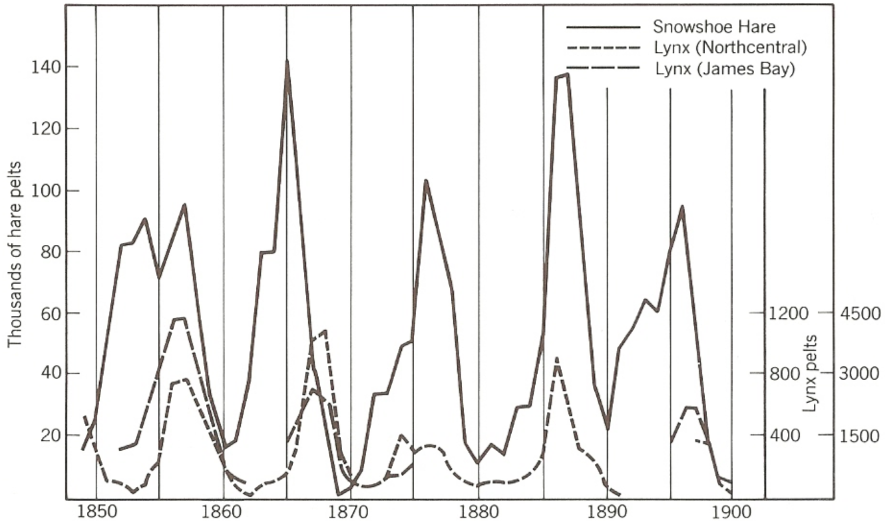


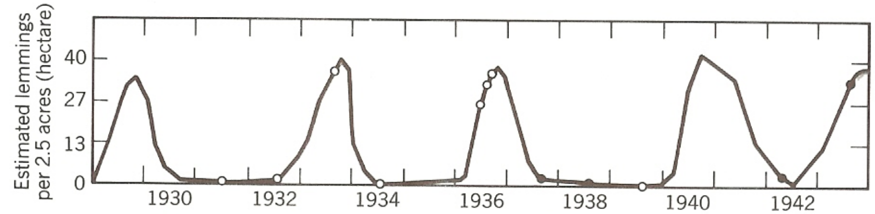


Figure 13.5 Lemming cycles in northern Manitoba. Data are from field censuses by Shelford. (From Finerty, 1980.)

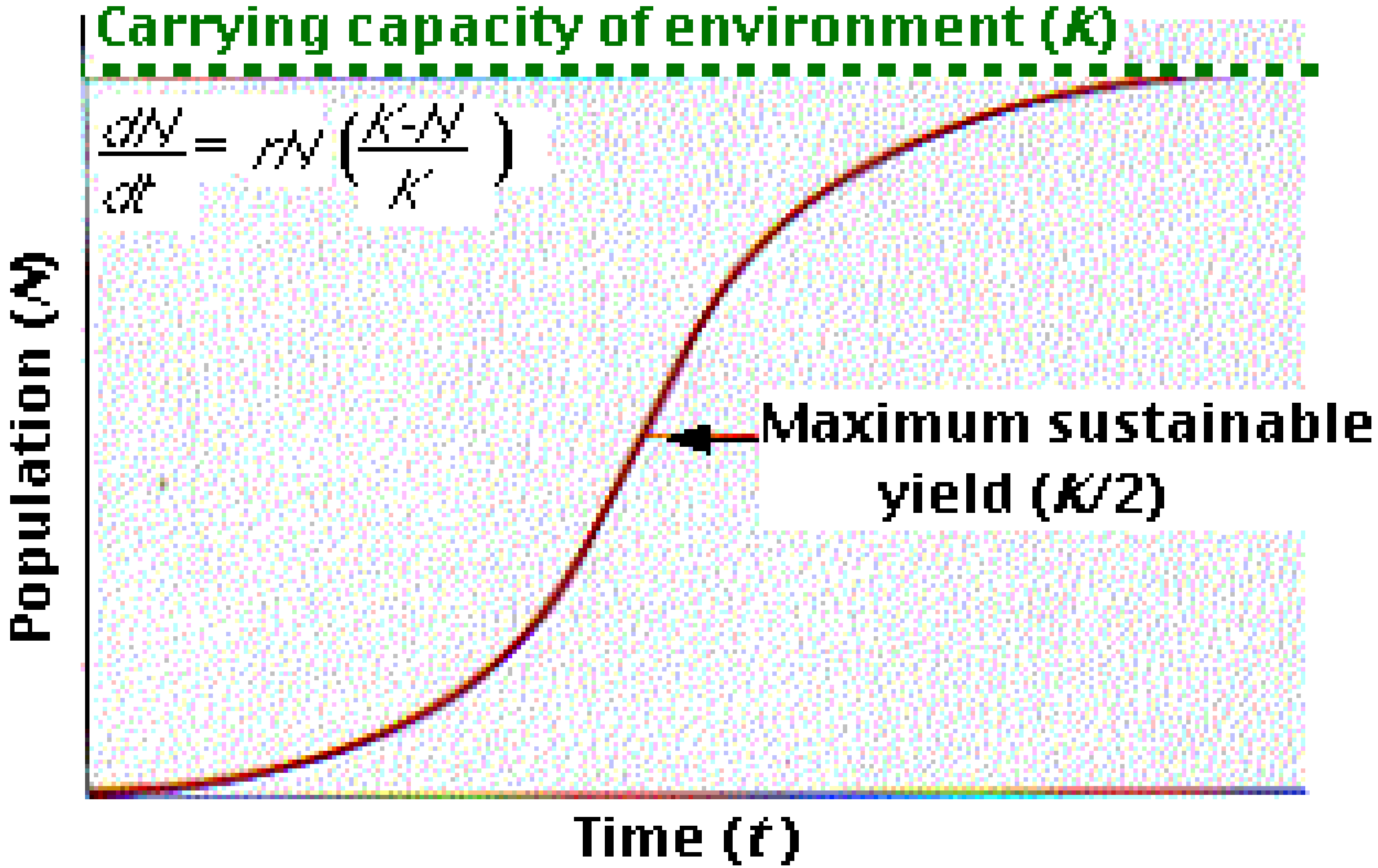
Ecology – Regulation, Fluctuations and Metapopulations

The Influence of Density on Population Growth and Consideration of Geographic Structure in Populations

Predictions of Logistic Growth

- The reality of nature dictates that organisms **will not (and cannot)** exhibit exponential for extended periods of time
- That is, $dN/dt=0$ at $N=K$ (remember the environmental resistance to growth)
- This is Logistic Population Growth

Graphically, this is logistic growth



Logistic Growth = Pop Regulation?

- Regulation of populations can be viewed from two very different perspectives; *density-dependent* and *density-independent*
- What sorts of things are we talking about with the density-dependent regulation?
- What about density-independent?

Density dependence

- Evaluating density-dependent population regulation, we are explicitly predicting that the greater the density, the greater the limiting influence that is exerted on the population growth rate
- What are density-dependent factors that limit the population size of a group of organisms?

Factors

- Resource availability, the feature predicted by Malthus, lack of resources to support the growing population
- What else? As density increases in a population, **you** are easier to find. Therefore predation pressure increases
- But also, disease and parasite effects
- And certainly waste accumulation (our fate?)

Look at the potential reproductive output based on habitat suitability

TABLE 16-1 Reproductive parameters of white-tailed deer (*Odocoileus virginianus*) in five regions of New York State, 1939–1949

Region*	Percentage of females pregnant	Embryos per female	Corpora lutea per ovary
Western (best range)	94	1.71	1.97
Catskill periphery	92	1.48	1.72
Catskill central	87	1.37	1.72
Adirondack periphery	86	1.29	1.71
Adirondack center (worst range)	79	1.06	1.11

**Arranged by decreasing suitability of range.*
(From Chaetum and Severinghaus 1950.)

Another exhibition of density effects, this time in a modified state

TABLE 16-2 Reproductive parameters of white-tailed deer (*Odocoileus virginianus*) in the DeBar Mountain area of the Adirondack Mountains of New York State before and after hunting

	Percentage of females pregnant	Embryos per female	Corpora lutea per ovary
1939–1943 (prehunting)	57	0.71	0.60
1947 (after heavy hunting)	100	1.78	1.86

(From Chaetum and Severinghaus 1950.)

And we see it in plants too!

