Demographic projections with matrix population models

SSA 200

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Applications to SSAs

- Output useful metrics on future resiliency and redundancy
  - Future abundance, extinction probability, population growth rate
- Use understanding of species' life history to predict future condition of the populations and characterize uncertainties
- Can be useful when little monitoring data exists (e.g., occupancy, current abundance) but we know a lot about species' life history from the literature and/or captive populations

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Lecture outline

- Building a matrix model
- Accounting for uncertainty and stochasticity
- Implementing future scenarios

Not just for demographic matrix models!

Lecture outline

- Building a matrix model
- Accounting for uncertainty and stochasticity
- Implementing future scenarios

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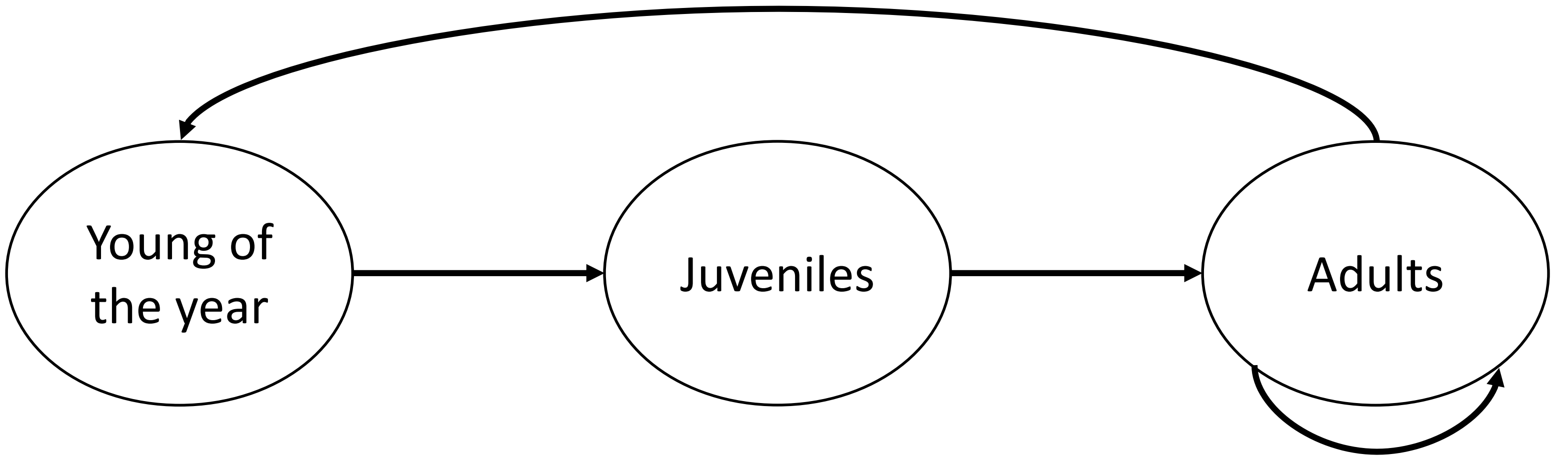
Building the demographic matrix model

1. Draw a life cycle diagram to understand key ages/stages that should be included



Structuring the life cycle model

- Age classes (Leslie Matrix)
  - Equal time intervals & all individuals advance at next time
    - Short lived species with age-specific data
- Stage classes (Lefkovitch Matrix)
  - Unequal time intervals
  - Population divided by developmental stage or size
    - Difficult to age individuals but can get length, height, etc.
    - Juvenile, subadult
    - Seeds, dormancy, small plants, large plants

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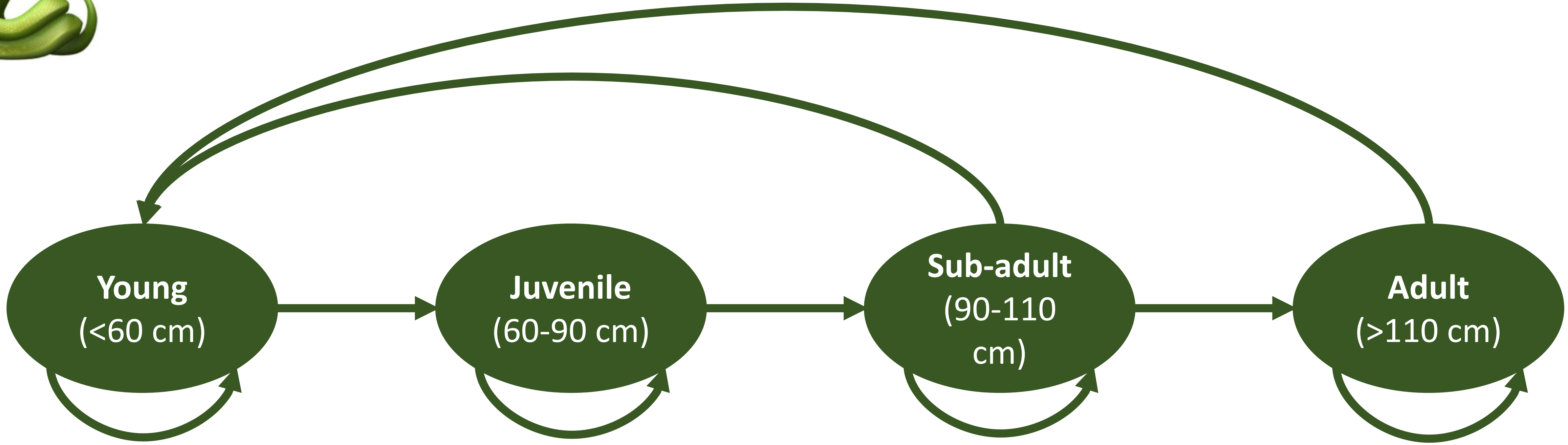
Puerto Rican boa

SSA in prep

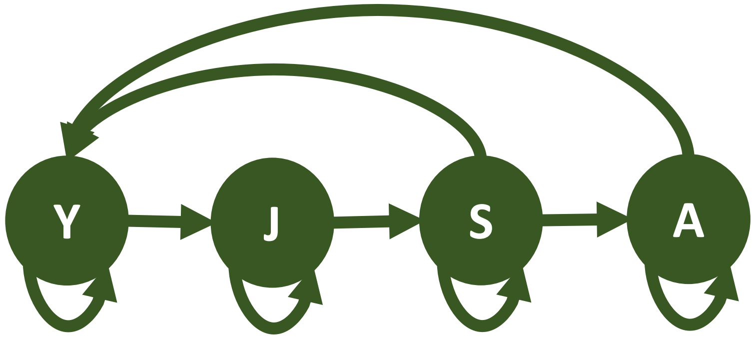

Young
(<60 cm)
Juvenile
(60-90 cm)
Sub-adult
(90-110
cm)
Adult
(>110 cm)

Building the model

1. Draw a life cycle diagram
2. Estimate vital rates (e.g., stage-specific survival probability, fecundity)

A number for each arrow

- Data analysis
  - Fecundity
    - Number of offspring/female -> Poisson GLM
    - Successful breeding (yes/no) -> Binomial GLM
  - Annual survival/mortality
    - Radio telemetry -> known-fate models
    - Individual CMR -> Cormack-Jolly-Seber (CJS) models
    - Proportion of marked plants alive next year
- Literature review
- Expert judgement



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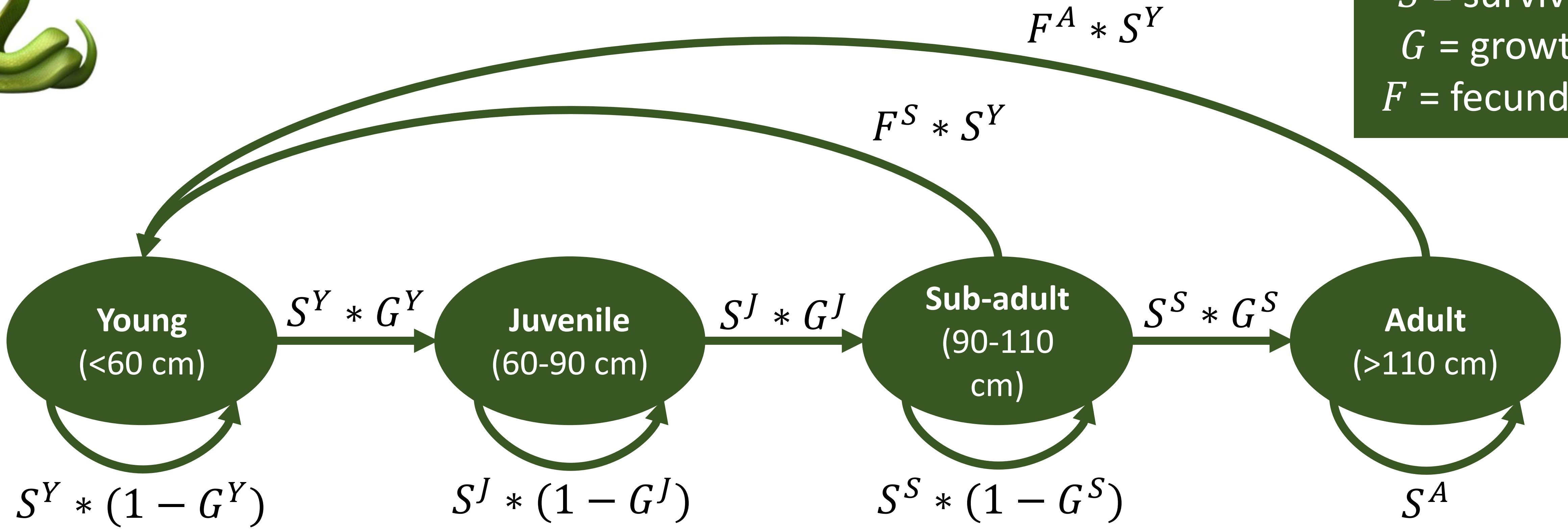
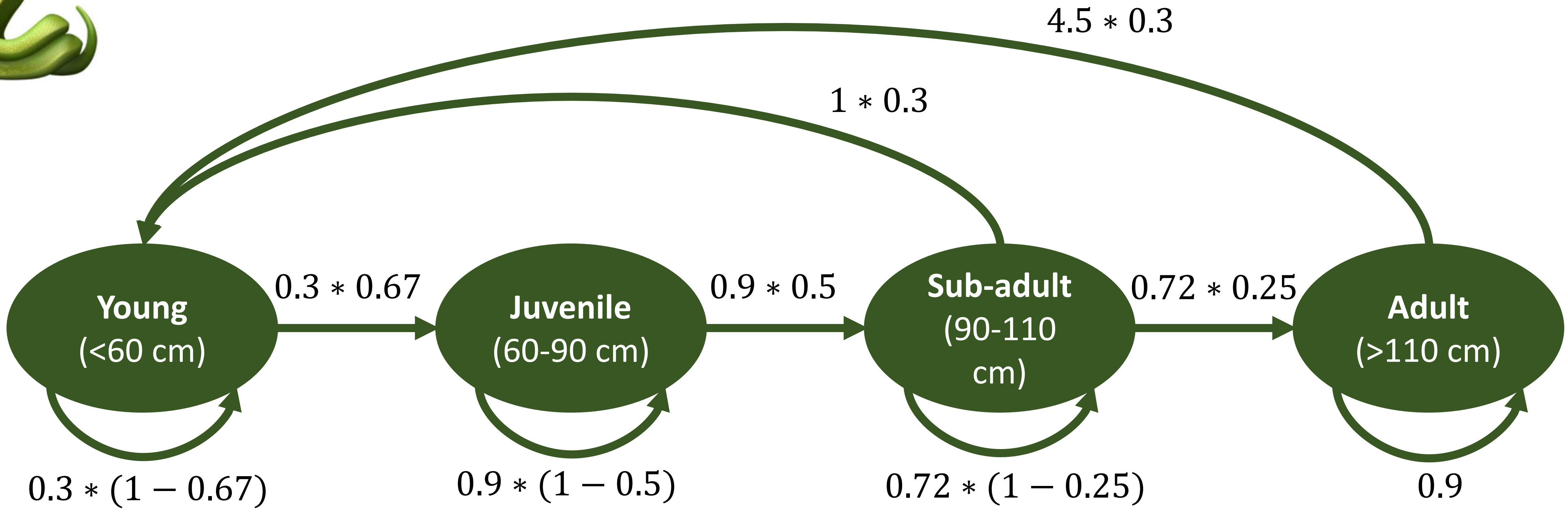
S = survival
G = growth
F = fecundity



