# Fundamentals of Ecology

Week 7, Ecology Lecture 3

Cara Brook

February 14, 2023

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- 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.

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***Structured populations***

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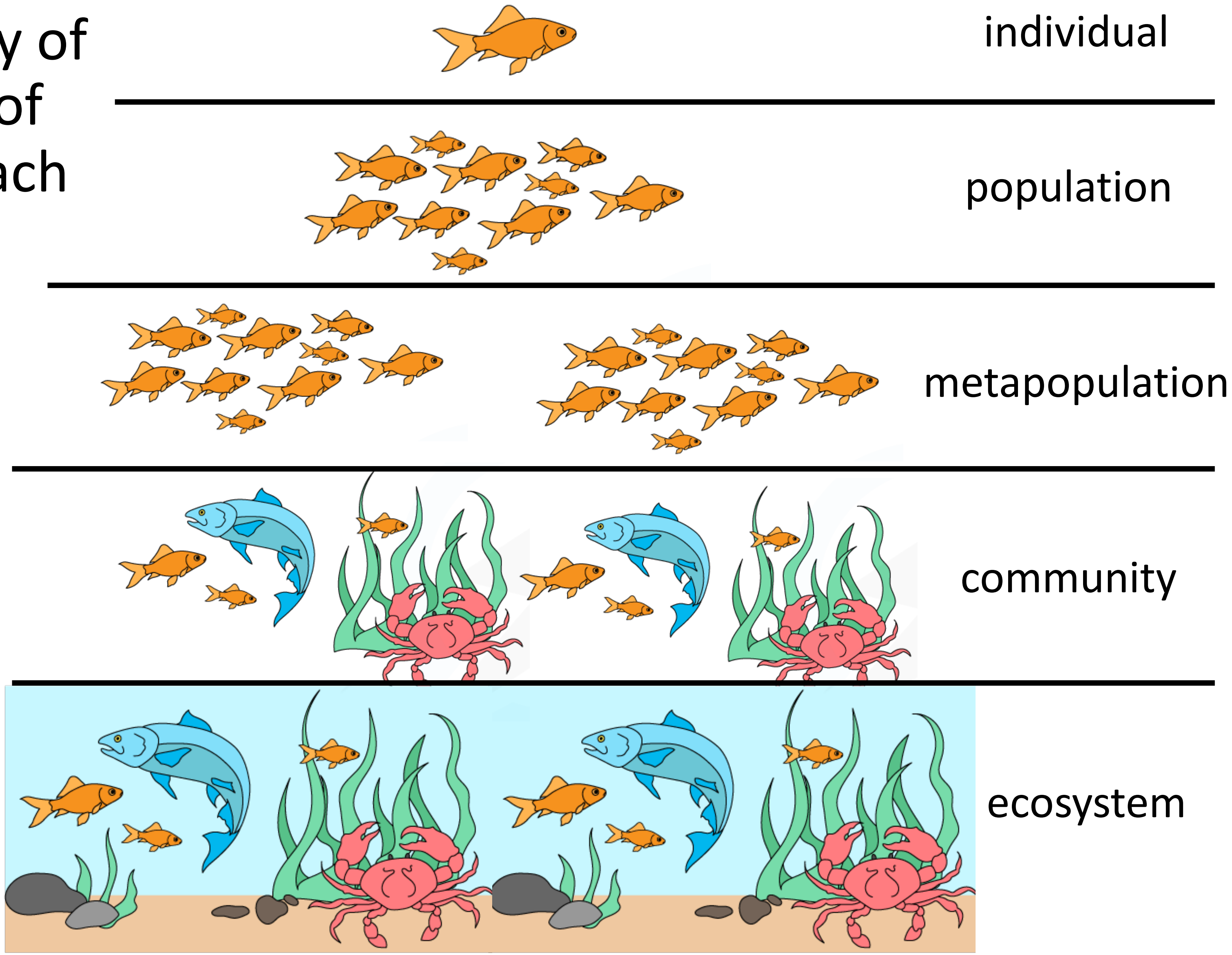
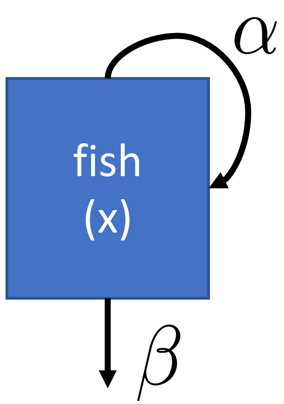
- The dominant eigenvalue of the transition matrix, $\lambda$, the population rate of increase, describes whether a structured population is increasing or decreasing
- Life tables are used to store demographic data to build transition matrices
- In humans, there are 5 stages to a demographic transition, 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

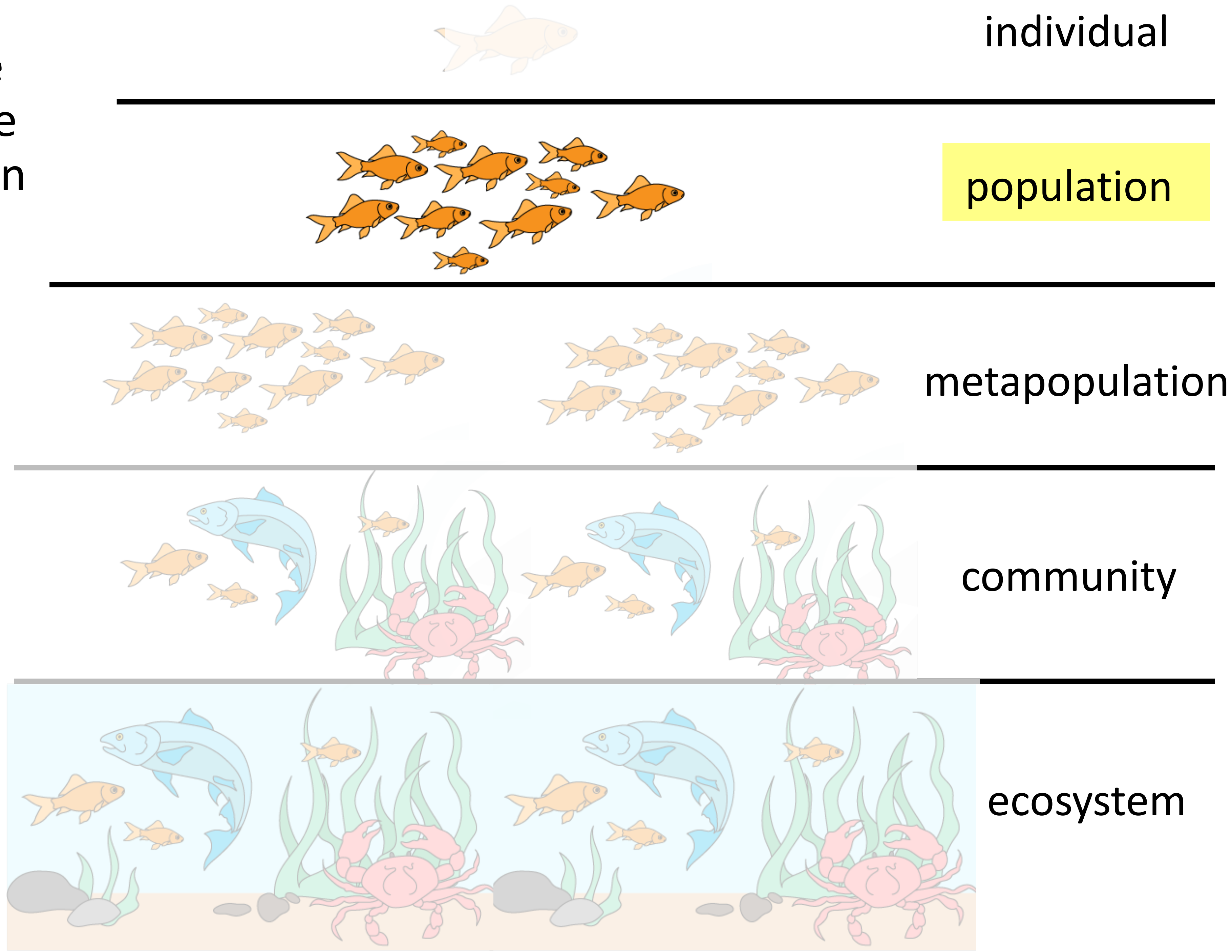
Ecology is the study of the **interactions** of **organisms** with each other and their **environment.**



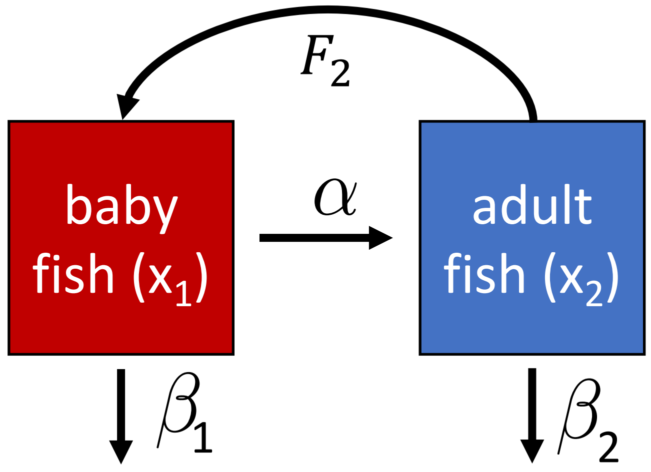
**Population** = multiple individuals of the same species (**conspecifics**) in the same habitat




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



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

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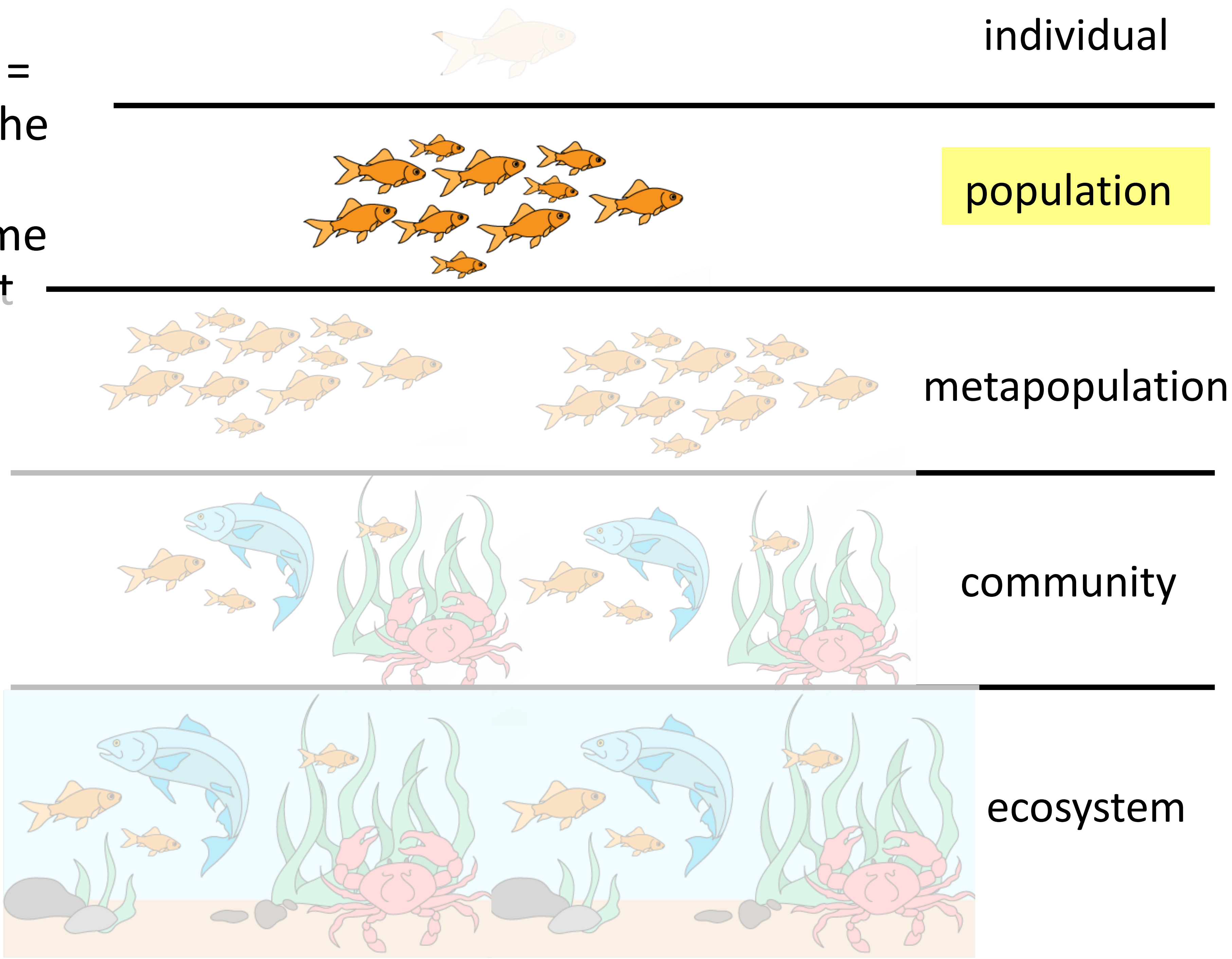
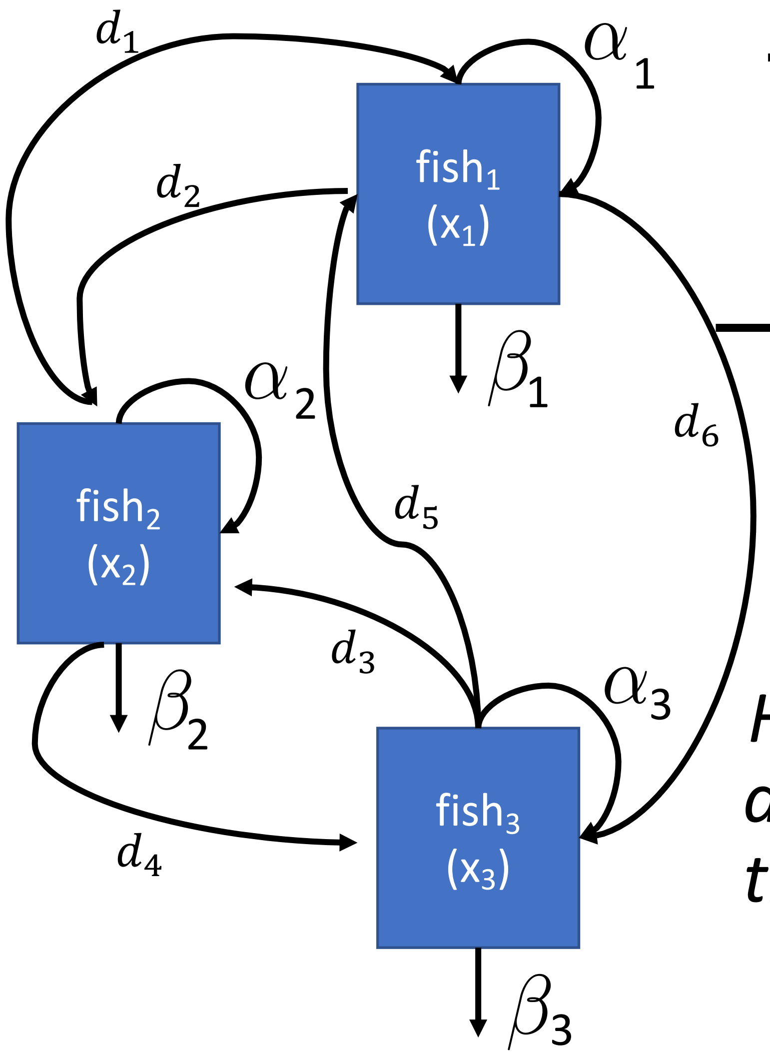
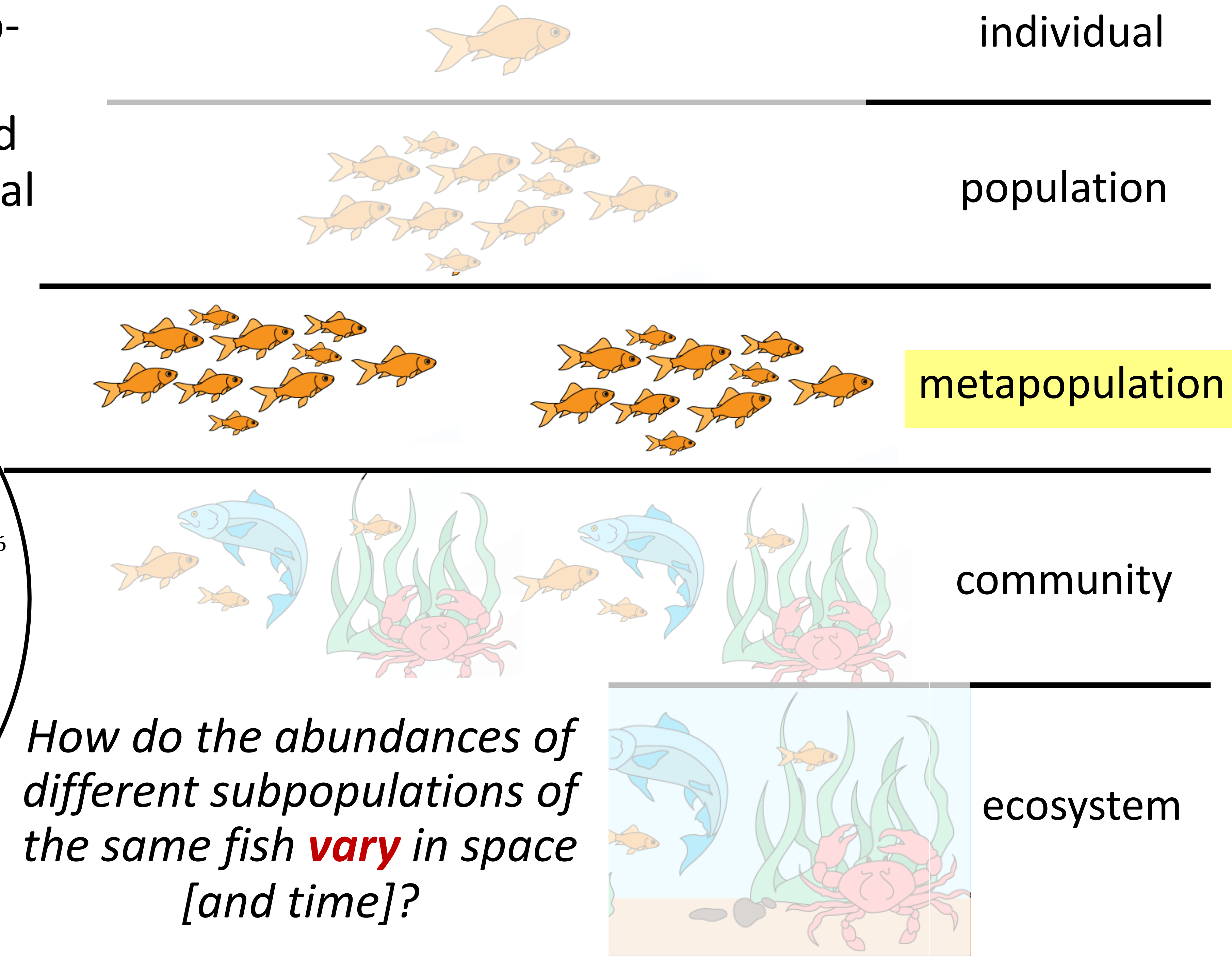


**Metapopulation** = sub-populations of conspecifics connected by migration or dispersal

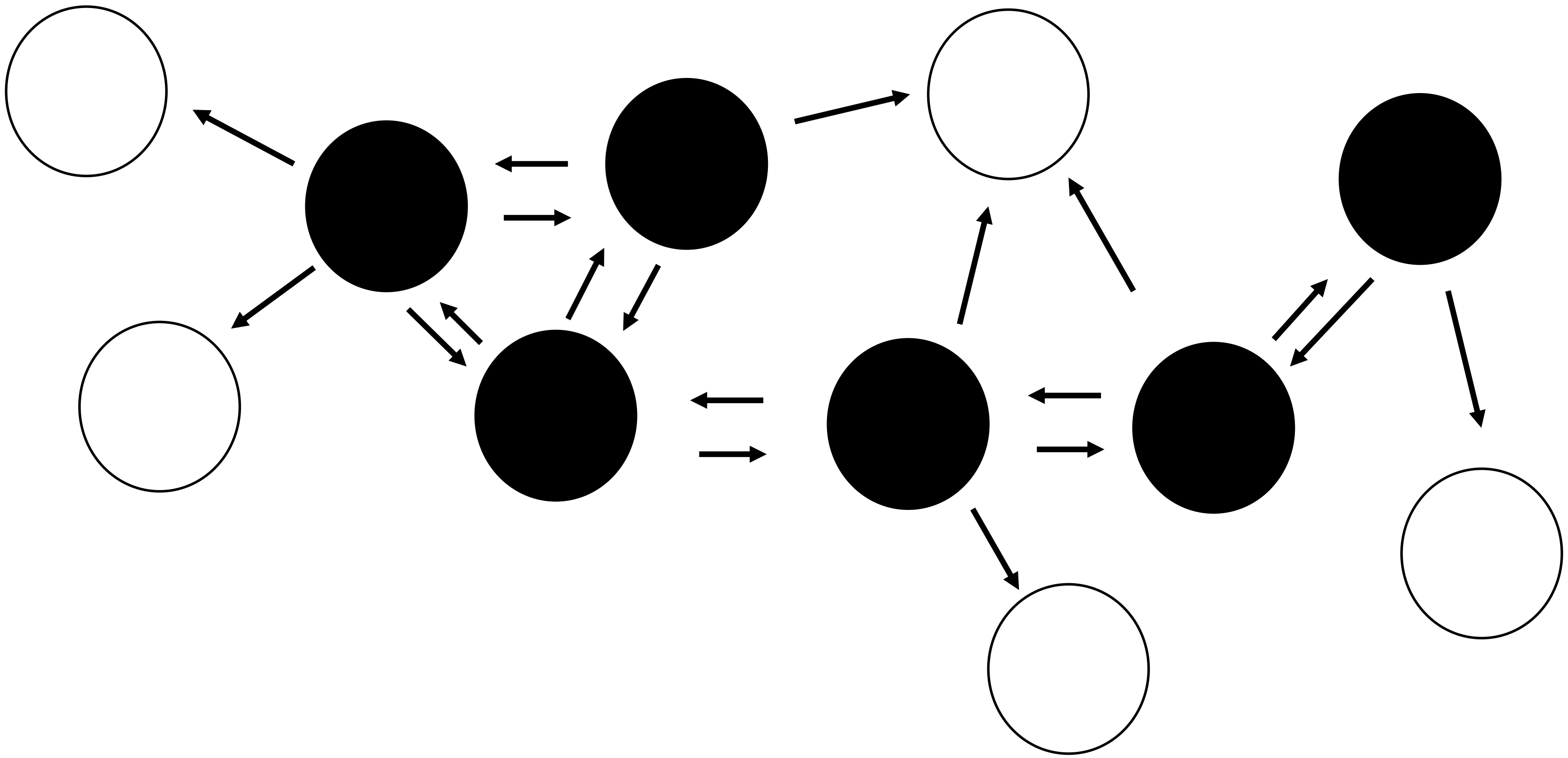



*How do the abundances of different subpopulations of the same fish **vary** in space [and time]?*

# Modeling metapopulation dynamics

- a “population of populations”            -Richard Levins 1969



# Modeling metapopulation dynamics

- a “population of populations” -Richard Levins 1969

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

fraction of patches occupied at a given time

colonization rate

extinction rate

# Modeling metapopulation dynamics

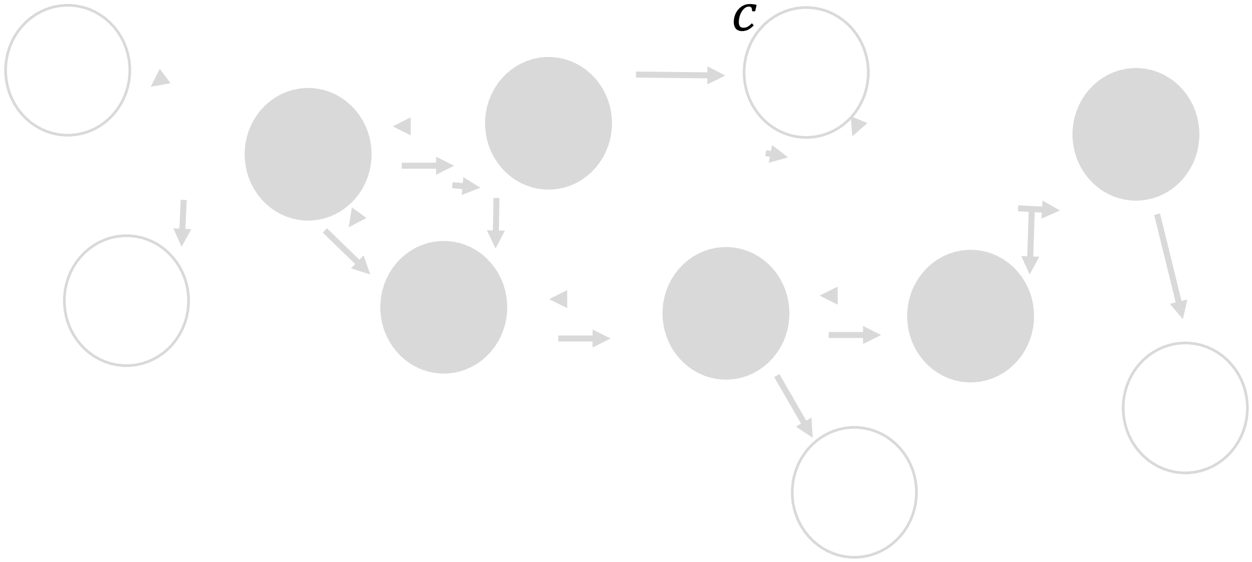
- a "population of populations" -Richard Levins 1969

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

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

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

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



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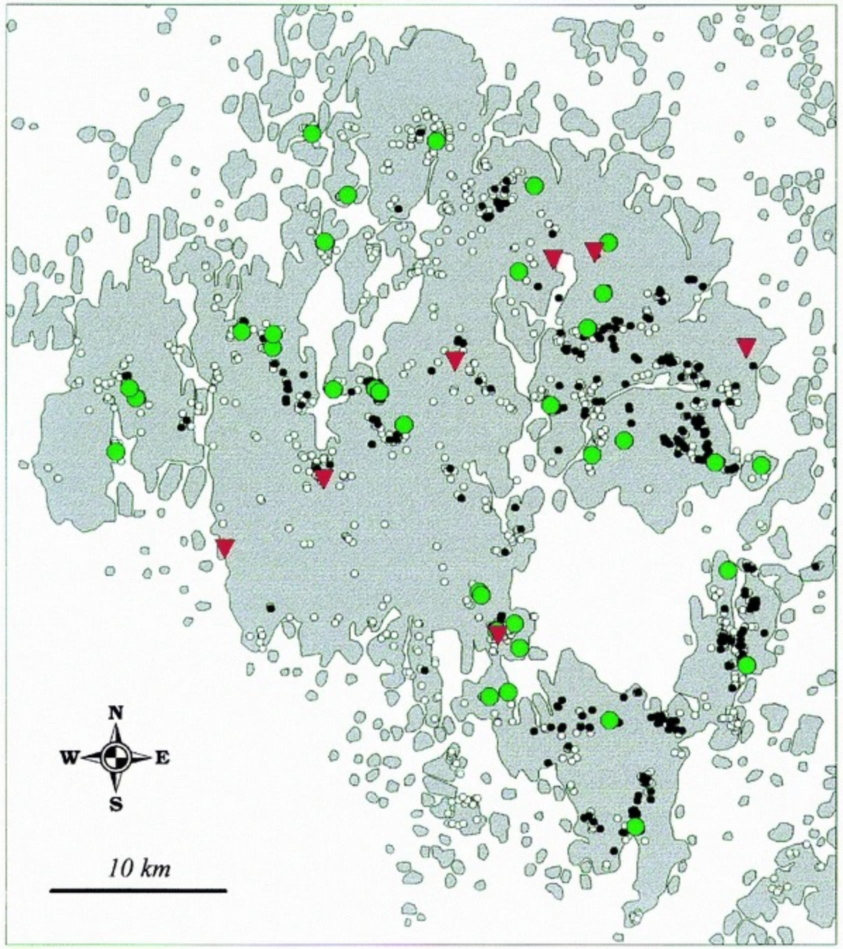
**rate of colonization increases when more patches are vacant and decreases as they become occupied**

(subpopulations within Levins’ metapopulation model are unstructured)

# Why do metapopulations matter?

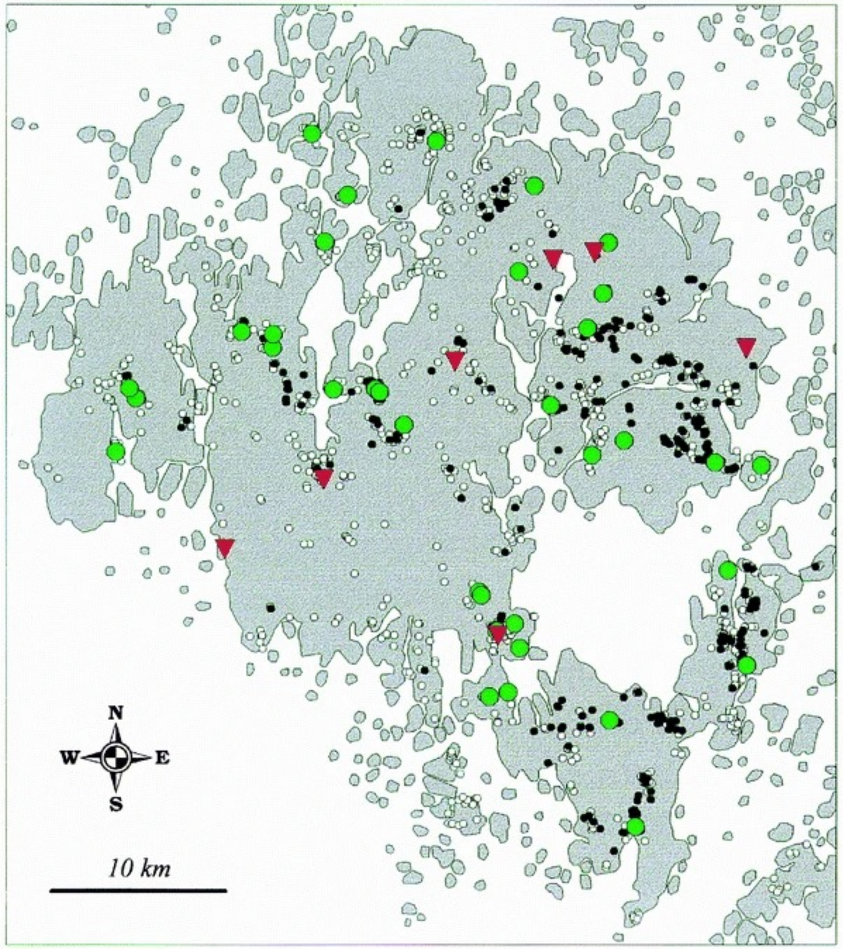



Saccheri et al 1998. *Nature.*

Glanville fritillary butterfly
*Melitaea cinxia*

Ilkka Hanski
1953-2016

# Why do metapopulations matter?

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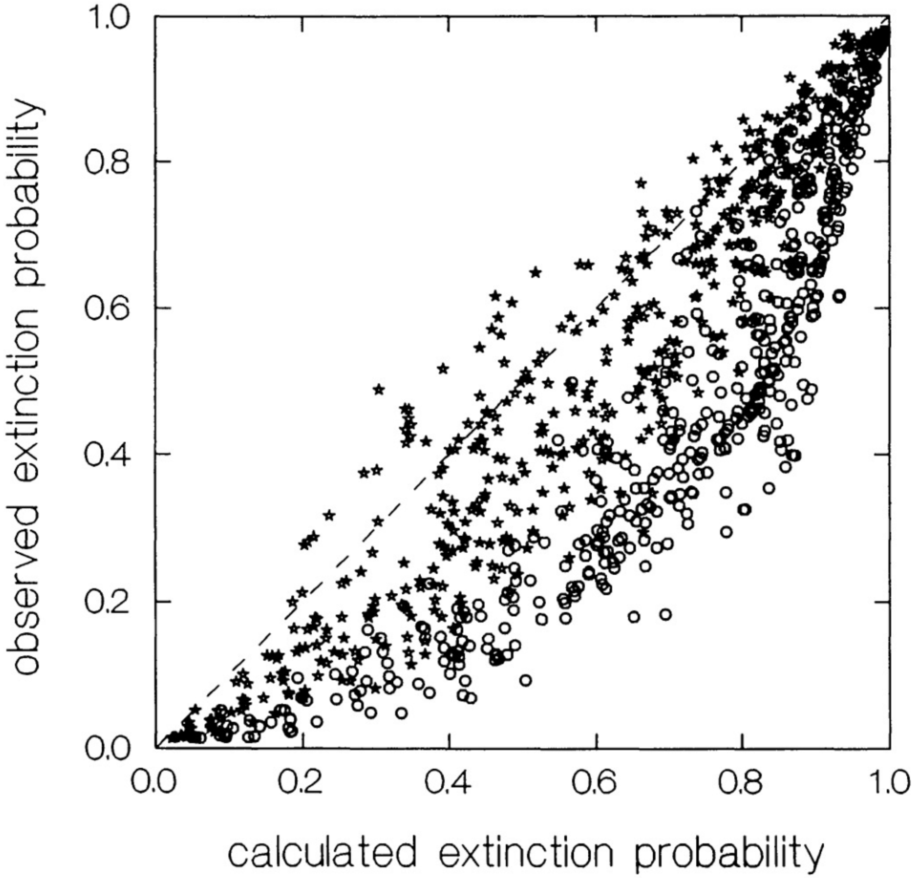
MINIMUM VIABLE METAPOPULATION SIZE

ILKKA HANSKI,[1] ATTE MOILANEN,[1] AND MATS GYLLENBERG[2]




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

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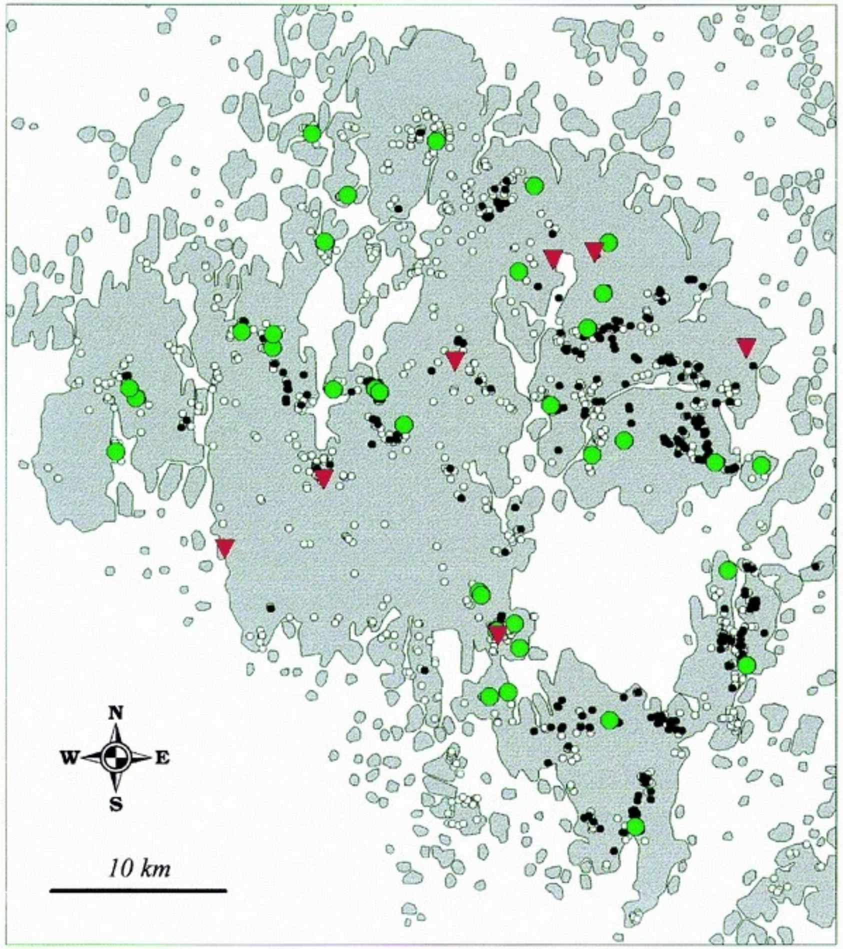