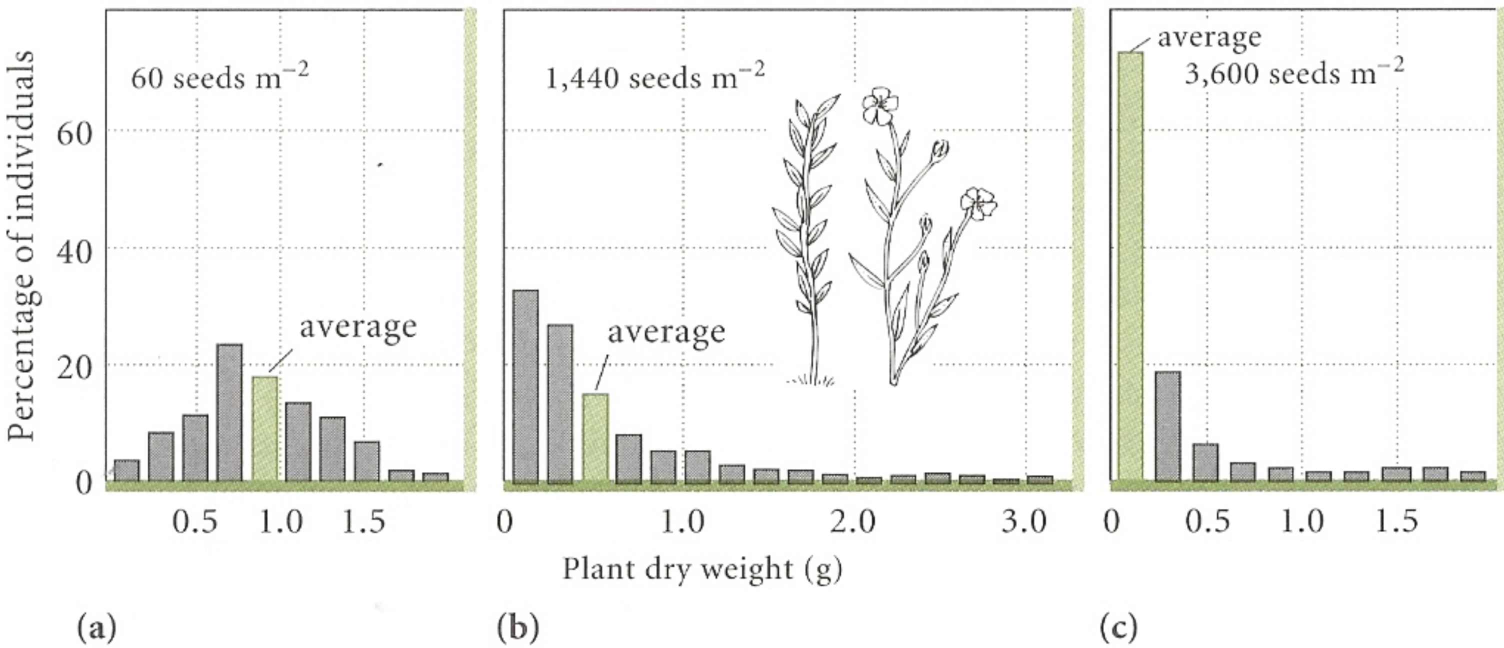


FIGURE 16-12 Distribution of dry weights of individuals in populations of flax (*Linum*) plants at a low density (a) and at two high densities (b and c). (*After Harper 1967.*)

Additional Effects of Density

- The density of individuals influences much more than the population growth patterns
- For example, as density increases, we see population specific breeding systems, social systems, etc.
- Density also influences movements of organisms and the distribution in space, for example, *ideal free distributions* (we will deal with this more later, but recall yesterday…)

What about density independence?

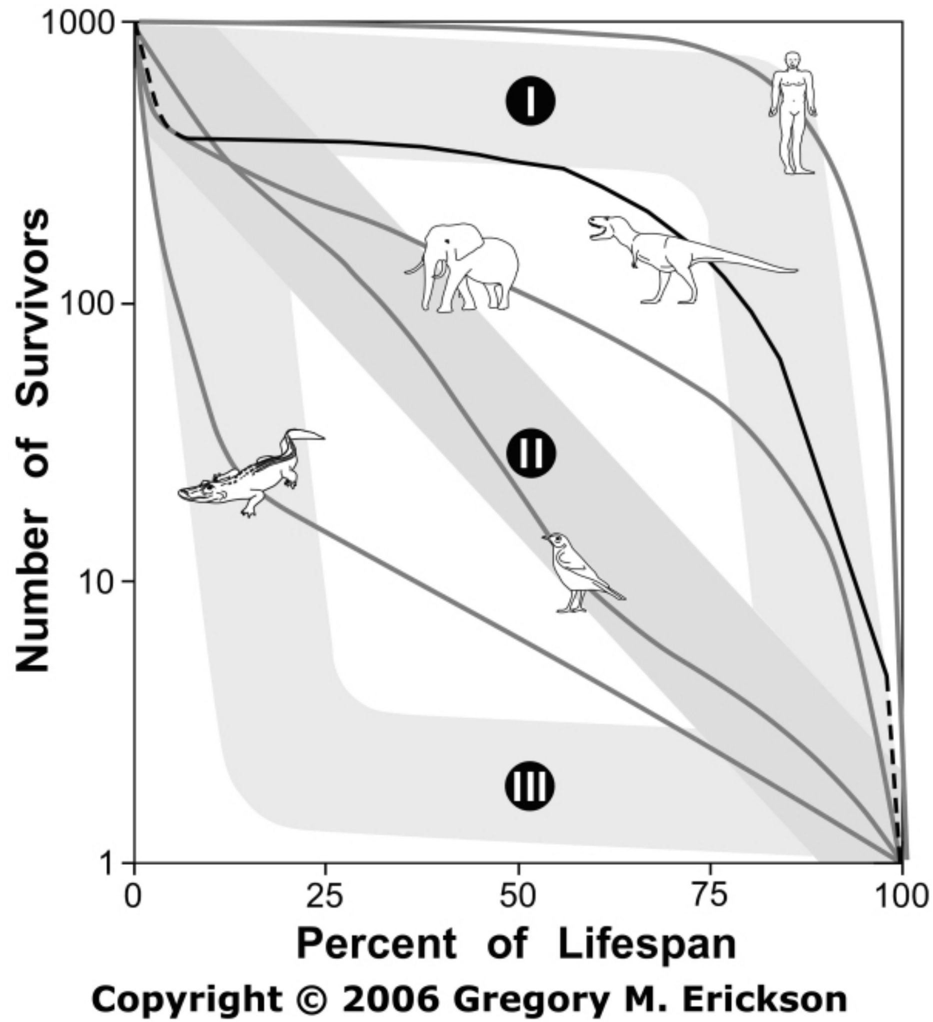
- Density-independent factors is regulation the density of the population without regard to the density level
- Regulation of the size of the population is, for the most part, a random process
- That is, just luck!

What sorts of features could be considered density-independent?

- It must be the environment
- Random environmental events are the typical factors associated with this unpredictable influences
- Natural disasters, typhoons, hurricanes, fires, etc. could all be considered random events, and not density-dependent

Reproductive Strategies

- Let us revisit the general types of reproductive strategies that we can identify



Let us compare Types I and III with regard to several characteristics

- Life span
- Stability of environment
- Onset of reproduction
- Number of reproductive events/lifetime
- Generation time
- Number of offspring
- Parental investment per offspring
- Factors that regulate population size
- Dispersal/colonizing ability

One more note on densities…

- Our model and qualitative treatment of this phenomenon may be an over-simplification of most situations
- There is stochasticity in both environmental factors and in demographic characteristics that often cause population sizes to vary widely

This is Density Vagueness

- Random effects of population characteristics are sometimes of greater significance than effects of the normal density-dependent variety
- This has resulted in the proposal by some that our models that point to self-regulation as the norm, may be the *exception* and not the rule

Fluctuations in Natural Populations – However, we still see patterns…

A struggle for existence inevitably follows from the high rate at which all organic beings tend to increase. Every being, which during its natural lifetime produces several eggs or seeds, must suffer destruction during some period of its life, and during some season or occasional year, otherwise, on the principle of geometrical increase, its numbers would quickly become so inordinately great that no country could support the product. Hence, as more individuals are produced than can possibly survive, there must in every case be a struggle for existence, either one individual with another of the same species, or with the individuals of distinct species, or with the physical conditions of life.

