Biological institutions: an institutional perspective on biological cooperation

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Diversity of life
Diversity of interactions
Cooperative interactions make life as we know it.

Natural selection shapes cooperation.
Ingredients of social evolution theory

<table>
<thead>
<tr>
<th>Cooperate</th>
<th>Don't cooperate</th>
</tr>
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<tr>
<td>Cooperate</td>
<td>R₁, R₂, S₁, T₂</td>
</tr>
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- Reproduction
- Dispersal of young
- Competition/Mortality

Behavioral dynamics & proximate mechanisms

Population structure (relatedness)
Ingredients of social evolution theory

**Game**

- **Cooperate**
  - \( R_1, R_2 \)
  - \( T_1, S_2 \)

- **Don't cooperate**
  - \( S_1, T_2 \)
  - \( P_1, P_2 \)

**Behavioral dynamics & proximate mechanisms**

**Life cycle**

- **Reproduction**
- **Dispersal of young**
- **Competition/Mortality**

**Population structure (relatedness)**
Ingredients of social evolution theory

- Reproduction
- Dispersal of young
- Competition/ Mortality
- Life cycle
- How do the games themselves and the way organisms play them evolve?

Behavioral dynamics & proximate mechanisms

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Cooperation in nature: examples

Potato grouper (*Epinephelus tukula*) being attended by cleaner wrasses (*Labroides dimidiatus*)
A cleaner fish economy

Some facts:

- Clients react to “cheating” by leaving
- Clients observe other clients’ interactions
- Cleaners prioritize fish that have choices
- Cleaners can learn new “rules of the game” in experiments

=> A market for cleaning services.

Some cleaning will most likely take place, but is it going to be efficient? Is there going to be “money left on the table”?
A cleaner fish economy

Some facts:

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=> A market for cleaning services.

Some cleaning will most likely take place, but is it going to be efficient? Is there going to be “money left on the table”?

Things like “false advertising” will reduce cooperation. (cleaners behaving differently when watched, and not otherwise)
Similar to the problem of merchants without international law in the Mediaeval Europe.

Long-distance trade, weak & small states: no guarantee that a foreign merchant or ruler of a foreign country will not cheat you.

Reputation effects by pure word of mouth inefficient.
The law merchant model (Milgrom et al. 1990): an institution for efficient record-keeping.

Designate some private individuals as arbitrators of disputes and keeper of records.

At equilibrium: everyone pays to check their counter-parties’ records and to arbitrate any disputes.

Provides effective incentives against cheating

(new problem: how to keep the law merchant from cheating?)
Cooperation in nature: examples

Fishy law merchants?

Cleaner wrasse territories often include small, resident clients.

Small residents get short shrift when compared to big roamers.

But can potentially give information to roamers about the resident client’s cooperativeness.

No explicit memory is needed: parasite loads of the small residents or tendency to visit the cleaner might be enough to signal cleaner cooperativeness.

Prediction: roaming clients should prefer cleaners with small resident clients that are in good shape.
Institutional perspective: a theory for natural history

Natural history of an interaction describes:

who interacts with whom, when, what strategies, information are available, in other words, “the rules of the game”.

Conventional evolutionary ecology takes natural history as given

Institutional perspective would ask how the rules themselves evolve.
This has been a very successful strategy. Not about to replace it, or drop it altogether.
Evolving games

How does natural selection act on structure of games?
How do game structure and individual behavior co-evolve?
Changing the game: perfect information

Take the Prisoner’s Dilemma game (aka the Dear Enemy game)

<table>
<thead>
<tr>
<th></th>
<th>make peace</th>
<th>fight</th>
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<tr>
<td>make peace</td>
<td>3, 3</td>
<td>0, 5</td>
</tr>
<tr>
<td>fight</td>
<td>5, 0</td>
<td>1, 1</td>
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Individually optimal to fight, but that’s mutually costly; hence the dilemma.
Changing the game: perfect information

Suppose a mutation arises that leads one bird to fight less viciously

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<td>make peace</td>
<td>3, 3</td>
<td>1.0, 3.5</td>
</tr>
<tr>
<td>fight</td>
<td>5, 0</td>
<td>1, 1</td>
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An “incentive” for the row-player to make peace with the incentive, even selfish individuals would cooperate.
Changing the game: perfect information

A diploid, well-mixed population with no assortative mating.

Two alleles:
Allele A codes for the original social dilemma
Allele B codes for an incentive “payment” $b$, but carries a direct cost $c$

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<thead>
<tr>
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<tbody>
<tr>
<td><strong>AA</strong></td>
<td></td>
<td></td>
</tr>
<tr>
<td>cooperate</td>
<td>$r, r$</td>
<td>$s, t$</td>
</tr>
<tr>
<td>defect</td>
<td>$t, s$</td>
<td>$p, p$</td>
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<td>cooperate</td>
<td>$r, r-c$</td>
<td>$s+b, t-c$</td>
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<tr>
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Original game

Game with the heterozygous mutant
Invasion of incentives

The original game; inefficient outcome (NE: Nash-equilibrium)

The game between the heterozygotes; efficient outcome

In a symmetric game, the outcome of an invasion is a diversity of games persisting in the population. Cooperating individuals on average are worse off than defecting ones. But cooperation persists: Diversity is not in the strategy, but in the games!
Changing the game through behavioral responses

Repeated PD w/ non-additive payoffs

Define responsiveness, $p$: Probability of copying the opponent’s action in last round

If not reciprocating, follow “intrinsic preference” (C or D)

<table>
<thead>
<tr>
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<th>D</th>
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<tbody>
<tr>
<td>C</td>
<td>b-c+d</td>
<td>-c</td>
</tr>
<tr>
<td>D</td>
<td>b</td>
<td>0</td>
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Suppose intrinsic cooperator plays
intrinsic defector;

Responsiveness of players of both
types: $p$

if at round $t$, they play \{C,D\}
Suppose intrinsic cooperator plays intrinsic defector.

