

Limits on Population Growth

EFB 370: Population Ecology

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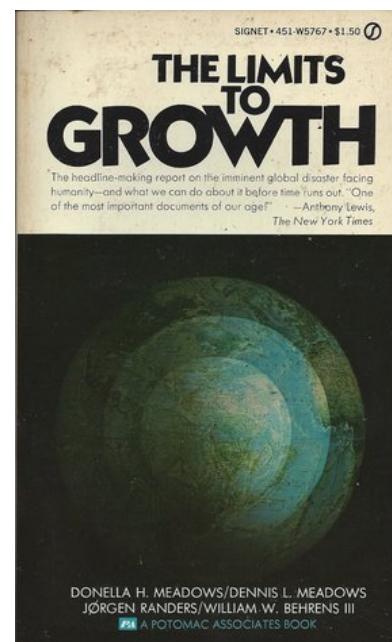


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As populations grow ...
they always hit **Limits to growth**

- Space limits
- Resource limitations
- Competition
- Predation
- Disease

All of these can and do interact



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Fundamental population equation

$$\Delta N = B - D + I - E$$

Exponential growth assumes these (especially **Birth & Death**) are proportional to **N**.

But at high N ... B can fall, or D can rise, or I can decrease or E can increase.

Density dependence

Means that the *rate* of a parameter, e.g. $b = B/N$ or $d = D/N$ is

- (a) NOT constant
- (b) dependent on total population (or density) N

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Meet the Squirlicorn (*Sciurus monocerus*)

Natural History Facts

Limited range: Only found on **Okie island**

Extremely territorial: Strictly ONE squirlicorn per oak tree.

One colonist ($N_0 = 1$) appears on Okie Island, which contains **K** oak trees

Reproduces **asexually** with some fixed probability p_b per year.



Offspring disperses to nearest tree.

If tree is occupied, existing squirlicorn **assassimates** newcomer with its horn.

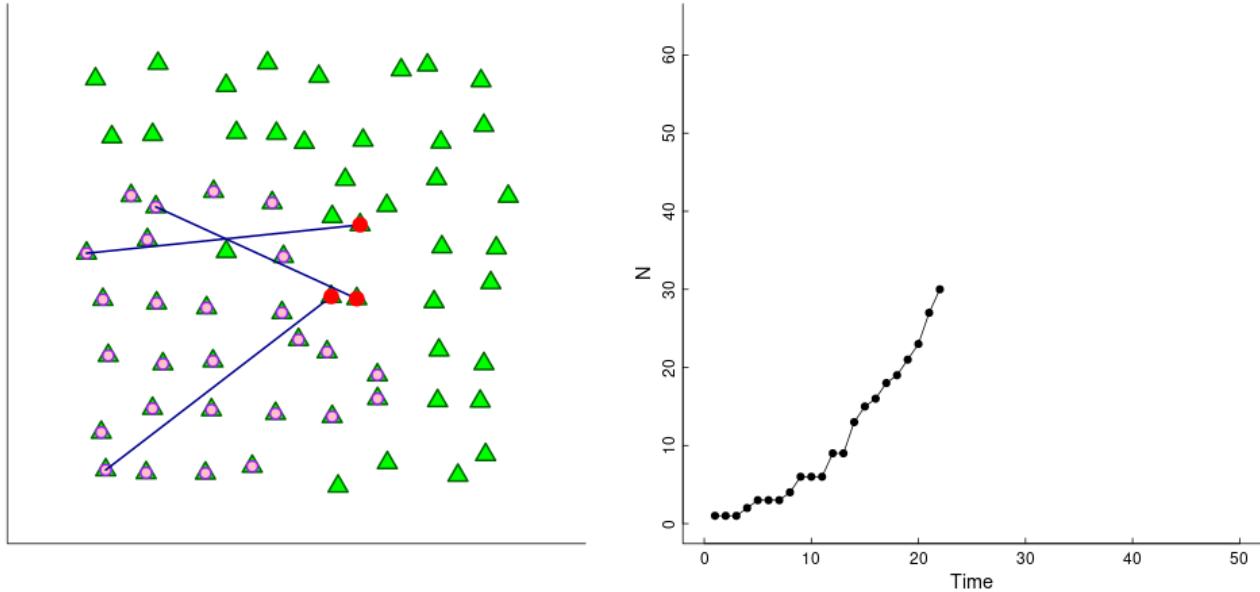
Is *immortal* (of course).

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Simulating limits on growth

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Squirlicorn Invasion



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Some math

$$E(N_{t+1}) = N_t + b \times N_t \times p_c$$

T_a = available trees, b - is birth rate, p_c - probability of successful colonization

Remember $E()$ is *expectation* (just a way to accept that we're talking about random variables and are interested in their **MEAN** behavior ... but we'll drop it from here on out).

