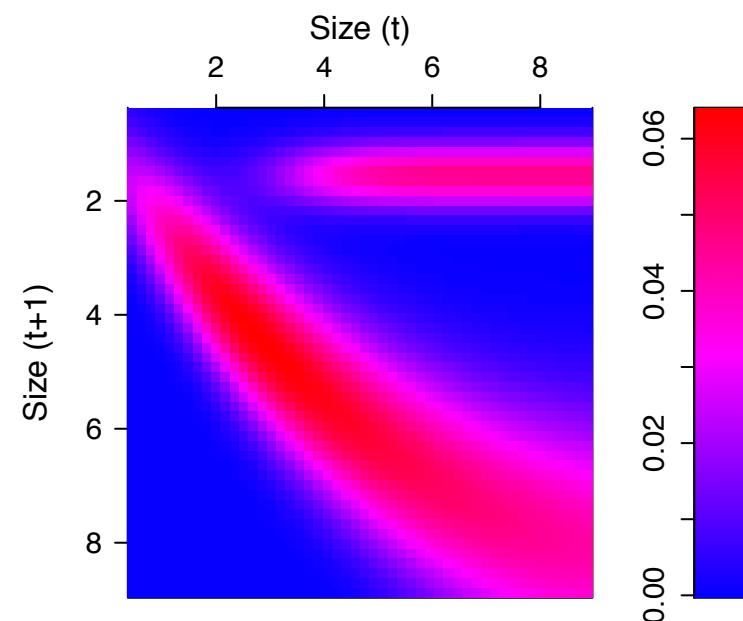


# AN INTRODUCTION TO INTEGRAL PROJECTION MODELS (IPMS)

---

Cory Merow  
Eelke Jongejans  
Sean McMahon  
Jessica Metcalf  
Rob Salguero-Gomez



# IPMs for stage-structured demography

## Process-based demography:

- Accurately represent stage structure
- Decompose life history to desired level of detail
- Link vital rates to environment or other covariates
- Include heterogeneity in vital rates

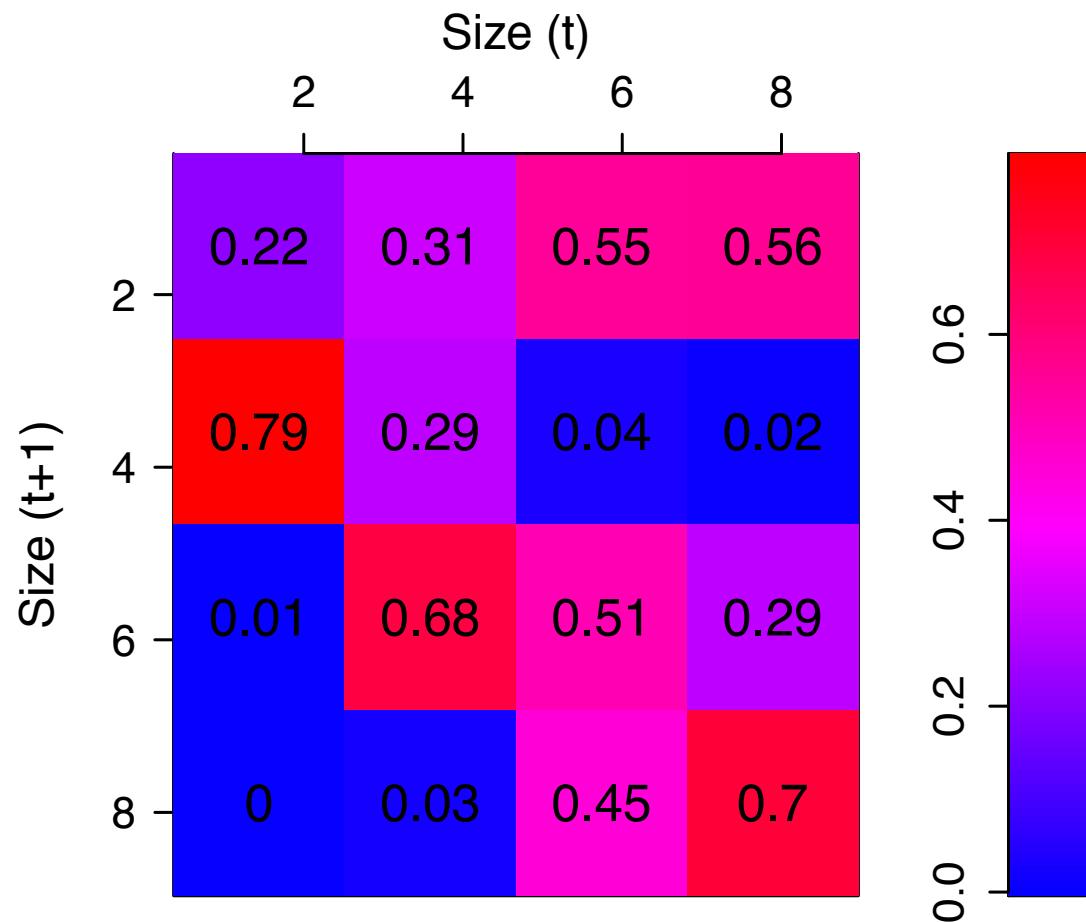
# What is an IPM?

Lefkovich matrix for a long-lived perennial plant

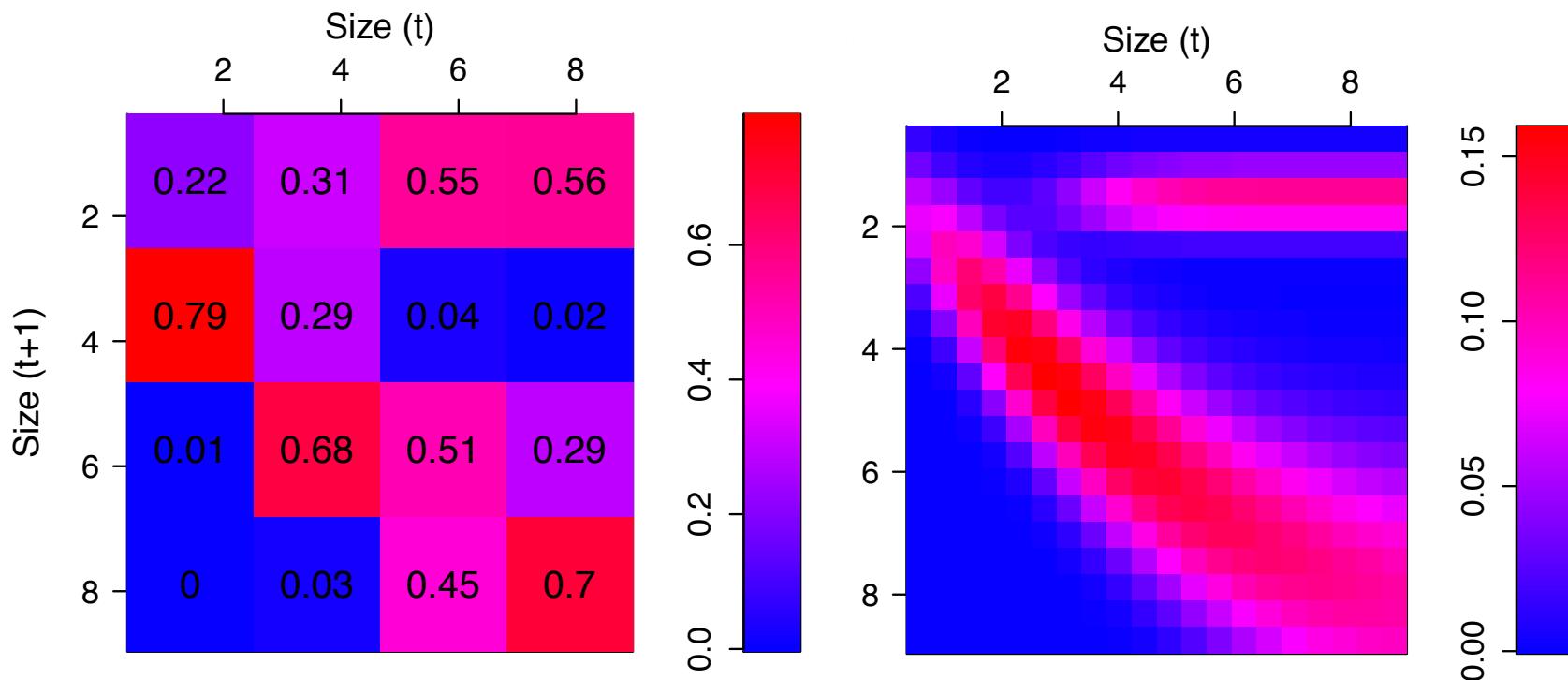
	Recruit	Juvenile	Non-flowering adult	Flowering adult
Recruit	0	0	0	4.074
Juvenile	0.093	0.667	0.098	0
Non-flowering adult	0	0.304	0.713	0.494
Flowering adult	0	0	0.180	0.503

# What is an IPM?

Lefkovich matrix for a long-lived perennial plant

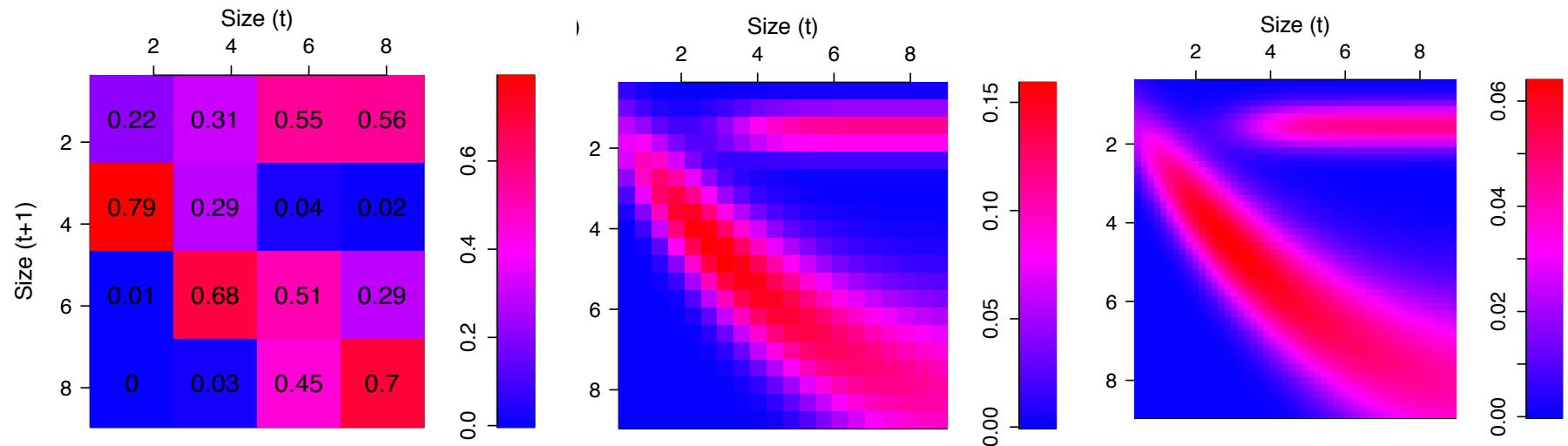


# What is an IPM?



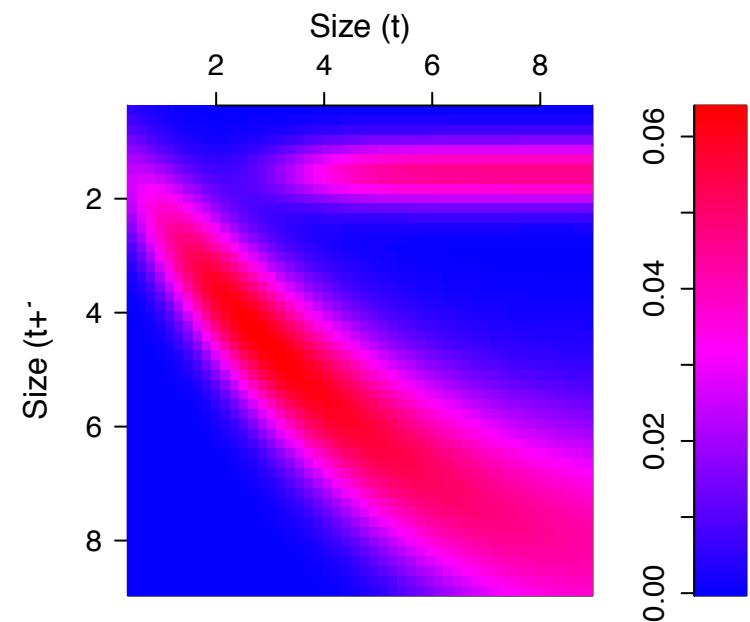
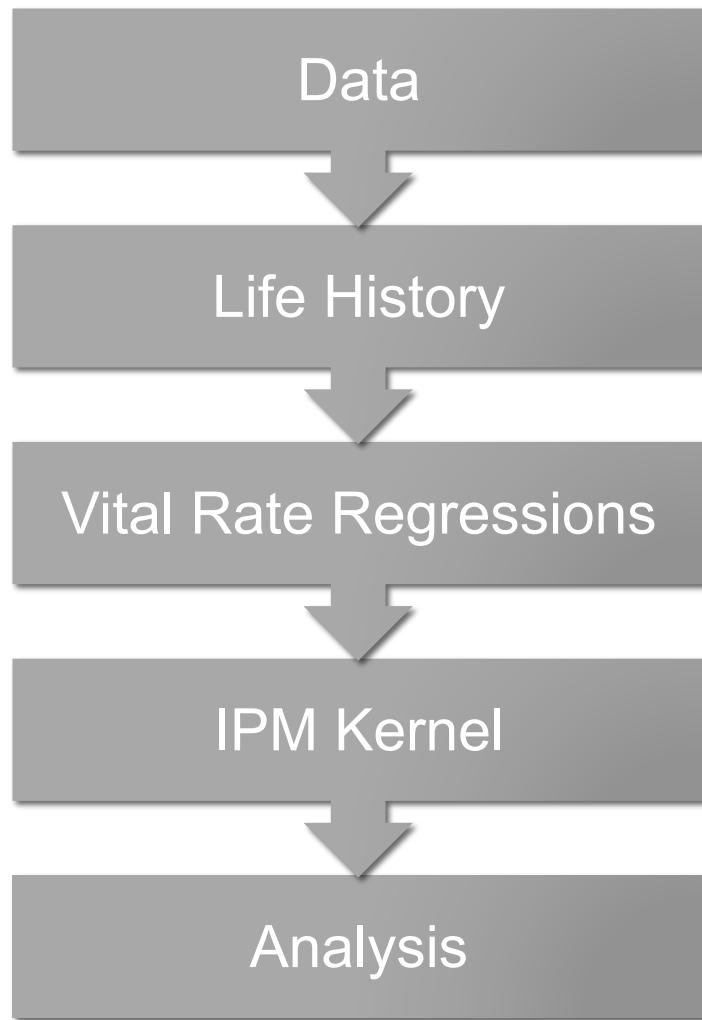
More stages = more heterogeneity

