I. General introduction to population ecology

II. Patterns of distribution and density (Ch. 9)
   A. General terms, principles
   B. The physical environment limits species distributions at large scales.
   C. At the smallest scale, distributions of individuals within populations are
determined by resource distribution and interactions with each other.
   D. At large scales, population densities vary within ranges.
   E. Rarity is a function of geographic distribution, habitat tolerance, and population
   size.

III. Population dynamics (Ch. 10)
   A. Patterns of distribution, abundance, and dynamics all depend on the
   interactions among death, birth, and migration.
   B. Life history tables combine information on birth and death over time.
      1. two main forms of life tables are cohort and static
      2. example of life table data
      3. survivorship curves summarize mortality patterns
      4. fecundity schedules summarize patterns of reproduction
   C. Life table information can be used to calculate important population parameters
   related to population growth:
      1. net reproductive rate $R_0$
      2. geometric (finite) rate of increase $r$
      3. generation time $T$
      4. per capita rate of increase $r$
   D. Migration can increase or decrease local population densities.

IV. Population growth (Ch. 11)
   A. In the presence of abundant resources, populations can grow geometrically or
   exponentially.
      1. Geometric growth occurs in species with non-overlapping generations, such as
      annual plants.
      2. The exponential model describes continuous growth in populations with overlapping
      generations.
      3. In nature, exponential growth can happen, at least for a limited time, when
      resources are abundant relative to population size.
   B. As resources decline, exponential population growth slows then stops.
      1. This pattern of growth is described by a sigmoidal curve.
      2. The logistic model describes sigmoidal growth by adding a term for
      environmental resistance to the exponential model.
      3. In logistic growth, many different factors may combine to lower $r$ as
      populations approach carrying capacity.
   C. Population dynamics vary within and among species.
      1. Among species, population growth rates are strongly correlated with
      body size.
      2. Within species, population growth rates are strongly influenced by age
      structure.
   D. Population dynamics are correlated with many features of an organism’s
   environment and life history (Ch. 12 pp. 290-291).
I. General introduction to population ecology

A. Among the major questions population ecologists ask are
   1. Where do they live? (distribution)
   2. How many individuals are in the population? (abundance)
   3. Is populations size changing? If so, how rapidly? (dynamics)

B. Because populations are complex and exist on larger spatial and temporal scales than do individuals,
   1. we have a hard time “seeing” the important patterns and understanding the important processes underlying the questions above
   2. so, we use a variety of mathematical models, especially for questions of abundance and dynamics

II. Patterns of distribution and density

A. General terms/principles
   1. population = group of individuals of a single species that interact more with each other (inhabit a specific area) than with other members of the species
   2. Populations have a number of characteristics of interest to ecologists; we’ll focus on distribution, density, abundance, growth first, then look at interactions among populations within communities later

B. The physical environment limits species distributions at large scales.
   1. distribution = full geographic & ecological range inhabited by members of a species over their lifetimes (note implications for migratory spp)
   2. In general, distribution will be a function of 2 key factors:
      a. distribution of habitat whose biotic, abiotic conditions are suitable
      b. ability of organisms to disperse into suitable habitat
   3. At largest scale, climate is often key factor in distributions
      a. organisms can’t establish/maintain populations where too much energy is being spent on homeostasis (compensating for environmental conditions outside range of tolerance)
b. effect of climate may be direct or indirect:
   i. **direct** = conditions of light, temperature, moisture, etc. may be inappropriate
   ii. **indirect** = climatic conditions may affect more “biotic” factors such as food production, the presence of competitors or pathogens, etc.

c. e.g. – **on your own, find out why there are no kangaroo species in northern Australia**

