Population growth

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Modeling populations

How populations change

- I survey a population in 2005, and again in 2009. I get a different answer the second time.
- What is one reason I might get different numbers?

Model choices

- Model choices are guided by:
  - Your questions and goals
  - A search for simplicity (parsimony)
  - Linking assumptions to outcomes as clearly as possible

What processes to include

- We start here with birth and death
- If a population is interacting with other populations, we might want to model immigration and emigration
- We also might want to include all the different populations in the same model (a *metapopulation* model)

How to structure the population

- Our model dandelion population has *no structure*: all individuals are equivalent
- The rabbit population does (we keep track of adults and juveniles separately)
- Name one (type of) organism for which you would use unstructured models

How to model time (continuous vs. discrete)

- Instantaneous rate of change vs. fixed time steps
- Continuous-time models are conceptually simpler, although they don't usually feel that way
  - Don't have to decide on order of events
  - Dynamics can be simpler (no overshoots)
- Discrete-time models are easier for structured populations, and the math is easier (no calculus)
- Some organisms have more continuous, and some more discrete, schedules of reproduction and development
- Name one (type of) organism with a discrete reproduction schedule

Interactions

- We care about interaction because it can change birth & death rates
- Do organisms interact with others in the population (**conspecifics**)?
- Does the environment affect organisms, or do they affect their environment?
- Do they interact with other organisms (predators, prey)?
- We will ignore all of these things to start with (i.e., we will treat them *implicitly*)

Stochastic vs. deterministic

- **Deterministic** models use rules to describe what will happen in a given situation
- **Stochastic** models use rules to describe the *probability* of different outcomes in a given situation
- Describe one advantage of stochastic models

Discrete-time models

Conceptual model

- Imagine censusing a population at regular time intervals Δt
- Typically $\Delta t = 1$ year
- Imagine that all individuals are the same at the time of census
- (i.e., an **unstructured** population)

Implementation

- If we have N individuals after T time steps, what determines how many individuals we have after $T+1$ time steps?
- Assuming no stochasticity, population structure or interactions:
  - A fixed proportion p of the population (on average) survives to be counted at time step $T+1$
  - Each individual creates (on average) f new individuals that will be counted at time step $T+1$
- What is the answer if individuals first survive, then reproduce?

Calculation

- $\lambda = p + f$ is the **finite rate of increase** of the population
- So $N_{T+1} = \lambda N_T$
- The solution to this equation is $N_T = N_0 \lambda^T$
- See math supplement

Time steps

- We use T to represent a *unitless* quantity measuring the number of time steps that has passed
- The amount of *time* that has passed is $t = T \cdot \Delta t$
- λ is unitless, but it is *associated with* the time step Δt
- This means it is potentially confusing! It is often better to use r or R (see below).

Fecundity

Fecundity components

- Recall the definition of f: it has no units (average *number* of offspring)
- Need to measure consistently across the annual cycle
- from seed to seed, or sprout to sprout, or adult to adult
- the answer should be the same however you count, as long as you count consistently
- Multiply:
  - Probability of surviving from census to reproduction
  - Expected number of offspring when reproducing
  - Probability of offspring surviving to census

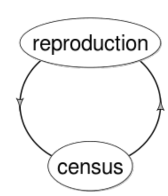

Figure 1: plot of chunk plotstage

Gypsy moth calculation

- Researchers studying a gypsy moth population estimate that:
  - The average reproductive female lays 600 eggs
  - 10% of eggs hatch into larvae
  - 10% of larvae mature into pupae
  - 50% of pupae mature into adults
  - 50% of adults survive to reproduce
- All adults die after reproduction
- What is λ for this population?
- Where in the cycle should we start counting?

Dealing with sexes

- Male reproductive output is highly variable, and often very hard to measure

- In animals with sexual reproduction, usually more convenient to ignore males completely

- e.g., λ is calculated using female offspring per (adult) female

- So the best answer to the problem above would be 0.75

- But it's not always safe to assume a 1:1 sex ratio
(except for class exercises)

Survival

Measuring survival

- p is the proportion of individuals who survive one cycle
- Need to measure consistently
- from seed to seed, or sprout to sprout, or adult to adult
- the answer should be the same however you count, as long as you count consistently
- Multiply:
  - Probability of surviving from census to reproduction
  - Probability of surviving reproduction
  - Probability of surviving from reproduction to census

Populations with overlapping generations

- When $p > 0$, some organisms survive from year to year
- Name a potential problem with unstructured models in this case
- How can we mitigate the problem without using a different model?
- What if this assumption breaks down for the question you are asking?

Assumptions

- What are we assuming if $p = 0$?
- What about $p = 1$?
- What about intermediate values?

Lifetime

- If p is the proportion of individuals that survive, then:
- If $\mu = 0.25$, how many time steps do you expect to live?

Thresholds

Threshold behaviour

- What is the behaviour of this model?

Birth and death

- If p is the proportion of individuals that survive, then:
- What if we rewrite the threshold condition $\lambda = f + p > 1$ using μ instead?

