Population regulation

Ben Bolker

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Introduction

The first law of population dynamics

- If individuals are behaving independently:
- the population-level rate of growth (or decline) is proportional to the population size
- the population grows (or declines) exponentially

The second law of population dynamics

- Exponential growth (or decline) cannot continue forever
- Something is changing the average rate at which populations we observe grow

The third law of population dynamics

- The changes in average rate must depend on the population size
- Populations are, directly or indirectly, affecting their own growth rates
- **Density dependence** (or preferably **density-dependent processes**)

Long-term growth rates

- Populations maintain long-term growth rates very close to $r = 0$
- This is almost certainly because factors affecting their growth rate change with the size of population.
- What is one density-dependent mechanism that could feed back on the growth rate?

Population regulation

- All the populations we see are *regulated*

- On average, population growth is higher when the population is lower
- Maybe with a time delay
- Lots of populations don't *seem* to be regulated

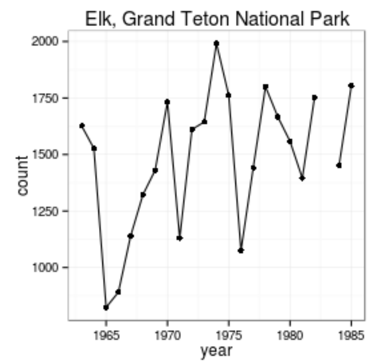


Figure 1: plot of chunk elk1

Mechanisms of regulation

- Dense populations experience more within-species competition
- e.g. for food or space: *per capita* resources proportional to $1/N$
- Dense populations may damage environments or resources that they need
- Dense populations attract more **natural enemies**
- Dense populations may overflow onto poor habitat

Figure 2: rabbits in New Zealand

Regulation may be hard to see

- Some species seem to completely fill a niche (mangroves), or deplete their own food resources (rabbits)
- Other species seem like they could easily be more common (pine trees)
- May be controlled by cryptic (hard to see) natural enemies (disease, parasites
- May be controlled by food limitation at bad times (e.g., droughts)
- Density **vagueness** (Strong 1986) ?
- Ecological data are **noisy**: need statistical methods to see regulation
- In the long term, every species is controlled in part by factors which respond to the species population size
- Otherwise, in the long term, it would increase forever or decline to extinction (random walk)

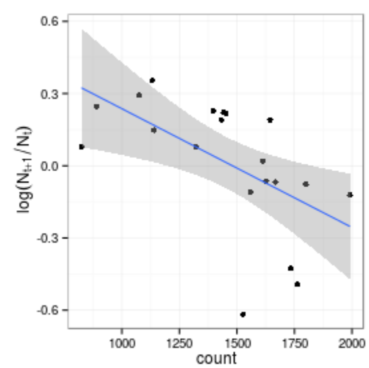


Figure 3: plot of chunk elkdiff

Regulation works over the long term

- Not every species experiences population regulation all the time
- Maybe expanding into a niche (e.g., because of climate change)
- Maybe controlled by big outbreaks of disease
- Maybe species outbreaks into marginal habitat, and spends most of the time contracting back to their "core" habitat

How do we know it's regulation?

- Why don't we believe that population growth is controlled by factors that don't depend on the population itself?

The great density-dependence debate

- Ecologists spent 40 years arguing about how important density-dependent processes are (Schmitt, Holbrook, and Osenberg 1999)
- *Field ecologists*: "We see strong density-independent processes operating!"
- *Theoreticians*: "There must be density-dependence somewhere!"
- Leaky bucket: $dW/dt = [\text{input}] - [\text{leakiness}]W \to W^* = [\text{input}]/[\text{leakiness}]$
- Field ecologists are right: *variation* in D-I processes explains lots of the *variation* we see
- Theoreticians are right: D-D most likely > 0 for most species
- Statisticians are right: better methods for measuring D-D (Dennis and Taper 1994)

Modeling framework

Modeling

- Start with a discrete-time or continuous-time population model
- How can we add regulation?