Key calculation ... the **probability of colonization** is just the **proportion of available trees**:

$$p_c = (K - N_t)/K$$

Plugging back in:

$$N_{t+1} = N_t + bN_t \left(\frac{K - N_t}{K} \right)$$

Slightly more generally with a death rate:
 $\lambda = b - d$

$$\Delta N_t = \lambda N_t \left(1 - \frac{N_t}{K} \right)$$

Let's just divide both sides by Δt , squeeze time, and replace $\lambda/\Delta t$ with r_0 (much like in exponential growth) to make this differential equation:

$$\frac{\Delta N_t}{\Delta t} = r_0 N_t \left(1 - \frac{N_t}{K} \right)$$

$$\frac{dN}{dt} = r_0 N_t \left(1 - \frac{N_t}{K} \right)$$

This is the:

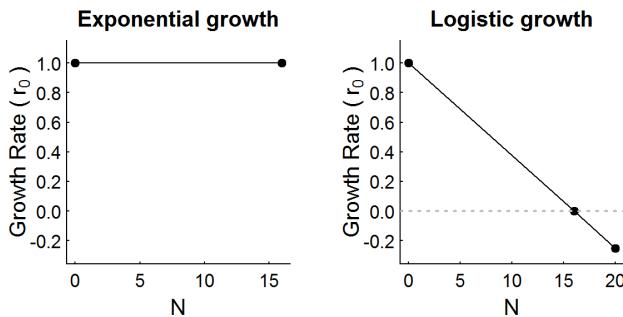
logistic population growth model

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Properties and Assumptions

$$\frac{dN}{dt} = rN_t \left(1 - \frac{N_t}{K}\right)$$

The key assumption is that *growth rate* decreases linearly with *population*.

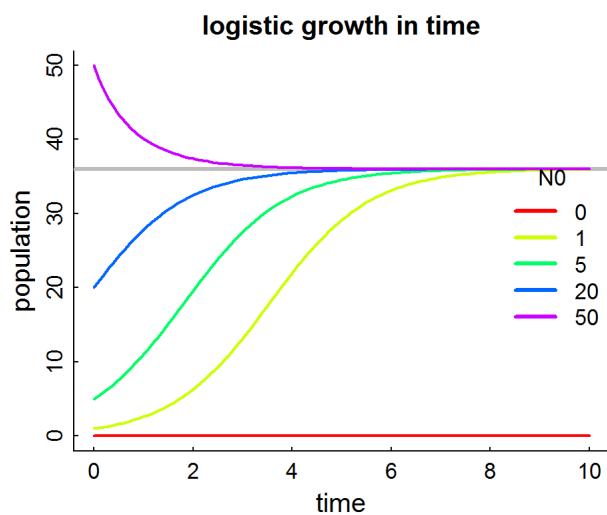


- At $N = 0$ - growth = 0
- At N slightly above 0 - growth $\approx r_0$
- At $N = K$ - growth = 0
- At $N > K$ - growth < 0

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Logistic Growth Curves

Here's how the process looks, at values: $r_0 = 1$, $K = 36$ and a selection of values for N_0 .



Starts out looking *Exponential* (at low N_0 , low values of time)

Typical "S" shape coming from below ... Slows down at K

Decays to K if $N_0 > K$

K is famously known as

Carrying Capacity

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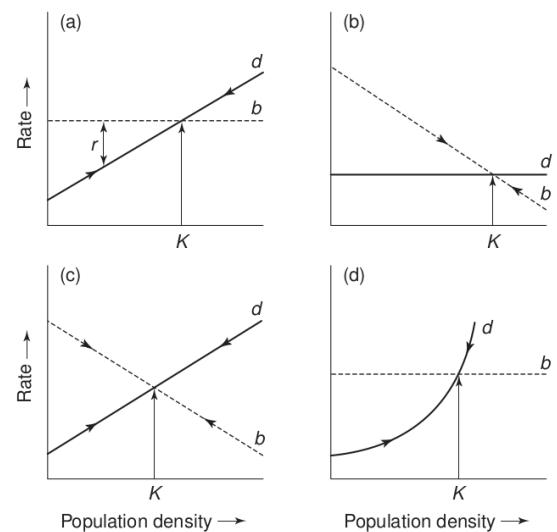
Different models of density dependence

What is it that depends on density?

Is it birth? Is it death? Is it linear? Is it curvy?

What changes for the squirlicorn? Is it linear?

