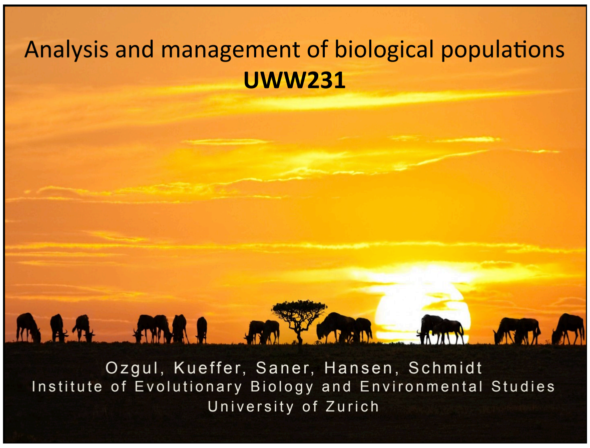


Analysis and management of biological populations
UWW231

Ozgul, Kueffer, Saner, Hansen, Schmidt
Institute of Evolutionary Biology and Environmental Studies
University of Zurich

Course Outline

Applied Population Ecology (Arpat Ozgul)
Life history theory, basic population models, introduction to population analysis and biodemography.

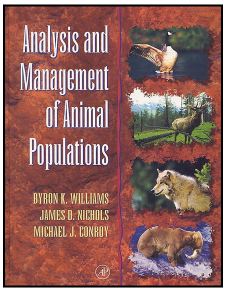
Invasion Biology (Christoph Kueffer)
Basics of invasion biology, scientific and policy aspects of invasive species, how to use population biology theory in controversial science-policy settings.

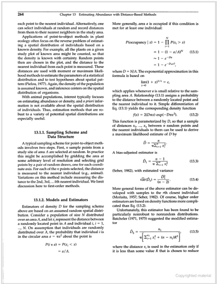
Restoration Ecology (Philippe Saner)
Strategies of ecosystem restoration, fragmentation, species diversity, wildlife corridors, Borneo case study, role of rare species

Rewilding (Dennis Hansen)
Concept of "rewilding", extant species to functionally replace extinct species, controversy in conservation and restoration, a rewilding proposal grounded in ecological theory.

Biodiversity monitoring (Benedikt Schmidt)
Key principles for designing biodiversity surveys, pros and cons of some state variables used to describe biodiversity trends, example cases from real-world monitoring programs.

Applied Population Ecology





Arpat Ozgul
Institute of Evolutionary Biology and Environmental Studies

www.popecol.org

Lecture Outline

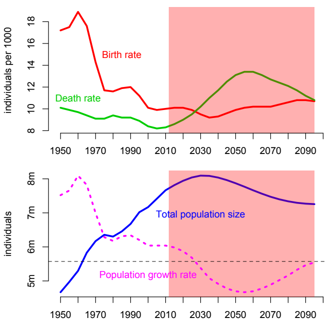
- A very brief intro to bio-demography
- Life history theory
  - Traits and trade-offs
- Linking reproduction and survival together
  - Matrix population models

arpat.net/lecture.pdf

arpat.net/practical.pdf

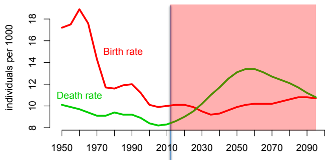
Demography

Swiss Population



(United Nations Report, 2011)

Demography



Measurement & Analysis

Demographic parameters
(birth, death, migration, …)

Social and environmental factors

Prediction & Modeling

Predicting population trends

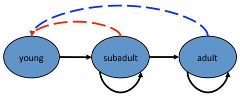
Assessing population persistence

Biodemography / Population Ecology

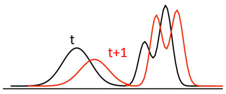
Measurement & Analysis

$$\phi_2^{11} p_3^1 [\phi_3^{11}(1-p_4^1)\phi_4^{12} + \phi_3^{12}(1-p_4^2)\phi_4^{22}] p_5^2$$

Prediction & Modeling



$$\begin{bmatrix} 0 & S_P\Psi_{PR}\ \theta & S_R\Psi_{RR}\ \theta \\ S_J\Psi_{JP} & S_P\Psi_{PP} & 0 \\ 0 & S_P\Psi_{PR} & S_R\Psi_{RR} \end{bmatrix}$$



Ecological and Evolutionary Knowledge

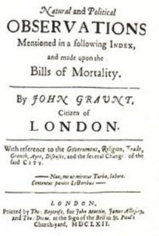
Organism → Population → Species

Biological conservation

Sustainable harvest

Pest control

History: Beginning



Natural and Political
OBSERVATIONS
Mentioned in a following INDEX,
and made upon the
Bills of Mortality.

By JOHN GRAUNT,
Citizen of
LONDON.

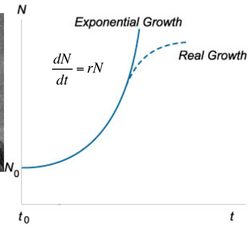
With reference to the Government, Religion, Trade, Growth, Ayre, Diseases, and the several Changes of the said CITY.

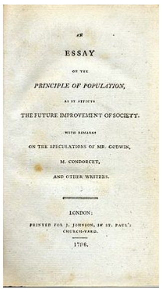
—— Non, me ut miretur Turba, laboro,
Contentus paucis Lectoribus ——

LONDON,
Printed by Tho: Roycroft, for John Martin, James Allestry, and Tho: Dicas, at the Sign of the Bell in St. Paul's Church-yard, MDCLXII.

John Graunt (1662)

History: Exponential growth



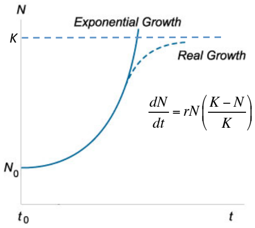


AN
ESSAY
ON THE
PRINCIPLE OF POPULATION,
AS IT AFFECTS
THE FUTURE IMPROVEMENT OF SOCIETY.
WITH REMARKS
ON THE SPECULATIONS OF MR. GODWIN,
M. CONDORCET,
AND OTHER WRITERS.

LONDON:
PRINTED FOR J. JOHNSON, IN ST. PAUL'S
CHURCH-YARD.
1798.

Thomas Robert Malthus (1789)

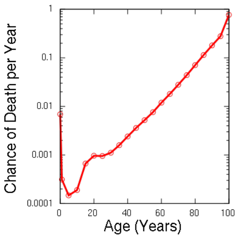
History: Logistic growth



Pierre Francois Verhulst (1838)

History: Mortality law

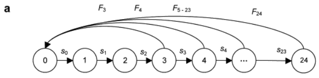
$$y(t) = ae^{be^{ct}}$$



Benjamin Gompertz (1825)

History: Age structure

Patrick H. Leslie (1945)

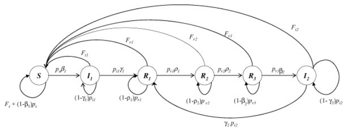


b

$$\mathbf{A} = \begin{bmatrix} F_0 & F_1 & F_2 & F_3 & F_4 & \dots & F_{23} & F_{24} \\ s_0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & s_3 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & s_4 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & s_{23} & s_{24} \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & f_4 \cdot p_4 \cdot s_3 & f_5 \cdot p_5 \cdot s_4 & \dots & f_{24} \cdot p_{24} \cdot s_{23} & 0 \\ s_0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & s_1 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & s_2 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & s_3 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & s_4 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & \dots & s_{23} & 0 \end{bmatrix}$$

History: Stage structure

Leonard P. Lefkovitch (1965)



$$\mathbf{A}= \begin{pmatrix} F_s+(1-\beta_1)p_s & F_{i1} & F_{r1} & F_{r2} & F_{r3} & F_{i2} \\ p_s\beta_1 & (1-\gamma_1)p_{i1} & 0 & 0 & 0 & 0 \\ 0 & p_{i1}\gamma_1 & (1-\rho_1)p_{r1} & 0 & 0 & \gamma_2 p_{i2} \\ 0 & 0 & p_{r1}\rho_1 & (1-\rho_2)p_{r2} & 0 & 0 \\ 0 & 0 & 0 & p_{r2}\rho_2 & (1-\beta_2)p_{r3} & 0 \\ 0 & 0 & 0 & 0 & p_{r3}\beta_2 & (1-\gamma_2)p_{i2} \end{pmatrix}$$

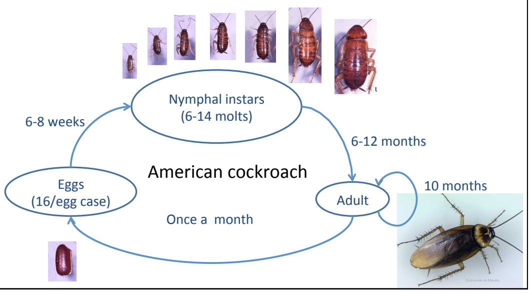
Lecture Outline

- A very brief intro to bio-demography
- Life history theory
  - Traits and trade-offs
- Linking reproduction and survival together
  - Matrix population models

Life history theory

What is life history?

