

# Why do populations go extinct?

## Key concepts

- Stochastic and deterministic models
- Demographic and environmental stochasticity
- Gillespie's direct method
- Population viability analysis

## Extinction

Extinction is a fundamental ecological process. For instance, for species that exhibit a metapopulation spatial structure, the species distribution and overall occupancy of habitats is determined by a balance between local extinction and recolonization<sup>1</sup>. At the community level, the theory of island biogeography<sup>2</sup> and neutral theory of biodiversity<sup>3</sup> both take the extinction of populations as a fundamental process in the regulation of local species richness. Finally, at the global scale, the current number of species on earth is the outcome of eons of speciation and extinction and the corresponding balance between them<sup>4</sup>. The contemporary “extinction crisis” refers to the global acceleration in extinction rates due to human activities<sup>5</sup>.

Why do populations go extinct? Can the lifetime of a population be predicted? What is the chance that a particular population will persist until some time in the future? Models studied so far do not admit answers to these questions. Rather, they allow only that a population may increase in size until it reaches the carrying capacity of the environment or else decline asymptotically toward extinction without ever quite reaching it. Our goal in this chapter is to understand extinction as the outcome of a *stochastic process* and to understand the sources of stochasticity that lead to extinction.



Figure 1: The grizzly bear (*Ursus arctos*) was listed as “threatened” according to the Endangered Species Act on 1973. Since the early 1980s populations have grown significantly and in 2013 the Yellowstone Ecosystem subcommittee and Interagency Grizzly Bear Study Team recommended that grizzly bears be removed from Threatened status.

<sup>1</sup> I Hanski. Metapopulation dynamics. *Nature*, 396(4):41–49, 1998

<sup>2</sup> R H MacArthur and E O Wilson. *The theory of island biogeography*, volume 1 of *Monographs in population biology*. Princeton University Press, 1967

<sup>3</sup> Gottfried Jetschke. *The Unified Neutral Theory of Biodiversity and Biogeography*, volume 83 of *Monographs in Population Biology*. Princeton University Press, 2002

<sup>4</sup> Sean Nee. Birth-Death Models in Macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, 37(1):1–17, 2006

<sup>5</sup> John H Lawton and Robert M May. *Extinction Rates*. Oxford University Press, Oxford, 1995

## *North American grizzly bear in the Greater Yellowstone Ecosystem*

Yellowstone National Park, an 8,983 km<sup>2</sup> area in the state of Wyoming, was established as the first National Park in the world by an act of the US Congress in 1872. The Greater Yellowstone Ecosystem had by then become well known for both its geothermal activity and wildlife, including American bison, grey wolves, and grizzly bears. By the early 1900s, Yellowstone National Park had become a major tourist destination. Grizzly bears (*Ursus arctos horribilis*), particularly are an iconic species in the Greater Yellowstone Ecosystem and for many years had been permitted to feed at garbage dumps associated with the parks camps, habituating the bears to human presence and leading to human-animal encounters that were often lethal for the animals. During the middle part of the 20th century, censuses of adult female bears showed the population to be declining and in 1963 the National Parks “Leopold Report” recommended the preservation of natural ecological interactions, including interactions between predators and prey. In 1967, the park began closing the garbage dumps. In 1975 the species was listed as threatened under the US Endangered Species Act and further protections were put in place in 1983.

Estimates of the adult female population size from 1955 to 1997 are recorded in Table 1 and plotted in Figure 2. Clearly, there is evidence that the population was declining prior to the closing of the dumps and species listing and one suspects that the reversal of this trend was in fact a result of these policies. Suppose, however, that the National Park Service and Fish and Wildlife Service had not acted when they did. How long would the Greater Yellowstone population have persisted? Further, population growth from its minimum of  $N = 33$  (in 1973) to its maximum of  $N = 99$  (in 1997) is encouraging, but is it enough. Given the history of observations from 1973 to 1997, what can be said about the chances of long term persistence? These and other questions all require that we develop a theory of stochastic population extinction.

### *Types of stochasticity*

The models introduced up to this point have all been *deterministic*, meaning that the equations for change and initial conditions together and uniquely determine the future state of the population for all times. By contrast, a *stochastic* model is one in which changes in the state of the population are probabilistic. Reasons for probabilistic change may be categorized as *demographic* or *environmental*. Demographic stochasticity is a kind of intrinsic “noise” that arises because

Year ( $t$ )	$N_t$	Year ( $t$ )	$N_t$	Year ( $t$ )	$N_t$
1959	44	1974	36	1989	65
1960	47	1975	34	1990	74
1961	46	1976	39	1991	69
1962	44	1977	35	1992	65
1963	46	1978	34	1993	57
1964	45	1979	38	1994	70
1965	46	1980	36	1995	81
1966	40	1981	37	1996	99
1967	39	1982	41	1997	99
1968	39	1983	39		
1969	42	1984	51		
1970	39	1985	47		
1971	41	1986	57		
1972	40	1987	48		
1973	33	1988	60		

Table 1: Estimates of the number of adult female grizzly bears in the Greater Yellowstone Ecosystem, 1959-1997.

