



# Population Principles – Malthus and natural populations (TSC 220)

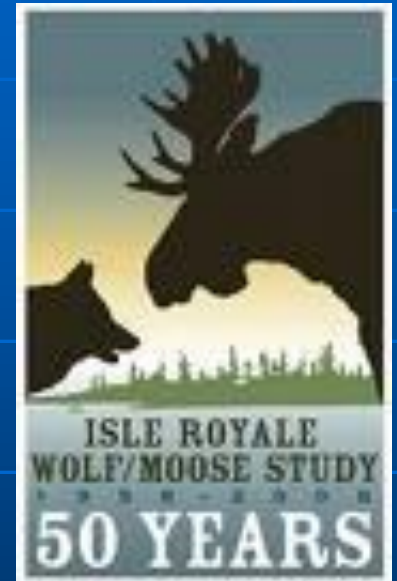
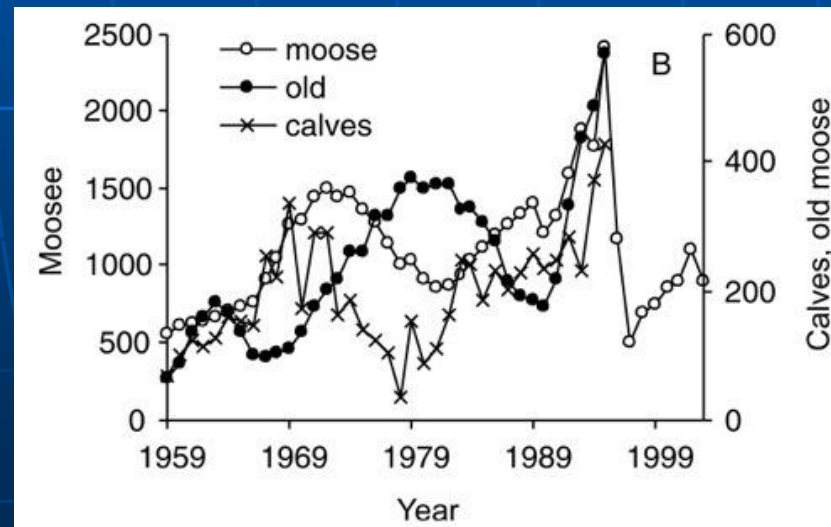
# Definitions

**Population** – individuals of the same species in a defined area

Examples:

- a wildlife ecologist might study the moose and wolves on Isle Royale
- a human demographer might study the individuals in a village in Africa
- or attempt to census the population of the USA on April 1st!

To study populations, we note of the importance of **geographic boundary** that defines the population and the implied emphasis on the **time dynamics**



# Historical perspective

**Demography** – study of vital characteristics of population life cycle traits, i.e. the birth, death and dispersal rates

Human motivation to understand population dynamics and to be aware of numbers in relation to resources extends to ancient times

Egyptians and Babylonians may have conducted a census

King David counted the Israelites in approximately 1000 BC

# Early recognition of potential for explosive population growth

- Giovanni Botero (1588) enunciated that populations ultimately did not grow because resources of the environment were insufficient
- John Graunt (1662) pioneered analytical side of demography with studies of the age-specific mortality of people of London
- Thomas Malthus (1798) drew attention to population growth at a time when England was worried about overpopulation

# Malthus

- **Principle of Population** first published in 1798 in a pre-industrial world; resources were animal and vegetable (i.e. food, clothing) and not mineral (oil, coal)
- Effectively resources were constant or slowly increasing so population growth must be braked by economic constraints on demography
- Articulated that population growth rate is a balance between fertility (**b**) and mortality (**d**) – which we will see in simple models

# Malthus

- If **b** is high then **d** must reach equally high level – living standards severely depressed, Malthus called this the “high pressure or Chinese case”
- In contrast, if **b** and **d** are balanced because **b** responds to deteriorating standard of living and falls to meet **d** before mortality is too high and living conditions have declined then real incomes need only fall modestly
- This latter condition could be described as an early recognition of the goal of sustainability
- Malthus predicted that the world would run out of food supply by the mid 1800's, which has not happened for a host of reasons

# Population Processes: the simplest biological model

The rate of change in a population:

$$\frac{dN}{dt} = rN = (b - d)N$$

In words this equation is:

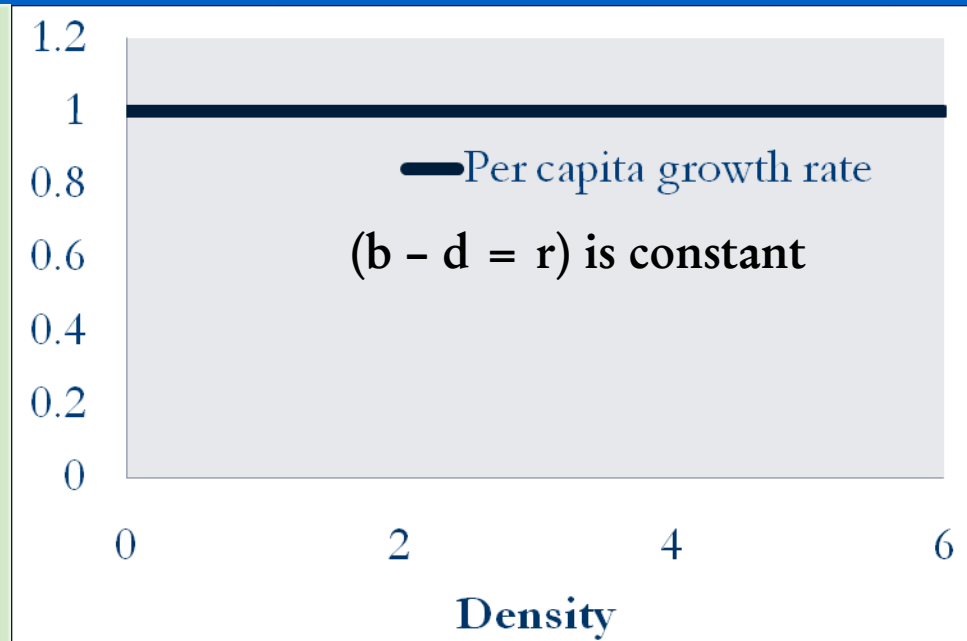
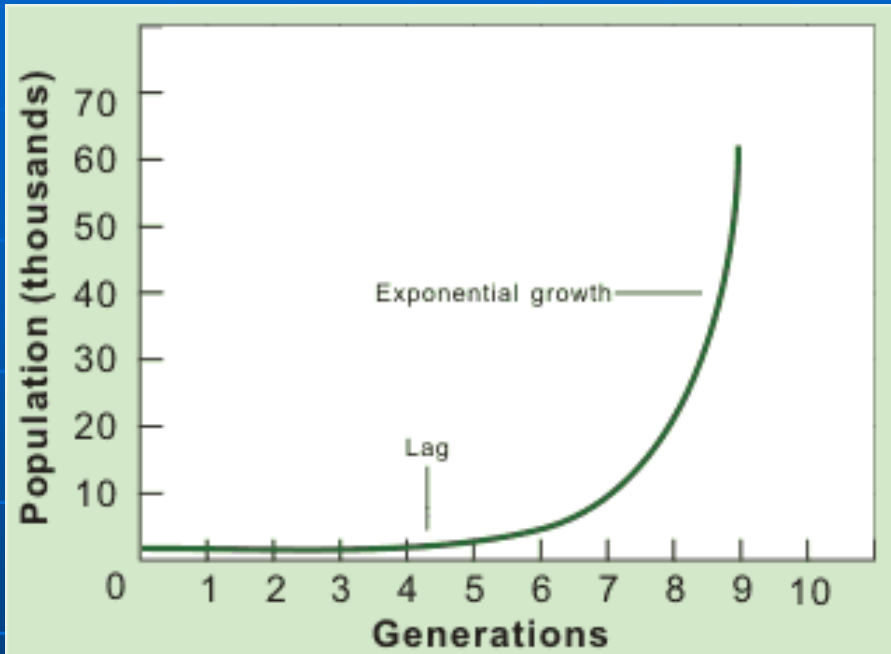
change in N/time = (birth rate - death rate) N

$$\frac{dN}{dt} / N = r$$

Divide through by N to visualize the per capita rate of change which is constant (Density Independent i.e. resources do not limit b or d; **r** is often called the **Malthusian parameter**)