Life history of an organism is the timing of key "life events"
from birth to death.



Nymphal instars
(6-14 molts)

6-8 weeks

6-12 months

American cockroach

Eggs
(16/egg case)

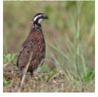
Adult

10 months

Once a month

Life history theory explains why…

- Organisms are small or large
- They have a short or a long life
- They mature early or late
- They have few or many offspring

Northern bobwhite			Black-browed albatross	
	38cm 160g 1-2yr 10months 12-15eggs *3	Wingspan Weight Longevity Age at 1st reproduction Fecundity	240cm 4kg 40yrs 6-15yrs 1egg	

Life history traits (LHT)

When is the 1st breeding?	Age / Size at maturity
How many times?	Iteroparity / Semelparity
How many offpsring?	Litter / Clutch size Reproductive effort Offspring sex-ratio
Stay or leave?	Natal dispersal / Migration
When to die?	Age / Size-specific reproductive and survival schedule Longevity / Senescence

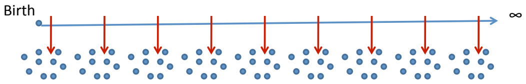
Life history & fitness

- Timing of events is shaped by natural selection to produce the largest possible number of surviving offspring
- Fitness: expected genetic contribution of an individual or genotype to future generations
- Natural selection is expected to favor a combination of traits that maximize fitness.
- LHT = fitness components. Many of them are demographic variables of the considered organism.

Life history & fitness

	Year 1	Year 2	Year 3
Genotype A	0	1	1
Genotype B	0	0	2

- Measuring fitness is not easy.
- Some statistics commonly used:
  - LRS (Lifetime reproductive success = total number of offspring produced in lifetime)
  - R_o (Net reproductive rate, from life tables)
  - r (from life tables) and λ (from matrix models)
- Best way to max fitness:



=> "Darwinian demons" (Law 1979)

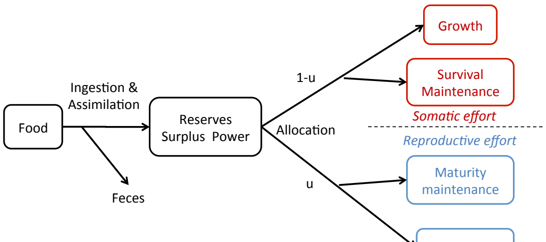
Trade-offs & principle of allocation

- However, such organisms cannot exist because life histories are constrained by external factors (resources, competitors, predators, etc.) and trade-offs among LHTs.

Allocation of resources

- **Principle of allocation** (Levins 1968): each organism has a limited amount of energy that can be allocated for maintenance, survival, growth and reproduction. Energy allocated to survival is not available for reproduction or growth.

Trade-offs & principle of allocation



Energy budget model

Trade-offs

- Central to life history theory
- Represent the cost paid in the currency of fitness when a beneficial change in one trait is linked to a detrimental change in another
- The most prominent life-history trade-off is the cost of reproduction (Stearns 1989) in terms of survival and future reproduction
  - Reproduce or survive? Now or later?
- Reproductive value = Current Reproduction + Residual Reproductive Value

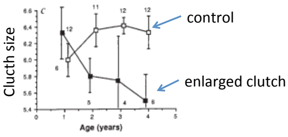
expected contribution to the population through both current and future reproduction

"left" for future reproduction

- So, reproductive value is not only related to reproduction, but also to survival.

Trade-offs

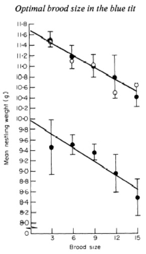
- Intra-individual trade-offs:
  - Current reproduction vs. survival
  - Current vs. future reproduction
  - Reproduction vs. growth
  - Reproduction vs. condition



Collared flycatcher
Gustaffson and Part (1990)

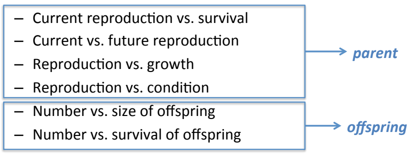
Trade-offs

- Intra-individual trade-offs:
  - Current reproduction vs. survival
  - Current vs. future reproduction
  - Reproduction vs. growth
  - Reproduction vs. condition
  - Number vs. size of offspring
  - Number vs. survival of offspring



Blue tit experiments
(Nur 1984,1988)

Trade-offs

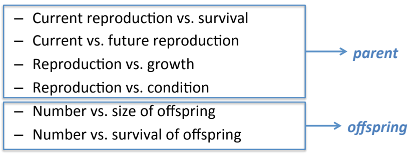


- Intra-individual trade-offs:
  - Current reproduction vs. survival
  - Current vs. future reproduction
  - Reproduction vs. growth
  - Reproduction vs. condition
  - Number vs. size of offspring
  - Number vs. survival of offspring

parent

offspring

Trade-offs

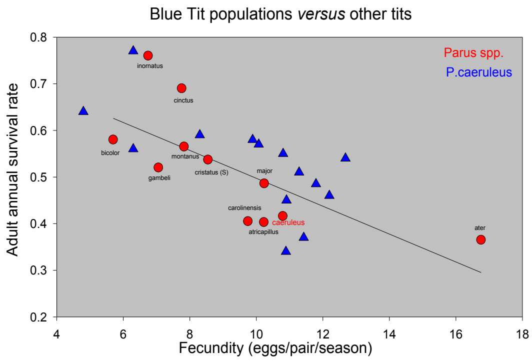


- Intra-individual trade-offs:
  - Current reproduction vs. survival
  - Current vs. future reproduction
  - Reproduction vs. growth
  - Reproduction vs. condition
  - Number vs. size of offspring
  - Number vs. survival of offspring

parent

offspring

- Inter-generational trade-offs (parent-offspring conflicts):
  - Number of offspring vs. parental survival
  - Offspring condition vs. parental survival



Dhondt 2001 (Ardea 89:155-166)

r-K selection

The r-K selection
(Pianka 1970)

- A heuristic (and much debated) way to classify species based on Verhulst's logistic equation of population regulation:

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

Rate of population change

Per capita population growth rate

Population size

Carrying capacity

- r-selected = high growth rate (r)
- K-selected = subsist near the carrying capacity of their environment (K)
- Attempt to place species along the r-K continuum

---

r-K selection

Trait	r-selected	K-selected
Maturity	Early	Late
Offspring	Many, small	Few, large
Parental care	Low	High
Survival	Low	High
Body size	Small	Large
Generation time	Short	Long
Lifespan	Short	Long
Environment	Unpredictable	Predictable
Succession	Early	Late
Refer to	Colonizers	Competitors
Example	mice	elephants

Criticism of the r-K selection

- Fast-slow continuum (Promislow & Harvey 1990)

Fast
Live a "fast" life
Die young

Slow
Live a "slow" life
Live long

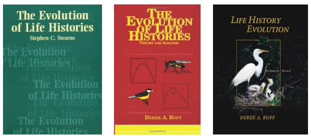
r-strategy

K-strategy

- See Gaillard et al. (1989) and Stearns (1992) for criticism of the r-K selection theory for focusing on density-dependent selection.
- The r-K selection paradigm was replaced by new paradigm that focused on age-specific mortality (Wilbur et al. 1974, Stearns 1976, Charlesworth 1980):
  - a more mechanistic link between an environment and an optimal life history
  - age/stage structured models as a framework (next section)

Further reading

- Stearns (1992) The evolution of life histories
- Roff (1992) The evolution of life histories
- Roff (2002) Life history evolution



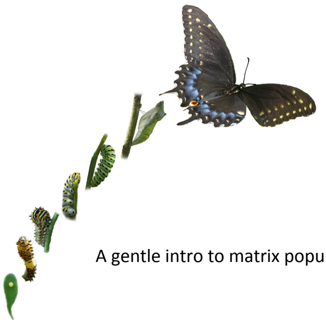
- Watch Stearns' lecture online at: http://academicearth.org/lectures/life-history-evolution

---

Lecture Outline

- A very brief intro to bio-demography
- Life history theory
  - Traits and trade-offs
- Linking reproduction and survival together
  - Matrix population models

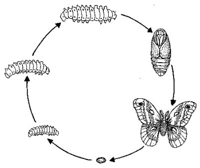
Linking reproduction and survival together



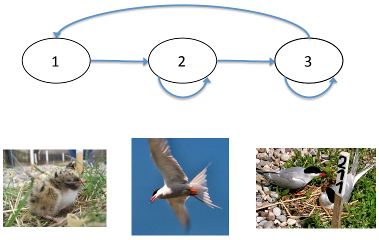
A gentle intro to matrix population models

Life goes through stages …

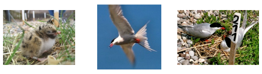
- When there are obvious differences in the performances of different life history stages and these differences are hypothesised to be important, we use structured population models.



