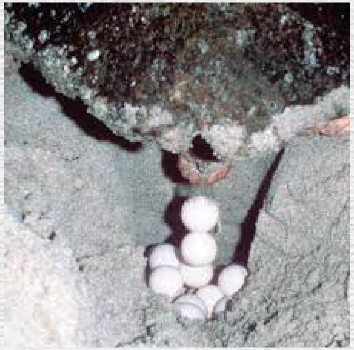
Sensitivity analysis

Which demographic rates are most important to a population's stability?

The real value of demographic monitoring – knowing what's broken

- Measuring population growth rate is important
  - Provides trend information from a (relatively) short time series
  - Mechanistic – based on the actual birth/death processes that determine the growth rate
- If the population is declining, what to do?
- Example of the loggerhead sea turtle, with $\lambda = 0.945$

Threats on the beach



Direct, observable, personal

For sea turtles, the beach is about reproduction

- Adult mortality on beaches *can* be a problem
  - Primarily due to poaching
  - But, poaching is illegal now – if enforced effectively, adult mortality on the beach is low
- Most of the persistent problems for turtles on the beach are about reproduction
- Headstarting increases fecundity

Headstarting

That feels so much better!
Does it work?

https://youtu.be/MRrJ2B1nLzM

Is headstarting enough?

- Fecundity is often not terribly important to a long-lived species
  - Adults have many opportunities to breed
  - Only need to replace themselves on average for population stability
  - Large numbers of offspring produced implies heavy mortality is to be expected
- Is it possible to stabilize the population by only improving reproduction?

The matrix model

TABLE 4. Stage-class population matrix for loggerhead sea turtles based on the life table presented in Table 3. For the general form of the matrix and formulae for calculating the matrix elements see Theoretical Population Projections.

From

To

	Eggs, hatchlings	Small juveniles	Large juveniles	Subadults	Novice breeders	1st-yr remigrants	Mature breeders
Eggs, hatchlings	0	0	0	0	127	4	80
Small juveniles	0.6747	0.7370	0	0	0	0	0
Large juveniles	0	0.0486	0.6610	0	0	0	0
Subadults	0	0	0.0147	0.6907	0	0	0
Novice breeders	0	0	0	0.0518	0	0	0
1st-yr remigrants	0	0	0	0	0.8091	0	0
Mature breeders	0	0	0	0	0	0.8091	0.8089

Estimating λ

	A	B	C	D	E	F	G	H
1		Hatchlings	Small juvie	Large juvie	Subad.	Novice breed.	1st yr remig.	Mature breeders
2	Hatchlings	0	0	0	0	127	4	80
3	Small juvie	0.6747	0.737	0	0	0	0	0
4	Large juvie	0	0.0486	0.661	0	0	0	0
5	Subad.	0	0	0.0147	0.6907	0	0	0
6	Novice breed.	0	0	0	0.0518	0	0	0
7	1st yr remig.	0	0	0	0	0.8091	0	0
8	Mature breeders	0	0	0	0	0	0.8091	0.8089
9								
10		Lambda	0.945030963					
11								
12	L - lambda I	-0.945030963	0	0	0	127	4	80
13		0.6747	-0.208030963	0	0	0	0	0
14		0	0.0486	-0.284030963	0	0	0	0
15		0	0	0.0147	-0.254330963	0	0	0
16		0	0	0	0.0518	-0.945030963	0	0
17		0	0	0	0	0.8091	-0.945030963	0
18		0	0	0	0	0	0.8091	-0.136130963
19								
20		Determ.	6.46124E-10					

Measuring the effect of each demographic rate on λ

- We want to know: how important is each demographic rate have to λ?
- Two basic approaches:
  - Sensitivity = change in λ per unit change in a parameter
  - Elasticity = percent change in λ per percent change in a parameter
- Can be estimated empirically, or analytically