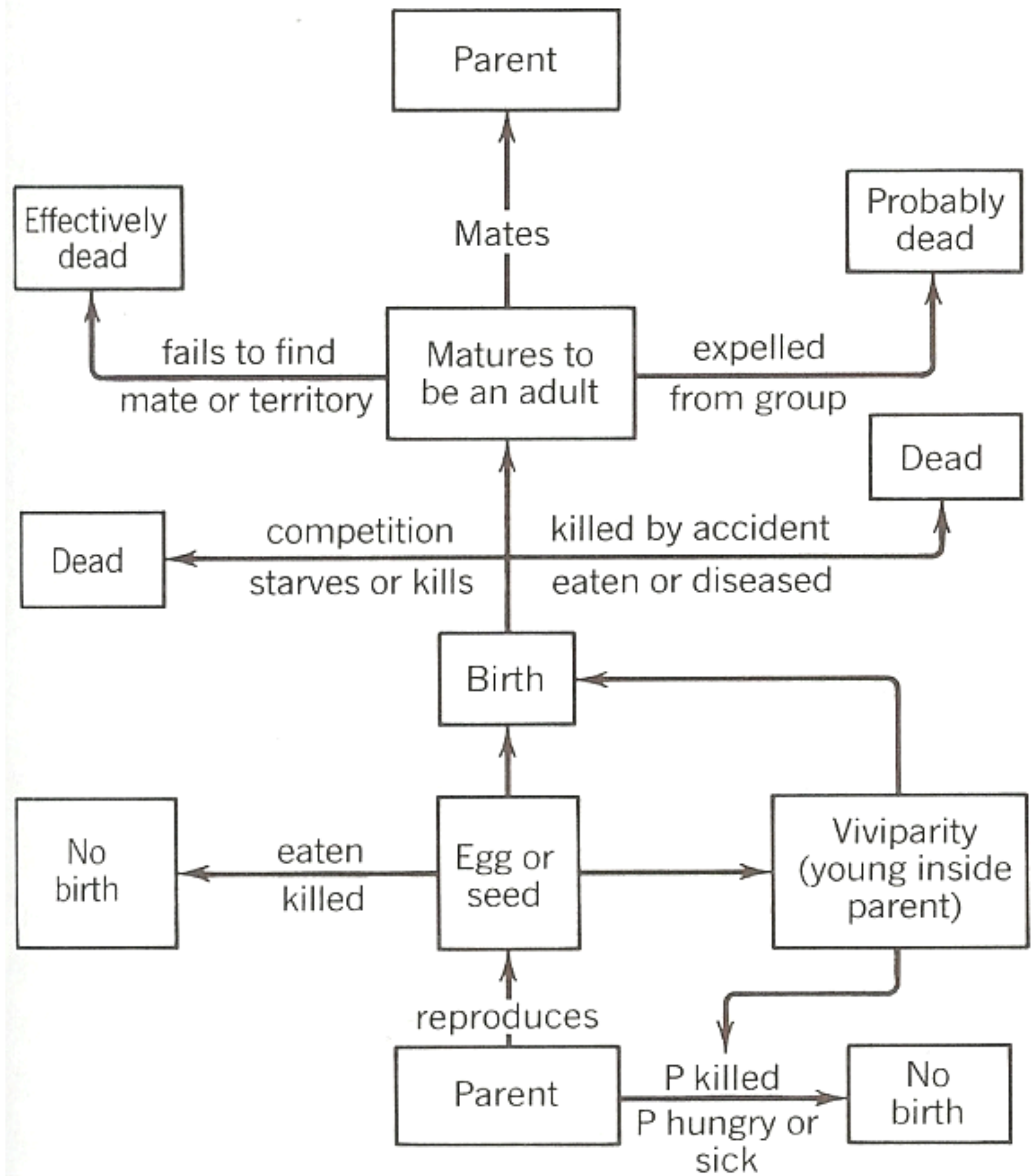
Charles Darwin from *The Origin of Species*

Population Regulation

- Darwin's proposal of the survival of organisms translates into the death of individuals not capable of surviving (talk about the negative view of things!)
- Those features that may come into play:
  - Starvation (lack of food resources)
  - Malnutrition (limited essential nutrients)
  - Predation
  - Parasites or Disease
  - Environmental Stochasticity

Density dependent factors (bracketing: Starvation, Malnutrition, Predation, Parasites or Disease)

This is the parent-to-parent cycle. At any point in this cycle, there is the potential for loss of life. Many of these features are extrinsic, including the effects of environmental variation and fluctuations. But there is also the potential for intrinsic regulation



Predation as the determining factor?

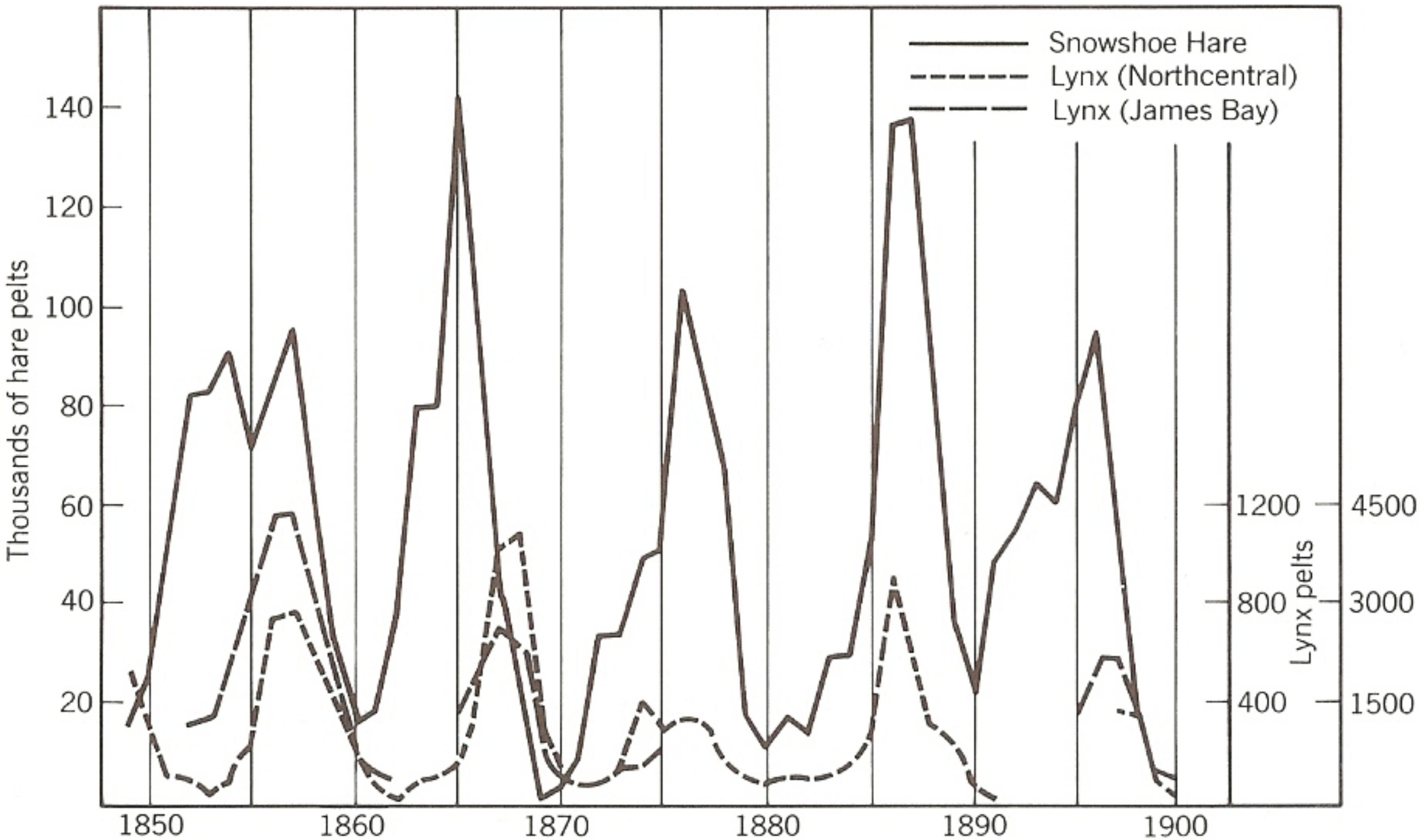


Figure 13.4 Relationship of hare and lynx populations in the Canadian arctic. Data are from sales records of traders dealing in both hare (*Lepus americanus*) and lynx (*Lynx canadensis*) skins. Lynx records are from two nearby trapping regions. The data show not only that the populations are linked but that numbers of the predator follow numbers of the prey. (From Finerty, 1980.)