4. Although climate is a major factor, it’s not the only factor influencing large-scale distribution patterns: examples

a. Nine-banded armadillo distribution is limited by **climate and geography**:
   i. armadillos (Dasypus novemcinctus) dig shallow burrows for shelter and root through surface soil layers to feed on soil invertebrates
   ii. to north, winters are too cold for juveniles (who haven’t attained adult weights yet)
   iii. to west, insufficient rainfall to support adequate soil invertebrate supply
   iv. to northeast, dispersal barriers such as rivers (Illinois, southeastern Tennessee, Kentucky) and mountainous topography (N. Alabama, Georgia), limit dispersal into potentially suitable habitat

b. **climate change and dispersal** have influenced tiger beetle distribution (Cicindela longilabris) in North America
   i. distribution extends throughout boreal forest in N. America, but also south into Arizona and New Mexico
   ii. southern populations confined to high elevation coniferous forests
   iii. fossil record shows that, during last glacial period, beetle range extended far south of present, & included lower elevations -- (during glacial maximum, cool, moist conditions were widespread)
   iv. hypothesis: following glacial retreat, populations followed “suitable climate” north & up in elevation
   v. studies of physiological ecology show
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a) across range, this species has higher MR and lower preferred temperatures than do other tiger beetles – suggesting they’re adapted to cooler climate

b) southern, high-elevation populations have virtually same preferred temps, metabolic rates, etc. as northern populations even after 10,000 years!

vi. suggests that, not only does the abiotic environment limit distribution, but that both the limits and the distributions can be stable over very long periods of time

c. Distribution of *Encelia* species within its geographic range is a function of *microclimate* as well as *macroclimate*

i. In general, Encelia spp. distribution correspond to moisture/temperature gradient

a) *E. californicus* has least pubescence; confined to coolest climates in west

b) to east, replaced by species w/ more pubescence, corresponding to hotter climates

ii. exception = *E. fructescens*: almost no pubescence, lives in hottest climate! How does it avoid overheating?

a) high transpiration rate allows evaporative cooling

b) within its geographic range, confined to ephemeral stream channels and/or washes -- where more water is available

d. Barnacle distributions are a consequence of both abiotic and biotic environment

i. Along coast of Scotland, *Chthamalus stellatus* lives in upper intertidal while *Balanus balanoides* lives in lower intertidal

ii. *Balanus* limited to lower intertidal because of low resistance to desiccation during low tide (abiotic factor)

iii. *Chthamalus* can live in lower intertidal, but only when *Balanus* absent -- *Balanus* outcompetes *Chthamalus* in lower intertidal (biotic factor)
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C. At the smallest scale, distributions of individuals within populations are determined by resource distributions and interactions with each other.

1. note on terms: large scale vs. small scale
   a. small scale = area over which there is little environmental change relevant to the individual under study
   b. large scale = area over which there is substantial environmental change
   c. obviously, depends on size/nature of organism!

2. On local (small) scale, distribution pattern also called dispersion.

3. On small scale, organisms exhibit one of three basic types of distribution/Dispersion:
   a. regular = even: individuals are uniformly spaced. Results from (combination of)
      i. even distribution of resources
      ii. negative (antagonistic) interactions among individuals
   b. clumped = individuals are more likely to be found together results from
      i. clumped distribution of resources
      ii. neutral or positive interactions among individuals
   c. random = individuals equally likely to be found anywhere (location of one individual independent of location of others) -- looks like combination of above; results from
      i. random resource distribution
      ii. neutral interactions among individuals

4. Examples
   a. stingless bee colonies in same habitat have different dispersion patterns (dispersion of nests):
      i. In one habitat, 9 species are present and classified as either:
         a) aggressive:
            i) forage on high-density clusters of nectar sources
            ii) defend nest sites aggressively against colonies of own or other
species

b) non-aggressive:
   i) feed singly or in small groups on widely distributed flowers
   ii) don’t interact aggressively with other individuals/colonies (think about why not)

ii. all species nest in trees

iii. investigators predicted that aggressive species should be evenly/regularly distributed while non-aggressive species should be randomly distributed
   a) prediction based on the assumption that nest sites are both randomly distributed and abundant (why?) – prediction met

iv. Investigators were able to map 5 species accurately – found that
   a) 4 aggressives were regularly distributed
   b) 1 non-aggressive was randomly distributed

v. Note here that on the most immediate level, dispersion is a function of interactions among individuals within species – but note also that the nature of those interactions (aggressive vs. neutral) may be a function of the dispersion of resources:
   a) clumped nectar sources are defensible resources, so aggressiveness is favored (and this could apply to nest sites as well)
   b) widely dispersed sources are indefensible, so neutrality toward other individuals is favored

b. Patterns of dispersion in desert creosote change over time
   i. young shrubs tend to be clumped because
      a) seeds don’t disperse far from parent plants
      b) seeds only germinate in a limited number of “good” sites
      c) asexually produced “offspring” are, of course, found next to parent plants
   ii. as plants grow, clumped pattern shifts to random, then to even pattern:
      a) as plants within clumps grow, some die, reducing clumping and producing a random distribution (some clumped, some not)
b) competition among roots for water, nutrients increases mortality in clumped plants, producing even pattern

