Matrix Population Models for Wildlife Conservation and Management

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Introduction to Population Ecology & Modeling

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What is a population?

- Population:
  - a group of organisms (plants, animals, or microorganisms) of the same species coexisting at the same time and place.
- Population ecology:
  - the scientific study of the dynamics, regulation, persistence and evolution of biological populations.

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How do we study populations?

- Empirical (field/lab) study
  - Data and statistical analyses
  - Population parameters/characteristics
- Population models
  - Empirical and theoretical models

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Population characteristics/ parameters

- Abundance
- Rate of birth (birth rate)
- Rate of death (death rate)
- Emigration/immigration rate
- Rate of increase (population growth rate)
- Sex ratio
- Age or stage structure
- Other: spatial distribution, …

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Population models

- Needed for understanding things like
  - Future dynamics
  - Persistence and viability
  - Scenario planning
  - …
- Typically, population characteristics are used as model parameters

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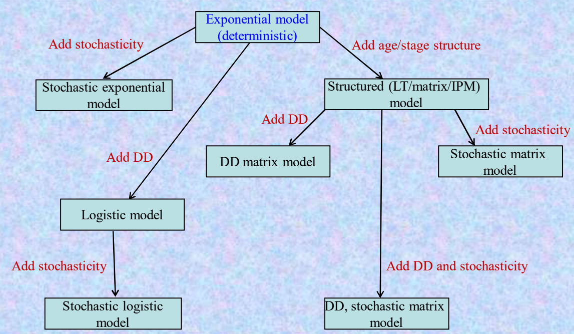
Taxonomy of population models

"Base model"



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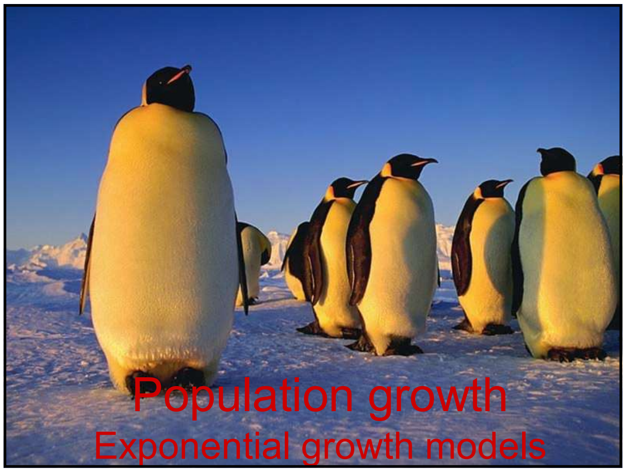

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Population growth

- Processes by which individuals are added to a population:
  1. Birth (*B*)
  2. Immigration (*I*)
- Processes by which individuals are removed from a population
  1. Death (*D*)
  2. Emigration (*E*)
- Using these parameters, N_1 is:

$$N_1 = N_0 + B + I - D - E.$$

BIDE model

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Assumptions

1. Unlimited, homogeneous, and constant environment
2. No immigration or emigration: closed population (geographic closure)
3. Constant birth and death rates (= constant growth rate)
   - No density-dependence or stochasticity
4. No age/stage (or spatial) structure

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Discrete exponential growth model

BIDE equation:

$$N_1 = N_0 + B + I - D - E.$$

By assumption 2 (I = E = 0),

$$N_1 = N_0 + B - D.$$

Divide both sides by N_0:

$$\frac{N_1}{N_0} = \frac{N_0}{N_0} + \frac{B}{N_0} - \frac{D}{N_0} = 1 + \frac{B}{N_0} - \frac{D}{N_0}.$$

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- Define:
  $b = B/N_0$
  = birth rate = # births/individual*unit time
  $d = D/N_0$
  = death rate = # deaths/individual*unit time
- With these replacements, we now have:

$$\frac{N_1}{N_0} = 1 + b - d.$$

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$$\frac{N_1}{N_0} = 1 + b - d, \text{ or } N_1 = N_0(1 + b - d).$$

