Demographic models for variability in lifetime reproductive output: how to go beyond R_0

Hal Caswell

Biology Department

Outline

Outline

Net reproductive rate

$$R_0 = \int_0^\infty \ell(x) m(x) dx$$

R_0

age-classified

$$\ell(x) = P[\text{survival to age } x]$$
$$m(x) = E[\text{reproduction at age } x]$$

$$R_0 = \int_0^\infty \ell(x)m(x)dx$$

stage-classified

$$\mathbf{A} = \mathbf{U} + \mathbf{F}$$
$$\mathbf{N} = (\mathbf{I} - \mathbf{U})^{-1}$$

$$R_0 = \max \text{eig}\,(\mathbf{FN})$$

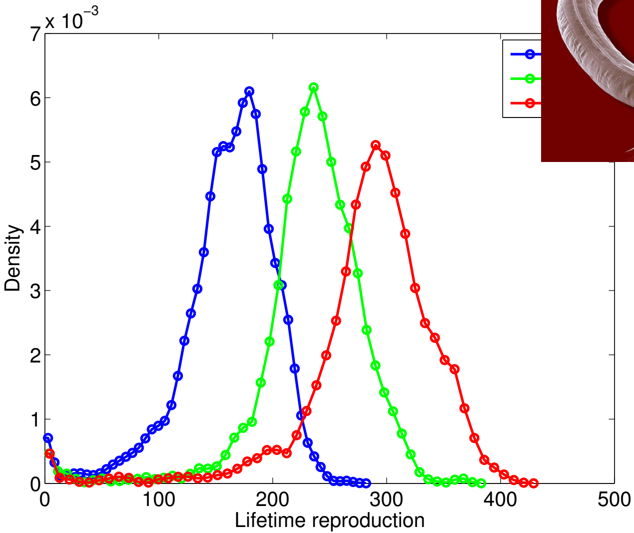
R_0

- mean lifetime reproduction
- per-generation growth rate
- indicator function for population growth

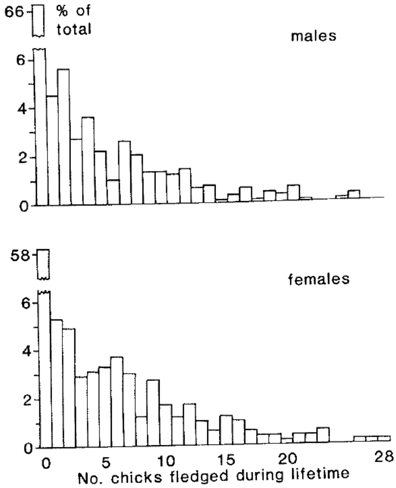
$$
\begin{aligned}
R_0 > 1 \quad &\Rightarrow \quad \text{population increase} \\
R_0 < 1 \quad &\Rightarrow \quad \text{population decline}
\end{aligned}
$$

- demography, epidemiology, evolution

Observation



Observation



Black-legged kittiwake

photo: Angsar Walk, CC

Observation

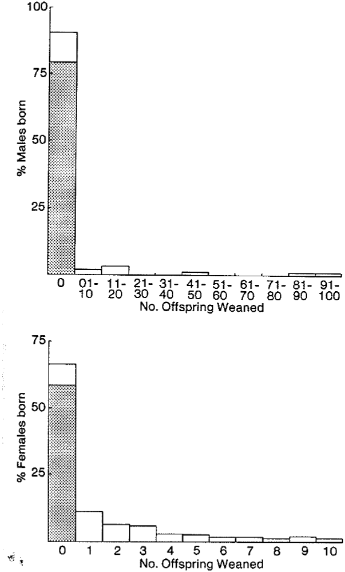


photo by Mike Baird, CC

Interpretation

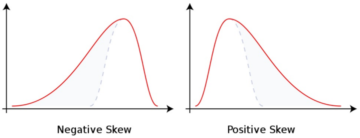
- Variability and skewness implies heterogeneity.
- Heterogeneity implies opportunity for selection.
- ... or does it

Problem: no way to calculate the variability *implied by* a particular life cycle and reproductive pattern in the absence of heterogeneity. Someone should do something about that.