# Exponential Growth



The familiar J-shaped curve of explosive growth

The key biological feature is that the per capita rate of growth is **density independent**

# Estimates of $\underline{r}$ and doubling time

Organism	$\underline{r}$ (indiv./indiv./time)	Doubling time
Bacterium	58.7/day	17 minutes
Protozoan	1.59/day	10.5 hours
Beetle	0.101/day	6.9 days
Brown rat	0.0148/day	46.8 days
Deer	0.26/year ( $\sim 0.0007$ /day)	$\sim 2.7$ years
Blue whale	0.007/year ( $\sim 0.000019$ /day)	$\sim 99$ years
Human (Africa)*	0.024/year ( $\sim 0.000065$ /day)	$\sim 29$ years
Human (North America)*	0.005/year ( $\sim 0.000014$ /year)	$\sim 139$ years

\* Data from Population Reference Bureau

# Population Processes: the logistic model (Pierre-Francois Verhulst 1838)

The rate of change in a population:

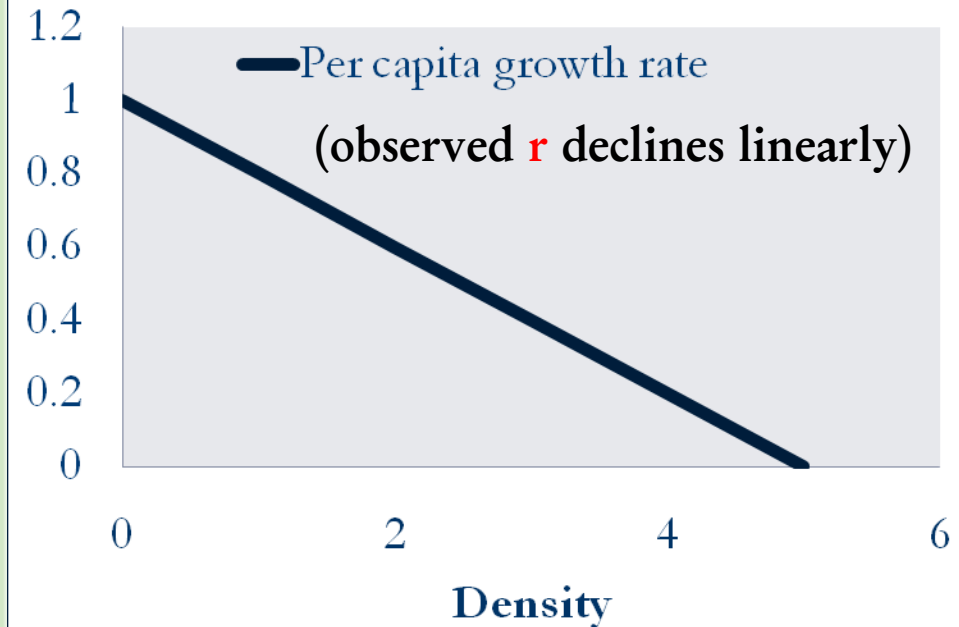
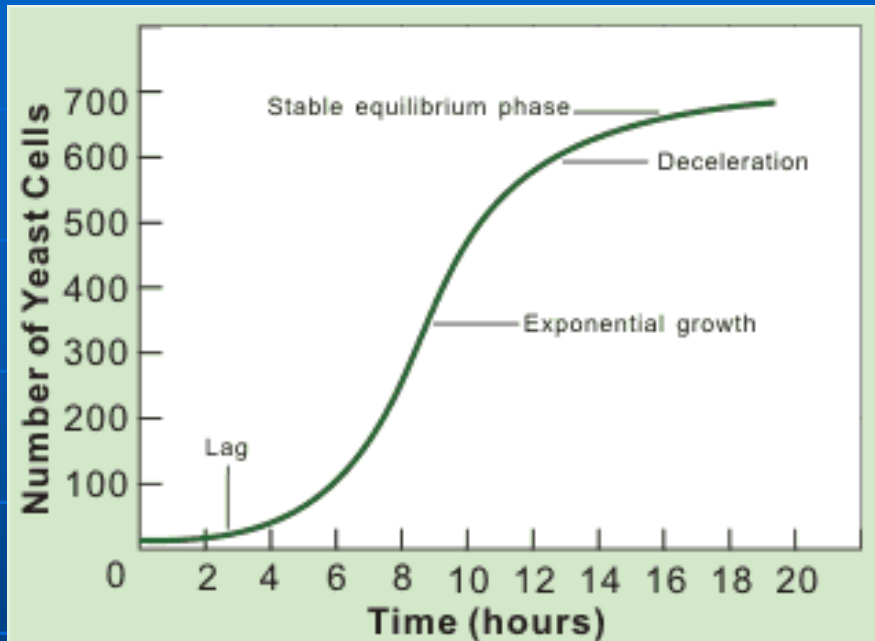
$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

In words this equation is: change in N/time =  
(exponential rate modified by term that quantifies the  
relative ratio of N to K)

$$\frac{dN}{dt} / N = r - \frac{r}{K} N$$

The per capita rate of change declines linearly from a high level when the population is not limited by resources and reaches zero net rate of growth when  $N = K$  ( the population reaches “carrying capacity”); this is Density Dependent i.e. resources limit growth

