Matrix population models

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Introduction

- Problems for endangered species
  - Demographic parameters, i.e. survival and reproduction not always known.
  - Life history is mostly approximately known.
  - Trend is known, but not how to counteract.
- Getting insight in population dynamics
  - Use life history to design a (simple) matrix population model.
  - If not all parameter values are known
    use known values and trend
    infer values for missing parameters
  - If all parameter values are known
    Compute yearly growth factor and the elasticities to determine which parameter influences the growth factor the most.

House Sparrow

Red-backed Shrike

Otter

Introduction

House Sparrow

Klok et al. (2006) Acta Biotheoretica.

- Data based matrix models for threatened species were developed.
  - House Sparrow (*Passer domesticus*)
  - Red-backed Shrike (*Lanius collurio*)
- Also for the re-introduction of the otter (*Lutra lutra*).

Red-backed Shrike

Hemerik et al. (2015) J. Ornith.

- For both birds a breeding pulse was included in the model (birth pulse model)
- The otter can reproduce year-round (birth flow model)

Otter

Seignobosc et al. (2011) Int. J. Ecol.

Introducing the notation

Simple Matrix Model with two age classes

Redshank

- Assumptions:
  - sex ratio is 1:1
  - length of sub-adult class is 1 year
  - birth pulse (breeding season)
- Parameters:

p part of the year after breeding (census moment)

a yearly survival of adults

q first year survival (juvenile survival)

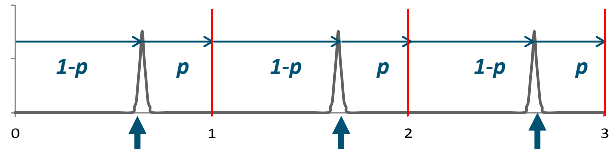
m mean number of offspring per female

Red-backed Shrike

Hemerik and Klok (2006) Anim. Biol.

Model with one year to maturation

Explanation of the census moment



Breeding pulse

Census moments

Special cases are

- Post-breeding: $p \downarrow 0$
- Pre-breeding: $p \uparrow 1$

House Sparrow

Hemerik and Klok (2006) Anim. Biol.

Model with one year to maturation

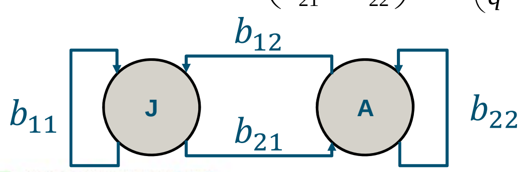
We model the population at the census moment p

- juveniles $J(t)$ and adults $A(t)$ at time t
- Project one year into the future

$$B(a,q,m)\begin{pmatrix} J(t) \\ A(t) \end{pmatrix} = \begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix}$$

- With matrix

$$B(a,q,m) = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} = \begin{pmatrix} \frac{m}{2}q & a^{1-p}\frac{m}{2}q^{p} \\ q^{1-p}a^{p} & a \end{pmatrix}$$



Hemerik and Klok (2006) Anim. Biol.

Model with one year to maturation

- The matrix $\begin{pmatrix} \frac{m}{2}q & a^{1-p}\frac{m}{2}q^{p} \\ q^{1-p}a^{p} & a \end{pmatrix}$
- Its characteristic equation $g(\lambda)=\lambda^2-\left(a+\frac{mq}{2}\right)\lambda$
- Sensitivity with respect to a parameter can be derived by differentiation of the dominant eigenvalue $\lambda = a+\frac{mq}{2},\ s(a)=\frac{\partial\lambda}{\partial a}=1,\ s(m)=\frac{\partial\lambda}{\partial m}=\frac{q}{2},\ s(q)=\frac{\partial\lambda}{\partial q}=\frac{m}{2}.$
- Elasticities are "relative sensitivities"

$$e(a)=\frac{a}{\lambda}\frac{\partial\lambda}{\partial a}=\frac{2a}{2a+mq} \qquad e(m)=\frac{m}{\lambda}\frac{\partial\lambda}{\partial m}=\frac{mq}{2a+mq} \qquad e(q)=\frac{q}{\lambda}\frac{\partial\lambda}{\partial q}=\frac{mq}{2a+mq}$$

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Hemerik and Klok (2006) Anim. Biol.

