# Evolution of motivations and behavioral responses
# Integrating the proximate and ultimate causes of behavior

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# Cooperation is ubiquitous

# Proximate and ultimate causation

- Proximate causes: mechanisms of behavior (e.g. hormones, firing of the neural circuitry, etc.)

- Ultimate cause: fitness consequences of behavior, selection

- Usual argument
  "Proximate questions are *different* than ultimate questions, need to be *separated*, but can *interact* and both are worthwhile"

- In practice, much more emphasis on separation, and at least for theory, much more emphasis on the ultimate causes

# Quotes

- Trivers, 2002 (p.7):
  "*You begin with the effect of behavior on actors and recipients; you deal with the problem of internal motivation, which is a secondary problem, afterward. [...]If you start with motivation, you have given up the evolutionary analysis at the outset.*"

- West et al., in press (Table 3)
  "*Proximate answers cannot provide a solution to ultimate problems.*"
  (in response mainly to attempts by Gintis and colleagues to explain human cooperation by strong reciprocity, which West et al. take as avoiding the question of evolutionary origin.)

# My take

- The ultimate vs. proximate distinction is logically sound
- But proximate mechanisms are still crucial to understand ultimate, evolutionary questions

- Here, a theoretical argument.

# Central thesis

- The ultimate vs. proximate distinction is logically sound
- But proximate mechanisms are still crucial to understand ultimate, evolutionary questions
- 

Every model of ultimate causation by necessity implies a proximate causation.

It pays to be explicit about the proximate mechanisms.

So we need a theory that integrates:
(i) ultimate and proximate causation, and
(ii) behavioral dynamics with natural selection.

# Topics *du jour*

Behavioral dynamics and social motivations in the evolution of cooperation

Role of behavioral responses in the evolution of group-optimal behaviors

## Part I

## Evolution of other-regarding motivations

- A model for proximate causation and behavioral dynamics
- How do other-regarding motivations evolve?
- Synergism and other-regard

## Part II

## Behavioral responses and group-optimal behaviors

- General model for selection in structured populations with behavioral responses
- What does it take to achieve group optimality?
- Interactions between relatedness and behavioral responses

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Jeremy Van Cleve, Santa Fe Institute

# Other-regarding motivations

an intrinsic motivation to increase
another individual's welfare, even at a cost to self

Humans

Capuchin monkeys[1]

Marmosets[2]

Chimpanzees (?)[3,4]


[1] Lakshminarayanan and Santos 2008 Curr. Bio.
[2] Burkart et al. 2007 PNAS
[3] Silk et al. 2005 Nature
[4] Warneken et al. 2007 PLoS Biology

# Can other-regarding motivations evolve?
(without kin- or group-selection)




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Motivations:
proximate cause

Natural selection:
ultimate cause

# Can other-regarding motivations evolve?
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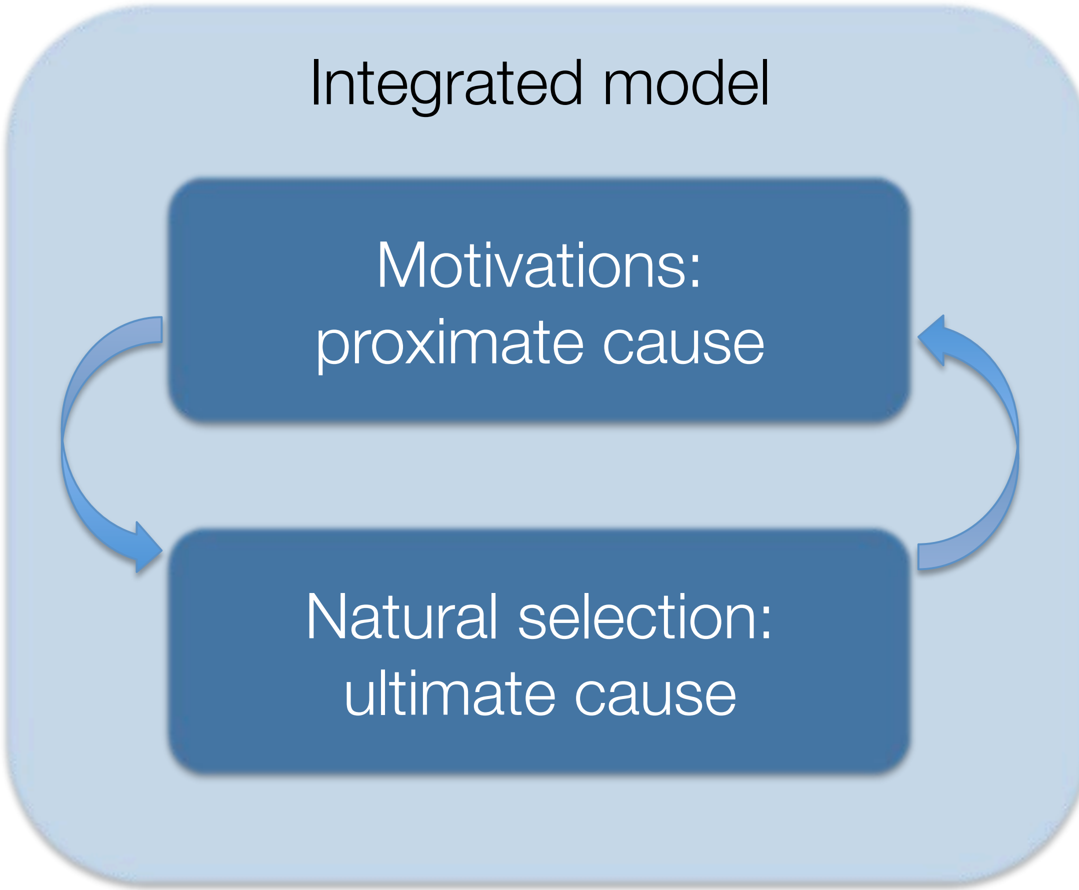