# What is an IPM?



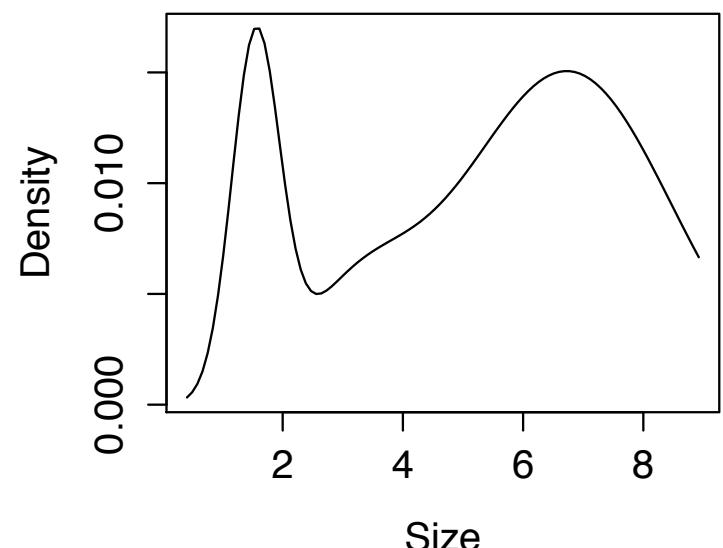
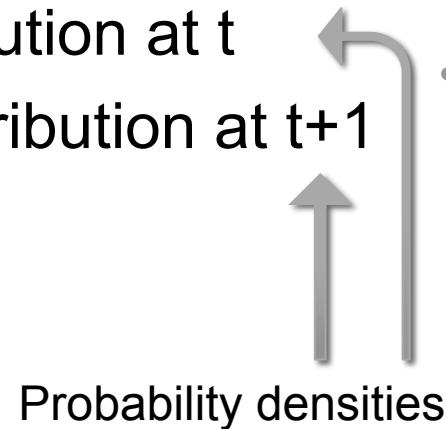
Matrix models and IPMs arrive at matrices for  
different reasons

# Workflow



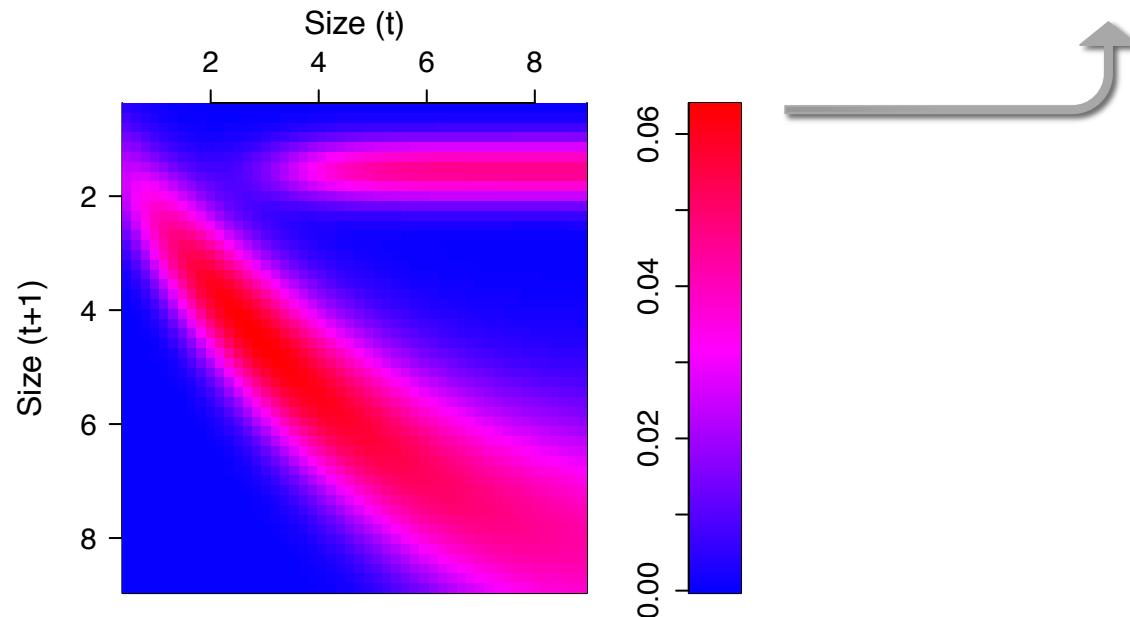
# The model

- $t$  = time
  - $x$  = size at  $t$
  - $y$  = size at  $t+1$
  - $n(x,t)$  = size distribution at  $t$
  - $n(y,t+1)$  = size distribution at  $t+1$
- $K(x,y)$  = full kernel
  - $P(x,y)$  = growth/survival kernel
  - $F(x,y)$  = fecundity kernel



# The model

- $t$  = time
- $x$  = size at  $t$
- $y$  = size at  $t+1$
- $n(x,t)$  = size distribution at  $t$
- $n(y,t+1)$  = size distribution at  $t+1$
- $K(x,y)$  = full kernel
- $P(x,y)$  = growth/survival kernel
- $F(x,y)$  = fecundity kernel



# The model

- $t$  = time
  - $x$  = size at  $t$
  - $y$  = size at  $t+1$
  - $n(x,t)$  = size distribution at  $t$
  - $n(y,t+1)$  = size distribution at  $t+1$
- $K(x,y)$  = full kernel
  - $P(x,y)$  = growth/survival kernel
  - $F(x,y)$  = fecundity kernel

$$\mathbf{n}(t+1) = \mathbf{A} \quad \mathbf{n}(t) \quad (Matrix)$$

$$n(y,t+1) = \int_{\substack{\text{all} \\ \text{sizes}}} K(y,x) \ n(x,t) dx \quad (IPM)$$

# The model

- $t$  = time
- $x$  = size at  $t$
- $y$  = size at  $t+1$
- $n(x,t)$  = size distribution at  $t$
- $n(y,t+1)$  = size distribution at  $t+1$
- $K(x,y)$  = full kernel
- $P(x,y)$  = growth/survival kernel
- $F(x,y)$  = fecundity kernel

$$\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \quad (Matrix)$$

$$n(y,t+1) = \int_{\substack{\text{all} \\ \text{sizes}}} K(y,x) n(x,t) dx \quad (IPM)$$

$$n(y,t+1) = \int_{\substack{\text{all} \\ \text{sizes}}} [P(x,y) + F(x,y)] n(x,t) dx$$

# The model

- $t$  = time
- $x$  = size at  $t$
- $y$  = size at  $t+1$
- $n(x,t)$  = size distribution at  $t$
- $n(y,t+1)$  = size distribution at  $t+1$
- $K(x,y)$  = full kernel
- $P(x,y)$  = growth/survival kernel
- $F(x,y)$  = fecundity kernel

$$\mathbf{n}(t+1) = \mathbf{A} \mathbf{n}(t) \quad (Matrix)$$

$$n(y,t+1) = \int_{\substack{\text{all} \\ \text{sizes}}} K(y,x) n(x,t) dx \quad (IPM)$$

$$n(y,t+1) = \int_{\substack{\text{all} \\ \text{sizes}}} [P(x,y) + F(x,y)] n(x,t) dx$$

$$size(y)_{t+1} = \int_{\substack{\text{all} \\ \text{sizes}}} [growth(size x \rightarrow y) + offspring(size x \rightarrow y)] size(x)_t dx$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 1: Shrub

$$\begin{aligned} P(x, y) &= (\text{survival probability at size } x) * (\text{growth from } x \text{ to } y) \\ &= s(x) * g(x, y) \end{aligned}$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 1: Shrub

$$\begin{aligned} P(x, y) &= (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= s(x) * g(x, y) \end{aligned}$$

$$\begin{aligned} F(x, y) &= (\text{mean # seeds of size } x \text{ parent}) * \\ &\quad (\text{establishment probability}) \\ &\quad (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \\ &= f_{\text{seeds}}(x) * p_{\text{estab}} * f_{\text{recruit}}(x, y) \end{aligned}$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 1: Shrub

$$\begin{aligned} P(x, y) &= (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= s(x) * g(x, y) \end{aligned}$$

$$\begin{aligned} F(x, y) &= (\text{mean # seeds of size } x \text{ parent}) * \\ &\quad (\text{establishment probability}) \\ &\quad (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \\ &= f_{\text{seeds}}(x) * p_{\text{estab}} * f_{\text{recruit}}(x, y) \end{aligned}$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 1: Shrub

$$\begin{aligned} P(x, y) &= (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= \boxed{s(x)} * \boxed{g(x, y)} \end{aligned}$$

$$\begin{aligned} F(x, y) &= (\text{mean # seeds of size } x \text{ parent}) * \\ &\quad (\text{establishment probability}) \\ &\quad (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \\ &= \boxed{f_{\text{seeds}}(x) * p_{\text{estab}}} * \boxed{f_{\text{recruit}}(x, y)} \end{aligned}$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 2: Monocarpic perennial

$$\begin{aligned} P(x, y) &= ([\text{not}] \text{ flowering probability of size } x \text{ parent})^* \\ &\quad (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= [1 - p_{\text{flower}}(x)] * s(x) * g(x, y) \end{aligned}$$

# Life History

$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 2: Monocarpic perennial

$$\begin{aligned} P(x, y) &= ([\text{not}] \text{ flowering probability of size } x \text{ parent})^* \\ &\quad (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= [1 - p_{\text{flower}}(x)] * s(x) * g(x, y) \end{aligned}$$

$$\begin{aligned} F(x, y) &= (\text{flowering probability of size } x \text{ parent})^* \\ &\quad (\text{mean # recruits of size } x \text{ parent})^* \\ &\quad (\text{establishment probability})^* \\ &\quad (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \\ &= p_{\text{flower}}(x) * f_{\text{recruits}}(x) * p_{\text{estab}} * f_{\text{recruit}}(x, y) \end{aligned}$$

# Life History

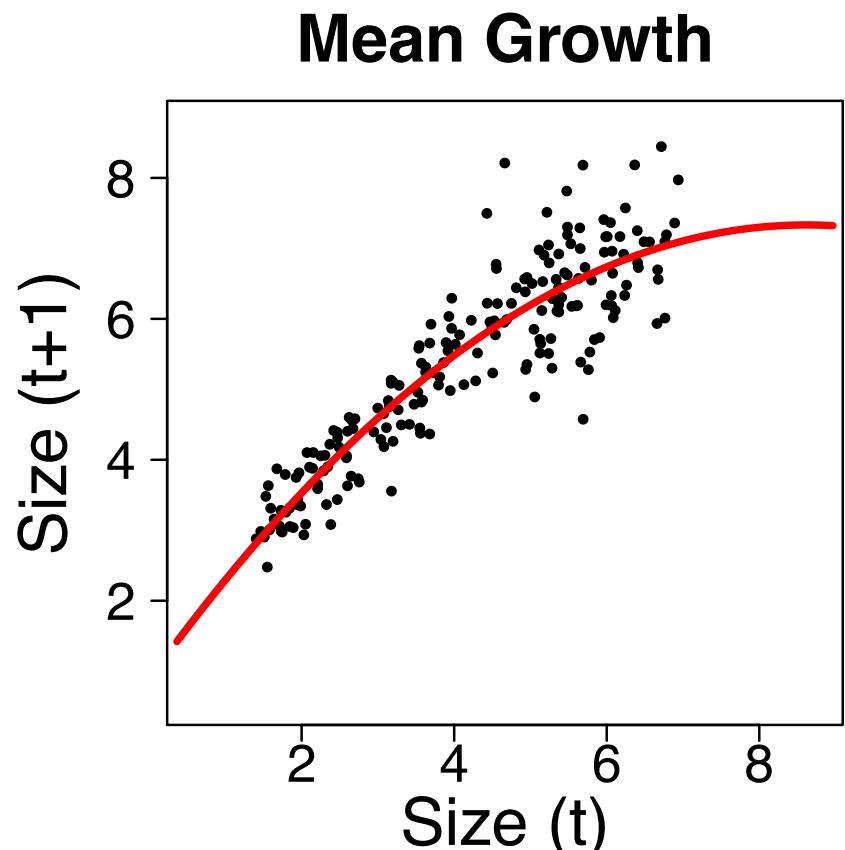
$$n(y, t+1) = \int_{\Omega} [P(x, y) + F(x, y)] n(x, t) dx$$

Example 2: Monocarpic perennial

$$\begin{aligned} P(x, y) &= (\text{[not] flowering probability of size } x \text{ parent}) * \\ &\quad (\text{survival at size } x) * (\text{growth from } x \text{ to } y) \\ &= [1 - p_{\text{flower}}(x)] * s(x) * g(x, y) \end{aligned}$$

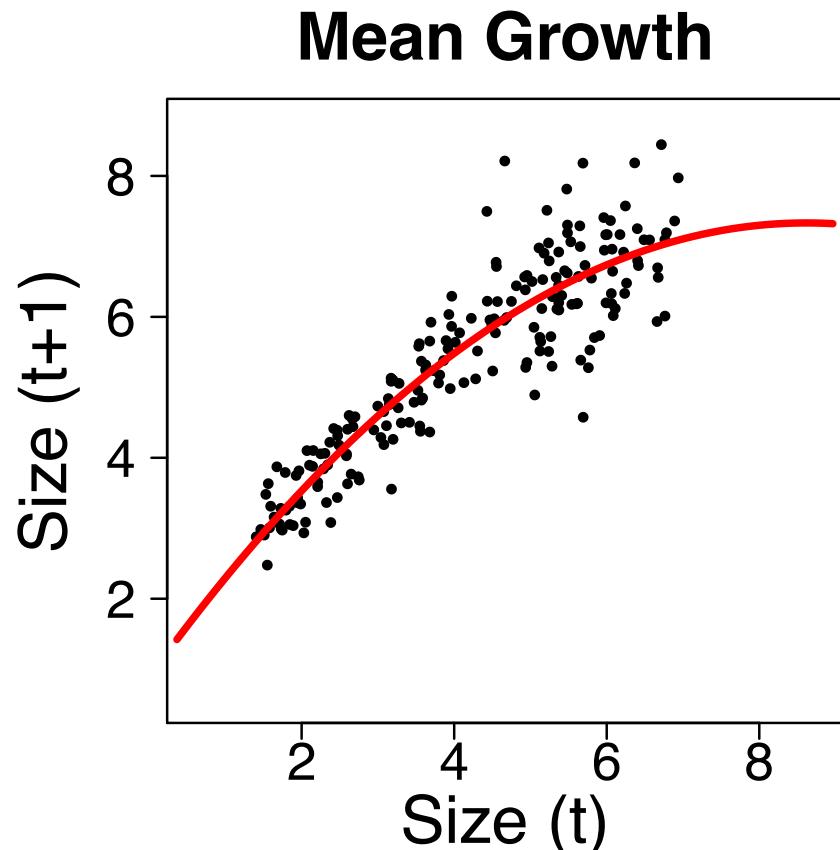
$$\begin{aligned} F(x, y) &= (\text{flowering probability of size } x \text{ parent}) * \\ &\quad (\text{mean # recruits of size } x \text{ parent}) * \\ &\quad (\text{establishment probability}) * \\ &\quad (\text{probability of size } y \text{ offspring from size } x \text{ parent}) \\ &= p_{\text{flower}}(x) * f_{\text{recruits}}(x) * p_{\text{estab}} * f_{\text{recruit}}(x, y) \end{aligned}$$

