

Introduction

Reading

Caughley 1970

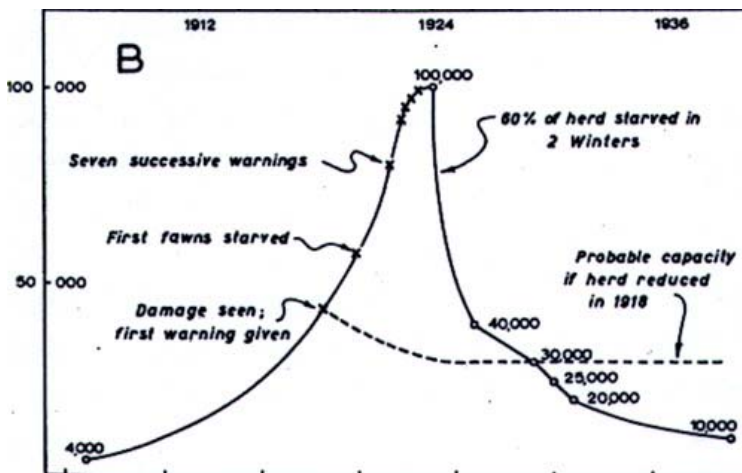
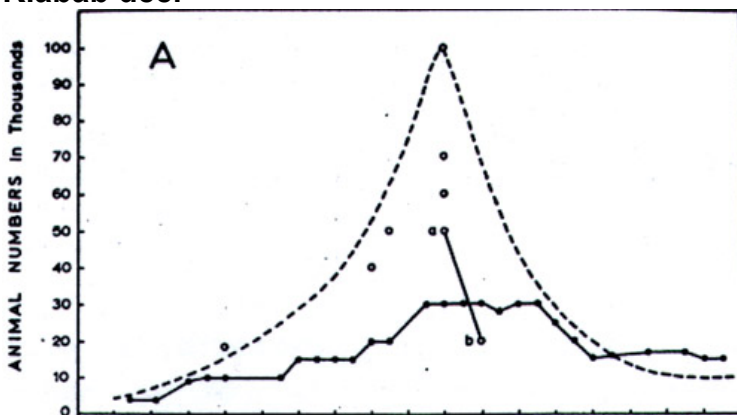
Population Ecology

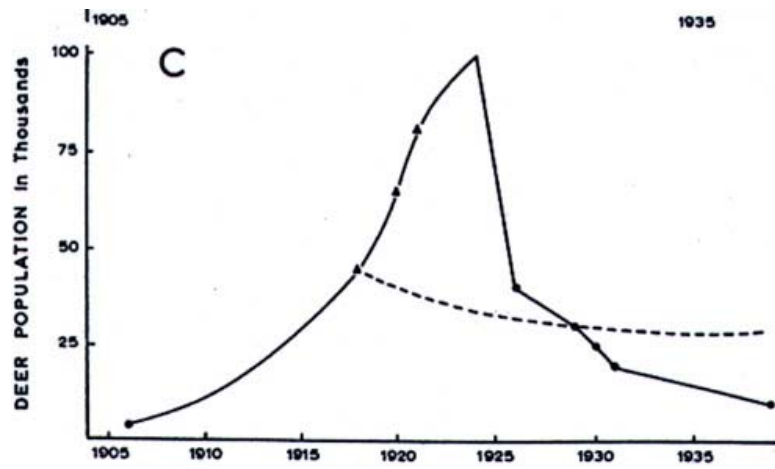
"The study of the sizes (and to a lesser extent the distributions) of plant and animal populations, and of the processes--particularly the biological processes--which determine those sizes." -Begon and Mortimer 1986

Population

"the organisms inhabiting a particular area or biotype"- Webster

Kiabab deer





MODELS

Reading

Chapter 2 in, White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory Publication LA-8787-NERP.

Definitions

Model- Mathematical description of the relationship between 2 or more variables. An abstraction of reality.

There are 3 basic types of models that we use in population ecology

1. Theoretical models- abstract relationship between variables. Generally derived using a deductive approach rather than being generated from the data.

ex) exponential growth model- $N_t = N_0 e^{rt}$

2. Statistical model- Model used to estimate a parameter of interest.

ex) Lincoln-Petersen model- $\hat{N} = \frac{n_1 n_2}{m_2}$

where n_1 =number caught in trapping session 1,

n_2 =number caught in trapping session 2, and

m_2 = number of marked animals recaptured in the second trapping session

3. Data based models- Relationship between 2 or more variables derived from data rather than deductively.

STATISTICAL CONCEPTS

Census- a type of survey in which each member of the population of interest is surveyed

Sample- Measurement of a subset of the population from which you make inferences to the whole population.

PARAMETERS- true population values expressed as numbers.

- ex) the density of microtus in a field in the Arcata bottoms
- ex) the number of golden-crowned kinglets in the Arcata community forest
- ex) home range size of fishers in Humboldt County
- ex) survival of adult Varied Thrushes in northern California

ESTIMATOR- mathematical expression that indicates how to calculate an estimate of the parameter from the sample data. (often denoted by \hat{N}) i.e. $\hat{N} = \frac{n_1 n_2}{m_2}$

ESTIMATE- numerical value resulting from substituting the sample data into the estimator.

Variance components- Sampling variance vs spatial or temporal variation. Sampling variation occurs when we sample a population and estimate a parameter rather than making a complete census. Spatial and temporal variation refers to the true environmental variation that we are interested in measuring and understanding.

ACCURACY, BIAS, AND PRECISION

ACCURACY- how close an estimator is to the parameter.

BIAS- The difference between the expected value of an estimator and the parameter it estimates. i.e.

If $E(\hat{N}) = N$, then \hat{N} is not biased.

PRECISION- Repeatability of a result- measured by sampling variance or standard error of the estimate.

RELIABILITY- refers to how often the estimator can be expected to be close to the parameter being estimated as specified by the measure of precision.

