Problems of small populations

The initial effect man has on all species is to divide them into semi-isolated populations

The next effect is to begin reducing the size of those populations.

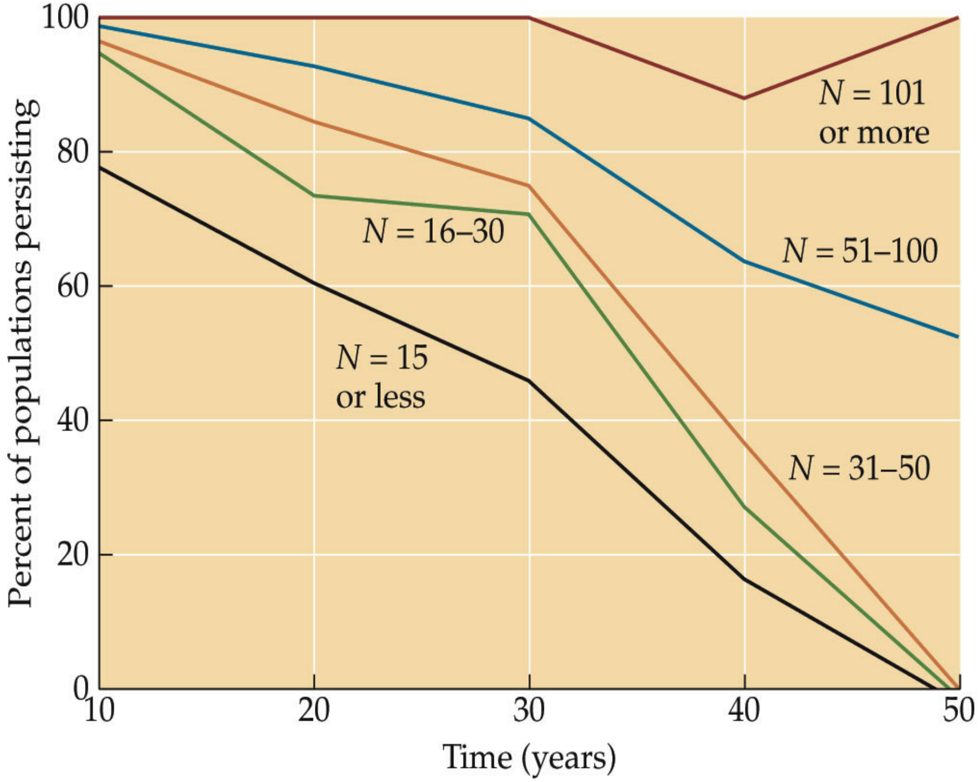
These lead to a cascading series of problems that often lead to the extirpation of local populations and often to the extinction of the entire species

The population becomes the local focal point and conservation must address preservation at that level

The key concept becomes the *minimum viable population* (MVP)

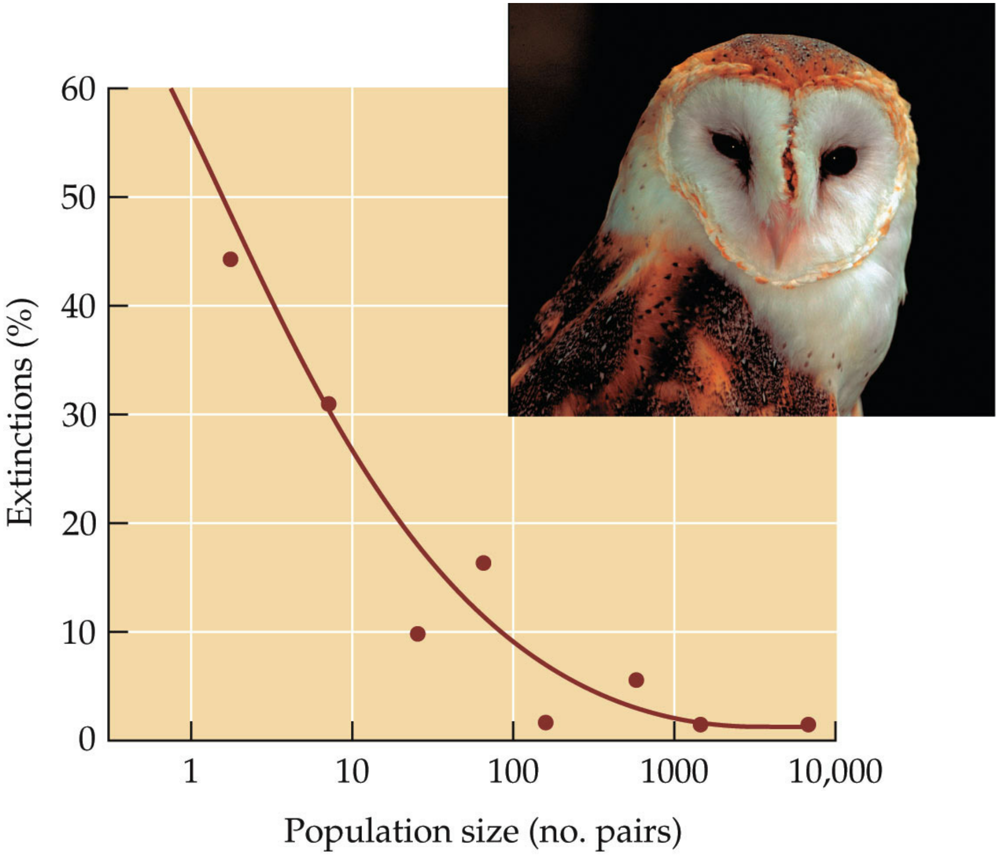
The MVP is the smallest population that can guarantee persistence for some number of years – 50 or 100 or 1000 – values that are arbitrary at best

Larger populations have a higher chance of persisting



Studies of bighorn sheep indicate that only populations with at least 100 individuals will persist for 50 or more years

Larger populations have a higher chance of persisting



the same result is seen in studies of barn owls on the Channel Islands

Small population face three types of problems

1. Loss of genetic variation – this stems from random genetic drift and inbreeding
2. Environmental stochasticity – this stems from fluctuations in predation, competition, food supplies, disease and weather; it is also driven by periodic catastrophes such as floods, fires and droughts
3. Demographic stochasticity – this stems from the sequence of birth and death events in a population

Not surprisingly, biologists differ on ranking the relative importance of these problems

Your author ranks them as 1, 3 and 2 (but he has #3 wrong)

I rank them as 3, 2 and 1

Loss of genetic variation

Individuals who are heterozygous and populations that contain genetic variation are better able to persist.

As individuals, this has to do in part with the simple fact that having 2 different alleles at a locus doubles your chances of one of them providing a reasonable solution to environmental challenges

For the population, increased numbers of different alleles raises the likelihood that there will be some individuals able to persist if and when the environment changes

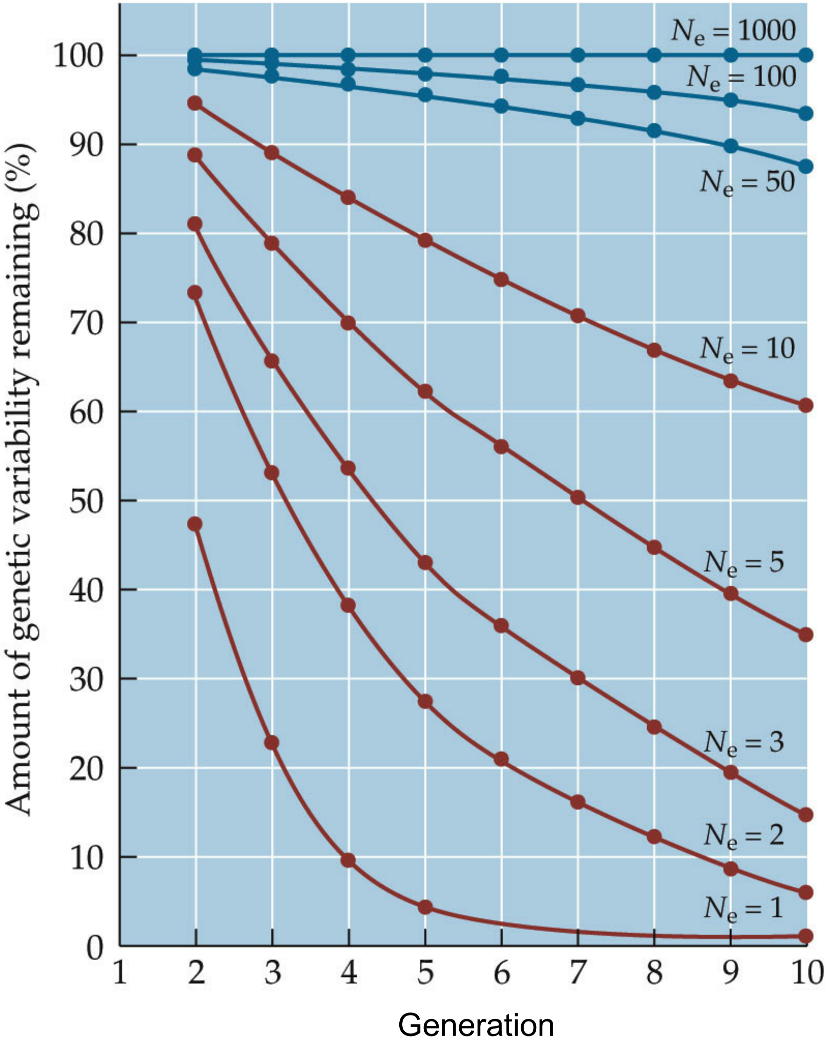
Genetic drift is a random process whereby some variation is lost each generation just due to sampling

If a population has 50% red alleles and 50% blue alleles in generation 1, the chances there are still 50:50 in generation 2 goes down as the population gets smaller

This is no different than the chance of tossing 50:50 heads to tails declines with the number of coins tossed