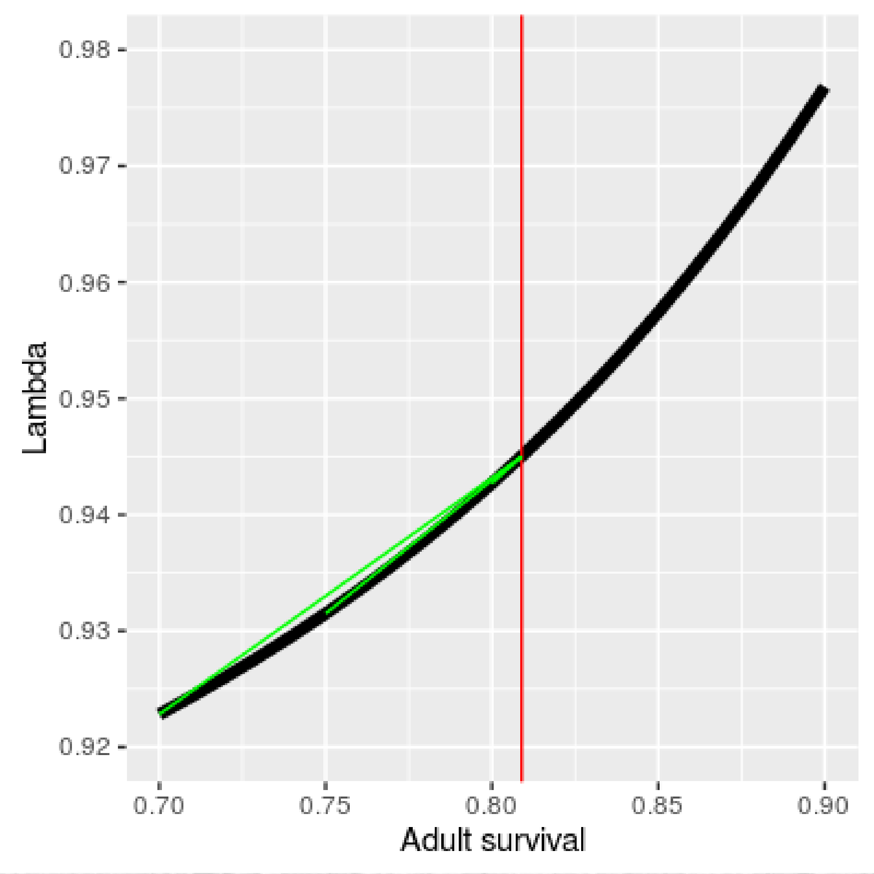
Empirically

Change the parameter (adult survival) by a small amount

Calculate the new λ

Divide the change in λ by the change in the parameter

The smaller the change in parameter the better the estimate



The empirical approach to sensitivity

1. Change one parameter by 0.01

	A	B	C	D	E	F	G	H
1		Hatchlings	Small juvie	Large juvie	Subad.	Novice breed.	1st yr remig.	Mature breeders
2	Hatchlings	0	0	0	0	127	4	80
3	Small juvie	0.6647	0.737	0	0	0	0	0
4	Large juvie	0	0.0486	0.661	0	0	0	0
5	Subad.	0	0	0.0147	0.6907	0	0	0
6	Novice breed.	0	0	0	0.0518	0	0	0
7	1st yr remig.	0	0	0	0	0.8091	0	0
8	Mature breeders	0	0	0	0	0	0.8091	0.8089
9								
10		Lambda	0.945030963		Lambda for sens.	0.944312609		
11								

2. Use Solver to estimate the new lambda value

3. Divide the difference between the lambdas by the difference between the parameters (0.01)

Parameter	Empirical sensitivity
T hatchling	0.0717

One parameter at a time...