Let λ = (1 + *b* – *d*), and solve for N_1:

$$N_1 = \lambda N_0$$

Assume: λ (finite growth rate) constant over time

$$N_2 = \lambda N_1 = \lambda\lambda N_0 = \lambda^2 N_0$$
$$N_3 = \lambda N_2 = \lambda\lambda\lambda N_0 = \lambda^3 N_0$$
$$\vdots$$
$$\boxed{N_t = \lambda^t N_0}$$

Discrete exponential (or geometric) growth model

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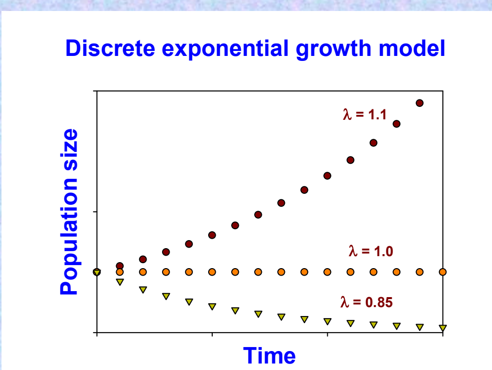

$$\boxed{N_t = \lambda^t N_0}$$

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Exponential growth model

$$\frac{dN}{dt} = rN$$

$$\boxed{\begin{aligned}\frac{dN}{dt} &= \lim_{\Delta t \to 0} \frac{\Delta N}{\Delta t} \\ &= \frac{\Delta N}{\Delta t} \text{ for small } \Delta t \ (\Delta t \to 0)\end{aligned}}$$

r = instantaneous or continuous population growth rate
= Malthusian parameter
= Continuous time, per-capita population growth rate
= ln(λ)

Linear Ordinary Differential Equation (ODE)

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Solution

$$\frac{dN}{dt} = rN$$

- A linear ODE
- A typical initial value problem
- Solve it to get (with N at time zero = N_0):

$$\boxed{N_t = N_0 e^{rt}}$$

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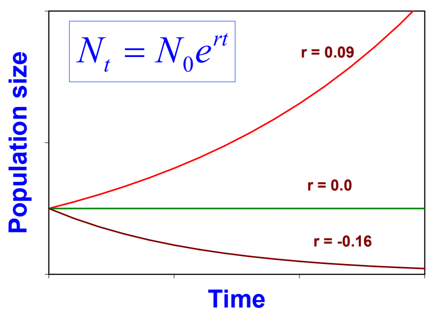
Continuous exponential growth model



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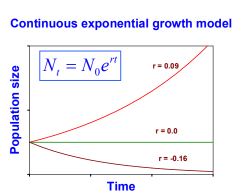
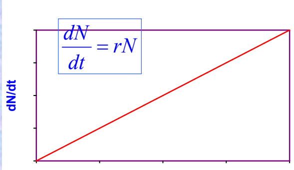
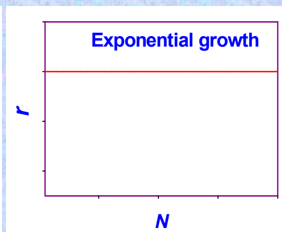
Exponential model: some relationships







- Density-independent, deterministic, unstructured, single population model
- A linear model

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Doubling/tripling time

- Doubling time

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

- Tripling time

$$t_{triple} = \frac{\ln(3)}{r}$$

- Quadrupling time

$$t_{quadruple} = \frac{\ln(4)}{r}$$

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Working with real data: the whooping cranes

- Only remaining natural migratory flock
- Nearly extinct: only 22 remaining in 1940's

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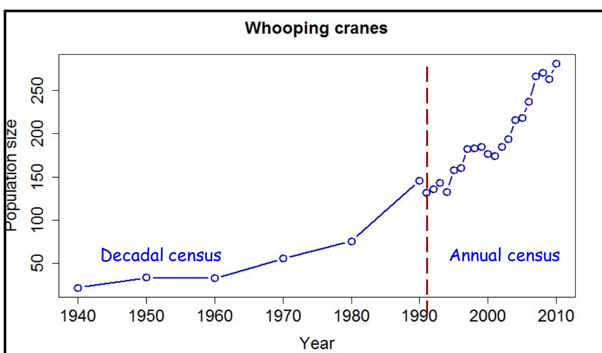