The Hare and the Lynx

- The explanation is obvious – predators over-consumed prey causing a crash in the prey with a subsequent crash in the predator populations, then cycling
- This was "***proof***" of something called the **coupled oscillation hypotheses** of the Lotka-Volterra predator-prey system – where each are interdependent upon the other with respect to population sizes…

Observations of other systems

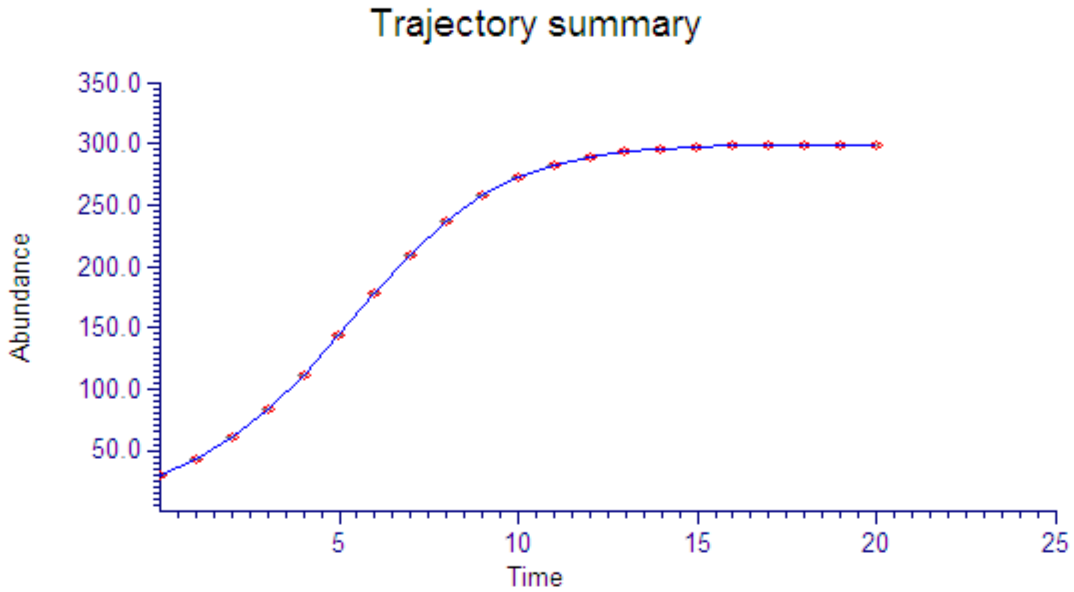
- However, evidence was accumulating suggesting that this was not a simple relationship
- Predators may indeed be dependent on the prey population size (we know that from a food standpoint), **but** where predation pressures are low, prey still exhibit fluctuations - ***oops***
- Something else is going on with the prey, either environmental or some other biological factor

Generalizations and Life Histories

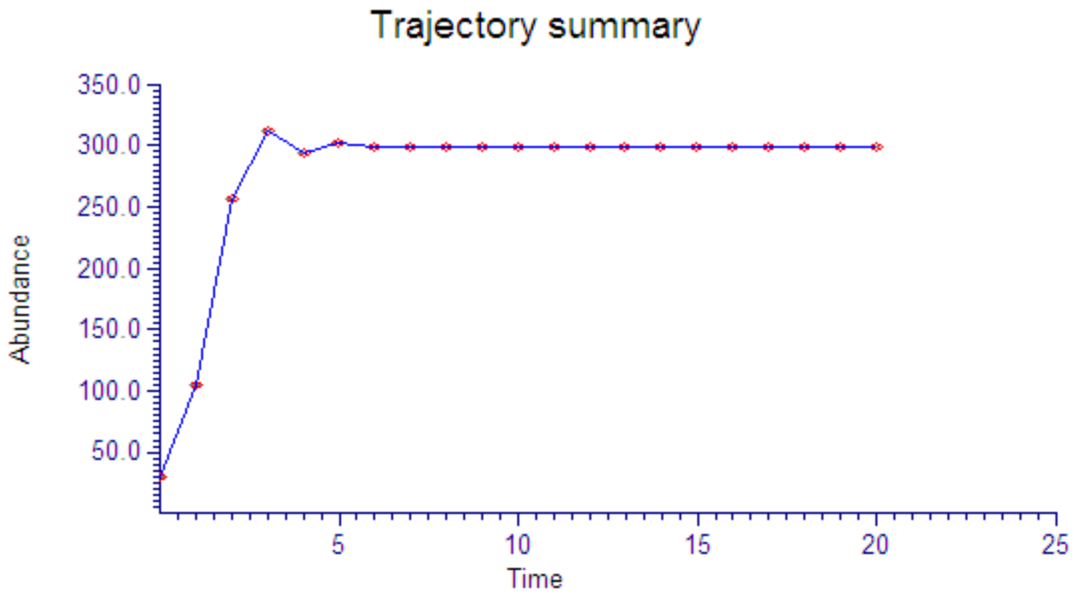
- Observation and measurements of natural populations suggest *some* generalizations of these cycles based upon life history patterns
- For example, short-lived, small forms that exhibit *high turnover rates* tend to fluctuate widely in nature

Contribution of Growth Rate?

- Here we are specifically addressing the issue of the magnitude of ***r***
- What did we note before regarding the magnitude of this variable?
- What growth patterns do we see in populations that exhibit a large ***r*** vs. populations that are characterized by a small ***r***?



r=1.5 compared to r=4.0



This allows more rapid tracking

- When ***r*** is large, variation in the conditions that regulate the population size are more closely ***tracked*** by these populations than when ***r*** is small
- Additionally, the response tends to "over-do" the response of the population, just as we observed in the models of logistic growth

Oscillations may also be a by-product of time delays in responses

- The birth and death rates do not, and realistically cannot respond instantaneously to changes in the environment
- Regardless of the nature of the changes, there is a delay in the response of the production of young, or death of individuals with limitations in resources

So, what does it all mean?

- We have considered features such as:
  - Life span
  - Age structure
  - The magnitude of ***r***
  - The time delay.
- Is that all? (I am not trying to be funny)
- Not in the least!

Consider environmental changes

- Our consideration of the modeling is dependent upon some sort of predictability
- Observational data of some of the most spectacular cyclical species *suggest* predictable patterns of variation

Table 13.1
Arctic Animals for Which 4-Year and 10-Year Cycles Have Been Demonstrated
For each cycle an array of predators specialize on the cycling numbers of the primary rodent prey. (From Finerty, 1980.)

	Lagomorpha	Rodentia	Carnivora		
Cycle	Leporidae	Muridae	Canidae	Mustelidae	Felidae
4-year	*Lemmus* *Dicrostonyx* spp.	*Alopex lagopus* *Vulpes* spp.	*Martes americana* (?)		
10-year	*Lepus americana*	*Ondatra zibethica*	*Alopex lagopus* *Vulpes* spp. *Canis latrans*	*Martes americana* *Martes pennanti* *Mustela vison*	*Lynx canadensis*

What is the importance of environmental stochasticity?

- Historical data regarding environmental variables suggest that predictability is not possible with any level of accuracy
- The evidence further suggests that these processes approach a random pattern
- So how do we model that in any predictable fashion? Look at another graph

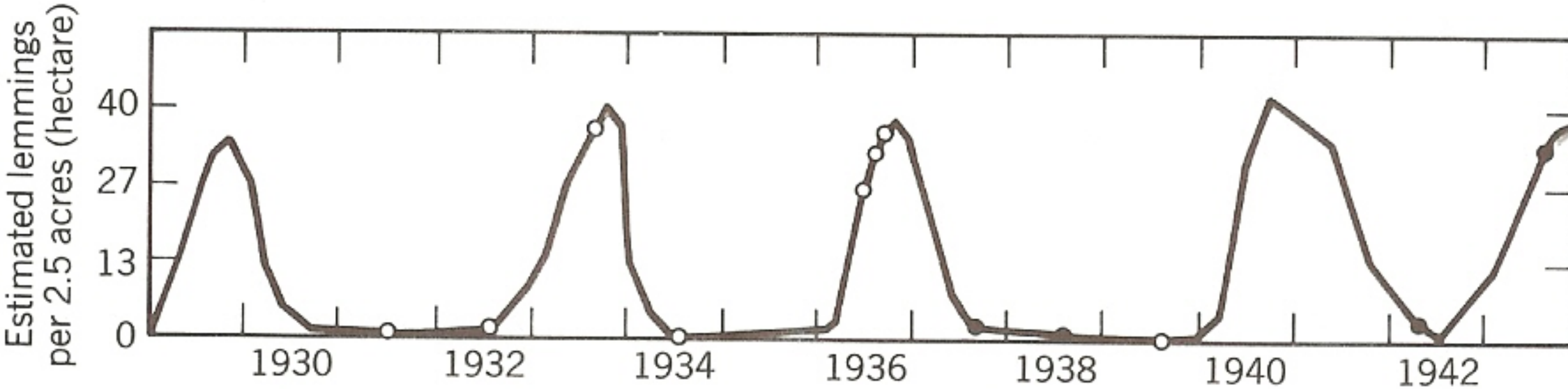


Figure 13.5 Lemming cycles in northern Manitoba. Data are from field censuses by Shelford. (From Finerty, 1980.)