0. Set first one back to its actual value

1. Change the next one by 0.01

	A	B	C	D	E	F	G	H
1		Hatchlings	Small juvie	Large juvie	Subad.	Novice breed.	1st yr remig.	Mature breeders
2	Hatchlings	0	0	0	0	127	4	80
3	Small juvie	0.6747	0.727	0	0	0	0	0
4	Large juvie	0	0.0486	0.661	0	0	0	0
5	Subad.	0	0	0.0147	0.6907	0	0	0
6	Novice breed.	0	0	0	0.0518	0	0	0
7	1st yr remig.	0	0	0	0	0.8091	0	0
8	Mature breeders	0	0	0	0	0	0.8091	0.8089
9								
10		Lambda	0.945030963		Lambda for sens.	0.942757182		

2. Use Solver to estimate the new lambda value

3. Divide the difference between the lambdas by the difference between the parameters (0.01)

Parameter	Empirical sensitivity
T hatchling	0.0717
S small juvie	0.2273

The full set

Parameter	Empirical sensitivity
T hatchling	0.0717
S small juvie	0.2273
T small juvie	1.0787
S large juvie	0.1669
T large juvie	4.7659
S subad.	0.1862
T subad.	1.0064
T novice	0.0456
T 1st yr	0.0452
S mature	0.2608
F novice	3.32E-08
F 1st yr	3.32E-08
F mature	0.0004

Analytical approach

- Instantaneous – slope of a line tangent to the relationship between the parameter and λ
- Sensitivities can be calculated from:
  - Stable age distribution (derived from **right eigenvector**)
  - Reproductive values (derived from **left eigenvector**)
- Remember, we calculated stable age distribution by recognizing:

$$Lw = \lambda w$$

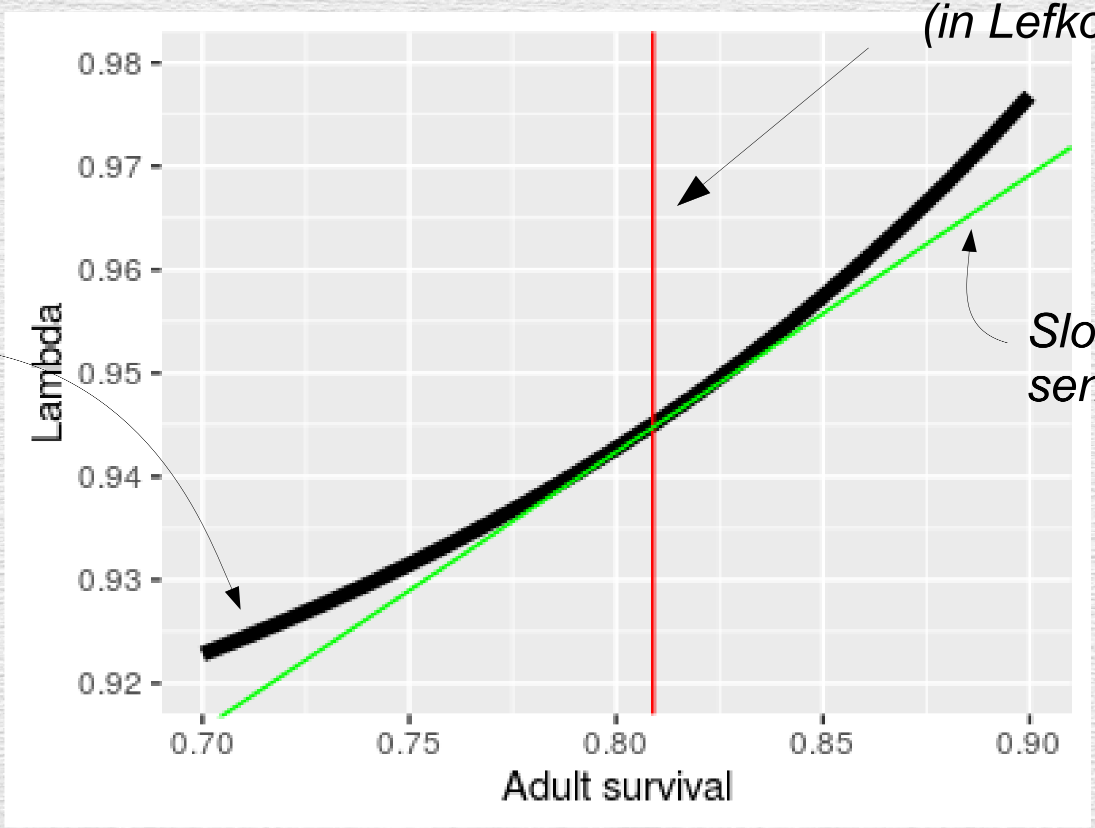
- We can get the left eigenvector the same way

$$vL = v\lambda$$

Analytical sensitivity is the slope of a tangent line at the estimate

Adult survival estimate (in Lefkovitch matrix)