First step of the model: A life cycle



Number of individual at each stage



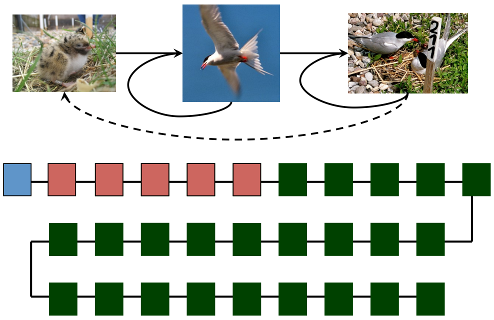
	Juvenile	Subadult	Adult	**Sum**
1. year	207	81	140	**428**
2. year	89	66	150	**305**

$$\begin{pmatrix}89\\66\\150\end{pmatrix} = \text{Population model} * \begin{pmatrix}207\\81\\140\end{pmatrix}$$

$$\begin{pmatrix}89\\66\\150\end{pmatrix} = \begin{pmatrix}0 & 0 & 0.64\\0.32 & 0 & 0\\0 & 0.31 & 0.89\end{pmatrix}\begin{pmatrix}207\\81\\140\end{pmatrix}$$

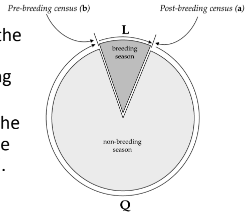
$$\mathbf{n_{t+1} = A \,.\, n_t}$$

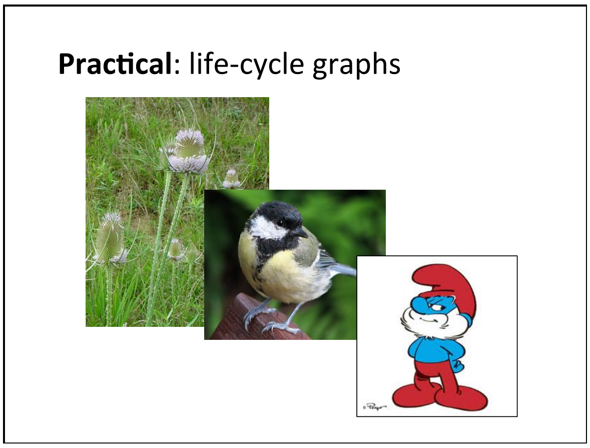
Age ~ Stage



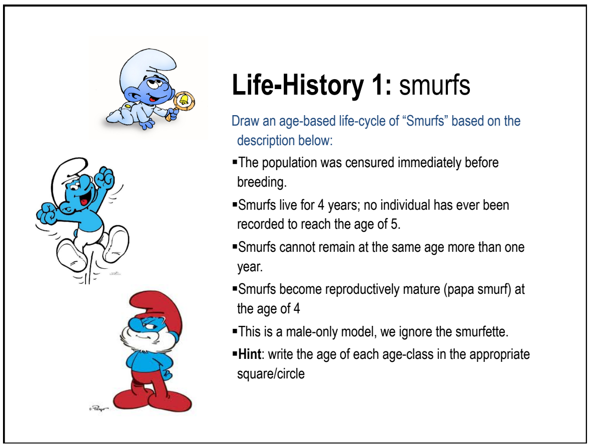
Data collection: When to census?

- Two popular variants:
  - Pre-breeding: assume that the census is carried out immediately before breeding the subsequent year.
  - Post-breding: assume that the census is carried out at some point after the "birth pulse".
  - Cooch et al. (2003) give an excellent description of the difference.





Practical: life-cycle graphs



Life-History 1: smurfs

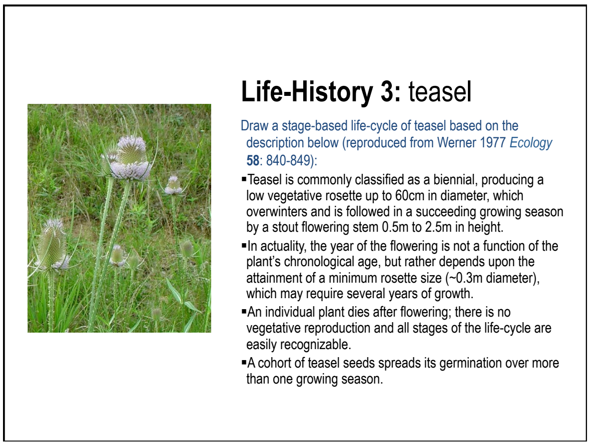
Draw an age-based life-cycle of "Smurfs" based on the description below:

- The population was censured immediately before breeding.
- Smurfs live for 4 years; no individual has ever been recorded to reach the age of 5.
- Smurfs cannot remain at the same age more than one year.
- Smurfs become reproductively mature (papa smurf) at the age of 4
- This is a male-only model, we ignore the smurfette.
- **Hint**: write the age of each age-class in the appropriate square/circle

Life-History 2: great tits

Draw the great tit life-cycle according to the description below

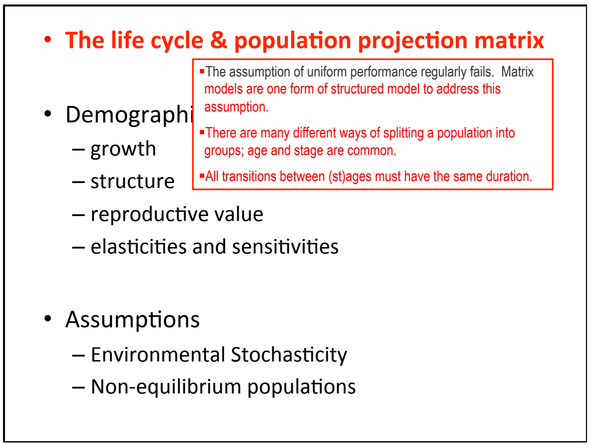
- The population was censured immediately before breeding.
- Great tits can live up to 9 years of age (and perhaps even older).
- Data is sparse when great tits become older than 5; pool these age-classes together.
- Great tits are able to reproduce after their first year.



Life-History 3: teasel

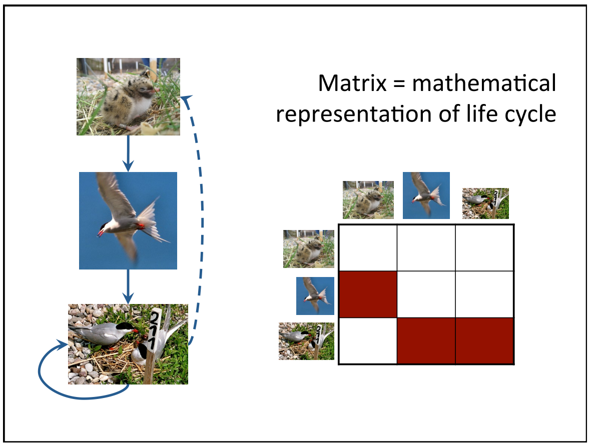
Draw a stage-based life-cycle of teasel based on the description below (reproduced from Werner 1977 *Ecology* **58**: 840-849):

- Teasel is commonly classified as a biennial, producing a low vegetative rosette up to 60cm in diameter, which overwinters and is followed in a succeeding growing season by a stout flowering stem 0.5m to 2.5m in height.
- In actuality, the year of the flowering is not a function of the plant's chronological age, but rather depends upon the attainment of a minimum rosette size (~0.3m diameter), which may require several years of growth.
- An individual plant dies after flowering; there is no vegetative reproduction and all stages of the life-cycle are easily recognizable.
- A cohort of teasel seeds spreads its germination over more than one growing season.

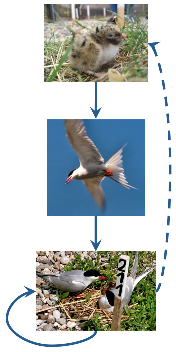


- **The life cycle & population projection matrix**
- Demographi
  - growth
  - structure
  - reproductive value
  - elasticities and sensitivities
- Assumptions
  - Environmental Stochasticity
  - Non-equilibrium populations

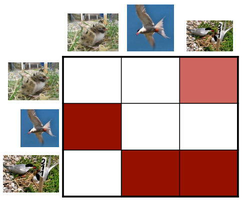
- The assumption of uniform performance regularly fails. Matrix models are one form of structured model to address this assumption.
- There are many different ways of splitting a population into groups; age and stage are common.
- All transitions between (st)ages must have the same duration.



