Fundamentals of Ecology

Week 6, Ecology Lecture 3

Cara Brook

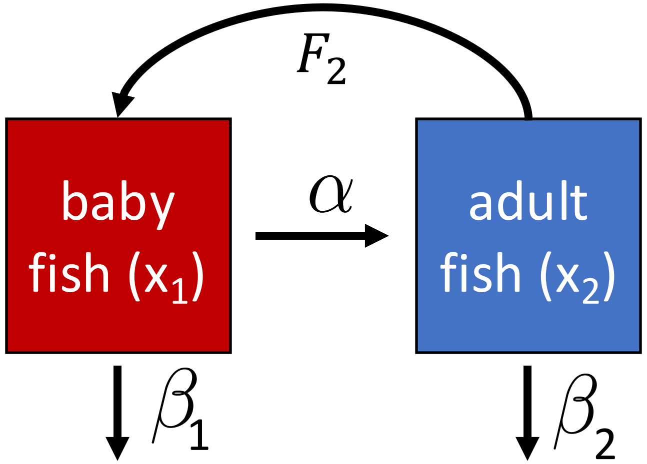
February 11, 2025

Learning objectives from Lecture 2

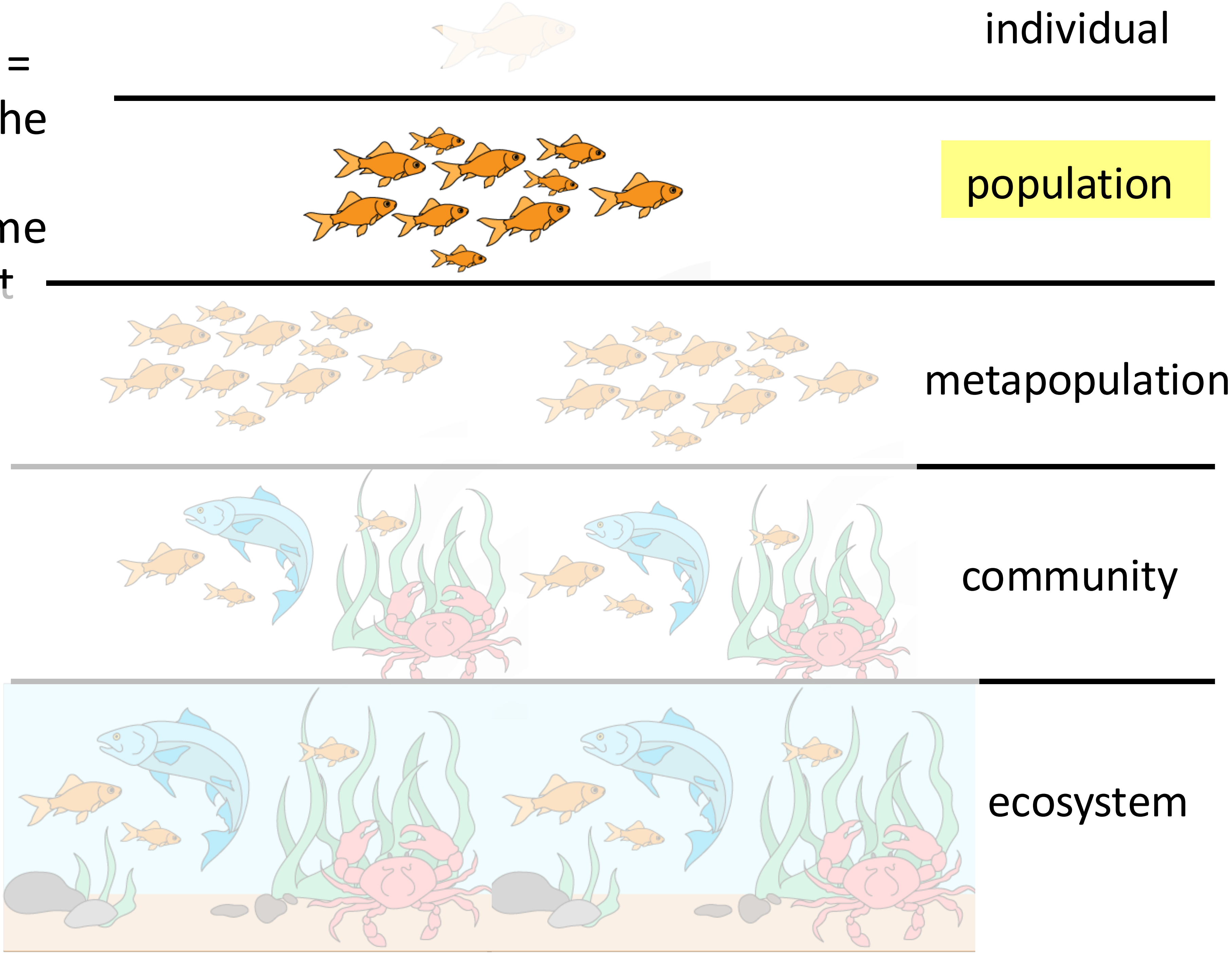
You should be able to:

- 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

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

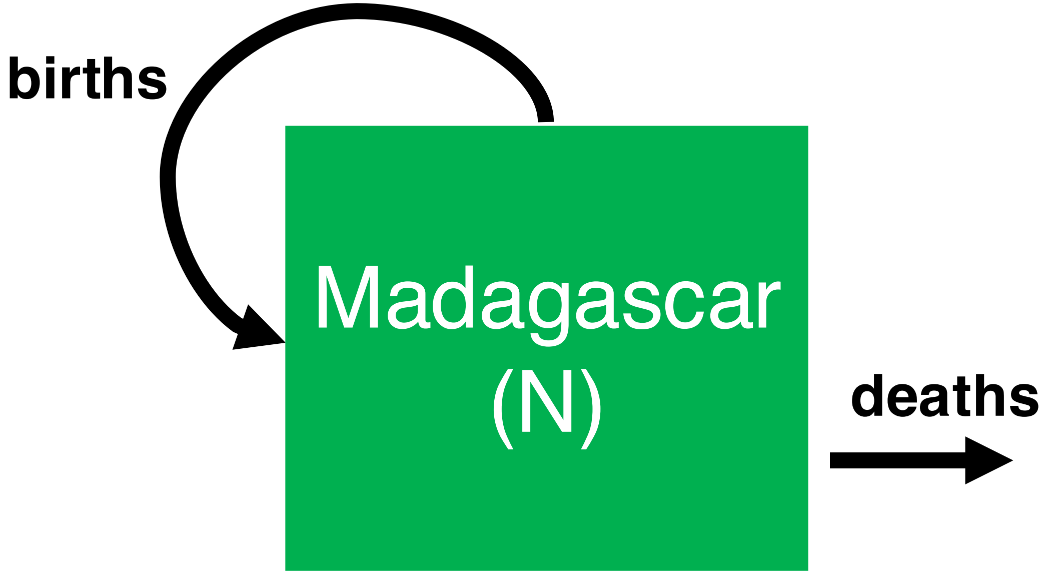


*How does the abundance of fish **change** through time?*



Modeling demographic complexity

1. Populations are divided into compartments
2. Individuals within a compartment are homogenously 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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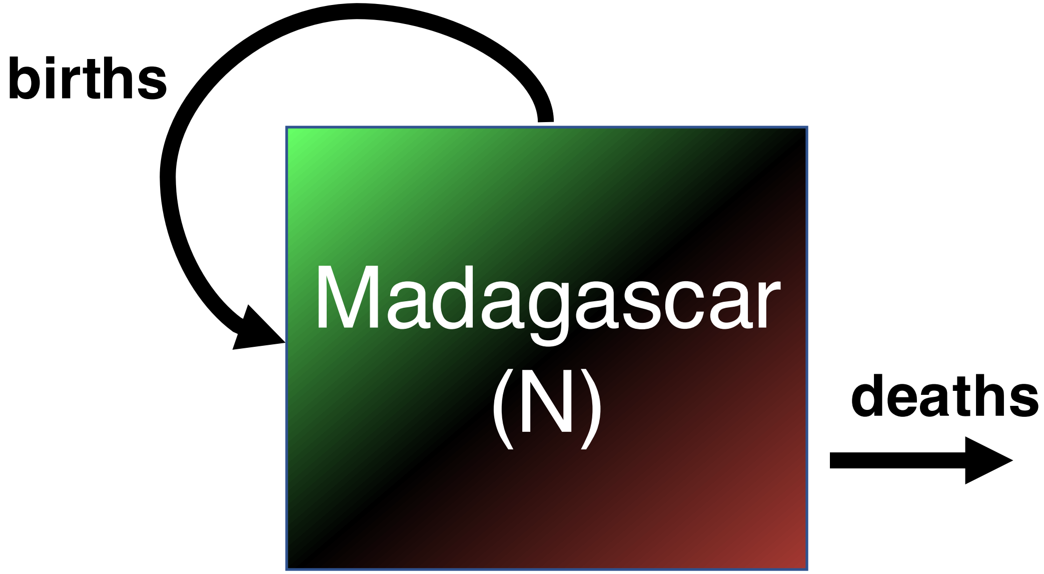

What is wrong about this model?

Modeling demographic complexity

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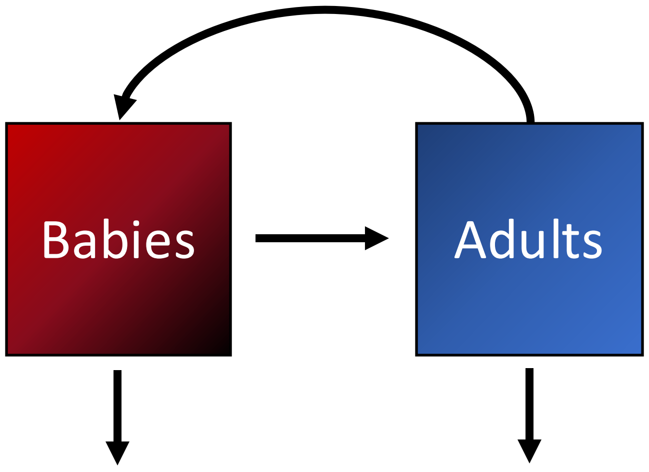

The structured population model

Modeling demographic complexity

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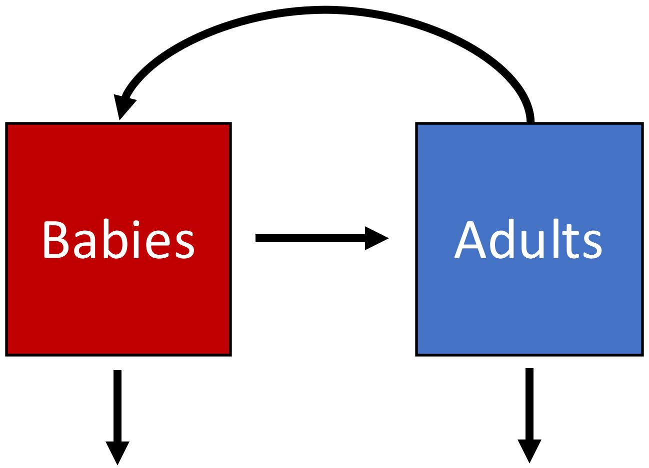

The structured population model

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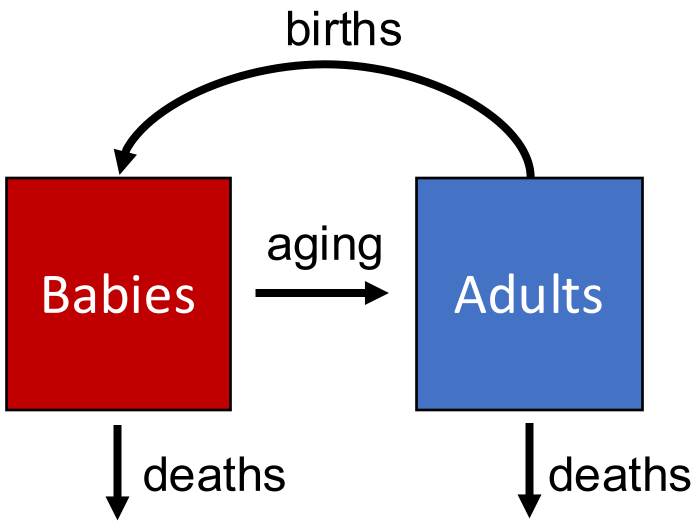


The structured population model

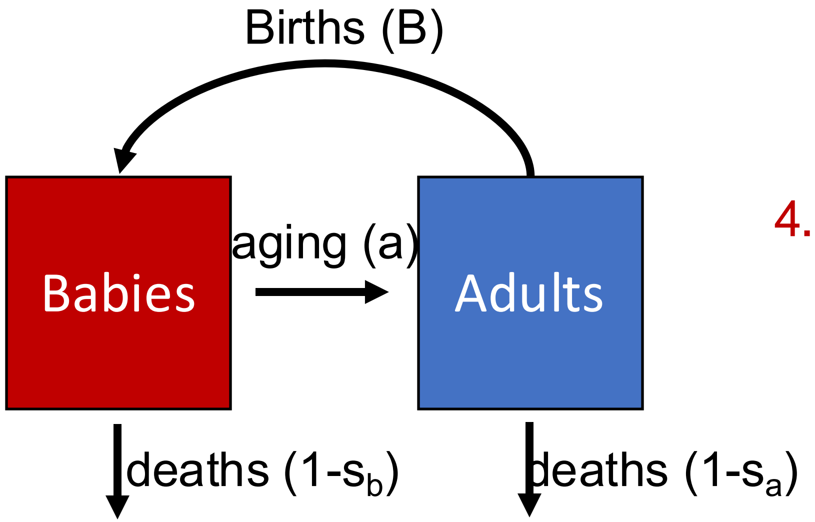
The structured population model

Population rate of increase

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

pop size at t

pop size at t + 1



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

matrix of survival and fecundity rates

vector of population sizes

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

***Discrete time**

The structured population model

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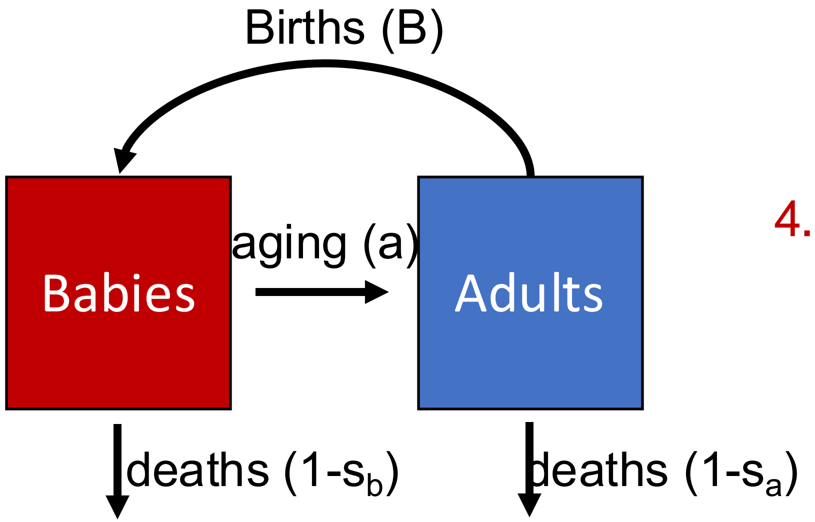


$$N_{t+1} = A^* \, N_t$$

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

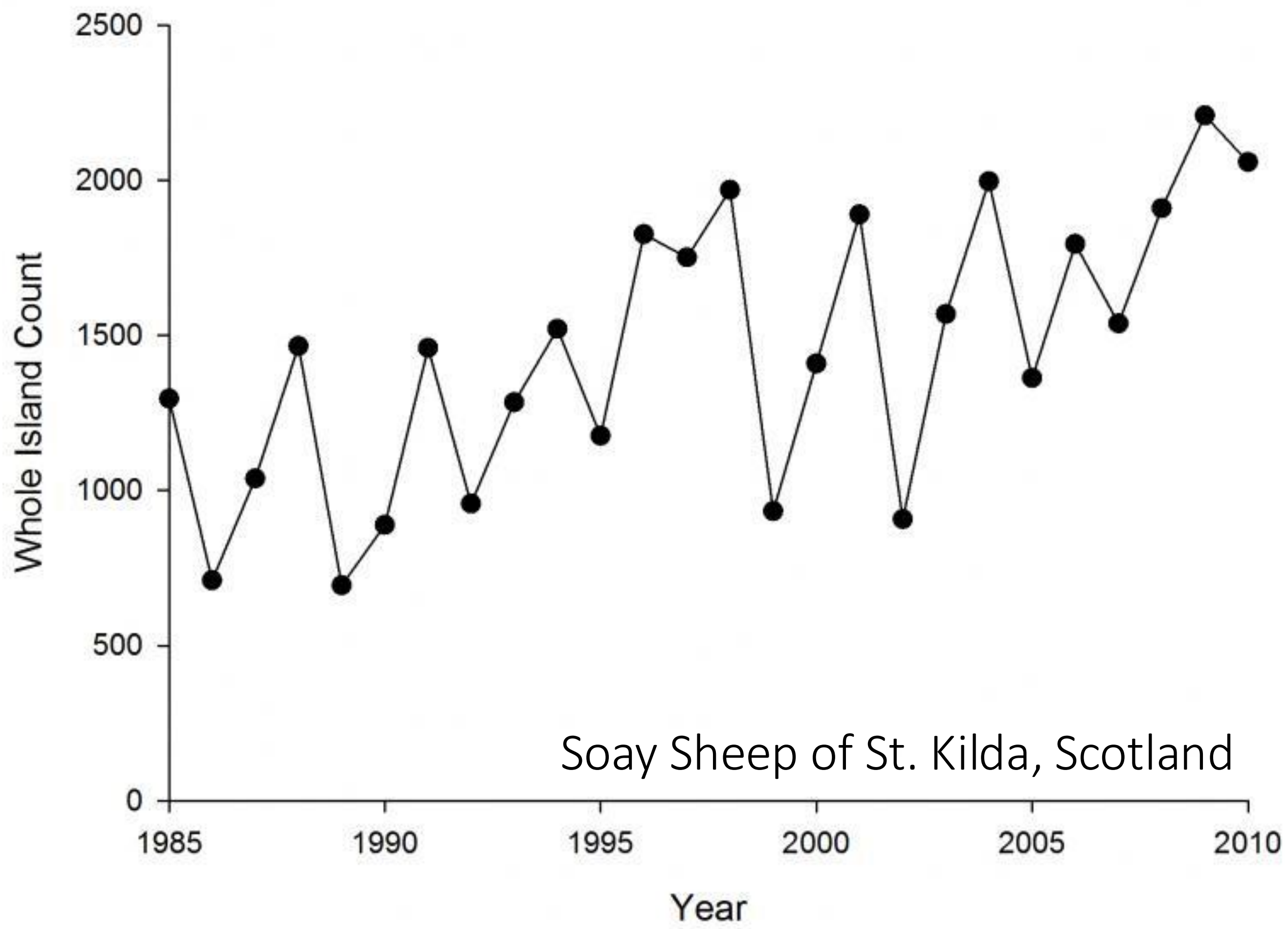
λ

$$\underset{\mathbf{A}}{\begin{bmatrix} s_b(1-a) & B \\ s_b a & s_a \end{bmatrix}} \times \underset{\mathbf{N_t}}{\begin{bmatrix} N_b \\ N_a \end{bmatrix}} = \underset{\mathbf{N_{t+1}}}{\begin{bmatrix} s_b(1-a)\, N_b + BN_a \\ s_b\, a\, N_b + s_a N_a \end{bmatrix}}$$

Population growth will depend on population structure!

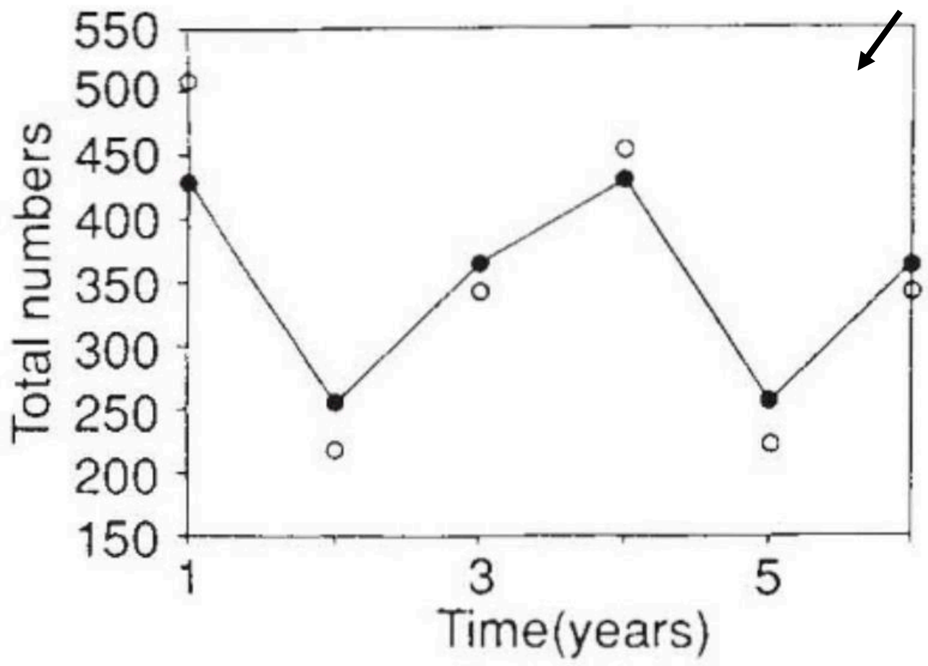
(pop grows @ $\lambda > 1$ & declines @ $\lambda < 1$)

Structured populations in practice



Soay Sheep of St. Kilda, Scotland

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

Structured populations in practice

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

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

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

population at t+1

average fecundity

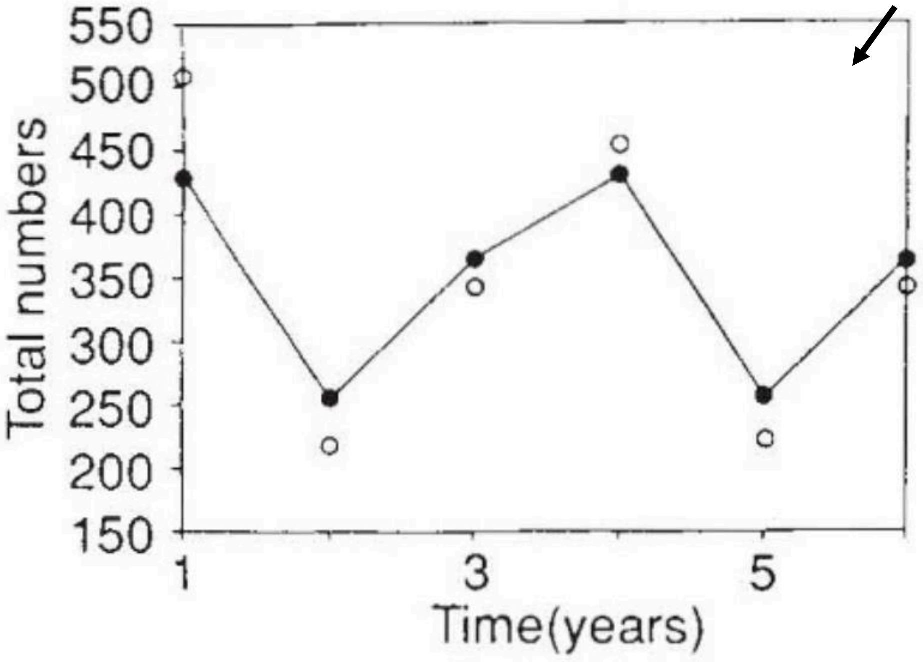
growth rate

population at t

Similar to the simple logistic growth equation!

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

Model compared against data



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Structured populations in practice

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

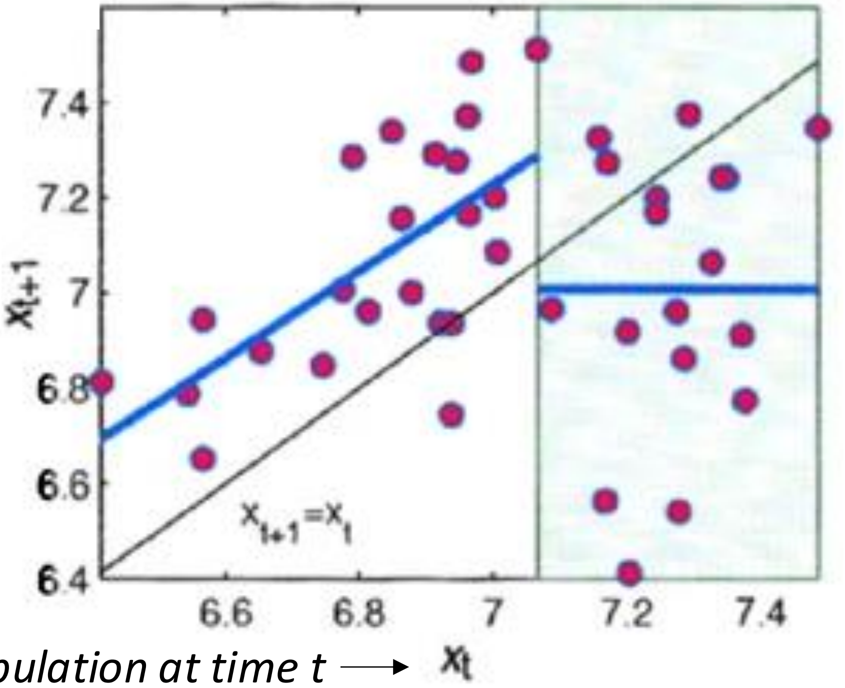
Noise and determinism in synchronized sheep dynamics

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

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

sheep population at time t+1



sheep population at time t

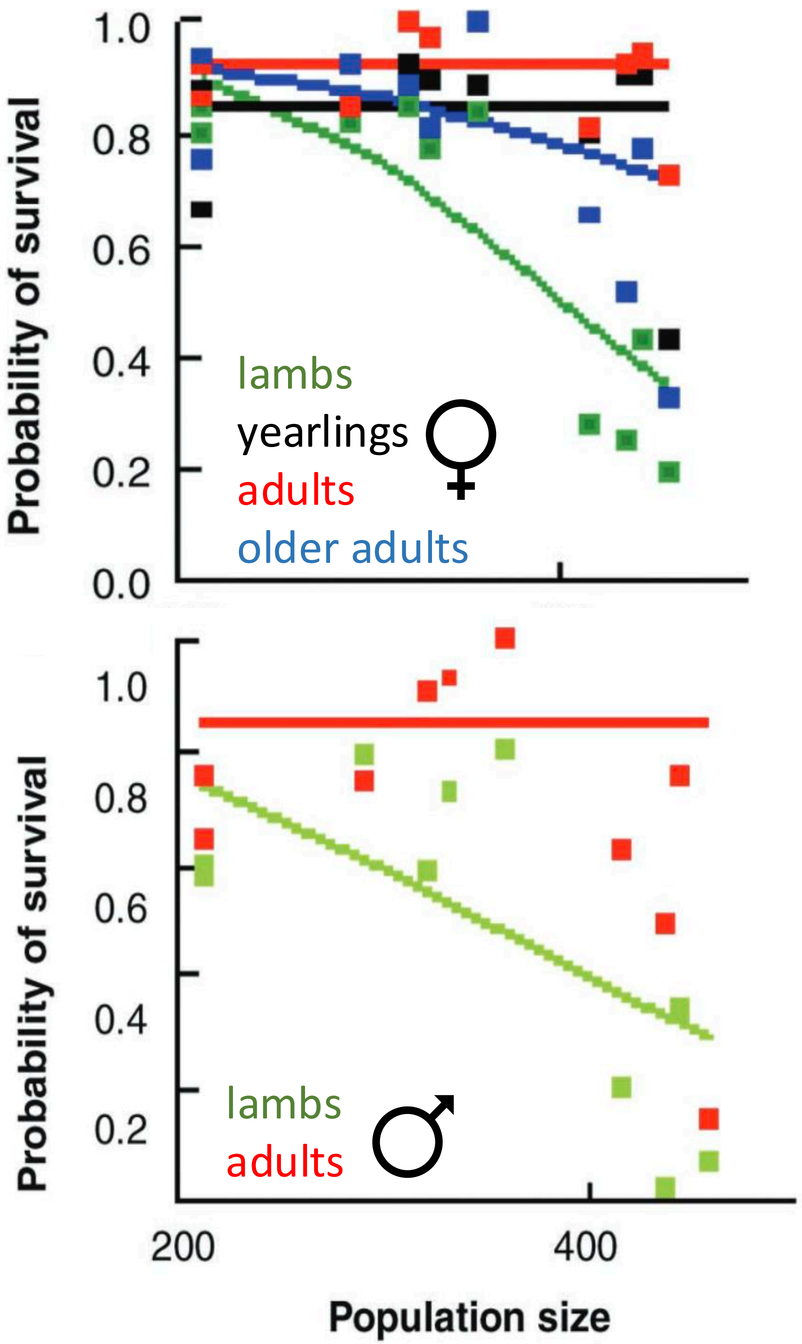
Structured populations in practice

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

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

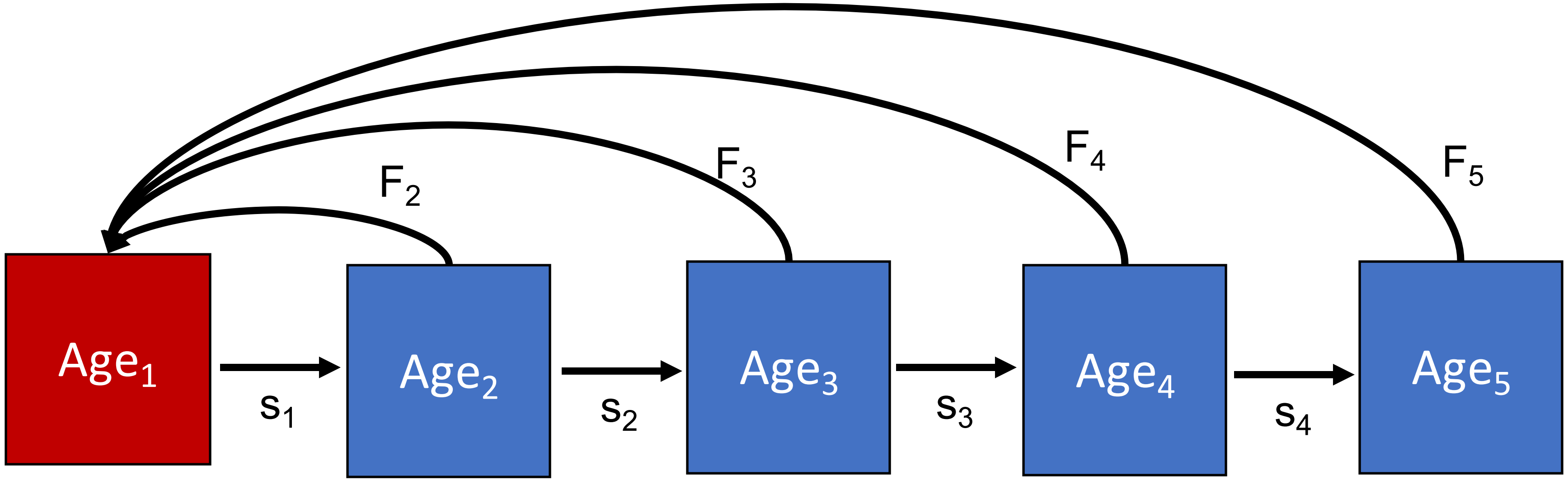
T. Coulson,[1*†] E. A. Catchpole,[2] S. D. Albon,[3] B. J. T. Morgan,[4] J. M. Pemberton,[5] T. H. Clutton-Brock,[6] M. J. Crawley,[6] B. T. Grenfell[7]

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.

