

# Fundamentals of Ecology

Week 7, Ecology Lecture 3

Cara Brook

February 13, 2024

# Let's recap a bit!

## **Harvesting**

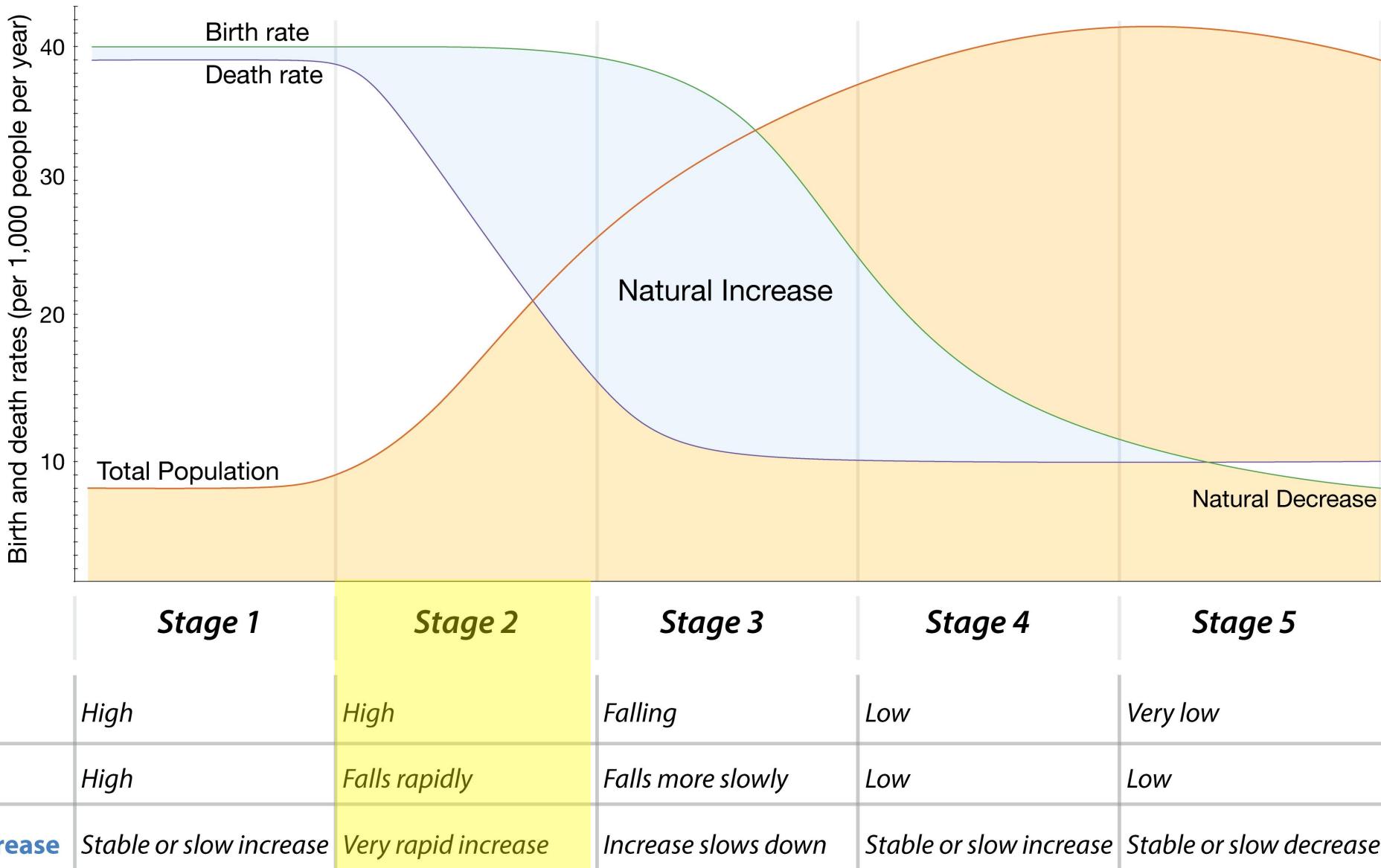
- Humans have attempted to leverage the density-dependent growth rate of the logistic growth equation to sustainable harvest populations, especially fisheries.
- The maximum sustainable yield (MSY) is the highest theoretical harvest that can be extracted sustainably, when the population is growing maximally at half carrying capacity.  $H_{MSY} = rK/4$
- There are many problems with MSY – can you name a few?
  - Single species, no pop structure, constant harvesting
  - Stochastic (as opposed to deterministic) processes and a semi-stable equilibrium
- Overfishing is one form of an ecological ‘Tragedy of the Commons’, depletion of a common-pool resource. Managers attempt to mitigate this with strategies like TAC, IFQs, and ITQs.

# Let's recap a bit!

## **Structured populations**

- Structured populations, including humans, can be modeled using matrix models (Leslie or Lefkovich)
- The dominant eigenvalue of the transition matrix,  $\lambda$ , the population rate of increase, describes whether a structured population is increasing or decreasing
- Life tables are used to store demographic data to build transition matrices
- In humans, there are 5 stages to a demographic transition, starting with high birth/death rates, then transitioning to low birth/death rates
- Populations grow fastest in stage 2 where death rates fall while birth rates remain high

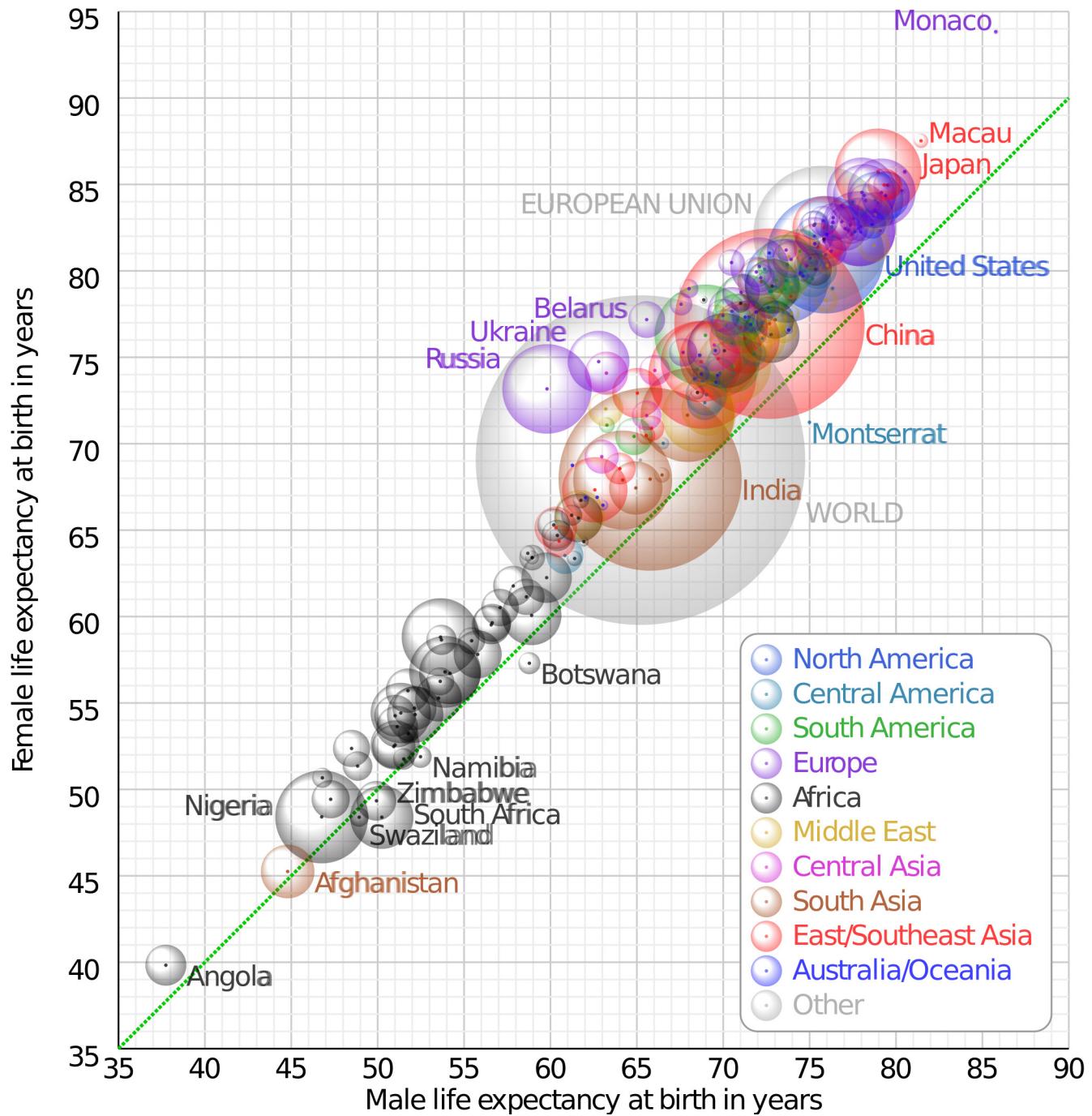
# Demographic transition



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>

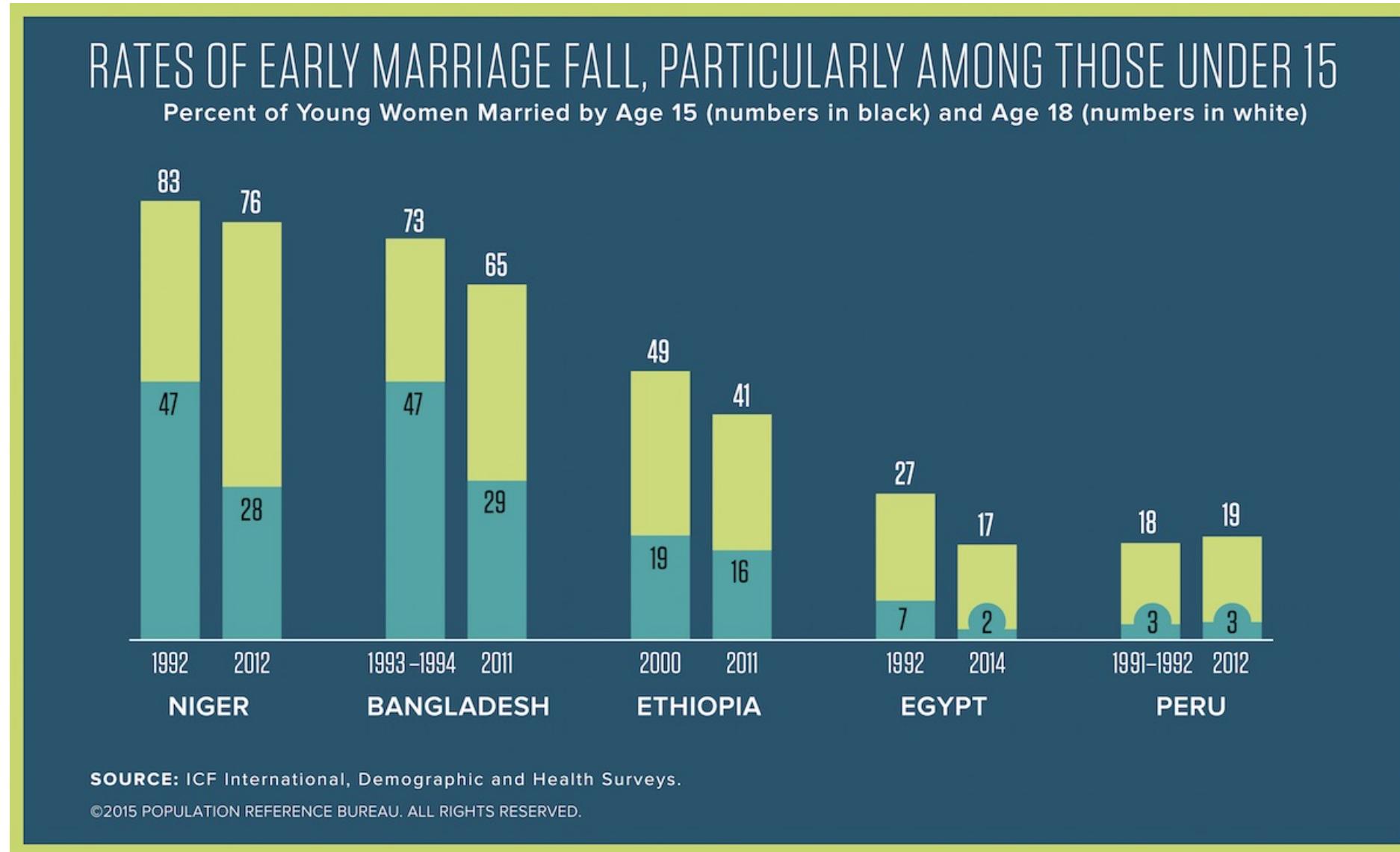
# Demographic transition

Death rates are falling globally...

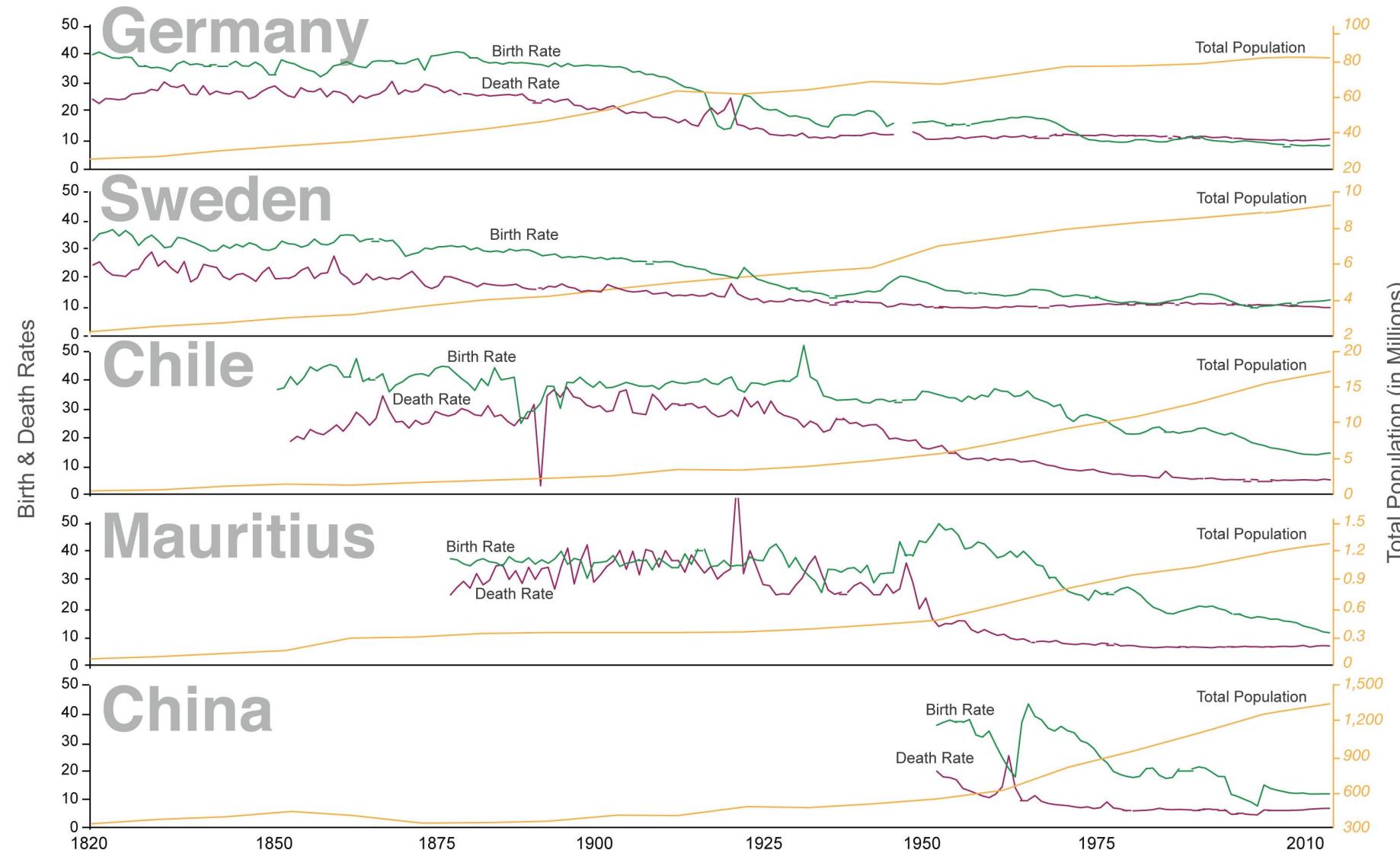


# Demographic transition

And birth rates  
are also falling...



# Demographic transition



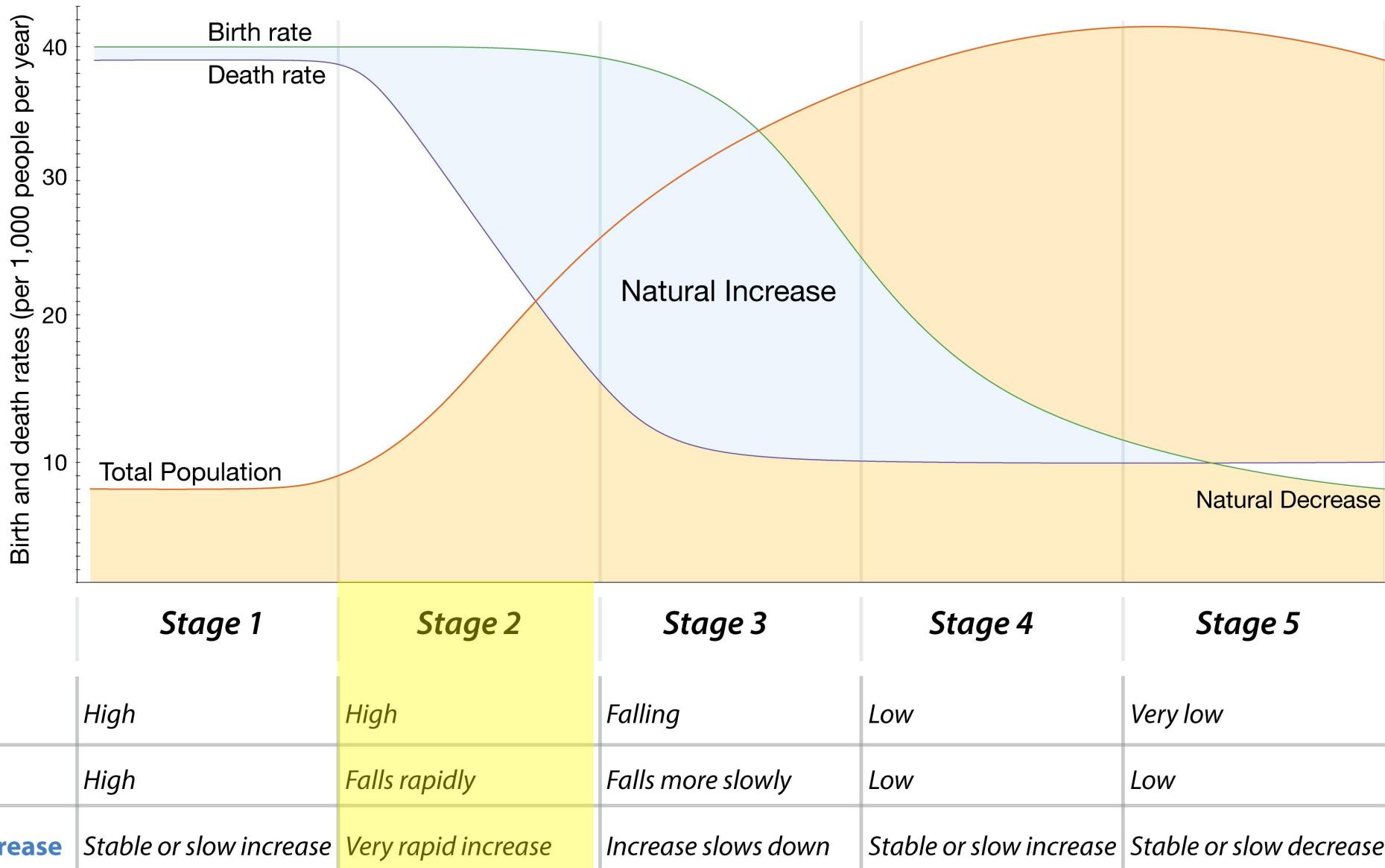
Data source: The data on birth rates, death rates and the total population are taken from the International Historical Statistics, edited by Palgrave Macmillan (April 2013).

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

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

# Demographic transition

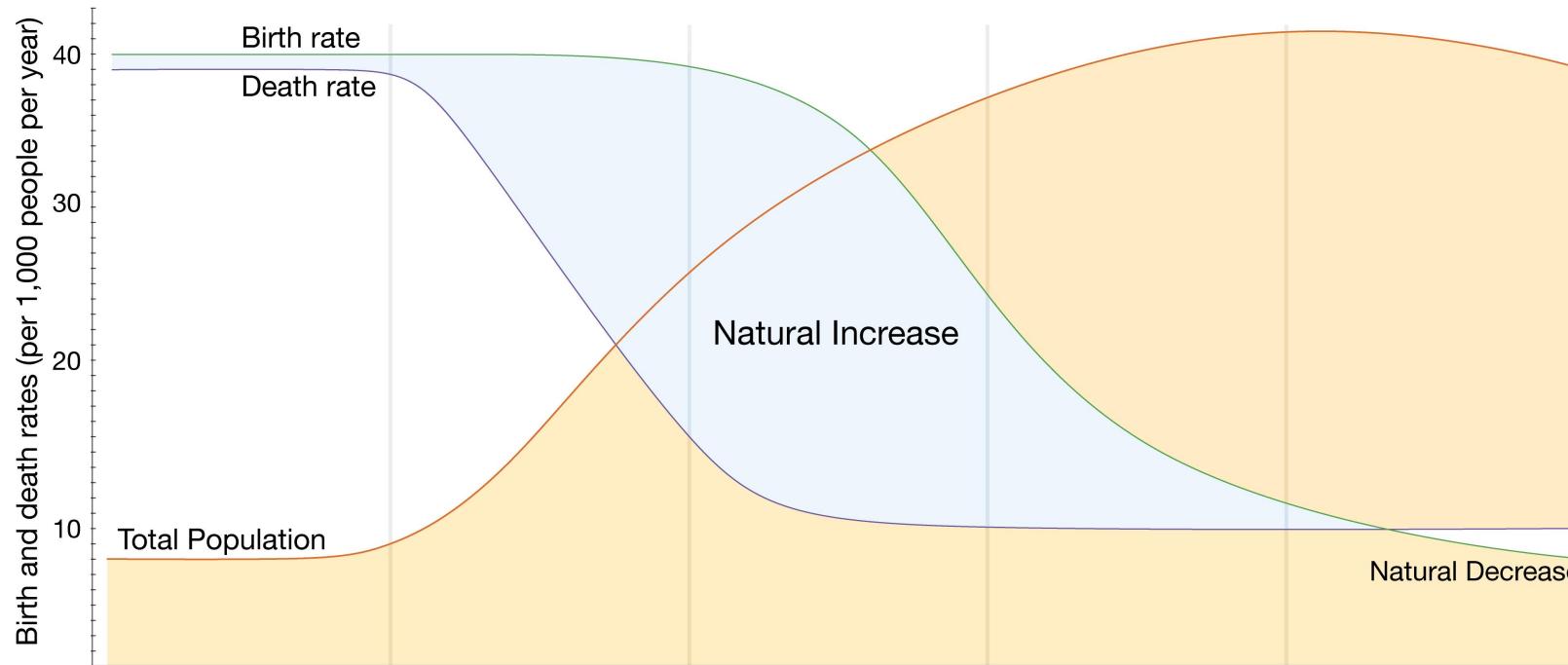
How does age structure predict population growth?



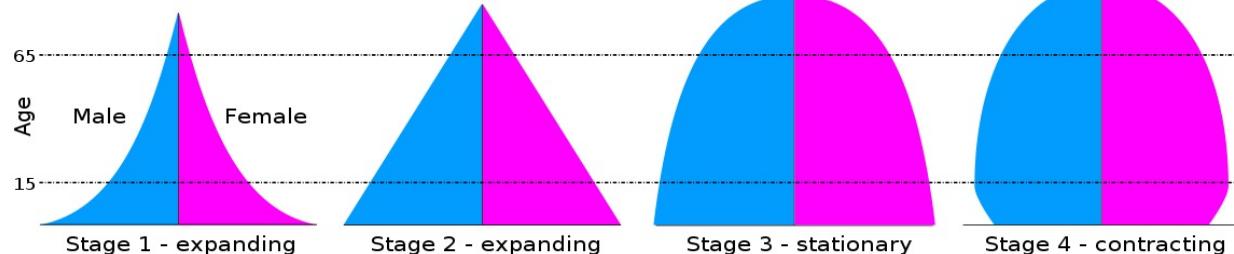
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# Demographic transition

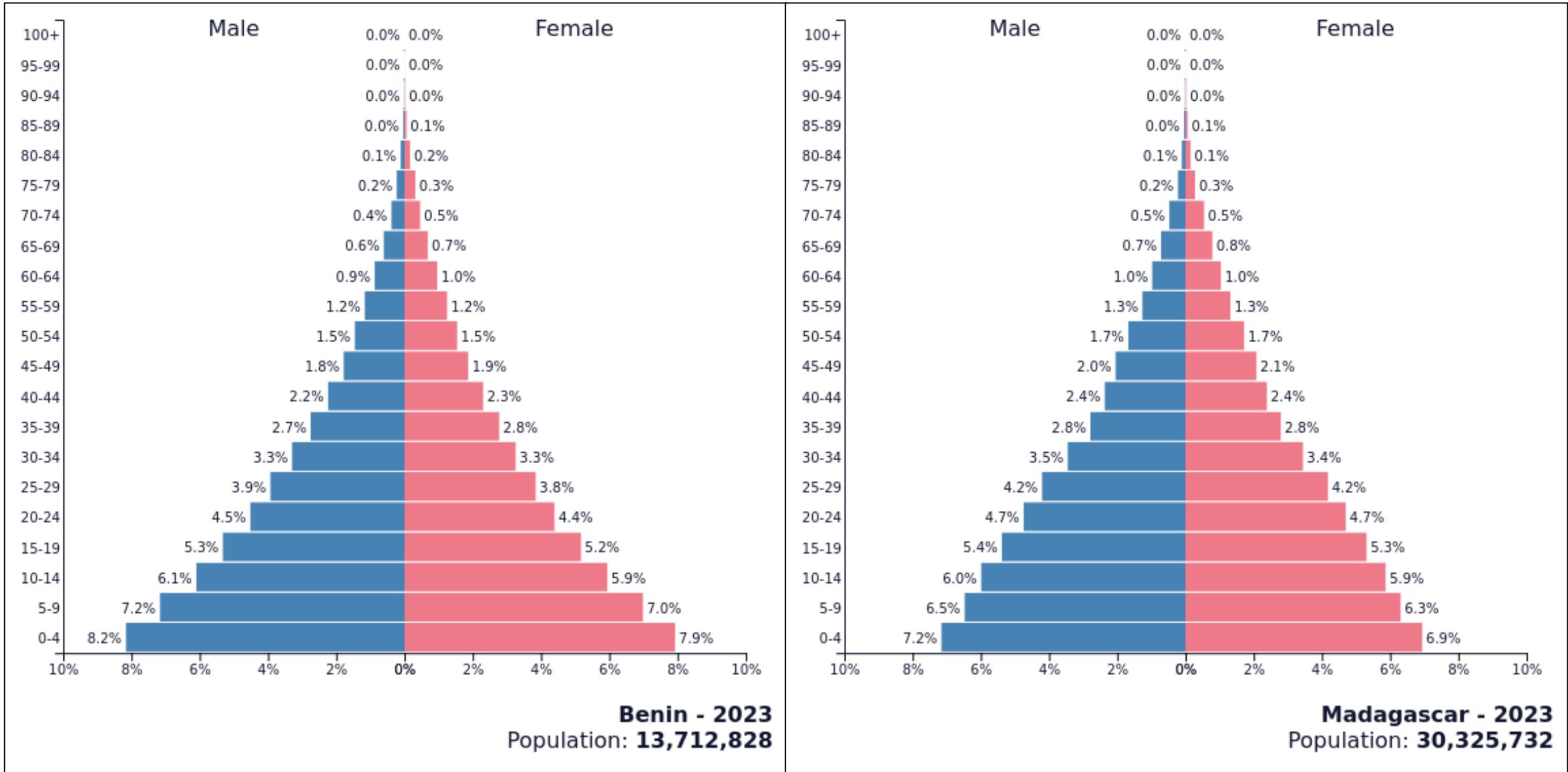
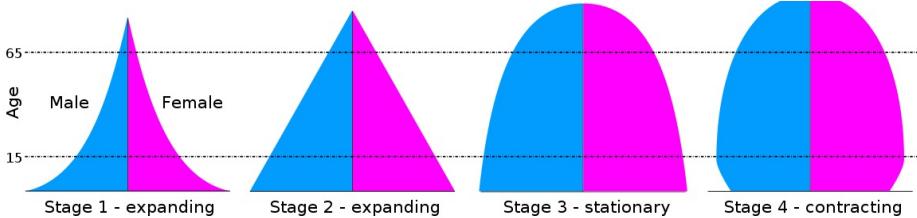
# How does age structure predict population growth?