Questions

1. Name three species which biologists are able to accurately census.
2. Mark Colwell found that there was a strong inverse relationship between shorebird density and grass height in pasture lands in the Arcata Bottoms. What kind of model does this describe?
3. Suppose you trapped small mammals in a clear-cut in the Arcata Community Forest. Using a mark-recapture model, you calculate that there are 167 animals/ha on your plot. Is this value an estimate, a parameter, or a census?
4. Why is a model needed to estimate parameters from data?

EXPONENTIAL GROWTH MODELS

Reading

Gotelli Ch.1

There are 4 factors that influence population size: births, deaths, imm/emigration:

$$N_{t+1} = N_t + B - D + I - E .$$

Where N_t = no. indiv. in the pop. at time t , B = no. births in interval, D = no. deaths in interval, I = no. immigrants, E = no. emigrants. Assume for simplicity no imm- or emigration then:

$$N_{t+1} = N_t + B - D$$

We are interested in describing the change in population size from one time step to the next. This is the difference in population size between the last time and this time or:

$$N_{t+1} - N_t = N_t - N_t + B - D \quad \text{or} \quad \Delta N = B - D$$

In continuously growing populations, population growth may be described using a differential equation:

$$\frac{dN}{dt} = B - D \quad (1)$$

Now let $B=bN$ and $D=dN$, where **b** is the **instantaneous birth rate** (births/indiv. per time) and **d** is the **instantaneous death rate** (deaths/indiv. per time). We define **r** as the **instantaneous rate of increase** and **r=b-d**. Substituting we get:

$$\frac{dN}{dt} = (b - d)N \quad \text{and,}$$

$$\frac{dN}{dt} = rN \quad (2)$$

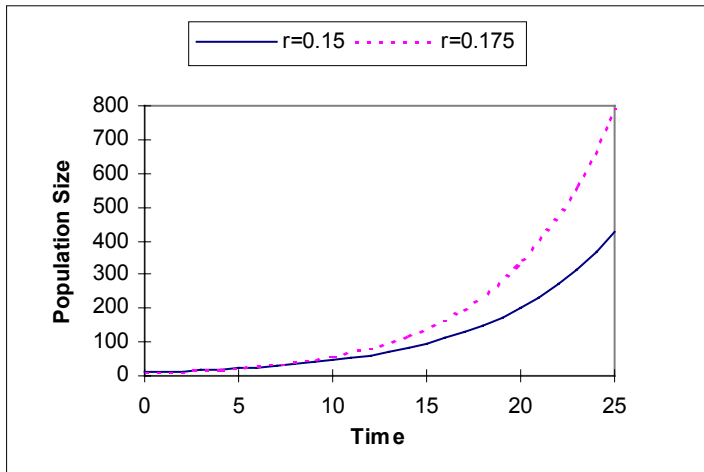
This is known as a differential equation. To predict population size we must integrate this equation using calculus to obtain the integrated form of the equation. This is commonly referred to as the **exponential growth equation**:

$$N_t = N_0 e^{rt} \quad (3)$$

$r < 0$, pop. declines,
 $r = 0$ -pop. stable,
 $r > 0$ -pop. increases

r has units indiv./indiv. per unit time. It expresses growth rate on a per individual basis.

The exponential growth equation gives the familiar exponential growth curve:

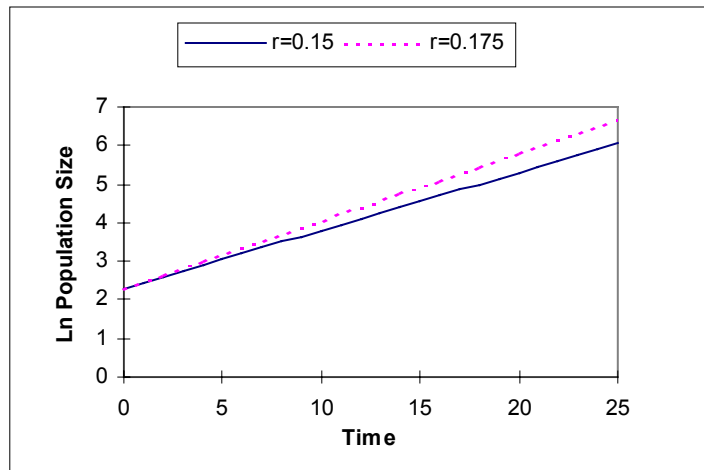


The exponential equation can be linearized by taking the log of both sides or,

$$\ln(N_t) = \ln(N_0) + rt \quad (4)$$

Which is of the general form: $y = a + bx$

On a log scale the exponential growth curve will be linear with slope = r .



The **doubling time** for a population can be calculated as:

$$t_{\text{double}} = \frac{\ln(2)}{r} \quad (5)$$

Assumptions of the exponential growth equation

1. The population is closed.
2. Constant b and d rates.
3. No genetic variation in the population for b and d rates.
4. No age or size structure.
5. Continuous growth with no resource limitation or time lags.

Geometric equations for population growth- applies to pulse breeding species with non overlapping generations such as many insect populations. It is a useful approximation for many wildlife populations that produce offspring during one time of year. The assumptions are the same as for the exponential growth equation except that now the reproduction occurs only once during each time step (usually one year).

Assume 100 individuals in a population, each produces one offspring per time step, and no mortality. How will the number of individuals change over time?

100 --> 200 --> 400 --> 800

i.e. a doubling in each generation or a 100% increase each generation.

A simple model

Let λ = the finite rate of increase of the population from one time step to the next (includes births and deaths).