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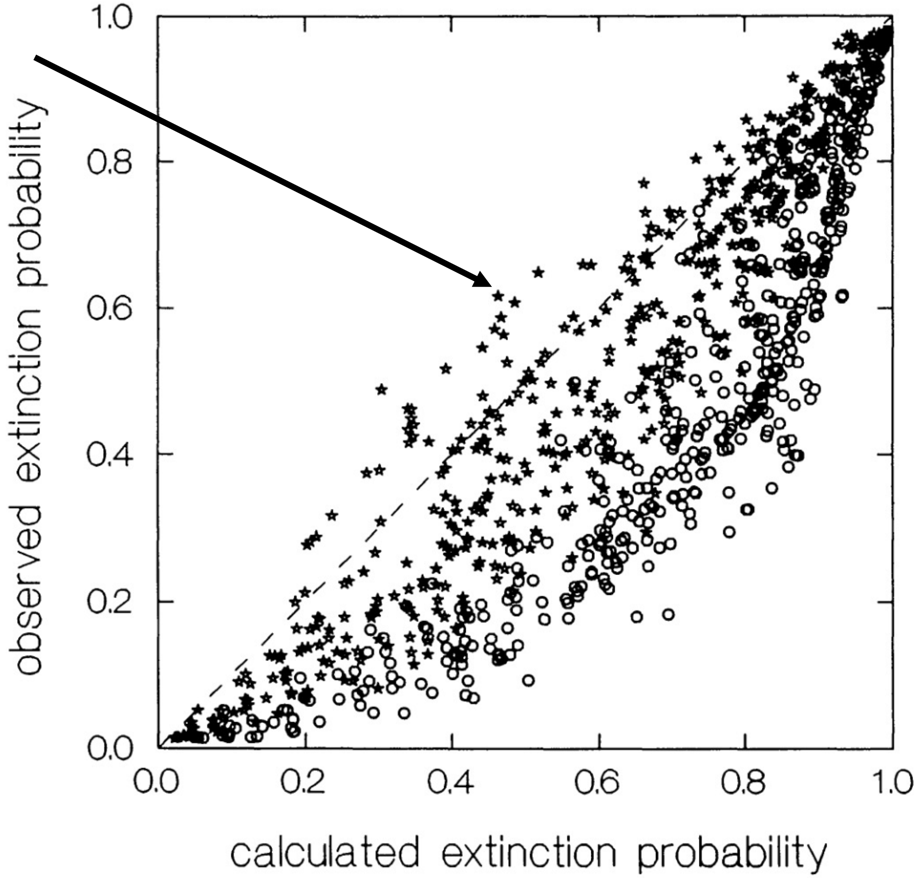
star points recalculated with **rescue effect** from Levins' model

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

Dr. Christopher Golden, Harvard University

Dr. James Herrera, Duke University

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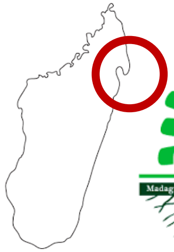
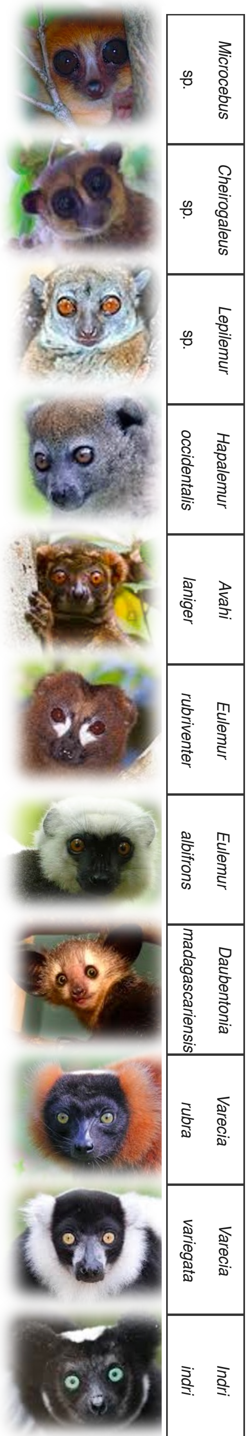
Hervet Randriamady, Harvard University

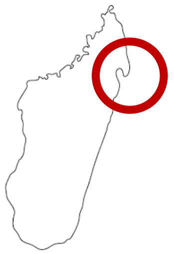
B.J. Rodolph Rasolofoniaina, MAHERY

Dr. Emma Fuller, Fractal Agriculture






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



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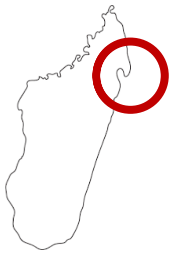

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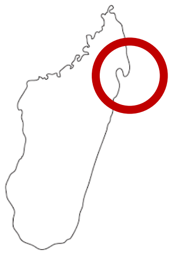

- 103 extant species of lemur
- **94%** under some **IUCN category of threat**
  - 24 Critically Endangered
  - 49 Endangered
  - 20 Vulnerable
  - 3 Near Threatened
  - 3 Least Concern
  - 4 Data Deficient
- The **most imperiled group of mammals** on earth

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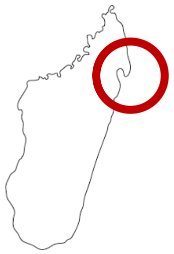

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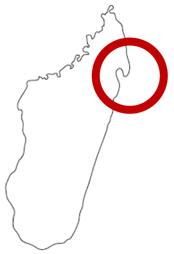

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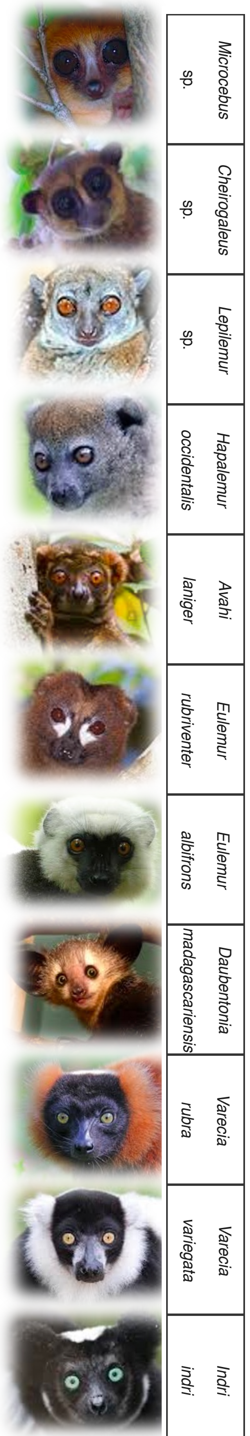


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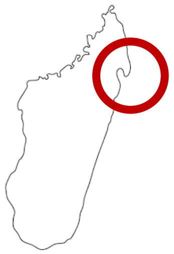

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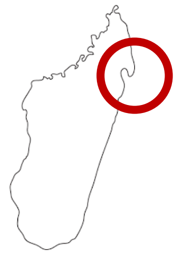

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- Local hunters from one village outfitted with **diaries to record harvested species**

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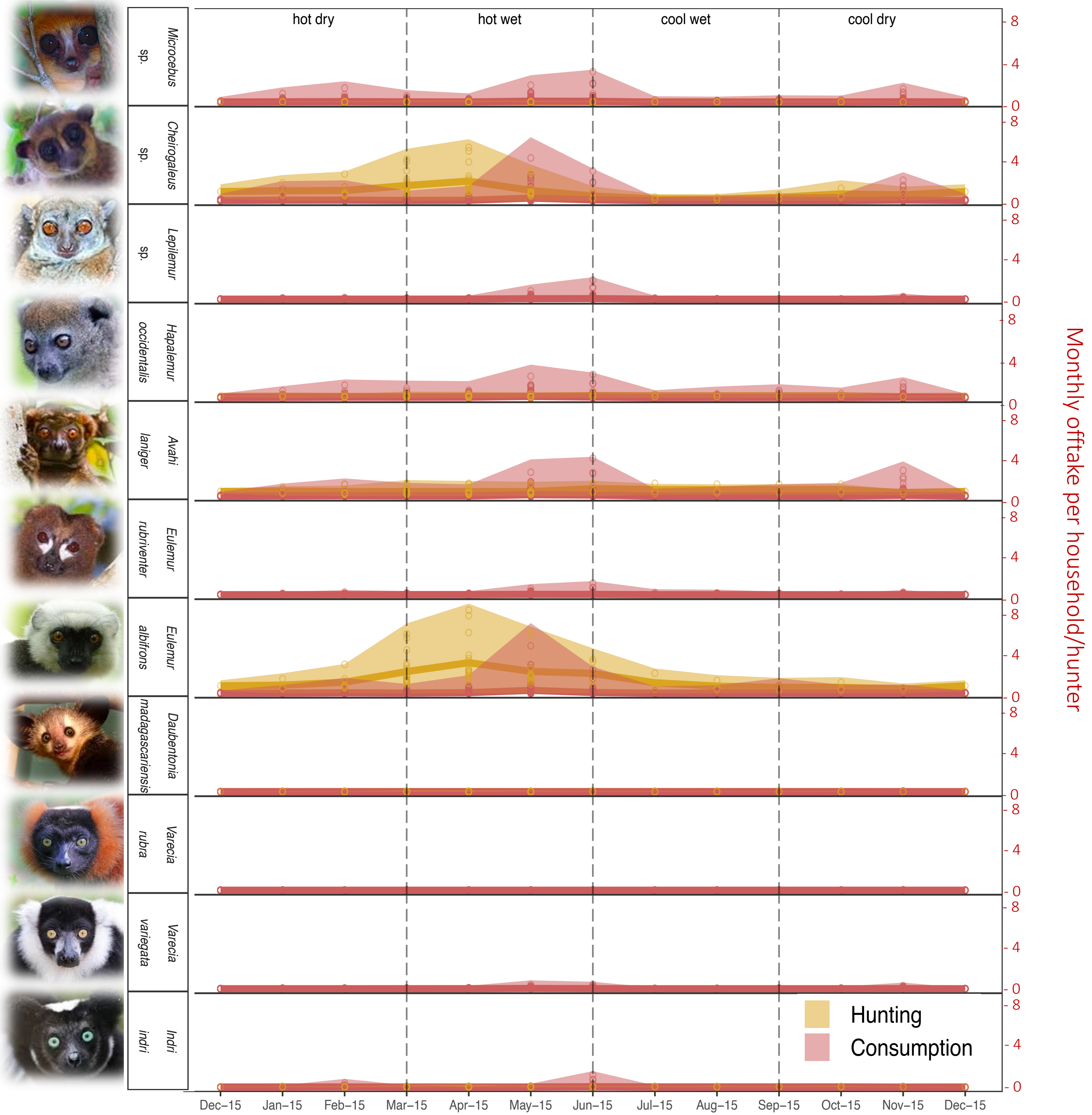


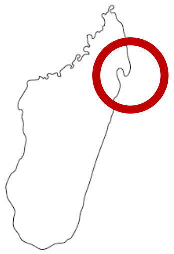

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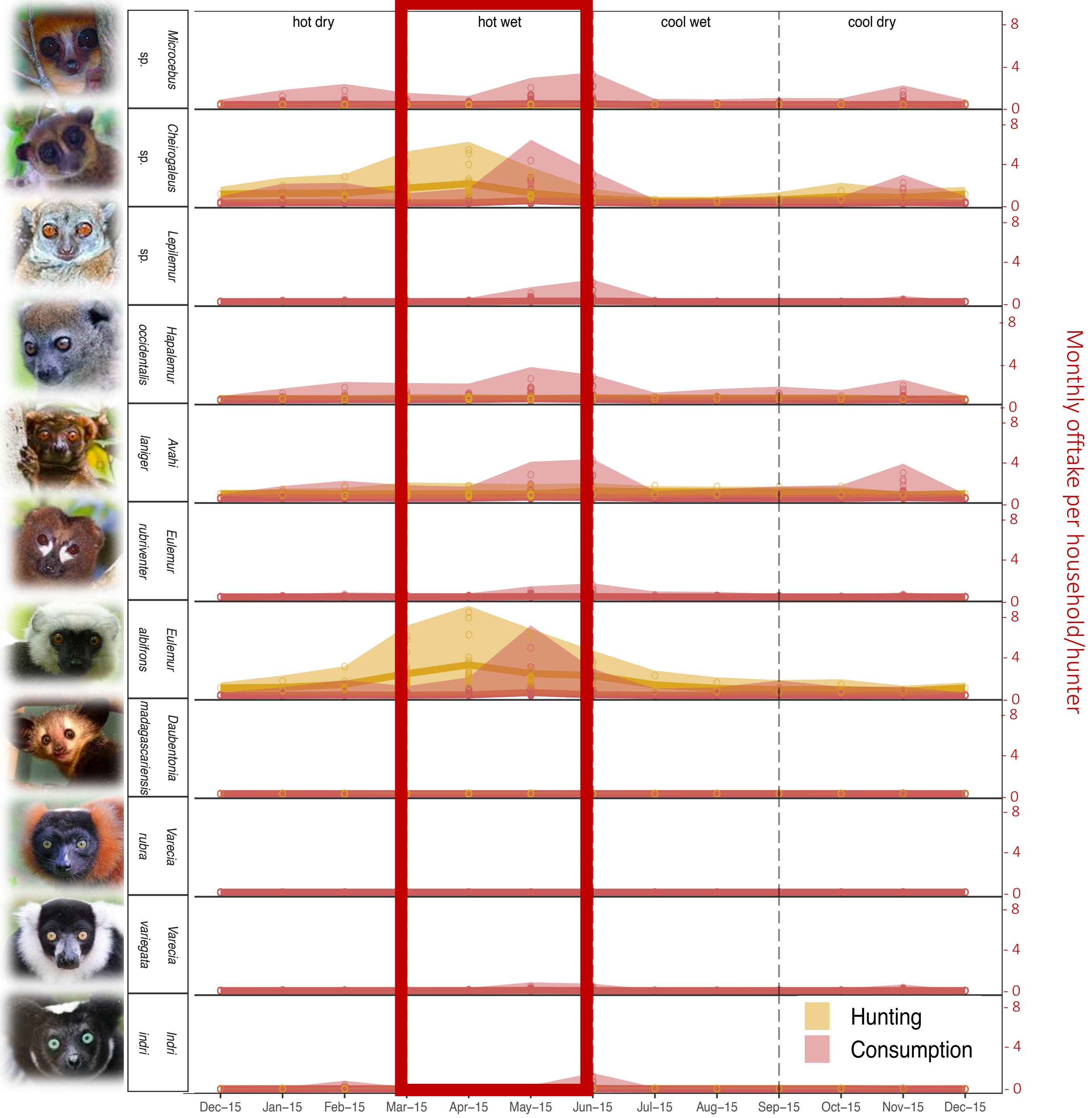
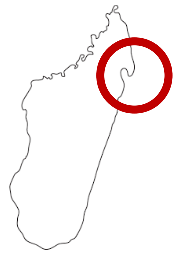



Lemurs are primarily hunted and consumed in the **hot wet season**.



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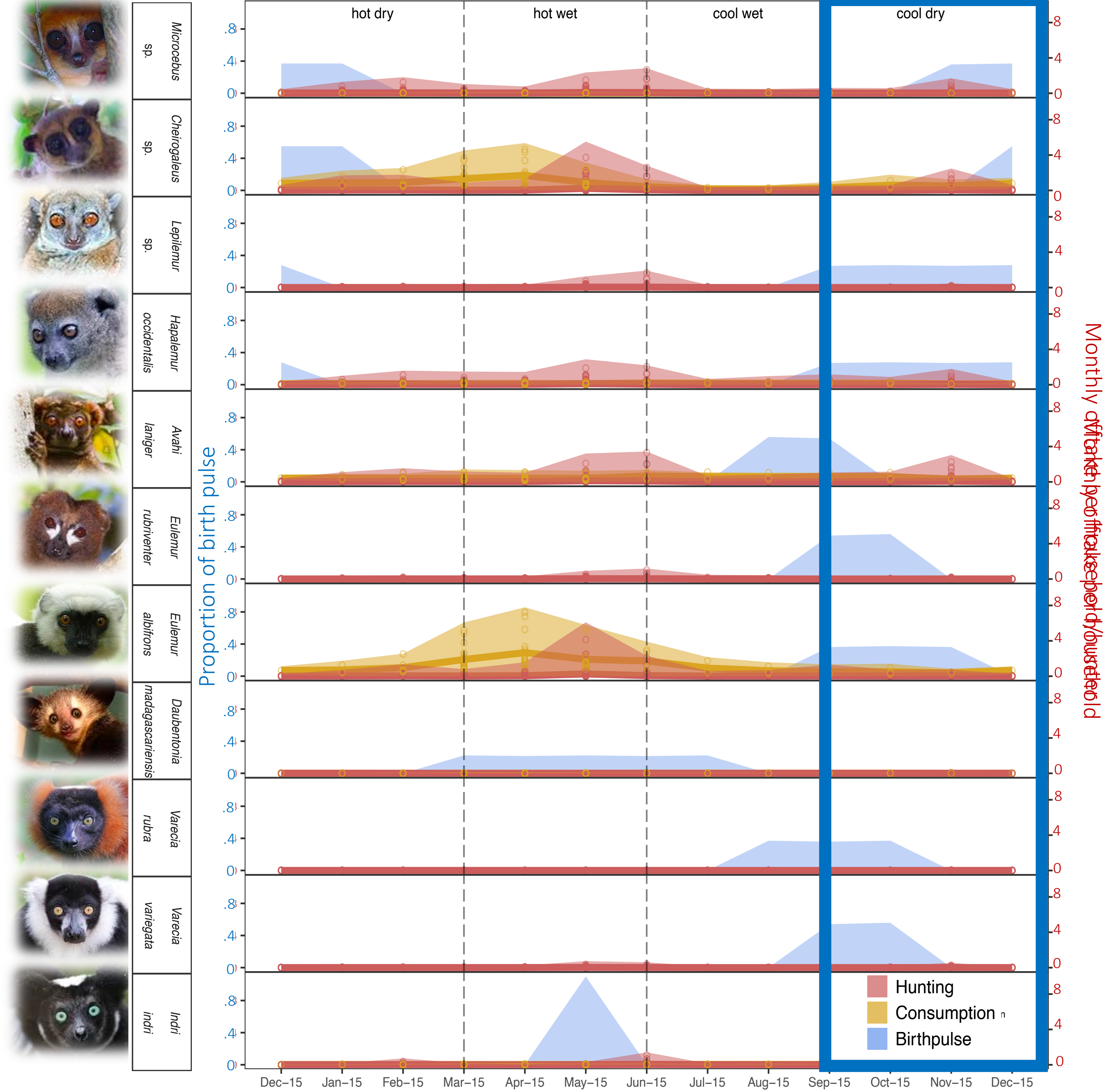


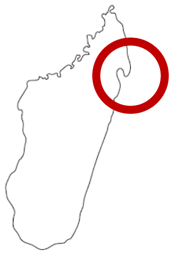

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Most spp. **birth** in the **cool dry season**, offset from the hunt.

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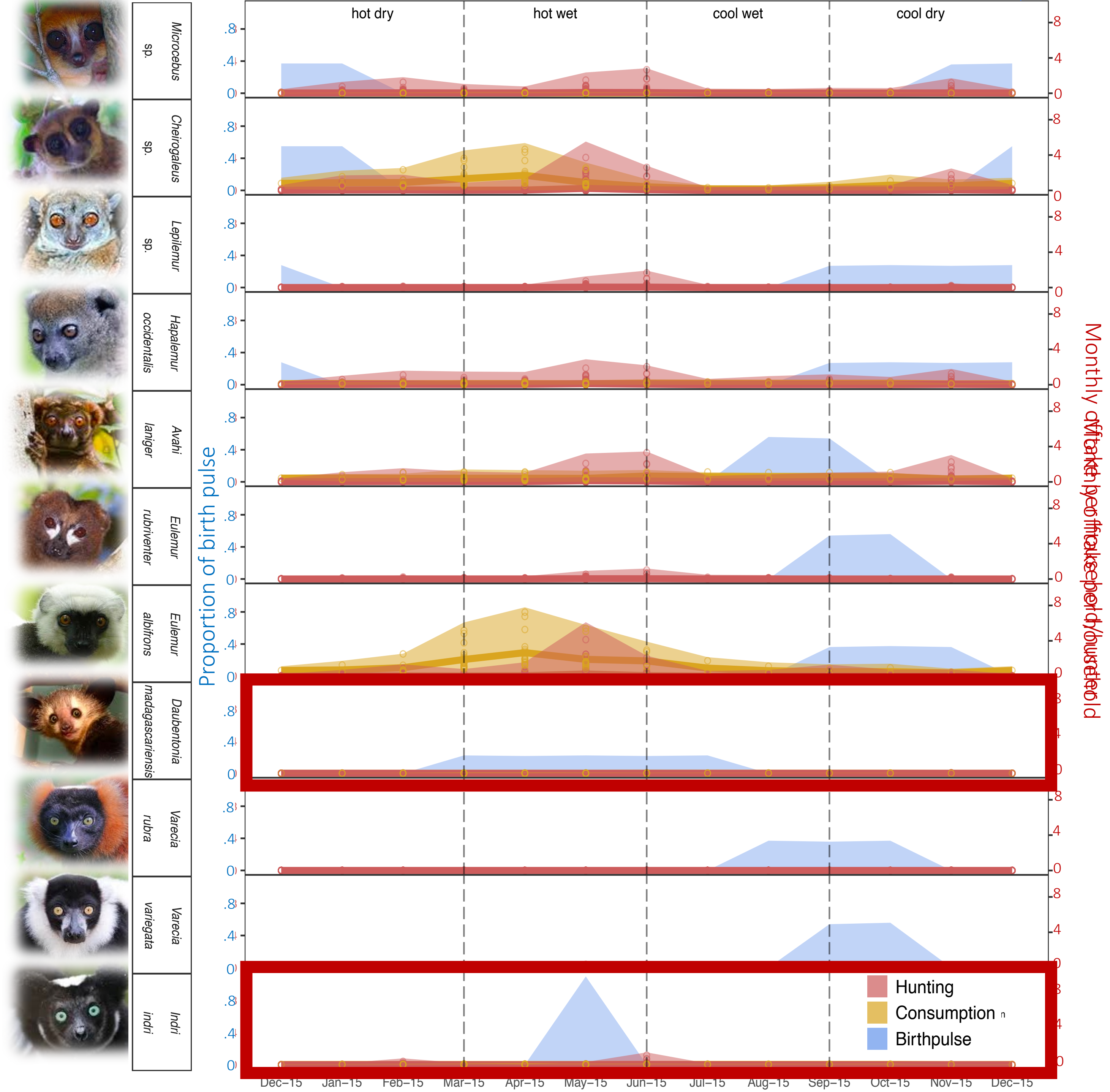


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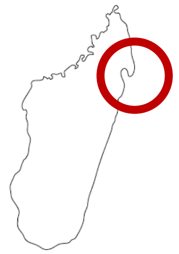

Most spp. **birth** in the **cool dry season**, offset from the hunt.

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

Brook et al. 2018. *Conservation Biology.*

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

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

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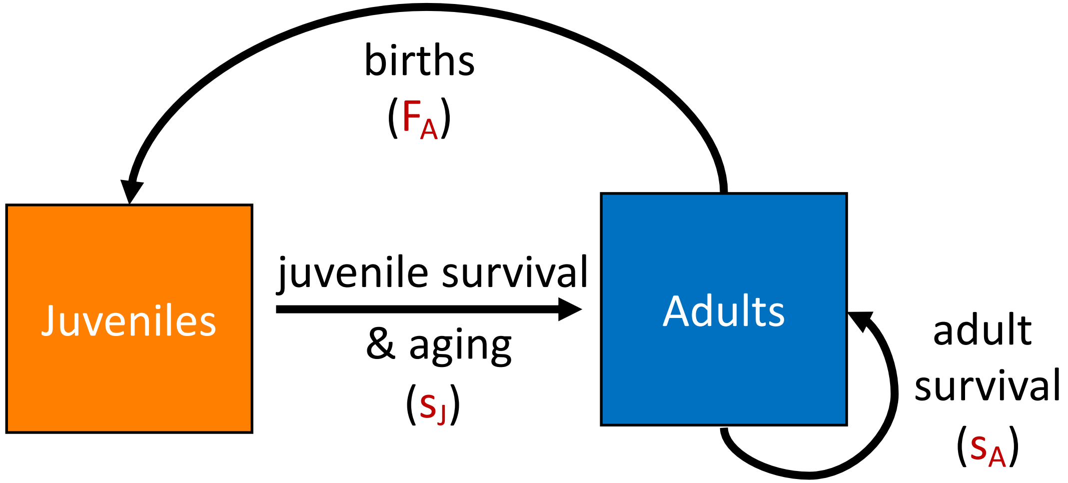


**Assumptions:**

- **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.*
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***N*** = *population vector*
***A*** = *transition matrix*

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

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

*(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 $F_A$.*

Brook et al. 2018. *Conservation Biology.*
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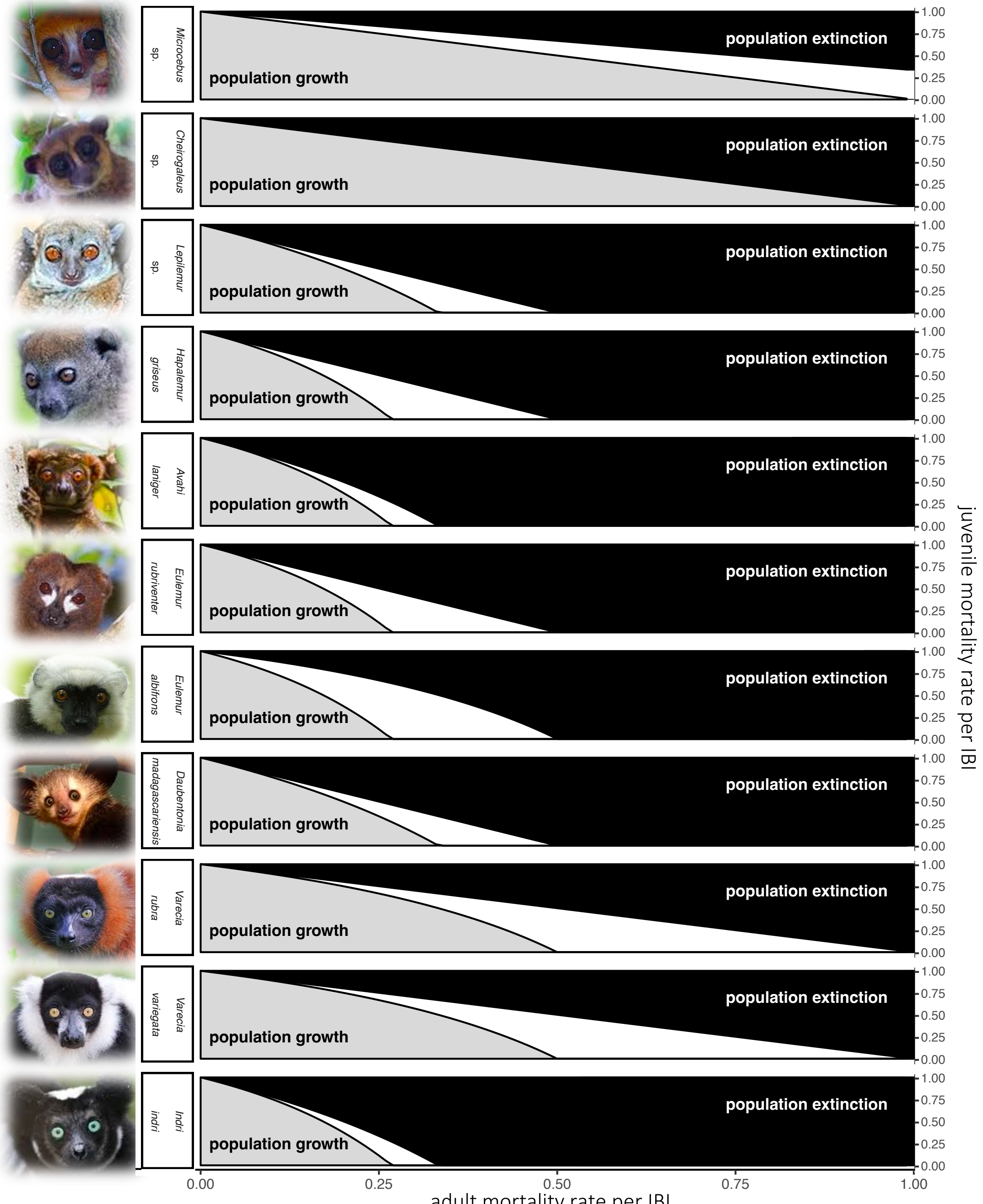


We plotted **zero-growth isoclines** to evaluate lemur population trajectories across different **mortality rates**.

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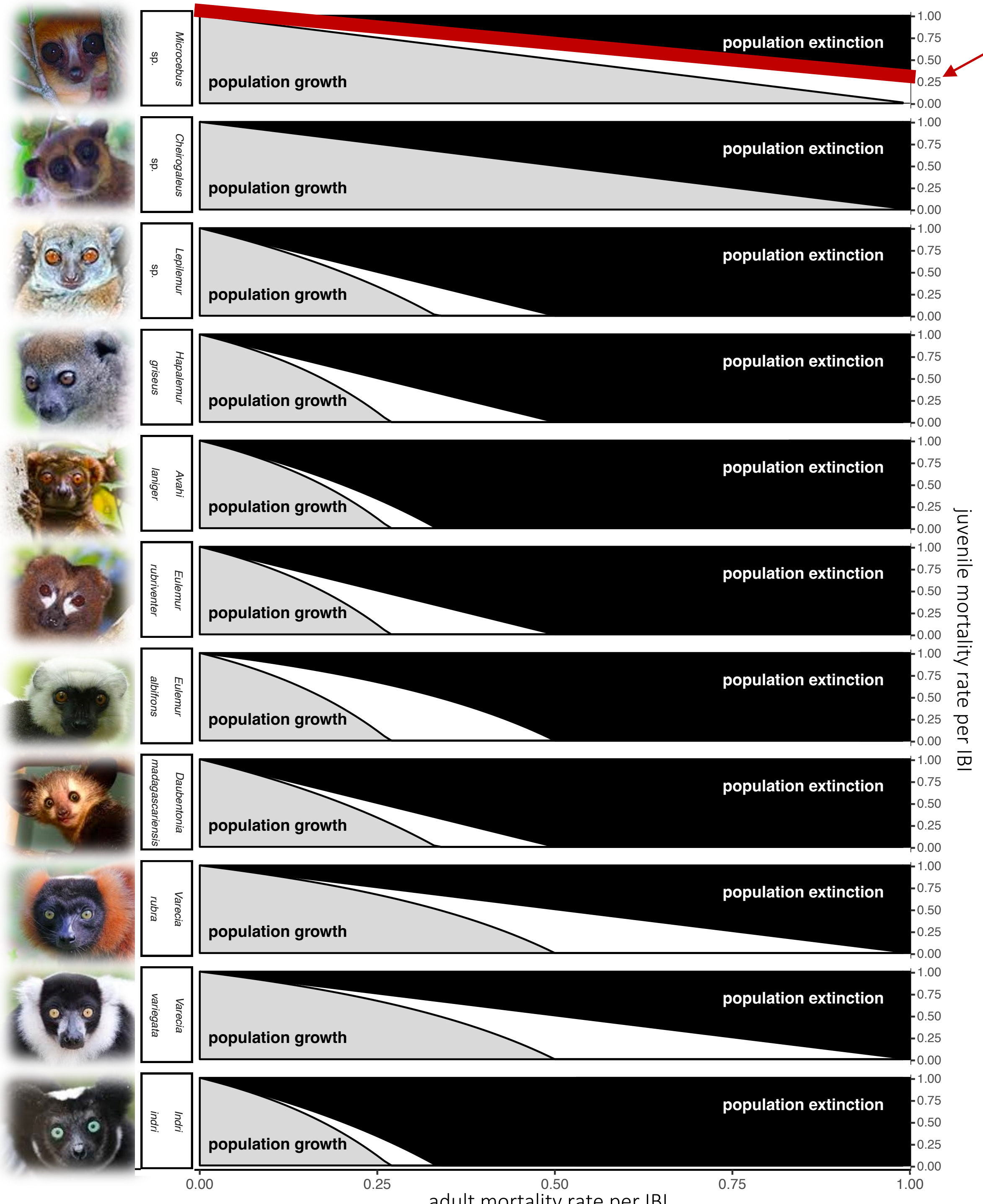
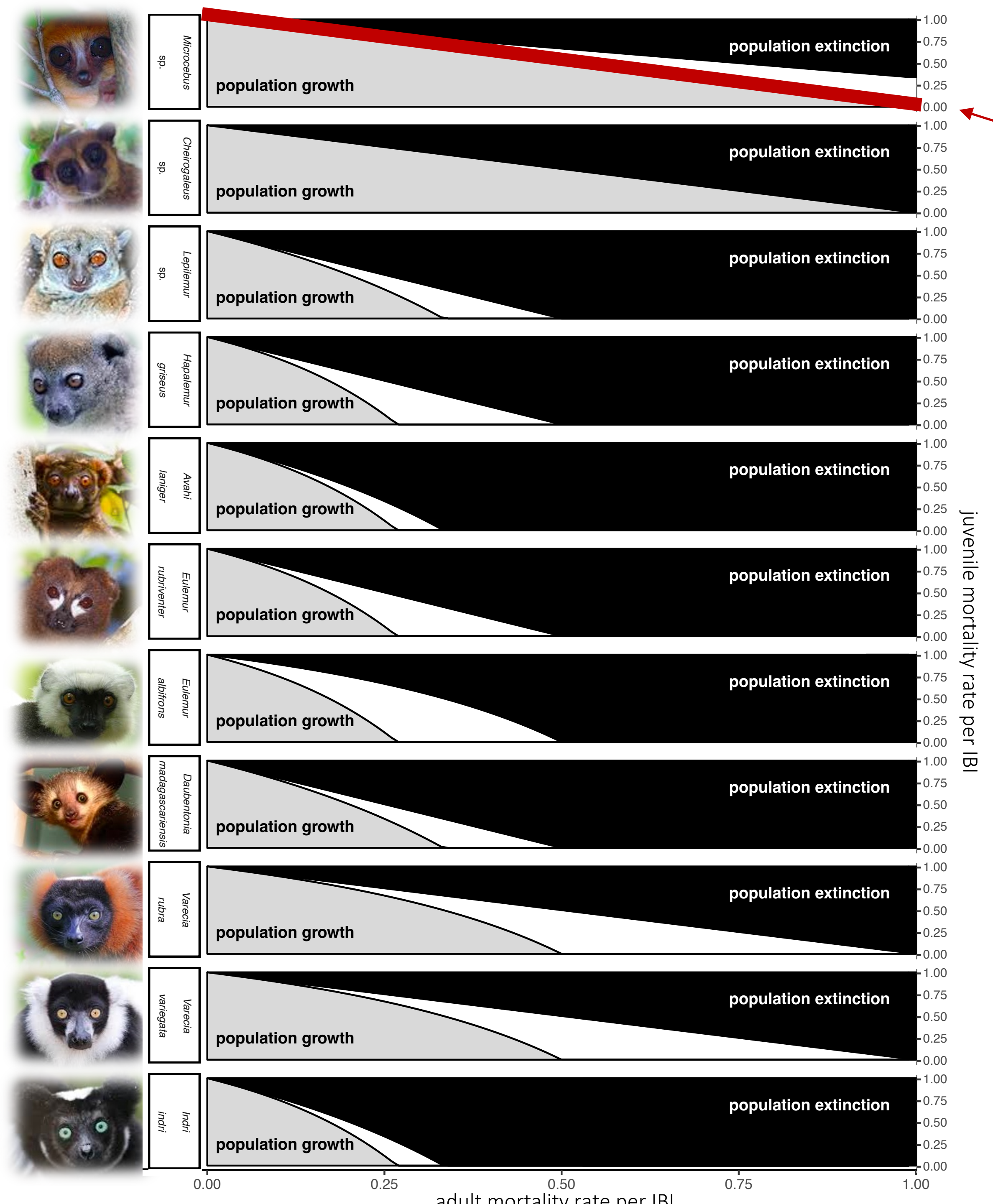


