Structured populations

i. Why we care about population structure

a. Ecology: Modeling population dynamics

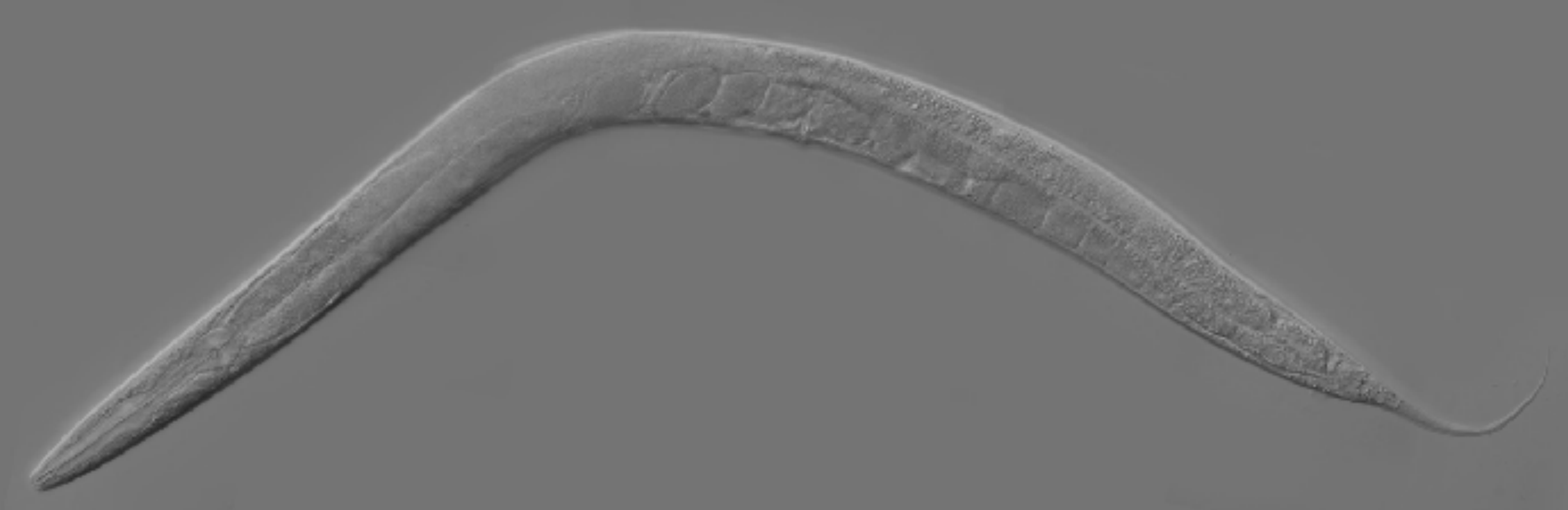
b. Evolution: Relative fitness; life history strategies

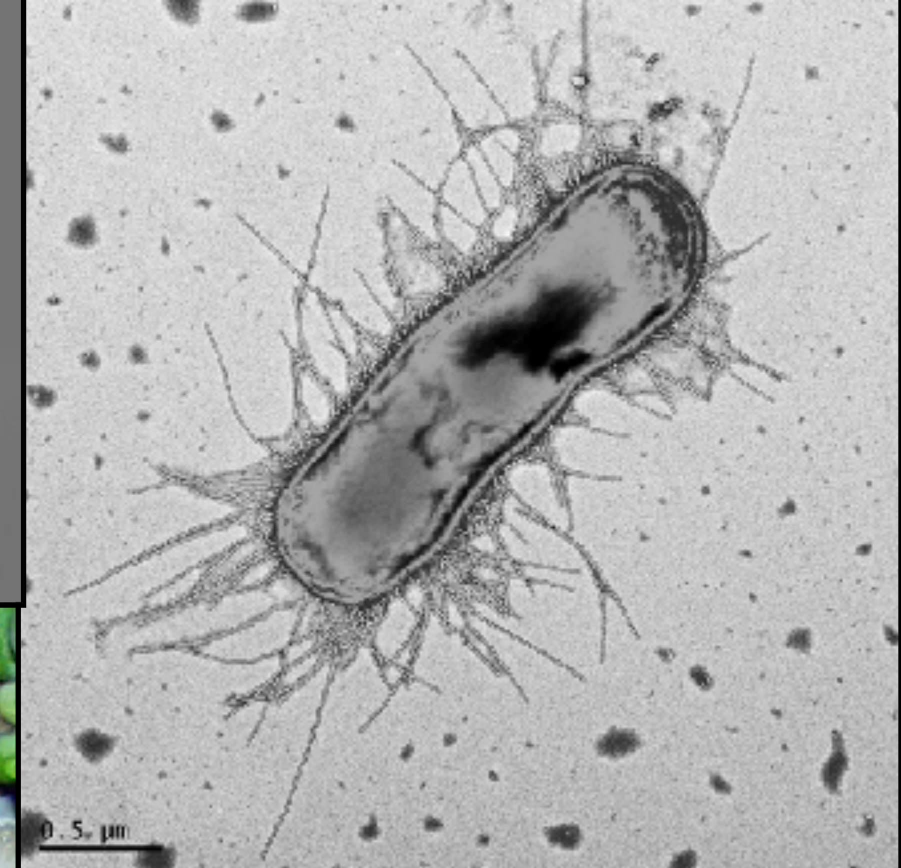
c. Conservation: Rare & invasive species

