

# DEMOGRAPHY OF SMALL POPULATIONS

## Introduction

Stochastic threats arise from the simple fact that it is always possible for a population to decline over a series of generations even if it tends to increase from generation to generation on average. As we saw last time, the following very simple model provides an excellent model of the dynamics for an annual plant population without a seed bank (or for a univoltine insect, for that matter):<sup>1</sup>

$$\begin{aligned}N_{t+1} &= (1 + R_t)N_t \\ &= (1 + R_t)(1 + R_{t-1})N_{t-1} \\ &= (1 + R_t)(1 + R_{t-1})(1 + R_{t-2})N_{t-2} \\ &= (1 + R_t)(1 + R_{t-1})(1 + R_{t-2}) \cdots (1 + R_0)N_0\end{aligned}$$

Let's put some numbers into this equation:

$$\begin{aligned}N_{t+1} &= (1 + 0.02)(1 - 0.02)(1 + 0.01)(1 - 0.01)(10000) \\ &= 9995 \quad .\end{aligned}\tag{1}$$

Last time we calculated  $\bar{R}$ , the average population growth rate in this populations

$$\frac{(1 + 0.02) + (1 - 0.02) + (1 + 0.01) + (1 - 0.01)}{4} = 1 + \bar{R} \quad .$$

That suggests that, on average, the population is neither growing nor declining. But the calculation in equation (1) clearly shows that the population has declined—not by much, admittedly, but it's still declined. What gives? Maybe this will give you a clue. Suppose we multiply each  $R_t$  by ten.  $\bar{R}$  won't change. It will still be 0, but

$$\begin{aligned}N_{t+1} &= (1 + 0.2)(1 - 0.2)(1 + 0.1)(1 - 0.1)(10000) \\ &= 9504 \quad .\end{aligned}$$

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<sup>1</sup>As we'll see when we get to discussing population viability analysis, it's even a reasonable way to get some idea of what's going on in circumstances where we have multiple age classes and other complications.

So  $\bar{R}$  is the same, but the variation around  $\bar{R}$ , the *variance*, is larger, and the result is a larger decline in population size.

Instead of calculating the average growth rate as the *arithmetic* mean,<sup>2</sup> which is what we just did, suppose we calculated the *geometric* mean, i.e.,

$$\begin{aligned} [(1 + 0.02)(1 - 0.02)(1 + 0.01)(1 - 0.01)]^{(1/4)} &= 0.999875 \\ ((1 + 0.2)(1 - 0.2)(1 + 0.1)(1 - 0.1))^{(1/4)} &= 0.9873625 \quad . \end{aligned}$$

Now  $(0.999875)^4 = 0.9995$  and  $(0.9873625)^4 = 0.9504$ , so the geometric mean is clearly what we want to use to calculate long-term growth rates of populations when the growth rate varies among generations. Why? Because the long-term growth rate of a population is the *product* of generation-to-generation growth rates, not the *sum*.

The first important thing this example illustrates is that when dealing with variation in rates, the usual arithmetic mean isn't nearly as important as the geometric mean. The long-term growth fate of a population is determined by the *geometric* mean of  $1 + R_t$ , not by the *arithmetic* mean.<sup>3</sup> If you want a formula to compare the two, here it is:

$$\begin{aligned} \bar{x}_{a.m.} &= (1/K) \sum_i x_i \\ \bar{x}_{g.m.} &= \left( \prod_i x_i \right)^{(1/K)} \\ &= \exp \left( (1/K) \sum_i \ln x_i \right) \quad . \end{aligned}$$

The second important thing this example illustrates is that the geometric mean is always less than the arithmetic mean.<sup>4</sup> As a result, the long-term growth rate of a population may be negative even if the arithmetic mean growth rate is positive. In other words, a population may decline over the long term even if it tends, on average, to increase in size from one year to the next.

