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Which are you?

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je suis pret!

estoy listo!

SEE MORE ▾

Fundamentals of Ecology

Week 6, Ecology Lecture 3

Cara Brook

February 11, 2025

Learning objectives from Lecture 2

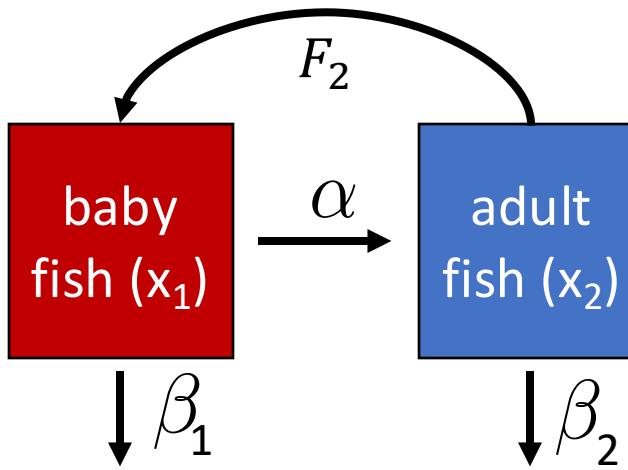
You should be able to:

- Recognize a logistic growth curve and define its equilibria.
- Predict a population's trajectory if starting from various points on the logistic growth curve.
- Recognize a logistic growth curve in the presence of harvesting, and evaluate whether equilibria on this curve are stable or unstable.
- Define MSY and know at what value of N MSY occurs
- Understand why MSY fails in practice, including understanding the tragedy of the commons
- Describe management approaches taken to mitigate the tragedy of the commons
- Understand the difference between deterministic and stochastic models
- Explain environmental and demographic stochasticity and how they contribute to problems with MSY

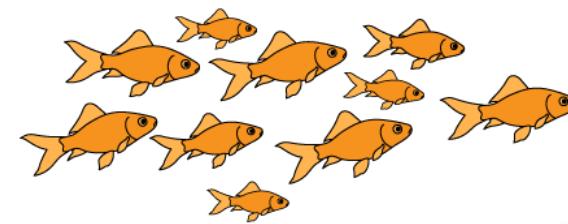
individual



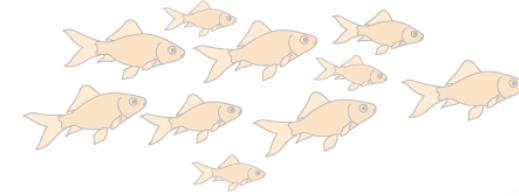
Structured Population =
multiple individuals of the
same species
(conspecifics) in the same
habitat but in different
life history stages



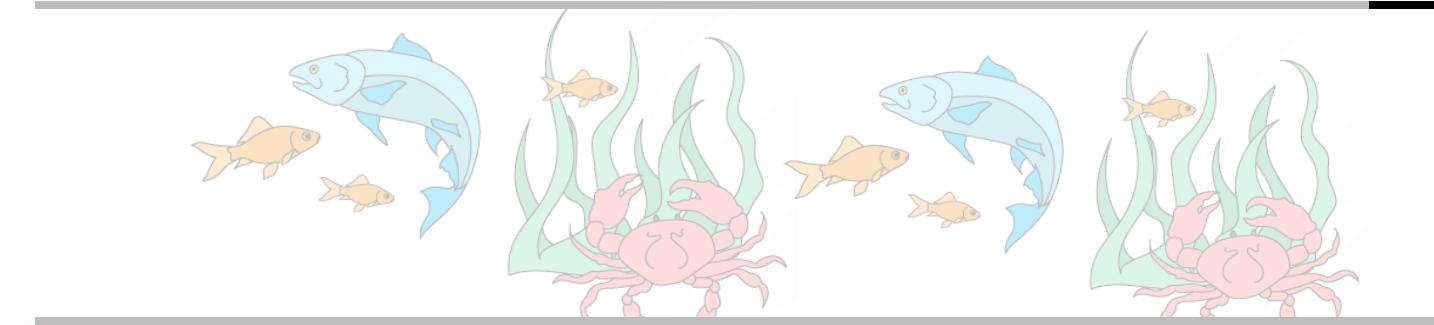
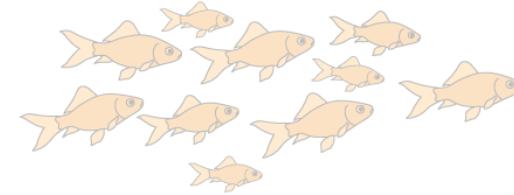
population



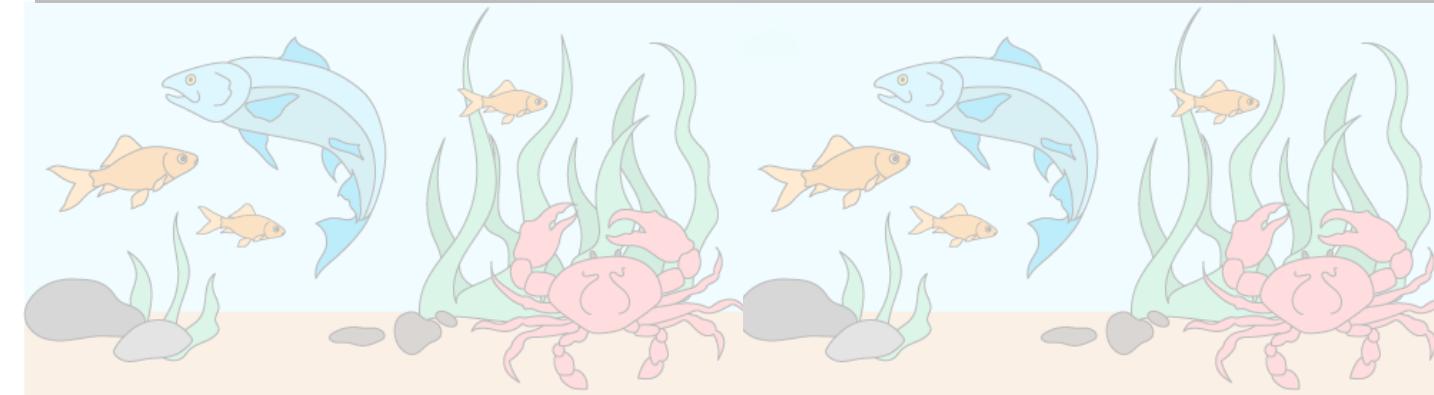
metapopulation



community



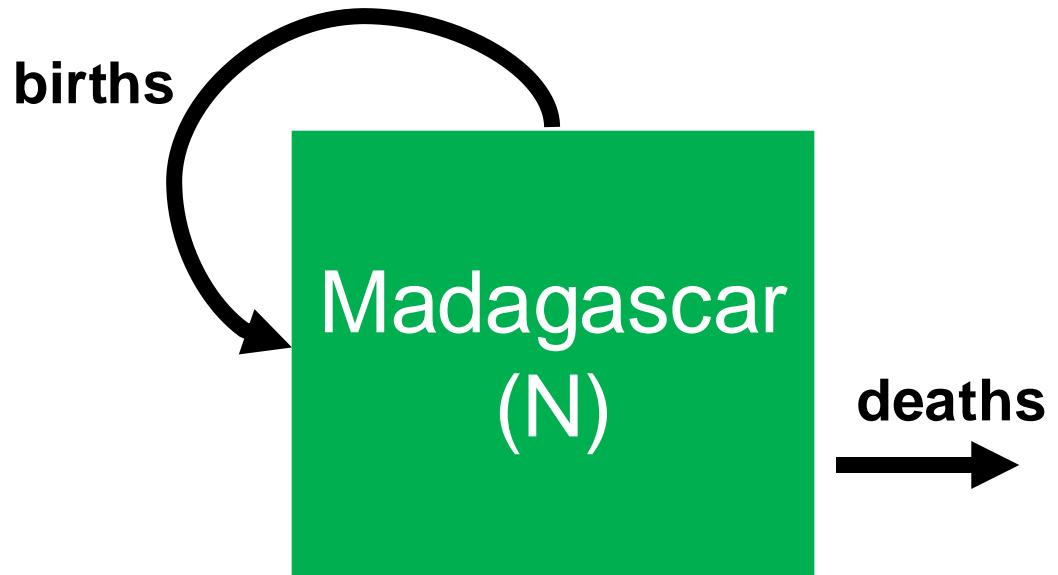
ecosystem



*How does the
abundance of fish
change through time?*

Modeling demographic complexity

Modeling demographic complexity

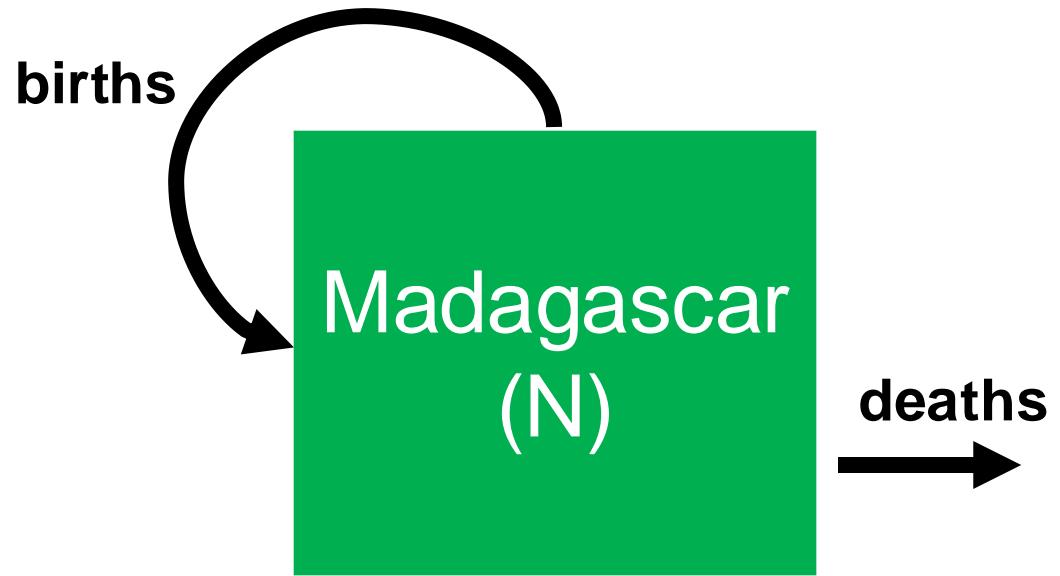


1. Populations are divided into compartments
2. Individuals within a compartment are homogeneously mixed
3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



The simplest population model

Modeling demographic complexity

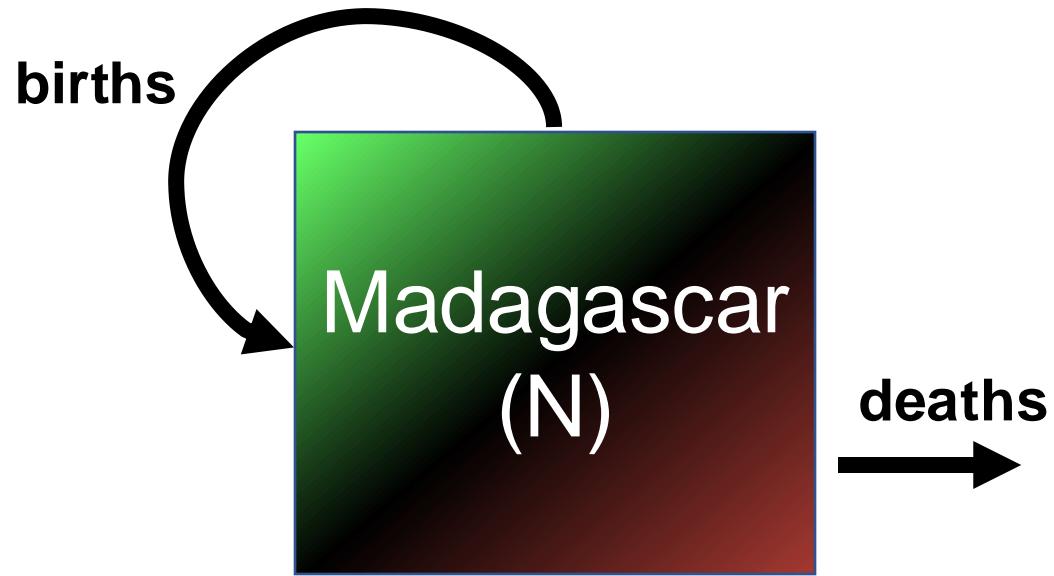


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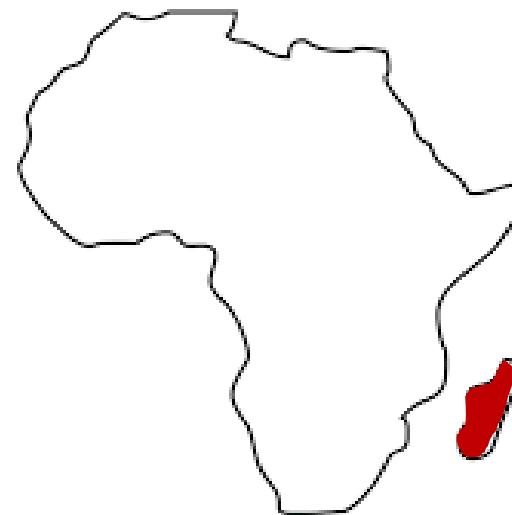


What is wrong about this model?

Modeling demographic complexity



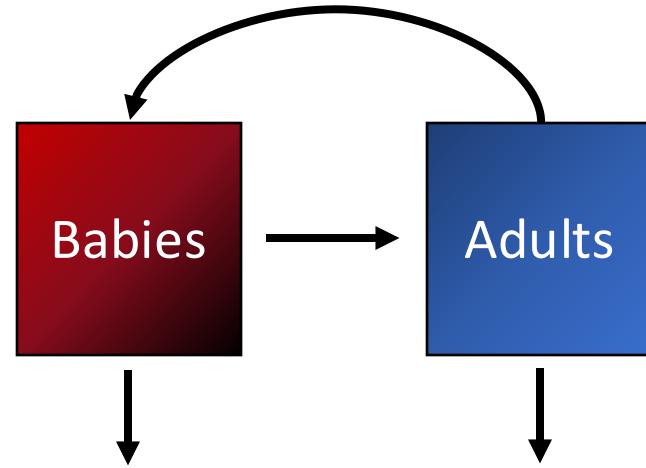
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What is wrong about this model?

Modeling demographic complexity

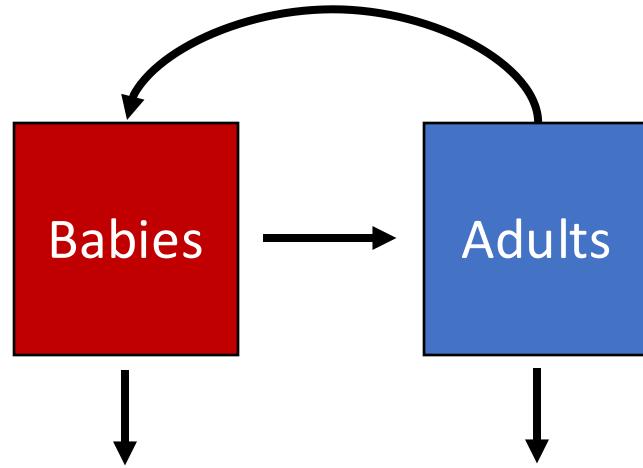
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The structured population model

Modeling demographic complexity

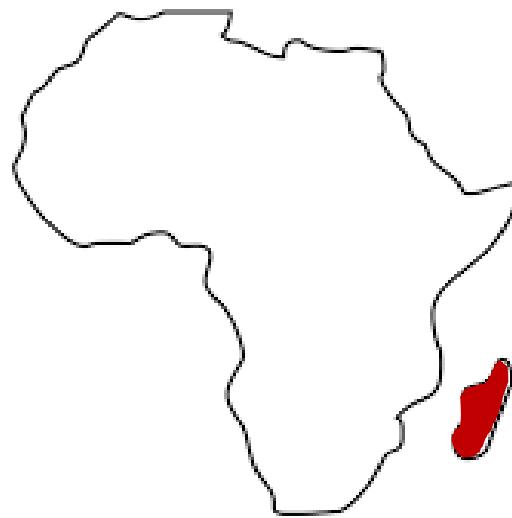
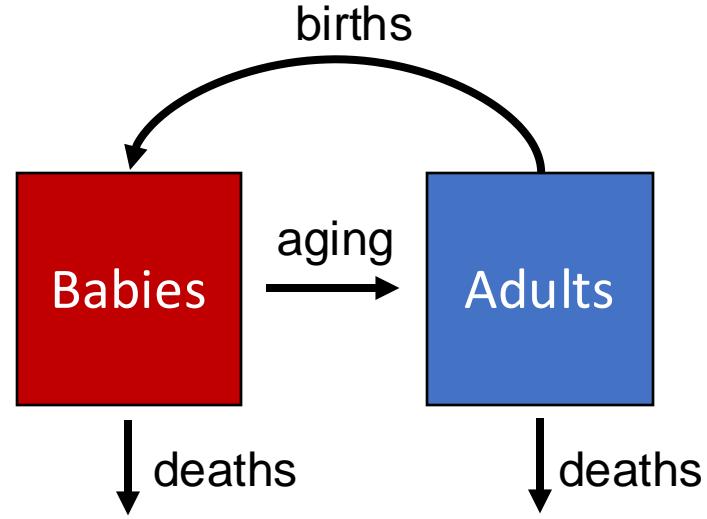
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The structured population model

Modeling demographic complexity

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4. Rates of transferring between compartments are expressed mathematically



The structured population model

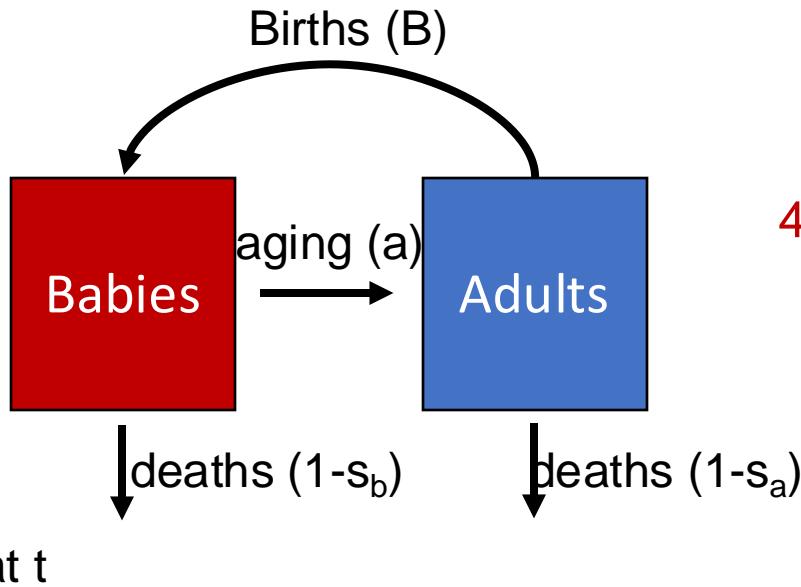
The structured population model

Population rate of increase

$$\lambda = \frac{N_{t+1}}{N_t}$$

pop size at t + 1

pop size at t



1. Populations are divided into compartments
2. Individuals within a compartment are homogeneously mixed
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4. Rates of transferring between compartments are expressed mathematically

$$N_{t+1} = A^* N_t$$

matrix of survival
and fecundity rates

| | |
|------------|-------|
| $s_b(1-a)$ | B |
| $s_b a$ | s_a |

vector of
population sizes

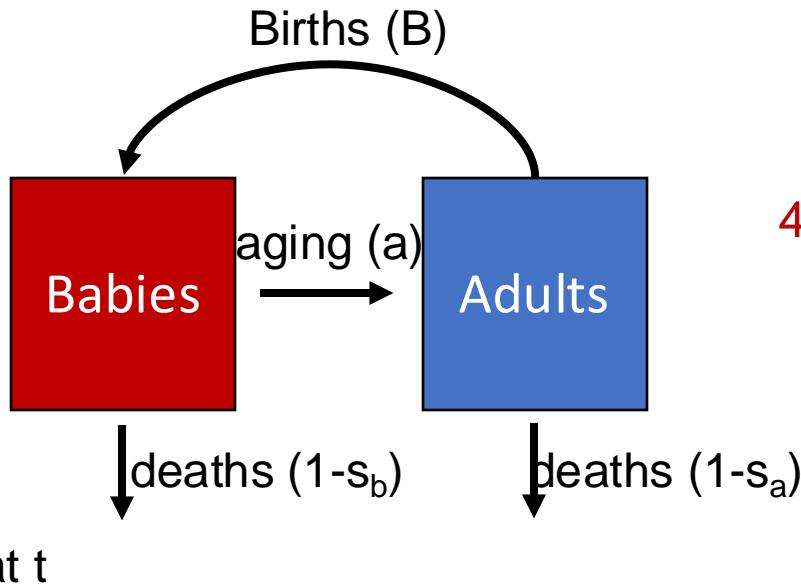
The structured population model

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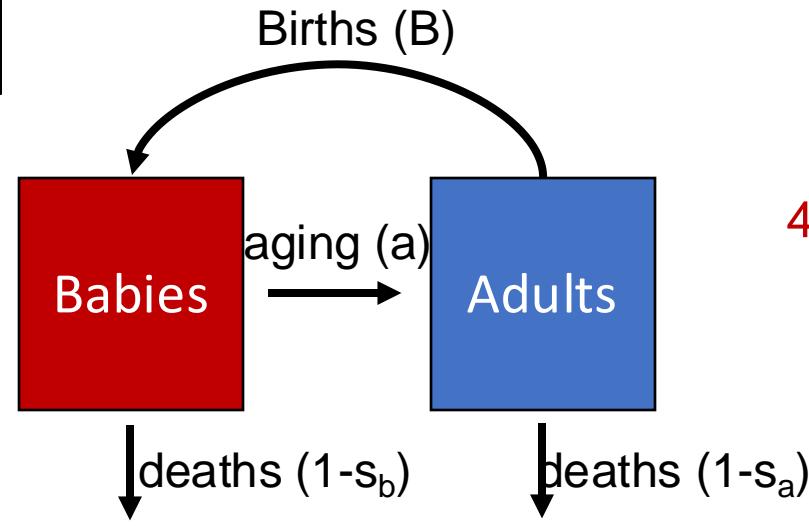
matrix of survival
and fecundity rates

| | |
|------------|-------|
| $s_b(1-a)$ | B |
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vector of
population sizes

*Discrete time

The structured population model

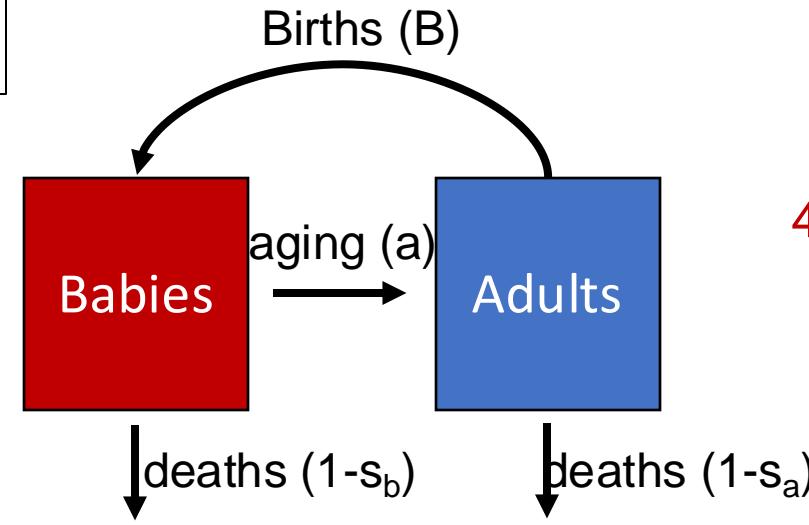


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$$N_{t+1} = A^* N_t$$

$$\begin{array}{c} \mathbf{A} \\ \begin{matrix} s_b(1-a) & B \\ \hline s_b a & s_a \end{matrix} \end{array} \times \begin{array}{c} \mathbf{N}_t \\ \begin{matrix} N_b \\ \hline N_a \end{matrix} \end{array} = \begin{array}{c} \mathbf{N}_{t+1} \\ \begin{matrix} s_b(1-a) N_b + B N_a \\ \hline s_b a N_b + s_a N_a \end{matrix} \end{array}$$

The structured population model



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$$N_{t+1} = A^* N_t$$

Population rate of increase – can be derived from the transition matrix!

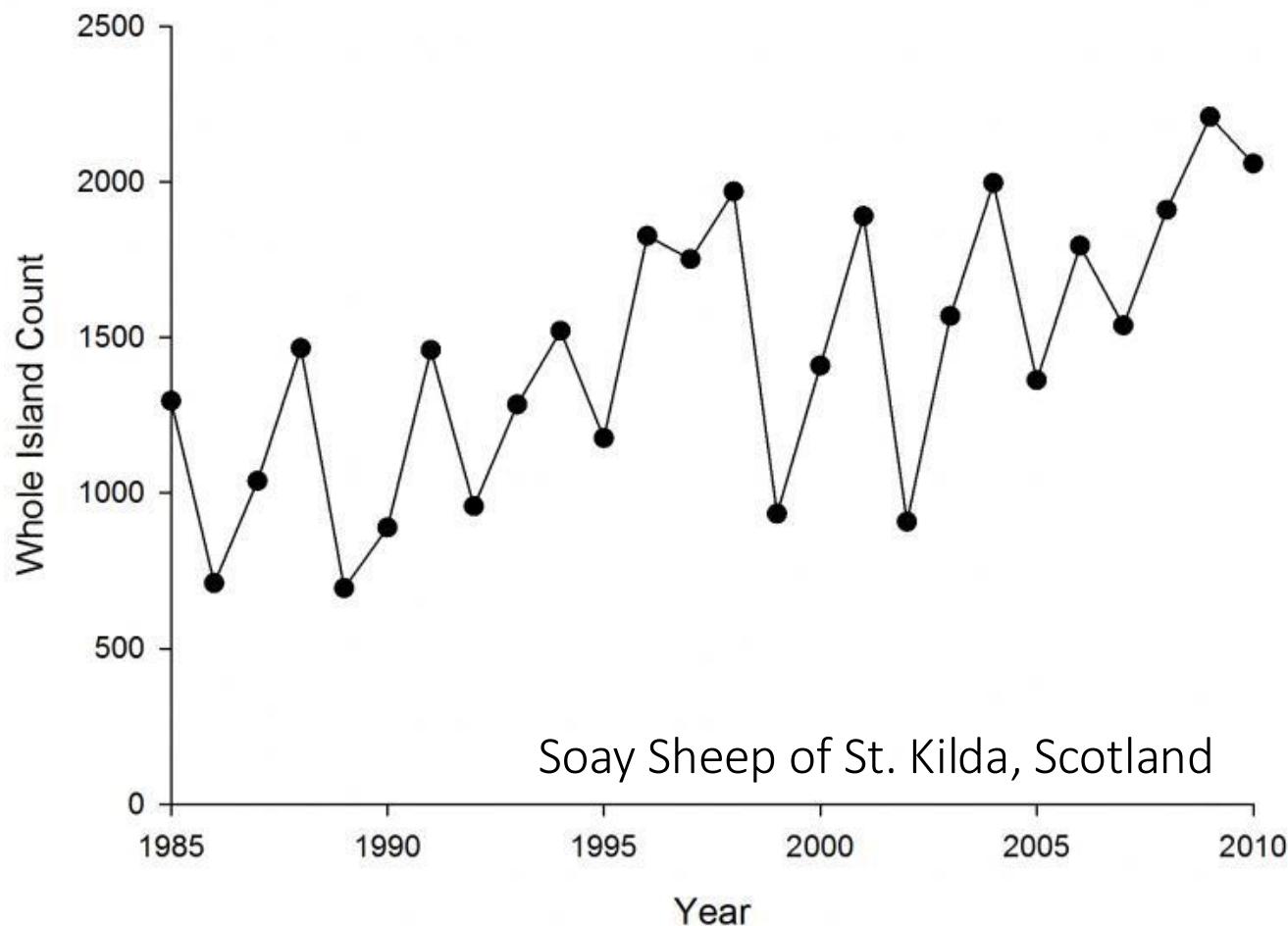
λ

$$\begin{array}{c} \mathbf{A} \\ \xrightarrow{\quad} \begin{matrix} s_b(1-a) & B \\ \hline s_b a & s_a \end{matrix} \end{array} \times \begin{matrix} N_b \\ N_a \end{matrix} = \begin{matrix} s_b(1-a) N_b + B N_a \\ s_b a N_b + s_a N_a \end{matrix}$$

Population growth will depend on population structure!

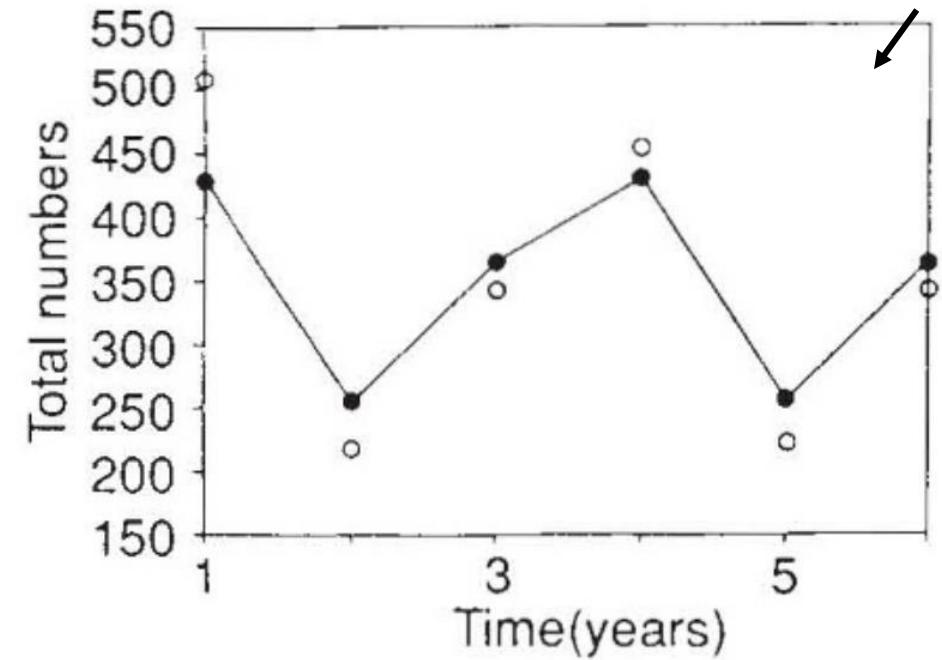
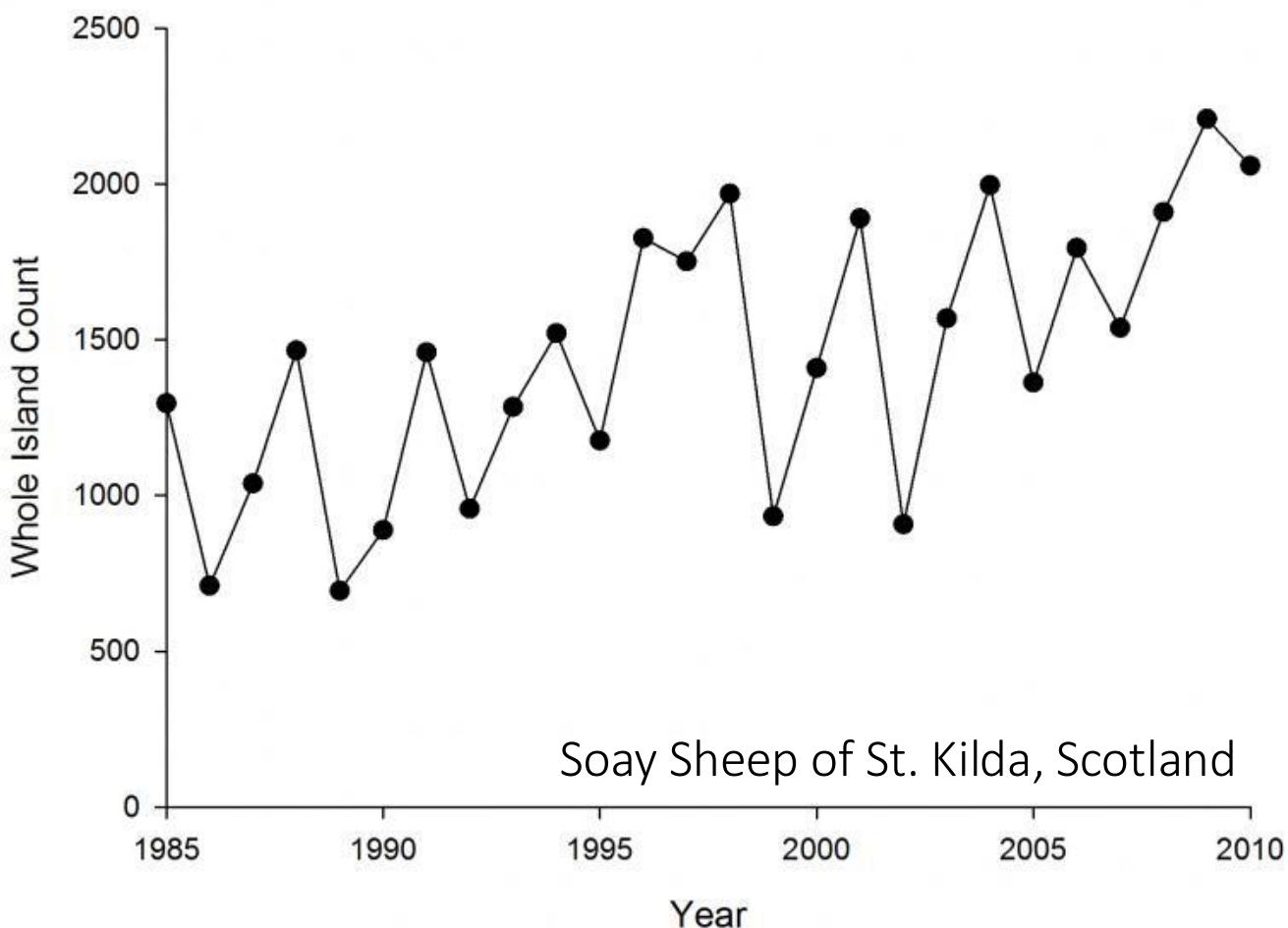
(pop grows @ $\lambda > 1$ & declines @ $\lambda < 1$)

Structured populations in practice



Structured populations in practice

Model
compared
against
data



Overcompensation and population cycles in an ungulate

[B. T. Grenfell](#), [O. F. Price](#), [S. D. Albon](#) & [T. H. Glutton-Brock](#)

[Nature](#) 355, 823–826 (1992) | [Cite this article](#)

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Model
compared
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data

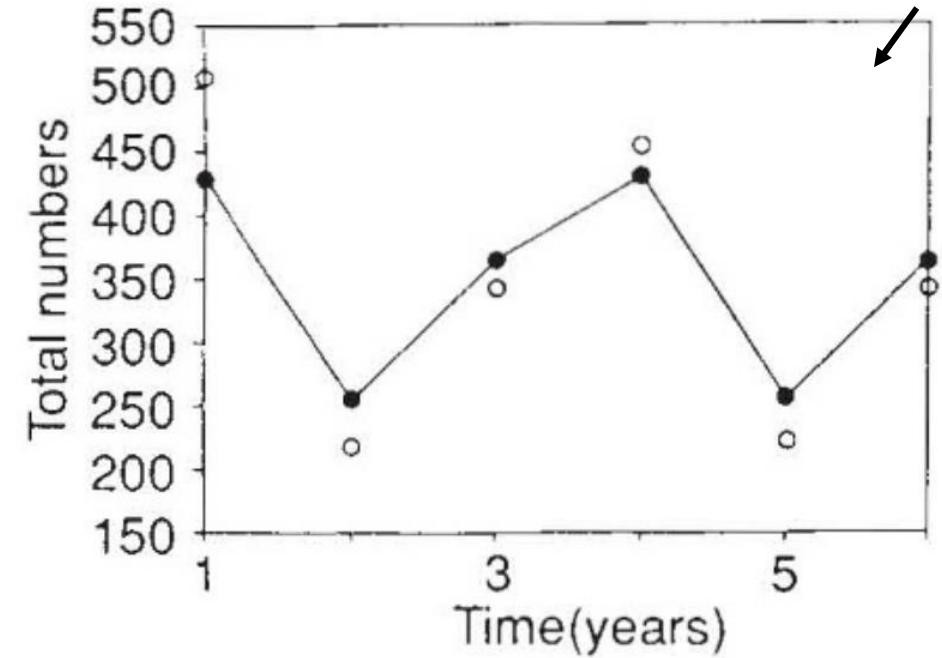
Structured populations in practice

These results used a simple **density-dependent** model only!

$$N_{t+1} = \lambda d N_t / (1 + (aN_t)^b)$$

↑ ↑ growth rate }
population at t+1 average fecundity population at t

a and *b* control the strength of density dependence.



Overcompensation and population cycles in an ungulate

[B. T. Grenfell](#), [O. F. Price](#), [S. D. Albon](#) & [T. H. Glutton-Brock](#)

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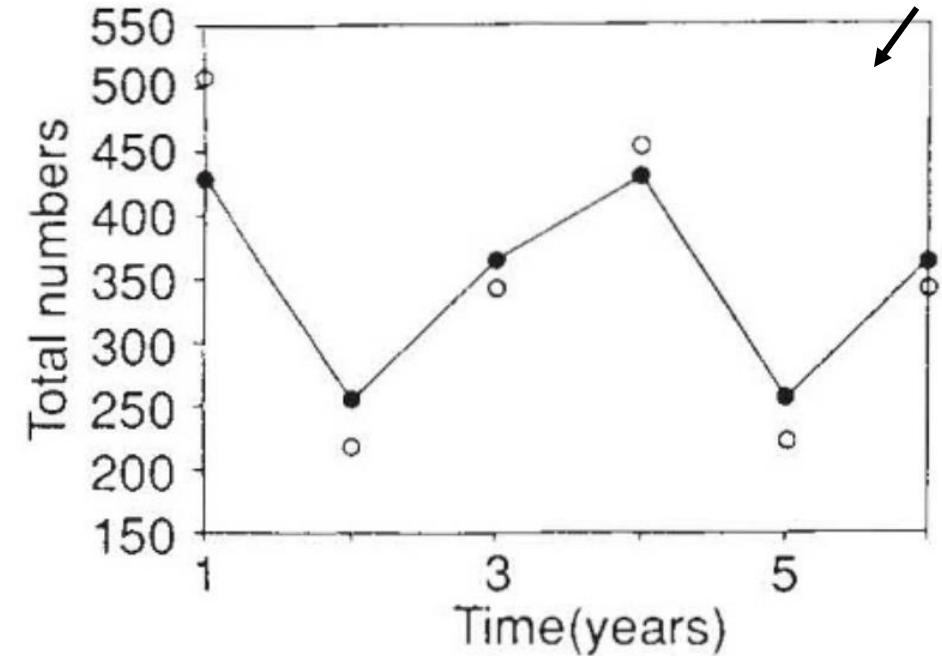
$$N_{t+1} = \lambda d N_t / (1 + (aN_t)^b)$$

↑ ↑ growth rate }
population at t+1 average fecundity population at t

a and *b* control the strength of density dependence.

Similar to the simple logistic growth equation!

$$N_{t+1} = N_t \left(1 - \frac{N_t}{K}\right)$$



Overcompensation and population cycles in an ungulate

[B. T. Grenfell, O. F. Price, S. D. Albon & T. H. Glutton-Brock](#)

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Structured populations in practice

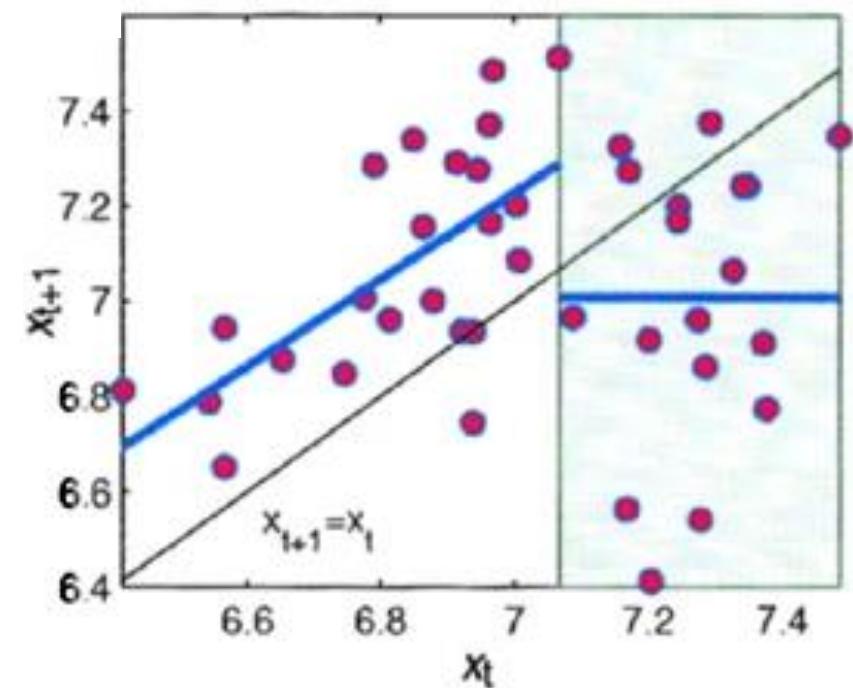
In later work, the authors added **environmental stochasticity** (bad weather) to **better represent** the data.....