5. Dispersion patterns can also be considered patterns of density on a local scale: clumped and random have some areas of high density and some of low; uniform is evenly low density throughout population

D. At large scales, population densities vary within ranges
1. At continental scale, density for most (all?) species is “clumped” within the species range -- density varies from high in some spots to very low in others
   a. pattern holds for widely-distributed species as well as those with limited ranges
   b. areas of high density = “hot spots”; generally areas where conditions good (appropriate climate, good resource base, few competitors, etc.)
   c. e.g., North American bird species
2. Similar patterns are found at smaller scales across environmental gradients – e.g., montane trees along moisture gradients
   a. mountain slopes have ~ regular environmental gradients of temperature and moisture from low to high elevations
   b. tree distributions are clumped according to moisture conditions

E. Rarity is a function of geographic distribution, habitat tolerance, and population size
1. The notion of “rarity” is obviously important for conservation -- we want to preserve rare species (or prevent rarity from occurring in the first place!)
2. Rarity can be hard to define, though: different people may mean different things
3. Deborah Rabinowitz (1981) laid out the problem by developing a classification of rarity based on three factors:
   a. three factors are
      i. geographic range: extensive or restricted
      ii. habitat tolerance (tolerance ranges): broad or narrow
      iii. local population size (large or small)
   b. eight possible combinations of these factors exist (OH) -- of those, seven have
at least one attribute of rarity

4. We can use “forms of rarity” as framework to assess extinction risks and develop conservation strategies
   a. species with more attributes of rarity are at higher extinction risk, generally, than species with one or none
   b. identifying “forms” of rarity helps us identify appropriate conservation strategies (habitat preservation, habitat restoration, protection from exploitation, etc.)

5. As a general rule, “island” organisms most at risk:
   a. tend to combine all three forms of rarity
   b. note don’t have to be islands in ocean; any small, restricted, isolated habitat can be an island!

III. Population dynamics

A. The interactions among death, birth, and migration (dispersal) underlie major population patterns and processes:
   1. **Distribution**: think of individuals dispersing out from an area of high density
      a. dispersal brings them to new areas; possibly new habitats
      b. interactions of individuals with the biotic and abiotic conditions in new habitats affect birth and death rates
      c. if birth rates exceed death rates over time, populations are maintained and the “new” area becomes part of the range of the species
   2. **Abundance** = how many individuals
      a. birth, immigration add individuals to a population
      b. death, emmigration remove them
   3. **Dynamics** = kind, rates of change in population size over time depend on rates of births, deaths, migration

B. **Life tables** (or life history tables) are essentially spread sheets biologists use to keep track of information on births and deaths
   1. Several kinds of life tables exist
a. **cohort** life tables
   i. are based on following a group of individuals born at the same time (a cohort) from birth to death
   ii. the data needed to build cohort life tables are the hardest to gather, but results are the best for studying population processes (so that’s what we’ll use)

b. **static** life tables use information on births and deaths at one point in time
   i. age at death and at maternity estimated using a variety of techniques
   ii. often much easier than following a cohort, but interpreting information requires simplifying assumptions -- so not as useful

2. Sample life table data (see handouts at end of notes)
   a. **time intervals** \( (x) \) are selected as appropriate for the organism under study
   b. count (estimate) number surviving and dying from one interval to the next
to calculate **survivorship** \( (l_x) = \text{proportion surviving (or probability of surviving)} \)
   c. determine number of (female) offspring females have during different intervals to calculate **fecundity** \( (m_x) \)
   d. note that proportions used, rather than “raw numbers”, so that populations of different size can be compared to one another

