

# Fundamentals of Ecology

Week 6, Ecology Lecture 2

Cara Brook

February 9, 2023

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## Population growth, specifically

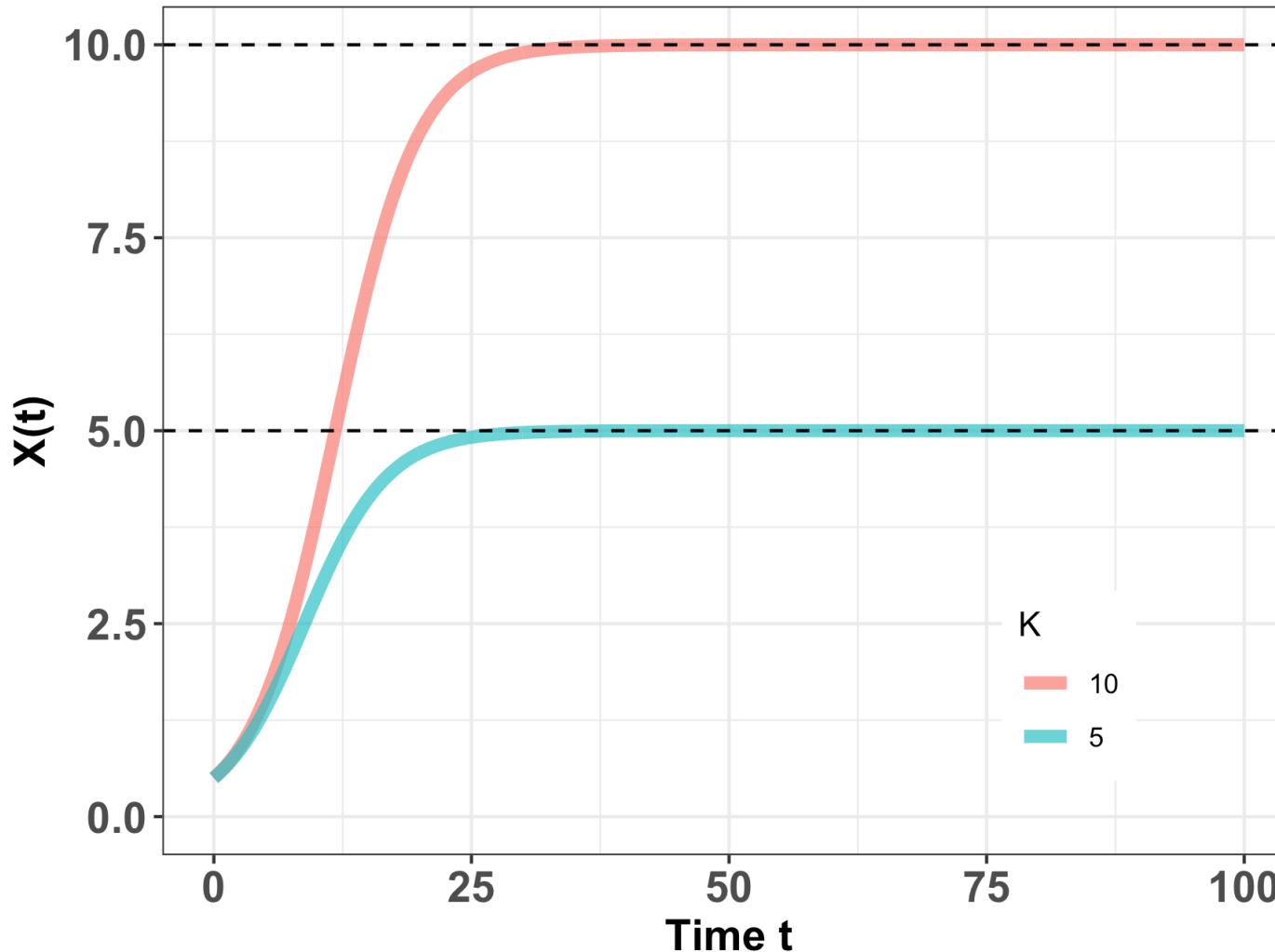
- We can model population growth as geometric in discrete time or exponential in continuous time
- Logistic growth models describe density-dependent growth rates that limit population growth as abundance approaches some specified carrying capacity
- Logistic growth models imply a stable equilibrium where the population size ( $N$ ) is equal to the carrying capacity ( $K$ )
- Despite the dire predictions of Malthus in the late 1700s, most human populations do not appear to yet be approaching carrying capacity

# Logistic growth and equilibrium

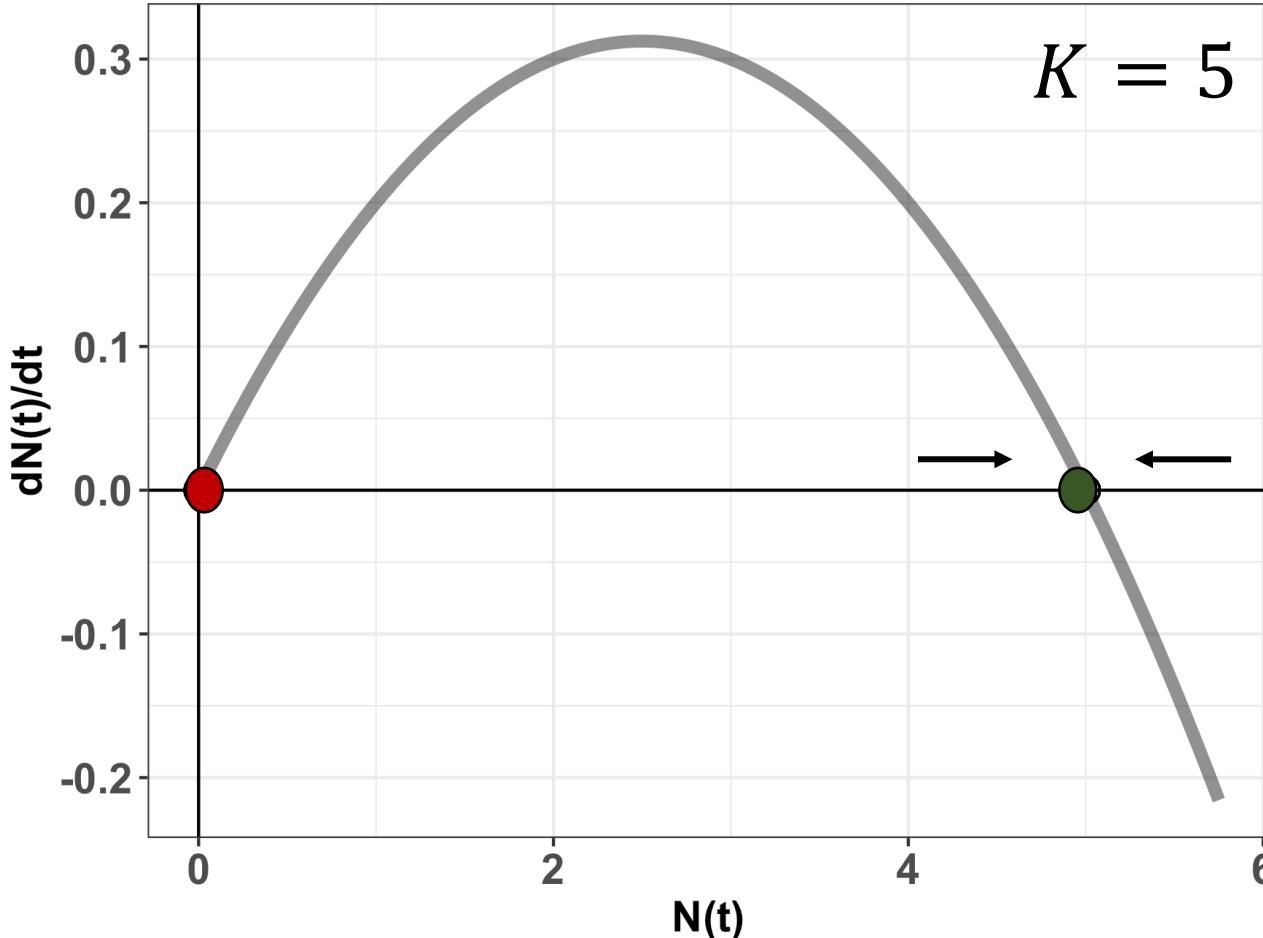
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

$$\frac{dN}{dt} = 0$$

When population size is not changing, the population is said to be at **equilibrium**.



# Logistic growth and equilibrium



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When population size is not changing, the population is said to be at **equilibrium**.

Mathematically, the carrying capacity ( $K$ ) can be shown to be a **stable equilibrium**, meaning that if the system is perturbed, growth will accelerate or decelerate to return the population to  $K$ .

# Logistic growth and harvesting

Humans have attempted to leverage density-dependent growth rates for **sustainable harvesting**, which refers to the offtake of individuals within a population's capacity for replenishment. Frequently, this refers to the harvesting of animals for human consumption.

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$$\text{change in population size with time} \longrightarrow \frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - H$$

Diagram illustrating the logistic growth equation with annotations:

- change in population size with time** →  $\frac{dN}{dt}$
- intrinsic growth rate** →  $rN$
- density-dependence** →  $\left(1 - \frac{N}{K}\right)$
- carrying capacity** →  $K$
- population size** →  $N$
- harvesting rate** →  $H$

# Logistic growth and harvesting

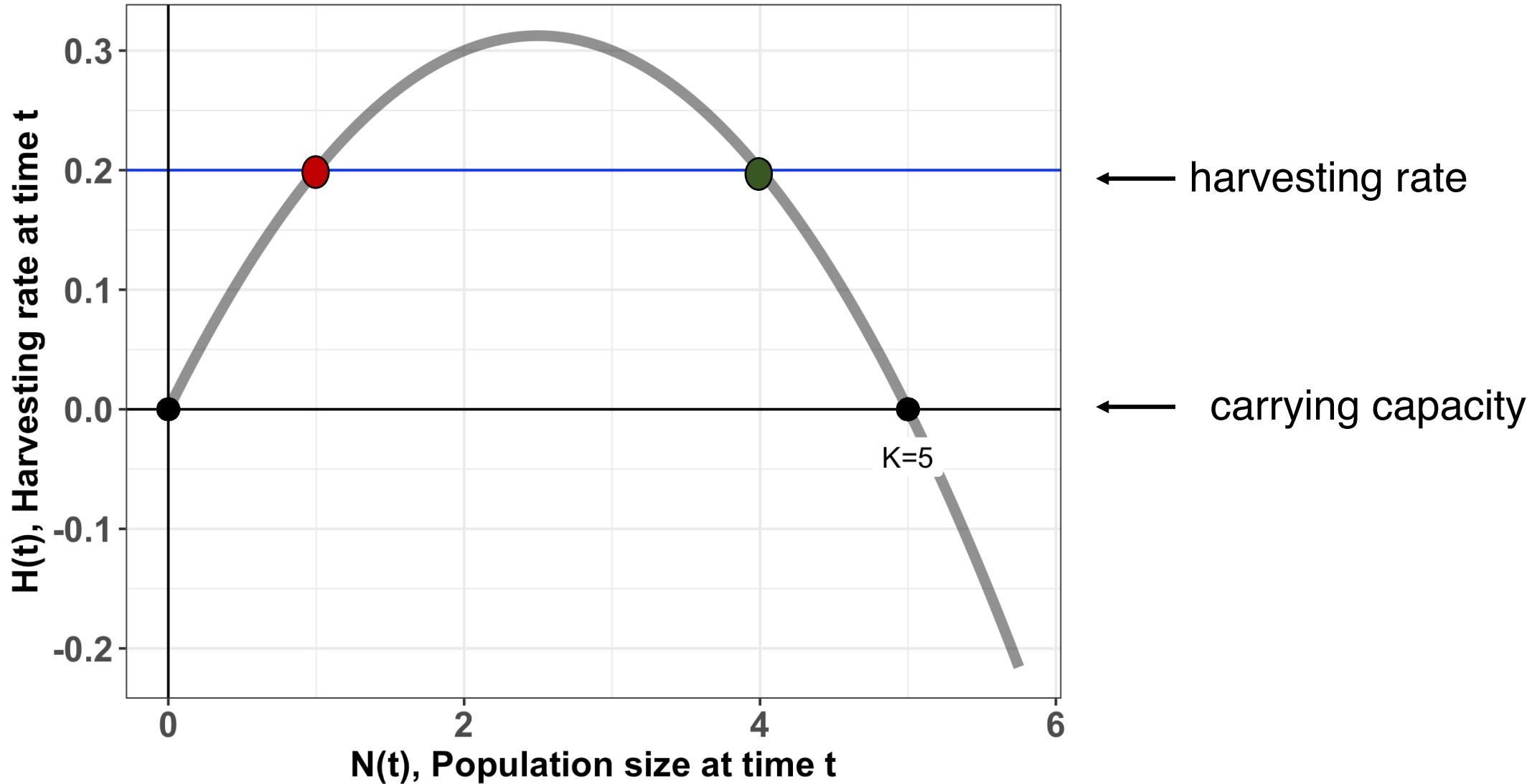
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right) - H$$

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

For a harvested population, **theoretically**, the population size is at equilibrium if the **harvest rate equals the growth rate**.

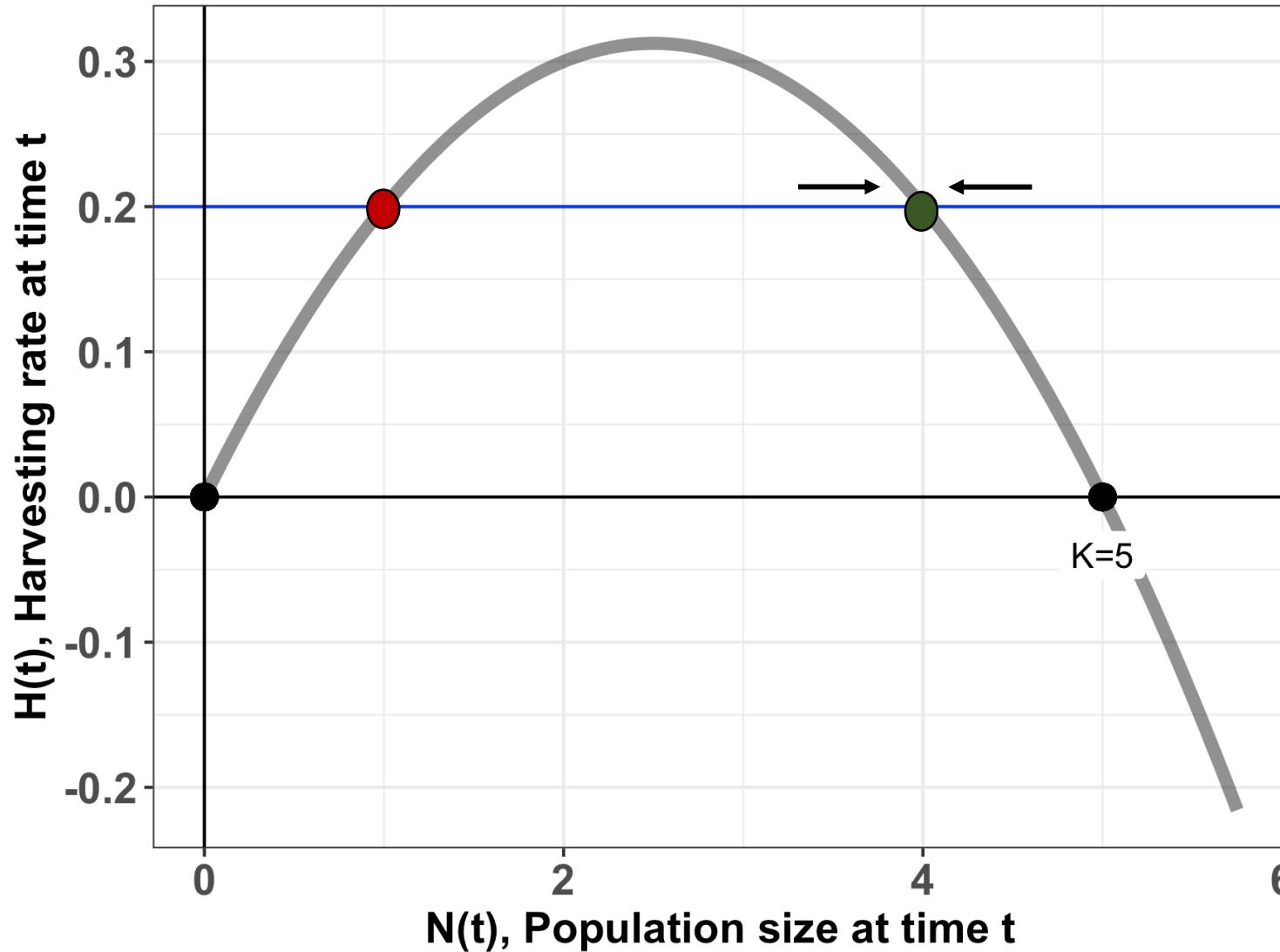
The stability of harvesting depends on population size.

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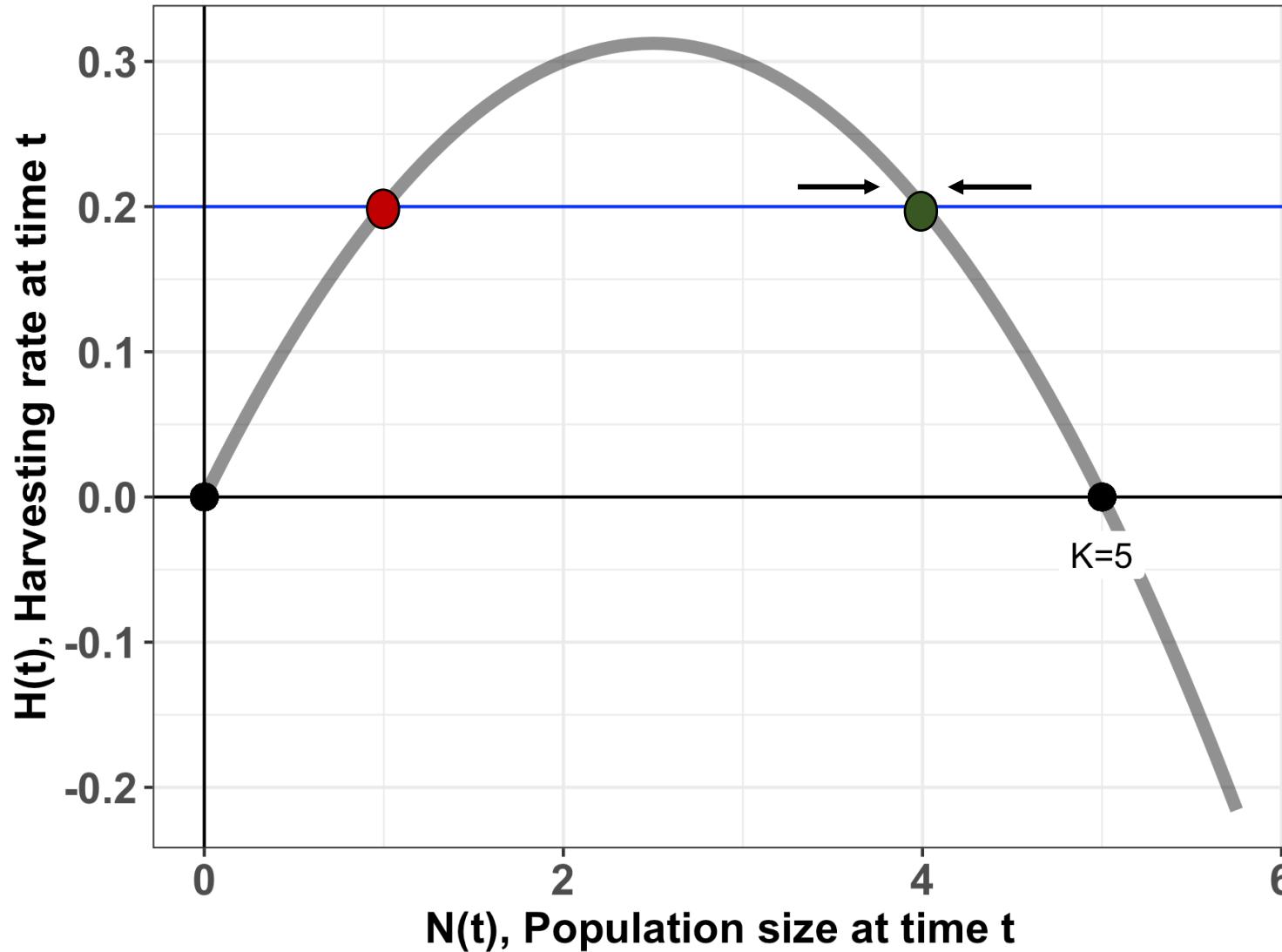
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**stable equilibrium**  
For a population of  $N=4$ ,  
a harvest rate of 0.2  
(animals/timestep)  
results in a stable  
equilibrium (**sustainable  
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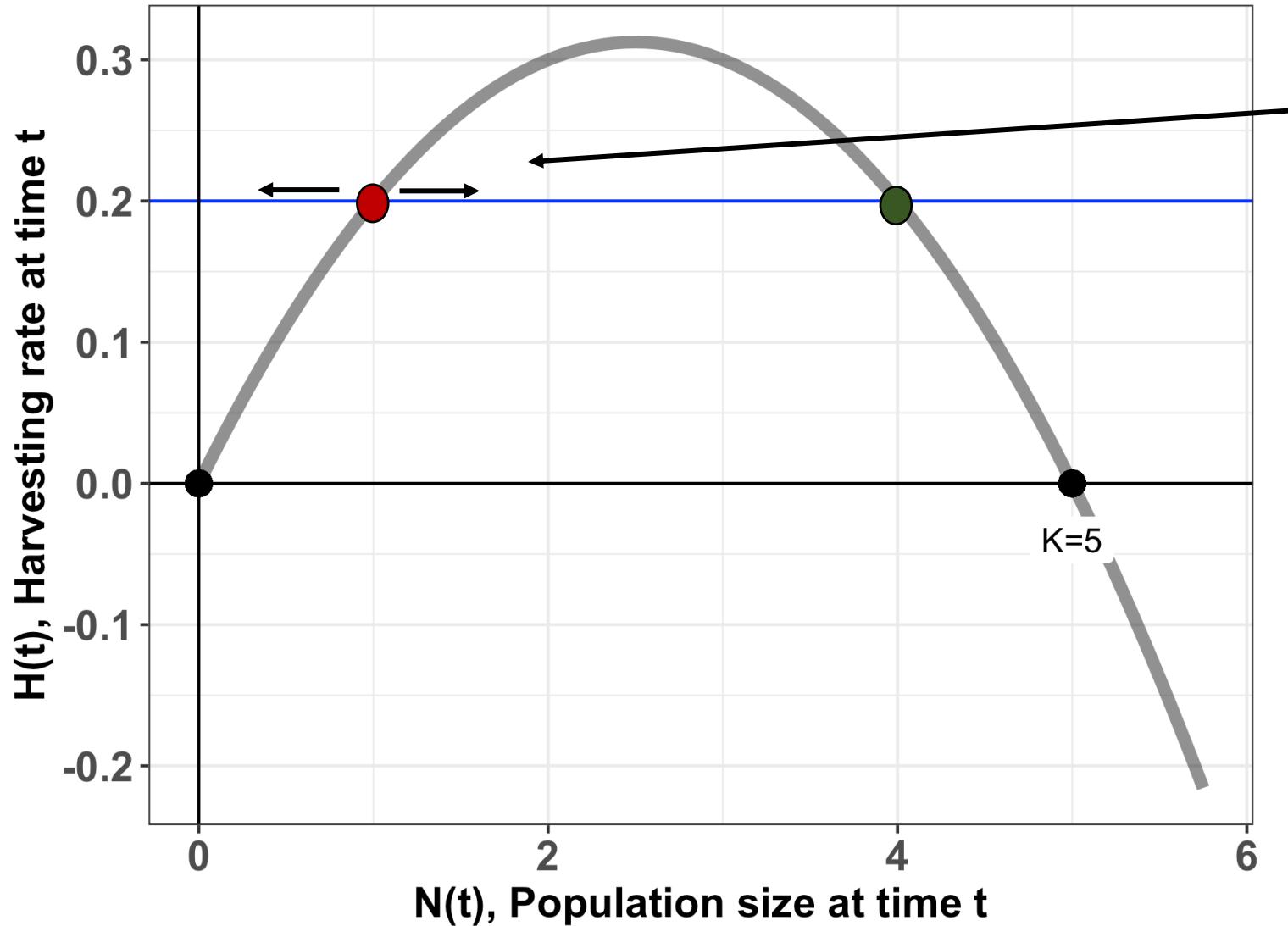


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Increases or decreases  
in population size will be  
compensated to return  
the system to  $N=4$ .

The stability of harvesting depends on population size.

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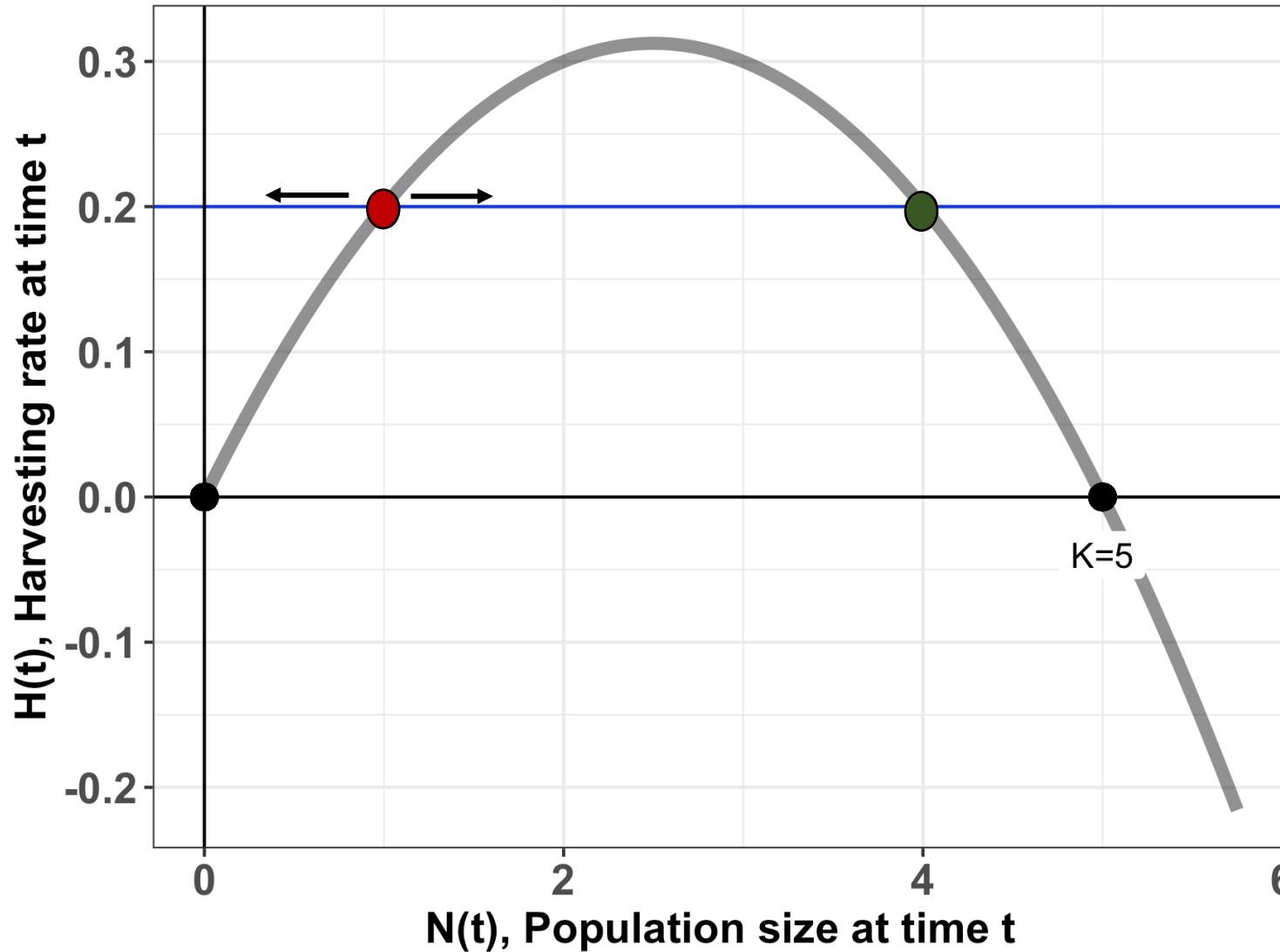


### unstable equilibrium

For a population of  $N=1$ , a harvest rate of 0.2 (animals/timestep) results in an unsustainable equilibrium.

The stability of harvesting depends on population size.

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



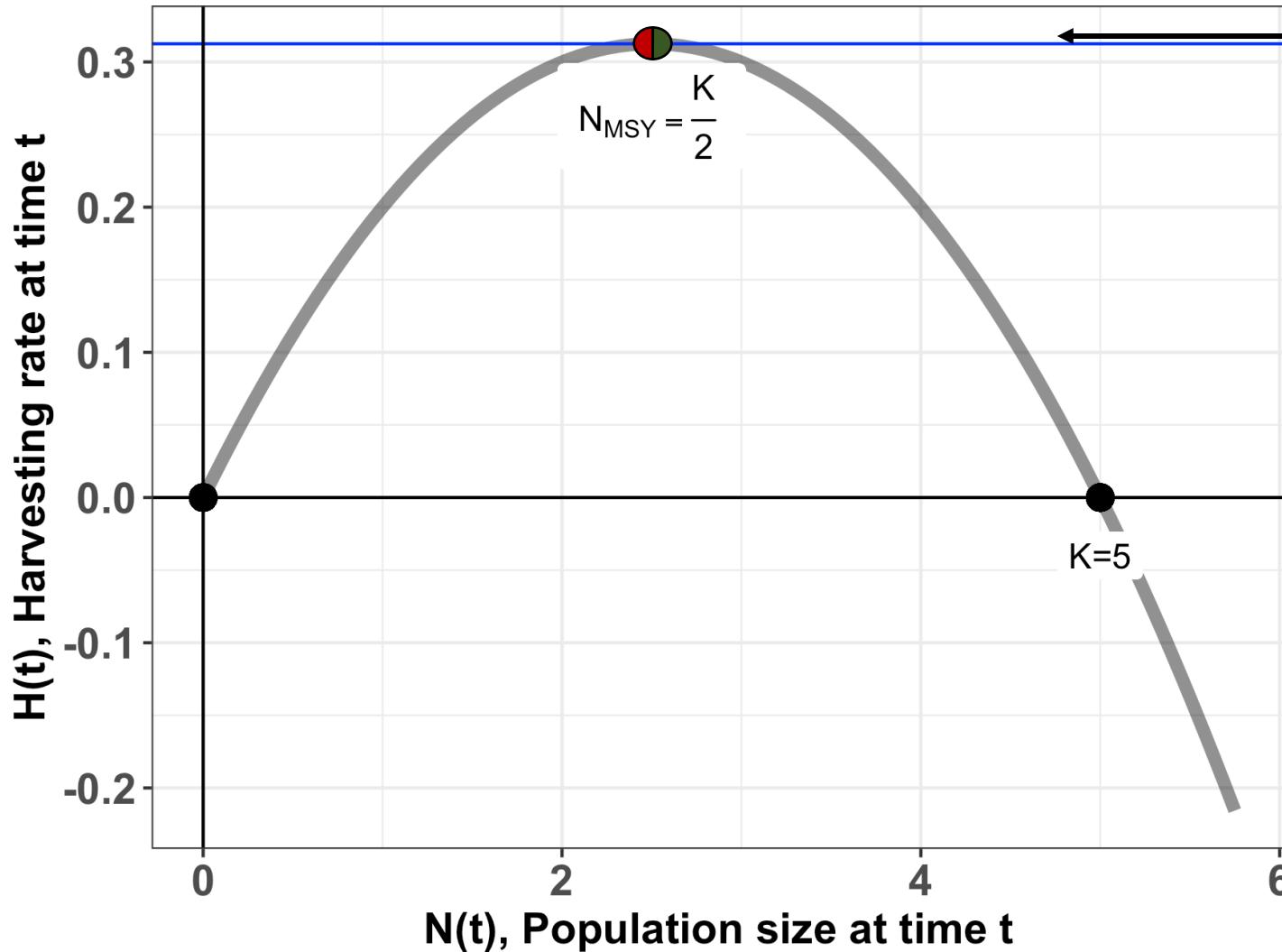
### unstable equilibrium

For a population of  $N=1$ , a harvest rate of 0.2 (animals/timestep) results in an unsustainable equilibrium.

Random increases or decreases in population size will result in the population moving away from  $N=1$  to, respectively,  $N=4$  or  $N=0$  (the latter is a **population collapse**).

# Maximum sustainable yield (MSY)

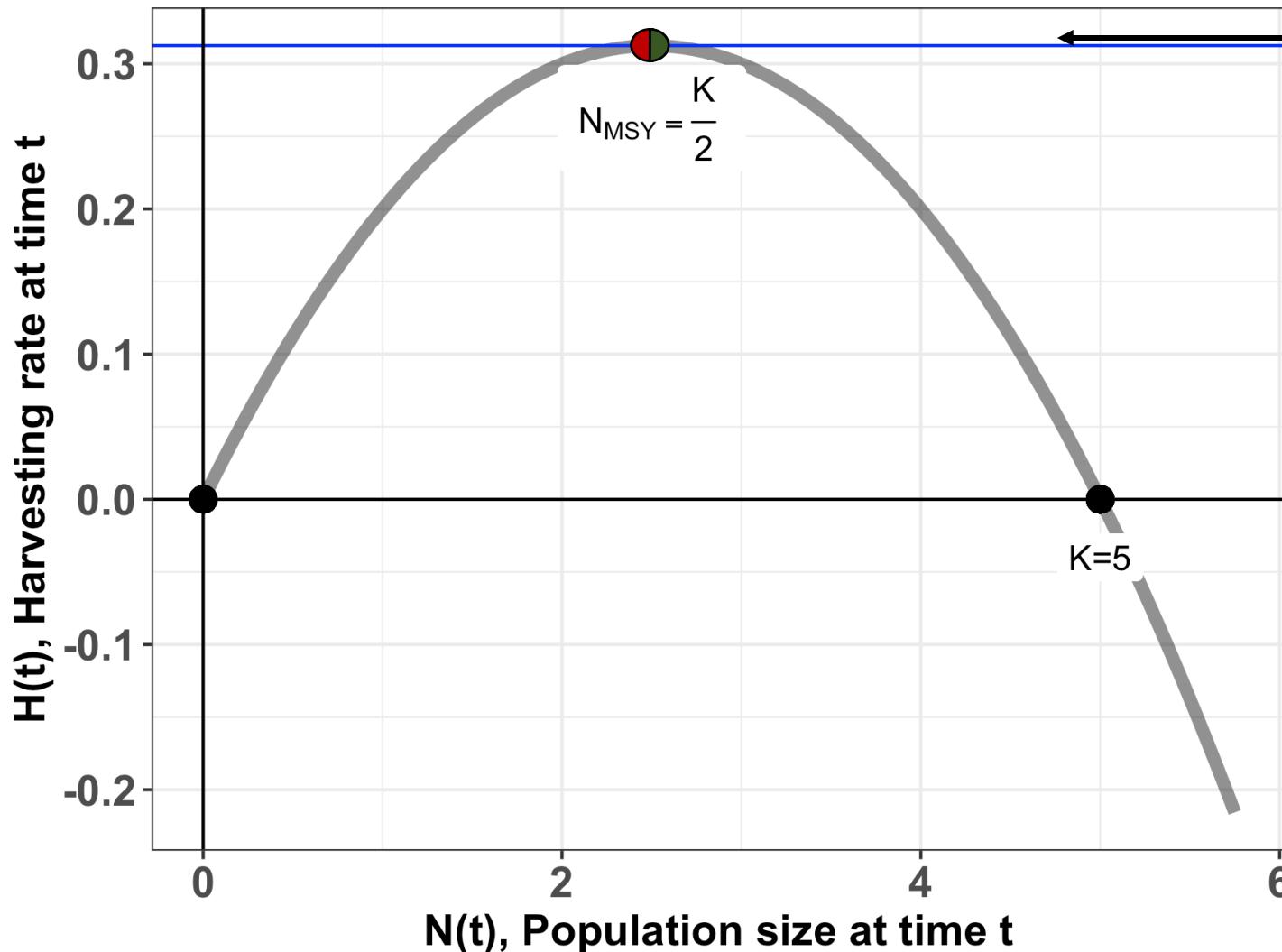
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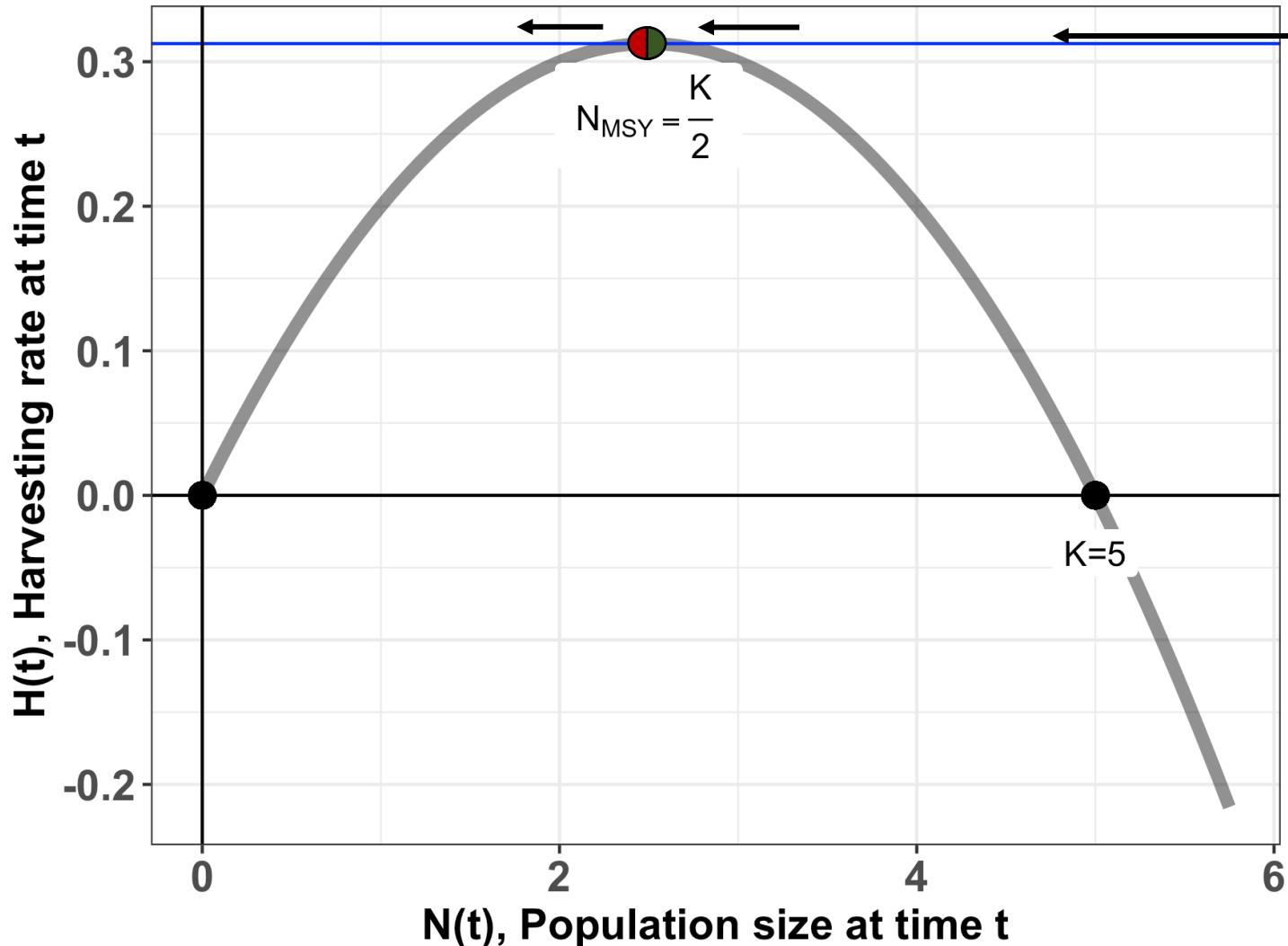
Theoretically, harvest could be maximized here as well:

$$\text{MSY: } H_{max} = \frac{rK}{4}$$

*take the derivative with respect to  $N$*

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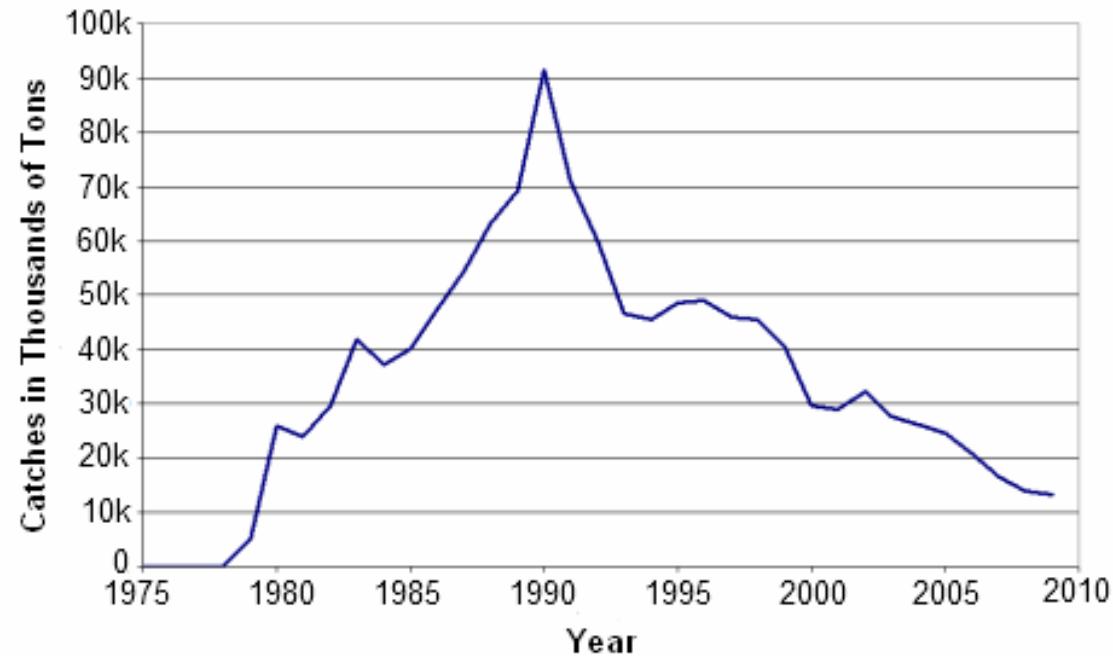
The MSY is a **semi-stable equilibrium**, meaning that small gains in population size ( $N$ ) will be compensated to return the system to  $N_{MSY}$ , while small losses will result in the system collapsing to  $N=0$ .