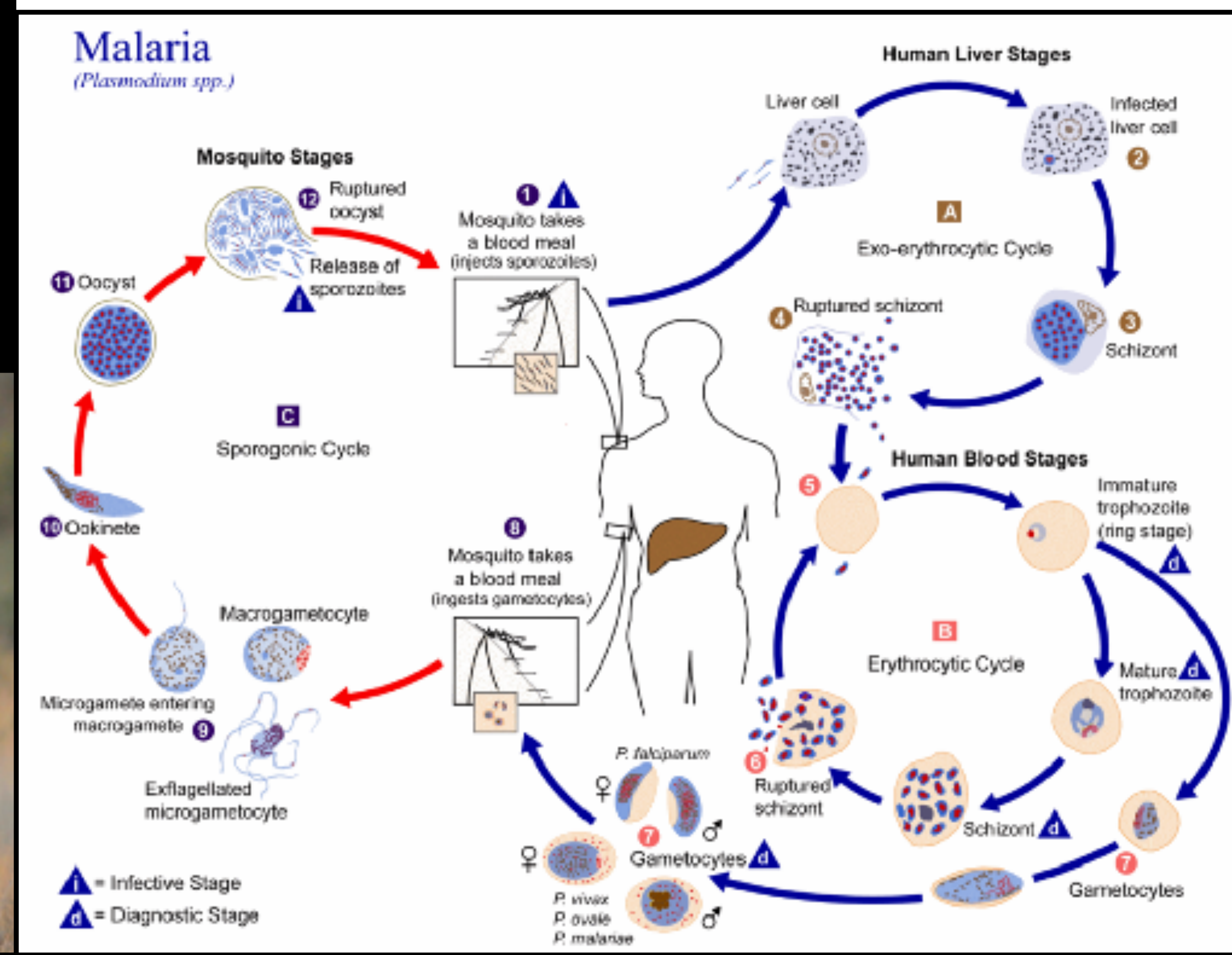
ii. Life cycle → Model

iii. Basic matrix model analysis

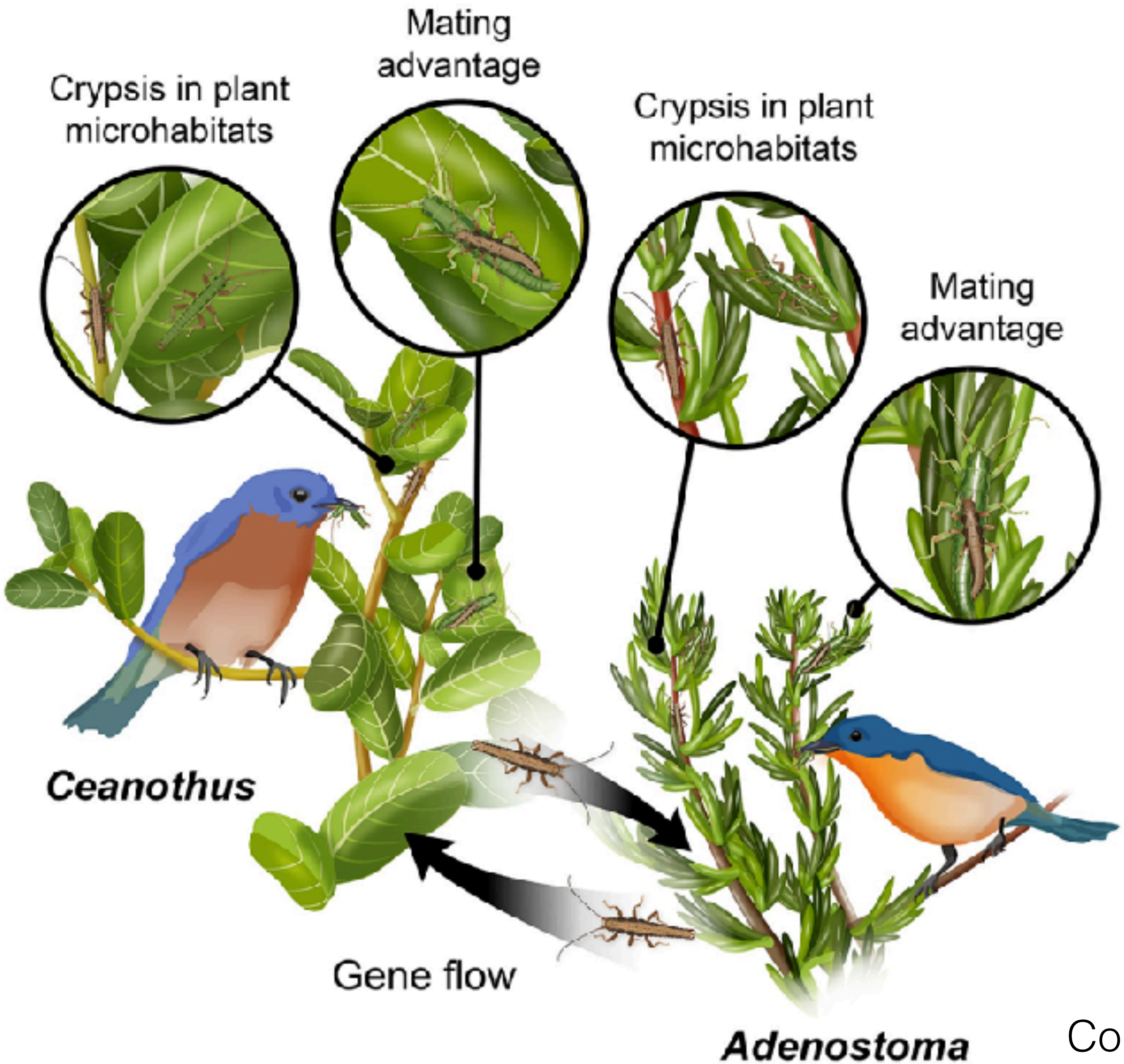
iv. Exercises




0.5 µm


Malaria
(Plasmodium spp.)
Human Liver Stages
Liver cell
Infected liver cell
2
A
Exo-erythrocytic Cycle
3 Schizont
4 Ruptured schizont
Mosquito Stages
12 Ruptured oocyst
Release of sporozoites
1 Mosquito takes a blood meal (injects sporozoites)
11 Oocyst
C
Sporogonic Cycle
10 Ookinete
8 Mosquito takes a blood meal (ingests gametocytes)
Macrogametocyte
Microgamete entering macrogamete 9
Exflagellated microgametocyte
Human Blood Stages
5
Immature trophozoite (ring stage)
B
Erythrocytic Cycle
Mature trophozoite
6 Ruptured schizont
Schizont
7 Gametocytes
P. falciparum
P. vivax
P. ovale
P. malariae
Gametocytes
i = Infective Stage
d = Diagnostic Stage

Evolution



Comeault *et al.* 2015
Curr. Biol.