Beyond R_0: goals

- statistics of lifetime reproduction
  - variability: variance, standard deviation, CV (scale parameters)
  - skewness (shape parameter)

$$\gamma = \frac{E\left(x - \bar{x}\right)^3}{V(x)^{3/2}}$$

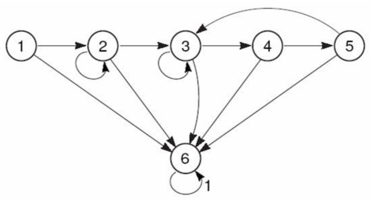


Wikipedia

- any kind of model
  - age- or stage-classified
  - time-invariant or time-varying
  - single or multiple types of reproduction
- can use many kinds of data

Outline

Demographic models as Markov chains



- absorbing markov chain
- transient states = stages in life cycle
- absorbing states = death
- projection matrix

$$\mathbf{P} = \left(\begin{array}{c|c} \mathbf{U} & 0 \\ \hline \mathbf{M} & \mathbf{I} \end{array} \right)$$

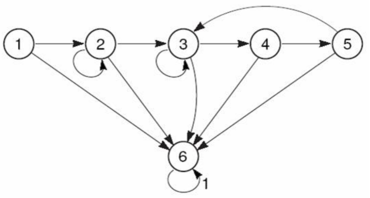
Markov chains with (random) rewards

- A Markov process with the collection of a "reward" at each transition:

  $$\text{transition } j \longrightarrow i = \text{reward of } r_{ij}$$

  r_{ij} is a random variable.
- rewards accumulate: we want the lifetime accumulated reward
  - pick a terminal time; rewards *still to be accumulated* at terminal time are zero
  - calculate rewards at previous time
  - iterate

Sources of variability in accumulated rewards?



- variability among pathways taken by individuals
- variability in rewards within pathways
- heterogeneity among individuals in p_{ij} and/or r_{ij}

Outline

Reproduction as a reward

Reproductive output depends on current stage

$$r_{ij} = r_j \qquad \text{independent of i}$$

for some measure of reproductive output (must specify what this is).

Howard's equation for mean reward

Specify a terminal time; let t = time remaining to terminal time

Conditional expectation:

$$E\left[\rho_j(t) \middle| j \longrightarrow i\right] = E\left\{r_{ij} + \beta E\left[\rho_i(t-1)\right]\right\}$$

Unconditional expectation:

$$E\left[\rho_j(t)\right] = \sum_i p_{ij} E\left\{r_{ij} + \beta E\left[\rho_i(t-1)\right]\right\}$$

Rewards: notation

Moments of rewards

$$\mathbf{R}_m = E \begin{pmatrix} r_{11}^m & \cdots & r_{1s}^m \\ \vdots & & \vdots \\ r_{s1}^m & \cdots & r_{ss}^m \end{pmatrix}$$

Moments of accumulated rewards

$$\boldsymbol{\rho}_m = E \begin{pmatrix} \rho_1^m \\ \vdots \\ \rho_s^m \end{pmatrix}$$

Howard's equation in matrix form

$$E\left[\rho_j(t)\right] = \sum_i p_{ij} E\left\{ r_{ij} + \beta E\left[\rho_i(t-1)\right]\right\}$$

$$\boldsymbol{\rho}_1(t) = \left(\mathbf{P} \circ \mathbf{R}_1\right)^{\mathsf{T}} \mathbf{1} + \beta \mathbf{P}^{\mathsf{T}} \boldsymbol{\rho}_1(t-1)$$

The problem: extend this to higher moments.

Rewards: equations for moments

$$
\begin{aligned}
\rho_1(t+1) &= (\mathbf{P}\circ\mathbf{R}_1)^{\mathsf{T}}\mathbf{1} + \mathbf{P}^{\mathsf{T}}\rho_1(t) \\
\rho_2(t+1) &= (\mathbf{P}\circ\mathbf{R}_2)^{\mathsf{T}}\mathbf{1} + 2\,(\mathbf{P}\circ\mathbf{R}_1)^{\mathsf{T}}\rho_1(t) + \mathbf{P}^{\mathsf{T}}\rho_2(t) \\
\rho_3(t+1) &= (\mathbf{P}\circ\mathbf{R}_3)^{\mathsf{T}}\mathbf{1} + 3\,(\mathbf{P}\circ\mathbf{R}_2)^{\mathsf{T}}\rho_1(t) + 3\,(\mathbf{P}\circ\mathbf{R}_1)^{\mathsf{T}}\rho_2(t) \\
&\quad + \mathbf{P}^{\mathsf{T}}\rho_3(t)
\end{aligned}
$$

