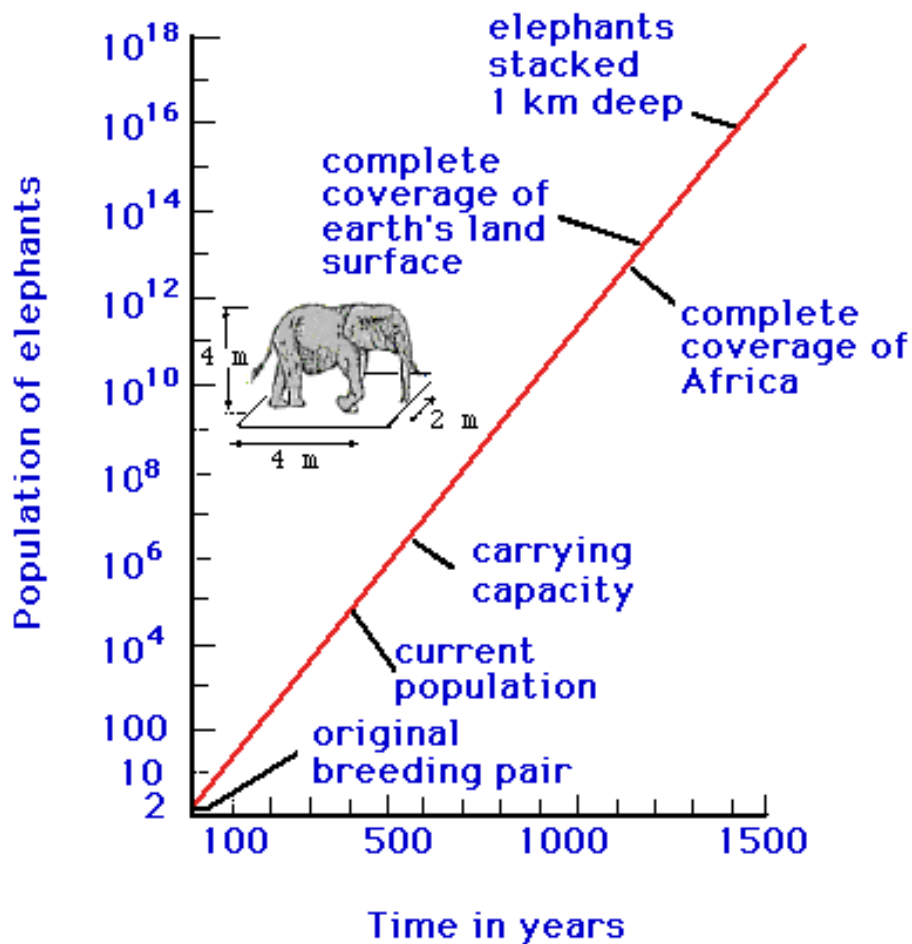
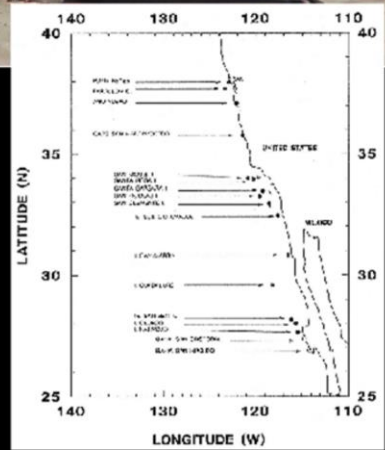
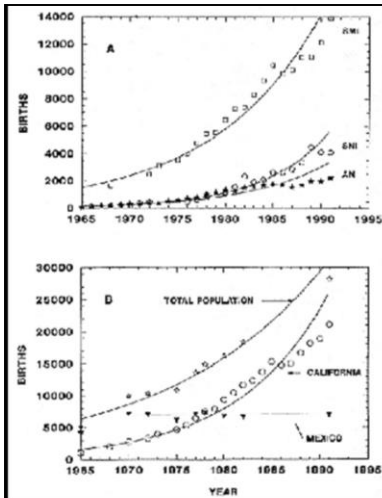




Populations have the potential to grow until something stops them – something becomes *limiting*. So the basic question about populations becomes, *what might limit population growth? And how?* Fundamentally, population growth rate can change only through two processes – changes in birth rate, or changes in death rate. (Note how this simplification echoes the approach of MacArthur and Wilson in thinking about what might regulate the number of *species* on an island.)



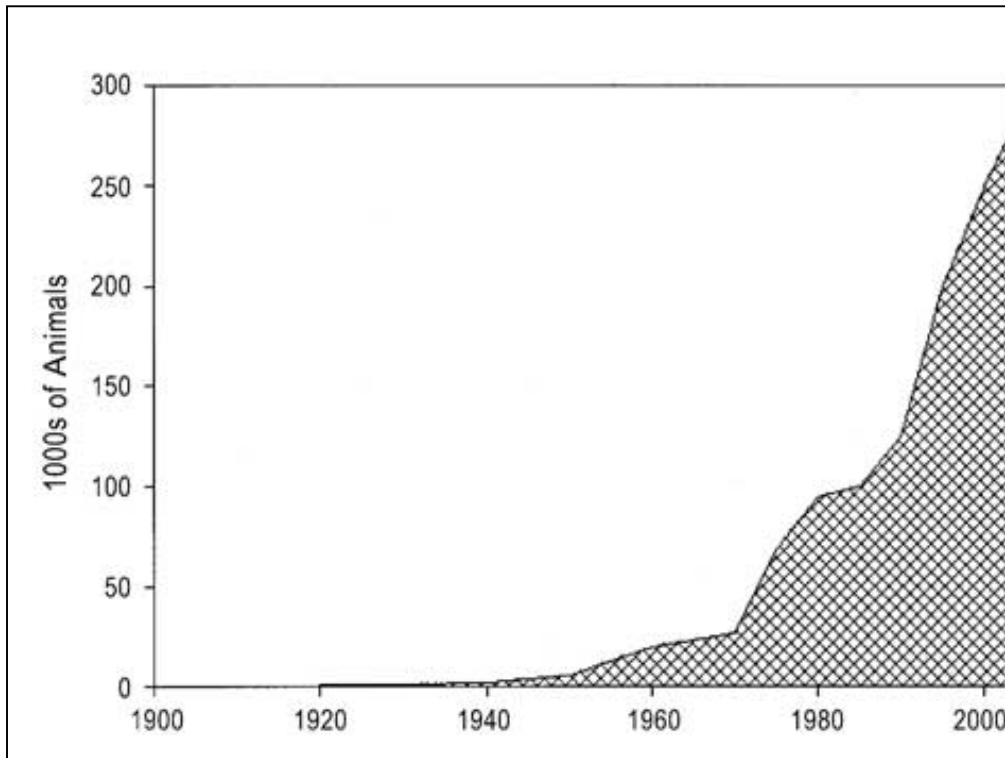
As long as reproduction is unconstrained, rate of addition of individuals to population will be a constant proportion of the population size (or the number of individuals available to reproduce). If death rate does not change, this yields GEOMETRIC or EXPONENTIAL growth. Resulting population trajectory is linear function of time IF plotted on a logarithmic axis. Some terms: r = intrinsic rate increase (net number added per time unit per existing individual) = $b-d$ = birth rate (# born per time unit per existing individual) – death rate (proportion dying per year). Remember that these are all RATES, so they must be thought of as numbers *per* something – or numbers as a proportion of existing population. They might be stated as (for example), “ $b = 2$ births per 100 individuals per year” or “ $b=2\%$ ”; these mean the same thing. **SO, RATE OF GROWTH** = dN/dt = population change per unit time = rN where N is current number in population (NOTE: if you’ve had calculus, you’ll note that this is stated as a derivative, which can be thought of as a rate, and you can do things like integrate it; if not, just think of “ dN/dt ” as rate of growth in N – change in numbers per change in time). From this equation, we can derive: $N_t = N_0e^{rt}$ which predicts population at time t (t time units from time 0) given a *rate of growth*, and the current population (time 0); e is a constant (root of natural logs).



Northern elephant seal

- $N \sim 20$ in 1890s
- protected 1920s
- $r \sim 6-8\%/yr$
- late 70s, $N > 40,000$
- N currently $> 120,000$ (about same as pre-exploitation?)
- by 2100, $N > 27,000,000$

If you look at exponential growth without the logarithmic transformation of the N axis, it looks like the graph upper left; an accelerating curve – an explosive positive-feedback process. Eventually, it will reach a point where the population would very rapidly become infinitely large (or at least as large as you could imagine...).



A real case of sort-of-exponential growth -- CA sea lions following protection. On a linear scale, exponential growth shows a concave-upward curve; initial small positive slopes rapidly become steeper; populations have the potential to approach infinity in startlingly short times. Various interesting properties: DOUBLING TIME is constant under exponential growth with constant r . (So is time for any proportional change, but doubling time = approximately $.70/r$). BUT THIS ASSUMES SEVERAL THINGS THAT ARE IMPLAUSIBLE; summarize assumptions as “ r never changes”. Now take that apart and think about constituent assumptions – why r MIGHT change, or even why r *would have to change*? A more specific list of assumptions of the exponential growth model might include things like: birth and death rates are never affected by population size (N); all individuals in population have same likelihood of living or dying...