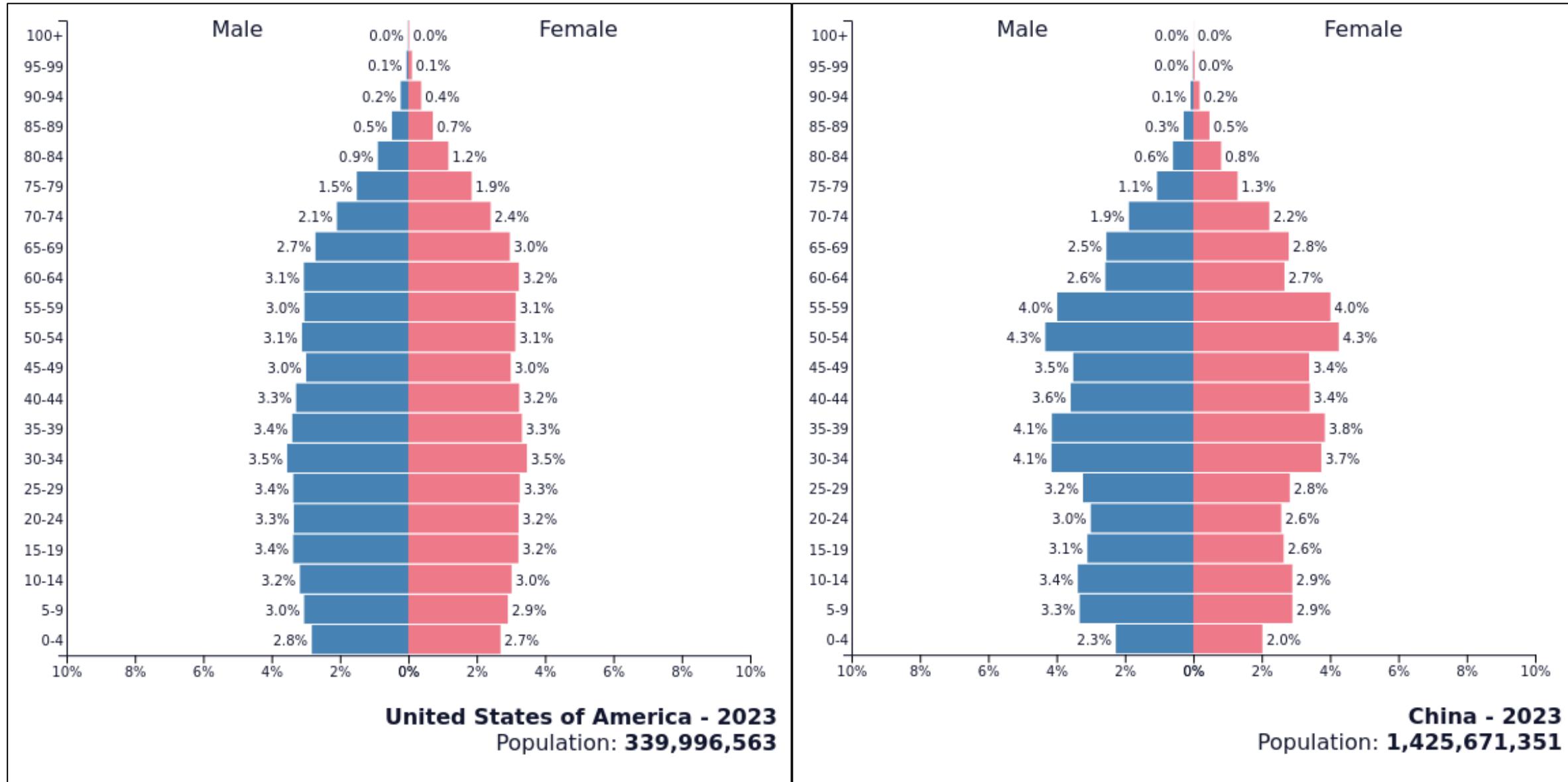
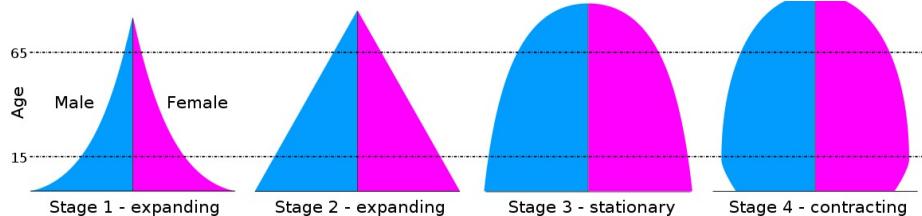
|                         |                         |                     |                     |                         |                         |
|-------------------------|-------------------------|---------------------|---------------------|-------------------------|-------------------------|
| <b>Birth rate</b>       | High                    | High                | Falling             | Low                     | Very low                |
| <b>Death rate</b>       | High                    | Falls rapidly       | Falls more slowly   | Low                     | Low                     |
| <b>Natural increase</b> | Stable or slow increase | Very rapid increase | Increase slows down | Stable or slow increase | Stable or slow decrease |



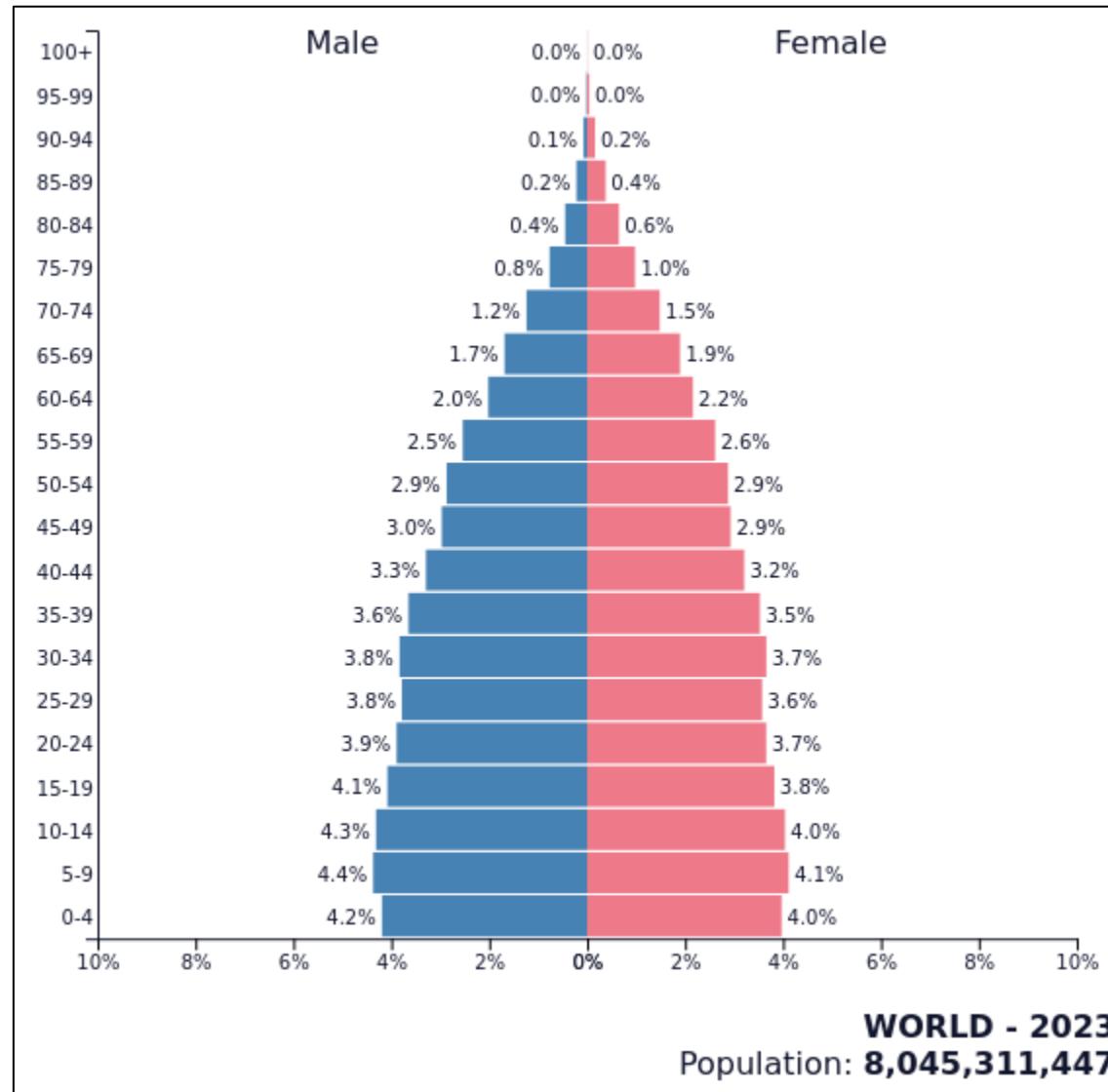
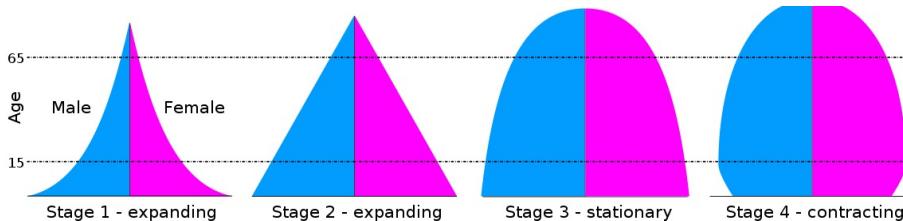
# Where are we globally?



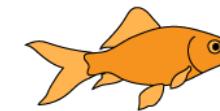
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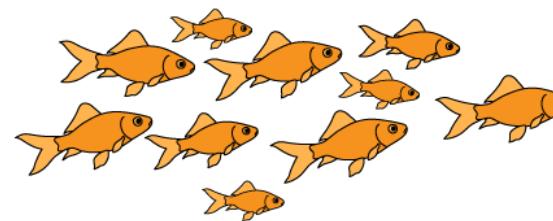
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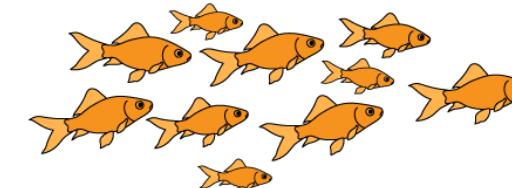
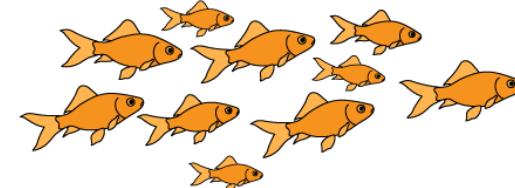
Ecology is the study of  
the **interactions** of  
**organisms** with each  
other and their  
**environment.**



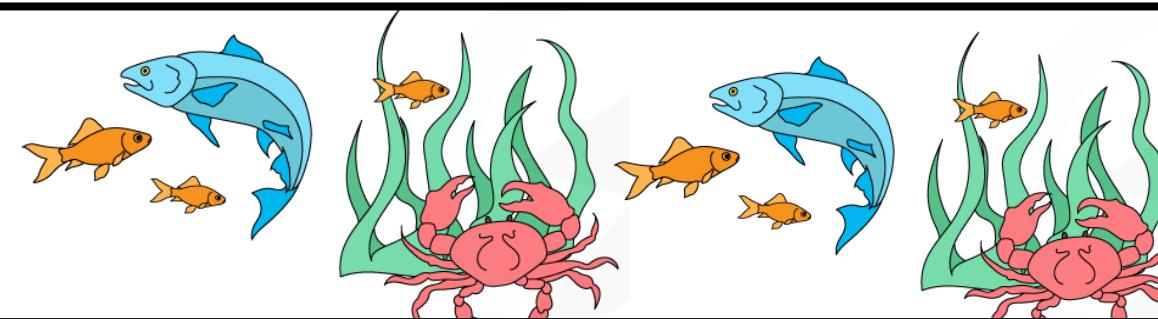
individual



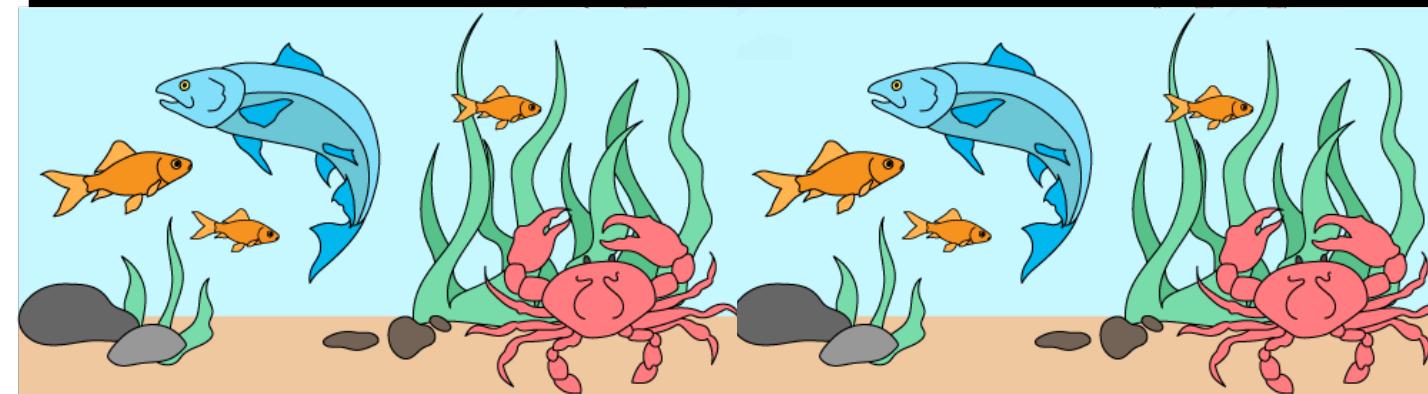
population



metapopulation

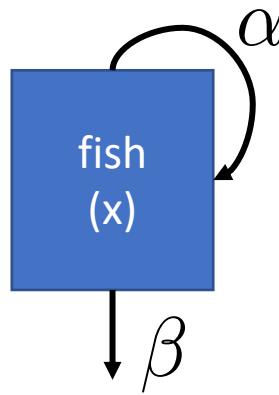


community

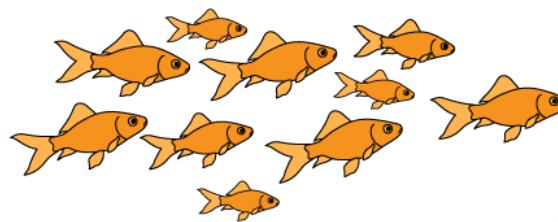


ecosystem

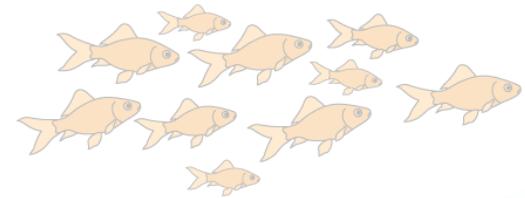
**Population** = multiple individuals of the same species (**conspecifics**) in the same habitat



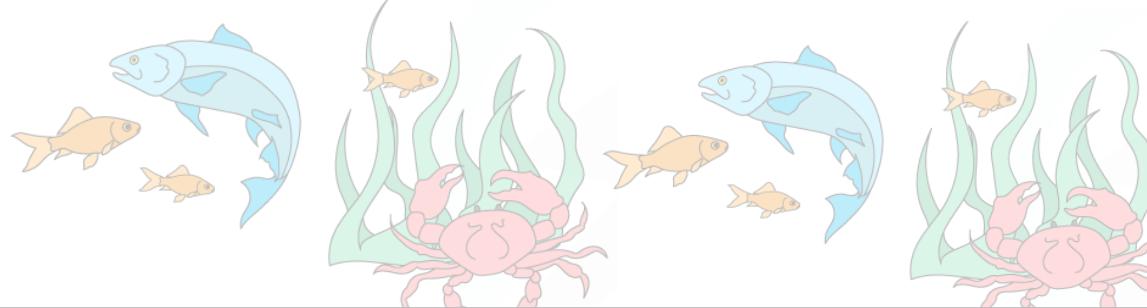
individual



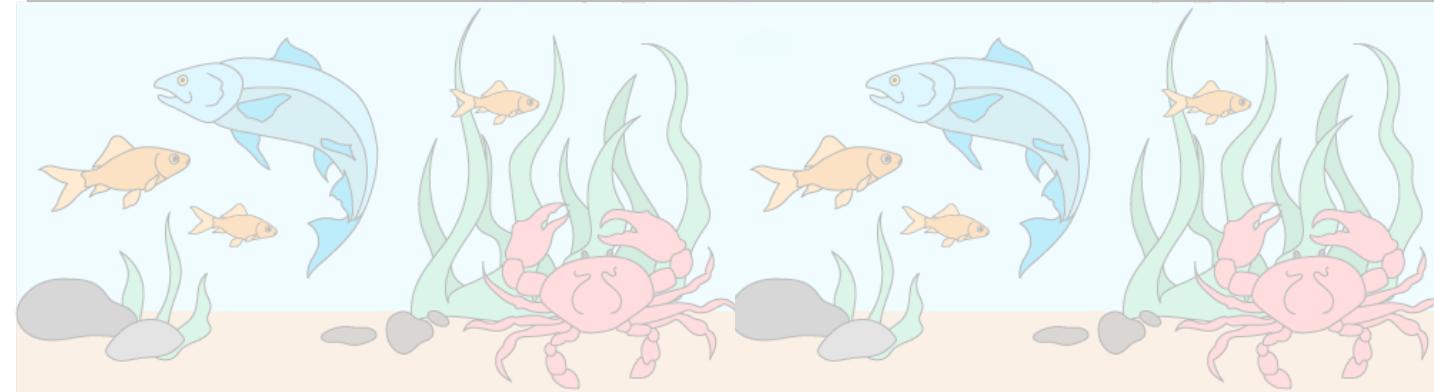
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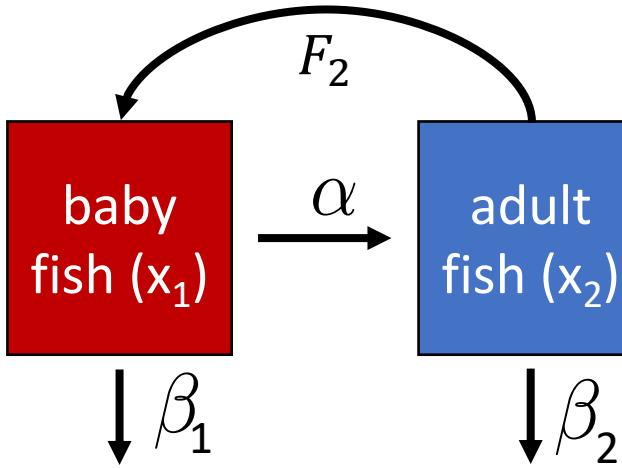
community



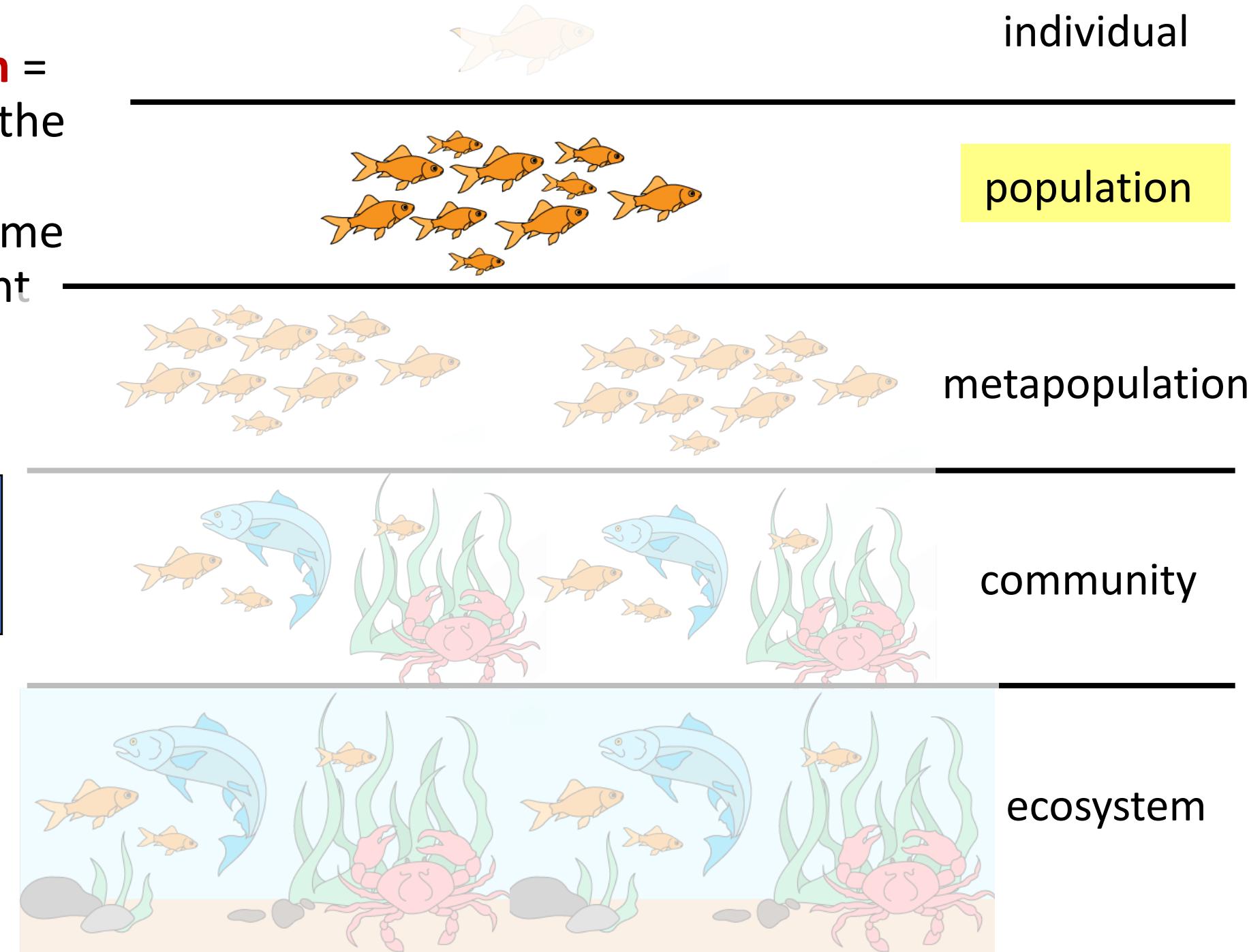
ecosystem

*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

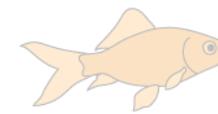


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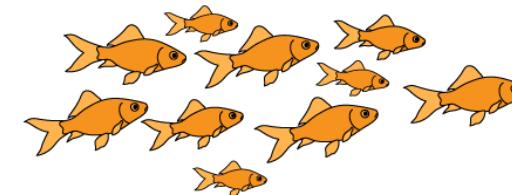
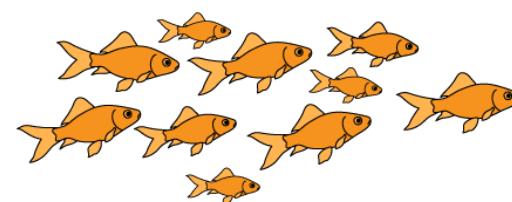
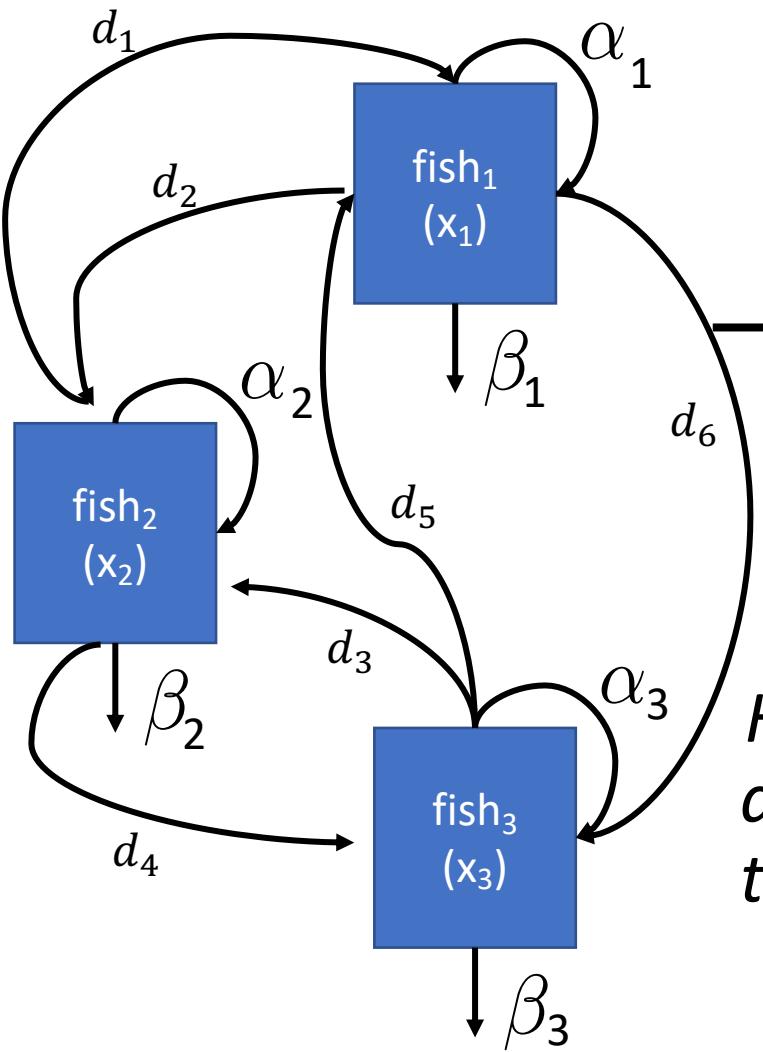
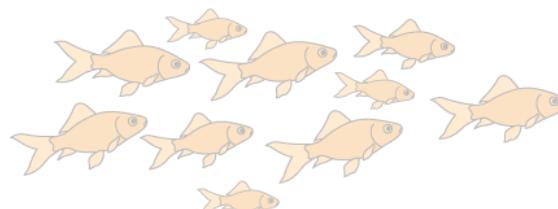


**Metapopulation** = sub-populations of conspecifics connected by migration or dispersal

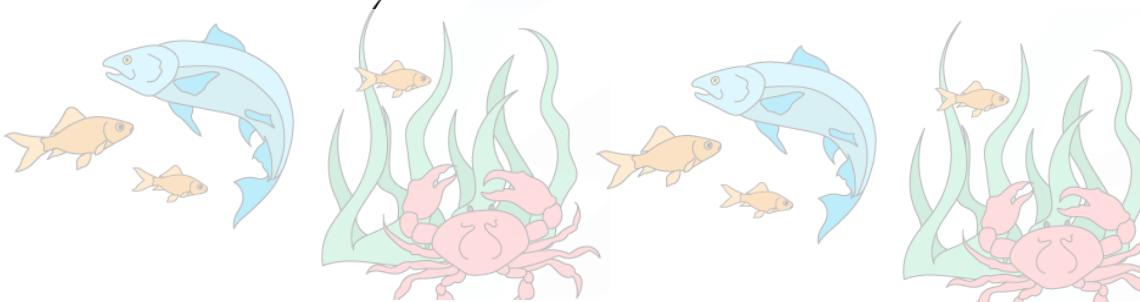
individual



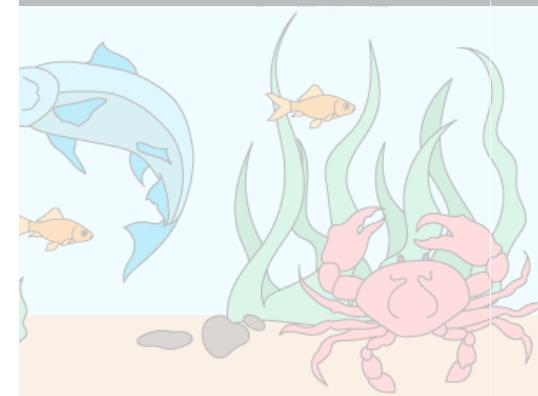
population



metapopulation



community



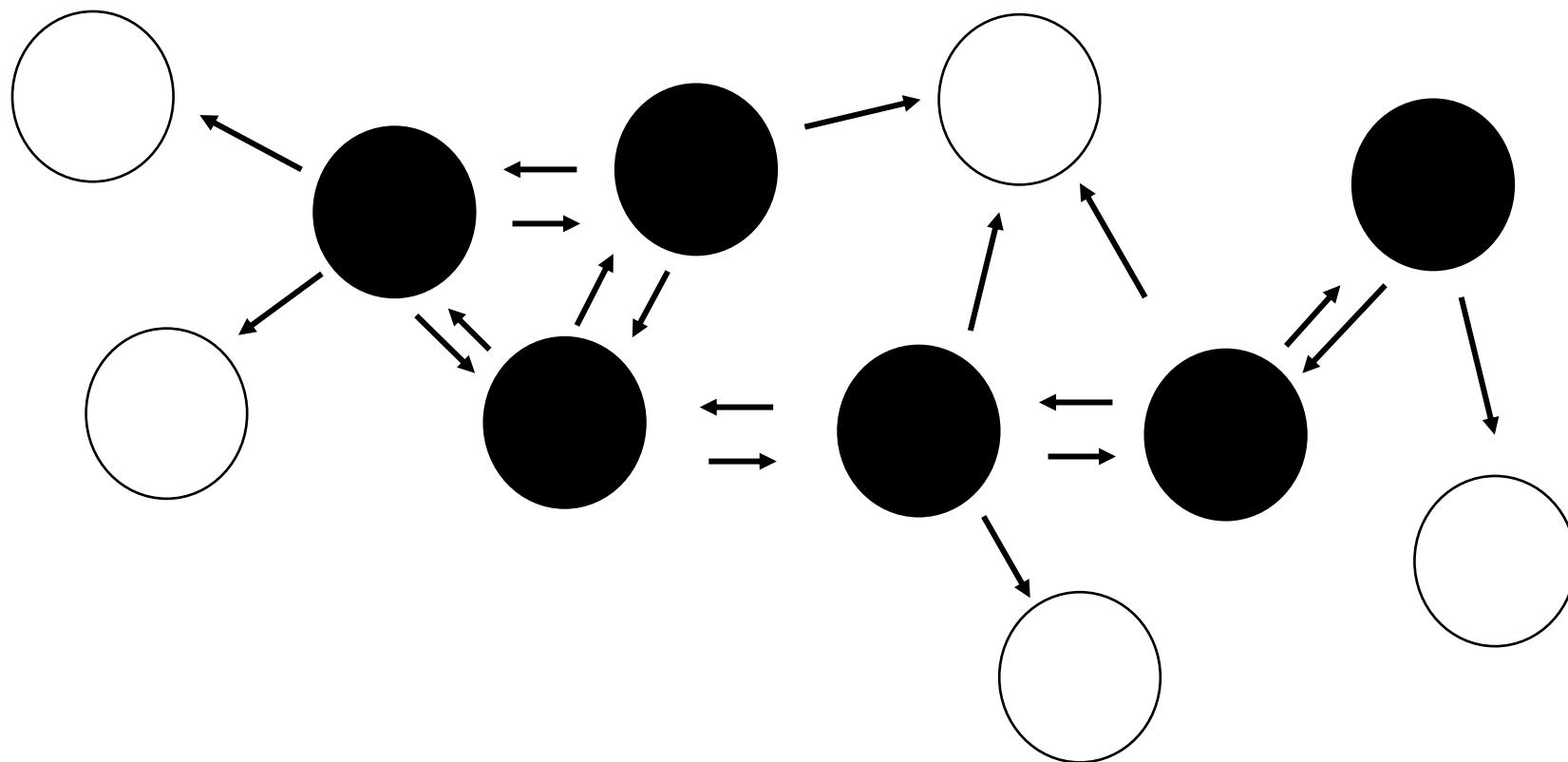
ecosystem

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

# Modeling metapopulation dynamics

- a “population of populations”