# Case Study: Orange Roughy



- Found in deep waters of eastern Pacific (Chile), western Pacific (Australia/NZ), and southeastern Atlantic (Namibia to South Africa)

Worldwide Catches of Orange Roughy 1975 - 2009



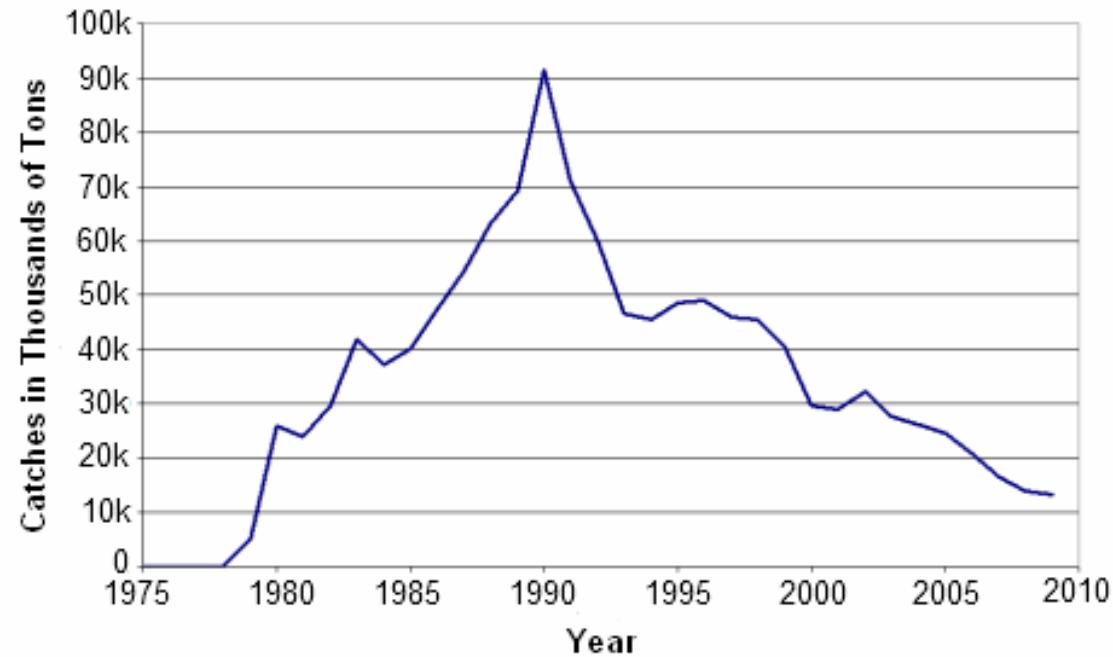
Source: FAO (Fisheries and Agriculture Organisation of the United Nations) Fisheries and Aquaculture Information and Statistics Service. © L. Baumont

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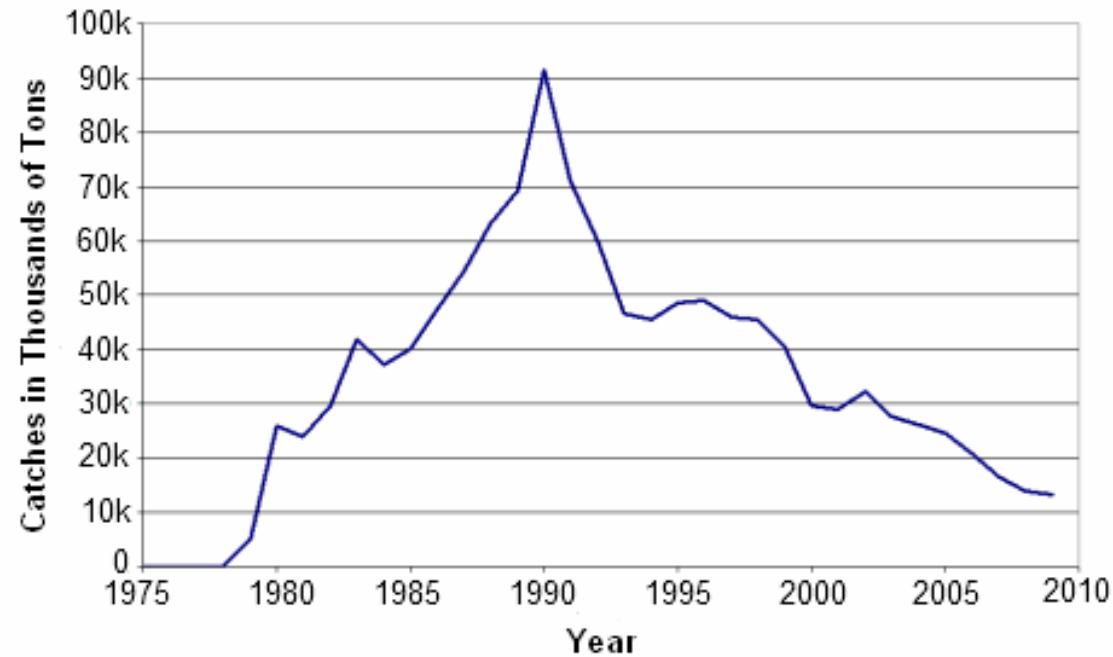
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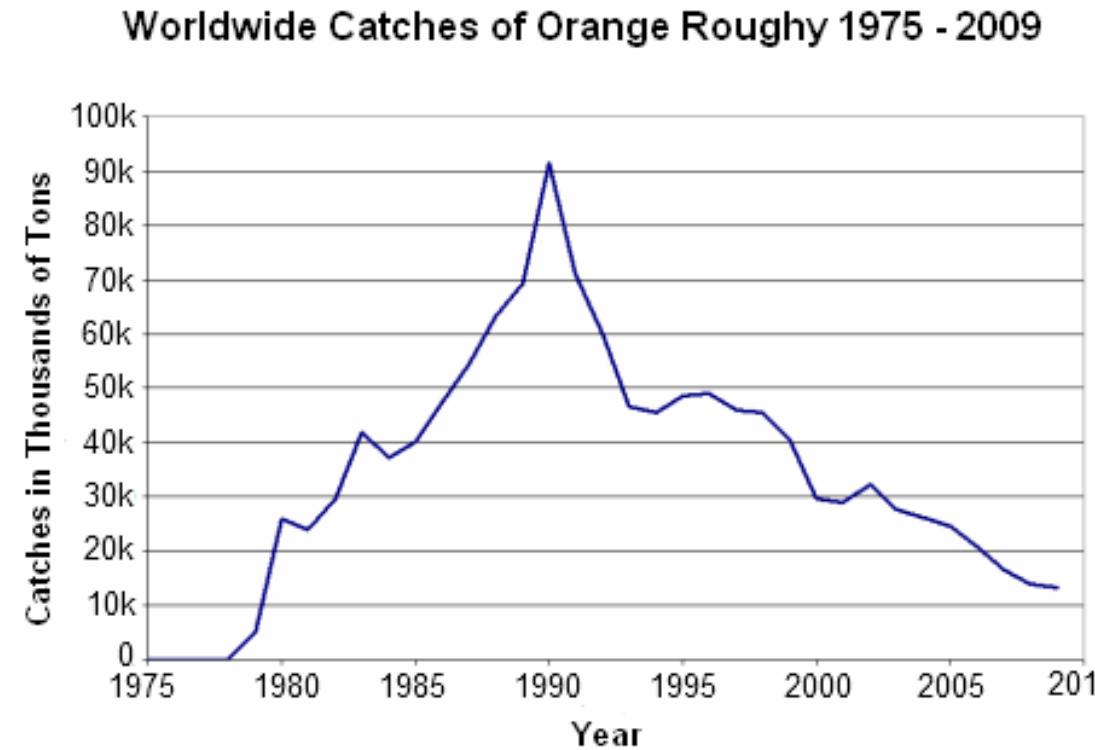


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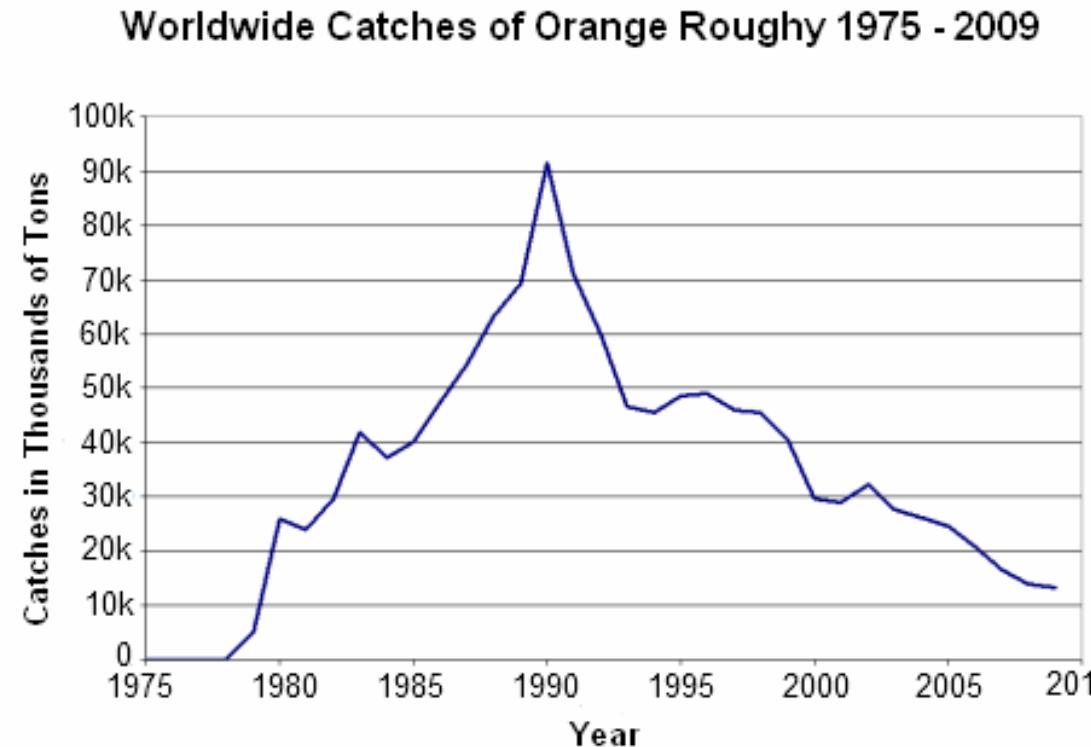


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- Annual global catches began in 1979 and increased to over 90,000 tons in the late 1980s.
- High catch levels quickly decreased as stocks were fished down. By the late 1990s, three of the eight NZ orange roughy fisheries had collapsed and were closed.



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

The case of the orange roughy highlights many of the **inherent problems with MSY**



- $r$  and  $K$  and  $N$  are difficult to measure.

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# Overfishing: A Tragedy of the Commons



- Tragedy of the Commons: A situation in which individual users, who have open access to a common pool resource, cause depletion of the resource through their uncoordinated actions.
  - Idea was popularized by ecologist Garret Hardin in 1968, a Malthus-like reference to the overpopulation of the Earth

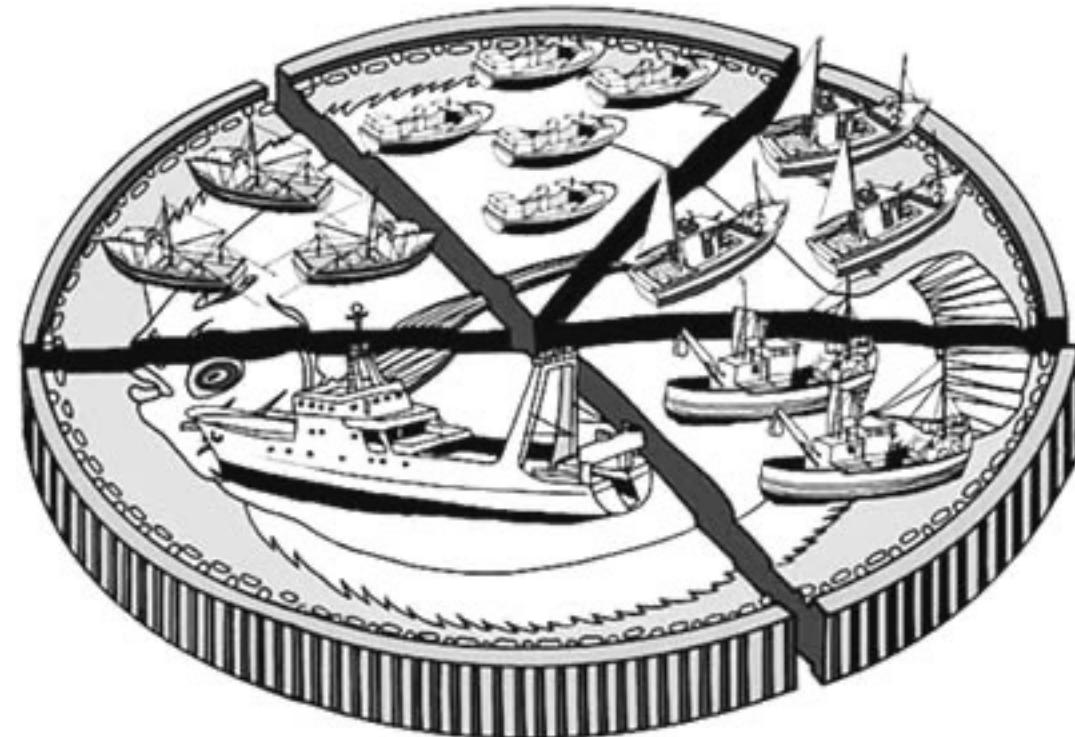
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- Fisheries provide a classic example of Tragedy of the Commons because property rights are incomplete and access is open.
- Many examples of fisheries collapse:
  - Sturgeon in Caspian sea in 2000s
  - Atlantic cod in Canada & elsewhere in 1990s
  - Orange roughy in NZ in 1990s

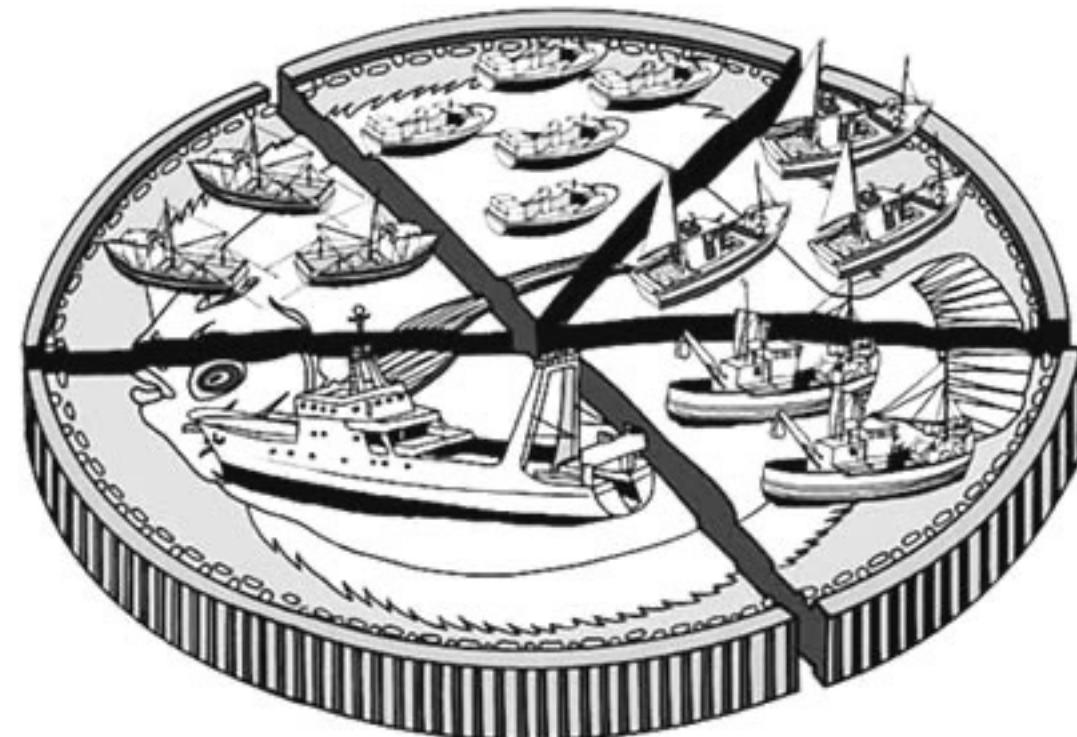
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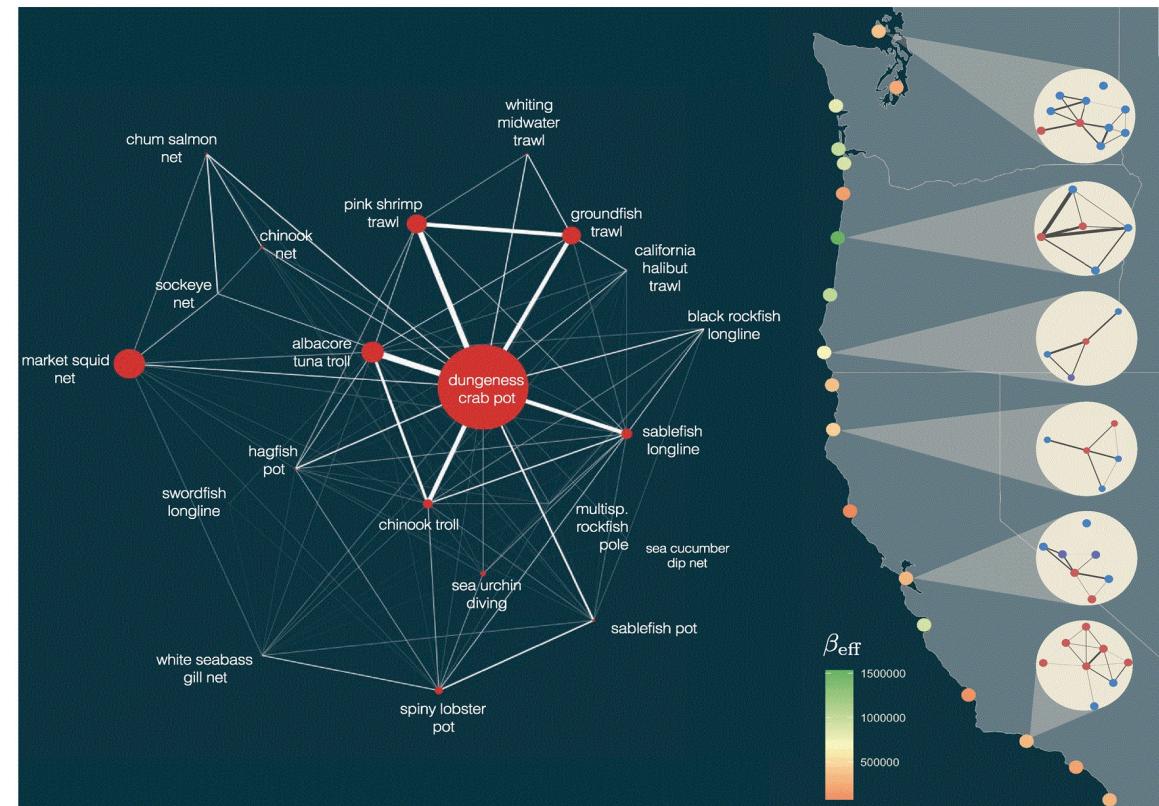
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- The work of Elinor Ostrom showed that some of these challenges can be overcome when the limits of a resource are clearly defined, when the group of stakeholders is small, and when communication is high.



Dr. Emma Fuller,  
Fractal Agriculture



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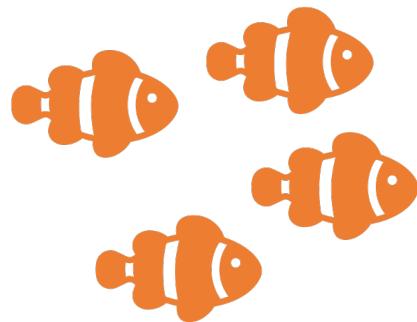
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- Simple harvesting models assume constant harvest.
- MSY fails to acknowledge the reality of **overfishing**.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in  $N$  can be devastating
  - environmental **stochasticity**
  - demographic **stochasticity**

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# Deterministic vs. Stochastic

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starting population

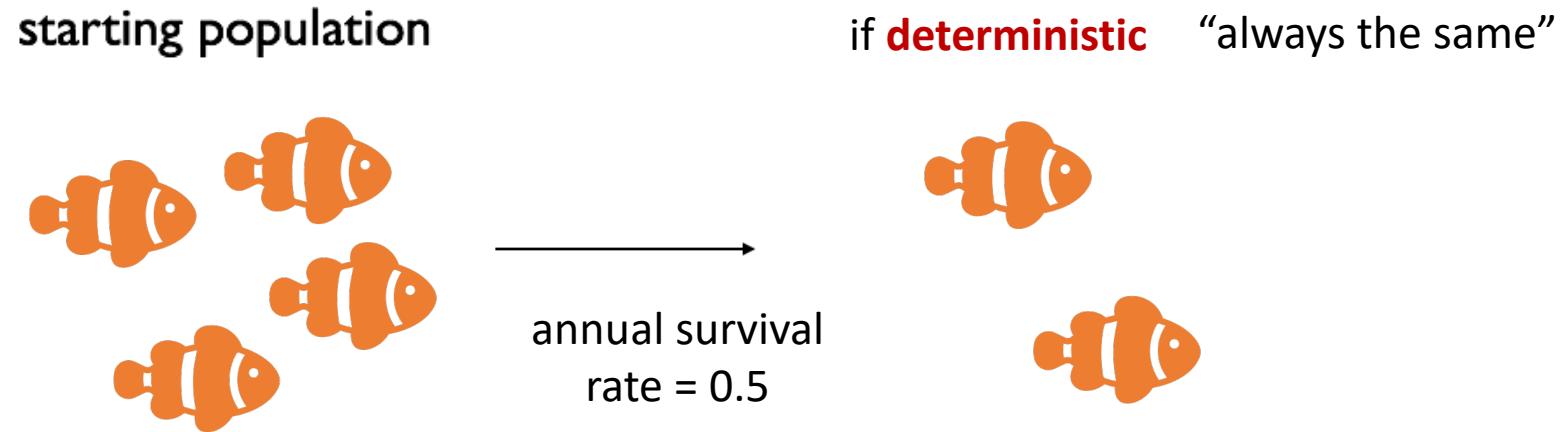


if **deterministic** “always the same”

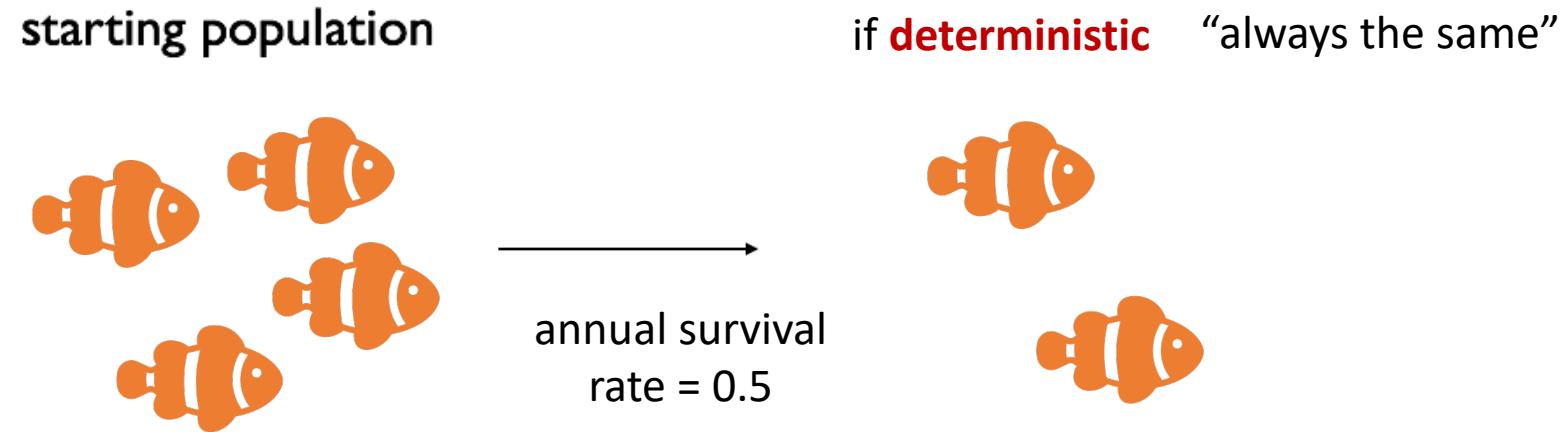


annual survival  
rate = 0.5

# Deterministic vs. Stochastic

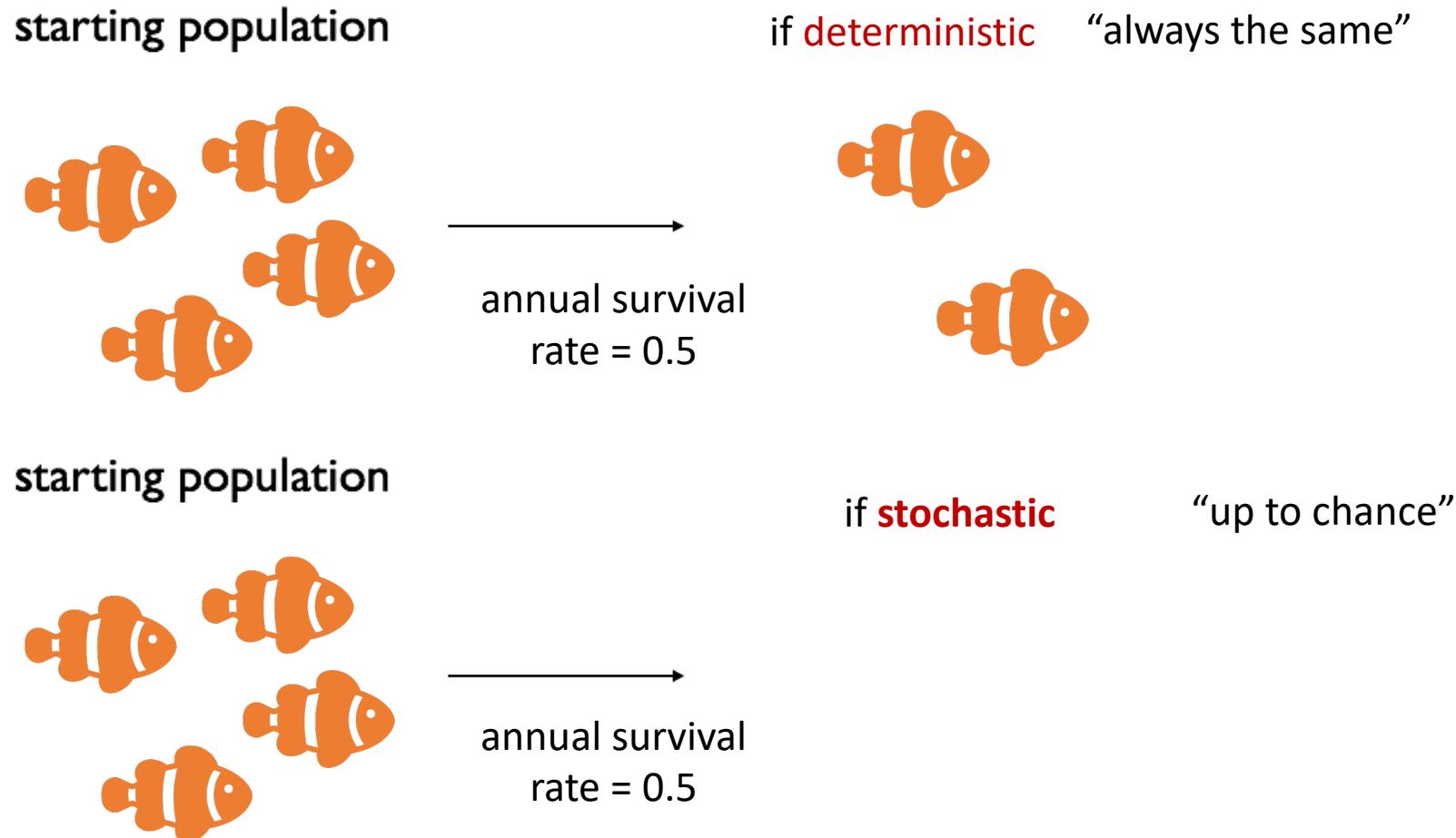


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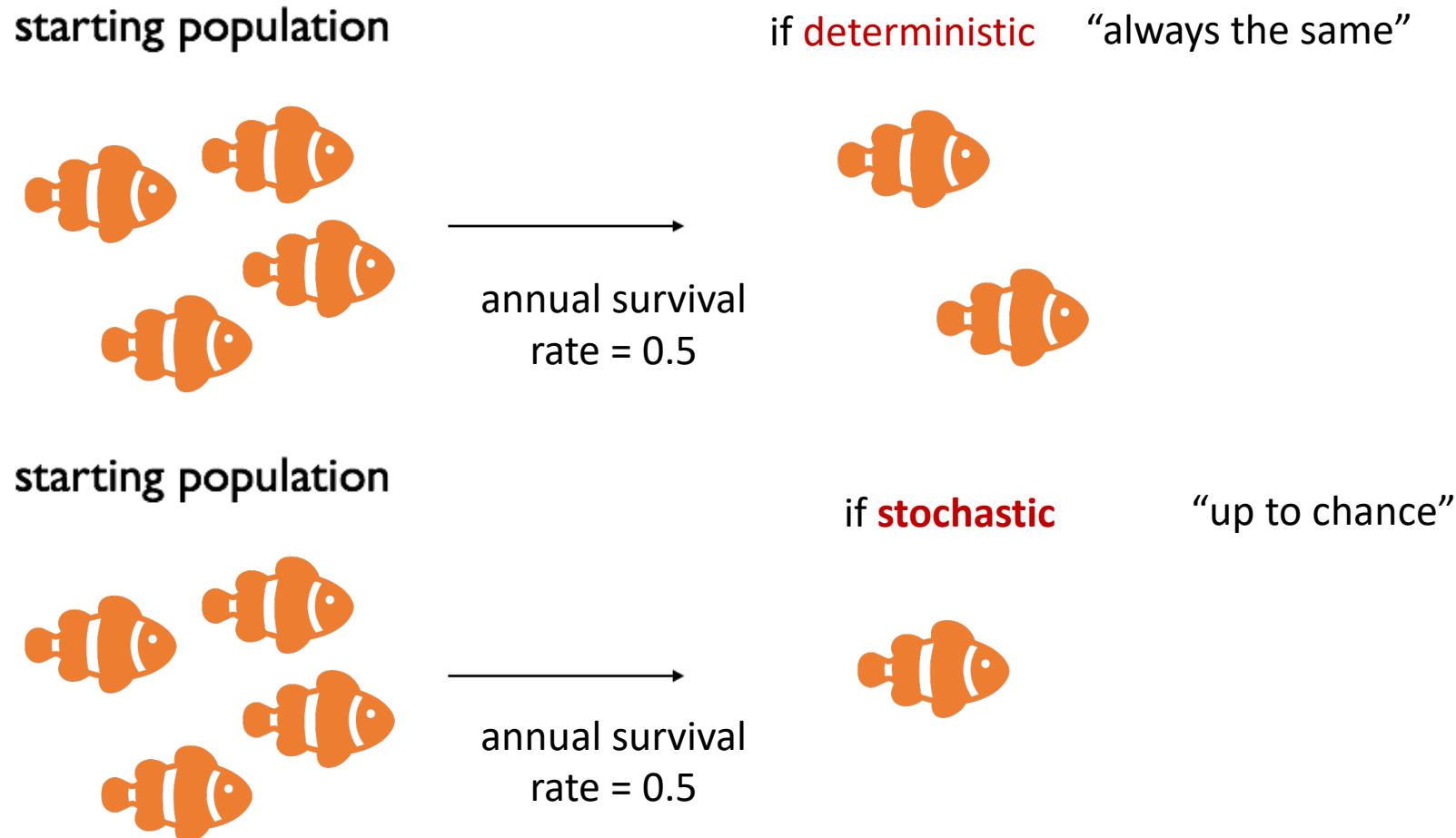


All the models we have looked at so far have been deterministic!

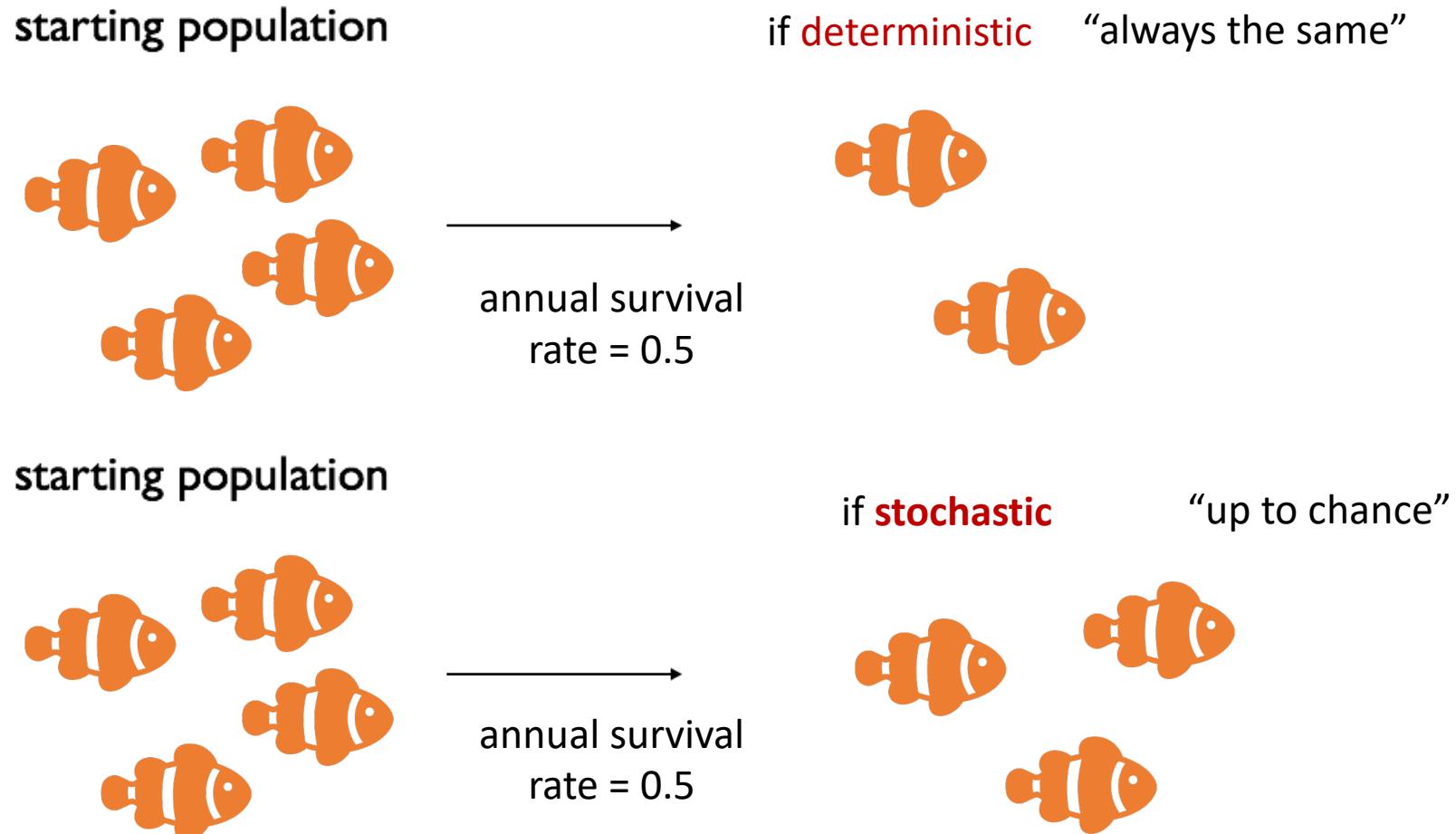
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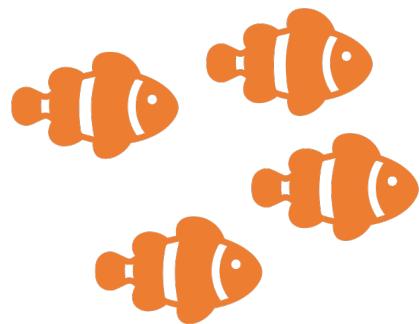
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# The case of the orange roughy highlights many of the **inherent problems with MSY**



starting population



if **stochastic**

“up to chance”

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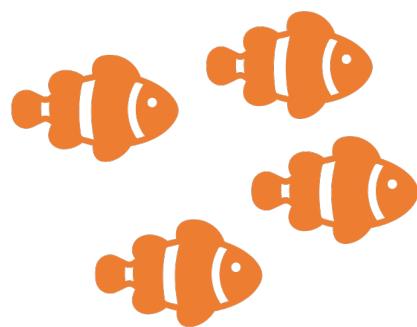
cyclone year!

- $r$  and  $K$  and  $N$  = difficult to measure.
- Neglect population structure.
- Single species models.
- Assumes constant harvest.
- Ignores reality of overfishing.
- Because of the **semi-stable equilibrium** at MSY, small (natural) decreases in  $N$  can be devastating
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    - temporal changes in mortality or reproductive rate (e.g. due to climate)

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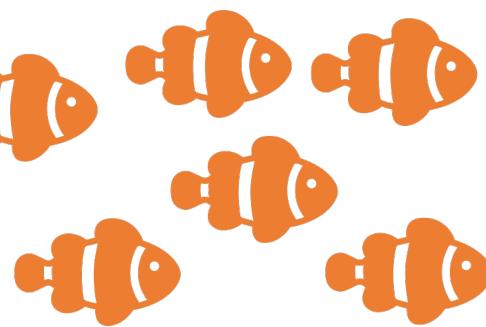


starting population



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annual fecundity  
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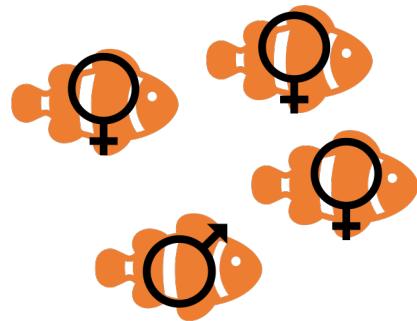


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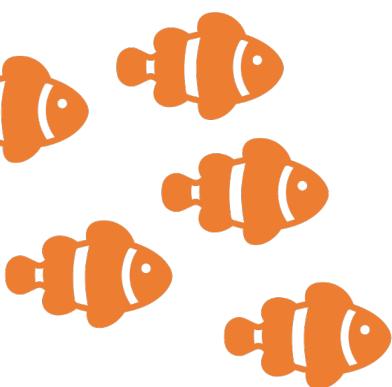
starting population



if stochastic

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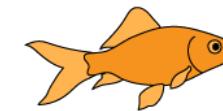
“up to chance”



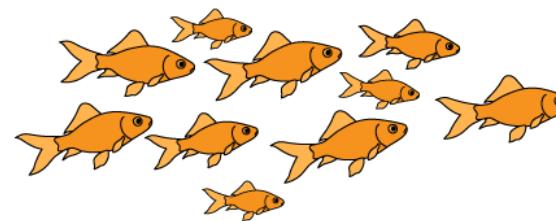
Only one male encounters only one female, so only 1 new fish is born!

