Escaping an infestation of parasites by ‘*outrunning*’ them

— *insights from a simple stochastic model*

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Background:
population† dynamics in complex systems

† generic term to describe the number of individuals in a given system

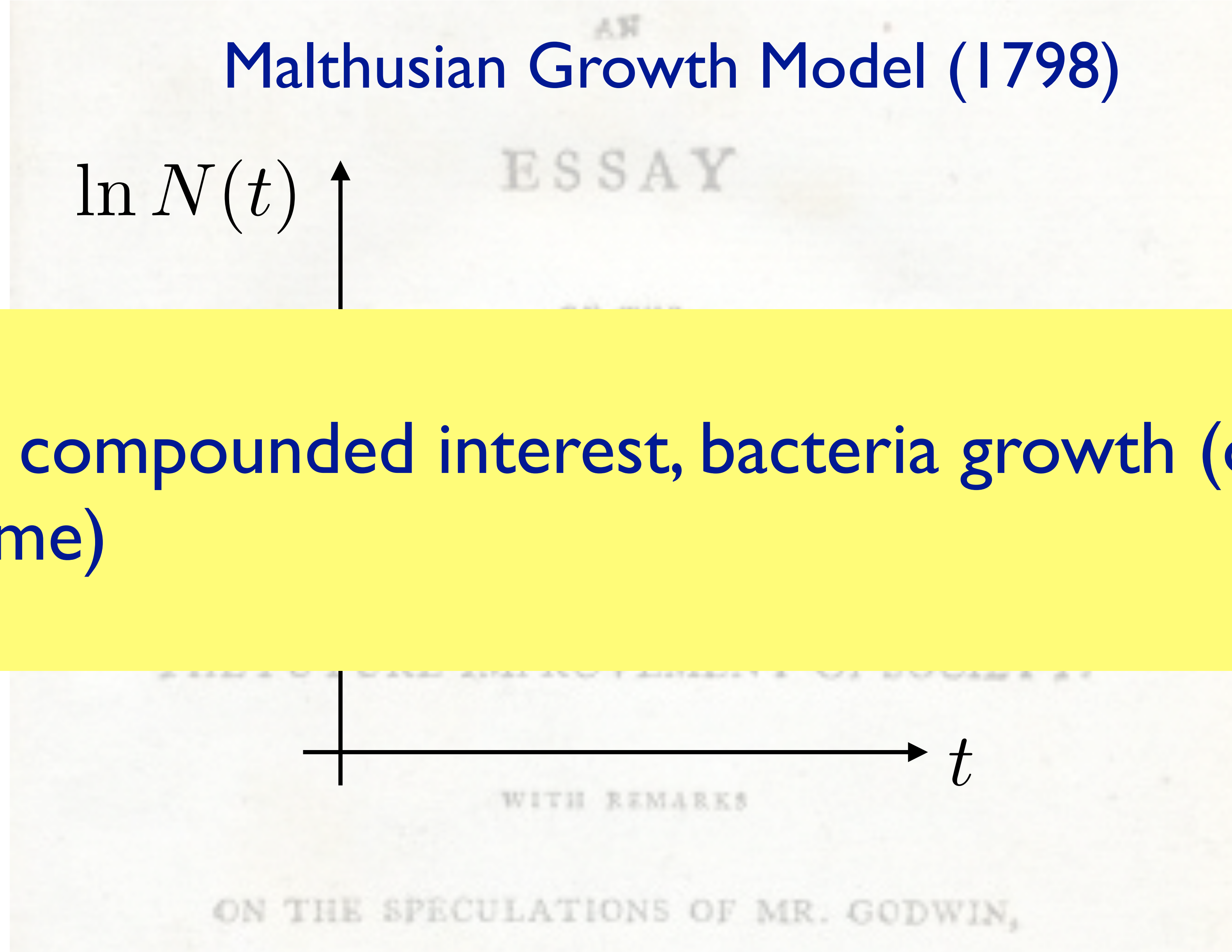
Scenario 1: when growing at a constant rate, how does the population change as a function of time, i.e. what is ***N*(t)**?

change = newborns - death

$$\frac{dN(t)}{dt} = \lambda \cdot N(t) \rightarrow N(t) = N_0 e^{\lambda t}$$

$N(t)$: size of population at time t; N_0 : initial population; λ : birth - death

Malthusian Growth Model (1798)



Examples: compounded interest, bacteria growth (only for a limited time)

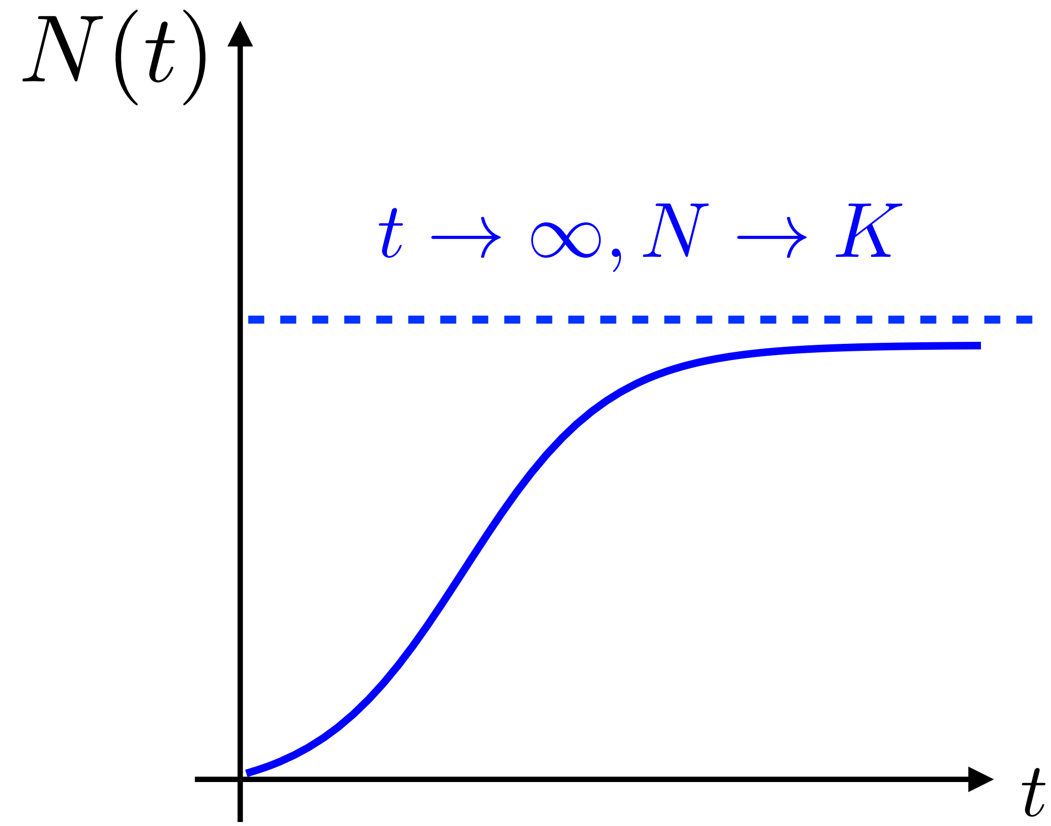
Scenario II: when growth is **limited** by resources, and the maximal individuals that can be sustained is *K*

K : Carrying capacity

$$\frac{dN}{dt} = \lambda(1 - \frac{N}{K})N$$ Verhulst logistic equation, 1838

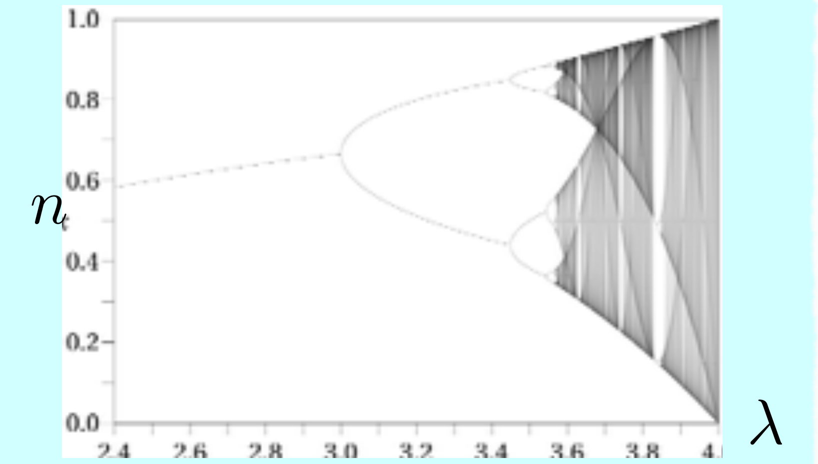
$$N(t) = \frac{1}{\frac{1}{K} + \left(\frac{1}{N_0} - \frac{1}{K}\right)e^{-\lambda t}}$$

$$\rightarrow N_0 e^{\lambda t} \quad \text{when} \quad K \rightarrow \infty$$



$$n_{t+1} = \lambda(1 - n_t)n_t$$

- depending on λ:
  - period doubling,
  - chaotic regime etc, summarized in bifurcation map



Logistic Bifurcation map

A few more complications:

- spatial structure:
  - inhomogeneous resource distribution;
  - immigration / emigration, "diffusion"

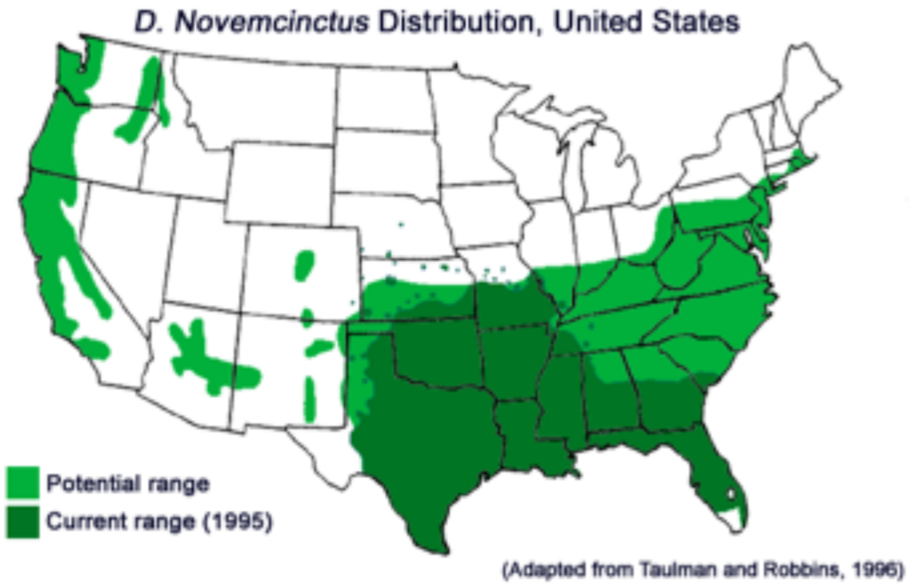
$$N(t) \Rightarrow N(\vec{r}, t)$$

nine-banded armadillo

$$\frac{\partial N(\vec{r}, t)}{\partial t} = \nabla \cdot [D(N, \vec{r}) \nabla N(\vec{r}, t)] \text{ + newborns - death}$$

special case: ***D*** = constant

$$\frac{\partial N(\vec{r}, t)}{\partial t} = D \nabla^2 N(\vec{r}, t)$$



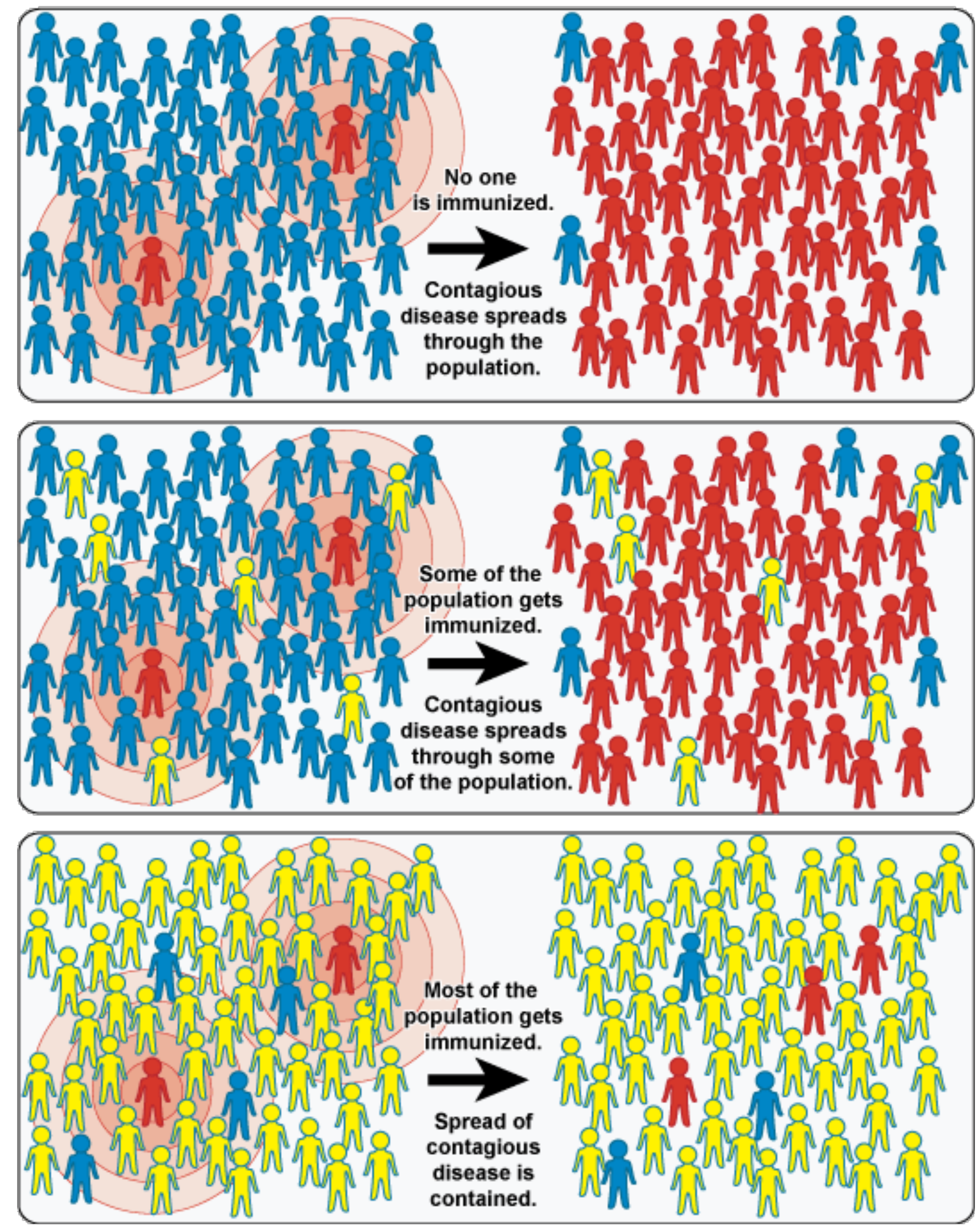
A few more complications:

- multiple species: e.g.
  - predator-prey;
  - epidemics: Susceptible Infected Recovered

$$N(t) \Rightarrow S(t) + I(t) + R(t)$$

$$\frac{dS}{dt} = -\beta SI/N$$
$$\frac{dI}{dt} = \beta SI/N - \gamma I$$
$$\frac{dR}{dt} = \gamma I$$
$$S + I + R = N$$

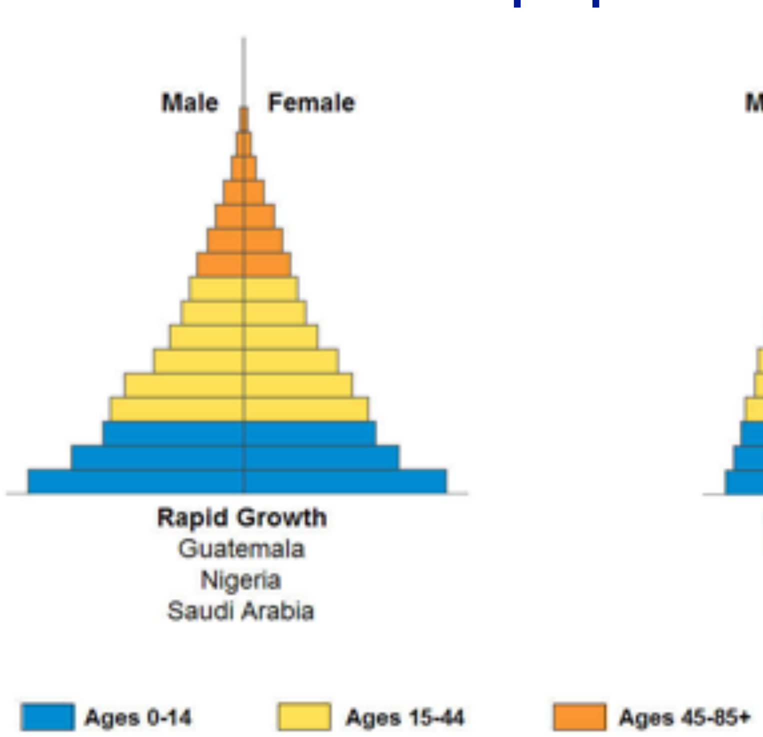
β : infection rate γ : recover rate

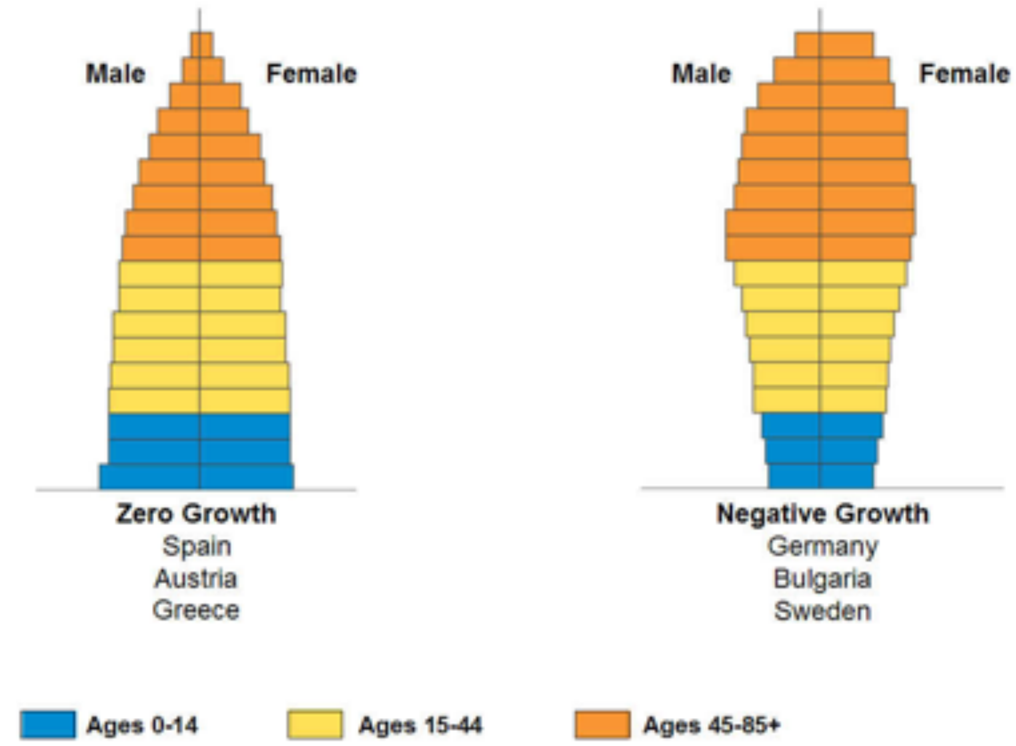


National Institute of Allergy and Infectious Diseases

A few more complications:

- structured population: e.g. age





b = 1.5 - 3%; Rapid Growth   b = 0.3 - 1.4 %; Slow Growth   b = 0 - 0.2%; Zero Growth   b < 0 Negative Growth

$$N(t) \Rightarrow \int_0^\infty n(a,t)da$$

$$\frac{\partial n(a,t)}{\partial t} + \frac{\partial n(a,t)}{\partial a} = -\mu(a,t)n(a,t)$$ McKendrick equation, 1926

A few more complications:

- stochastic description: (c.f. deterministic differential equations)
  - each individual has a certain **probability** to give birth or die
  - what is the probability to find $N(t)$ starting with N_0 ,
    i.e. need a probability distribution $P(N(t))$.

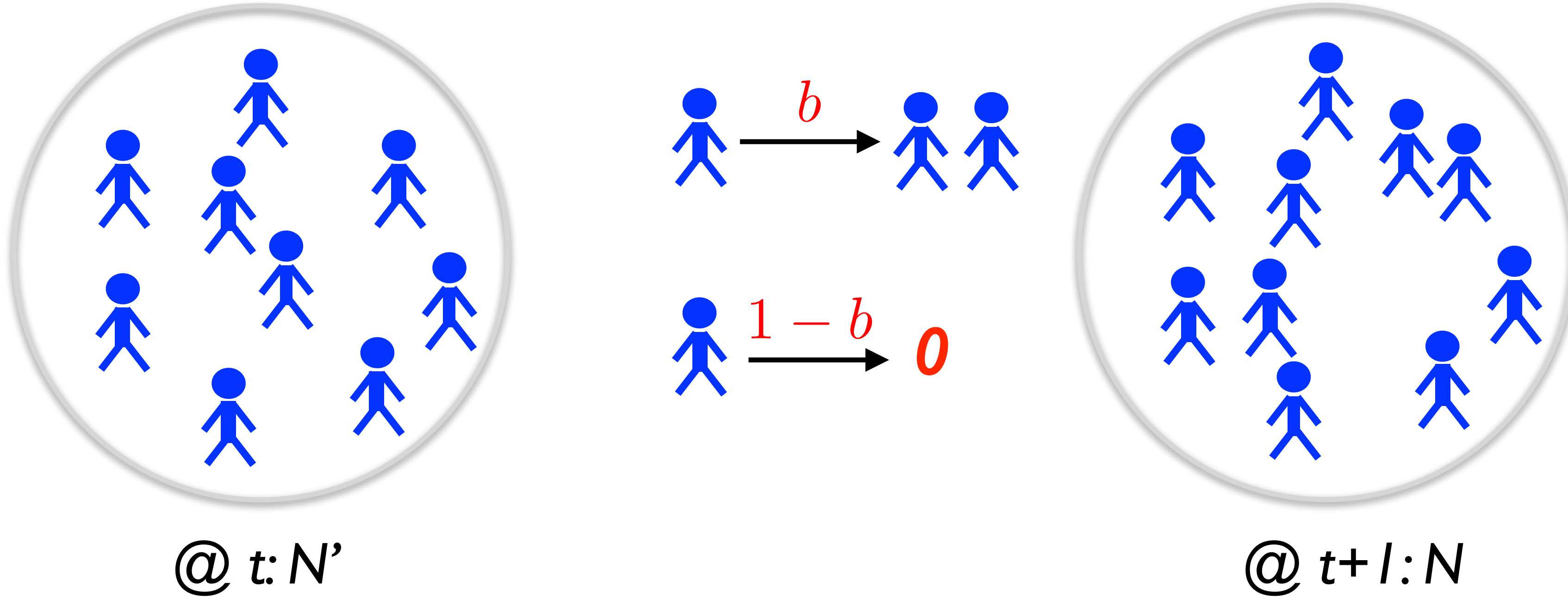
master equation

$$P(N, t+1) = \sum_{N'} P(N', t) W(N' \to N)$$

transition probability from N' individuals to N

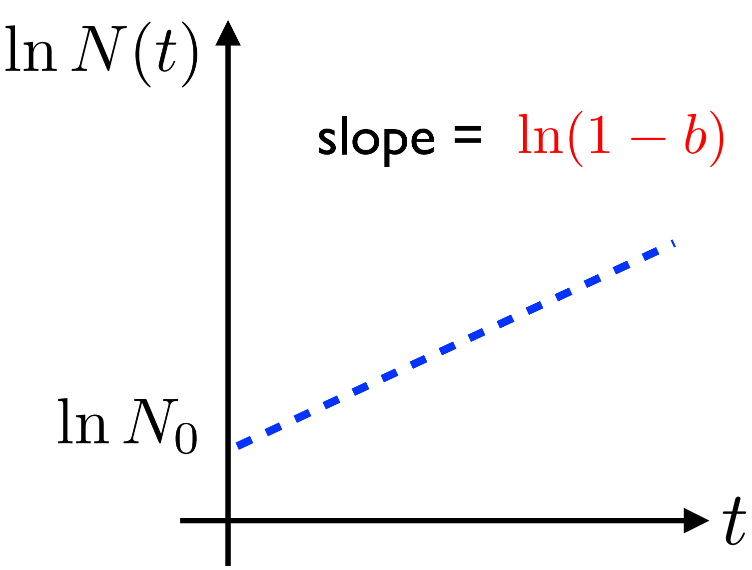
$$1 = \sum_{N'} W(N' \to N)$$

Example:



$$W(N' \to N) = \sum_k \binom{N'}{k} b^k (1-b)^{N'-k} \delta_{N,N'-k}$$ Kronecker delta function

$$\langle N \rangle_{t+1} \equiv \sum_N N \cdot P(N, t+1) = \sum_{N'} P(N', t) \sum_N N \cdot W(N' \to N)$$



recover Malthusian Model *and*

- fluctuations: $\langle (N - \langle N \rangle)^2 \rangle$
- correlations: $\langle N_t \cdot N_{t'} \rangle$

$$\delta_{N,N'-k} = \begin{cases} 1 & : N = N' - k \\ 0 & : N \neq N' - k \end{cases}$$

a tale of *host and parasites:*

birth, death, and migration

parasites and single stationary host:

fleas: birth + death + migration

Some flea ecology:

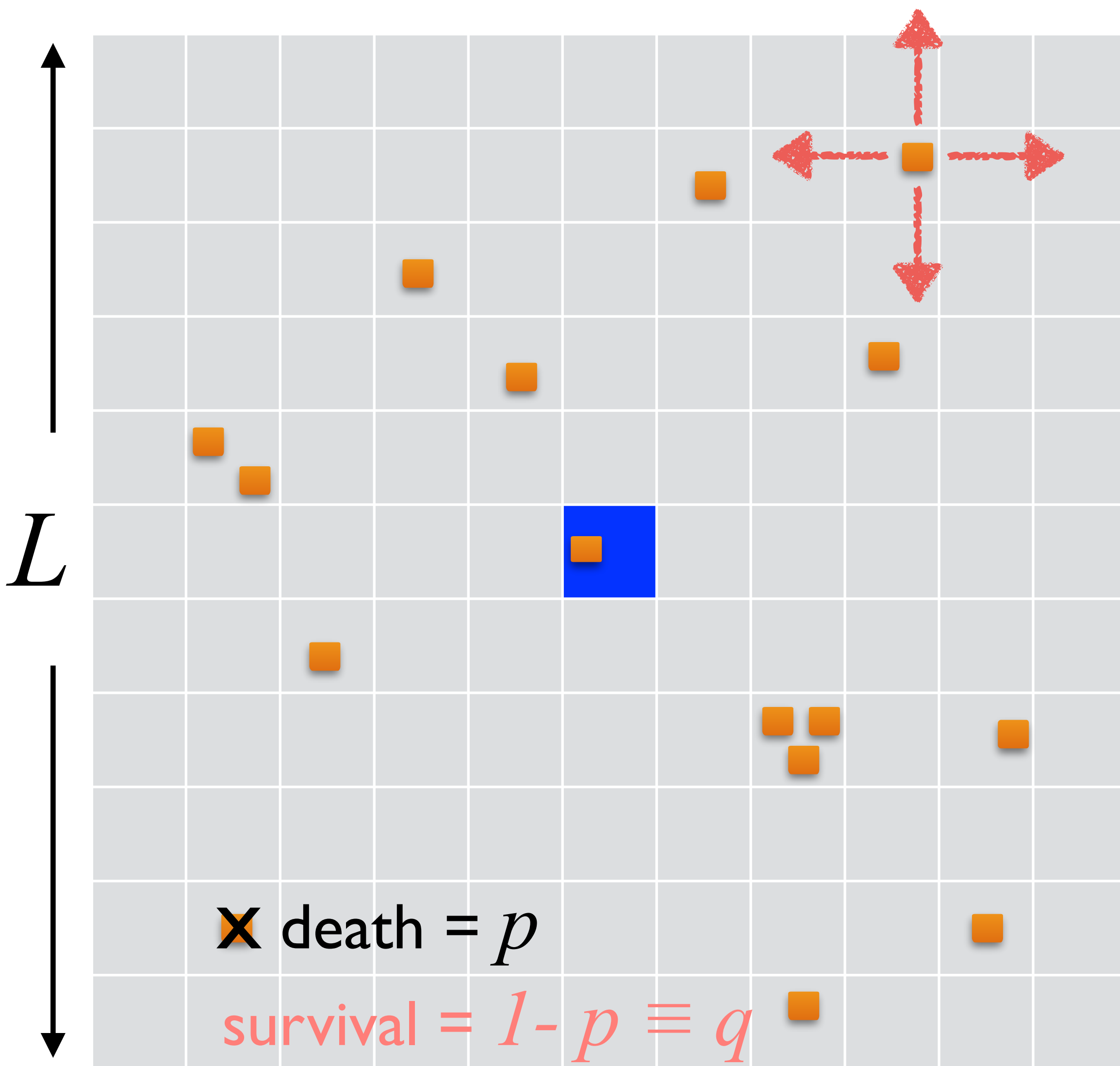
- reproduction requires blood from the host ➡ physical contact
- life cycle of parasites ≪ life cycle of host

Questions: (for a curious theoretical physicist)

1. What happens in long times (steady state distribution)?
   - How long will it take for fleas to die out? (or do they ever?)
   - How does such transition depend on parasites' life cycle and migration?
   - How do the host's location and motion affect this distribution?
2. What if multiple hosts are introduced?

… …

parasites and single stationary host:



periodic boundary condition

fleas

distribution	$\rho(\vec{r}, t)$
death *survival*	p $q \equiv 1 - p$
birth	$B = B_0 V(\rho)$

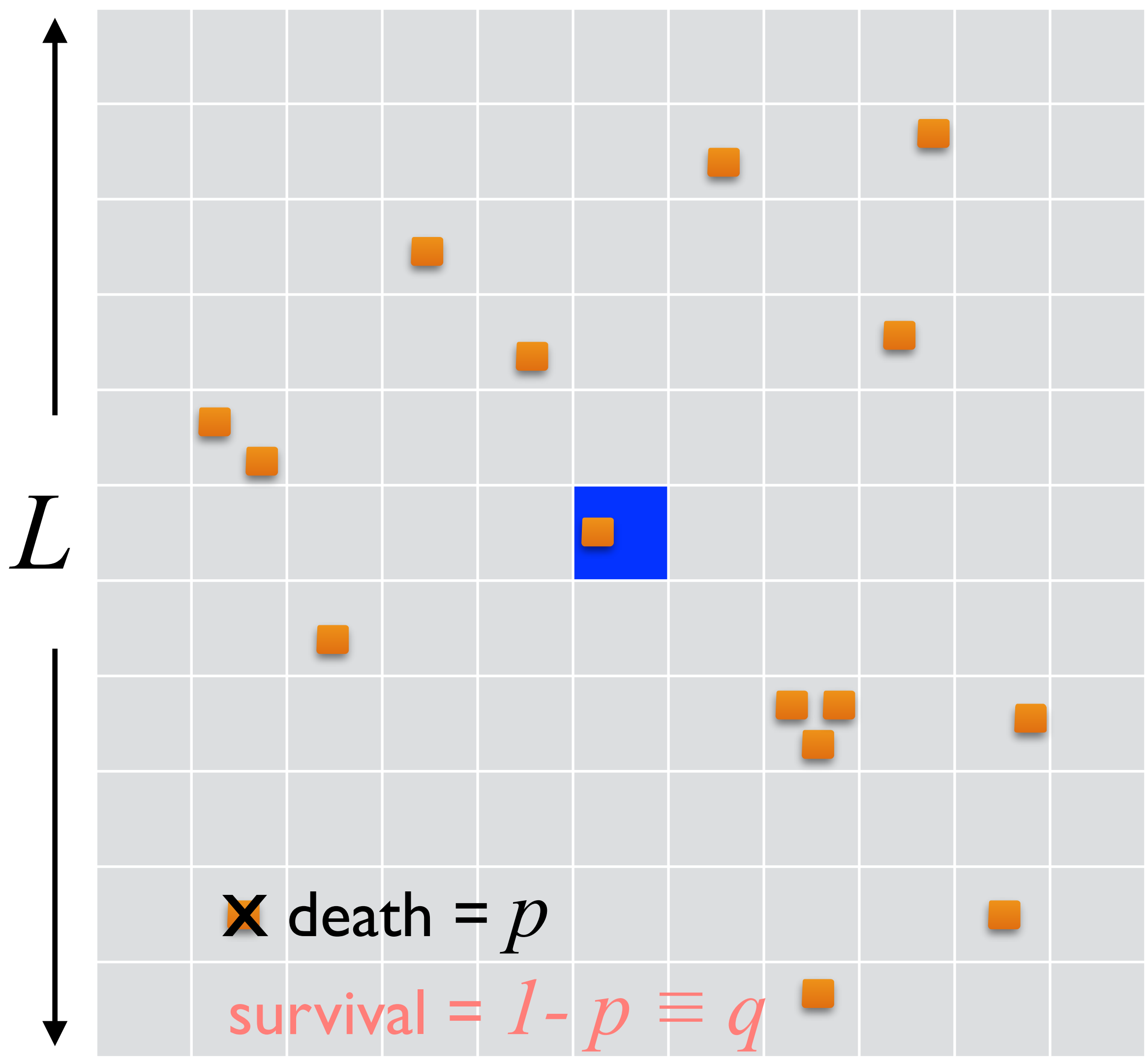
only occurs on cat

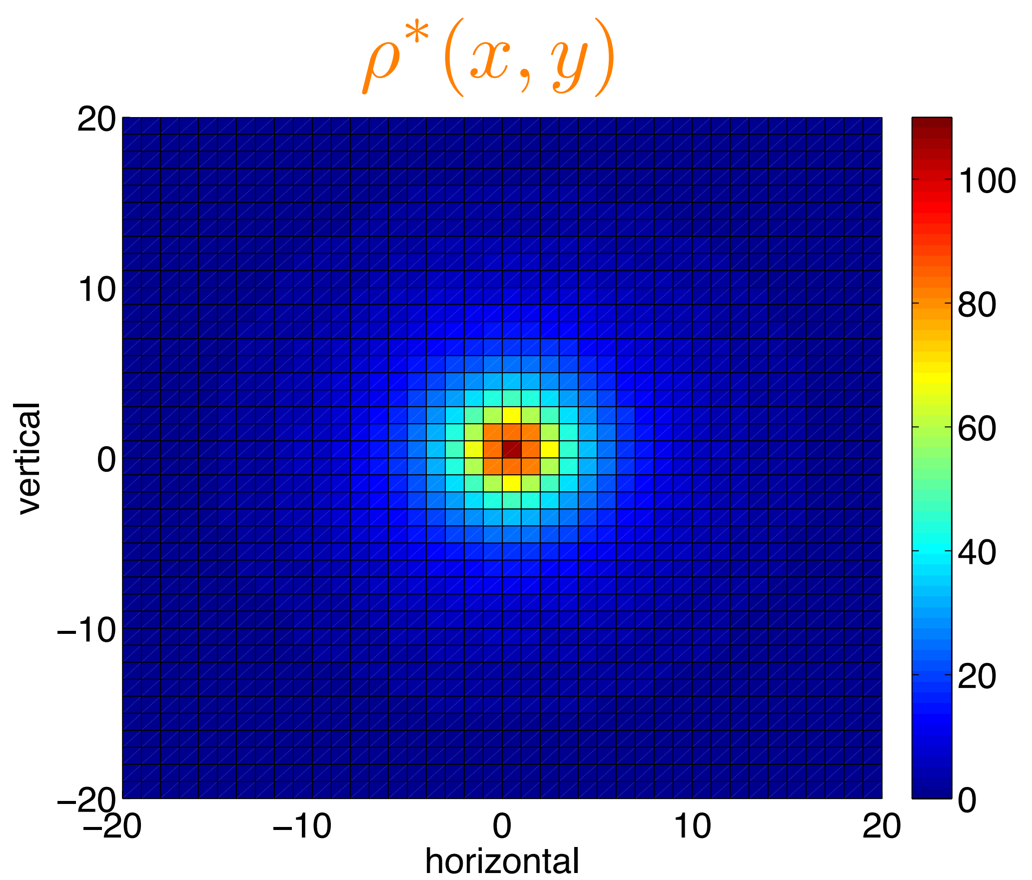
fecundity (B_0)

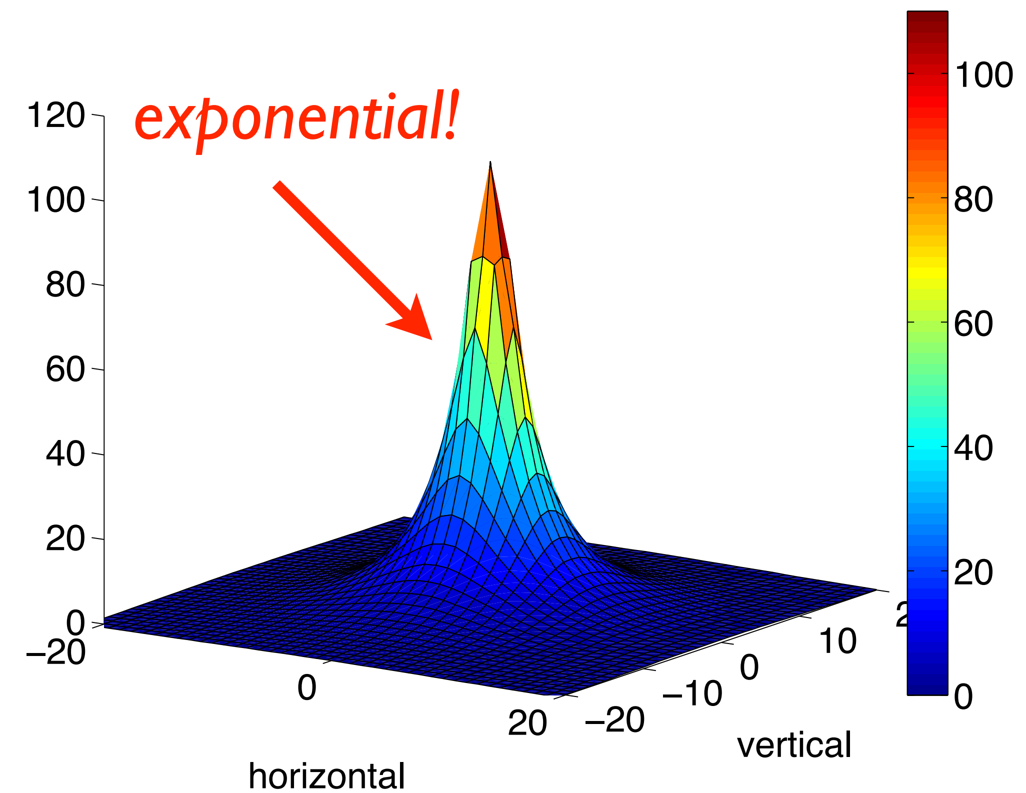
Verhulst factor, dep. on local density (ρ), carrying capacity (K) … ($V(\rho)$)

e.g. $B = B_0 \exp(-\rho/K)$

no bias — simulation results







$p = 0.01;\ B_0 = 2.5;\ K = 100$

no bias — theoretical understanding

continuous equation: $$\frac{\partial \rho(\vec{r},t)}{\partial t} = \underbrace{D\nabla^2 \rho(\vec{r},t)}_{\text{wander}} + \underbrace{b(\vec{r},\vec{r}_{\mathrm{h}},t)}_{\text{birth}} - \underbrace{p\rho(\vec{r},t)}_{\text{death}}$$

d = 2: $$b(\vec{r},\vec{r}_{\mathrm{h}},t) = \delta(\vec{r}-\vec{r}_{\mathrm{h}}) \cdot a^2 \cdot \rho(\vec{r},t) \cdot B_0 \exp\left(-\frac{\rho(\vec{r},t)}{K}\right)$$