# Vital Rate Regression: Growth – $g(x,y)$

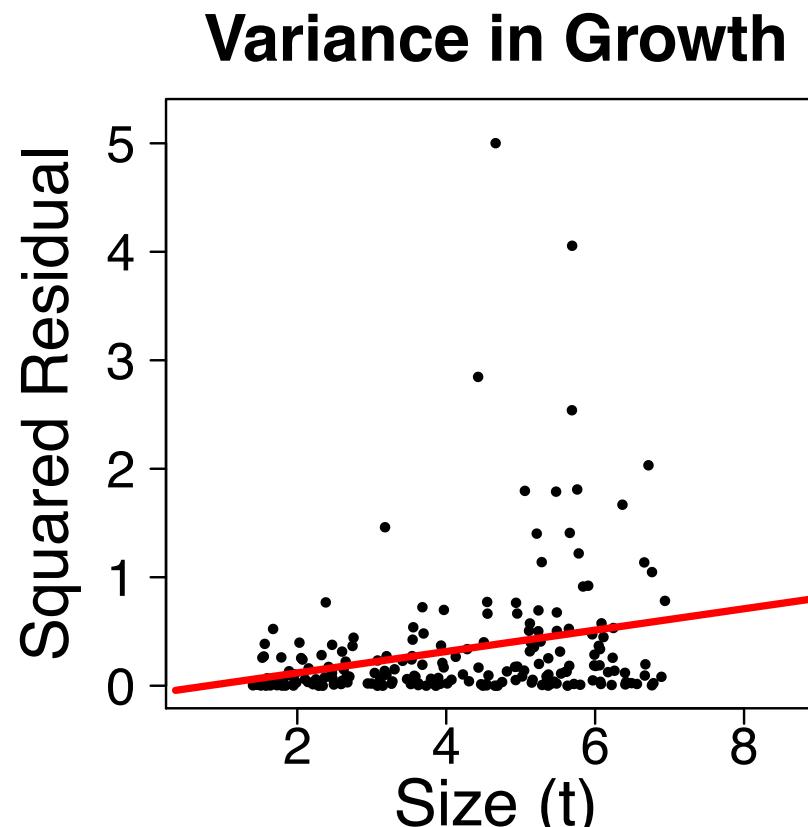


$$\mu(x) = b_0 + b_1 x + b_2 x^2$$

# Vital Rate Regression: Growth – $g(x,y)$

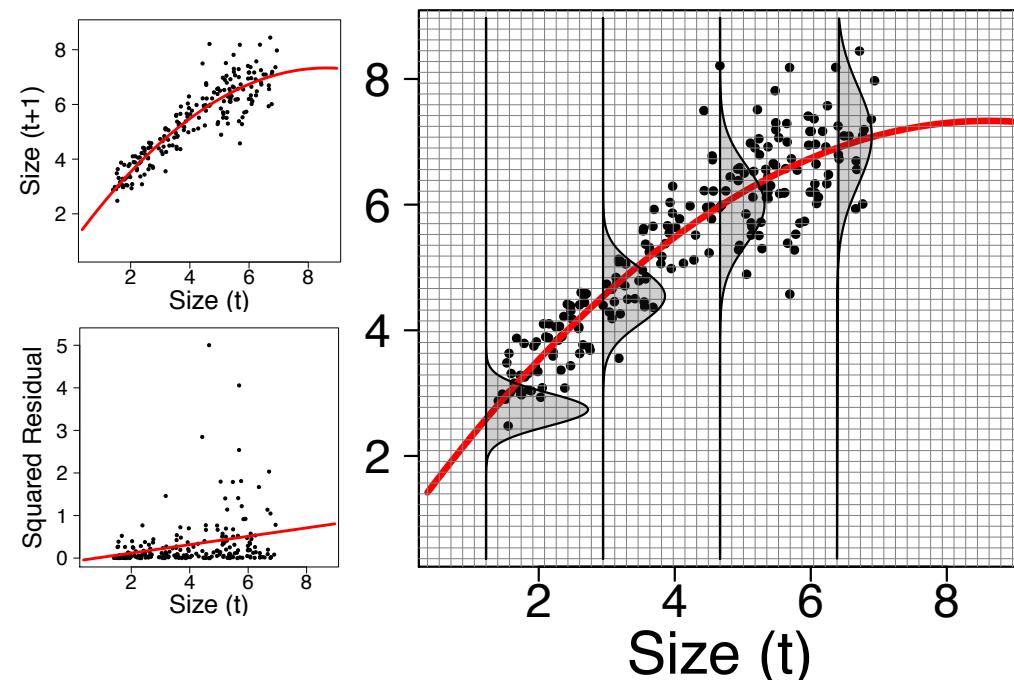


$$\mu(x) = b_0 + b_1 x + b_2 x^2$$

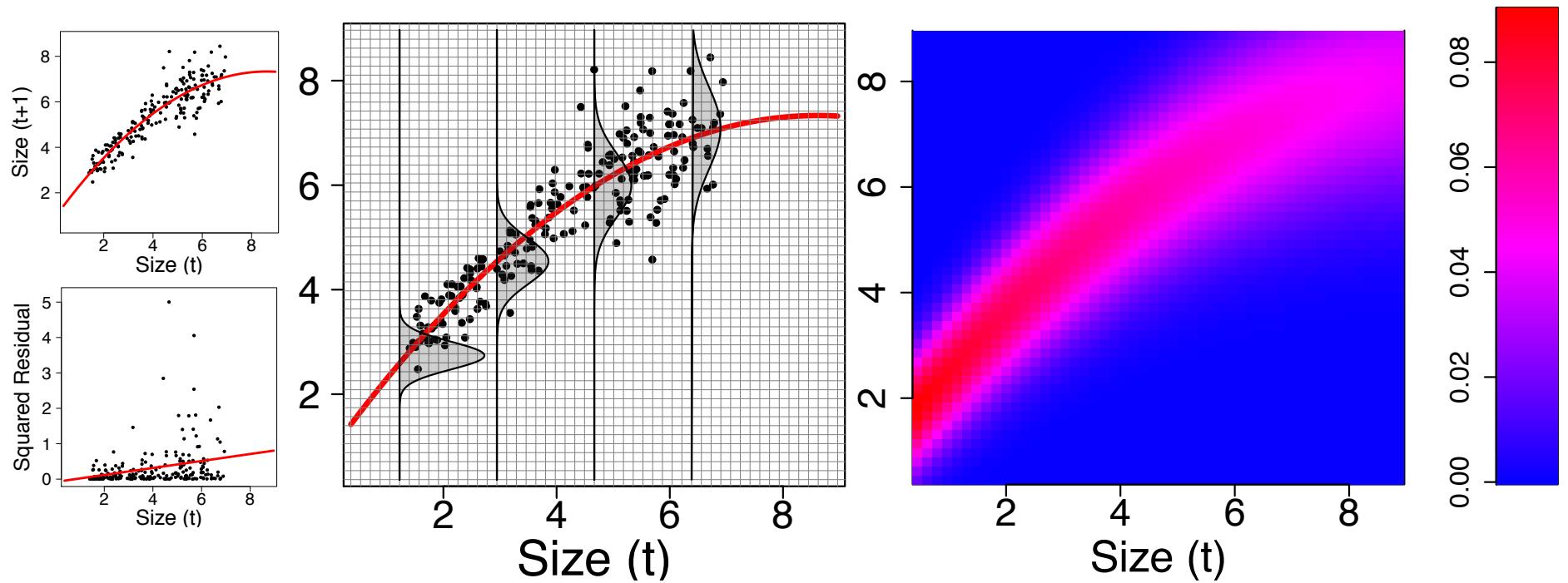


$$\sigma(x) = a_0 + a_1 x$$

# Vital Rate Regression: Growth – $g(x,y)$

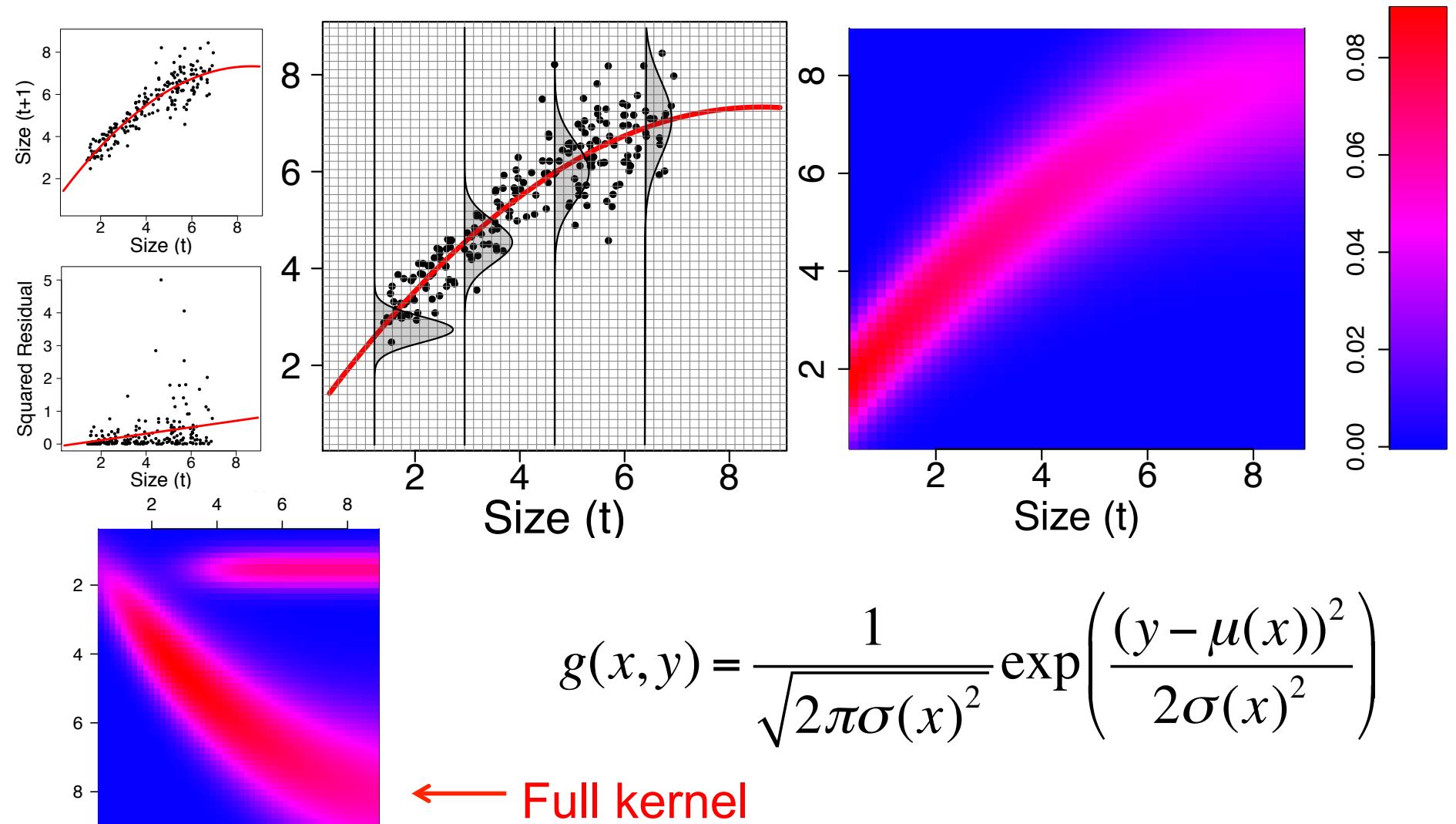


# Vital Rate Regression: Growth – $g(x,y)$



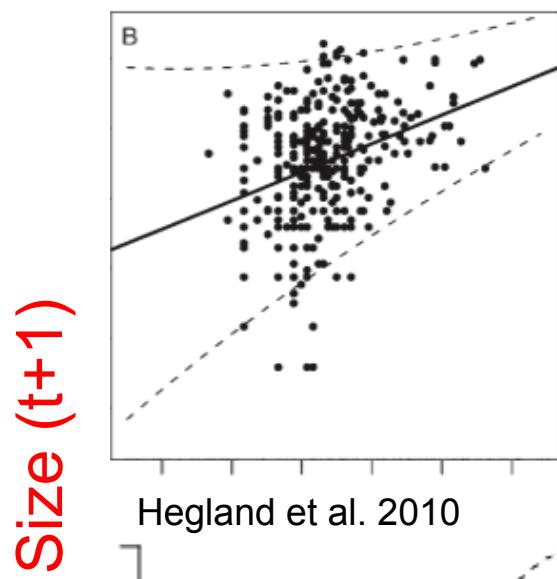
$$g(x, y) = \frac{1}{\sqrt{2\pi\sigma(x)^2}} \exp\left(-\frac{(y - \mu(x))^2}{2\sigma(x)^2}\right)$$

# Vital Rate Regression: Growth – $g(x,y)$

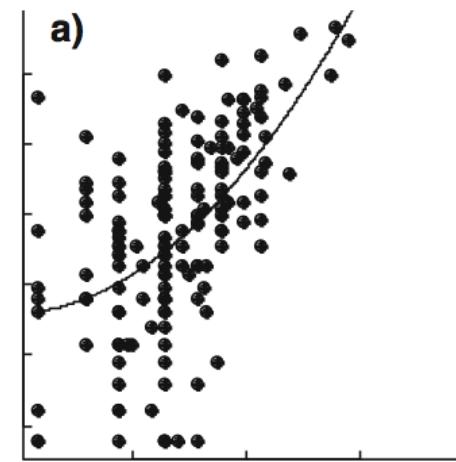


# Vital Rate Regression: Growth – $g(x,y)$

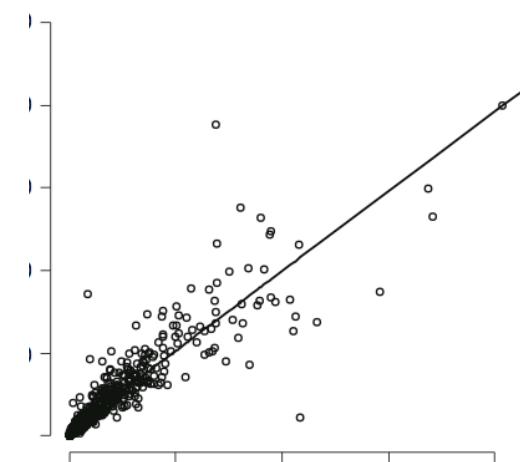
Jongejans et al. 2011



Metcalf et al. 2008

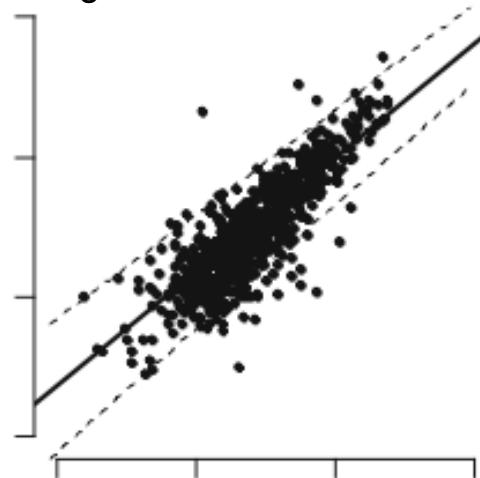


Ferrer-Cervantes et al. 2012

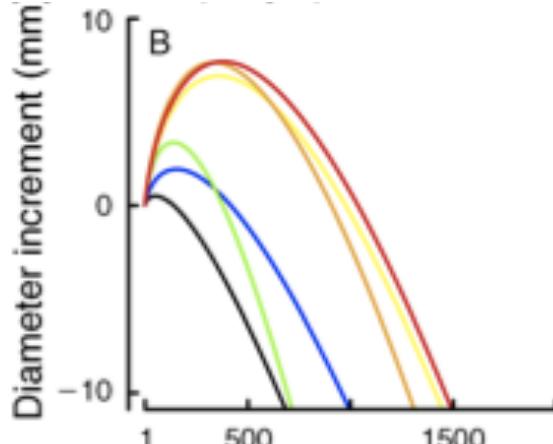
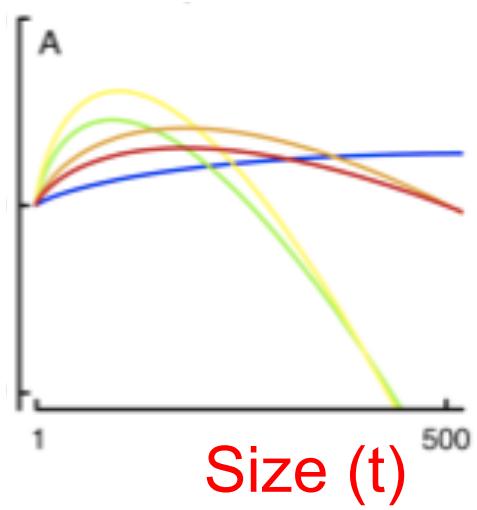