Model with one year to maturation

For our special cases holds

- Post-breeding: $p \downarrow 0$ $\quad B(a,q,m)=\begin{pmatrix} \frac{mq}{2} & \frac{ma}{2} \\ q & a \end{pmatrix}$
- Pre-breeding: $p \uparrow 1$ $\quad B(a,q,m)=\begin{pmatrix} \frac{mq}{2} & \frac{mq}{2} \\ a & a \end{pmatrix}$

We have shown that

- Matrix models with different census moments have the same population growth factor $\lambda = a+\frac{mq}{2}$.
- Eigenvectors associated with this dominant eigenvalue are different.
- The elasticities of a, q, m to this growth factor are for both these models

$e(m)=\frac{m}{\lambda}\frac{\partial\lambda}{\partial a}=\frac{mq}{2\lambda},\quad e(a)=\frac{a}{\lambda}\frac{\partial\lambda}{\partial a}=\frac{a}{\lambda}.$ and $e(a)=\frac{a}{\lambda}\frac{\partial\lambda}{\partial a}=\frac{a}{\lambda}.$

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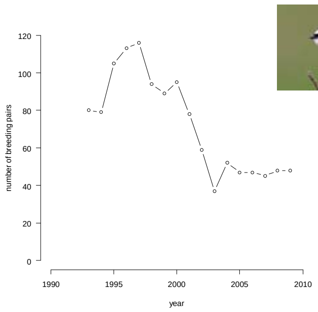
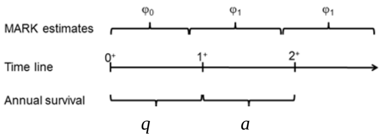
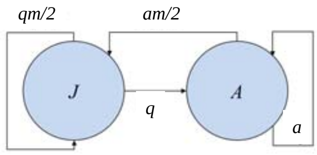
Hemerik and Klok, 2006, Anim. Biol.

The dynamics of a local Red-backed Shrike population in the Netherlands





$s(m) = 0.08, s(q) = 1.45, s(a) = 1$



- mean adult (juvenile) survival is 0.54 (0.16)
- reproductive success 2.91

- the resulting population growth factor is 0.80 thus requiring immigrants.

$e(m) = e(q) = 0.29, e(a) = 0.68$

- the most plausible driver is food availability requiring a landscape with a patchwork of different habitat types and a large diversity of invertebrate prey species

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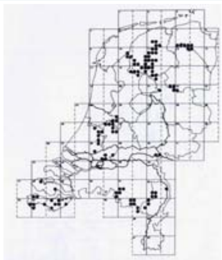
Hemerik L., M. Geertsema, S. Waasdorp, R.P. Middelveld, H. van Kleef, C. Klok (2014) Survival, reproduction, and immigration explain the dynamics of a local Red-backed Shrike population in the Netherlands. Journal of Ornithology 156: 35-46 DOI 10.1007/s10336-014-1120-2

Introduction of the otter in the Netherlands

1900



1962

1965 - 1981

Last otter was found dead in the year 1989

In 2001 the otter was (re)introduced

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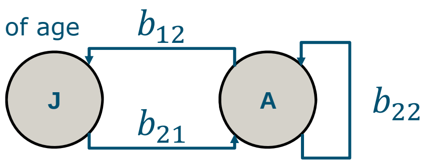
Seignobosc et al. (2011) Int. J. Ecol.

Birth flow model for the otter

We model the population at time t

- juveniles $J(t)$ of half a year
- adults $A(t)$ older than one and a half year
- adults reproduce from two years of age



- project one year into the future $B\begin{pmatrix} J(t) \\ A(t) \end{pmatrix} = \begin{pmatrix} J(t+1) \\ A(t+1) \end{pmatrix}$
- with matrix

$$B = \begin{pmatrix} b_{11} & b_{12} \\ b_{21} & b_{22} \end{pmatrix} = \begin{pmatrix} 0 & \sqrt{a}\frac{m}{2}\sqrt{q} \\ \sqrt{q}\sqrt{a} & a \end{pmatrix}$$

Seignobosc et al. (2011) Int. J. Ecol.

