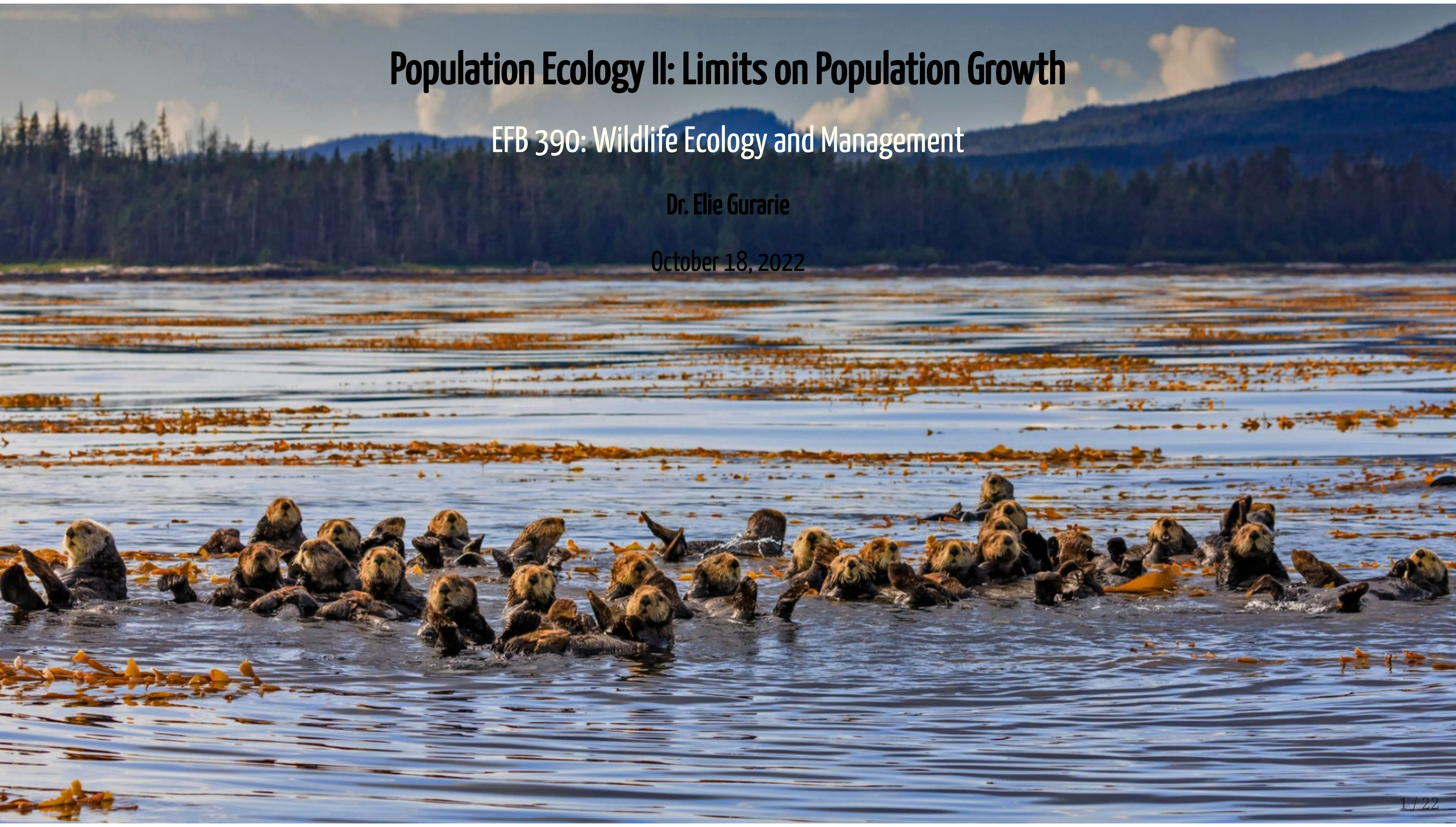


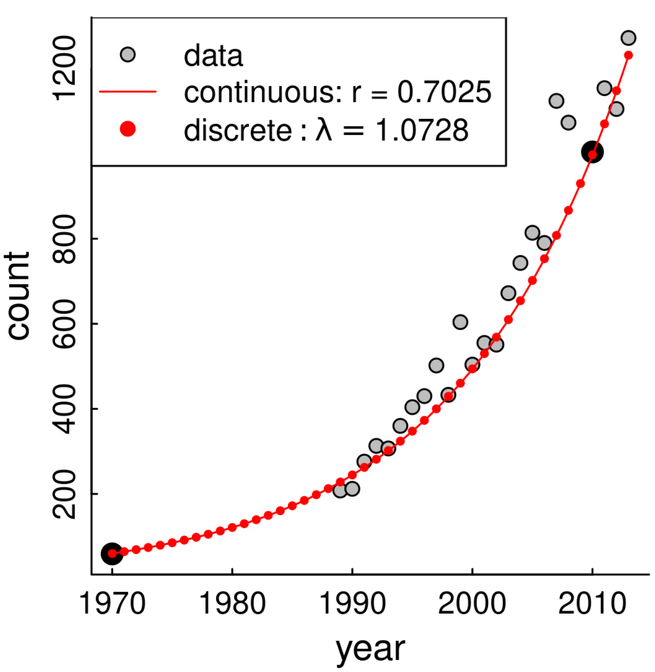
Population Ecology II: Limits on Population Growth

EFB 390: Wildlife Ecology and Management

Dr. Elie Gurarie

October 18, 2022

Estimating exponential growth rate from two points



We fitted this with just two points:

year	N
1970	60
2010	1000

by solving for:

$N_{2010} = N_{1970} \times \lambda^{(2010-1970)}$

In a single formula:

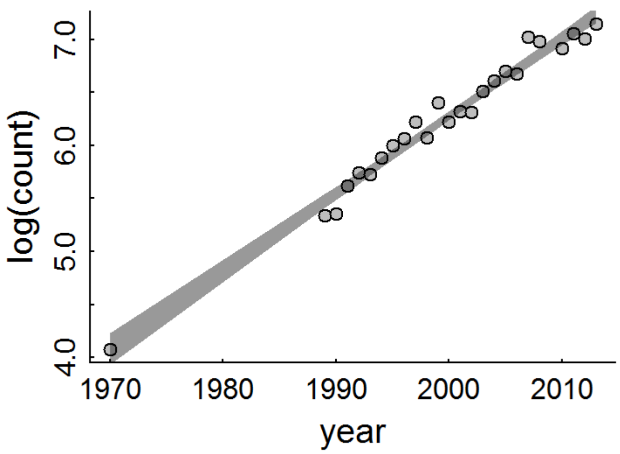
$$\lambda = \exp\left(\frac{\log N_t - \log N_0}{t}\right)$$

