Evolutionary dynamics in finite populations: Oscillations, diffusion, and drift rever

Jens Christian Claussen



1. Lizards, E.coli, Mice, . . . and Rock-Paper-Scissors.
2. Evolutionary game theory. Coevolution.
   How to describe coevolutionary dynamics in finite populations?
3. Microscopical processes: Moran process, Local update.
   Mean-field theory in finite populations:
   Derive replicator equations (and FPEs for internal fluctuations).
4. Consequences: Drift reversal in asymmetric conflicts.

Claussen & Traulsen, Phys. Rev. E 71, 025101 (R) (2005)
Traulsen, Claussen & Hauert, Phys. Rev. Lett. 95, 238701 (2005); Phys. Rev. E 74, 011901 (2006)
Claussen & Traulsen, submitted (2007), Claussen, submitted (2007)

Cyclic coevolution: Side-blotched Lizards *(Uta stansburiana)*

Cyclical games: Lizards "playing" a rock-scissors-paper game[c]

- Orange-throated males establish large territories holding several females. Can be invaded by yellow-striped males ("sneakers"), not contributing to defense

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- Yellow-striped populations can be invaded by blue-striped males,
  which defend a small territory that can hold one female and defend it against sneakers.
- Once sneakers are rare, i.e. blue-striped have taken over,
  it is advantageous to defend a large territory holding several females.

This allows for cyclic invasion O $\rightarrow$ Y $\rightarrow$ B $\rightarrow$ O

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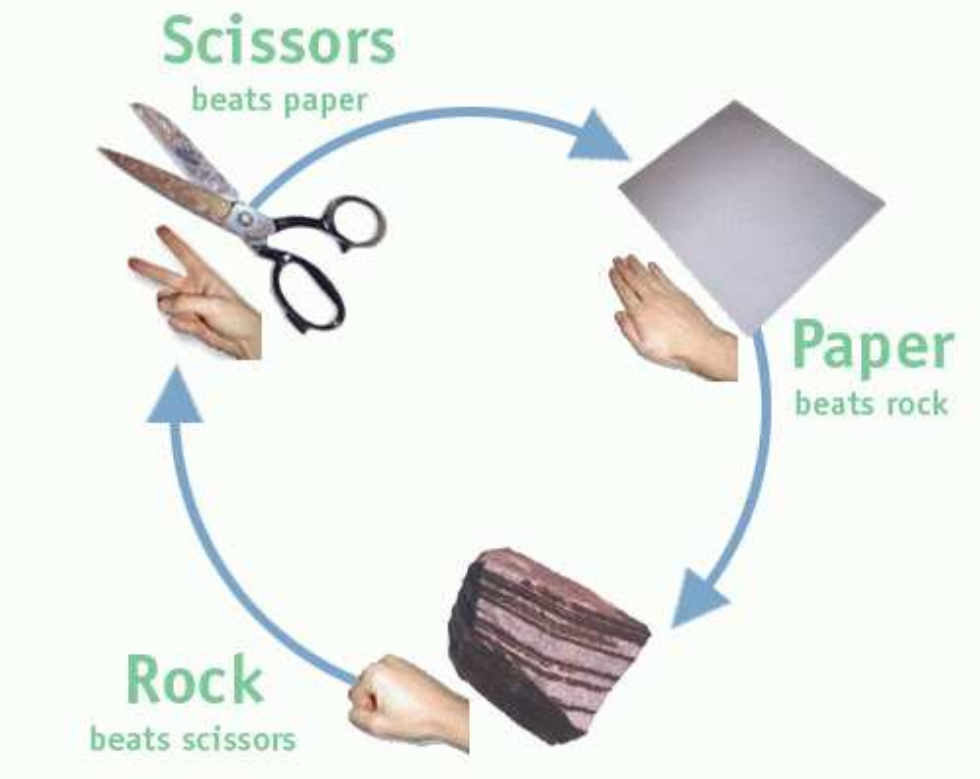
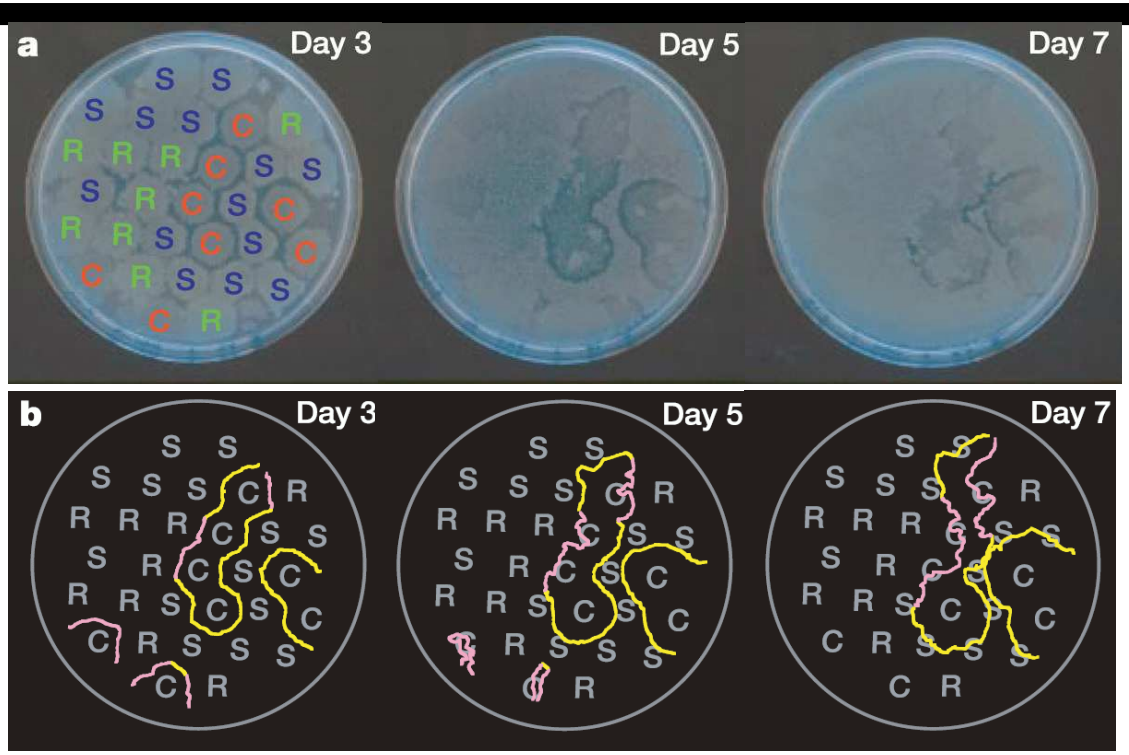
Cyclic games