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<sup>2</sup>Just in case you haven't heard the word "mean" in this context before, it's just another word for "average." Statisticians tend to like to talk about the "mean" of a distribution or the "mean" of a sample, rather than the average. Since I have an adjunct appointment in our Department of Statistics, that's the terminology I'll use.

<sup>3</sup>Similarly, the long-term growth rate of your retirement portfolio is determined by the *geometric* mean of your annual returns, not the *arithmetic* mean.

<sup>4</sup>Notice that I said that this example "illustrates" that the geometric mean is always less than the arithmetic mean. But it doesn't actually "illustrate" it very well, does it? All it really shows is that the arithmetic mean and the geometric mean aren't equal. The proof that the geometric mean is always smaller than the arithmetic mean, for anyone who cares, follows from Jensen's inequality. If you don't know what Jensen's inequality is, don't worry about the proof. Just take my word for it.

It can be shown that the long-term growth rate of a population will be negative, i.e, the population will tend to decline, whenever the variance in growth rate is more than about twice its mean.<sup>5</sup> To be more precise, if

$$N_{t+1} = (1 + R_t)N_t$$

and  $\bar{R}$  is the average  $R_t$  and  $s_R^2$  is the variance of  $R_t$  then the long-term growth rate of a population will be negative if

$$\bar{R} < \frac{s_R^2}{2} .$$

## Demographic vs. environmental stochasticity

Remember that demographic stochasticity refers to the inevitable variability in *actual* population growth rate that occurs even if the population vital rates (expected rates of survival and reproduction) don't change from one season to the next. Environmental stochasticity refers to the variability in population growth rate that occurs because vital rates differ from one season to the next. Making an analogy with evolutionary processes may help: Demographic stochasticity is like genetic drift. It is non-directional and non-deterministic. Environmental stochasticity is like a variable selection pressure. In any one generation there is a directional change and it is deterministic. It's just that the direction of that deterministic influence may change from one generation to the next. It would be very useful if we could tease apart these two stochastic influences on population dynamics so that we could more accurately assess their effect.

Unfortunately, the relative contributions of demographic and environmental stochasticity to variation in population growth rate cannot be directly measured. All we know is that we see  $N_{t+1}$  plants or animals at time  $t+1$  and  $N_t$  at time  $t$ . Now if we had a large enough set of data, we might be able to predict pretty closely what  $N_{t+1}$  should be in terms of  $N_t$  and the relevant demographic parameters. The  $N_{t+1}$  we observe will almost certainly be different from the one we expect. But how much of this difference is because the environment in generation  $t$  was different from its long-term average and how much is because of inherent randomness associated with birth and reproduction? There's no way to tell.<sup>6</sup>

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<sup>5</sup>The math isn't too hard. It's in appendix A of [4], if you'd like to see it. By the way, the same calculations apply to your retirement portfolio. The value of your retirement investment will decline if the variance in annual rate of return is more than about twice the mean annual rate of return. That's one reason why it's important to pay attention not only to what the annual rate of return on an investment is, but on how variable that return is, i.e., how risky it is.

<sup>6</sup>Actually, that's not quite true. By fitting a hierarchical Bayesian model to a time series of population

Species	$\bar{r}$	Variance	Equivalent $N$	Observed $N$
Great tit	0.20 (-0.045,0.44)	0.4151	3	20–95
Heron	0.025 (-0.035,0.084)	0.01438	71	274–484
Laysan finch	0.89 (0.33,1.44)	0.0802	24	5000–21000
Palila	0.52 (-0.66,1.70)	0.3625	5	2000–6400
Palila	0.0017 (-1.0,1.0)	0.3931	3	2000–6400
Grizzly bear	-0.0018 (-0.036,0.032)	0.006444	155	33–47

Table 1: Demographic *versus* environmental stochasticity for several animal populations (from [4])

