Demographic monitoring

The state of the art

- Demographic monitoring is used to assess population trends using estimates of survival and reproduction
- It is much more informative than statistical trend estimation because:
  - The causes of population change are modeled explicitly
  - The relative effect of different demographic parameters on rates of population change can be assessed
  - It's possible to accurately estimate growth rate under circumstances that cause problems with trend analysis

The basic approach

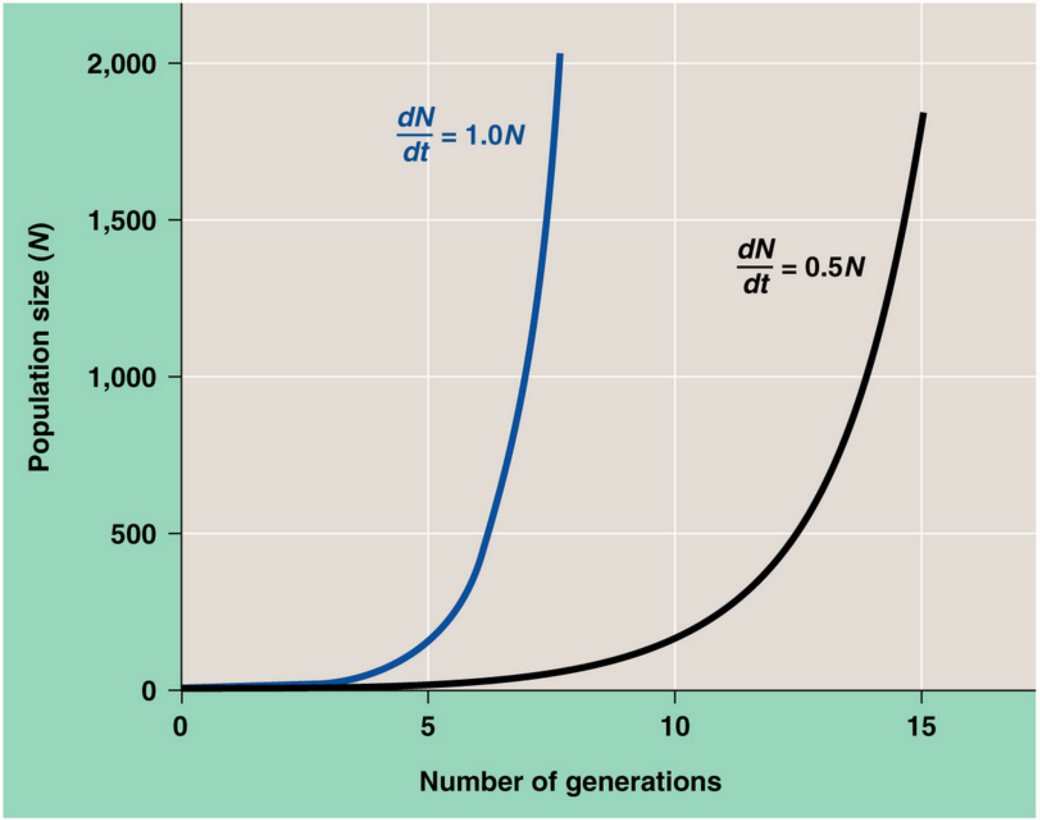
- We want to know if a population is stable ($\Delta N = 0$), increasing ($\Delta N > 0$), or decreasing ($\Delta N < 0$)
- Population change is due to a balance between:
  - Births + Immigration, and Deaths + Emigration
  - BIDE model: $\Delta N = B + I – D – E$
- If the population is geographically closed, there are no immigrants or emigrants
  - BD model: $\Delta N = B – D$
- To understand population change, minimally we need to know births and deaths
  - In a stable population, births balance deaths
  - In changing populations births are greater than deaths (increasing), or births are less than deaths (decreasing)