And the answer is…

- The questions still exist
- The coupled oscillation hypotheses tend to be accurate with regard to one of the species (or the species of a particular trophic level)
- But it does not explain the coupled aspect
- Similarly, patchy distribution of habitats may help explain part of the observations
- The seemingly regular periodicity may be telling us something completely different and remains to be studied in terms of the biological rhythms that are being displayed by these creatures

Break Time

The Metapopulation Concept

- Metapopulations are collections of localized groups of individuals of the same species (a.k.a. localized populations)
- A more convenient way of thinking about these groups is a “population of populations”
- This is a growing movement in Ecology to look at a more inclusive view of a species

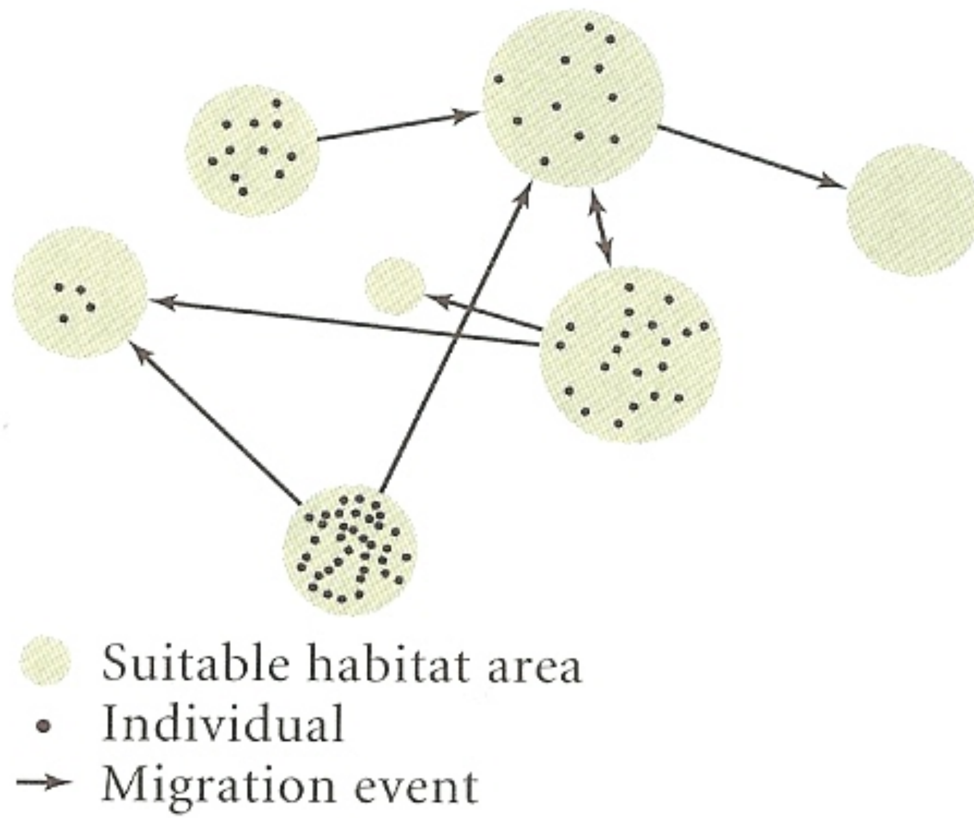


FIGURE 17-1 A metapopulation can be portrayed as a set of discrete local populations with partially independent local population dynamics. At any one time, some patches of suitable habitat may be occupied while others are not. Individuals may migrate from occupied patches to colonize unoccupied patches.

The basic issues

- Many, if not most, resources are not equally or even randomly distributed in the environment,
- These patches are occupied by the individuals creating isolated local populations in space
- These are not necessarily completely isolated, but may communicate via gene flow with one another by migration among the subpopulations

Foundations of Metapopulations

- The original proposal of work regarding subdivided populations looks *very* similar to other models – any ideas?
- The MacArthur and Wilson model of species on islands is nearly identical in the parameters that are important for this model

Components of the Model

- This distribution pattern presents some biological realities
- Can you think of any?
- **Can you think of any issues associated with small populations that are isolated from other such populations?**
- What happens when there is open habitat?

Extinctions and Colonization

- Particularly in small populations, these entities are subject to stochasticity of intrinsic and extrinsic factors that may ultimately lead to population extinction
- If migration is possible, there is also the potential for colonization of empty habitats, or simply gene flow among subpopulations

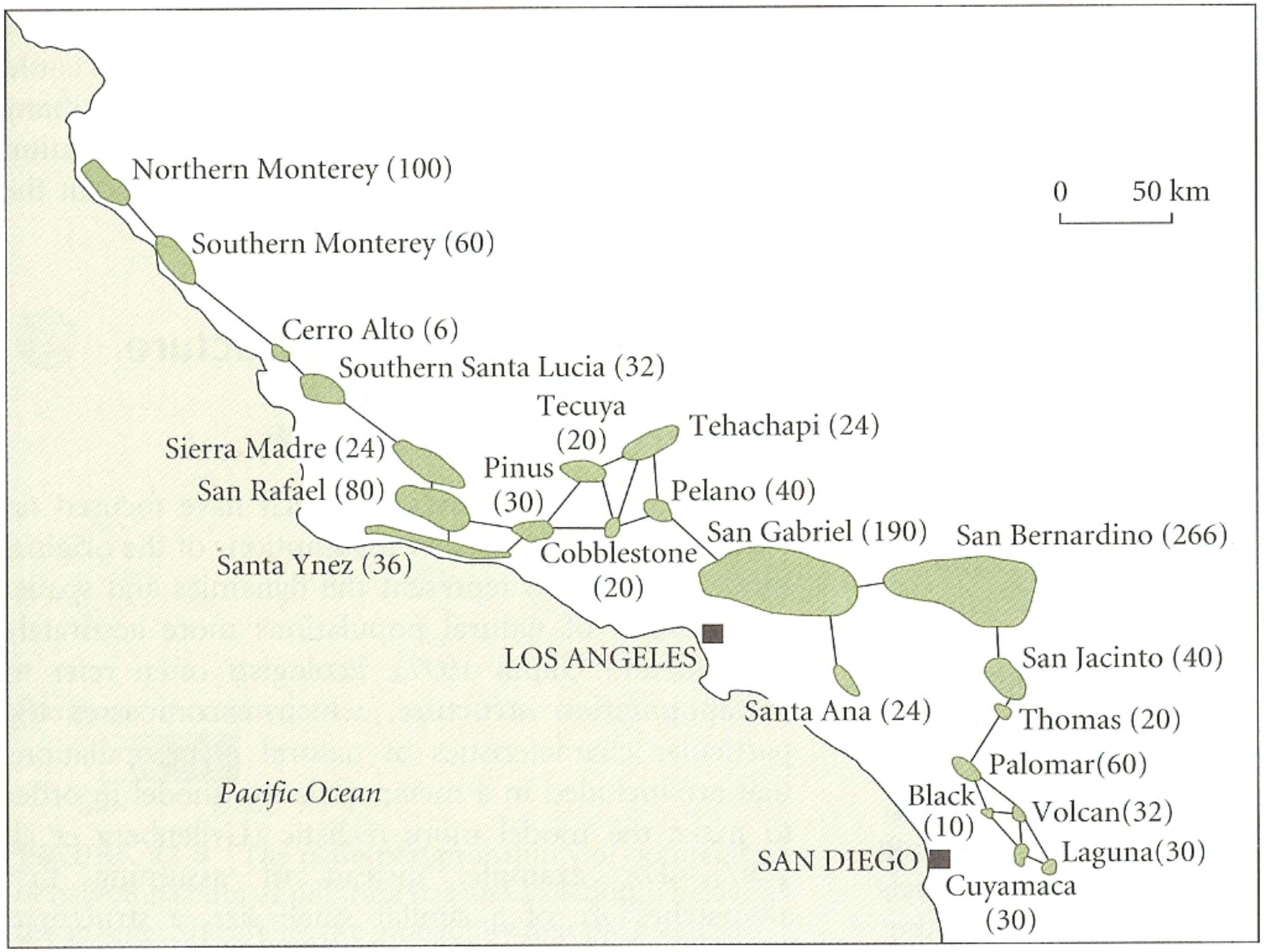


FIGURE 17-2 Metapopulation of the Southern California spotted owl in the San Bernardino Mountains. The numbers given in parentheses represent estimated carrying capacities for each patch. (*From Lahaye et al. 1994.*)

