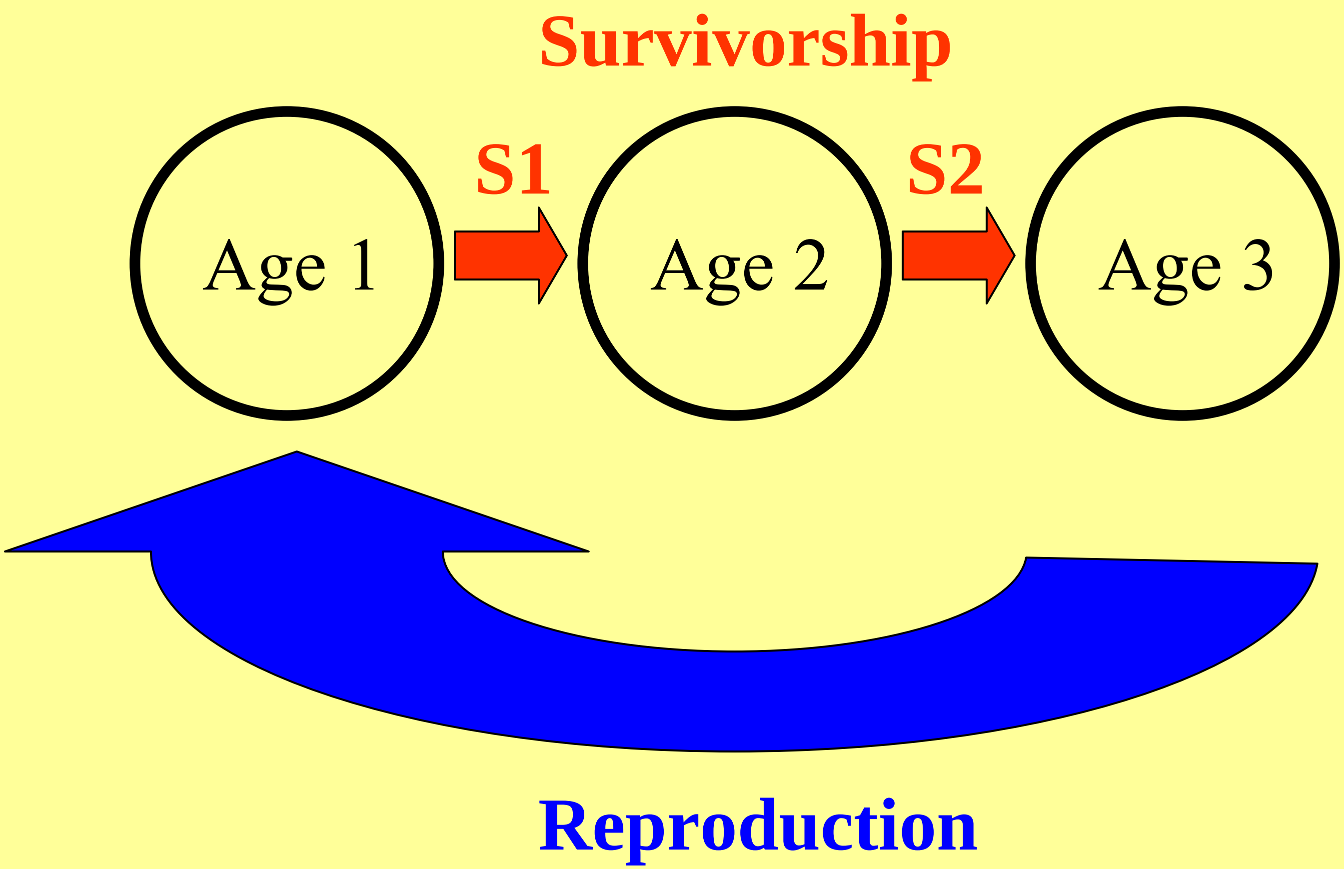
Leslie Matrix Modelling



Life Table Review

- Definition: Age (stage, size) specific schedule of a population used to calculate vital rates
- Important Terms:

x = age interval

n_x = number survivors start of age interval x

d_x = number dying during interval x to x+1

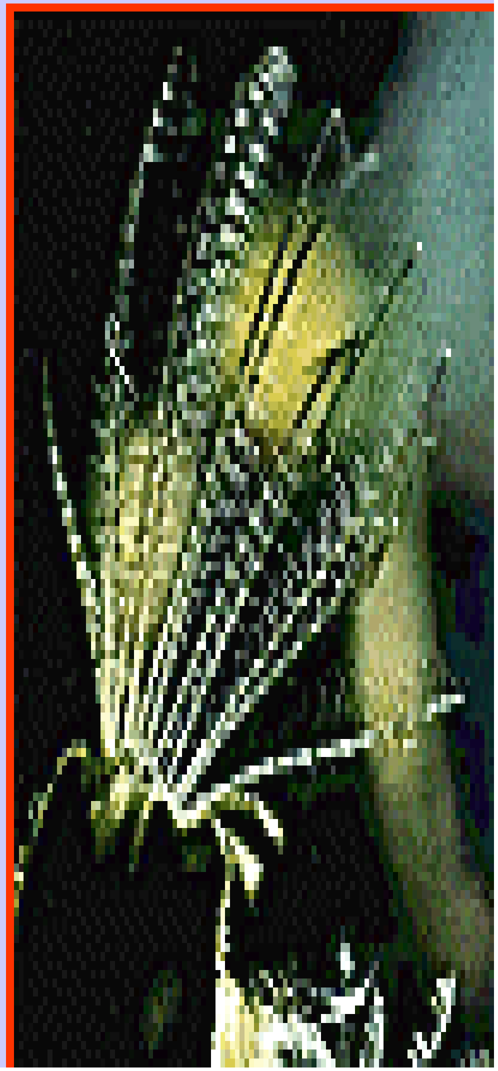
q_x : (dx / nx) = rate of mortality during interval x to x+1

s_x : 1 - (dx / nx) = survivorship rate during interval x to x+1

m_x: Fertility Rate = mean number offspring / female age x

Barnacle Life Table (Connell 1970)

Age (x)		Nx	Lx	Mx	LxMx
0	1	$1X10^6$	1	0	0
1		62	.000062	4600	.285
2		34	.000034	8700	.296
3		20	.000020	11600	.232
4	2	15.5	.0000155	12700	.197
5		11	.0000110	12700	.140
6		6.5	.0000065	12700	.082
7	3	2	.0000020	12700	.025
8		2	.0000020	12700	.025
					1.282