Demographic rates and continuous growth

$$\frac{dN}{dt} = rN$$

$$\frac{dN}{Ndt} = b - d = r$$

$$N_t = N_0 e^{rt}$$



Exponential growth rate, r, is a balance between per-capita birth and death rate

Balancing births and deaths

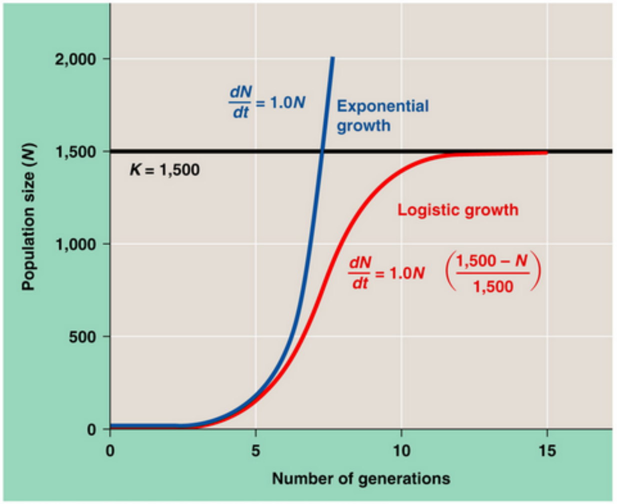
- Birth and death rate are **per-capita** numbers
  - Births per individual = b ← a positive decimal number
  - Deaths per individual = d ← a probability
- Intrinsic rate of increase is r = b-d
  - Values of r > 0 are increases
  - Values of r < 0 are decreases
- r is used for models of change in continuous time

Continuous growth with environmental resistance

- Populations can't grow exponentially for long
  - Density increase → density-dependent reduction in b, increase in d
- If the population...
  - Is in an area with a fixed capacity to support a population indefinitely (when N = K, carrying capacity)
  - Decreases in growth rate with each added individual
- ...the population will exhibit logistic growth

$$\frac{dN}{dt} = rN\left(\frac{K-N}{K}\right)$$

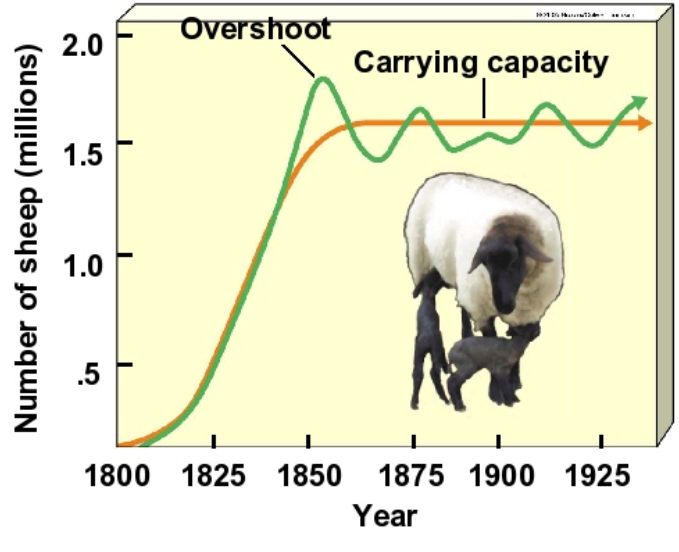
$$N_t = \frac{K}{1+\left[\left(K-N_0\right)/N_0\right]e^{-rt}}$$

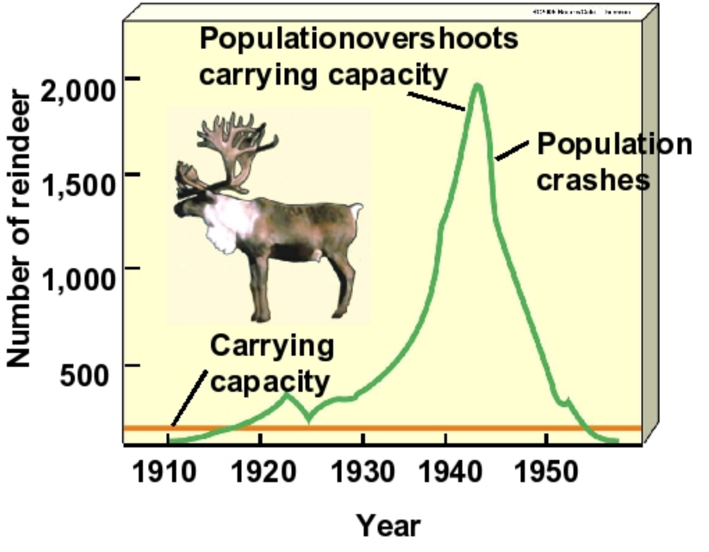


Discrete time

- Most species have some degree of seasonality in their reproduction and mortality
  - Distinct breeding seasons
  - Periods of harsh conditions, limited food
- Important distinction – continuous time models aren't capable of representing some real phenomena that discrete time models can