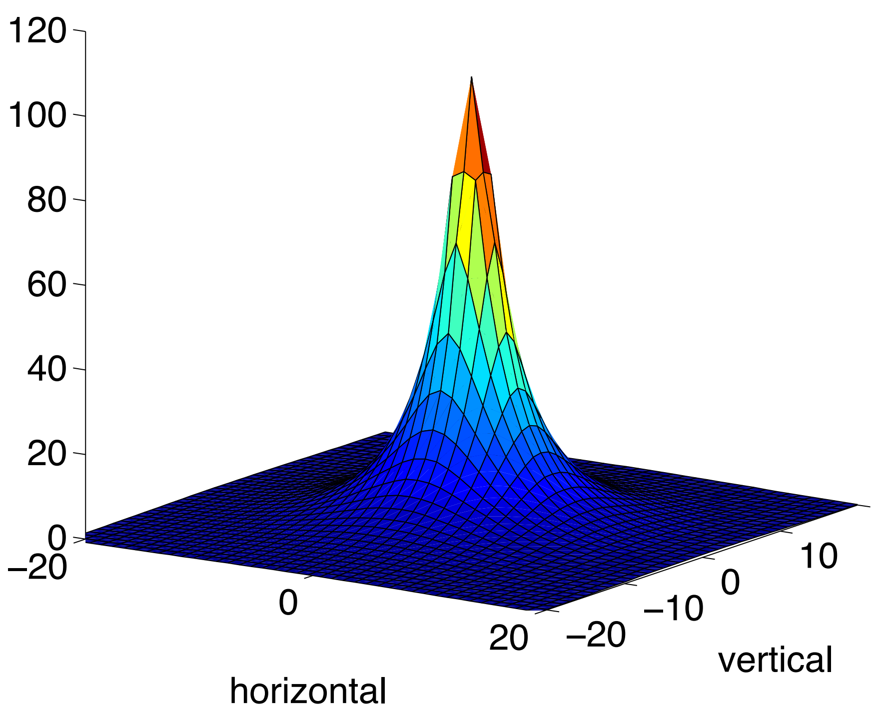
steady state $\frac{\partial \rho(\vec{r},t)}{\partial t} = 0$:

for parasites NOT on host: $(D\nabla^2 - p)\rho^*(\vec{r}) = 0$

$$\longrightarrow \rho^*(\vec{r}) \sim e^{-r/r_0} = e^{-r/\sqrt{D/p}}$$

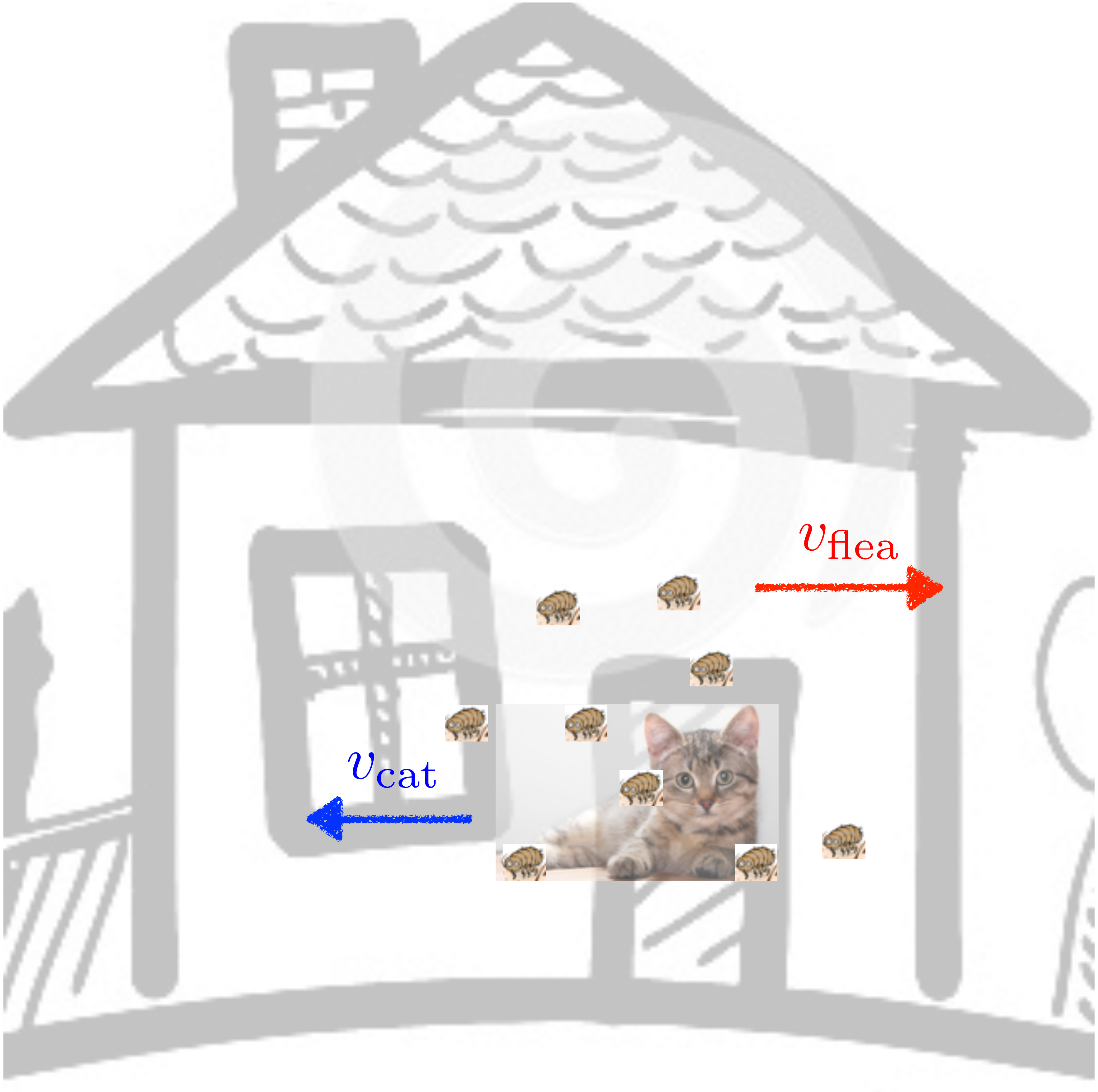
r_0: how far do you wander before you die

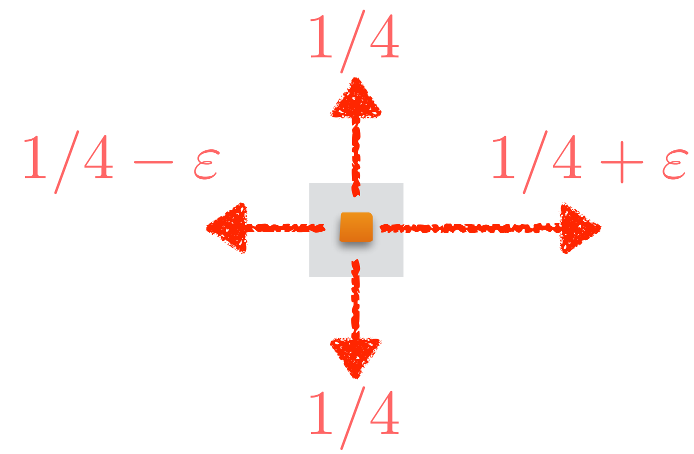
for $p = 0.01, D = 1/2d = 1/4 \Rightarrow r_0 \sim 5$



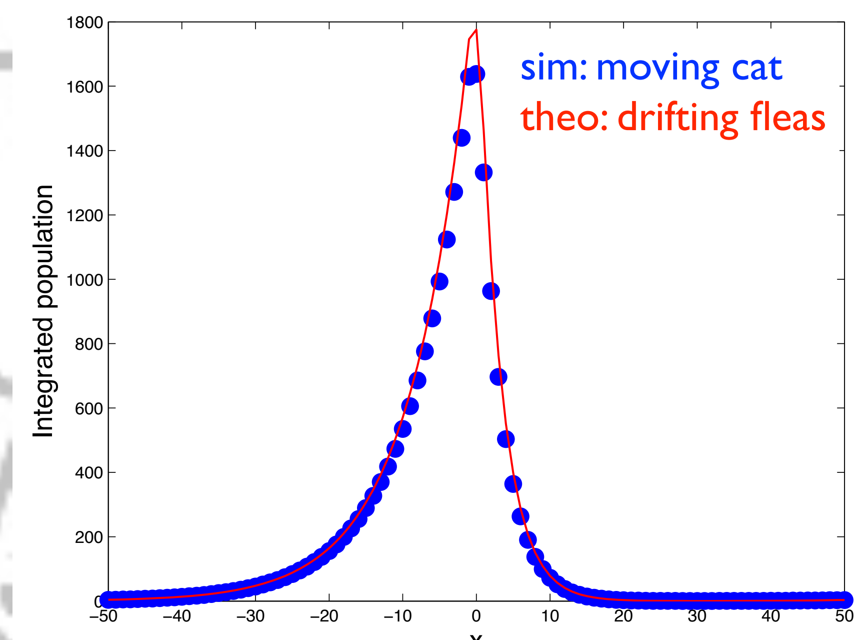
in *d*=3: $(\nabla^2 - \lambda)\underbrace{U^*(\vec{r})}_{\text{Yukawa potential}} = 0$

parasites and moving host:





$$v_{\text{flea}} = 2\varepsilon$$



with bias — theoretical understanding

discrete equation: $\rho(\vec{x}, t+1) = \frac{1}{2d}\sum_{\vec{a}} \rho(x, \vec{y}+\vec{a}, t)\,[q + B\delta(\vec{y}+\vec{a})\delta(x)]$

$$+ \frac{1}{2d}\sum_{\tau=\pm 1} \rho(x+\tau, \vec{y}, t)\,[q(1+\tau\varepsilon) + B\delta(x+\tau)\delta(\vec{y})]$$

live + wander | birth

steady state
Fourier transform

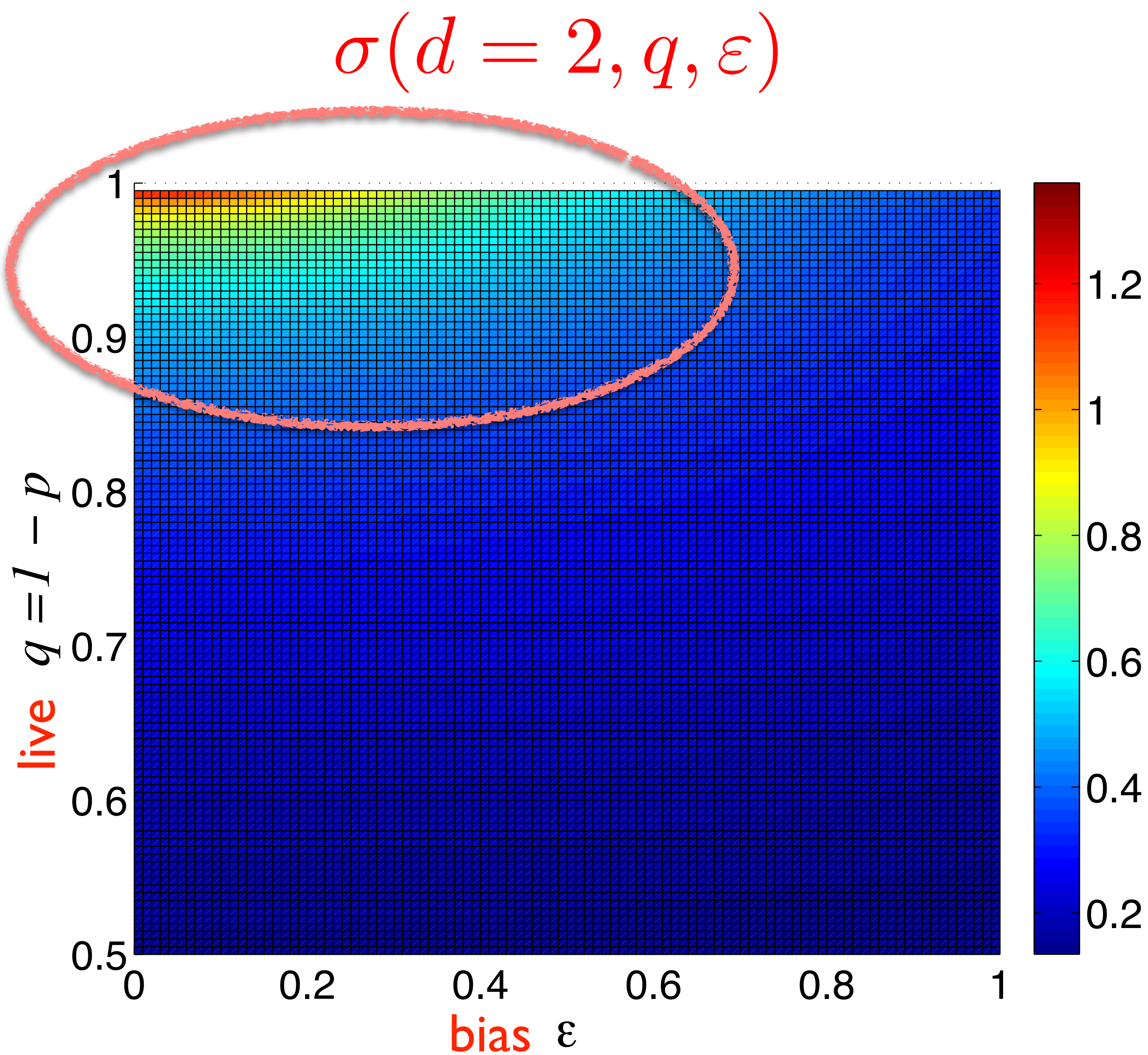
$$\rho_0^* = \rho_0^* B(\rho_0^*)\sigma(d, q, \varepsilon)$$