Noise and determinism in synchronized sheep dynamics

[B. T. Grenfell](#) , [K. Wilson](#), [B. F. Finkenstädt](#), [T. N. Coulson](#), [S. Murray](#), [S. D. Albon](#), [J. M. Pemberton](#), [T. H. Clutton-Brock](#) & [M. J. Crawley](#)

[Nature](#) **394**, 674–677 (1998) | [Cite this article](#)

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Structured populations in practice

In later work, the authors added **environmental stochasticity** (bad weather) to **better represent** the data.....

At high population sizes, population crashes can occur due to density dependence – but these happen preferentially in bad weather!

Noise and determinism in synchronized sheep dynamics

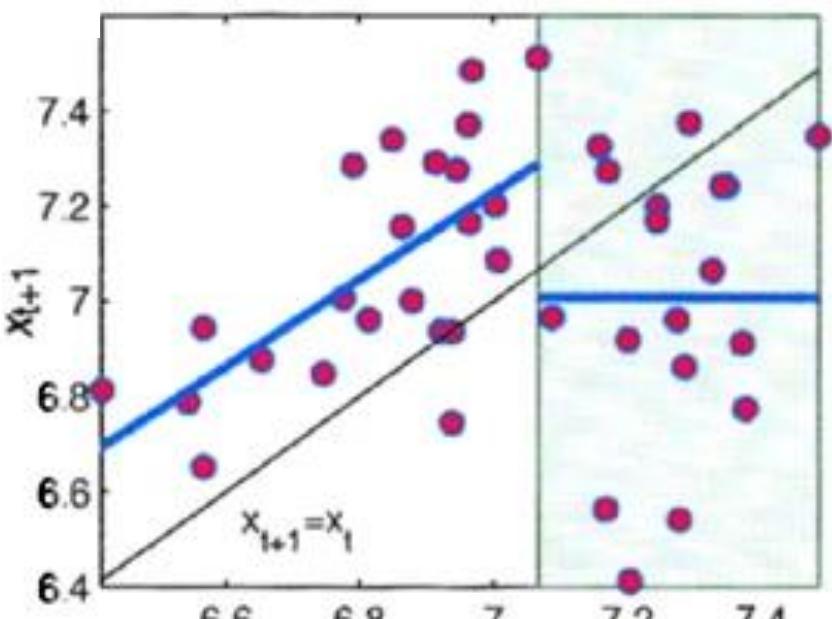
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sheep
population at
time $t+1$

sheep population at time t → x_t



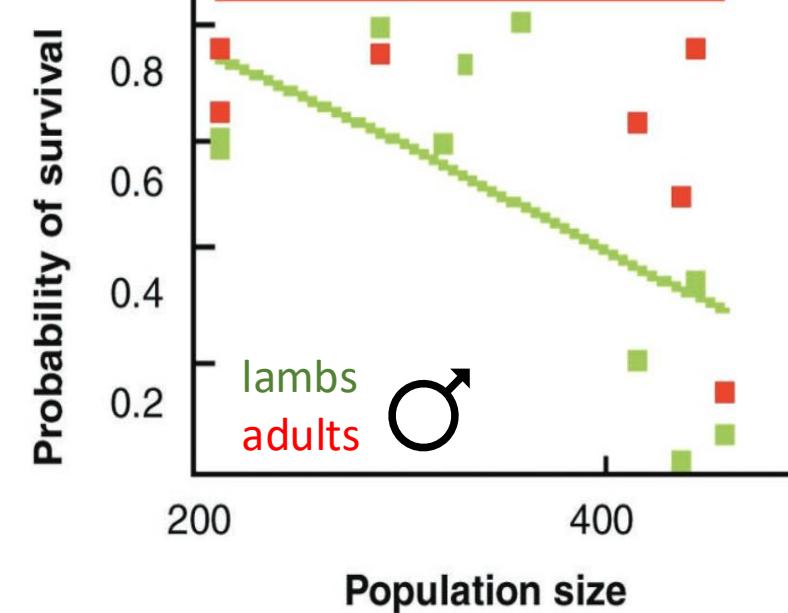
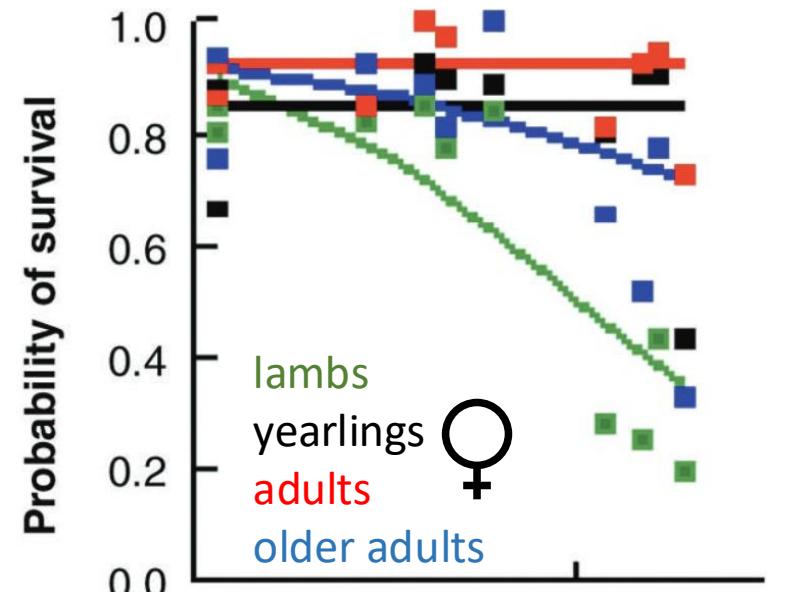
Structured populations in practice

And, finally, they added in **population structure** as well!

Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep

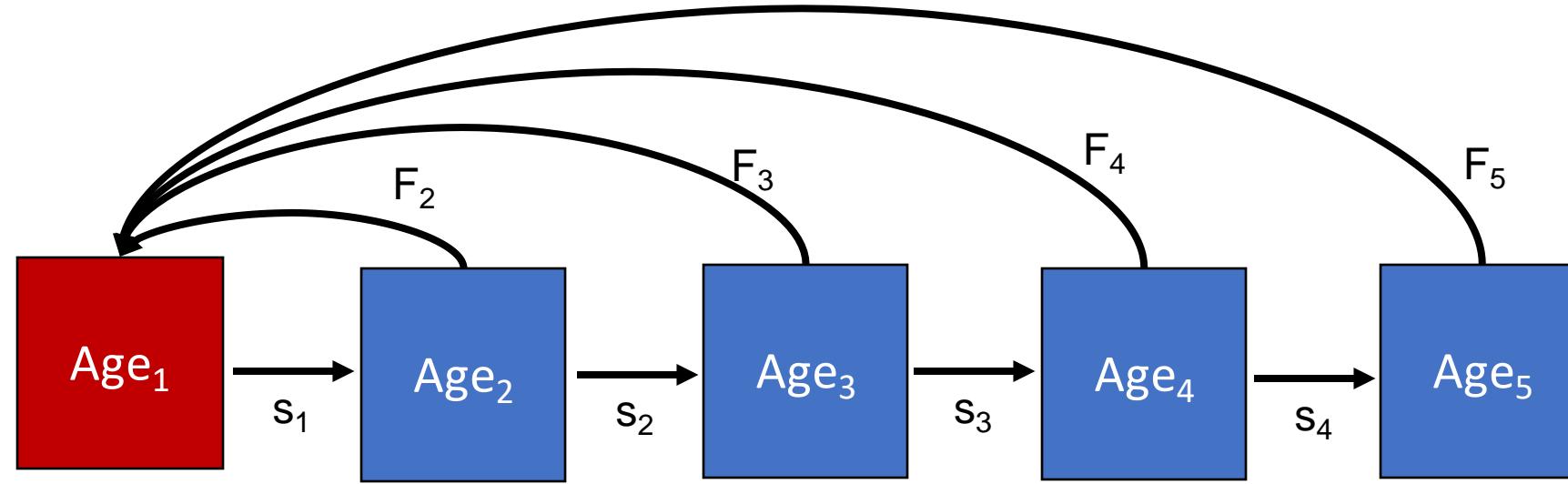
T. Coulson,^{1*}† E. A. Catchpole,² S. D. Albon,³ B. J. T. Morgan,⁴
J. M. Pemberton,⁵ T. H. Clutton-Brock,⁶ M. J. Crawley,⁶
B. T. Grenfell⁷

25 MAY 2001 VOL 292 SCIENCE www.sciencemag.org



The structured population model

If data are available, we can model much more detailed population structures using the same approach.

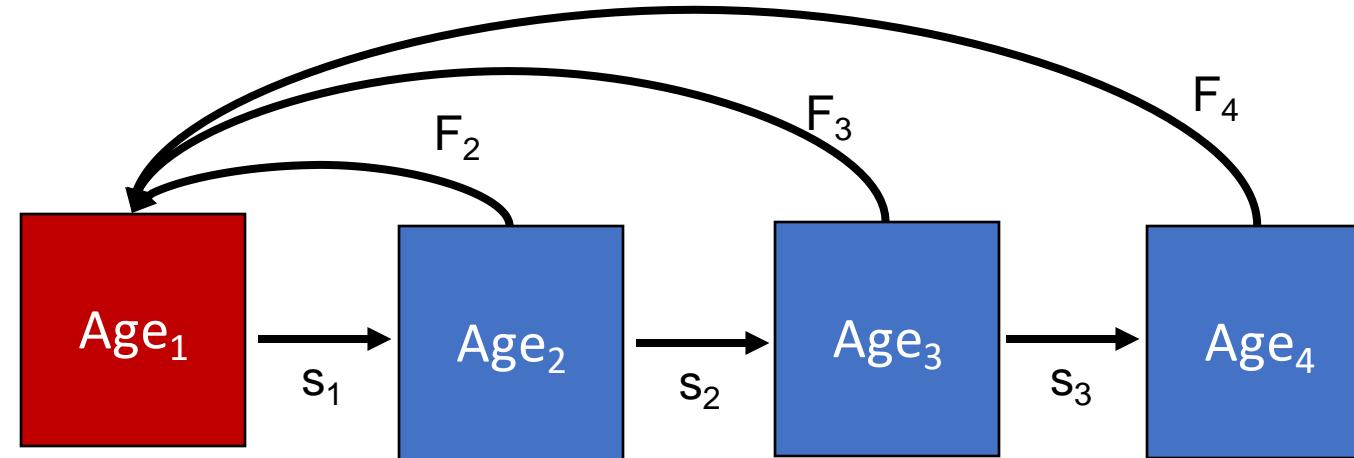


The **Leslie matrix** model divides classes based on age.

The **Lefkovitch matrix** model divides classes based on life stage.

The structured population model

If data are available, we can model much more detailed population structures using the same approach.



λ =can be
derived from
transition matrix

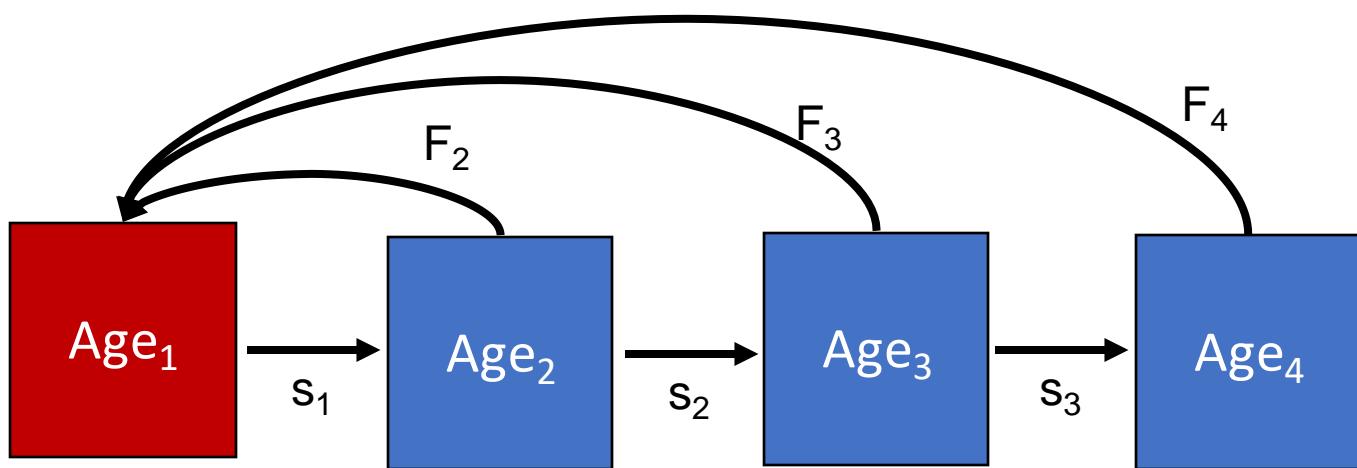
$$\rightarrow \begin{matrix} & \mathbf{A} \\ \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} & \times \begin{bmatrix} N_t \\ N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} = \begin{bmatrix} N_{t+1} \\ N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} \end{matrix}$$

$$N_{t+1} = A^* N_t$$

Leslie 1945 *Biometrika*. Leslie 1948 *Biometrika*.
Lefkovitch 1965 *Biometrics*.

The structured population model

Demographers collect these rates in life tables



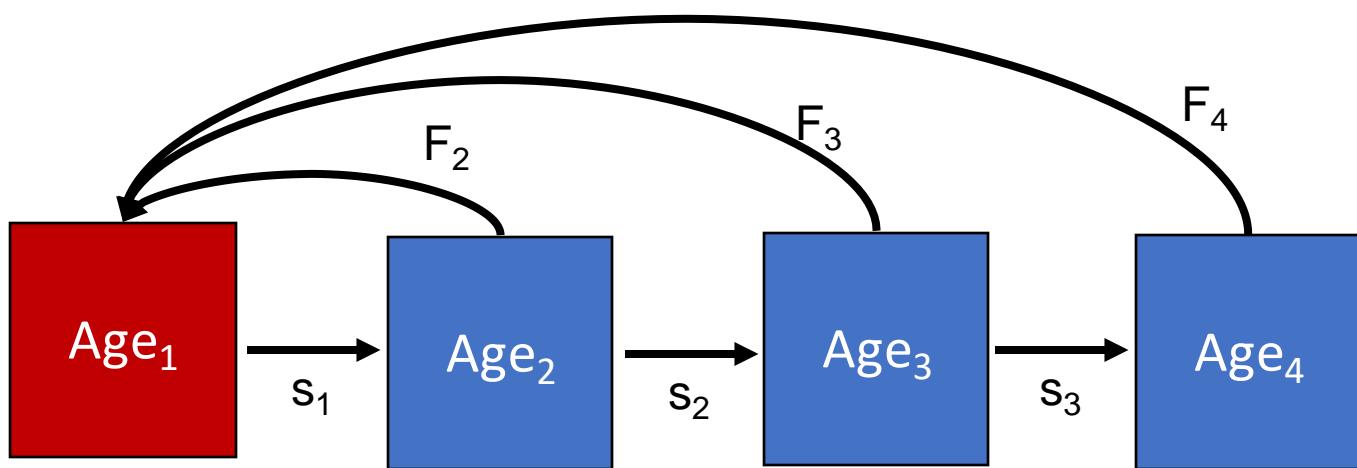
| x (age) | N _x (number in cohort) | I _x (survivorship to age x) | m _x (fecundity) | I _x m _x |
|---------|-----------------------------------|--|----------------------------|-------------------------------|
| 0 | 100 | 1 | 0 | 0 |
| 1 | 60 | .6 | 2 | 1.2 |
| 2 | 30 | .3 | 3 | 0.9 |
| 3 | 10 | .1 | 1 | 0.1 |
| 4 | 1 | .01 | 1 | 0.01 |



Gross reproductive rate (GRR): $\sum m_x = 7$

The structured population model

Demographers collect these rates in life tables



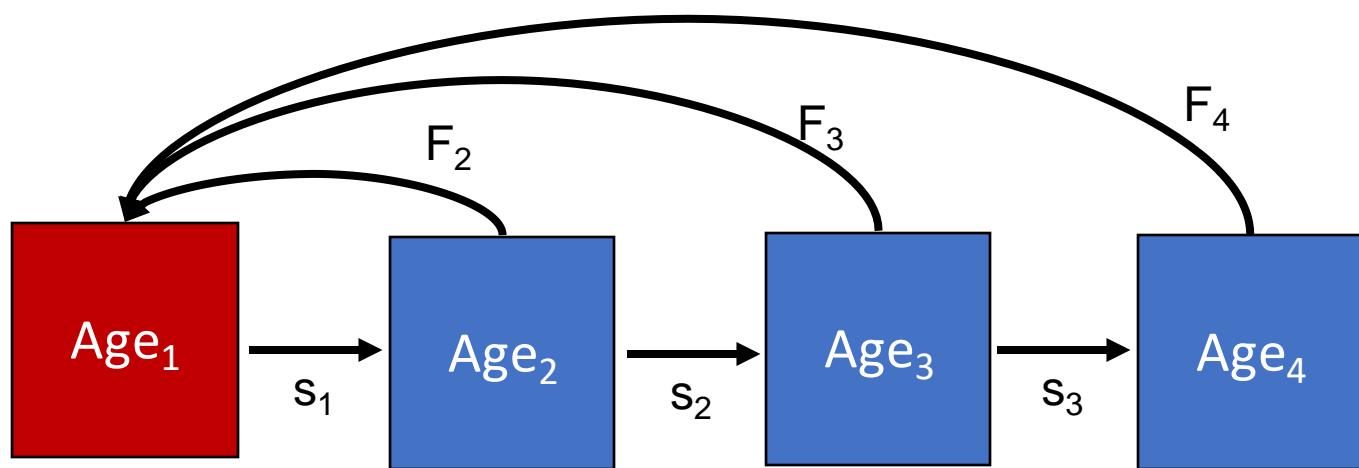
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Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

The structured population model

Demographers collect these rates in life tables



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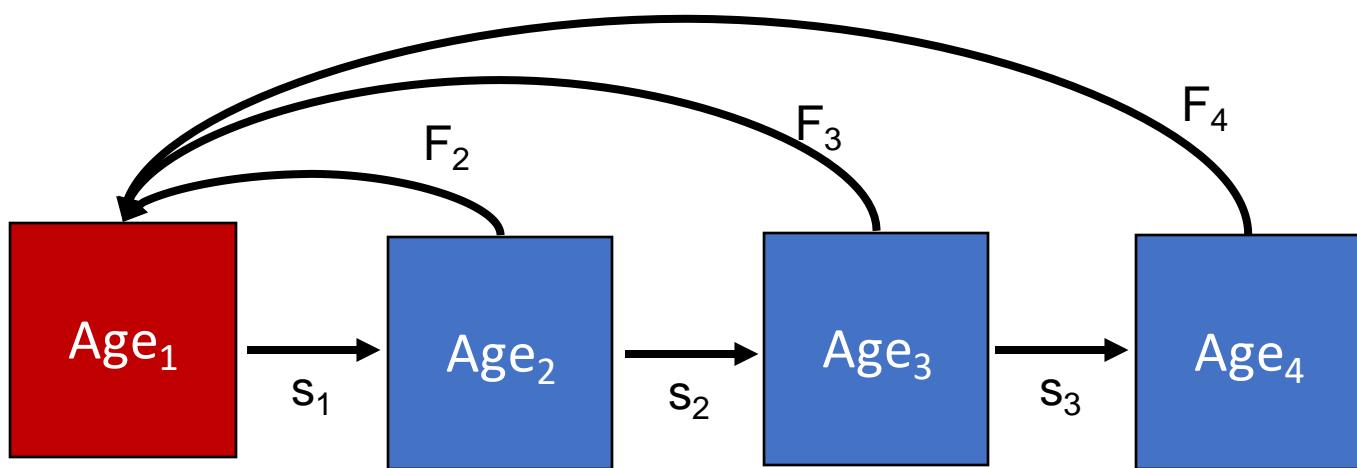


Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

(pop grows at $R_0 > 1$ and declines at $R_0 < 1$)

The structured population model

Demographers collect these rates in life tables



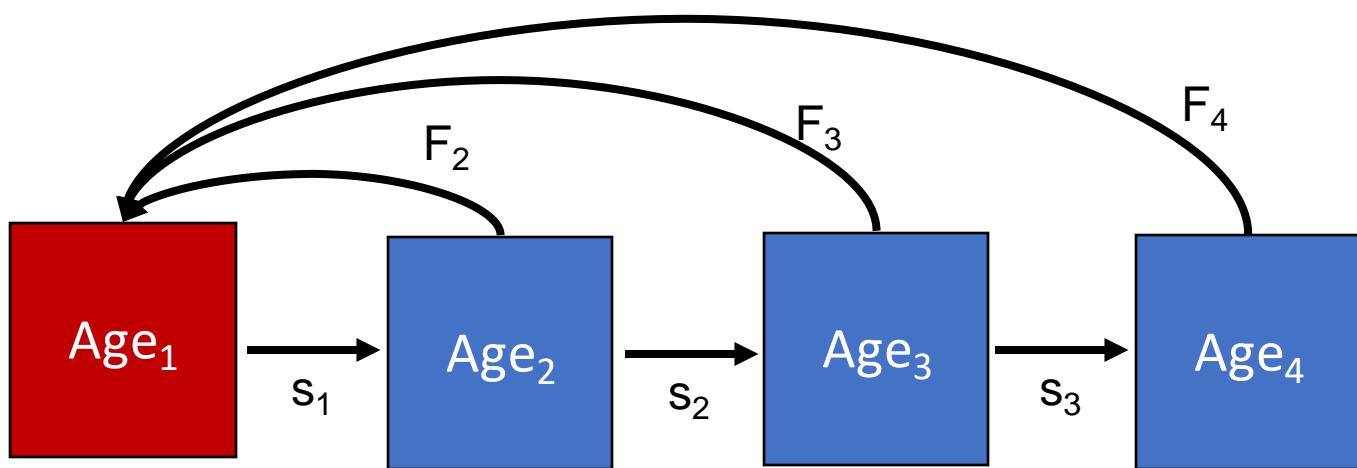
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| 4 | 1 | .01 | 1 | 0.01 |



Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

$\lambda = R_0^{1/G}$ where G = length of a generation (often 1 year)

The structured population model



| x (age) | N _x (number in cohort) | I _x (survivorship to age x) | m _x (fecundity) | I _x m _x |
|---------|-----------------------------------|--|----------------------------|-------------------------------|
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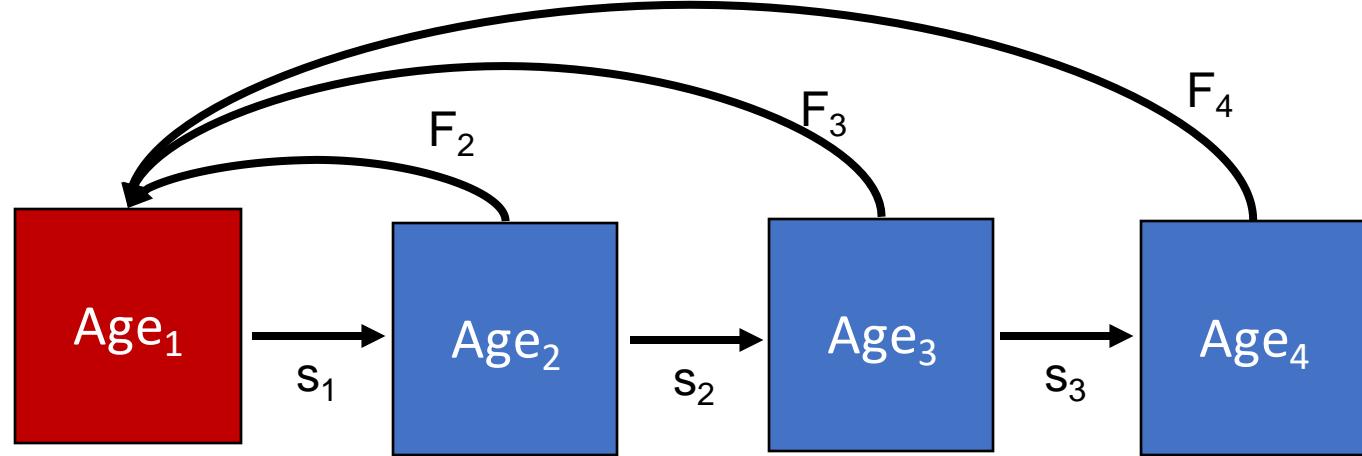
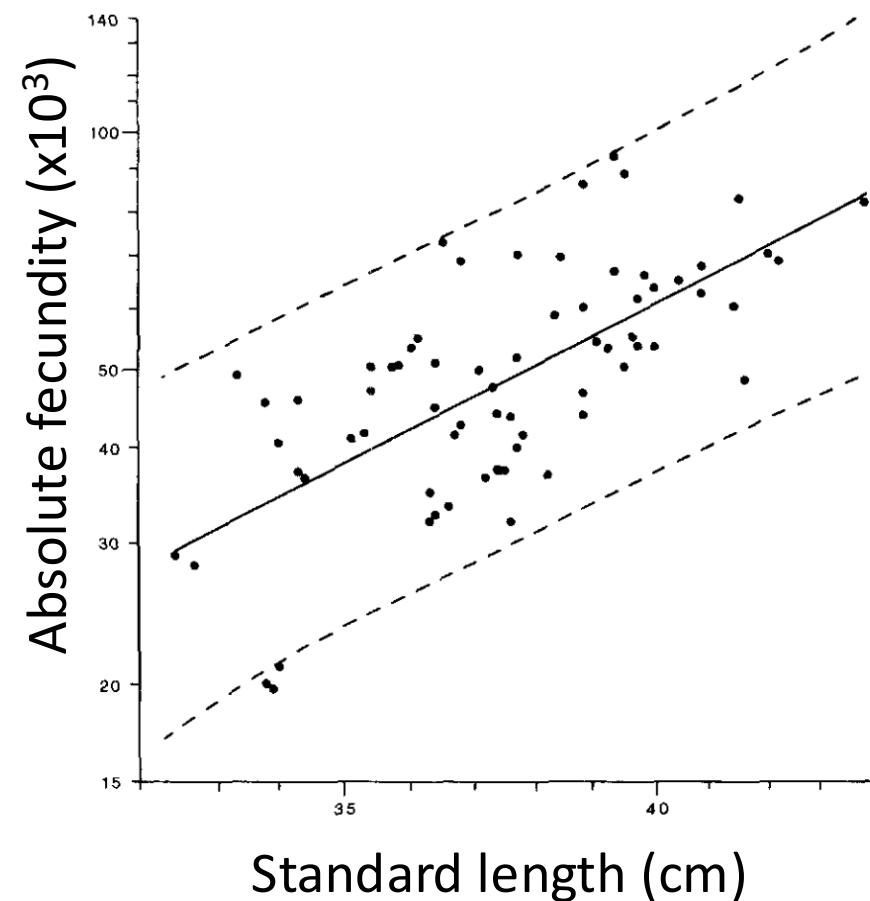


⋮

Orange roughy can live up to 200 years!

Net reproductive rate (R_0): $\sum l_x m_x = \dots$

The structured population model



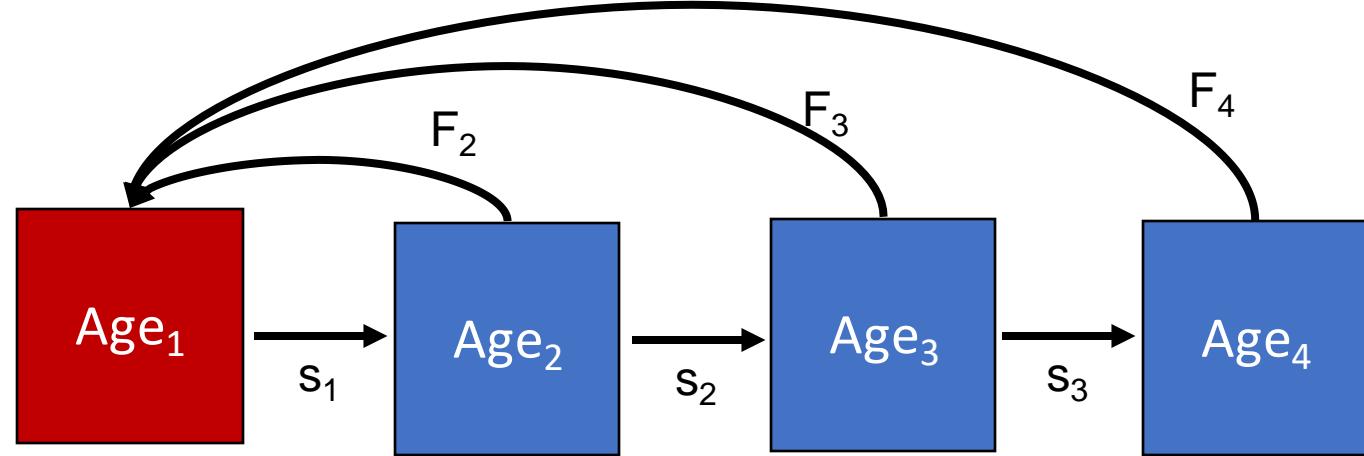
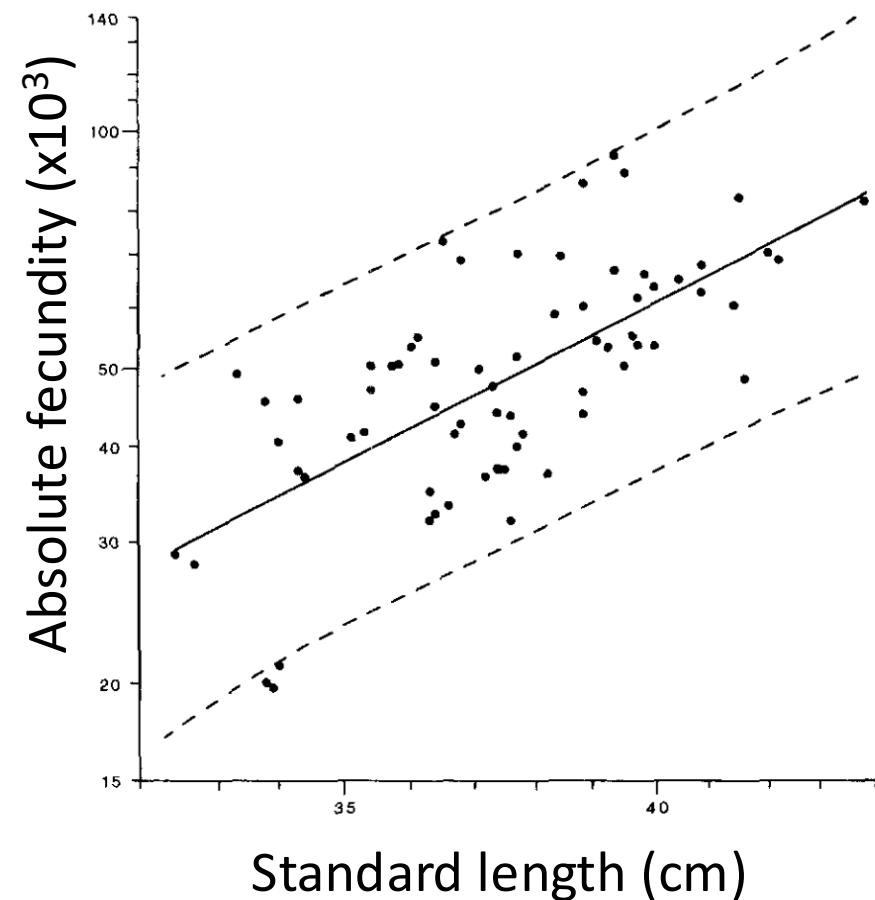
A brace on the left side of the text block groups the fecundity arrows. The text states:

Fecundity (eggs)
increases in older,
bigger fish!

Pankhurst & Conroy 1987

NZ J of Marine & Freshwater Res

The structured population model



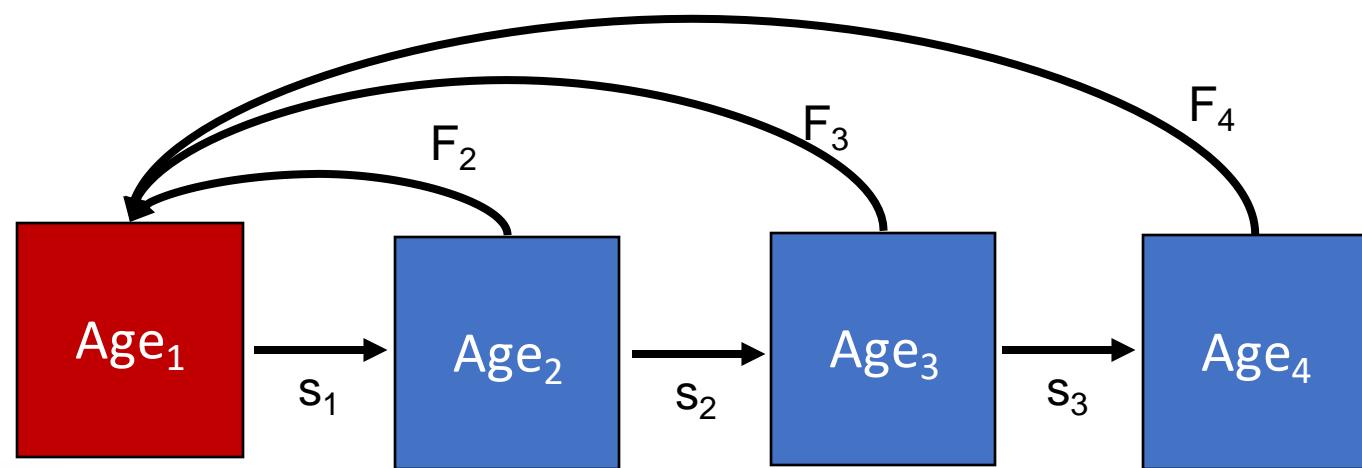
Fecundity (eggs)
increases in older,
bigger fish!

These are precisely
the fish we like to
catch! One of the
problems with
MSY...

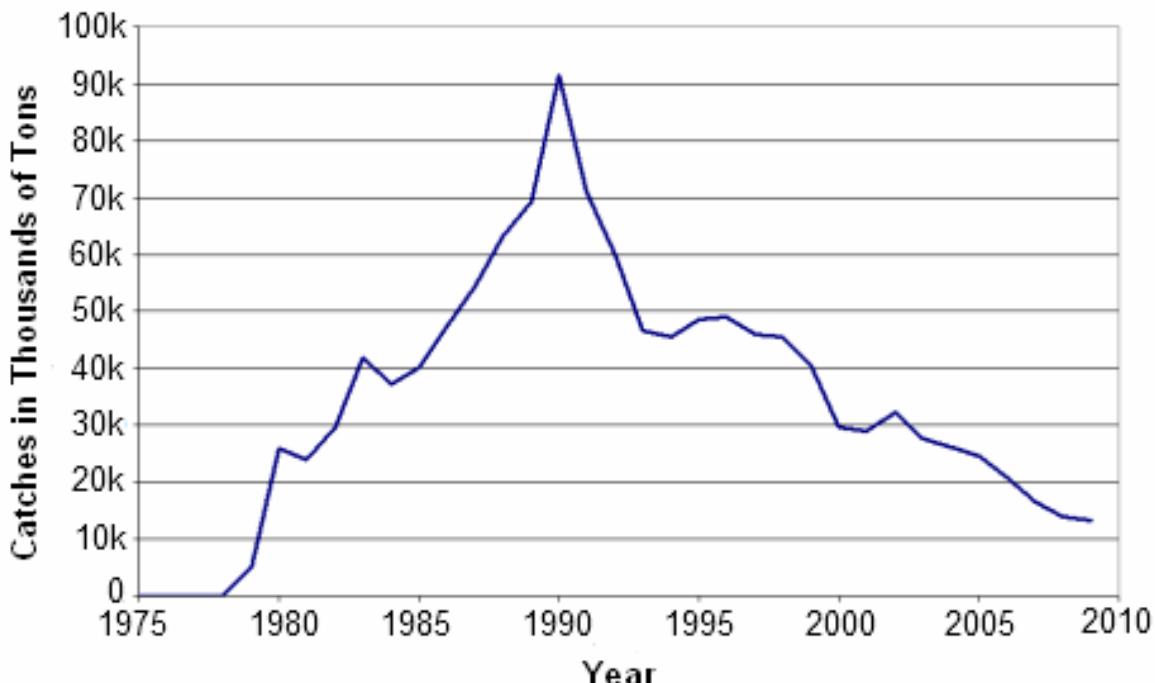


Norway 1910
(Norsk folkemuseum)

The structured population model



Worldwide Catches of Orange Roughy 1975 - 2009



Source: FAO (Fisheries and Agriculture Organisation of the United Nations) Fisheries and Aquaculture Information and Statistics Service. © L. Baumont

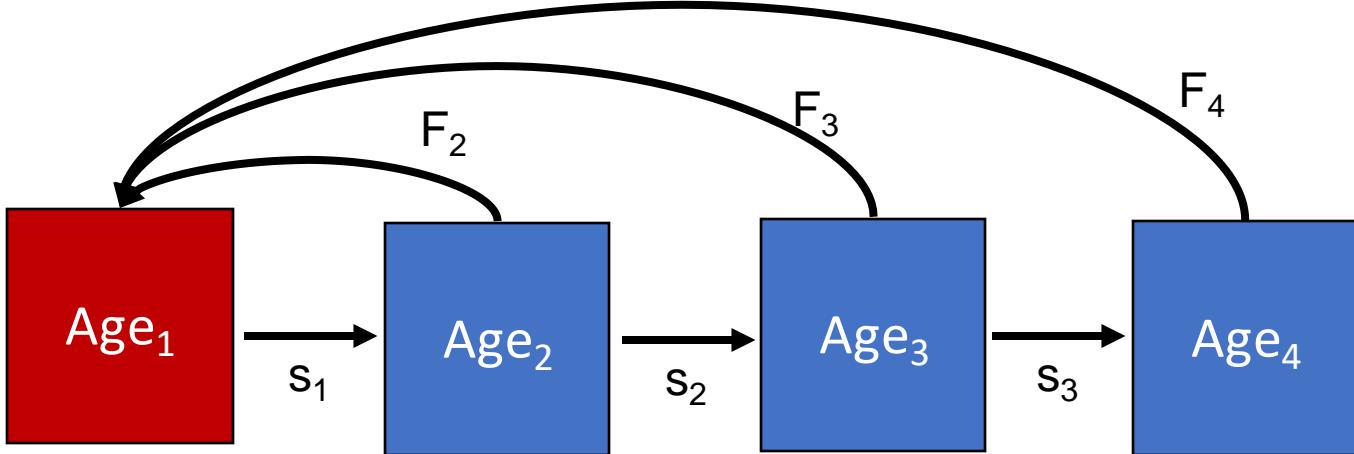
Poor modeling projections has led to severe overexploitation, a common problem in fisheries...

In 2008, the international TAC for orange roughy was reduced from 1470 tons to 914 tons... down from over 90,000 tons in the early 1990s...



The structured population model

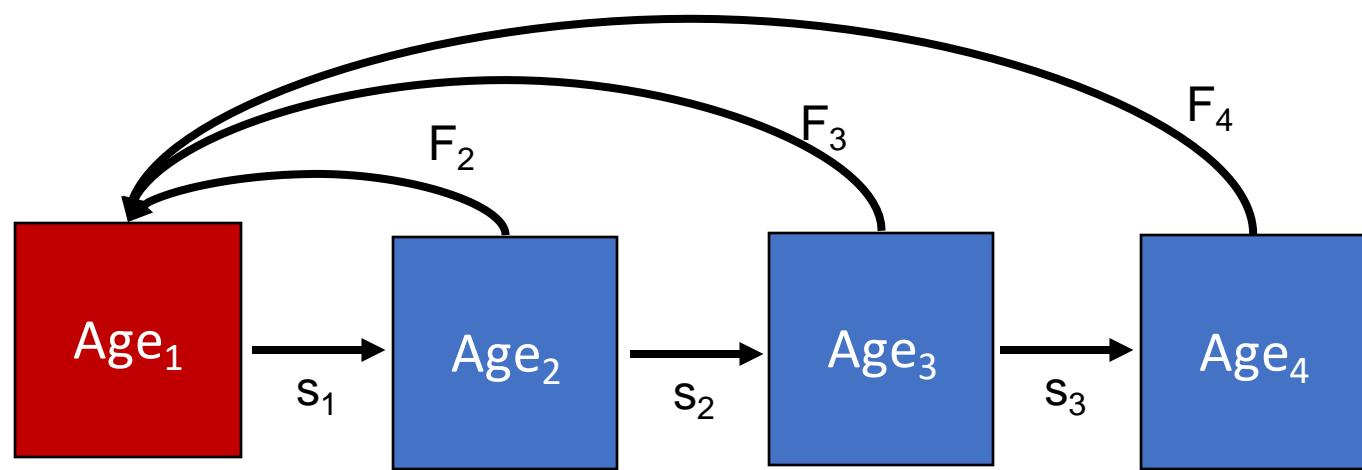
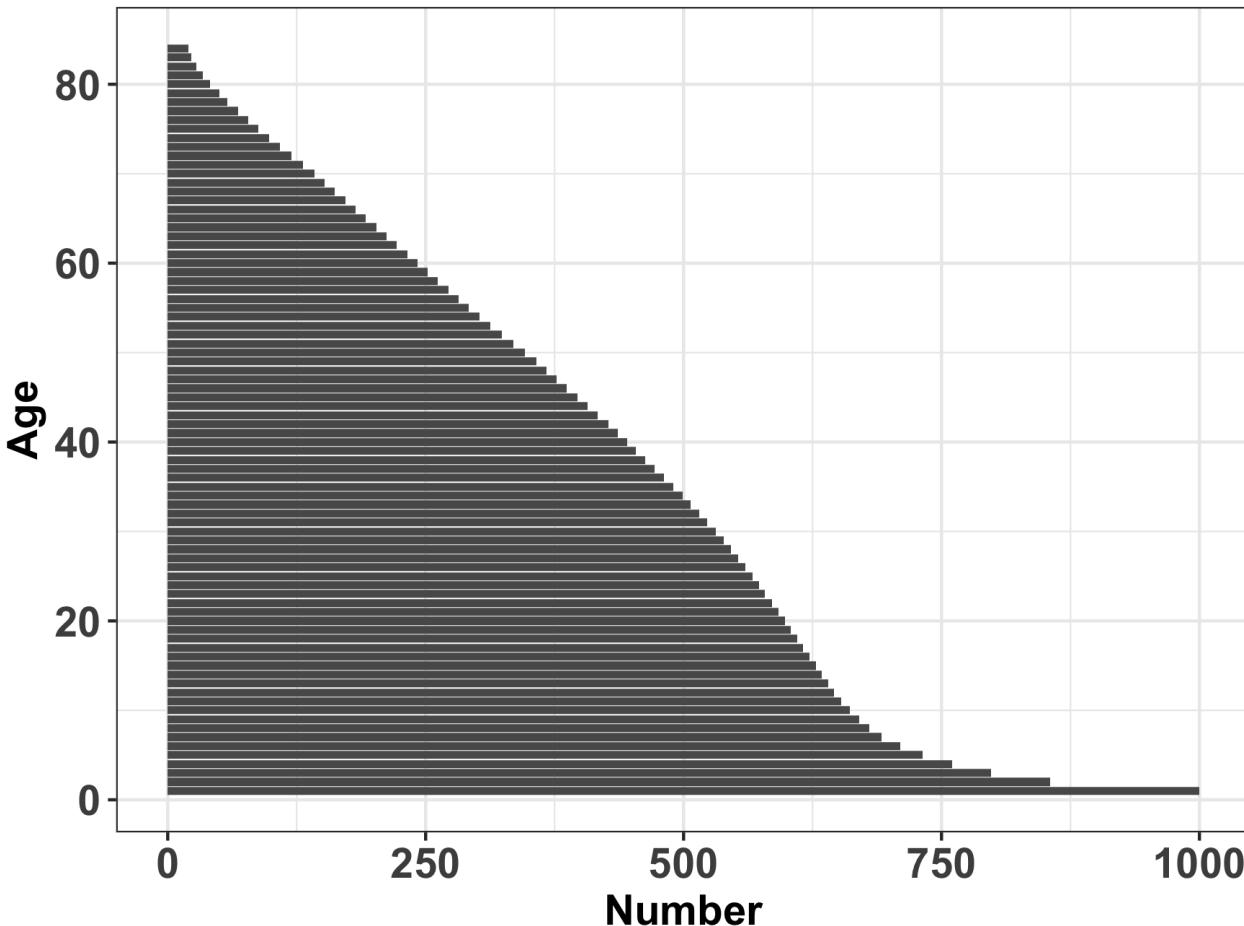
Life table analysis is also used extensively in **human demography**.