- Code file: Ex_1_exponential_model.R
- Data: whooping_crane.csv
- Things to do: calculate r, sd(r), project N under deterministic and stochastic scenarios

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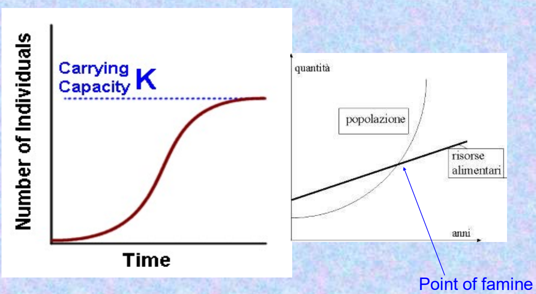
Logistic population growth model



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Density-dependence (DD)

- Dependence of *per capita* population growth rate (*r*) on present or past population density
- Density-dependent models: models that incorporate the effects of population density on population dynamics

DD generally implies a negative relationship

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Density-dependence: mechanisms

- Competition for resources
  - Food
  - Territories, nest sites, mates, and other limiting resources
- Intra-specific strife
  - Black bears, Florida panthers
- Stress response
  - Small mammals
- Disease transmission
  - Risk of transmission can increase with density

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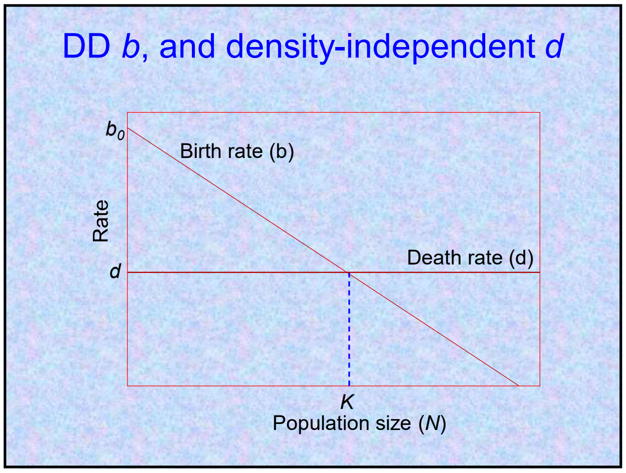
DD b, and density-independent d
b0
Birth rate (b)
Rate
d
Death rate (d)
K
Population size (N)

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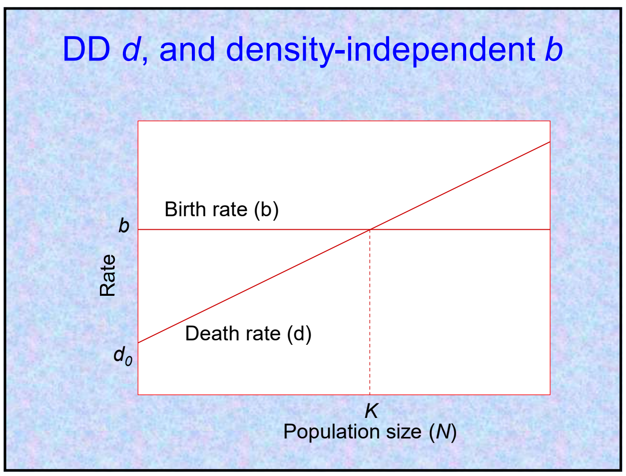
DD d, and density-independent b
Birth rate (b)
b
Rate
Death rate (d)
d0
K
Population size (N)

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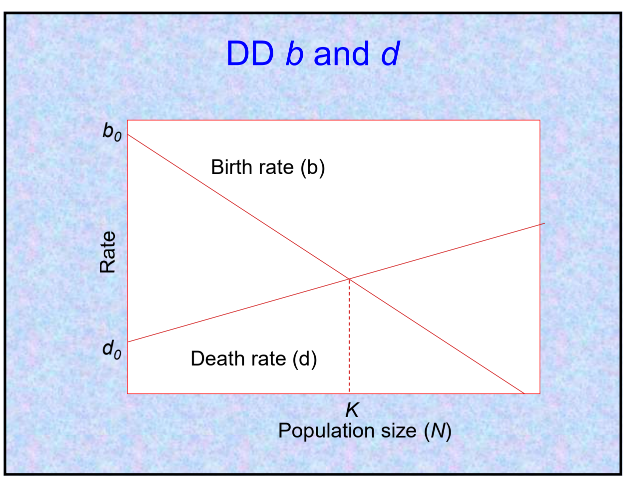
DD b and d
b0
Birth rate (b)
Rate
d0
Death rate (d)
K
Population size (N)

