

**Lecture 4. Population Models Incorporating Stochasticity.**

## Reading:

Renshaw (1991) Chapters 2 Simple birth-death processes, and 3 General birth-death processes, Pages 15-86.

## Optional:

Lebreton, J.-D. 1990. Modeling density dependence, environmental variability, and demographic stochasticity from population counts: an example using Wytham Wood Great Tits. Pages 89-102 *in* Population Biology of Passerine Birds, J. Blondel (ed.). Springer-Verlag Berlin Heidelberg.

## Paraphrase of Renshaw (1991:2):

Why would we not accept the weight of one Scotchman as representative of the entire population of Scotland, but will accept the time trace of a population as representative of the population's dynamics?

How important is stochasticity? Consider a simple example patterned from an example in Morris and Doak (2002:26) where  $\lambda_t$  can take on 2 values with equal probability: 0.83 and 1.17. Thus, the arithmetic mean of the possible values of  $\lambda$  is exactly 1.0, so the population should remain stable. Right? WRONG! Here's why. Change in population size is expressed as the product of the  $\lambda_t$  values,  $\prod_{t=1}^T \lambda_t$ .

Half the time,  $\lambda_t$  is equal to 0.83, and half the time it is 1.17. The product of these 2 values is 0.9711, and is thus the expected value of the change in the population over a 2-year interval is the geometric mean of 0.9711, not the arithmetic mean of 1.0. Therefore, the expected value of the above product is  $0.9711^{T/2}$ , and is thus  $<1$ , so that the population will decline. The key point of this example is that the geometric mean is what is important, and the geometric mean of a series is always less than the arithmetic mean. Variation in values of  $\lambda$  is important because the geometric mean of these values can be  $<1$  even when the arithmetic mean is  $>1$ .

Types of stochasticity. Variation in population sizes can be classified into 2 general mechanisms. The true population may vary through time and space, even though a deterministic model predicts a constant population. Variation in the true population size is termed process variation, because of stochasticity in the population growth process. Several mechanisms can cause process variation.

Bernoulli or penny-flip variation (Demographic).

Individual heterogeneity, including phenotypic and genotypic.

Spatial variation (Environmental).

Temporal variation (Environmental).

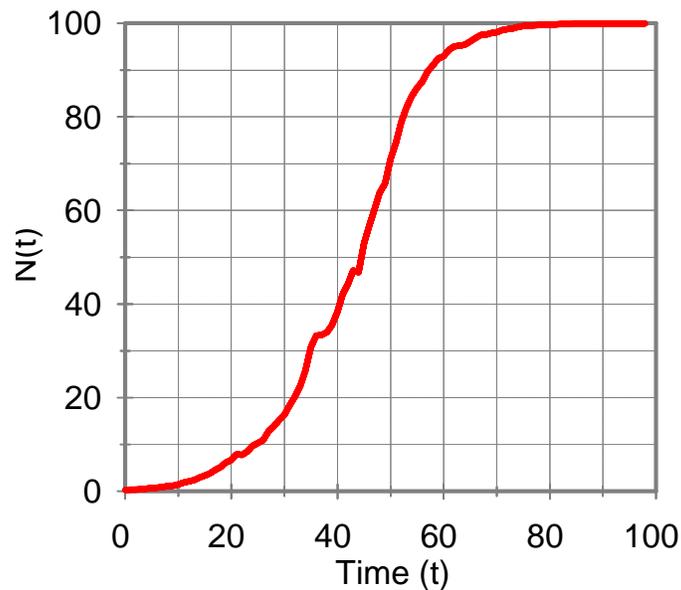
Small annual variation, such as typical weather patterns might generate.

Catastrophes, such as severe storms might generate (impact of a

hurricane or tornado on a habitat).