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

The structured population model

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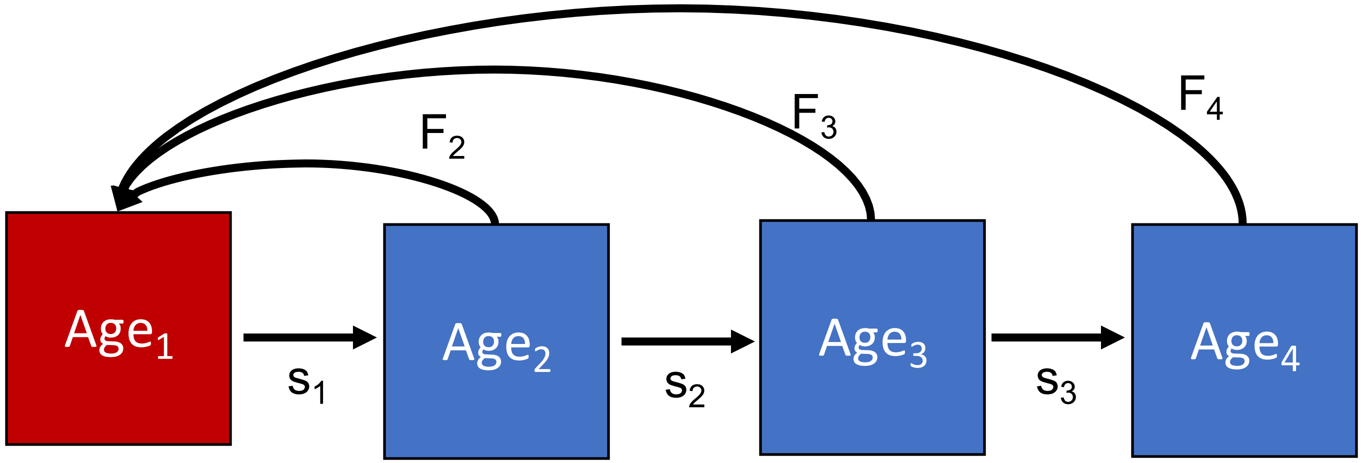


λ=can be derived from transition matrix →

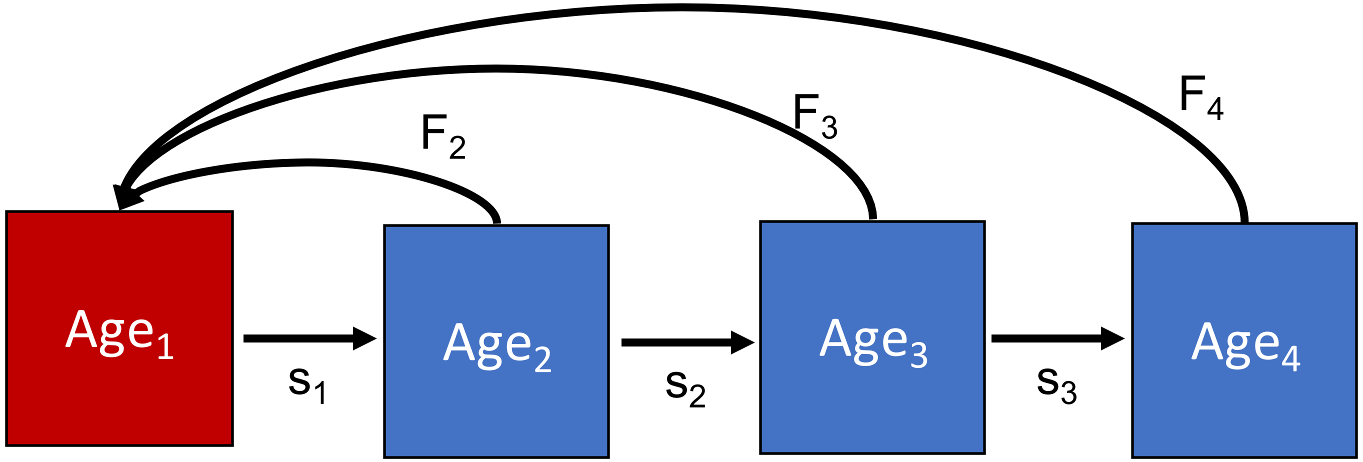
$$\mathbf{A} \quad \mathbf{N_t} \quad \mathbf{N_{t+1}}$$

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

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

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

The structured population model

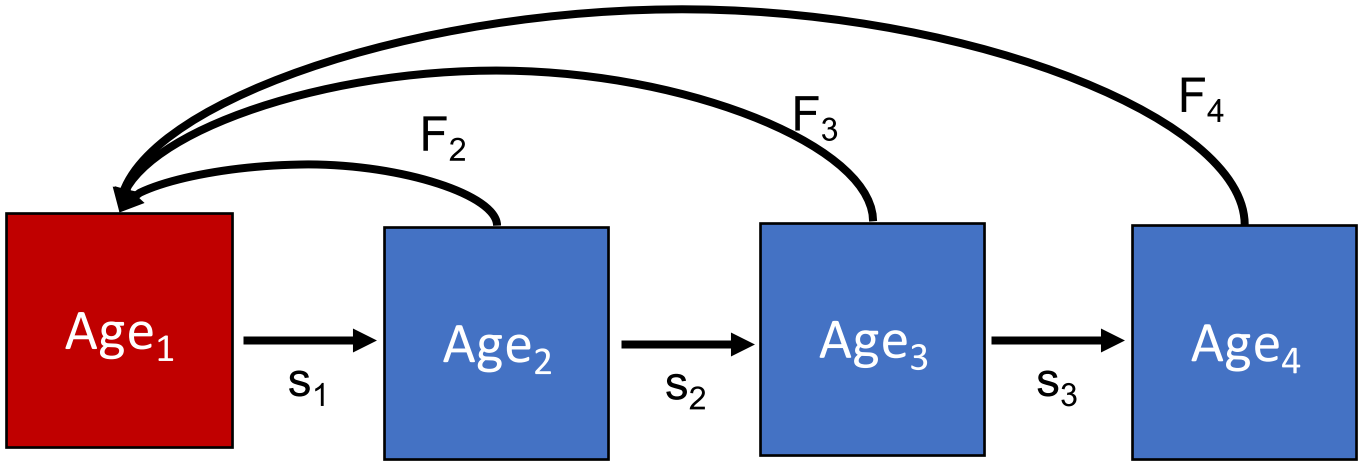


Demographers collect these rates in life tables

x (age)	N_x (number in cohort)	l_x (survivorship to age x)	m_x (fecundity)	$l_x m_x$
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



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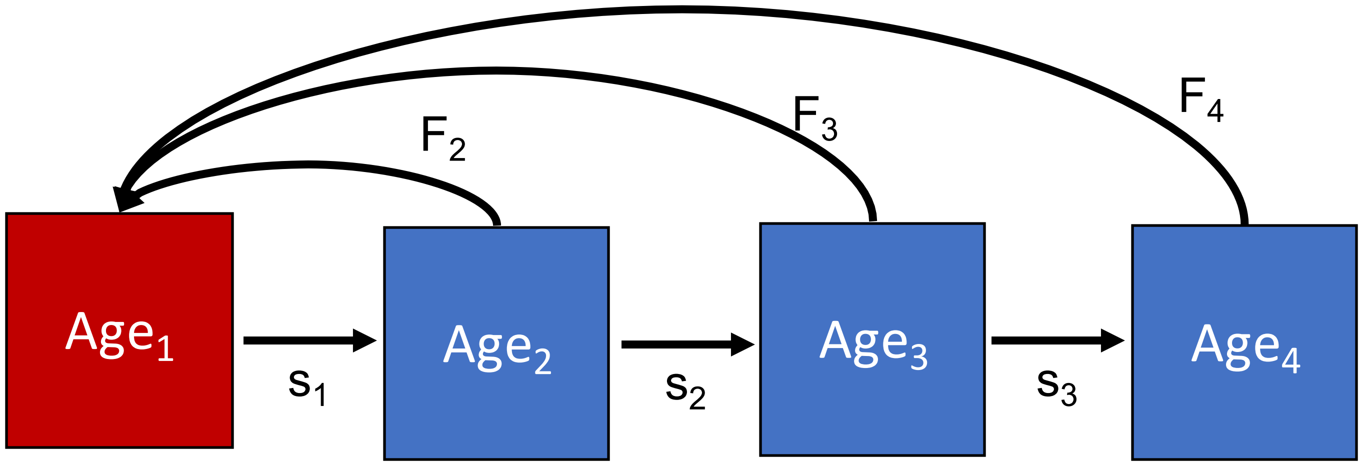
Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

The structured population model



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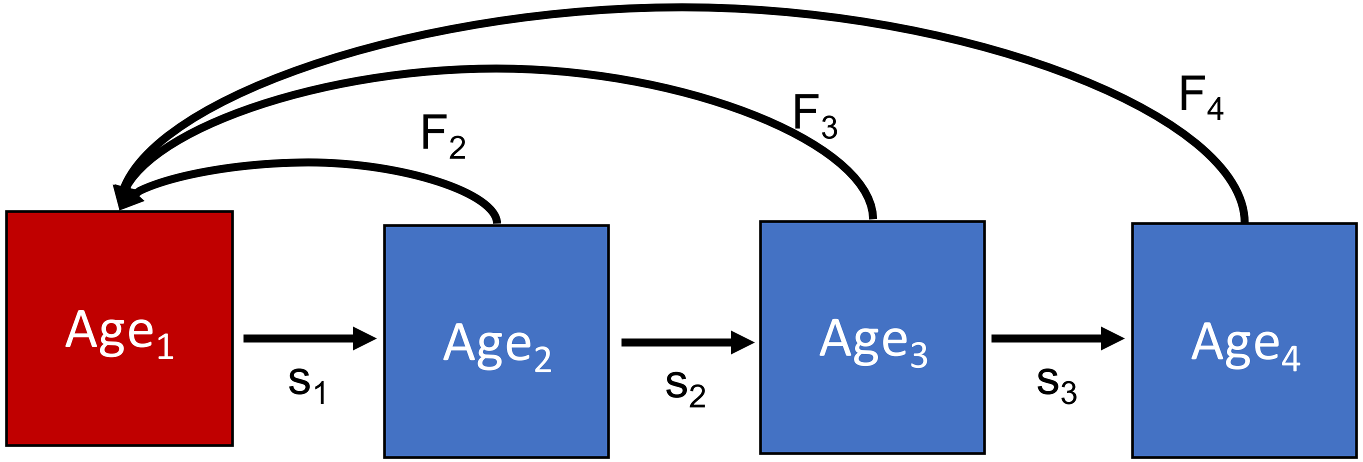
(pop grows at $\boldsymbol{R_0}$ >1 and declines at $\boldsymbol{R_0} < 1$)

The structured population model



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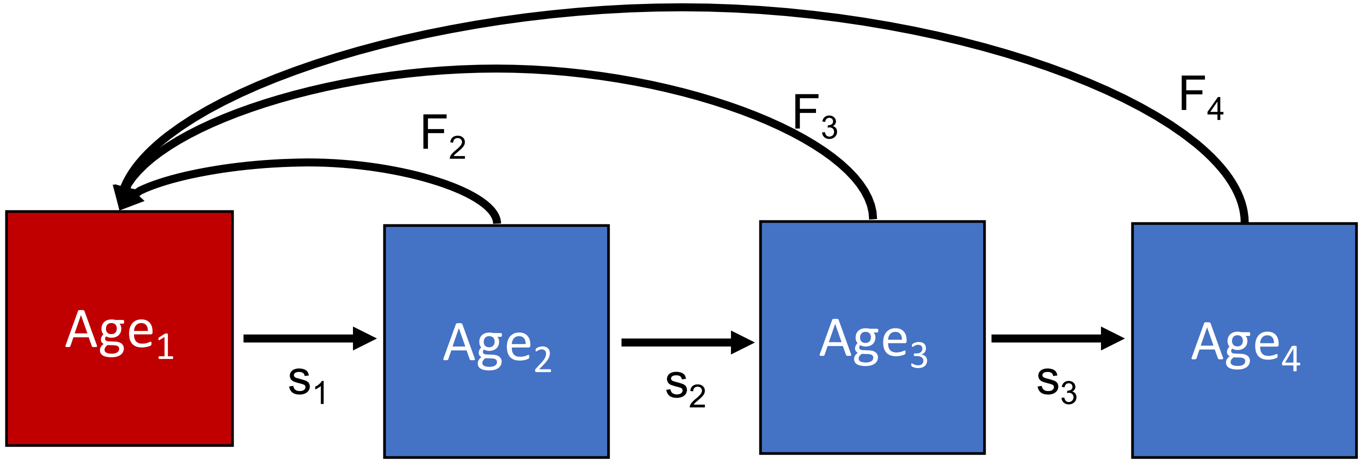
Net reproductive rate (R_0): $\sum l_x m_x = 2.21$

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

The structured population model



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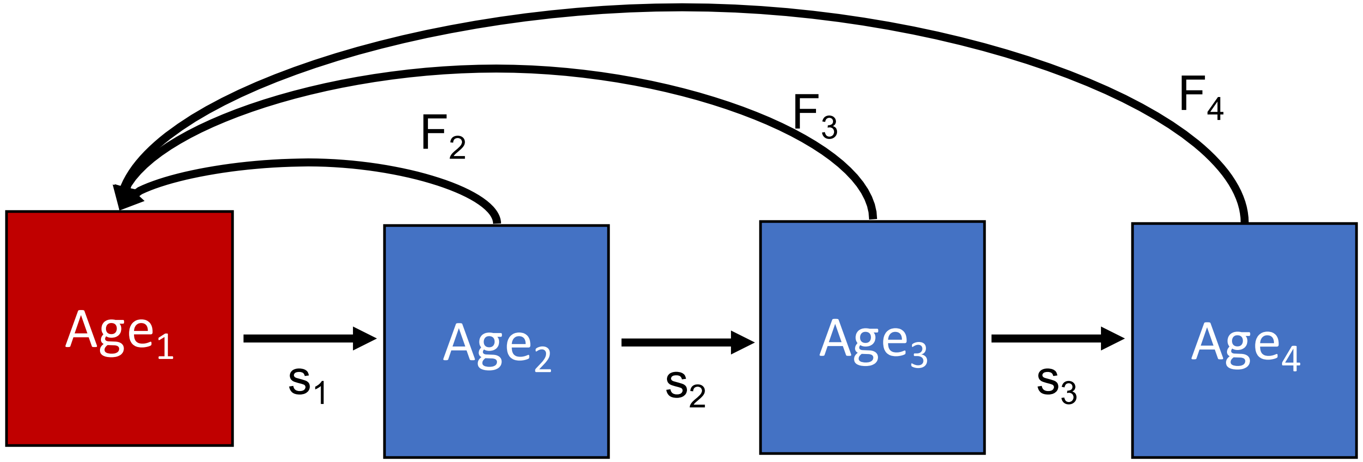
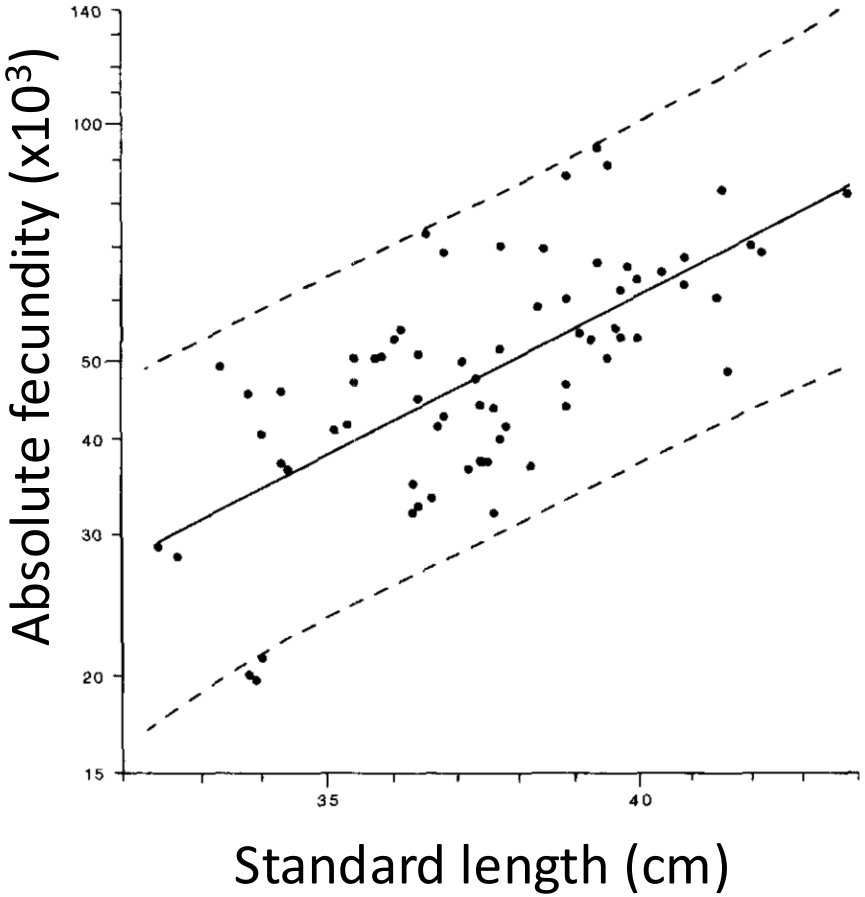
⋮

Orange roughy can live up to 200 years!

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

The structured population model



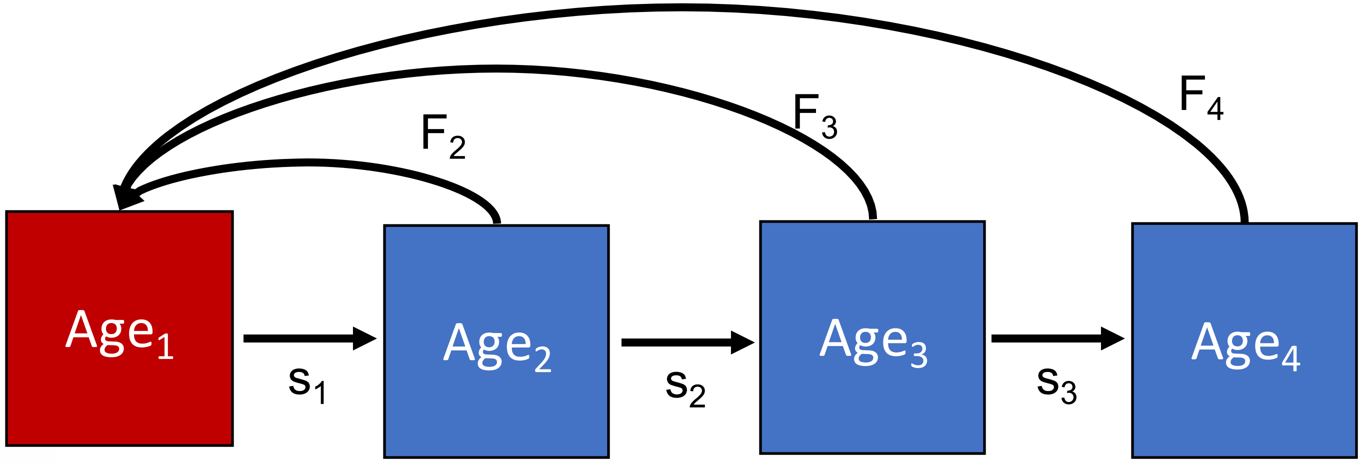


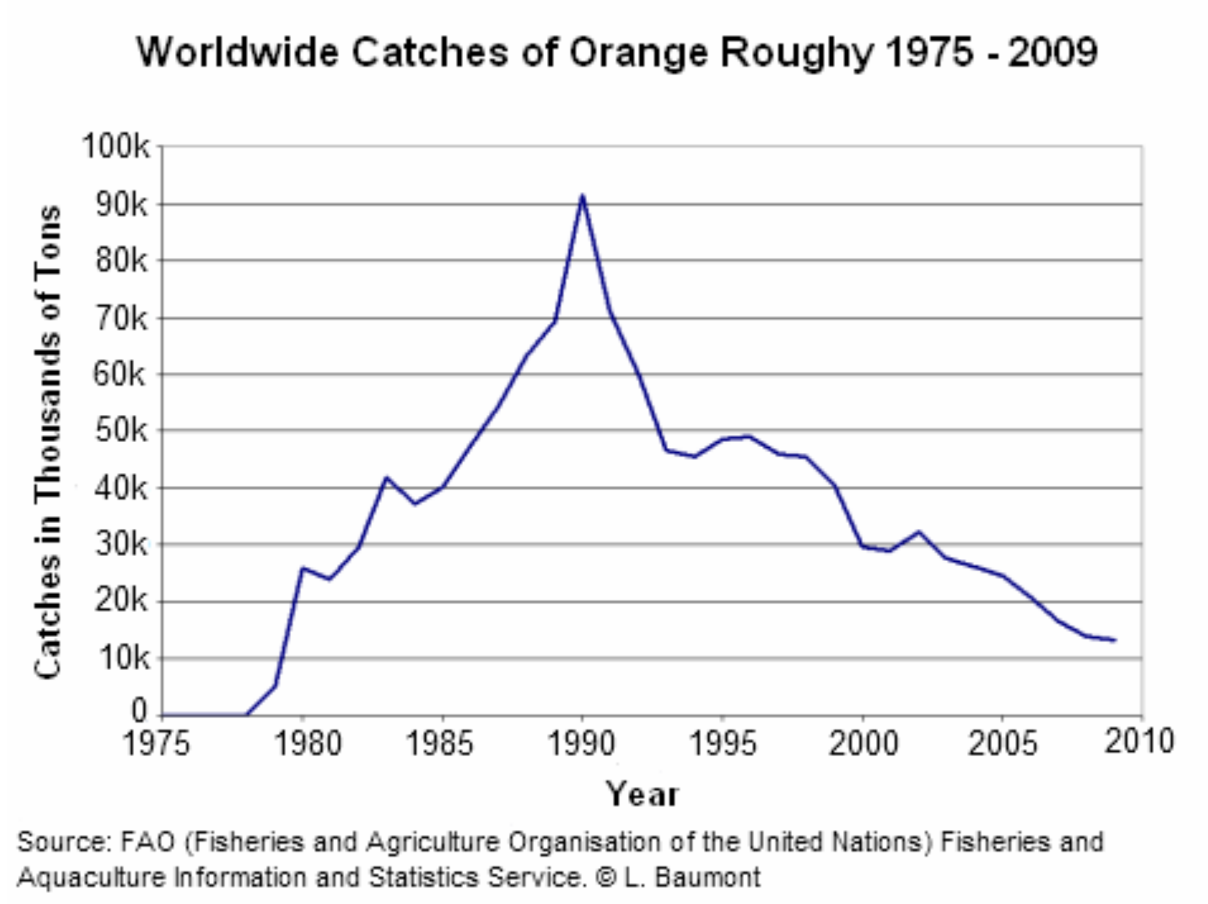
Fecundity (eggs) increases in older, bigger fish!

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

Norway 1910
(Norsk folkemuseum)

The structured population model

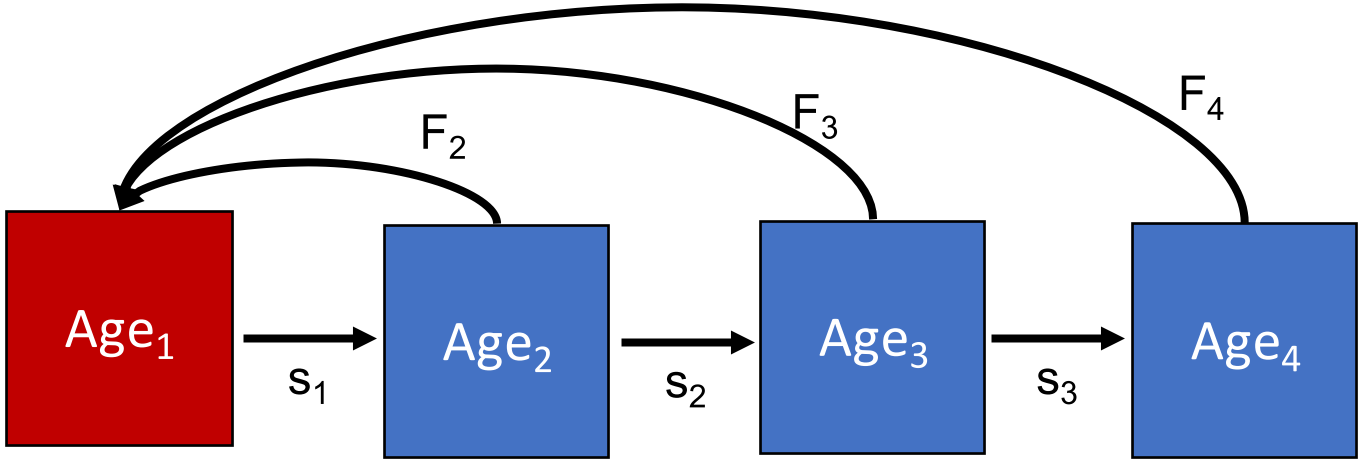




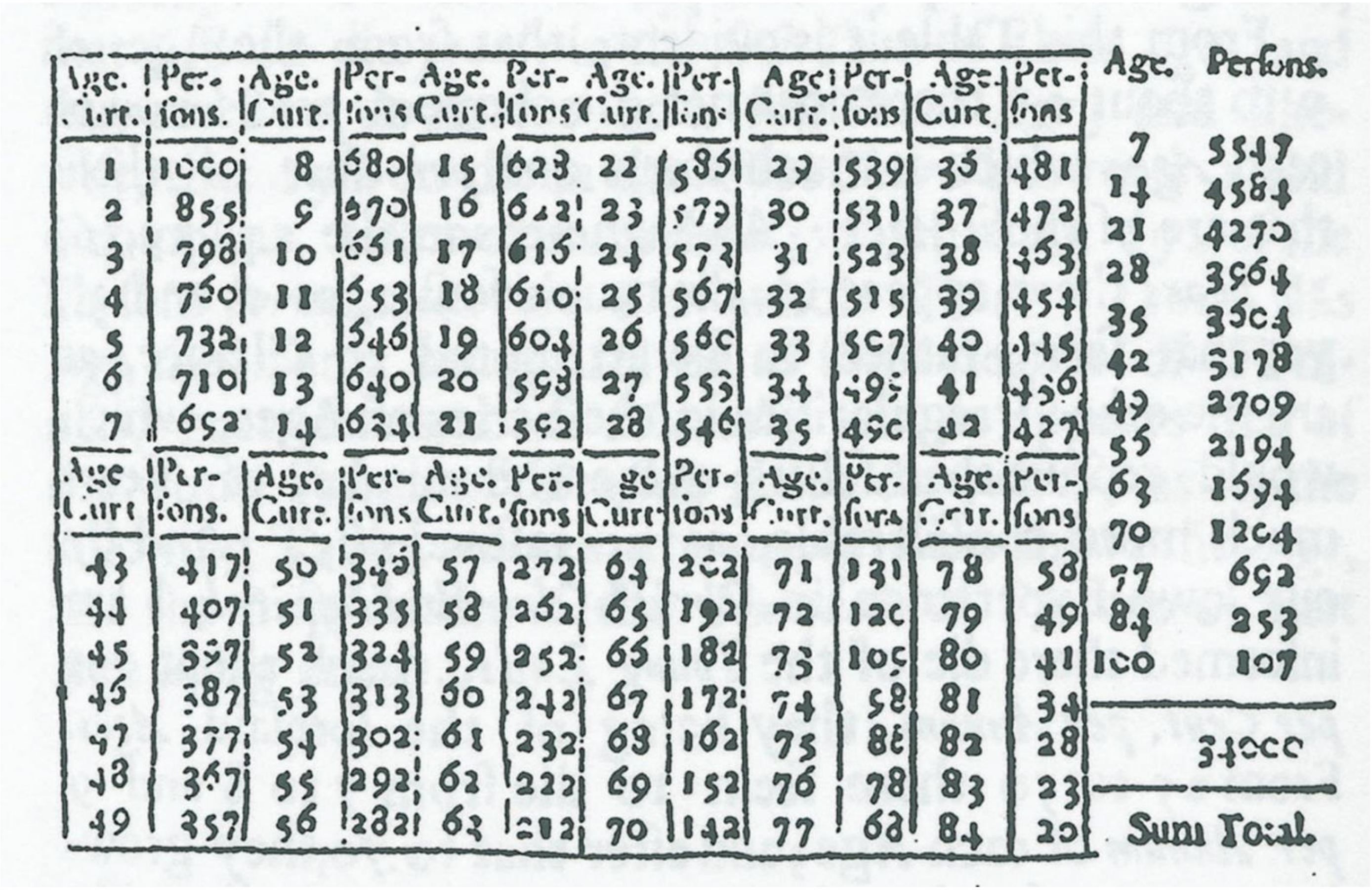
Poor modeling projections has led to severe overexploitation, a common problem in fisheries…

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**.



Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons
1	1000	8	680	15	628	22	586	29	539	36	481
2	855	9	670	16	622	23	579	30	531	37	472
3	798	10	661	17	616	24	573	31	523	38	463
4	760	11	653	18	610	25	567	32	515	39	454
5	732	12	646	19	604	26	560	33	507	40	445
6	710	13	640	20	598	27	553	34	499	41	436
7	692	14	634	21	592	28	546	35	490	42	427

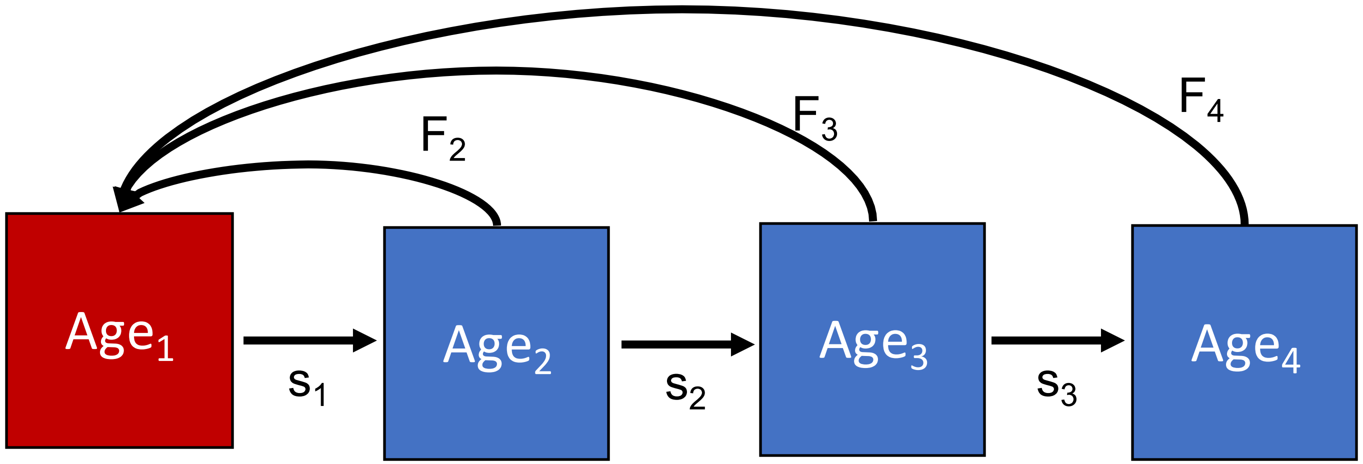
Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons	Age Curt.	Persons
43	417	50	346	57	272	64	202	71	131	78	58
44	407	51	335	58	262	65	192	72	120	79	49
45	397	52	324	59	252	66	182	73	109	80	41
46	387	53	313	60	242	67	172	74	98	81	34
47	377	54	302	61	232	68	162	75	88	82	28
48	367	55	292	62	222	69	152	76	78	83	23
49	357	56	282	63	212	70	142	77	68	84	20

Age.	Persons.
7	5547
14	4584
21	4270
28	3964
35	3604
42	3178
49	2709
56	2194
63	1694
70	1204
77	692
84	253
100	107
	34000
	Sum Total.