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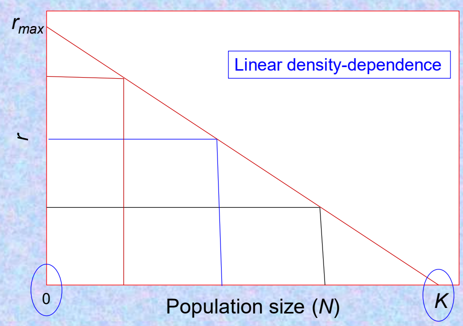
Density-dependent r



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Density-dependence

- When $N = K$, $b = d$, and $r = 0$, and the population stops growing
  - K: carrying capacity (or equilibrium density)
  - When $N = K$, $r = 0$; $dN/dt = 0$
- K can be viewed as the maximum number of individuals an environment can support
  - $N \leq K$, always!

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DD population growth

- Assume:
  1. Linear decline in r as N increases (linear density-dependence), and
  2. K is constant

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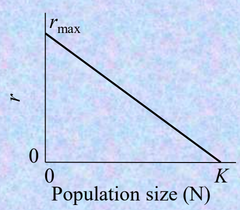
Density-dependence



•The linear regression equation is (FYI only):

$Y = a + bX,$

And, we have

$$a = r_{max},$$

$$b = -\frac{r_{max}}{K},$$

$$X = N,$$

$$Y = r$$

So, our regression equation is:

$$r = r_{max} + \left(-\frac{r_{max}}{K}\right)N$$

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Logistic growth model

$$r = r_{max} + \left(-\frac{r_{max}}{K}\right)N$$

$$= r_{max}\left(1 - \frac{N}{K}\right)$$

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

Exponential:

$$\frac{dN}{dt} = rN$$

Ordinary non-linear differential equation

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Logistic growth model

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

- The simplest non-linear population growth model!
- First derived by Pierre Francois Verhulst in 1838!!
- Solve this differential equation to get the integral form of the logistic growth model

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Integral form

$$N_t = \frac{K}{1 + \left[\frac{K - N_0}{N_0}\right] e^{-rt}}$$

- Notes:
  - *N* can never exceed *K*
  - Note that *r* here is really r_{max}

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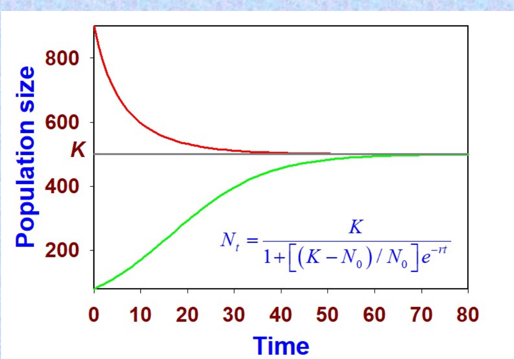
Model behavior



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Assumptions

1. No immigration or emigration: “closed” population (geographic closure)
2. No age/stage (or spatial) structure
3. No stochasticity
4. Linear decline in *r* as *N* increases ➔ linear density-dependence
5. Carrying capacity (*K*) constant

Note:
Assumptions of unlimited environment and constant *r* are replaced by assumptions 4 and 5;
r is no longer constant

