Population Viability Analyses for Populations without Age Structure

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Date

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1   Introduction

Population biologists define a population as a group of individuals of a single species, living in a defined area at a particular time, having the potential for genetic exchange. Consider salmon as an example. These fish hatch in streams and spend their first year or more living in freshwater. They subsequently swim to the ocean to finish maturing. After up to five years at sea, they return to their natal (home) stream to spawn (reproduce). Salmon die shortly after spawning. Thus, salmon who have returned to their natal stream to spawn are considered as one population. Salmon at sea come from many populations.

The goal of a population viability analysis (PVA) is to estimate the probability that a population of interest will persist for a certain amount of time. Population viability analyses are most often applied to species that are endangered; that is, they are at high risk of going extinct.

2   Deterministic Population Growth Models

The first element of a PVA is a deterministic population growth model, and these models differ dramatically depending on whether or not a population has age structure. Whether or not a population has age structure is, in turn, determined by the biology of the species. A species can be either semelparous or iteroparous. A semelparous species produces all of its offspring at one time and then dies, whereas an iteroparous species produces offspring at more than one time during its life. Annual plants (those that live only one year), many insects and salmon are semelparous. Trees, deer and humans are examples of iteroparous species. Iteroparous species give rise to populations with age structure (different aged individuals in the same population at the same time.) Semelparous species generally give rise to populations without age structure; that is, generations do not overlap. The remainder of this paper focuses on population viability analyses for populations without age structure.

Non-age structured population growth models are based on one of the

two following sets of assumptions. First, survival and birth rates are constant across all individuals, and generations are non-overlapping. This means that only one age class is alive at a given time, as occurs for semelparous organisms where individuals mature at the same rate. Second, there are only two age classes: adults and offspring. In this case, adults have constant per capita survival and birth rates, and offspring have both a constant per captia survival rate and a constant rate of maturation. Most models are based on the assumption that offspring become reproductively mature before the next breeding cycle begins, but some models allow for a time lag in maturation. A non-age structured model is fit to a time series of total population size estimates.

Furthermore, non-age structured population growth models are generally based on two parameters: r and K. The former is known by names including the intrinsic rate of increase, the exponential growth rate and the Malthusian parameter. Populations that are not limited by competition or effects of crowding grow geometrically, and they are modeled as growing at the rate of e^r or $1 + r$. Carrying capacity (K) is defined as the point at which the population size at one time step equals the population size at the next time step. Biologists consider carrying capacity to represent the maximum number of animals a habitat can support over a long period of time; however, this is a very general concept, not a mathematical definition.

It is worth noting that population growth models do produce non-integer population sizes. Extinction, however, is always defined by whole numbers. That is, a simulated population that has dropped below one is considered extinct. Usually, a quasi-extinction level is defined. For example, a population of sexually reproducing organisms is effectively extinct when the population drops below two, and effective extinction may occur at higher numbers because of inbreeding or behavioral problems. For example, if the few individuals remaining in a population live in a vast area, they may not be able to find each other to mate. Such as population would be effectively extinct at a whole number greater than two.

The simplest population growth models describe density independent growth. Density independence refers to situations without overcrowding; because of this, the growth rate is independent of population size. This type of growth is typical of founding populations, where population size is

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small, and resources such as food and nest or den sites are easily available. The discrete form of density independent population growth is given by the following equation,

$$\Delta N = rN_t, \quad \text{where} \tag{1}$$

N = population size
t = time
r = intrinsic rate of increase.

It follows from Equation (1) that

$$N_{t+1} = N_t + rN_t = (1 + r)N_t. \tag{2}$$

The predominant characteristics of this model are that population growth is unlimited and population size in the next time step is directly proportional to the current size of the population.

In continuous time, Model (1) becomes

$$\frac{dN}{dt} = rN, \tag{3}$$

which integrates to

$$ln(N) = rt + C,$$

giving

$$N = e^{rt}C'.$$

Finally, solving for C' at $t = 0$ and $N = N_0$ gives

$$N_t = N_0 e^{rt}. \tag{4}$$

Most populations residing at high lattitudes are birth-pulse populations, meaning that individuals give birth during a short portion of the year. Density independent growth for birth-pulse populations is best modeled in discrete time. At low lattitudes, animals often reproduce year round,

making the continuous time model more appropriate. Because $1 + r$ is the first order Taylor approximation of e^r at $r = 0$, the discrete time model and the continuous time model give very similar results for r near zero; however, as the distance between zero and r increases, the results of the two models diverge (Figure 1). When $-0.2 < r < 0.2$ the discrete time model and the continuous time model give results that are similar enough to be used interchangeably (Case 2000).

Because populations cannot grow without limit for an indefinite period of time, density dependent population growth models have been developed. These growth curves have a sigmoidal shape showing essentially density independent growth at small population sizes, and a decreasing growth rate as population size increases. When growth is density dependent, the discrete time models and the continuous time models produce qualitatively different growth curves (Case 2000), thus the decision to model in discrete or continuous time is made by choosing the population growth curve that best fits the data. Discrete logistic growth (Figure 2) is governed by the following equation,

$$\Delta N = N_t r\left(\frac{K - N_t}{K}\right), \quad \text{where} \tag{5}$$

N = population size
t = time
r = intrinsic rate of increase
K = carrying capacity.

It follows from (5) that

$$N_{t+1} = N_t\left(1 + r\left(\frac{K - N_t}{K}\right)\right).$$

At very small population sizes, $N_{t+1} \approx (1 + r)N_t$, and population growth is essentially density independent. At $N_t = K$, the equation becomes $N_{t+1} = N_t$, and the population is at equilibrium. Population size can easily overshoot carrying capacity when r is large. When population size exceeds carrying capacity, the discrete logistic equation yields negative growth. Both exceedence of carrying capacity and negative population growth are observable in nature. However, in the model of discrete logistic growth,

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if the population size exceeds $\frac{K(r+1)}{r}$, the model will produce a negative population size in the following time step, obviously a biological impossibility.