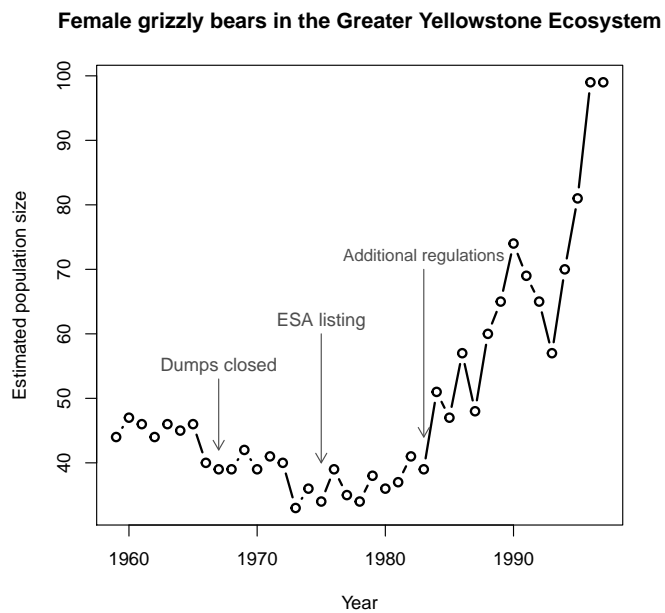


Figure 2: Estimates of the number of adult female grizzly bears in the Greater Yellowstone Ecosystem, 1959-1997.

individuals exhibit differences in reproduction or lifespan. In 1999, the average number of grizzly bear cubs associated with an adult female was 1.9, but no litter consisted 1.9 cubs. Rather, most females had two offspring while some gave birth to only one (or only one survived). Thus, one point of view holds that the cause of demographic stochasticity is the discreteness of individual members of the population. Environmental stochasticity is extrinsic noise which reflects unpredictable year-to-year variation in environmental conditions affecting all individuals similarly. The effects of these two types of noise are different and these differences are important for understanding extinction.

### *The simple birth-death process*

This section introduces a model for density-independent stochastic population dynamics in continuous time called the *simple birth-death process*. Although the model itself is relatively uncomplicated (it has only two parameters), its solution requires some effort. This effort is well rewarded, however, because the result is analytical insight into stochastic population dynamics in general. Any more complicated model is typically much less tractable so the general insights obtained here are especially valuable.

The derivation of the model proceeds as follows. First, as before, let  $b$  be the per capita birth rate and  $d$  be the per capita death rate. In keeping with the principle that demographic stochasticity reflects that individuals are discrete, we will require that the number of individuals in the population be an interval, *i.e.*,  $n \in \{0, 1, 2, \dots\}$ . Additionally, we will assume that births and deaths in the population depend only on the size of the population and are otherwise independent of each other. This means that in any small interval of time  $h$ , the probability that a given individual reproduces is the product  $p(\text{birth}) = bh$  and the probability that it dies is  $p(\text{death}) = dh$ .

### *Gillespie's direct method*

Individual realizations of this process can be simulated using *Gillespie's direct method*. The independence assumption implies that this birth-death process is a continuous time Markov chain. Gillespie's direct method is a simple algorithm for computing such processes and comprises two steps.

1. Determine the time that must elapse between the present time and the time of the next birth or death in the population; we call this birth or death the "event". This is an exponential random variable with mean  $[n(b + d)]^{-1}$ .

2. Determine whether the next event is a birth or death. Births must happen randomly with a long run frequency of  $b/(b+d)$  so that deaths occur with a long run frequency of  $1 - b/(b+d)$ .

Some realizations of the simple birth-death process obtained using Gillespie's direct methods are shown in Figure 3.

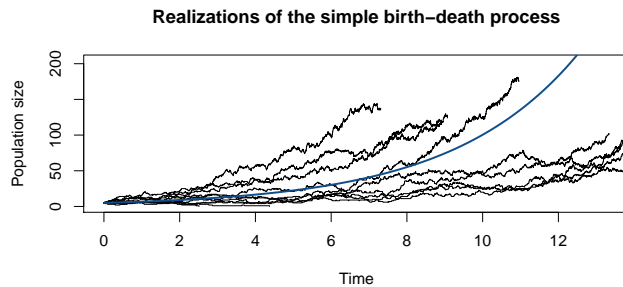


Figure 3: Realizations of the simple birth-death process using  $n_0 = 5$ ,  $b = 1.3$ , and  $d = 1$ . The blue line is the growth of the mean population size given by equation 8.

