The rock-paper-scissors (RPS) game everywhere

Barry Sinervo
Frequency-dependent selection

Negative FDS (self-limitation), stabilizing
• Rare advantage
  apostatic selection, cryptic types
• Common disadvantage
  self poisoning, overly aggressive strategy

Positive FDS (self-reinforcing), destabilizing
• Aposematic selection (Fisher 1930)
  Model with a signal reinforced by toxicity
• Cooperation
Male color morph cycle
NSF support 1989-2010

RPS cycle

Paternity results:
Zamudio & Sinervo, PNAS, 2000
Calsbeek & Sinervo, PNAS, 2003
Calsbeek & Sinervo, JEB, 2003
Sinervo & Clobert Science, 2003
Sinervo et al. PNAS, 2006

Genetics (theory & data):
Sinervo, Genetica, 2001
Sinervo et al., Evolution, 2001
Sinervo et al., PNAS, 2006
Lacerta
Louvie, 3 sites: LT, LC, LS

Lacerta
Aubisque

Lacerta
Gabas
Lacerta vivipara
Rare Strategy

Common Strategy
True RPS (in discrete time)

<table>
<thead>
<tr>
<th>Rare genotype</th>
<th>Common genotype</th>
<th></th>
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</thead>
<tbody>
<tr>
<td></td>
<td>$r$</td>
<td>$s$</td>
</tr>
<tr>
<td>$r$</td>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>$s$</td>
<td>$\frac{1}{2}$</td>
<td>1</td>
</tr>
<tr>
<td>$p$</td>
<td>2</td>
<td>$\frac{1}{2}$</td>
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</table>

![Bar chart showing the frequency of r, s, and p]
Mating system RPS

• **Side-blotched lizards** (Sinervo & Lively 1996)
• **Female damselflies** (Svensson et al 2005)
• **Isopods** (Shuster and Wade 1991)
• The Ruff (Lank et al. 1995, Jukema Piersma 2006)
• Gouldian Finches (Pryke et al. 2005)
• **Blue-gilled sunfish** (*Gross 1991*)
• Elephant seals (Lebeouf 1972)
• **European common lizards** (Sinervo et al. 2007)

RPS everywhere

• *E. coli* -- Bacterial RPS (Kerr et al. 2002)
• Public Goods Game (Seemann et al. 2004)
• Brood Parasites (Sinervo, Kuchta, Lyon in prep.)
• Aposematic mimics (Kuchta & Sinervo in prep.)
Cooperation versus Scissors

B Altruism versus O

Rock versus Usurpation

B mutualism versus Y

Paper versus Deception

Sinervo et al. (2006) PNAS
Where do the three strategies of the RPS come from?

Let us consider the pairs of players:

OB, OY, and BB
Hawk-Dove

Blue vs Orange resembles HD
Yellow vs Orange resembles HD

Is the relationship between cooperating blue males a Prisoner’s Dilemma?
Beneficiary -- gains fitness from the social interaction with a genetically similar male.

Altruist -- Looses fitness from the social interaction.

Note the variation in the number of O males.

Most bb are “Loners” and do not find a genetically similar male.
$N_0(t)$ for $bb$ males

$W(t) =$ Fitness or recruits

Year

Beneficiary
Donor (Altruist)
Loner
$\begin{array}{c|c|c}
C & \text{cooperate} & \text{sucker's payoff} \\
D & \text{temptation} & \text{punishment} \\
\end{array}$

$D\vert C > C\vert C > D\vert D > C\vert D$

- $D\vert C$ is referred to as the temptation to defect.
- $C\vert C$ is referred to as mutual cooperation
- $D\vert D$ is the punishment for mutual defection
- $C\vert D$ is the sucker's payoff

Player A should defect as $D\vert C$ is the best payoff. However, player B should do the same. When both defect they get the worst payoff. In the long run then it pays to Cooperate as it provides the second highest payoff. Therein lies the dilemma. The prisoner’s dilemma always applies for payoffs with a reward structure as follows:

**Temptation > Cooperation > Mutual defection > Sucker's payoff**
When Orange is Common: payoffs to blue strategies

<table>
<thead>
<tr>
<th></th>
<th>C</th>
<th>D</th>
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<tbody>
<tr>
<td>C</td>
<td>0.4</td>
<td>0</td>
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<tr>
<td>D</td>
<td>0.7</td>
<td>0.2</td>
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D|C > C|C > D|D > C|D
When Yellow is Common: payoffs to blue strategies

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<tr>
<td>C</td>
<td>0.7</td>
<td>0.3</td>
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<tr>
<td>D</td>
<td>0.3</td>
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The RPS as 3 two-strategy games

