Biology of small populations — Introduction

Introduction

It almost seems a truism to say it, but it's a simple fact that we can't ignore when dealing with endangered species: Small populations are more likely to go extinct than large ones. Over the next couple of weeks we'll be talking in detail about the reasons for this, but it was recognized many years ago that when pouplations get too small they may be unsustainable — the Allee effect. But even that idea wasn't new. Like so many other things in biology where we think that we've had an original idea, it turns out that Darwin [2, p. 109] already had the same insight:

> Rarity . . . is the precursor to extinction. We can . . . see that any form represented by few individuals will, during fluctuations in the seasons or in the number of its enemies, run a good chance of utter extinction.

The peril small populations face may be either deterministic (the result of systematic forces that cause population decline, e.g., loss of pollinators, inability to find mates, inability to defend against predators) or stochastic (the result of random fluctuations that have no systematic direction).

Deterministic *versus* stochastic threats

So far in this course we've mentioned only *deterministic threats* to the persistence of species.[1] Deterministic forces are guaranteed to drive a population to extincition in a relatively short period of time. Overexploitation, development, deforestation, and disease are examples of deterministic threats to persistence. Deterministic threats to persistence are traditionally where conservationists have focused most of their efforts. We eliminate the use of DDT, we set aside reserves or national parks, we use captive breeding to increase the number of

[1] A *deterministic process* is one in which the future state can be exactly specified given knowledge of the present state.

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individuals. More generally, first we try to identify the factors that are causing a species to decline, and then we try to find ways to mitigate or eliminate those factors.

One of the important insights from population genetics and population ecology that was incorporated into conservation thinking in the 1980s was the idea that random events in small populations may have a large impact on population dynamics and population persistence. In other words, in addition to any deterministic threats they may face, small populations may also face *stochastic threats* to their persistence.[2] If the rate of population growth varies from one generation to the next, a series of unlucky generations in which there are successive declines in population size can lead to extinction even if the population is growing, on average.

A (slightly) mathematical digression

You've probably got the idea, but let's be a little more formal about this.[3] Let N_t be the size of a population at time t. Then no matter how complicated the population dynamics actually are, it is always possible to write the population size at some later time, $t+1$, as

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

You should recognize that R_t could vary from one time period to the next for many different reasons, e.g., "fluctuations in the seasons or in the number of ... enemies". The weather might be different in different years. A disease might sweep through the population. The number of individuals added to or subtracted from the population might depend on the number already there. Chance events may cause the population to increase or decline.

Suppose, however, that we're dealing with an annual plant, one that doesn't have a seed bank, and that we've counted the number of individuals present for many years. As a result, we have a whole list of R_t's. Suppose we take the average of these R_t's, call it $\bar{R}$. If $\bar{R} > 0$, then the population is growing on average. Another way of saying that is to say that $N_{t+1} > N_t$, on average. If $\bar{R} < 0$, then the population is declining on average (and $N_{t+1} < N_t$, on average). Deterministic threats are those, like the ones we've talked about so far in this course, that make $\bar{R} < 0$. Deterministic threats cause population sizes to decline, on average, year after year. So what are stochastic threats?

Well, let's think about that annnual plant again. We have a list of R_t's from when we started to count up to the present. In every generation

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

[2]A *stochastic process* is one in which only the probability distribution for future states can be specified, even given exact knowledge of the present state.

[3]This is the first of several mathematical models you're going to be seeing over the next few lectures, so take a deep breath and hold on.

But if you think about it a little longer, you realize that this isn't the whole story. Since that equation applies in every generation, we can do the following:

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

So what's the big deal? Well, the population will have grown over this period *only* if the product $(1+R_t)(1+R_{t-1})(1+R_{t-2})\cdots(1+R_0)$ is greater than one. It turns out that this product can be less than one even if $\bar{R} > 0$. In other words, the population can decline over the long-run even if it increases, on average, every generation.

That undoubtedly sounds paradoxical, but there's a mathematical theorem showing that it's true.[4] We'll go into the details next time, but for now just consider a simple example, an annual plant without a seed bank that increases in size by 2% one year, decreases by 2% the following year, increases by 1% the following year, and decreases in size by 1% in the fourth year. Then

$$\begin{aligned} 1+\bar{R} &= \frac{(1+0.02)+(1-0.02)+(1+0.01)+(1-0.01)}{4} \\ &= 1 \\ \bar{R} &= 0 \quad . \end{aligned}$$

In other words, the population size isn't changing on average. Now consider this. Suppose the population size in the first year was 10000. Then the population size after 4 years will be

$$10000(1+0.02)(1-0.02)(1+0.01)(1-0.01) = 9995 \quad .$$

What isn't obvious from this simple example is that a long-term decline can happen even when $\bar{R} > 0$ if there's lots of variability among the R_t. In fact, if the variation in R_t is big enough, a population is guaranteed to decline even if $\bar{R} > 0$. Stochastic threats are those that arise from the variability of R_t.

- *Deterministic threats*—Those that cause $\bar{R} < 0$.
- *Stochastic threats*—Those that arise because of the variability of R_t.

[4] You'll be happy to hear that we're not going to prove that theorem. If you're interested, though, I'd be happy to walk through the proof with you.