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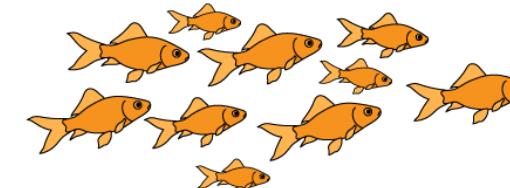
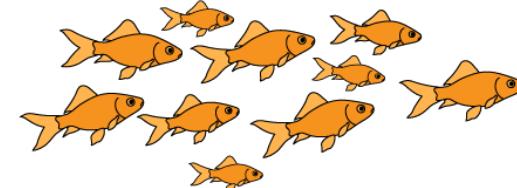
Ecology is the study of  
the **interactions** of  
**organisms** with each  
other and their  
**environment.**



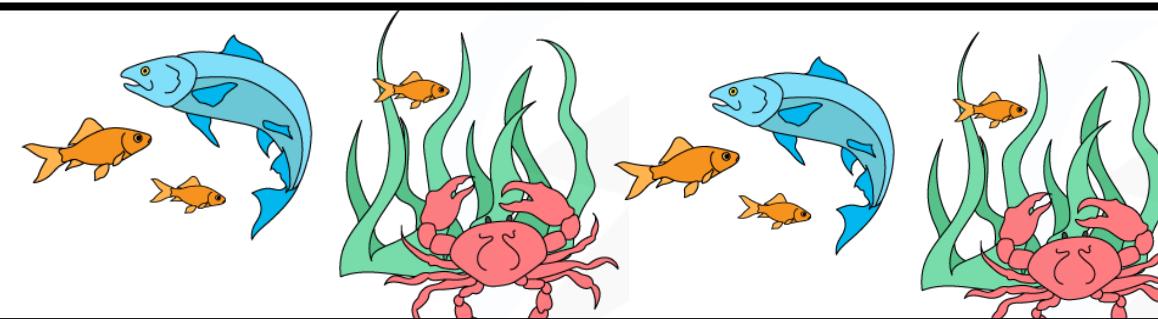
individual



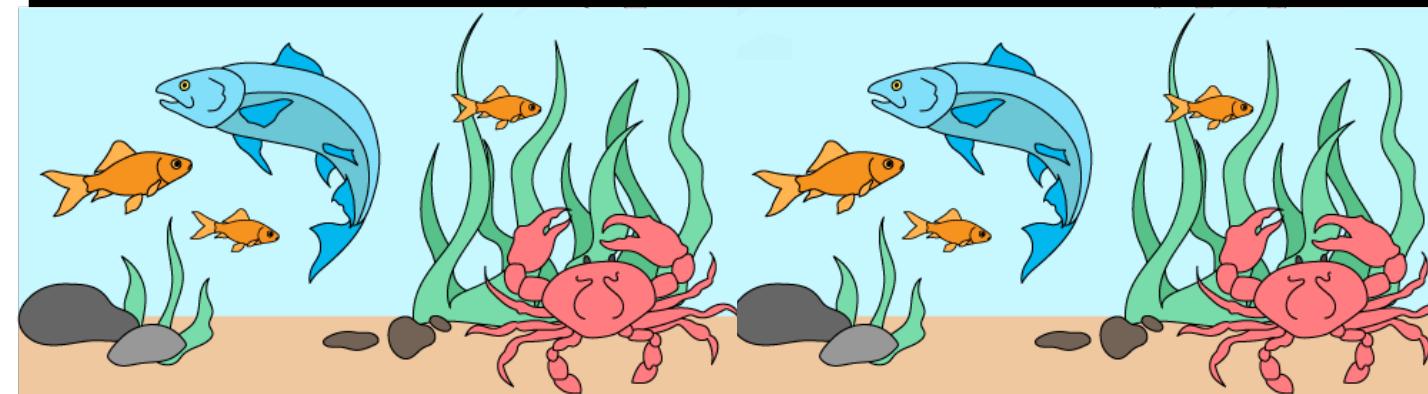
population



metapopulation

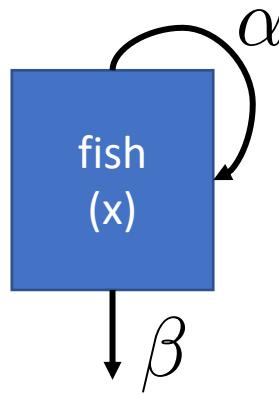


community

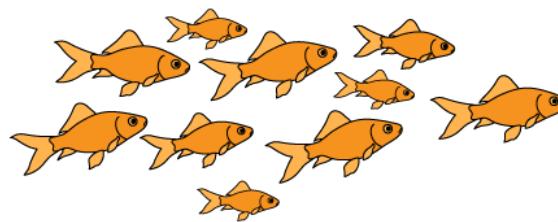


ecosystem

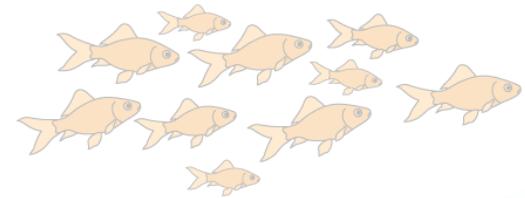
**Population** = multiple individuals of the same species (**conspecifics**) in the same habitat



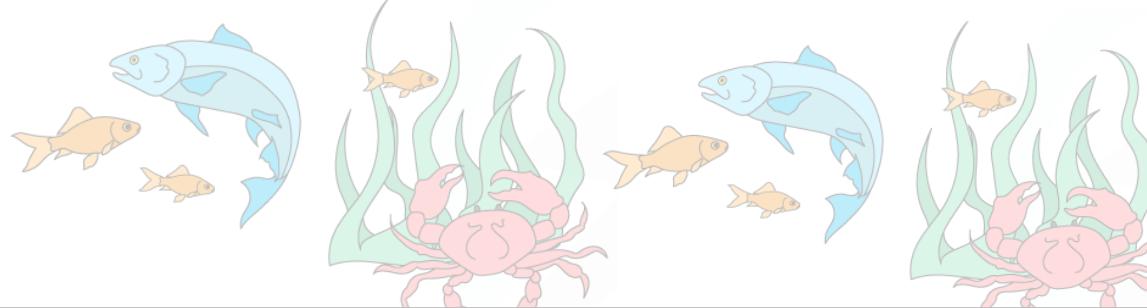
individual



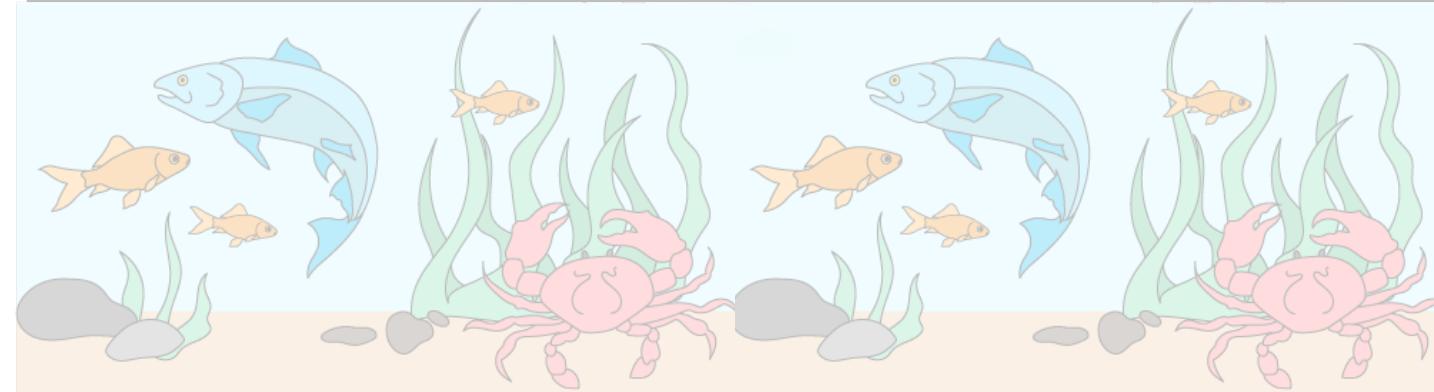
population



metapopulation



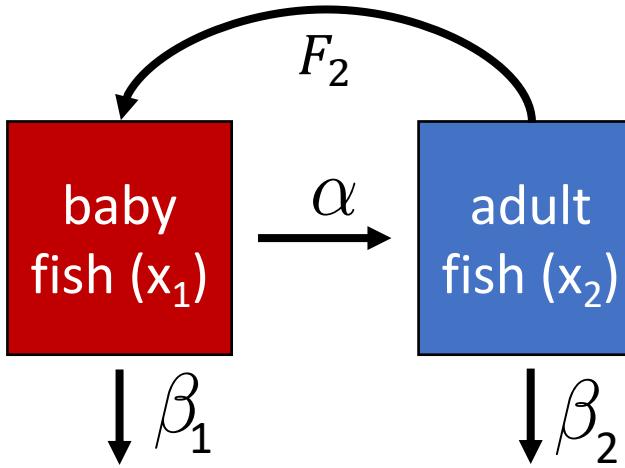
community



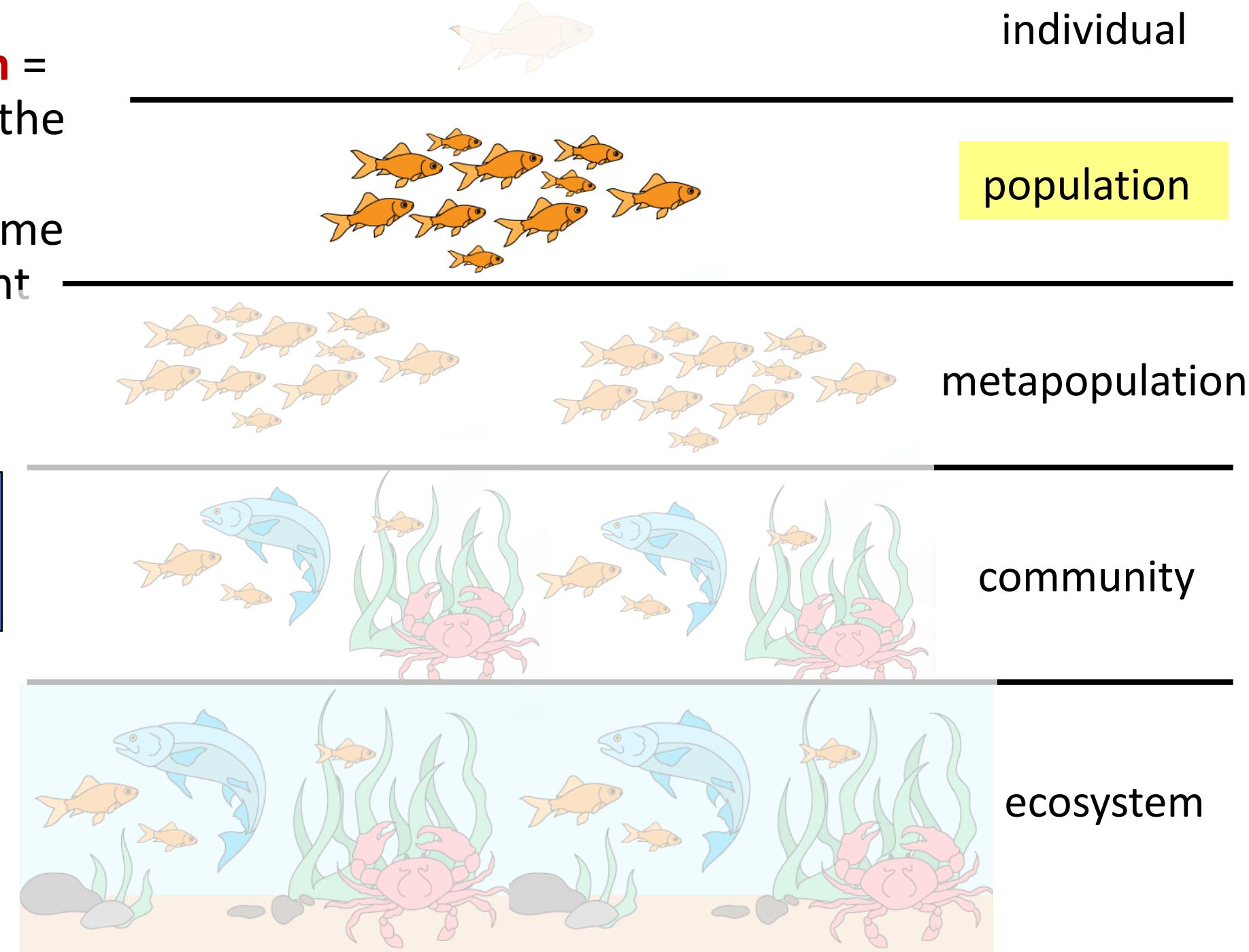
ecosystem

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

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



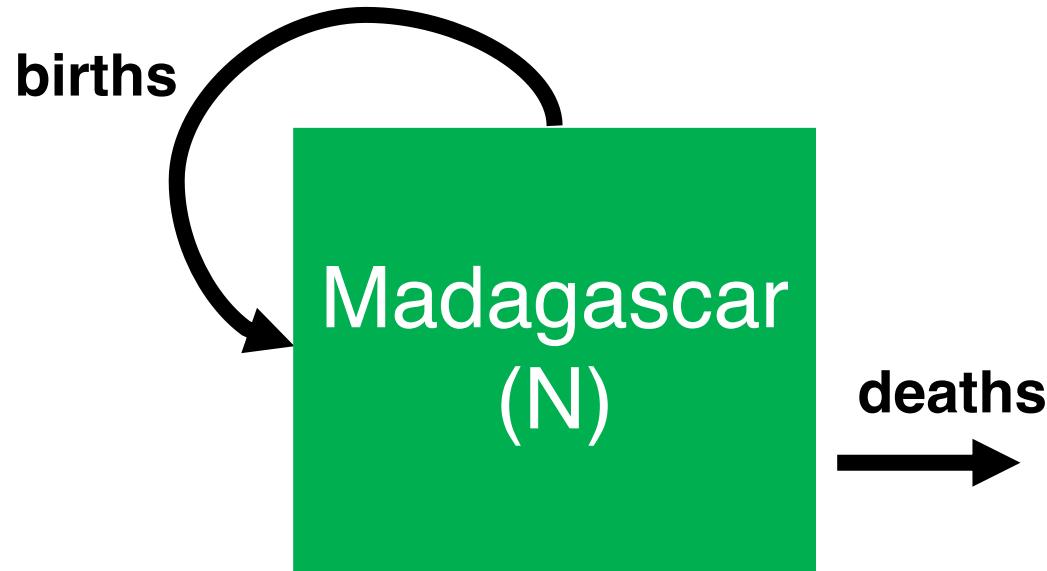
*How does the  
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# Modeling demographic complexity

# Modeling demographic complexity

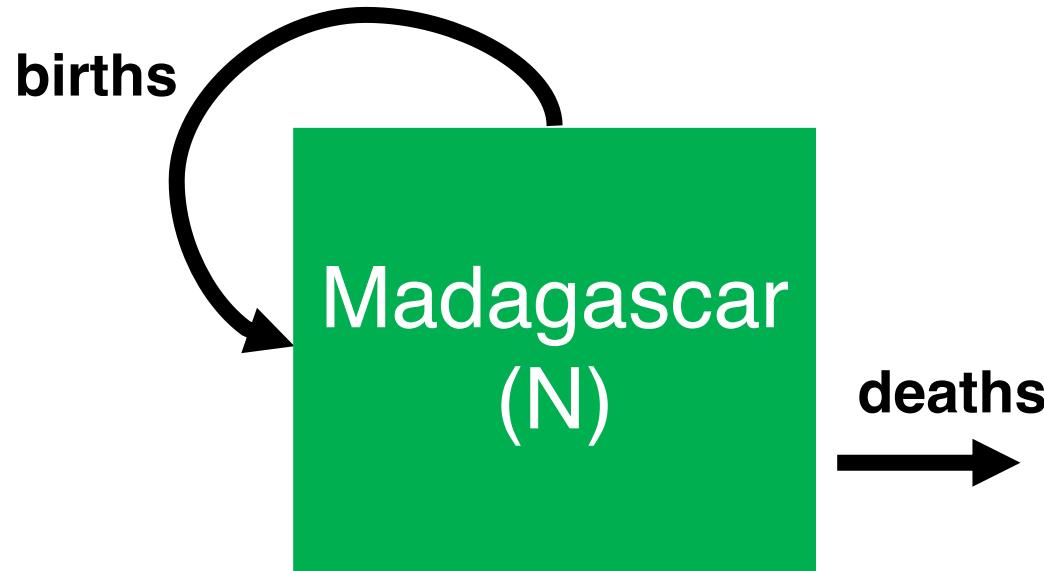
1. Populations are divided into compartments
2. Individuals within a compartment are homogeneously mixed
3. Compartments and transition rates are determined by biological systems
4. Rates of transferring between compartments are expressed mathematically



The simplest  
population model

# Modeling demographic complexity

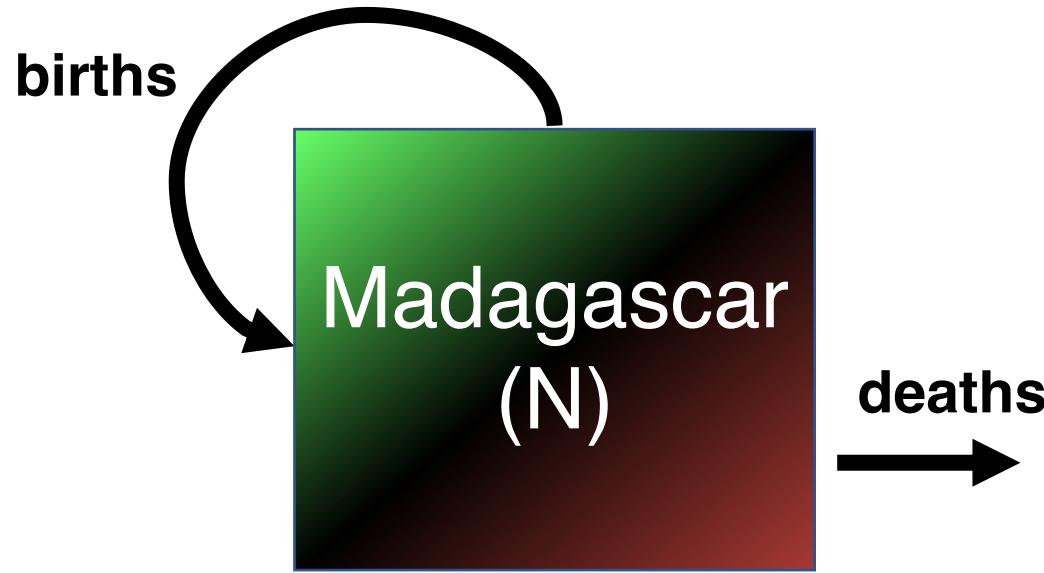
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**What is wrong about this model?**

# Modeling demographic complexity

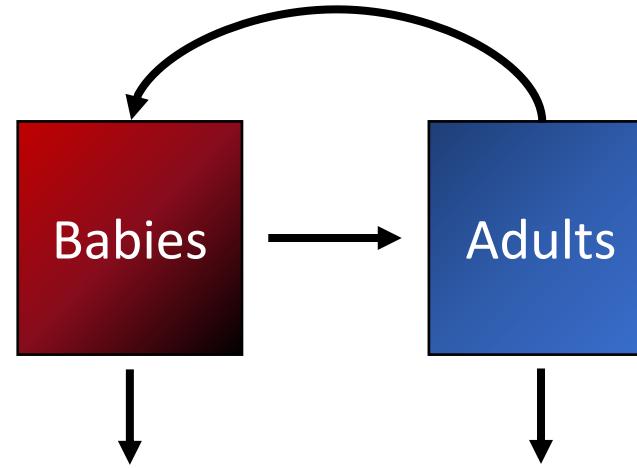
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**What is wrong about this model?**

# Modeling demographic complexity

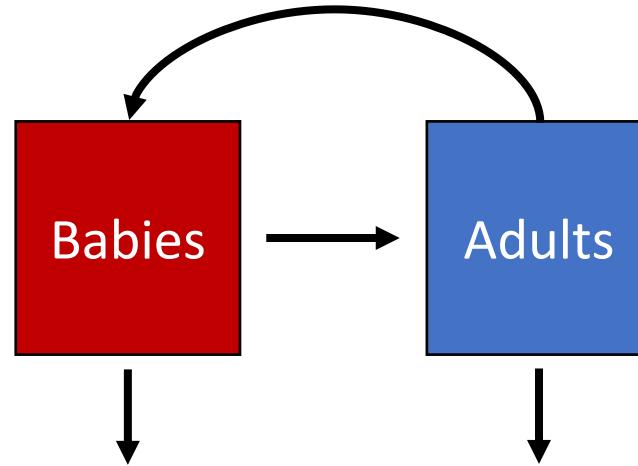
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**The structured population model**

# Modeling demographic complexity

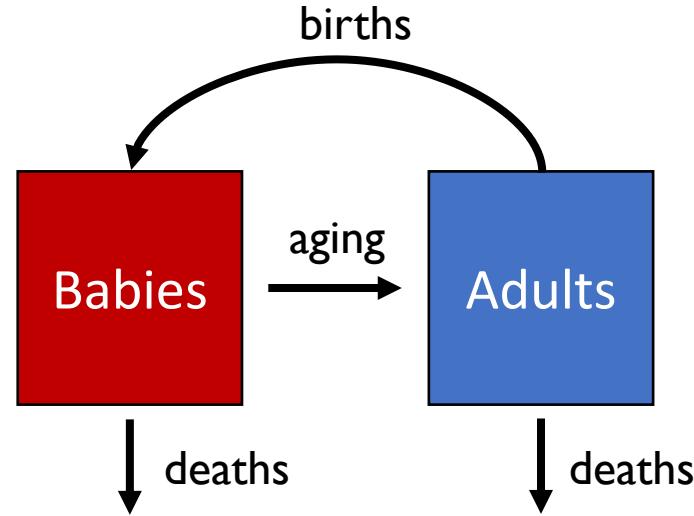
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The structured population model

# Modeling demographic complexity

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2. Individuals within a compartment are homogeneously mixed
- 3. Compartments and transition rates are determined by biological systems**
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**The structured population model**

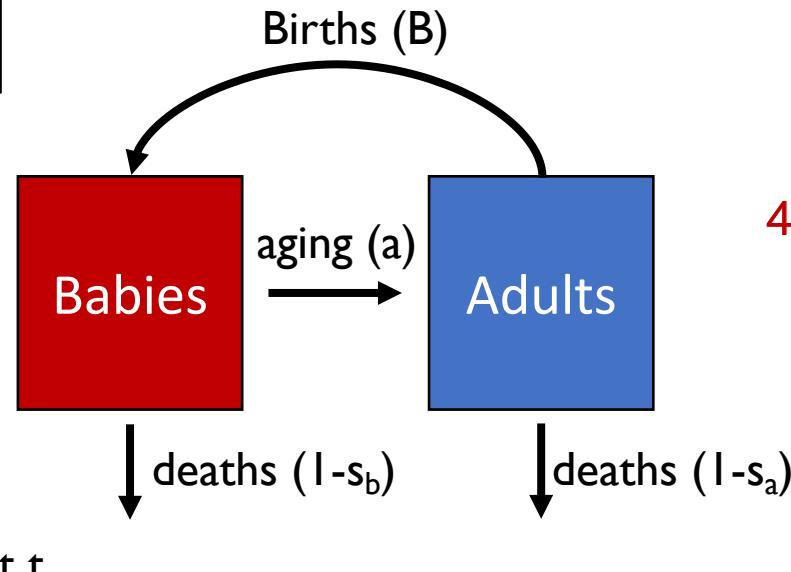
# The structured population model

Population rate of increase

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

pop size at  $t + 1$

pop size at  $t$



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

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

vector of  
population sizes

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

matrix of survival and  
fecundity rates

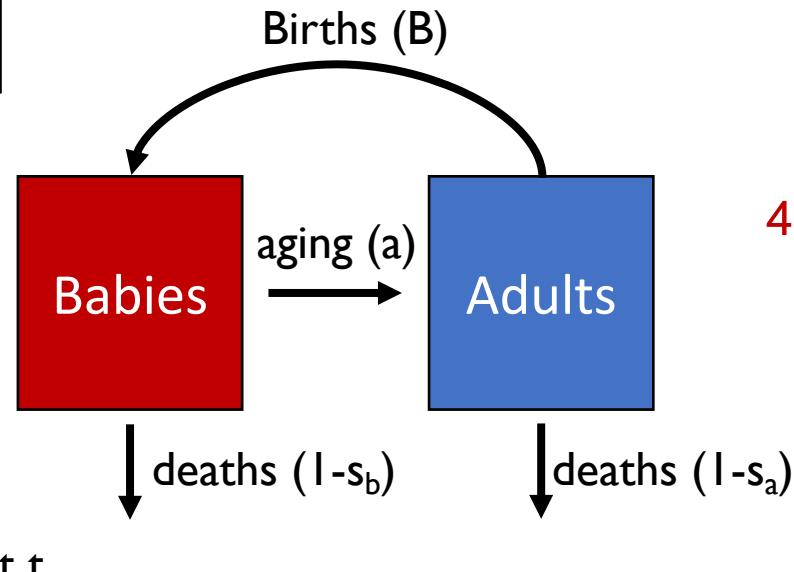
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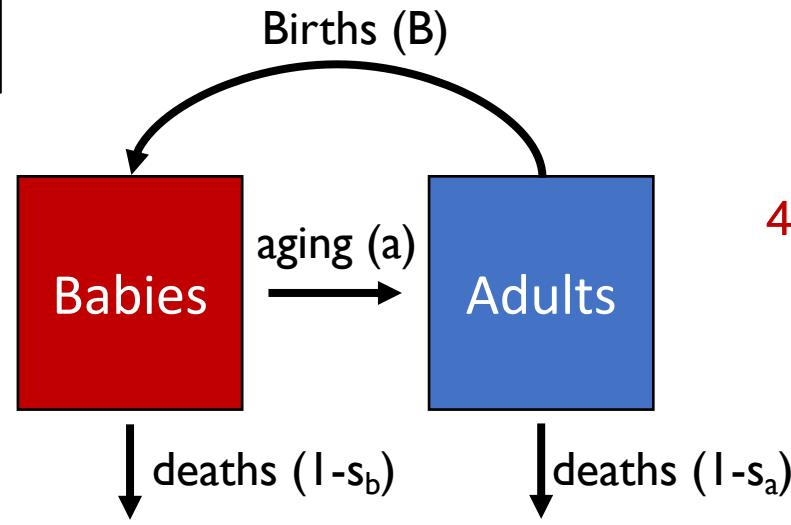
vector of  
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$s_b(1-a)$	$B$
$s_b a$	$s_a$

matrix of survival and  
fecundity rates

\*Discrete time

# The structured population model

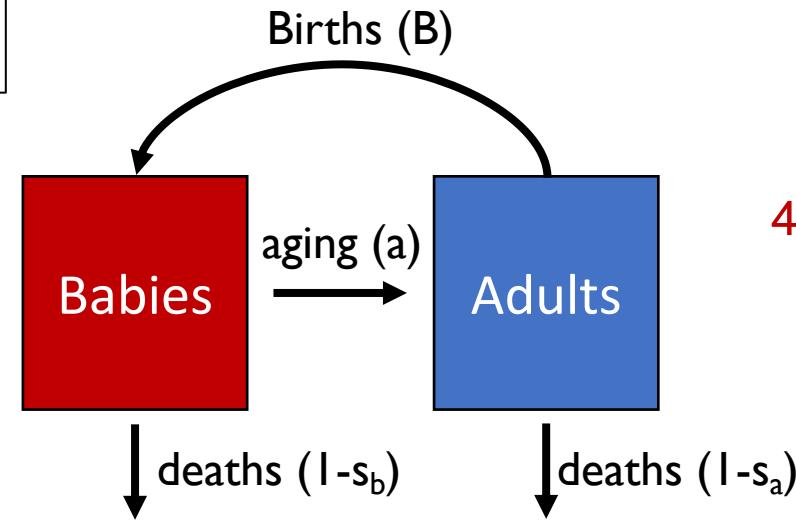


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$$N_{t+1} = A^* N_t$$

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

# The structured population model



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

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

Population rate of increase

$\lambda$  = dominant eigenvalue of transition matrix

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

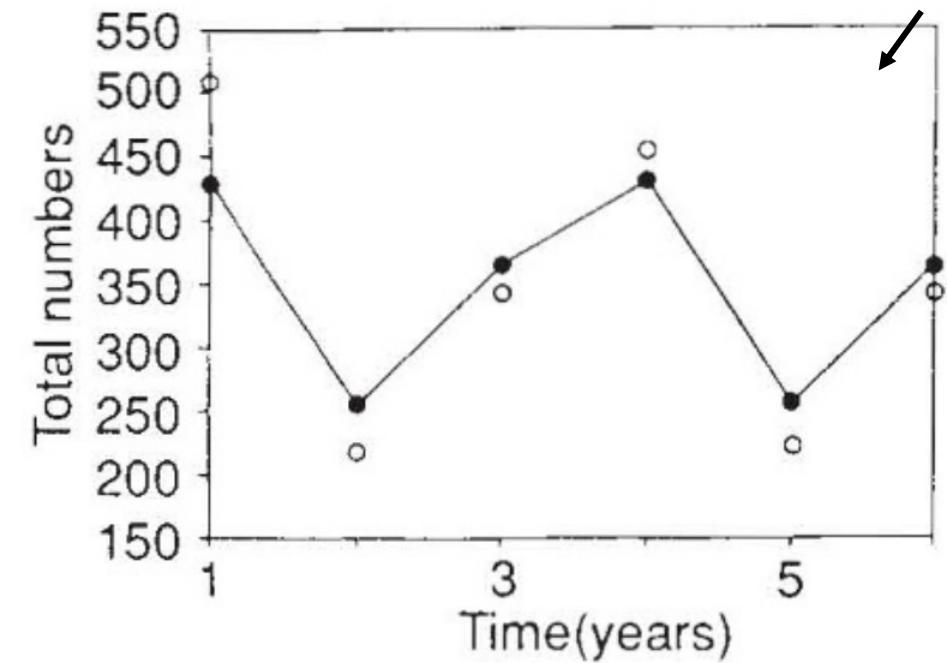
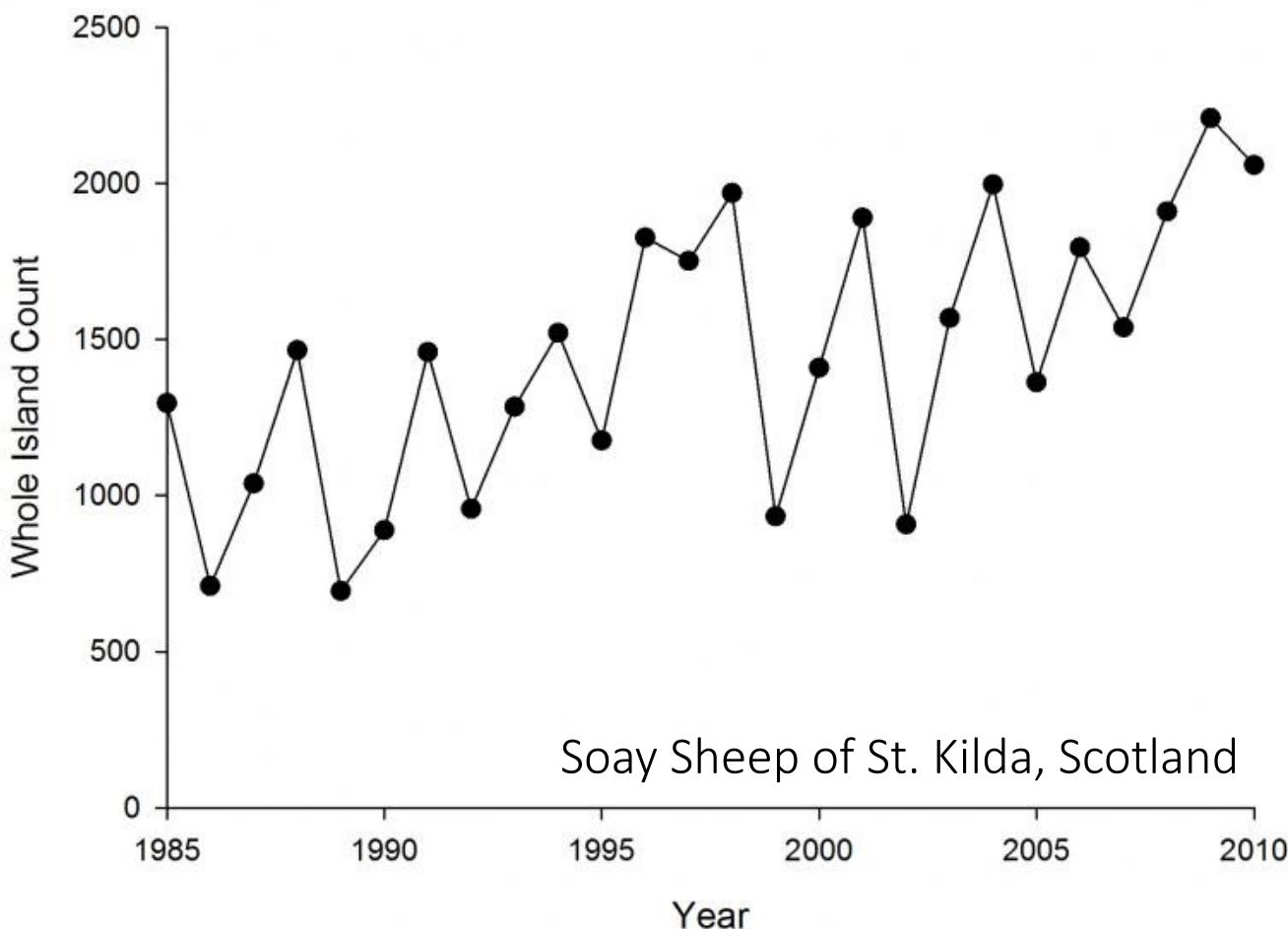
Population growth will depend on population structure!

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

# Structured populations in practice



# Structured populations in practice



**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  
against  
data

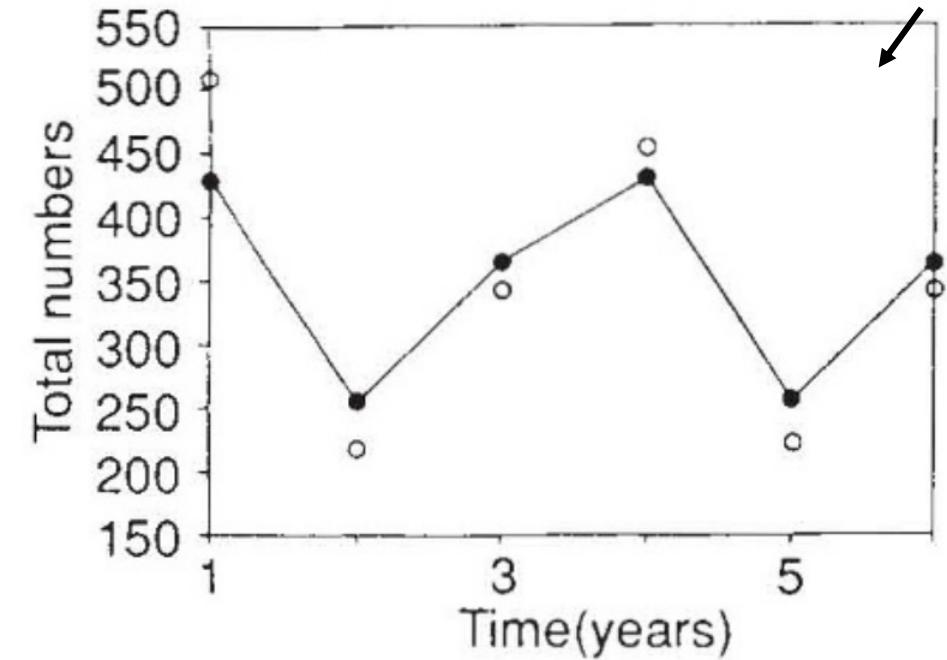
# Structured populations in practice

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

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

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

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



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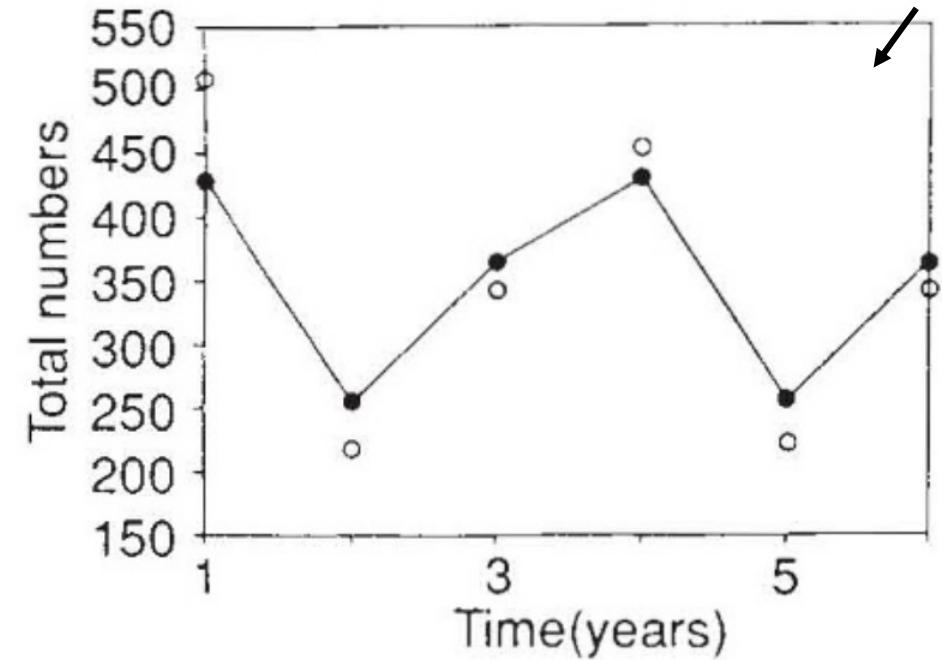
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↑      ↑      ↑  
population   average   growth  
at t+1      fecundity   rate  
                ↑  
                population  
                at t

} *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**

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# Structured populations in practice

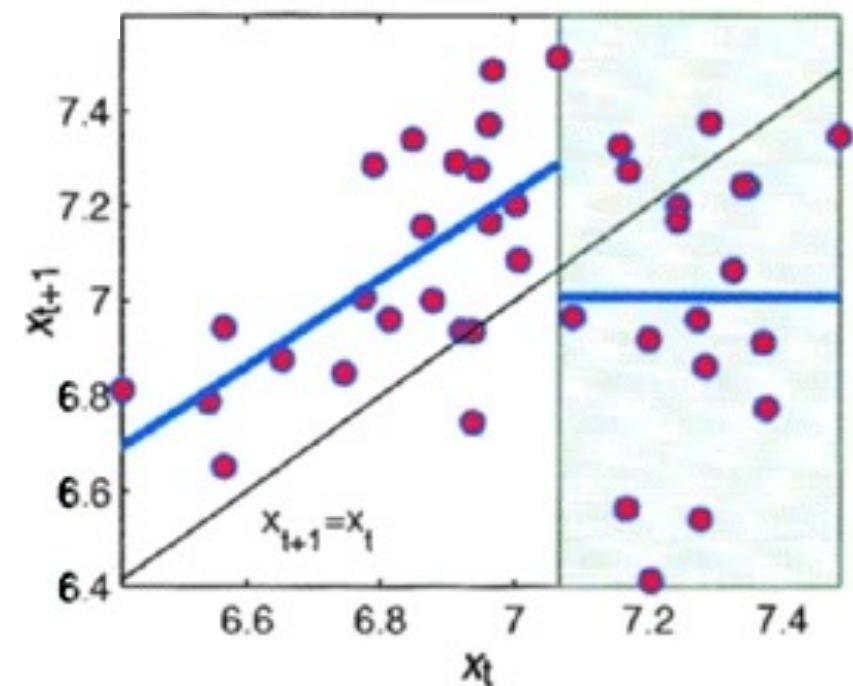
In later work, the authors added **environmental stochasticity** (bad weather) to **better represent** the data.....

## 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](#)

1746 Accesses | 414 Citations | 4 Altmetric | [Metrics](#)



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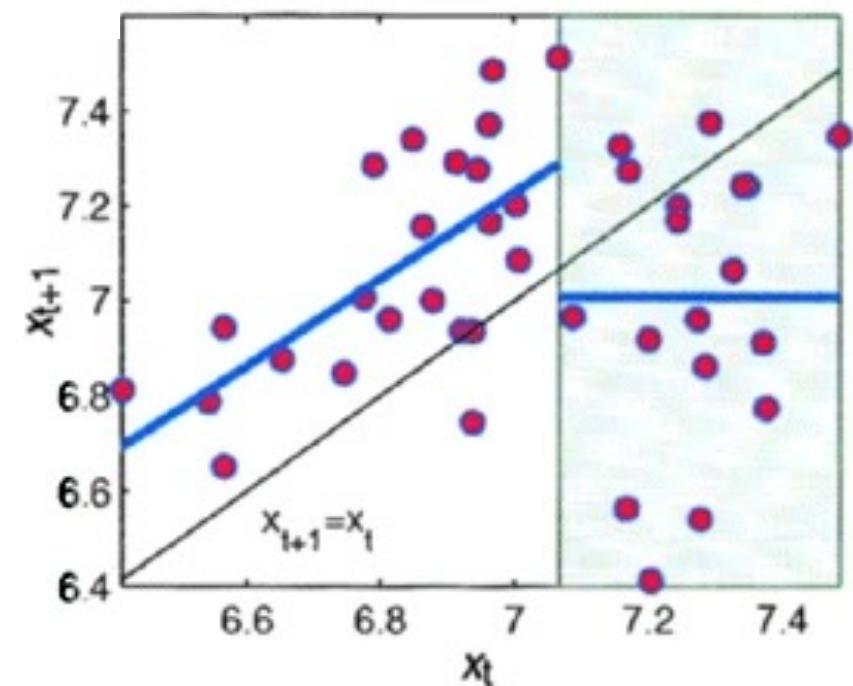
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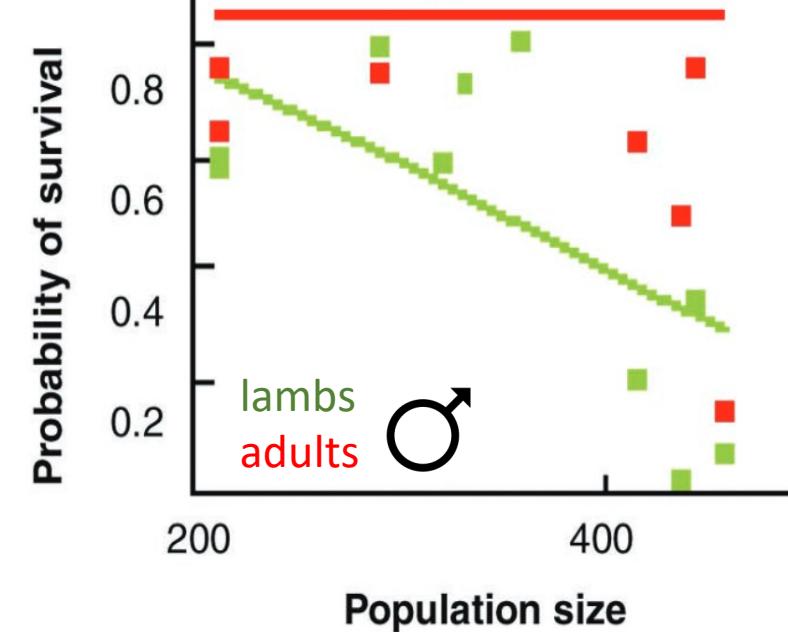
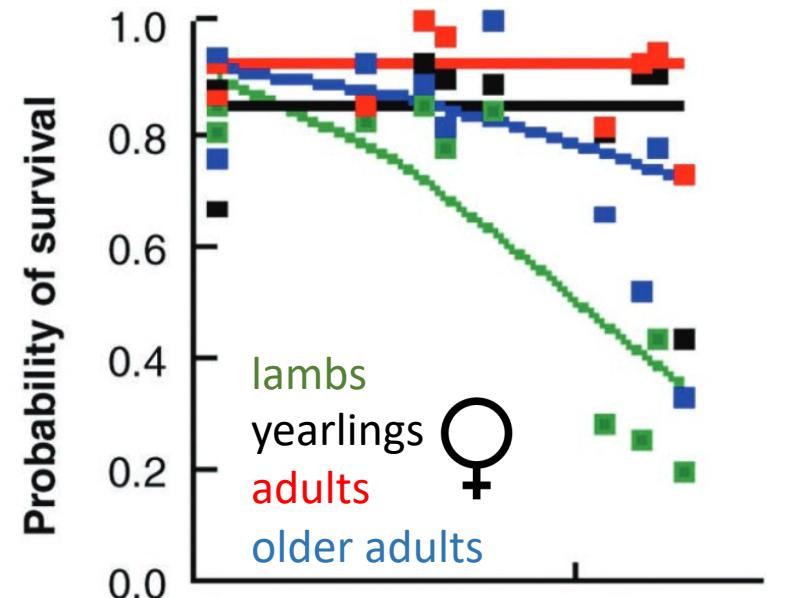
# Structured populations in practice

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

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

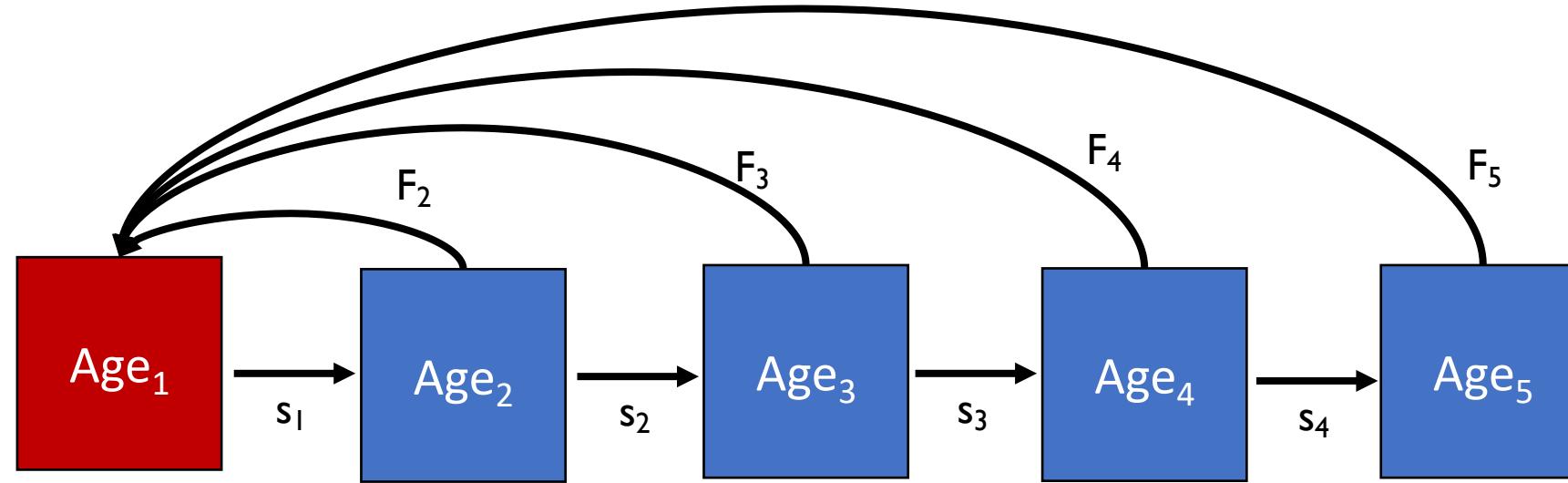
T. Coulson,<sup>1\*</sup>† E. A. Catchpole,<sup>2</sup> S. D. Albon,<sup>3</sup> B. J. T. Morgan,<sup>4</sup>  
J. M. Pemberton,<sup>5</sup> T. H. Clutton-Brock,<sup>6</sup> M. J. Crawley,<sup>6</sup>  
B. T. Grenfell<sup>7</sup>

25 MAY 2001 VOL 292 SCIENCE [www.sciencemag.org](http://www.sciencemag.org)



# The structured population model

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

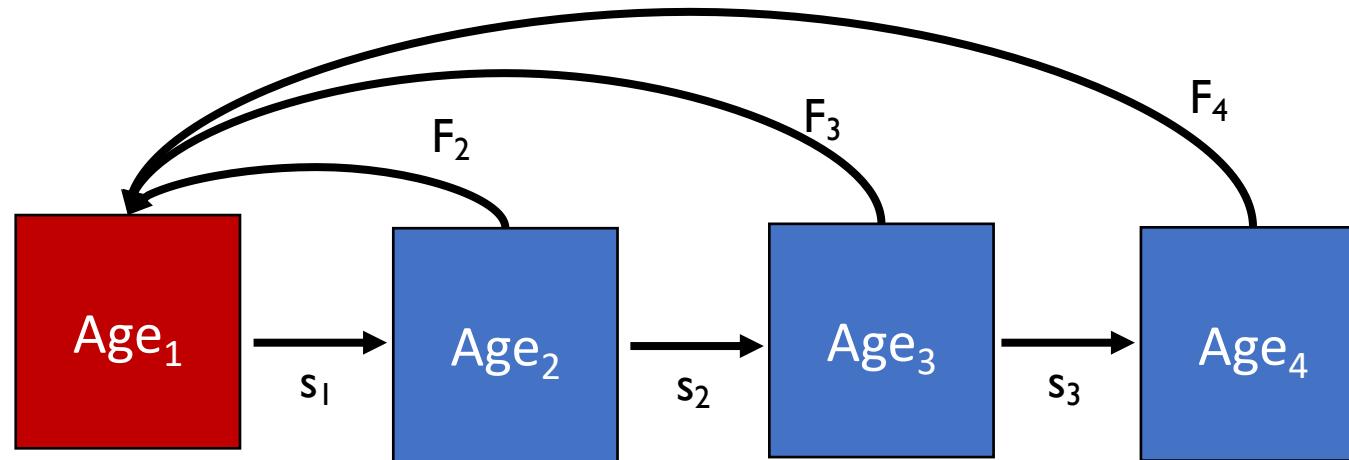


The **Leslie matrix** model divides classes based on age.