If, however, we assume that the number of births and deaths are approximately distributed as independent Poisson random variables, then the demographic variance is equal to  $(1 + R)/N$ . We can use this observation to calculate the population size (labeled “Equivalent  $N$ ” in Table 1) that would produce a variance in population growth rate equivalent to what is observed in a particular data set.<sup>7</sup> For example, the observed variance in population growth rate of a British heron population is 0.01438. Given that its observed growth rate,  $R$ , is 0.025, we can calculate the “equivalent  $N$ ” from

$$\begin{aligned}
(1 + R)/N &= \text{Var}(R) \\
(1 + 0.025)/N &= 0.01438 \\
N &= 1.025/0.01438 \\
&= 71
\end{aligned}$$

Such calculations give us a way of assessing whether it’s reasonable to think that the observed magnitude of population fluctuations we see are consistent with purely demographic variability or if it’s more reasonable to think that there must be some environmental variability, too.

Notice that the equivalent  $N$  is much smaller than the observed  $N$  for every species except the grizzly bear. That means that in every species except grizzly bear there is substantially more variation in population growth rate than is likely to be accounted for by demographic stochasticity, i.e., it is likely that environmental stochasticity makes a large contribution to the population dynamics of the other species. This may not be much of a surprise, but the

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sizes, it is possible to distinguish between intrinsic process variability and variability that is the result of measurement error. But doing it isn’t easy. Take a look at [1] if you’re interested.

<sup>7</sup>Those of you familiar with population genetics will recognize this as a trick analogous to the one population geneticists use for defining the effective size of populations with respect to genetic drift.

quantitative results suggest that environmental stochasticity is 10-100 times more important than geographic stochasticity.

## Demography of chance extinction

When we're managing a threatened species, our primary focus is identifying strategies to prevent it from going extinct. The primary conceptual tools for organizing our thinking are related to extinction, specifically the probability that a population goes extinct within a specified time period (typically 100 years) or the expected time to extinction.<sup>8</sup> We'll talk more about this when we discuss population viability analysis next week.

Probabilists have studied *birth-and-death processes* for many years. Individuals die with a given probability between seasons. Surviving individuals give birth to a random number of individuals. For a population of size  $N$ , the expected time to extinction is

$$T_{(N)} = \sum_{x=1}^N \sum_{y=x}^{N_m} \frac{2}{y[yV_{(y)} - r_{(y)}]} \prod_{z=x}^{y-1} \frac{V_{(z)}z + r_{(z)}}{V_{(z)}z - r_{(z)}} \quad ,$$

where  $r_{(n)}$  is the mean per capita growth rate and  $V_{(n)}$  is its variance when the population size is  $n$  [3].  $N_m$  is maximum possible population size—the population ceiling.

If all variance in population growth rates were due to events that affect individuals independently and all individuals have the same probability distribution governing death rates and fecundity rates then

$$V_{(n)} = \frac{V_1}{N} \quad ,$$

where  $N$  is the population size and  $V_1$  is the variance of the per capita offspring production rate. This approach incorporates only demographic stochasticity.

Alternatively, all variance in population growth rates may be due to population-wide variation in the vital rates, with all individuals behaving identically. Then

$$V_{(n)} = V_e \quad ,$$

where  $V_e$  is a measure of environmental stochasticity.<sup>9</sup> This approach incorporates only environmental stochasticity.

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<sup>8</sup>We'll come back to this when we talk about population viability analysis, but for now think about this question. Why did I say that we talk about the probability that a population goes extinct *within a specified time period*?

<sup>9</sup>Notice that we are implicitly assuming density-independent population dynamics here (except for the “hard” cap on population size,  $N_m$ ), or at least that the magnitude of variation in population growth rate is overwhelmingly determined by factors unrelated to the current size of populations.

To incorporate both

$$V_{(n)} = V_e + \frac{V_1}{N} \quad . \quad (2)$$

Note: This ignores any covariance between  $V_1$  and environment, which is likely to inflate the variance. From equation (2) we would expect demographic stochasticity to have a large influence only when population sizes are very small. This entire approach ignores age/stage structure within the population, but analysis of these types of models still provide some indications of the qualitative features of the extinction process.