Sheep on Tasmania





Caribou on St. Paul Island, AK

Discrete time models use difference equations

- Predict population size at discrete time steps, usually one year at a time
- Changes in population size between the time points not modeled
- The natural measure of growth rate for discrete growth is the finite rate of increase = λ = N_t/N_{t+1}
- What is λ in:
  A growing population?
  A declining population?
  A stable population?

$$\frac{N_{t+1}}{N_t}=\lambda$$

$$N_{t+1}=\lambda N_t$$

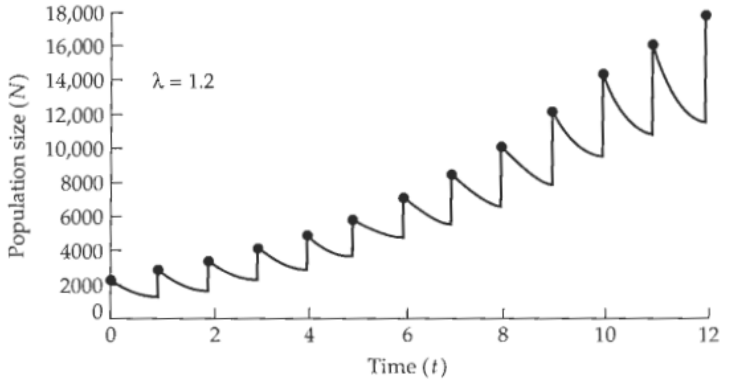


Figure 1.2 Discrete population growth. In this example, births are pulsed at the beginning of the year, and deaths occur continuously.

Geometric growth

- Growth without environmental resistance in discrete time is called **geometric growth**
- We can predict the population with $N_t = \lambda^t N_0$
- But, can't grow at a geometric rate for long
- In the presence of environmental resistance, the model becomes:

$$N_{t+1} = N_t + \overbrace{r_d N_t \underbrace{\left(\frac{K - N_t}{K}\right)}_{\text{Density dependence}}}^{\text{Number added}}$$