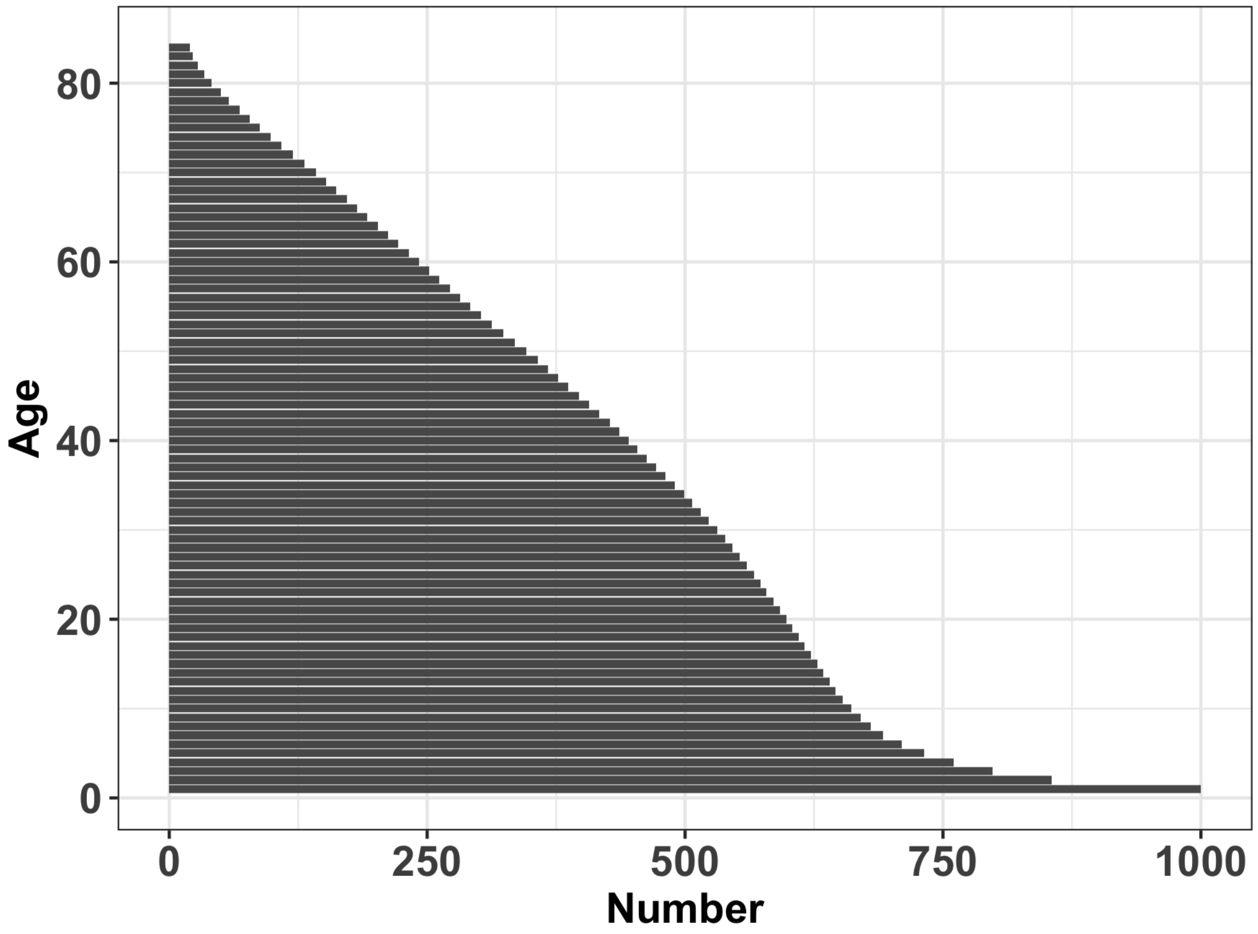
Edmond Halley, 1693

"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



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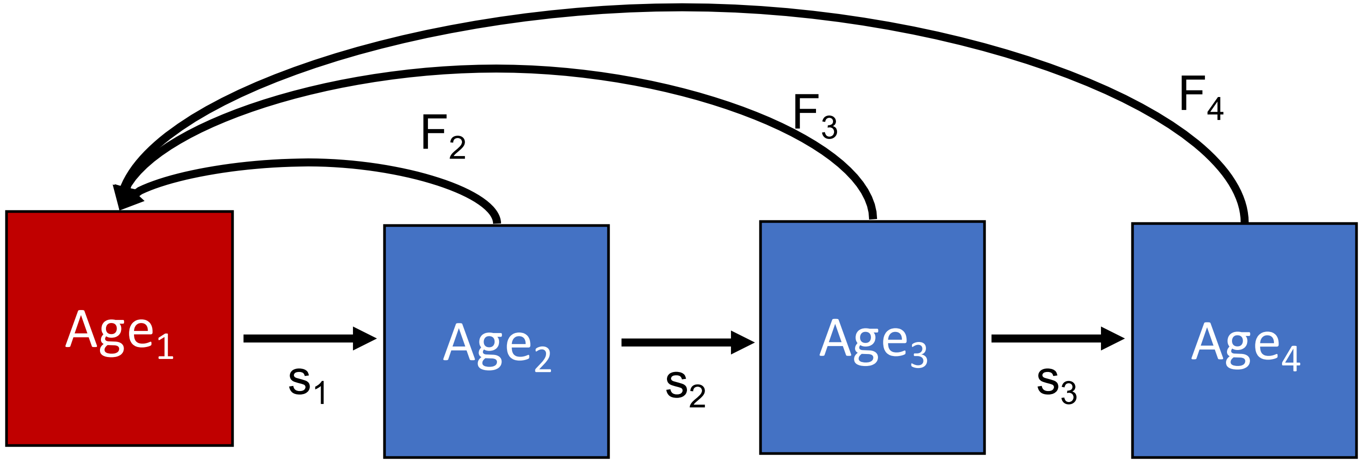
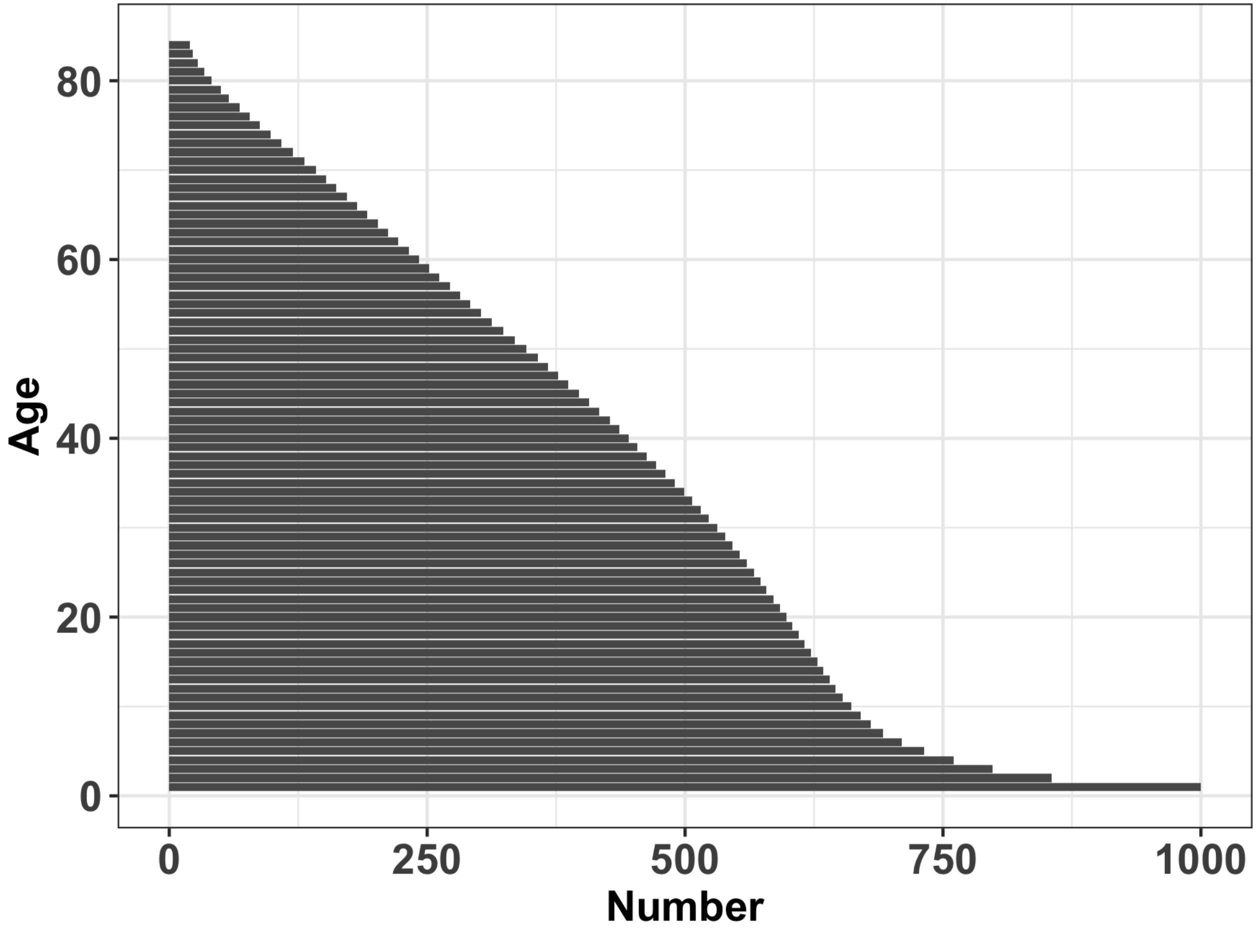


Population pyramid for Breslau

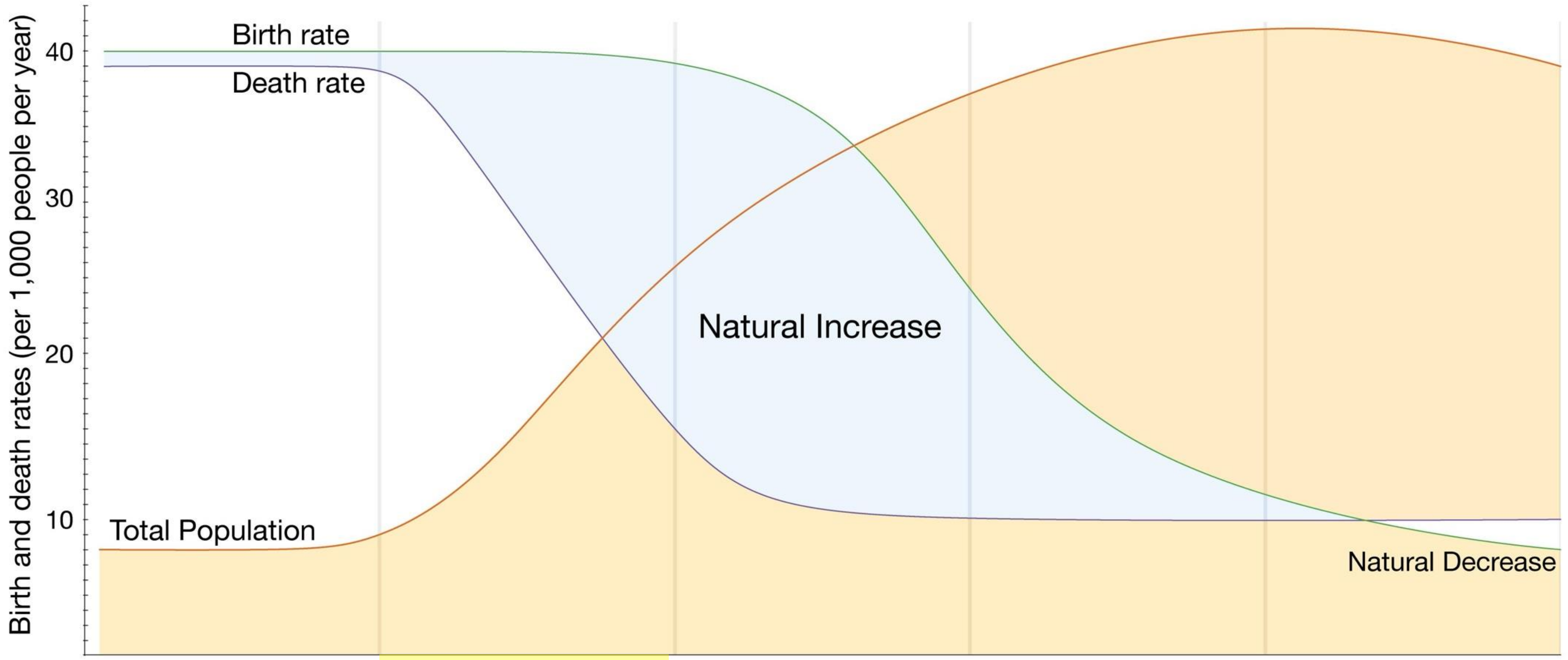


Humans are not like fish!
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

Younger human populations that start <u>giving birth earlier</u> grow faster!

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

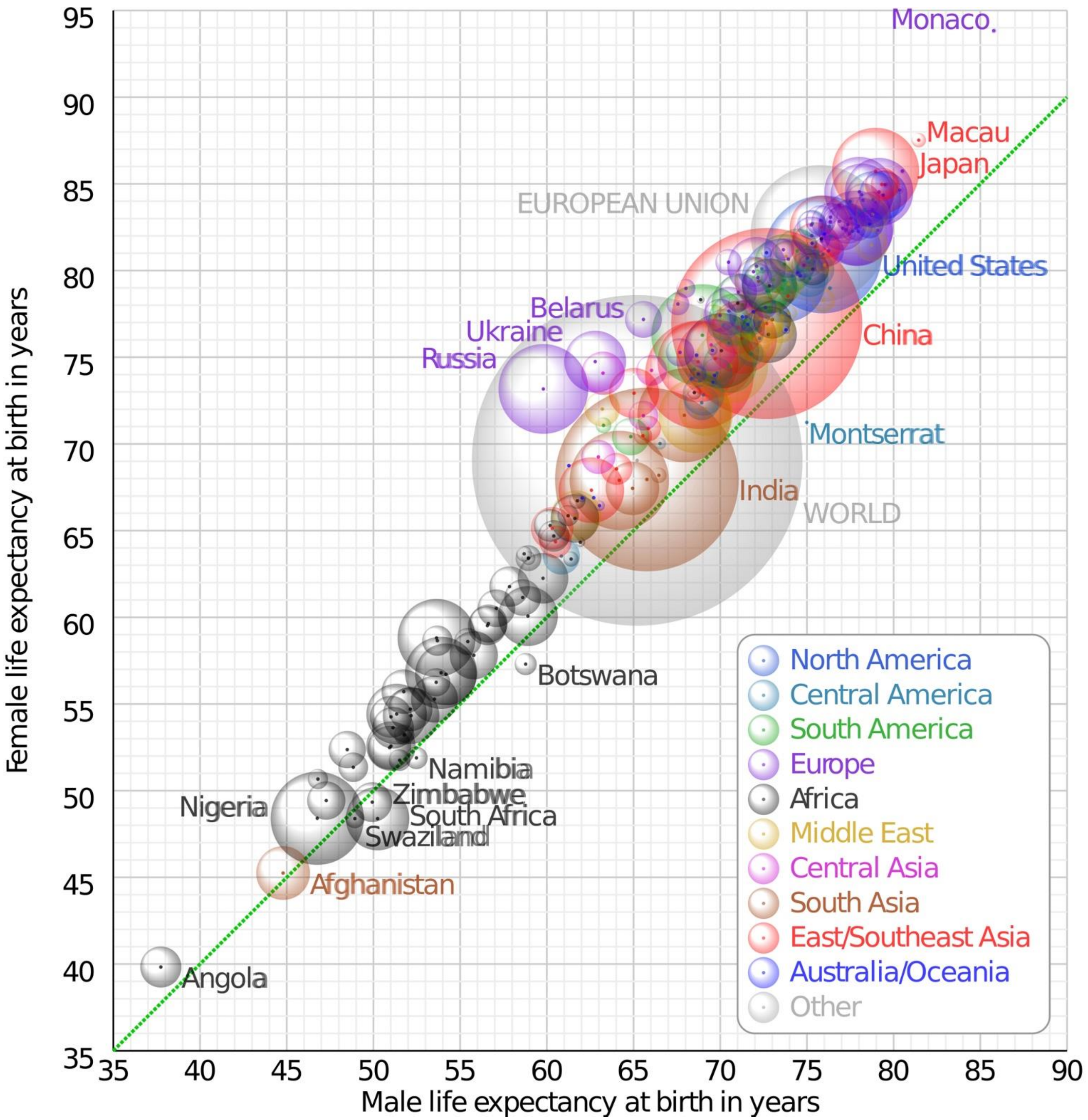
Demographic transition



	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*

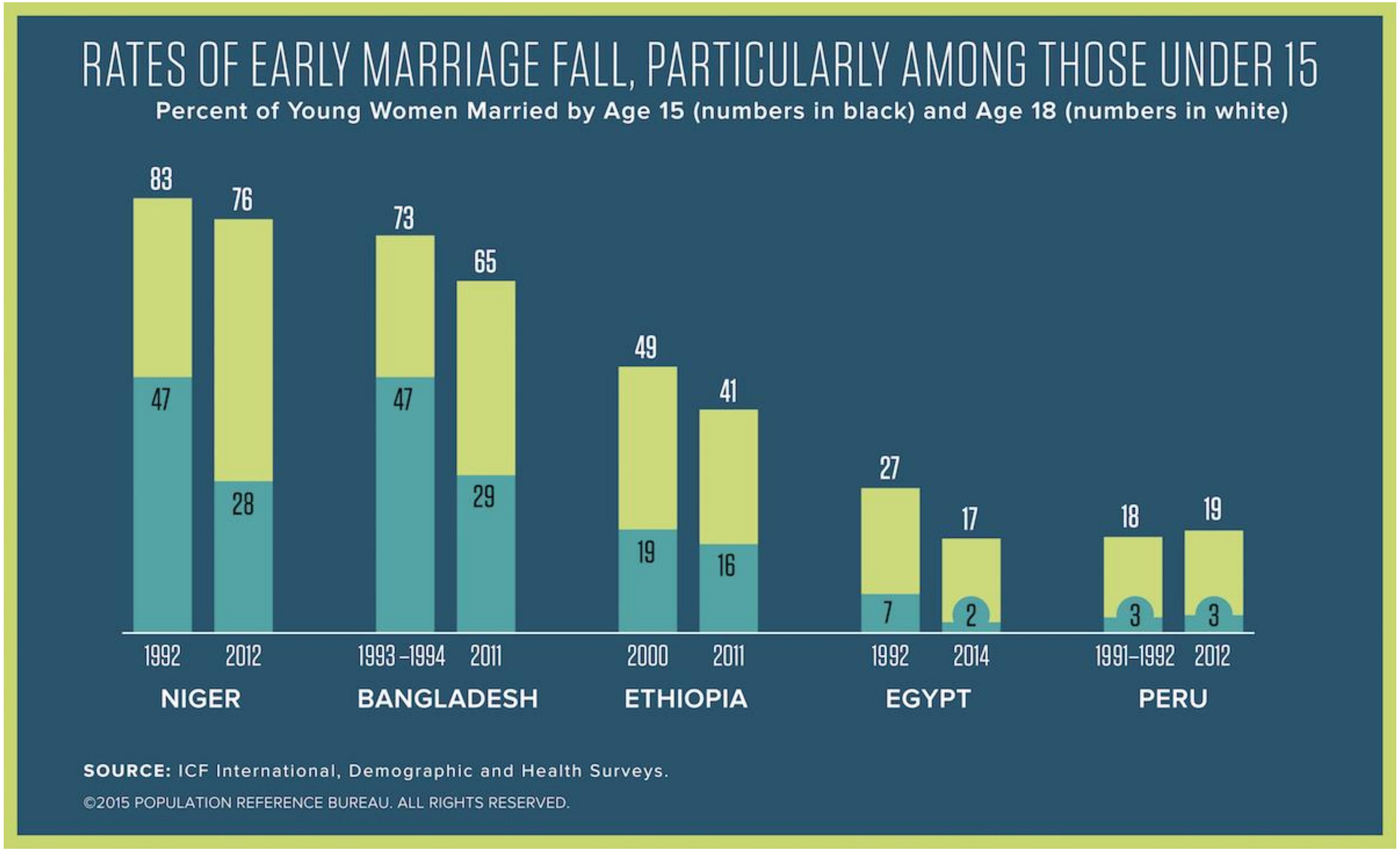
Demographic transition

Death rates are falling globally…

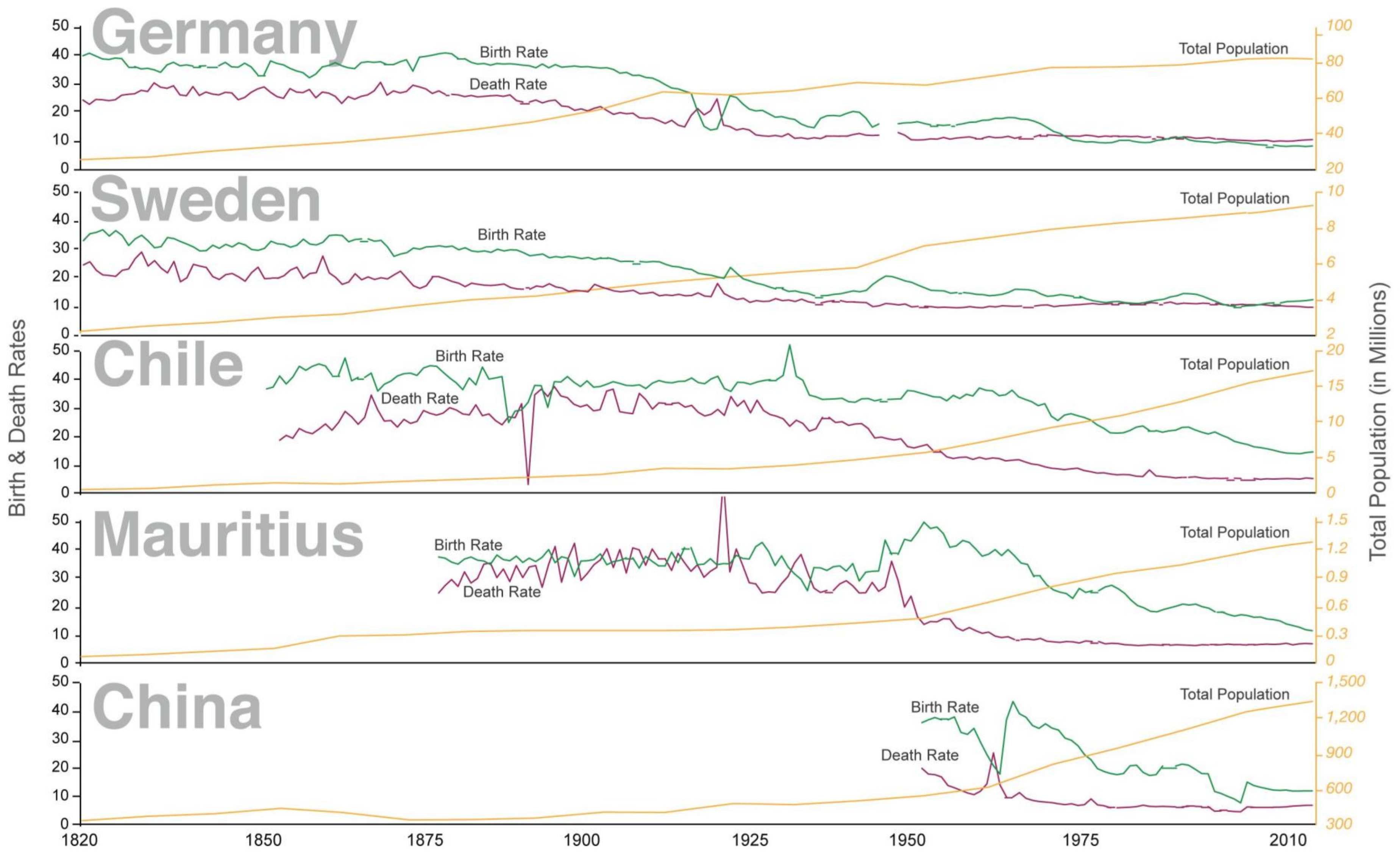


Demographic transition

And birth rates are also falling…



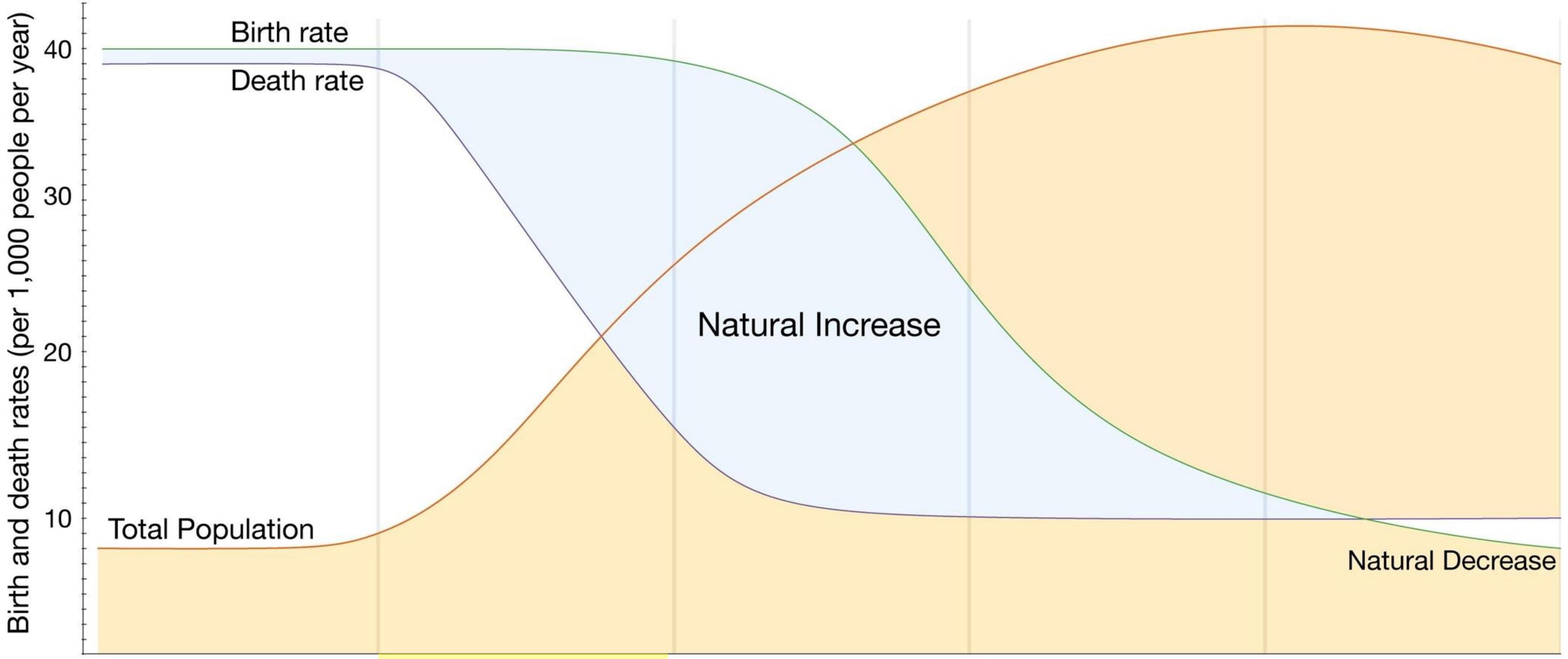
Demographic transition



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.

Demographic transition

How does age structure predict population growth?



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Demographic transition

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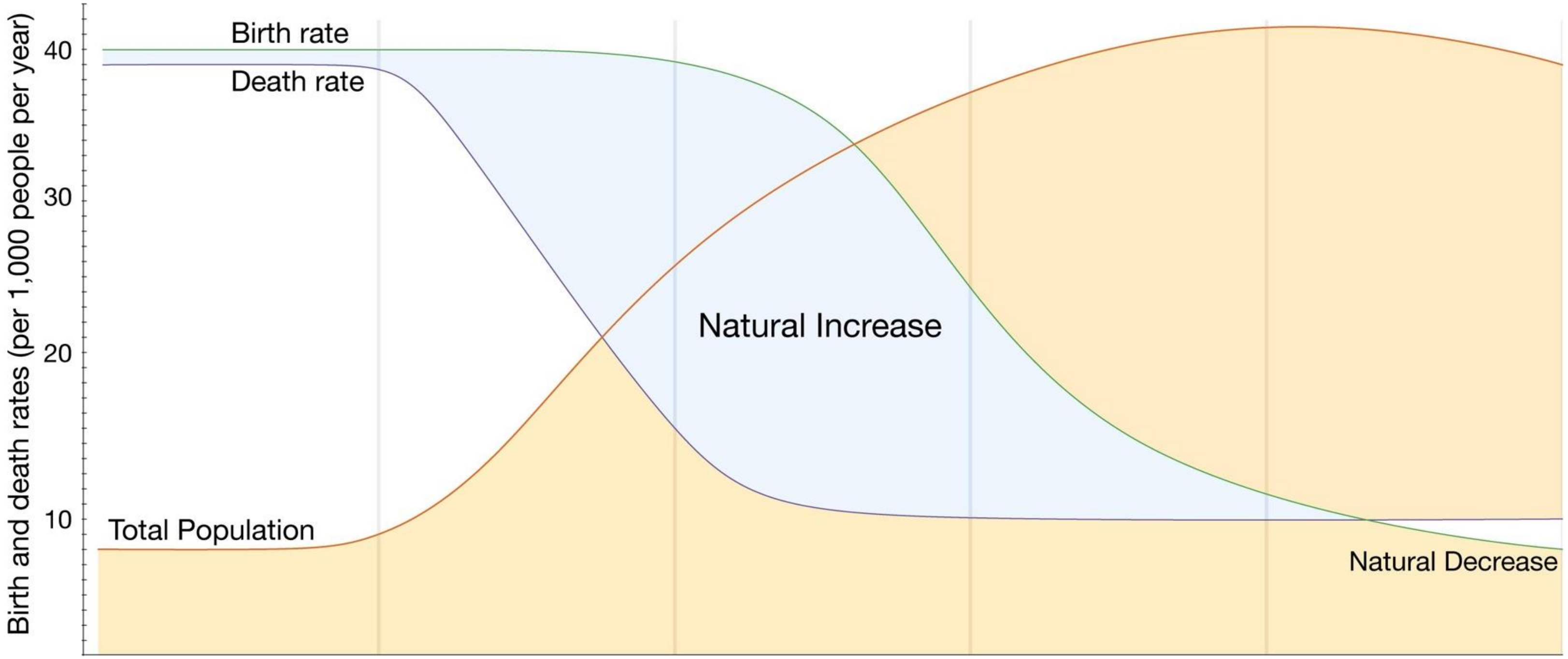