Matrix = mathematical representation of life cycle

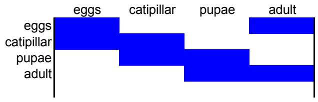


Matrix = mathematical representation of life cycle

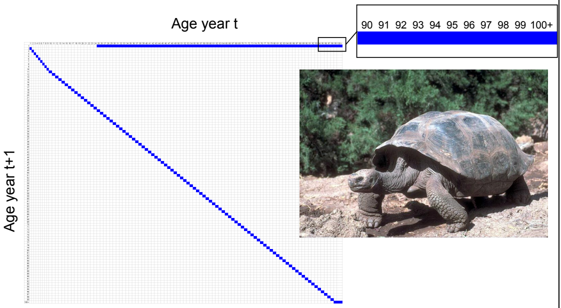


Examples of matrices from biological systems

Blue parts of the matrices represent non-zero elements

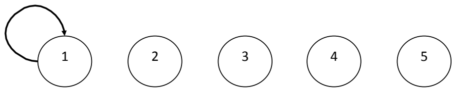


Examples of matrices from biological systems



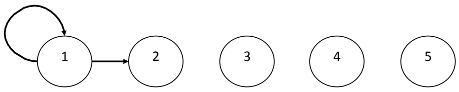
What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1				
	2					
	3					
	4					
	5					



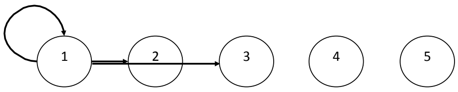
What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1				
	2	1 --> 2				
	3					
	4					
	5					



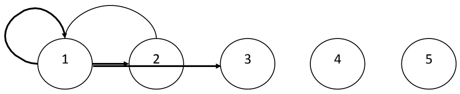
What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1				
	2	1 --> 2				
	3	1 --> 3				
	4					
	5					



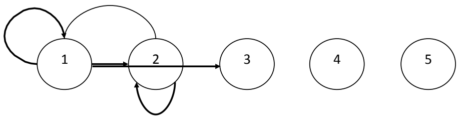
What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1	2 --> 1			
	2	1 --> 2				
	3	1 --> 3				
	4					
	5					



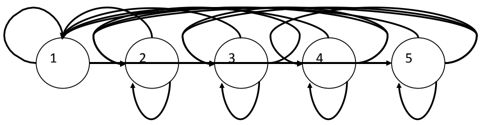
What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1	2 --> 1			
	2	1 --> 2	2 --> 2			
	3	1 --> 3				
	4					
	5					



What do the elements of a matrix mean?

		Class in year t				
		1	2	3	4	5
Class in year t+1	1	1 --> 1	2 --> 1	3 --> 1	4 --> 1	5 --> 1
	2	1 --> 2	2 --> 2	3 --> 2	4 --> 2	5 --> 2
	3	1 --> 3	2 --> 3	3 --> 3	4 --> 3	5 --> 3
	4	1 --> 4	2 --> 4	3 --> 4	4 --> 4	5 --> 4
	5	1 --> 5	2 --> 5	3 --> 5	4 --> 5	5 --> 5



$$\mathbf{A} = \begin{bmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{bmatrix}.$$

THE BIOLOGY The top row of the matrix **often** represents fecundity (recruitment). In a **pre-breeding matrix** , then this the per capita number of offspring that are almost 1 year old, i.e. that reach the time of the subsequent census.

$$\mathbf{A} = \begin{bmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{bmatrix}.$$

THE BIOLOGY The sub-diagonal of the matrix represents progression from one class to the subsequent one.

In **age-structured matrices**, this contains individuals of age A that survive to be one year older in the subsequent year.

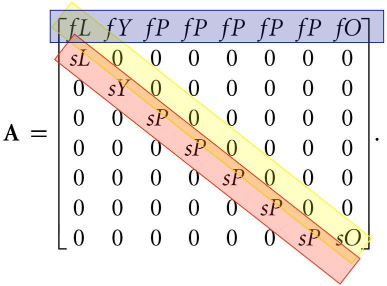
In **stage-structured matrices**, this contains individuals of stage S that grow to stage S+1 in the subsequent year.

$$\mathbf{A} = \begin{bmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{bmatrix}.$$

THE BIOLOGY The main diagonal of the matrix represents stasis.

In **pure age-structured matrices**, this value is always zero (individuals either age or die).

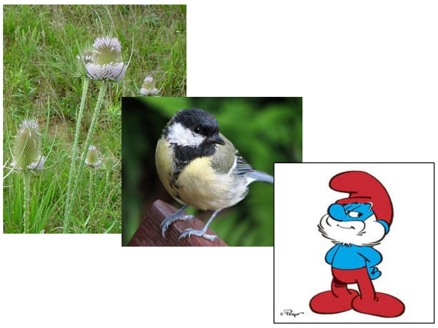
In **stage-structured matrices**, this contains individuals of stage S that remain in stage S in the subsequent year.



$$\mathbf{A} = \begin{bmatrix} fL & fY & fP & fP & fP & fP & fP & fO \\ sL & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & sY & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & sP & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & sP & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & sP & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & sP & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & sP & sO \end{bmatrix}.$$

N.B. Other values need not be zero. For example, the super-diagonal reflects regression, e.g. shrinkage from size S+1 to size S from one year to the next.

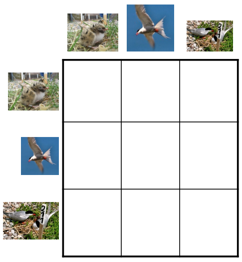
Practical: “active” cells in transition matrices



- The life cycle & population projection matrix
- Demographic inference from
  - growth
  - structure
  - reproductive value
  - elasticities and sensitivities
- Assumptions
  - Environmental Stochasticity
  - Non-equilibrium populations

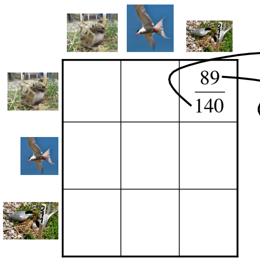
- A matrix is a mathematical representation of the life-cycle graph.
- Read the transitions **from** the column number **to** the row number.
- Stage-structured matrices have more active cells than age-structured matrices.

Matrix elements



- 1. year
  - 207 juveniles
  - 81 subadults
  - 140 adults
- 2. year
  - 89 juveniles
  - 66 subadults
  - 150 adults
    (25 new, 125 old)

Matrix elements



- 1. year
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  - 81 subadults
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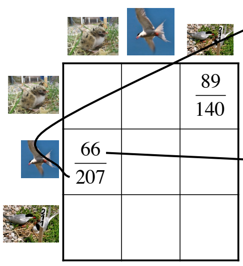
Matrix elements



- 1. year
  - 207 juveniles
  - 81 subadults
  - 140 adults
- 2. year
  - 89 juveniles
  - 66 subadults
  - 150 adults
    (25 new, 125 old)

Matrix elements

0	0	$\frac{89}{140}$
$\frac{66}{207}$	0	0
0	$\frac{25}{81}$	$\frac{125}{140}$

- 1. year
  - 207 juveniles
  - 81 subadults
  - 140 adults
- 2. year
  - 89 juveniles
  - 66 subadults
  - 150 adults
    (25 new, 125 old)

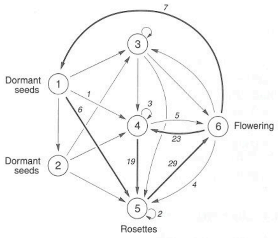
Matrix elements

0	0	0.636
0.319	0	0
0	0.308	0.893

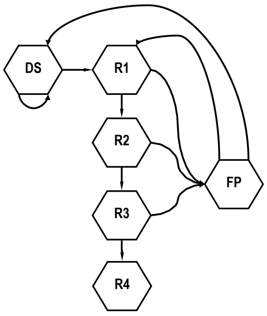
- 1. year
  - 207 juveniles
  - 81 subadults
  - 140 adults
- 2. year
  - 89 juveniles
  - 66 subadults
  - 150 adults
    (25 new, 125 old)

	Yr 1	Yr 2
Age 1	90	160
Age 2	60	27
Age 3	100	24
Age 4	80	90

Werner & Caswell (1977) proposed a life-cycle for Teasel (*Dipsacus sylvestris* Huds.)

