Cox Cox (1975) is based entirely on the conditional distribution of the current response, given past responses, and past covariate information. The likelihood (6) leads to the following partial likelihood:

$$PL(\alpha, \tau, \theta | \mathbf{N}) = \prod_{k=2}^m P(N_k | N_{k-1}) \quad (7)$$

substituting (5) in (7), we have,

$$PL(\alpha, \tau, \theta | \mathbf{N}) \propto \tau^{\frac{m-1}{2}} \exp \left\{ -\frac{\tau}{2} \sum_{k=2}^m \left(y_k - \alpha_0 - \alpha_1 N_{k-1}^{(\theta)} \right)^2 \right\} \quad (8)$$

Let us consider the $(m-1) \times 1$ vector \mathbf{Y} the vector defined as,

$$\mathbf{Y} = (y_2, y_3, \dots, y_m)'_{(m-1) \times 1} \quad (9)$$

and the $(m-1) \times 2$ matrix $\mathbf{X}^{(\theta)}$ defined as

$$\mathbf{X}^{(\theta)} = \begin{pmatrix} 1 & N_1^\theta \\ 1 & N_2^\theta \\ \vdots & \vdots \\ 1 & N_{m-1}^\theta \end{pmatrix}_{(m-1) \times 2} \quad (10)$$

From (9) and (10), the likelihood function for $\alpha = (\alpha_0, \alpha_1)'$, τ and θ given the observations $\mathbf{N} = \{N_1, N_2, \dots, N_m\}$ can be written as:

$$L(\alpha, \tau, \theta | \mathbf{N}) \propto \tau^{\frac{m-1}{2}} \exp \left\{ -\frac{\tau}{2} (\mathbf{Y} - \mathbf{X}^{(\theta)} \alpha)' (\mathbf{Y} - \mathbf{X}^{(\theta)} \alpha) \right\}$$

that is,

$$L(\alpha, \tau, \theta | \mathbf{N}) \propto \tau^{\frac{m-1}{2}} \exp \left\{ -\frac{\tau}{2} [\nu \hat{\sigma}^{2(\theta)} + (\alpha - \hat{\alpha}^{(\theta)})' \mathbf{X}^{(\theta)'} \mathbf{X}^{(\theta)} (\alpha - \hat{\alpha}^{(\theta)})] \right\}, \quad (11)$$

where,

$$\hat{\alpha}^{(\theta)} = (\mathbf{X}^{(\theta)'}\mathbf{X}^{(\theta)})^{-1}\mathbf{X}^{(\theta)'}\mathbf{Y} \quad (12)$$

$$\hat{\sigma}^2(\theta) = \frac{1}{\nu}(\mathbf{Y} - \hat{\mathbf{Y}}^{(\theta)})'(\mathbf{Y} - \hat{\mathbf{Y}}^{(\theta)}), \quad (13)$$

and $\nu = m - 1$, $\hat{\mathbf{Y}} = \mathbf{X}^{(\theta)}\hat{\alpha}^{(\theta)}$ and $\hat{\tau}^{(\theta)} = 1/\hat{\sigma}^2(\theta)$. The profile log-likelihood function for the parameter θ , is given by:

$$l_p(\theta|\mathbf{N}) = \ln L(\hat{\alpha}^{(\theta)}, \hat{\tau}^{(\theta)}, \theta|\mathbf{N}) \quad (14)$$

$$l_p(\theta|\mathbf{N}) \propto \frac{(m-1)}{2} \ln \hat{\tau}^{(\theta)} \quad (15)$$

Replacing $\hat{\tau}^{(\theta)} = 1/\hat{\sigma}^2(\theta)$ in equation (15), we can write the profile log-likelihood function for the parameter θ , as:

$$l_p(\theta|\mathbf{N}) \propto -\frac{(m-1)}{2} \ln \hat{\sigma}^2(\theta) \quad (16)$$

The estimate θ^* of the parameter θ is the maximum profile likelihood estimate, subject to the constraint $\theta \in \Theta = [a, b]$, $a < b$, given by:

$$\theta^* = \max_{\theta \in \Theta} l_p(\theta|\mathbf{N}) \quad (17)$$

where $\Theta = [a, b]$, $a < b$, $\theta \in \Theta$. The set Θ can be chosen based on some prior knowledge about the population's intrinsic growth rate.

When we have small sample sizes, the confidence intervals are likely with large range and there are many case studies where we have prior intervals $\Theta = [a, b]$, $a < b$, inside the confidence intervals.

Optimization algorithms can be used to compute the maximum likelihood estimate and the information matrix subject to the constraint. But in general, this way is not easy because those algorithms require the second order derivative of the likelihood function at the parameter θ and there are no evidence that the unconditional estimates will be more accurate than conditional estimates.

3.1 Model Inference

Often, it is of interest to test if the parameter θ of the model is equal to a known value $\theta^{(0)}$, that is, $H_0 : \theta = \theta^{(0)}$. In this way, we can easily obtain from the profile a likelihood ratio (LR) statistics $w = 2 \{l_p(\theta^*|\mathbf{N}) - l_p(\theta^{(0)}|\mathbf{N})\}$ to test $\theta = \theta^{(0)}$ which has an asymptotical Chi-square χ_1^2 distribution with one degree of freedom. From this result we can construct a large sample confidence interval for θ by inverting the LR test. An approximate confidence interval for θ is then readily obtained from $\{\theta \mid l_p(\theta|\mathbf{N}) > l_p(\theta^*|\mathbf{N}) -$