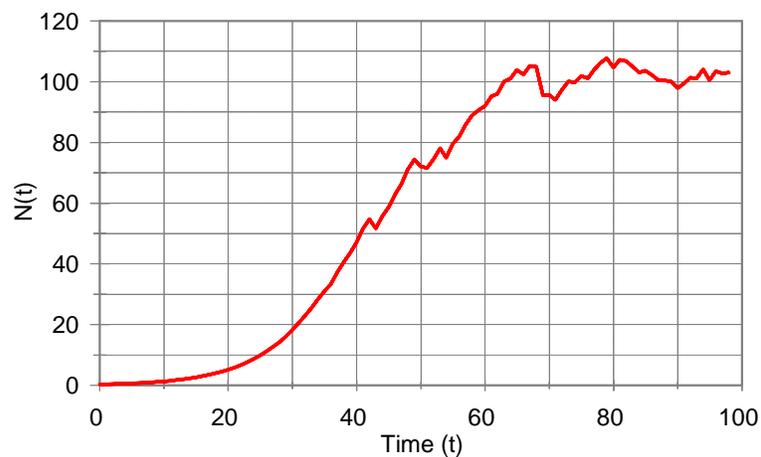
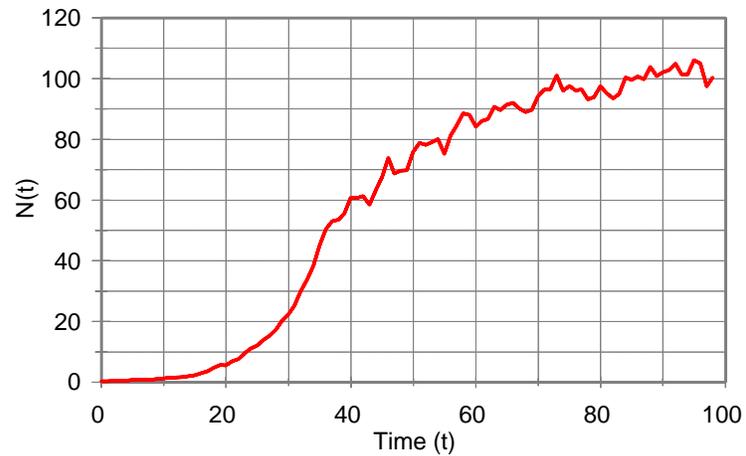
In contrast to process variation, sampling variation is not variation in the population size, but only our inability to measure the population without error. Thus, we observe only estimates of population size,  $\hat{N}_t$ , instead of true population size  $N_t$ .

Environmental stochasticity can be incorporated into a model by making the parameters random variables. As an example, consider the logistic growth model  $N_{t+1} = N_t[1 + R_0(1 - N_t/K)]$ . By setting  $K$  equal to 100 and making  $R_0$  a random variable that is normally distributed with mean 0.15 and standard deviation 0.075, population growth might look like the following. Variation in population growth is predominantly at small population sizes, with little variation at populations around  $K$ .



Making just  $K$  a random variable with mean 100 and standard deviation 20 and setting  $R_0$  to 0.15 results in the following graph. Note that the variation in population growth is now predominantly at higher levels.

By making both  $K$  and  $R_0$  random variables with the same normal distributions as used above, the following graph results. Now, variation in population growth is evident at all population sizes.



We can envision how such variation occurs in the natural world:  $K$  could easily vary from year to year because of weather effects. Good rains result in lush growth for herbivores, whereas drought results in little growth and poor conditions, with the population above carrying capacity because of the smaller value of  $K$ . Note that the average population size is not the mean of the distribution of  $K$  because the population will drop faster to reach a decreased  $K$  than it will grow to reach an increased  $K$  (Gotelli 1998:38). Likewise, lush

growth should result in larger values of  $R_0$ , whereas drought conditions would result in smaller, even negative, values of this parameter.

Incorporation of demographic stochasticity into a population model can be in the form of a differential equation with continuous time, or in a difference equation with discrete time. In the continuous time models, the time to the next event is the random variable modeled. This is the approach generally presented in Renshaw (1991). If time to the next event is modeled as an exponential random variable, then analytical solutions can generally be derived, and a huge mathematical literature exists on this type of stochastic process (known as a Poisson process). For the exponential distribution, the probability density function is

$$f(t) = \lambda e^{-\lambda t} ,$$

giving a mean of  $1/\lambda$  and variance of  $1/\lambda^2$ . The cumulative density function is

