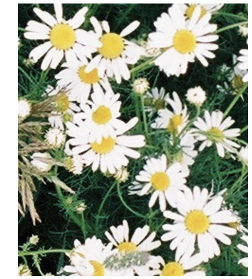
R_0 and Stage-Structured Invaders

Mark Lewis

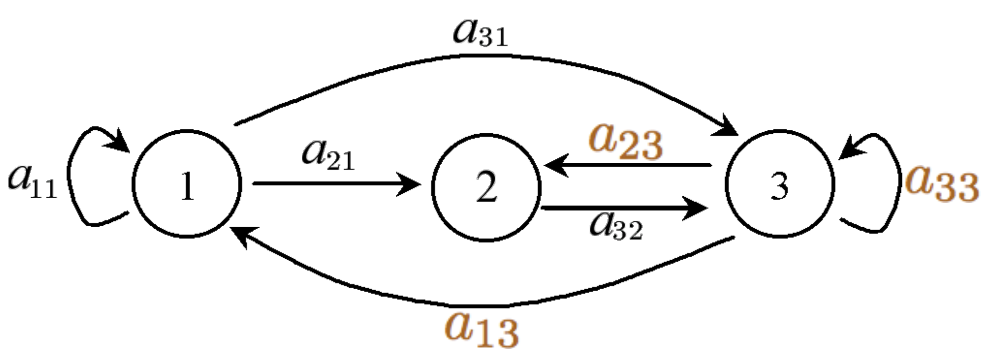
The Mathematics Behind Biological Invasions

A Canadian weed



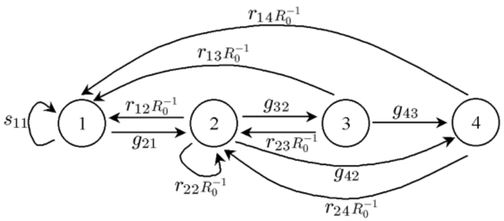
Case Study:
Scentless chamomile (*Matricaria perforata*)

- Annual, biennial or short-lived perennial
- Prefers disturbed habitats (poor competitor)
- Invades agricultural ecosystems
- Three distinctive life cycle stages: (1) seeds (2) rosettes, and (3) flowering plants
- Stage-structured life cycle:

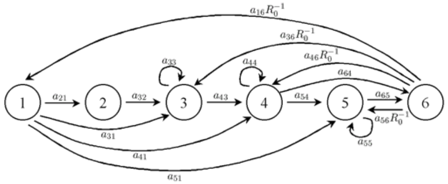


Complex Stage-Structures of Some Invaders

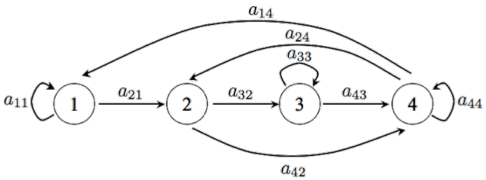
Nodding thistle
(*Carduus nutans*)



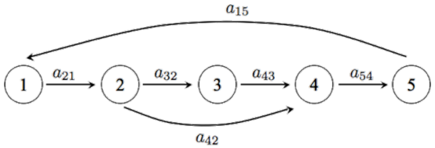
Common teasel
(*Dypsacus sylvestris*)



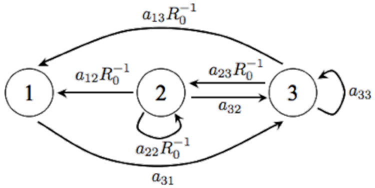
Tansy ragwort
(*Senecio jacobaea*)



Bullfrog
(*Rana catesbeiana*)



Common cat's ear
(*Hypochaeris radicata*)



Outline

- Classical methods to evaluate growth of invaders using eigenvalue and elasticity analysis
- New methods to evaluate growth growth of invaders using the basic reproductive rate
- Application to control of scentless chamomile

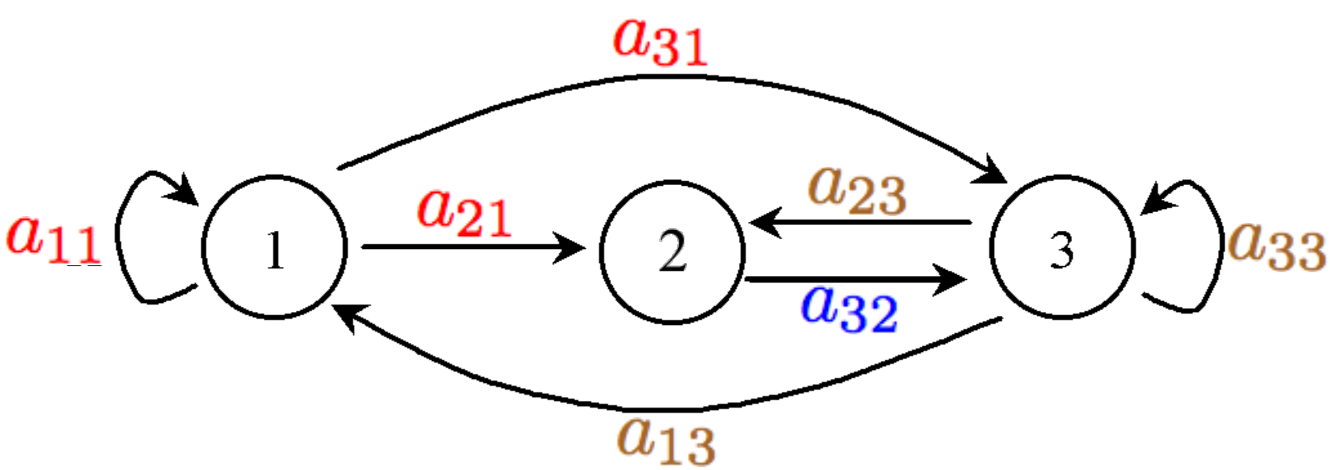
Matrix Population Models

Matrix model:

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t$$

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_t$$

Life cycle graph:



Matrix Population Models

Population growth rate (λ):

Dominant eigenvalue of **A** $\begin{cases} \lambda < 1 & \text{decrease} \\ \lambda = 1 & \text{constant} \\ \lambda > 1 & \text{increase} \end{cases}$

Elasticity analysis:

Measures the relative contributions of transitions to population growth

$$\mathbf{E} = \left[\frac{a_{ij}}{\lambda} \frac{\partial \lambda}{\partial a_{ij}} \right]$$