Relationship between growth rate and adult survival



Slope of this line is sensitivity

Right eigenvector → stable age

	A	B	C	D	E	F	G	H	I	J	K	L	M
1		H	SJ	LJ	SuA	NB	1Y	MB		Stable age (w)		L w	Lambda w
2	Hatchlings	0	0	0	0	127	4	80		0.2065		0.195	0.195
3	Small juvie	0.6747	0.737	0	0	0	0	0		0.6698		0.633	0.633
4	Large juvie	0	0.0486	0.661	0	0	0	0		0.1146		0.108	0.108
5	Subad.	0	0	0.0147	0.6907	0	0	0		0.0066		0.006	0.006
6	Novice breed.	0	0	0	0.0518	0	0	0		0.0004		0.000	0.000
7	1st yr remig.	0	0	0	0	0.8091	0	0		0.0003		0.000	0.000
8	Mature breeders	0	0	0	0	0	0.8091	0.8089		0.0018		0.002	0.002
9													
10		Lambda	0.945031								SS	1.22188E-16	
11													

Left eigenvector → reproductive value

	A	B	C	D	E	F	G	H
1		H	SJ	LJ	SuA	NB	1Y	MB
2	Hatchlings	0	0	0	0	127	4	80
3	Small juvie	0.6747	0.737	0	0	0	0	0
4	Large juvie	0	0.0486	0.661	0	0	0	0
5	Subad.	0	0	0.0147	0.6907	0	0	0
6	Novice breed.	0	0	0	0.0518	0	0	0
7	1st yr remig.	0	0	0	0	0.8091	0	0
8	Mature breeders	0	0	0	0	0	0.8091	0.8089
9								
10		Lambda	0.945031					
11								
12		Determ.	5.9E-11					
13								
14	Reproductive value (v)	0.000559	0.000783	0.003353	0.064788	0.318099	0.283755	0.328662
15								
16	vL	0.000529	0.00074	0.003169	0.061226	0.300613	0.268158	0.310596
17	v Lambda	0.000529	0.00074	0.003169	0.061226	0.300613	0.268158	0.310596
18								
19	SS	1.2E-13						
20								

Reproductive value is the average contribution of individuals in an age class to the population

VW

									Stable age (w)
Reproductive value (v)	0.0006	0.0008	0.0034	0.0648	0.3181	0.2838	0.3287	x	0.207
									0.670
									0.115
									0.007
									0.000
		vw							0.000
0.0006x0.207 + 0.0008x0.670 + ... =		**0.0023**							0.002

Matrix multiply reproductive value (v) by stable age (w) – single number

Calculating sensitivity

1. Multiply the "from" class stable age...

	H	SJ	LJ	SuA	NB	1Y	MB		Stable age (w)
Hatchlings	0	0	0	0	127	4	80		0.207
Small juvie	0.6747	0.737	0	0	0	0	0		0.670
Large juvie	0	0.0486	0.661	0	0	0	0		0.115
Subad.	0	0	0.0147	0.6907	0	0	0		0.007
Novice breed.	0	0	0	0.0518	0	0	0		0.000
1st yr remig.	0	0	0	0	0.8091	0	0		0.000
Mature breeders	0	0	0	0	0	0.8091	0.8089		0.002
									vw
Reproductive value (v)	0.0006	0.0008	0.0034	0.0648	0.3181	0.2838	0.3287		**0.0023**
	Sensitivity of lambda to:								
	T hatching	0.071							

2. ..by the "to" class reproductive value...