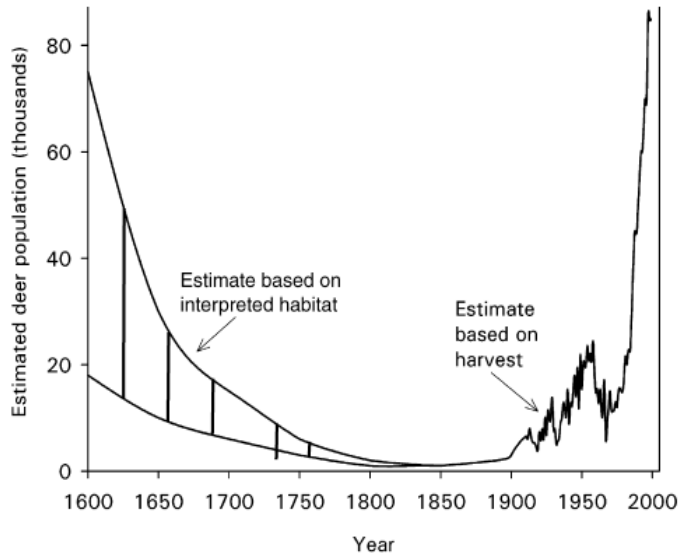
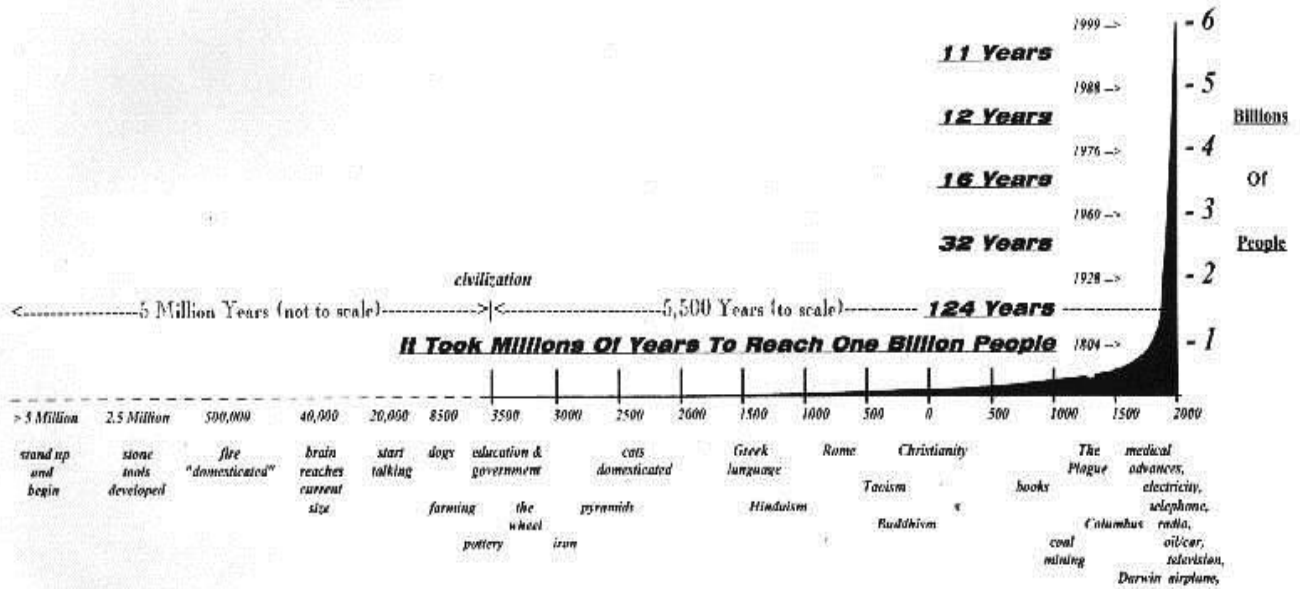


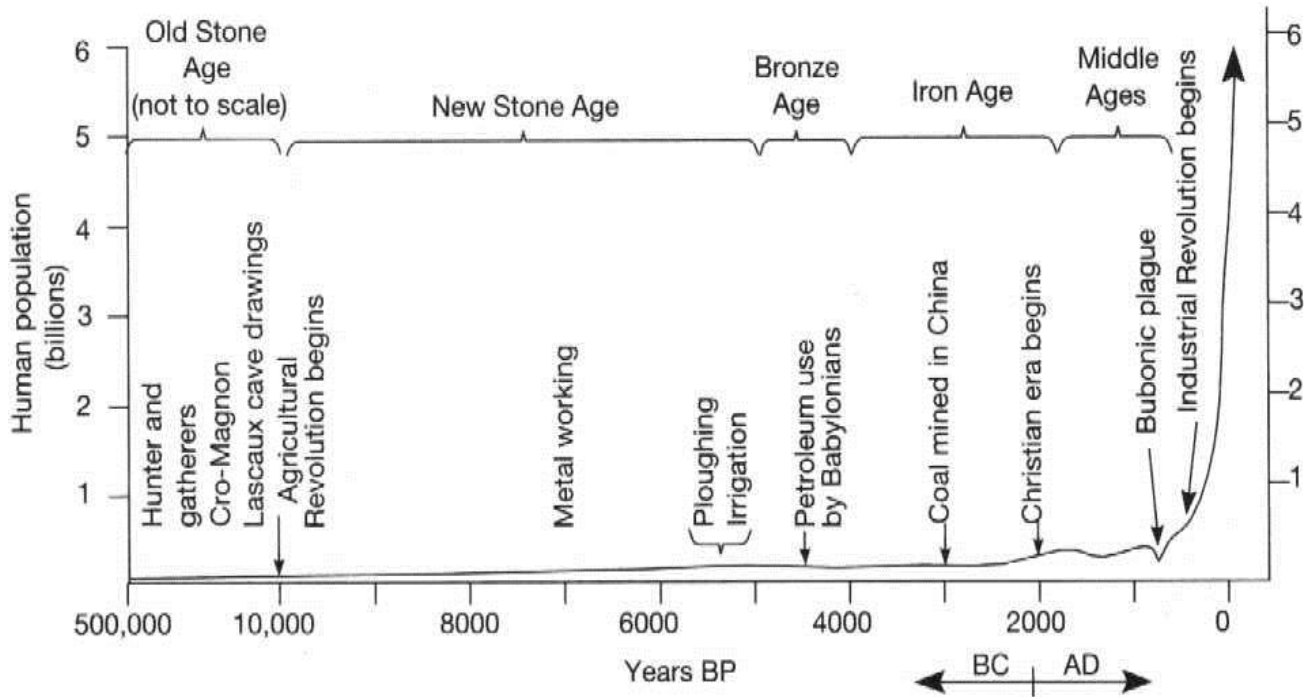
Figure 5 Historical changes in the population of white-tailed deer in Massachusetts. Two early scenarios are depicted that bracket the extreme high and low estimates at the time of European settlement.

Deer in MA

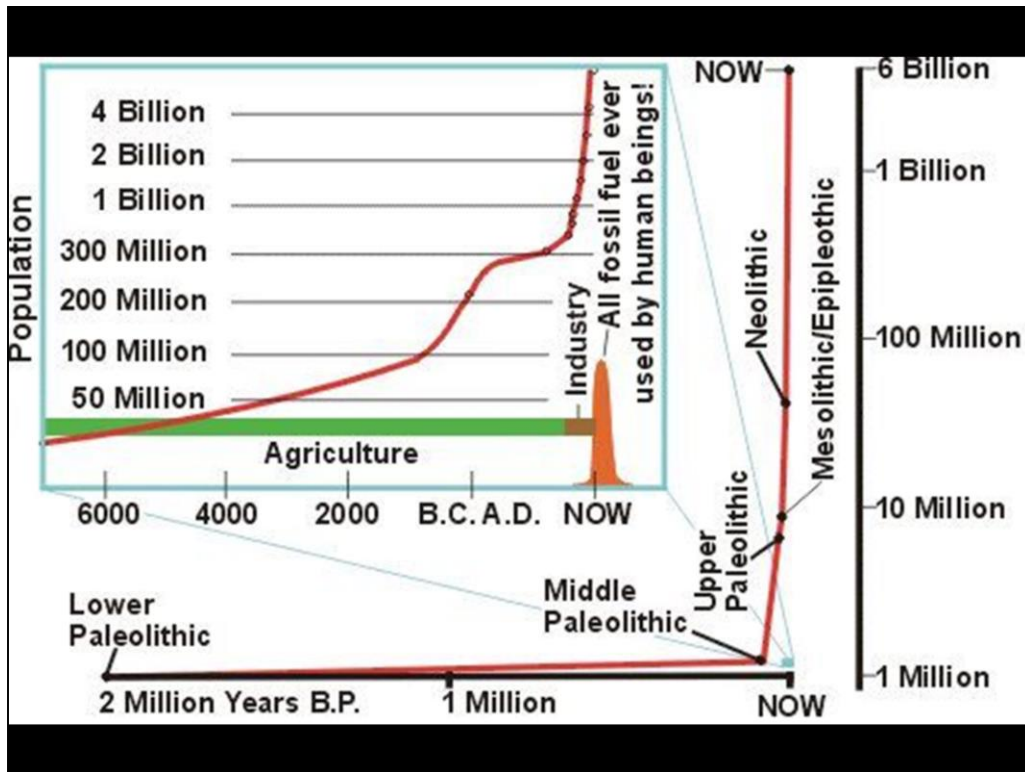
HUMAN HISTORY AND POPULATION



Here, note that doubling time actually gets shorter for some periods (124 years from 1 to 2 billion; only 48 from 2 to 4 billion); that means r is INCREASING. Either b is going up or d going down or both. Hypotheses?



Note that the bubonic plague is one of the very few events in known history that probably caused a significant drop in global population – but the dip lasted only about a century...



Some human demographers (or demographers of humans) suggest that there have been points in human history where r increased (either b increased, or d decreased) because of particular cultural transitions (agriculture, industrialization, etc.)

