



Anais da Academia Brasileira de Ciências

ISSN: 0001-3765

aabc@abc.org.br

Academia Brasileira de Ciências

Brasil

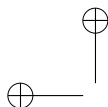
Loibel, Selene; Andrade, Marinho G.; Val, João B.R. do; Freitas, Alfredo R. de
Richards growth model and viability indicators for populations subject to interventions
Anais da Academia Brasileira de Ciências, vol. 82, núm. 4, 2010, pp. 1107-1126
Academia Brasileira de Ciências
Rio de Janeiro, Brasil

Available in: <http://www.redalyc.org/articulo.oa?id=32717686027>

- How to cite
- Complete issue
- More information about this article
- Journal's homepage in redalyc.org

redalyc.org

Scientific Information System
Network of Scientific Journals from Latin America, the Caribbean, Spain and Portugal
Non-profit academic project, developed under the open access initiative



Anais da Academia Brasileira de Ciências (2010) 82(4): 1107-1126
(Annals of the Brazilian Academy of Sciences)
ISSN 0001-3765
www.scielo.br/aabc

Richards growth model and viability indicators for populations subject to interventions

SELENE LOIBEL¹, MARINHO G. ANDRADE², JOÃO B.R. DO VAL³
and ALFREDO R. DE FREITAS⁴

¹Departamento de Estatística, Matemática Aplicada e Computação, Instituto de Geociências e Ciências Exatas,
Universidade Estadual Paulista “Julio de Mesquita Filho”, Av. 24 A, 1515, 13000-900 Rio Claro, SP, Brasil

²Departamento de Matemática Aplicada e Estatística, Instituto de Ciências Matemáticas e de Computação,
Universidade de São Paulo, Caixa Postal 668, 13560-970 São Carlos, SP, Brasil

³Departamento de Telemática, Faculdade de Engenharia Elétrica e de Computação, Universidade de Campinas,
Av. Albert Einstein, 400, Cidade Universitária Zeferino Vaz, 13083-852 Campinas, SP, Brasil

⁴EMBRAPA Pecuária Sudeste, Caixa Postal 339, 13560-970 São Carlos, SP, Brasil

Manuscript received on December 12, 2008; accepted for publication on August 16, 2010

ABSTRACT

In this work we study the problem of modeling identification of a population employing a discrete dynamic model based on the Richards growth model. The population is subjected to interventions due to consumption, such as hunting or farming animals. The model identification allows us to estimate the probability or the average time for a population number to reach a certain level. The parameter inference for these models are obtained with the use of the likelihood profile technique as developed in this paper. The identification method here developed can be applied to evaluate the productivity of animal husbandry or to evaluate the risk of extinction of autochthon populations. It is applied to data of the Brazilian beef cattle herd population, and the the population number to reach a certain goal level is investigated.

Key words: Richards growth model, population risk, harvested populations, parametric estimation, likelihood profile function.

INTRODUCTION

There are multiple reasons for modeling the growth of a population of a certain species. A growth model of a population is an important tool for understanding how environmental uncertainties affect growth. It provides the foundations to growth control policies, slaughter control, etc. These models help to forecast population behavior and to evaluate the risk of extinction or, in the other extreme, population explosion. From the stochastic viewpoint, they allow calculations of the probability of extinction, explosion



populational characteristics are known as population viability indicators. The population viability analysis (PVA) is one of the central tools for conservation planning and evaluation of management options. Compared to other methods, PVA has several advantages (Boyce 1992, Omlin and Reichert 1999, Akçakaya and Sjögren-Gulve 2000). PVA provides a rigorous methodology that can use different types of data a way to incorporate uncertainties, natural variabilities and products or predictions that are relevant to conservation and management goals. The disadvantages of PVA include its single-species focus and requirements for data that may not be available for many species.

There are many works dealing with the population growth of a single population with growth rates depending on its size (see Ludwig 1996, 1999, Allen and Allen 2003, Matis and Kiffe 2004). In (Ludwig 1996, 1999), the Gompertz and the logistic model for single species are considered to calculate extinction probability. In (Matis and Kiffe 2004), a stochastic (Markovian) logistic population growth model with immigration and multiple births is derived, and the equilibrium distribution of the population is approximated to provide the extinction time of a species. The use of some of these models to evaluate the economic impact of population growth control can be found in (Yamauchi 2000). In (Matis et al. 2007), it was developed a generalization of the deterministic and stochastic population size model based on power-law kinetics for the black-margined pecan aphid. Deriso et al. (2008) present a framework for evaluating the cause of fishery declines by integrating covariates into a fisheries stock assessment model. In (Polansky et al. 2008), it was used simulated data to quantify the relative effects of sample size, population disturbances and environmental stochasticity on statistical inference. They focused on the key parameters that inform population dynamics predictions in a generalized Beverton-Holt model. In (Jiao et al. 2009), a hierarchical Bayesian approach for population dynamics modelling was developed to simulate variability in the population growth rates of three fish species.

In this paper, PVA is used to estimate the limiting probability of a population to reach a certain level, or the expected time for the occurrence of this event. It considers the population dynamics described by the Richards model, (Richards 1959), also known as generalized logistic model. As implied, it generalizes the logistic and also the Gompertz growth model (see Loibel et al. 2006). The Richards model was first used for the growth of animals (weight \times age) and only later it was applied to model the populational growth (Fitzhugh 1974). A variation of this model, proposed by Gilpin and Ayala (1973), is known as theta-logistic, and it is used by Saether et al. (2000, 2002a, b) for the study of different populations.

Most of the works found in the literature relies on the logistic or the Gompertz models due to the difficulties to estimate the form parameter of the Richards model. The models with two parameters have a growth rate per capita that is symmetric near the inflexion point at mid level of the carrying capacity. However, this is not the case of populations of large mammals (see Fowler 1981). A three parameter model, such as Richards', is able to fit better to an asymmetric growth rate per capita due to the extra form parameter (see Sibly et al. 2005). In addition to the usual Richards model, we introduce an extension to take into account exogenous interventions on the population. Modeling with interventions becomes very important when we need to identify the growth parameters of a population subjected to human intervention with economic and/or ecological motivations.



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

second place in bovine herd size and in production of beef meat, only surpassed by the USA. The Brazilian bovine population has presented growth in recent years, having about 169 million head of cattle, a increase of more than 10 million just in the last ten years (see ANUALPEC 2008).

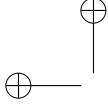
The Brazilian cattle production in the last decades presented constant growth rates in production, export and consumption. Brazil has a potential domestic market for food consumption mainly for the beef meat. The domestic cattle production has always been characterized by an extensive system, since the cattle are mostly bred as unconfined herds, being relying on pastures. In recent years, with the incorporation of new technologies that aim at increasing productivity, the intensive systems of production increased in some regions, being called confined or semi-confined. However, the physical space and other production resources needed for further growth are bound to be scarce in the future, creating a saturation of the growth rate. These models are well described by the class of growth models here studied.

The development of cattle raising becomes even more attractive when the social-economic potential of the meat production chain is considered. The agro-industrial system of animal meat has the largest contribution on the Gross National Product, and the segment denominated “steer” alone is responsible for more than US\$ 30 million a year. According to Pineda (2002), a goal for Brazil is to take advantage of its full potential and to definitely hold the position as one of the international main producers and exporters of bovine meat. This would be to keep a bovine population stable with more than 200 million animals.

Several factors contribute to the growth of bovine populations, which assign an stochastic behavior to the growth process. As a result, the use of methodologies that provide accurate estimates of the population growth in the country is important, as they contribute to the organization of this sector and support to policies on internal consumption, exports and marketing, among others. In this work, we study specifically the Richards model with exogenous interventions on the population to make estimates of the probability of the population beef cattle to achieve a particular goal. The model also allows the estimation of the time up to the occurrence of these events by taking into account the interventions on the population.