-Richard Levins 1969



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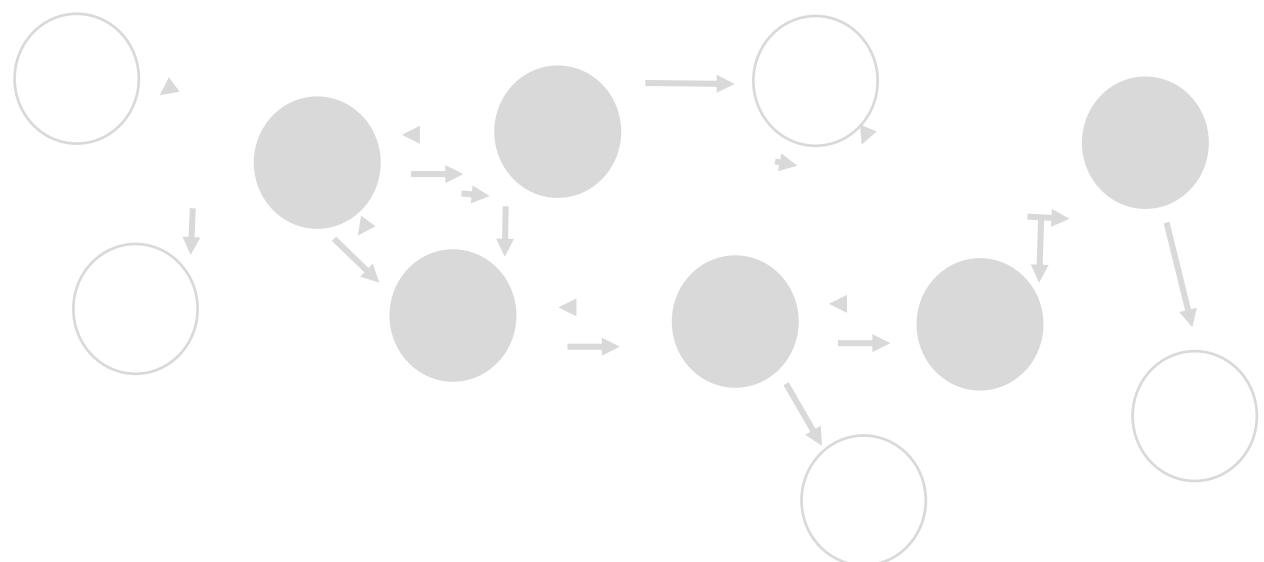
$$\frac{dp}{dt} = cp(1 - p) - ep \leftarrow$$

colonization rate      extinction rate

↑      ↘      ↑

proportion of unoccupied patches

fraction of patches occupied at a given time



# Modeling metapopulation dynamics

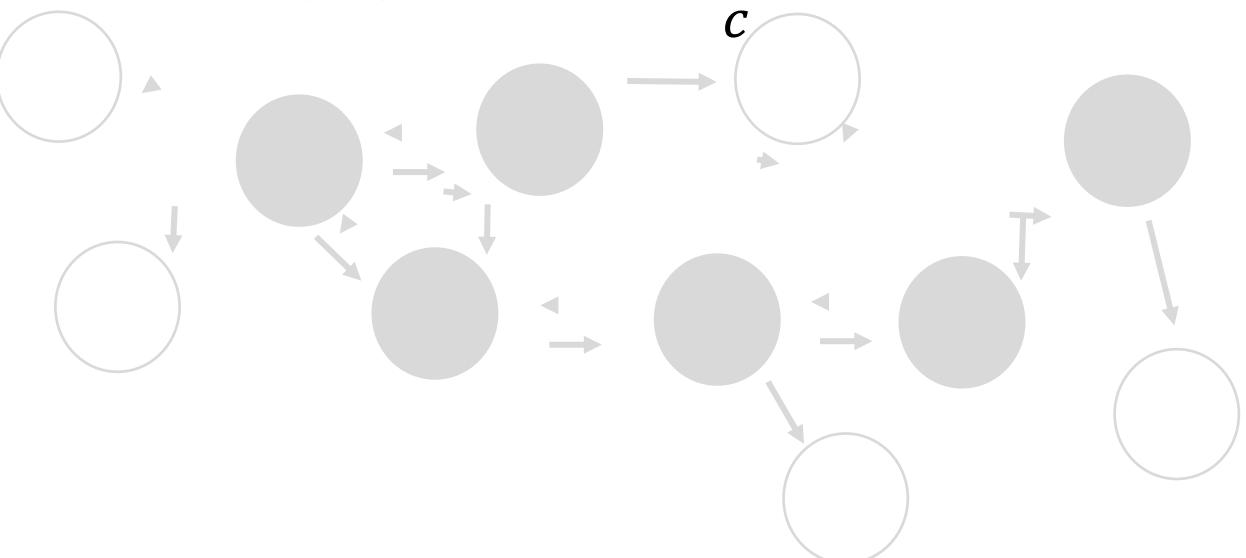
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$$\frac{dp}{dt} = cp(1 - p) - ep$$
$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K}\right)$$

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

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



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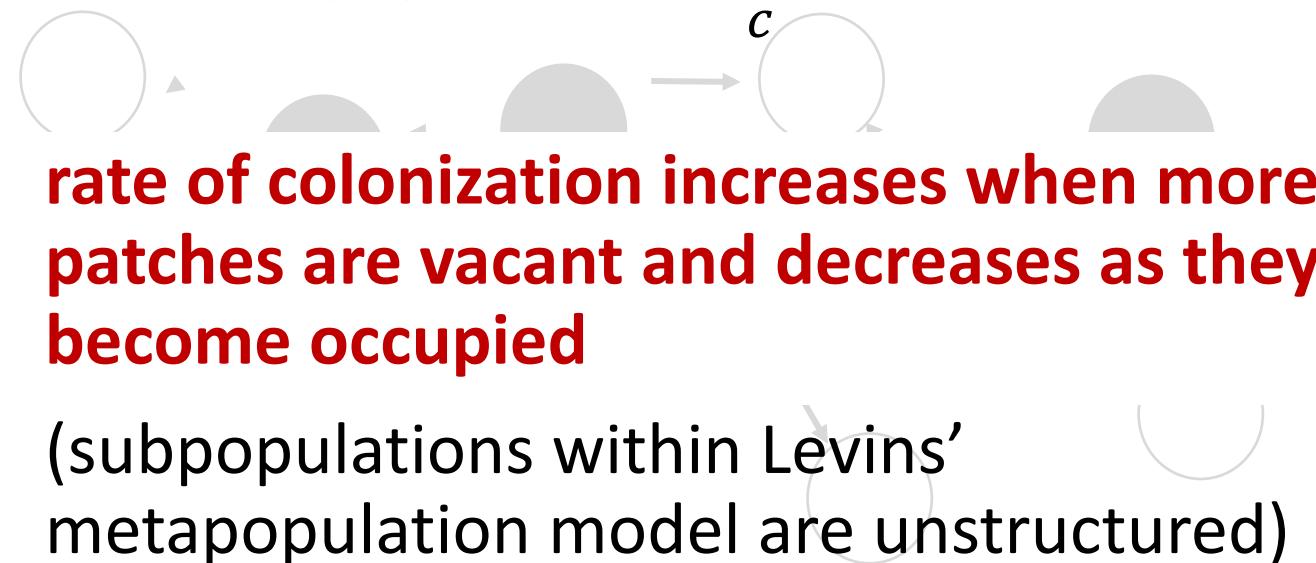
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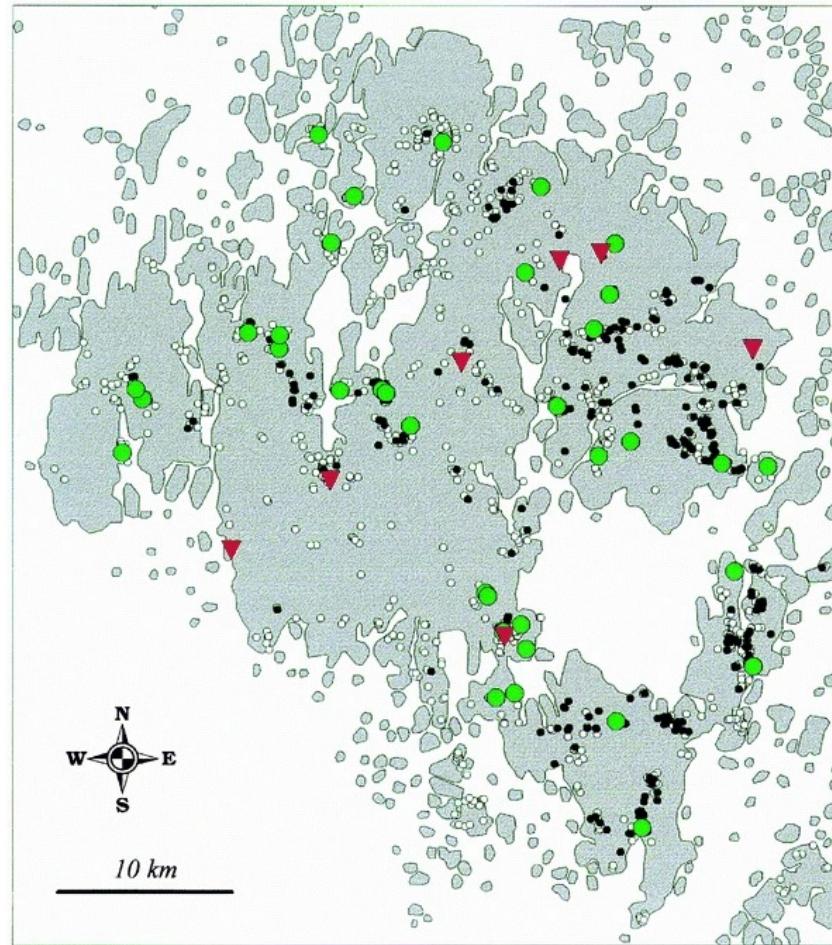


rate of colonization increases when more patches are vacant and decreases as they become occupied  
(subpopulations within Levins' metapopulation model are unstructured)

# Why do metapopulations matter?



Ilkka Hanski  
1953-2016

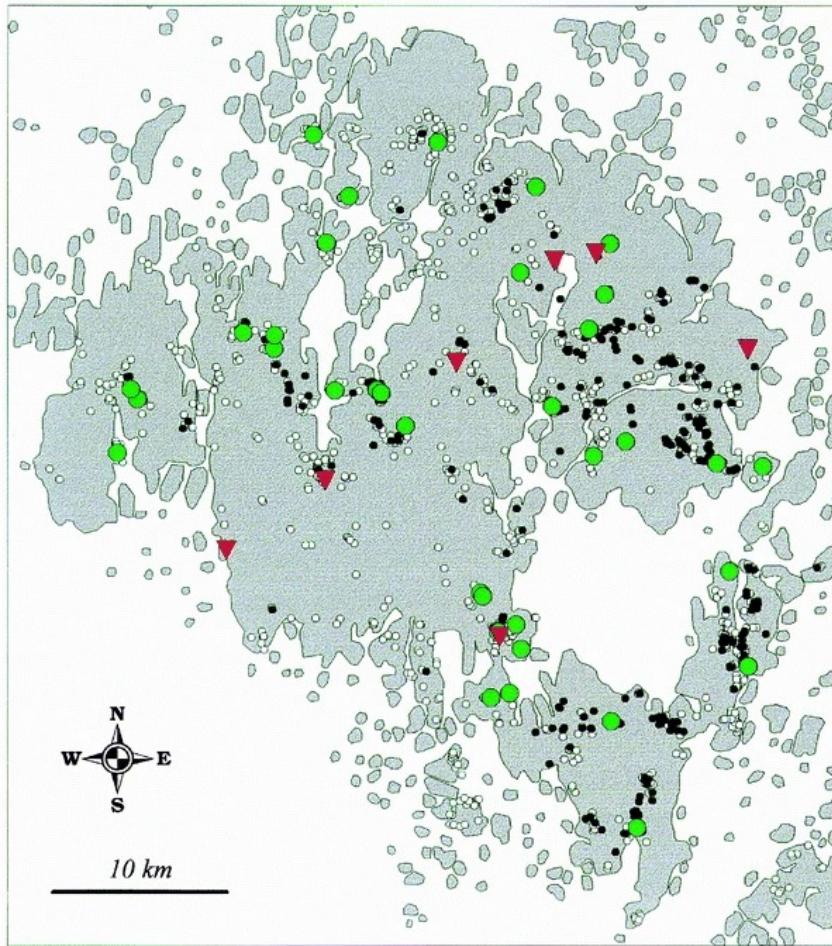


Saccheri et al 1998. *Nature*.



Glanville fritillary butterfly  
*Melitaea cinxia*

# Why do metapopulations matter?

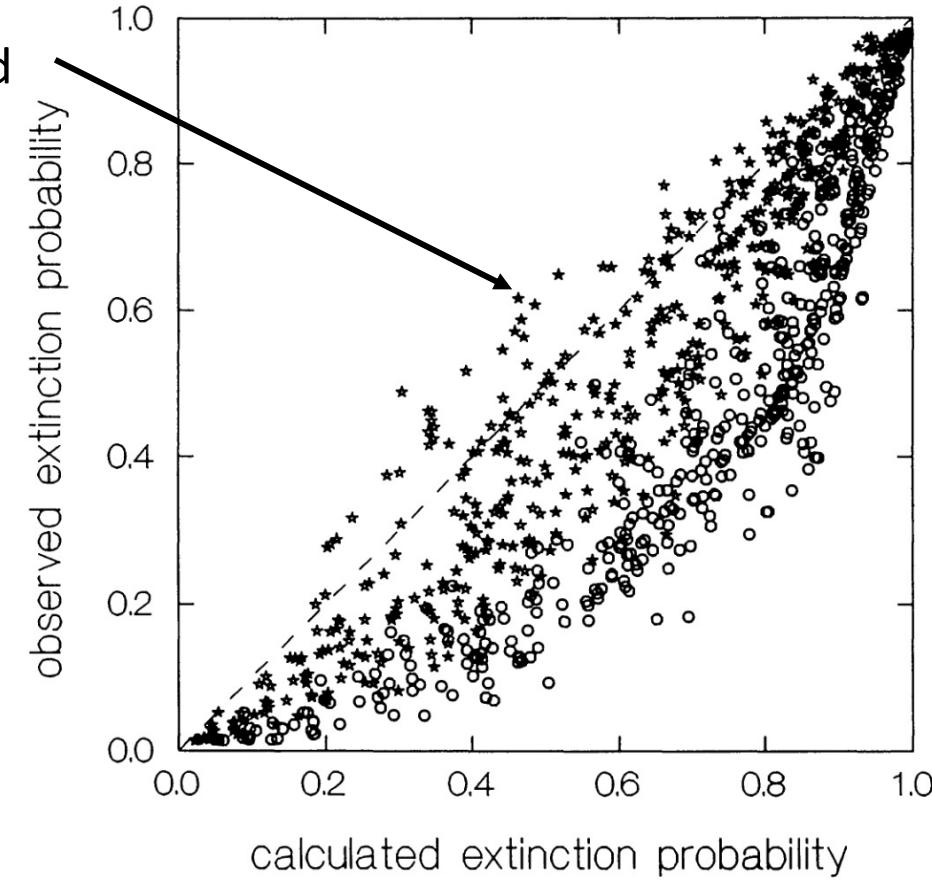


Saccheri et al 1998. *Nature*.

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

## 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*.

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

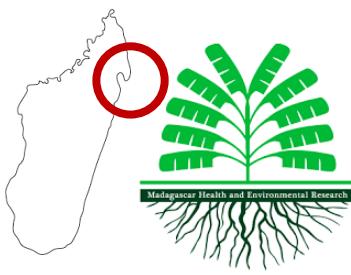
*Conservation Biology*



*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?**

- 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



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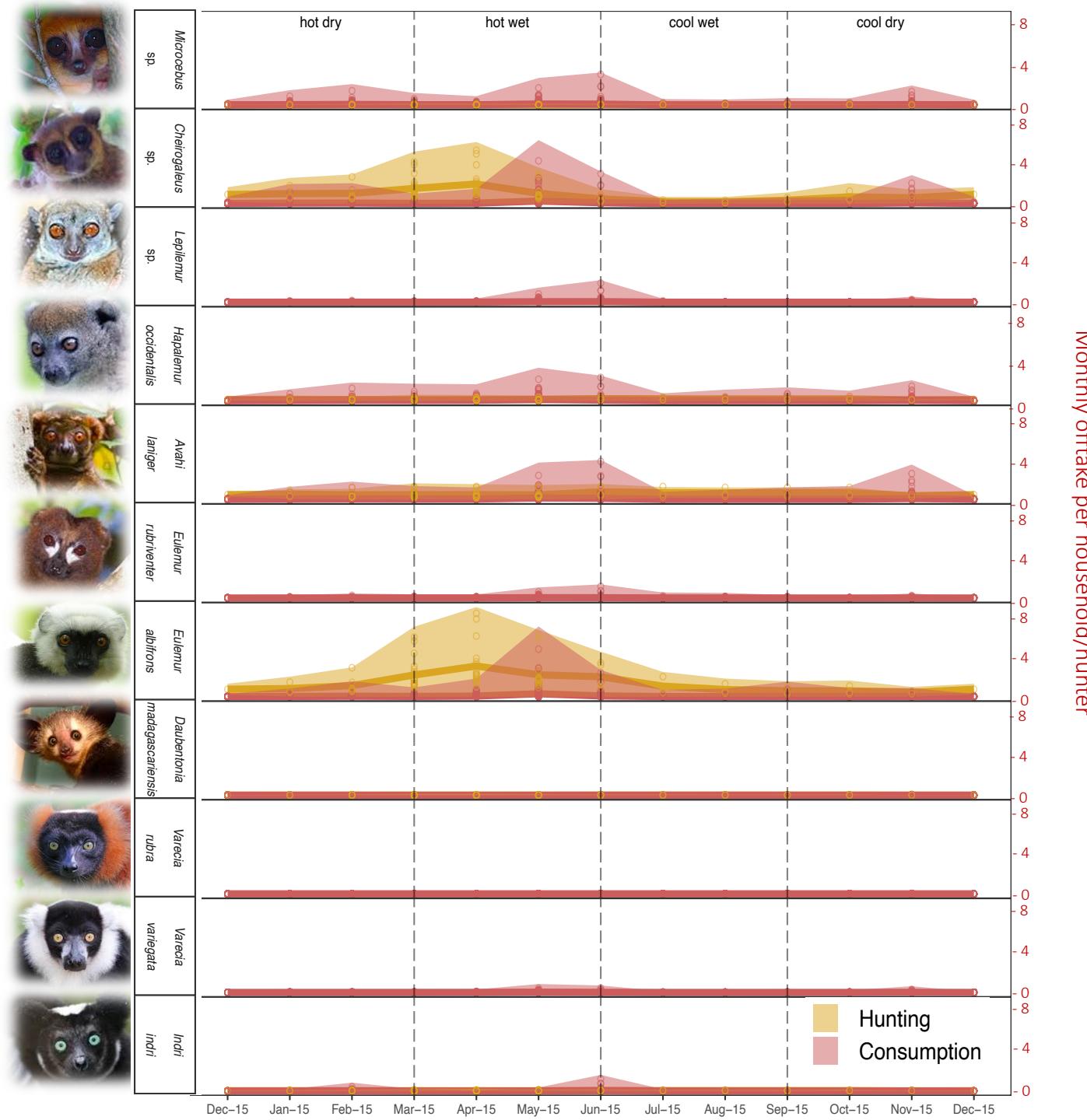
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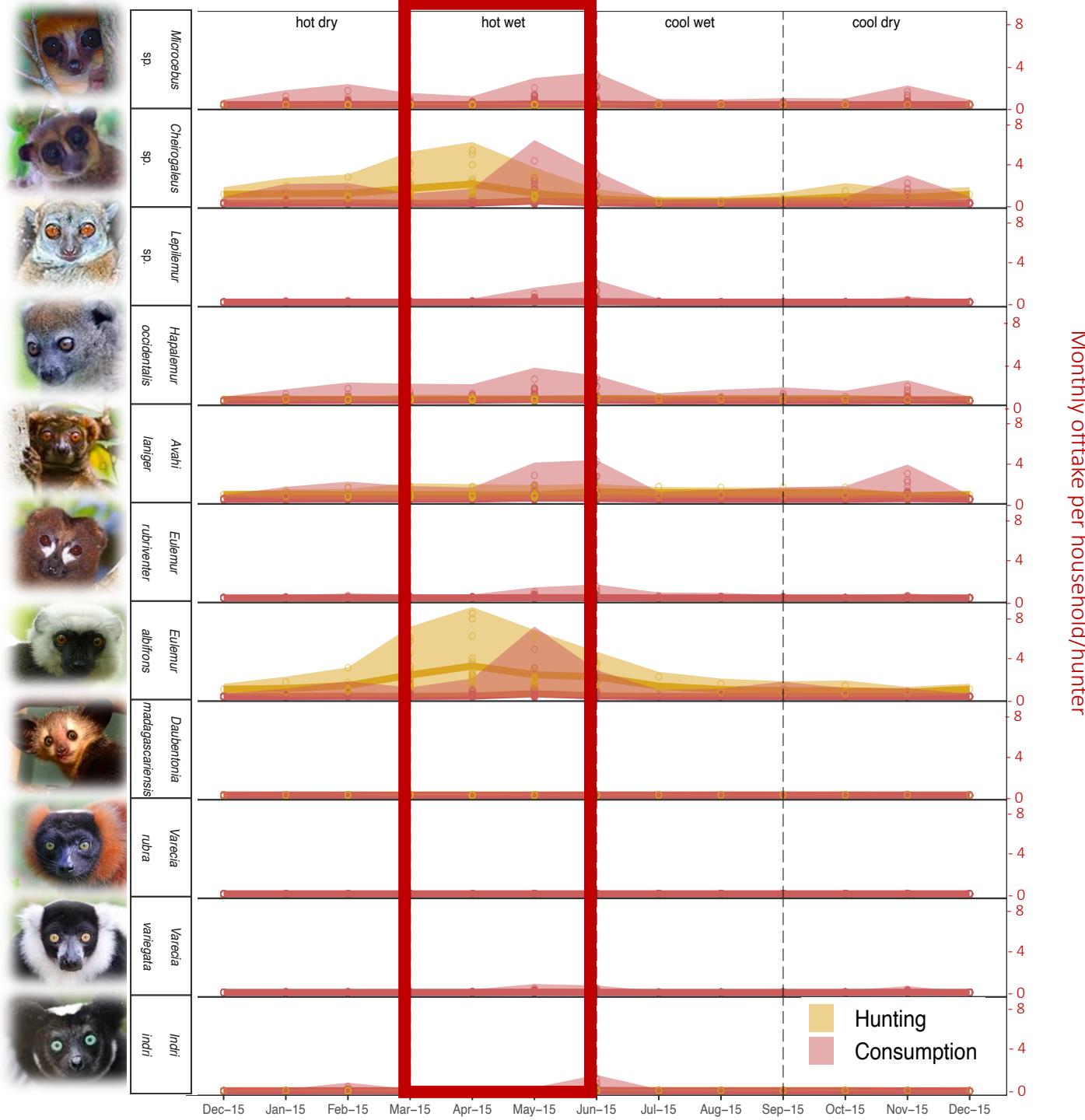


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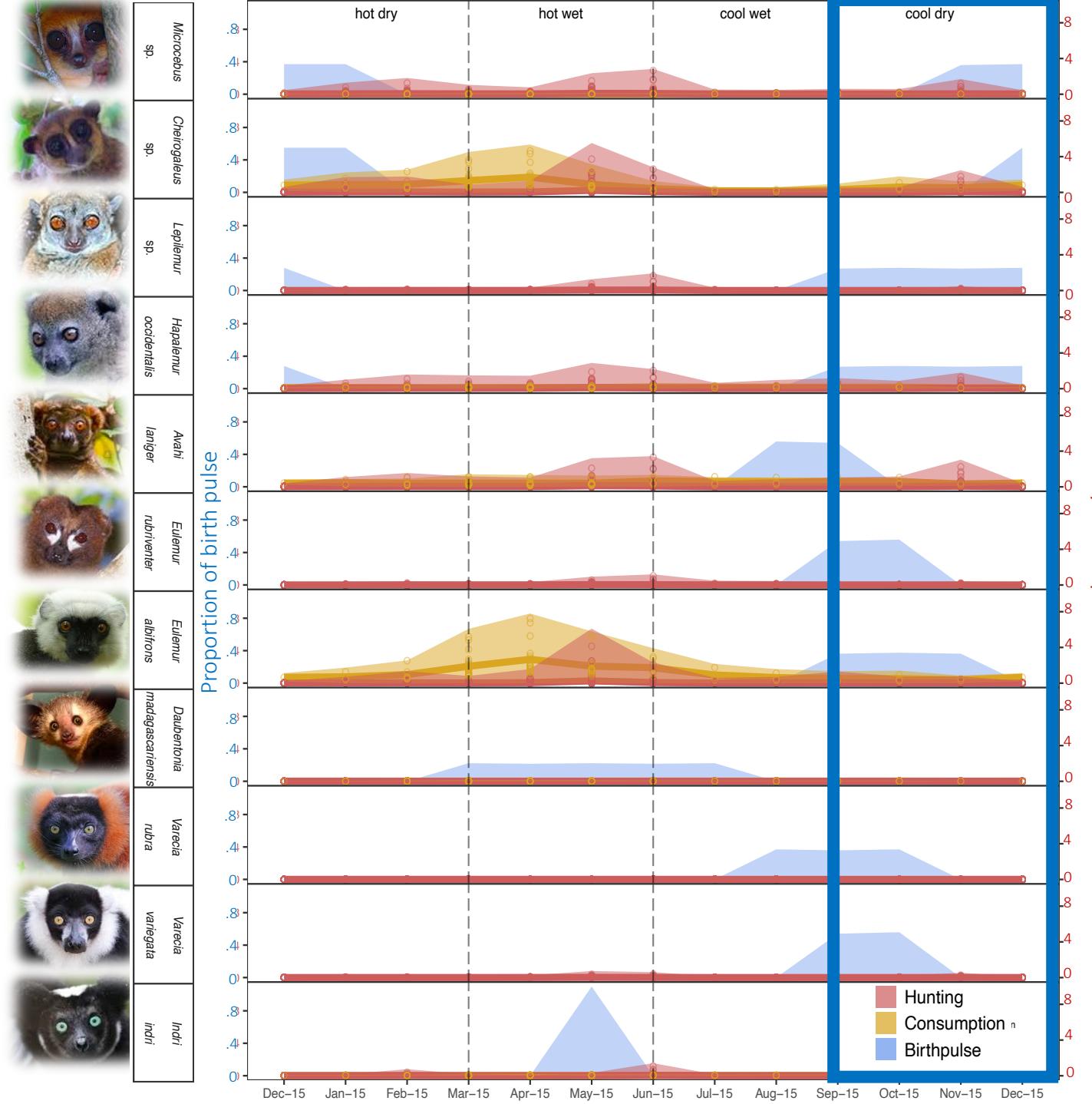


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- MAHERY conducted monthly **dietary recall interviews** for target taxa in households from 2005-2013
- Local hunters from one village outfitted with **diaries to record harvested species**





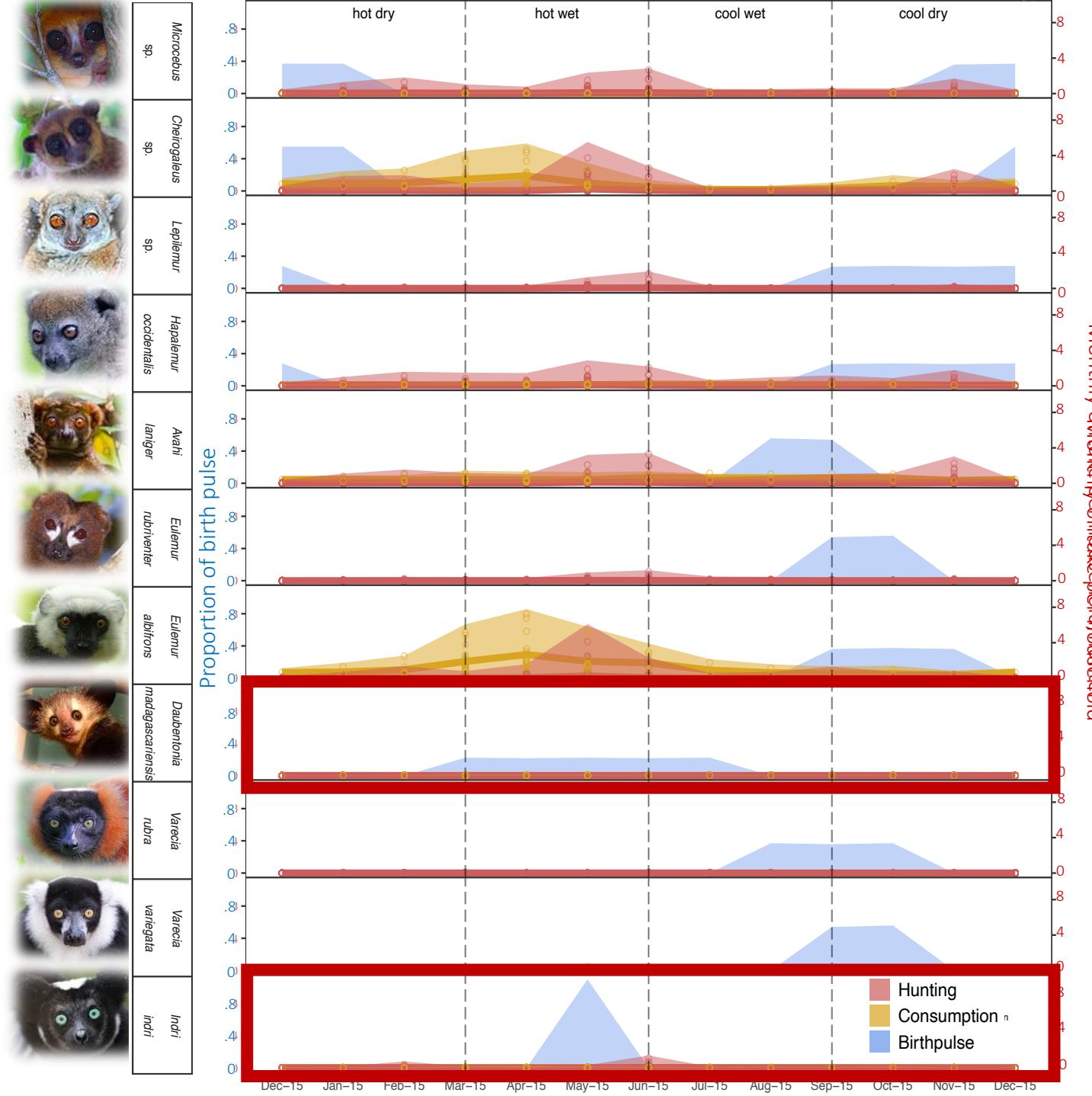
Lemurs are primarily hunted and consumed in the **hot wet season**.



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





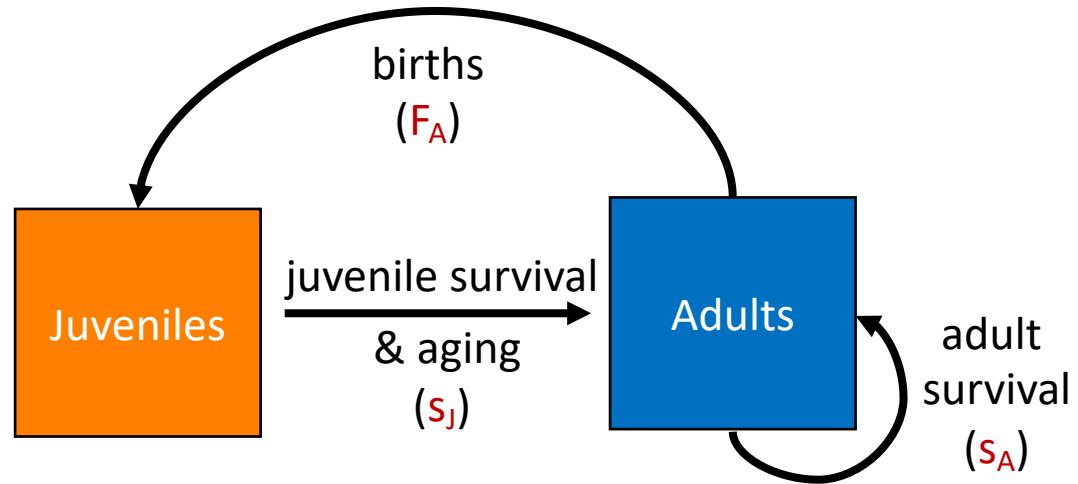
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Most spp. birth in the **cool dry season**, offset from the hunt.

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.