Edmond Halley, 1693
“An estimate of the degrees of the mortality of mankind, drawn from curious tables of the births and funerals at the city of Breslau, with an attempt to ascertain the price of annuities upon lives...”

The structured population model

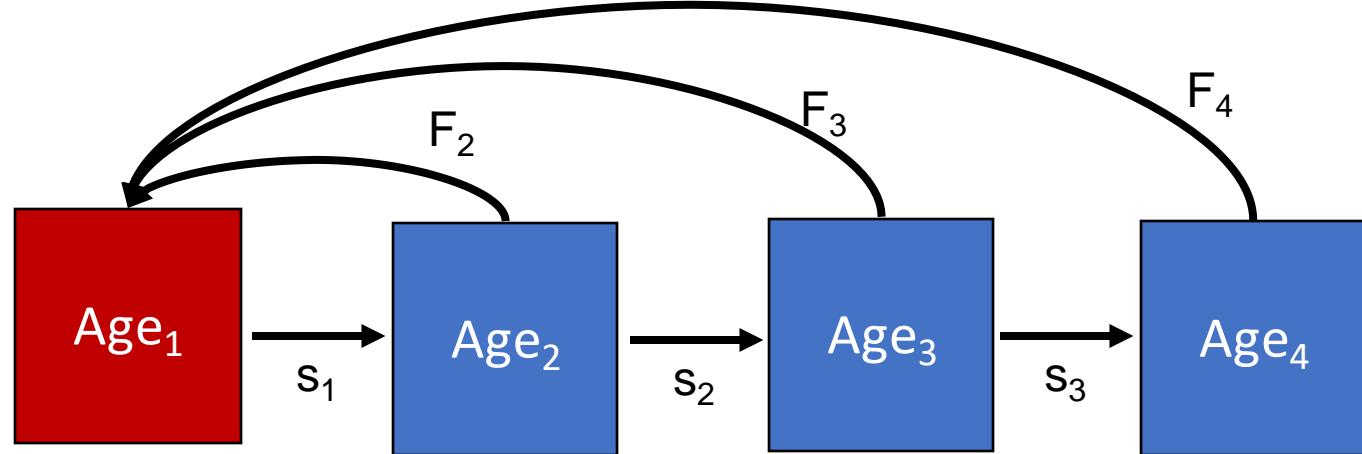
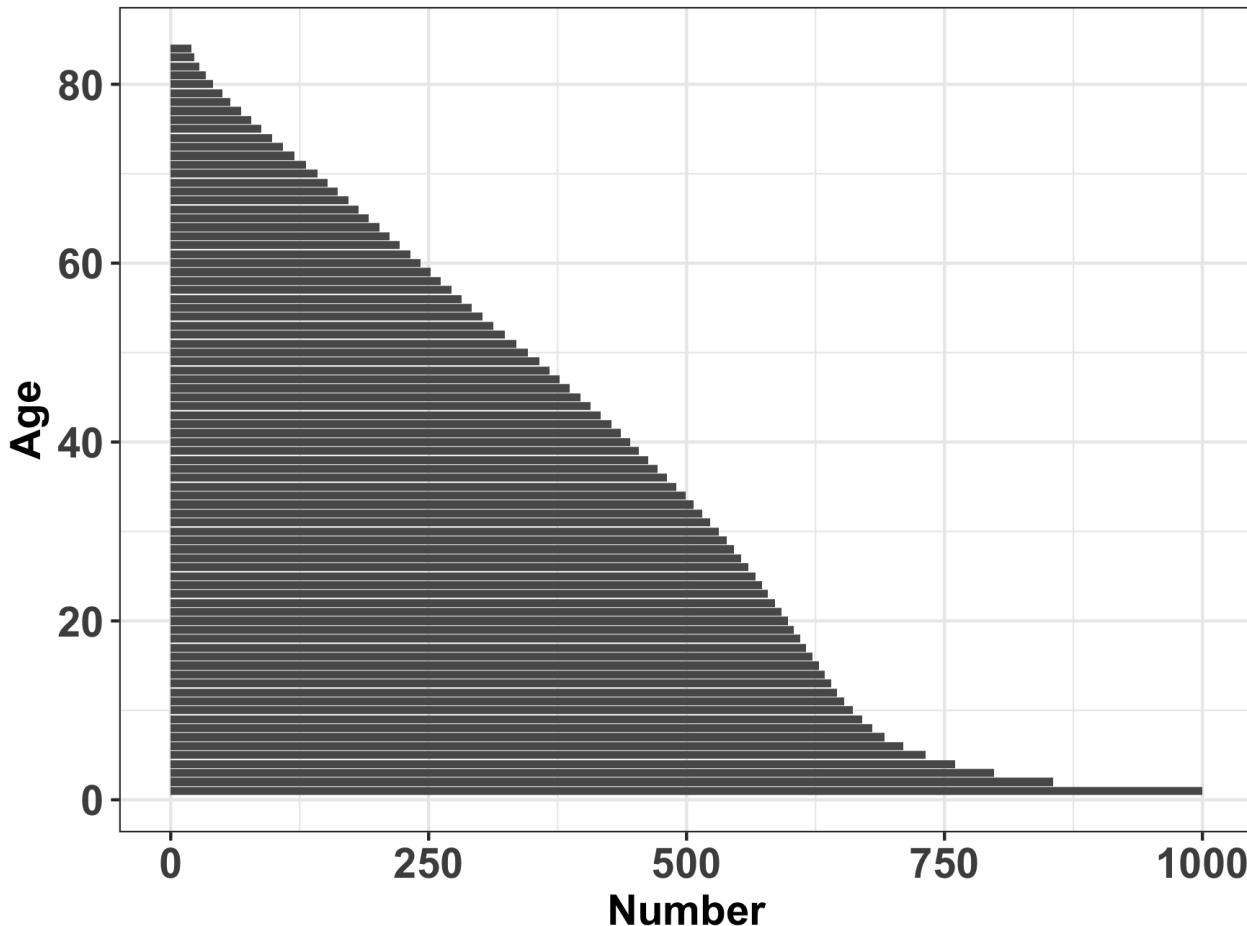
Population pyramid for Breslau



Edmond Halley, 1693
“An estimate of the degrees of the mortality of mankind, drawn from curious tables of the births and funerals at the city of Breslau, with an attempt to ascertain the price of annuities upon lives...”

The structured population model

Population pyramid for Breslau



Humans are not like fish!
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

Younger human populations that start giving birth earlier grow faster!

$$\begin{bmatrix} A & N_t & N_{t+1} \\ \begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} & \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} & = \begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} \end{bmatrix}$$



0.0



**The number of individuals in age class 3 in the next year
is given by:**

$$\begin{bmatrix} 0 & F_2 & F_3 & F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \times \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

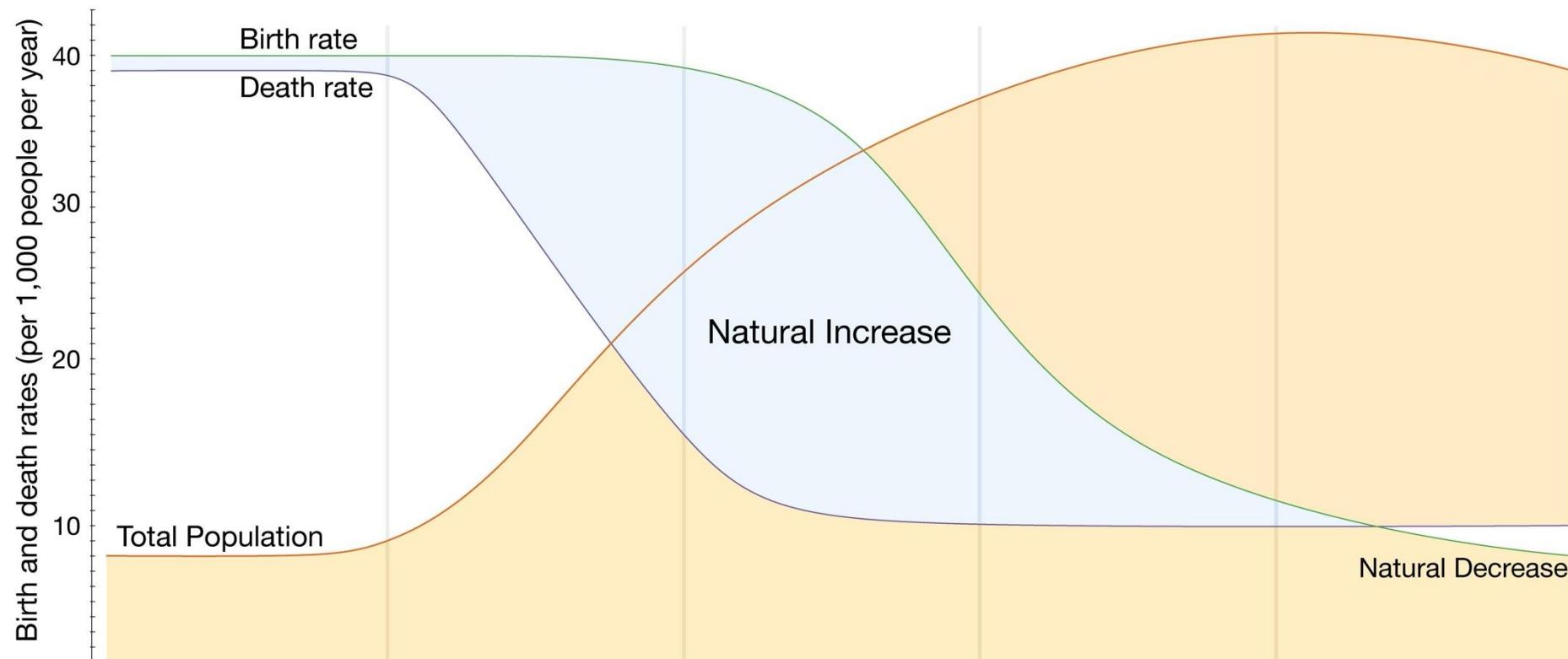
A. $F_2 N_2 + F_3 N_3 + F_4 N_4$

SEE MORE



00%

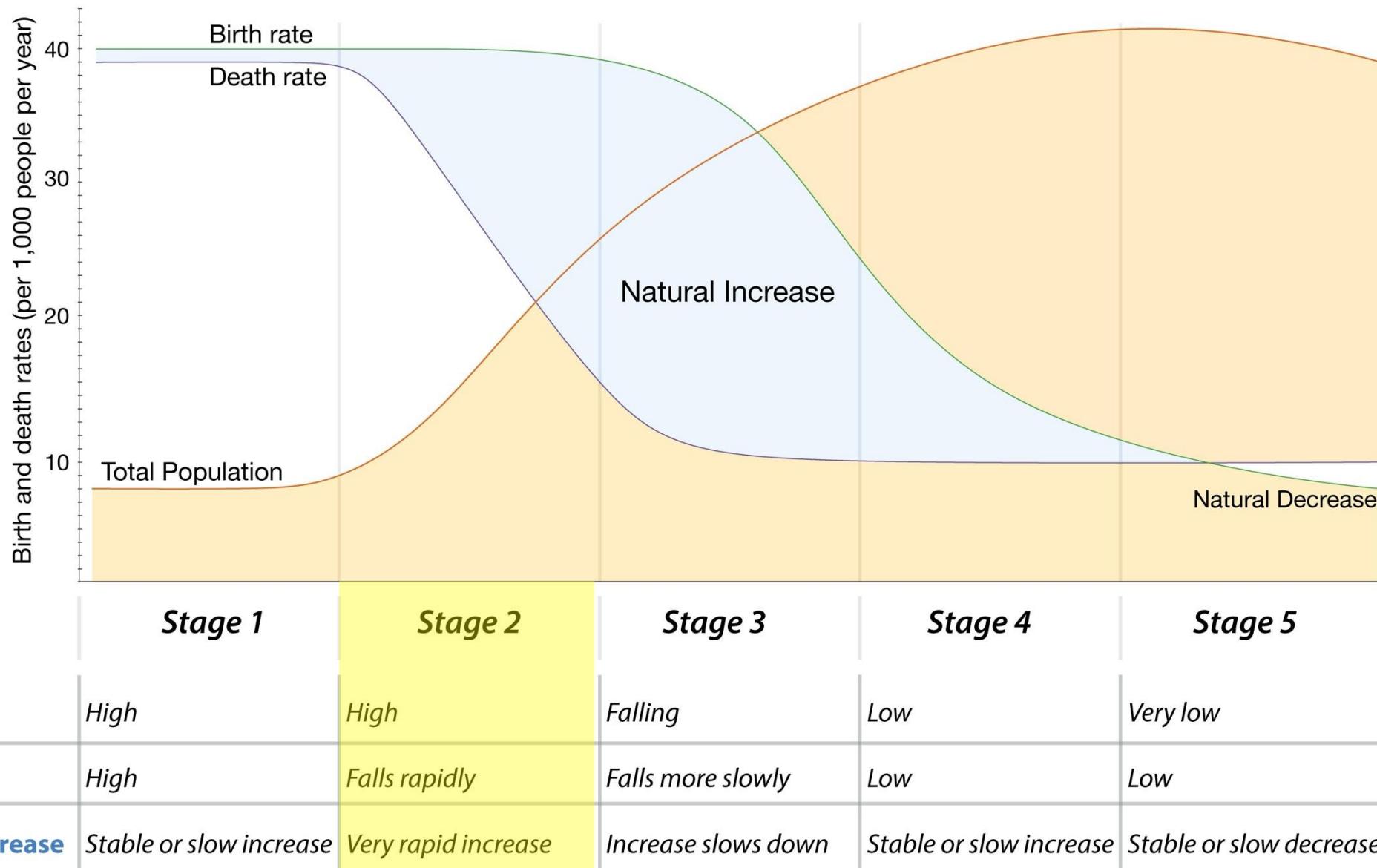
Demographic transition



| | <i>Stage 1</i> | <i>Stage 2</i> | <i>Stage 3</i> | <i>Stage 4</i> | <i>Stage 5</i> |
|-------------------------|-------------------------|---------------------|---------------------|-------------------------|-------------------------|
| Birth rate | High | High | Falling | Low | Very low |
| Death rate | High | Falls rapidly | Falls more slowly | Low | Low |
| Natural increase | Stable or slow increase | Very rapid increase | Increase slows down | Stable or slow increase | Stable or slow decrease |

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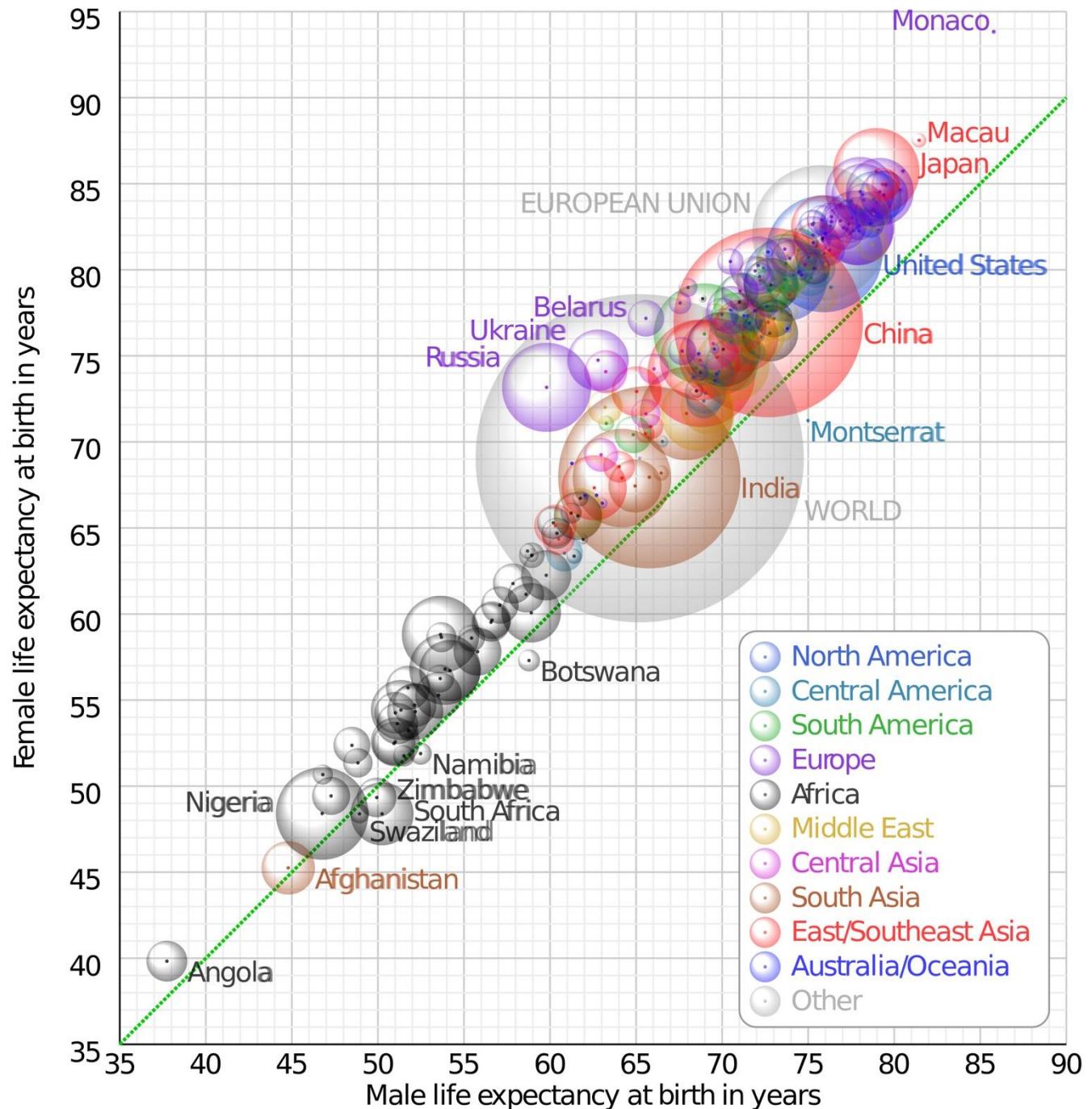
Demographic transition



The author Max Roser licensed this visualisation under a CC BY-SA license. You are welcome to share but please refer to its source where you find more information: <http://www.OurWorldInData.org/data/population-growth-vital-statistics/world-population-growth>

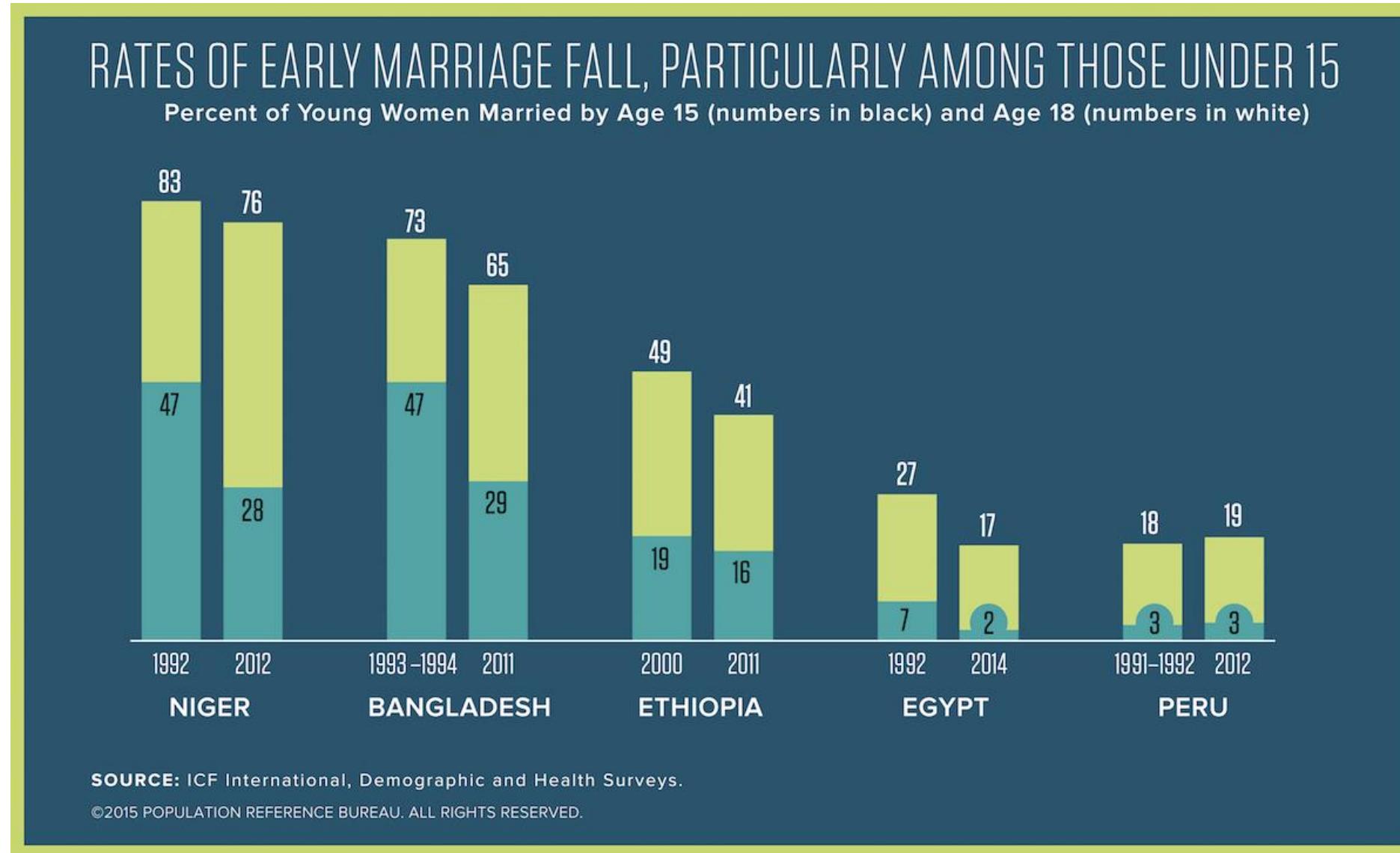
Demographic transition

Death rates are falling globally...

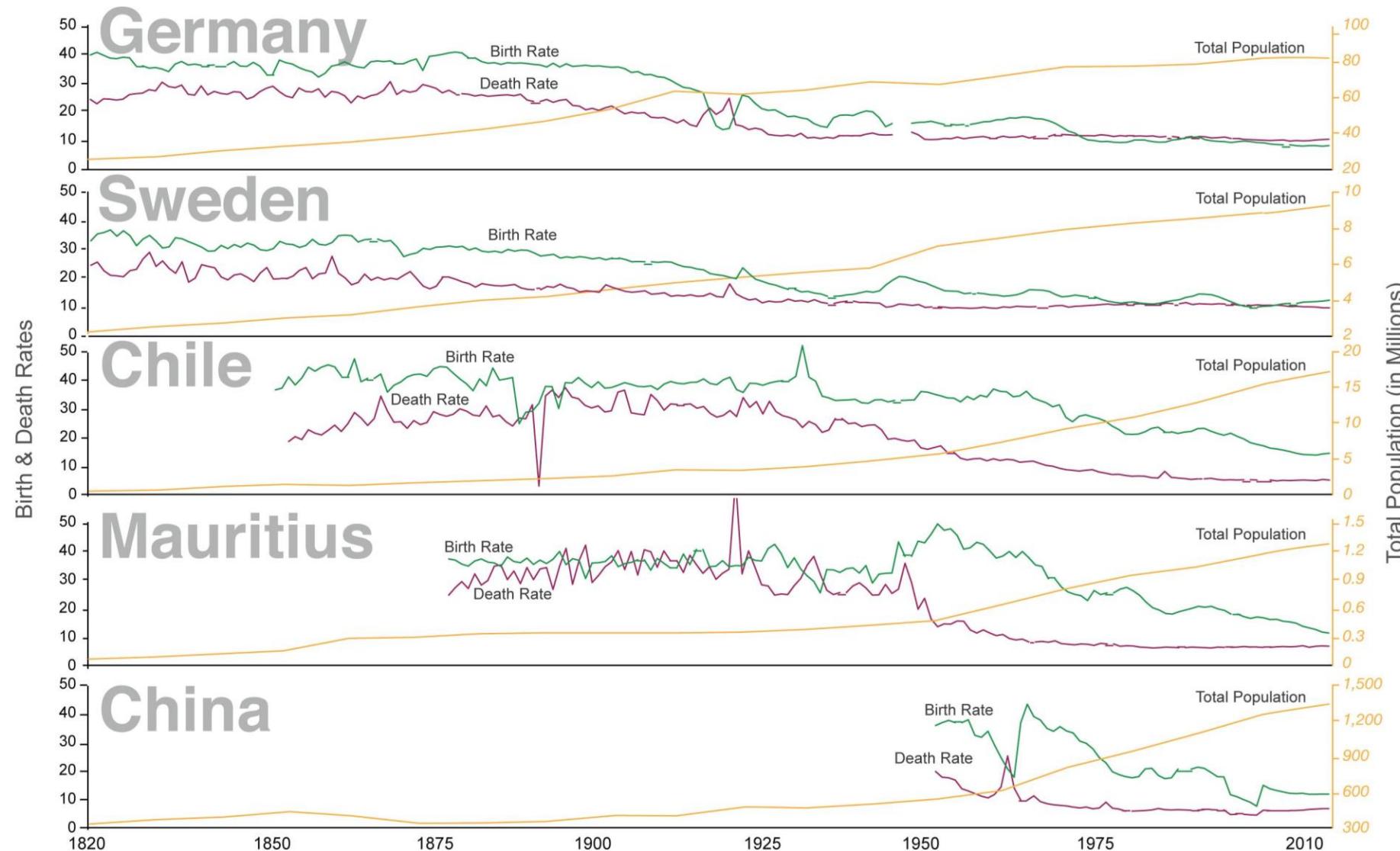


Demographic transition

And birth rates
are also falling...



Demographic transition



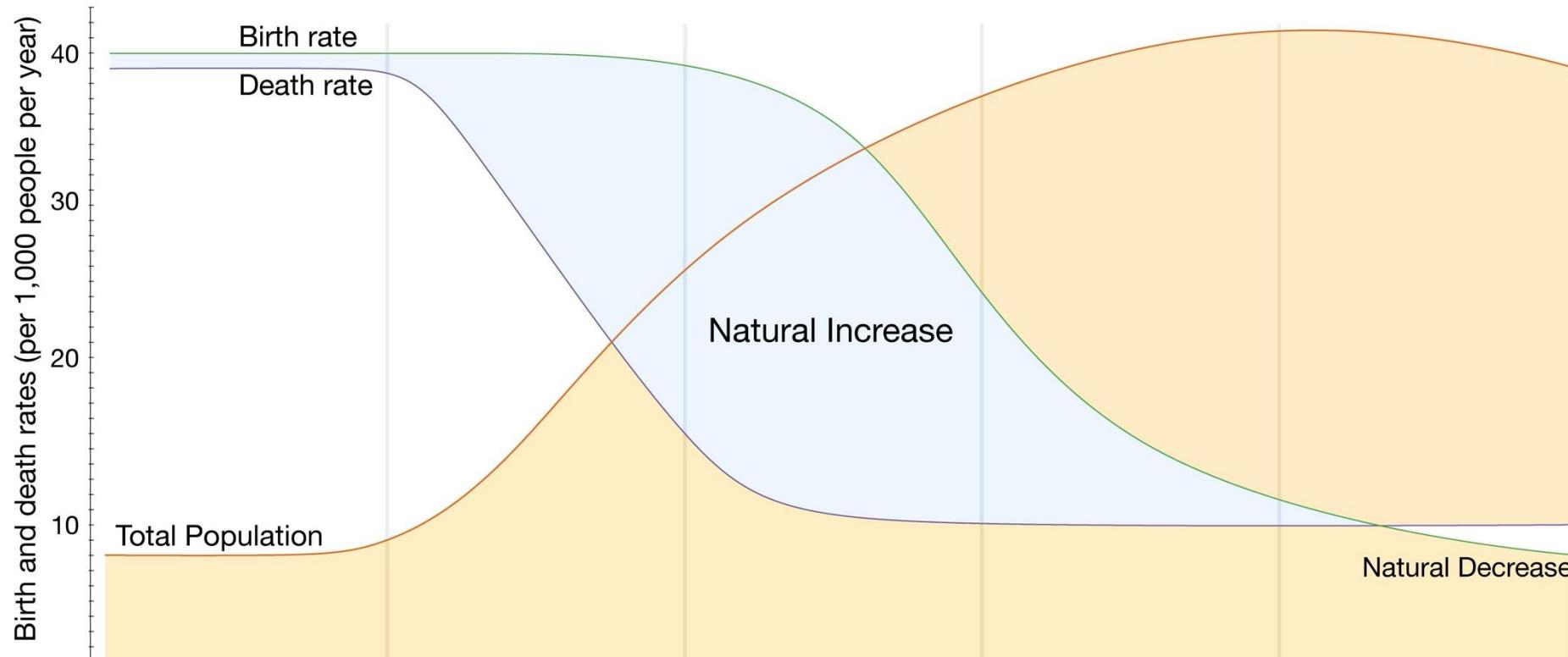
Data source: The data on birth rates, death rates and the total population are taken from the International Historical Statistics, edited by Palgrave Macmillan (April 2013).

The interactive data visualisation is available at OurWorldInData.org. There you find the raw data and more visualisations on this topic.

Licensed under CC-BY-SA by the author Max Roser.

Demographic transition

How does age structure predict population growth?

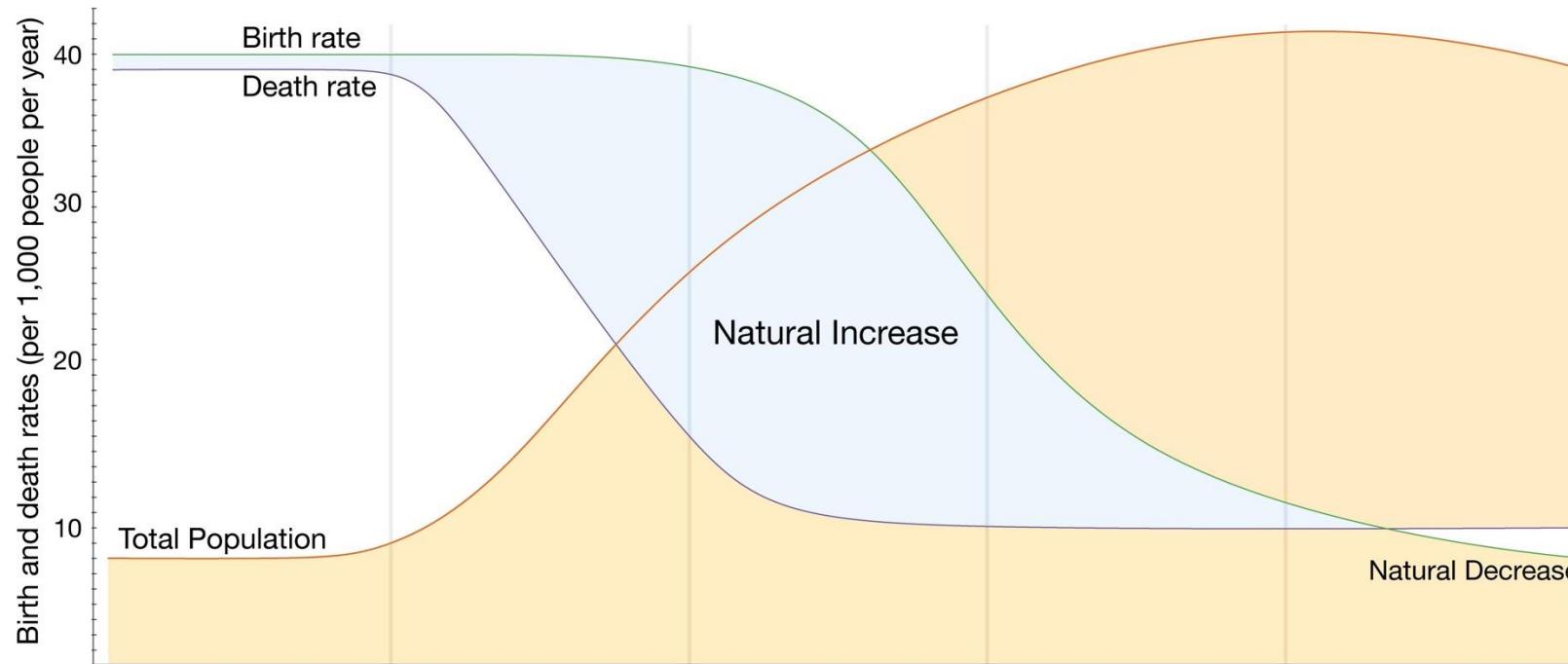


| | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 |
|-------------------------|-------------------------|---------------------|---------------------|-------------------------|-------------------------|
| Birth rate | High | High | Falling | Low | Very low |
| Death rate | High | Falls rapidly | Falls more slowly | Low | Low |
| Natural increase | Stable or slow increase | Very rapid increase | Increase slows down | Stable or slow increase | Stable or slow decrease |

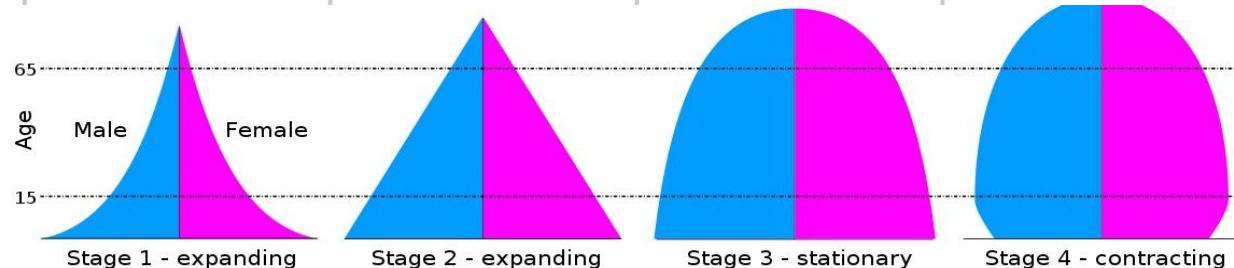
The author Max Roser licensed this visualisation under a CC BY-SA license. You are welcome to share but please refer to its source where you find more information: <http://www.OurWorldInData.org/data/population-growth-vital-statistics/world-population-growth>

Demographic transition

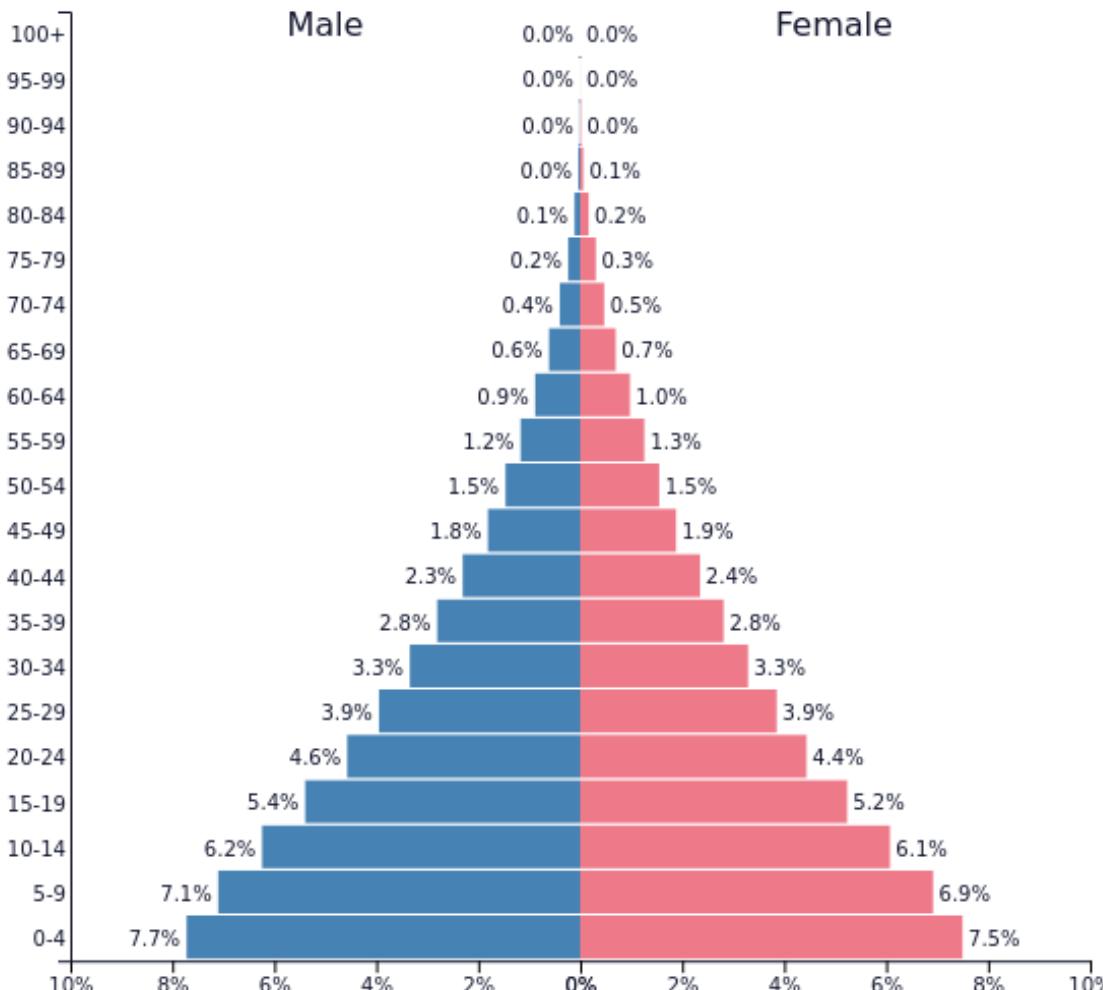
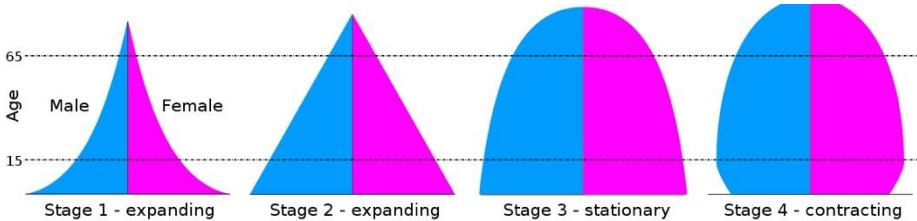
How does age structure predict population growth?