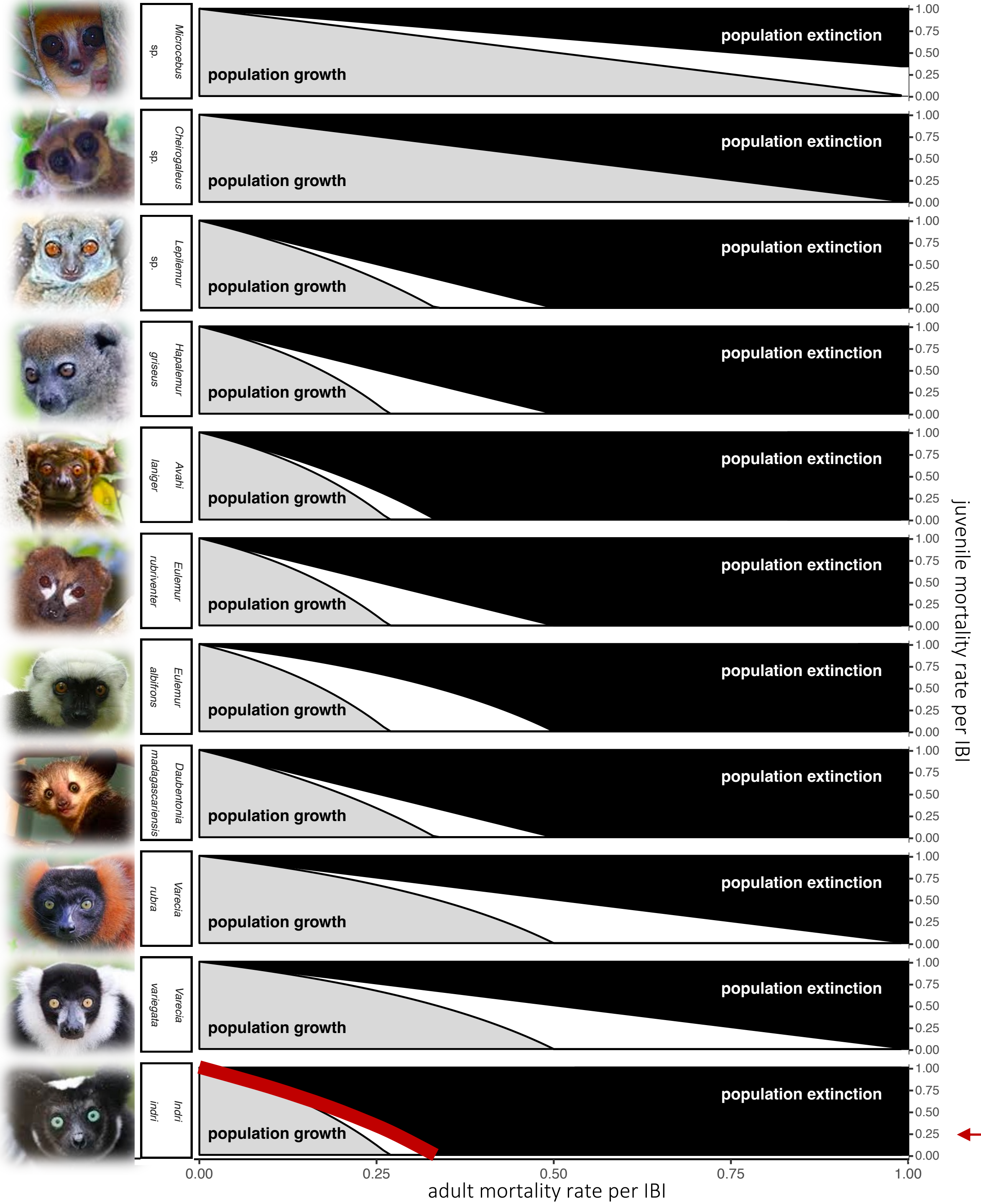

3 offspring / IBI

Brook et al. 2018. *Conservation Biology.*



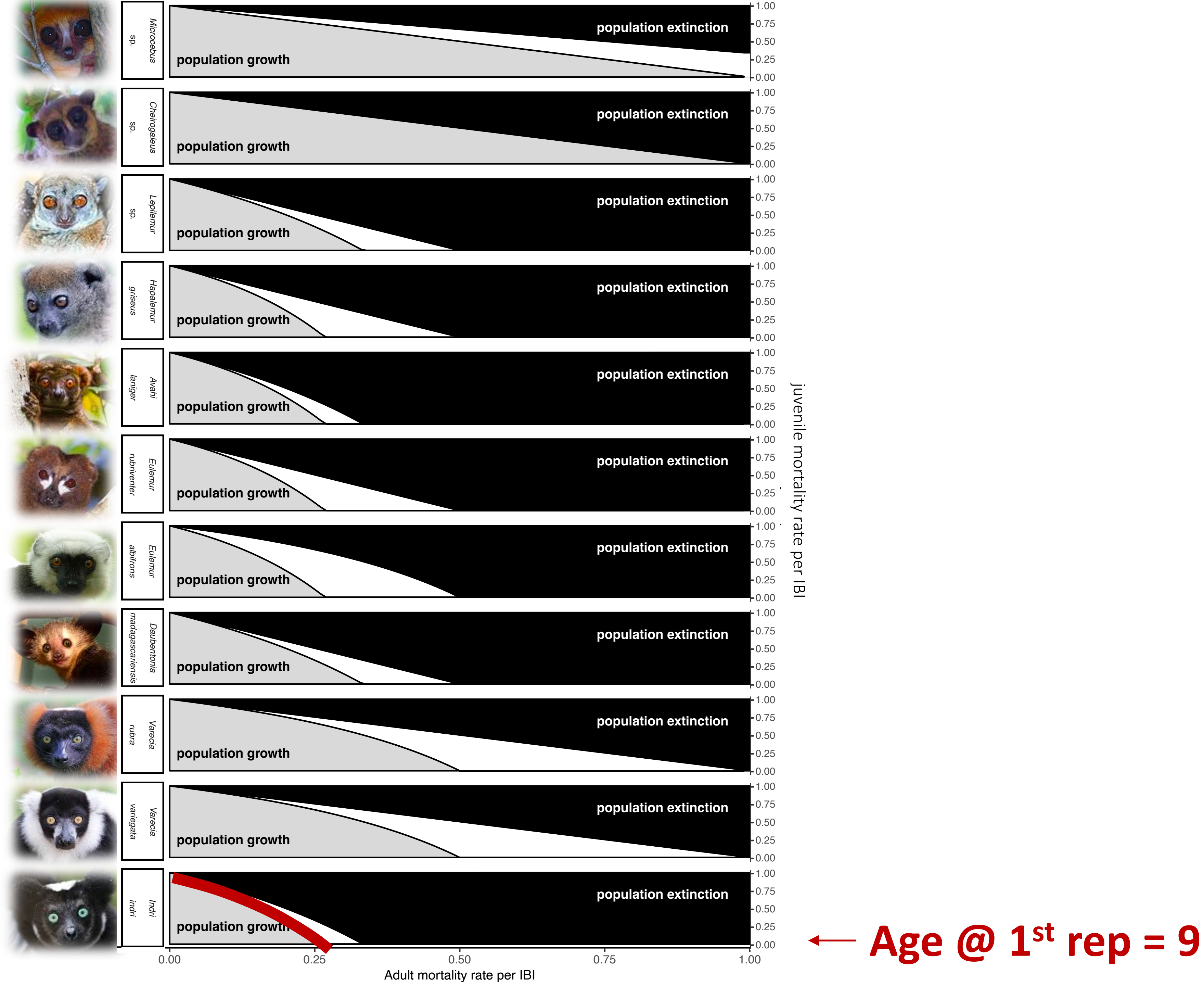

**2 offspring / IBI**

Brook et al. 2018. *Conservation Biology.*




**Age @ 1$^{st}$ rep = 6**

Brook et al. 2018. *Conservation Biology.*

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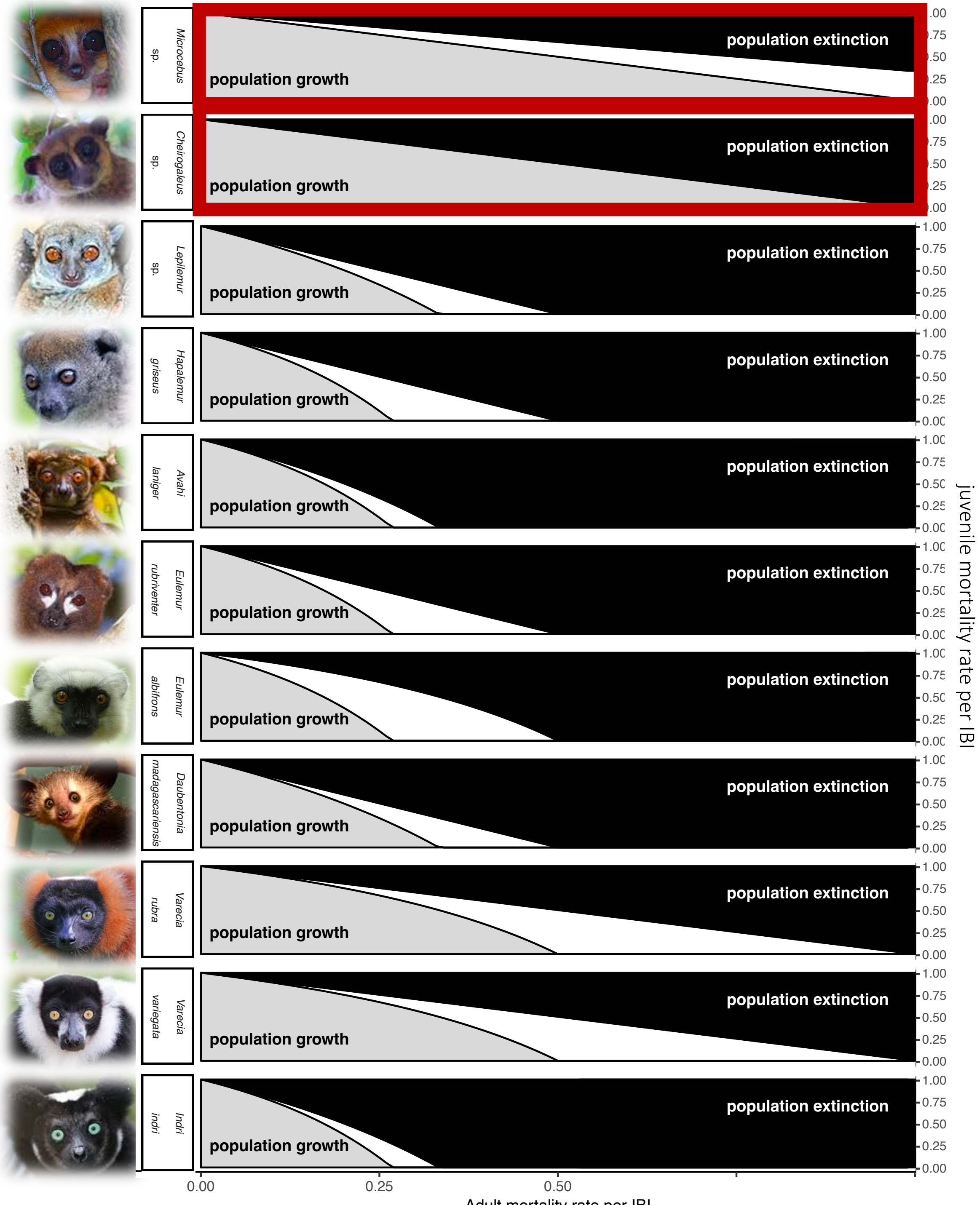
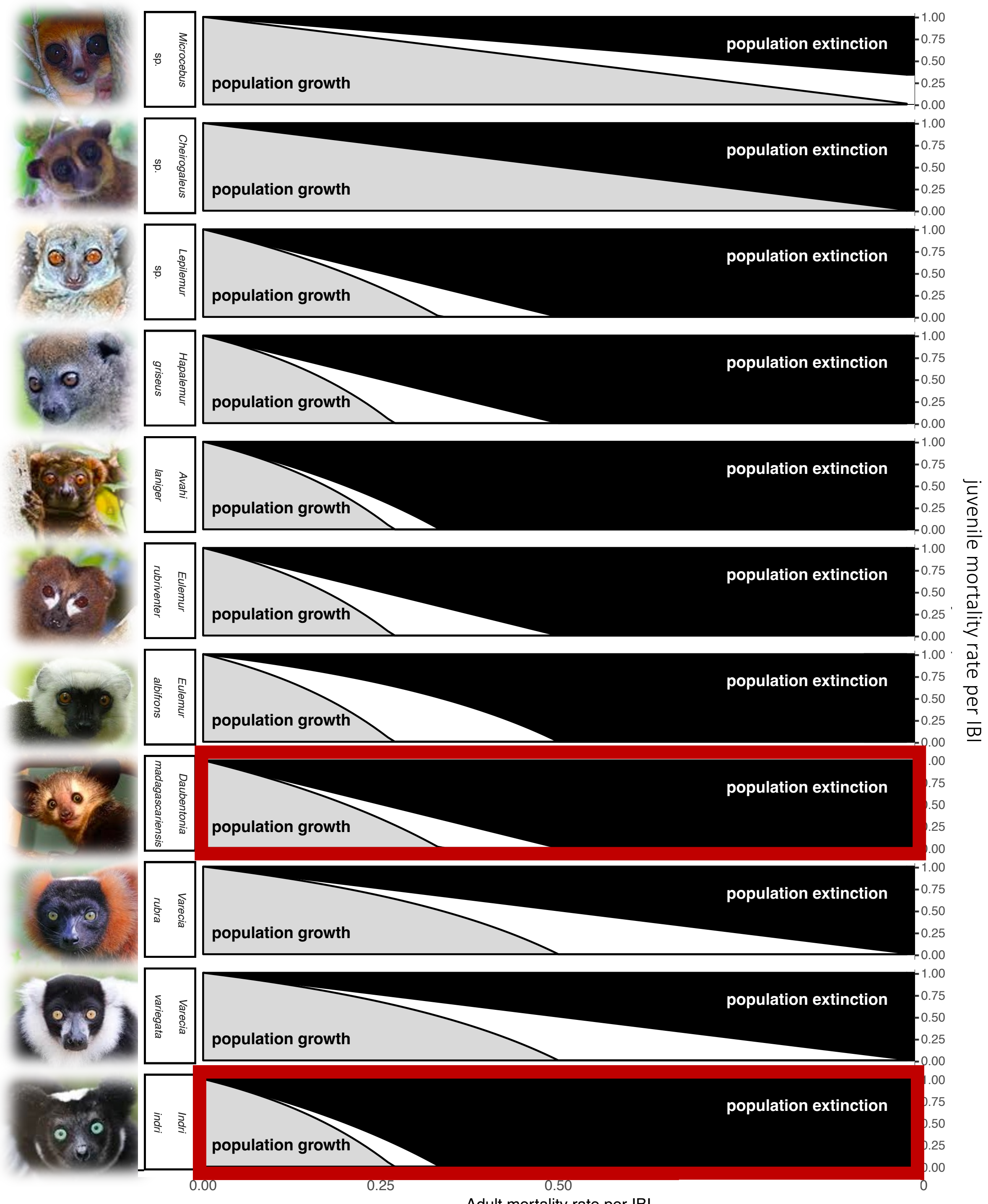



We plotted **zero-growth isoclines** to evaluate lemur population trajectories across different **mortality rates**.

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

Brook et al. 2018. *Conservation Biology.*

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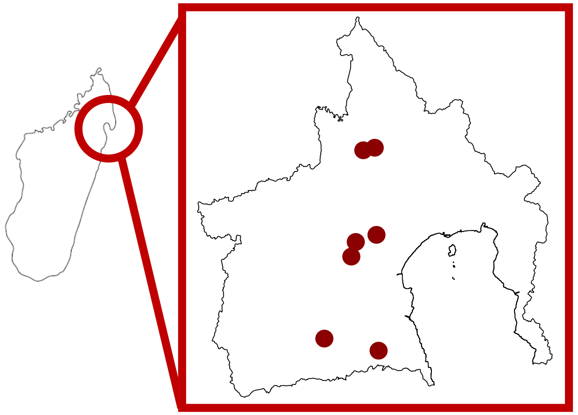
Lemurs with **faster life histories** are resilient to **mortality**.

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

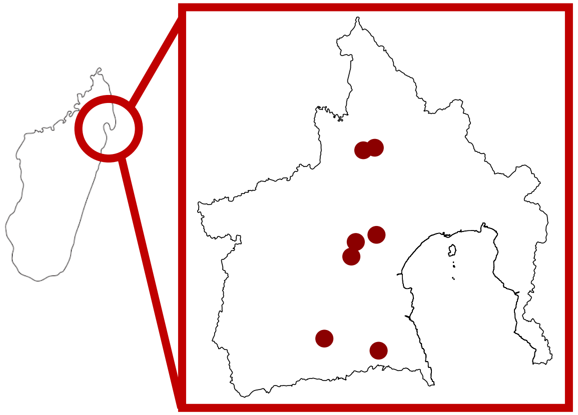
Brook et al. 2018. *Conservation Biology.*

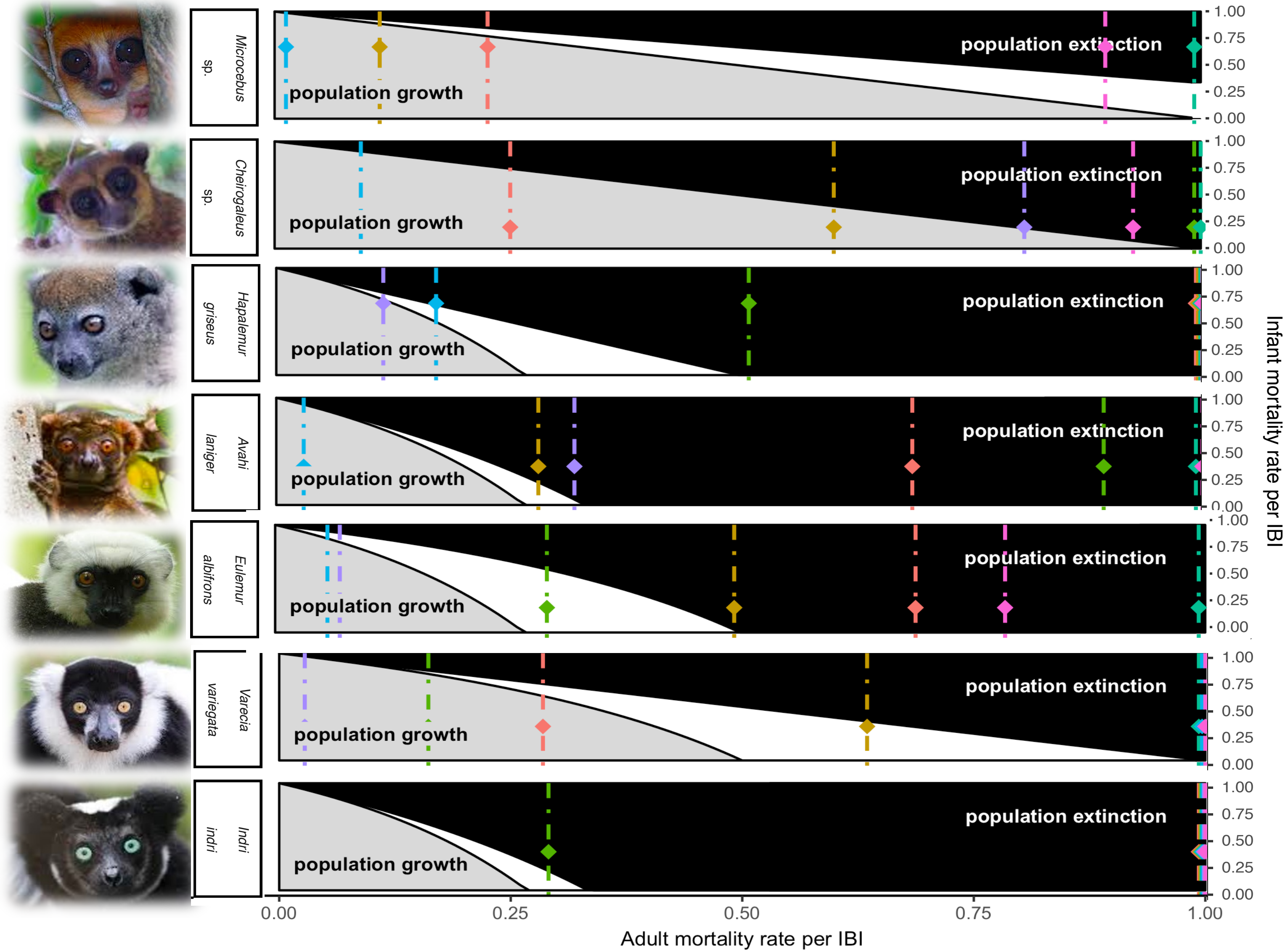
We paired household consumption data with **lemur densities** for 7 species at 7 sites to estimate hunt-based **mortality rates** and assess **harvest sustainability**.



Brook et al. 2018. *Conservation Biology.*

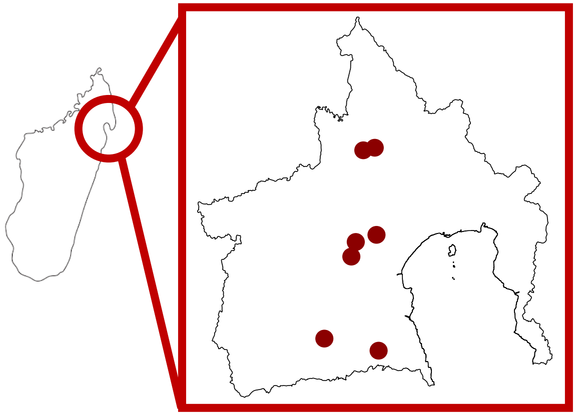
We paired household consumption data with **lemur densities** for 7 species at 7 sites to estimate hunt-based **mortality rates** and assess **harvest sustainability**.

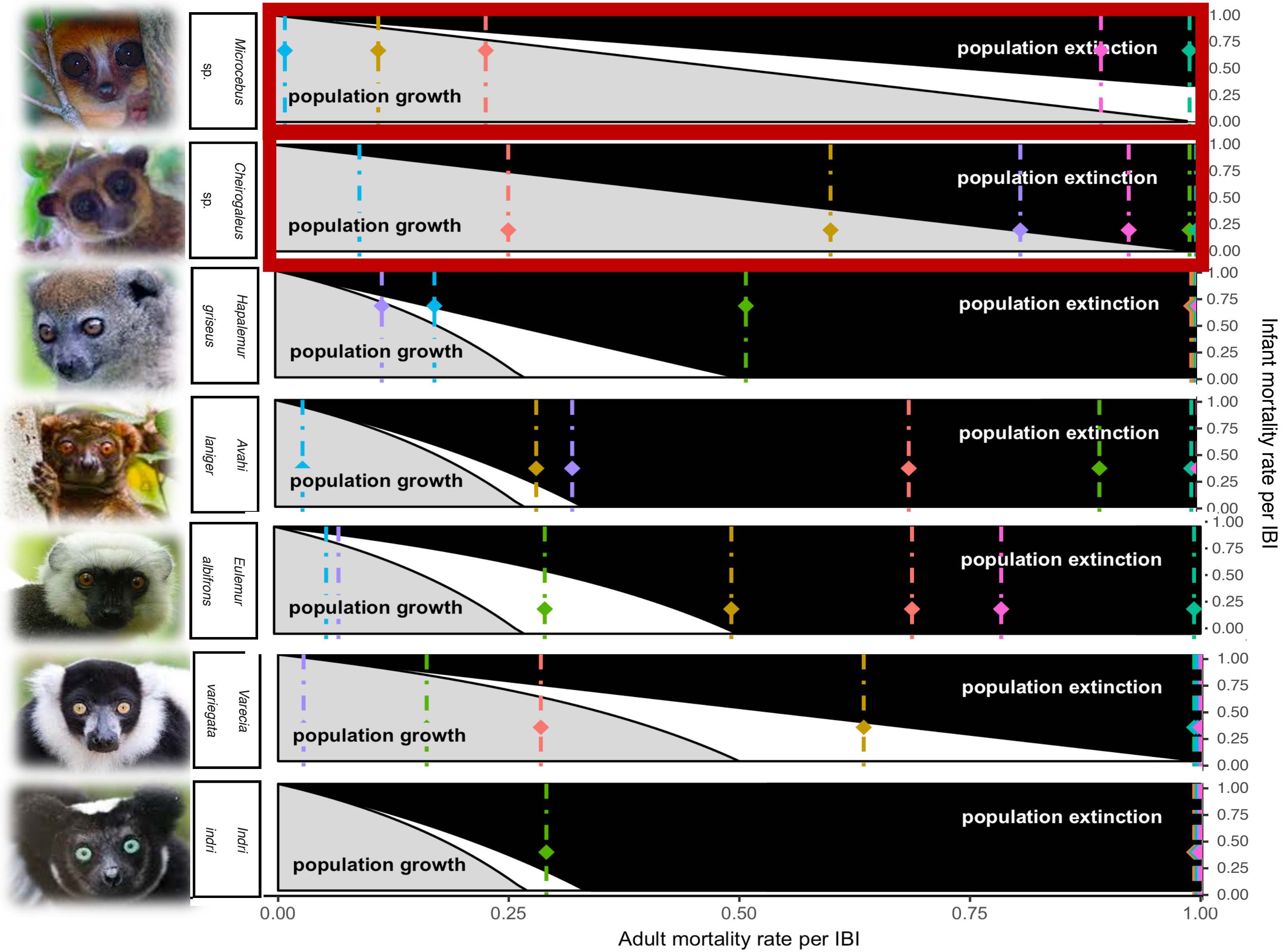





Brook et al. 2018. *Conservation Biology.*

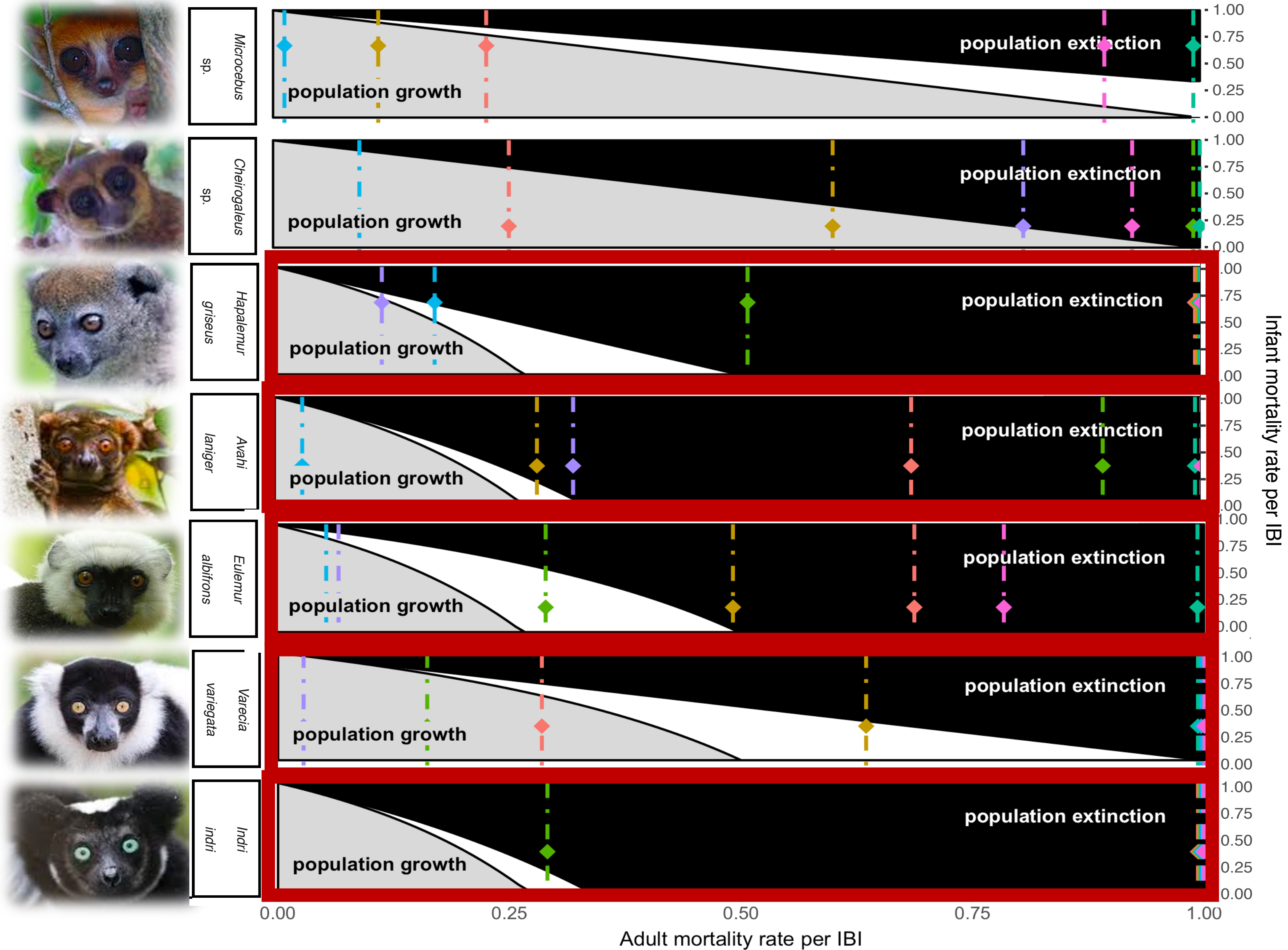
# **Small-bodied lemurs** are largely **harvested at sustainable rates** on the Makira-Masoala peninsula.

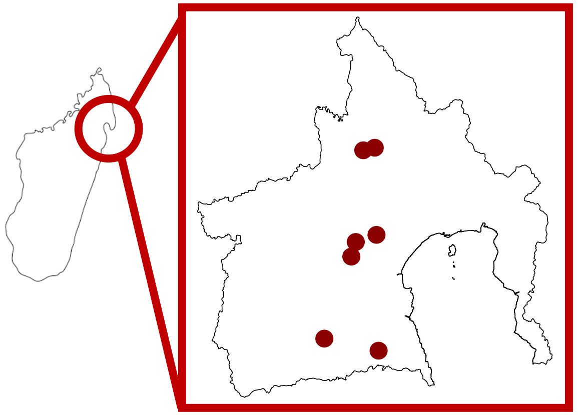





Brook et al. 2018. *Conservation Biology.*

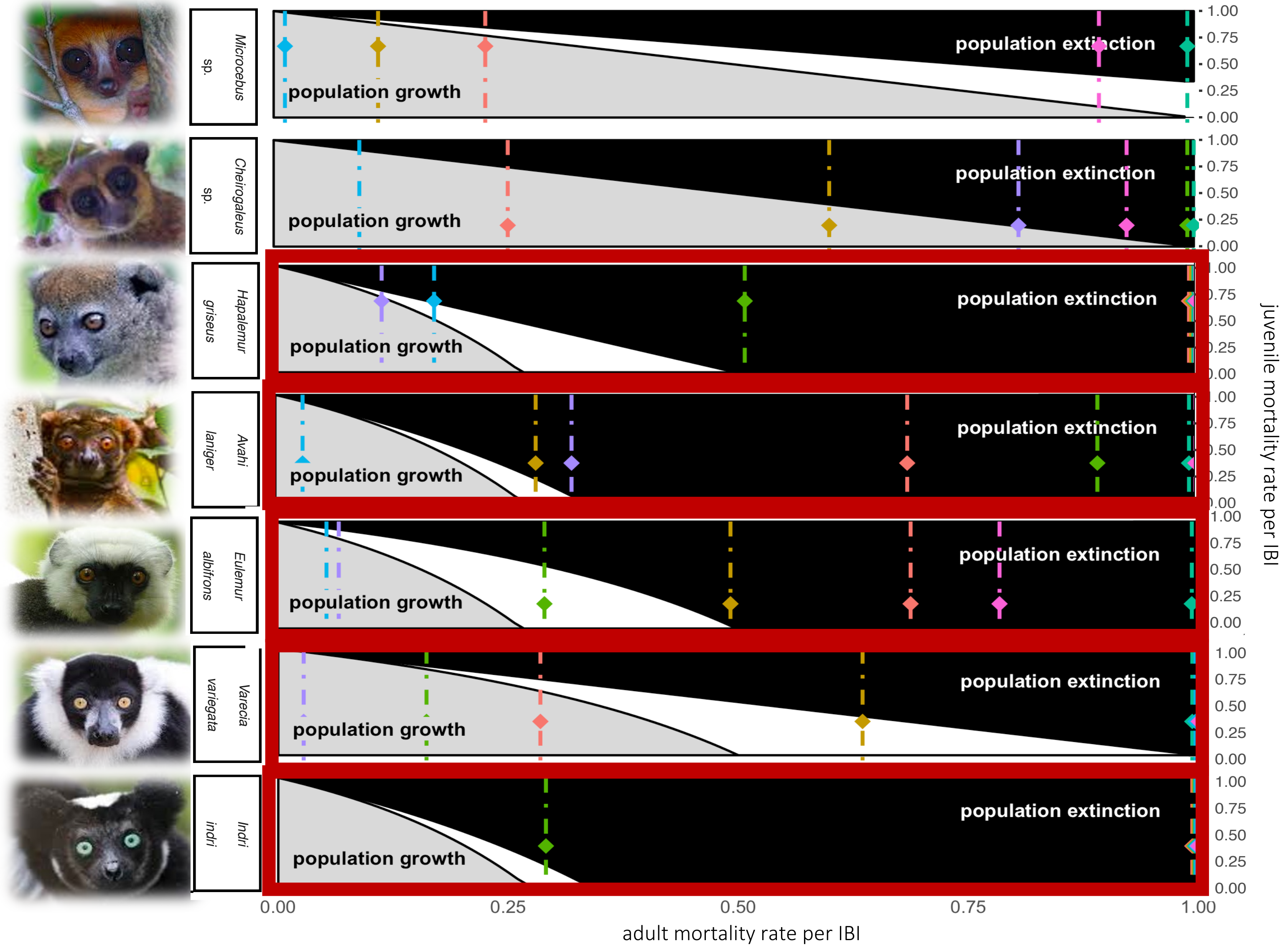
# By contrast, **larger-bodied lemurs** are severely **threatened**.

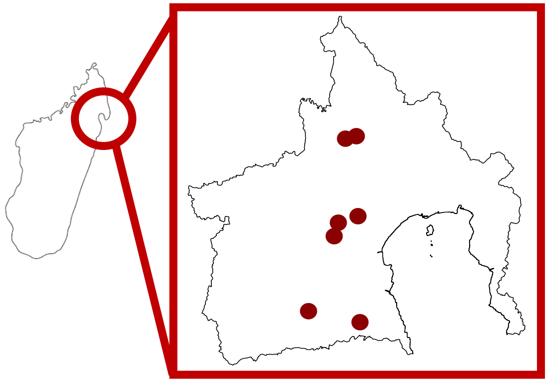


Brook et al. 2018. *Conservation Biology.*

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



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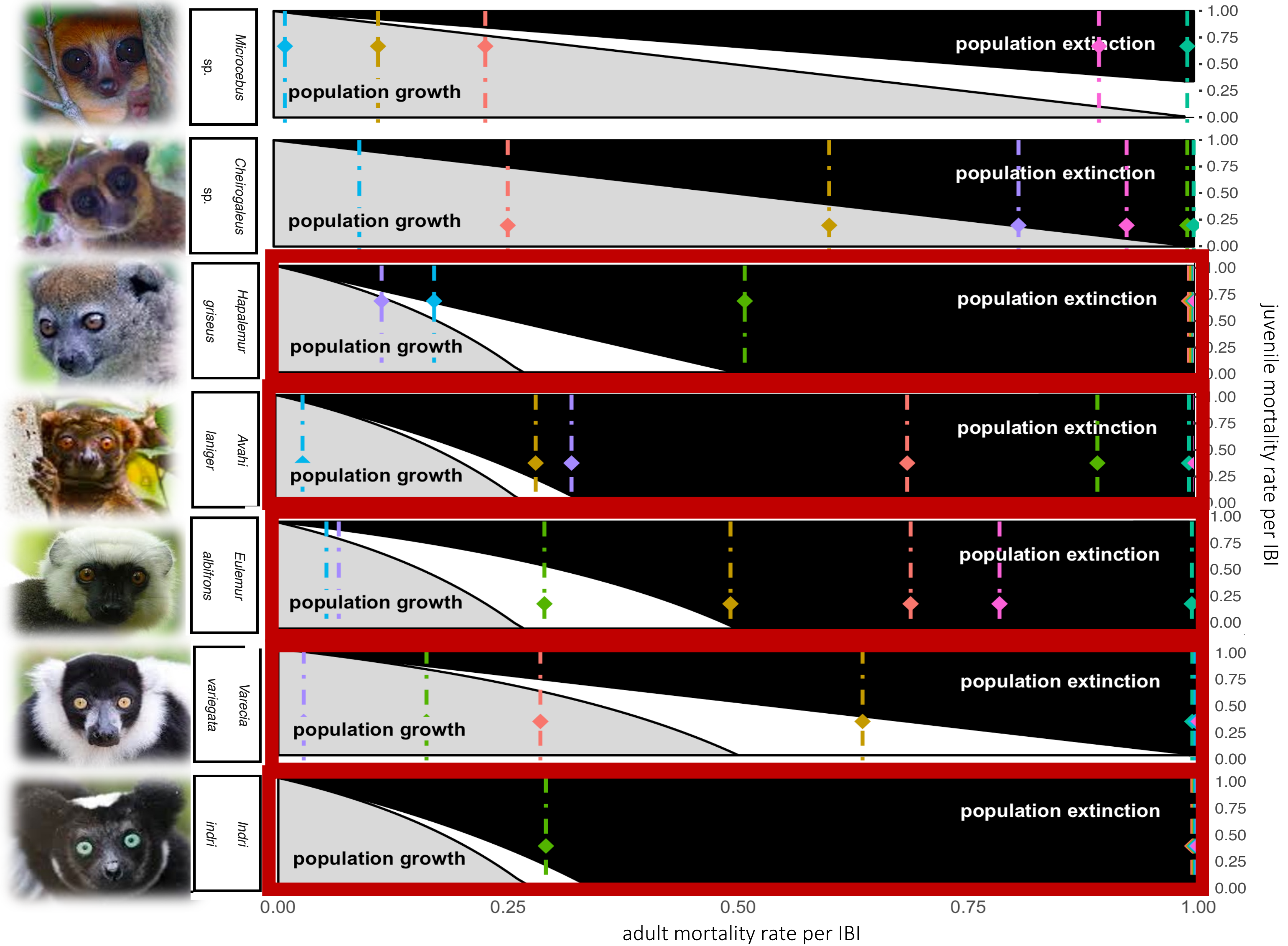
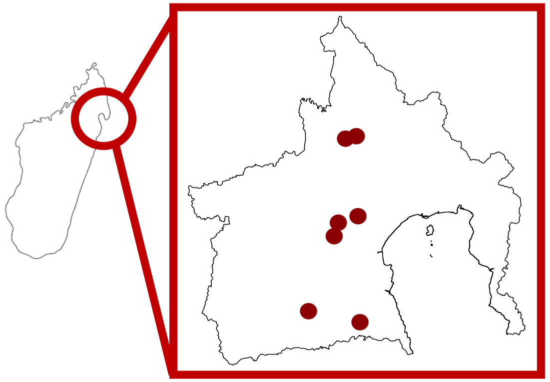


The **'Allee effect'** describes the correlation between population size and population 'fitness', often measured by the population rate of increase, $\lambda$.

