## Who laughs last? perturbation theory of games

Tibor Antal, Program for Evolutionary Dynamics, Harvard


- games in phenotype space
- perturbation method: two key aspects
- further examples, general results
with: C Tarnita, H Ohtsuki, J Wakeley, P Taylor, A Traulsen, F Fu, NWage, M Nowak


## What is the question?

Two strategies: A and B : Which one is better?
John Forbes Nash, John Maynard Smith fixation probabilities ...

C Taylor, Nowak


Or: Which outnumbers the other in the long run? with two way mutation $u$ (who laughs last?)
$\langle x\rangle>1 / 2$
Kandori '93


## Evolution in phenotype space



## Evolution in phenotype space



## Evolution in phenotype space


disperse or condense?


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





$$
\begin{aligned}
\mu & =2 N u \\
r & =2 N \beta
\end{aligned}
$$

$$
\left.\begin{array}{l}
\quad \text { Coop } \\
\text { Coop } \\
\text { Def } \\
\text { Def } \\
1 \\
\hat{S} \\
\hat{T}
\end{array}\right) \quad \text { 人 } \quad \hat{T}<\hat{S}+1+\sqrt{3}
$$



## Perturbation method: 2 key points



Wright-Fisher
$u$ mutation probability

$\Delta x^{\mathrm{tot}}=\Delta x^{\mathrm{sel}}-\frac{u}{2}\left(x+\Delta x^{\mathrm{sel}}\right)+\frac{u}{2}\left(1-x-\Delta x^{\mathrm{sel}}\right)$
$\langle x\rangle=\frac{1}{2}+\frac{1-u}{u}\left\langle\Delta x^{\mathrm{sel}}\right\rangle$

$$
\langle x\rangle>\frac{1}{2} \Longleftrightarrow\left\langle\Delta x^{\mathrm{sel}}\right\rangle>0
$$

## Perturbation method: 2 key points

$$
\begin{aligned}
& \text { when playing agoinst } \\
& \text { Payoff }=1+\delta \times \text { payoff of } \mathrm{A} \begin{array}{|lll}
\mathrm{a}_{11} & \mathrm{a}_{12} & x
\end{array} \text { frequency of } \mathrm{A} \\
& \text { Payoff }=1+\delta \times \text { payoffof } \begin{array}{l}
\text { B } \\
\mathrm{a}_{21}
\end{array} \mathrm{a}_{22} \quad \delta \text { selection strength } \\
& u \text { mutation probability } \\
& \langle x\rangle>\frac{1}{2} \Longleftrightarrow\left\langle\Delta x^{\text {sel }}\right\rangle>0
\end{aligned}
$$

Easy perturbation method for small $\delta$

$$
\langle\Delta x\rangle=\sum \Delta x_{i} \pi_{i} \quad \begin{aligned}
& \Delta x_{i}=0+\delta \Delta x_{i}^{(1)} \\
& \pi_{i}=\pi_{i}^{(0)}+\delta \pi_{i}^{(1)}
\end{aligned}
$$

$\langle\Delta x\rangle=\delta \sum \Delta x_{i}^{(1)} \pi_{i}^{(0)}+\mathcal{O}\left(\delta^{2}\right)$


One parameter to rule them all

A wins iff $\quad \sigma a+b>c+\sigma d$
single parameter for all structures payof of ${ }_{\mathrm{B}}^{\mathrm{A}}\left(\begin{array}{ll}a & b \\ c & d\end{array}\right)$
classical well mixed $\sigma=1$

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

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

## when playing against

$$
\text { payoff of } \begin{array}{cc}
\mathrm{A} & \mathrm{~B} \\
\mathrm{~B}
\end{array}\left(\begin{array}{ll}
a & b \\
c & d
\end{array}\right)
$$

\# strategies \# parameters

$$
\begin{array}{r}
2 \\
\geq 3
\end{array}
$$

Relations to relatedness

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

same size islands

$$
R=\frac{\operatorname{Pr}\left(S_{k}=S_{q} \mid X_{k}=X_{q}\right)-\operatorname{Pr}\left(S_{k}=S_{q}\right)}{1-\operatorname{Pr}\left(S_{k}=S_{q}\right)}
$$

fluctuating size islands, phenotype walk

$$
\left(\frac{b}{c}\right)^{*}=\frac{z-h}{g-h} \quad R=\frac{\operatorname{Pr}\left(S_{k}=S_{q} \mid X_{k}=X_{q}\right)-\operatorname{Pr}\left(S_{l}=S_{k} \mid X_{k}=X_{q}\right)}{1-\operatorname{Pr}\left(S_{l}=S_{k} \mid X_{k}=X_{q}\right)}
$$

TA '09, Taylor 'IO
more general structures
is there always a relatedness interpretation of the general formulas?

## Final slide

general method to study weak selection

TA, Ohtsuki, Wakeley, Taylor, Nowak, PNAS '09
some papers can be found on my website
thanks