Estimating Vital Rates

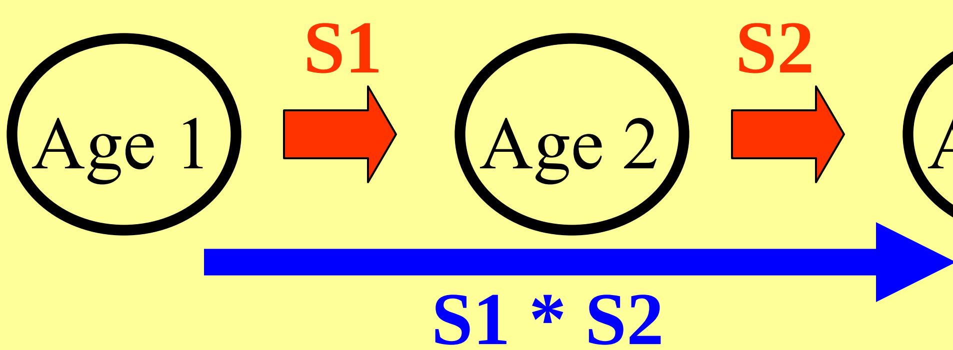
Age (x)	Nx	Sx	Lx
0	1×10^6	0.000062	1
1	62	-	0.000062

$$Sx = \frac{62}{1000000}$$

$$Sx = 0.000062$$

Lx = Proportion surviving to start of age interval x

Think of cumulative survivorship to age x



Comparing Vital Rates of Age Classes

Age Group	Sx	Lx	Mx
Just – Settled (0)	0.000062	1	0
Middle-Age (4)	0.709677	0.0000155	12700
Old-Timers (7)	1	0.000002	12700

LxMx: Discount age-specific fertility rates by the probability of survivorship to that age

Helps us to understand which age classes are contribute most to the population growth

Barnacle Life Table (Connell 1970)

Age (x)		Nx	Lx	Mx	LxMx
0	1	$1X10^6$	1	0	0
1		62	.000062	4600	.285
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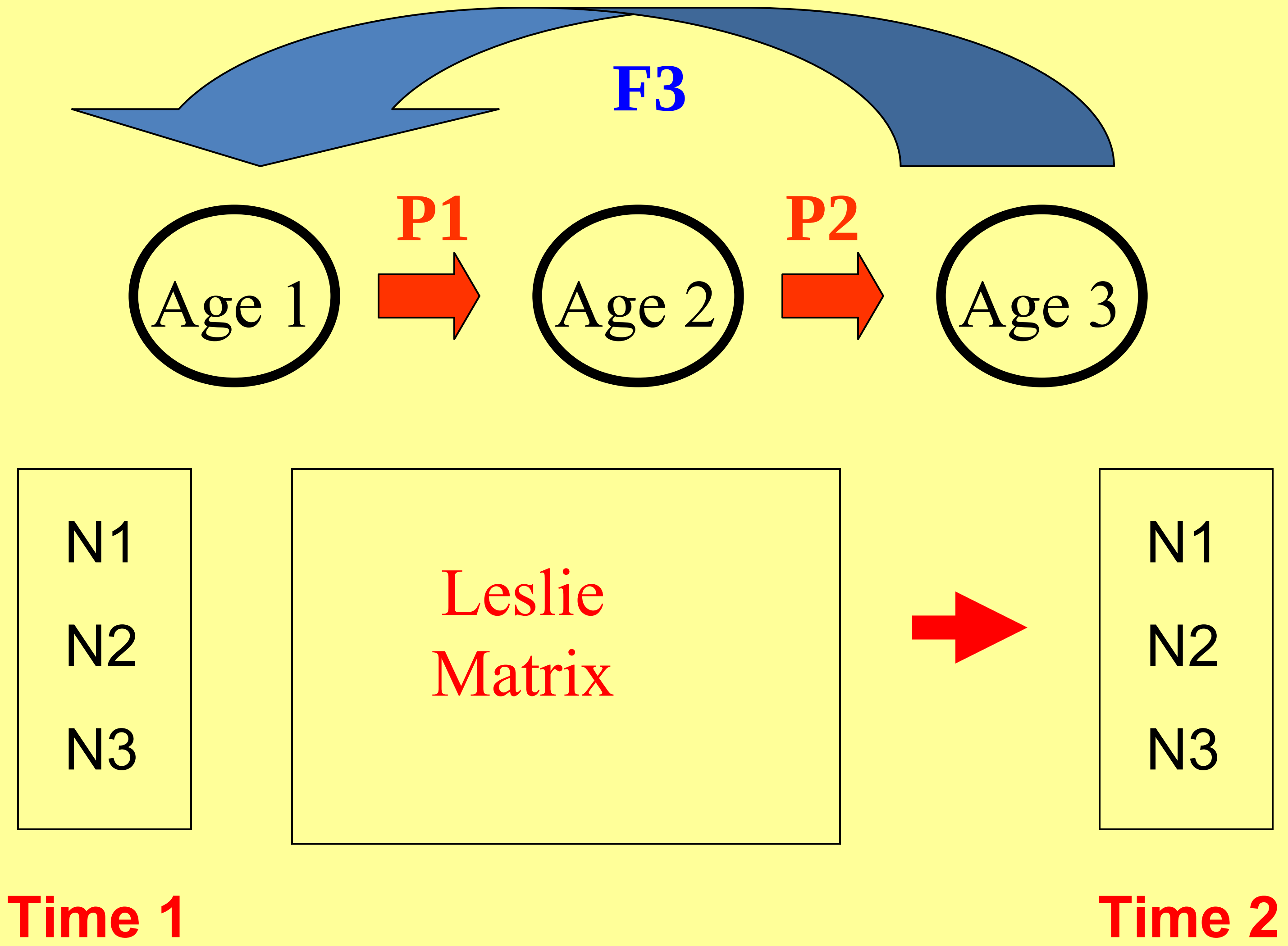
Leslie Matrix Modelling