$\frac{1}{2}\chi_1^2(\delta)\}$ and the accuracy of this approximation follows from the fact that $Pr\{w \geq \chi_1^2(\delta)\} = \delta + O(m^{-1/2})$. Model inference can be done through considering the log-likelihood function of (11). The elements of the the observed information matrix are given by:

$$\begin{aligned} I_{\alpha^{(\theta)}\alpha^{(\theta)}} &= \widehat{\tau}^{(\theta)}(\mathbf{X}^{(\theta)'}\mathbf{X}^{(\theta)}) & I_{\alpha^{(\theta)}\theta} &= \widehat{\tau}^{(\theta)}(\mathbf{X}^{(\theta)'}\dot{\mathbf{e}} + \frac{d\dot{\mathbf{e}}'}{d\alpha}\mathbf{e}) & I_{\alpha^{(\theta)}\tau} &= \mathbf{X}^{(\theta)'}\mathbf{e} \\ I_{\theta\alpha^{(\theta)}} &= \widehat{\tau}^{(\theta)}(\mathbf{X}^{(\theta)'}\dot{\mathbf{e}} + \dot{\mathbf{X}}^{(\theta)'}\mathbf{e}) & I_{\tau^{(\theta)}\tau^{(\theta)}} &= \frac{(m-1)}{2\widehat{\tau}^{(\theta)2}} & I_{\tau^{(\theta)}\theta} &= \mathbf{e}'\dot{\mathbf{e}} \\ I_{\theta\theta} &= \widehat{\tau}^{(\theta)}(\dot{\mathbf{e}}'\dot{\mathbf{e}} + \mathbf{e}'\ddot{\mathbf{e}}) \end{aligned} \quad (18)$$

where $\mathbf{e}(\alpha, \theta) = \mathbf{Y} - \mathbf{X}^{(\theta)}\alpha$ and $\dot{\mathbf{e}} = d\mathbf{e}/d\theta$, $\ddot{\mathbf{e}} = d^2\mathbf{e}/d\theta^2$. Using the information matrix above, we can write, after some algebra,

$$Var^{-1}(\widehat{\theta}) = I_{\theta\theta} - I_{\theta\alpha^{(\theta)}}I_{\alpha^{(\theta)}\alpha^{(\theta)}}^{-1}I_{\alpha^{(\theta)}\theta} - I_{\theta\tau^{(\theta)}}I_{\tau^{(\theta)}\tau^{(\theta)}}^{-1}I_{\tau^{(\theta)}\theta} \quad (19)$$

Consider the original vector of parameters $\phi^{(\theta)} = (\rho^{(\theta)}, K^{(\theta)}, \tau^{(\theta)})$ conditioned on the parameter θ , and the vector of parameters $\gamma^{(\theta)} = (\alpha_1^{(\theta)}, \alpha_2^{(\theta)}, \tau^{(\theta)})$ given by parametrization $\alpha_1 = \rho$, $\alpha_2 = -\rho/K^\theta$. The observed information matrix $I_{\phi^{(\theta)}\phi^{(\theta)}}$ can be calculated with the observed information matrix $I_{\gamma^{(\theta)}\gamma^{(\theta)}}$ and the Jacobian of the transformations $\alpha_1 = \rho$, $\alpha_2 = -\rho/K^\theta$ (to details, see Seber and Wild (1989)). The matrix $I(\phi^{(\theta)})$ is given by

$$I_{\phi^{(\theta)}\phi^{(\theta)}} = J'_{\gamma\phi} I_{\gamma^{(\theta)}\gamma^{(\theta)}} J_{\gamma\phi}, \quad (20)$$

where the Jacobian of the transformations $J_{\gamma\phi}$ is given by,

$$J_{\gamma\phi} = \frac{\partial\gamma^{(\theta)}}{\partial\phi^{(\theta)}} = \begin{pmatrix} 1 & 0 & 0 \\ -K^{-\theta} & \theta\rho K^{-(\theta+1)} & 0 \\ 0 & 0 & 1 \end{pmatrix}. \quad (21)$$

The confidence intervals for $\phi^{(\theta)}$ can be calculated using the asymptotic normal approximation to the finite sample distribution of the maximum likelihood estimate (conditioned on the parameter θ).

$$\widehat{\phi}^{(\theta)} - \phi^{(\theta)} \sim N(0, I_{\widehat{\phi}^{(\theta)}\widehat{\phi}^{(\theta)}}^{-1}) \quad (22)$$

4 The Bayesian approach

The Bayesian approach of the Theta-logistic model (1) starts by considering the parameters ρ , K and θ in the model (1) as random quantities and quantifying the uncertainty of the parameter's values in the form of a

prior probability distribution that represent some prior knowledge about the population. We know that $\rho \in (0, 1)$ and $K > K_0 \geq 1$, where $K_0 > 0$ is the minimum viable population size, below which the population is considered extinct (call it “realistic” extinct). Certainly $K_0 = 2$ is a possible choice because with less than two individuals there is no reproduction but we can, if there are Allee effects, choose larger values of K_0 .

This knowledge must be used to build a prior probability density. In special situations when more refined information are available, a more appropriate informative prior probability density can be built.

For the parameter $K > 0$ we consider a gamma prior distribution $G(\kappa_0, \lambda_0)$ with mean κ_0/λ_0 and variance κ_0/λ_0^2 . For the parameters $\rho \in [0, 1]$, we consider a beta prior distribution, $B(p_0, q_0)$ with mean $p_0/(p_0 + q_0)$ and variance $p_0q_0/(p_0 + q_0)^2(p_0 + q_0 + 1)$. For the parameter $\tau > 0$ we also consider a gamma prior distribution, $G(\nu_0, \beta_0)$ with mean ν_0/β_0 and variance ν_0/β_0^2 . The choice of a distribution $G(\nu_0, \beta_0)$ for τ corresponds to choose an inverse-gamma distribution for σ^2 . We are assuming the hyperparameters $k_0, \lambda_0, p_0, q_0, \nu_0, \beta_0$ all known. Assuming independence for K, ρ and τ we can write the joint prior density as:

$$\pi_0(K, \rho, \tau) \propto \rho^{p_0-1} (1 - \rho)^{q_0-1} K^{\kappa_0-1} \tau^{\nu_0-1} \exp\{-(\lambda_0 K + \beta_0 \tau)\} \quad (23)$$

It is possible to use a “weak” prior for K and τ with small values for λ_0 and β_0 . The weak prior indicates that one is unsure about an informative prior distribution.