1. **Persistence time increases greatly as population ceiling is increased:** Management implication, small reserve areas have small population ceilings (at least for large animals), therefore extinction is more likely in small reserves than large ones.
2. **Demographic stochasticity is unimportant in populations with more than about 50 reproductive individuals:**<sup>10</sup> Management implication, direct manipulation of reproduction is unlikely to be needed except in very small populations
3. **Persistence time is drastically shortened by environmental stochasticity:**<sup>11</sup> Management implication, populations must be very large to buffer environmental stochasticity without direct intervention
4. **Distribution of persistence times is roughly geometric:** If mean persistence time is  $\bar{t}$  probability of extinction after  $n$  generations is

$$\left(\frac{1}{\bar{t}}\right) \left(1 - \frac{1}{\bar{t}}\right)^{n-1}$$

Management implication, there is a greater than 50% of extinction before  $\bar{t}$ .

- (a) 63% chance of extinction by  $\bar{t}$
- (b) 50% chance of extinction by  $0.7\bar{t}$

5. **Persistence time increases exponentially with carrying capacity if  $\bar{R} > \frac{s_R^2}{2}$ , but only logarithmically with carrying capacity if  $\bar{R} < \frac{s_R^2}{2}$ :** Management implication, increasing the size of a managed population has less impact on its long-term persistence than reducing the variability in growth rate. Only when variability in population growth rate is small<sup>12</sup> are isolated populations likely to persist without frequent management intervention.

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<sup>10</sup>age/stage structure can complicate this a lot, if reproduction is heavily concentrated in one age or stage

<sup>11</sup>Holds true with age or stage structure

<sup>12</sup>What counts as “small” depends on the average population growth rate. Variability is small if  $\bar{R} > \frac{s_R^2}{2}$ .

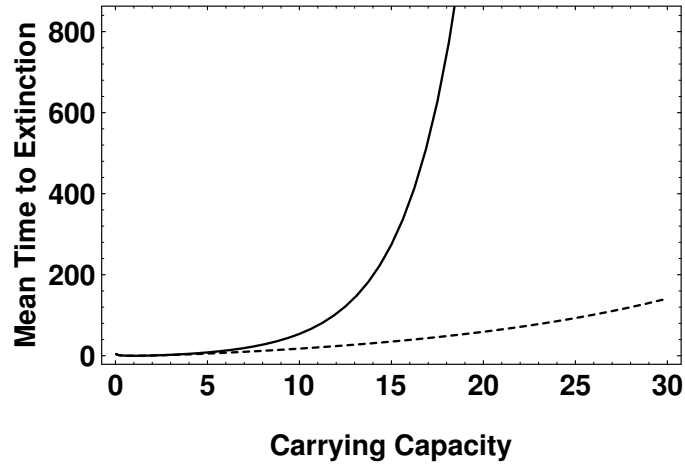


Figure 1: Effect of demographic stochasticity on persistence times. Solid line has  $r = 0.2$ . Dotted line has  $r = 0.05$ . Individual variance in reproductive success is equal to 1.

## Catastrophes

In thinking about the influence of catastrophes on population persistence, it is useful to think of them as events that happen very rarely, but eliminate a fixed proportion of the population whenever they occur.

Definitions [2]:

- $\alpha$  = probability of a birth in the population in a small time interval
- $\beta$  = probability of a death in the population in a small time interval
- $\gamma$  = probability of a catastrophe in the population in a small time interval
- $p$  = individual survival probability in a catastrophe
- $n$  = initial population size