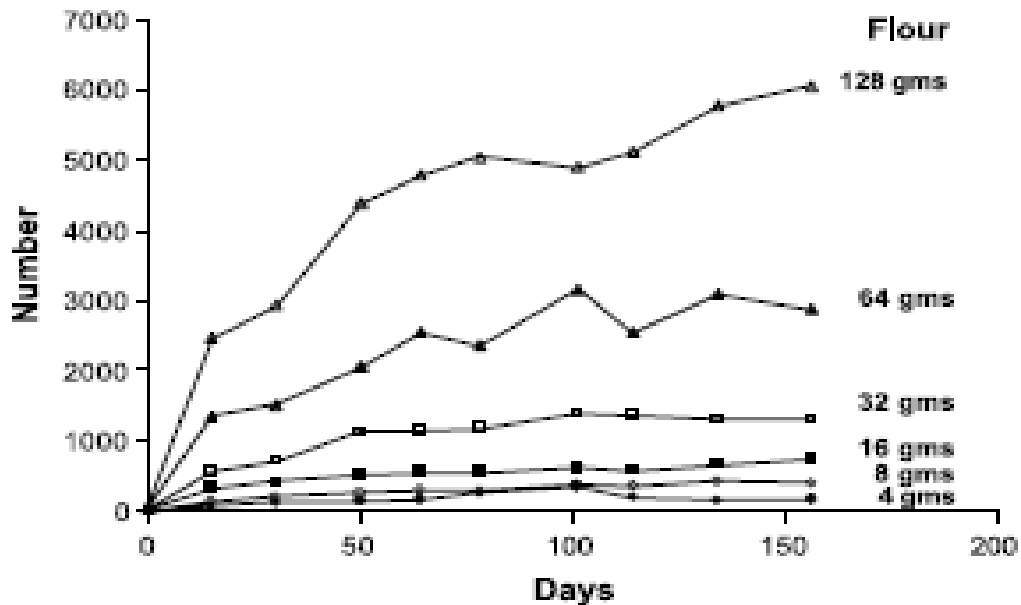
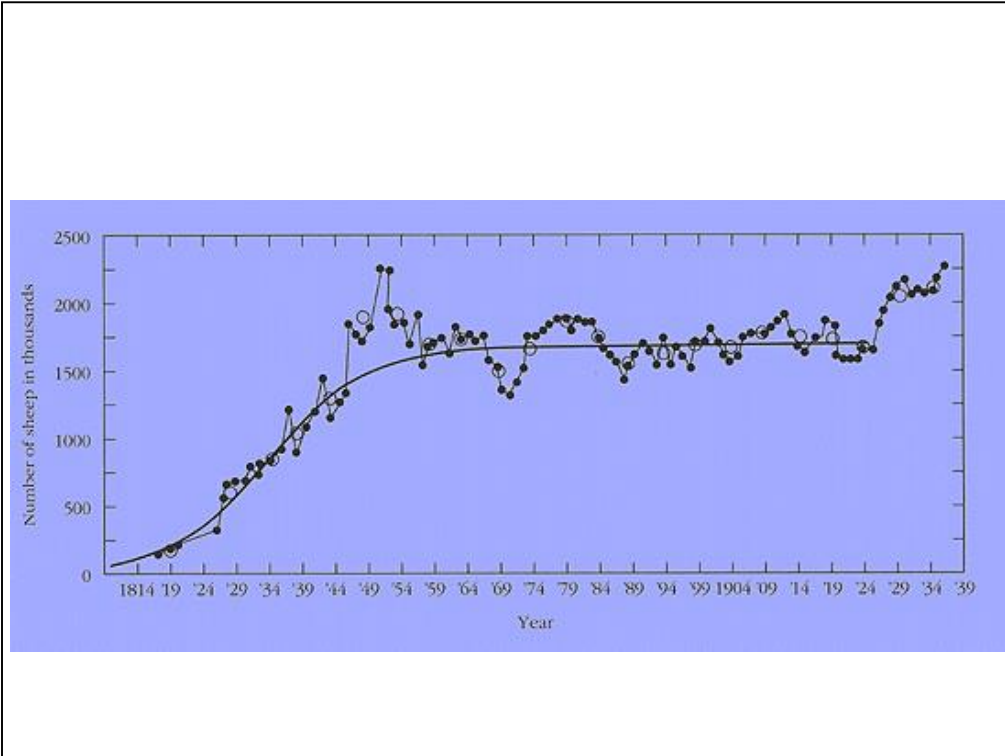
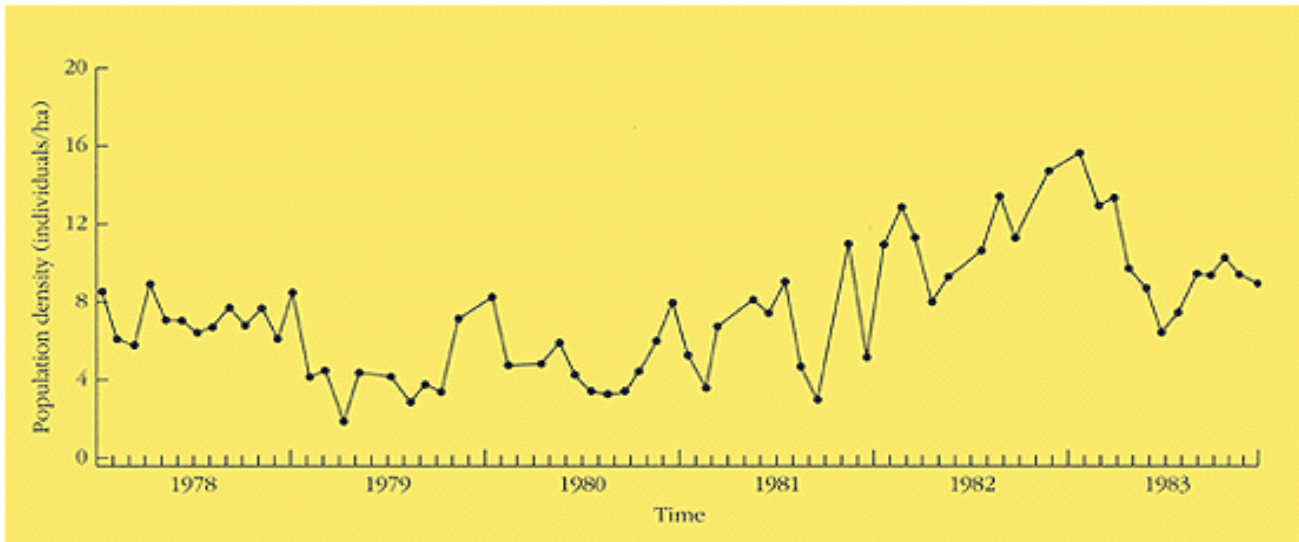


Fig. 1. Growth of six *Tribolium confusum* populations in the laboratory (27°C) when provided with specific quantities of whole wheat flour at the time of sampling (data from Chapman 1928).

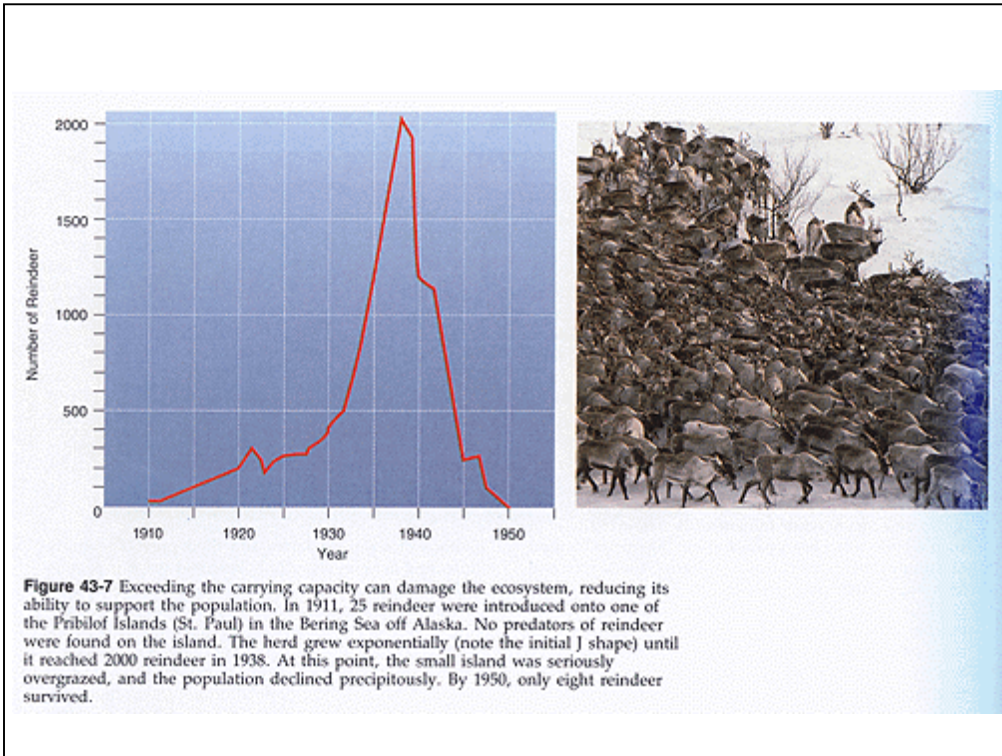
But most often we expect that r must go down as numbers become large relative to available resources, violating assumption that r is the same no matter the value of N . Populations can't become infinite because resources are finite; as populations get large, resources per individual decline and, at some point, this must mean either less reproduction or higher mortality, or both. Simple lab experiments can show this sort of *negative feedback*; here, in a population of flour beetles grown on constant resource supply in the lab. In a simple feedback system of this sort, we might anticipate population leveling off (meaning $b=d$, so $r=0$) at a size where resources are being consumed at same rate they're being supplied. The value of N at this point is often denoted as K or 'carrying capacity' (obviously, habitat specific...). One formula that produces such behavior is the logistic formula, $dN/dt = rN[(K-N)/K]$. BUT this is STILL a simple model with various assumptions that are not typically realistic. For example, it assumes that a) negative feedback of increasing N on decreasing r is instantaneous (no time lags in the number-resource-growth rate interaction); b) all individuals are equivalent; c) resource supply is constant. And some others. Think about how growth dynamics might vary depending how these assumptions are NOT met. "Neat" logistic growth curves are almost never seen in nature.



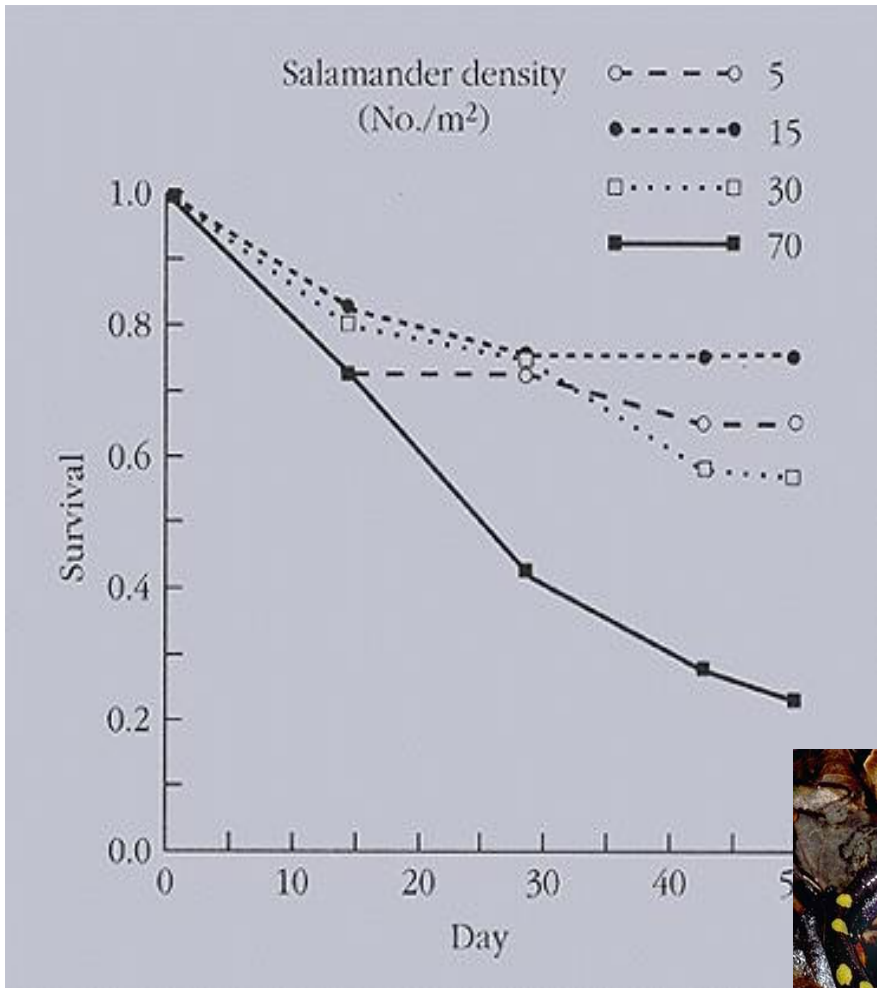
A sort-of-logistic growth pattern in a sort-of-managed population -- sheep in Tasmania. But even here, population fluctuates quite a bit with overshoots and crashes. Still, this population has a clear *density-dependent* dynamic; it's numeric behavior changes with population size/density.