$$
\rho_1(0) = \rho_2(0) = \rho_3(0) = \mathbf{0}
$$

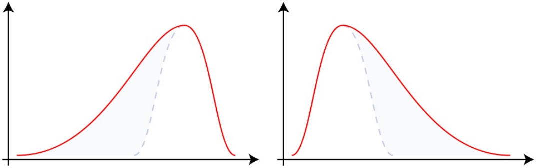
Caswell (in prep.)

Rewards: equations for moments

$$\rho_m(t+1) = \sum_{k=0}^{m} \binom{m}{k} \left(\mathbf{P} \circ \mathbf{R}_{m-k}\right)^{\mathsf{T}} \rho_k(t)$$

Caswell (in prep.)

Rewards: variance and skewness



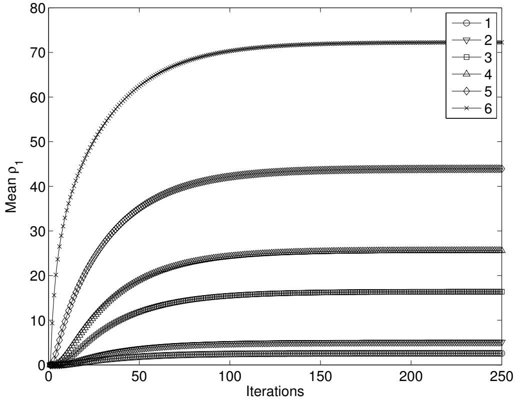
Wikipedia

Variance and skewness

$$V(\rho) = \rho_2 - \rho_1 \circ \rho_2$$
$$Sk(\rho) = \mathcal{D}\left[V(\rho)\right]^{-3/2} \left(\rho_3 - 3\rho_1 \circ \rho_2 + 5\rho_1 \circ \rho_1 \circ \rho_1\right)$$

Rewards: convergence of moments

Trillium grandiflorum



Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & i \text{ is absorbing, } j \text{ is transient} \\ 0 & \text{otherwise} \end{cases}$$

What does this measure? What are the mean and variance of lifetime reward?

Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & j \text{ is transient} \\ 0 & j \text{ is absorbing} \end{cases}$$

Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & j \text{ is transient} \\ 0 & j \text{ is absorbing} \end{cases}$$

Measuring or modelling reproductive rewards

- full measurement of the distribution of the r_{ij}
- Poisson model: random assortment of offspring among parents

$$
\begin{aligned}
E\left(r_{ij}\right) &= \mu \\
E\left(r_{ij}^2\right) &= \mu\left(1+\mu\right) \\
E\left(r_{ij}^3\right) &= \mu\left(1+3\mu+\mu^2\right)
\end{aligned}
$$

so

$$
\begin{aligned}
V\left(r_{ij}\right) &= \mu \\
Sk\left(r_{ij}\right) &= \mu^{-1/2}
\end{aligned}
$$

Reward models (cont'd.)

- fixed reward model (the "fraction of a baby" model)

$$
\begin{aligned}
E\left(r_{ij}\right) &= \mu \\
E\left(r_{ij}^2\right) &= \mu^2 \\
E\left(r_{ij}^3\right) &= \mu^3
\end{aligned}
$$

with

$$
\begin{aligned}
V\left(r_{ij}\right) &= 0 \\
Sk\left(r_{ij}\right) &= \text{NaN}
\end{aligned}
$$

Outline

A gallery of examples

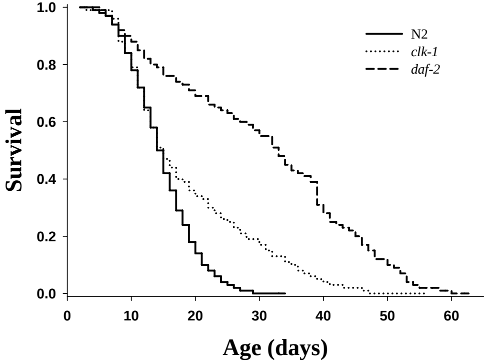
The nematode *Caenorhabditis elegans*

longevity mutants

- *clk*-1
- *daf*-2
- N2 (lab standard)