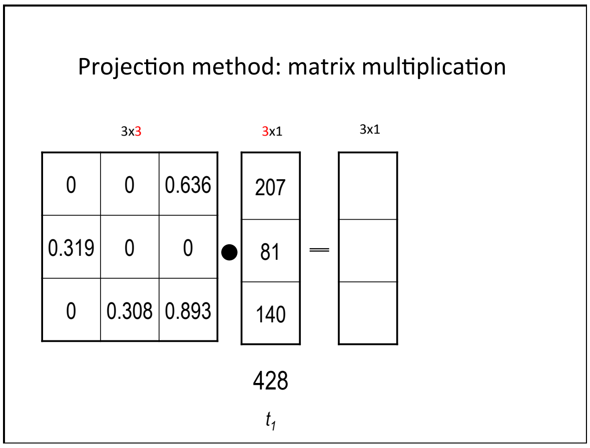


Practical: the Teasel transition matrix



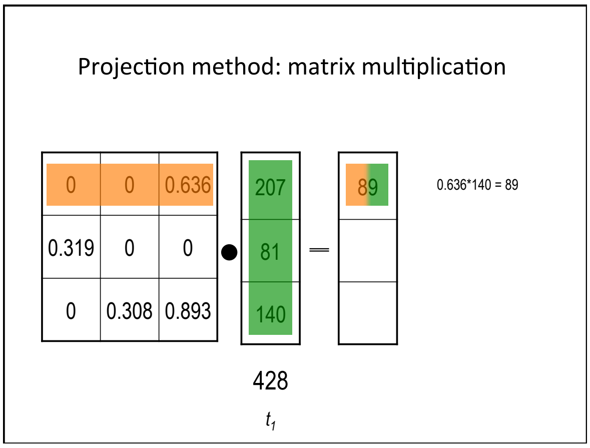
0.961	0	0	0	0	322.4
0.039	0	0	0	0	108.6
0	0.132	0	0	0	0
0	0	0.378	0	0	0
0	0	0	0.357	0	0
0	0.004	0.352	0.429	0	0

- The life cycle & population projection matrix
- **Demographic inference from matrix models**
  - **growth**
  - **structure**
  - **reproductive value**
  - **elasticities and sensitivities**
- Assumptions
  - Environmental Stochasticity
  - Non-equilibrium populations



Projection method: matrix multiplication

$$\begin{array}{ccccc} 3\times3 & & 3\times1 & & 3\times1 \\ \begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix} & \bullet & \begin{bmatrix}207\\81\\140\end{bmatrix} & = & \begin{bmatrix}\;\\\;\\\;\end{bmatrix} \\ & & 428 & & \\ & & t_1 & & \end{array}$$



Projection method: matrix multiplication

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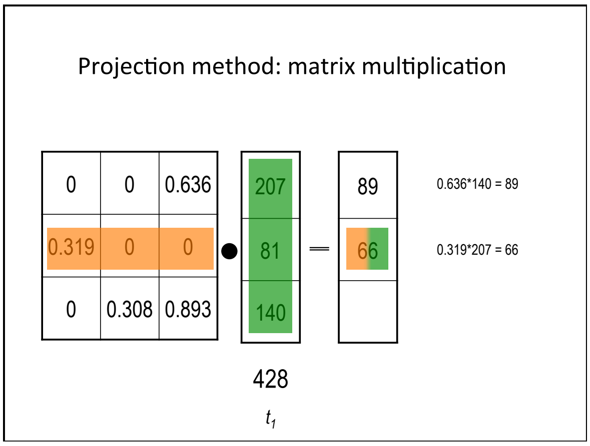
0.636*140 = 89



Projection method: matrix multiplication

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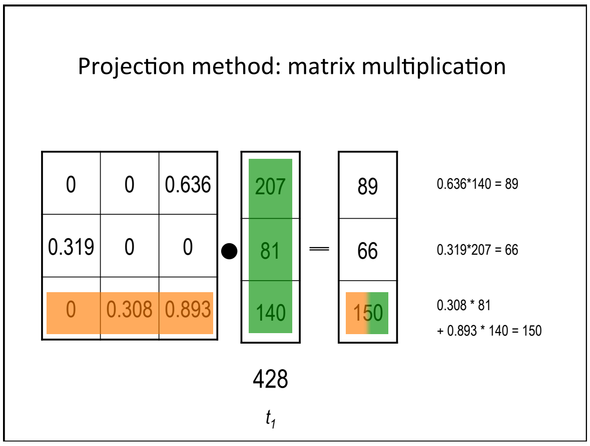
0.636*140 = 89

0.319*207 = 66



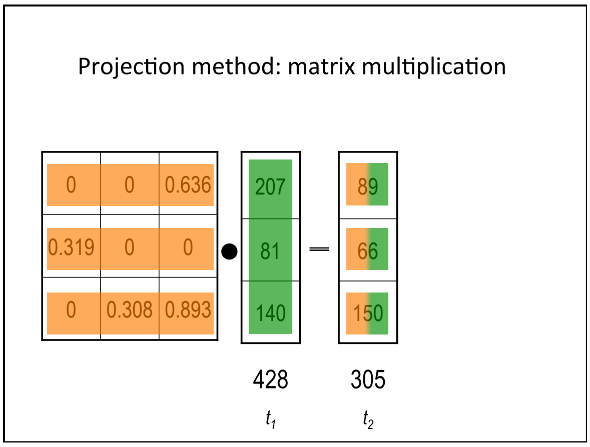
Projection method: matrix multiplication

$$\begin{array}{ccccc} \begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix} & \bullet & \begin{bmatrix}207\\81\\140\end{bmatrix} & = & \begin{bmatrix}89\\66\\150\end{bmatrix} \\ & & 428 & & \\ & & t_1 & & \end{array}$$

0.636*140 = 89

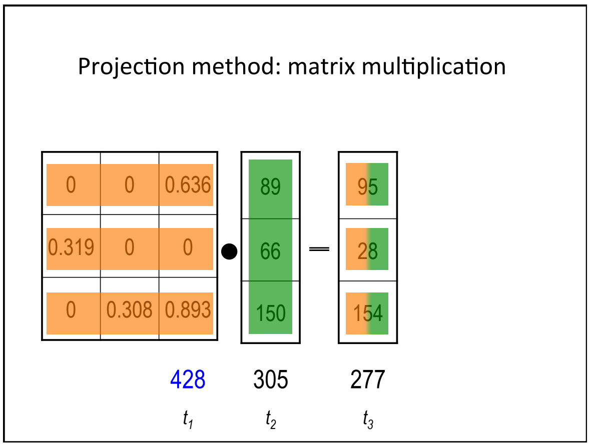
0.319*207 = 66

0.308 * 81
+ 0.893 * 140 = 150



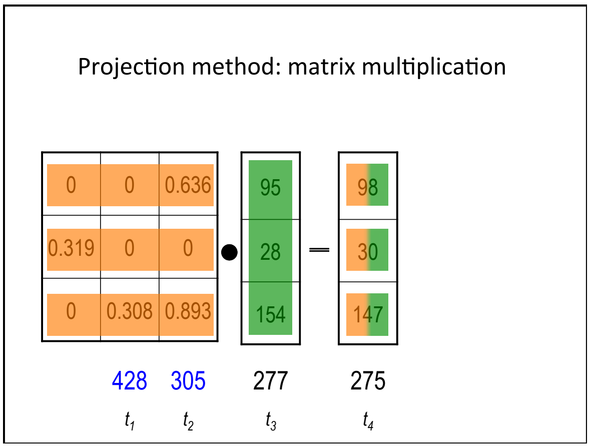
Projection method: matrix multiplication

$$\begin{array}{ccccc} \begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix} & \bullet & \begin{bmatrix}207\\81\\140\end{bmatrix} & = & \begin{bmatrix}89\\66\\150\end{bmatrix} \\ & & 428 & & 305 \\ & & t_1 & & t_2 \end{array}$$



Projection method: matrix multiplication

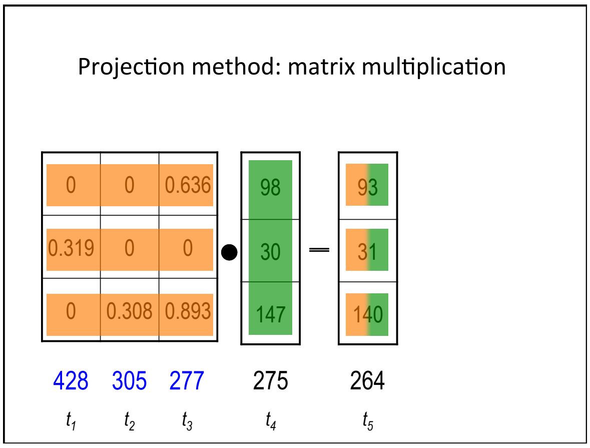
$$\begin{array}{ccccc} \begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix} & \bullet & \begin{bmatrix}89\\66\\150\end{bmatrix} & = & \begin{bmatrix}95\\28\\154\end{bmatrix} \\ 428 & & 305 & & 277 \\ t_1 & & t_2 & & t_3 \end{array}$$