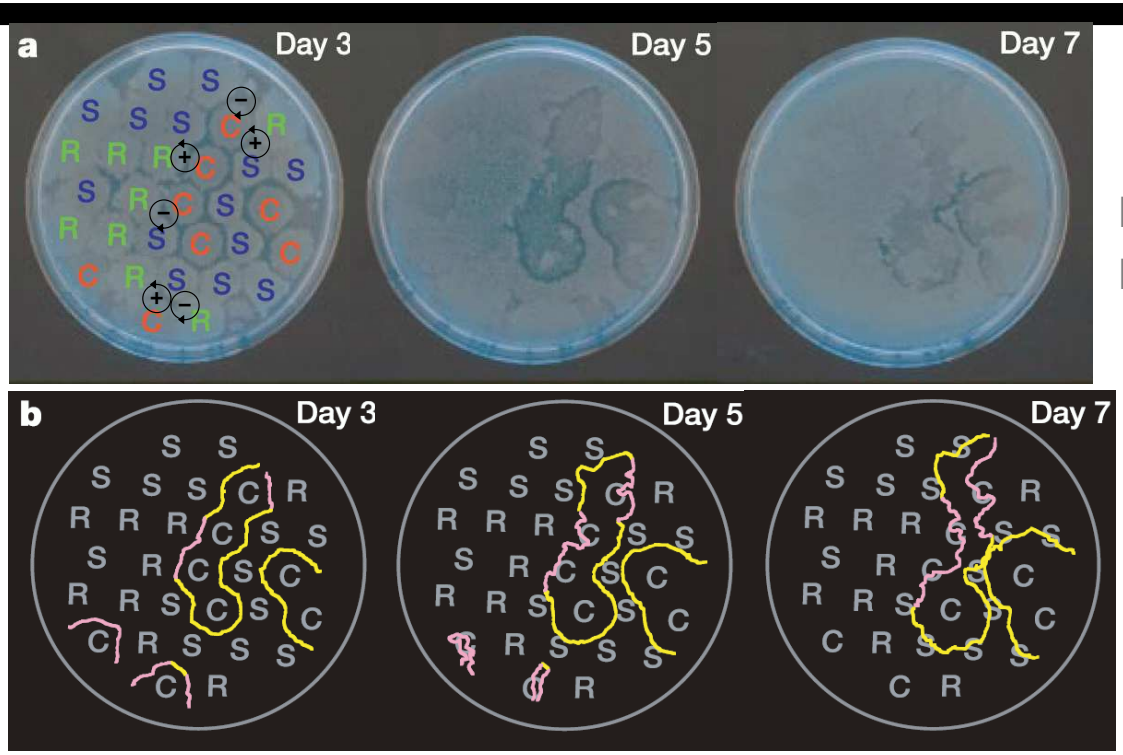
			
	0	-1	1
	1	0	-1
	-1	1	0

Cyclic coevolution: E.coli “play” RPS in vitro



Kerr, Riley, Feldman, Bohannan, Nature 428, 412 (2004)

Cyclic coevolution: E.coli “play” RPS in vitro ... and in mice!