The Ricker equation (Ricker 1954, 1958; Figure 3) corrects this deficiency and can be written as

$$N_{t+1} = N_t e^{r\left(\frac{K-N_t}{K}\right)}. \tag{6}$$

As population size becomes vanishingly small, $N_{t+1} \approx N_t e^r$, and population growth again becomes density independent. At $N_t = K$, $N_{t+1} = N_t$, again showing an equilibrium. Exceedence of K produces negative growth, and a very large population size will precipitate a population crash; however, the population size will not go below zero.

The behavior of both of these density dependent models depends very much on the magnitude of the intrinsic rate of increase. When projected through time, both the discrete logistic model and the Ricker model grow to carrying capacity if the intrinsic rate of increase is is greater than zero and less than or equal to one. Between one and two, the population trajectory oscillates, but dampens to K. As r increases above two, stable oscillations are produced, and as r increases toward three, the population trajectory becomes chaotic.

Another commonly used model of density dependent population growth is the Beverton-Holt model (Beverton and Holt 1957, Figure 4), which also is referred to as continuous logistic growth. This model can be written as

$$\frac{dN}{dt} = r\left(\frac{K-N}{K}\right). \tag{7}$$

Rearranging (7) gives

$$\left[\frac{1}{N(K-N)}\right]dN = \frac{r}{K}dt$$

$$\frac{1}{K}\left[\frac{N+(K-N)}{N(K-N)}\right]dN = \frac{r}{K}dt$$

$$\frac{1}{K}\left[\frac{N}{N(K-N)} + \frac{(K-N)}{N(K-N)}\right]dN = \frac{r}{K}dt$$

$$\frac{1}{K}\left[\frac{1}{(K-N)} + \frac{1}{N}\right]dN = \frac{r}{K}dt$$

Integrating with respect to N and t yields

$$\frac{ln(N)}{K} - \frac{ln(N-K)}{K} = \frac{rt}{K} + C,$$

which can be rearranged as

$$ln\left[\frac{N}{N-K}\right] = rt + C'$$

$$\frac{N}{N-K} = e^{rt}C''.$$

Solving for C'' at $t = 0$ and $N = N_0$ gives

$$\frac{N}{N-K} = \frac{N_0 e^{rt}}{N_0 - K},$$

and solving for N gives

$$N = \frac{N_0 e^{rt}}{1 + N_0\frac{(e^{rt}-1)}{K}}. \tag{8}$$

As in the Ricker model, extremely small population sizes experience essentially geometric growth, because

$$\frac{N_0 e^{rt}}{1 + N_0\frac{(e^{rt}-1)}{K}} = N_0 e^{rt} + O(N_0{}^2),$$

and if $N_0 = K$,

$$\frac{N_0 e^{rt}}{1 + N_0\frac{(e^{rt}-1)}{K}} = K,$$

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showing an equilibrium at K.

However,

$$\lim_{t \to \infty} \frac{N_0 e^{rt}}{1 + N_0 \frac{(e^{rt}-1)}{K}} = K,$$

and

$$\lim_{N_0 \to \infty} \frac{N_0 e^{rt}}{1 + N_0 \frac{(e^{rt}-1)}{K}} = \frac{e^{rt}K}{(e^{rt}-1)},$$

meaning that over time, the population grows to carrying capacity, and a population initialized above K grows to the population ceiling, which is, in fact, larger than K. Thus, the functional difference between the Ricker model and the Beverton-Holt model is that at high population levels, the former models a population that crashes to zero, whereas the latter models a population that simply stops growing. The Ricker model describes scramble competition: if the population size is too large for the available resources, then everyone suffers, hence the population crash. Species that respond in this manner are said to be r-selected, and their adaptations include good colonization abilities and high intrinsic rates of increase. The Beverton-Holt model describes contest competition: if the population size is too large for the available resources, then there are winners and losers. Species that respond in this manner are said to be K-selected, and their primary adaptation is competitive ability. Although there are multiple models of density dependent population growth, the most striking difference among the models is this response to large population sizes.

All of the density dependent models considered here produce nonsensical results if the population size is initialized above K and the growth rate is negative. For discrete logistic growth, if $N_t > K$ and $r < 0$, then $r(1 - \frac{N_t}{K})$ is positive, and the population will exhibit unlimited positive growth. Under the same circumstances, the Ricker curve also will exhibit unlimited positive growth. The Beverton-Holt model yields a population that will crash to a negative size. Clearly, none of these equations would be appropriate to model a population that had exceeded carrying capacity and then changed from a positive to a negative growth rate because of a density-independent factor, such as hunting or an environmental catastrophe.

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The final density dependent model to be considered is the Schnute model (Schnute 1981, Figure 5),

$$N_{t+1} = \frac{\alpha N_t}{(1+\beta\gamma N_t)^{\frac{1}{\gamma}}}, \quad \text{where} \tag{9}$$

N = population size
t = time
α = a function of the intrinsic rate of increase
β = a function of the intrinsic rate of increase and the carrying capacity
γ = a shape parameter that determines the nature of the density dependent response.

When $\gamma = 1$,

$$N_{t+1} = \frac{\alpha N_t}{(1 + \beta N_t)}, \tag{10}$$

which is simply a reparameterization of the Beverton-Holt model where $\alpha = e^r$ and $\beta = \frac{e^r - 1}{K}$.

Furthermore,

$$\lim_{\gamma \to 0} \frac{\alpha N_t}{(1+\beta \gamma N_t)^{\frac{1}{\gamma}}}$$

$$= \frac{\lim_{\gamma \to 0} \alpha N_t}{\lim_{\gamma \to 0} (1+\beta \gamma N_t)^{\frac{1}{\gamma}}}$$

$$= \frac{\alpha N_t}{\lim_{\gamma \to 0} (1+\beta \gamma N_t)^{\frac{1}{\gamma}}}$$

$$= \frac{\alpha N_t}{\lim_{\gamma \to 0} e^{ln((1+\beta \gamma N_t)^{\frac{1}{\gamma}})}}$$

$$= \frac{\alpha N_t}{\lim_{\gamma \to 0} e^{\frac{1}{\gamma} ln(1+\beta \gamma N_t)}}$$

$$= \frac{\alpha N_t}{e^{\lim_{\gamma \to 0} \frac{1}{\gamma} ln(1+\beta \gamma N_t)}}$$

$$= \frac{\alpha N_t}{e^{\lim_{\gamma \to 0} \frac{\beta N_t}{1+\beta \gamma N_t}}} \qquad \text{by l'Hopital's rule}$$

$$= \frac{\alpha N_t}{e^{\beta N_t}}$$

which is a reparameterization of the Ricker curve, where $\alpha = e^r$ and $\beta = \frac{r}{K}$. For values of γ between zero and one, the Schnute curve represents a mixture of the Ricker and Beverton-Holt response. When the data are not sufficient to determine the nature of a population's response to overcrowding, the Schnute model gives a more accurate representation of the uncertainty surrounding predictions about the populations future than would be given by choosing either the Ricker or the Beverton-Holt model.