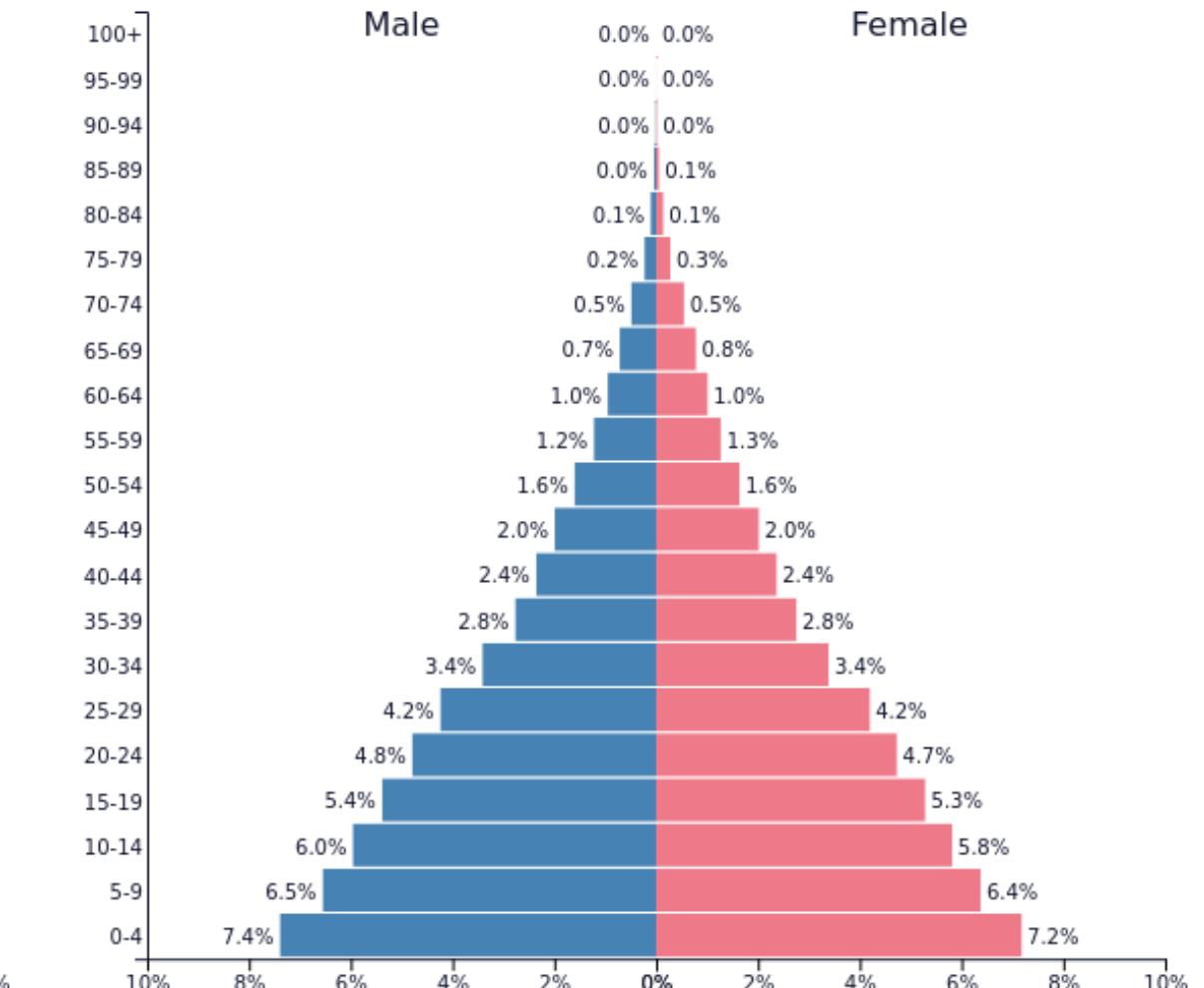
| | Stage 1 | Stage 2 | Stage 3 | Stage 4 | Stage 5 |
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Where are we globally?

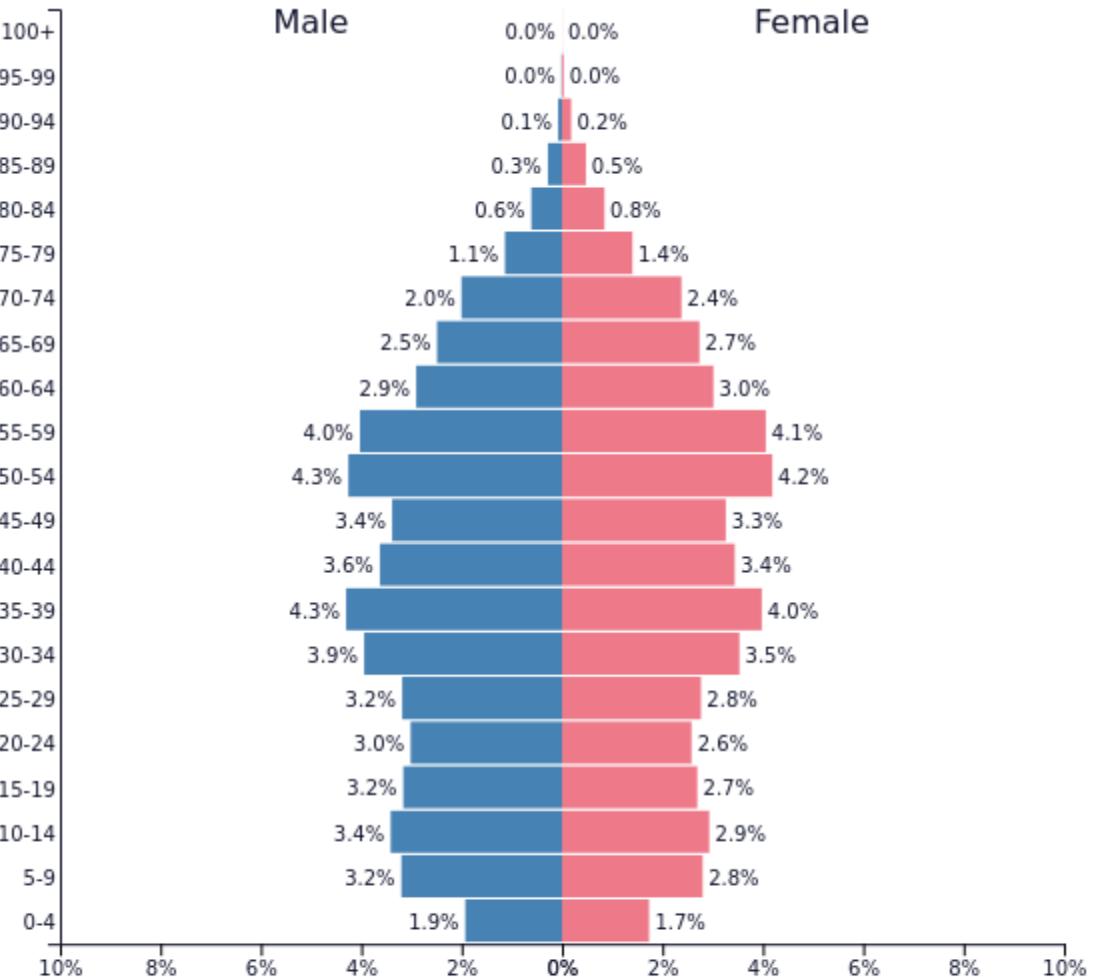
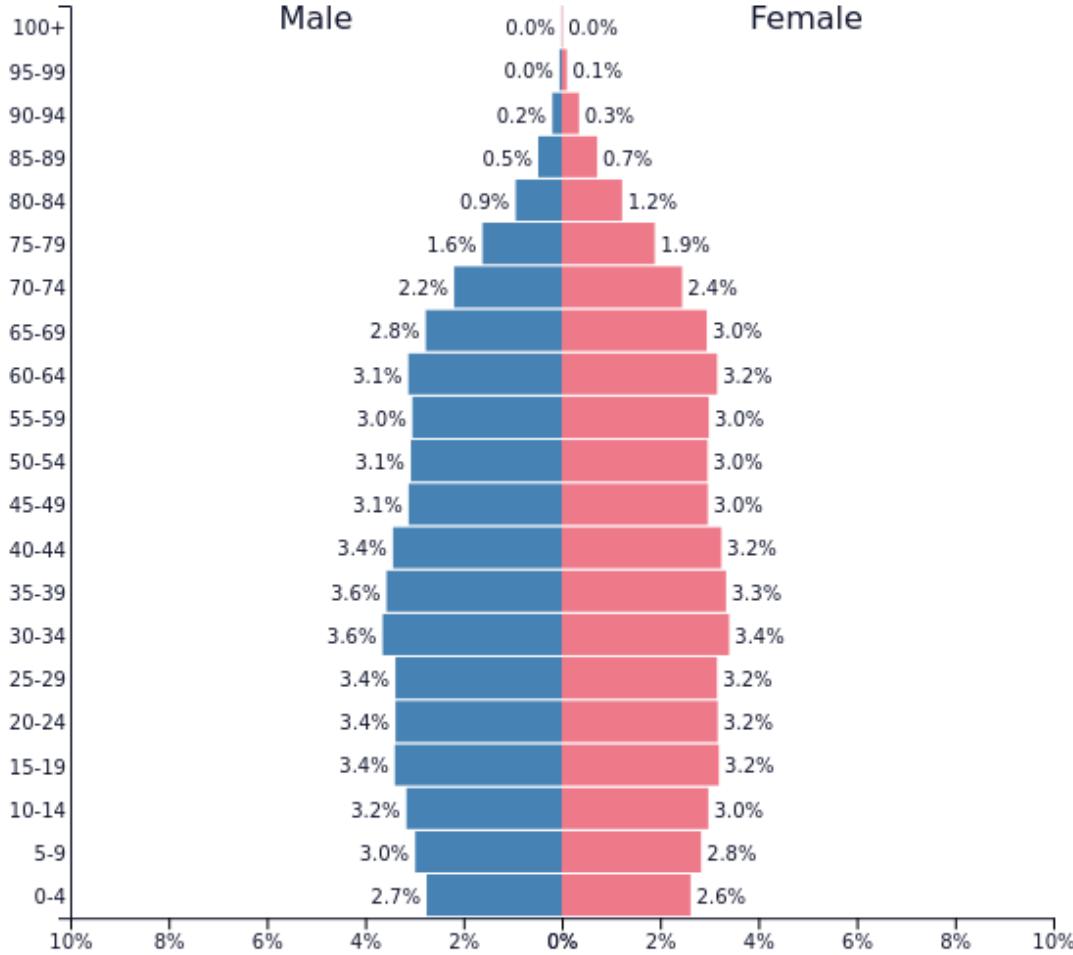
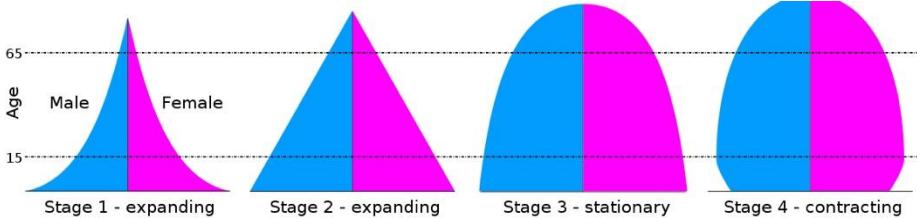


Benin - 2024
Population: **14,462,724**

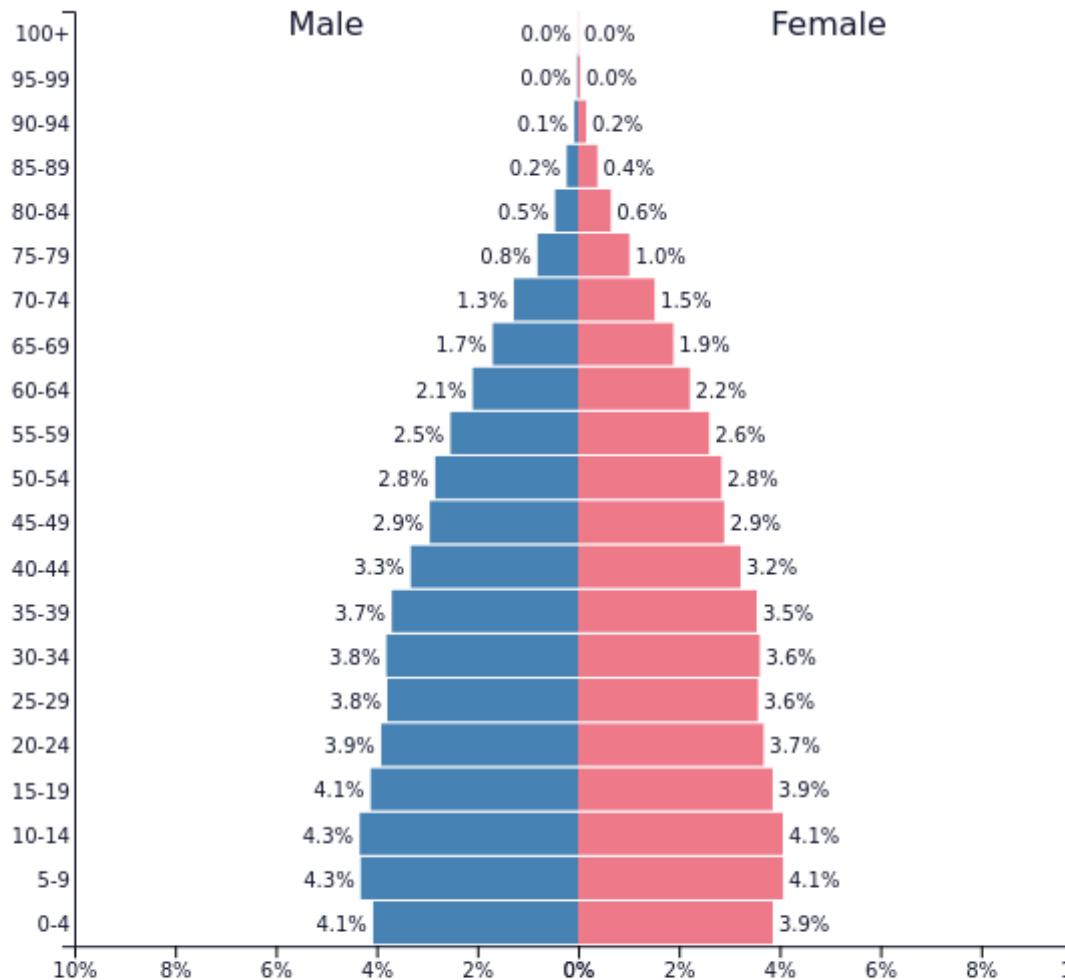
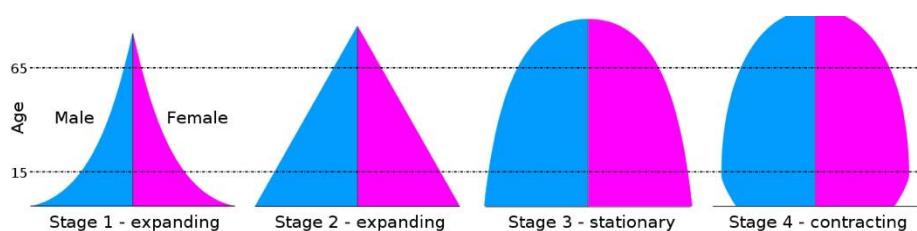


Madagascar - 2024
Population: **31,964,956**

Where are we globally?



Where are we globally?



WORLD - 2024

Population: **8,161,972,572**

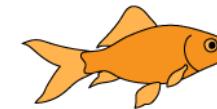


A population with this pyramid is likely:

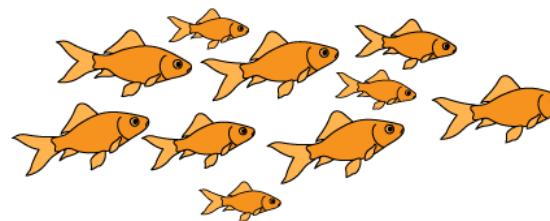
80 +
75 - 79
70 - 74
65 - 69
60 - 64
55 - 59
50 - 54
45 - 49
40 - 44
35 - 39
30 - 34



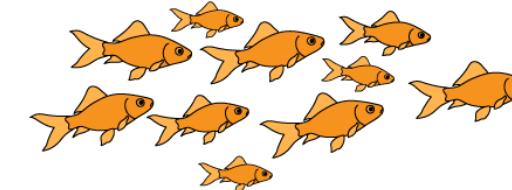
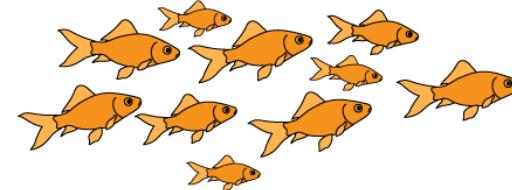
Ecology is the study of
the **interactions** of
organisms with each
other and their
environment.



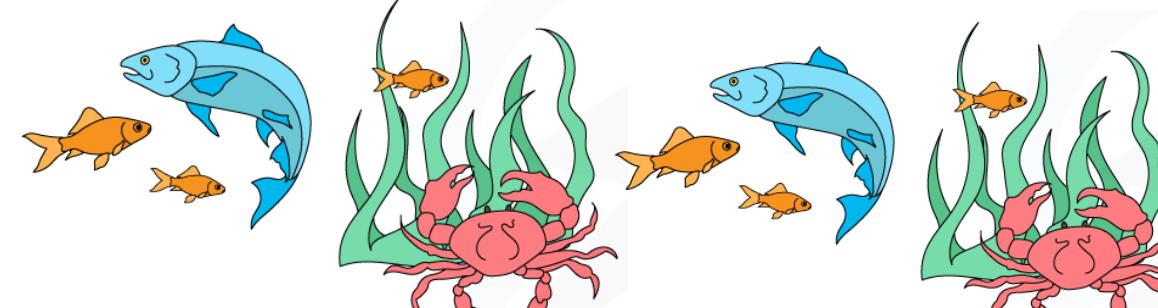
individual



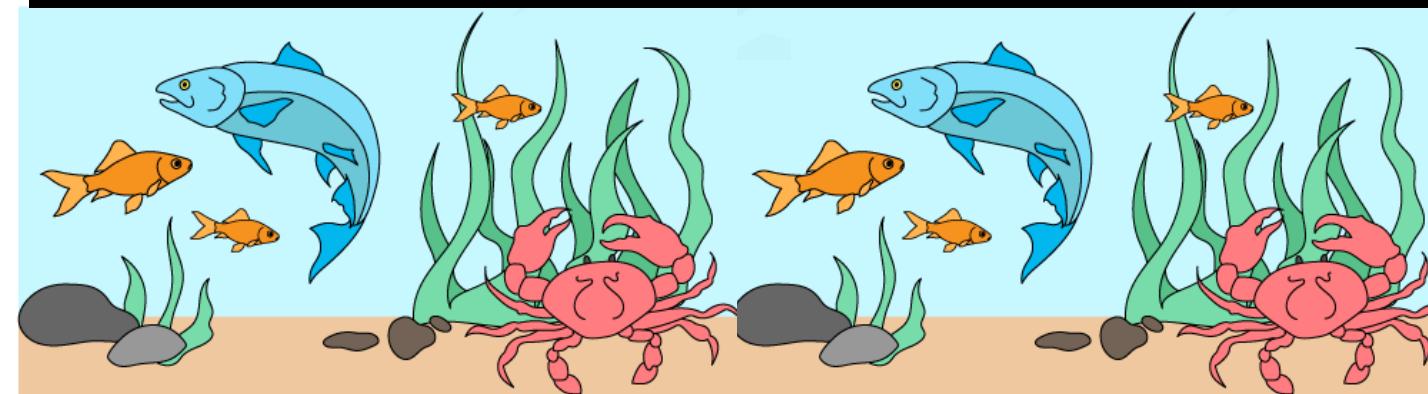
population



metapopulation

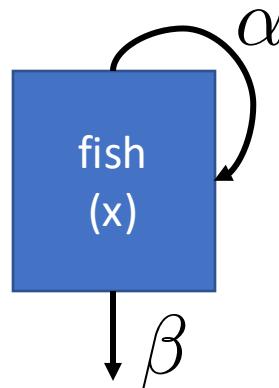


community

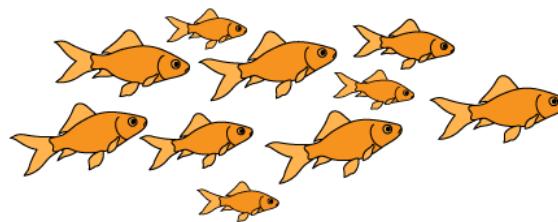


ecosystem

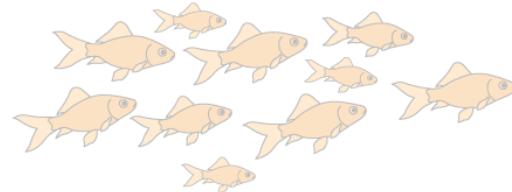
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



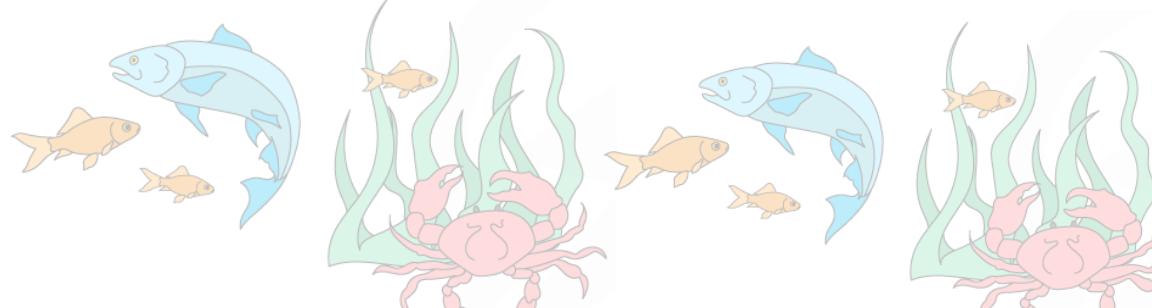
individual



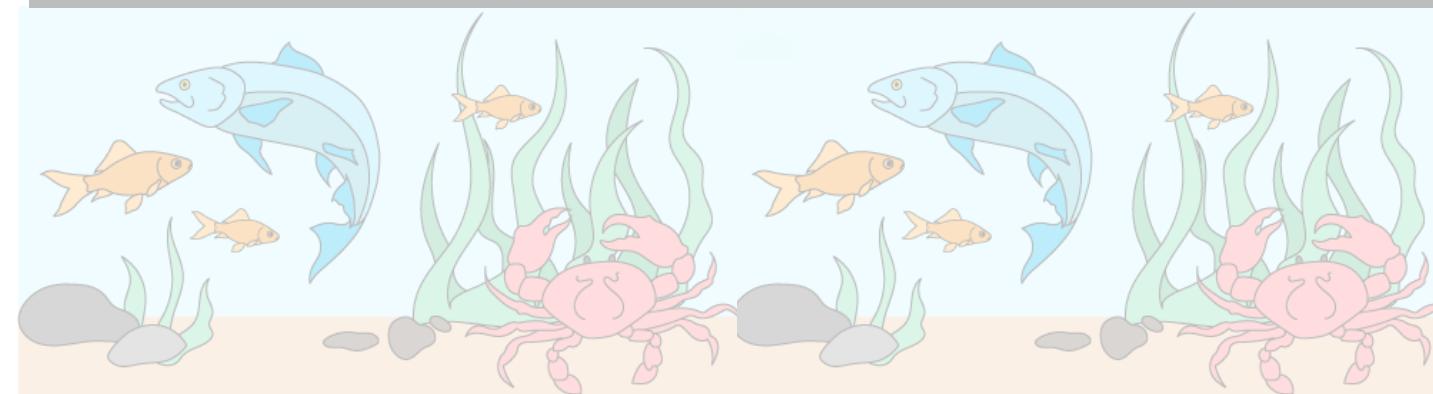
population



metapopulation



community



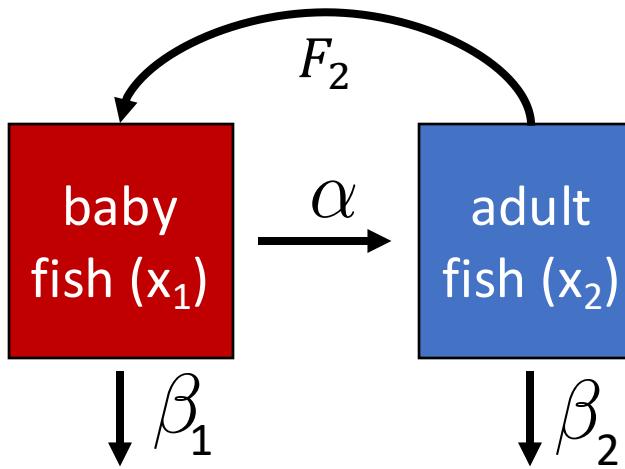
ecosystem

*How does the abundance of fish **change** through time?*

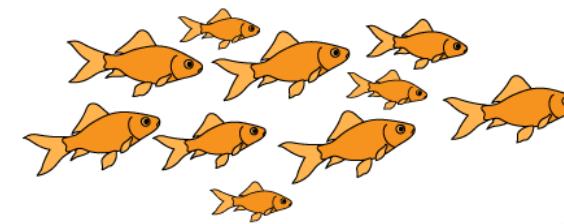
individual



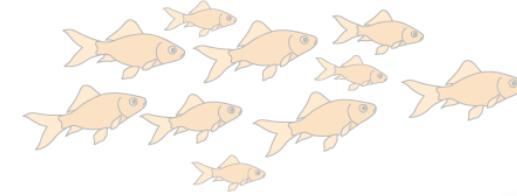
Structured Population =
multiple individuals of the
same species
(conspecifics) in the same
habitat but in different
life history stages



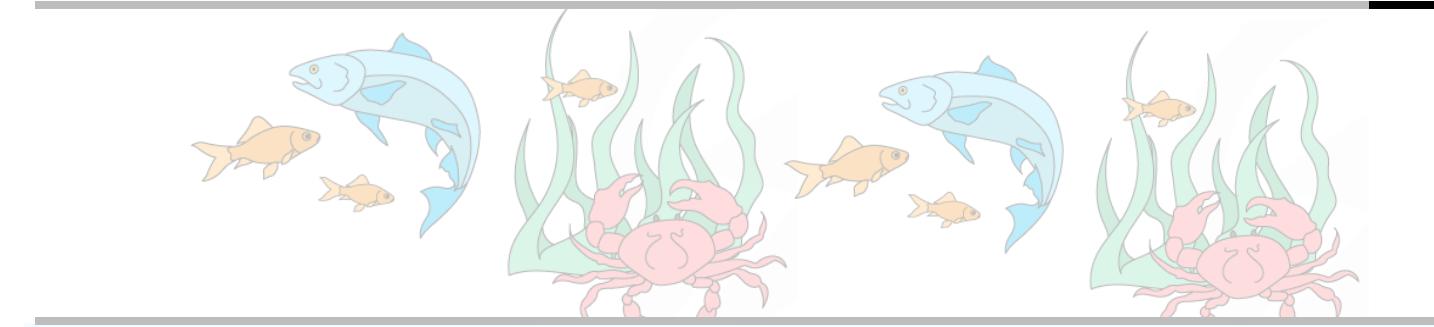
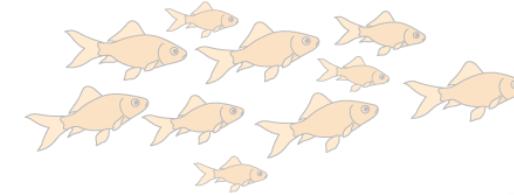
population



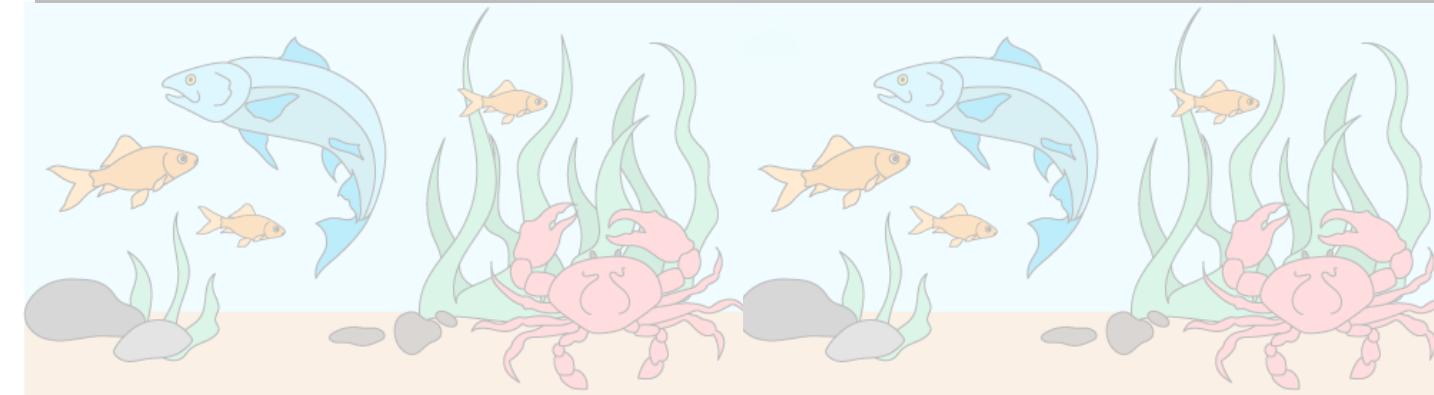
metapopulation



community



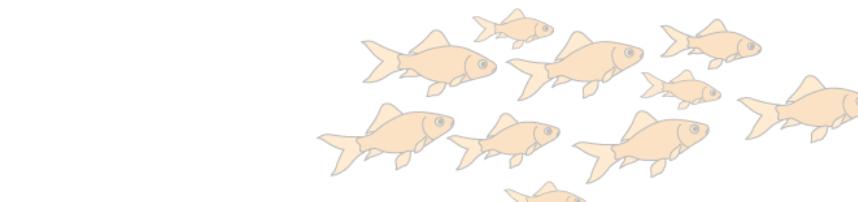
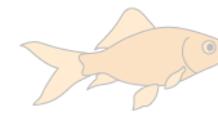
ecosystem



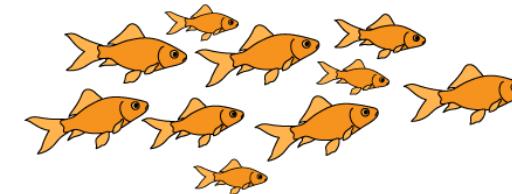
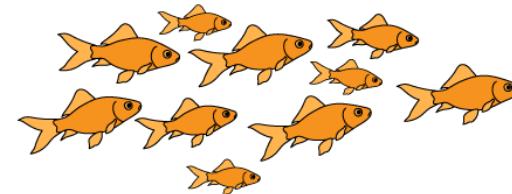
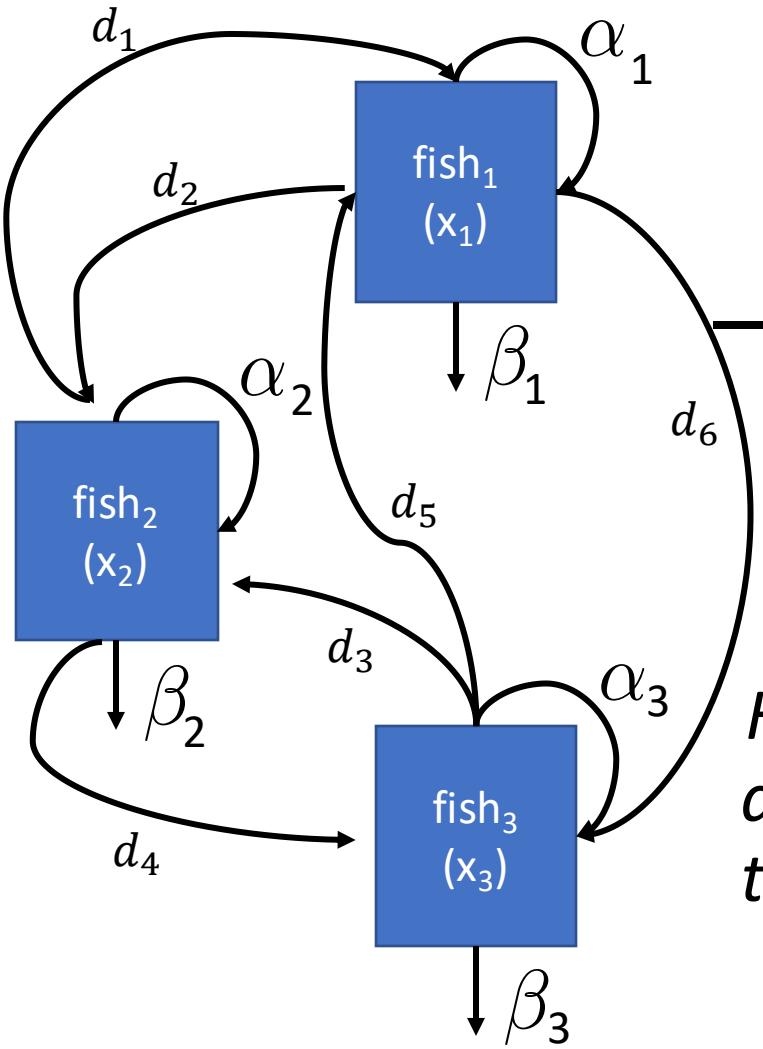
*How does the
abundance of fish
change through time?*

Metapopulation = sub-populations of conspecifics connected by migration or dispersal

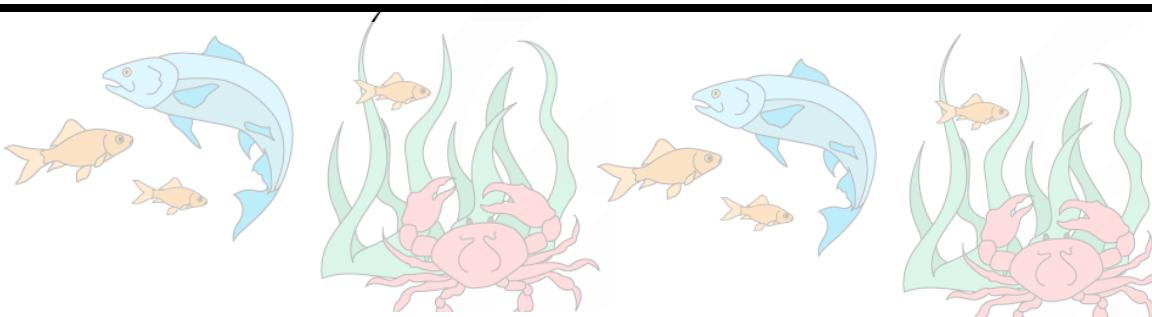
individual



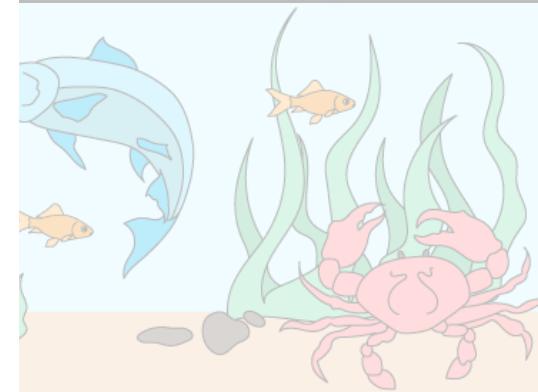
population



metapopulation



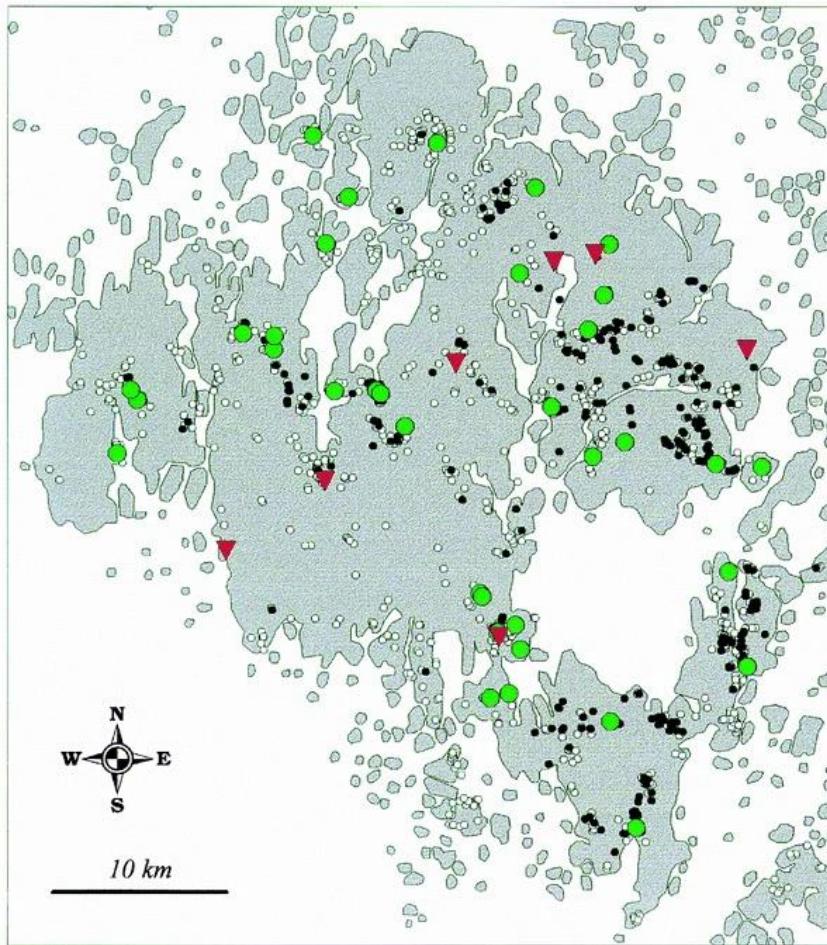
community



ecosystem

*How do the abundances of different subpopulations of the same fish **vary** in space [and time]?*

Why do metapopulations matter?



Saccheri et al 1998. *Nature*.



Glanville fritillary butterfly
Melitaea cinxia

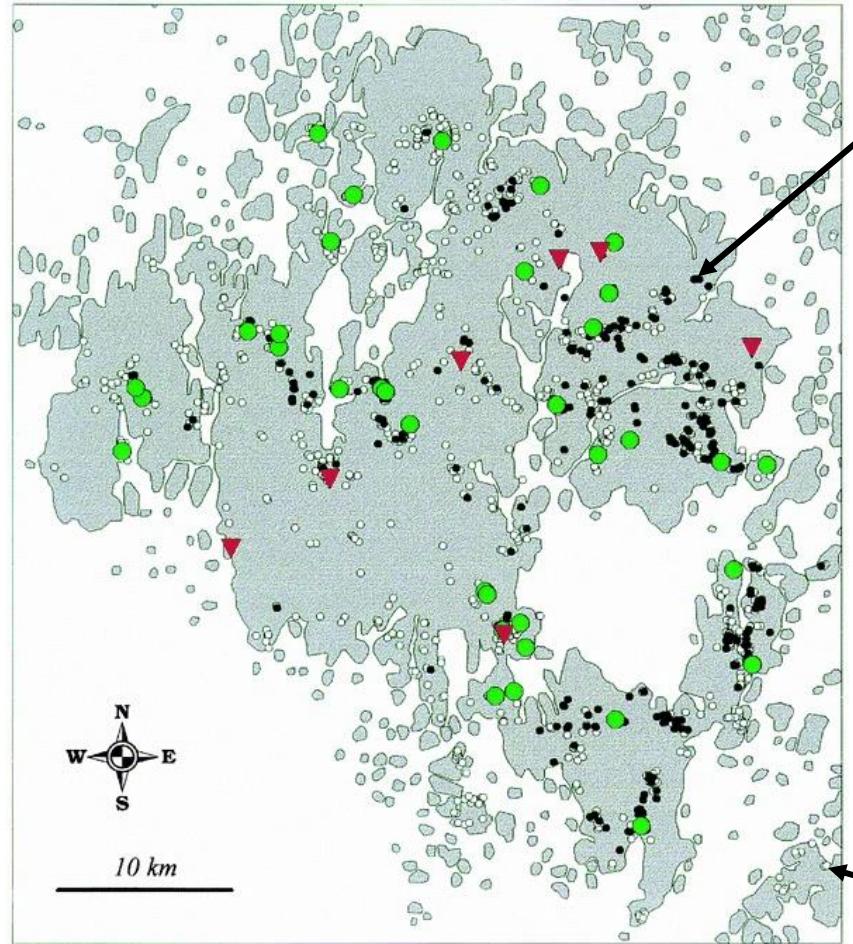


Ilkka Hanski
1953-2016

Why do metapopulations matter?



Ilkka Hanski
1953-2016



Saccheri et al 1998. *Nature*.

black dots = patches
occupied in 1995



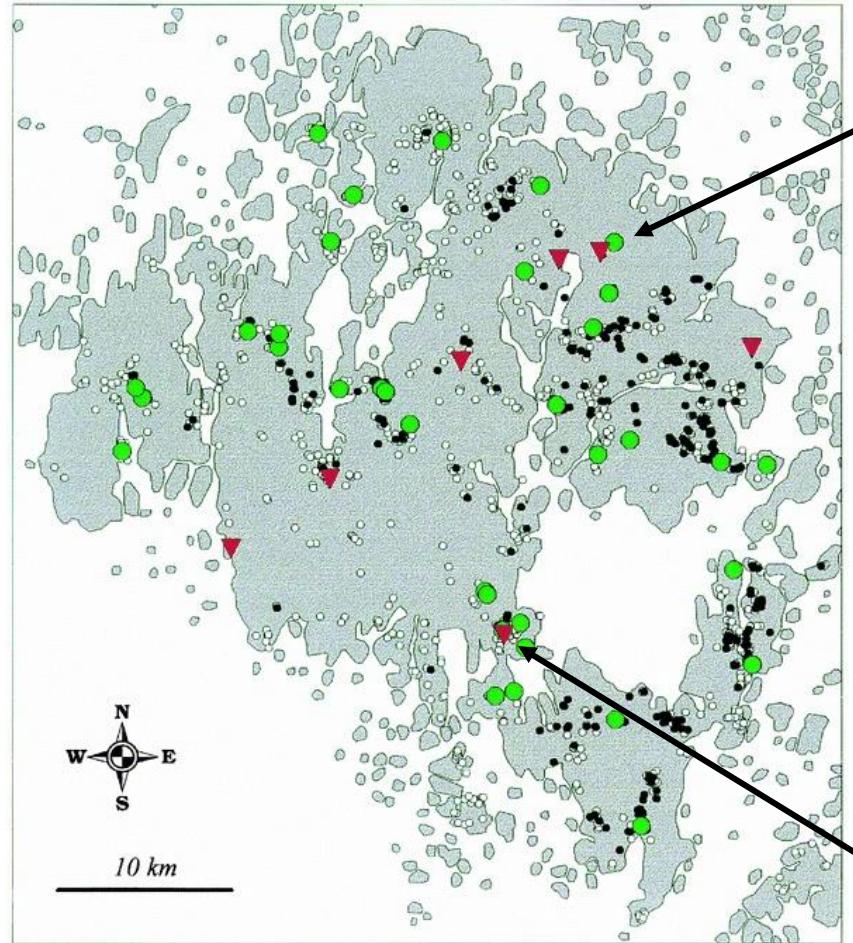
Glanville fritillary butterfly
Melitaea cinxia

white dots = patches
vacant in 1995

Why do metapopulations matter?