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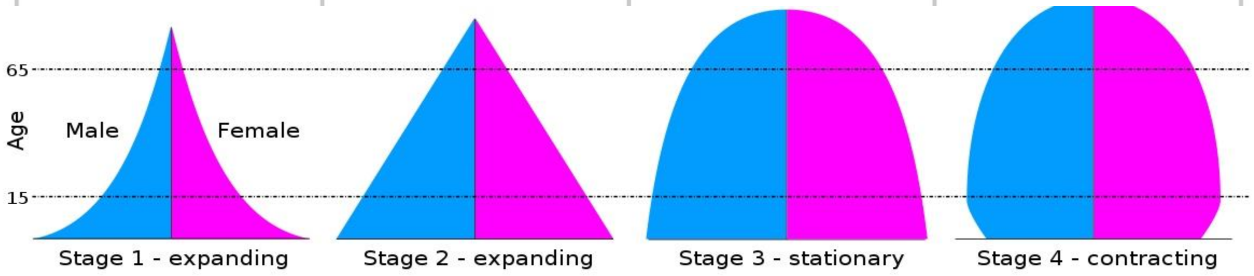
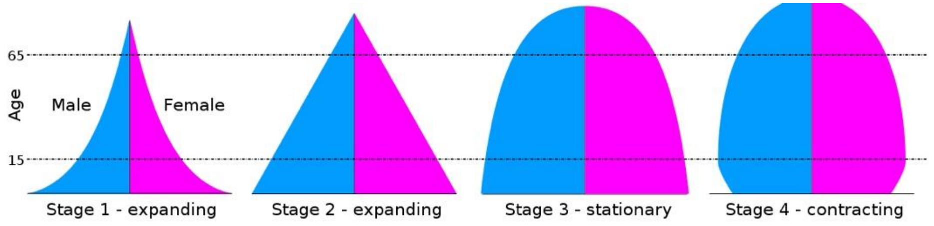
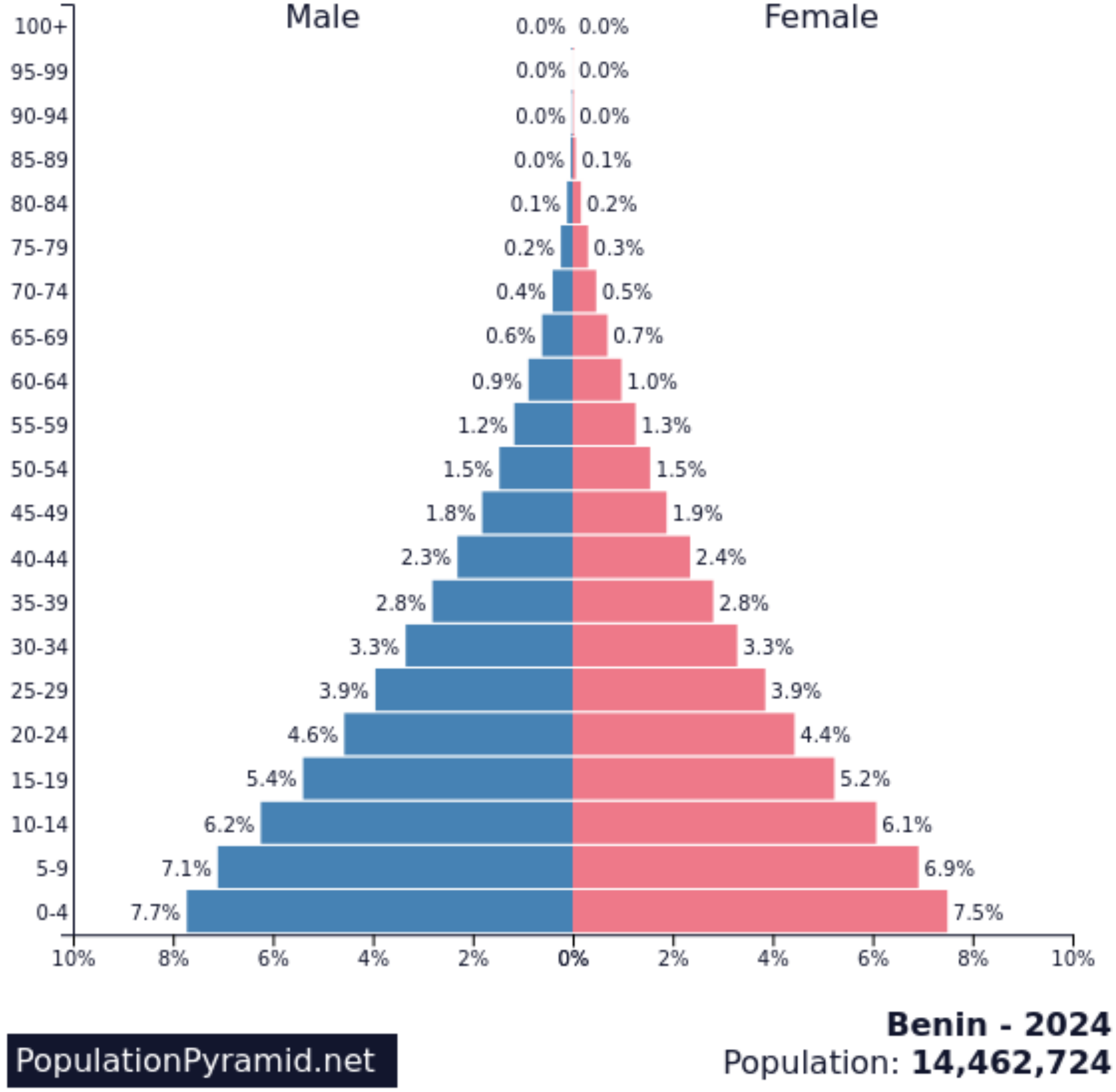
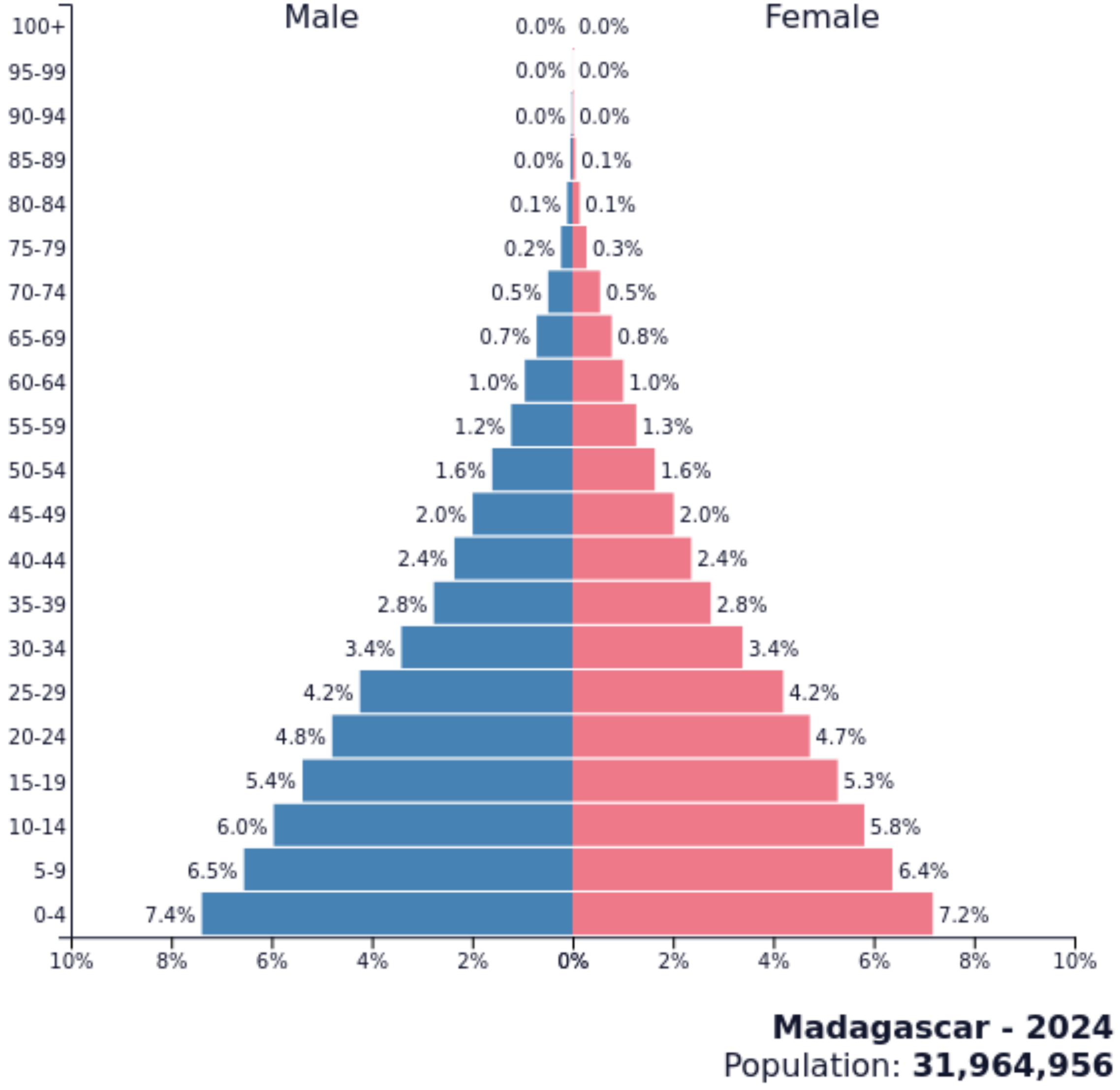
Natural increase	*Stable or slow increase*	*Very rapid increase*	*Increase slows down*	*Stable or slow increase*	*Stable or slow decrease*



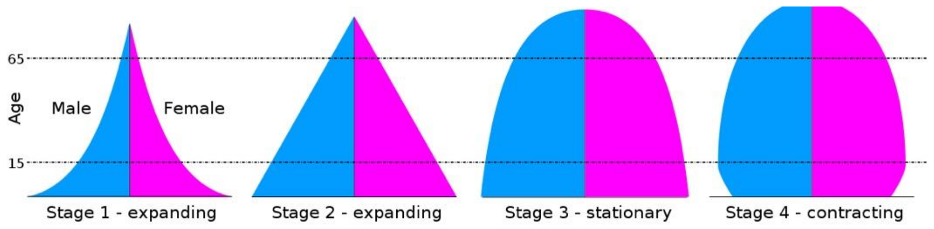
Where are we globally?

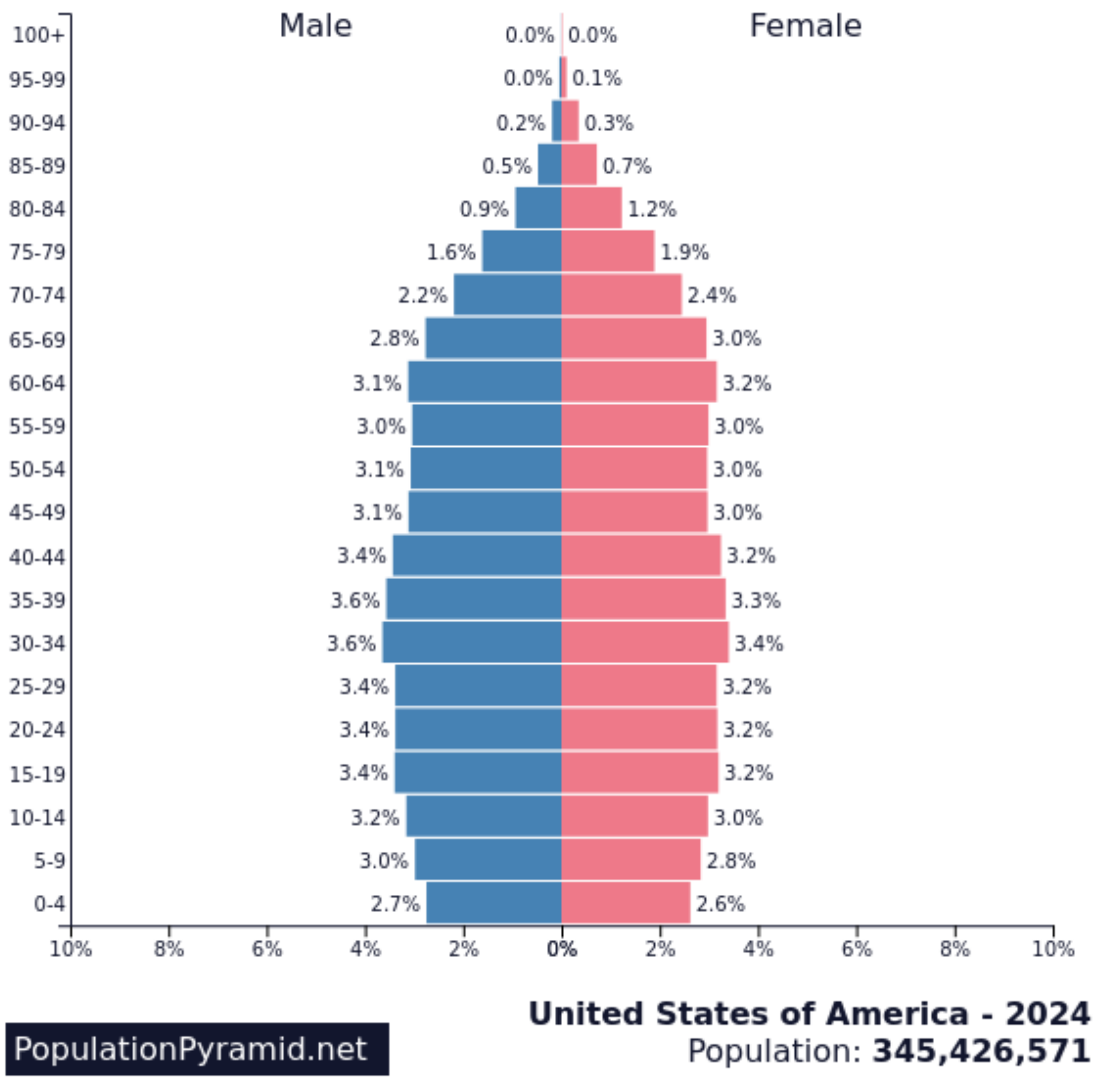


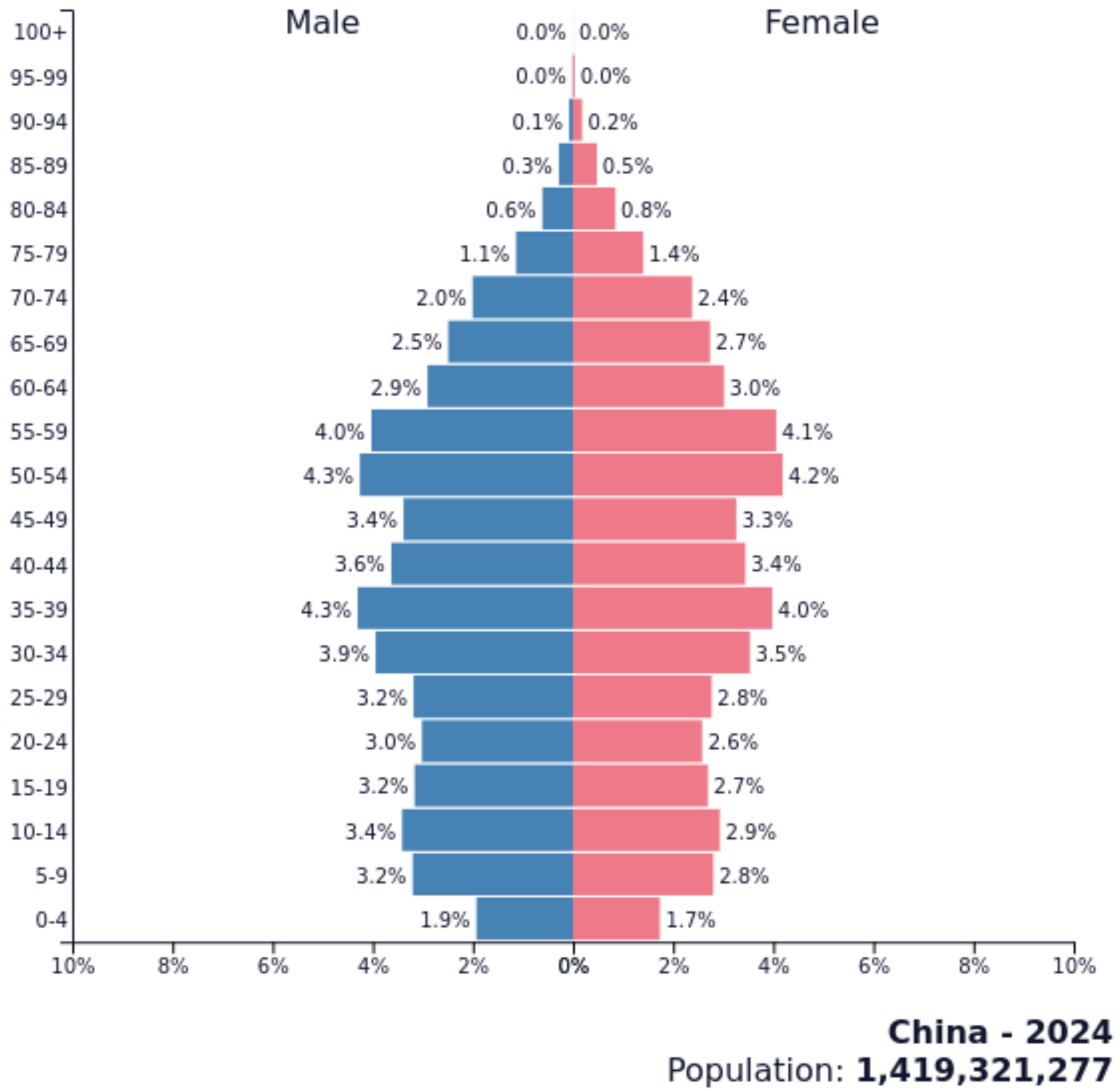




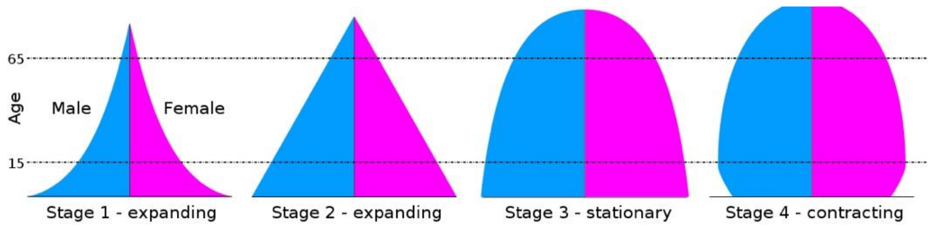
Where are we globally?

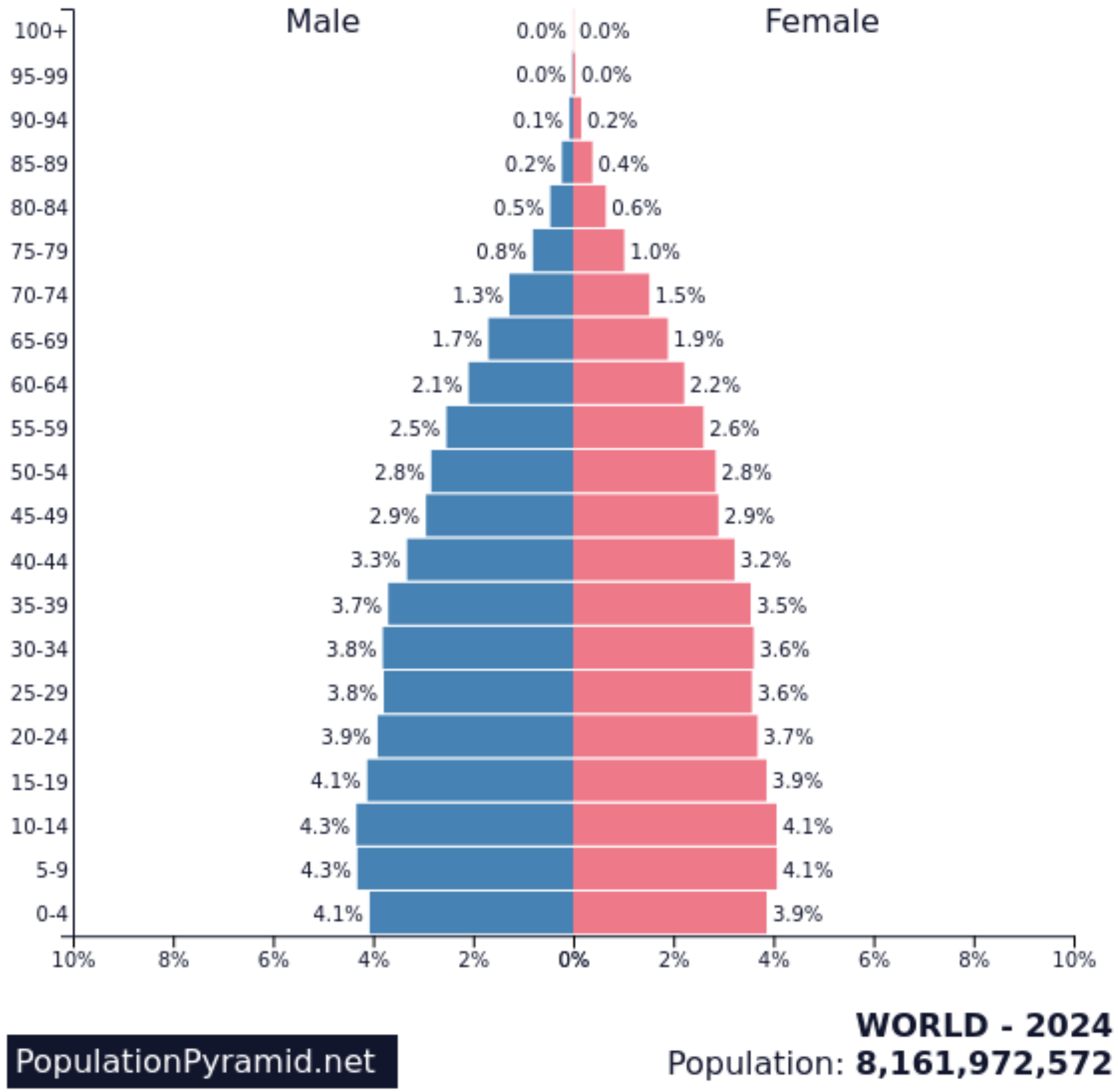




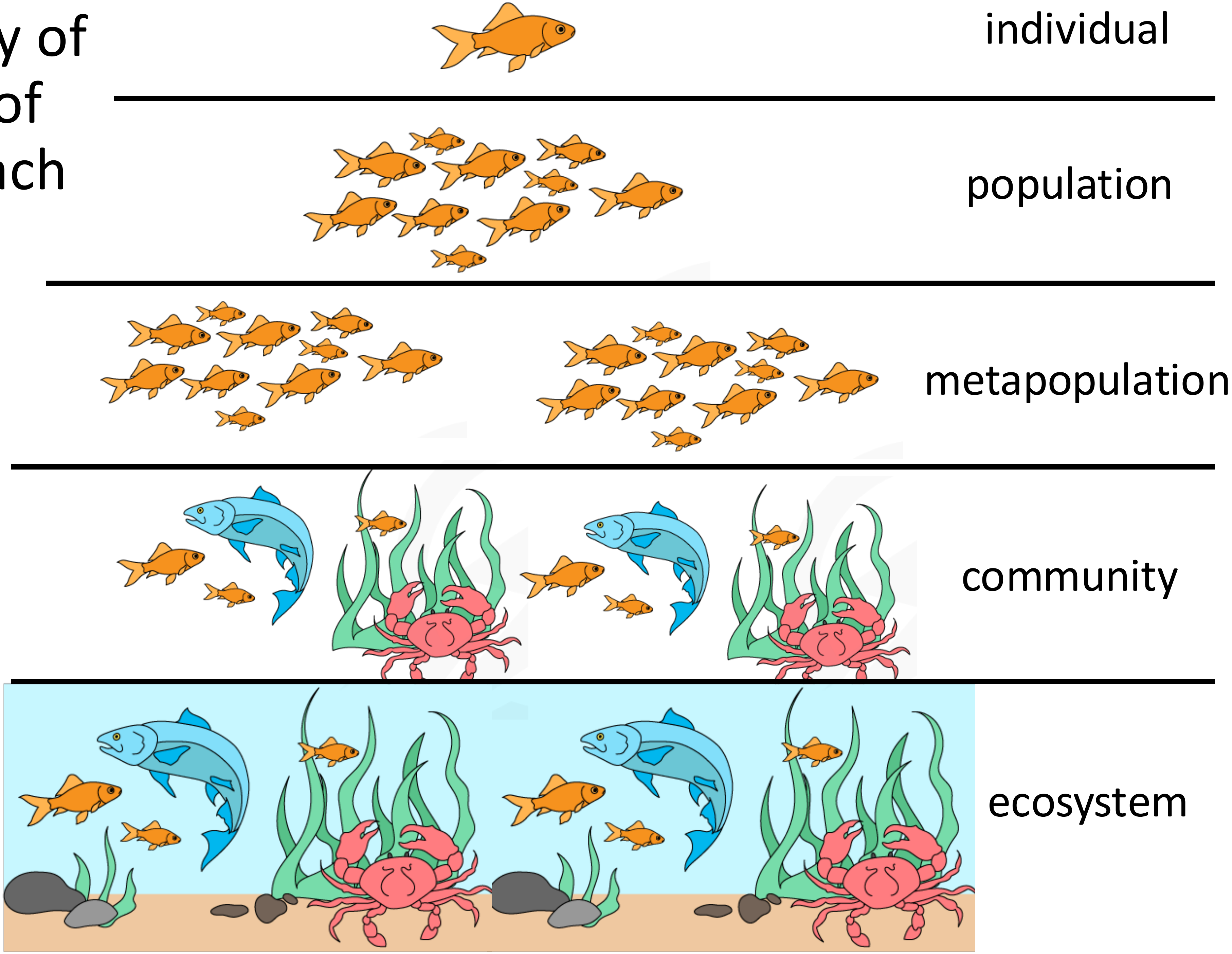


Where are we globally?

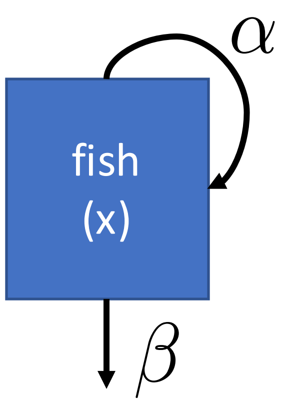




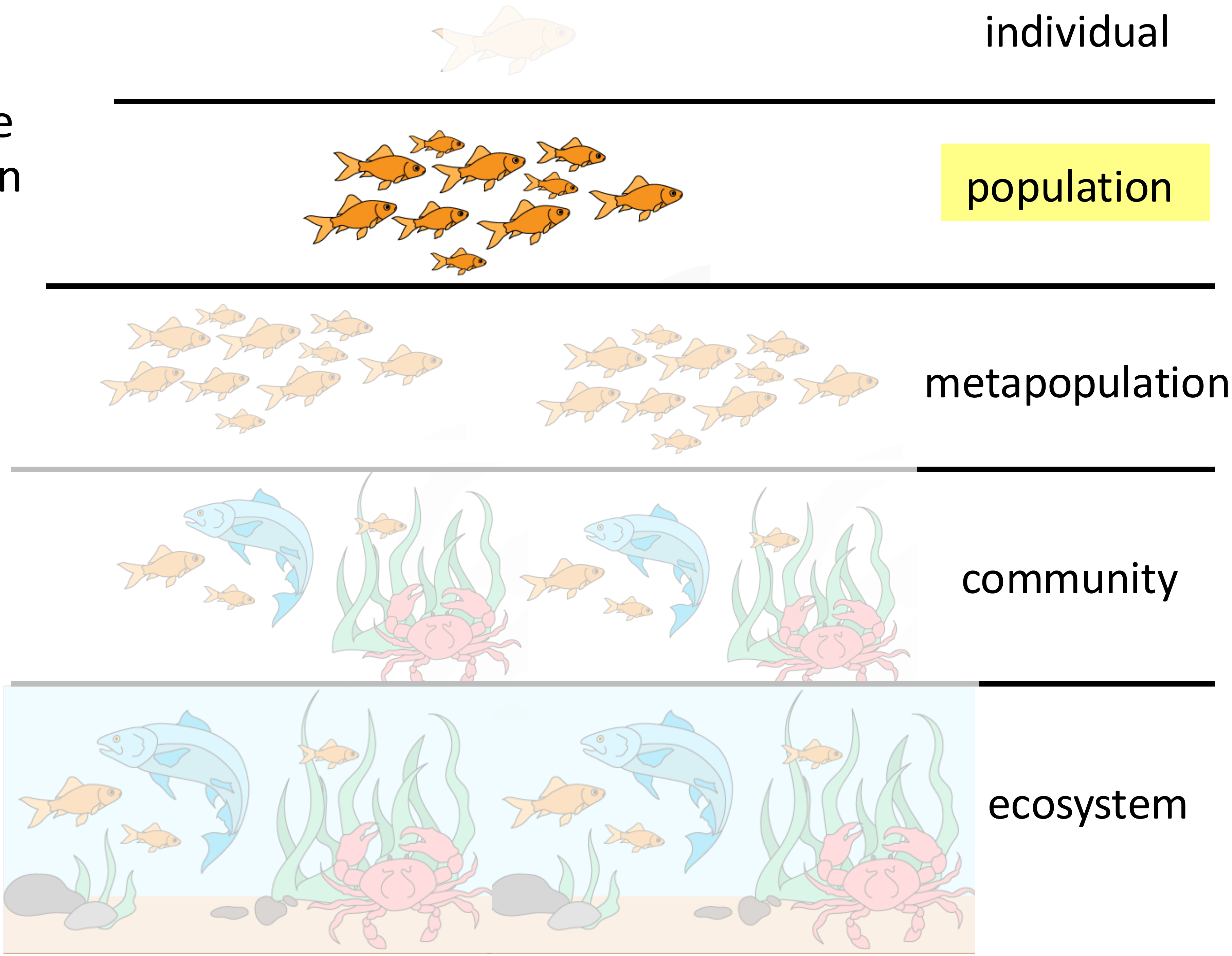
Ecology is the study of the **interactions** of **organisms** with each other and their **environment.**



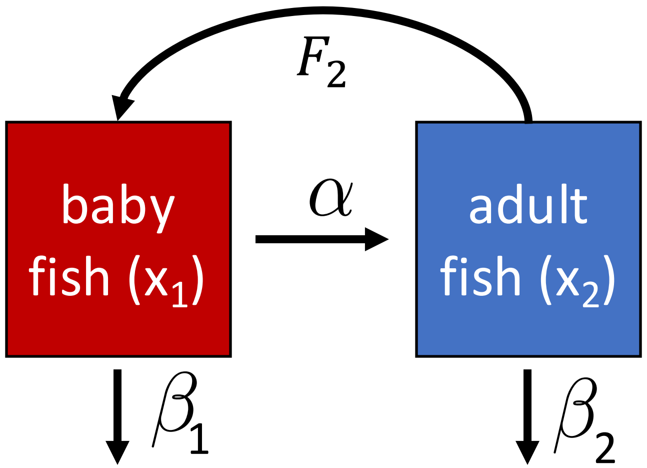
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



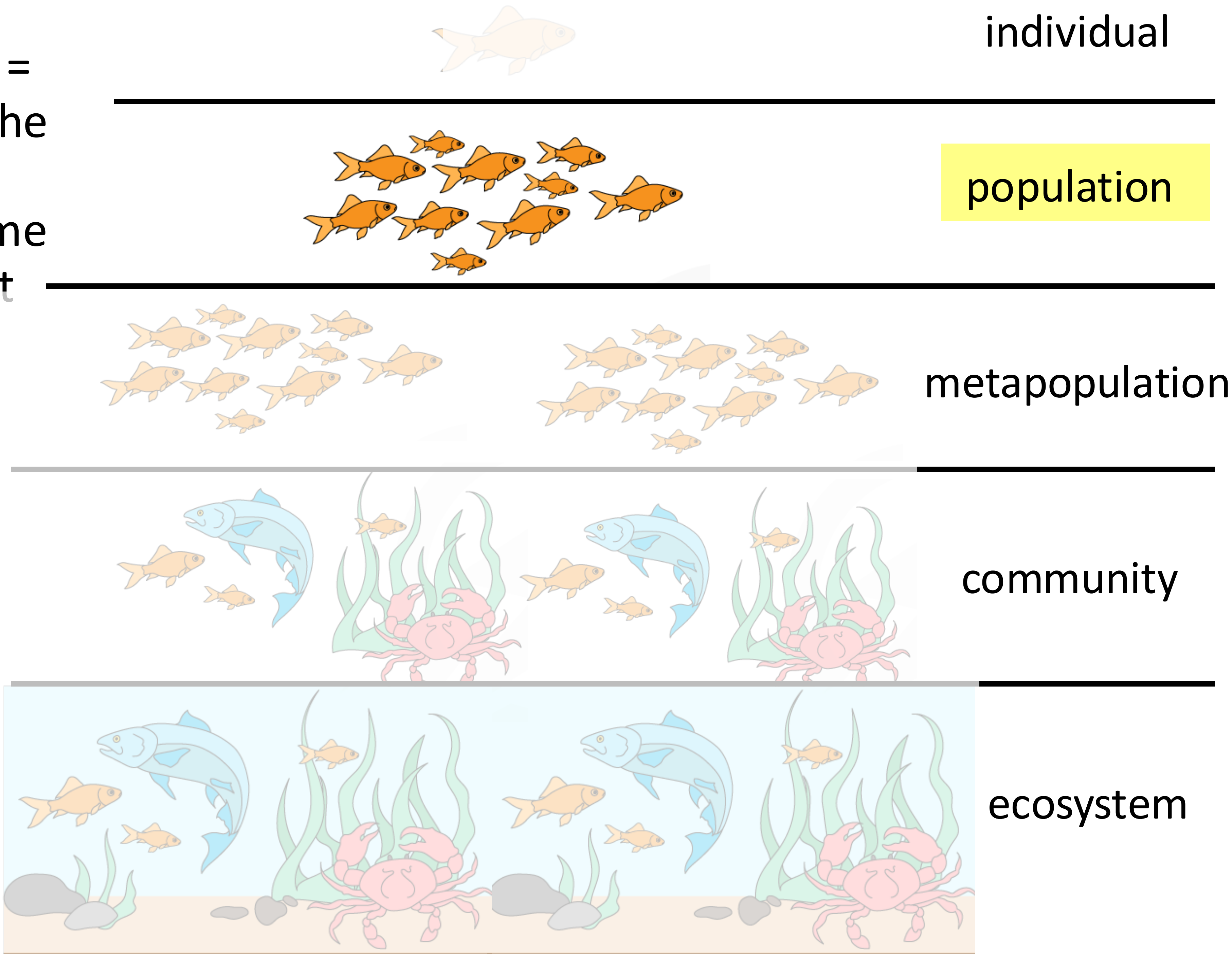
*How does the abundance of fish **change** through time?*



