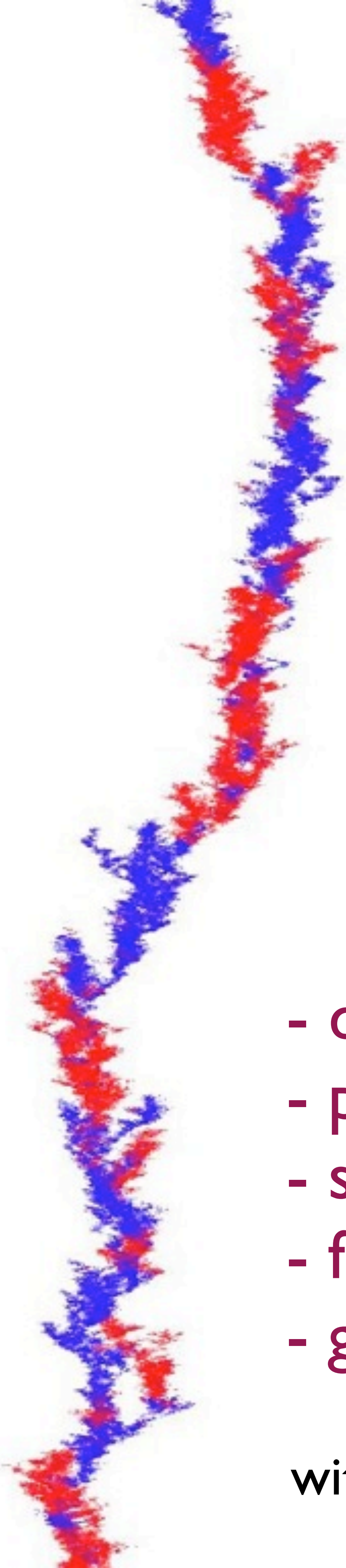


Who laughs last?

perturbation theory of games

Tibor Antal, Program for Evolutionary Dynamics, Harvard

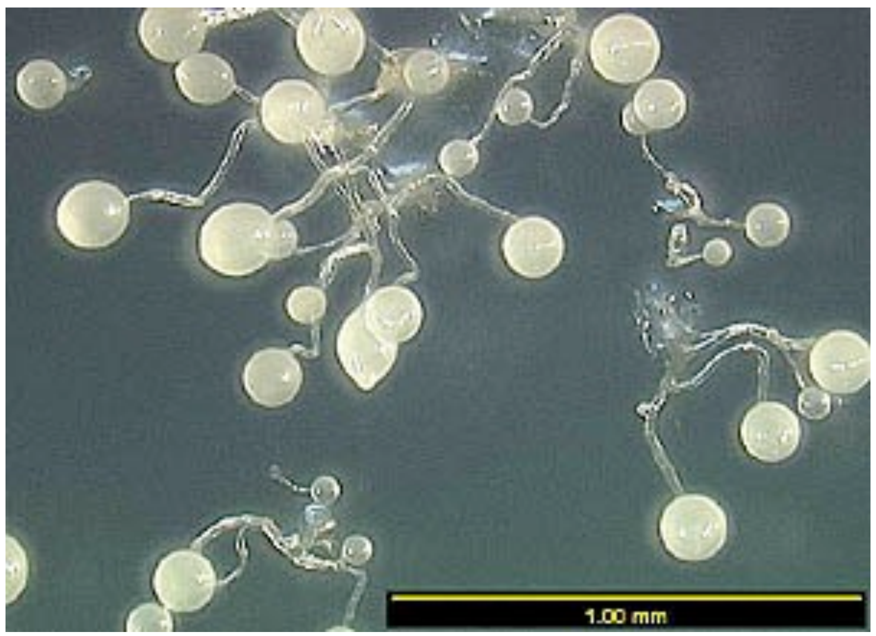
- dynamics, question
- perturbation method: two key aspects
- simplest case: well mixed 2*2
- further examples: n strategies, structured populations
- general results

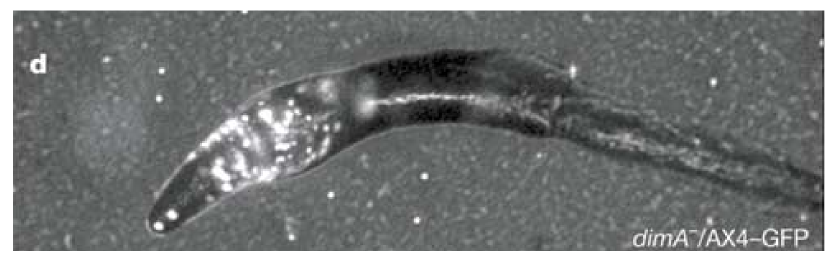
with: C Tarnita, H Otsuki, J Wakeley, P Taylor, A Traulsen, M Nowak

Cooperation

humans, bacteria, trees, slime molds, ...

Foster '04





Social amoeba fruiting bodies

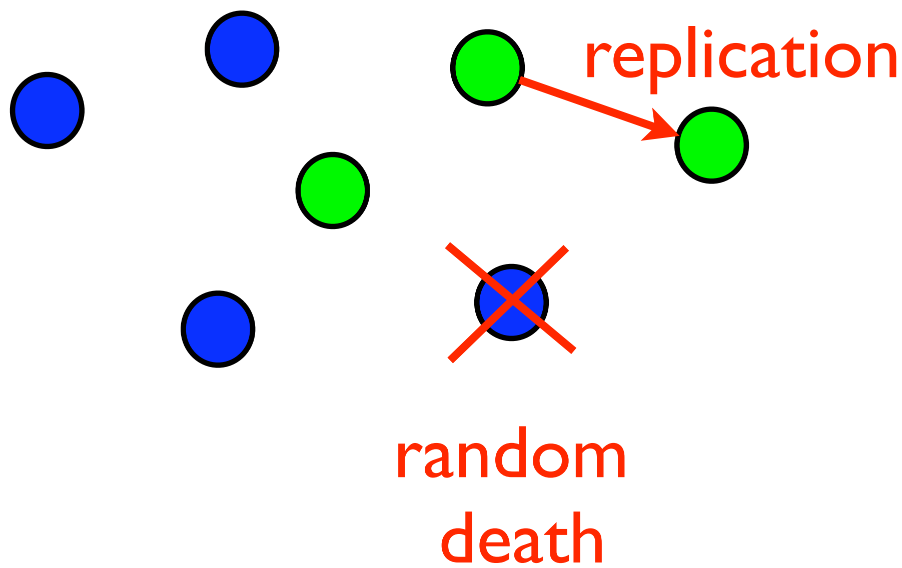
prisoner's dilemma

$$\begin{array}{cc} & \begin{array}{cc} \mathcal{C} & \mathcal{D} \end{array} \\ \begin{array}{c} \mathcal{C} \\ \mathcal{D} \end{array} & \begin{pmatrix} 10 & 1 \\ 11 & 2 \end{pmatrix}. \end{array}$$

defectors win!

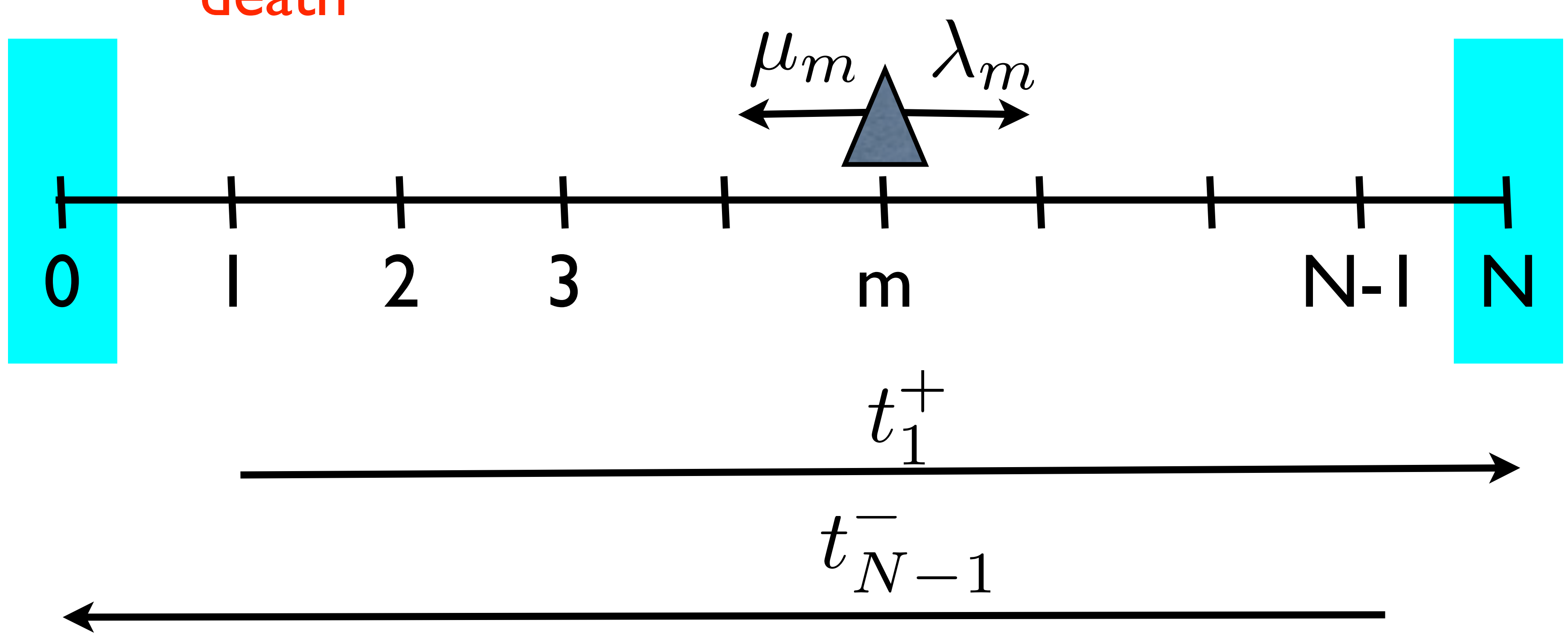
Evolutionary Dynamics

Moran process, N players



Game

		when playing against	
		A	B
payoff of	A	a_{11}	a_{12}
	B	a_{21}	a_{22}



$$\boxed{t_1^+ = t_{N-1}^-}$$

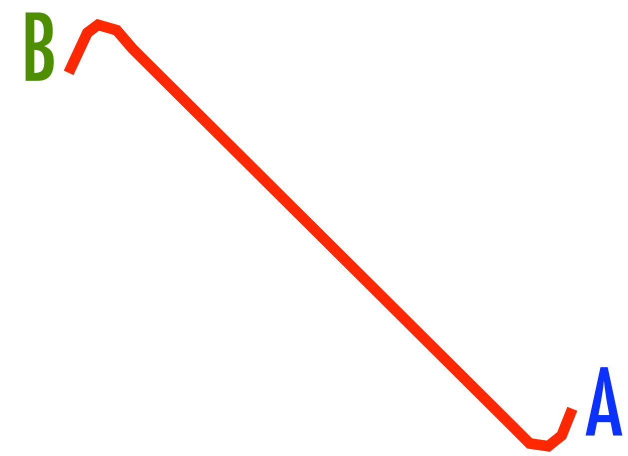
TA, Scheuring '06

What is the question?