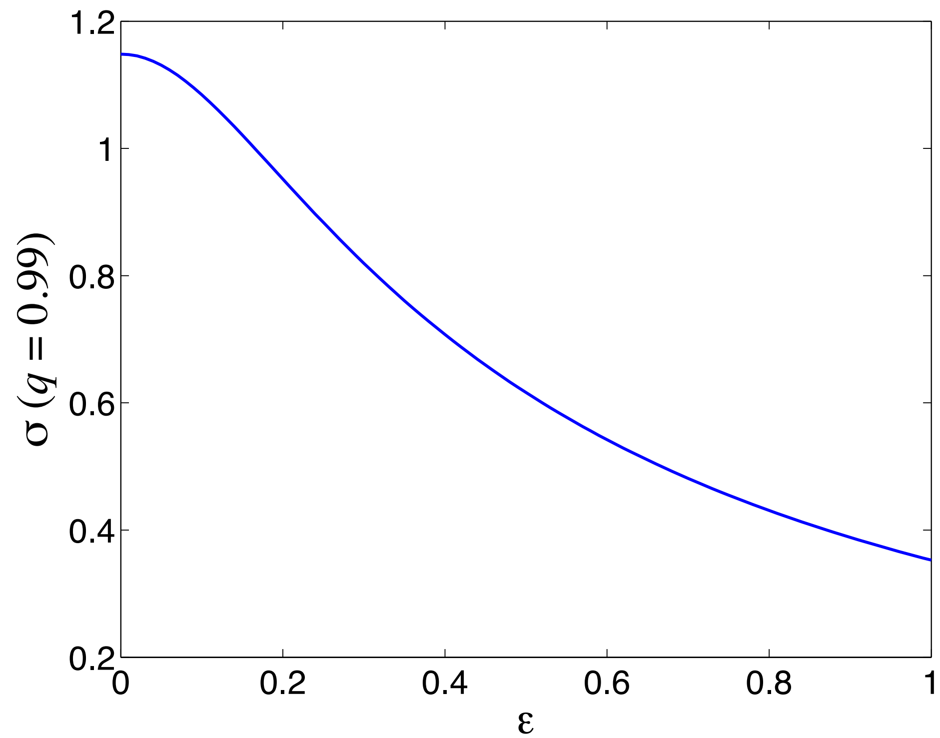
- extinction when $\rho_0^* = 0$
- survival if: $B(\rho_0^*)\sigma(d, q, \varepsilon) = 1$

  tot. flea population $N_{\text{tot}} = \tilde{\rho}^*(\vec{0}) = B\frac{\rho_0^*}{1-q}$

$\rho_0^* \equiv \rho^*(\vec{0})$ $\quad \sigma(d, q, \varepsilon) = \frac{1}{L^2}\sum_{\vec{k}} \frac{A(k, \vec{p})}{d - qA(k, \vec{p}) + i\varepsilon q \sin ka}$ $\quad A(k, \vec{p}) = \cos ka + \sum_{i=2}^{d} \cos p_i a$

Parsing survival condition: $B(\rho_0^*)\sigma(d,q,\varepsilon) = 1$

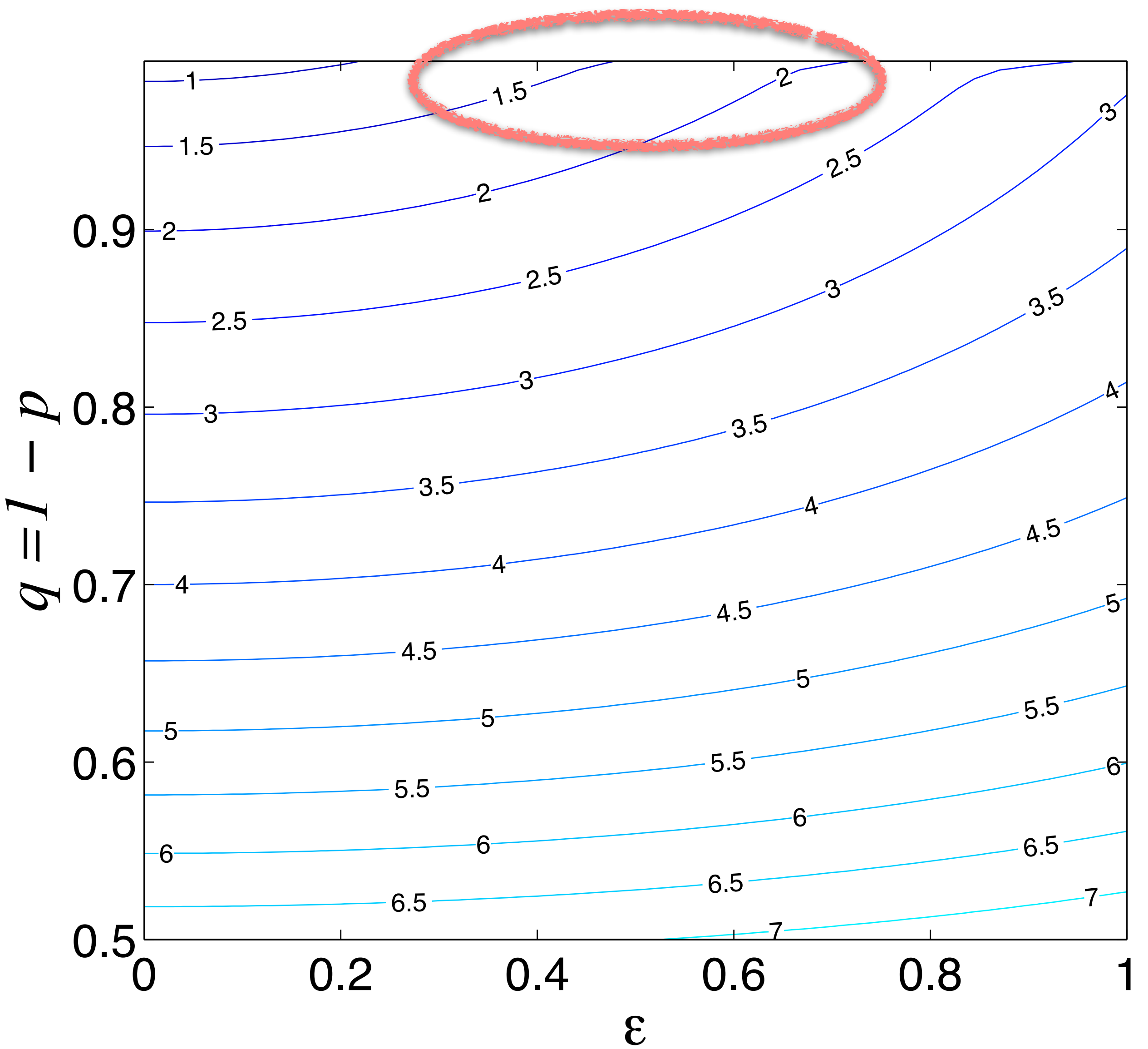




$$\sigma(d,q,\varepsilon) = \frac{1}{L^2}\sum_{\vec{k}} \frac{A(k,\vec{p})}{d - qA(k,\vec{p}) + i\varepsilon q \sin ka}$$

Parsing survival condition: $B(\rho_0^*)\sigma(d,q,\varepsilon) = 1$

$$B_{\min} = 1/\sigma$$



- minimum birth to survive

$$\sigma(d,q,\varepsilon) = \frac{1}{L^2}\sum_{\vec{k}} \frac{A(k,\vec{p})}{d - qA(k,\vec{p}) + i\varepsilon q \sin ka}$$

total parasite population

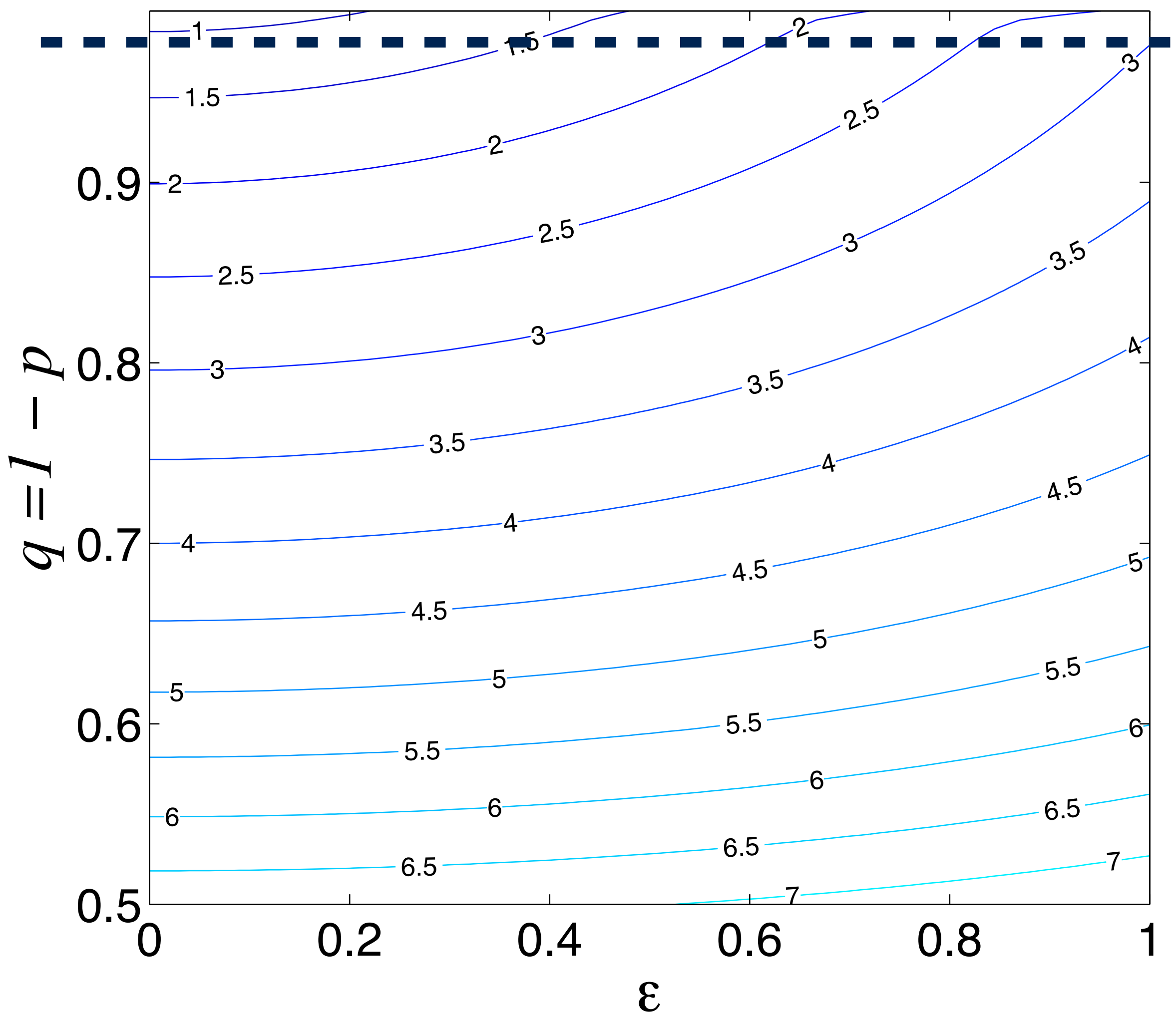
$$N_{\rm tot} = \frac{\rho_0^*}{\sigma(1-q)}$$