Number next year

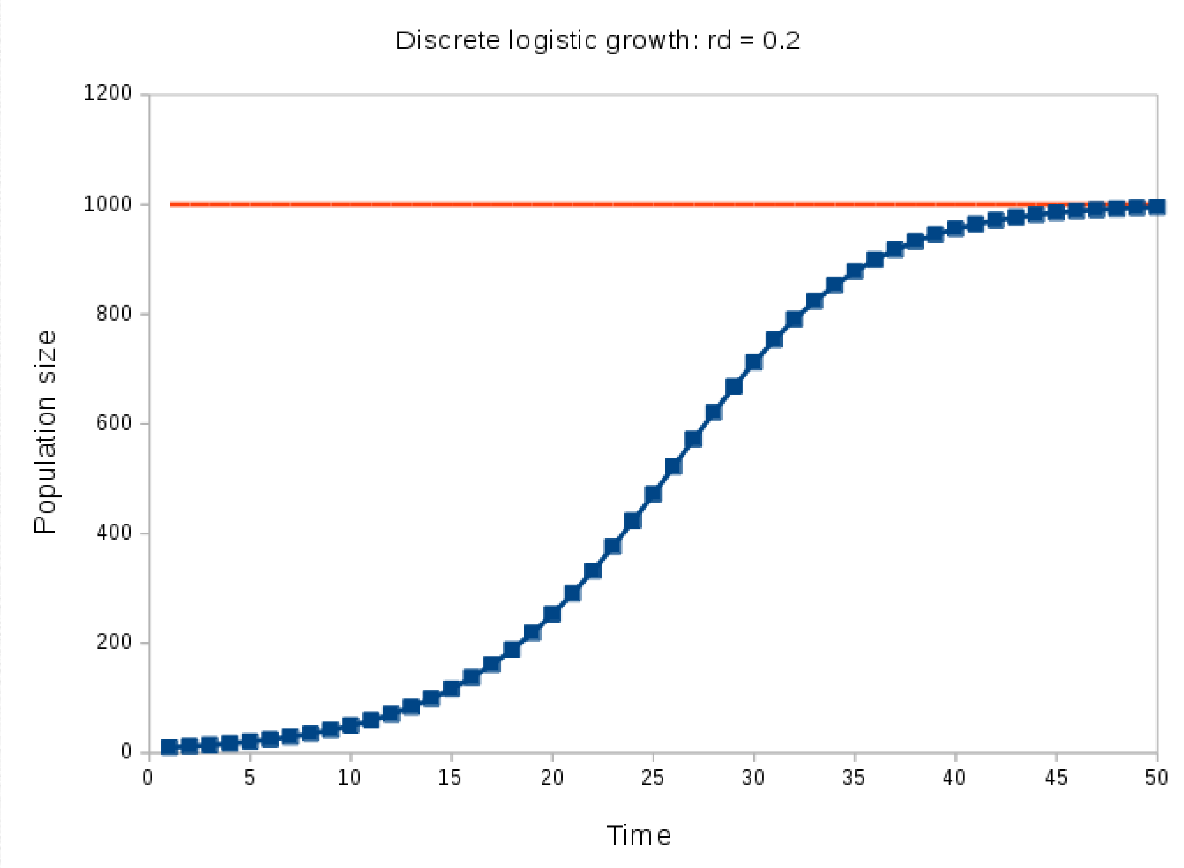
Number this year

Proportion added if no density dependence

Does this matter?

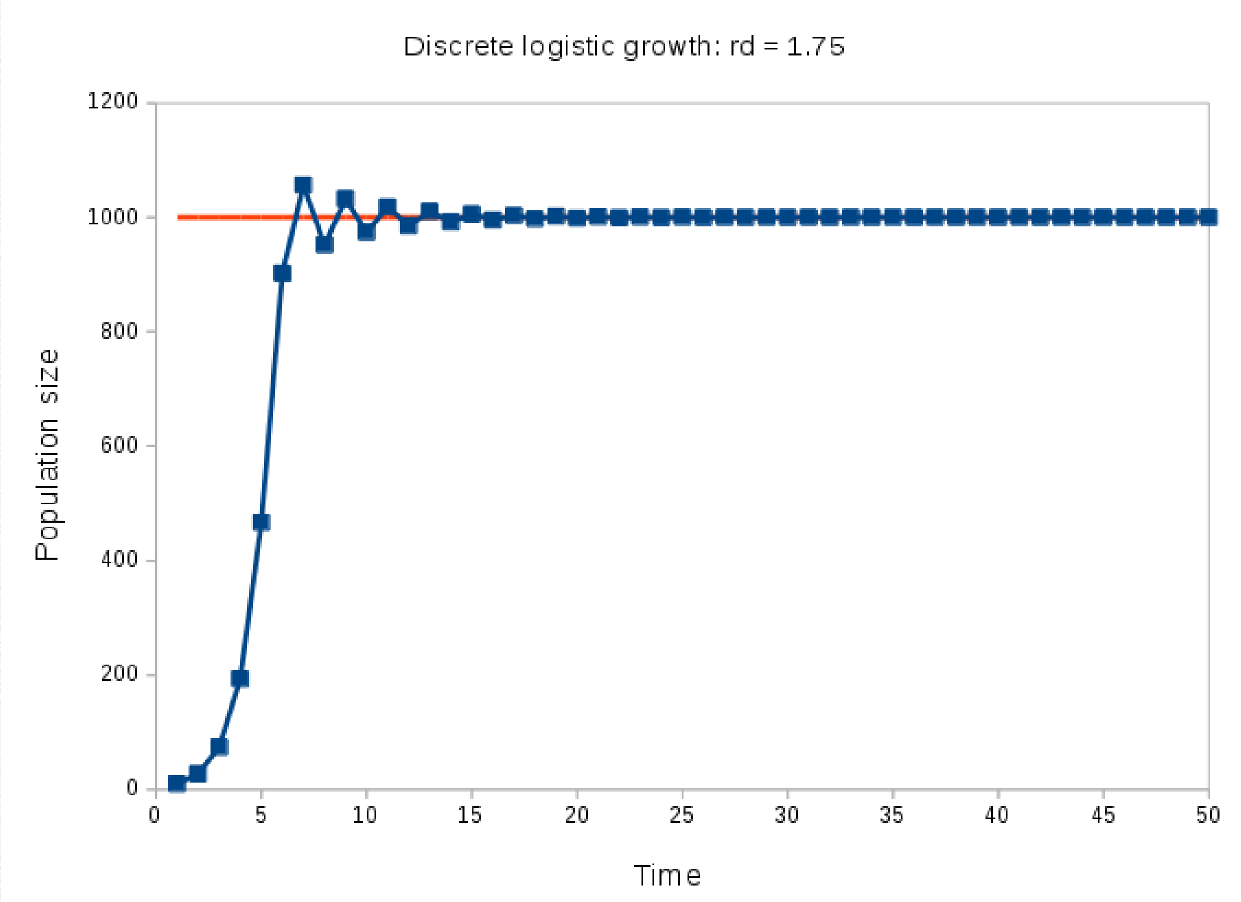
To CougarCourses...