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.



$\lambda$ =dominant eigenvalue of transition matrix

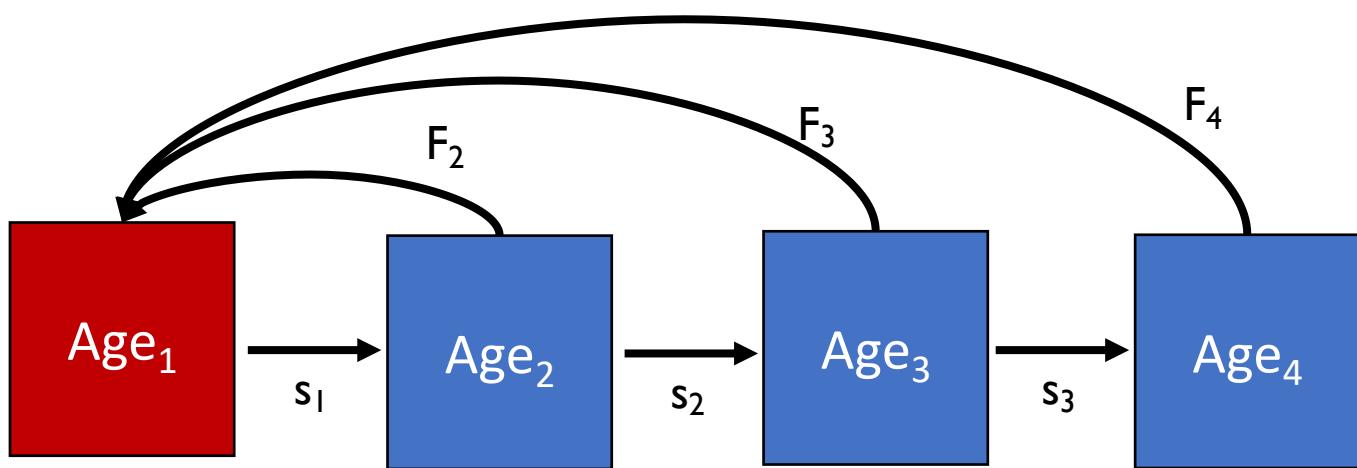
$$\xrightarrow{\lambda \text{=dominant eigenvalue of transition matrix}} \begin{matrix} \mathbf{A} \\ \begin{bmatrix} 0 & s_1F_2 & s_2F_3 & s_3F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{bmatrix} \times \begin{bmatrix} N_t \\ \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix} \end{bmatrix} = \begin{bmatrix} N_{t+1} \\ \begin{bmatrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{bmatrix} \end{bmatrix} \end{matrix}$$

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

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

# The structured population model

Demographers collect these rates in life tables



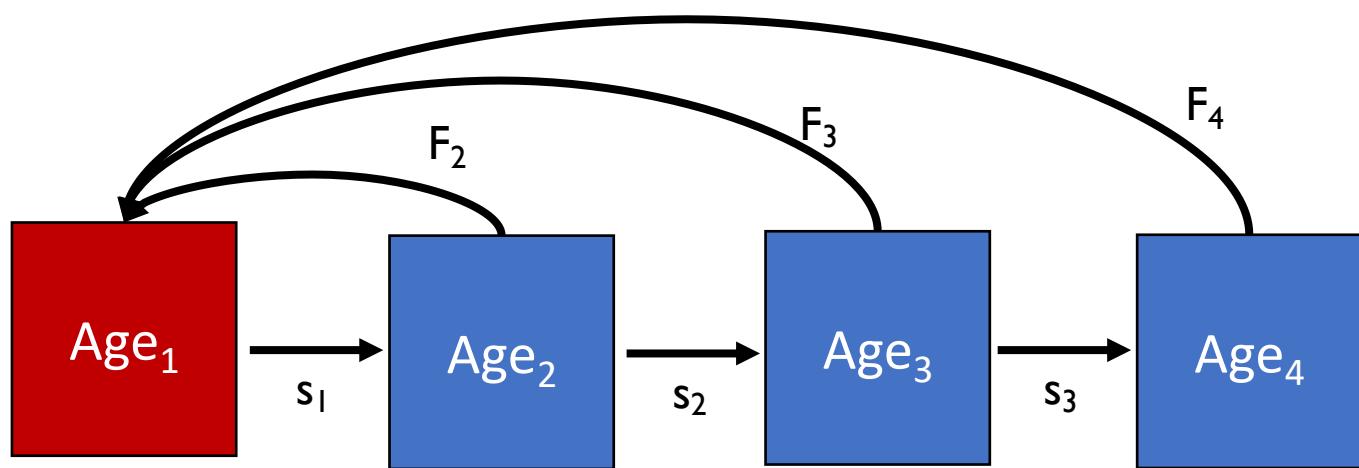
x (age)	N <sub>x</sub> (number in cohort)	I <sub>x</sub> (survivorship to age x)	m <sub>x</sub> (fecundity)	I <sub>x</sub> m <sub>x</sub>
0	100	1	0	0
1	60	.6	2	1.2
2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01



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

# The structured population model

Demographers collect these rates in life tables



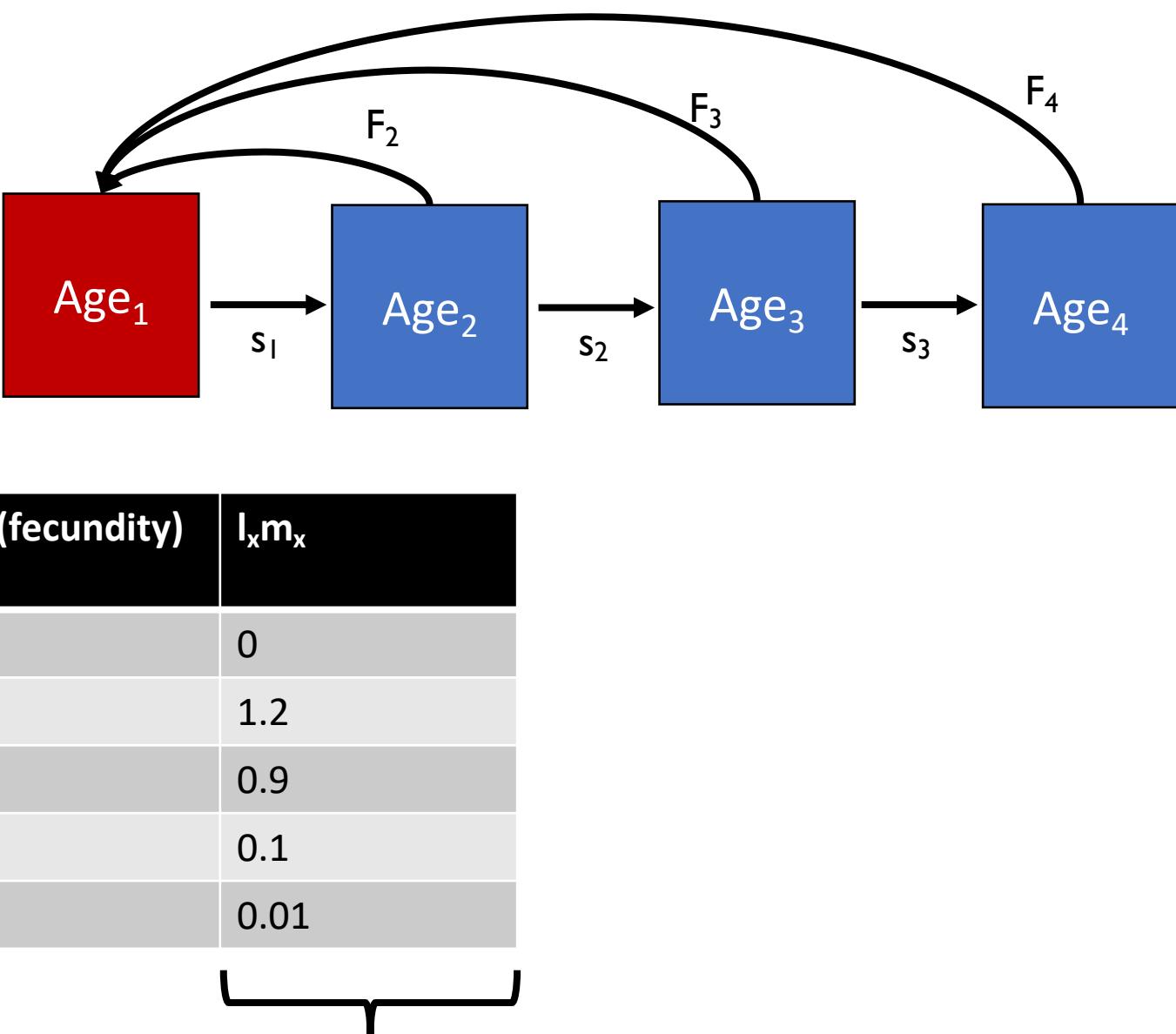
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**Net reproductive rate ( $R_0$ ):**  $\sum l_x m_x = 2.21$

# The structured population model

Demographers collect these rates in life tables

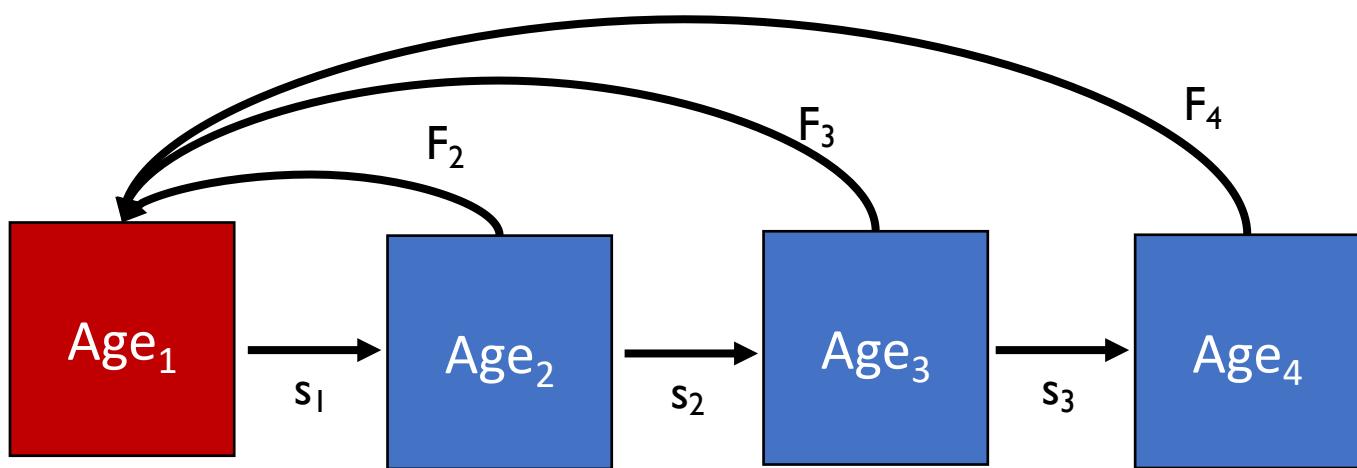


**Net reproductive rate ( $R_0$ ):**  $\sum l_x m_x = 2.21$

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

# The structured population model

Demographers collect these rates in life tables



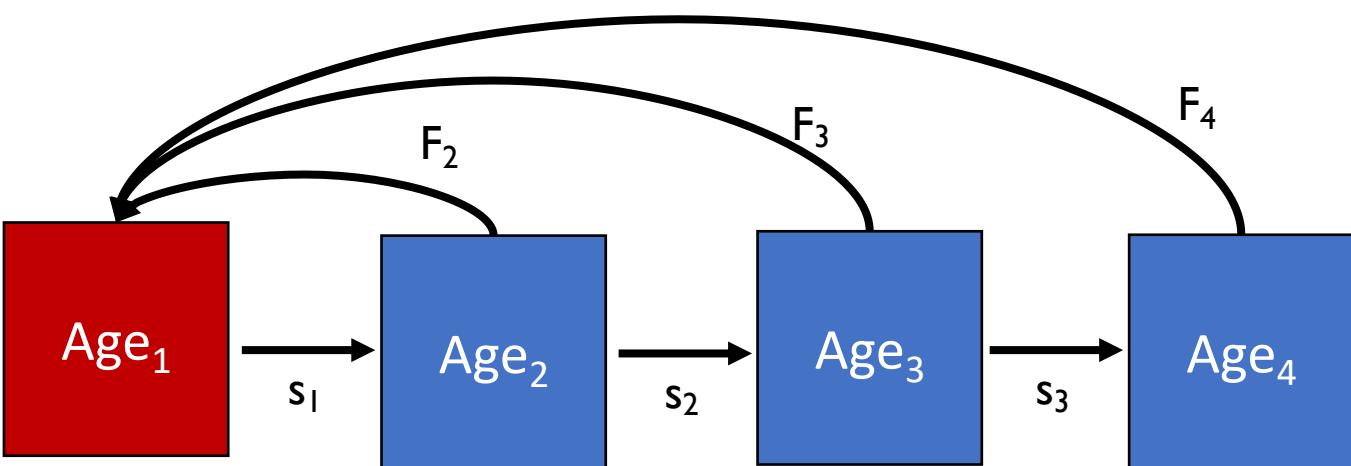
x (age)	N <sub>x</sub> (number in cohort)	l <sub>x</sub> (survivorship to age x)	m <sub>x</sub> (fecundity)	l <sub>x</sub> m <sub>x</sub>
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2	30	.3	3	0.9
3	10	.1	1	0.1
4	1	.01	1	0.01



**Net reproductive rate (R<sub>0</sub>):**  $\sum l_x m_x = 2.21$

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

# The structured population model



x (age)	N <sub>x</sub> (number in cohort)	I <sub>x</sub> (survivorship to age x)	m <sub>x</sub> (fecundity)	I <sub>x</sub> m <sub>x</sub>
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

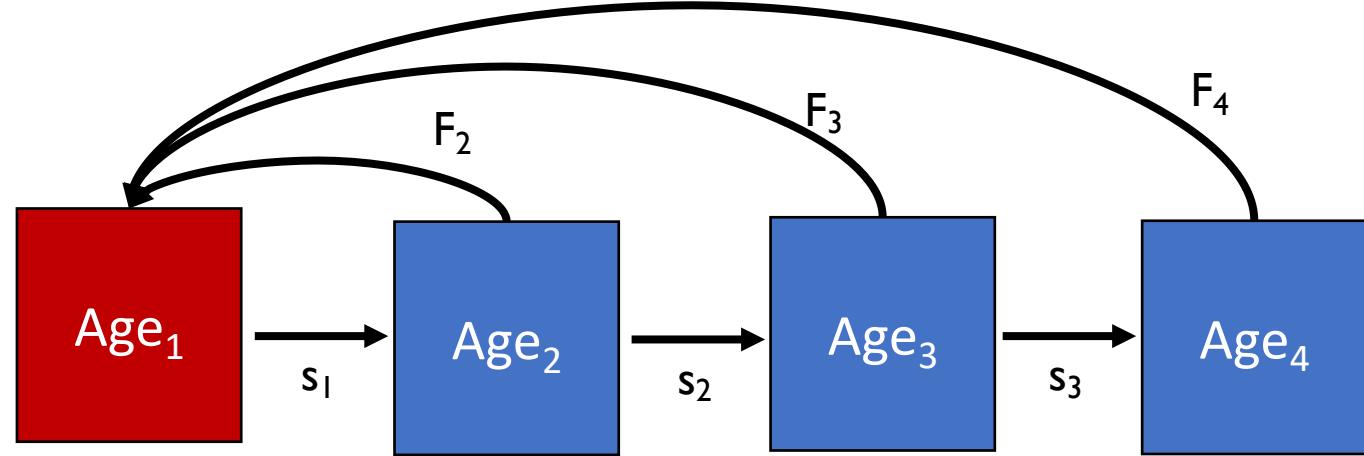
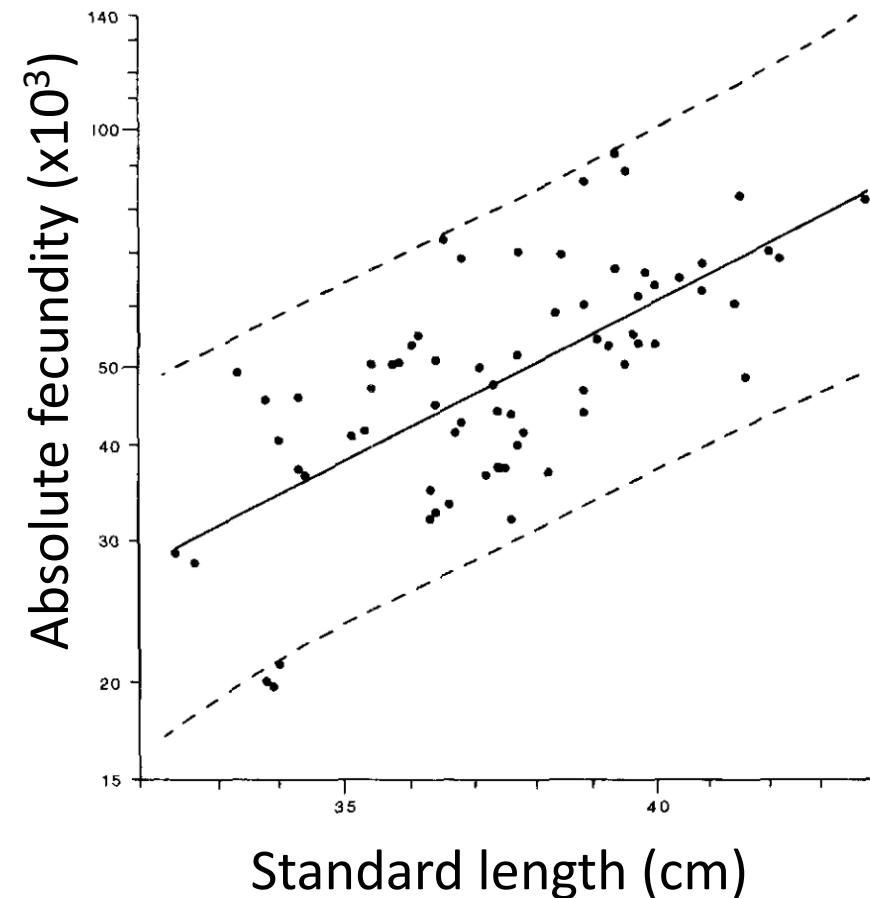


⋮

Orange roughy can live up to 200 years!

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

# The structured population model

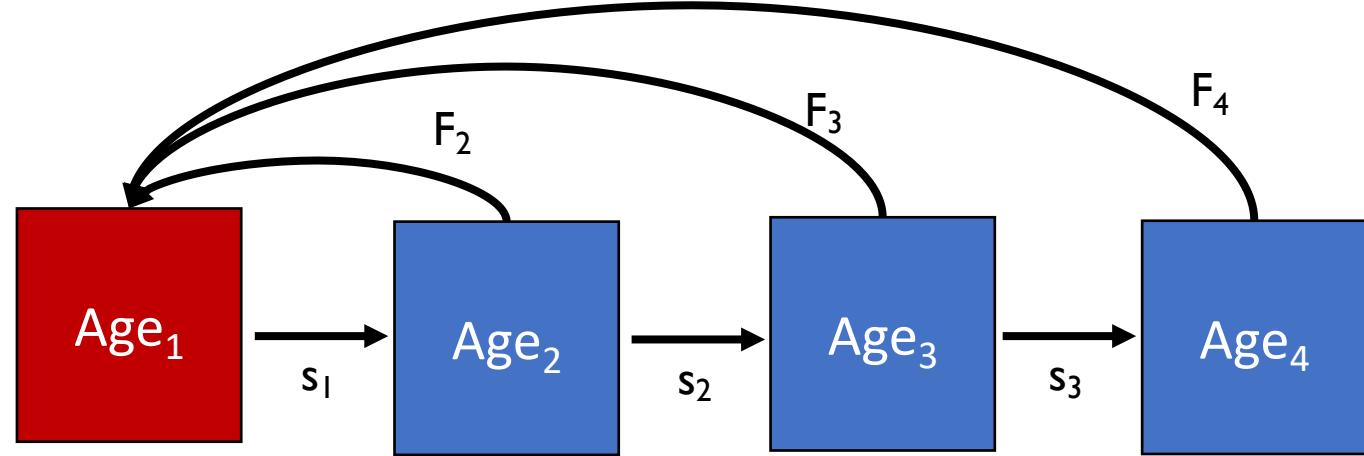
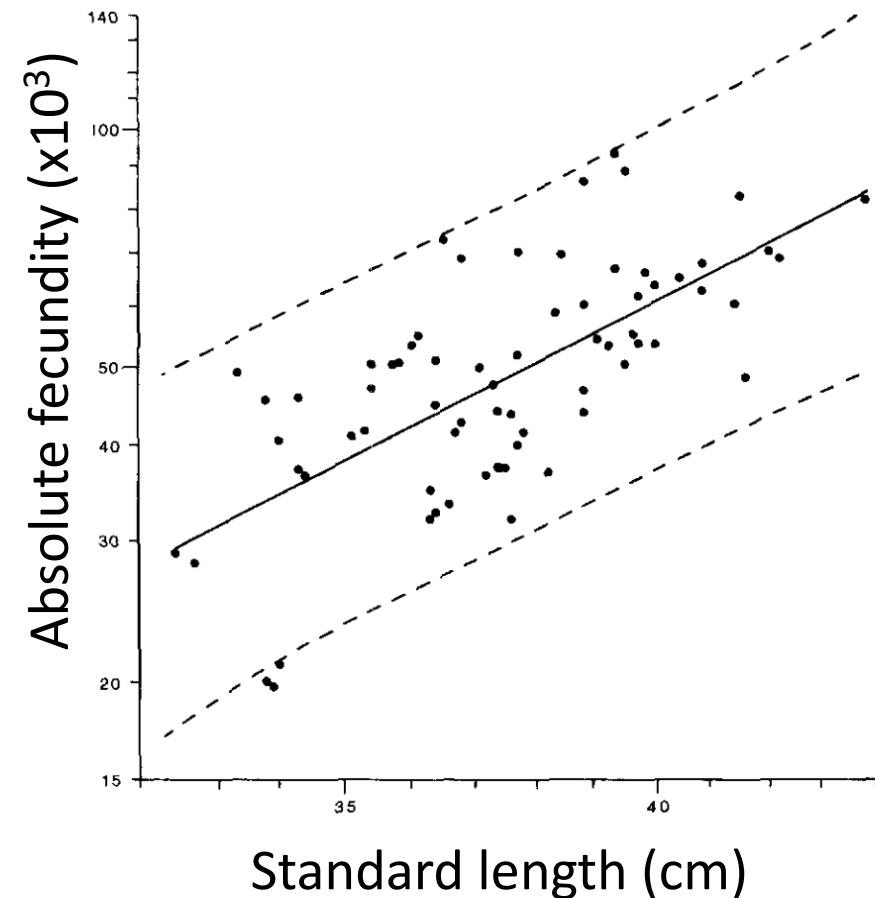


A brace on the right side of the graph points to the data points, with the text:  
Fecundity (eggs)  
increases in older,  
bigger fish!

Pankhurst & Conroy 1987

*NZ J of Marine & Freshwater Res*

# The structured population model



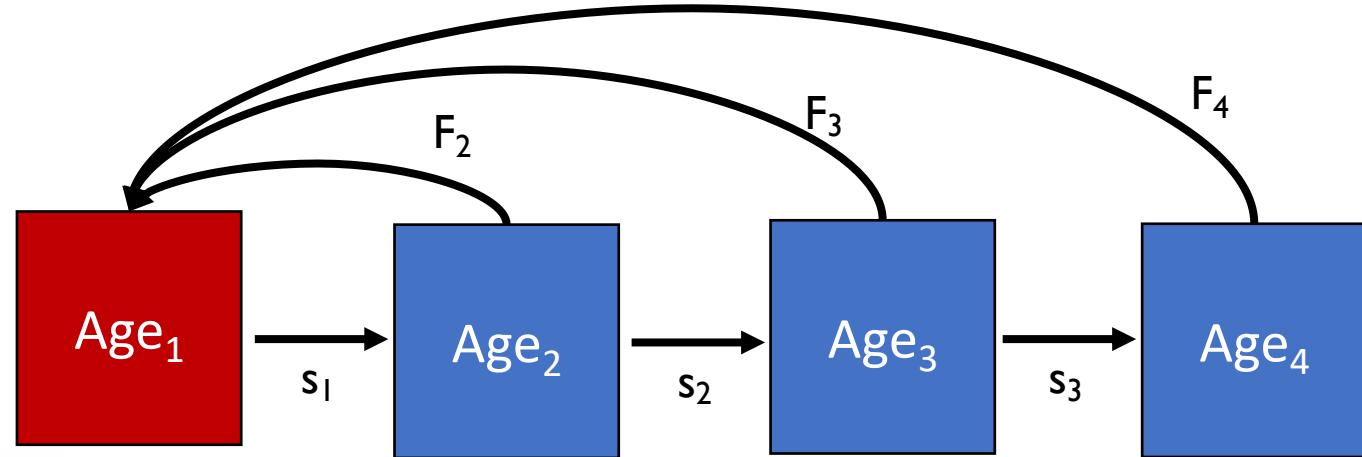
Fecundity (eggs)  
increases in older,  
bigger fish!

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

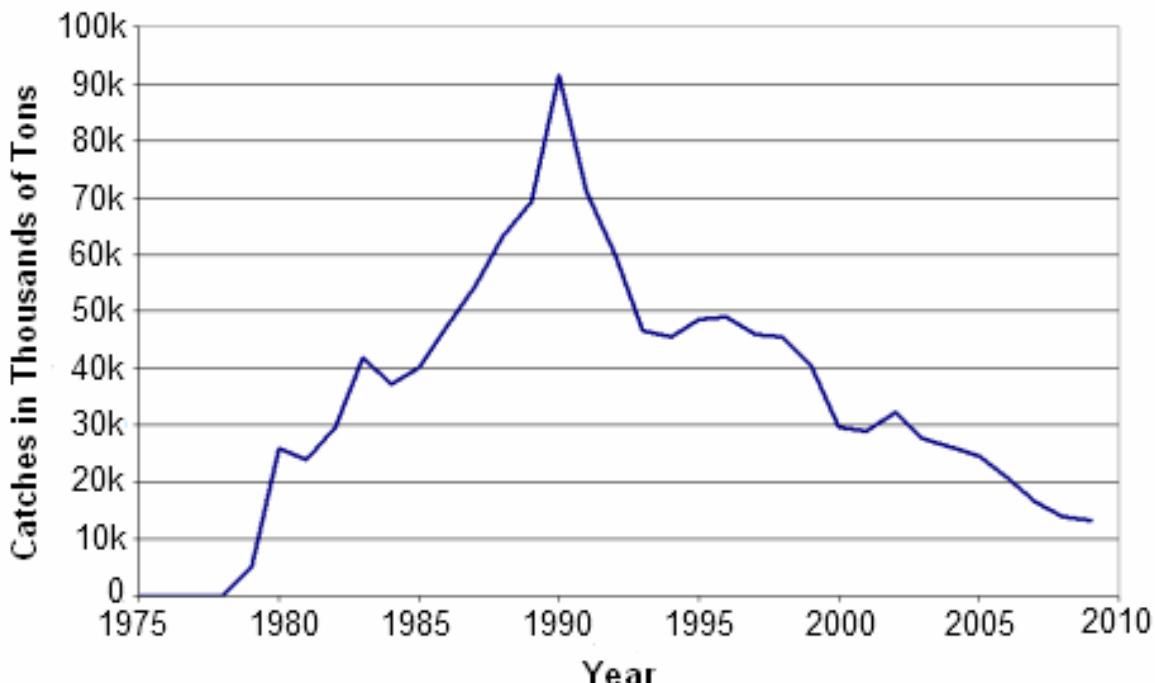


Norway 1910  
(Norsk folkemuseum)

# The structured population model



Worldwide Catches of Orange Roughy 1975 - 2009



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

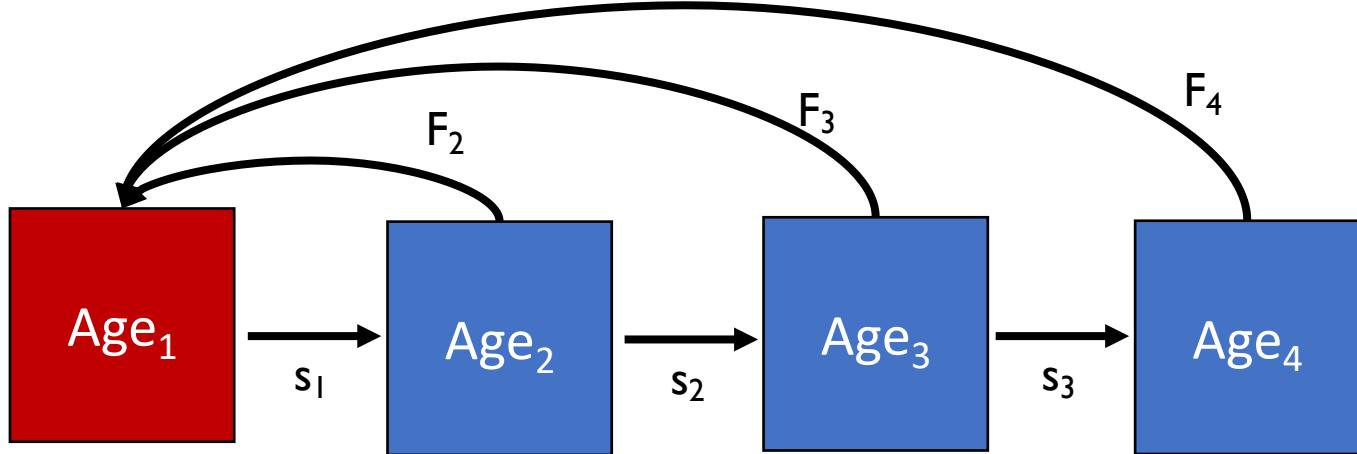
In 2008, the international TAC for orange roughy was reduced from 1470 tons to 914 tons... down from over 90,000 tons in the early 1990s...



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

# The structured population model

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

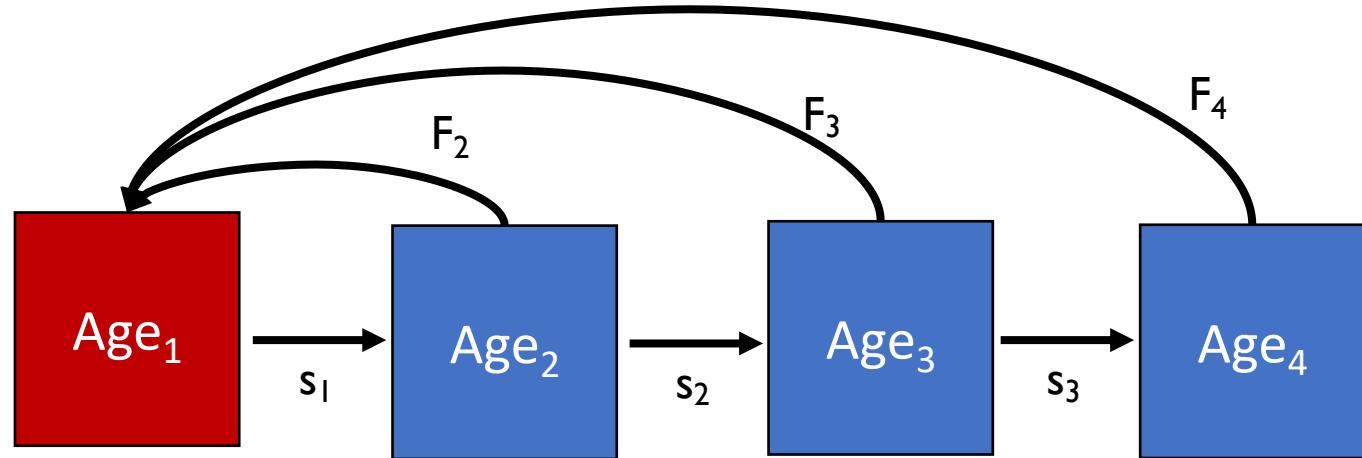
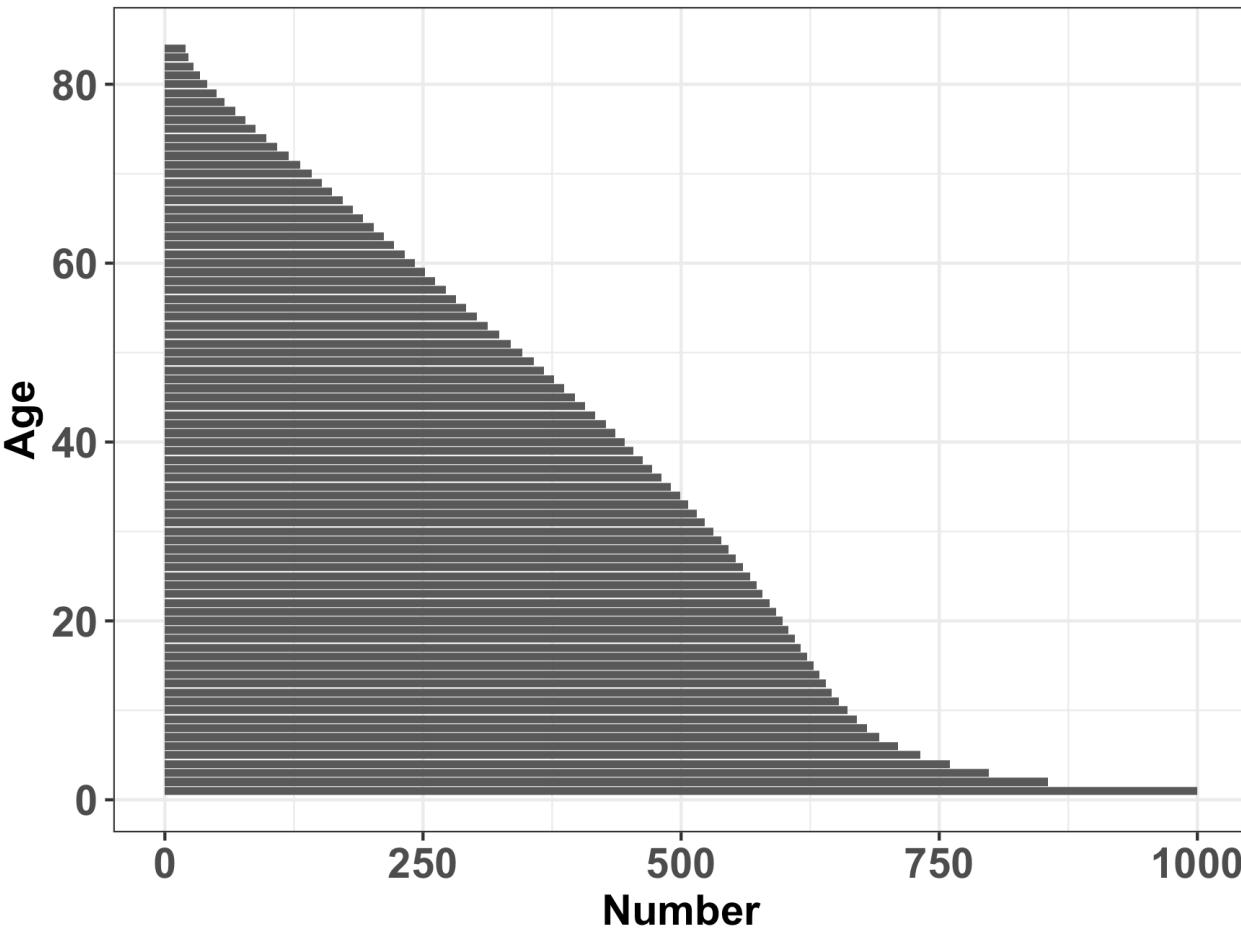


Age. Year.	Per- sons.	Age. Cur.	Per- sons.								
1	1000	8	680	15	623	22	585	29	539	35	481
2	855	9	570	16	612	23	579	30	531	37	472
3	798	10	651	17	615	24	573	31	523	38	453
4	750	11	553	18	610	25	567	32	515	39	454
5	732	12	546	19	604	26	560	33	507	40	445
6	710	13	640	20	593	27	555	34	495	41	436
7	652	14	634	21	592	28	546	35	490	42	427
Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.	Age. Cur.	Per- sons.
43	417	50	345	57	272	64	202	71	131	78	58
44	407	51	333	58	252	65	192	72	120	79	49
45	397	52	324	59	252	65	182	73	105	80	41
46	387	53	313	60	242	67	172	74	98	81	34
47	377	54	302	61	232	68	162	75	92	82	28
48	367	55	292	62	222	69	152	76	88	83	23
49	357	56	282	63	212	70	142	77	83	84	20
											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

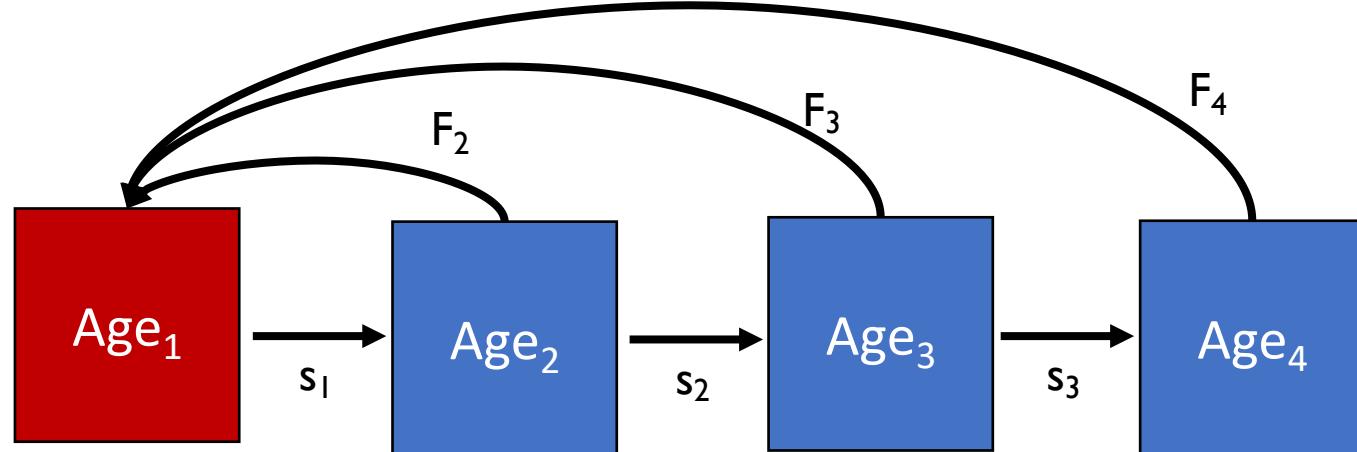
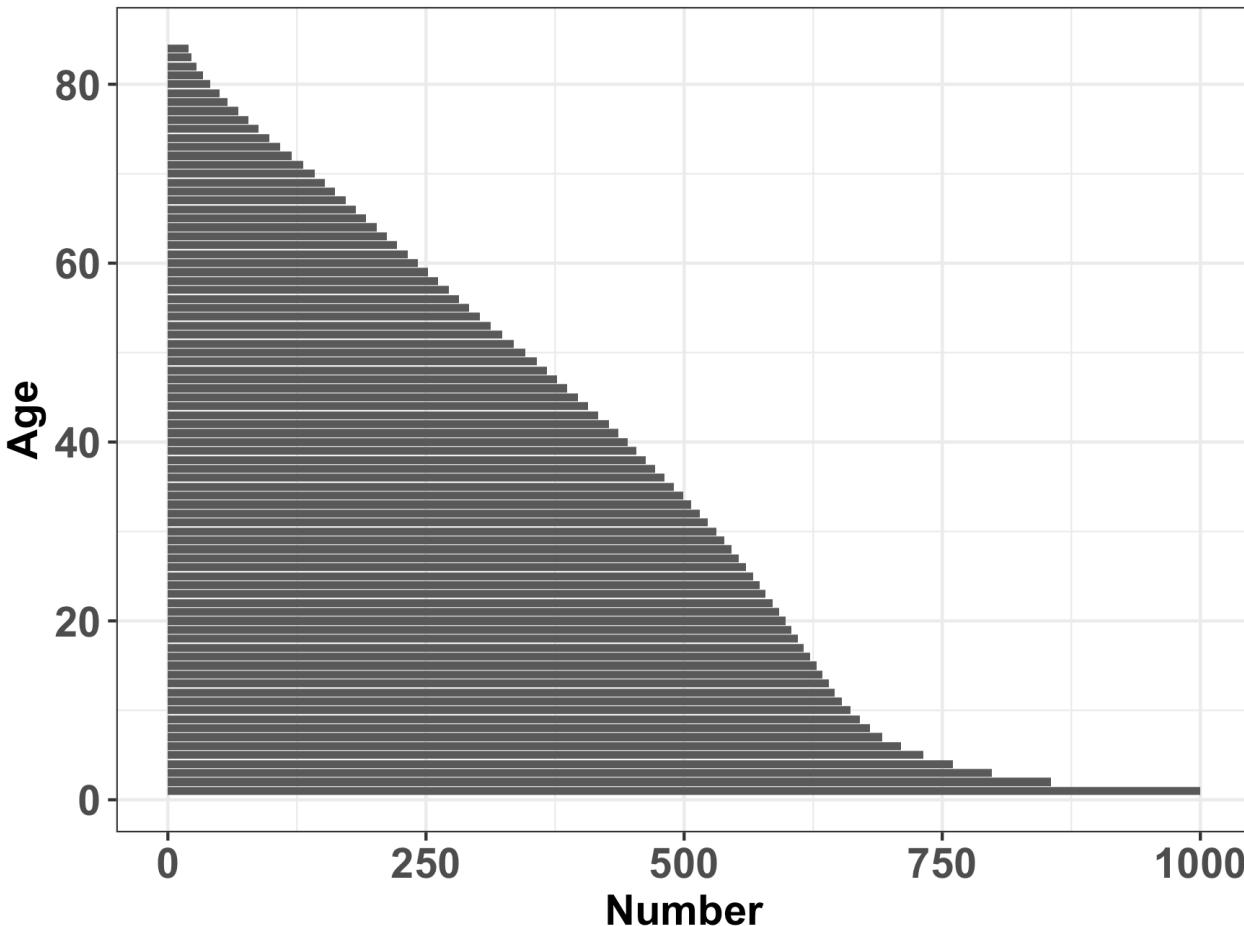
Population pyramid for Breslau