Iterated
Prisoner’s Dilemma

Hawk-Dove

Deception

Hawk-Dove
Two kinds of RPS

- Apostatic RPS (damselflies): rare advantage to both strategies, and common disadvantage

- True RPS (*Uta* lizards): rare advantage to only 1 strategy, disadvantage to the other

- Isopods (Apo-True mixed)
# True RPS

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</table>

![Bar chart](image.png)
True RPS

Payoff Matrix

Siring Success

Rare
Common

Genetics  oo, bo, yo  bb  by, yy

10X

Evolutionary Dynamic

Sinervo and Calsbeek AREEs 2006
Apostatic RPS

Payoff Matrix

<table>
<thead>
<tr>
<th>Fecundity</th>
<th>A I IO</th>
<th>A I IO</th>
<th>A I IO</th>
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<tbody>
<tr>
<td>Rare</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
<tr>
<td>Common</td>
<td>1</td>
<td>2</td>
<td>4</td>
</tr>
</tbody>
</table>

Genetics: $aa, ai, ao$  $ii, io$  $oo$

Evolutionary Dynamic

Sinervo and Calsbeek *AREES* 2006
Based on Svensson et al. *Amer. Natur.* 2004
Female morph RPS in butterflies
*Papilio dardanus*
Clark & Peddard 1960
Cook et al. 1994

Black and white Batesian mimic of
*Amauris niavius niavius*

**hipponcooonides**

*trimeni*
Male mimic

*lamborni*
Ageing male mimic
Mixture of the True and Apostatic RPS

Sinervo and Calsbeek AREES 2006

Perfect female mimic
Jukema Piersma (2006)
The Ruff

Sinervo 2001

Move to new Lek

Cooperate to attract males

Benefits from many Residents?

Gouldian finches, *Chloebia gouldiae*, photo by Sara Pryke
Gouldian finches

Red (30%)

Assortative mating

Black (70%)

Assortative mating

Yellow (0.1%)
Bluegill Sunfish are an RPS

Gross et al. 1982
Gross 1991
Fu et al. 2000

Reanalysis of data from Mart Gross’ lab by Sinervo, unpublished
Salmon

Gross 1994 and Others,
Reanalysis of data ongoing by Sinervo & J. Moore
Size Polymorphism in *Xiphophorus*

- Male growth is relatively determinate.
- Growth nearly ceases at maturity.
- There is variation in time to and size at maturity leading to polymorphism.
- *X. nigrensis* exhibits three size morphs.
- Y-linked gene

*Peocilia parae*, an ancestor of the common guppy

Godfrey Bourne et al. *Naturwissenschaften* 2003

Felix Breden et al. *Heredity* 2004
Rock-Paper-Lizards-Scissors-Spock

It's simple:
- Scissors cuts paper
- Paper disproves spock
- Spock vaporizes rock
- Rock crushes scissors
- Lizard eats paper
- Paper covers rock
- Rock crushes lizard
- Lizard poisons spock
- Spock smashes scissors
Or hand symbology

- Paper covers Rock
- Paper cuts Scissors
- Rock crushes Lizard
- Rock vaporizes Spock
- Lizard poisons Scissors
- Lizard smashes Paper
- Scissors crushes Rock
- Spock poisons Paper
- Scissors smashes Lizard
Lacerta
Louvie, 3 sites: LT, LC, LS

Lacerta
Aubisque

Lacerta
Gabas
Lacerta vivipara

A) Common adult o
   Fitness o recruits
   P = 0.01

   Fitness w recruits
   P = 0.05

   Fitness y recruits
   P = 0.05

   Adult male o allele
   P = 0.04

   Adult male w allele
   P = 0.01

   Adult male y allele
   P = 0.58
Rare Strategy

Common Strategy
Podarcis millesenensis (Croatia, Lastovo)

Podarcis muralis (France Pyrenees)

Podarcis milensis (Greece, Milos)
Sceloporus minor, a Mexican species with the RPS
Barry Stephenson et al.
**E. coli RPS cycle**

Toxin producing

Resistant \[\rightarrow\] Undefended

Kin altruism:
Large fields at junction between clones undergo lysis to release toxin!

Kerr et al. 2002 *Nature*
Elephant seals and a life history RPS

\[ \alpha \]

\[ \beta=6,7,8 \]

\[ \gamma=3... \]

Elliot et al. in prep.

Sinervo, Habib and Friedman
Public goods game

Cooperate

Loner

Defect

Seemann et al. *Nature* 2004
Hauert et al. *PRSB* 2006
Intended and Unintended Receivers
Communication Theory for Signalers and Receivers

Cooperate

Aggression

Deception
Ecosystem RPS

• Human ecology – public goods game
  Seemann et al. Nature; Friedman (UCSC Econ) & Sinervo in prep.