As a consequence, small populations lose variation due to genetic drift

Genetic variation is lost more quickly in small populations



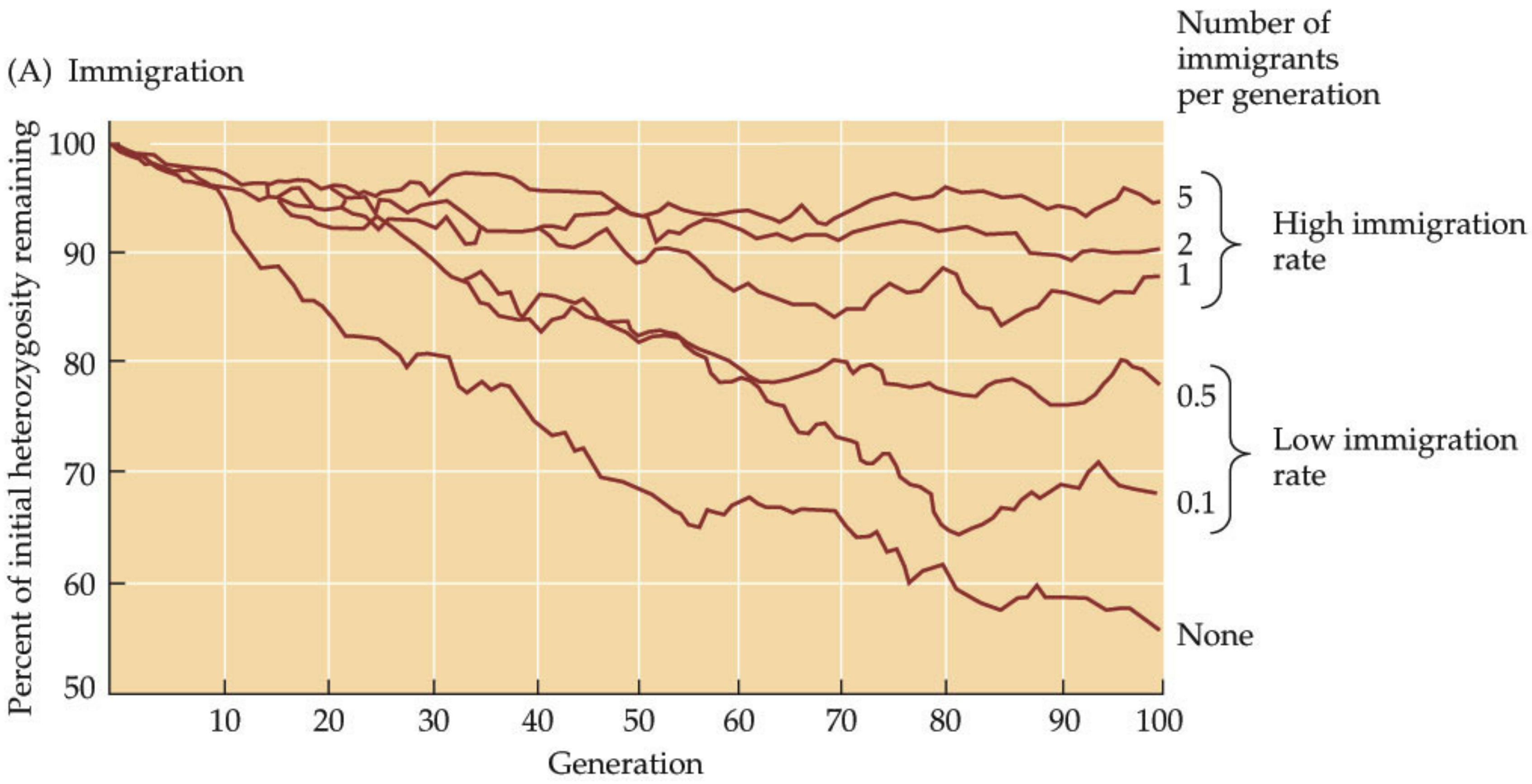
In a “perfect population”, you always have equal numbers of males and females, equal reproductive success, random mating, etc.

“Real populations” never meet these assumptions so we compute the *effective size of a population* (N_e) as the size of a perfect population that would behave genetically like the real one we are studying

The proportion of heterozygosity remaining in a population after each generation is $H = 1 – 1/(2N_e)$

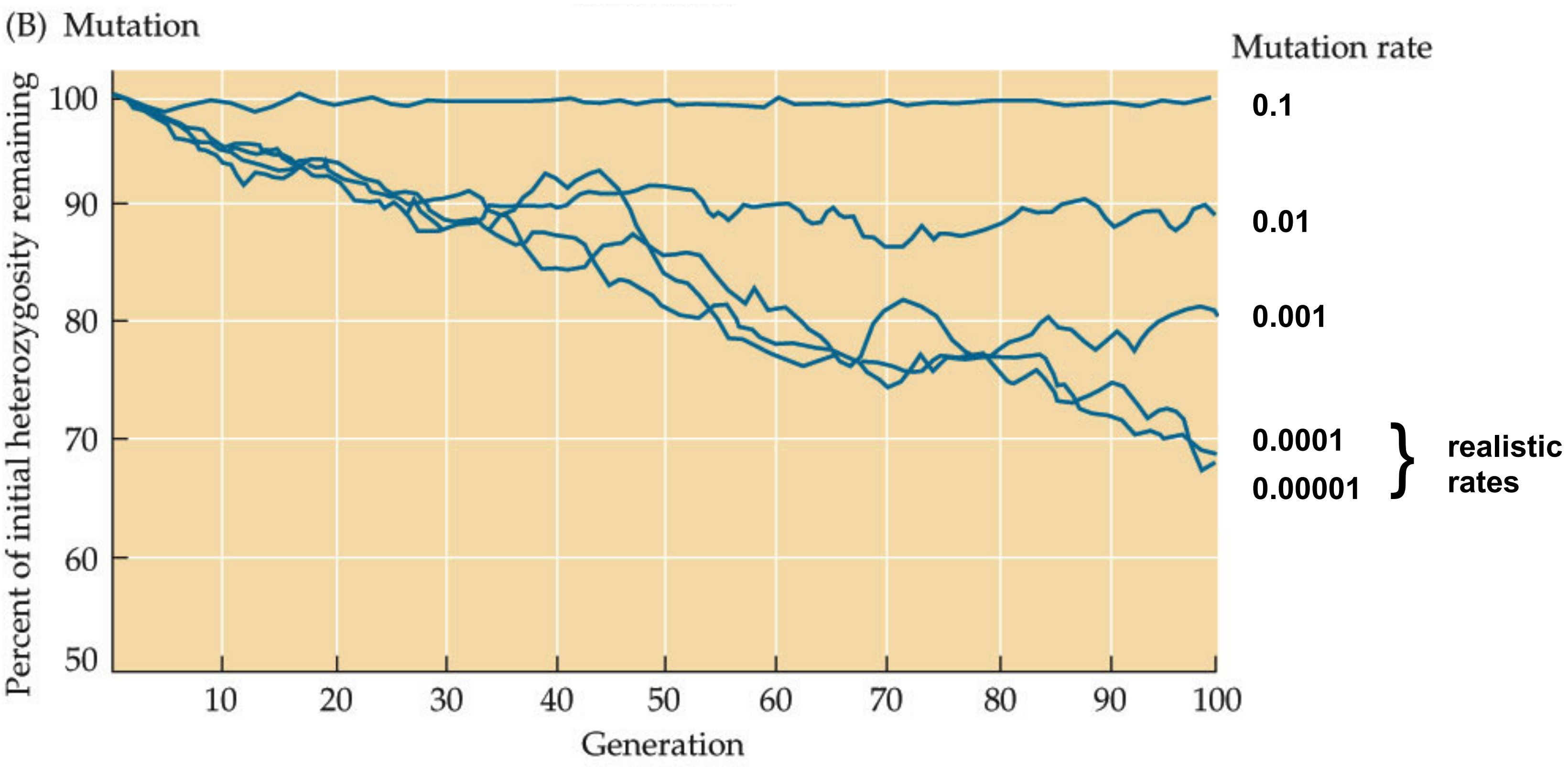
for populations < 1000, this declines and increasingly so for small populations

Loss of genetic variation can be countered by even low immigration rates



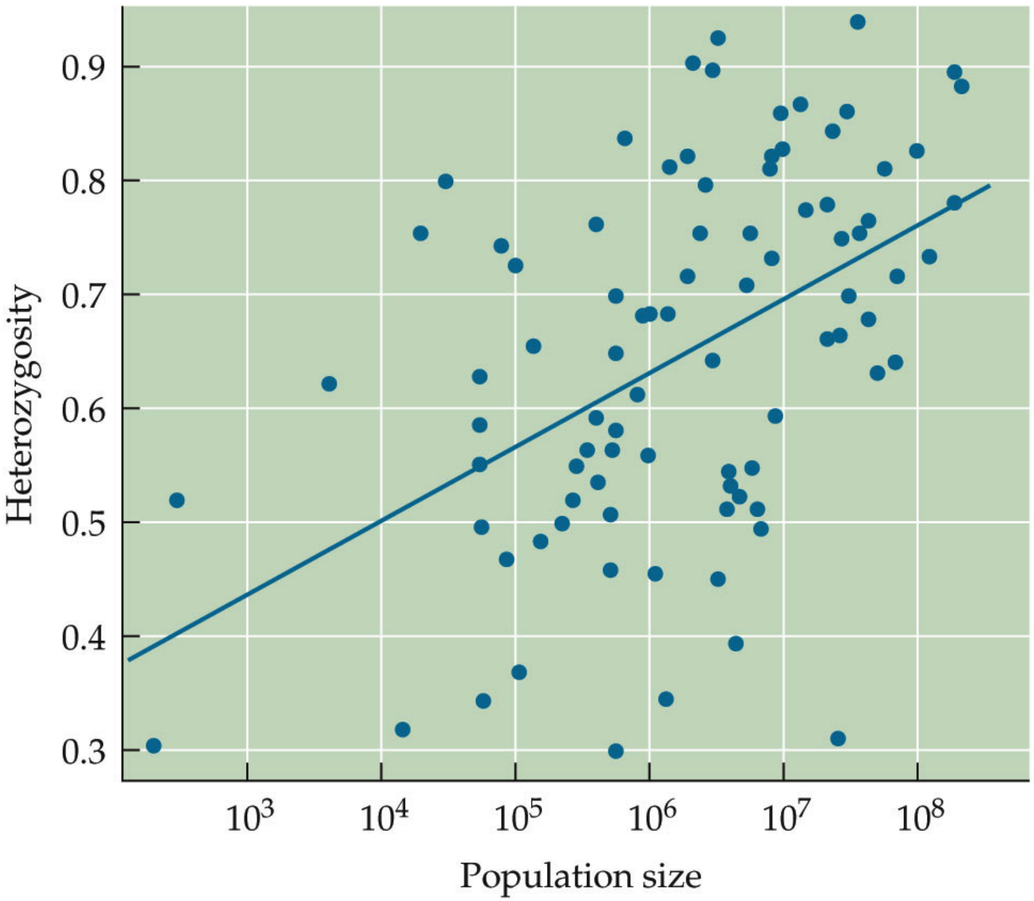
These simulations assume $N_e = 120$ and even 1 immigrant per generation is sufficient to maintain genetic variation.