$\lambda = \exp(0.07) = \mathbf{1.0725}$

7.25% annual growth

But you could/should use ALL the data!

Using linear model of $\log(N)$ to estimate growth rate



Look how linear it's become!

]

Population Growth model:

$$N_t = N_0 \lambda^t$$

Log of both sides:

$$\log(N_t) = \log(N_0) + \log(\lambda) \times t$$

this is a linear model!

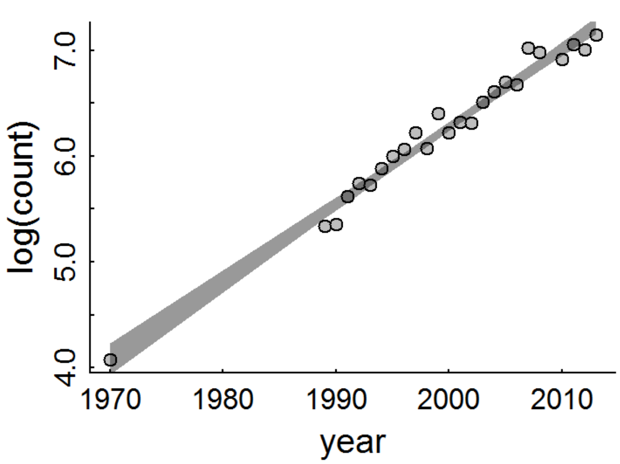
$$Y = \alpha + \beta X$$

where

$\widehat{\beta} = \log(\widehat{\lambda})$ - so - $\hat{\lambda} = \exp\left(\widehat{\beta}\right)$

But you could/should use ALL the data!