Two strategies: A and B: Which one is better?

John Forbes Nash,
John Maynard Smith

fixation probabilities ...



Or: Which outnumbers the other in the long run?

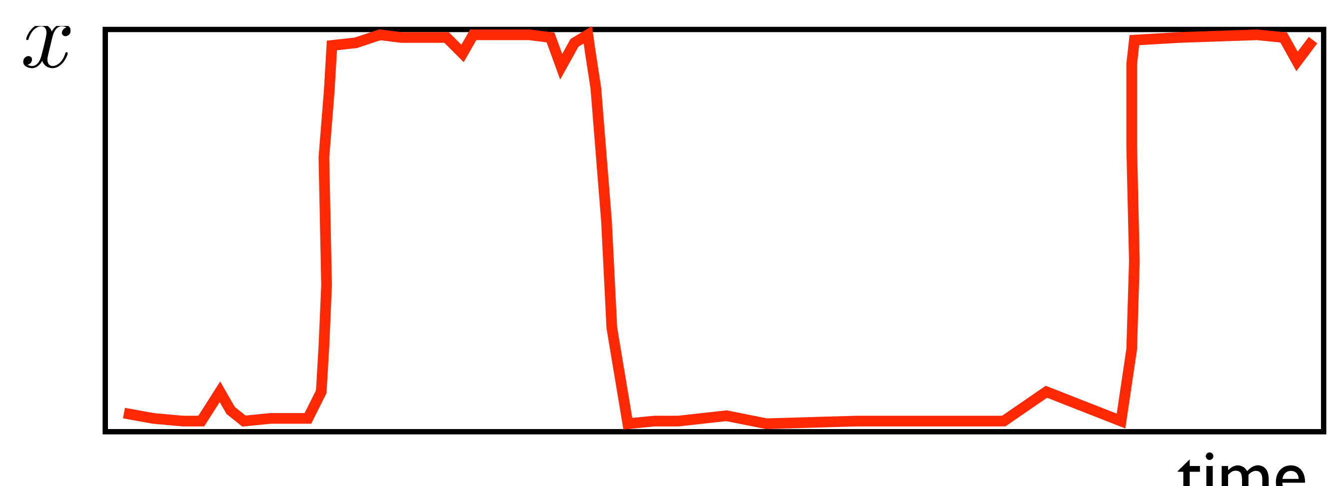
with two way mutation u

$$\langle x \rangle > 1/2$$

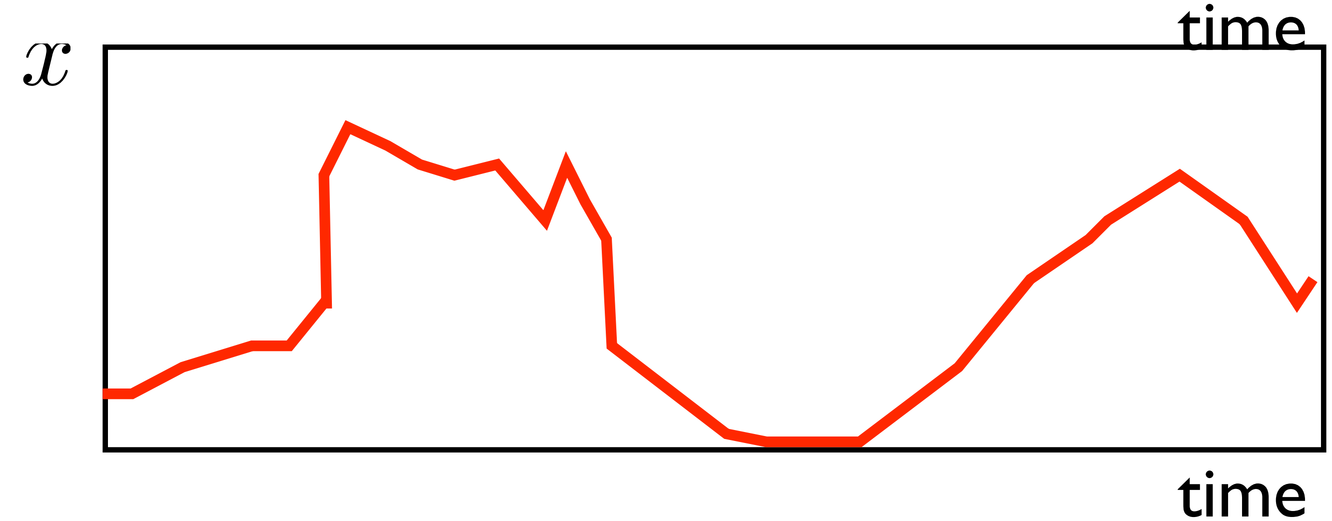
Kandori '93

$u \to 0$

fixation probabilities
$\rho_A > \rho_B$



general u



Perturbation method: 2 key points

Payoff = $1 + \delta \quad \times$ payoff of

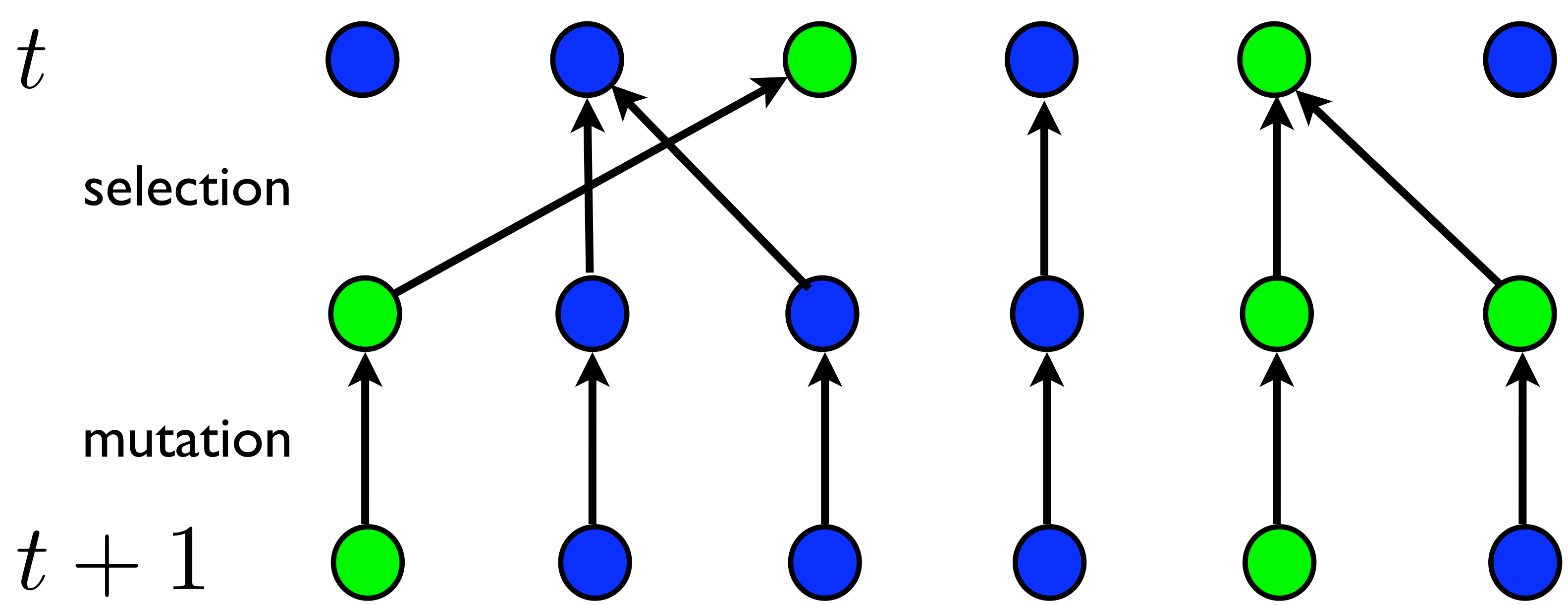
	when playing against A	B
A	a_{11}	a_{12}
B	a_{21}	a_{22}

x frequency of A

δ selection strength

u mutation probability

Wright-Fisher



Δx^{sel}

Δx^{mut}

$$\Delta x^{\text{tot}} = \Delta x^{\text{sel}} - \frac{u}{2}(x + \Delta x^{\text{sel}}) + \frac{u}{2}(1 - x - \Delta x^{\text{sel}})$$

$$\langle x \rangle = \frac{1}{2} + \frac{1-u}{u} \langle \Delta x^{\text{sel}} \rangle$$

$$\boxed{\langle x \rangle > \frac{1}{2} \iff \langle \Delta x^{\text{sel}} \rangle > 0}$$

Perturbation method: 2 key points

$$\text{Payoff} = \quad 1 + \delta \quad \times \quad \text{payoff of} \quad \begin{array}{c|cc} & \multicolumn{2}{c}{\text{when playing against}} \\ & A & B \\ \hline A & a_{11} & a_{12} \\ B & a_{21} & a_{22} \end{array}$$

x frequency of A

δ selection strength

u mutation probability

$$\boxed{\langle x \rangle > \frac{1}{2} \Longleftrightarrow \langle \Delta x^{\text{sel}} \rangle > 0}$$

Easy perturbation method for small δ

$$\langle \Delta x \rangle = \sum \Delta x_i \, \pi_i$$

$$\Delta x_i = 0 + \delta \Delta x_i^{(1)}$$

$$\pi_i = \pi_i^{(0)} + \delta \pi_i^{(1)}$$

$$\boxed{\langle \Delta x \rangle = \delta \sum \Delta x_i^{(1)} \, \pi_i^{(0)} + \mathcal{O}(\delta^2)}$$

neutral probabilities only !