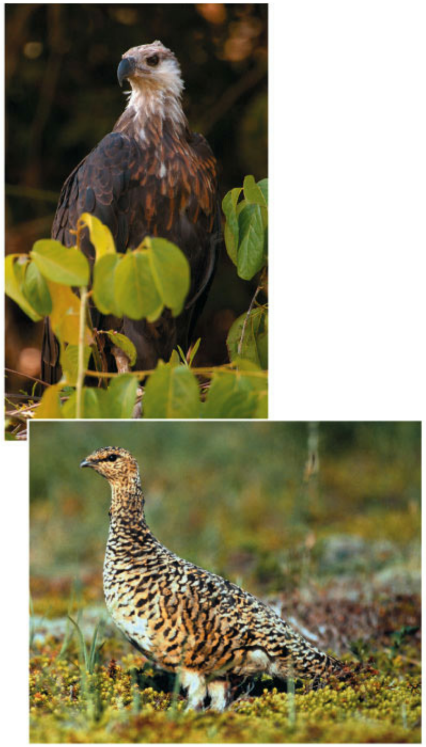
Mutation is not nearly as effective at maintaining heterozygosity



N_e is again 120 and only unrealistic rates of mutation can counter the effect of random genetic drift in reducing heterozygosity

Field data show that smaller populations have lower heterozygosity





In this study, heterozygosity and population size were determined for 89 species of birds

The 50/500 rule

The loss of genetic variation is increased when relatives mate with each other, a process called *inbreeding*

when populations get small, the likelihood of mating with a relative, even by chance, goes up

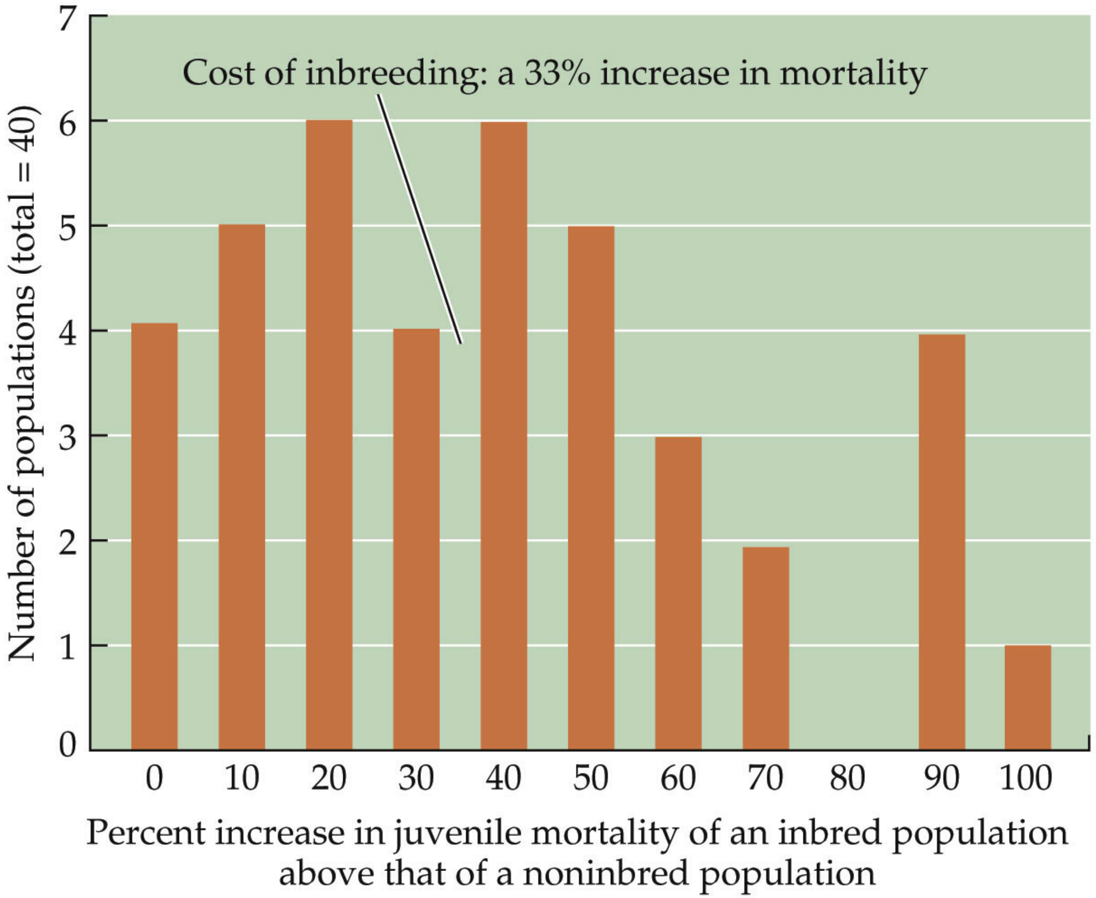
Franklin calculated that as long as $N_e > 50$ reductions in heterozygosity due to inbreeding are reduced enough to avoid negative effects

Franklin also calculated that in the absence of intentional inbreeding, realistic mutation rates are sufficient to offset reductions in heterozygosity as long as $N_e > 500$

These estimates make a lot of assumptions

Consequences of the loss of genetic variation

As heterozygosity is lost, so is the ability of individuals to mask the effects of deleterious recessive alleles