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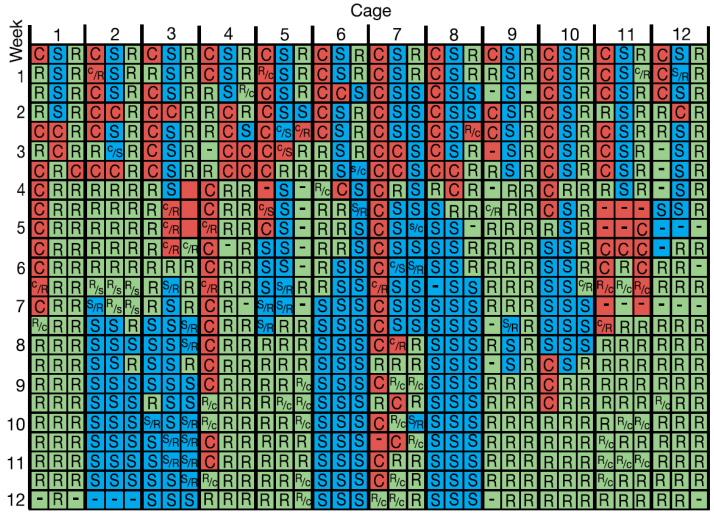


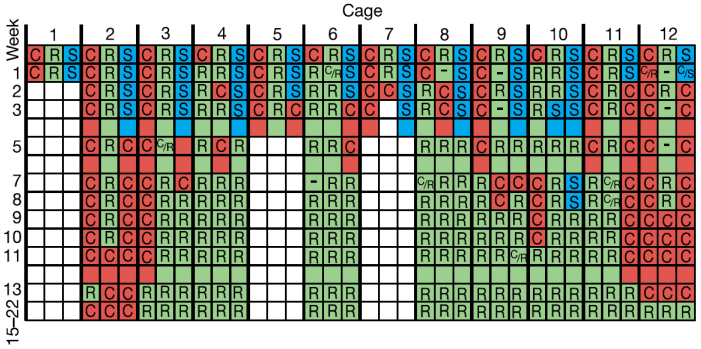


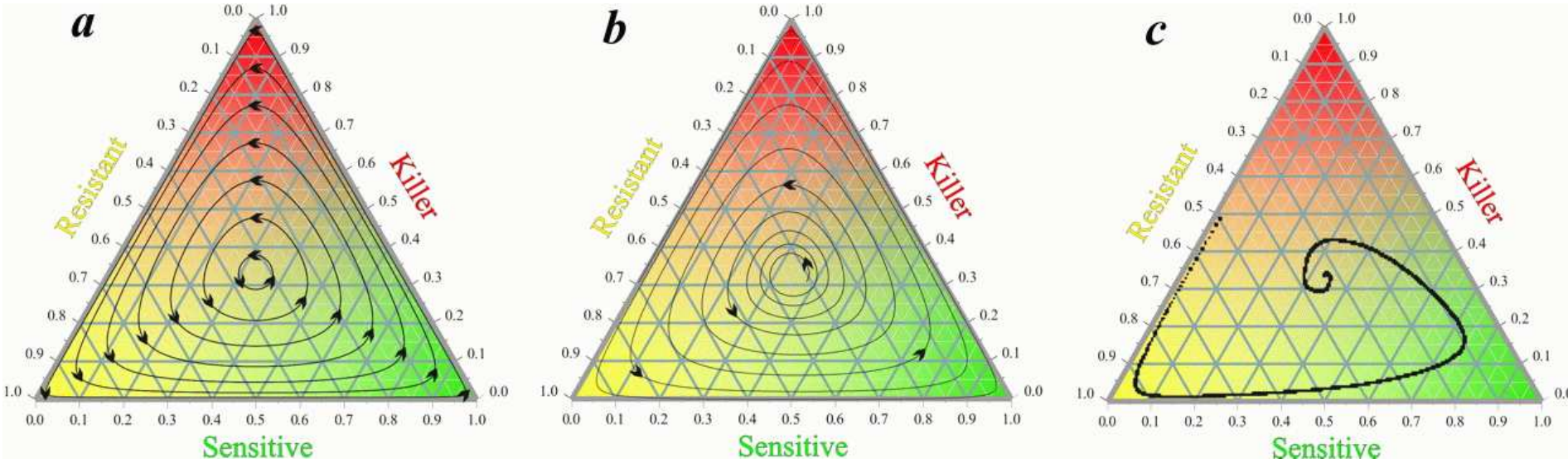
Figure 2 Occupation of co-caged mice by dominant strain: colicin E2. The boxes are coloured to show the dominant strain occupying each mouse. Red represents colicinogenic (C_{E2}); green, resistant; blue, sensitive. Cages 1, 5 and 7 were discontinued because of mice fighting.