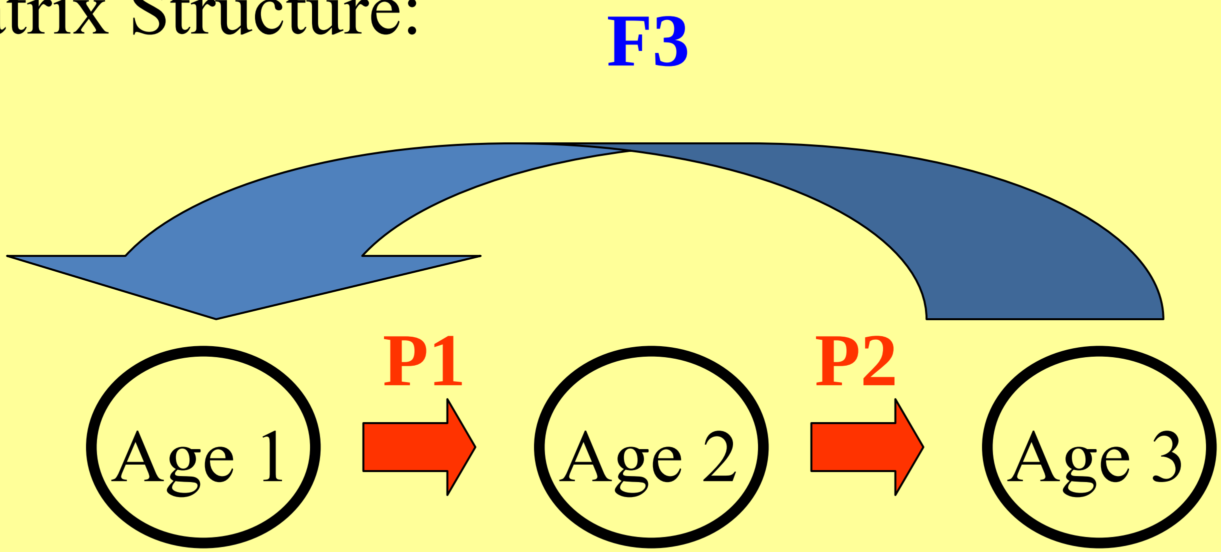
POP TOOLS

http://www.cse.csiro.au/poptools/

- Versatile add-in for PC versions of Microsoft Excel
- Facilitates analysis of matrix population models and stochastic simulations
- Originally written to analyze ecological models, but has much broader application
- Used for studies of population dynamics, calculation of bootstrap and resampling statistics

POP TOOLS

- Leslie Matrix Structure:



Time 1

Time 2

1 to 1	0	F3
P1	2 to 2	0
0	P2	3 to 3

POP TOOLS

➢ Calculate and plug-in vital rates:

Time 1: 100 age-2
Time 2: 50 age-3

Time 1: 100 age-3
Time 2: 50 age-3

Time 1: 100 age-0 (newborns)
Time 2: 100 age-1

FROM

TO

1	**0.5**	**0.5**
0.5	0	0
0	**0.5**	**0.5**

POP TOOLS

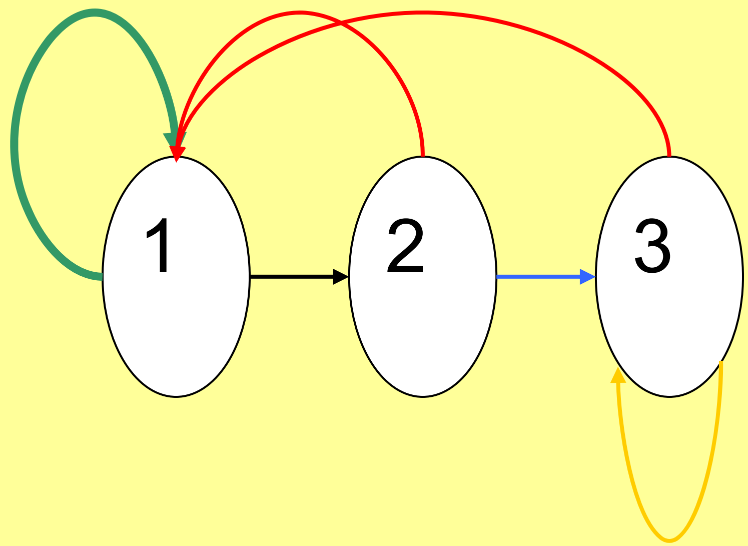
- Draw Life Diagram:

Use POPTOOLS
(MATRIX TOOLS / DRAW LIFE CYCLE)

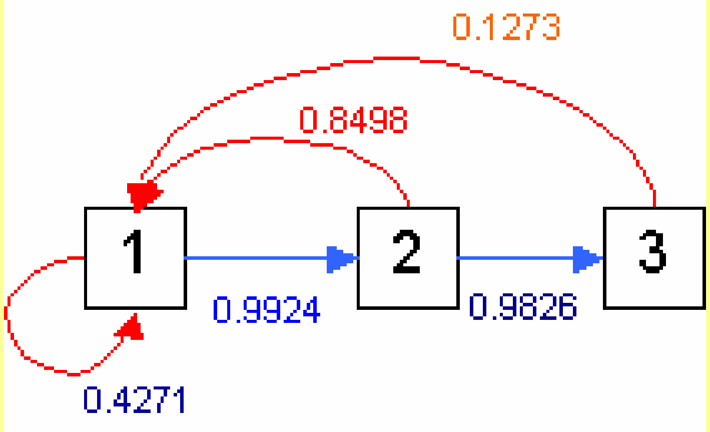
FROM

TO

1	**0.5**	**0.5**
0.5	0	0
0	**0.5**	**0.5**



POP TOOLS



FROM

$$\mathbf{A} = \begin{array}{c} \\ \textit{TO} \\ \\ \end{array} \begin{array}{c} 1 \\ 2 \\ 3 \end{array} \overset{\begin{array}{ccc} 1 & \quad\quad 2 & \quad\quad 3 \end{array}}{\left[\begin{array}{ccc} 0.4271 & 0.8498 & 0.1273 \\ 0.9924 & 0 & 0 \\ 0 & 0.9826 & 0 \end{array} \right]}$$

- Three age stages (labeled 1, 2 and 3)
- Red arrows represent reproduction (females per female surviving to stage 1); the blue arrows indicate survival across single time step
- To construct the appropriate projection matrix, look at the source and destination of each arrow. An arrow leading from stage X to stage Y, should be represented in the projection matrix by an entry in column X and row Y of the projection matrix

POP TOOLS

- Analysis of Population Matrix:

To analyze this model use POPTOOLS (MATRIX TOOLS/BASIC ANALYSIS)

