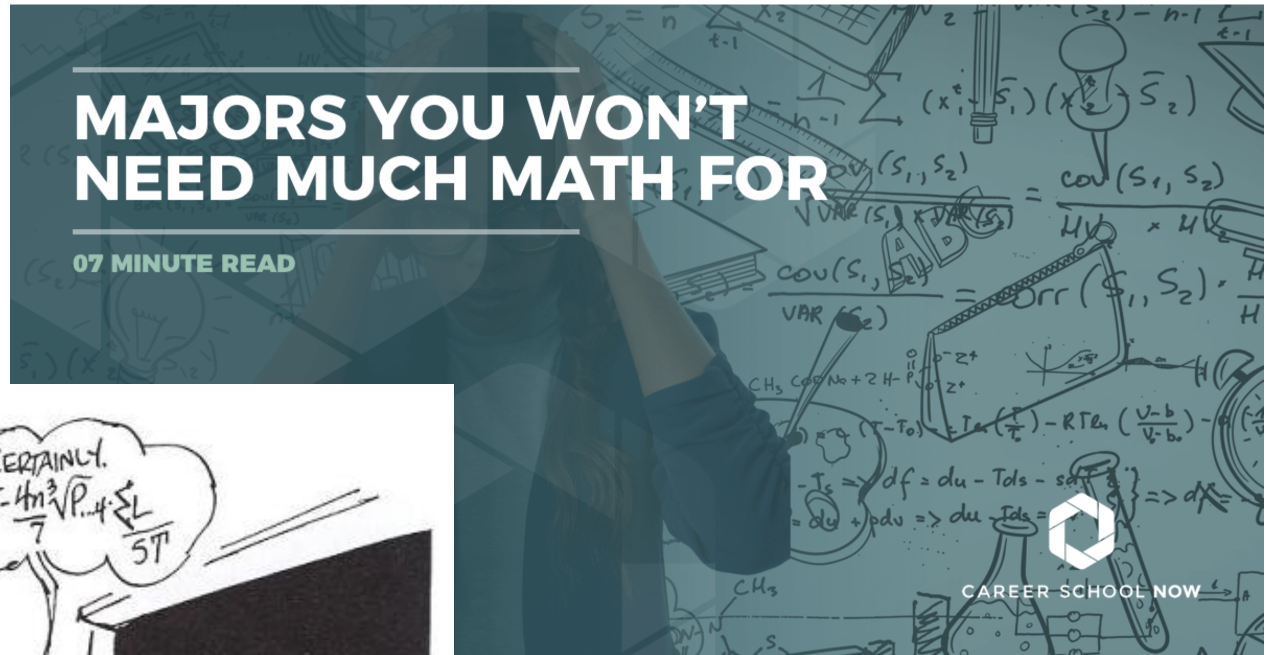
Mathematical models in evolutionary research

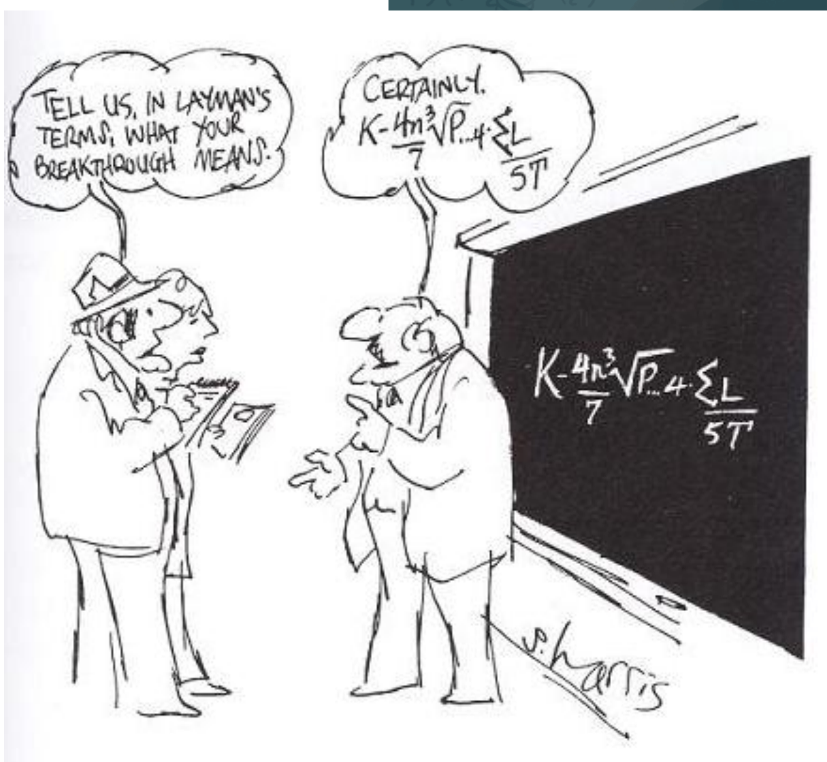
Maria E. Orive
Ecology and Evolutionary Biology
University of Kansas
@MEOrive

NABT Professional Development Conference
November 10, 2018

Scott Williamson

mathematics and biologists





mathematical models in ecology and evolution

Journal (2001)	Number of articles	Models used generally[1]	Models used specifically[2]	Equations![3]
American Naturalist	105	96%	59%	58%
Ecology	274	100%	35%	38%
Evolution	231	100%	35%	33%

[1]General use: includes statistical or phylogenetic analysis with a mathematical basis, e.g. ANOVA, regression, etc.

[2]Specific use: mathematical model used to obtain results

[3]Equations present: excluding standard statistical equations

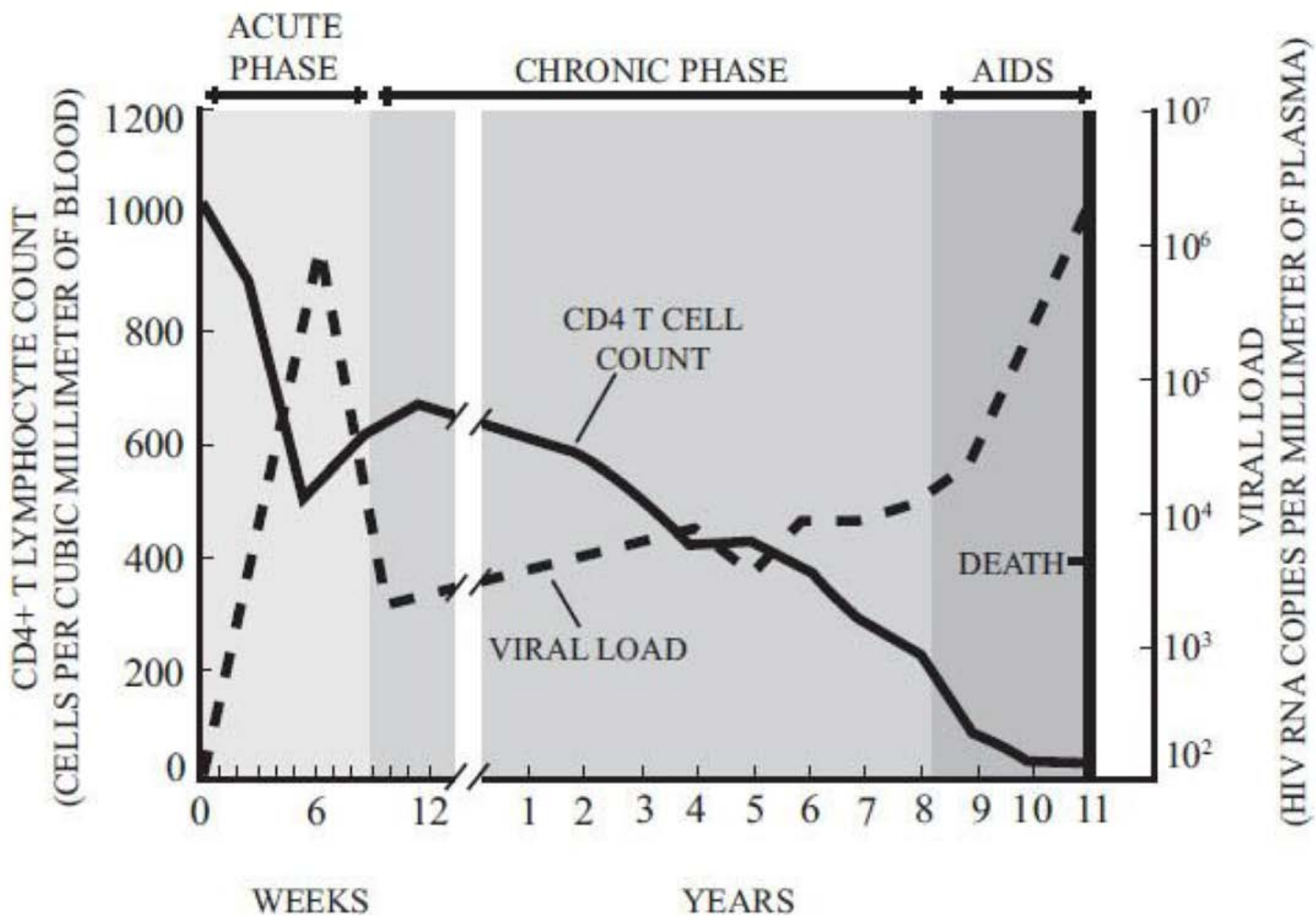
adapted from Otto and Day (2007)

two ways we can use models to make sense of biology

- Explain what we *do see*
  - Specific test of hypotheses
  - Example: dynamics of HIV after infection

- Predict what we *might see*
  - Generate hypotheses
  - Example: evolutionary lag and rescue with complex life histories

Time course of HIV infection within an individual



from Otto & Day (2007)
data from Fauci et al. (1996)

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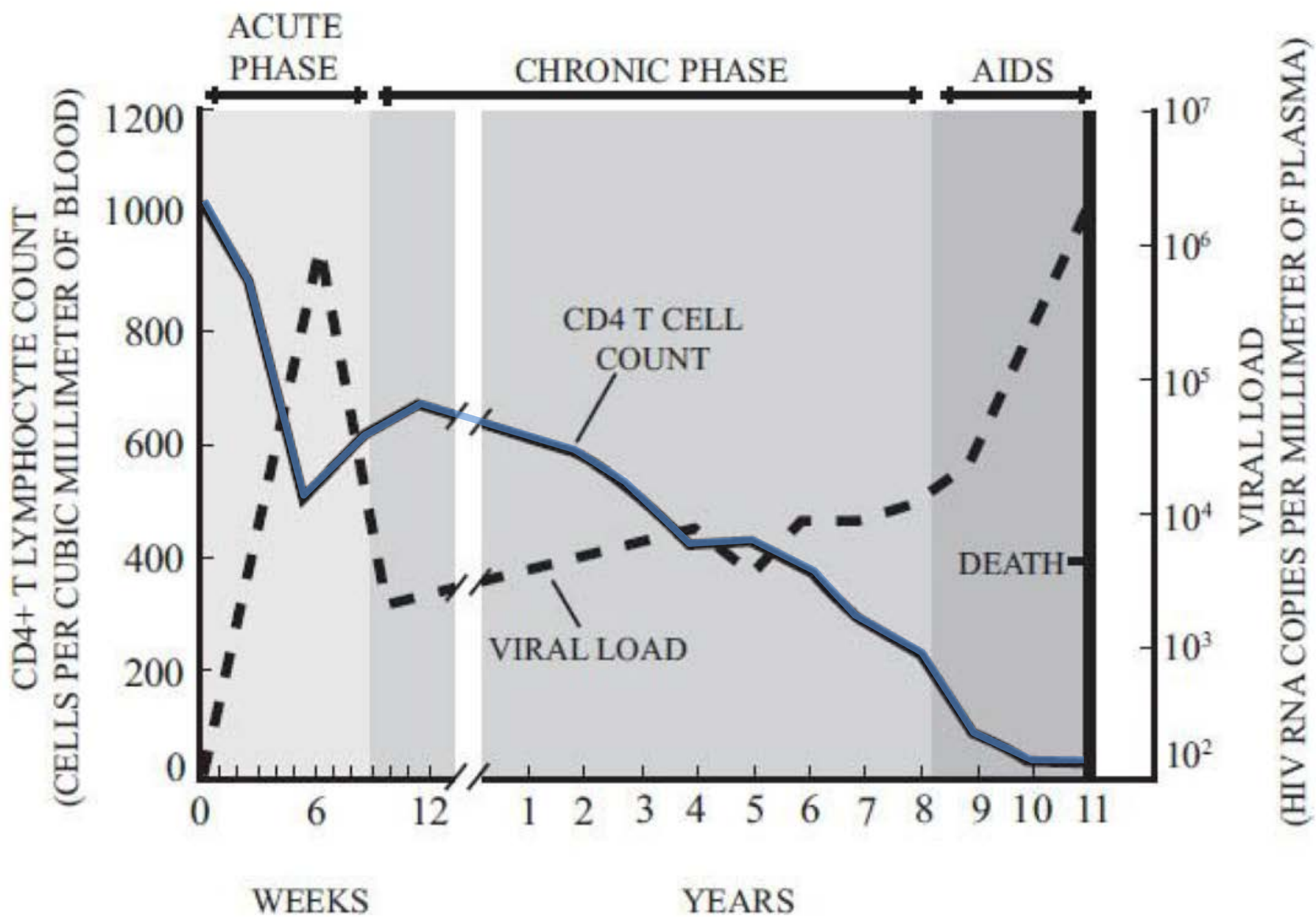

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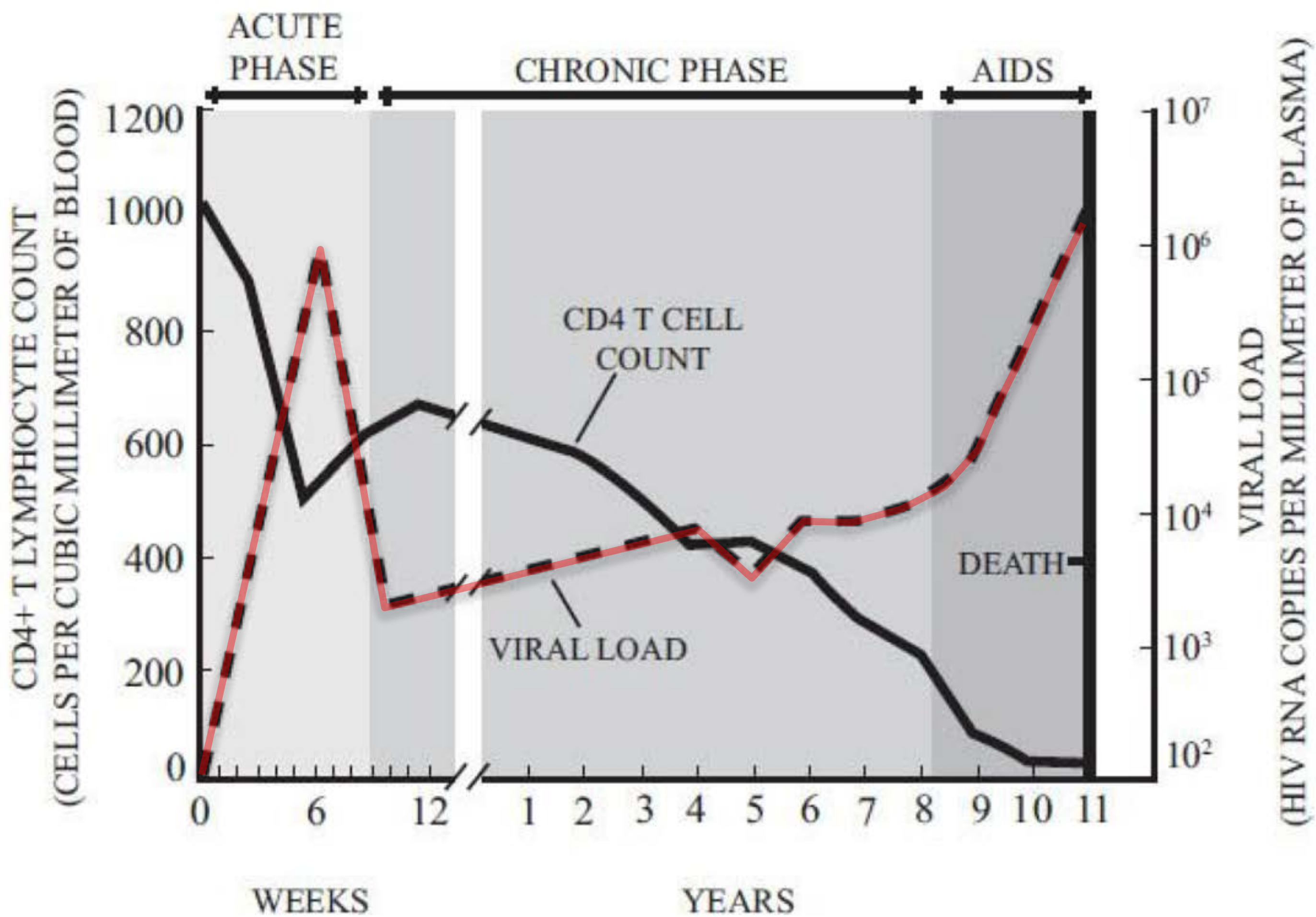

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dynamical models:
describing systems that change over time

differential equations – describe the *rate* at which
a variable changes over time;
continuous in time

$$\frac{d\,n(t)}{dt} = \text{"}some\ function\ of\ n(t)\text{"}$$

recursion equations – describe the *value* of a variable
in the next time step;
discrete in time

$$n(t+1) = \text{"}some\ function\ of\ n(t)\text{"}$$

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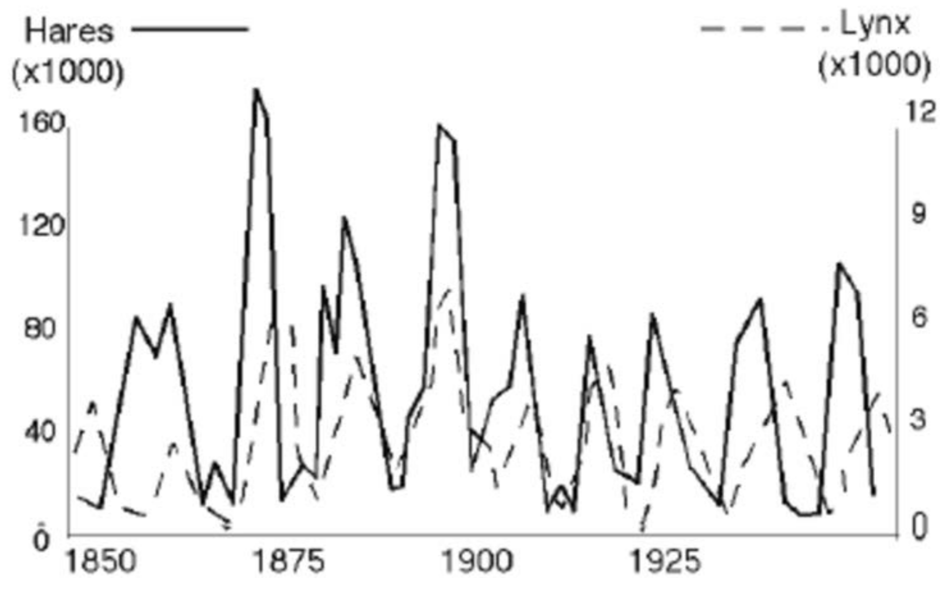
example: predator-prey model



example: predator-prey model

prey $$\frac{d\,x(t)}{dt} = a\,x(t) - b\,x(t)\,y(t)$$

predator $$\frac{d\,y(t)}{dt} = -c\,y(t) + p\,x(t)\,y(t)$$

example: predator-prey model

prey $$\frac{d\,x(t)}{dt} = a\,x(t) - b\,x(t)\,y(t)$$

a = growth rate of prey (hares)

example: predator-prey model

prey $$\frac{d\,x(t)}{dt} = a\,x(t) - b\,x(t)\,y(t)$$

b = capture rate (death rate of prey)

example: predator-prey model

p = growth rate of predator (lynx)

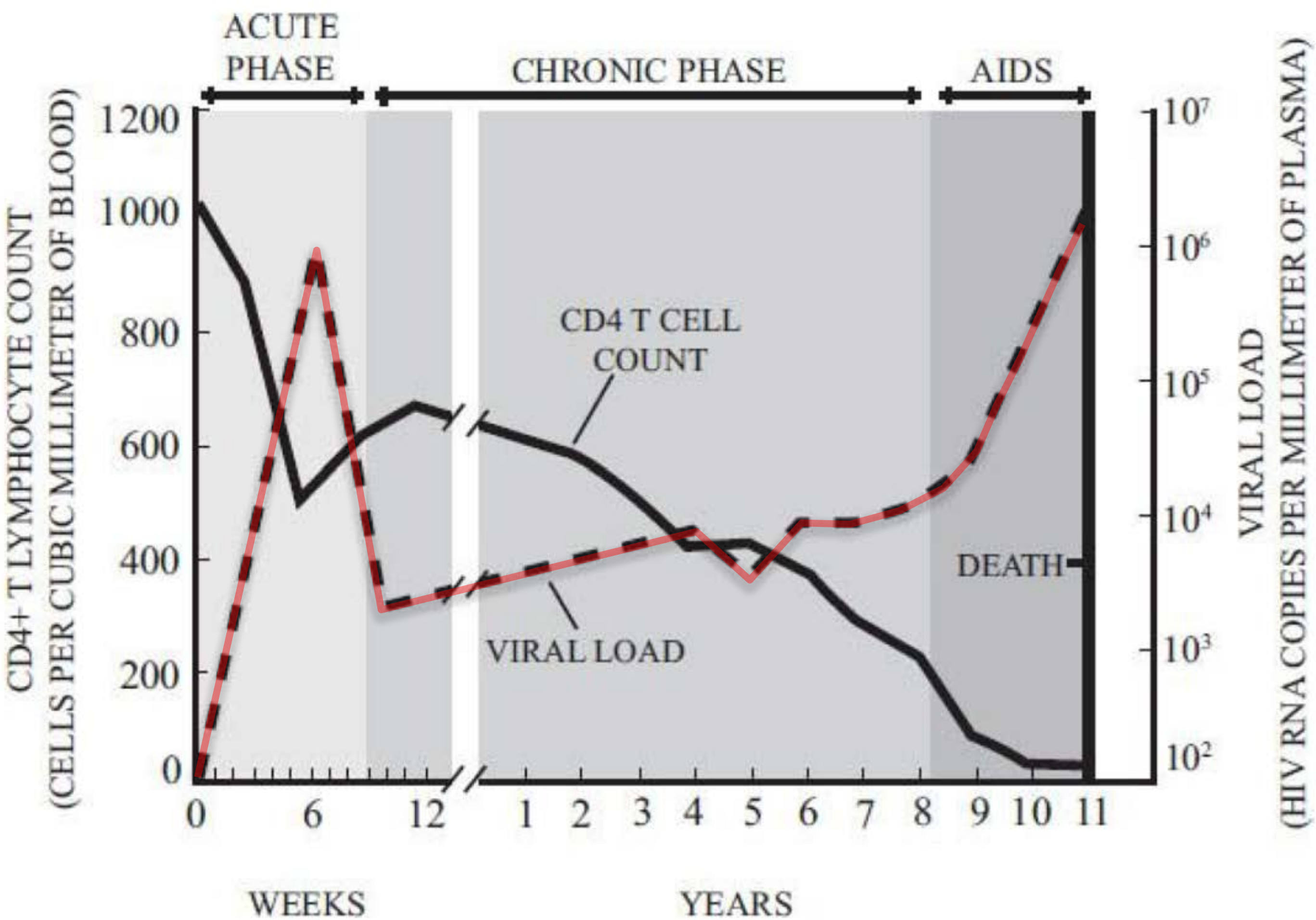
predator $$\frac{d\,y(t)}{dt} = p\,x(t)\,y(t) - c\,y(t)$$

example: predator-prey model

c = death rate of predator (lynx)

predator $$\frac{d\,y(t)}{dt} = p\,x(t)\,y(t) - c\,y(t)$$

Time course of HIV infection within an individual



from Otto & Day (2007)
data from Fauci et al. (1996)

model of within-individual HIV infection (Phillips 1996)

susceptible CD4+ cells $$\frac{dR(t)}{dt} = \Gamma\,\tau - \mu\,R(t) - \beta\,V(t)\,R(t)$$

latently infected CD4+ cells $$\frac{dL(t)}{dt} = p\,\beta V(t) R(t) - \mu\,L(t) - \alpha\,L(t)$$

actively infected CD4+ cells $$\frac{dE(t)}{dt} = (1-p)\,\beta\,V(t)\,R(t) + \alpha\,L(t) - \delta\,E(t)$$

virus particles $$\frac{dV(t)}{dt} = \pi\,E(t) - \sigma\,V(t) - \beta\,V(t)\,R(t)$$