Projection method: matrix multiplication

$$\begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix}\bullet\begin{bmatrix}95\\28\\154\end{bmatrix}=\begin{bmatrix}98\\30\\147\end{bmatrix}$$

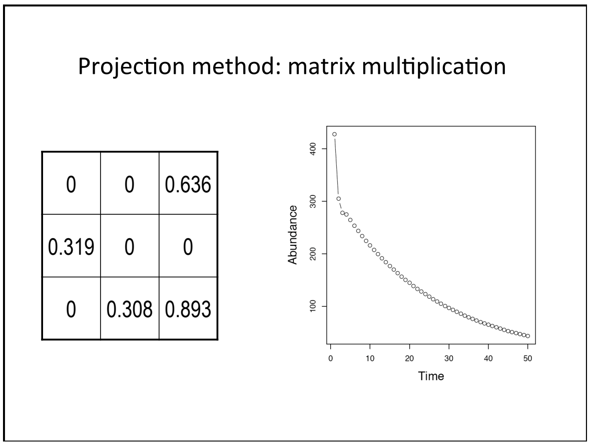
428	305	277	275
t_1	t_2	t_3	t_4



Projection method: matrix multiplication

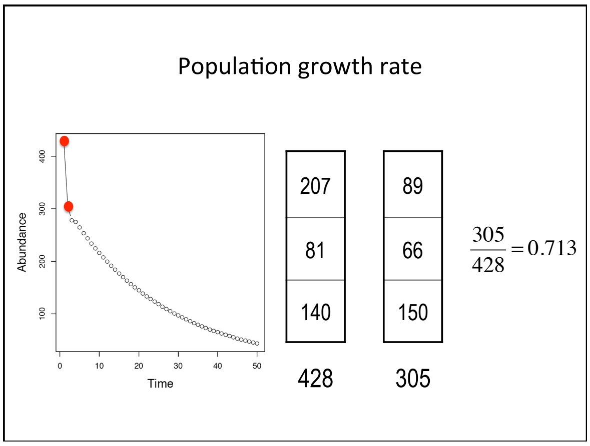
$$\begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix}\bullet\begin{bmatrix}98\\30\\147\end{bmatrix}=\begin{bmatrix}93\\31\\140\end{bmatrix}$$

428	305	277	275	264
t_1	t_2	t_3	t_4	t_5



Projection method: matrix multiplication

$$\begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix}$$

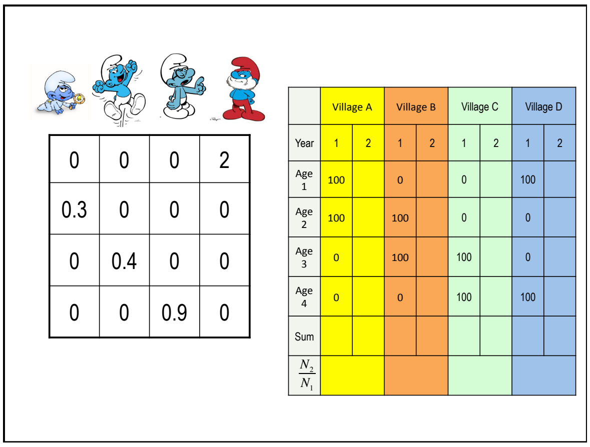


Population growth rate

$$\begin{bmatrix}207\\81\\140\end{bmatrix}\quad\begin{bmatrix}89\\66\\150\end{bmatrix}$$

428	305

$$\frac{305}{428}=0.713$$



$$\begin{bmatrix}0&0&0&2\\0.3&0&0&0\\0&0.4&0&0\\0&0&0.9&0\end{bmatrix}$$

	Village A		Village B		Village C		Village D	
Year	1	2	1	2	1	2	1	2
Age 1	100		0		0		100	
Age 2	100		100		0		0	
Age 3	0		100		100		0	
Age 4	0		0		100		100	
Sum								
$\frac{N_2}{N_1}$								

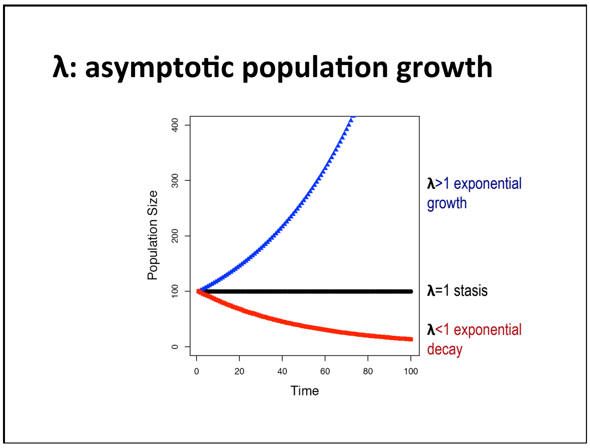
What if we don't know the number of individuals?

$$\begin{bmatrix}0&0&0.636\\0.319&0&0\\0&0.308&0.893\end{bmatrix}$$

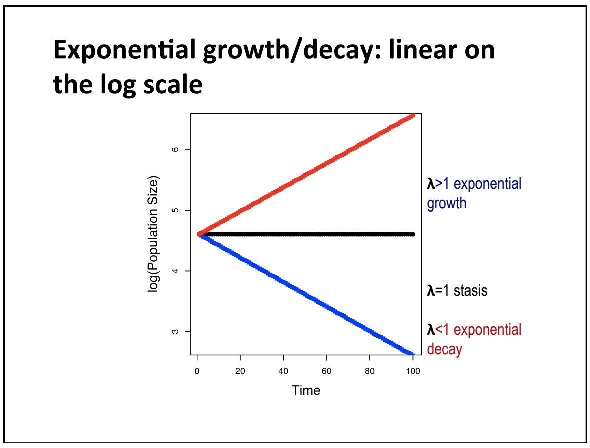
Characteristic equation: det(A-λI) = 0

- Lambda (λ) = **dominant eigenvalue**
- Lambda (λ) = **population growth rate**

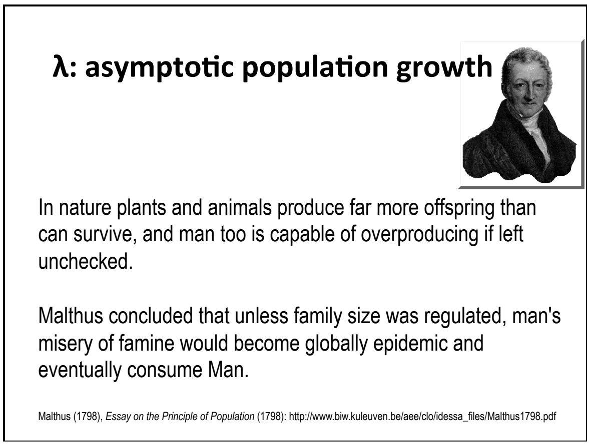
- Right eigenvector (v_λ) = **stable (st)age structure**
- Left eigenvector (w_λ) = **reproductive value**



λ: asymptotic population growth



Exponential growth/decay: linear on the log scale

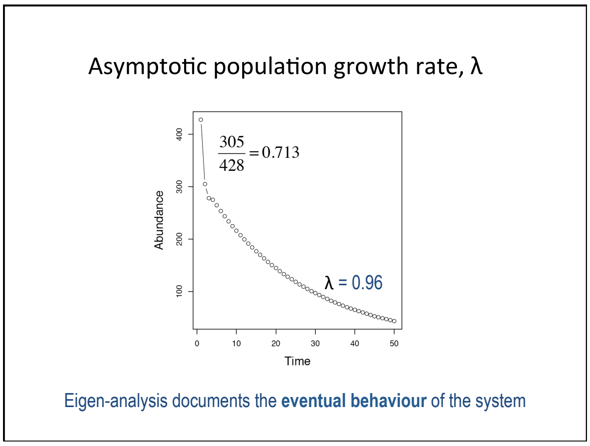


λ: asymptotic population growth

In nature plants and animals produce far more offspring than can survive, and man too is capable of overproducing if left unchecked.