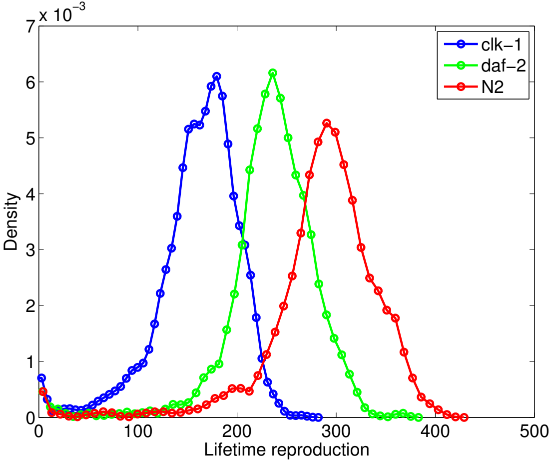
lab cohort study
age-classified
genetically identical

The nematode *Caenorhabditis elegans*



Chen, J., D. Senturk, J.L. Wang, H.G. Muller, J.R. Carey, H. Caswell, and E.P. Caswell-Chen. 2007. A demographic analysis of the fitness cost of extended longevity in *Caenorhabditis elegans*. Journal of Gerontology: Biological Sciences 62A:126-135.

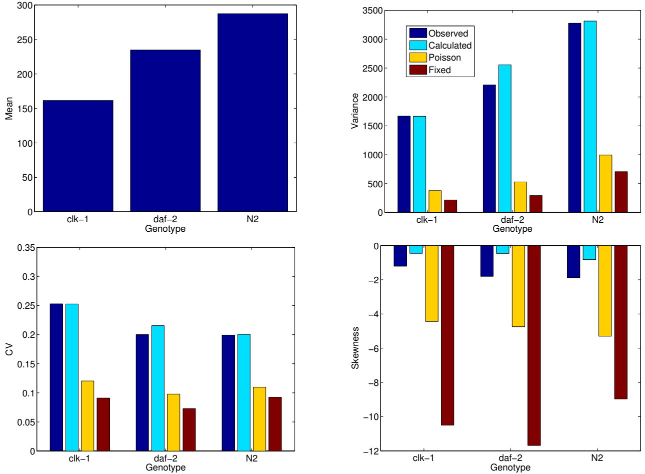
The nematode *Caenorhabditis elegans*



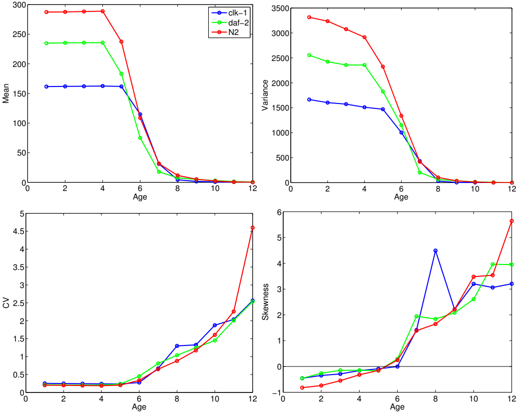
The nematode *Caenorhabditis elegans*

- reward = egg production
- models
  - full measured individual egg production
  - Poisson model
  - fixed reward model
- because it's a cohort study, measured distribution of lifetime reproduction available