The identification problem of the Richards model without intervention and a detailed analysis of the inference of the model parameters were previously addressed in Loibel et al. (2006) by using bootstrap techniques. As in this case, the inference of the present model is treated with the use of the likelihood function technique that, roughly speaking, fix some parameters (the nuisance parameters) to estimate the others (see also (Seber and Wild 1989)). Here the intervention is taken into account as part of the population dynamics, which is removed, which may be brought about by fishing, hunting or slaughter in the case of animal husbandry. In these cases, we are interested in estimating the parameters of the model, not only the ones related to the free trajectory of the process $\{N_t, t \geq 0\}$, but also those associated with the intervention $\{h_t(N_t)\}$, modeled as a stochastic process.

This work is organized in the following way: in section 2, we present Richards’ population growth model with intervention. In section 3, we present the procedure for identification of the parameters of the model employing the maximum likelihood profile function technique. In section 4, we present a Monte Carlo simulation approach to evaluate the indicators of the populational viability. In section 5, we present the results of this analysis for the data gathered over a period of 25 years (1983 to 2008) regarding the Brazilian bovine population.



an adequate slaughter policy is established. Apart from its own importance, this case study offers signposts for similar populational studies.

RICHARDS MODEL WITH INTERVENTION

We consider the size of the population as a stochastic process $\{N_t, t \in \mathbb{N}\}$, where \mathbb{N} is the set of non-negative integers $\{0, 1, 2, \dots\}$. This population consists of adults and young, but only adults can be recruited to slaughter. Denoting the number of slaughtered individuals by $\{H_t, t \in \mathbb{N}\}$, the number of individuals who remain in the population is $R_t = N_t - H_t$, where R_t represents the stock of animals available for slaughter in the next instant $t + 1$.

To write a growth model with an intervention function (or slaughter), we consider the population size N_t and N_{t+1} in two consecutive instants t and $t + 1$, respectively, and the number of slaughtered individuals H_{t+1} . The total number of individuals N_{t+1} can be written as a function of the population size in the instant t (we denote this function by $f(N_t)$) subtracted from individuals who will be slaughtered in the instant $t + 1$. Then, the dynamic model can be written as $R_{t+1} = N_{t+1} - H_{t+1} = f(N_t) - H_{t+1}$.

We model the interventions on this population as a function $\{h_t(R_t), t \in \mathbb{N}\}$, where $0 \leq h_t(R_t) \leq 1$ represents the fraction of R_t of a “removed” population in the instant $t + 1$. Then, the number of slaughtered individuals H_{t+1} is given by $H_{t+1} = h_t(R_t)R_t$. Then, the dynamic model can be written as a cause-effect relation as

$$R_{t+1} = f(N_t) - h_t(R_t)R_t. \quad (1)$$

Supposing that the total population N_{t+1} and N_t are related by the Richards growth function, then we can write that

$$f(N_t) = N_t \exp \left\{ \frac{\rho}{q} \left[1 - \left(\frac{N_t}{K} \right)^q \right] + \epsilon_t \right\}, \quad (2)$$

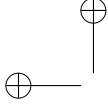
where ϵ_t is a stochastic process in which each value is independent and identically distributed (*i.i.d*) with distribution $N(0, \tau^{-1})$ for $\tau > 0$. It represents the random effects of environment on the growth rate of the Richards model. Parameters ρ is the intrinsic growth rate, K is the carrying capacity, and $q \neq 0$ is a form parameter that changes the shape of the growth curve.

Replacing the equation (2) in (1), we can write the complete model in the presence of interventions as:

$$R_{t+1} = N_t \exp \left\{ \frac{\rho}{q} \left[1 - \left(\frac{N_t}{K} \right)^q \right] + \epsilon_t \right\} - h_t(R_t)R_t \quad (3)$$

To elaborate the intervention function, note that it should depend on the available population, and an admissible model for $h_t(R_t)$ is a linear piecewise model given by:

$$h_t(R_t) = \begin{cases} 0, & \text{if } R_t \leq R_0, \\ h_0 \left(\frac{R_t - R_0}{K - R_0} \right), & \text{if } R_0 < R_t \leq K, \\ h_0, & \text{if } R_t > K. \end{cases} \quad (4)$$



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

there is no reproduction, but we can choose larger values for R_0 , if there are Allee effects. The parameter h_0 , $0 < h_0 \leq 1$, is the maximum intervention rate due to the technological and physical limitations of the intervention action. The equation (4) can be written as:

$$h_t(R_t) = \phi_0 + \phi_1 R_t + \varpi_t \quad \text{for } R_0 < R_t \leq K,$$

where ϖ_t is a non-correlated *i.i.d.* stochastic process with distribution $N(0, \eta^{-1})$, with $\eta > 0$. We assume that ϵ_t and ϖ_t are independent processes; therefore, we have that $E(\epsilon_t \varpi_t) = 0$. In (5) we consider $\phi_0 = -h_0 R_0 / (K - R_0)$, $\phi_1 = h_0 / (K - R_0)$ or $R_0 = -\phi_0 / \phi_1$, and $h_0 = \phi_1 (K + \phi_0 / \phi_1)$. Considering the model in (5) for the rate of intervention $h_t(R_t)$ as a function of the available population R_t , we have the conditional distribution density $P(h_t(R_t)|R_t)$ is a Gaussian $N(\phi_0 + \phi_1 R_t, \eta^{-1})$.

The equation (3) can be written as:

$$(R_{t+1} + h_t(R_t)R_t)^q = N_t^q \exp \left\{ \rho \left[1 - \left(\frac{N_t}{K} \right)^q \right] + q\epsilon_t \right\}.$$

We denote $N_{t+1}^{(q)} = N_{t+1}^q = (R_{t+1} + h_t(R_t)R_t)^q$ and $N_t^{(q)} = N_t^q$, and also set $y_{h,t}^{(q)} = q \ln(N_{t+1}^{(q)} / N_t^{(q)})$ and $z_t = q\epsilon_t$. We can, then, rewrite the equation (6) as a linear relation:

$$y_{h,t}^{(q)} = \alpha_0 + \alpha_1 N_t^{(q)} + z_t,$$

with $\alpha_0 = \rho$ and $\alpha_1 = -\rho/K^q$.

From the fact that ϵ_t is a *i.i.d* stochastic process with distribution $N(0, \tau^{-1})$, it follows that $y_{h,t}^{(q)}$ is also *i.i.d* stochastic process with Gaussian density with zero mean and variance $\tau_0^{-1} = q^2 \tau^{-1}$. We can then, conclude from the equation (7) that the conditional density $P(y_{h,t}^{(q)}|N_t, R_t, h_t(R_t))$ is Gaussian with mean $\alpha_0 + \alpha_1 N_t^{(q)}$ and variance $\tau_0^{-1} = q^2 \tau^{-1}$. We use this characterization to formulate the identification problem for the Richards model.