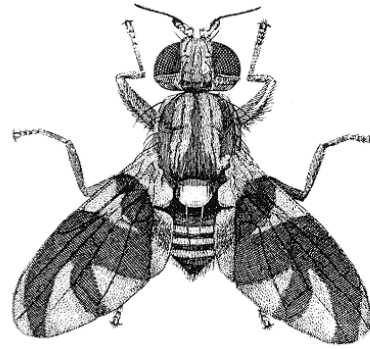
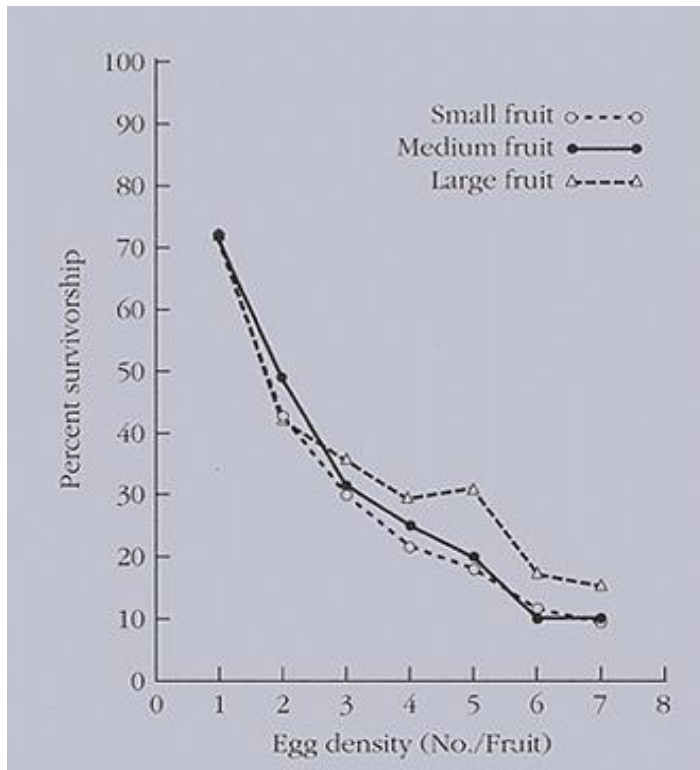
And sometimes no detectable trend towards leveling off at a carrying capacity at all. This graph shows population size for a kangaroo rats in an area of the Mojave Desert in southern CA. This sort of pattern has been taken to suggest that environmental circumstances are so dramatically fluctuating that populations are often controlled by occasional catastrophes instead of number-resource feedbacks at all; ‘crises’ cause high mortality regardless of density, and between crises populations tend to grow rapidly without constraint. Population regulatory factors whose effect depends on numbers of the population are referred to as *density-dependent*; those where chance of mortality is unrelated to numbers (as might be the case with these kangaroo rats) are *density-independent*. Meteorite impacts and tidal waves would be nearly purely density-independent in their effects; your chance of survival is not influenced by N (the size of your population). Effects of food availability on birth or death rates would generally be density-dependent.



An extreme ‘boom and bust’ population history. Why might something like this happen? Consider in terms of how assumptions of exponential and simple logistic models might be violated. Most interpretations suggest that this is a result of a *time-lag* in the response of population properties to resource limits; i.e., the effects of increasing population aren’t evident immediately in form of changes in birth or death rates.

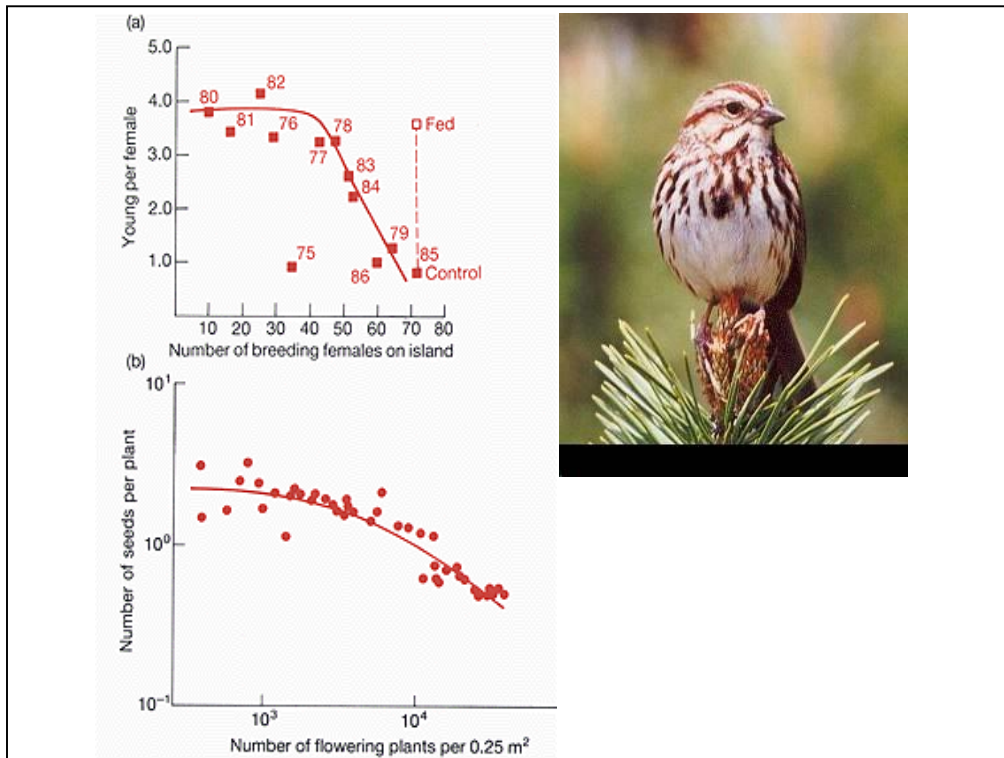


Much attention has been focused on ways of testing for density-dependence in a range of species and circumstances. Fundamentally, this requires showing that birth or death rates are a function of population size or density – that birth rates decrease with increasing N at some point, OR d increases. Here (with spotted salamanders of the genus *Ambystoma*), survival (the inverse of death rate) DOES decline as population density (N) increases – but only above a threshold density. There is generally an *assumption* that such changes are a result of *competition for resources among individuals of the population* ('intraspecific' competition); could there be other processes that would affect survival in this way?



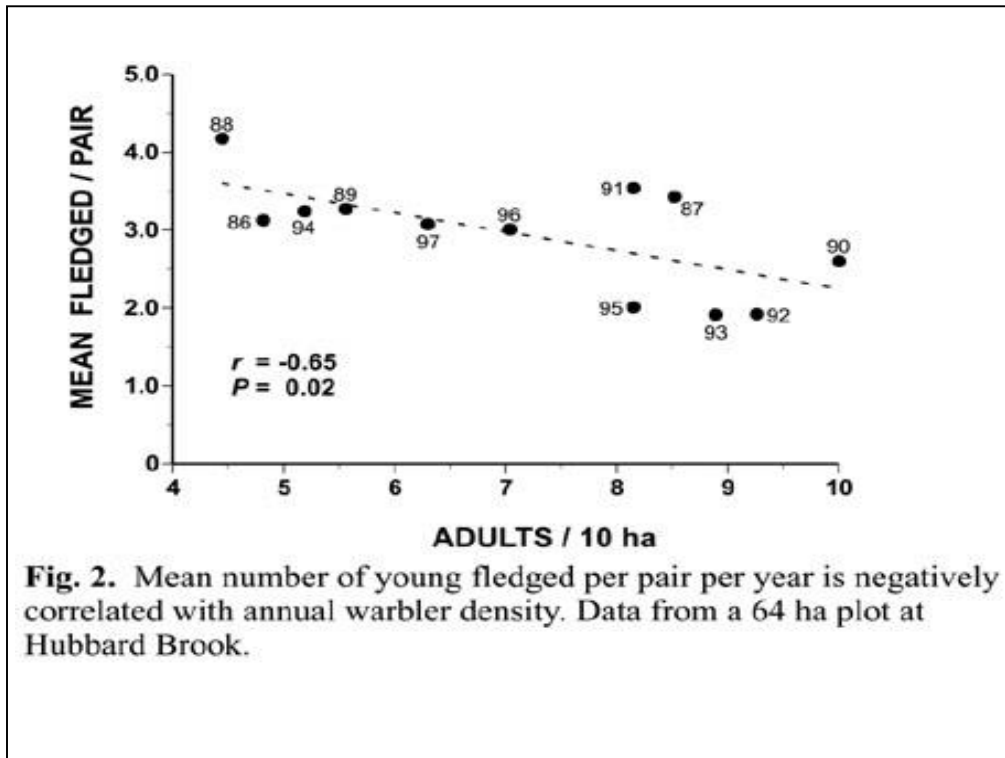
Rhagoletis pomonella

Interpret this graph in a similar way.

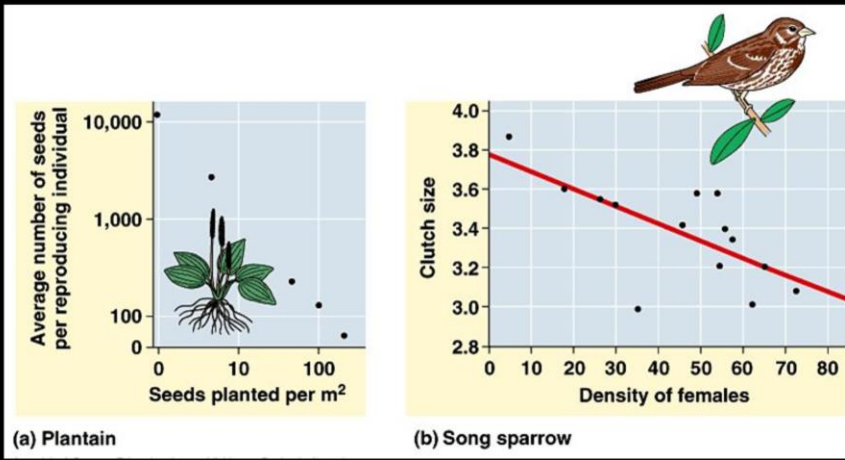


Density-dependence can be a result of limited resources other than food; breeding birds defend territories, and space is finite (focus on top graph, for song sparrows on Mandarte I, British Columbia; each point shows size of breeding female population and number of young fledged per female for a particular year). Consider how results of competition for nesting territories might differ from results of competition for food (hint: you either get a territory or you don't; a loser gets nothing. In competition for food, that might not be so true...) Note that, when song sparrow nests are offered supplemental food even when number of breeders is high, number of young fledged returns to numbers similar to nests in low-density years. What does this imply?

IN GENERAL, then, density dependent population effects can be related to competition for some specific limiting resource. And IF there is density-dependence in population dynamics, there is at least the potential for populations to be regulated by resource competition.



