Extinction, Cope's Rule, and the dynamics of starvation and recovery




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Organisms condition reproduction on energetic state

Sometimes these activities are partitioned to reinforce the conditional relationship

Via life-history
-Space
-Time

Or mediated by behavioral state

Roadmap for this talk:

1) Briefly describe the Nutritional State-structured Model (NSM)
2) Implications for extinction risk as a function of mass
3) Predictions for contemporary species
4) A mechanism for Cope's Rule based on competition dynamics

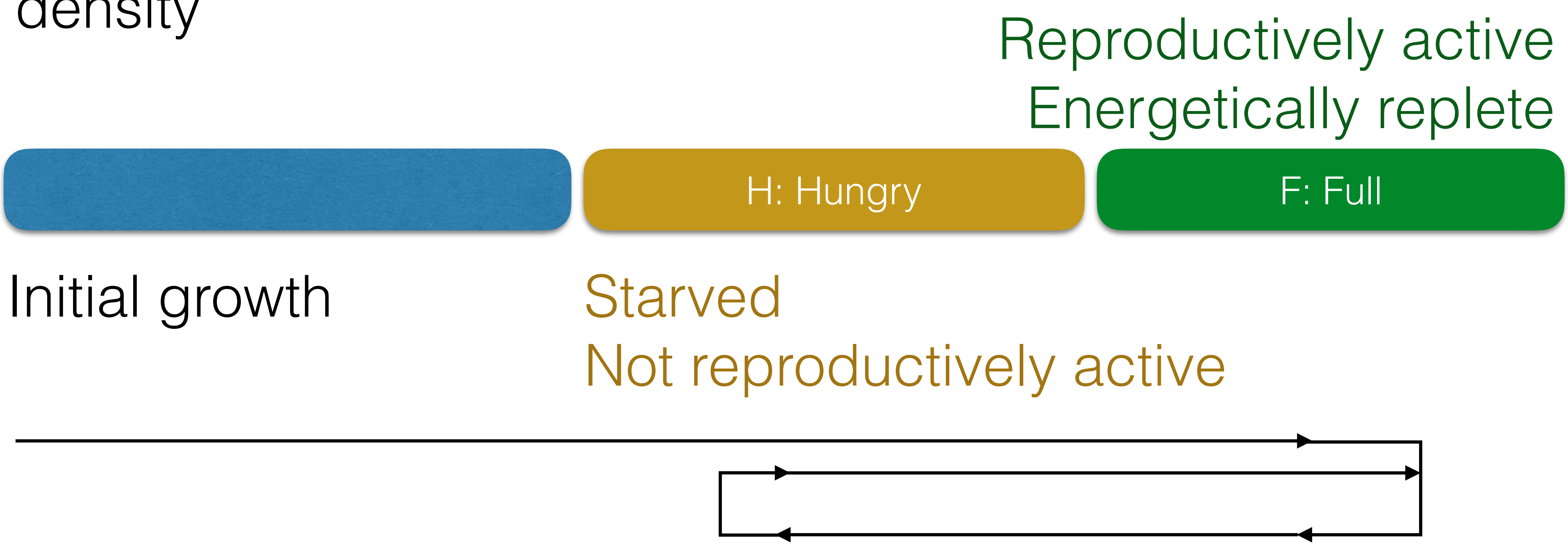
What is a <u>minimal model</u> to incorporate

- -Growth
- -Starvation
- -Recovery

Deriving an *explicit* version:

Full & **H**ungry consumer class (C=F+H)

**The transition from H→F, F→H is driven by resource density



Nutritional State Model (NSM)

consumer growth — recovery — starvation

$$\dot{F} = \lambda F + \xi \rho R H - \sigma (1 - R) F,$$
$$\dot{H} = \sigma (1 - R) F - \xi \rho R H - \mu H,$$
$$\dot{R} = \alpha R (1 - R) - (\rho R + \delta) H - \beta F$$

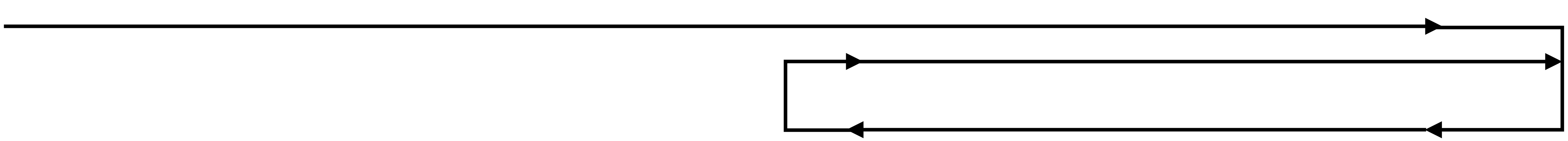
(NPP) — maintenance

Reproductively active
Energetically replete

H: Hungry — F: Full

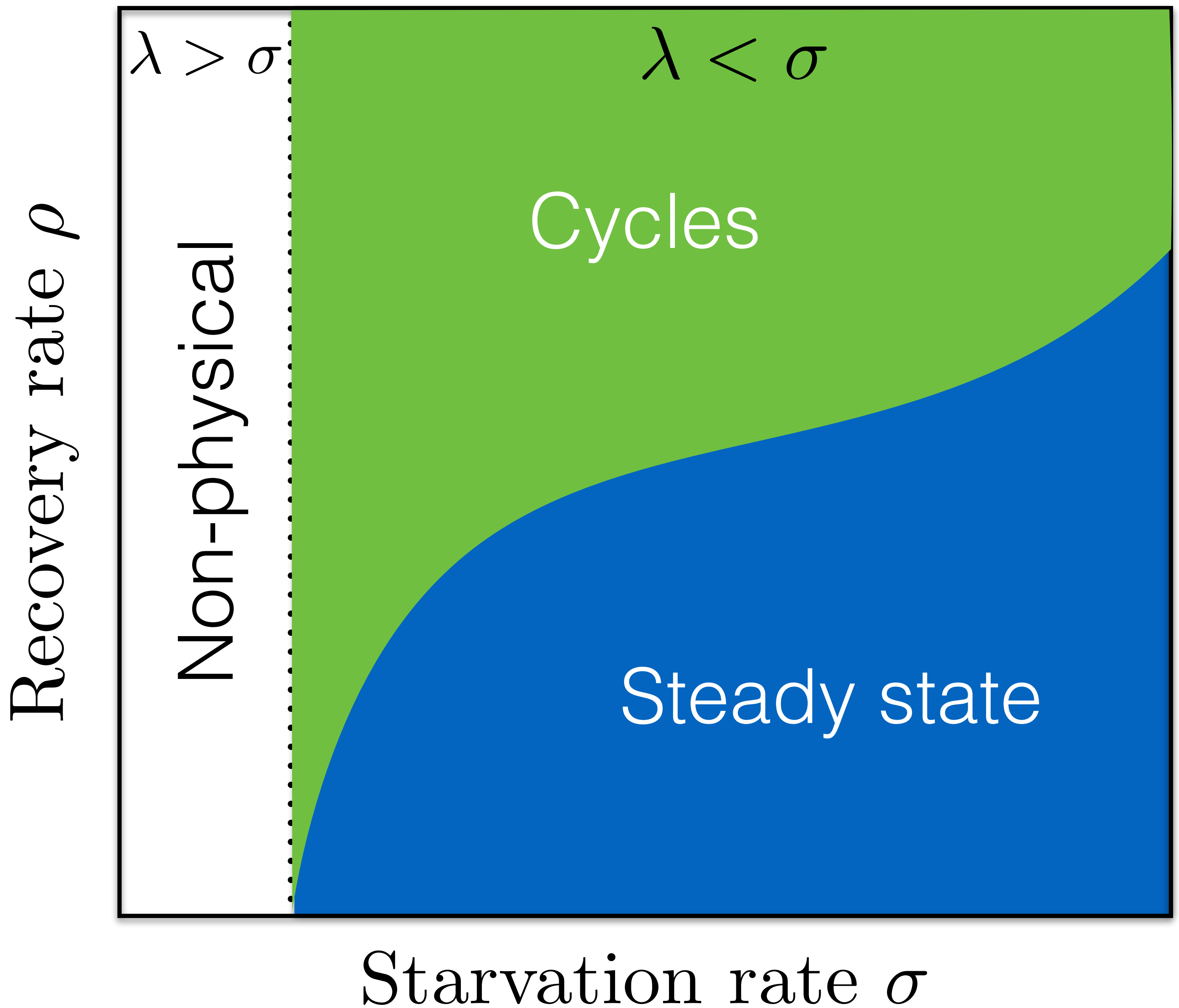
Initial growth

Starved
Not reproductively active



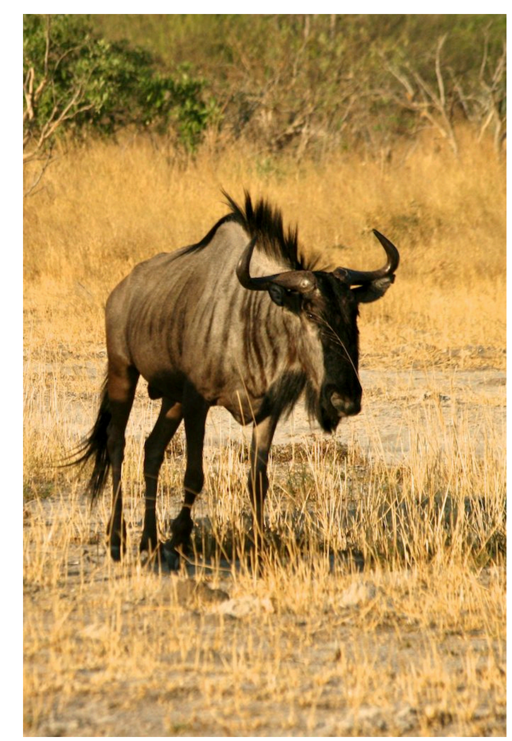
The general dynamics of the system

$$\dot{F} = \lambda F + \xi \rho R H - \sigma (1 - R) F,$$
$$\dot{H} = \sigma (1 - R) F - \xi \rho R H - \mu H,$$
$$\dot{R} = \alpha R (1 - R) - (\rho R + \delta) H - \beta F$$