The parameter θ assumes any continuous value in the interval $\Theta = [a, b]$, where $a < b$ and we consider a truncated normal prior distribution $NT(\mu_\theta, \sigma_\theta^2)$. The truncated normal prior probability density function is given by

$$\pi_0(\theta) = \frac{1}{\Phi \sqrt{2\pi\sigma_\theta^2}} \exp\left\{-\frac{(\theta - \mu_\theta)^2}{2\sigma_\theta^2}\right\} \mathbf{I}_R(\theta), \quad a < \theta < b, \quad (24)$$

where Φ is a constant not needed to be known when we used the Metropolis-Hastings algorithms, $R = [a, b]$, and the hyperparameters μ_θ and σ_θ^2 are calculated as $\mu_\theta = (a + b)/2$ and $\sigma_\theta^2 = (b - a)^2/12$ and $\mathbf{I}_R(\alpha)$ is a indicator function that takes the value 1 if $\theta \in R$, and the value 0 otherwise.

Bayesian analysis of the constrained parameter and truncated data problems within a Gibbs sampling framework can be found in Damien and Walker (2001). The joint prior probability density for the parameters K, ρ, τ and θ is given by $\pi_0(K, \rho, \tau, \theta) = \pi_0(K, \rho, \tau)\pi_0(\theta)$

The joint posterior density function for the parameters K, ρ, τ, θ can be obtained from the Bayes theorem as:

$$\pi(K, \rho, \tau, \theta | \mathbf{N}) \propto L(K, \rho, \tau, \theta | \mathbf{N}) \pi_0(K, \rho, \tau, \theta)$$

From (11), the joint posterior density function, can be written as

$$\begin{aligned} \pi(K, \rho, \tau, \theta | \mathbf{N}) &\propto \rho^{p_0-1} (1-\rho)^{q_0-1} K^{\kappa_0-1} \tau^{\frac{2\nu_0+m}{2}-1} \exp\{-(\lambda_0 K + \beta_0 \tau)\} \times \\ &\times \exp\left\{-\frac{\tau}{2} [\nu \widehat{\sigma}^2(\theta) + (\alpha - \widehat{\alpha}^{(\theta)})' \mathbf{X}^{(\theta)'} \mathbf{X}^{(\theta)} (\alpha - \widehat{\alpha}^{(\theta)})]\right\} \pi_0(\theta) I_R(\theta) \end{aligned} \quad (25)$$

where $\widehat{\alpha}_B^{(\theta)}$ and $\widehat{\sigma}^2(\theta)$ are given in (12) and (13) respectively and $\alpha = (\rho, -\rho/K^\theta)'$ denote the vector of the parameter functions.

However, in order to obtain the marginal densities for α and τ we first need to integrate out θ in (25). This problem can be only tackled by numerical methods. In this paper, we employ Monte Carlo Markov Chain (MCMC) and, more specifically, we used a combination of Gibbs sampling and Metropolis-Hastings sampling, because MCMC methods are most conveniently built upon full conditional distributions.

4.1 MCMC Procedure

In order to obtain the marginal densities for each of the unknown parameters we built a MCMC procedure upon full conditional distributions. The posterior conditional densities are found easily through equation (25).

To facilitate the identification of the conditional densities, it is convenient to rewrite (25) in different ways. In each case we condition on the two parameters. First, we rewrite (25) conditional on values for τ and θ and the posterior conditional probability density for $\alpha = (\rho, -\rho/K^\theta)'$ can be written as:

$$\begin{aligned} \pi(\rho, K | \tau, \theta, \mathbf{N}) &\propto \rho^{p_0-1} (1-\rho)^{q_0-1} K^{\kappa_0-1} \exp\{-\lambda_0 K\} \times \\ &\times \exp\left\{-\frac{\tau}{2} (\alpha - \widehat{\alpha}^{(\theta)})' \mathbf{X}^{(\theta)'} \mathbf{X}^{(\theta)} (\alpha - \widehat{\alpha}^{(\theta)})\right\} \end{aligned} \quad (26)$$

In the same way, the posterior conditional probability density for τ conditional on values for ρ, K , and θ , can be written as:

$$\pi(\tau | \rho, K, \theta, \mathbf{N}) \propto \tau^{\frac{2\nu_0+m}{2}-1} \exp\left\{-\frac{\tau}{2} \left[\nu \widehat{\sigma}^2(\theta) + (\alpha - \widehat{\alpha}^{(\theta)})' \mathbf{X}^{(\theta)'} \mathbf{X}^{(\theta)} (\alpha - \widehat{\alpha}^{(\theta)}) \right]\right\} \quad (27)$$

that is,

$$\tau | \rho, K, \theta, \mathbf{N} \sim G\left(\frac{2\nu_0 + m}{2}, \frac{b(\theta, \alpha)}{2}\right)$$

where

$$b(\theta, \alpha) = (\alpha - \widehat{\alpha}^{(\theta)})' \mathbf{X}^{(\theta)'} \mathbf{X}^{(\theta)} (\alpha - \widehat{\alpha}^{(\theta)}) + \nu S^2(\theta)$$

and the posterior conditional probability density for θ conditional on ρ, K and τ , is given by

$$\pi(\theta | \rho, K, \tau, \mathbf{N}) \propto \Psi(\rho, K, \tau, \theta) \pi_0(\theta) \quad (28)$$

where

$$\Psi(\rho, K, \tau, \theta) = \exp \left\{ -\frac{\tau}{2} b(\alpha, \theta) \right\} \quad (29)$$