Conservation

Which life stage would be best to **help**?

Conservation

Which life stage would be best to **harm**?

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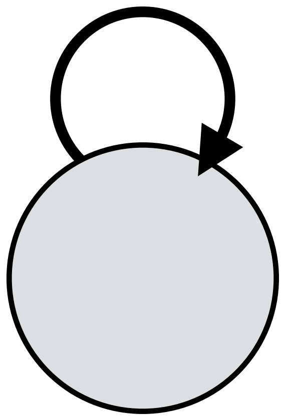
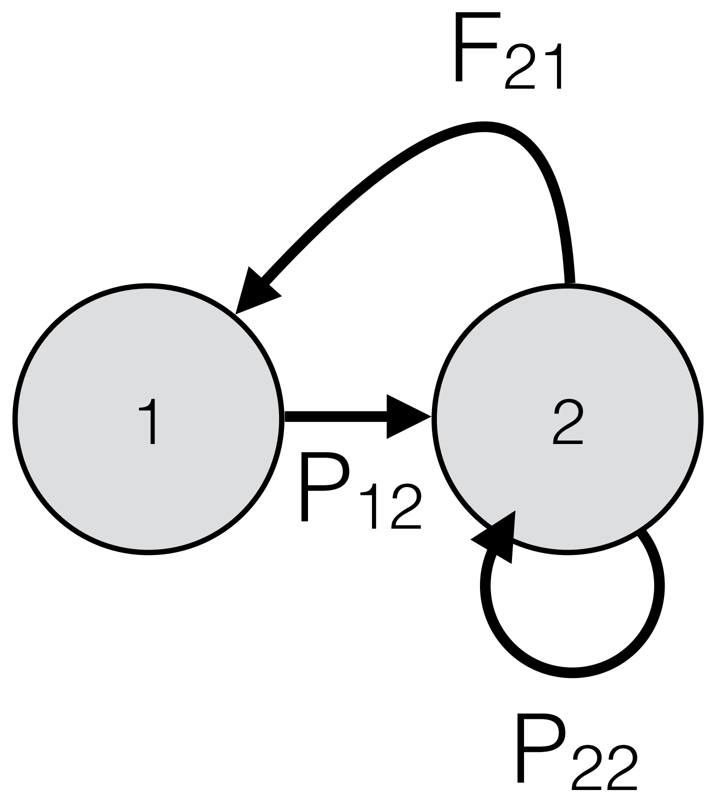
Unstructured population models

$$
\begin{aligned}
N_{t+1} &= N_t + (b - d)N_t \\
&= N_t + rN_t \\
&= (1 + r)N_t \\
&= \lambda N_t
\end{aligned}
$$