Ilkka Hanski
1953-2016



Saccheri et al 1998. *Nature*.

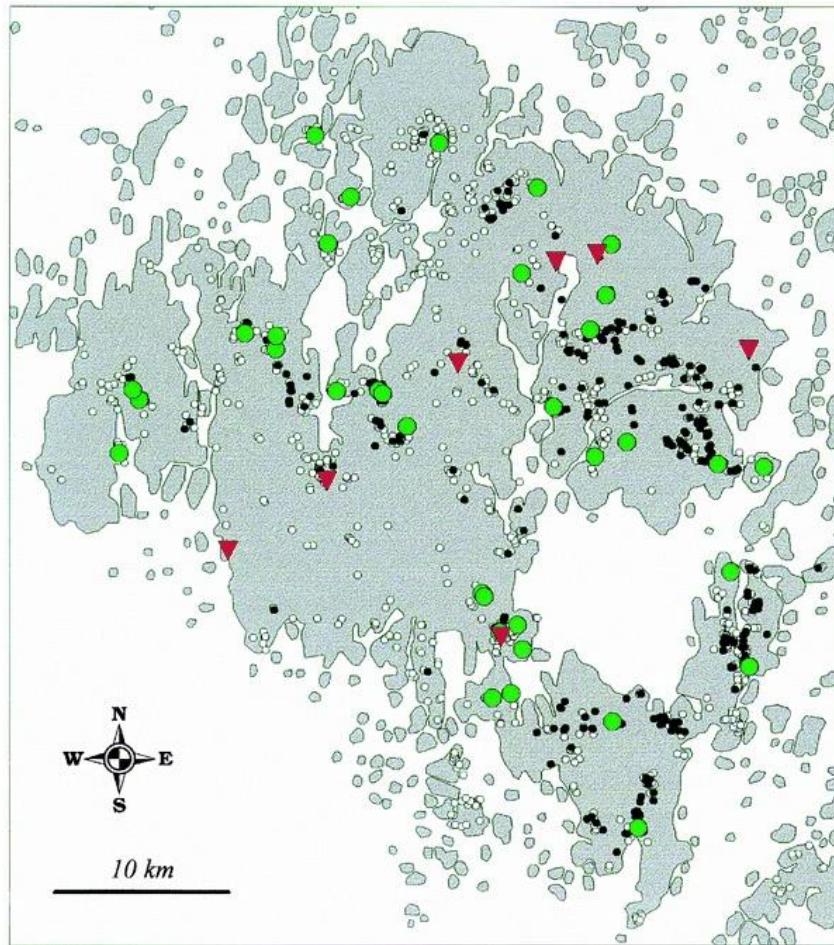
green dots = patches
still occupied in 1996



Glanville fritillary butterfly
Melitaea cinxia

red dots = patches
extinct in 1996

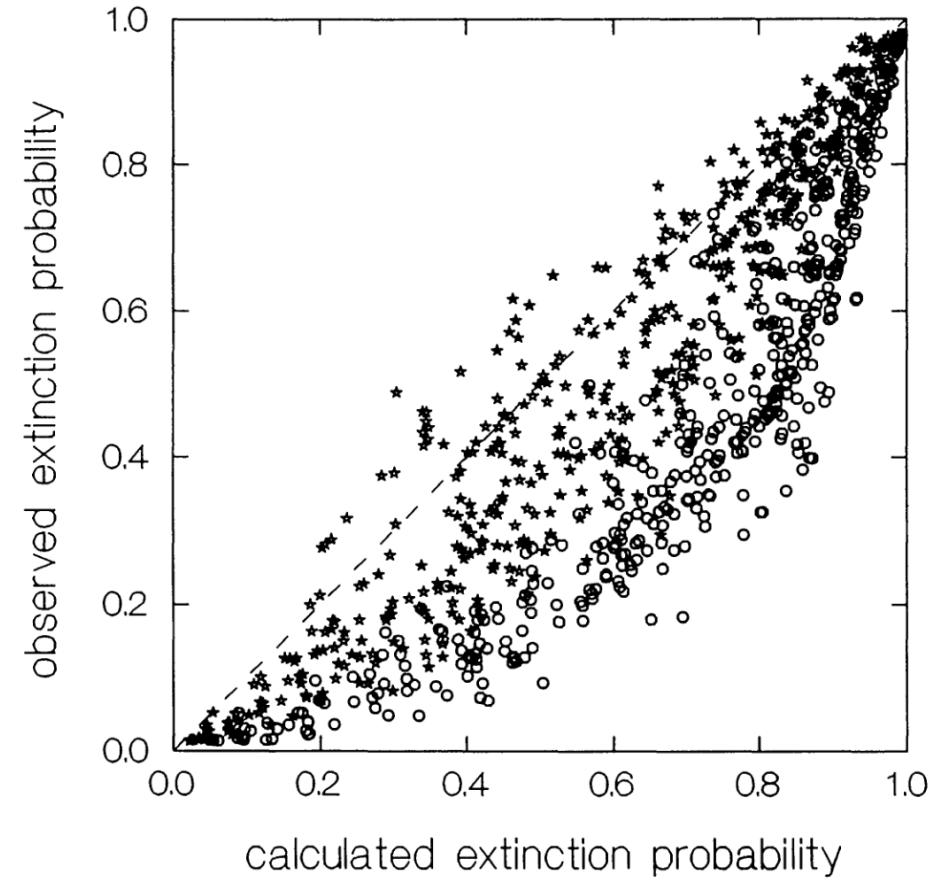
Why do metapopulations matter?



Saccheri et al 1998. *Nature*.

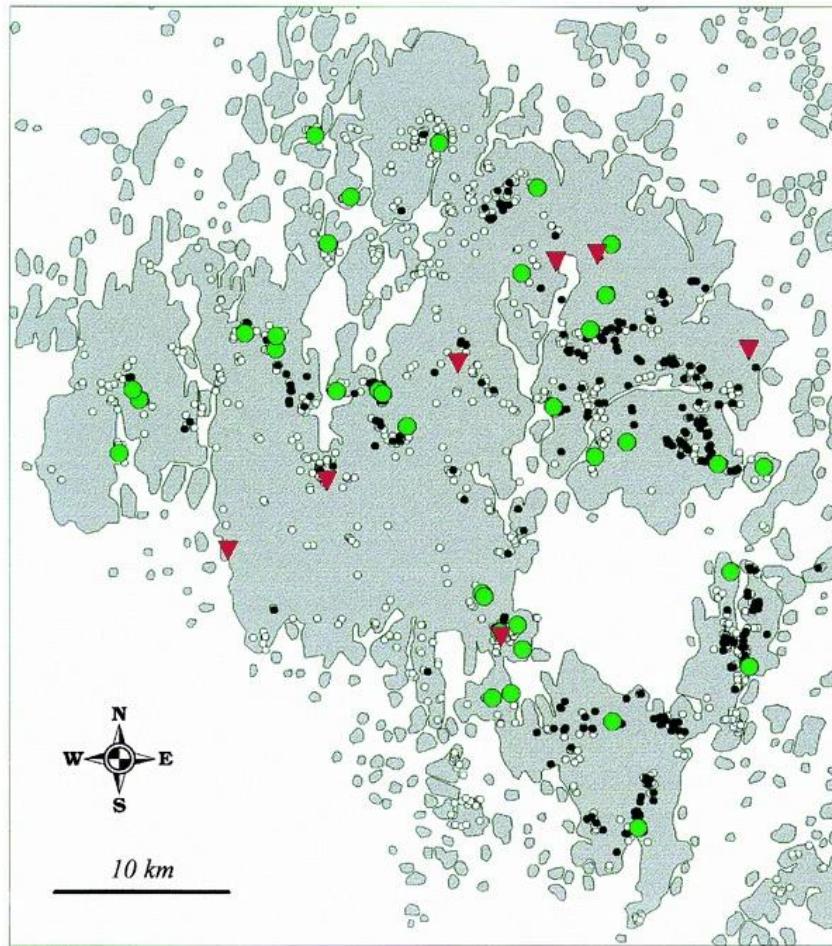
MINIMUM VIABLE METAPOPULATION SIZE

ILKKA HANSKI,¹ ATTE MOILANEN,¹ AND MATS GYLLENBERG²



Hanski et al. 1996. *The American Naturalist*.

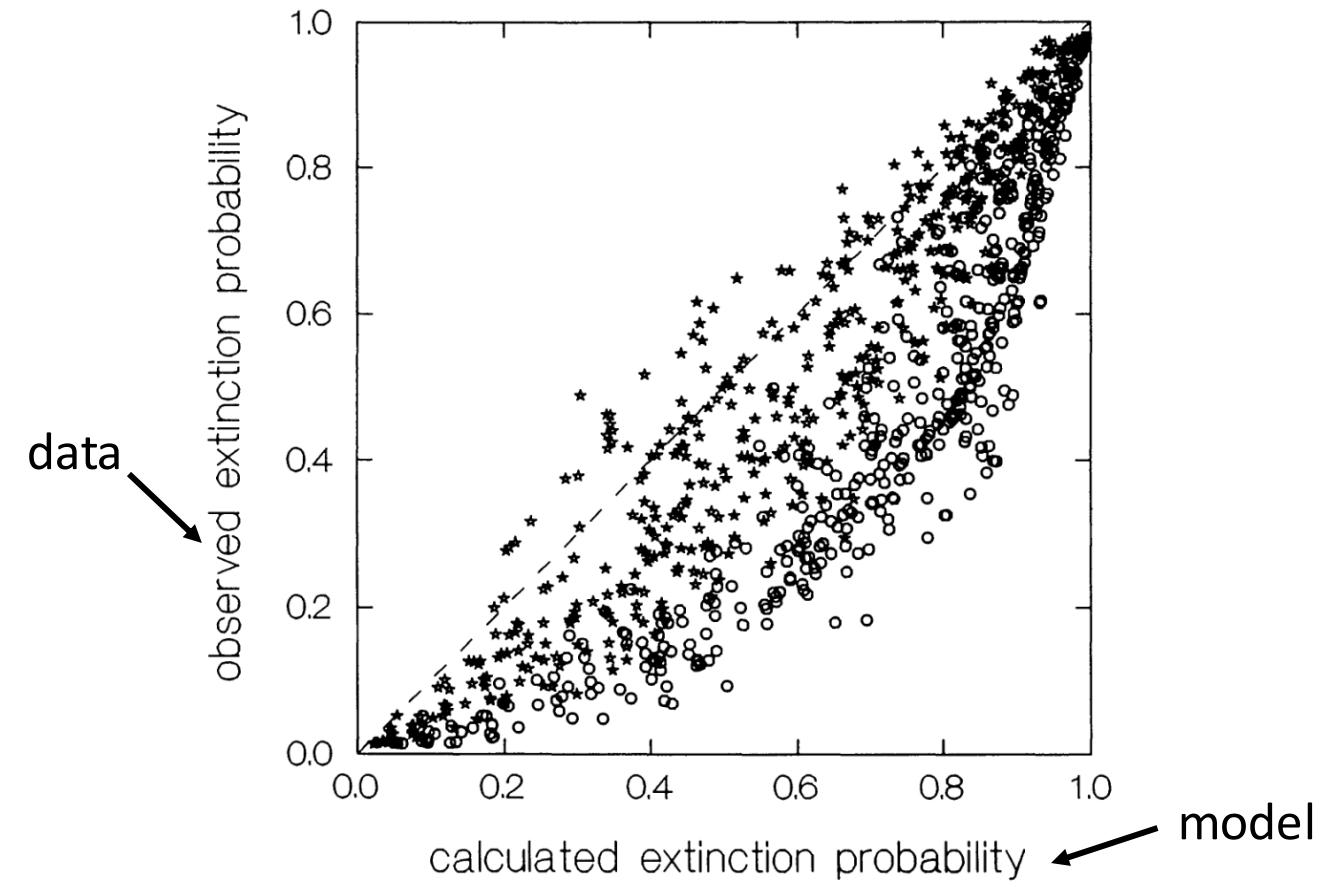
Why do metapopulations matter?



Saccheri et al 1998. *Nature*.

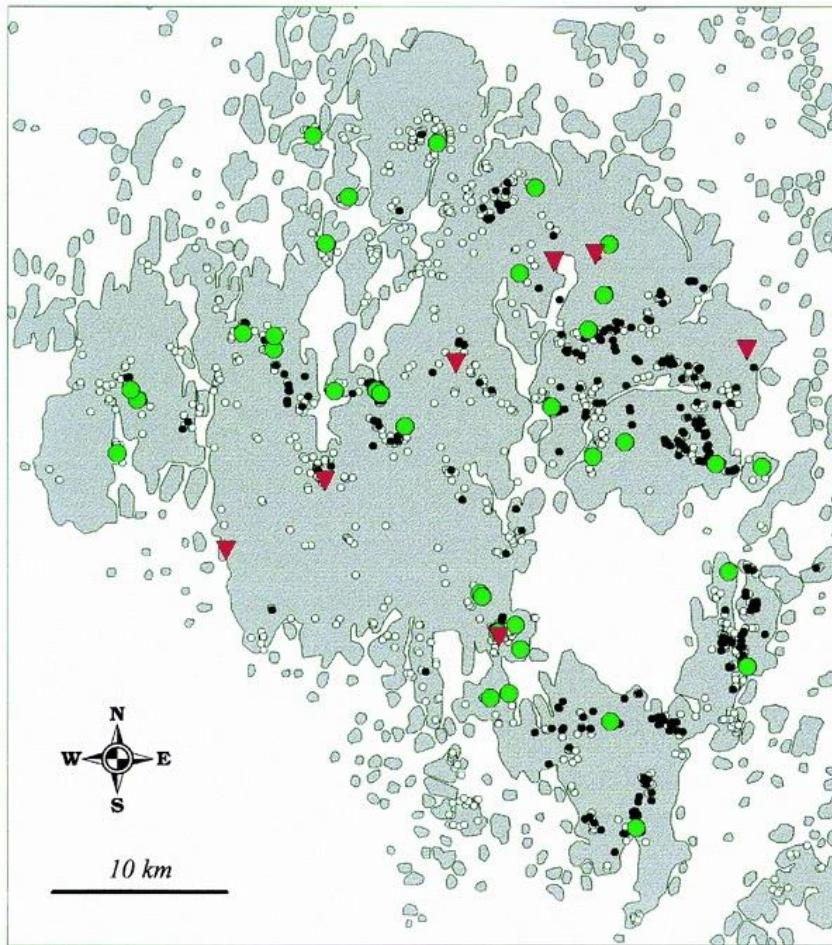
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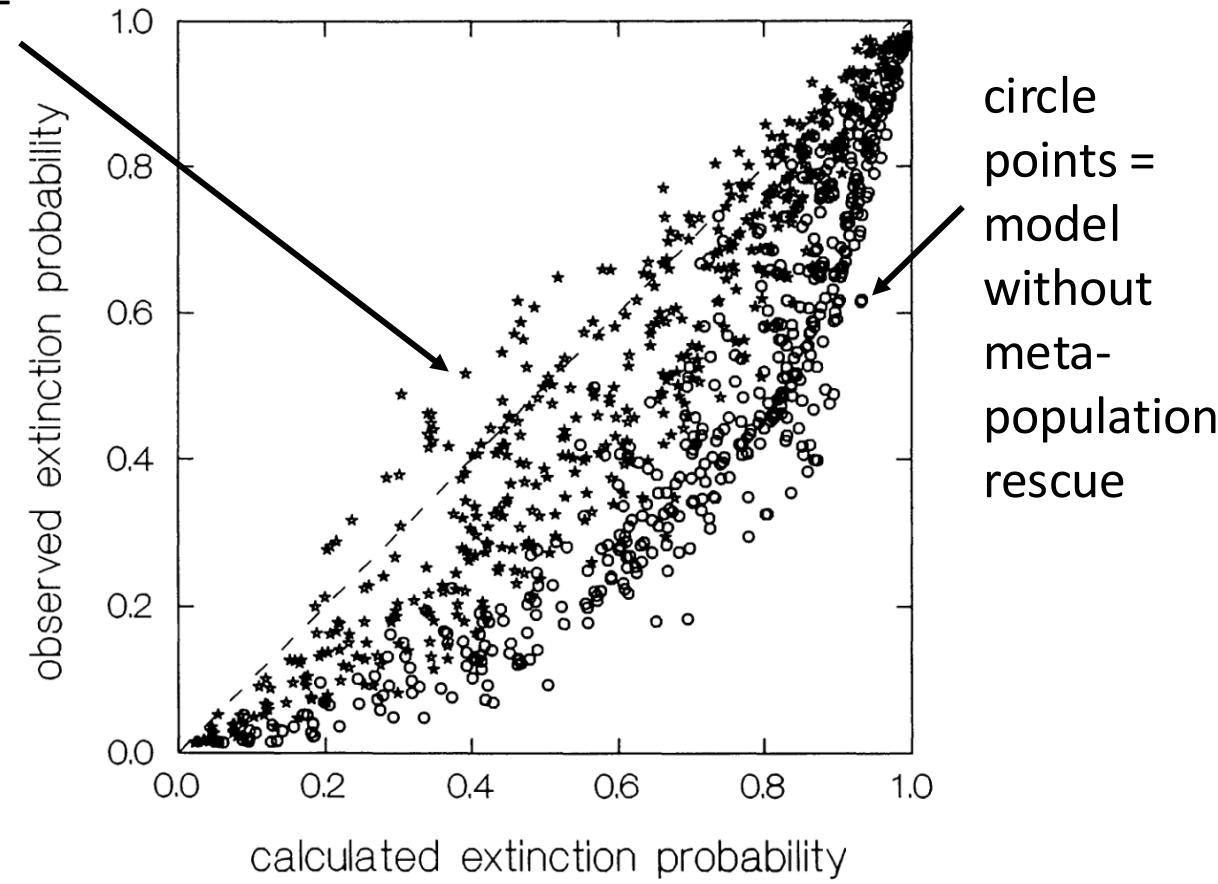


Saccheri et al 1998. *Nature*.

star points =
model
including
meta-
population
rescue
effects

MINIMUM VIABLE METAPOPULATION SIZE

ILKKA HANSKI,¹ ATTE MOILANEN,¹ AND MATS GYLLENBERG²

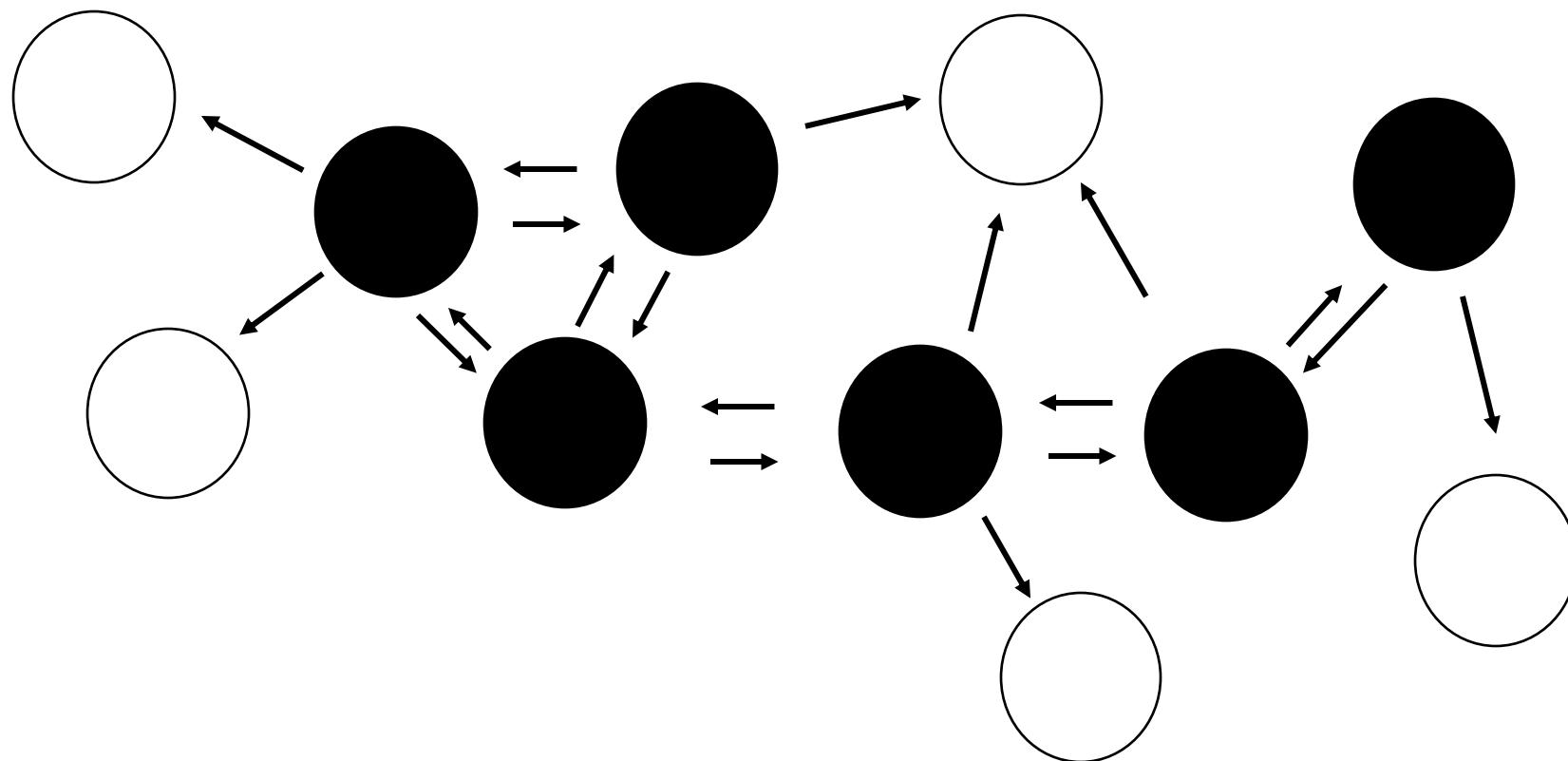


Hanski et al. 1996. *The American Naturalist*.

Modeling metapopulation dynamics

- a “population of populations”

-Richard Levins 1969



Modeling metapopulation dynamics

- a “population of populations”

-Richard Levins 1969

$$\frac{dp}{dt} = cp(1 - p) - ep \leftarrow$$

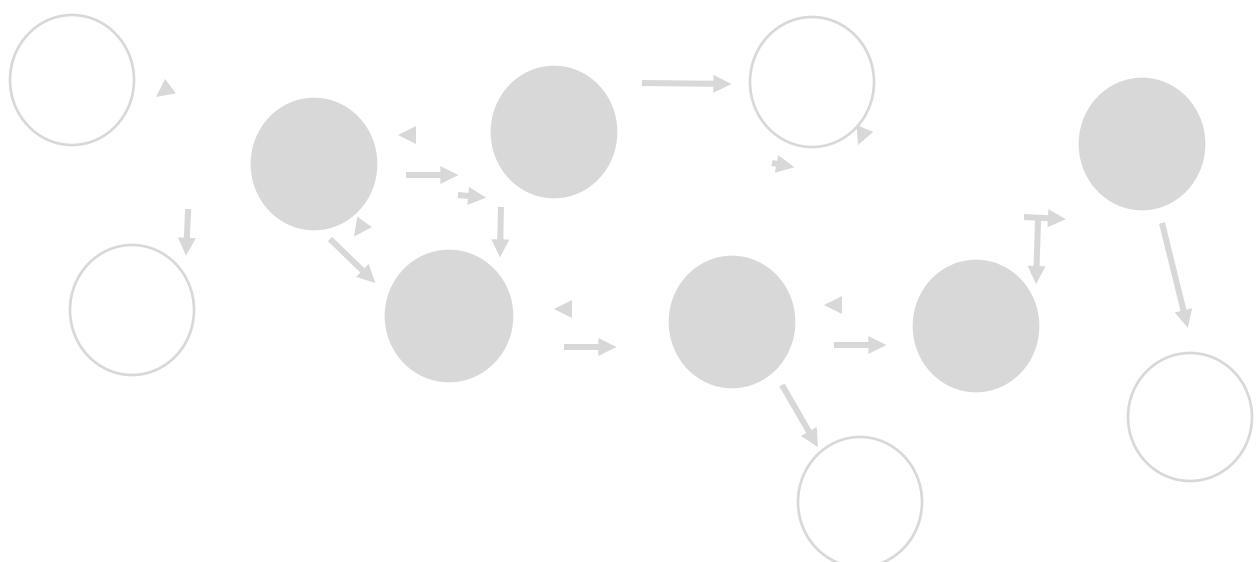
colonization rate

extinction rate

proportion of unoccupied patches

fraction of
patches
occupied at a
given time

“patch dynamics”



Modeling metapopulation dynamics

- a “population of populations”

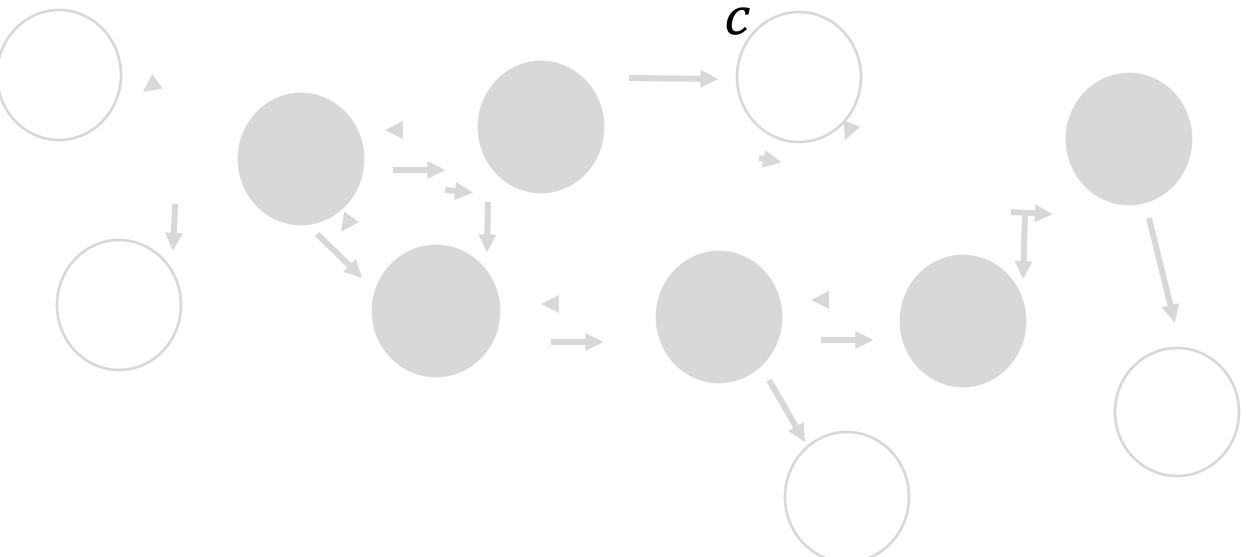
-Richard Levins 1969

$$\frac{dp}{dt} = cp(1 - p) - ep$$

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

$$\frac{dN}{dt} = (c - e)N \left(1 - \frac{N}{\left(1 - \frac{e}{c}\right)}\right)$$

mathematically equivalent to the logistic growth equation when
 $r = c - e$ and $K = 1 - \frac{e}{c}$



Modeling metapopulation dynamics

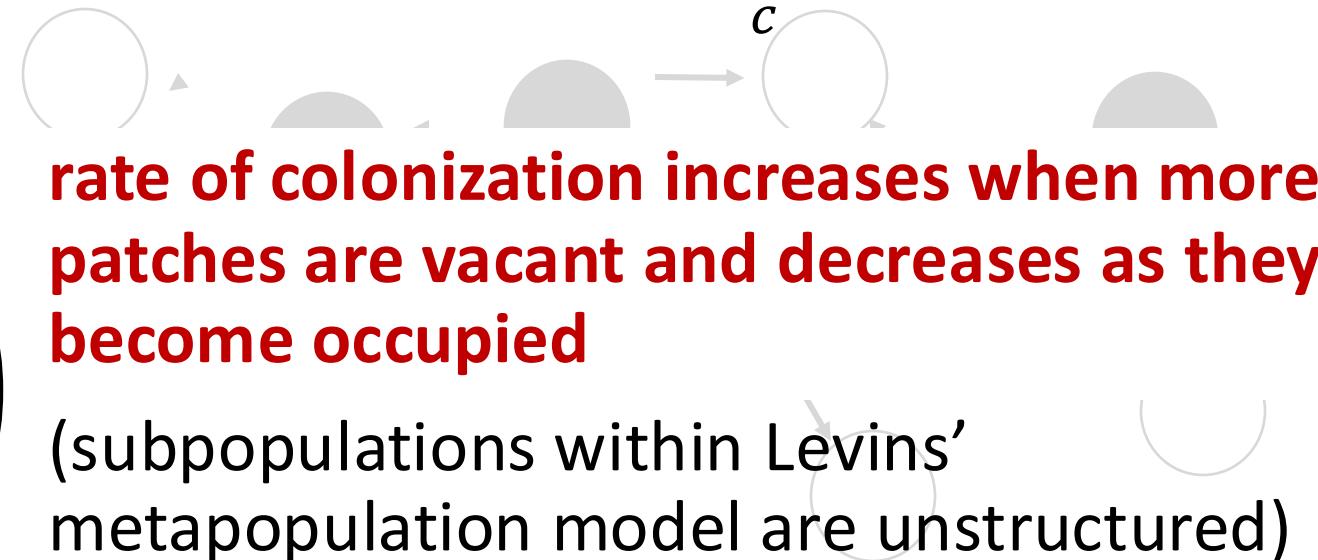
- a “population of populations” -Richard Levins 1969

$$\frac{dp}{dt} = cp(1 - p) - ep$$

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

$$\frac{dN}{dt} = (c - e)N \left(1 - \frac{N}{\left(1 - \frac{e}{c}\right)}\right)$$

mathematically equivalent to the logistic growth equation when
 $r = c - e$ and $K = 1 - \frac{e}{c}$



rate of colonization increases when more patches are vacant and decreases as they become occupied
(subpopulations within Levins' metapopulation model are unstructured)

Structured population models and **metapopulation models** can be **combined**, depending on the data and question at hand

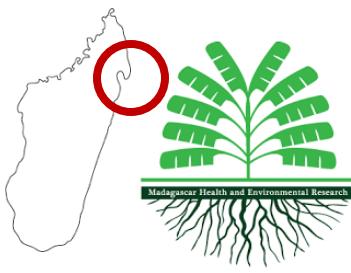
Conservation Biology



Contributed Paper

Population viability and harvest sustainability for Madagascar lemurs

Cara E. Brook  ^{1,*} James P. Herrera,² Cortni Borgerson,³ Emma C. Fuller,¹ Pascal Andriamahazoarivosoa,⁴ B. J. Rodolph Rasolofoniaina,⁴ J. L. Rado Ravoavy Randrianasolo,⁴ Z. R. Eli Rakotondrafarasata,⁴ Hervet J. Randriamady,⁴ Andrew P. Dobson,¹ and Christopher D. Golden^{3,4}



Dr. Christopher Golden,
Harvard University



Dr. James Herrera,
Duke University



Dr. Cortni Borgerson,
Montclair University



Hervet Randriamady,
Harvard University



B.J. Rodolph
Rasolofoniaina, MAHERY



Dr. Emma Fuller,
Fractal Agriculture





What are the **future population trajectories** for hunted lemurs on Madagascar's **Makira-Masoala peninsula?**



| | | | | | | | | | | |
|--------------------------|----------------------------|-------------------------|---|--------------------------------|-------------------------------------|------------------------------------|---|--------------------------------|------------------------------------|------------------------------|
| <i>Microcebus</i> sp. | <i>Cheirogaleus</i> sp. | <i>Lepilemur</i> sp. | <i>Hapalemur</i> <i>occidentalis</i> | <i>Avahi</i> <i>laniger</i> | <i>Eulemur</i> <i>rufiventer</i> | <i>Eulemur</i> <i>albifrons</i> | <i>Daubentonia</i> <i>madagascariensis</i> | <i>Varécia</i> <i>ribba</i> | <i>Varécia</i> <i>variegata</i> | <i>Indri</i> <i>indri</i> |
|--------------------------|----------------------------|-------------------------|---|--------------------------------|-------------------------------------|------------------------------------|---|--------------------------------|------------------------------------|------------------------------|



What are the **future population trajectories** for hunted **lemurs** on Madagascar's **Makira-Masoala peninsula?**

- 103 **extant** species of **lemur**





| | | | | | | | | | | |
|--------------------------|----------------------------|-------------------------|---|--------------------------------|-------------------------------------|------------------------------------|---|--------------------------------|------------------------------------|------------------------------|
| <i>Microcebus</i> sp. | <i>Cheirogaleus</i> sp. | <i>Lepilemur</i> sp. | <i>Hapalemur</i> <i>occidentalis</i> | <i>Avahi</i> <i>laniger</i> | <i>Eulemur</i> <i>rufiventer</i> | <i>Eulemur</i> <i>albifrons</i> | <i>Daubentonia</i> <i>madagascariensis</i> | <i>Varécia</i> <i>ribba</i> | <i>Varécia</i> <i>variegata</i> | <i>Indri</i> <i>indri</i> |
|--------------------------|----------------------------|-------------------------|---|--------------------------------|-------------------------------------|------------------------------------|---|--------------------------------|------------------------------------|------------------------------|

What are the **future population trajectories** for hunted lemurs on Madagascar's **Makira-Masoala peninsula?**



- 103 extant species of lemur
- **94% under some IUCN category of threat**
 - 24 Critically Endangered
 - 49 Endangered
 - 20 Vulnerable
 - 3 Near Threatened
 - 3 Least Concern
 - 4 Data Deficient
- The **most imperiled group of mammals** on earth

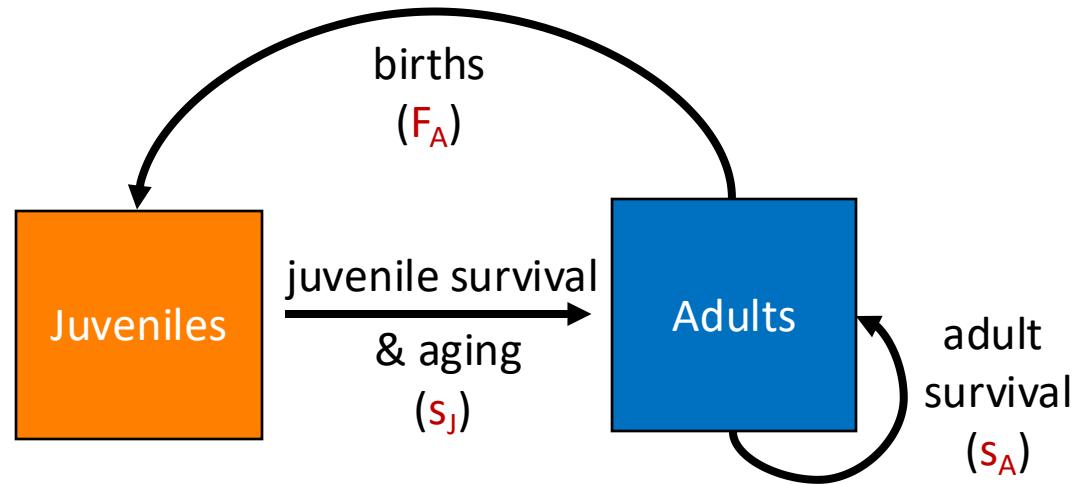


What are the **future population trajectories** for hunted lemurs on Madagascar's **Makira-Masoala peninsula?**

- 103 extant species of lemur
- 94% under some IUCN category of threat
- The most imperiled group of mammals on earth
- Aimed to highlight what **quantitative population viability analysis** can add to conservation management and pinpoint data gaps

We next used a **Lefkovitch matrix** approach to explore the **limits of population persistence** for each lemur species.

We next used a **Lefkovitch matrix** approach to explore the **limits of population persistence** for each lemur species.



Assumptions:

- Time-steps in units of Interbirth Intervals (IBI)
- Model only females
- Stable age structure
- F_A parameters derived from the literature

Brook et al. 2018. *Conservation Biology*.
Leslie 1945 *Biometrika*. Leslie 1948 *Biometrika*.
Lefkovitch 1965 *Biometrics*.

We next used a **Lefkovitch matrix** approach to explore the **limits of population persistence** for each lemur species.

N = population vector

A = transition matrix

$$\begin{aligned} \mathbf{N}_{t+1} &= \mathbf{A} \mathbf{N}_t \\ \begin{bmatrix} J \\ A \end{bmatrix}_{t+1} &= \begin{bmatrix} 0 & \mathbf{A} \\ S_J & S_A F_A \end{bmatrix} \begin{bmatrix} J \\ A \end{bmatrix}_t \end{aligned}$$

(where:

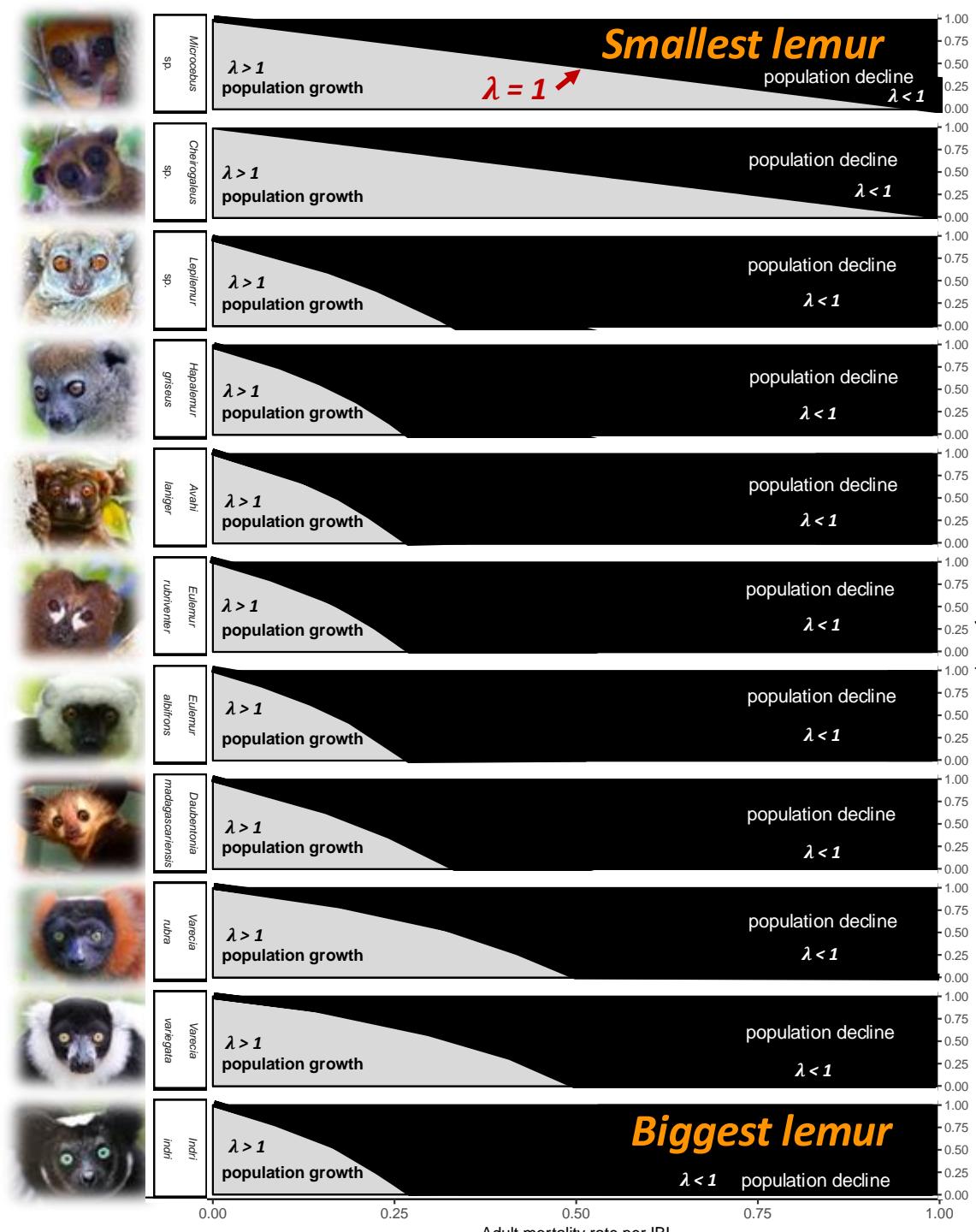
S_J = juvenile IBI survival

S_A = adult IBI survival

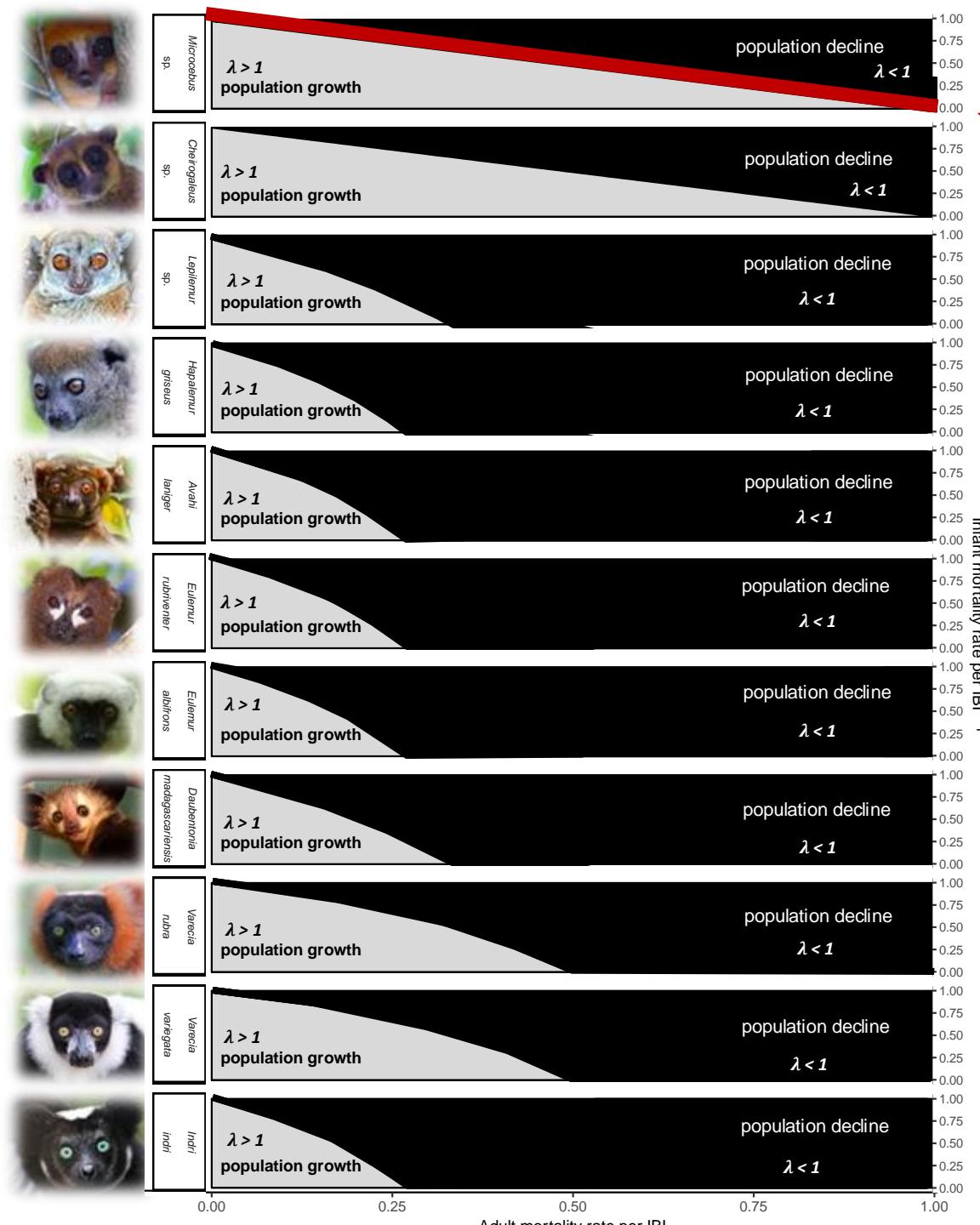
F_A = adult IBI fecundity)

We can explore the
zero-population growth line at $\lambda = 1$
for differing values of s_J , s_A , and F_A .