Eigenvalues	
Real	Imaginary
1.209336988	0
-0.166781531	0
-0.615455457	0

Dominant Eigenvalue = λ

POP TOOLS

- Analysis of Population Matrix:

To analyze this model use POPTOOLS (MATRIX TOOLS/BASIC ANALYSIS)

Eigenvectors (R&L)	
Age / Stage Structure	Reproductive value
40.2%	52.8%
33.0%	41.6%
26.8%	5.6%

Balancing Current / Future Reproduction

Reproductive Value (Vx): The expected relative contribution of an individual to the population, by reproducing now and in the future

Trade-off Between Current and Future Reproduction

$$Vx = F\ present + V\ future$$

POP TOOLS

- Analysis of Population Matrix:

To analyze this model use POPTOOLS (MATRIX TOOLS/BASIC ANALYSIS)

Ro	1.394	(number of replacements)
T	1.749	(generation time)
r	0.190	(rate of increase)

POP TOOLS

- Analysis of Population Matrix:

To analyze this model use POPTOOLS (MATRIX TOOLS/BASIC ANALYSIS)

Ro = Replacement Rate = Σ (lx * mx) = 1.394

$$T = \text{Generation Time} = \frac{\Sigma\,[\,(x) * lx * mx]}{\Sigma\,(lx * mx\,)} = 1.749$$

(weighed by the age class)

r = Rate of Increase = ln (Ro)/T = ln (1.394) /1.749 = 0.190

POP TOOLS

$$\frac{\Delta \lambda}{\Delta a}$$

➢ Sensitivity of the Population Trajectory to Small Changes in Demographic Rates:

To calculate sensitivity use POPTOOLS (MATRIX TOOLS / MATRIX SENSITIVITY)

	1	2	3
1	0.4271	0.8498	0.1273
2	0.9924	0	0
3	0	0.9826	0

0.582	0.477	0.388
0.459	0	0
0	0.050	0

- Change each parameter by an equal small amount (absolute change) and record change in Lambda
- Values are not absolute (+ / - sign)

Problems with Sensitivity

Unambiguous metric of response of population growth (Lambda) to a perturbation in demographic parameters.

- However, there are two problems:

Scale: Demographic rates are measured differently:

Transition probabilities (0 – 1)

Fecundity rates (larger than 1)

Interpretations: S quantifies "importance"
(small change in a causes large change in Lambda) …
but does not address the "contribution" to Lambda

POP TOOLS

$$\frac{a}{\lambda}\ \frac{\Delta \lambda}{\Delta a}$$

➢ Elasticity of the Population Trajectory to Small Changes in Demographic Rates:

To calculate sensitivity use POPTOOLS (MATRIX TOOLS / MATRIX ELASTICITY)

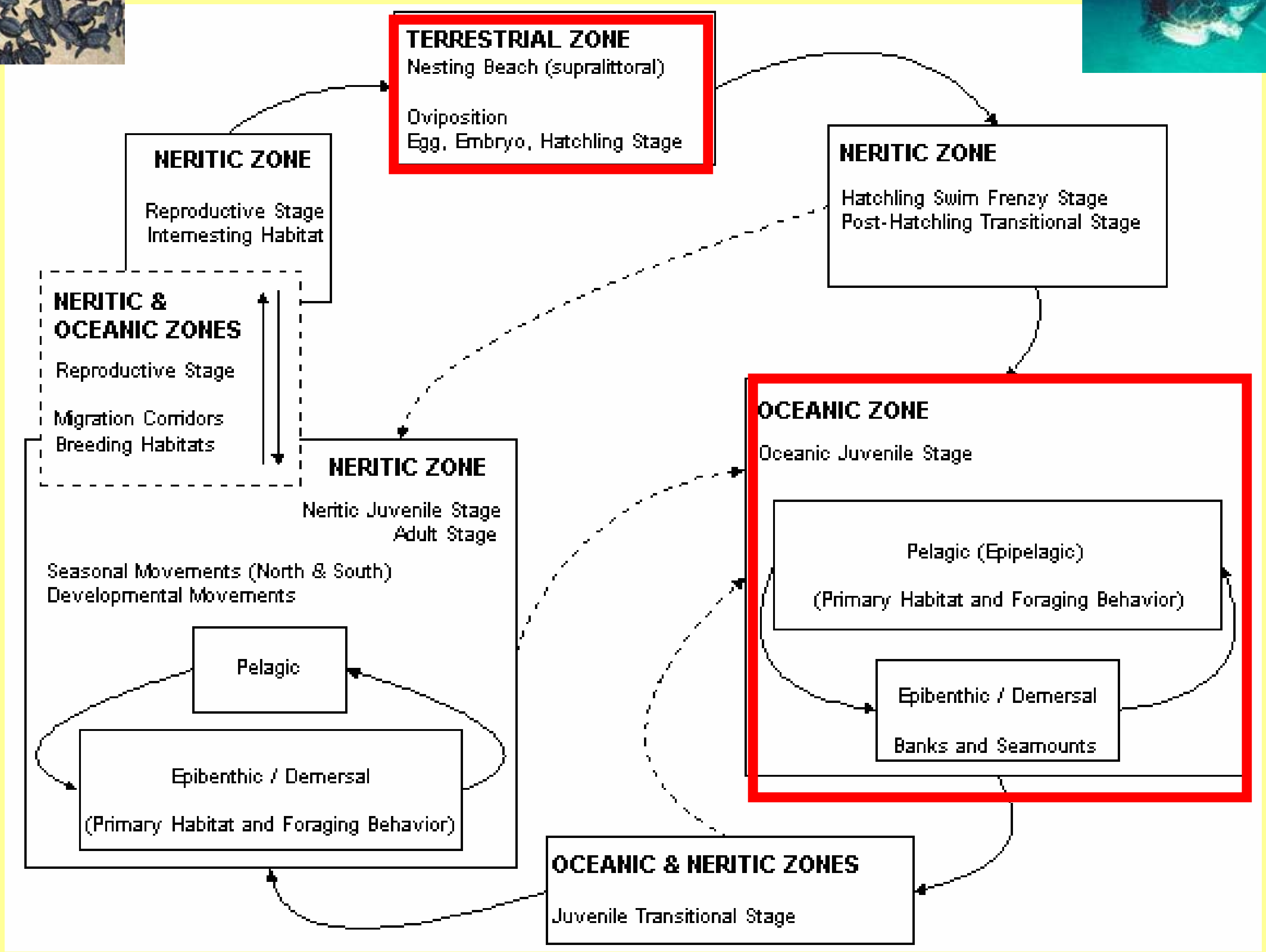
	1	2	3
1	0.4271	0.8498	0.1273
2	0.9924	0	0
3	0	0.9826	0