Summarizing, the combination of Gibbs sampling and Metropolis-Hastings steps consists of:

1. Start with initial values $\theta^{(0)}$, $\tau^{(0)}$ and compute $\alpha^{(0)} = (\rho^{(0)}, -\rho^{(0)}/K^{(0)\theta^{(0)}})'$; then proceed with the following steps:
2. Generate ξ_K from $G(\kappa_0, \lambda_0)$, and ξ_ρ from $B(p_0, q_0)$ and compute $\alpha^{(j+1)} = (\xi_\rho, -\xi_\rho/\xi_K^{\theta^{(j)}})'$
3. Calculate the probability of this new proposal to be accepted as the next value by

$$p = \min \left\{ 1, \frac{\exp \left\{ -\frac{\tau^{(j)}}{2} (\alpha^{(j+1)} - \hat{\alpha}^{(\theta^{(j)})})' \mathbf{X}^{(\theta^{(j)})'} \mathbf{X}^{(\theta^{(j)})} (\alpha^{(j+1)} - \hat{\alpha}^{(\theta^{(j)})}) \right\}}{\exp \left\{ -\frac{\tau^{(j)}}{2} (\alpha^{(j)} - \hat{\alpha}^{(\theta^{(j)})})' \mathbf{X}^{(\theta^{(j)})'} \mathbf{X}^{(\theta^{(j)})} (\alpha^{(j)} - \hat{\alpha}^{(\theta^{(j)})}) \right\}} \right\}$$

4. Generate $u \sim \text{Uniform}[0, 1]$. Then the new proposal ξ is chosen according to the following rules.:

$$(\rho^{(j+1)}, K^{(j+1)}) = \begin{cases} (\xi_K, \xi_\rho) & \text{if } u \leq p \\ (\rho^{(j)}, K^{(j)}) & \text{if } u > p \end{cases}$$

5. Generate a new proposed sample ξ_θ from $\pi_0(\theta)$ and compute $\alpha(\xi_\theta) = (\rho^{(j+1)}, -\rho^{(j+1)}/K^{(j+1)\xi_\theta})'$
6. Calculate the probability of this new proposal to be accepted as the next value given by

$$p = \min \left\{ 1, \frac{\Psi(\alpha(\xi_\theta), \tau^{(j)}, \xi_\theta)}{\Psi(\alpha^{(j+1)}, \tau^{(j)}, \theta^{(j)})} \right\}$$

7. Generate $u \sim U(0, 1)$. Then the new proposal ξ_θ is chosen according to the following rules.:

$$\theta^{(j+1)} = \begin{cases} \xi_\theta & \text{if } u \leq p \\ \theta^{(j)} & \text{if } u > p \end{cases}$$

8. Generate $\tau^{(j+1)}$ from $G\left(\frac{2\nu_0 + m}{2}, \frac{b(\alpha^{(j+1)}, \theta^{(j+1)})}{2}\right)$.

9. Increase $j \leftarrow j + 1$ and repeat the steps (2)-(8).

We could monitor the convergence of the mixed Gibbs samples and Metropolis-Hastings algorithms using Gelman and Rubin's method that uses the analysis of variance technique to determine whether further iterations are needed Gelman and Rubin (1992), Geweke criterion, Geweke (1992), graphical methods and standard existing indexes (see Gilks et al. (1998) for details).

Considering Gibbs with Metropolis-Hastings algorithms, we get Monte Carlo estimates for the posterior quantities of interest. In order to obtain inferences on the parameters of the model, both point estimates and interval estimates are required. Considering Gibbs with Metropolis-Hastings algorithms, this may be readily obtained by Monte Carlo expectation based on the sample $\omega^{(j)} = \{\rho^{(j)}, K^{(j)}, \theta^{(j)}, \tau^{(j)}\}$, $j = 1, \dots, M$, generated from the posterior distributions, as:

$$\hat{g}(\omega_k^{MC}) = \frac{1}{M} \sum_{j=1}^M g(\omega_k^{(j)}).$$

In order to obtain the Credibility Intervals (IC) estimates, $[\hat{\omega}_k^{MC}(1 - \gamma), \hat{\omega}_k^{MC}(\gamma)]$, considering Gibbs with Metropolis-Hastings algorithms, we get Monte Carlo estimates for the posterior quantities of interest, so that

$$P[\hat{\omega}_k^{MC}(1 - \gamma) \leq \omega_k^{MC} \leq \hat{\omega}_k^{MC}(\gamma)] = \gamma.$$

Credibility intervals are legitimate probability statements about the unknown parameters, since these parameters now are considered random, not fixed. Generally one use $\gamma = 95\%$ and $IC(\gamma)$ is the 95% Bayesian Credibility Interval.

5 Model selection methods

There are many model selection methods to choose the best model to be fitted by time series data under the Bayesian approach (see for example Gamerman (2002)). We have considered some of these methods to choose between the Theta-logistic model ($\theta \neq 1$) and Logistic model ($\theta = 1$); the methods considered in this paper are described below.

5.1 Bayesian information Criterion (BIC)

The Bayesian Information Criterion (*BIC*) is a model selection criterion introduced by Schwarz (1978) and modified by Carlin and Louis (2000) (see also Raftery et al. (2006)) to be used considering the posterior density for the parameter of the fitted models. This criterion weights between the maximized

log-likelihood function and the number of parameters of the models. The best model is the one that gives a larger value of BIC , given by,

$$BIC = E\{\log L(\rho, K, \tau, \theta|\mathbf{N})\} - \frac{p}{2} \ln(m - 1) \quad (30)$$

where $L(\rho, K, \tau, \theta|\mathbf{N})$ is the partial-likelihood function (11) and $E\{\log L(\rho, K, \tau, \theta|\mathbf{N})\}$ is the expected value of the log-partial-likelihood function based on the posterior density for (ρ, K, τ, θ) ; p is the dimension of the parameter vector and m is the sample size.