Simplest example

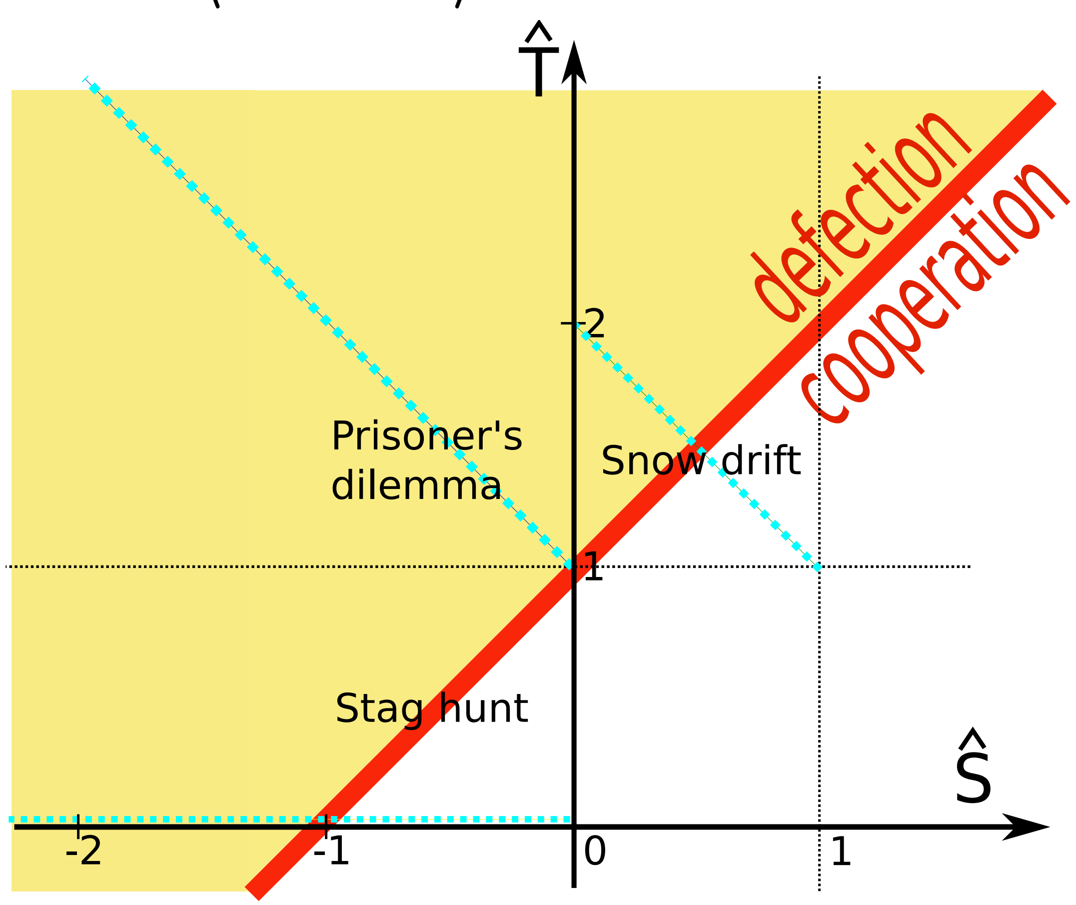
$$\begin{pmatrix} 1 & S \\ T & 0 \end{pmatrix}$$ **well-mixed**

payoffs:
$$f_A = 1 + \delta\left[X - 1 + S(N - X)\right]$$
$$f_B = 1 + \delta(XT + 0)$$

$$\Delta x^{\text{sel}} = \delta N\left[(x^3 - x^2)(1 - S - T) + (x - x^2)(S - 1/N)\right]$$

average in the neutral stationary state $\langle \Delta x \rangle = \delta \sum \Delta x_i^{(1)} \pi_i^{(0)} + \mathcal{O}(\delta^2)$

$$\langle \Delta x^{\text{sel}} \rangle > 0 \Longleftrightarrow T < 1 - S + \left(S - \frac{1}{N}\right)\underbrace{\frac{\langle x \rangle - \langle x^2 \rangle}{\langle x^2 \rangle - \langle x^3 \rangle}}_{= 2}$$



$$T < S + 1 - \frac{2}{N}$$

neutral correlations from coalescence

Kandori '93,
TA, Traulsen, Nowak '09

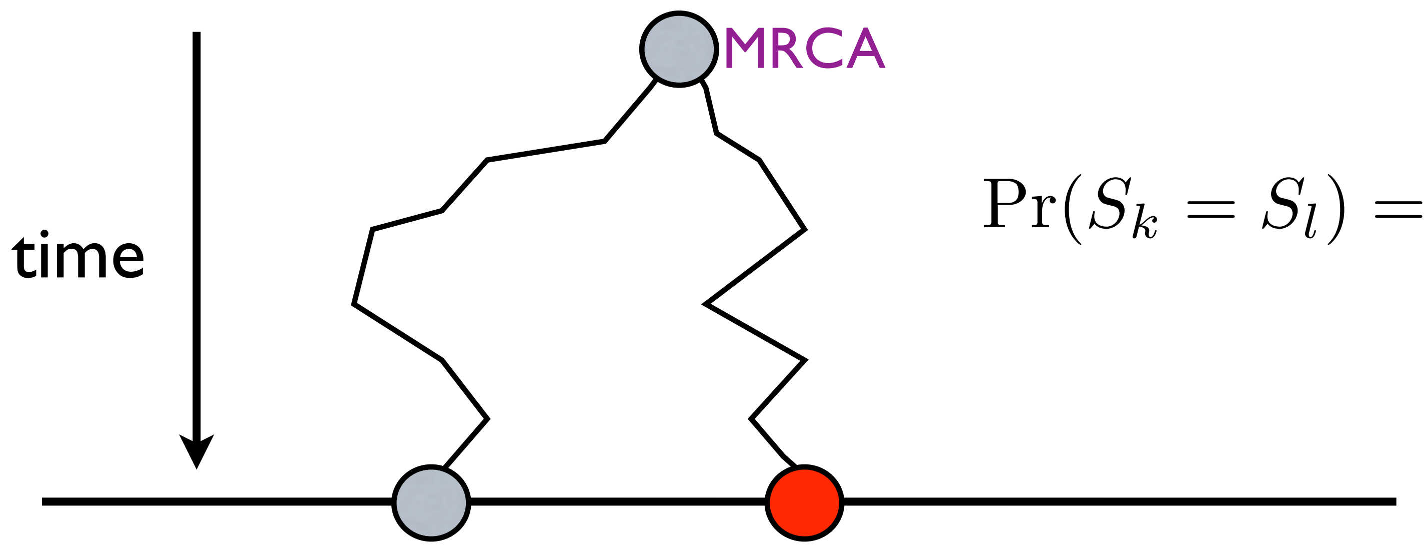
Example: $T = 1, \quad S = \frac{1}{2}$

A wins for N=5,
but B wins for N=3

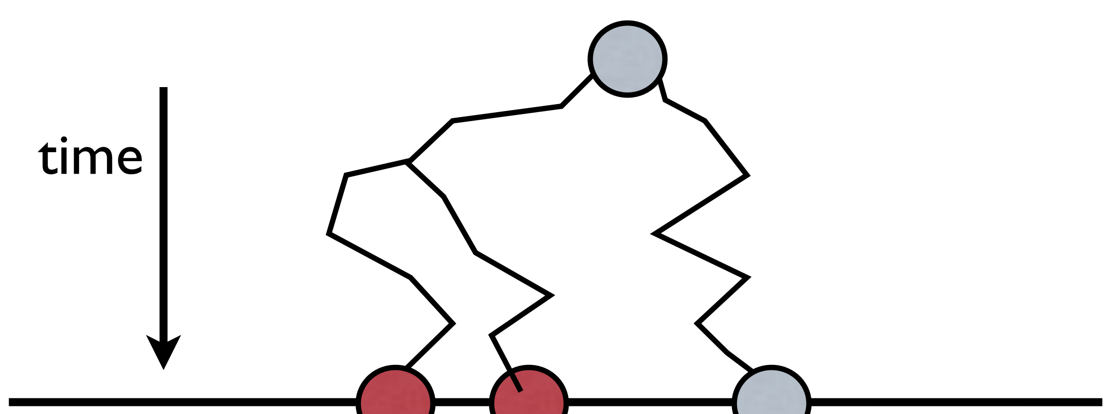
Correlations from coalescent

$$\frac{\langle x \rangle - \langle x^2 \rangle}{\langle x^2 \rangle - \langle x^3 \rangle} = 2$$

$$\langle x \rangle = \frac{1}{2} \qquad \langle x^2 \rangle = \frac{1}{2}\mathrm{Pr}(S_k = S_l) \qquad \langle x^3 \rangle = \frac{1}{2}\mathrm{Pr}(S_k = S_l = S_q)$$



$$\mathrm{Pr}(S_k = S_l) = \sum_t \mathrm{Pr}(S_k = S_l | T = t)\mathrm{Pr}(T = t)$$



n strategies: when is k better than average?

$$\begin{pmatrix} a_{11} & a_{12} & \dots & a_{1n} \\ \vdots & & & \vdots \\ a_{n1} & \dots & \dots & a_{nn} \end{pmatrix}$$

Low mutation

$$L_k = \frac{1}{n}\sum_{i=1}^{n}(a_{kk} + a_{ki} - a_{ik} - a_{ii}) > 0$$

$n = 2 : a_{11} + a_{12} > a_{21} + a_{22}$

High mutation

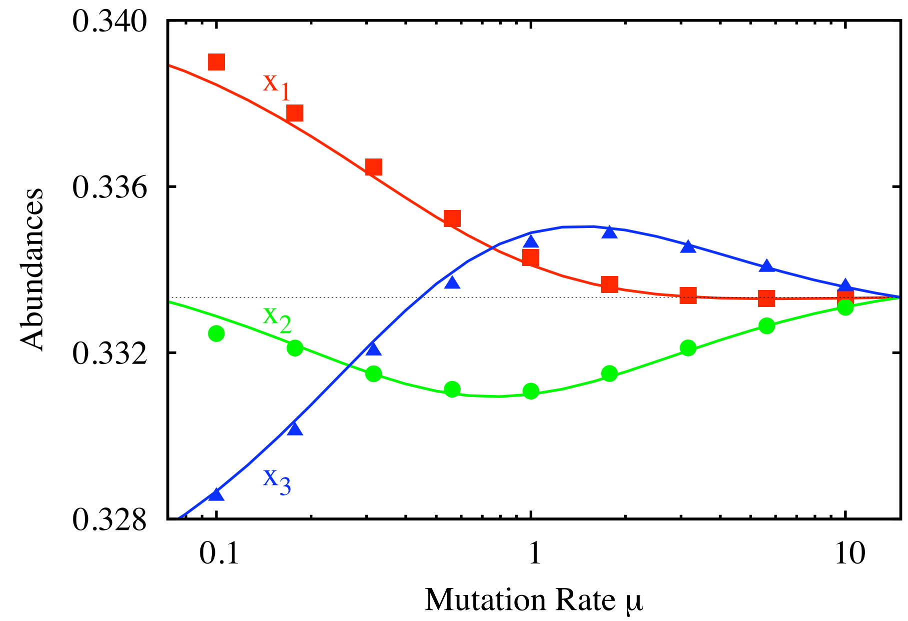
$$H_k = \frac{1}{n^2}\sum_{i=1}^{n}\sum_{j=1}^{n}(a_{kj} - a_{ij}) > 0$$

Arbitrary mutation

$$L_k + NuH_k > 0$$

Example 1

$$
\begin{array}{c|ccc}
 & S_1 & S_2 & S_3 \\
\hline
S_1 & 1 & 0 & 13 \\
S_2 & 0 & \lambda & 8 \\
S_3 & 0 & 7 & 9
\end{array}
$$