Density-dependent processes

- *How* do *per capita* **vital rates** (birth rate, death rate) change with population density?
- *Shape*: is the response straight, curved, curved more than once?
- *Scale*: how much does additional density affect vital rates?
- Two curves may have the same shape but different scales
- When does the curve cross zero?
- What does the zero-crossing point mean?

Different scales (per capita)

Different scales (absolute growth)

Different shapes (per capita)

Different shapes (absolute)

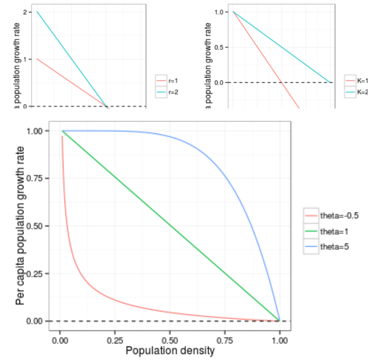


Figure 6: plot of chunk shape1

Mathematical details

- Linear *per capita* rates: **logistic model**, $r(N) = r_0(1 - N/K)$
- Do birth rates, or death rates, or both, change?
- Maybe we only care about $r(N) = b(N) - d(N)$
- If birth, have to stop at $b(N) = 0$; can chop it off but this is unrealistic/mathematically ugly
- Mortality rate can grow arbitrarily large (lifespan approaches zero)

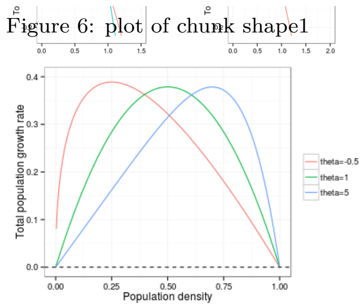


Figure 7: plot of chunk shape2

Mathematical details (2)

- More flexible model: **theta-logistic model**, $r(N) = r_0(1 - (N/K)^\theta)$
- Have to be careful when $\theta < 0$
- Hard to separate birth and death: **phenomenological** model (vs. **mechanistic** alternatives)
- Hard to estimate: (Sæther, Engen, and Matthysen 2002; Sibly et al. 2005; Clark et al. 2010)

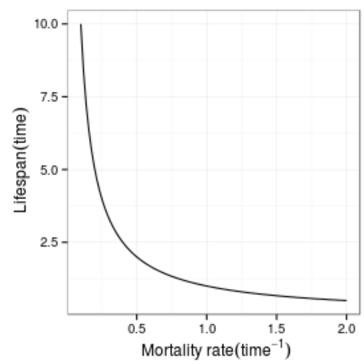


Figure 8: plot of chunk mort1

Another model

- In principle we can pick *any* model with decreasing (or constant) fecundity and increasing (or constant) birth rates
- *exponential-fecundity* model
- constant death rates, $d(N) \equiv d$
- birth rate declines exponentially with density, $b(N) \equiv b(0)\exp(-N/N_b)$
- What are the units of N_b?

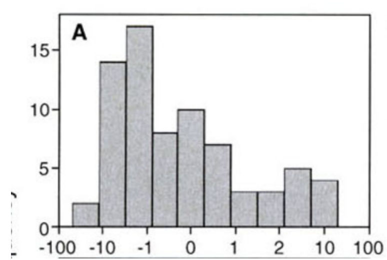


Figure 9: θ for mammal populations (Sibly et al. 2005)

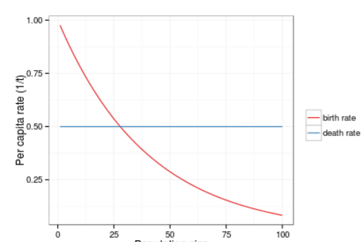
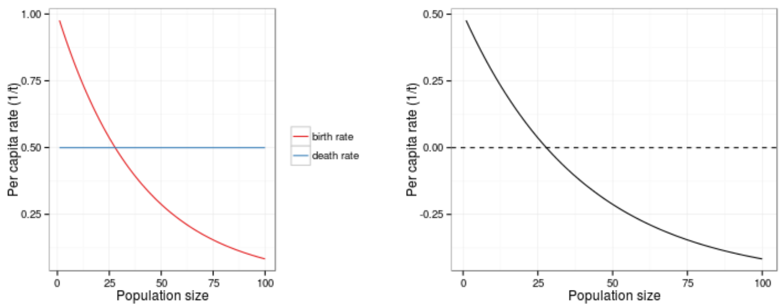