• Aposematic Mimicry
  Sinervo and Shawn Kuchta (Post-doc) in prep.

• Brood parasites
  Sinervo and Bruce Lyon (UCSC) in prep.

• Ant (mutualist/cheater)-Aphid-Predator
  Kailen Mooney and Sinervo (UC Irvine)

• Plant - Mutualistic Ant - Cheater Ant
  Sinervo and Paulo Guimarães (UCSC) and Thiago Izzo
  (Universidade Estadual de Campinas, Sao Paulo)

• Plant – Pollinator – Nectar Robbers
  Sinervo and Kathleen Kay (UCSC)
  Christophe Thebaud, E. Tastard (CNRS) and Sinervo
Ecosystem RPS
Two population games!

- Brood parasites
- Aposematic Mimicry
- Mimicry, Crypsis systems
- Competition
Brood parasitism as an RPS

Egg rejection Strategies

HONEST

DISHONEST

Beats the DISHONESTY

Parent

Offspring Conflict

Parent

Begging

Chick

RPS

Brood Parasite

Extreme mimicry

+ve Aggregation with self

DISHONEST
Phenotypic Variation in the salamander *Ensatina eschscholtzii*

Blotched subspecies are distributed along the inland axis

Un-blotched subspecies are distributed along the coastal axis

*E. e. xanthoptica* is a Batesian mimic of newts (*Taricha*)

Northern populations of *E. e. eschscholtzii* may also possess aposematic colors
Sinervo, Martin, & Kuchta, unpublished
Predation Experiment at UCSC using clay replicas of salamanders

Sinervo, Martin, & Kuchta, unpublished
Does the Western Jay Care about the color?
The Jay’s perspective: Individual variation among jays

Time to First Contact

- Taricha torosa
- E. e. xanthoptica
- E. e. oregonensis

Seconds

Individual Western Scrub Jays
Learning Crypsis systems
Rock-paper-scissors and Predator learning

With Costs = 0.6 for model (relative to 1 for no costs)
The game space sectored
The cycling gamescape
Crypsis and Thermoregulation

With Mitchel Mulks
Aposematism and Mimicry in California Mountain Kingsnakes

PREDATOR

MODEL

CRYPTIC
Crypsis and Thermoregulation

MIMIC

Tradeoff
Network Theory
A) **HD or snowdrift**

- **r-K game**

- **stable point**

- **a**

- **b**

- **c**

- **c invades**

- **c is lost**

- **stable oscillator**

B) Network evolves a short-circuit due to FDS:

- **d evolves to exploit b.**

C) Three entrained RPS systems with flow reversal (c→b, changes to b→c)

- **Network evolves short-circuits due to FDS**

D) **RPS for b,c,d**

- **a**

- **b**

- **c**

- **d**

- **c contributes least to FD flow**

- **c is lost**
Milo et al 2002 - Networks of 3 and 4 nodes

A

\( X \rightarrow Y \) represents

- transcription network
- neuron synaptic connection network
- ecological food web

gene x gene y

B

1 2 3 4 5 6 7
8 9 10 11 12 13

A

real network

B

randomized networks

Concentration of Feedforward loop vs Subnetwork size
Milo et al 2002 - Networks of 3 and 4 nodes

<table>
<thead>
<tr>
<th>Network</th>
<th>Gene regulation (transcription) E. coli S. cerevisiae</th>
<th>Feed-forward loop</th>
<th>Bi-fan</th>
</tr>
</thead>
<tbody>
<tr>
<td>Neurons C. elegans</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Food webs</td>
<td></td>
<td></td>
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<tr>
<td>Electronic circuits (forward logic chips)</td>
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<tr>
<td>Electronic circuits (digital fractional multipliers)</td>
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<tr>
<td>World Wide Web</td>
<td></td>
<td></td>
<td>Four-node feedback loop</td>
</tr>
</tbody>
</table>

- **Feedback with two mutual dyads**
- **Fully connected triad**
- **Uplinked mutual dyad**
- **Three chain**
- **Bi-parallel**
- **Bi-fan**
- **Bi-parallel**
Rock-Paper-Scissors and Ecosystem Analysis

A) +ve cooperation

B) +ve Innate or Learning Reinforcement

C) altruism

D) +ve Parent Care

E) +ve Immunity or immune memory
Frequency-dependent selection

Negative FDS (self-limitation), stabilizing

• Rare advantage
  apostatic selection, cryptic types

• Common disadvantage
  self poisoning, overly aggressive strategy

Positive FDS (self-reinforcing), destabilizing

• Runaway sexual selection (Fisher 1930)
  male trait, female preference

• Aposematic selection (Fisher 1930)
  Model with a signal reinforced by toxicity

• Cooperation