3 Error Structure

Once a deterministic mathematical model has been chosen to describe the population dynamics of a species, an error structure must be incorporated into that model. Because population growth is a geometric process, its error is best described by a multiplicative, not an additive, process. The error on

population growth is considered to be lognormally distributed, giving the intrinsic rate of increase a normal distribution.

4 Confronting Models with Data

The next step in a population viability analysis is to estimate the model parameters based on a time series of population size estimates. The models presented above are simple because all individuals are treated alike; that is, populations are modeled without age structure or demographic stochasticity. Yet despite the simplicity of these models, the amount of varibility in ecological systems and the logistics of collecting field data often make it difficut to accurately estimate the model parameters. Ten years of population count data are often considered the minimum needed, even for the simplest of PVA's (Morris and Doak 2002). Thirty years of data could well represent a career's worth of work for a biologist, yet statistically, this sample size is barely adequate.

Demonstrating how a species responds to competition can be difficult even with many years of data, either because the population has not been observed over a large range of sizes or because of the variation due to both process and observation error. For example, application of the Schnute model to a salmon population yielded such a broad posterior distribution on γ that the species' response to increasing density could not be determined (Goodman 2004). If a population is suspected to be density dependent, but the data do not allow for estimation of both r and K, the population may be modeled by using a density independent model, but allowing r to vary over time (Goodman 2006). Fitting density dependent models becomes much easier if one can obtain an estimate of carrying capacity independent of the population trajectory being analyzed. Finally, it is noteworthy that PVA's for aged structured populations are sometimes conducted by fitting non-age structured models to time series of population estimates simply because age-structured data are unavailable.

5 Future projections

After the inference is complete, the model, the parameter estimates and the error structure are used to conduct stochastic simulations of population growth. Future projections of interest include the probability the population will persist for a certain number of years, the expected population size at a given date and the expected time to extinction.

It is particularly important in a PVA to distinguish between process variation and observation error, making the measurement of observation error an important component of study design. Observation error should not be used in the forward projections of a PVA, because the population does not actually experience the variability due to observation error. Furthermore, inclusion of observation error will bias low the estimate of the mean growth rate. Consider the K observed population growth rates (λ_t) derrived from a time series of $K + 1$ population size estimates.

$$\frac{N_{t+1}}{N_t} = \lambda_t.$$

Furthermore, note that population growth is a geometric process, governed by the geometric mean of λ_t,

$$\lambda_G = [\prod_{t=1}^{K} \lambda_t]^{\frac{1}{K}}.$$

Let λ_t be generated from a lognormal distribution with mean, θ, and variance, τ^2, and note that by a Taylor series expansion around θ,

$$log(\lambda_t) = log(\theta) + \frac{1}{\theta}(\lambda_t - \theta) - \frac{1}{2\theta^2}(\lambda_t - \theta)^2 + O_p[(\lambda_t - \theta)^3]$$

Taking expectations and simplifying gives,

$$E[log(\lambda_t)] \approx log(\theta) - \frac{\tau^2}{2\theta^2}$$

Furthermore,

$$E[log(\lambda_t)] = E[\frac{1}{K}\sum_{t=1}^{K} log(\lambda_t)] = E[log((\prod_{t=1}^{K} \lambda_t)^{\frac{1}{K}})] = E[log(\lambda_G)].$$

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Thus,

$$E[log(\lambda_G)] \approx log(\theta) - \frac{\tau^2}{2\theta^2},$$

meaning that the expectation of the log of the geometric mean of λ_t decreases as the variance of λ_t increases. Because the natural logarithm is a monotonic, increasing function, the expectation of the geometric mean of λ_t also decreases as the variance of λ_t increases. Therefore, inclusion of observation error in the forward projections of a PVA will result in an increase in the variance of λ_t and therefore a decrease in its expected geometric mean, biasing low the future population size projections.

6   Example PVA

Population viability analyses come in many different flavors. In the example below, I used simulated data to present one way to conduct a PVA. I try to be explicit about the assumptions made for this particular example. I used a density independent, continuous time model, and I incorporated process variation in the PVA by allowing the intrinsic rate of increase to vary on an annual basis. However, I made the simplifying assumption that these growth rates do not show serial correlation.

I simulated ten years (t) of population size estimates (n), which are presented below, along with the resulting estimates of growth rates (λ) and intrinsic rates of increase (r). The data were generated using an initial population size of 100 and ten independent values for r drawn from a N(-.017, 0.035) distribution. I chose this distribution because it is representative of parts of the decline of the Steller sea lion, and I simulated ten years of data because that is considered the minimum needed for a simple PVA.

From the above data, I first conducted a numerical, Bayesian inference on the true mean and standard deviation of r, which were both unknown. I specified $r_t \sim iid\, N(\mu, \sigma^2)$, Specifically, the likelihood function was

$$f(\mathbf{r}|\mu, \sigma^2) \;\; = \;\; \frac{1}{(\sqrt{2\pi\sigma^2})^n} \, e^{\frac{1}{2\sigma^2}[(n-1)s^2 + n(\bar{r}-\mu)^2]}.$$

t	n	$\lambda = e^r$	r
1	99	0.9900	0.0683
2	106	1.0707	0.0279
3	109	1.0283	-0.0092
4	108	0.9908	0.0000
5	108	1.0000	0.0364
6	112	1.0370	-0.0090
7	111	0.9911	0.0000
8	111	1.0000	-0.0182
9	109	0.9820	0.0091
10	110	1.0092	

Table 1: Time step (t), population size estimates (n), growth rates (e^r), and intrinsic rates of increase (r). $\bar{r} = 0.0117$, $s = 0.0276$.