Discrete-time with low r_d looks logistic



With a positive growth rate that is not very big, looks just like continuous time

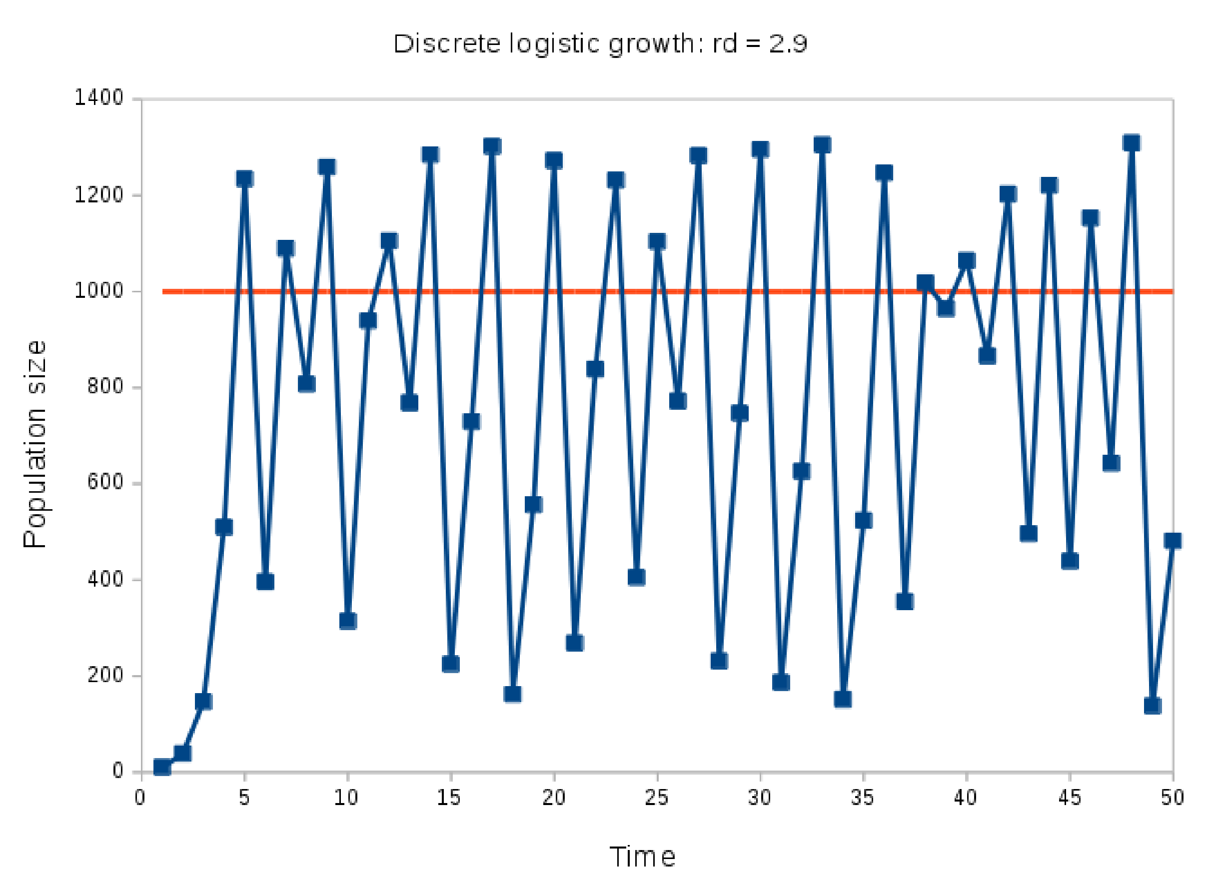
Overshooting K is possible



Larger growth rate allows overshoot

Damped oscillations back to K

Big growth rates lead to deterministic chaos



Discrete-time models are the most common in monitoring

- Discrete time models are most appropriate for species with seasonal reproduction, or seasonally high mortality
- The measure of growth rate will be λ
- We will need measures of births per individual and survival (1-deaths per individual) to estimate λ
- Today we will focus on reproduction

Reproduction terminology

- Fertility = number of offspring per mature female
- Fecundity = viable offspring per mature (reproductive age) female
  - Fertility with neonate mortality subtracted
- Birth rate (natality) = number of offspring per individual in the population (of all ages and sexes)
- Recruitment = number of viable offspring per individual in the population
  - Birth rate - neonate mortality

Example: raptors

Measuring raptor reproduction

- Breeding happens in stages:
  - Pair formation, territory occupancy
  - Nest building
  - Egg laying
  - Hatching
  - Rearing
  - Fledging
- Measuring any one will give you useful information about reproduction
- Measuring all of them will tell you where reproductive problems are occurring

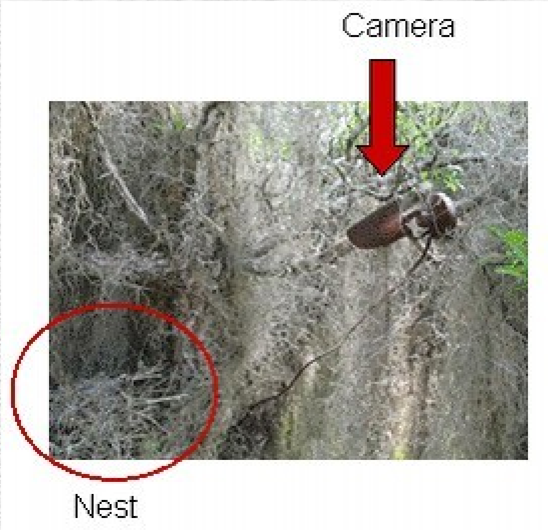
Territory occupancy, nest construction

- Pre-breeding
- Count of the number of territories found
  - Observing pairs, defending an area from conspecifics
- Many raptors re-use territories, so occupancy is useful as a measure of re-use
  - If an increasing number of territories are not re-used, indicate a declining breeding population