$$F_T(t) = \Pr(T \leq t) = 1 - e^{-\lambda t} .$$

Thus, the probability of surviving at least  $T$  or longer is given by

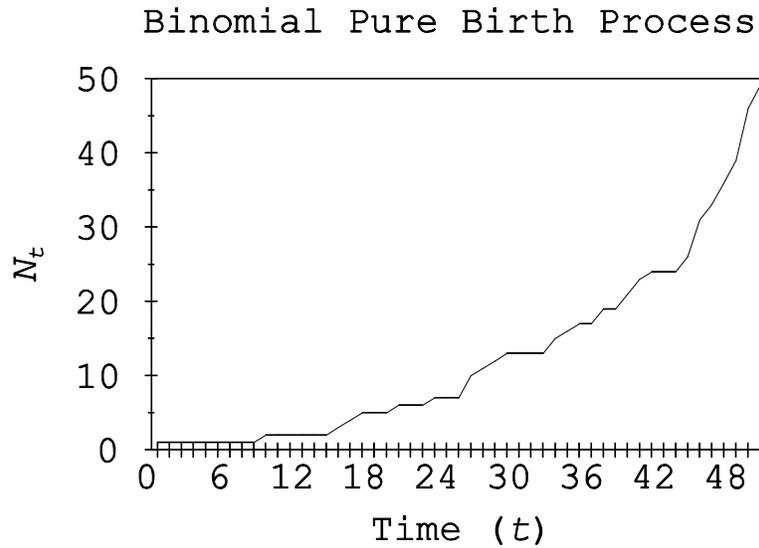
$$\Pr(T \geq t) = 1 - F(T) = e^{-\lambda t} .$$

If the proportion of the population undergoing the process (giving birth or dying) over a finite time interval is taken as the random variable, then a binomial process results. Just as difference equations become identical to differential equations as the time interval becomes infinitely small, so do binomial process models become the same as Poisson process models. For most of the populations we are interested in this course, a binomial process is much more reasonable. Births are a pulse in time, and mortality is not a constant rate across time, but more severe at certain months of the year. The lack of a constant instantaneous mortality rate (hazard rate) makes the simple Poisson process models unrealistic for most fishery and wildlife populations.

#### Pure Birth Process -- Binomial model

Each individual undergoes a Bernoulli trial to determine if it gives birth (splits) in this finite interval.

Only binomial variation is present.



For a population of  $N$  individuals with probability  $p$  of having a single young, the probability of having  $B$  young is

$$Pr(B) = \binom{N}{B} p^B (1 - p)^{(N - B)}$$

For example, let  $N = 5$ , and  $p = 0.7$ . Then:

$b$	$Pr(B = b)$	$Pr(B \leq b)$
0	0.00243	0.00243
1	0.02835	0.03078
2	0.13230	0.16308
3	0.30870	0.47178
4	0.36015	0.83193
5	0.16807	1.00000
Total	1.00000	

The values of the binomial function can be generated with the @BINOMDIST( $b,N,p,cum$ ) function. If  $cum = 0$ , the  $Pr(B = b)$  is returned, whereas  $cum = 1$  returns  $Pr(B \leq b)$ . For example, @BINOMDIST(1,5,0.7,0) = 0.02835, and

@BINOMDIST(1,5,0.7,1) = 0.03078.

To generate random observations from the binomial distribution in Quattro Pro, use the @CRITBINOM( $N,p,\alpha$ ) function. This function calculates the maximum value of  $B$  that can occur before the cumulative probability expressed by  $\alpha$  is exceeded. To check this function, I generated 1000 observations of  $B$ , and tabulated them against the expected distribution.

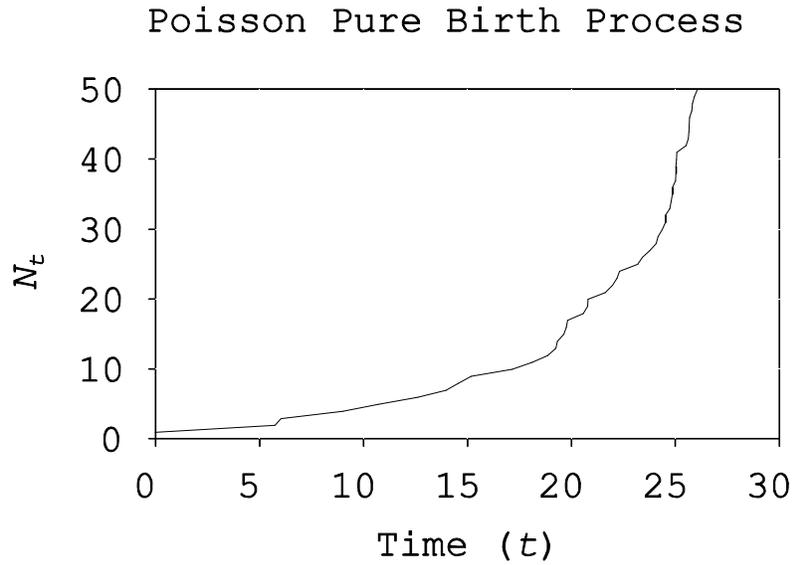
$b$	Observed Frequency	Expected Frequency	Chi-Square
0	3	2.43	0.1337
1	30	28.35	0.0960
2	132	132.30	0.0007
3	315	308.70	0.1286
4	360	360.15	0.0000
5	160	168.07	0.3875
Total	1000	1000.00	0.7465

Pure Birth Process -- Poisson model.