3. Patterns of mortality (“reverse” of survivorship) are summarized in survivorship curves
   a. Curve plots the **logarithm** of number surviving against time (usually adjusted to starting population of 1000 for convenience)
   b. Examples/patterns (see graphs at end of notes):
      i. Note: most organisms have at least a short period of high juvenile mortality right at birth/hatching/germination; the patterns described below refer primarily to what happens after that period
      ii. high survival among the young
         a) offspring surviving to some early age have a high probability of surviving
into adulthood

b) beyond some critical later age, mortality rates increase sharply
   (senescence or “death in old age”)

c) examples include Dall sheep, *Phlox* (note early period of high mortality first)

iii. constant rates of survival

a) over largest portion of lifespan, survivorship linear -- individuals have equal chance of surviving to next interval regardless of age

b) usually have increase in mortality at youngest and oldest intervals

c) examples include mud turtles, Uinta ground squirrels (also many birds, at least after fledging)

iv. High juvenile mortality (continuing beyond the earliest period)

a) for many organisms, juvenile mortality is extremely high: huge numbers of young produced, but young extremely vulnerable

b) get high juvenile mortality, then mortality declines with age

c) examples include *Balanus* (and marine invertebrates generally)

c. patterns generalized into three major “types”

i. **Type I = high juvenile survival**

ii. **Type II = uniform survival**

iii. **Type III = high juvenile mortality**

iv. note that many (if not most!) fall somewhere “in between” ideal (e.g., thar)

4. Fecundity schedules summarize patterns of reproduction

a. note that, for sexually reproducing organisms with 1:1 sex ratios, we use only female offspring of females to assess fecundity; need to make adjustments for other situations (but we won’t worry about those!)

b. Like survivorship, fecundity tends to fall into a few basic patterns

i. **semelparity** = organisms have single reproductive episode in their lifetimes
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a) annual plants, many kinds of insects, etc.
b) usually produce lots of offspring (we’ll talk about why later)

ii. **iteroparity** = multiple reproductive episodes; many patterns, but the
   most common are
   a) steadily increasing fecundity with age until death
   b) fecundity increases with age to peak then declines

C. Life table information can be used to calculate important population parameters related to population growth (discussed in more detail in the next section):

1. **net reproductive rate** $R_0$
   a. this is a measure of individual reproduction, but can give us information about
      the population as a whole
   b. defined as average number of female offspring per female in the population
   c. is a function of both number of offspring per time interval and mortality rates from one interval to the next
   d. mathematically, sum of $l_i m_x$ for all intervals
   e. tells us whether the population is growing, declining, or stable (but not much more detail than that): $R=1$ is stable; $R>1$ is growing; $R<1$ is declining

2. **geometric (finite) rate of increase**
   a. this is a measure of population growth/decline over a specific time period
   b. defined as the proportional change in population size from one point in time to another
   c. mathematically = ratio of population size at later time to size at earlier time: $\left( \frac{N_{t+1}}{N_t} \right)$
   d. only provides an accurate measure of population growth/decline when the population has non-overlapping generations (i.e., adults all die before their offspring start reproducing)

3. **generation time** $T$
   a. when generations overlap within a population, we need a measure of generation
time to let us analyze overall rates of change in population size with more precision

b. generation time can be thought of as the average age of all the parents of a group of individuals born at the same time (the average age of the parents of a cohort)

c. can also be thought of as the average time to reproduction for an individual
d. calculated as the sum of $x(l_0)(m_x)/R_0$ (don’t worry about why!)

4. **per capita rate of increase = instantaneous rate of increase $r$**

a. tells us the average increase/decrease in population per individual for population as a whole, at any instant in time

b. defined as the per capita birth rate ($b$) minus the per capita death rate ($d$)
   i. so, logically, if $r=0$, population is stable; $r>1$ population is growing; $r<0$, population is declining

c. mathematically, estimated as $\ln R_0/T$: $r$ will increase as
   i. number of offspring per female increases AND
   ii. as generation time decreases (i.e., the younger organisms reproduce, the faster the population will grow)
   iii. note relationship between $r$ and $R_0$:
      a) when $R_0 = 1$, $\ln R_0 = 0$ and $r = 0$ (stable population)
      b) when $R_0 > 1$, $\ln R_0$ is positive and $r > 0$ (growing population)
      c) when $R_0 < 1$, $\ln R_0$ is negative and $r < 0$ (declining population)

d. the **intrinsic rate of natural increase $r_{max}$ or $r_m$** is related to $r$:
   i. $r$ is the realized rate of growth; it will vary depending on environmental conditions
   ii. each species has a theoretical upper limit to birth rate and a lower limit to death rate (assuming ideal conditions) – this is $r_{max}$
   iii. note that $r$ is almost always less than $r_{max}$