Another natural experiment where evidence is consistent with density-dependence, for warblers in forests of northeastern U.S.. Statistics review: the $P=0.02$ means that a pattern with equal or stronger negative correlation between density and fledging rates has only a 0.02 chance of appearing by chance in a data-set of this size and structure if the null hypothesis of no interaction were, in fact, true. Since this is a low probability, we would typically ‘reject’ the null hypothesis – proceed as if the correlation were ‘real’. That does NOT mean we’ve shown direct causality, however.



More examples of density dependence.

| | ALL | WILD | NEG | NOT HARVEST |
|---------|-----|------|-----|-------------|
| INVERTS | 5 | 0 | 0 | 0 |
| INSECTS | 17 | 10 | 1 | 1 |
| FISH | 7 | 7 | 4 | 0 |
| BIRDS | 23 | 23 | 14 | 12 |
| MAMMALS | 19 | 19 | 14 | 3 |

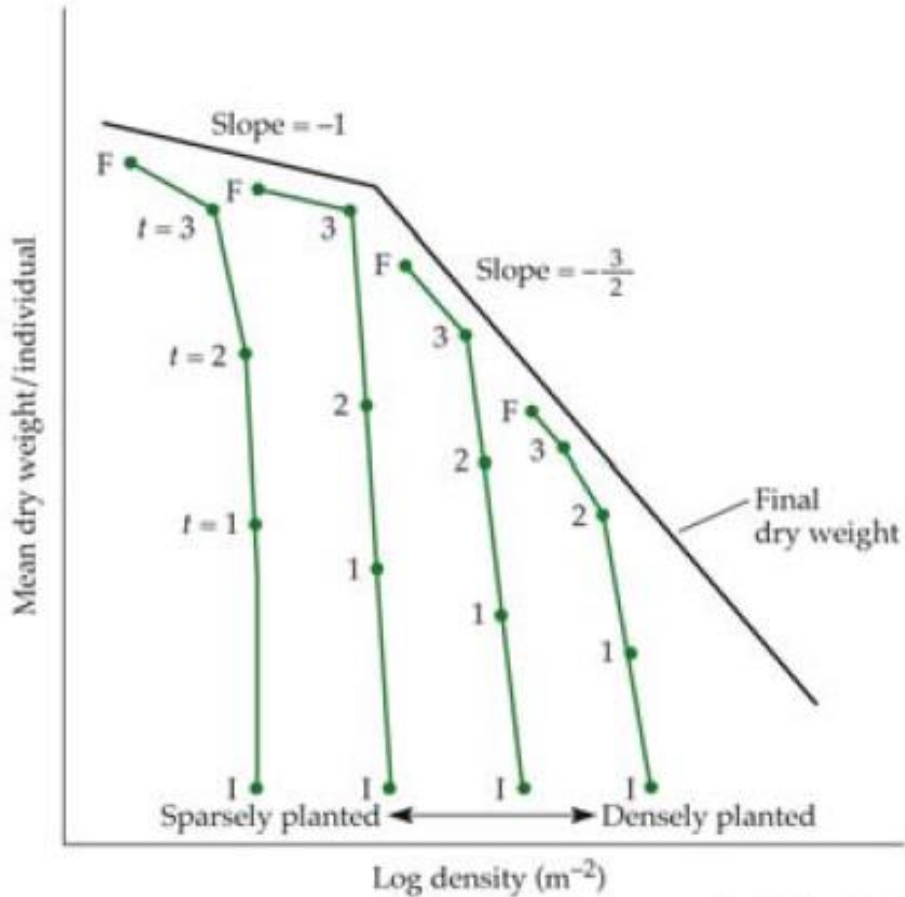
Studies demonstrating density-dependence are proportionally more frequent for birds and mammals. This table tallies published studies showing negative feedback between N and r (the “Neg” column) – that is, as N goes up r goes down. It’s an old compilation, but the pattern has remained about the same.



The actual mechanisms for the negative feedback of *resource competition* on *population growth* (either birth or death rates) differ depending on the nature of the resource and the organisms, and the effects can be very different as a consequence. Birds competing for nesting sites (like peregrine falcons, who nest on cliff ledges, which can be scarce, and defend an area around their nest site from other falcons), *actively confront* one another; this is often referred to as ***contest competition***, and is ‘winner takes all’. Aside from the risk of energy, the winning bird may experience little or no negative consequence, but the loser may fail to reproduce altogether. Crowded aspen trees (left), however, are not sequestering and defending resources (light, soil nutrients...) from each other; they’re simply ‘grabbing’ what they can before another individual gets it. Some individuals may get more than others and become ‘dominant’, but even the ‘losers’ get some resources (at least for a while). This ***scramble competition*** is typically manifest in differences in vigor (and, eventually, survival) among individuals. These models of competition are sometimes referred to as *interference* and *exploitation*.



Male elephant seals exhibit an extreme version of contest/interference competition for mating opportunities; males maintain harems of up to several dozen females and actively battle other males over control of the harem; fighting among males frequently leads to severe injuries and even death.



If you're interested in some more sophisticated models and quantitative relationships, focus on the next three pages...

'Scramble' competition can produce interesting patterns, like the '-3/2 power thinning law' in plants. Each green curve shows a single experimental population over time since planting (from "1" through time 1, 2, 3); where-ever you start, density-wise, as plants grow, they eventually start dying off at a rate related to average size – and all experimental population converge on the same line!

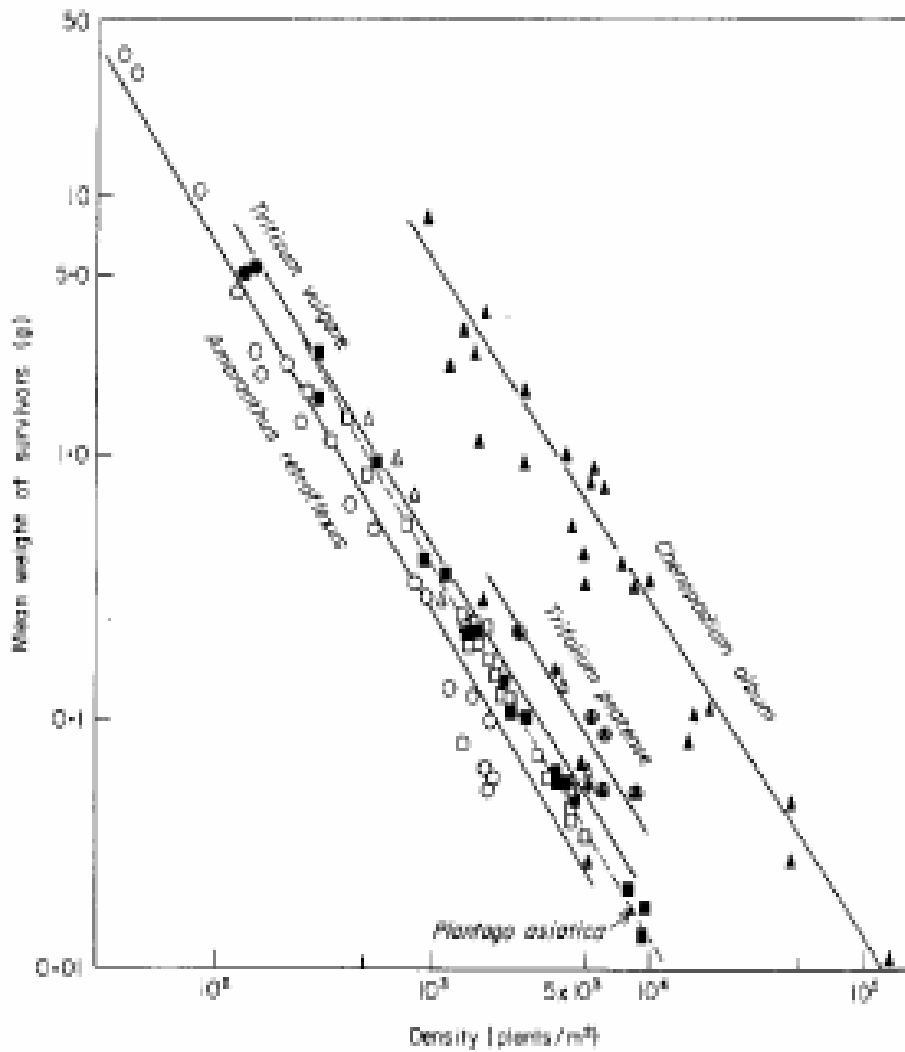
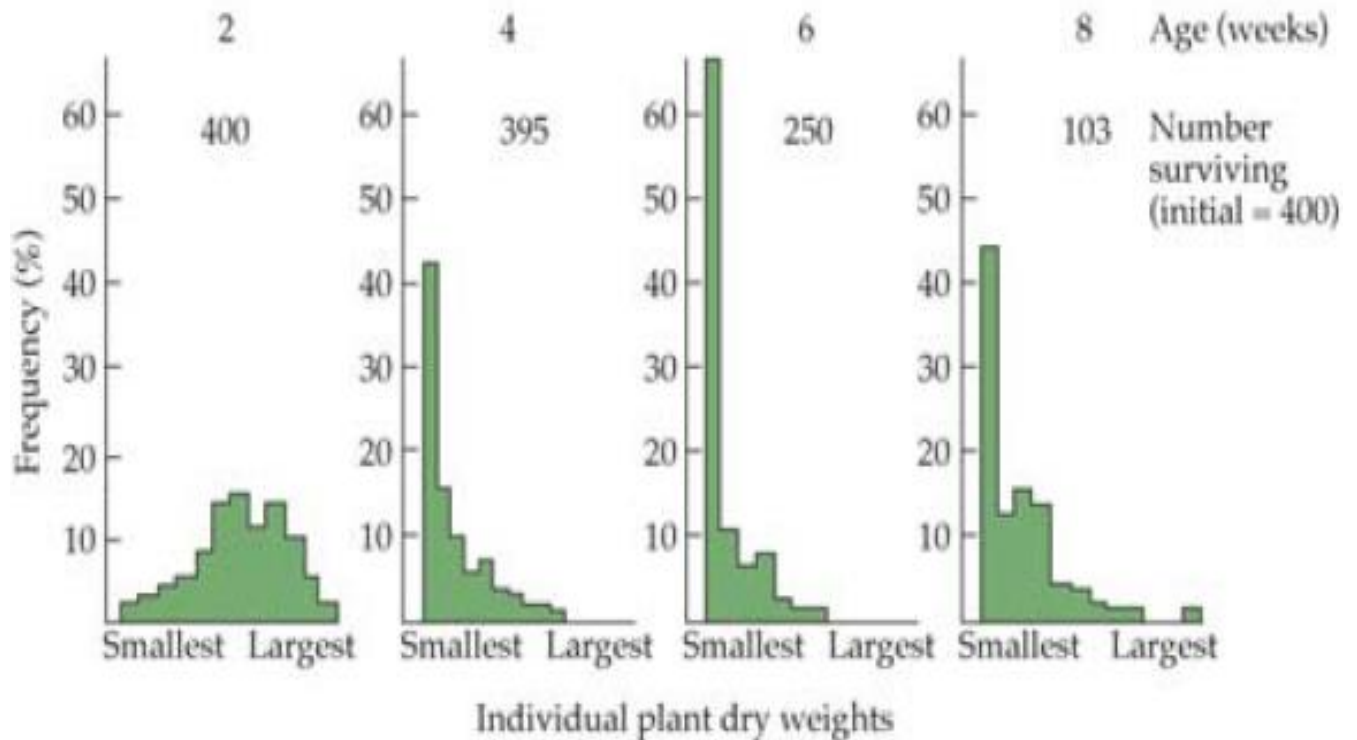