3. ...divide the product by vw

Sensitivity from w and v

- The full set of empirical and analytical sensitivities
- Not identical – analytical is instantaneous, better

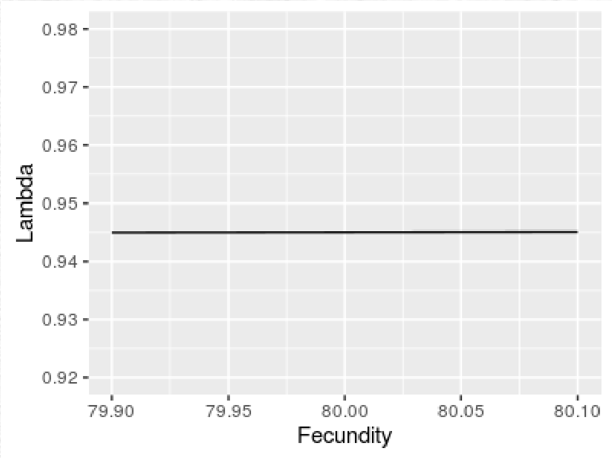
Parameter	Empirical sensitivity	Analytical sensitivity
T hatchling	0.0717	0.0714
S small juvie	0.2273	0.2317
T small juvie	1.0787	0.9917
S large juvie	0.1669	0.1697
T large juvie	4.7659	3.2788
S subad.	0.1862	0.1895
T subad.	1.0064	0.9305
T novice	0.0456	0.0455
T 1st yr	0.0452	0.0451
S mature	0.2608	0.2681
F novice	3.32E-08	0.0001
F 1st yr	3.32E-08	0.0001
F mature	0.0004	0.0005

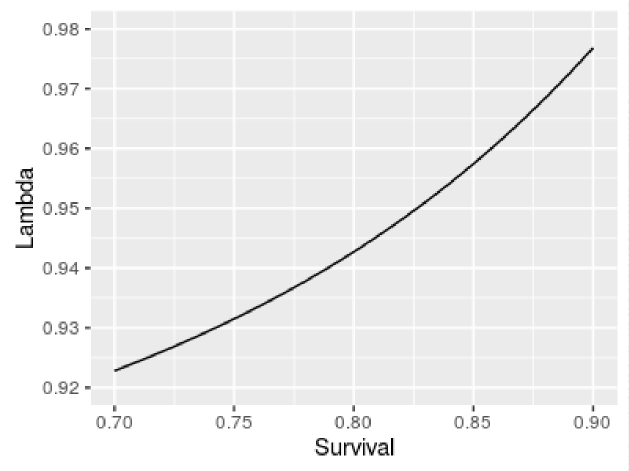
Differences in units make sensitivities hard to interpret

- Sensitivities for reproduction are low, but the scale is very different
  - Fecundities can be any positive number (can be huge)
  - Survival is constrained to fall between 0 and 1
- Elasticity scales the sensitivities to a proportional scale
  - If we changed each parameter by the same proportional amount (10% of the value, rather than the same 0.01) we would measure elasticity
- Analytically, if we multiply sensitivity by the parameter and then divide by λ we get elasticity