Figure 10: plot of chunk fecmodel

Another model

- can also reduce the model from birth & death to growth (birth-death):



Continuous-time models

Mathematical model

- Suppose population has constant *per capita* birth rates $b(N)$ and death rates $d(N)$
- Our mathematical model is: $\frac{dN}{dt} = (b(N) - d(N))N \equiv r(N)N$
- This tells us how fast the population is changing at any instant
- Recall: when we model a population using its size, we are assuming we can treat all individuals as the same

Recruitment

- **Recruitment** is when an organism moves from one life stage to another
- e.g. Seed $\rightarrow$ seedling $\rightarrow$ sapling $\rightarrow$ tree
- Egg $\rightarrow$ larva $\rightarrow$ pupa $\rightarrow$ adult moth
- In simple continuous-time population models, recruitment is included in birth:
- b is the rate at which adults produce new adults (or seeds produce new seeds)

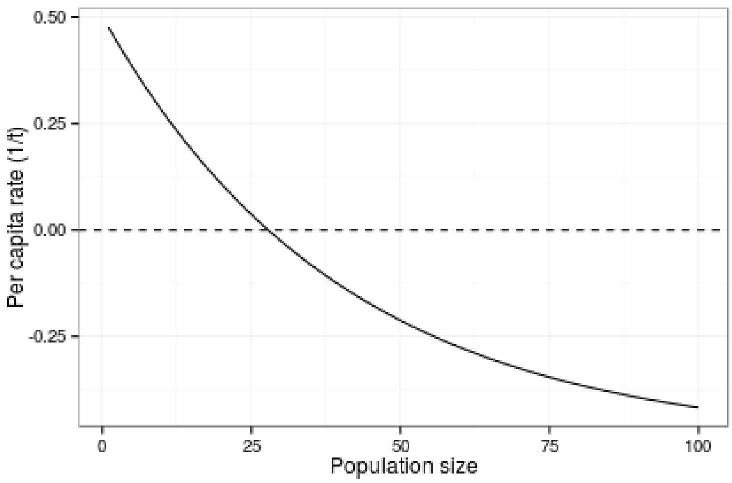
Density dependent processes

- What will normally happen to the (per capita) birth rate when population density is high?

- What will normally happen to the (per capita) death rate when population density is high?

Density-dependent regulation

- "Density dependent" means that:
  - Above some level of population density, the reproductive number R goes down when density goes up:
  - eventually R crosses from > 1 to < 1, r from positive to negative



Model behaviour

Dynamics

- What sort of **dynamics** do we expect from our conceptual population?
- i.e., how will it change through time?
- What will the population do if it starts near zero?
- ... near the equilibrium?
- ... at a high value?

What will this model do?

Exponential-fecundity model:

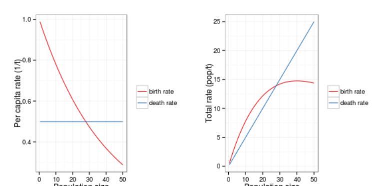


Figure 11: plot of chunk unnamed-chunk-1

Time dynamics

Time dynamics (log scale)

Time dynamics (high starting value)

Time dynamics (different θ)

Time dynamics (different θ, log scale)

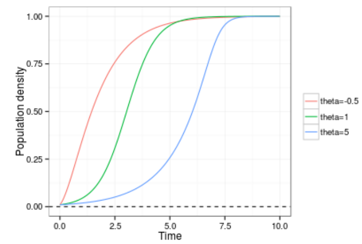
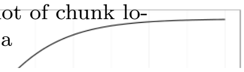