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predator

virus particles
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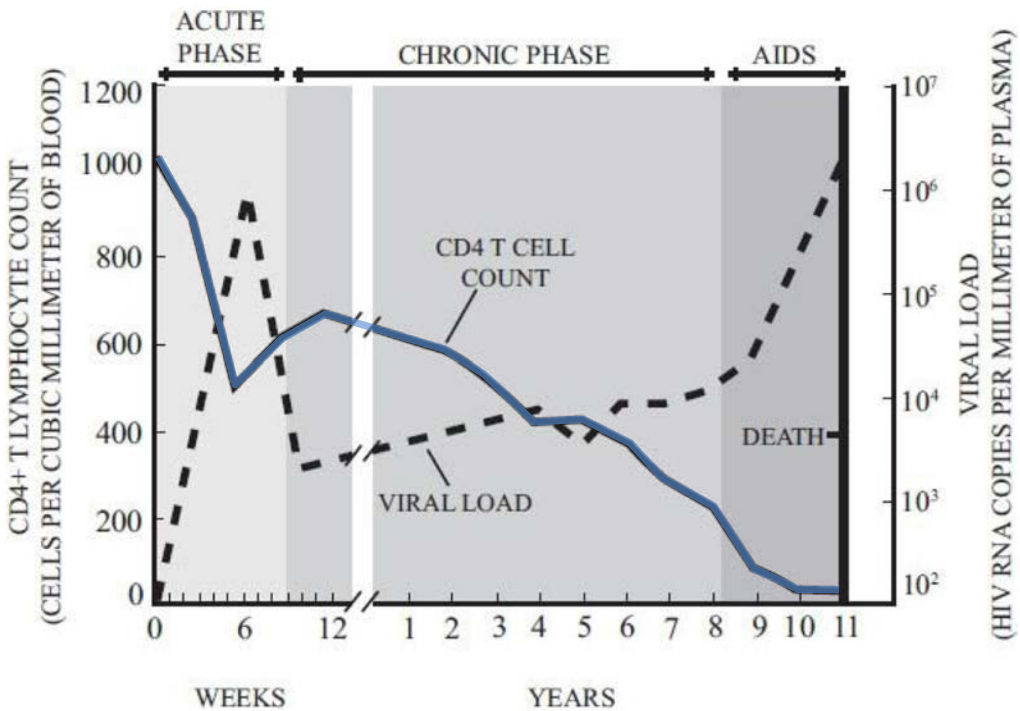
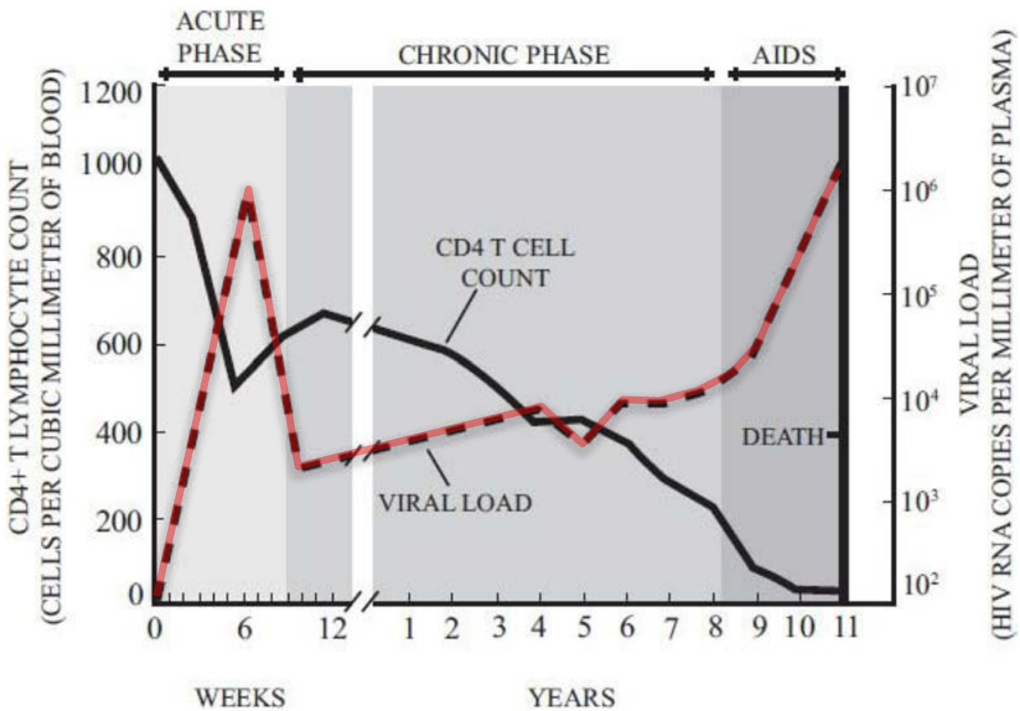


number of CD4+ cells

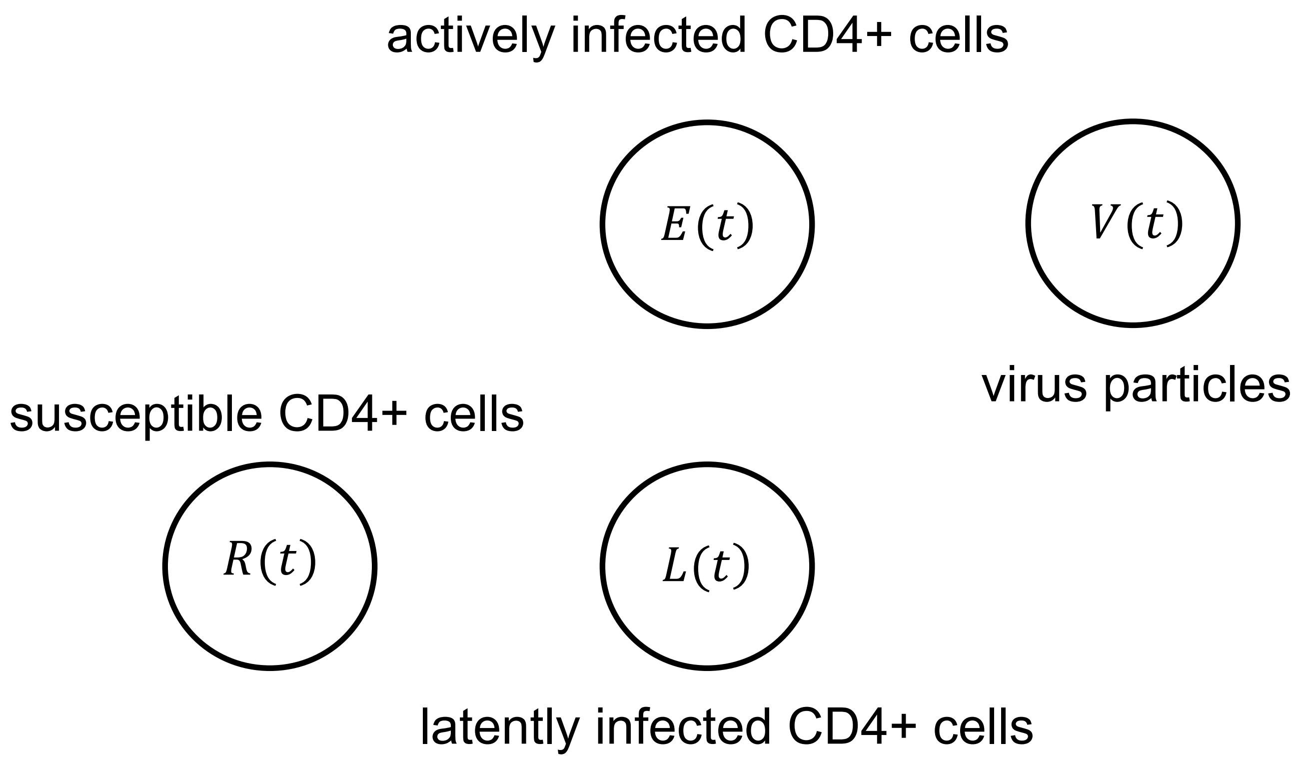
(susceptible + latent + active)

$$
\begin{cases}
\dfrac{dR(t)}{dt} = \Gamma\,\tau - \mu\, R(t) - \beta\, V(t)\, R(t) \\[2ex]
\dfrac{dL(t)}{dt} = p\,\beta V(t) R(t) - \mu\, L(t) - \alpha\, L(t) \\[2ex]
\dfrac{dE(t)}{dt} = (1-p)\,\beta\, V(t)\, R(t) + \alpha\, L(t) - \delta\, E(t)
\end{cases}
$$

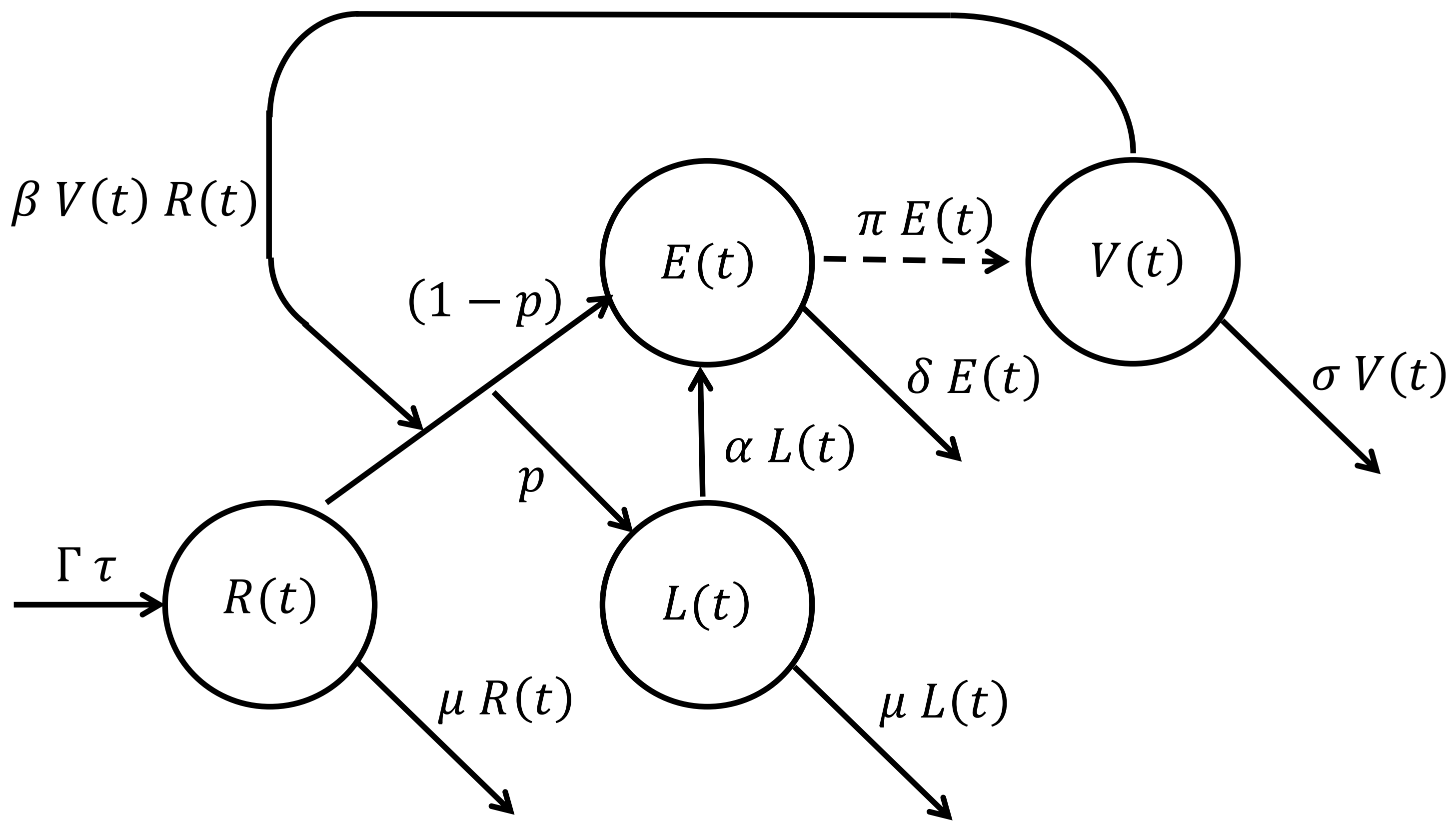


number of virus particles

$$\frac{dV(t)}{dt} = \pi\, E(t) - \sigma\, V(t) - \beta\, V(t)\, R(t)$$



Flow diagram for Phillips (1996) model
adapted from Otto & Day (2007)



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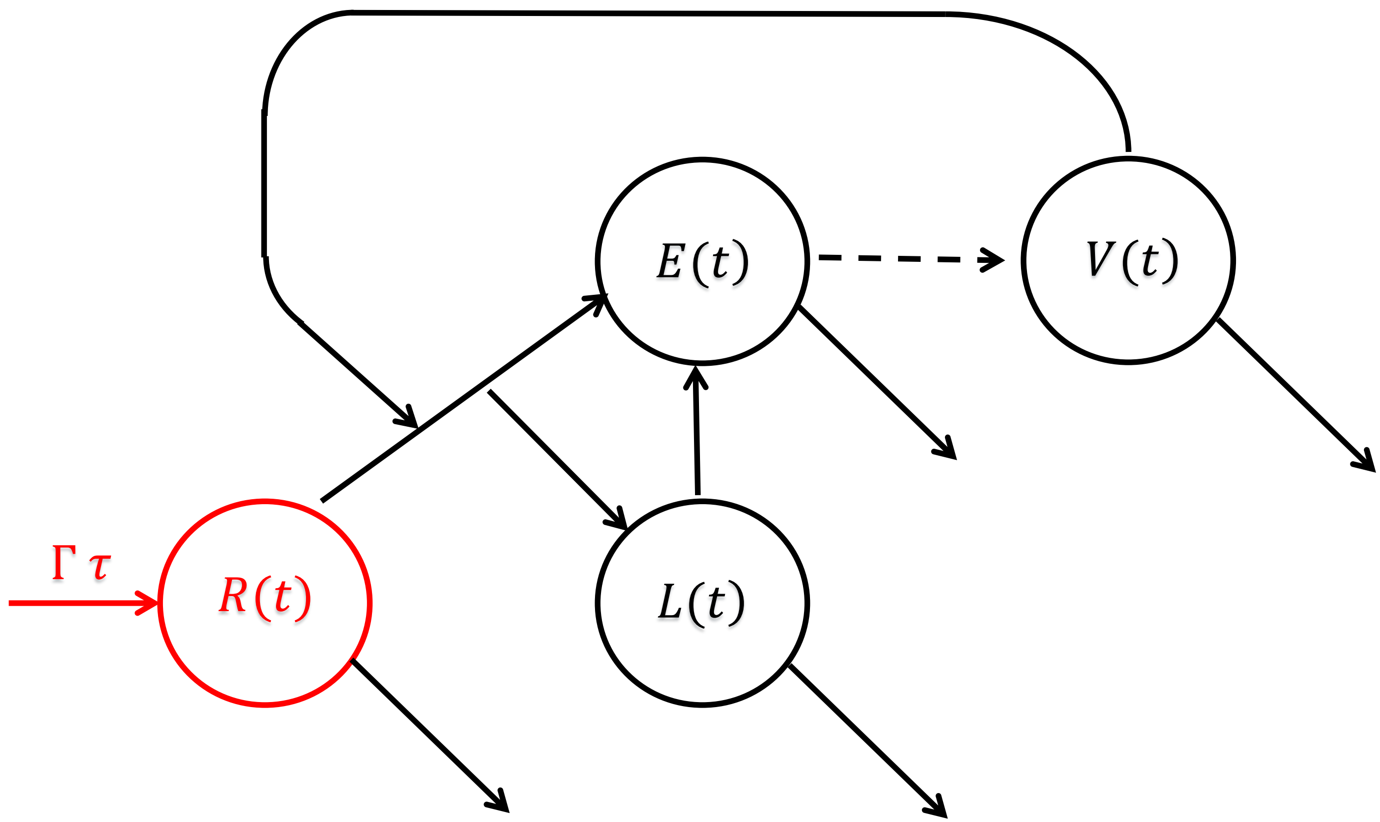
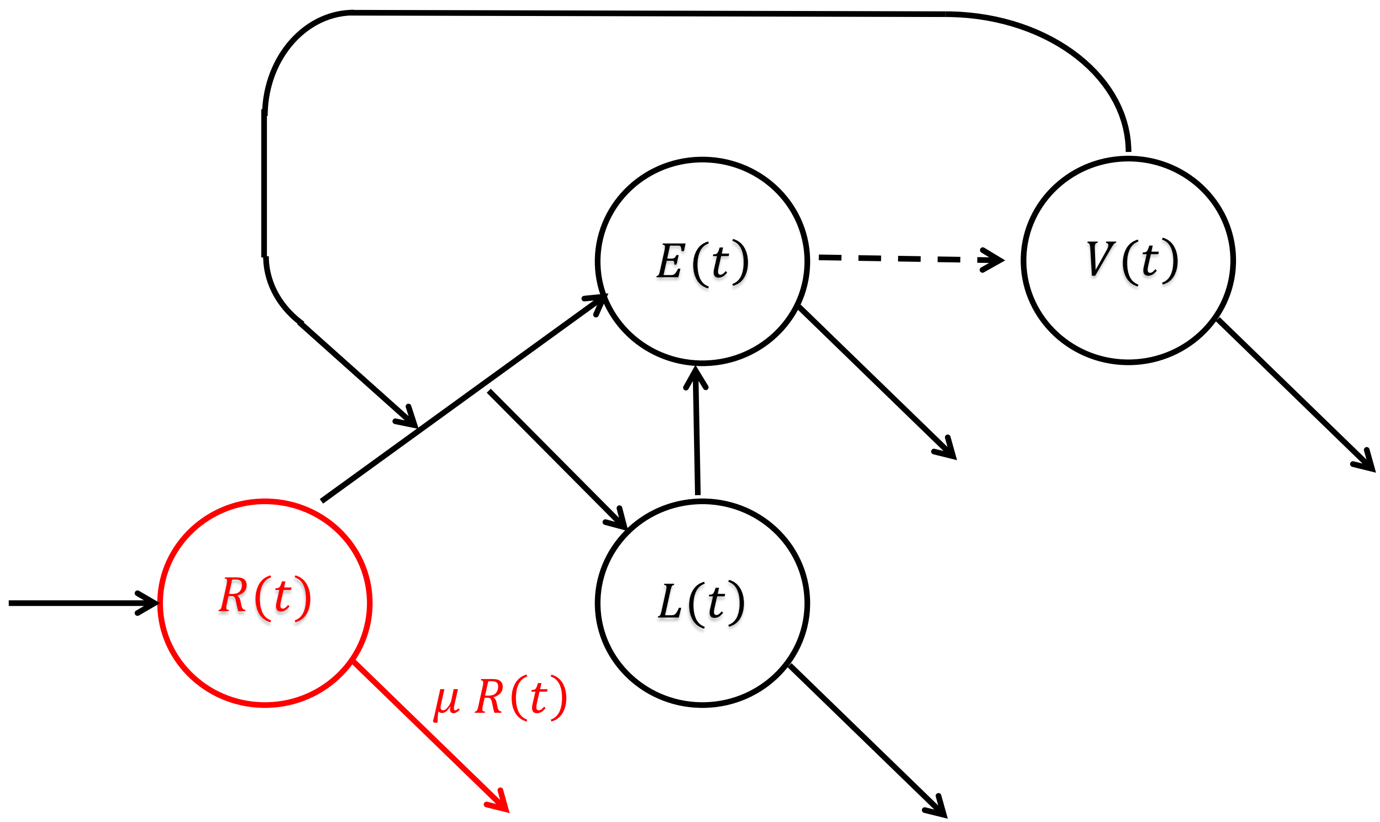


susceptible CD4+ cells

$$\frac{dR(t)}{dt} = \Gamma\,\tau - \mu\,R(t) - \beta\,V(t)\,R(t)$$

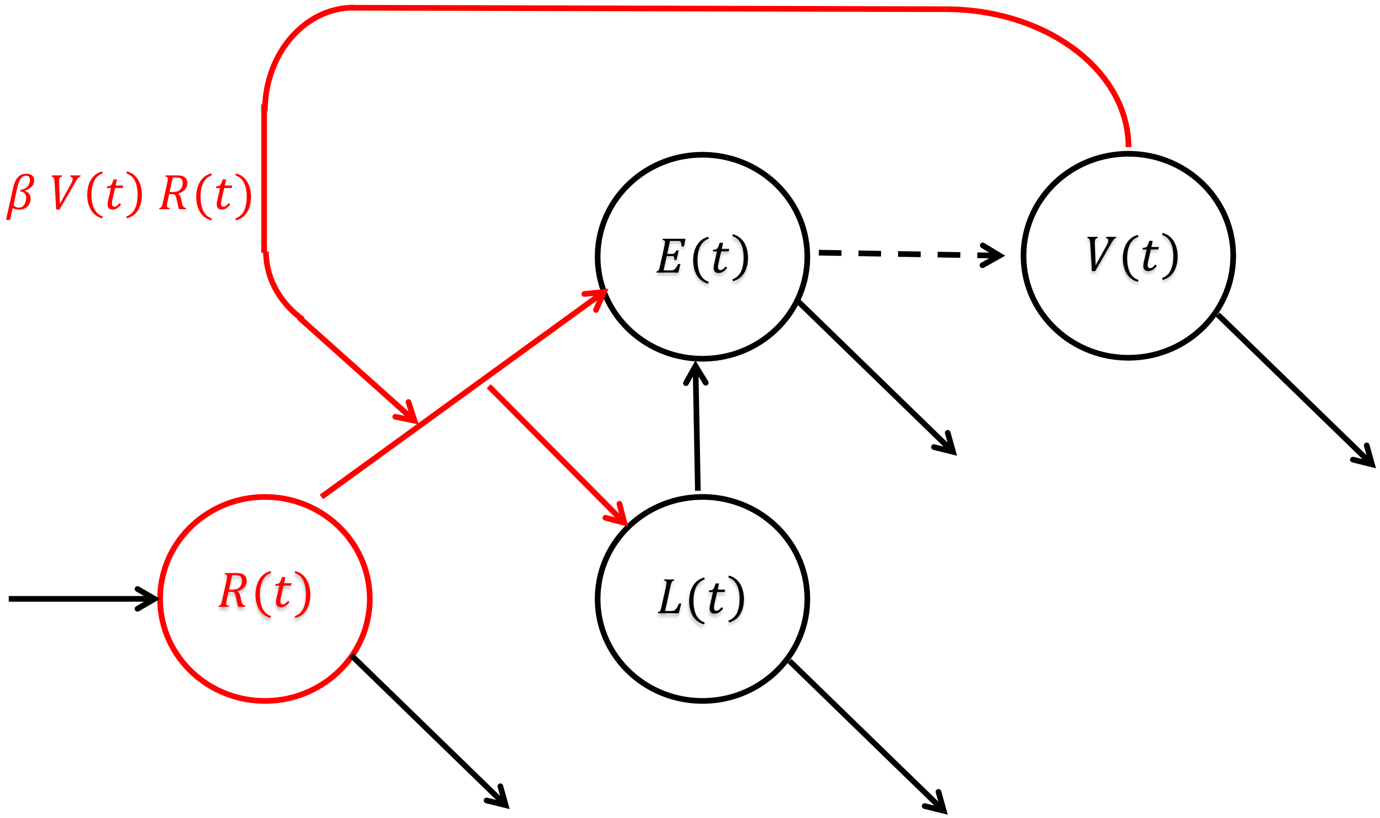
$\Gamma\,\tau$ = input of susceptible cells from immune system