#### 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:

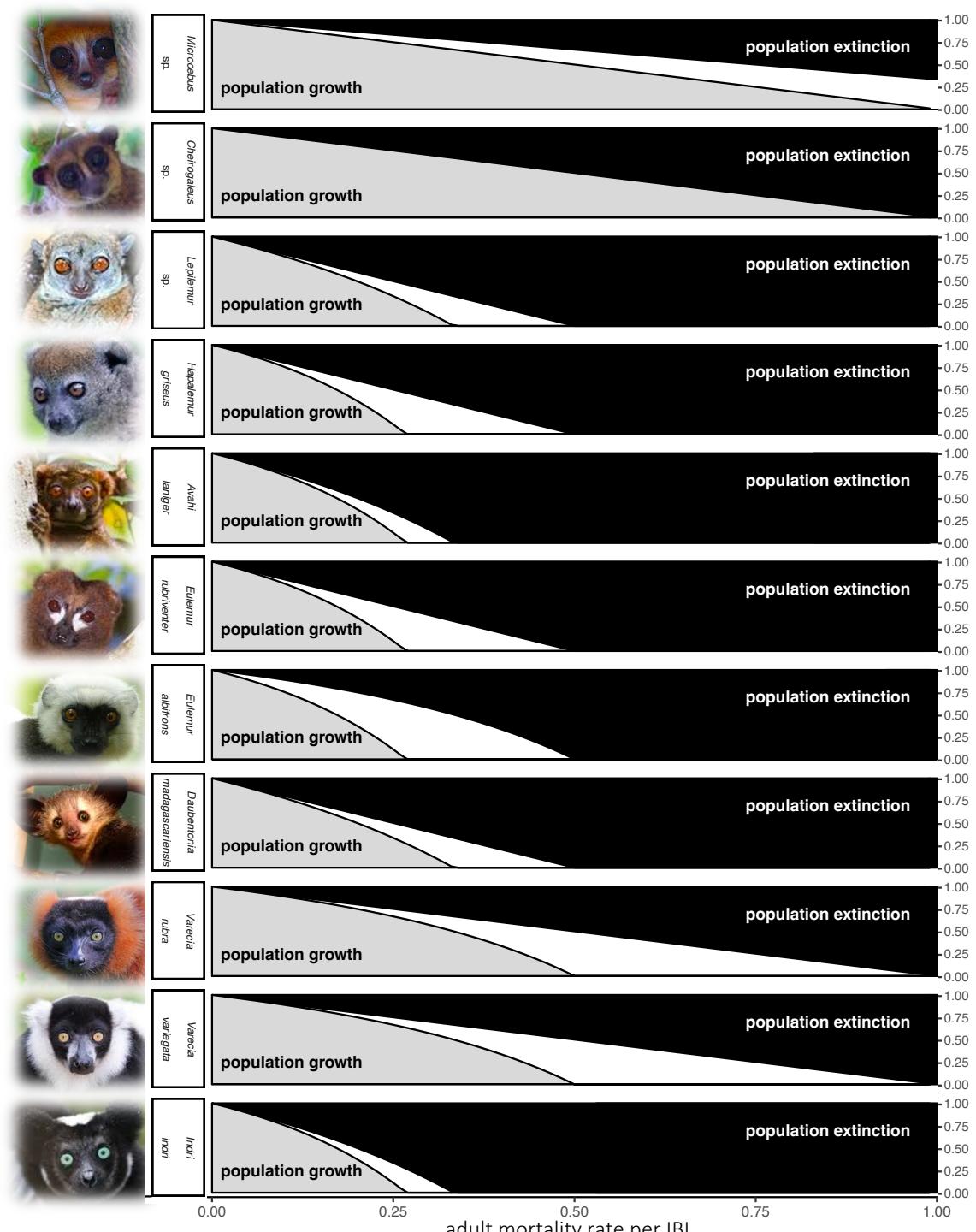
$S_J$  = juvenile IBI survival

$S_A$  = adult IBI survival

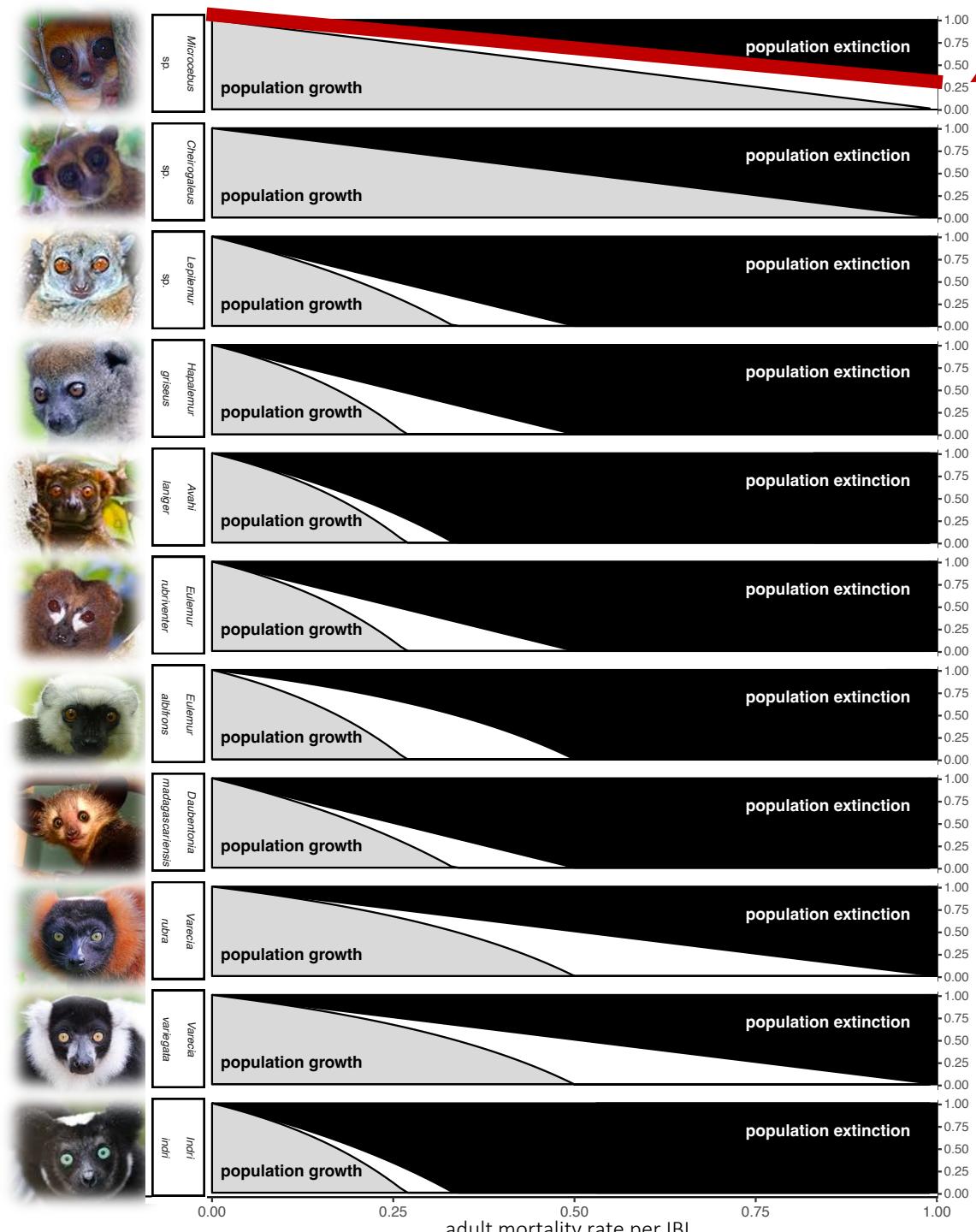
$F_A$  = adult IBI fecundity)

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

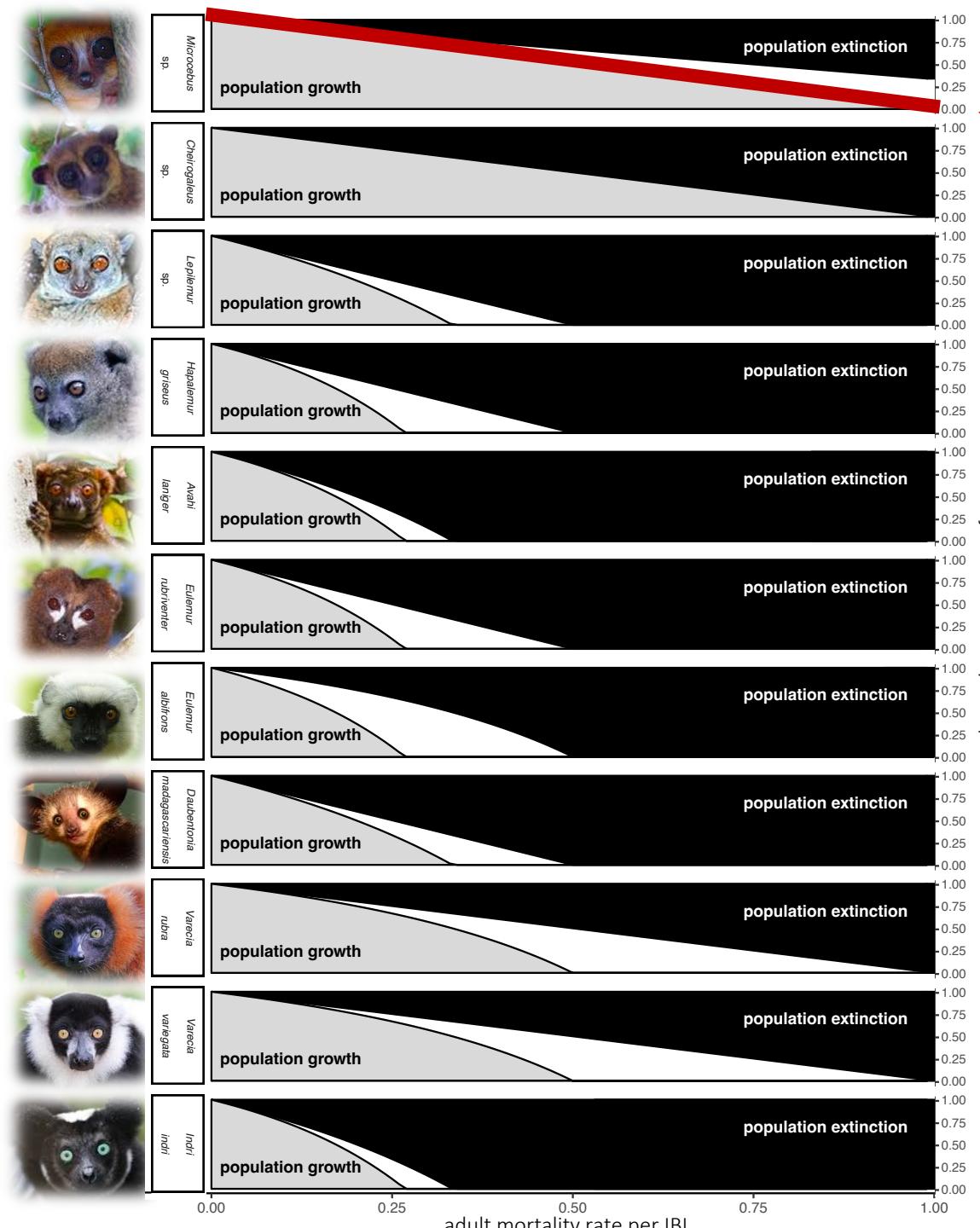
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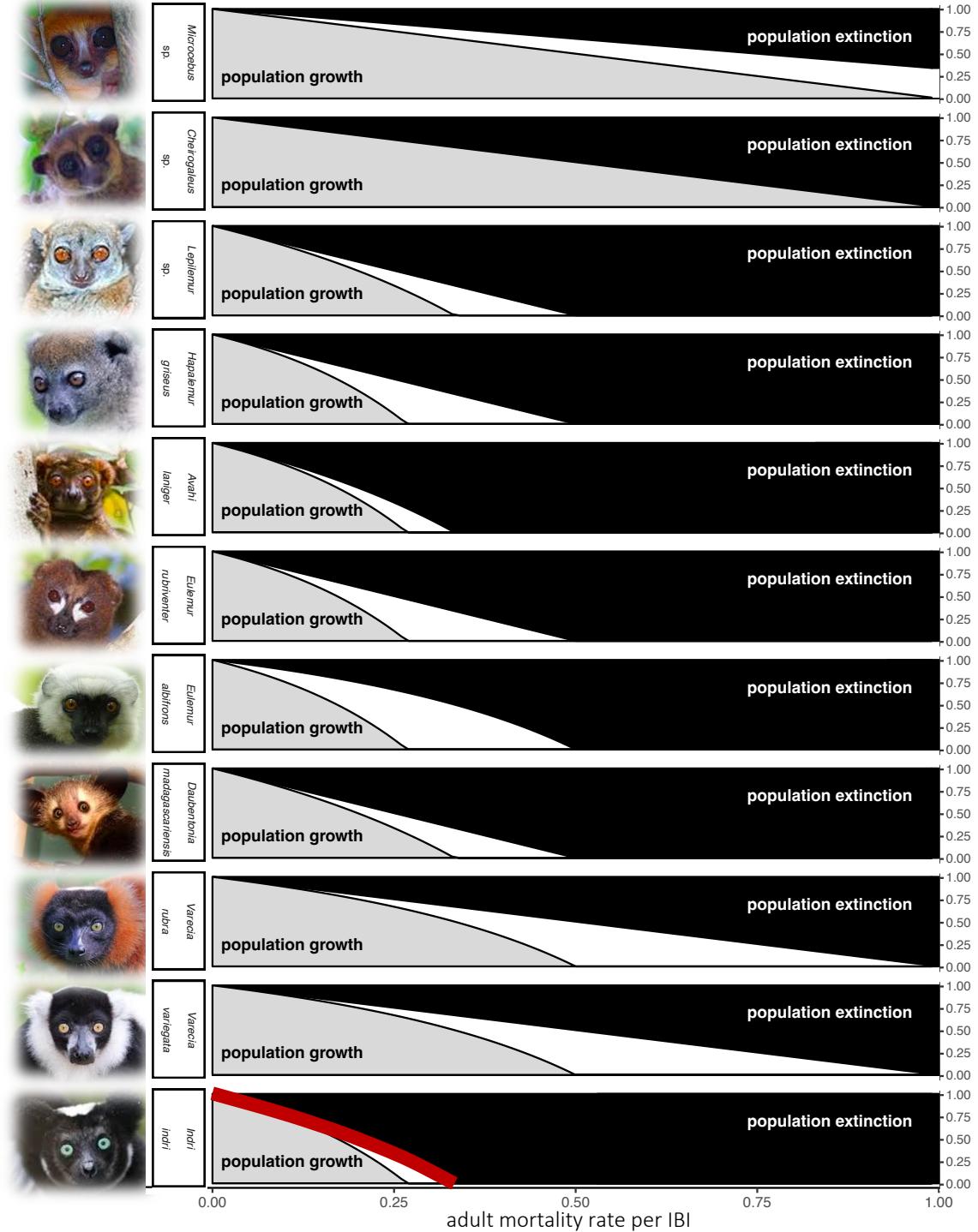


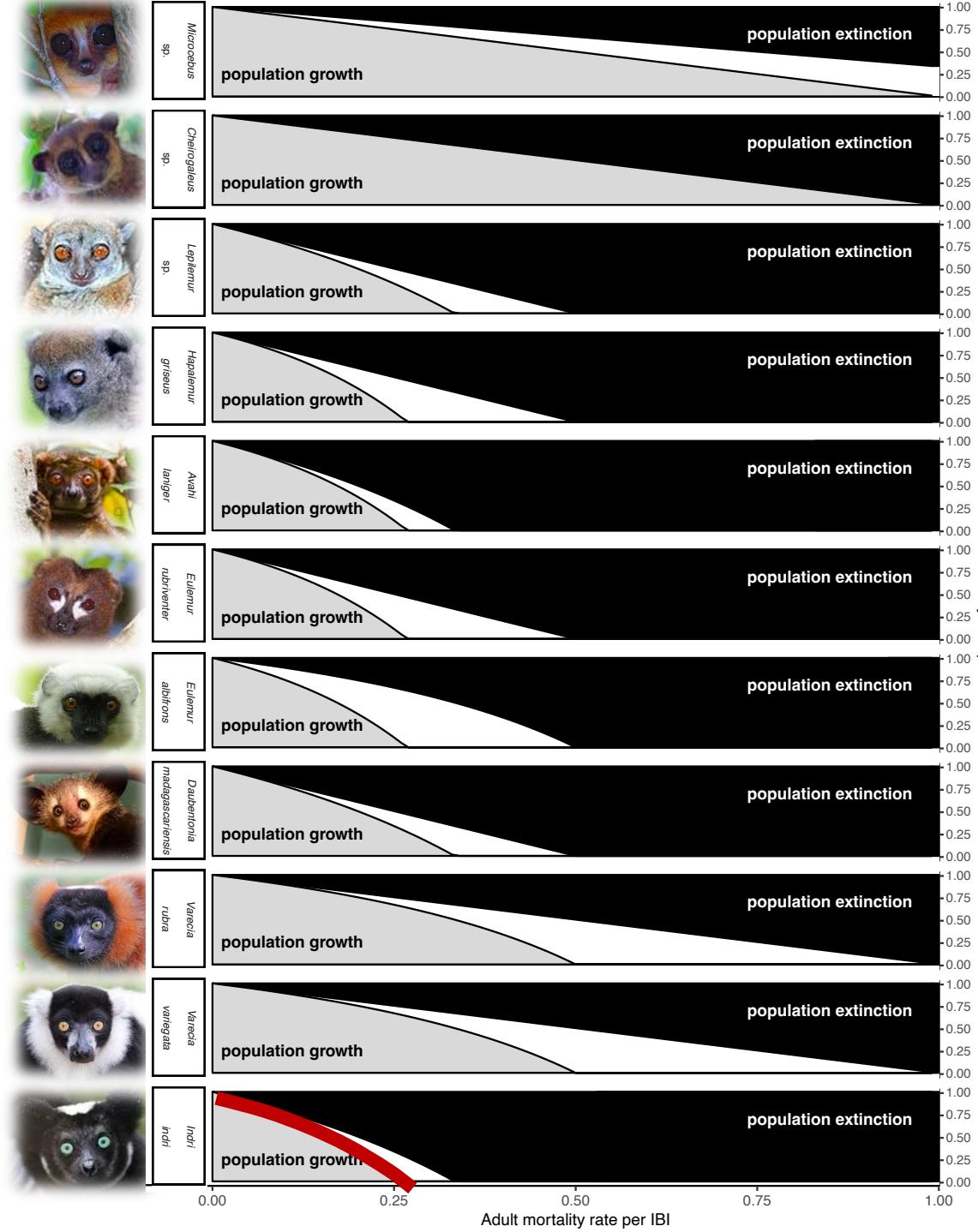
We plotted  
**zero-growth lines** to  
evaluate lemur  
population trajectories  
across different  
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3 offspring / IBI

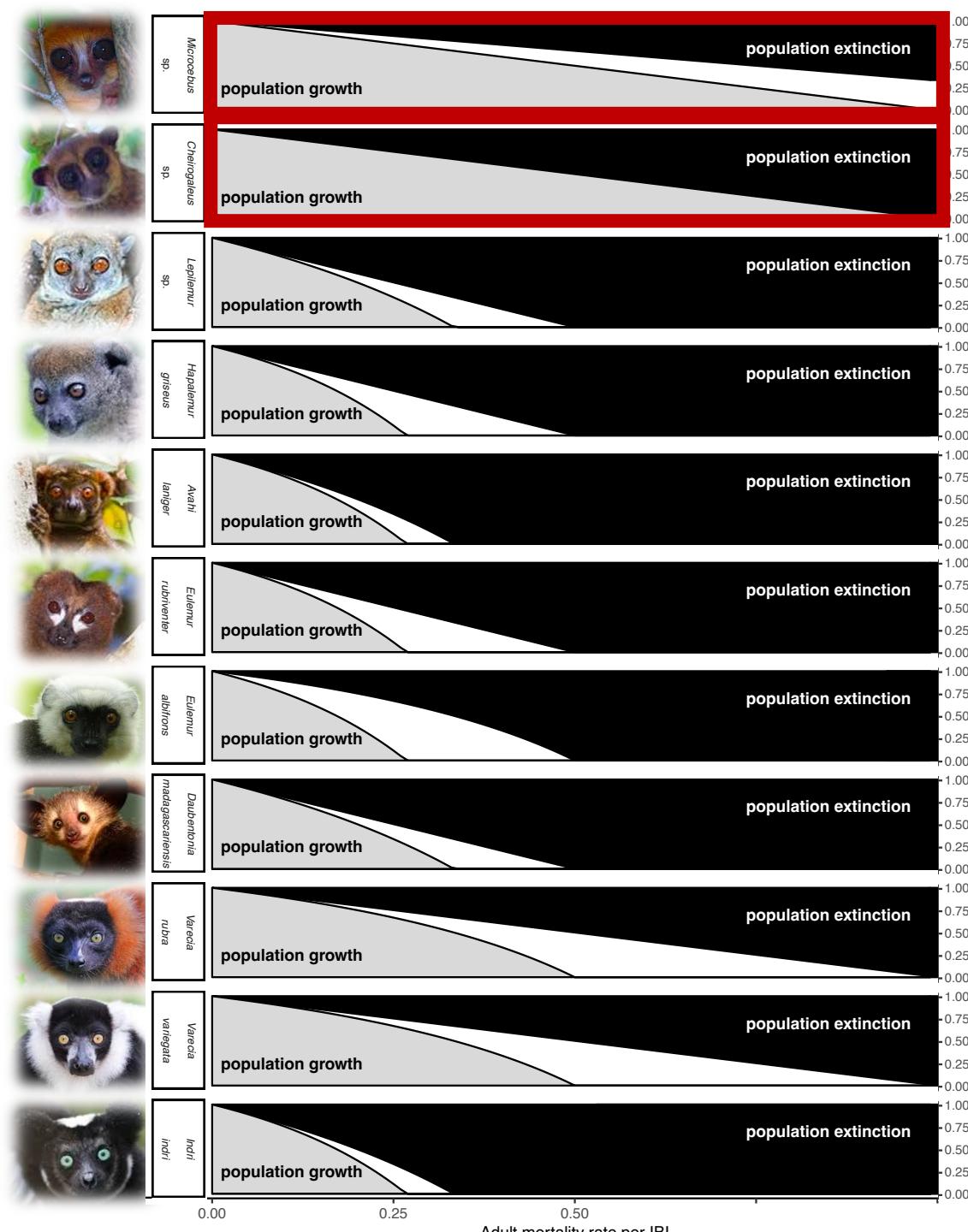






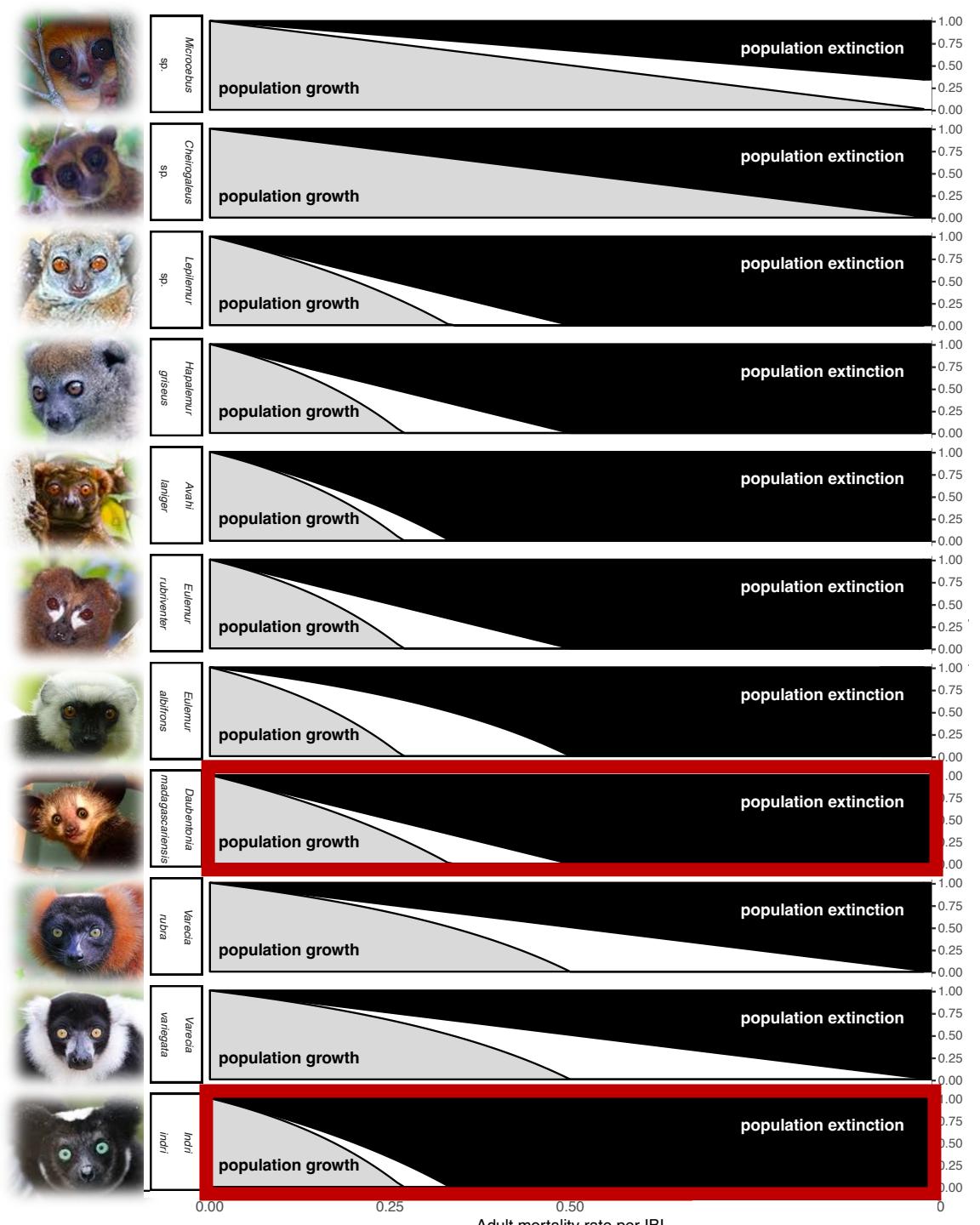
← Age @ 1<sup>st</sup> rep = 9

Brook et al. 2018. *Conservation Biology*.



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

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

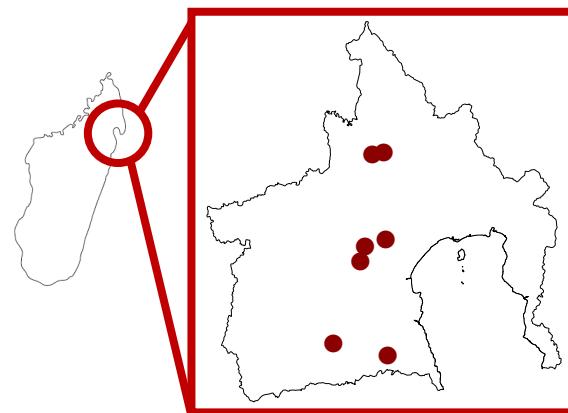


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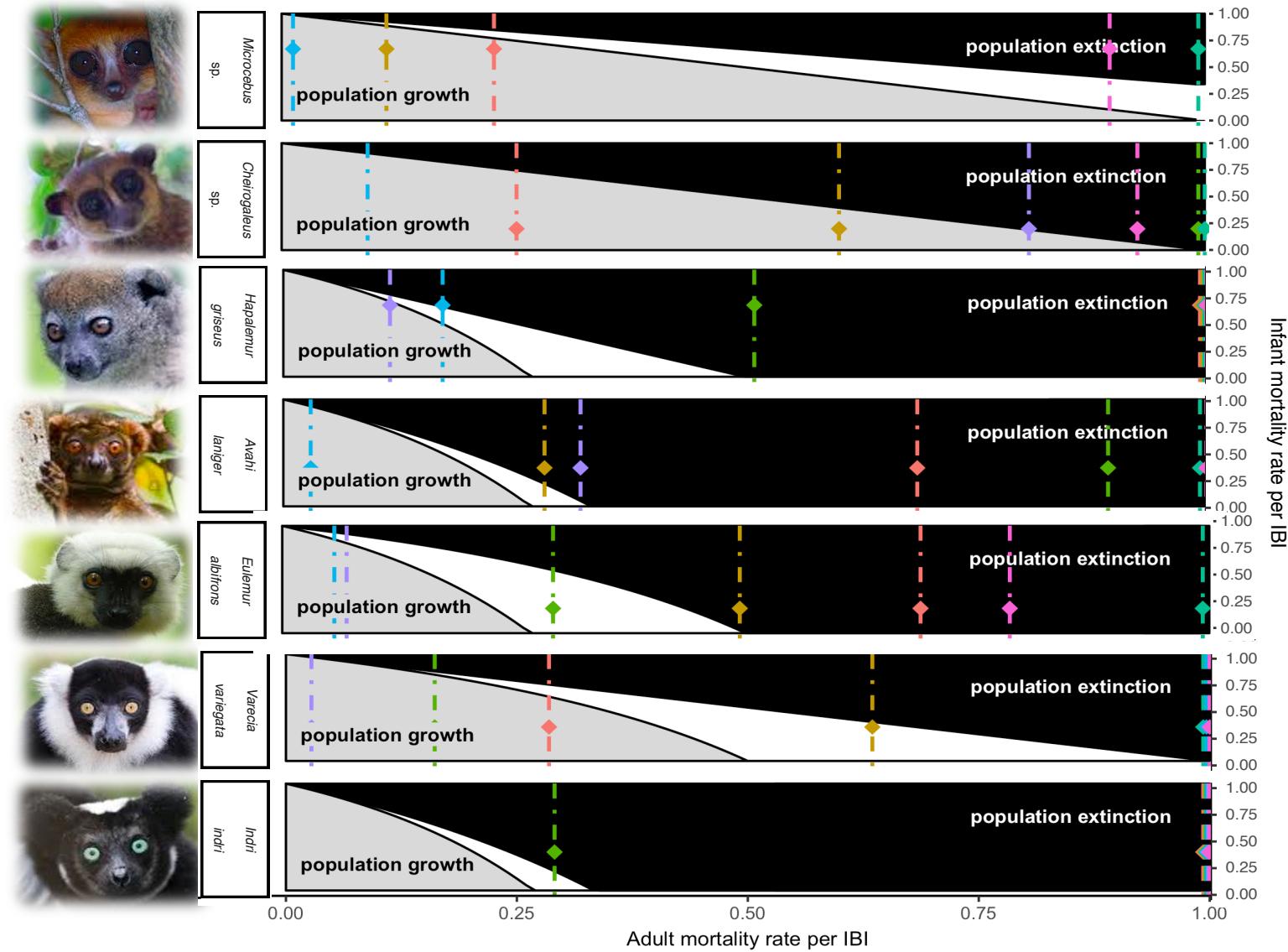
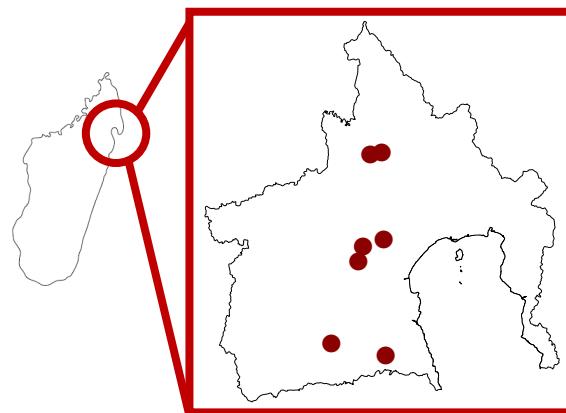
Lemurs with faster life histories are resilient to mortality.