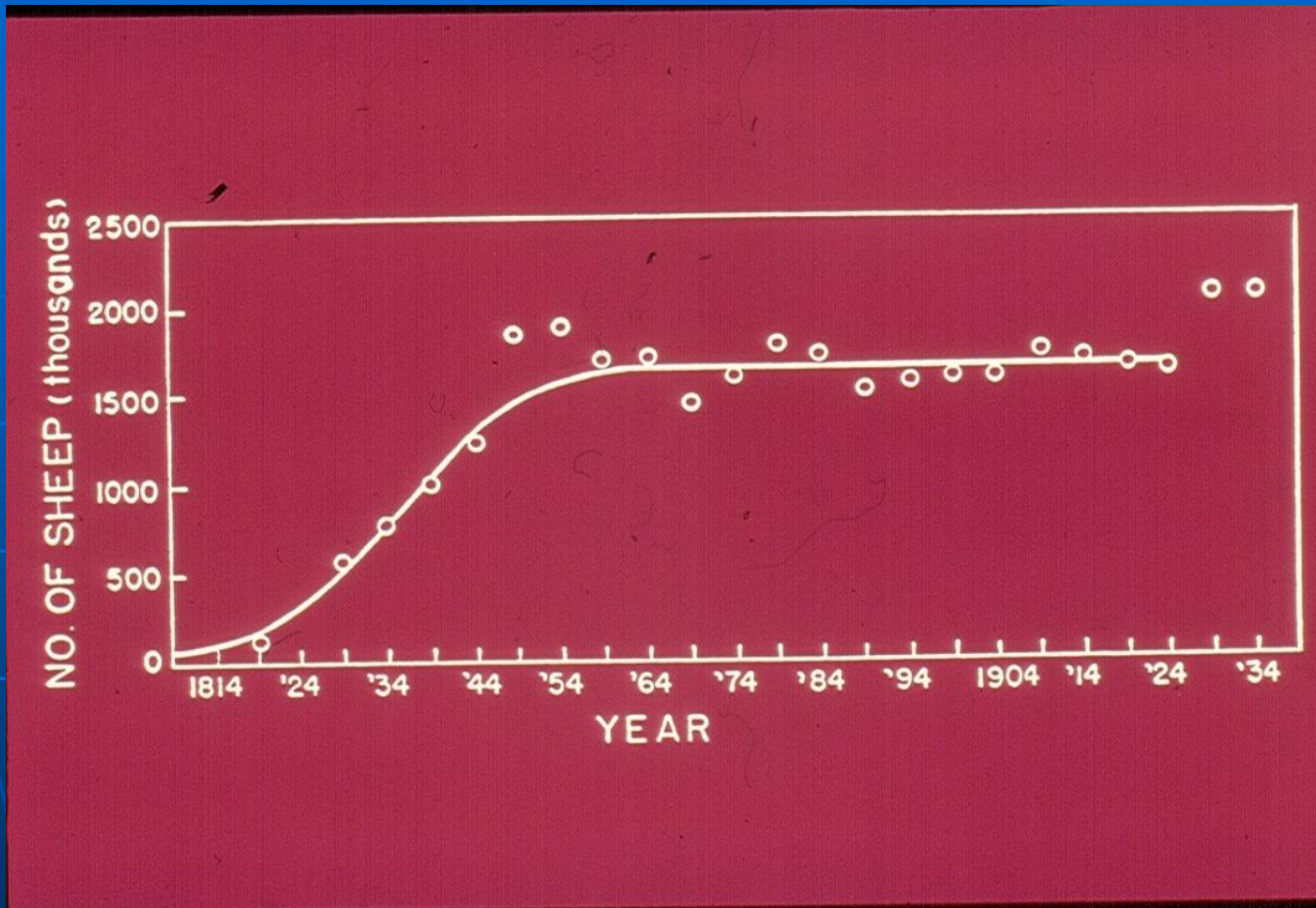
# Limited Growth: the logistic



S-shaped curve of limited growth

The key biological feature is that the per capita rate of growth is **density dependent**

# Examples of limited growth

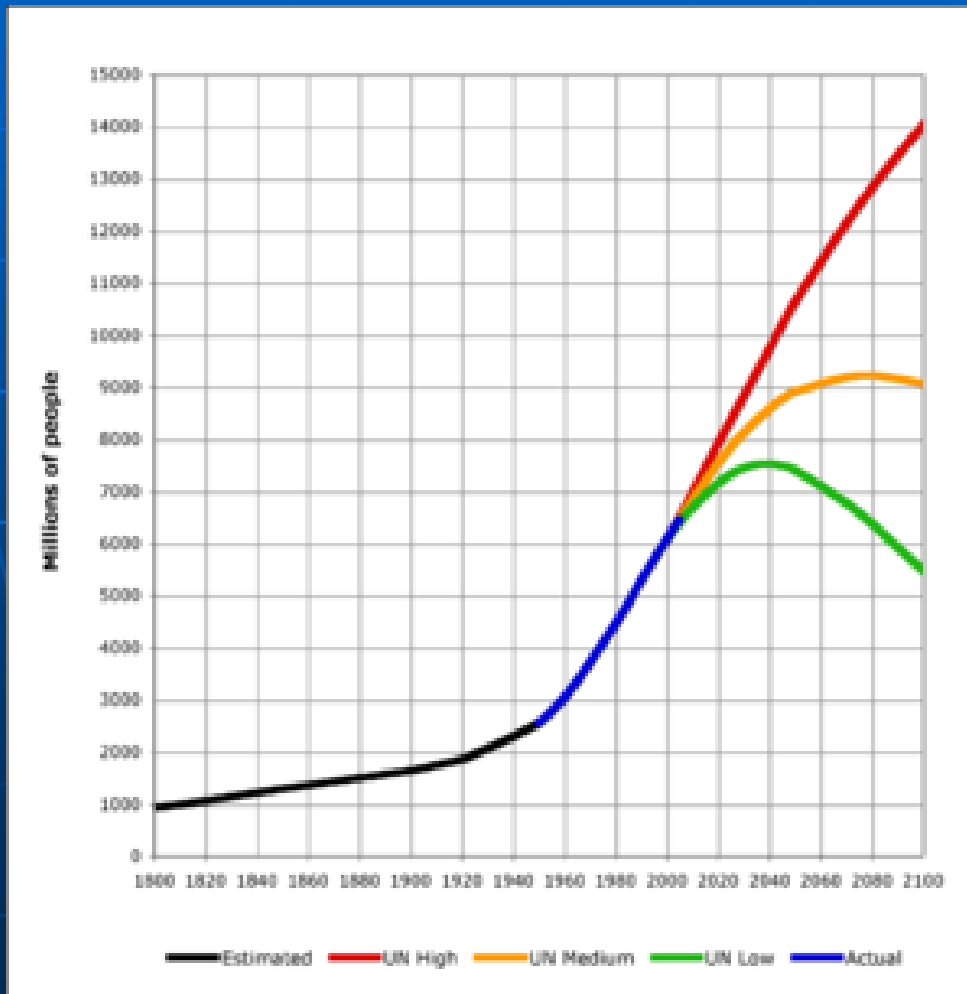


Fit of logistic to population growth of sheep introduced to Tasmania

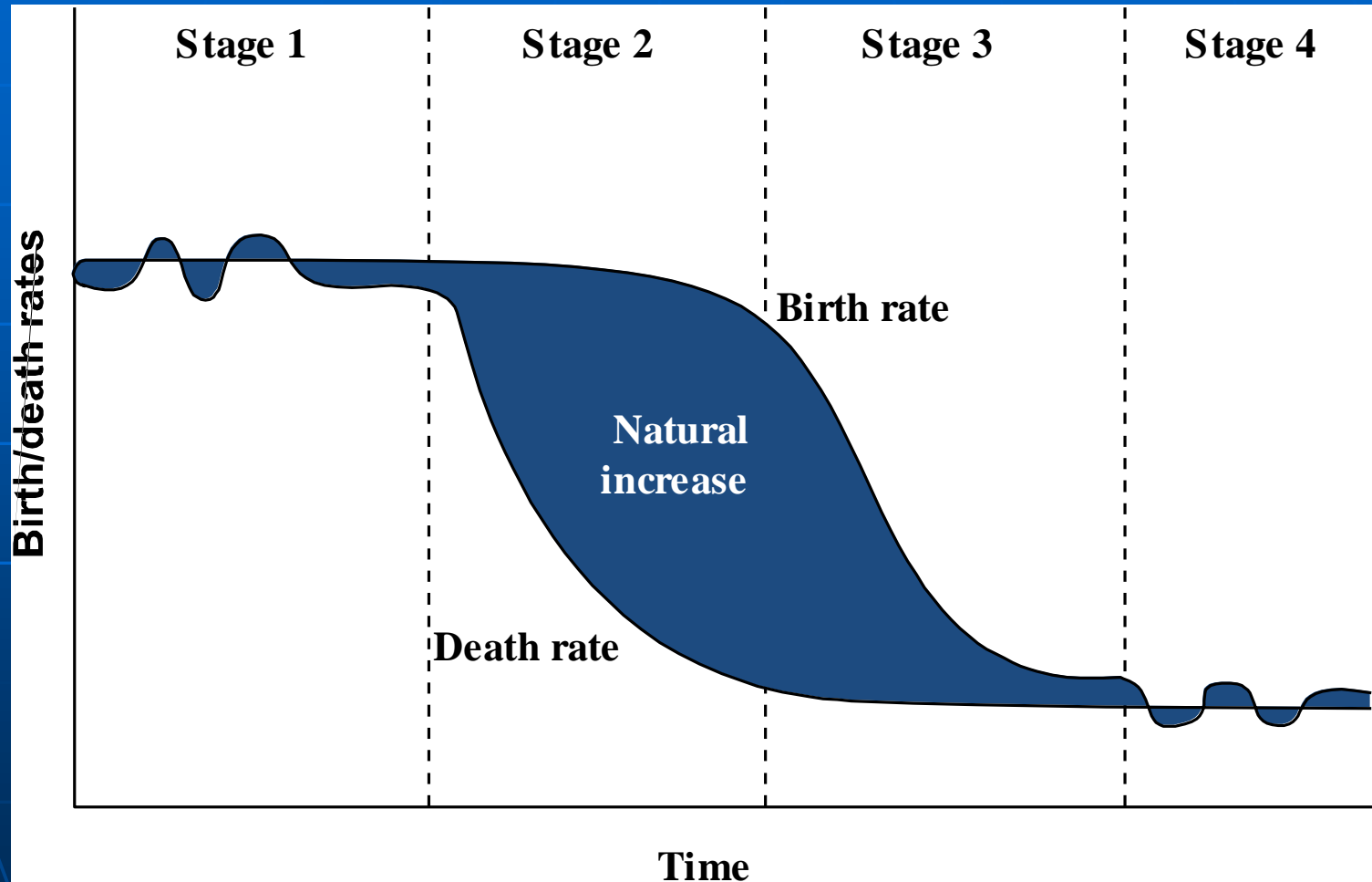
# Limited growth models of human populations