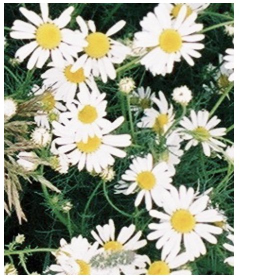
Caswell (2001)

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters
2. Calculate population growth rate λ
3. Calculate **E** and target transitions with higher elasticities
4. Verify is control agents affect transitions with high elasticities

Demographic Analysis



Case Study:
Scentless chamomile (*Matricaria perforata*)

- Annual, biennial or short-lived perennial
- Seed production of up to 256,000 seeds/plant
- Three distinctive life cycle stages: seeds (n_1), rosettes (n_2), and flowering plants (n_3):

$$\begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t+1} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix} \begin{bmatrix} n_1 \\ n_2 \\ n_3 \end{bmatrix}_{t}$$

Demographic Analysis

Case Study: Scentless chamomile (*Matricaria perforata*)

Data collected in Vegreville, AB, 2003-2005




Demographic Analysis

Case Study: Scentless chamomile (*Matricaria perforata*)

2004

$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 36376.45 \\ 0.27 & 0 & 517 \\ 0.04 & 0.45 & 297.85 \end{bmatrix}$$

$$\lambda = 303.46$$

$$\mathbf{E} = \begin{bmatrix} 0.00041 & 0 & \mathbf{1.57} \\ 0.016 & 0 & 0.25 \\ \mathbf{1.55} & 0.26 & \mathbf{96.35} \end{bmatrix}$$

2005

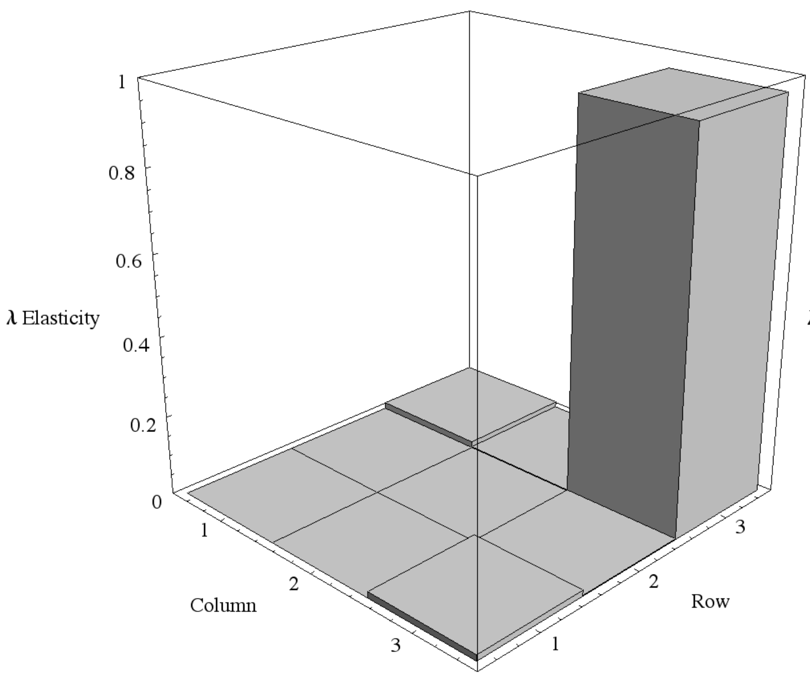
$$\mathbf{A} = \begin{bmatrix} 0.08 & 0 & 1775.22 \\ 0.27 & 0 & 25.24 \\ 0.04 & 0.45 & 14.53 \end{bmatrix}$$

$$\lambda = 19.37$$

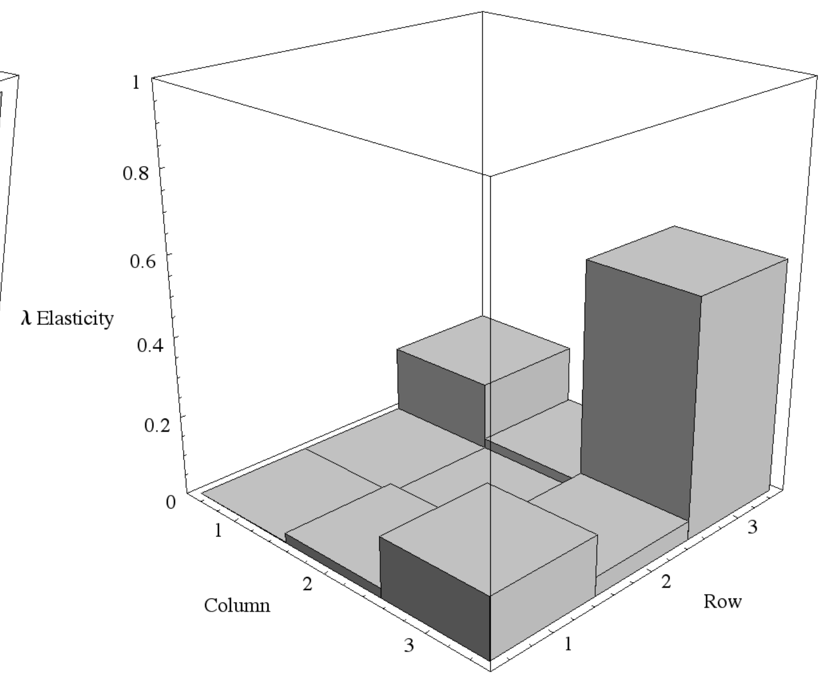
$$\mathbf{E} = \begin{bmatrix} 0.071 & 0 & \mathbf{17.16} \\ 2.32 & 0 & 2.36 \\ \mathbf{14.83} & 4.69 & \mathbf{58.56} \end{bmatrix}$$

Control Target: flower to flower transition

Demographic Analysis—Elasticity



2004



2005

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters
2. Calculate population growth rate λ
3. Calculate **E** and target transitions with higher elasticities
4. Verify is control agents affect transitions with high elasticities

Is this a robust method for assessing control?

Demographic Analysis

Matrix models for control:

1. Determine life cycle and estimate parameters
2. Calculate population growth rate λ
3. Calculate **E** and target transitions with higher elasticities
4. Choose control agents that affect transitions with high elasticities

Is this a robust method for assessing control?