susceptible CD4+ cells

$$\frac{dR(t)}{dt} = \Gamma\,\tau - \mu\, R(t) - \beta\, V(t)\, R(t)$$

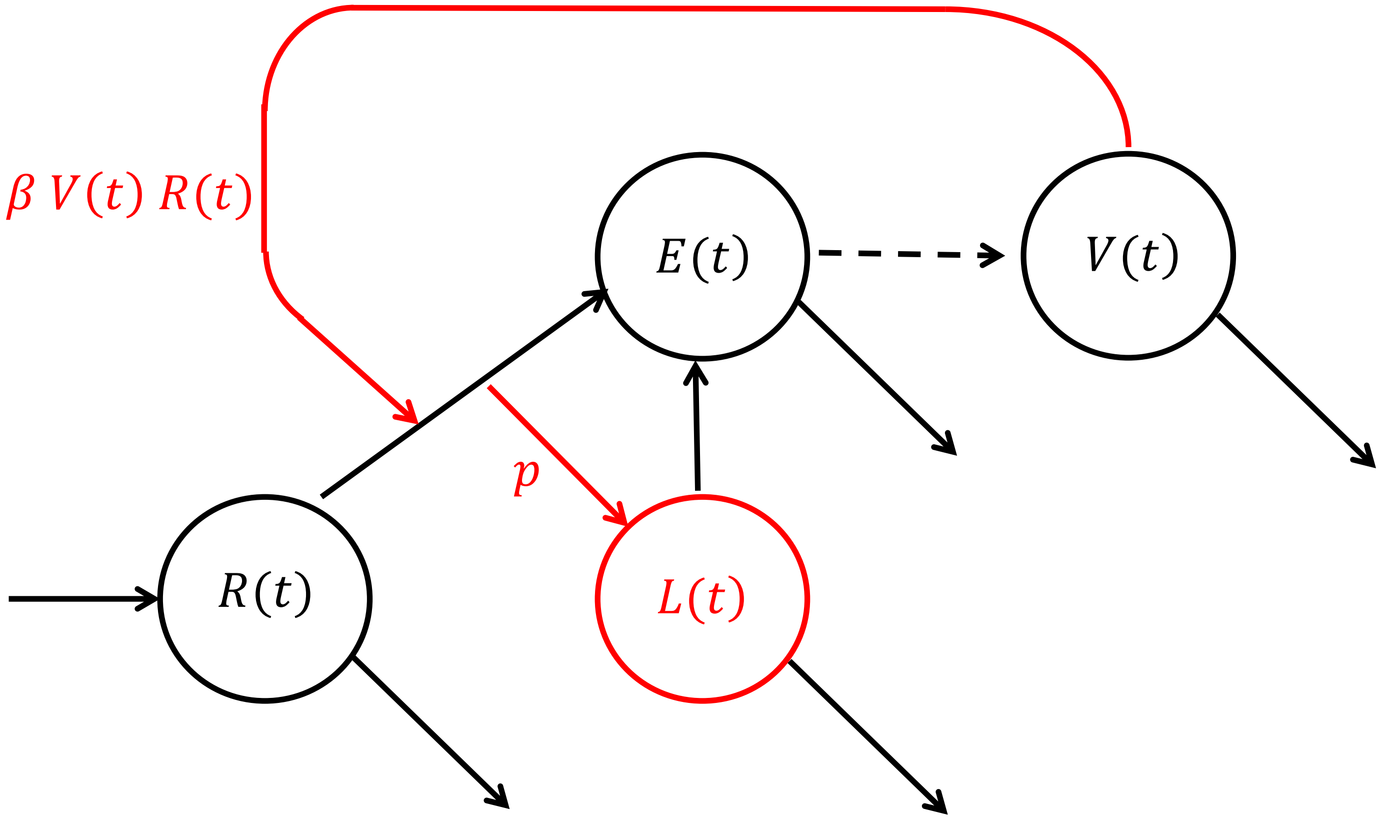
μ = death rate of CD4+ cells



susceptible CD4+ cells

$$\frac{dR(t)}{dt} = \Gamma\, \tau - \mu\, R(t) - \beta\, V(t)\, R(t)$$

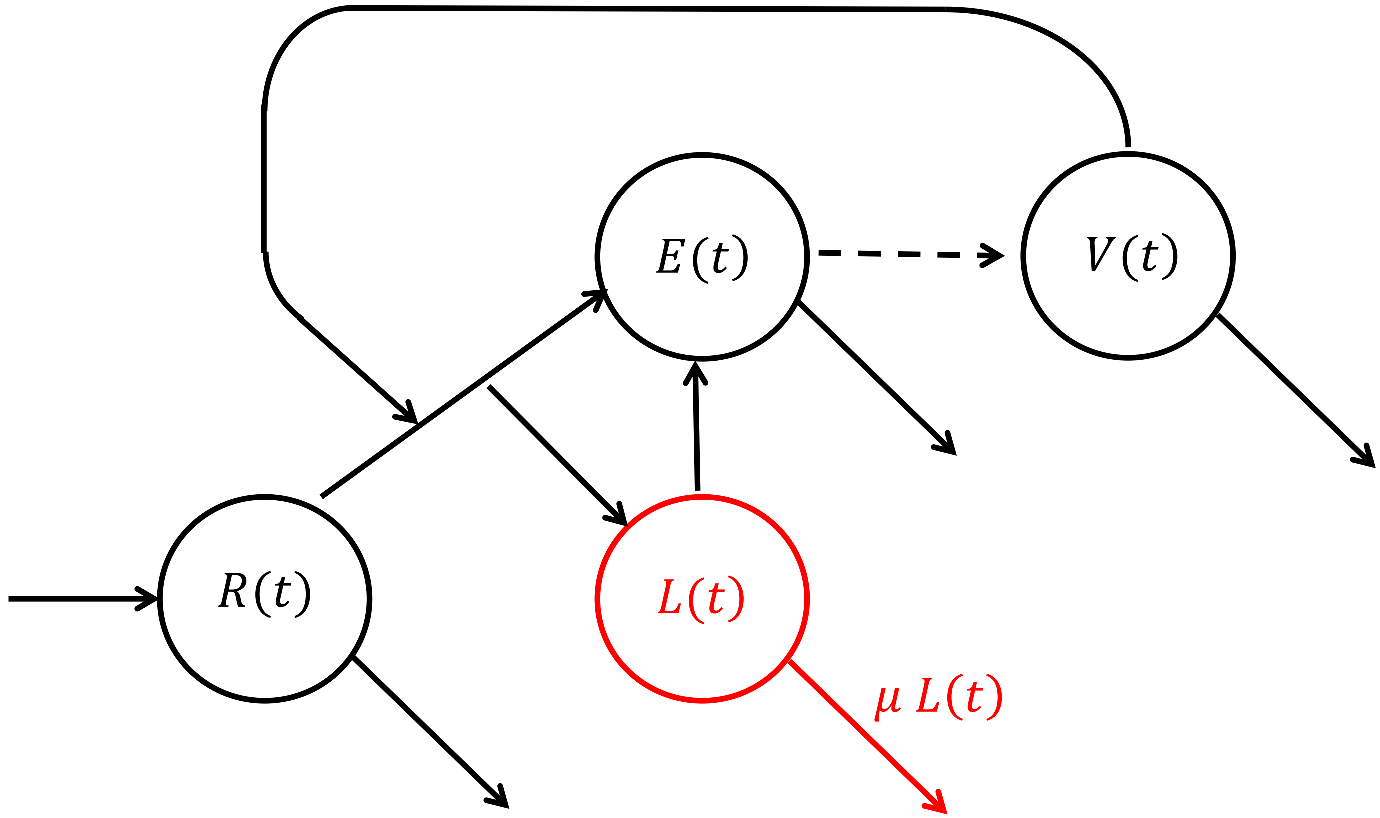
β = infection rate of susceptible cells



latently infected CD4+ cells

$$\frac{dL(t)}{dt} = p\ \beta V(t) R(t) - \mu\ L(t) - \alpha\ L(t)$$

p = probability HIV in infected cell is latent



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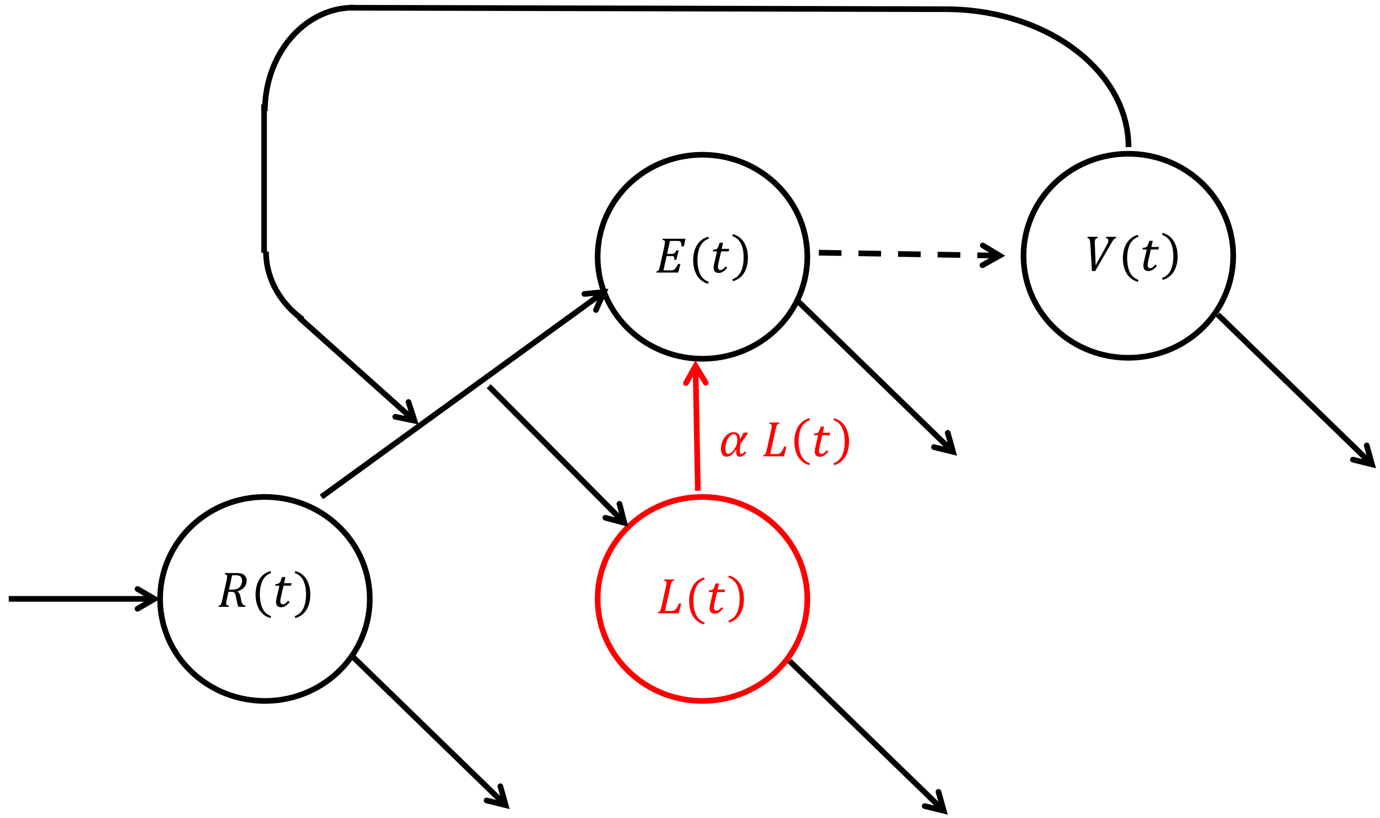
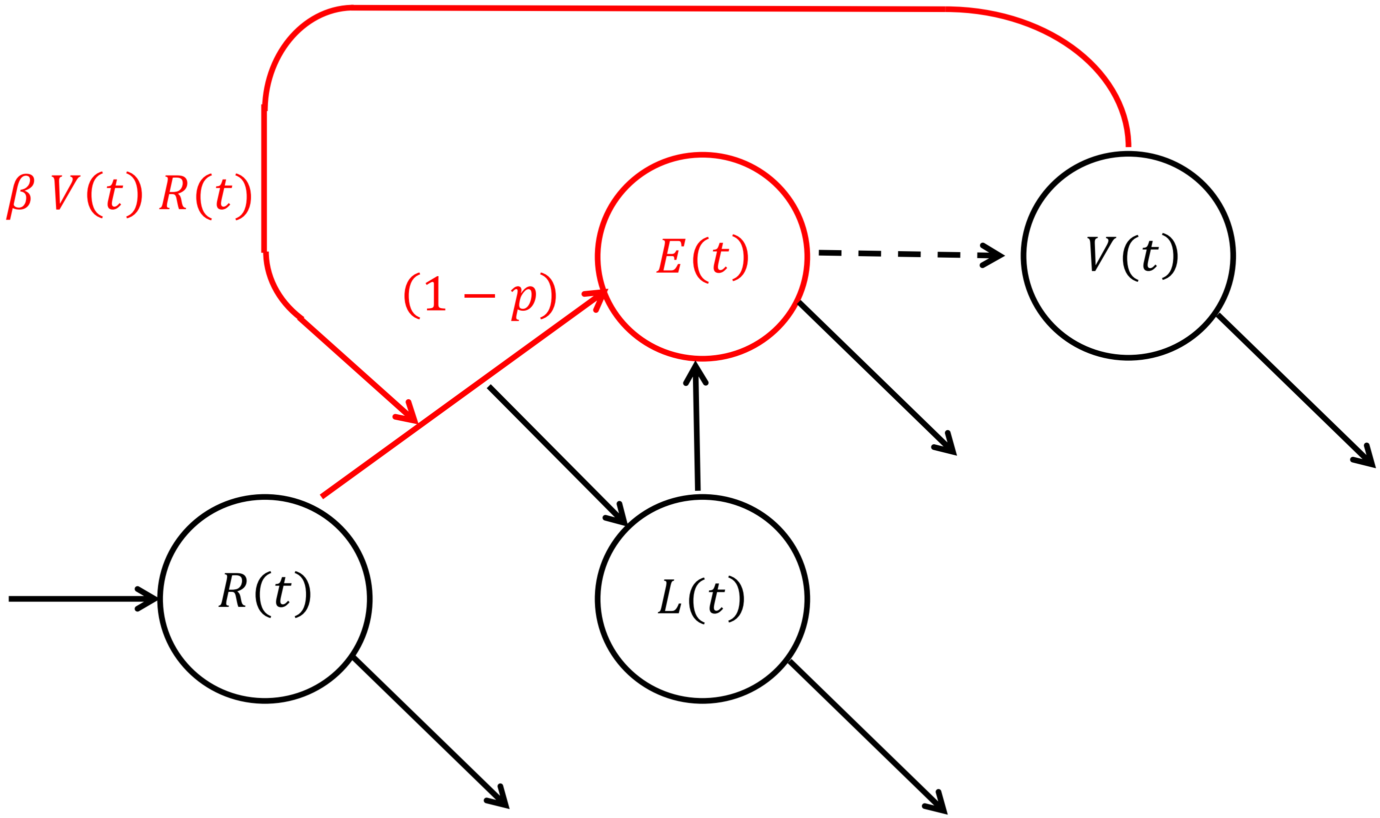


latently infected CD4+ cells

$$\frac{dL(t)}{dt} = p\,\beta V(t)R(t) - \mu\,L(t) - \alpha\,L(t)$$

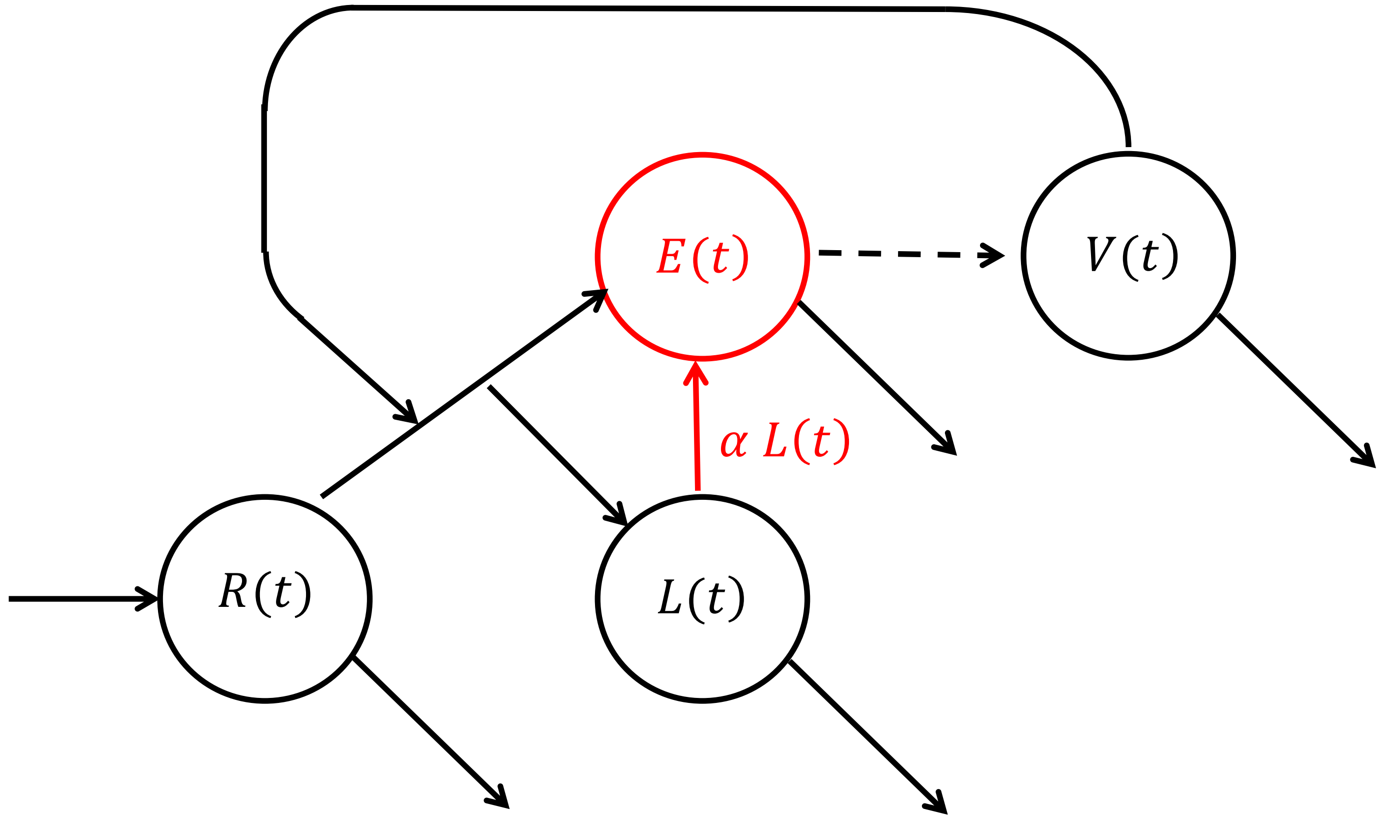
α = conversion rate from latent to active



actively infected CD4+ cells

$$\frac{dE(t)}{dt} = (1-p)\,\beta\, V(t)\, R(t) + \alpha\, L(t) - \delta\, E(t)$$