Raymond Pearl (1920) applied Verhulst's logistic model to census data of USA

We are currently approaching 7 billion, moderate growth projects ~ 9 billion, low growth projects peak in year 2040

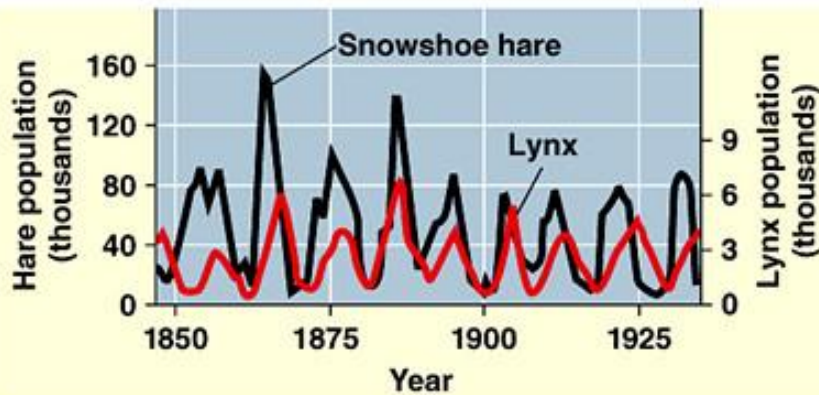


# The Classic Stages of Demographic Transition

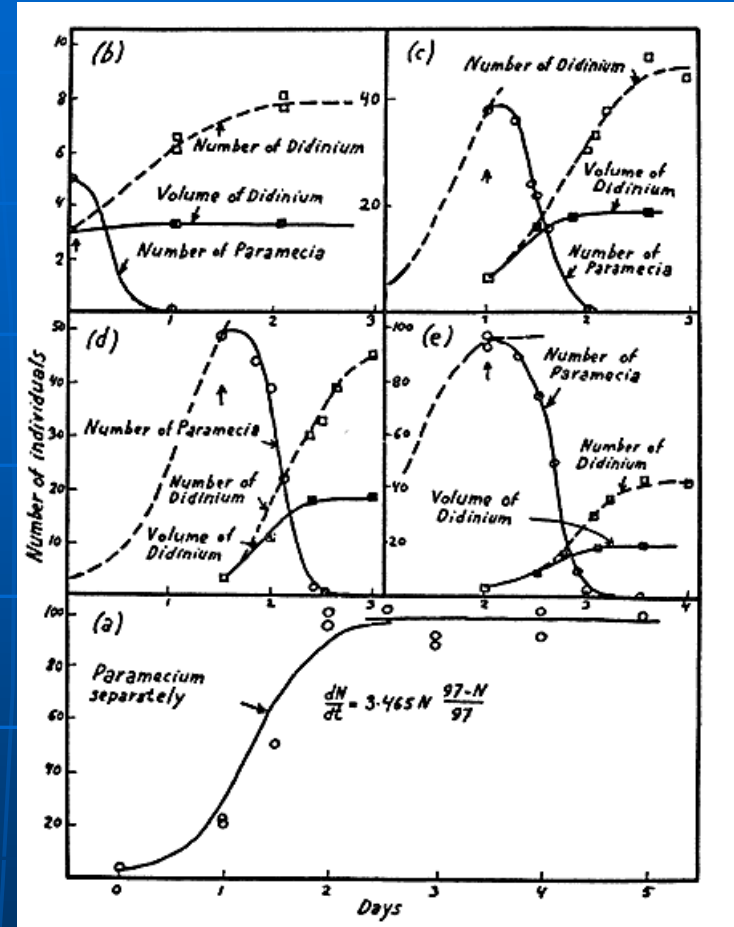


Note: Natural increase is produced from the excess of births over deaths.

# Logistic models: fundamental to ecological theory about food web dynamics



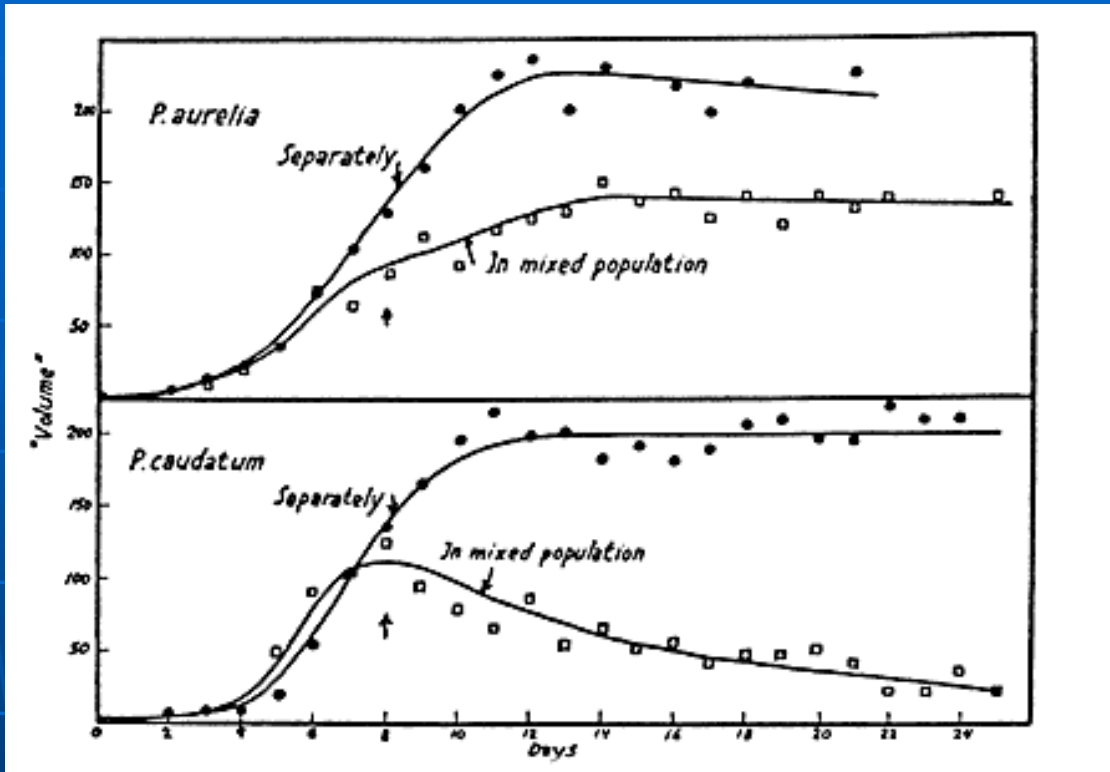
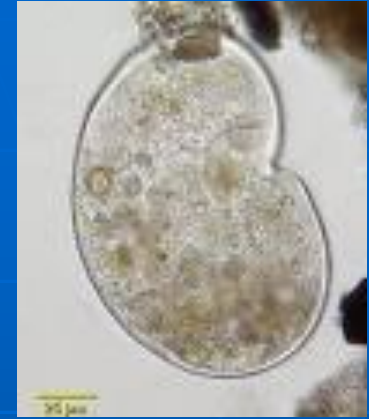
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Predator prey models of Paramecium and Didinium, Georgy Gause (1934) "The Struggle for Existence," with contemporary mathematician Vito Volterra



