Mutualists Don't Look Back in Anger

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Economics slides

Biggest problem in theory of symbiosis: two theories

- Ed Wilson on NPR: biggest problem cooperation
  - Advanced organisms=cooperating sub-organisms
- Inter-specific more challenging: no inclusive fitness
- Concrete examples: ant-plant mutualism
  - Ants protect plant from herbivores, plant gives food+shelter
  - Why don't ants slack off, collect food instead?
- Two major theories
  1. *Partner Fidelity Feedback* (PFF)
     - Bull et. al. (1991), Sachs et. al. (2004) survey
     - If plant dies, ants lose home; natural feedback enough
  2. *Host Sanctions* (HS)
     - Denison (2000) propose, West et. al. (2002)
     - Natural feedback *insufficient*
     - Plant punishes ants for bad behavior to sustain cooperation

Role of economics

Theories certainly distinct, but conflated

- Edwards et. al. (2006) find shoot dies after leaves eaten
- Waste to keep alive or means of punishment?

Economic theory can formalize, help distinguish

- PFF like rehabilitation, incapacitation
- HS more like deterrence, “look back in anger”
    - Becker (1968): minimize cost of punishing by severity
- Plants know how to deal with enemies
    - If HS, should observe this behavior towards ants...
    - Fact that we don’t already strong indication for PFF
- But maybe plant limited in how it can react
    - With economic model, still two sharp experiments
        1. Punishment-value signals indicating or not cheating
        2. Cheating actions giving rationale or not for “punishment

Outline

1. Model
2. Formal definition of theories
3. Testable predictions
4. Experimental application: *Allomerus*-*Cordia* system
   - Introduce system
   - Applying the experiments
   - (Predicted) Results
5. Existing application: *Rhizobia*-legume interactions
6. Discussion and conclusion

Model

- *Agent* takes good action $a^\star$ or bad a_1, a_2
- *Principal* gets signal $S = \{s_1, \ldots, s_N\}$
  - *Smoking guns* for a_1, a_2 are S_1, S_2
- Principal decides on punishment π
- Payoffs

1. Principal: $u^P(s, \pi)$, concave in π
2. Agent: $u^A(a, s, \pi) = \underbrace{u^s(a)}_{\text{short-term}} + \underbrace{fu^P(s, \pi)}_{\text{PFF}} - \underbrace{\pi}_{\text{punishment}}$
   - $f \in [0, 1]$
3. Principal has a *policy* $\pi(s)$
   - Natural policy is *prospectively optimal* $\pi^\star(s) \equiv \text{argmax}_\pi u^P(s, \pi)$
   - Payoff under policy $U^A(a; \pi)$ is expected payoff to agent

Formalizing the theories

Key assumption of equilibrium underlies all tests:

Assumption

Subject to constraints of theory, actions optimal.

Now we can define theories

Definition

PFF: $\pi^\star$ used and $U^A(a^\star;\pi^\star) > U^A(a_1;\pi^\star), U^A(a_2;\pi^\star)$

"No commitment"

Definition

a_1 disciplined by HS if $U^A(a^\star;\pi^\star) < U^A(a_1;\pi^\star)$ and minimum cost enforcement: π used has $U^A(a^\star;\pi) = U^A(a_1;\pi)$

Solved by Holmström (1979), spirit of Becker (1968)

Test 1: comparing signals

- Clearly very different in theory
  - But in practice hard to measure full fitness function
  - Want generally applicable, clean experiments to test
- First experiment: compare punishment after two signals
  1. Find two signals, s and s' with $u^P(s, \cdot) = u^P(s', \cdot)$
  2. s smoking gun for a_1, s' not smoking gun at all
  3. HS says s must be punished more than s'
     - Otherwise wasting a chance to punish
     - Depends on smoothness, concavity
  4. PFF says should be equally punished
- Thus sharply distinguishes theories
- Easy, general methodology (see below)

Test 2: comparing cheats

Second experiment compares consequences two cheats

1. a_2 as much cheating as a_1: $u^s(a_2) \geq u^S(a_1)$
2. a_2 leads to, on average, at least as fit a principal
3. a_2 less punished, on average, under $\pi^\star$

- Then PFF says a_2 less punished than a_1
- But HS says a_2 at least as punished as a_1
  - Gives as much cheating benefit
  - So if less punished, then could punish a_1 less
  - Under HS, this would be cheaper

  $\Longrightarrow$ a_2 must be at least as punished
- Again sharp, simple, easy and general