The nematode *Caenorhabditis elegans*



The nematode *Caenorhabditis elegans*



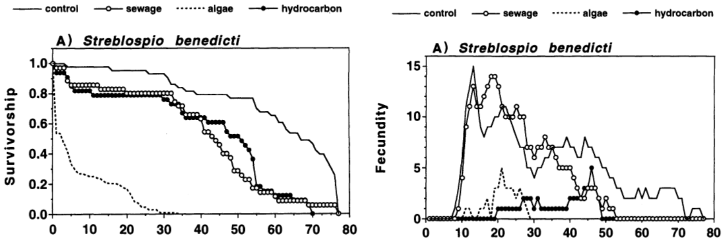
The polychaete *Streblospio benedicti*

pollutant stress response

- control
- sewage
- fuel oil
- blue-green algae

genetically heterogeneous

The polychaete *Streblospio benedicti*

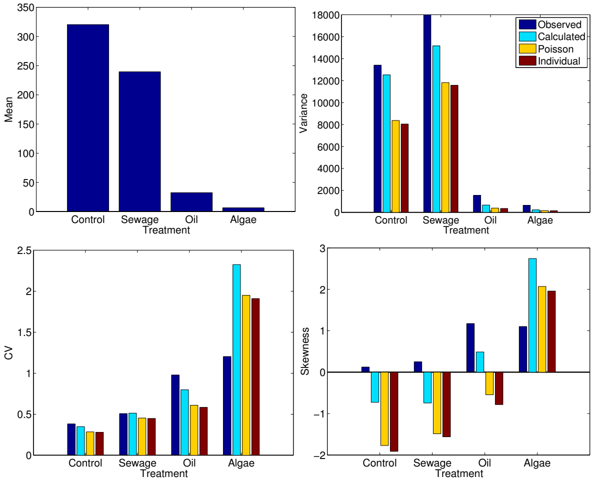


Levin, L. A., H. Caswell, T. Bridges, C. DiBacco, D. Cabrera, and G. Plaia. 1996. Demographic response of estuarine polychaetes to pollutants: Life table response experiments. Ecological Applications 6:1295-1313.

The polychaete *Streblospio benedicti*

- reward = larval production
- models
  - full measured individual larval production
  - Poisson model
  - fixed reward model
- because it's a cohort study, measured distribution of lifetime reproduction available

The polychaete *Streblospio benedicti*



These studies age-classified, with large clutches of offspring. What about an age-classified species with small clutch size?

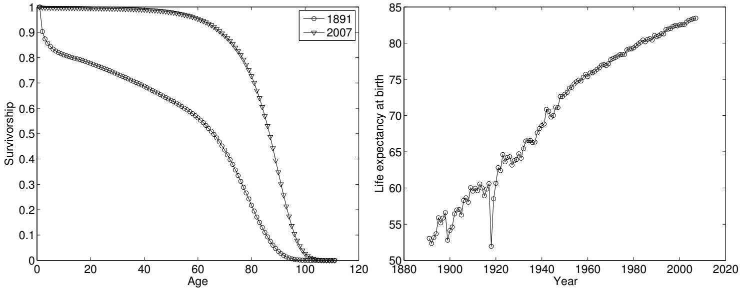
Swedes

- age-classified
- monovular species (more or less)
- time series 1891–2007

The human population of Sweden

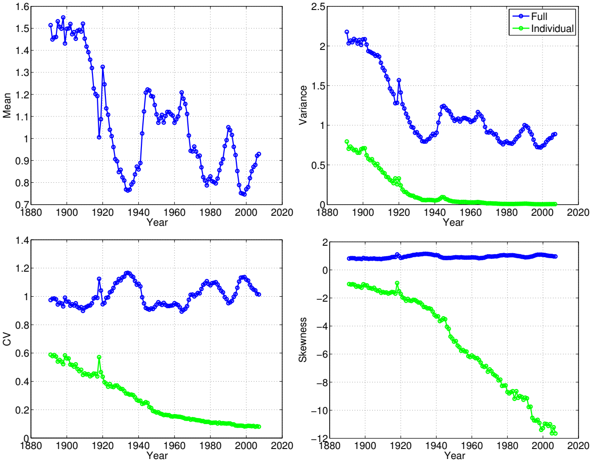
- reward = female births
- models
  - full individual variation (binomial)
  - fixed reward model
- cross-sectional study; no measured distribution of lifetime reproduction

The human population of Sweden



Source: Human Mortality Database

The human population of Sweden



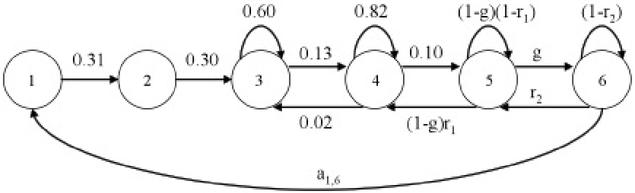
A forest understory plant *Trillium grandiflorum*