1. There is no simple formulae for the eigenvalue λ , for high order polynomials
2. Both **E** and λ have to be calculated numerically for a particular dataset

Net Reproductive Rate

Transition and fecundity matrix:

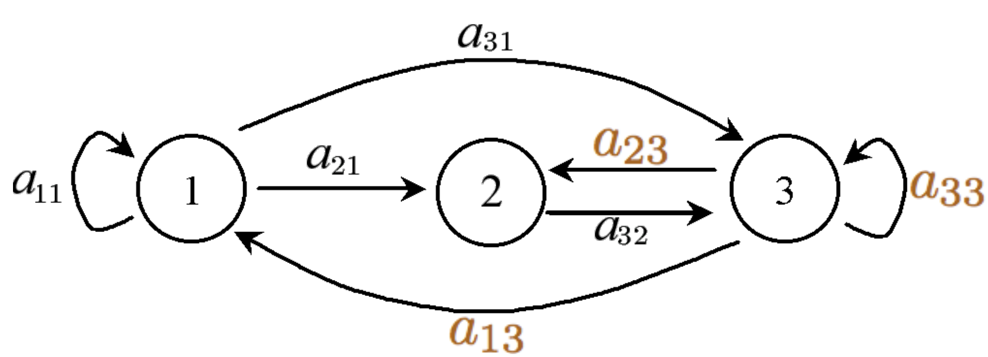
$$\mathbf{A} = \mathbf{T} + \mathbf{F} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Transition matrix
(Survival)

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Fecundity matrix
(Fecundity)



Net Reproductive Rate

Next generation operator (**Q**):

$$\mathbf{n}_{t+1} = \mathbf{A}\mathbf{n}_t = (\mathbf{T} + \mathbf{F})\mathbf{n}_t$$

$$\mathbf{n}_{t+gen} = \mathbf{Q}\mathbf{n}_t = (\underbrace{\mathbf{F}}_{\text{Year 1}} + \underbrace{\mathbf{F}\mathbf{T}}_{\text{Year 2}} + \underbrace{\mathbf{F}\mathbf{T}^2}_{\text{Year 3}} + \ldots)\mathbf{n}_t = \mathbf{F}(\mathbf{I} - \mathbf{T})^{-1}\mathbf{n}_t$$

Net Reproductive rate (R_0):

This is the number of individuals that one individual produces over its lifetime. It is the largest eigenvalue of the next generation operator **Q**. The population grows if $R_0>1$ and dies out if $R_0<1$

$$R_0 > 1 \quad \text{if and only if} \quad \lambda > 1$$

Cushing and Yicang (1994)

Net Reproductive Rate

Transition and fecundity matrix:

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Transition matrix
(Survival)

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Fecundity matrix
(Fecundity)

$$[I - T]^{-1} = \begin{bmatrix} \frac{1}{1-a_{11}} & 0 & 0 \\ \frac{a_{21}}{1-a_{11}} & 1 & 0 \\ \frac{a_{32}a_{21}+a_{31}}{1-a_{11}} & a_{32} & 1 \end{bmatrix}$$

$$F[I - T]^{-1} = \begin{bmatrix} \frac{a_{13}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{13}a_{32} & a_{13} \\ \frac{a_{23}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{23}a_{32} & a_{23} \\ \frac{a_{33}(a_{32}a_{21}+a_{31})}{1-a_{11}} & a_{33}a_{32} & a_{33} \end{bmatrix}$$

$$R_0 = \frac{(a_{31} + a_{21}a_{32})a_{13}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Net Reproductive Rate

Transition and fecundity matrix:

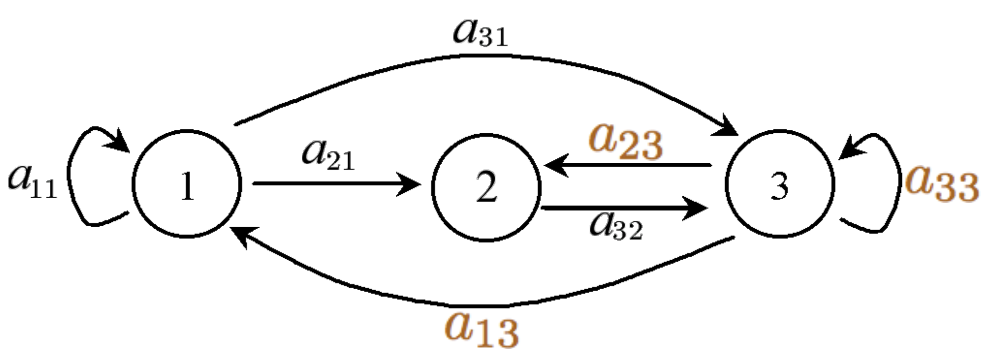
$$\mathbf{A} = \mathbf{T} + \mathbf{F} = \begin{bmatrix} a_{11} & 0 & a_{13} \\ a_{21} & 0 & a_{23} \\ a_{31} & a_{32} & a_{33} \end{bmatrix}$$

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}$$

Transition matrix
(Survival)

$$\mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

Fecundity matrix
(Fecundity)



Net Reproductive Rate

Is this a robust method for assessing control?

As with λ we still need to calculate an eigenvalue, now of the next generation operator **Q**

However, this eigenvalue R_0 can be written down easily and explicitly using…

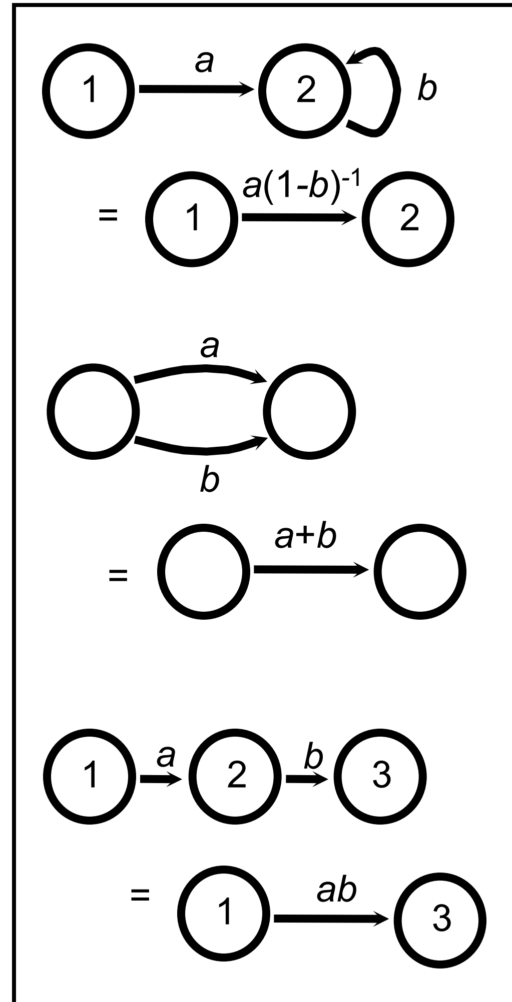
A simple method for calculating R_0:

1. Calculates R_0 for complex models
2. Uses graph theoretic approach
3. Easy to implement-little math needed
4. Groups terms in the R_0 expression according to lifecycle pathways

De Camino Beck and Lewis (2006)

Method for calculating R_0

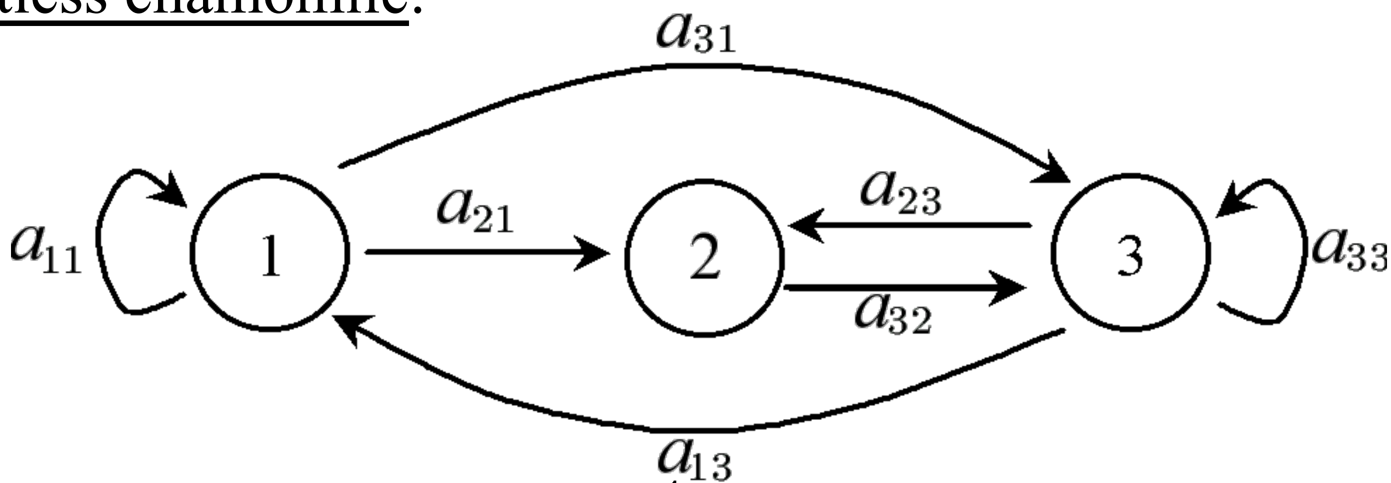
1. Create a graph where the fecundities (entries of **F**) are multiplied by R_0^{-1}
2. Reduce graph to a single node, using Mason's graph reduction rules.
3. Set the weight for the final node equal to 1 and solve for R_0



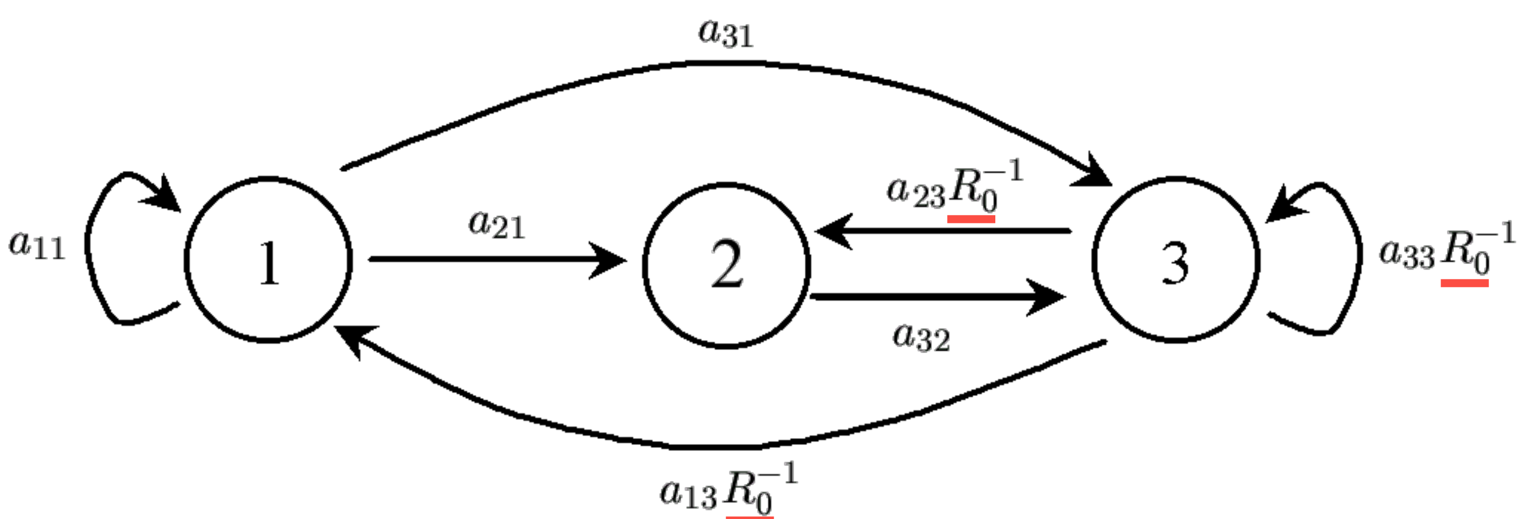
De Camino Beck and Lewis (2006)

$$\mathbf{T} = \begin{bmatrix} a_{11} & 0 & 0 \\ a_{21} & 0 & 0 \\ a_{31} & a_{32} & 0 \end{bmatrix}, \text{ and } \mathbf{F} = \begin{bmatrix} 0 & 0 & a_{13} \\ 0 & 0 & a_{23} \\ 0 & 0 & a_{33} \end{bmatrix}$$