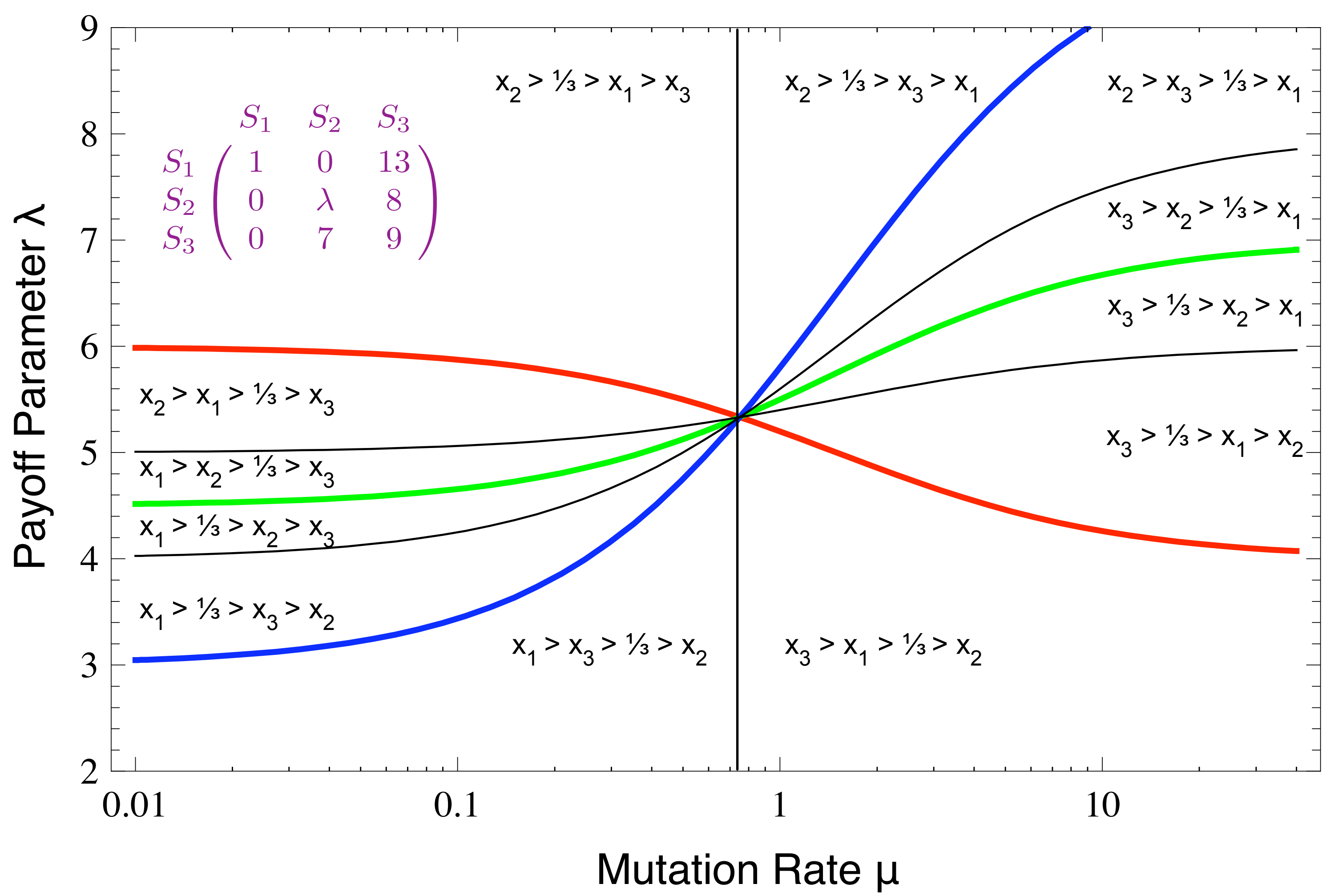


$\lambda = 4.6$

$N = 30$

$\delta = 0.003$

$\mu = Nu$



Example 2

$$\begin{array}{c} \\ \mathcal{C} \\ \mathcal{D} \end{array} \begin{array}{c} \begin{array}{cc} \mathcal{C} & \mathcal{D} \end{array} \\ \begin{pmatrix} 10 & 1 \\ 11 & 2 \end{pmatrix} \end{array}.$$

Defectors beat Cooperators

since $a_{11} + a_{12} < a_{21} + a_{22}$

$$\begin{array}{c} \\ \mathcal{C} \\ \mathcal{D} \\ \mathcal{L} \end{array} \begin{array}{c} \begin{array}{ccc} \mathcal{C} & \mathcal{D} & \mathcal{L} \end{array} \\ \begin{pmatrix} 10 & 1 & 0 \\ 11 & 2 & 0 \\ 0 & 0 & 0 \end{pmatrix} \end{array}$$

But lets add Loners

$$L_{\mathcal{C}} = \frac{8}{3}, \qquad L_{\mathcal{D}} = \frac{4}{3}, \qquad L_{\mathcal{L}} = -4$$ C win

$$H_{\mathcal{C}} = 1, \qquad H_{\mathcal{D}} = \frac{5}{3}, \qquad H_{\mathcal{L}} = -\frac{8}{3}$$ D win

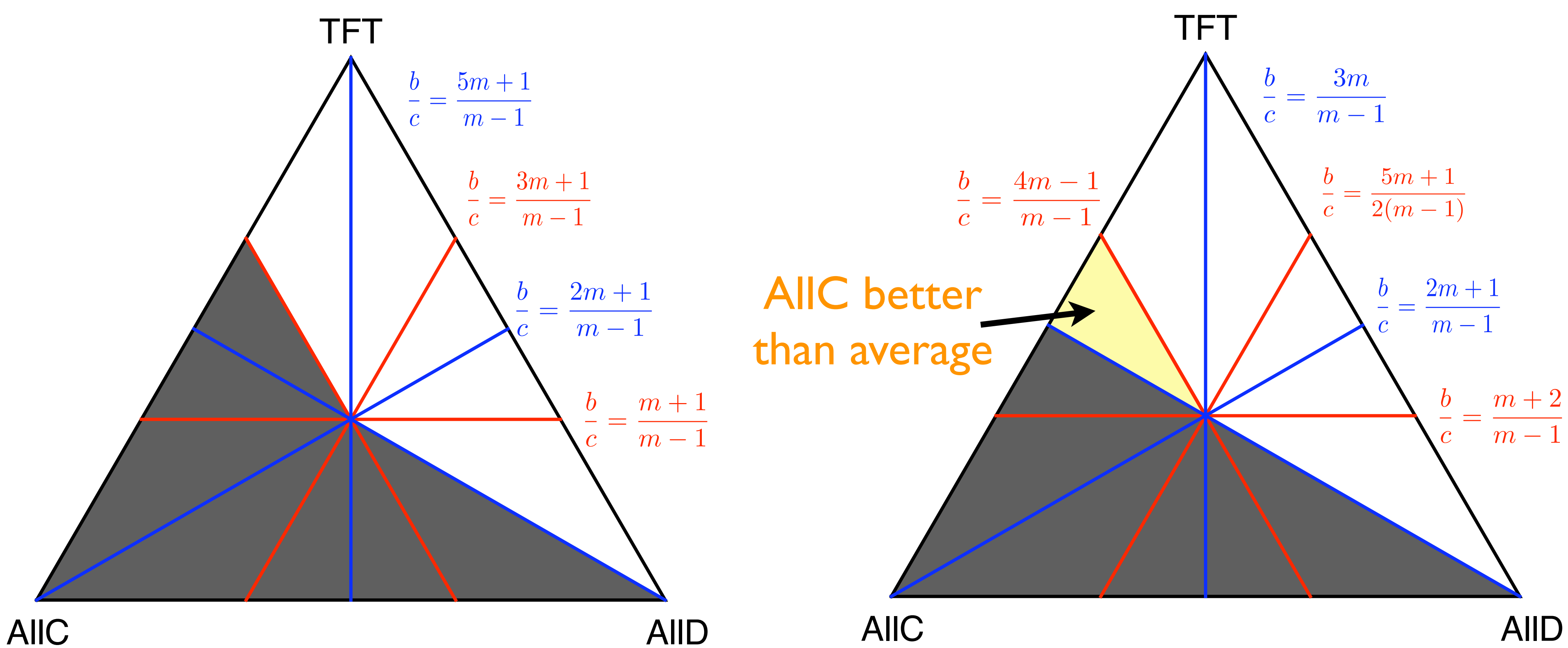
General, C win for $\mu < \mu^* \equiv 1$

Example 3 m round Prisoner's dilemma

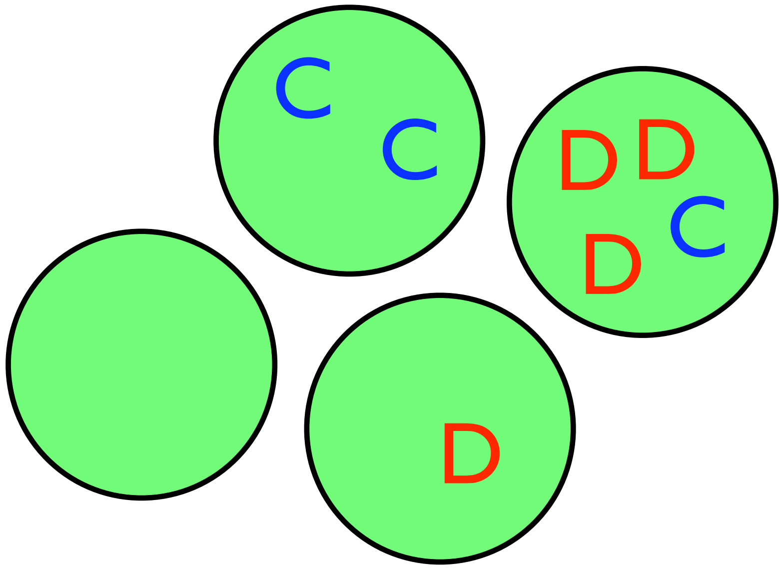
b benefit, c cost

$$
\begin{array}{cc}
 & \begin{array}{ccc} \text{AllC} & \text{AllD} & \text{TFT} \end{array} \\
\begin{array}{c} \text{AllC} \\ \text{AllD} \\ \text{TFT} \end{array} &
\begin{pmatrix}
(b-c)m & -cm & (b-c)m \\
bm & 0 & b \\
(b-c)m & -c & (b-c)m
\end{pmatrix}
\end{array}
$$

(a) Low mutation rates (b) High mutation rates



Islands: simplest structured population



u strategy mutation

β position mutation

$$\begin{array}{cc} & \begin{array}{cc} \text{C} & \text{D} \end{array} \\ \begin{array}{c} \text{C} \\ \text{D} \end{array} & \begin{pmatrix} b-c & -c \\ b & 0 \end{pmatrix} \end{array}$$

$$y = \Pr(S_k = S_q)$$
$$z = \Pr(X_k = X_q)$$
$$g = \Pr(S_k = S_q,\ X_k = X_q)$$
$$h = \Pr(S_l = S_k,\ X_k = X_q)$$