Size ( $t+1$ )

Hegland et al. 2010



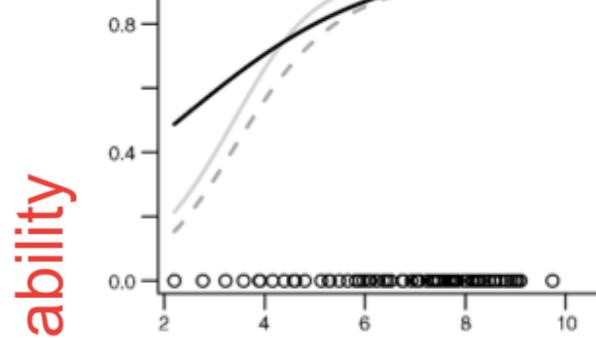
Metcalf et al. 2009



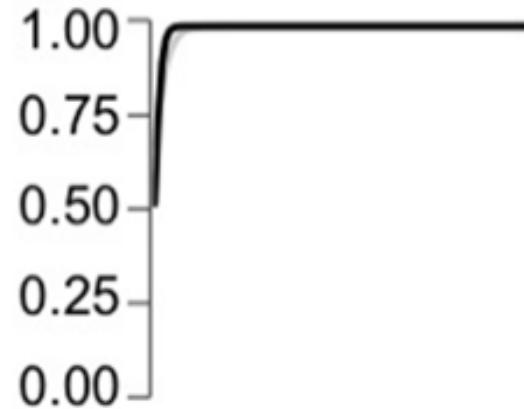
Size ( $t$ )

# Vital Rate Regression: Survival – $s(x)$

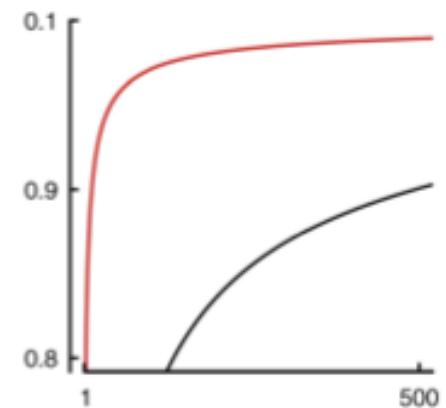
Dahlgren et al. 2011



Salguero-Gomez et al. 2012

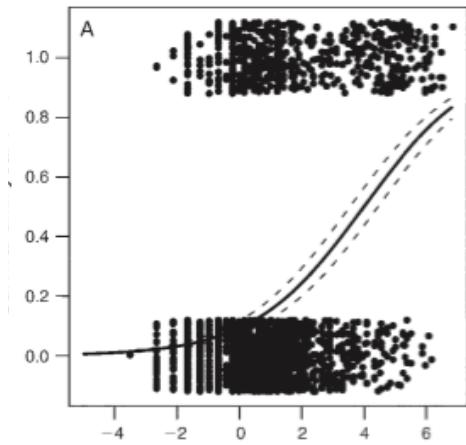


Metcalf et al. 2009

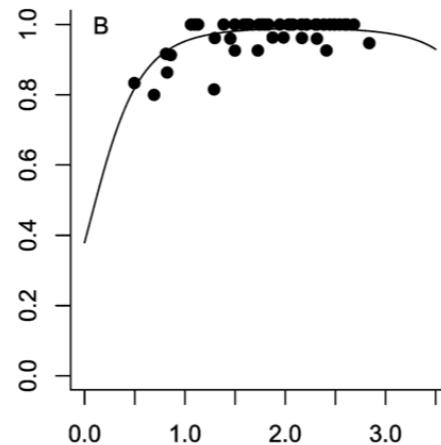


Survival Probability

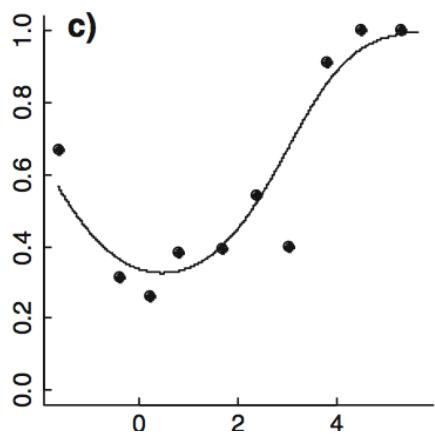
Jongejans et al. 2011



Hesse et al. 2008

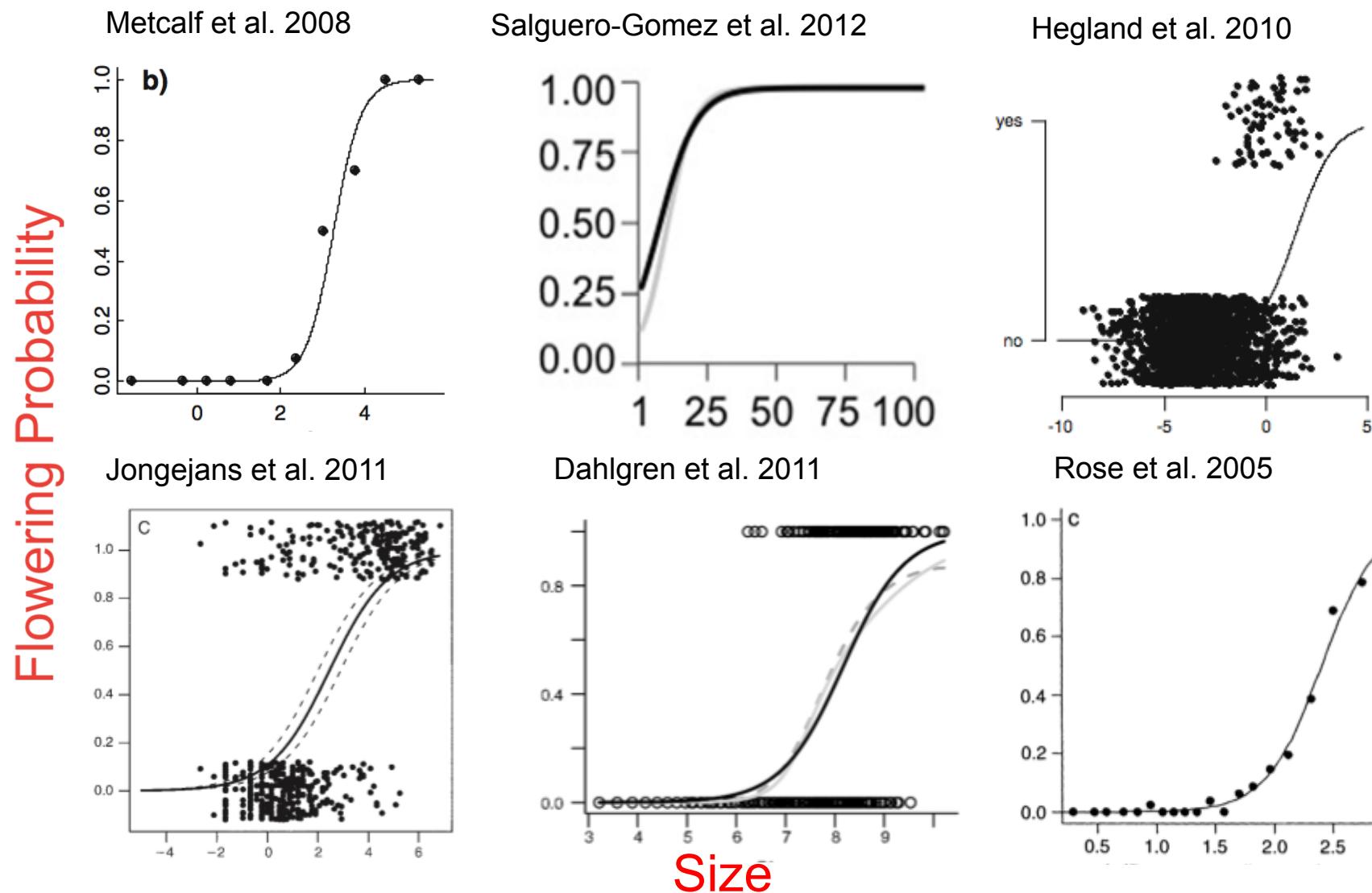


Metcalf et al. 2008



Size

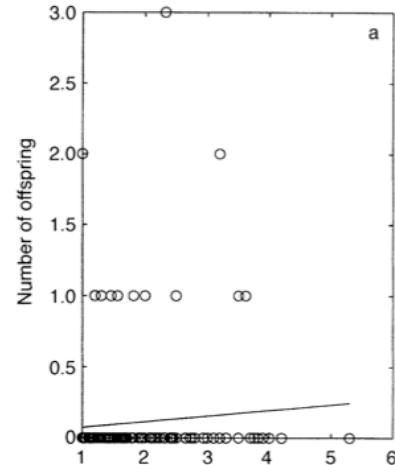
# Vital Rate Regression: Flowering – $p_{\text{flower}}(x)$



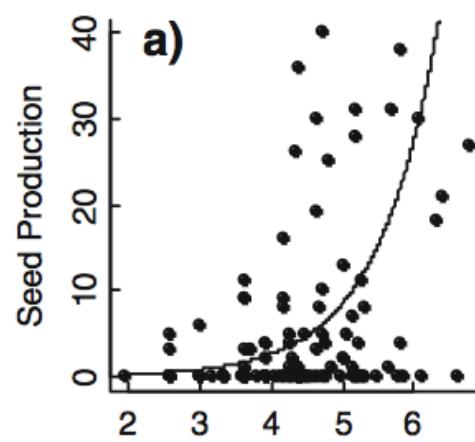
# Vital Rate Regression: Fecundity – $f_{\text{seeds}}(x)$

Easterling et al. 2000

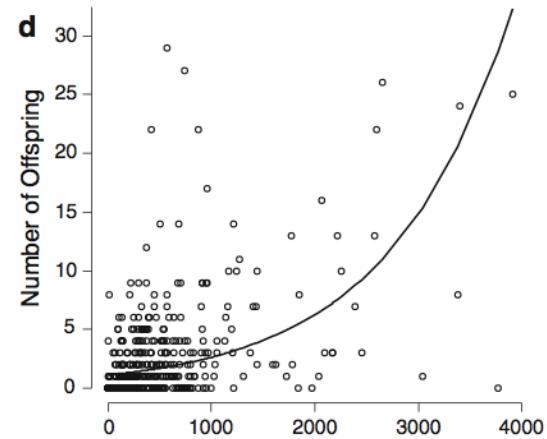
Number of Babies



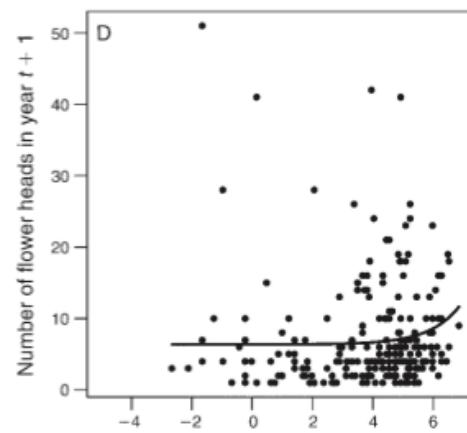
Metcalf et al. 2009



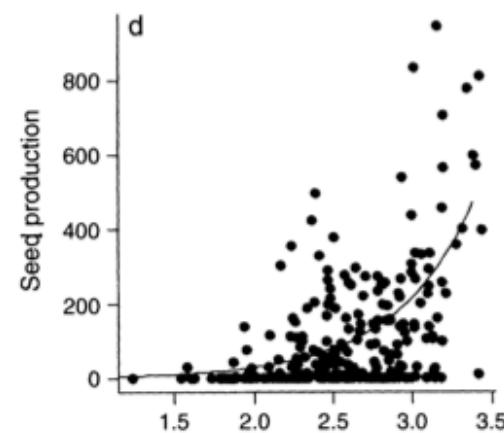
Ferrer-Cervantes et al. 2012



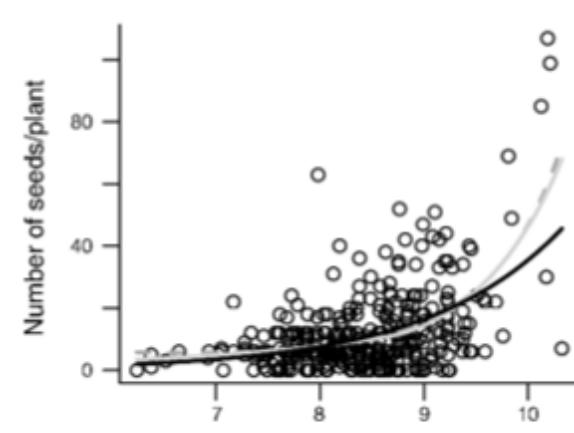
Jongejans et al. 2011



Rose et al. 2005



Dahlgren et al. 2011

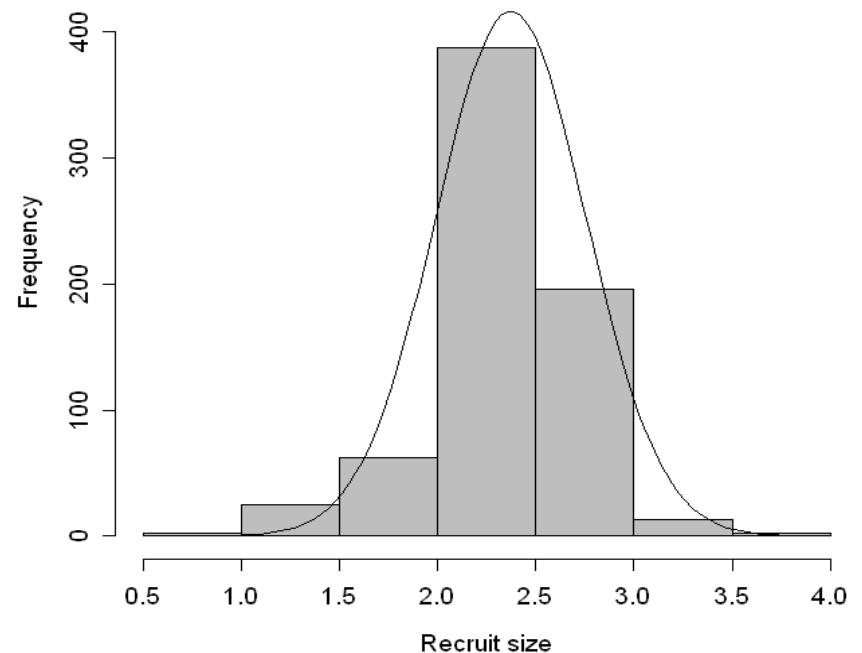


Size

# Vital Rate Regression: Fecundity – $f_{recruit}(x,y)$

*Usually...*

$$f_{recruit}(y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(-\frac{(y-\mu)^2}{2\sigma^2}\right)$$