The balance between extinctions and recolonization events

- Parameters:
  - *p* represents the number of patches occupied and 1 – *p* the number empty
- The rate of change in the number of occupied patches, *p,* will be:

$$\frac{dp}{dt} = mp(1 - p) - ep,$$

Predictions of the model

- The equilibrium condition is $dp/dt = 0$
- The equilibrium p will be given by $1 - e/m$
- The assumption is that the colonization rate m will be greater than the extinction rate e (otherwise p will = 0)

Patch size and density

- Average size in area of the patches *should* influence the number of patches occupied, and
- Density of patches *should* influence the number of patches that are occupied
- Why would we expect these two characteristics to contribute to occupation?

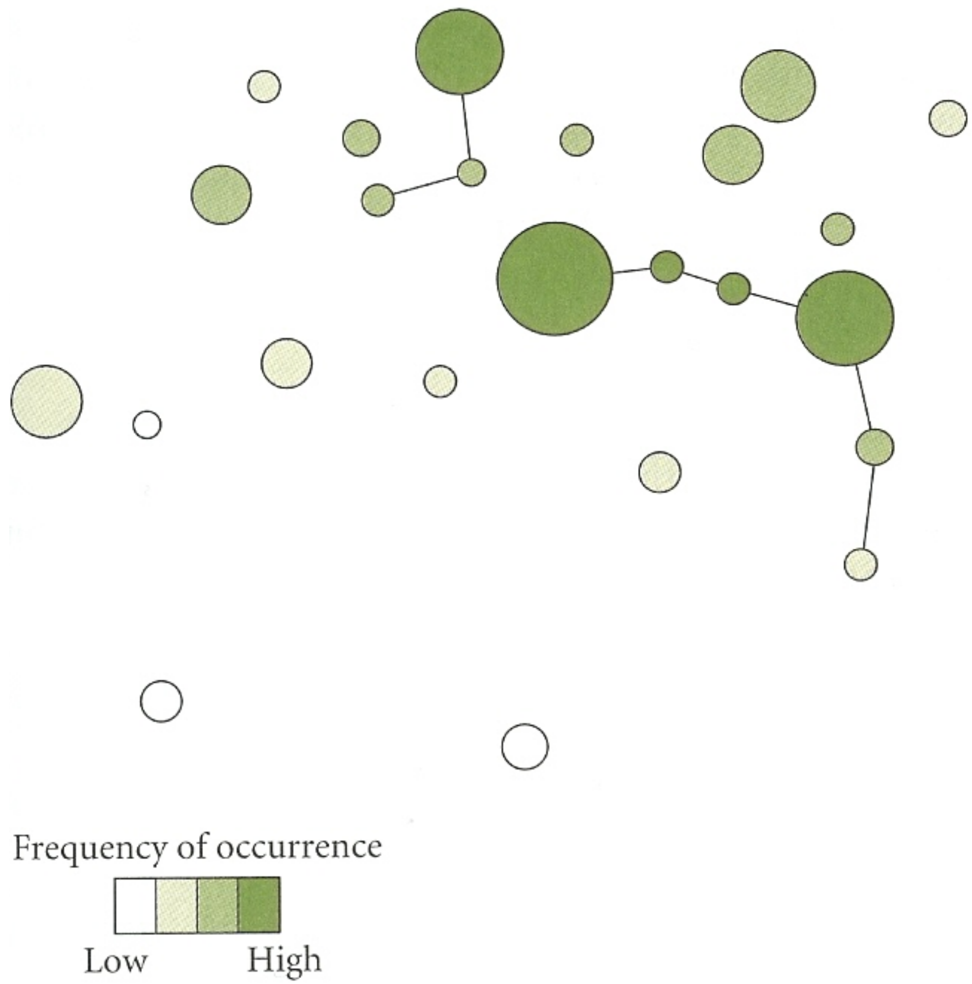


FIGURE 17-3 The pattern of probability of occupancy of habitat patches of differing size and isolation. The darker the shading, the higher the probability that the patch will be occupied. In general, large patches and patches that are close to another population have a higher probability of being occupied than those that are small and isolated. (*From Opdam 1991.*)

Now, some real data

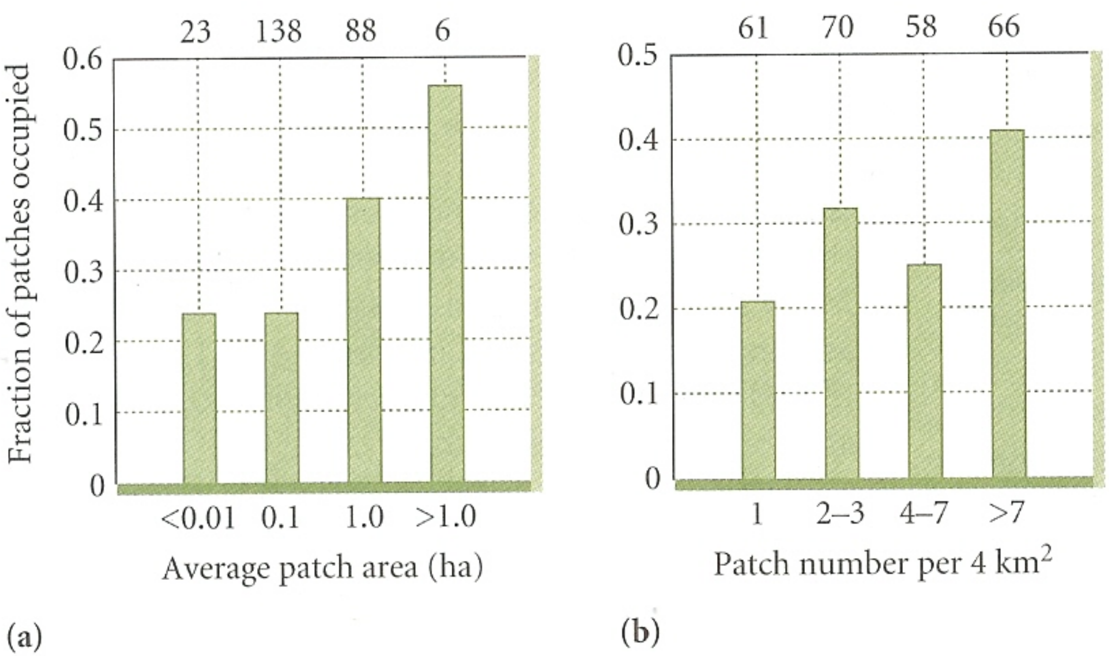


FIGURE 17-4 (a) Effect of patch area on the fraction of patches occupied in a metapopulation of the Glanville fritillary butterfly (*Melitaea cinxia*). The proportion of occupied patches was higher for large patches. (b) Effect of the density of patches. The proportion of occupied patches was highest for areas with the highest density of patches. (*From Hanski et al. 1995.*)

Different types of models

- The **Source-Sink Metapopulation** model categorizes populations in terms of their growth characteristics:
  - Source populations grow at low densities
  - Sink populations decline w/o immigration
- The **Mainland-Island Metapopulations** model depicts a series of small patches located near a single large patch (similar to a model you have seen before)

Let us return to the model

- Let us go back to our consideration of *m*
- Colonization rate *will* be a function of the distance between patches, that is intuitive
- Similarly, the extinction rate *e* will depend on the size of the habitat patches
- This is not necessarily intuitive, but logical
  – Why?