We will revisit this!

Brook et al. 2018. *Conservation Biology.*

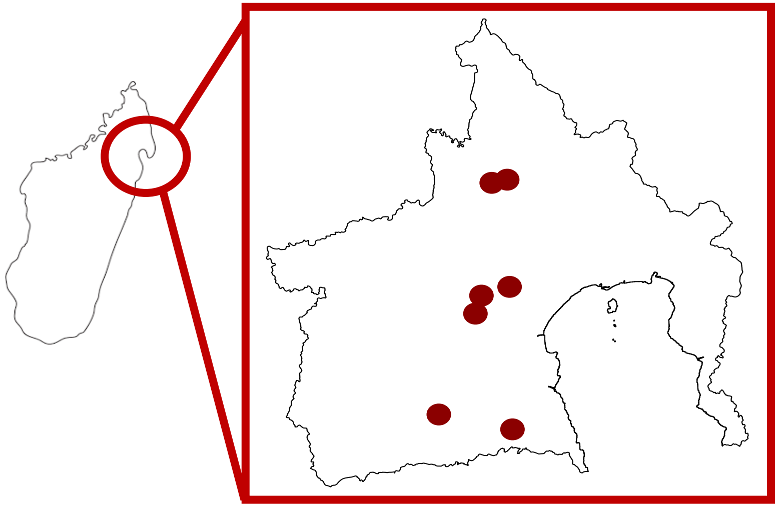
Finally, we built a regional **metapopulation model** to simulate population dynamics into the future.


Brook et al. 2018. *Conservation Biology.*

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


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- Starting population of 200 lemurs per site
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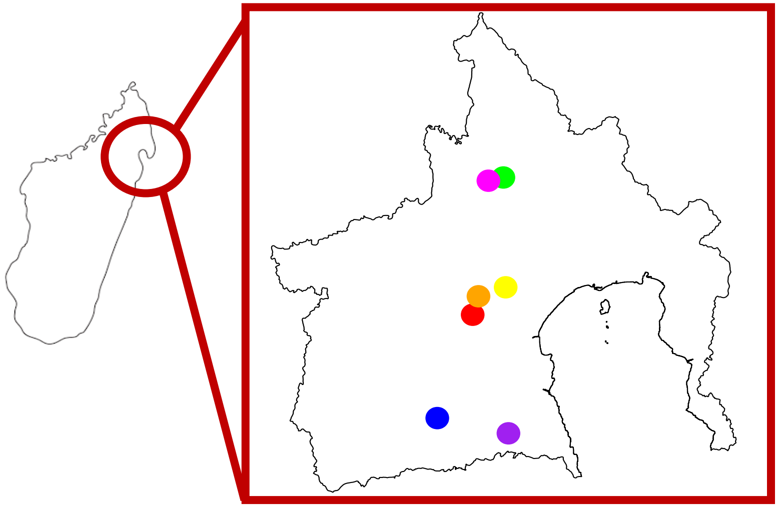

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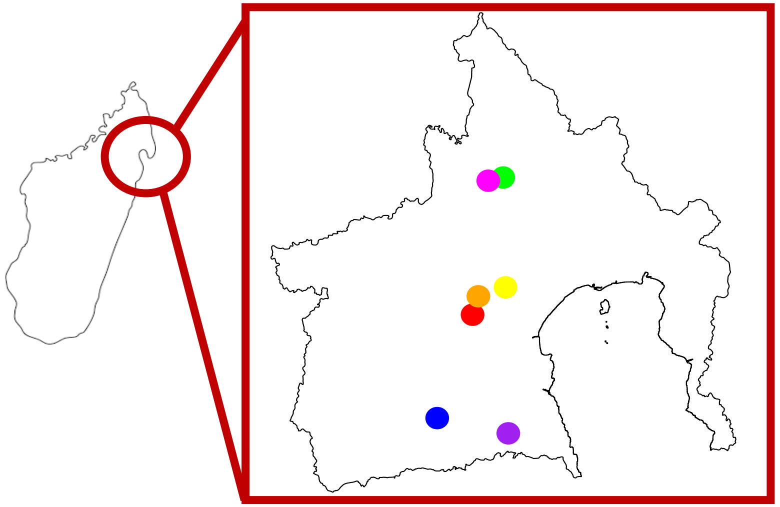

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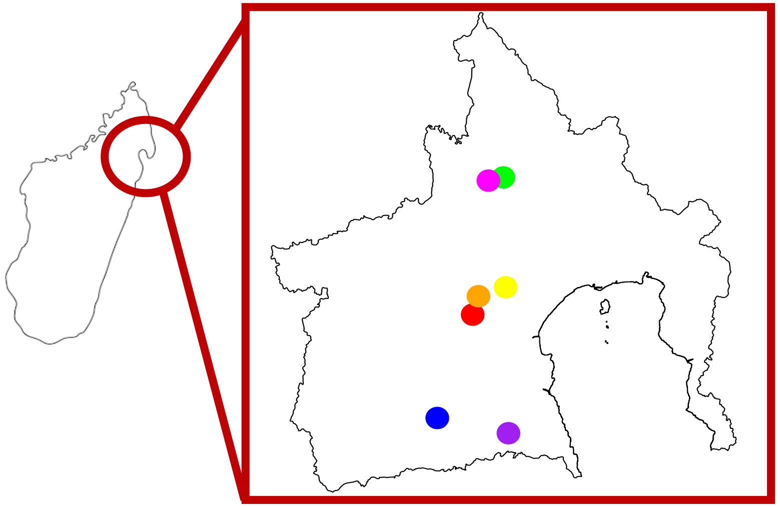

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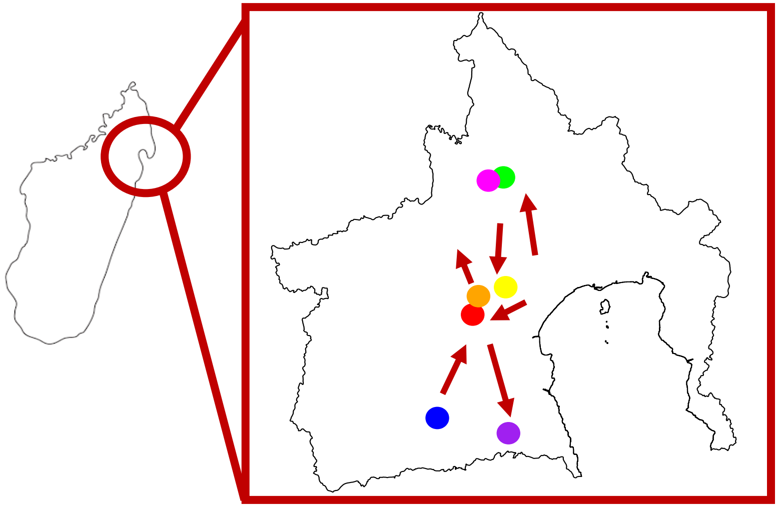
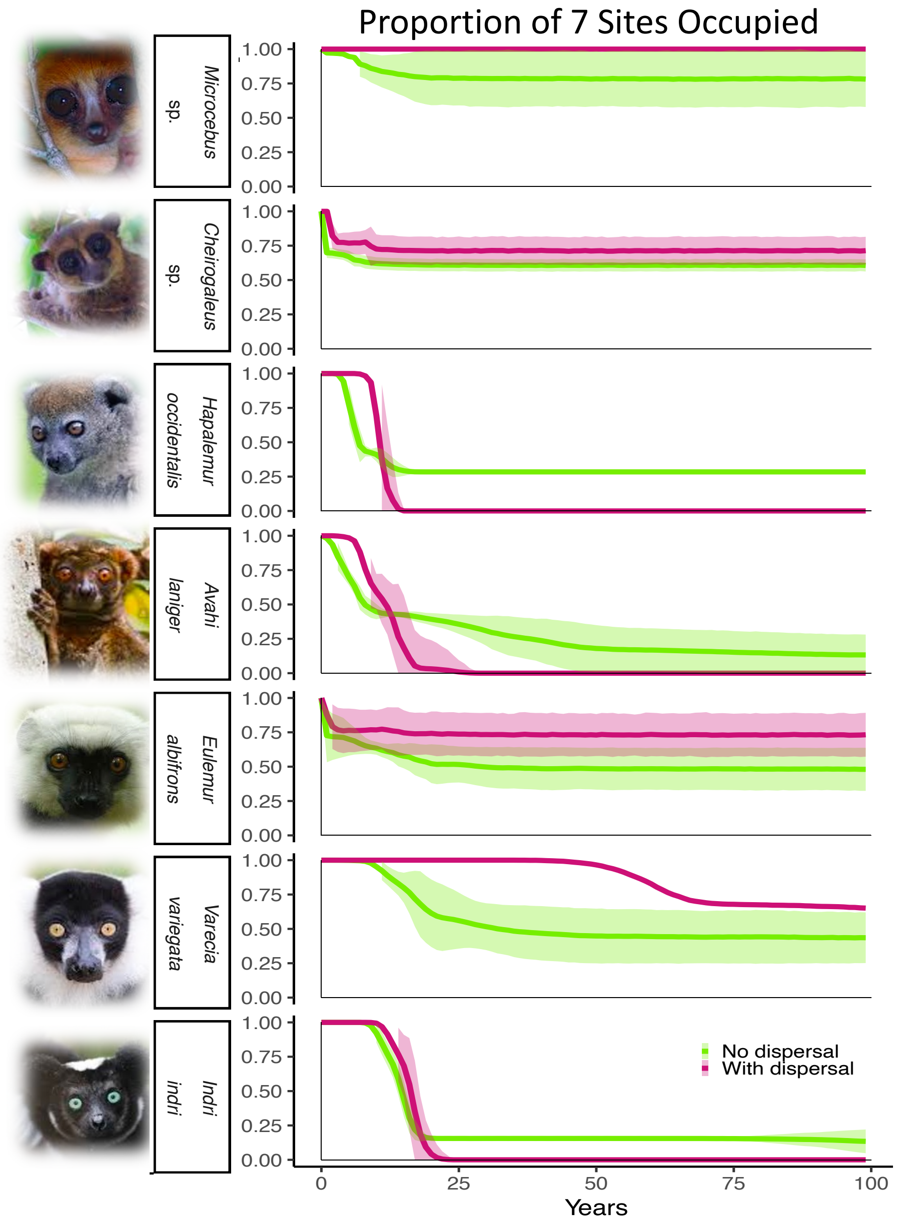
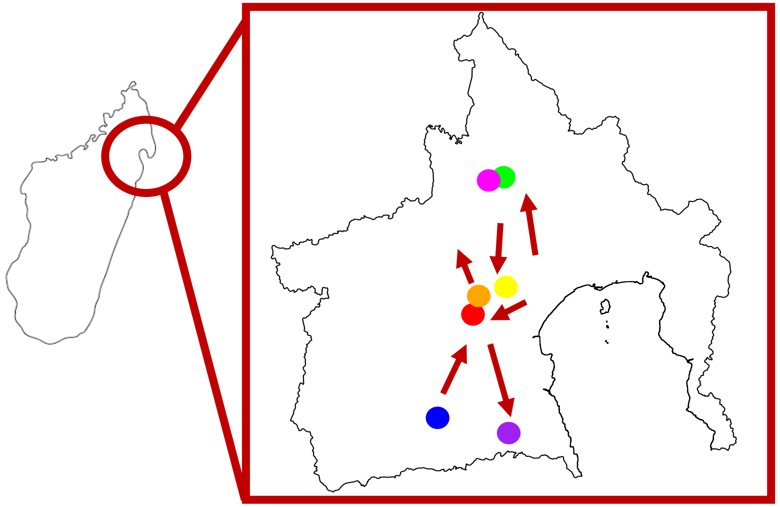
- Density dependent effects on fecundity
- Compared **no dispersal scenarios** vs. scenarios allowing for **stochastic dispersal** mediated by geographic distance



Brook et al. 2018. *Conservation Biology.*

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



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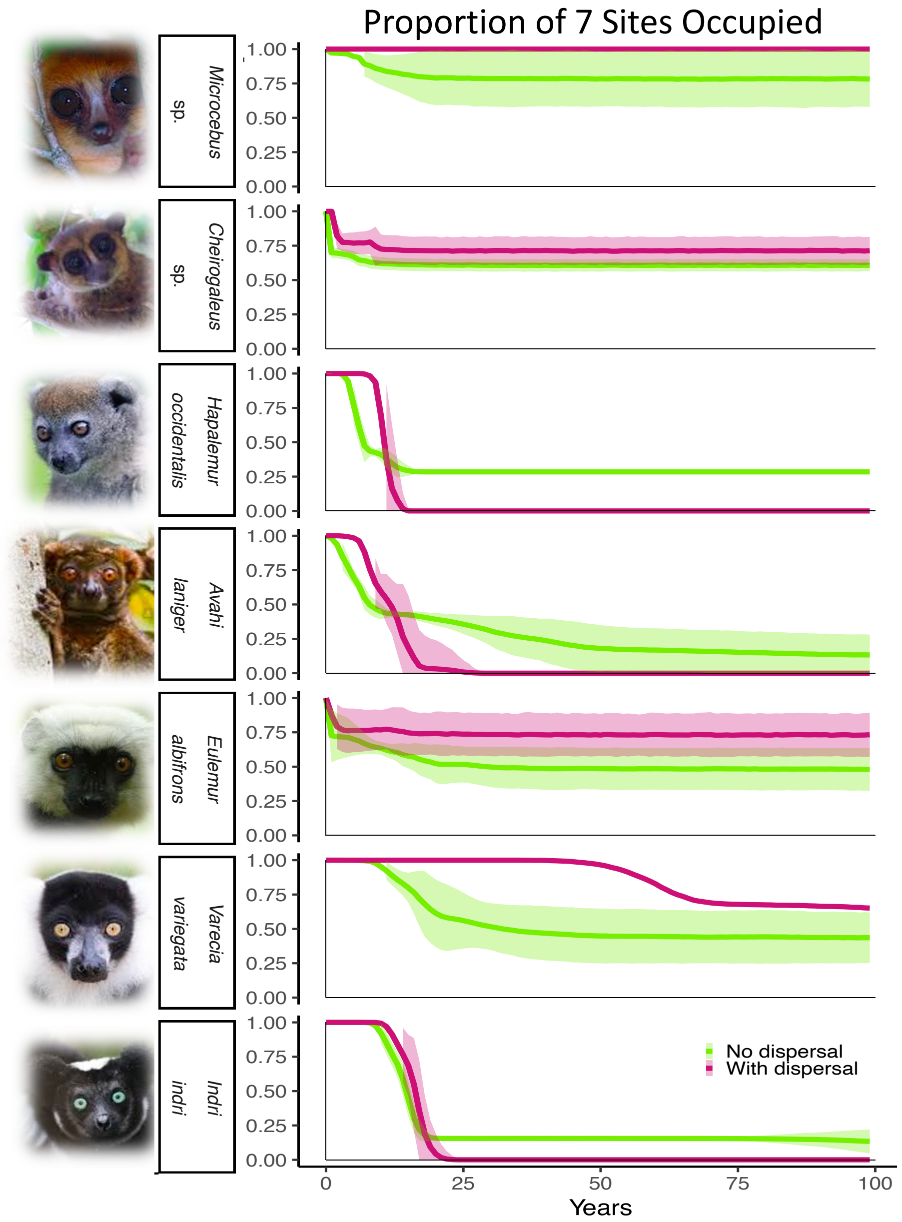
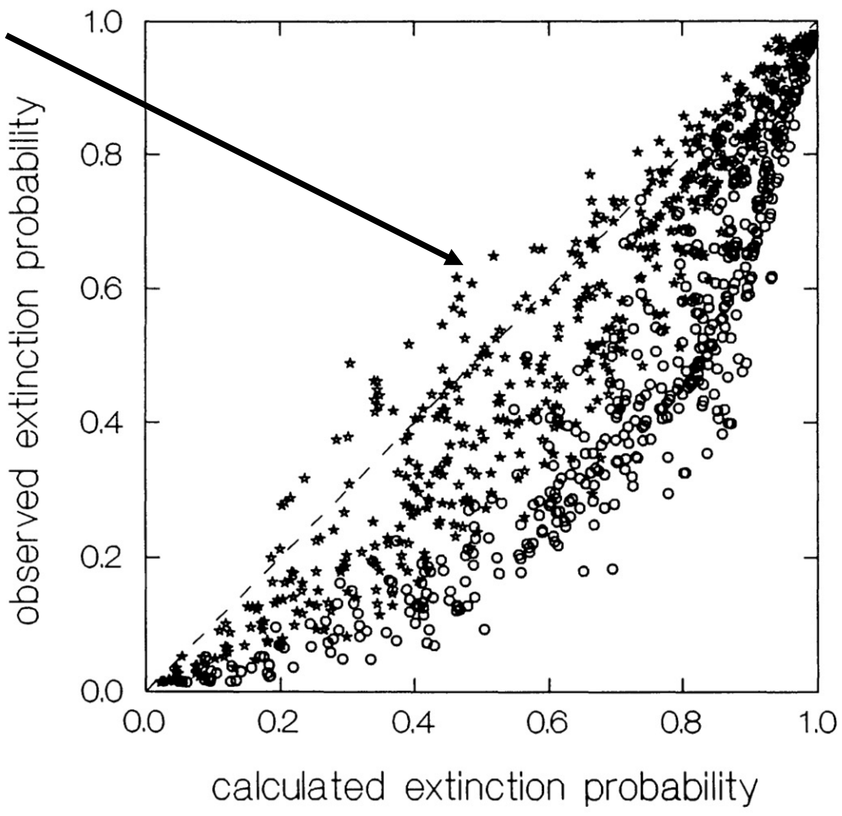



## In contrast to the rescue effect observed in Hanski!

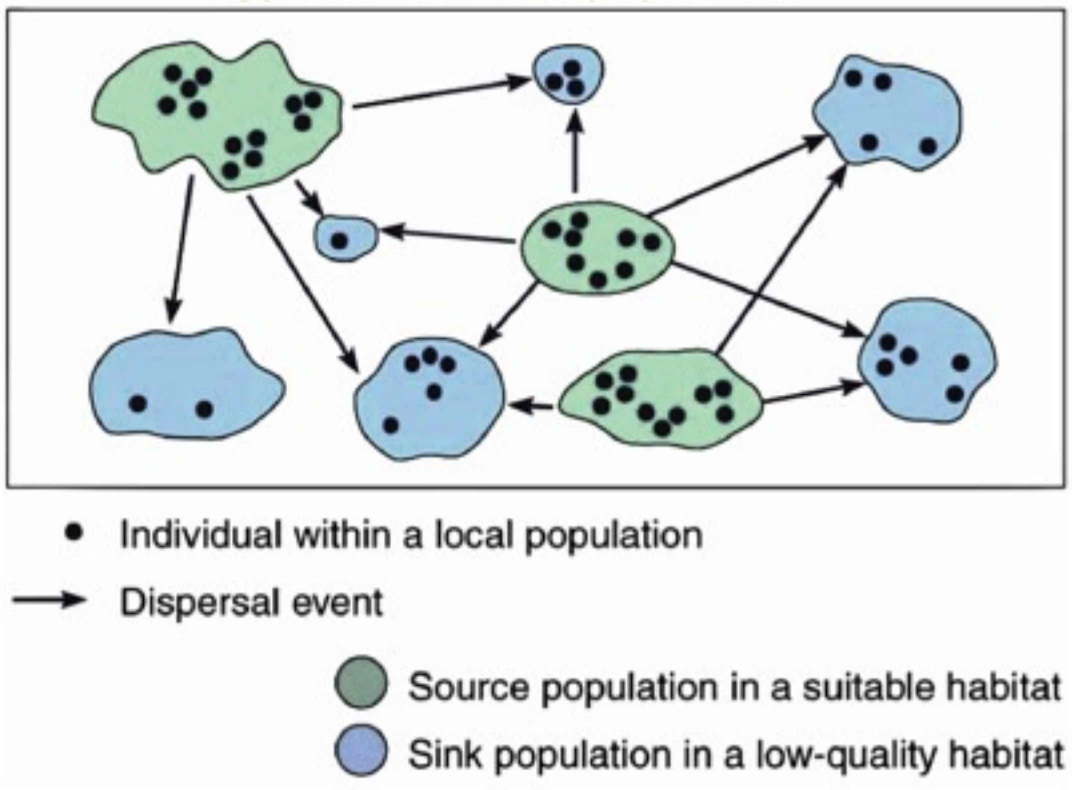
star points recalculated with rescue effect from Levins' model




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.

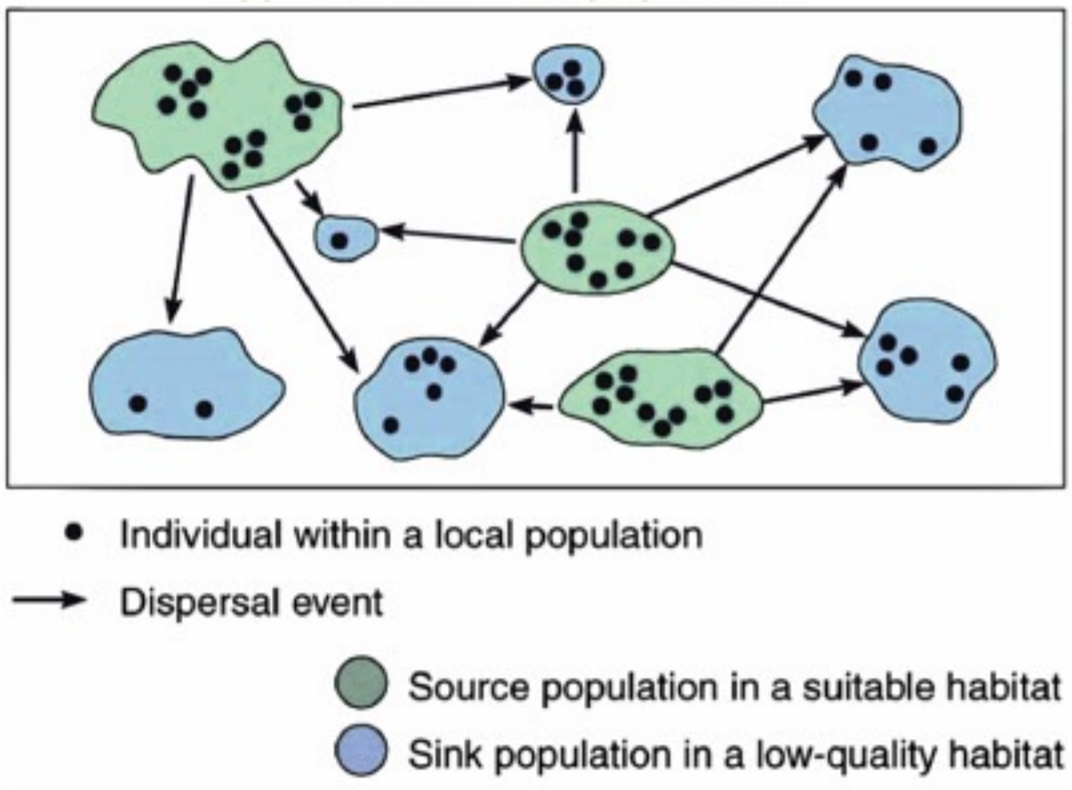
- Dispersal can drive **extinction** if the majority of sites function as **population sinks**.




Pulliam 1988. *The American Naturalist.*

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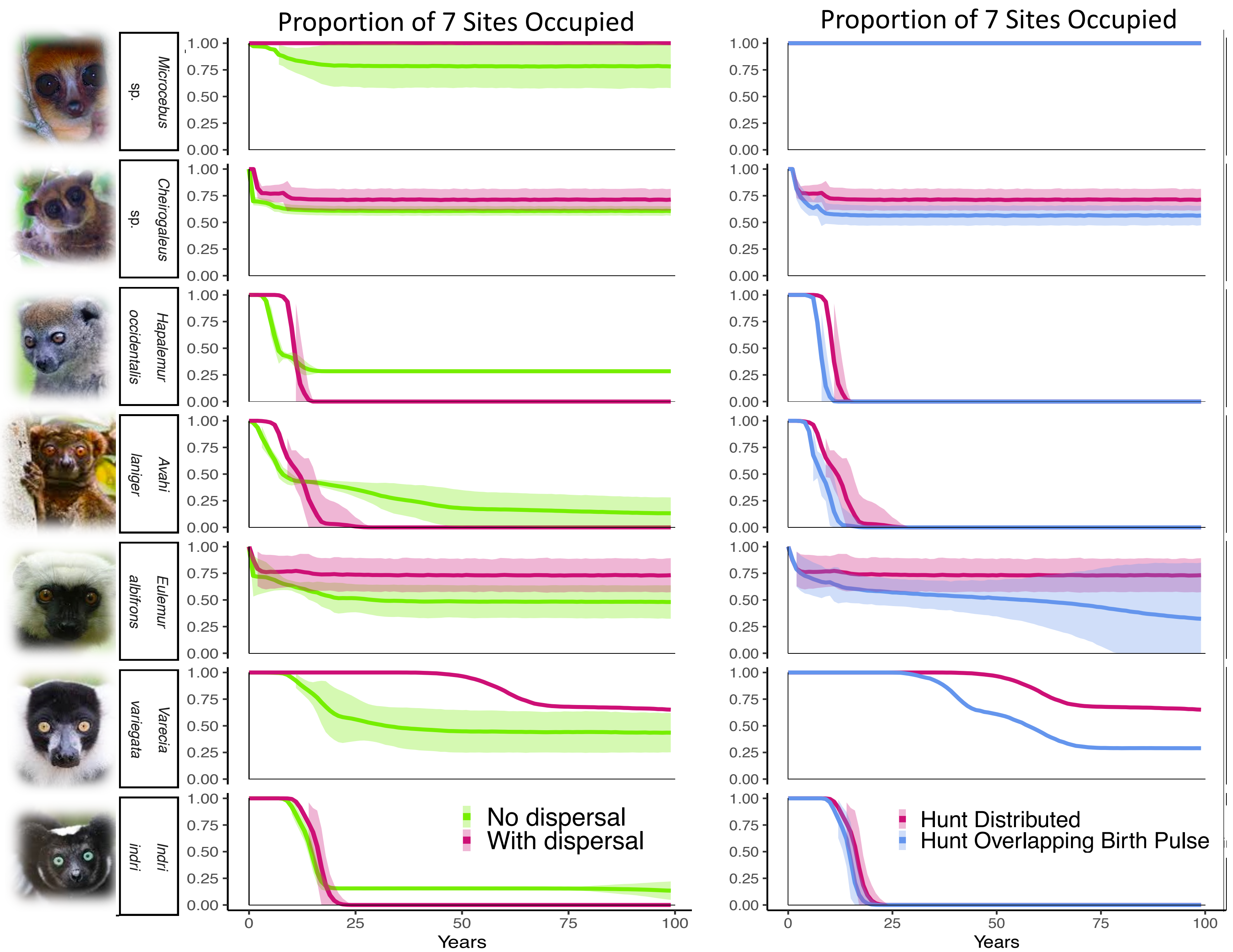
# Species are even **further threatened** when **hunt seasonality** overlaps the **annual birth pulse**.

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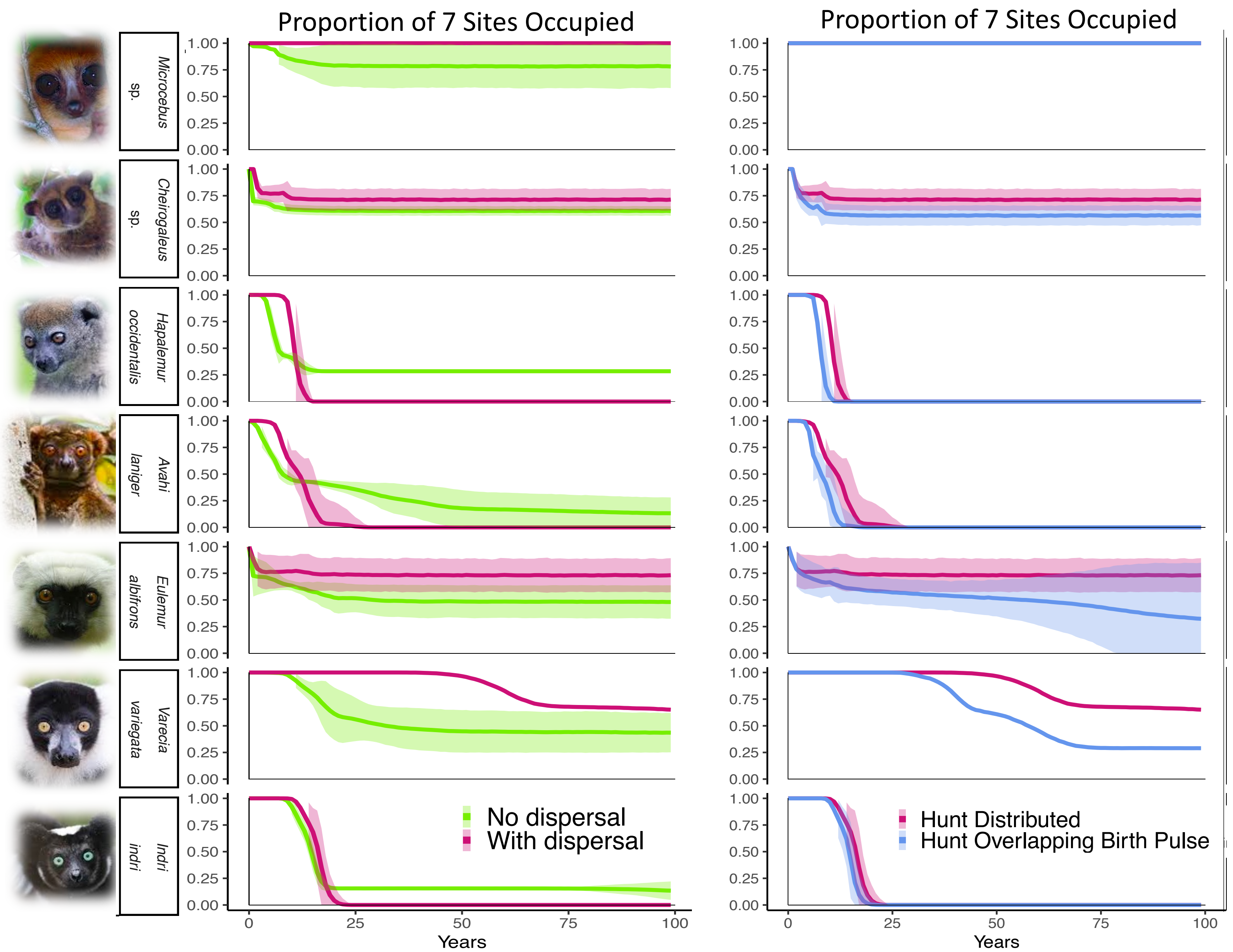


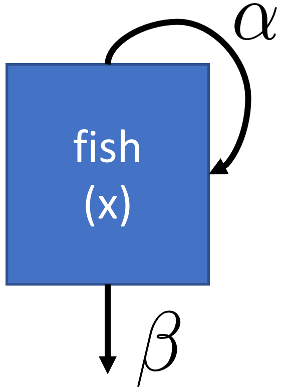

Our lemur model highlights some of the earlier challenges discussed with modeling '**maximum sustainable yield**' in fisheries!

Simplest representations of MSY:

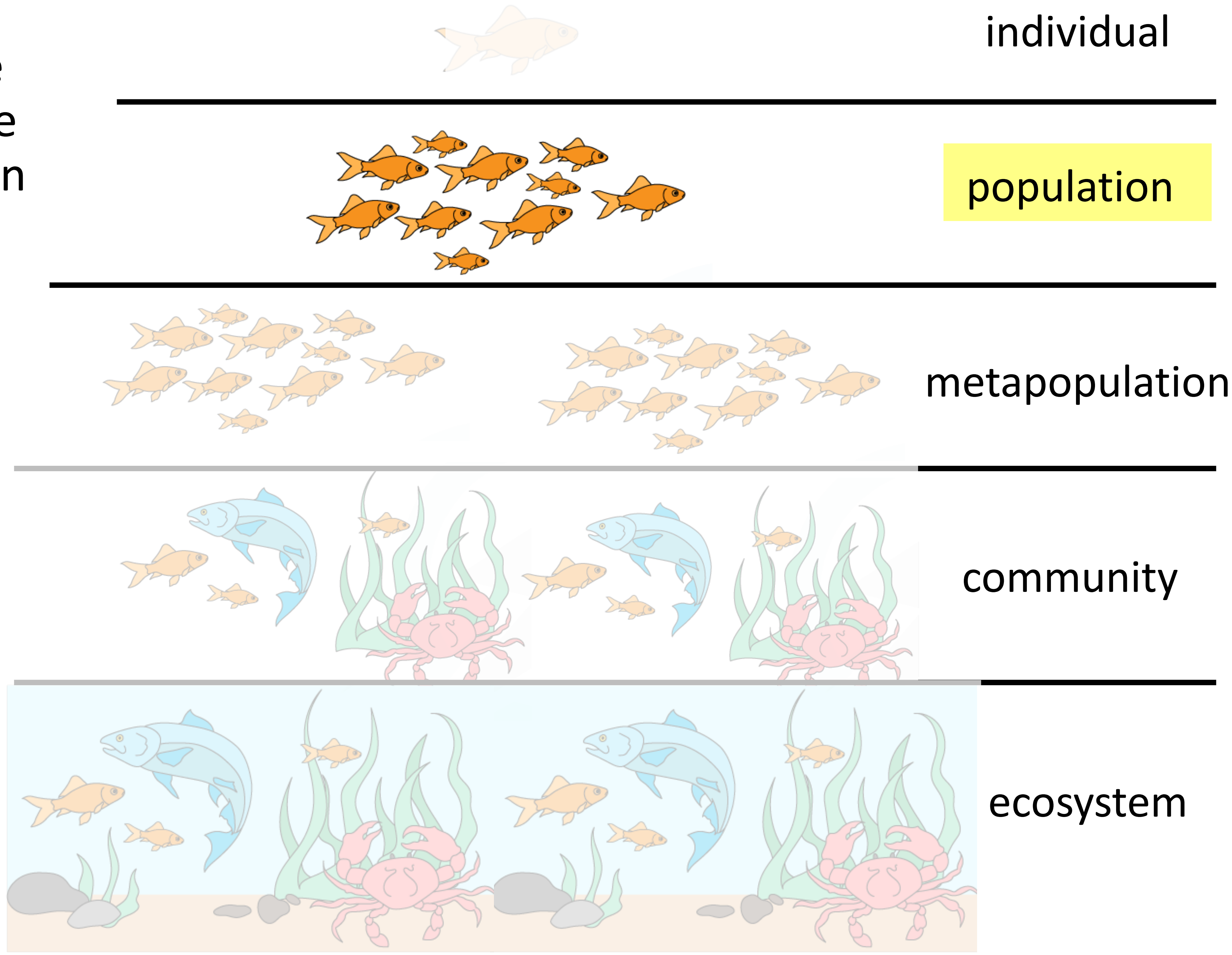
- Neglect population structure.
- Assume constant harvest.
- Ignore environmental and demographic stochasticity

Brook et al. 2018. *Conservation Biology.*

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




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



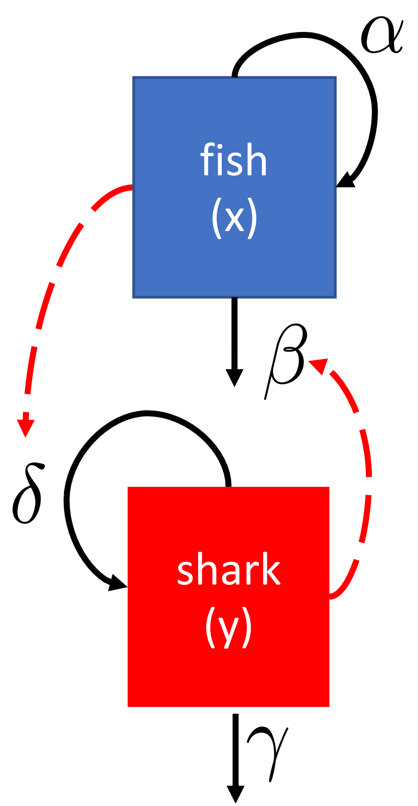
The logistic growth equation offers an explanation for population self-regulation, an example of **intraspecific competition**.