Kirkup and Riley, Nature 428, 412 (200

Cyclic games

“Chemical warfare between microbes promotes biodiversity”

(Czárán, Hoekstra, Pagie, PNAS 99, 786 (2001))



RSP replicator dynamics - same, but small interaction cost - spatial system

Stability of evolutionary cycles: Possible mechanisms?

What determines the (in)stability of the fixed point (=coexistence)?

- Payoff (fitness) values (for non-zero-sum games)
- Spatial structure (stabilizes coexistence)
- Finiteness of population (usually destabilizes coexistence)
- Dynamics of the (microscopic) interaction process
  (and resulting replicator equations)

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What happens in reality?

- E.coli (mixed system): Fixates to border. 
- Lizards: damped oscillations $\rightarrow$ stable fixed point. 
- Social strategies: Many strategies do coexist. 
- Mating (& parental care) behaviour: Fixates to border (typically). 

Coevolutionary dynamics in finite populations? Meanfield theory.

Main questions:

- How do ("microscopic") evolutionary processes and replicator equations $\dot{x} = x(1-x)(\pi^A(x) - \pi^B(x))$ relate?
- Deterministic limit for N$\rightarrow \infty$. What happens in finite populations?
- Is the discretization stochasticity simply Gaussian noise?

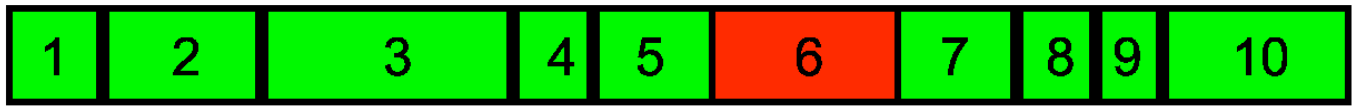
Methods and Approach:

- Use explicitely ("microscopic") dynamics: Moran process and Local update
- Analyze meanfield ("macroscopic") equations of motion
  - Perform N$\rightarrow \infty$ explicitely yielding replicator-type equations
  - What are the dynamical 1/N corrections?

Microscopic processes: Moran process and local update

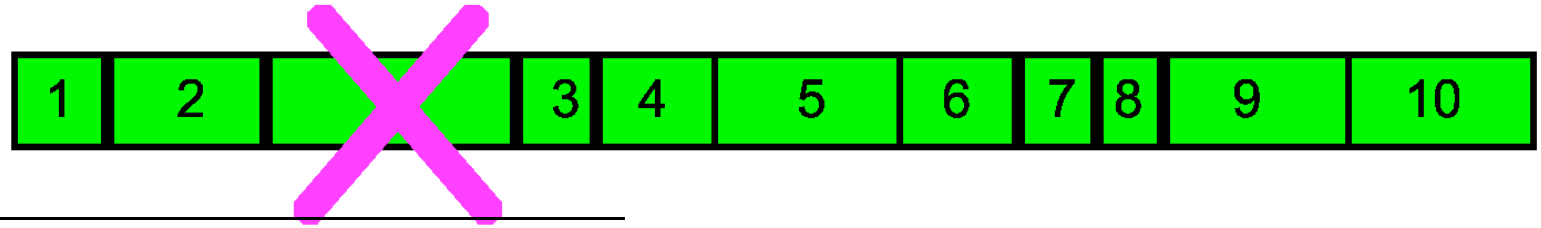
The frequency-dependent Moran Process[ab]

- N individuals
- Choose an individual at random proportional to its payoff



- Create identical offspring

- Remove one random individual



[a] Moran, The Statistical Processes of Evolutionary Theory (1962).