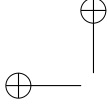
MODEL FITTING

In order to formulate the problem of fitting the Richards model with intervention, by maximum likelihood method, it is necessary to know the joint distribution of the processes $\{N_t, R_t, h_t(R_t), t \geq 0\}$. If we know the stochastic processes R_t and $h_t(R_t)$, we can recover the stochastic process N_t using the relation $N_t = R_t + h_t(R_t)R_t$. We begin the evaluations with the joint distribution of the processes $\{y_{h,t}^{(q)}, h_t(R_t), R_t\}$, we have, therefore:

$$P(y_{h,t}^{(q)}, h_t(R_t)|N_t, R_t) = P(y_{h,t}^{(q)}|N_t, R_t, h_t(R_t))P(h_t(R_t)|N_t, R_t),$$

To write the joint density for the original processes, $P(N_{t+1}, h_t(R_t)|N_t, R_t)$, we should consider the Jacobian of the transformation $y_{h,t}^{(q)} = q \ln(N_{t+1}/N_t)$ given by:

$$J_{Y,N} = \left| \frac{dy_{h,t}^{(q)}}{dN_{t+1}} \right| = \frac{q}{N_{t+1}}.$$



Considering the model in (5) and (7), we can write the joint conditional density (10) for $\{N_{t+1}, h_t(R_t)\}$ as:

$$P(N_{t+1}, h_t(R_t)|N_t, R_t) \propto \frac{q\tau_0^{\frac{1}{2}}\eta^{\frac{1}{2}}}{N_{t+1}} \exp\left\{-\frac{\tau_0}{2}\left(y_{h,t}^{(q)} - \alpha_0 - \alpha_1 N_t^{(q)}\right)^2\right\} \exp\left\{-\frac{\eta}{2}(h_t(R_t) - \phi_0 - \phi_1 R_t)^2\right\}. \quad (11)$$

With (11) we can construct the likelihood function used to estimate the parameters of the model.

LIKELIHOOD FUNCTION

Adopting the matrix notation $\mathbf{N}' = (N_1, \dots, N_n)$, $\mathbf{R}' = (R_1, \dots, R_n)$, $\mathbf{h}' = (h_1(R_1), \dots, h_n(R_n))$, $\mathbf{D} = (\mathbf{N}, \mathbf{R}, \mathbf{h})$, $\alpha' = (\alpha_0, \alpha_1)$, $\phi' = (\phi_0, \phi_1)$, we conclude that the likelihood function for the Richards model with stochastic intervention is given by:

$$L(\alpha, \phi, \tau_0, \eta, q|\mathbf{D}) = \prod_{t=1}^{n-1} P(N_{t+1}, h_t(R_t)|N_t, R_t) \quad (12)$$

and

$$L(\alpha, \phi, \tau_0, \eta, q|\mathbf{D}) \propto q^{n-1} \tau_0^{\frac{n-1}{2}} \eta^{\frac{n-1}{2}} \exp\left\{-\frac{\tau_0}{2}(\mathbf{Y}^{(q)} - \mathbf{X}^{(q)}\alpha)'(\mathbf{Y}^{(q)} - \mathbf{X}^{(q)}\alpha)\right\} \exp\left\{-\frac{\eta}{2}(\mathbf{h} - \mathbf{V}\phi)'(\mathbf{h} - \mathbf{V}\phi)\right\} \left(\prod_{t=1}^{n-1} \frac{1}{N_{t+1}}\right). \quad (13)$$

In the equation (13), we are using the notation $\mathbf{Y}^{(q)'} = [y_{h,1}^{(q)}, \dots, y_{h,n}^{(q)}]$, $\mathbf{N}^{(q)'} = [N_1^{(q)}, \dots, N_n^{(q)}]$ and $\mathbf{X}^{(q)} = [\mathbf{1}, \mathbf{N}^{(q)}]$, $\mathbf{V} = [\mathbf{1}, \mathbf{R}]$, with $\mathbf{1}$ being a $n \times 1$ vector of ones. Due to the separability of $L(\alpha, \phi, \tau_0, \eta, q|\mathbf{D})$ regarding the parameters (α, τ_0) and (ϕ, η) , we can write the log-likelihood function as:

$$l(\alpha, \phi, \tau_0, \eta, q|\mathbf{D}) = l_1(\alpha, \tau_0, q|\mathbf{D}) + l_2(\phi, \eta|\mathbf{D}), \quad (14)$$

where:

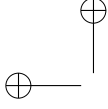
$$l_1(\alpha, \tau_0, q|\mathbf{D}) = \frac{n-1}{2} \ln(\tau_0) - \frac{\tau_0}{2}(\mathbf{Y}^{(q)} - \mathbf{X}^{(q)}\alpha)'(\mathbf{Y}^{(q)} - \mathbf{X}^{(q)}\alpha) + (n-1) \ln(q) - \sum_{t=1}^{n-1} \ln(N_{t+1}) \quad (15)$$

and

$$l_2(\phi, \eta|\mathbf{D}) = \frac{n-1}{2} \ln(\eta) - \frac{\eta}{2}(\mathbf{h} - \mathbf{V}\phi)'(\mathbf{h} - \mathbf{V}\phi). \quad (16)$$

To make inference about model parameters it is necessary to calculate the Fisher information matrix. We adopted the matrix notation $\theta = (\alpha', \tau_0)$ and $\gamma = (\phi', \eta)$. Then, for a fixed q , the Fisher information matrix for θ and γ has the form:

$$\mathbf{I}^{(q)} = \begin{bmatrix} \mathbf{I}_{\theta\theta}^{(q)} & 0 \\ 0 & \mathbf{I}_{\gamma\gamma}^{(q)} \end{bmatrix}, \quad (17)$$



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

THE ESTIMATION OF THE PARAMETERS $\theta^{(q)}$

We use the likelihood function for the Richards model (15), for a fixed value of the parameter q to calculate the maximum likelihood estimates (MLE) of the parameters $\theta^{(q)} = (\alpha^{(q)}, \tau_0^{(q)})$, conditioned to a particular value of q . We denote these estimators by $\hat{\theta}^{(q)} = (\hat{\alpha}^{(q)}, \hat{\tau}_0^{(q)})$. Substituting these estimators in equation (15), we have the profiled likelihood function for parameter q given by

$$l_p(q|\mathbf{D}) = \frac{n-1}{2} \ln(\hat{\tau}_0^{(q)}) + (n-1) \ln(q) - \sum_{t=1}^{n-1} \ln(N_{t+1}).$$

The equation (18) is a modified version of the profile likelihood function for the Richards model (Loibel et al. (2006)), which includes the presence of the intervention in the vector $N_{t+1} = N_{t+1} - h_{t+1}(R_{t+1})R_{t+1}$. We should find the maximum profile likelihood estimate (MPLE) q^* of the parameter q evaluating the function (18) for many values of the parameter $q \in [q_{\min}, q_{\max}]$, and finding q^* that maximizes the function (18).

$$q^* = \max_{q \in [q_{\min}, q_{\max}]} l_p(q|\mathbf{D}).$$

The maximum likelihood estimates (MLE) of the parameters $\theta^{(q)} = (\alpha^{(q)}, \tau_0^{(q)})$, conditioned to $q = q^*$ are given by

$$\hat{\alpha}^{(q^*)} = (\mathbf{X}^{(q^*)'} \mathbf{X}^{(q^*)})^{-1} \mathbf{X}^{(q^*)'} \mathbf{Y}^{(q^*)}$$

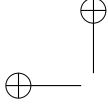
$$\hat{\tau}_0^{(q^*)} = \frac{(n-1)}{(\mathbf{Y}^{(q^*)} - \mathbf{X}^{(q^*)} \hat{\alpha}^{(q^*)})' (\mathbf{Y}^{(q^*)} - \mathbf{X}^{(q^*)} \hat{\alpha}^{(q^*)})}.$$

The variance for these conditional maximum likelihood estimators is analogous to the one derived in Loibel et al. (2006). The variance for $\hat{\alpha}^{(q)}$ can be calculated using the result of the asymptotic theory of Seber and Wild (1989), $Var(\hat{\alpha}^{(q)}) = (\hat{\tau}^{(q)})^{-1} (\mathbf{X}^{(q)'} \mathbf{X}^{(q)})^{-1}$. Consider the original vector of parameters $\beta^{(q)} = (\rho^{(q)}, K^{(q)})$ conditioned on the parameter q and the vector of parameters $\alpha^{(q)} = (\alpha_1^{(q)}, \alpha_2^{(q)})$ by parametrization $\alpha_1 = \rho$, $\alpha_2 = -\rho/K^q$. The observed information matrix $I(\alpha^{(q)}) = \hat{\tau}^{(q)} (\mathbf{X}^{(q)'} \mathbf{X}^{(q)})$ can be calculated with the observed information matrix $I(\beta^{(q)})$ and the Jacobian of the transformation $\alpha_1 = \rho$, $\alpha_2 = -\rho/K^q$ (to details, see Seber and Wild (1989)), given by

$$J_{\alpha\beta} = \frac{\partial \alpha^{(q)}}{\partial \beta^{(q)}} = \begin{pmatrix} 1 & 0 \\ -K^{-q} & q\rho K^{-(q+1)} \end{pmatrix}.$$