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

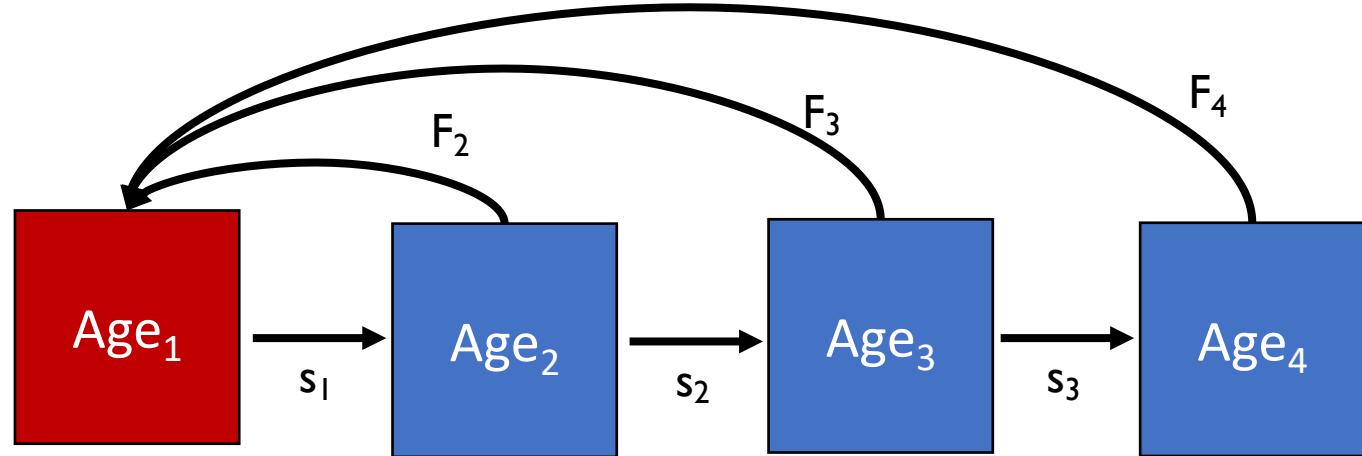


Humans are not like fish!  
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

**Younger human populations that start giving birth earlier grow faster!**

$$\begin{matrix} \mathbf{A} & \mathbf{N}_t & \mathbf{N}_{t+1} \\ \left[ \begin{matrix} 0 & s_1 F_2 & s_2 F_3 & s_3 F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{matrix} \right] & \times & \left[ \begin{matrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{matrix} \right] = \left[ \begin{matrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{matrix} \right] \end{matrix}$$

# The structured population model

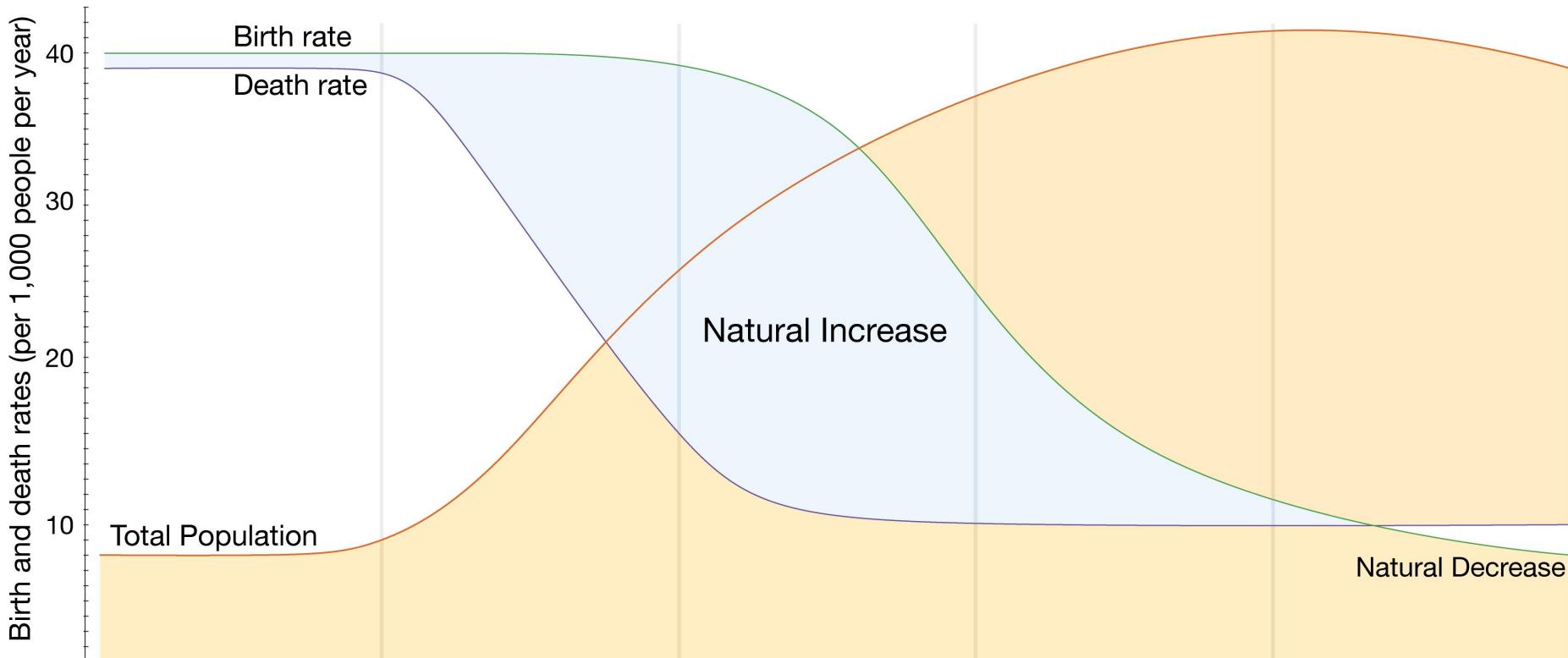


Humans are not like fish!  
Fecundity tends to decrease in older age classes due to **reproductive senescence**.

**Younger human populations that start giving birth earlier grow faster!**

$$\begin{matrix}
 & \mathbf{A} & \mathbf{N}_t & \mathbf{N}_{t+1} \\
 \left[ \begin{matrix} 0 & s_1 F_2 & s_2 F_3 & s_3 F_4 \\ s_1 & 0 & 0 & 0 \\ 0 & s_2 & 0 & 0 \\ 0 & 0 & s_3 & 0 \end{matrix} \right] \times \left[ \begin{matrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{matrix} \right] = \left[ \begin{matrix} N_{1,t+1} \\ N_{2,t+1} \\ N_{3,t+1} \\ N_{4,t+1} \end{matrix} \right]
 \end{matrix}$$

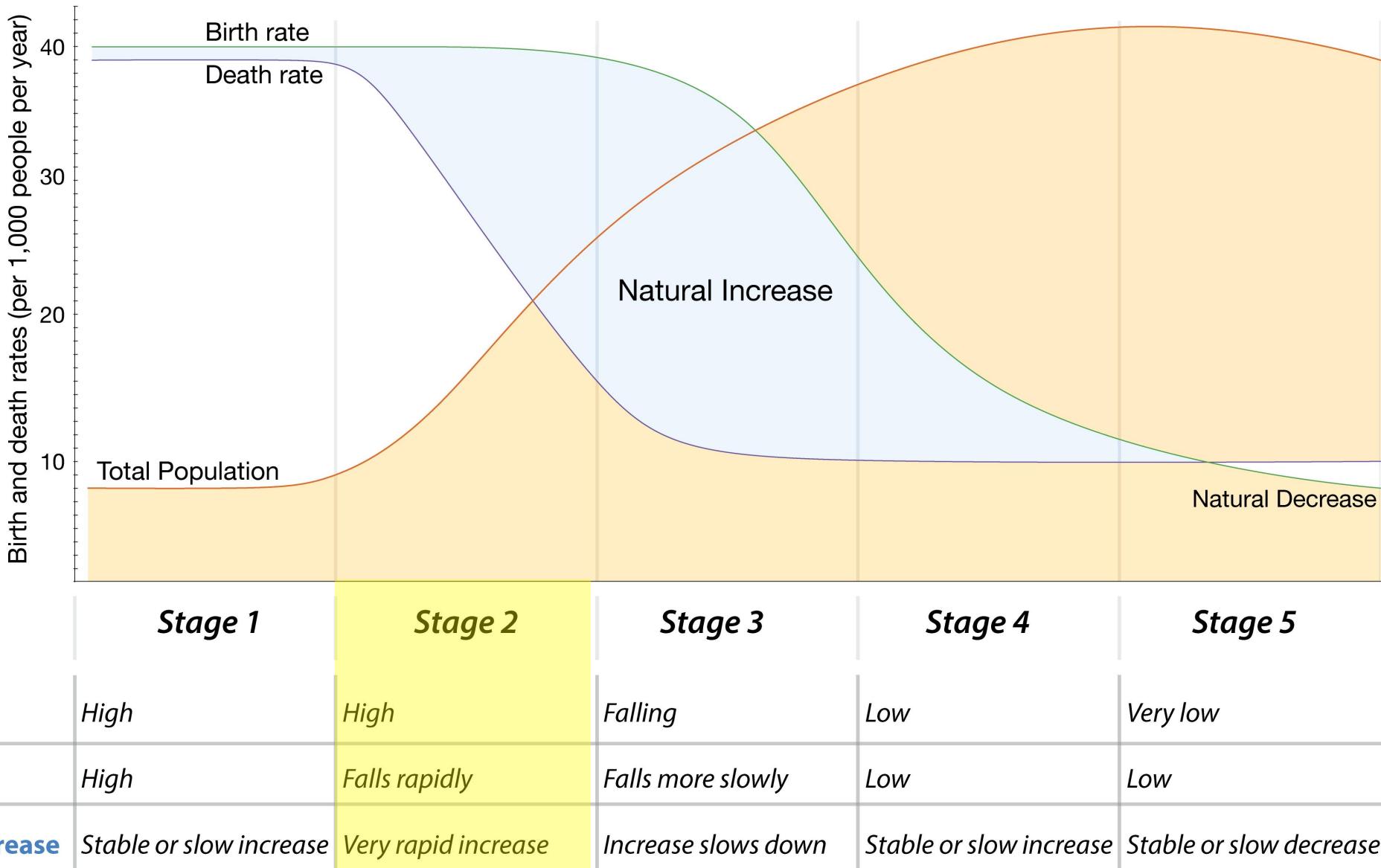
# Demographic transition



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

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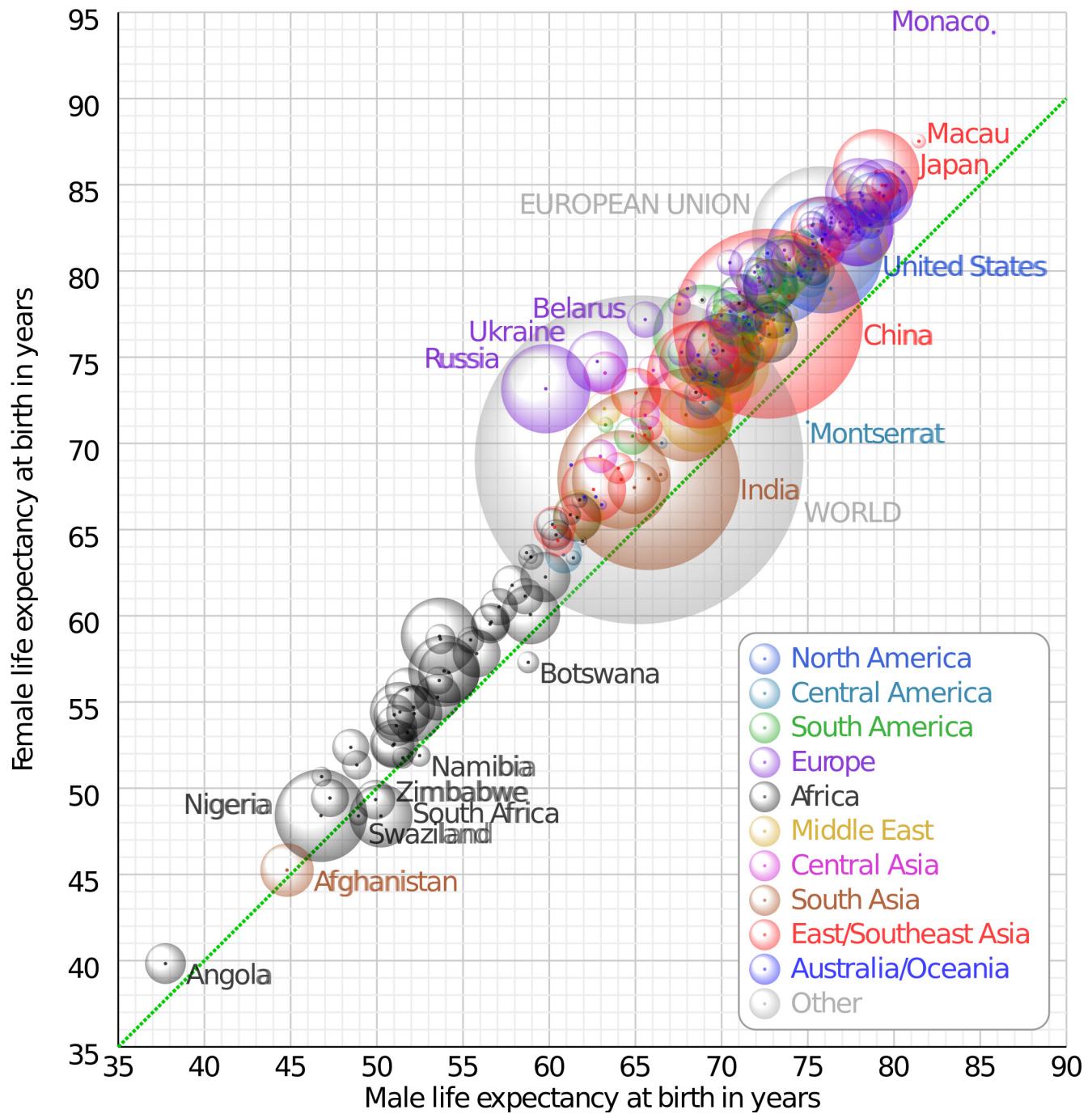
# Demographic transition



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>

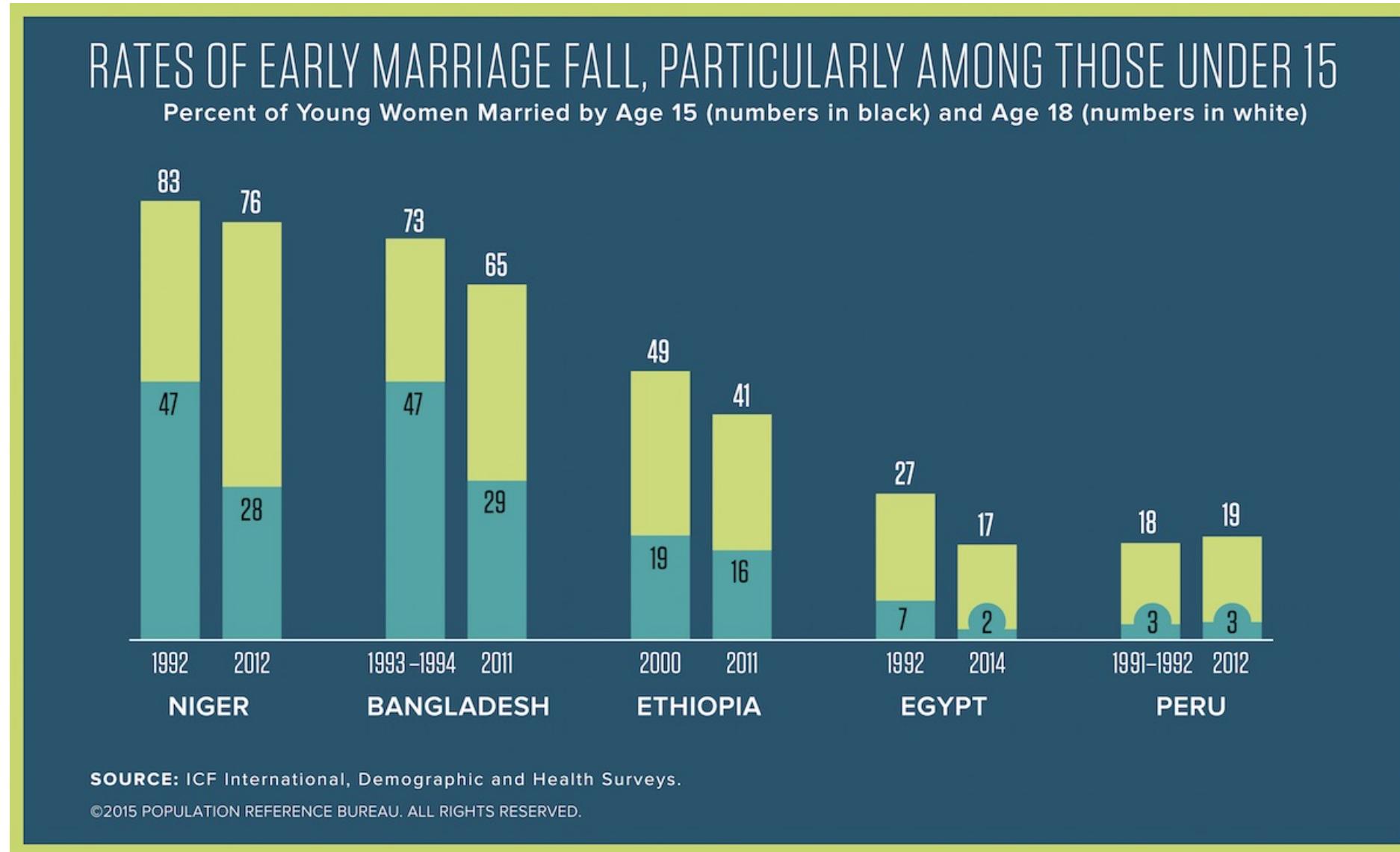
# Demographic transition

Death rates are falling globally...

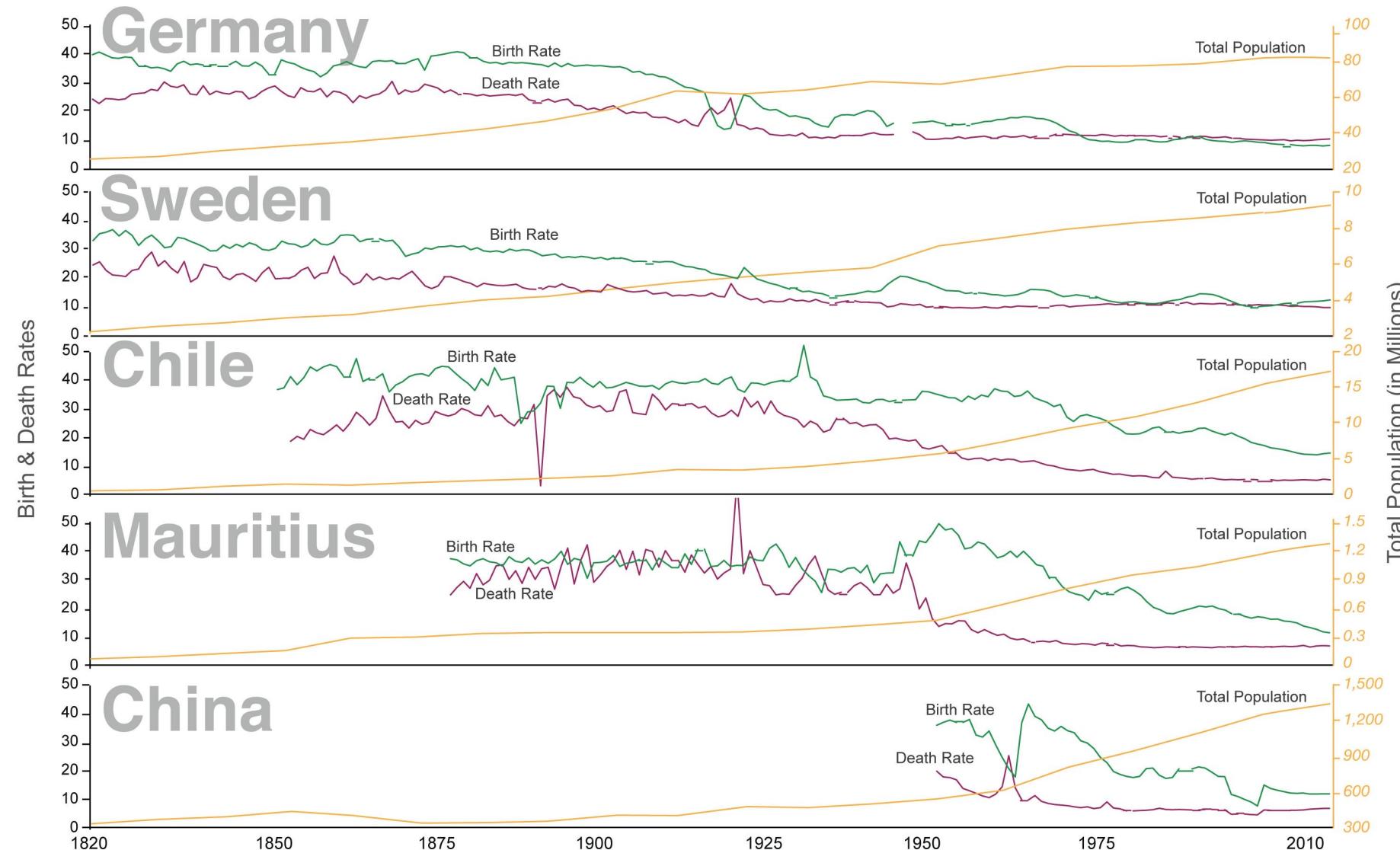


# Demographic transition

And birth rates  
are also falling...



# Demographic transition



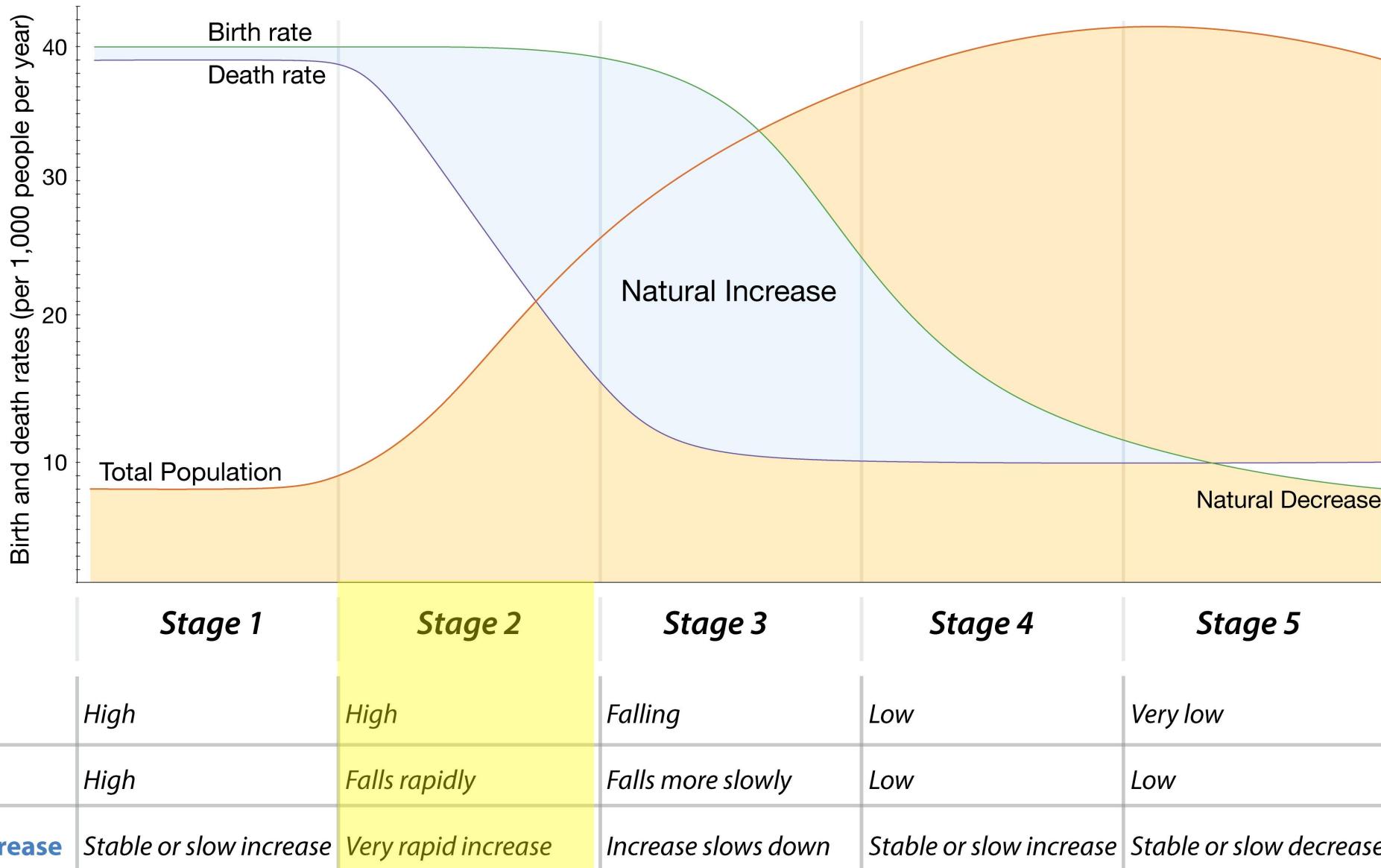
Data source: The data on birth rates, death rates and the total population are taken from the International Historical Statistics, edited by Palgrave Macmillan (April 2013).

The interactive data visualisation is available at [OurWorldInData.org](http://OurWorldInData.org). There you find the raw data and more visualisations on this topic.

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# Demographic transition

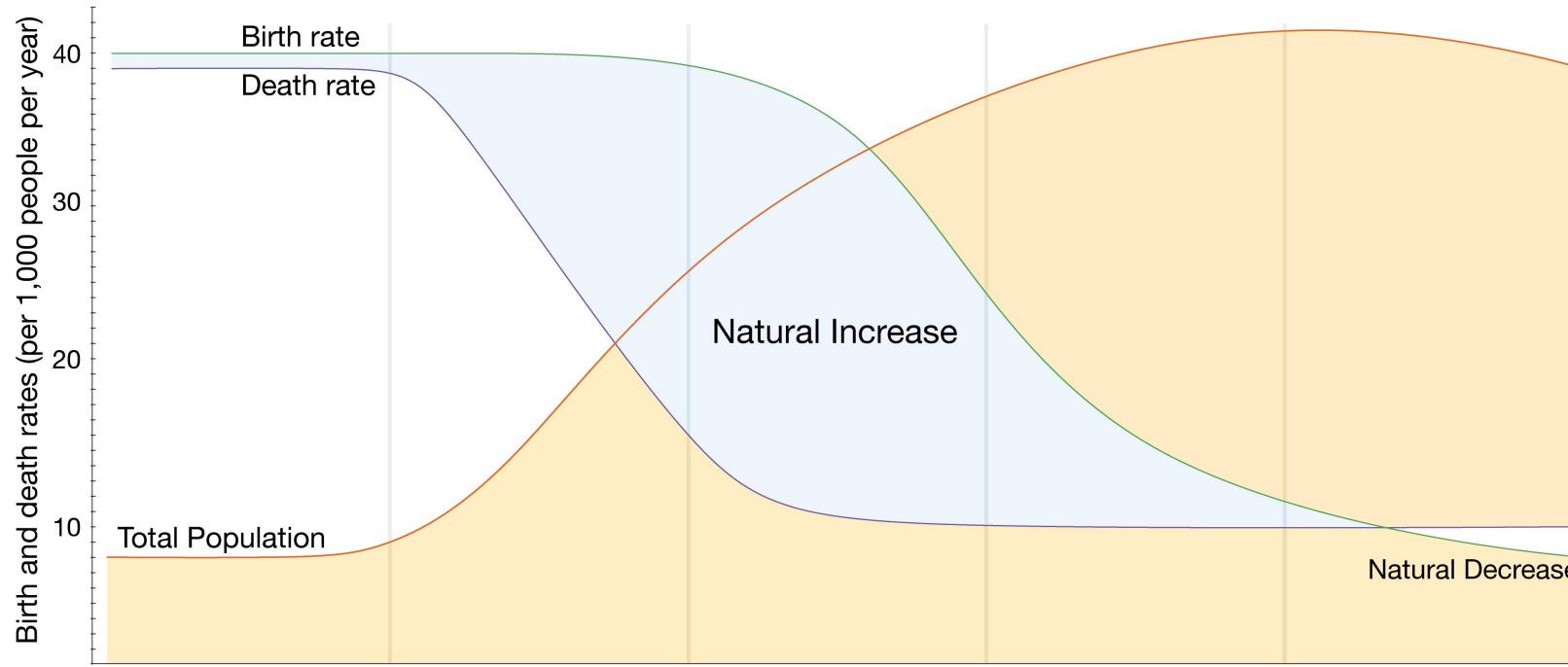
How does age structure predict population growth?



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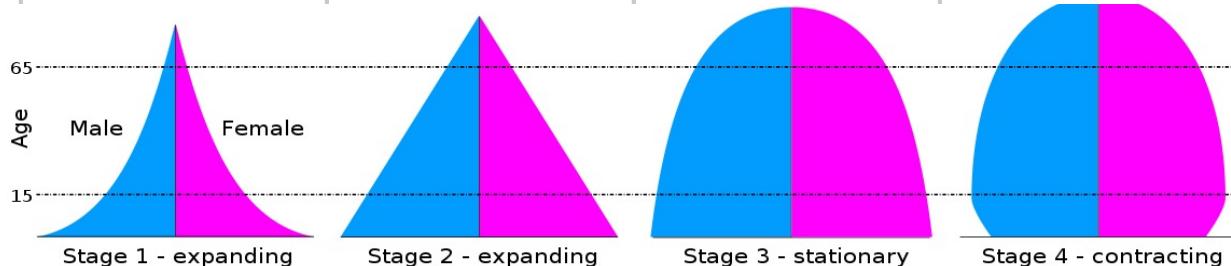
# Demographic transition

How does age structure predict population growth?

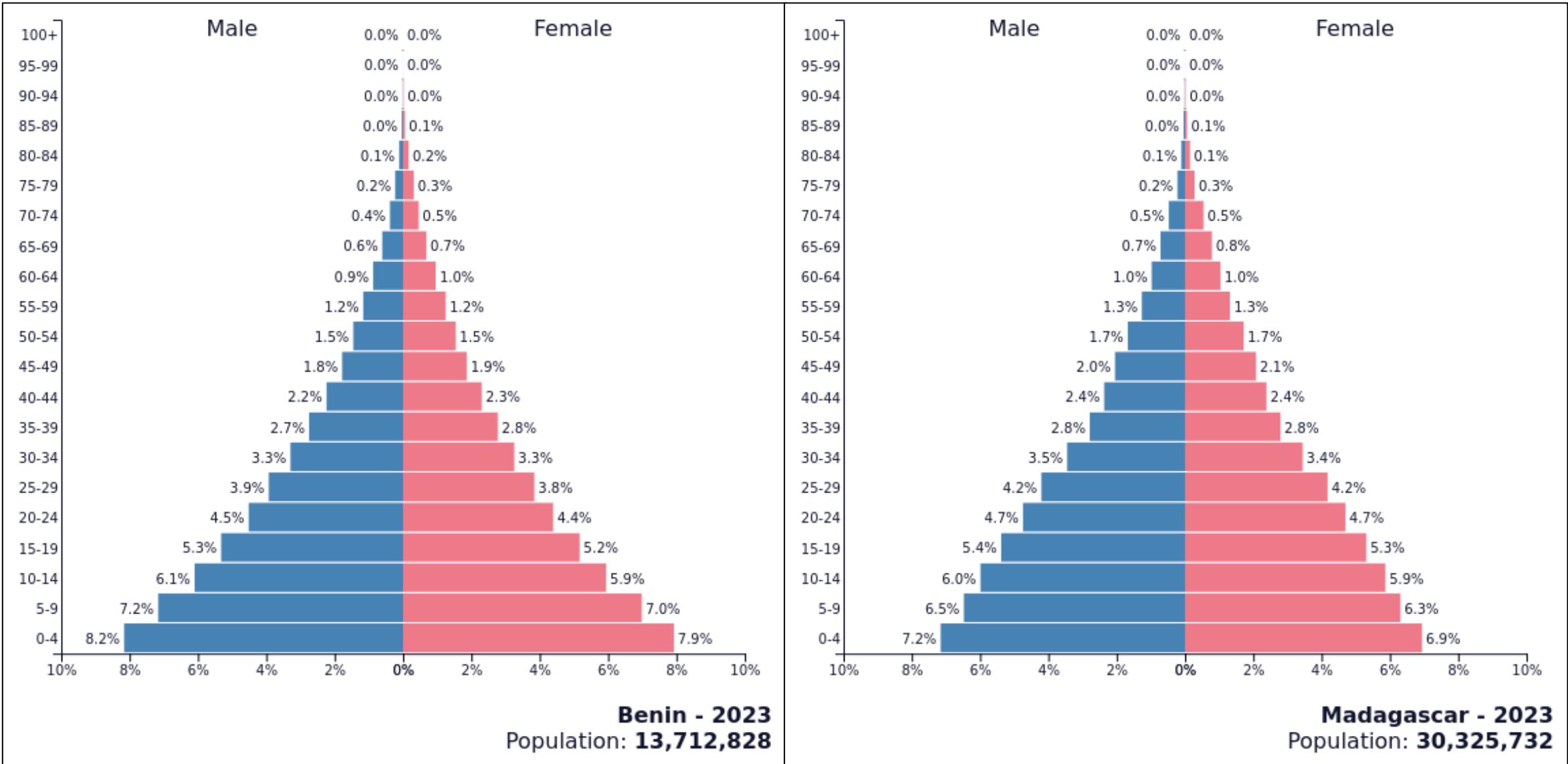
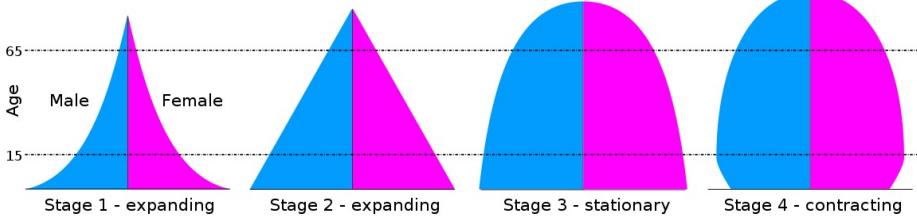


Stage 1      Stage 2      Stage 3      Stage 4      Stage 5

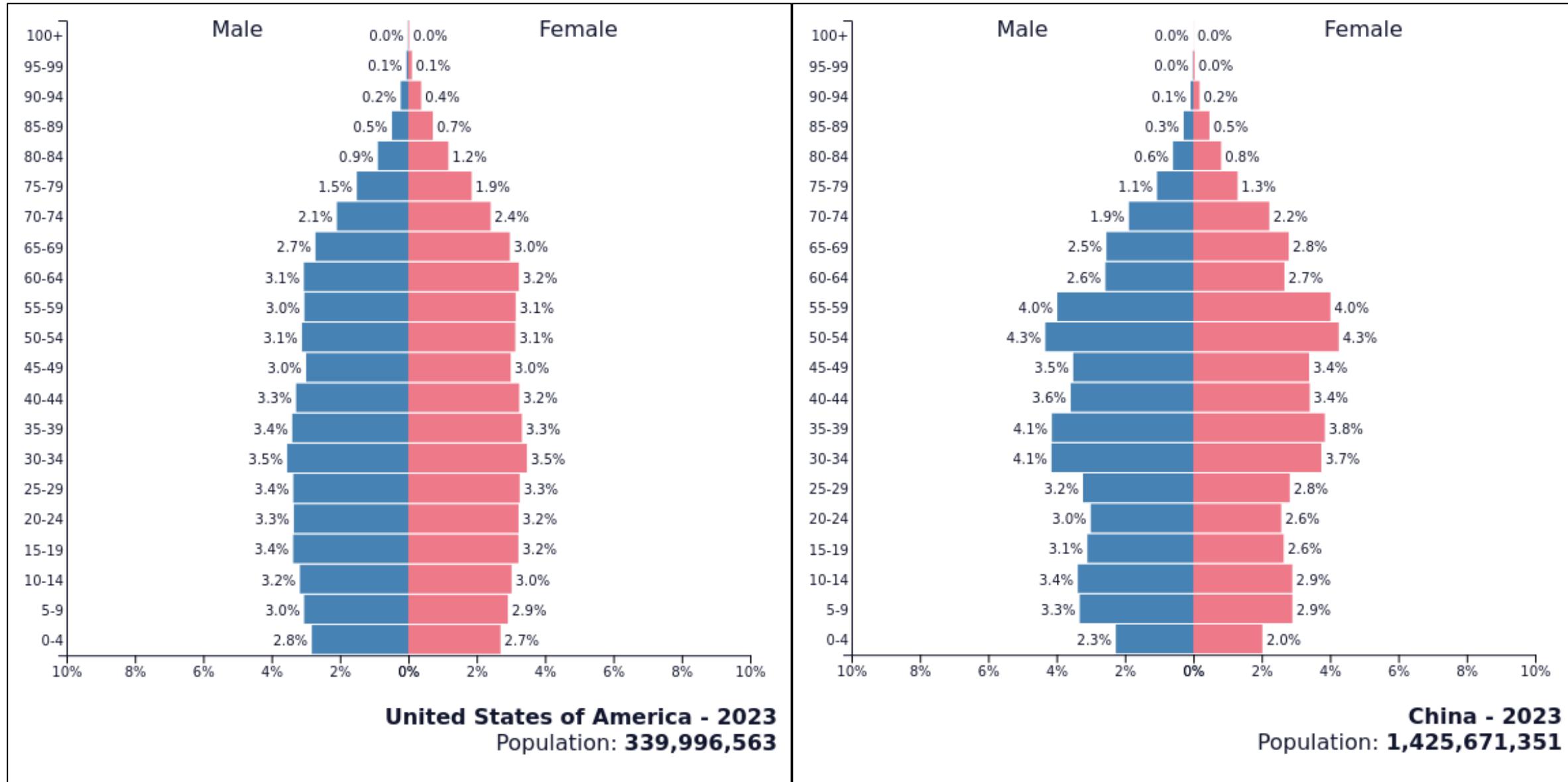
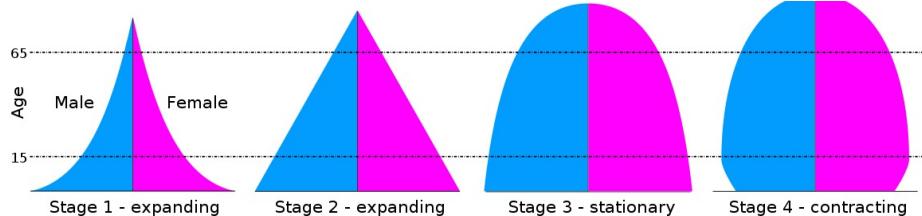
<b>Birth rate</b>	High	High	Falling	Low	Very low
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<b>Natural increase</b>	Stable or slow increase	Very rapid increase	Increase slows down	Stable or slow increase	Stable or slow decrease



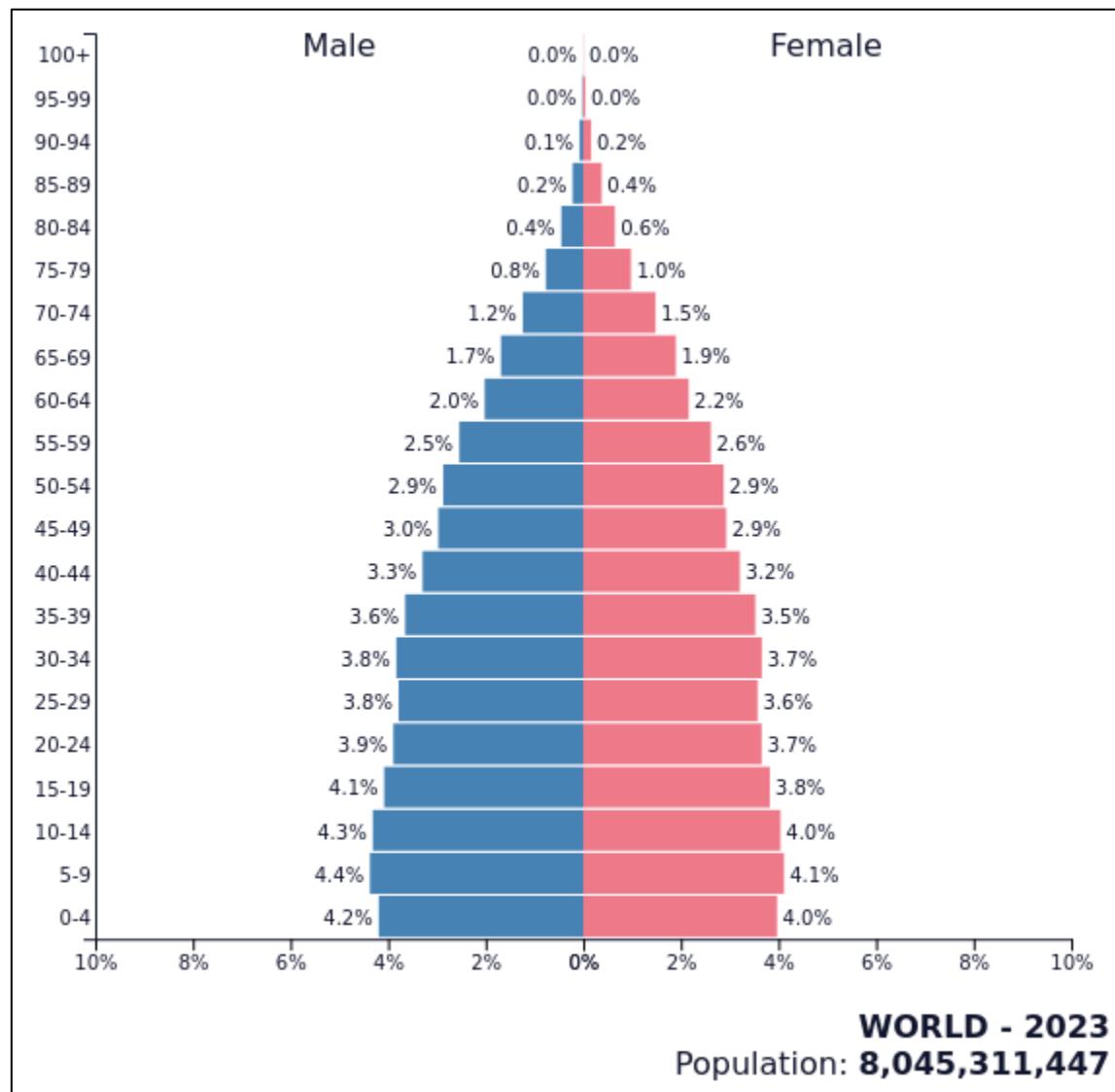
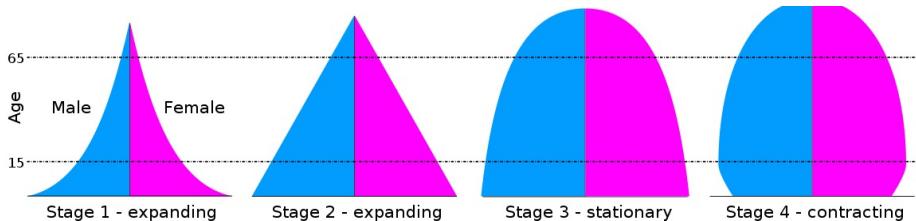
# Where are we globally?