0.205	0.335	0.040
0.376	0	0
0	0.040	0

- All elasticities for a matrix sum to 1
- Values are not absolute (+ / - sign)

Decision Making for Effective Conservation

(Loggerhead Turtles)

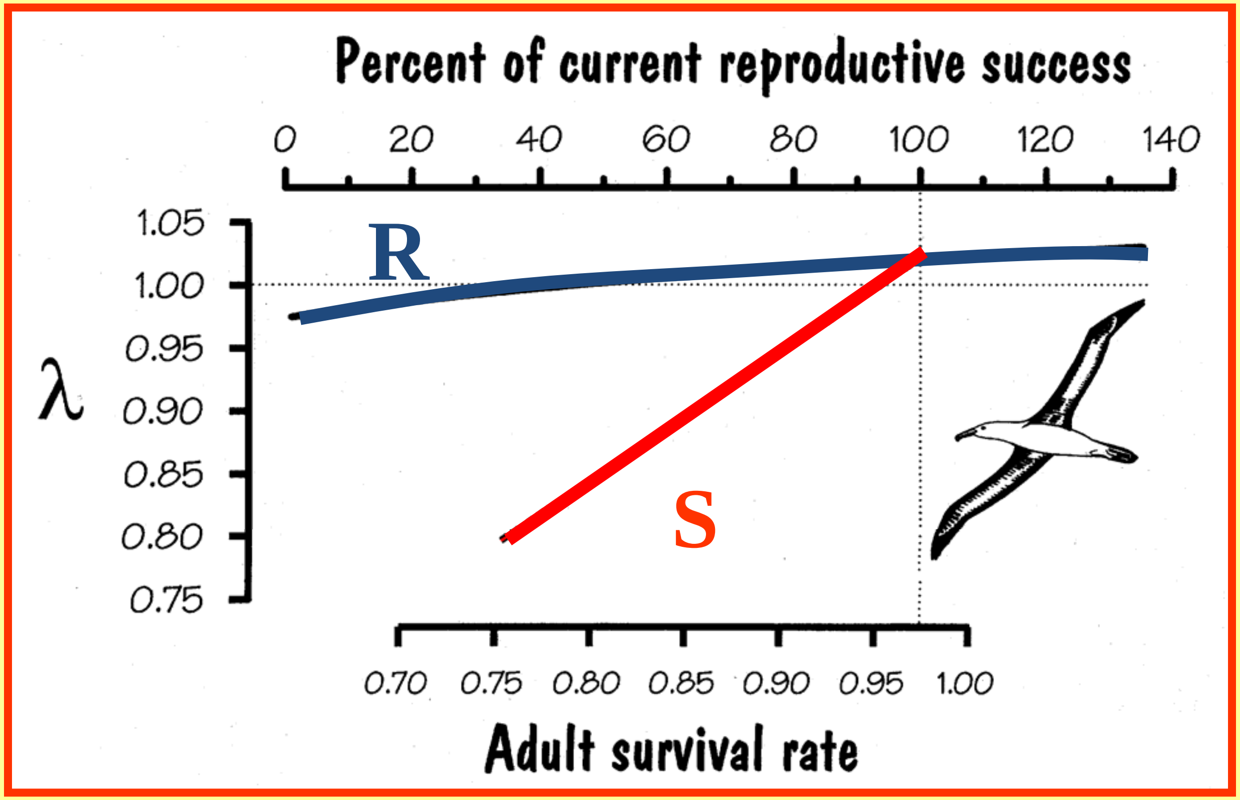


(U.S. Fish & Wildlife Service, National Marine Fisheries Service)

Interpreting Sensitivity and Elasticity

• Visualizing trade-offs between changes in survivorship and fecundity for population growth (λ)

• Slope
(sign / size)



(Russell 1999)

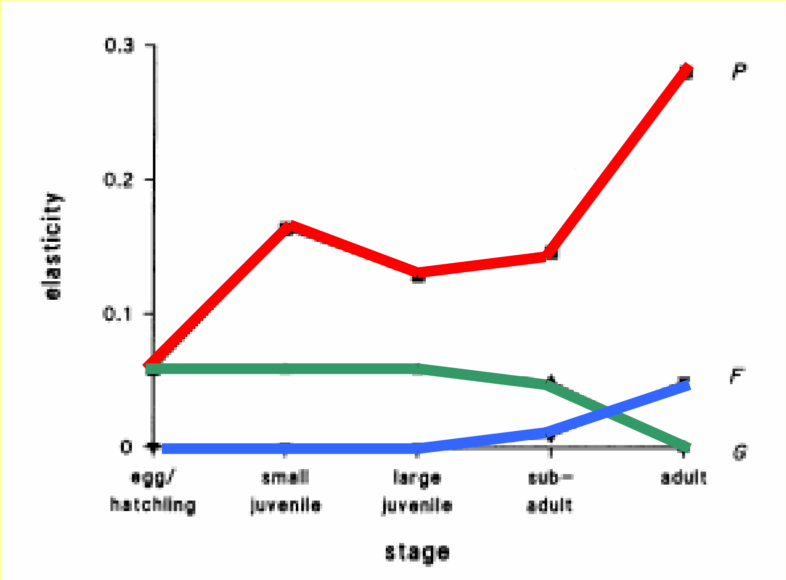
Decision Making for Effective Conservation

(Loggerhead Turtles)

• Comparison of effects of different rates (S, F) on overall population growth

• Age-specific "returns" to conservation investments

• Common currency (λ)



P: Survivorship

F: Fecundity

G: Growth

(Crowder et al. 1994)

Decision Making for Effective Conservation

Caveats:

- Elasticity is a mathematical construct…
  the biology may not be able to attain certain parameter values (especially fecundity rates)