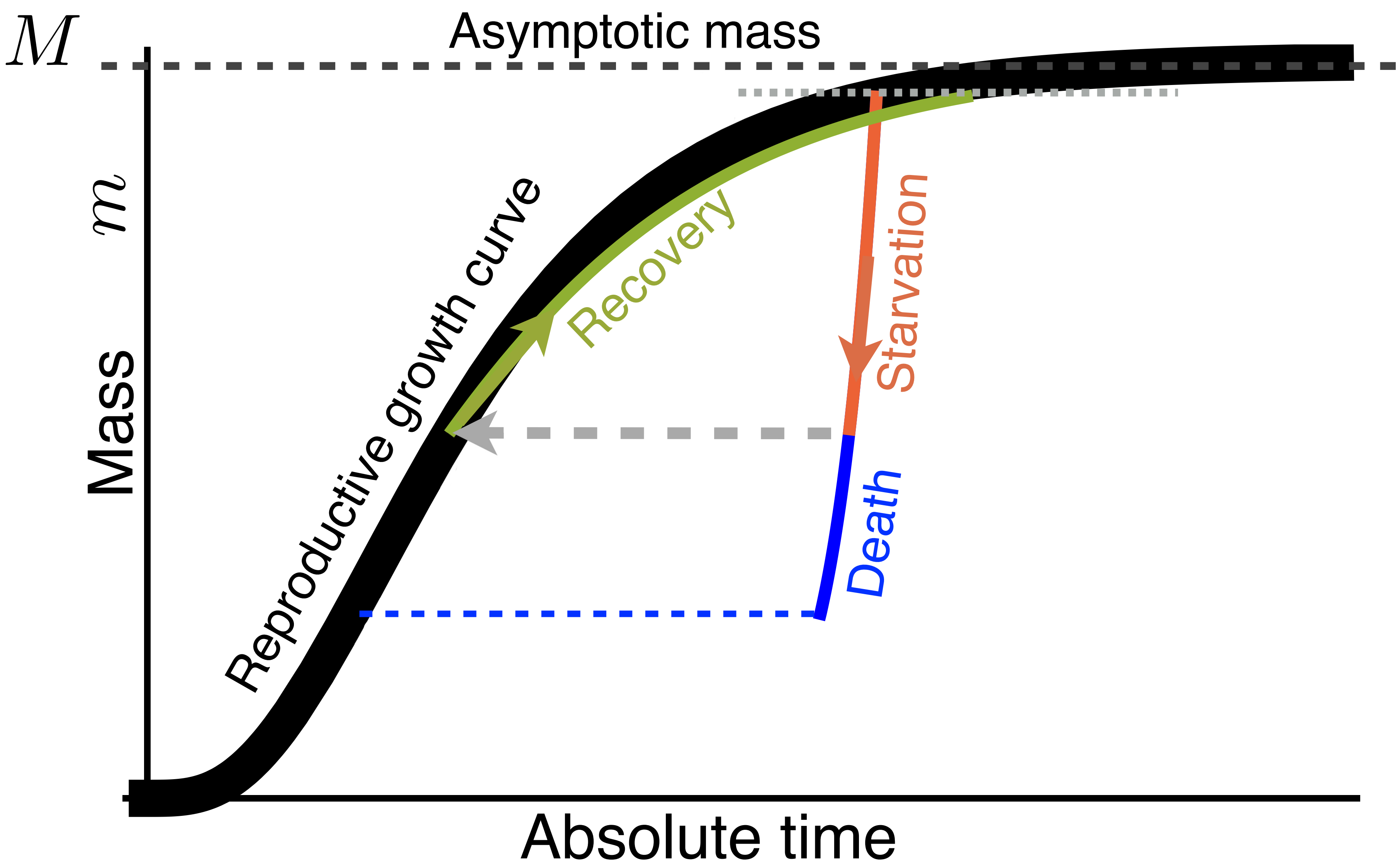


These rates are constrained by metabolism…

Body size!



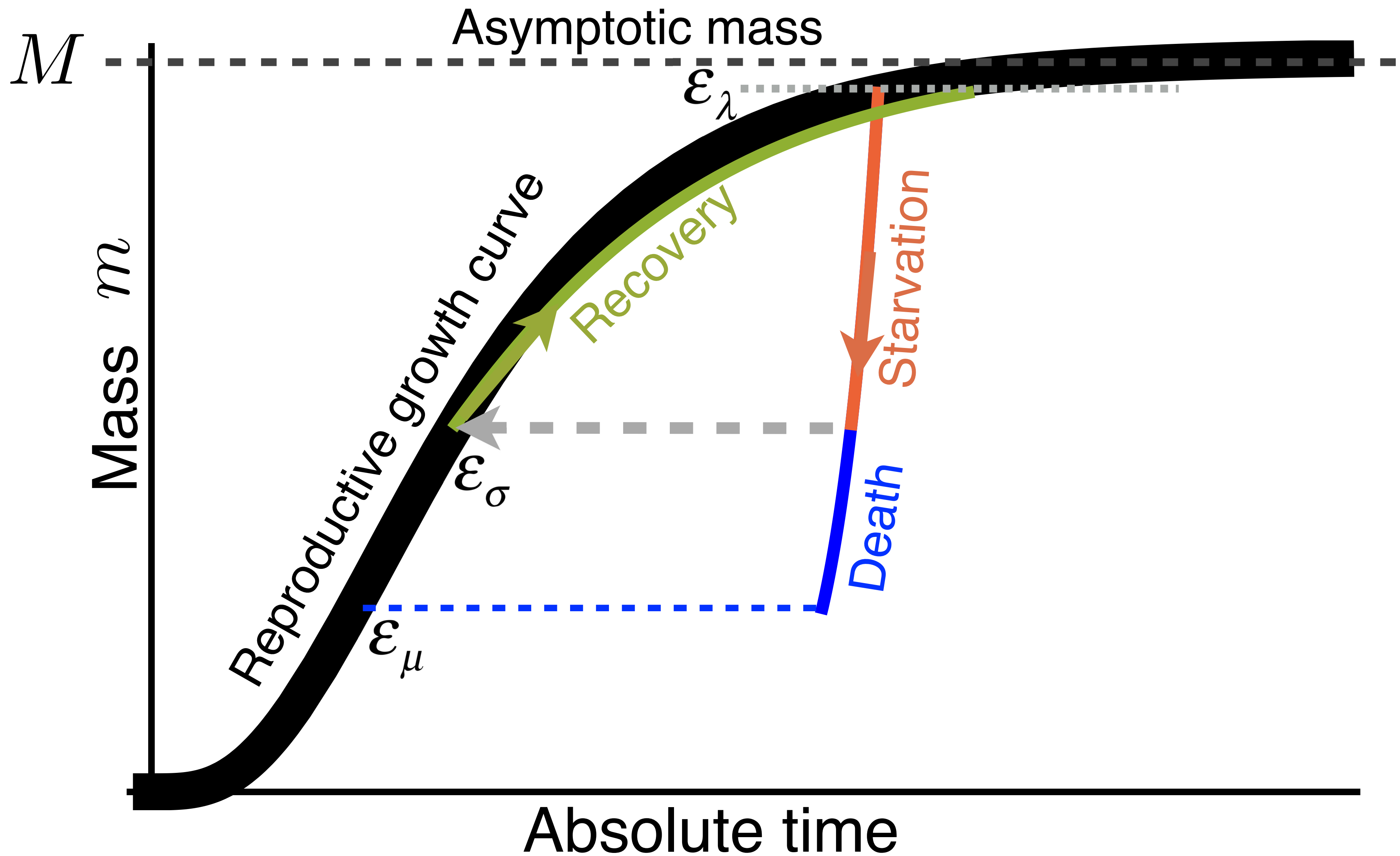
Model for ontogenetic growth supplies nearly all of the rates