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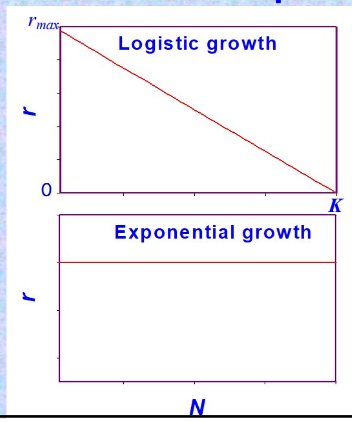
Comparison



r is linearly density-dependent

$$r = r_{\max}\left(1 - \frac{N}{K}\right)$$

r is constant and density-independent

$$r = r_{\max}$$

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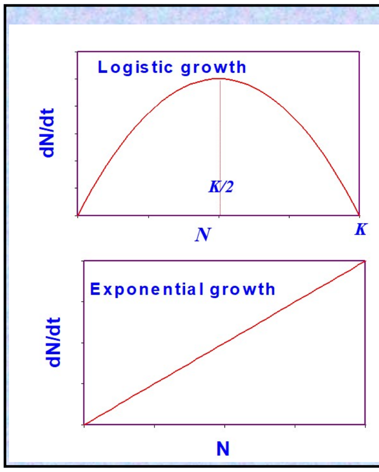

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right)$$

dN/dt maximum when $N = K/2$ (inflection point)

$$\frac{dN}{dt} = rN$$

dN/dt is a linear function of N

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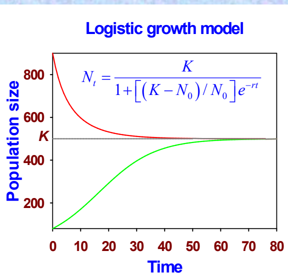
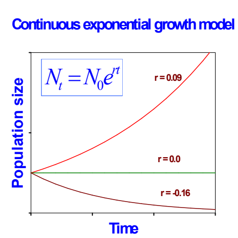


$$N_t = \frac{K}{1 + \left[\left(K - N_0\right)/N_0\right]e^{-rt}}$$



$$N_t = N_0 e^{rt}$$

- Stable equilibrium at $N = K$
- Non-linear model

- Unbounded growth or decline ("boom" or "bust")
- No stable equilibrium
- Linear model

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China's population growth

- Data: china_pop_size.csv
- Code: Logistic_growth_3.R
- Things to do:
  - Estimate r_{max} and K
  - Perform population projection using estimated parameters
  - Perform stochastic population projection under various scenarios

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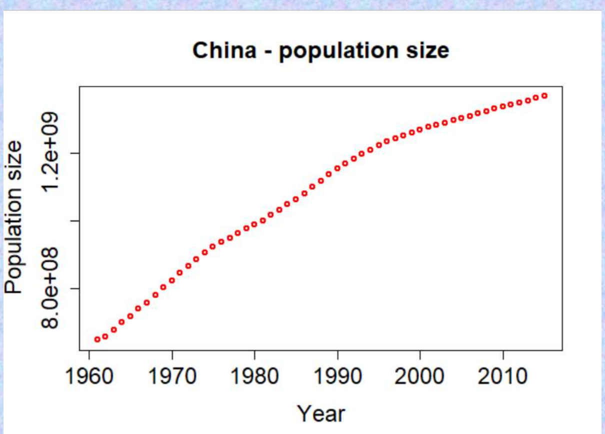

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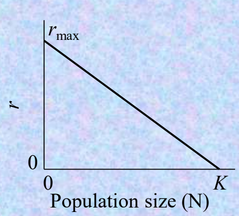
Estimating r and K

1. Plot $r_t = \ln(N_{t+1}/N_t)$ against N_t. If r declines linearly as N increases ➔ evidence of DD
2. Perform linear regression with Y = r_t against N_t

$$r_t = a + b*N_t$$

3. $r_{max} = a$ (Y-intercept)
   $K = - r_{max}/b$ (X-intercept)



Alternative:
non-linear regression

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Discrete logistic growth model

$$N_{t+1} = N_t + N_t r_d \left[1 - \frac{N_t}{K}\right]$$

Difference equation ➔ discrete time model

r_d = "discrete growth factor" = λ - 1

➢ λ = 1 + r_d

➢ Ricker and Beverton-Holt recruitment models also are discrete time DD models

(May 1974)

