Biology of Small Populations – the fewer you are the more problems you have

The Heath Hen
- Relative of the prairie chicken.
- Once found in the eastern United States from Maine to Virginia.
- Very edible and subjected to intolerable hunting pressure.
- By the 1870s only on Martha’s Vineyard.
- In 1907 there were only 50 heath hens left in a 1600-acre sanctuary established for their protection.

Decline factors
- The original 50 protected birds reproduced rapidly and there were 2000 individuals by 1915.
- In 1916 a fire wiped out much of the habitat that heath hens used for breeding.
- Following winter was unusually harsh, with an influx of goshawks, a predatory bird that fed on the heath hens.
- Poultry disease introduced to the island by domestic turkeys.

End of the species...
- Only 13 heath hens left by 1927 and most of these were males.
- Last living heath hen, the final survivor of his species, was seen on March 11, 1932.
- Why did the heath hen become extinct?
  - “Small population phenomena”
  - In former range, could have survived any one of these stresses, or even all of them in combination.
Another example: Colorado Big horn sheep

Small populations are generally at a greater risk of extinction than large populations.

- loss of genetic variability and related problems of inbreeding and genetic drift
- demographic fluctuations due to random variations in birth and death rate
- environmental fluctuations due to variation in predation, competition, disease and food supply
- Natural catastrophes that occur at irregular intervals, such as fires, floods, volcanic eruptions, storms and droughts.

Extinction Vortex

Genetic Issues

Allelic diversity

- What is an allele?
- any of two or more alternative forms of a gene occupying the same chromosomal locus; such as that which determines flower petal color in peas
**Heterozygosity**

- % of individuals in a population that possess heterozygosity at a particular locus
- % of loci in an individual that are heterozygous

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**Why is genetic diversity important?**

- Adaptability at the population level to changing environments
- Buffering of individuals against change during their lifetimes

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**Genetic Drift**

- Allele frequencies “drift” around
- If an allele occurs at a low frequency in a small population it has a significant probability of being lost by chance in each generation
- Gradual loss of rare alleles from a population changes the overall genotype (pool of available genes) of the population

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*Figure 1: Distribution of correlations between refire selection fitness and genetic diversity for a surrogate theory. The distribution’s weighted mean is 0.452 and the median is 0.445.*

*Figure 2: Genetic drift in a small population of 100 individuals. Initially, 50% of the population is homozygous for allele A and 50% homozygous for allele a. Over time, due to genetic drift, the frequency of allele A decreases, and the population becomes more homozygous for allele a.*
Example

- Consider a rare allele that occurs in 5% of all individuals present.
- **Large Population** = 1000 individuals, then 100 copies of the allele are present in the population (1000 individuals x 2 copies per individual (diploid species) x .05).
- **Small Population** = 10 individuals there will only be 1 copy of the allele present in the population (10 x 2 x .05) = 1.

Genetic Drift

- finite population size alone results in a change in allele frequency (which results in a decline in heterozygosity).
- Genetic Drift is a process that leads to random genetic changes in populations.
- While it occurs in all populations, drift can be a major driving force for changing allele frequencies in small populations.
- Like selection, drift is a process of differential reproductive success; however, the key element of genetic drift is which individuals survive and reproduce is random (unrelated to their phenotype and genotype).

Effective Size

- The total population (census size) is **not** a meaningful number.
- All the animals in the population will not be involved in breeding (juveniles, old, ill, small, sterile or weak individuals will not breed).
- Instead, we must consider **Effective Population Size** (N_e), the number of individuals in the population able to breed.

\[
\frac{N_e}{N_c}
\]

- The Effective Population Size is often approximately 10% of the overall population (N_e = 0.1 N_c).
- For example, in a study of alligators (N=1,000) only 10 animals were found to be of the right age and health to breed with one another. In this case N_e = 0.01 N_c!
Population Fluctuation and Bottlenecks

- $N_e$ greatly affected by years with very low population size
- A single generation with either a very large or a very small population will have a major effect on $N_e$.
- Multiple generations with small numbers can have a profound effect

Asian bramble (*Rubus alceifolius*)