Figure 15: plot of chunk logist_dt_theta



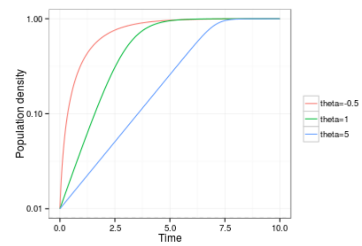


Figure 16: plot of chunk thetalogist_dt_log

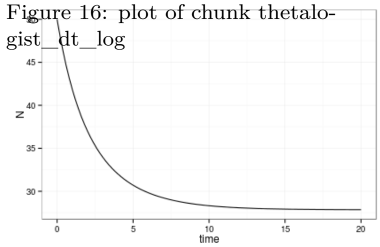


Figure 14: plot of chunk logist_dt_high

Simulations

- We will simulate the behaviour of populations in continuous time using the program R
- http://lalashan.mcmaster.ca/theobio/3SS/index.php/BirthDeath

Characteristic Time

- If a population is growing (or declining) exponentially at rate r, we can call $1/r$ the **characteristic time** (e-folding time) of population change
- Bacteria death example: they are continuously dying at a rate of 0.05 deaths per individuals per hour
- Characteristic time is 20 hours. If the rate *didn't decrease with population size*, they would disappear completely in 20 hours

Human growth example

- Long-term average growth rate is 0.0003/yr
- When growing at that rate:

Doubling time

- The characteristic time of growth (decline) is very similar to the doubling time (half life)

- Characteristic time is more closely related to instantaneous dynamics, so it's used more often in dynamic modeling

Equations

- $N = N_0 \exp(t/T_c)$ for growth
- $N = N_0 \exp(-t/T_c)$ for decline

- If $t \ll T_c$ change is close to linear
- If $t \gg T_c$ change (should be) extreme!

Characteristic scale

- A **characteristic scale** for density dependence is analogous to a characteristic time
- We rewrite the exponential equation to have a scale constant with the same units as the population.
- For example: $b(N) = b_0 \exp(-N/N_b)$
- N_b is the characteristic scale of density-dependence in birth rate
- If $N \ll N_b$, density dependence is linear (and weak)
- If $N \gg N_b$, density dependence is extreme (virtually no births)

Analyzing behaviour

- Dynamics of density-dependent populations
- Recall $\frac{dN}{dt} = (b(N) - d(N))N$

Equilibria

- In this simple model, when does equilibrium occur?
- Does our model have any **stable** equilibria?
- Does it have any **unstable** equilibria?

Stable and unstable equilibria

- If we are at an equilibrium we expect to stay there
- At least in our simplified model
- An equilibrium is defined as stable if we expect to approach the equilibrium when we are near it
- An equilibrium is defined as unstable if we expect to move away from the equilibrium when we are near it

What kind of equilibrium?

- How can we tell an equilibrium is stable?
- If population is just below the equilibrium:
- If population is just above the equilibrium:

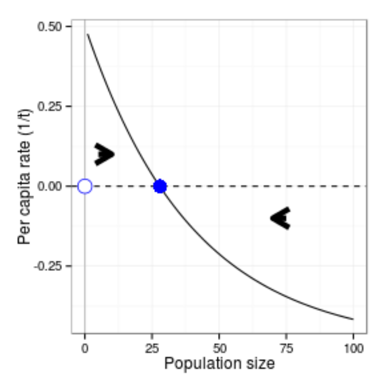


Figure 17: plot of chunk stabplot

Invasion

- We say a species can **invade** a community if its rate of change is positive when the population is small.
- In other words, population can invade if the **extinction equilibrium** $N = 0$ is not stable
- In this conceptual model, this is the same as saying $b(0) > d(0)$
- We can define a new value $R_0 = b(0)/d(0)$

Carrying capacity

- In a simple system with density dependence:
- When $R_0 < 1$, $R(N)$ is always < 1, and the population never persists
- When $R_0 > 1$, the population has a single, stable equilibrium:

Dynamics of density-dependent populations

- Populations following this model change *smoothly*
- Equations tell how the population will change at each instant
- They have no memory
- Birth rate and death rate are determined by population size alone
- Cycling is impossible

Dynamics of real-world populations

- Initial exponential growth and leveling off frequently observed
- Exponential approach to equilibrium hard to observe
- Real populations are subject to **stochastic**(random) effects
- Real populations are subject to changing conditions
- Some species exhibit cycles

Competition and depletion

- **Competition** occurs when organisms interfere with each others' use of resources
- Competition may or may not involve **depletion** of resources (reducing the amount of resource available in the future)

Resource competition

- What is a resource that is competed for but not depleted?