$$B_0 m^{\eta} = E_m \frac{dm}{dt} + B_m m$$

Metabolic rate = Growth + Maintenance

Model for ontogenetic growth supplies nearly all of the rates



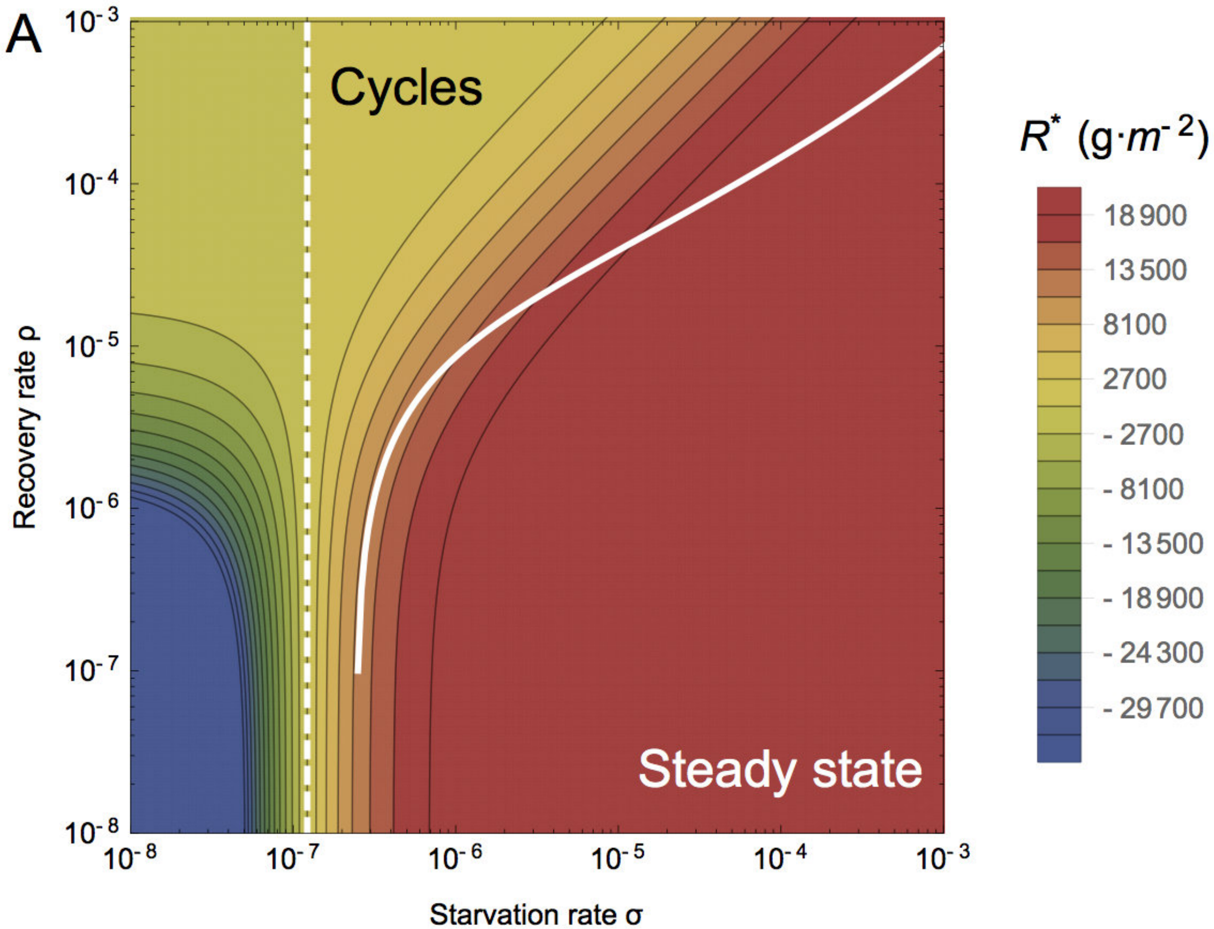
% body fat

ϵ_λ =0.95*M

ϵ_σ =Organism depleted of fat reserves $\epsilon_\sigma = 1 - f_0 M^\gamma / M$

ϵ_μ =Organism depleted of fat+muscle reserves

$$\epsilon_\mu = 1 - \left(f_0 M^\gamma + u_0 M^\zeta \right) / M$$

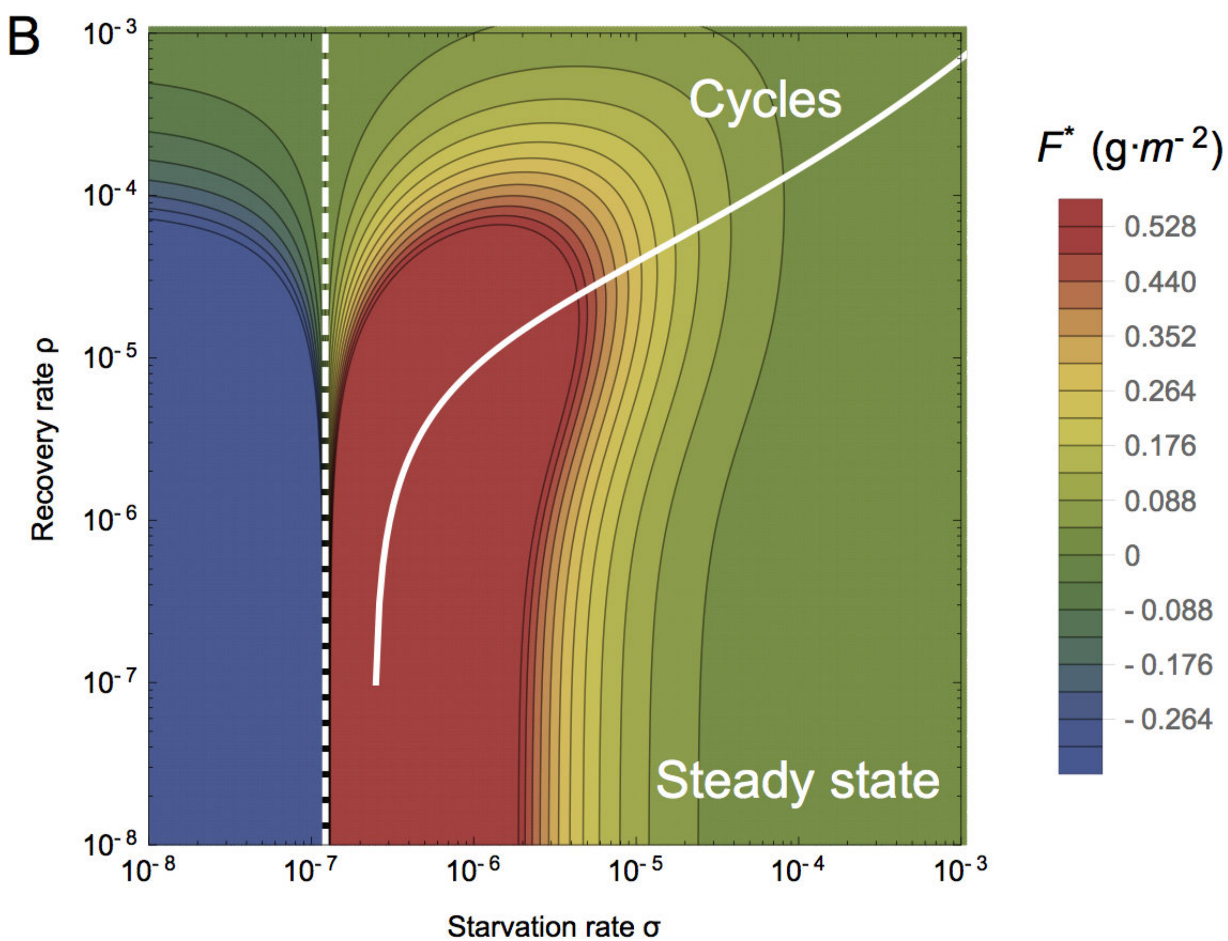


Kangaroo rat

$M = 100\text{g}$

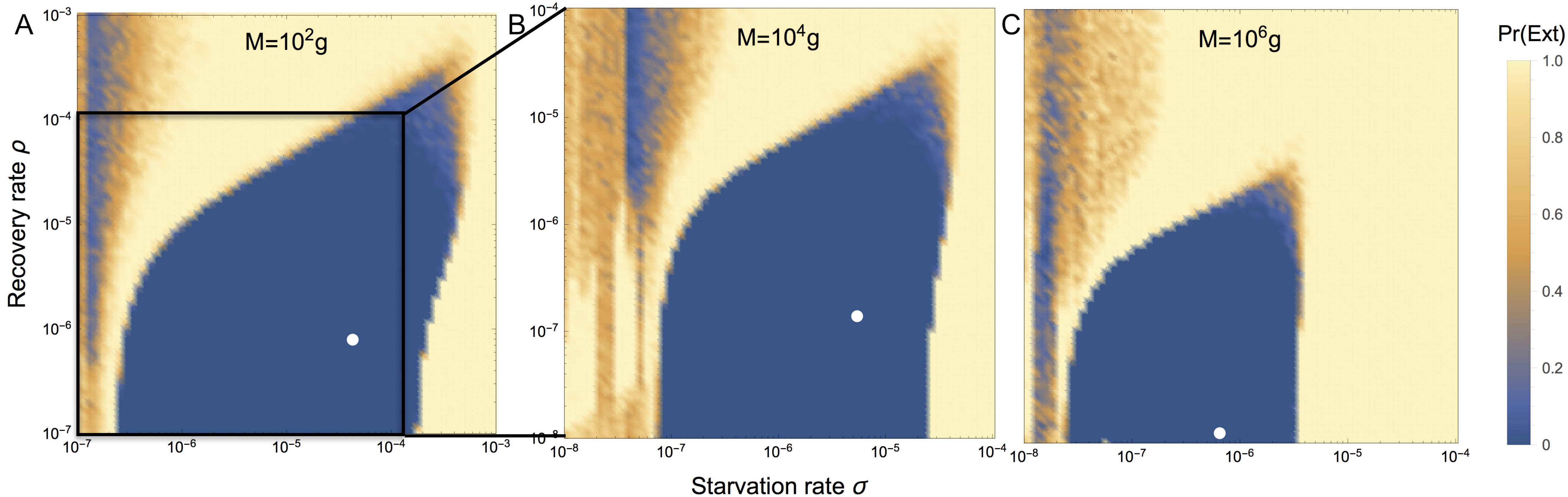
Transcritical bifurcation - - - - - -

Hopf bifurcation ———



Generally, rates of starvation and recovery close to transitions result in highest biomass densities for the consumer