- Introduced weed on some Pacific islands.
- In its native range (Viet Nam) this species is highly polymorphic, while in an introduced population (the island of Réunion) no polymorphisms are observed.
Lions (*Panthera leo*) of the Ngorongoro Crater, Tanzania

Details

- This population totaled roughly 60 to 75 lions until 1962.
- Exceptionally heavy rains permitted the biting fly *Stomoxys calcitrans* to breed constantly for more than six months.
- Most lions became emaciated and covered with festering sores.
- Became so ill they were no longer able to hunt.
- By the time the rains finally abated, at least 70 lions had been reduced to about ten.
10 = 9 females and 1 male (some later migration by males)

Despite this influx, and an increase in population to 75-125 animals, the crater lions still exhibit evidence of a genetic bottleneck.

**Symptoms**

- reduced genetic viability,
- high levels of sperm abnormality,
- reduced reproductive rate (relative to the nearby Serengeti lion population).
- cause for concern for status of population

**Loss versus Gain of Alleles**

Won’t mutation just make up for drift?

**Loss versus Gain of Alleles**

- When alleles are lost through genetic drift the population suffers a loss of overall genetic variability.
- To balance the loss due to genetic drift, new alleles may be introduced to the population by either
  - mutation
  - immigration of individuals from other populations of the same species

**Relative Rates of Loss versus Gain of Alleles**

- A small amount of immigration (2 to 5 individuals per generation) will serve to maintain the level of heterozygosity.
- But mutation rates range from about **0.001 to 0.0001 mutations per gene per generation** -- totally insignificant in a small population over the short-term!
Why does mutation not simply mitigate for drift?

- The mutation rate would have to be between $10X$ and $100X$ greater than normal in order for mutation alone to preserve the heterozygosity of a small population.
- Also, generally mutations are deleterious.
- Unlikely to be sufficient.

The big consequence:

- Natural selection needs:
  - Heritability
  - Selection
  - Variation
- Loss of genetic diversity means loss of evolutionary flexibility.

Inbreeding Depression

- Inbreeding = mating by close relatives.
- Inbreeding depression: decline in average fitness of a population due to exposure of deleterious recessive alleles in homozygous state.

Cystic Fibrosis

- most common, severe autosomal recessive disorder in the Caucasian population.
- ~5% of North Americans are carriers; they are completely asymptomatic.
- 1/2000 live births are affected by CF.
- $(q = 0.022; p = 0.978; 2pq = 0.043 (~5\%))$

Sickle Cell Anemia

- affects 1 in 500 black Americans.
- Frequency of homozygous recessive:
  - $q^2 = 1/500 = 0.002$ or 0.2%
  - $q = 0.002 = 0.0447$ or 4.47%
  - $p = 1 - q = 0.9553$ or 95.53%
- Frequency of heterozygotes = $2pq = 0.0854$
- 91.26% homozygous normal
- 8.5% heterozygous (1 in 12 are carriers)
- 0.2% homozygous sickle.
- Heterozygotes are fairly common.
Consequences

- Small populations increase likelihood of mating with relatives
- With inbreeding, a population suffers from higher mortality among offspring, fewer offspring, and weak and sterile offspring which will have low mating success.

Phenotypic consequences of inbreeding

- Some populations can "breed through" inbreeding depression and purge all the deleterious recessives
- Inbreeding is not always bad: can be good if you live in a constant environment, i.e., selfing in many plant species

Adders (Vipera berus)

Some 35 years ago, the number of adders living around the Swedish town of Smygehuk on the Baltic Sea began to drop (to just 40).

- Fewer young adders were being born. Those that were suffered deformities or were born dead.
- Had become isolated from other populations on a small, grassy, coastal strip for about 100 years

Management

- Starting in 1992, 20 adult males introduced from large and genetically rich snake groups from elsewhere in Sweden.
- From 1996 to 1999, a considerable increase in the population
- 32 recently-matured males being recorded 1999 -- the highest number recorded during 19 years of data collection in Smygehuk.
- Also a rapid increase in the genetic variability during this time, as well as a fall in the number of still born offspring.
Inbreeding versus Outbreeding

- Most mating systems are a compromise between inbreeding and outbreeding depression: mating with distant relatives best.