# And...ecological theory about competition and community diversity

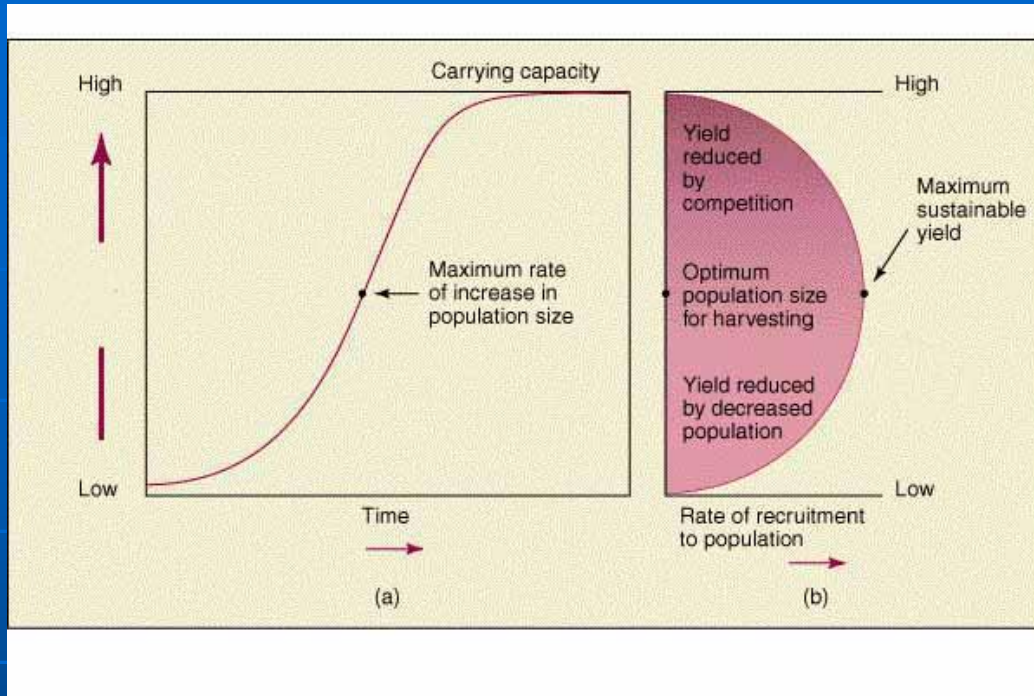


Two species of Paramecium, competitive exclusion principle, Gause-Volterra models of competition



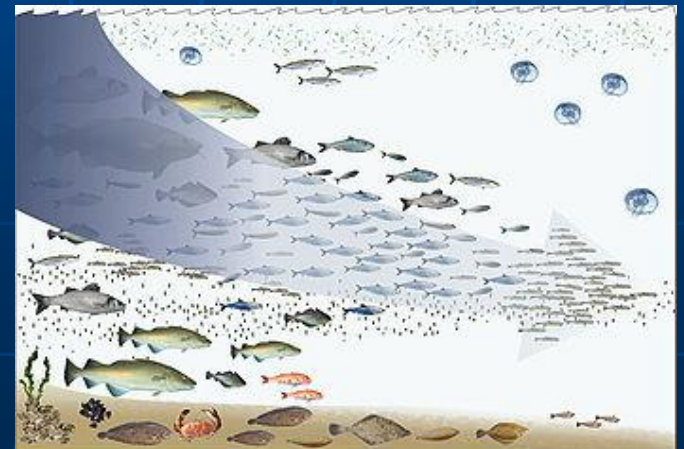
Competition and predation in the rocky intertidal, biological interactions that structure community diversity

# Furthermore...practical aspects of sustainable harvest

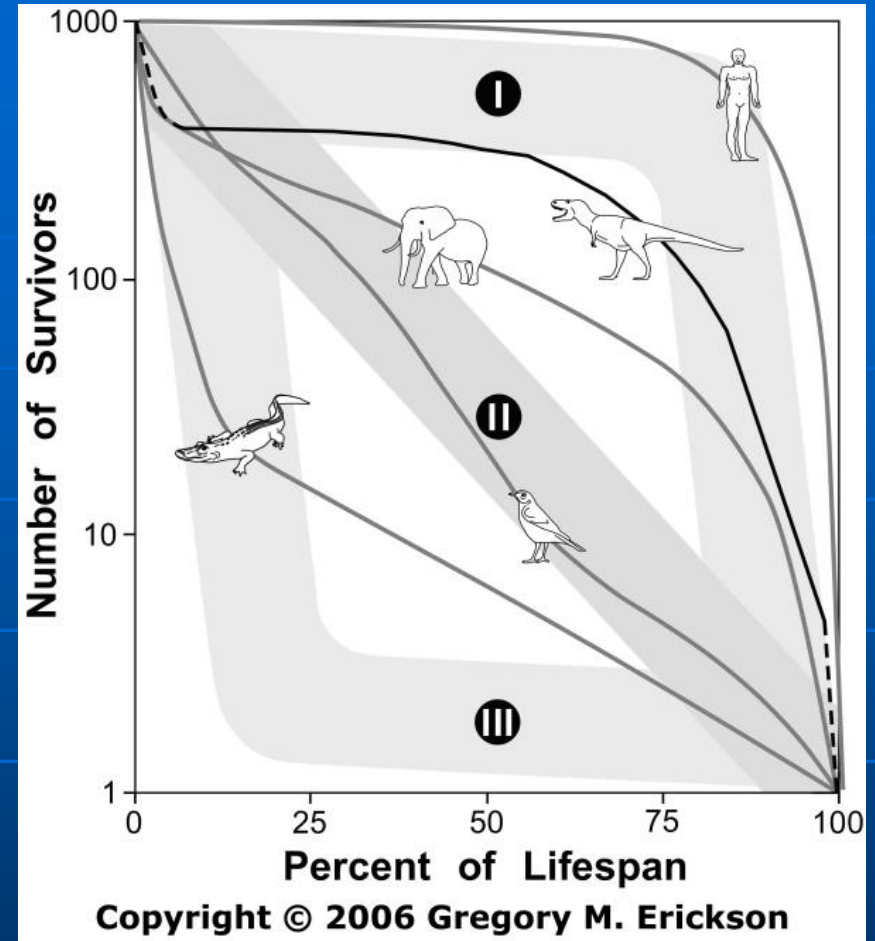
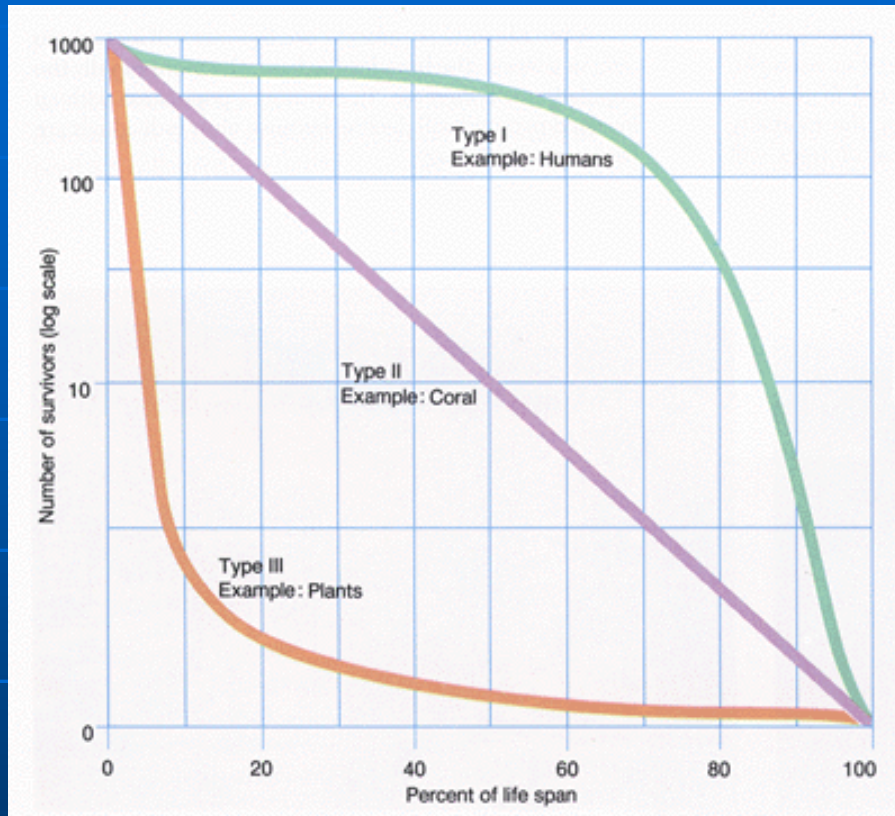


...collapse of cod fishery,  
“fishing down” the size  
(age structure)

Logistic model with maximum  $dN/dt$  at  $N = K/2$ ; application to fisheries biology assumes the population can sustain repeated removal of the increment (MSY); but because of difficulty in monitoring, time lags, economic realities...