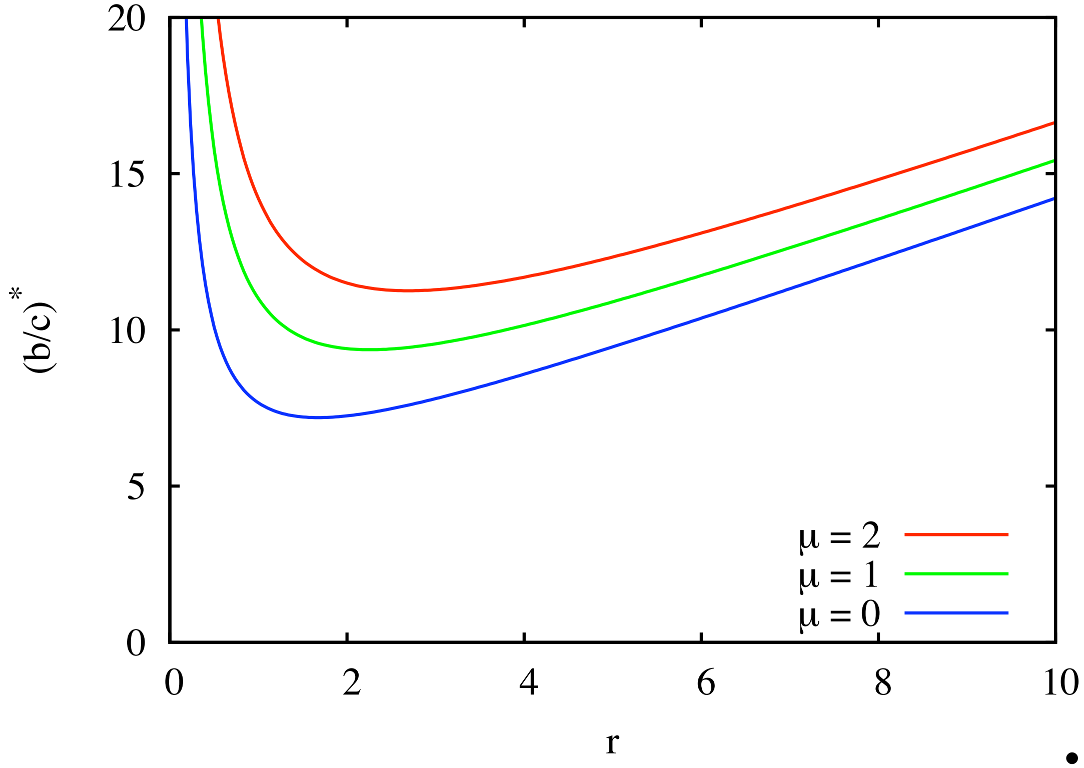
S_k **strategy**

X_k **position**

$$\left(\frac{b}{c}\right)^* = \frac{z-h}{g-h}$$

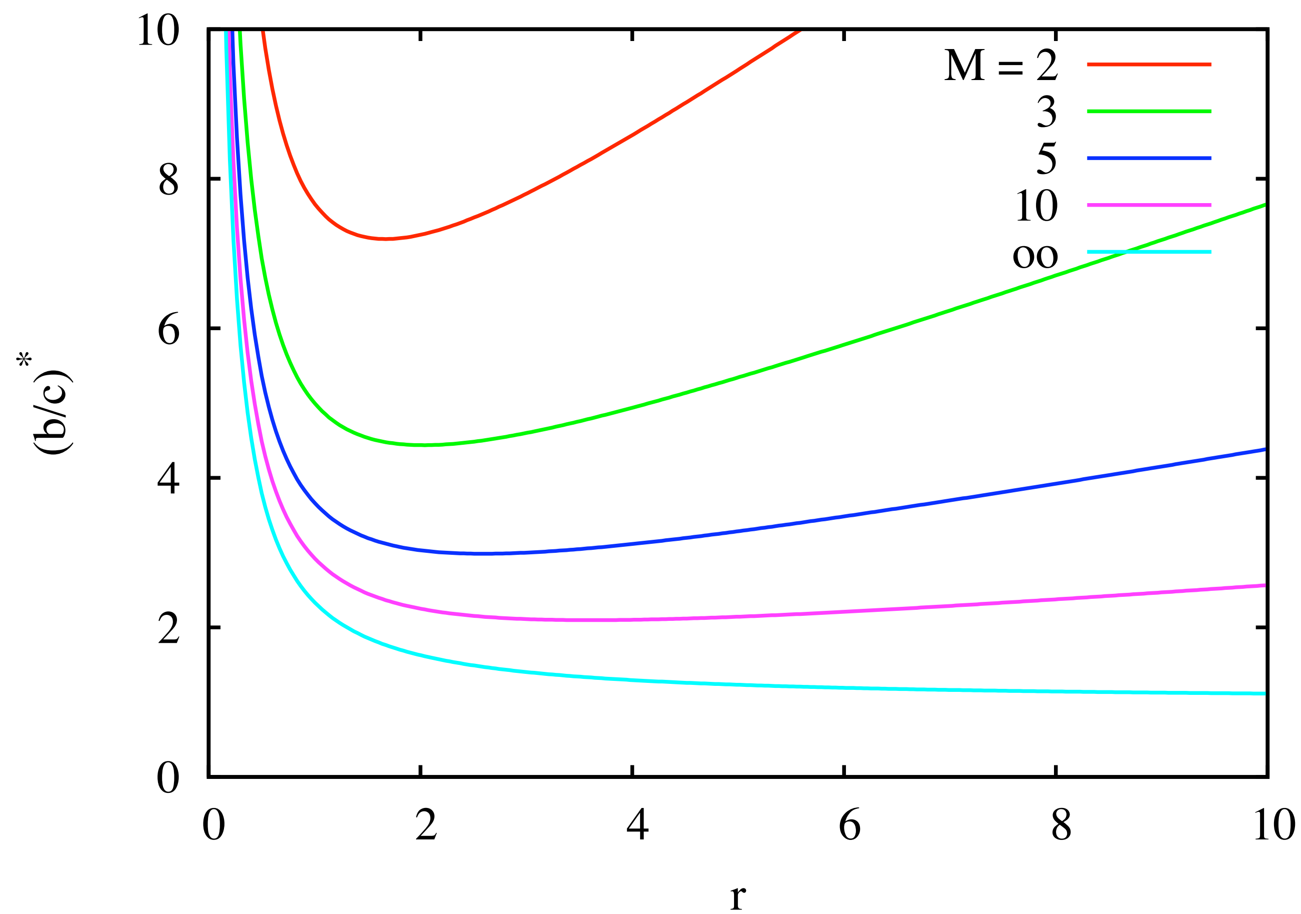
M=2 islands

$$\left(\frac{b}{c}\right)^* = \frac{M+r+2+\mu}{M-1} + \frac{M(1+\mu)}{(M-1)(2+\mu)}\left[\frac{3+\mu}{r} - \frac{1}{r+2+\mu}\right]$$