$1 - p$ = probability HIV in infected cell is active



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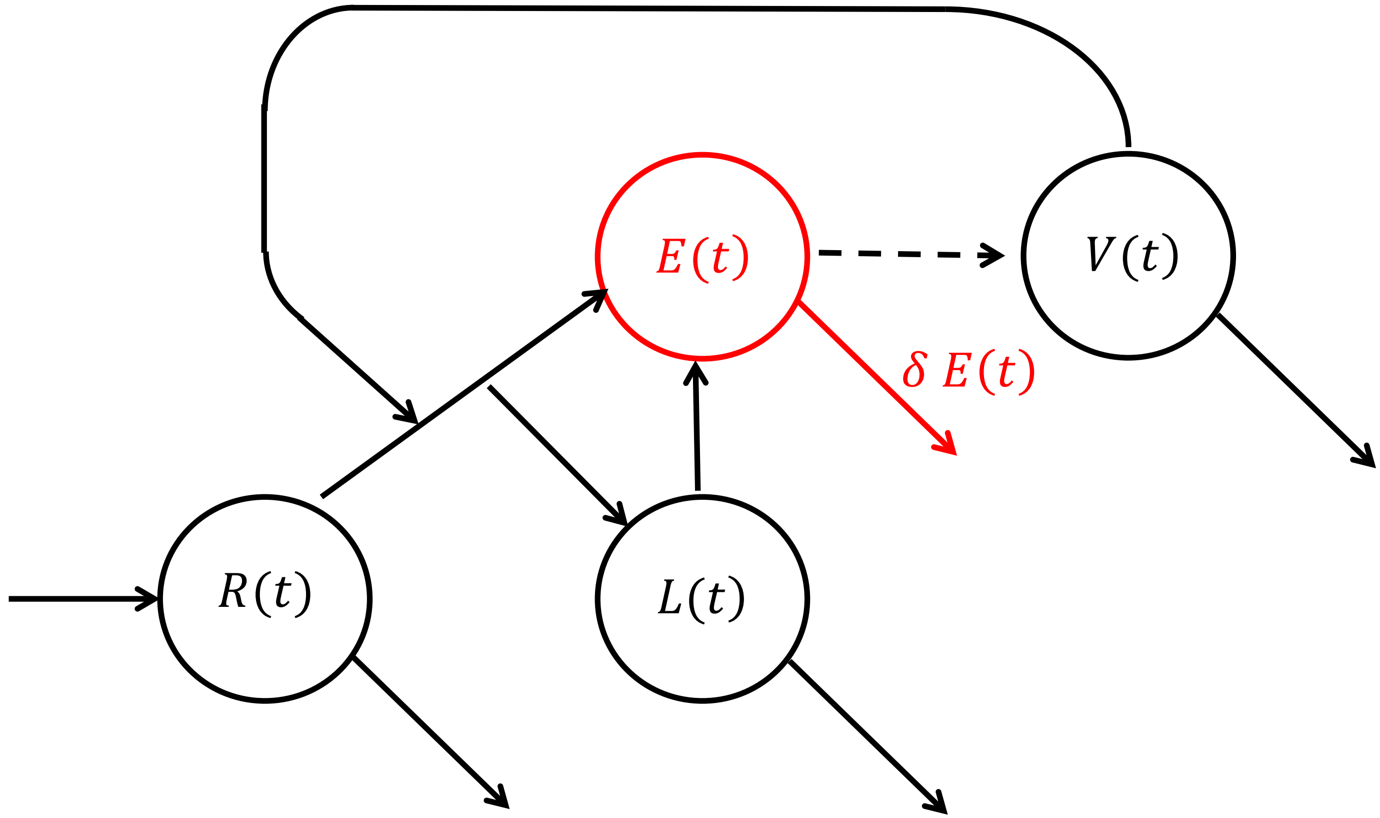
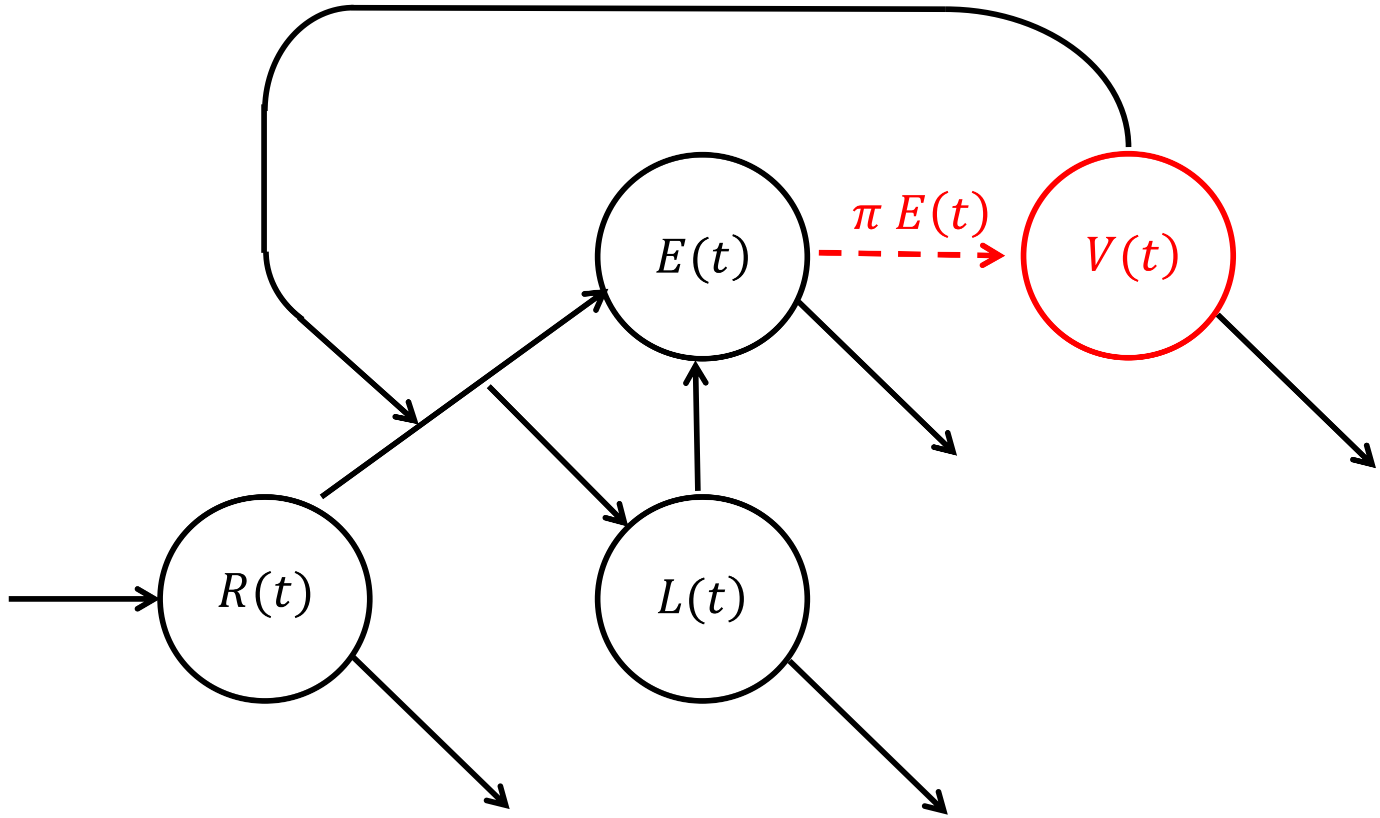


actively infected CD4+ cells

$$\frac{dE(t)}{dt} = (1-p)\ \beta\ V(t)\ R(t) + \alpha\ L(t) - \delta\ E(t)$$

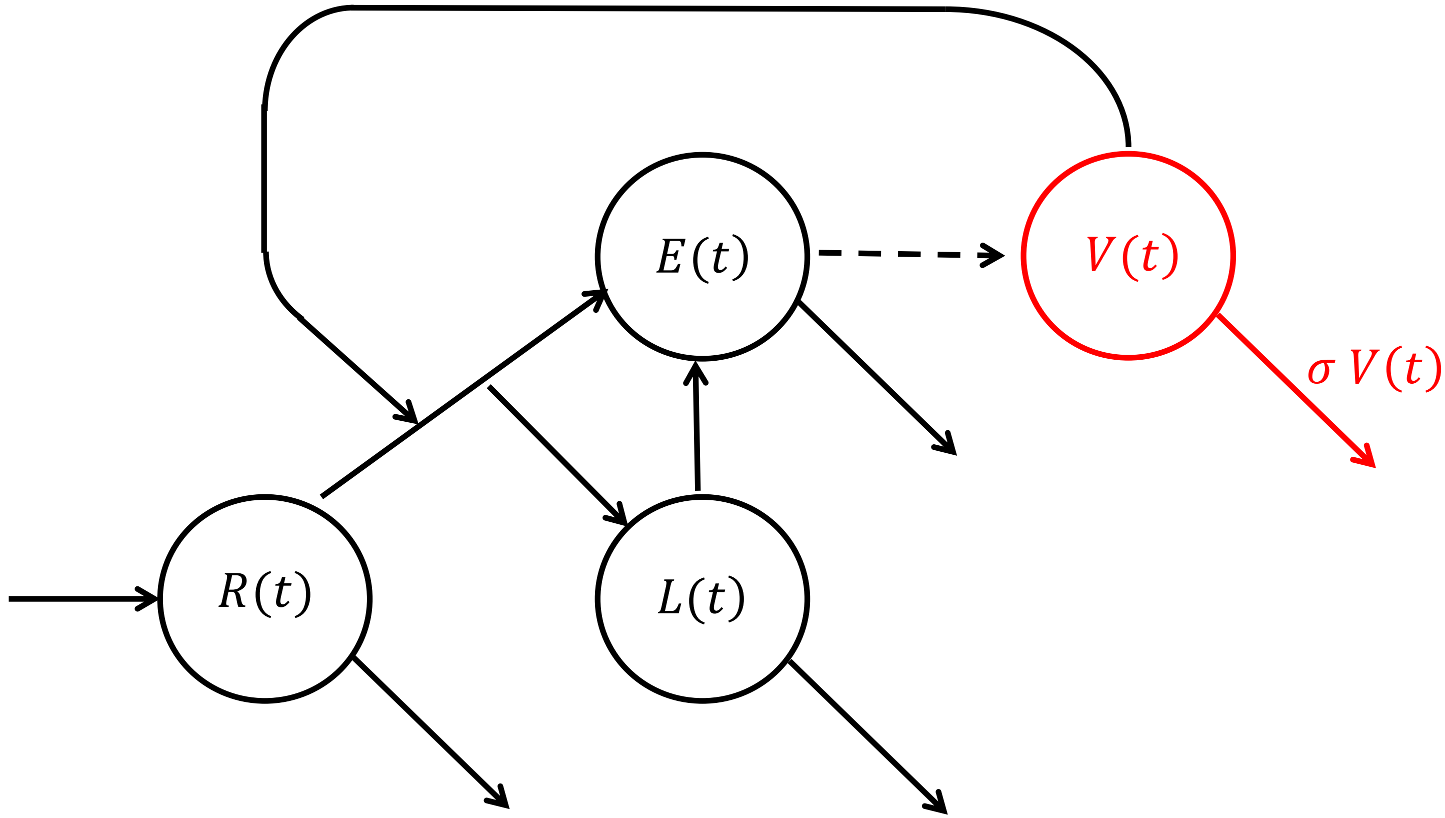
δ = death rate of actively infected CD4+ cells



virus particles

$$\frac{dV(t)}{dt} = \pi\, E(t) - \sigma\, V(t) - \beta\, V(t)\, R(t)$$

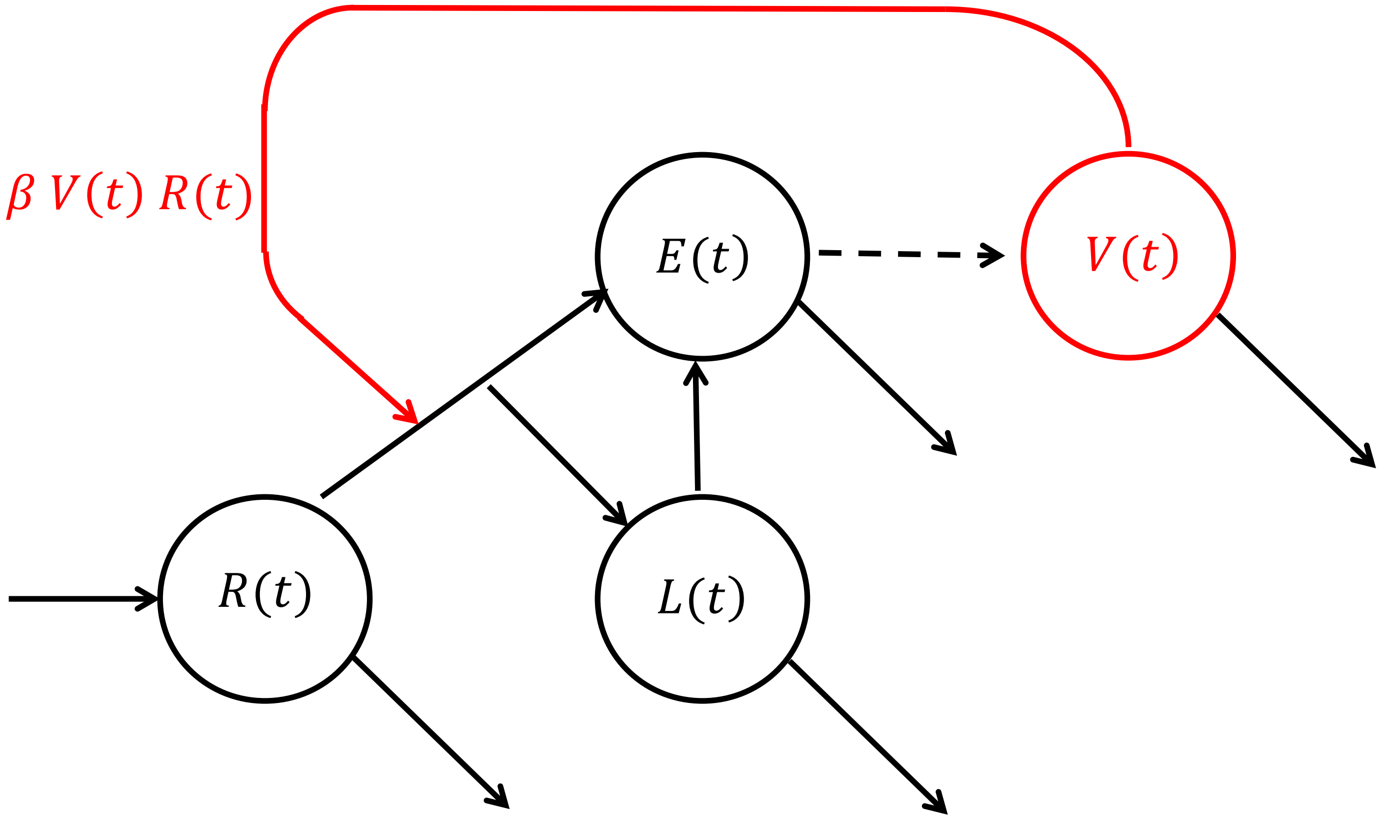
π = budding rate of virus particles from infected cells



virus particles

$$\frac{dV(t)}{dt} = \pi\, E(t) - \sigma\, V(t) - \beta\, V(t)\, R(t)$$

σ = clearance rate of virus particles



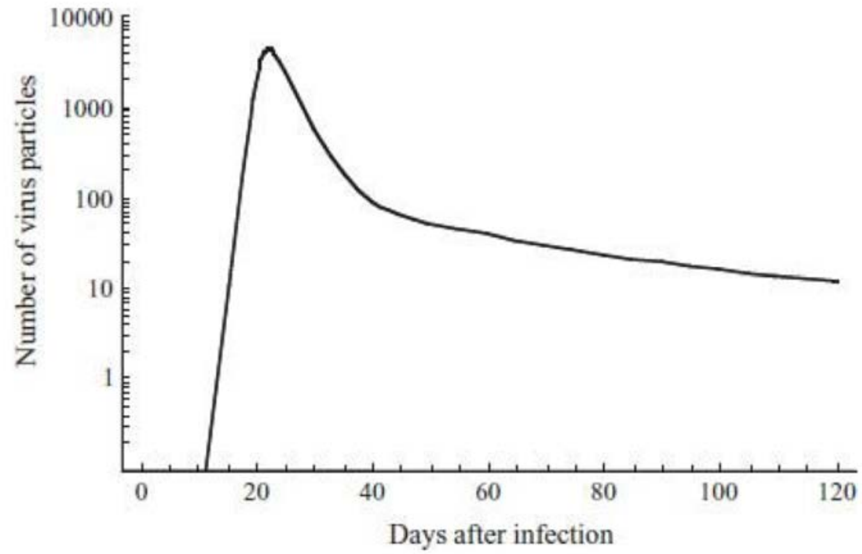
virus particles

$$\frac{dV(t)}{dt} = \pi\, E(t) - \sigma\, V(t) - \beta\, V(t)\, R(t)$$

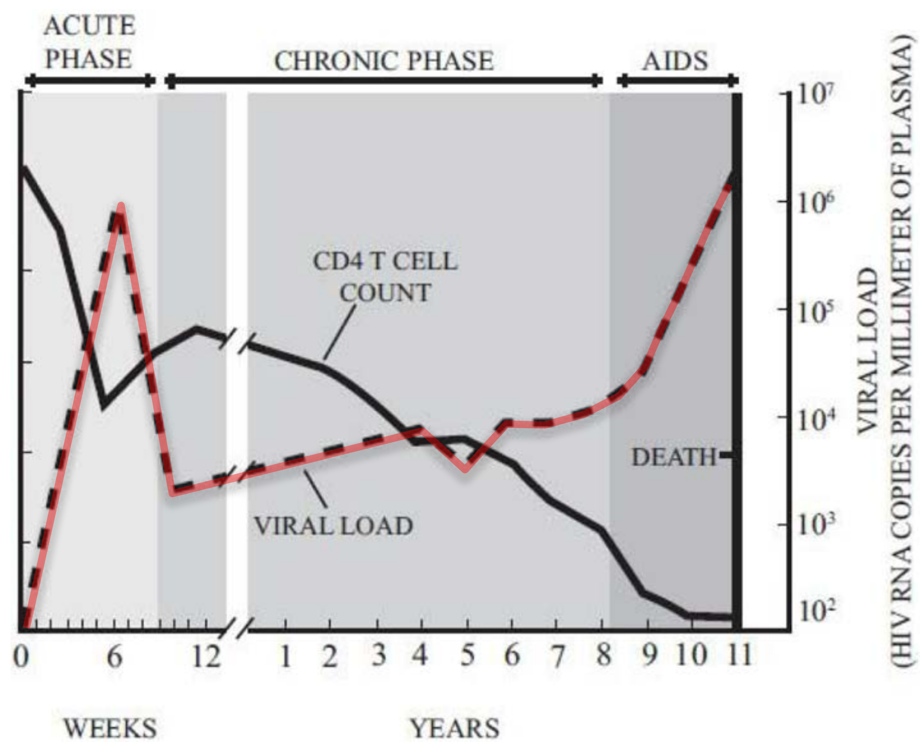
β = infection rate

Number of virus particles over time

Model: Phillips (1996)



Data: Fauci et al. (1996)



VOL. 162, NO. 1 THE AMERICAN NATURALIST JULY 2003

Linking Dynamical and Population Genetic Models of Persistent Viral Infection

John K. Kelly,[1,*] Scott Williamson,[1] Maria E. Orive,[1] Marilyn S. Smith,[2] and Robert D. Holt[3]

Kelly, Williamson, et al. 2003 *Am Nat*

Adaptation in the *env* Gene of HIV-1 and Evolutionary Theories of Disease Progression

Scott Williamson
Department of Ecology and Evolutionary Biology, University of Kansas

Williamson 2003 *Mol Biol Evol*

A Statistical Characterization of Consistent Patterns of Human Immunodeficiency Virus Evolution Within Infected Patients

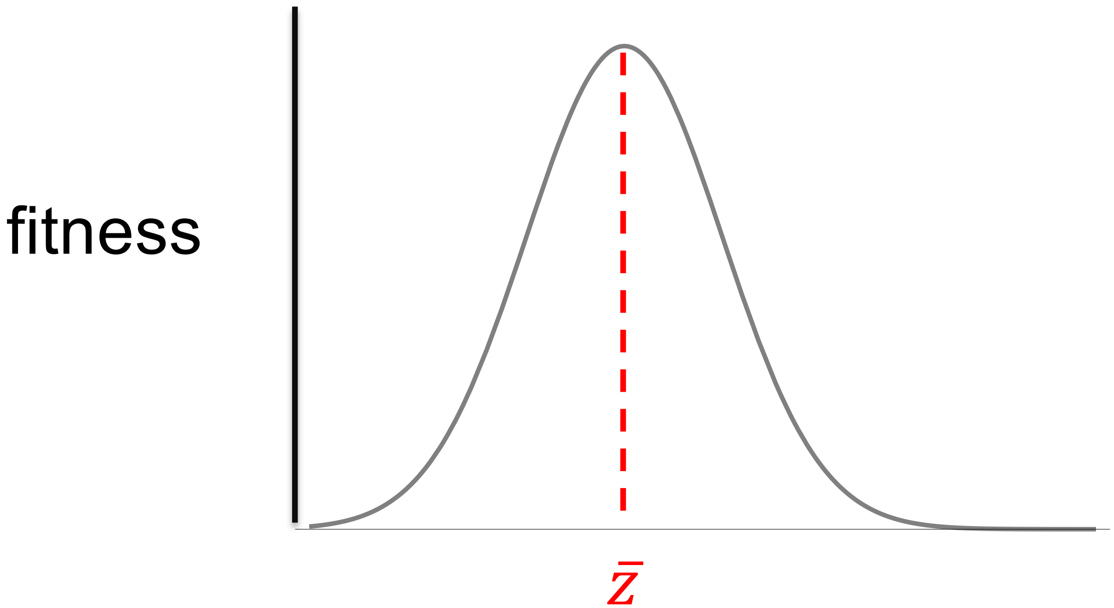
Scott Williamson,† Steven M. Perry,† Carlos D. Bustamante,* Maria E. Orive,† Miles N. Stearns,† and John K. Kelly†*
*Department of Biological Statistics and Computational Biology, Cornell University, Ithaca, New York; †Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence

Williamson et al. 2005 *Mol Biol Evol*

two ways we can use models to make sense of biology

- Explain what we *do see*
  - Specific test of hypotheses
  - Example: dynamics of HIV after infection
- Predict what we *might see*
  - Generate hypotheses
  - Example: evolutionary lag and rescue with complex life histories

tracking environmental change



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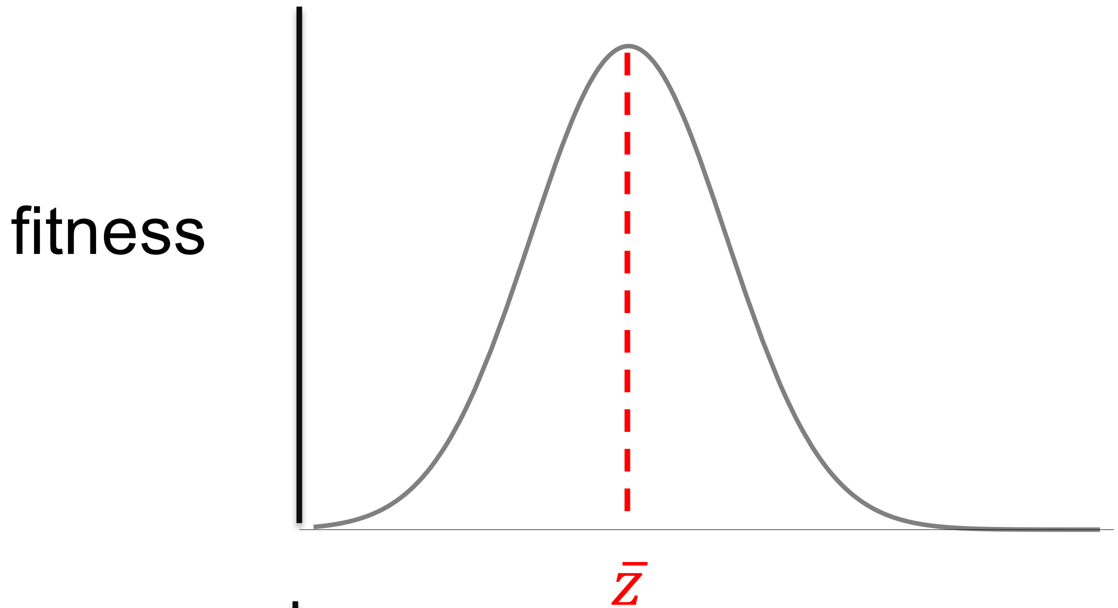

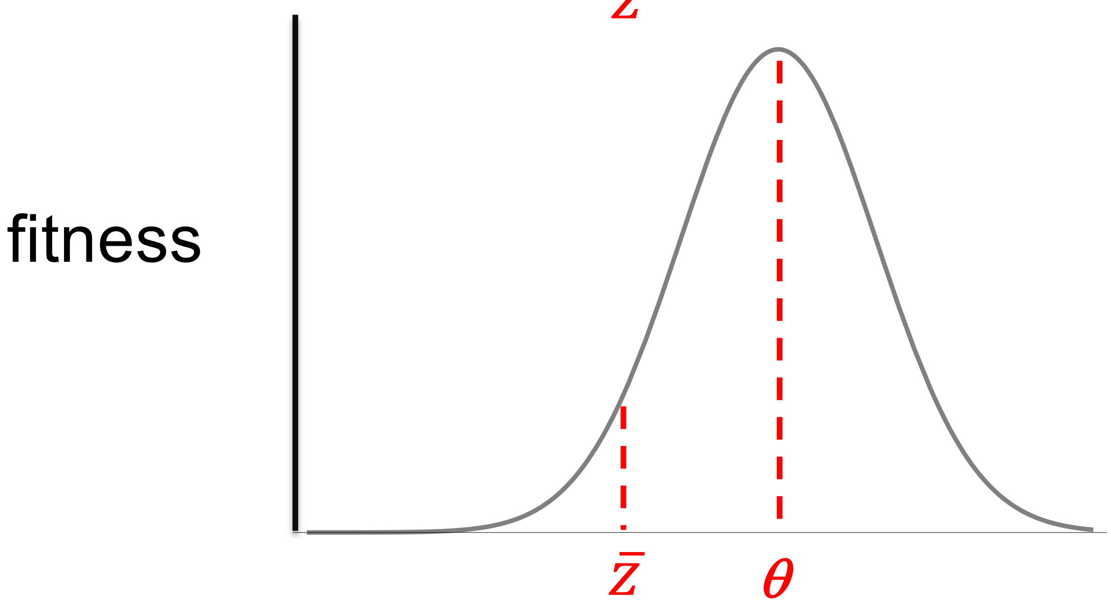

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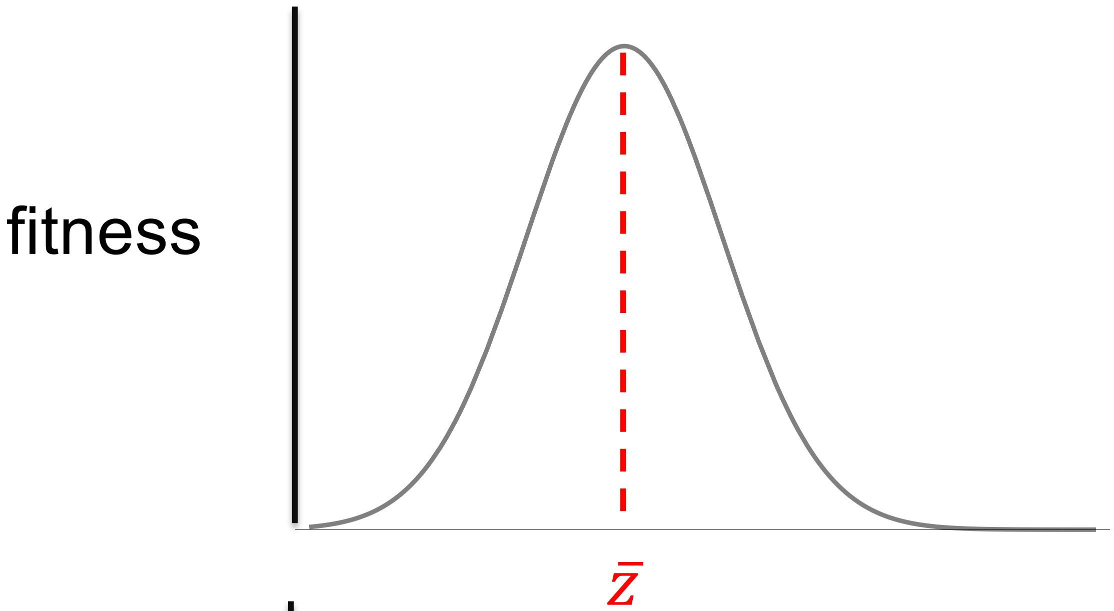