I used independent, improper uniform priors on both μ and $log(\sigma^2)$. Because the prior on $log(\sigma^2)$ was uniform, the prior on σ^2 was proportional to the reciprocal of σ^2, resulting in a joint posterior where

$$f(\mu, \sigma^2 | \mathbf{r}) \propto \frac{1}{\sigma^{n+2}} e^{\frac{1}{2\sigma^2}[(n-1)s^2 + n(\bar{r}-\mu)^2]}.$$

Integrating over μ shows that

$$f(\sigma^2 | \mathbf{r}) \propto (\sigma^2)^{-\frac{n-1}{2}} e^{-\frac{(n-1)s^2}{2\sigma^2}},$$

indicating that the marginal posterior on σ^2 is a scaled inverse χ^2 distribution of the form

$$\sigma^2 | \mathbf{r} \sim Inv \, \chi^2(n-1, s^2).$$

Integrating the joint posterior over σ^2 shows that

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$$f(\mu|\mathbf{r}) \propto \left[1 + \frac{n(\mu - \bar{r})^2}{(n-1)s^2}\right]^{-\frac{n}{2}},$$

meaning that the marginal posterior on μ is a t distribution of the form

$$\mu|\mathbf{r} \sim t_{n-1}\left(\bar{r}, \frac{s^2}{n}\right).$$

In other words,

$$\left.\frac{\mu - \bar{r}}{s/\sqrt{n}}\right|\mathbf{r} \sim t_{n-1}.$$

Note that μ and σ^2 are not independent in the joint posterior, thus the joint posterior cannot be obtained by sampling from the respective marginal posteriors. However, the joint posterior can be factored as follows:

$$f(\mu, \sigma^2|\mathbf{r}) = f(\mu|\sigma^2, \mathbf{r})f(\sigma^2|\mathbf{r}).$$

Thus, σ^2 can be sampled from its marginal posterior and μ can then be sampled from its posterior conditioned on σ^2, which is normally distributed as

$$f(\mu|\sigma^2, \mathbf{r}) \sim N(\bar{r}, \frac{\sigma^2}{n}).$$

I obtained the joint posterior distribution in this manner, using a sample size of 100,000,000. I next projected population size 100 years into the future for each of the 100,000,000 simulated populations. For each year in each population projection, I sampled a new r from the $N(\mu_i, \sigma^2_i)$ distrubution. I then calculated the next year's population size using the continuous time, density independent model of population growth. A population was considered extinct if its size became smaller than two individuals. I assumed the variability in the posterior distribution came from process variation, not observation error.

The chance of extinction during a 100 year time frame was estimated at 5.7%. Figures 6 - 9 show the posterior distributions of μ, σ^2, the natural logarithm of population size in 100 years and time to extinction given the

population went extinct within 100 years. Given the small sample size (ten years), it is not surprising that the posterior mean of μ was substantially different than the true mean used to generate the data, with the former showing an average 1.2% per year increase, and the latter showing an average 1.7% per year decline. This is a sobering commentary on the nominally minimal sample size of ten.

7 Conclusion

Population viability analyses are used to estimate the probability that a population of interest will persist for a certain amount of time. The three components needed to conduct a PVA are a deterministic population model, an error structure and data. For a population without age structure, the data are time series of population estimates. The two steps to a PVA are inference on the model's parameters and subsequent use of the parameter estimates to simulate future population growth. Although PVA model theory is well developed, data requirements are rarely met, underscoring the need for parsimony.

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Exponential Growth

Points for Discrete Growth, Lines for Continuous Growth
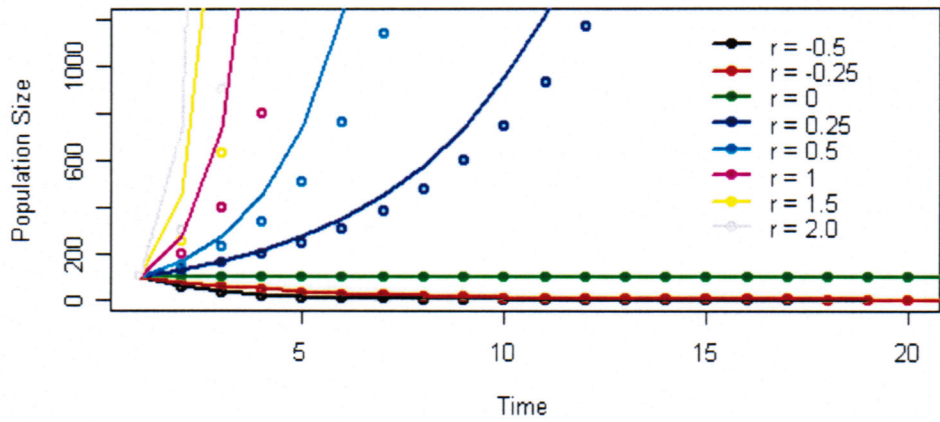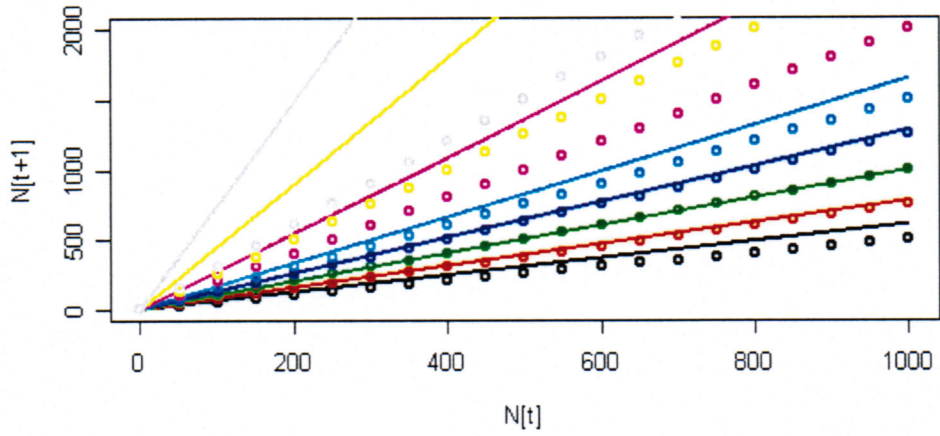
Figure 1.