Vital rates:
- Annual survival of each stage (S)
- Annual growth probability for each stage (G)
- Annual fecundity for each stage (F)

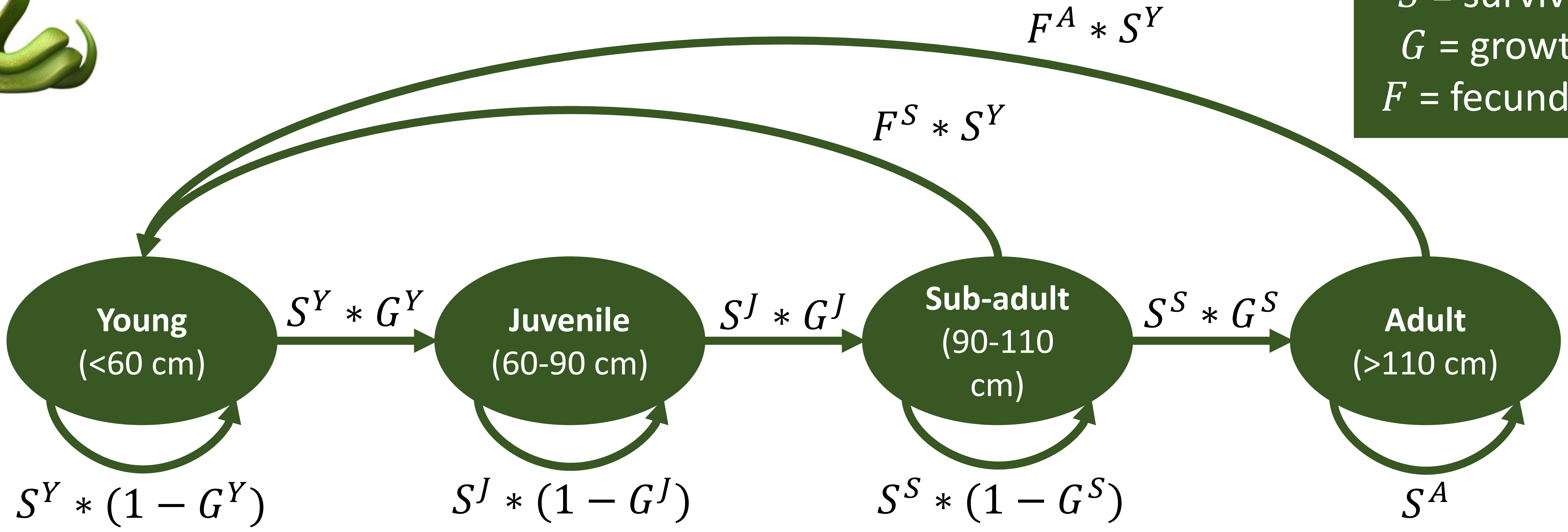


Demographic rates were estimated by the expert team or drawn from the literature

Building the model

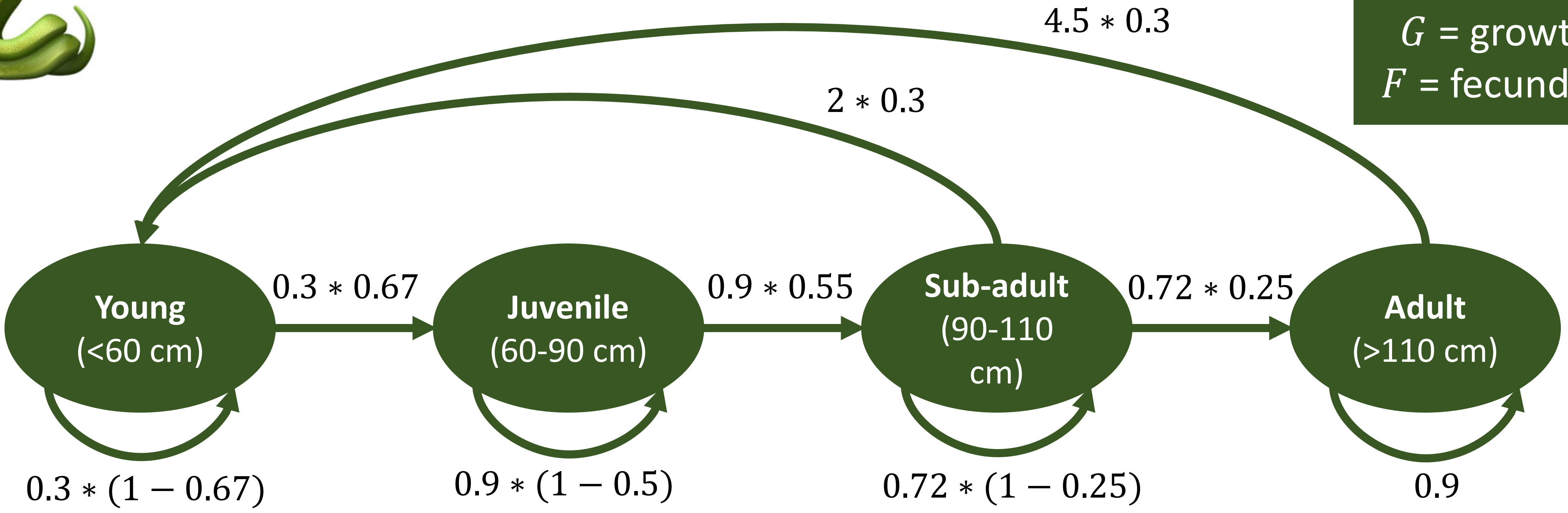
1. Draw a life cycle diagram
2. Estimate vital rates
3. Construct the population matrix and use it to project the population into the future

S = survival
G = growth
F = fecundity



$$\begin{bmatrix} N_t^Y \\ N_t^J \\ N_t^S \\ N_t^A \end{bmatrix} = \begin{bmatrix} \boldsymbol{S^Y * (1 - G^Y)} & \boldsymbol{0} & \boldsymbol{F^S * S^Y} & \boldsymbol{F^A * S^Y} \\ \boldsymbol{S^Y * G^Y} & \boldsymbol{S^J * (1 - G^J)} & \boldsymbol{0} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{S^J * G^J} & \boldsymbol{S^S * (1 - G^S)} & \boldsymbol{0} \\ \boldsymbol{0} & \boldsymbol{0} & \boldsymbol{S^S * G^S} & \boldsymbol{S^A} \end{bmatrix} x \begin{bmatrix} N_{t-1}^Y \\ N_{t-1}^J \\ N_{t-1}^S \\ N_{t-1}^A \end{bmatrix}$$

S = survival
G = growth
F = fecundity



$$\begin{bmatrix} N_t^Y \\ N_t^J \\ N_t^S \\ N_t^A \end{bmatrix} = \begin{bmatrix} \mathbf{0.1} & \mathbf{0} & \mathbf{0.6} & \mathbf{1.35} \\ \mathbf{0.2} & \mathbf{0.41} & \mathbf{0} & \mathbf{0} \\ \mathbf{0} & \mathbf{0.50} & \mathbf{0.54} & \mathbf{0} \\ \mathbf{0} & \mathbf{0} & \mathbf{0.18} & \mathbf{0.9} \end{bmatrix} x \begin{bmatrix} N_{t-1}^Y \\ N_{t-1}^J \\ N_{t-1}^S \\ N_{t-1}^A \end{bmatrix}$$