Introduction of the otter in the Netherlands

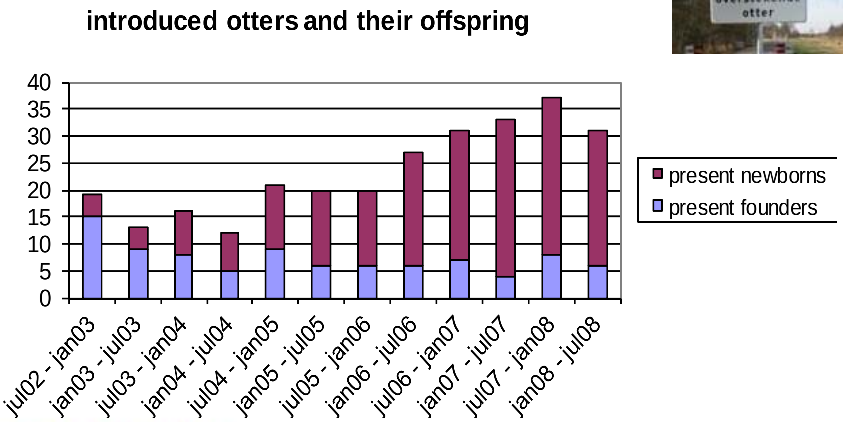
$$\begin{pmatrix} 0 & \frac{m}{2}\sqrt{qa} \\ \sqrt{qa} & a \end{pmatrix} = \begin{pmatrix} 0 & 0.690 \\ \sqrt{0.946\ 0.786} & 0.786 \end{pmatrix}$$

- Population growth factor from model was 1.26
- Elasticity of adult survival is the largest

Seignobosc et al. (2011) Int. J. Ecol.

Introduction of the otter in the Netherlands

Population growth factor from model was 1.26



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Seignobosc et al. (2011) Int. J. Ecol.

Model with more than one year to maturation

Simple Matrix Model with three stages

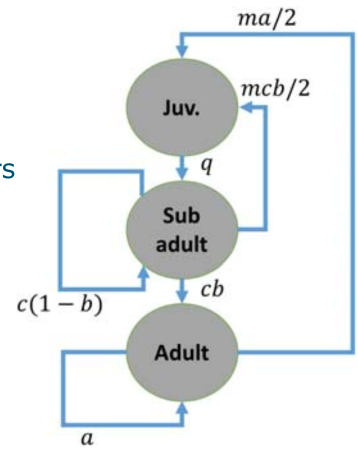
- Assumptions:
  - sex ratio is 1:1
  - length of juvenile class is 1 year
  - length of sub-adult class is T years
  - birth pulse (breeding season)
  - census moment post-breeding
- Parameters:

a yearly survival of adults

q first year survival (juvenile survival)

c first yearly survival of sub-adults

m mean number of offspring per female



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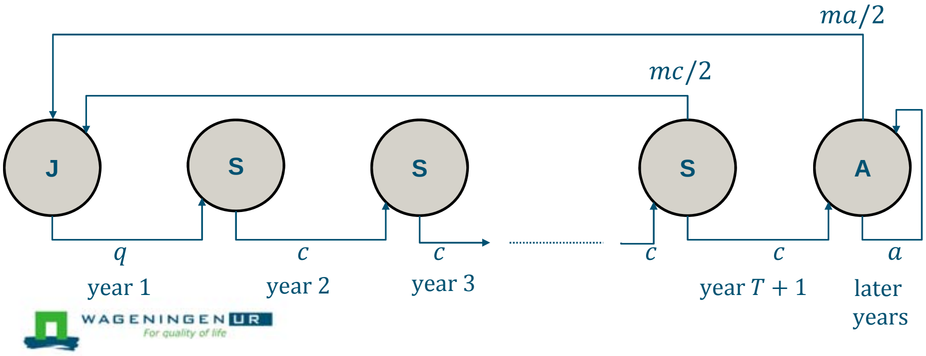
Hemerik and Klok (2006) Anim. Biol.