Using linear model of $\log(N)$ to estimate growth rate



Look how linear it's become!

```
lm(log(count)~year, data = WA_seaotters)
```

Model output:

	Estimate	Std. Error	t value	Pr(>|t|)
(Intercept)	-140.2227	4.7318	-29.6344	0
year	0.0733	0.0024	30.9533	0

Using ALL THE DATA, we get the benefit of a precision estimate as well:

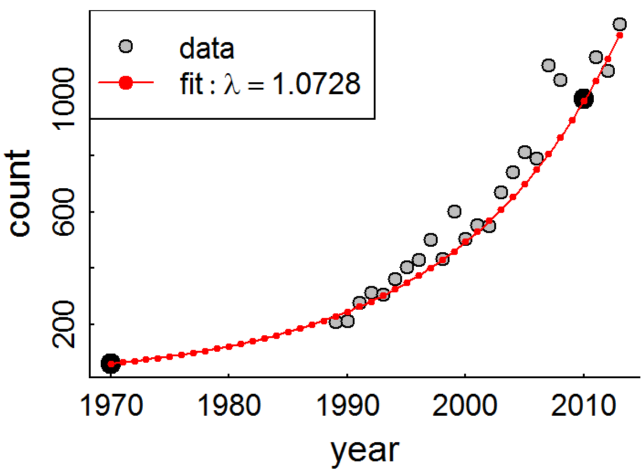
$$\widehat{\lambda} = \exp(\widehat{\beta});\ \widehat{\lambda} = 1.076 \pm 0.005$$

(actually, 95% confidence interval is not quite symmetric:

$$\exp(\widehat{\beta} - 2\sigma_\beta), \exp(\widehat{\beta} + 2\sigma_\beta)$$

but close enough)

Sources of variation?



Observation error.

- How **precise**/**accurate** is the actual estimate?

Unexpected immigration / emigration.

- check assumptions about "closed population"

Environmental Stochasticity

Environment good / bad affecting **birth** and **death** for all animals.

Demographic Stochasticity

Stochasticity means: **randomness** in **time**.

Demography is the **Science of Population Dynamics**. Often it refers specifically to **births** and **deaths** (and **movements** ... but we're still looking at closed population).

Individually, *all* demographic processes are stochastic. An individual has some **probability** of dying at any moment. An individual has some *probability* of reproducing (or some probability distribution of number of offspring) at a given time.

Question: How important is the randomness of *individual* events for a *population* process?

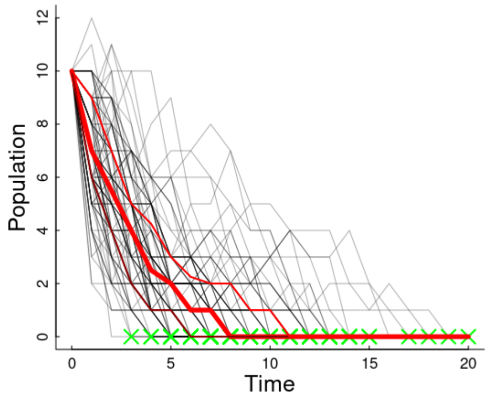
More specific Q: What is the probability of extinction?