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

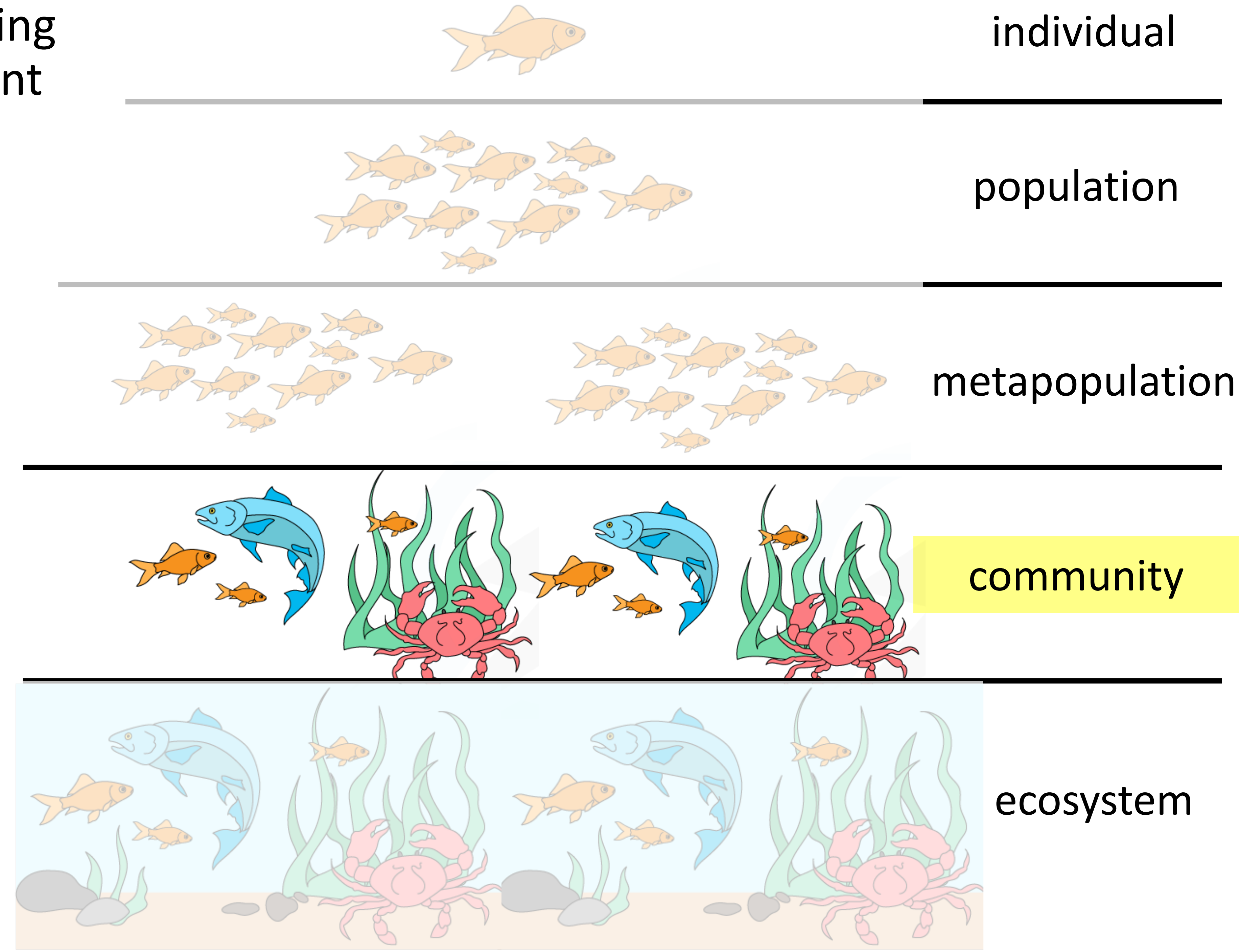
THE CROCODILE'S FRIEND.

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

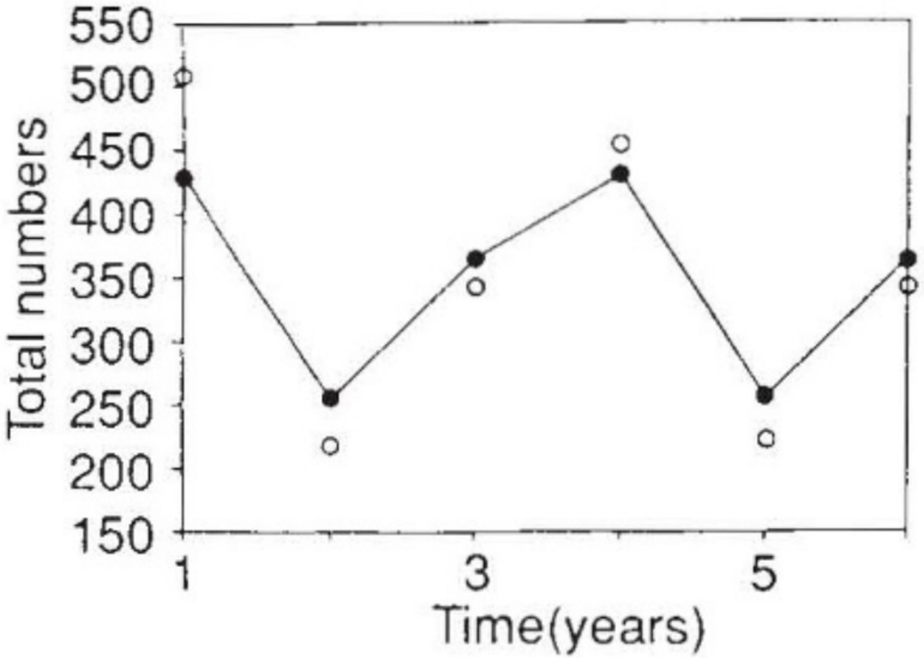



*How does fish abundance **vary** with **changes** in shark abundance?*



# Remember those Soay sheep…


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

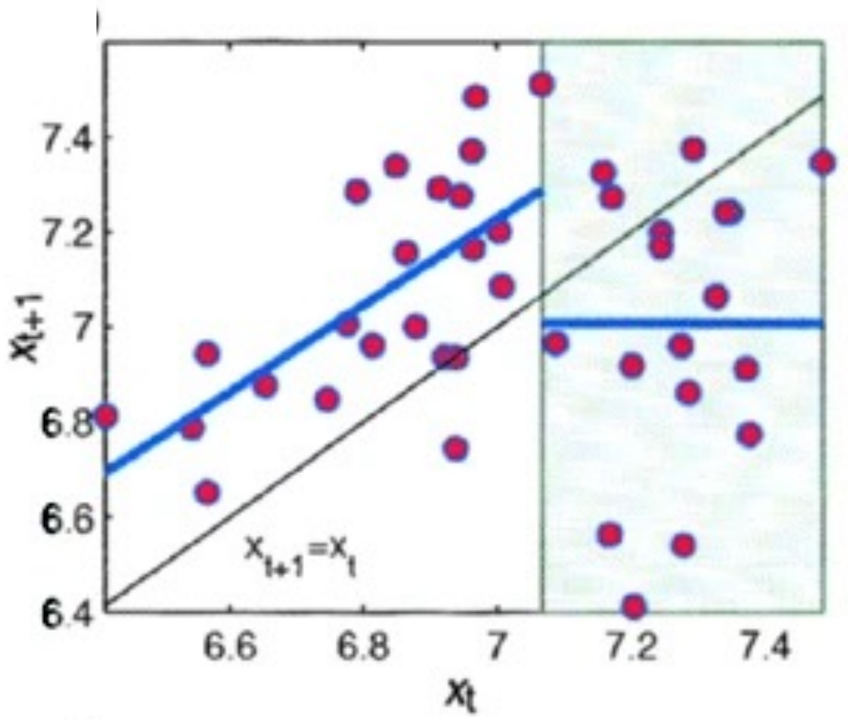




**Overcompensation and population cycles in an ungulate**

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

*Nature* **355**, 823–826 (1992) | Cite this article

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



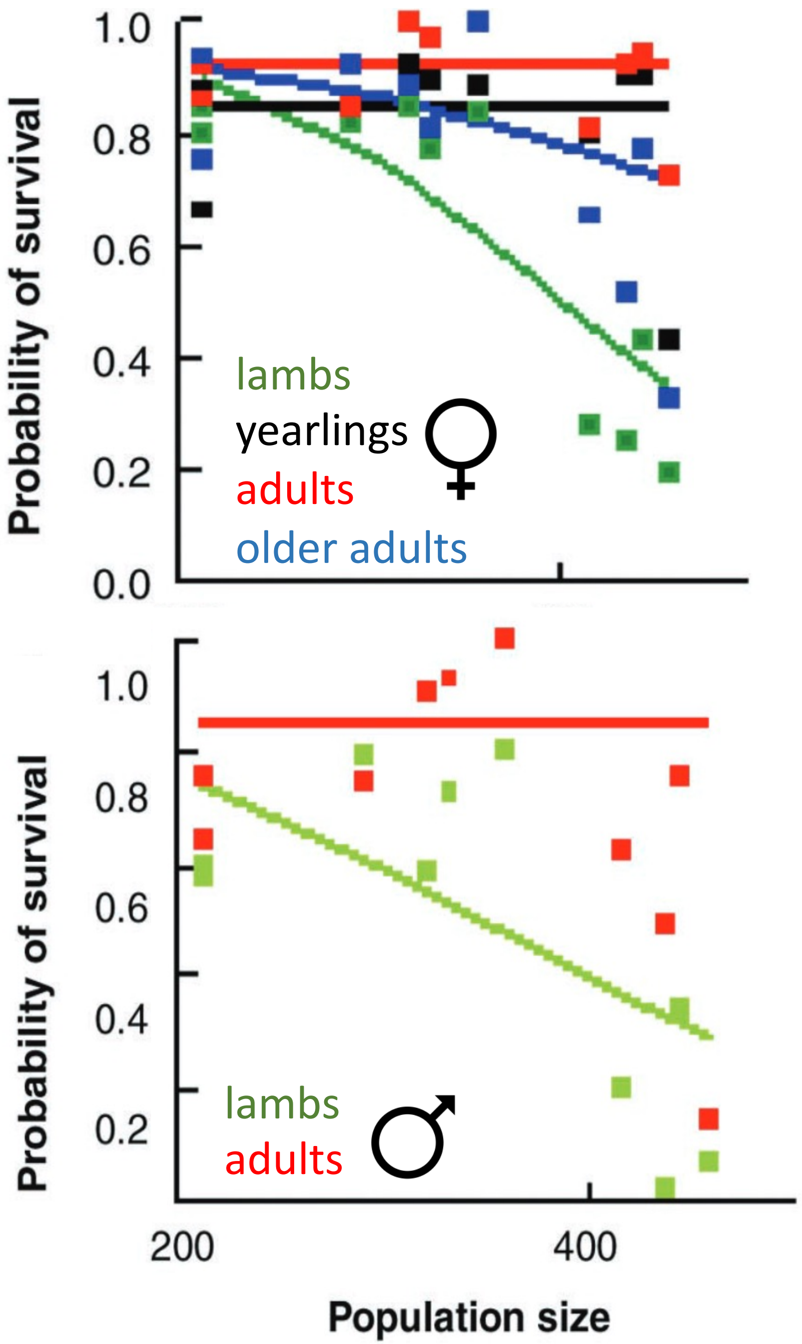
*Nature* **394**, 674–677 (1998) | Cite this article

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

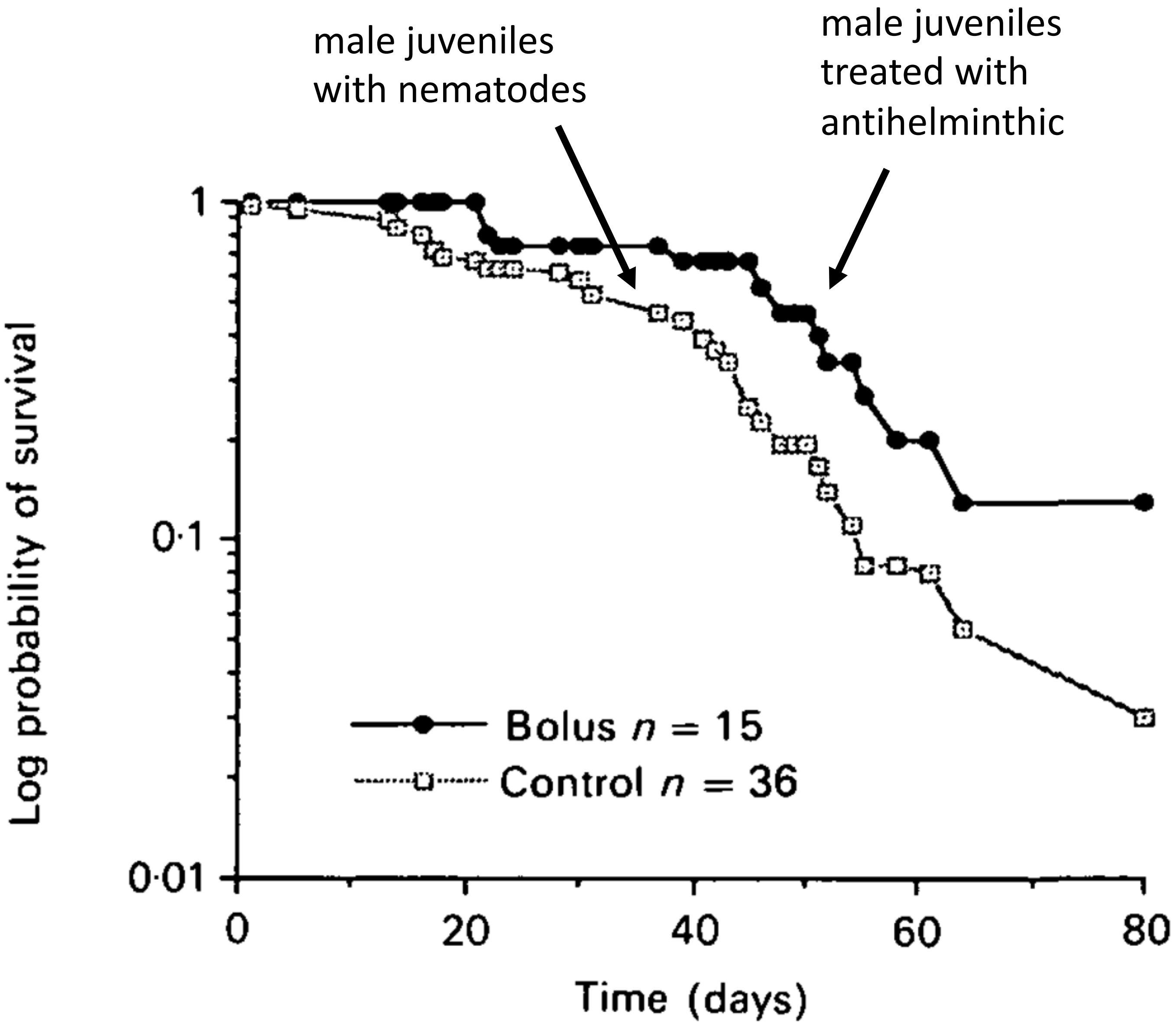
# Age, Sex, Density, Winter Weather, and Population Crashes in Soay Sheep

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

25 MAY 2001 VOL 292 SCIENCE www.sciencemag.org



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




Gulland 1992. *Parasitology.*

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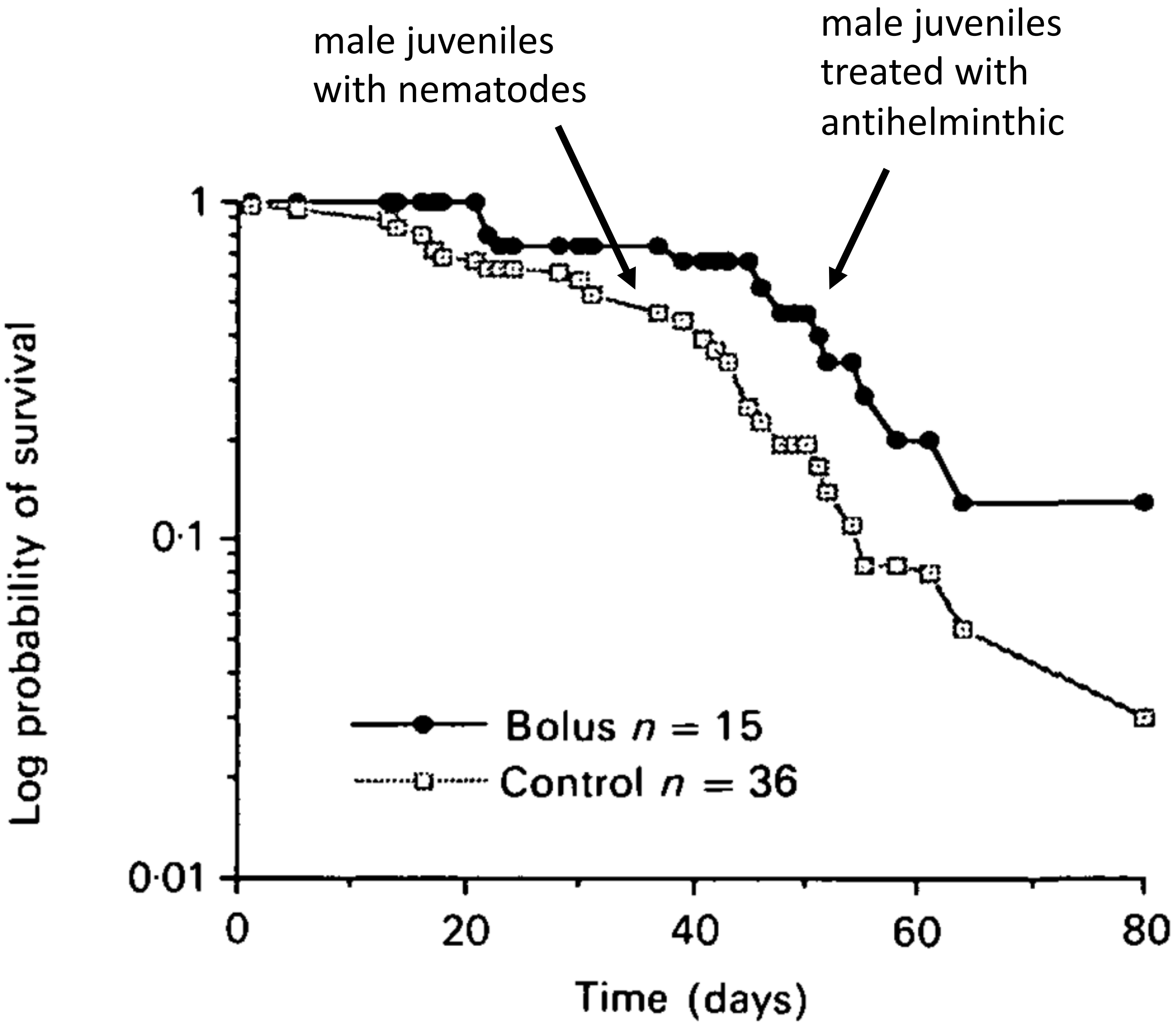
The team is actively working on a model that incorporates **nematode-sheep (parasite-host) interactions** to explain longterm sheep population dynamics.




Gulland 1992. *Parasitology.*

# 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
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"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**."

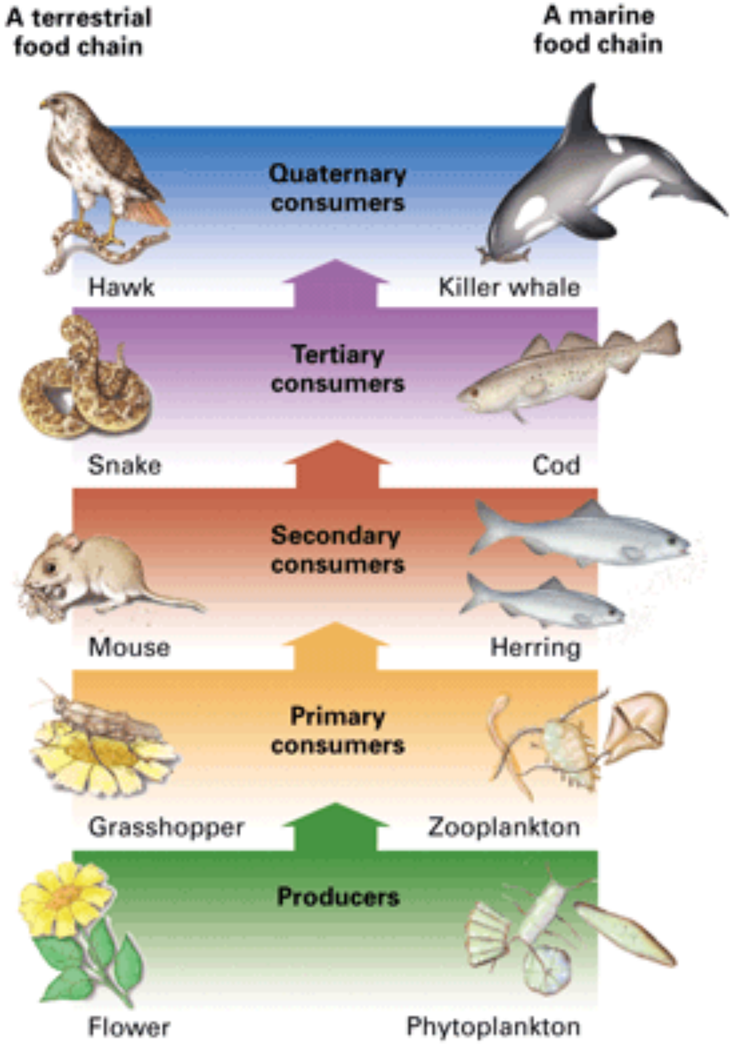
-John Steinbeck

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

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

- **Trophic levels** refer to hierarchal 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.



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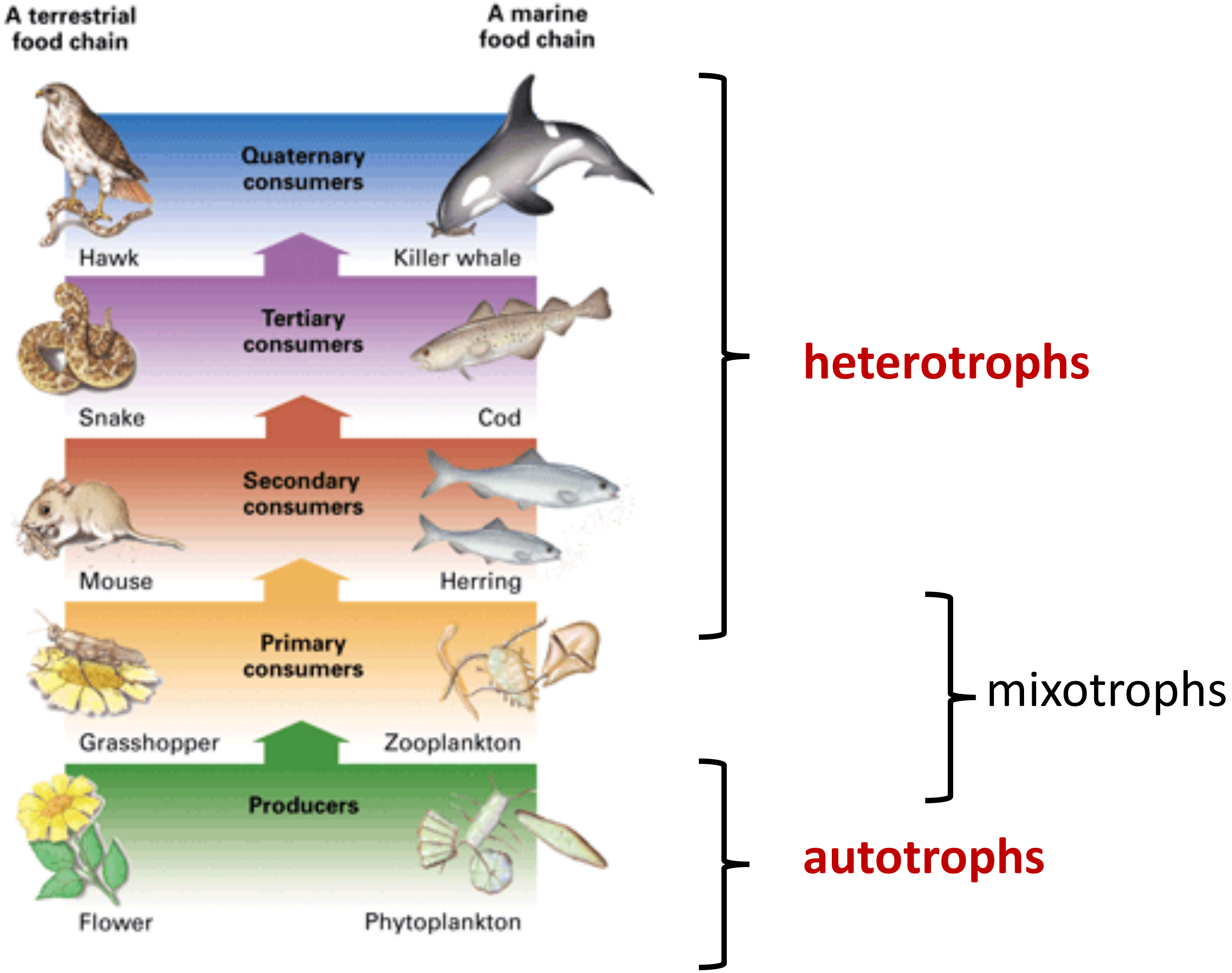

# **Food webs** more accurately represent the complexity of ecological interactions that span multiple **trophic levels**

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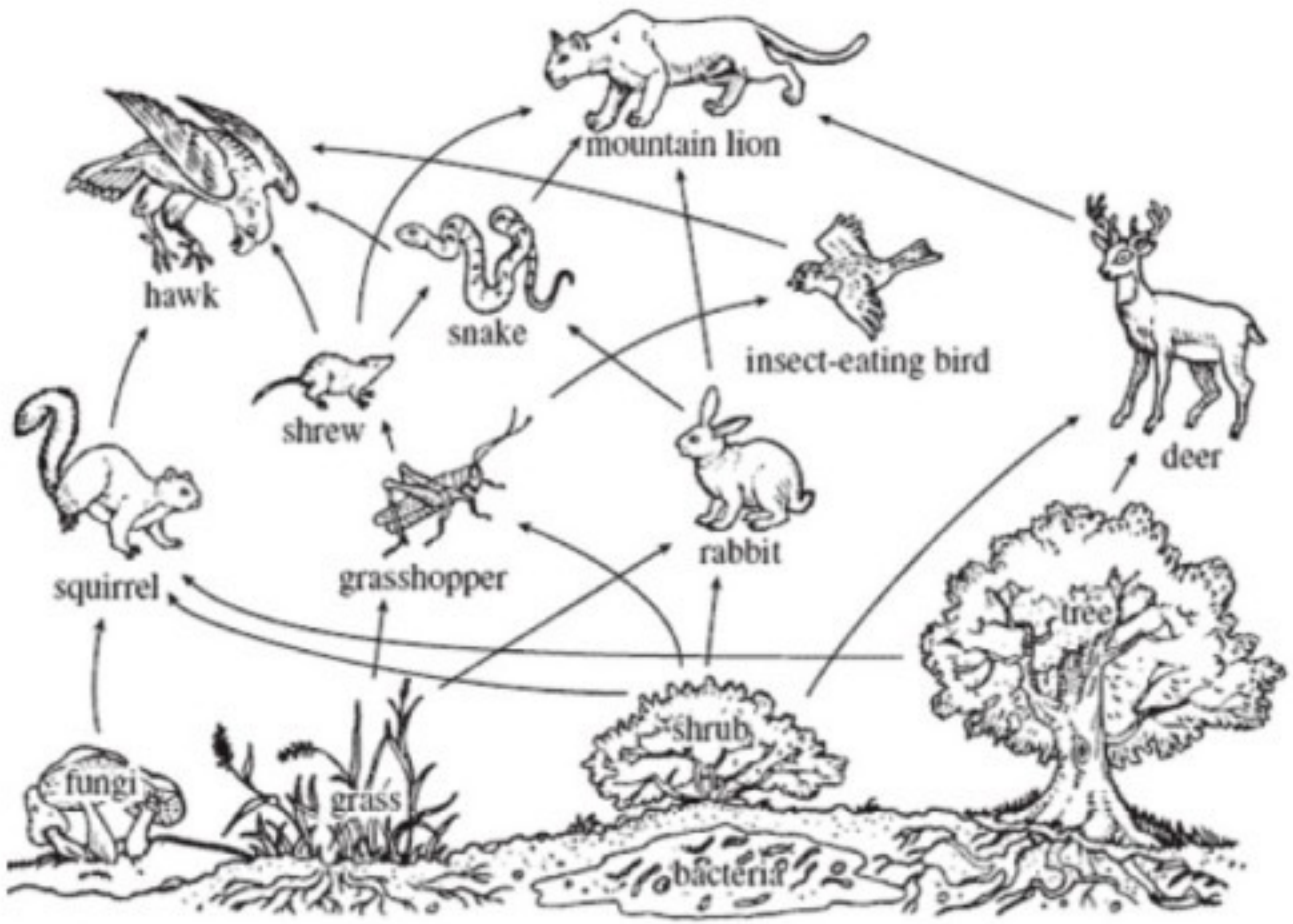


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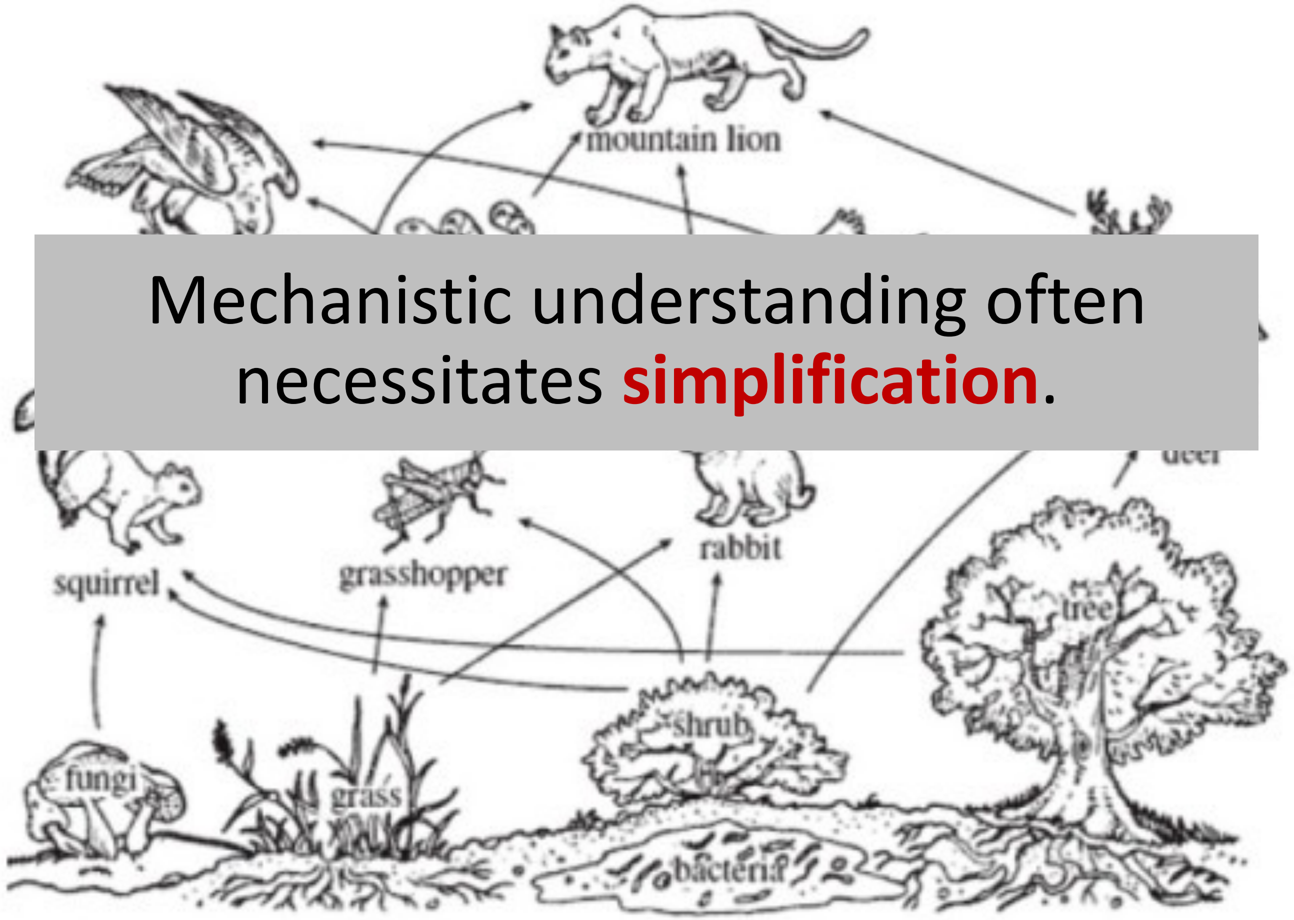


Mechanistic understanding often necessitates **simplification**.

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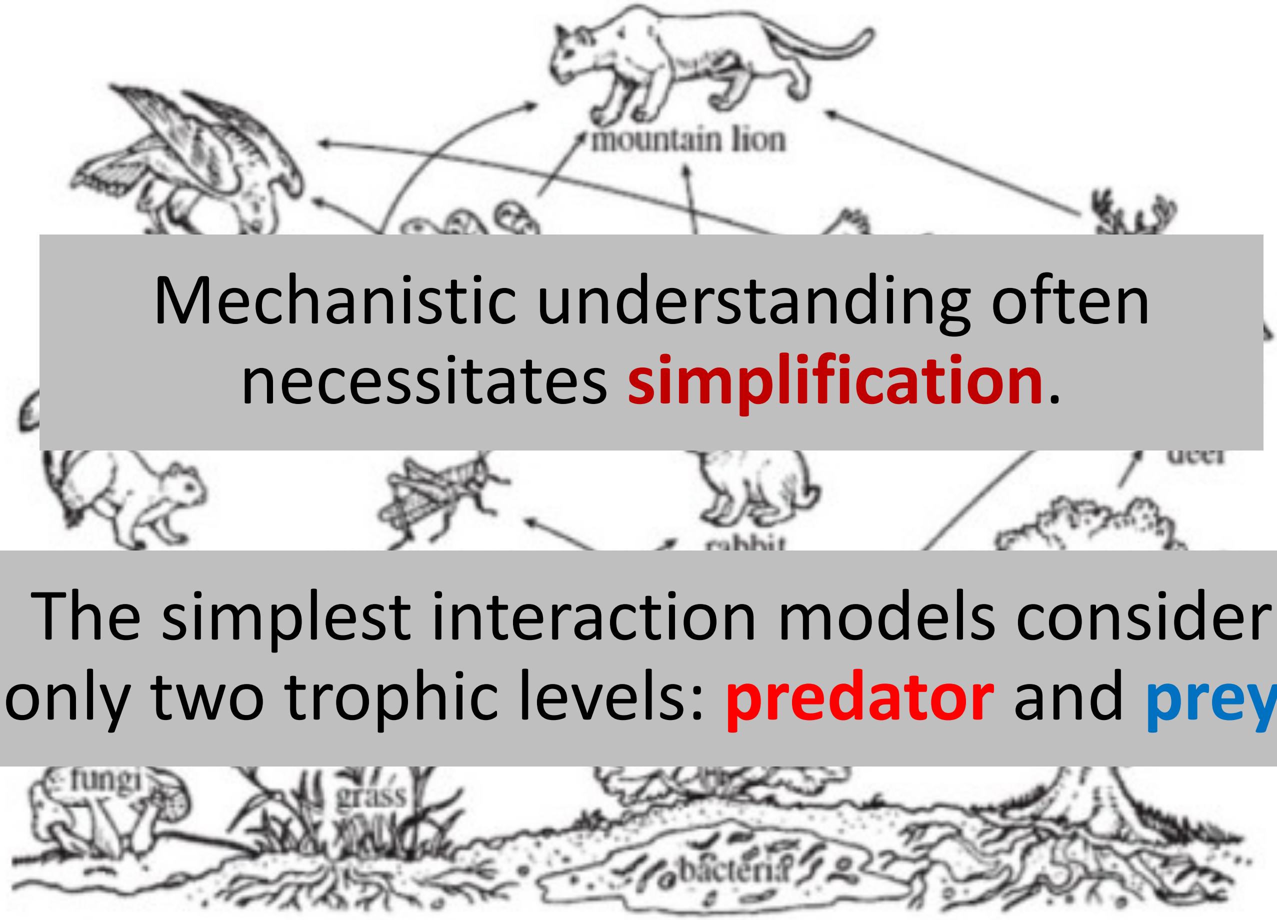
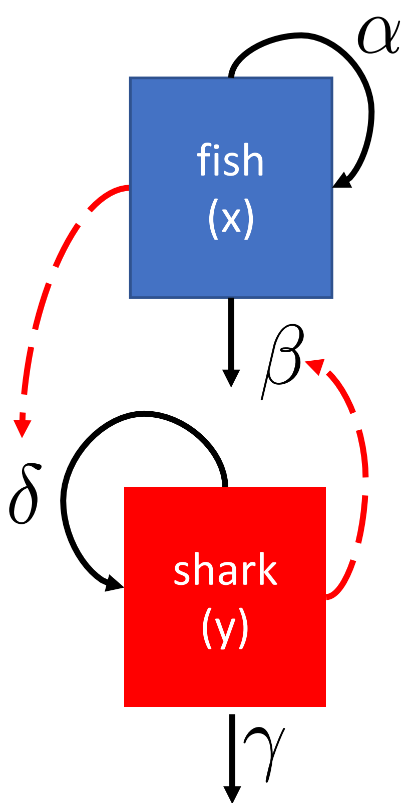



Mechanistic understanding often necessitates **simplification**.