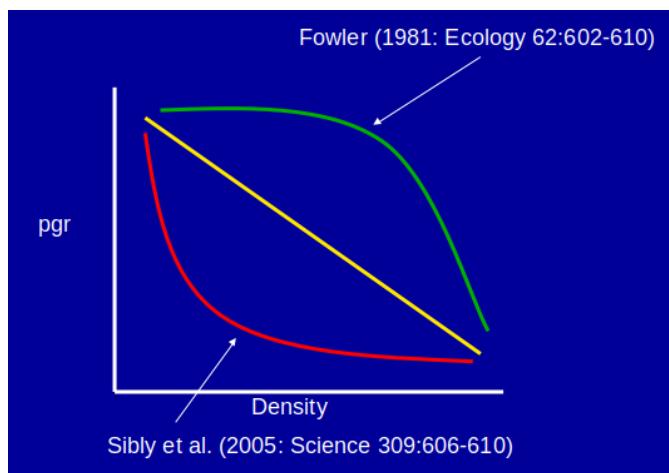
Fig. 8.4 Model of density-dependent and density-independent processes.
(a) Birth rate, b , is held constant over all densities while mortality, d , is density dependent. The population returns to the equilibrium point, K , if disturbed. The instantaneous rate of increase, r , is the difference between b and d . (b) As in (a) but b is density dependent and d is density independent. (c) Both b and d are density dependent. (d) d is curvilinear so that the density dependence is stronger at higher population densities.



Fryxell chapter 8.

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Density Dependence



Any relationship where r or λ depends on N is called **Density Dependence**.

It does not *have* to be linear. (That's just easiest to model)

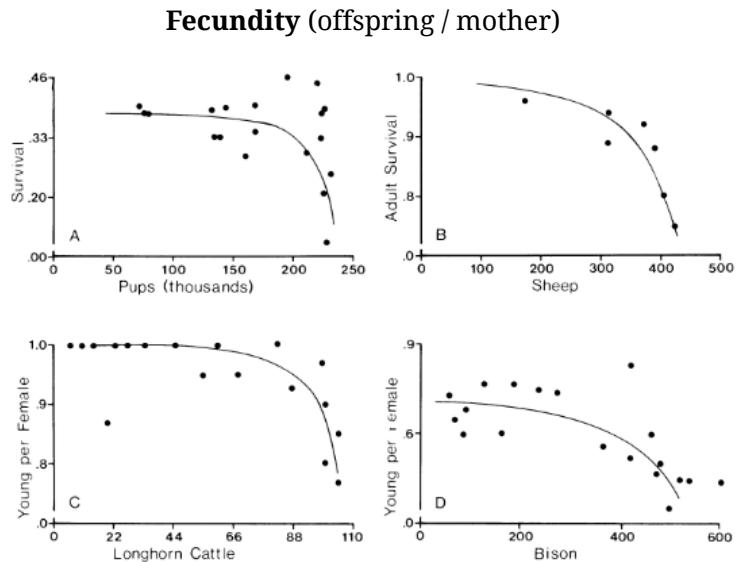
These different curves are different **forms** of density dependence.

Typically for large mammals ...

Calf / pup / juvenile mortality is highest when densities are highest.

Fecundity (# of offspring per female) falls at high densities...

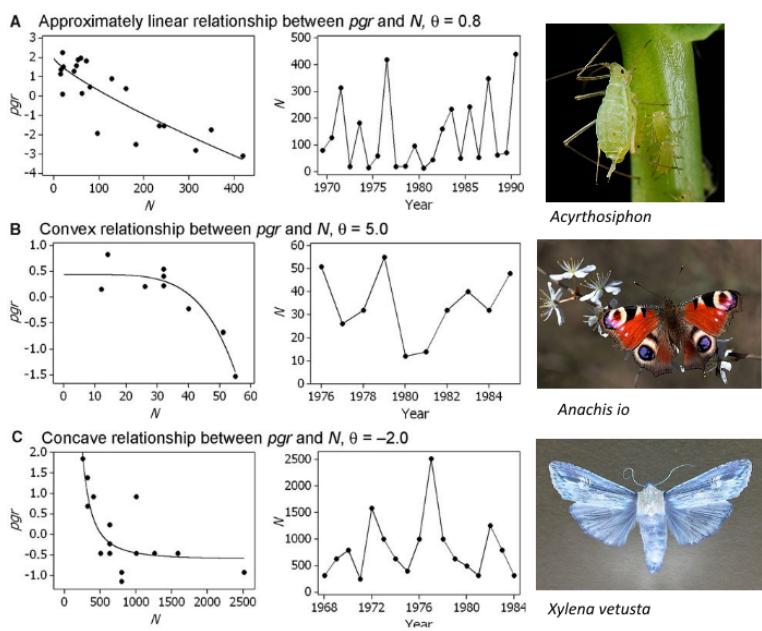
... but this effect mainly kicks in at very high numbers (not linear).