The time to the next birth in the population is exponentially distributed. Thus, the time  $S$  to the next birth in the population of size  $N$  with an instantaneous birth rate of  $b$  is  $\Pr(S > s) = \exp(-bNs)$ , with  $s > 0$ . The distribution of  $N$  after some time  $t$  is distributed as a negative binomial distribution,

$$\Pr(N) = \binom{N - 1}{N_0 - 1} e^{-bN_0t} (1 - e^{-bt})^{(N - N_0)}$$

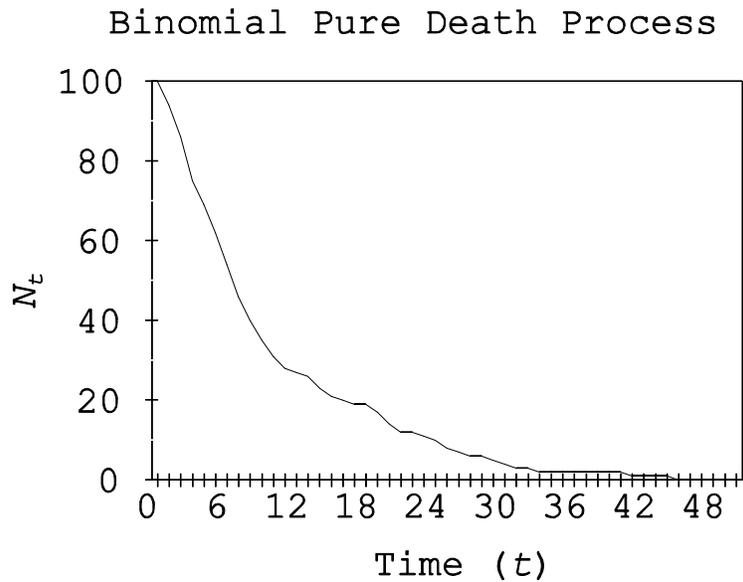
To simulate values of  $S$ , recognize that  $\exp(-bNS)$  has a uniform distribution between 0 and 1. Thus, if  $Y$  is selected as a random Uniform(0,1),  $S = -[\log(Y)]/bN$ . In Quattro Pro,  $Y$  is generated as @RAND. Thus,  $S = -@LN(@RAND)/(bN)$ . To simulate this model in Quattro Pro, each row of the spreadsheet corresponds to a population size, so that row 1 contains  $N_0$ , row 2 contains  $N_0 + 1$ , etc., and the time at which this population size is reached is the current time plus  $S$ .



Pure Death process -- Binomial process.

Each individual undergoes a Bernoulli trial to determine if it will die in this interval.

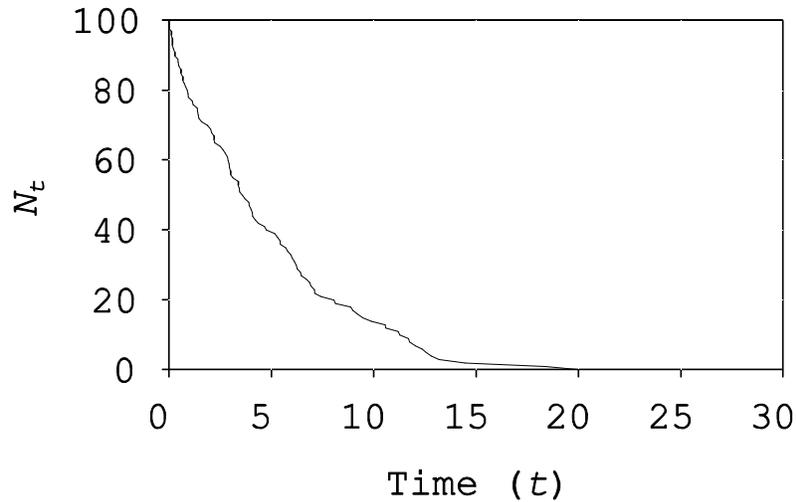
Only binomial variation is present.