Outbreeding Depression

- Caused by the interbreeding of different subspecies ( = races) leading to diminished fitness of offspring.
- Generally, there are strong ecological, behavioral, physiological and morphological isolating mechanisms which prevent the interbreeding of subspecies.
- Possibly the result of locally adapted gene complexes

Ibex (Capra ibex)

- This species was extirpated in the High Tatra Mountains of Czechoslovakia in the late 19th Century
- Later restored with new stocks which included two other subspecies (C. hircus and C. nubiana), both of which come from warmer climates.

- Capra ibex usually mated in midwinter so that the young would be born during the relatively mild months of April and May.
- The cross of C. ibex with C. hircus and C. nubiana resulted in summer mating (the time when the warmer climate subspecies usually mated) with juveniles born in the winter months.
- The harsh winter conditions led to the deaths of the juveniles.
“Allee effects”

- Some process in demography that collapses when a threshold density is reached

Allee Effects

- Named after the British ecologist Warder Allee
- The per capita birth rate declines at low densities
- For smaller populations, the reproduction and survival of individuals decrease
- A low density equilibrium could be sustained in a deterministic equilibrium where the birth rate equals the death rate.
- However, given stochasticity, the population could be driven below the low density equilibrium, and thus slide into extinction.

Passenger pigeon population collapse

- The decline in numbers circumvented the social facilitation necessary for the flocks to find enough mast for a successful nesting.
- Once a population went below a minimum viable size, the remaining individuals were unable to find food patches at an adequate rate.

Sluggishness of great whale population recovery despite protection

- Southern Hemisphere Population of Blue Whales
  - 1980-2000
  - 400-1,400
  - CV=0.4
Failure of canopy trees to fruit in fragments of tropical forests

Purely “stochastic” events

Dusky Seaside Sparrow *Ammodramus maritimus nigrescens*

- The last 6 birds brought into captivity in 1980 from a Florida marsh were all males!
- Declared extinct in December, 1990

Only 13 heath hens left by 1927; most of these were males
PVA or Population Viability Analysis

Predicting the Future

Some questions PVA can address…

- What is the chance of recovery of the Spotted Owl from its current threatened status?
- What is the risk of extinction of the Florida Panther in the next 50 years?
- Is it better to prohibit hunting or to provide more habitat for elephants?
- Is captive breeding and reintroduction to natural habitat patches a viable strategy for conserving Black-footed Ferrets?
- If so, is it better to reintroduce 100 Black-footed Ferrets to one habitat patch or 50 each to two habitat patches?

Is it worthwhile to translocate endangered Helmeted Honeyeaters from their current populations to empty habitat patches to spread the risk of local extinctions?

Is it better to preserve one large fragment of old-growth forest, or several smaller fragments of the same total area?

Is it better to add another habitat patch to the nature reserve system, or enhance habitat corridors to increase dispersal among existing patches?

General idea behind PVA:

- We cannot understand the complexity of interactions among the variables we can influence unless we model the population.
- We cannot predict population size with certainty but we can specify the probability of particular outcomes.

Population viability analysis

Demographic models

- Initial population size
- Number of breeding individuals
- Number of young produced by each breeder

Add the new individuals
Population viability analysis

Demographic models
- Initial population size
- Number of breeding individuals
- Number of young produced by each breeder
- Juvenile survival rate
- Adult survival rate

Without stochasticity, the model will always predict the exact same thing. But in the real world little is certain, so we need to know the range of possible outcomes. For each variable, the model picks some number from a range of potential numbers. Hence every simulation produces a slightly different result.

Population viability analysis

To determine population viability, we need to:
- Run model for a given time
- Incorporate stochasticity
- Run multiple simulations
- See how many simulations result in the population going extinct (or declining significantly)

Types of stochasticity

1) Genetic
   - drift
   - mutations

2) Demographic
   - % male vs. % female offspring
   - mean reproductive success
   - random events of survival
### Types of stochasticity

1) Genetic
   - drift
   - mutations

2) Demographic
   - % male vs. female offspring
   - mean reproductive success
   - random events of survival

3) Environmental
   - food, competitors, predators, parasites, etc.
   - weather, flooding, etc.
   - catastrophes