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

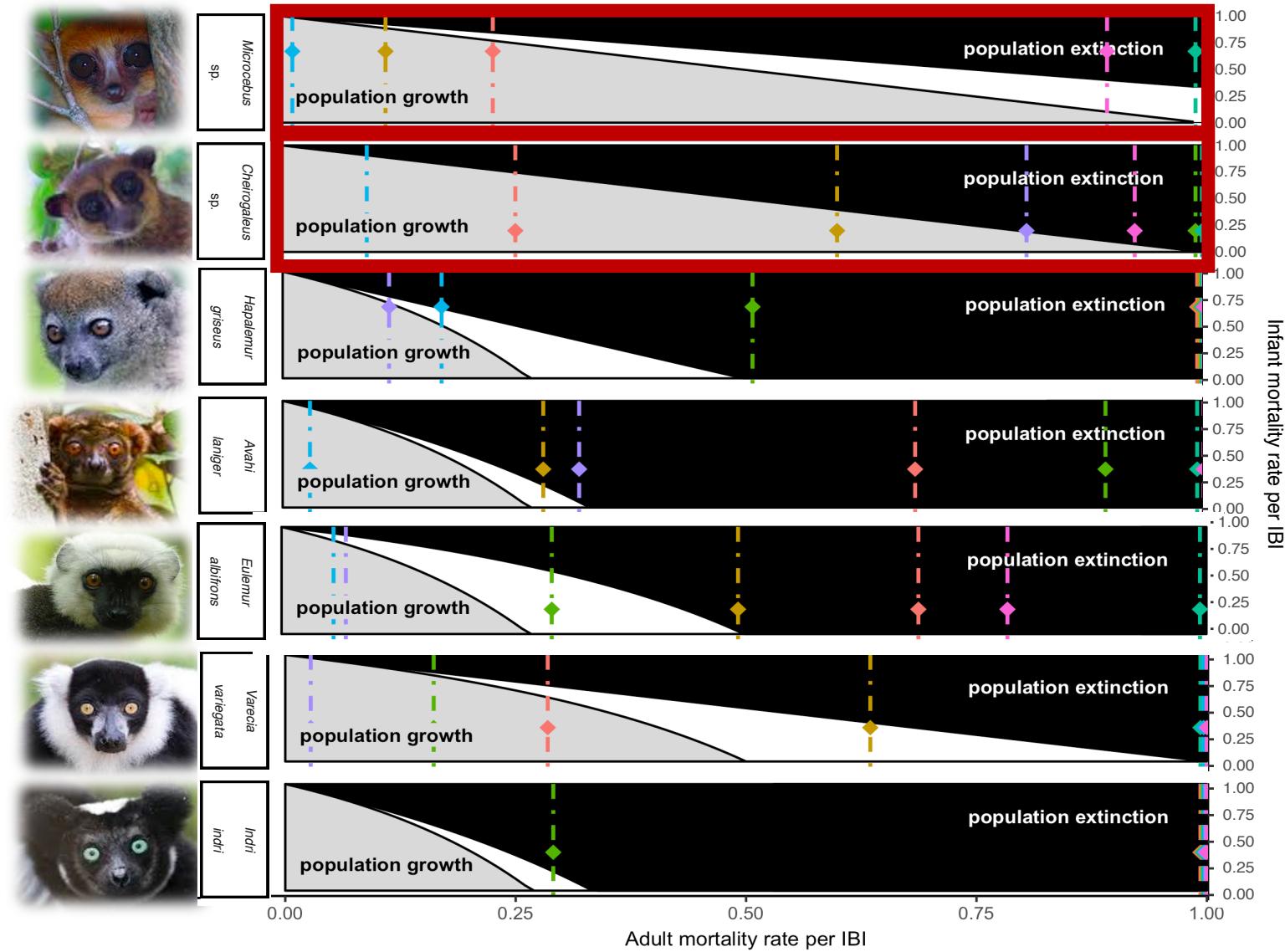
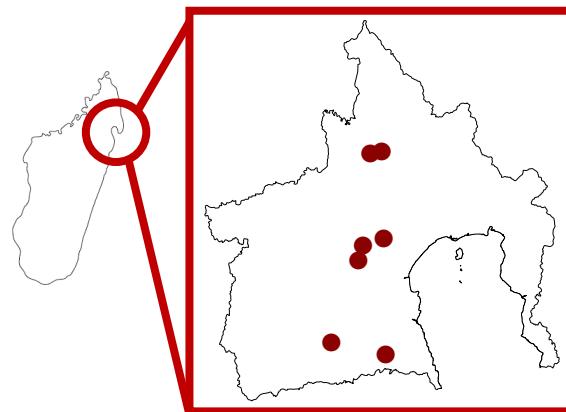
We paired household consumption data with **lemur densities** for 7 species at 7 sites to estimate hunt-based **mortality rates** and assess **harvest sustainability**.



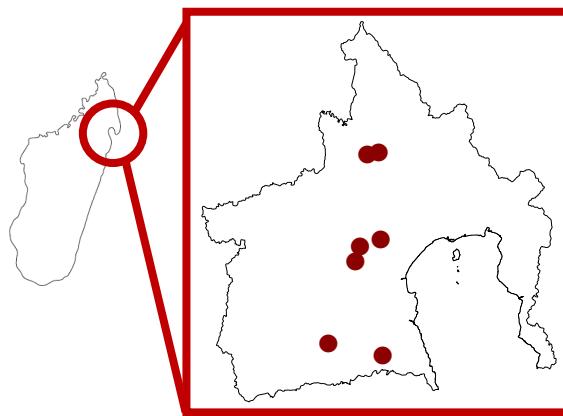
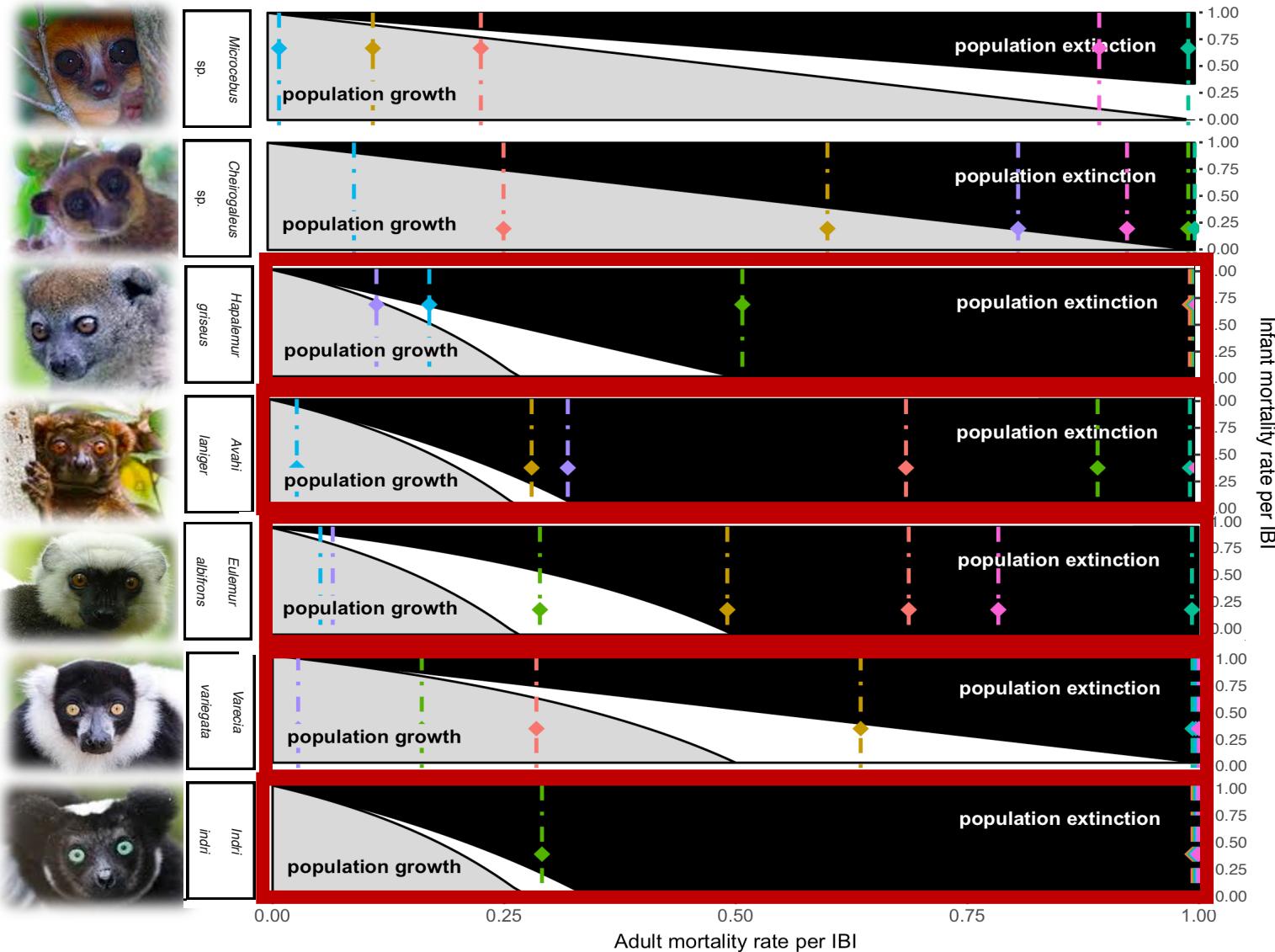
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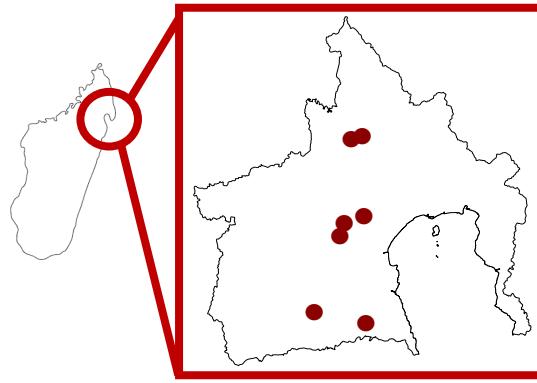
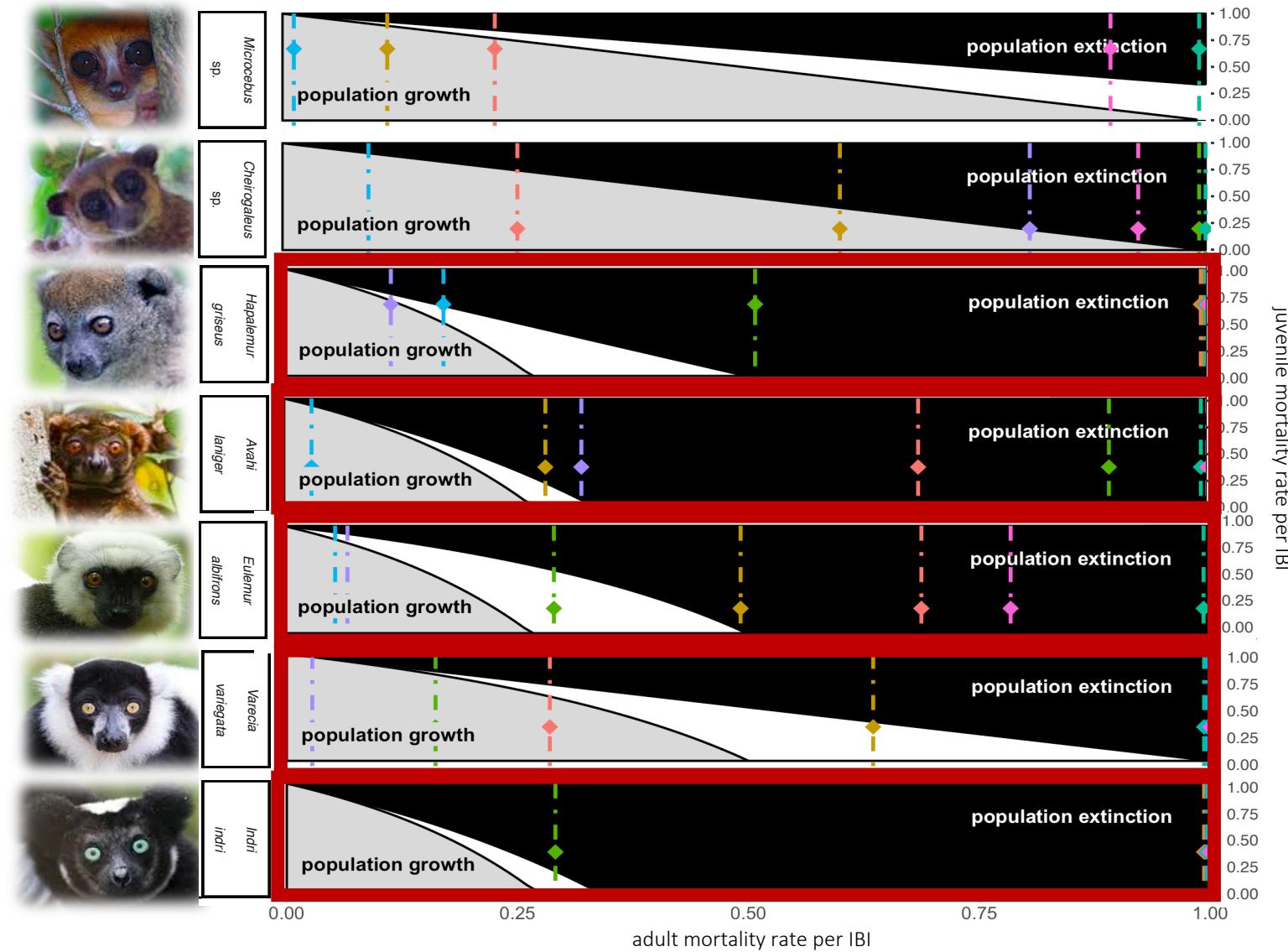
# Small-bodied lemurs are largely harvested at sustainable rates on the Makira-Masoala peninsula.



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



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



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

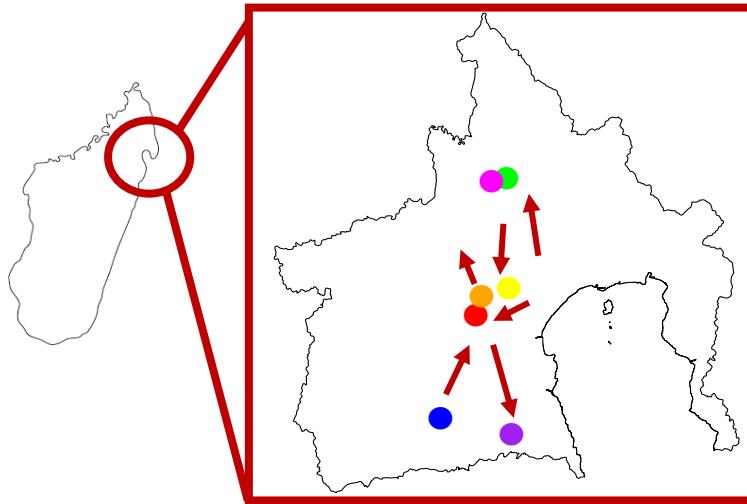
We will revisit this!

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

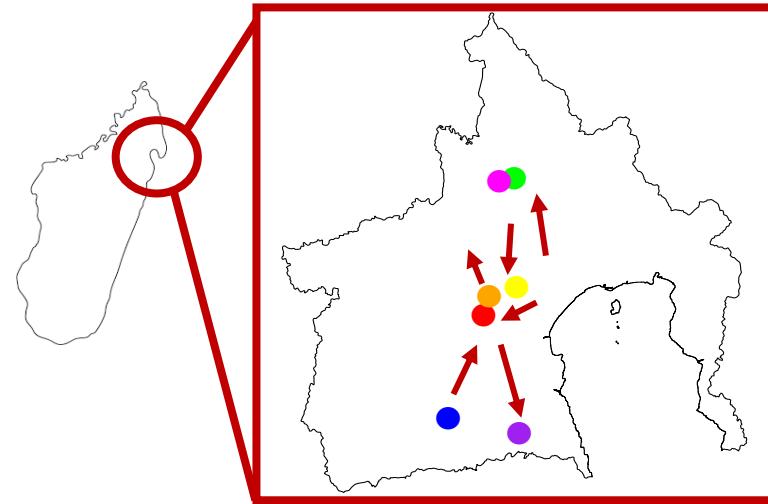
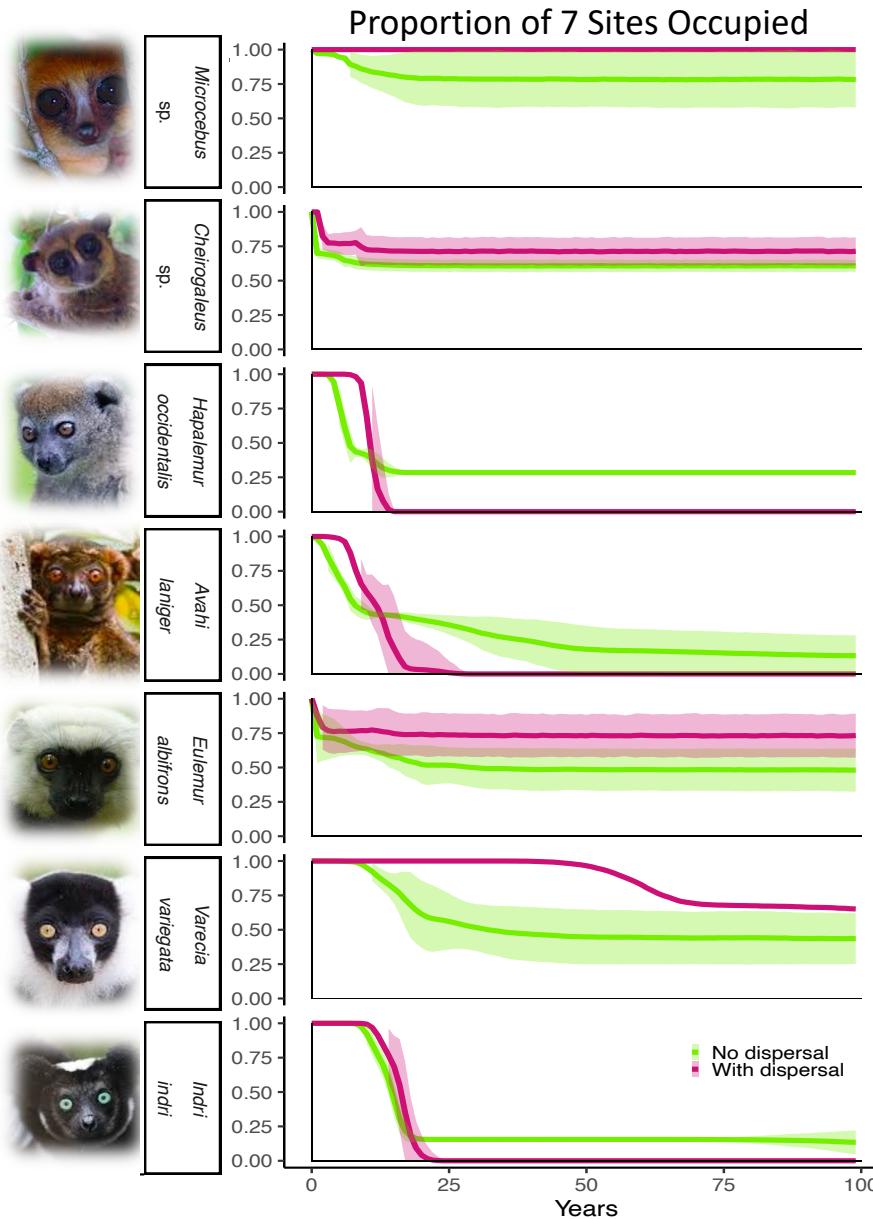


### Assumptions:

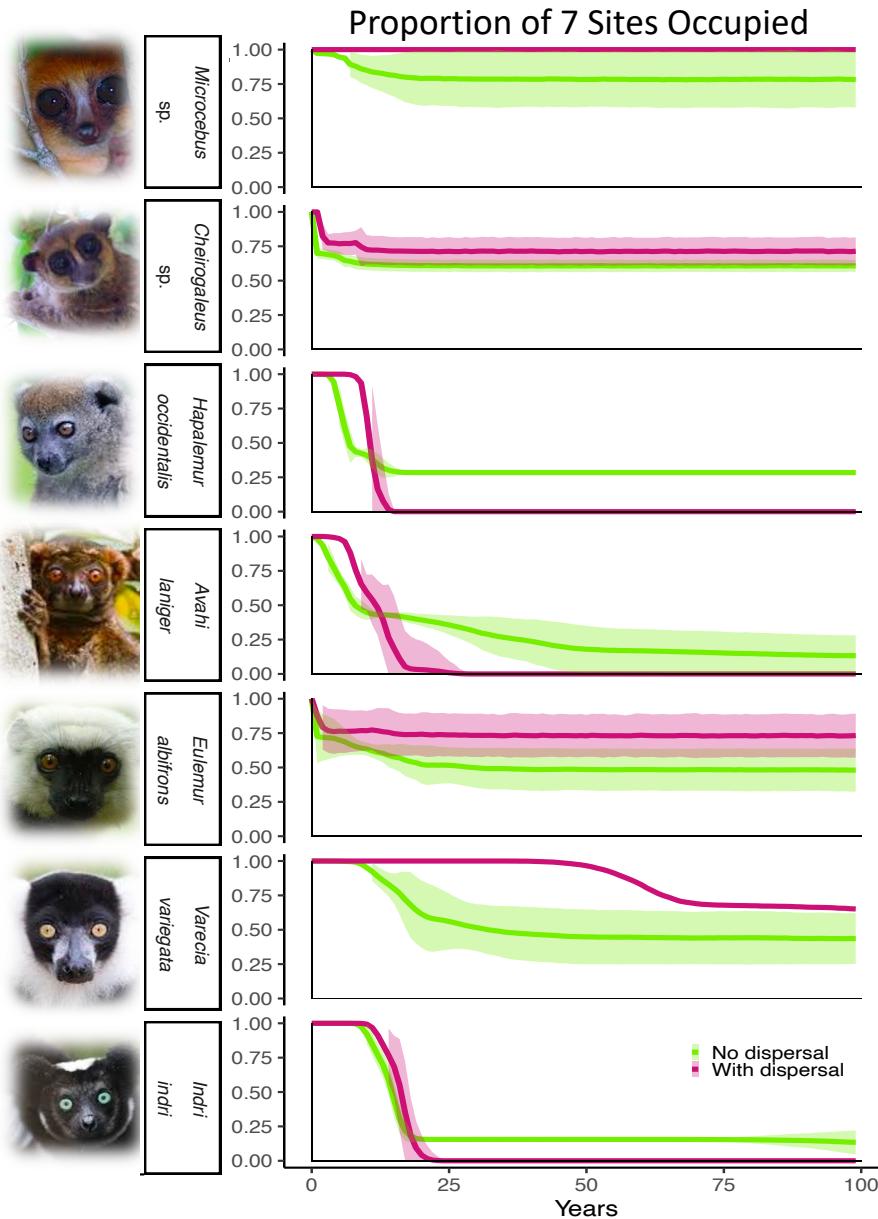
- Starting population of 200 lemurs per site
- Site-specific mortality rates derived from field studies
- Density dependent effects on fecundity
- Compared **no dispersal scenarios** vs. scenarios allowing for **stochastic dispersal** mediated by geographic distance



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

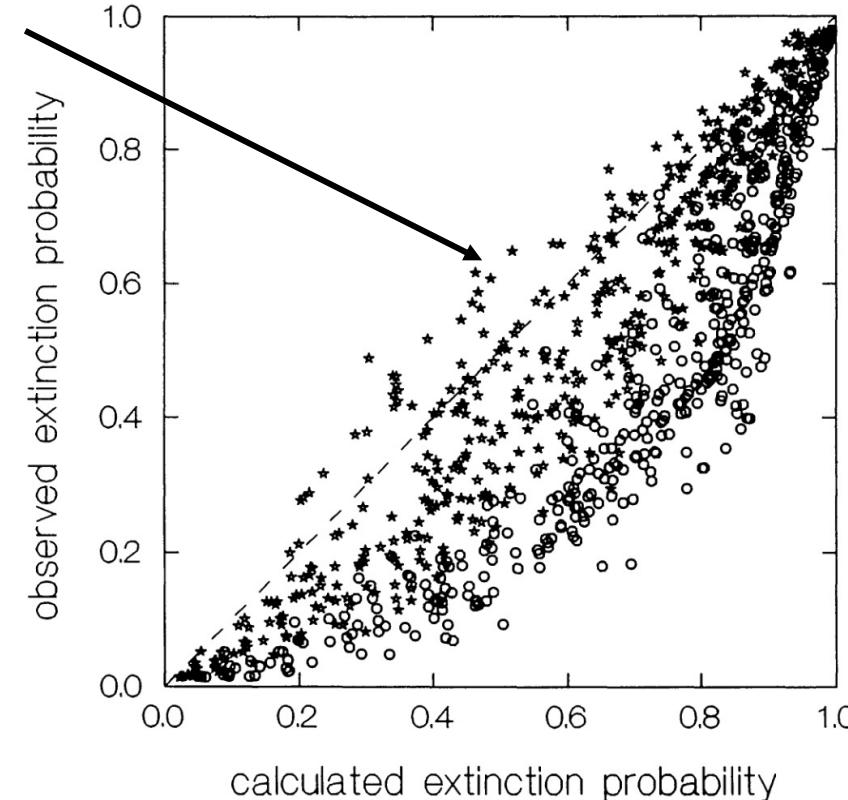


# Dispersal can drive regional extirpation if the majority of local sites function as population sinks.



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

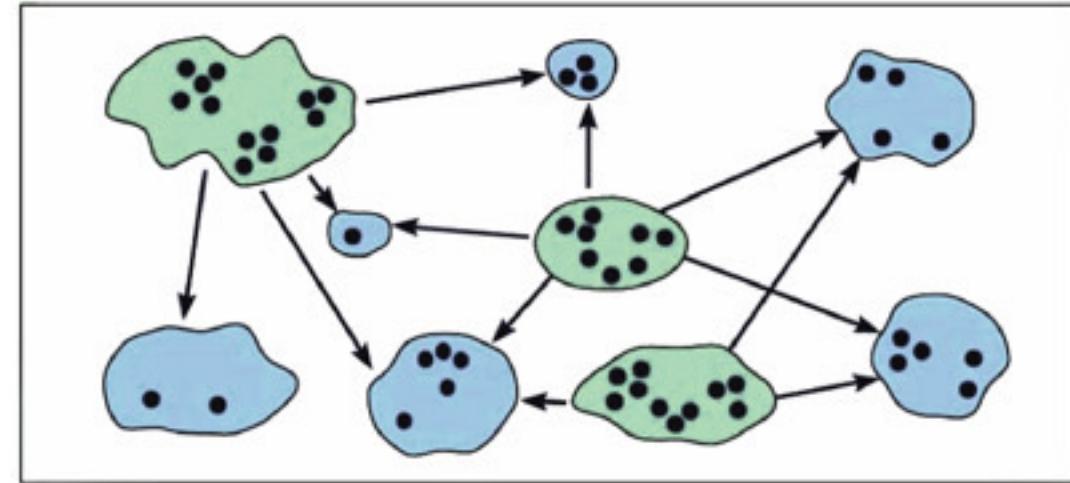
In contrast to the **rescue effect**  
observed in Hanski!



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

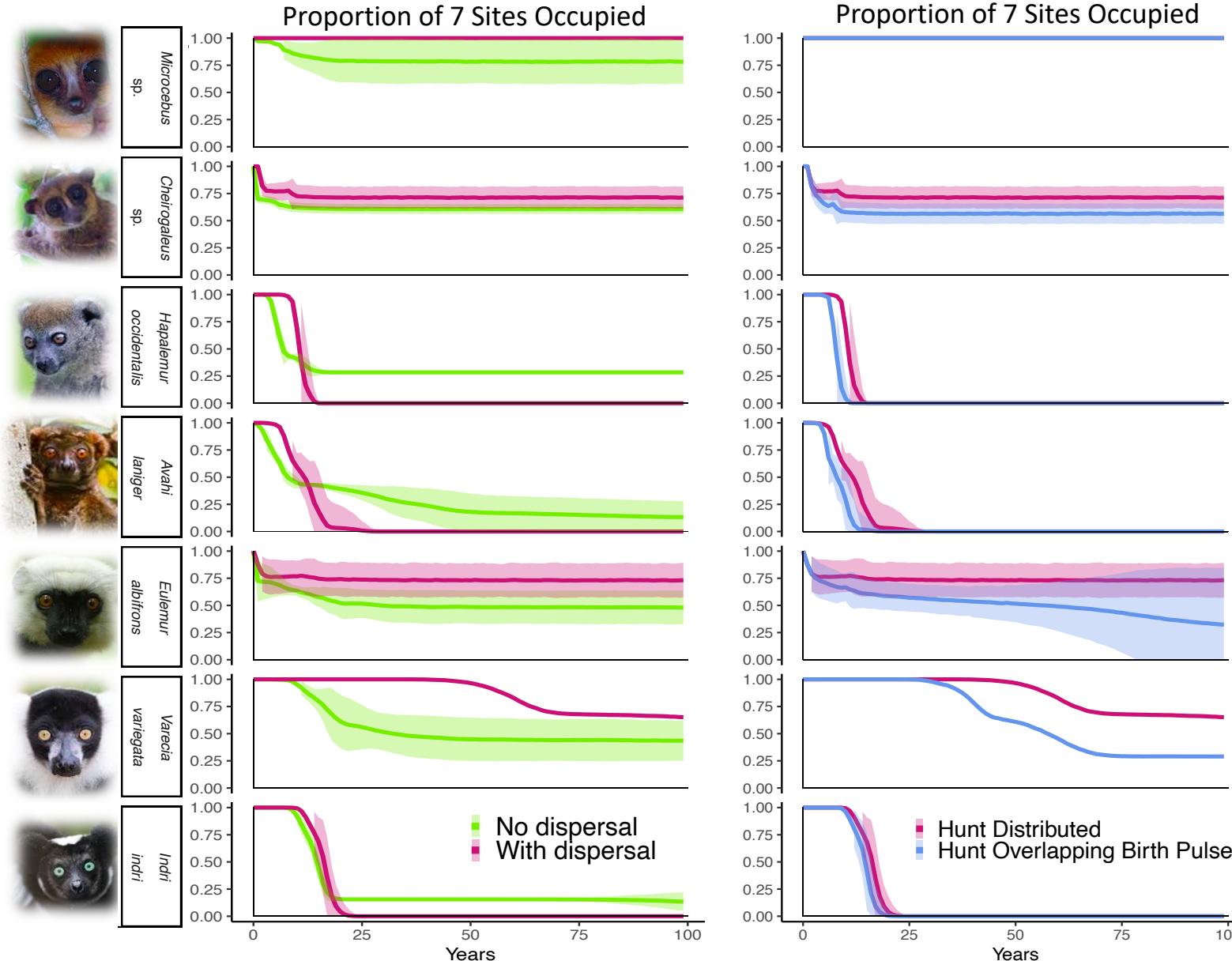
# Source-sink theory describes how variation in habitat may affect population dynamics.