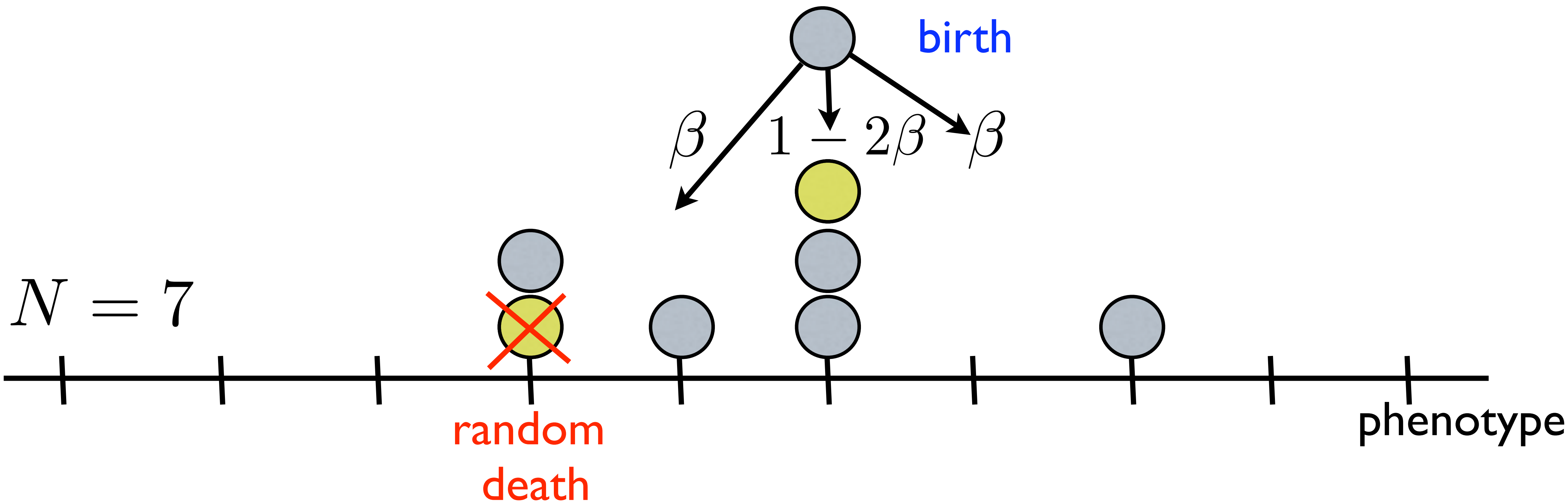


$$\mu = 2Nu$$
$$r = 2N\beta$$

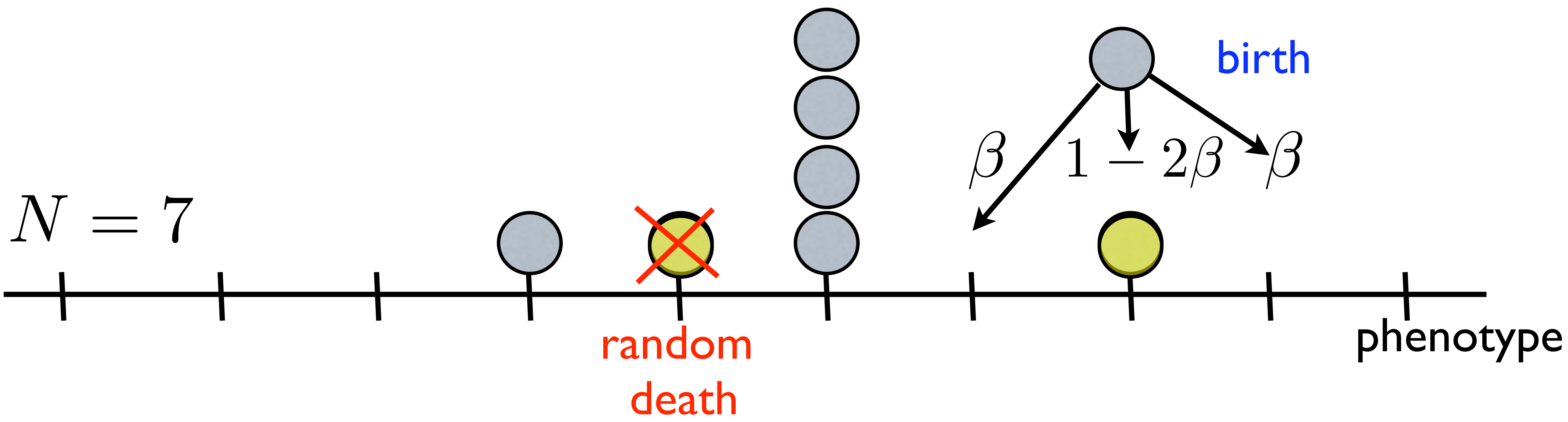
island size dependence $(\mu = 0)$



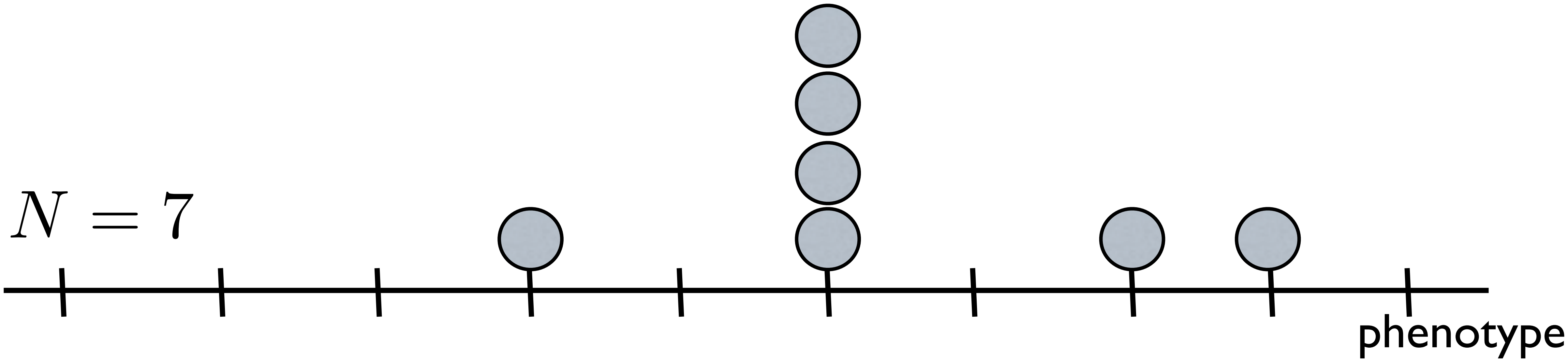
Evolution in phenotype space



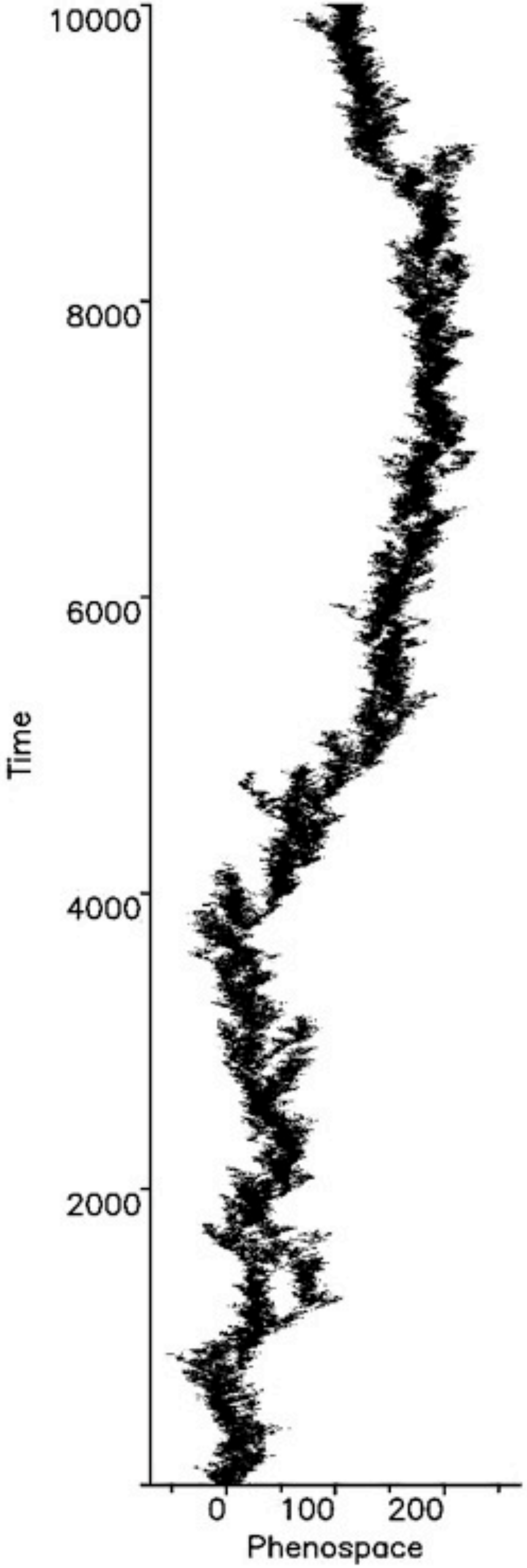
Evolution in phenotype space



Evolution in phenotype space

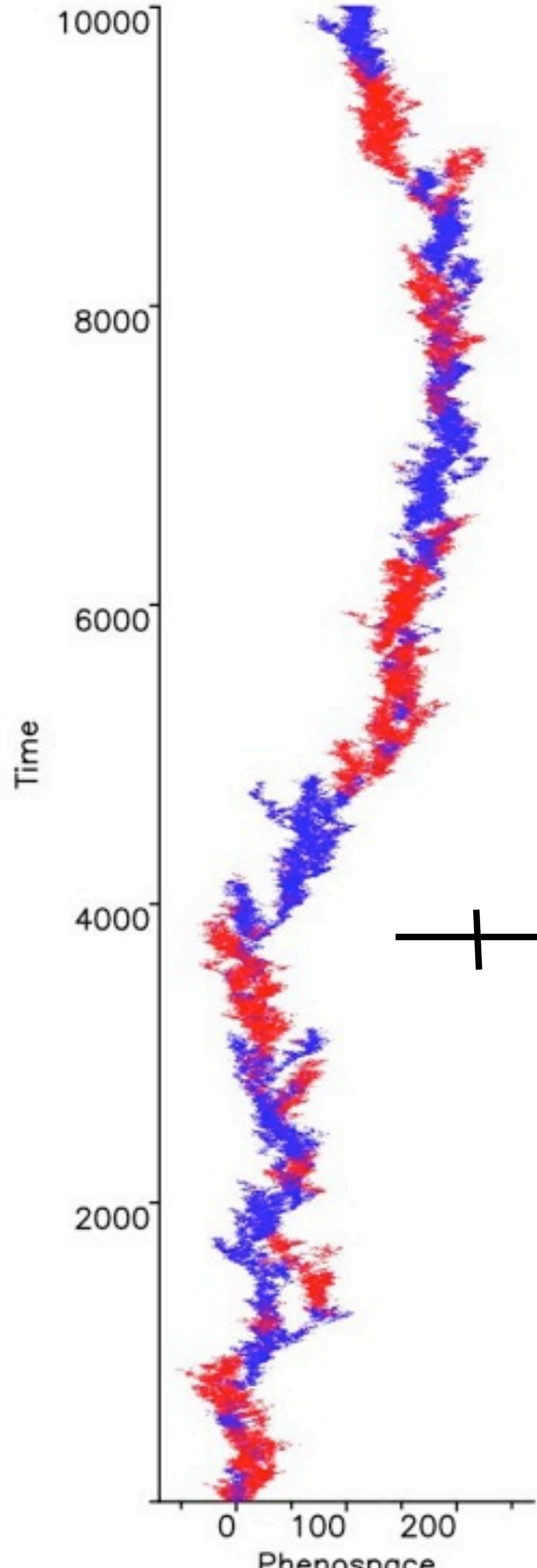


disperse or condense ?

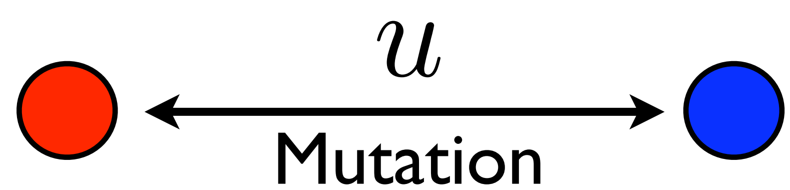


Group of size $\sqrt{r}$ diffuses as $D = r/2$

$r = N\beta$

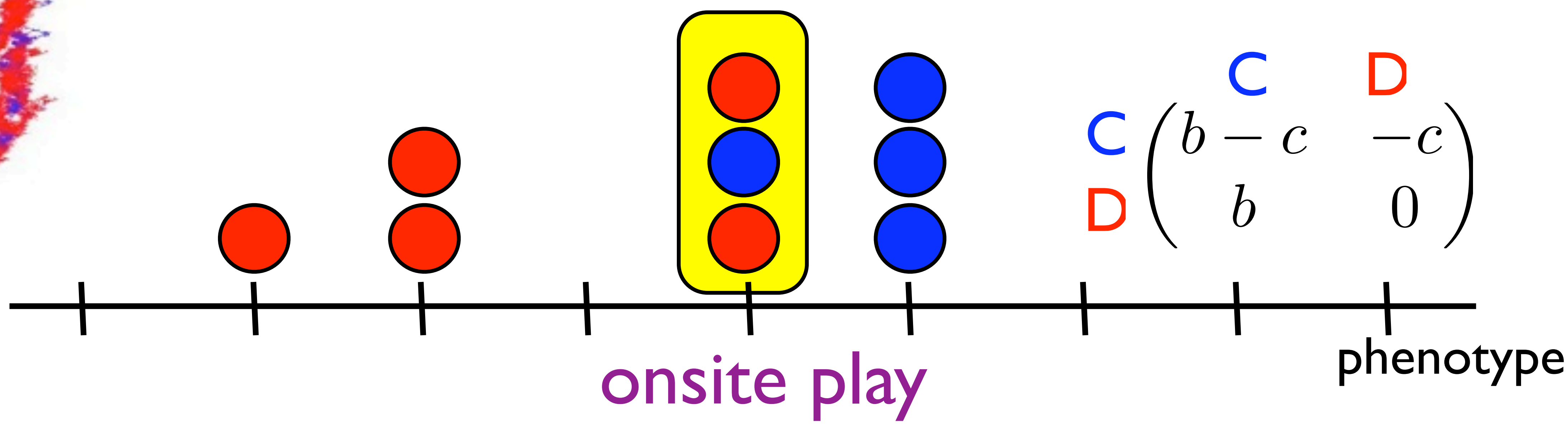


Colors



$$y = \Pr(S_k = S_q)$$
$$z = \Pr(X_k = X_q)$$
$$g = \Pr(S_k = S_q,\ X_k = X_q)$$
$$h = \Pr(S_l = S_k,\ X_k = X_q)$$