Human Experiment

- 15 students
- Flip a survival coin.
  - If you die (tails) sit down, if you live (heads) stay standing
- Flip a reproduction coin.
  - If you reproduce (heads) call on another student to stand

Cranking this experiment very many times.

https://egurarie.shinyapps.io/StochasticGrowth/



On average, the number of individuals at time $t+1$ is the number that survived + the number that reproduced of those that survived.

$$E(N_{t+1}) = p_s N_t + p_b \, p_s N_t = p_s(1+p_b) N_t$$

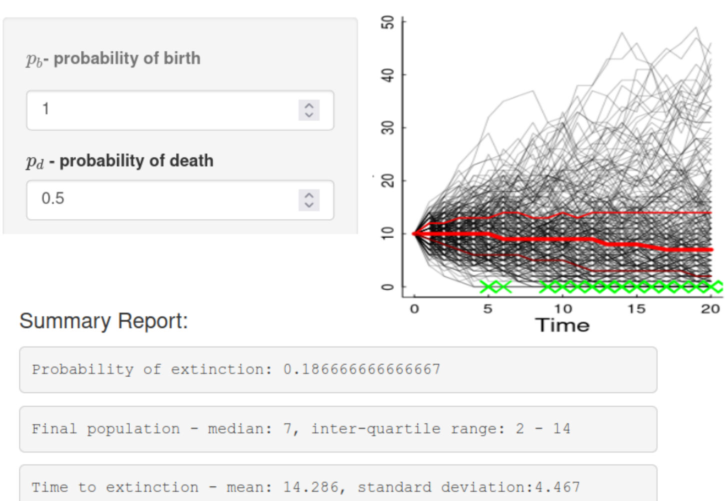
So (in our coin flip example)

$$\widehat{\lambda} = p_s(1+p_b) = 0.75$$

What does that mean for our population!?

Extinction is inevitable!

Even when population growth is 0...



Even if the population growth is 0 (neither growing nor falling) ....

$$\widehat{\lambda} = 0.5 \times (1+1) = 1$$

demographic stochasticity leads to *some* probability of extinction always.

Main take-away

Demographic stochasticity is important only for *small* populations.

Environmental Stochasticity

- Affects entire population
- Can ALSO increase risk of extinction
- or at least drive populations

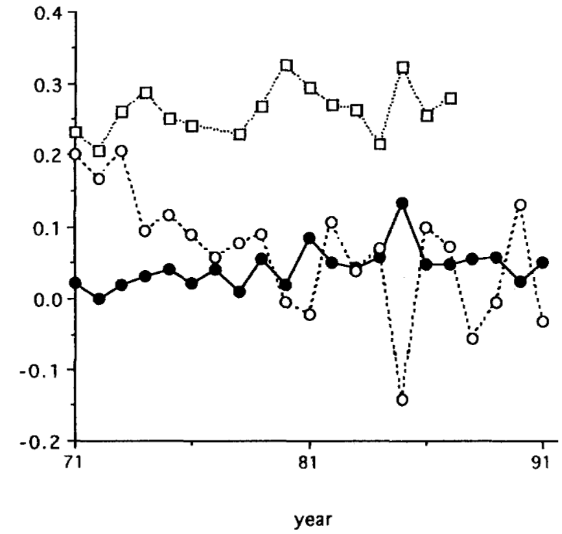


Figure 2. Time series of annual rainfall (01.06–31.05 each year) (squares), adult mortality (over same periods) (filled circles) and the multiplicative increase in population size from year to year (open circles). The correlation between adult mortality and rainfall = 0.549 ($p < 0.02$) and that between change in population size and rainfall = −0.695 ($p < 0.001$).

red deer, *Cervus elephas*

As populations grow ...

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.