with survival condition

$$B(\rho_0^*)\sigma(d,q,\varepsilon) = 1$$

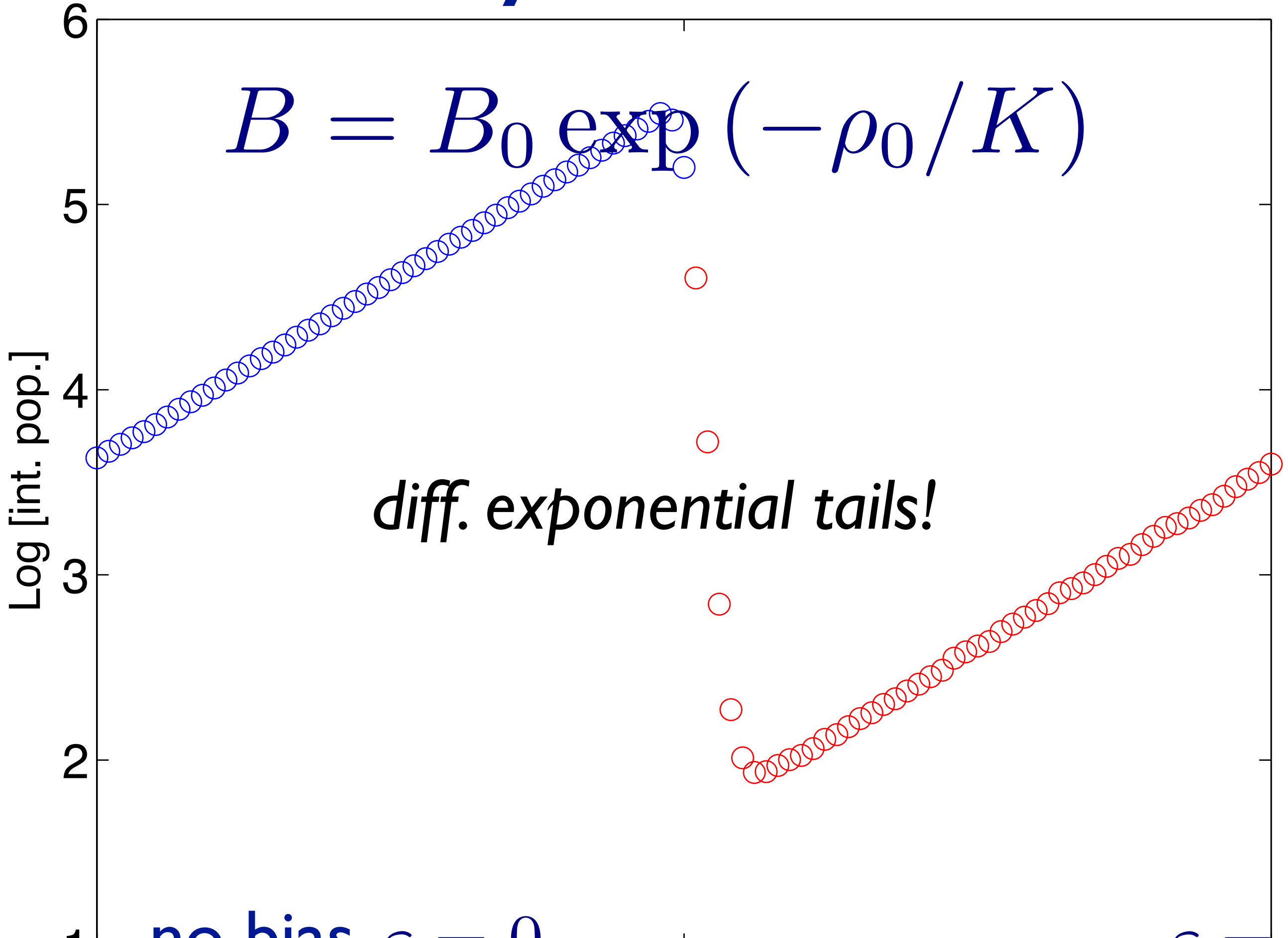
Q: How does bias affect total population?

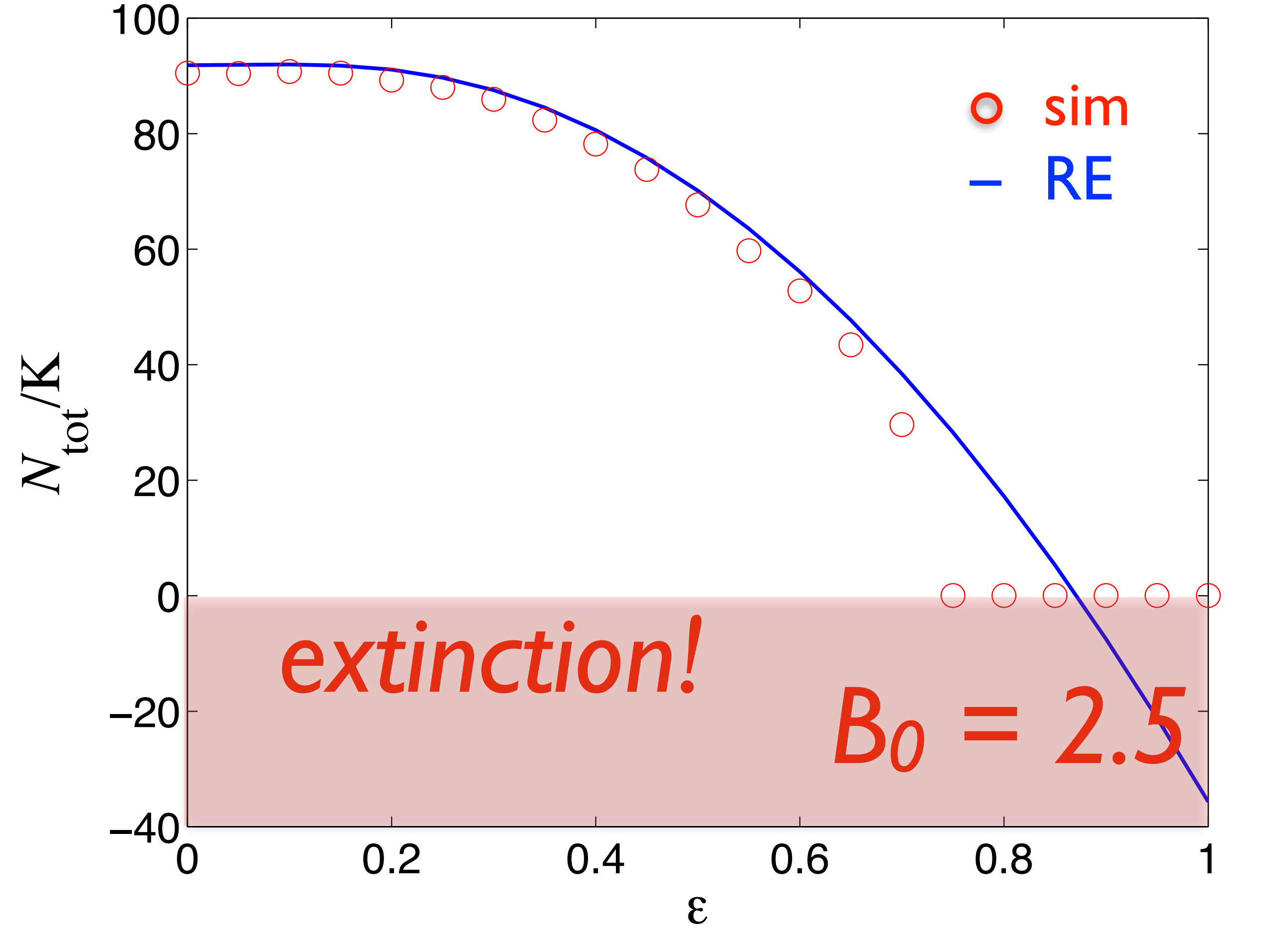
case study:
(*d*=2, *L*=101)