- Nest construction/maintenance behavior indicates intention to breed
  - Number of territories with nests / total territories can indicate a change in readiness to breed over time

Looking into nests

- From the ground, possible to establish that a pair is incubating, that chicks have hatched, and how many fledge
- But, measuring clutch size, hatching success, loss of eggs or nestlings all require looking into the nest
- Difficult to see into a nest that is up in the top of a tree, or on a cliff face, etc.
- Variety of methods used to get above a nest to see inside

Video cameras



Continuous (daytime) monitoring

Minimal disturbance at nest (aside from battery changes)

Clutch size

- Average number of eggs laid
  - Different on average between species
  - Variable within species
- Sensitive to body condition of the females
  - Years of low food abundance → smaller clutch sizes
  - If females are having trouble forming eggs, it would show up here
- Timing is important
  - Most raptors lay one egg every 2-5 days
  - Nest predation can reduce the number of eggs → under-estimate CS
  - Best CS estimates come from finding a nest early, and following it until the number of eggs maximizes
- Problem: repeated visits can be disturbing, may cause adults to abandon nests

Counting chicks

- At early stages, like counting eggs – need to look into nests
- Ideally, combined with a clutch size measure, so that hatching success can be calculated
  - # chicks/# eggs
  - If there are problems with embryonic development, they would show up here

- Timing:
  - Asynchronous laying → asynchronous hatching
  - For hatching success, as soon after hatching as possible – waiting too long leads to brood reduction
  - To measure loss of chicks during the nestling phase, can re-visit the nest repeatedly