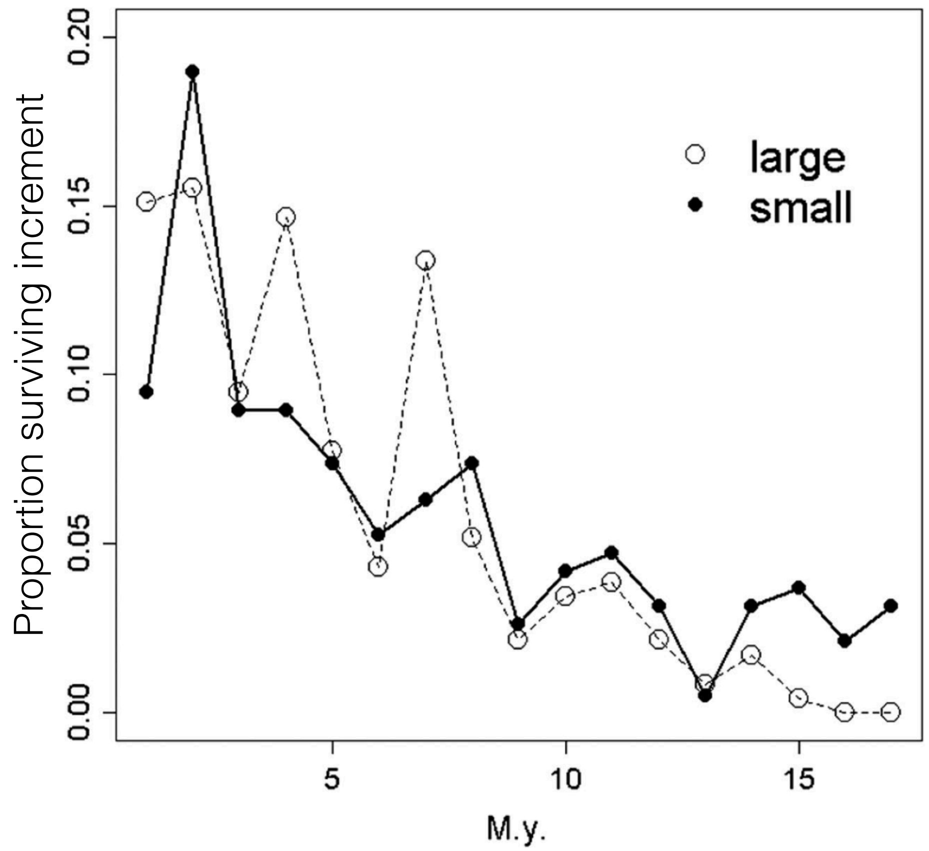
There are risks in both the cyclic regime and steady state regime



Two boundaries to persistence
-Death by transience
-Death by scarcity

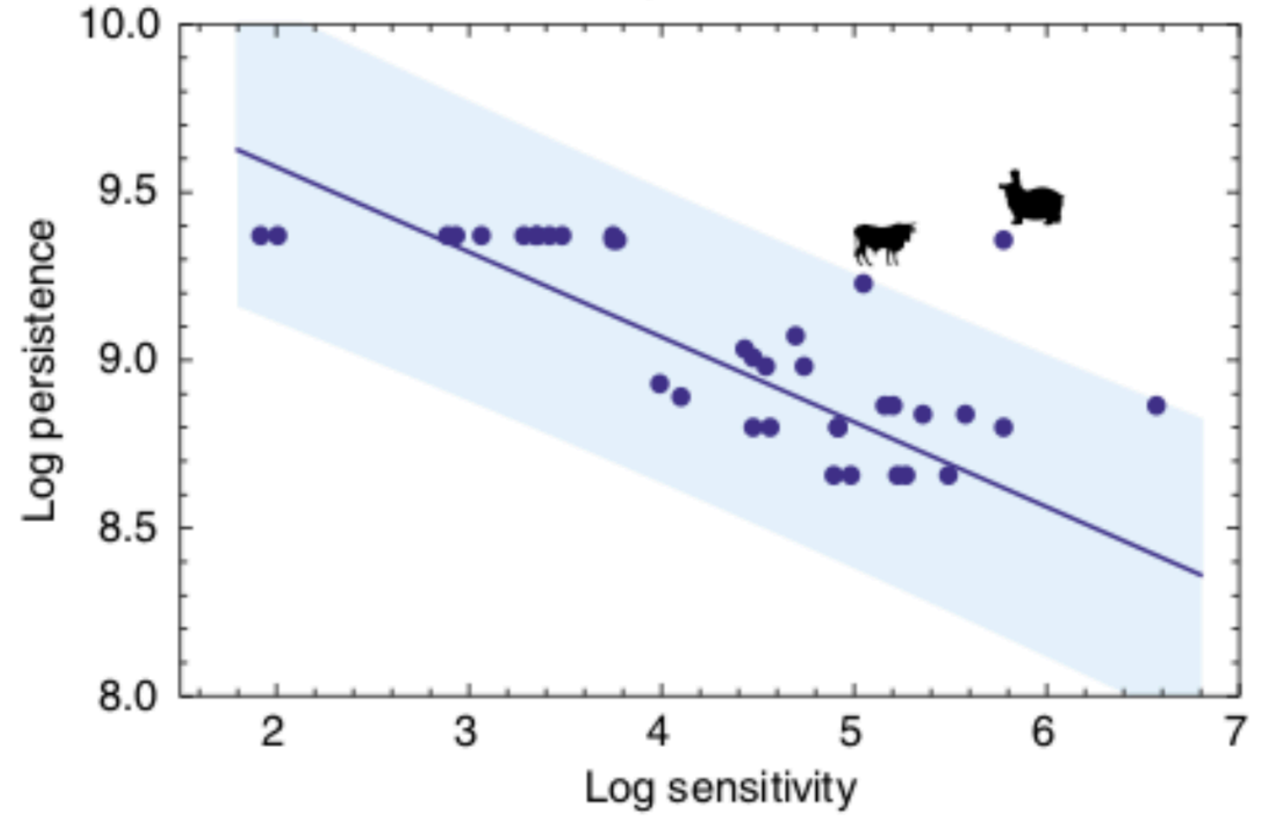
1) There is an ‘extinction refuge’, and the expected starvation and recovery rates are found within this range
2) This refuge becomes smaller for larger organisms… Suggests larger organisms are at greater risk based on the starvation-recovery dynamics in the NSM

Narrow extinction refuge for larger mammals has qualitative support



Large-bodied genera have shorter durations (significant but weak)