Allomerus octoarticulatus and *Cordia nodosa*

- Work with Megan Frederickson, Doug Yu, Naomi Pierce
  - All experts on particular ant-plant mutualism in Amazon
  - Particularly common in Peruvian Amazon basin
- Many such mutualisms, but particularly abundant
  - Including really nasty ones (adulterer tree)
  - *Allomerus* attacks herbivores, particularly on new shoots
  - *Cordia* makes *domatia* at bottom of shoots for ants to live in
  - Only one colony (essentially an individual) per plant
- *Allomerus* has big benefits; protected plants grow faster
- Cost to protection: foraging, protecting brood, die in battle

Cordia plant

Figure: *Cordia nodosa* and its domatia (thanks to Gabe Miller)

Ants in their home

Figure: *Allomerus octoarticulatus* in domatium home (Mark Moffett)

Allomerus defending a new shoot

Figure: *Allomerus* defending a young *Cordia* shoot (Gabe Miller)

What happens without ants

Figure: *Cordia* without ants to defend it, being eaten (Gabe Miller)

Edwards et. al. (2006): evidence for HS?

- Edwards et. al. (2006) claim to find evidence for HS
  1. Cut off much of new shoot's leaves
  2. Domatium growth slows, or even falls off
  3. The more cut, the more domatium affected
- But plant would kill shoot anyway...
- Kill shoot to save or to punish?
- Regardless, natural frame for our test

Applying experiment 1

- Two different signals w/ opposite message, same fitness
  1. Let caterpillars eat some of the leaves
  2. Do same amount of damage mechanically (scissors)
- Both types of damage occur in nature (sticks)
- Plant can distinguish them (alarm chemicals)
- Same effect on prospective fitness value of shoot
  - But only caterpillar damage could indicate cheating
  - Twenty plants in each treatment+control for insecticide
    1. Exclude ants, let damage on one shoot
    2. Mechanical damage (scissors), same distribution as natural
  - Come back 28 days later and measure growth of domatium

Control group

Figure: A control group for experiment 1, protected from herbivores (Alison Ravenscraft)

Applying experiment 2

- Two different cheats, different effects on fitness
  1. Remove ants, exclude from new shoot
     - Good prospective fitness reason to kill shoot
  2. Remove ants (distributed damage, common)
     - No reason to kill anything, otherwise suicide
- But equal cheating benefit
  - Distributed removal better for plant (revealed preference)
  - Ant opportunity cost is lost foraging (number of ants)
- Again twenty plants in each treatment, again control
  1. Exclude ants from shoot, killing all ants on the shoot
  2. Remove ants typically killed in exclusion, but no exclusion
- Come back in 28 days, measure *all* domatia growth

Putting the experiment into action

Figure: Getting my hands dirty with data, literally (Megan)

Predicted results (if only economics were like this!)

- The beautiful thing about biology...
  - Is that people actually know something!
  - My co-author believes she knows exactly what will happen
  - Thus we can write the paper without knowing results...
  - Just plug in results at the end
  - Should have actual results within a week or two
- What Megan thinks will happen (PFF wins!)
  1. No difference between ways of cutting off leaves
  2. No “punishment” of distributed, but usual of concentrated
- Would give clear evidence of PFF over HS

Background on *Rhizobia*-legume mutualism

- We want to claim general methodology
- So would be useful to have another application
  - But who wants to run another damn experiment?
- So why not use others' data against them?
- Perfect opportunity is most famous example of "HS"
  - *Rhizobia*-legume mutualism
    - Legumes need ammonium ($NH4^+$) to create proteins
    - But much nitrate-poor
    - So legumes grow *nodules* in roots
    - *Rhizobia* bacteria live in nodules, fix nitrogen
    - In exchange, receive carbohydrates from plant
    - Why don't *Rhizobia* just not fix, take food and run?

Legume roots

Figure: Nodules on the root of a Soya bean plant (Inga Spence)

Rhizobia in a legume nodule

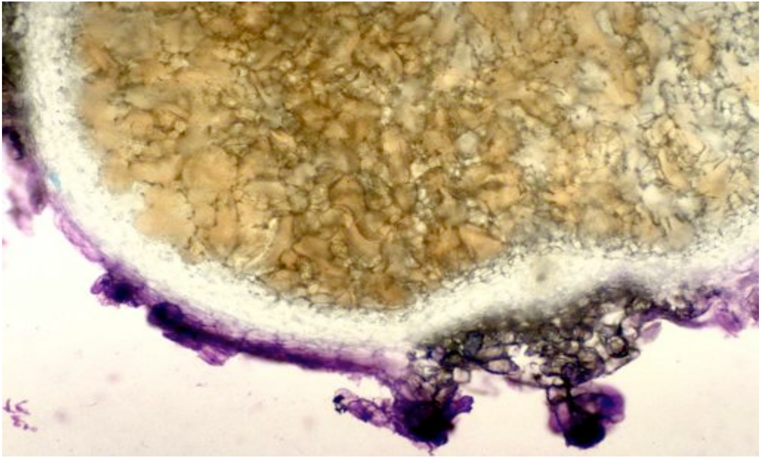

Figure: Nitrogen-fixing *Rhizobia* in a legume nodule (Inga Spence)