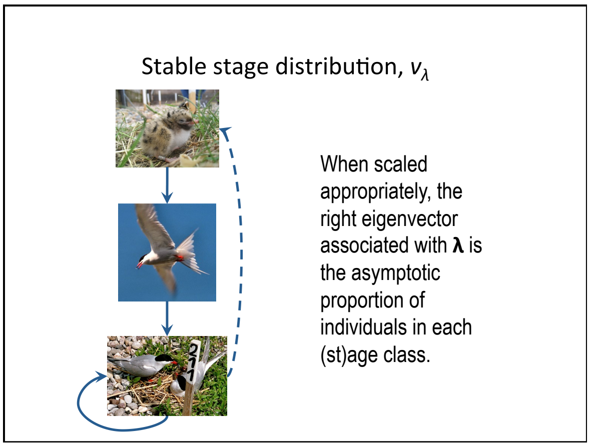
Malthus concluded that unless family size was regulated, man's misery of famine would become globally epidemic and eventually consume Man.

Malthus (1798), *Essay on the Principle of Population* (1798): http://www.biw.kuleuven.be/aee/clo/idessa_files/Malthus1798.pdf



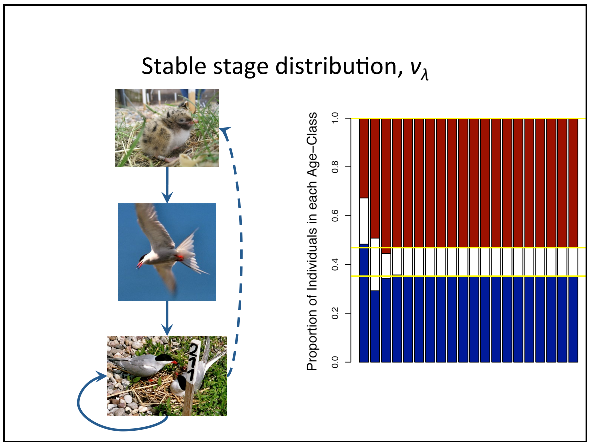
Asymptotic population growth rate, λ

Eigen-analysis documents the **eventual behaviour** of the system

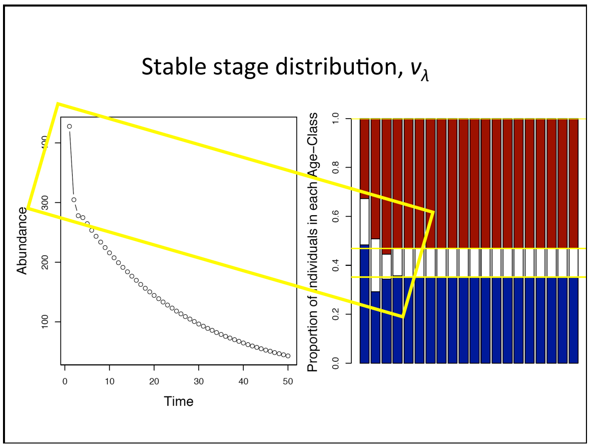


Stable stage distribution, v_λ

When scaled appropriately, the right eigenvector associated with **λ** is the asymptotic proportion of individuals in each (st)age class.



Stable stage distribution, v_λ



Stable stage distribution, v_λ

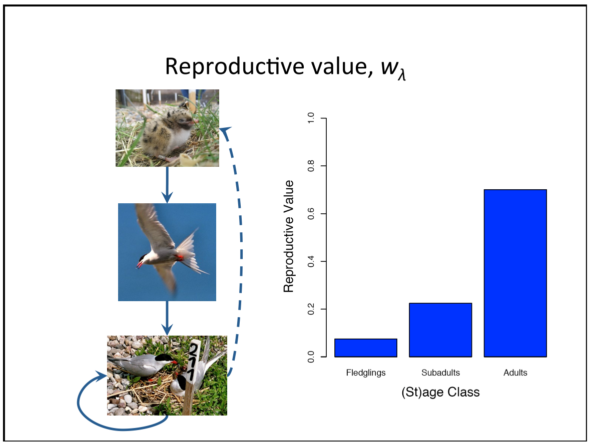
Back to reproduction: Reproductive value

- There is also a left eigenvector (**w**) which gives reproductive values of each stage for the population at equilibrium structure
- Reproductive value (Fisher 1930):

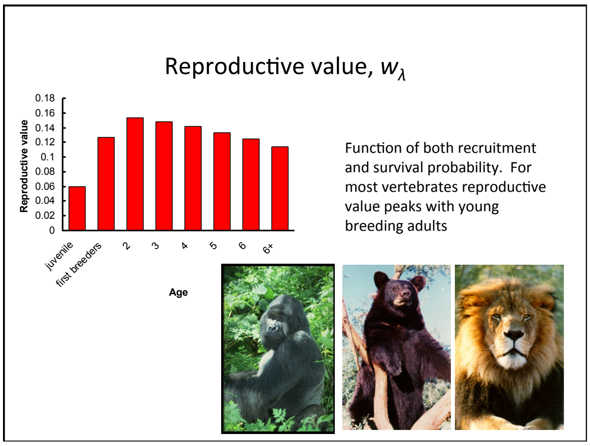
  "To what extent will persons of this age, on the average, contribute to the ancestry of future generations?

  This question is of some interest, since the direct action of Natural Selection must be proportional to this contribution."

- Reproductive value = Current Reproduction + Residual Reproductive Value

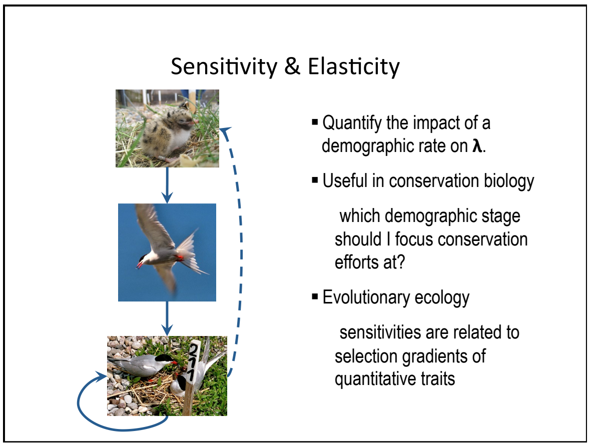


Reproductive value, w_λ



Reproductive value, w_λ

Function of both recruitment and survival probability. For most vertebrates reproductive value peaks with young breeding adults

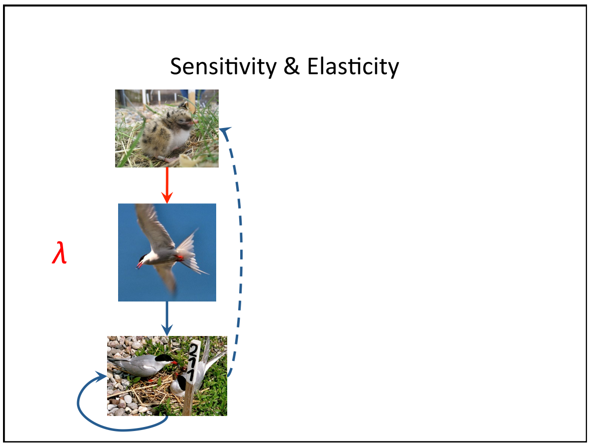


Sensitivity & Elasticity

- Quantify the impact of a demographic rate on **λ**.
- Useful in conservation biology

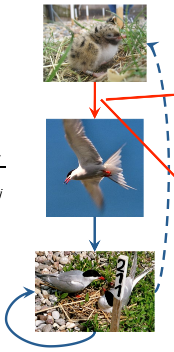
  which demographic stage should I focus conservation efforts at?
- Evolutionary ecology

  sensitivities are related to selection gradients of quantitative traits



Sensitivity & Elasticity

Sensitivity



$$\frac{\partial\lambda}{\partial a_{ij}}$$

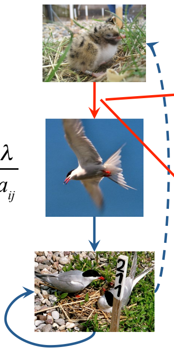
0	0	0.64
0.32	0	0
0	0.31	0.89

λ=0.96

0	0	0.64
0.32 + 0.01	0	0
0	0.31	0.89

λ_p=0.963

Elasticity



$$\frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}}$$

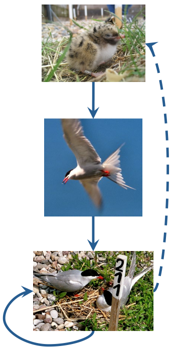
0	0	0.64
0.32	0	0
0	0.31	0.89

λ=0.96

0	0	0.64
0.32 x 1.01	0	0
0	0.31	0.89

λ_p=0.961

Elasticity = Proportional sensitivity



0	0	0.09
0.19	0	0
0	0.19	0.88

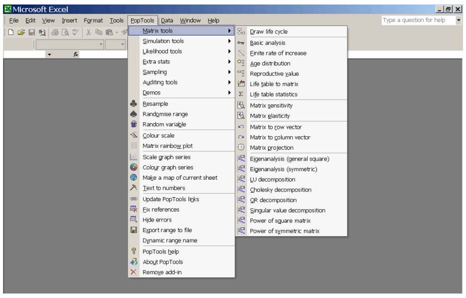
$$\frac{\partial\lambda}{\partial a_{ij}}$$