# Vital Rate Regression: Fecundity – $f_{\text{recruit}}(x,y)$

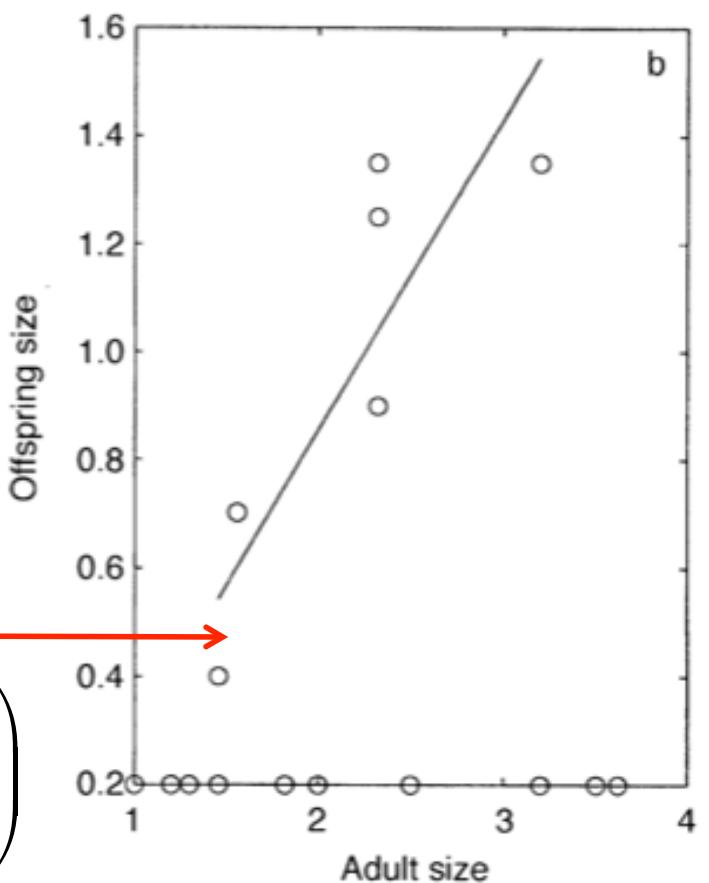
*Usually...*

$$f_{\text{recruit}}(y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y-\mu)^2}{2\sigma^2}\right)$$

*but sometimes...*

$$\mu(x) = ax + b$$

$$f_{\text{recruit}}(x,y) = \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(y-(ax+b))^2}{2\sigma^2}\right)$$

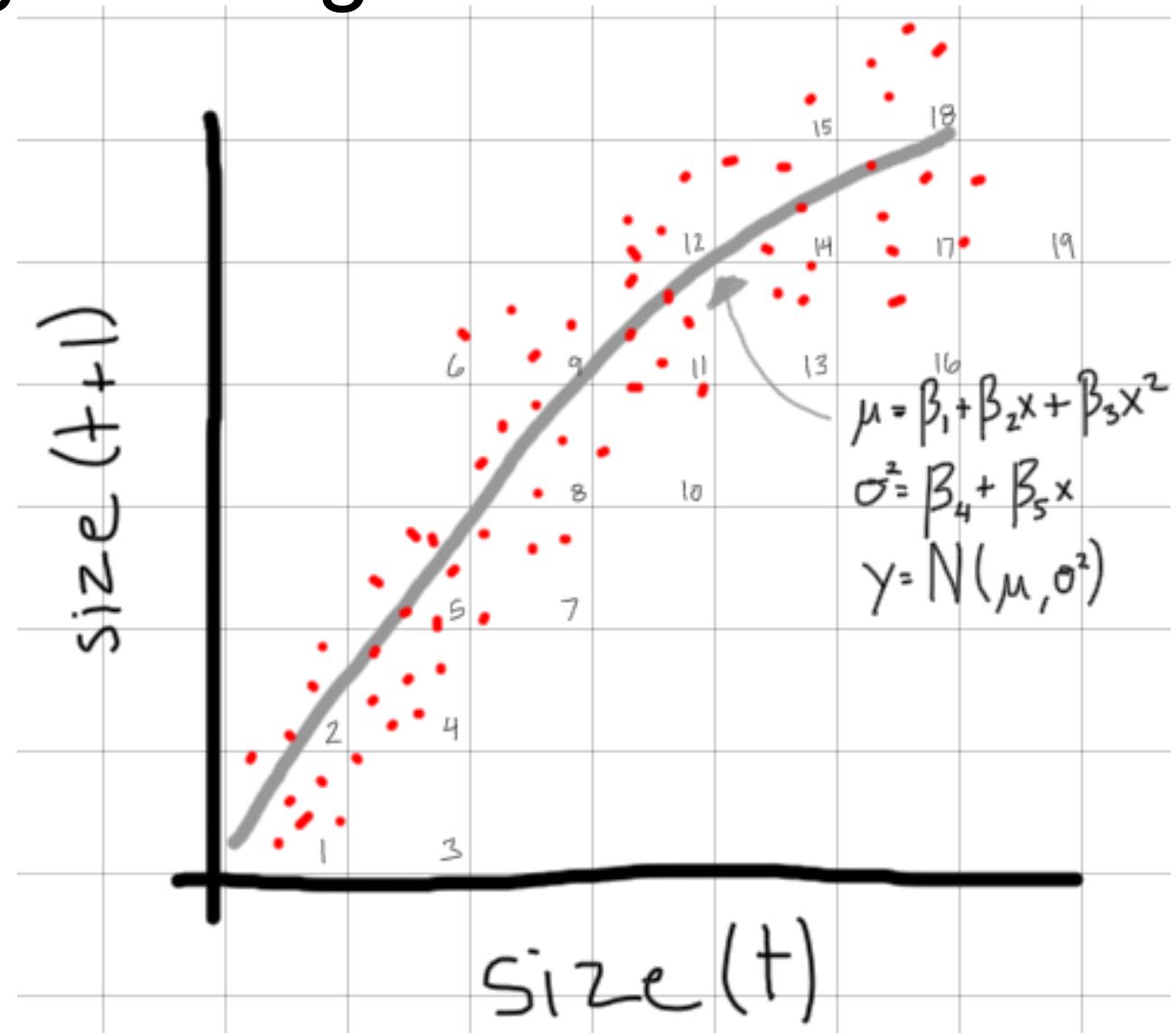


Easterling et al. 2000

Lots of advantages to using regression....

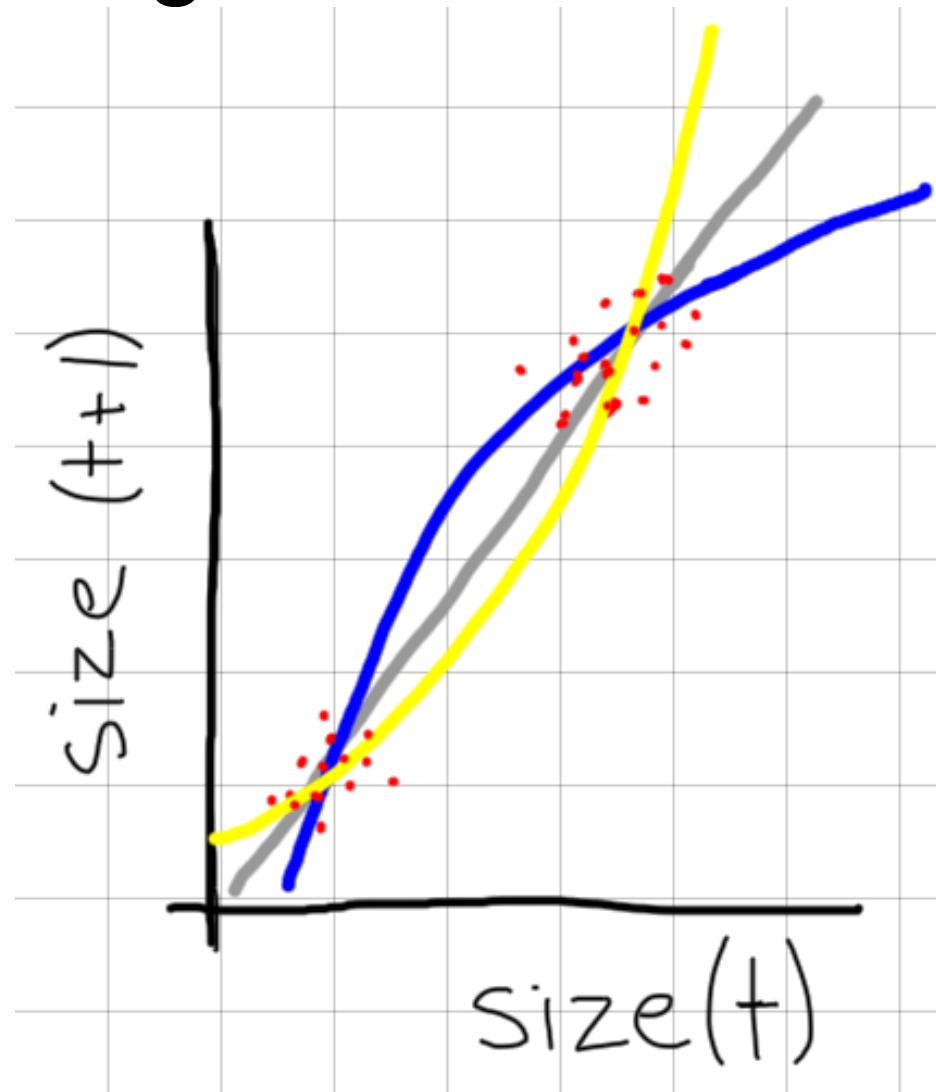
# Advantages of regression

IPMs have  
relatively few  
parameters



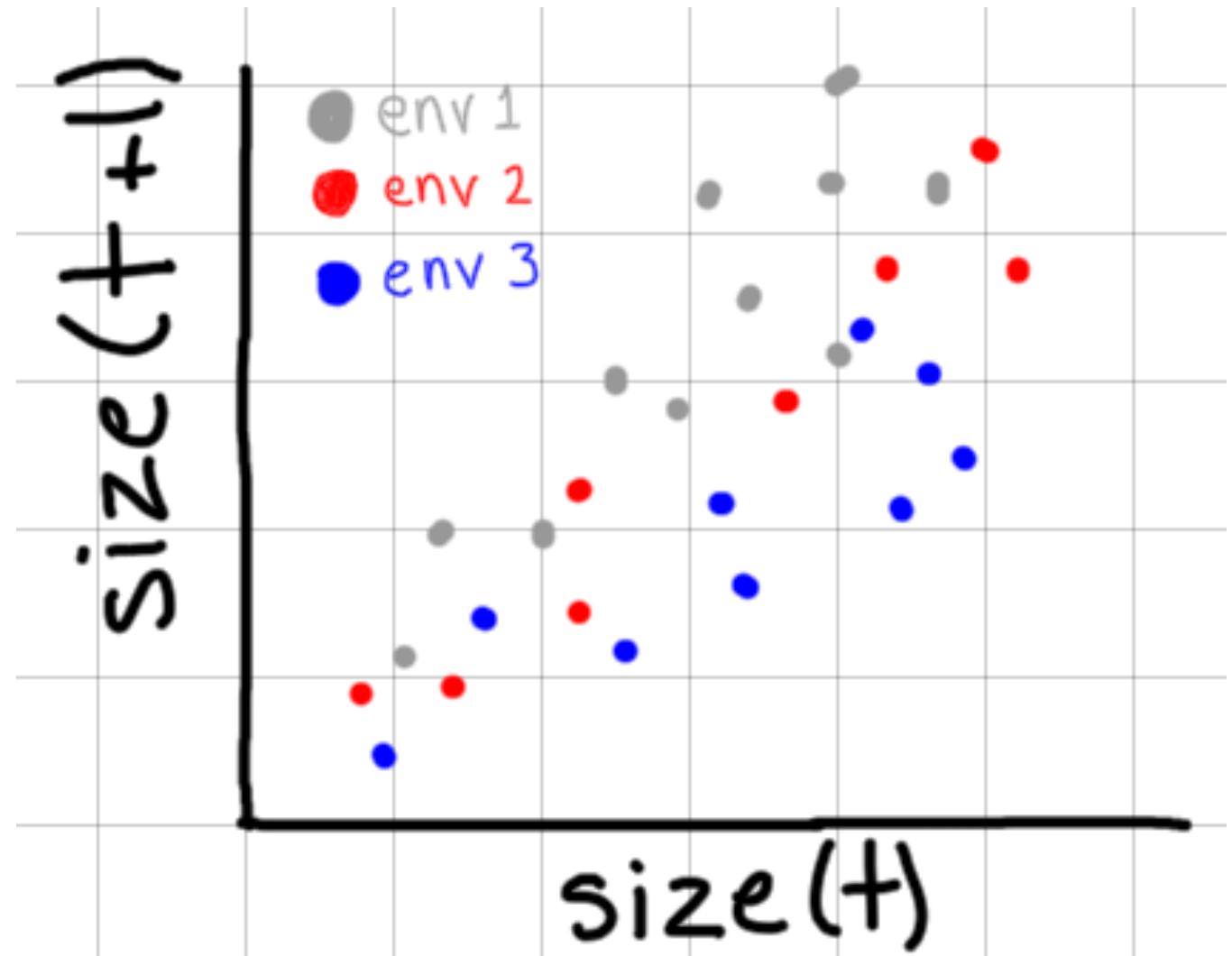
# Advantages of regression

Borrow strength  
across stages



# Advantages of regression

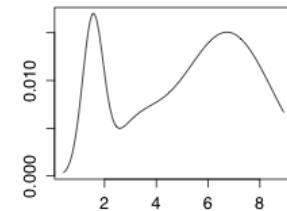
Borrow  
strength  
across  
environments



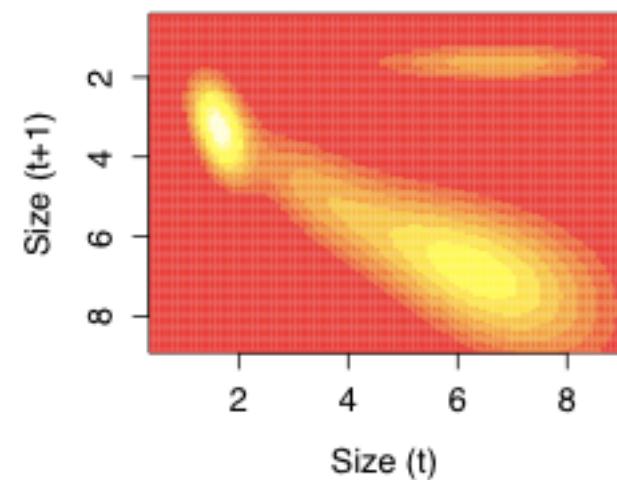
# Analysis

- Want the same things from IPMs as from matrix models
  - Eigenvalues
  - Eigenfunction (vectors)
- Can do all the same analyses with IPMs as matrix models
  - Elasticity/sensitivity
  - Forward projections
  - Stochastic dynamics
  - Life table response experiments
  - Etc...

$$\lambda$$



Elasticity



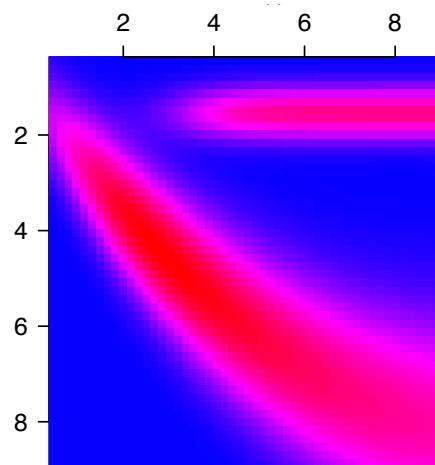
# Full kernel function

$$size(y)_{t+1} = \int_{all\ sizes} [growth(size\ x \rightarrow y) + offspring(size\ x \rightarrow y)]\ size(x)_t dx$$