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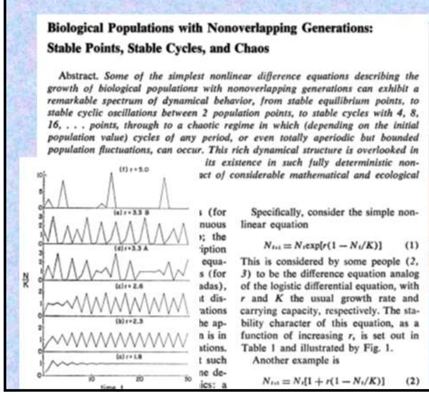
Lord May of Oxford



Biological Populations with Nonoverlapping Generations: Stable Points, Stable Cycles, and Chaos

Abstract. *Some of the simplest nonlinear difference equations describing the growth of biological populations with nonoverlapping generations can exhibit a remarkable spectrum of dynamical behavior, from stable equilibrium points, to stable cyclic oscillations between 2 population points, to stable cycles with 4, 8, 16, . . . points, through to a chaotic regime in which (depending on the initial population value) cycles of any period, or even totally aperiodic but bounded population fluctuations, can occur. This rich dynamical structure is overlooked in*

its existence in such fully deterministic non-

act of considerable mathematical and ecological

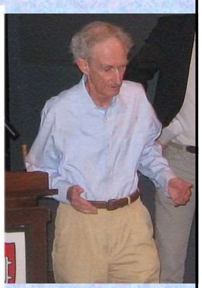
Specifically, consider the simple nonlinear equation

$$N_{t+1} = N_t \exp[r(1 - N_t/K)] \quad (1)$$

This is considered by some people (2, 3) to be the difference equation analog of the logistic differential equation, with r and K the usual growth rate and carrying capacity, respectively. The stability character of this equation, as a function of increasing r, is set out in Table 1 and illustrated by Fig. 1.

Another example is

$$N_{t+1} = N_t[1 + r(1 - N_t/K)] \quad (2)$$



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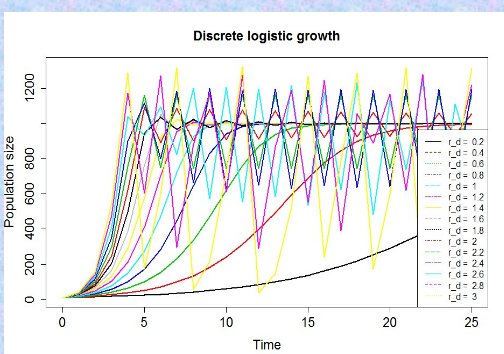

Chaos

Sensitive dependence on initial conditions

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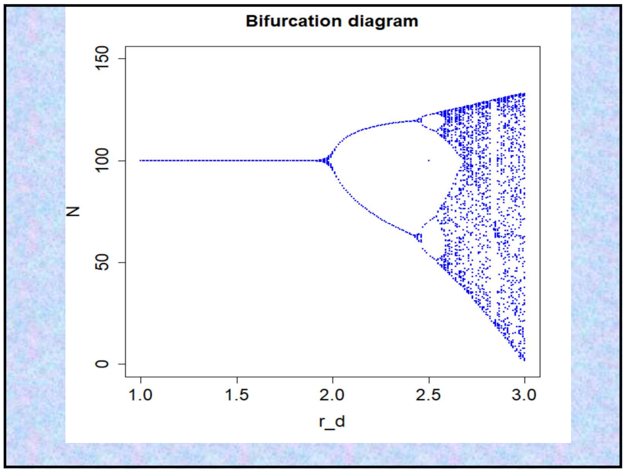
Bifurcation diagram
N
r_d
0
50
100
150
1.0
1.5
2.0
2.5
3.0