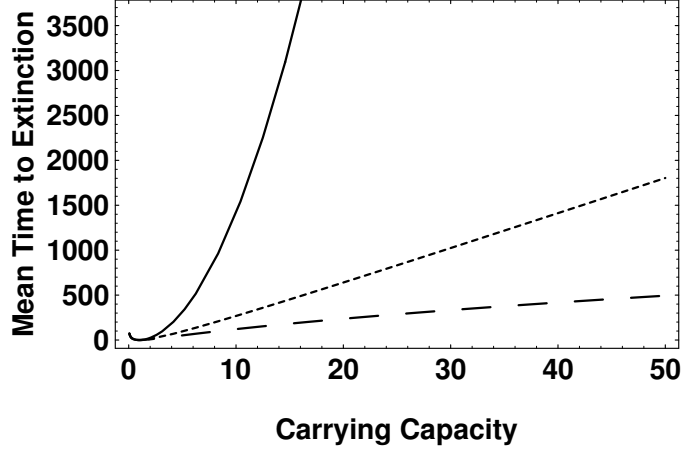


Figure 2: Effect of environmental stochasticity on persistence times.  $r = 0.05$  for all lines.  $V_e = 1/30$  for the solid line,  $1/20$  for the dotted line, and  $1/15$  for the dashed line.

$$P(\text{population extinction} \leq t) \approx \exp \left[ - \exp \left( - \frac{t - a_n}{b_n} \right) \right] ,$$

where  $b_n = 0.7797\sigma_n$ ,  $a_n = \mu_n - 0.5772b_n$ , and  $\mu_n$  and  $\sigma_n^2$  are the mean and variance of the extinction time.<sup>13</sup>

$$\mu_n = -(\ln n)/(\alpha - \beta + \gamma \ln p) , \tag{3}$$

$$\sigma_n^2 = -(\ln n)[\gamma(\ln p)^2]/(\alpha - \beta + \gamma \ln p)^3 \tag{4}$$

**Note:** This formula can only be used if  $\alpha < \beta - \gamma \ln p$ .

Mean lifetime for an individual	$\beta^{-1}$
Mean number of offspring for an individual	$\alpha\beta^{-1}$
Mean time between catastrophes	$\gamma^{-1}$

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<sup>13</sup> $0.7797 = \sqrt{6}/\pi$ ,  $-0.5772 = \Gamma'(1)$

## Example

We can use these results to find the time by which the population has a 50% chance of going extinct. Suppose that in each catastrophe that occurs 95% of the population is eliminated, and that we're dealing with a species that has 2 offspring over its lifetime, lives about 20 years, and to which catastrophes occur about every 50 years. Suppose that we start with a population of 100 individuals.

Mean lifetime for an individual	20 years
Mean number of offspring for an individual	2
Mean time between catastrophes	50 years
Proportion of population surviving	0.05
Current population size	100
$\beta = 1/20$	0.05
$\alpha = \beta(2) = (1/20)(2)$	0.1
$\gamma = 1/50$	0.02
Mean time to extinction (from 3)	464
Variance of extinction time (from 4)	850,000
$b_n$	718
$a_n$	50
$t$ to 50% probability of extinction	313
Notice that $(0.7)464 \approx 325$ , which is pretty close to 313.	

Properties:

- Effect of catastrophes depends dramatically on their frequency (Figure 3).
- Effect of catastrophes depends dramatically on proportion of population surviving after catastrophe (Figure 4).
- Resistance to catastrophes increases only very slowly with population size (Figure 5)

These results are for density-independent population growth. It is also possible to study similar models of density-dependent population growth. Instead of expressing results in terms of persistence given the current population size, they are expressed in terms of persistence given a particular carrying capacity. The results are much more complicated, but the general pattern holds [5]:

- Persistence time is proportional to the *logarithm* of the current population size (in the case of density-independent population growth) or to a power  $< 1$  of carrying capacity (in the case of density-dependent population growth) if  $r = \alpha - \beta < -\gamma \ln p$ .