Pure Death process -- Poisson process.

The time till the next death is an exponentially distributed variable.

Poisson Pure Death Process



Birth and Death Process -- Binomial process.

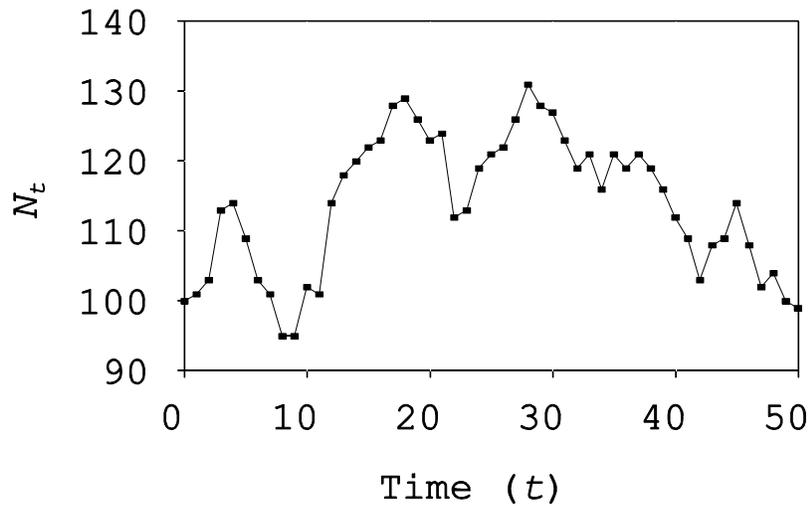
Each individual first undergoes a Bernoulli trial to determine if it gives birth at the start of the interval.

Then, another Bernoulli trial determines if it lives to the start of the next interval.

The result is a random walk model, commonly used to detect density dependence (Murdoch 1994).

As with the simple birth process, the binomial distribution is used for  $N$  animals, all with the same probability of dying. How valid is this assumption?

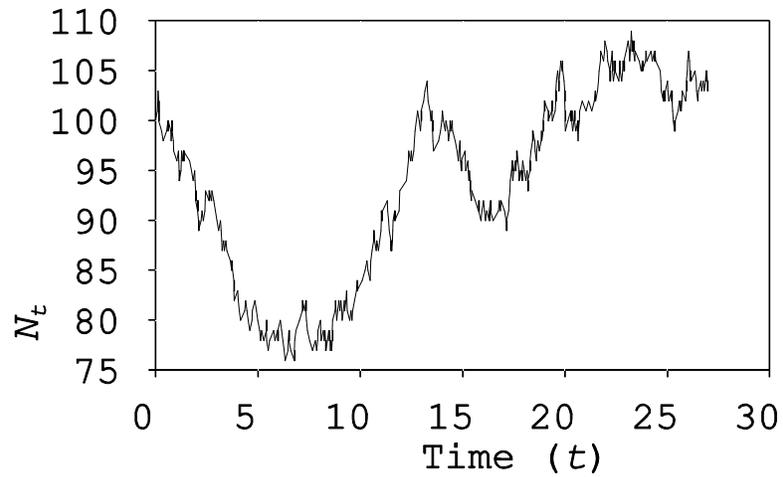
Binomial Birth and Death Process



Birth and Death Process -- Poisson process.

The time to the next event, either a birth or death, is modeled as an exponentially distributed variable. Then, whether the event is a birth or a death is determined from a Bernoulli trial.