Types of stochastic threats

Boyce [1] suggested that we distinguish among four classes of stochasticity affect small populations:

1. Genetic stochasticity
2. Demographic stochasticity
3. Environmental stochasticity
4. Catastrophes

Genetic stochasticity

Genetic stochasticity refers to changes in the genetic composition of a population unrelated to systematic forces (selection, inbreeding, or migration), i.e., genetic drift. It can have a large impact on the genetic structure of populations, both by reducing the amount of diversity retained within populations and by increasing the chance that deleterious recessive alleles may be expressed. The loss of diversity could limit a population's ability to respond adaptively to future environmental changes. In addition, the increased frequency with which deleterious recessive alleles are expressed (because of increased homozygosity) could reduce the viability and reproductive capacity of individuals. I am generally skeptical about the extent to which genetic stochasticity poses a threat to most endangered species of animals or plants, for reasons we'll discuss in some detail later. For now, suffice it to say that most frequently I suspect the lack of genetic diversity in endangered species is a symptom of their endangerment, not a cause.

Demographic stochasticity

Demographic stochasticity refers to the variability in population growth rates arising from random differences among individuals in survival and reproduction within a season. This variability will occur even if all individuals have the same expected ability to survive and reproduce and if the expected rates of survival and reproduction don't change from one generation to the next. Even though it will occur in all populations, it is generally important only in populations that are already fairly small.[5]

[5] In other words, it's like genetic stochasticity. It's a symptom of endangerment, not a cause.

To make this concrete, let's compare two populations, one of size 10, one of size 10,000. We'll asssume that individuals produce 2 offspring, on average, but that the actual number of offspring any one individual produces is a Poisson random variable, i.e.,

$$P(N = n) = \frac{\lambda^n e^{-\lambda}}{n!} \qquad ,$$

where $\lambda = 2$. We'll also assume that the offpring have a 50% chance of survival. The combination of an average of two offspring per individual and 50% survival means that the population size doesn't change, on average, i.e. $\bar{R} = 0$.

- Population of 10,000
  - Expected number of offspring in next generation is $20,000$
  - Variance in number is $20,000$. Standard deviation is 141.
  - Therefore, $20,000 \pm 300$ offspring produced, half of which (on average) survive.
  - Results of a little simulation.
    - Generate 1000 random numbers from a Poisson distribution with a mean of 20,000, matching the number of offspring produced in this hypothetical example.
    - For each of these 1000 numbers, randomly determine whether each individual survives to reproduction with probability $p = 0.5$.
    - Here's the code in R[6]

```
> n <- rpois(1000, 20000)
> n.surv <- numeric(0)
> for (i in 1:1000) n.surv[i] <- rbinom(1, n[i], 0.5)
> mean(n)
[1] 20002.28
> var(n)
[1] 19284.28
> mean(n.surv)
[1] 9999.959
> var(n.surv)
[1] 9370.934
```

[6] R is an open source statistical package largely compatible with the commercial S-Plus. It is extremely powerful and flexible, although if you're used to SAS, it takes a little getting used to. If you'd like to get a copy, you can download executables for Windoze, Macintosh, or Linux at http://www.r-project.org/.

```
> quantile(n.surv)
      0%      25%      50%      75%     100%
 9734.00  9931.75  9999.00 10070.00 10322.00
```

So in this simulation the maximum decline (from 10,000 to 9734) was a little less than 3%, and the median outcome was indistinguishable from stability. Another way of summarizing these results is to say that $\mathrm{Var}(R_t) = \frac{1}{N_t^2}\mathrm{Var}(\mathtt{n.surv}) \approx 1.0 \times 10^{-4}$.

- Population of 10
  - Expected number of offspring in next generation is 20
  - Variance in number is 20. Standard deviation is 4.5.
  - Therefore, 20 ± 9 offspring produced.
  - Simulation results:

```
> n <- rpois(1000, 20)
> n.surv <- numeric(0)
> for (i in 1:1000) n.surv[i] <- rbinom(1, n[i], 0.5)
> mean(n)
[1] 20.102
> var(n)
[1] 19.01261
> mean(n.surv)
[1] 10.016
> var(n.surv)
[1] 10.46621
> quantile(n.surv)
  0%  25%  50%  75% 100%
   2    8   10   12   23
```

So in this simulation the maximum decline (from 10 to 2) was 80%, even though the median outcome was stability and the individuals in this population had exactly the same reproductive potential as those in the population of 10,000. Another way of summarizing these results is to say that $\mathrm{Var}(R_t) \approx 1.0 \times 10^{-1}$, three orders of magnitude greater than the variance when $N = 10,000$.

Like genetic stochasticity, demographic stochasticity is likely to be important only in populations that are already small.[7] It may pose an additional threat to species that are already endangered, but it is unlikely to cause the endangerment of those with reasonably large populations.

Environmental stochasticity

Environmental stochasticity is the type of variability in population growth rates that probably occurred to you when I first brought the subject up. It refers to variation in birth and death rates from one season to the next in response to weather, disease, competition, predation, or other factors external to the population. Environmental stochasticity can affect even populations that are quite large. We'll see quantitative examples of just how large the effect can be a little later.

Catastrophes

Catastrophes are in one sense, merely an extreme form of environmental stochasticity. It is, however, useful to distinguish them for several reasons:

1. Often distinguished as events happening at random intervals in which a large proportion of the individuals in the population die.

2. Even though catastrophic declines may occur very rarely, they have a large impact on whether populations are able to persist.

3. Catastrophes occur infrequently, and we're not likely to see one or to see how large its effect is while we're watching. Even a relatively long time-series may not include them. Nonetheless, if catastrophes are big enough, meaning that they eliminate a large enough fraction of the population, they may be the greatest threats to a population's persistence, even if they occur only once every 50 or 100 years.

References

[1] M S Boyce. Population viability analysis. *Annual Review of Ecology & Systematics*, 23:481–506, 1992.

[7] If you're reading footnotes, you'll notice that I already pointed this out once, but it's an important point, so it's worth making twice.

[2] C R Darwin. *On the Origin of Species by Means of Natural Selection.* John Murray, London, 1859.

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