Discrete Logistitic Growth with K = 1000
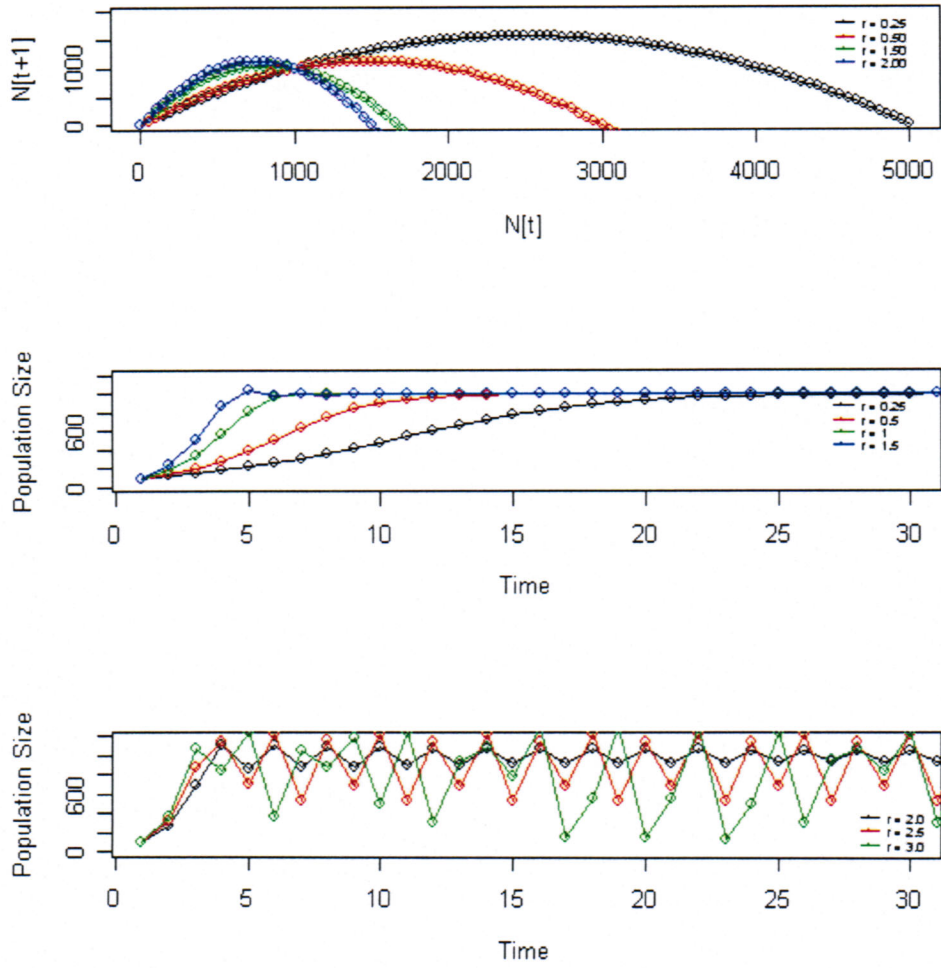
Figure 2.

Ricker Curve with K = 1000
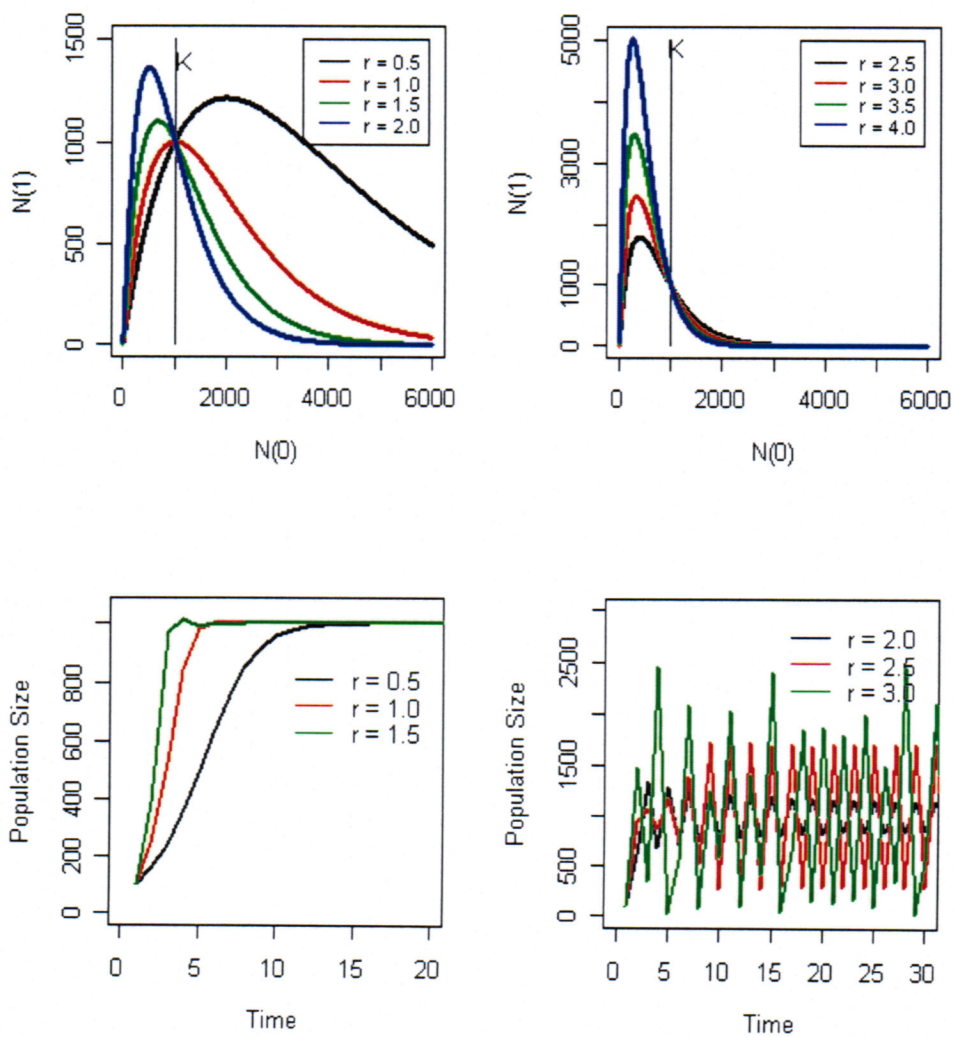
Figure 3.