The Fisher information matrix for the original vector of parameters is given by

$$I(\beta^{(q)}) = \hat{\tau}^{(q)} J_{\alpha\beta}' (\mathbf{X}^{(q)'} \mathbf{X}^{(q)}) J_{\alpha\beta},$$



ESTIMATION OF THE PARAMETER $\gamma^{(q)}$

The estimators of maximum likelihood for ϕ and η are calculated by maximizing the function $l(\gamma|D)$ given in (16). Therefore, we have:

$$\hat{\phi} = (\mathbf{V}'\mathbf{V})^{-1}\mathbf{V}'\mathbf{h} \quad (24)$$

$$\hat{\eta} = \frac{(n-1)}{(\mathbf{h} - \mathbf{V}\hat{\phi})'(\mathbf{h} - \mathbf{V}\hat{\phi})}. \quad (25)$$

The variance for $\hat{\phi}$ can be calculated straightforward by $Var(\hat{\phi}) = \hat{\eta}^{-1}(\mathbf{V}'\mathbf{V})^{-1}$. The relation $R_0 = -\phi_0/\phi_1$ and $h_0 = \phi_1(K + \phi_0/\phi_1)$ are used to estimate the parameters present in the slaughter function h_t . The variance for the vector of original parameters $\psi = (h_0, R_0)$ can be estimated with the observed information matrix $I(\phi) = \hat{\eta}(\mathbf{V}'\mathbf{V})$ calculated with the observed information matrix $I(\phi)$ and the Jacobian of the transformations $R_0 = -\phi_0/\phi_1$ and $h_0 = \phi_1(K + \phi_0/\phi_1)$ (to details, see Seber and Wild (1989)), given by

$$J_{\phi\psi} = \frac{\partial \phi}{\partial \psi} = \begin{pmatrix} \frac{-R_0}{K - R_0} & \frac{-h_0 K}{(K - R_0)^2} \\ \frac{1}{K - R_0} & \frac{h_0}{(K - R_0)^2} \end{pmatrix}. \quad (26)$$

The Fisher information matrix for the original vector of parameters is given by

$$I(\psi) = \hat{\eta} J_{\phi\psi}' (\mathbf{V}'\mathbf{V}) J_{\phi\psi}, \quad (27)$$

the variance for the estimates of the original parameters $\psi = (h_0, R_0)$ is given by

$$Var(\psi) = \hat{\eta}^{-1} (J_{\phi\psi})^{-1} (\mathbf{V}'\mathbf{V})^{-1} (J_{\phi\psi}')^{-1}$$

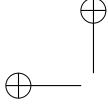
and the variance for $\hat{\eta}$ is given by $Var(\hat{\eta}^{-1}) = 2/(n-1)\hat{\eta}^2$.

ESTIMATION OF THE PARAMETER q

It is often of interest to test if the parameter q of the Richards model is equal to a known value $q^{(0)}$, that is, $H_0 : q = q^{(0)}$. In this way, we can easily obtain from the profile a likelihood ratio (LR) statistics $w = 2\{l_P(q^*|\mathbf{D}) - l_P(q^{(0)}|\mathbf{D})\}$ to test $q = q^{(0)}$, which has an asymptotical Chi-square χ_1^2 distribution with one degree of freedom, (Barndorff-Nielsen and Cox 1994). From this result, we can produce a large sample confidence interval for q by inverting the LR test. An approximate confidence interval for q is, then, readily obtained from $\{q | l_P(q|\mathbf{D}) > l_P(q^*|\mathbf{D}) - \frac{1}{2}\chi_1^2(\delta)\}$, and the accuracy of this approximation comes from the fact that $Pr\{w \geq \chi_1^2(\delta)\} = \delta + O(n^{-1/2})$.

CALCULATION OF VIABILITY INDICATORS

In general, the growth models are adjusted to allow the calculation of viability indicators of a population, such as the probability of the population to reach a determined upper level defined by $G = \{x \in \mathbb{R}_+ : x \leq$



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

MONTE CARLO SIMULATION APPROACH

We consider the populational growth model given by equations (3) and (5), remembering that ϵ_t and ω_t are independent processes, with ϵ_t , *i.i.d.* $N(0, \tau^{-1})$ and ω_t , *i.i.d.* $N(0, \eta^{-1})$. With these models, we simulate the behavior of a population over a long period of time and generate possible trajectories of the processes $\{N_t^{(j)}, R_t^{(j)}, h_t^{(j)}(R_t), j = 1, \dots, J\}$ for values of time beginning with $t = T_0$, for a certain instant T_0 of interest. In this way, we estimate the risk or probability of the population reaching a goal by counting how many trajectories were necessary for this goal to be achieved among all of the J generated trajectories. We denote the time elapsed to achieve this goal by T_G , with $T_G = \inf\{k > T_0 : N_k \in G\}$ and the number associated to these occurrences by $\#\{T_G < \infty\}$. Therefore, we have the probability estimate of the population reaching a certain goal by:

$$\widehat{P}(N_k \in G | N_{T_0}) = \frac{\#\{T_G < \infty | N_{T_0}\}}{J}.$$

In some cases, we may be interested in calculating not only the probability of the population to reach a certain state, but also to evaluate the expected time for the population to reach a certain state. The time necessary for the population to reach a goal is a stop time T_G and its expected value can be estimated using the generated trajectories by simply evaluating the time to reach the level to each realization $j = 1, 2, \dots, J$. We, then, have the estimate:

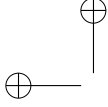
$$\overline{T}_G = \frac{1}{J} \sum_{j=1}^J T_G^{(j)}.$$

We should adopt a very large number of J trajectories in view of the law of large numbers to ensure the convergence of the estimators (28) and (29) for the true values. Another difficulty found in the practical application of this technique is that, depending on the intervention policy adopted $\{h_t, t \geq T_0\}$, the goal may become unreachable or perhaps reachable with a very low probability. It is necessary, therefore, to establish a limit for the maximum simulation time that will be associated to the infinite time. We denote the infinite time by T_∞ , that is, $\{T_k < \infty\} \equiv \{T_k < T_\infty\}$. Then, in the simulation process N_t , we have $N_t < G$ for $t \leq T_\infty$, and we consider that the goal was not reached.

DETERMINISTIC INTERVENTION

There are situations in which we can consider the intervention h_t as a deterministic function. One of these situations occurs when we want to evaluate the impact of an intervention, for example, in a population where a government policy establishes that the removal of a population should be done in a certain percentage of the year. An estimate of the mean removal can be established, and we wish to evaluate the impact of this average removal on the population. Another situation occurs in long-term studies when we wish to evaluate the impact on the population when a mean removal is carried out over a long period of time.

In these cases, the estimates of the parameters and the risk of extinction are obtained for a pre-determined intervention policy. Assuming that $\{h_t(R_t), t \geq 0\}$, which means a deterministic function



MARKOV CHAIN WITH DETERMINISTIC INTERVENTION

When the intervention h_t is deterministic, the recursive equation (2) can generally be written as

$$N_{t+1} = f_h(N_t, \epsilon_t). \quad (30)$$

The subscript h indicates that, somehow, the function $f_h(\cdot)$ depends on the action h . In the model proposed in this paper, the intervention h affects the maximum likelihood estimators of the parameters of the function $f_h(\cdot)$, which are calculated using the equations (19)–(21). The process $\{\epsilon_t, t = 0, 1, \dots\}$ is independent and identically distributed, with $E(\epsilon_t) = 0$ and $E(\epsilon_t \epsilon_{t+s}) = 0$, if $s \neq 0$ and $E(\epsilon_t^2) = \tau^{-1}$.