The simplest interaction models consider only two trophic levels: **predator** and **prey**.

# 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.

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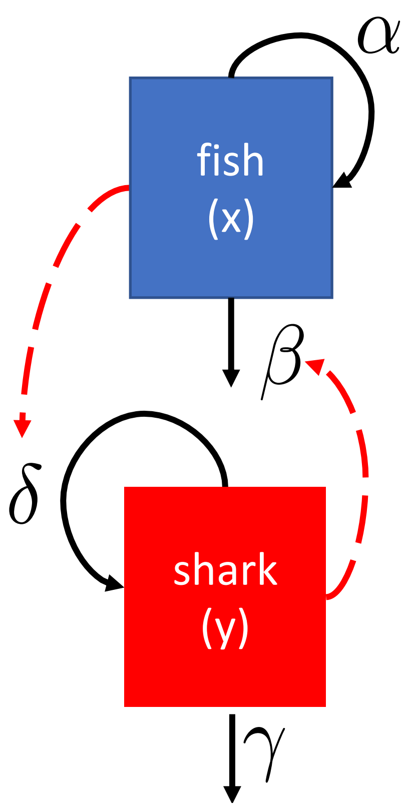


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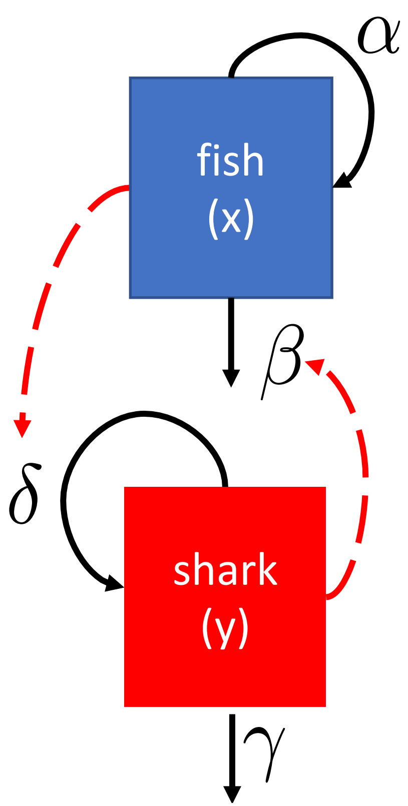


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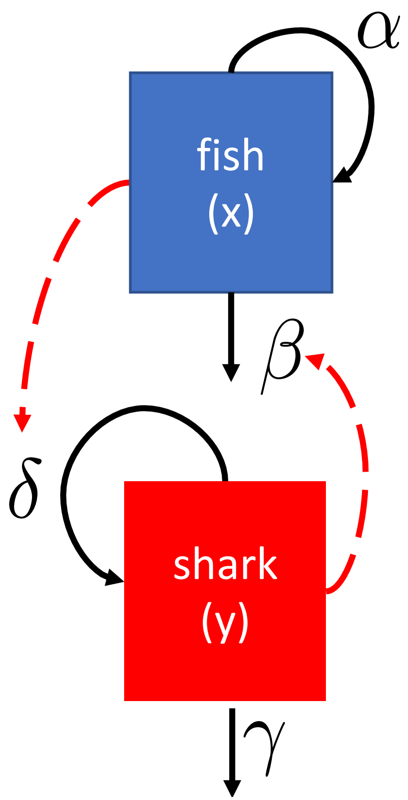


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- Idea that **interspecies interactions** regulate populations

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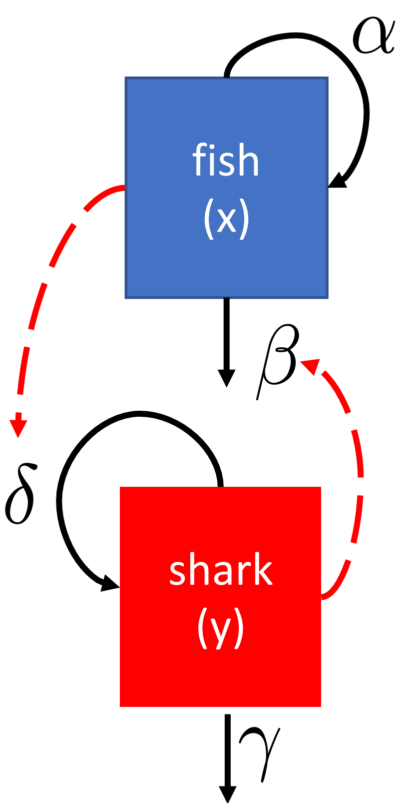


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$$\frac{dx}{dt} = \overbrace{\alpha x}^{\text{growth rate of prey, independent of predator}} - \beta xy$$

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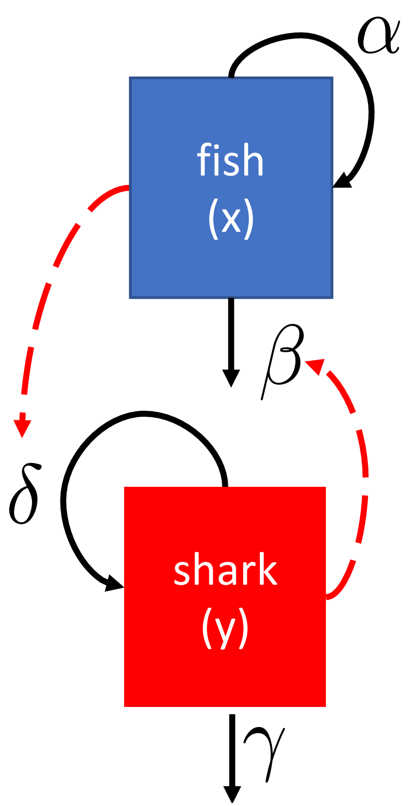
# The **Lotka-Volterra** **predator**-**prey** model




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

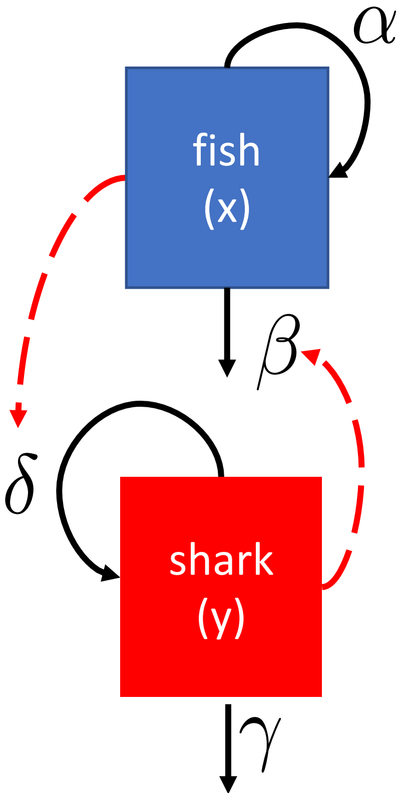
growth rate of prey, independent of predator

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

death rate of prey, depends on abundance of predator

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

# The Lotka-Volterra predator-prey model




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

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

death rate of prey, depends on abundance of predator

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

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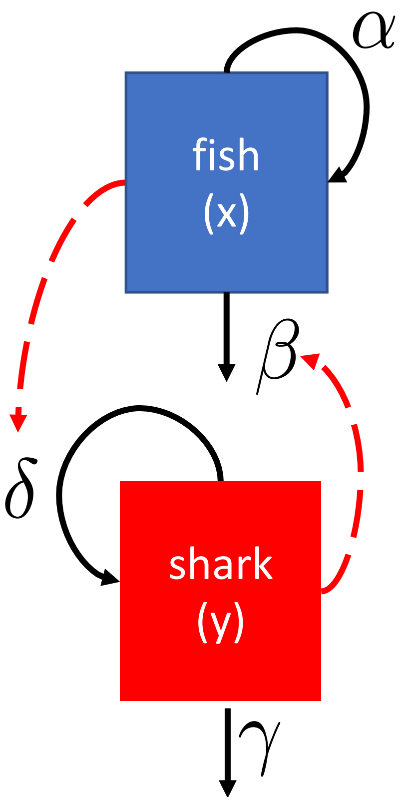


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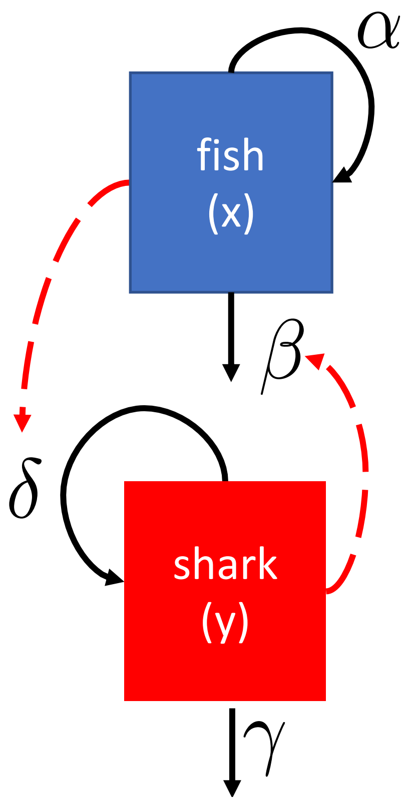
$\beta xy$: death rate of prey, depends on abundance of predator

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

$\gamma y$: death rate of predator, independent of prey

# The Lotka-Volterra predator-prey model



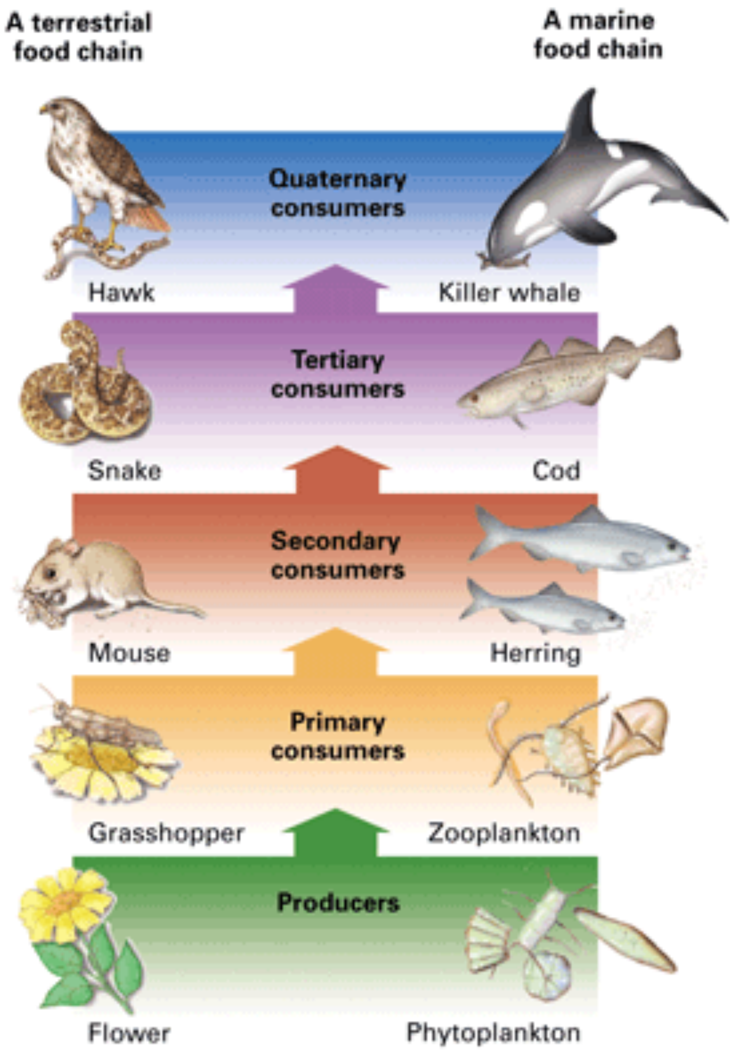

$$\frac{dx}{dt} = \boxed{\alpha x} - \beta xy$$

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

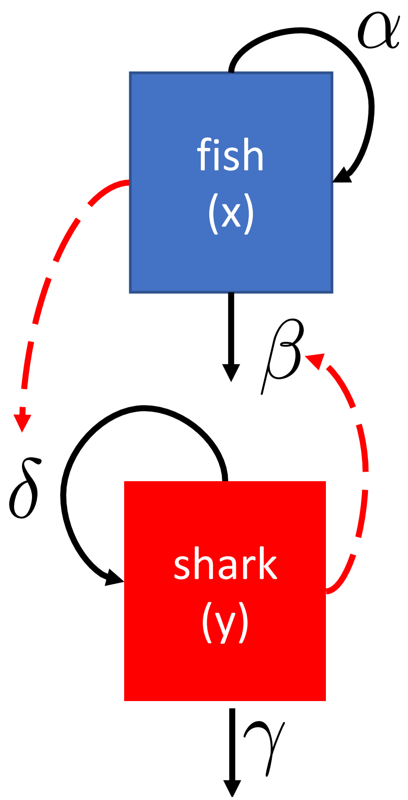
*How does* ***fish*** *abundance* ***vary*** *with* ***changes*** *in* ***shark*** *abundance?*

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

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



# The Lotka-Volterra predator-prey model

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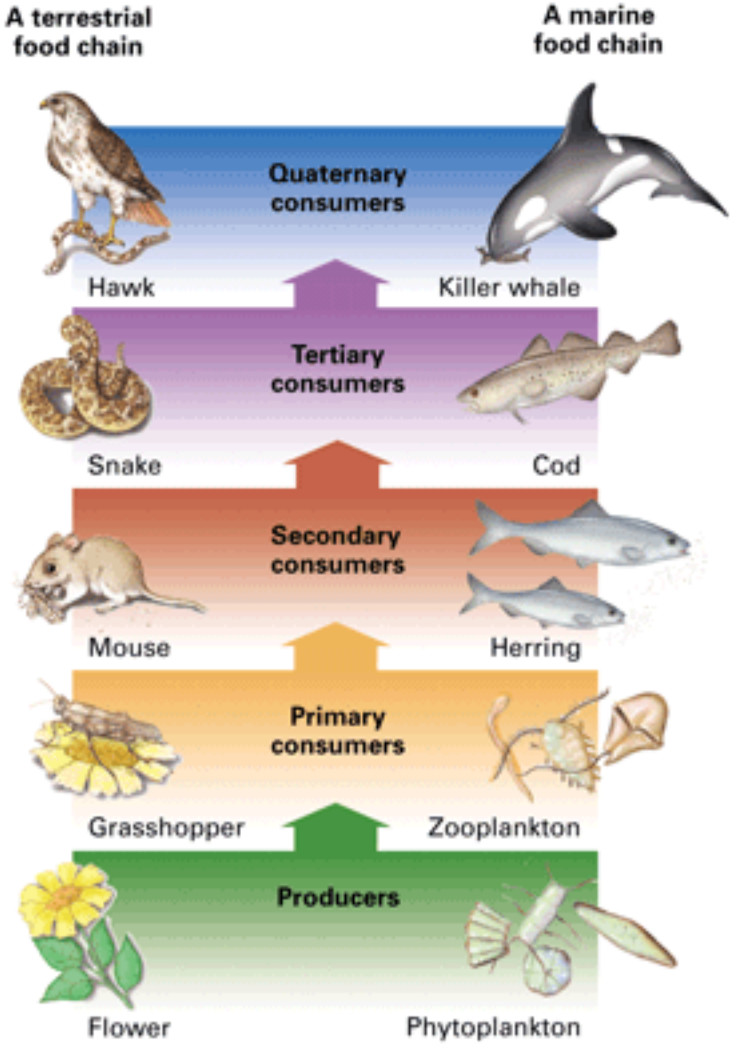
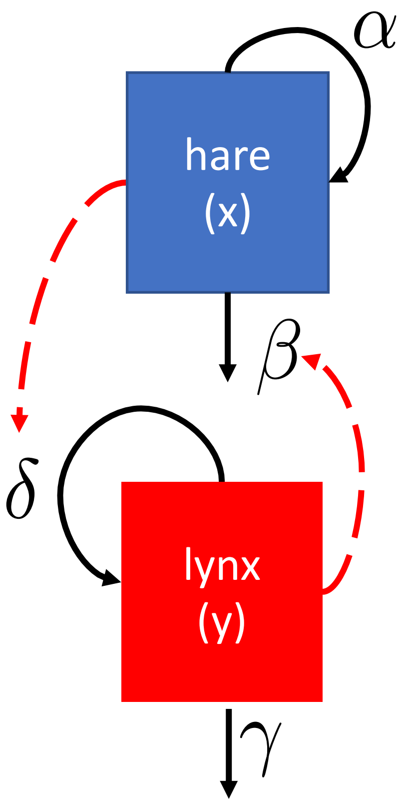


# **Lotka-Volterra** predator-prey models with data

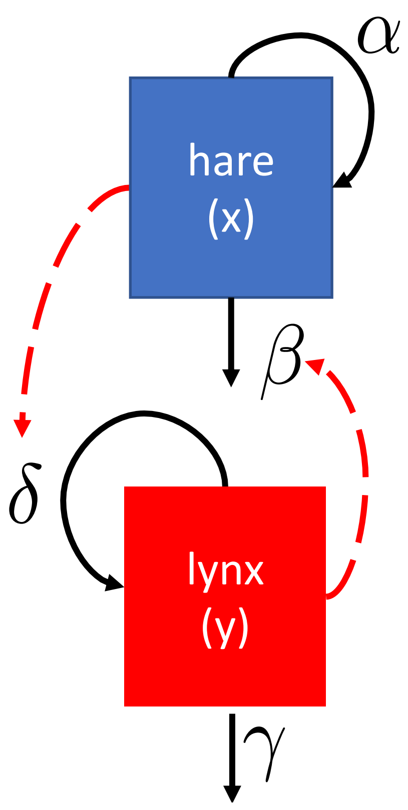



*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

HUDSON'S BAY

INCORPORATED 2 MAY 1670

# Lotka-Volterra predator-prey models with data

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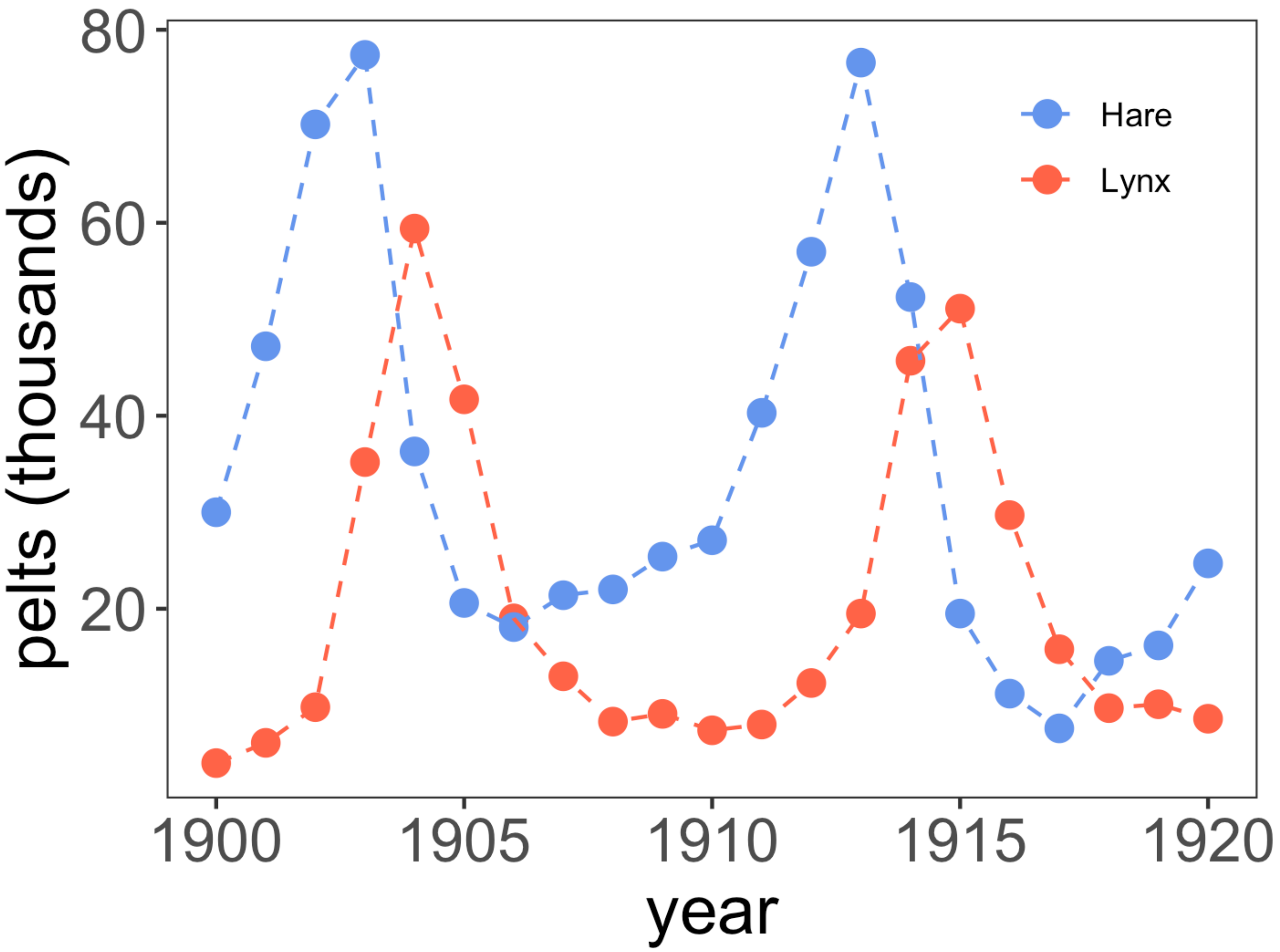
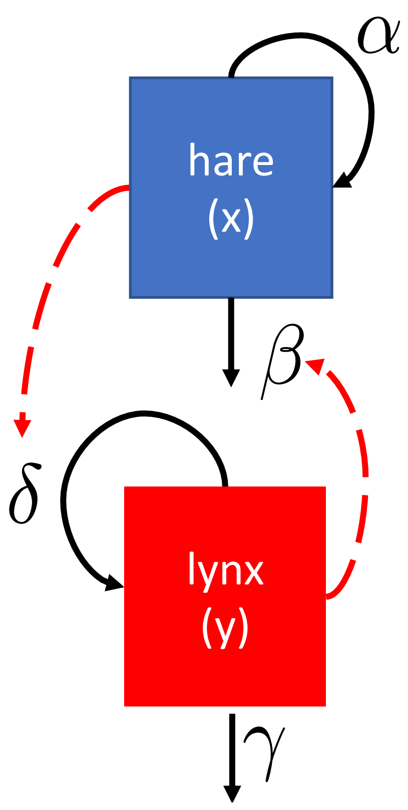


# Lotka-Volterra predator-prey models with data

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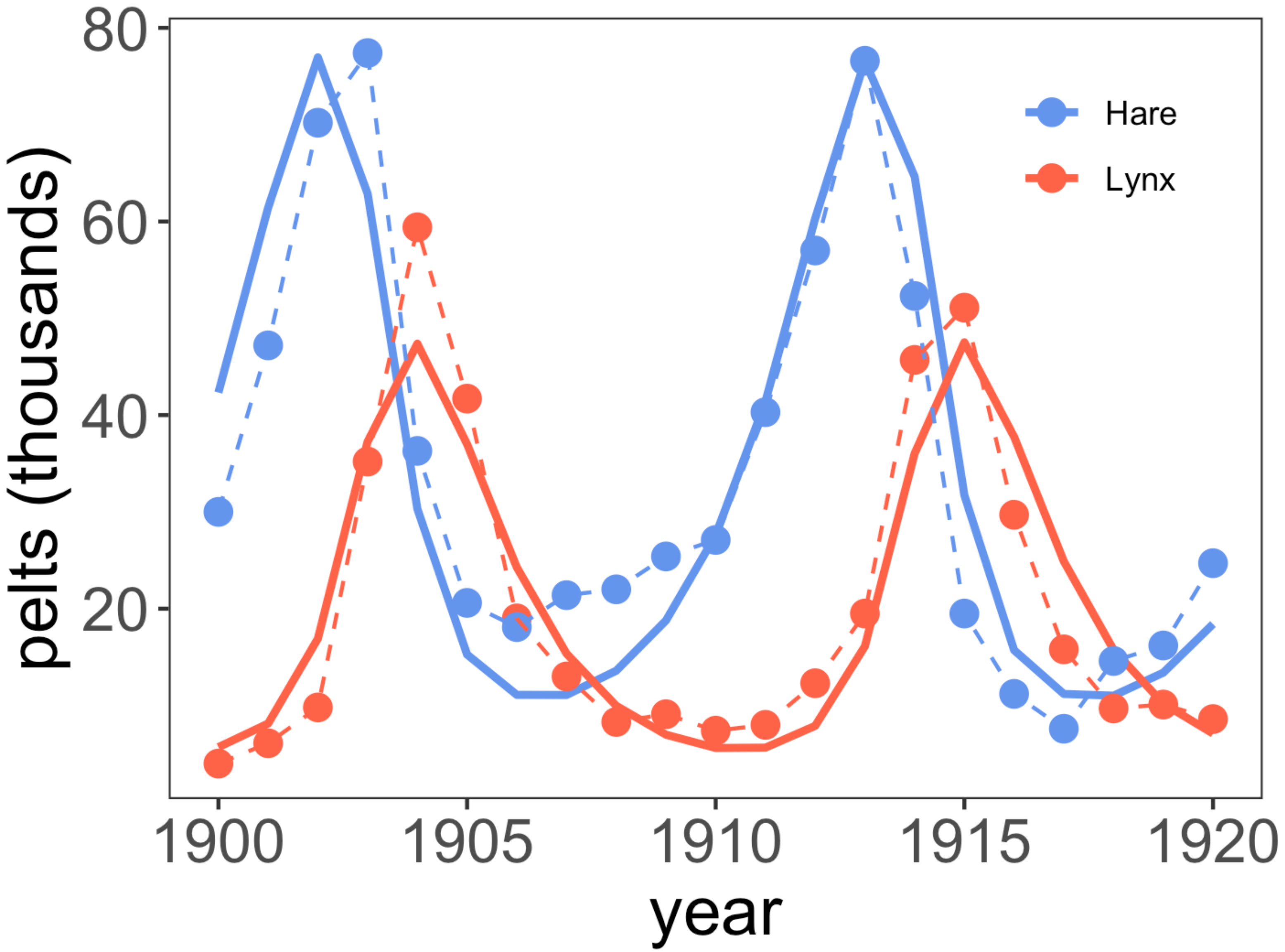

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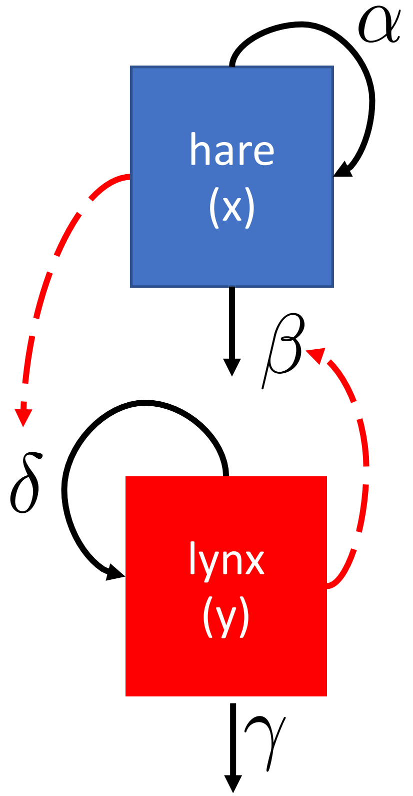
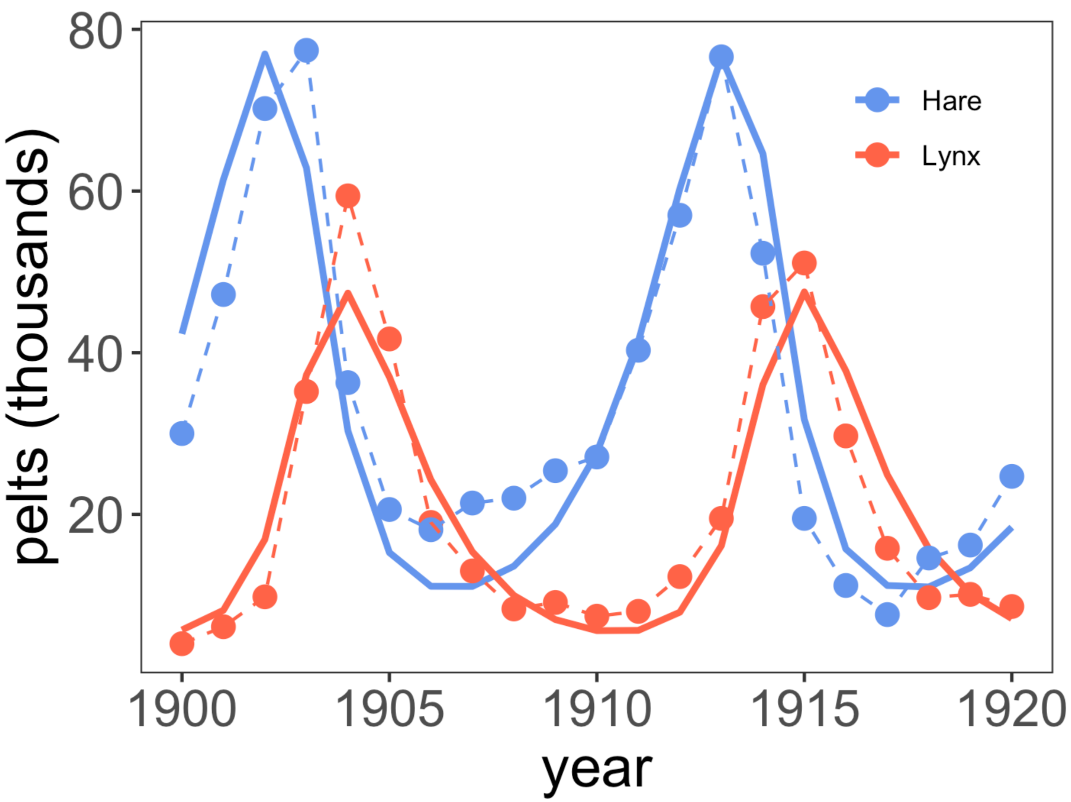



- Fitting a model to data allows us to estimate parameters – remember those growth rates from the human population models!
- Here, we can explore the growth rate of the prey under exponential growth ($\alpha$), the efficiency of kill ($\beta$) and digestion ($\delta$) by the predator, and the natural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

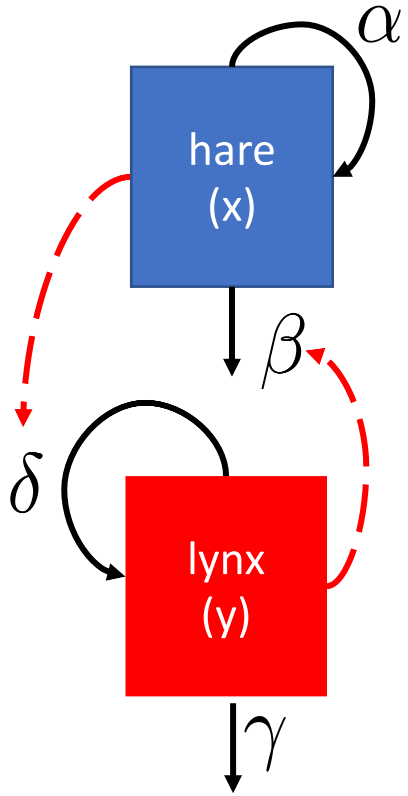
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

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

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

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

# **Lotka-Volterra** predator-prey models with data

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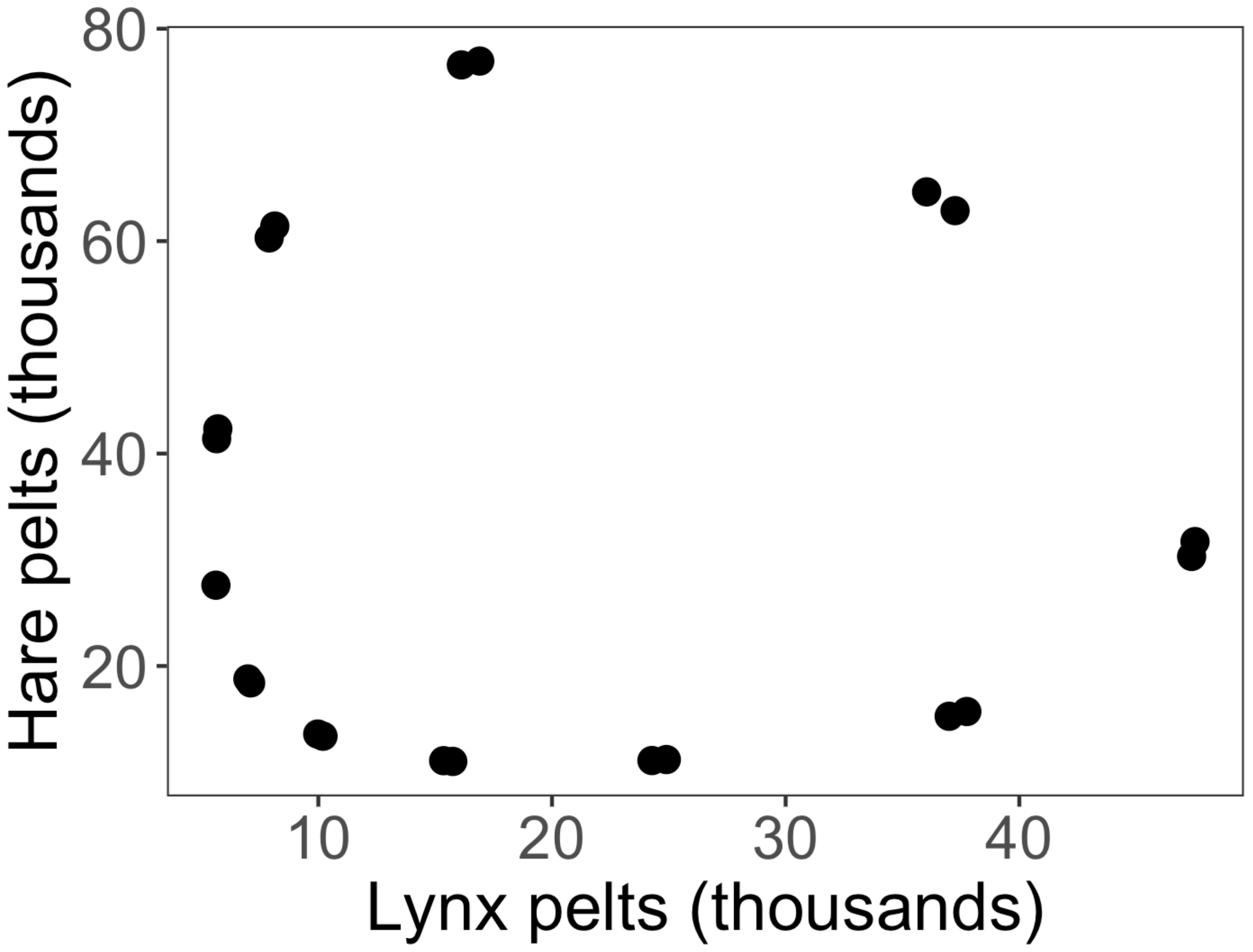
*How does **hare** abundance **vary** with **changes** in **lynx** abundance?*

Predator-prey cycles can be visualized as oscillations.