Beverton-Holt Curve with K = 1000
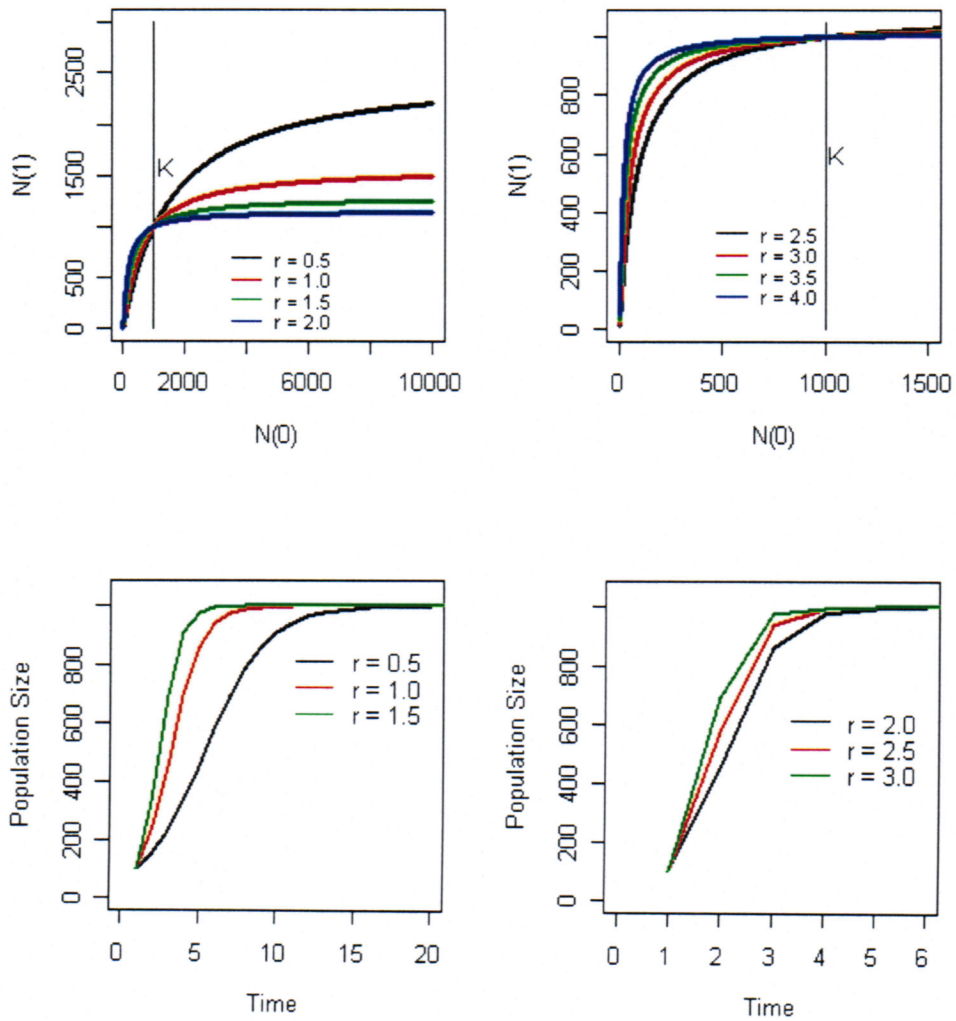
Figure 4.