Model with more than one year to maturation

We model the population at a post-breeding census moment

- juveniles $J(t)$, sub-adults $S(t)$ and adults $A(t)$ at time t
- Project one year into the future
- With a Leslie matrix



General Lesliematrix for 3 classes (1)

- Juvenile (1 yr), Sub-adult (T yr) and Adult
- Sex ratio 1:1
- After $T+1$ years reproduction starts
- q Juvenile survival
- c yearly survival in sub-adult stage
- a yearly adult survival
- Leslie-matrix for fictitious animal:

$$Z_{T+2} = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & \frac{mc}{2} & \frac{ma}{2} \\ q & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & c & 0 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & c & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & c & a \end{pmatrix}$$

General Leslie matrix (2)

$$Z_n = \begin{pmatrix} 0 & 0 & 0 & \cdots & 0 & \frac{mq}{2} & \frac{ma}{2} \\ q & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & q & 0 & \cdots & 0 & 0 & 0 \\ \vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots \\ 0 & 0 & 0 & \cdots & 0 & 0 & 0 \\ 0 & 0 & 0 & \cdots & q & 0 & 0 \\ 0 & 0 & 0 & \cdots & 0 & q & a \end{pmatrix}$$

Sei whale (*Balaenoptera borealis)*

- Special cases: $c = q$ or $c = a$
- We go to the example of the Sei whale where
- $c = q = 0.934$, $a = 0.942$ and $m = 0.27$
- Reproduction for the first time at age 5, so T=4

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Characteristic equation and elasticities

- For Z_6 with $c = q$the characteristic equation is

$$g(\lambda) = 0$$

$$Z_6 = \begin{pmatrix} 0 & 0 & 0 & 0 & \frac{mq}{2} & \frac{ma}{2} \\ q & 0 & 0 & 0 & 0 & 0 \\ 0 & q & 0 & 0 & 0 & 0 \\ 0 & 0 & q & 0 & 0 & 0 \\ 0 & 0 & 0 & q & 0 & 0 \\ 0 & 0 & 0 & 0 & q & a \end{pmatrix}$$

- With $g(\lambda) = \lambda^6 - a\lambda^5 - \frac{mq^5\lambda}{2}$
- And the elasticities are e.g. $e_6(a) = \frac{a}{\lambda}\frac{\partial\lambda}{\partial a}$

$$e_6(a) = \frac{a\lambda^4}{g'(\lambda)} \qquad e_6(q) = \frac{5mq^5}{2g'(\lambda)} \qquad e_6(m) = \frac{mq^5}{2g'(\lambda)}$$

- It is clear that $e_6(q) > e_6(m)$
- We can derive explicit relations for

$$e_6(a) = e_6(q) \qquad e_6(a) = e_6(m)$$

- But not for the dominant eigenvalue

Sei whale (*Balaenoptera borealis)*

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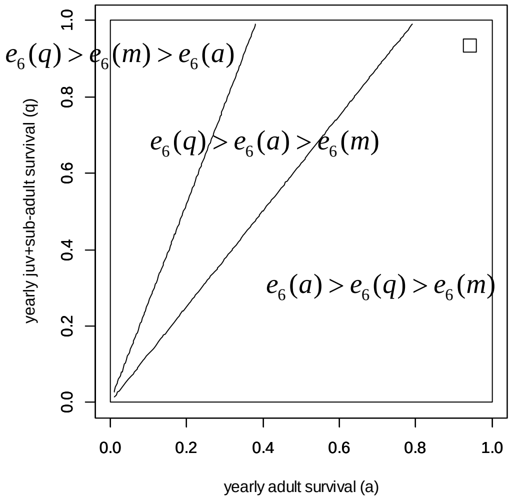
Leslie elasticities

Sei whale
(*Balaenoptera borealis*)