Conclusion

- We expect models of resource competition *without* depletion to exhibit smooth behaviours:
- The models in this section are not suitable for populations for which resource depletion is important

Allee effects

Small-population effects

- What would happen if I released one butterfly into a new, highly suitable habitat?

Allee effects

- Effects which cause small populations to have low per-capita growth rates are called **Allee effects**
- Equivalent to saying that medium-sized populations have larger per-capita growth rates than small ones
- Why might per capita growth rates decrease in small populations?

Allee effect models

Allee effect example

Allee effect: stability analysis

Allee effects

- Population may go extinct if it drops below a certain threshold (**strong Allee effect**: $r(0) < 0$, $R(0) < 1$)
- **Weak** Allee effect: *per capita* growth rate decreases toward zero, but doesn't go negative ($r(0) > 0$, $R(0) > 1$)
- How do populations establish in the presence of Allee effects?

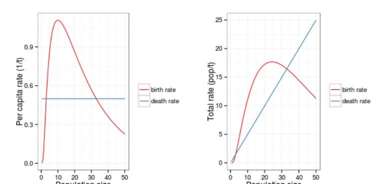


Figure 18: plot of chunk allee1

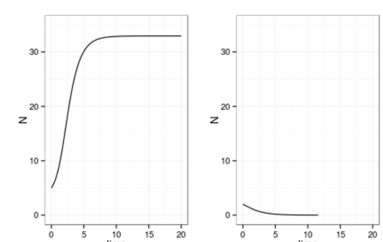


Figure 19: plot of chunk allee2

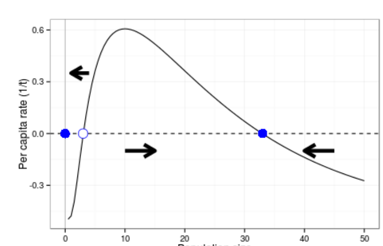


Figure 20: plot of chunk allee3

Invasion

- When Allee effects are present, it's no longer true that a species that can't invade can't persist
- We may have $R_0 < 1$, but $R(N) > 1$ for some intermediate value.
- Whether this is good or bad depends on your goal

Stochastic effects

- The world is complicated and biological populations are not perfectly predictable
- Real populations don't go smoothly to equilibria, instead they bounce around (or sometimes do other wild stuff)
- We divide stochastic (or random) effects into demographic and environmental stochasticity

Example

- Female butterflies of a certain species lay 200 eggs on average, of which:
- Half are female
- 50% hatch successfully into larvae
- 10% of larvae successfully pupate
- 60% of pupae become adults
- Half of adult females successfully reproduce
- A single gravid (pregnant) female butterfly is blown away by a freak storm, and lands by chance on a suitable island with no butterflies
- What do you expect to happen?

Butterfly example

- Depending on unknown conditions, especially in that first season, all of those probabilities could change dramatically

- Even if we knew the *probabilities*, that would not guarantee an exact result

- What if $\lambda < 1$?

Demographic stochasticity

- **Demographic** stochasticity is stochasticity that operates at the level of individuals

- Individuals don't increase gradually, they die or give birth
- Individuals don't produce 1.2 offspring: they produce 0, 1, 2 or 3 ...
- Even if we control conditions perfectly, we can't exactly predict the dynamics of small populations
- Demographic stochasticity averages out in large populations
- Important in extinction, disease trough dynamics

Environmental stochasticity

- **Environmental** stochasticity is stochasticity that operates at the level of the population
- e.g,. weather, pollution
- Environmental stochasticity can have large effects on any population
- But small populations are the ones in danger of going extinct

References

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