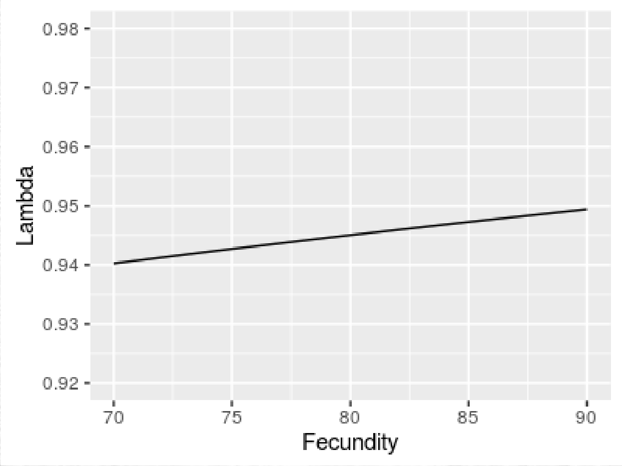
	Adult fecundity	Adult survival

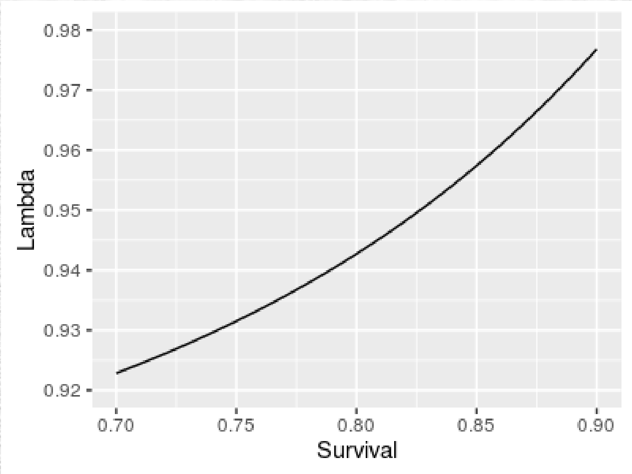
Sensitivity – change in lambda with the same small amount of change in the parameter





Elasticity – change in lambda with the same small proportional change in the parameter





Elasticity is a unitless ratio

$$sensitivity = \frac{\partial \lambda}{\partial s}$$

$$elasticity = \frac{\partial \lambda}{\partial s} \times \frac{s}{\lambda} = \frac{\partial \lambda}{\lambda} \div \frac{\partial s}{s}$$

Elasticities

Parameter	Empirical sensitivity	Analytical sensitivity	Elasticity
T hatchling	0.0717	0.0714	0.0510
S small juvie	0.2273	0.2317	0.1807
T small juvie	1.0787	0.9917	0.0510
S large juvie	0.1669	0.1697	0.1187
T large juvie	4.7659	3.2788	0.0510
S subad.	0.1862	0.1895	0.1385
T subad.	1.0064	0.9305	0.0510
T novice	0.0456	0.0455	0.0390
T 1st yr	0.0452	0.0451	0.0386
S mature	0.2608	0.2681	0.2295
F novice	3.32E-08	0.0001	0.0121
F 1st yr	3.32E-08	0.0001	0.0003
F mature	0.0004	0.0005	0.0386

What the elasticities tell us

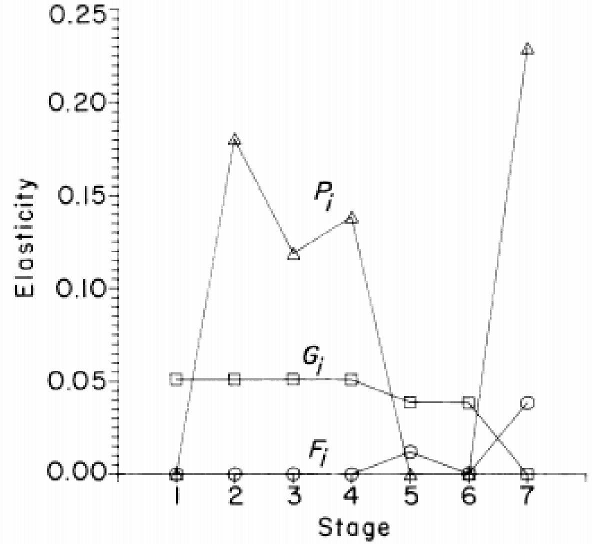


FIG. 3. The elasticity, or proportional sensitivity, of λ_m to changes in fecundity F_i (○), survival while remaining in the same stage P_i (△), and survival with growth G_i (□). Because the elasticities of these matrix elements sum to 1, they can be compared directly in terms of their contribution to the population growth rate r.

The most important parameter is mature adult survival

The most important fecundity parameter is fecundity of mature adults, but it is never nearly as important as adult survival

Some caveats...