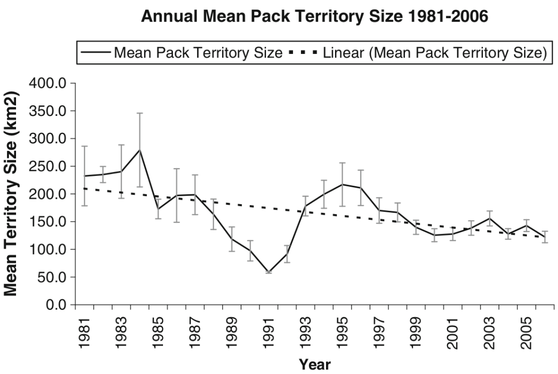
Density dependence

Means that the *rate* of a parameter(e.g. $b = \frac{B}{N}$ or $d = \frac{D}{N}$ is:

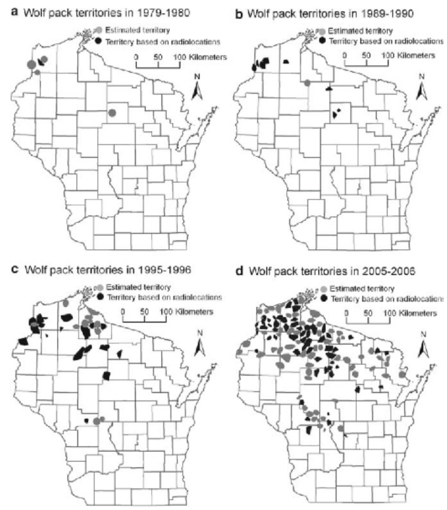
- (a) NOT constant
- (b) dependent on total population (or density) N.

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



Human-wolf experiment model

basics of model

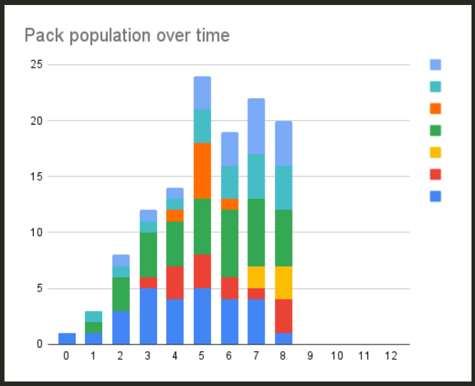
- 8 possible territories
- 1 initial dispersing wolf (female)

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

Results of Human Wolf Experiment



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

Modeling wolf population

Population equation:

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

Death rate is constant: $d = 0.25$

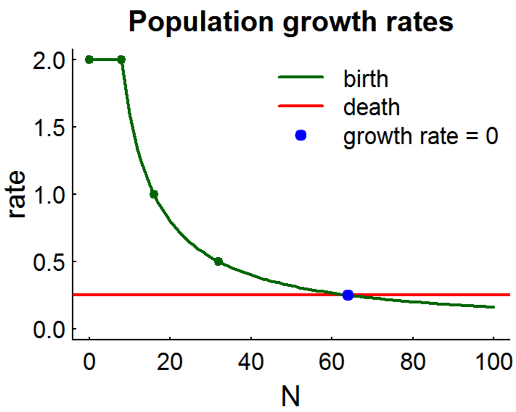
Birth rate is high when population is low: $b_0 = 2$

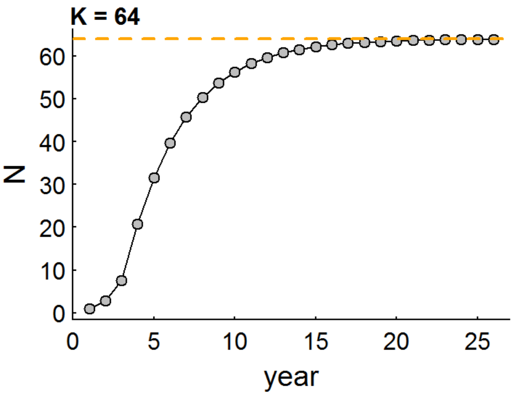
Birth rate is small when population is high:

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

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

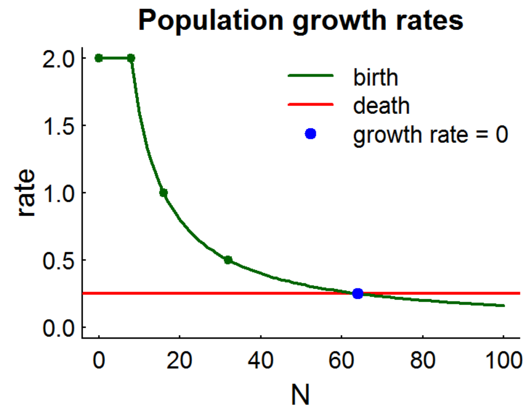
- $N = 32; B = 16; b = 1/2$
- $N = 64; B = 16; b = 1/4$

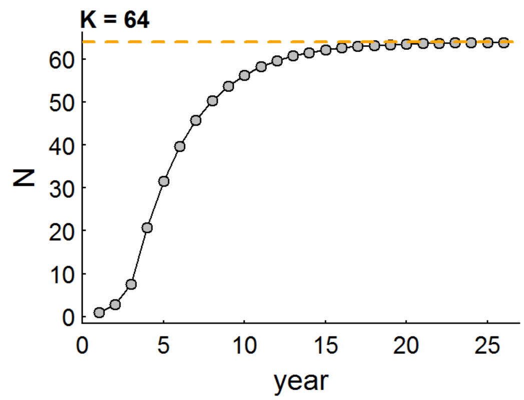




Some Concepts

- Natural populations are always eventually limited
- The "cap" on a population is called the ***Carrying Capacity*** (symbol: **K**). This is
- When population rates (b, d, also i, e) depend on the **total population**, this is called: ***Density Dependence***.
- The maximum growth rate (max $b - d$) is called the **intrinsic growth rate**.

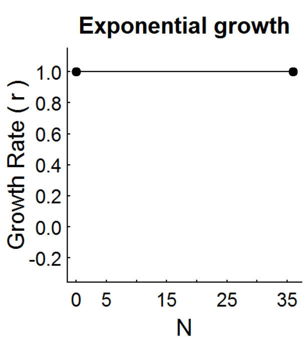


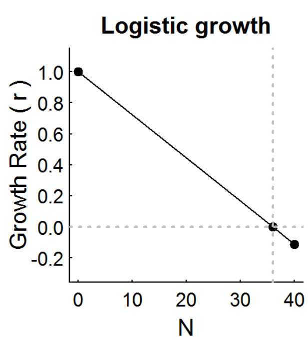


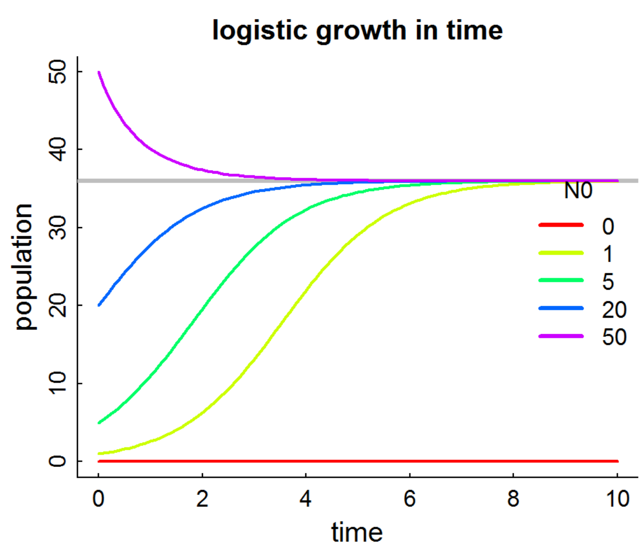
Logistic growth

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

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







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

Intrinsic growth rates

Strong Relationships with body size:

$$r_0 = 1.5\,W^{-0.36}$$

(`W`) is live weight in kilograms

Q. Why would this be the case?

Fig. 6.2 Intrinsic rate of increase of mammals plotted against body weight. (After Caughley and Krebs 1983.)