Then,

$$\lambda = \frac{N_{t+1}}{N_t} \quad (6)$$

and the growth of the population can be described as follows:

year	0	1	2	3	4	... t
pop. size	N_0	$N_0\lambda$	$N_0\lambda^2$	$N_0\lambda^3$	$N_0\lambda^4$	$N_0\lambda^t$

Thus we have,

$$N_t = N_0\lambda^t \quad (7)$$

$\lambda > 1$, population is increasing

$\lambda = 1$, population is stable

$\lambda < 1$, population is decreasing

λ is usually expressed as a % formed by subtracting 1 from λ and multiplying by 100. Thus $\lambda = 1.2$ would be expressed as a rate of increase of 20%.

Difference equations- another approach to modeling discrete population growth

$$N_{t+1} = N_t + N_t * R$$

$$N_{t+1} = N_t * (1 + R)$$

Assume a constant proportion (R) is added to the population in each time step. Then,

$$N_t = N_0 * (1 + R)^t$$

or

R is known as the finite rate of growth of the population and $\lambda = 1+R$.

Note: $\lambda = e^r = 1+R$ also note that $r \neq R$

Various interpretations of r.

1. r_{\max} - maximum growth under ideal (laboratory) conditions -almost never measured for wildlife populations.
2. r_0 - rate of population growth without competition -maximum growth rate observed in nature.
3. **current r**- rate at which population is currently growing. This will decline as population size approaches carrying capacity if density dependence is operating in the population.

Density-dependent population growth models: logistic, Ricker; Effects of time delays

Reading

Gotelli Ch. 2

Derivation of the differential form of the logistic equation

We wish to create a model in which the per capita rate of change is a function of the population size

$$\frac{dN}{Ndt} f(N)$$

Now assume that the per capita growth rate decreases as individuals are added to the population

$$\frac{dN}{Ndt} = r - aN$$

Where a is an arbitrary constant that represents the amount the growth rate is reduced by adding a single individual to the population.

For what values of N will the per capita rate = 0?

$$\frac{dN}{dt} = N(r - aN) = 0$$

Answer: $N=0$, and $r-aN=0$, or $N=r/a$. We call this larger value K or the **carrying capacity**. Now rewrite the above equation without a .

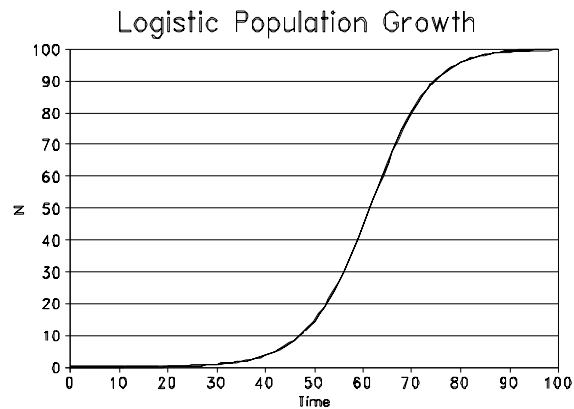
$$\frac{dN}{dt} = N(r - aN) = N\left(r - \frac{r}{K}N\right) = rN\left(1 - \frac{N}{K}\right) = rN\left(\frac{K - N}{K}\right) \quad (9)$$

If we integrate this equation we get,

$$N_t = \frac{K}{1 + \left(\frac{K}{N_0} - 1\right)e^{-rt}} \quad (10)$$

Which allows us to find N at some time in the future.

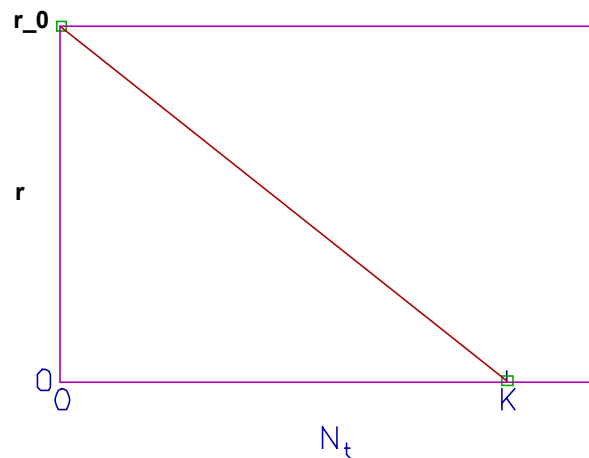
Plotting N as a function of time gives us the familiar logistic curve.



$N > K$ dN/dt is negative

$N < K$ dN/dt is positive

Another way to think about this is that r decreases with increasing N .



Assumptions of logistic growth equation

1. Same as exponential growth equation except with respect to resource limitation.
2. The population size is limited by the carrying capacity of the environment, K , which is constant.
3. There is a negative linear relationship between r and N .

Discrete logistic

Like the exponential growth model we can also model logistic growth as a discrete process using a difference equation. In this case R is a function of population size, N_t , such that:

$$R = R_0 \left(1 - \frac{N_t}{K} \right) \quad (11)$$

and the change in population size can be described by:

$$N_{t+1} = N_t \left[1 + R_0 \left(1 - \frac{N_t}{K} \right) \right] \quad (12)$$

and the per capita finite rate of increase is:

$$\frac{N_{t+1} - N_t}{N_t} = R_0 - \frac{R_0 N_t}{K} \quad (13)$$

The discrete logistic equation can exhibit some unusual behavior including, damped oscillations, continuous oscillations, and chaos. We will explore the behavior of the discrete logistic in lab.

Time lags

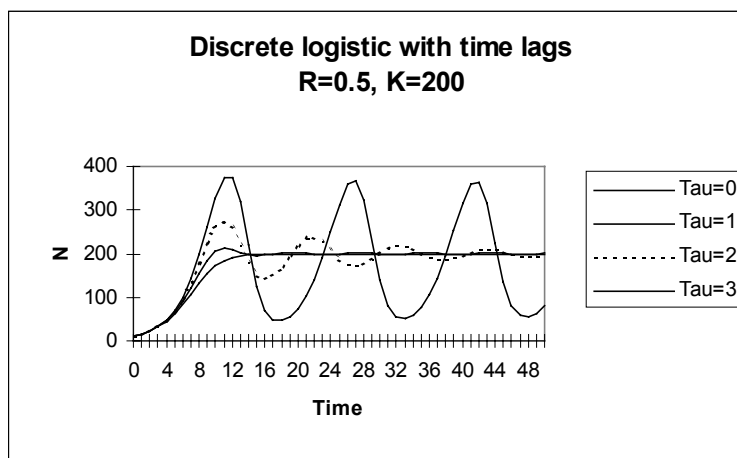
Time lags can be incorporated into the discrete logistic equation.

$$N_{t+1} = N_t \left[1 + R_0 \left(1 - \frac{N_{t-T}}{K} \right) \right] \quad (14)$$

Where T is the time lag in units of t .