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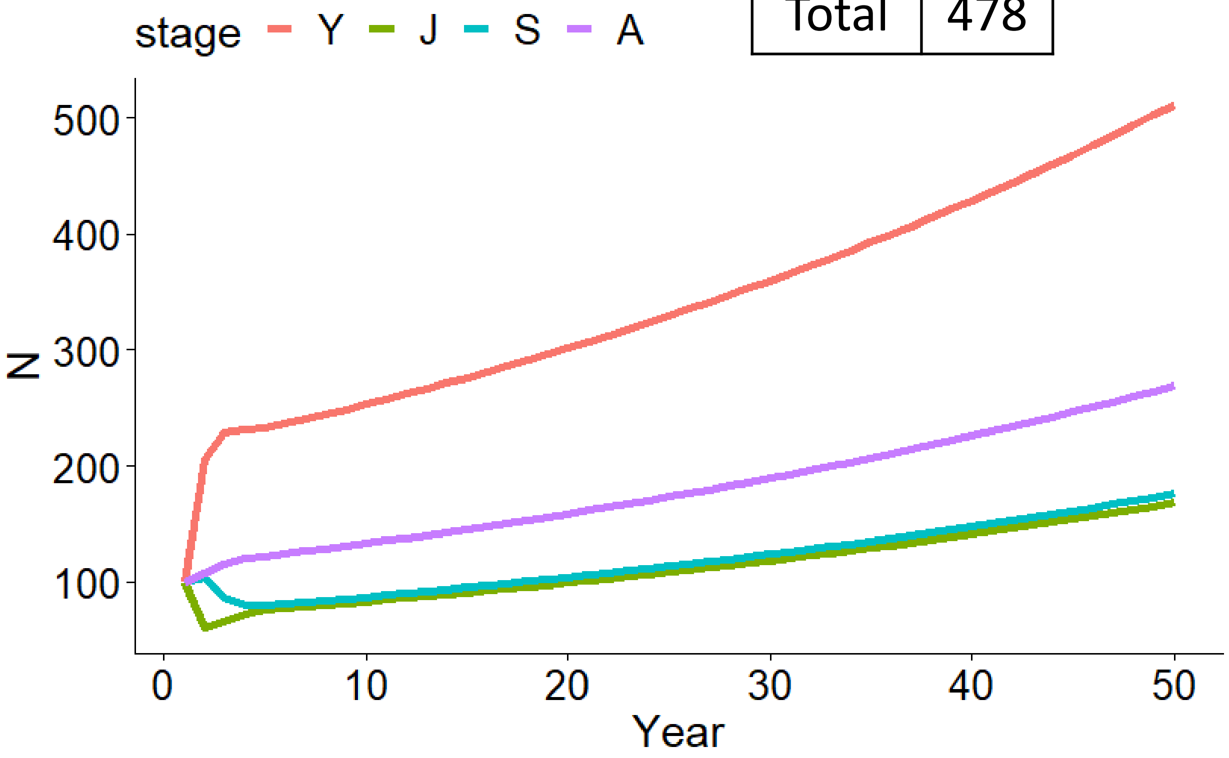
Year 1	
Stage	**N**
Y	100
J	100
S	100
A	100
Total	400

$$\begin{bmatrix} 0.1 & 0 & 0.6 & 1.35 \\ 0.2 & 0.41 & 0 & 0 \\ 0 & 0.50 & 0.54 & 0 \\ 0 & 0 & 0.18 & 0.9 \end{bmatrix}$$

Year 2	
Stage	**N**
Y	205
J	61
S	104
A	108
Total	478

$$\begin{bmatrix} 0.1 & 0 & 0.6 & 1.35 \\ 0.2 & 0.41 & 0 & 0 \\ 0 & 0.50 & 0.54 & 0 \\ 0 & 0 & 0.18 & 0.9 \end{bmatrix}$$

Year 3	
Stage	**N**
Y	229
J	66
S	87
A	116
Total	498



*This is a **deterministic** projection--every time we run this model we would get the exact same output*

Matrix projection outputs

- Abundance over time
- Population growth rate (λ)
  - $\lambda = 1.0 \rightarrow$ no change
  - $\lambda = 1.10 \rightarrow$ increasing 10% per year
  - $\lambda = 0.90 \rightarrow$ decreasing 10% per year
- Probability of extinction and/or quasi-extinction
- Sensitivity and elasticity
  - Which vital rates are most important for population stability?

Population Resiliency

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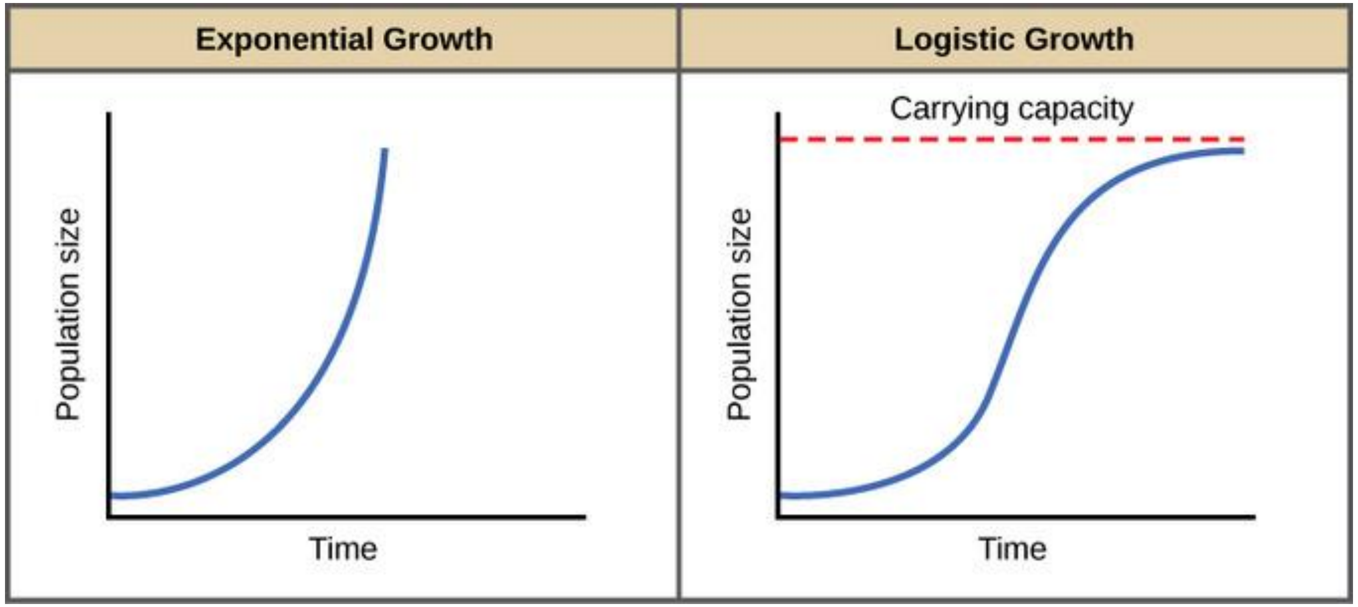
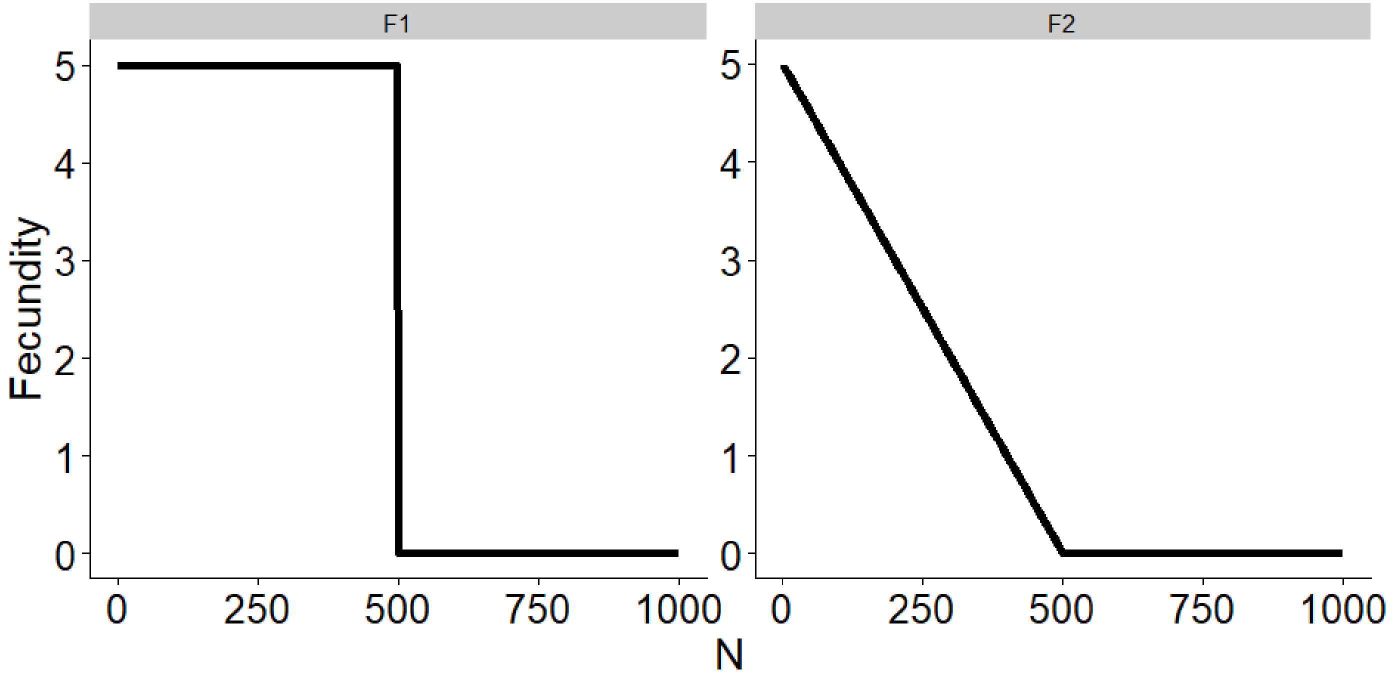
Density dependence

- Most (all?) wildlife populations cannot grow exponentially forever
- Allowing for exponential growth could lead to overestimating future abundance or population growth rate
- Functional forms of density dependence poorly understood for most species