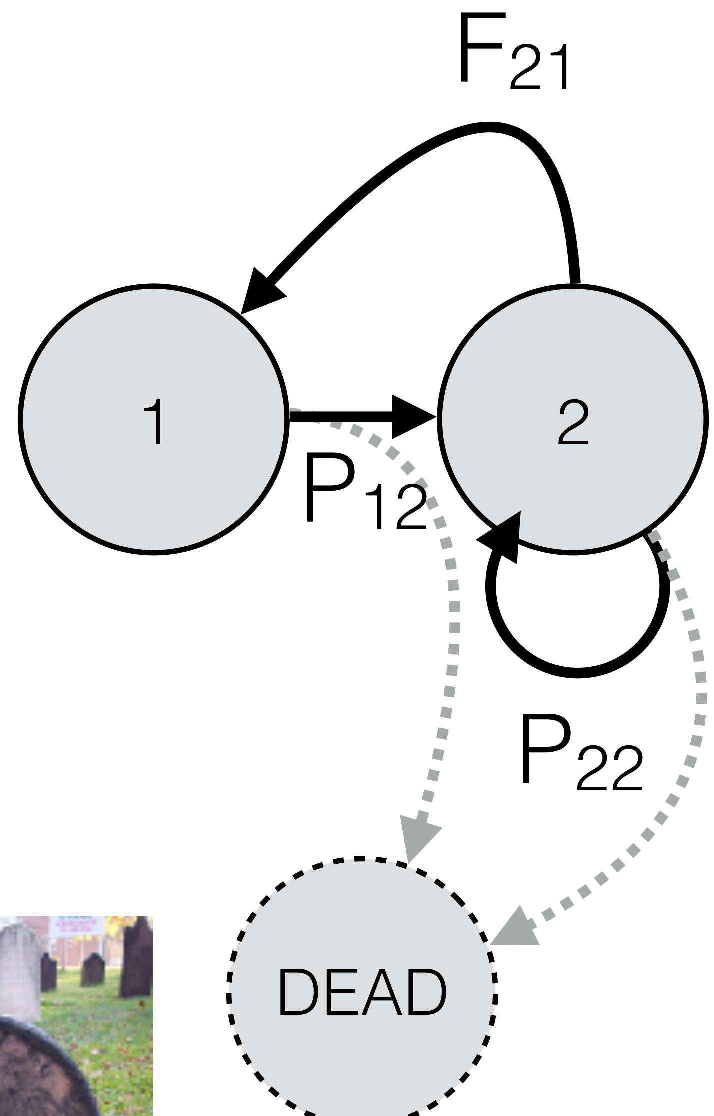
Finite rate of increase



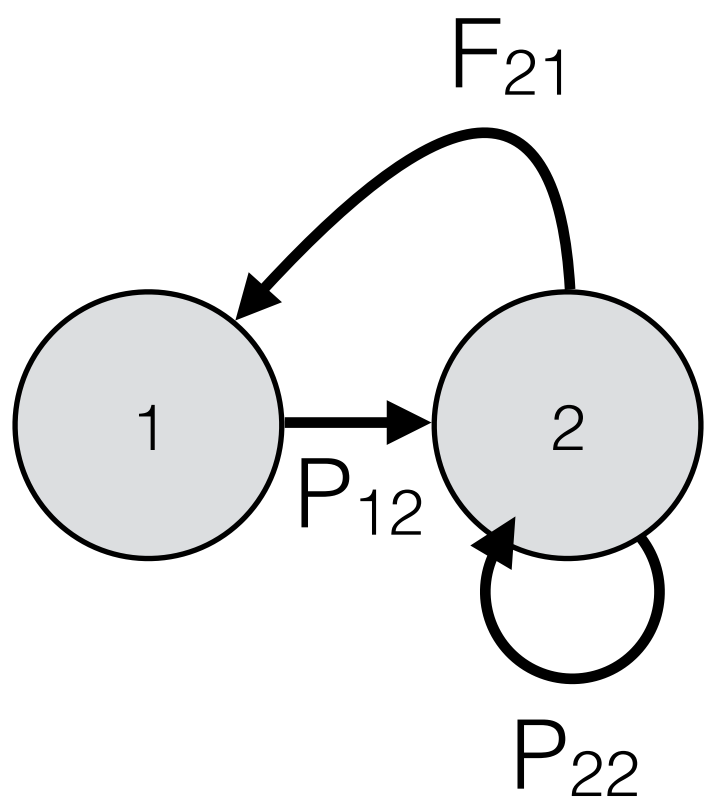
A simple structured life cycle



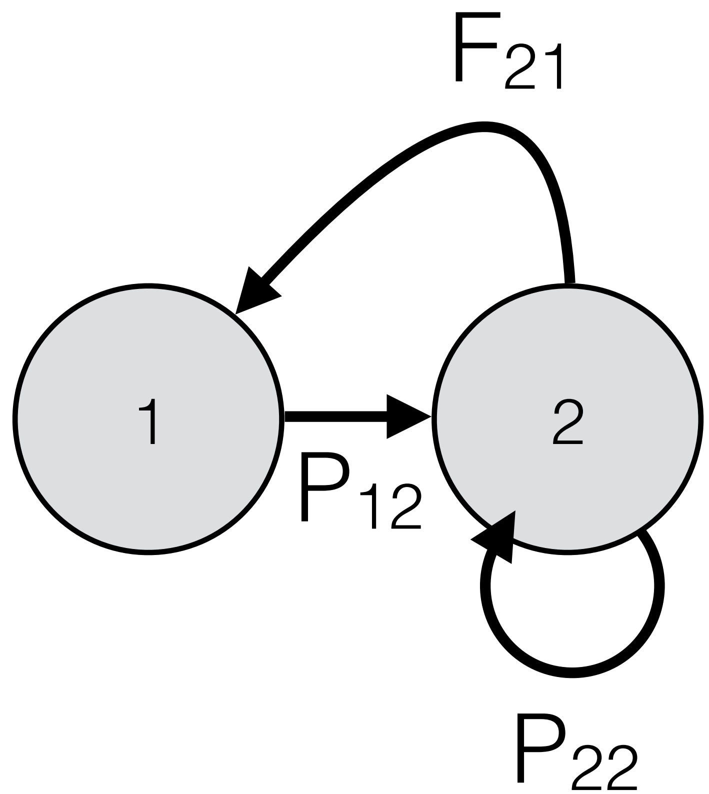
A simple structured life cycle



Stage-specific equations



Stage-specific equations



$$
\begin{aligned}
N_{1,t+1} &= F_{21} N_{3,t} \\
N_{2,t+1} &= P_{12} N_{1,t} + P_{22} N_{2,t}
\end{aligned}
$$