Ex) 17-year locusts, salmon, large mammals?

Behavior of difference equation logistic model with time lags – cycles.

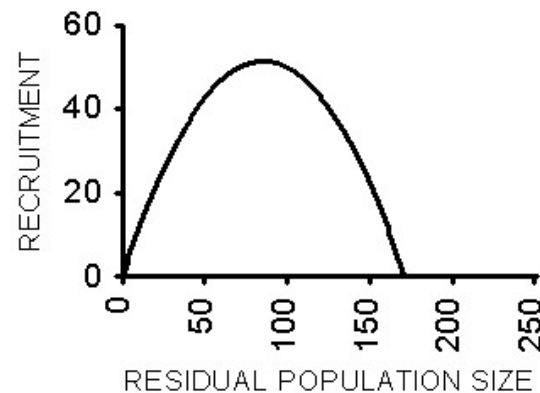


Fisheries biologists often use the Ricker equation to describe density-dependent population growth.

$$N_{t+1} = N_t \exp \left[R_0 \left(1 - \frac{N_t}{K} \right) \right] \quad (15)$$

Recruitment vs N

Recruitment is the number of individuals that are added to a population in a given period of time. With the logistic equation, recruitment is maximized at $K/2$.



Allee effect -the per capita birth rate declines at low densities because, for example, of the increased difficulty of finding a mate. This is known as *Allee-type behavior* (of the per capita birth rate), and its effect on the growth rate $R(t)$ is called an *Allee effect* (Allee 1931, *Animal aggregations: A study in general sociology*. Univ. Chicago Press, Chicago).

Carrying capacity

There are two general definitions of K carrying capacity:

1. Carrying capacity is the population size at which birth rate equals death rate described by the logistic growth equation.
2. The maximum density of a species in its preferred habitat (Leopold 1933).

Most ecologists now equate carrying capacity with the former but this is often difficult to determine in the field.

In the logistic equation, carrying capacity is assumed to be constant but it almost certainly varies through time.

Questions

1. If $N_0=100$ and $r=0.05$, calculate N_t for $t=2, 5, 10$, and 20 . Do the same for $r=0.1$. Now calculate N_t for the same initial population size using the geometric equation with $R=0.05$ and 0.1 . What value of R will give you the same values for N_t as the exponential model?
2. Calculate r and R for $\lambda=0.85, 1.05$, and 1.15 .
3. Suppose you are monitoring a population and your census indicates there are 110 animals in the population in 1980 and 150 in 1985. Assuming the population is growing exponentially, what is r for this population? Would this value represent r_{\max} , r_0 , or current r ?
4. Suppose you wanted to fit the data in question 3 to a logistic growth model. What additional information would you need?
5. If $N_0=10, K=250$ and $r=0.05$, calculate N_t for $t=2, 5, 10, 20, 50$.

Population Models Incorporating Stochasticity.

Reading

Gotelli Ch. 1,2

Additional literature

Lebreton, J. D. 1990. Modeling density dependence, environmental variability, and demographic stochasticity from population counts: an example using Wytham Wood Great Tits. Pages 89-102. *In* Population Biology of Passerine Birds, J. Blondel (ed.). Springer-Verlag, Berlin Heidelberg.

The models we have presented so far are deterministic models. However, most populations do not grow deterministically but are affected by stochastic factors. There are four types of stochastic variation that may influence populations: demographic, environmental, heterogeneity, and genetic. The first three are covered here.

Types of stochasticity

Demographic stochasticity- sometimes called binomial stochasticity. Demographic stochasticity arises because organisms reproduce (and die) in discrete units. Thus, the actual number of individuals in a population is a function of the sequence of births and deaths in the population. Demographic stochasticity does not affect the average population size at time t but it does affect the variation in population size ($\sigma^2_{N_t}$). If birth and death rates are equal then:

$$\sigma^2_{N_t} = 2N_0bt \quad (16)$$

If birth and death rates are unequal then:

$$\sigma^2_{N_t} = \frac{N_0(b+d)e^{rt}(e^{rt}-1)}{r} \quad (17)$$

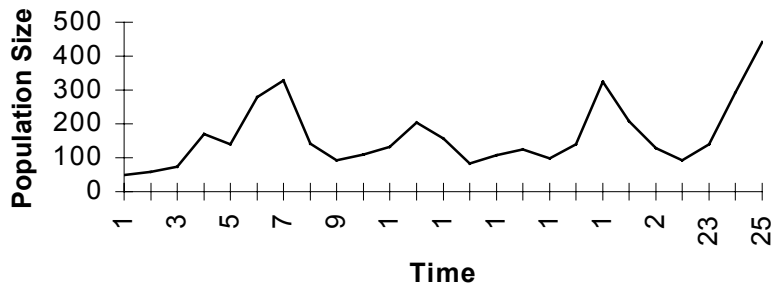
and the probability of extinction for the population is:

$$P(\text{extinction}) = \left(\frac{d}{b}\right)^{N_0} \quad (18)$$

Example of demographic stochasticity-

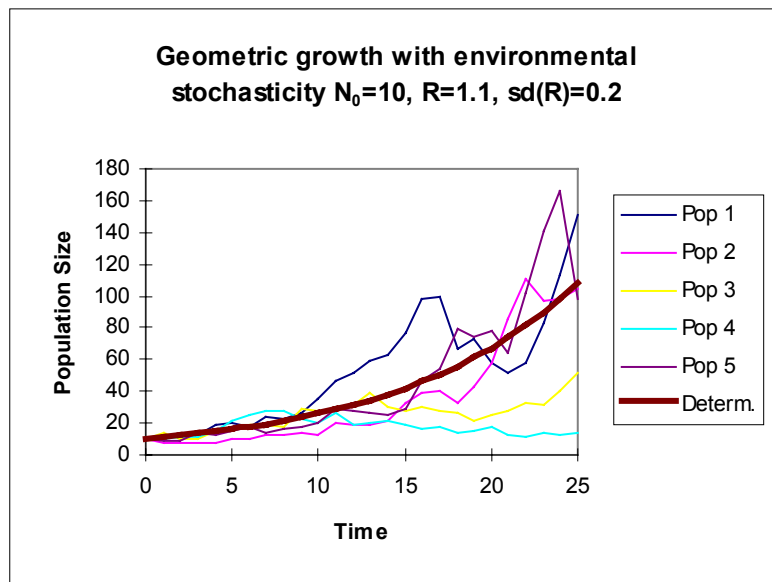
For each individual in the population, a coin is flipped to determine if it gives birth at the start of the interval. Then, a coin flip determines whether each individual lives to the start of the next interval. In a population with equal birth and death rates, the change in population size with demographic stochasticity may look like this:

Exponential growth with stochastic variation



Environmental stochasticity- variability associated with yearly fluctuations in birth and death rates. This source of variation is generally associated with climatic variation (the general meaning of environmental stochasticity) or large cataclysmic events (generally referred to as **catastrophes**). Variation in birth and death rates from place to place within a population would also be considered environmental stochasticity- in this case it would be called spatial environmental stochasticity. Again, the average population size at time t is unaffected by environmental stochasticity but the variance in population size at time t can be described by:

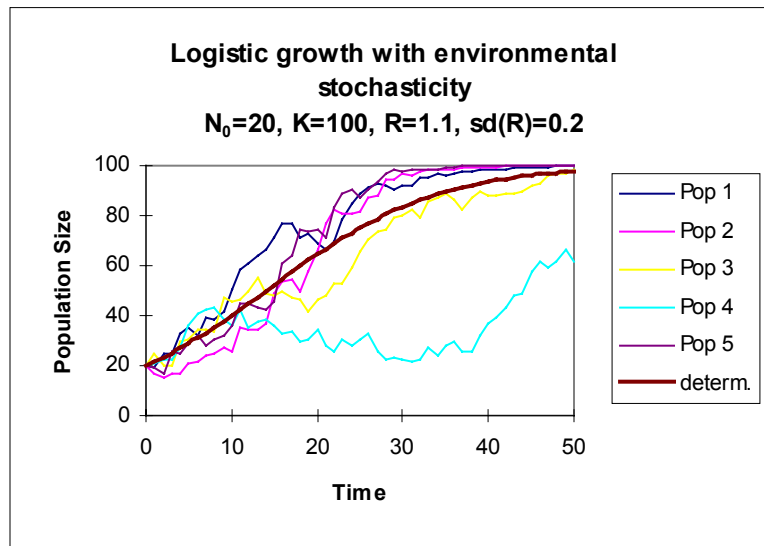
$$\sigma^2_{N_t} = N^2_0 e^{2\bar{r}t} (e^{\sigma^2_{rt}} - 1) \quad (19)$$



Heterogeneity- Variation in birth and death rates between individuals in the population.

Logistic models

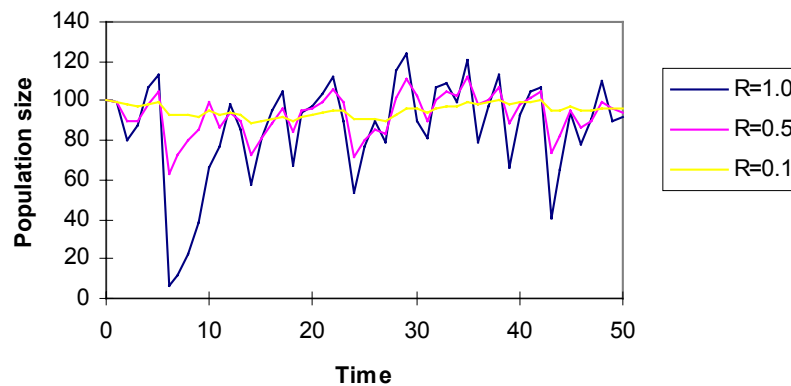
There are two ways to incorporate environmental stochasticity into logistic models, random variation in R or random variation in K . In most wildlife populations, both factors probably vary randomly. Random variation in R with a constant K causes the population to rise erratically to K at which point it stabilizes very close to K .



If K varies randomly through time, the average population size will be below the carrying capacity because the population responds more sluggishly when below than above K (see figure 2.2 in Gotelli). The difference between N and K depends on the variance in K :

$$\bar{N} \approx \bar{K} - \frac{\sigma_K^2}{2} \quad (20)$$

Logistic growth with random variation in K
 $K=100$, $sd(K)=20$



Questions:

1. Suppose you are studying an endangered population of salamanders, for which $b=0.0041$ births/(individual per year) and $d=0.004$ deaths/(individual per year). The current population size is 50. A new highway bypass is planned that will eliminate half of the population. Estimate the effect of the bypass on the probability of extinction of the population. Assume the population is growing exponentially.
2. How is the variation in population size related to N_0 , t , and b in the exponential equation with demographic stochasticity (assuming $b=d$)?
3. Name and describe the four types of stochasticity.
4. How is the average population size related to the carrying capacity when there is random variation in K ?
5. Which of the previous stochastic models do you think most closely approximates natural systems?