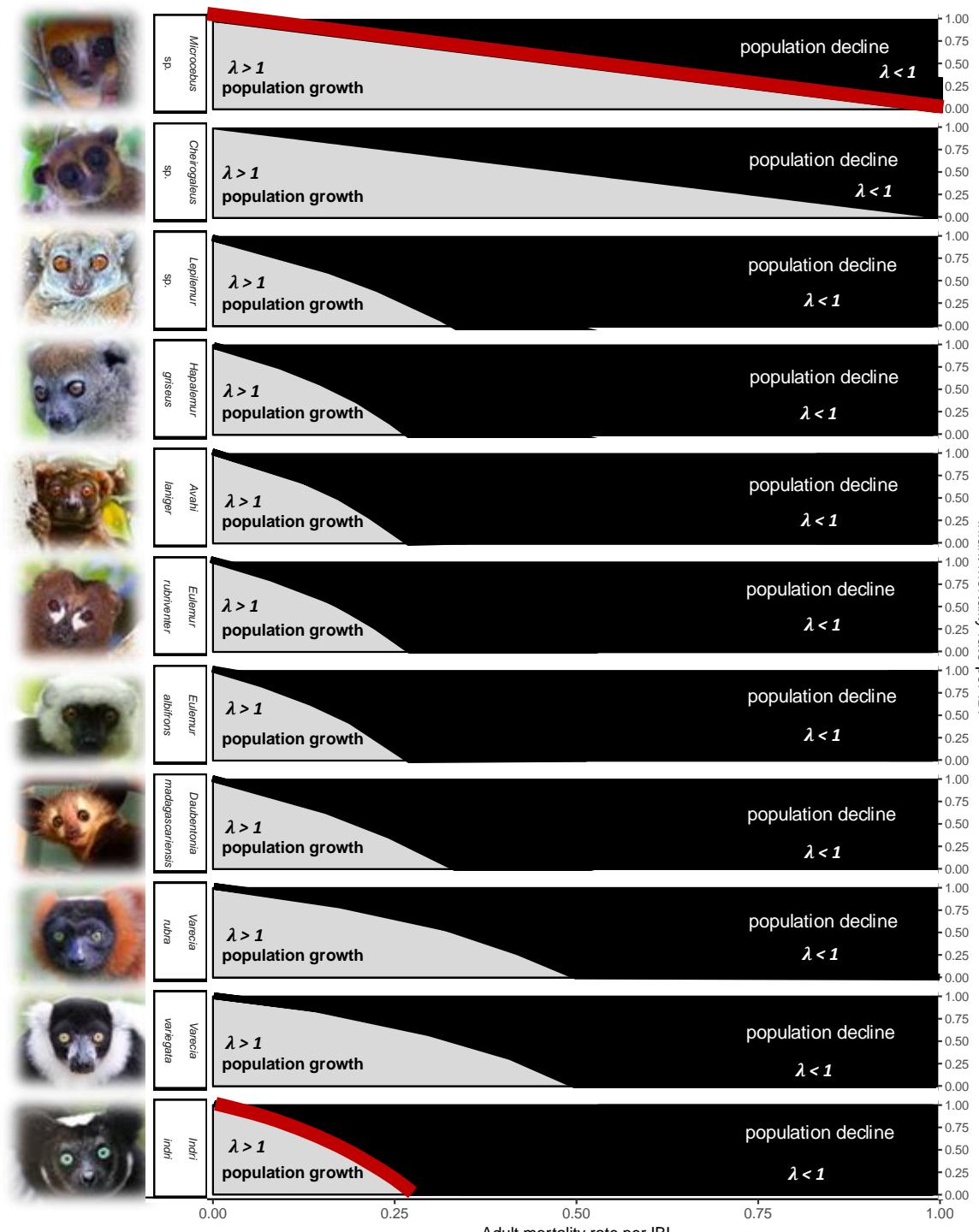
Brook et al. 2018. *Conservation Biology*.
Leslie 1945 *Biometrika*. Leslie 1948 *Biometrika*.
Lefkovitch 1965 *Biometrics*.



We plotted
zero-growth lines to
evaluate lemur
population trajectories
across different
mortality rates.

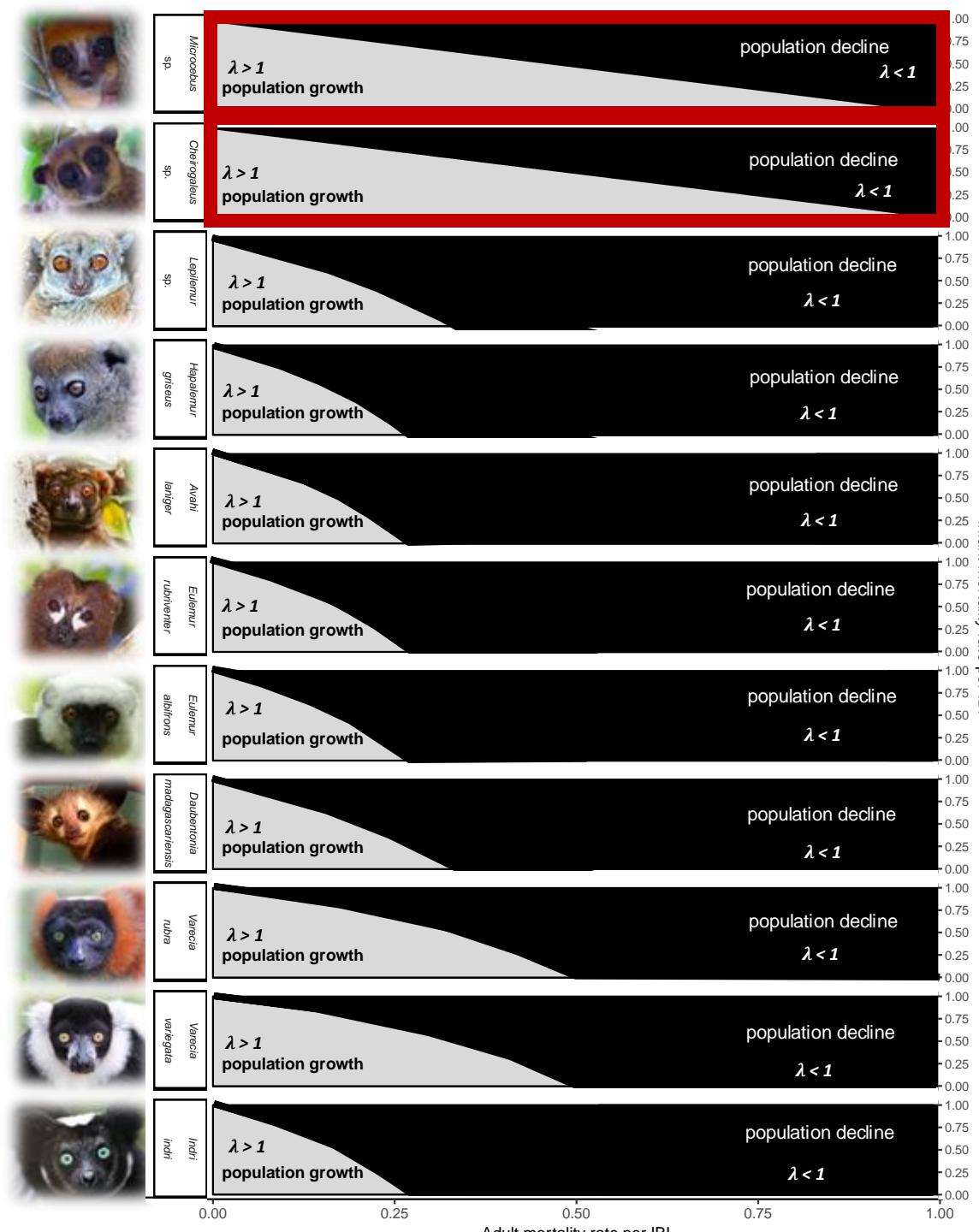


Age @ 1st reproduction = 1 yr
2x babies/ 1 year



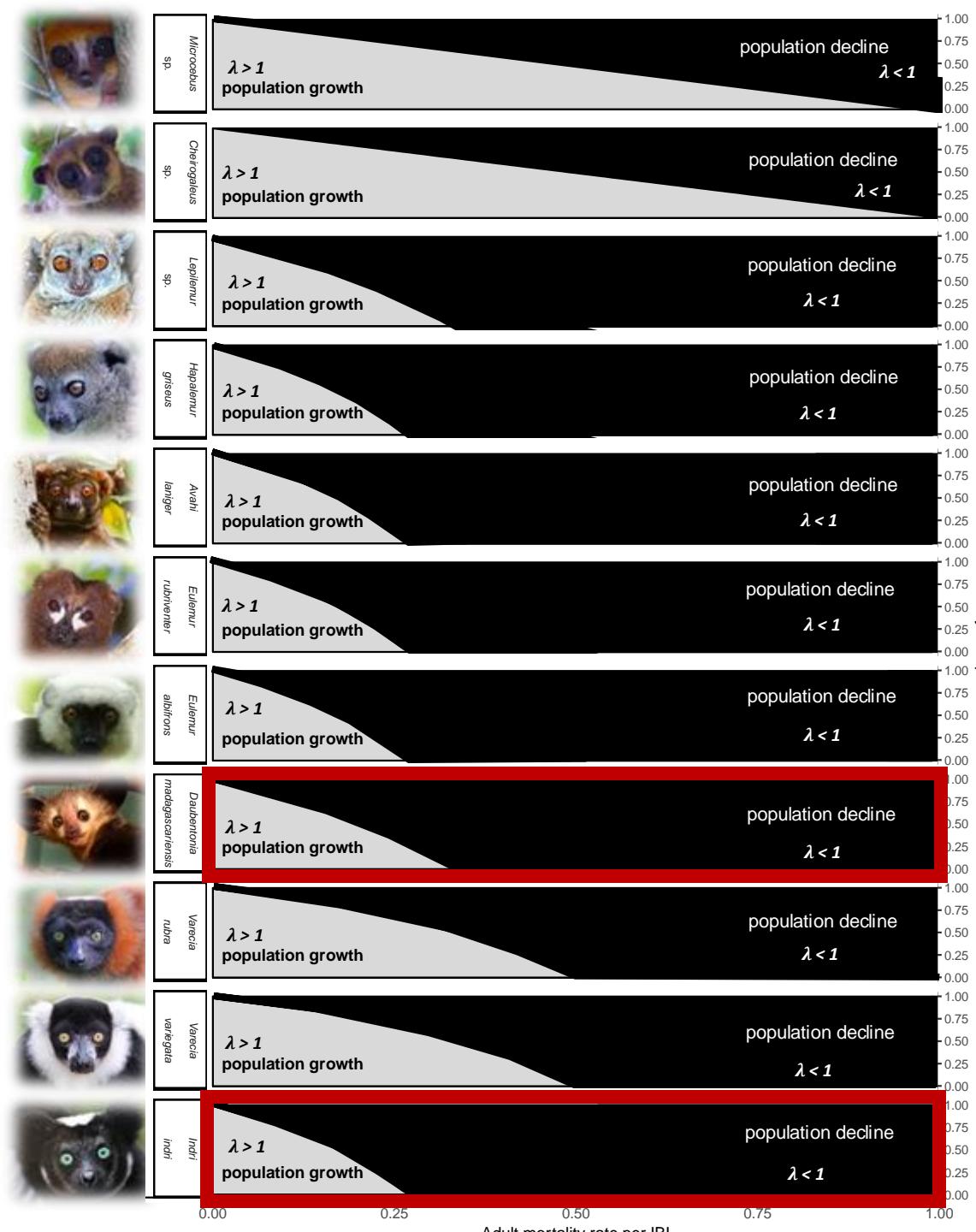
Age @ 1st reproduction = 1 yr
2x babies/ 1 year

← Age @ 1st reproduction = 9 yrs
1x baby/ 3 years Brook et al. 2018. *Conservation Biology*.



We plotted zero-growth lines to evaluate lemur population trajectories across different mortality rates.

Smaller lemurs with **faster life histories** are resilient to **mortality**.

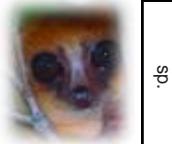


We plotted zero-growth lines to evaluate lemur population trajectories across different mortality rates.

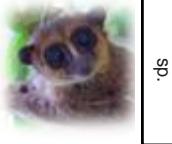
Smaller lemurs with faster life histories are resilient to mortality.

Bigger lemurs with **slower life histories** are particularly **vulnerable**.

We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



Microcebus
sp.



Cheirogaleus
sp.



Hapalemur
occidentalis



Avahi
laniger



Eulemur
albifrons



Varécia
variegata



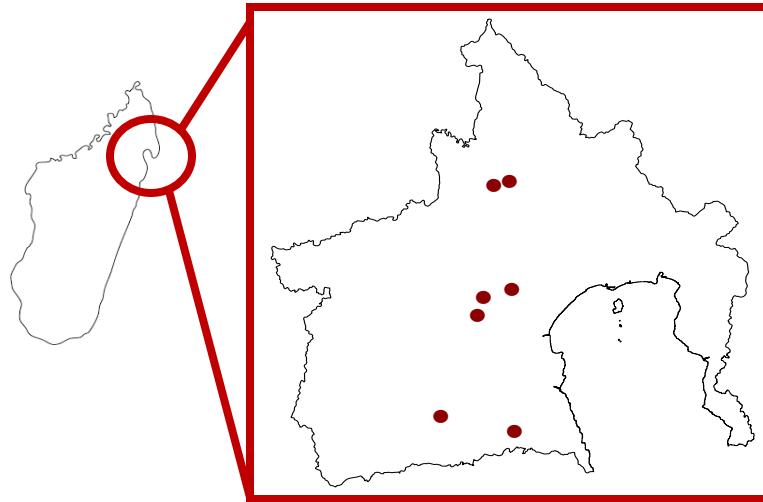
Indri
indri

We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



Assumptions:

- Starting population of 200 lemurs per site

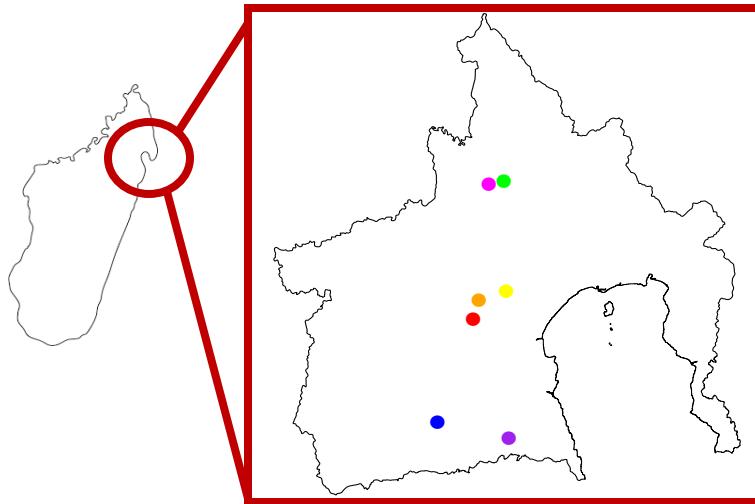


We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



Assumptions:

- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies

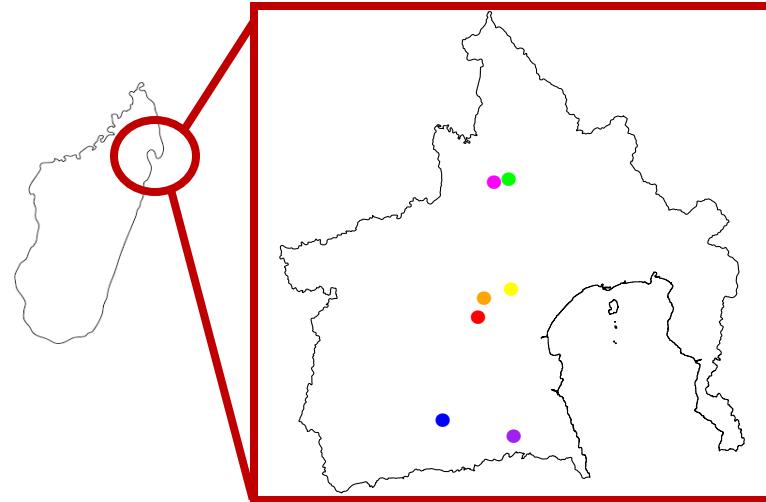


We built a regional **metapopulation model** to simulate population dynamics into the future for a subset of species.



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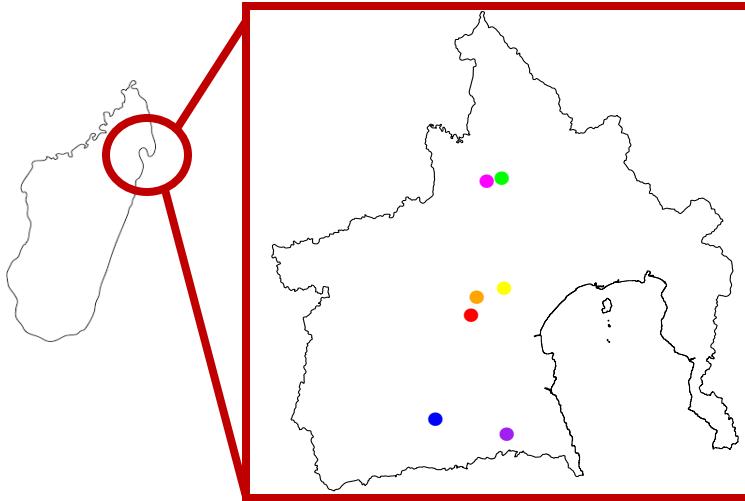


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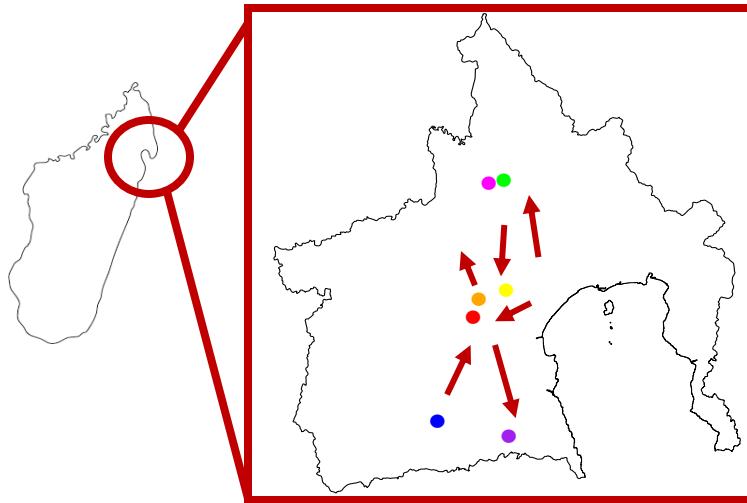


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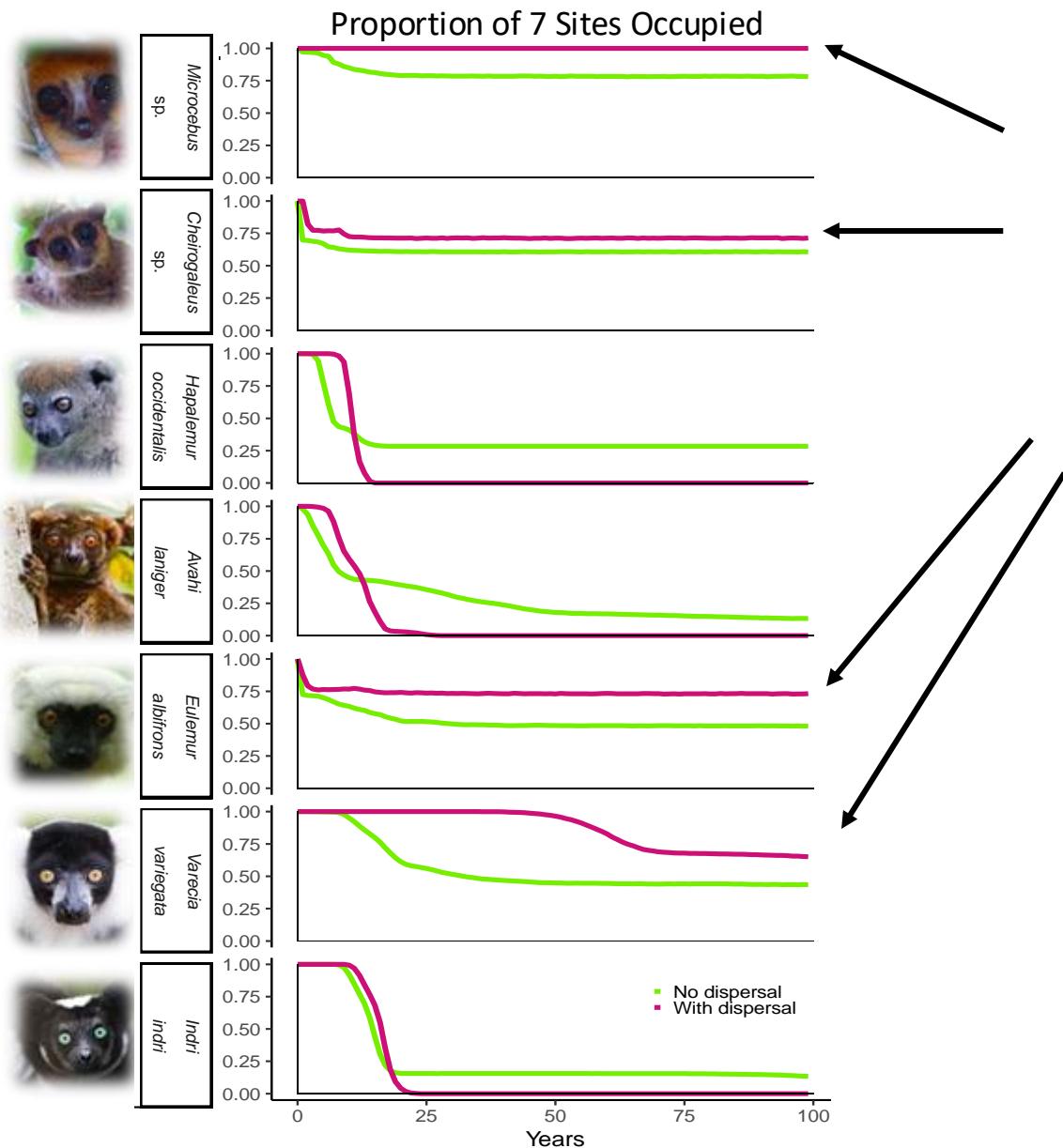


Assumptions:

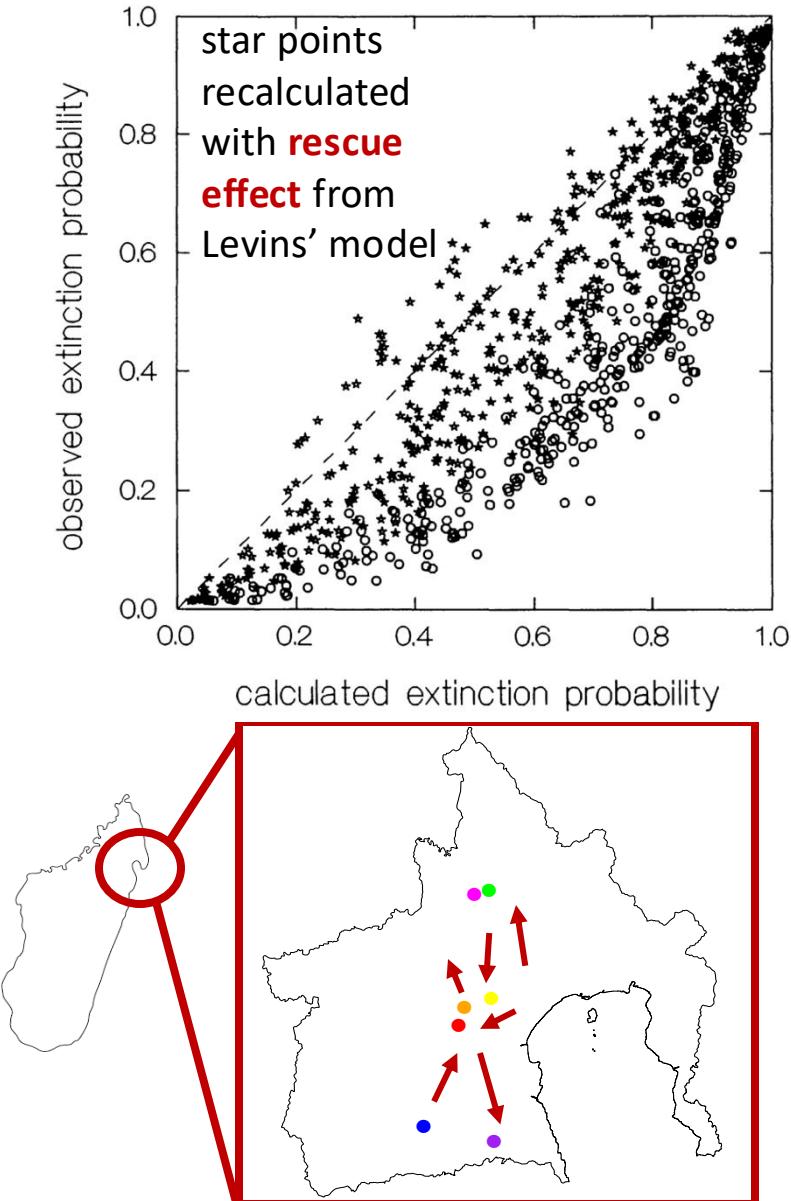
- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies
- Density dependent effects on fecundity
- Compared **no dispersal scenarios** vs. scenarios allowing for **stochastic dispersal** mediated by geographic distance



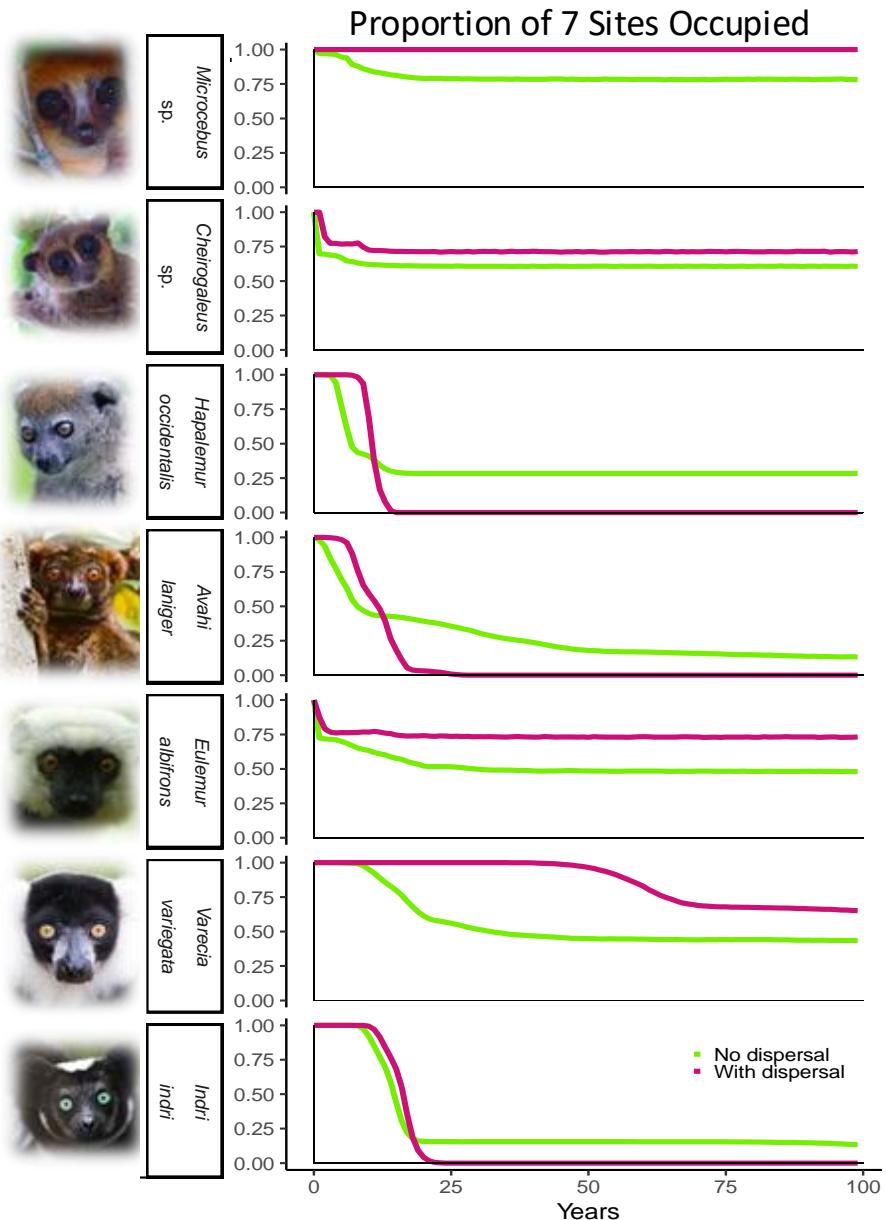
Dispersal sometimes promoted **rescue effects** as seen in Hanksi's work.



Metapopulation dynamics can promote more lemurs at more sites across the landscape!

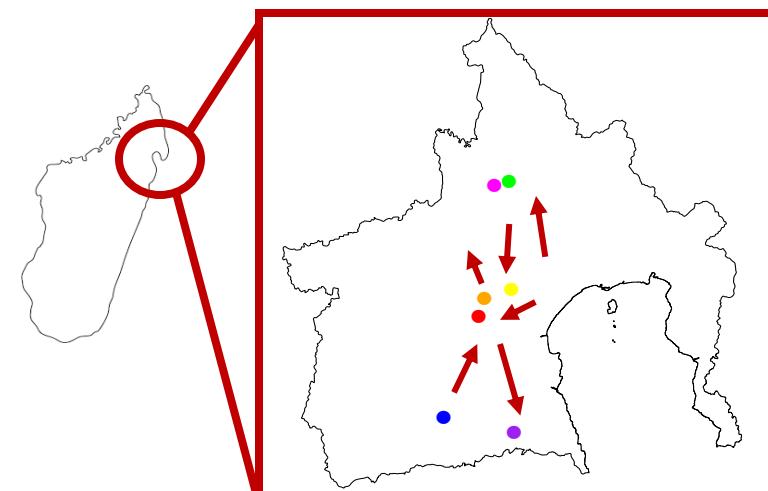
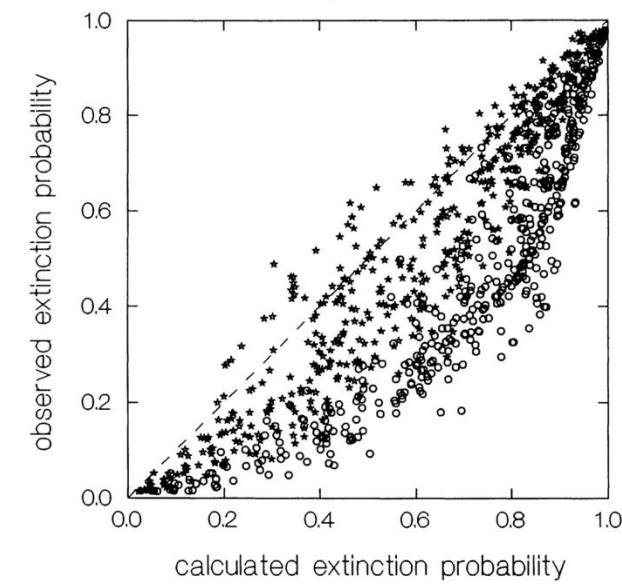


Dispersal can drive **regional extirpation** if the majority of local sites function as **population sinks**.



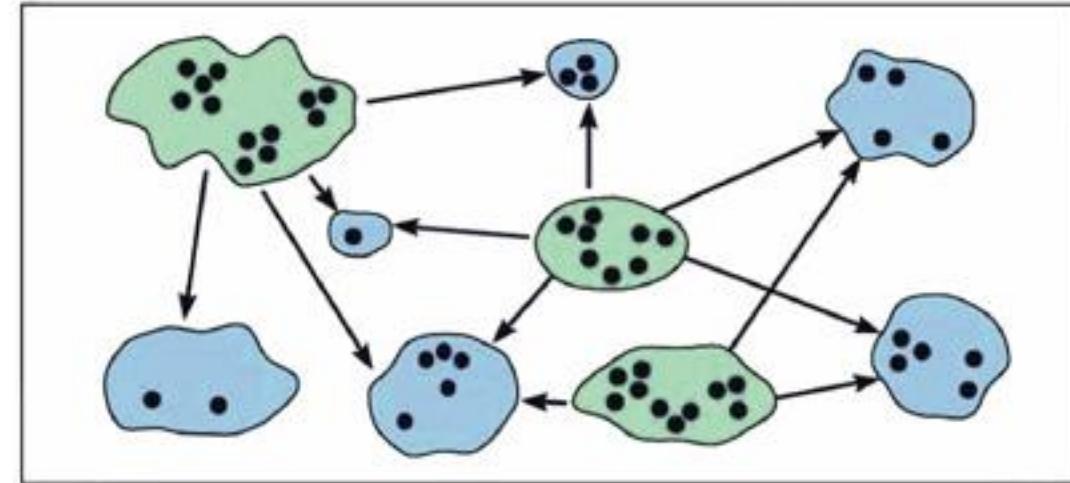
In contrast to the **rescue effect** observed in Hanski!

Metapopulation dynamics can drive regional declines in other cases!



Source-sink theory describes how variation in habitat may affect population dynamics.

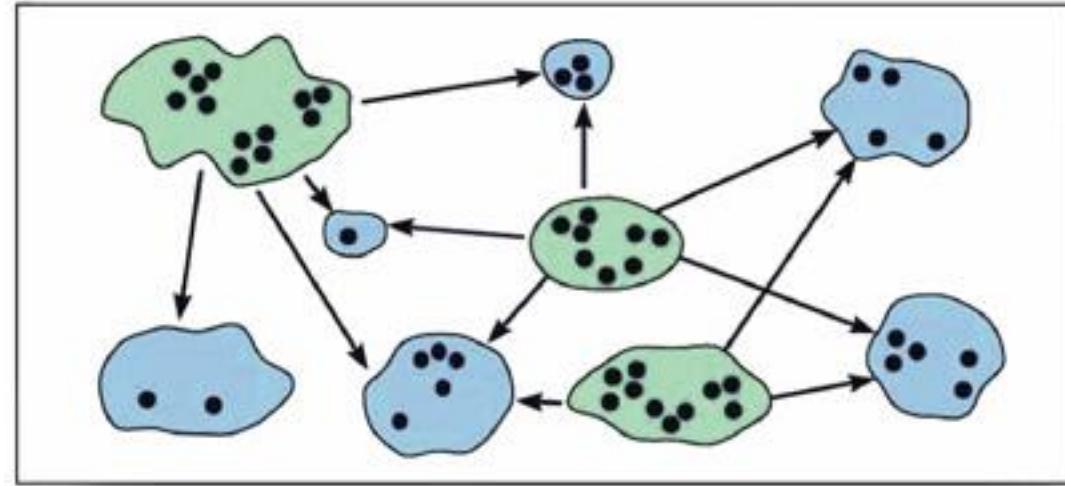
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.



- Individual within a local population
- Dispersal event
- Source population in a suitable habitat
- Sink population in a low-quality habitat

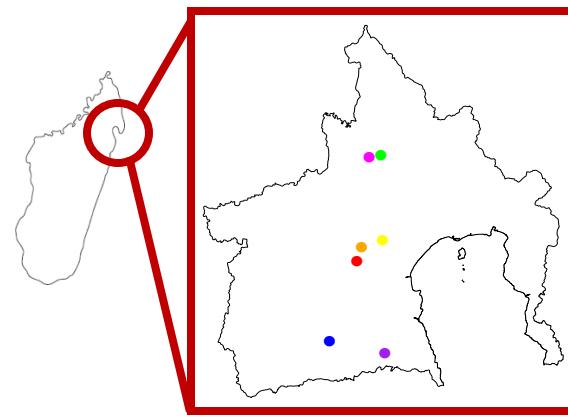
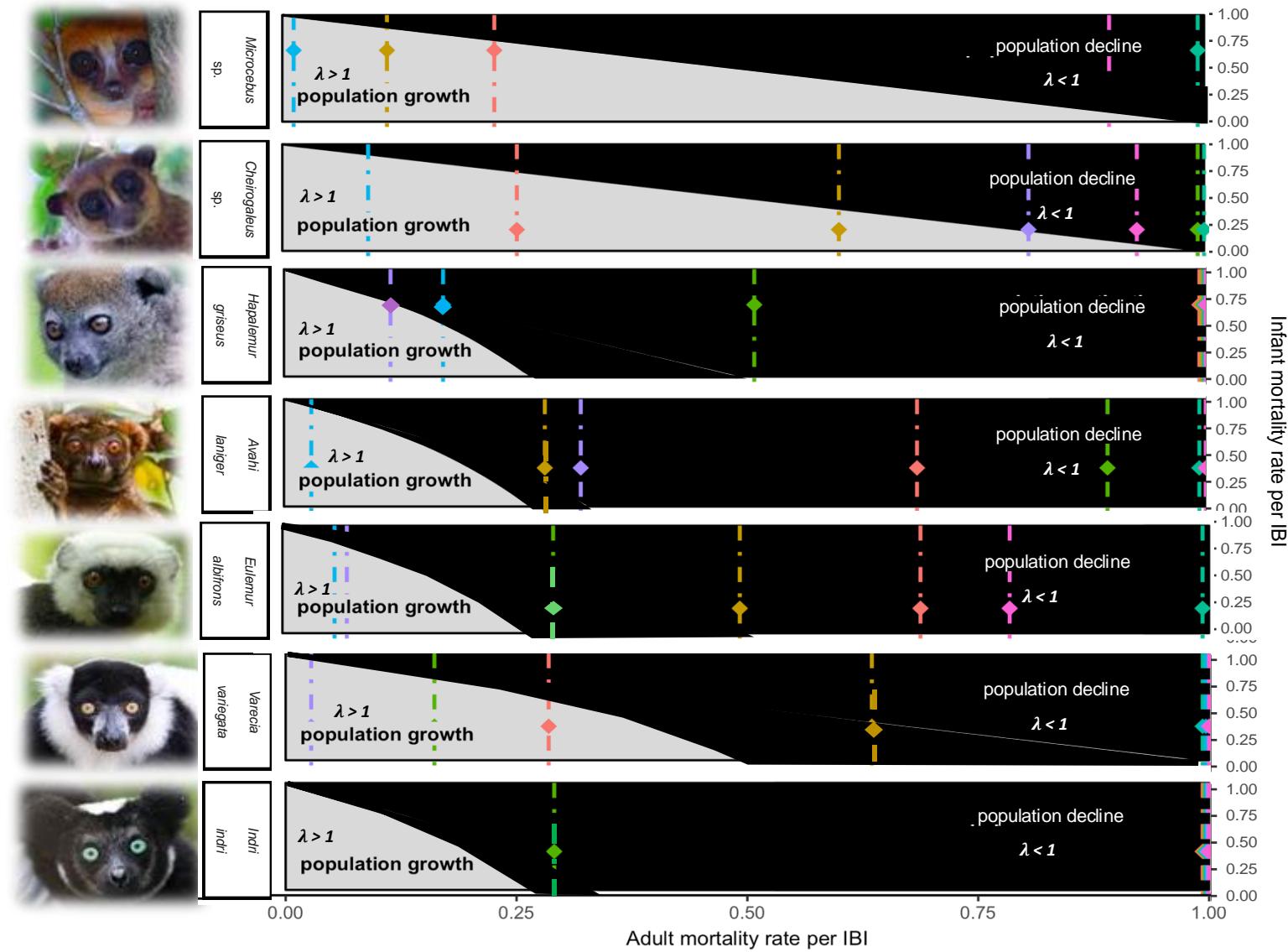
Source-sink theory describes how variation in habitat may affect population dynamics.

- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.
- An **ecological trap** is an organism's preference for poor quality habitat
 - Ex: polarized light pollution & insect ovipositing



- Individual within a local population
 - Dispersal event
- Source population in a suitable habitat
○ Sink population in a low-quality habitat

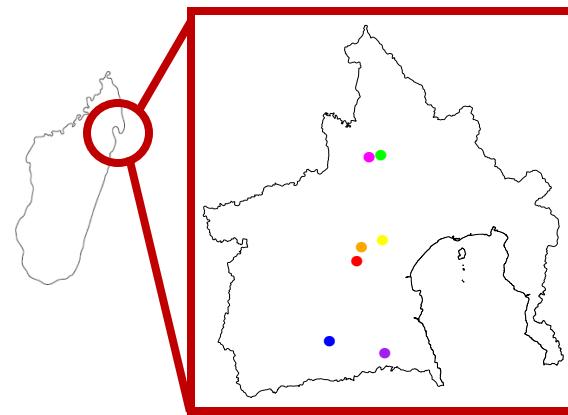
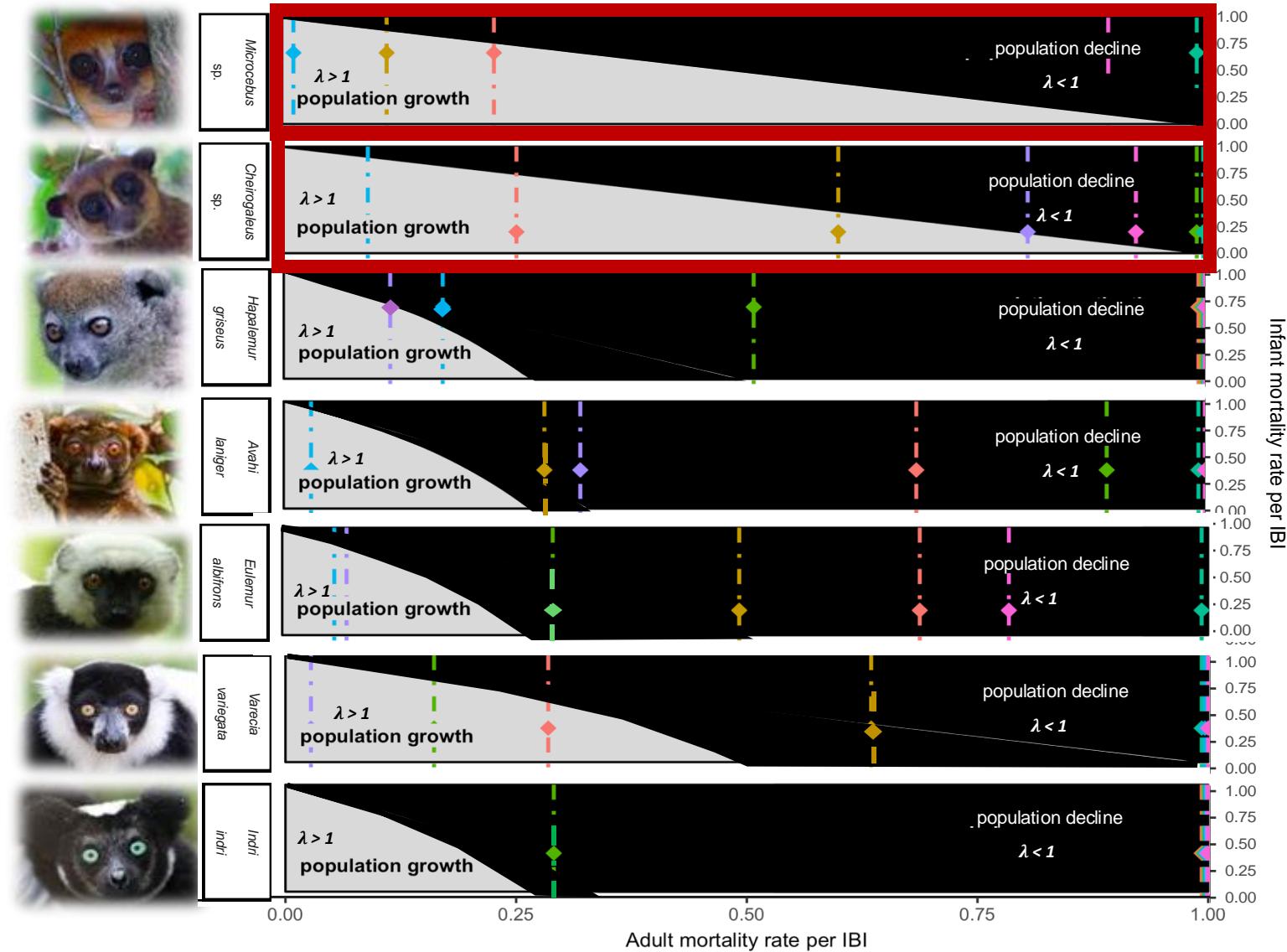
We also evaluated **excess mortality due to human hunting** to assess **harvest sustainability**.



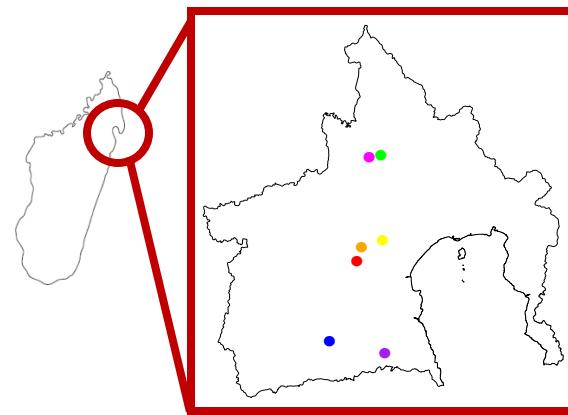
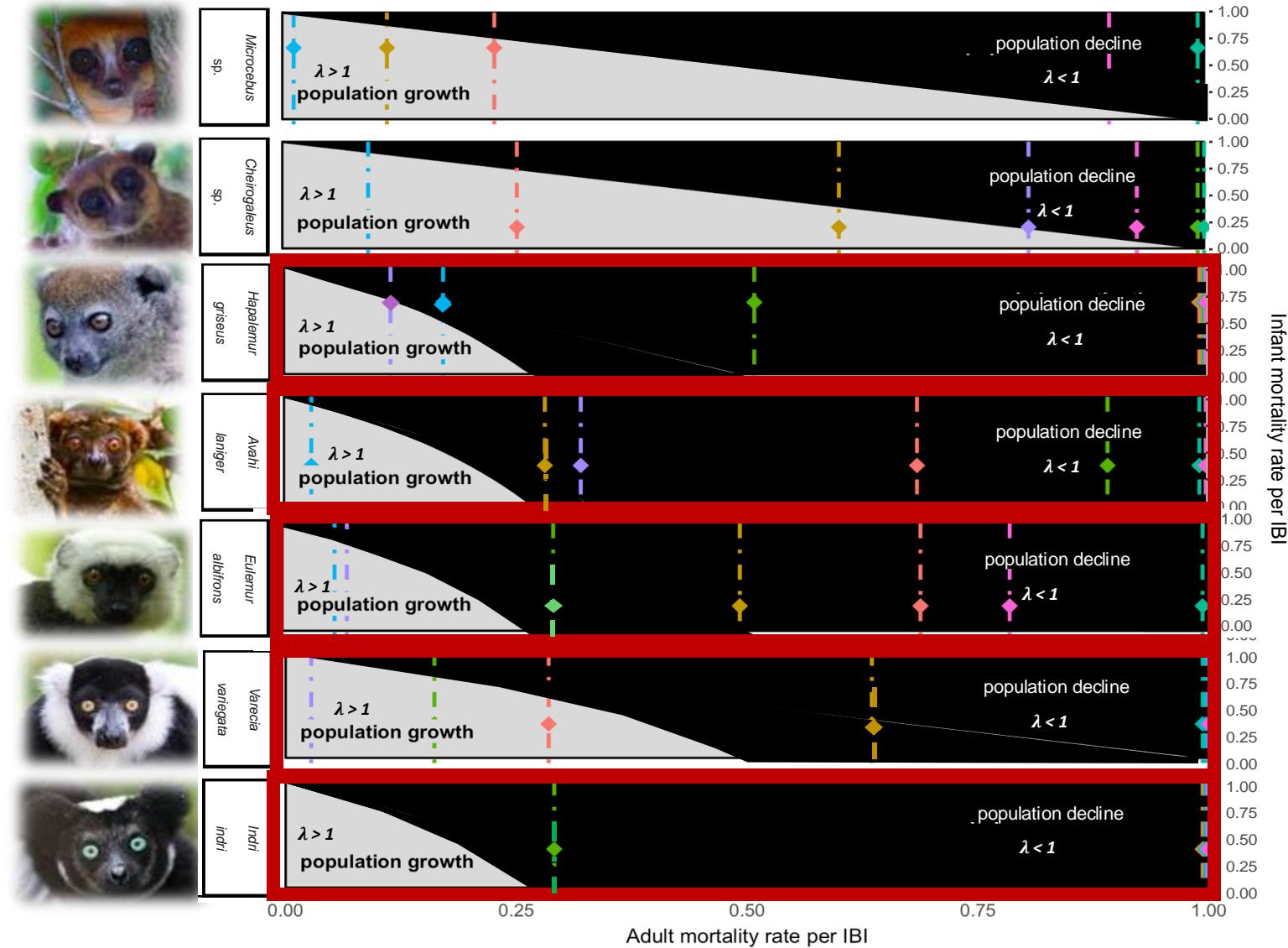
Colored vertical lines give **site-specific hunting rates** for adult lemurs.

Diamonds correspond to the intersection of that hunt rate with estimated juvenile mortality.

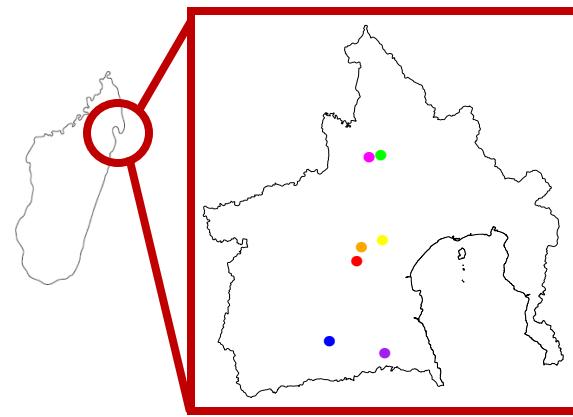
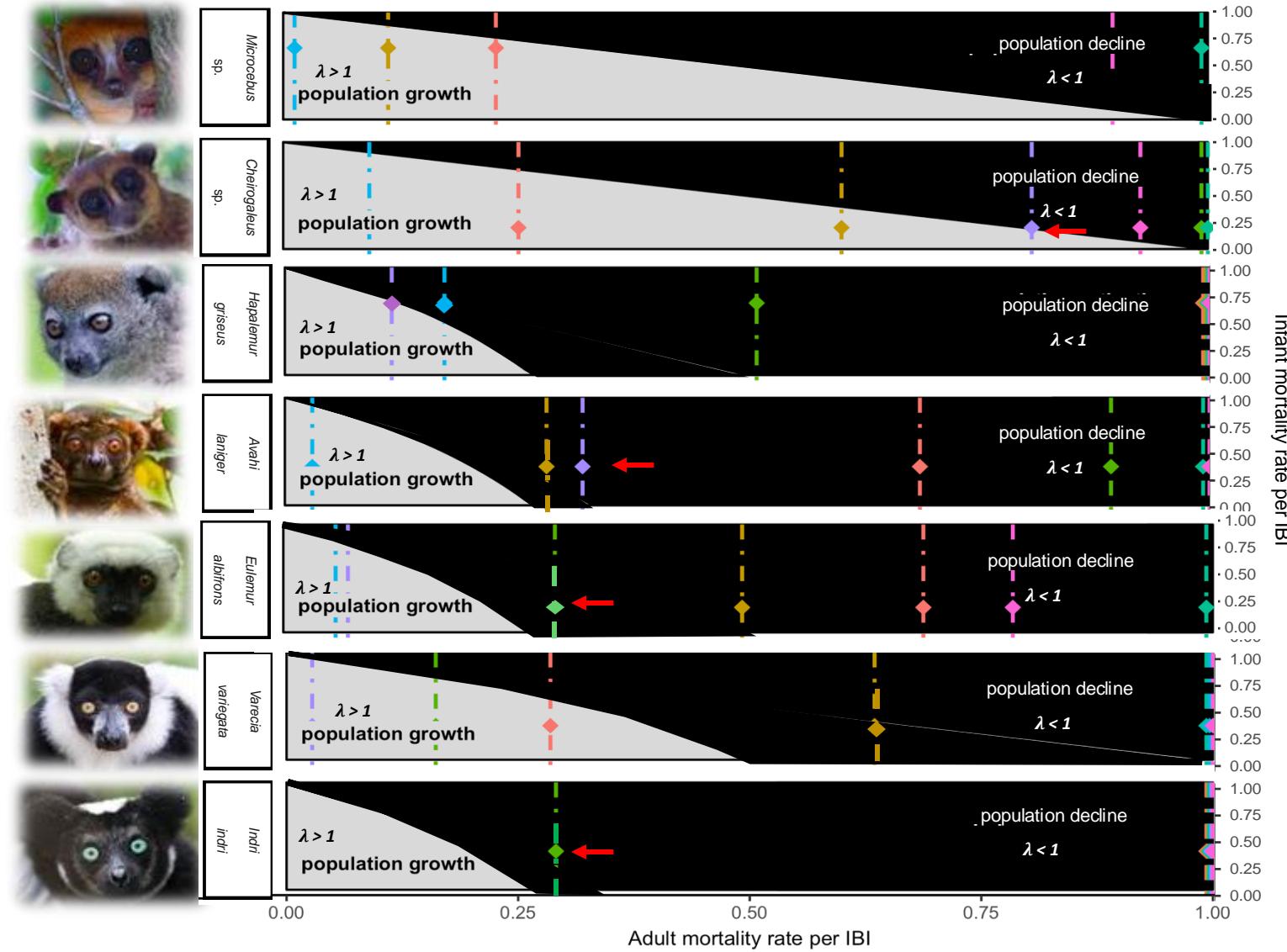
Small-bodied lemurs are largely harvested at sustainable rates on the Makira-Masoala peninsula.



By contrast, larger-bodied lemurs are severely threatened.



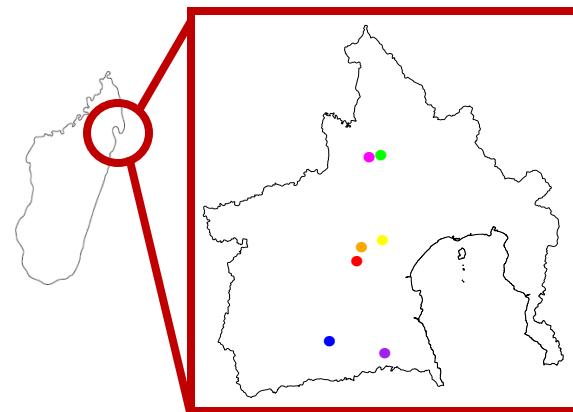
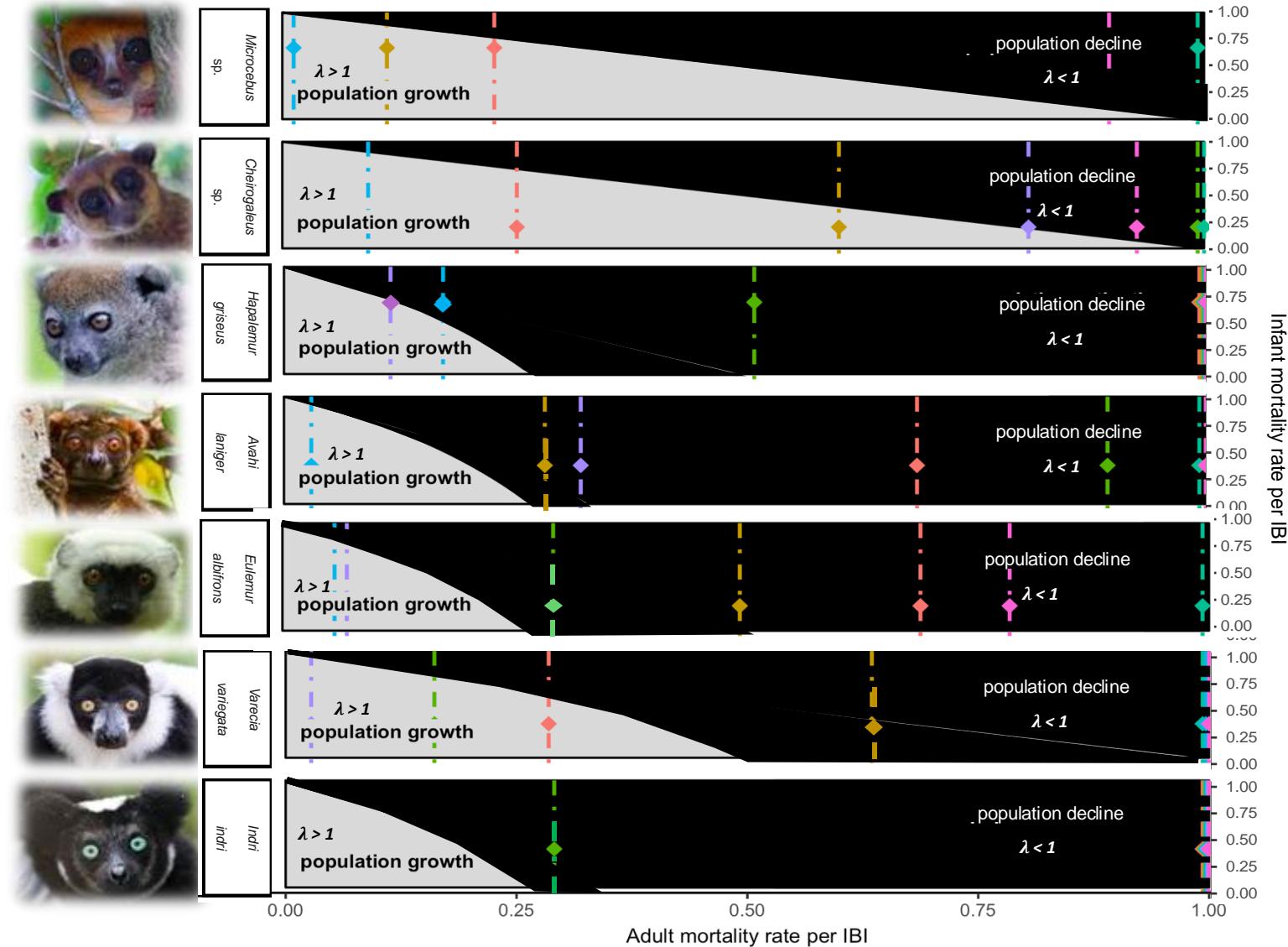
Harvesting near the zero-growth curve highlights the problems inherent with MSY!



Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating:

- environmental **stochasticity**
- demographic **stochasticity**

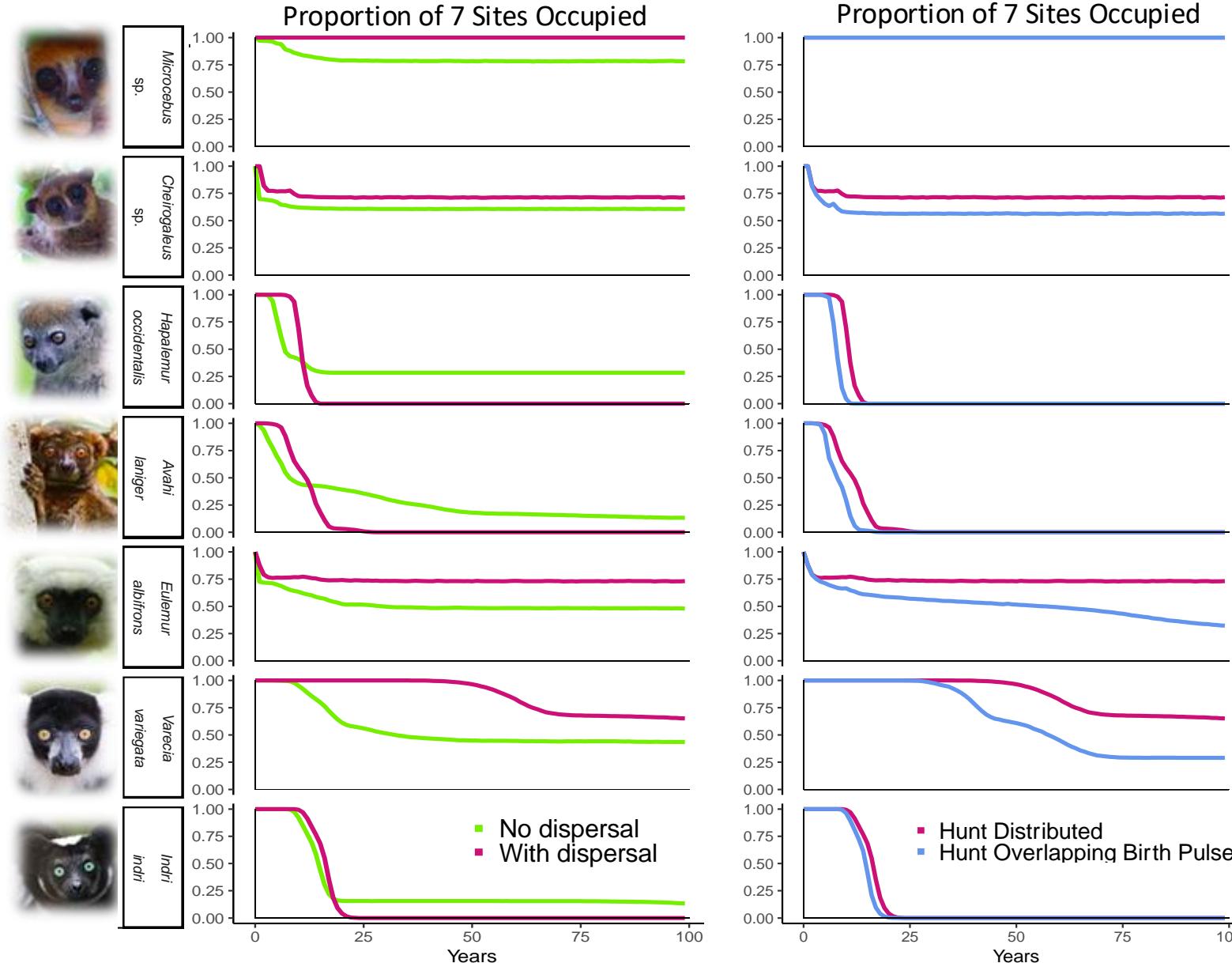
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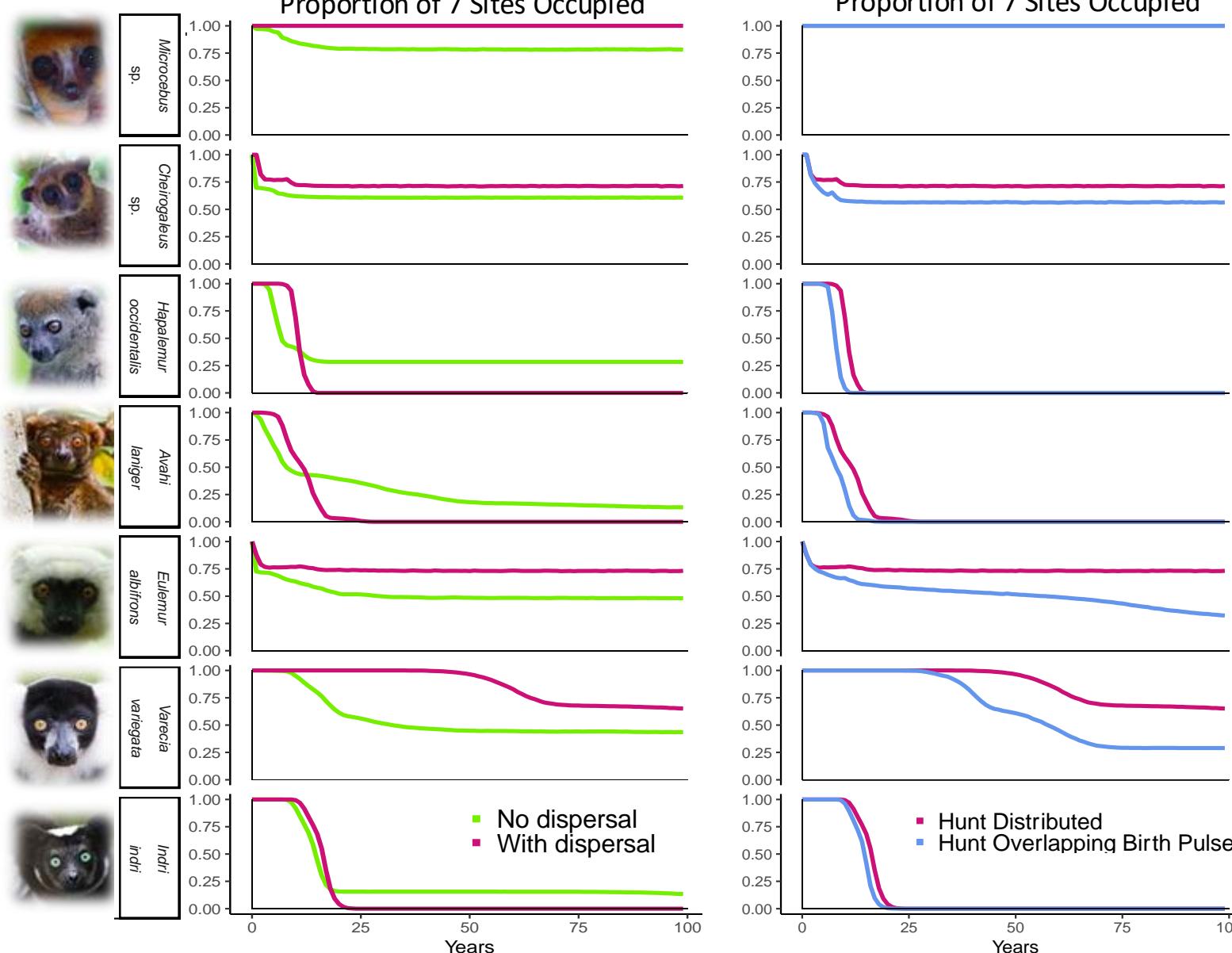
The '**Allee effect**' describes the correlation between population size and population 'fitness', often measured by the population rate of increase, λ .

Large animals tend to have **smaller population sizes**, which are often associated with **lower λ** .

Species are even **further threatened** when hunt seasonality overlaps the **annual birth pulse**.



Species are even **further threatened** when **hunt seasonality** overlaps the **annual birth pulse**.



Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

Simplest representations of MSY:

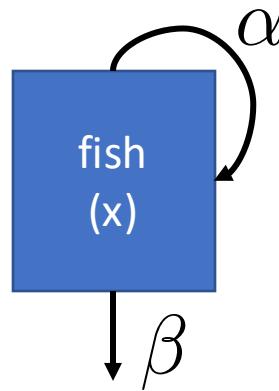
- Neglect population structure.
- Assume constant harvest.
- Ignore environmental and demographic stochasticity



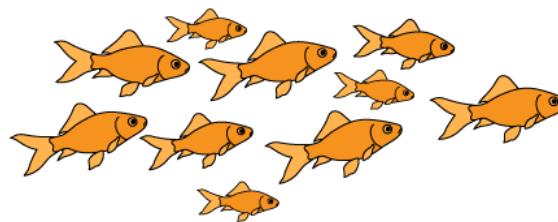
Which of the following statements is correct?

- A The greater the number of subpopulations with... 0%
- B Fragmentation can facilitate population persistence. 0%
- C Butterflies are going extinct in Finland. 0%
- D Ecological traps occur when species migrate to high qual... 0%

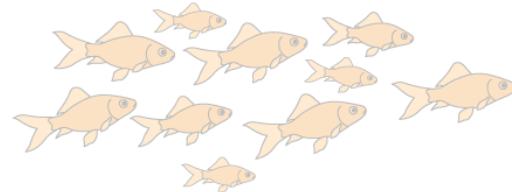
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



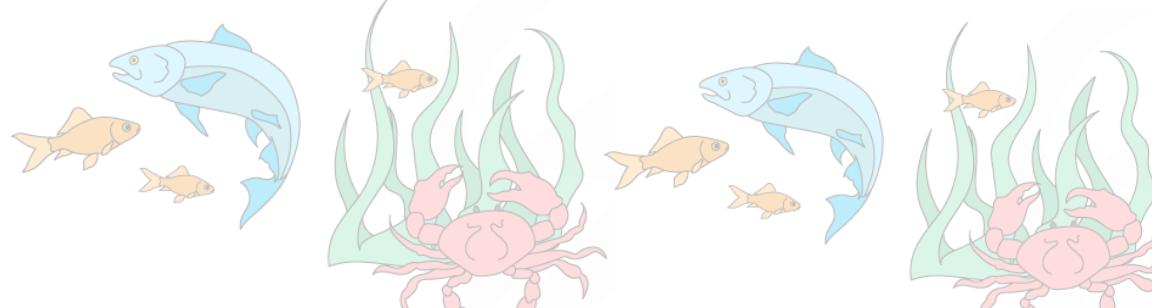
individual



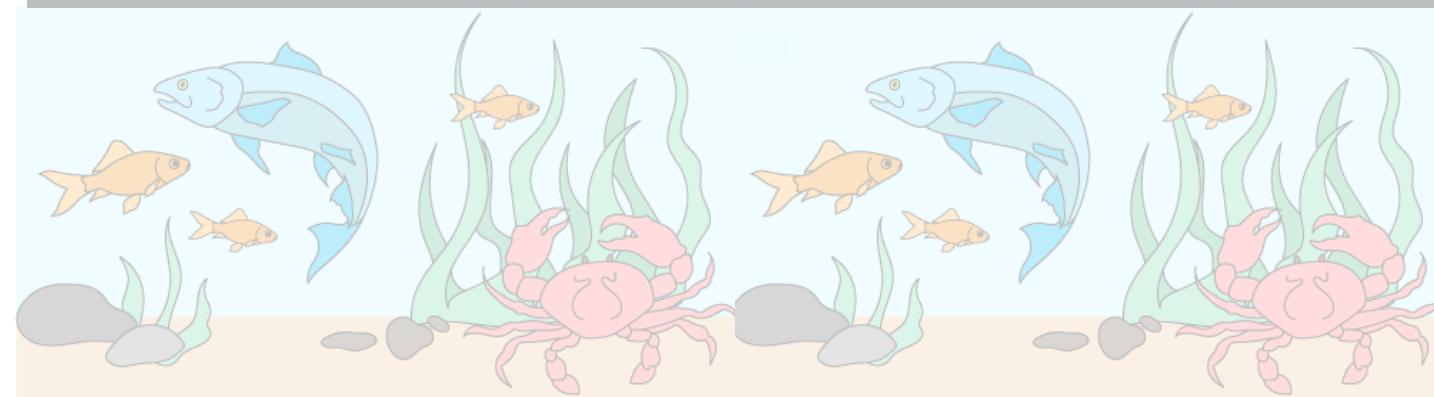
population



metapopulation



community



ecosystem

*How does the abundance of fish **change** through time?*

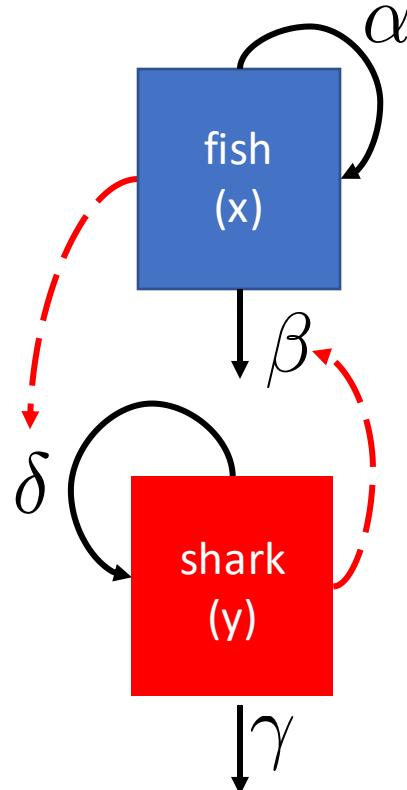
The logistic growth equation offers an explanation for population self-regulation, an example of **intraspecific competition**.

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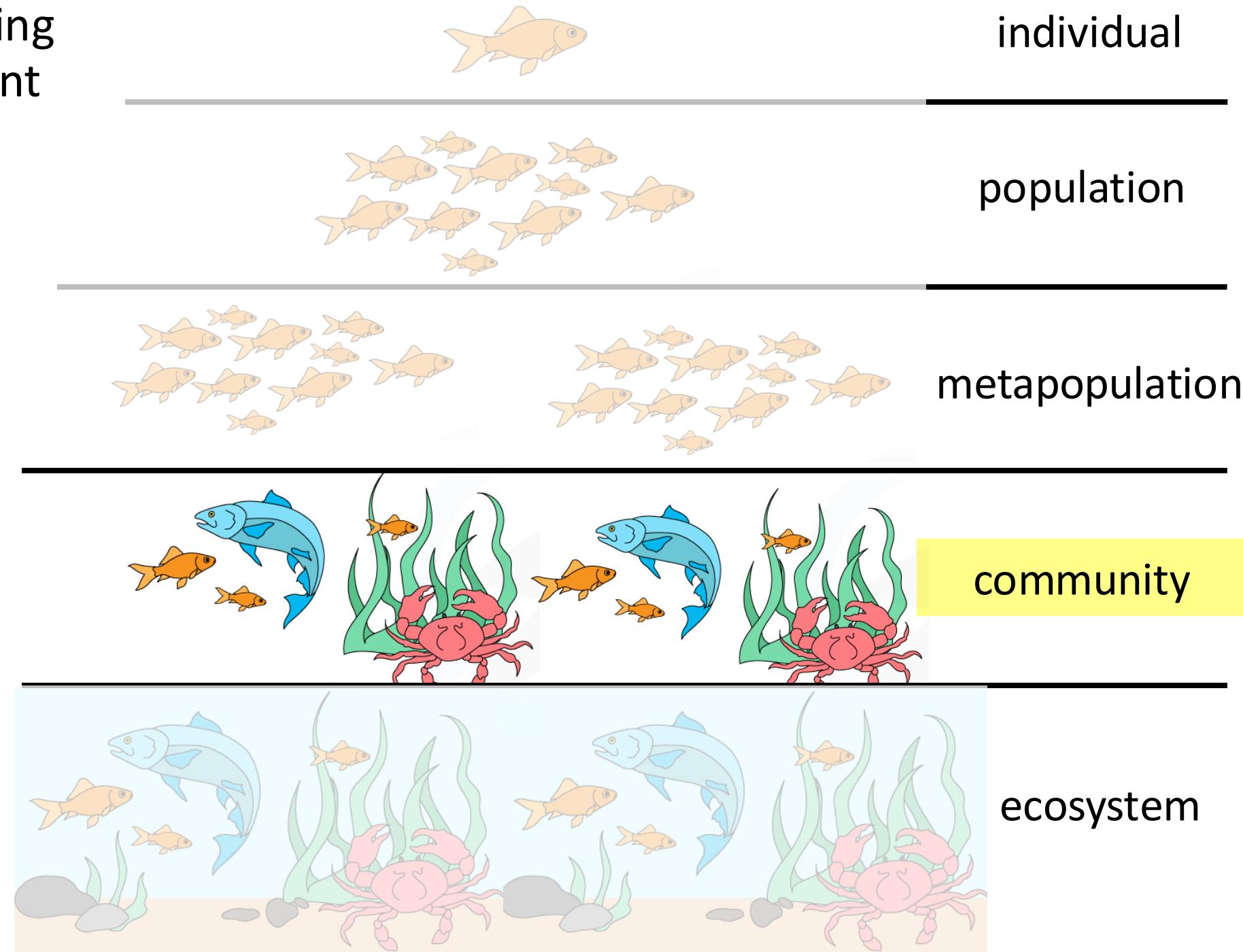


But ecology is the study of the **interactions** of organisms with each other and their environment, and in some cases, **interspecific interactions** are essential to understanding ecological systems.

Community = interacting populations of different species

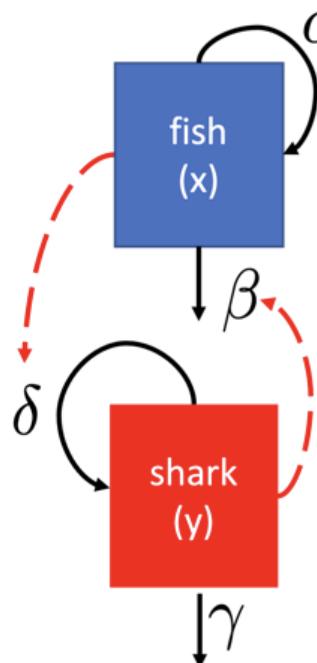


How does fish abundance **vary** with changes in shark abundance?





What are the state variables in this predator-prey system?



A β and γ

B α and δ

D fish (x) and sharks (y)

E The red dashed lines

C Both "A" and "B"

0%

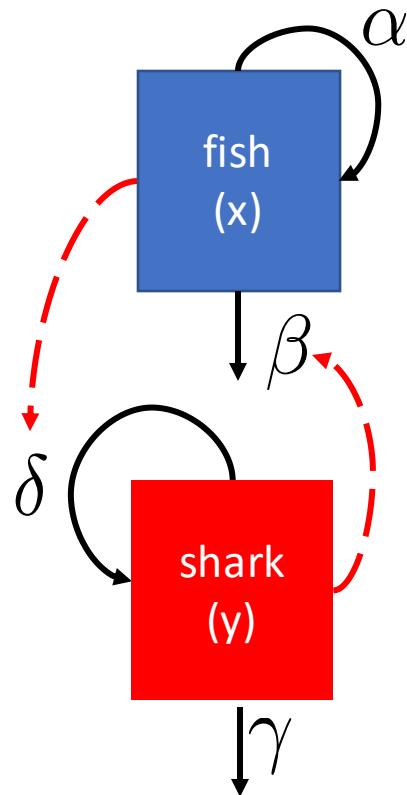
0%

0%

0%

0%

The Lotka-Volterra predator-prey model



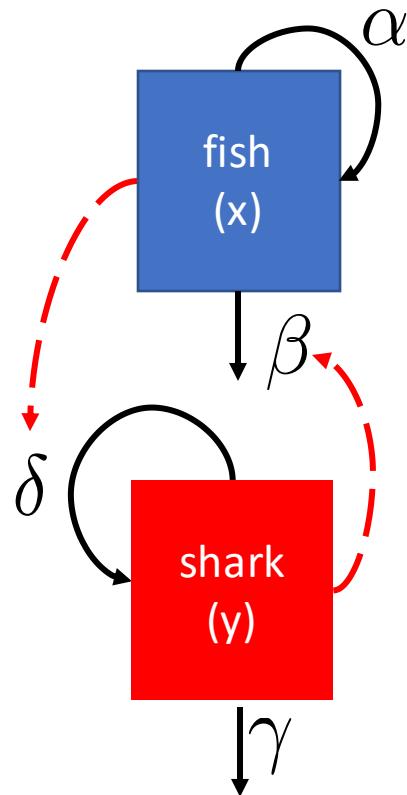
$$\frac{dx}{dt} = \alpha x - \beta xy$$

$$\frac{dy}{dt} = \delta xy - \gamma y$$

*How does **fish** abundance **vary** with changes in **shark** abundance?*

- First proposed by Polish-born American mathematician & chemist, Alfred J. Lotka, in 1920 to explain autocatalytic chemical reactions.

