## Extinction



## Quiz

- In the simple birth-death stochastic model, if birth rate $b>$ death rate $d$ then the ultimate probability of extinction is:
- A) $P=0$
- B) $P=1$
- C) $0<P<1$


## Key concepts

- Stochastic birth-death model
- Probability of ultimate (eventual) extinction
- Demographic stochasticity
- Square root scaling law
- Population viability
- IUCN criterion E


## The stochastic process of extinction

- A problem with deterministic geometric models: For finite time the solution of these models implies finite population size
- How does population extinction occur?
- Stochastic process: a dynamical process in which part of the rate of change is determined by a random variable



## The fundamental idealization: identical individuals

## Exponential Growth:

Discrete

$$
N_{t+1}=R N_{t}
$$

Continuous $\quad \frac{d N}{d t}=r N(t)$

Logistic Growth:
Discrete

$$
N_{t+1}=N_{t}\left(1+R\left(1-\frac{N}{K}\right)\right)
$$

Continuous

$$
\frac{d N}{d t}=r N\left(\frac{K-N}{N}\right)
$$

## Objection: Measurement shows individuals to be different



Individual variation well documented and the basis for developments of biological theory, i.e., evolution by natural selection

Sources of individual heterogeneity

- Heritable genetic variation
- Environmental variation
- Maternal effects
- Mutation


## Heterogeneity \& Stochasticity

- Heterogeneity refers to differences among individuals
- Stochasticity expresses the idea that variation is randomly distributed

Strategy: Begin by assuming all variation "un-attributable" (demographic stochasticity) and build in heterogeneity later


## Simple Birth-Death Process

- Denote per capita birth rate by $b$ and per capita death rate by $d$
- In a small interval of time $h$, the probability that a given individual reproduces is the product $p(b i r t h)=b h$ and the probability that it dies is $p($ death $)=d h$
- From this, we can write down the following equation

$$
p_{n}(t+h)=p_{n}(t)(1-n(b+d) h)+p_{n-1}(n-1) b h+p_{n+1}(n+1) d h
$$

- Dividing by $h$ and letting $h \rightarrow 0$ yields the following differential equation

$$
\frac{d p_{n}}{d t}=b(n-1) p_{n-1}-(b+d) n p_{n}+d(n+1) p_{n+1}
$$

- This differential equation can be solved using the method of generating functions
- If we start with $n_{0}=1$
$p_{0}(t)=\frac{d-d e^{-(b-d) t}}{b-d e^{-(b-d) t}}$


## Simple Birth-Death Process

- Since the dynamics are density independent, the probability of extinction for n0 individuals is just the joint probability of extinction of their independent lineages

$$
p_{0}(t)=\left(\frac{d-d e^{-(b-d) t}}{b-d e^{-(b-d t t}}\right)^{n_{0}}
$$

- For $b<d$, we can rewrite this equation as

$$
p_{0}(t)=\left(\frac{d e^{(b-d) t}-d}{b e^{(b-d) t}-d}\right)^{n_{0}}
$$

-Taking $t \rightarrow \infty$, we have the ultimate probability of extinction

$$
p_{0}(t)=\left(\frac{d e^{(b-d) t}-d}{b e^{(b-d) t}-d}\right)^{n_{0}} \rightarrow\left(\frac{-d}{-d}\right)^{n_{0}}=1
$$

## Simple Birth-Death Process

- For $b>d$ and $t \rightarrow \infty$, the ultimate probability of extinction is

$$
p_{0}(t)=\left(\frac{d-d e^{-(b-d) t}}{b-d e^{-(b-d) t}}\right)^{n_{0}} \rightarrow\left(\frac{d}{b}\right)^{n_{0}}
$$

- Further, for all times, we have the mean population size

$$
m_{n}(t)=n_{0} e^{(b-d) t}
$$

And variance in population size

$$
v_{n}(t)=n_{0}\left(\frac{b+d}{b-d}\right) e^{(b-d) t}\left(e^{(b-d) t}-1\right)
$$

## Simple Birth-Death Process

- The coefficient of variation $\operatorname{sqrt}(\mathrm{v}(\mathrm{t})) / \mathrm{m}(\mathrm{t})$ is thus

$$
c v_{n}(t)=(b+d)^{1 / 2}(b-d)^{-1 / 2} n_{0}^{-1 / 2}
$$

An example of the square root rule!

## Square root scaling rule

Square root scaling rule of demographic stochasticity: Demographic stochasticity is a kind of sampling error and gives rise to a relation between population size and its coefficient of variation over time such that the coefficient of variation is proportional to the inverse square root of the average population size.


## Demographic stochasticity: Discrete time example

$b=0.4$ (on average, each individual produces 0.4 offspring per year)
$s=0.6$ (each individual has an annual survivorship probability of 0.6 , implying that

$$
N_{t+1}=N_{t}+b N_{t}-d N_{t}
$$ on average $60 \%$ of the population will survive from one year to the next)

$$
N t=\begin{array}{ll}
\underline{\text { Pop1 }} & \underline{\text { Pop2 }} \\
10 & 25
\end{array}
$$

## Demographic stochasticity example

$b=0.4$ (on average, each individual produces 0.4 offspring per year)
$s=0.6$ (each individual has an annual survivorship probability of 0.6 , implying that $N_{t+1}=N_{t}+b N_{t}-d N_{t}$ on average $60 \%$ of the population will survive from one year to the next)

|  | Pop1 |  |
| :--- | :--- | :--- |
| Nt $=$ | Pop2 <br>  <br> Ind. | Random |
| 10 | 0.5938 | no offspring |
| 2 | 0.2348 | one offspring |
| 3 | 0.4284 | no offspring |
| 4 | 0.7927 | no offspring |
| 5 | 0.3123 | one offspring... |

## Demographic stochasticity example

$$
N_{t+1}=N_{t}+b N_{t}-d N_{t}
$$

|  | $\underline{\text { Pop1 }}$ | $\underline{\text { Pop2 }}$ |
| :--- | :--- | :--- |
|  |  |  |
| $N t=10$ | 25 |  |
| $N t+1=10$ | 25 | deterministic |

Remember death rate $=1-s=1-0.6=0.4$
So $b-d=0$

## Demographic stochasticity example



## Demographic stochasticity example



## Demographic stochasticity example



## Real World Example: Bighorn Sheep

Berger (1990) Conservation Biology


## Population viability analysis

Population viability analysis is an approach to risk analysis for species extinction that focuses on the potential outcomes of a stochastic population growth process.


Fender's Blue Butterfly (Icaricia icarioides fenderi)


Schultz \& Hammond (2003)

## Extinction probability and IUCN Criterion E

Criterion E. Quantitative analysis showing the probability of extinction in the wild is at least $20 \%$ within 20 years or five generations, whichever is the longer.


## Summary

- Individuals vary in ways that affect fitness
- Morphology, age, behavior, sex, location
- Unattributed variation gives rise to demographic stochasticity
- Demographic stochasticity gives rise to the possibility of extinction (even if mean $b>$ mean $d$ )
- Small populations more affected by demographic stochasticity (fewer samples of birth and death rates means less chance to average out)
- These theories are used for population viability analysis and IUCN criteria
- HOMEWORK: Extinction chapter, Q2, due 5pm on September 6th