Life Table Analysis

Reading

Gotelli Ch. 3

Summary of Life Table variables

Age- x- Age of individuals in cohort. By convention, newborns are age 0 and k refers to the final age in the life table. An individual of **age class** i is between the ages $i-1$ and i . Age class will be designated with a subscript thus, $f(x)=f_{x+1}$.

Number alive- $s(x)$ - Number of individuals of age x in the population.

Survival to age x- $l(x)$ - Proportion of newborns that survive to age x . $l(x)=s(x)/s(0)$

Where $s(x)$ = no. alive at age x , and $s(0)$ = no. of newborns (or no. in original cohort). Also,

$$l_x = g(0)g(1)g(2)...g(x-1) = \prod_{i=0}^{x-1} g(i)$$

Age specific survival- $g(x)$ (note: Many authors use $s(x)$)- Proportion of those alive at age x that survive to $x+1$. Also written as $P(10)=g(0)$, $P(21)=g(1)$, etc.

$$g(x) = s(x+1)/s(x) = l(x+1)/l(x) = 1-m(x)$$

Age specific mortality- $m(x)$ - Proportion of individuals of age x dying by age $x+1$.

Krebs uses $q(x)$ for age specific mortality.

$$m(x)=(s(x)-s(x+1))/s(x) = (l(x)-l(x+1))/l(x) = 1-g(x)$$

Fecundity- $b(x)$ - Average number of female offspring produced by females at age x .

Also denoted as $f(x)$ (Noon and Sauer 1992) or $m(x)$ in most life table analyses.

Other variables that are sometimes included

Number of individuals dying in each interval- $d(x)$

Number of individuals surviving each interval

Expectation of further life of individuals of age x - $e(x)$

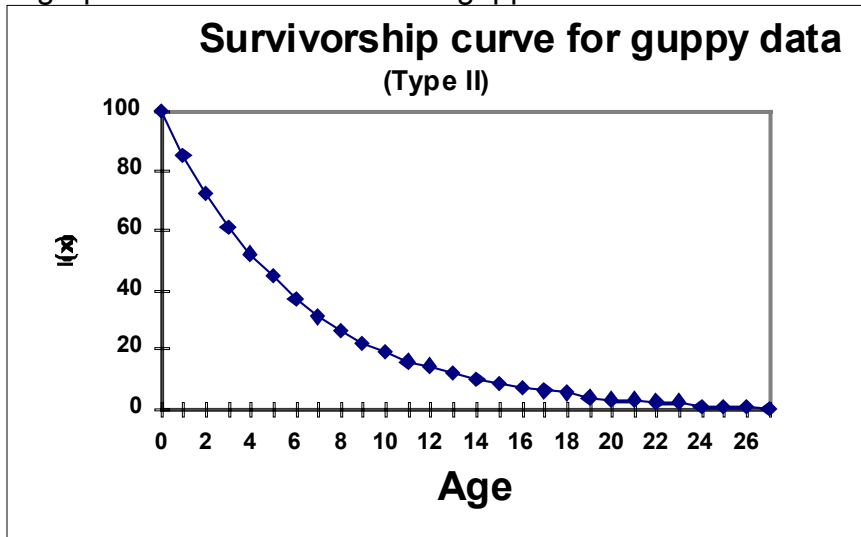
Killing rate- $k(x)$ - the exponential mortality rate between x and $x+1$. $k(x)=-\ln(g(x))$

Example using guppy data

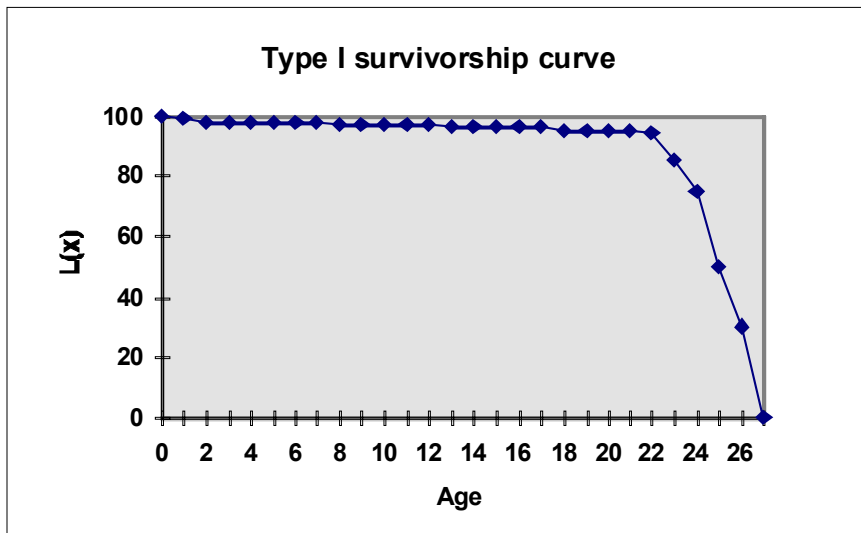
Assume you start with 100 newly hatched guppies and follow them until all of the individuals die. Age (x) is measured in weeks.

x	$s(x)$	$l(x)$	$d(x)$	$s(x)$	$m(x)$
0	100	1	15	0.85	0.15
1	85	0.85	13	0.85	0.15
2	72	0.72	11	0.85	0.15
3	61	0.61	9	0.85	0.15
4	52	0.52	8	0.85	0.15
5	44	0.44	7	0.84	0.16
6	37	0.37	6	0.84	0.16
7	31	0.31	5	0.84	0.16
8	26	0.26	4	0.85	0.15
9	22	0.22	3	0.86	0.14
10	19	0.19	3	0.84	0.16
11	16	0.16	2	0.88	0.13
12	14	0.14	2	0.86	0.14
13	12	0.12	2	0.83	0.17
14	10	0.1	2	0.80	0.20
15	8	0.08	1	0.88	0.13
16	7	0.07	1	0.86	0.14
17	6	0.06	1	0.83	0.17
18	5	0.05	1	0.80	0.20
19	4	0.04	1	0.75	0.25
20	3	0.03	0	1.00	0.00
21	3	0.03	1	0.67	0.33
22	2	0.02	0	1.00	0.00
23	2	0.02	1	0.50	0.50
24	1	0.01	0	1.00	0.00
25	1	0.01	0	1.00	0.00
26	1	0.01	1	0.00	1.00
27	0	0	0	0.00	0.00