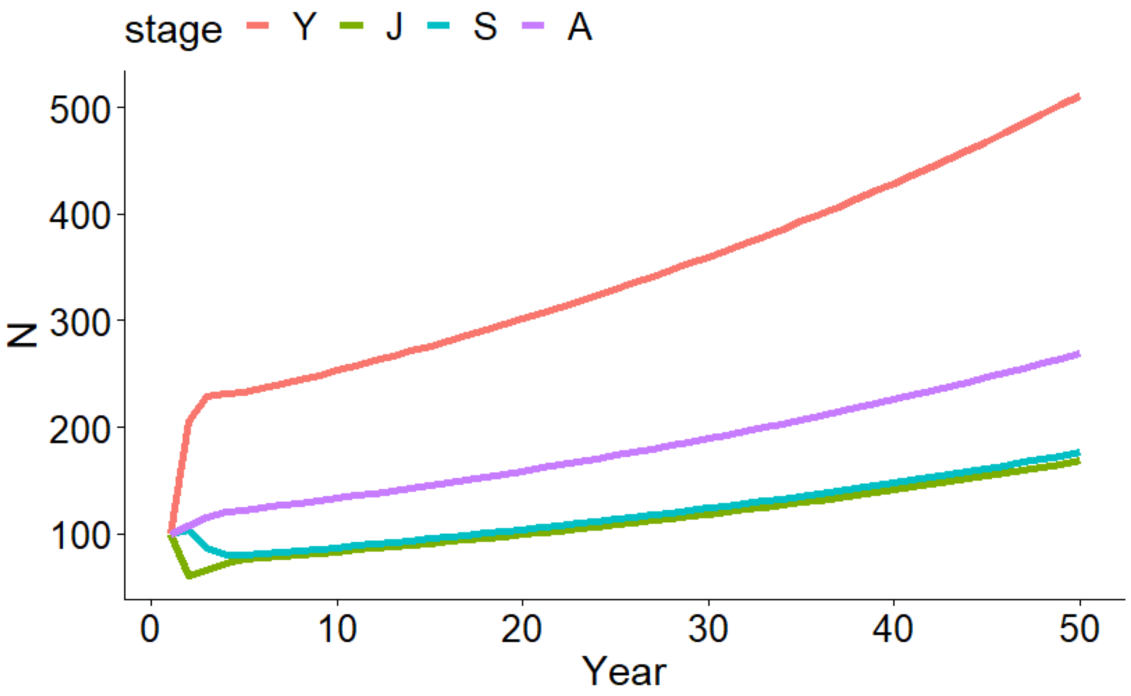


Modeling density dependence

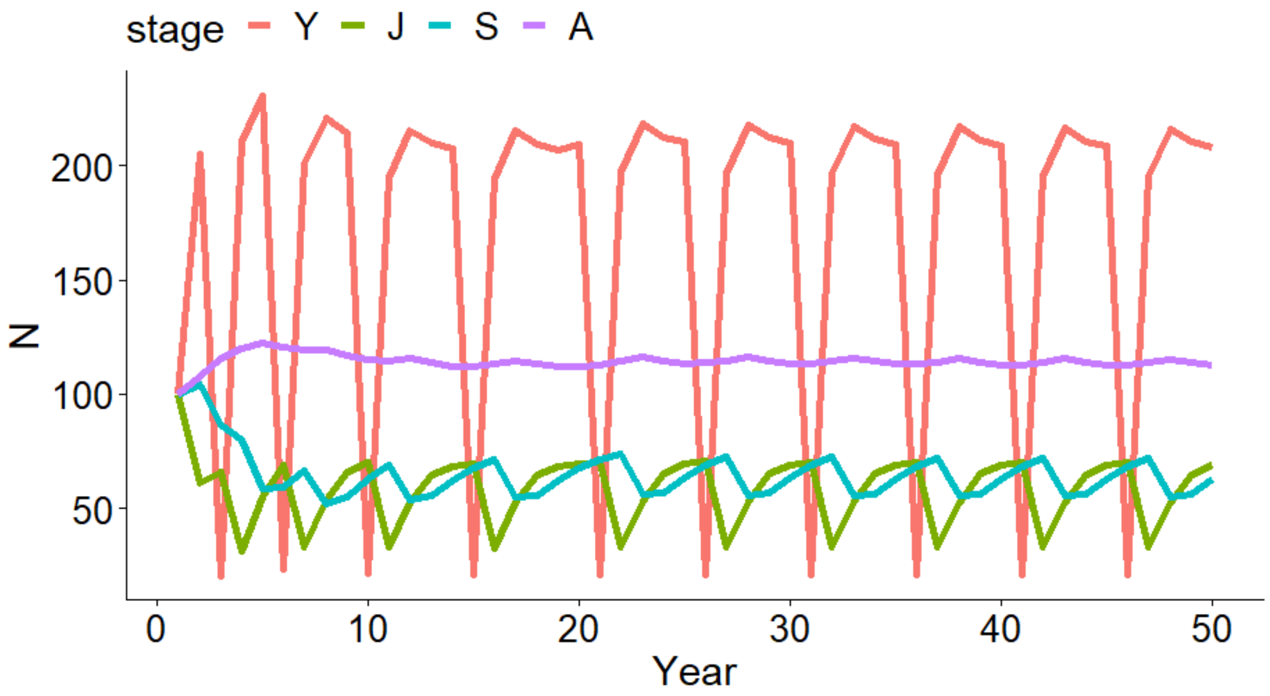
- Common approach: define a carrying capacity as a population ceiling, set a rule for how vital rates are affected by population size
    - If the population exceeds the carrying capacity, fecundity is equal to zero
    - OR, as the population approaches some ceiling threshold, fecundity gets smaller and smaller



Density independent growth



Density dependent growth, K = 450



If total population size exceeded K, fecundity was set equal to 0

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Lecture outline

- Building a matrix model
- Accounting for uncertainty and stochasticity
- Implementing future scenarios

Accounting for uncertainty

- Observational uncertainty
- Environmental stochasticity
- Demographic stochasticity

- Failing to account for uncertainty and stochasticity can lead to overly precise projections (we would underestimate our level of uncertainty about the future state of the system)
- Incorporate uncertainty via replicated projections

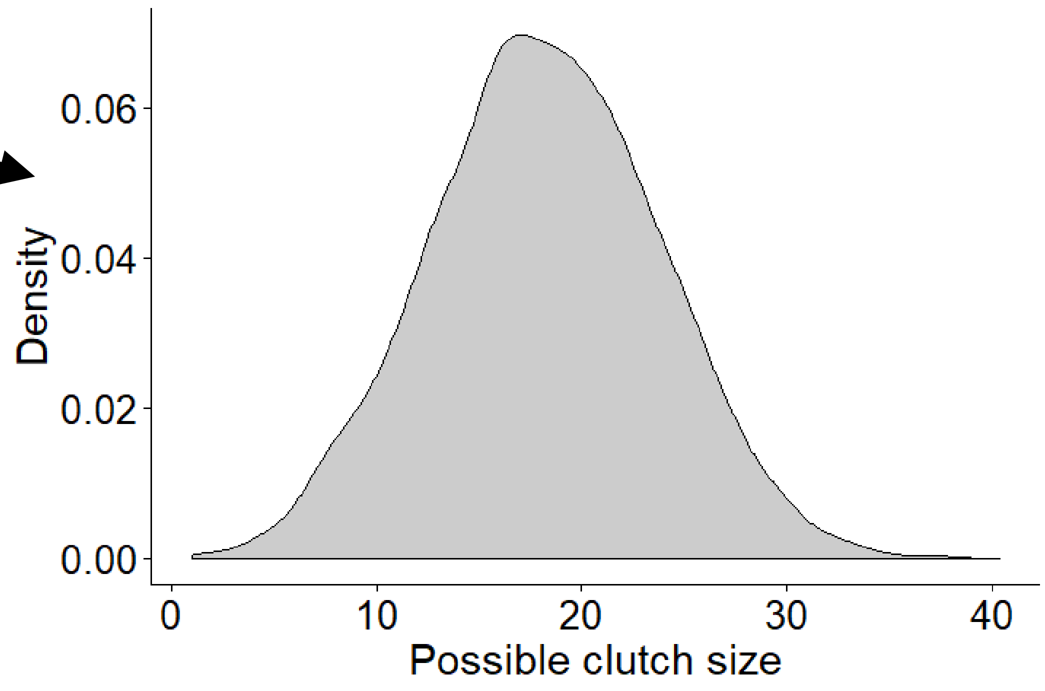
Observational uncertainty/parametric uncertainty

- We cannot perfectly observe wildlife populations, and therefore we cannot perfectly measure vital rates
- Vital rates are estimated with associated standard errors/confidence interval
- Estimates of parametric uncertainty:
  - output of data analysis
  - should be reported in the literature where vital rates were presented
  - can be derived from expert elicitation

from Puente-Rolon (2012) (dissertation on reproductive ecology of Puerto Rican boa):

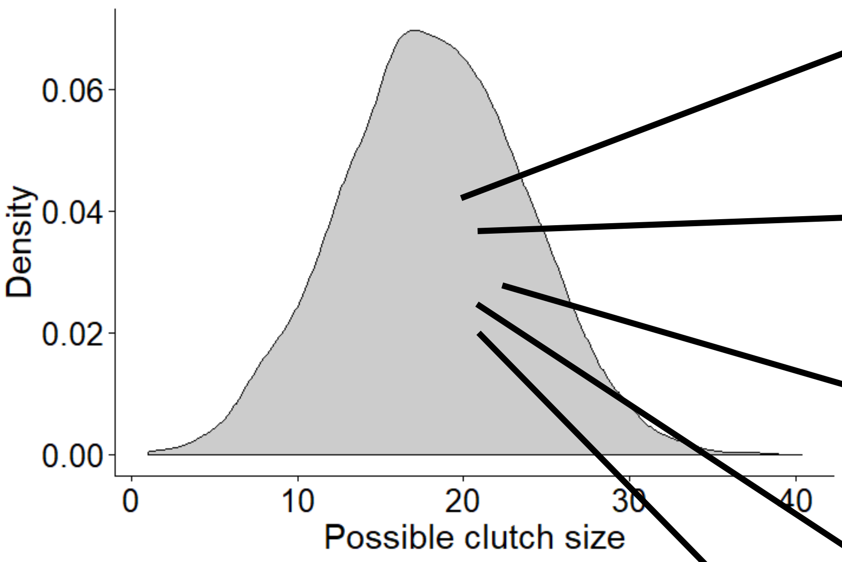
litters showed that courtship and fertilization occurred between early March and late May. Gravid snakes average 143.4±19.5cm SVL, and weighed an average of 1857.6 ± 547 g pre-partum and 1333.3 ± 407 g post-partum. The average clutch size for *E. inornatus* was 18.2 ± 5.6, with an average clutch mass of 524 ± 254 g. Neonates have a snout-vent length at birth of 34.20 ± 1.8 cm, tail length of 7 ± .53 cm, and a mass of 13.61 ± 1.6 g. Relative