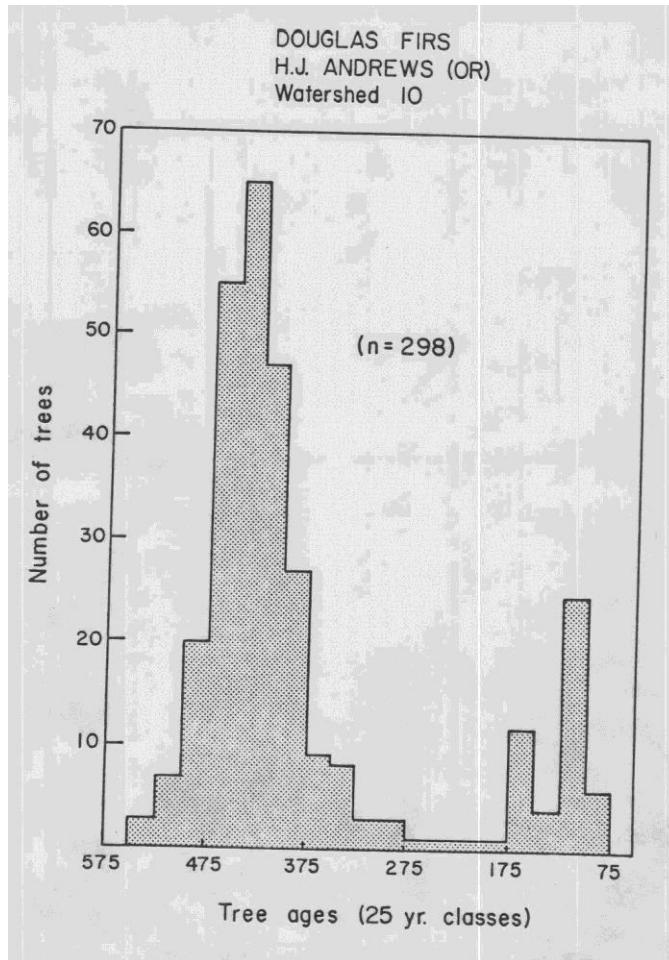
Fig. 6/22a. Changes in plant density and in mean plant weight with the passage of time. Data for *Chenopodium*, *Amaranthus*, and *Plantago* from Yoda et al., (1963); data for *Trifolium* and *Trifolium* from Harper and White (1970) after data of Black and of Packeridge.

And many species show similar pattern with same slope: slope = $-3/2$

Changes in size at constant starting density



Another common trend in density-dependent processes: size distributions become progressively 'skewed' with a very few LARGE individuals ('winners') and many small losers (the ones who die in thinning). This is referred to as strong DOMINANCE. Recall pine trees in the plantation; big trees get more light and so get bigger faster; winning a little means winning even more.



Simple models assume that all individuals in a population are identical – have same likelihood, for example, of dying or giving birth. For organisms where AGE matters, this assumption is generally inappropriate. *AGE STRUCTURES* describe how individuals in a population are distributed among age groups. A group of individuals of similar age in a population is referred to as a *cohort*. A population with an *AGE STRUCTURE* dominated by old trees might have very different growth rate than one dominated by young trees. Note also that an age structure like this one will necessarily change shape over time; it is unstable. This is obvious when younger age classes are less abundant than older; as trees in older classes ‘age out’ they can’t be replaced in equal abundance if younger classes are not there!

DOUGLAS - FIRS
H.J. ANDREWS (OR)
(Silver Fir/Foamflower Type)

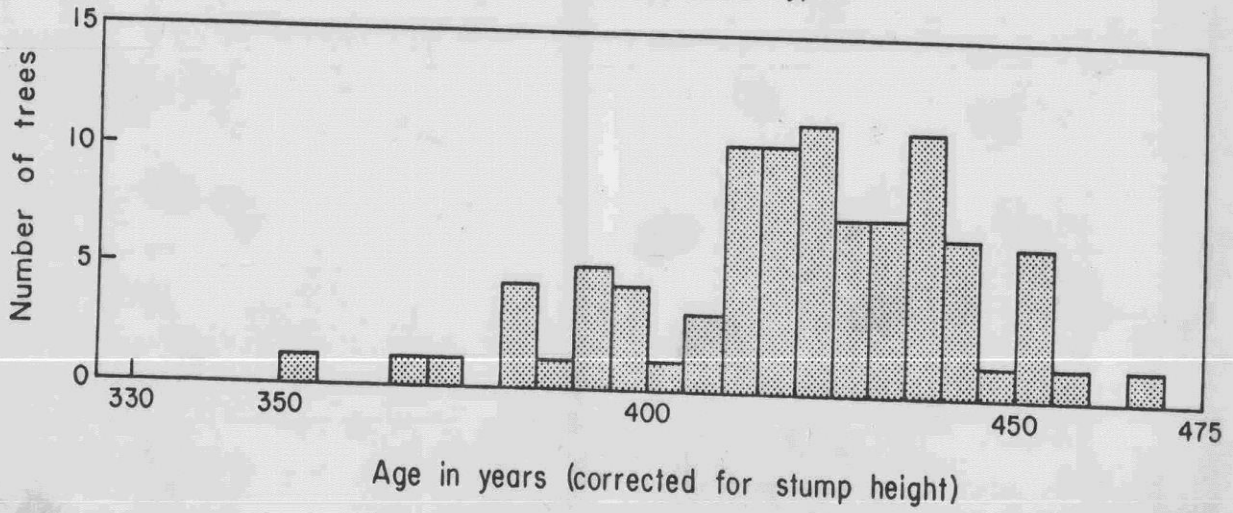
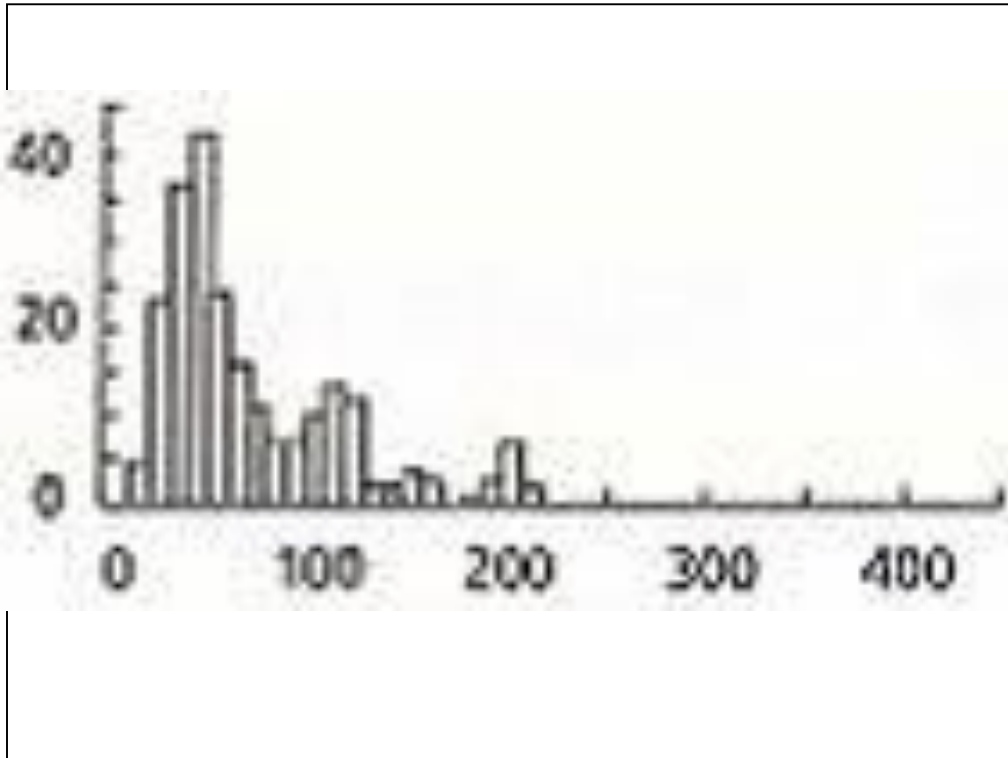
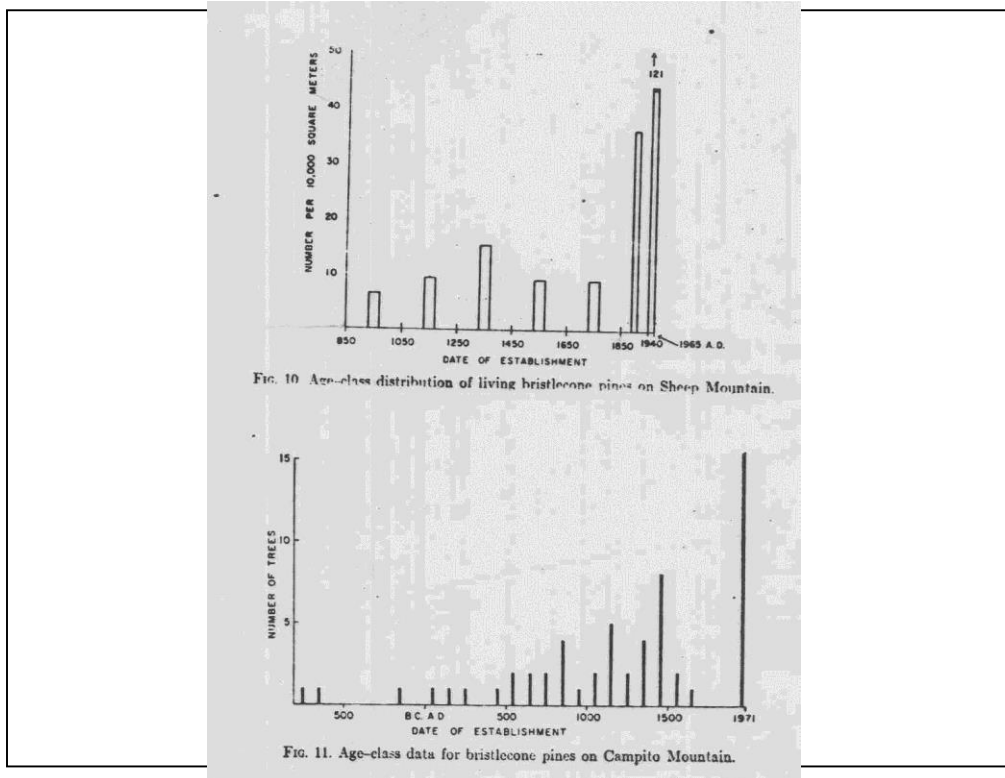