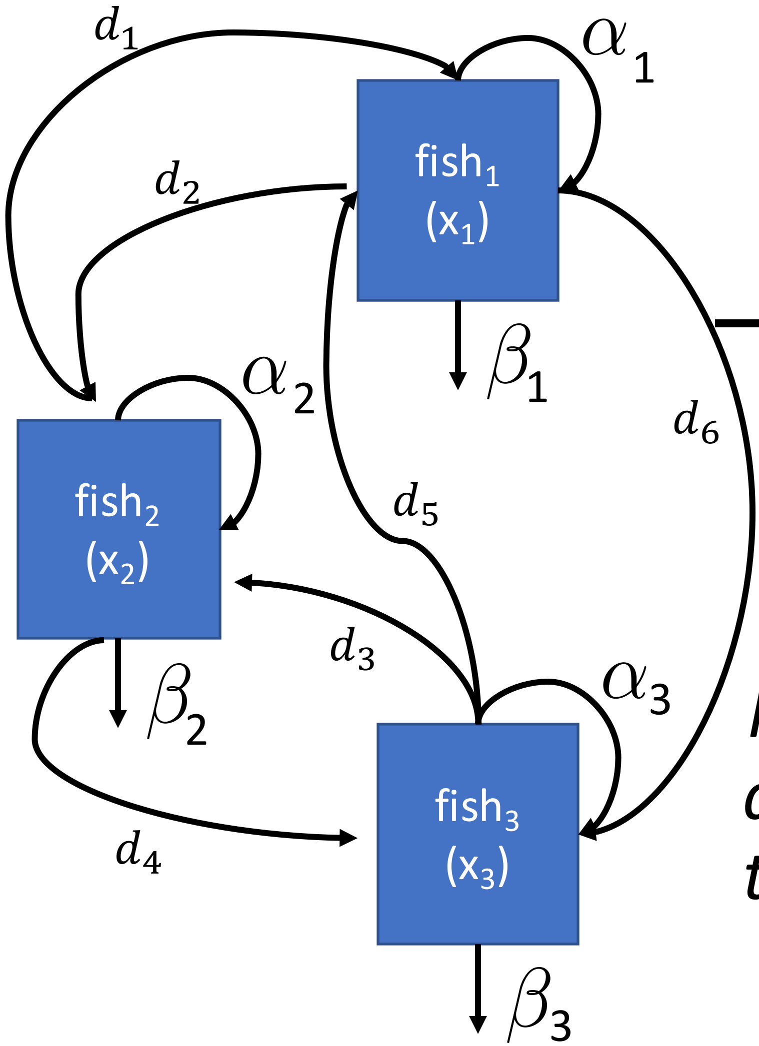
Structured Population =
multiple individuals of the same species (**conspecifics**) in the same habitat but in different life history stages

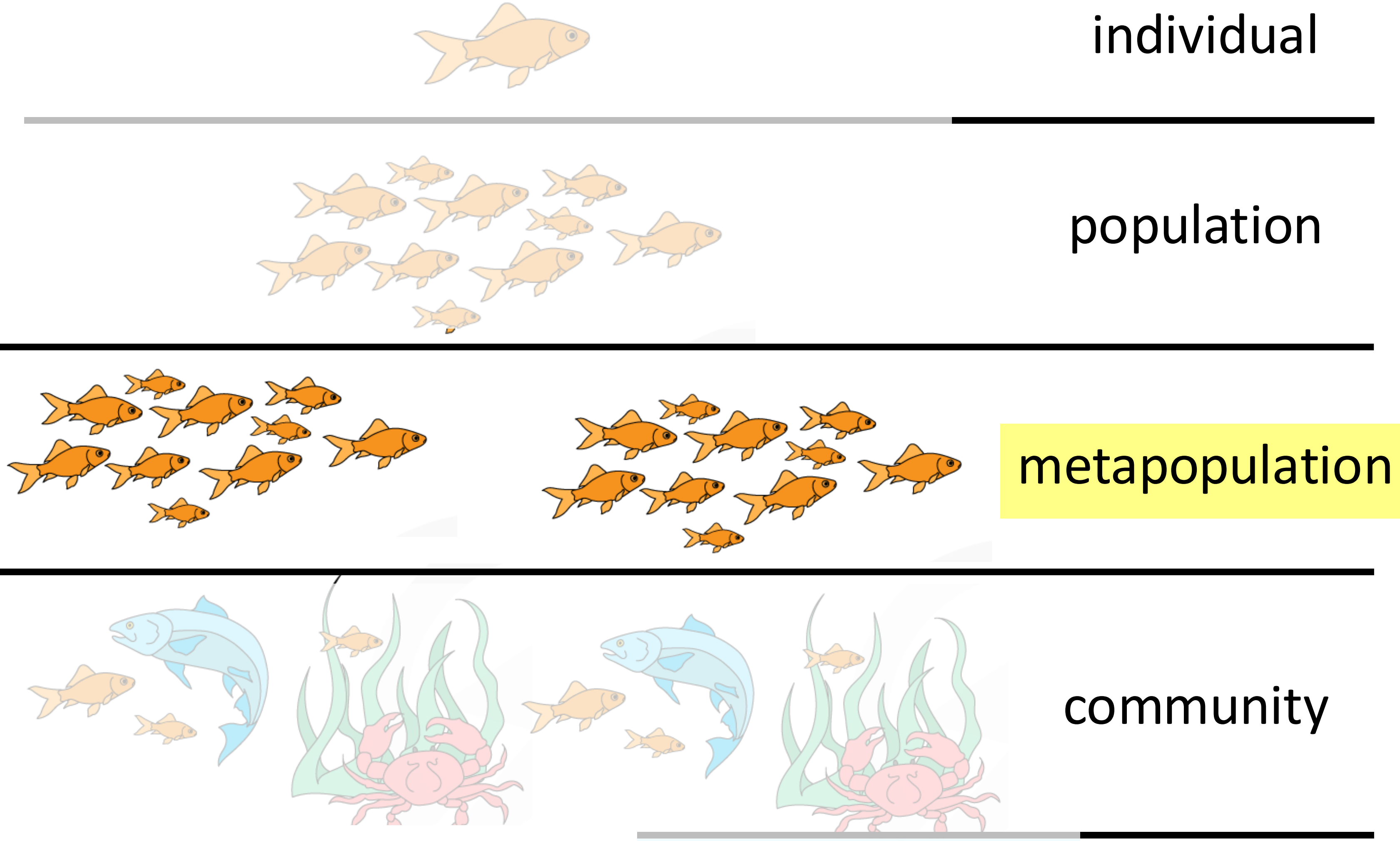


How does the abundance of fish ***change*** *through time?*



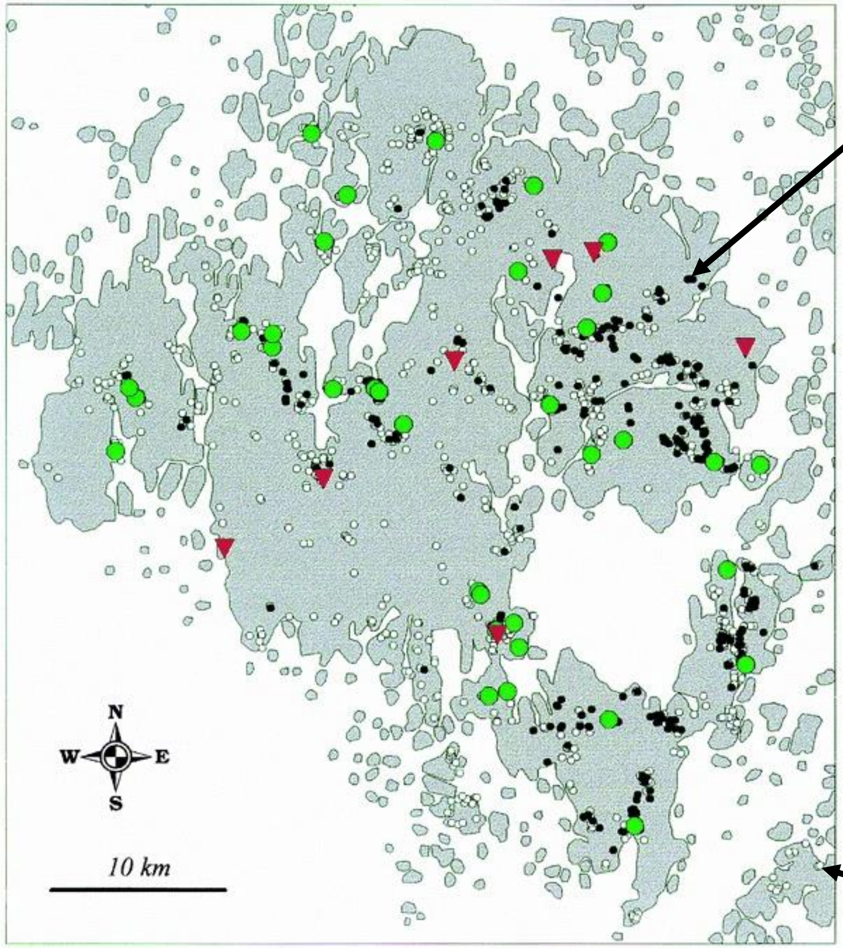
Metapopulation = sub-populations of conspecifics connected by migration or dispersal





*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.*

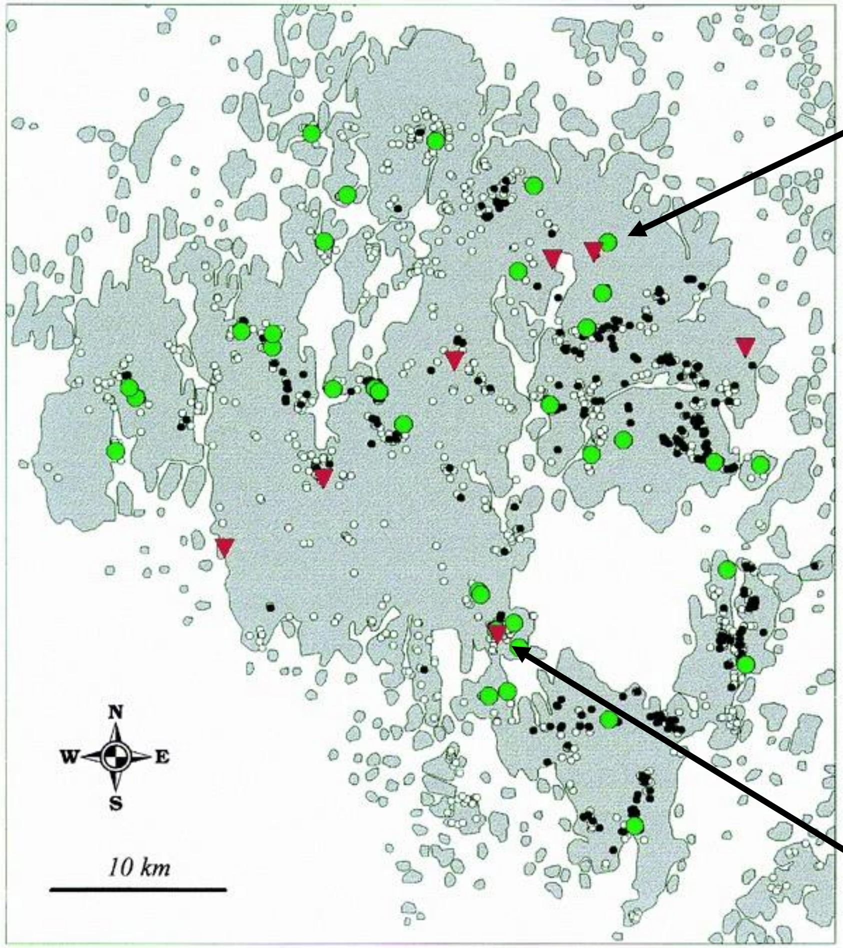
black dots = patches occupied in 1995

white dots = patches vacant in 1995

Glanville fritillary butterfly
Melitaea cinxia

Ilkka Hanski
1953-2016

Why do metapopulations matter?



green dots = patches still occupied in 1996

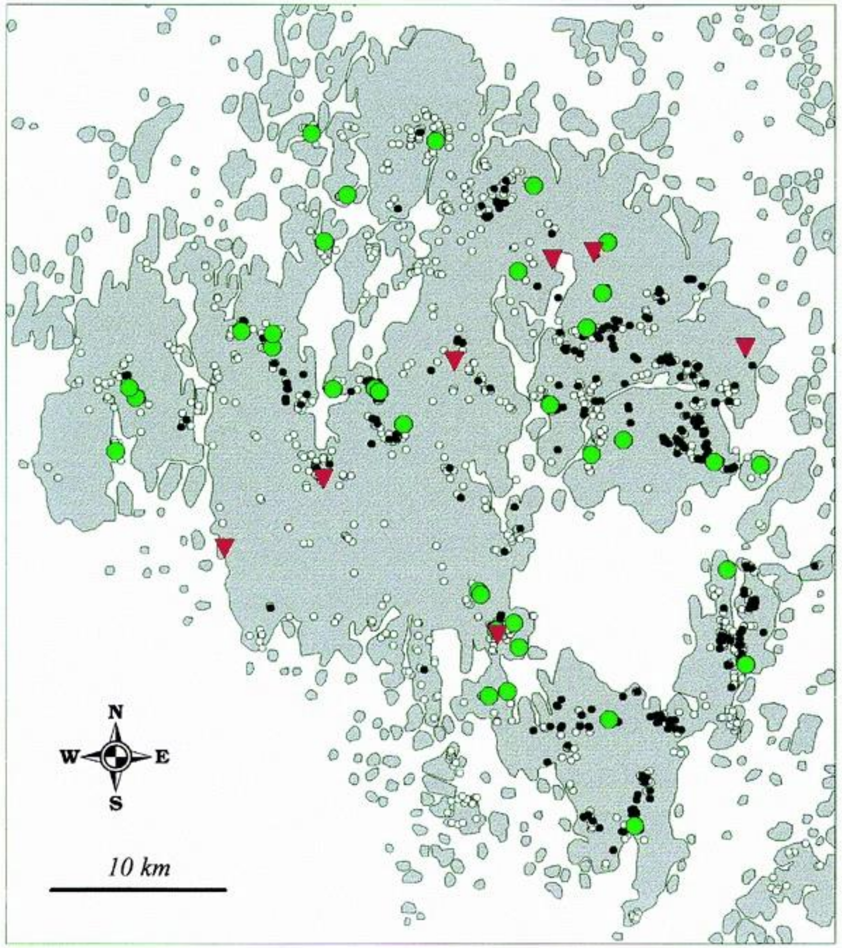
red dots = patches extinct in 1996

Saccheri et al 1998. *Nature.*

Glanville fritillary butterfly
Melitaea cinxia

Ilkka Hanski
1953-2016

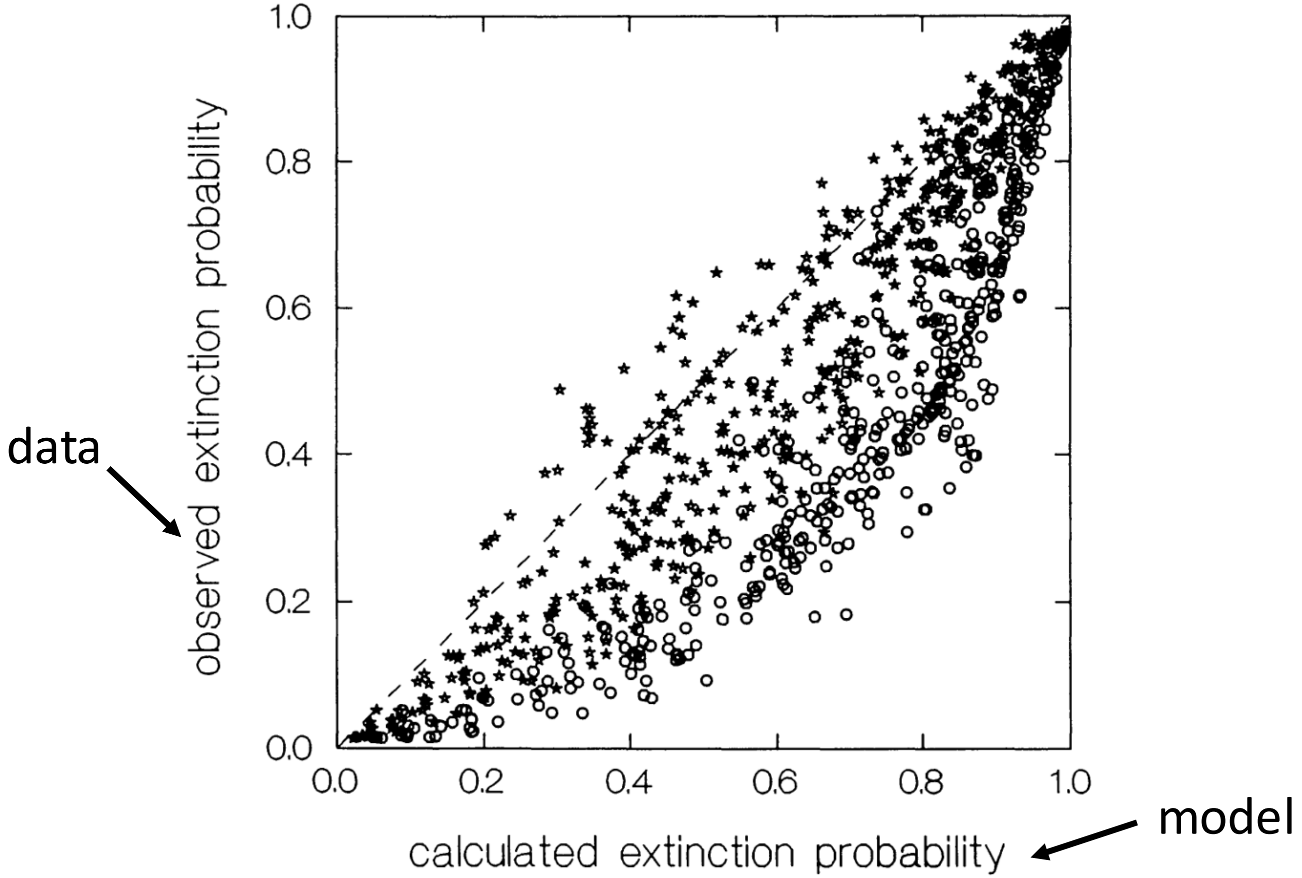
Why do metapopulations matter?



Saccheri et al 1998. *Nature.*

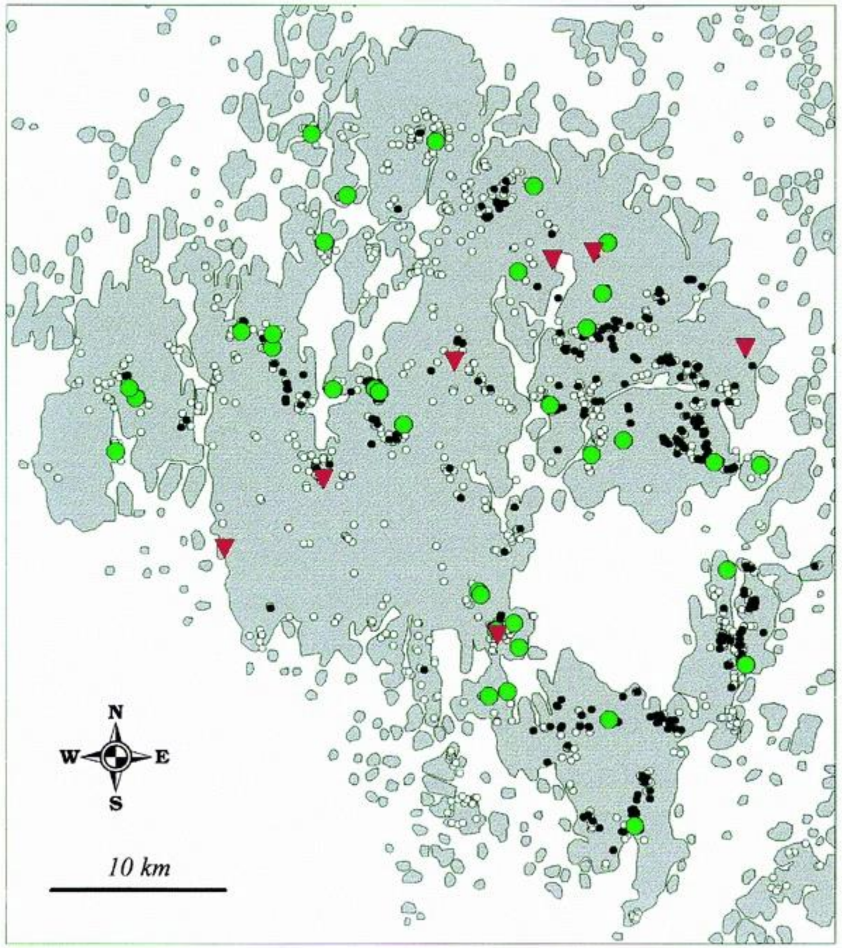
MINIMUM VIABLE METAPOPULATION SIZE

Ilkka Hanski,[1] Atte Moilanen,[1] and Mats Gyllenberg[2]

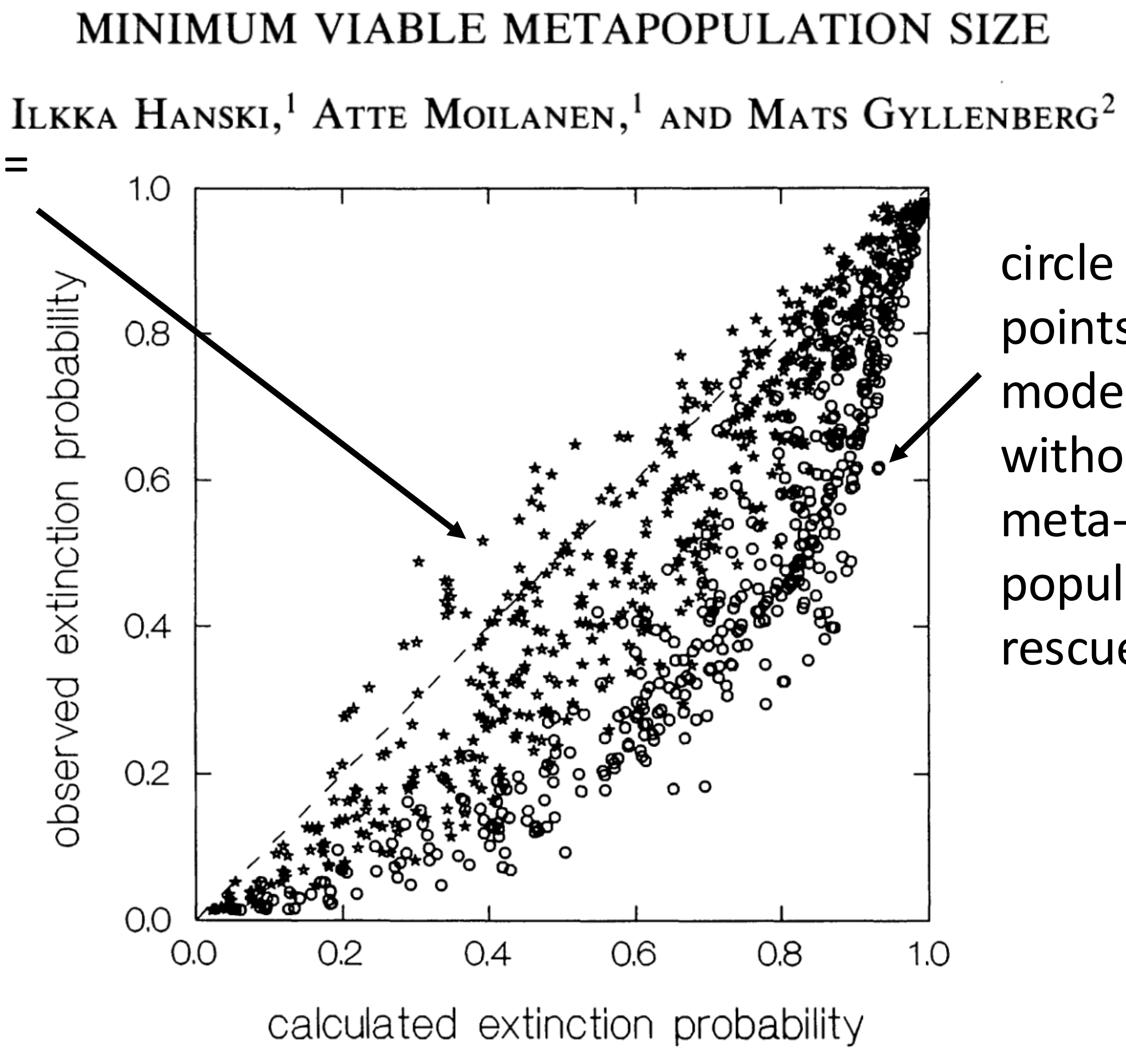


Hanski et al. 1996. *The American Naturalist.*

Why do metapopulations matter?



Saccheri et al 1998. *Nature.*



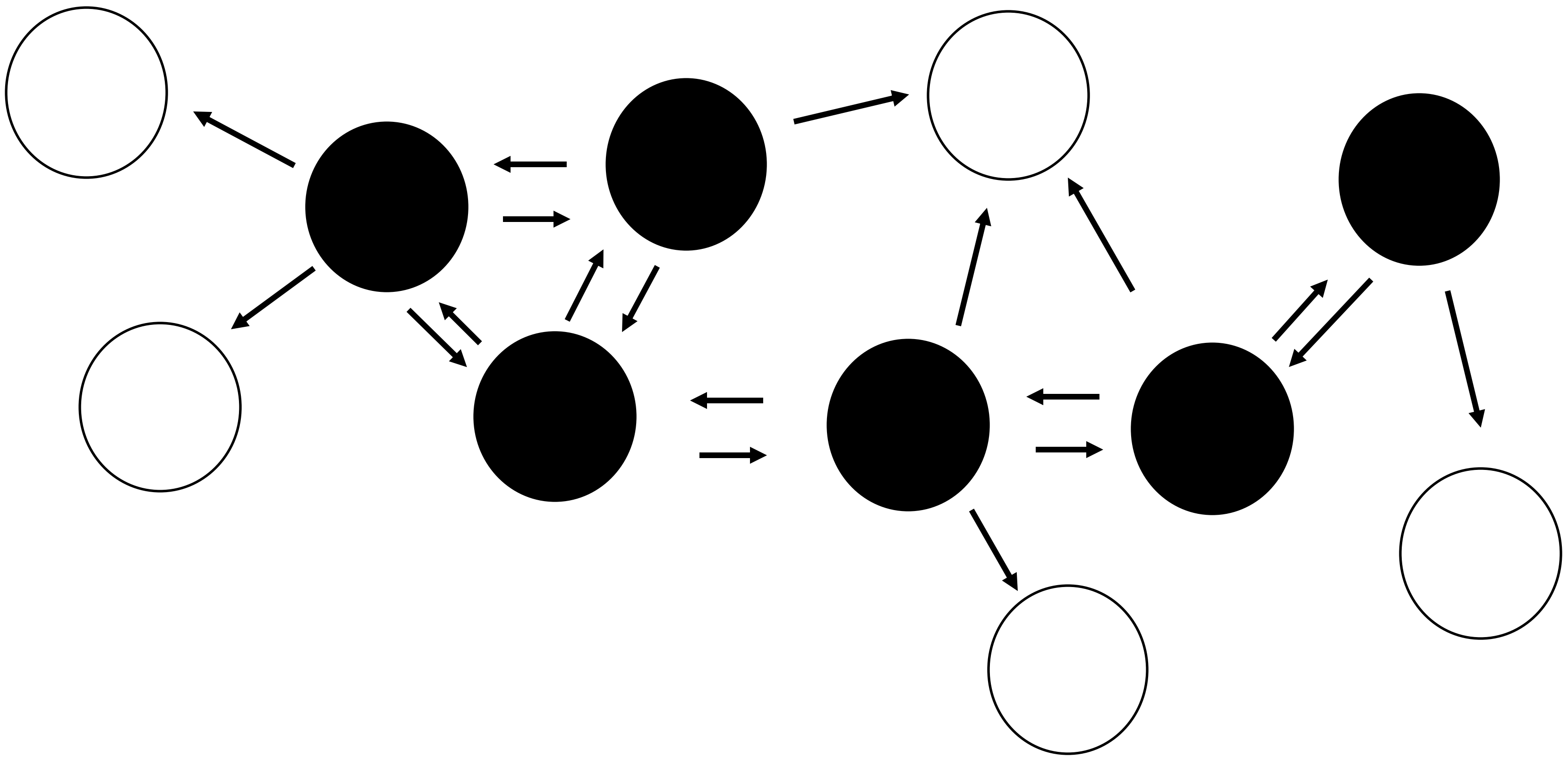
star points = model including meta-population **rescue** effects

circle points = model without meta-population rescue

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

$$\frac{dp}{dt} = cp\underbrace{(1-p)}_{\text{proportion of unoccupied patches}} - ep$$

fraction of patches occupied at a given time

colonization rate

extinction rate

“patch dynamics”

Modeling metapopulation dynamics

- a “population of populations” -Richard Levins 1969

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

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

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

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

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

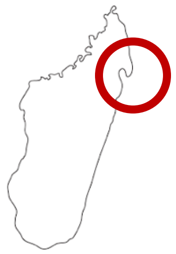
Dr. Cortni Borgerson, Montclair University

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?