Nest failure, brood reduction

- Loss of chicks during the nestling period can occur due to starvation, nest predation, or brood reduction
  - Brood reduction is usually siblicide, doesn't usually cause nest failure
  - Nest predation can result in complete loss (nest failure) or reduction in number of offspring
- For top predators, starvation is more common than nest predation
- Distinguishing between nest predation and brood reduction requires intensive observation

Nest predation

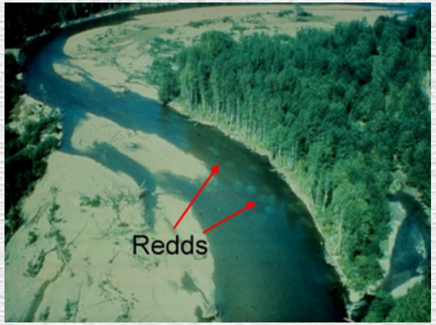
Fledging

- Fledging = chicks leaving the nest
  - Consider a chick fledged when it's seen out of the nest
  - Can usually measure from the ground
- Can express as:
  - Fledging success = # fledged/# eggs laid
  - Average number of chicks fledged – can be used to estimate recruitment
- Timing:
  - As close to the fledging event as possible, but can be on different days for each chick
  - Mortality of fledglings can be high – don't want to confuse post-fledging mortality for low fledging success
- Problems:
  - After leaving the nest, chicks are harder to find – can mistake a chick that is hidden/out of the area for a mortality
  - Some species (owls) leave the nest very early, before they can fly

Fledgling raptors

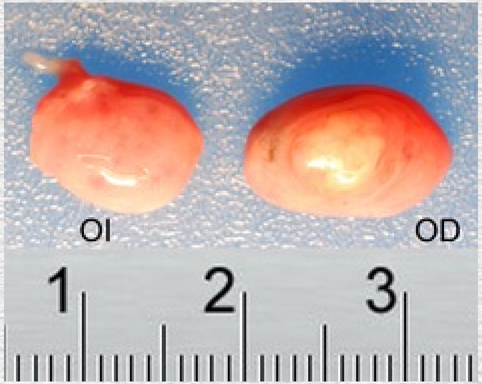
Reproduction in other egg-laying animals

- Some species that lay eggs provide no parental care
  - Count number of nests
  - Count clutch sizes
  - Hatching success = fledging success
- Some broadcast spawn
  - Sperm and egg both released into the water column
  - Fertilization happens externally, eggs develop and hatch in the plankton

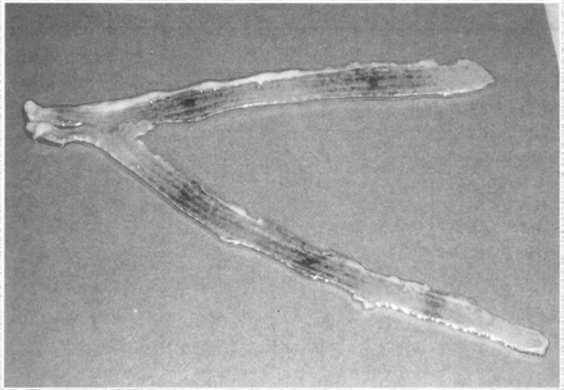


Reproduction in live-bearing animals

- Mammals, some herps
- Can count pregnant females, couple with estimated number of offspring per female
- Can come from histology
  - Count of corpus luteum, corpus albicans → recent pregnancy, past pregnancy
  - Count of placental scars → litter size
- Survey based:
  - Count of pups in dens
  - Count of offspring, females → recruitment