# A social interaction

Take two capuchin monkeys that have different food sources (e.g. apples and carrots).

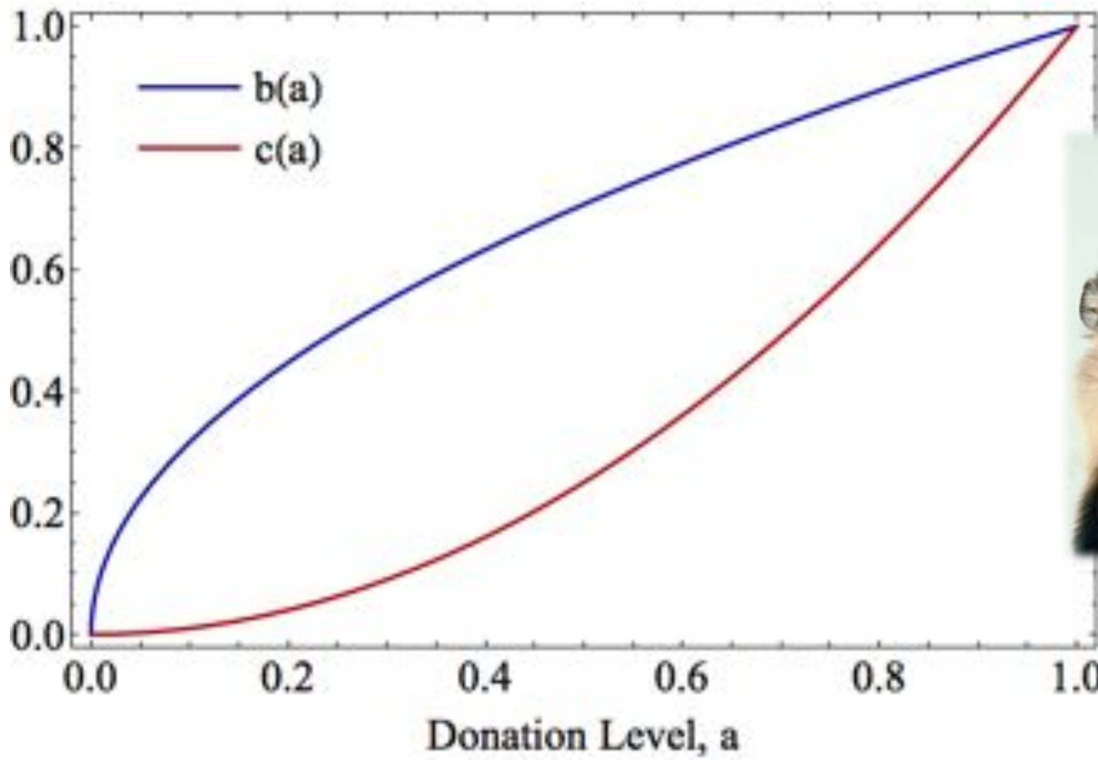
They can donate some of their food to each other

actions: $a_1, a_2$ (How much food 1 donates to 2 and *vice versa*)

payoffs: $u_1(a_1, a_2), u_2(a_1, a_2)$
(How much 1 and 2 grow at the end of the day)