survival rate
q = 0.99

case study: d=2, L=101

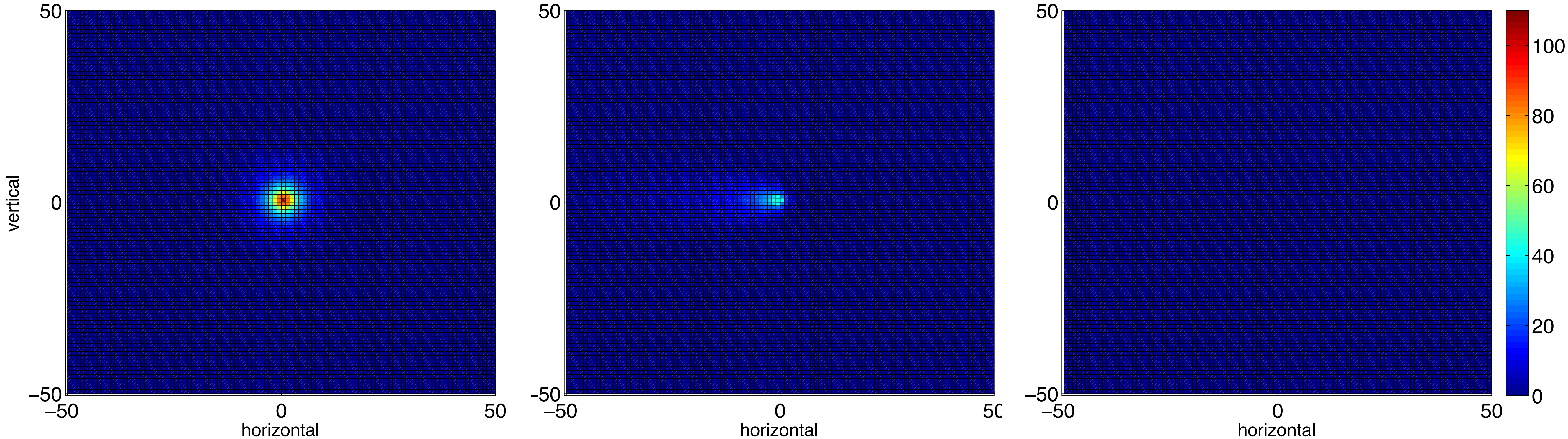




no bias $\varepsilon = 0$

$\varepsilon = 0.5$

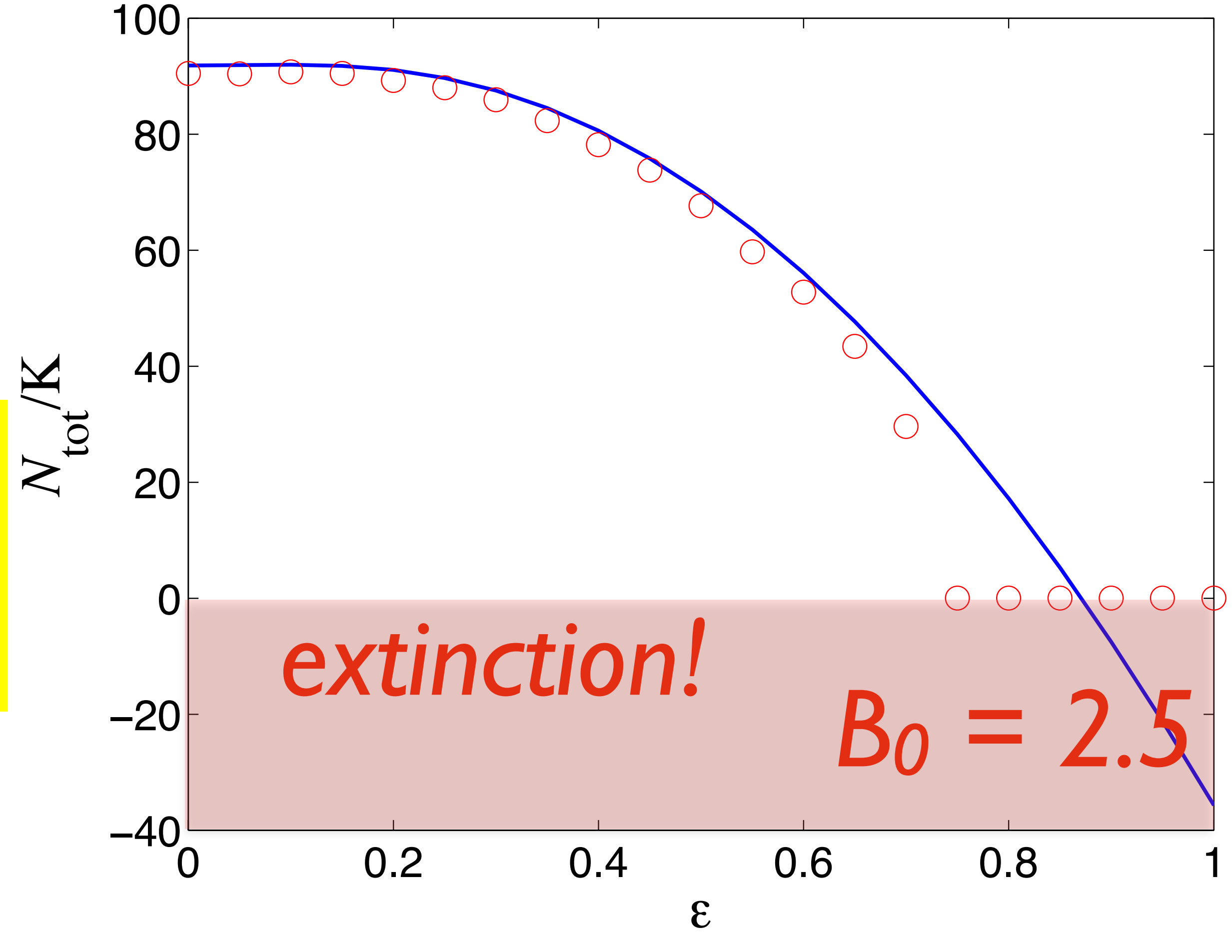
$\varepsilon = 0.85$



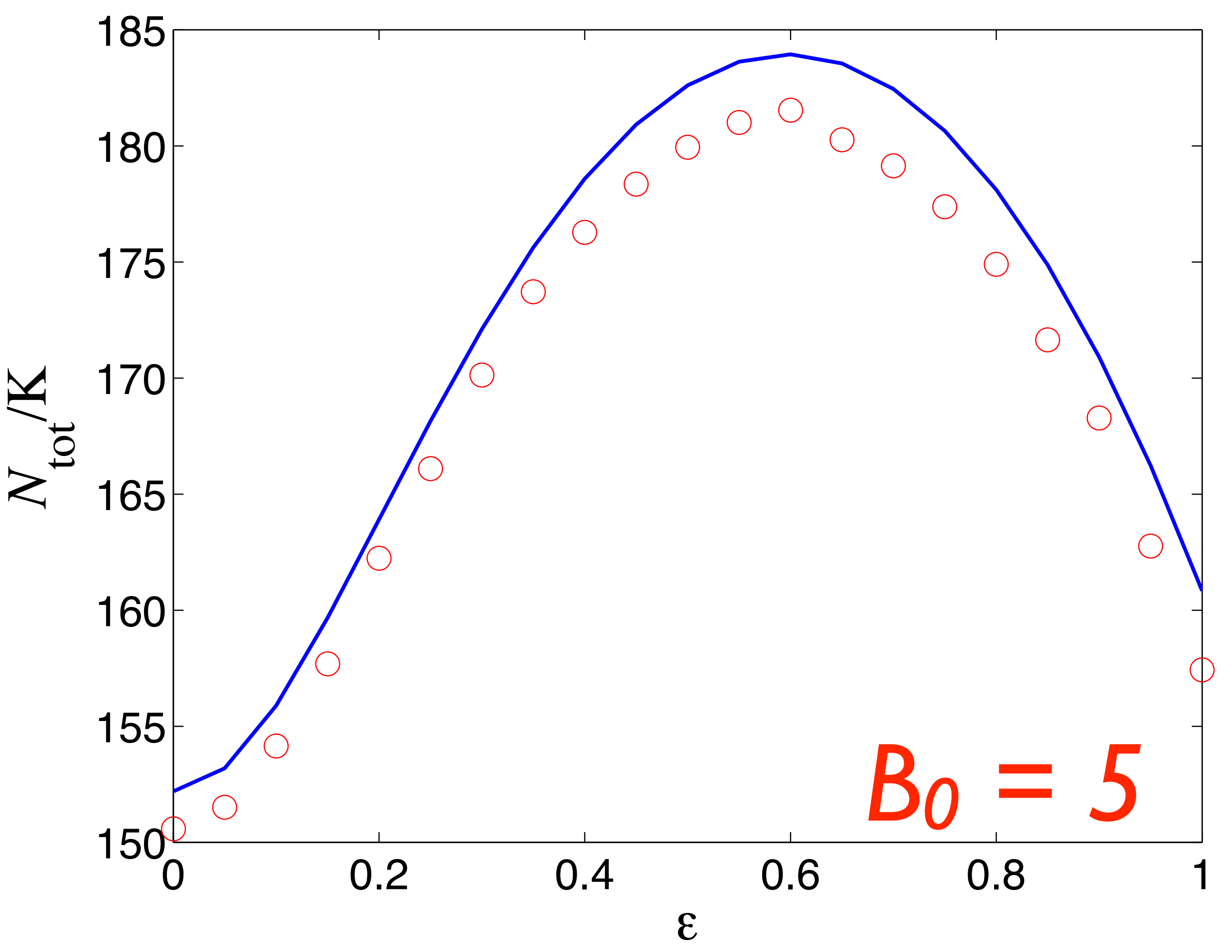
case study: d=2, L=101

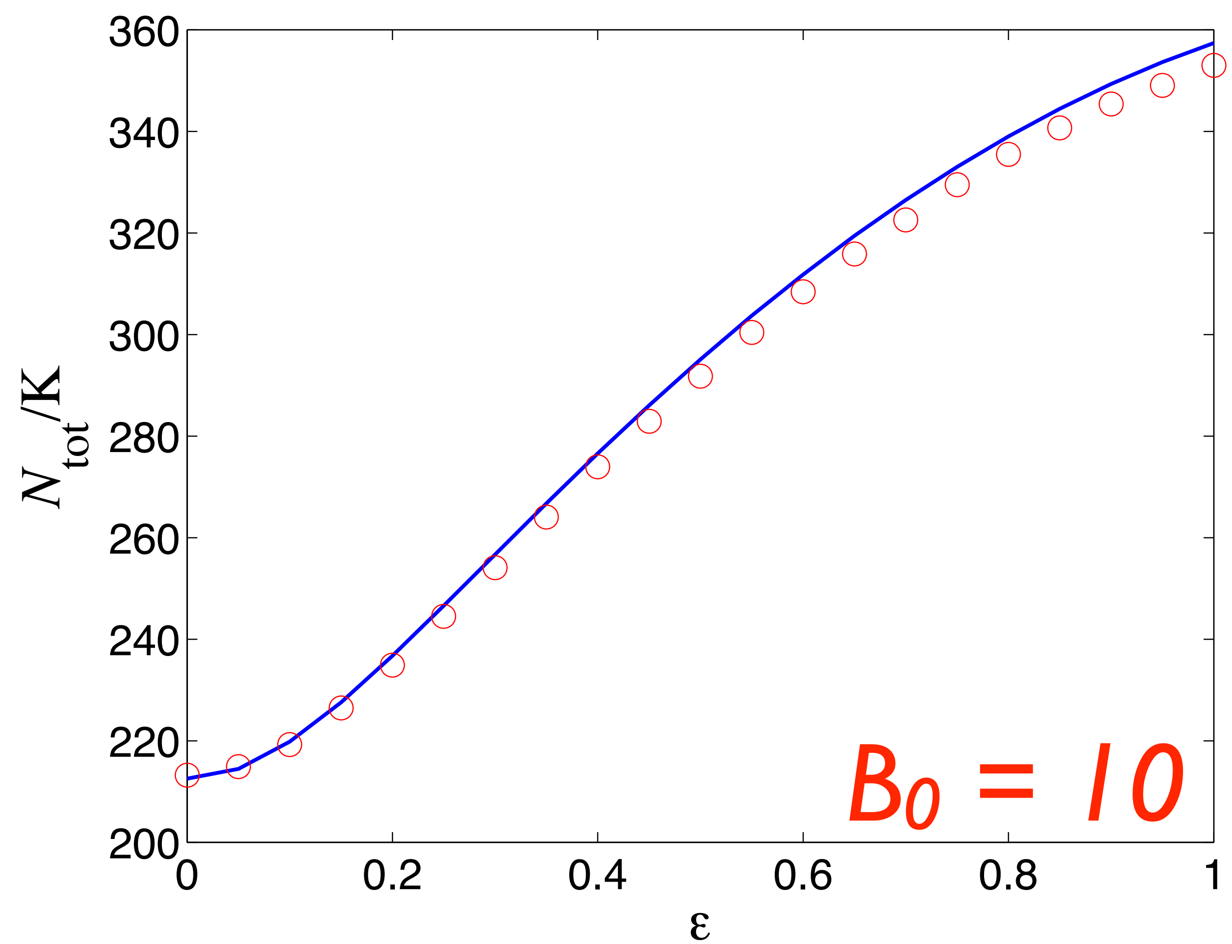
$$B = \boxed{B_0} \exp(-\rho_0^*/K)$$

Q: Is such monotonicity a general behavior?



non-monotonic!!





return to a *general* birth $B = B_0 V(\rho_0^*)$

- survival-extinction sheet $\sigma(d, q, \varepsilon)|_{\text{ext}} \cdot B(\rho_0^*) = 1$

$V(\rho_0^*) = 1/B_0\sigma$

$\rho_0^* = V^{-1}(1/B_0\sigma)$

$$N_{\text{tot}} = \frac{\rho_0^*}{\sigma(1-q)}$$

- condition for $N_{\text{tot, MAX}}$

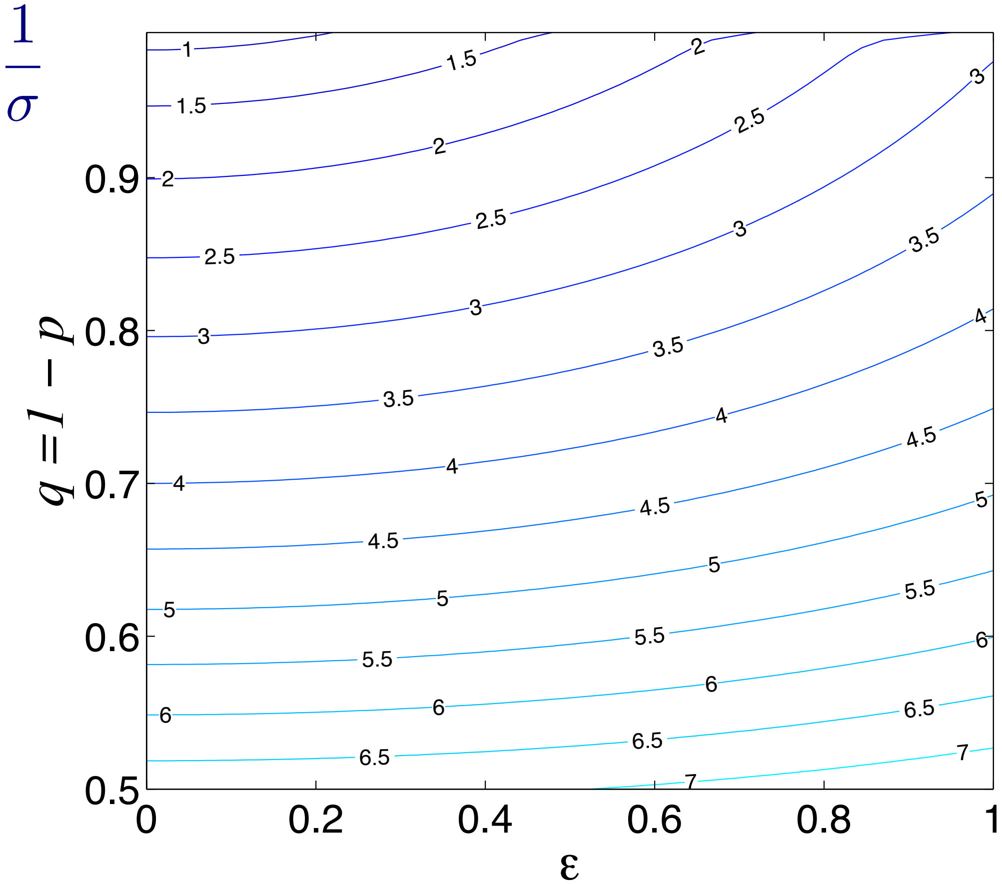
$$\frac{dN_{\text{tot}}}{d\varepsilon} = 0 \rightarrow -\frac{V'(\rho_0^*)}{V(\rho_0^*)} = \frac{1}{\rho_0^*}$$