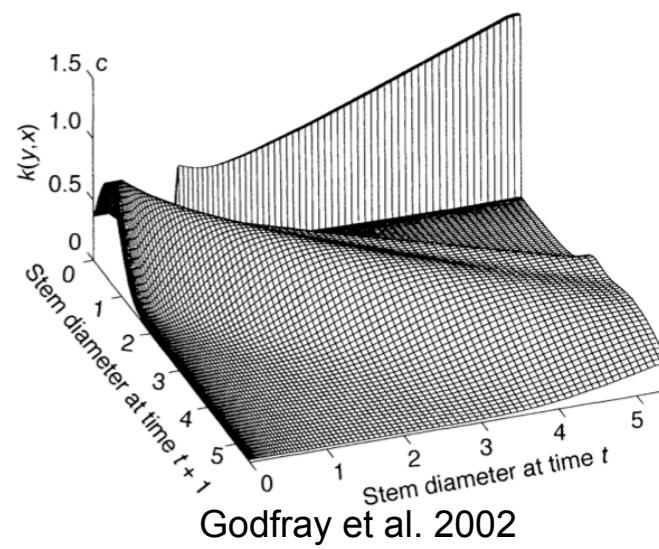
$$n(y, t+1) = \int_{\Omega} \left[ \logit(a_s x + b_s) * \frac{1}{\sqrt{2\pi(a_{g\sigma}x + b_{g\sigma})^2}} \exp\left(\frac{(x - (a_{g\mu}x + b_{g\mu}))}{2(a_{g\sigma}x + b_{g\sigma})^2}\right) + \right. \\ \left. \exp(a_{f\#}x + b_{f\#}) * \frac{1}{\sqrt{2\pi\sigma^2}} \exp\left(\frac{(x - (a_f x + b_f))^2}{2\sigma^2}\right) \right] n(x, t) dx$$

# Full kernel function

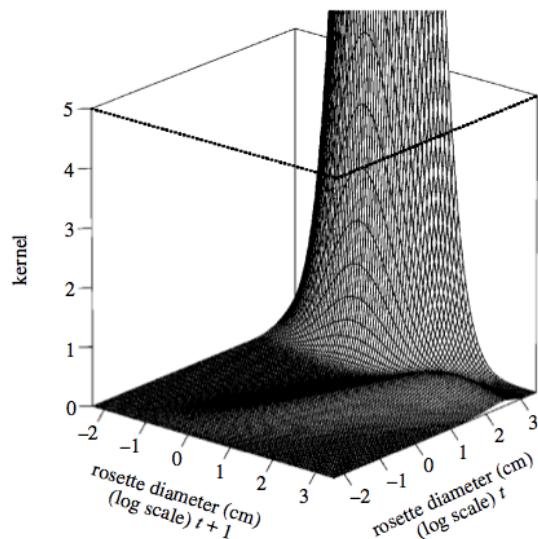
~Nicolé et al. 2011



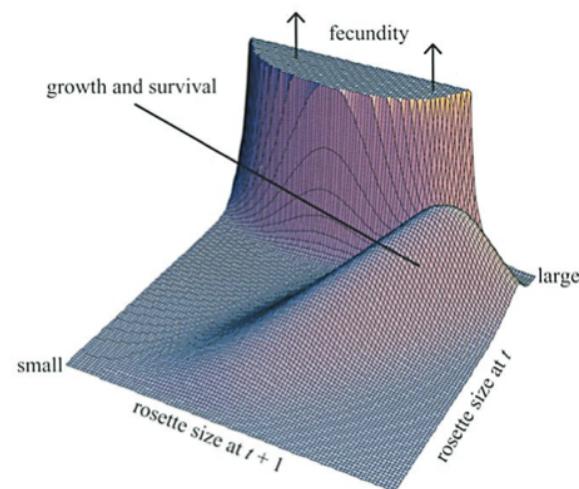
Easterling et al. 2000



Rees et al. 2002

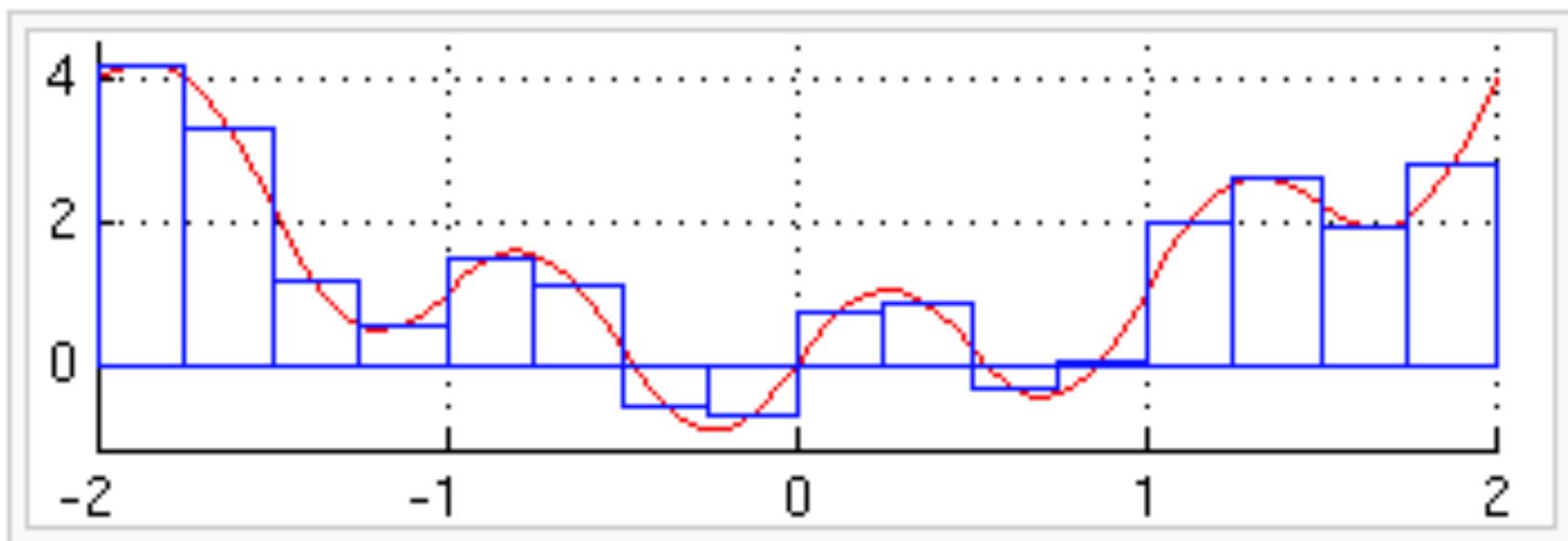


Godfray et al. 2002



# Numerical integration

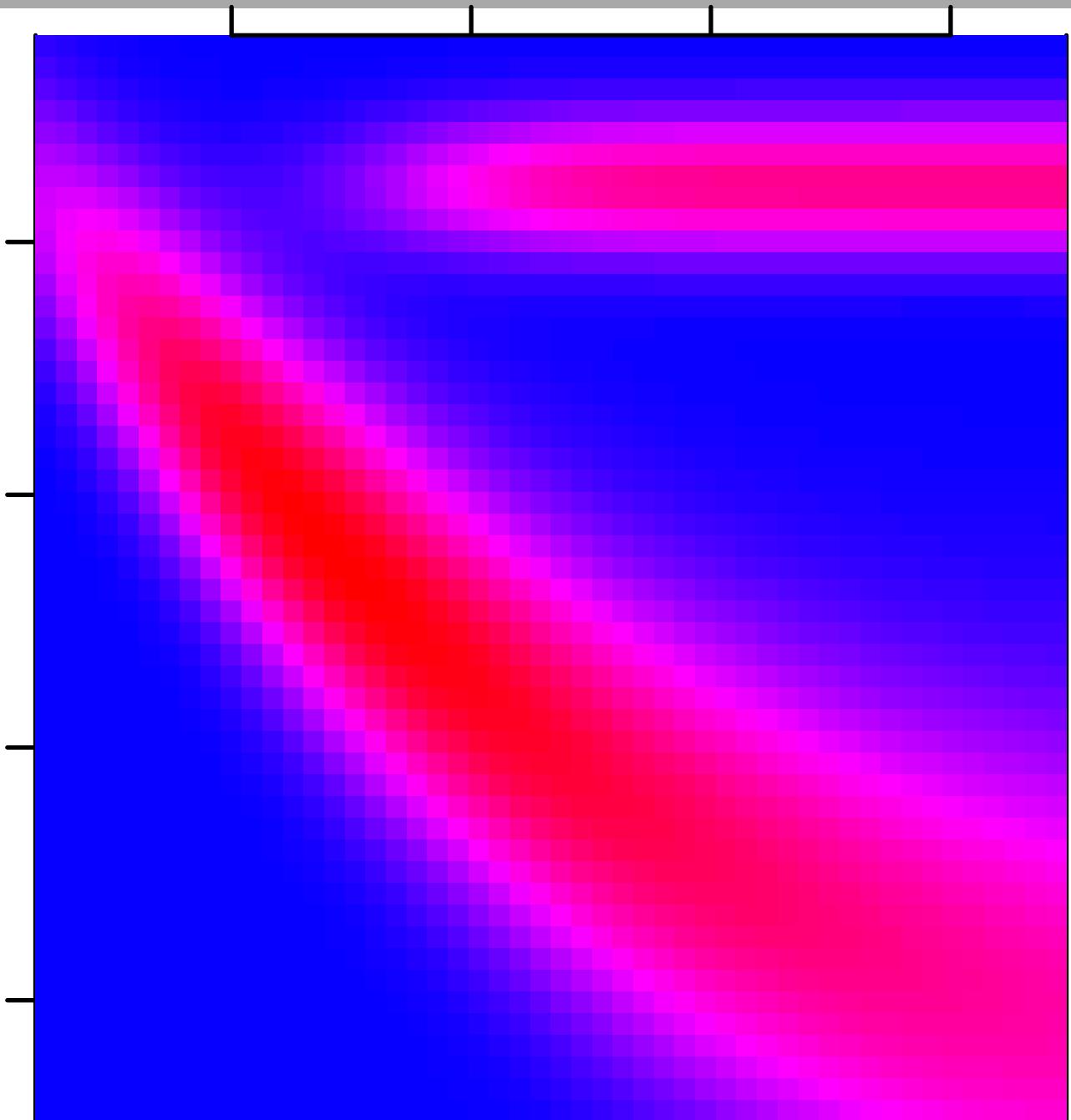
Midpoint rule



IPMs discretize for numerical integration

# Numerical integration

Evaluate kernel at midpoint of each cell to obtain a large matrix



# Numerical integration

Evaluate kernel at midpoint of each cell to obtain a large matrix

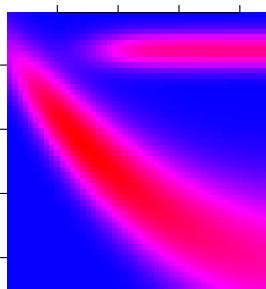
$$n(y, t+1) = \int_{\Omega} K(y, x) n(x, t) dx$$

↓

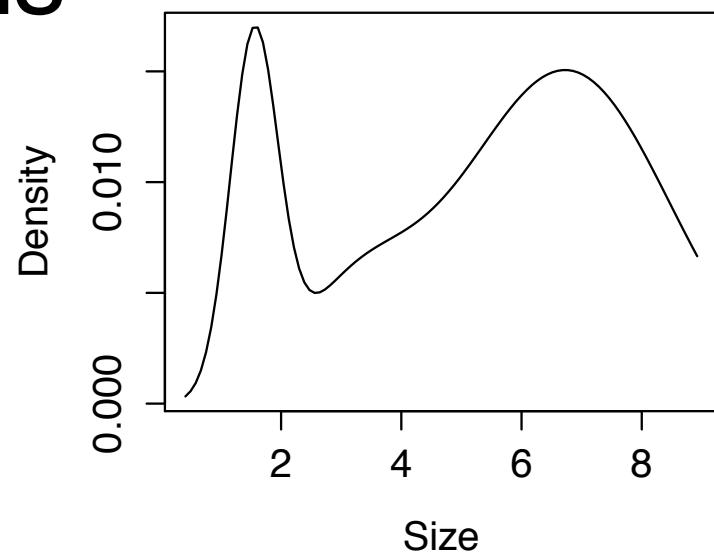
$$\mathbf{n}(t+1) = \mathbf{K} \mathbf{n}(t)$$