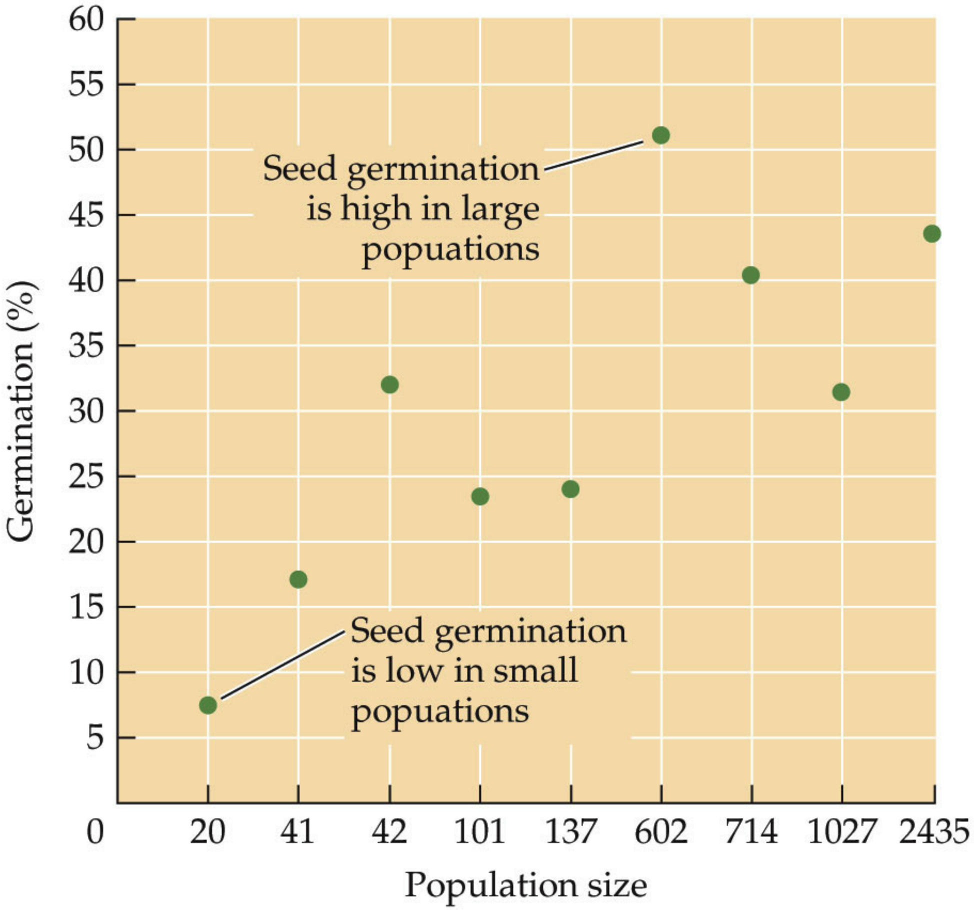


This is often referred to as *inbreeding depression* or the *cost of inbreeding*

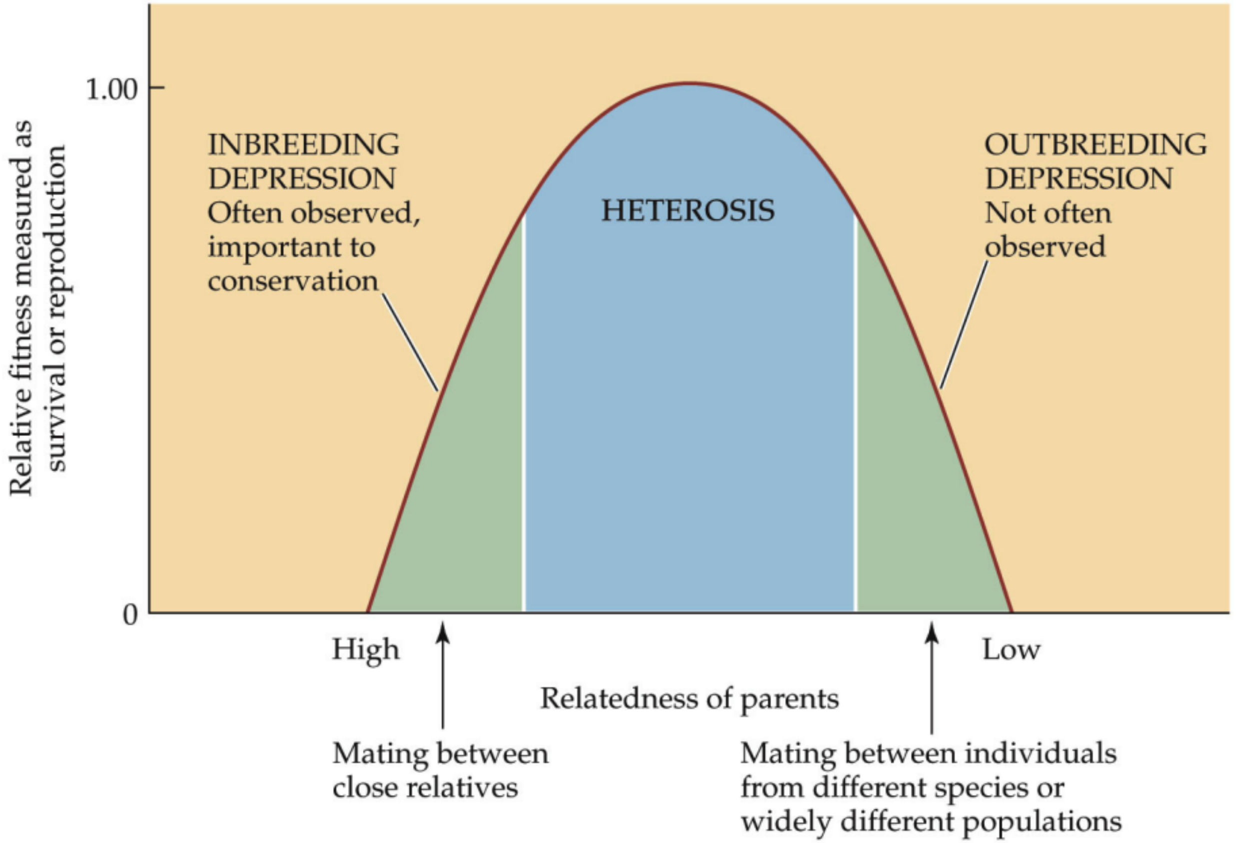
The x-axis depicts the relative cost in terms of increased juvenile mortality in 40 inbred mammal populations

On average, there was a 33% increase in mortality among the inbred populations in the study

Inbreeding depression often affects reproductive success



There is an optimal level of heterozygosity



Conservation plans sometimes fail by trying too hard to avoid inbreeding depression

Outbreeding depression results when coadapted gene complexes are destroyed by too much heterozygosity

Several factors affect the effective population size

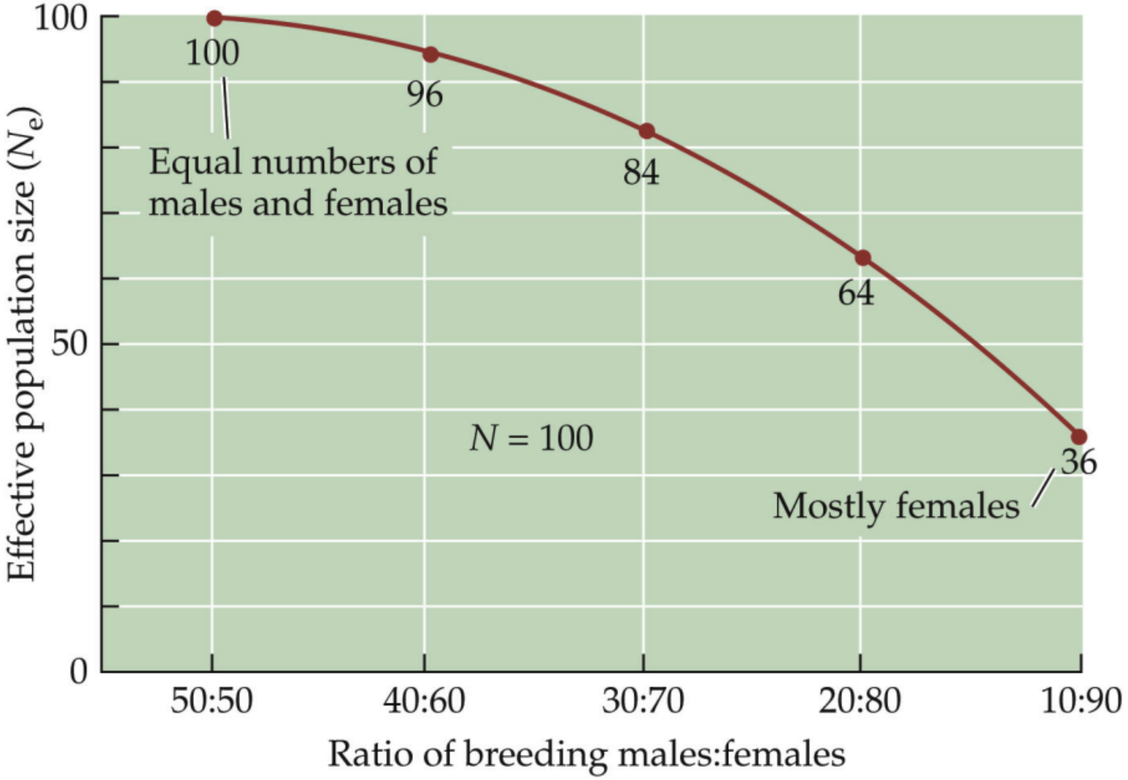
The negative effects of inbreeding depression can be offset by increasing the effective population size

This can sometimes be accomplished without increasing the actual number of individuals in the population

N_e depends on the operational sex ratio, variation in reproductive success among the members of the population and fluctuations in population size

Operational sex ratio is the ratio of the females and males who mate

In many species, a smaller number of males do much more of the mating so the operational ratio of males:females is less than the 50:50 you often find in the census



This inequality reduces the effective population size according to the relationship

$N_e = (4N_mN_f)/(N_m+N_f)$

As the relative number of males goes down, so does the effective population size

For some species, *increasing the equality of mating opportunity can reduce the level of inbreeding*

Variation in reproductive success

If a small number of individuals in the population do a disproportionate amount of reproducing then the effective size of the population will be less than the census size of the population

Rockwell and Barrowclough showed that if adult mortality remains constant as an animals ages and that reproductive success follows a random distribution with an equal mean and variance then:

$$N_e \approx N/2$$

They also showed that the effective size of the population can be increased (and inbreeding depression decreased) by making sure each female produces the same number of offspring

Fluctuations in population size can cause problems

Various factors can cause a population to temporarily decrease

These factors include storms and disease

Even these temporary reductions in N alter the effective population size

When populations go through such *bottlenecks*, the effective size is:

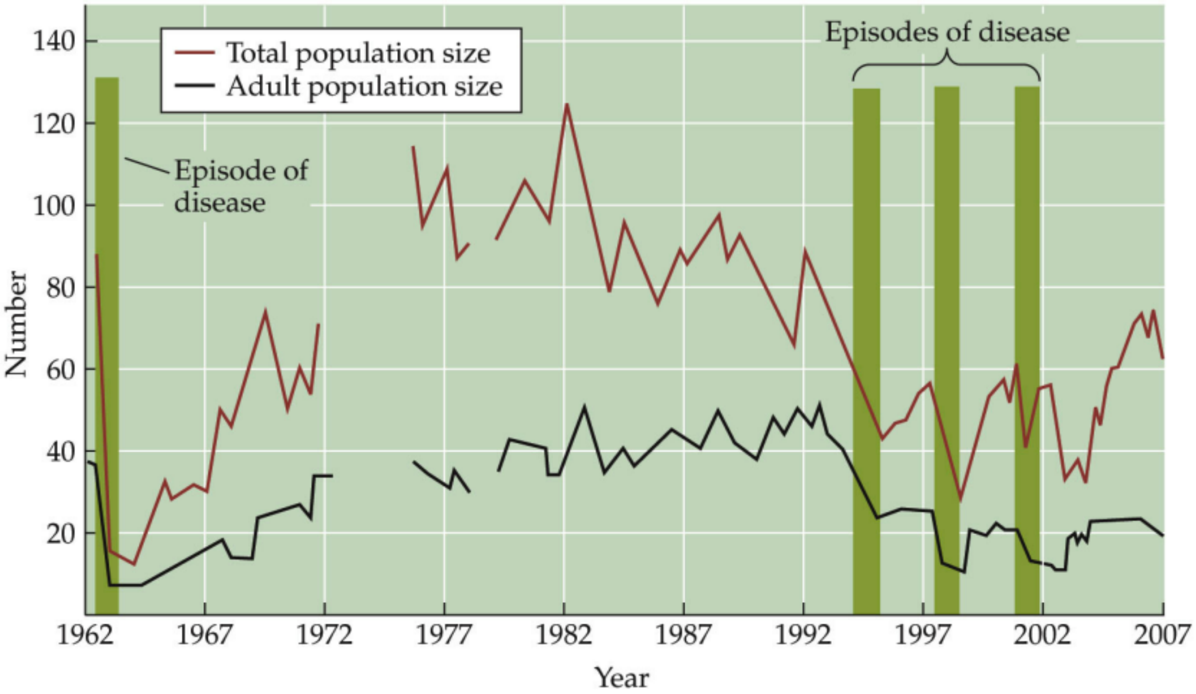
$N_e = t \times \Sigma(1/N_i)$ where

t is the number of years

N_i is the census size in year i

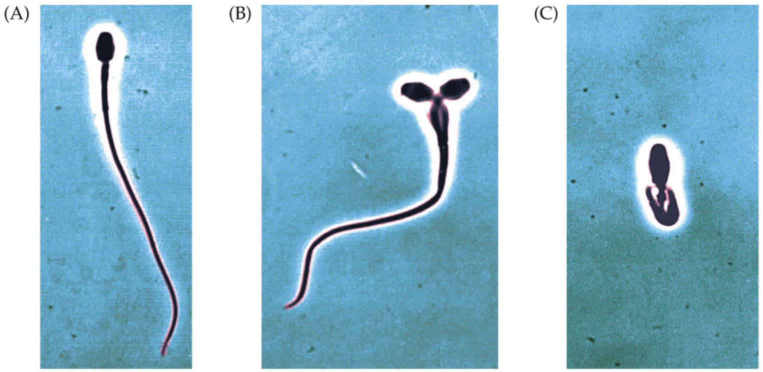
This is called a harmonic mean and because it is the sum of inverses, the smallest value has the largest effect

The effect of bottlenecks on lions



Periodic disease outbreaks reduced the lion population

This in turn led to an increase in inbreeding and a loss in heterozygosity



There is an increase in abnormal sperm (center and right) in the lions from this population

Environmental stochasticity

- **Catastrophes**

  Events such as storms, drought, volcanic eruption, tsunamis and war can drastically reduce populations in a short time span.