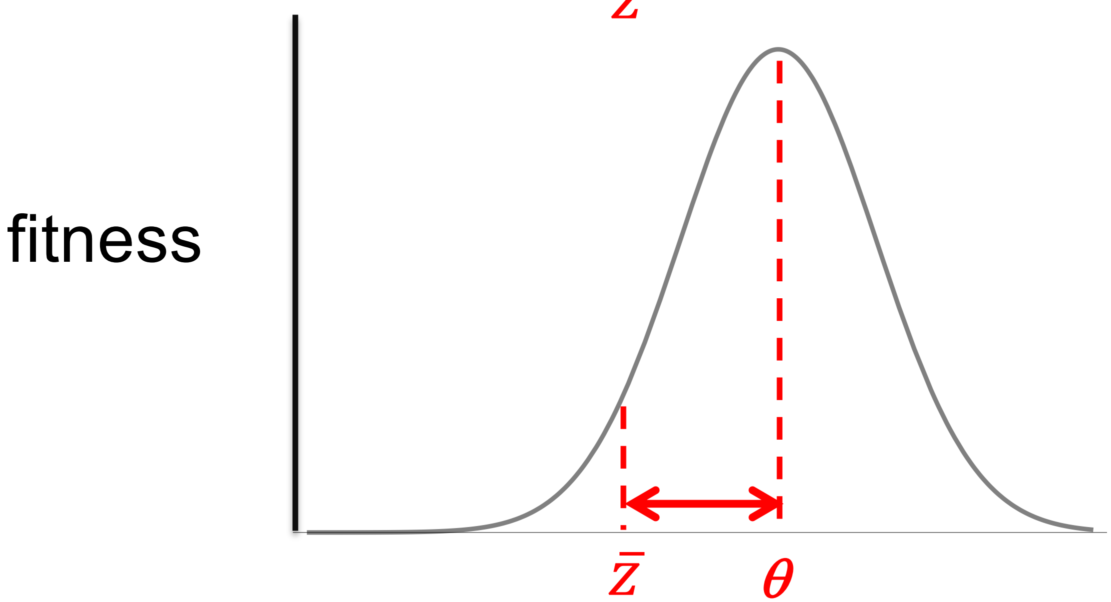

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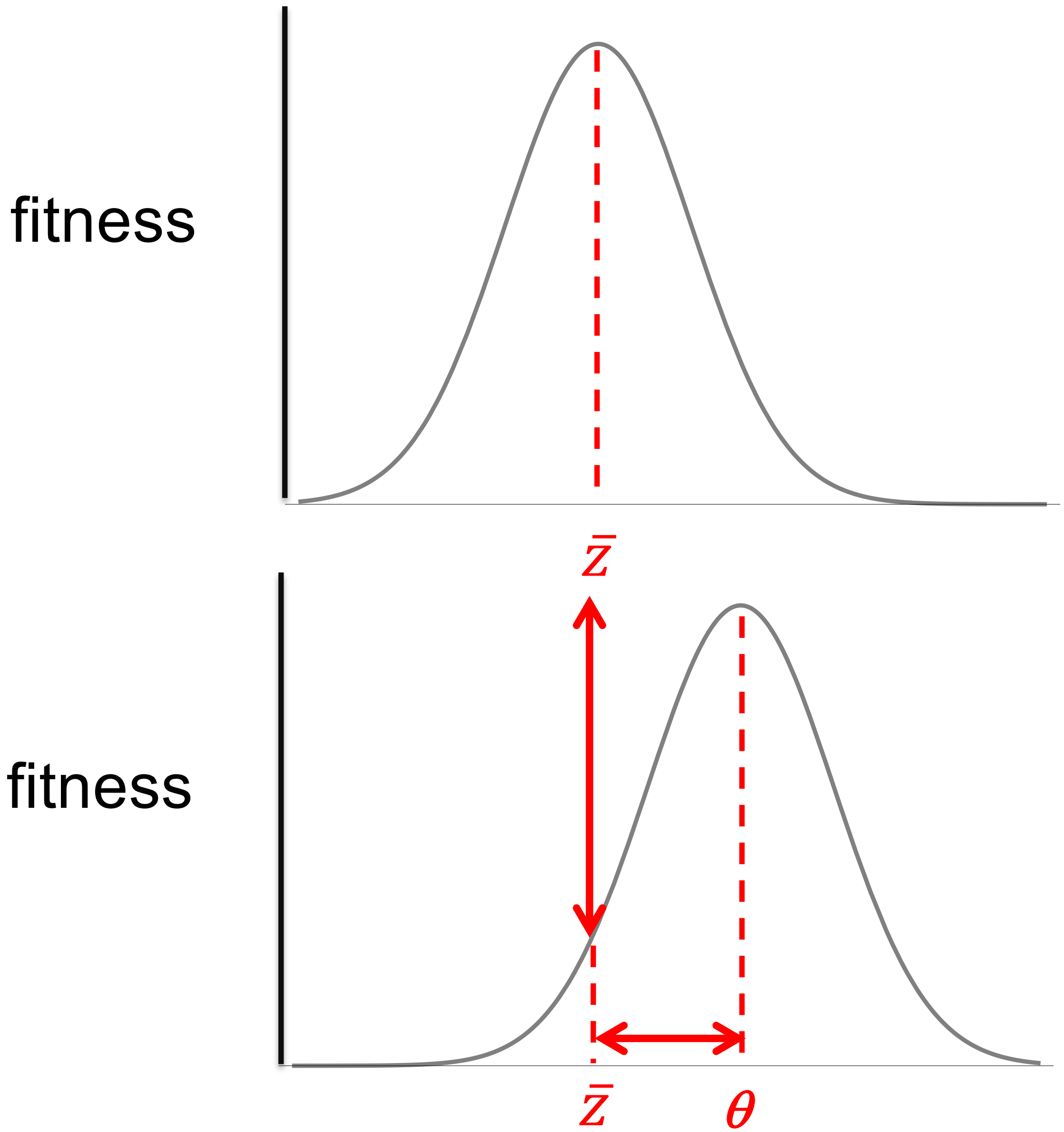


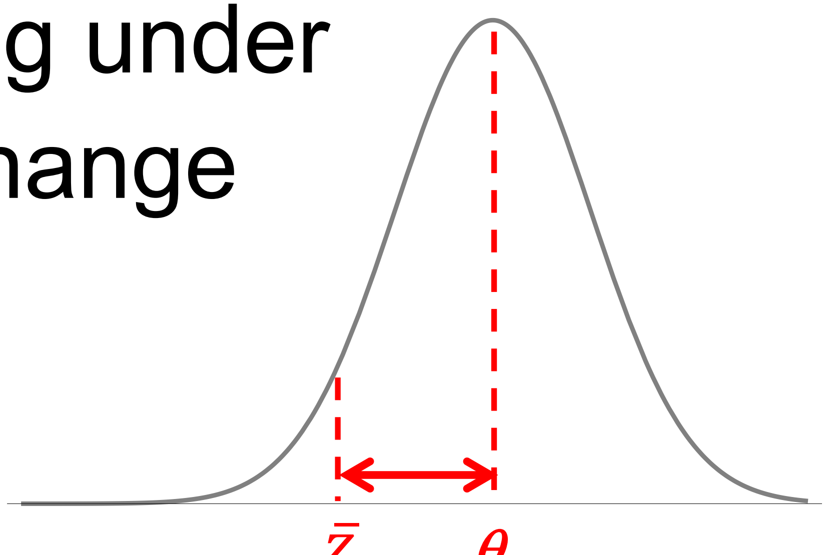
evolutionary lag

- evolutionary lag (or lag load)
  - difference between phenotypic trait mean and its optimum

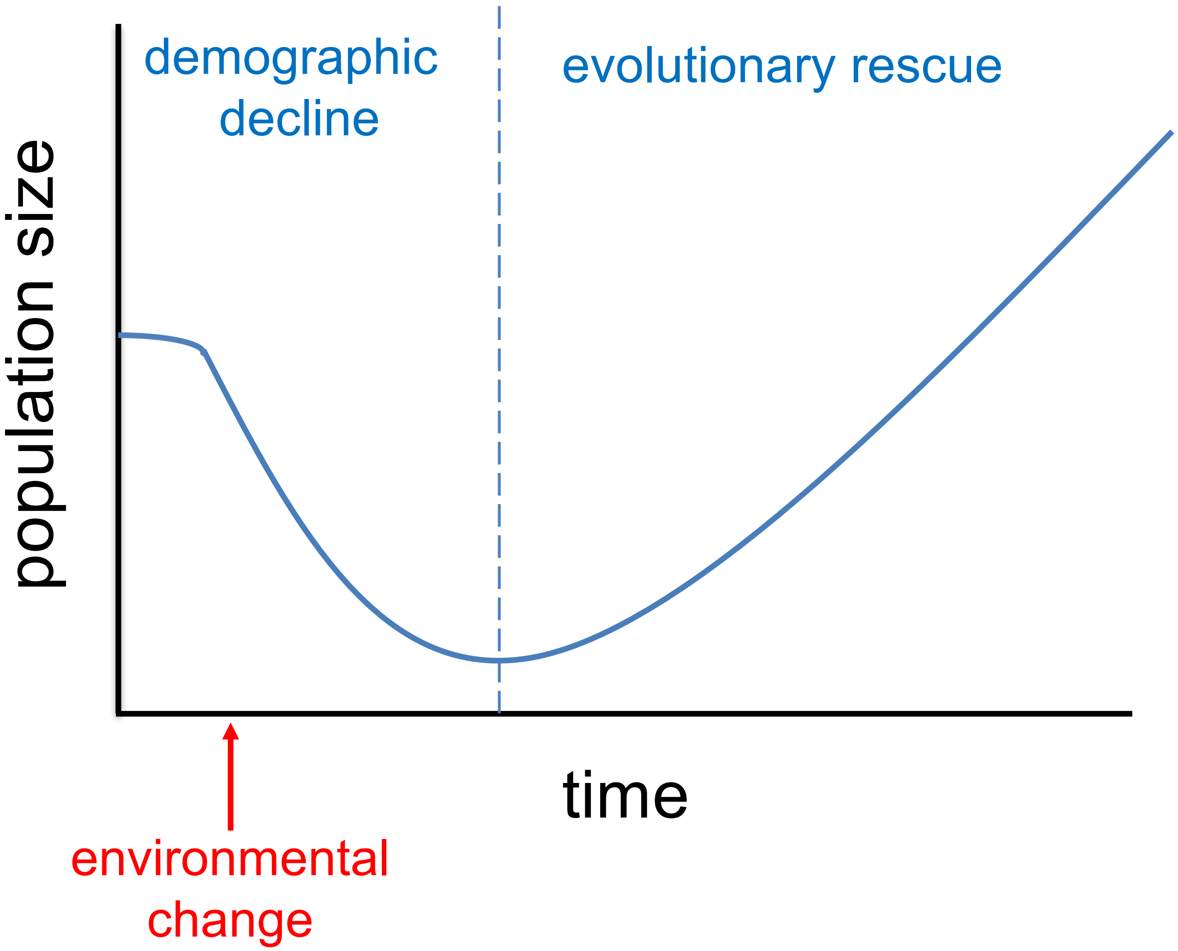
$$L_\theta = \frac{(\bar{z} - \theta)^2}{2\sigma_w^2}$$

Maynard Smith (1976)

- greater evolutionary lag under rapid environmental change

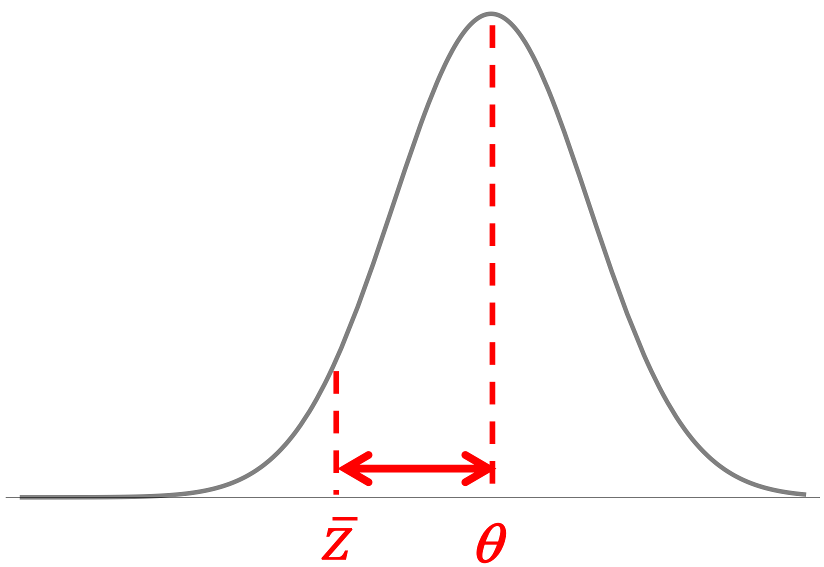


evolutionary rescue



complex life histories and adaptation

- how do stage structure and clonal reproduction affect a population's ability to track environmental change?



stage structure and clonality

image by Forest & Kim Starr.

image by Nadiatalent

image from Oxford Scientific

image from NOAA website

Life-history complexities

- mutation arising in somatic tissues
  - in gametes and/or independent clonal offspring
  - within-individual or somatic selection

somatic mutation

gametic reproduction

Image: Jouko Lehmuskallio

agametic (clonal) reproduction

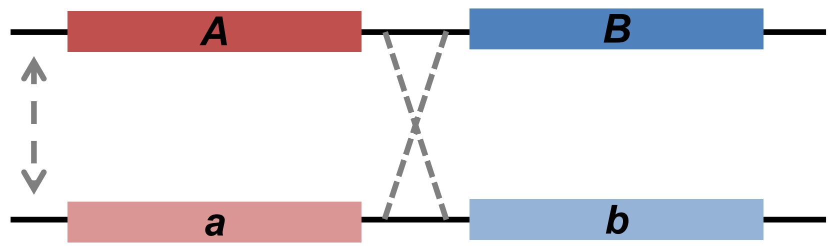
image from Oxford Scientific

Life-history complexities

- mutation arising in somatic tissues
  - in gametes and/or independent clonal offspring
  - within-individual or somatic selection
- reproduction without meiosis
  - shields from higher meiotic mutation rates
  - lacks genetic segregation (heterozygosity, homozygosity)
  - lacks recombination

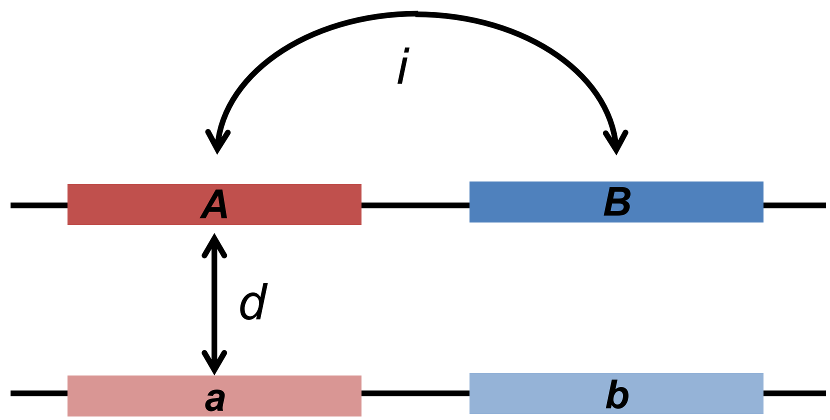
sexual reproduction

α



clonal reproduction

α, d, i



Life-history complexities

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  - within-individual or somatic selection
- reproduction without meiosis
  - shields from higher meiotic mutation rates
  - lacks genetic segregation (heterozygosity, homozygosity)
  - lacks recombination
- clonal offspring phenotypically distinct from sexual offspring

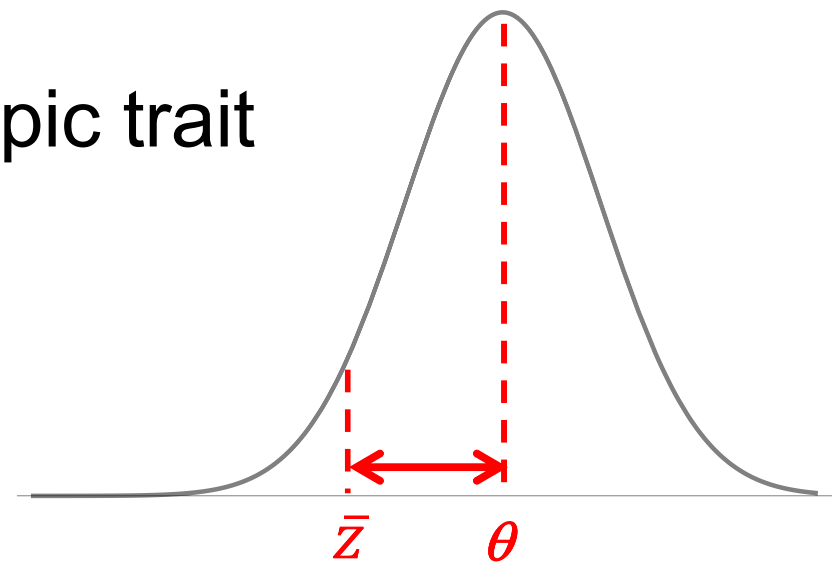
clonal reproduction and invasive spread

phenotypic evolution with stage-structured life histories

– multivariate phenotypic trait

$$\mathbf{z} = (z_1, z_2, \cdots, z_n)^T$$

$$\mathbf{z} = \mathbf{g} + \mathbf{e}$$



– N_i = number of individuals for each stage i

– $\bar{\boldsymbol{g}}_i$ = mean genotype of stage i

– $\bar{\boldsymbol{z}}_i$ = mean phenotype of stage i

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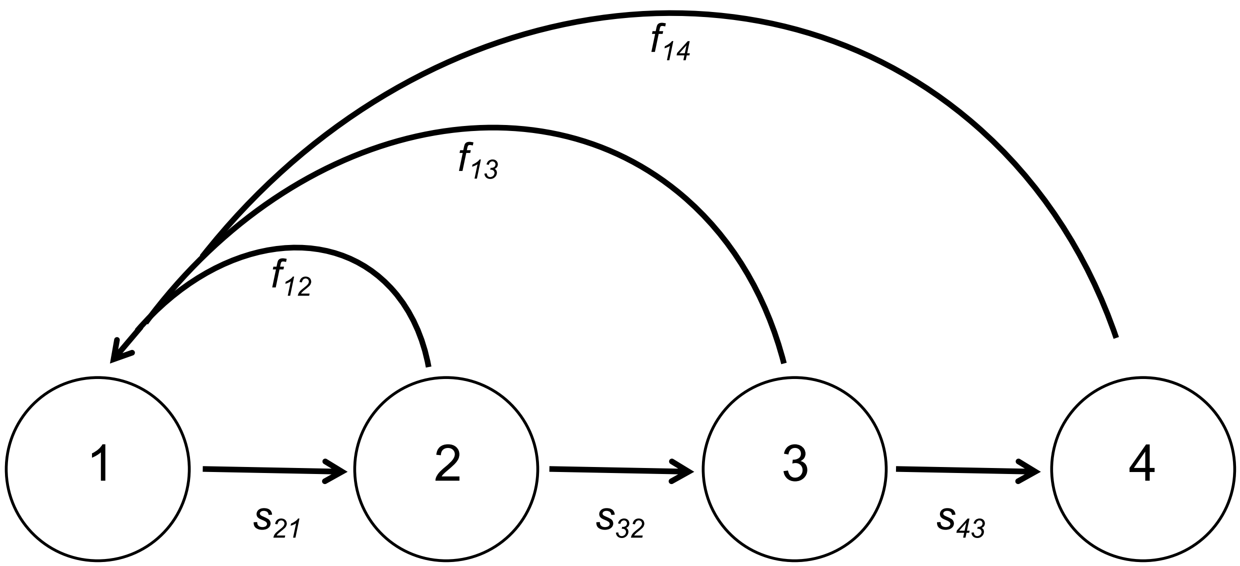
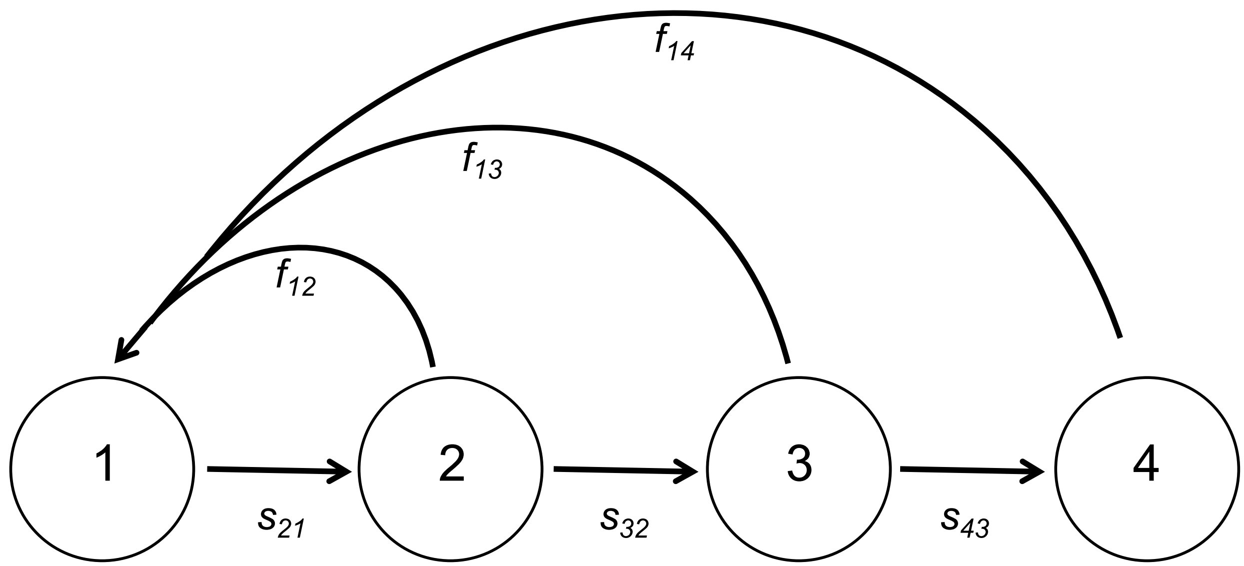
age-structured life history graph



$$N' = \mathbf{A}\,N \qquad \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}' = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ s_{21} & 0 & 0 & 0 \\ 0 & s_{32} & 0 & 0 \\ 0 & 0 & s_{43} & 0 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

age-structured life history graph



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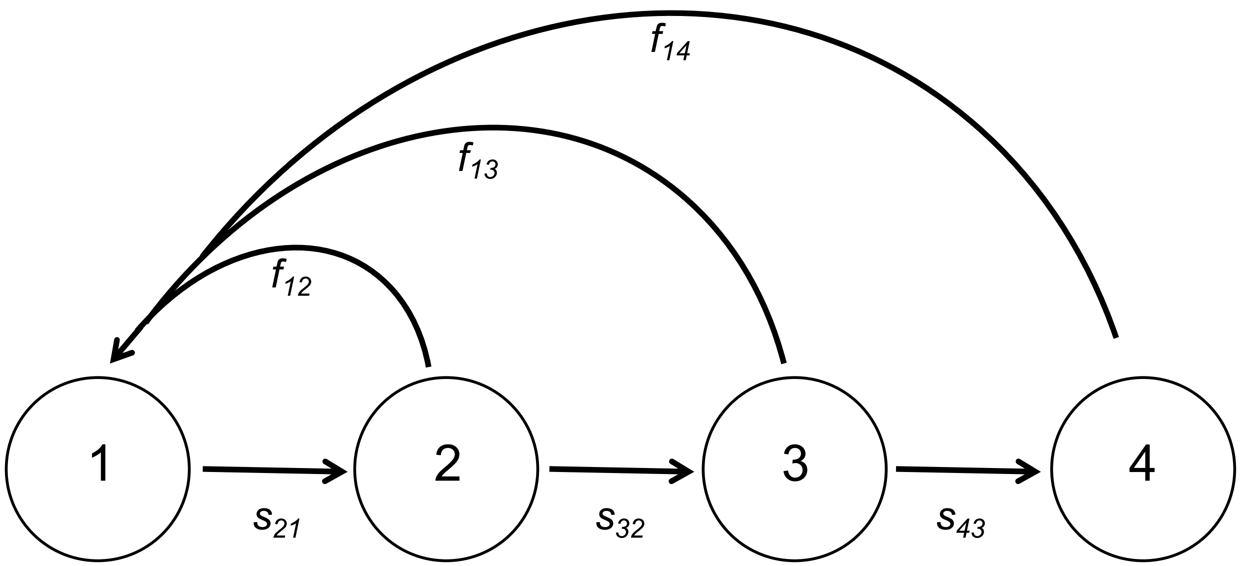
$$N_1' = f_{12}N_2 + f_{13}N_3 + f_{14}N_4$$