[b] M.A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature 428, 646 (2004),

Moran evolution dynamics in 2×2 games

- Arbitrary payoff matrix:

  $P = \begin{pmatrix} a & b \\ c & d \end{pmatrix}$. E.g.: $P_{\rm c} = \begin{pmatrix} a & a \\ c & c \end{pmatrix}$, $P_{\rm CG} = \begin{pmatrix} 0 & 1 \\ 1 & 0 \end{pmatrix}$, $P_{\rm PD} = \begin{pmatrix} 3 & 0 \\ 5 & 1 \end{pmatrix}$

- Frequency-dependent[a] Moran[b] process:

  Every agent interacts with a representative sample of the population:

$$\begin{aligned} \pi^A(i) &= \frac{a(i-1)+b(N-i)}{N-1} \\ \pi^B(i) &= \frac{c\,i+d(N-1-i)}{N-1}, \end{aligned}$$

  With probability $\pi^A(i)/\langle\pi\rangle$, a copy of an A agent replaces a randomly chosen individual.

[a] M.A. Nowak, A. Sasaki, C. Taylor, and D. Fudenberg, Nature 428, 646 (2004),

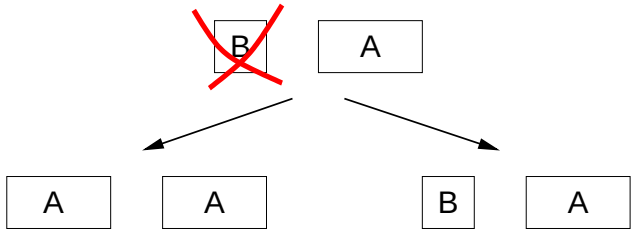
[b] P.A.P. Moran, *The Statistical Processes of Evolutionary Theory*, Oxford (1962).

Local update: a local microscopic process

- Moran process requires perfect global information via $\langle \pi_i \rangle$
- Local update: Microscopic process entirely based on local information

  A randomly chosen individual b compares its payoff to the payoff of a (also randomly chosen).
  It switches with probability

$$p_{b\to a} = \frac{1}{2} + \frac{w}{2}\frac{\pi_a - \pi_b}{\Delta\pi_{\max}}$$



Pure “2-particle” interaction

- Transition matrix:

$$T^+(i) = \left(\frac{1}{2} + \frac{w}{2}\frac{\pi_i^A - \pi_i^B}{\Delta\pi_{\max}}\right)\frac{i}{N}\frac{N-i}{N}$$

$$T^-(i) = \left(\frac{1}{2} + \frac{w}{2}\frac{\pi_i^B - \pi_i^A}{\Delta\pi_{\max}}\right)\frac{i}{N}\frac{N-i}{N}.$$

Meanfield dynamics
. . . and finite-size scaling: Fokker-Planck equation

Derivation of the FPE

Master equation

$$P^{\tau+1}(i) - P^{\tau}(i) = P^{\tau}(i-1)T^{+}(i-1) - P^{\tau}(i)T^{-}(i) + P^{\tau}(i+1)T^{-}(i+1) - P^{\tau}(i)T^{+}(i)$$

For $N \gg 1$: Taylor expansion of T and $\rho(x,t) = N\,P^{\tau}(i)$ $\quad (x = i/N,\, t = \tau/N)$

Fokker-Planck equation:

$$\boxed{\frac{d}{dt}\rho(x,t) = -\frac{d}{dx}\left[a(x)\rho(x,t)\right] + \frac{1}{2}\frac{d^2}{dx^2}\left[b^2(x)\rho(x,t)\right]}$$

with $a(x) = T^{+}(x) - T^{-}(x)$ and $b(x) = \sqrt{\frac{1}{N}[T^{+}(x) + T^{-}(x)]}$.

- Corresponding Langevin equation: $\dot{x} = a(x) + b(x)\xi$
- What about the limit $N \to \infty$?

Microscopic processes and replicator equations

For $N \to \infty$, $b(x)$ vanishes with $\frac{1}{\sqrt{N}}$, yielding deterministic equations:

Microscopic process	Deterministic equation
Moran process $p_{B\to A} = \frac{1-w+w\,\pi_i^A}{1-w+w\,\langle\pi_i\rangle}$	Adjusted replicator equation $\dot{x} = x(1-x)\frac{\pi^A(x)-\pi_i^B}{\Gamma+\langle\pi_i\rangle}$
Local update $p_{B\to A} = \frac{1}{2}+\frac{w}{2}\frac{\pi_i^A-\pi_i^B}{\Delta\pi_{\max}}$	(ordinary) Replicator equation $\dot{x} = \kappa x(1-x)(\pi^A(x)-\pi^B(x))$
Fermi process $p_{B\to A} = \frac{1}{1+\mathrm{e}^{\mp w(\pi_i^A-\pi_i^B)}}$	a nonlinear Replicator equation (TNP) $\dot{x} = \kappa x(1-x)\tanh(\pi^A(x)-\pi^B(x))$