Fowler (1981)

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Most density dependence is curvy

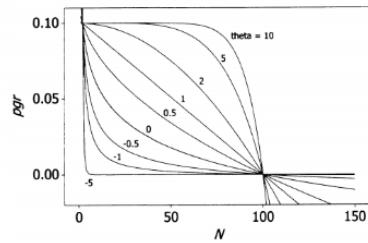


On the Regulation of Populations of Mammals, Birds, Fish, and Insects

Richard M. Sibly,^{1*} Daniel Barker,¹ Michael C. Denham,² Jim Hone,³ Mark Page¹

Theta-logistic model

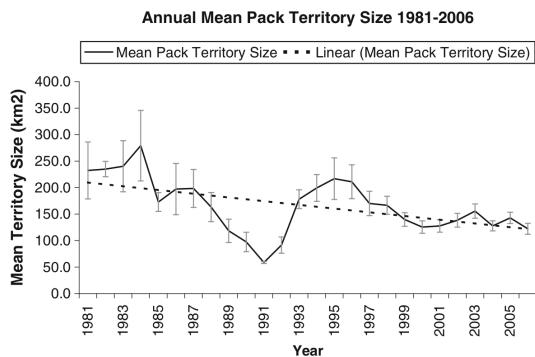
$$pgr = r_0[1 - (N/K)^\theta]$$



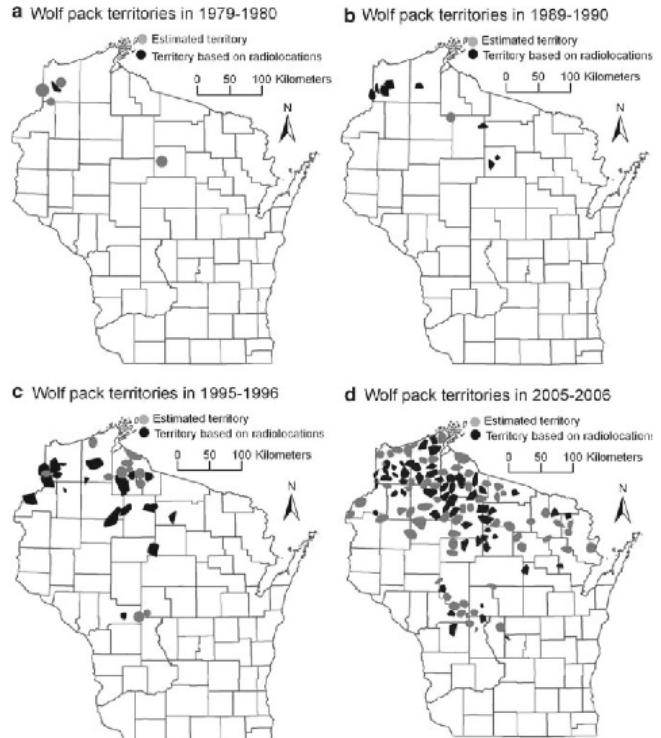
in fact, most density dependence might be concave

Example: Wolf populations

- Dispersal into new area, mainly wolf mating pairs.
- Highly territorial!
- Wolves produce up to 4 pups per litter that survive
- If there are no neighbors, wolves will disperse to found new packs
- Pack with 8 adults or 2 adults, still produces (about) 4 pups per litter
- If there are lots of neighbors, packs become larger (more individuals) in smaller territories.



Expansion of Wisconsin Wolves, 1970's to 2000's



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Human-wolf experiment model

basics of model

- 8 possible territories
- 1 initial dispersing wolf (female)

each season ...

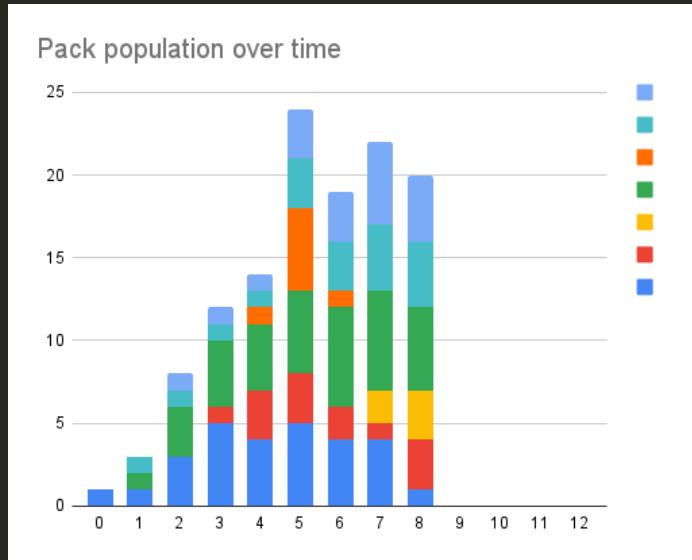
- One female / pack gives birth to 2 offspring
- Offspring can choose whether to disperse or not
- 1/4 of all wolves die each year