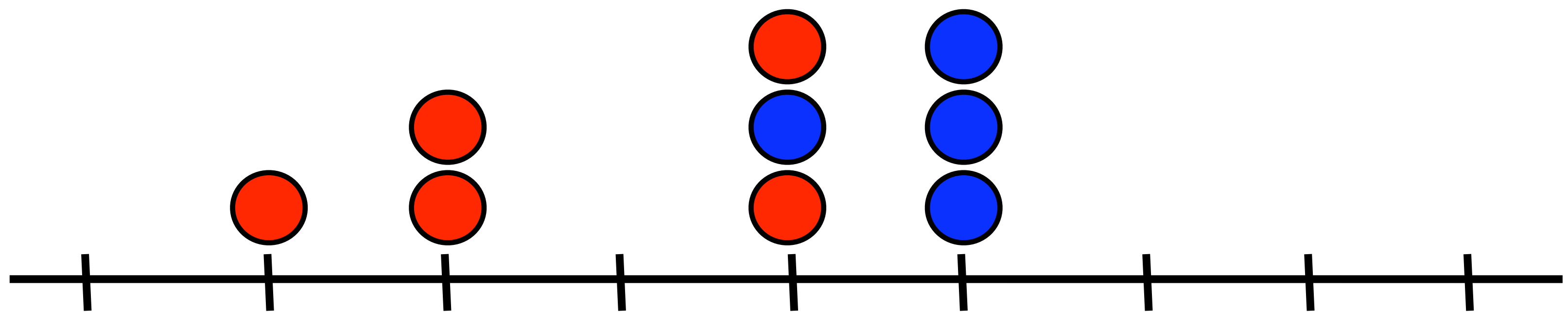
S_k strategy
X_k position



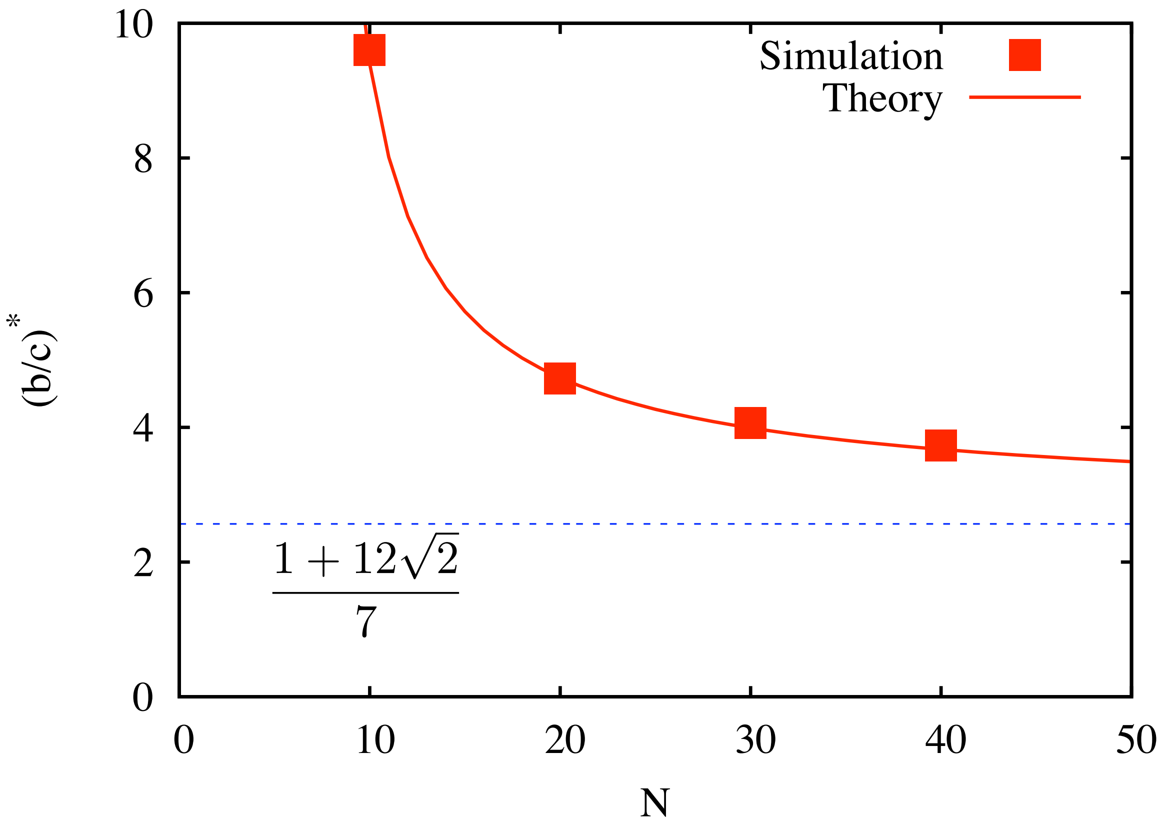
$$\begin{array}{ccc} & C & D \\ C & b-c & -c \\ D & b & 0 \end{array}$$

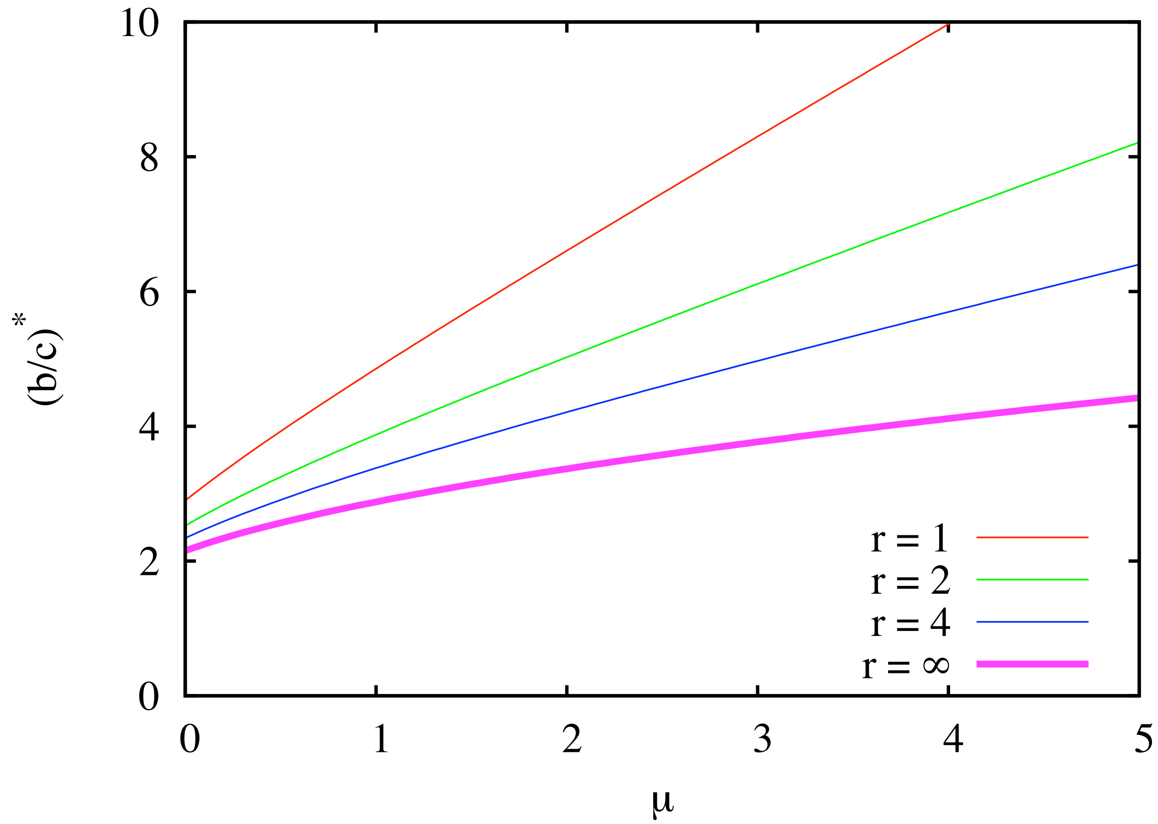
$$\left(\frac{b}{c}\right)^* = \frac{z-h}{g-h}$$