Liow et al. 2008

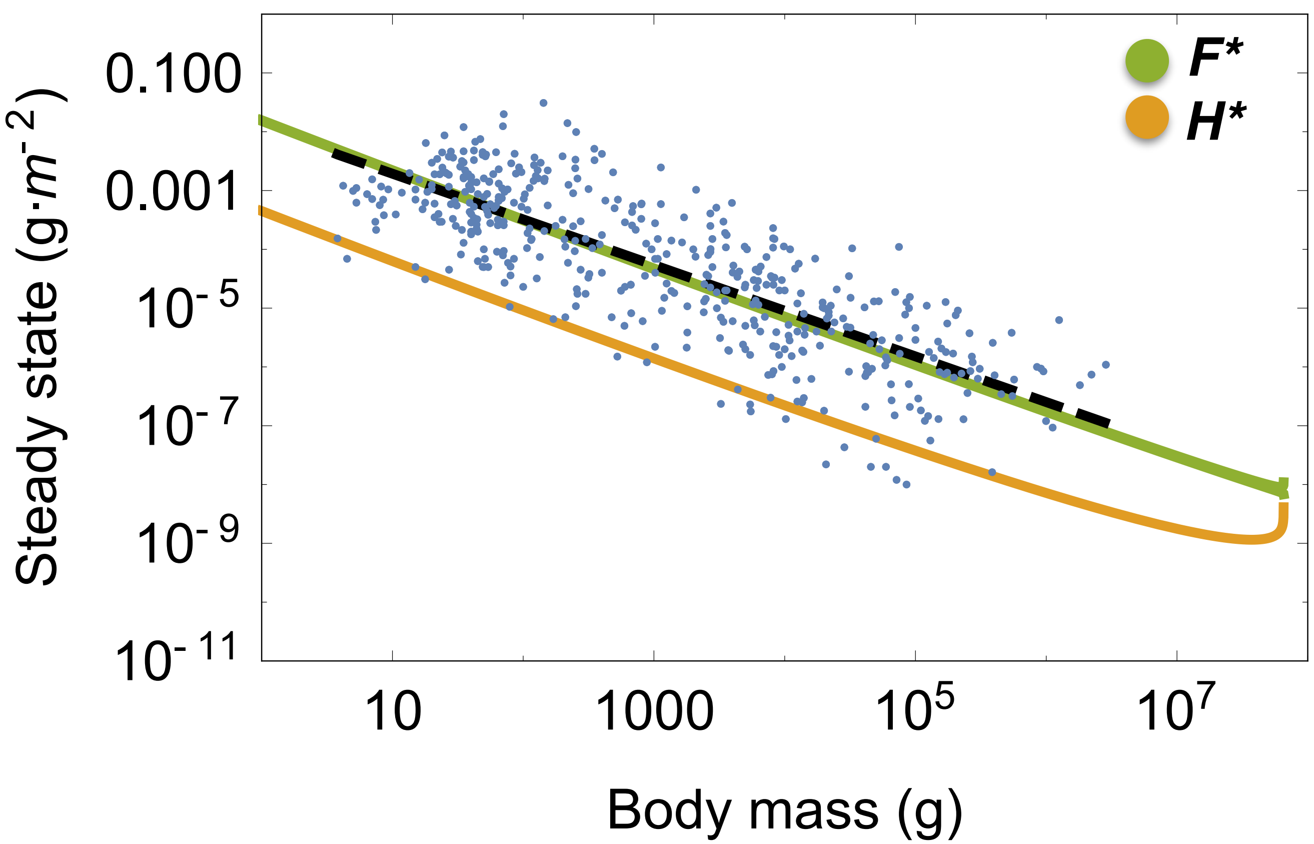


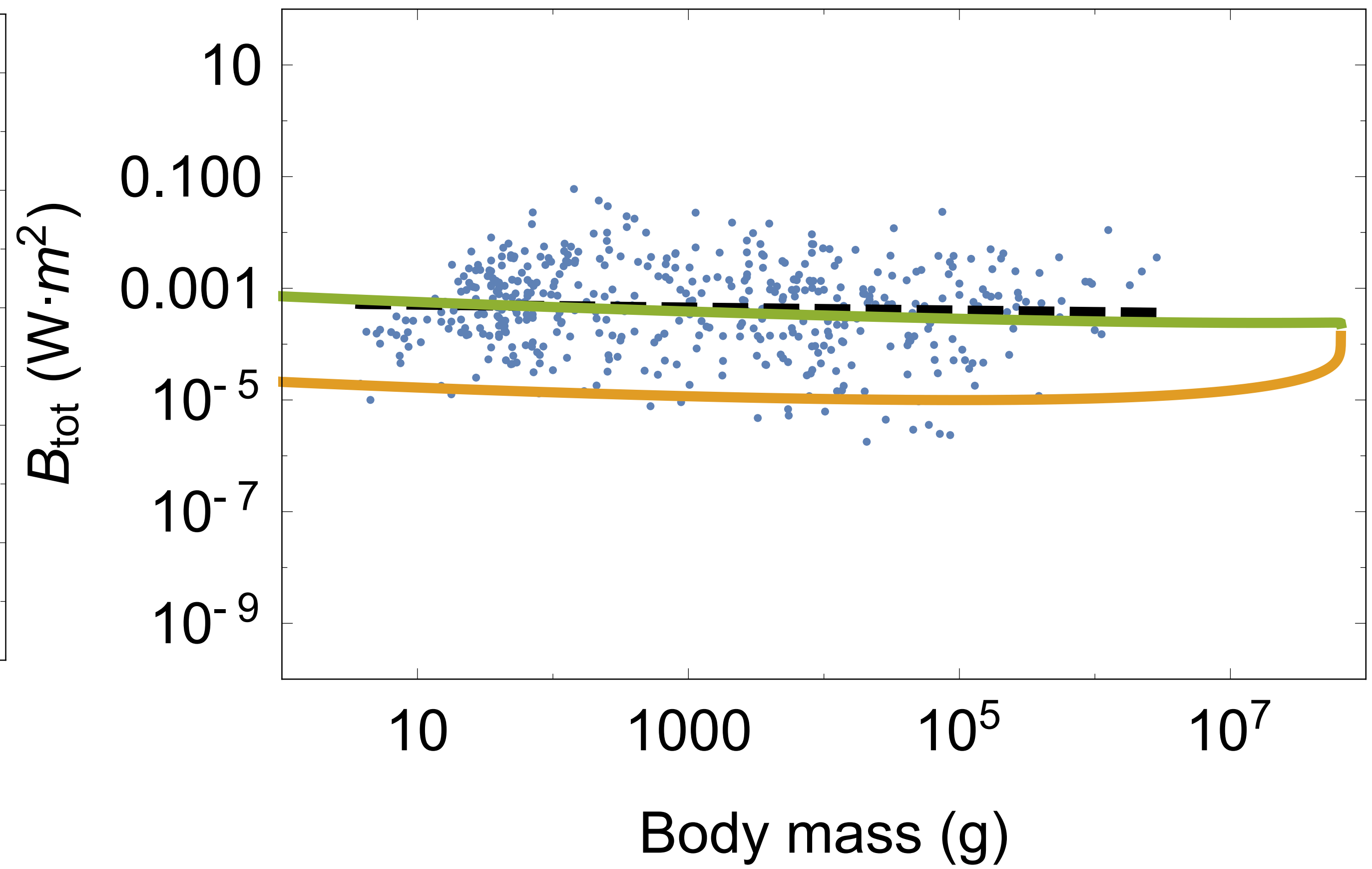
In Egypt, large mammals have persisted for shorter durations over the Holocene

Yeakel et al. 2014

Evolutionary feedback?

Does the NSM predict anything?