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



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

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

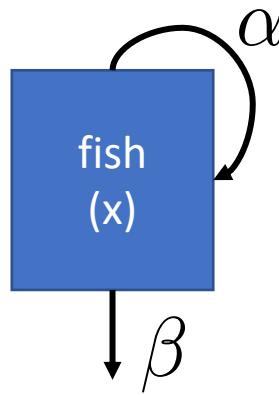


Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

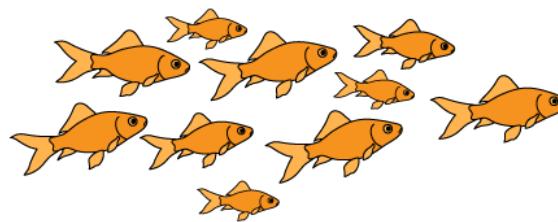
Simplest representations of MSY:

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

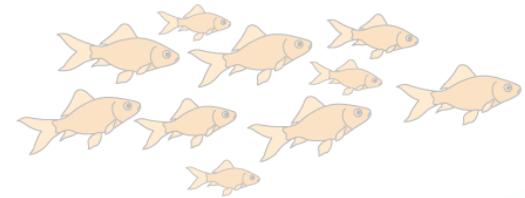
**Population** = multiple individuals of the same species (**conspecifics**) in the same habitat



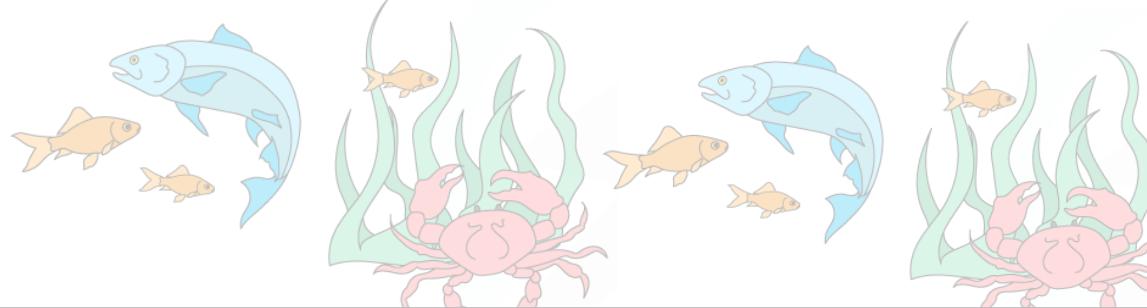
individual



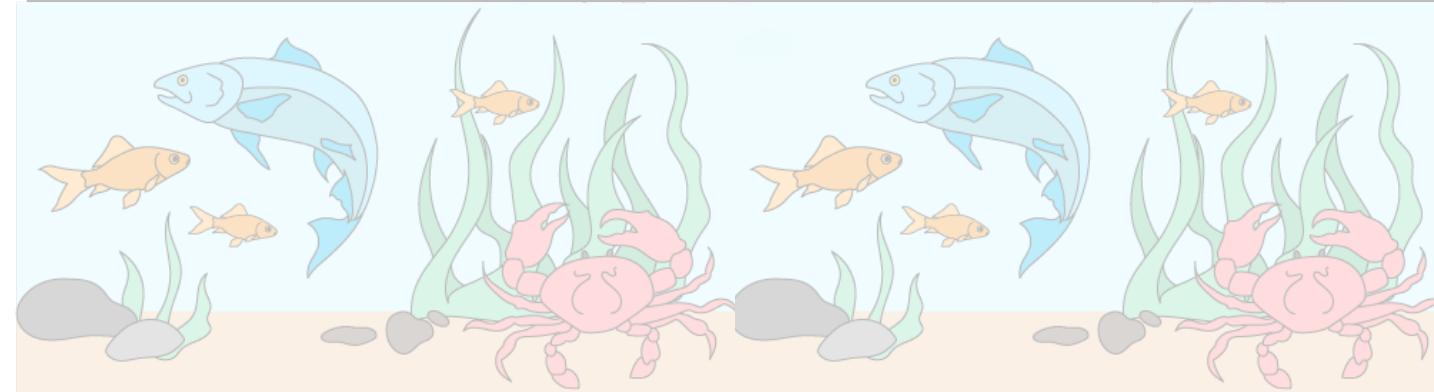
population



metapopulation



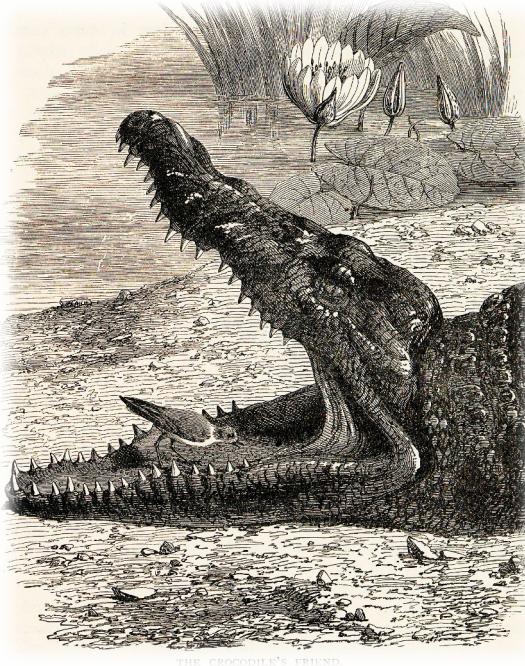
community



ecosystem

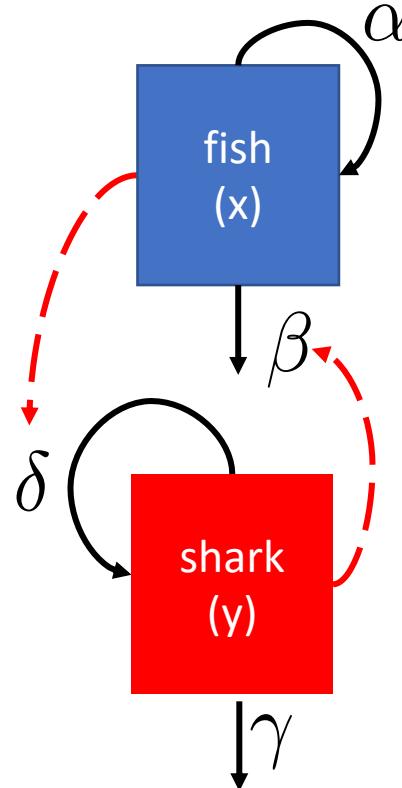
*How does the abundance of fish **change** through time?*

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

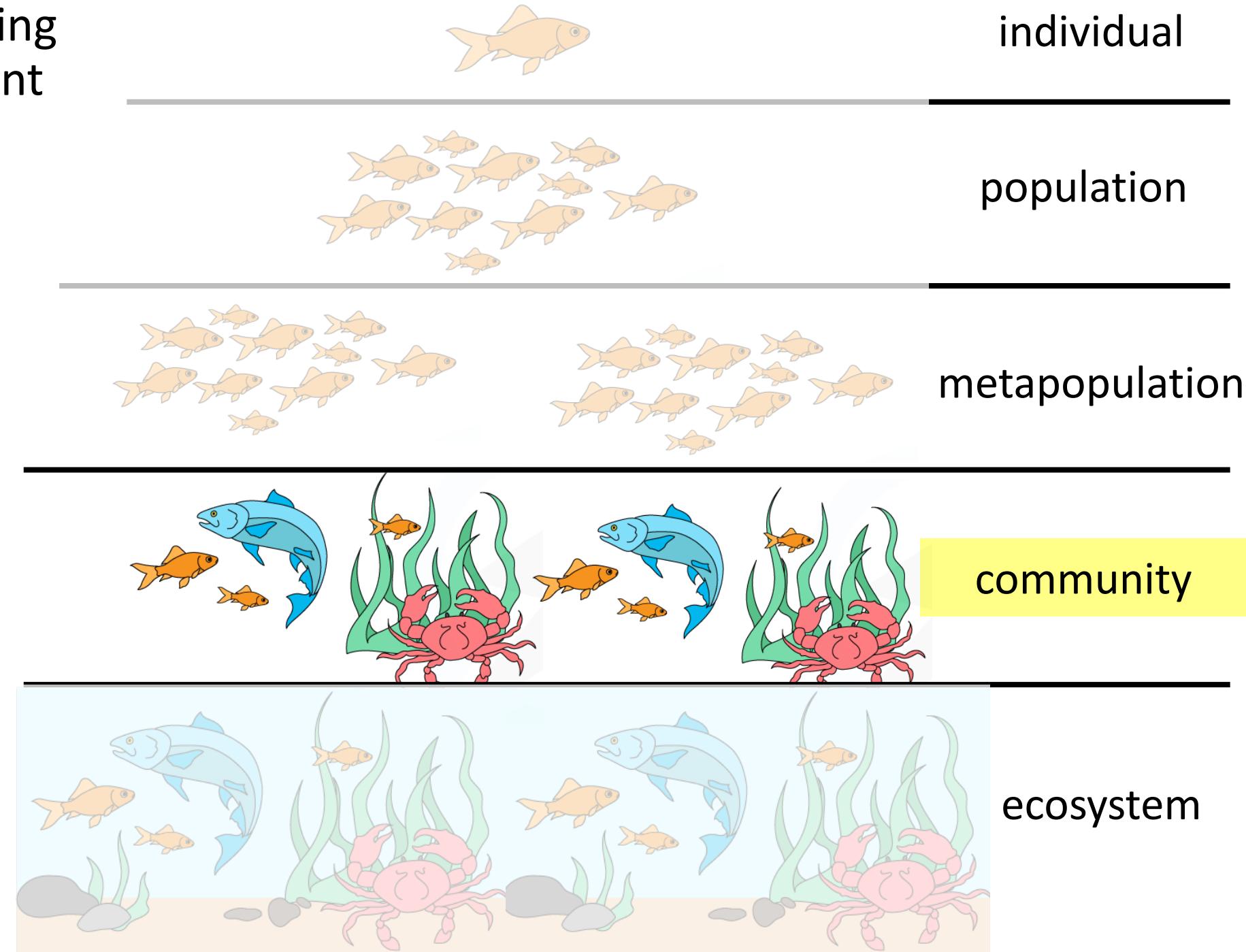


But ecology is the study of the **interactions** of organisms with each other and their environment, and in some cases, **interspecific interactions** are essential to understanding ecological systems.

**Community** = interacting populations of different species



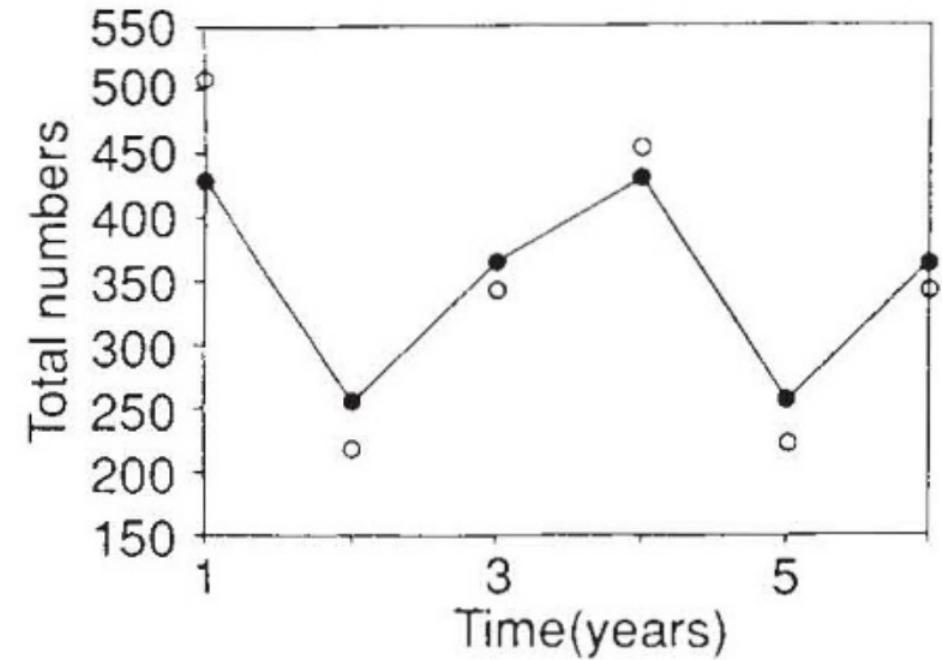
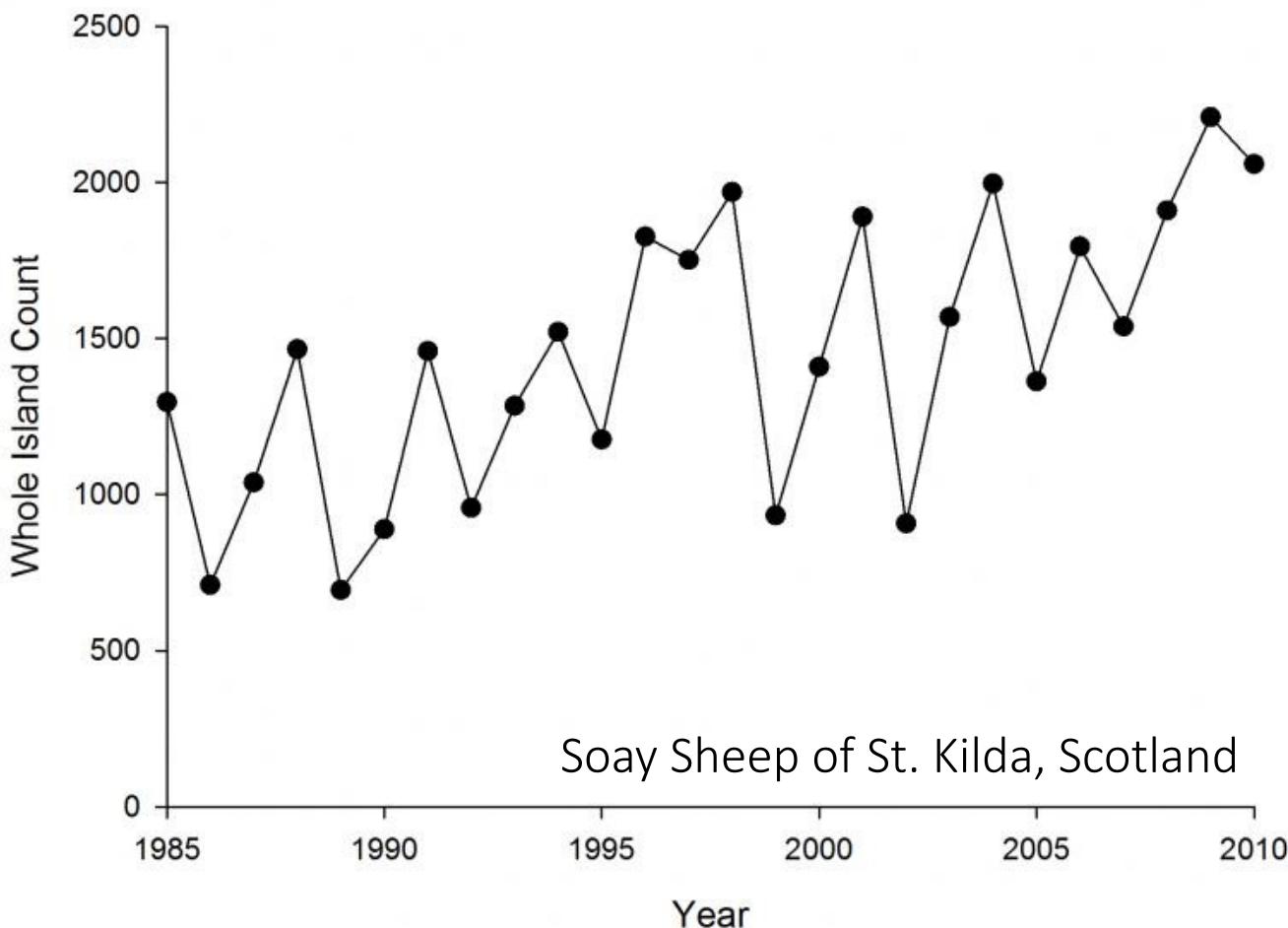
How does fish abundance **vary** with changes in shark abundance?



# Remember those Soay sheep...



The first model fit the data incorporating the effects of **intraspecific competition** (density dependent, logistic growth).



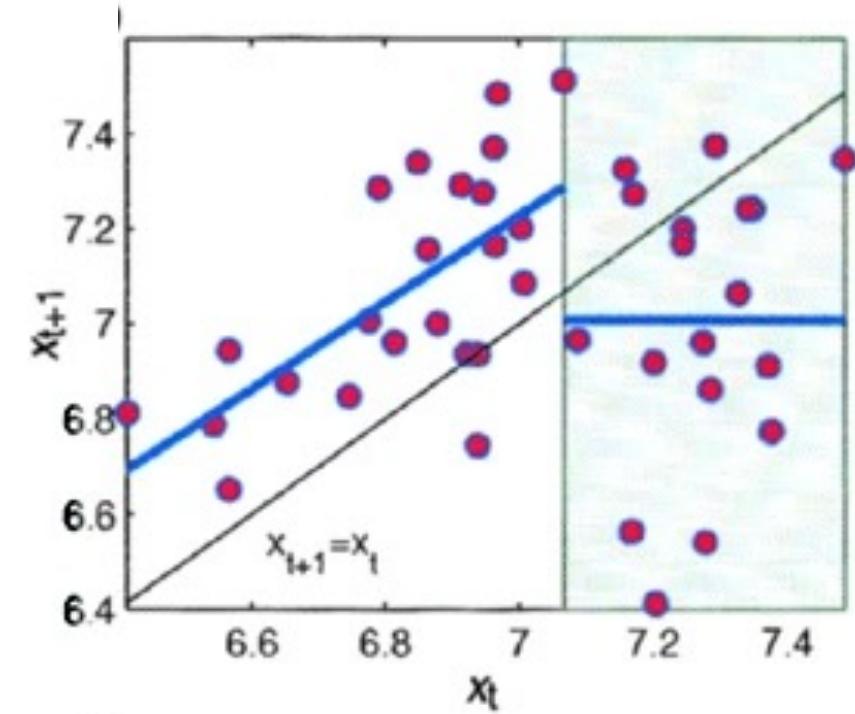
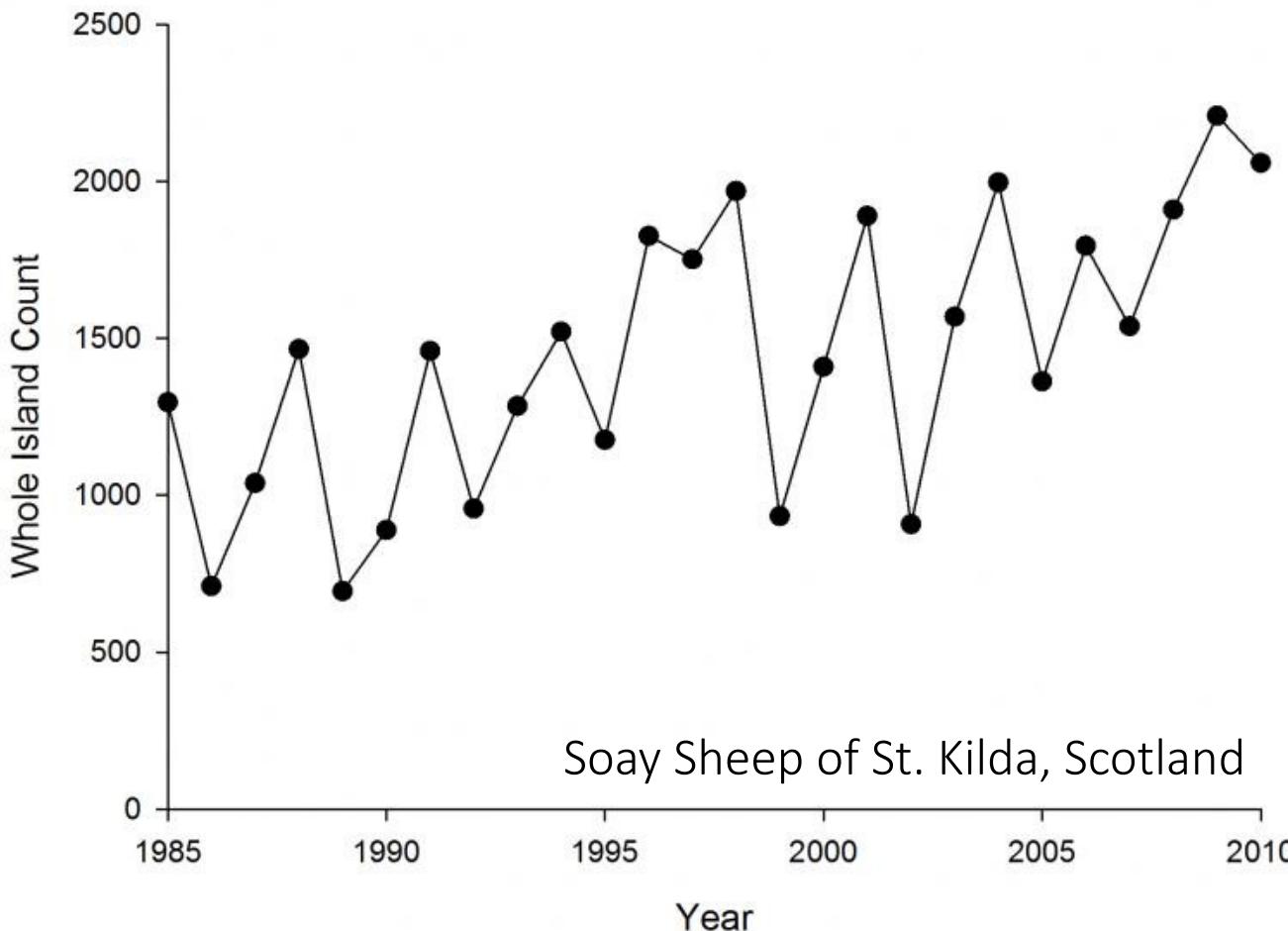
## Overcompensation and population cycles in an ungulate

B. T. Grenfell, O. F. Price, S. D. Albon & T. H. Glutton-Brock

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

589 Accesses | 107 Citations | [Metrics](#)

In the second model, 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

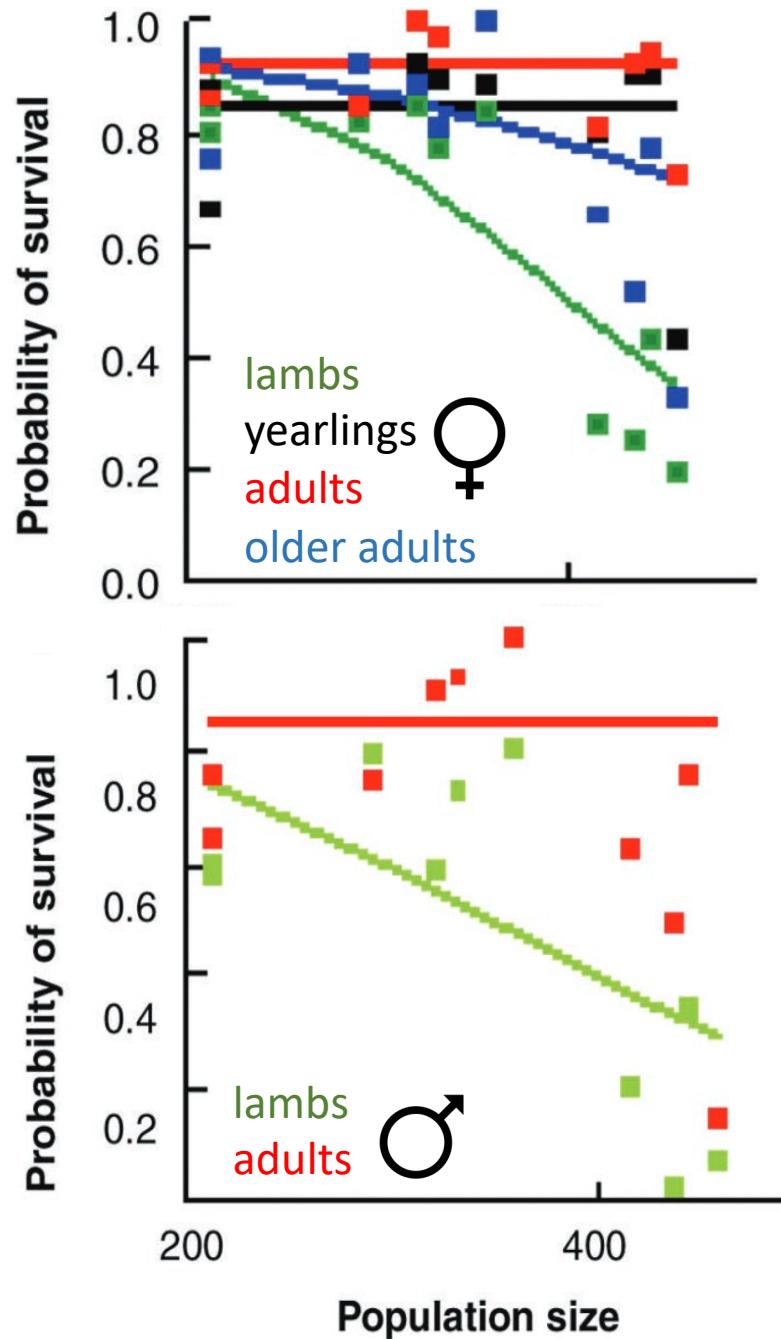
1746 Accesses | 414 Citations | 4 Altmetric | Metrics

Later still, they added **population structure** (age, sex) to do an *even better job* of recovering the data...

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

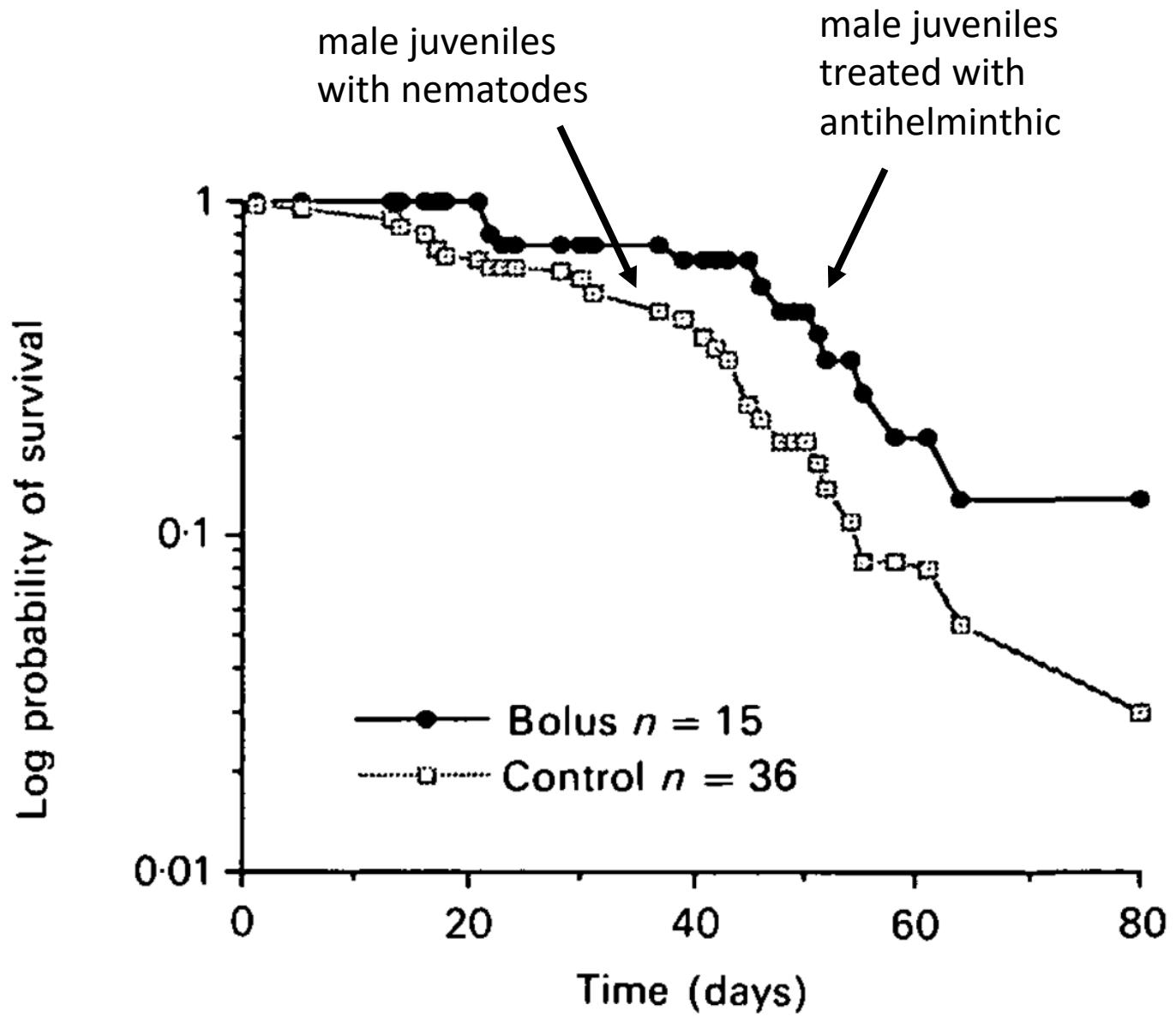
T. Coulson,<sup>1\*</sup>† E. A. Catchpole,<sup>2</sup> S. D. Albon,<sup>3</sup> B. J. T. Morgan,<sup>4</sup> J. M. Pemberton,<sup>5</sup> T. H. Clutton-Brock,<sup>6</sup> M. J. Crawley,<sup>6</sup> B. T. Grenfell<sup>7</sup>

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



But this team has known  
for some time that  
**interspecies interactions**  
impact Soay sheep survival  
in crash years as well!

The team is actively  
working on a model that  
incorporates **nematode-**  
**sheep (parasite-host)**  
**interactions** to explain  
longterm sheep  
population dynamics.