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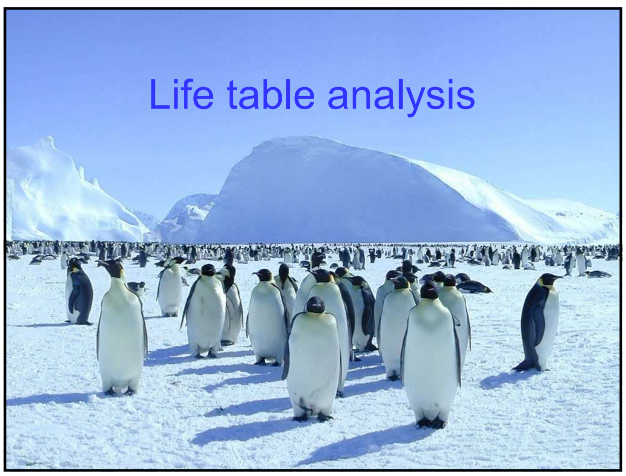
Life table analysis

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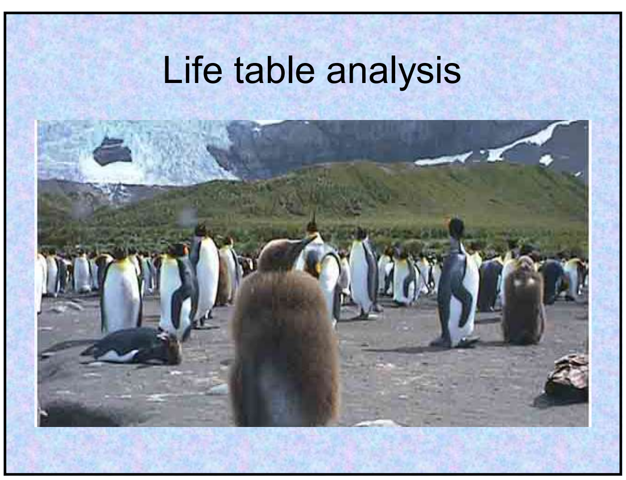
Life table analysis

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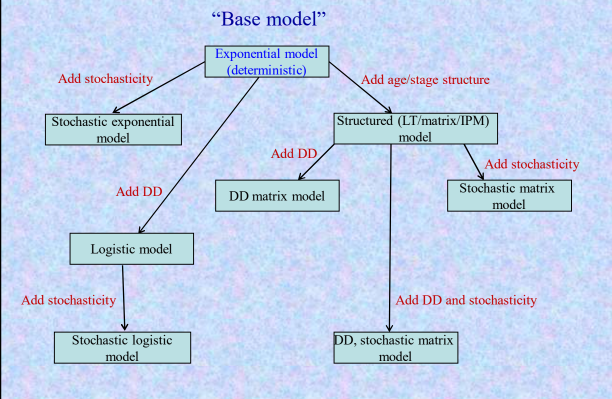
Taxonomy of population models



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Why worry about age structure?

1. Birth and death rates differ among age classes (or life-history stages)
2. Age structure can be used for structured demographic projections
   - Population size, age-structure
   - Possible management challenges (wildlife)
   - Health care costs, social security, workforce, dependency ratio (humans)
3. Age structure provides useful information regarding past history, present or future population growth

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Age structure matters!

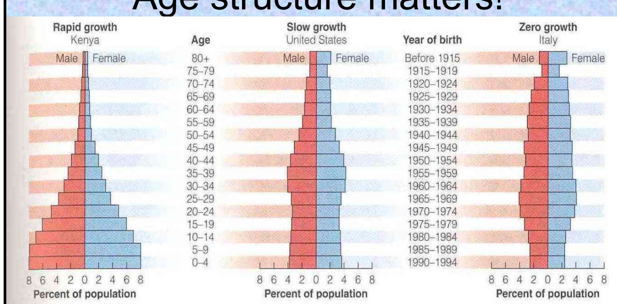

FIGURE 10.16
Age structure pyramids for the human population of Kenya (growing at 2.1% per year), the United States (growing at 0.6% per year), and Italy (zero growth) for 1995. (From McFalls 1998.)

"Age pyramids"

Age pyramid tool:
https://www.populationpyramid.net/

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What is a life table?

- Age-specific summary of survival (and reproduction)
- Originally developed by life insurance companies
- Routinely used in actuarial, medical and ecological research
- Age: important variable as it is assumed to influence survival and reproduction

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Ecological life tables

Age (x)	l_x	m_x
0	1	0
1	0.217	1.5
2	0.165	2
3	0.104	2.1
4	0.017	3.5
5	0.009	3.1
6	0.0	0

Key life table variables

x = Age

Survival:

l_x= Age-specific survivorship

q_x = Age-specific mortality

P_x = Age-specific survival rate (= 1- q_x)

Reproduction:

m_x= Age-specific fecundity rate→

The average number of daughters born to a female of age x per unit time.