Reproductive number

- The **reproductive number** is the average *lifetime* reproduction per individual
  (or females per female)
- R is the average number of offspring per year, multiplied by the average lifespan
- Unlike λ, R is independent of the time step Δt

Discrete-time R

- Mean lifetime is $1/(1-p) = 1/\mu$ time steps
- Average number of offspring per time step is f
- Why do we multiply by time steps instead of actual time?

Is the population increasing?

- What does λ tell us about whether the population is increasing?
- What does R tell us about whether the population is increasing?

Each individual is (on average) more than replacing itself over its lifetime

Thresholds for persistence

- What if the individuals in a population are growing, reproducing and establishing just fine, but the average lifetime number of offspring per individual is less than one?
- Thus, when we ask what species occur where, we don't just ask where they can survive, we ask where they can *survive and replace themselves*
- This answers the riddle from our first class

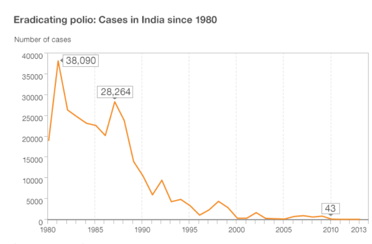

Figure 2: polio in India

Another example of $R < 1$

Proportionality

Proportionality

- If individuals are behaving independently, absolute birth and death rates should be *proportional* to population size
- This means the rate of change is *proportional* to population size, leading to:

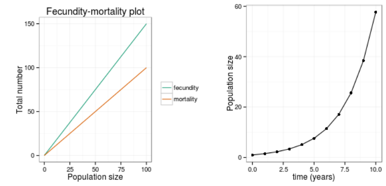

Figure 3: plot of chunk happymoths

Proportional rates

Per-capita view

- *per capita* is another way of saying "per individual"
- If individuals are behaving independently, *per capita* birth and death rates should remain constant
- If viewed geometrically (in terms of ratios), the population:

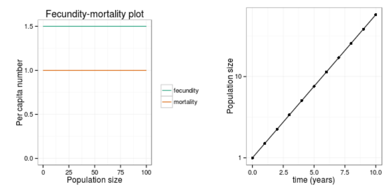

Figure 4: plot of chunk percap

Per-capita rates

Continuous time

Continuous-time models

- Continuous-time models deal in *instantaneous* change, instead of specifying what will happen over a time step
- As we will see, this is conceptually simpler in many ways, but it can also be more confusing
- Figuring out how instantaneous change relates to longer-term behaviour is basically what calculus is about
- But you don't need to understand calculus to do this course successfully

Examples

Bacterial death

- Imagine some bacteria in an unfavorable environment
- They are not reproducing, and are continuously dying at a rate of 0.05 deaths per individual per hour
- If we start with a density of 5 individual/ml, how many do we expect to see after one hour?
- After 12 hours?
- After one day?
- Remember that 0.05/hour means exactly and precisely the same thing as $24 \cdot 0.05 = 1.2/\text{day}$

Answers

Calculus

- This is what calculus is for:

(and vice versa) * The equation $N_0 \exp(rt)$, where r is a rate of (positive or negative) increase, is the **only** calculus result we will require or use * We will also use the *general* idea that a differential equation represents the rate of change (rate at which something is increasing or decreasing)

Euler's e

- This is also what e is for

Model

Conceptual model

- We imagine the population always changing continuously
- All individuals:
  - Reproduce at a constant rate
  - Die at a constant rate
  - (i.e., they are independent of each other)

Implementation

- $\frac{dN}{dt} = (b-d)N \equiv rN$
  - b is the birth rate
  - d is the death rate
  - $r \equiv b - d$ is the **instantaneous rate of increase**.
  - All of these quantities have units 1/[time].
  - The solution to this equation is $N(t) = N_0 \exp(rt)$.

Assumptions

- All individuals are the same, all the time
- Pretty hard to believe, even for bacteria
- But it still works pretty well in some cases

Life span

- Individuals die at rate d, regardless of how old they are
- This leads to a mean life span of $1/d$

Thresholds

- What is the behaviour of this model when $r < 0$?

Reproductive number

- How would we calculate R given the assumptions of this model?

Continuous-time R

- For this model, the mean lifetime is $1/d$
- The *per capita* rate at which offspring are produced on average is b
- Thus, $R = b/d$ for this model
- (This is actually a little bit tricky; it ignores compound interest)

Is the population increasing?

- What does r tell us about whether the population is increasing?

- What does R tell us about whether the population is increasing?

Proportionality

- Another way to think of the two perspectives:

- If we look at things from a population point of view, we are measuring arithmetic change

- If we look at things from the individuals (per capita) point of view, we are measuring geometric change

Population perspective

Individual perspective

Linking models

Linking models

- Discrete-time and continuous-time models can be used to model the same process
- $\lambda = e^{r\Delta t}$, where Δt is the time unit associated with λ.
- If we solve for r, we get a unitful version of the information in λ – better for comparing across time scales

Exploring exponential growth

- If species are following simple models like those above, they will grow (or decline) exponentially
- This poses some interesting issues

Exploring exponential growth

Darwin, On the origin of species (section 3, "Struggle for existence"):

- There is no exception to the rule that every organic being naturally increases at so high a rate, that if not destroyed, the earth would soon be covered by the progeny of a single pair . . . The elephant is reckoned to be the slowest breeder of all known animals, and I have taken some pains to estimate its probable minimum rate of natural increase: it will be under the mark to assume that it breeds when thirty years old, and goes on breeding till ninety years old, bringing forth three pair of young in this interval; if this be so, at the end of the fifth century there would be alive fifteen million elephants, descended from the first pair.
- Exponential growth → competition → natural selection!