$m = 0.27$



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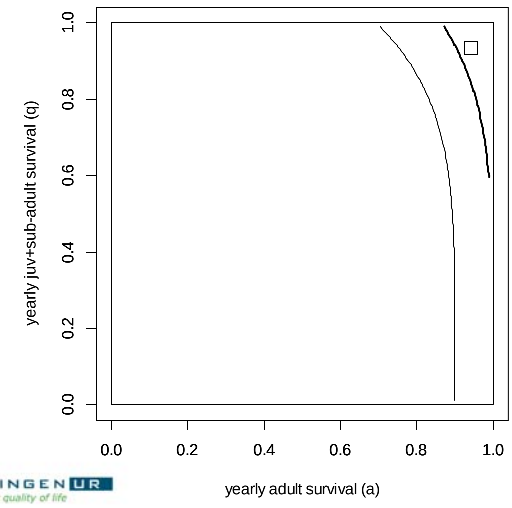
Leslie dominant eigenvalue

Sei whale
(*Balaenoptera borealis*)

$m = 0.27$



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Stage-structured matrix
Characteristic equation and elasticities

$$\begin{pmatrix} 0 & \frac{mqb}{2} & \frac{ma}{2} \\ q & q(1-b) & 0 \\ 0 & qb & a \end{pmatrix} \quad \text{with } b = \frac{q^3 - q^4}{1 - q^4}$$

- We distinguish Juvenile, Sub-adult and adult stage
- For this the characteristic equation is $f(\lambda) = 0$
- With $f(\lambda) = \lambda^3 - (q(1-b) + a)\lambda^2 - \lambda(\frac{mq^2 b}{2} - aq(1-b))$
- From this we can easily get a formula of the dominant eigenvalue
- The formulas for the elasticities are complicated

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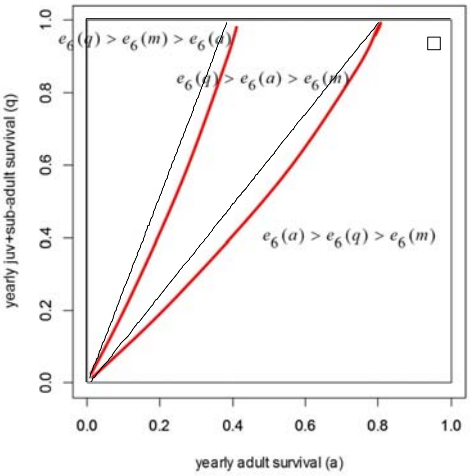
Stage-structured elasticities



$m = 0.27$

Sei whale
(*Balaenoptera borealis)*

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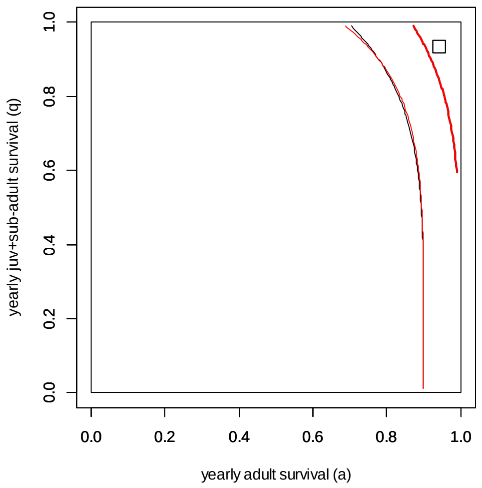
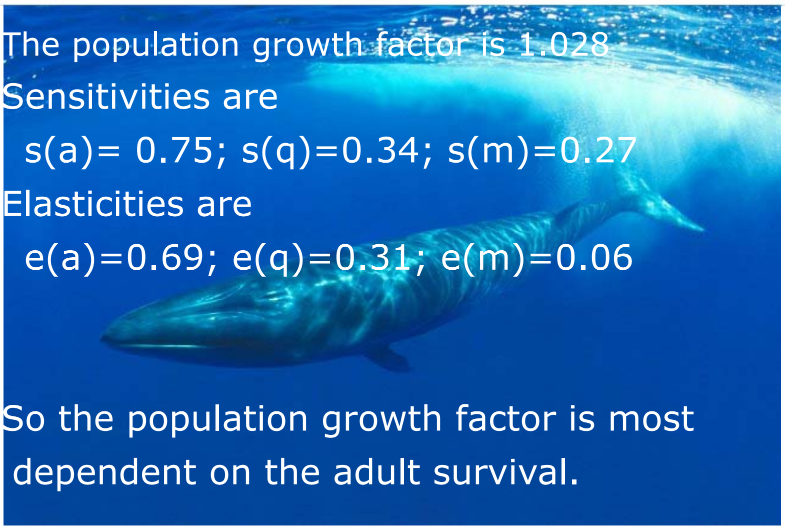
Stage-structured dominant eigenvalue (red)