# Conflict of interest

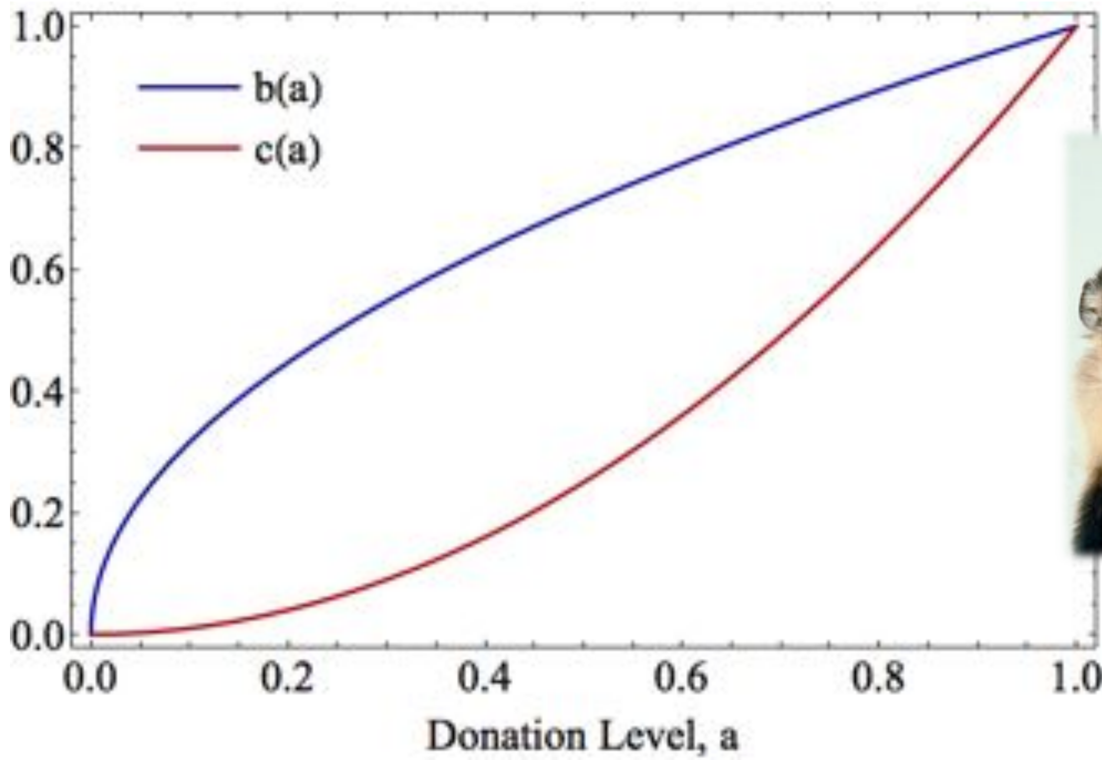
payoff=b(*donation received*)-c(*donation given*)




increasing one's payoff decreases the other's.

# Conflict of interest

payoff=b(*donation received*)-c(*donation given*)