- Speed of evolution: Moran process fixates faster
- Consequence: Drift reversal in asymmetric conflicts

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Drift reversal in asymmetric conflicts

Battle of the Sexes (Richard Dawkins)

- Payoff benefit for a child: $b = 15$
- Total cost of raising an offspring: $-2c = -20$, covered by both parents (except philanderer males meet fast females)
- Prolonged courtship (coy females insist on) costs both a burden of $-a = -3$

		Female	
		Coy	Fast
Faithful Male		2	5
		2	5
Philanderer		0	−5
		0	15

		Female	
		Coy	Fast
Faithful Male		−1	+1
		+1	−1
Philanderer		+1	−1
		−1	+1

The normalized payoff matrix qualitatively preserves the cyclic dominance.




Asymmetric conflicts: BOTS $P_x = \begin{pmatrix} +1 & -1 \\ -1 & +1 \end{pmatrix} = -P_y$

Standard replicator equations:

$$\begin{aligned} \dot{x} &= -2\,w\,x(1-x)(2y-1) \\ \dot{y} &= +2\,w\,y(1-y)(2x-1) \end{aligned}$$

Constant of motion $H = -x(1-x)y(1-y)$: $\rightarrow$ Closed trajectories.

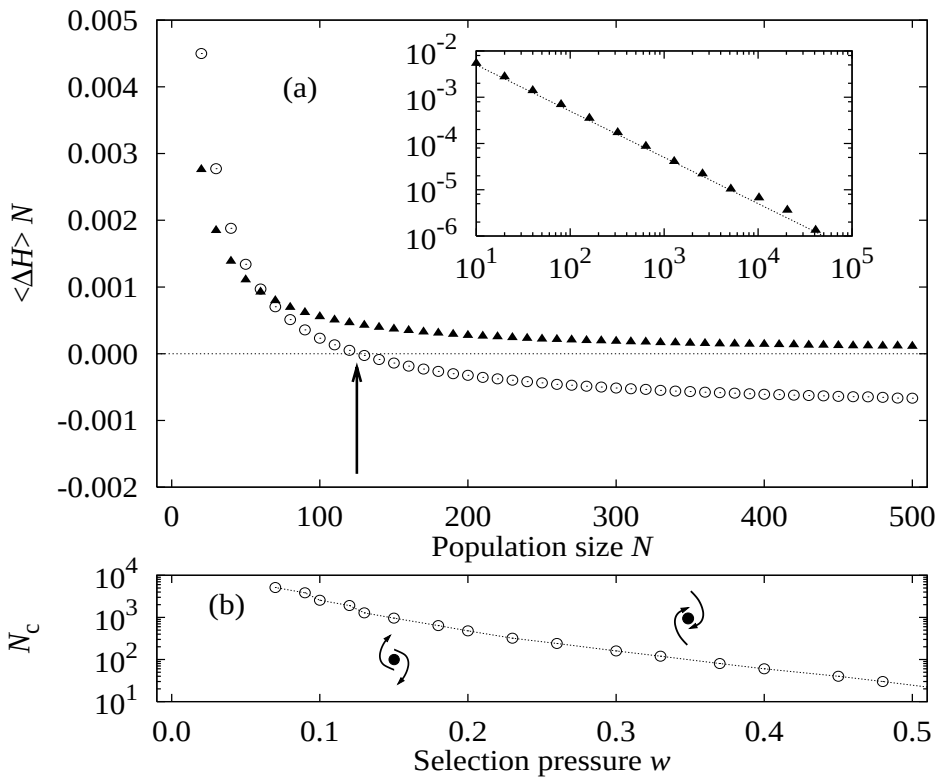
Adjusted replicator equations:

$$\begin{aligned} \dot{x} &= -2\frac{x(1-x)(2y-1)}{\frac{1-w}{w}+(2y-1)(2x-1)} \\ \dot{y} &= +2\frac{y(1-y)(2x-1)}{\frac{1-w}{w}-(2y-1)(2x-1)} \end{aligned}$$

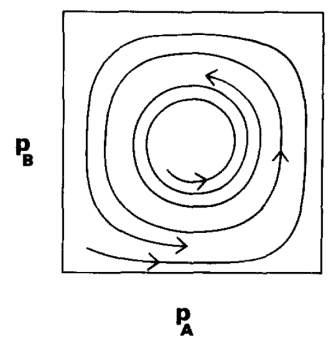
$\dot{H} \leq 0$. For $t \rightarrow \infty$: Nash eq. $(\frac{1}{2}, \frac{1}{2})$

Qualitatively different behavior!