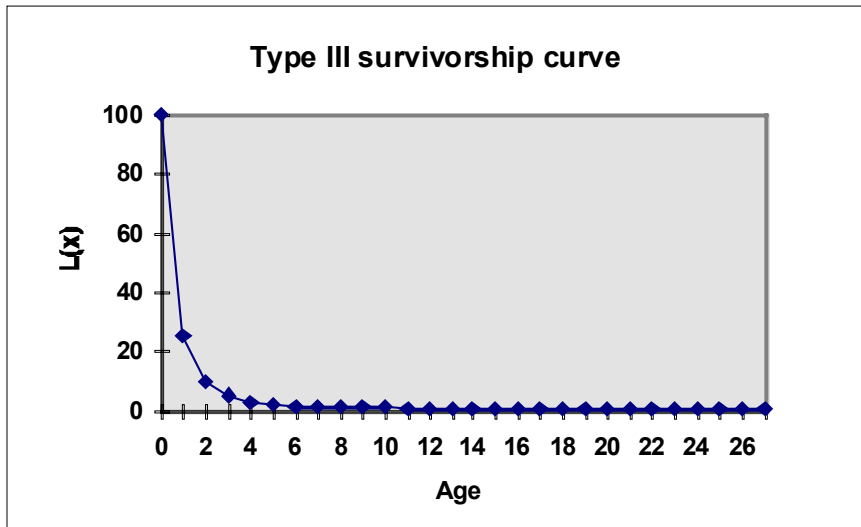
A graph of the survival of these guppies would look like this:



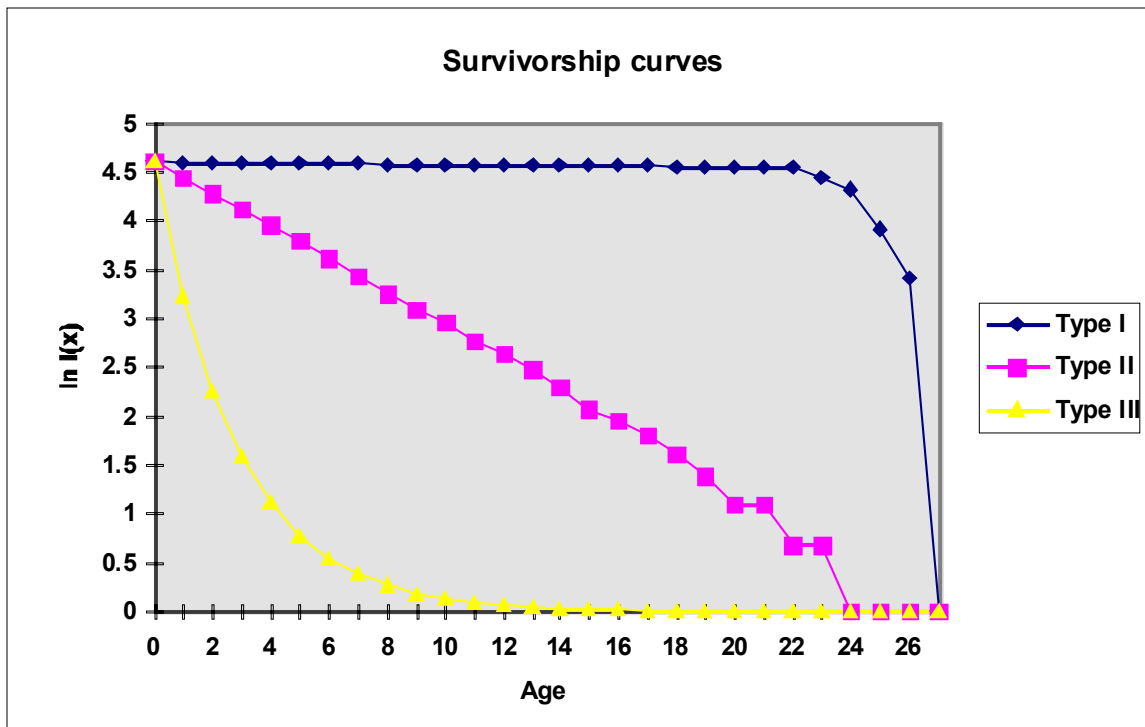
Now suppose that old age was the principal cause of mortality.



Suppose that the aquarium is invaded by a deadly pathogen at the beginning.

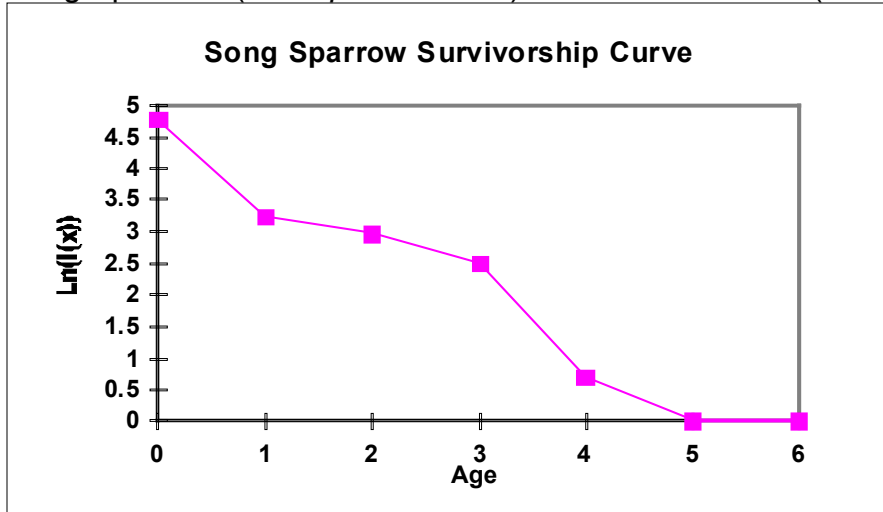


These are the three classic shapes of **survivorship curves**. They are generally plotted on a logarithmic scale.