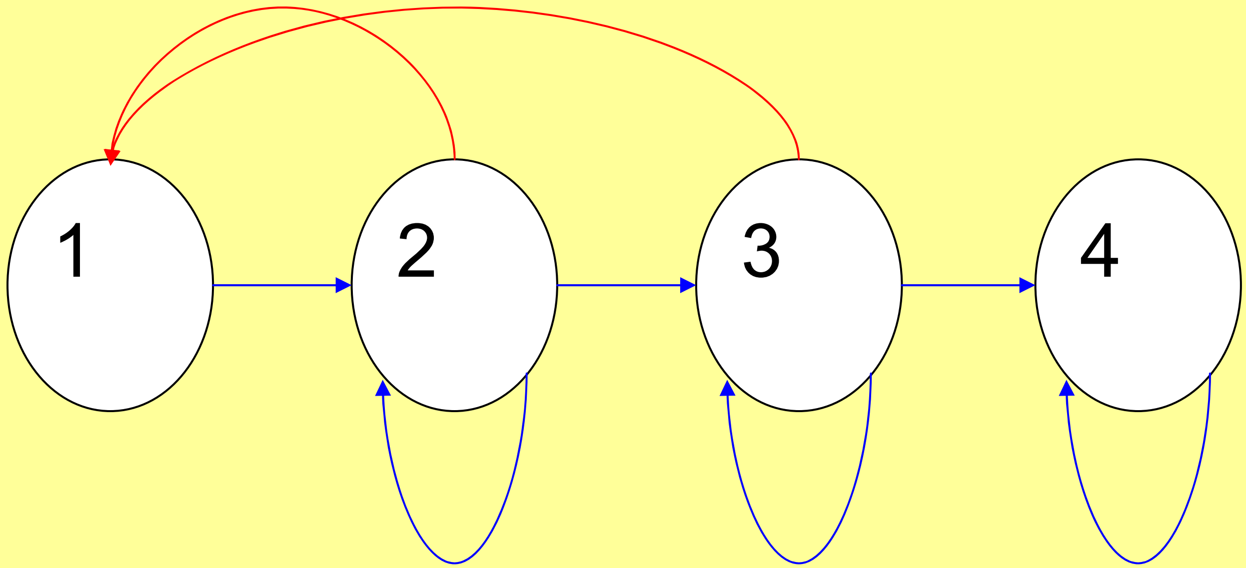
- Beware of the influence of
  "implementation costs"

- The most elastic rates may
  be the hardest to manage

More PopTools Examples – Killer Whales

Age First Rep: 13

Maximum Age: 60



A

	1	2	3	4
1	0	0.0043	0.1132	0
2	0.9775	0.9111	0	0
3	0	0.0736	0.9534	0
4	0	0	0.0452	0.9804

More PopTools Examples

T

	1	2	3	4
1	**0**	**0**	**0**	**0**
2	**0.9775**	**0.9111**	**0**	**0**
3	**0**	**0.0736**	**0.9534**	**0**
4	**0**	**0**	**0.0452**	**0.9804**

F

	1	2	3	4
1	**0**	**0.0043**	**0.1132**	**0**
2	**0**	**0**	**0**	**0**
3	**0**	**0**	**0**	**0**
4	**0**	**0**	**0**	**0**

More PopTools Examples – Killer Whales

Dominant Eigenvalue = λ = 1.19

r	0.179	(rate of increase)
Ro	1.634	(expected number of replacements)
T	2.739	(generation time)
mu1	2.846	(mean age of parents of offspring)

More PopTools Examples – Killer Whales

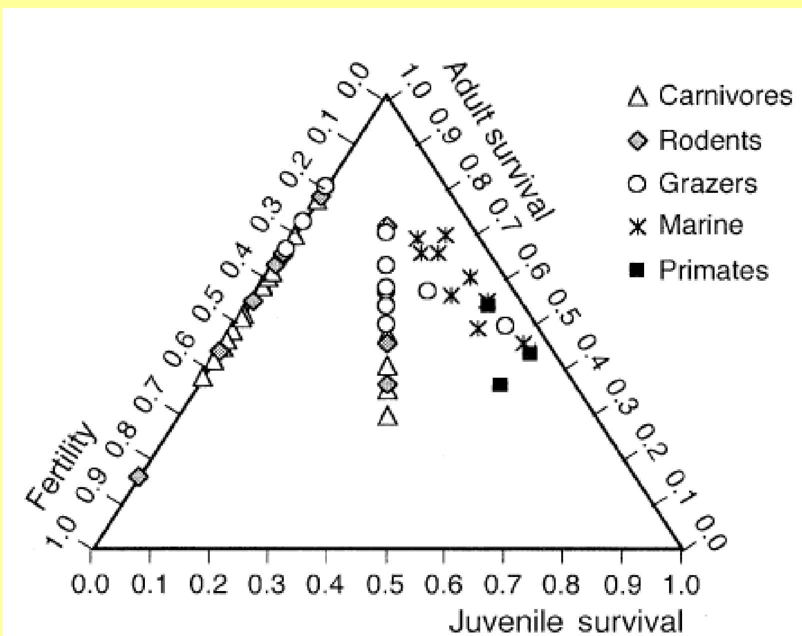
A

	1	2	3	4
1	**0**	**0.0043**	**0.1132**	**0**
2	**0.9775**	**0.9111**	**0**	**0**
3	**0**	**0.0736**	**0.9534**	**0**
4	**0**	**0**	**0.0452**	**0.9804**

0	**0**	**0.04**	**0**
0.04	**0.34**	**0**	**0**
0	**0.04**	**0.54**	**0**
0	**0**	**0**	**0**

Meta-Analysis of Demographic Rates

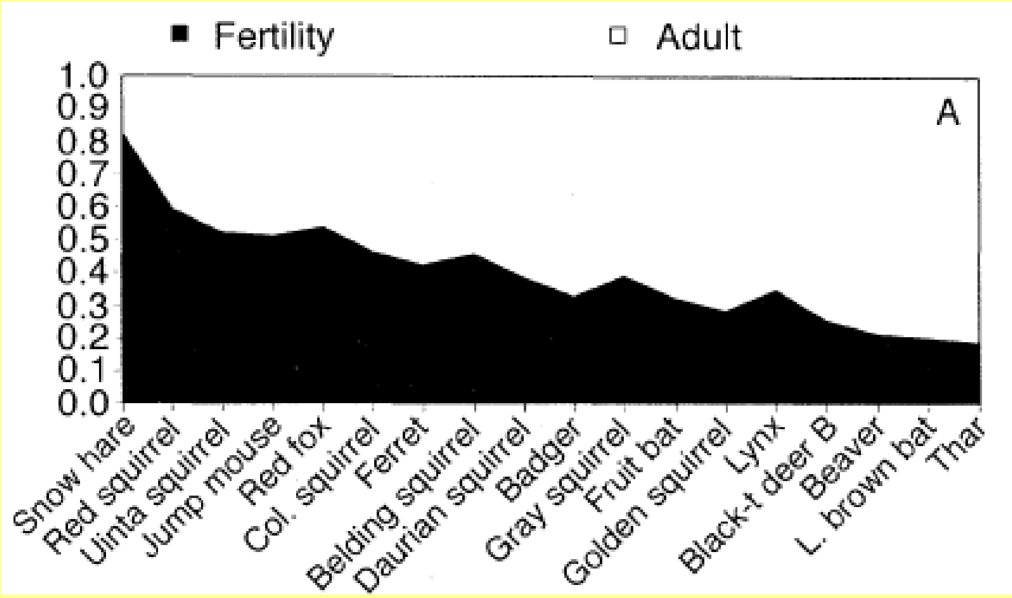
$$\mathbf{B} = \begin{bmatrix} 0 & 0 & \cdots & 0 & \bar{F} \\ P_1 & 0 & 0 & 0 & 0 \\ 0 & P_2 & 0 & 0 & \vdots \\ 0 & 0 & \ddots & 0 & 0 \\ 0 & 0 & 0 & P_{\alpha-1} & \bar{P} \end{bmatrix}$$