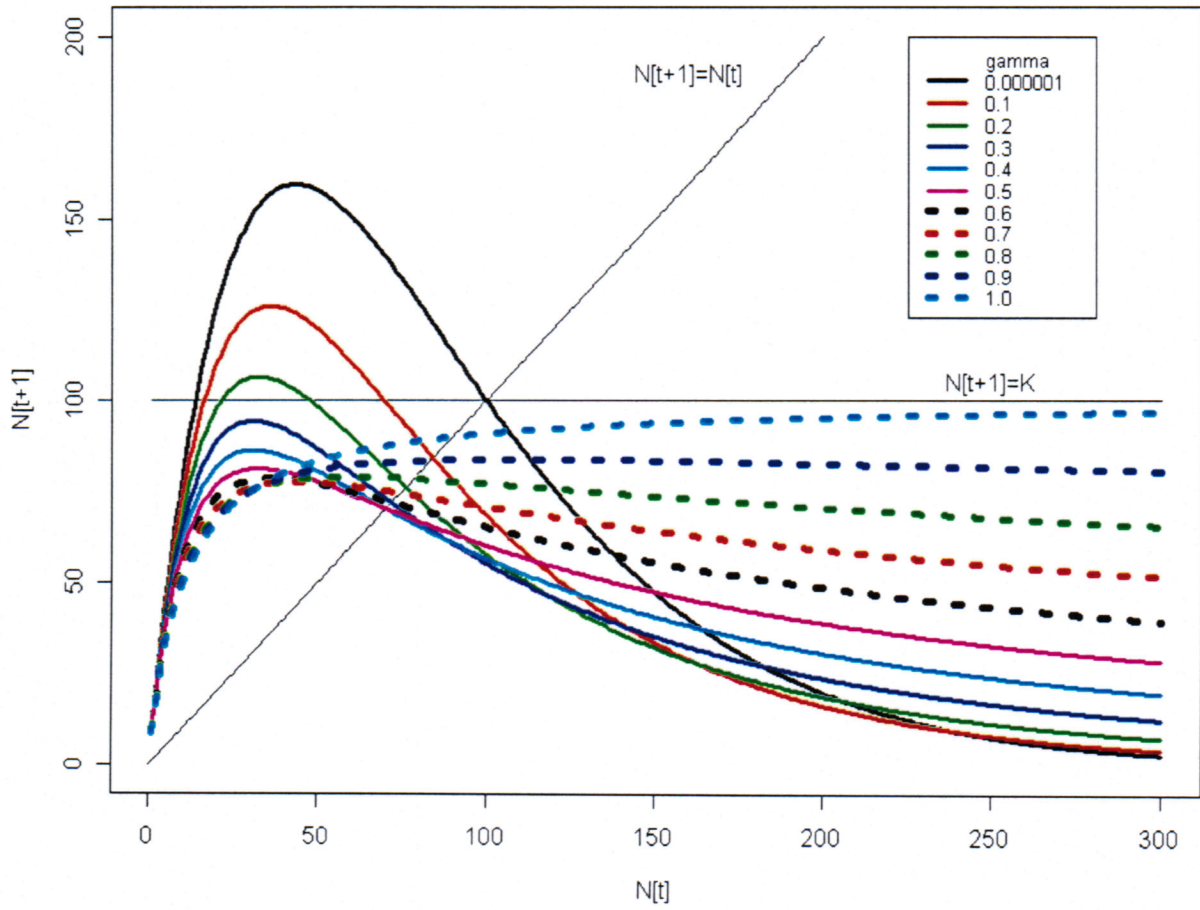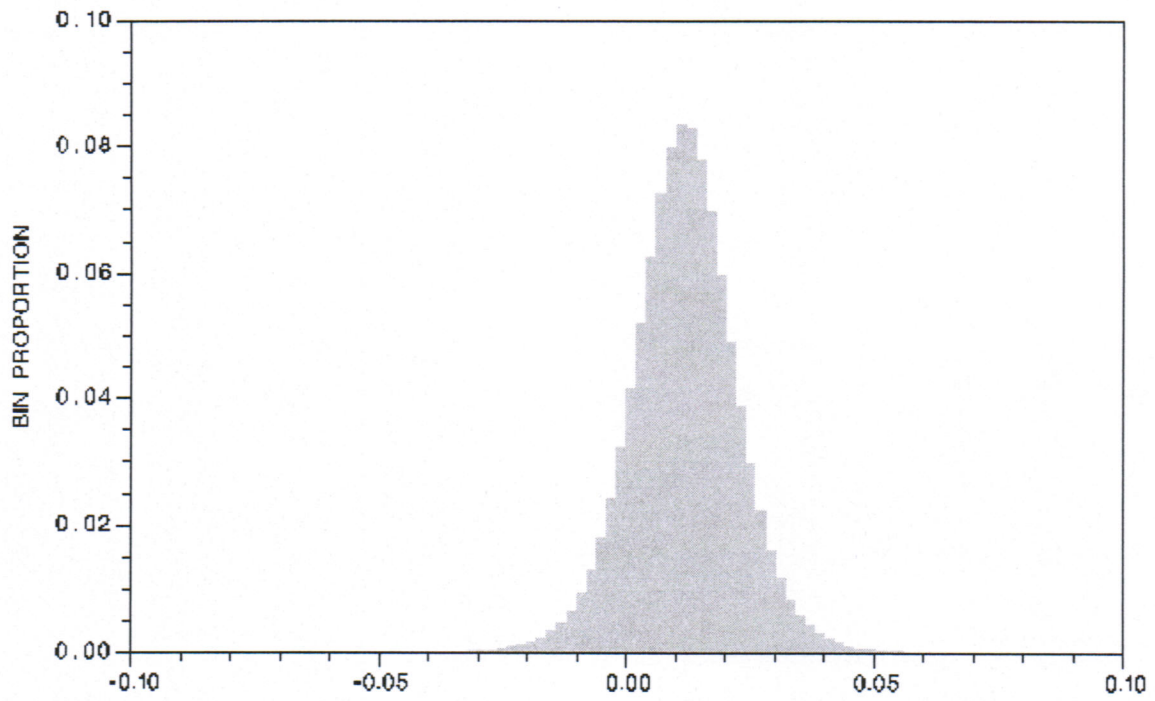Schnute Curve with K = 100 and alpha = 10, for gamma = 0.000001-1.0
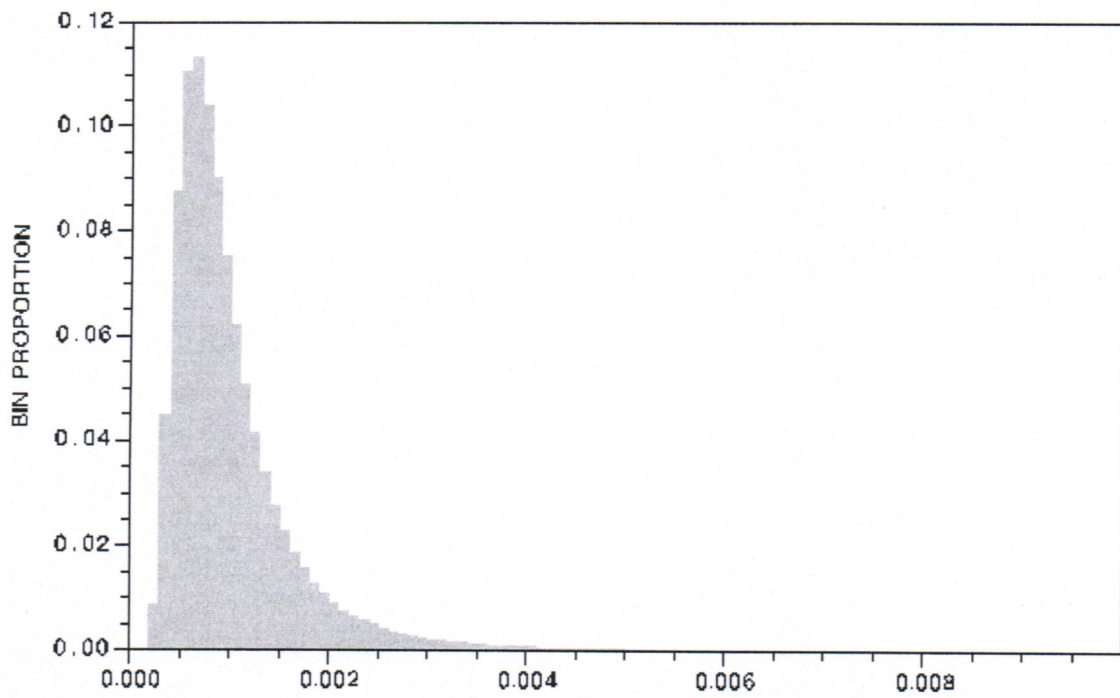
Figure 5.