We can adopt a discrete state space model for the problem of population growth whose continuous states space E can be decomposed into the disjoint union

$$E = \bigcup_{i=1}^{N_E} I_i \quad \text{with} \quad I_i \cap I_j = \emptyset, i \neq j. \quad (31)$$

The probability of the population to reach a certain state I_j at instant $t + 1$, given the records of the population $\mathcal{N}_t = \{N_1, N_1, \dots, N_t\}$ and of the intervention $\mathcal{H}_t = \{h_0, h_1, \dots, h_t\}$, is written as follows:

$$P(N_{t+1} \in I_j | \mathcal{N}_t, \mathcal{H}_t) = P(\mathcal{E}_t | \mathcal{N}_t, \mathcal{H}_t), \quad (32)$$

where $\mathcal{E}_t = \{\epsilon_t | f_h(N_t, \epsilon_t) \in I_j\}$.

From (30) we see that the random process $\{N_0, N_1, \dots, N_t\}$ is function of the basic random process $\{N_0, \epsilon_1, \dots, \epsilon_{t-1}\}$, which is independent of ϵ_t . Hence, ϵ_t is also independent of $\{N_0, N_1, \dots, N_t\}$. Under these conditions, we can write that

$$P(N_{t+1} \in I_j | \mathcal{N}_t, \mathcal{H}_t) = P(\epsilon_t | f_h(N_t, \epsilon_t) \in I_j). \quad (33)$$

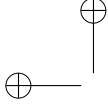
If $N_t \in I_i$, for some $I_i \subset E$, we can adopt a Markov chain model for the problem of population growth with the probability of transition between states I_i and I_j , $p_{ij} = P(N_{t+1} \in I_j | N_t \in I_i)$, given by:

$$p_{ij} = P(\epsilon_t | f_h(N_t, \epsilon_t) \in I_j) \quad \text{with} \quad N_t \in I_i \quad \text{for some} \quad I_i \subset E. \quad (34)$$

Let \mathbf{P} be a square matrix with the elements p_{ij} , defined for all $\{(i, j), 0 \leq i, j \leq N_E\}$. Then, \mathbf{P} is called Markov matrix over E if it satisfies the following properties:

$$p_{ij} \geq 0 \quad \text{and} \quad \sum_{j=1}^{N_E} p_{ij} = 1, \forall 0 \leq i, j \leq N_E. \quad (35)$$

We are interested in calculating the probability of the chain leaving a state I_i at instant t and reaching a state I_j at instant $t + s$, $s \geq 0$. Therefore, we should calculate the transition probability matrix in s steps



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

In many problems, we may be interested in calculating the probability of a population reaching a state above I_j . Thus, denoting $M = \bigcup_{k=j}^{N_E} I_k$, we have:

$$P(N_s \in M | N_0 \in I_i, 1 \leq i < j) = \sum_{l \geq j} P(N_s \in I_l | N_0 \in I_i).$$

In other words, the probability of reaching M is the sum of columns l , so that $l \geq j$ on line i of the matrix \mathbf{P}^s .

For the calculation of the transition matrix using the Richards model with intervention, we use $F_h(N_t) = (\rho/q)(1 - (N_t/K)^q)$ and rewrite the model (3) as:

$$N_{t+1} = N_t \exp\{F_h(N_t) + \epsilon_t\},$$

where $N_{t+1} = R_{t+1} + h_t(R_t)R_t$; then,

$$\epsilon_t = \ln\left(\frac{N_{t+1}}{N_t}\right) - F_h(N_t).$$

If I_i and I_j are any two states of space of states E , and assuming that $I_j = [A_j, B_j]$, then an interval $[a_j, b_j]$ exists so that we can calculate the transition matrix in one step with elements $p_{ij} = P(N_{t+1} \in I_j | N_t \in I_i)$ and rewrite the equation (34) by:

$$p_{ij} = P(a_j \leq \epsilon_t \leq b_j | f_h(N_t, \epsilon_t) \in I_j)$$

to find $[a_j, b_j]$. We can use the equation (37) to write:

$$P[A_j \leq N_{t+1} \leq B_j | N_t \in I_i] = P[A_j \leq N_t \exp\{F_h(N_t) + \epsilon_t\} \leq B_j | N_t \in I_i].$$

Then, we can write that

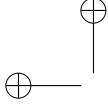
$$p_{ij} = P\left\{\log\left(\frac{A_j}{N_t}\right) - F_h(N_t) \leq \epsilon_t \leq \log\left(\frac{B_j}{N_t}\right) - F_h(N_t) | N_t \in I_i\right\}.$$

With equations (38) and (39), we can write that

$$\begin{aligned} a_j &= \log\left(\frac{A_j}{N_t}\right) - F_h(N_t) \\ b_j &= \log\left(\frac{B_j}{N_t}\right) - F_h(N_t). \end{aligned}$$

Assuming that ϵ_t is a process with Gaussian distribution $N(0, \tau^{-1})$, we can calculate p_{ij} from the standard Gaussian accumulated distribution function with:

$$p_{ij} = P(N_{t+1} \in I_j | N_t \in I_i) = \Phi(\tau^{1/2}b_j) - \Phi(\tau^{1/2}a_j).$$



population may assume within the intervals. The accuracy of this approach depends on the discretization refinement of the space of states.

Given that $N_0 \in I_i$, we wish to calculate the expected value $E(T)$, so that N_s makes the first passage for the state I_j . In practice, there are many situations where the calculation of first-passage time is important. In the case of control of populations that grow explosively, we want to calculate the time expected for the population to reach a point that justifies intervention, such as controlled slaughter.

DEFINITION 1. First-passage time: Let I_i and I_j be two states of a Markov chain $\{N_t, t \in \mathbb{I}_+\}$ with space of states E . If, for a given time t , $N_t \in I_i$, the first-passage time of the state I_i to state I_j is defined as:

$$T_{ij} = \inf\{s : s \in \mathbb{I}_+, N_{t+s} \in I_j\}. \quad (44)$$

DEFINITION 2. For any $s \in \mathbb{I}_+$, the probability function of T_{ij} is defined by:

$$g_{ij}(t) = P(T_{ij} = t) \quad \forall I_i, I_j \in E, t \in \mathbb{I}_+. \quad (45)$$

By convention, we adopt $g_{ij}(0) = 0$.

DEFINITION 3. Expected value of first-passage time:

$$\mu_{ij} = E[T_{ij}] \mu_{ij} = E[T_{ij}]. \quad (46)$$

PROPOSITION 1. For every pair of states $(I_i, I_j) \subset E$, we have:

$$g_{ij}(1) = p_{ij} \quad (47)$$

$$g_{ij}(t) = \sum_{k \neq j} p_{ik} g_{kj}(t-1). \quad (48)$$

PROOF. Using Definition 2 for $t = 1$, we have:

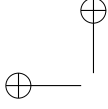
$$P(T_{ij} = 1) = P(N_1 \in I_j | N_0 \in I_i) \quad (49)$$

Therefore,

$$g_{ij}(1) = p_{ij} \quad (50)$$

Since $P(T_{ij} = t) = P(N_t \in I_j | N_0 \in I_i)$ and considering all of the possible states I_k with $k \neq j$, we have:

$$P(N_t \in I_j | N_0 \in I_i) = \sum_{k \neq j} P(N_t \in I_j | N_{t-1} \in I_k) P(N_{t-1} \in I_k | N_0 \in I_i). \quad (51)$$



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

PROPOSITION 2. $E = \bigcup_{k=1}^{NI} I_k$ with $I_i \cap I_j = \emptyset, \forall i \neq j$; let $N_0 \in I_i$ and $\mu = (\mu_{ij}, 0 \leq i \leq NI \text{ e } i \neq j)$ be the expected times to reach state I_j , starting from any I_i state. We can calculate μ by resolving the system of equations given by:

$$(\mathbf{I} - \mathbf{Q})\mu = \mathbf{1},$$

where \mathbf{I} is the matrix identity $(NI - 1) \times (NI - 1)$, $\mathbf{1} = (1, \dots, 1)'$ is a vector $(NI - 1) \times 1$, \mathbf{Q} is the matrix $((NI - 1) \times (NI - 1))$ obtained by removing the line and the column j from the matrix \mathbf{P} .