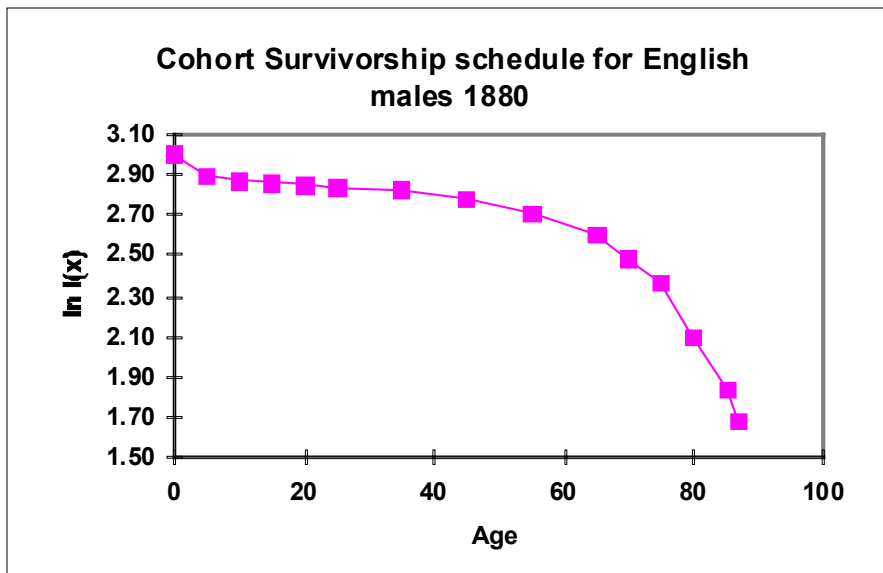


Some actual examples:

Song Sparrows (*Melospiza melodia*) on Mandarte Island (from Smith 1988).



Survivorship curve for men from England and Wales born in 1880 (from Krebs figure 11.3).



There are two basic ways that a survival schedule or survivorship curve can be estimated.

1. Cohort method- (also called the generation or horizontal method) follow a cohort of newborns from birth until the last individual dies.

2. Current method- (also called the static, stationary, time-specific, or vertical) calculated on the basis of a cross section of the population at a specific time.

Three approaches to estimating survival schedules using the current method:

- a. Count the number of individuals in each age class and estimate $l(x)$ from the distribution of individuals in the age classes.
- b. Follow individuals of each age class through one time step.
- c. Determine the age at death from skulls or other remains and estimate $l(x)$ from the proportion in each age class.

1. Cohort method- Consider 5 different cohorts, each beginning at 5 different times and with different numbers of newborns. Compute $l(x)$ using the cohort method.

t	N(1)	N(2)	N(3)	N(4)	N(5)
0	1000				
1	900	600			
2	750	540	80		
3	500	450	72	150	
4	100	300	60	135	200
5	0	60	40	112	180
6		0	8	75	150
7			0	15	100
8				0	20
9					0

Answer: $l(x)$ is identical for the 5 cohorts.

x	$l(x)$
0	1.00
1	0.90
2	0.75
3	0.50
4	0.10
5	0.00

2a. Current method- Suppose that you cannot distinguish between the cohorts, but you can determine the exact age of each individual. Consider time 4: you observe 200 newborns, 135 1 yr olds, 60 2 yr. olds, 300 3 yr. olds, and 100 4 yr. olds. You assume that the population is at a stationary state. Compute $l(x)$ only from the number of individuals observed at time 4 (Note: You must count newborns immediately after birth before any mortality has occurred).

x	$l(x)$
0	1.00
1	0.68
2	0.30
3	1.50
4	0.50
5	0.00

These data are nonsensical. Why?

2b. Current method- Observe the population at $t=5$ in addition to $t=4$. Compute the survival probabilities (transition probabilities) directly.

$$S(0) = 180/200 = 0.90$$

$$S(1) = 112/135 = 0.83$$

$$S(2) = 40/60 = 0.67$$

$$S(3) = 60/300 = 0.20$$

$$S(4) = 0/100 = 0.00$$

Now compute $l(x)$ from the above probabilities.

$$l(0) = 1 \text{ (by definition)}$$

$$l(1) = S(0) * l(0) = 0.9$$

$$l(2) = S(1) * l(1) = 0.83 * 0.9 = 0.75$$

$$l(3) = S(2) * l(2) = 0.67 * 0.75 = 0.50$$

$$l(4) = S(3) * l(3) = 0.20 * 0.50 = 0.10$$

$$l(5) = S(4) * l(4) = 0 * 0.10 = 0$$

These values correspond to the values we obtained from the cohort method.

2c. Current method- Now compute the $l(x)$ schedule based on dead animals that you find. Assume that you find and can age all of the individuals that die between time periods 4 and 5 (not an easy task!).

x at t=4	No. Alive at t=4	No. Alive at t=5	No. that die between t=4 and t=5
0	200	180	20
1	135	112	23
2	60	40	20
3	300	60	240
4	100	0	100
		Total	403

Now construct your $l(x)$ schedule assuming that you started with a cohort of 403 individuals.

x	No. alive	$l(x)$
0	403	1.00
1	383	0.95
2	360	0.89
3	340	0.84
4	100	0.25
5	0	0.00

This does not match the $l(x)$ schedule computed using the cohort method. Why not?