Population growth and decline

Key concepts

- Open *vs.* closed populations
- The fundamental equation of population ecology
- *Per captita* rates
- Estimating rates of growth and decline
- Predicting changes in population size
- Discrete *vs.* continuous time models

Changes in the population size of grizzly bears in Yellowstone National Park

The grizzly bear *Ursus arctos horribilis* used to inhabit most of North America, but these days its continental range is restricted to the northwestern US (including Alaska) and western Canada. The Yellowstone National Park population is one of the most southern in the US and has experienced recent periods of decline and growth (Figure 2). Grizzly bears are a species vulnerable to local extinction. They have one of the lowest birth rates among all terrestrial mammals in the US. Females typically have two cubs per litter, and caring for the cubs is a two year investment during which time no further mating will occur. Mating is seasonal, occurring in June and July, and the cubs are born in January. Depending on environmental conditions, females may not acquire sufficient energy for successful reproduction females and they may have to wait many years before successfully reproducing. Males tend to occupy large ranges and habitat fragmentation can limit the ability to find mates.

Figure 1: Grizzly bear (*Ursus arctos horribilis*).

To help us understand the changes in the grizzly bear population we can make use of certain facts. For instance, during the decline in the 1960s and 1970s coincided with closure of garbage dumps in the parks following a number of bear-inflicted human injuries. At the

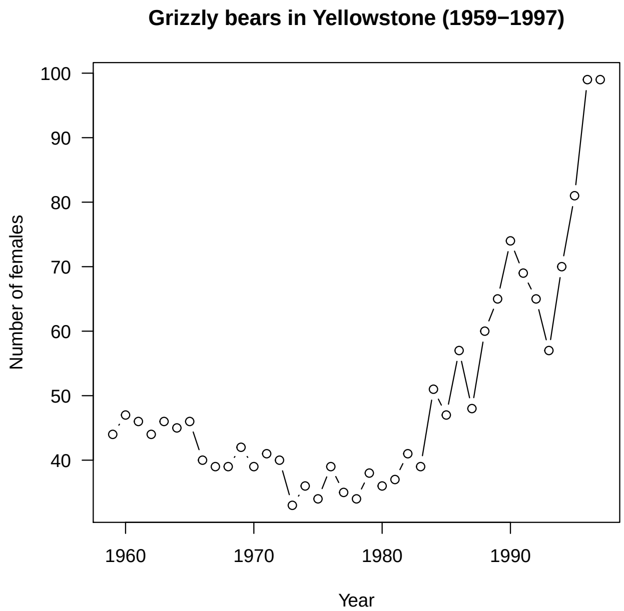

Figure 2: Changes in the grizzly bear population in Yellowstone.

beginning of the growth period the grizzly bear was listed as a threatened species in the lower 48 states under the Endangered Species Act (1975) and in the 1980s a recovery plan was developed and implemented in Yellowstone. While this narration helps us understand the trends, we can aim to answer more specific questions. Without interventions, when would the grizzly bear have gone extinct in Yellowstone? How much of an improvement in female survivorship (a key part of the recovery plan) was required to shift the balance from population decline to growth?

In many animal populations, only females are censused as they are the ones that reproduce. Assuming an equal sex ratio we double this number to estimate the total population size

The fundamental equation of population ecology

To answer such questions, we take into account the four factors that can lead to year-on-year changes in the population size as well as their positive or negative effect: birth (+), death (-), immigration (+), emigration (-). The inclusion of immigration and emigration refers to an *open* population, and when only births and deaths are considered, we refer to a *closed* population. Consequently, if we use n to denote the population size, the change (Δn) in a population between years can be written as

The fundamental equation of population ecology

$$\Delta n = n_{t+1} - n_t = B_n - D_n + I_n - E_n, \tag{1}$$

where B_n, D_n, I_n and E_n are the number of birth, death, immigration and emigration events experienced by a population of size n during the time interval $t, t+1$ (in this case one year).