# Where are we globally?

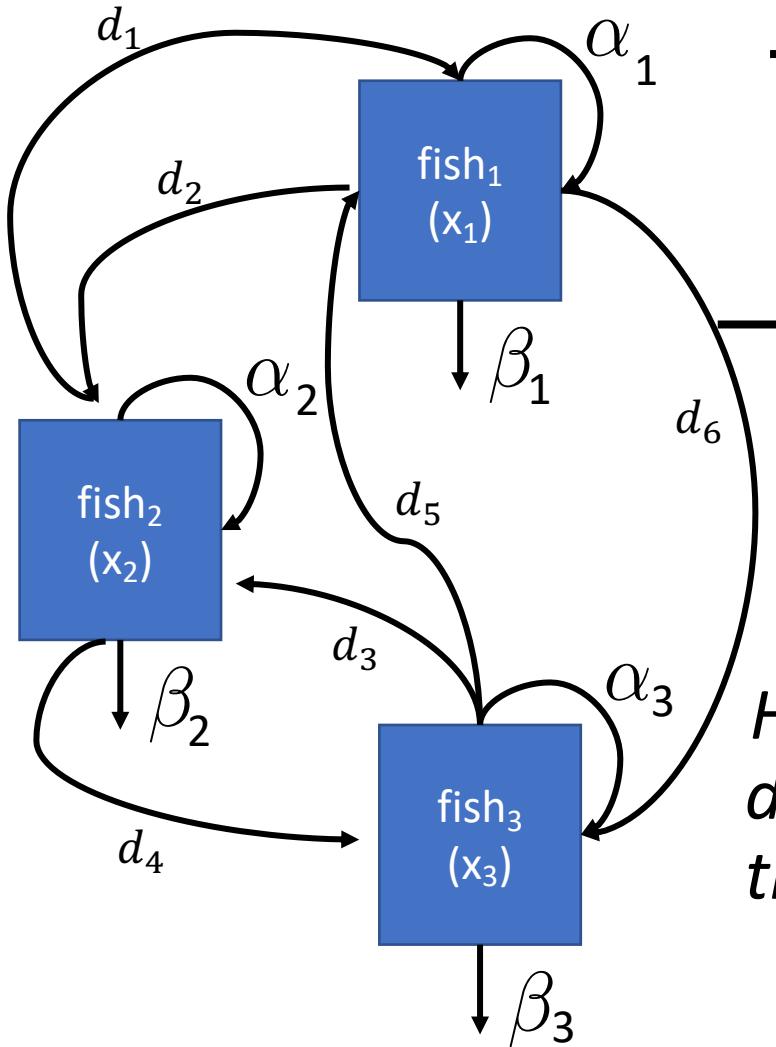


# Where are we globally?

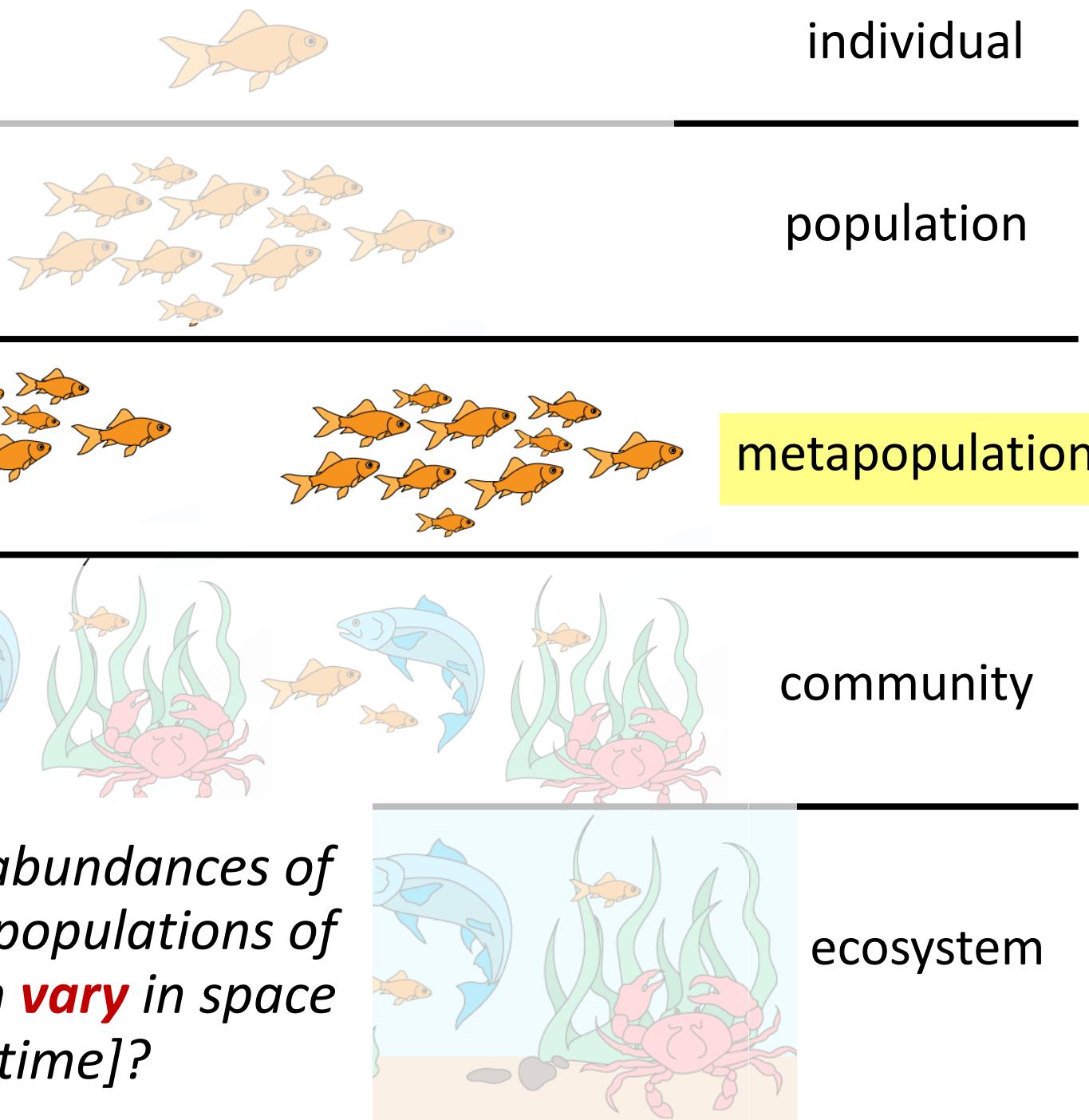


Structured population models can be scaled up to **metapopulation models**, depending on the data and question at hand

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



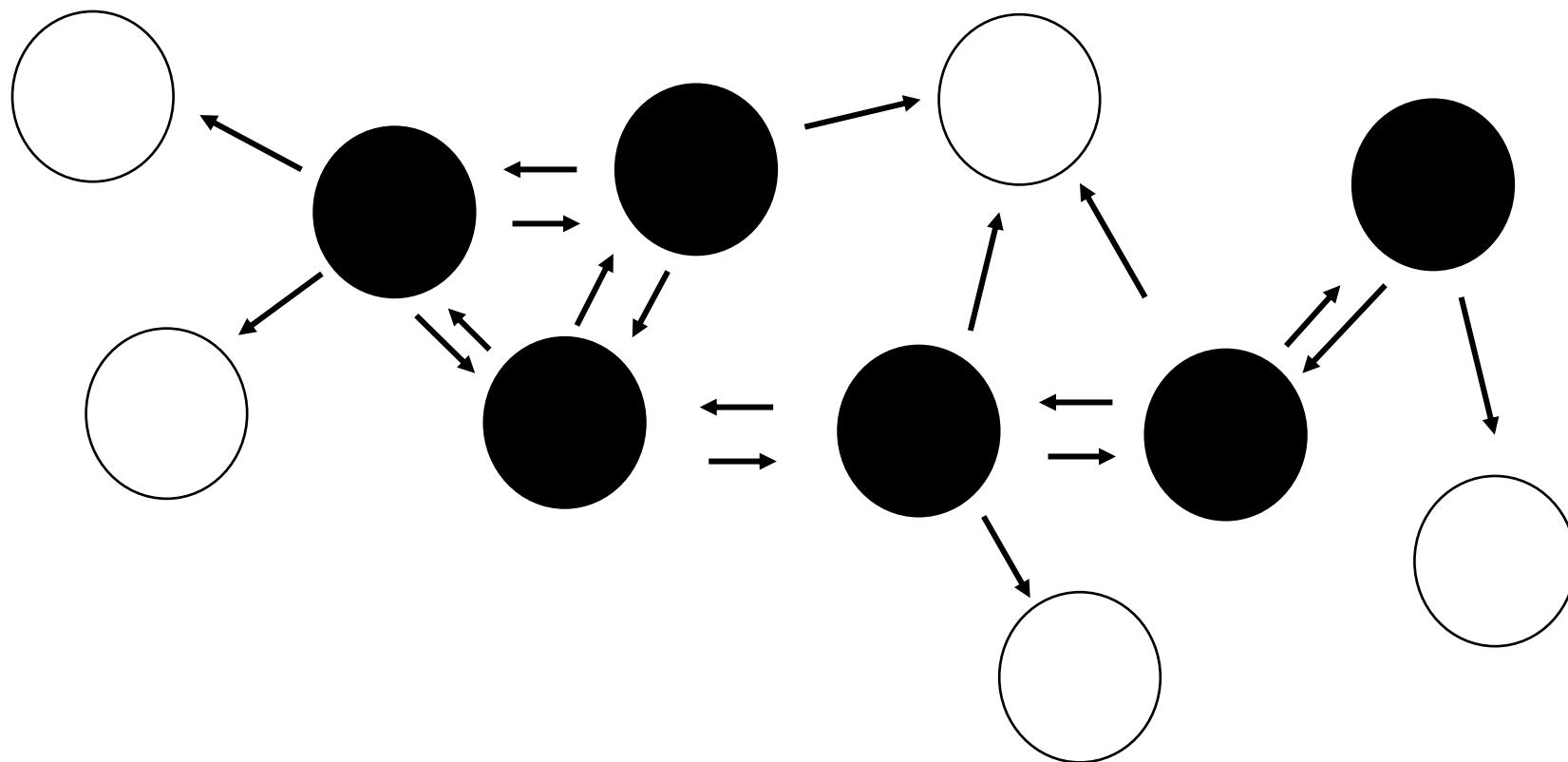
*How do the abundances of different subpopulations of the same fish **vary** in space [and time]?*



# Modeling metapopulation dynamics

- a “population of populations”

-Richard Levins 1969



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

colonization rate

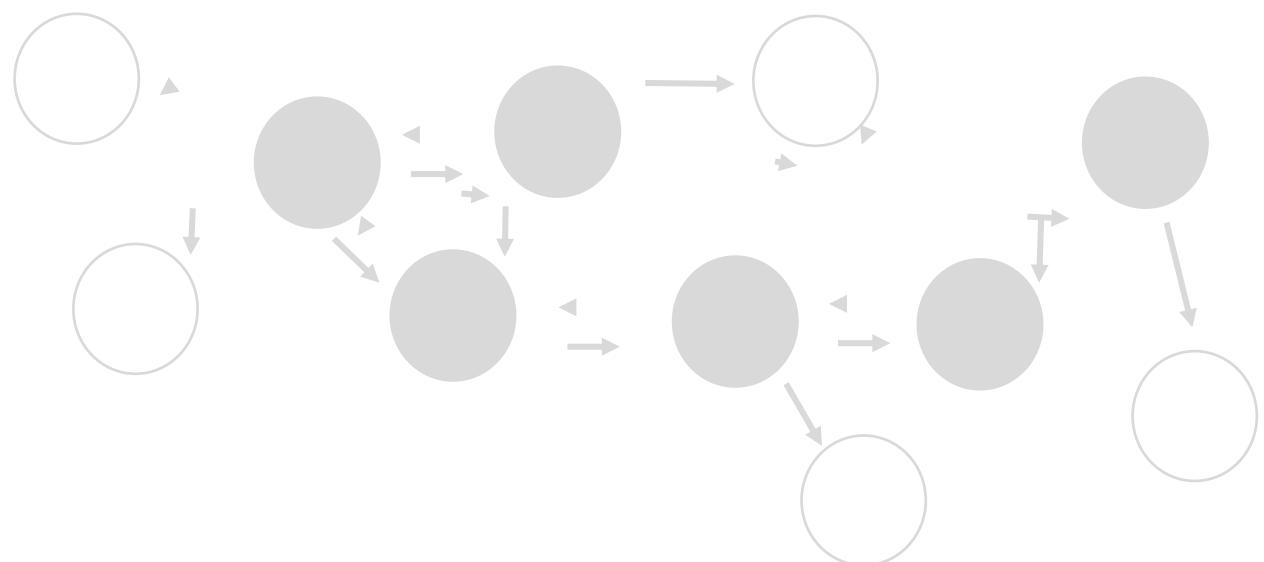
↑

proportion of unoccupied patches

extinction rate

↑

fraction of patches occupied at a given time



# Modeling metapopulation dynamics

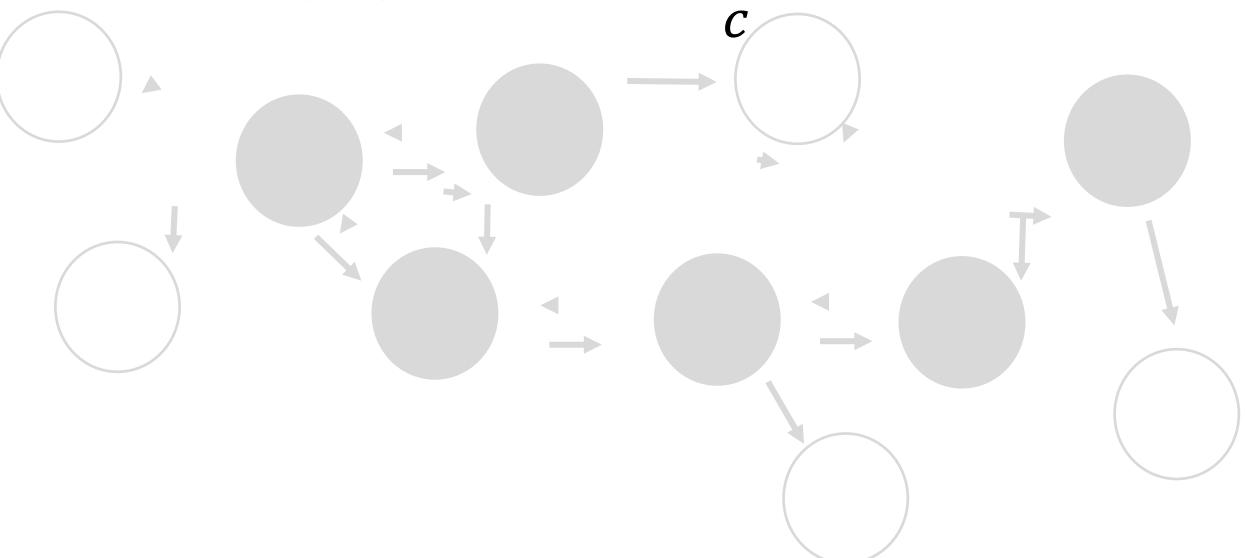
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$$\frac{dp}{dt} = cp(1 - p) - ep$$
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

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

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



# Modeling metapopulation dynamics

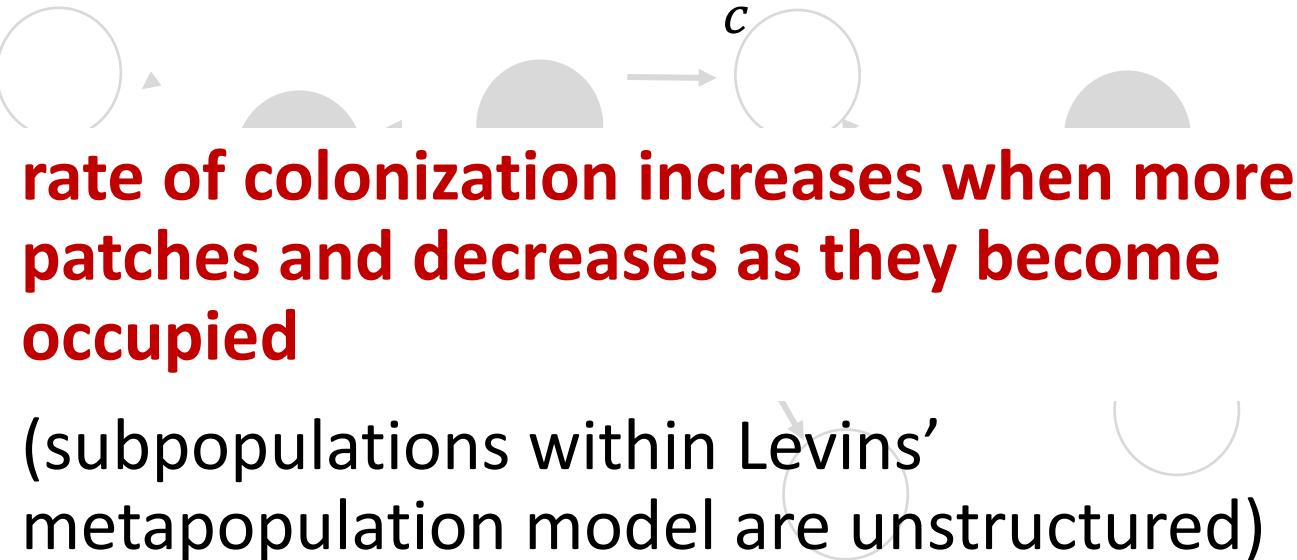
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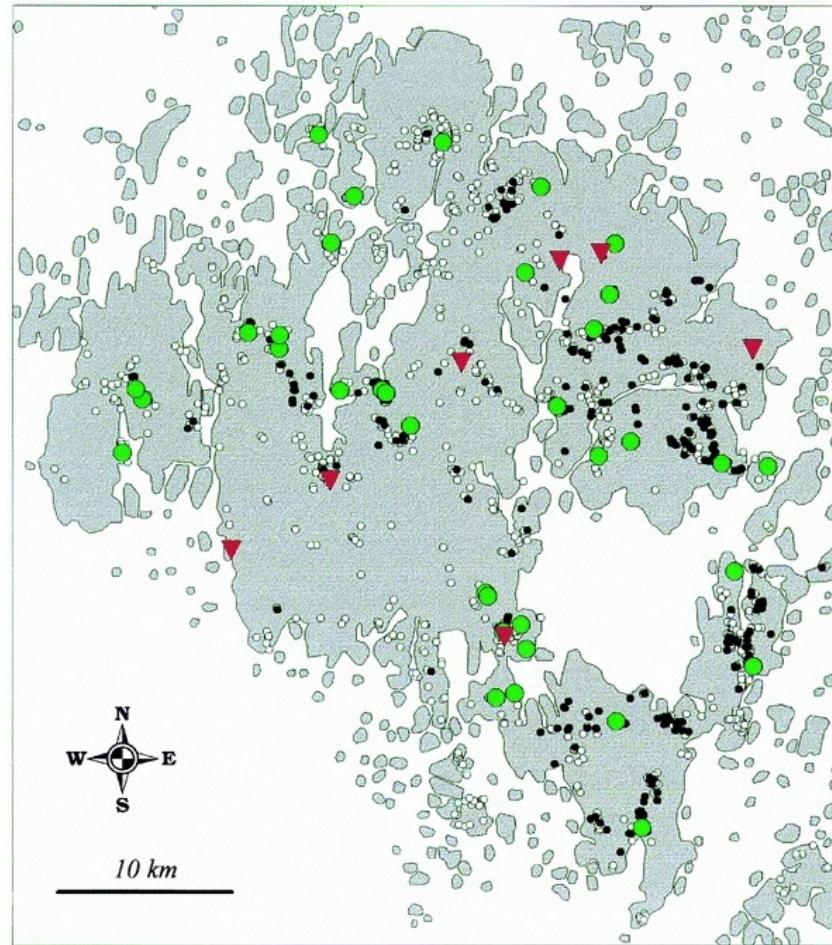
rate of colonization increases when more patches and decreases as they become occupied

(subpopulations within Levins' metapopulation model are unstructured)

# Why do metapopulations matter?



Ilkka Hanski  
1953-2016

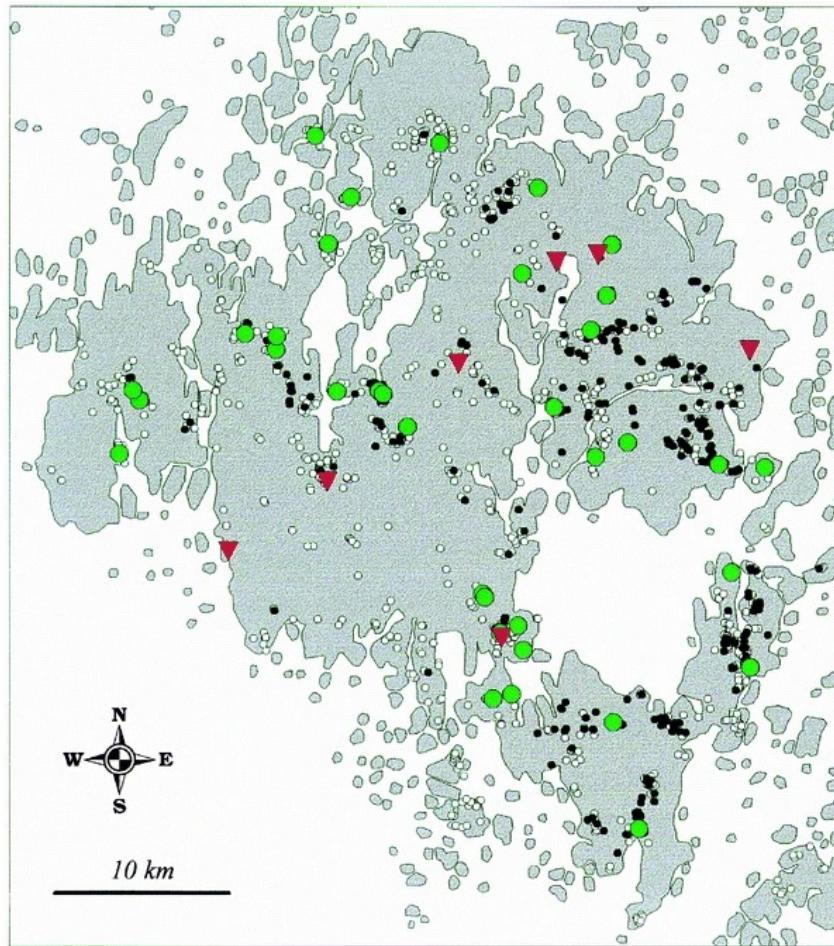


Saccheri et al 1998. *Nature*.



Glanville fritillary butterfly  
*Melitaea cinxia*

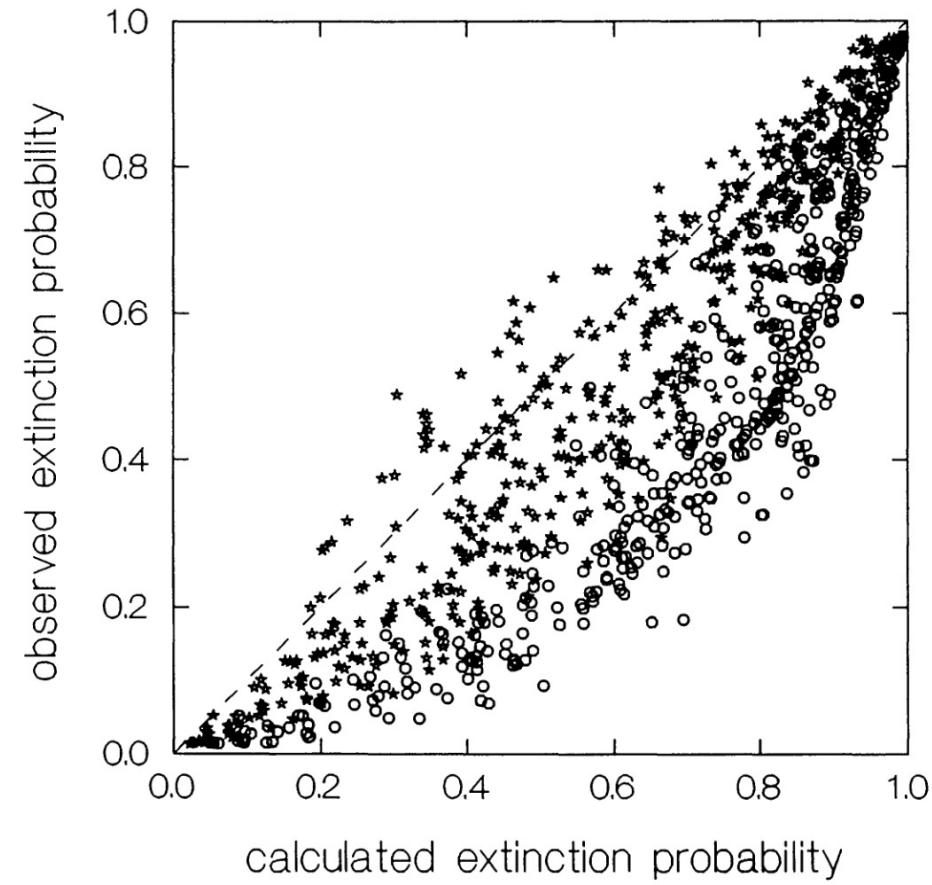
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Saccheri et al 1998. *Nature*.

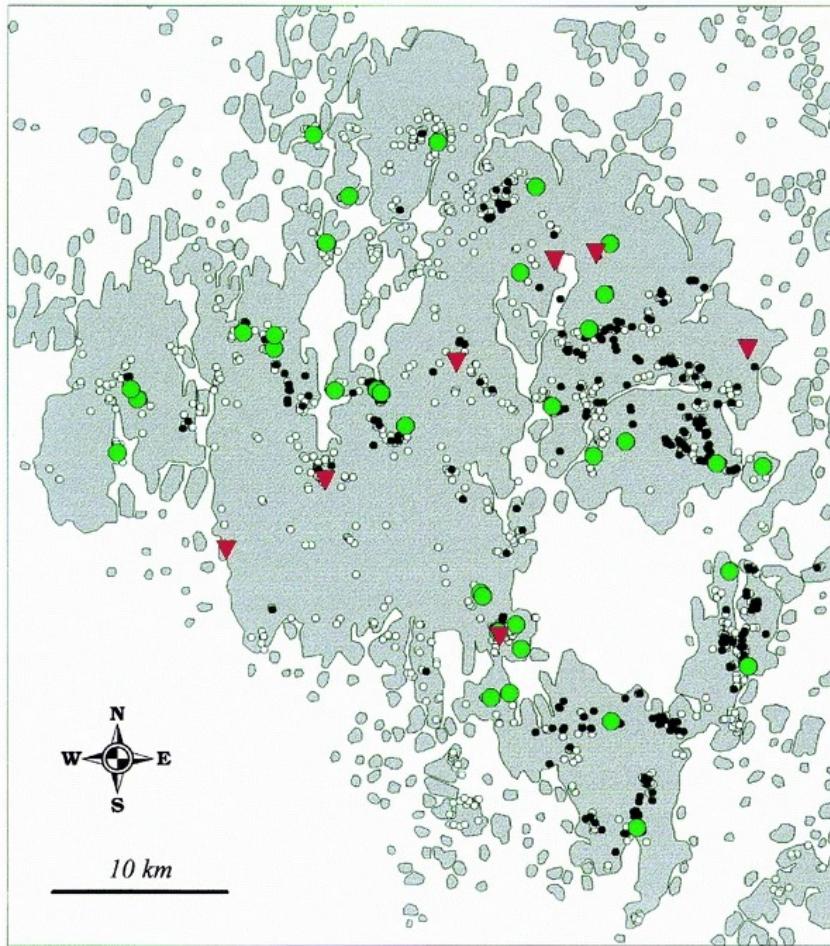
## MINIMUM VIABLE METAPOPULATION SIZE

ILKKA HANSKI,<sup>1</sup> ATTE MOILANEN,<sup>1</sup> AND MATS GYLLENBERG<sup>2</sup>



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

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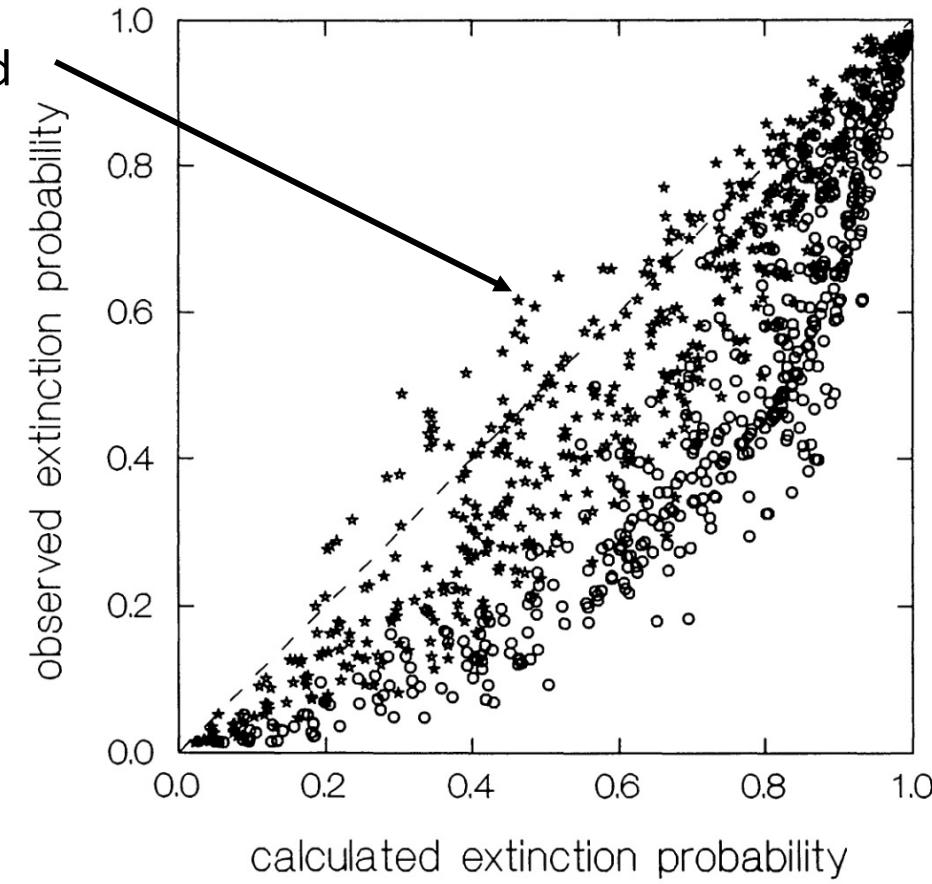


Saccheri et al 1998. *Nature*.

star points  
recalculated  
with **rescue  
effect** from  
Levins'  
model

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

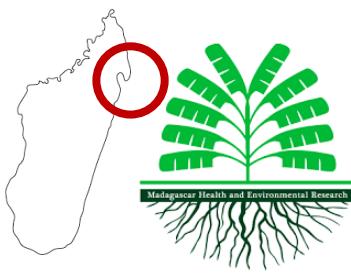
*Conservation Biology*



*Contributed Paper*

## Population viability and harvest sustainability for Madagascar lemurs

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



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?**





# 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>Varecia</i> <i>rubra</i>	<i>Varecia</i> <i>variegata</i>	<i>Indri</i> <i>Indri</i>
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# 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?**

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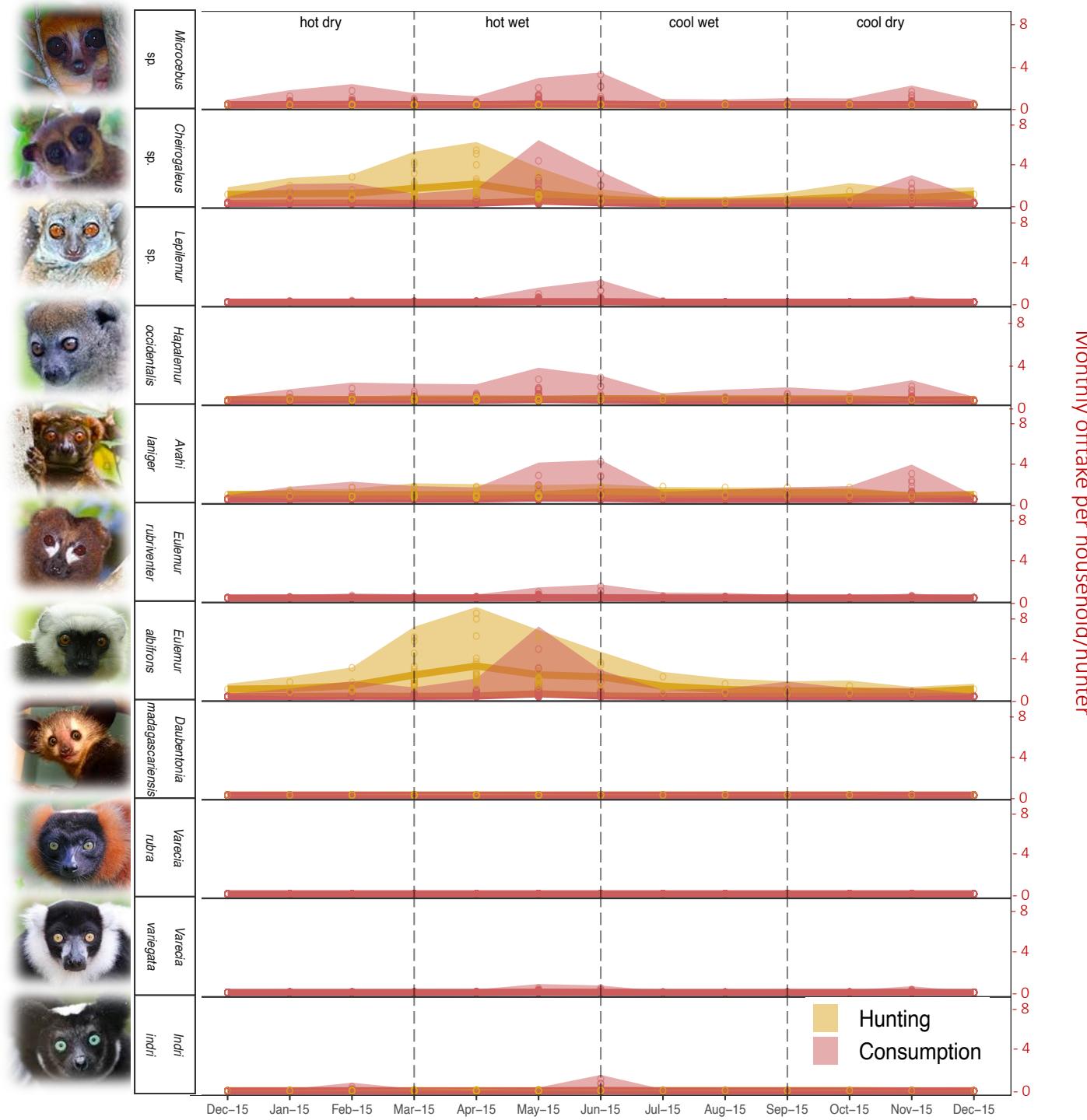
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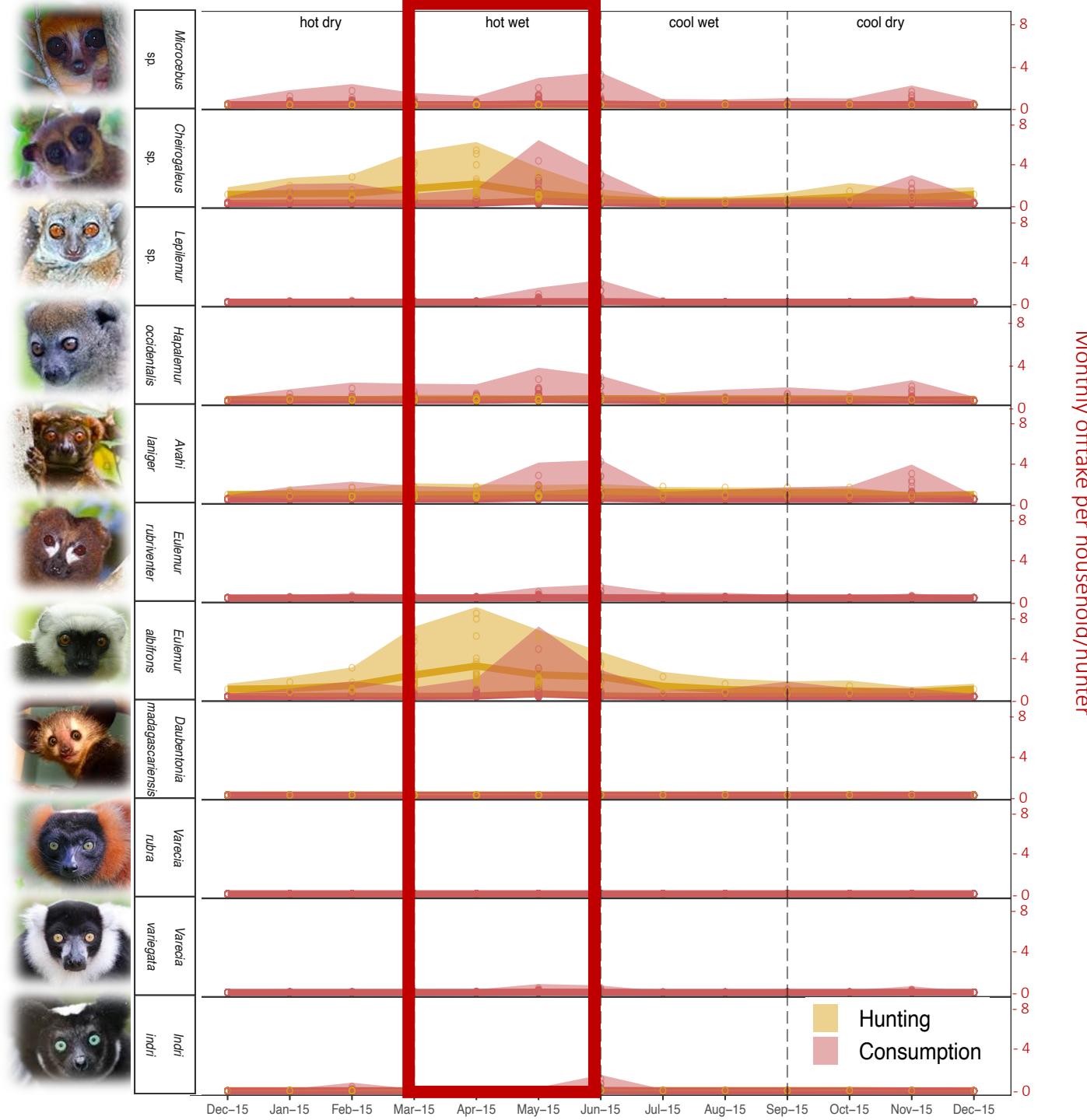


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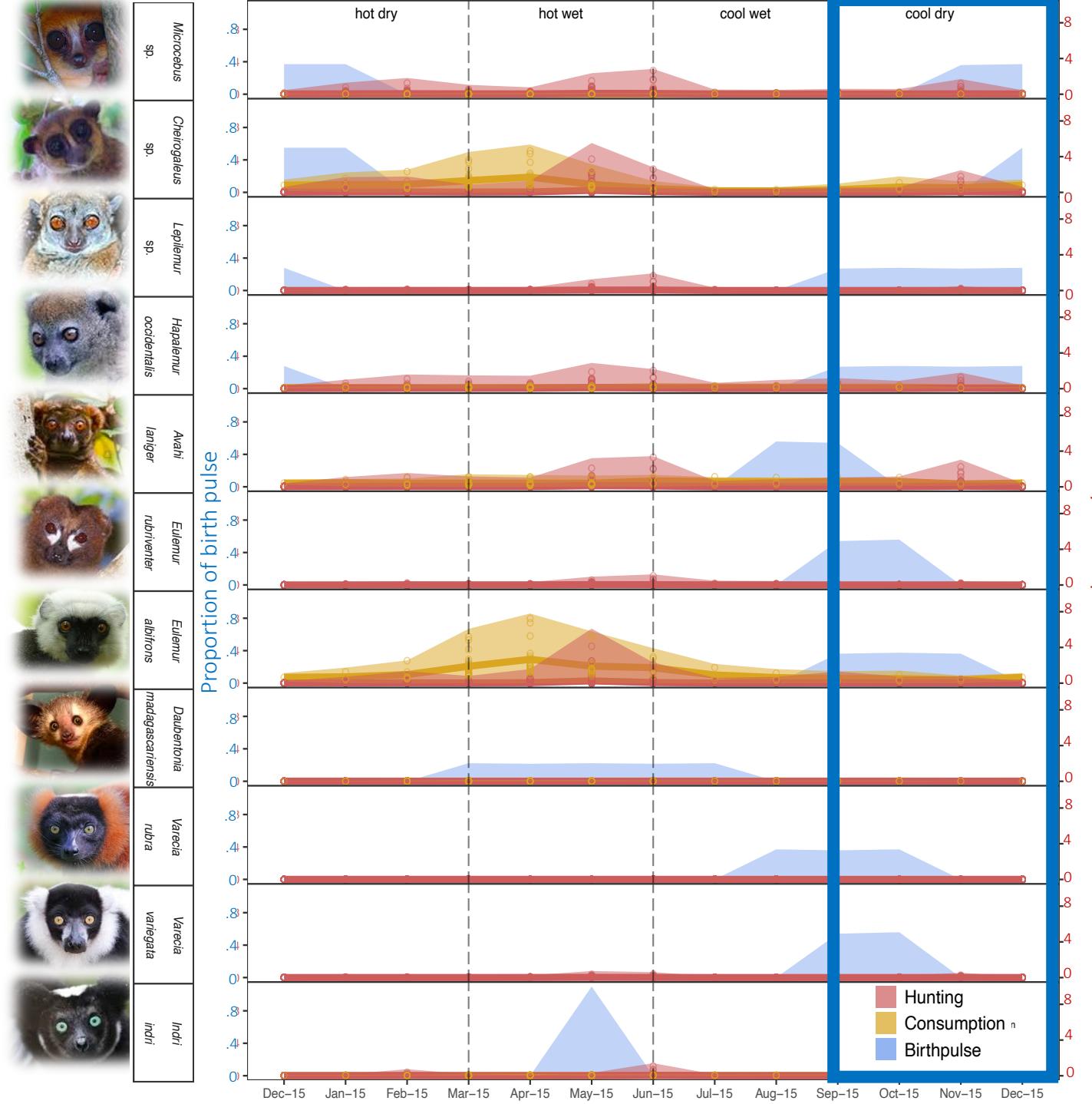


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- Local hunters from one village outfitted with **diaries to record harvested species**





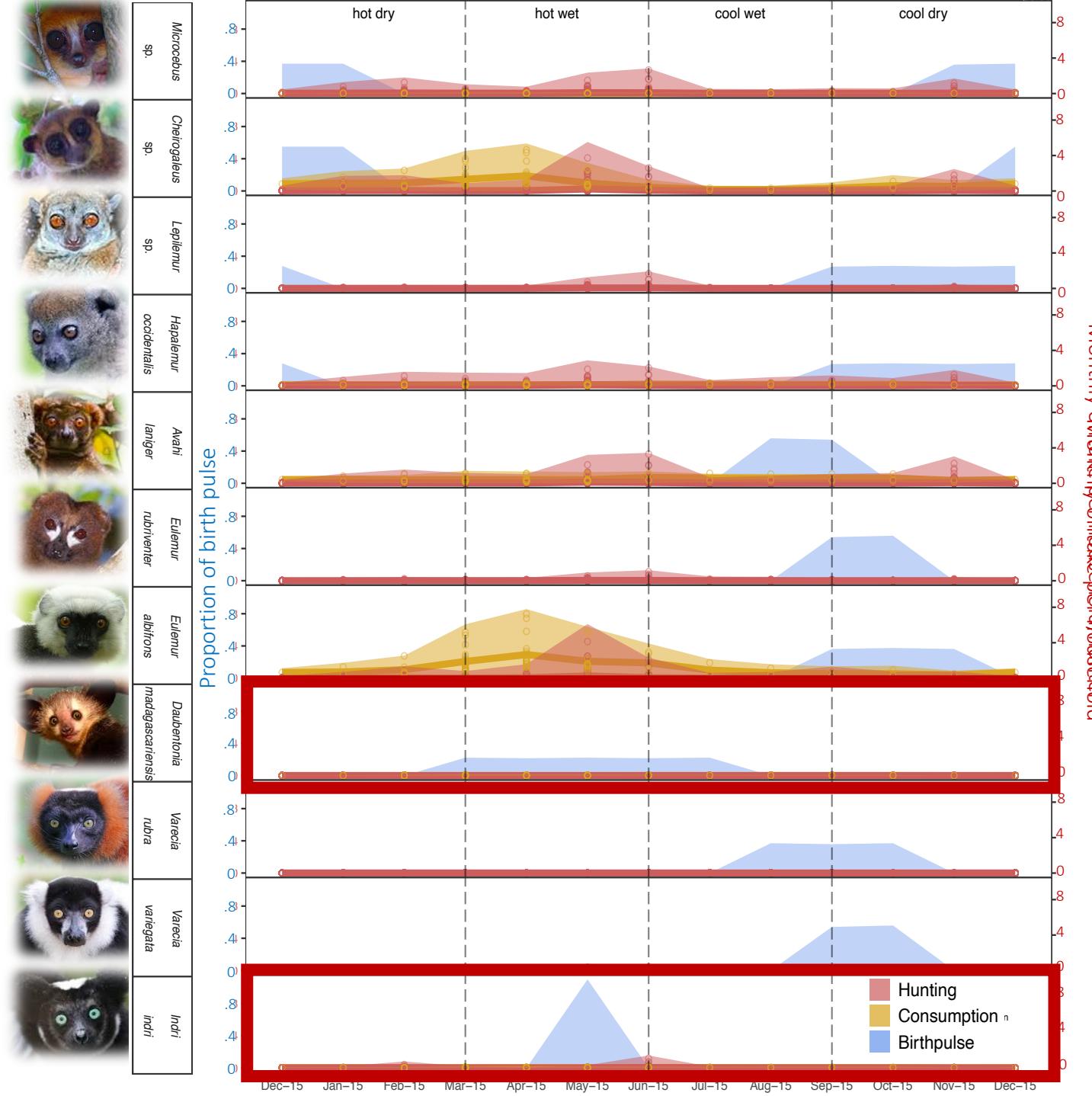
Lemurs are primarily hunted and consumed in the **hot wet season**.