- Leslie Matrix Approach
- N = 50 mammal species
- Young / Adult
- Survivorship / Fertility

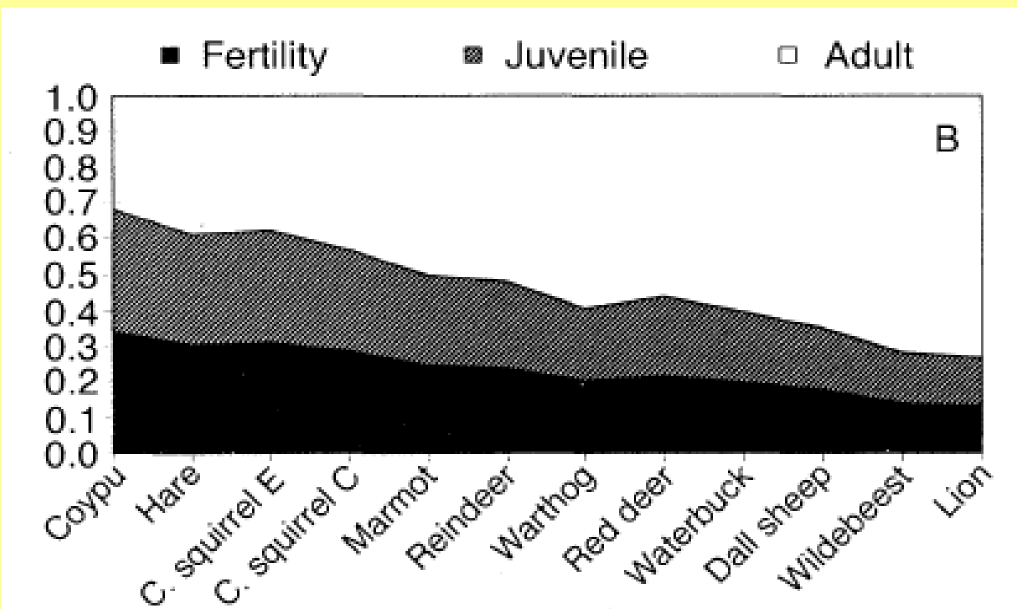
(Heppell et al. 2000)

Meta-Analysis of Demographic Rates



- Early first reproduction

age = 1yr (No Juveniles)