PROOF. We will consider that:

$$E[T_{ij}|N_1 \in I_k] = \begin{cases} 1 & k = j \\ 1 + \mu_{kj} & k \neq j. \end{cases}$$

We can write that:

$$\mu_{ij} = E[T_{ij}] = E_{N_1}\{E[T_{ij}|N_1 \in I_k]\} = \sum_k E[T_{ij}|N_1 \in I_k]p_{ik}.$$

Replacing (54) in (55), we have:

$$\mu_{ij} = 1 \cdot p_{ij} + \sum_{k \neq j} (1 + \mu_{kj})p_{ik} = p_{ij} + \sum_{k \neq j} p_{ik} + \sum_{k \neq j} \mu_{kj}p_{ik}$$

$$\mu_{ij} = E[T_{ij}] = 1 + \sum_{k \neq j} \mu_{kj}p_{ik}.$$

Establishing a j and writing (57) for $\mu = (\mu_{ij}, 0 \leq i \leq NI \text{ e } i \neq j)$, we have the system of equations given by:

$$(\mathbf{I} - \mathbf{Q})\mu = \mathbf{1}.$$

The Markov chain modeling can only be used together with a constant slaughter rate, and it is not appropriate for evaluation of scenarios in long-term planning. On the other hand, the Monte Carlo simulation approach can handle more general slaughter functions but it also requires a larger computational effort. A comparison between these two approaches, for constant slaughter rates is presented in the Results section.

RESULTS

In this study, we propose an evaluation of the growth of meat production in Brazil based on data regarding the number of cattle and annual slaughter between 1983 and 2008 (ANUALPEC 2008). The population and slaughter data referring to this period are presented on the graphs shown in Figures 1 and 2, in millions of heads, together with the adjusted values, according to the equations (3) and (5), respectively.

Table I presents the maximum likelihood estimates (MLE) and the standard deviation (SD) of the parameters of the Richards model adjusted to the population data in Figure 1, and of the parameters of the

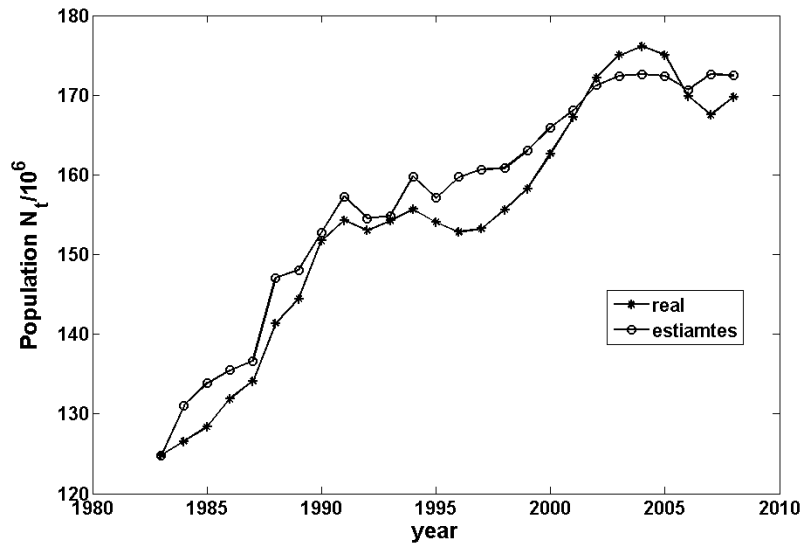


Fig. 1 – Bovine population in Brazil, in millions of heads, between 1983 and 2008.

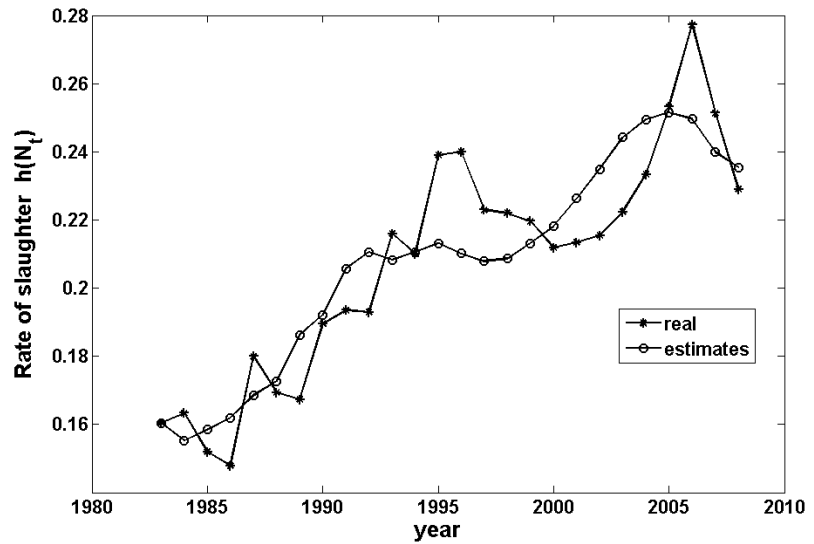


Fig. 2 – Slaughter of the bovine population in Brazil between 1983 and 2008.

TABLE I

The MLE and SD estimates of the Richards model parameters.

Population				
	K	q	ρ	τ^{-1}
MLE	217.5701	3.4	0.1389	2.7642×10^{-4}
SD	3.0419	1.554	0.01	7.9794×10^{-5}
Intervention				

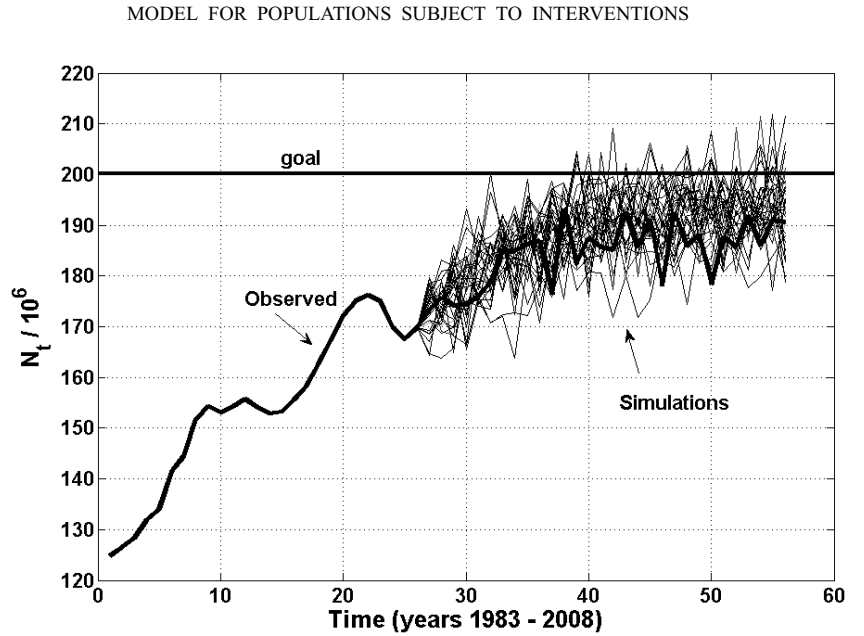
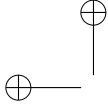


Fig. 3 – Simulation of the trajectories of N_t for 30 years ahead.