# Analysis

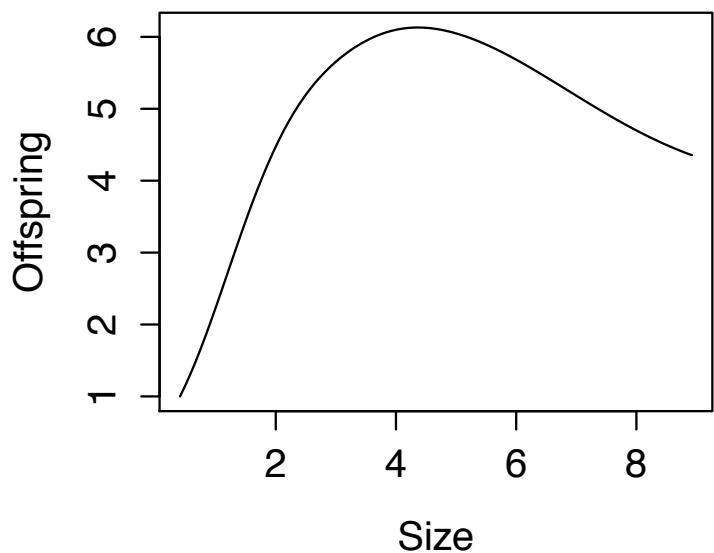
Kernel



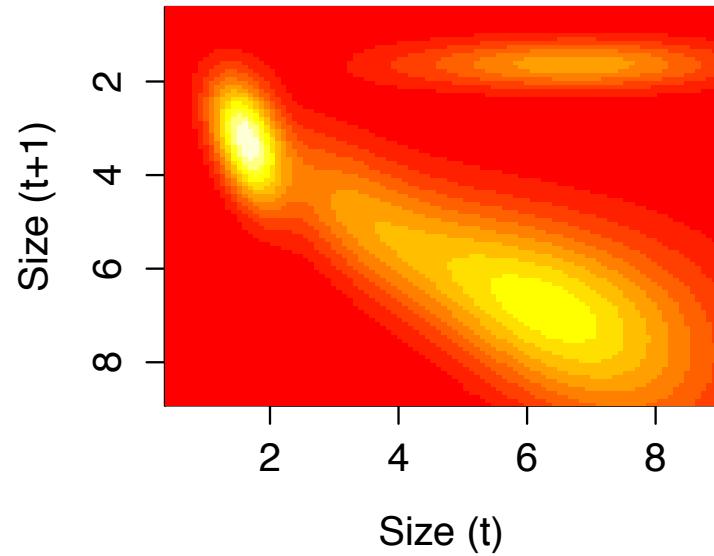
**Stable size distribution**



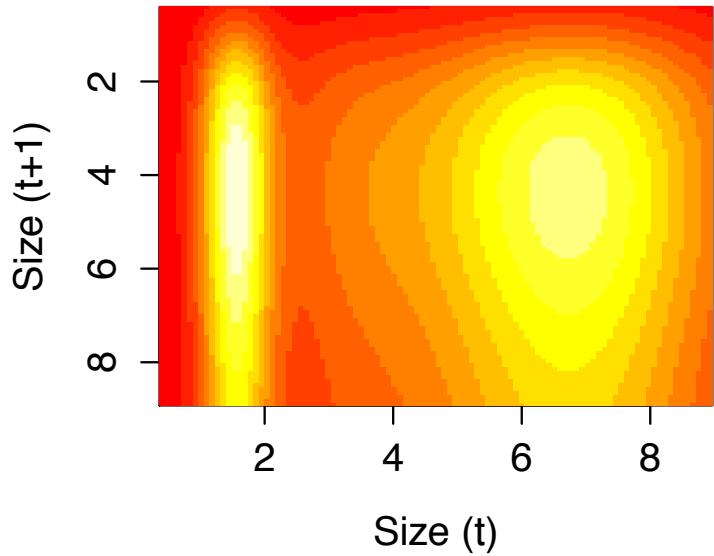
**Reproductive values**



**Elasticity**

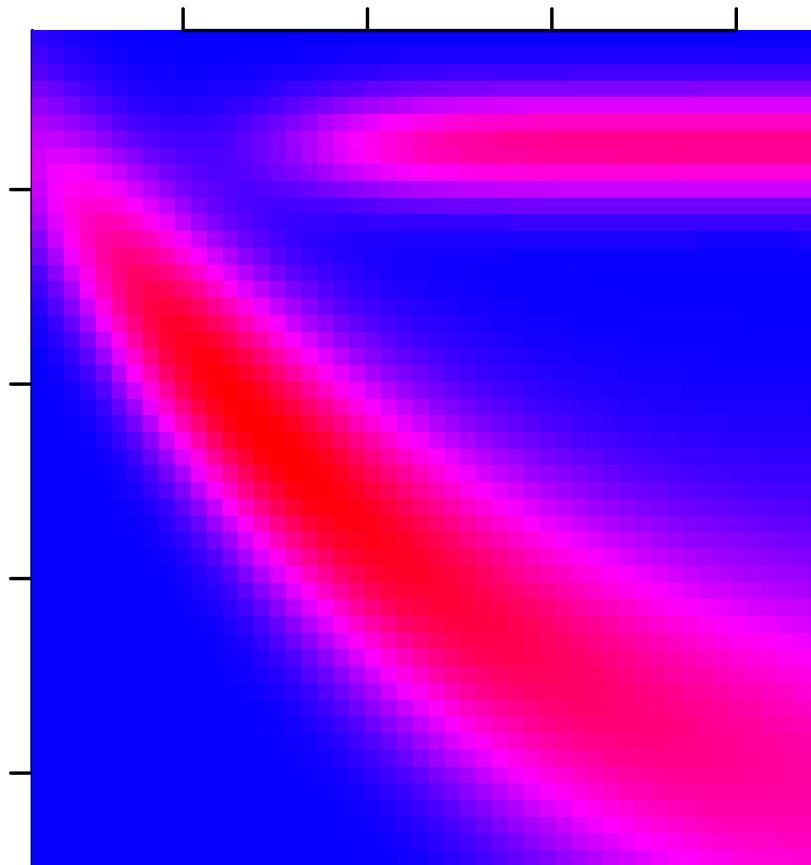


**Sensitivity**



# Additional tools for IPMs

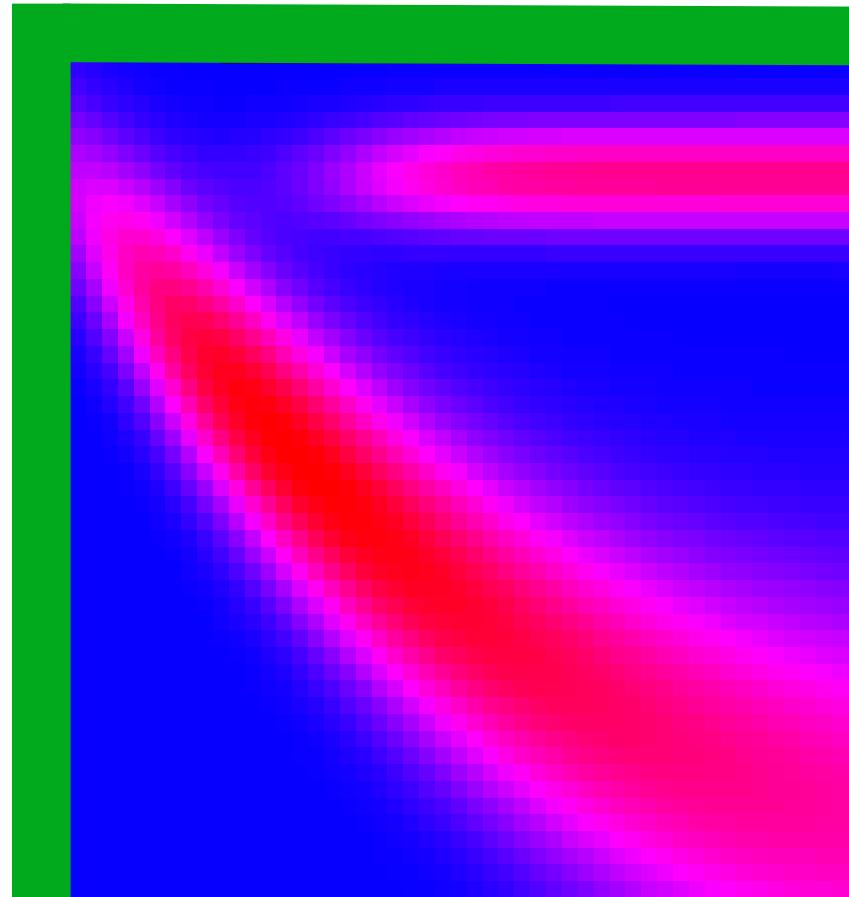
Add discrete states (seed banks, larval states)



# Additional tools for IPMs

Add discrete states (seed banks, larval states)

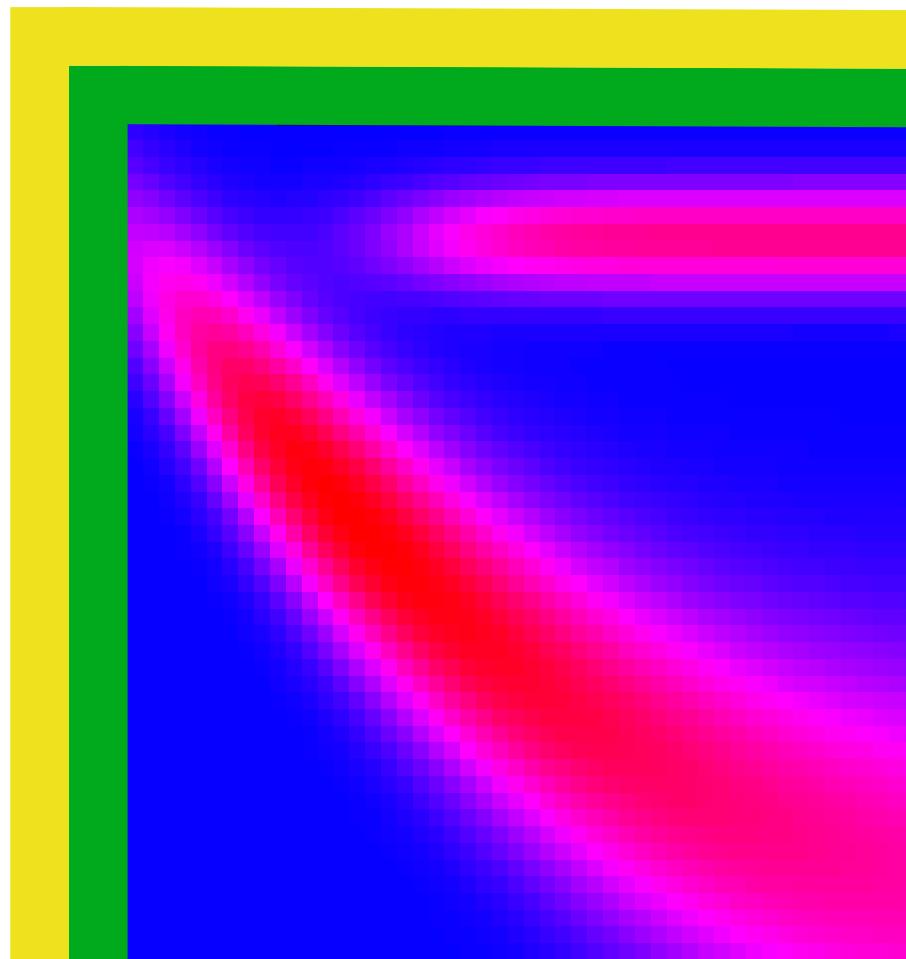
Different  
functions  
describe  
discrete  
transitions



# Additional tools for IPMs

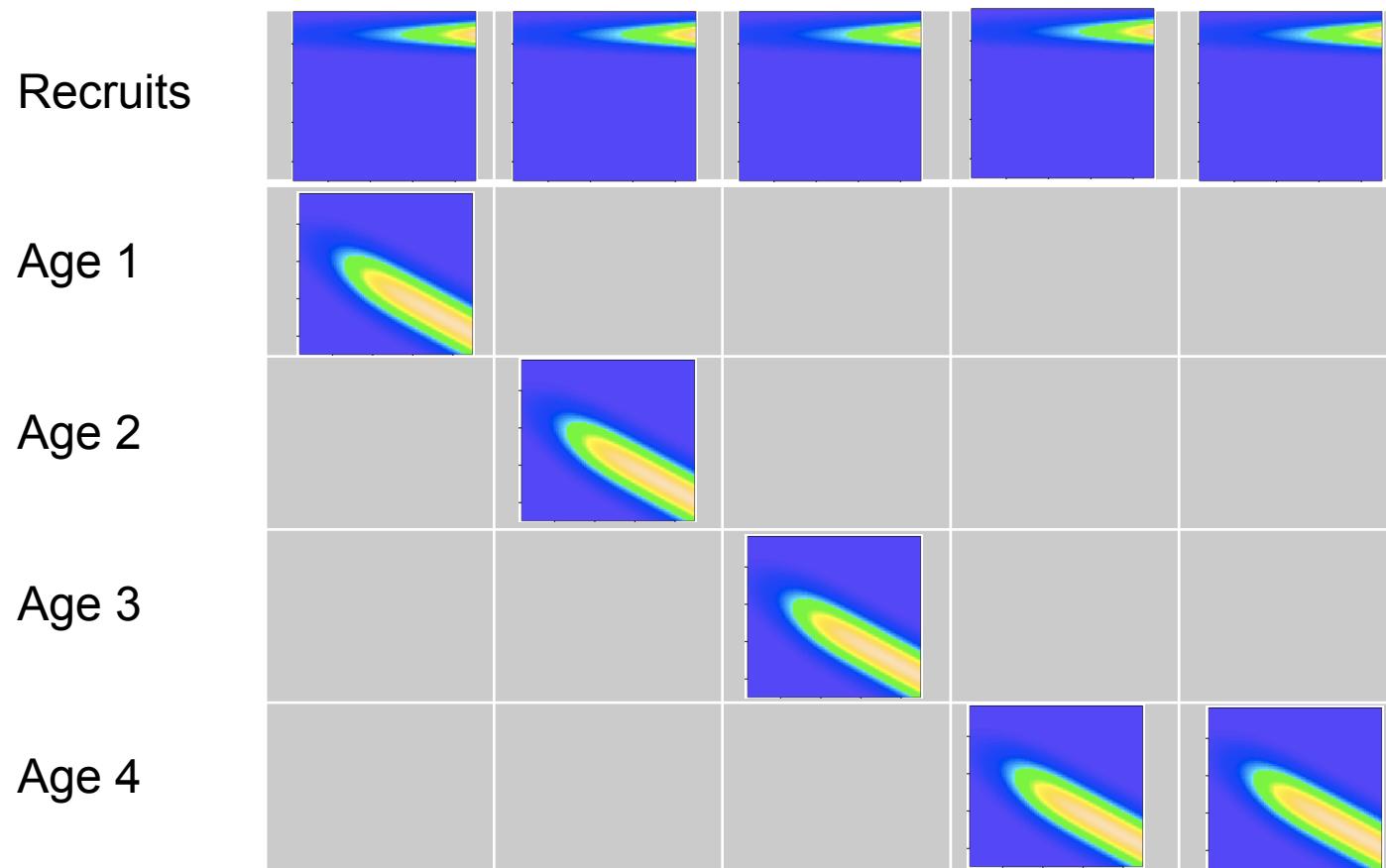
Add discrete states (seed banks, larval states)