Finite-size influence in asymmetric conflicts



Battle of the sexes for finite population size N. ($1 - w =$ backgr. fitn.)



- Replicator dynamics ($N \to \infty$) predicts eternal oscillations... Spurious result!
- Local update (▲): System spirals to the absorbing boundaries $\langle \Delta H \rangle > 0$.
- Moran process (○): For $N > N_c$ a drift reversal occurs towards the Nash eq. $(\frac{1}{2}, \frac{1}{2})$.
- In finite populations, the Battle of the Sexes always comes to rest.

Drift reversal: when and why?

Claussen (2007), submitted

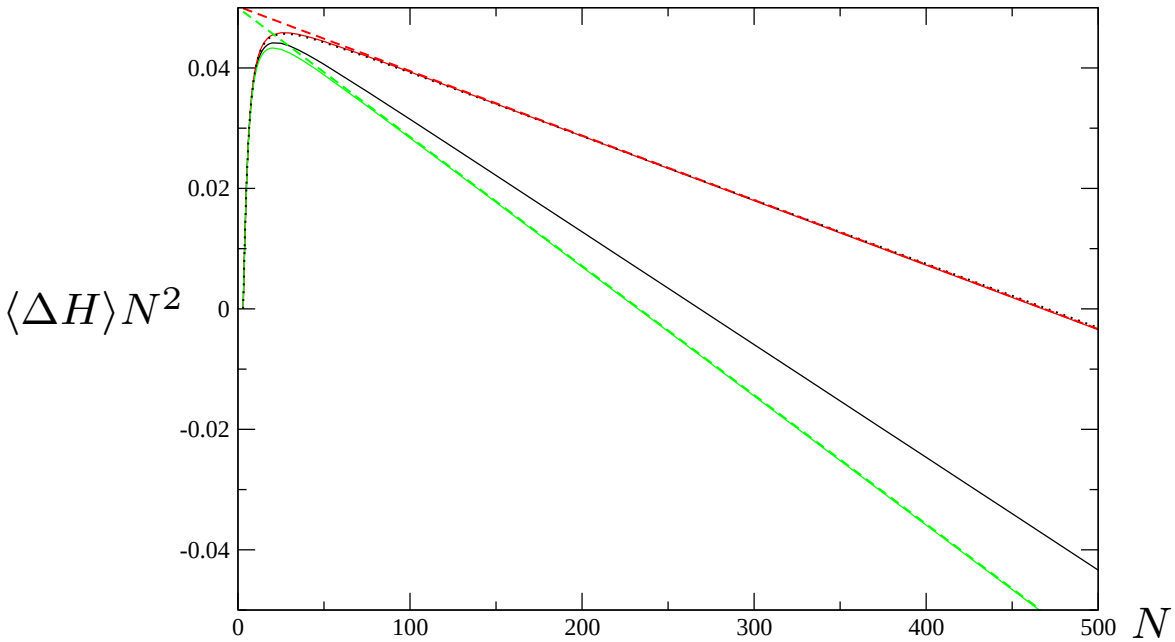
- Again, consider the zero-sum "Battle of the Sexes" with $(+1, -1)$ payoffs.
  Average drift can be calculated analytically!
  - Neutral case (payoffs zero): $\langle \triangle H \rangle_{\text{neutral}} = \frac{1}{18N^2}$, drift $\rightarrow$ outwards.
    Can be overriden by a $o(1/N)$ term $\leftrightarrow$ $\exists N_c$ where sign changes $\leftrightarrow$ "drift reversal".
  - Local update ($\&$ pairw.comp.), Fermi, ... *(quite general class!!!):* no drift reversal

- Now consider two limits of weak selection!
  - (Frequency-dependent) Moran process $\Phi_m^A = \frac{1-w+w\pi^A}{1-w+w\langle \pi_m \rangle}$ drift reversal occurs!
    (and can be calculated by expanding in $o(w)$ properly, confirming numerics...)
  - Moran process, linearized at process level, $\Phi_m^A = 1 + w(\pi^A - \langle \pi_m \rangle)$ no drift reversal!

- $\rightarrow$ For asymmetric conflicts, stability subtly depends on the underlying process.

Drift reversal also in RPS?

- For the zero-sum game with $(+1, -1)$ payoffs drift always goes outwards.
- For $(+1, -s)$ payoffs (and $s < 1$) again a drift reversal occurs!