Clutch size = 18.2 ± 5.6



$average = 18.2$

$SD = 5.6$



Replicate 1
$average = 10.1$

Replicate 2
$average = 22.5$

Replicate 3
$average = 21.1$

Replicate 4
$average = 15.2$

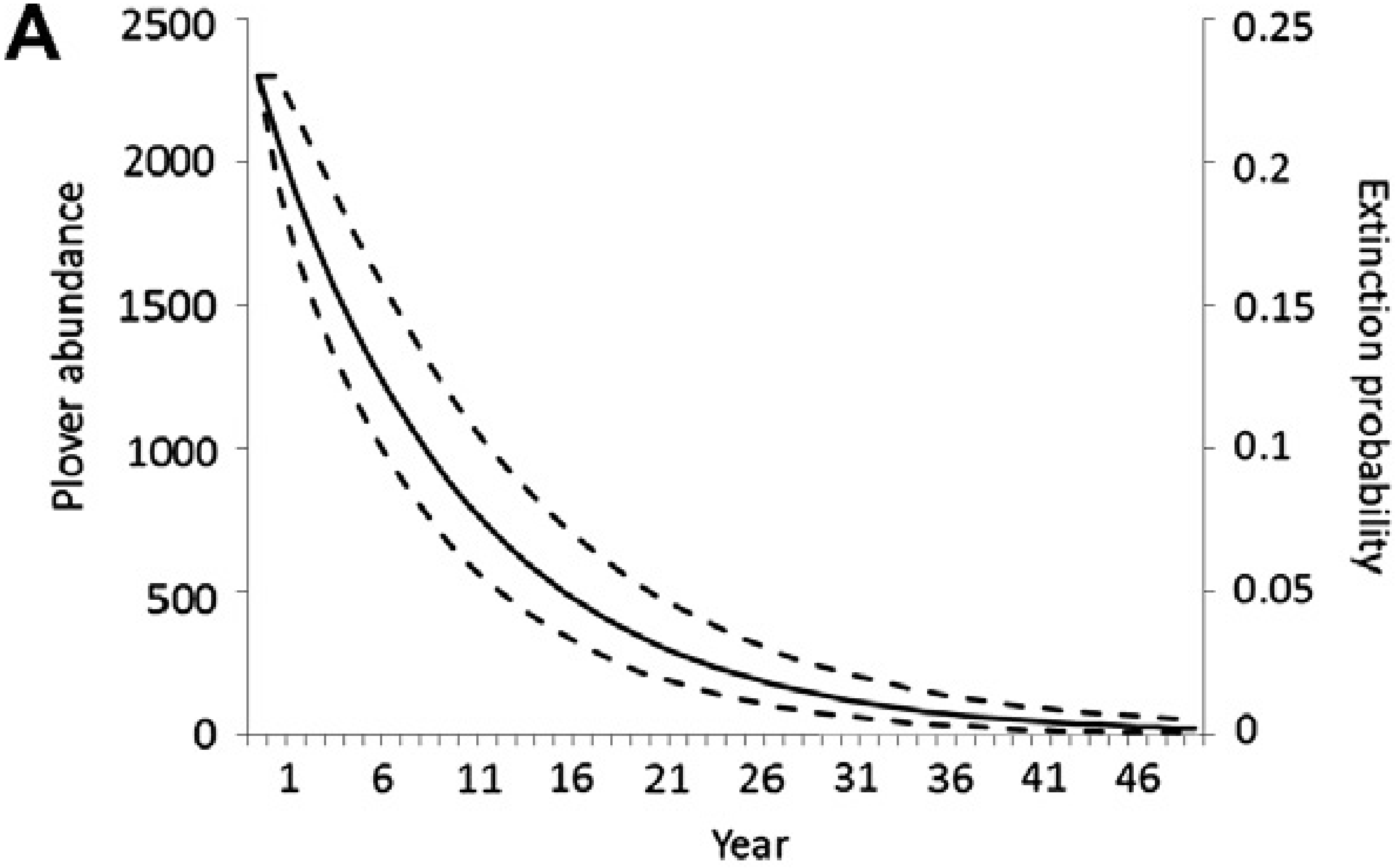
Replicate 5
$average = 19.4$

Randomly draw one value per replicate

Parametric uncertainty – uncertainty about the true average value

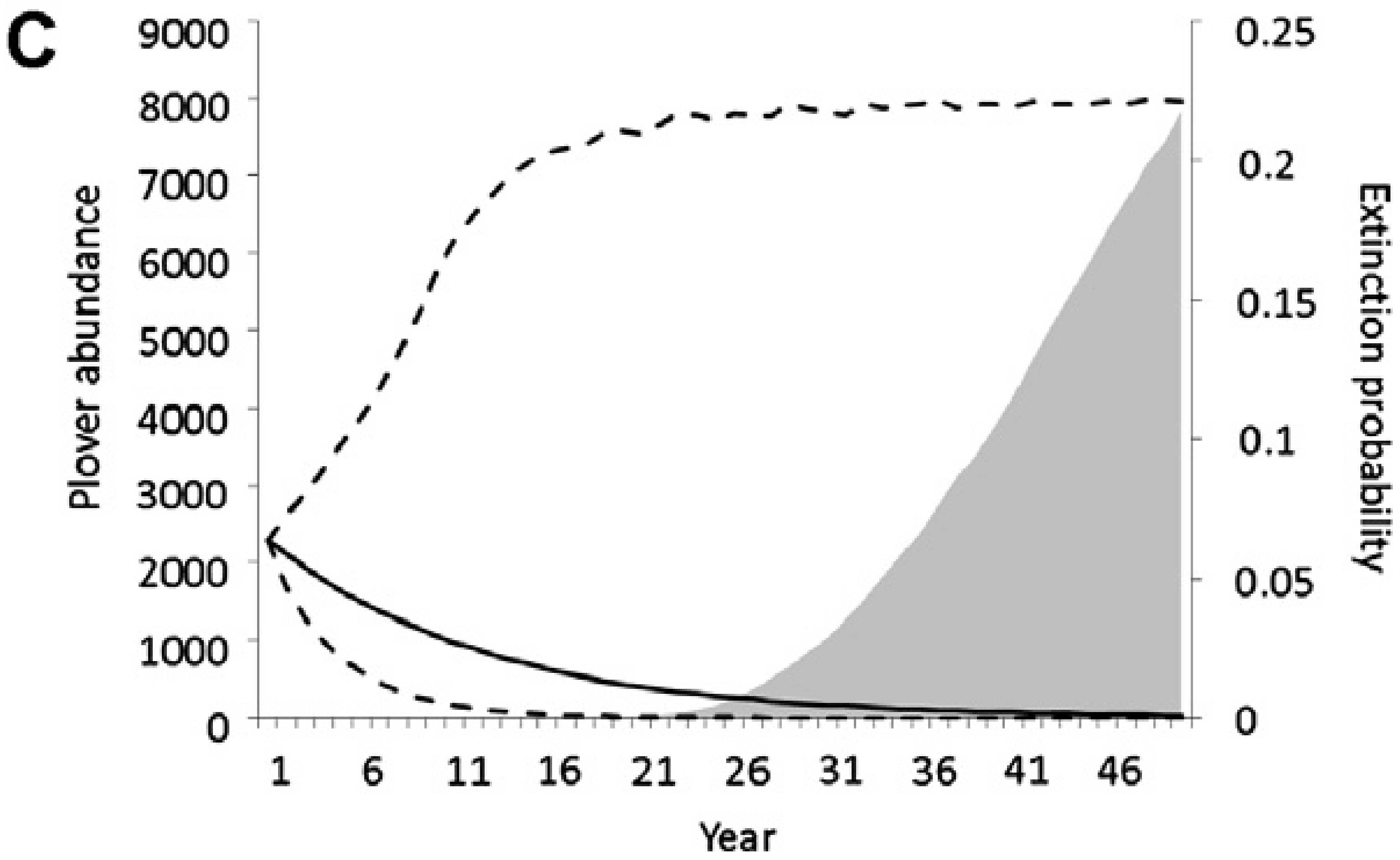
Draw a different average value for each replicate

Projection without parametric uncertainty



McGowan, C. P., M. C. Runge, and M. a. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Projection with parametric uncertainty



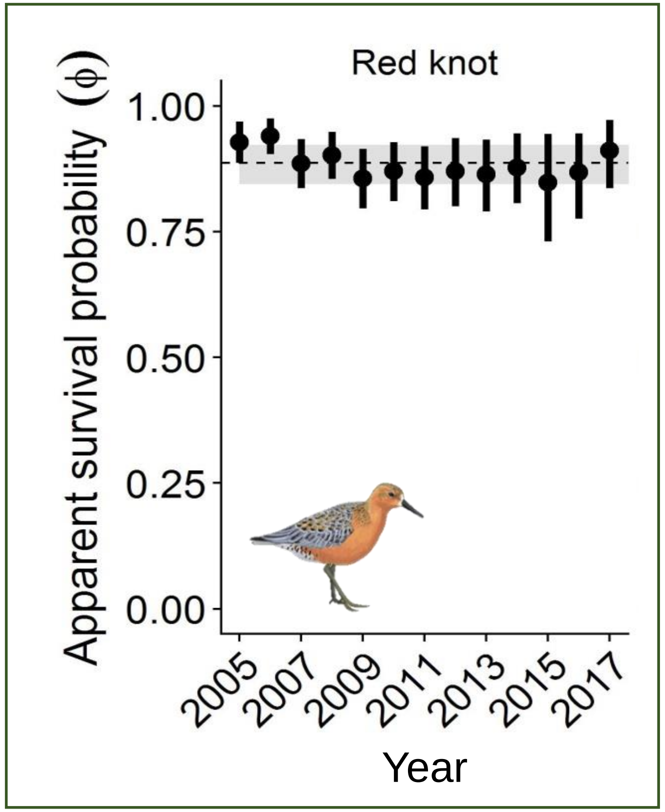
McGowan, C. P., M. C. Runge, and M. a. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Parametric uncertainty can be included for any input variable

- Vital rates
- Initial population size
- Carrying capacity
- Effects of stressors
- etc

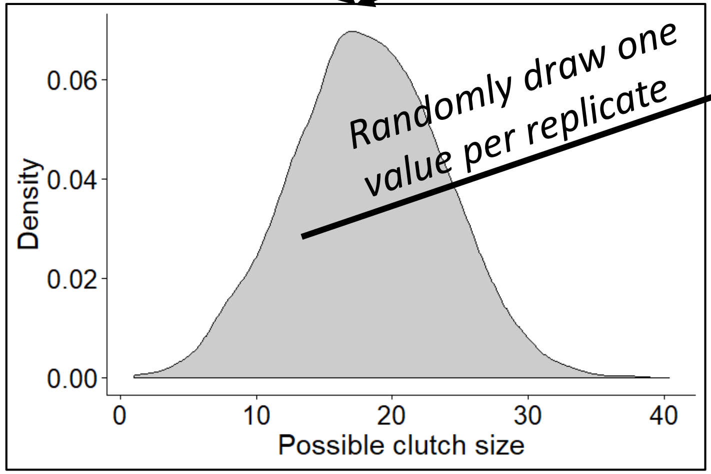
Environmental stochasticity

- Realized demographic rates in a given year usually vary stochastically based on random variation in the environment
- Estimating environmental stochasticity (process variation):
    - Analysis of long-term monitoring data (primary analysis or literature)
    - Expert elicitation
    - Assume that all demographic rates vary within some percent of the average among years