- 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

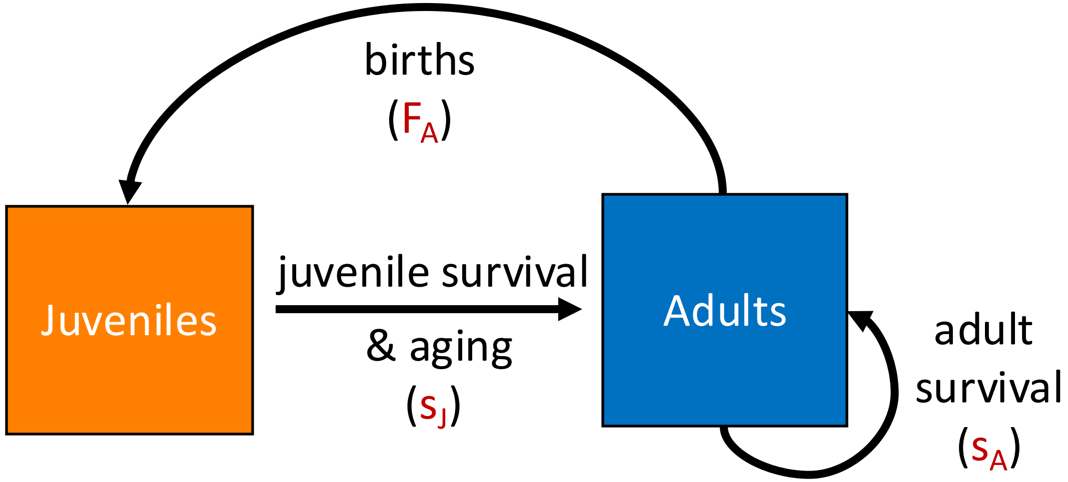
Brook et al. 2018. *Conservation Biology.*

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

Brook et al. 2018. *Conservation Biology.*

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*

$$N_{t+1} = AN_t$$

$$\begin{array}{ccc} \mathbf{N_{t+1}} & \mathbf{A} & \mathbf{N_t} \\ \begin{bmatrix} J \\ A \end{bmatrix}_{t+1} = & \begin{bmatrix} 0 & s_A F_A \\ s_J & s_A \end{bmatrix} & \begin{bmatrix} J \\ A \end{bmatrix}_t \end{array}$$

(where:

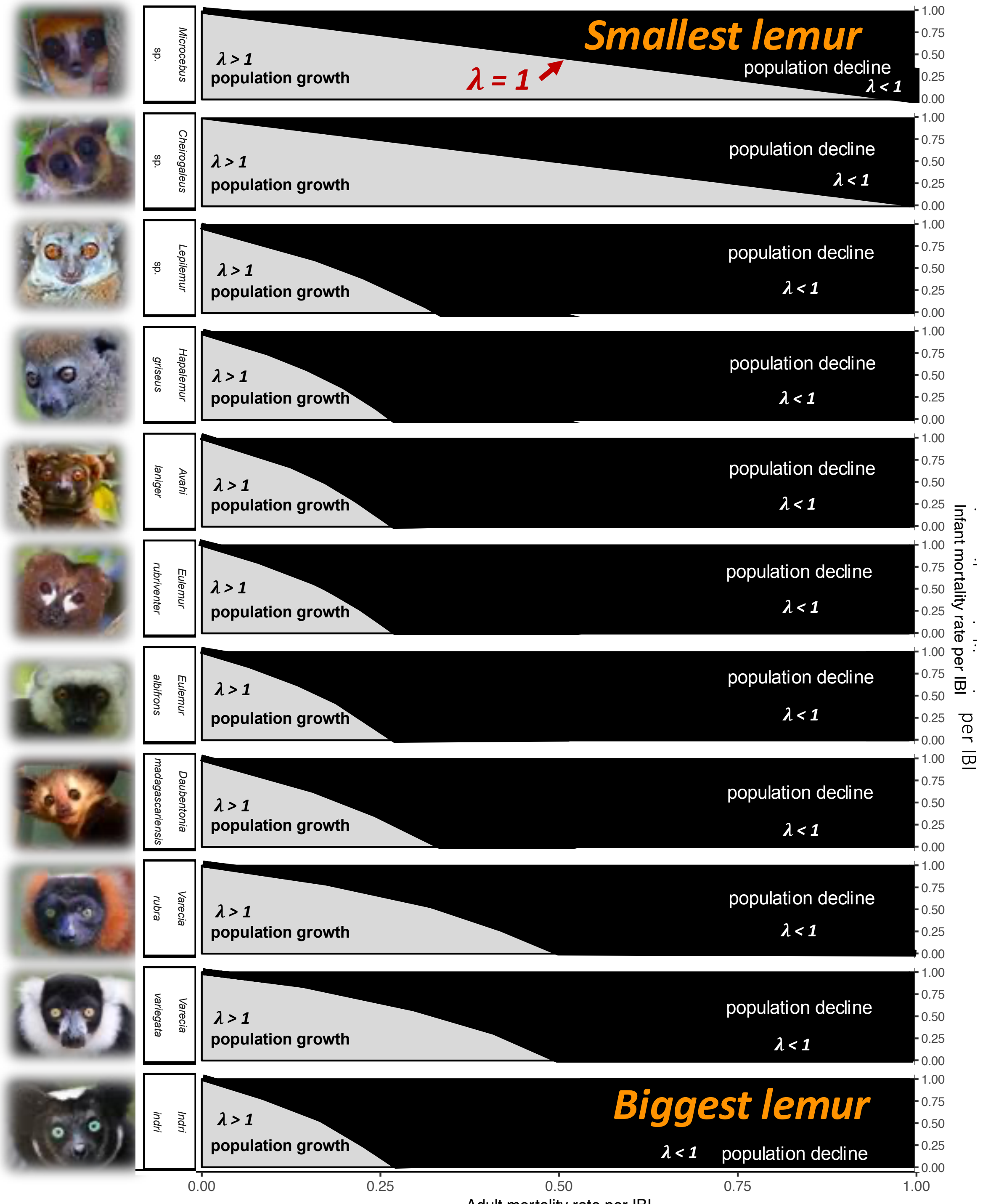
S_J = juvenile IBI survival

S_A = adult IBI survival

F_A = adult IBI fecundity)

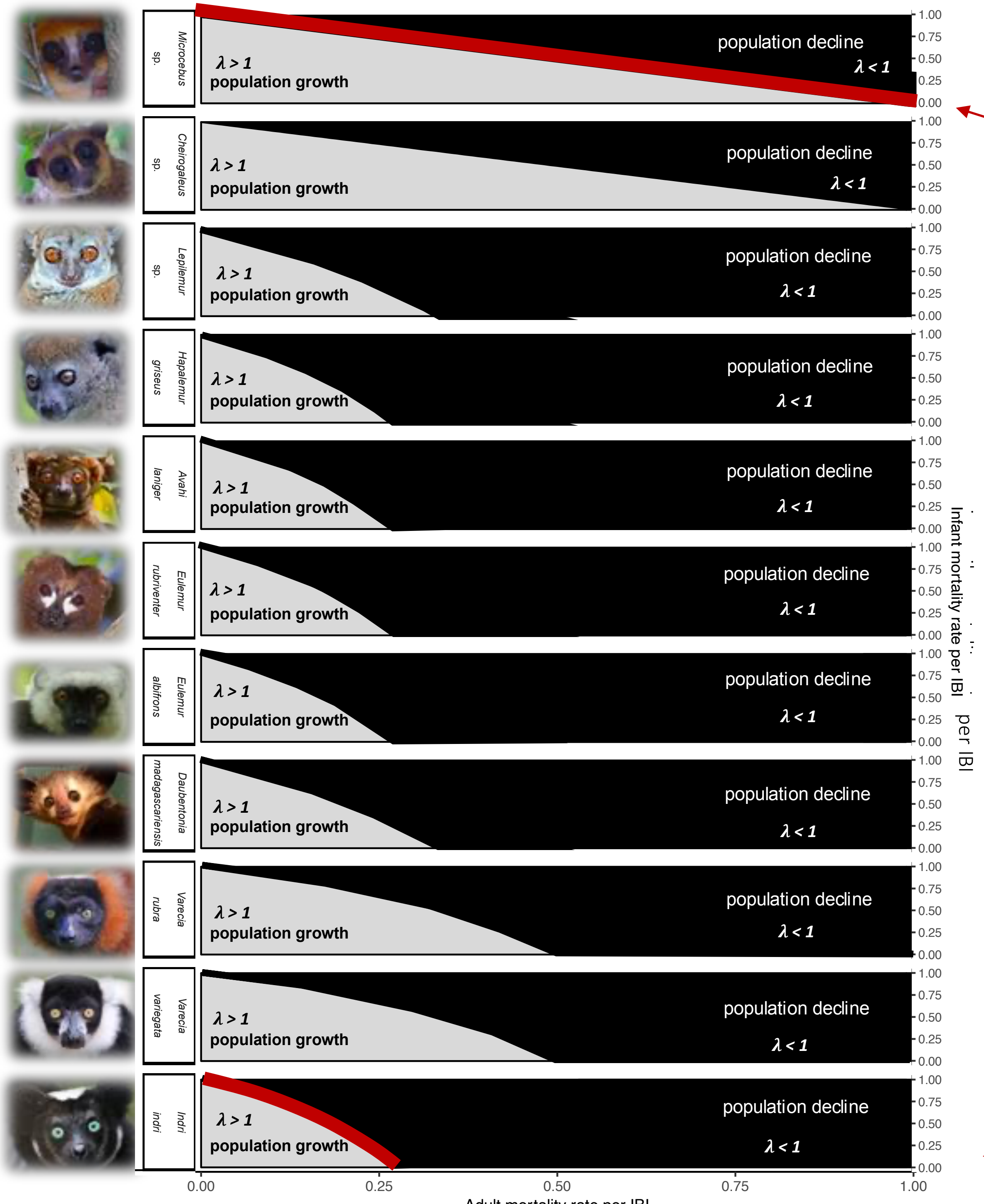
We can explore the
zero-population growth line at λ = 1
for differing values of s_J, s_A, and F_A.

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**.

Brook et al. 2018. *Conservation Biology.*



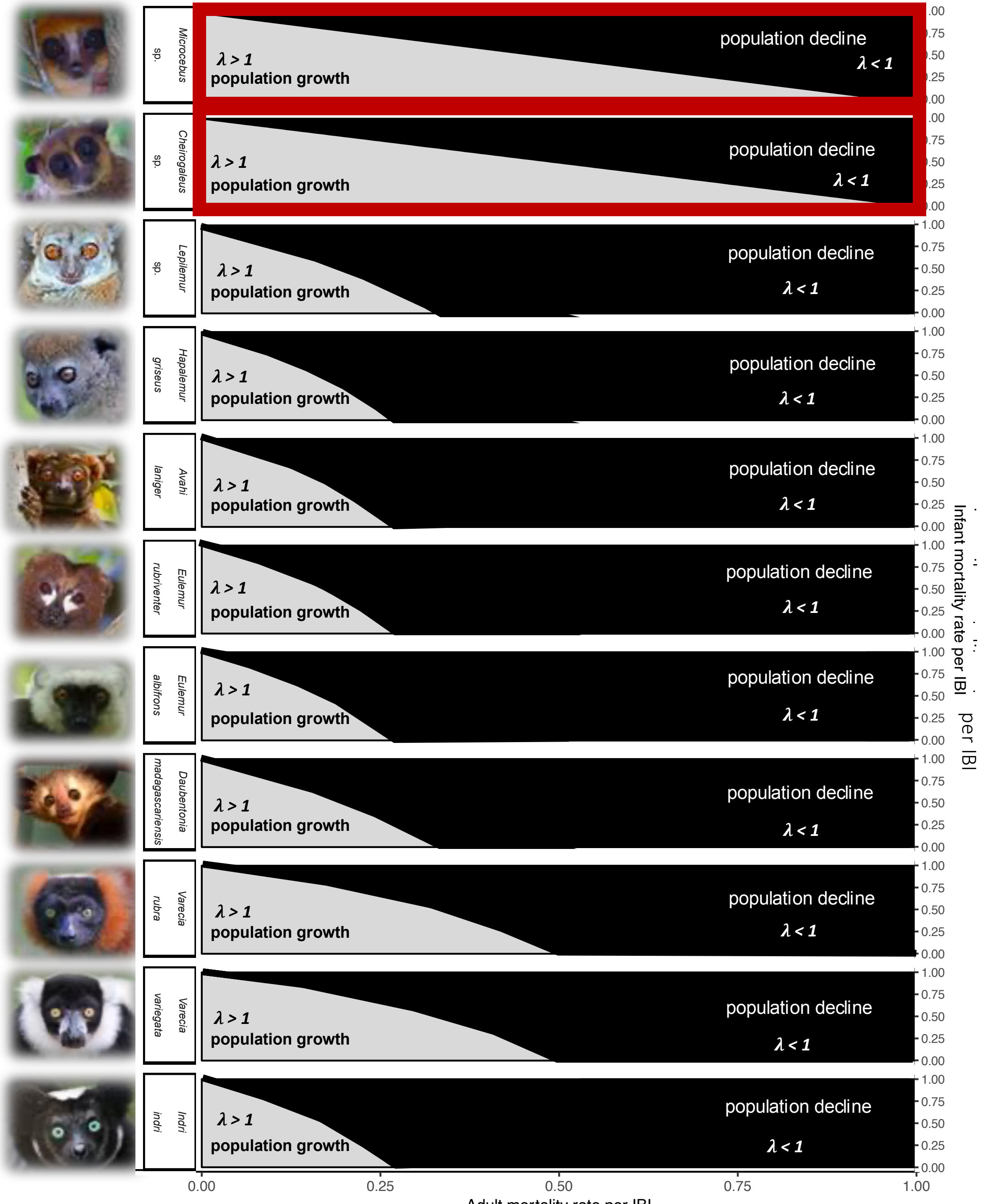
Age @ 1st reproduction = 1 yr

2x babies/ 1 year

Age @ 1st reproduction = 9 yrs

1x baby/ 3 years

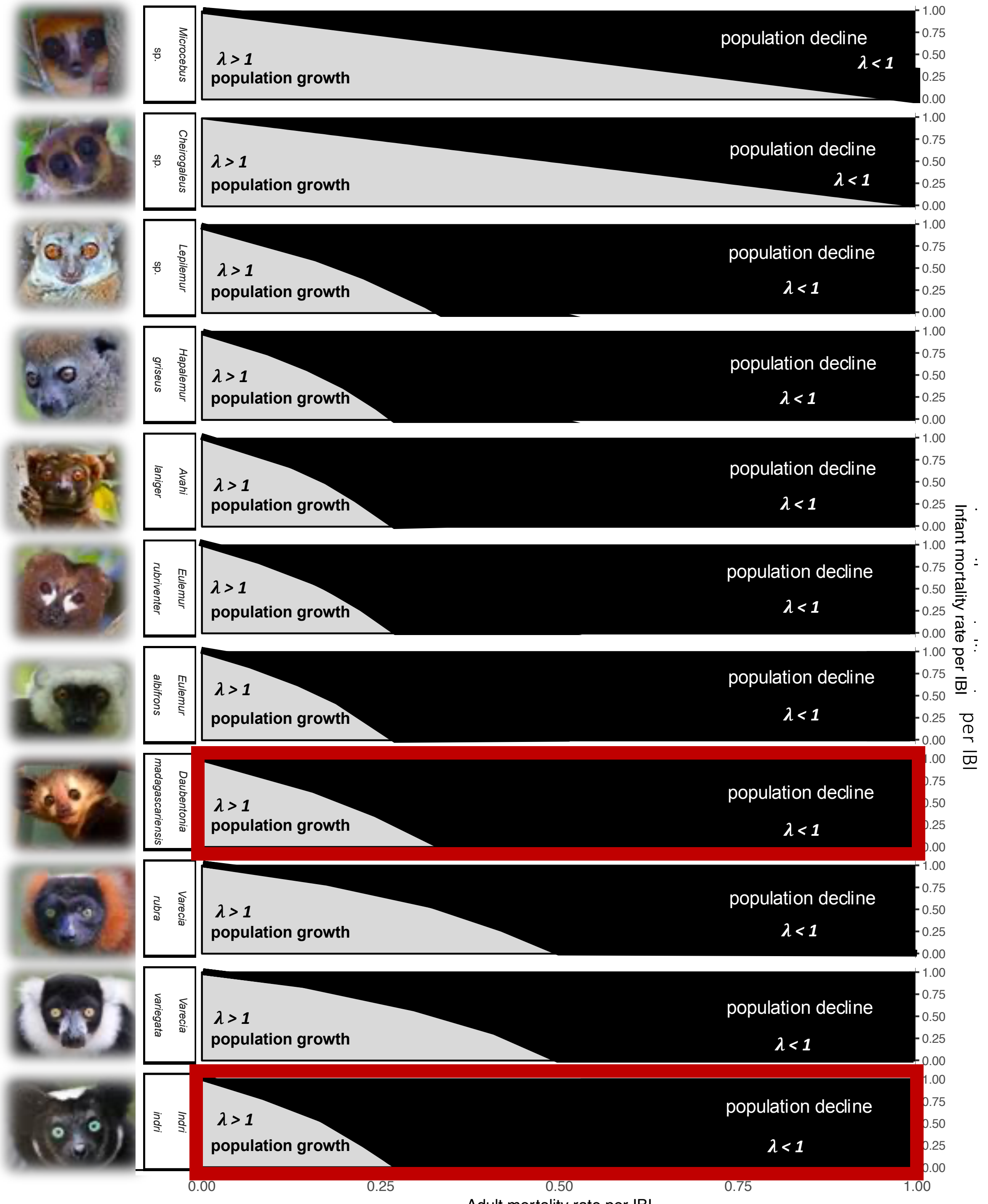
Brook et al. 2018. *Conservation Biology.*



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

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

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**.

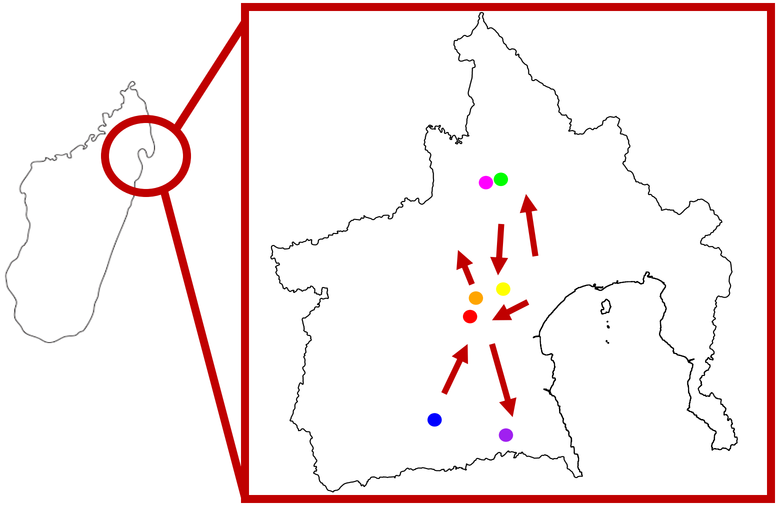
Bigger lemurs with **slower life histories** are particularly **vulnerable**.

Brook et al. 2018. *Conservation Biology.*

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

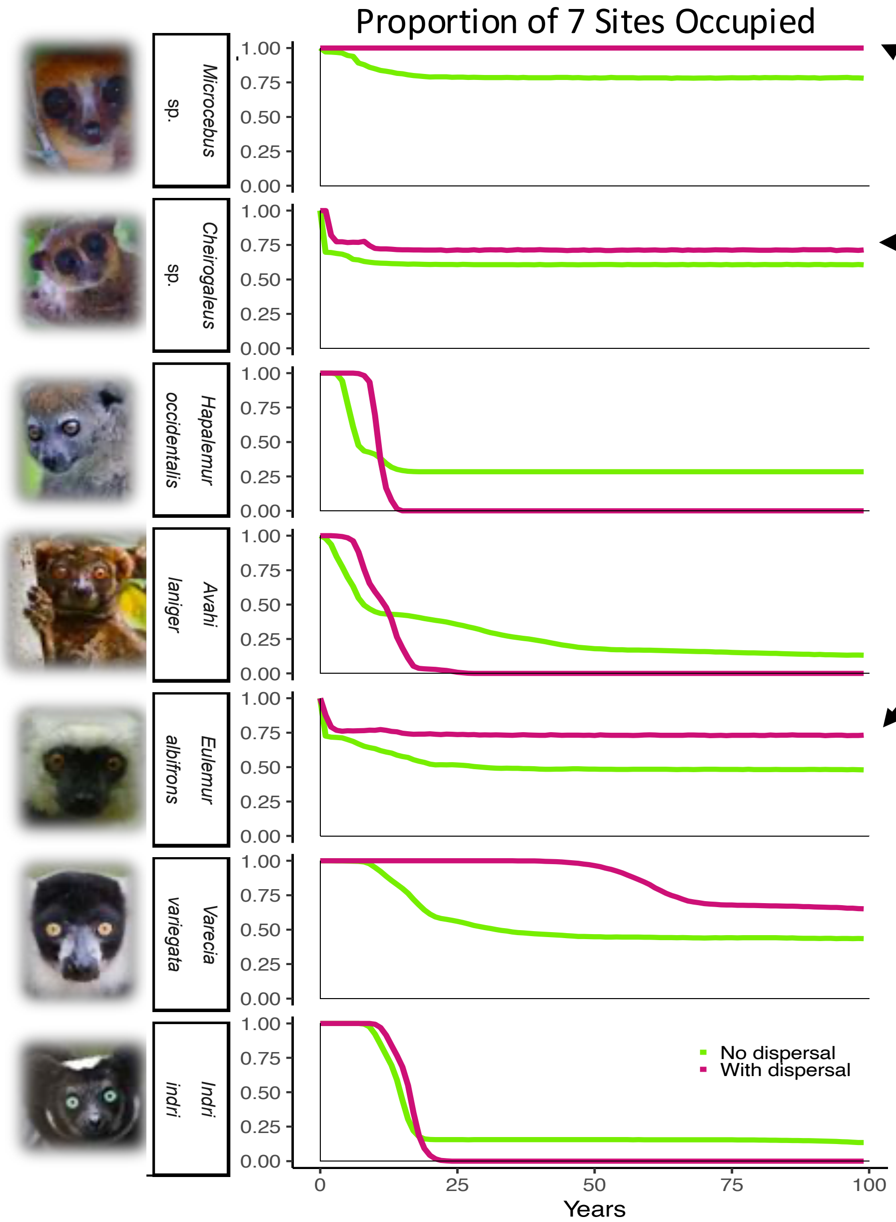
Assumptions:

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

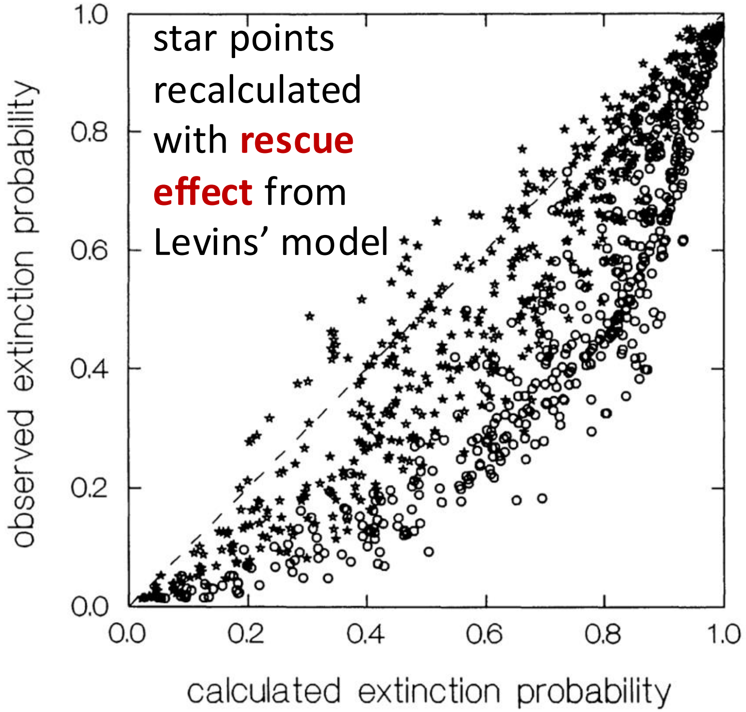


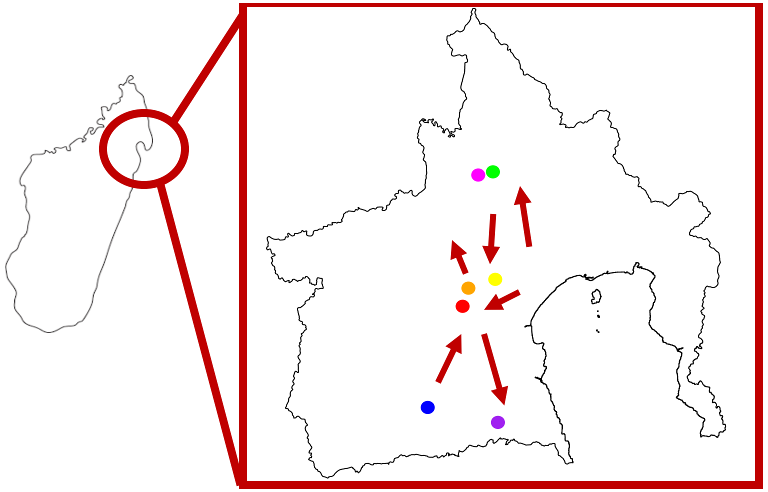
Brook et al. 2018. *Conservation Biology.*

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



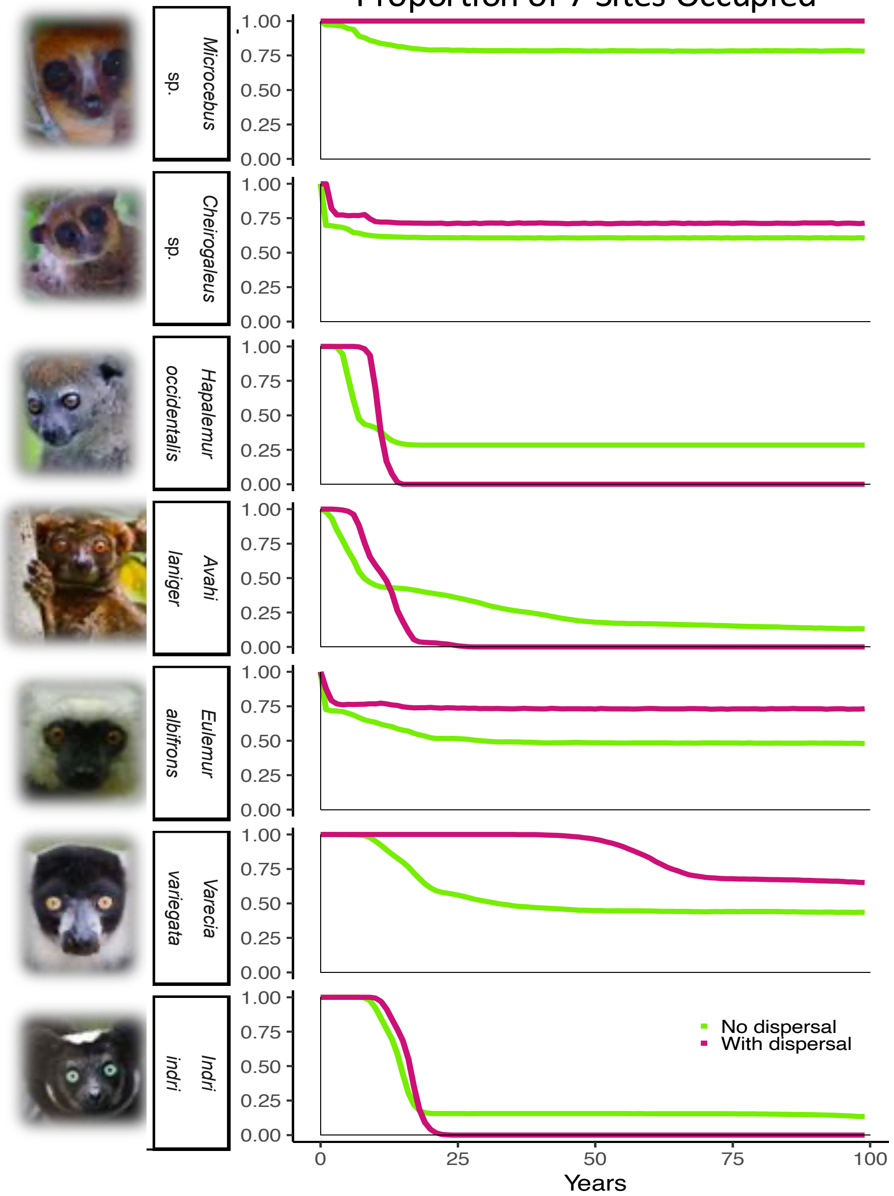
Metapopulation dynamics can promote more lemurs at more sites across the landscape!





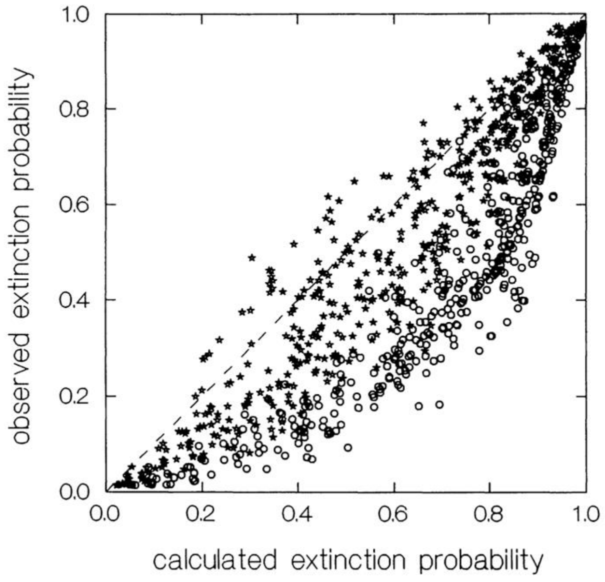
Brook et al. 2018. *Conservation Biology.*

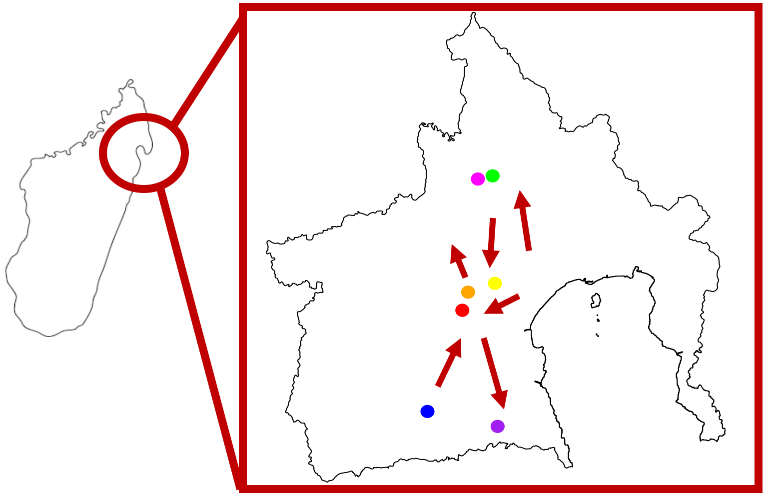
Dispersal can drive regional extirpation if the majority of local sites function as population sinks.



Metapopulation dynamics can drive regional declines in other cases!

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

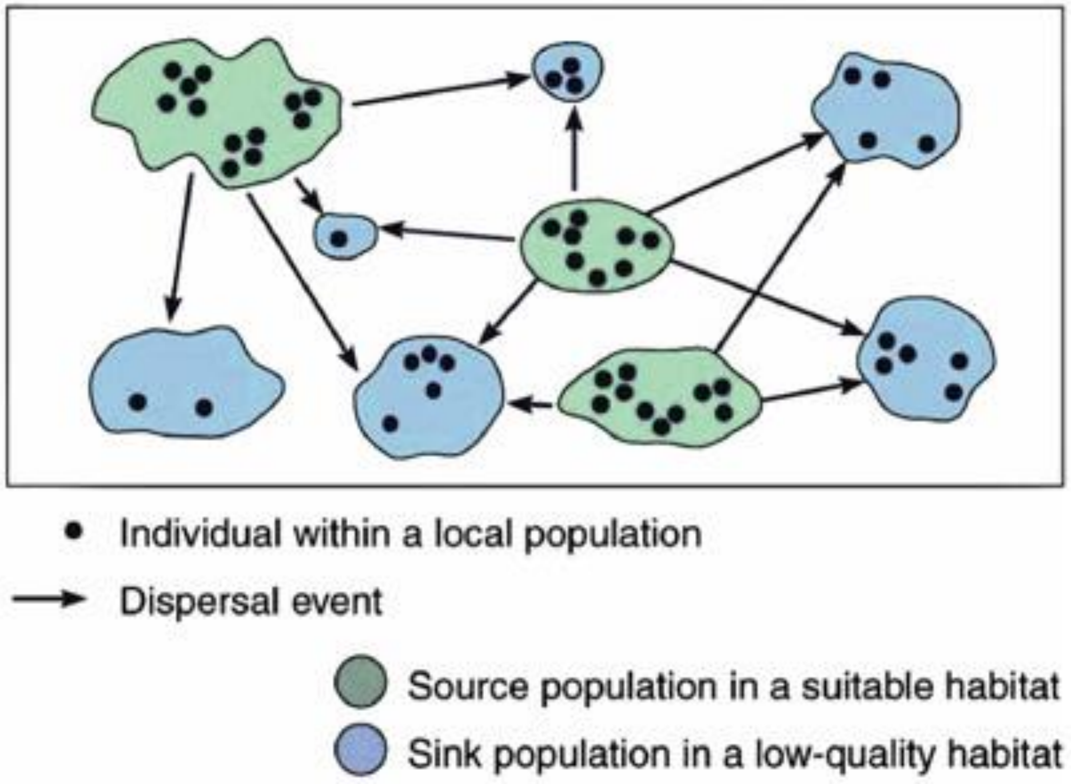




Brook et al. 2018. *Conservation Biology.*

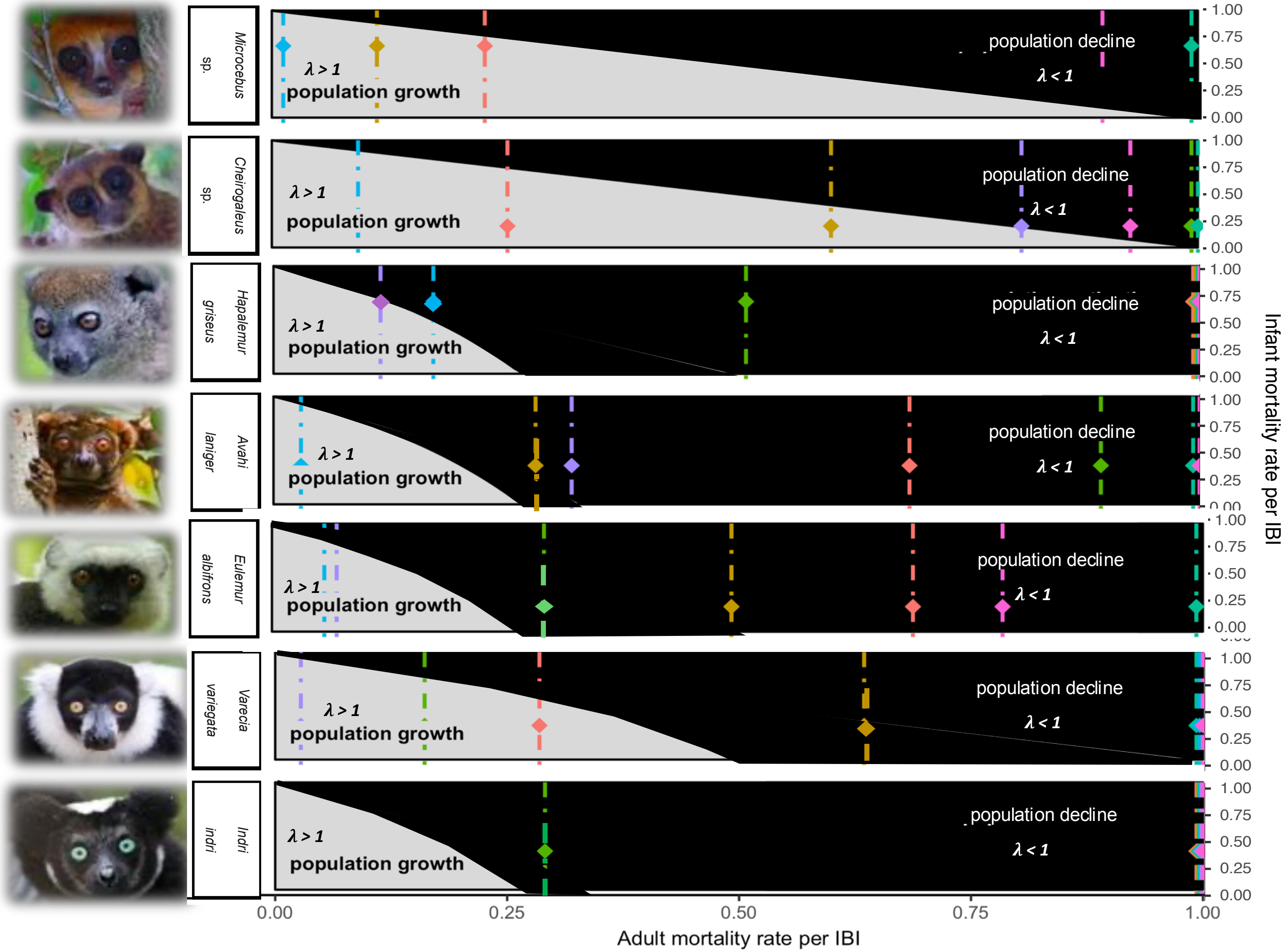
Source-sink theory describes how variation in habitat may affect population dynamics.