(Claussen & Traulsen 2005/2007)

- Can be calculated analytically! – Linear processes (dashed) fit well.
- Drift reversal (due to "cooperative" payoffs) occurs for all processes (but N_c varies)

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  Answers an open question asked by John Maynard Smith (1982)!
- First-order corrections have the form of a Fokker-Planck equation

  Noise is multiplicative and frequency-dependent!

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  Answers an open question asked by John Maynard Smith (1982)!
- First-order corrections have the form of a Fokker-Planck equation
  Noise is multiplicative and frequency-dependent!
- Different scenarios result! – Finite-size dependent drift reversal.
  For finite populations, the Battle of the sexes always comes to rest.

Claussen & Traulsen PRE 71, 025101(R) (2005), Traulsen & Claussen PRE 70, 046128 (2004)
Traulsen, Claussen & Hauert PRL 95, 238701 (2005) & PRE 74, 011901 (2006)
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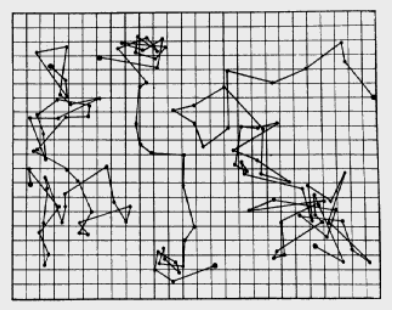
The Raleigh particle: an analogy from physics

- Stochastic motion of a large particle (mass M)

  driven by collisions with small particles (mass m)[a]

  Einstein/Perrin: $D = \frac{RT}{6\pi\nu a N_{\mathrm{A}}}$

  ($R =$ gas constant, $\nu =$ viscosity, $a =$ particle radius)



- Motion of the large particle for large (but finite) M/m:

  Can be described with a Fokker Planck equation

  with a fluctuations term scaling with $\sqrt{m/M}$ (van Kampen)

- For $M/m \to \infty$ again a deterministic trajectory is obtained.

[a] J. B. Perrin, Les Atomes, Paris, Alcan, 1913.

Dawkins Battle of the Sexes

Dawkins Battle of the Sexes

	Female: Coy	Female: Fast
Male: Faithful	-1, 1	1, -1
Male: Philanderer	1, -1	-1, 1

$(\pi_{♂}, \pi_{♀})$	$A_{♀}$	$B_{♀}$
$A_{♂}$	$(+1, -1)$	$(-1, +1)$
$B_{♂}$	$(-1, +1)$	$(+1, -1)$

- If males (♂) are philanderers ($B_{♂}$), it pays for females (♀) to be coy ($A_{♀}$),

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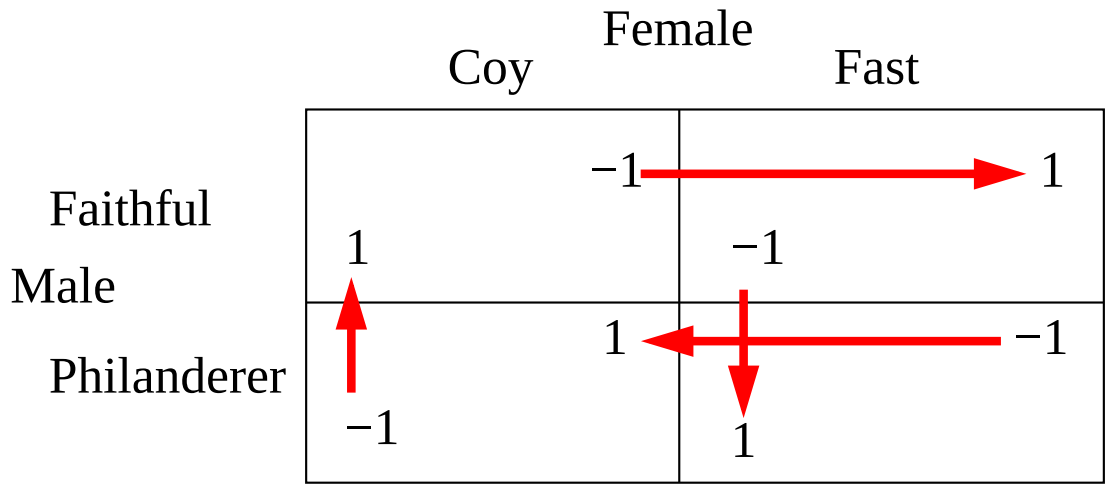

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- However, once most males are faithful ($A_{♂}$), fast females are favored ($B_{♀}$) avoiding the costs of courtship.
- Subsequently, the male investment into the offspring is no longer justified, philanderers are again favored ($B_{♂}$), and the cycle continues. Corresponds to ‘Matching pennies”.

Qualitatively different dynamics for adjusted/standard replicator equations!