Different  
functions  
describe  
discrete  
transitions



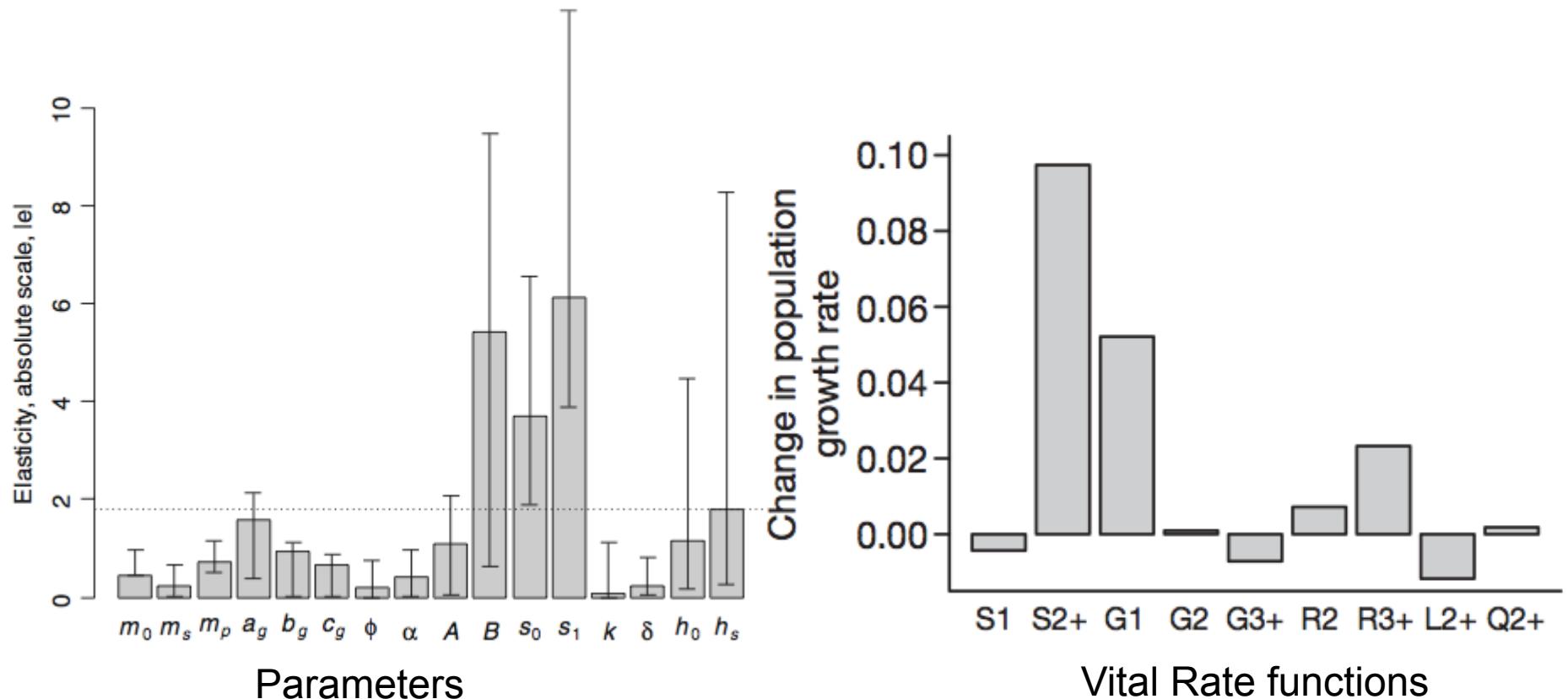
# Additional tools for IPMs

Age x Stage models



# Additional tools for IPMs

Parameter sensitivity – retrospective parameter perturbation

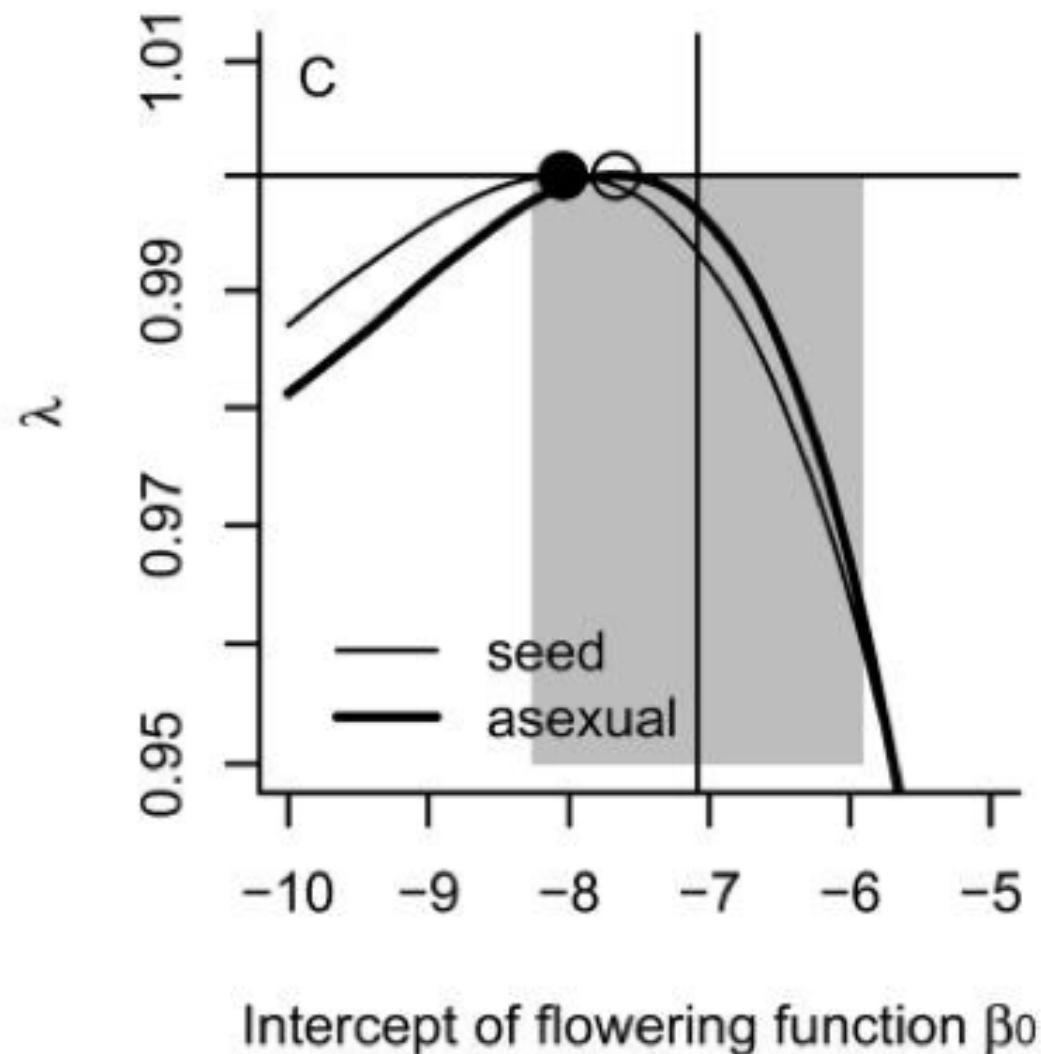


Metcalf et al. 2008

Ozgul et al. 2010

# Additional tools for IPMs

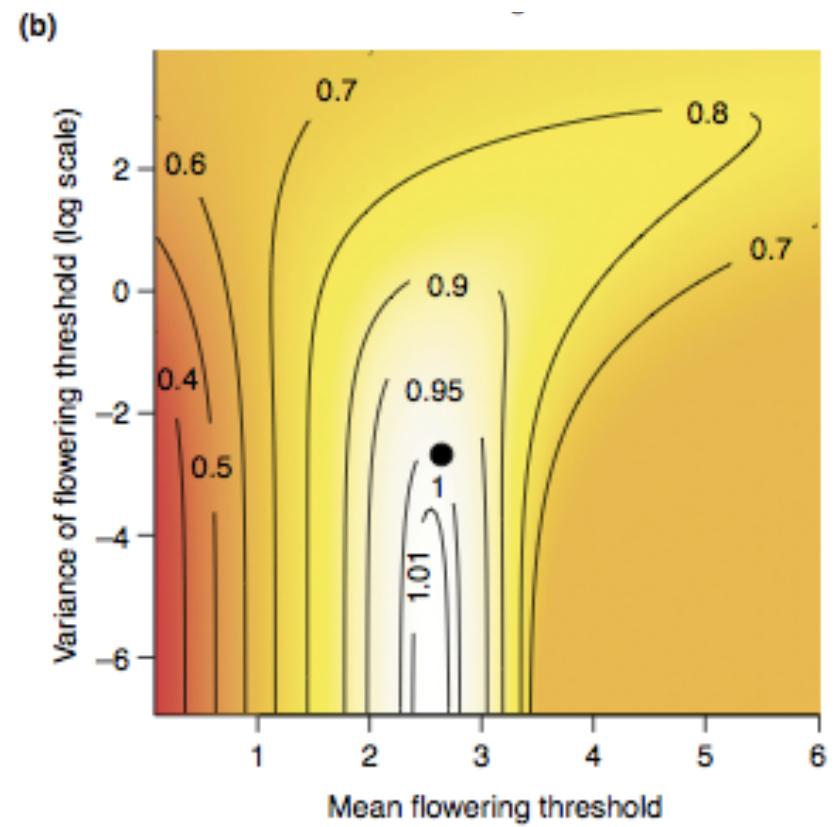
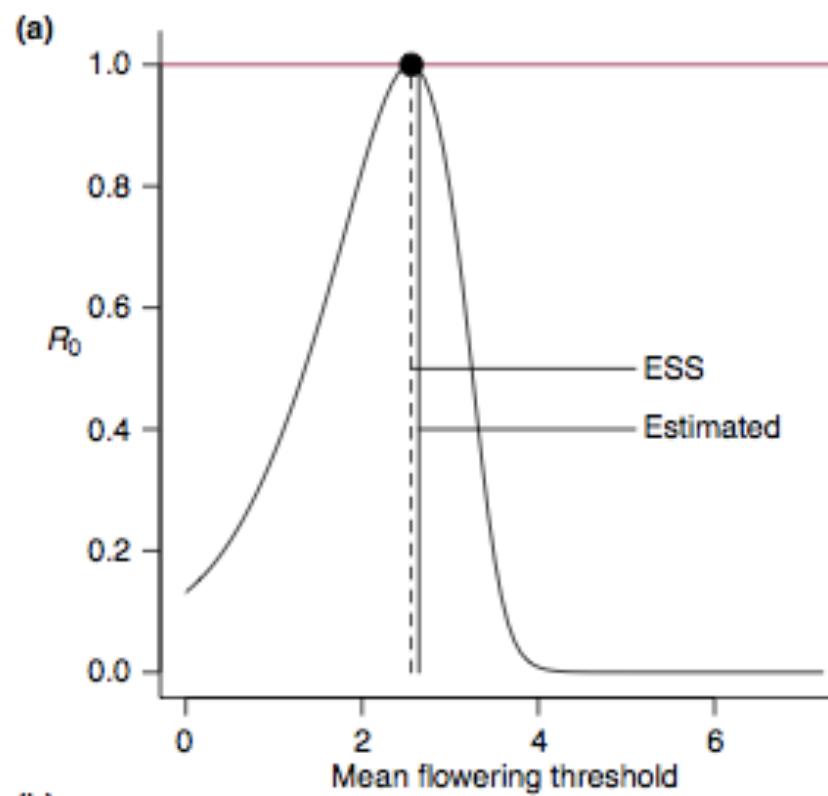
Optimizing  
parameters



Hesse et al. 2008

# Additional tools for IPMs

## Optimizing parameters



Metcalf et al. 2003

# Additional tools for IPMs

Regression allows some cool analyses

- Species interactions using spatial arrangement and frequency dependence to (Adler, Dalgleish, Ellner 2011)

# Additional tools for IPMs

Regression allows some cool analyses

- Species interactions using spatial arrangement and frequency dependence to (Adler, Dalgleish, Ellner 2011)
- Using other state variables
  - Age (Lots of papers)
  - Genotype (Coulson et al. 2011)
  - Space (Jongejans et al. 2011)
  - Infection (Bruno et al. 2010)

# Additional tools for IPMs

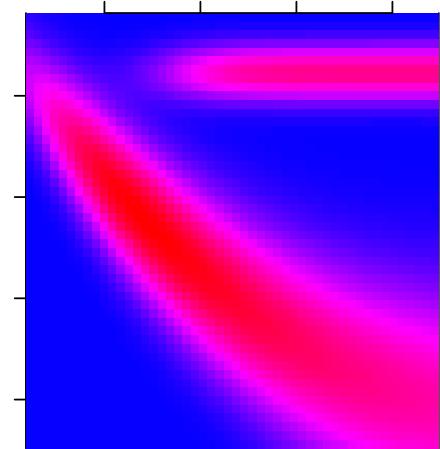
Regression allows some cool analyses

- Species interactions using spatial arrangement and frequency dependence to (Adler, Dalgleish, Ellner 2011)
- Using other state variables
  - Age (Lots of papers)
  - Genotype (Coulson et al. 2011)
  - Space (Jongejans et al. 2011)
  - Infection (Bruno et al. 2010)
- Nonlinear vital rate functions (Dahlgren et al. 2011)
- Hierarchical models linking covariates to vital rate coefficients
- Borrowing strength across species (or other things)

# Summary - Why IPMs?

## Process-based demography

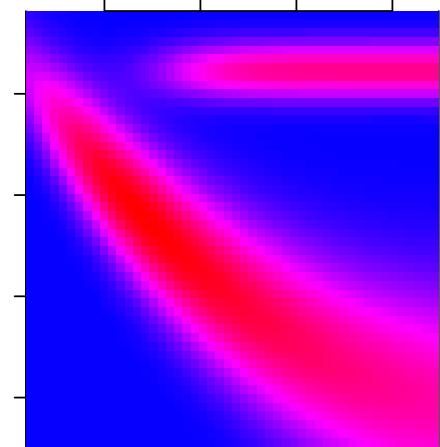
- Continuous stages
- Few parameters
- Account for heterogeneity
- Borrow strength across stages
- Multiple state variables
- Include covariates



# Summary - Why IPMs?

## Process-based demography

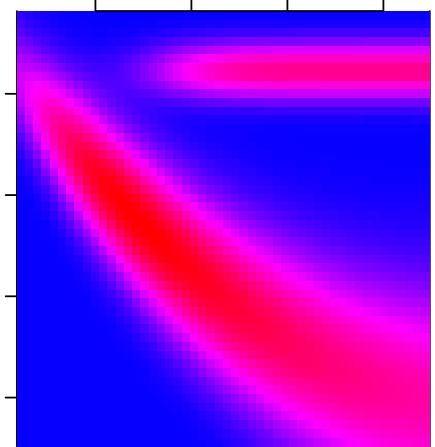
- Continuous stages
- Few parameters
- Account for heterogeneity
- Borrow strength across stages
- Multiple state variables
- Include covariates



IPMs make  
these easy

# Summary - Why IPMs?

Process-based demography



# Questions?

# Exercises

1. **Intro exercises**
2. IPMpack vignette
3. ESS
4. Discrete stages and environment
5. Modeling life expectancy and passage time in trees

# Exercises ~ 40 minutes

1. Download the following files from the workshop's dropbox folder, or ask for one of our flash drives
  - Data set: 'Intro IPM exercises ESA-data set.csv'
  - R script: 'Intro IPM exercises ESA.r'
2. Work through the sample code in the R script
3. Complete exercises 1 and 2 at the end of the R script
4. Ask us lots of questions
5. When finished make sure you've downloaded the latest version of IPMpack, released Friday
  - `install.packages("IPMpack")`

\* This code does not rely on IPMpack, and is meant to illustrate its underlying operations for a very simple case. We'll begin with IPMpack in the next talk.

# Answers

- Question 1a.

```
>growth.sd.reg=lm(abs(resid(growth.reg))~  
growth.reg$model$size)  
>summary(growth.sd.reg)
```

# Answers

- Question 1a.

```
>growth.sd.reg=lm(abs(resid(growth.reg))~  
growth.reg$model$size)
```

```
>summary(growth.sd.reg)
```

- Question 1b.

```
>params$growth.sd.int=  
coefficients(growth.sd.reg)[1]
```

```
>params$growth.sd.slope=  
coefficients(growth.sd.reg)[2]
```

# Answers

- Question 1a.

```
> growth.sd.reg=lm(abs(resid(growth.reg))~growth.reg$model  
$size)
```

```
> summary(growth.sd.reg)
```

- Question 1b.

```
> params$growth.sd.int=coefficients(growth.sd.reg)[1]
```

```
> params$growth.sd.slope=coefficients(growth.sd.reg)[2]
```

- Question 1c

```
> g.yx=function(xp,x,params) {  
  dnorm(xp,mean=params$growth.int+params$growth.slope*x,  
  sd=params$growth.sd.int+params$growth.sd.slope*x)  
}
```

# Answers

- Question 1a.

```
>growth.sd.reg=lm(abs(resid(growth.reg))~growth.reg$model  
$size)
```

```
>summary(growth.sd.reg)
```

- Question 1b.

```
>params$growth.sd.int=coefficients(growth.sd.reg)[1]
```

```
>params$growth.sd.slope=coefficients(growth.sd.reg)[2]
```

- Question 1c

```
> g.yx=function(xp,x,params) {  
  dnorm(xp,mean=params$growth.int+params$growth.slope*x,  
  sd=params$growth.sd.int+params$growth.sd.slope*x)  
}
```

- Question 1d.

```
>lambda=1.006311
```

# Answers

- Question 2

```
> growth.reg=lm(sizeNext~size+I(size^2),data=d)
> summary(growth.reg)
> params$growth.int=coefficients(growth.reg)[1]
> params$growth.slope=coefficients(growth.reg)[2]
> params$growth.sqrd=coefficients(growth.reg)[3]

> growth.sd.reg=lm(abs(resid(growth.reg))~growth.reg$model$size)
> summary(growth.sd.reg)
> params$growth.sd.int=coefficients(growth.sd.reg)[1]
> params$growth.sd.slope=coefficients(growth.sd.reg)[2]

> g.yx=function(xp,x,params) {
  dnorm(xp,mean=params$growth.int+params$growth.slope*x+
    params$growth.sqrd*x^2, sd=params$growth.sd.int+params
    $growth.sd.slope*x)
}
```

lambda=1.118804

# Answers

- Question 3

```
# 1. p.flower.x=function(x,params) {
  u=exp(params$flower.int+params$flower.slope*x)
  return(u/(1+u))
}

# 2. f.yx=function(xp,x,params) {
  p.flower.x(x,params)*
  params$establishment.prob*
  dnorm(xp,mean=params$recruit.size.mean, sd=params$recruit.size.sd)*
  exp(params$seed.int+params$seed.slope*x)
}

# 3. flower.reg=glm(fec.flower~size,data=d,family=binomial())
  summary(flower.reg)
  params$flower.int=coefficients(flower.reg)[1]
  params$flower.slope=coefficients(flower.reg)[2]

# 4. seed.reg=glm(fec.seed~size,data=d[d$fec.flower==1,],family=poisson())
  summary(seed.reg)
  params$seed.int=coefficients(seed.reg)[1]
  params$seed.slope=coefficients(seed.reg)[2]

# 6 . 0.996426
```