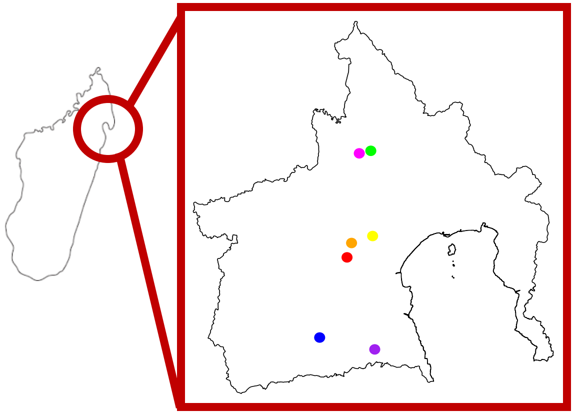
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.
- An **ecological trap** is an organism's preference for poor quality habitat
  - Ex: polarized light pollution & insect ovipositing



Pulliam 1988. *The American Naturalist.*

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



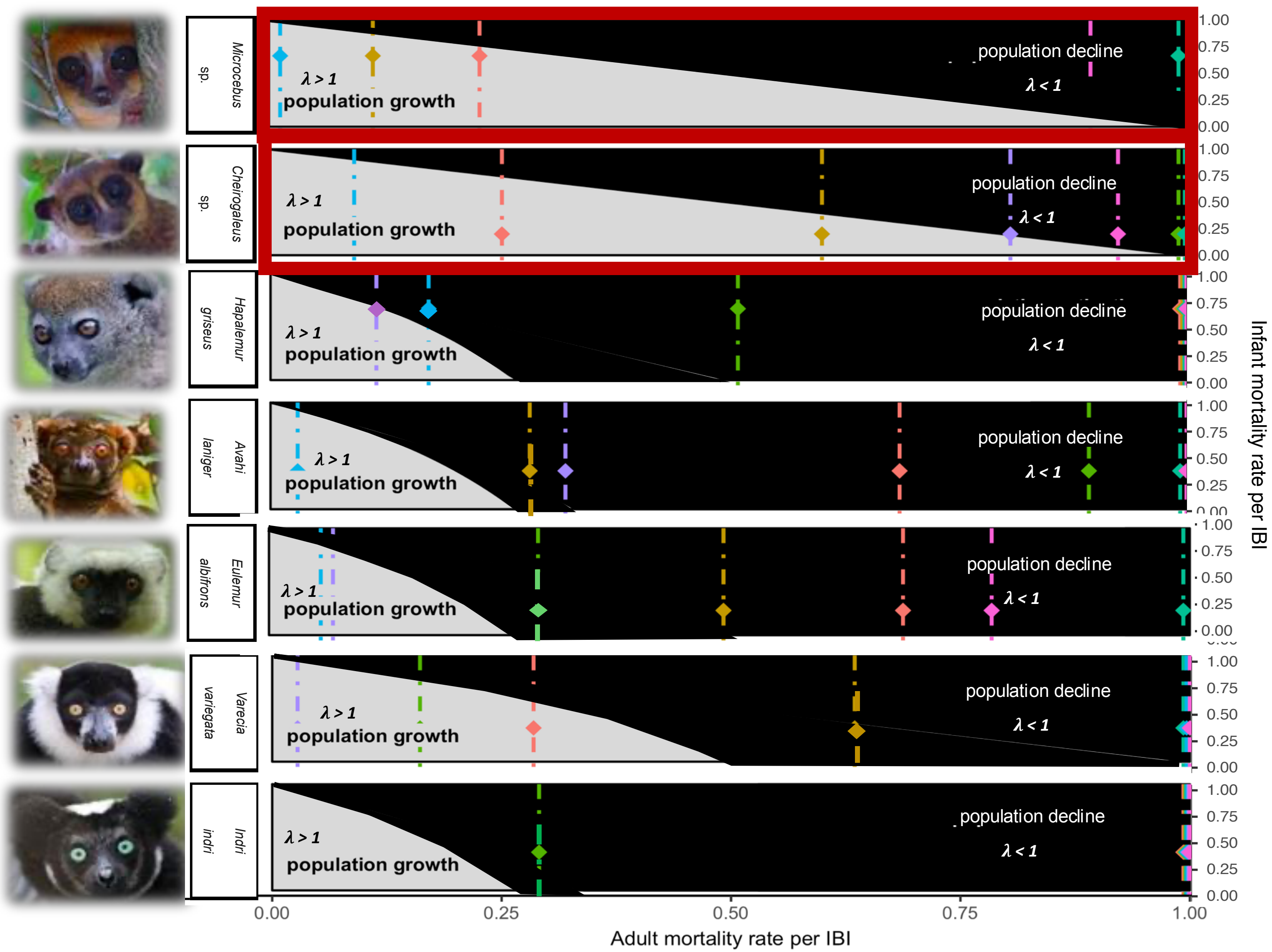


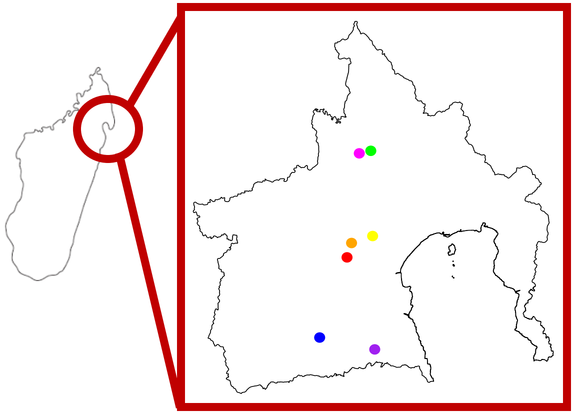
Colored vertical lines give **site-specific hunting rates** for adult lemurs.

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

Brook et al. 2018. *Conservation Biology.*

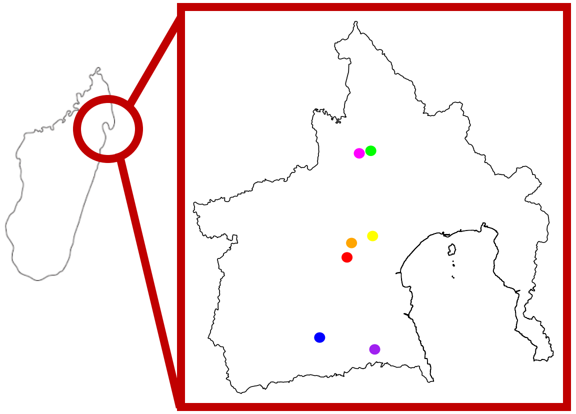
Small-bodied lemurs are largely **harvested at sustainable rates** on the Makira-Masoala peninsula.

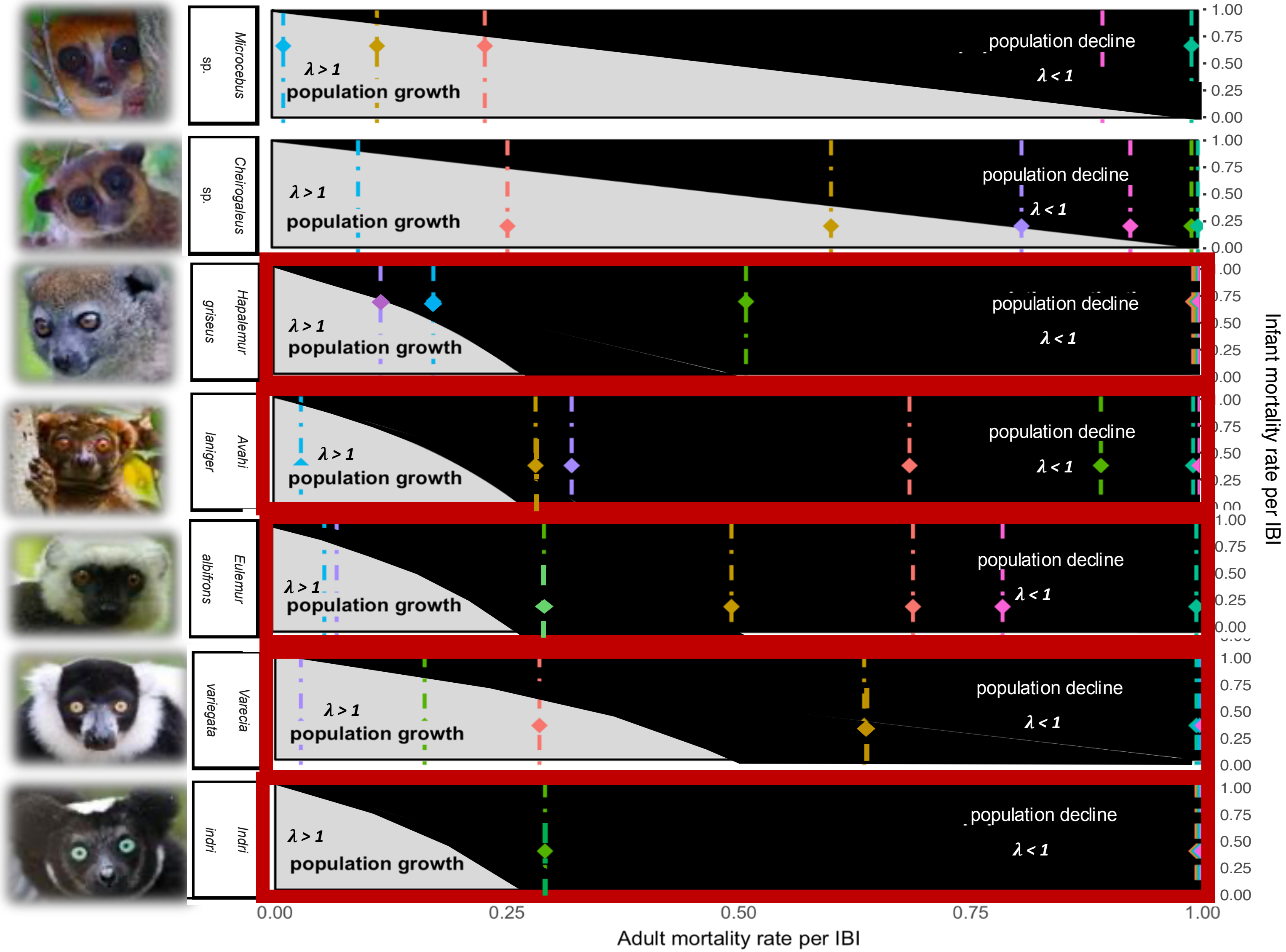




Brook et al. 2018. *Conservation Biology.*

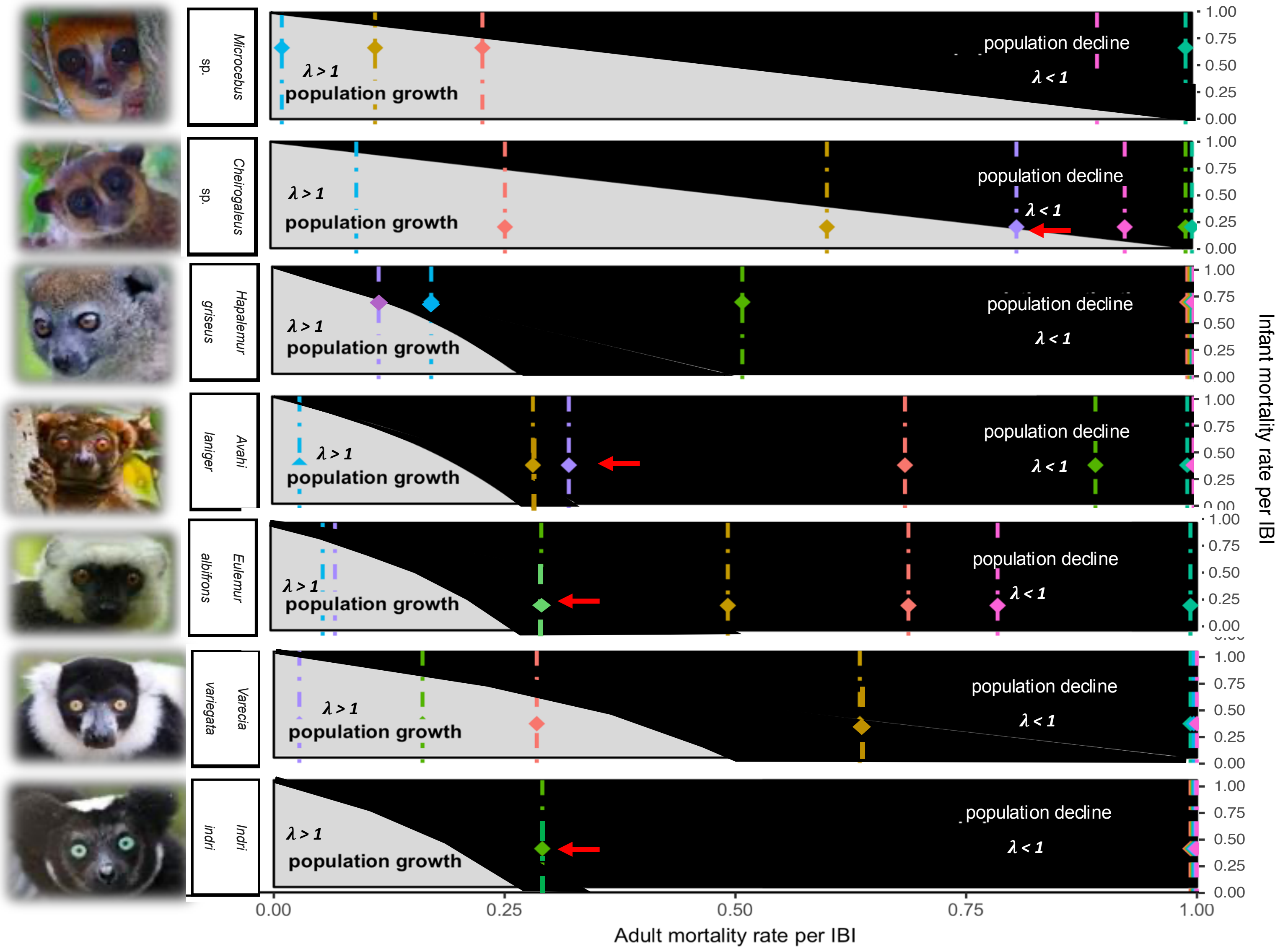
By contrast, **larger-bodied lemurs** are severely **threatened**.

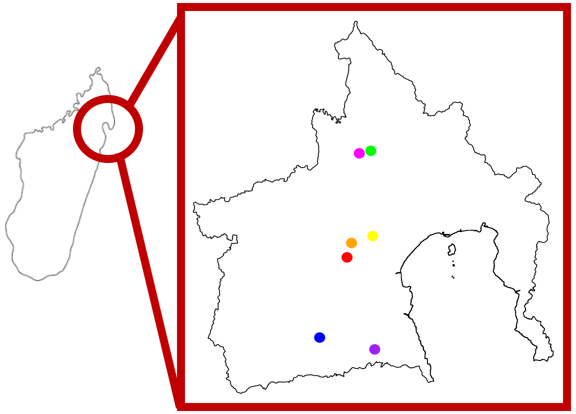




Brook et al. 2018. *Conservation Biology.*

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



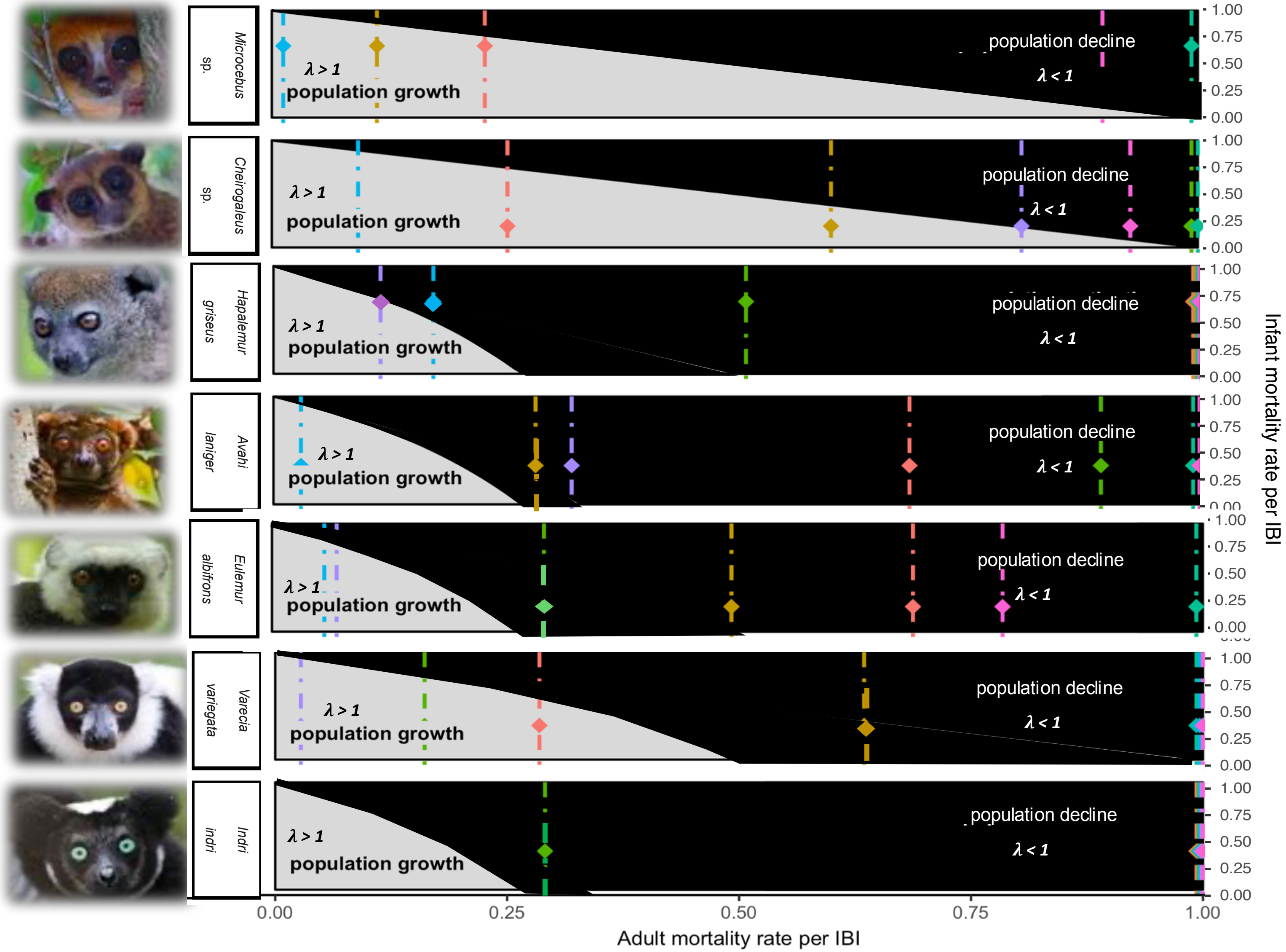


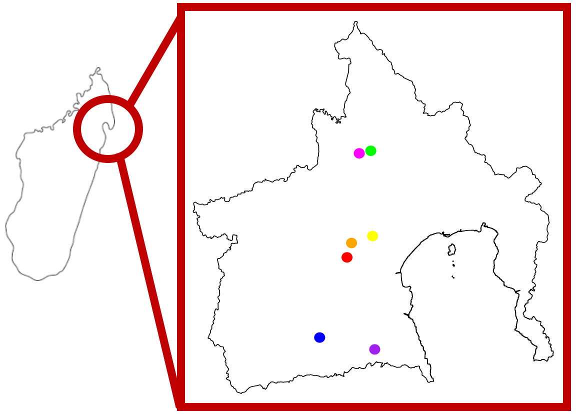
Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in N can be devastating:

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

Brook et al. 2018. *Conservation Biology.*

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



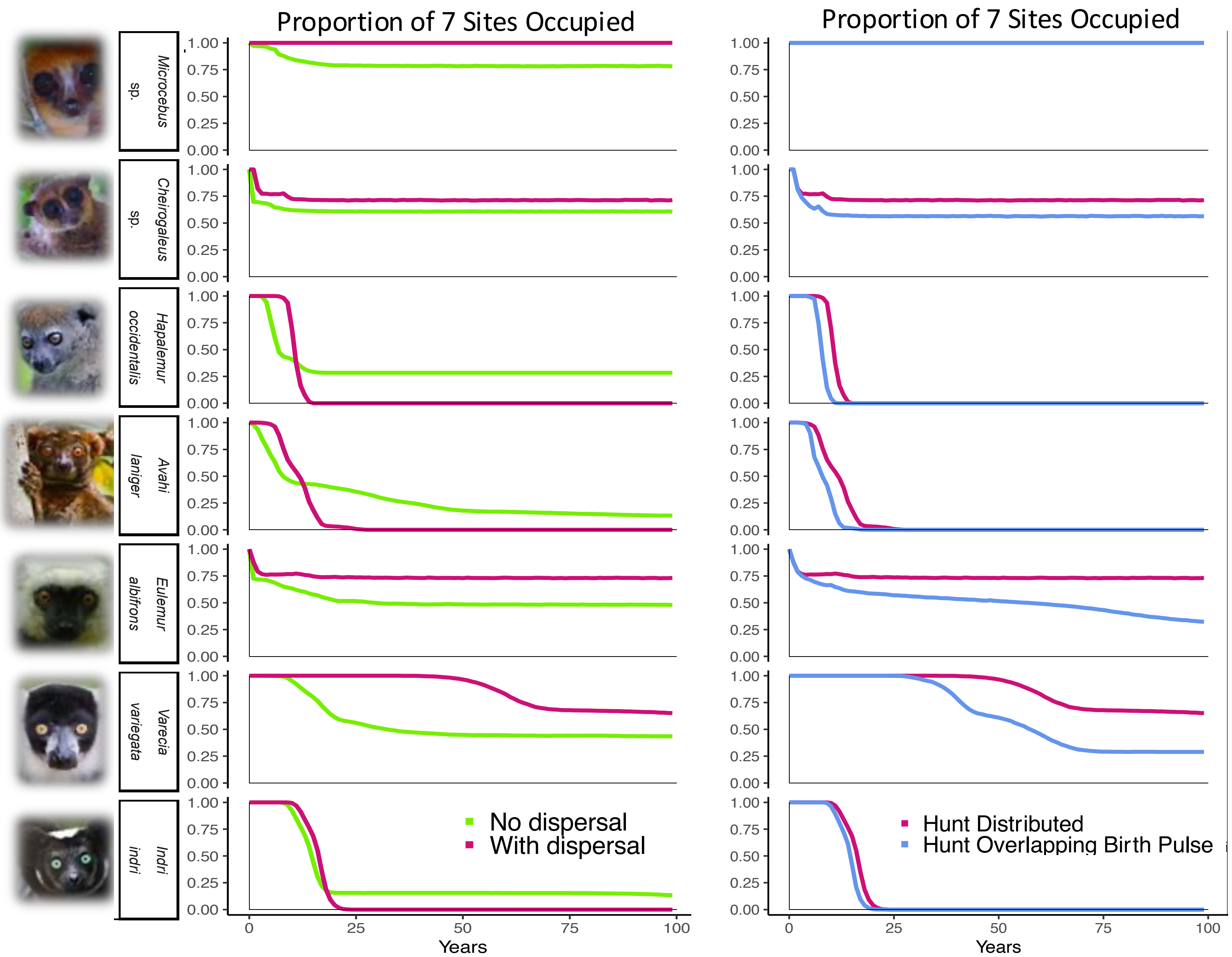


The **'Allee effect'** describes the correlation between population size and population 'fitness', often measured by the population rate of increase, λ.

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

Brook et al. 2018. *Conservation Biology.*

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



Brook et al. 2018. *Conservation Biology.*

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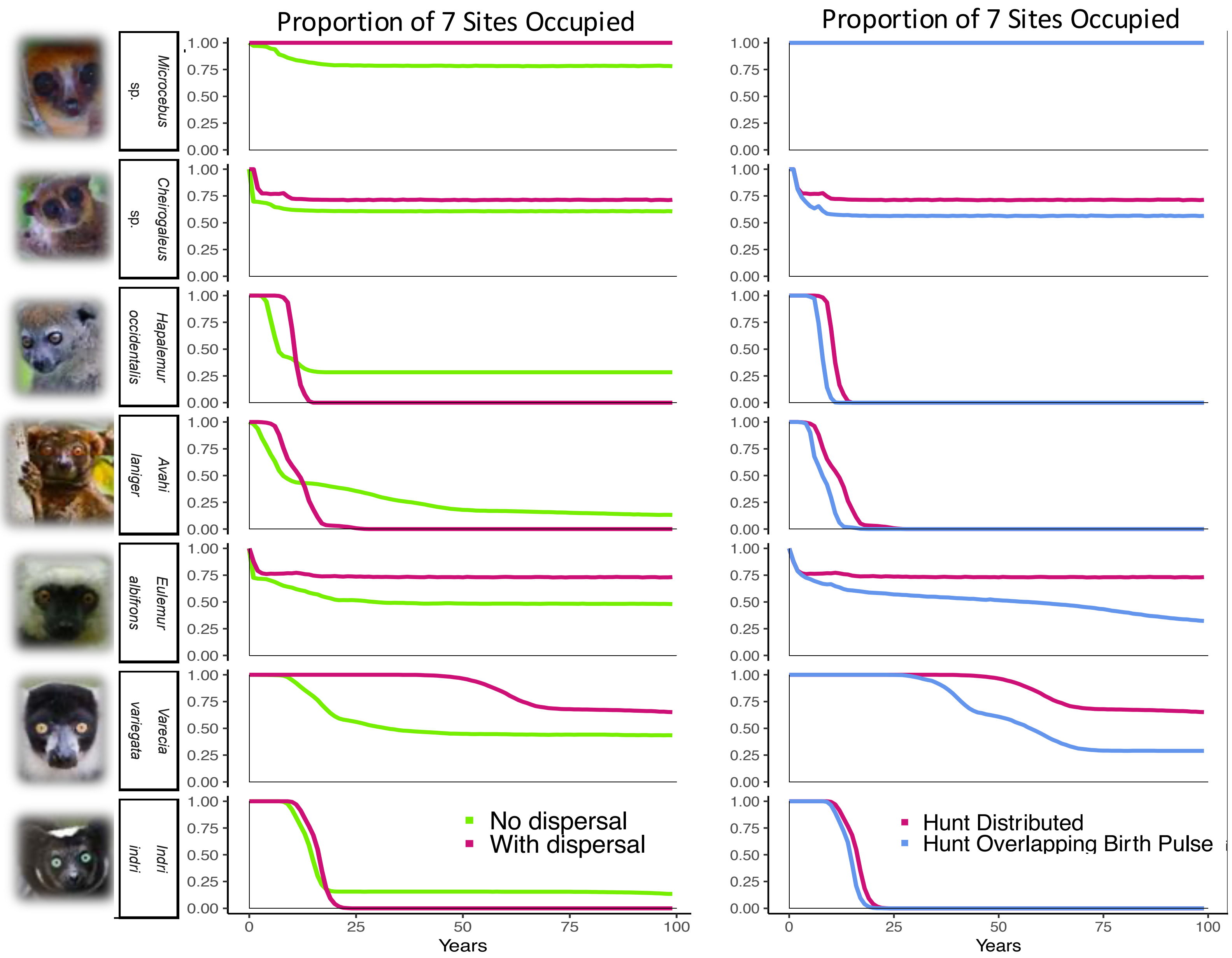


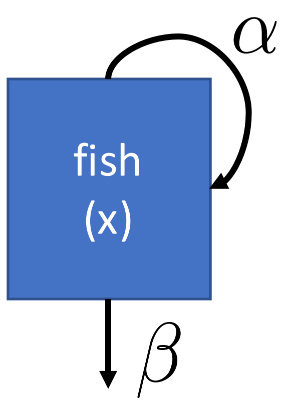
Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

Simplest representations of MSY:

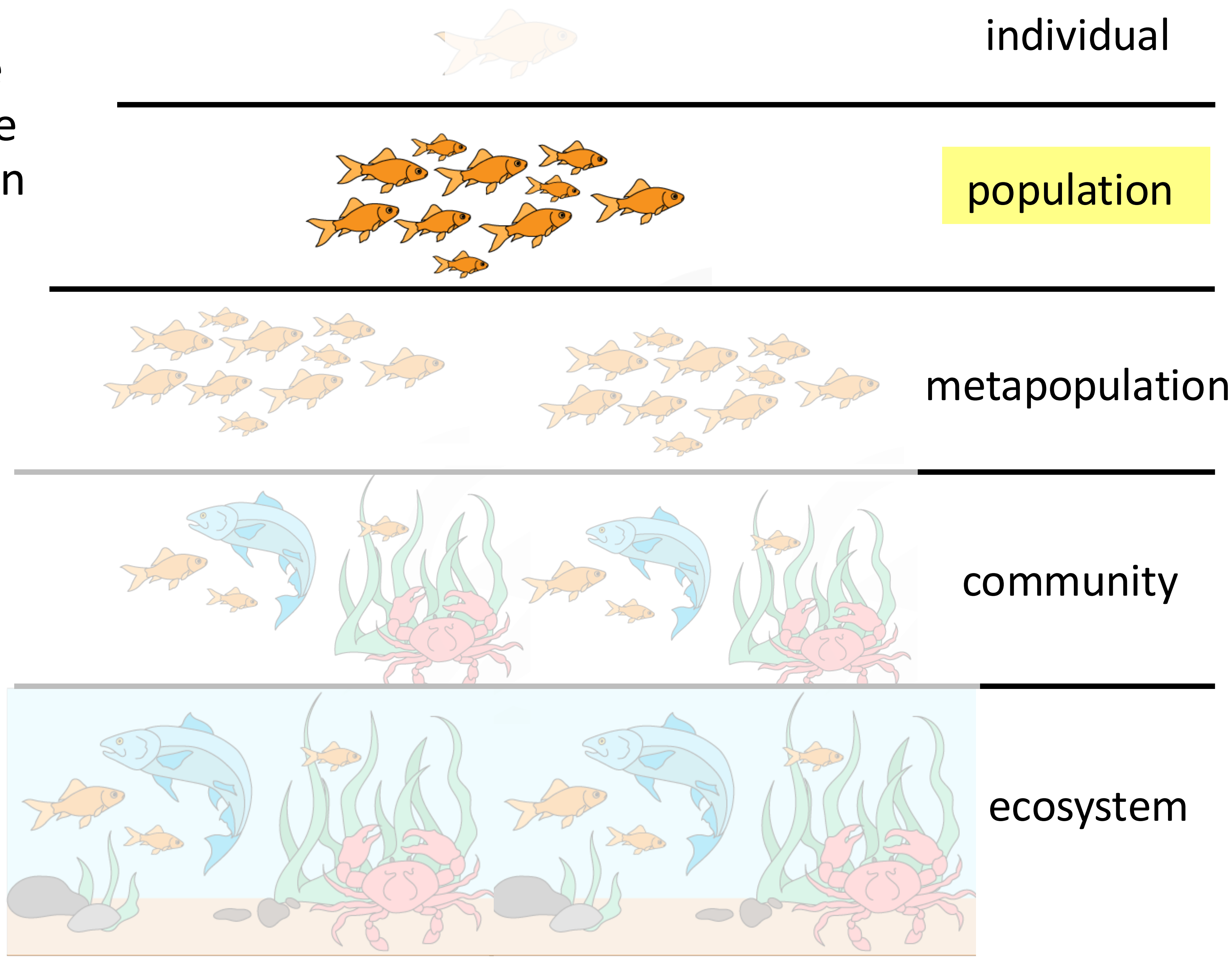
- Neglect population structure.
- Assume constant harvest.
- Ignore environmental and demographic stochasticity

Brook et al. 2018. *Conservation Biology.*

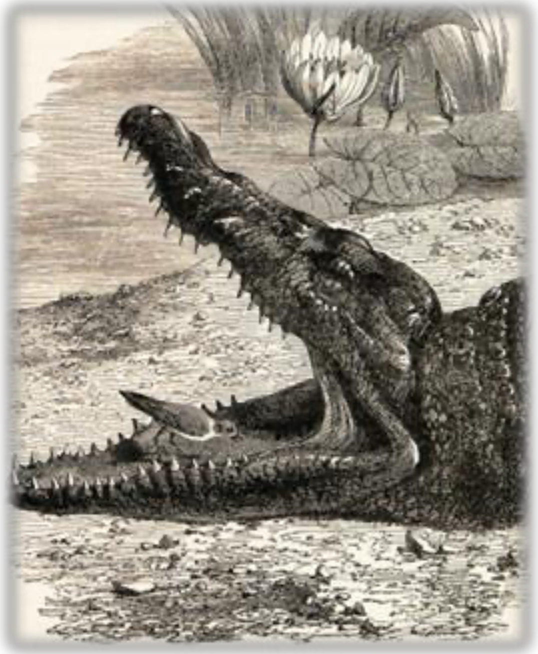
Population = multiple individuals of the same species (**conspecifics**) in the same habitat



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

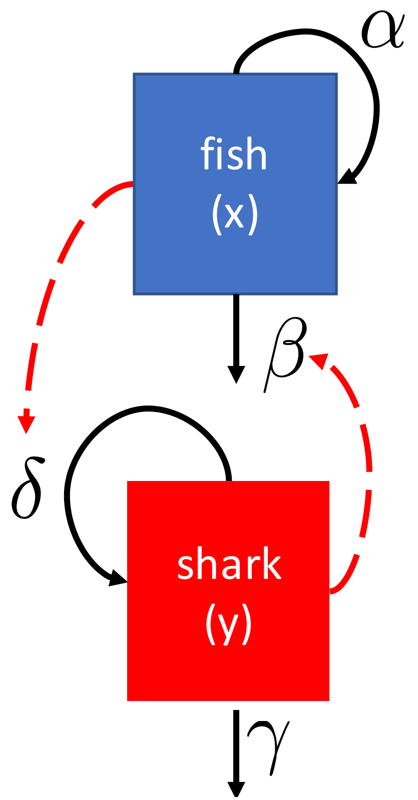


The logistic growth equation offers an explanation for population self-regulation, an example of **intraspecific competition**.