Figure 3

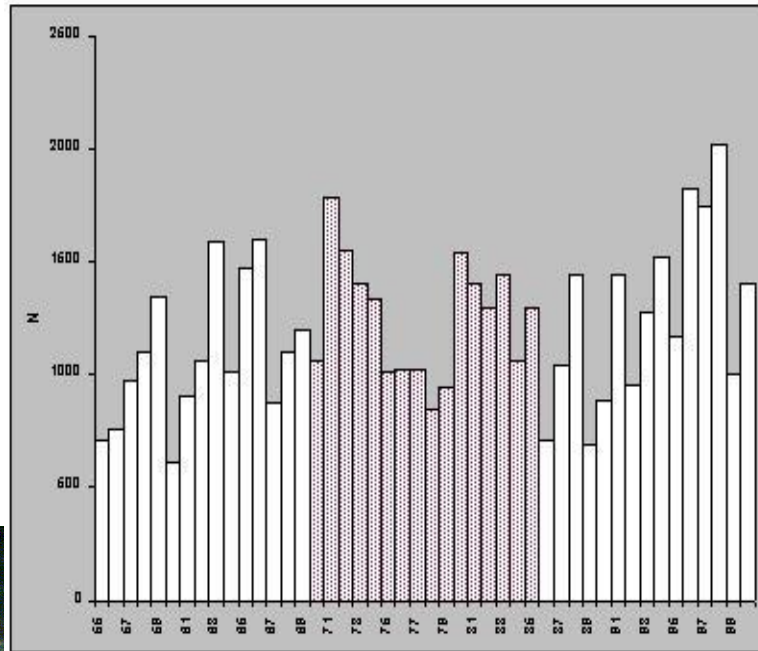
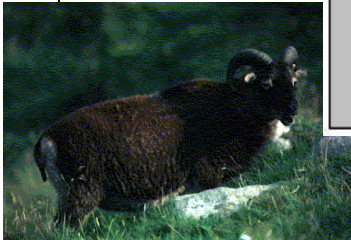
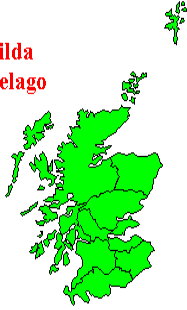


Age structure for a Scots pine population. Discounting the apparent rarity of trees < 20 years old (maybe due to their not being large enough to core), this age structure might be approximately *stable*; frequency of each progressively older age class is generally lower (although this pattern isn't perfect; there are some 'bulges' possibly reflecting large COHORTS establishing approximately 100 and 200 years ago).

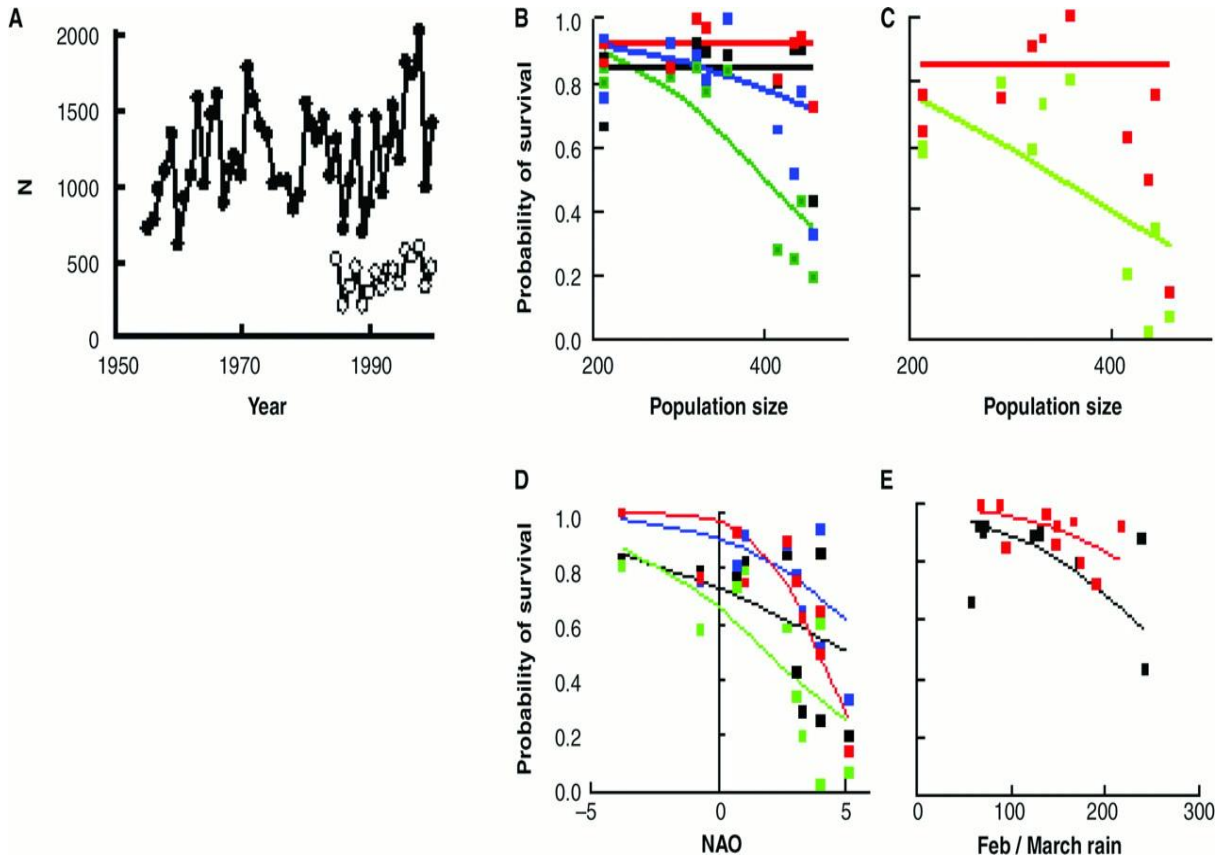


Bristle-cone age structures. Bristlecone pines can live several thousand years so, even though new cohorts may establish only every century or two or three, an age structure like that shown in bottom graph may be relatively stable. (we have a lot of age-structures for tree populations; few for long-lived animals. Why is that?)

St. Kilda
archipelago

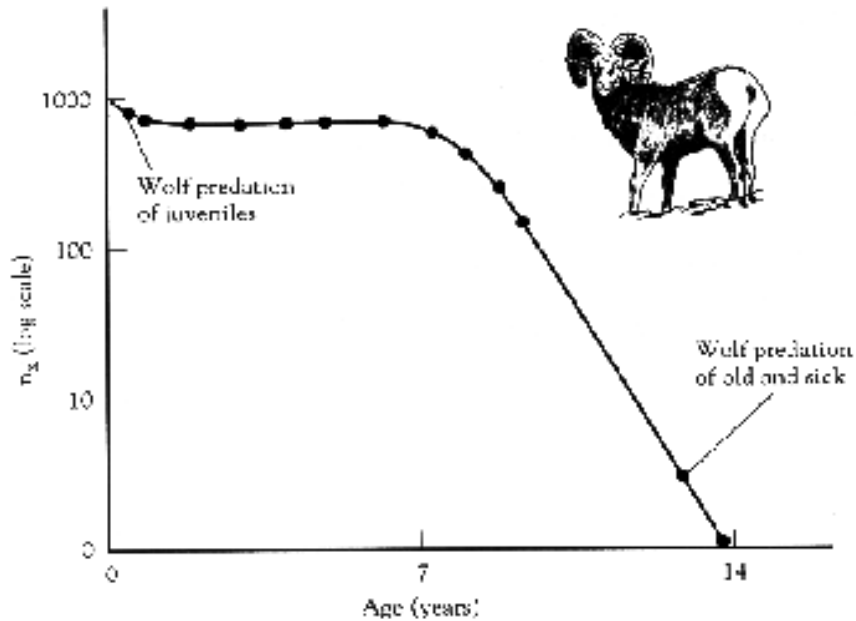


Feral sheep on St. Kilda Island – an isolated archipelago west of Scotland -- a classic study showing density-dependence in the wild. Here: numbers fluctuate from year to year over a wide range.



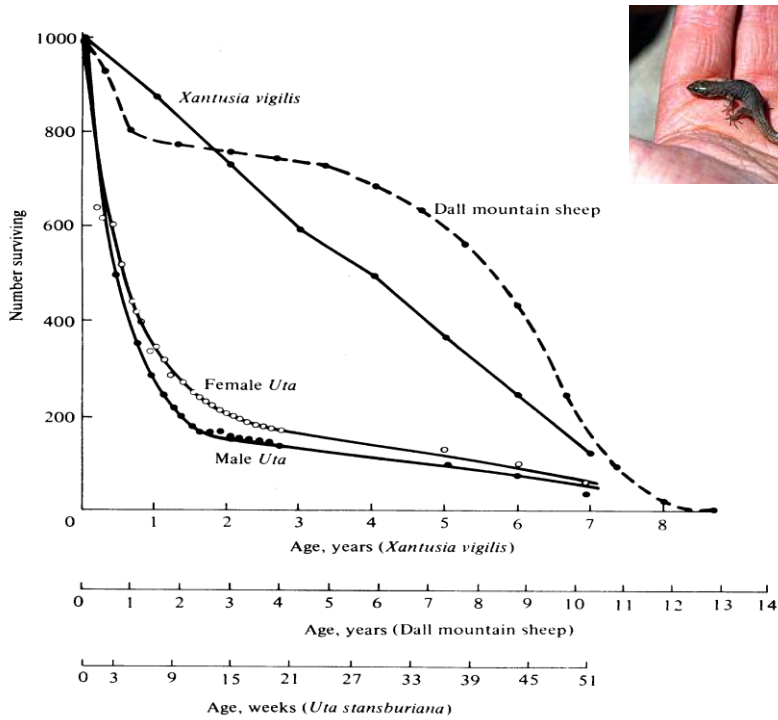
But note the relationship, in this multi-year data-set, between number and probability of survival from one year to next. Also note differences in survivorship curves for different age groups and sexes (graphs B and C). Again, assumption that individuals are demographically identical is violated. Figure B and C: Lambs have lower survivorship (higher mortality) than adults, and lamb mortality is strongly *density-dependent* (not so much for adults, although *old females* show increasing mortality at higher density). Figures D and E: The North Atlantic Oscillation is a pattern of fluctuating weather. Survival is much lower when it is at its 'higher' extreme...