Overall average
$average = 18.2$

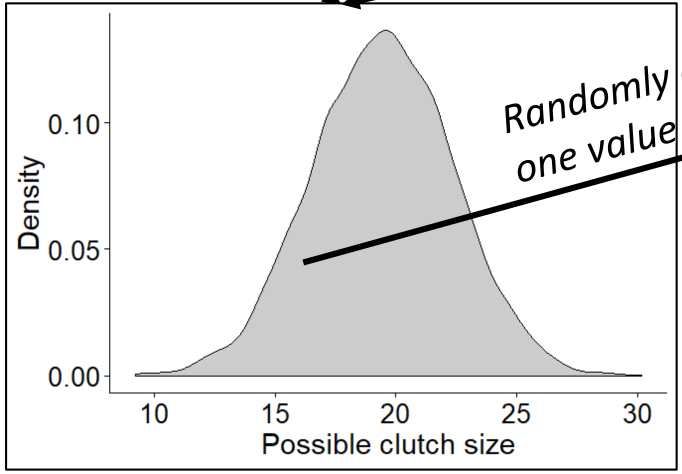
Parametric uncertainty
$SD = 5.6$



Randomly draw one value per replicate

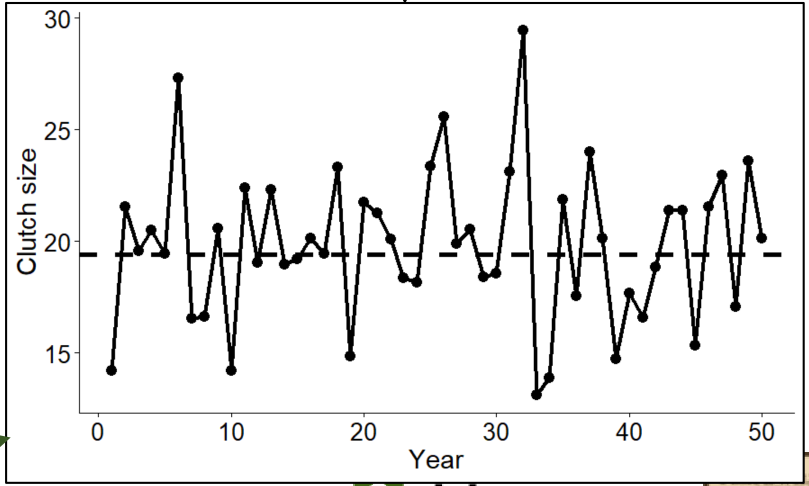
Replicate average
$average = 19.4$

15% annual variation
$SD = 19.4 * 0.15 = 2.91$



Randomly draw one value per year

Year-specific values



Parametric uncertainty – uncertainty about the true average value

Environmental stochasticity – random variation in realized rates from year to year

Demographic stochasticity

- Animals live or die as whole animals - not as fractions
  - *Without demographic stochasticity:* If average survival probability = 0.8, 6 individuals * 0.8 = 4.8 individuals at the next time step
- Demographic stochasticity refers to the random variation among individuals as to who lives or dies (or grows or reproduces) in a given year
  - *With demographic stochasticity*: Use Binomial distribution to determine who survives with probability = 0.8 for each "coin flip"
- Especially important to consider for small populations

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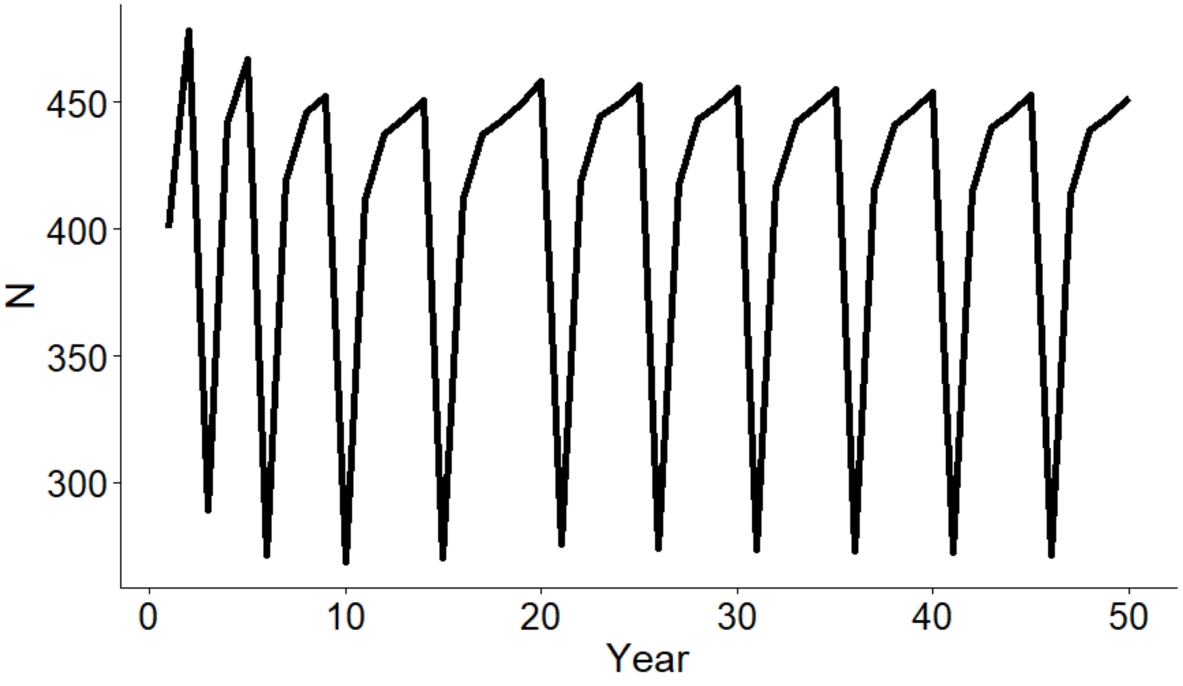
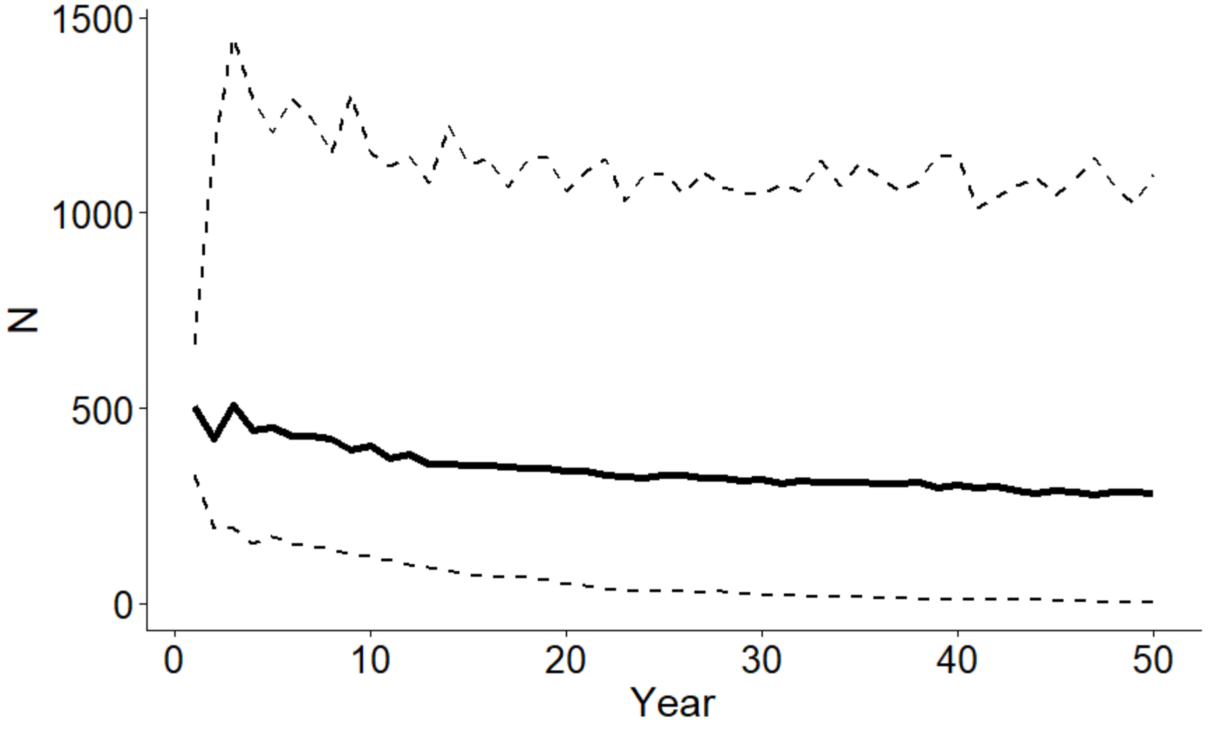
Deterministic projection



Stochastic projection with parametric uncertainty, environmental stochasticity, and demographic stochasticity (1000 reps)



Break?

Lecture outline

- Building a matrix model
- Accounting for uncertainty and stochasticity
- Implementing future scenarios

Implementing future scenarios

- Use sensitivity analysis to inform how the population will respond to future conditions
- Determine how environmental stressors and management actions will influence vital rates (arrows in the life cycle diagram), project the population under a few discrete scenarios
- Use triple-loop replication to project the population under a range of possible conditions, evaluate the importance of stressors using GLM

Simpler

More complex

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Implementing future scenarios

- Use sensitivity analysis to inform how the population will respond to future conditions

Sonoran desert tortoise

Global Ecology and Conservation 12 (2017) 119–130

Contents lists available at ScienceDirect

Global Ecology and Conservation

journal homepage: http://www.elsevier.com/locate/gecco

Original Research Article

Incorporating population viability models into species status assessment and listing decisions under the U.S. Endangered Species Act

Conor P. McGowan [a,*], Nathan Allan [b], Jeff Servoss [c], Shaula Hedwall [d], Brian Wooldridge [d]

[a] U.S. Geological Survey, Alabama Cooperative Fish and Wildlife Research Unit, Auburn University, Auburn, AL 36849, United States
[b] U.S. Fish and Wildlife Service, Southwest Region, Ecological Services, Austin, TX 78613, United States
[c] U.S. Fish and Wildlife Service, Arizona Ecological Services Office, Tucson, AZ 85745, United States
[d] U.S. Fish and Wildlife Service, Arizona Ecological Services Office, Flagstaff, AZ 86001, United States