# Survivorship, longevity, and age structure of populations



Note the log scale on both figures above

Type II survivorship is constant mortality rates at all ages (exponential decrease)

# Survivorship and age-specific reproduction has a big influence on population growth rate

X (Age Class)	$C_x$ (Age distribution)	$V_x$ (Reproductive value)
0-1	0.49	1.0
1-2	0.22	1.22
2-3	0.14	0.99
3-4	0.09	0.77
4-5	0.06	0.42



→ Matrix analyses

↓  
Annual Growth

$$r = 0.12$$

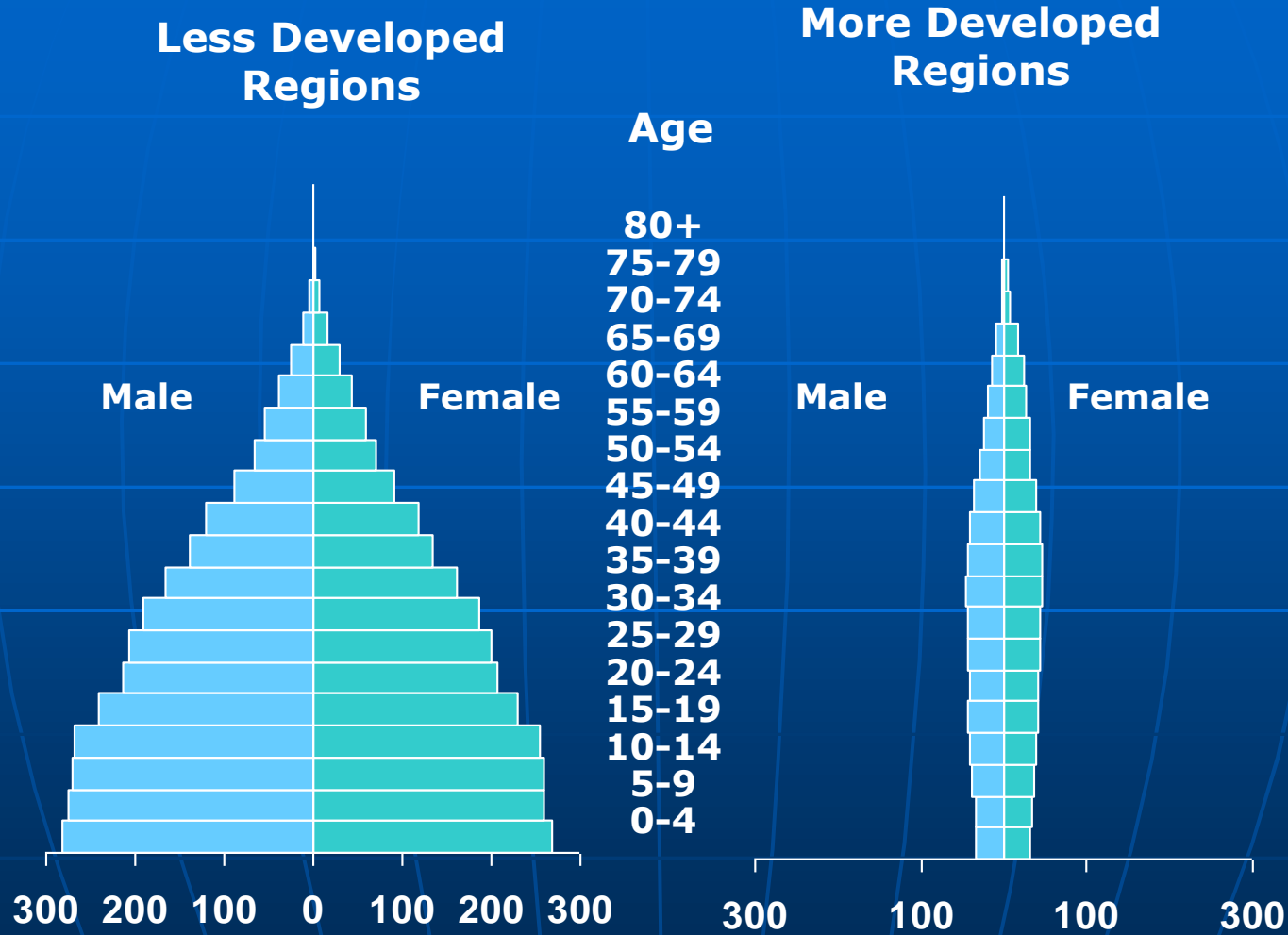
$C_x$  = proportion in each age class derived from survival rates

$V_x$  = current and future reproductive contribution

# Age Distribution of the World's Population

## Population Structures by Age and Sex, 2005

Millions

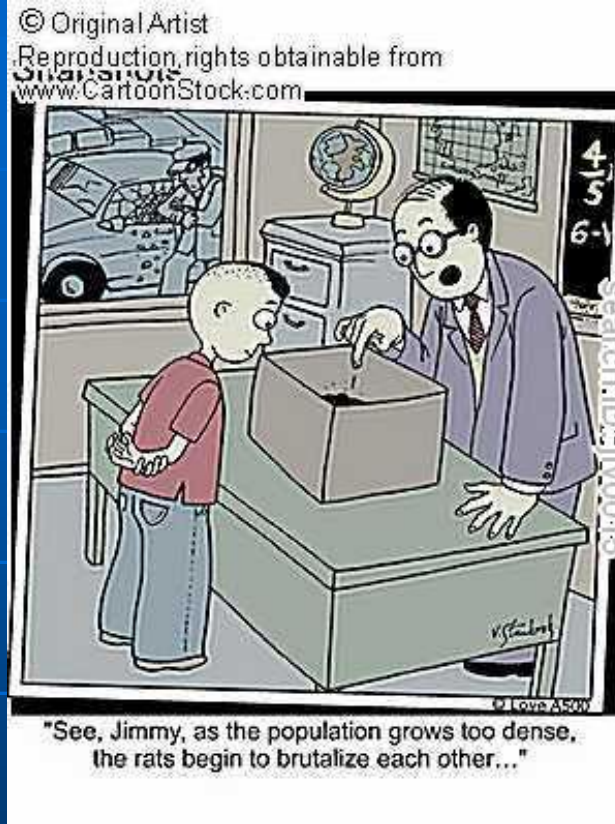


Source: United Nations, *World Population Prospects: The 2004 Revision*, 2005.

# Natural regulation: Behavior, physiology and genetics



- Behavioral and physiological stress (Christian 1950, based on General Adaptation syndrome of Selye), changes in levels of aggression and reproduction



Experimental enclosures for studies of mice emphasize the role of dispersal in population regulation



# Population Processes: the full model with dispersal

The rate of change in a population:

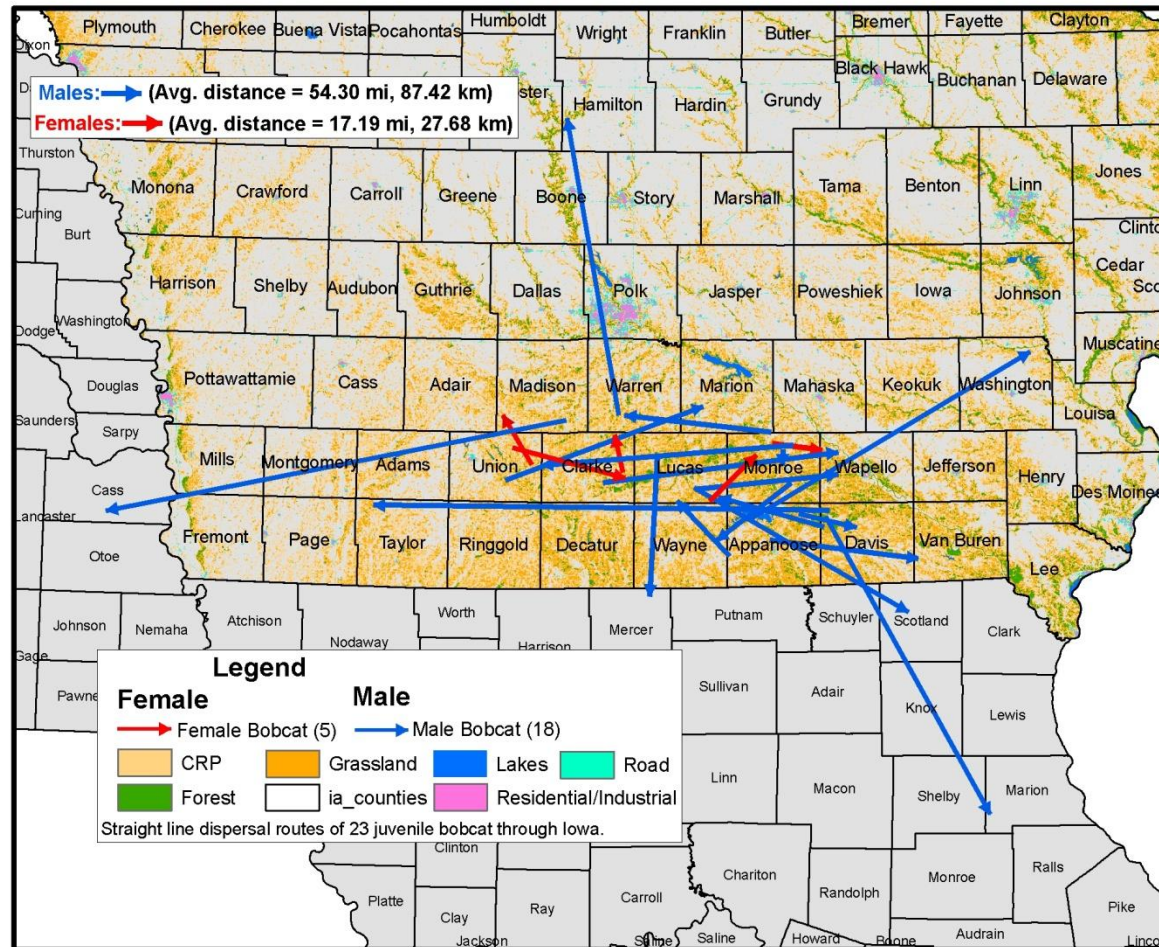
$$\frac{dN}{dt} = rN = (b - d + i - e)N$$

(birth rate - death rate + immigration rate - emigration rate)

Recall the initial statements about defining the boundaries of the population under study, populations “open” to movements result in spatial mosaics which are vastly more realistic and vastly more complicated

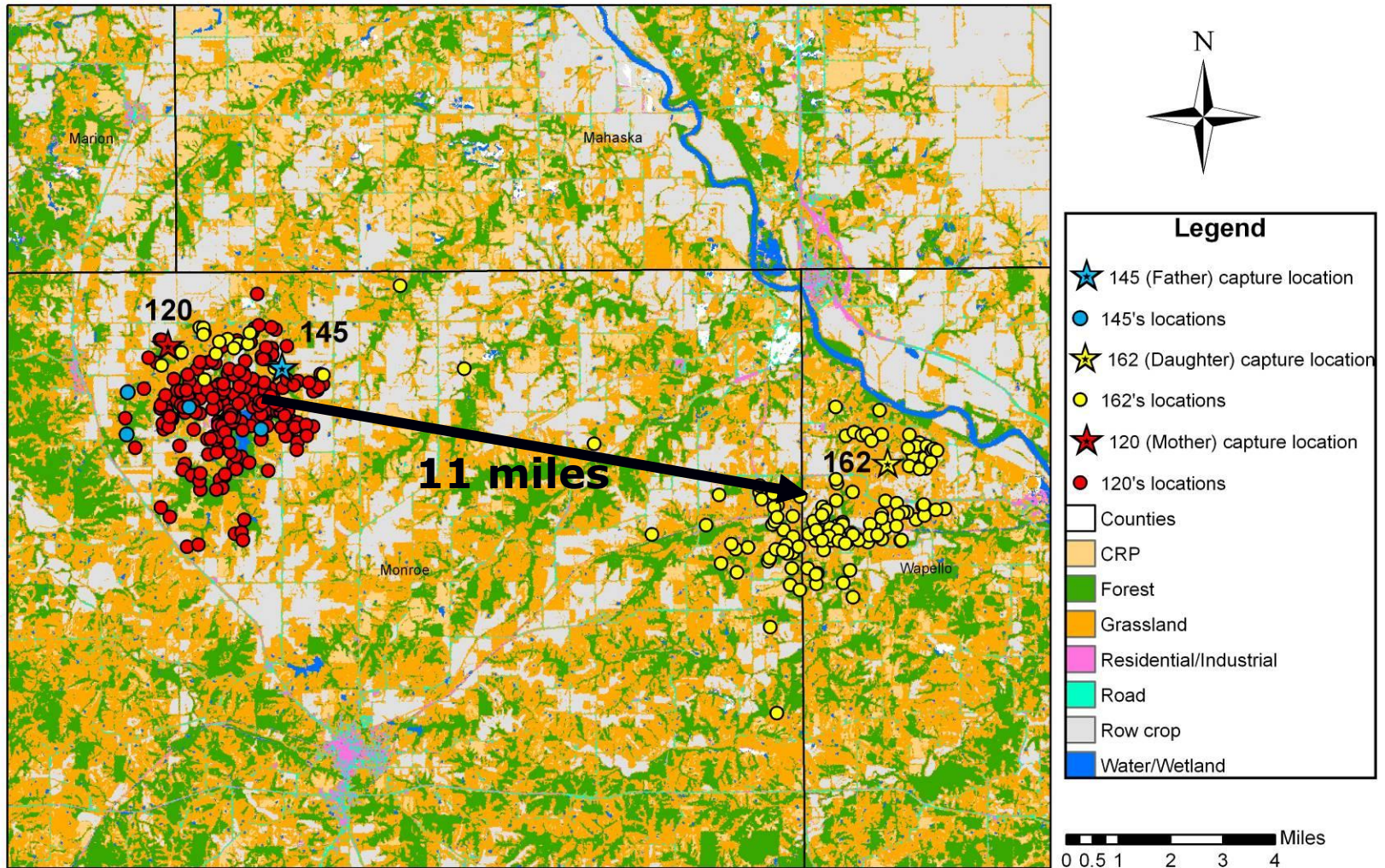
# Estimating immigration and emigration is very difficult in natural populations

Straight Line Dispersal Routes of Juvenile Bobcats (June 2003 - August 2008)