Enter data [here](#)

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Results of Human Wolf Experiment



Looks a lot like initial exponential growth stabilizes around 20 ind as die-offs balance out births.

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Modeling wolf population

Population equation:

$$N_t = (1 + b - d) \times N_{t-1}$$

Death rate is constant: $d = 0.25$

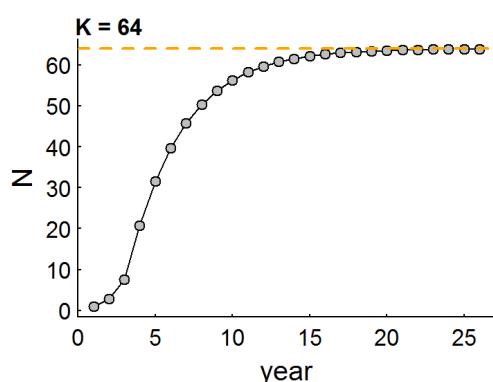
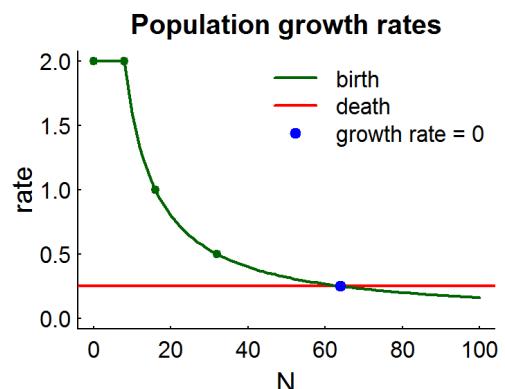
Birth rate is high when population is low: $b_0 = 2$

Birth rate is small when population is high:

- $N = 1; B = 2; b = 2$
- $N = 8; B = 16; b = 2$

But it hits an absolute maximum of 16 total. So if:

- $N = 32; B = 16; b = 1/2$
- $N = 64; B = 16; b = 1/4$



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Summary Concepts

Growth of natural populations is always *eventually* limited

When population rates (b , d , also i , e) depend on the **total population** or **density** (N), this is called: **Density Dependence**.

The maximum growth rate ($r_0 = \max(b - d)$) is called the **intrinsic growth rate**.

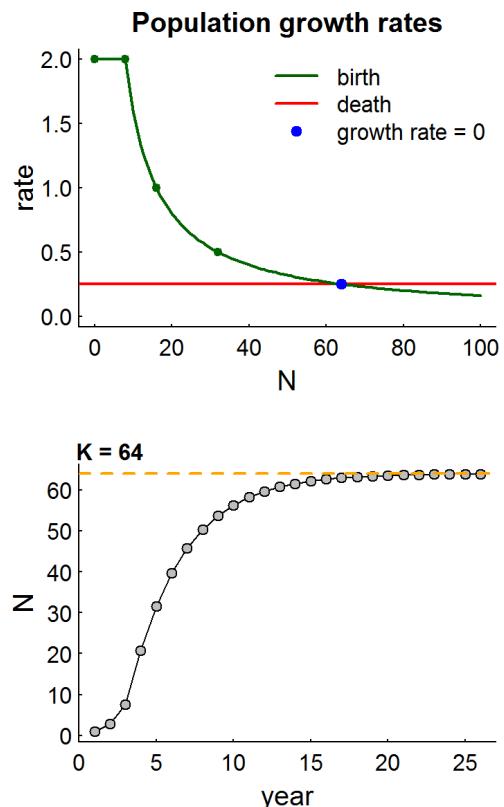
In density dependent growth, the **actual growth rate (r)** falls with higher density until it is 0. The point where that happens is the **Carrying Capacity (K)**. If N ever exceeds K , the growth becomes negative.

Logistic growth is a specific kind of Density Dependent growth where the relationship between r and N is **linear**. The formula is:

$$r = r_0(1 - N/K)$$

which leads to the following differential equation:

$$\frac{dN}{dt} = r_0 N \left(1 - \frac{N}{K}\right)$$



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Some references

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