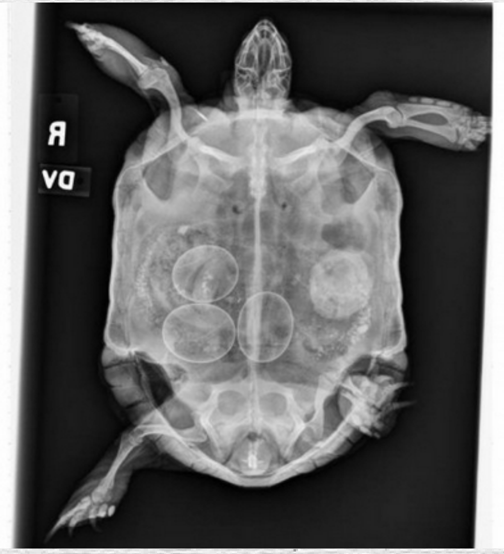
Pampas deer ovaries



A mink uterus

Portable medical imaging

X-ray on desert tortoise



Ultrasound on deer

Reproduction in plants

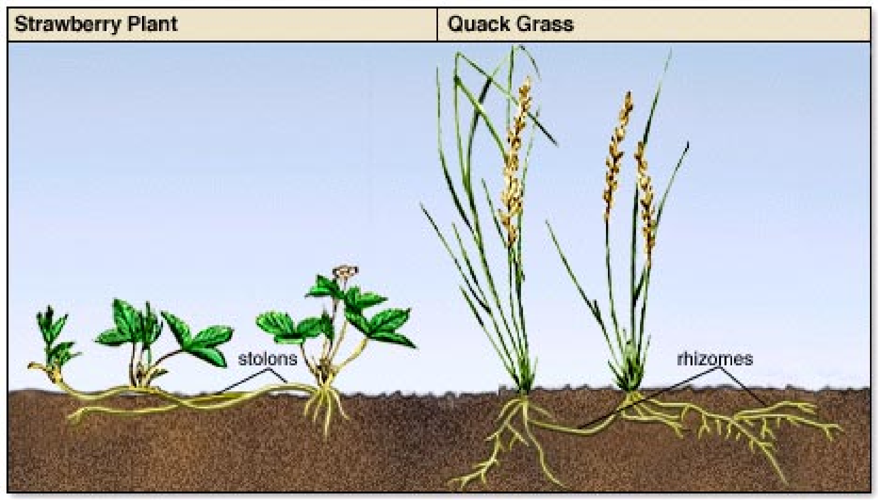
- Plants have both vegetative and sexual reproduction
  - Sexual reproduction through seeds
  - Vegetative reproduction through various structures (rhizomes, stolons)
- Both can be important for population regulation

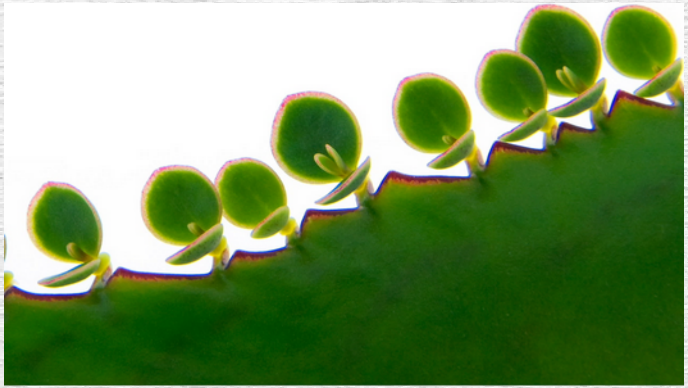
Plant sexual reproduction

- Reproduction in plants is seed production, followed by germination
- Germination is enough for estimating population growth, can be easier to measure than seed production
- Germination rate from a single plant is complicated if there is a seed bank
  - Long-term storage of non-germinated seeds in the ground
  - May take more than one year to go from seed to germinated seedling

Plant asexual reproduction

- Any reproduction that doesn't involve sex between different individuals
- Rhizomes, stolons, vegetative reproduction, fragments





Example – *Geum reptans*

- Long-lived alpine plant, found in the Alps
- Uses both sexual and asexual reproduction
- Weppler et al. 2006 estimated both modes of reproduction

Sexual reproduction

- Two censuses
  - First: every individual mapped, number of flower heads counted for each
  - Second: seedlings counted
- Seeds/head estimated from a sample of 10 in each life history stage once during the 3-year study
- Total seed production was seed heads x average seeds per head
- Per capita sexual reproduction was [(seed produced)/(total adults)] x germination rate

Asexual reproduction

- First census:
  number of stolons
- Second census:
  daughter rosettes at the ends of stolons counted
- Age-specific per-capita clonal reproduction was:

$$\frac{\text{Number of rosettes established}}{\text{Number of stolons produced per individual}}$$

Both reproductive modes equally important to population growth rate

- Reproductive rates were used along with survival measures to calculate population growth rates
- Using sensitivity analysis, they found that survival of adults was most important
- But, there was no difference in sensitivity of growth rate to sexual vs. asexual reproduction