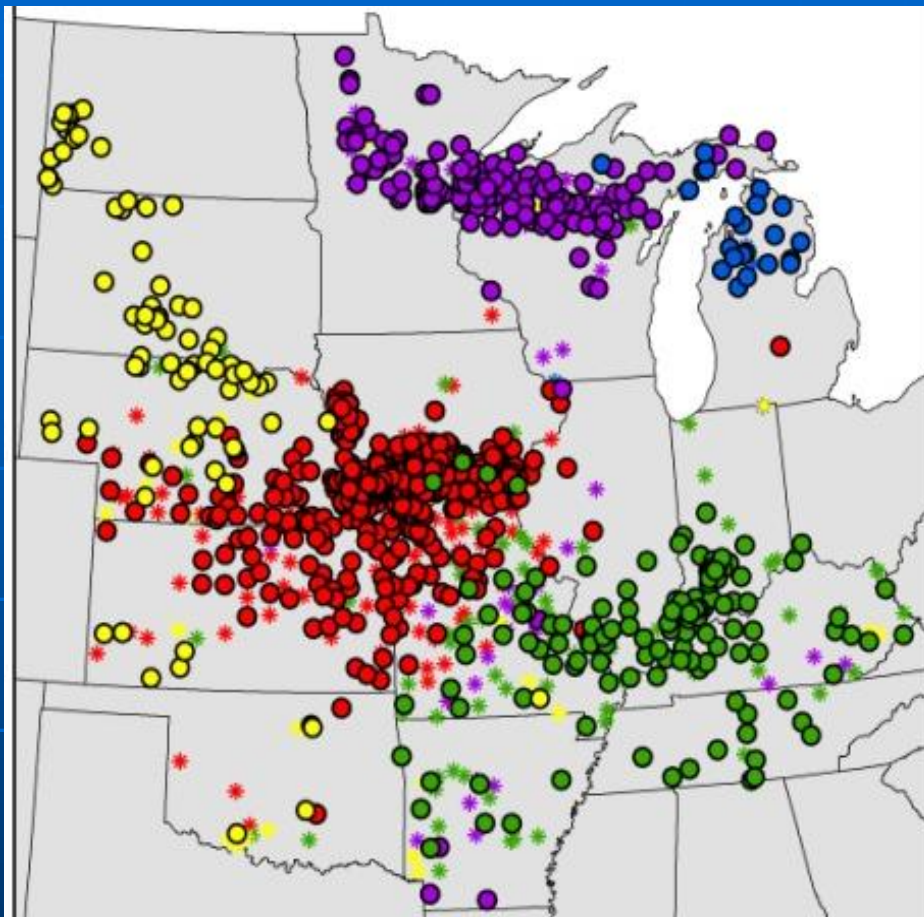




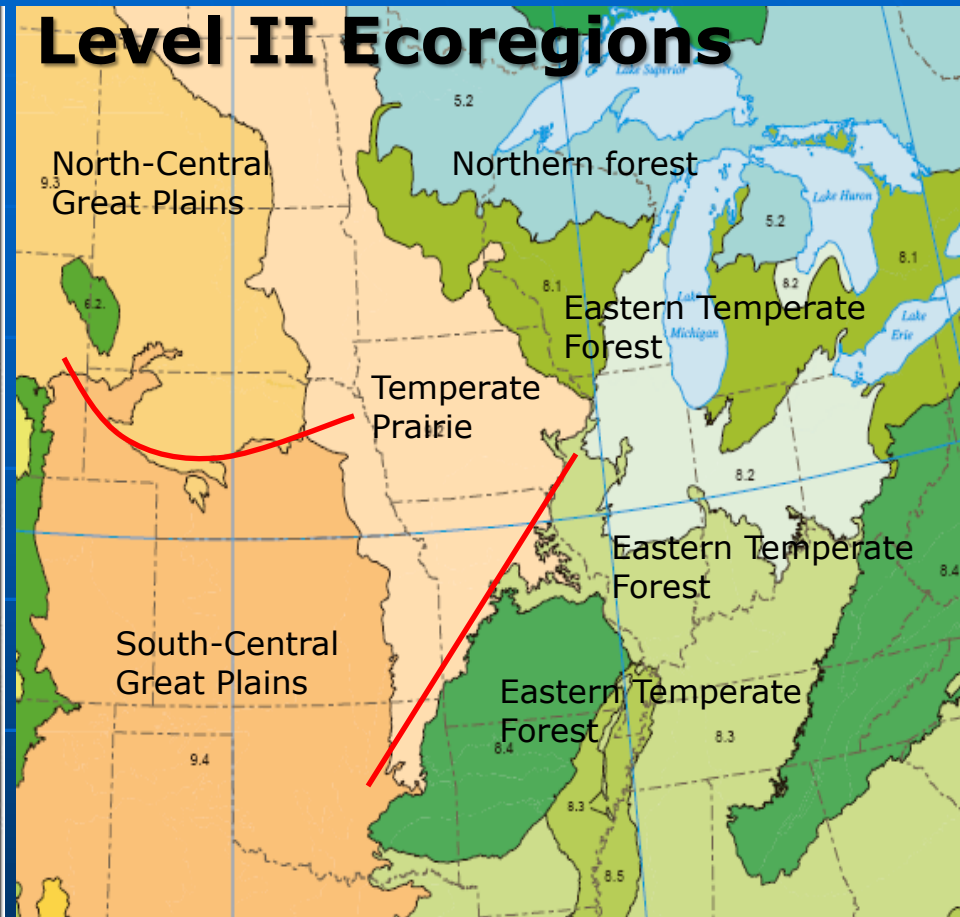
# A family of bobcats in Monroe County, IA, identified by DNA analysis



# The landscape is not a “black box”: heterogeneity adds to complexity



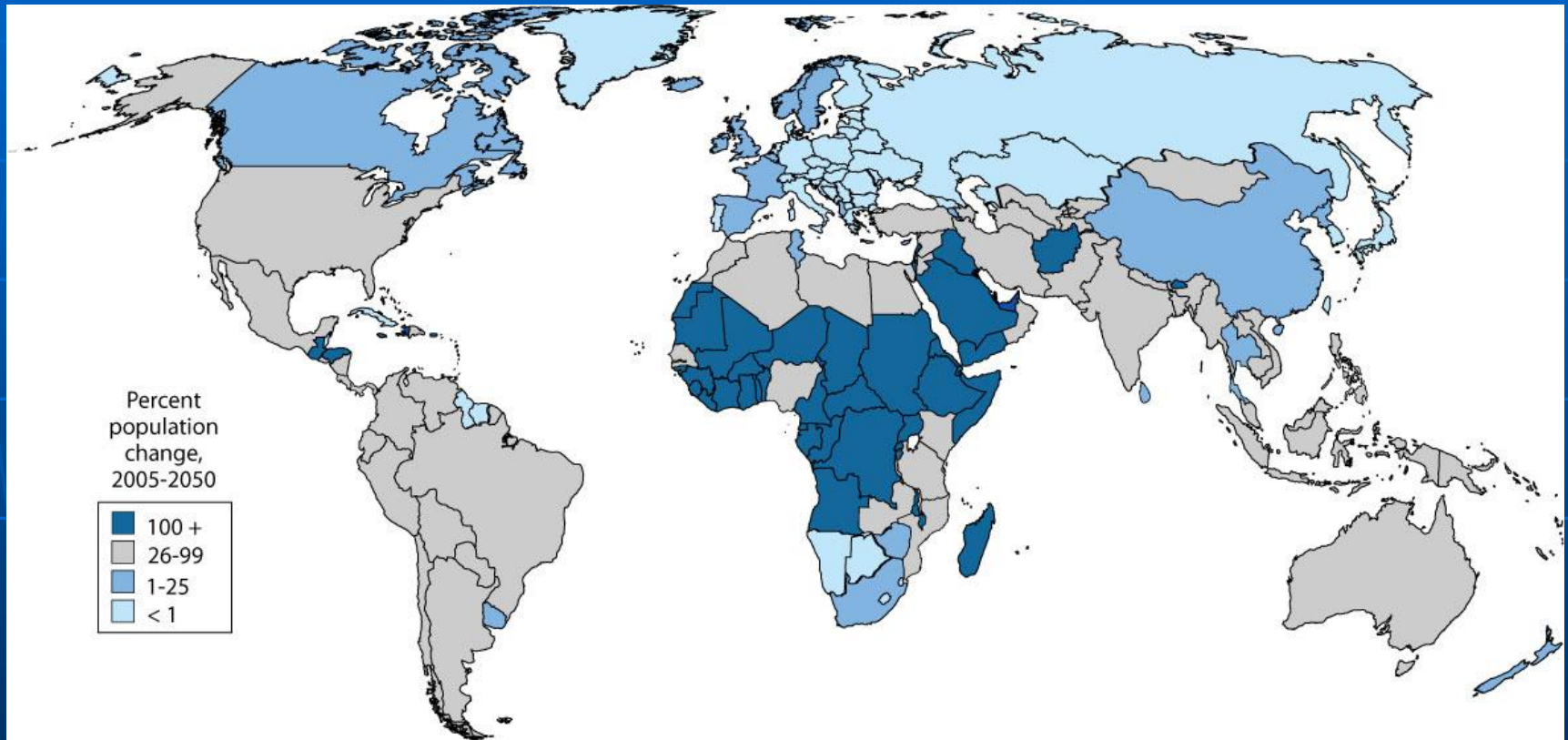
Genetic differentiation among bobcats in the Midwest



Cryptic barriers: habitat biased dispersal

# Now visualize the importance of migration in human demographics and the distribution of resources

## Percent Population Change, 2005-2050



Source: Population Reference Bureau, *2005 World Population Data Sheet*.