### Demographic stochasticity

Identical conditions in each simulation, but fate of each individual is uncertain:
- 30% chance of dying
- 50% chance of giving birth to one more individual

Without stochasticity: population would increase by 5% per year

### Environmental stochasticity

Average birth and death rates change from year to year:
- 20-40% chance of dying (ave = 30%)
- 40-60% chance of giving birth to one more individual (ave = 50%)
- Line A shows conditions with just demographic stochasticity

### Effect of catastrophes

This graph has conditions the same as before, except there is also a 2% chance per year that 90% of the population dies

### PVA: Step 1

- a single population projection is made over a specified time period
- population size at any given time step is a function of
  - the population size at the previous time step and
  - values drawn at random from distributions of numbers described by the model's parameters.

### PVA: Steps 2 & 3

- Many such projections are made (typically 500 or more).
- The proportion of projections in which the population reached a certain threshold is determined.
What comes out of a PVA:

- A prediction from a PVA generally has three elements:
  - a population threshold (often zero),
  - a probability (from 0 to 1, or 0% to 100%) that the population will reach that threshold,
  - an interval of time for which the prediction pertains.
- Insights available through sensitivity analysis
- A very valuable synthesis about what is known (or not known) about a species’ demography

A Case Study

Crowded Beach

Adult Piping Plover
Threats

• Commercial, residential, and recreational development have decreased the amount of coastal habitat available for piping plovers to nest and feed.

• Human disturbance often curtails breeding success.

Foot and vehicular traffic may crush nests or young.

Excessive disturbance may cause the parents to desert the nest, exposing eggs or chicks to the summer sun and predators.

Developments near beaches provide food that attracts increased numbers of predators such as raccoons, skunks, and foxes. Domestic and feral cats are also very efficient predators of plover eggs and chicks.

Young Piping Plover Chick
Interruption of feeding may stress juvenile birds during critical periods in their development.

Protections under the Endangered Species Act
- Became a protected species under the Endangered Species Act on January 10, 1986.
- Along the Atlantic Coast it is designated as threatened, which means that the population would continue to decline if not protected.
- Listing requires development of a recovery plan, which invoked a PVA to explore alternatives.

Basic Population Model
- The number of fledglings present in the population at the time of census is calculated as:
  \[ F(t+1) = F(t)\times SF \times PB \times CP + A(t)\times SA \times CP \]
- and the number of adults present as:
  \[ A(t+1) = F(t)\times SF + A(t)\times SA \]
where:
- \( F \) = number of fledglings,
- \( SF \) = annual survival rate of fledglings,
- \( CP \) = female chicks fledged per female per year (chicks per pair divided by 2),
- \( PB \) = proportion of 1-year old adults breeding,
- \( A \) = number of adults,
- \( SA \) = annual survival rate of adults

Recommended Delisting Criteria
- Based on > 95% probability of persistence for 100 years:
  - Increase all 4 subpopulations to current estimates of carrying capacity: Atlantic Canada = 400 pairs, New England = 600 pairs, New York/New Jersey = 550 pairs, Delaware to North Carolina = 450 pairs.
  - Maintain mean fecundity of 1.5 chicks fledged per pair for each of the 4 subpopulations and the Atlantic Coast population as a whole.
Results?
- Driven management and effort during last decade
- Recovery objectives were widely regarded as unachievable
- In 2002 there were:
  - 1650 pairs!
  - Mean fecundity was 1.32!

Limitations of PVA
- A model like any other model
- Incomplete knowledge of basic population and life history information
- A predictive tool, not a definitive equation.
- Unknown futures – initial conditions are never constant; what will the world be like in 100 years?

Summary of Small Populations

Some benchmarks...
- **Demographic stochasticity**—Unlikely to be a problem in populations with more than 50-100 individuals
- **Genetic stochasticity**—Not a problem in populations with greater than 100-300, therefore, not likely to be a problem in populations large enough to buffer demographic stochasticity

Summary (cont’d)
- **Environmental stochasticity**—Requires population sizes on the order of 1000-10,000 to buffer against
- **Natural catastrophes**—No single populations can ever be large enough to buffer against natural catastrophes
End

Small Populations