D. Dispersal can increase or decrease local population densities
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1. most (all?) organisms have at least some capacity for dispersal during their lifetimes
2. many kinds of organisms have adaptations specifically for dispersal; often permit very long-distance movements
3. patterns and processes of dispersal really complex, and really interesting; unfortunately, we don’t have time to explore in depth!
4. so, for now, just remember that, in open populations, immigration and emigration also play a role in population dynamics

IV. Population growth

Note that understanding patterns of population growth is critical to understanding many aspects of ecology. The patterns themselves are highly variable; we’re just going to focus on two common ones (there are plenty more we could look at!), with the goal of understanding both how they “work”, and how we can use the tools of mathematics to study ecological problems.

A. In the presence of abundant resources, populations can grow geometrically or exponentially
   1. **Geometric growth** occurs in species with non-overlapping generations, such as annual plants
      a. In species like this, population growth is “pulsed”
      b. the number of individuals at any point in time will depend on the number of individuals in the previous generation and in the average number of offspring they have
      c. if the average number of offspring stays constant over time, then we can use the geometric rate of increase ($\lambda$) to calculate population size
      d. The equation for population size will simply be $N_t = N_0 \lambda^t$ where
         i. $N_t = \text{the size of the population at the time we’re interested in (measured in days, months, years, etc.)}$
         ii. $N_0 = \text{the original number of individuals in the population}$
         iii. $\lambda = \text{the finite rate of increase}$
iv. \( t = \) the time interval we’re interested in

e. under conditions of geometric growth, even with constant \( r \), will get increasing rates of population growth as \( N \) increases: e.g., Phlox (fig. 11.3)

2. The **exponential model** describes continuous growth in populations with overlapping generations.

a. the exponential model describes population growth in terms of \( N \), \( r \), and \( t \)

   i. \( N \) will change over time as the population grows

   ii. \( r \) will be constant (this is important!)

   iii. generally, when conditions are suitable for exponential growth, \( r \) will be high (near \( r_{\text{max}} \))

b. two equations describe this pattern:

   i. equation for **population size** \( N \): \( N_t = N_0 e^{rt} \) where

      a) \( N_t = N \) at any time \( t \) and

      b) \( N_0 = \) starting population size

      c) note that this describes the curve itself

      d) in this case, curve goes up because \( t \) increases (assume \( r \) constant)

   ii. equation for **rate of population growth** \( dN/dt \):

      \( dN/dt = rN \)

      a) \( dN/dt = \) the rate of population change, not population size
b) biologically, this equation describes how fast the population is growing or shrinking.

c) mathematically, this describes the slope of the tangent line to the growth curve at any time t – this gives us an easy way to see how the rate of population growth changes over time.

d) note that, as population size (N) increases, rate of growth also increases (tangents get “steeper”; **the larger the population is, the faster it grows**).

e) means that, not only is population growing, but it’s growing at an ever-increasing (accelerating) rate.

f) happens because, although r is constant, N increases over time (number of individuals added per individual stays the same; number of individuals goes up!)

iii. remember that, in this model, r is constant.

3. In nature, exponential growth can happen, at least for a limited time, when resources are abundant relative to population size -- at these times, r will be very close to r_max -- e.g.

a. when populations become established in new, favorable environments

i. trees following glacial retreat in Britain

ii. collared doves following range expansion into W. Europe

iii. brown tree snakes (invasive exotic species) in Guam – population density reached 13,000/mi^2 after less than 20 years.

b. during transient times of high resource abundance

i. diatoms and other planktonic organisms in spring – exponential growth results in algal blooms

b. during recovery following some kind of exploitation (e.g., endangered species once they’re adequately protected; prey species when predators eliminated)