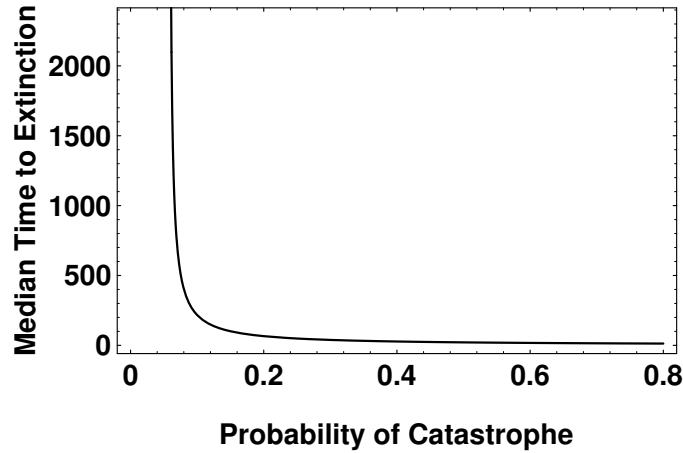


Figure 3: Effect of catastrophes depends dramatically on their frequency. ( $\alpha = 0.24$ ,  $\beta = 0.2$ ,  $p = 0.5$ ,  $n = 1000$ )

- Persistence time is proportional to a power  $> 1$  of carrying capacity if  $r = \alpha - \beta > -\gamma \ln p$ .<sup>14</sup>

## Demographic heterogeneity

A few years ago, Brett Melbourne and Alan Hastings [6] pointed out that there's another source of stochasticity to consider: demographic heterogeneity. Demographic stochasticity arises because individuals with the same probability of survival and the same expected fecundity may or may not survive and may have different numbers of offspring.

But there are also obviously differences among individuals in how likely they are to survive and in how many offspring they can expect to produce. Those differences reflect demographic heterogeneity. I know that most or all of you aren't as enamored of mathematical equations

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<sup>14</sup>Remember that we can't calculate persistence time for density-independent models in this case.

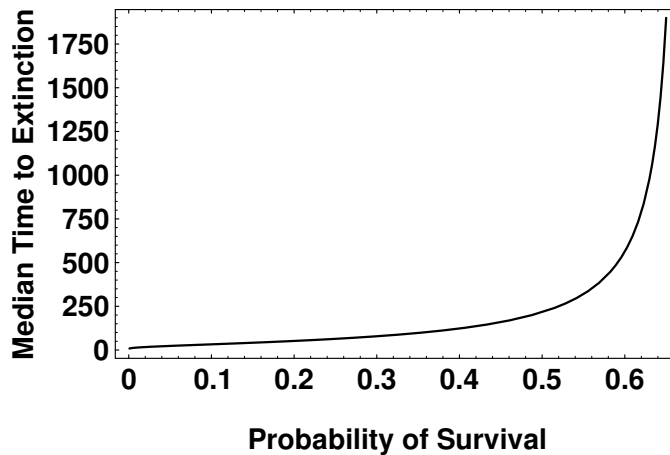


Figure 4: Effect of catastrophes depends dramatically on proportion of population surviving after catastrophe. ( $\alpha = 0.24$ ,  $\beta = 0.2$ ,  $\gamma = 0.1$ ,  $n = 1000$ )

as I am, but stick with me for a minute here. I think this mathematical digression will help you to see what's going on.

## A stochastic Ricker model

Let's start at time  $t$  with a population having  $N_t$  females. Assume that the  $i$ th female produces  $B_{i,t}$  offspring, where  $B_{i,t}$  is a Poisson random variable with mean and variance  $\beta_{i,t}$ .<sup>15</sup> Demographic stochasticity is reflected in the fact that the *actual* number of offspring the  $i$ th female produces is a random variable, i.e., we don't know it with certainty. We can only specify its mean and variance. Demographic heterogeneity is reflected in the fact that I have a subscript  $i$  on  $\beta_{i,t}$ , meaning that the expected number of offspring produced may differ from female to female. We'll assume that  $\beta_{i,t}$  is drawn from a gamma distribution with

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<sup>15</sup>If you don't know what a Poisson random variable is, all you really need to know is that it's a reasonable choice, and that it has the property that its mean and variance are equal to one another.