TA '09

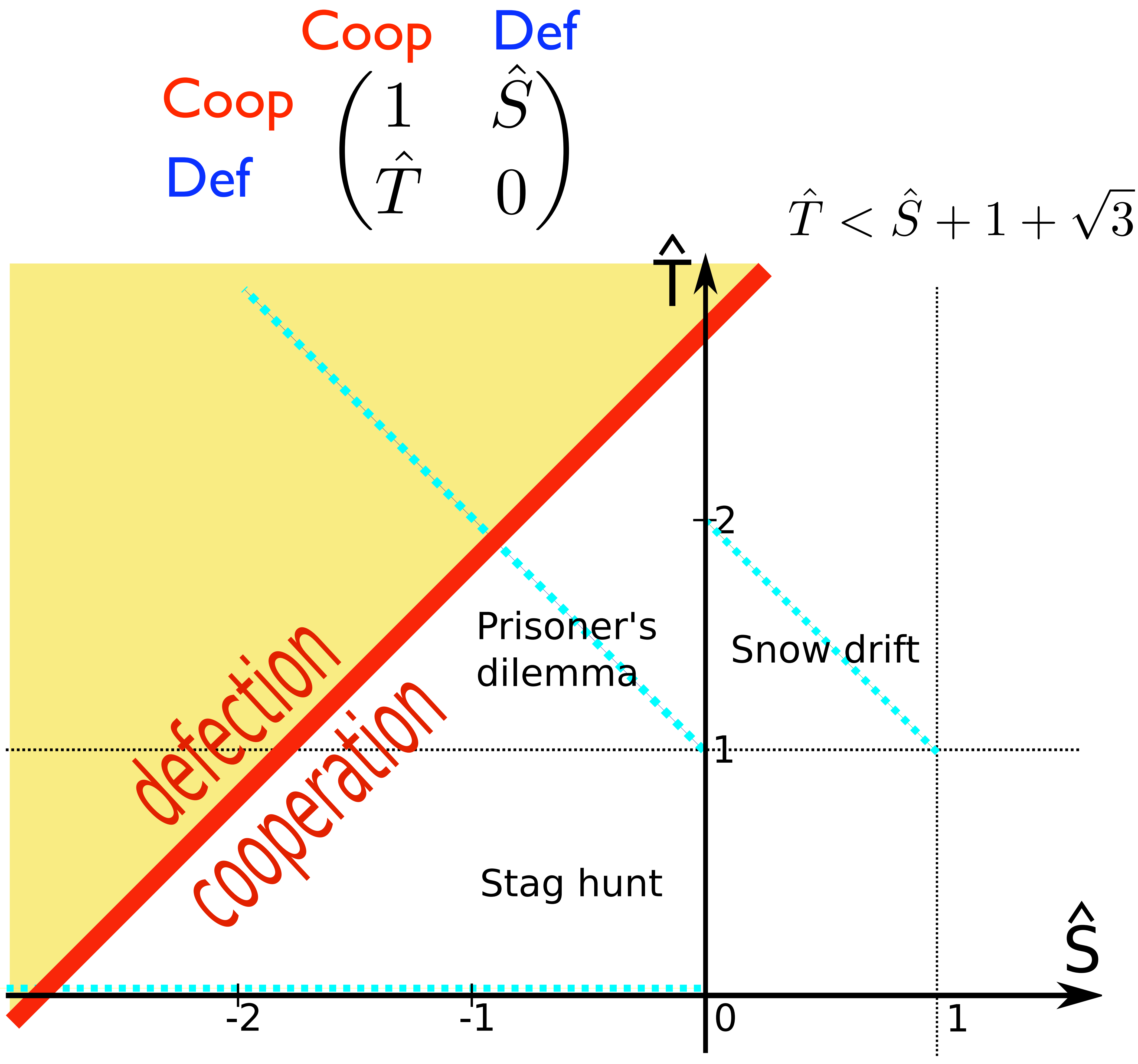


$\beta = 1/2, \ \mu = 1/2$



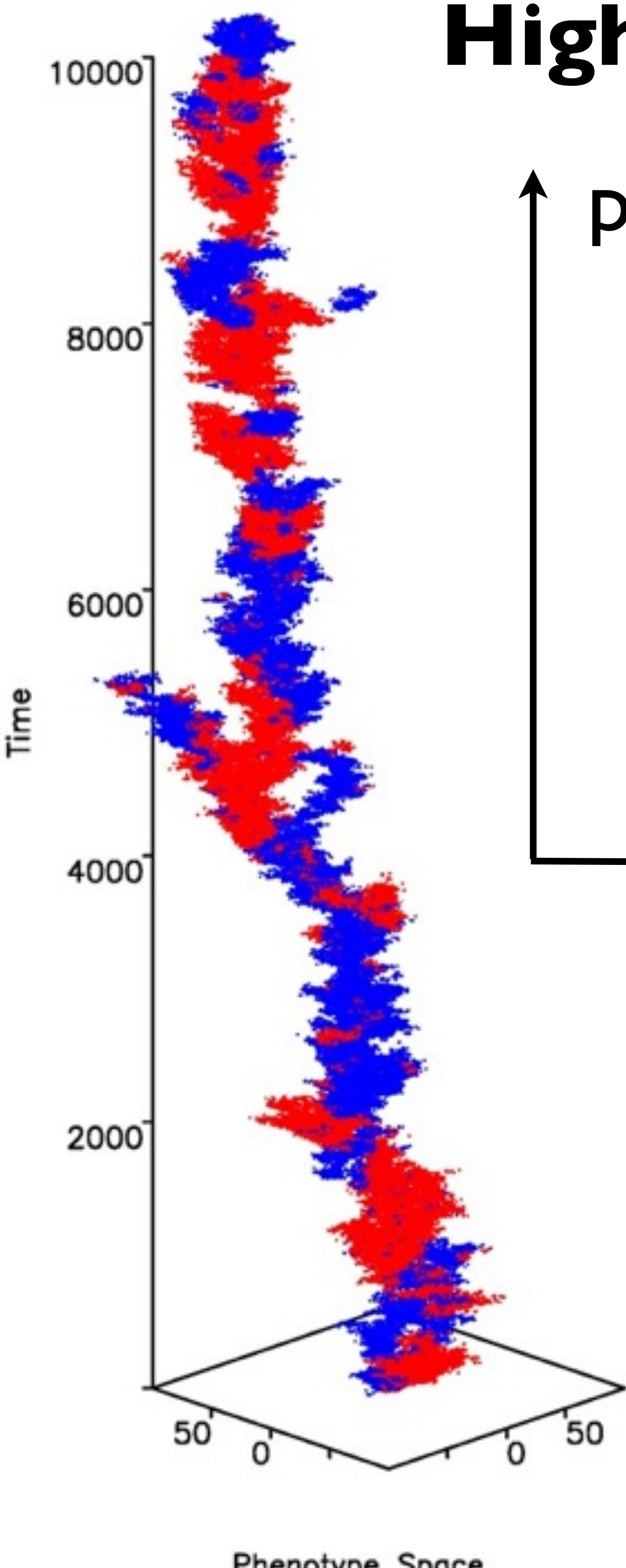


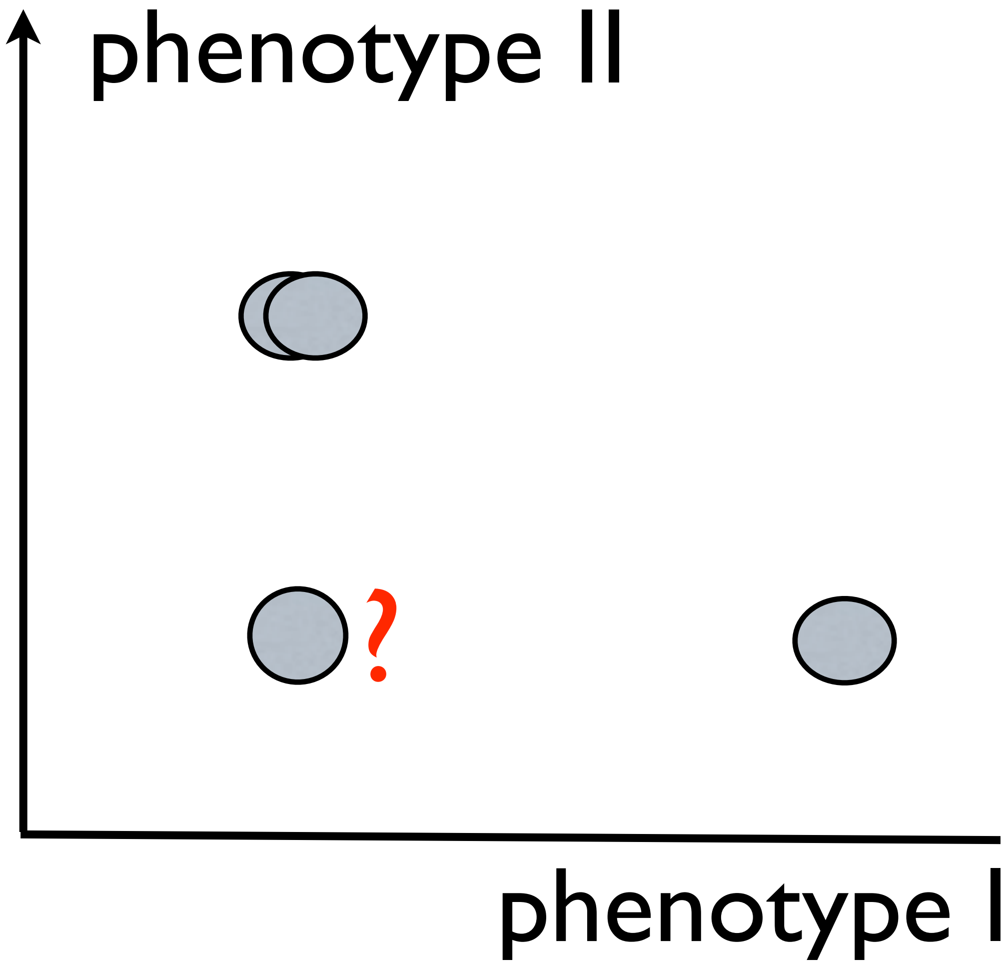
$$\mu = 2Nu$$
$$r = 2N\beta$$



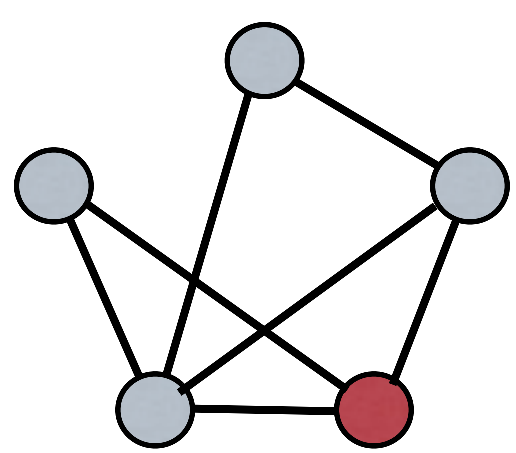
Coop
Def
Coop
Def
$\begin{pmatrix} 1 & \hat{S} \\ \hat{T} & 0 \end{pmatrix}$
$\hat{T} < \hat{S} + 1 + \sqrt{3}$
T̂
Ŝ
2
1
0
-2
-1
1
Prisoner's dilemma
Snow drift
Stag hunt
defection
cooperation

Higher dimensions

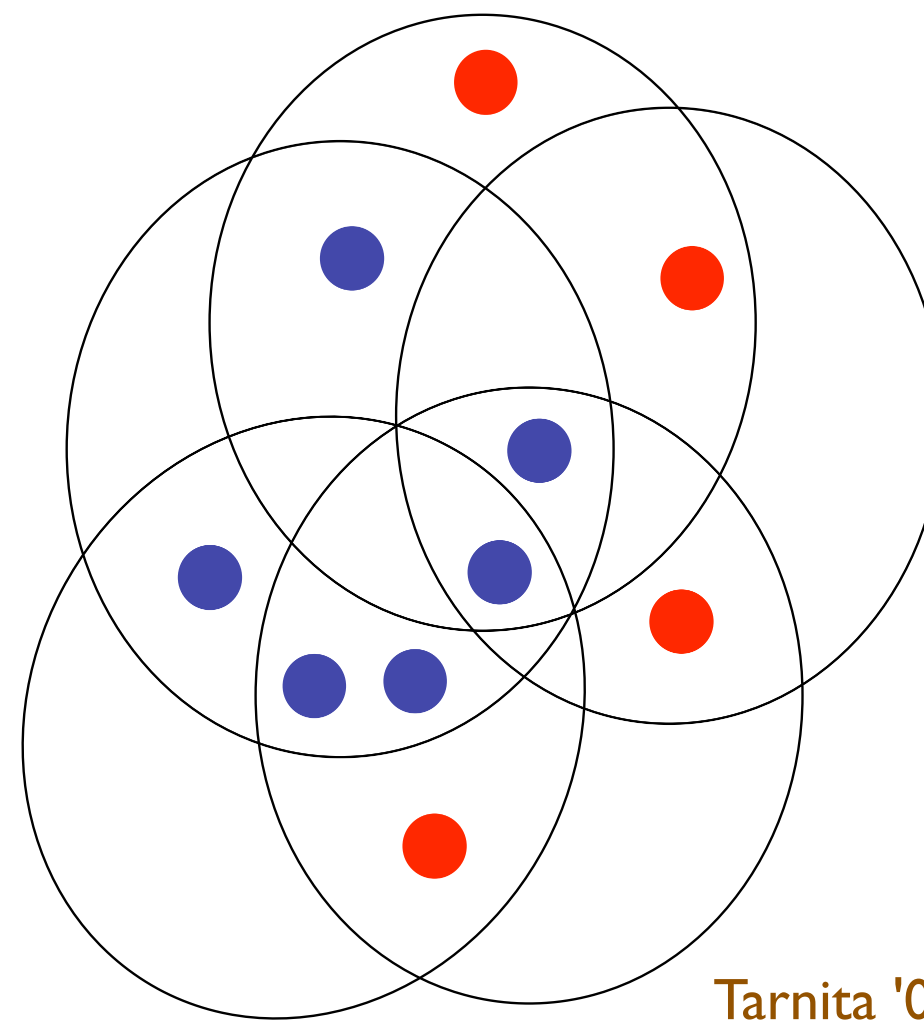




Graphs



Sets



Tarnita '09

One parameter to rule them all

Tarnita '09

A wins iff $\sigma a + b > c + \sigma d$

$$\begin{array}{ccc} & \text{when playing against} & \\ & \text{A} \quad \text{B} & \\ \text{payoff of} & \begin{array}{c}\text{A}\\ \text{B}\end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array}$$

single parameter for all structures

classical well mixed $\sigma = 1$

$a + b > c + d$ (risk dominance) or $\sigma = 1 - 2/N$

phenotype game $\sigma = 1 + \sqrt{3}$

more strategies on structure?

Wage, Tarnita '10

# strategies	# parameters
2	1
≥ 3	2

Relations to relatedness

A wins iff $\frac{b}{c} > \frac{1}{R}$ (Hamilton's rule)

same size islands

$$R = \frac{\Pr(S_k = S_q | X_k = X_q) - \Pr(S_k = S_q)}{1 - \Pr(S_k = S_q)}$$

fluctuating size islands,
phenotype walk

$$\left(\frac{b}{c}\right)^* = \frac{z-h}{g-h} \qquad R = \frac{\Pr(S_k = S_q|\ X_k = X_q) - \Pr(S_l = S_k|\ X_k = X_q)}{1 - \Pr(S_l = S_k|\ X_k = X_q)}$$

TA '09, Taylor '10

sets, more general
structures

no relatedness interpretation
of our general formulas

Final slide

general method to study weak selection

TA, Ohtsuki, Wakeley, Taylor, Nowak, PNAS '09

papers can be found on my website

thanks