### Master equation

Gillespie's direct method allows us to compute individual realizations of a birth-death process. Since such realizations are just a sample from a large set of possible outcomes of this process, they don't individually provide much insight. Of course, we can compute a large number of these solutions and analyze them numerically to determine such properties as the average growth, the range of possible outcomes, and frequency of extinction. However, in some cases this approach will be computationally prohibitive and in general it will not identify simple relationships between these quantities and the model parameters should any exist. In this section we see that we also can gain some general insight. From the assumptions above, we can also write down the *master equation*,

$$p_n(t+h) = p_n(t)(1 - n(b+d)h) + p_{n-1}(n-1)(bh) + p_{n+1}(n+1)(dh). \quad (1)$$

The left hand side of this equation is read as "the probability the population is of size  $n$  at time  $t+h$ ." So far we have only said that  $h$  is "small". To be more precise we will insist this means that at most only one "event" (a birth or a death) may occur in an interval of duration  $h$ . Then, there are only three ways that the population can be of size  $n$  at time  $t+h$ : (1) the population could have been of size  $n+1$  at time  $t$  and lost one individual through death, (2) the population could have been of size  $n-1$  at time  $t$  and gained one individual through birth,

or (3) neither of the first two events occurred since time  $t$  and the population was already of size  $n$ . The terms on the right hand side of 1, reading from right to left, are the rates at which these events occur. By construction these possibilities are mutually exclusive and all the possible events that may have occurred. Notice that the three events are weighted by the values  $n + 1$ ,  $n$ , and  $n - 1$  respectively, reflecting the fact that the rates of birth and death are proportional to the size of the population at time  $t$ . Also, since there is no population size of -1 we will interpret  $p_{-1}$  as zero.

Now, dividing both sides of 1 by  $h$  and letting  $h \rightarrow 0$ , we obtain a differential equation.

$$dp_n/dt = -(b+d)np_n + (n-1)bp_{n-1} + (n+1)d \quad (2)$$

This equation is similar to the models encountered previously in that it is a rate of change. However, instead of being the rate of change of the size of the population it is the rate of change of the *probability* that the population is of size  $n$ . (One might instead think of this as a system of an infinite number of equations, one for the probability that the population is of size 0, a second for the probability that the population is of size 1 a third for the probability that the population is of size 2, *etc.*)

If the initial population size is  $n = 1$  then  $p_1(0) = 1$  and one can use the method of *generating functions* to obtain the probability of extinction<sup>6</sup>:

$$p_0(t) = \frac{d - de^{-(b-d)t}}{b - de^{-(b-d)t}} \quad (3)$$

Since the dynamics are density independent, the probability of extinction for  $n_0$  individuals is just the joint probability of extinction of their independent lineages

$$p_0(t) = \prod_{i=1}^{n_0} \frac{d - de^{-(b-d)t}}{b - de^{-(b-d)t}} = \left( \frac{d - de^{-(b-d)t}}{b - de^{-(b-d)t}} \right)^{n_0} \quad (4)$$

For  $b < d$  we can write this equation as

$$p_0(t) = \left( \frac{de^{-(b-d)t} - d}{be^{-(b-d)t} - d} \right)^{n_0} \quad (5)$$

Taking  $t \rightarrow \infty$  we have

$$p_0(\infty) = \left( \frac{-d}{-d} \right)^{n_0} = 1 \quad (6)$$

This result says that if the birth rate is less than the death rate (so the intrinsic rate of increase is less than zero, a condition referred to as

<sup>6</sup> Eric Renshaw. *Stochastic Population Processes*. Oxford University Press, Oxford, 2011

*subcritical*), the population goes extinct with probability 1. However, if  $b > d$  (a *supercritical* population), equation 4 implies that the *ultimate chance of extinction* is

$$p_0(\infty) = \left(\frac{d}{b}\right)^{n_0}. \quad (7)$$

Since both  $d$  and  $b$  are positive and  $d$  is less than  $b$  then  $d/b$  and any power of  $d/b$  is a positive number less than one. Populations subject to demographic stochasticity have a non-zero probability of extinction for any set of vital rates, even for very large intrinsic rate of increase. The case where  $b = d$  exactly is known as the *critical* case and is the knife edge between population growth (on average) and population decline (on average).

In interpreting this result it is important to keep in mind the original assumption that per capita birth and death rates are fixed. There is no density dependence and this population can grow without bound. This might seem like a serious limitation. However, the result is still useful if considered as the chance of “escape” from small to large population size. For populations of large size, extinction via demographic stochasticity in any meaningful time frame is negligible. The chance that a population of small initial size reaches such a large size is given approximately by 7 where  $b$  and  $d$  are the vital rates at small population sizes.