$$N_{dead,t+1} = (1 - P_{12} N_{1,t}) + (1 - P_{22} N_{2,t})$$

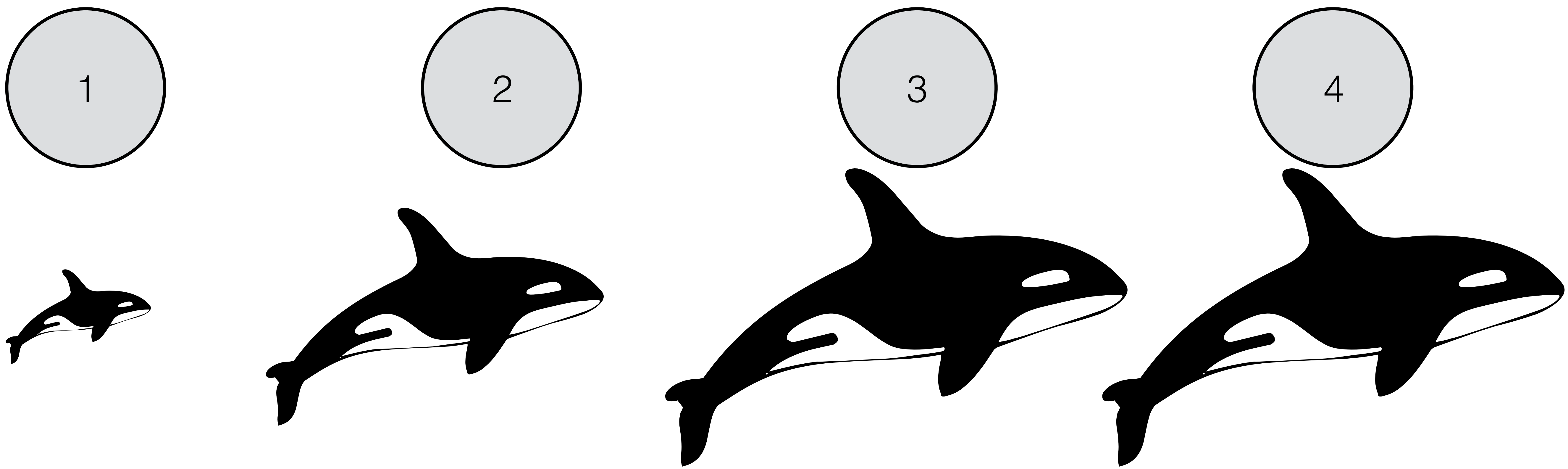
Group exercise: Orca life cycle

Calf

Small adult

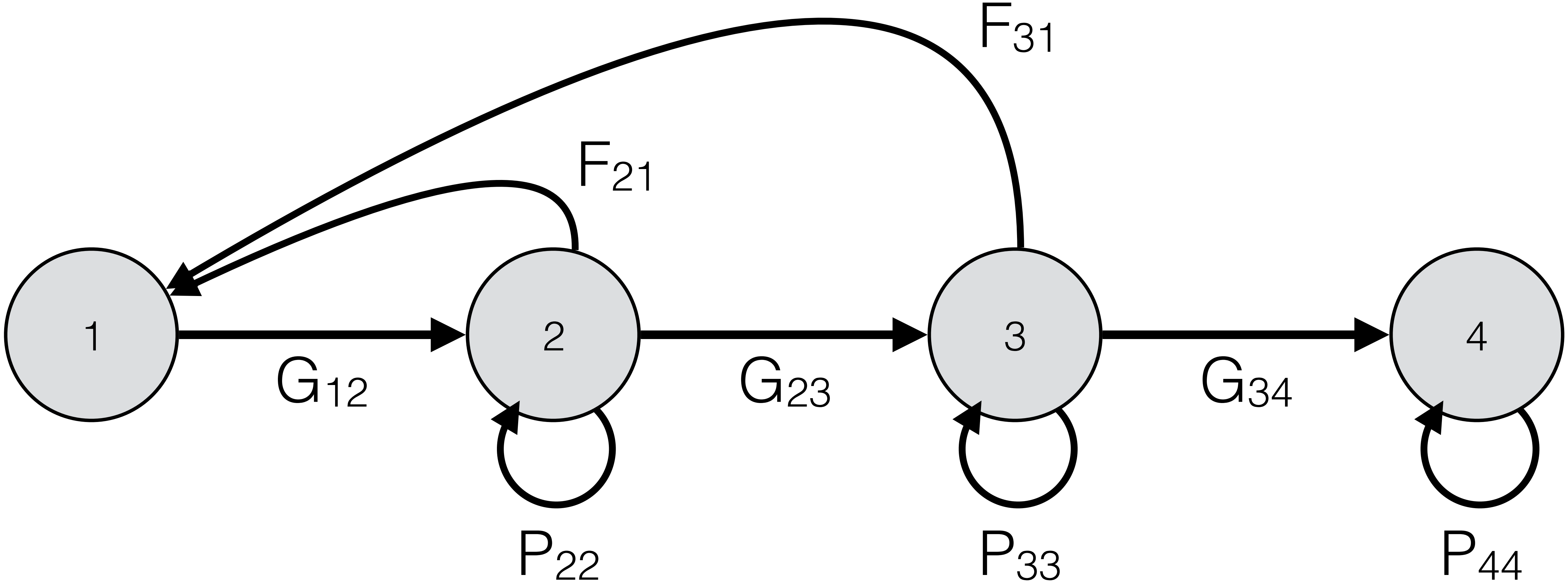
Large adult

Post-reproductive adult



Brault & Caswell 1993 Ecology

Group exercise: Orca life cycle



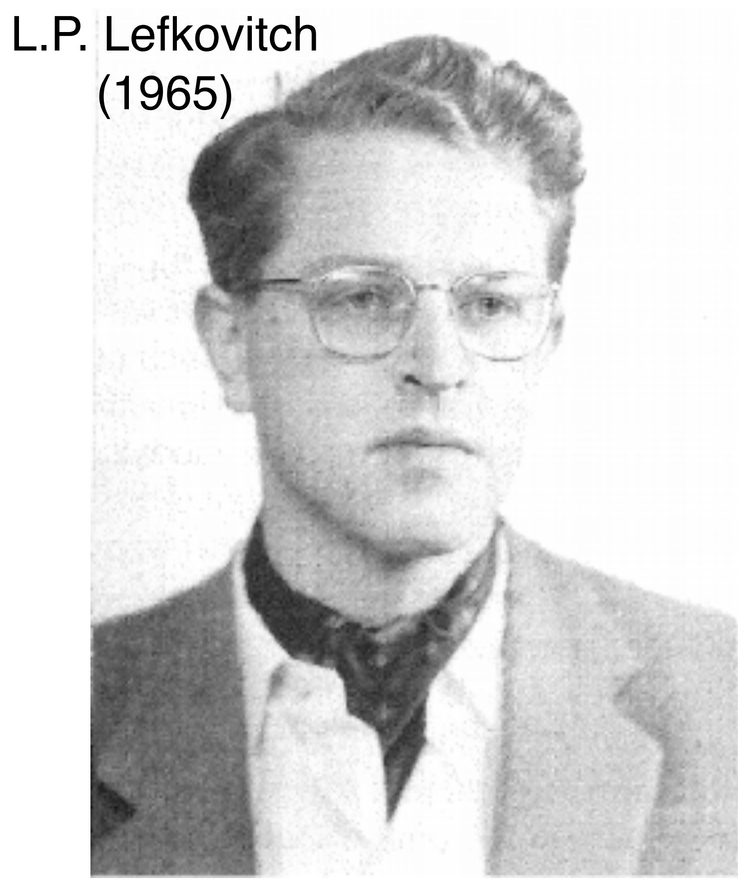
$$N_{1,t+1} = F_{21}N_{2,t} + F_{31}N_{3,t}$$

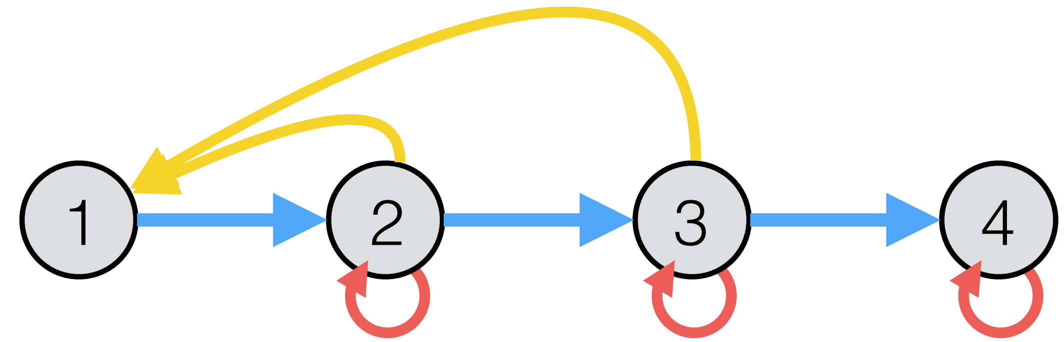
$$N_{2,t+1} = G_{12}N_{1,t} + P_{22}N_{2,t}$$

$$N_{3,t+1} = G_{23}N_{2,t} + P_{33}N_{3,t}$$

$$N_{4,t+1} = G_{34}N_{3,t} + P_{44}N_{4,t}$$

The transition matrix





$$
\begin{aligned}
N_{1,t+1} &= F_{21}N_{2,t} + F_{31}N_{3,t} \\
N_{2,t+1} &= G_{12}N_{1,t} + P_{22}N_{2,t} \\
N_{3,t+1} &= G_{23}N_{2,t} + P_{33}N_{3,t} \\
N_{4,t+1} &= G_{34}N_{3,t} + P_{44}N_{4,t}
\end{aligned}
$$

$$
\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} = \begin{bmatrix} 0 & F_{21} & F_{31} & 0 \\ G_{12} & P_{22} & 0 & 0 \\ 0 & G_{23} & P_{33} & 0 \\ 0 & 0 & G_{34} & P_{44} \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{bmatrix}
$$