5.2 Deviance Information Criterion (DIC)

The Deviance Information Criterion (DIC) is a generalization for the BIC . This criterion is specially useful for model selection under Bayesian approach where samples of the posterior distribution for the parameters of the models were obtained using Monte Carlo Markov Chain (MCMC) methods. Similarly to BIC criterion, this criterion is a asymptotical approximation for large sample size and when the posterior distribution is well approximated by a multivariate normal distribution.

The deviance is defined by:

$$D(\rho, K, \tau, \theta) = -2 \log L(\rho, K, \tau, \theta|\mathbf{N}) + C$$

where (ρ, K, τ, θ) is a vector of unknown parameters of the model; $L(\rho, K, \tau, \theta|\mathbf{N})$ is the partial-likelihood function (11) and C is a constant not needed to be known in comparison of two models. The DIC criterion introduced by Spiegelhalter et al. (2002), is given by

$$DIC = D(\hat{\rho}, \hat{K}, \hat{\tau}, \hat{\theta}) + 2p_D \quad (31)$$

where $D(\hat{\rho}, \hat{K}, \hat{\tau}, \hat{\theta})$ is the deviance evaluated at the posterior mean and p_D is the effective number of parameters of the model, given by $p_D = \bar{D} - D(\hat{\rho}, \hat{K}, \hat{\tau}, \hat{\theta})$, where $\bar{D} = E\{D(\rho, K, \tau, \theta)\}$ is the posterior mean deviance measuring the quality of the data fitted by the model. Smaller values of DIC indicate better models; these values also could be negatives.

5.3 Bayes Factor (B_{ij})

This criterion compares two models M_1 and M_2 using marginal densities or marginal likelihood functions. The model M_1 is better than the model M_2 if $P(\mathbf{N}|M_2) < P(\mathbf{N}|M_1)$. The marginal likelihood function is given by:

$$P(\mathbf{N}|M_i) = \int_{\Omega} L(\rho_i, K_i, \tau_i, \theta_i|\mathbf{N}, M_i) \pi_0(\rho_i, K_i, \tau_i, \theta_i|M_i) d\rho_i dK_i d\tau_i d\theta_i \quad (32)$$

where the integral on the right hand side of (32) represents a multiple integral in the parameter space $(\rho_l, K_l, \tau_l, \theta_l)$ and $L(\rho_l, K_l, \tau_l, \theta_l | \mathbf{N}, M_l)$, $l = 1, 2$ is the likelihood of the data under the hypothesis of model M_l and $\pi_0(\rho_l, K_l, \tau_l, \theta_l | M_l)$ is a prior density for the vector of parameters $(\rho_l, K_l, \tau_l, \theta_l)$. The Bayes factor is given by the ratio,

$$B_{ij} = \frac{P(D|M_i)}{P(D|M_j)} \quad (33)$$

A modification of the Bayes factor introduced by Aitkin (1991) replaces the prior density $\pi_0(\rho_l, K_l, \tau_l, \theta_l | M_l)$ in (32) by the posterior density for $(\rho_l, K_l, \tau_l, \theta_l)$. The multiple integral in equation (32) can be evaluated by Monte Carlo methods from the generated samples of the posterior distribution for $(\rho_l, K_l, \tau_l, \theta_l)$ using MCMC methods. The Monte Carlo estimator of the marginal likelihood is given by,

$$\hat{P}(D|M_l) = \frac{1}{M} \sum_{j=1}^M L(\rho_l, K_l, \tau_l, \theta_l | \mathbf{N}, M_l) \quad \text{for } l = 1, 2$$

Another discrimination criterion was introduced by Raftery (1995), (see also Raftery et al. (2006)) given by the harmonic mean of the likelihood function

$$\hat{f}(D|M_l) = \left\{ \frac{1}{M} \sum_{j=1}^M \frac{1}{L(\rho_l, K_l, \tau_l, \theta_l | \mathbf{N}, M_l)} \right\}^{-1} \quad \text{for } l = 1, 2$$

The model selection methods introduced in this section are used to select the best model to be fitted by the population time series considered in the next section.

6 Applications

The Bayesian approach introduced in this paper was applied to analyze two real data set. In both cases, we have considered a “burn-in-sample” of size 5,000; after this, we have simulated 50,000 mixed Metropolis–Hastings and Gibbs samples taking every 10th sample, to get approximated uncorrelated samples. The convergence of the mixed algorithms was monitored using , Geweke and Gelman and Rubin criterion, graphical methods and standard existing indexes (see, for example Gilks et al. (1998)).

6.1 The American Black bears population

The real time series representing the population of the common named American Black bears, (species name: *Ursus americanus*) living in Manitoba,

Canada, in the period of 1919 to 1981 is shown in the Figure 4. A complete description of this data set is given in The Global Population Dynamics Database, (1999). NERC Center for Population Biology, Imperial College (<http://www.sw.ic.ac.uk/cpb/cpb/gpdd.html>).

The prior densities functions are built in an empiric way, considering the maximum conditional likelihood estimates of the parameters. A summary of the prior densities for Theta-logistic models fitted to the American Black bears population time series is given in the Table 1.