Kiers et. al. (2003): evidence for host sanctions

- *Rhizobia*-legume most famous example of claimed HS
- Force some *Rhizobia* to cheat, show legume punishes
  - Split-root system
  - Expose some nodules to Argon instead of Nitrogen

    $\Longrightarrow$ *Rhizobia* cannot fix
    - Forced to cheat
  - *Rhizobia* forced receive less carbs, tend to die
  - Evidence of HS (?)
- Alternative interpretation: plant senses gas
  - If so, no gain from Argon-exposed nodules
  - So no reason to give reward

    $\Longrightarrow$ Layoff not firing

The Kiers et. al. (2003) set-up

Figure: A soya bean root system in the lab (E. Toby Kiers)

Treating individual nodules

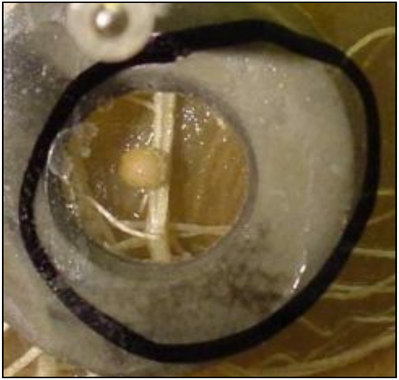

Figure: A gaseously isolated soya bean nodule (E. Toby Kiers)

Replacing with argon

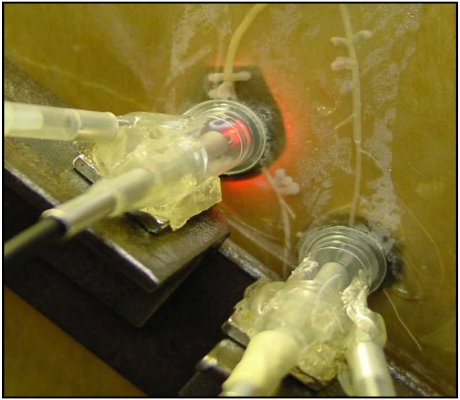

Figure: Replacing the N_2 in nodule with *Ar* (E. Toby Kiers)

Marco et. al. (2009) and Kiers et. al. (2006)

To implement our approach, need two things

1. Paired signal that doesn't indicate cheating
2. Paired cheating w/o fitness rationale for punishment

Luckily supplied by past research!

1. Kiers et. al. (2006): more Argon $\implies$ more punishment
   - Also providing more nitrates $\implies$ more punishment
   - But nitrates don't indicate cheating! Just reduces value
     - Nitrate saturation=pure Argon in $\pi^\star$
     - PFF $\implies =$ "punishment", HS $\implies > \pi$ of Argon
     - Not statistically distinguishable: PFF wins again!
2. Other half from Marco et. al. (2009): paired cheating
   - Knock-out fixing gene: cheating without changing value
   - Heath and Tiffin (2009) do with different natural species
     - Both: no effect on carbs to *Rhizobia*, fitness! PFF wins again

Why might contract theory not apply to biology?

- So, at least here, PFF seems right
- Indicates that contract theory may not apply well to biology
  - Ironic, given grant that supported us!
  - I couldn't make the shoe fit, which gave this paper
- Why not?
  - How would it evolve?
    - Have to make commitment; influence evolution of other
    - Maybe possible if life spans sufficiently different...
    - But seems hard to imagine
    - Ecological for one would have to be evolutionary for other
  - Also may require some memory

$\Longrightarrow$ Mutualists don't look back in anger! (you heard us say)

- Contracts/retribution needs higher cognition? Distinct to...?

Conclusion

Paper makes two contributions

1. General, clean methodology for testing theories
2. In two canonical systems, PFF beats HS

Suggests many directions for future research

- What we're working on
  1. Why doesn't PFF unravel backwards?
     - Rotten kid theorem and the end of the life-cycle
     - *Allomerus* and *Azteca* with *Cordia*
  2. Life-cycle limiting reagent? Broad empirical analysis
- Other ways to go
  1. Contract theory+: screening=partner choice (Archetti, Yu)
  2. Applying our methodology to other mutualisms
  3. Economics: formalizing biological theories for tests
     - Make bio-econ theory more applied/system-oriented

Thanks to Megan!

Figure: My co-author, Megan Frederickson, deserves special thanks for getting me interested in all of this (Gabe Miller)