### Poisson Birth and Death Process

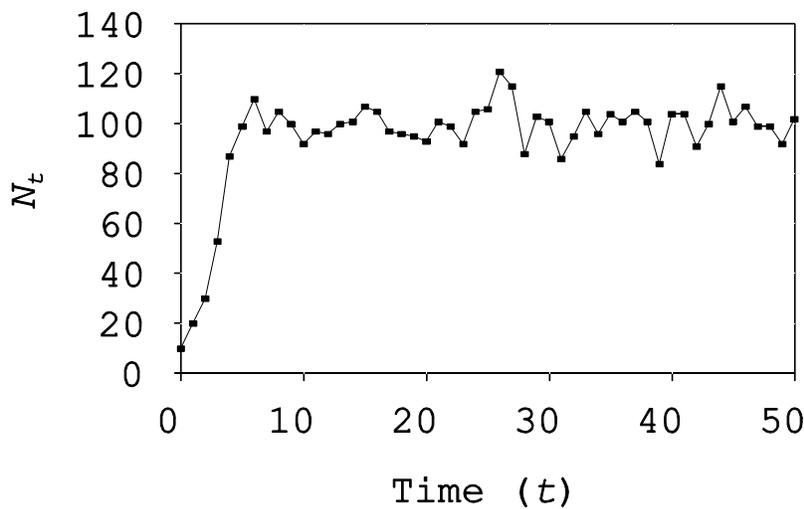


Birth and Death Process with Logistic growth -- Binomial model.

Each individual first undergoes a Bernoulli trial to determine if it gives birth at the start of the interval. The probability of birth is a linear function of the population size. For models where the population size is just after the birthing season, this order would be reversed.

Then, it determines if it lives to the start of the next interval, again with a Bernoulli trial. Again, the probability of death is a linear function of the population size.

Binomial Logistic Birth and Death

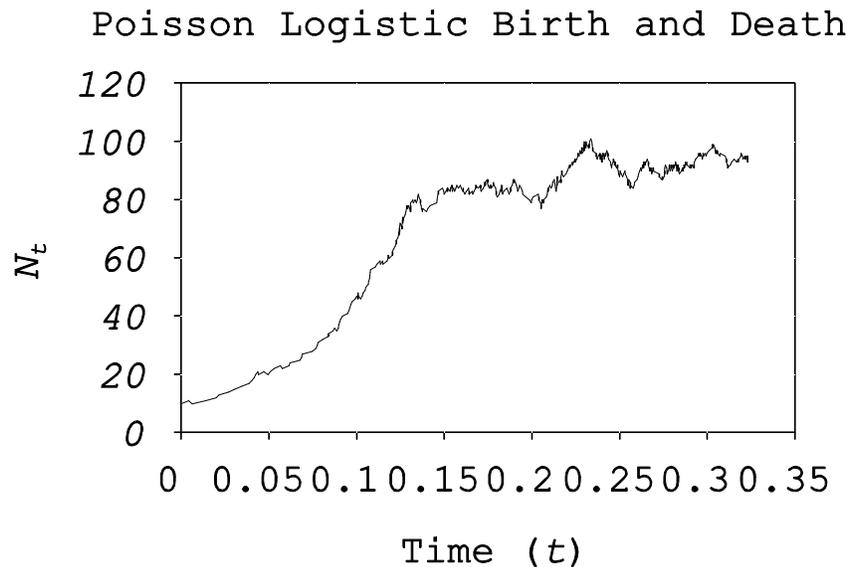


If we specify the change in the birth rate as  $a_1 - b_1N$  and the change in the death rate as  $a_2 + b_2N$ , then  $K = \frac{a_1 - a_2}{b_1 + b_2}$ . If we want to specify  $K$ ,

then the constraint can be imposed on one of the remaining parameters, but the above relationship must hold.

Birth and Death Process with Logistic growth -- Poisson model.

The time to the next event is modeled as an exponentially distributed variable, where the mean of the distribution is a linear function of the current population size. Then, whether the event is a birth or a death is determined by a Bernoulli trial based on the probability of a birth versus the probability of a death.



These processes only incorporate demographic variation.

Individual heterogeneity could be incorporated if each individual had a different probability of birth and death.

Spatial variation would be incorporated if birth and death probabilities differed by areas.

Temporal variation would be incorporated if birth and death probabilities differed in time.

Time to extinction.

Minimum viable population size.

The models discussed in this lecture only incorporate demographic stochasticity, and hence do not provide valid models for real populations where other sources of stochasticity should be considered, such as individual variation and environmental variation.

How to incorporate individual variation into these models: individual based models, IBM.

Spreadsheets are clumsy for this process, and you generally have to use a real programming language.

Improper stochasticity -- incorporating sampling error of parameter estimates into the population process.

Sampling variation

Process variation

### Literature Cited

Morris, W. F., and D. F. Doak. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Incorporated, Sunderland, Massachusetts, USA.

Murdoch, W. W. 1994. Population regulation in theory and practice. *Ecology* 75:271-287.

Renshaw, E. 1991. Modelling biological populations in space and time. Cambridge University Press, New York, New York, USA. 350 pp.