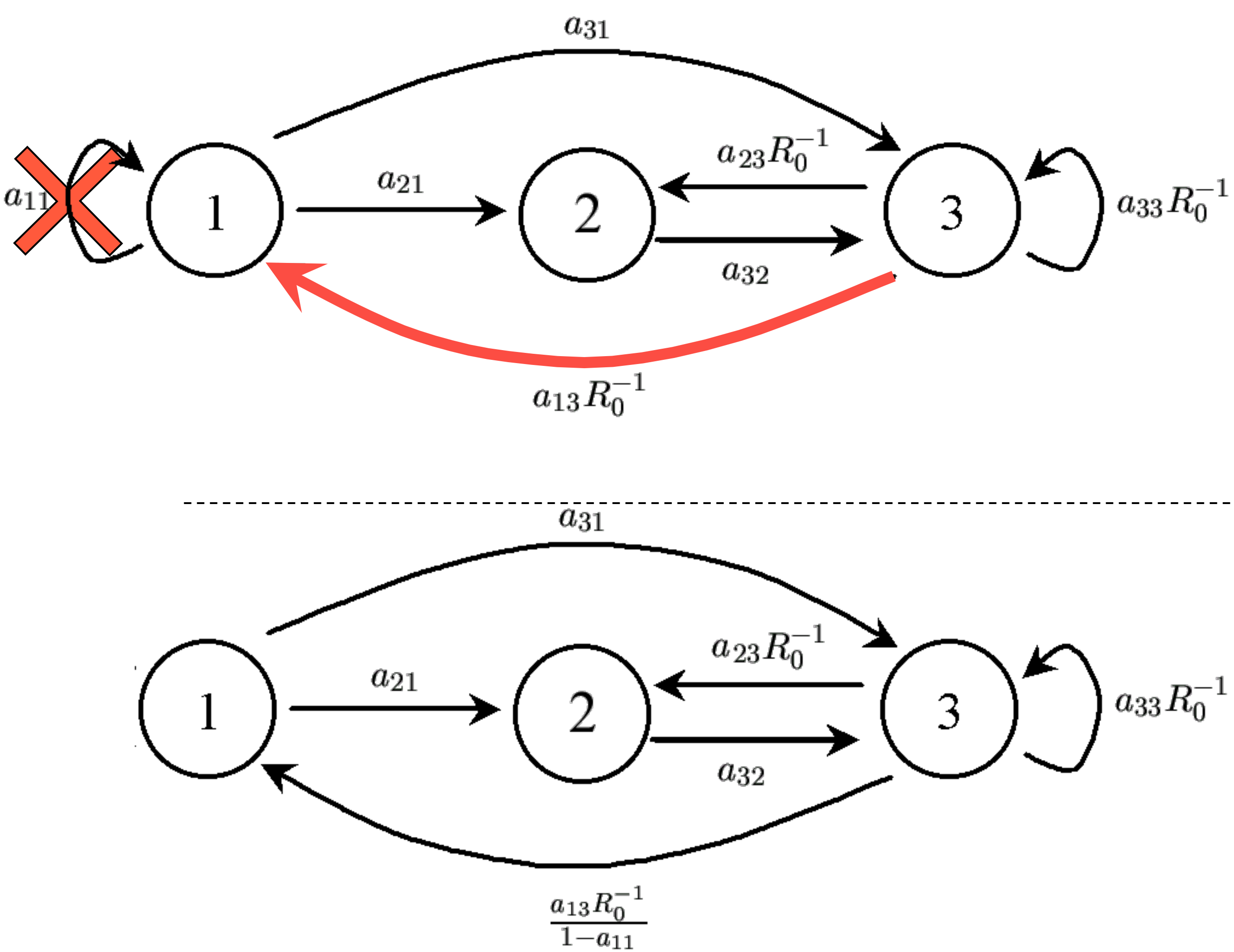
Scentless chamomile:

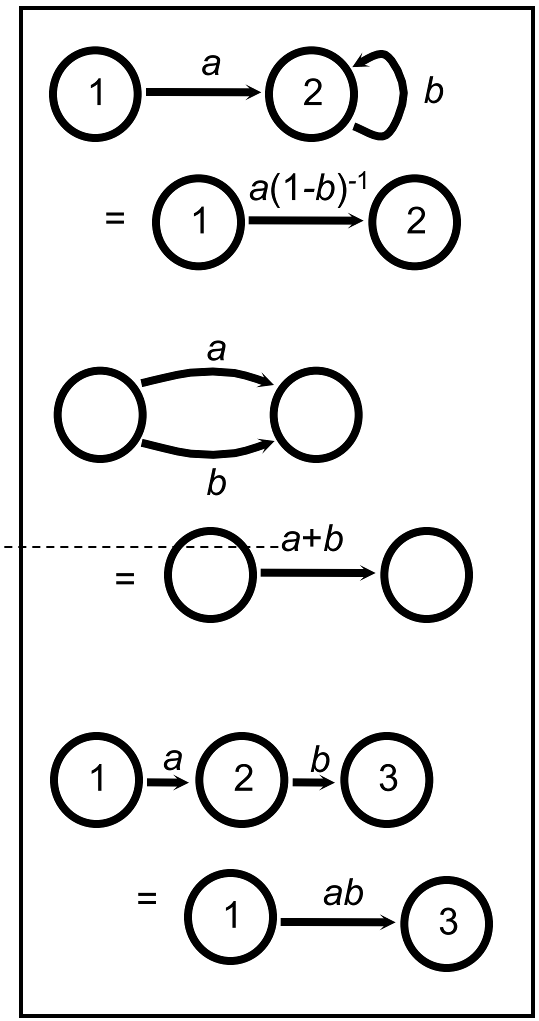


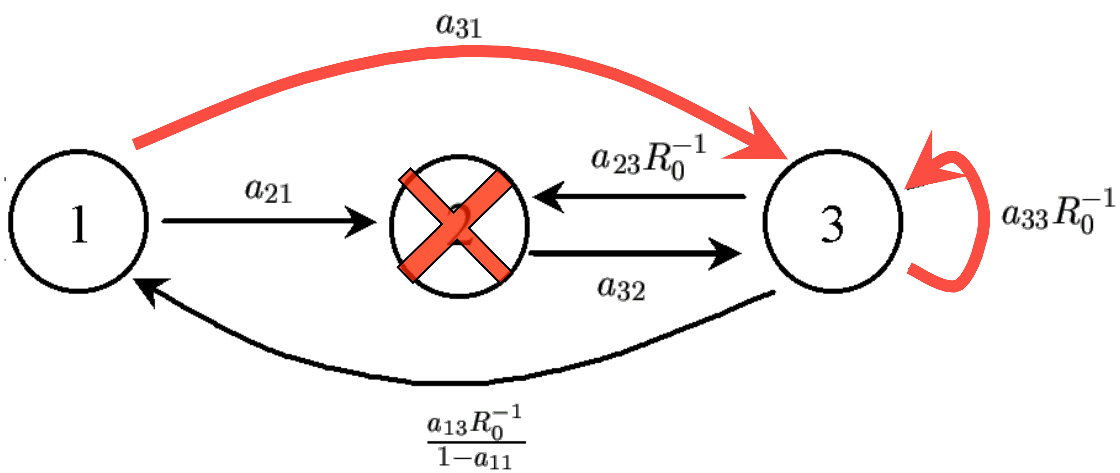
1. Multiply fecundities by R_0^{-1}



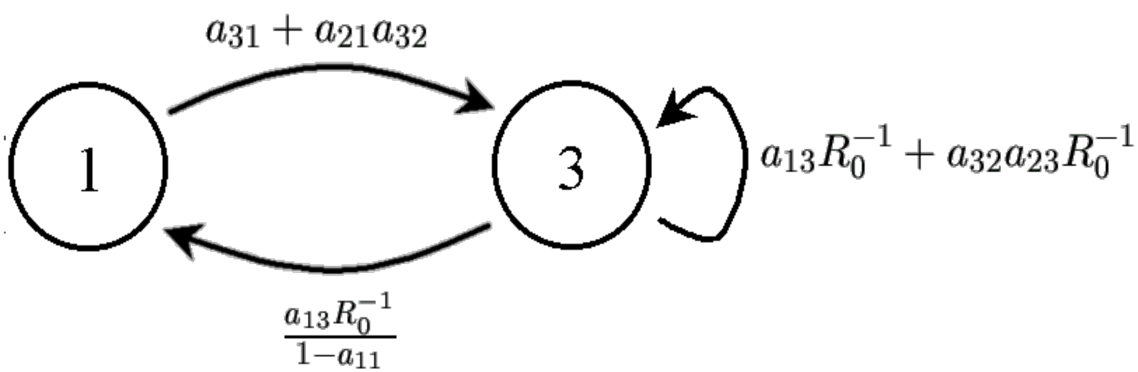
2. Reduce graph

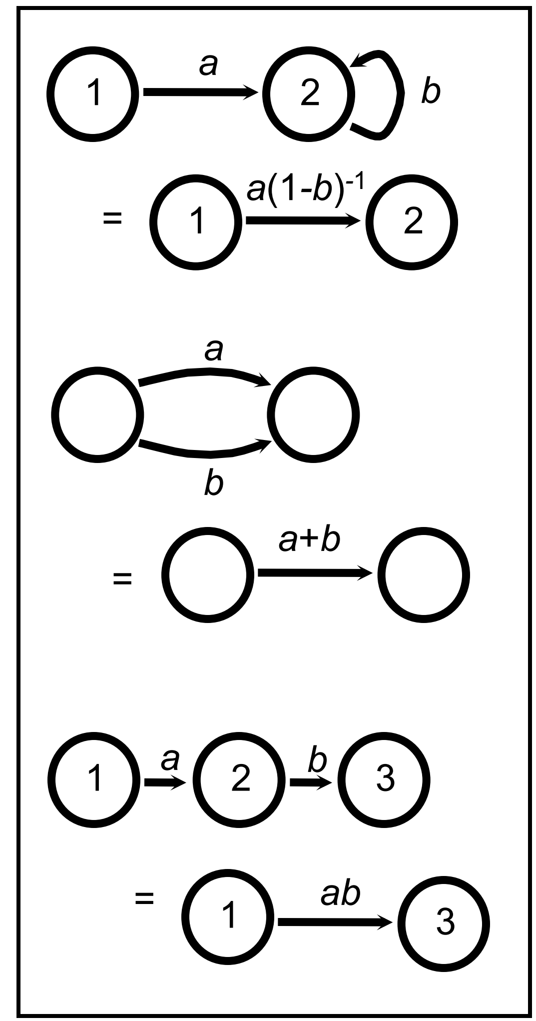




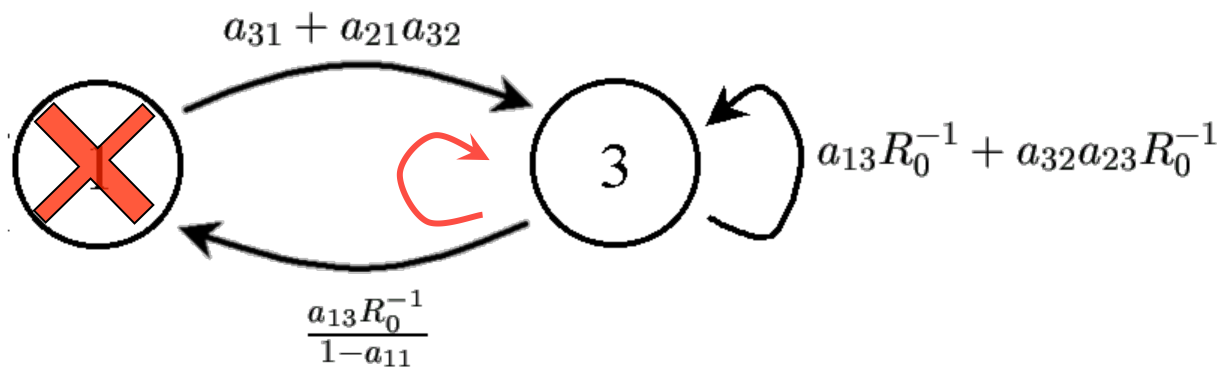


Node 2 eliminated

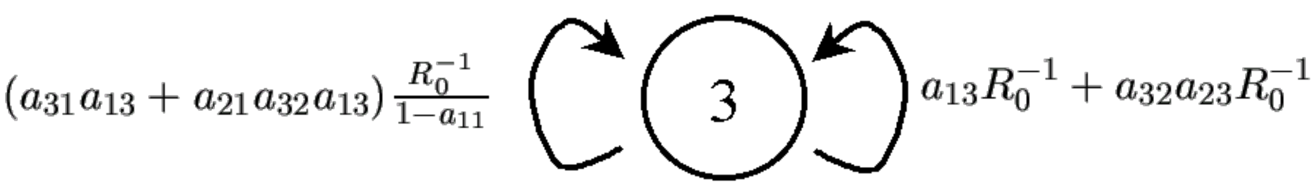


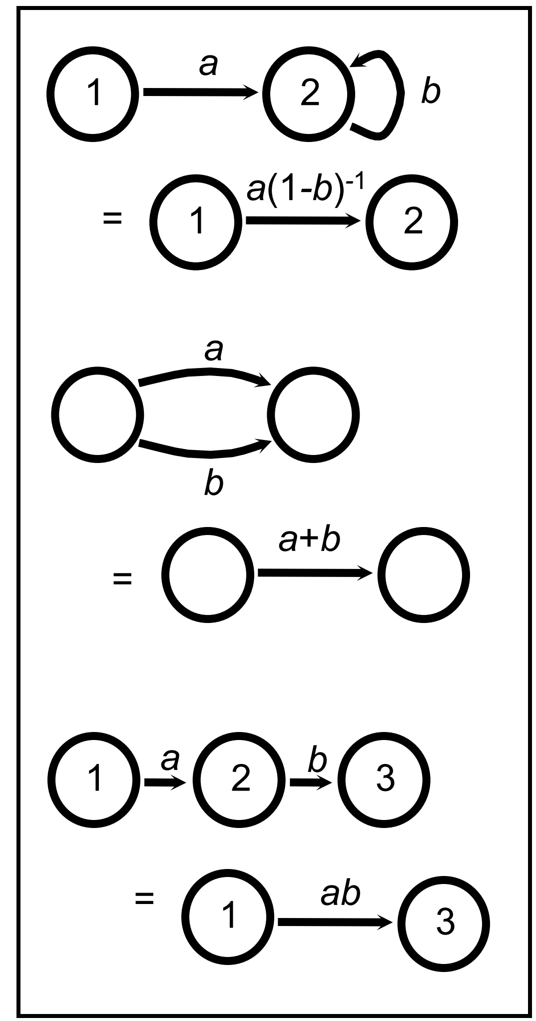


Mason's rules



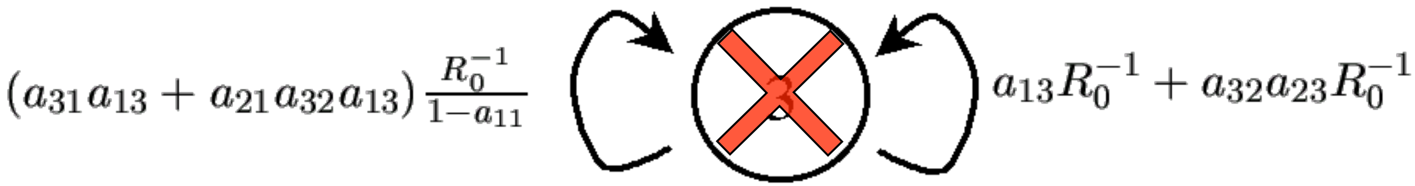
Node 1 eliminated





Mason's rules

Set the final node equal to 1 and solve for R_0



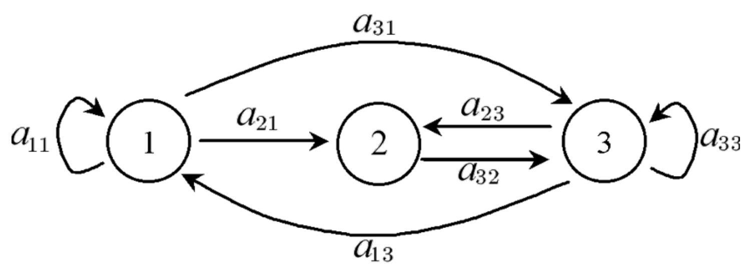
$$R_0 = \frac{(a_{31} + a_{21}a_{32})a_{13}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Net Reproductive Rate

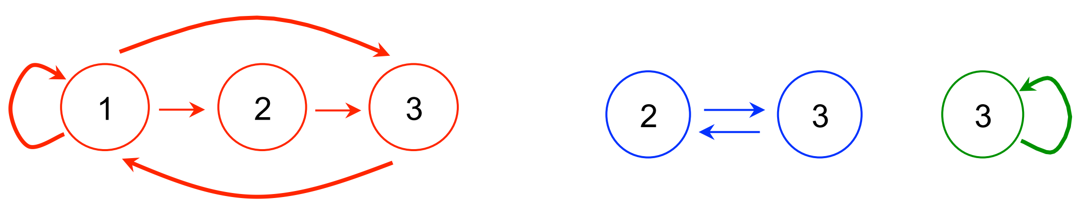
Scentless chamomile:

2004	2005
$R_0 = 6385.65 + 232.74 + 297.85$	$R_0 = 311.63 + 11.36 + 14.53$

1. Seeds
2. Rosettes
3. Flowering plants



$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$



Seed bank pathway