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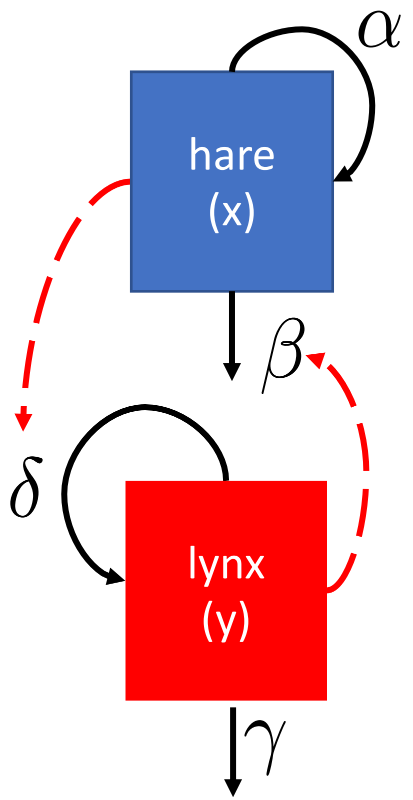


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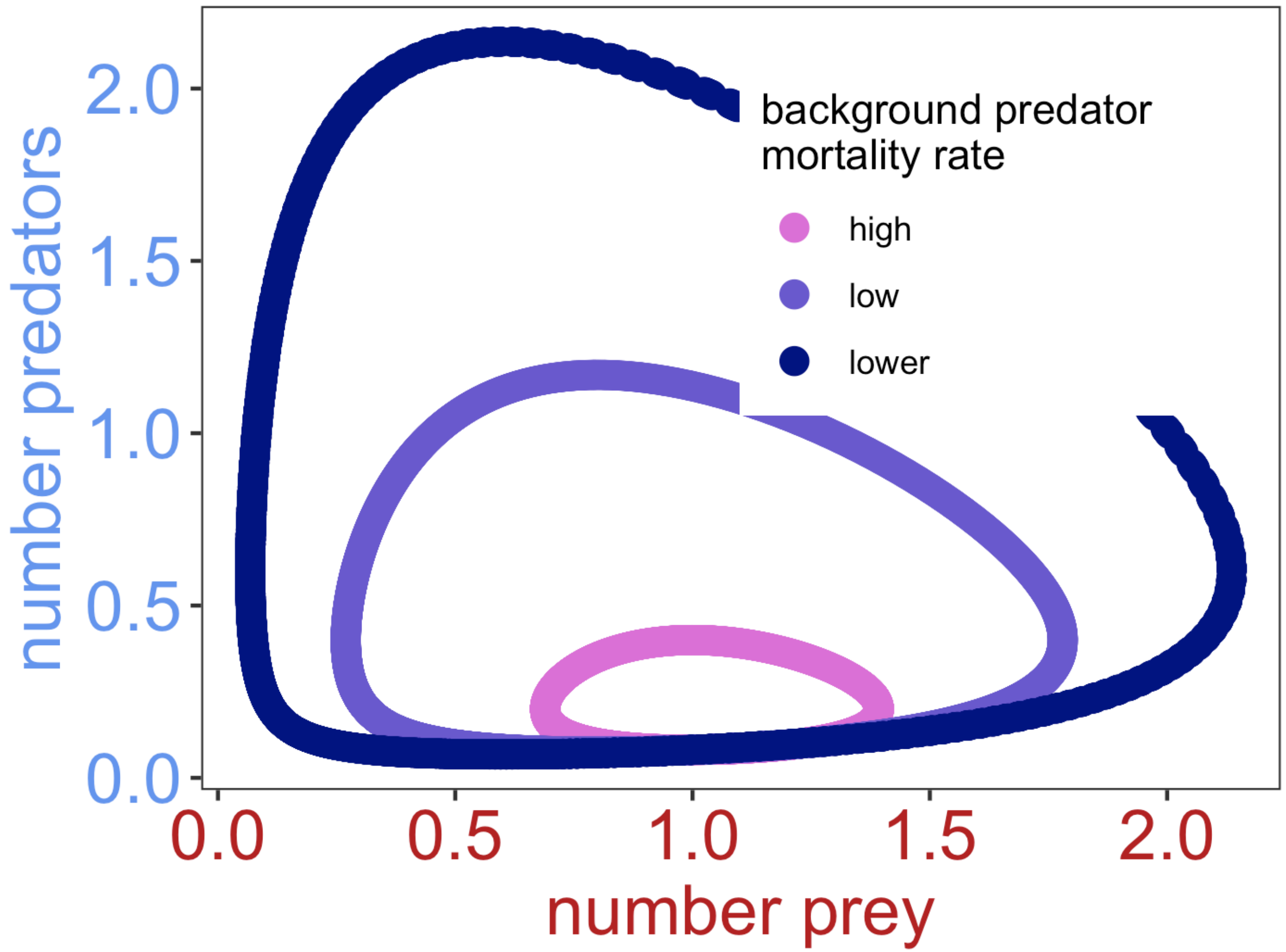
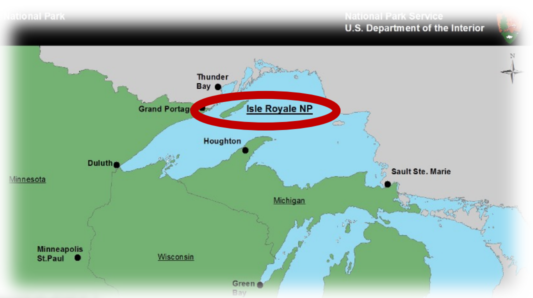


# Another famous example: Wolf-Moose on Isle Royale

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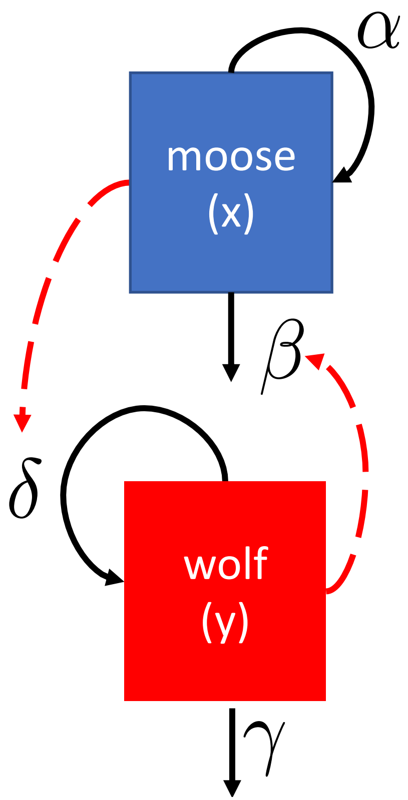


*How does **moose** abundance **vary** with **changes** in **wolf** abundance?*

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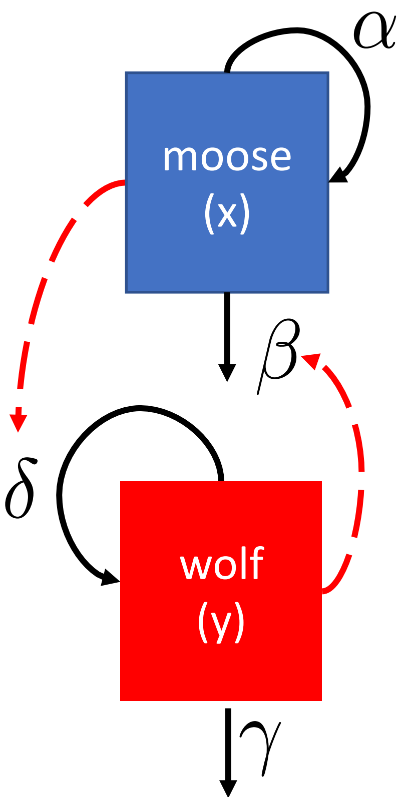
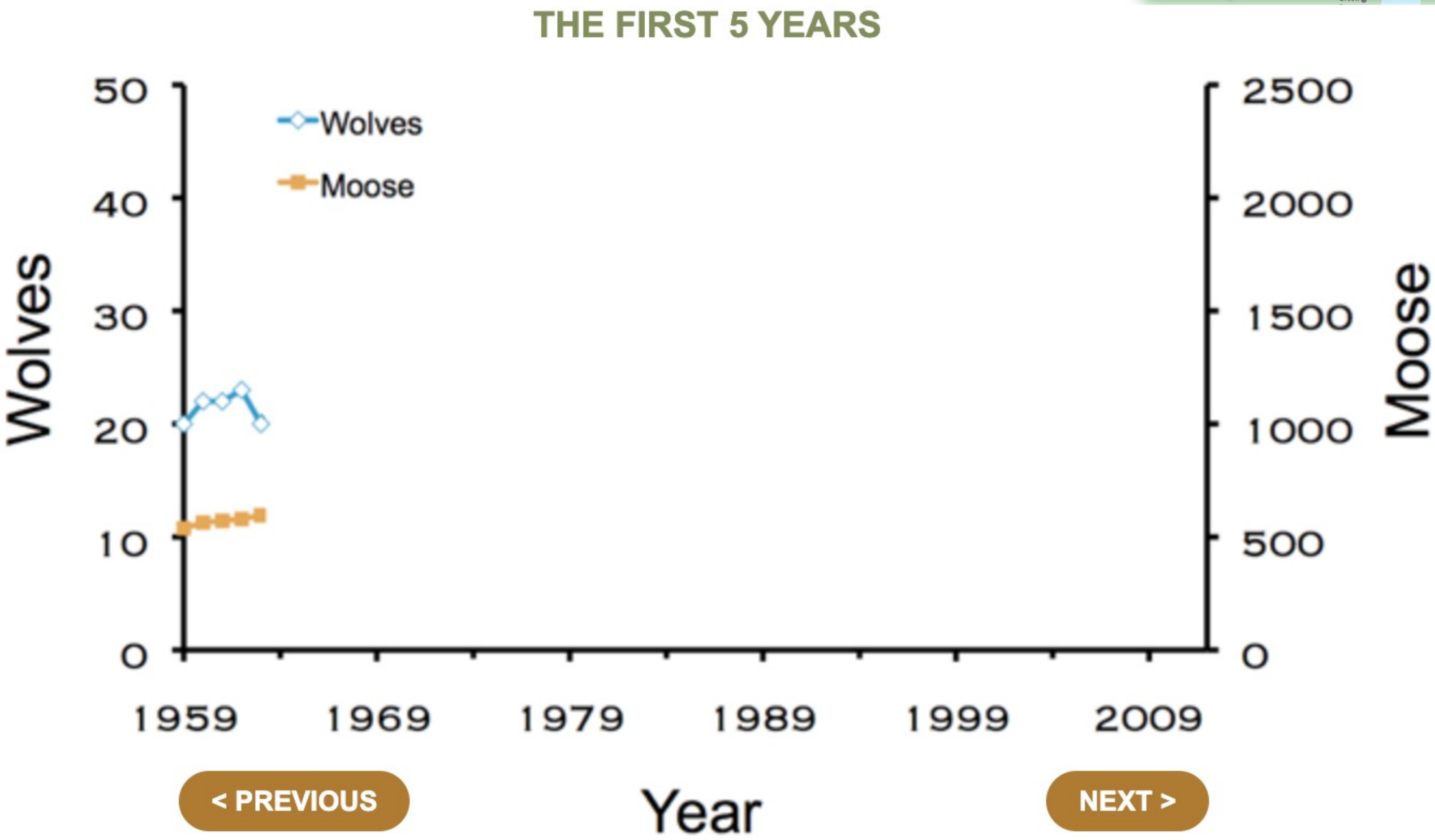



*How does* ***moose*** *abundance* ***vary*** *with* ***changes*** *in* ***wolf*** *abundance?*




After observing relatively constant abundances for five years, it seemed that the wolves and moose of Isle Royale had struck some kind of a balance of nature.

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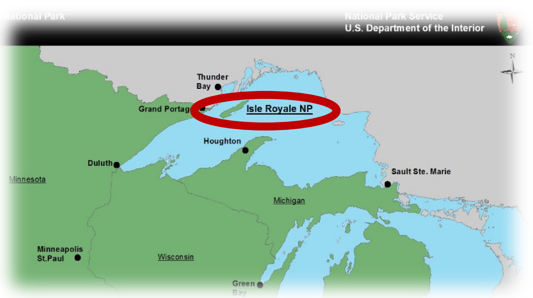


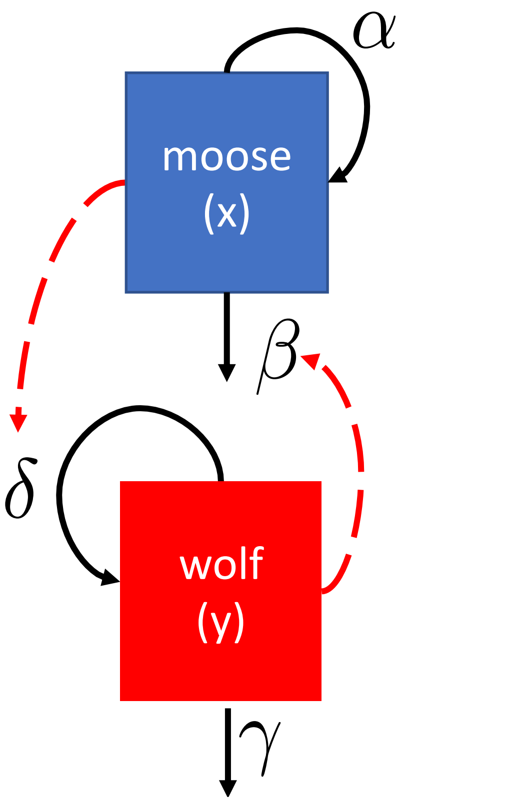


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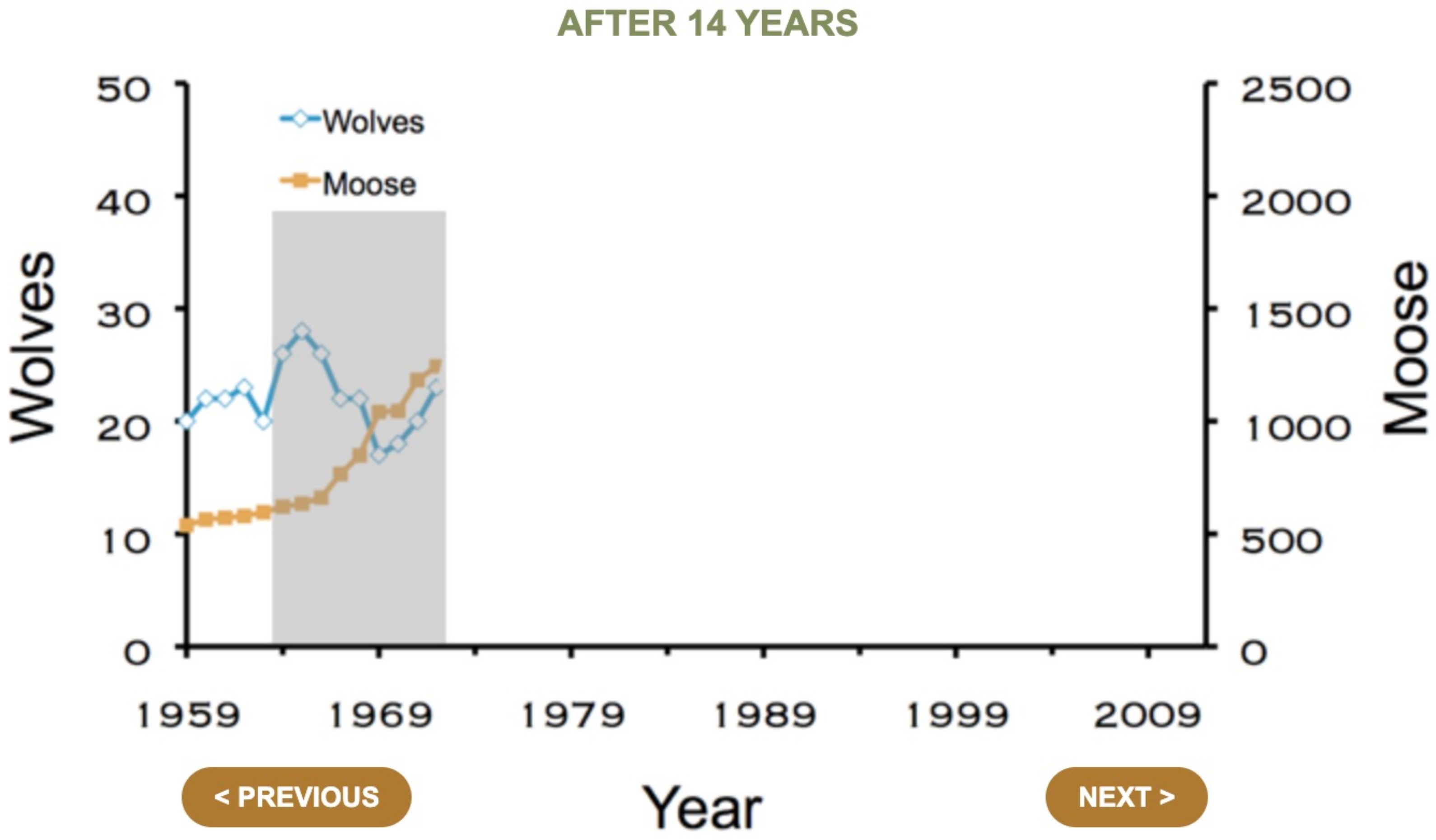


Over time wolf abundance fluctuated a bit. But, after a series of mild winters moose abundance doubled. There'd been a major shift in the balance.

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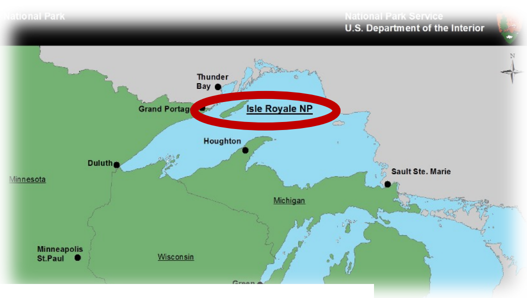
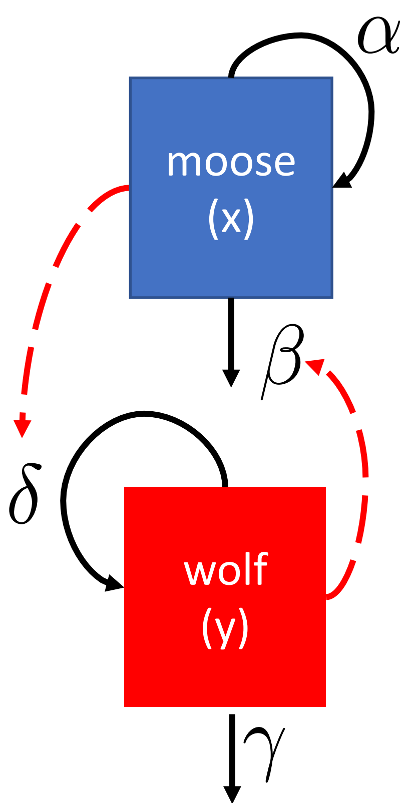
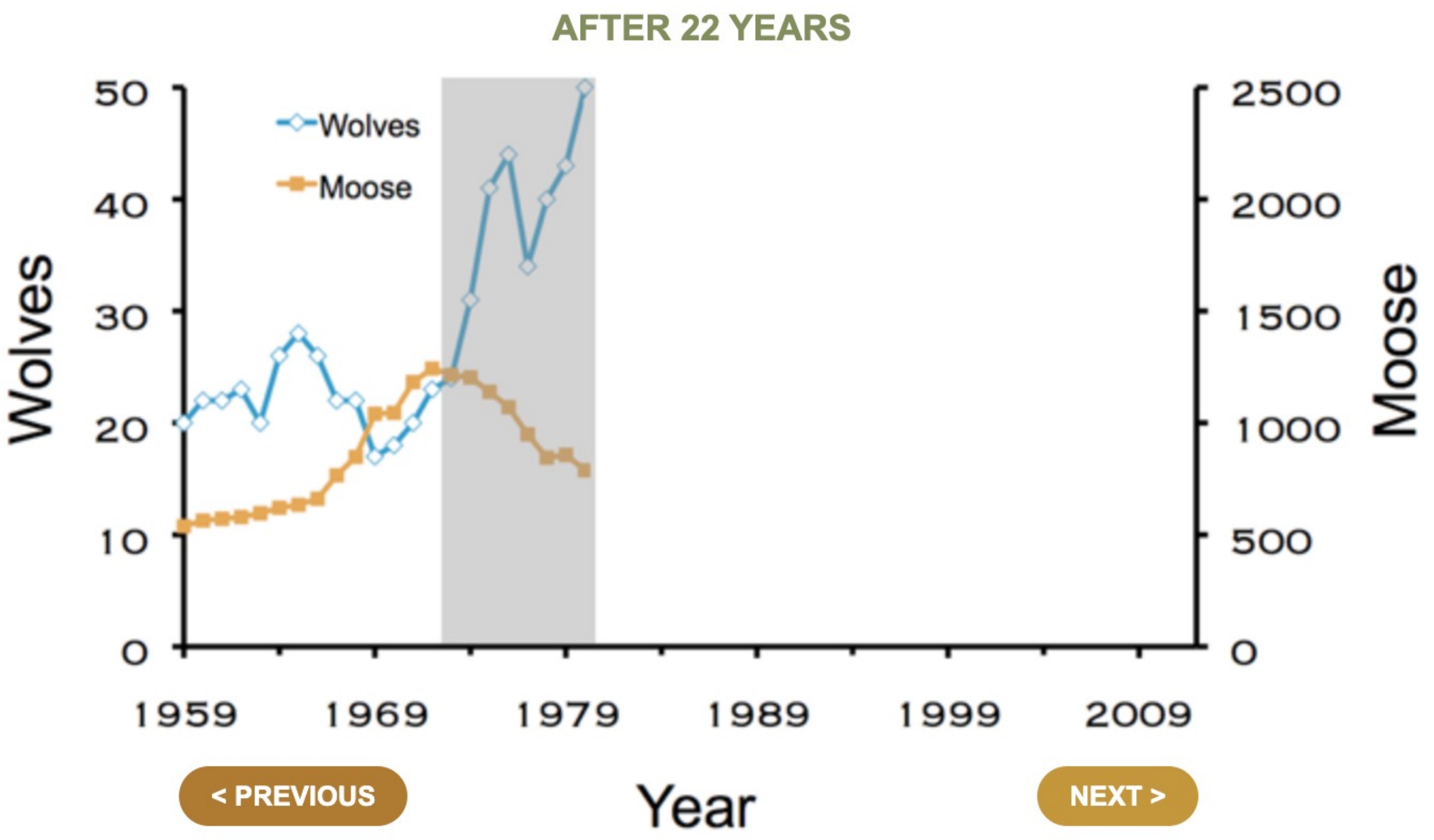
# Another famous example: Wolf-Moose on Isle Royale




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




Then a series of severe winters, increased wolf predation, and moose abundance was cut in half. Wolves soared to 50 individuals.

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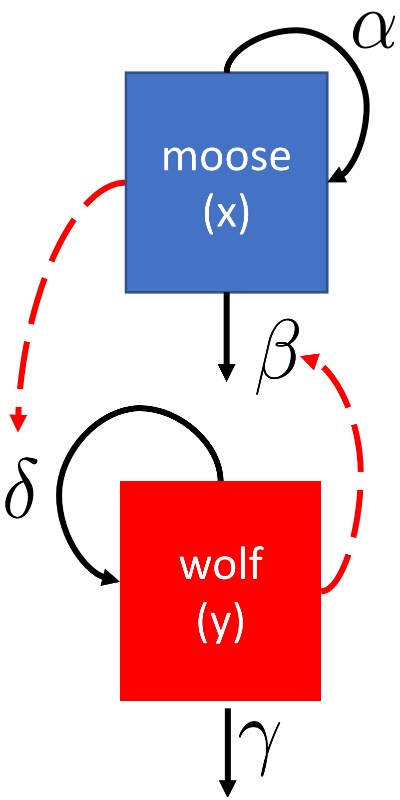
# Another famous example: Wolf-Moose on Isle Royale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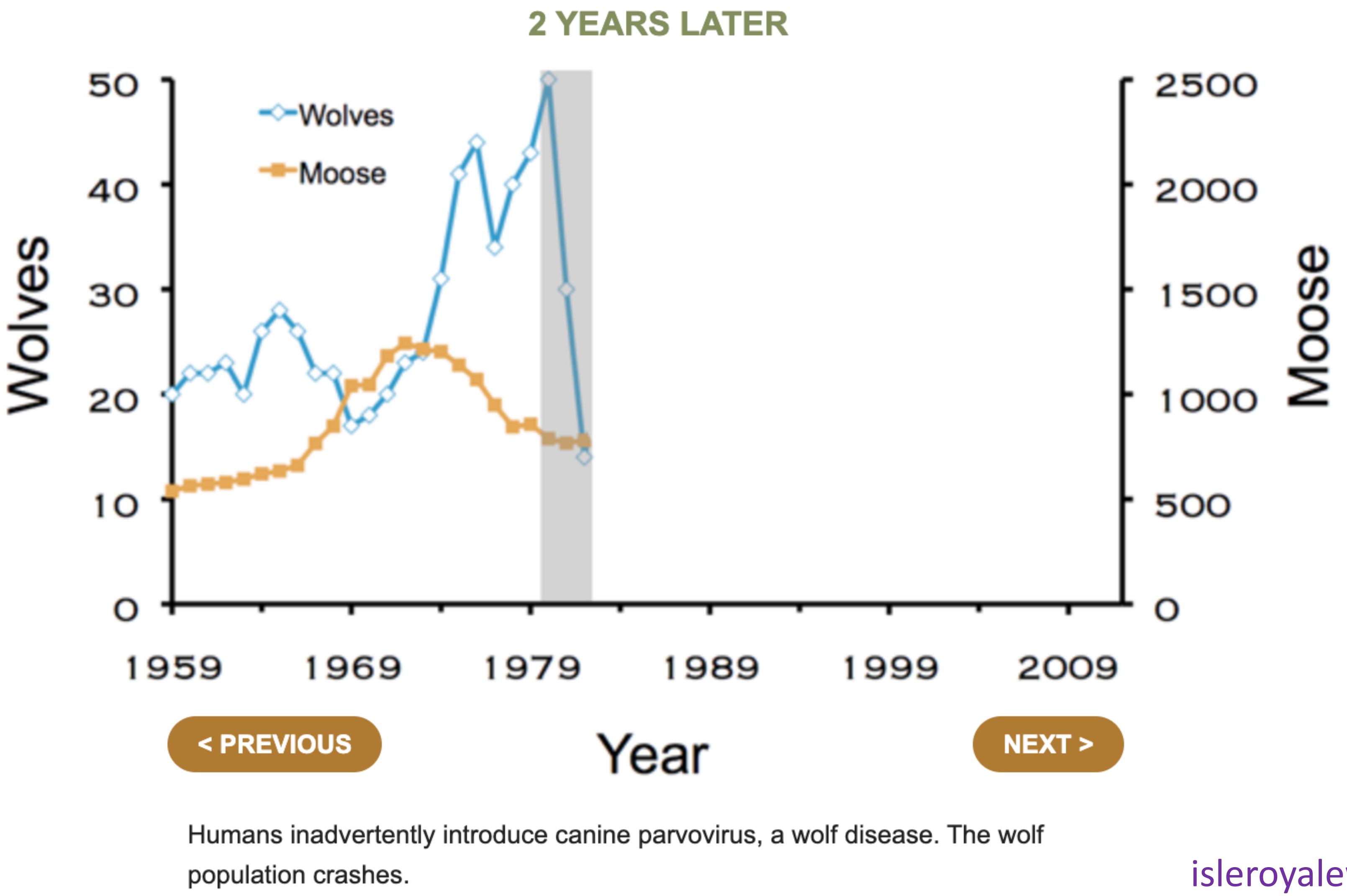


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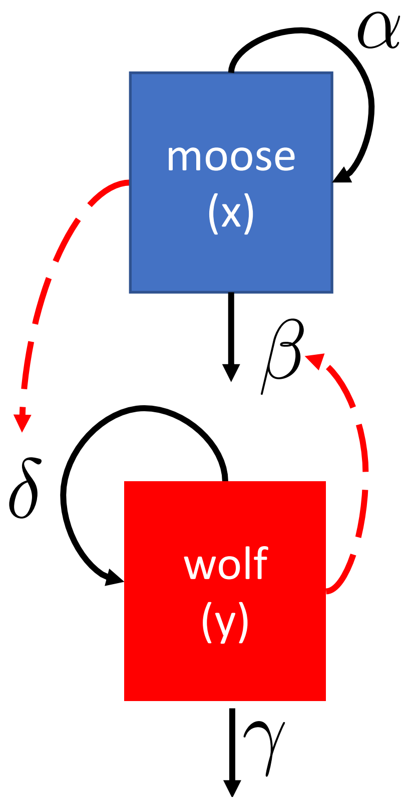


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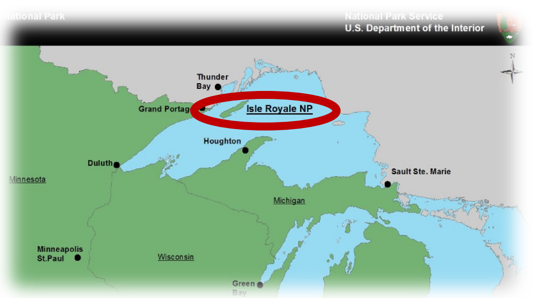


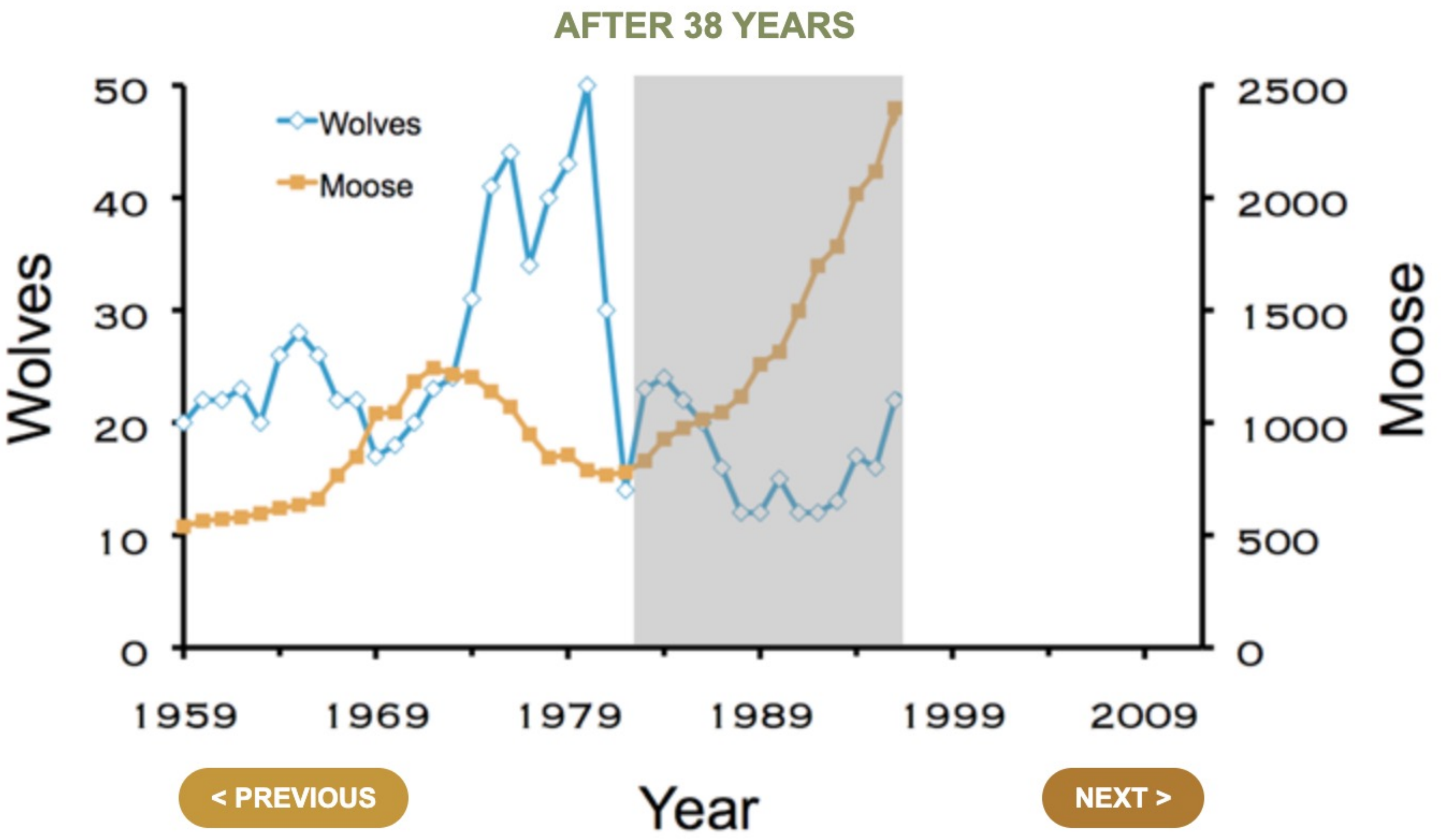


With a reprieve from wolf predation, the moose population explodes. We begin to think, but cannot yet prove, that inbreeding among wolves explains why they languor in low abundance for over a decade.

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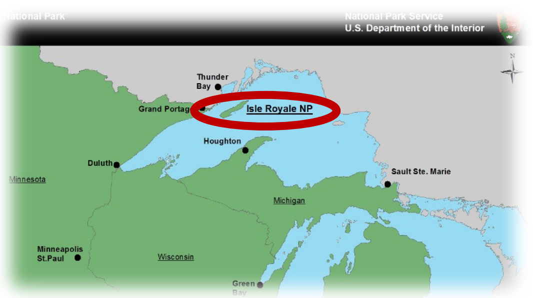
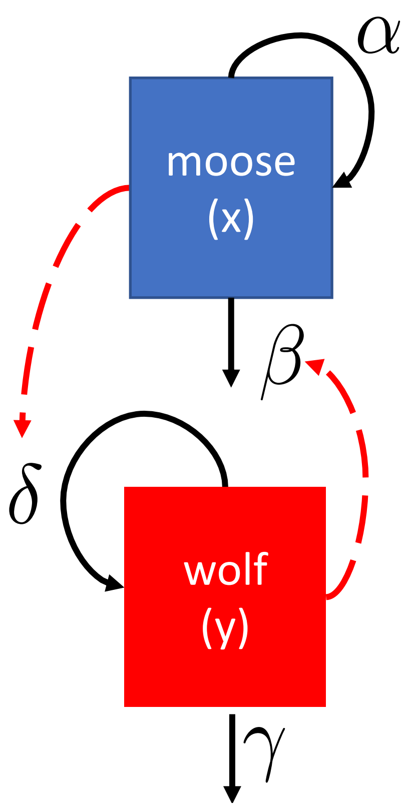
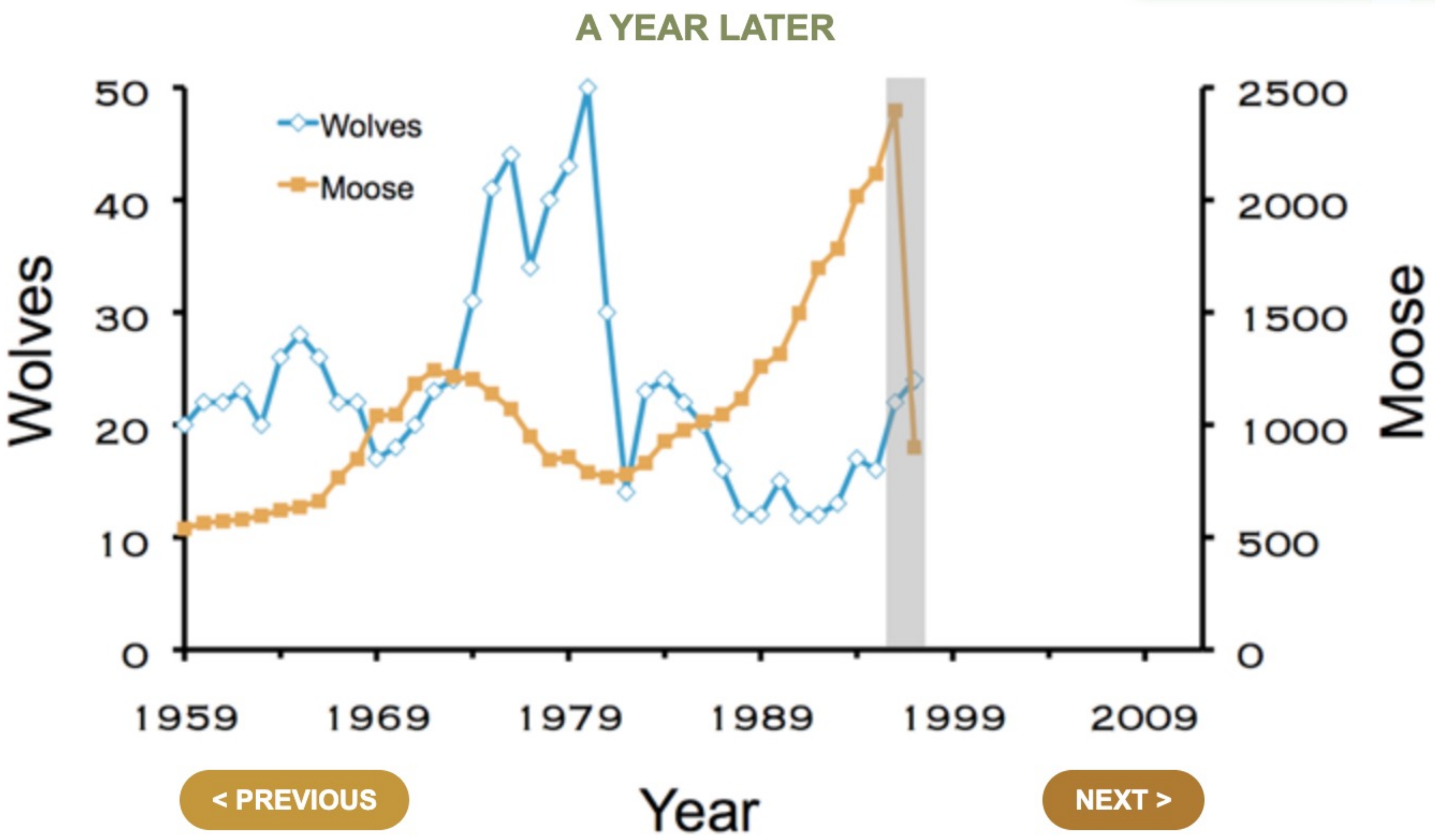
# Another famous example: Wolf-Moose on Isle Royale




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




Intense competition for a declining forage, an outbreak of winter ticks, and the severe winter. They all conspired against the moose population which collapsed in 1996.