Although grizzly bears can move in an out of Yellowstone, we will treat the population as a closed population. In addition, we'll assume that all individuals are the same regarding the fecundity and survivorship during a year and that births and deaths don't depend on population density.

Later chapters will explore heterogeneity and density dependence

Our fundamental equation 1 reduces to

$$\Delta n = n_{t+1} - n_t = bn_t - dn_t. \tag{2}$$

B_n and D_n represent the number of births and deaths, whereas b and d are the *per capita* births and deaths in the time interval $t, t+1$

Relationship between population sizes at different times

This description of population change allows us to represent the population size in one year based on its value in the preceding year

$$n_{t+1} = bn_t - dn_t + n_t = \lambda n_t. \tag{3}$$

We define $\lambda = b - d + 1$, which has a constant value provided *per capita* birth and death rates are constant over time

But better than that, from knowledge of the population size in a given year, we can project any number of years forward

$$\begin{aligned} n_{t+1} &= \lambda n_t & (4)\\ n_{t+2} &= \lambda n_{t+1} = \lambda^2 n_t, & (5) \end{aligned}$$

and in general

$$n_t = \lambda^t n_0, \tag{6}$$

where n_0 is the initial population size.

The parameter λ is often referred to as the reproductive ratio of the population since $\lambda = n_{t+1}/n_t$. Equation 6 describes geomteric growth ($\lambda > 1$) or decline ($\lambda < 1$), with examples shown in Figures 3 and 4.

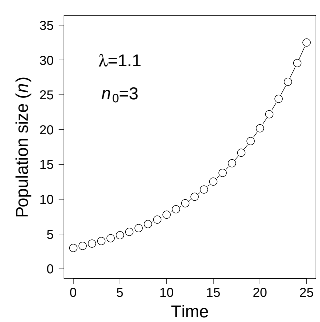

Figure 3: Geometric growth

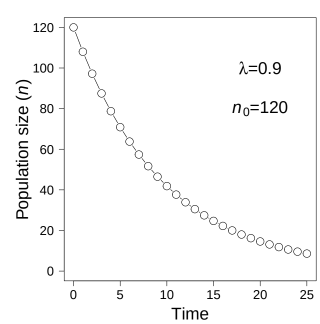

Figure 4: Geometric decline

Estimating λ from data

If we assume that a population is growing or declining in a geometric fashion over some period of time (0-t), we can estimate the associated value of reproductive ratio, λ.

$$\begin{aligned} n_t &= \lambda^t n_0 & (7)\\ n_t/n_0 &= \lambda^t & (8)\\ \ln(n_t/n_0) &= \ln(\lambda^t) & (9)\\ \ln(n_t/n_0) &= t\ln(\lambda) & (10)\\ \frac{\ln(n_t/n_0)}{t} &= \ln(\lambda) & (11) \end{aligned}$$

$$\boxed{e^{\ln(n_t/n_0)/t} = \lambda} \tag{12}$$

While there are more statistically rigorous methods to estimate λ from data, this straightforward approach provides a simple formula to assess rates of population growth and decline.

Discrete vs. continuous time models of population dynamics

The grizzly bear data was in the form of annual estimates of the population size, and we developed a related model where the population is updated each year accounting for all the births and deaths that occurred during the preceding year. A combination of data and the seasonal reproduction and mortality of grizzly bears motivated such a *discrete time* model. However, other populations may be better described by a *continuous time* model. For example, many species of tropical fish reproduce year round, and experience many sources of mortality through the year. In such situations, we may assume the per capita birth and death rates are continuous and we can track the instantaneous change in poulation size with time, dn/dt, using a differential equation that can be solved by integration