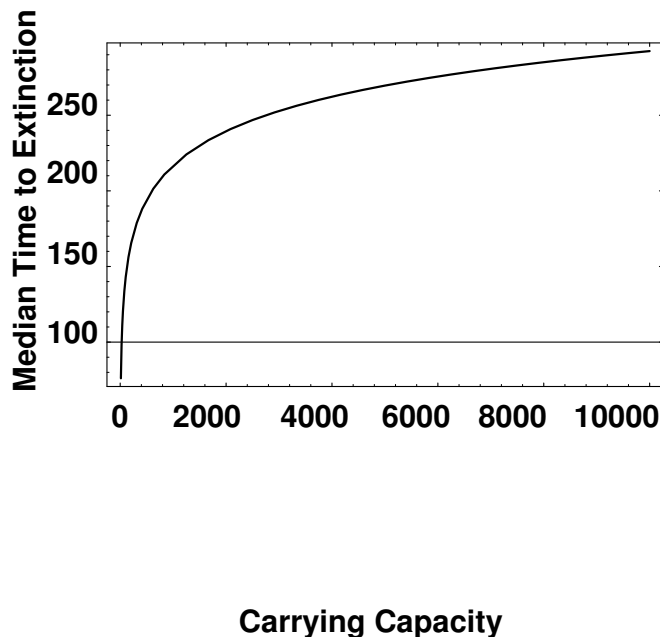


Figure 5: Resistance to catastrophes increases only very slowly with population size ( $\alpha = 0.24$ ,  $\beta = 0.2$ ,  $\gamma = 0.1$ ,  $p = 0.5$ ).

mean  $\beta_t$  and shape parameter  $k_D$ .<sup>16</sup> The fact that I also have a subscript  $t$  on  $\beta_{i,t}$  should clue you in to the fact that I'm going to let  $\beta_t$  vary over time. That's environmental stochasticity. We'll assume that  $\beta_t$  is drawn from a gamma distribution with mean  $\beta$  and shape parameter  $k_E$ .

Now suppose that each offspring (irrespective of whether it's male or female) survives to adulthood with probability  $se^{-aN_t}$ , i.e., that there's demographic stochasticity in survival, but no demographic heterogeneity and no sex-specific survival. We will also suppose that each surviving offspring is female with probability  $z$ , i.e., that there's demographic stochasticity associated with sex determination.

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<sup>16</sup>If you don't know what a gamma distribution is, don't worry. All you need to know is that it's a handy distribution, and that the shape parameter is related to the variance. The smaller the shape parameter, the larger the variance.

Stochasticity	R	$\alpha$	$k_D$	$k_E$	$L$	$\Delta\text{AIC}$
None	2.526	0.003636	-	-	-406.5	336
Demographic	2.638	0.003744	0.01463	-	-246.3	18
Environmental	2.706	0.003800	-	1.9913	-265.3	148
Demographic & sex	2.621	0.003731	0.3876	-	-245.8	17
Environmental & sex	2.770	0.003831	-	13.1014	-242.6	10
All	2.613	0.003731	1.1475	26.6221	-236.4	

Table 2: Parameter estimates for different models fit to an experimental population of *Tribolium castaneum* [6].  $R = \beta(1 - m)$ .  $L$  is the log likelihood at its maximum.  $\Delta\text{AIC}$  is a measure of how much worse each model is than the one below it. Differences of 10 or more are regarded as very substantial.

## An application

This model may seem complicated, but it’s still relatively simple. For example, we don’t allow generations to overlap, and we assume that sexes survive with the same probability and that there’s no individual heterogeneity in probability of survival. Still it’s complicated enough to capture what seem to be the most important features of population dynamics in one simple experimental system: laboratory populations of the flour beetle, *Tribolium castaneum*.

The results in Table 2 clearly show that all sources of stochasticity contribute importantly to population dynamics in this experimental population. Interestingly, the variance associated with demographic heterogeneity is substantially greater than the variance associated with environmental stochasticity, i.e., differences among individuals *within* a generation matter more than differences *among* generations.

## References

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