**Discrete, non-additive case**

<table>
<thead>
<tr>
<th>Outcome</th>
<th>{C,C}</th>
<th>{C,D}</th>
<th>{D,C}</th>
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<tr>
<td>Probability @stationary distribution</td>
<td>(p/(1-p)^2)</td>
<td>(1/(1-p)^2)</td>
<td>(p^2/(1-p)^2)</td>
<td>(p/(1-p)^2)</td>
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Responsiveness of C- and D- players:

- \(p_c\)
- \(p_d\)

So we can look at the stationary distribution of outcomes.
### Transforming the evolutionary game

#### Evolutionary game

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<td><strong>b+d-c</strong></td>
<td>( \frac{p(bp + b + d) - c(p + 1)}{(1 + p)^2} )</td>
</tr>
<tr>
<td><strong>p(b - c + d) + b - cp^2</strong></td>
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#### Behavioral game

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\frac{p(bp + b + d) - c(p + 1)}{(1+p)^2}
\] |
| Intrinsic defector | \[
\frac{p(b - c + d) + b - cp^2}{(1+p)^2}
\] | 0 |

#### Diagram

- **Stag Hunt (coordination)**
- **Mutualism**
- **Prisoner’s Dilemma**
- **Hawk Dove**

Probability of reciprocating (responsiveness), \( \rho \)
Transforming the evolutionary game

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Responsiveness (p) and synergism (d) interact synergistically.
Changing the game: imperfect information

Why are benefits from group living divided equally (low skew) in some species and unequally (high skew) in others?

Low skew (egalitarian)  High skew (despotic)
Reproductive transactions theory

central hypothesis:
Natural selection favors a division of reproduction such that all group members are better off within the group than outside.

Sandra Vehrencamp

NC: non-cooperative outcome
Reproductive transactions theory

Where exactly the outcome ends up depends on model assumptions

Also, how skew varies with relatedness, outside options, etc.

Indeterminacy is due to perfect information assumption

Dominant’s “outside option”

Subordinate’s “outside option”

Range of divisions compatible with cooperation

NC: non-cooperative outcome
If there is variation in outside options

Individuals will be uncertain about their partner’s outside options

Trade-off between losing out on cooperation and getting a larger share

Outcome still depends on what game they play
Imperfect information

If there is variation in outside options
Individuals will be uncertain about their partner’s outside options

Trade-off between losing out on cooperation and getting a larger share

Outcome still depends on what game they play
=> Apply mechanism design to get “game-free” results
Game setup

Take two males: Male 1 and Male 2, related to each other with $r$.

They can either form a group, or breed alone.

Each expects a breeding success of $T_1$ and $T_2$ when breeding alone. Privately known; probability distributions $F_j(T_j)$ commonly known.

When breeding together, the total group reproduction will be $\Omega$. Commonly known

Male 1 gets $x$ out of $\Omega$; Male 2 gets $\Omega-x$ ($x$ to be determined)
Analog to bilateral trade

The canonical trade problem (Myerson & Satterthwaite)
A seller has an item that’s worth $v_s$ to her, and $v_b$ to a potential buyer. Valuations are privately known.

Negotiate a price at which both are willing to trade (which exists whenever $v_b > v_s$)

(substitute $T_i$ for $v_s$ and $\Omega - T_j$ for $v_b$)

Reproductive skew w/ imperfect information = Myerson&Satterthwaite w/ other-regarding preferences.
When cooperating may not be mutually beneficial and unless relatedness is high enough

**no game exists that allows natural selection to guarantee cooperation whenever it is mutually beneficial**

\[- \int_{a_2}^{b_2} F_1(t)(1 - F_2(t))dt + r \int_{a_1}^{a_1+b_2-a_2} F_1(t)(1 - F_2(t))dt \geq 0\]
When cooperating may not be mutually beneficial and unless relatedness is high enough, **no game exists that allows natural selection to guarantee cooperation whenever it is mutually beneficial.**

\[
- \int_{a_2}^{b_2} F_1(t)(1 - F_2(t))dt + r \int_{a_1}^{a_1 + b_2 - a_2} F_1(t)(1 - F_2(t))dt \geq 0
\]

**Will natural selection acting on game structure (non-direct mechanisms) result in second-best outcomes?**
Concluding remarks

In biology as in economics, conflict between individual interest and collective benefit is a common theme.

Institutions in human life frequently (but not always) align individual interest with common good.

Hypothesis: natural selection shapes many interactions in nature to do the same, within informational and commitment constraints.
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