Populations have potential to grow until something limits them
As long as reproduction is unconstrained, rate of addition of individuals to population will be a constant proportion of the population size (the number of individuals available to reproduce), yielding GEOMETRIC or EXPONENTIAL growth. Resulting population trajectory is linear on a logarithmic axis. Some terms: \( r \) = intrinsic rate increase = \( b - d \) = birth rate (#’s born per year as proportion of pop size) – death rate (proportion dying per year). RATE OF GROWTH = \( \frac{dN}{dt} = rN \) where \( N \) is current number in population (NOTE: “\( dN/dt \)” just means rate of groth – change in numbers per change in time). \( N_t = N_0e^{rt} \) predicts population at time \( t \) given population now (time 0); \( r \) is a constant (root of natural logs).
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.
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.
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?
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 \( N \). 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, \( \frac{dN}{dt} = rN\frac{(K-N)}{K} \). BUT this is STILL a simple model with various assumptions that are not typically realistic. For example, it assumes that a) 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.

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**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).**
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.
And sometimes no detectable trend towards leveling off at a carrying capacity at all. 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 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.
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.
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.
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.

**Fig. 2.** Mean number of young fledged per pair per year is negatively correlated with annual warbler density. Data from a 64 ha plot at Hubbard Brook.
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.

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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. 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)

Number of trees

Age in years (corrected for stump height)
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 (we have a lot of age-structures for tree populations; few for long-lived animals. Why is that?
Feral sheep on St. Kilda Island – an isolated archipelago west of Scotland -- a classic study showing density-dependence in the wild. Here: numbers fluctuate.
But note the relationship, in 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. Again, assumption that individuals are demographically identical is violated. Figure 1. (A) The size of the whole island (solid circles) and the Village Bay populations (open circles). Associations between survival and (B) density in females (green, lambs, black, yearlings, red, adults, blue, older adults), (C) density in males (red, adults, green, lambs) (D) the North Atlantic Oscillation in males and females (red, adult males, blue, older females, black, female lambs, green, male lambs) and (E) March/February rain in females (red, adult females, black, yearling females)
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.

From Stiling 1999
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....
Human survivorship curves. Most modern curves are typical of high-parental care species (like the Dall sheep); note the vertical axis is linear, not exponential; on exponential axis, all of these would look more like the Dall sheep curve.
Human populations have a strong ‘Type I’ – mammal-like – survivorship curve with relatively high survivorship in early years, very low mortality through adult years, and rapid decline of cohort size only in senescence. This is generally associated with high levels of parental care. Which of these AGE STRUCTURES, given similar survivorship curves of this sort (they are) can be approximately stable?
Effects of human exploitation on wild populations can be most evident in altered age structures;

**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.

Unstable age structure due to baby boom…
Competition for resources (and density-dependent effects) can take different forms: ‘exploitation’ or ‘scramble’ competition is when individuals simply consume resources making them unavailable to others; ‘interference’ or ‘contest’ competition involves active confrontation over resources (e.g. nest sites for peregrine falcons).
‘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 “I” 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 Triticum from Harper and White (1970) after data of Black and of Packeridge.

And many species show similar pattern with same slope: slope = -3/2
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.
Isle Royale and population regulation of moose and wolf
Isle Royale is 544 km² in area

http://www.nps.gov/isro/home.htm
Moose arrived in early 20th century by swimming
Moose populations grew exponentially and depleted primary winter food sources (they browse on twigs and conifer needles)
Habitat differences. Moose eat a lot of aquatic vegetation for sodium. Some trees provide more nutritious browse...
Wolves arrived in mid-20th century by crossing ice
And starting eating moose. Note that wolves are extremely social; hunting success depends on pack dynamics. Reproduction is in packs only and usually involving only one pair of wolves in the pack.
In 1996 carcasses of 175 dead moose were examined, and skulls and other specimens accumulated at the summer research cabin on Rock Harbor.

Long-term studies of wolf predation, moose mortality, etc. Check out http://www.isleroyalewolf.org/wolfhome/home.html
Not all moose are equally vulnerable to wolves; they prey disproportionately on young and old moose.
Populations of both have fluctuated dramatically since long-term studies began. Are moose populations regulated by predation or food? Wolves by food or disease (or inbreeding)? Or both, indirectly by climate?
Wolves don’t always hunt ‘efficiently’; sometimes they kill lots more than they eat. (graphic didn’t translate well; but) When times are good (25% of the time), wolves get 2-4 times more food than when times are bad (25% of the time). Maximum kill rate is 2-1/2 times typical kill rate.

Minimum kill rate is 15% of typical kill rate.
This seems to be related to snowfall; moose are easier to kill in high-snowfall years because they are hungrier and can’t move around as easily.
High moose populations are correlated with low bone-marrow fat.
Lower NAO index = greater snow depth correlates with larger wolf packs
Kill rate per pack (and per individual wolf) increases with wolf pack size
So climate interacts with moose vulnerability interacts with kill success interacts with pack size interacts with kill rate…
Wolf pack interactions have varied greatly, with more packs, there can be more wolves – but packs fight for territory. Some packs are better hunters than others. Some years kills are concentrated along shore (where ‘yarding’ areas allow moose to overwinter in less deep snow); other years more widely scattered...
Some data suggest climate differences regulate plant productivity and drive everything from the ‘bottom up’. Some suggest ‘top down’ regulation by wolves; when wolves depress moose populations, plant populations respond by increased growth…) “Fir” curves show measured growth rates (ring-widths) for fir trees in two areas. Note that “AET” is actual evapotranspiration - related to rate at which trees pump water through foliage -- but don’t worry about that too much.
And food availability for moose may simply be changing due to long-term change in abundance of fir trees as they are competitively displaced by other species.