An important observation refers to the estimated values of K and h_0 that represent the carrying capacity and maximum slaughtering allowed, respectively. Note that the carrying capacity estimate $K = 217.5701$ exceeded the maximum population level $N_{26} = 176.1144$ million head of cattle observed in 2004 (see Figure 1) and $h_0 = 0.3294$ that represents an estimate of the maximum slaughter rate is exceeding the maximum rate, which was about 0.2772, observed in 2006 (see Figure 2). K and h_0 are the two main parameters that affect the population growth. In this work, we perform simulations of population growth for different values of K and h_0 , close to estimated values, in order to estimate the probability and the expected time of the population to reach a given goal.

The graph in Figure 3 presents some of the 100 thousand simulations of trajectories of the population that were generated to calculate the probability of the population reaching the goal of 200 million head.

In Table II, we present the probability p (Percent) and the expected time T (year) for this event to occur, considering scenarios with K increased from the estimated value to the value of 250 million head and h_0 increased from the actual observed value 0.21 to the estimated value 0.3294 given in Table I.

Note that the probability that the Brazilian herd will reach the goal of 200 million head proposed by Pineda (2002) when $h_0 = 0.3294$ and $K = 217$ million heads is only $p = 0.02\%$, and the time expected for this event to occur is $T \approx 74$ years. These results point out that an optimized slaughter policy is not enough together with investments in technology that improve the reproduction rates and carrying capacity of the Brazilian bovine herd and make possible to reach the population goal in a desirable time interval as 74 years with $p \approx 94\%$, which can be achieved with $h_0 \approx 0.25$ and $K \approx 250$ million head.



TABLE II
Indicators estimates via Monte Carlo simulation.

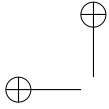
Rate h_0	Carrying capacity (K)									
	217		220		230		240		250	
	p	T	p	T	p	T	p	T	p	T
0.21	9.21	60.27	15.73	52.02	60.04	21.10	92.29	11.34	99.06	8.18
0.22	5.67	64.77	10.80	57.69	50.81	24.59	88.45	12.58	98.44	8.94
0.23	3.53	68.13	6.62	62.83	41.78	29.01	82.61	14.41	97.57	9.73
0.24	2.29	70.28	4.60	66.06	32.52	34.14	76.53	15.92	96.15	10.68
0.25	1.30	71.78	2.75	68.99	24.85	39.61	69.48	17.89	93.96	11.63
0.26	0.82	72.53	1.44	71.04	18.16	45.54	60.90	20.43	90.44	12.72
0.27	0.45	73.13	0.98	72.10	12.97	51.04	52.56	23.11	86.84	13.79
0.28	0.21	73.59	0.61	72.71	9.59	55.72	43.70	26.33	82.14	15.08
0.29	0.10	73.78	0.41	73.24	6.49	60.52	36.40	29.40	76.59	16.36
0.3294	0.02	73.97	0.06	73.90	1.26	70.48	14.05	47.59	48.18	23.87

two methods we presented, in Figure 4, both indices calculated with each of the methodologies presented, considering $K = 230$. Estimates made by the Monte Carlo simulation are in the third column of Table I. An analysis of the curves in Figure 4 shows a great similarity between the two approaches. However, being practical, the modeling by Markov chain requires some careful with the choice of size and the discretization of the space state. These results can be seen in Table III and on the graphs in Figure 4.

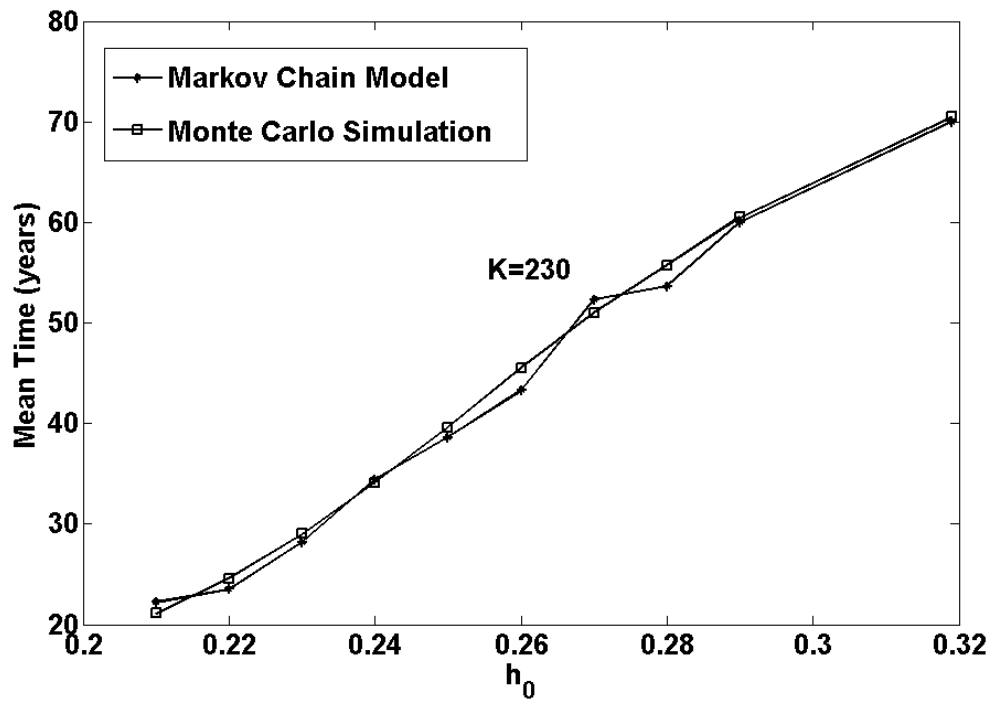
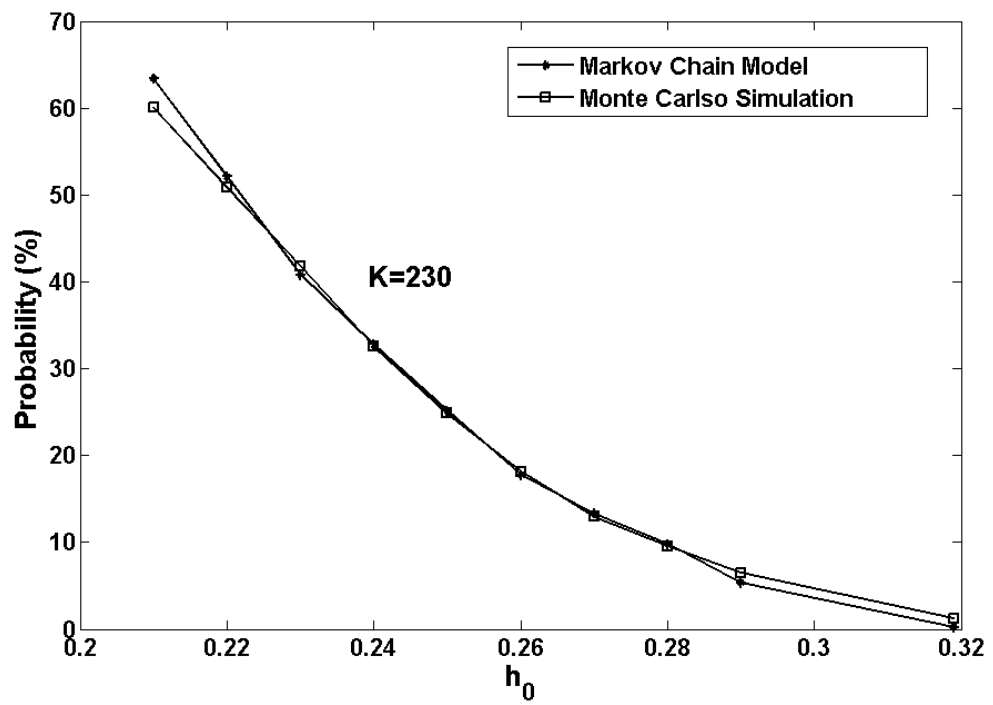
TABLE III
Estimates of the indicators by Markov chain
as function of maximum slaughter rate.

h_0	Time-MC	Prob-MC
0.21	22.2439	0.6340
0.22	23.5111	0.5211
0.23	28.1966	0.4079
0.24	34.4267	0.3279
0.25	38.6040	0.2514
0.26	43.2941	0.1775
0.27	52.3350	0.1333
0.28	53.6280	0.0983
0.29	60.0000	0.0537
0.30	T_∞	0.0135
0.3294	T_∞	0.0020

From the results of Table III we note that, with a maximum slaughter rate of 21%, we reach the population goal with the probability of 63% and a mean time period of 22 years for this event to occur.