The relationship between *m* and D

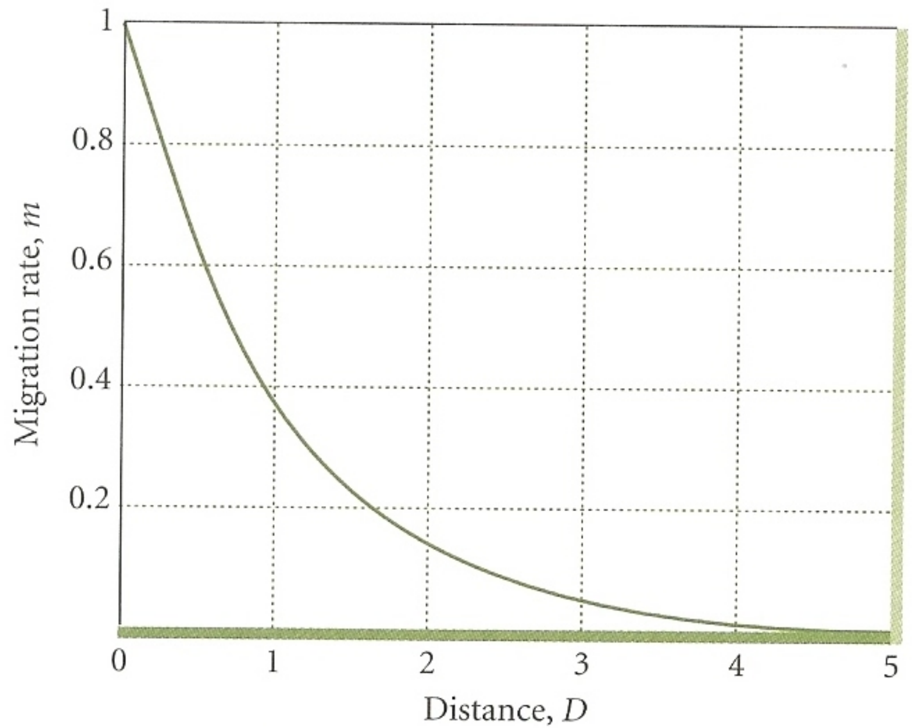


FIGURE 17-5 Negative exponential relationship between migration rate, m, and distance of patch isolation, D ($m = m_0e^{-aD}$, where m_0 and a are parameters). The relationship between extinction rate, e, and patch area, A ($e = e_0e^{-bA}$, where e_0 and b are parameters) will have the same shape.

The dynamic nature of occupancy

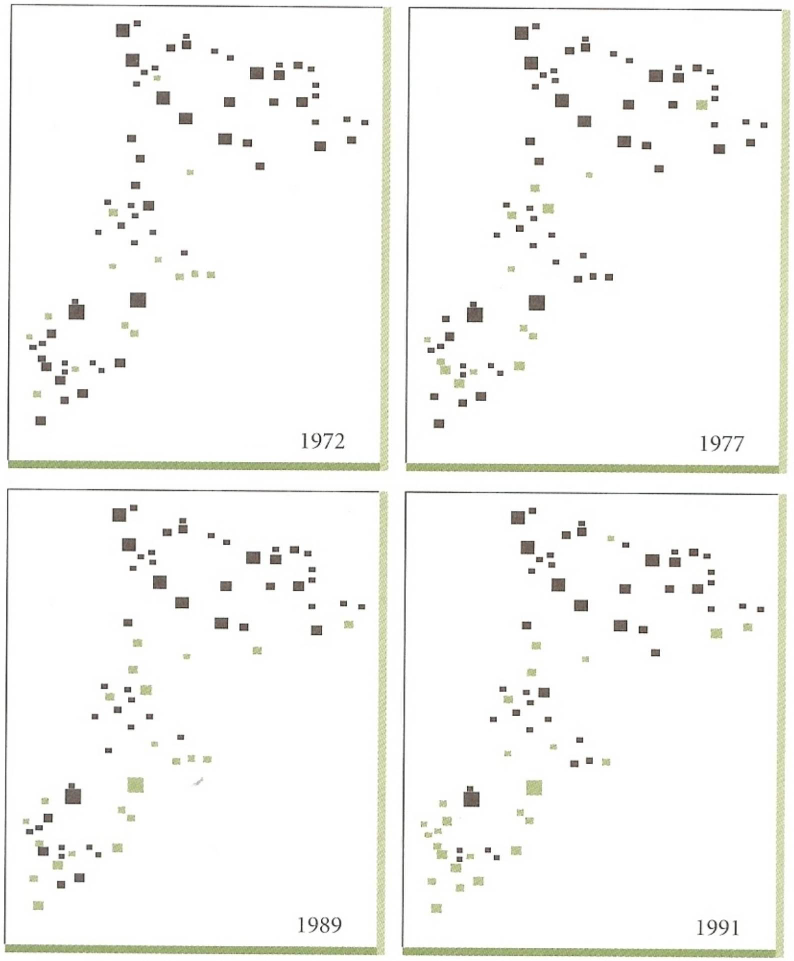


FIGURE 17-8 Occupied (black) and unoccupied (green) patches in the American pika (*Ochotona princeps*) metapopulation near Bodie, California. The size of each square is proportional to its carrying capacity. The figure shows a decrease in the proportion of occupied patches in 1989 and 1991, with more extinctions in the southern portion of the metapopulation range. (*From Smith and Gilpin 1997.*)

The previous example is stable?

- The variability of the patches inhabited and the densities of the patches that are inhabited can change through time

TABLE 17-1 Census data for a metapopulation of American pika (*Ochotona princeps*) near Bodie, California

	Census year			
	1972	1977	1989	1991
Average size of occupied patch (perimeter, m)	96.0	90.5	96.9	85.9
Average interpatch distance (m)	101.5	110.1	102.6	193.4
Number of patches censused	78	78	77	78
Percentage of patches occupied	60.3	57.7	44.2	43.6

(Data from Smith and Gilpin 1997.)

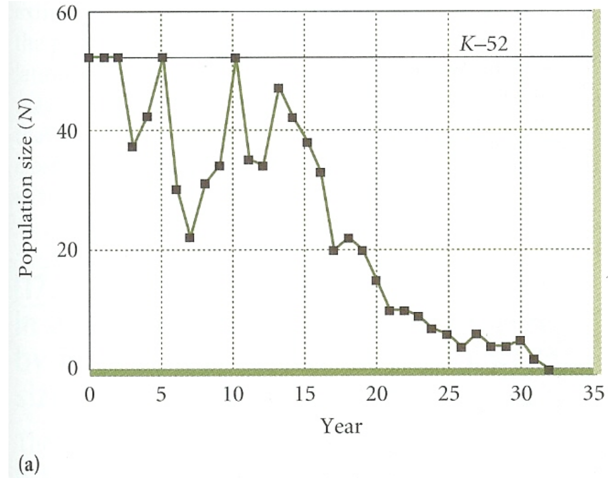
Variation can be extreme

- At least in part, stochasticity may impact a population, but there are internal factors influencing population survivorship
- Remember back to population fluctuations?
- What is at the heart of population fluctuations in real biological terms?

Let us look at *m* more closely

- With our evaluation of *m* and distance is that the closer patches are to one another, the more likely they will be occupied
- There is more. *m* can be thought of as not just a value of colonization or recolonization, but a value for migration between or among patches

Where populations are completely isolated, particularly small populations, the fate will be extinction, and there is very little debate about that fact. The other issue here is that even with low rates of immigration, populations tend **not** to go extinct, a phenomenon called the **rescue effect**.



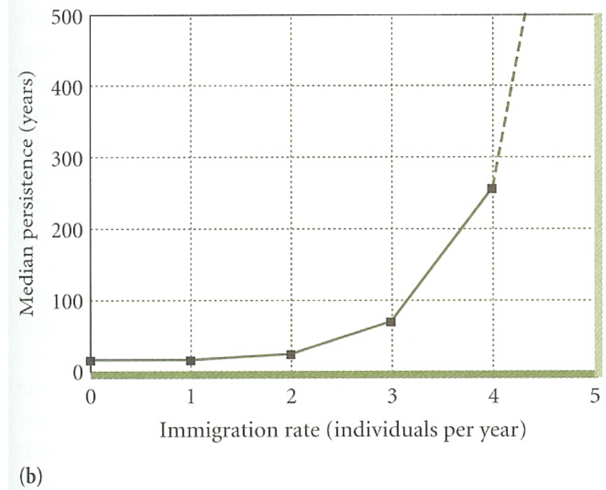


FIGURE 17-11 Results of a simulation of population size in a population of acorn woodpeckers (*Melanerpes formicivorus*) in central New Mexico. Demographic parameters from previous studies were used to construct the simulation. (a) Projected population trend if it is assumed that the population receives no migrants. (b) The number of years that the population is expected to persist at different migration rates. These figures show that even a small amount of migration will rescue the population from extinction. (*From Stacey et al. 1997.*)

There is still more going on here

- What is it about small populations that make them more susceptible to extinctions than large populations?