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Net reproductive rate (R_0)

- The average (expected) number of daughters produced by a female in her lifetime. $$R_0 = \sum l_x m_x$$
- Unit: no. of daughters per female, per generation
- A measure of per-generation population growth rate
  - $R_0 > 1$ → Increasing population
  - $R_0 < 1$ → Decreasing population
  - $R_0 = 1$ → Stable population

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Age (x)	l_x	m_x	l_x*m_x
0	1	0	1*0 = 0
1	0.217	1.5	0.217*1.5 =0.326
2	0.165	2	0.165*2 = 0.33
3	0.104	2.1	0.104*2.1 = 0.218
4	0.017	3.5	0.017*3.5 = 0.06
5	0.009	3.1	0.009*3.1 = 0.03
6	0.0	$R_0 =$	$\sum l_x m_x = 0.96$

R_0 = 0.96
(per fem*gen)

Note: *R_0 in this context is conceptually identical to R_0 of COVID-19 or other infectious diseases*

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Generation time (G)

- The mean age of the mothers of a newborn "cohort",
- The time required for the population to grow by a factor of R_0

$$G = \frac{\sum x l_x m_x}{R_0}$$

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Age (x)	l_x*m_x	x*l_x*m_x
0	0	0*0 = 0
1	0.326	1*0.326 = 0.326
2	0.33	2*0.33 = 0.66
3	0.218	3*0.218 = 0.655
4	0.06	4*0.06 = 0.24
5	0.03	5*0.03 = 0.15
6		$\sum x l_x m_x = 2.018$

R_0 = 0.96

$$G = \frac{\sum x l_x m_x}{R_0} = \frac{2.018}{0.96} = 2.099 \text{ yrs.}$$

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Per capita population growth rate (r)

- Approximate r:

$$r \approx \frac{\ln R_0}{G}$$
$$= \frac{\ln(0.96)}{2.099}$$
$$= -\ 0.0188 \text{ / individual*year}$$
$$\lambda \approx e^r = e^{-\ 0.0188} = 0.981$$

- Exact r ➔ Use Lotka-Euler equation

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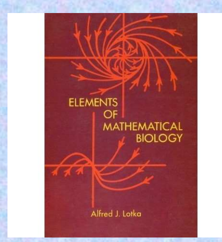
The Lotka-Euler equation

- Continuous:

$$1 = \int_{\alpha}^{\omega} l_x m_x e^{-rx} dx$$

- Discrete:

$$1 = \sum_{\alpha}^{\omega} l_x m_x e^{-rx}$$



- Solved iteratively

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The Lotka-Euler equation

$$\boxed{1 = \int_{\alpha}^{\omega} l_x m_x e^{-rx} dx} \qquad \boxed{1 = \sum_{\alpha}^{\omega} l_x m_x e^{-rx}}$$

- Foundation of stable age theory
  - Underlies ALL animal, plant or human demography
- Life history evolution and evolutionary studies rely on this theory
- r is possibly the single most important quantity in ecology, evolutionary biology and wildlife management!!

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Solving Lotka-Euler equation

$$1 = \sum_{\alpha}^{\omega} l_x m_x e^{-rx}$$

- Solved iteratively (i.e., by "trial and error")
- Calculate R_0 and G
- Calculate approximate r:

$$r \approx \frac{\ln R_0}{G}$$

- Re-arrange the equation, write a function:

$$1 - \sum_{\alpha}^{\omega} l_x m_x e^{-rx} = 0$$

- Use *uniroot* function in R to find the (the largest) root
  - Use approximate r to create a search interval

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Yellow-bellied marmots, RMBL, Colorado

- Data: marmot_lt_female2. csv
- Code: Ex_3_Life_table_analysis.R
- Things to do: Calculate R_0, G, and exact r.

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Lecture concludes!

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