Figure 6. The posterior distribution on μ.
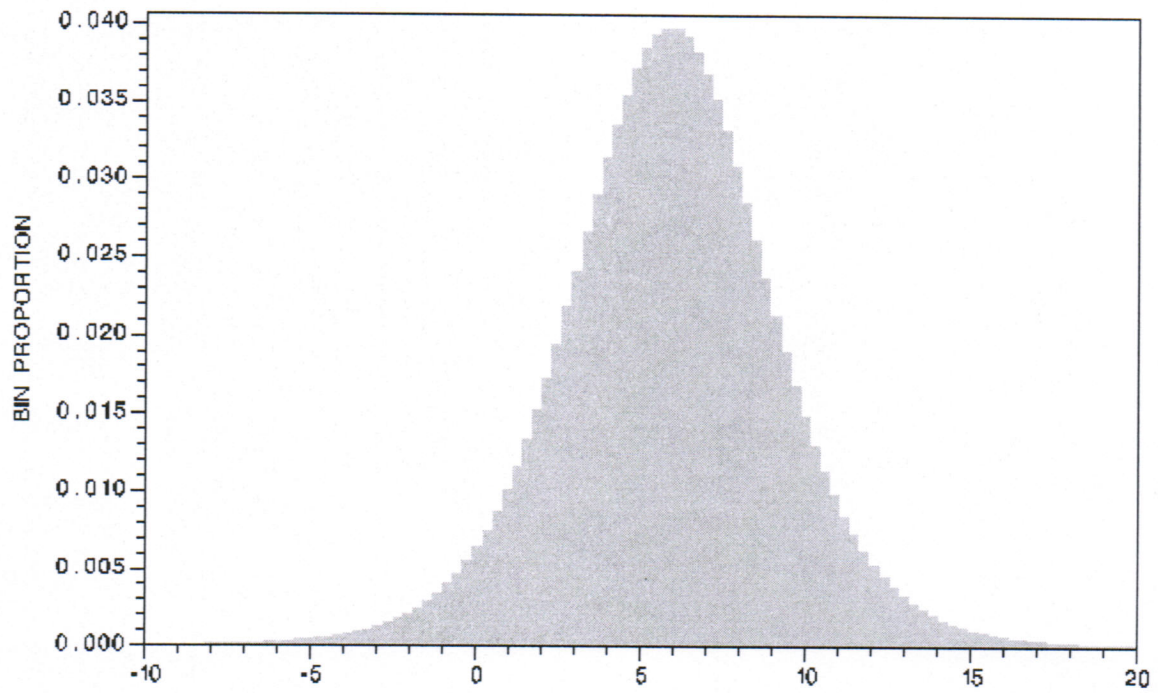

Figure 7. The posterior distribution on σ^2.

Figure 8. The posterior distribution on ln(population size in 100 years).
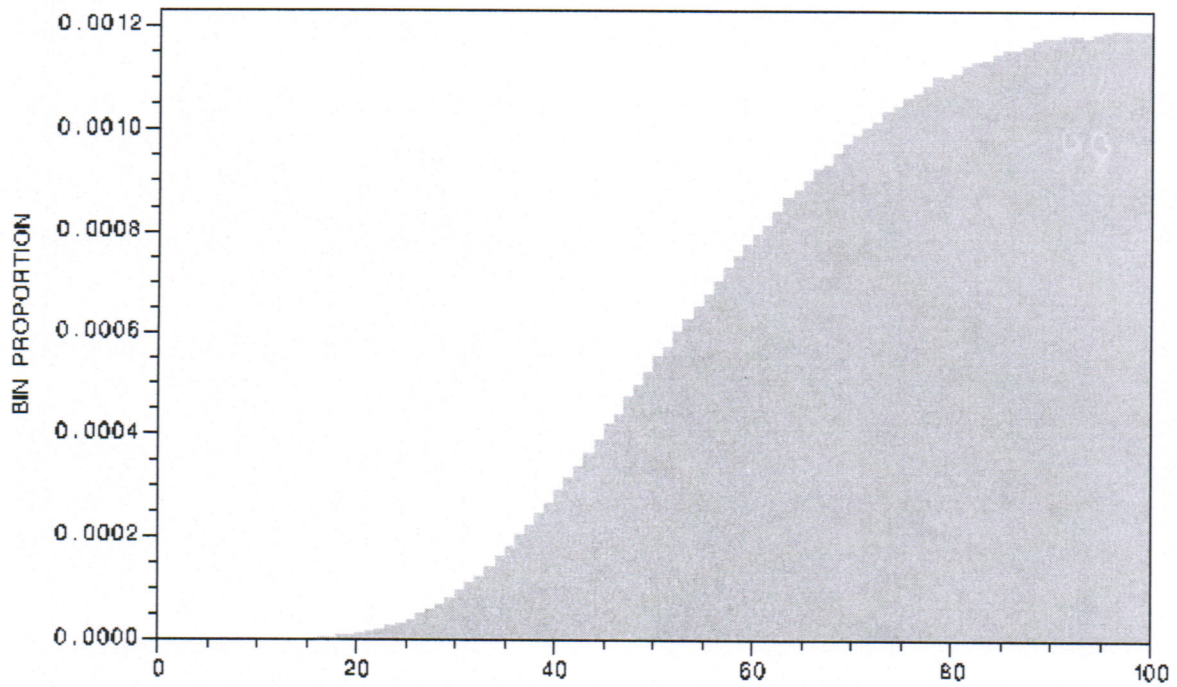

Figure 9. The posterior distribution on number of years to extinction given that the population went extinct.