B. As resources decline, exponential population growth slows then stops.
1. in simplest pattern, decline in resources will cause a reduction in $r$:
   a. as resources decline, per-capita birth rates will decline and per-capita death rates will increase – so $r$ decreases
   b. result will be that the population growth rate will decrease, eventually reaching 0: individuals reproduce enough to replace themselves only, and population size stabilizes
2. Pattern described by sigmoidal curve (e.g., barnacles, yeast, buffalo etc.)
3. The logistic model describes sigmoidal growth by adding a term for environmental resistance to the exponential model
   a. carrying capacity ($K$) = maximum number of individuals of that species the environment can support
   b. can be determined by a variety of factors
      i. barnacles = space
      ii. buffalo = grass
      iii. yeast = accumulation of own waste (alcohol)
   c. rate of population growth (logistic growth equation) derived from the equation for exponential growth by incorporating a term for environmental resistance such that, as the population approaches the carrying capacity, $r$ will decrease
      i. note that, in this model, $r$ will no longer remain constant – it will change depending on the size of $N$ relative to $K$
      ii. mathematically, set $r = r_{max}(1-N/K)$ where $N/K = \text{environmental resistance}$
         a) $r_{max}$ is constant and sets the upper limit to growth rate
         b) as $N$ approaches $K$, environmental resistance increases
         c) by setting $r = r_{max}(1-N/K)$, model specifies that, as $N$ increases:
            i) $N$ approaches $K$
            ii) environmental resistance ($N/K$) increases
iii) \((1-N/K)\) decreases

iv) \(r\) declines

d) substitute into equation for exponential growth:
\[
dN/dt = r_{\text{max}} N(1-N/K)
\]

iii. note that this equation specifies the tangent line to the sigmoidal growth curve – note how the slope changes at different points along the curve!

a) at one extreme, when \(N\) is very small relative to \(K\),

i) \(r \sim r_{\text{max}}\) and growth is exponential \((dN/dt \sim r_{\text{max}} N)\)

ii) biologically, when the population is much smaller than the carrying capacity, then resources will be abundant and organisms will be reproducing at near maximum

b) at the other extreme, when \(N = K\)

i) \(r = 0\) (the per-capita birth rate = per-capita death rate) so the growth rate is 0

ii) biologically, when the carrying capacity has been reached, organisms have only enough resources to replace themselves (on average), so the population size is stabilized

c) between those two points, \(r\) declines as \(N\) increases, so growth rate also decreases (slows down)

iv. NOTE difference: until \(N=K\), population size increases, but growth rate decreases (car is still moving forward even though speed is being reduced)

4. In logistic growth, many different factors may combine to lower \(r\) as populations approach carrying capacity

a. birth and death rates affected by numerous biotic and abiotic factors interacting in complex ways

b. in theory, though, we can recognize a general difference between the effects of biotic and abiotic factors:
i. effects of biotic factors like disease, parasitism, predation, competition should vary with population size:
   a) as population increases, should act to decrease birth and increase death rates & vice-versa
   b) so should get “negative feedback” between biotic factors and population size, especially when population is near carrying capacity: as N approaches K, factors have stronger effect -> r declines -> growth rate declines -> N drops -> factors have weaker effect -> r increases -> N increases etc.
   c) these mechanisms called density-dependent factors; in theory, help maintain population at or near K
      i) density-dependent because the “strength” of the effect increases with population size

ii. in contrast, direct effects of abiotic factors like temperature, precipitation, etc., shouldn’t depend on density:
   a) e.g., frost will kill insects regardless of population size; drought will kill salamanders regardless of population size, etc. – the risk of being affected is independent of density
   b) often, abiotic factors called density-independent factors; although they definitely affect growth rates, they don’t have a “feedback” effect

iii. in “real life”, of course, interactions between biotic and abiotic factors can be very complex: e.g., Opuntia population declines 1983-1986 in Galápagos
   a. El Niño caused heavy rains in 1983 (abiotic factor). This caused
      a) some Opuntia to absorb so much water roots couldn’t hold; blown over and died. (direct abiotic effect)
      b) rapid growth in a vine that strangled many Opuntia (biotic effect caused by abiotic effect), reducing flower and seed production
      c) coastal plants damaged by salt spray during storms produced fewer
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flowers (direct abiotic effect)

ii. Drought from 1984-1985
   a) fewer flowers develop (direct abiotic effect)
   b) more flowers eaten by finches as their other food sources decline (biotic effect caused by abiotic effect)

d. we’ll look at biotic interactions among populations in detail in later units

C. Population dynamics vary within and among species for lots of reasons We’ll look briefly at two:

1. Among species, population growth rates are strongly inversely correlated with body size (the larger the animal, the lower the population growth rate)
   a. growth rate is function of birth rate, death rate
   b. large organisms typically have lower birth rates
      i. as simple consequence of larger size of offspring (take longer to develop)
      ii. as consequence of smaller litter/clutch sizes (fewer offspring per reproductive episode)
   c. e.g., for comparison (think about conservation issues!)
      i. small (1g) pelagic tunicate can increase population 1000X in 8 days
      ii. gray whales (25,000,000 g) doubled population in 25 years