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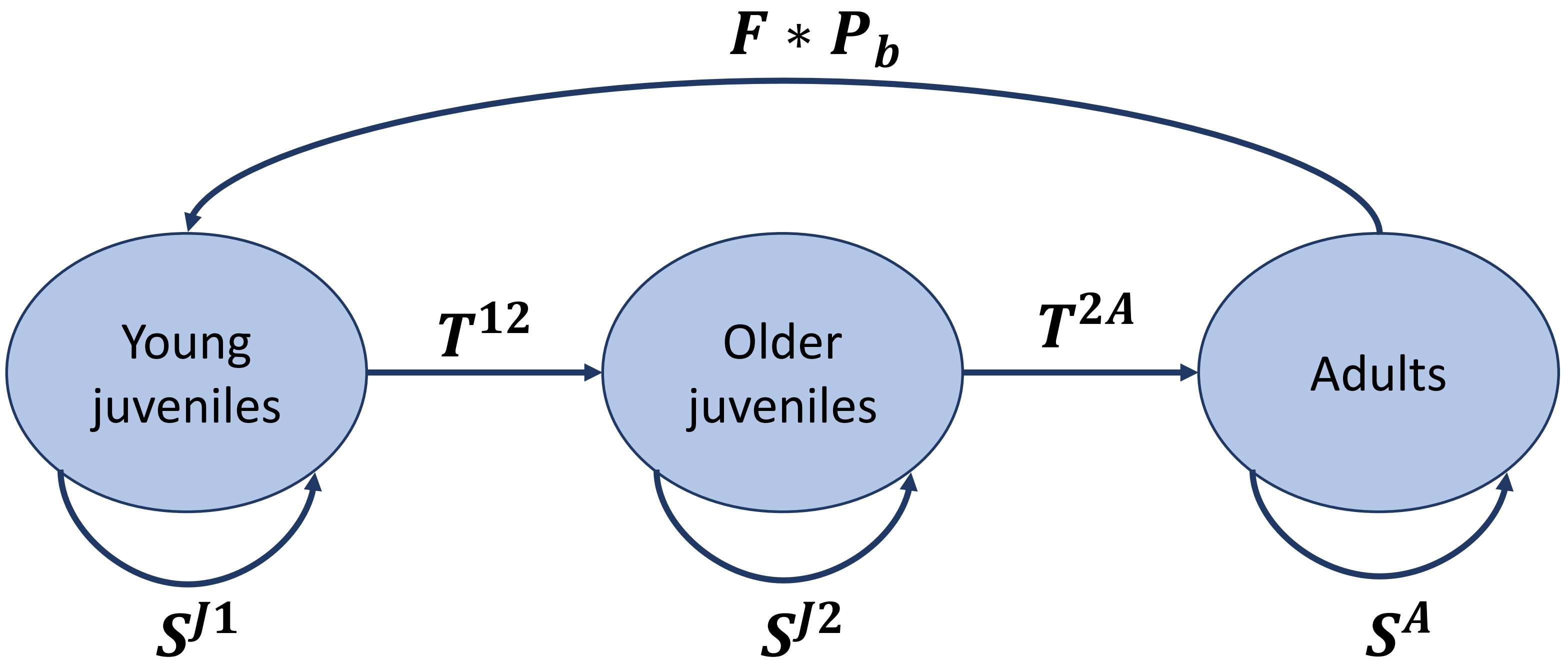
Sonoran desert tortoise life cycle model



$$\begin{bmatrix} N_t^{J1} \\ N_t^{J2} \\ N_t^{A} \end{bmatrix} = \begin{bmatrix} \boldsymbol{S^{J1}} & \mathbf{0} & \boldsymbol{F * P_b} \\ \boldsymbol{T^{12}} & \boldsymbol{S^{J2}} & \mathbf{0} \\ \mathbf{0} & \boldsymbol{T^{2A}} & \boldsymbol{S^{A}} \end{bmatrix} x \begin{bmatrix} N_{t-1}^{J1} \\ N_{t-1}^{J2} \\ N_{t-1}^{A} \end{bmatrix}$$

Sensitivity analysis

- Which vital rate(s) is most important for population stability?
- Elasticity = the proportional change in population growth rate (λ) resulting from a 1% change in each rate
- Can calculate using the poptools add-in for Excel or popbio package for R

Population matrix → $\begin{bmatrix} S^{J1} & 0 & F * P_b \\ T^{12} & S^{J2} & 0 \\ 0 & T^{2A} & S^{A} \end{bmatrix}$ → $\begin{bmatrix} 0.006 & 0 & 1.3 \\ 0.083 & 0.67 & 0 \\ 0 & 0.1 & 0.95 \end{bmatrix}$

Elasticity matrix → $\begin{bmatrix} 0 & 0 & 0.031 \\ 0.031 & 0.066 & 0 \\ 0 & 0.031 & 0.841 \end{bmatrix}$

Position with the greatest value corresponds to the vital rate that has the strongest effect on λ

1% change in adult survival will result in a 84.1% change in λ

Using elasticities to assess future conditions

- Using sensitivity and/or elasticity output (example)
  - Results indicate population growth is most sensitive to **adult survival**
    - Conceptual modeling and lit review suggest that adult survival is negatively affected by drought frequency
    - Climate projections indicate that drought frequency will increase over next 50 years
  - What can we expect given this information?
    - Adult survival will likely decrease
    - Population growth will likely decrease
    - If climate predictions are accurate, future resiliency will decrease

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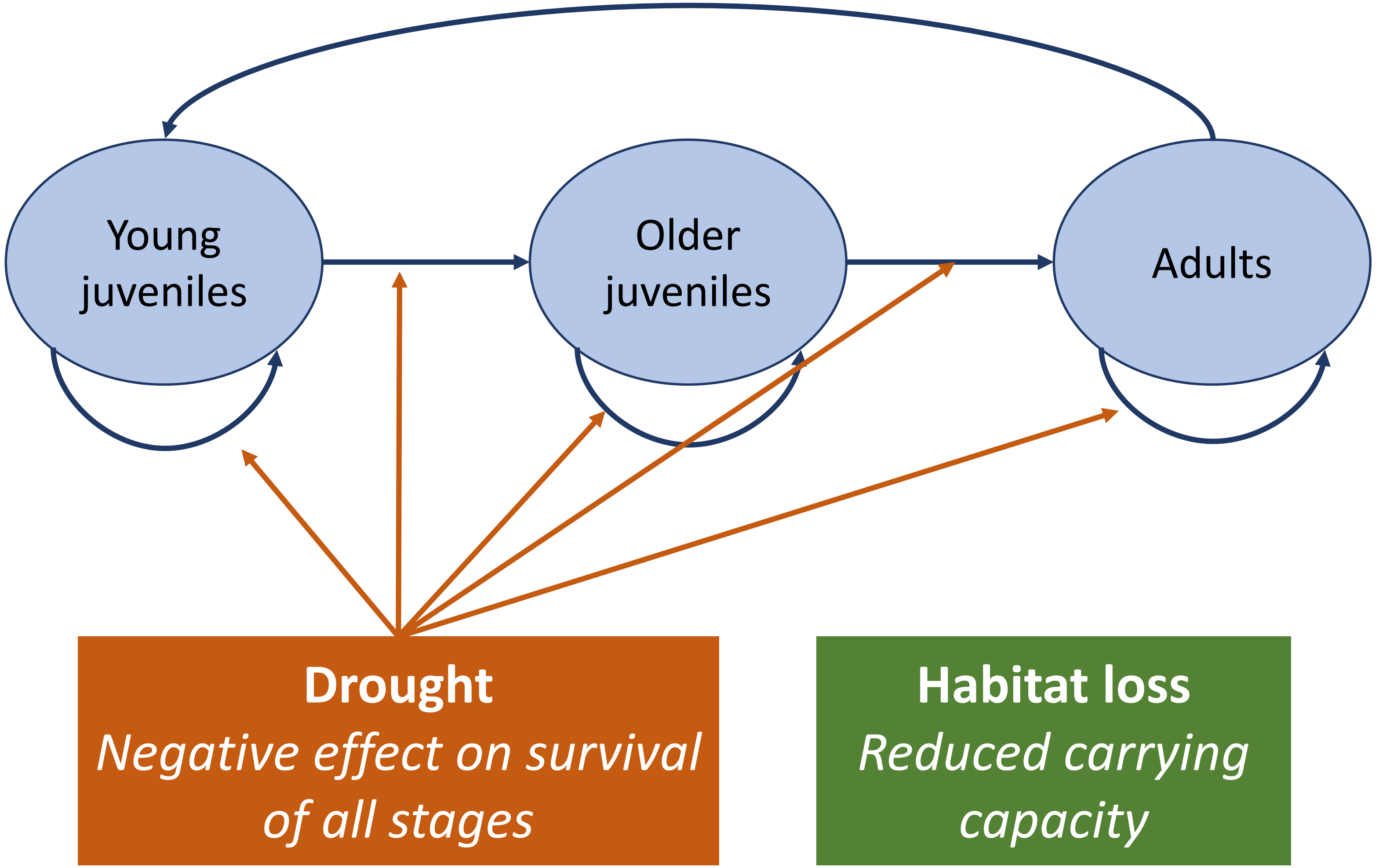
Implementing future scenarios

- Use sensitivity analysis to inform how the population will respond to future conditions
- Determine how environmental stressors and management actions will influence vital rates (arrows in the life cycle diagram), project the population under a few discrete scenarios

Key threats = drought and habitat loss



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Modeling drought

- Used historical drought data to estimate the annual proportion of the range affected by drought and variability
- In each model replicate, randomly draw proportion of range affected by drought
- Survival rates are a weighted average of animals exposed and not exposed to drought

$$S_t^A = \underbrace{(P_{drought} * S_t^A * DE_t)}_{\textit{Exposed to drought}} + \underbrace{((1 - P_{drought}) * S_t^A)}_{\textit{Not exposed to drought}}$$

Proportion of range exposed to drought

Drought effect:
1% - 20% reduction in survival

Can model droughts with different magnitudes and extents by varying inputs for $\boldsymbol{P_{drought}}$ and $\boldsymbol{DE}$

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Modeling habitat loss

- Included a ceiling density dependence function—if population exceeded carrying capacity, $\boldsymbol{P_b} = 0$
- Carrying capacity (Pop_{max}) determined based on amount of habitat available in different types and estimates of tortoise density in each habitat type

$$Pop_{max} = (D_P + A_P) + (D_S + A_S) + (D_T + A_T)$$

Density in primary habitat (17.1 per km^2)

Area of primary habitat (km^2)

Can model changes in habitat area and quality by varying inputs for $\boldsymbol{A_P}$, $\boldsymbol{A_S}$, or $\boldsymbol{A_T}$