For any donation received, the payoff is maximized by not donating at all

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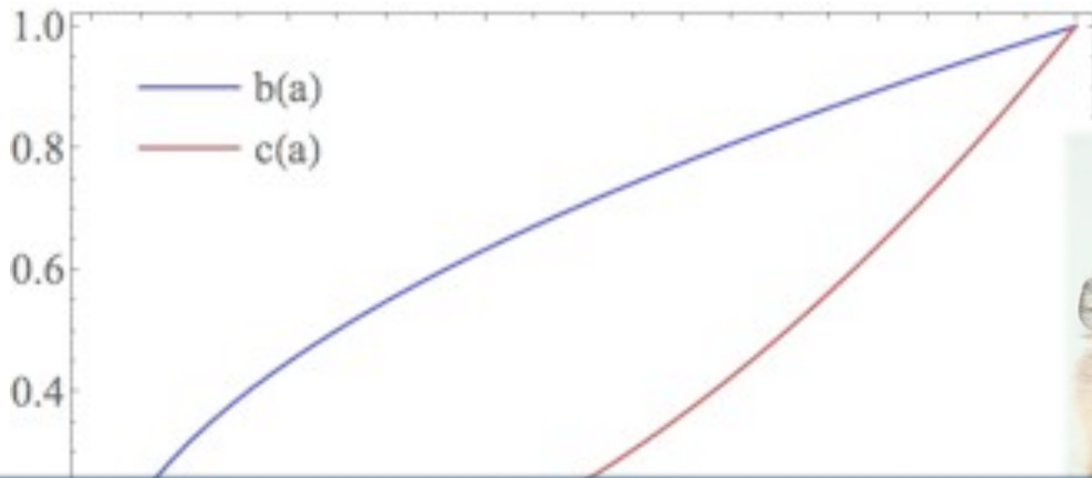


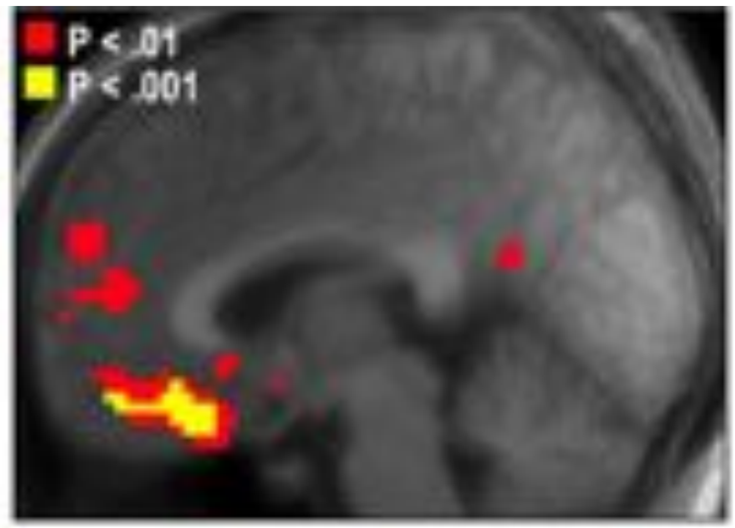

What would motivate them to donate at all?

For any donation received, the payoff
is maximized by not donating at all

Motivations: proximate cause

# Goal-oriented decision making

An innate objective function $x_{1,2}(a_1, a_2)$ represents the internal reward sensation as a function of the actions



Kim et al. 2006 PLoS Biology

Determines the motivations

Two examples:

**Selfish**

$$x_1(a_1, a_2) = u_1(a_1, a_2)$$

**Other-regarding**

$$x_1(a_1, a_2) = u_1 u_2$$

Motivations: proximate cause

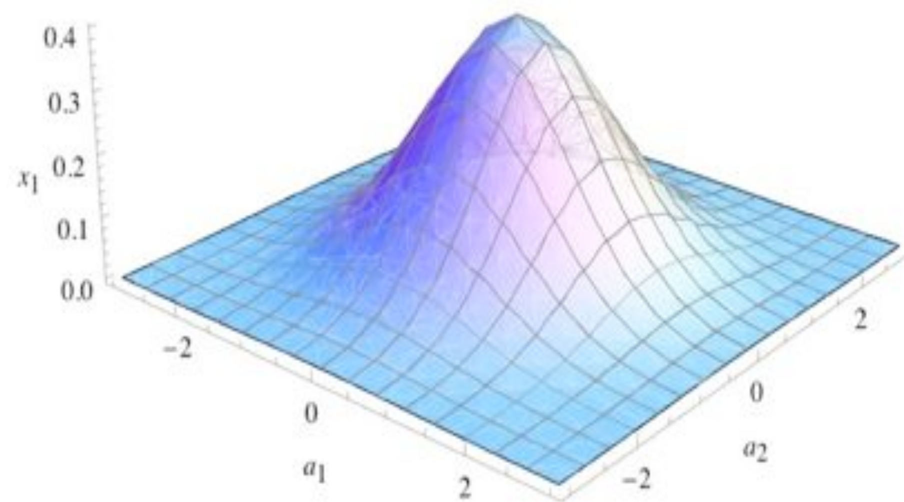
# The behavioral dynamics

Adjust actions to increase reward sensation:

- If increasing $a_1$ increases $x_1$, increase $a_1$ (motivated to donate more)
- If decreasing $a_1$ increases $x_1$, decrease $a_1$ (motivated to donate less)

Hill-climbing process:

$$\frac{da_1}{dt} = \frac{\partial x_1}{\partial a_1}, \quad \frac{da_2}{dt} = \frac{\partial x_2}{\partial a_2}$$



Motivations: proximate cause

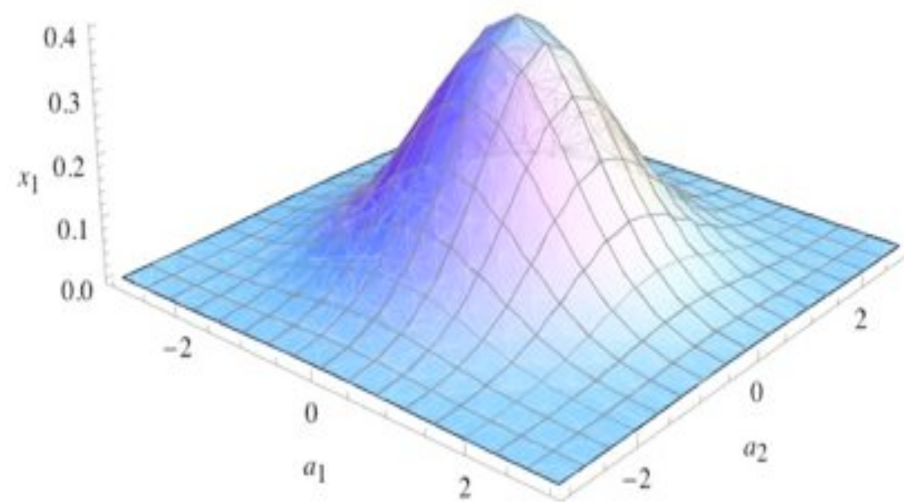
# The behavioral equilibrium

no player can further increase their reward sensation (not motivated to change their actions)

$$(a_1^*, a_2^*)$$

Fitness = payoff at the behavioral equilibrium

$$w_1 = u_1(a_1^*, a_2^*)$$



Can other-regarding motivations evolve
(without kin- or group-selection?)




Reformulate the question:

Which objective function will be evolutionarily stable?

Selfish? $x_1 = u_1$

Other-regarding? $x_1 = u_1 u_2$

Selection: ultimate cause

Define a range of objective functions, parameterized by the evolutionary strategy, $\beta$

$$x_1(a_1, a_2) = u_1 u_2^{\beta_1}$$

$\beta$ is a genetic trait;
determines how rewards are encoded in the brain
changes the behavioral equilibrium, fitness

| | | |
|---|---|---|
| Selfish | $\beta = 0$ | $x_1 = u_1$ |
| Other-regarding | $\beta = 1$ | $x_1 = u_1 u_2$ |

Selection:
ultimate cause

# Evolutionary stability conditions

Evolutionarily stable strategy (ESS):

Mutants cannot invade the population

Fitness maximized at the ESS

The first-order condition

(with small-effect mutants)

$$\frac{dw_1}{d\beta_1} = 0$$

Selection: ultimate cause

# Evolutionary stability conditions

Evolutionarily stable strategy (ESS):

Mutants cannot invade the population

Fitness maximized at the ESS

The first-order condition after some algebra:

$$\frac{\partial u_1}{\partial a_1} - \left( \frac{\partial^2 x_2}{\partial a_1 \partial a_2} \Big/ \frac{\partial^2 x_2}{\partial a_2^2} \right) \frac{\partial u_1}{\partial a_2} = 0$$

Selection: ultimate cause

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How 1's payoff changes with 1's own action

Selection: ultimate cause

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How 1's payoff changes with 2's action

Selection:
ultimate cause

# Evolutionary stability conditions

Evolutionarily stable strategy (ESS):