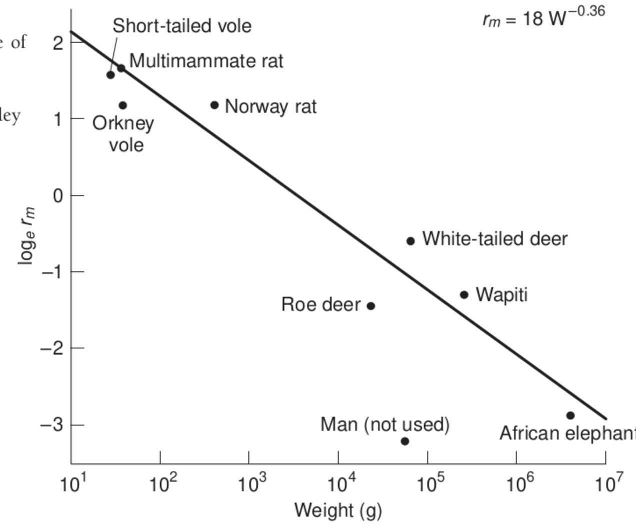


Table 6.1 Expected intrinsic rates of increase r_m on a yearly basis for herbivorous mammals as estimated from mean adult live weight.

Weight (kg)	r_m
1	1.50
10	0.65
100	0.29
1000	0.08

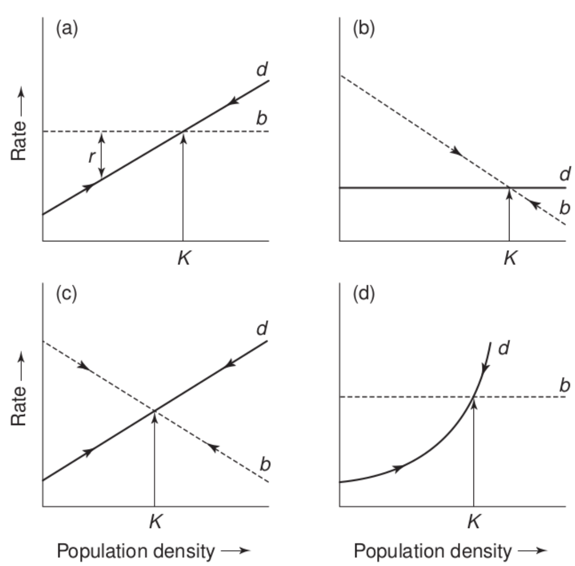
Fryxell chapter 6

Different models of density dependence

What is it that depends on density?

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

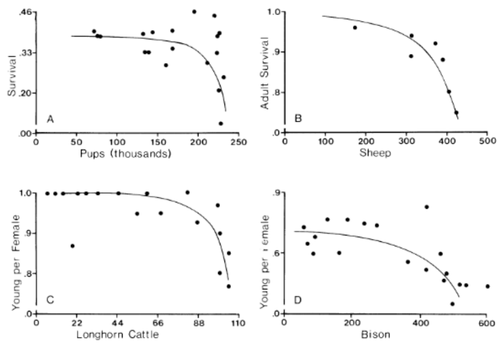
Fig. 8.4 Model of density-dependent and density-independent processes. (a) Birth rate, *b*, is held constant over all densities while mortality, *d*, is density dependent. The population returns to the equilibrium point, *K*, if disturbed. The instantaneous rate of increase, *r*, is the difference between *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.