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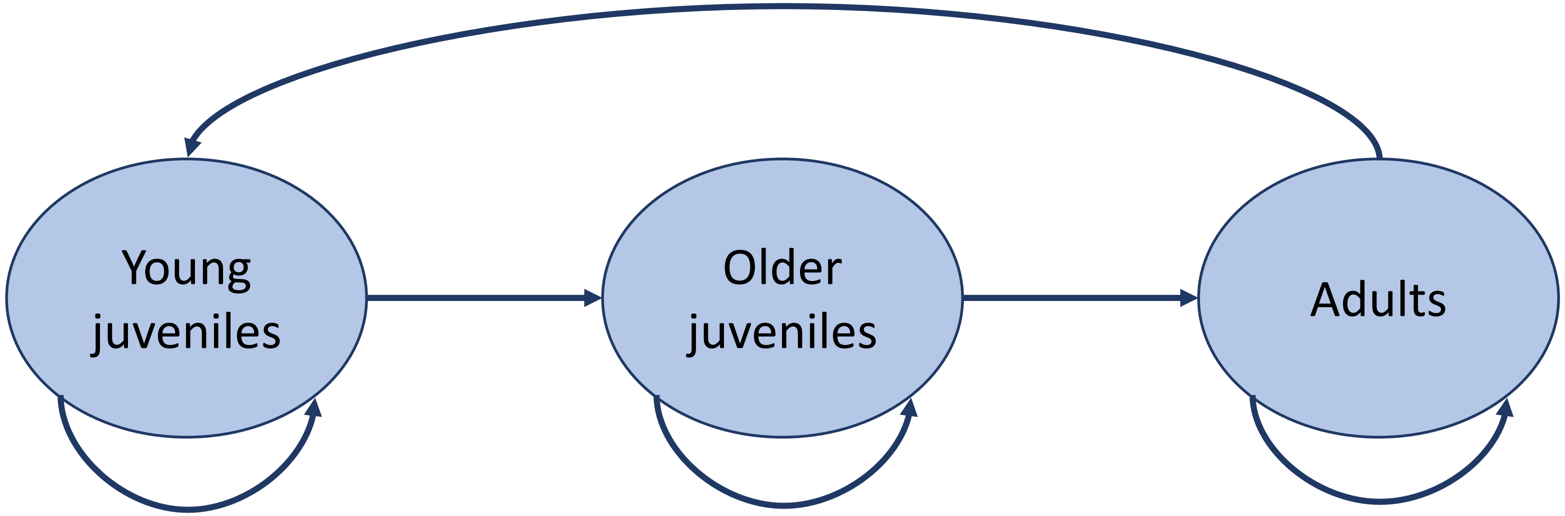
Choosing future scenarios

- Use the conceptual model and sensitivity analysis to guide scenarios
  - What ecological factors affect the most sensitive parameters?
- Design scenarios to explore the expected range of future variation in important covariates



Choosing future scenarios

- Identify key stressors and define relationships between stressors and demographic rates
- Develop a few discrete scenarios, run with different model inputs and compare results

Scenario	Drought extent	Drought severity	Habitat area	Habitat quality
1	=	↑	=	↓
2	↑	↑	=	=
3	=	=	↓	↓
4	↑	↑	↓	↓

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Table 1

Predicted population growth rates, change in median female abundances, and the probabilities of quasi-extinction (model outputs) for the baseline, four continuation of current conditions scenarios (“Scenarios 1–4”), and four projected future conditions scenarios (“Scenarios 5–8”) in Arizona, U.S. at 50 and 100 years into the future. The scenarios had varying droughts, maximum population sizes (Max Pop), habitat loss rates, initial population sizes (Initial Pop), and quasi-extinction thresholds (Qe threshold).

Scenario inputs						Scenario outputs				
	Drought	Max Pop	Habitat loss rate	Initial Pop	Qe Threshold	Population growth rate	Median population change, 50 years	Qe 50 yrs	Median population change, 100 years	Qe 100 yrs
Baseline	Historic Drought	320,000	0	320,000	7000	0.997	6433	0.000	−3294	0.000
Scenario 1	Historic Drought 10%	290,000	0	290,000	7000	0.996	−12,507	0.000	−33,684	0.001
Scenario 2	Historic Drought 10%	140,000	0	140,000	12,000	0.996	−1880	0.000	−5887	0.031
Scenario 3	Historic Drought 10%	240,000	0	240,000	7000	0.995	−5726	0.000	−10,987	0.002
Scenario 4	Historic Drought 10%	120,000	0	120,000	12,000	0.995	−789	0.000	−6076	0.031
Scenario 5	Historic Drought 15%	290,000	9%	290,000	7000	0.996	−7955	0.000	−26783	0.000
Scenario 6	Historic Drought 15%	140,000	9%	140,000	12,000	0.996	−2575	0.000	−13767	0.030
Scenario 7	Historic Drought 25%	240,000	9%	240,000	7000	0.995	−14323	0.000	−42031	0.001
Scenario 8	Historic Drought 25%	120,000	9%	120,000	12,000	0.995	−11247	0.000	−28780	0.047

Implementing future scenarios

- Use sensitivity analysis to inform how the population will respond to future conditions
- Determine how environmental stressors and management actions will influence vital rates (arrows in the life cycle diagram), project the population under a few discrete scenarios
- Use triple-loop replication to project the population under a range of possible conditions, evaluate the importance of stressors using GLM

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Evaluate range of future scenarios using GLMs

- Generate lots of output values (abundance, P(extinction), etc.) with lots of corresponding input values
  - Evaluate stressors across entire range of possible values, not just a few
- Use a multi-variate GLM to assess the importance of each variable of interest:
  - $\mathrm{P}(extinction) \sim b_1(Initial\ N) + b_2(drought\ freq) + b_3(MaxPop)$

    (this is a binomial GLM)

- Determine which factors most effect the output metric of interest (here, quasi-extinction probability)

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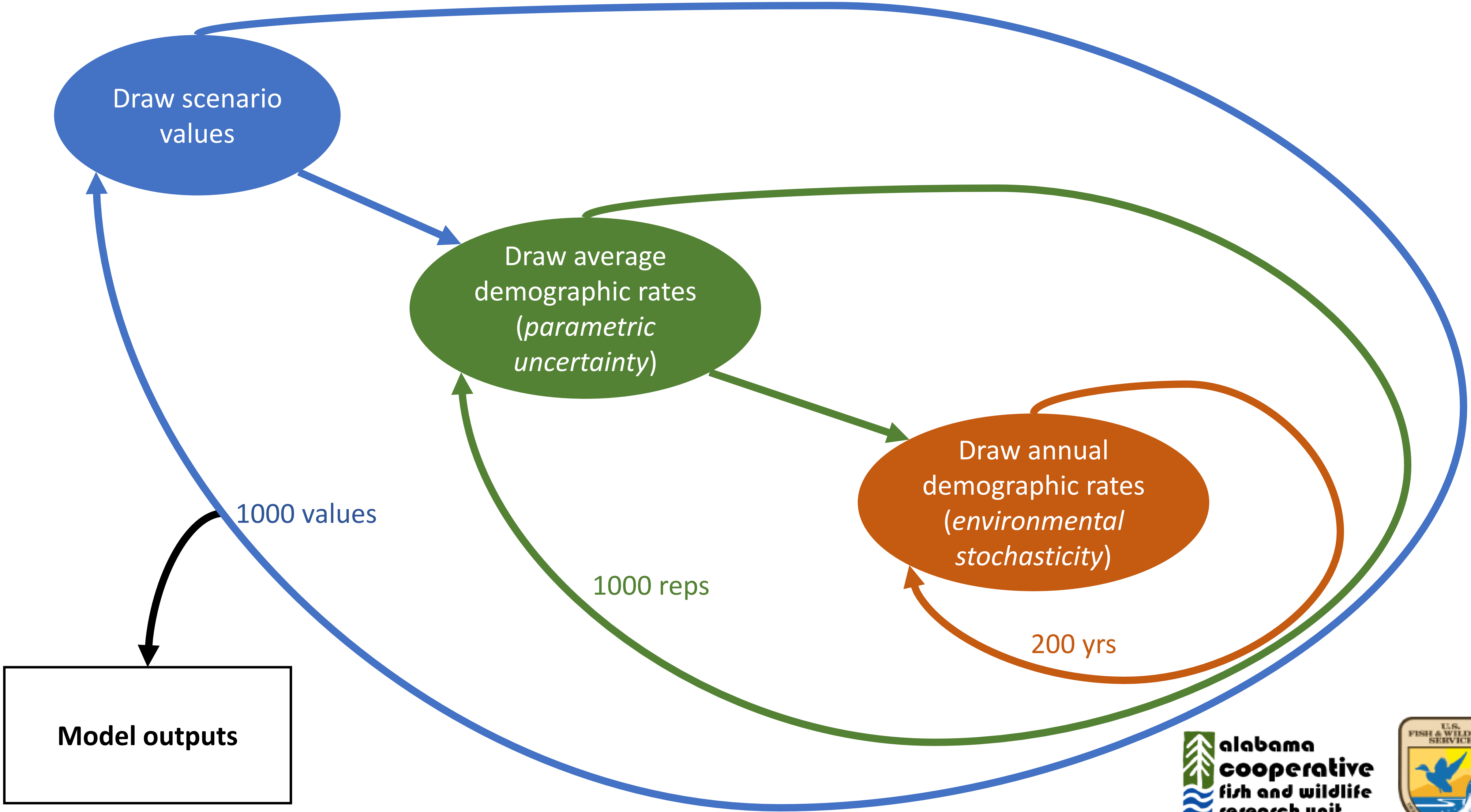
Draw scenario values
Draw average demographic rates (*parametric uncertainty*)
Draw annual demographic rates (*environmental stochasticity*)
1000 values
1000 reps
200 yrs
Model outputs

GLM output

- MDR = mean drought rate
- NAI = Initial Number of adults
- MaxPop = habitat based maximum population size

$$P(Qe100) =- 5.602 + (18.42\ x\ MDR) - (5.363e - 6x\ NAI) - (1.797e - 6x\ MaxPop)$$

Drought exposure has a large, positive effect on quasi-extinction probability

GLM output

Table 3
Quasi-extinction probability (i.e., the probability of falling below 8000 females) at 100 years, given 350,000 females as the maximum population size and varying values for initial female abundance and mean drought exposure.

100 years	Max pop = 350,000 females						
	Starting population size						
Magnitude of drought	100,000	150,000	200,000	250,000	300,000	350,000	400,000
0.10	0.013	0.010	0.008	0.006	0.005	0.004	0.003
0.15	0.033	0.025	0.019	0.015	0.011	0.009	0.007
0.20	0.078	0.061	0.047	0.037	0.028	0.022	0.017
0.25	0.176	0.141	0.111	0.087	0.068	0.053	0.041
0.30	0.349	0.291	0.239	0.194	0.155	0.123	0.097

Review

- Matrix population models use species life history to make predictions about future population size
  - Useful when we know a good amount about the basic ecology but don't have a lot of historic/current monitoring data
- Outputs can be used to assess current and future resiliency (population growth rate, quasi-extinction probability, etc.)
- Important to include sources of uncertainty/stochasticity to capture all uncertainties and avoid overly-precise projections
- Scenarios built on knowledge of how stressors influence specific demographic rates

Questions