example: $B = B_0 \exp(-\rho_0^*/K)$

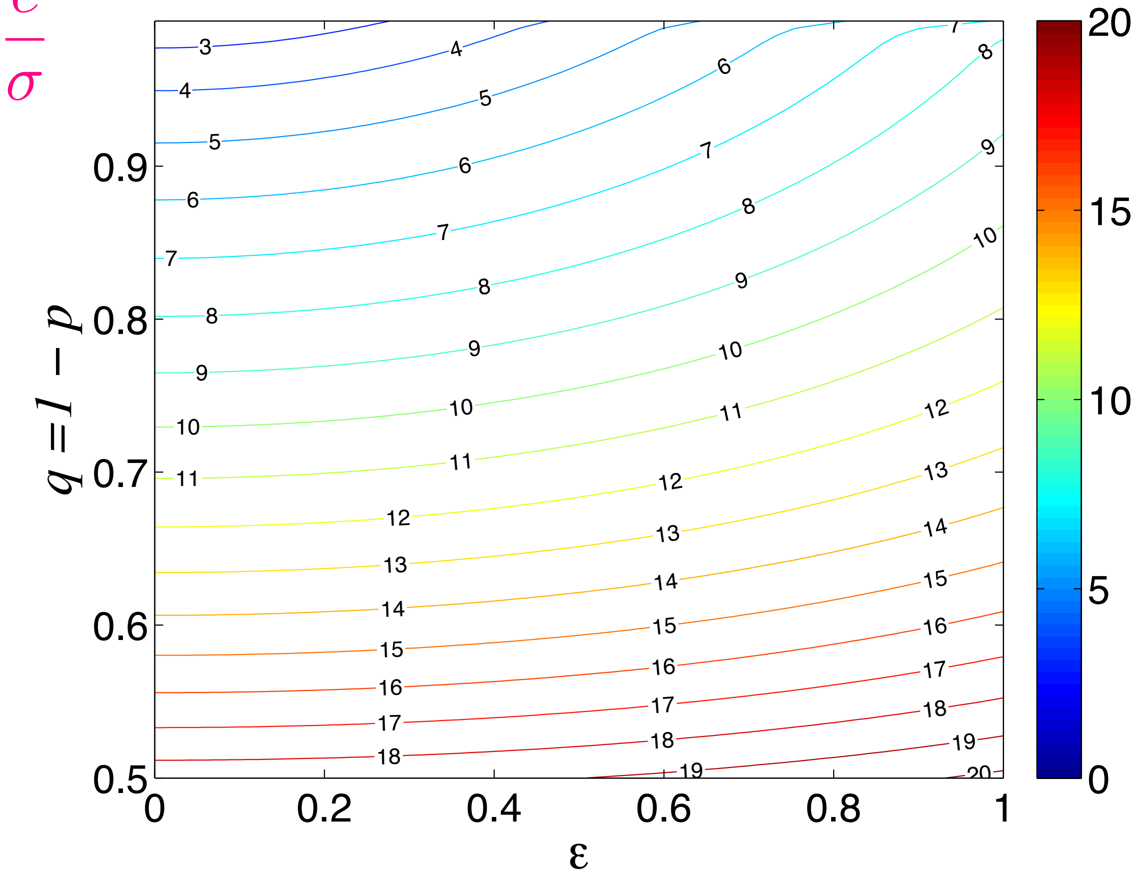
$\sigma B_0 = e$

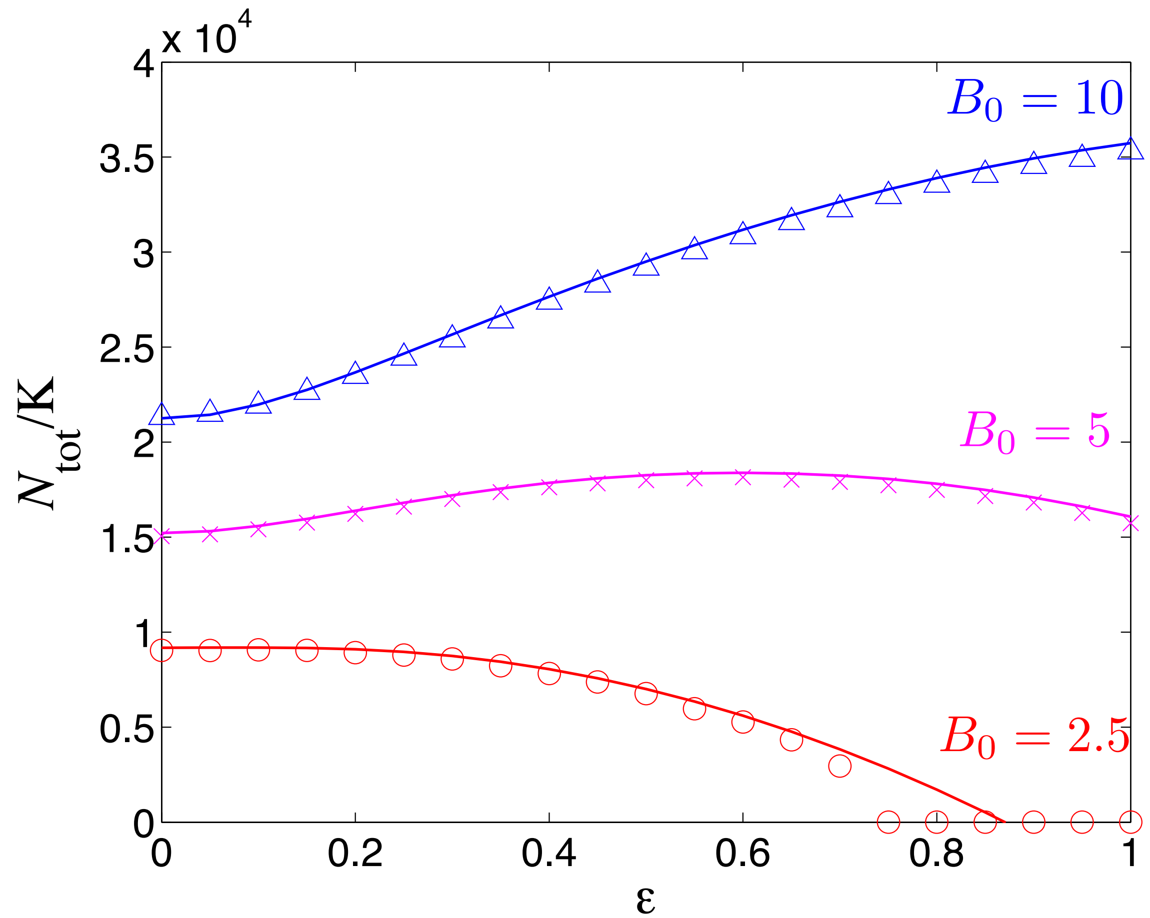
survival vs. prosperity

$B_0 = \frac{1}{\sigma}$



$B_0 = \frac{e}{\sigma}$

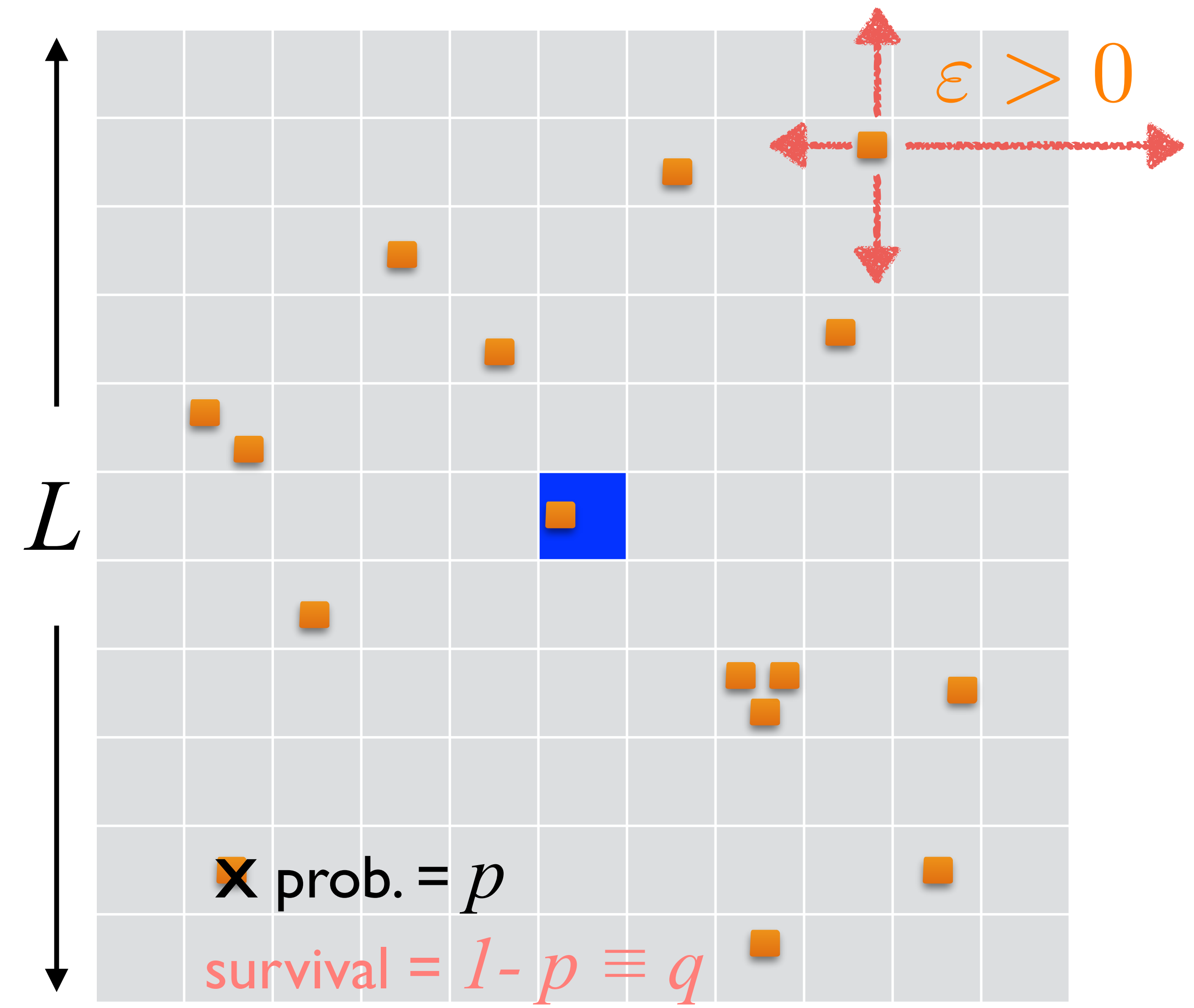




summary

- PH model: biased diffusion+b/d
  - survival vs. prosperity
  - general non-monotonicity

- ongoing explorations:
  - “dumb” vs “smart” host
  - multiple hosts, flea spatial distribution



periodic boundary condition

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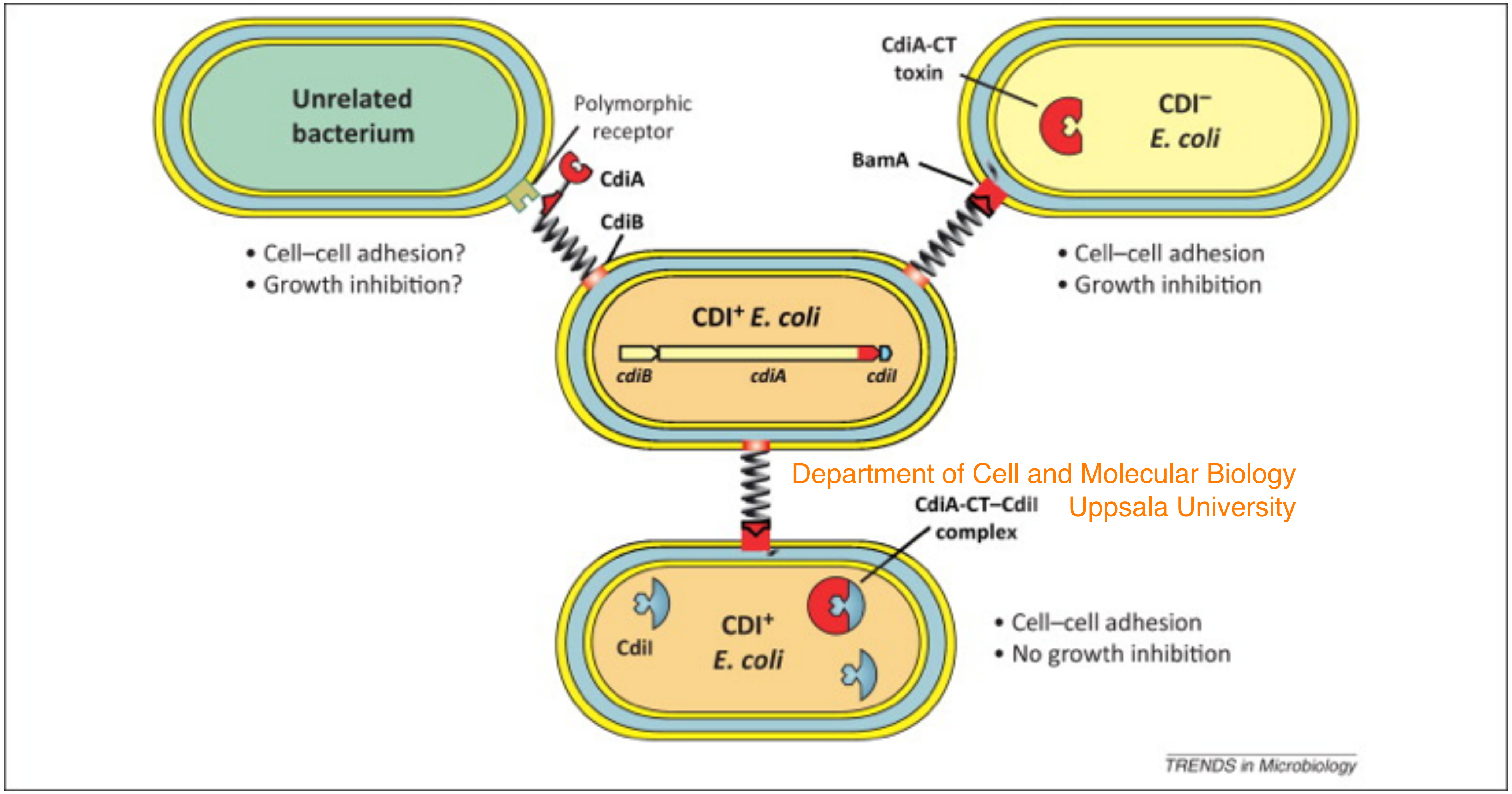
arXiv:1506.07624

Contact Dependent Inhibition in bacteria:



Department of Cell and Molecular Biology
Uppsala University

Bacterial contact-dependent growth inhibition

Zachary C. Ruhe, David A. Low and Christopher S. Hayes, Trends in Microbiology, 21, 5, 2013



Zach Ruhe,Sanna Koskiniemi, David Low
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