Density dependent mortality & fecundity

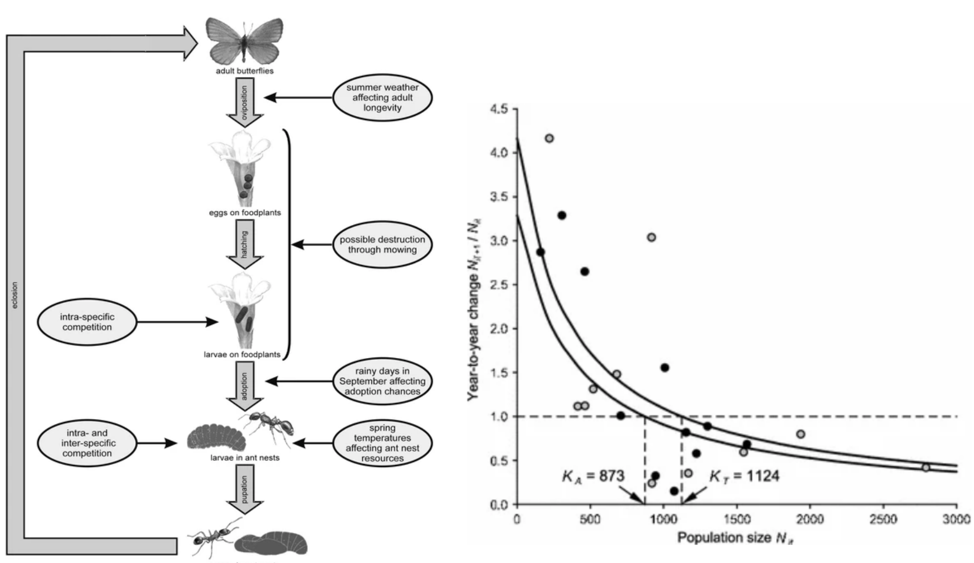
- Calf / pup / juvenile mortality is highest when densities are highest.
- **Fecundity** (# of offspring per female) falls at high densities.
- This effect mainly kicks in at very high numbers (not linear).



Fowler (1981)

Concave curves: Butterflies

Note that the **density dependent effects** kick in when populations are **small** rather than **large**.



(Nowicki et al. 2009)

Carrying capacity

Ecological carrying capacity

Basically - *K* of a logistic growth

Limited (almost always) by:

- resources:
    - food
    - shelter
    - breeding **habitat**
- space
- interactions (predation / parasites / disease)

For the **Howework assignment** you will explore different ways in which **Carrying Capacity** is estimated, and why it is an important question for wildlife ecologists to ask.

Some references

- Benton, T. G., A. Grant, and T. H. Clutton-Brock. 1995. Does environmental stochasticity matter? Analysis of red deer life-histories on Rum. Evolutionary Ecology 9:559–574.
- Chapman, E. J., and C. J. Byron. 2018. The flexible application of carrying capacity in ecology. Global Ecology and Conservation 13:e00365.
- Fowler, C. W. 1981. Density Dependence as Related to Life History Strategy. Ecology 62:602–610.
- Laidre, K. L., R. J. Jameson, S. J. Jeffries, R. C. Hobbs, C. E. Bowlby, and G. R. VanBlaricom. 2002. Estimates of carrying capacity for sea otters in Washington state. Wildlife Society Bulletin:1172–1181.
- McClelland, C. J. R., C. K. Denny, T. A. Larsen, G. B. Stenhouse, and S. E. Nielsen. 2021. Landscape estimates of carrying capacity for grizzly bears using nutritional energy supply for management and conservation planning. Journal for Nature Conservation 62:126018.
- Nowicki, P., S. Bonelli, F. Barbero, and E. Balletto. 2009. Relative importance of density-dependent regulation and environmental stochasticity for butterfly population dynamics. Oecologia 161:227–239.
- Potvin, F., and J. Huot. 1983. Estimating Carrying Capacity of a White-Tailed Deer Wintering Area in Quebec. The Journal of Wildlife Management 47:463.
- Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the Regulation of Populations of Mammals, Birds, Fish, and Insects. Science 309:607–610.
- Thébault, J., T. S. Schraga, J. E. Cloern, and E. G. Dunlavey. 2008. Primary production and carrying capacity of former salt ponds after reconnection to San Francisco Bay. Wetlands 28:841–851.
- Wydeven, A. P., T. R. Van Deelen, and E. J. Heske, editors. 2009. Recovery of Gray Wolves in the Great Lakes Region of the United States: An Endangered Species Success Story. Springer New York, New York, NY.