Table 1 summary of the prior densities for Theta-Logistic model

K	ρ	$\theta \in (1.8, 2.8)$	τ
$G(\kappa_0, \lambda_0)$	$B(p_0, q_0)$	$NT(\mu_\theta, \sigma_\theta^2)$	$G(\nu_0, \beta_0)$
$\kappa_0 = 75.1931$	$p_0 = 6.3315e + 007$	$\mu_q = 2.65$	$\nu_0 = 30.9968$
$\lambda_0 = 0.2050$	$q_0 = 1.1193e + 009$	$\sigma_q^2 = 1.19$	$\beta_0 = 4.8162$

The maximum likelihood estimates (MLE) and Bayesian estimates with MCMC method are presented in the Table 2 as mean/(standard deviation). The asymptotic confidence intervals were calculated by $mean \pm 2Sd$ and the credibility intervals as proposed in the Section 4.

Table 2. Bayesian and Likelihood estimates for *Ursus americanus*

	Bayesian		MLE	
	Mean/(<i>Sd</i>)	CI(95%)(*)	Mean / (<i>Sd</i>)	CI(95%)(**)
K	355.2 (37.1826)	(288.2, 434.4)	366.8 (42.3)	(282, 2.451.4)
ρ	0.05354 (6.5524×10^{-6})	(0.0535, 0.0536)	0.05354 (6.546×10^{-6})	(0.0535, 0.0536)
θ	2.243 (0.1941)	(1.8742, 2.6214)	2.65 (1.092)	(0.466, 4.834)
τ	6.37 (0.7901)	(4.9137, 7.9979)	6.436 (1.156)	(4.124, 8.748)
σ^2	0.1594 (0.0200)	(0.1250, 0.2035)	0.1554 (0.04834)	(0.0587, 0.2521)

Sd: Standard deviation, (*)Credibility Interval, (**)Confidence Interval

To test if the parameter θ of the model is equal to a known value $\theta^{(0)} = 1$ (the logistic model), we can easily obtain from the profile likelihood ratio (LR) a statistics $w = 2 \{l_P(\theta^*|N) - l_P(\theta^{(0)}|N)\}$ to test $\theta = \theta^{(0)}$ which has an asymptotical Chi-square χ_1^2 distribution with one degree of freedom, where

$l_P(\theta^*|N)$ is given by (16). For the MLE given in Table 2 we have $l_P(\theta^*|N) = 57.7177$, $l_P(\theta^{(0)}|N) = 56.7979$ and $w = 1.8396 < \chi_{1,0.95}^2$ ($\chi_{1,0.95}^2 = 3.8414$); thus, we do not reject the null hypothesis $H_0 : \theta = 1$ (the Logistic model) and we conclude that, there is not evidence in favor of the alternative hypotheses of the Theta-logistic model. On the other hand under the Bayesian approach we use the model selection criteria given in Section 5 to choose among the Logistic and Theta-logistic models, the best model to be fitted by the time series data. All the selection criteria based posterior sample shown in the Table 3 indicate that Theta-logistic model is the best model to be fitted by American Black bears population time series data.

Table 3. The Bayesian model selection criteria based posterior sample

Model	BIC	DIC	$f(N M_i)$	$P(N M_i)^{(*)}$
$M_1 : \text{Logistic } (\theta = 1)$	17.35	-46.69	7.166×10^{-11}	1.887×10^{10}
$M_2 : \text{Theta-logistic } (\theta)$	19.75	-51.17	6.413×10^{-12}	2.154×10^{11}

$$(*) B_{2,1} = P(N|M_2)/P(N|M_1) = 11.4149$$

The Bayesian estimates of the growth rate and per capita growth rate are shown respectively in Figures 2 and 3 and the real and estimate time series representing the population of the American Black bears is shown in Figure 4.

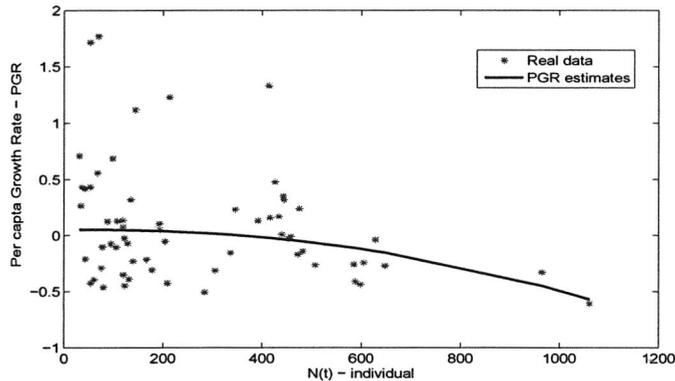


Figure 2. Per capita growth Bayesian estimates for American Black bears

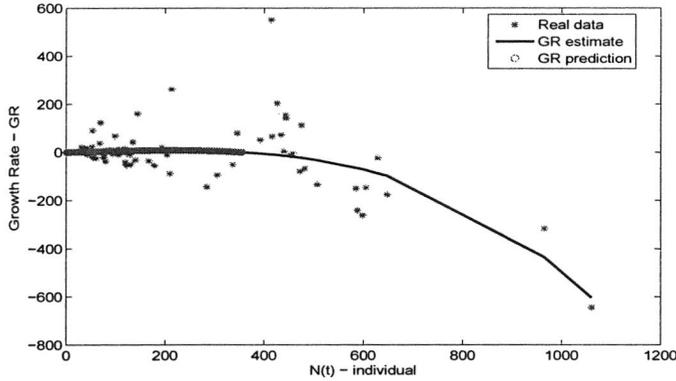


Figure 3. Growth Bayesian estimates for American Black bears

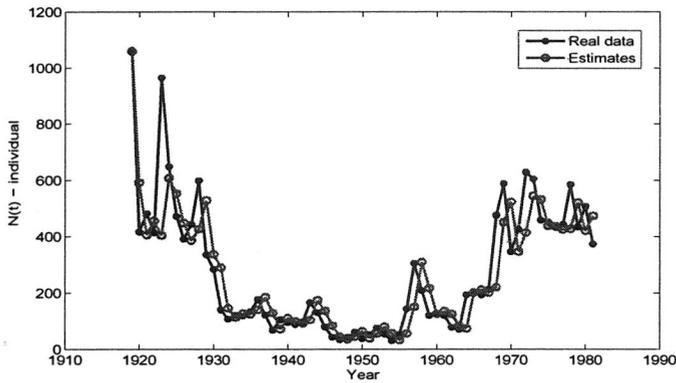


Figure 4. The Bayesian estimates of American Black bears based on real population data of Manitoba Canada the period of 1919 to 1981