stage-classified
pollen-limited
pollen supplementation experiment

- control
- pollen supplementation

A forest understory plant *Trillium grandiflorum*

cross-sectional field study



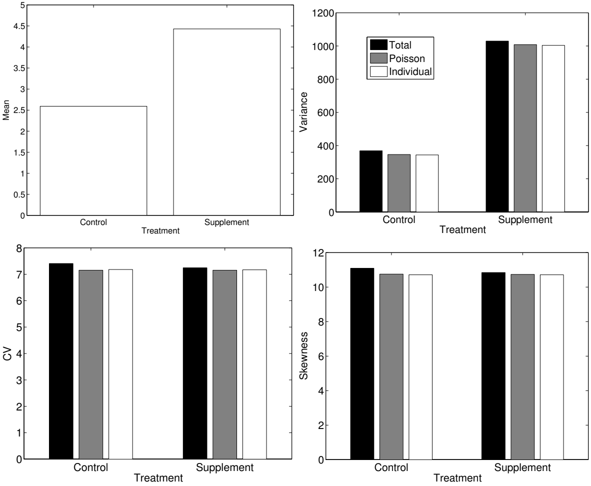
Stages: 1= germinant, 2=seedling, 3=one-leaf, 4=small 3-leaf, 5=large 3-leaf, 6=reproductive.

Knight, T.M. 2004. The effects of herbivory and pollen limitation on a declining population of *Trillium grandiflorum*. Ecological Applications 14:915–928.

A forest understory plant *Trillium grandiflorum*

- stage-classified projection matrix
- reward = seed production
- rewards models
  - full measured seed production
  - Poisson model
  - fixed reward model
- cross-sectional study; no measured distribution of lifetime reproduction available

A forest understory plant *Trillium grandiflorum*



Time-varying models

environmental states

$$E(1) \longrightarrow E(2) \longrightarrow \cdots E(t) \longrightarrow$$

transition matrices

$$\mathbf{P}[E(1)] \longrightarrow \mathbf{P}[E(2)] \longrightarrow \cdots \mathbf{P}[E(t)] \longrightarrow$$

reward matrices

$$\mathbf{R}_i[E(1)] \longrightarrow \mathbf{R}_i[E(2)] \longrightarrow \cdots \mathbf{R}_[E(t)] \longrightarrow$$

Outline

Time-varying models

Classify individuals jointly by stage and by state of the environment:

$$\mathbb{P} = \left(\begin{array}{c|c|c} \mathbf{P}[1] & & \\ \hline & \ddots & \\ \hline & & \mathbf{P}[q] \end{array}\right)$$

$$\mathbb{R}_j = \left(\begin{array}{c|c|c} \mathbf{R}_j[1] & \cdots & \mathbf{R}_j[q] \\ \hline \vdots & & \vdots \\ \hline \mathbf{R}_j[1] & \cdots & \mathbf{R}_j[q] \end{array}\right) \qquad j = 1, 2, 3$$

Time-varying models

$$\mathbb{M} = \left(\begin{array}{c|c|c} \mathbf{M}_1 & & \\ \hline & \ddots & \\ \hline & & \mathbf{M}_s \end{array}\right)$$

where

$$\mathbf{M}_i = \begin{cases} \begin{pmatrix} 0 & 0 & 1 \\ 1 & 0 & 0 \\ 0 & 1 & 0 \end{pmatrix} & \text{periodic} \\ \text{environment transition matrix} & \text{Markovian} \end{cases}$$

Time-varying models

$$\tilde{\mathbf{P}} = \mathbb{M}\mathbf{K}\mathbb{P}\mathbf{K}^{\mathsf{T}}$$

$$\tilde{\mathbf{R}}_j = \mathbb{R}_j\mathbf{K}^{\mathsf{T}} \qquad j = 1, 2, 3.$$

where **K** is the vec-permutation matrix
Calculations proceed as before.