- **Environmental stochasticity**

  The environment is not constant and annual variation in such variables as temperature, rain and snow fall and cloud cover can affect the growth rates of populations

  The growth of a population can be represented as:

  $N_{t+1} = \lambda \times N_t$ where λ is the annual growth rate

  Environmental stochasticity leads to variation in the growth rate such that it is best represented as a mean (λ_m) and variance (V_λ)

  Because of this the realized growth rate of the population is

  $\lambda_s \approx \lambda_m - V_\lambda/2$

  Populations whose mean growth rate is $\lambda_m > 1$ may actually decline since $\lambda_s < 1$ if $V_\lambda > 2 \times (\lambda_m - 1)$

Demographic stochasticity

The population growth rate λ is a function of the difference between birth rate (b) and death rate (d)

Birth and death rates are estimated over the whole population and allow for the fact that some individuals may die before reproducing

The order of birth and death events becomes increasingly important when populations get small

Assume N=8 and each individual can have 1 birth event (b) and of course has to have 1 death event (d)

If the order is bbbbbbbbdddddddd then N=8 the next generation

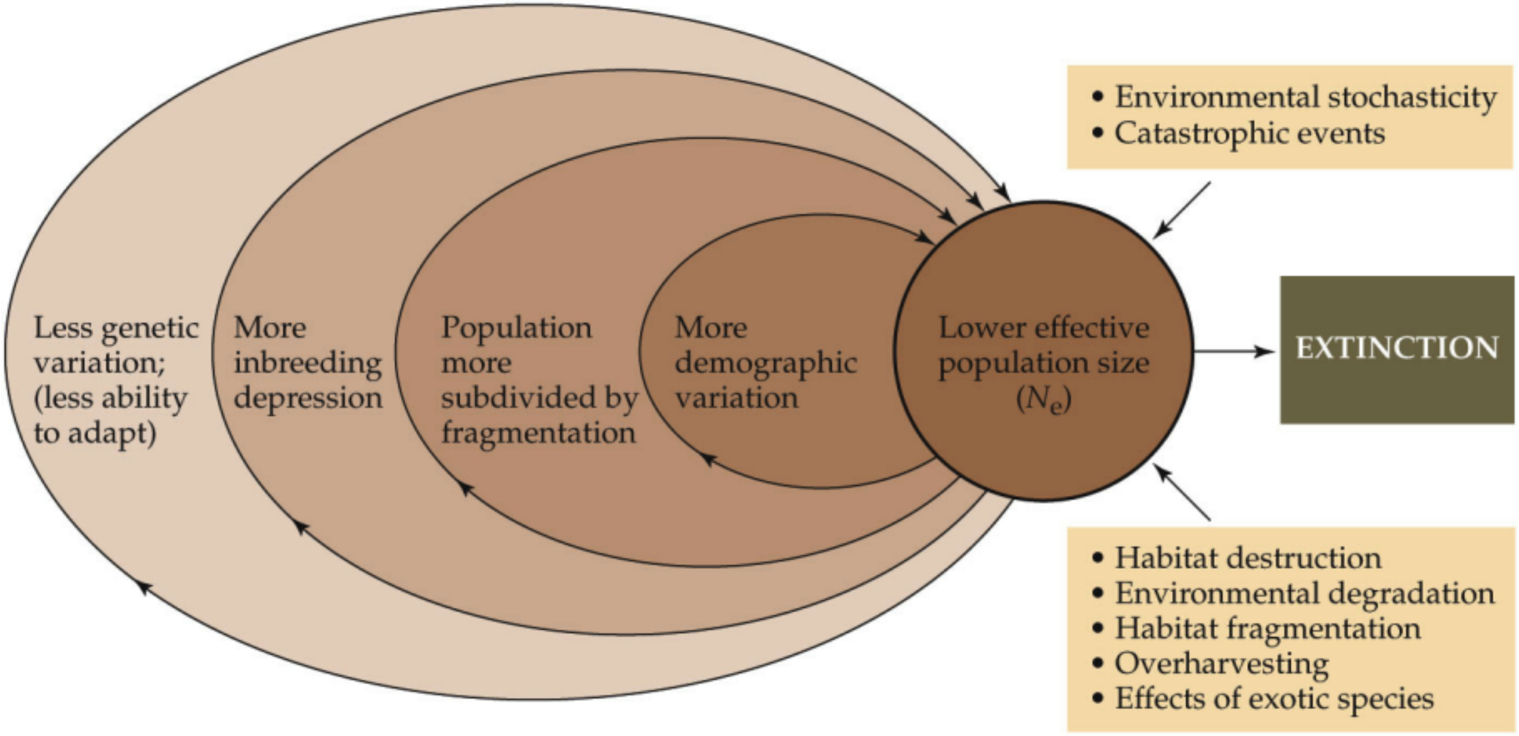
The same is true if each individual reproduces and then dies

But suppose 4 individuals die before birthing – ddddbdbdbdbd and N=4

Worse, we could have dddddddd and N=0

The odds that all death events precede any birth events increases as N declines just as the odds of tossing all tails goes up as the number of coins goes down

Extinction vortex



Simply put, as a population becomes smaller, all of the factors act to reduce it further and at a faster rate, increasing the likelihood of extinction

Applied population biology

For most species, by the time we recognize they are in trouble there is little time to gather the information needed to help them

Basically the kinds of information needed fall into two categories:

- *natural history* – including basic ecology and distinctive characteristics
- *population biology* – distribution, population size and dynamics

Types of information needed

- *Environment* – what are the habitats where the species is found, how much of it is there and what is the condition of that habitat?
- *Distribution* – what is the distribution of the species relative to that available habitat?
- *Biotic interactions* – how does the species interact with other species in the same geographic area and habitat? what is its trophic level?
- *Morphology* – what does the species look like? is it distinct from other closely related species? does it have special “issues”?
- *Physiology* – what are its environmental tolerances? what does it eat? how efficiently does it process food and water?
- *Demography* – what is its population size N and growth rate λ? what are its life history characteristics?
- *Behavior* – how does it behave? do any of its behaviors put it at risk?
- *Genetics* – how much genetic variation is there? how is it distributed?
- *Human interactions* – how does the species react to human activity?

How do you get this information?

- *Published literature* – the best form of information is peer-reviewed publications and the simplest way to find them is to perform species-specific searches using computer-based search engines like:
  - Web of Science
  - Scopus
  - Google Scholar
- *Unpublished (gray) literature* – this is information found in the reports of government agencies like USFWS and NGO's like World Wildlife Fund. Finding this information is more difficult and it is important to confirm it from several independent sources. The best starting points are:
  - Government agency and NGO websites
  - Google
  - Yahoo

Again, it is crucial that gray information be confirmed from several independent sources!!

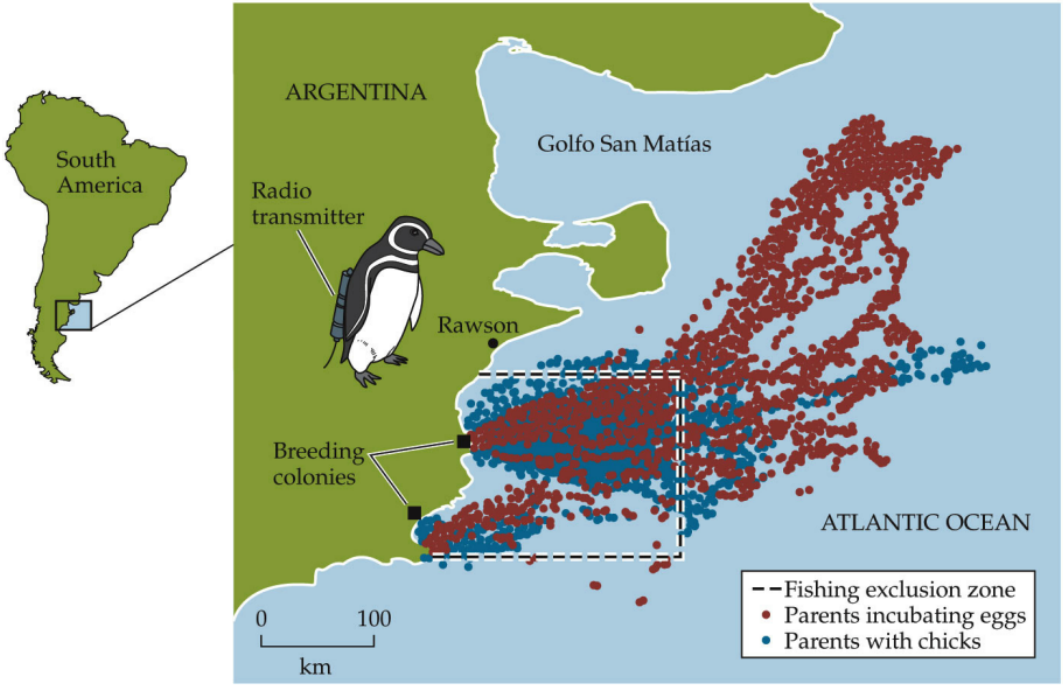
How do you get this information?

- *Fieldwork* – for many species, there is very little known and data have to be collected directly. This is not easy and must be done both quickly and thoroughly.

  Such work is usually be done in conjunction with government agencies or NGO's.