6.2 The Brazilian Capybara population

The second time series that we analyzed is the population of the Brazilian Capybara (*Hydrochoerus hydrochaeris*). This animal is the largest rodent of the world, measuring up to 1,30 meters of length and 0,50m to 0,60m of height. It can weigh up to 100Kg, but its medium weight is about 50Kg for females and 60Kg for males. They are found in the flooded zones of the savannas in Colombia and Venezuela and in the swampland of the Mato-Grosso state, in Brazil and in Paraguay. In Figure 7 we have the monthly average of Capybara population for a community of Capybara that inhabits

the riverine area of the Atibaia river, near of the Piracicaba city, this average was calculated based in the weekly observations accomplished in the period of July, 1998 to July, 2002, measured by researchers of the USP/ESALQ (a total of 200 observations).

The hyperparameters of the prior densities for Theta-logistic models are given in Table 4, these prior densities functions is built in an empirical way considering the maximum conditional likelihood estimates of the model, fitted to the the population of Brazilian Capybara population time series.

Table 4 Summary of the prior densities for Theta-Logistic model

K	ρ	$\theta \in (1.5, 4.0)$	τ
$G(\kappa_0, \lambda_0)$	$B(p_0, q_0)$	$NT(\mu_\theta, \sigma_\theta^2)$	$G(\nu_0, \beta_0)$
$\kappa_0 = 195$	$p_0 = 2.07 \times 10^7$	$\mu_\theta = 3.41$	$\nu_0 = 23.49$
$\lambda_0 = 3.08$	$q_0 = 1.76 \times 10^8$	$\sigma_\theta^2 = 2.14$	$\beta_0 = 1.33$

The maximum likelihood estimates (MLE), Bayesian estimates with MCMC method as mean/(standard deviation), the confidence intervals calculated by $mean \pm 2Sd$ and the Bayesian credibility intervals are presented in Table 5.

Table 5. Bayesian and Likelihood estimates for *Hydrochoerus hydrochaeris*

	Bayesian		MLE	
	Mean/(<i>Sd</i>)	CI(95%)(*)	Mean / (<i>Sd</i>)	CI(95%)(**)
K	62.24 (3.8313)	(55.17, 70.09)	63.22 (4.53)	(54.16, 72.28)
ρ	0.1055 (2.182×10^{-5})	(0.1054, 0.1056)	0.1055 (2.192×10^{-5})	(0.1054, 0.1056)
θ	2.635 (0.3269)	(1.9368, 3.2401)	3.41 (1.462)	(0.4864, 6.3336)
τ	17.48 (2.5412)	(12.89, 22.80)	17.63 (3.637)	(10.36, 24.90)
σ^2	0.05846 (8.675×10^{-3})	(0.0438, 0.0776)	0.05672 (2.027×10^{-2})	(0.0162, 0.0973)

Sd: Standard deviation, (*)Credibility Interval, (**)Confidence Interval

Using the profile likelihood ratio (LR) statistics w (see section 3.1) to test $\theta^{(0)} = 1$ (the logistic model) we have $l_P(\theta^*|N) = 67.4359$, $l_P(\theta^{(0)}|N) = 67.0172$ and $w = 0.8374 < \chi_{1,0.95}^2$ ($\chi_{1,0.95}^2 = 3.8414$). That is, we do not reject the null hypothesis $H_0 : \theta = 1$ (the Logistic model) and we conclude that, there is not evidence in favor of the alternative.hypotheses of the

Theta-logistic model. On the other hand under the Bayesian approach all the selection criteria based posterior sample shown in Table 6 indicate that Theta-logistic model is the best model to be fitted by American Black bears population time series data.

Table 6. The Bayesian model selection criteria based posterior sample

Model	BIC	DIC	$f(N M_l)$	$P(N M_l)^{(*)}$
M_1 : Logistic ($\theta = 1$)	35.51	-82.2	1.38×10^{-18}	9.624×10^{17}
M_2 : Theta-logistic (θ)	37.41	-85.6	2.01×10^{-19}	6.546×10^{18}

$$^{(*)}B_{2,1} = P(N|M_2)/P(N|M_1) = 6.8017$$

The Bayesian estimates of the growth rate and per capita growth rate are shown respectively in Figures 5 and 6 and the real and estimate time series representing the population of the Brazilian Capybara is shown in Figure 7.