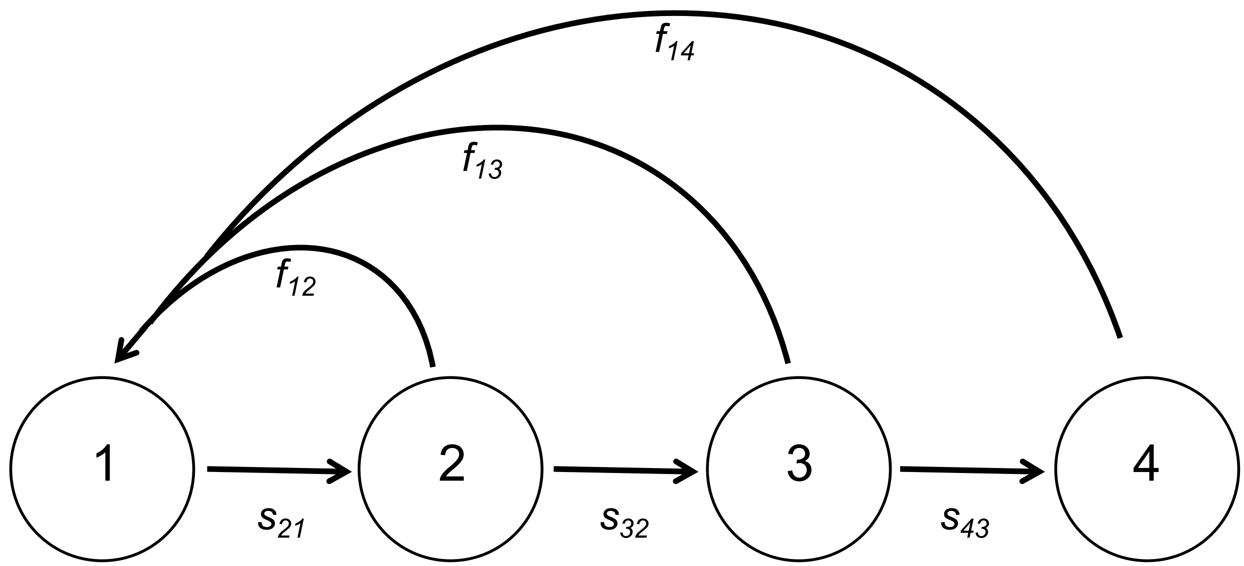
age-structured life history graph



$$N' = \mathbf{A}\,N \qquad \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}' = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ s_{21} & 0 & 0 & 0 \\ 0 & s_{32} & 0 & 0 \\ 0 & 0 & s_{43} & 0 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

$$N_2' = s_{21} N_1$$

age-structured life history graph



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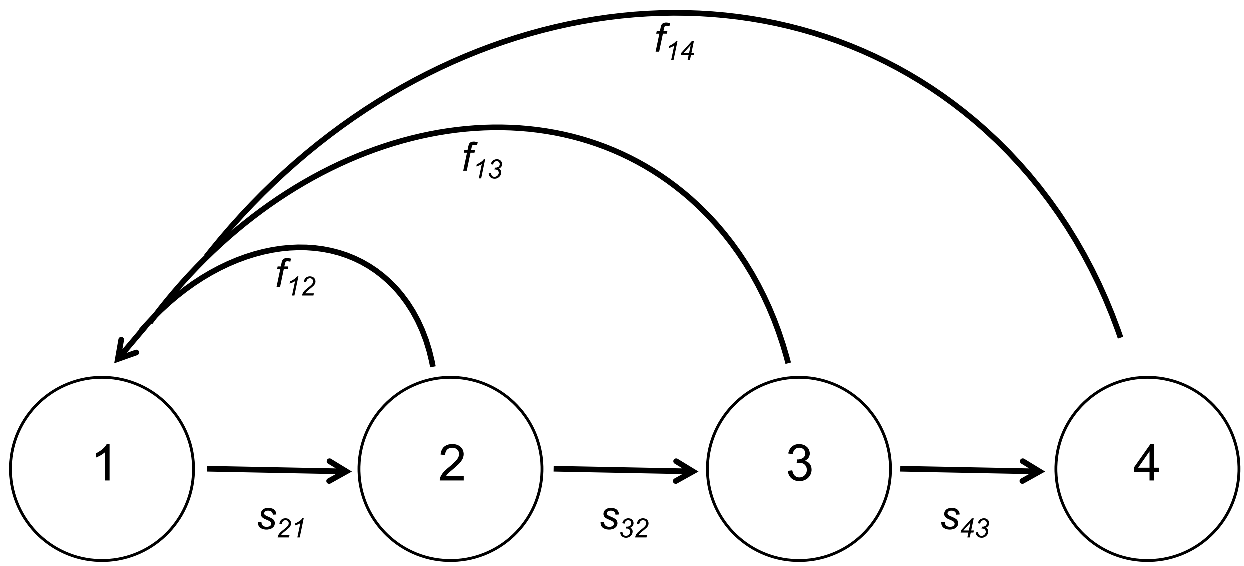
$$N_3' = s_{32} N_2$$

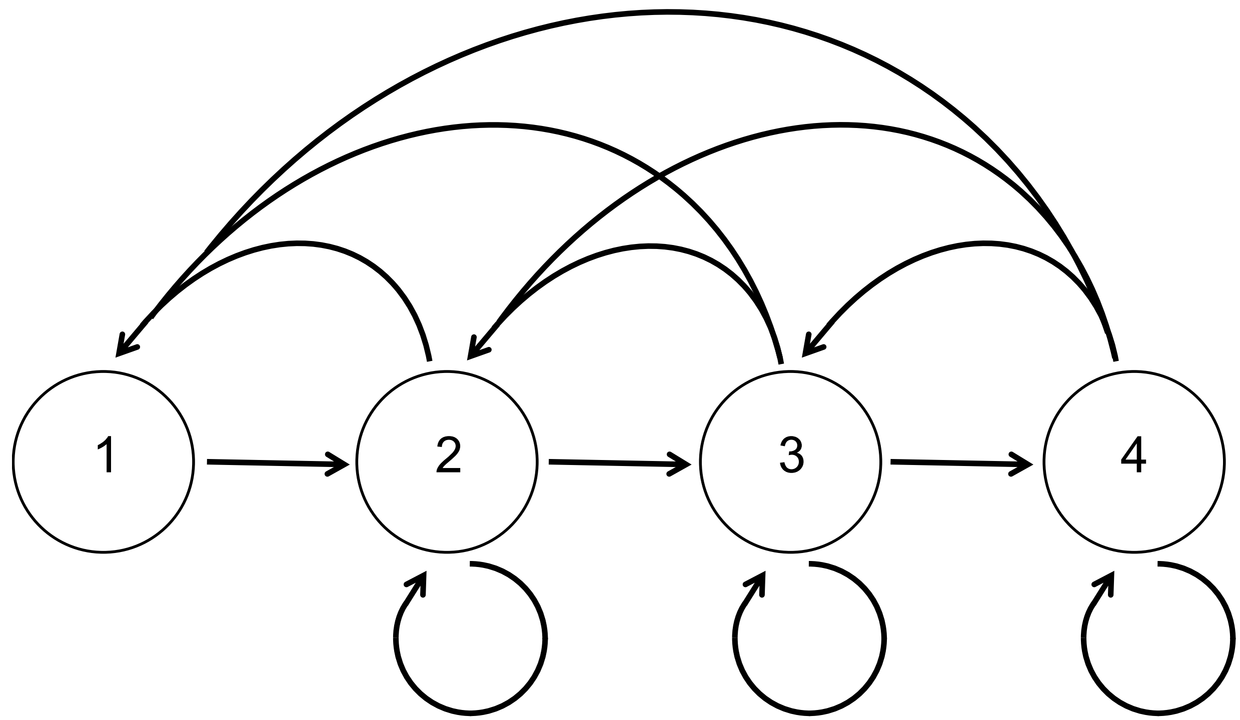
age-structured life history graph



$$N' = \mathbf{A}\, N \qquad \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}' = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ s_{21} & 0 & 0 & 0 \\ 0 & s_{32} & 0 & 0 \\ 0 & 0 & s_{43} & 0 \end{bmatrix} \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

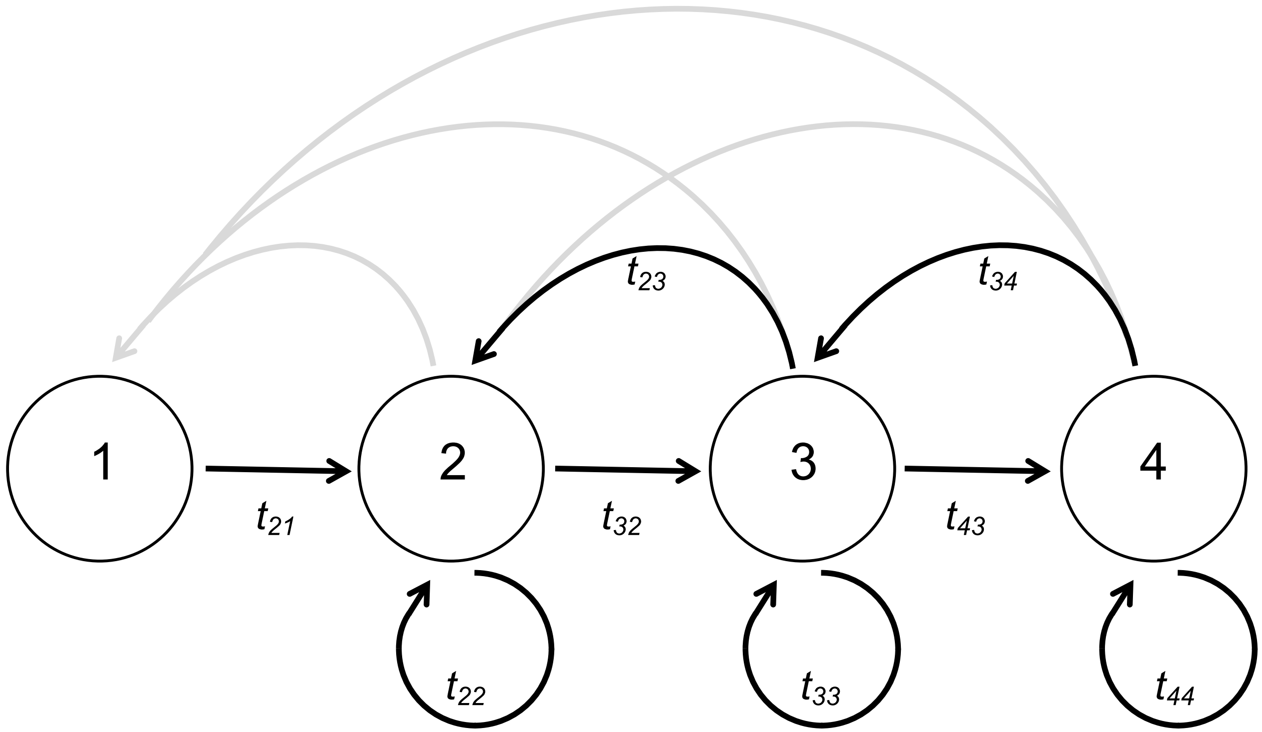
$$N_4' = s_{43} N_3$$

stage-structured life history graph



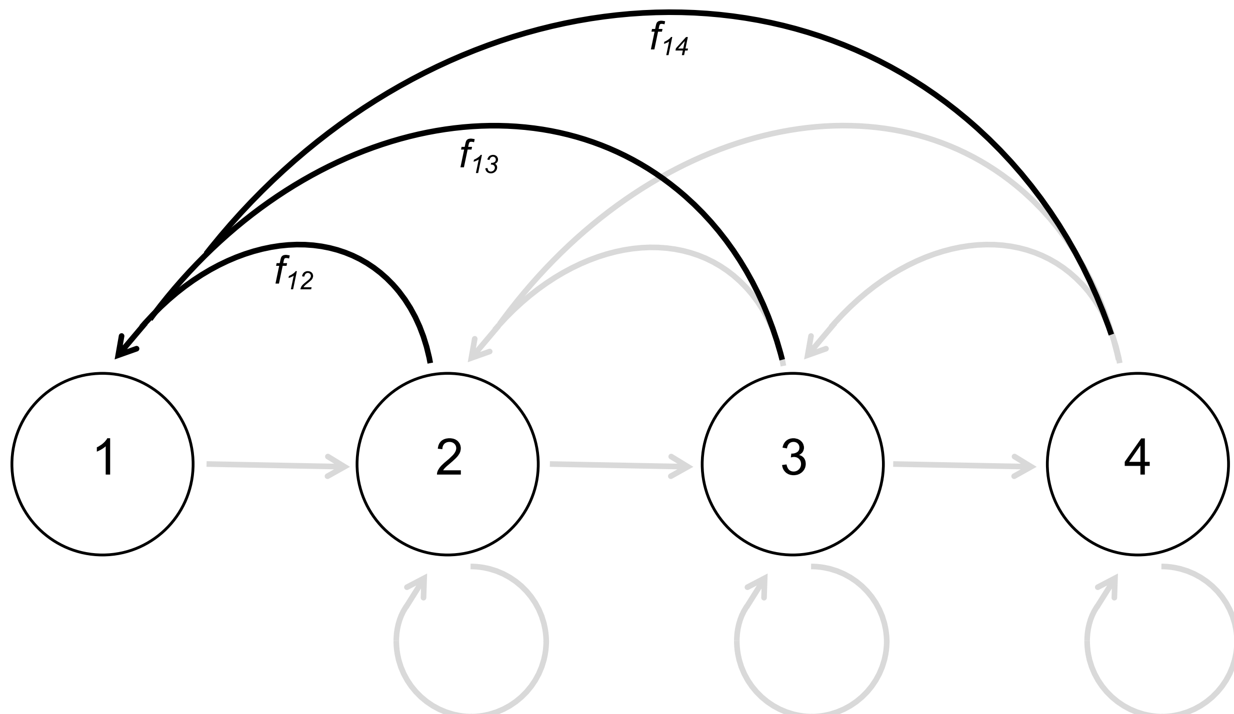
$$N' = \mathbf{A}\,N \qquad \mathbf{A} = \begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ t_{21} & t_{22} & t_{23} + c_{23} & c_{24} \\ 0 & t_{32} & t_{33} & t_{34} \\ 0 & 0 & t_{43} & t_{44} \end{bmatrix} \qquad N = \begin{bmatrix} N_1 \\ N_2 \\ N_3 \\ N_4 \end{bmatrix}$$

transitions



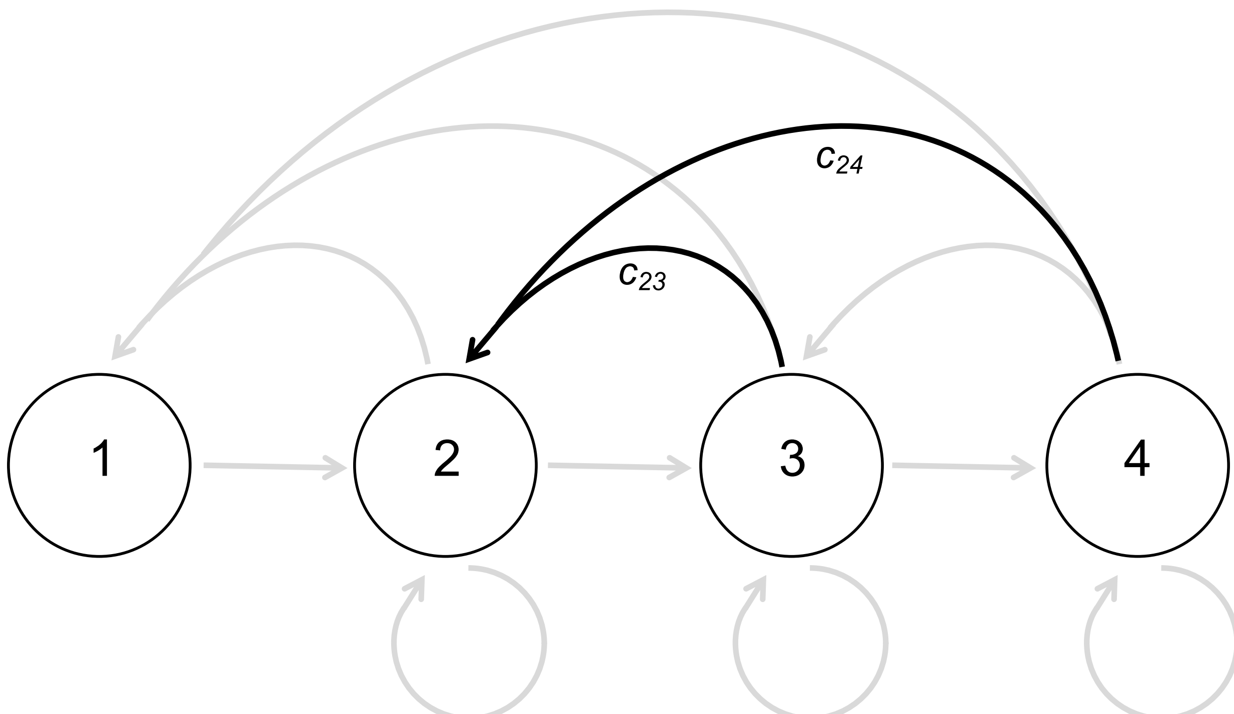
$$\begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ t_{21} & t_{22} & t_{23} + c_{23} & c_{24} \\ 0 & t_{32} & t_{33} & t_{34} \\ 0 & 0 & t_{43} & t_{44} \end{bmatrix}$$

sexual reproduction



$$\begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ t_{21} & t_{22} & t_{23} + c_{23} & c_{24} \\ 0 & t_{32} & t_{33} & t_{34} \\ 0 & 0 & t_{43} & t_{44} \end{bmatrix}$$

clonal reproduction



$$\begin{bmatrix} 0 & f_{12} & f_{13} & f_{14} \\ t_{21} & t_{22} & t_{23} + c_{23} & c_{24} \\ 0 & t_{32} & t_{33} & t_{34} \\ 0 & 0 & t_{43} & t_{44} \end{bmatrix}$$

Explicitly considering clonal reproduction

- three types of movements

$$N_i' = \sum_j N_j \bar{a}_{ij} = \sum_j N_j \left(\bar{t}_{ij} + \bar{f}_{ij} + \bar{c}_{ij}\right)$$

$$= \sum_j N_j \bar{t}_{ij} + \sum_j N_j \bar{f}_{ij} + \sum_j N_j \bar{c}_{ij} = T_i' + F_i' + C_i'$$

t_{ij} = transition from stage j to stage i

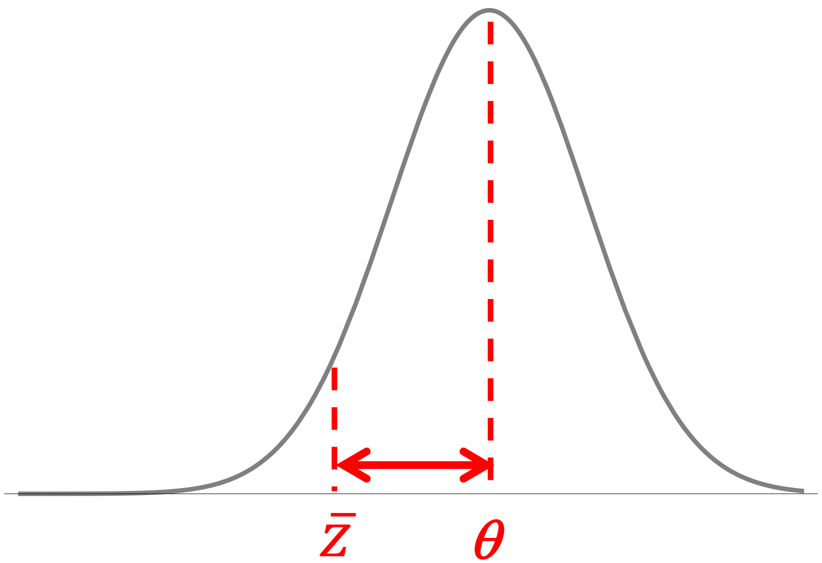
f_{ij} = sexual reproduction from stage j to stage i

c_{ij} = clonal reproduction from stage j to stage i

phenotypic evolution

z = phenotypic trait

z = g + e



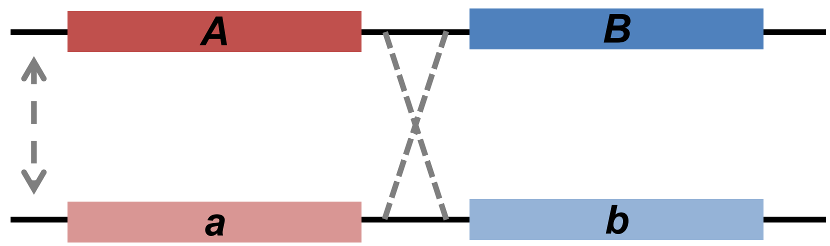
g = additive genetic factor

e = non-additive genetic
+ random environmental factor

What makes up **e**?