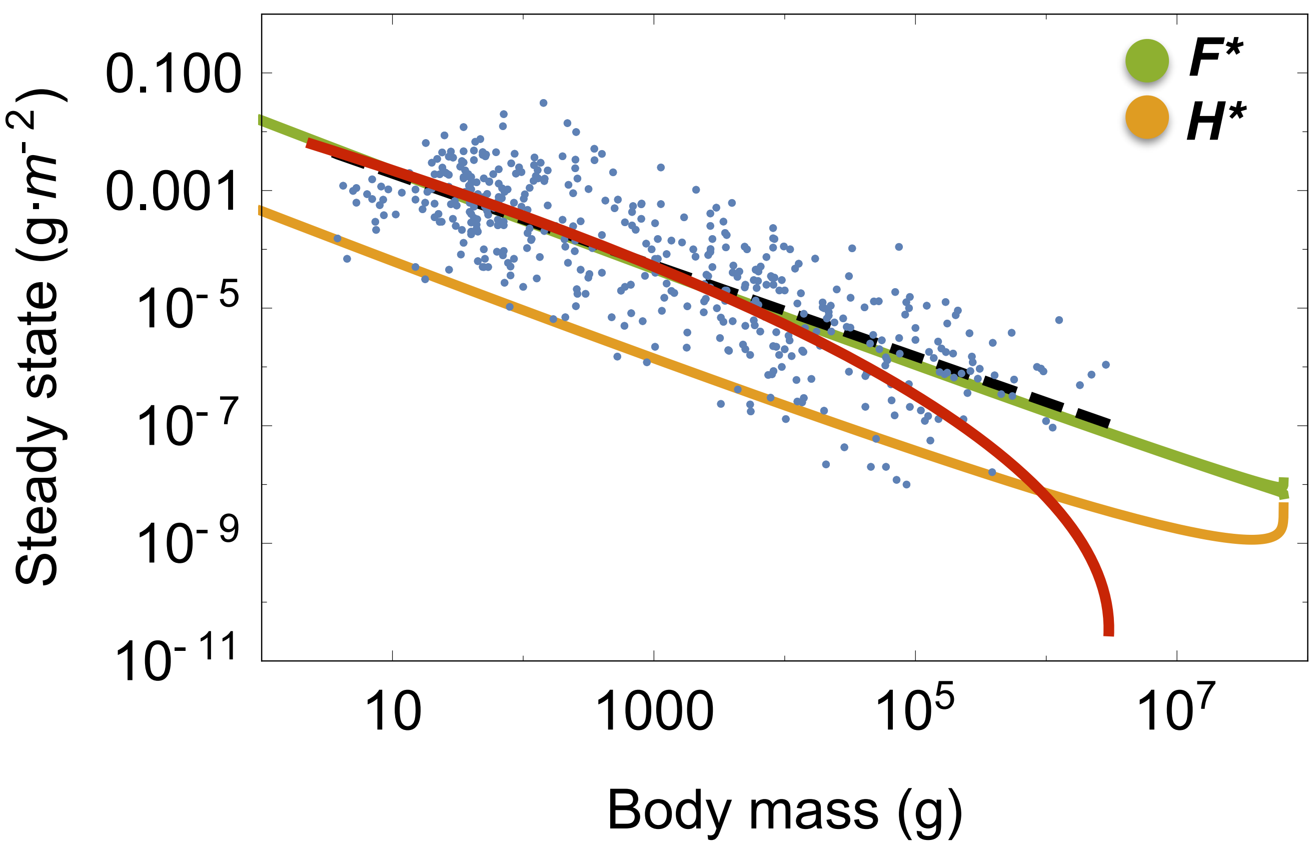


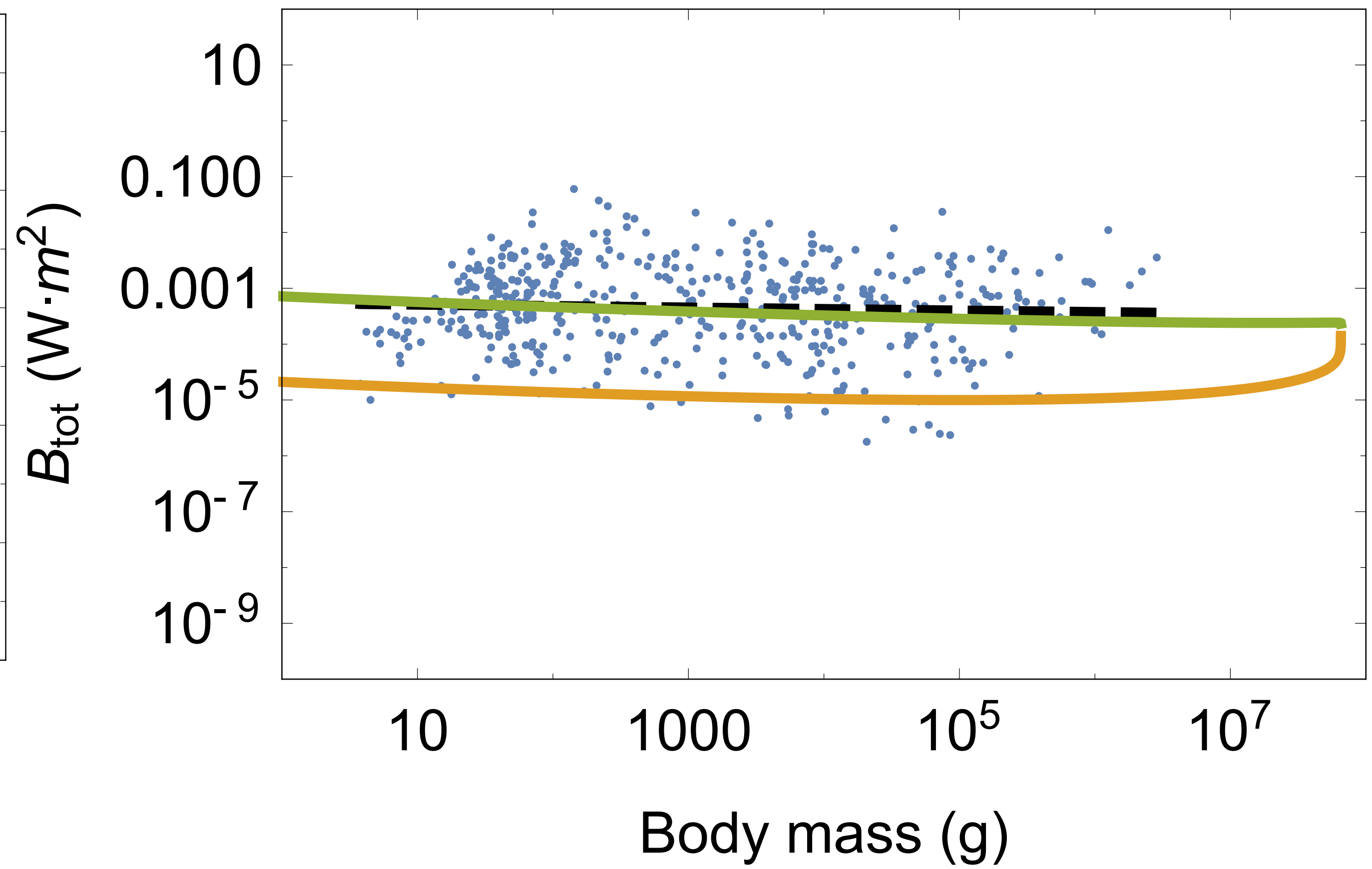
1) Intercept scales with resource growth rate
2) Slope purely a function of the dynamics and rate equations

$$F^* = (\sigma - \lambda)\frac{\alpha\lambda\mu^2(\mu + \xi\rho)}{A(\lambda\rho B + \mu\sigma(\beta\mu + \lambda(\delta + \rho)))}$$

3) Suggests starvation dynamics are important
4) Supports Damuth's Law
5) Additional mortality load asymmetrically effects large body sizes ~ extinction risk
6) Weird asymptotes at large *M*

Does the NSM predict anything?





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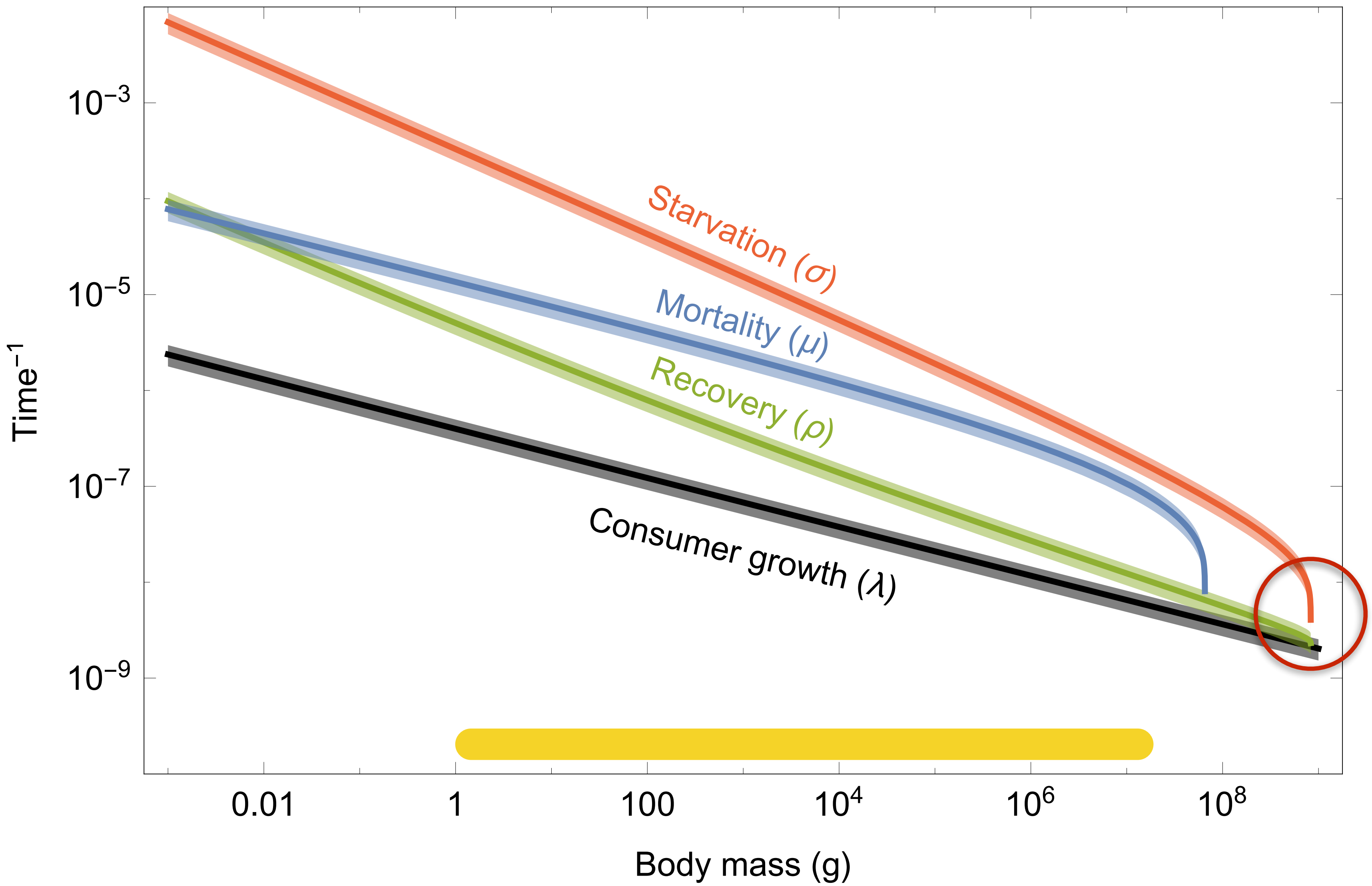
Does this provide any insight to Cope's Rule, or the evolution of larger body size?



$\lambda < \sigma$ for all realistic values of M

Strong upper-bound to body mass… when body = 100% fat, meaning starvation time is infinitely long