Death is an absorbing state

Time *t*

Time *t+1*

$$
\begin{array}{c|c|c}
 & \textbf{Alive} & \textbf{Dead} \\
\hline
\textbf{Alive} & \begin{bmatrix} 0 & F_{21} & F_{31} & 0 \\ G_{12} & P_{22} & 0 & 0 \\ 0 & G_{23} & P_{33} & 0 \\ 0 & 0 & G_{34} & P_{44} \end{bmatrix} & 0 \\
\hline
\textbf{Dead} & m & 1
\end{array}
$$

U = survival & growth

F = fecundity

C = clonality

$$A = \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{bmatrix} + \begin{bmatrix} 0 & 0.0043 & 0.1132 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix} + \begin{bmatrix} 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 \end{bmatrix}$$

$$\sum_{i=1}^{n} a_{ij} = \begin{bmatrix} 0.9775 & 0.9847 & 0.9986 & 0.9804 \end{bmatrix}$$

Stage-specific
survival rates

Brault & Caswell 1993 Ecology

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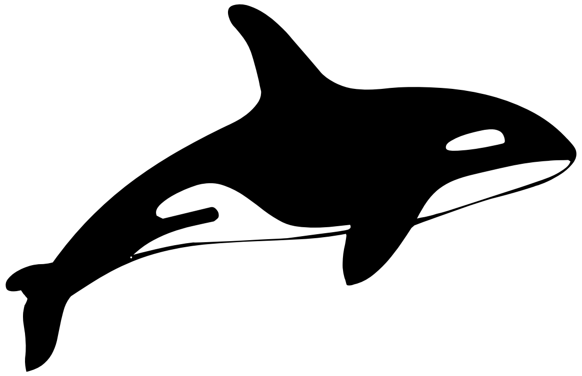
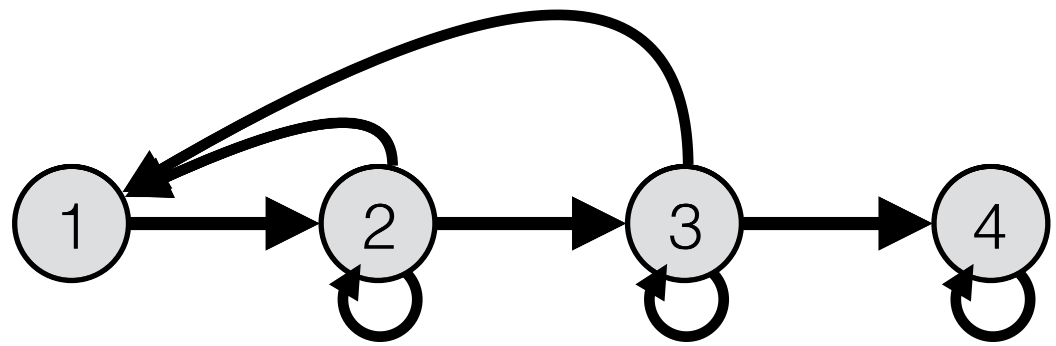


Projection



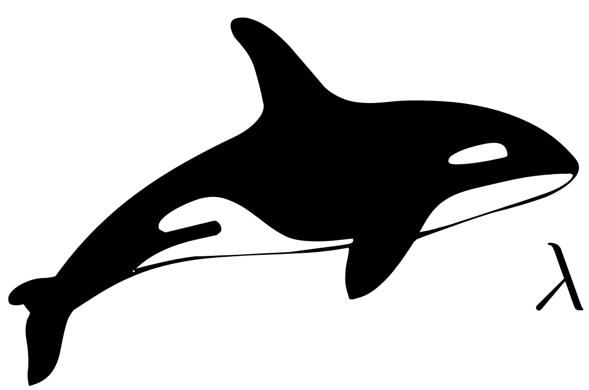
$$\begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} = \begin{bmatrix} 0 & 0.0043 & 0.1132 & 0 \\ 0.9775 & 0.9111 & 0 & 0 \\ 0 & 0.0736 & 0.9534 & 0 \\ 0 & 0 & 0.0452 & 0.9804 \end{bmatrix} \begin{bmatrix} N_{1,t} \\ N_{2,t} \\ N_{3,t} \\ N_{4,t} \end{bmatrix}$$

Matrix multiply,
& iterate

Brault & Caswell 1993 Ecology

Equilibrium: Population growth (λ)

$$\begin{bmatrix} \mathrm{a}_{11} & \dots & \mathrm{a}_{1n} \\ \vdots & \ddots & \vdots \\ \mathrm{a}_{n1} & \dots & \mathrm{a}_{nn} \end{bmatrix} \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix} = \lambda \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix}$$



$$\lambda = 1.025$$

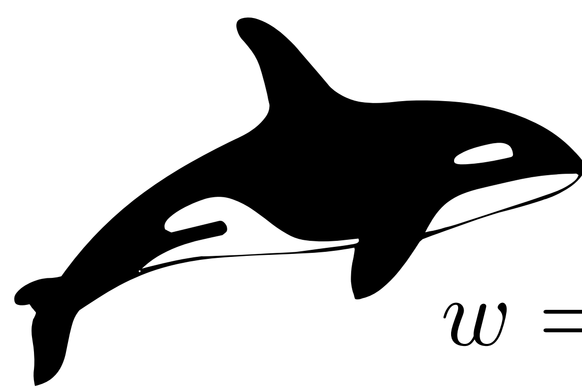
Brault & Caswell 1993 Ecology

	Population size	Population decline	Population growth rate (λ)
Critically endangered	–	≥ 80% 10 years	$\lambda \leq (1-0.8)^{\frac{1}{10}}$ ≤ 0.851
	N < 250	≥ 25% 3 years	≤ 0.909
Endangered	–	≥ 50% 10 years	≤ 0.933
	N < 2500	≥ 20% 5 years	≤ 0.956
Vulnerable	–	≥ 20% 10 years	≤ 0.978
	N < 10000	≥ 10% 10 years	≤ 0.990

IUCN
Caswell 2001

Equilibrium: Stage structure (*w*)

$$\begin{bmatrix} \mathrm{a}_{11} & \cdots & \mathrm{a}_{1n} \\ \vdots & \ddots & \vdots \\ \mathrm{a}_{n1} & \cdots & \mathrm{a}_{nn} \end{bmatrix} \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix} = \lambda \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix}$$



$$w = \begin{bmatrix} 0.0370 \\ 0.3161 \\ 0.3229 \\ 0.3240 \end{bmatrix} = \begin{bmatrix} 3.70\% \\ 31.61\% \\ 32.29\% \\ 32.40\% \end{bmatrix}$$

Brault & Caswell 1993 Ecology

Structured vs. unstructured population dynamics

orca.R

Shiny app
[server.R, ui.R]

Which stages have the biggest impact on λ?

seaturtle.R

$$\begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix}$$

$\lambda = 0.952$ Endangered

Crowder *et al.* 1994 Ecol. Appl.