The Lotka-Volterra predator-prey model

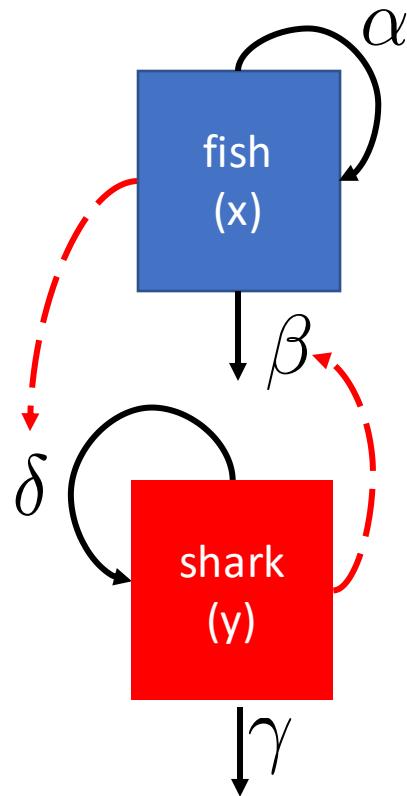


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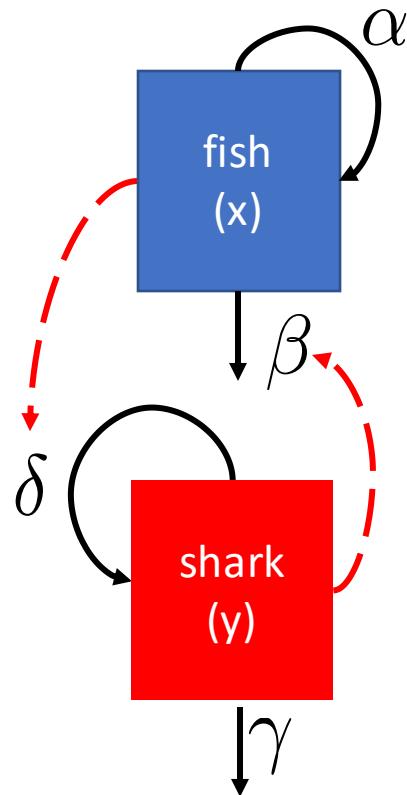


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The Lotka-Volterra predator-prey model

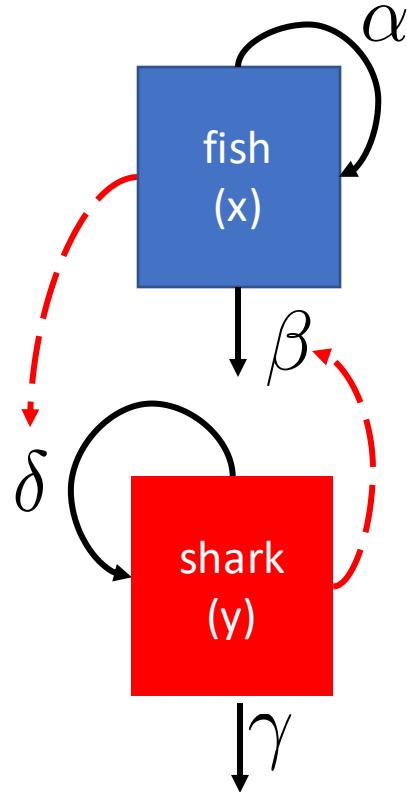


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- Idea that **interspecies interactions** regulate populations

The Lotka-Volterra predator-prey model



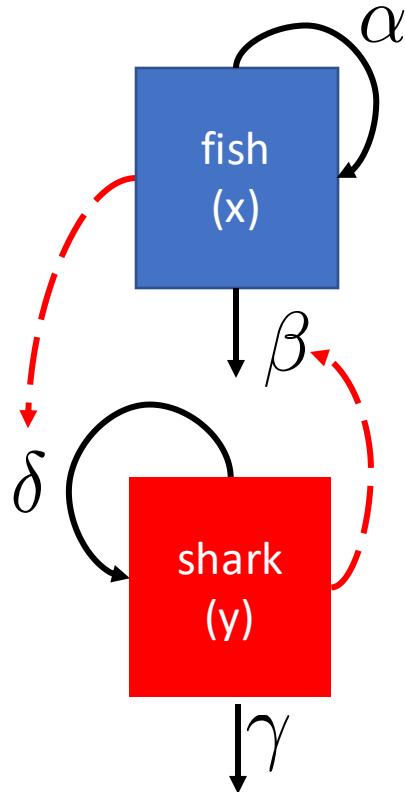
growth rate of prey,
independent of predator

$$\frac{dx}{dt} = \underbrace{\alpha x}_{\text{growth rate}} - \beta xy$$

$$\frac{dy}{dt} = \delta xy - \gamma y$$

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The Lotka-Volterra predator-prey model



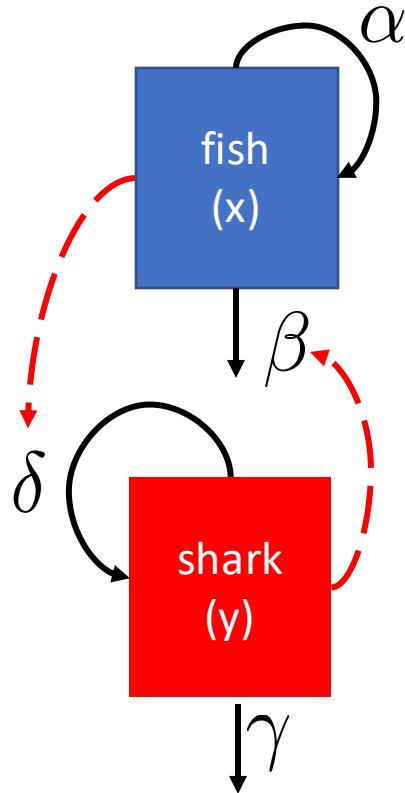
growth rate of prey,
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$$\left. \begin{aligned} \frac{dx}{dt} &= \alpha x - \beta xy \\ \frac{dy}{dt} &= \delta xy - \gamma y \end{aligned} \right\}$$

death rate of prey,
depends on
abundance of
predator

*How does **fish**
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The Lotka-Volterra predator-prey model



*How does **fish** abundance **vary** with changes in **shark** abundance?*

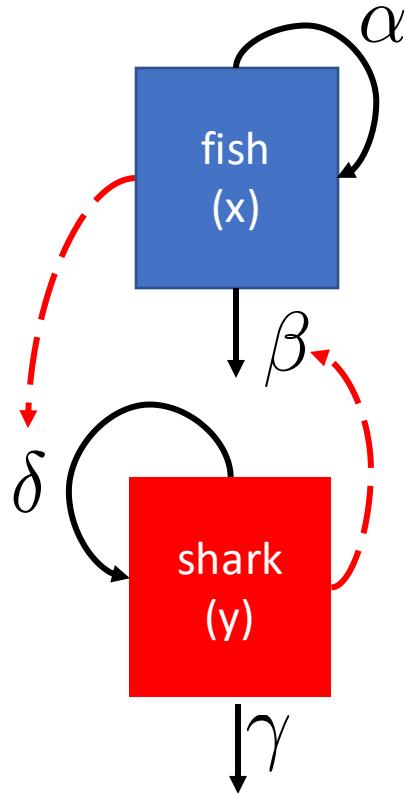
growth rate of prey,
independent of predator

$$\frac{dx}{dt} = \underbrace{\alpha x}_{\text{growth rate of prey, independent of predator}} - \beta xy \quad \}$$

$$\frac{dy}{dt} = \delta xy - \underbrace{\gamma y}_{\text{death rate of prey, depends on abundance of predator}}$$

growth rate of predator, depends on abundance of prey
(and efficiency of consumption)

The Lotka-Volterra predator-prey model



*How does **fish** abundance **vary** with changes in **shark** abundance?*

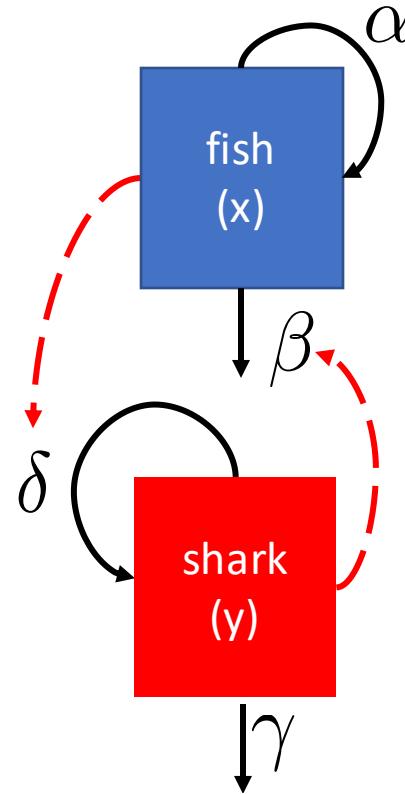
growth rate of prey,
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$$\frac{dy}{dt} = \underbrace{\delta xy}_{\text{growth rate of predator, depends on abundance of prey (and efficiency of consumption)}} - \underbrace{\gamma y}_{\text{death rate of predator, independent of prey}}$$

growth rate of predator, depends on abundance of prey (and efficiency of consumption)

The Lotka-Volterra predator-prey model



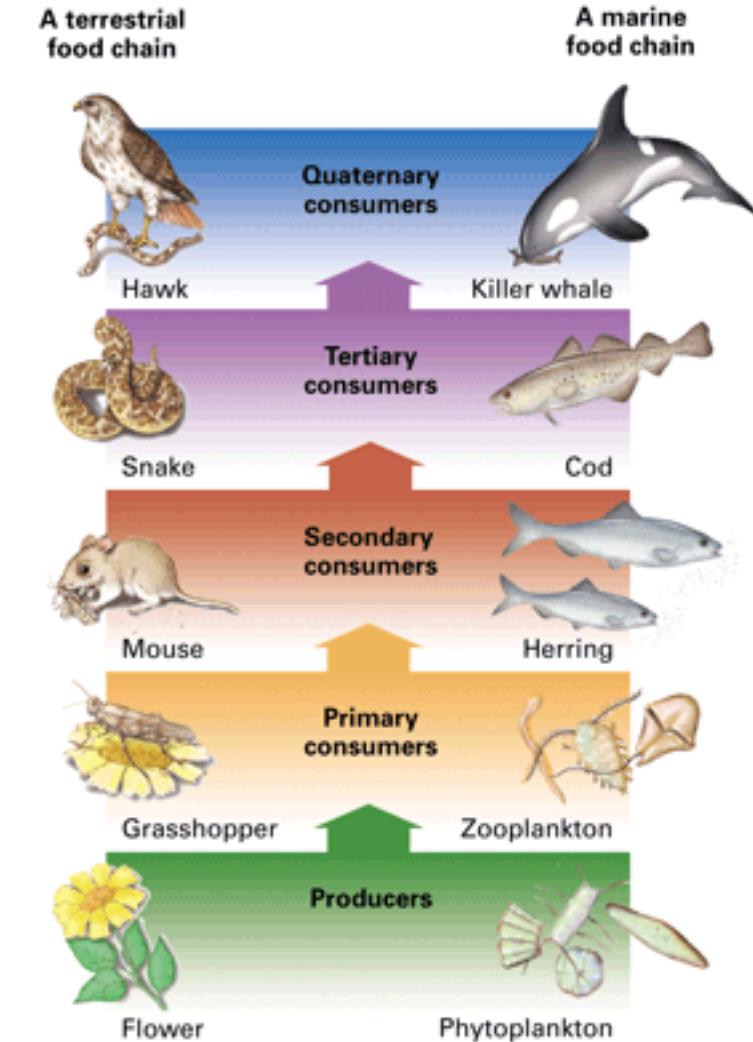
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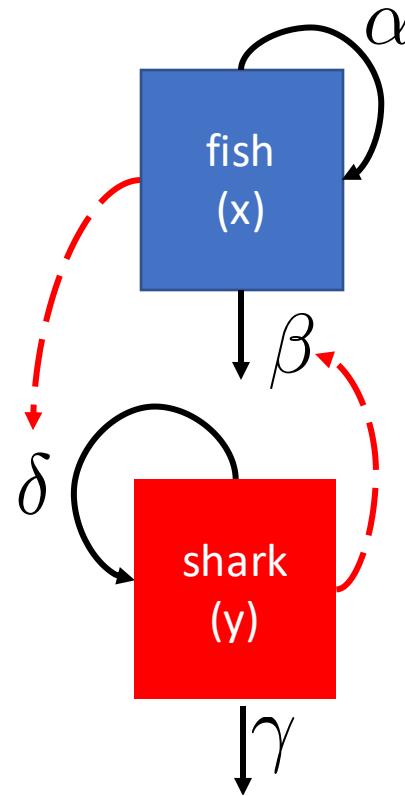
$$\frac{dy}{dt} = \delta xy - \gamma y$$

Bottom-up processes describe ecosystems regulated via production from lower trophic levels.

Top-down processes describe ecosystems regulated via consumption from higher trophic levels.



The Lotka-Volterra predator-prey model



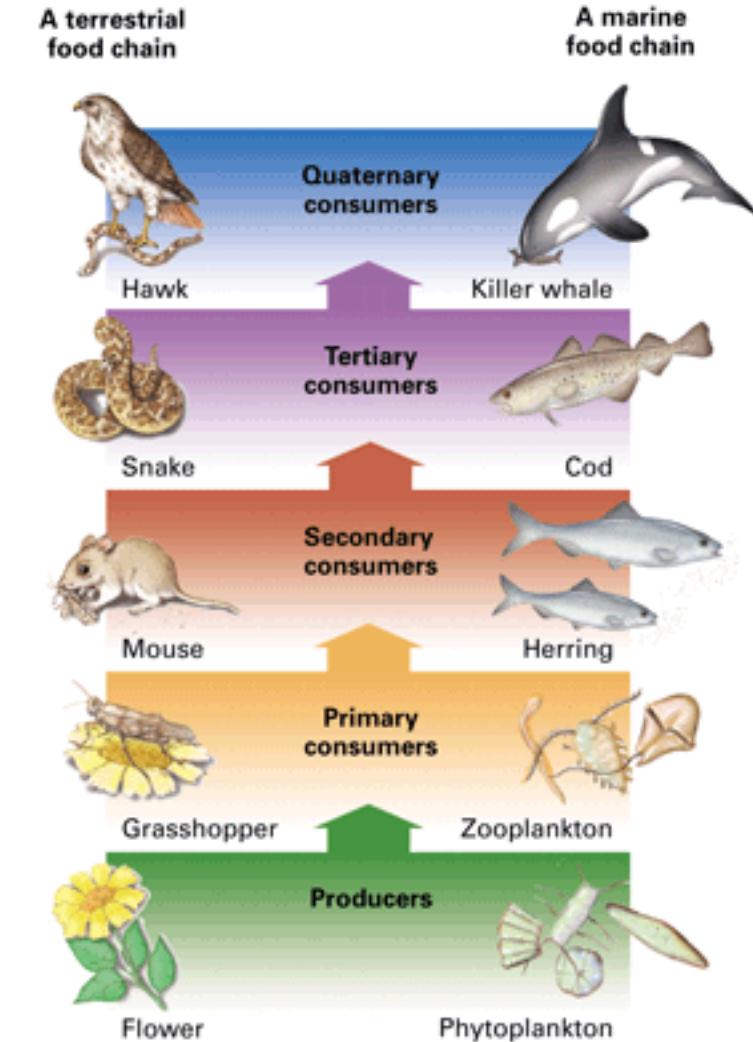
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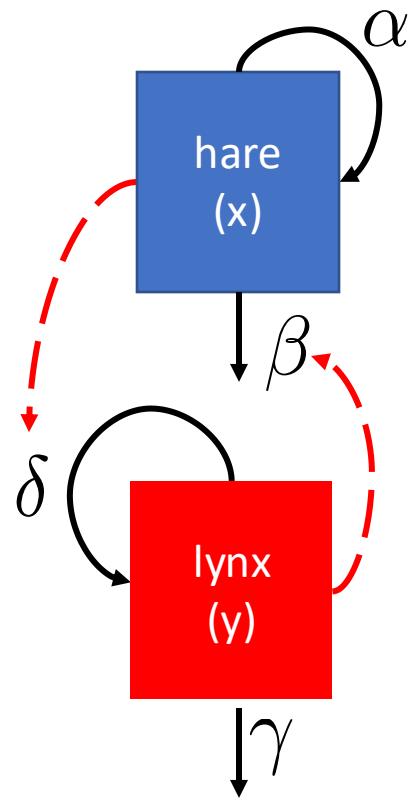
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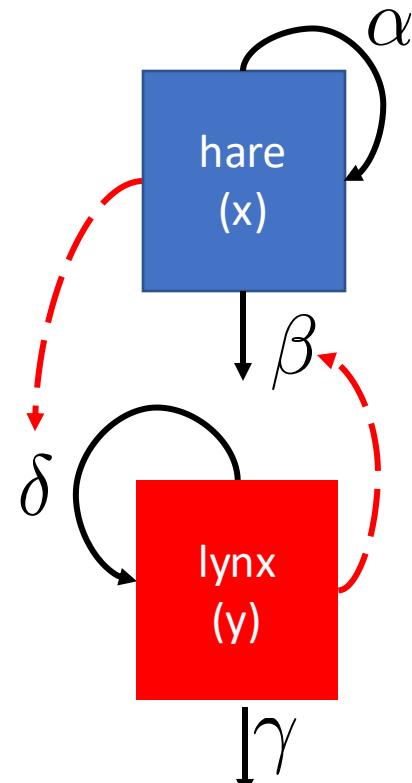
Lotka-Volterra predator-prey models with data



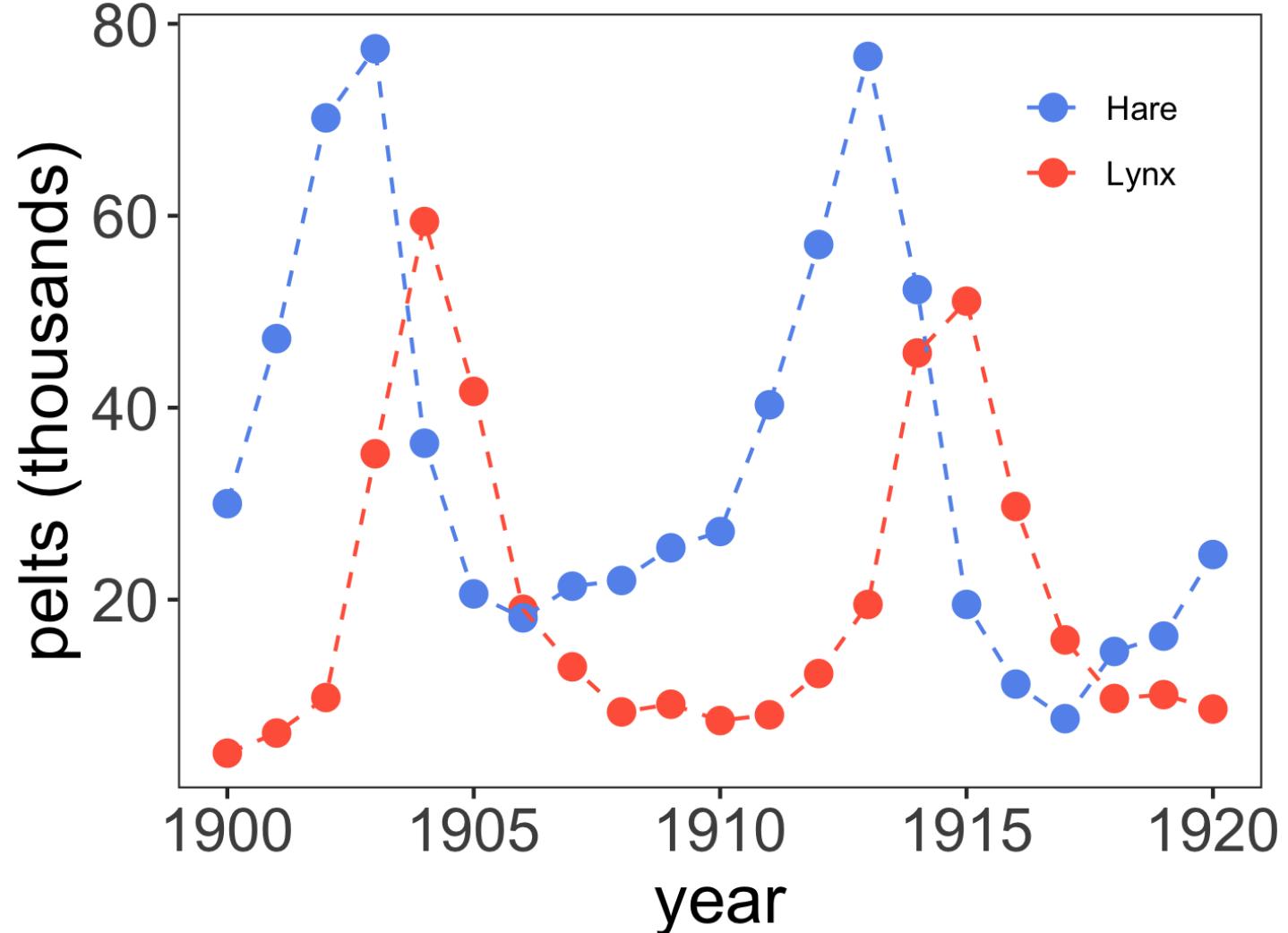
How does **hare** abundance **vary** with changes in **lynx** abundance?



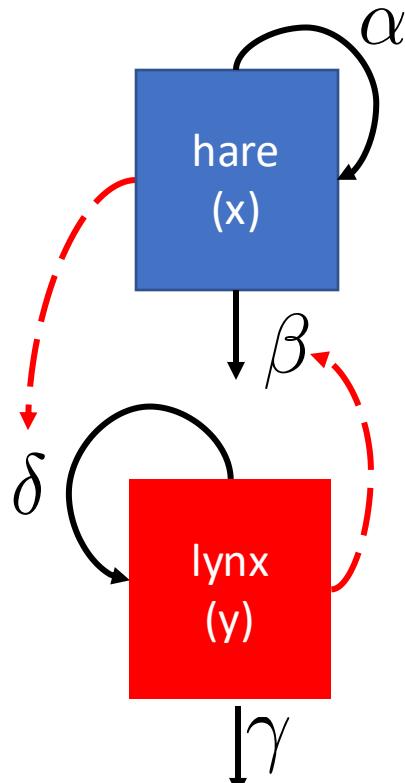
Lotka-Volterra predator-prey models with data



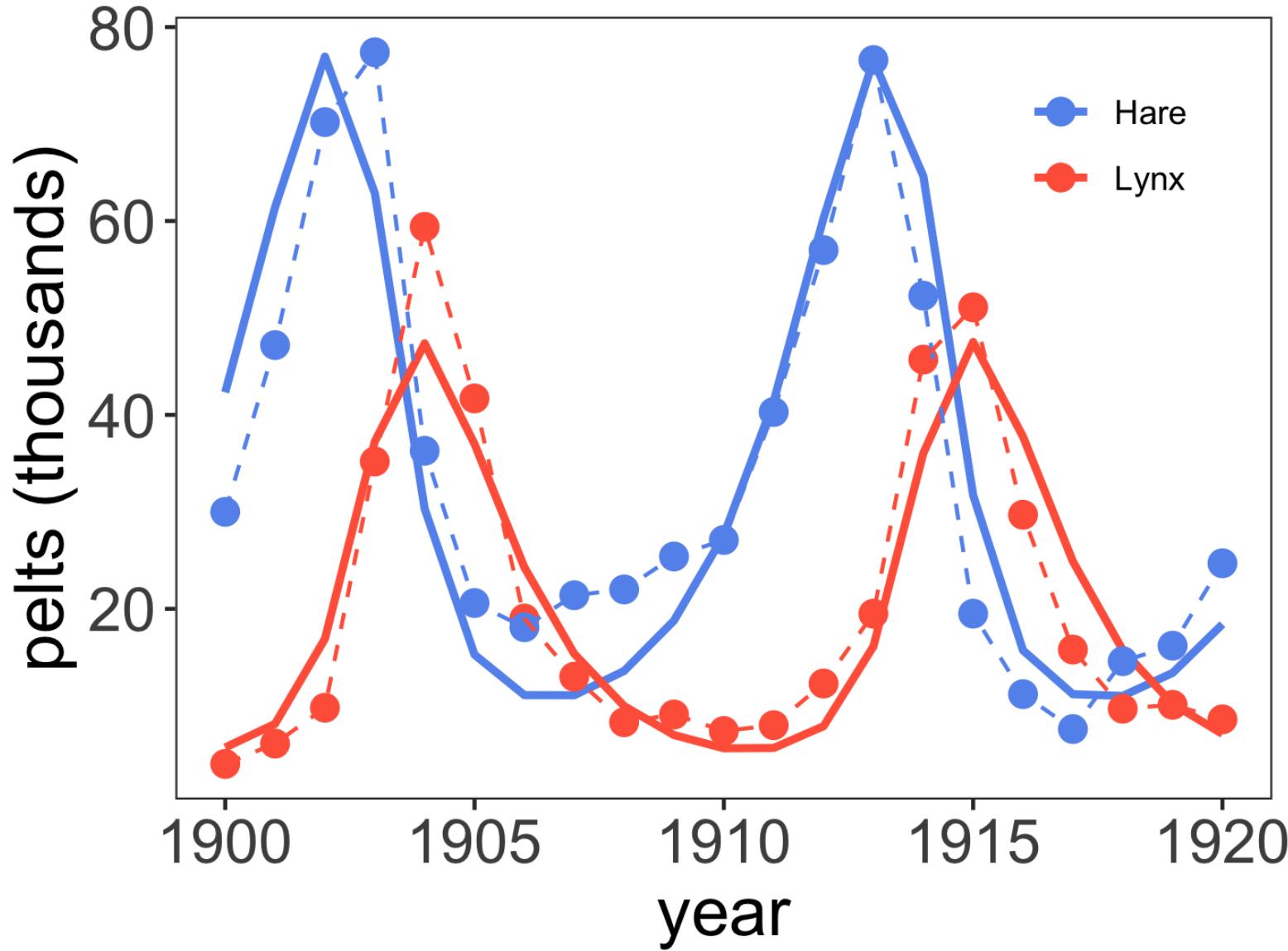
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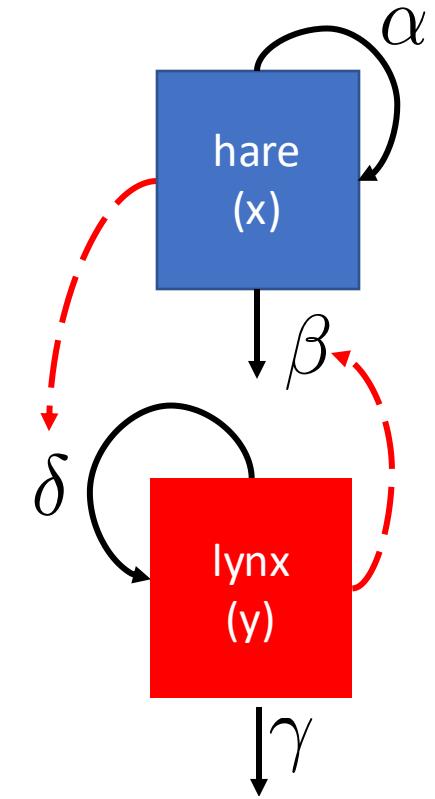
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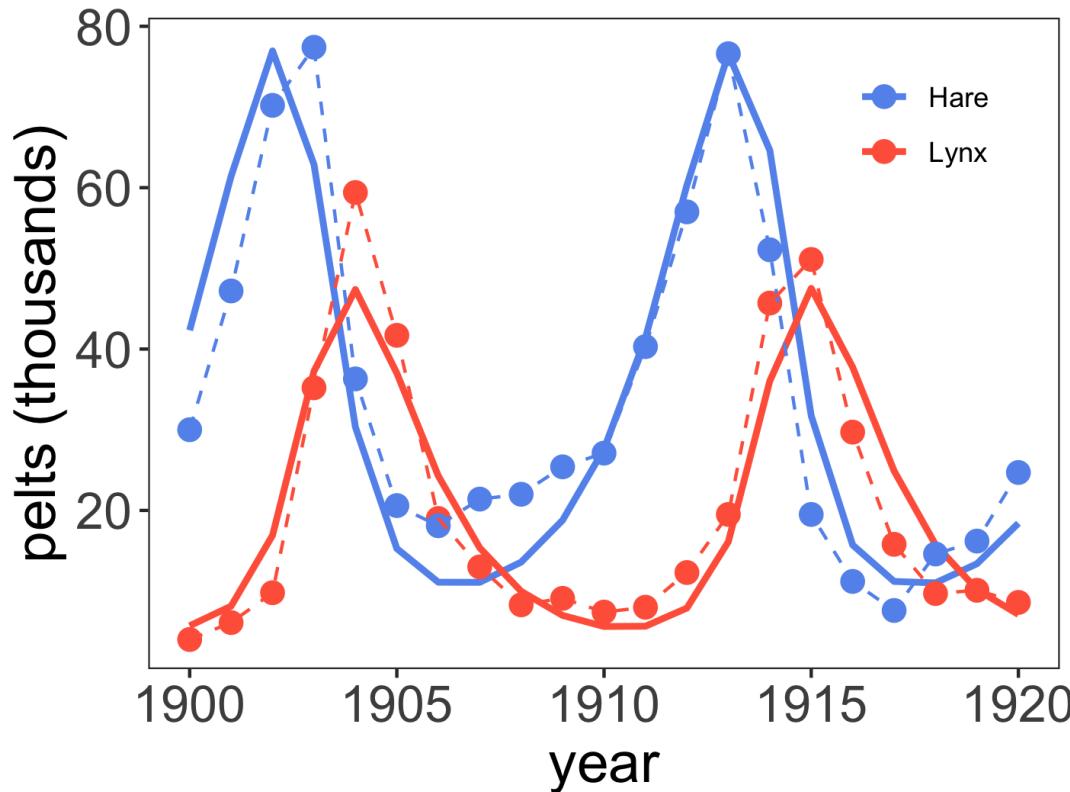
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Lotka-Volterra predator-prey models with data



How does **hare** abundance **vary** with changes in **lynx** abundance?



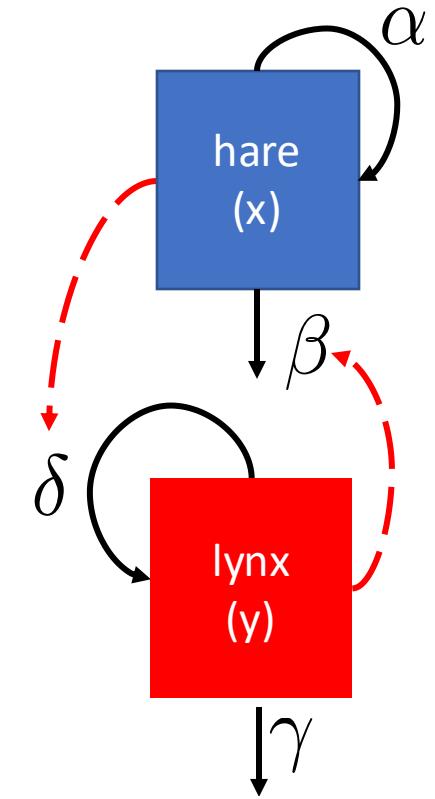
$$\frac{dx}{dt} = \alpha x - \beta xy$$

$$\frac{dy}{dt} = \delta xy - \gamma y$$

- Fitting a model to data allows us to estimate parameters – remember those growth rates from the human population models!
- Here, we can explore the growth rate of the prey under exponential growth (α), the efficiency of kill (β) and digestion (δ) by the predator, and the natural death rate of the predator (γ).

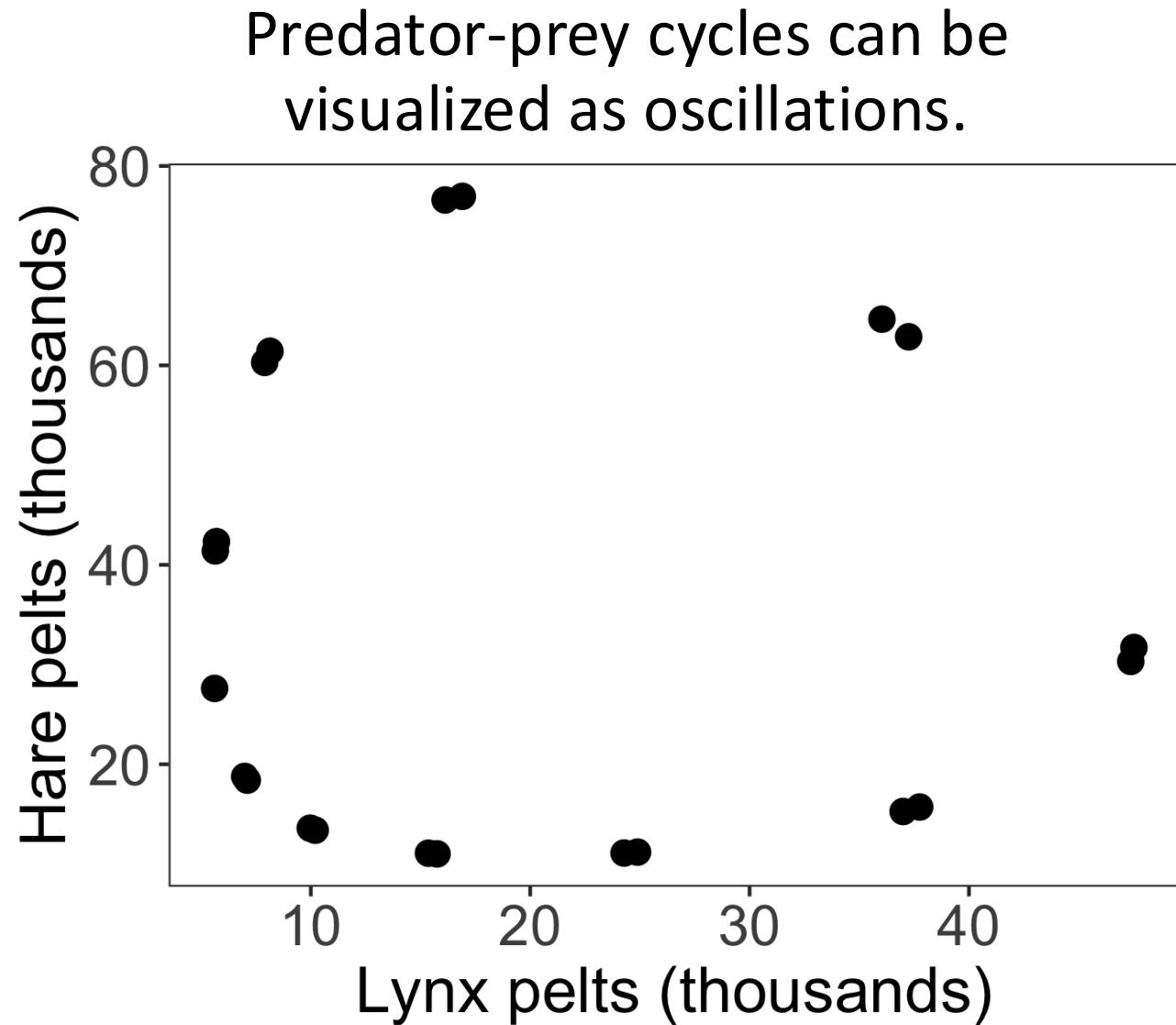
- $\alpha = .0897$ hare/year
- $\beta = .0000157$ hare/lynx/year
- $\delta = .0250$ lynx/hare/year
- $\gamma = .0174$ lynx /year

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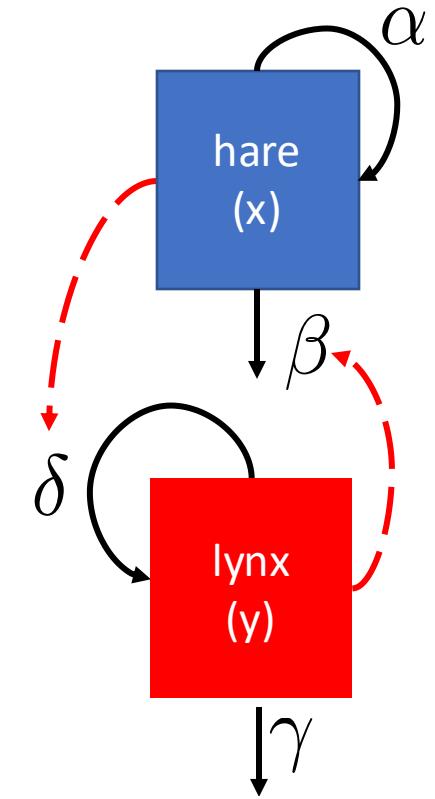


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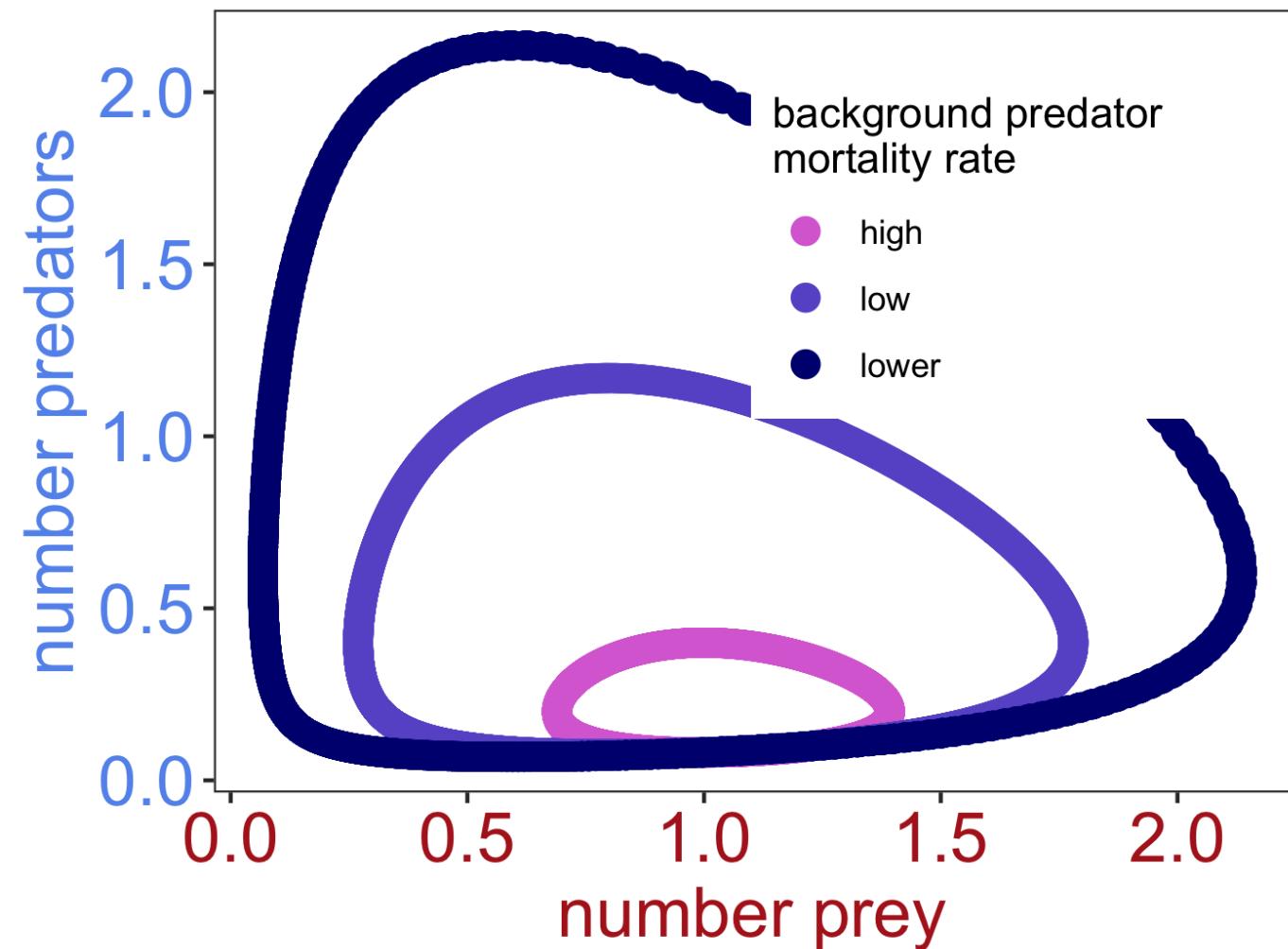


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Predator-prey cycles can be visualized as oscillations.



Supplemental

Derivation of the zero-growth isocline.

We express juvenile survival in terms of adult survival to establish zero-growth isoclines from demographic parameters:

$$\begin{bmatrix} \mathbf{N}_{t+1} \\ \mathbf{J} \\ \mathbf{A} \end{bmatrix}_{t+1} = \begin{bmatrix} 0 & s_A F_A \\ i s_A & s_A \end{bmatrix} \begin{bmatrix} \mathbf{N}_t \\ \mathbf{J} \\ \mathbf{A} \end{bmatrix}_t$$

(where:

s_A = adult annual survival

i = modifier for juvenile survival

F_A = adult annual fecundity)

Brook et al. 2018 *Conservation Biology*.

Brook et al. 2019 *Biological Conservation*.

Dobson and Lyles 1989 *Conservation Biology*.

Lyles and Dobson 1988 *Ecol & Behav Food-Enhanced Primates*.

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Now, recall that: $\mathbf{AN} = \lambda \mathbf{N}$

We can rearrange this as: $(\mathbf{A} - \lambda \mathbf{I})\mathbf{N} = 0$

And matrix algebra tells us that the above is only satisfied when:

$$\det(\mathbf{A} - \lambda \mathbf{I}) = 0$$

Eventually, we set $\det(A - \lambda I) = 0$ and solve for λ :

$$\det \begin{bmatrix} -\lambda & s_A F_A \\ is_A & s_A - \lambda \end{bmatrix} = 0$$

For a 2×2 matrix, recall that:

$$\det \begin{bmatrix} a & b \\ c & d \end{bmatrix} = ad - bc$$

which gives us:

$$\lambda^2 - \lambda s_A - is_A^2 F_A = 0$$

If we rearrange the characteristic equation:

In terms of λ :

$$\lambda^2 - \lambda s_A - i s_A^2 F_A = 0$$

$$\lambda = \frac{i s_A^2 F_A}{\lambda - s_A}$$

We can infer the following inequality
for a growing population ($\lambda > 1$):

$$i s_A^2 F_A > 1 - s_A$$

And compute the zero-growth isocline at:

$$i = \frac{1 - s_A}{F_A s_A^2}$$