Hunter and Caswell (2005) Ecological Modelling 188:15-21.
Caswell (2009) Oikos 118:1763-1782

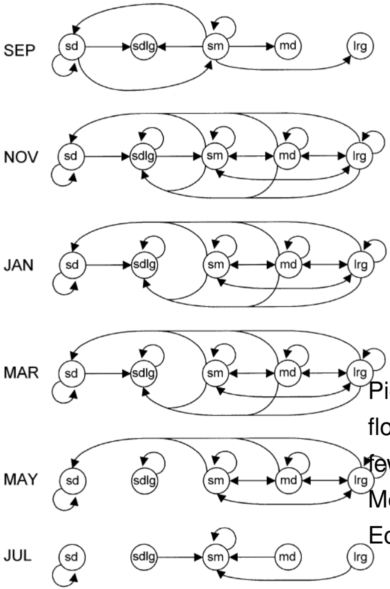
Outline

Let's look at some examples

A perennial plant *Lobularia maritima* in a seasonal environment

- short-lived perennial
- Mediterranean basin
- extended flowering period (10 months)
- periodic seasonal model

Lobularia maritima in a seasonal environment



- cross-sectional field study
- 6 seasons (2 months each)
- stages
  - seeds
  - seedlings
  - small adults
  - medium adults
  - large adults

Pico et al. 2002. An extended flowering and fruiting season has few demographic effects in a Mediterranean perennial herb. Ecology 83:1991–2004.

Lobularia maritima in a seasonal environment

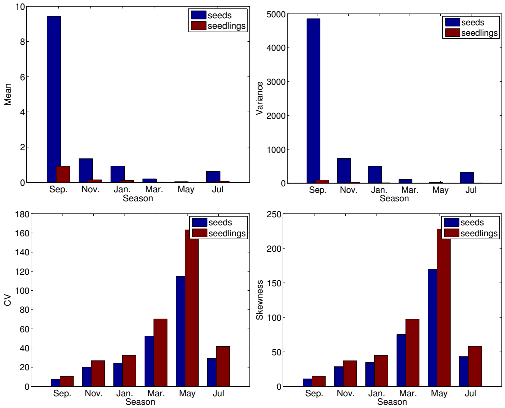
- periodic time-varying matrix model

$$\tilde{\mathbf{P}} = \mathbb{M}\mathbf{K}^{\mathsf{T}}\mathbb{P}\mathbf{K}$$

$$\mathbf{M} = \begin{pmatrix} 0 & 0 & 0 & 0 & 0 & 1 \\ 1 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 \end{pmatrix}$$

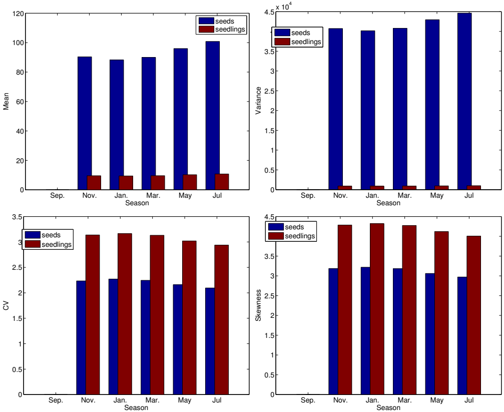
- rewards
  - seed production
  - seedling production
- reward models
  - Poisson model
  - fixed reward model
- "treatment" = season of origin

Lobularia maritima – reproduction by seeds



Poisson and fixed reward models nearly identical.

Lobularia maritima – reproduction by seedlings



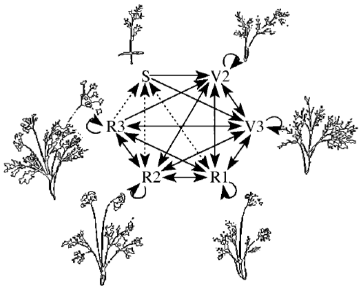
Poisson and fixed reward models nearly identical.

A prairie plant *Lomatium bradshawii* in a stochastic fire environment

- endangered perennial prairie plant
- dependent on frequent fires

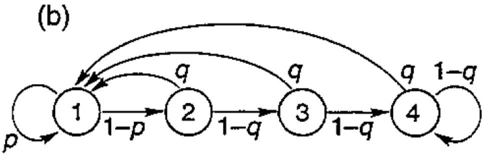
Caswell, H. and T.N. Kaye 2001. Stochastic demography and conservation of an endangered perennial plant (*Lomatium bradshawii* in a dynamic fire regime. Advances in Ecological Research 23:1–51.