Sei whale
(Balaenoptera borealis)

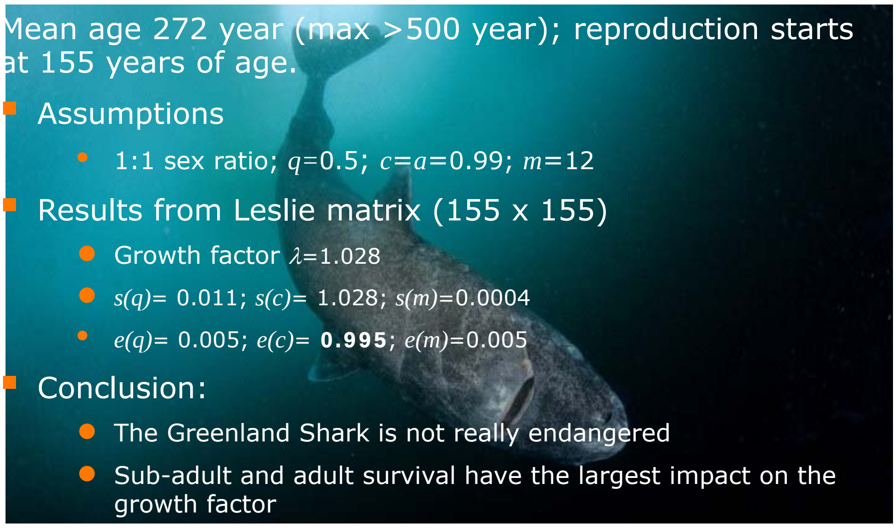
Conclusion for the Sei whale



- The population growth factor is 1.028
- Sensitivities are
  s(a)= 0.75; s(q)=0.34; s(m)=0.27
- Elasticities are
  e(a)=0.69; e(q)=0.31; e(m)=0.06
- So the population growth factor is most dependent on the adult survival.

Greenland Shark

© Waterframe / Alamy



Mean age 272 year (max >500 year); reproduction starts at 155 years of age.

- Assumptions
  - 1:1 sex ratio; q=0.5; c=a=0.99; m=12
- Results from Leslie matrix (155 x 155)
  - Growth factor λ=1.028
  - $s(q)$= 0.011; $s(c)$= 1.028; $s(m)$=0.0004
  - $e(q)$= 0.005; $e(c)$= **0.995**; $e(m)$=0.005
- Conclusion:
  - The Greenland Shark is not really endangered
  - Sub-adult and adult survival have the largest impact on the growth factor

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Nielsen, J.; Hedeholm, R.B.; Heinemeier, J.; Bushnell, P.G.; Christiansen, J.S.; Olsen, J.; Ramsey, C.B.; Brill, R.W.; Simon, M.; Steffensen, K.F. and Steffensen, J.F., 2016, "Eye lens radiocarbon reveals centuries of longevity in the Greenland shark (*Somniosus microcephalus*)", Science 353(6300): 702–704

Conclusion

- Leslie and stage-structured matrices have
  - The same dominant eigenvalue
  - approximately the same elasticities of underlying parameters
- From stage-structured we get an analytic formula of the dominant eigenvalue
- For the Leslie matrix the formulas for the elasticities are easily obtained

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Thank you for your attention

And my co-authors for exploring these models with me.