Rosette pathway

Flowering plant pathway

Net Reproductive Rate

Scentless chamomile:

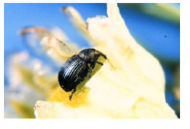
2004	2005
$R_0 = 6385.65 + 232.74 + 297.85$	$R_0 = 311.63 + 11.36 + 14.53$

$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

Seed bank pathway — Rosette pathway — Flowering plant pathway

Control Agents:

- ☐ Seed Weevil (*Omphalapion* (Apion) *hookeri*)
- ☐ Gall midge (*Rhopalomyia sp.*)

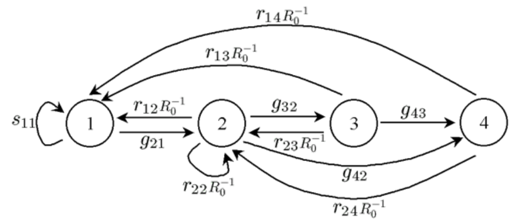


Tomas de Camino Beck
(Grad (Mathbio) *studenticus*)

Mechanical control (removal of seed head and destruction of stems) used to simulate control agents and validate model

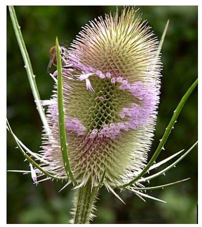
Net Reproductive Rate

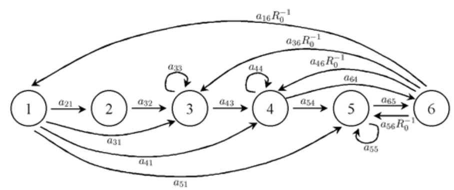
Nodding thistle
(*Carduus nutans*)



$$R_0 = r_{22} + g_{42}r_{24} + g_{32}r_{23} + g_{32}g_{43}r_{24} + \frac{g_{21}r_{12} + g_{21}g_{32}r_{13} + g_{21}g_{42}r_{14} + g_{32}g_{43}g_{21}r_{14}}{1 - s_{11}}$$