- No matter how small the sensitivity/elasticity, no parameter can drop to 0 and have the population persist
- There are other considerations
  - Headstarting is a way for people to get involved in sea turtle conservation
  - Baby turtles make people care more about sea turtles
- But, if you want to actually stop the population decline, you'll have a bigger impact by protecting adults

Management alternatives

- What can be done?
- How much improvement is needed to stabilize the population?
- Headstarting – how many more offspring per individual needed to achieve a λ of 1?

Improvement to reproduction needed

	H	SJ	LJ	SuA	NB	1Y	MB
Hatchlings	0	0	0	0	127	4	80
Small juvie	0.6747	0.737	0	0	0	0	0
Large juvie	0	0.0486	0.661	0	0	0	0
Subad.	0	0	0.0147	0.6907	0	0	0
Novice breed.	0	0	0	0.0518	0	0	0
1st yr remig.	0	0	0	0	0.8091	0	0
Mature breeders	0	0	0	0	0	0.8091	0.8089
	Lambda	1					
	Determ.	-0.0033					

2. Have solver increase adult fecundity...

1. Set lambda to 1

3. ...until the determinant is 0

Huge increase needed...

	H	SJ	LJ	SuA	NB	1Y	MB
Hatchlings	0	0	0	0	127	4	284.384
Small juvie	0.6747	0.737	0	0	0	0	0
Large juvie	0	0.0486	0.661	0	0	0	0
Subad.	0	0	0.0147	0.6907	0	0	0
Novice breed.	0	0	0	0.0518	0	0	0
1st yr remig.	0	0	0	0	0.8091	0	0
Mature breeders	0	0	0	0	0	0.8091	0.8089
	Lambda	1		Multiple	3.5548		
	Determ.	3.3E-10					

...even if all three fecundities increased

	H	SJ	LJ	SuA	NB	1Y	MB
Hatchlings	0	0	0	0	346.939	10.9272	218.544
Small juvie	0.6747	0.737	0	0	0	0	0
Large juvie	0	0.0486	0.661	0	0	0	0
Subad.	0	0	0.0147	0.6907	0	0	0
Novice breed.	0	0	0	0.0518	0	0	0
1st yr remig.	0	0	0	0	0.8091	0	0
Mature breeders	0	0	0	0	0	0.8091	0.8089
	Lambda	1		Multiple	2.7318		
	Determ.	-6E-18					

Fecundity would have to increase by 2.7318 times for all age classes to stabilize the population

Increasing adult survival...

	H	SJ	LJ	SuA	NB	1Y	MB
Hatchlings	0	0	0	0	127	4	80
Small juvie	0.6747	0.737	0	0	0	0	0
Large juvie	0	0.0486	0.661	0	0	0	0
Subad.	0	0	0.0147	0.6907	0	0	0
Novice breed.	0	0	0	0.0518	0	0	0
1st yr remig.	0	0	0	0	0.8091	0	0
Mature breeders	0	0	0	0	0	0.8091	0.94624
	Lambda	1		Multiple	1.16979		

A much smaller increase in adult survival alone stabilizes the population

...less still if all adult survival rates improve

	H	SJ	LJ	SuA	NB	1Y	MB
Hatchlings	0	0	0	0	127	4	80
Small juvie	0.6747	0.737	0	0	0	0	0
Large juvie	0	0.0486	0.661	0	0	0	0
Subad.	0	0	0.0147	0.6907	0	0	0
Novice breed.	0	0	0	0.0518	0	0	0
1st yr remig.	0	0	0	0	0.92928	0	0
Mature breeders	0	0	0	0	0	0.92928	0.92905
	Lambda	1		Multiple	1.14854		
	Determ.	1.4E-11					

Only a 14.8% increase in all adult survival probabilities needed to stabilize the population

Protecting adults

Turtle excluder devices

Pollution control

Reducing dumping

Take-home: sensitivity/elasticity

- Elasticity is the better measure – unitless, better for comparing among rates
- Useful for identifying which demographic rates are most important for population growth/stability
- The models can be used to evaluate management alternatives
  - How much improvement is needed?
  - Is the amount of improvement needed achievable, or even possible?