### *The square root scaling law*

Besides providing expressions for the chance of extinction the simple birth-death process can also be solved for summary quantities such as the mean and variance in population size<sup>7</sup>. Specifically, the mean population size is given by

$$m(t) = n_0 e^{(b-d)t} \quad (8)$$

and the variance by

$$v(t) = n_0 \frac{b+d}{b-d} e^{(b-d)t} (e^{(b-d)t} - 1). \quad (9)$$

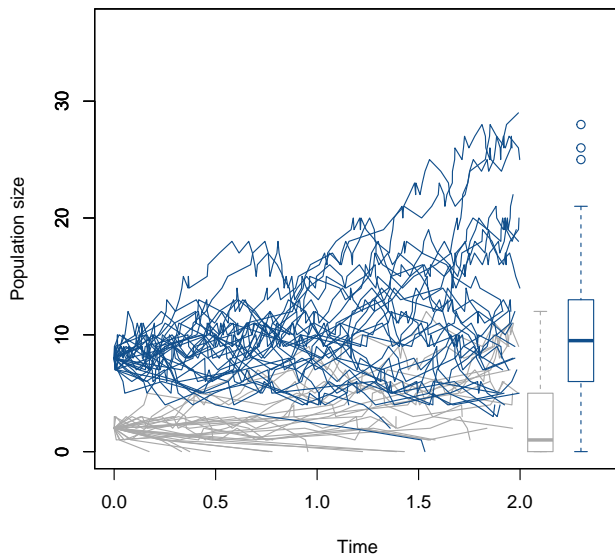
On defining  $r = b - d$  we see that the mean of the demographically stochastic model for density-independent population growth and solution of the deterministic model  $dn/dt = rn$  are equivalent. Further, we can combine these two expressions to obtain a result that is consistent with a very general property known as the *square root scaling law*. The square root scaling law holds that the magnitude of fluctuations in population size due to demographic stochasticity scale inversely with the square root of population size, that is they are proportional

<sup>7</sup> Eric Renshaw. *Stochastic Population Processes*. Oxford University Press, Oxford, 2011

to  $1/\sqrt{n}^8$ . Fluctuations in any quantity can be quantified relative to the mean by calculating the *coefficient of variation*, which is the ratio of the standard deviation of the fluctuations to the mean. Combining equations 8 and 9, we have

$$CV = \frac{\sqrt{v(t)}}{m(t)} \approx \sqrt{\frac{b+d}{b-d}} n_0^{-1/2} = \sqrt{\frac{b+d}{r}} n_0^{-1/2}. \quad (10)$$

Thus, we see that the square root law holds for demographically stochastic populations in growth phase, that the coefficient of proportionality  $(b+d)/(b-d)$  is a quantity that relates the absolute speed of demography to the intrinsic rate of increase, and is itself also inversely proportional to the intrinsic rate of increase.



<sup>8</sup> Robert a. Desharnais, R. F. Costantino, J. M. Cushing, Shandelle M. Henson, Brian Dennis, and Aaron a. King. Experimental support of the scaling rule for demographic stochasticity. *Ecology Letters*, 9(5): 537–547, may 2006

Figure 4: Thirty realizations each of the birth-death process with  $n_0 = 2$  (grey) and  $n_0 = 8$ ; other parameters are  $b = 1.3$  and  $d = 1$ . Box-and-whisker plots show the distribution of population sizes after two years.

As an illustration, Figure 4 shows some realizations of the simple birth-death process with initial population sizes  $n_0 = 2$  and  $n_0 = 8$ . Not surprisingly, the spread is greater in the population that started at a larger size, but how does this spread scale relative to the average population size at the same time? Figure 5 shows the coefficient of variation in 100 simulations of the birth-death over a wider range of initial conditions, illustrating numerically what is shown analytically by equation 10.

### *Environmental stochasticity*

Among the results of our analysis of demographic stochasticity is a scaling law (equation 7) for the chance of extinction in a supercritical



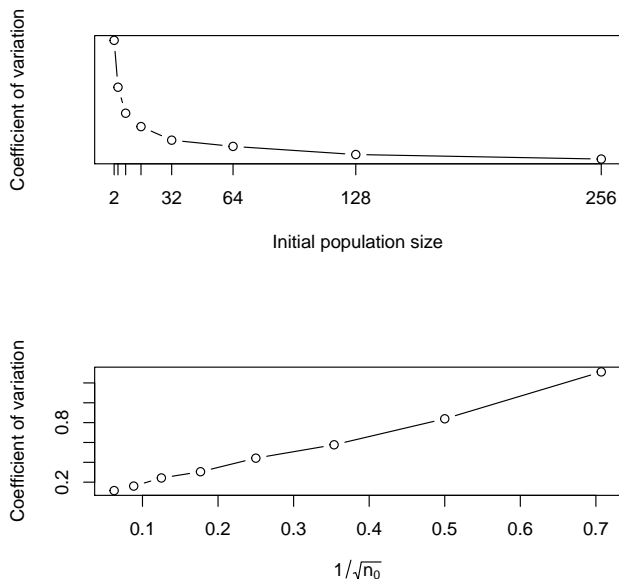


Figure 5: Coefficient of variation in population size after two years from 100 realizations of the simple birth-death process with  $b = 1.3$  and  $d = 1$ . The top panel shows the decline in coefficient of variation as the initial population size increases from  $n_0 = 2$  to  $n_0 = 256$ . The bottom panel shows that this decline follows the inverse square root rule.

population. Evaluating this equation for some arbitrarily chosen values of  $b$  and  $d$  shows that even if the birth rate only slightly exceeds the death rate, then the chance of extinction for even a very modest population (say  $n = 10$ ) is practically zero. Further, as even Darwin observed, virtually all species produce a prodigious number of propagules, implying also that their intrinsic rate of increase is very large, at least under reasonably hospitable conditions. Yet, local extinction is nevertheless an extraordinarily common event in nature, so common in fact that many species have evolved life histories or dispersal strategies to rapidly recolonize habitat sites vacant due to local extinction. What, then, is the cause of these extinctions?