There is still more going on here

- What is it about small populations that make them more susceptible to extinctions than large populations?
- Well, I can think of two:
  - One issue is potential density-independent events that takes members of the population
  - What is another?

The bottom line is heterozygosity

- That is, variability
- This is not just some theory of survivorship pattern as predicted by models, this is a real phenomenon
- The considerations here are not just limited to the level of heterozygosity (but let us consider this aspect)

Local extinctions are anticipated and the recolonization events yield a loss of genetic variability in the cycling of these metapopulations. What does this model predict with regard to the long-term survival of a geographically subdivided species?

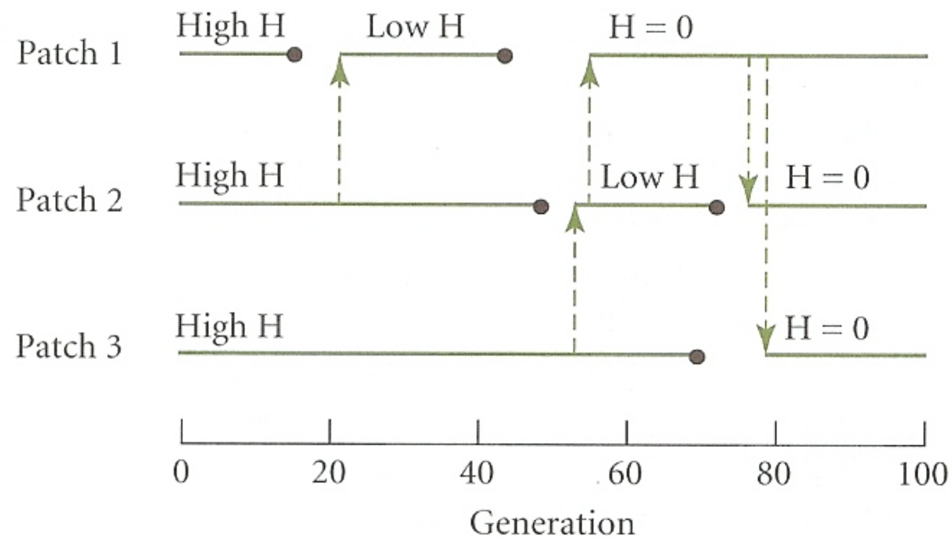


FIGURE 17-14 A metapopulation having three patches, each initially with high levels of heterozygosity (H), may lose genetic diversity by repeated recolonization of extinct patches. Extinction events are noted as breaks in the green line; recolonization with vertical arrows. The population in patch 1 goes extinct in generation 18 and is recolonized in generation 20 by individuals from patch 2. Because the recolonization involves only a few individuals, the level of heterozygosity in patch 1 is reduced. A similar event occurs in patch 2 around generation 47. A second extinction and recolonization event occurs in patch 1 between generations 40 and 60. Because of the reduced genetic variation of the colonizers from patch 2, the level of heterozygosity in patch 1 becomes 0. Subsequent recolonization events in which patch 1 (H = 0) serves as the source population result in a metapopulation having no genetic variation. (*From Hedrick and Gilpin 1997.*)

Are subdivided populations always negative for the group as a whole?

- Most of our discussion has focused on the extinction and recolonization and the limitations and, and, and
- Beyond the simplistic consideration of the single species, look at the potential interspecific relationship and how that might influence the species under consideration

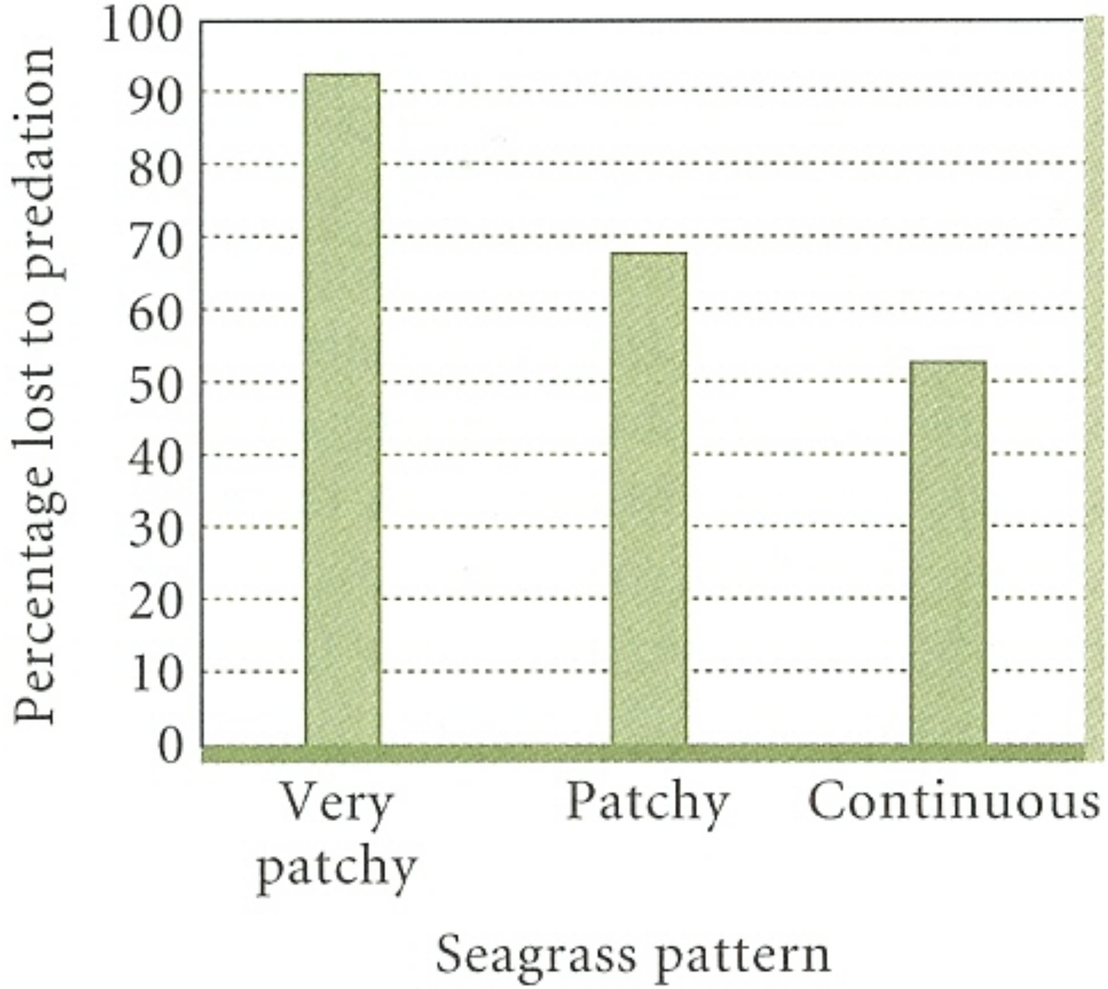


FIGURE 17-15 Rates of predation over a 4-week period on juvenile scallops placed in continuous seagrass habitat and in areas of seagrass with two levels of patchiness. (*From Irlandi et al. 1995.*)

In this case of predation, yes it is!

- Habitat patches and the coincident occurrence of edges allow greater access of the predators to the interior of patches
- With continuously distributed habitats, the edge effects are minimized and there is substantially higher survivorship among the juvenile forms in this situation

What about competition?

- When we add the potential effects of competitors, we need to look at the **coincident occurrence** of the competitor, and the same sorts of distributional issues it is facing
- It is facing local extinctions and recolonizations
- This ***may*** **facilitate** the survival of inferior competitors in isolated patches that would otherwise be excluded by a superior competitor

How do we evaluate features?

- How can we assess the degree of connectedness among populations?
- How can we assess the sizes of the localized populations?
- How can we evaluate boundaries or movement among local populations?

Genetic Differentiation

- Isolation leads to differentiation in genetic characteristics and we can use molecular tools to evaluate the amount of differentiation among forms
- This can be used to evaluate levels of gene flow among these isolated populations and the predicted rate of movement among these entities