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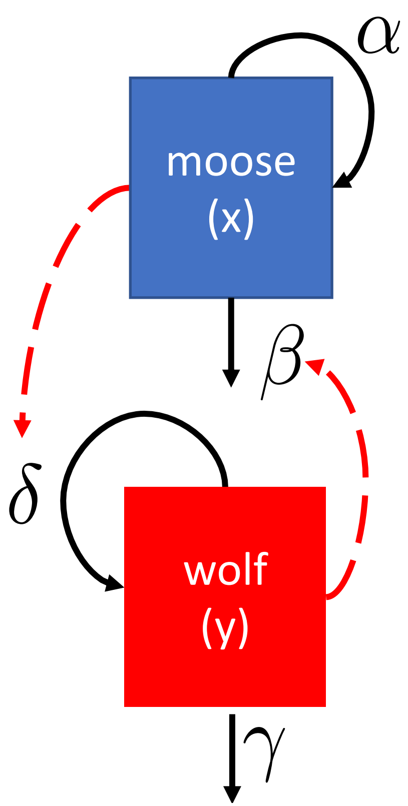
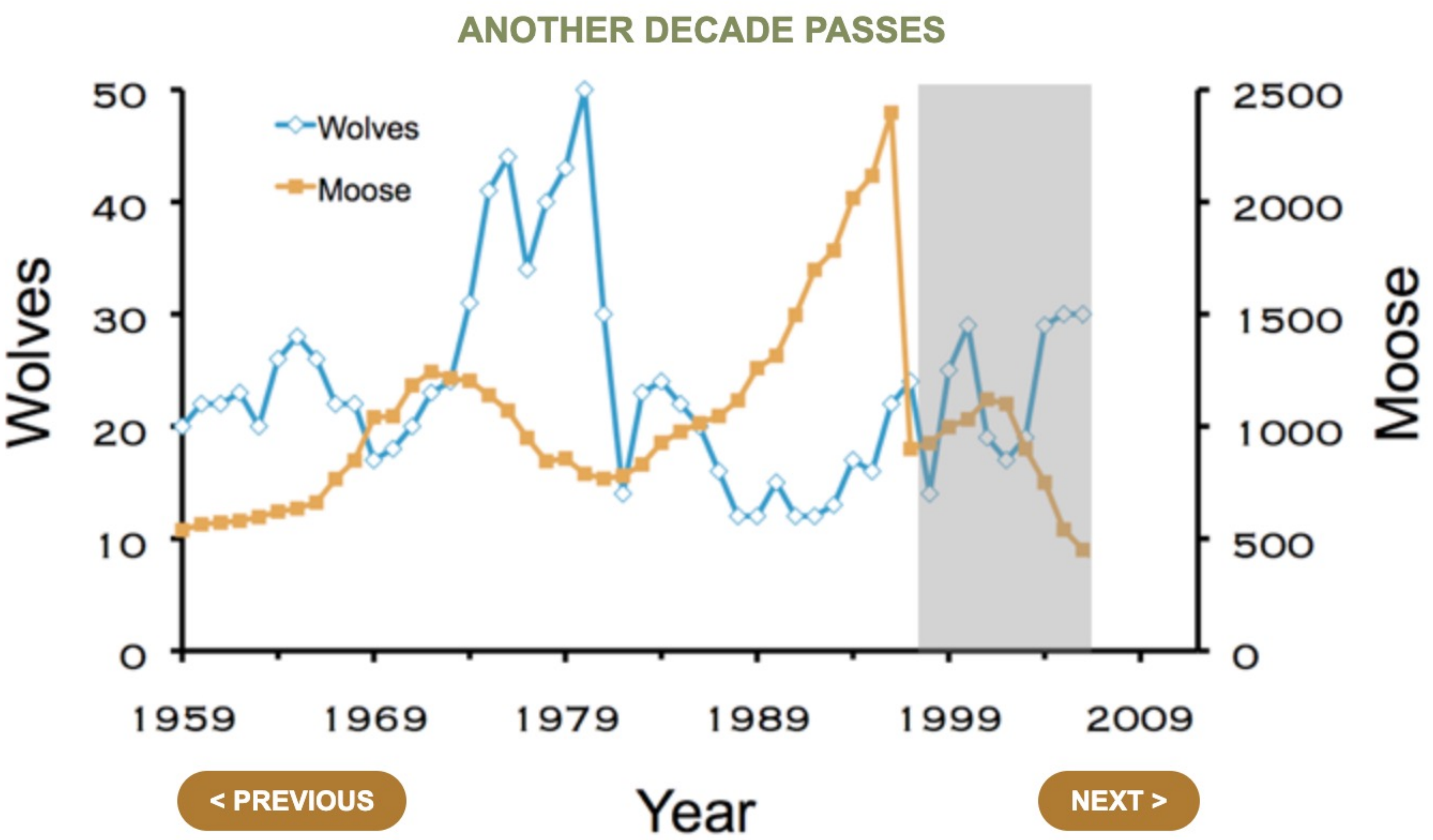
# Another famous example: Wolf-Moose on Isle Royale


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




Moose continue to dwindle. In 1997, a wolf immigrates from Canada, bringing an infusion of new genes. The wolves increase erratically.

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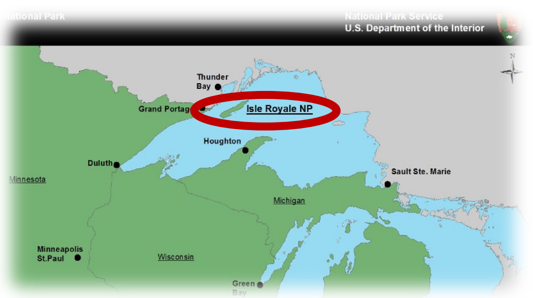
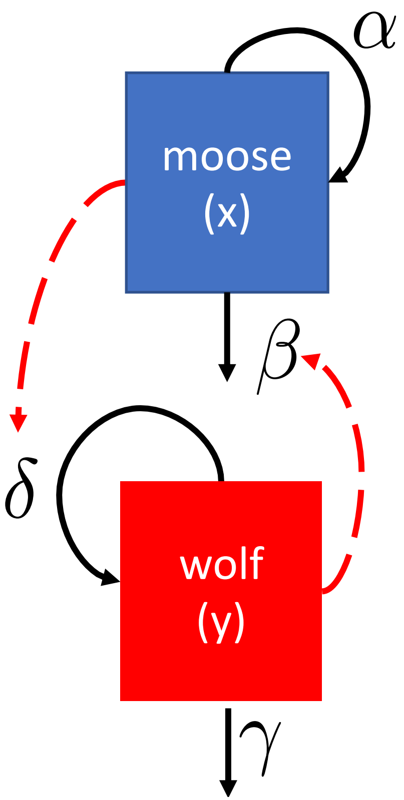
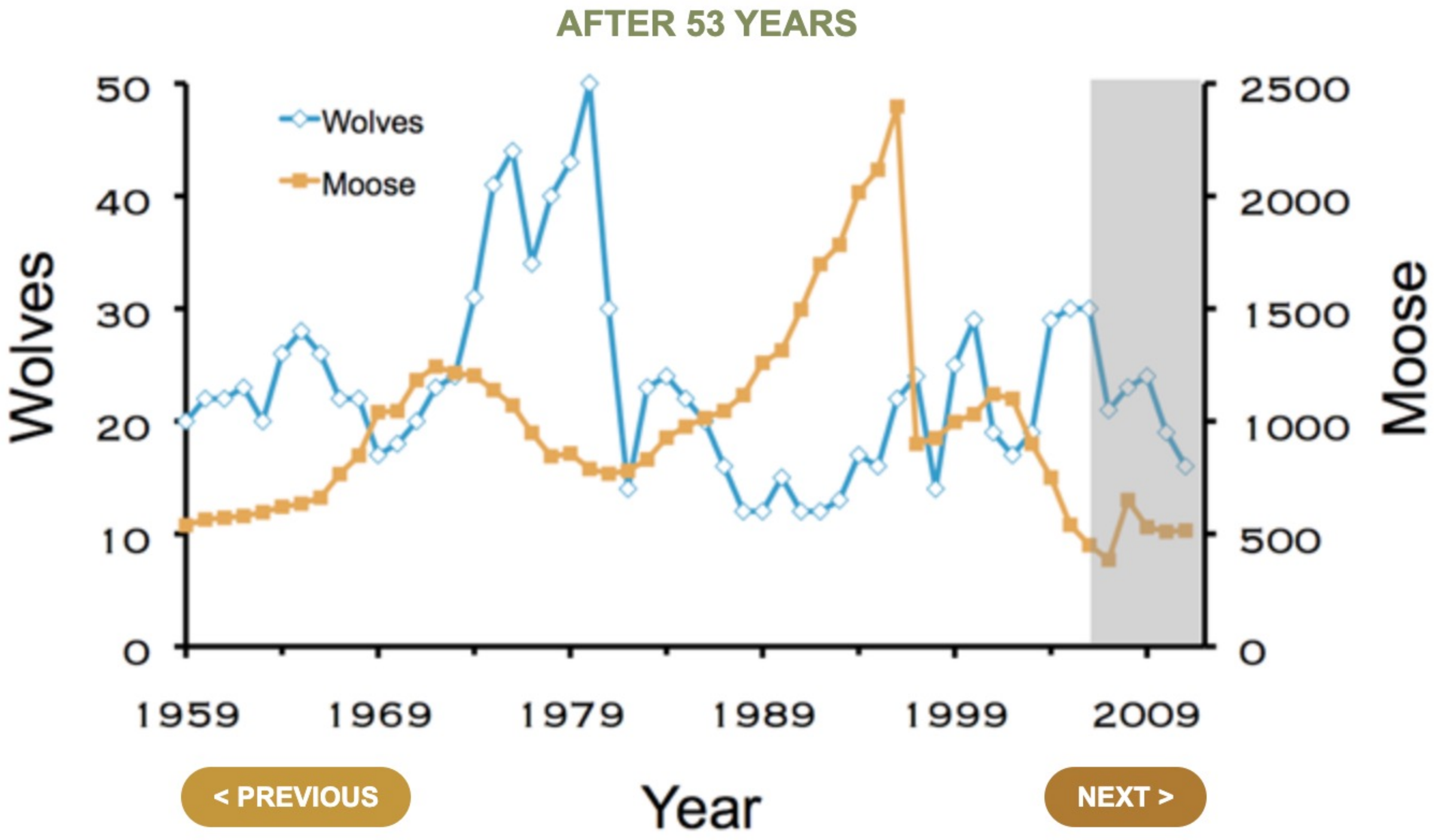
# Another famous example: Wolf-Moose on Isle Royale




*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.

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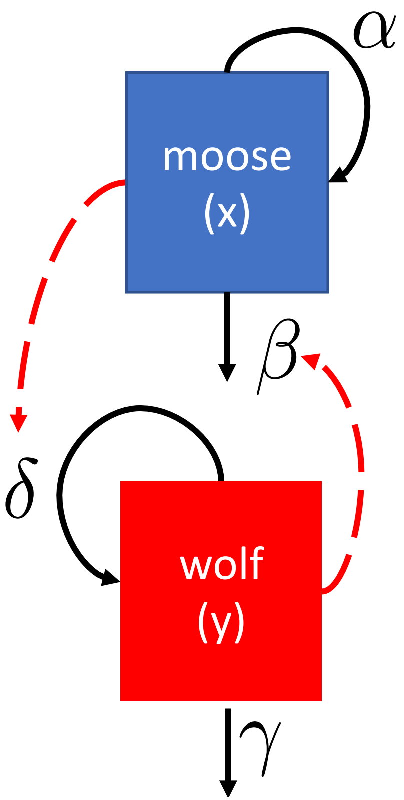
# Another famous example: Wolf-Moose on Isle Royale




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

## Field Work Opportunity for College Students

This could be you!

### 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.

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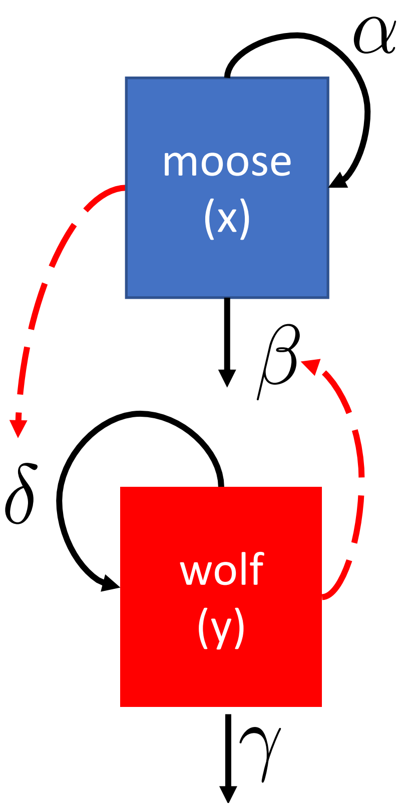
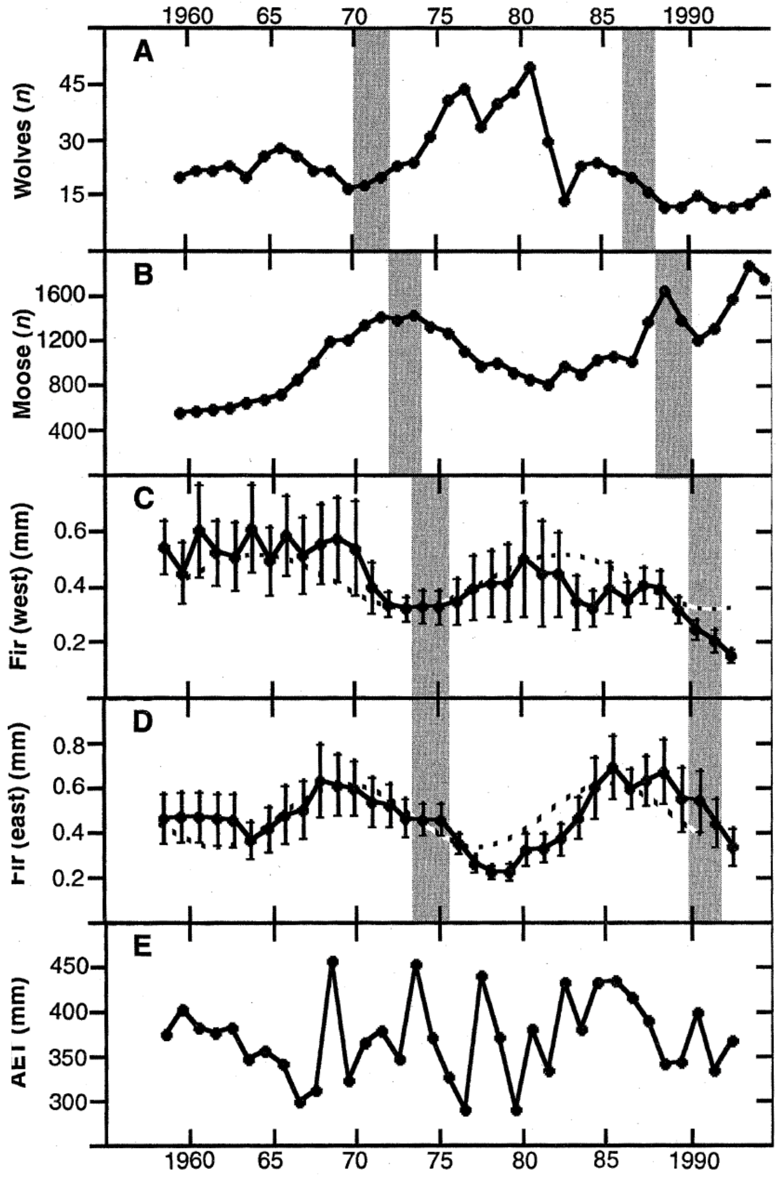
# Another famous example: Wolf-Moose on Isle Royale




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



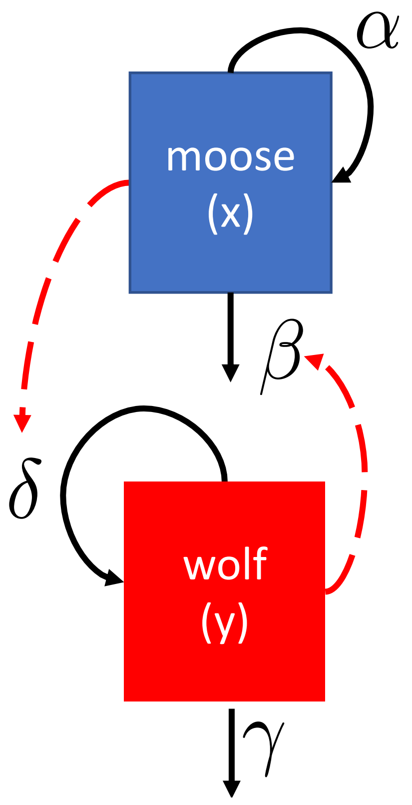

Wolf-moose dynamics on Isle Royale are **more complex than simple predator-prey**.

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

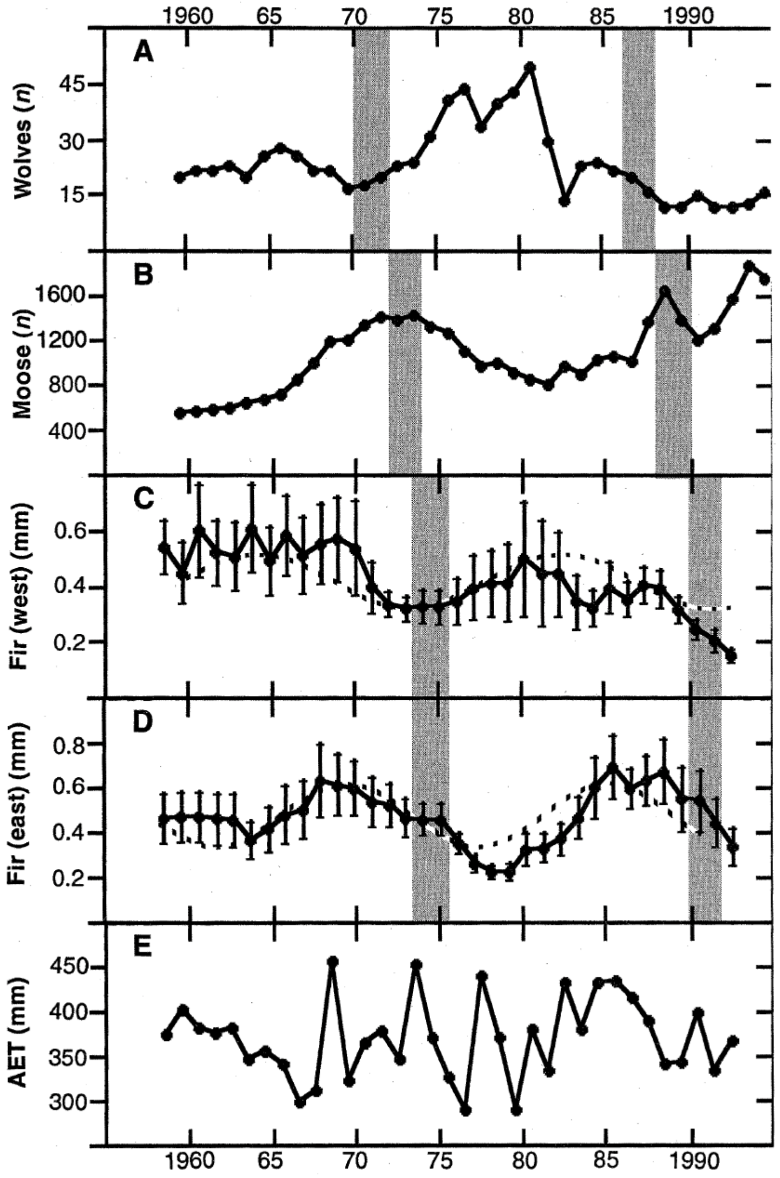
B. E. McLaren* and R. O. Peterson

SCIENCE • VOL. 266 • 2 DECEMBER 1994

# 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**.

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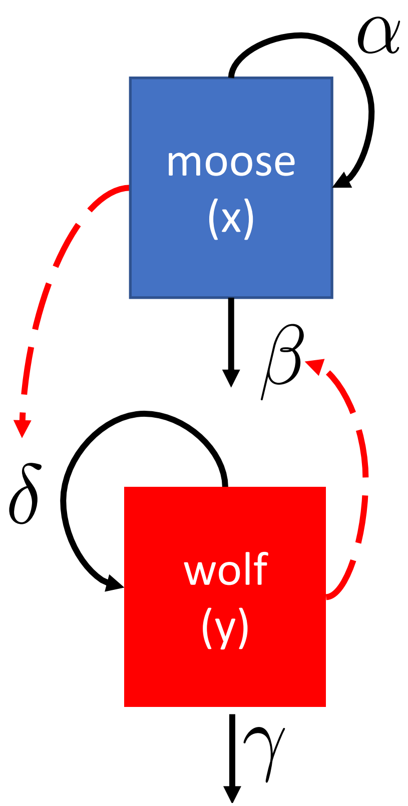


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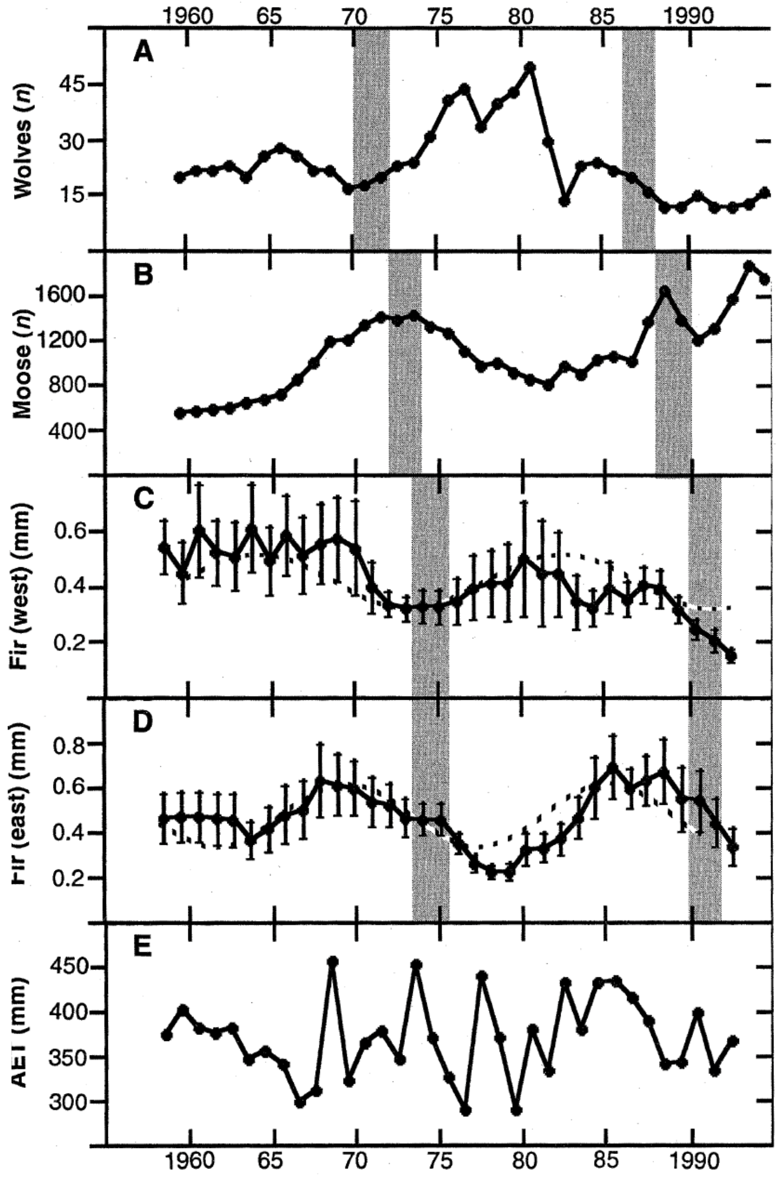


Wolf-moose dynamics on Isle Royale are **more complex than simple predator-prey**.

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.

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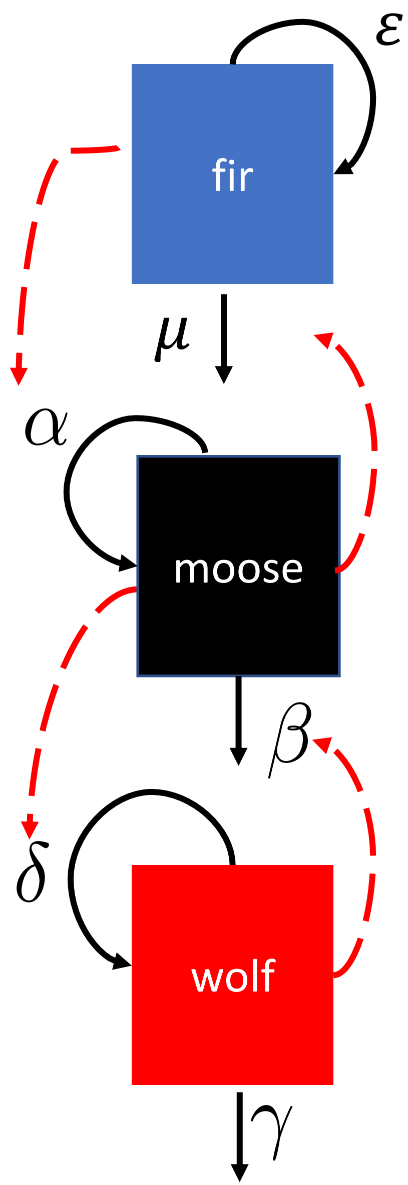
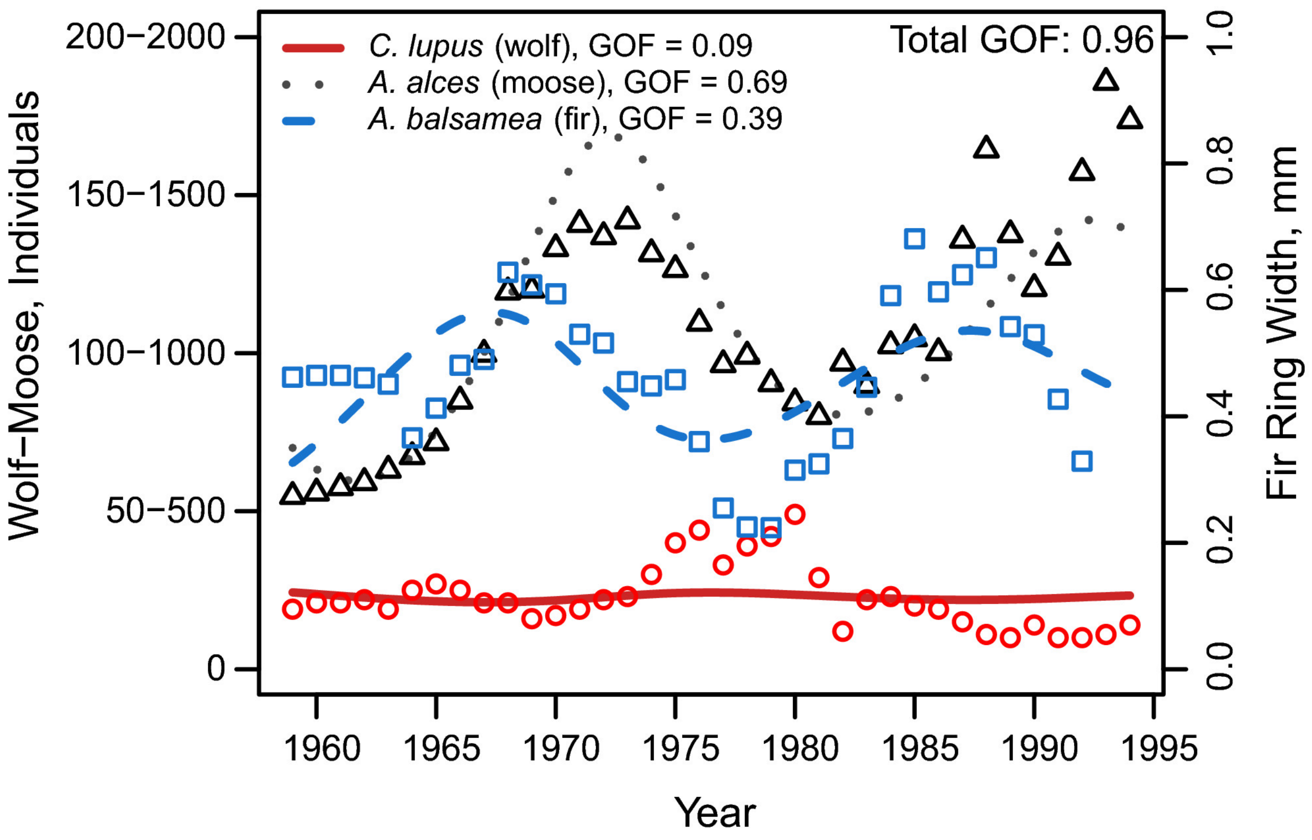
# Another famous example: Wolf-Moose on Isle Royale




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

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

Mülhbauer et al. 2020. *Ecology & Evolution.*

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

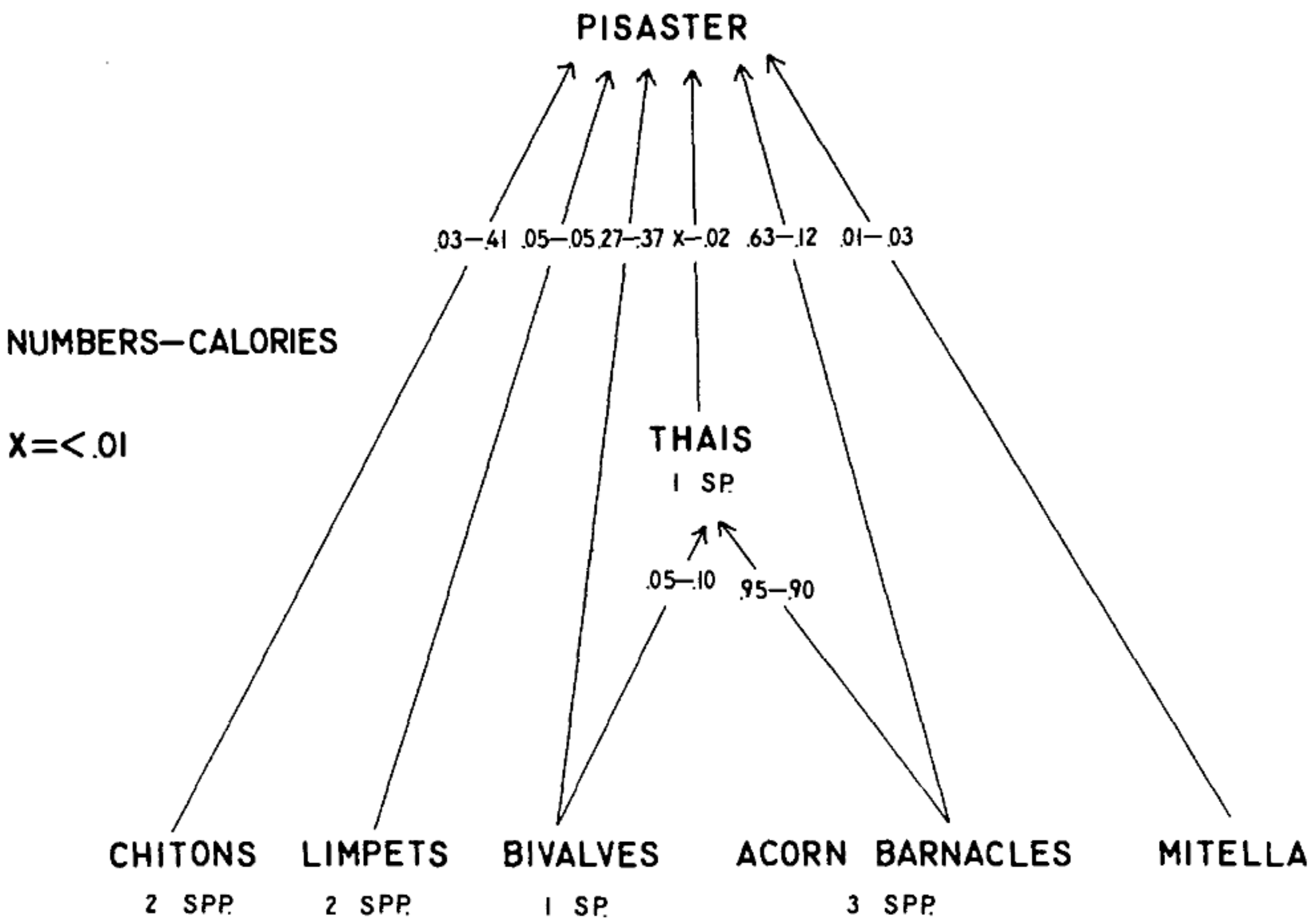
Vol. XCIV, No. 879 The American Naturalist November–December, 1960

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’)

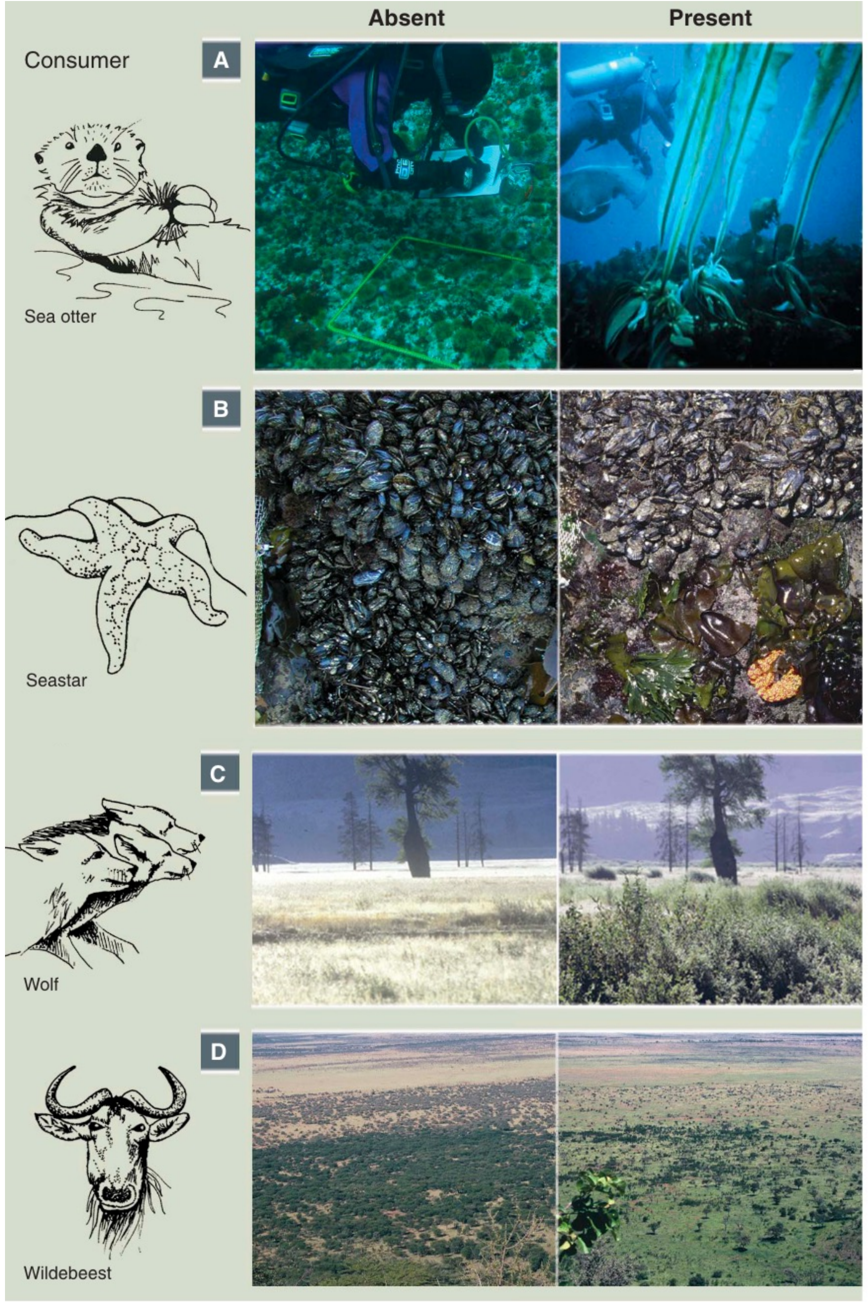
# This work inspired empirical studies on **trophic cascades**: *Pisaster* removal on Tatoosh Island




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*)