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Most spp. birth in the **cool dry season**, offset from the hunt.





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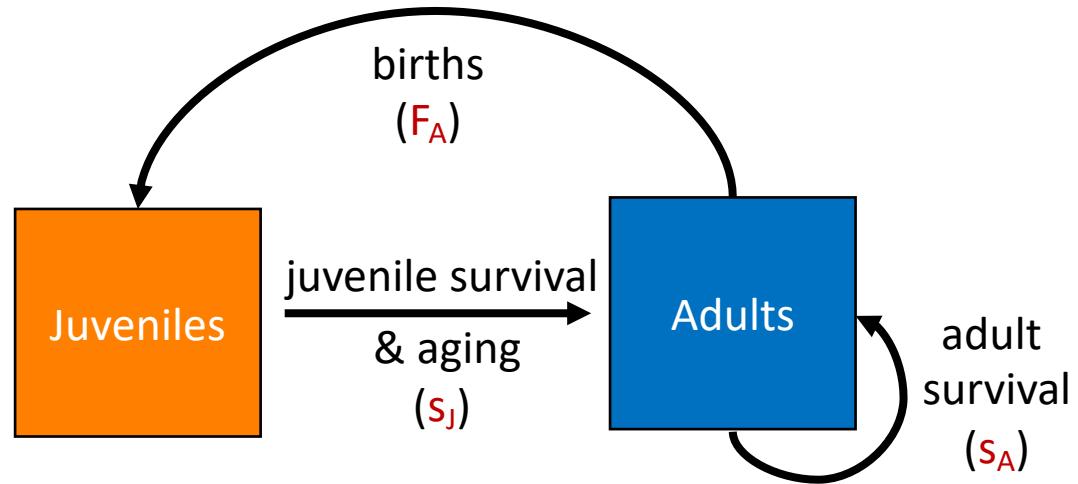
Most spp. birth in the **cool dry season**, offset from the hunt.

For **Indri & Aye-Aye**, peak hunt overlaps the **birth pulse**.



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

**N<sub>t+1</sub>**

$\begin{bmatrix} J \\ A \end{bmatrix}_{t+1}$

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

$$\begin{bmatrix} A \\ S_A F_A \\ S_A \end{bmatrix} \begin{bmatrix} J \\ A \end{bmatrix}_t$$

(where:

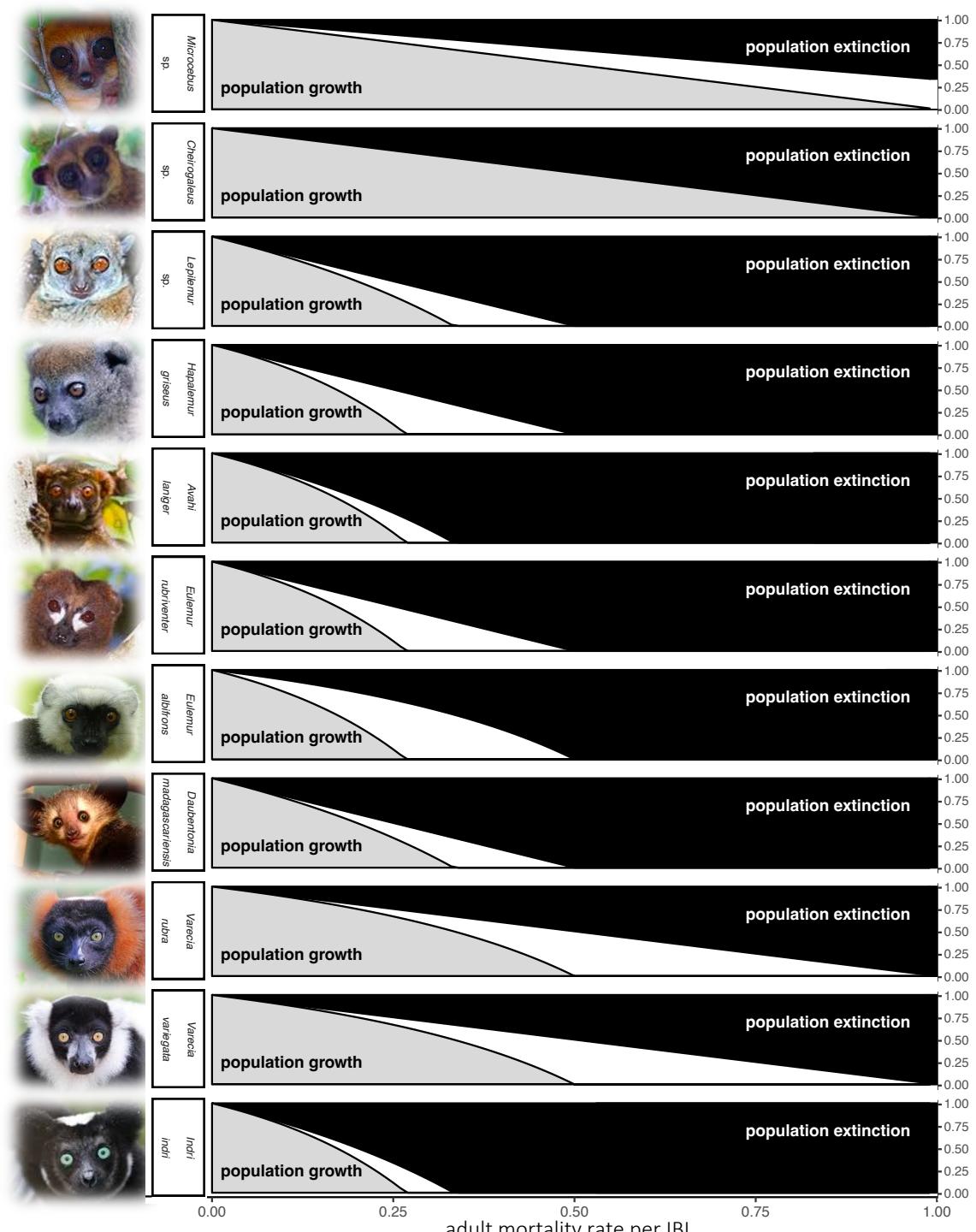
$S_J$  = juvenile IBI survival

$S_A$  = adult IBI survival

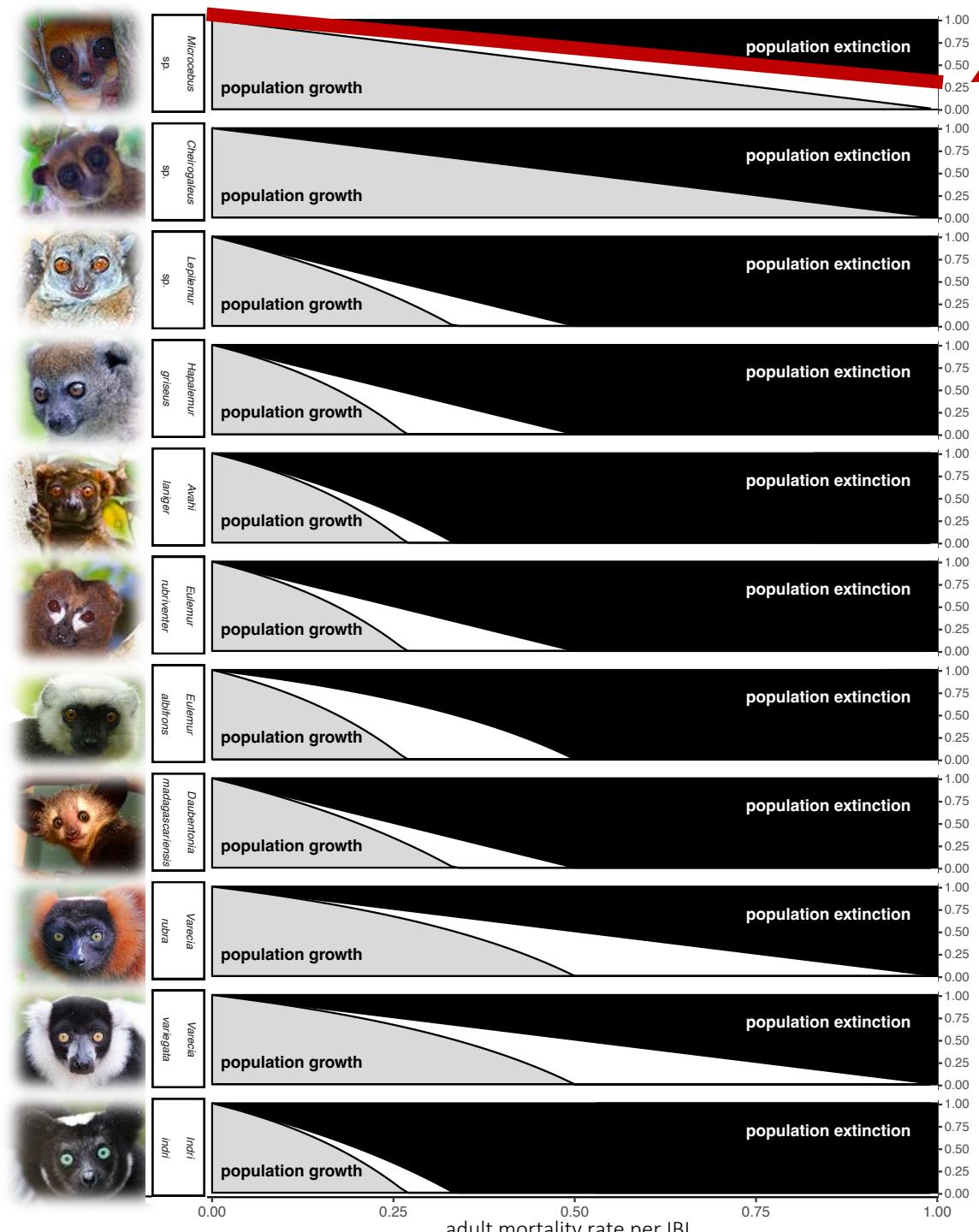
$F_A$  = adult IBI fecundity)

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

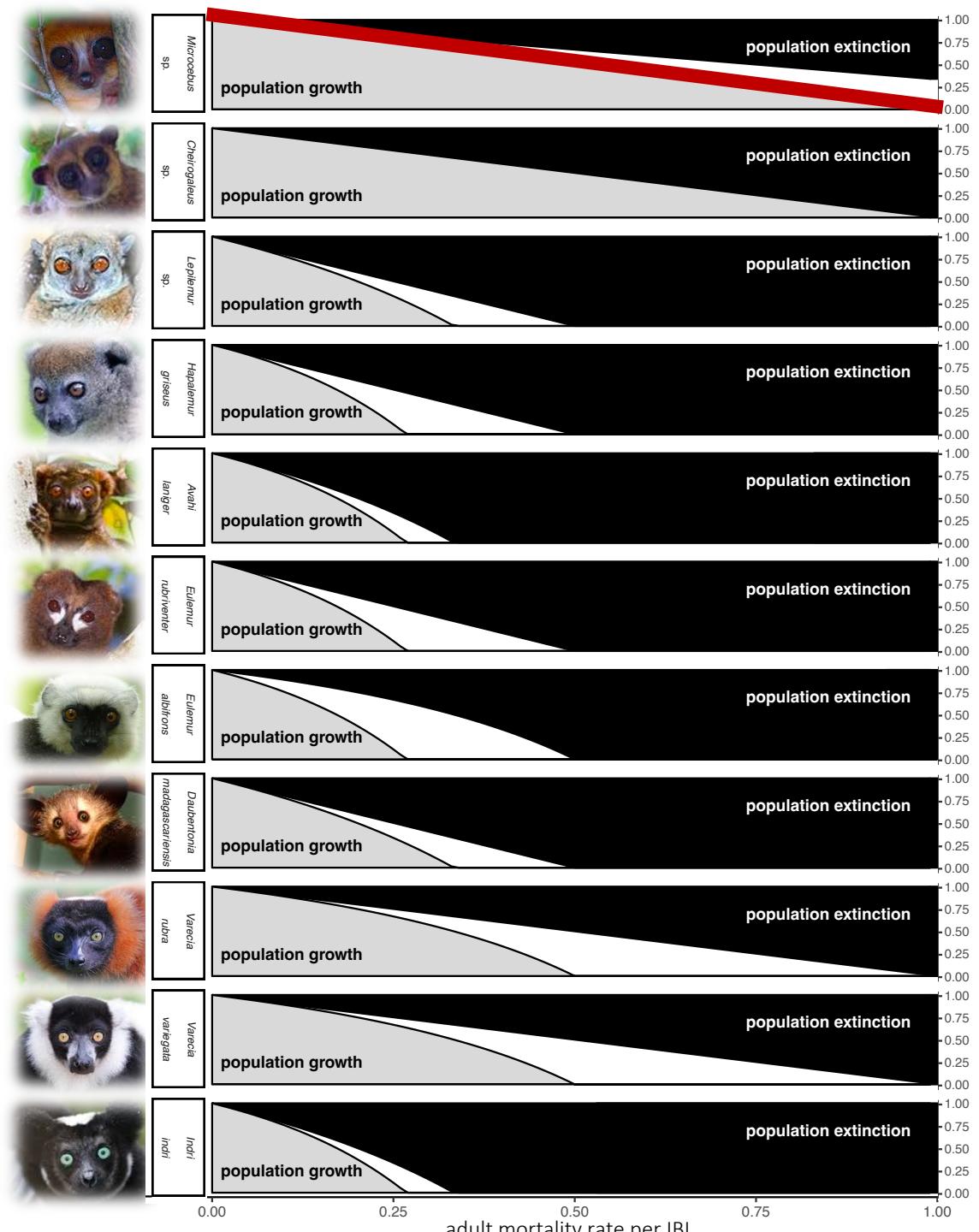
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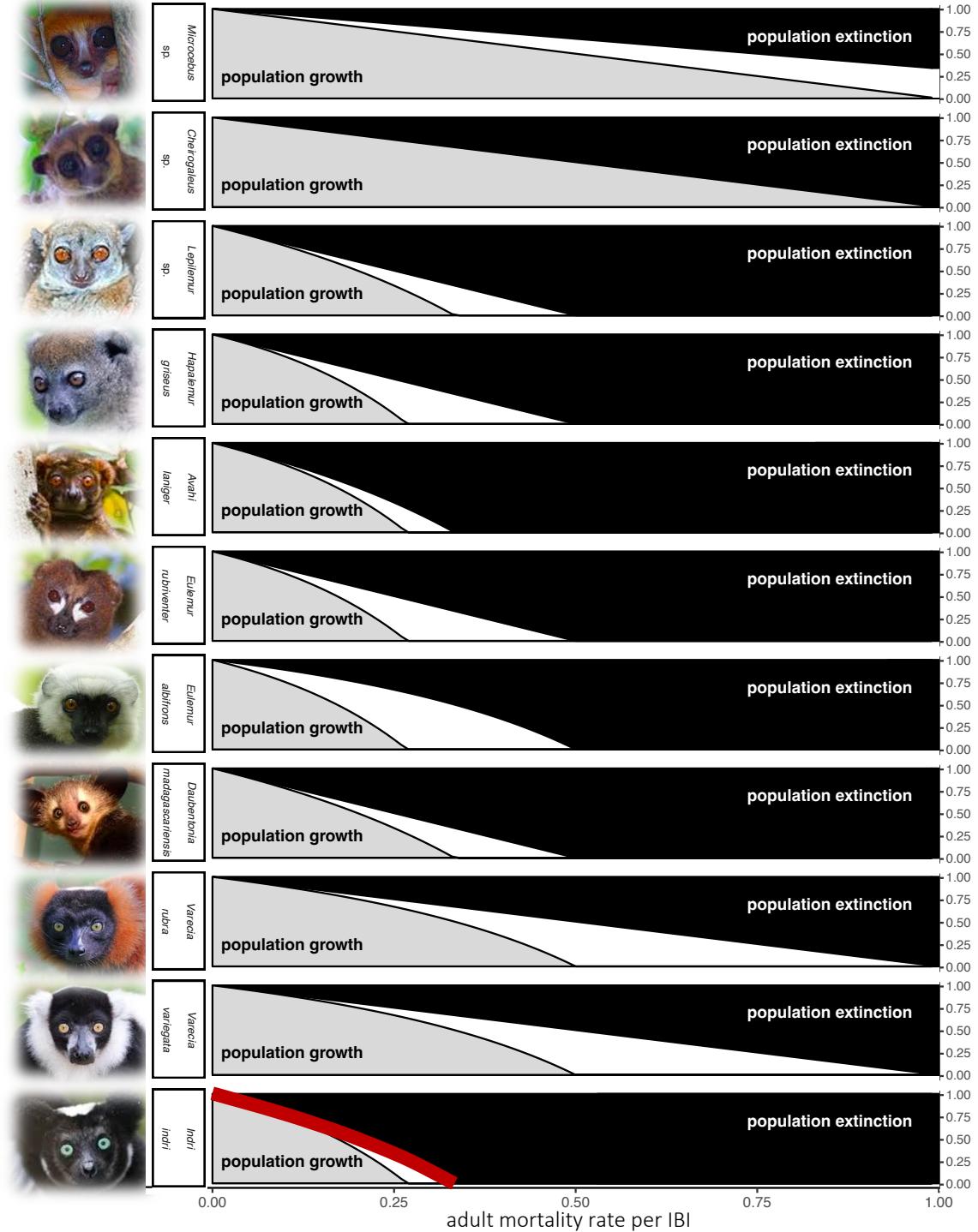


We plotted  
**zero-growth isoclines**  
to evaluate lemur  
population trajectories  
across different  
**mortality rates.**

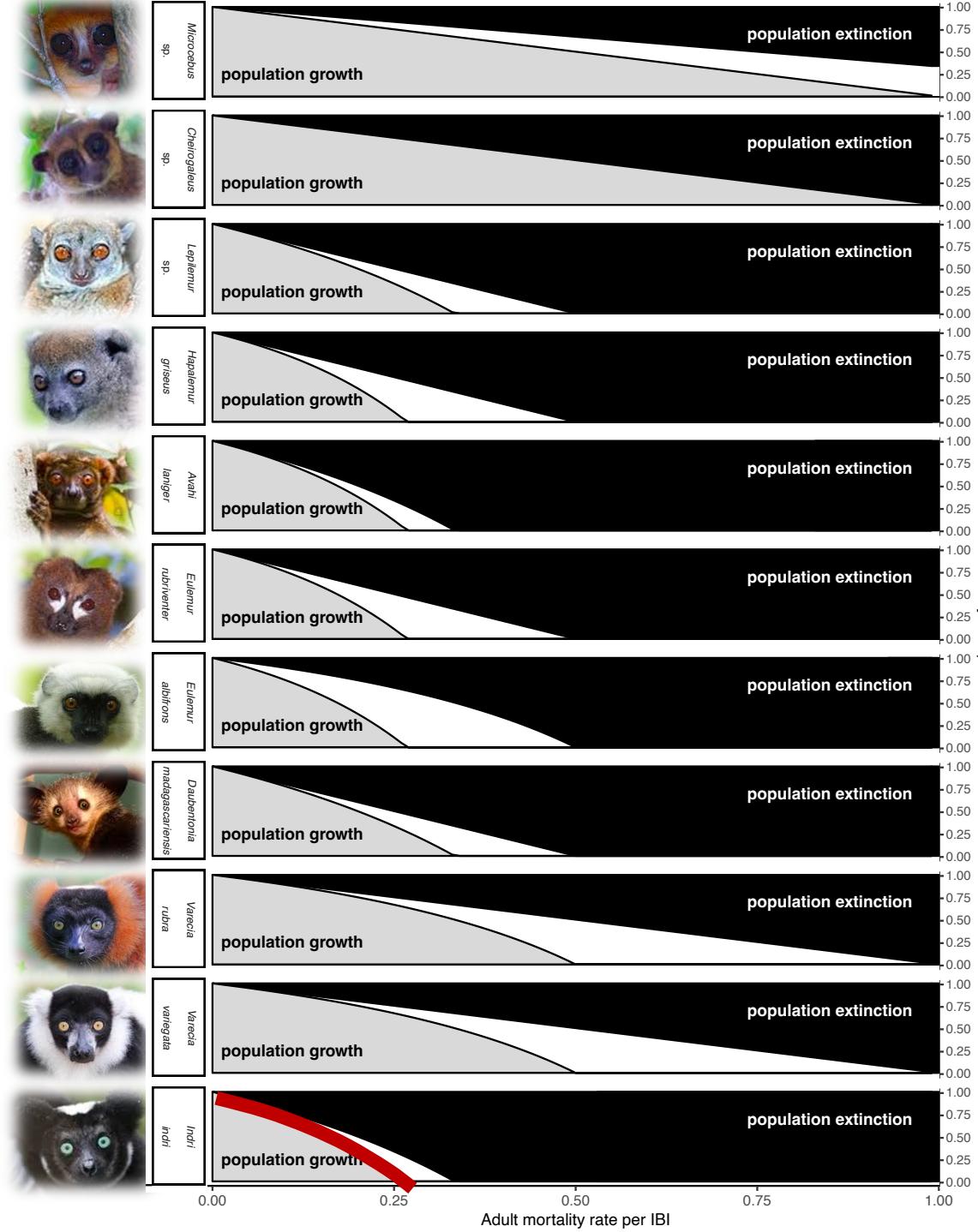


3 offspring / IBI



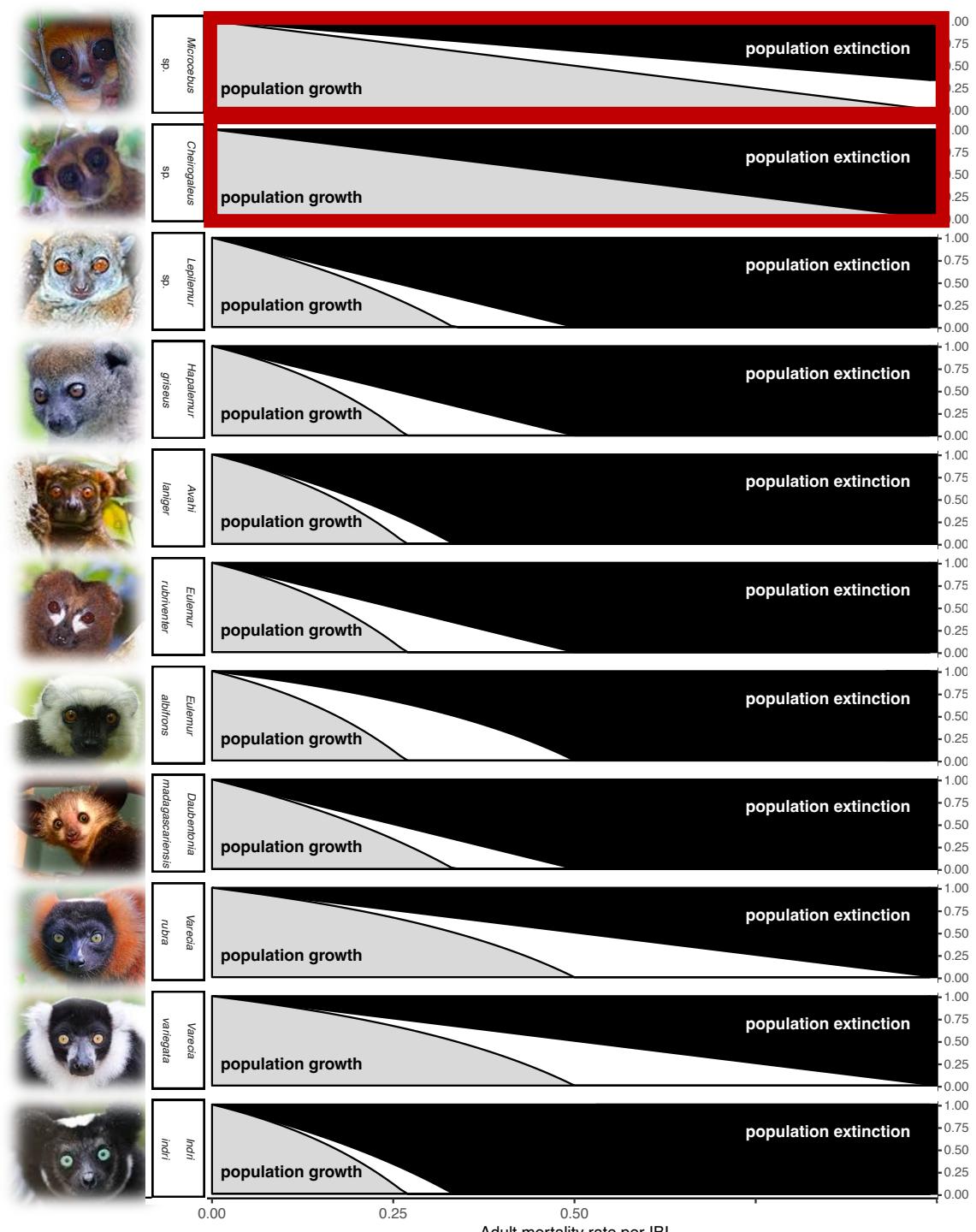


← Age @ 1<sup>st</sup> rep = 6



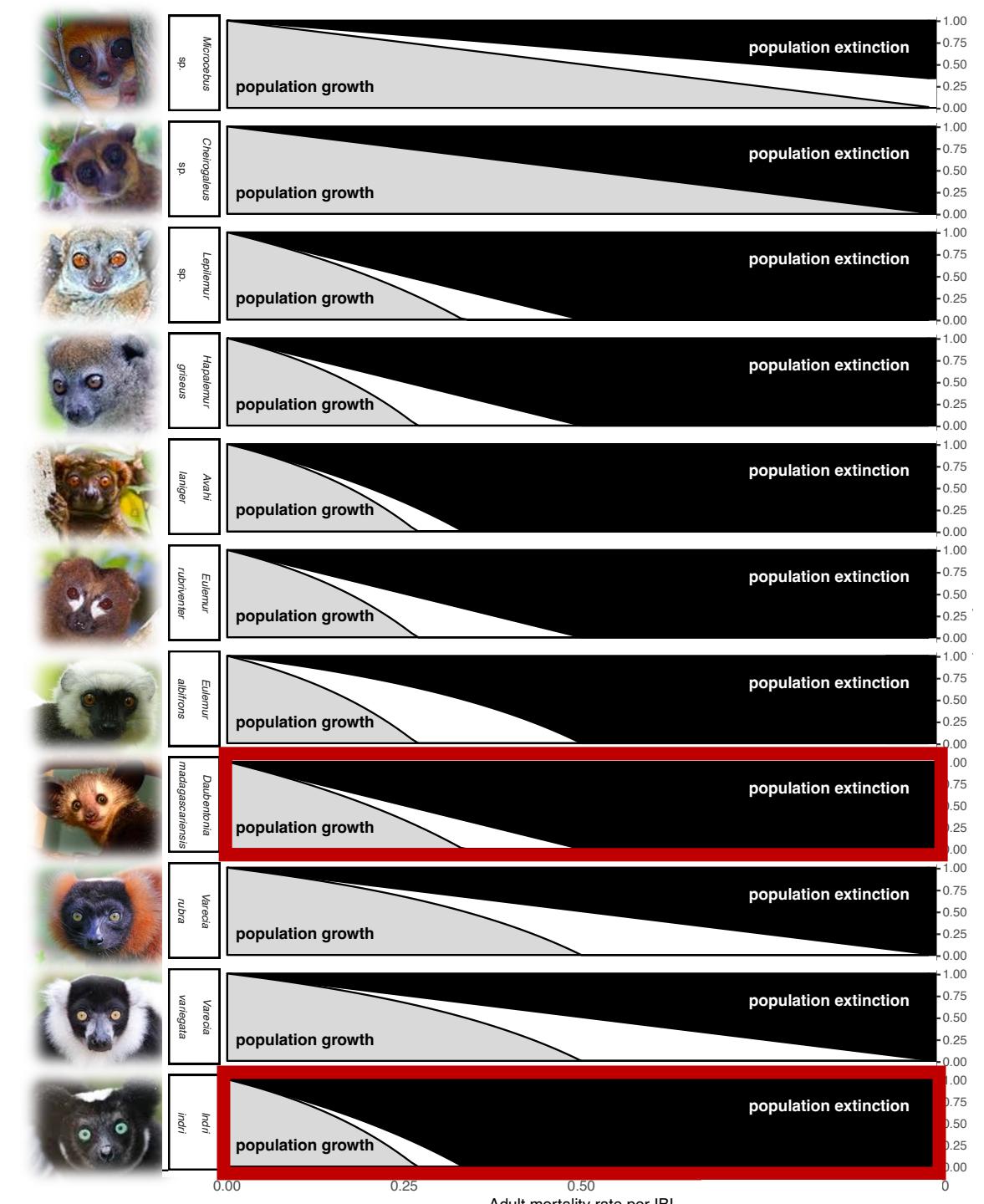
← Age @ 1<sup>st</sup> rep = 9

Brook et al. 2018. *Conservation Biology*.



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

Lemurs with **faster life histories** are resilient to **mortality**.

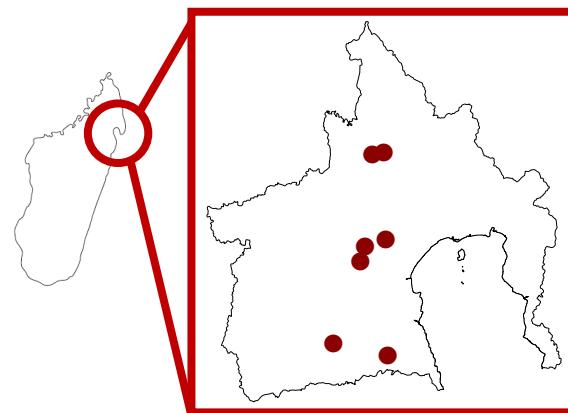


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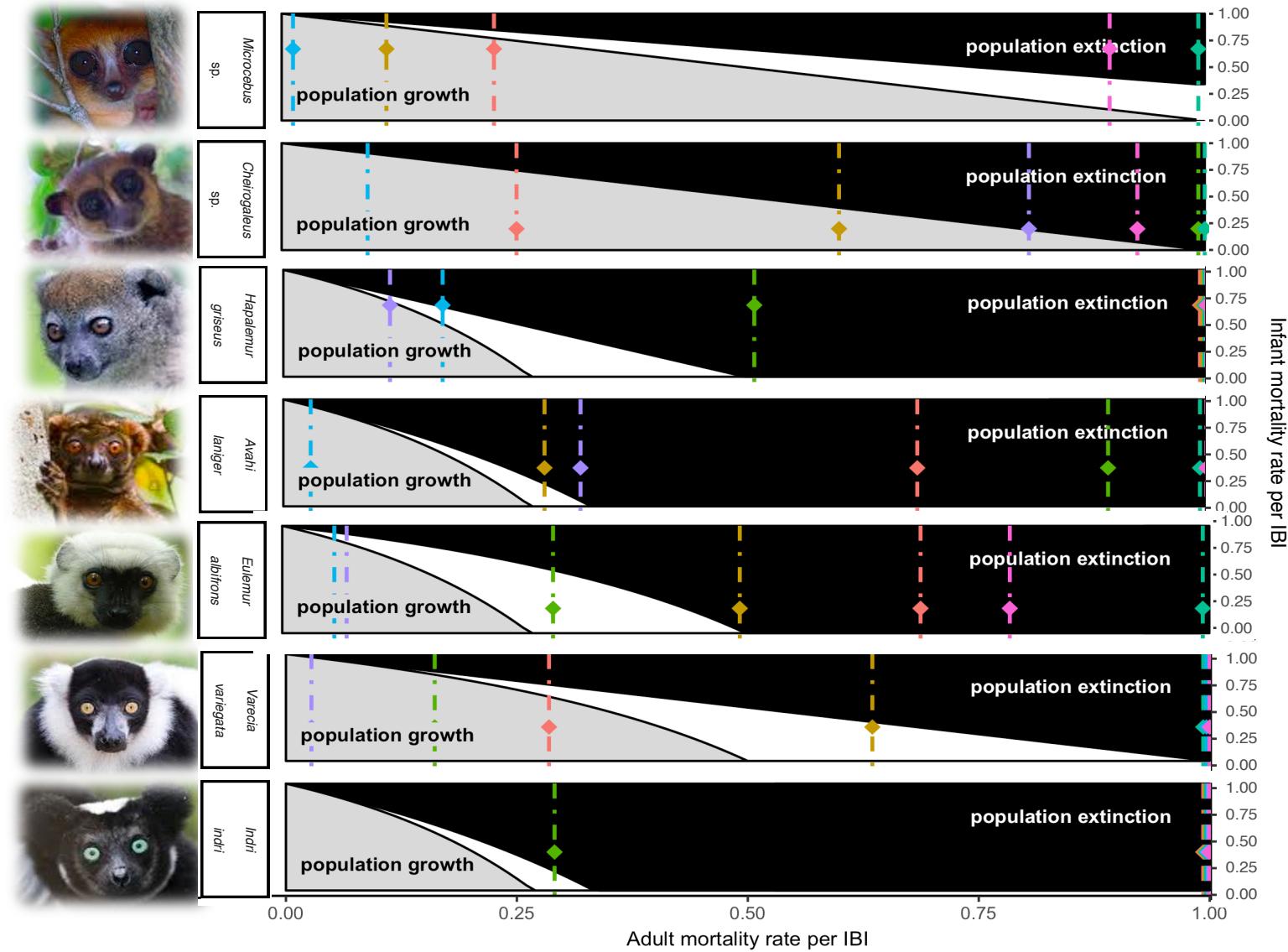
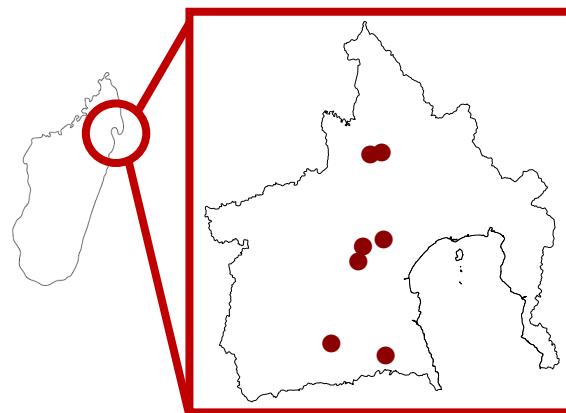
Lemurs with faster life histories are resilient to mortality.

Lemurs with **slower life histories** are particularly **vulnerable**.

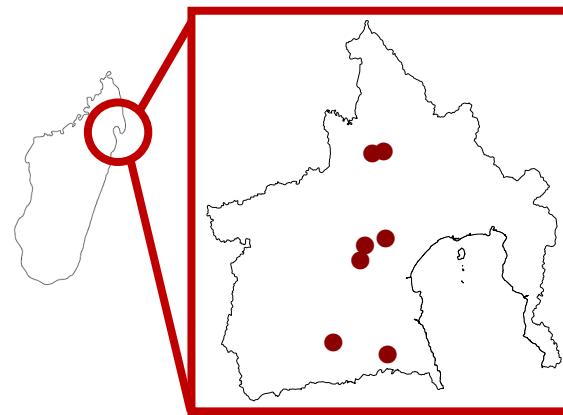
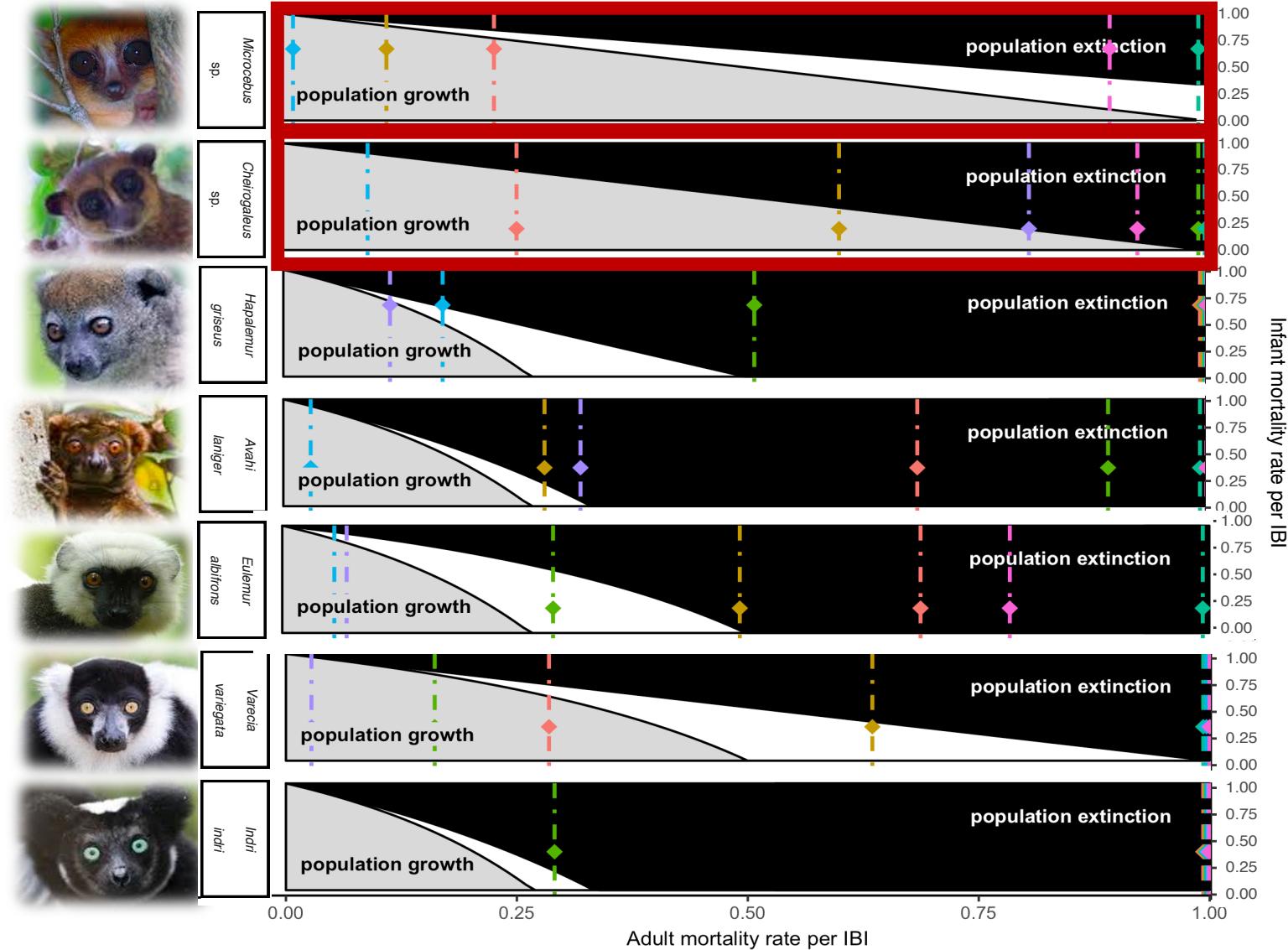
We paired household consumption data with **lemur densities** for 7 species at 7 sites to estimate hunt-based **mortality rates** and assess **harvest sustainability**.