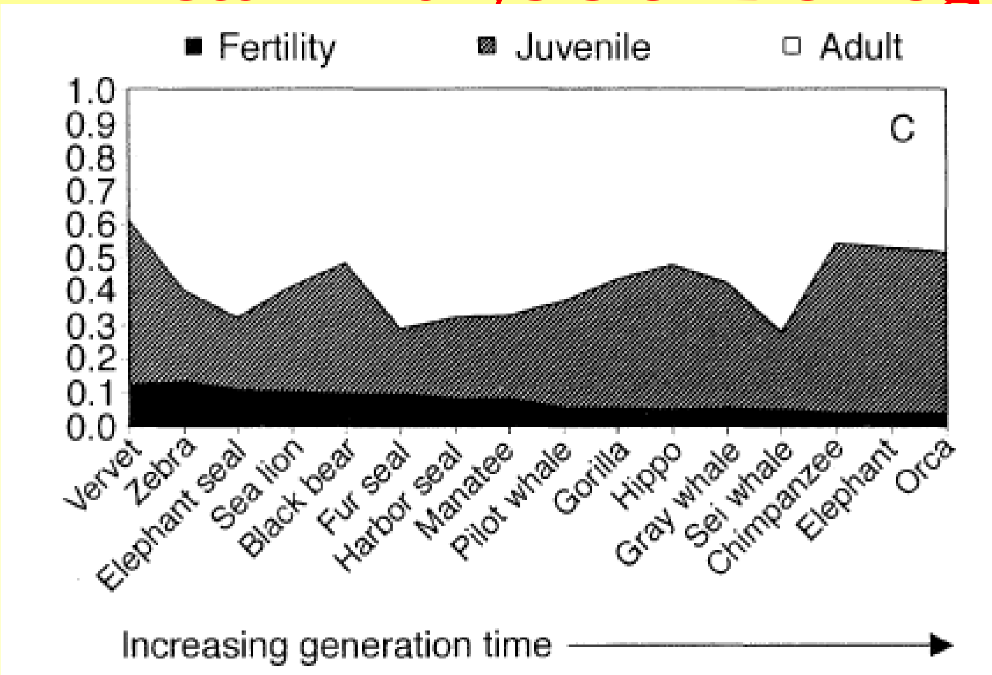


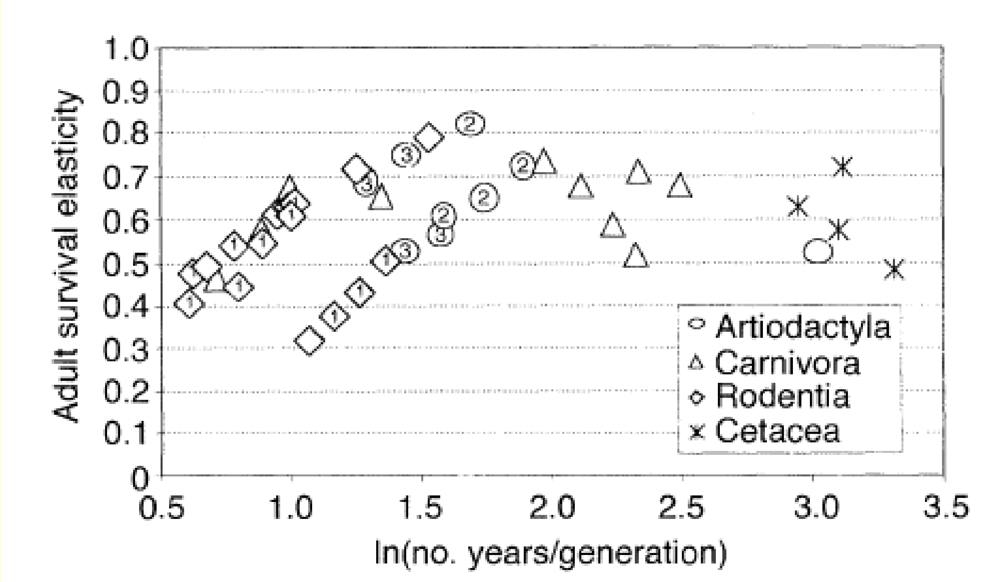
- Age first reproduction

2 yrs (2 age classes)

(Heppell et al. 2000)

Meta-Analysis of Demographic Rates





- Late first reproduction

➢2 yrs (max: 14)

- Adult survivorship increasingly important for longer-lived species

(Heppell et al. 2000)

Meta-Analysis of Demographic Rates

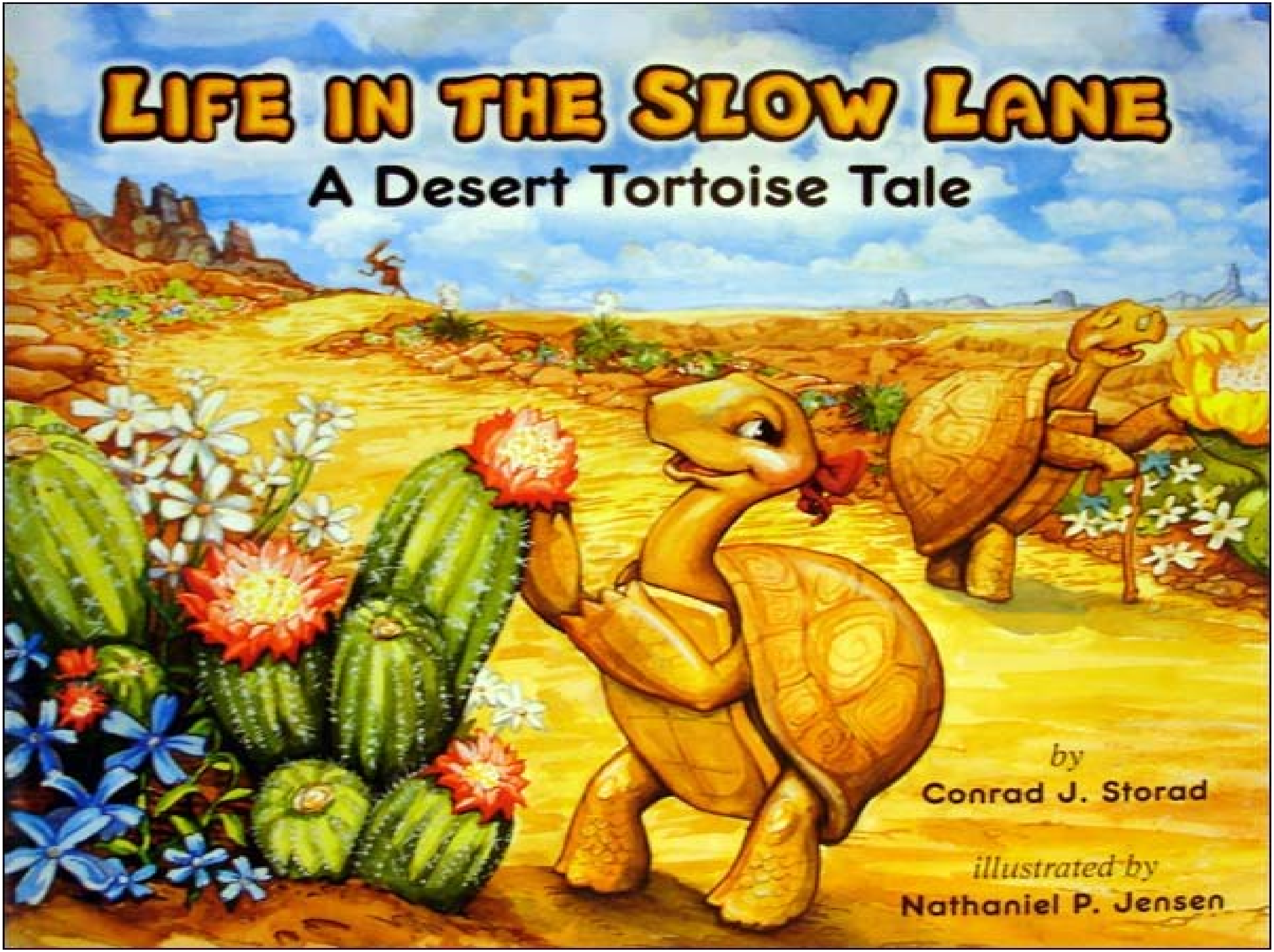
Variable	All life tables (N = 50)
Age at earliest maturity (α)	−0.192
Maximum age (k)	0.317*
Fertility ($\overline{F}$, weighted mean; includes survival to age 1)	−0.375**
Adult annual survival ($\overline{P}$, weighted mean)	0.300*
λ	−0.091
R_0	−0.056
Generation time (T_c)	0.252
Survivorship to maturity	0.310*
Life expectancy at birth ($\mathring{e}_0$)	0.258
Life expectancy at maturity ($\mathring{e}_\alpha$)	0.313*

Note: Coefficients have been corrected for ties (Zar 1984).
* $P < 0.05$, ** $P < 0.01$.

- Spearman rank correlation of various demographic variables and the elasticity of adult survivorship

(Heppell et al. 2000)

(Data: http://www.esapubs.org/archive/ecol/E081/006/appendix-A.htm)


LIFE IN THE SLOW LANE
A Desert Tortoise Tale
by
Conrad J. Storad
illustrated by
Nathaniel P. Jensen