Protect hatchlings

$$\begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix} \quad \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 1.000 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix}$$

$$\lambda_{\text{control}} = 0.952$$

Endangered

$$\lambda_{\text{hatchling protection}} = 0.974$$

Vulnerable

Crowder *et al.* 1994 Ecol. Appl.

Turtle Exclusion Device

$$\begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix} \quad \begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.757 & 0 & 0 \\ 0 & 0 & 0.022 & 0.769 & 0 \\ 0 & 0 & 0 & 0.069 & 0.877 \end{bmatrix}$$

$$\begin{bmatrix} 0.675 & 0.750 & 0.676 & 0.743 & 0.8091 \end{bmatrix} \quad \begin{bmatrix} 0.675 & 0.750 & 0.77918 & 0.83814 & 0.876703 \end{bmatrix}$$

$$\lambda_{\text{control}} = 0.952 \qquad \lambda_{\text{TED}} = 1.027$$

Endangered

Recovering

Crowder *et al.* 1994 Ecol. Appl.

Sensitivity

"Fixed change in λ for a fixed change in a_{ij}"

$$\frac{\partial \lambda}{\partial \mathrm{a}_{ij}} = \frac{v_i w_j}{w \cdot v}$$

$$\begin{bmatrix} \mathrm{a}_{11} & \dots & \mathrm{a}_{1n} \\ \vdots & \ddots & \vdots \\ \mathrm{a}_{n1} & \dots & \mathrm{a}_{nn} \end{bmatrix} \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix} = \lambda \begin{bmatrix} w_1 \\ \vdots \\ w_n \end{bmatrix}$$

$$\begin{bmatrix} v_1 & \dots & v_n \end{bmatrix} \begin{bmatrix} \mathrm{a}_{11} & \dots & \mathrm{a}_{1n} \\ \vdots & \ddots & \vdots \\ \mathrm{a}_{n1} & \dots & \mathrm{a}_{nn} \end{bmatrix} = \lambda_L \begin{bmatrix} v_1 & \dots & v_n \end{bmatrix}$$

Elasticity

"Proportional change in λ for a proportional change in a_{ij}"

$$e_{ij} = \frac{\mathrm{a}_{ij}}{\lambda}\frac{\partial\lambda}{\partial\mathrm{a}_{ij}}$$

$$\begin{bmatrix} 0 & 0 & 0 & 4.665 & 61.896 \\ 0.675 & 0.703 & 0 & 0 & 0 \\ 0 & 0.047 & 0.657 & 0 & 0 \\ 0 & 0 & 0.019 & 0.682 & 0 \\ 0 & 0 & 0 & 0.061 & 0.8091 \end{bmatrix}$$

Sensitivity

0	0	0	0.002	0.001
0.082	0.222	0	0	0
0	1.173	0.187	0	0
0	0	2.901	0.204	0
0	0	0	0.768	0.329

Elasticity

0	0	0	0.009	0.049
0.058	0.164	0	0	0
0	0.058	0.129	0	0
0	0	0.058	0.147	0
0	0	0	0.049	0.28

Crowder *et al.* 1994 Ecol. Appl.

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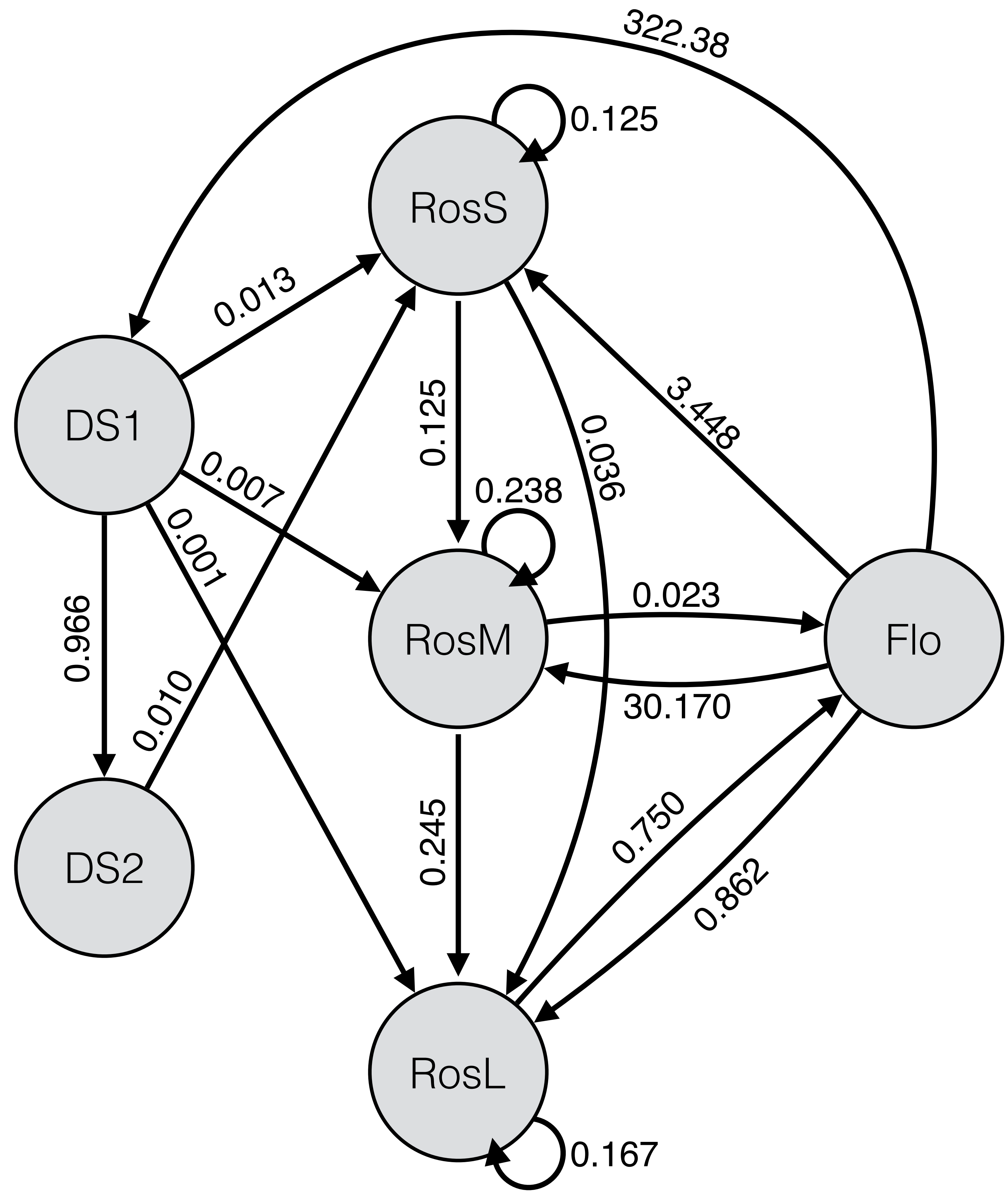
Dipsacus sylvestris
Werner & Caswell 1977