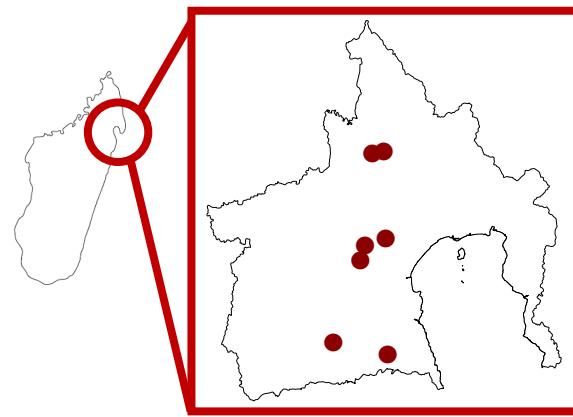
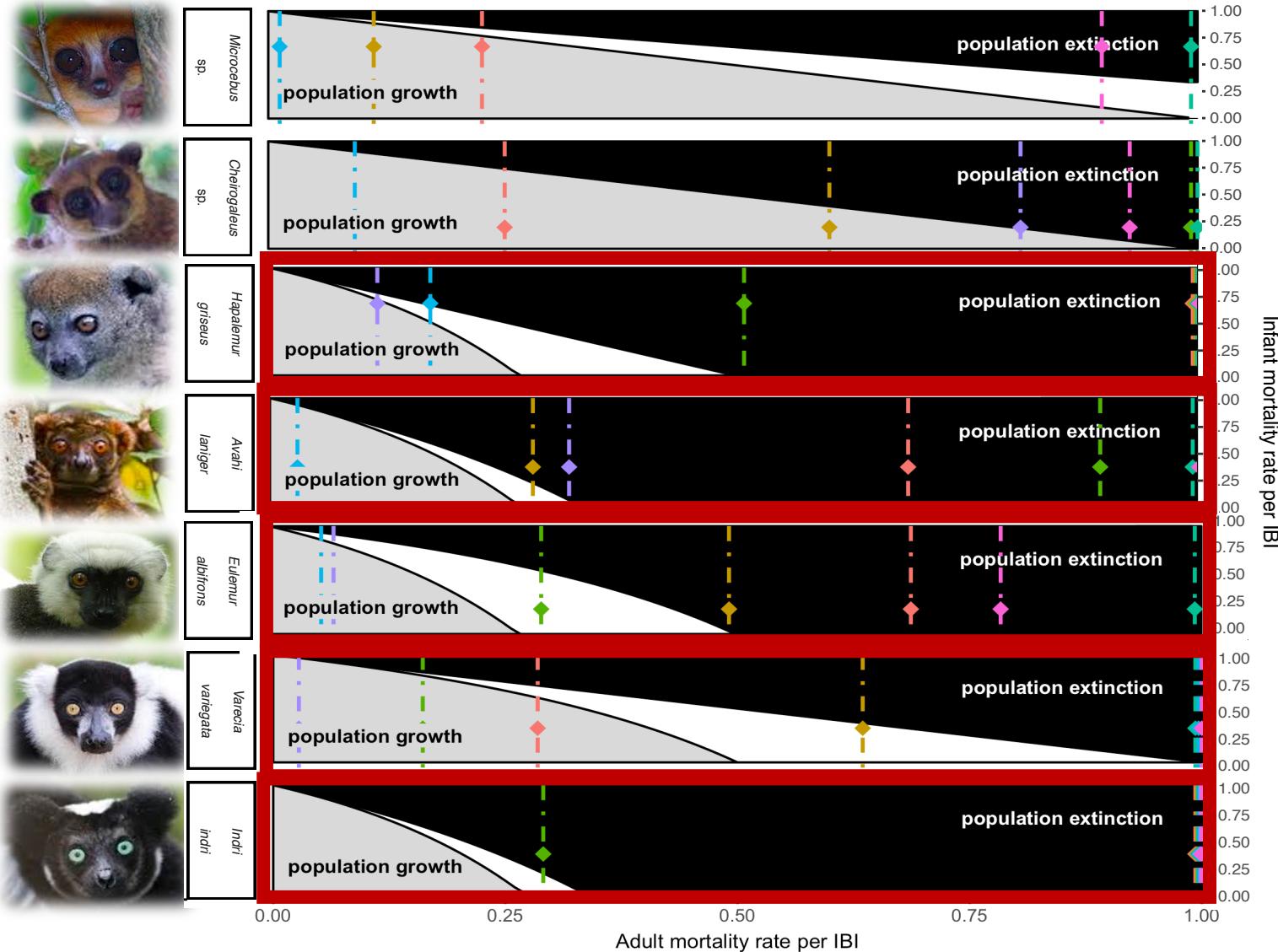
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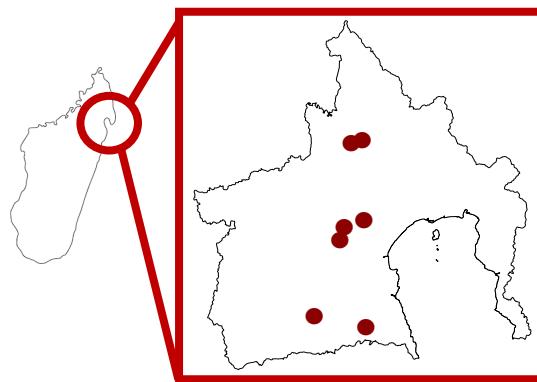
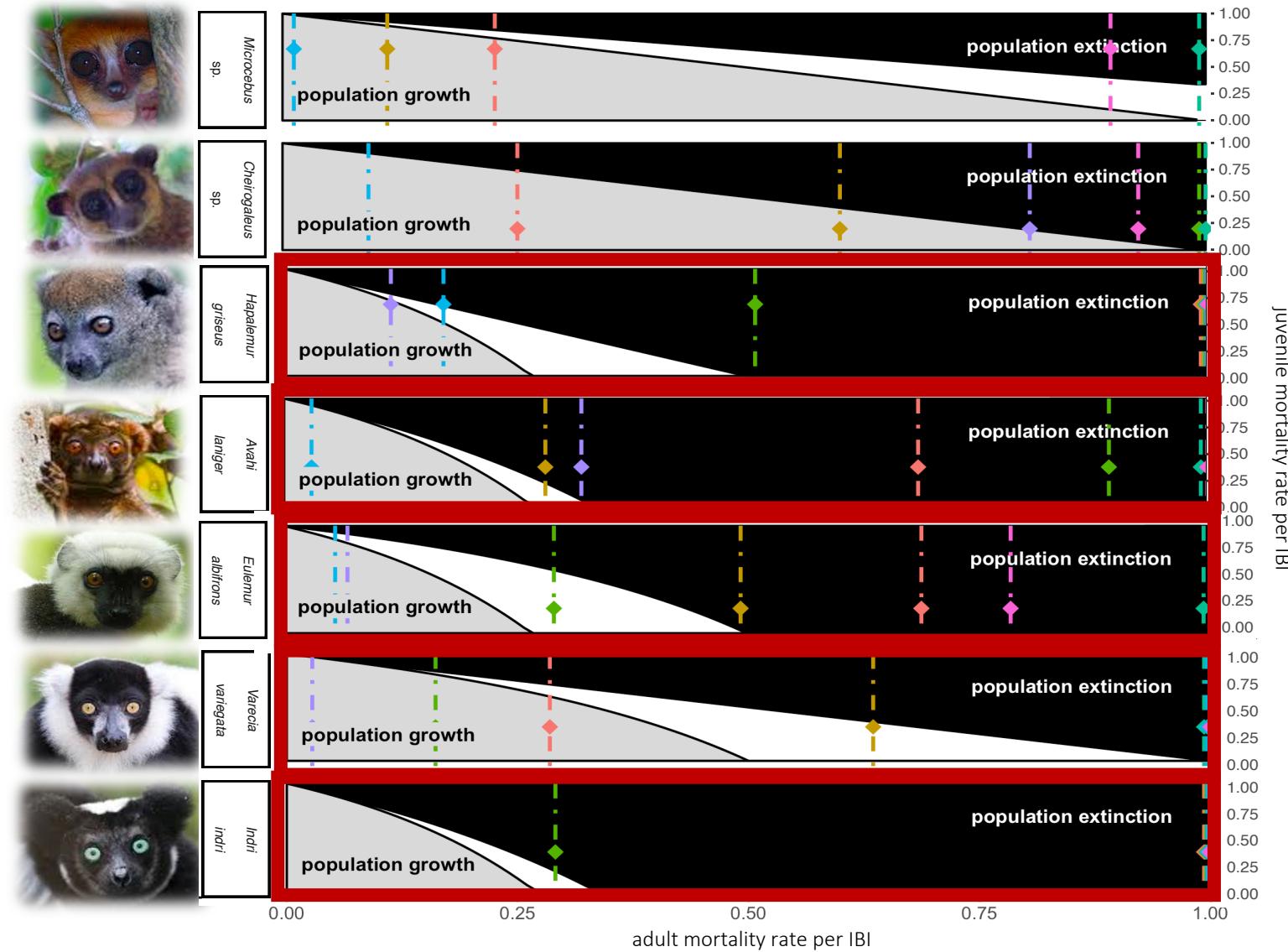
# Small-bodied lemurs are largely harvested at sustainable rates on the Makira-Masoala peninsula.



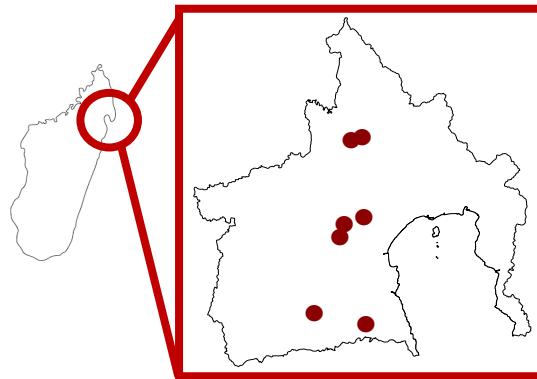
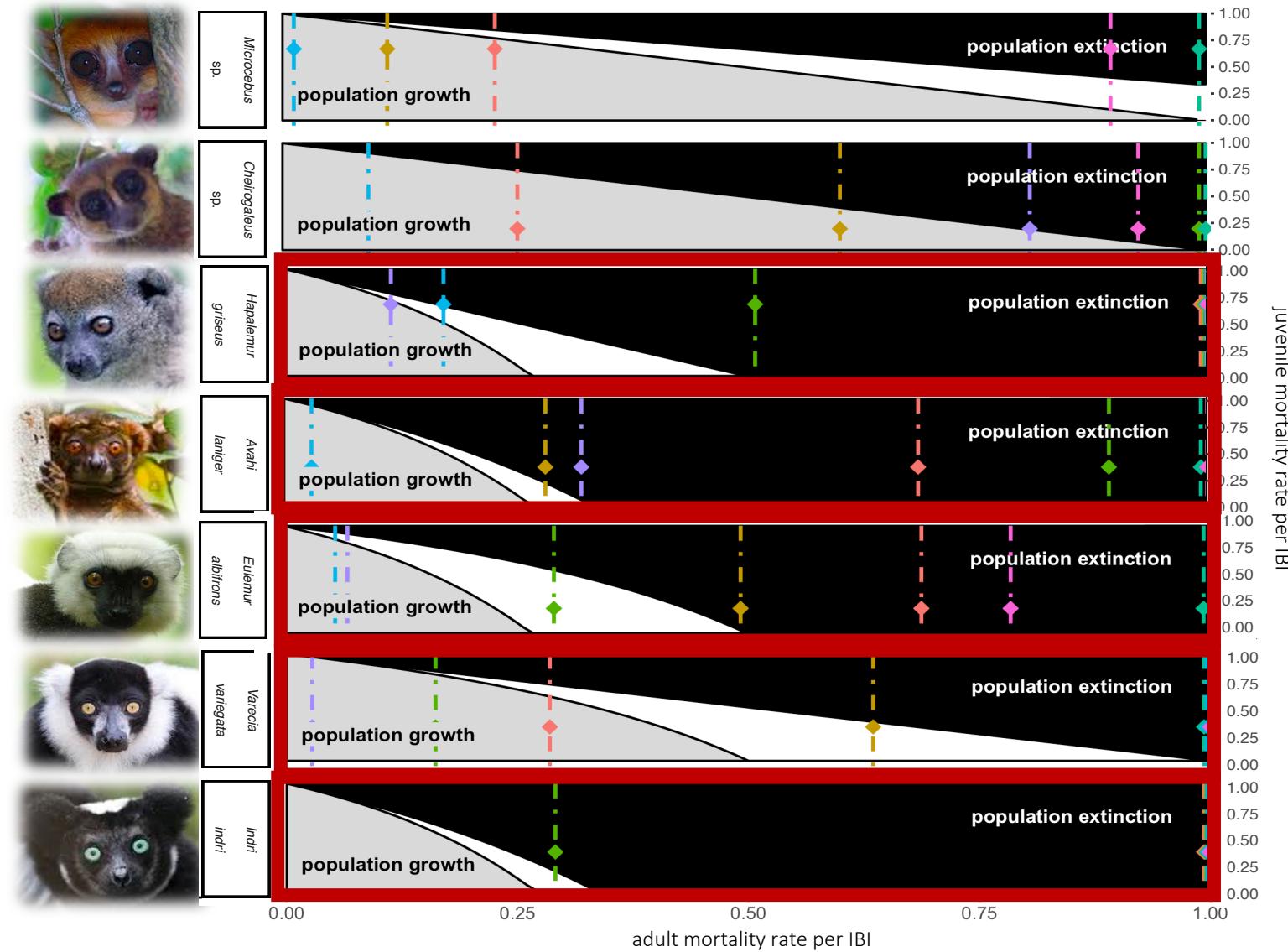
By contrast, larger-bodied lemurs are severely **threatened**.



# Natural **background mortality** and **Allee effects** may exacerbate threats to extirpation.



# Natural **background mortality** and **Allee effects** may exacerbate threats to extirpation.



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

We will revisit this!

Finally, we built a regional **metapopulation model** to simulate population dynamics into the future.



*Microcebus*  
sp.



*Cheirogaleus*  
sp.



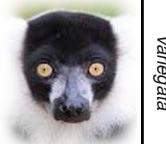
*Hapalemur*  
*occidentalis*



*Avahi*  
*laniger*



*Eulemur*  
*albifrons*



*Varécia*  
*variegata*

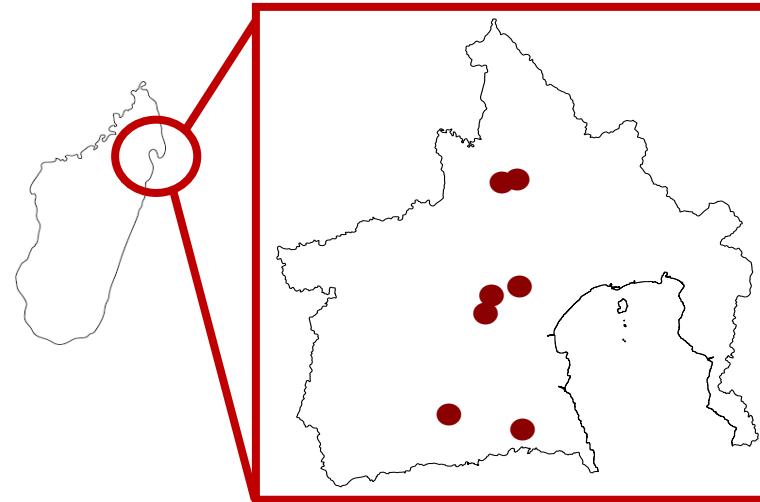


*Indri*  
*indri*

Finally, we built a regional **metapopulation model** to simulate population dynamics into the future.

### Assumptions:

- Starting population of 200 lemurs per site



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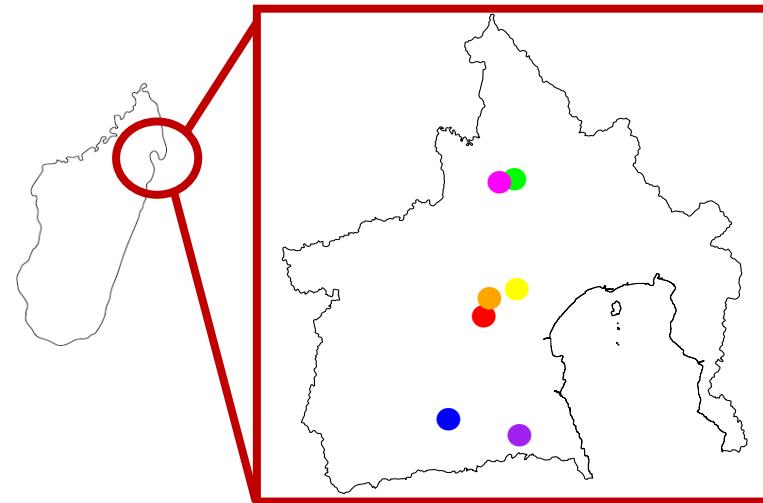


*Indri*  
*indri*

Finally, we built a regional **metapopulation model** to simulate population dynamics into the future.

### Assumptions:

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

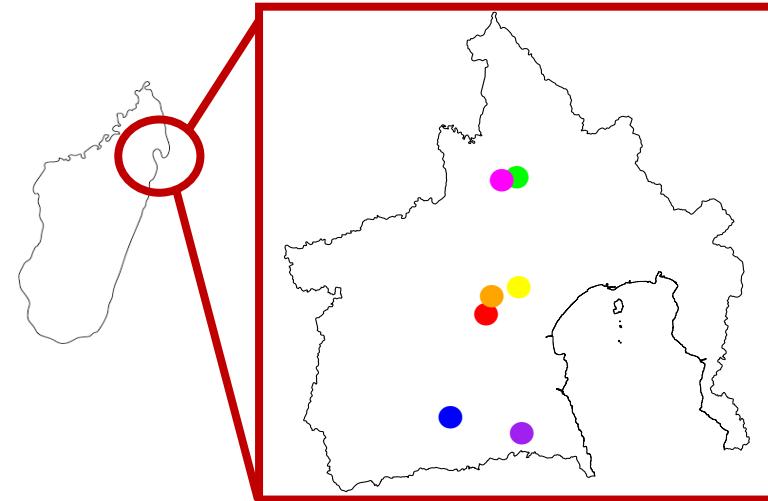


Finally, we built a regional **metapopulation model** to simulate population dynamics into the future.



### Assumptions:

- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies
- Density dependent effects on fecundity

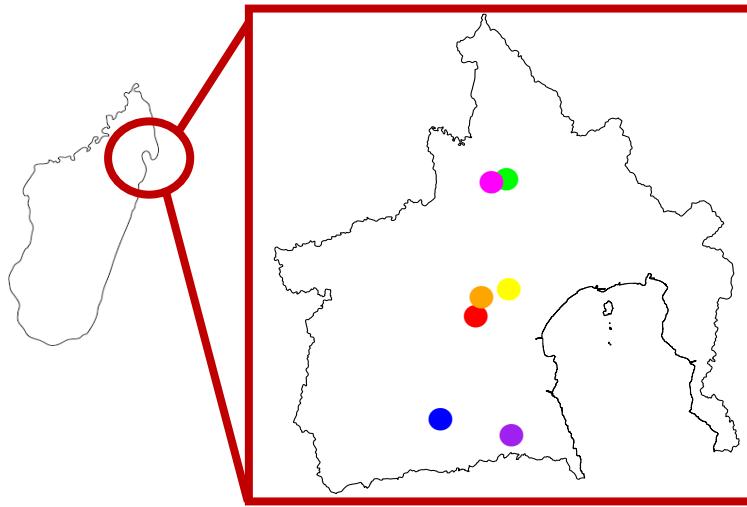


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### Assumptions:

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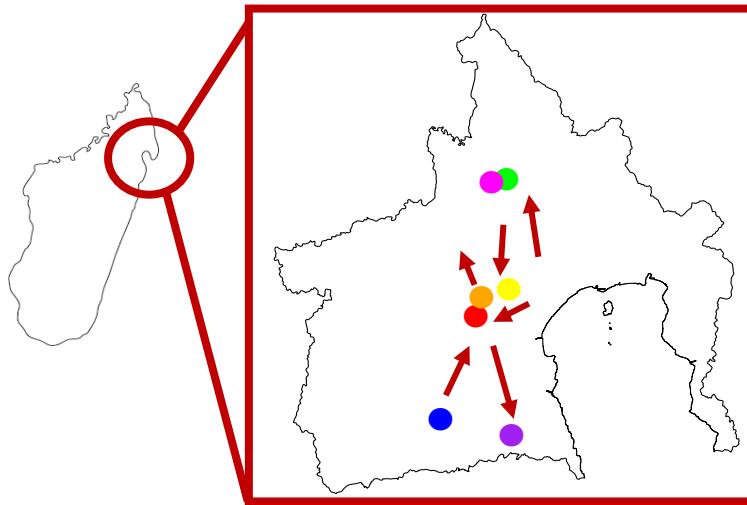


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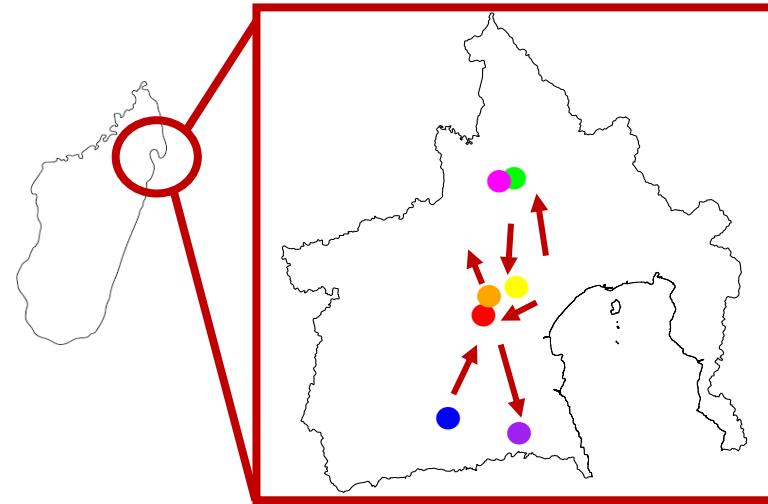
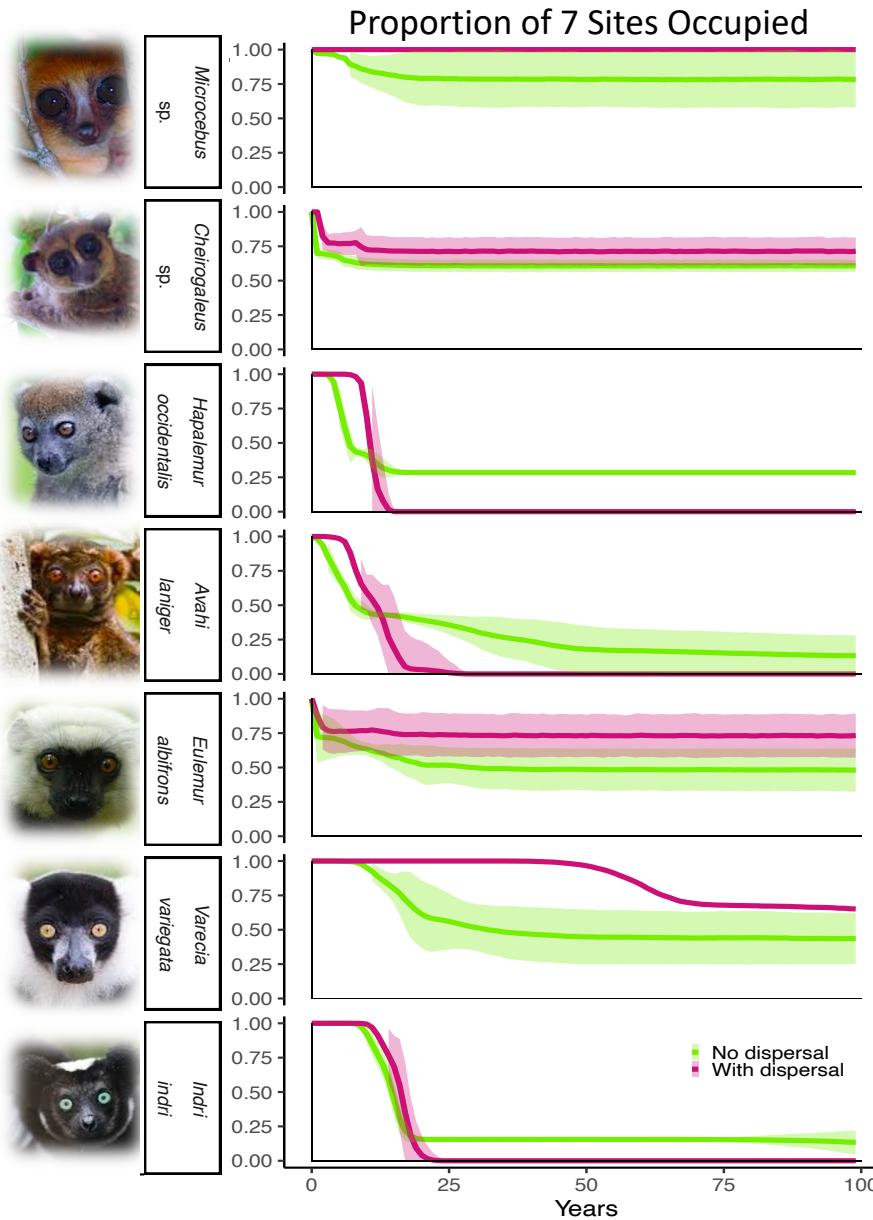


### Assumptions:

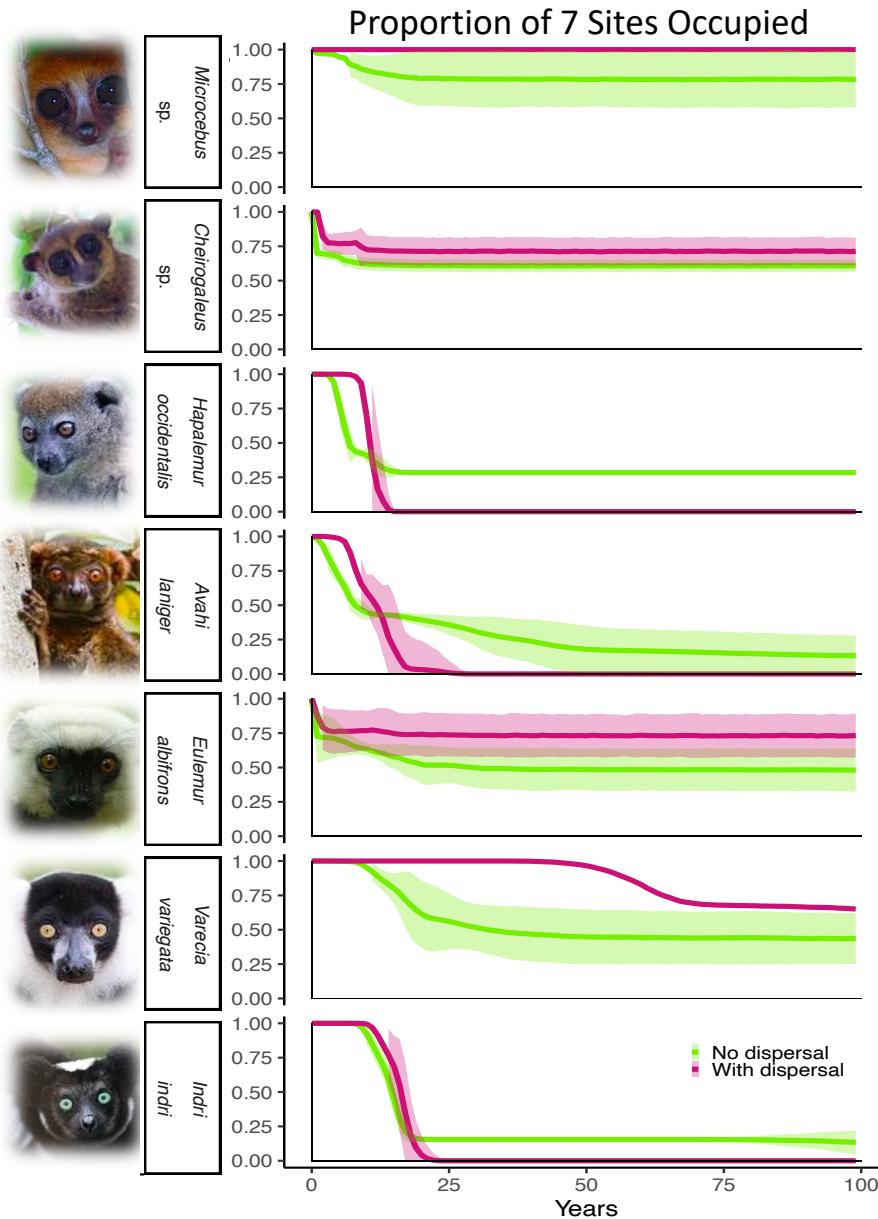
- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies
- Density dependent effects on fecundity
- Compared **no dispersal scenarios** vs. scenarios allowing for **stochastic dispersal** mediated by geographic distance



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

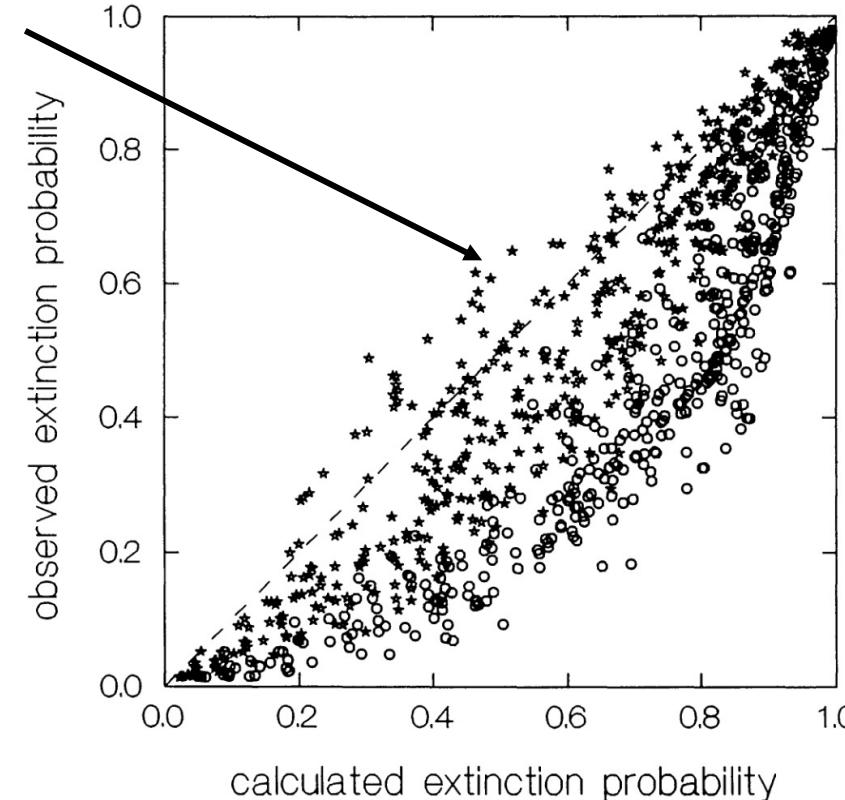


# Dispersal can drive regional extirpation if the majority of local sites function as population sinks.



star points  
recalculated  
with **rescue  
effect** from  
Levin's  
model

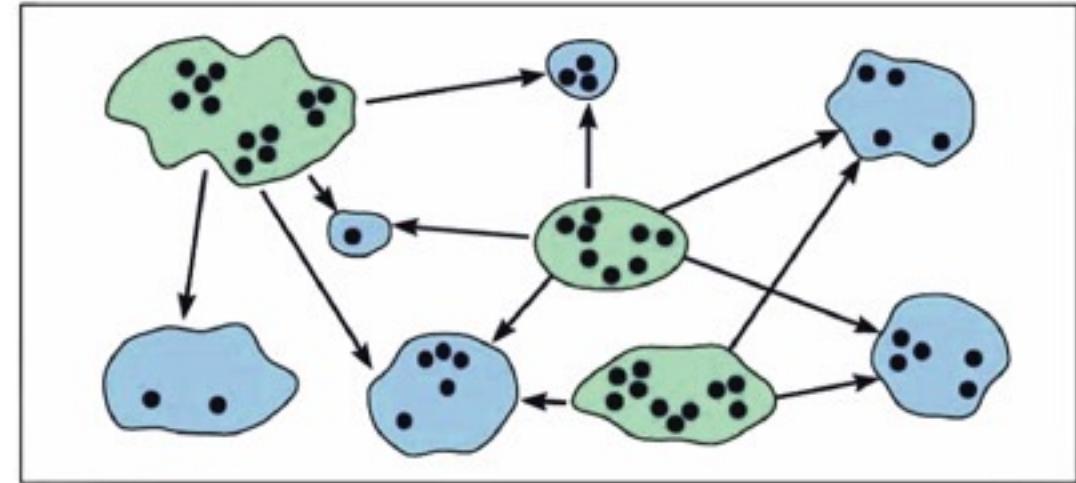
In contrast to the **rescue effect**  
observed in Hanski!



Hanski et al. 1996. *The American Naturalist*.  
Brook et al. 2018. *Conservation Biology*.

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

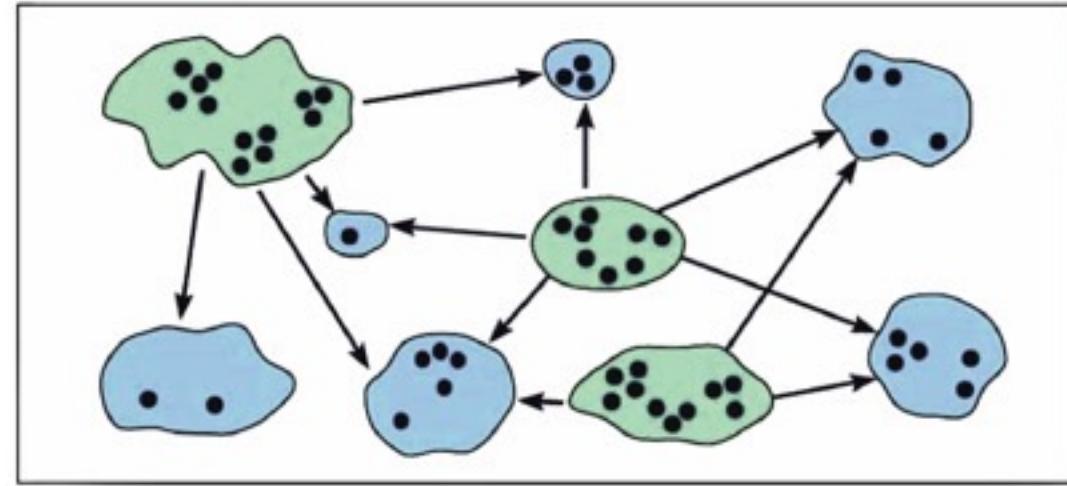
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.



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

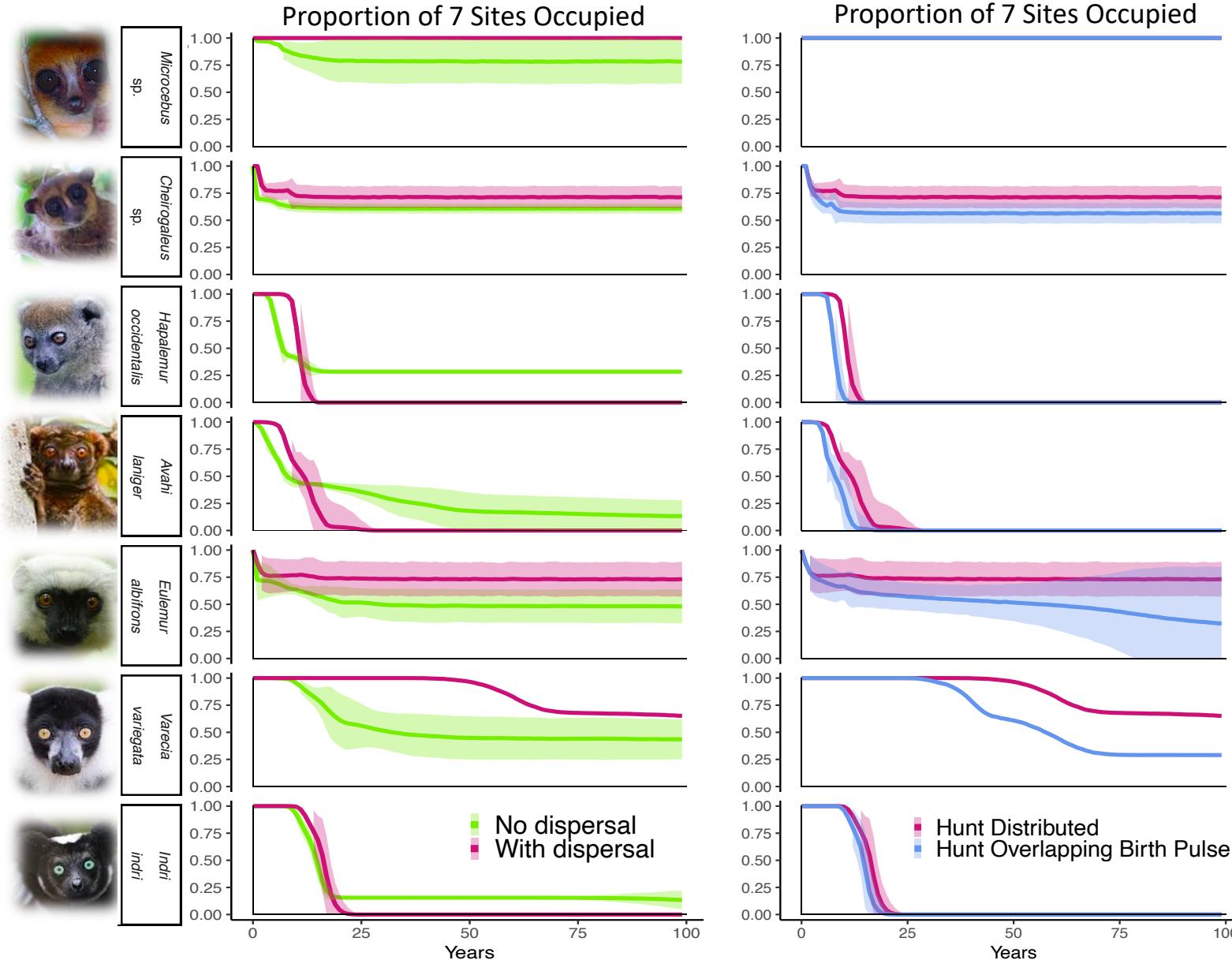
# Source-sink theory describes how variation in habitat may affect population dynamics.

- 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

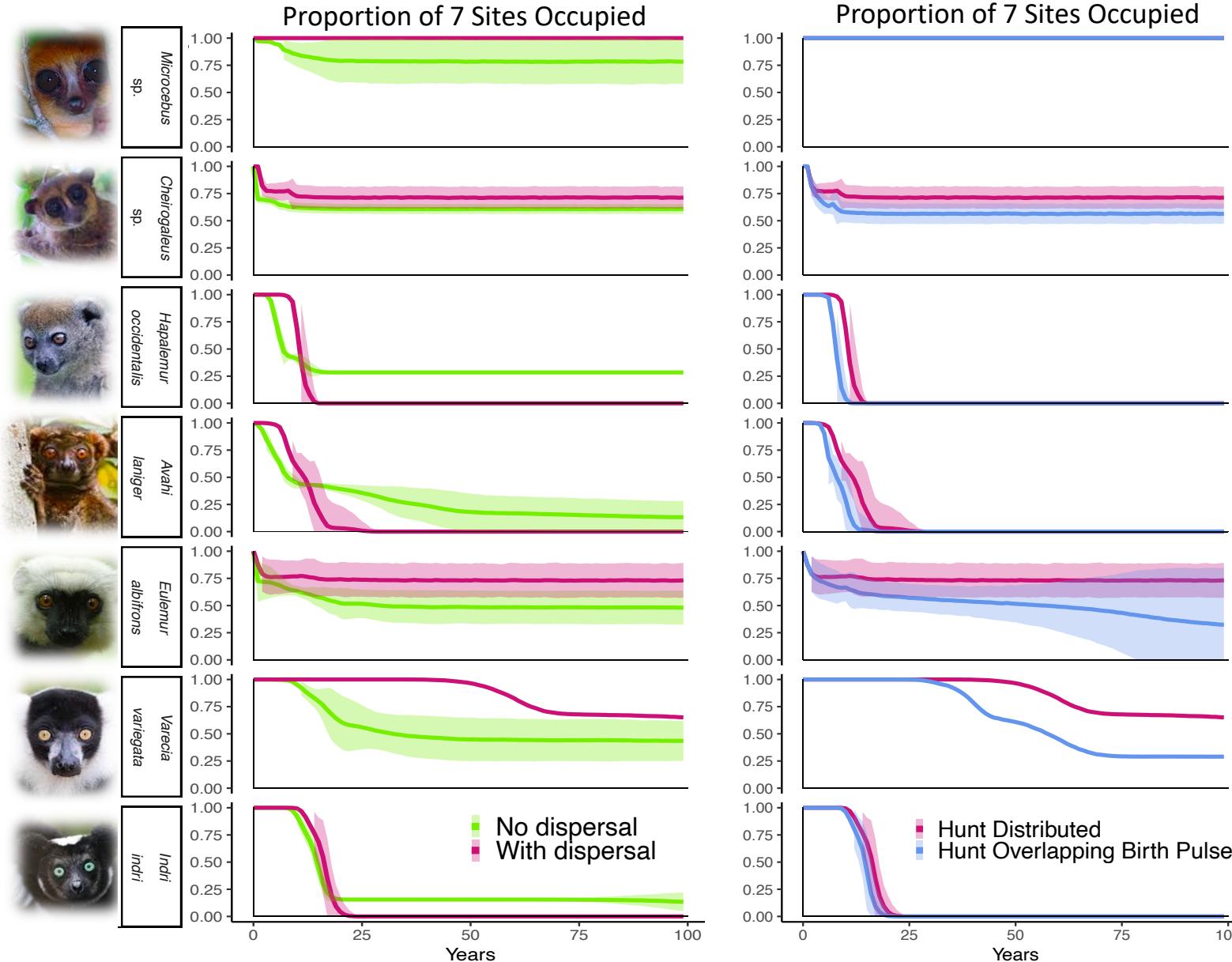


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# Species are even **further threatened** when hunt seasonality overlaps the **annual birth pulse**.



# 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