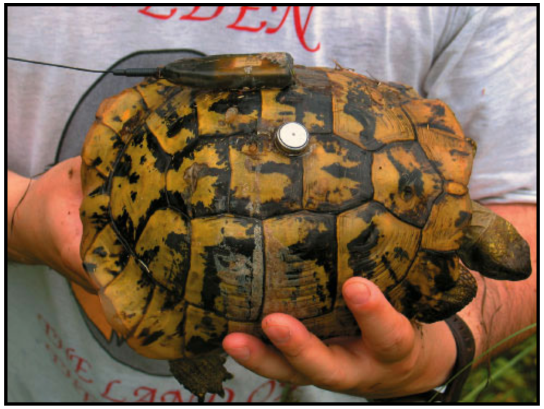
Quick but detailed studies of magellanic penguins using satellite transmitters showed they foraged much further offshore than thought

Government shifts in fishing exclusion zones improved survival

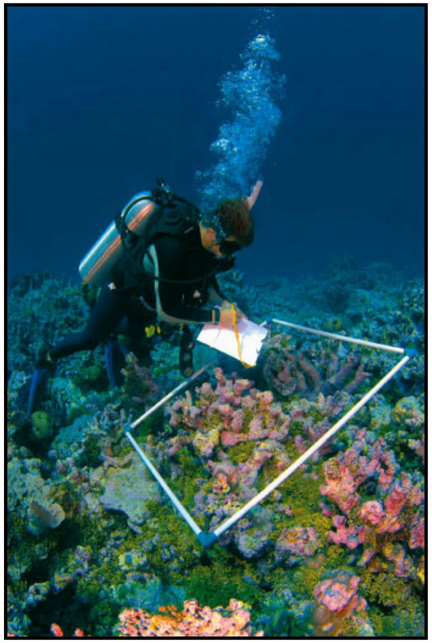


How do you get this information?

- *Monitoring* – at the very least, populations of species need to be monitored for population size and growth rate. Often simply knowing that $\lambda < 1$ is sufficient to force conservation actions by governments.



abundance of turtles can be monitored with satellite telemetry

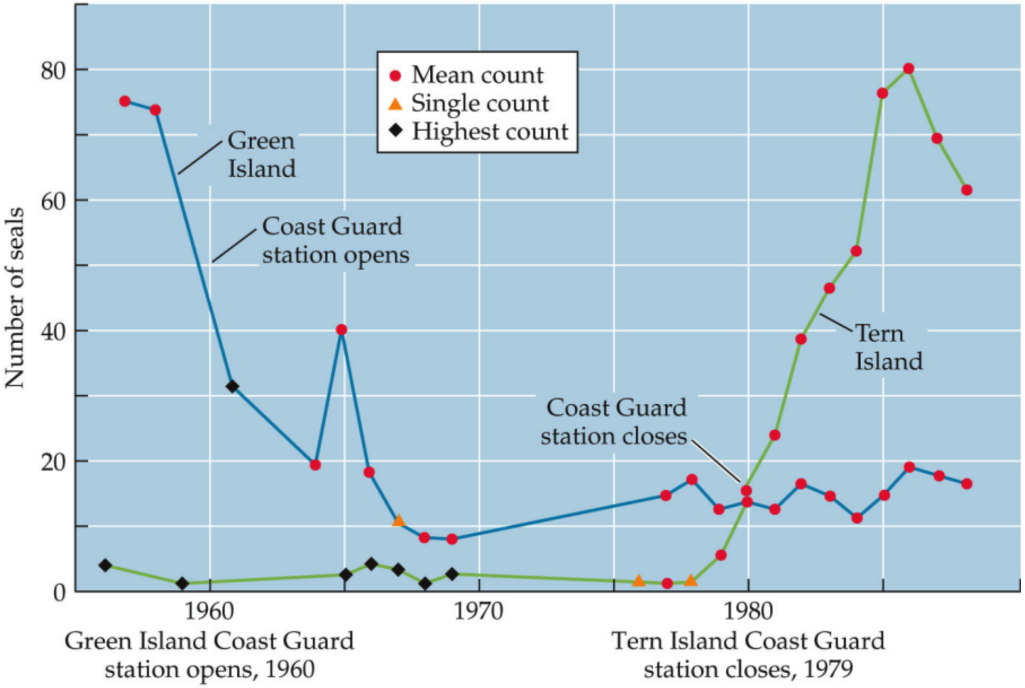


coral abundance and distribution can be monitored directly

plant productivity can be monitored remotely

How do you get this information?

- *Census* – this is a monitoring technique that can be done inexpensively for some species and provide crucial data

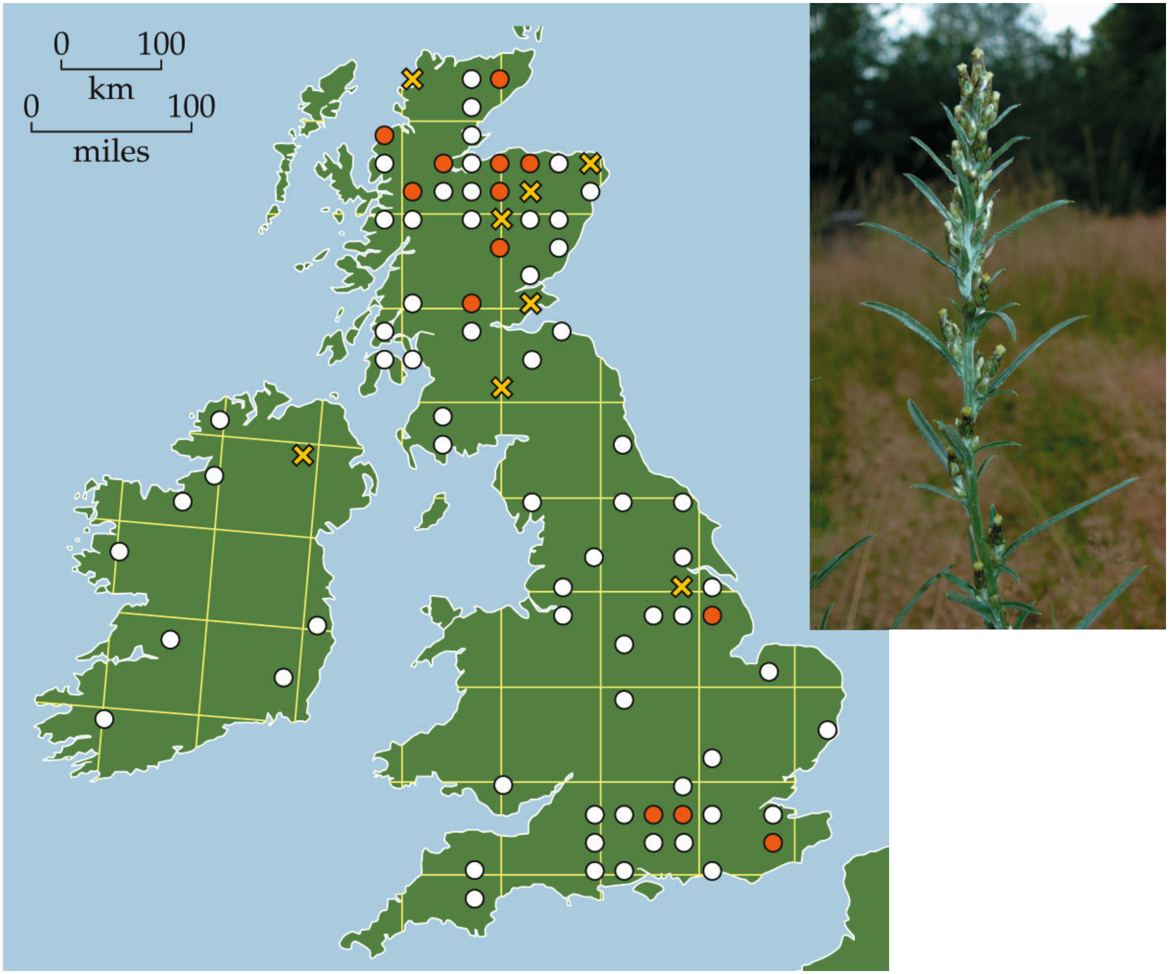


Consistently done counts of monk seals hauled out on beaches of two islands showed that the numbers were changing and that coast guard station activities were likely causing declines

How do you get this information?

- *Census* – repeated assessment of fixed sampling points can often document changes in abundance and distribution

Detailed annual sampling of numerous plant in Britain has shown that the woodland cudweed has disappeared from many sites ○, has persisted in a few sites ● and has spread to some others ✕



How do you get this information?

- *Surveys* – are used to estimate population abundance and growth when direct counts are not possible either because the species is difficult to find, occurs over a large area or has a large population size.

Techniques include random sampling, capture-mark-recapture and various non-invasive methods such as foot print traps, camera traps and even scat detection

Quinoa searches the Hudson Bay coast for piles of polar bear scat

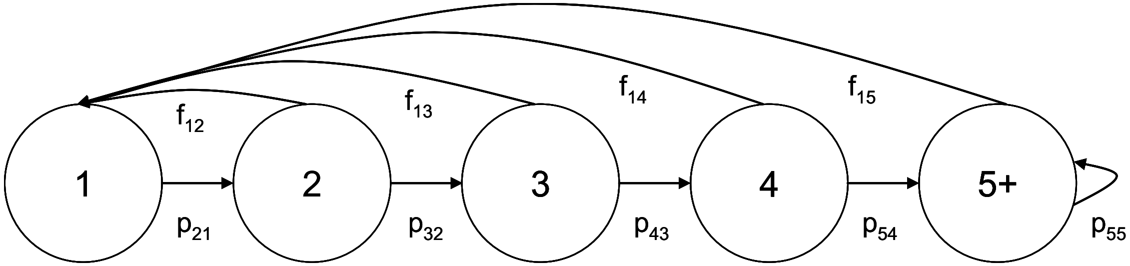
He signals on each one, some of which are less obvious than others

How do you get this information?