0	0	0.06
0.06	0	0
0	0.06	0.82

$$\frac{a_{ij}}{\lambda}\frac{\partial\lambda}{\partial a_{ij}}$$

Software: λ, **w**, **v**, sensitivities and elasticities

- Poptools in Excel (http://www.cse.csiro.au/poptools/)



λ, w, v, sensitivity, elasticity

Caswell, H. Matrix population models. John Wiley & Sons, Ltd, 1989.

```
mat<-matrix(c(0,0.32,0,0,0,0.31,0.64,0,0.89),nrow=3,ncol=3)

w<-Re(eigen(mat)$vectors[,1]); v<-Re(eigen(t(mat))$vectors[,1])

lambda<-Re(eigen(mat)$value[1]) # LAMBDA
sad<-w/sum(w)                     # STABLE AGE DISTRIBUTION
rv<-v/v[1]                     # REPRODUCTIVE VALUES

temp<-rv %*% sad; temp<-as.vector(temp)
transp.sad<-t(sad);temp.mat<-rv %*% transp.sad

sens<-round(temp.mat/temp,2)    # SENSITIVITIES

temp<-mat/Re(eigen(mat)$value[1])

elas<-sens*temp;               # ELASTICITIES
```

```
# or:
library(popbio)
eigen.analysis(mat)
```

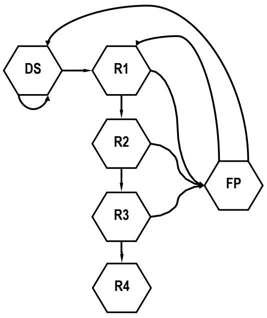
- The life cycle & population projection matrix

- **Demographic inference from**
  - **growth**
  - **structure**
  - **reproductive value**
  - **elasticities and sensitivities**

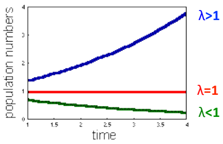
- Assumptions
  - Environmental Stochasticity
  - Non-equilibrium populations

- Deterministic approach: if **λ**<1, then the population will go extinct if everything remains constant.
- Describes the eventual dynamics of a system; an initial transient phase can have different characteristics.
- Elasticities and sensitivities are measures of the importance of a demographic rate on **λ**.
- Elasticities are more readily comparable than sensitivities across demographic rates that differ by large amounts.

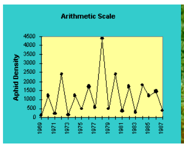
Practical: Simulation & demographic inference



- The life cycle & population projection matrix
- Demographic inference from matrix models
  - growth
  - structure
  - reproductive value
  - elasticities and sensitivities
- **Assumptions**
  - **Non-equilibrium populations**
  - **Environmental Stochasticity**



Most populations don't grow or decline exponentially, or remain static



Adult sycamore lace bug.

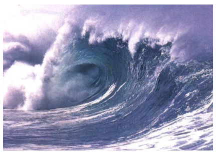
Demographic rates influenced by a wide range of factors

Predation

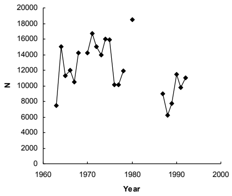
Disease

Climate

Competition for resources

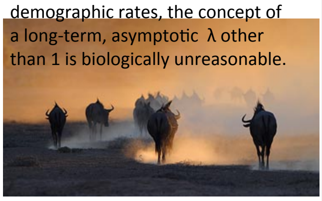


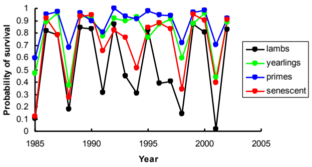
Catastrophes



Variation in population size (N) and population growth (λ) caused by temporal variation in demographic rates

Because of the variation in demographic rates, the concept of a long-term, asymptotic λ other than 1 is biologically unreasonable.





What processes do deterministic matrices ignore?

ENVIRONMENTAL PROCESSES

- Density-dependence
- Environmental stochasticity

EVOLUTIONARY PROCESSES

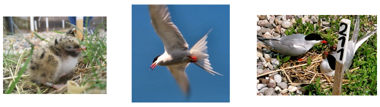
- Adaptation
- Demographic stochasticity (genetic drift)

Demographic rate variation

- The incorporation of variation in demographic rates into matrices requires matrix elements to be functions

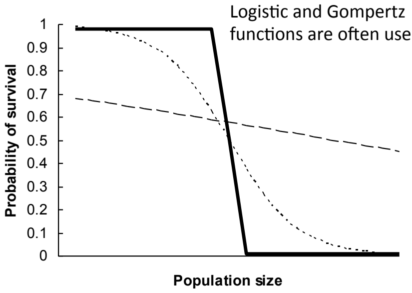
These become functions

$$\begin{pmatrix} 0 & 0 & 1.56 \\ 0.15 & 0 & 0 \\ 0 & 0.17 & 0.74 \end{pmatrix}$$

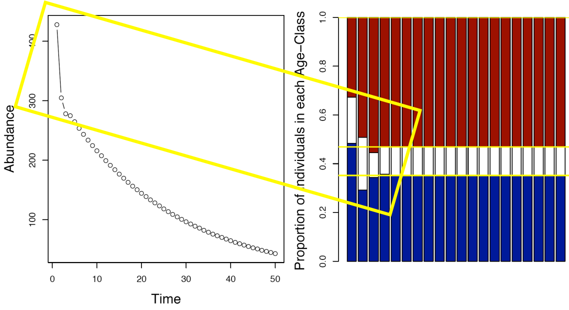


Example of a function

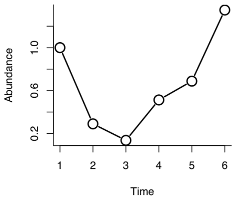
Logistic and Gompertz functions are often used



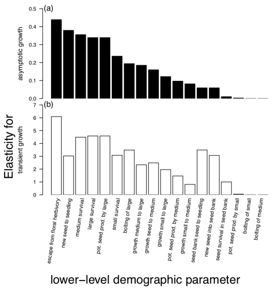
Transients

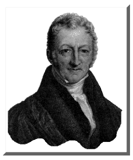


Transient growth can be very different from asymptotic growth



Elasticities of asymptotic and transient growth can be quite different





Thomas Malthus
(1766-1834)

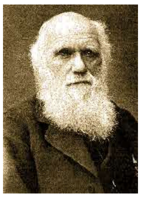
Essay on the Principle of Population (1798)

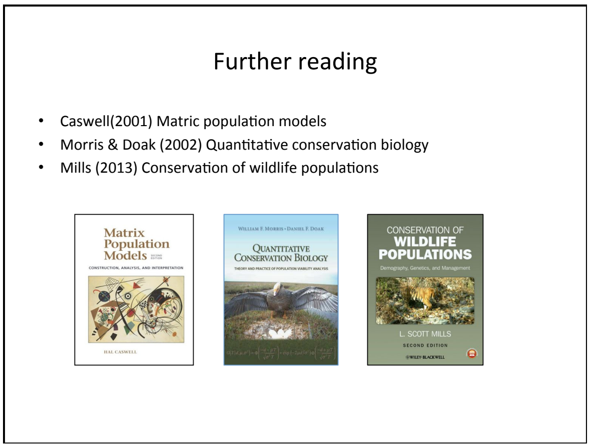
In nature plants and animals produce far more offspring than can survive, and man too is capable of overproducing if left unchecked. Malthus concluded that unless family size was regulated, man's misery of famine would become globally epidemic and eventually consume Man.

Population growth is geometric!

http://www.ac.wwu.edu/~stephan/malthus/malthus.0.html

In October 1838, that is, fifteen months after I had begun my systematic inquiry, I happened to read for amusement Malthus on *Population*, and being well prepared to appreciate the struggle for existence which everywhere goes on from long- continued observation of the habits of animals and plants, it at once struck me that under these circumstances favourable variations would tend to be preserved, and unfavourable ones to be destroyed. The results of this would be the formation of a new species. Here, then I had at last got a theory by which to work.





Further reading

- Caswell(2001) Matric population models
- Morris & Doak (2002) Quantitative conservation biology
- Mills (2013) Conservation of wildlife populations