Survivorship for Dall mountain sheep (Murie 1944)

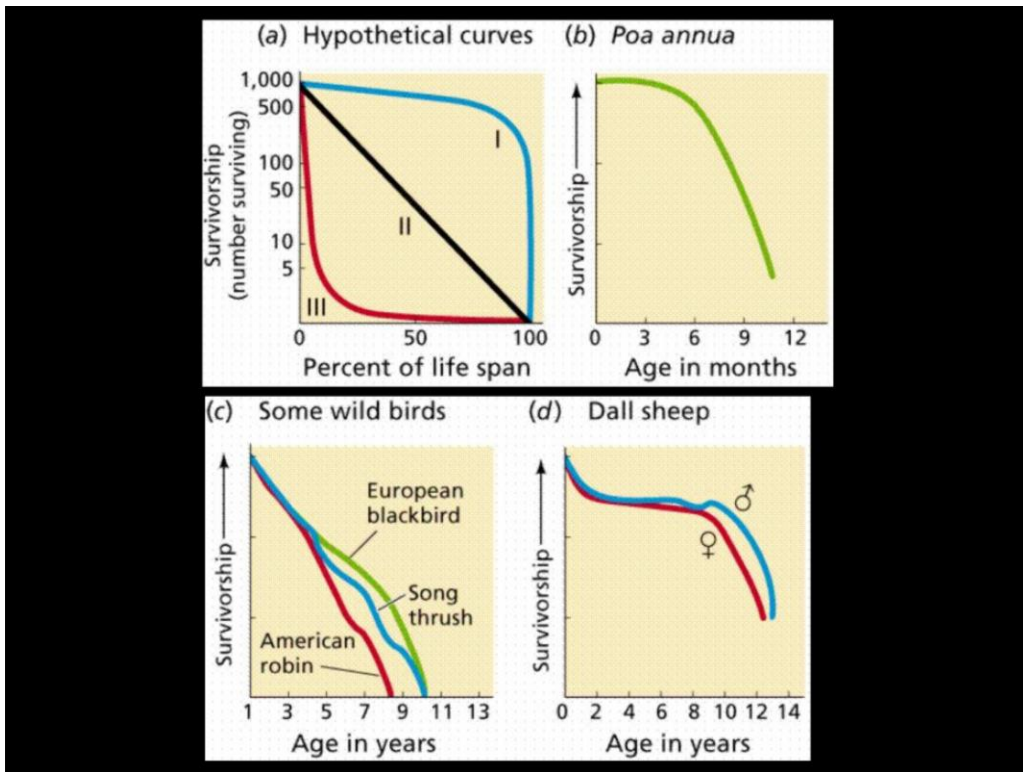


From Stiling 1999

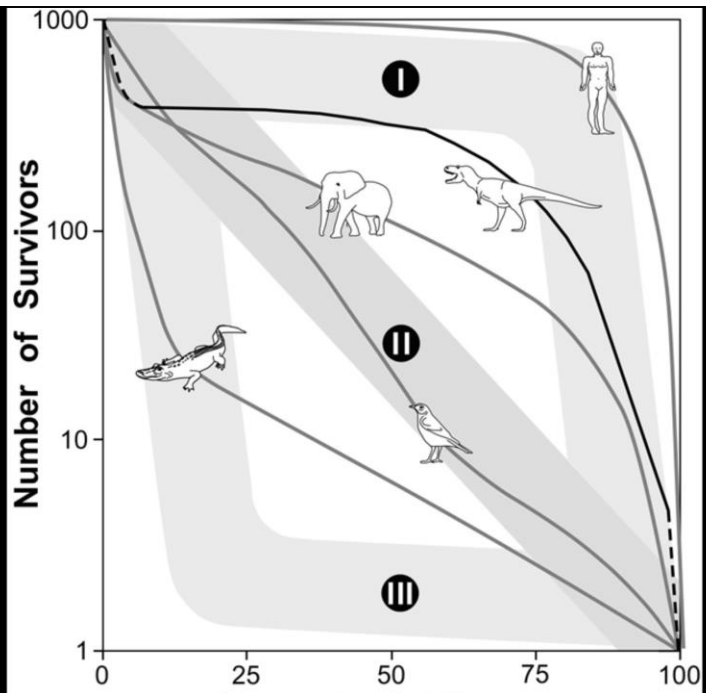
Another demographic/population property is the SURVIVORSHIP CURVE. In concept, this represents the number surviving over time from an original COHORT of 1000 (sometimes standardized to 100). Note exponential vertical axis. This is a typical mammalian survivorship curve; it shows that, after early losses of lambs, 'adolescent' and young adult sheep survive very well until about age 7, when numbers begin to decline exponentially. Mortality in this study is due mostly to predation.



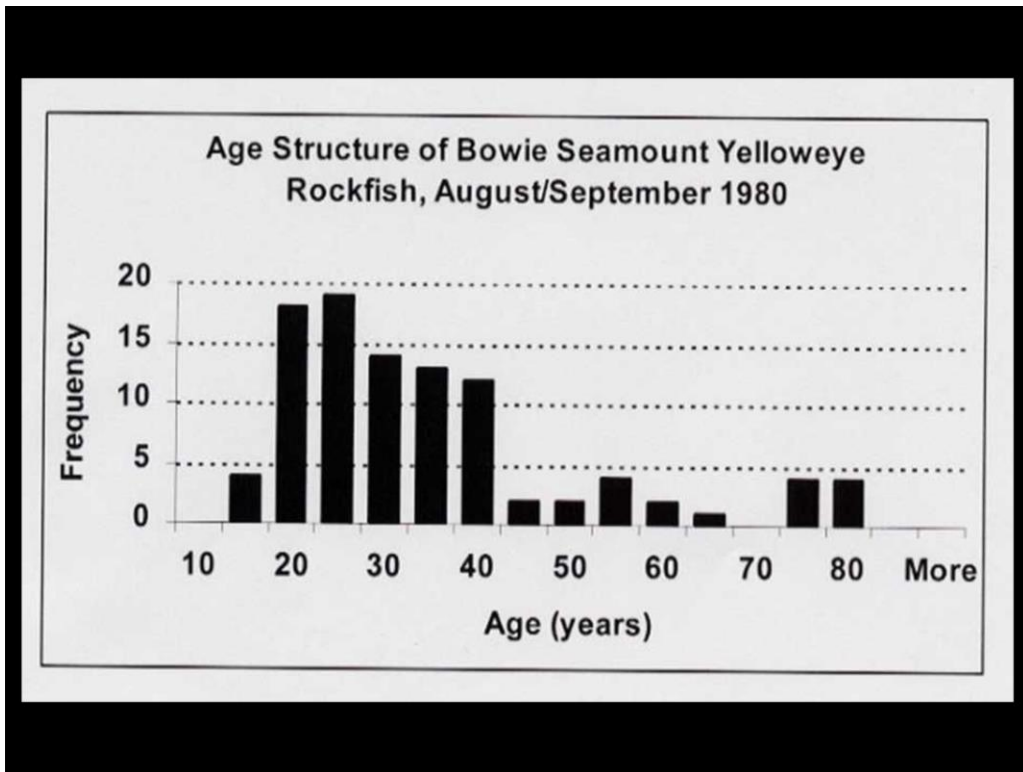
But some creatures show very different survivorship patterns with age. CONSIDER how shape of age structure and shape of survivorship curve are related. An age structure MAY be stable ONLY if it has similar shape to survivorship curve. THINK ABOUT IT....



Some more survivorship curves. Demographers talk about three general types of survivorship curves; type I (high survivorship until old age), II (constant mortality rate), and III (very high early mortality, but high survival once adulthood is achieved). Of course all intermediate shapes occur, but these 'models' help think about how different chief causes of mortality might affect populations and how different life-histories might play out. What sorts of organisms would you imagine showing each type of curve? WHY?.



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POPULATION BIOLOGY CONCEPTS have important practical applications: for instance, the age structure of a harvested fish population can say a lot about whether harvests are sustainable or not.

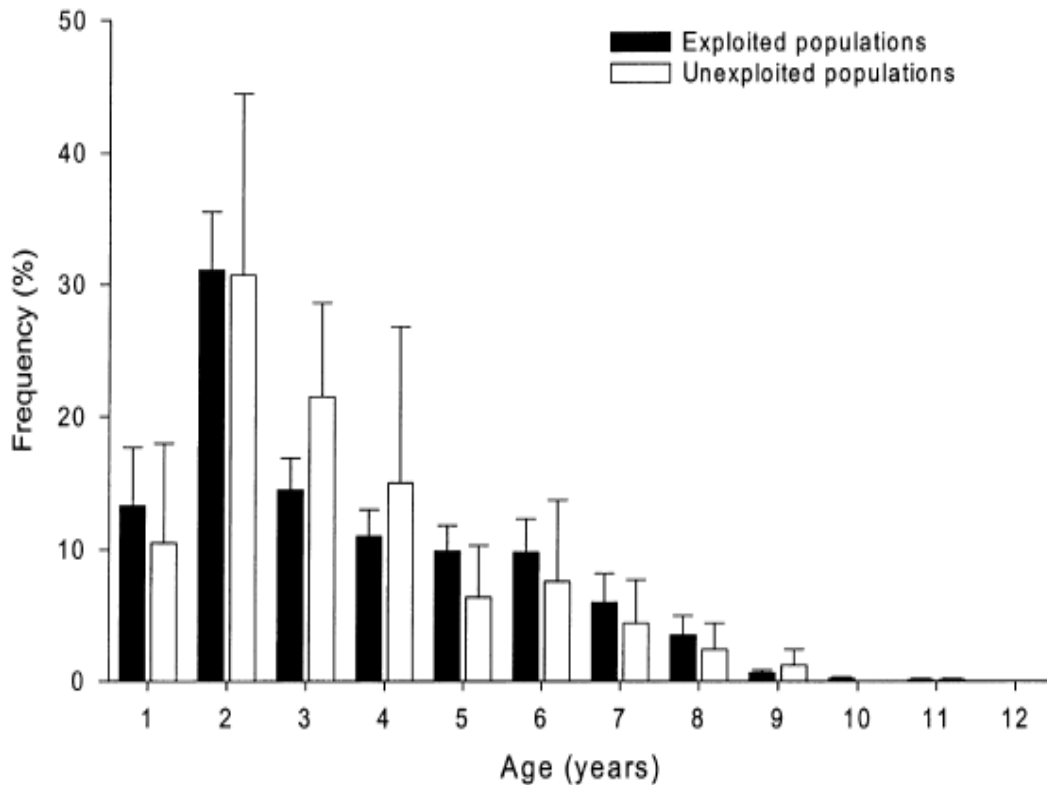


Figure 1. Age structure of exploited and unexploited yellow perch populations in Nebraska Sandhill lakes sampled in 1998 and 1999. Values for each age group represent the mean relative frequency with error bars representing ± 1 SE.

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In fact, effects of human exploitation on wild populations can be most evident in altered age structures; a fisheries manager can use this information. If an ‘exploited’ population exhibits *younger* cohorts that are smaller than *older* ones, that strongly indicates unsustainable over-exploitation...