One candidate answer to this question is *environmental stochasticity*, which refers to the fact that the average rates themselves ( $b$  and  $d$  in our example) fluctuate through time in a seemingly random way in response to fluctuations in weather, the presence of other species with which they interact (*e.g.*, predators), and other changes in the environment (such as the availability of resources or territories). There are two causal routes by which environmental stochasticity can elevate extinction risk. One simple way that environmental stochasticity can affect extinction risk is analogous to the effect of demographic stochasticity. Just as the birth-death process allows with some probability (vanishingly small as population size gets large) that the next sequence of demographic events will all be deaths, the model of environmental stochasticity allows that there may be runs of “bad” years with low

growth rates. How much the population suffers from these sequences will depend on the population size at the start of the sequence. A second effect of environmental stochasticity arises because population size compounds like interest in a bank account. A consequence of compounding is that the long run growth rate of the population is the *geometric mean growth rate* of the growth rate realized over smaller intervals,

$$\bar{\lambda}_g = \left( \prod_i^n \lambda_i \right)^{1/n}, \quad (11)$$

which is not the same as the average (the *arithmetic mean*),

$$\bar{\lambda}_a = \frac{1}{n} \left( \sum_i^n \lambda_i \right). \quad (12)$$

In fact, it is the antilog of the arithmetic mean of the natural logarithm, *i.e.*,

$$\bar{\lambda}_g = \left( \prod_i^n \lambda_i \right)^{1/n} = \exp \left( \frac{1}{n} \sum_i^n \ln \lambda_i \right) \quad (13)$$

Due to *Jensen's inequality*, the geometric mean must always be less than or equal to the arithmetic mean. It is possible, in fact, that the arithmetic mean of a sequence of reproductive multipliers may be greater than one (on average the population grows), while the geometric mean is less than one (the long run behavior of the population is to decline). In this sense, the drag on population growth exerted by random environmental variation may be sufficiently great even to reverse the long run direction of the population. One way to express this result is to say that the average growth of a population in a fluctuating environment is less than the growth of the average population in that environment. If the extinction hazard due to demographic stochasticity is not sufficiently large to explain observed extinctions in nature, perhaps the hazard due to environmental stochasticity is.

Here we seek to add this concept of a fluctuating vital rate to our theoretical analysis. Previously, we had written  $n_{t+1} = bn_t - dn_t + n_t$  as a recursive equation for population size in discrete time. Now we modify this expression slightly

$$n_{t+1} = b_t n_t - dn_t + n_t \quad (14)$$

to allow that the parameter  $b$  is itself a Gaussian random variable with mean  $b$  and variance  $\sigma^2$ . Equivalently, we can write the model as

$$n_{t+1} = (b + \delta)n_t - dn_t + n_t \quad (15)$$

where  $\delta$ , a Gaussian random variable with mean 0 and variance  $\sigma^2$ , is an annual deviation from the intrinsic rate  $b$ . This formulation preserves the meaning of  $b$ , allowing us to consider the effect of environmental variation on a population where everything else remains the same. Of course, we could also allow  $d$  to be a random variable.