$$dn/dt = bn - dn \tag{13}$$

Define $r = b - d$ as the intrinsic growth rate

$$dn/dt = (b - d)n \tag{14}$$

$$dn/dt = rn \tag{15}$$

Separate the variables n and t

$$\frac{1}{n}dn = r\,dt \tag{16}$$

$$\int \frac{1}{n}dn = \int r\,dt \tag{17}$$

c is the constant of integration

$$\ln(n) = rt + c \tag{18}$$

$$e^{\ln(n)} = e^{rt+c} \tag{19}$$

Recall: $x^{a+b} = x^a x^b$

$$n = e^{rt}e^{c} \tag{20}$$

Note: when $t = 0$, $n = e^c$ so we rename $e^c = n_0$ to represent the initial population size

$$n = n_0 e^{rt} \tag{21}$$

If the birth rate is greater than the death rate then $r = b - d > 0$ and the population exhibits exponential growth (Figure 5). Conversely, if the death rate dominates then $r = b - d < 0$ and the population declines exponentially (Figure 6).

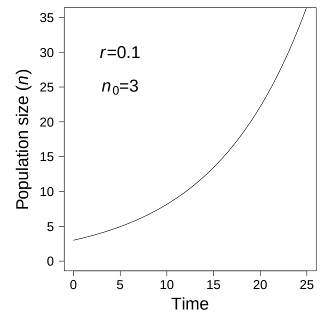

Figure 5: Exponential growth

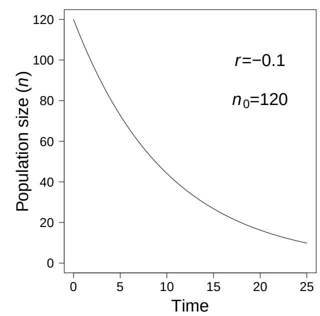

Figure 6: Exponential decline

We see from equation 21 that to calculate the population size at t time units from the initial point, we multiply the initial population size n_0 by e^{rt}. Comparing with equation 6 we see that the multiplying factor e^{rt} in the continuous time model is equivalent to the factor λ^t in the discrete time model. This helps us derive the relationship between the reproductive ratio, λ, and the intrinsic growth rate, r

$$
\begin{aligned}
e^{rt} &= \lambda^t && (22)\\
\ln(e^{rt}) &= \ln(\lambda^t) && (23)\\
rt &= t \ln\lambda && (24)\\
r &= \ln(\lambda). && (25)
\end{aligned}
$$

In both the discrete and continuous time models, populations are predicted to grow or decline in a multiplicative way. In the discrete time formulation, populations grow geometrically if $\lambda > 1$ and decline geometrically if $\lambda < 1$. In the continuous time formulation, populations grow exponentially if $r > 0$ and decline exponentially if $r < 0$.

Test yourself

- What is the difference between an open and closed population?
- Why do we characterize some population dynamics with discrete time, rather than continuous time, models?
- What information is required to predict a population's size at a future time point?
- Why might the presented method to estimate λ, equation 12, sometimes be innacurate? What improvements can you think of?

Homework

1. Given that the female grizzly bear population was 44 in 1959 and 34 in 1975, estimate the reproductive ratio (λ) during this time.

2. Starting from 1975, if there were no interventions (i.e., λ did not change) how many female grizzly bears would there be after 5 years (rounding to the nearest individual)?

3. In the same scenario of no interventions in 1975, and assuming an equal sex ratio, in which year would the total Yellowstone population first drop below two individuals?

Q3 Hint: equation 10 can be used to determine a time interval. What biological factors might contribute to the answer being an over-estimate?

4. Consider a population in a reserve with year-round births (b=0.2 offspring per individual per year), deaths (d=0.16 per individual per year), and emigration (a=0.5 per individual per year). Will this population grow or decline?

5. Now, suppose emigration is eliminated by the construction of a barrier around the reserve. Does this change the qualitative behavior of the population (i.e., growth versus decline)?

6. If the population size at the time the barrier is constructed is $n_0 = 10$, what will the population size be in 50 years?

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Bibliography

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