$$f_0 M^{\gamma - 1} = 1$$

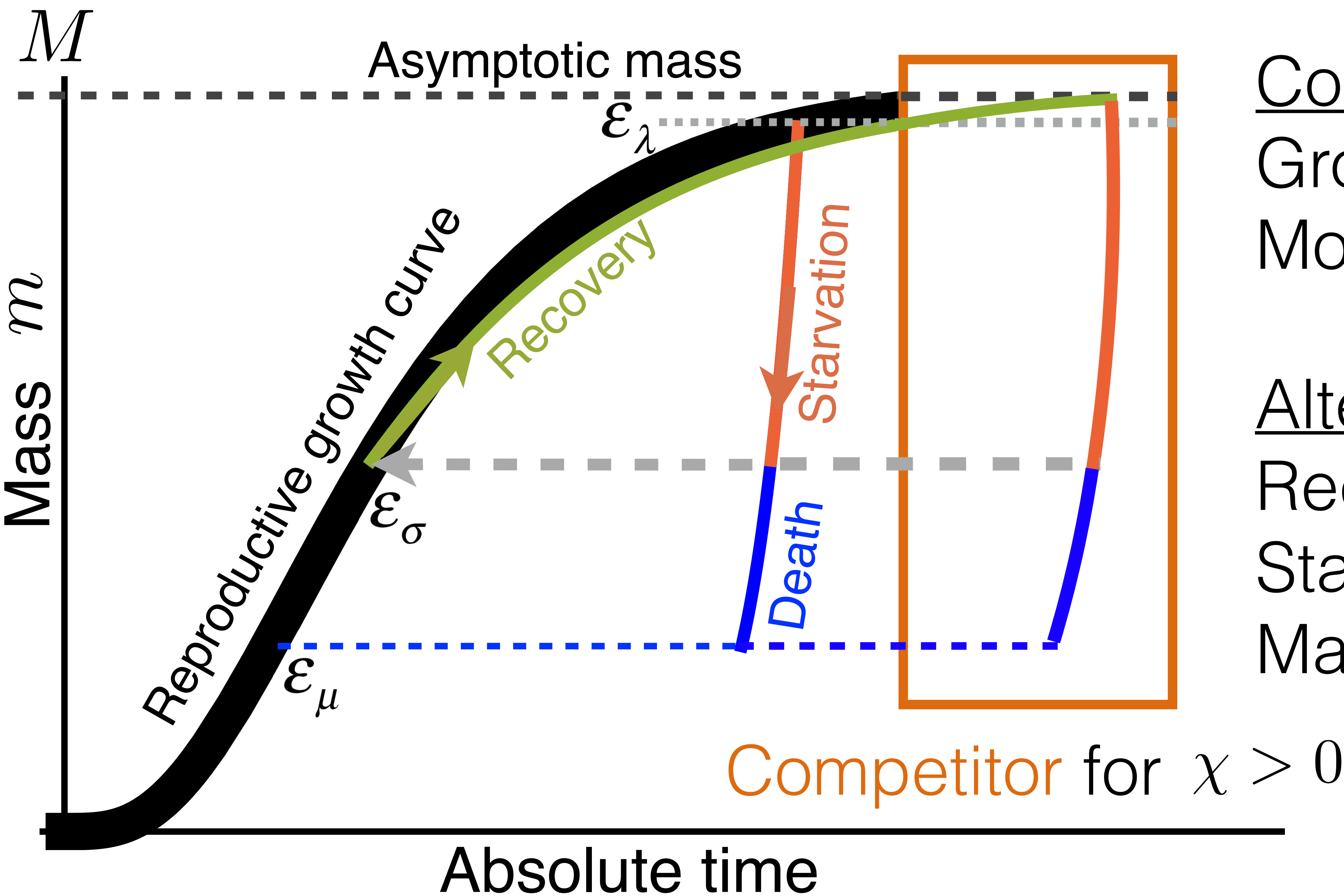
Strong upper-bound to body mass… when body = 100% fat, meaning the rate of starvation become infinite

$$f_0 M^{\gamma-1} = 1$$

$M = 8.3 \times 10^8$ …an organism the size of 120 male African elephants

This is fun, but doesn't introduce a selective mechanism for Cope's rule

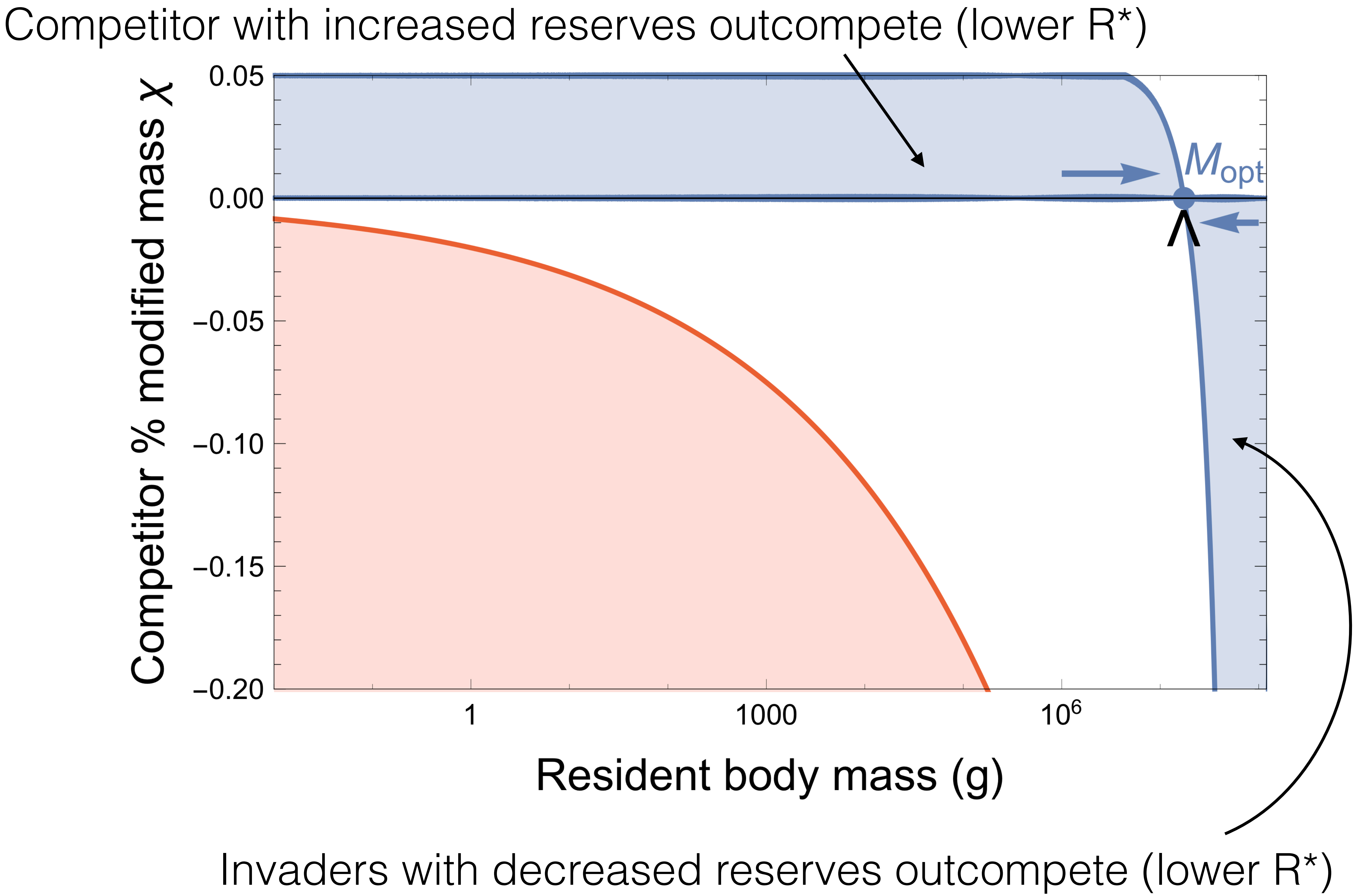
Characterizing the rates of a competing species



<u>Conserved</u>
Growth rate
Mortality rate

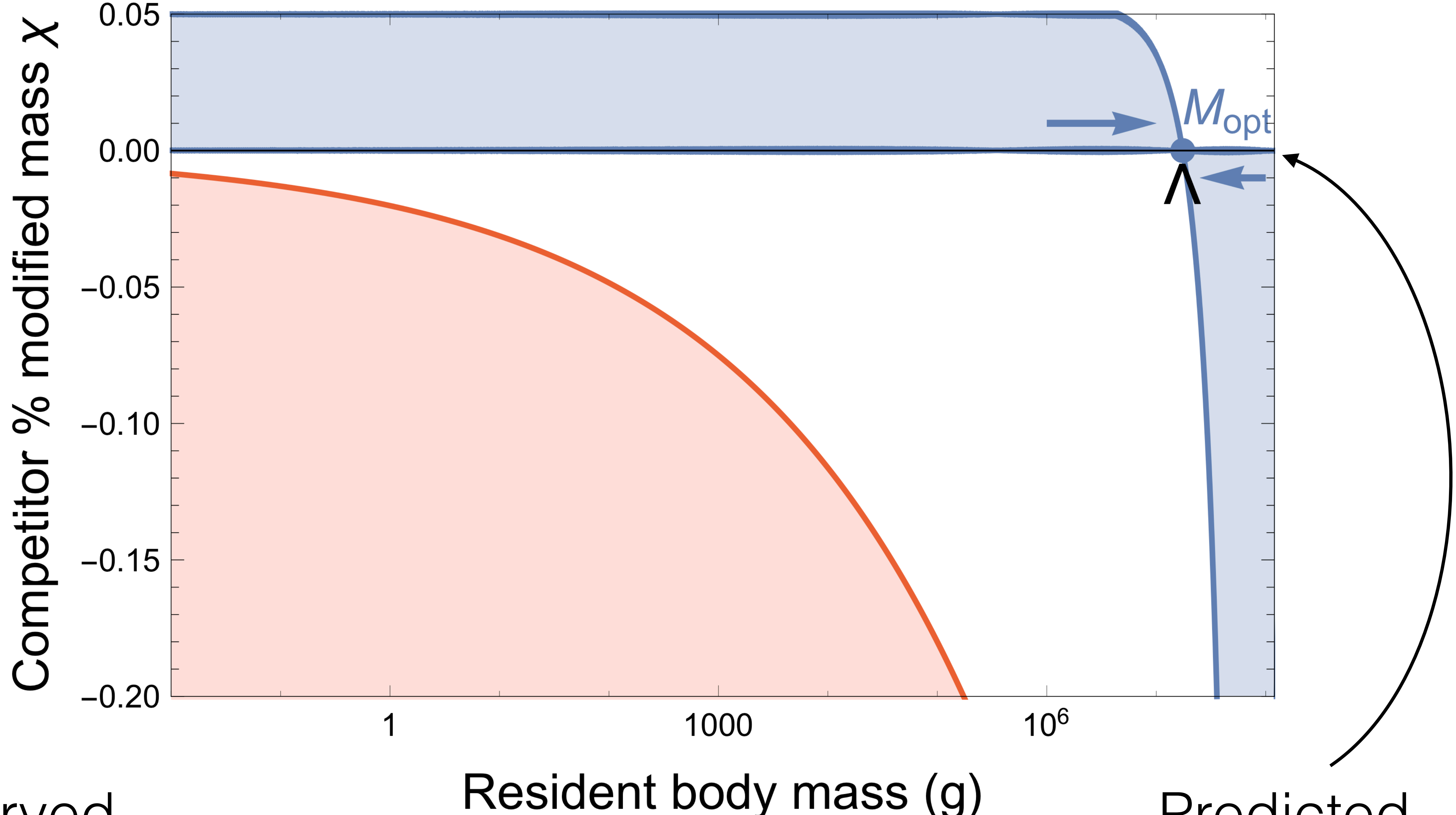
<u>Altered</u>
Recovery rate
Starvation rate
Maintenance rates

Selection via: who can push resource densities lower?
[R* theory]



Competitor with increased reserves outcompete (lower R*)
0.05
0.00
−0.05
−0.10
−0.15
−0.20
Competitor % modified mass χ
1
1000
10^6
Resident body mass (g)
M_opt
Invaders with decreased reserves outcompete (lower R*)

Evolutionary attractor?