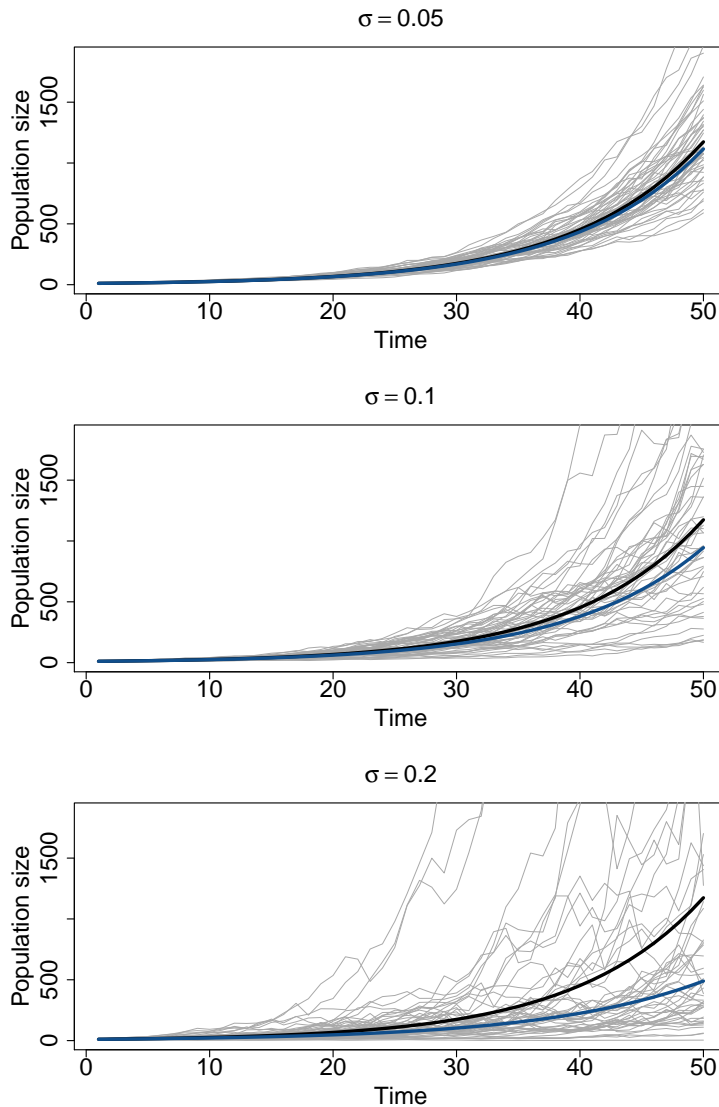


Figure 6: Fifty realizations of the environmentally stochastic model in equation 15 with  $b = 1.1$  and  $d = 1$  at three different levels of environmental variation. For comparison, the heavy black line shows the growth of deterministic model and the heavy blue line shows the growth of the average population size among stochastic realizations. The difference between these lines shows the drag on population growth that results from environmental variation.

Engen *et al.*<sup>9</sup> have shown that the variance in the change in size of a population subject to demographic and environmental stochasticity may be decomposed into two components,

$$\text{var}(\Delta n | n) = v(n) = v_1(n)n + v_2(n)n^2 \quad (16)$$

In this equation (and, technically, also assuming no *demographic co-*

<sup>9</sup> S Engen, B.-E. Sæther, and B E Saether. Stochastic population models: some concepts, definitions and results. *Oikos*, 83(2):345–352, 1998

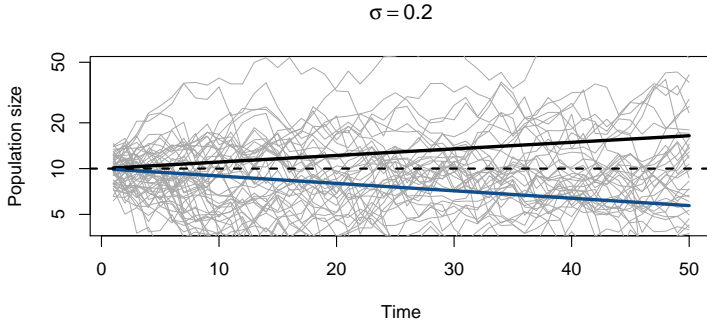


Figure 7: Fifty realizations of the environmentally stochastic model in equation 15 with  $b = 1.1$  and  $d = 1$ . In this case environmental variation causes the average population size to decline over time (blue line) despite the fact that the average value of  $\lambda$  is greater than one and a population growing deterministically at the average population growth rate would increase (black line). The dashed line at  $n_0 = 10$  shows the initial population size so that trajectories above this line have increased whereas trajectories below this line exhibit decline.

variance), the coefficient  $v_1$  corresponds to the contribution to variance from demographic stochasticity while  $v_2$  represents the contribution from environmental stochasticity. Using a technique called the *diffusion approximation* allows us to derive a *stochastic differential equation* as a continuous time approximation to the growth process with variance in the form of equation 16<sup>10</sup>.

$$dn = f(n)dt + \sqrt{v(n)}dW, \quad (17)$$

where  $f(n)$  is the “mean field” or “deterministic” component to population growth or decline, *i.e.*,  $rn$ , and  $v(n)$  is the random fluctuations. Here, the unusual term  $dW$  is the derivative of a Wiener process, also called “Brownian motion”. The formulation of the stochastic differential equation has many advantages, including formulas for such properties as the stationary distribution, mean, and variances (where they exist) and probability densities for *first passage times*, such as the time to extinction. For the birth-death process, we substitute equations 8 and 9, and have

$$dn = rndt + \sqrt{(b-d)(b+d)}\sqrt{n}dW. \quad (18)$$

The  $\sqrt{n}$  in this equation is another expression of the square root rule. If we ignore demographic stochasticity but consider environmental stochasticity, we have

$$dn = rndt + \sqrt{v_2}ndW, \quad (19)$$

where the fluctuations scale with the population size itself. Together, these results imply that unless population size is very small ( $n \approx 1$ ) environmental stochasticity will swamp demographic stochasticity. For many purposes, it may therefore be acceptable to neglect the effects of demographic stochasticity and focus on equation 19, which is considerably more tractable than equation 17. Particularly, it has been known for a long time that the solution to equation 19 is a random