Competition

- What will happen if two different varieties of a species are growing (or declining) exponentially at different rates?

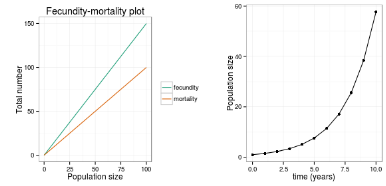

Figure 5: plot of chunk pop2

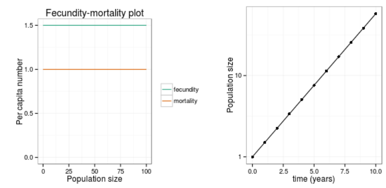

Figure 6: plot of chunk percap2

Example

- Regular dandelions have $\lambda = 2$ in a particular environment (*assume they're annual*: $\Delta t = 1$, $p = 0$)
- A new kind has $\lambda = 3$ in the same environment
- We introduce the same number of each
- What are the proportions after 10 years?

Cole's paradox

- If $\lambda = p + f$, then changing strategy from an annual plant ($p = 0$) to an immortal plant ($p = 1$) is equivalent to having just one more offspring
- In other words, you should "pull a salmon" and devote all of your energy to reproduction, if that would increase your expected f even by one
- Why do any plants bother to reproduce more than once? (Cole 1954,**???**)

Regulation

Regulation

- If populations *tend* to grow or shrink exponentially, what keeps them under control?

Long-term growth rate

- What is the long-term average exponential growth rate (using either r or λ) of:
- A successful population?
- An unsuccessful population?

Example: Human population growth

- In the last 50,000 years, the human population has increased from ≈ 1000 to ≈ 7 billion
- What is the value of r?
- If we use a time step of 20-year generations, what is λ?

Long-term growth rate

- What is the long-term average exponential growth rate (using either r or λ) of:
- A successful population?
- An unsuccessful population?

Balance

- If populations grow and shrink proportionally to their size, why don't they go exponentially to zero or infinity?

Stochastic variation

- Suppose we think that population growth can be stabilized by stochastic variation in growth rates (Davidson and Andrewartha 1948)
- assume variation is *independent of population size*
- The population growth rate in year t is λ_t
- What happens to the population in the long run?

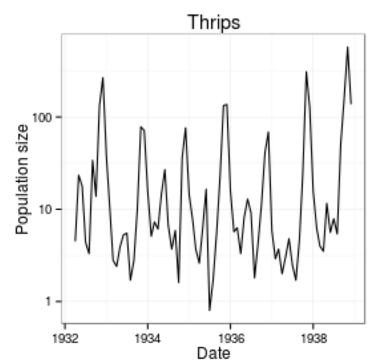

Figure 7: plot of chunk thrips

Stochastic variation (2)

- $N_2 = \lambda_1 N_1$
- $N_3 = \lambda_2 N_2 = \lambda_2 \lambda_1 N_1$
- $N_4 = \lambda_3 N_3 = \lambda_3 \lambda_2 \lambda_1 N_1$
- ...
- $N_t = \lambda_{t-1} \ldots \lambda_1 N_1 = M^{t-1} N_1$
- M is the **geometric mean** of the growth rate
- $= \sqrt[t-1]{\lambda_{t-1} \ldots \lambda_1}$
- or $\exp(\sum(\ln \lambda)/(t-1))$

What does this mean?

- even in the long run, the population *never* stabilizes
- all populations are on a (geometric) **random walk** from speciation to extinction
- this is a plausible position (Price 1980)

- ... but you have to have the courage of your convictions; you can only talk about *differences* in population size, not population size itself

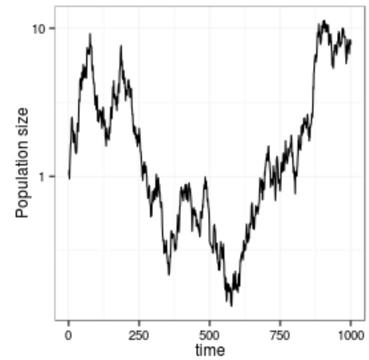

Figure 8: plot of chunk rwalk

Changing growth rates

- What sort of factors can make species growth rates change?

Regulation

- What do we expect to happen if a population's growth rate is affected only by seasons and climate?

References

Cole, L. C. 1954. "The Population Consequences of Life History Phenomena." *Quarterly Review of Biology* 29: 103–137.

Davidson, J., and H. G. Andrewartha. 1948. "Annual Trends in a Natural Population of Thrips Imaginis (Thysanoptera)." *Journal of Animal Ecology* 17 (2) (November): 193–199. doi:10.2307/1484. http://www.jstor.org/stable/1484.

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