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS





CONCLUSIONS

In this work, we presented the adjustment of the Richards growth model for the bovine population in Brazil taking into consideration the populational losses due to the slaughter intervention. With the model adjustment that includes the stochastic intervention and posteriorly Monte Carlo simulations, we were able to estimate the indicators of the population viability. By considering deterministic intervention, we calculated the indicators, assuming that the population can be modeled by a Markov chain. We also employed Monte Carlo simulations to compare the results between these two methods. The Markov chain model would be the most natural manner of obtaining estimates of a population viability indicators, but it depends on the discretization of the space of states. On the other hand, the method using Monte Carlo simulation requires the establishment of an upper limit that, in this work, we call T_{∞} . This limitation may impair the accurate calculation of the time expected to reach the population goal.

The analysis of the numerical results shows that a slaughter rate higher than 25% can make the growth of the population difficult and, in the future, lead to the reduction of bovine meat production in Brazil. To reach a higher goal, such as 200 million heads in a period less than 20 years, an optimized slaughter policy is fundamental in order to maximize a certain expected return within a finite horizon.

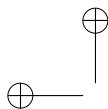
Considering the stochastic intervention, we simulated 10 scenarios changing the maximum slaughter rate and the carrying capacity, and concluded that the goal will be reached in 8 to 20 years (with $K = 250$). This leads us to believe that the use of a fixed intervention equal to 25% (slaughter in 2005) does not guarantee a sustainable production for $K < 240$. Given the present scenario, we can conclude that the Brazilian bovine herd will not reach the goal of 200 million heads in the expected time of 15 years.

ACKNOWLEDGMENTS

Research partially supported by Fundação de Amparo à Pesquisa do Estado de São Paulo (FAPESP), Grant 07/007612-0 and by Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq), Grant number 300235/2005-5.

RESUMO

Neste trabalho estudamos o problema de identificação do modelo de uma população utilizando um modelo dinâmico discreto baseado no modelo de crescimento de Richards. A população é submetida a intervenções devido ao consumo, como no caso de caça ou na criação de animais. A identificação do modelo permite-nos estimar a probabilidade ou o tempo médio de ocorrência para que se atinja um certo número populacional. A inferência paramétrica dos modelos é obtida através da técnica de perfil de máxima verossimilhança como desenvolvida neste trabalho. O método de identificação desenvolvido pode ser aplicado para avaliar a produtividade de criação animal ou o risco de extinção de uma população autóctone. Ele foi aplicado aos dados da população global de gado de corte bovino brasileiro, e é



MODEL FOR POPULATIONS SUBJECT TO INTERVENTIONS

REFERENCES

- AKÇAKAYA HR AND SJÖGREN-GULVE P. 2000. Population viability analysis in conservation planning: an overview. *Ecol Bull* 48: 8–21.
- ALLEN LJS AND ALLEN EJ. 2003. A comparison of three different stochastic population models with respect to persistence time, *Theor Popul Biol* 64: 439–449.
- ANUALPEC. 2008. Anuário da Pecuária Brasileira (Annual of Brazilian Cattle, in Portuguese), Published by ANUALPEC, 359 p.
- BARNDORFF-NIELSEN OE AND COX DR. 1994. Inference and Asymptotics, Chapman & Hall, 360 p.
- BOYCE MS. 1992. Population Viability Analysis. *Annu Rev Ecol Syst* 23(4): 481–506.
- DERISO RB, MAUNDER MN AND PEARSON WH. 2008. Incorporating covariates into fisheries stock assessment models with application to Pacific herring. *Ecological applications: a publication of the Ecol Soc Am* 18(7): 1270–1286.
- FITZHUGH JR HA. 1974. Analysis of growth curves and strategies for altering their shapes. *J Anim Sci* 38: 1036–1051.
- FOWLER CW. 1981. Density Dependence as Related to Life History Strategy. *Ecology* 62: 602–610.
- GILPIN ME AND AYALA FJ. 1973. Global Model of Growth and Competition. *Proc Nat Acad Sci* 70(12): 3593.
- JIAO Y, HAYES C AND CORTÉS E. 2009. Hierarchical Bayesian approach for population dynamics modeling of fish complexes without species-specific data. *ICES J Mar Sci* 66(2): 367–377.
- LOIBEL S, ANDRADE MG AND VAL JBR. 2006. Inference for the Richards Growth Model Using Box-Cox Transformation and Bootstrap Techniques. *Ecol Model* 191(3-4): 501–512.
- LUDWIG D. 1996. Uncertainty and the Assessment of Extinction Probabilities. *Ecol Appl* 6(4): 1067–1076.
- LUDWIG D. 1999. Is it meaningful to estimate a probability of extinction. *Ecology* 1(80): 298–310.
- MATIS JH AND KIFFE TR. 2004. On Stochastic Logistic Population Growth Models With Immigration and Mortality. *Theor Popul Biol* 65: 89–104.
- MATIS JH, KIFFE TR, MATIS TI AND STEVENSON DE. 2007. Stochastic modeling of aphid population dynamics with nonlinear, power-law dynamics. *Math Biosci* 208: 469–494.
- OMLIN M AND REICHERT P. 1999. A Comparison of Techniques for the Estimation of Models Prediction Intervals under Uncertainty. *Ecol Model* 115: 45–59.
- PINEDA NR. 2002. Cenário da cadeia Produtiva de Carne Bovina no Brasil. *Revista da Associação Brasileira de Criadores de Zebuinos-ABCZ* 2(10): 186–187.
- POLANSKY L, DE VALPINE P, LLOYD-SMITH JO AND GETZ WM. 2008. Parameter estimation in a general stochastic discrete-time model of density dependence. *Theor Ecol* 1: 221–229.
- RICHARDS JF. 1959. A flexible growth function for empirical use. *J Exp Bot* 1(10): 290–310.
- SAETHER BE, ENGEN S, LANDE R, ARCESE P AND SMITH JNM. 2000. Estimating the time extinction probability for populations subject to interventions. *Ecol Appl* 10(1): 1–11.



- SAETHER BE, ENGEN S, FILL F, AANES R, SCHRODER W AND ANDERSEN R. 2002b. Stochastic population dynamics of an introduced swiss population of the Ibex. *Ecology* 83(12): 3457–3465.
- SEBER GAF AND WILD CJ. 1989. *Nonlinear Regression*. J Wiley & Sons, 774 p.
- SIBLY RM, BARKER D, DENHAM MC, HONE J AND PAGEL M. 2005. On the Regulation of Populations of Mammals, Birds, Fish, and Insects, *SCIENCE* www.sciencemag.org. 309(22): 607–610.
- YAMAUCHI A. 2000. Population Persistence Time Under Intermittent Control in Stochastic Environments. *Theor Popul Biol* 57: 391–398.