# Species can interact in several distinct ways

- **Mutualism** – both species benefit
- **Commensalism** – one species benefits, the other is unaffected
- **Predation** – one species benefits, the other is harmed (eaten!)
- **Competition** – two species compete for the same limiting resource, both harmed by the interaction
  - Direct = wolves and coyote at a moose carcass
  - Indirect = diurnal cheetah, nocturnal leopard at a giraffe carcass
- **Parasitism** – one species (the parasite) lives *in* or *on* the other species (the host)

“It is interesting to contemplate a tangled bank, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have **all been produced by laws acting around us.**”

- *On the Origin of Species* (1859) by Charles Darwin



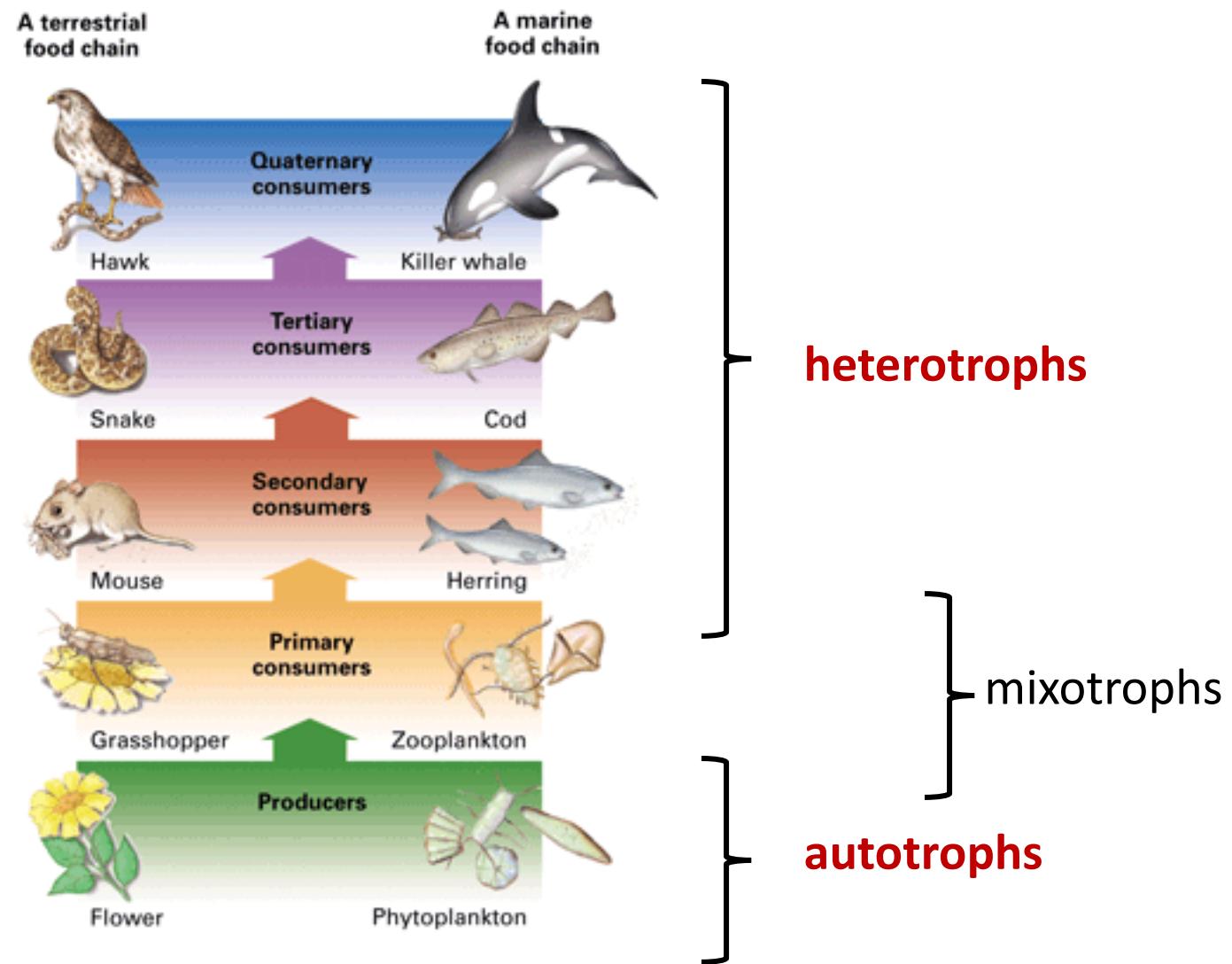
**“Ecology** has a synonym which is **ALL.**”

-John Steinbeck

*The Log from the Sea of Cortez* (1941)

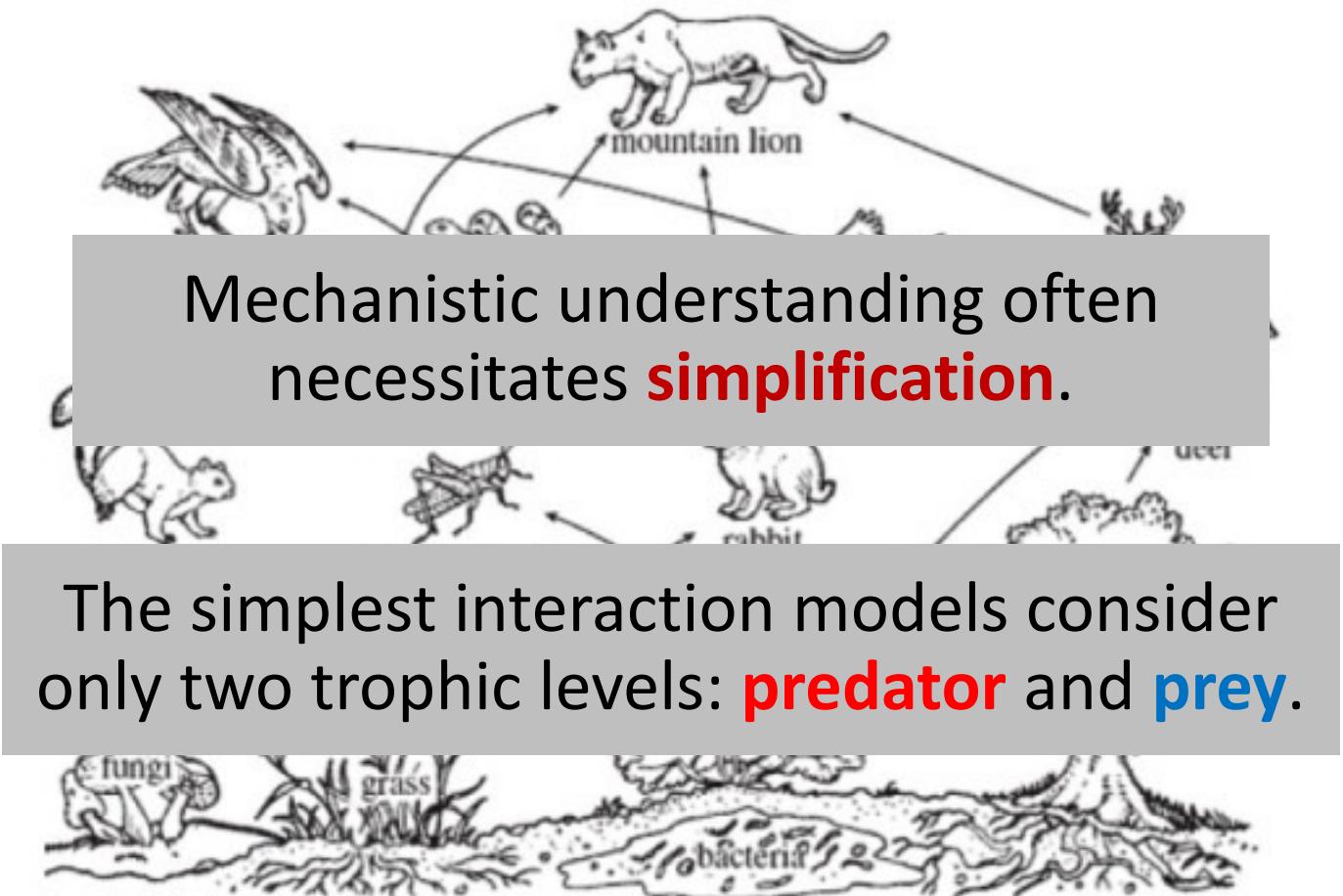
# Ecological communities can be organized by **trophic level**

- **Trophic levels** refer to hierachal levels of organization in an ecosystem, comprised of organisms that share the same function in the **food chain** and the same nutritional relationship to the primary sources of energy.
- **Food chains** are organized with arrows pointing in the direction of energy flow.

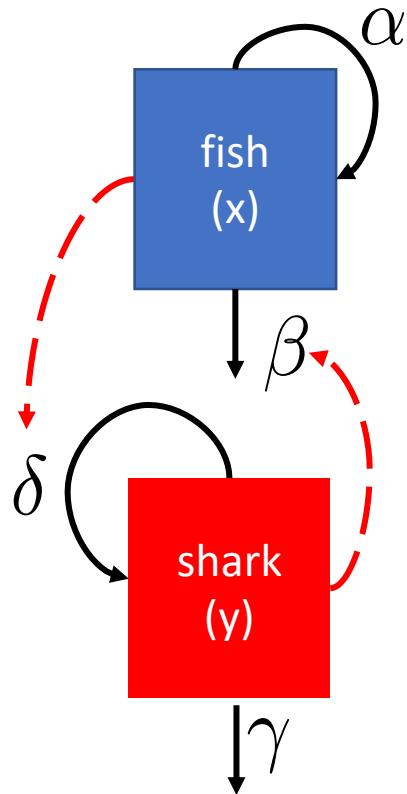


**Food webs** more accurately represent the complexity of ecological interactions that span multiple **trophic levels**

“It is interesting to contemplate a **tangled bank**, clothed with many plants of many kinds, with birds singing on the bushes, with various insects flitting about, and with worms crawling through the damp earth, and to reflect that these elaborately constructed forms, so different from each other, and dependent upon each other in so complex a manner, have **all been produced by laws acting around us.**”



# The Lotka-Volterra predator-prey model

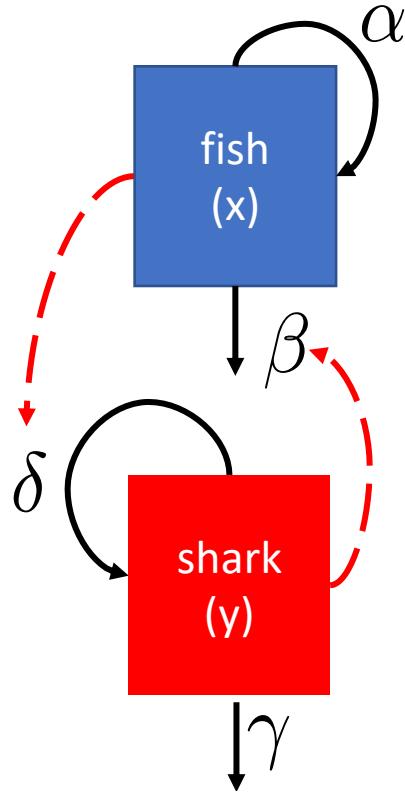


*How does **fish** abundance **vary** with changes in **shark** abundance?*

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$

- 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 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?*

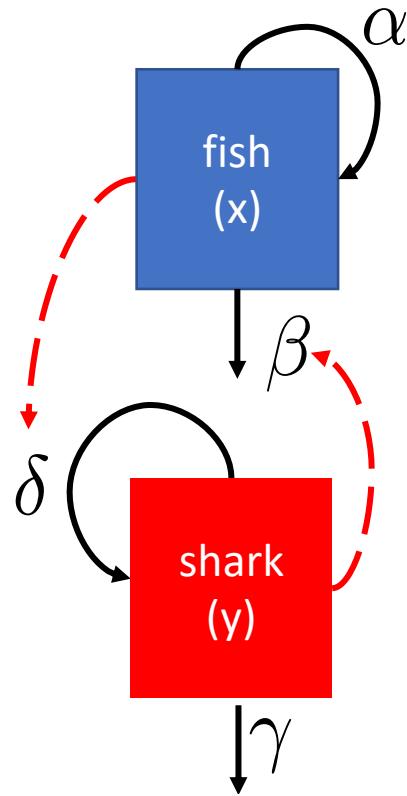
growth rate of prey,  
independent of predator

$$\frac{dx}{dt} = \alpha x - \beta xy \quad \left. \begin{array}{l} \text{death rate of prey,} \\ \text{depends on} \\ \text{abundance of} \\ \text{predator} \end{array} \right\}$$

$$\frac{dy}{dt} = \delta xy - \gamma y \quad \left. \begin{array}{l} \text{death rate of} \\ \text{predator,} \\ \text{independent of} \\ \text{prey} \end{array} \right\}$$

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

# The Lotka-Volterra predator-prey model



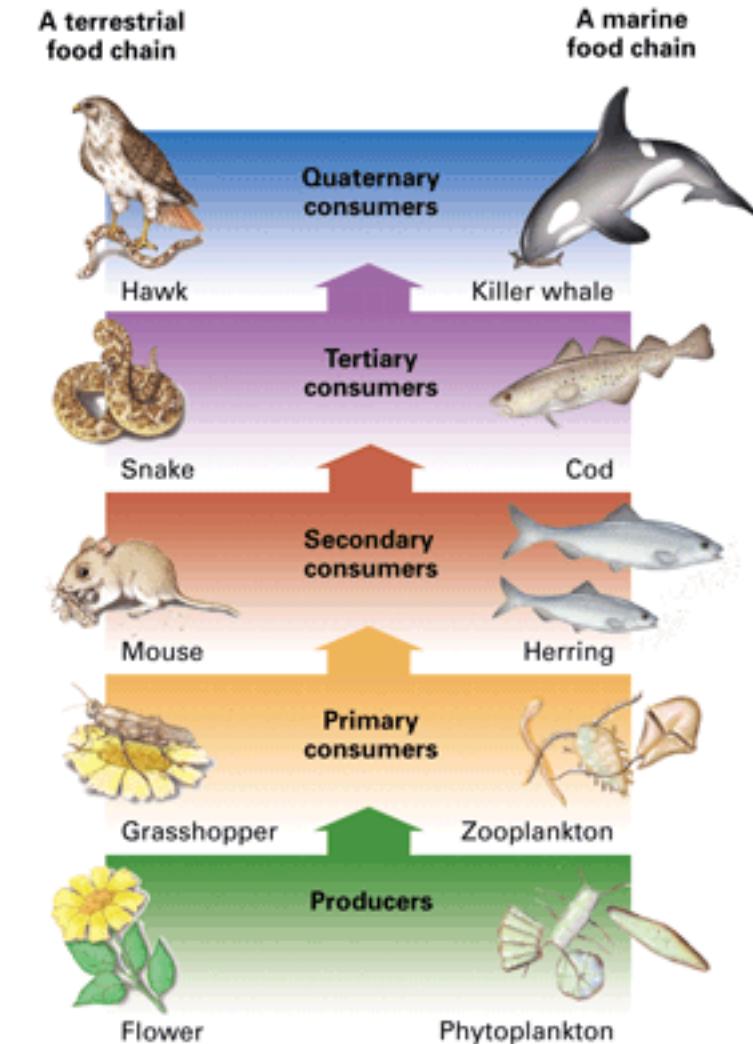
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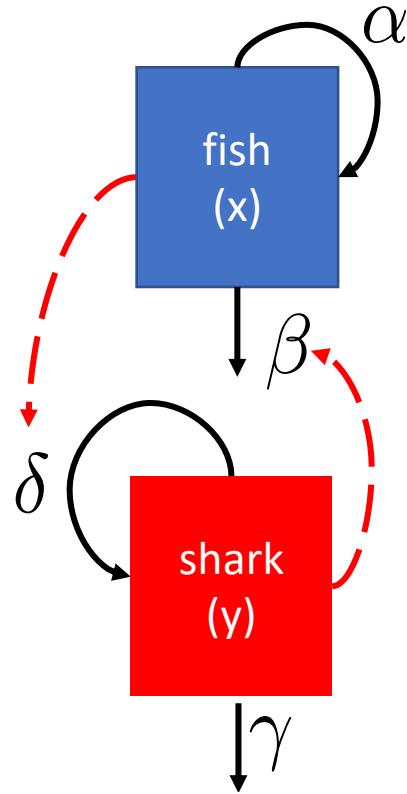
$$\frac{dy}{dt} = \delta xy - \gamma y$$

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

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



# The Lotka-Volterra predator-prey model



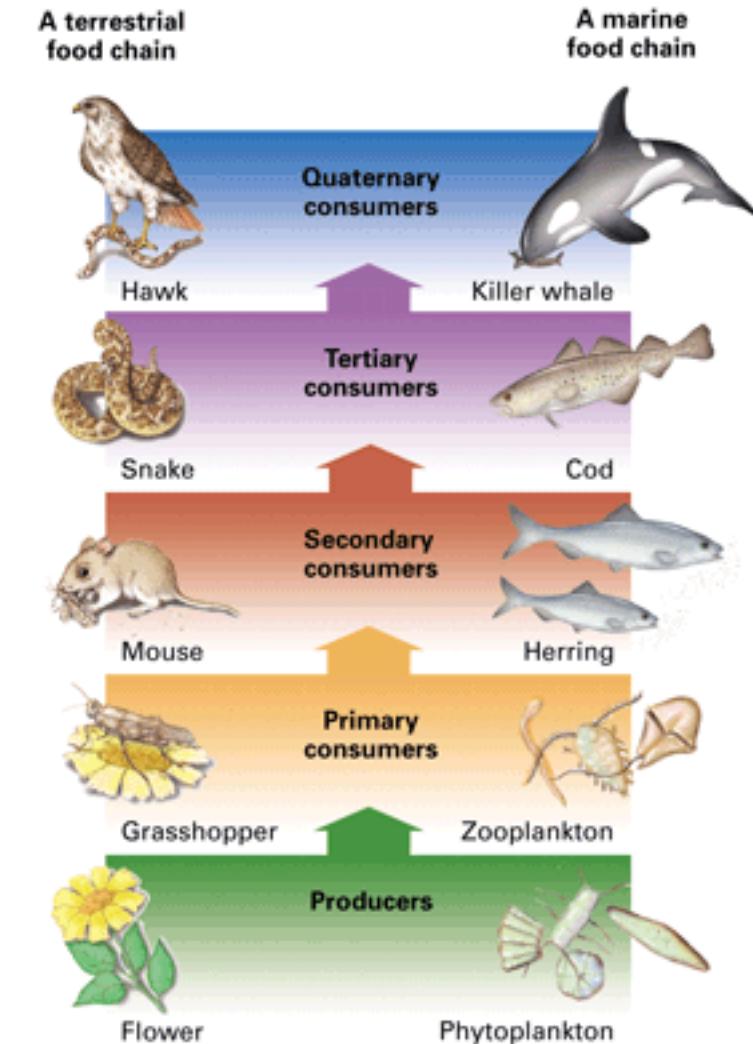
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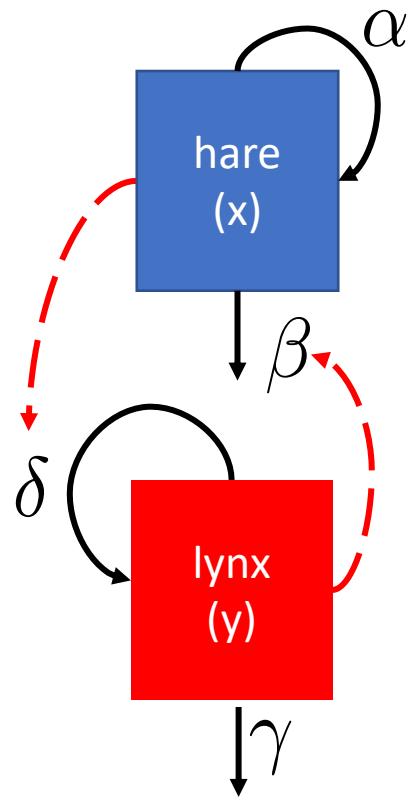
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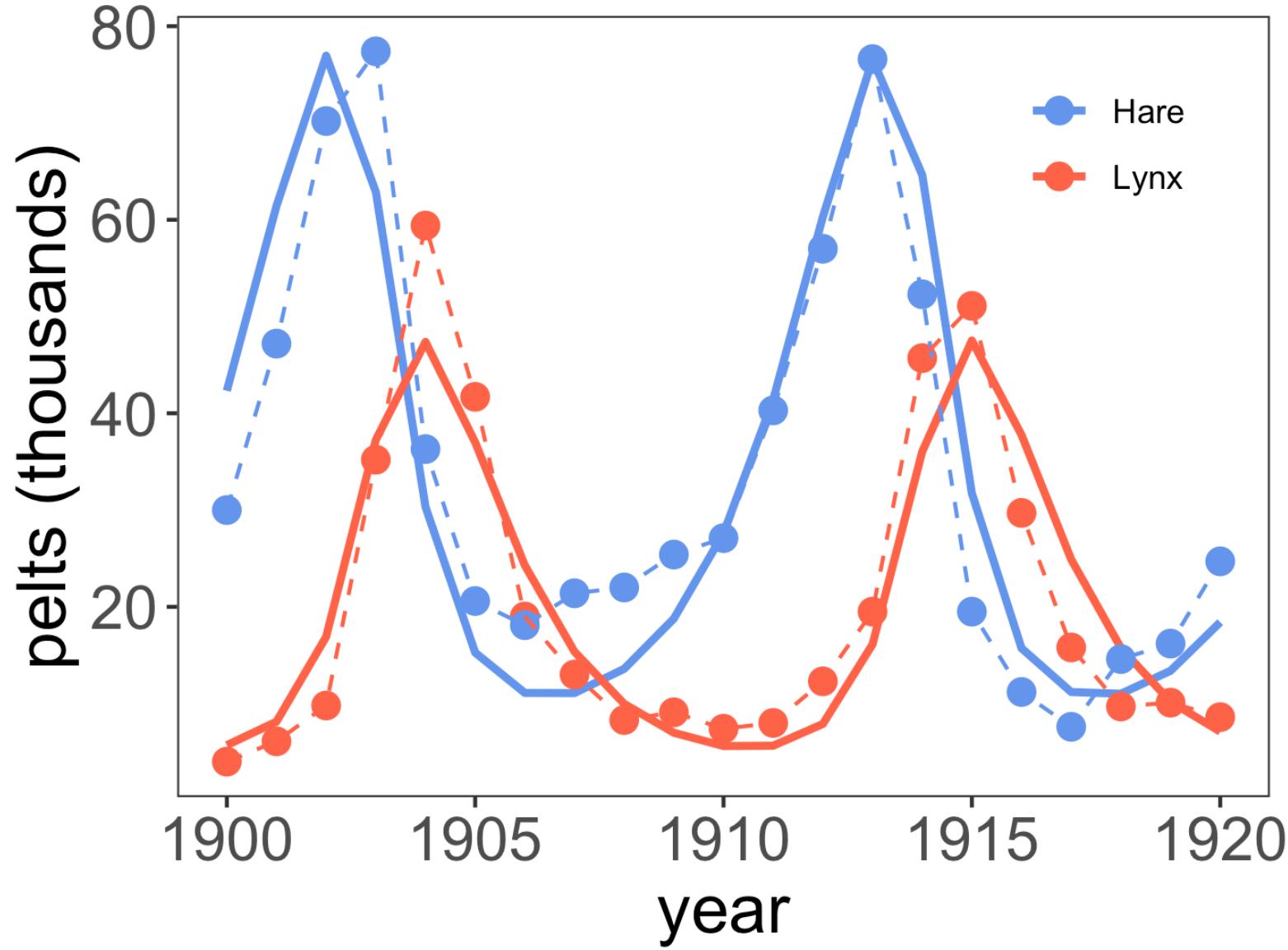
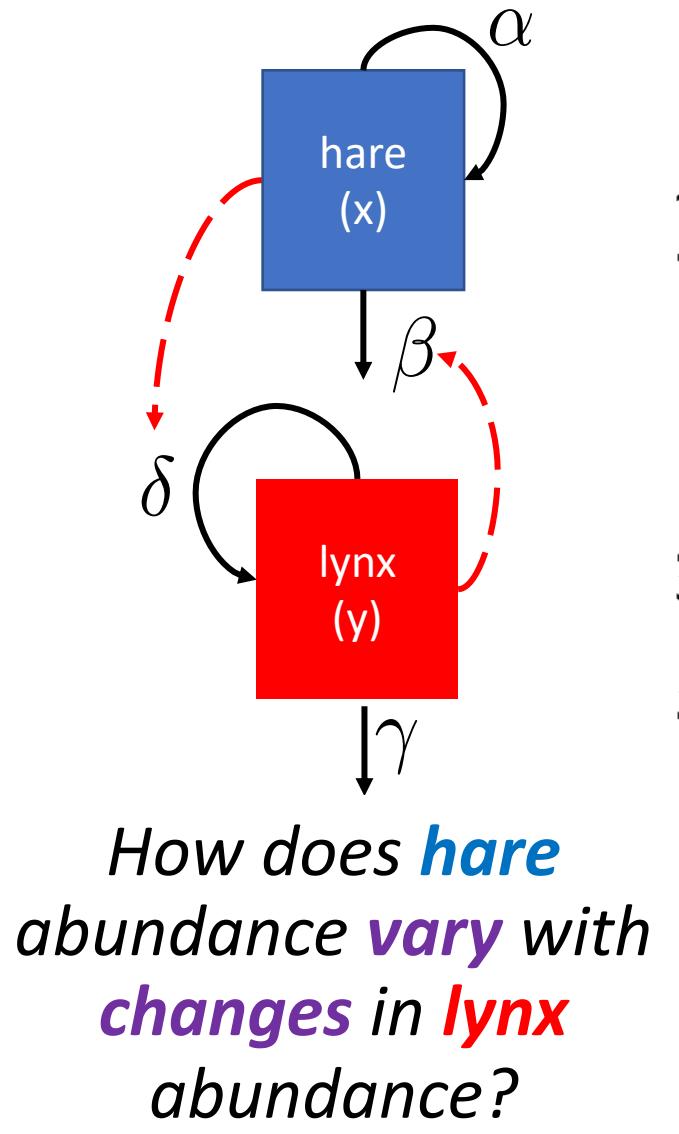
# Lotka-Volterra predator-prey models with data



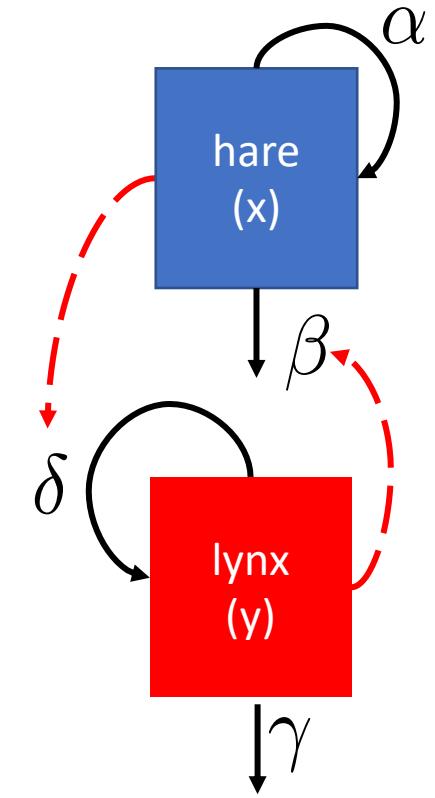
How does **hare** abundance **vary** with changes in **lynx** abundance?



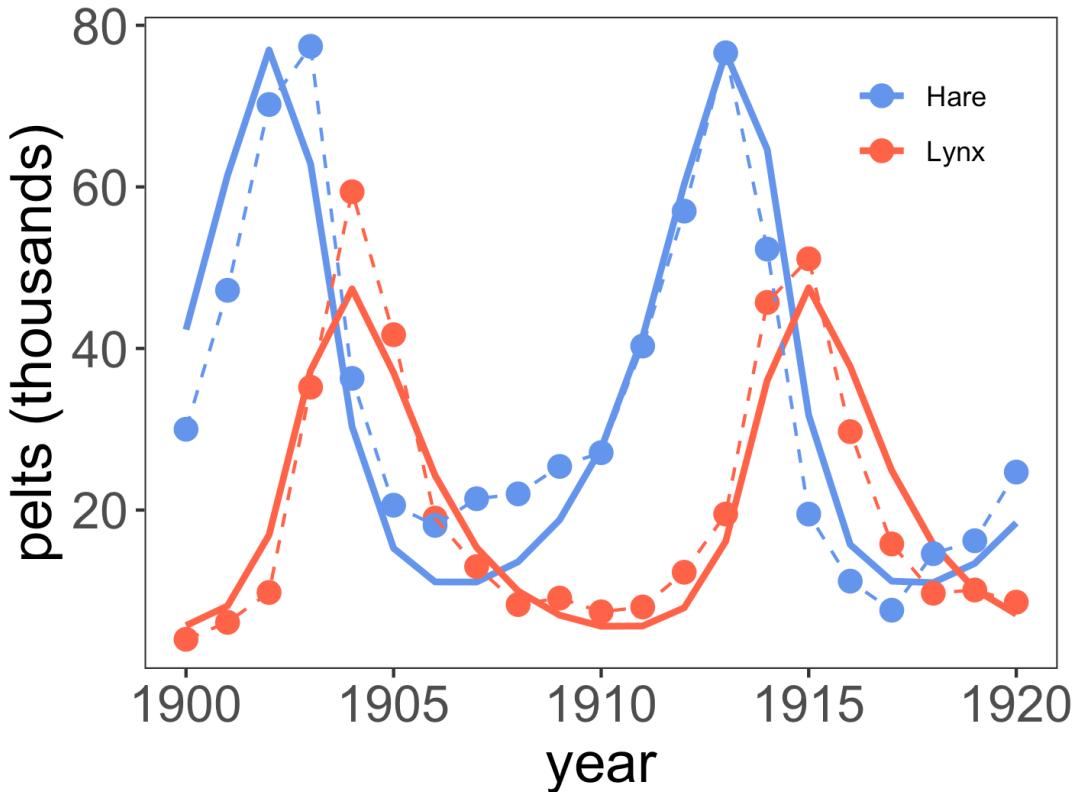
# Lotka-Volterra predator-prey models with data



# Lotka-Volterra predator-prey models with data



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



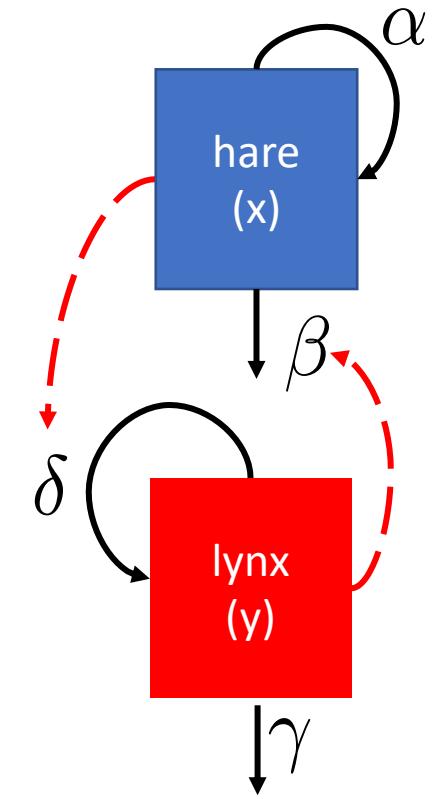
- Fitting a model to data allows us to estimate parameters – remember those growth rates from the human population models!
- Here, we can explore the growth rate of the prey under exponential growth ( $\alpha$ ), the efficiency of kill ( $\beta$ ) and digestion ( $\delta$ ) by the predator, and the natural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

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

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

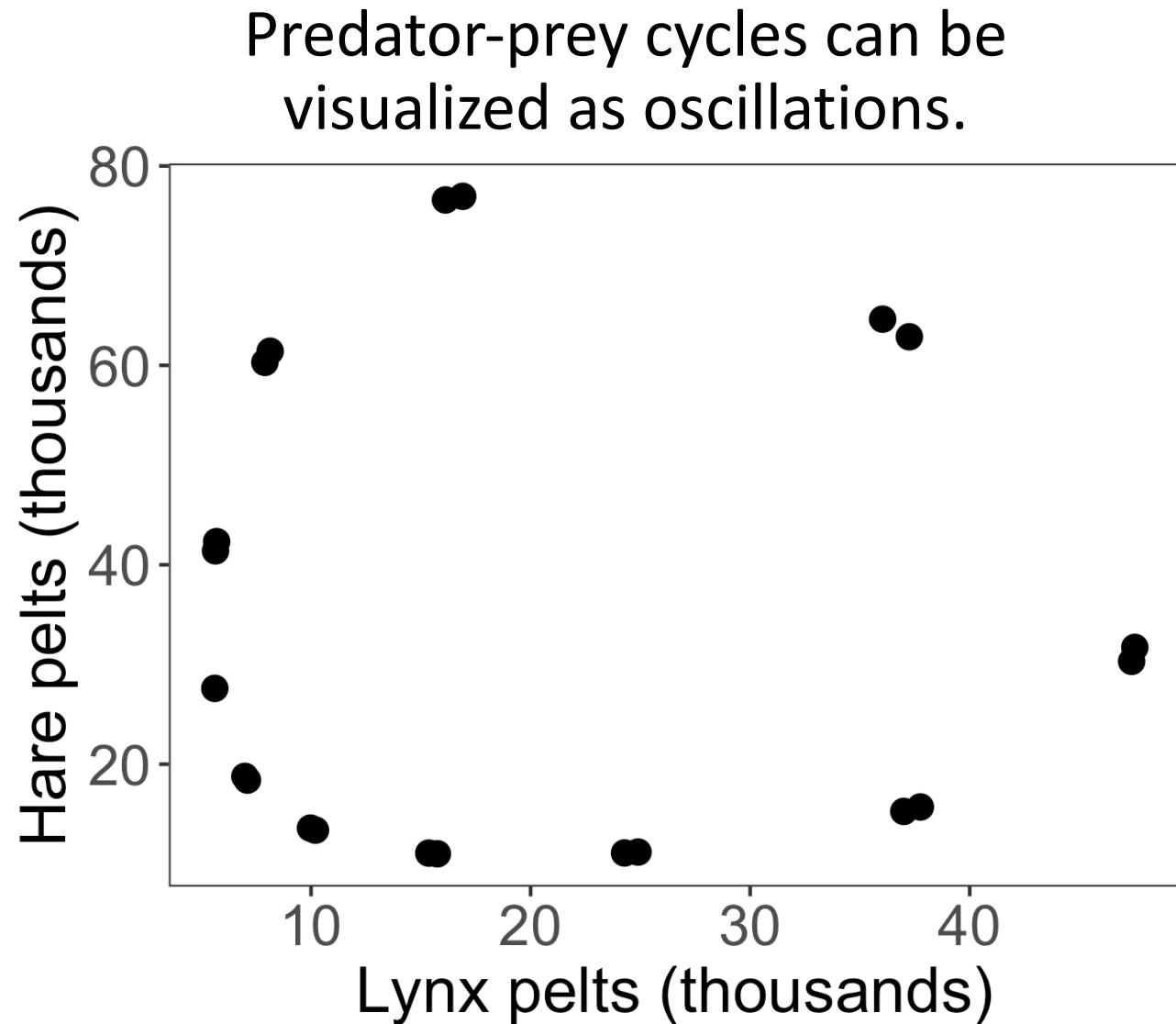
$$\frac{dy}{dt} = \delta xy - \gamma y$$