2. Within species, population growth rates are strongly affected by the age structure of the population (in combination with survivorship)
   a. age structure = distribution of individuals among age classes, usually divided into pre-reproductive, reproductive, and post-reproductive
      i. note that our earlier discussion of population growth ignored this!
   b. three general “shapes” possible
      i. “uniform” = approximately the same number of individuals in each group
      ii. “pyramid” = pre-reproductive is largest class, followed by reproductive with post-reproductive smallest
      iii. “mushroom” = more post-reproductive than reproductive or pre-
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reproductive

c. shape of age distribution affects population growth -- note that the following assumes Type I survivorship (high juvenile survivorship):
   i. in a uniform distribution, growth stays steady as number of individuals no longer reproducing (entering post-reproductive class) is balanced by individuals entering reproductive class
   ii. in a “pyramid”, more individuals enter the reproductive class than leave --so more individuals are born per capita (per total number in the population) and population size increases even if fecundity is low
   iii. in “mushroom”, more individuals leave the reproductive age class than enter it -- population growth will decline unless fecundity is very high

d. examples from human population
   i. note that human population growth currently exponential
   ii. although fertility in developed countries declining, two problems:
      a) most individuals live in developing countries
      b) developing countries typically have “pyramid” age distributions
   iii. so, even though fertility is declining, growth rates are staying high and relatively rapid growth is projected to continue for another few decades at least

D. Population dynamics are correlated with many features of an organism’s environment and life history

1. Let’s “tie up” threads of discussions on abiotic environment, physiological ecology, and population ecology by examining relationships among environment, physiology, and population dynamics
2. Although there’s a lot of variation, many organisms show common patterns –some kinds of traits tend to co-occur in some kinds of environments
3. In older terminology, groups of correlated life history traits were called “r and K selected”; now, we generally identify according to broad environmental conditions:
equilibrial and non-equilibrial life history strategies

4. Begin by identifying two broad types of environment:

a. **non-equilibrial**: K changes dramatically over time
   i. typical, e.g., of new or disturbed habitats
   ii. habitats tend to be variable and/or unpredictable

b. **equilibrial**: K stays approximately constant, at least over long periods of time relative to organism’s life span

![Graph showing K and Time]
5. Given different kinds of environments, what kinds of characteristics do we see?

Identify major selective pressures and responses given allocation principle and developmental constraints:

<table>
<thead>
<tr>
<th>Characteristic</th>
<th>Equilibrial strategy (K-selected)</th>
<th>Non-equilibrial strategy (r selected)</th>
</tr>
</thead>
<tbody>
<tr>
<td>major selection pressure</td>
<td>be competitive at high population densities</td>
<td>“swamp the gene pool” with your offspring so they’re the ones that make it through the time of low K</td>
</tr>
<tr>
<td>reproductive strategy</td>
<td>relatively few, high-quality offspring</td>
<td>as many offspring as possible (lottery)</td>
</tr>
<tr>
<td>allocation pattern</td>
<td>allocate to factors affecting offspring quality</td>
<td>allocate to offspring numbers</td>
</tr>
<tr>
<td>homeostasis</td>
<td>regulator (performance advantage)</td>
<td>conformer (don’t waste energy on homeostasis)</td>
</tr>
<tr>
<td>body size</td>
<td>large (improves competitiveness)</td>
<td>small (don’t waste energy on growth)</td>
</tr>
<tr>
<td>life span</td>
<td>long (needed for growth)</td>
<td>short (don’t waste energy)</td>
</tr>
<tr>
<td>offspring body size</td>
<td>large</td>
<td>small (constraint + allocation)</td>
</tr>
<tr>
<td>fecundity</td>
<td>relatively low (constraint)</td>
<td>high</td>
</tr>
<tr>
<td>parental care</td>
<td>significant</td>
<td>none</td>
</tr>
<tr>
<td>r_max</td>
<td>relatively low</td>
<td>high</td>
</tr>
<tr>
<td>population regulation</td>
<td>density-dependent</td>
<td>density-independent</td>
</tr>
</tbody>
</table>