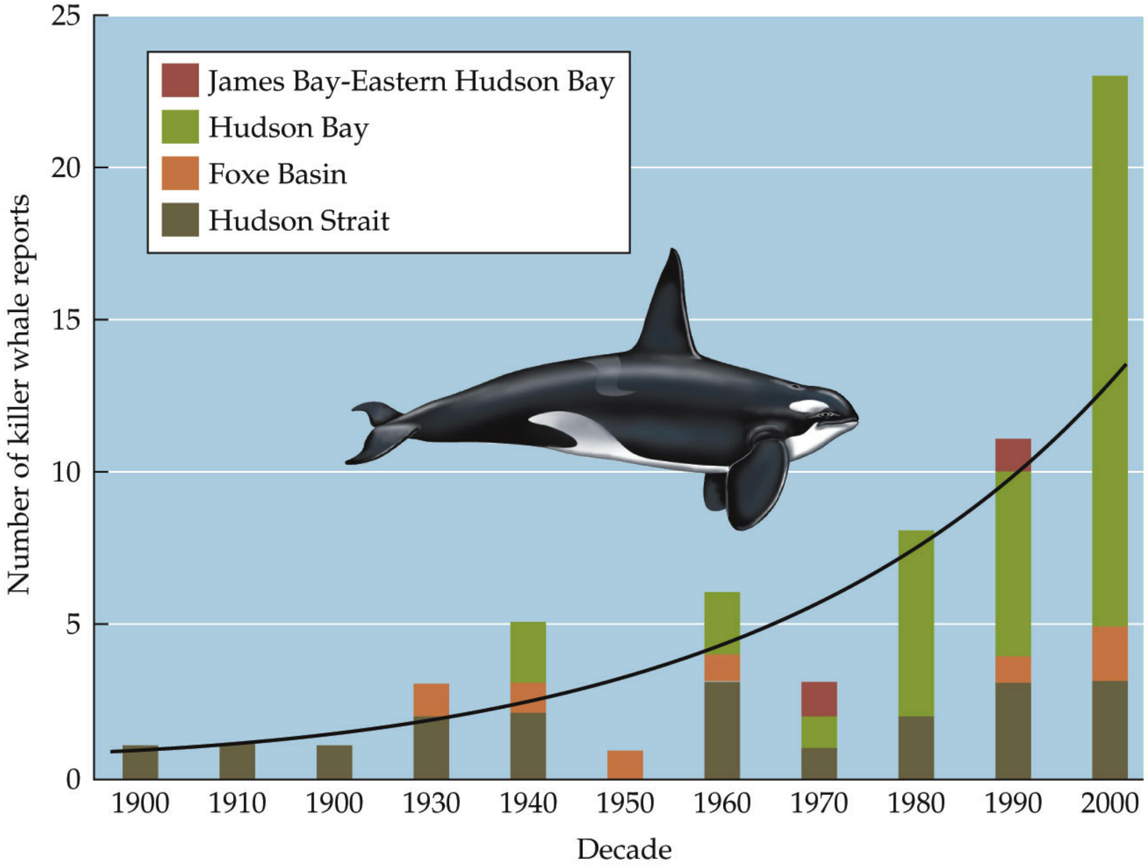
- *Demographic studies* – these are used to estimate demographic variables like reproductive success and survival in populations with age structure

  Those variables can then be used in population projection models to estimate population growth rates and determine if populations are at risk

  Unfortunately, these studies require more years of data than can be collected on species at risk

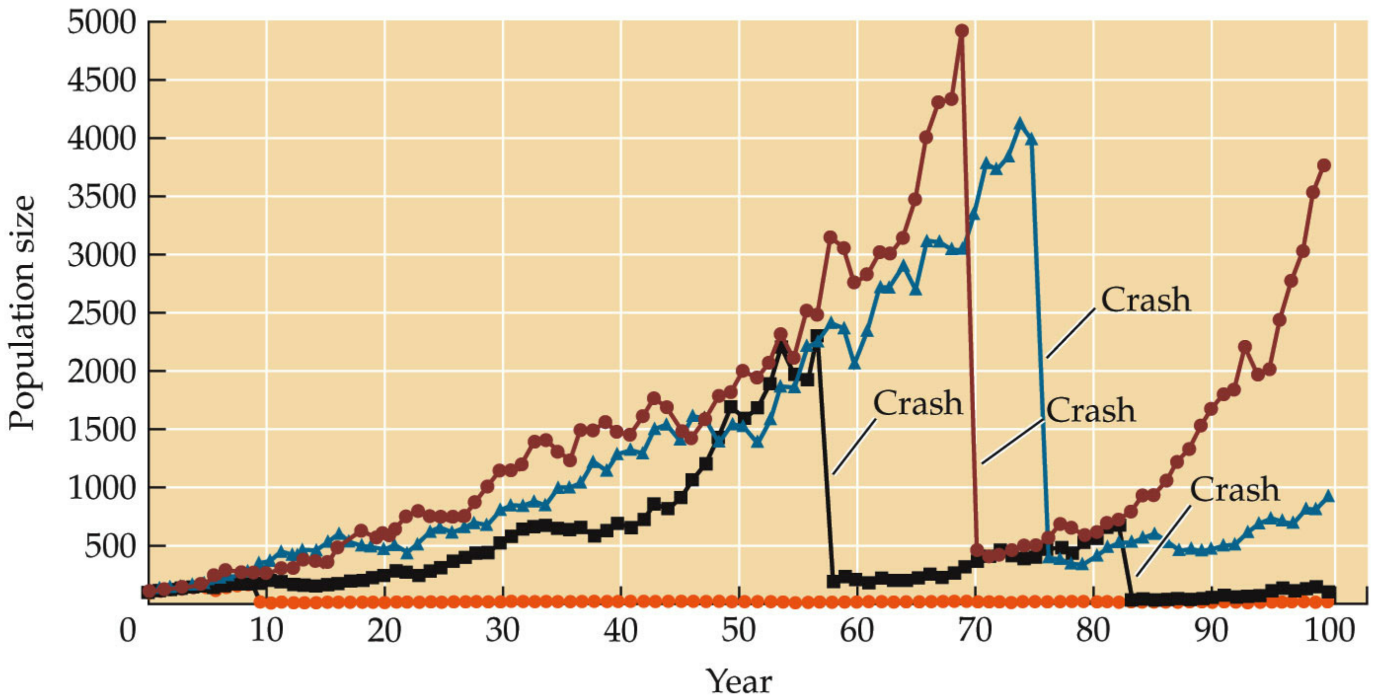


Killer whale sightings have increased coincident with reduced ice cover



However, so have the numbers of people looking for killer whales!!!!

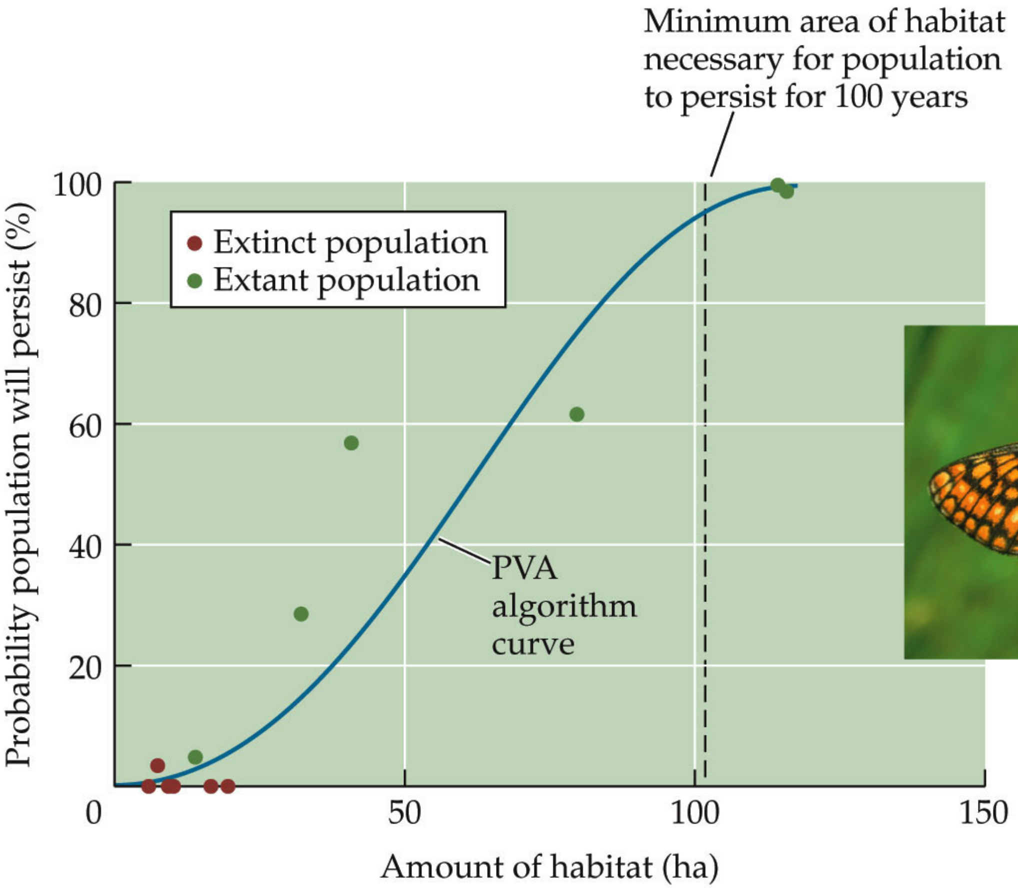
Population viability Analyses



Computer models that include stochastic variation and the chance of catastrophes can be built and used to project possible outcomes for populations at risk

These are very *assumption based* so using them for management must be done with care

PVA can be used to project the amount of habit needed for persistence



Again, assumptions need to be evaluated prior to implementation

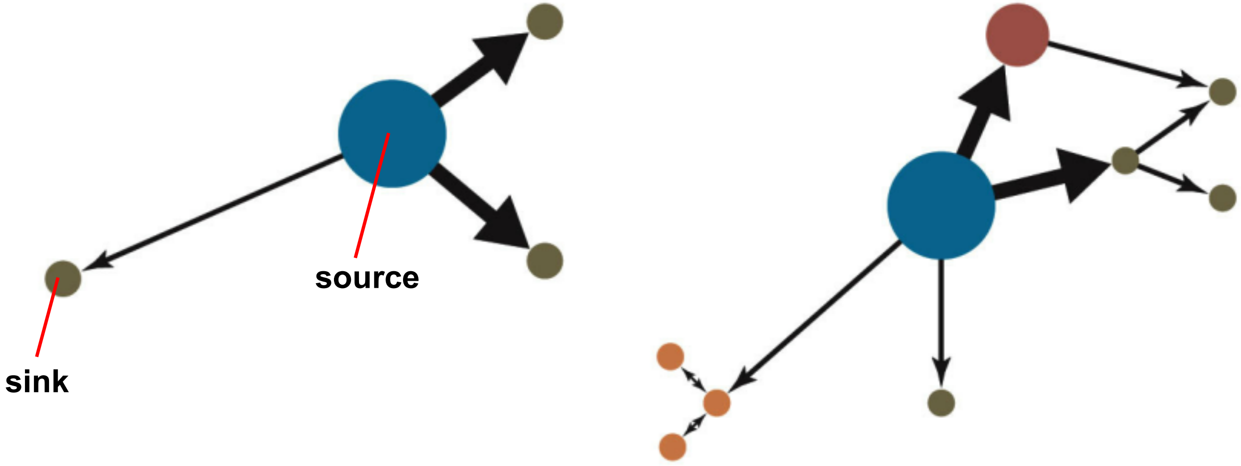
Habitat fragmentation leads to metapopulation structures