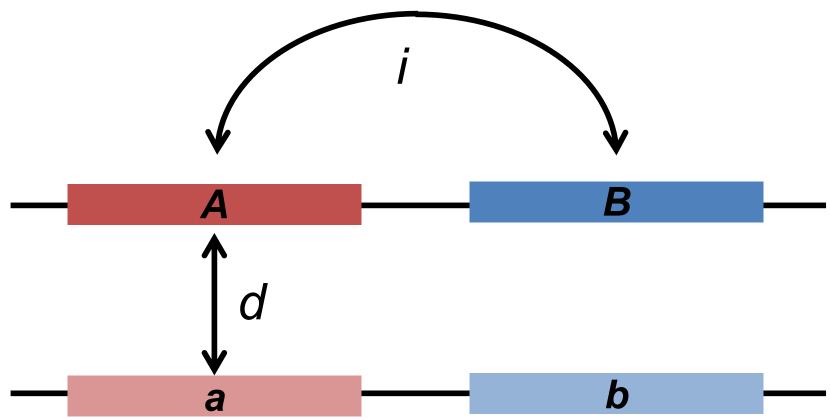
sexual reproduction

α



clonal reproduction

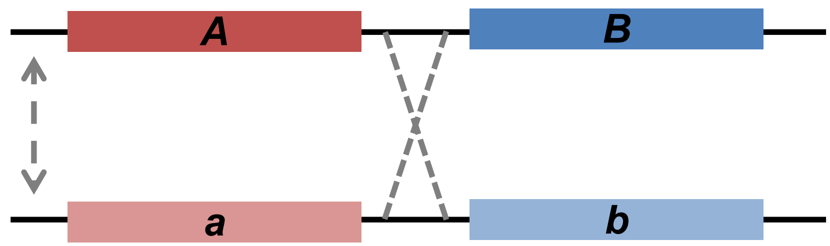
α, d, i



What makes up **e**?

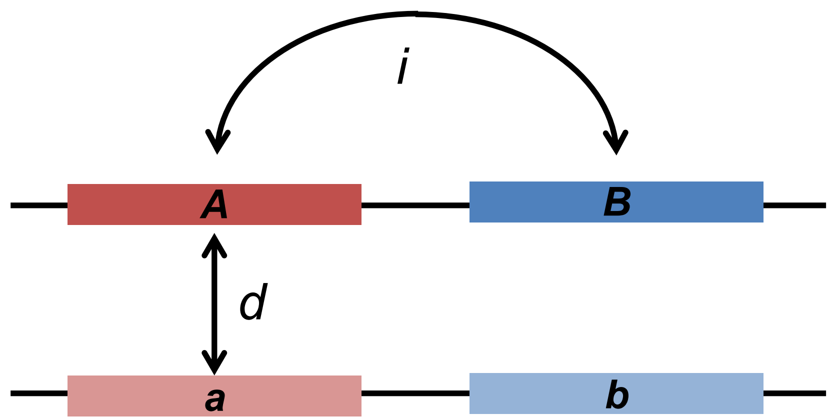
sexual reproduction

α



clonal reproduction

α, *d*, *i*

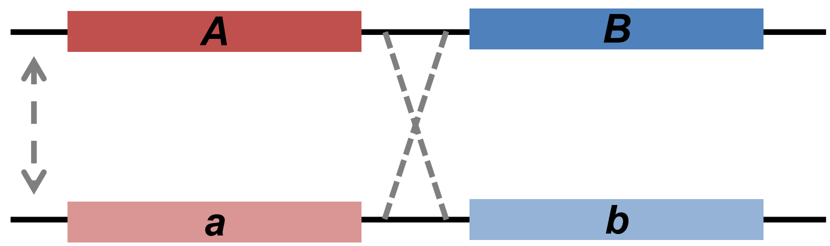


non-additive genetic factors
(dominance, epistatis)

What makes up **e**?

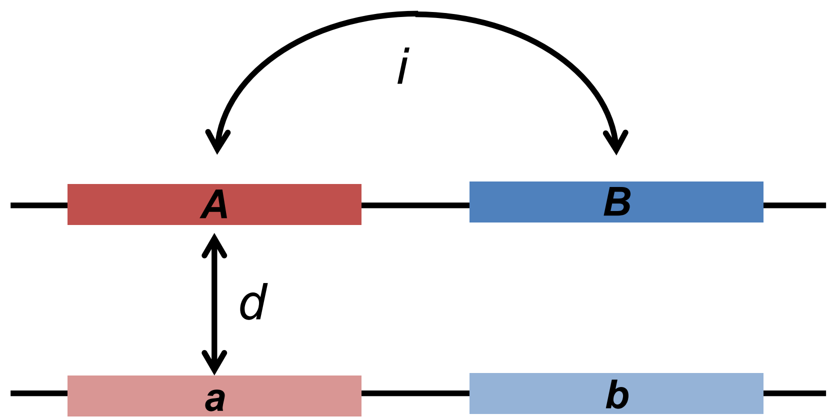
sexual reproduction

α



clonal reproduction

α, d, i



non-additive genetic factors (dominance, epistatis) + random environmental factors

ρ = association between **e** in parent and clonal offspring

ρ close to 0

Joerg Hauke/Getty Images

ρ close to 1

recursions for phenotypic and genotypic means

$$\bar{\boldsymbol{z}}_{\boldsymbol{i}}' = \sum_{\boldsymbol{j}} \Big[\big(d_{ij}^{t} + \mathbf{R} d_{ij}^{c}\big) \bar{\boldsymbol{z}}_j + \big(d_{ij}^{f} + (\mathbf{I} - \mathbf{R}) d_{ij}^{c}\big) \bar{\boldsymbol{g}}_j$$

$$+ \frac{d_{ij}}{\bar{a}_{ij}} \Big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{f}_{ij} + \mathbf{R}\, \boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} + (\mathbf{I} - \mathbf{R}) \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} \Big) \Big]$$

$$\bar{\boldsymbol{g}}_i' = \sum_j d_{ij}\ \bar{\boldsymbol{g}}_j + \sum_j d_{ij}\, \boldsymbol{G}_j\, \boldsymbol{\nabla}_{\bar{\mathbf{z}}_{\boldsymbol{j}}}\ \mathbf{ln}\, \bar{\boldsymbol{a}}_{\boldsymbol{ij}}$$

$\boldsymbol{P}_j$ = phenotypic covariance matrix

$\boldsymbol{G}_j$ = additive genetic covariance matrix

$\bar{a}_{ij} = \bar{t}_{ij} + \bar{f}_{ij} + \bar{c}_{ij}$

$d_{ij} = \bar{a}_{ij} N_j / N_{\boldsymbol{i}}'$

$d_{ij}^{t} = \bar{t}_{ij} N_j / N_{\boldsymbol{i}}',\ d_{ij}^{f} = \bar{f}_{ij} N_j / N_{\boldsymbol{i}}',\ d_{ij}^{c} = \bar{c}_{ij} N_j / N_{\boldsymbol{i}}'$

$$\boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} = (\partial/\partial\, \bar{z}_1, \partial/\partial\, \bar{z}_2, \cdots, \partial/\partial\, \bar{z}_m)^{\mathrm{T}}$$

$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

recursions for phenotypic and genotypic means

$$\bar{\boldsymbol{z}}_{\boldsymbol{i}}' = \sum_{\boldsymbol{j}} \Big[\big(d_{ij}^t + \mathbf{R} d_{ij}^c\big) \bar{\boldsymbol{z}}_j + \big(d_{ij}^f + (\mathbf{I} - \mathbf{R}) d_{ij}^c\big) \bar{\boldsymbol{g}}_j$$

$$+ \frac{d_{ij}}{\bar{a}_{ij}} \Big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{f}_{ij} + \mathbf{R}\, \boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} + (\mathbf{I} - \mathbf{R}) \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} \bar{c}_{ij} \Big) \Big]$$

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recursions for phenotypic and genotypic means

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$$+ \frac{d_{ij}}{\bar{a}_{ij}}\big(\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{t}_{ij} + \boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{f}_{ij} + \mathbf{R}\,\boldsymbol{P}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij} + (\mathbf{I}-\mathbf{R})\boldsymbol{G}_j \boldsymbol{\nabla}_{\bar{\mathbf{z}}_j}\bar{c}_{ij}\big)\Big]$$

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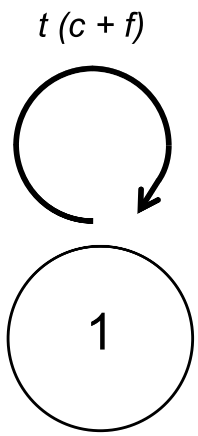
$$\boldsymbol{\nabla}_{\bar{\mathbf{z}}_j} = (\partial/\partial\,\bar{z}_1, \partial/\partial\,\bar{z}_2, \cdots, \partial/\partial\,\bar{z}_m)^{\mathrm{T}}$$

$$\mathbf{R} = \begin{bmatrix} \rho_1 & 0 & \cdots & 0 \\ 0 & \rho_2 & & 0 \\ \vdots & & \ddots & \vdots \\ 0 & \cdots & \cdots & \rho_m \end{bmatrix}$$

Simple life history



clonal and sexual reproduction

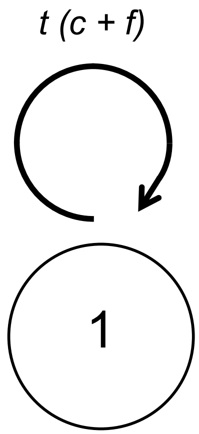
selection on survival probability $t = \exp\left[-\frac{(\bar{z}_1 - \theta)^2}{(2\omega^2)}\right]$

amount of clonal reproduction $r_c = c/(f + c)$

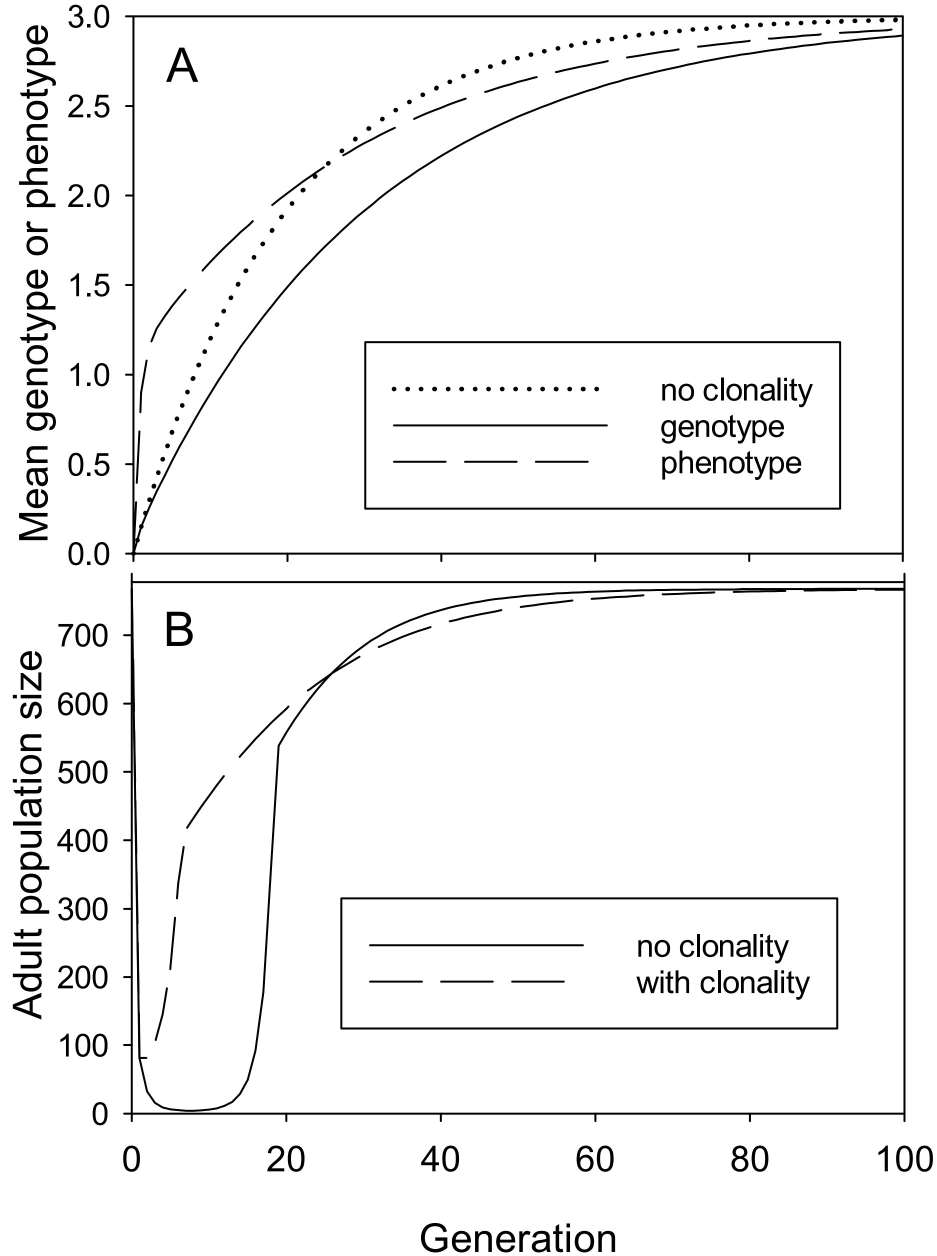
$$\Delta\bar{z} = (1 - r_c\rho)(\bar{g} - \bar{z}) + \{r_c\rho P + (1 - r_c\rho)G\}\frac{\theta - \bar{z}}{\omega^2}$$

$$\Delta\bar{g} = G\,\frac{\theta - \bar{z}}{\omega^2}$$

analytical results – effect of clonality

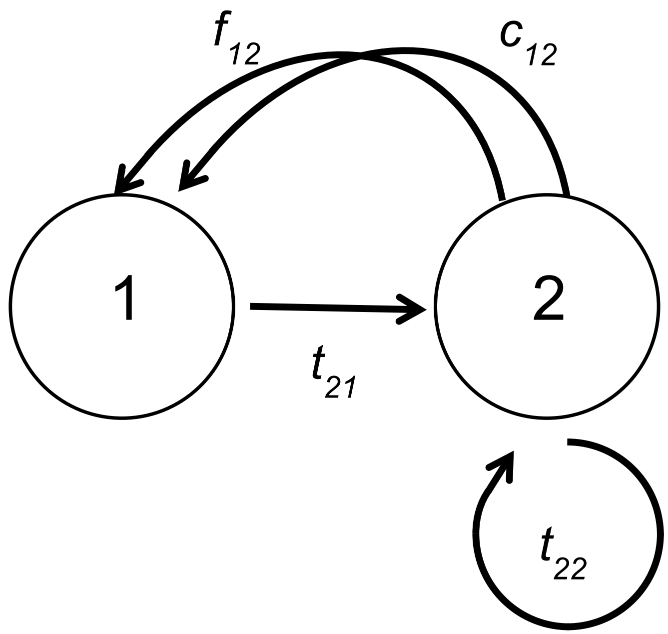


no clonality ($r_c \rho = 0$)
vs.
with clonality ($r_c \rho = 0.5$)



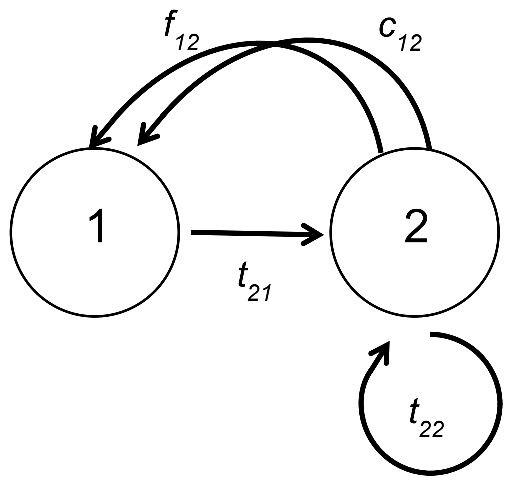
Orive et al. (2017) *Am Nat*

Life history with stage structure



$$\begin{pmatrix} N_1 \\ N_2 \end{pmatrix}' = \begin{pmatrix} 0 & c_{12} + f_{12} \\ t_{21} & t_{22} \end{pmatrix} \begin{pmatrix} N_1 \\ N_2 \end{pmatrix}$$

Life history with stage structure



selection on juvenile survival

$$\bar{t}_{21} = t_{\max}\exp\left[-\frac{(\bar{z}_1-\theta)^2}{(2\omega^2)}\right]$$

$$r_c = c_{12}/(c_{12}+f_{12})$$

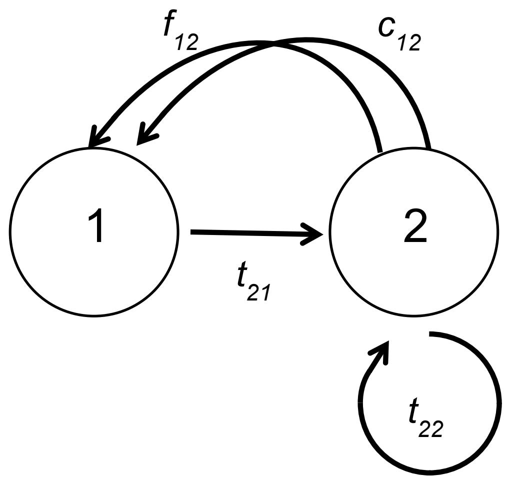
$$\bar{z}_1' = r_c\rho(\bar{z}_2-\bar{g}_2)+\bar{g}_2$$

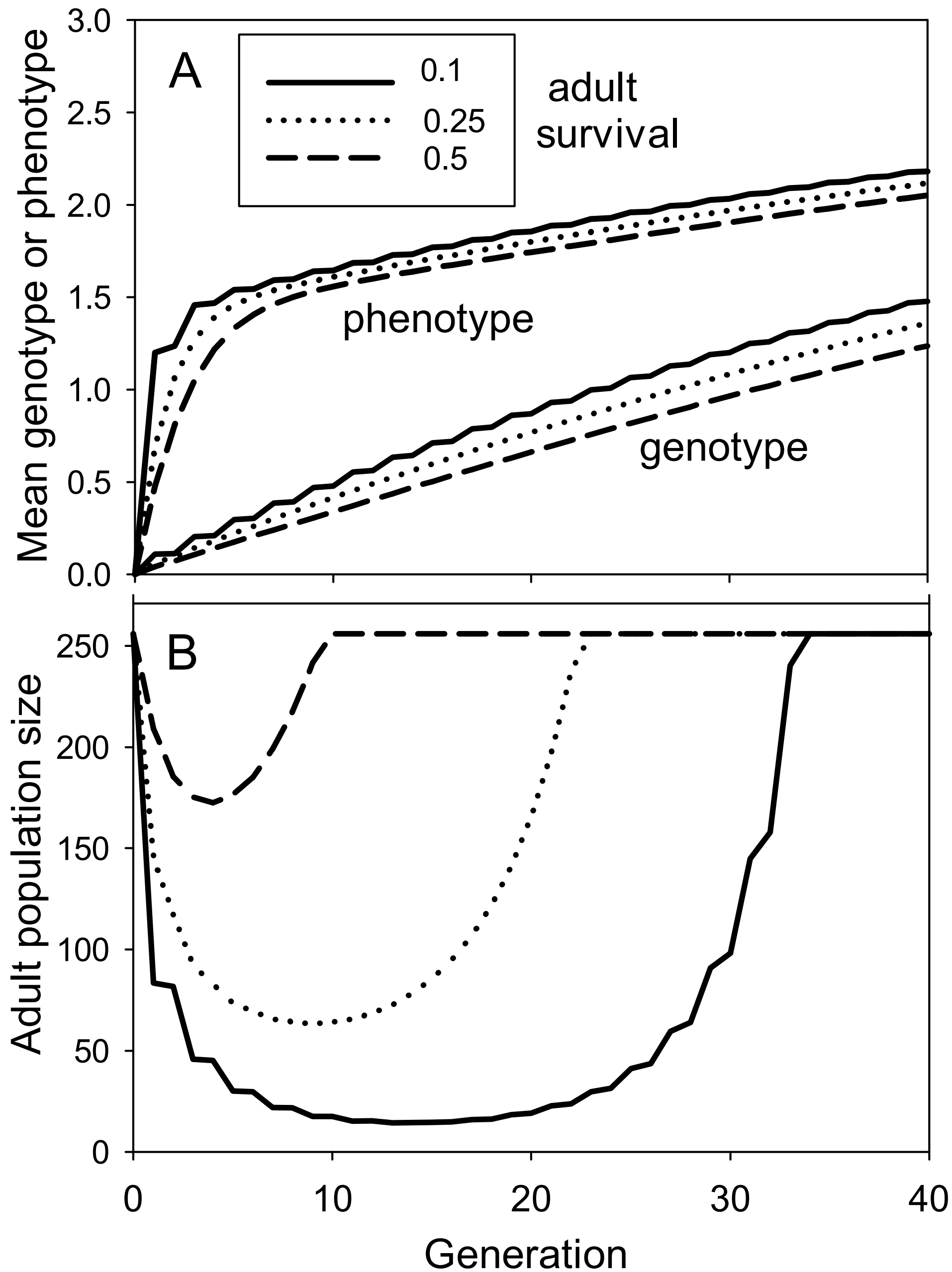
$$\bar{z}_2' = \bar{z}_2 + \frac{N_1}{\bar{t}_{21}N_1+\bar{t}_{22}N_2}\bar{t}_{21}\left[(\bar{z}_1-\bar{z}_2)+P_1\left(\frac{\theta-\bar{z}_1}{\omega^2}\right)\right]$$

$$\bar{g}_1' = \bar{g}_2$$

$$\bar{g}_2' = \bar{g}_2 + \frac{N_1}{\bar{t}_{21}N_1+\bar{t}_{22}N_2}\bar{t}_{21}\left[(\bar{g}_1-\bar{g}_2)+G_1\left(\frac{\theta-\bar{z}_1}{\omega^2}\right)\right]$$

analytical results – increased adult survival





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evolutionary lag in clonal organisms