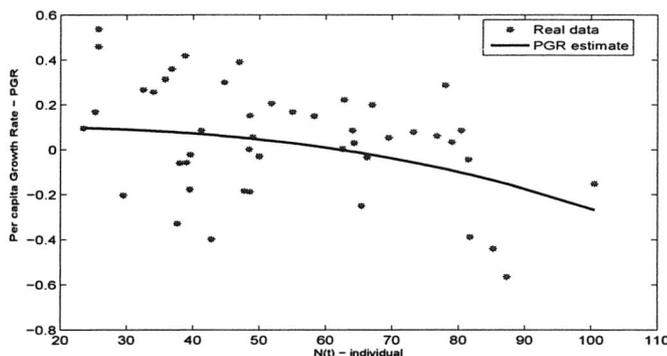


Figure 5. Per capita growth Bayesian estimates for Brazilian Capybara

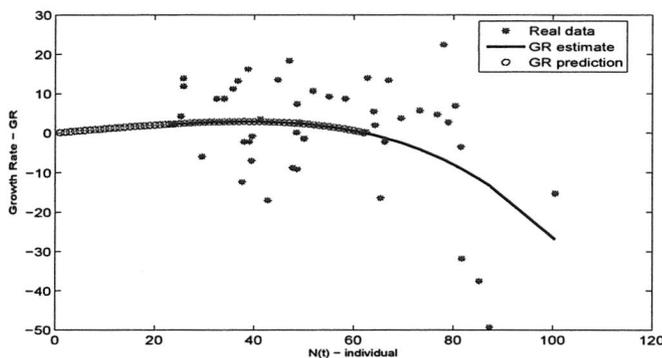


Figure 6. Growth Bayesian estimates for Brazilian Capybara

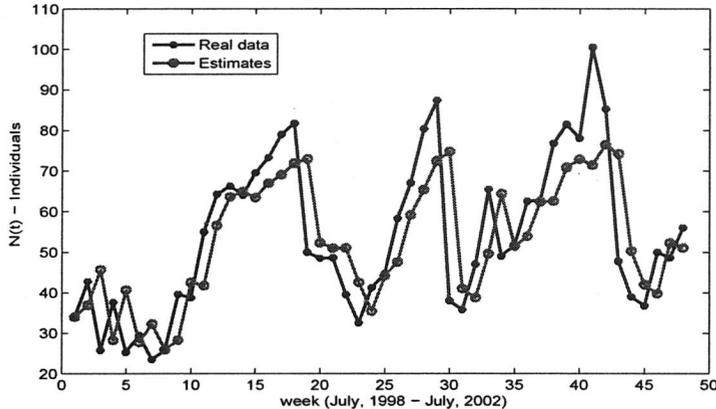


Figure 7. The Bayesian estimates of the Brazilian Capybara population based on real population data of the Atibaia river of July, 1998 to July, 2002

In an appendix at the end of this paper we have the *WinBugs* code for population data analyzed in this paper using another prior: distributions (prior 1 and 2) built with the MLE information. The results obtained with these prior distribution (prior 1 and 2) are similar to the obtained results in the Tables 2 and 5.

7 Conclusions

The Bayesian approach introduced in this paper is applied to two real data sets: the population of American Black Bears (*Ursus americanus*) and the Brazilian Capybara (*Hydrochoerus hydrochaeris*). This paper shows that the Bayesian model with MCMC methods jointly to the criteria for model selection based posterior sample can be used to choose the best model to fit be fitted by time series data. This approach is an efficient approach for the Theta-logistic population growth model identification. The identification method developed here can be applied to evaluate the asymmetric growth rate per capita, due to the consideration of a shape parameter (θ). In this way we use these discrimination methods to identify the models of best fit among the Logistic ($\theta = 1$) or the Theta-logistic model (θ unknown). The Bayesian approach given more accurate interval estimates for the parameter θ . The posterior summaries can be obtained easily using standard software (in this paper we used Matlab and *WinBugs*).

A Appendix: *WinBugs* Codes

In Table A1 we have the *WinBugs* programming for American Black bears population using (a) Prior 1 distributions built with the MLE information, given by: $\rho \sim \text{uniform}(0.10, 0.20)$; $K \sim \text{uniform}(200, 500)$; $\theta \sim \text{uniform}(1, 3)$; $\tau \sim \text{gamma}(0.1, 0.1)$ and (b) Prior 2 distributions; Beta prior for ρ with mean 0.15 and standard-deviation 0.25 and uniform(0.5,4) prior for θ .

Table A1: *WinBugs* codes for American Black bears population

Prior 1 (a)	Prior 2 (b)
<pre>{ for(i in 1 : n) { Y[i]~dnorm(mu[i], tau) a[i] <- N[i] / k mu[i] <- rho*(1- pow(a[i] , theta)) } rho ~dunif(0.10,0.20) k ~dunif(200,500) theta ~dunif(1,3) tau ~dgamma(0.1, 0.1) sigma <- 1 / sqrt(tau) }</pre>	<pre>{ for(i in 1 : n) { Y[i]~dnorm(mu[i], tau) a[i] <- N[i] / k mu[i] <- rho*(1- pow(a[i] , theta)) } rho ~dbeta(0.15,0.85) k ~dunif(200,500) theta ~dunif(0.5,4) tau ~dgamma(0.1, 0.1) sigma <- 1 / sqrt(tau) }</pre>

Replacing the prior distribution of the *WinBugs* codes given in Table A1 by the prior given in Table A2 we have the *WinBugs* codes for Brazilian Capybara population using (a) Priors 1 distributions built with the MLE information, given by: $\rho \sim \text{uniform}(0.01, 0.20)$; $K \sim \text{uniform}(20, 200)$; $\theta \sim \text{uniform}(1, 5)$; $\tau \sim \text{gamma}(0.1, 0.1)$ and (b) Prior: 2 distributions; Beta prior for ρ with mean 0.15 and standard-deviation 0.25; $K \sim \text{uniform}(20, 500)$ and uniform(0.5,5) prior for θ .

Table A2: *WinBugs* priors densities for Brazilian Capybara population

Prior 1 (a)	Prior 2 (b)
$\rho \sim \text{dunif}(0.10, 0.20)$	$\rho \sim \text{dbeta}(0.15, 0.85)$
$k \sim \text{dunif}(20, 200)$	$k \sim \text{dunif}(20, 500)$
$\theta \sim \text{dunif}(1, 5)$	$\theta \sim \text{dunif}(0.5, 5)$
$\tau \sim \text{dgamma}(0.1, 0.1)$	$\tau \sim \text{dgamma}(0.1, 0.1)$
$\sigma <- 1 / \text{sqrt}(\tau)$	$\sigma <- 1 / \text{sqrt}(\tau)$

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