## Lotka-Volterra predator-prey models with data

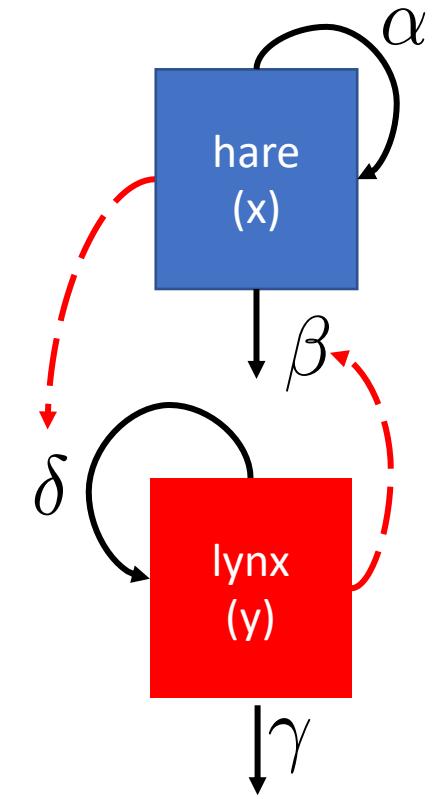


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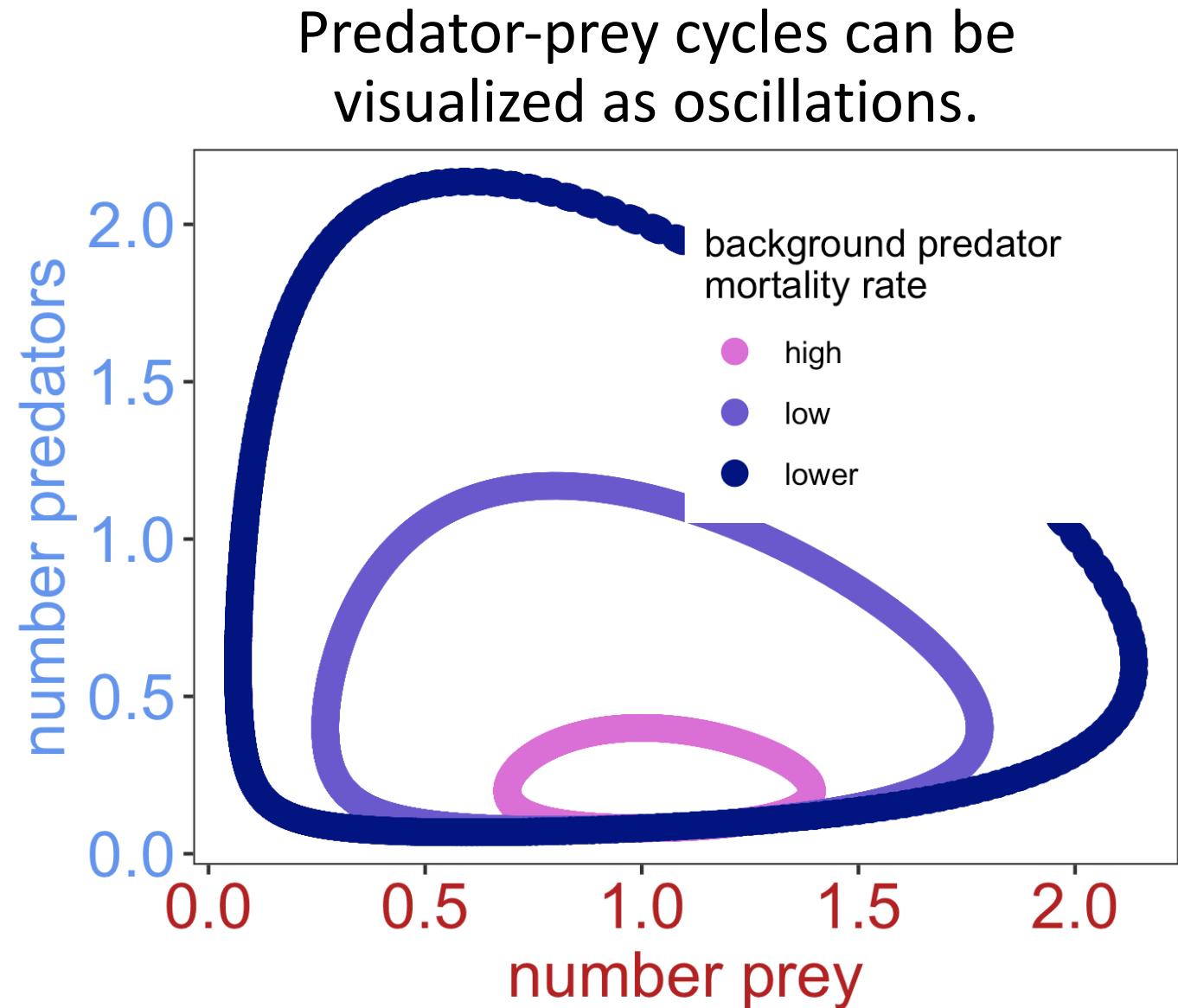


# Lotka-Volterra predator-prey models with data

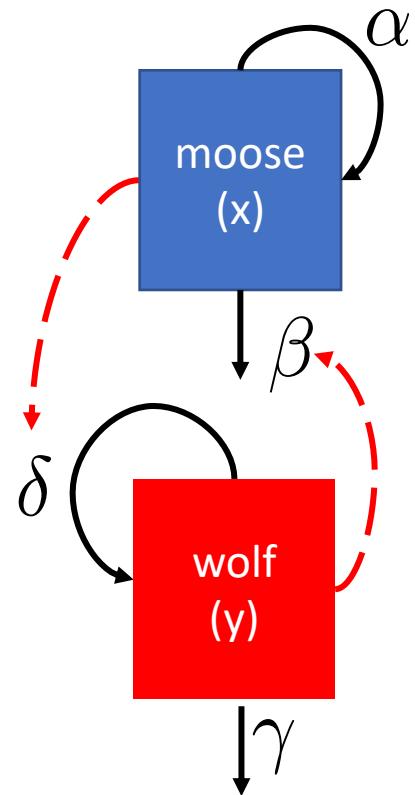


How does **hare** abundance **vary** with changes in **lynx** abundance?

$$\frac{dx}{dt} = \alpha x - \beta xy$$
$$\frac{dy}{dt} = \delta xy - \gamma y$$



# Another famous example: Wolf-Moose on Isle Royale

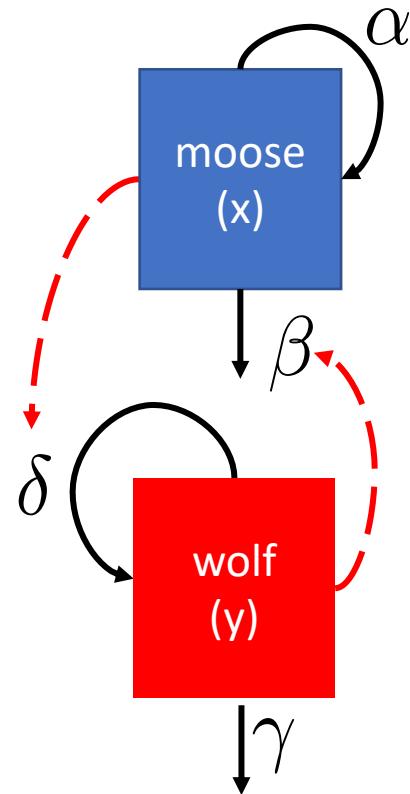


How does **moose** abundance **vary** with **changes** in **wolf** abundance?

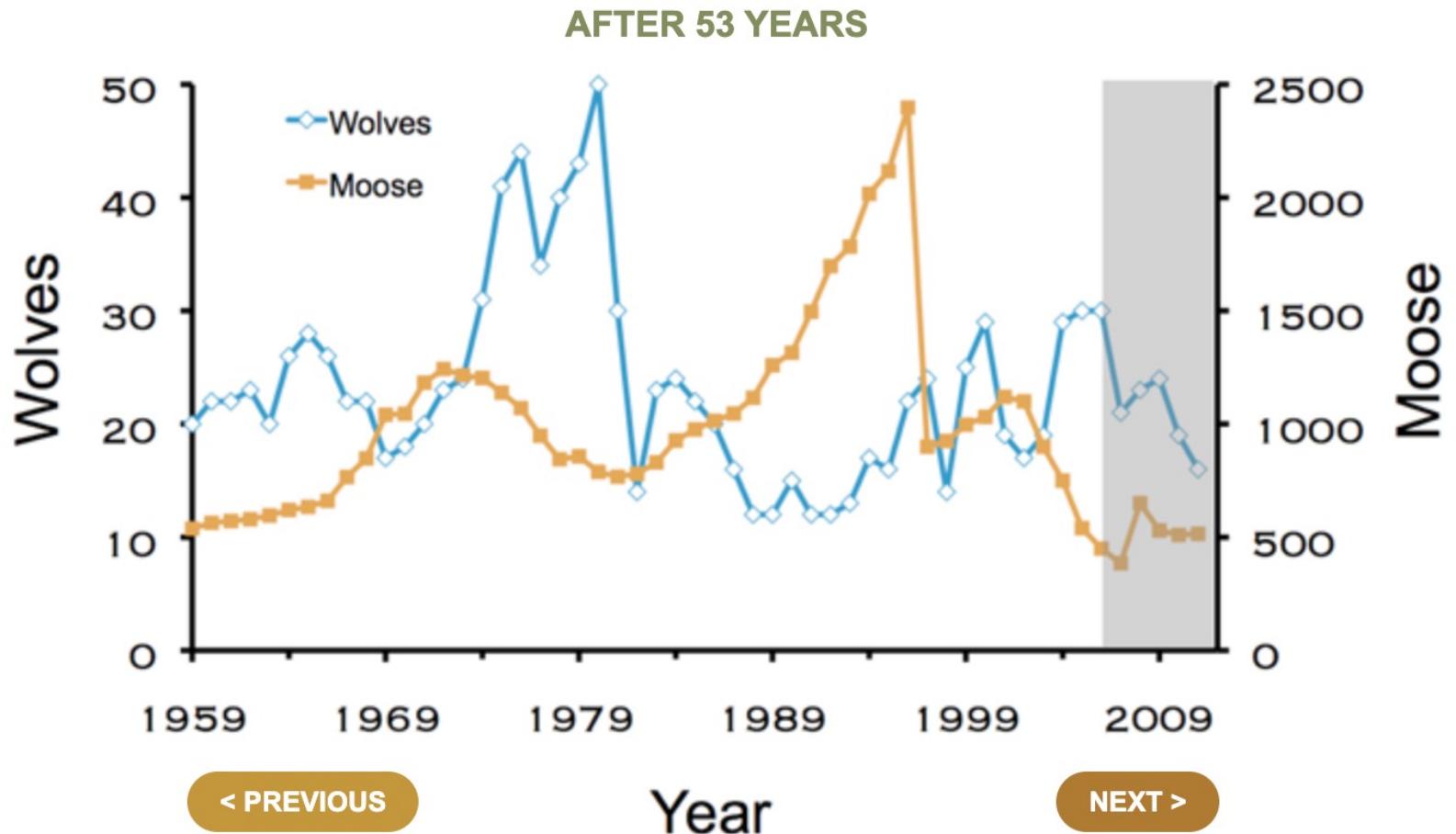


[isleroyalewolf.org](http://isleroyalewolf.org)

# Another famous example: Wolf-Moose on Isle Royale



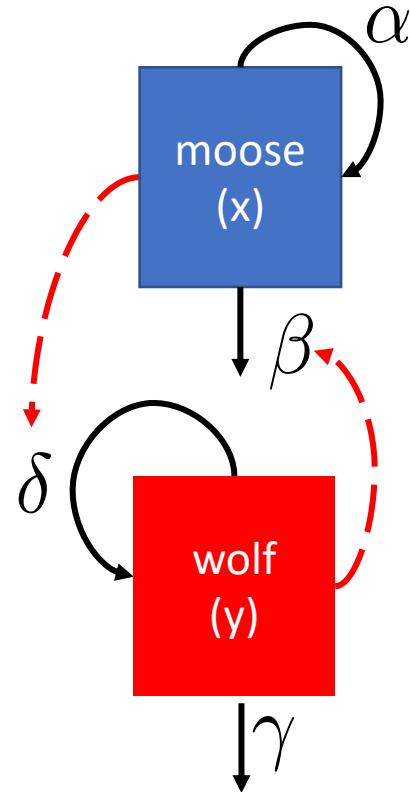
How does **moose** abundance **vary** with changes in **wolf** abundance?



The wolf population eventually stumbles as the moose continue to be kept low by high rates of predation, ticks, and hot summers.



# Another famous example: Wolf-Moose on Isle Royale



*How does **moose** abundance **vary** with changes in **wolf** abundance?*

## Field Work Opportunity for College Students



### FIELD WORK OPPORTUNITY FOR COLLEGE STUDENTS FOR MAY/JUNE 2023

We are seeking volunteers to assist with data collection for the 2023 summer field season. This is a great opportunity to gain valuable field experience while working in the remote and beautiful Isle Royale National Park.



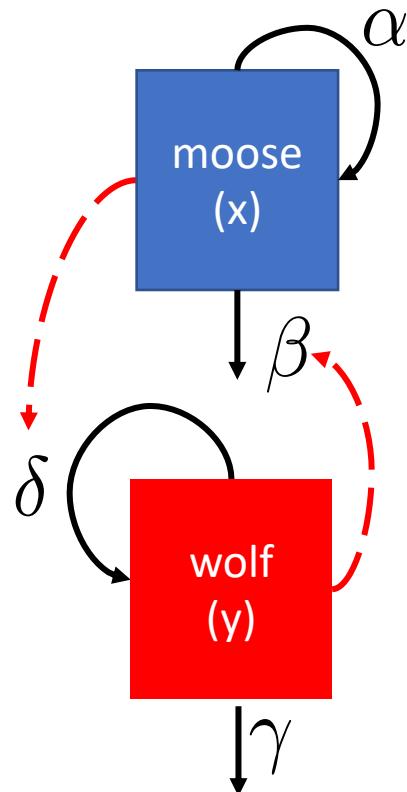
Duration: Approximately 4-5 weeks between early-May and mid-June.

Work Environment: Work is conducted on-trail and off-trail throughout Isle Royale. This is a physically demanding position; the climate, insects (mosquitoes and black flies), and terrain are often difficult. Volunteers may be required to carry up to 60 lbs. for varying distances (up to 10 miles per day) over trail and cross-country conditions. The primary mode of living is backpacking. Most travel is by foot.

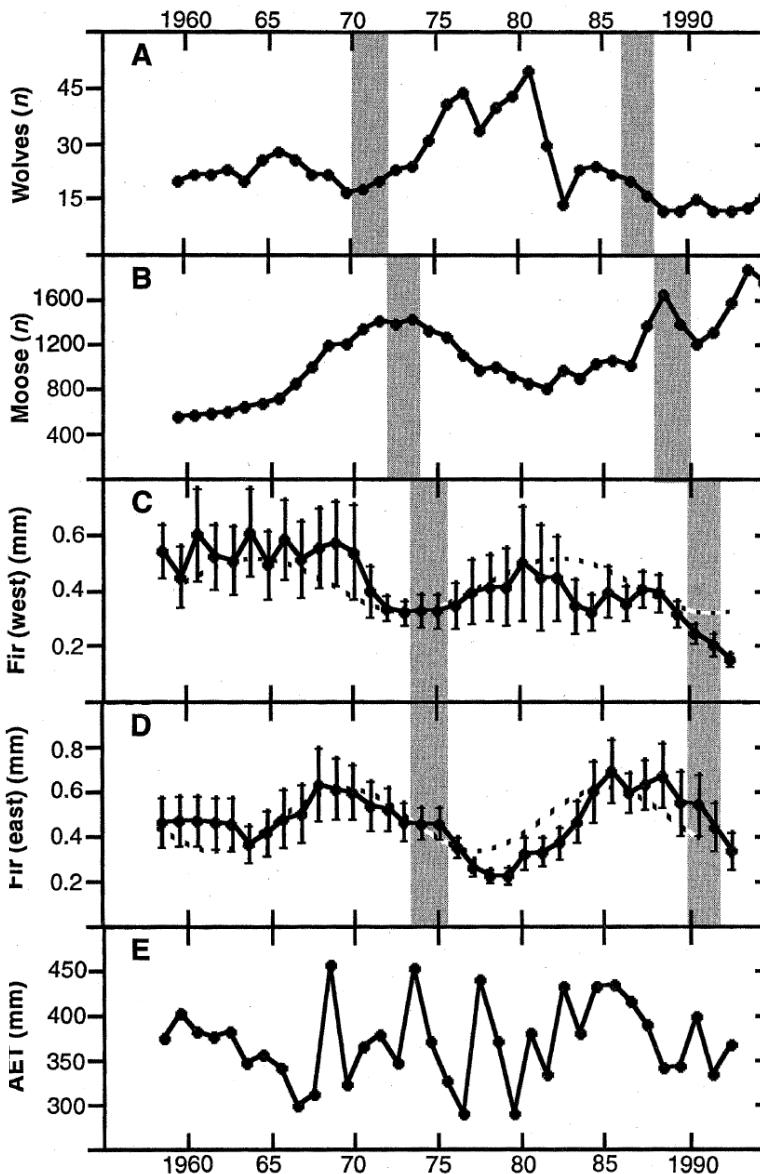
Work Schedule: Typically spend 6-8 days in the field followed by 1-2 days at base camp. Work schedule varies depending upon conditions, project needs and logistics.

This could  
be you!

# Another famous example: Wolf-Moose on Isle Royale



How does **moose** abundance **vary** with changes in **wolf** abundance?



Wolf-moose dynamics on Isle Royale are **more complex than simple predator-prey**.

This 3-way interaction is an example of a **trophic cascade**.

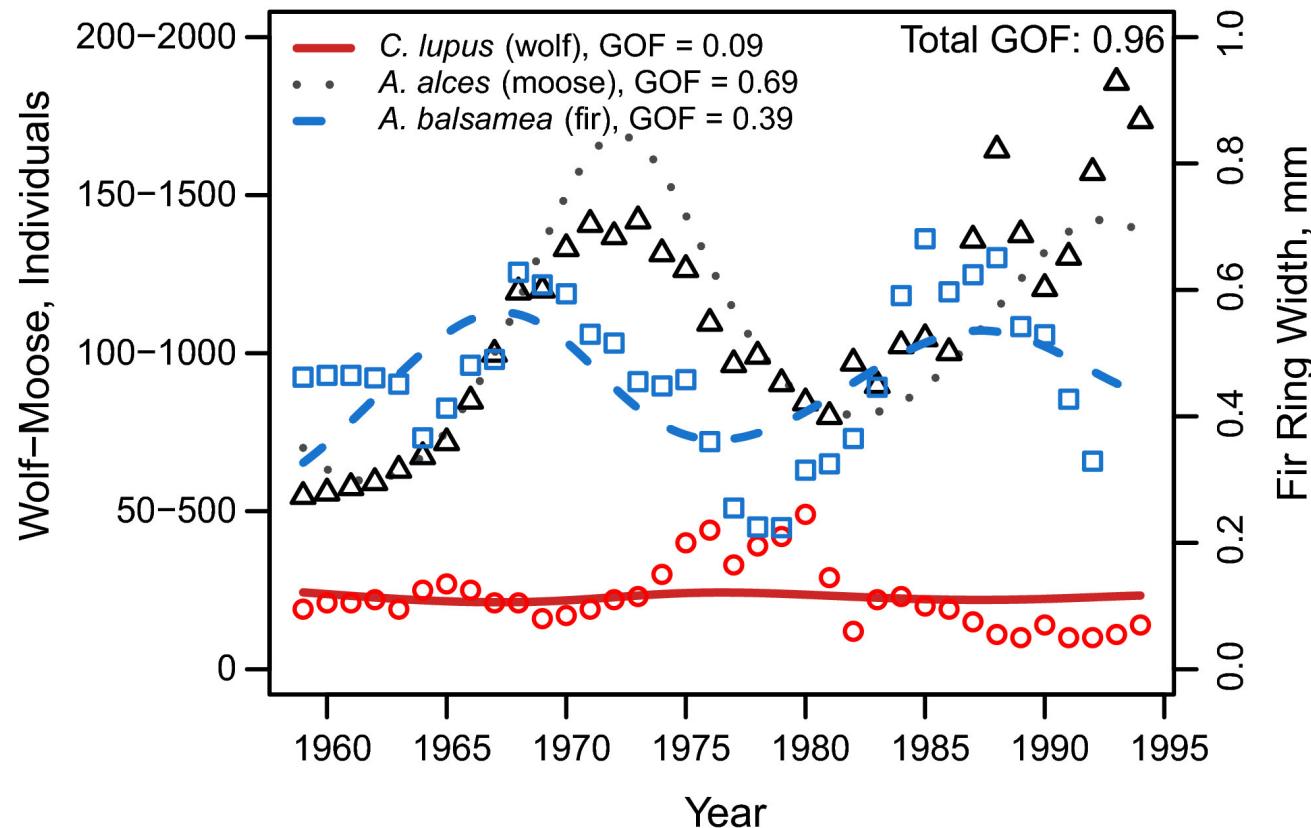
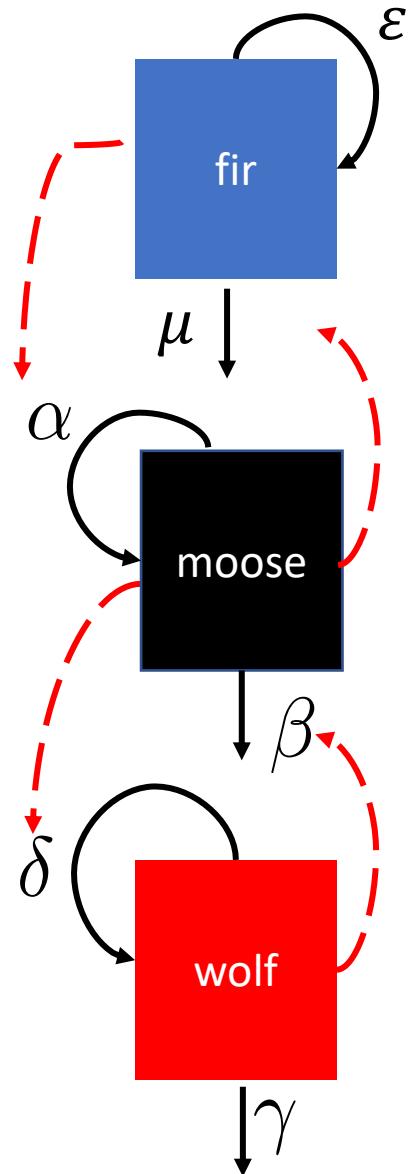
By definition, **trophic cascades span at least 3 trophic levels**, highlighting the process of **top-down** ecosystem control.

## Wolves, Moose, and Tree Rings on Isle Royale

B. E. McLaren\* and R. O. Peterson

Investigation of tree growth in Isle Royale National Park in Michigan revealed the influence of herbivores and carnivores on plants in an intimately linked food chain. Plant growth rates were regulated by cycles in animal density and responded to annual changes in primary productivity only when released from herbivory by wolf predation. Isle Royale's dendrochronology complements a rich literature on food chain control in aquatic systems, which often supports a trophic cascade model. This study provides evidence of **top-down control** in a forested ecosystem.

# Another famous example: Wolf-Moose on Isle Royale



How does **fir growth** vary with **moose** abundance, which varies with changes in **wolf** abundance?

Models incorporating >2 trophic levels can be challenging, but ecologists do sometimes attempt them!

# HSS: The first theory of **top-down regulation** of trophic levels

Vol. XCIV, No. 879

The American Naturalist

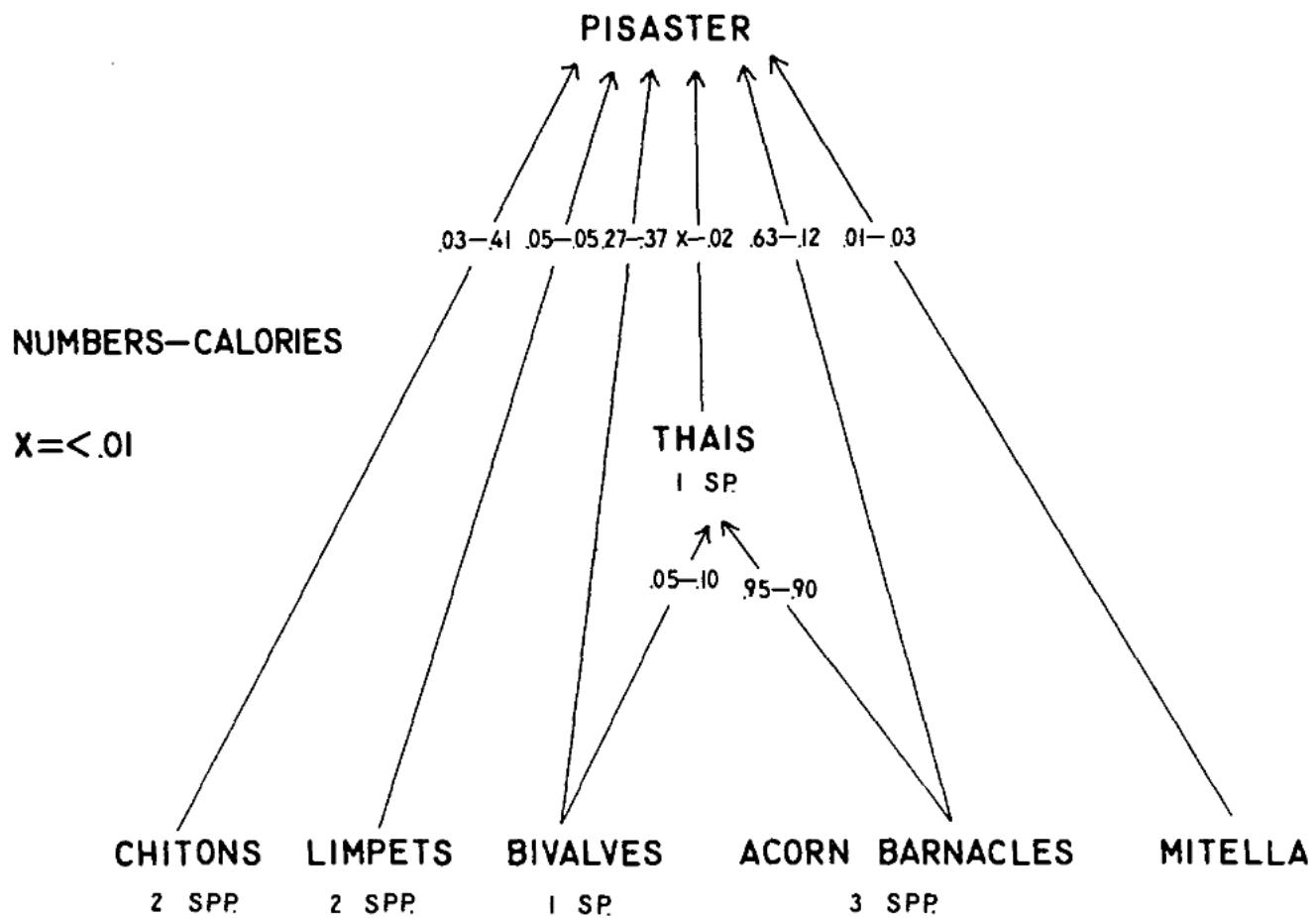
November–December, 1960

## COMMUNITY STRUCTURE, POPULATION CONTROL, AND COMPETITION

NELSON G. HAIRSTON, FREDERICK E. SMITH,  
AND LAWRENCE B. SLOBODKIN

1. Producers, decomposers, and carnivores are **bottom-up controlled** in a density-dependent fashion
2. **Interspecific competition** mediates these interactions
3. Herbivores are **top-down controlled** (because the ‘the world is green’)

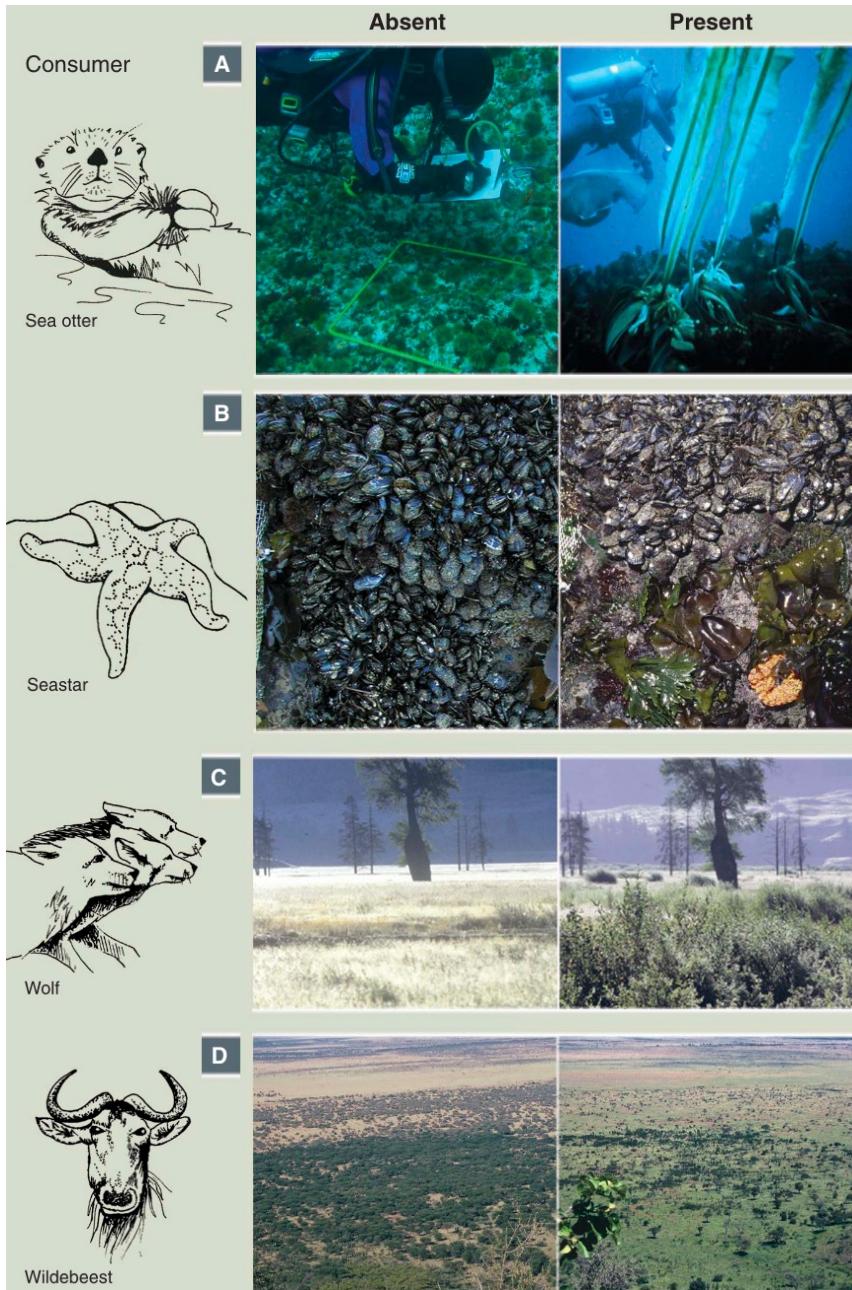
This work inspired empirical studies on **trophic cascades**:  
*Pisaster* removal on Tatoosh Island



Paine 1966. *The American Naturalist*.

# Other famous **trophic cascades**:

Estes et al. 2011. *Science*.



CA sea otters maintain kelp forest diversity by consuming herbivorous sea urchins. (Estes & Duggins 1995. *Ecological Monographs*)

Starfish maintain diversity in Pacific intertidal by consuming space-dominating mussels. (Paine 1966 *The American Naturalist*)

Yellowstone wolves promote willow recovery by consuming overbrowsing elk (Ripple & Beschta 2005. *Forest Ecology & Management*)

Rinderpest eradication releases wildebeest populations that control savanna, limit fire, and promote tree regrowth (Holdo et al. 2009. *PLoS Biology*)