<sup>10</sup> C. Tier and F. B. Hanson. Persistence in density dependent stochastic populations. *Mathematical Biosciences*, 53(1-2):89–117, 1981; and S Engen, B.-E. Sæther, and B E Saether. Stochastic population models: some concepts, definitions and results. *Oikos*, 83(2):345–352, 1998

walk on a logarithmic scale. That is, if we log-transform the population size to obtain a new variable  $x = \ln(n)$  and consider fluctuations in  $x$ , then the change in population size is as if  $x$  is diffusing equally in both directions from  $x_0$  (Figure 8). A consequence of this result is that we can calculate the probability that any other population size  $n_*$  is achieved at time  $t$  (conditioning on the event occurring at all) using the formula<sup>11</sup>

$$p_n(t) = \frac{\ln n_0 - \ln n_*}{\sqrt{2\pi v_2 t^3}} \exp\left(-\frac{((\ln n_0 - \ln n_*) - |r - v_2/2|t)^2}{2v_2 t}\right). \quad (20)$$

If we set the extinction threshold to  $x = 0$  (which is  $n = 1$  on the untransformed scale), then the probability density for the time to extinction is

$$p_1(t) = \frac{\ln n_0}{\sqrt{2\pi v_2 t^3}} \exp\left(-\frac{(\ln n_0 - |r - v_2/2|t)^2}{2v_2 t}\right). \quad (21)$$

These equations can be integrated numerically to obtain the probability that extinction will occur by time  $t$  given that it does occur. The ultimate chance of extinction is

$$p_0(\infty) = \begin{cases} 1 & \text{if } r - v_2/2 \leq 0 \\ \exp(-2 \ln n_0 (r - v_2/2)/v_2) & \text{if } r - v_2/2 > 0. \end{cases} \quad (22)$$

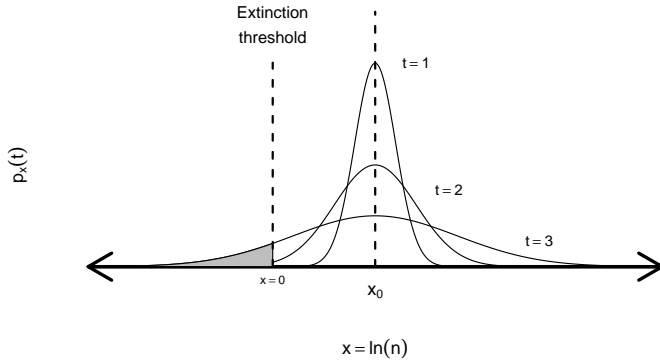


Figure 8: The probability density of log-transformed population size “diffuses” symmetrically over the number line. Initial population size is designated by the vertical dashed line at  $x_0$ . The extinction threshold occurs at  $x = 0$ . The extinction probability is the portion of the probability density that falls to the left of the extinction threshold.

Additional quantities that can be obtained from the extinction time distribution are the expected extinction time (time to  $x = 0$  or  $n = 1$ ),

$$m(t) = \log(n_0)/|r - v_2/2|, \quad (23)$$

and the variance in extinction time,

$$\text{var}(t) = \log(n_0)v_2/|r - v_2/2|^3. \quad (24)$$

<sup>11</sup> Brian Dennis, Patricia L. Munholland, and J. Michael Scott. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61(2):115–143, jun 1991

Further, the tools of ordinary linear regression provide a battery of methods for generating confidence intervals, performing hypothesis tests, and diagnosing fit to model assumptions. See Dennis et al.<sup>12</sup> for details.

These results imply that the main threat to population persistence is the variation in environmental fluctuations, measured by the quantity  $v_2(n)$  in equation 16 since the contribution to variance from demographic stochasticity is large only when the population size is small. Of course, for populations comprised of discrete individuals, the final decline from  $n = 2$  to  $n = 1$  to  $n = 0$  is necessarily a discrete process and may be said to be due to demographic stochasticity. Thus, one view of the relationship of environmental and demographic stochasticity to extinction is that it is environmental stochasticity – random fluctuations in the environment that affect all individuals in the population similarly – that results in the vulnerability of populations, but demographic stochasticity – the chance sequence of birth and death events in the population – that delivers the final stroke.