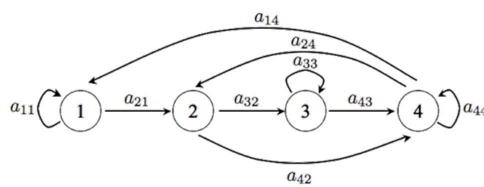
Common teasel
(*Dypsacus sylvestris*)





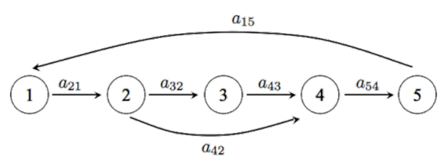
$$R_0 = a_{16}\alpha_1 + \alpha_2$$

Tansy ragwort
(*Senecio jacobaea*)



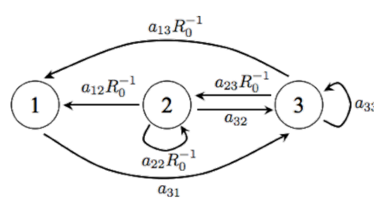
$$R_0 = \left[\frac{a_{21}a_{14}}{1 - a_{11}} + a_{24}\right]\left[\frac{a_{32}a_{43}}{(1 - a_{33})(1 - a_{44})} + \frac{a_{42}}{(1 - a_{44})}\right].$$

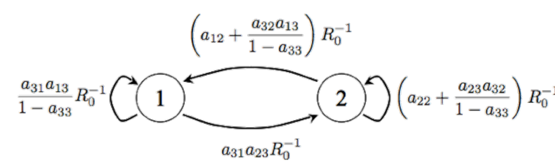
Bullfrog
(*Rana catesbeiana*)



$$R_0 = a_{12}a_{42}a_{54}a_{15} + a_{21}a_{32}a_{43}a_{54}$$

Common cat's ear
(*Hypochaeris radicata*)





Net Reproductive Rate

Why R_0?

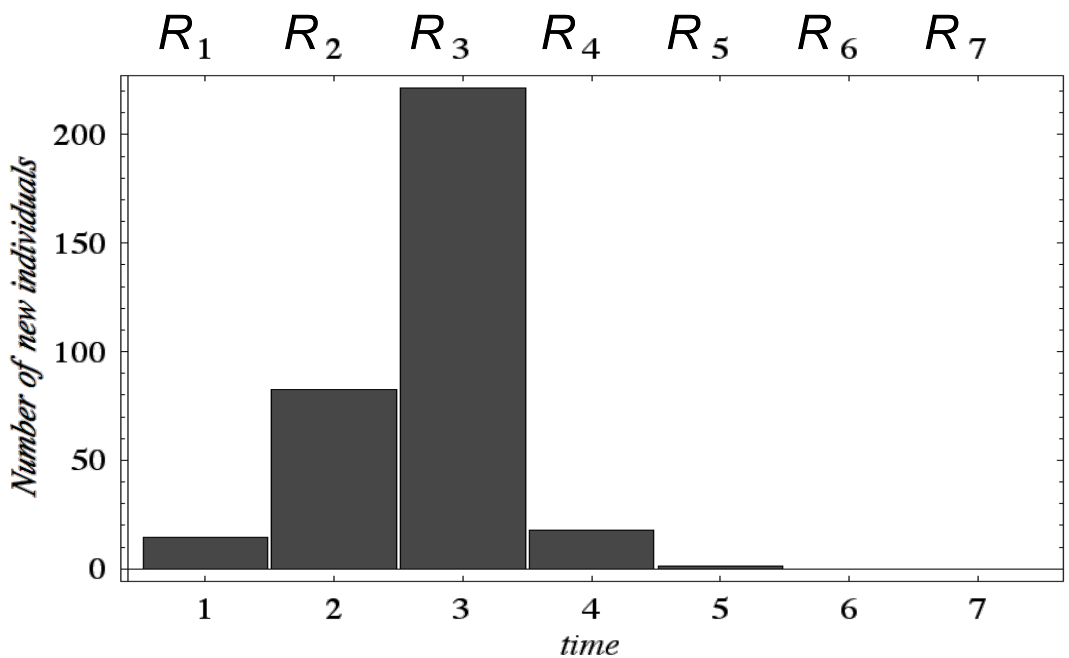
1. An analytical formula can be calculated
2. All reproductive pathways are represented in R_0
3. Life history traits can be analyzed in a general framework
4. It can complement demographic analysis of λ
5. Allows for evaluation of control strategies

Generation Time

Explicit R_0 formulae can be used to determine when the new offspring are produced (fecundity profile)

Relates to Cole (1954):

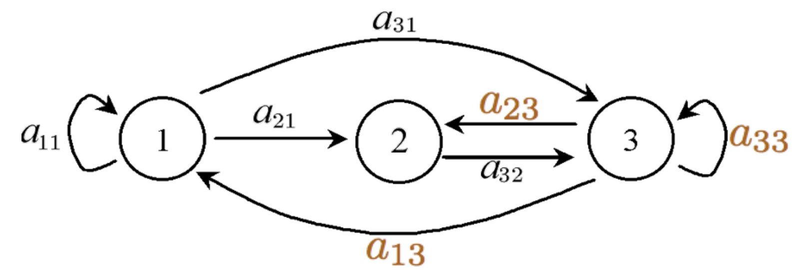
Effect of life history traits on population growth and Generation-Law method



De Camino Beck and Lewis (2007)

Generation Time

Number of new individuals:



$$R_0 = \frac{a_{31}a_{13} + a_{13}a_{21}a_{32}}{1 - a_{11}} + a_{32}a_{23} + a_{33}$$

R_0 generating function

$$R(T) = \frac{a_{31}a_{13}T^2 + a_{13}a_{21}a_{32}T^3}{1 - a_{11}T} + a_{32}a_{23}T^2 + a_{33}T$$

$$= R_1 T + R_2 T^2 + \ldots$$

$$R_0 = R(1) = R_1 + R_2 + \ldots$$

$$R_1 = R'(0)$$

$$R_2 = R''(0)/2$$

$$\vdots$$

From this it is possible to calculate mean generation time $\bar{T}$ and generation time variance $\mathrm{Var}[T]$

References

- Caswell, H. (2001). Matrix population models: Construction, analysis and interpretation, 2nd Ed. John Wiley & Sons, Ltd.
- Cushing, J. M., Yicang, Z. (1994). The net reproductive value and stability in matrix population models. *Natural Resource Modeling*. **8**: 297-333.
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- de Camino Beck, T., Lewis, M.A. July (2008). On net reproductive rate and the timing of reproductive output. *American Naturalist*. **172**: 128-39.