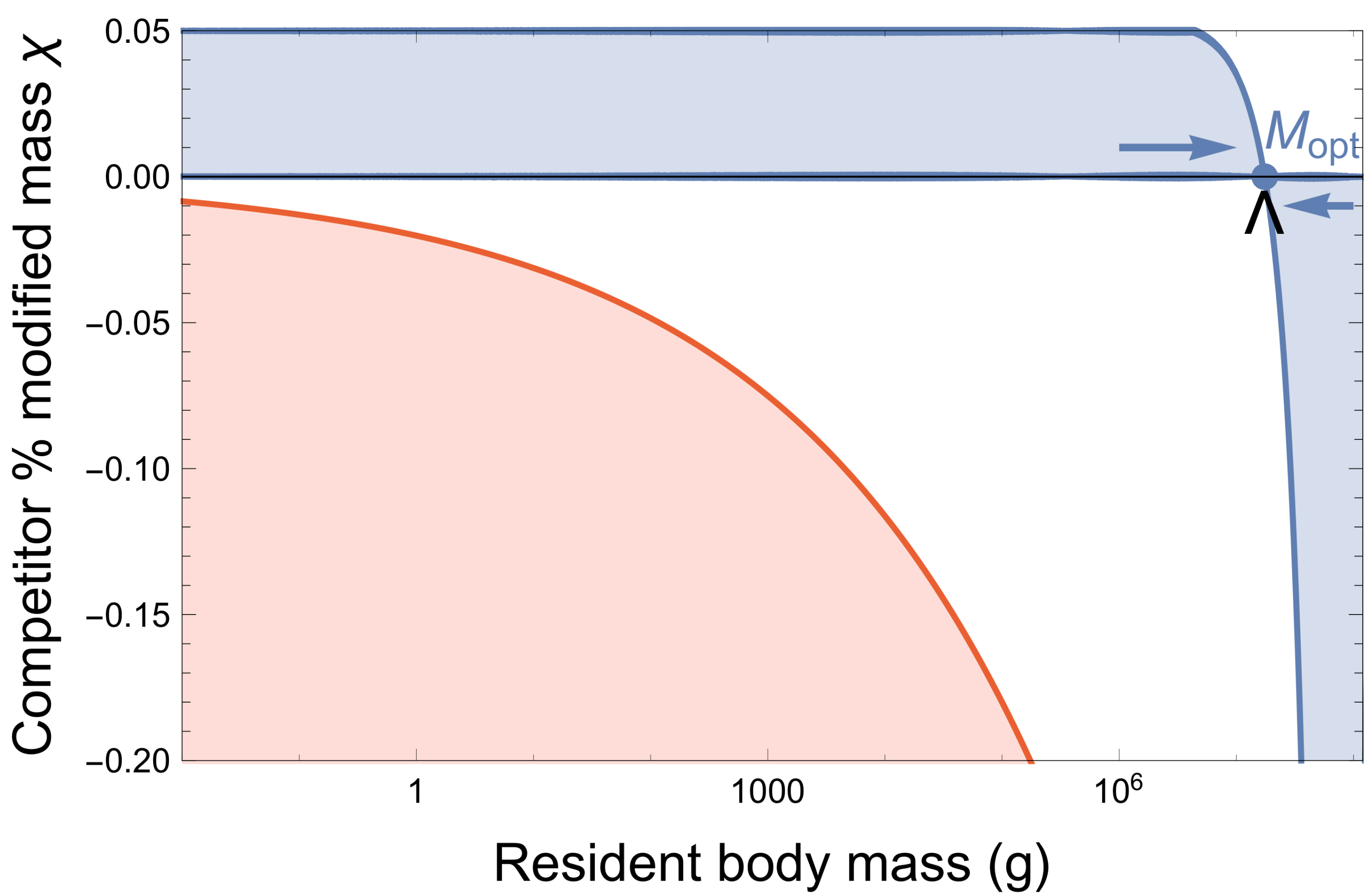
Observed

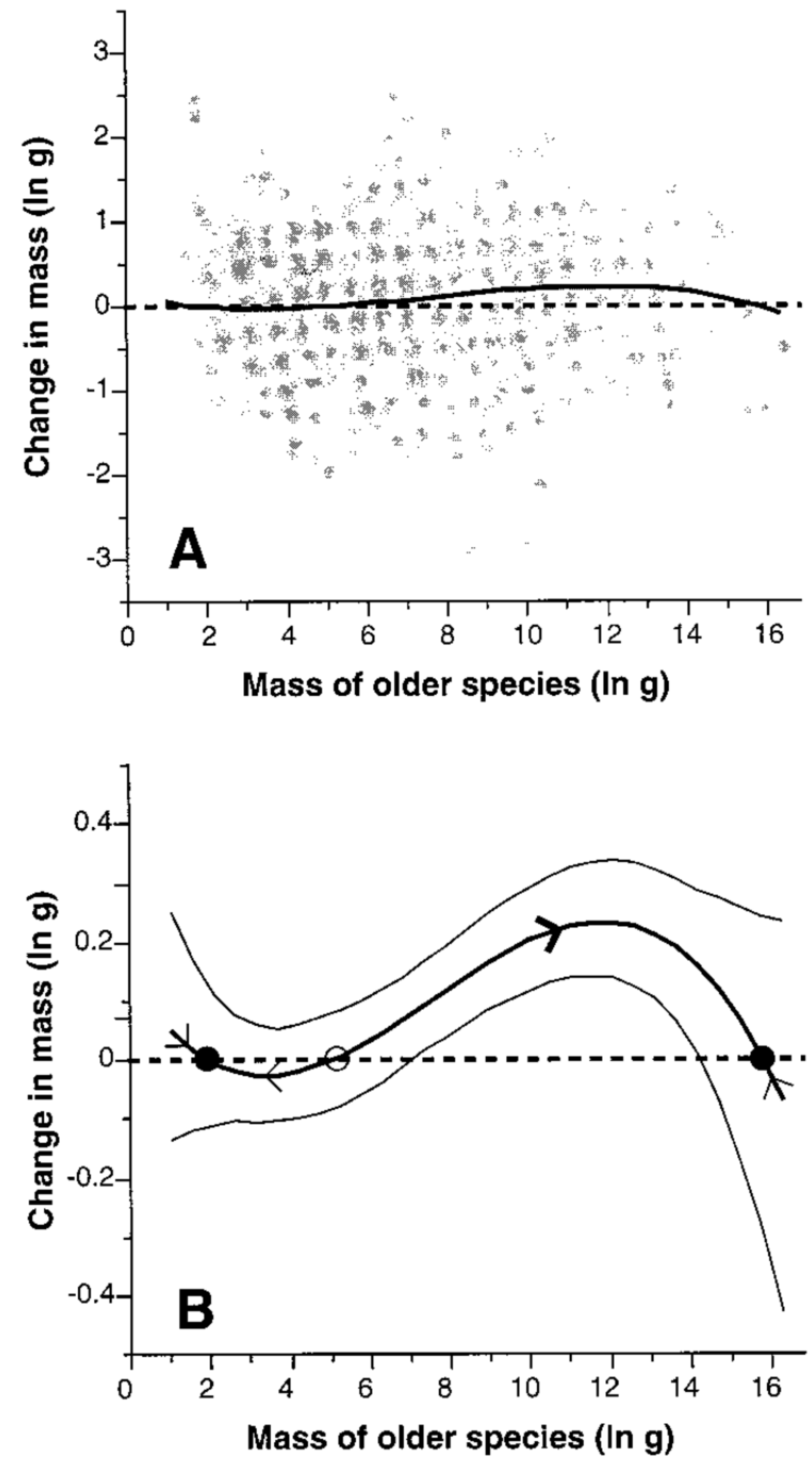
$$M_{Indricotherium} = 1.5 \times 10^7$$
$$M_{Deinotherium} = 1.74 \times 10^7$$

Predicted

$$M_{\text{opt}} = 1.748 \times 10^7$$

Evolutionary attractor?





No sign of a lower bound, but the NSM is pretty minimal…
Higher trophic effects?

Alroy, 1998

Thank you!