### *Estimating the probability of extinction*

A practical application of extinction theory is the estimation of extinction probabilities or *population viability analysis*<sup>13</sup>. We have already argued that the main threat to population viability is the magnitude of environmental fluctuations, measured by  $v(n)$  in equation 17. If we ignore demographic stochasticity (because it is small relative to environmental stochasticity) then we only need values for the parameters in equations 21 and 22 to estimate the the probability of extinction. Dennis et al.<sup>14</sup> showed that one can estimate the parameters of this model from simple count data as follows:

1. Transform counts  $n$  to  $x$  by taking logarithms.
2. Calculate growth/decline increments by taking subsequent differences of  $x$ , *i.e.*,  $y_i = x_{i+1} - x_i$ .
3. Calculate time intervals for growth/decline intervals as  $\tau = t_{i+1} - t_i$ .
4. Regress  $y_i = x_i / \sqrt{\tau_i}$  on  $\sqrt{\tau_i}$  using least squares regression forcing the fit regression line through the origin; the slope parameter is an estimate of  $r - v_2/2$  and the mean squared error is a biased estimate of  $\sigma^2$ . (Most regression packages will return an unbiased estimate as well.) In the special case of regularly sampled time series, these are just the mean and variance of  $y$ .

The regression analysis also provides confidence intervals on  $r$  and  $v_2$  that can be used to propagate uncertainty through to put intervals on

<sup>12</sup> Brian Dennis, Patricia L. Munholland, and J. Michael Scott. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61(2):115–143, jun 1991

<sup>13</sup> S R Beissinger. Population viability analysis: past, present, future. In S R Beissinger and D R McCullough, editors, *Population Viability Analysis*, chapter 1, pages 5–17. University of Chicago Press, 2002

<sup>14</sup> Brian Dennis, Patricia L. Munholland, and J. Michael Scott. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61(2):115–143, jun 1991

the estimated probability of extinction.

Performing this procedure using the data in Table 1 for the years 1959 to 1973 we obtain  $\hat{r} = -0.018$  and  $\hat{\vartheta}_2 = 0.006$ . Substituting these values into equation 21 and integrating we estimate that if the National Park Service had not acted as it did to preserve the Yellowstone grizzly bear population, the probability of extinction within 100 years was a serious 8.1%, rising to 89.3% within 200 years. By contrast, applying the procedure to the data for 1973 to 1997 we obtain  $\hat{r} = 0.055$  and  $\hat{\vartheta}_2 = 0.016$  providing an estimate of the extinction probability of approximately  $1.3 \times 10^{-14}$  for the following 100 years. If these calculations may be interpreted to signify the effectiveness of measures taken in response to the observed decline of the grizzly bear and subsequent recommendations of the Leopold report, then the conservation of the grizzly bear in the Greater Yellowstone Ecosystem should be considered an unambiguous success.

### *Homework*

1. Derive the coefficient of variation in equation 10 from equations 8 and 9.
2. Estimate the expected time to extinction of the Yellowstone grizzly bear population from 1973, had the park not acted as it did.
3. The example above assumes that the dynamics of Yellowstone grizzly bears should be considered in two epochs, before and after the 1973 legislation. However, it is possible that the legislation had no effect at all and that the minimum size of the grizzly bear population reached around that time was merely coincidental with conservation actions, in which case the data should be analyzed all together. Perform this analysis and estimate the ultimate extinction probability, the probability of extinction in 100 years, and the mean time to extinction, starting with  $n_0 = 99$  corresponding to 1997 (the last year in Table 1).
4. Devise a test to determine if the Endangered Species Act and other measures taken around 1973 had a statistically detectable effect on the population dynamics of grizzly bears. Test for effects on both mean and variation in change in population size over time.





# *Bibliography*

- S R Beissinger. Population viability analysis: past, present, future. In S R Beissinger and D R McCullough, editors, *Population Viability Analysis*, chapter 1, pages 5–17. University of Chicago Press, 2002.
- Brian Dennis, Patricia L. Munholland, and J. Michael Scott. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs*, 61(2):115–143, jun 1991.
- Robert a. Desharnais, R. F. Costantino, J. M. Cushing, Shandelle M. Henson, Brian Dennis, and Aaron a. King. Experimental support of the scaling rule for demographic stochasticity. *Ecology Letters*, 9(5): 537–547, may 2006.
- S Engen, B.-E. Sæther, and B E Saether. Stochastic population models: some concepts, definitions and results. *Oikos*, 83(2):345–352, 1998.
- I Hanski. Metapopulation dynamics. *Nature*, 396(4):41–49, 1998.
- Gottfried Jetschke. *The Unified Neutral Theory of Biodiversity and Biogeography*, volume 83 of *Monographs in Population Biology*. Princeton University Press, 2002.
- John H Lawton and Robert M May. *Extinction Rates*. Oxford University Press, Oxford, 1995.
- R H MacArthur and E O Wilson. *The theory of island biogeography*, volume 1 of *Monographs in population biology*. Princeton University Press, 1967.
- Sean Nee. Birth-Death Models in Macroevolution. *Annual Review of Ecology, Evolution, and Systematics*, 37(1):1–17, 2006.
- Eric Renshaw. *Stochastic Population Processes*. Oxford University Press, Oxford, 2011.
- C. Tier and F. B. Hanson. Persistence in density dependent stochastic populations. *Mathematical Biosciences*, 53(1-2):89–117, 1981.