322.38
0.125
RosS
0.013
DS1
0.125
0.036
3.448
0.007
0.001
0.238
0.966
RosM
0.023
Flo
0.010
30.170
DS2
0.245
0.750
0.862
RosL
0.167

Assignment:

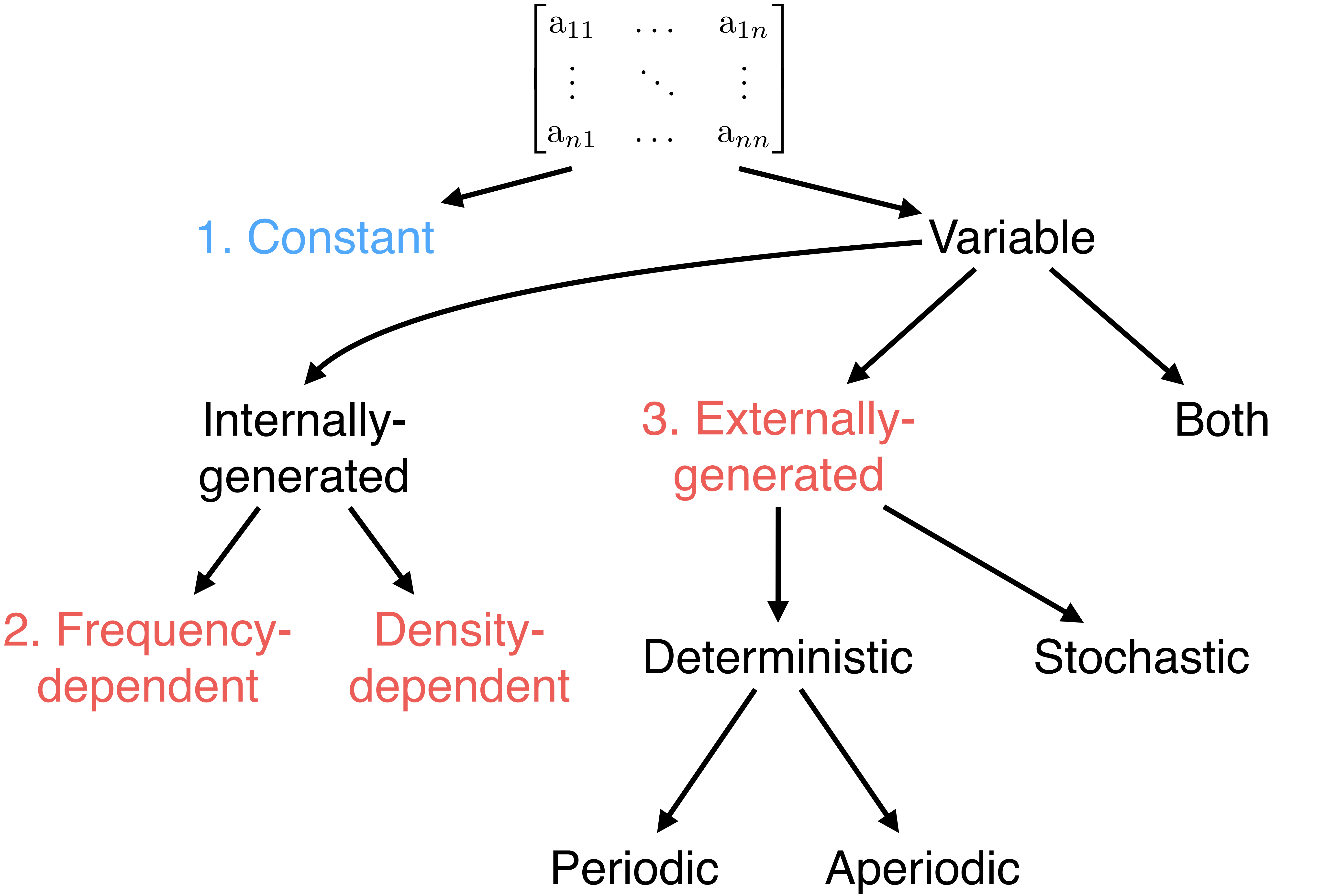
This matrix model for teasel was constructed in the United States, where teasel is invasive. Propose and evaluate an intervention to reduce the population growth of this species. The intervention strategy can use one or more mechanical, chemical, or biological controls. Please include:

i) A brief description of the intervention.
ii) Matrices (**A=U+F+C**) for a teasel population under the intervention with modified transition rates. The transition rates that are changed by the intervention should be indicated.
iii) A comparison of equilibrium population growth rates, $\lambda_{control}$ and $\lambda_{intervention}$. Do you predict that the intervention will drive the teasel population to extinction?

Submit your assignment as a Word, PDF, or similar file format by email to will.petry@usys.ethz.ch by 17:00 on Monday 1 May.

COM(P)ADRE

- Plant (COMPADRE) and animal (COMADRE) databases of matrix models for comparative demography
- 695 plant species, 405 animal species
- *ca.* 9000 matrices
- Error checked
- Regularly updated
- http://www.compadre-db.org/



$\begin{bmatrix} a_{11} & \cdots & a_{1n} \\ \vdots & \ddots & \vdots \\ a_{n1} & \cdots & a_{nn} \end{bmatrix}$
1. Constant
Variable
Internally-generated
3. Externally-generated
Both
2. Frequency-dependent
Density-dependent
Deterministic
Stochastic
Periodic
Aperiodic