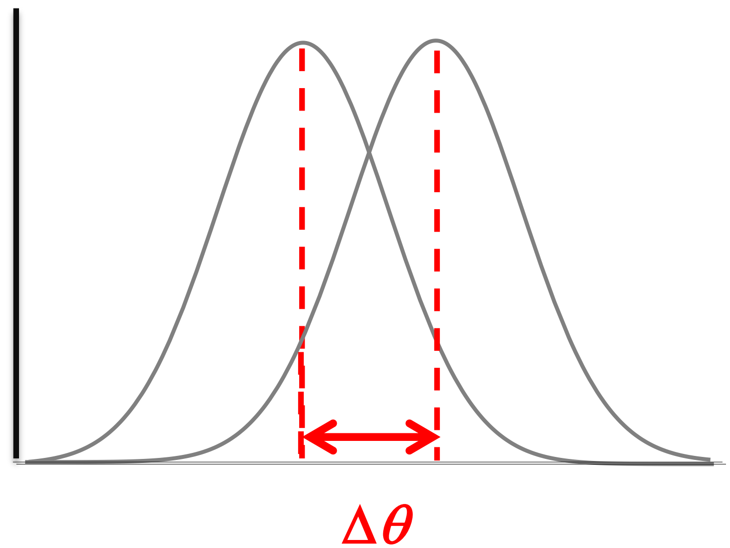
- analytical results
  - clonality ($r_c\,\rho > 0$) and adult survival (stage structure) both slow approach to equilibrium phenotype
  - but both also reduce both extent and duration of population size decrease
    - demographic advantage

individual-based simulations

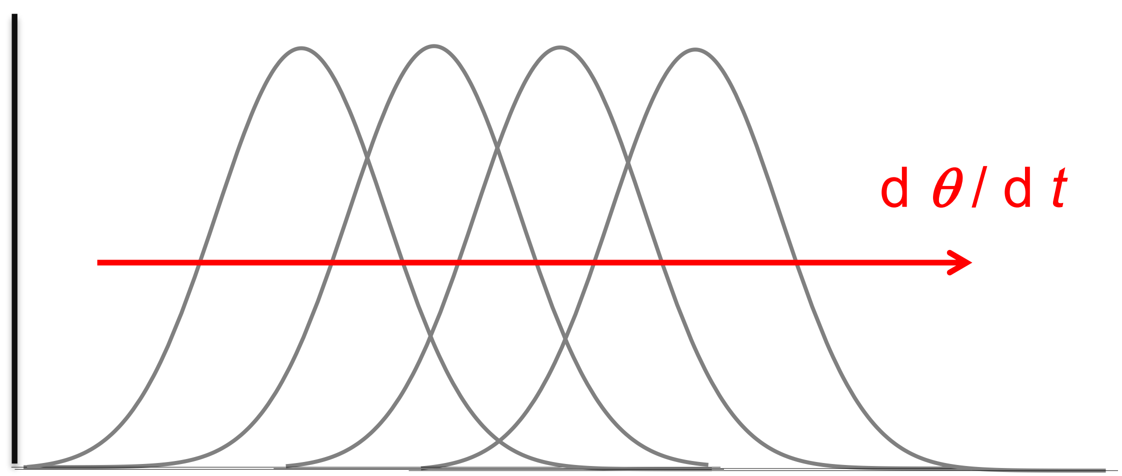
- single polygenic trait z
  - $n = 10$ loci, additive allelic effects
- **e** normally distributed, mean 0, variance 1
- $\mu_g = 100\mu_s$
- population size ceiling, K
- relative amounts of clonal reproduction, $r_c = c/(c + f)$
- association parameter, ρ
- change in optimum phenotype
  - one-step change
  - continuous, linear change

change in optimum phenotype

one-step change



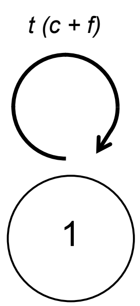
continuous change



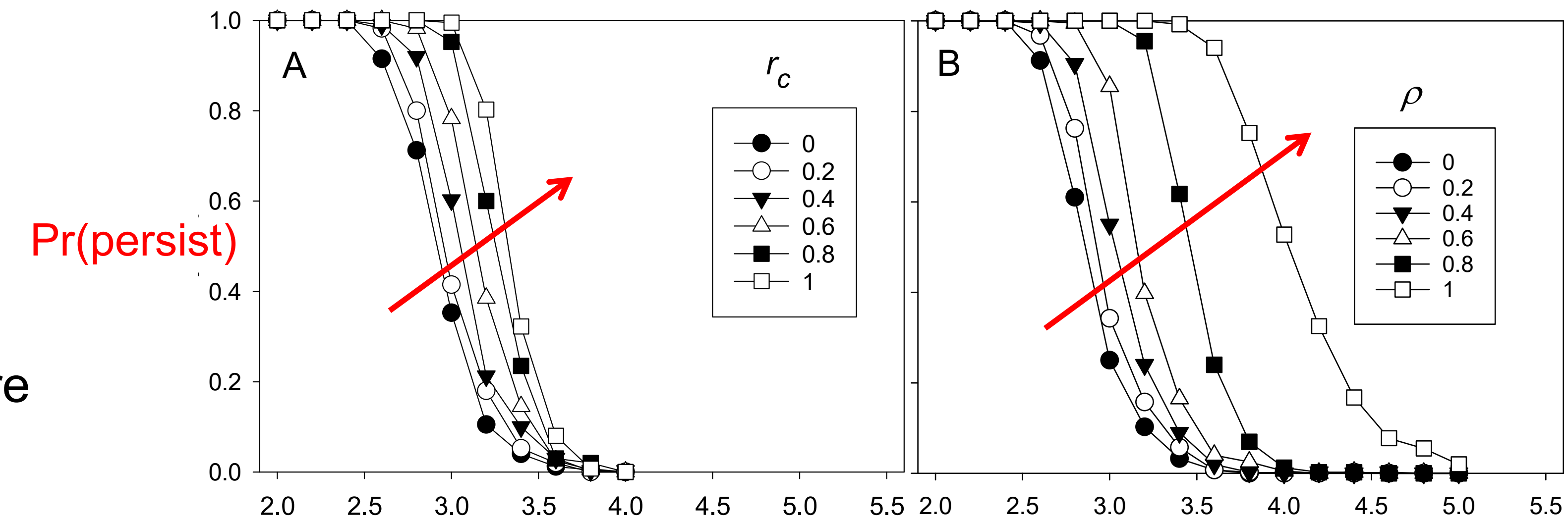
one-step change in optimal phenotype

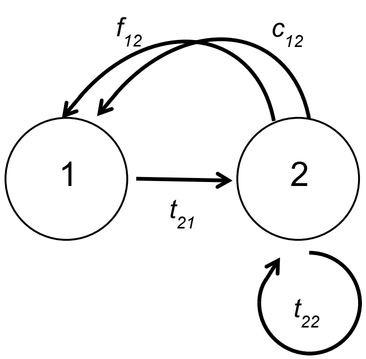
clonal reproduction r_c — $\rho = 0.5$

association parameter ρ — $r_c = 0.5$

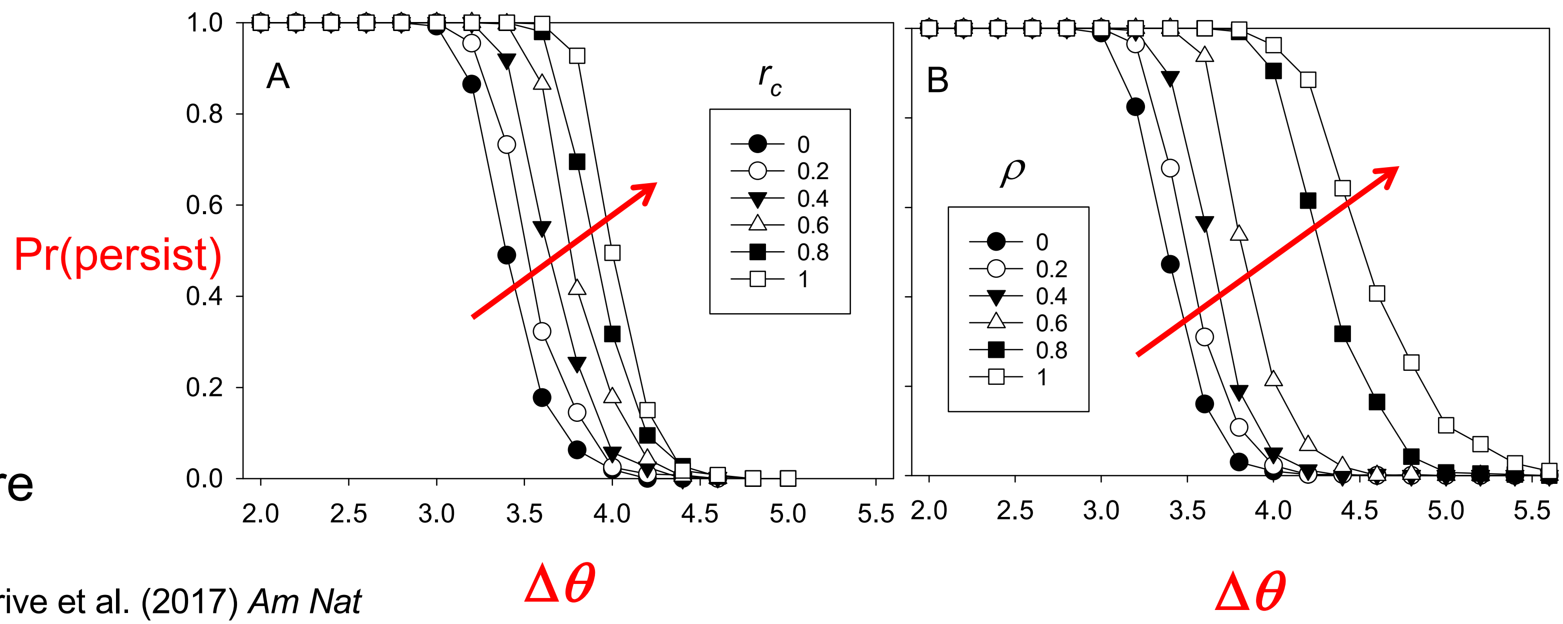


no stage structure





with stage structure



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one-step change in optimal phenotype

- greater population persistence with more clonal reproduction (r_c) and higher environmental component association (ρ)
  - standing genotypic variation

one-step change in optimal phenotype

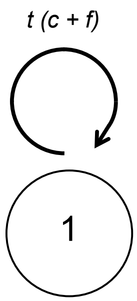
- greater population persistence with more clonal reproduction (r_c) and higher environmental component association (ρ)
  - standing genotypic variation

- stage structure increases probability of population persistence
  - demographic advantage

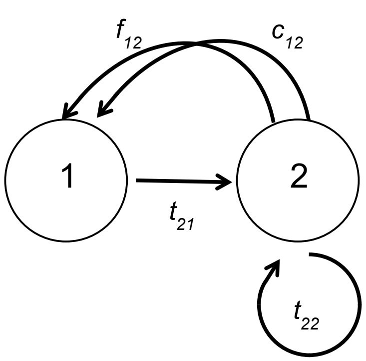
continuous change in optimal phenotype

clonal reproduction r_c — $\rho = 0.5$

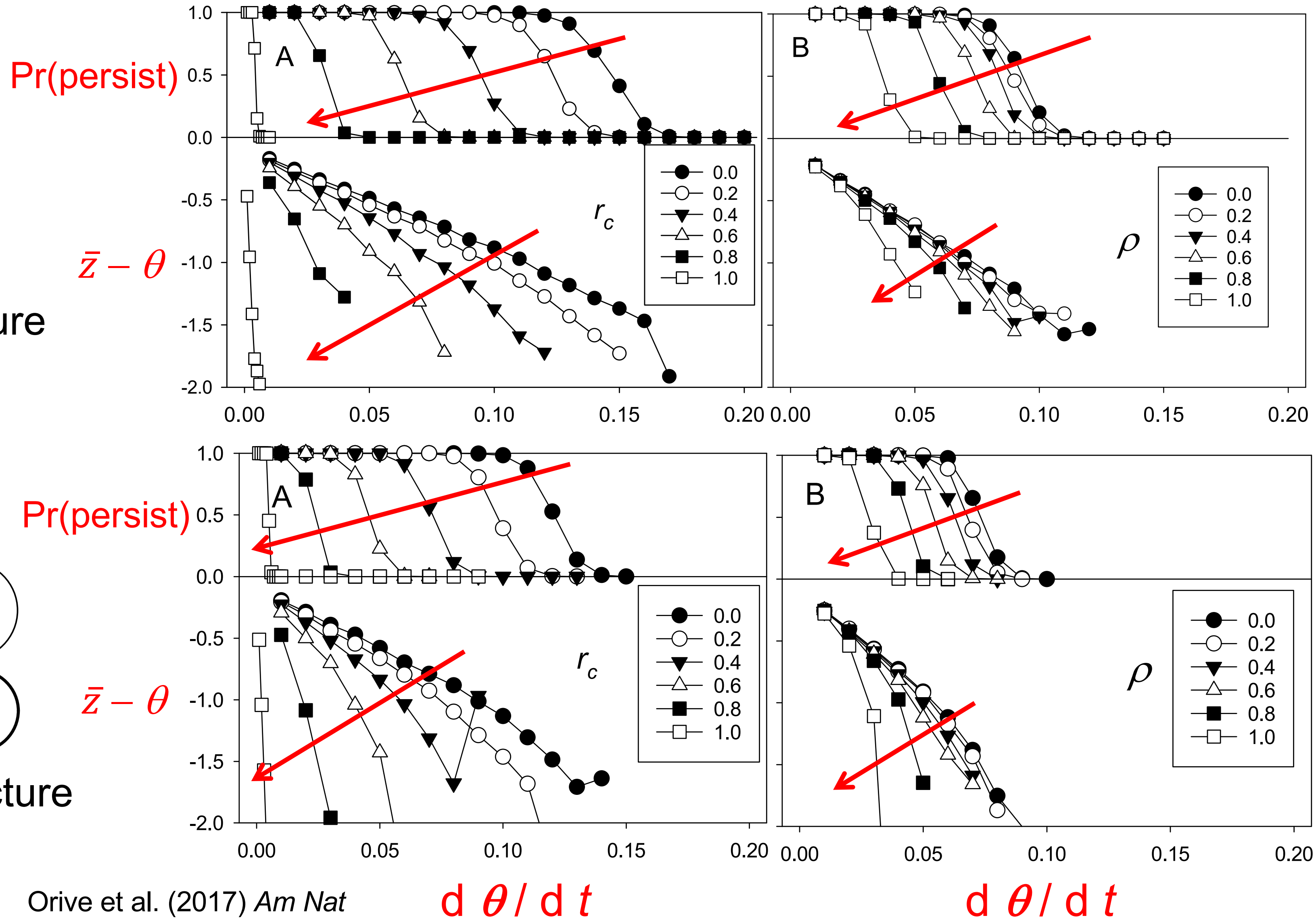
association parameter ρ — $r_c = 0.5$



no stage structure



with stage structure



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continuous, linear change in optimal phenotype

- decreased persistence and greater lag with more clonal reproduction, higher ρ
  - de novo genotypic variation

continuous, linear change in optimal phenotype

- decreased persistence and greater lag with more clonal reproduction, higher ρ
  - de novo genotypic variation

- stage structure decreases persistence and increases lag
  - increased generation time
  - decreased N_e of component of population experiencing phenotypic selection
  - maladaptive “gene flow through time”

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

- scale of change – whether population experiences that change as a single transition or not

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?
- scale of change – whether population experiences that change as a single transition or not
- amount of phenotypic matching between organisms and their clonal offspring

evolutionary lag in clonal organisms

- how will clonal organisms respond under rapid environmental change?

- scale of change – whether population experiences that change as a single transition or not

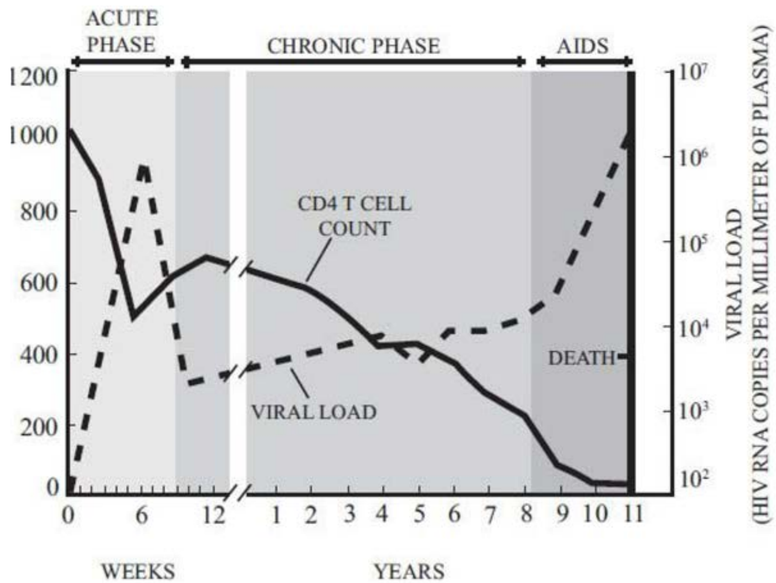
- amount of phenotypic matching between organisms and their clonal offspring

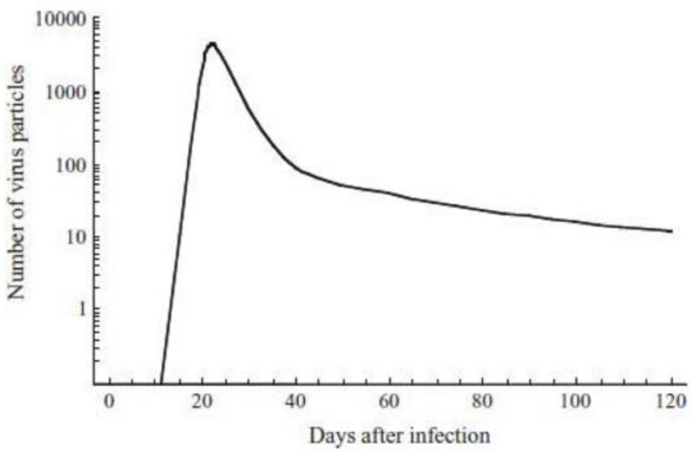
- existence of stage structured life histories

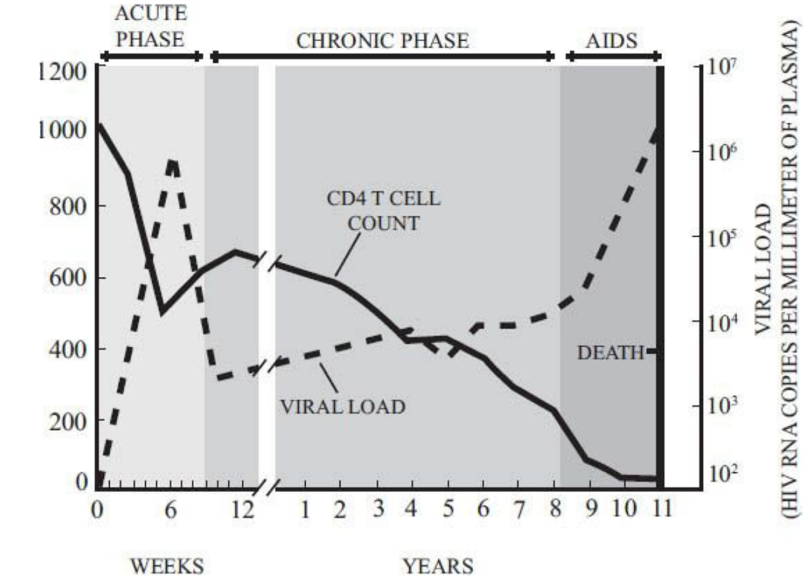
two ways we can use models to make sense of biology

- Explain what we *do see*
  - Specific test of hypotheses
  - Example: dynamics of HIV after infection

- Predict what we *might see*
  - Generate hypotheses
  - Example: evolutionary lag and rescue with complex life histories


ACUTE PHASE
CHRONIC PHASE
AIDS
1200
1000
800
600
400
200
0
CD4 T CELL COUNT
VIRAL LOAD
DEATH
0
6
12
1 2 3 4 5 6 7 8 9 10 11
WEEKS
YEARS
10^7
10^6
10^5
10^4
10^3
10^2
VIRAL LOAD
(HIV RNA COPIES PER MILLIMETER OF PLASMA)


10000
1000
100
10
1
Number of virus particles
0 20 40 60 80 100 120
Days after infection


ACUTE PHASE
CHRONIC PHASE
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1200
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200
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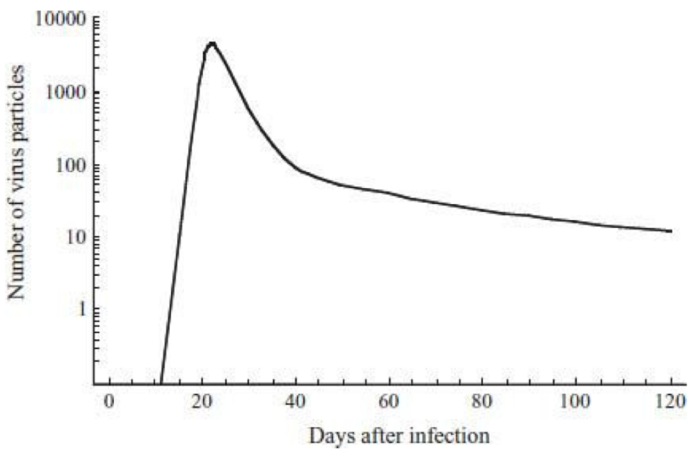
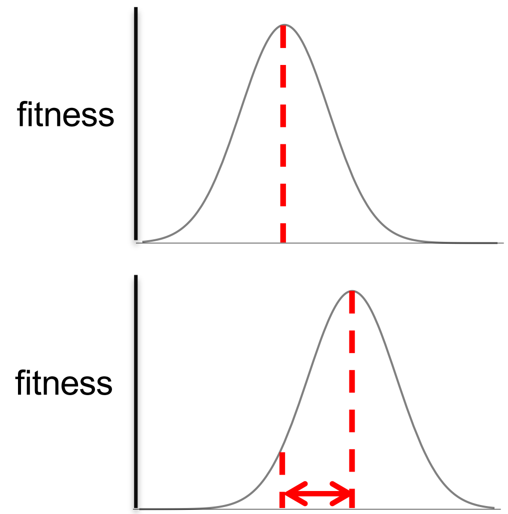
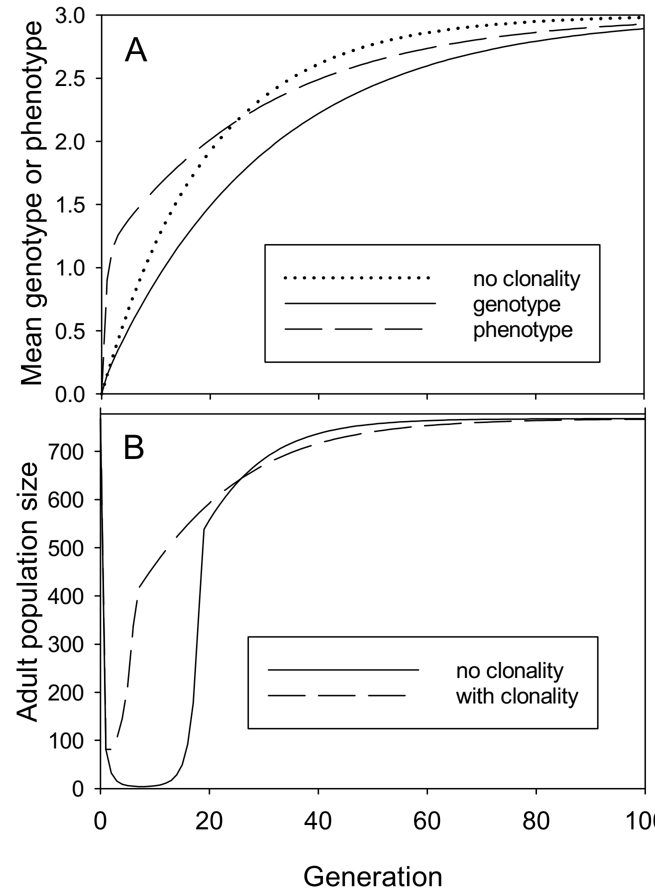
CD4 T CELL COUNT
VIRAL LOAD
DEATH
10^7
10^6
10^5
10^4
10^3
10^2
VIRAL LOAD (HIV RNA COPIES PER MILLIMETER OF PLASMA)
0 6 12
1 2 3 4 5 6 7 8 9 10 11
WEEKS
YEARS


Number of virus particles
10000
1000
100
10
1
0 20 40 60 80 100 120
Days after infection


fitness
fitness


A
Mean genotype or phenotype
3.0
2.5
2.0
1.5
1.0
0.5
0.0
no clonality
genotype
phenotype
B
Adult population size
700
600
500
400
300
200
100
0
no clonality
with clonality
0 20 40 60 80 100
Generation

acknowledgments

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questions?

Website: http://www.orive.faculty.ku.edu/

Email: morive@ku.edu

Twitter: @MEOrive