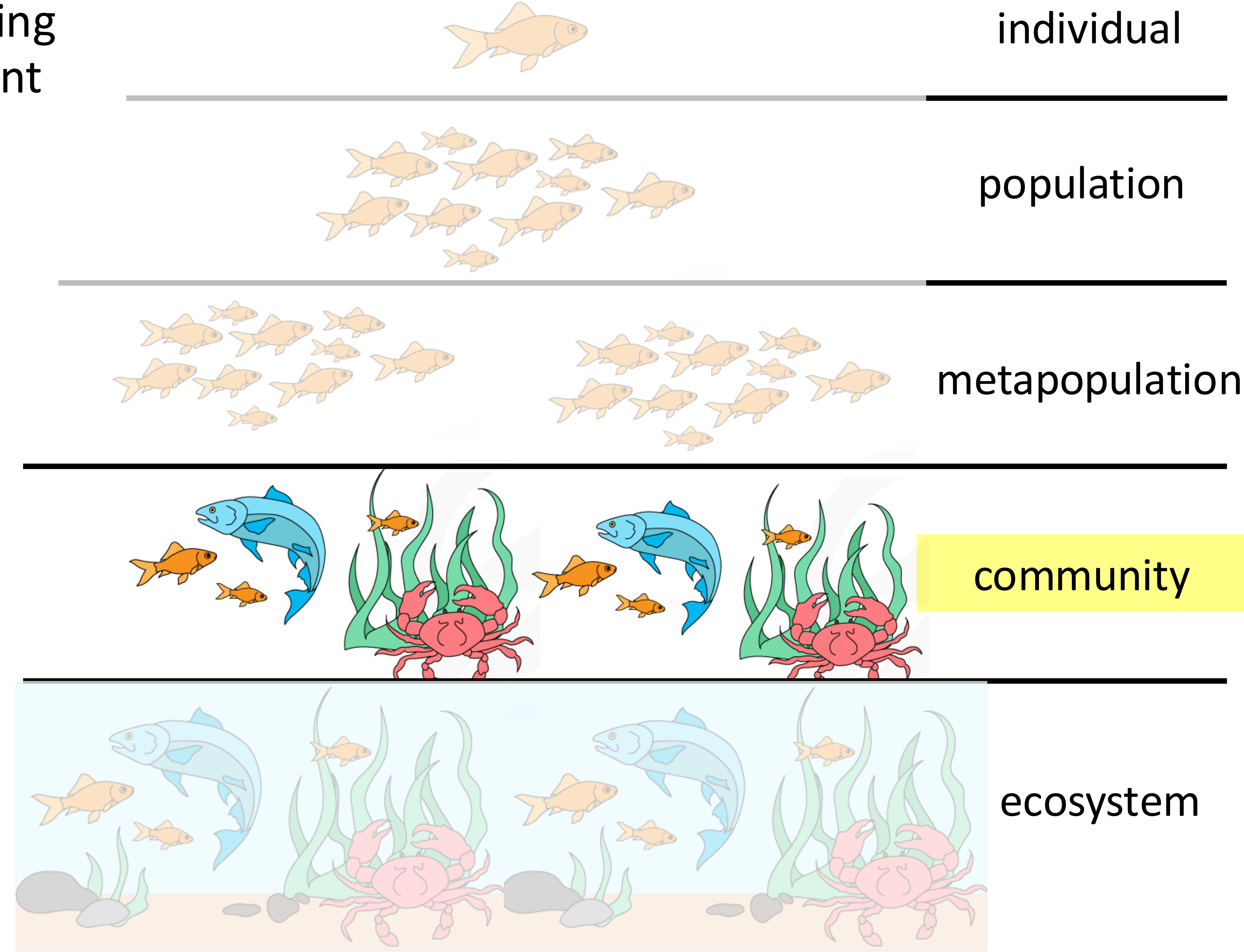


But ecology is the study of the **interactions** of organisms with each other and their environment, and in some cases, **interspecific interactions** are essential to understanding ecological systems.

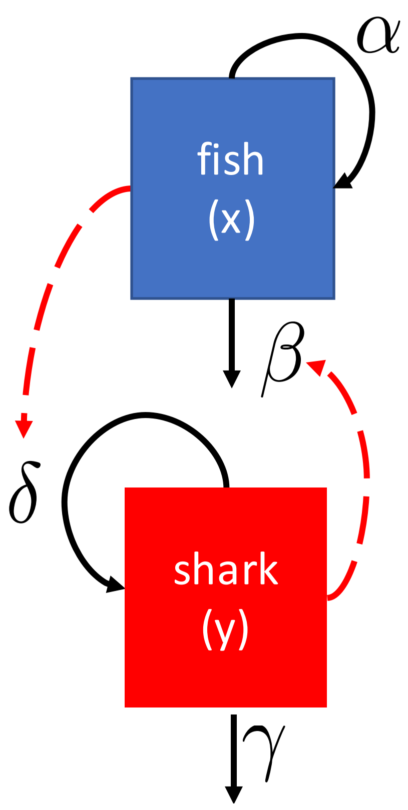
Community = interacting populations of different species



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



The Lotka-Volterra predator-prey model



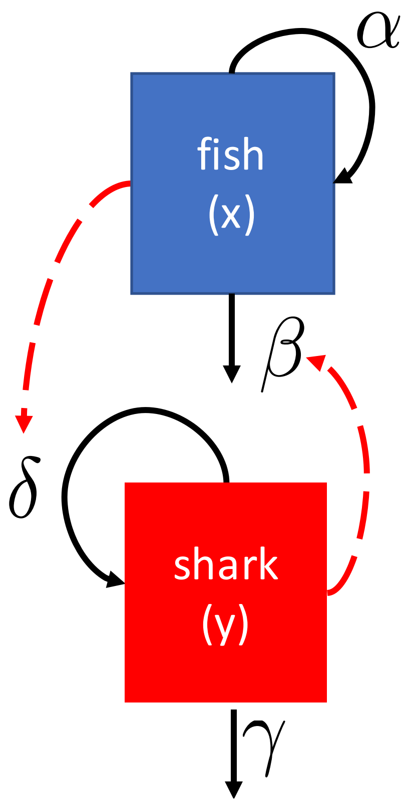
*How does **fish** abundance **vary** with **changes** in **shark** abundance?*

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

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

- First proposed by Polish-born American mathematician & chemist, Alfred J. Lotka, in 1920 to explain autocatalytic chemical reactions.
- Lotka worked with Soviet mathematician Andrey Kolmogorov to extend the model to "organic systems", originally studying plant-herbivore interactions.
- In 1926, Italian mathematician Vito Volterra independently developed the same model to explain the dynamics of predatory fish catches which increased immediately following WWI after years of low fishing.
- Idea that **interspecies interactions** regulate populations

The Lotka-Volterra predator-prey model



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

growth rate of prey, independent of predator

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

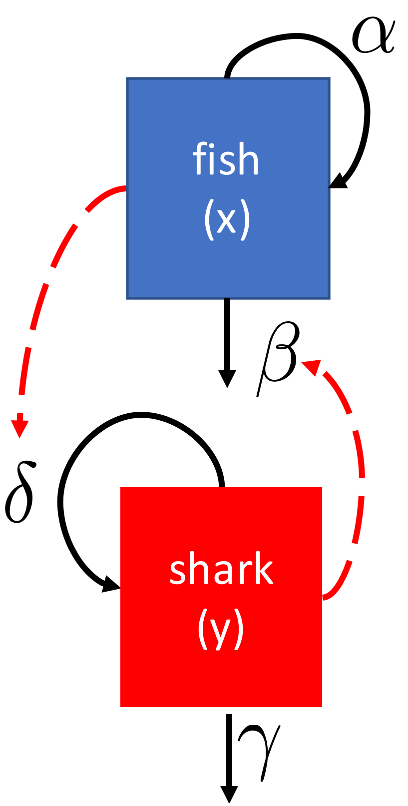
death rate of prey, depends on abundance of predator

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

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



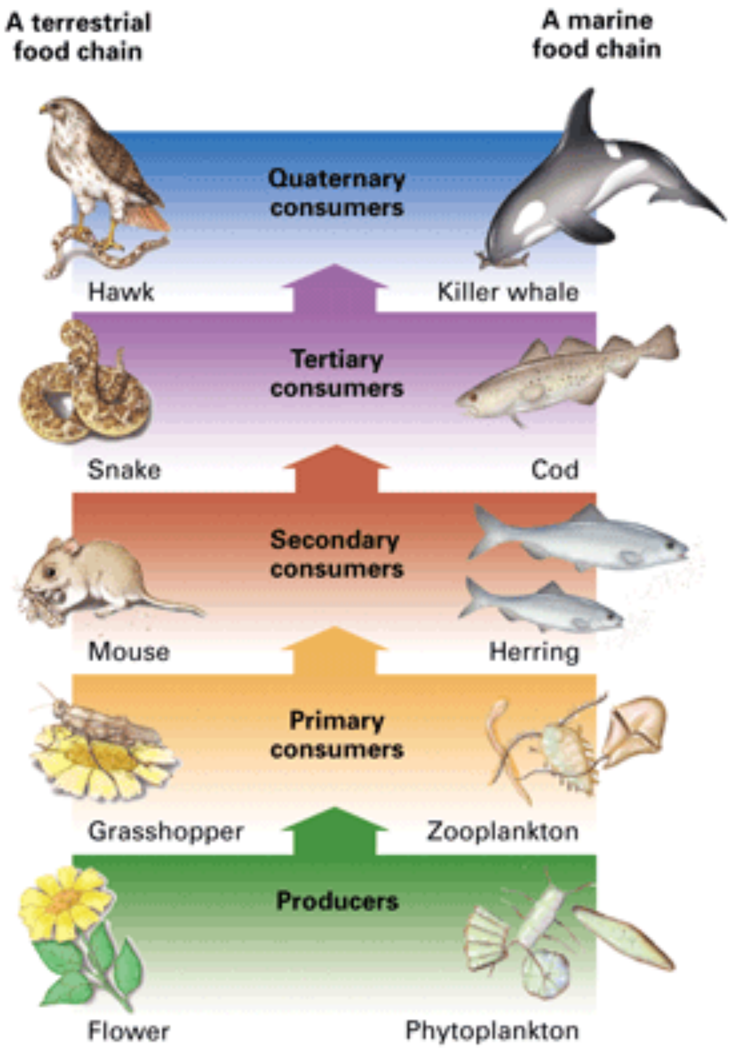
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

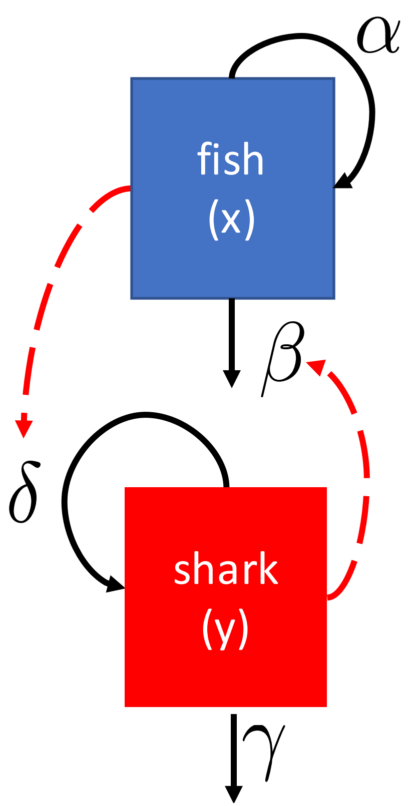
*How does **fish** abundance **vary** with **changes** in **shark** abundance?*

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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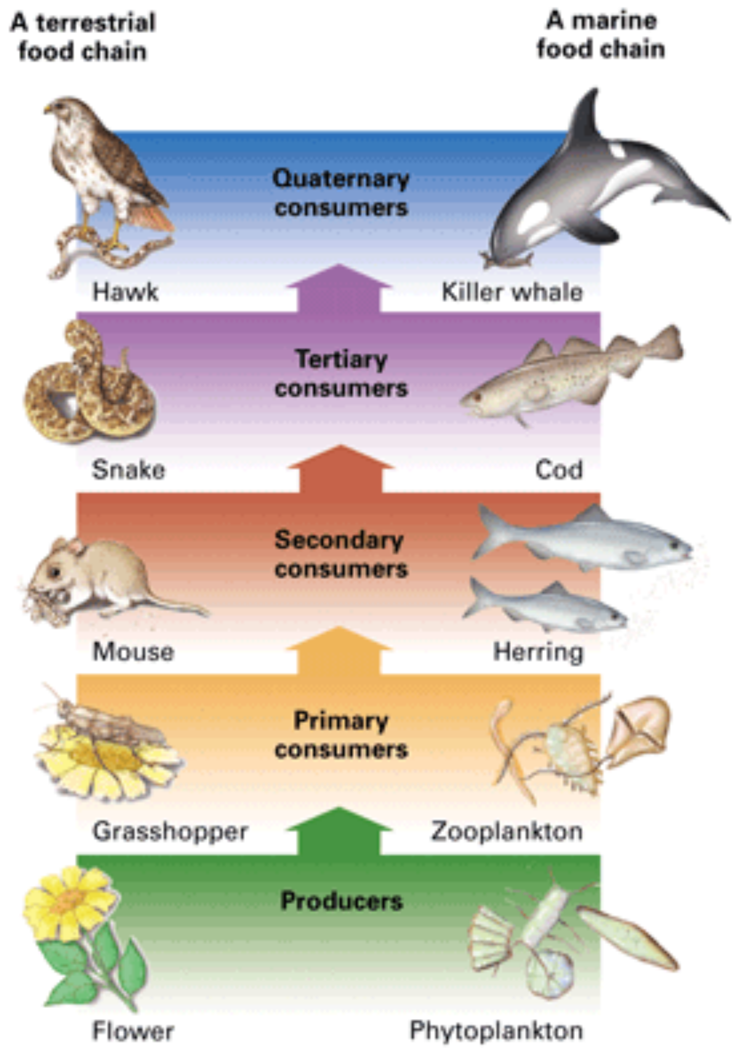
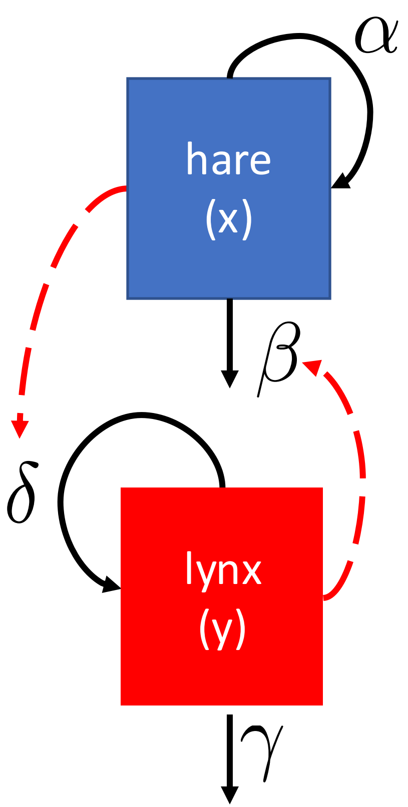


Lotka-Volterra predator-prey models with data



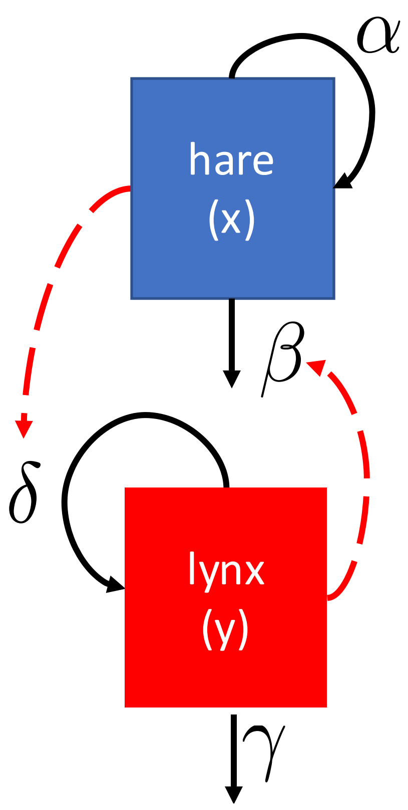
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

PRO PELLE CUTEM

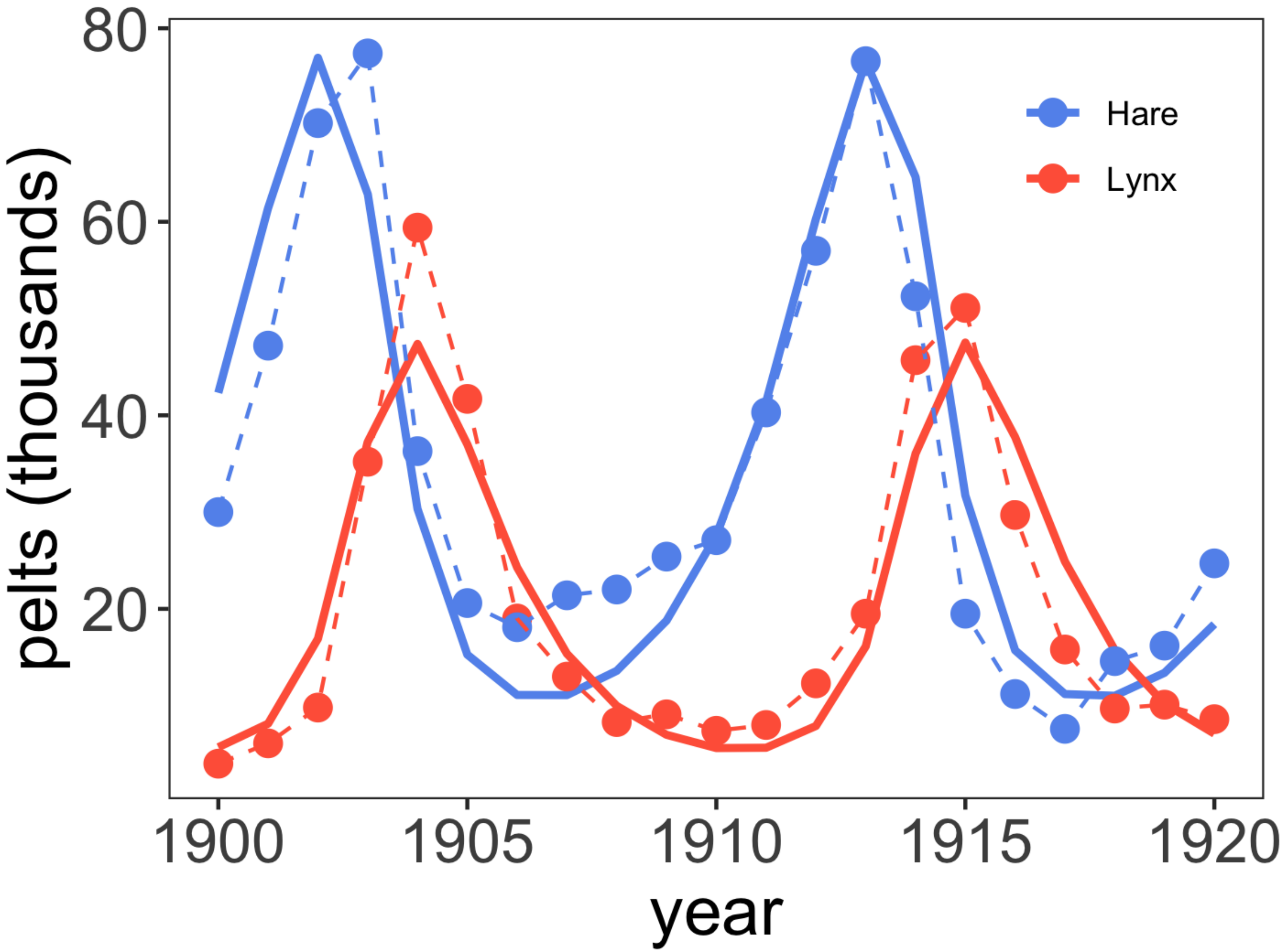
HUDSON'S BAY

INCORPORATED 2 MAY 1670

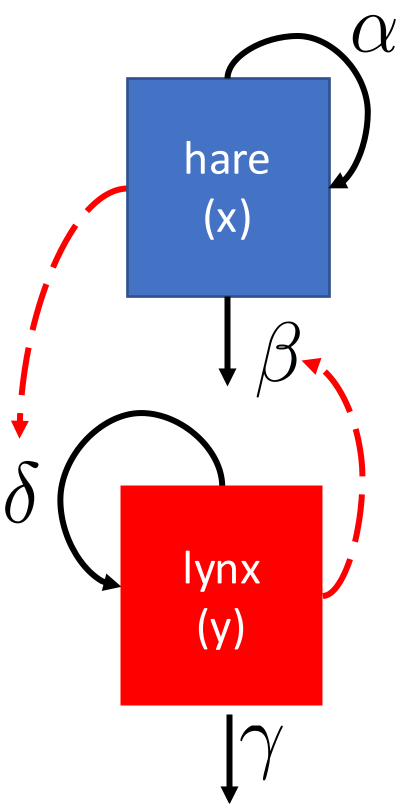
Lotka-Volterra predator-prey models with data

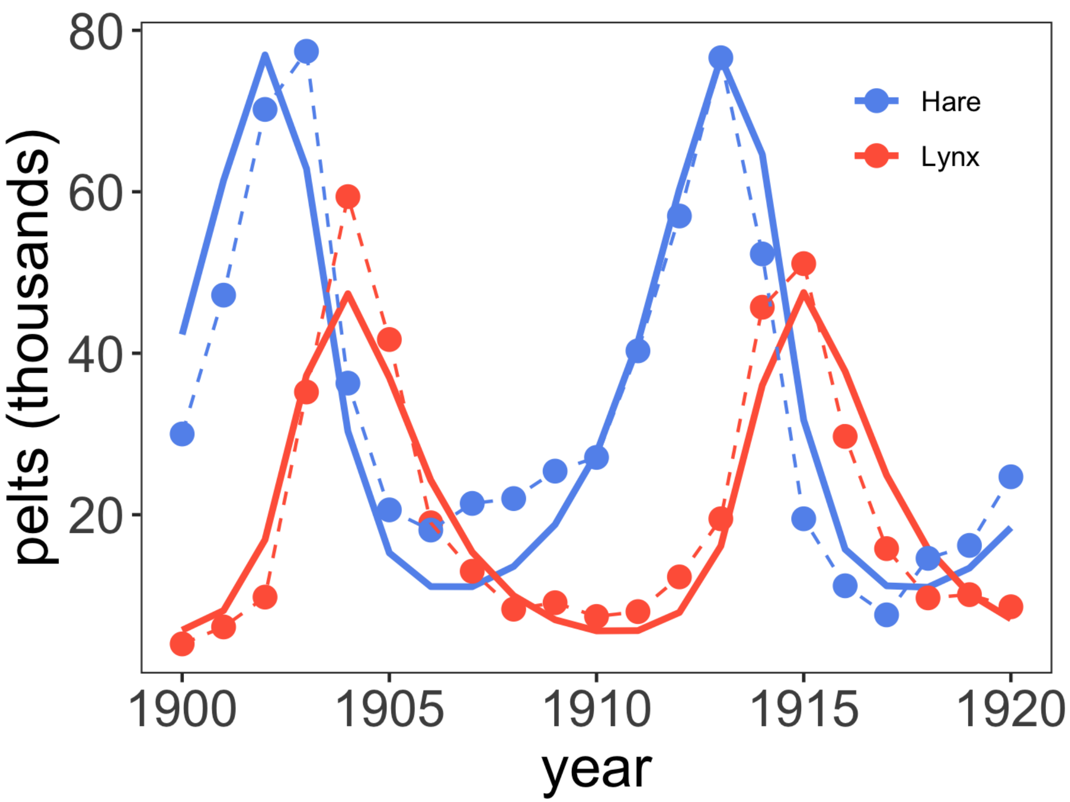


*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*



Lotka-Volterra predator-prey models with data





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

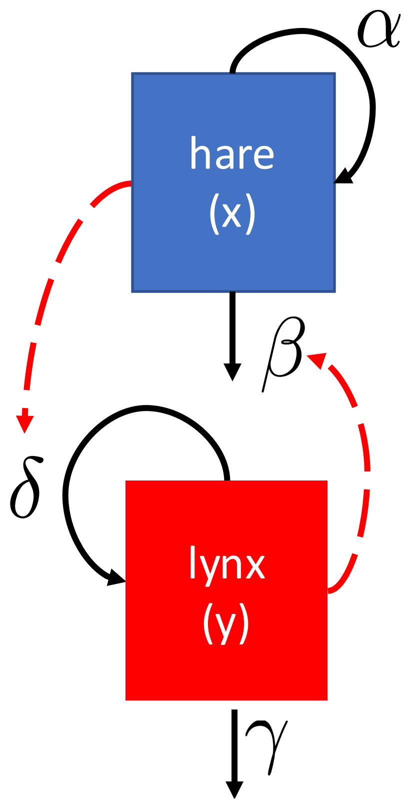
$$\frac{dx}{dt} = \alpha x - \beta xy$$

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

- 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

Lotka-Volterra predator-prey models with data



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

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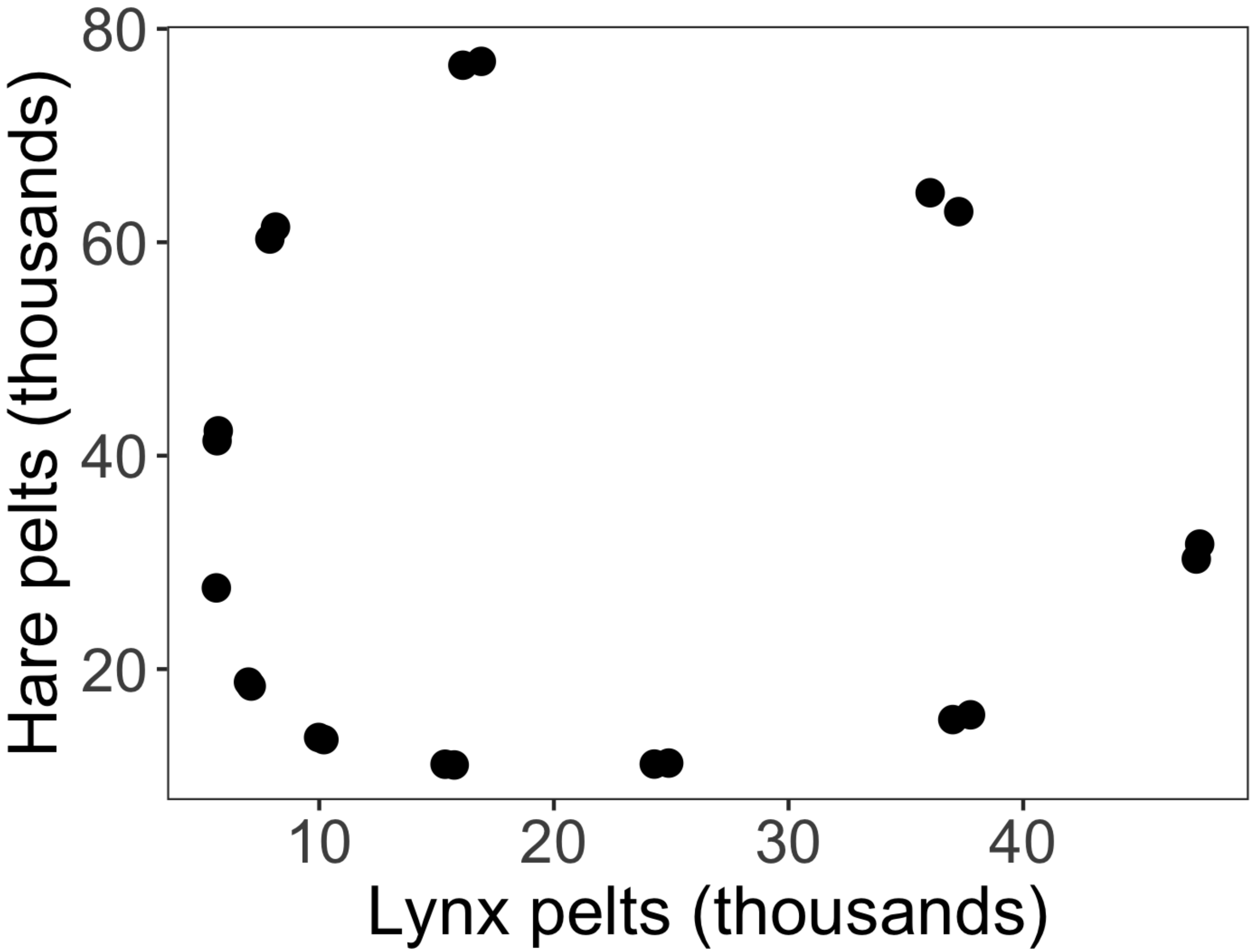
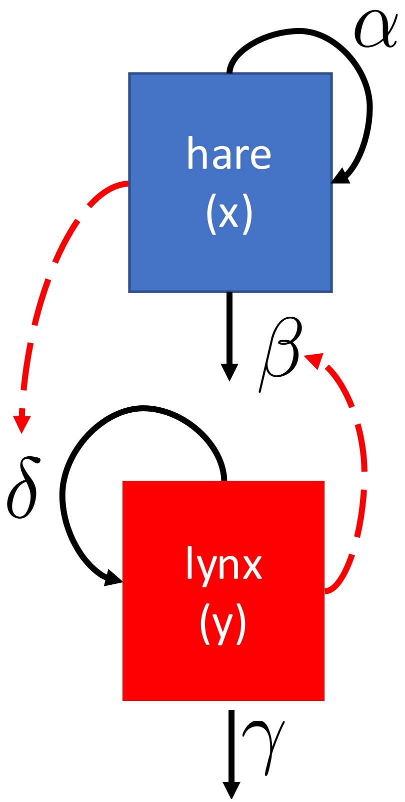
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

Predator-prey cycles can be visualized as oscillations.



Lotka-Volterra predator-prey models with data



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