Lomatium bradshawii in a stochastic fire environment



- cross-sectional field study
- experimental fire treatments
- stages
  - yearling vegetative plants
  - small vegetative
  - large vegetative
  - small reproductive
  - medium reproductive
  - large reproductive

Lomatium bradshawii in a stochastic fire environment



Environmental states

- 1 = year of fire
- 2 = 1 year post-fire
- 3 = 2 years post-fire
- 4 = $\geq$ 3 years post-fire

Lomatium bradshawii in a stochastic fire environment

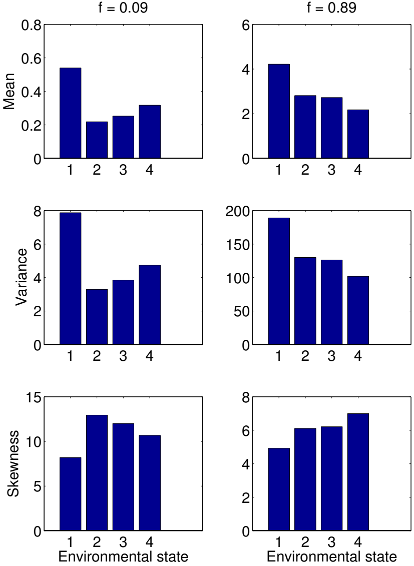
- stochastic stage-classified model

$$\tilde{\mathbf{P}} = \mathbb{M}\mathbf{K}^{\mathsf{T}}\mathbb{P}\mathbf{K}$$

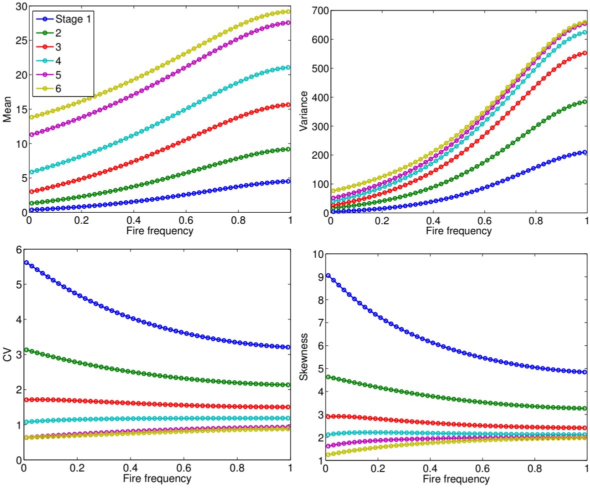
$$\mathbf{M} = \begin{pmatrix} p & q & q & q \\ 1-p & 0 & 0 & 0 \\ 0 & 1-q & 0 & 0 \\ 0 & 0 & 1-q & 1-q \end{pmatrix}$$

- rewards = reproduction of new yearlings
- reward models
  - Poisson model
  - fixed reward model
- “treatments” = fire frequency, initial environmental state

Lomatium bradshawii in a stochastic fire environment



Lomatium bradshawii in a stochastic fire environment



Outline

Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & i = a, j \neq a \\ 0 & \text{otherwise} \end{cases}$$

Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & j \neq a \\ 0 & j = a \end{cases}$$

Some other interesting rewards

transient states $1, \ldots, s$
absorbing state a

$$r_{ij} = \begin{cases} 1 & j \neq a \\ 0 & j = a \end{cases}$$

Some other interesting rewards

transient states $1, \ldots, s$, absorbing state a

$$r_{ij} = \begin{cases} 1 - \delta_j & j \neq a \\ 0 & j = a \end{cases}$$

where δ_j is prevalence of disability in stage j

Disability-free life expectancy and moments of DF longevity (equivalent to Sullivan method [?], but not restricted to age-classification or to means).

Some other interesting rewards

transient states $1, \ldots, s$, absorbing state a

$$r_{ij} = \begin{cases} Q_j & j \neq a \\ 0 & j = a \end{cases}$$

where Q_j measures quality of life in stage j

Mean and moments of Quality-Adjusted Life Years (I think).

Some topics for further research

- Sensitivity analysis
- Multivariate rewards
- Application to health status, quality of life, economic costs
- Connection to optimization via dynamic programming

Conclusions

- it works
- there appear to be patterns
- permits generalizations of R_0 and variability to time-varying environments
- other kinds of rewards
  - health status (health expectancy, quality-adjusted life years)
  - economic costs (treatment of illness or disability)
- open problems: connection to population dynamics, perturbation analysis
- I am eager to hear about possible applications.

Thanks to National Science Foundation for funding.