6. Although this scheme does a good job of describing character suites in some organisms, doesn’t work well for all – so other schemes have been developed (e.g., for plants, fish). But serves as a good starting point for consideration of tradeoffs and constraints.
## Life tables

<table>
<thead>
<tr>
<th>x (age or interval yrs)</th>
<th>( l_x ) (survivorship)</th>
<th>( m_x ) (fecundity)</th>
<th>( l_x m_x )</th>
<th>( x l_x m_x )</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>proportion surviving to interval ( x ) or probability of survival to interval ( x )</td>
<td>average number of (female) offspring per individual (female) during interval ( x )</td>
<td>average number of offspring per female per interval adjusted for mortality</td>
<td>used to calculate generation time ( T )</td>
</tr>
<tr>
<td>0</td>
<td>1.00</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>1</td>
<td>0.80</td>
<td>0.7</td>
<td>0.56</td>
<td>0.56</td>
</tr>
<tr>
<td>2</td>
<td>0.78</td>
<td>1.0</td>
<td>0.78</td>
<td>1.56</td>
</tr>
<tr>
<td>3</td>
<td>0.50</td>
<td>1.0</td>
<td>0.50</td>
<td>1.50</td>
</tr>
<tr>
<td>4</td>
<td>0.30</td>
<td>1.0</td>
<td>0.30</td>
<td>1.20</td>
</tr>
</tbody>
</table>

Information on survivorship and fecundity from field data; precise methods depend on the species under study.

\[ \text{sum} = 2.14 = R_0 \]
\[ \text{sum} = 4.82 \]

**survivorship curve** = plot of \( l_x \) over time

**geometric rate of increase** \( \lambda = \frac{N_{t+1}}{N_t} \)

**net reproductive rate** \( R_0 = \) average number of female offspring per female in the population

\[ \text{if } R_0 > 1, \text{ the population is growing} \]

**generation time** \( T = \frac{\sum x l_x m_x}{R_n} \) used to calculate per-capita rate of increase

**(realized) per capita rate of increase** \( r = \) the number of individuals added to or lost from the population per individual per unit time

\[ = \text{the per-capita birth rate minus the per-capita death rate} \ (b-d) \]

**estimated as** \( r = \frac{(\ln R_0)}{T} \)

**if } r > 0, \text{ the population is growing} \]

**intrinsic rate of increase** \( r_m = \) maximum per-capita rate of increase possible under ideal conditions

\( r_m \) is usually greater than \( r \)
Life table worksheet

1. Complete the life table. Remember that survivorship is calculated as the number surviving to each interval divided by the original number in the cohort.

2. Use the data from the life table to calculate $R_0$, $T$, and $r$.

3. Which of the three general types of survivorship does this population most closely approximate? What is the general fecundity pattern?

<table>
<thead>
<tr>
<th>$x$ (years)</th>
<th>number surviving</th>
<th>$l_x$</th>
<th>$m_x$</th>
<th>$l_xm_x$</th>
<th>$xl_xm_x$</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>1000</td>
<td></td>
<td>0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>158</td>
<td></td>
<td>0.33</td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>154</td>
<td></td>
<td>0.8</td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>151</td>
<td></td>
<td>2.4</td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>147</td>
<td></td>
<td>3.1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>136</td>
<td></td>
<td>2.5</td>
<td></td>
<td></td>
</tr>
<tr>
<td>7</td>
<td>105</td>
<td></td>
<td>3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>8</td>
<td>74</td>
<td></td>
<td>8.6</td>
<td></td>
<td></td>
</tr>
<tr>
<td>9</td>
<td>22</td>
<td></td>
<td>4.3</td>
<td></td>
<td></td>
</tr>
<tr>
<td>10</td>
<td>0</td>
<td></td>
<td>0</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$R_0 =$

$T =$

$r =$
Patterns of survivorship

- **Survivorship in Phlox**
- **Survivorship in Dall sheep**
- **Survivorship in mud turtles**
- **Survivorship in Uinta ground squirrels**
- **Survivorship in Balanus**
- **Survivorship in female thar**