(A) Three independent populations

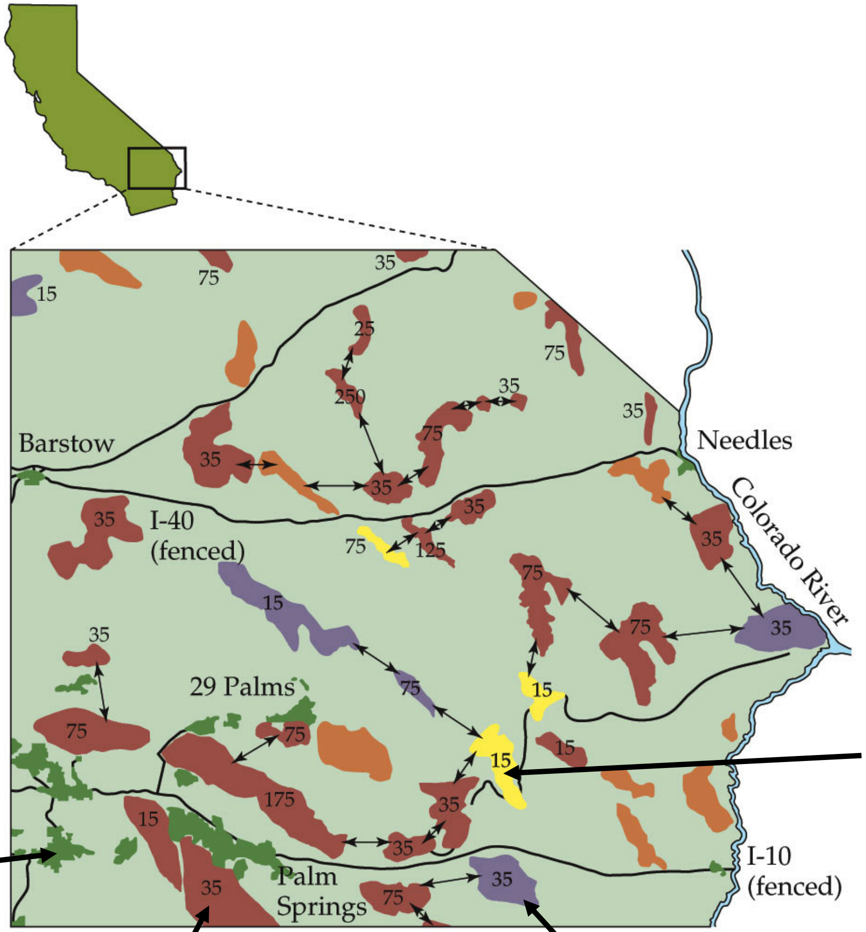
(B) Simple metapopulation of three interacting populations

(C) Metapopulation with a large core population and three satellite populations

(D) Metapopulation with complex interactions



Mountain sheep in California are managed as a metapopulation



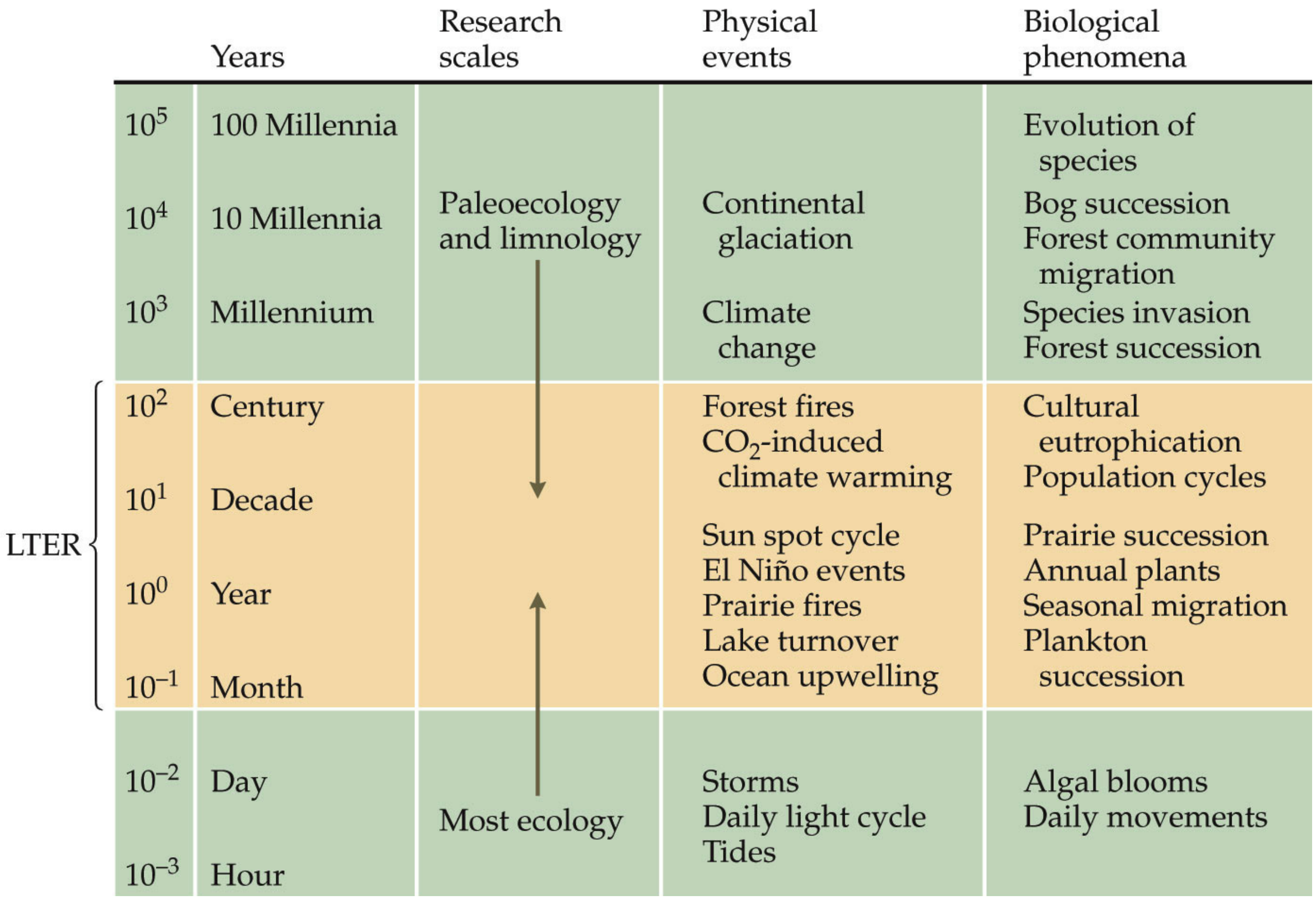
recolonized elements

lost elements

“stable” elements

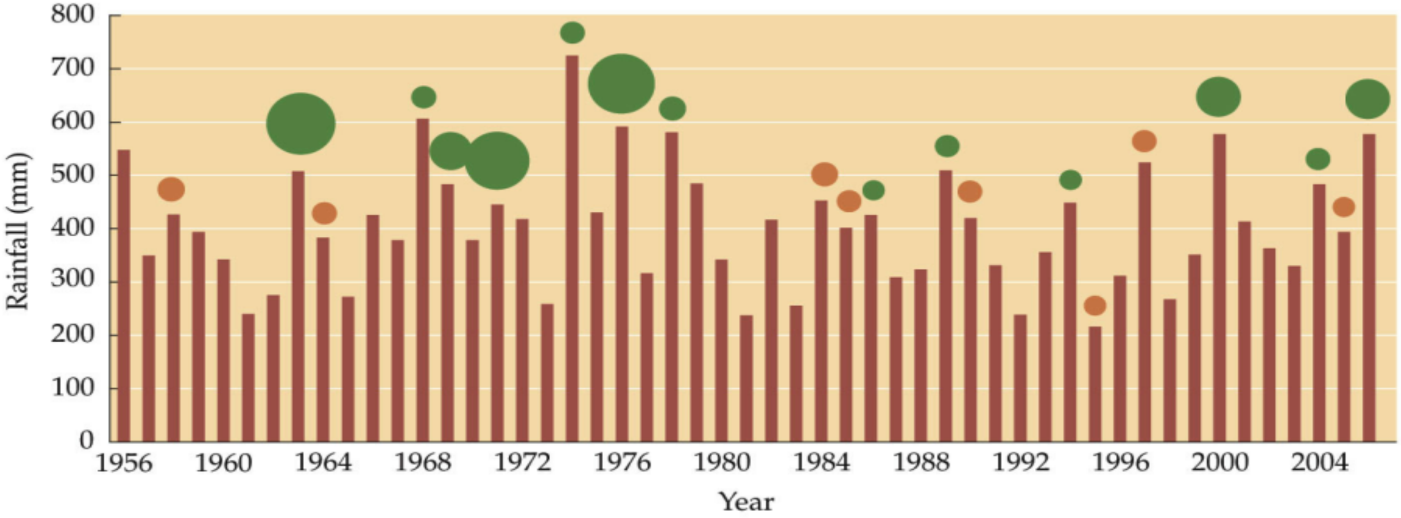
reintroduced elements

Long-term ecological research



		Years	Research scales	Physical events	Biological phenomena
	10^5 10^4 10^3	100 Millennia 10 Millennia Millennium	Paleoecology and limnology	Continental glaciation Climate change	Evolution of species Bog succession Forest community migration Species invasion Forest succession
LTER	10^2 10^1 10^0 10^{-1}	Century Decade Year Month		Forest fires CO_2-induced climate warming Sun spot cycle El Niño events Prairie fires Lake turnover Ocean upwelling	Cultural eutrophication Population cycles Prairie succession Annual plants Seasonal migration Plankton succession
	10^{-2} 10^{-3}	Day Hour	Most ecology	Storms Daily light cycle Tides	Algal blooms Daily movements

Long-term research can often uncover underlying drivers



●	**1000’s**
●	**100’s**
●	**<100**
●	**failed**
blank	**no attempt**

years of no nesting or failure are associated with reduced rainfall

years of more successful nesting are associated with increased rainfall

there is an overall decline in successful nesting