Mutants cannot invade the population

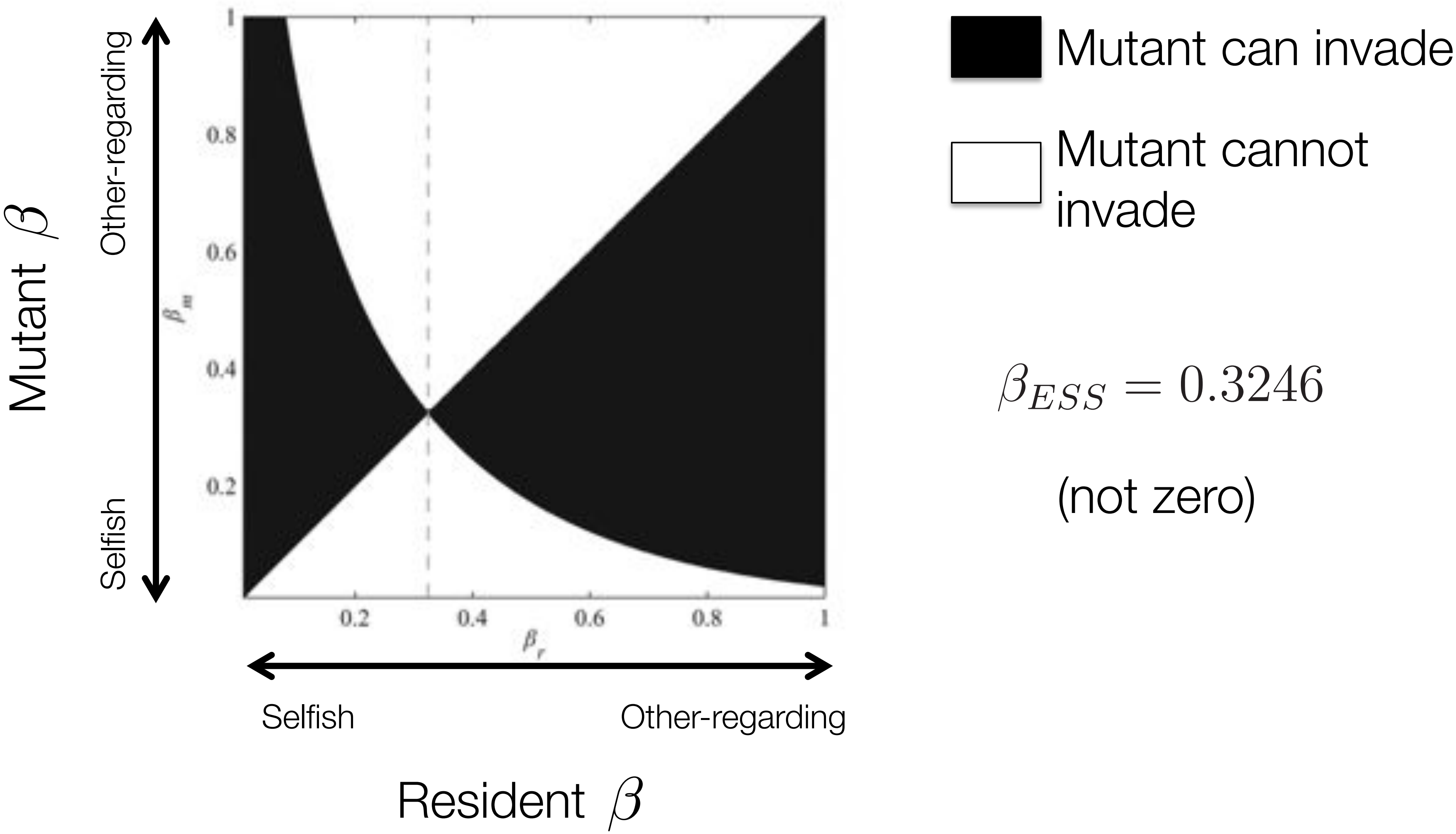
Fitness maximized at the ESS

The first-order condition after some algebra:

$$\frac{\partial u_1}{\partial a_1} - \left( \frac{\partial^2 x_2}{\partial a_1 \partial a_2} \Big/ \frac{\partial^2 x_2}{\partial a_2^2} \right) \frac{\partial u_1}{\partial a_2} = 0$$

How 2 responds to changes in 1's action defines the response coefficient $\rho$

# Other-regarding objectives are ESS




$$\beta_{ESS} = 0.3246$$

(not zero)

Akçay, Van Cleve et al. 2009 PNAS

# Why?

$$\frac{\partial u_1}{\partial a_1} - \left( \frac{\partial^2 x_2}{\partial a_1 \partial a_2} \Big/ \frac{\partial^2 x_2}{\partial a_2^2} \right) \frac{\partial u_1}{\partial a_2} = 0$$

Other-regarding objectives lead to positive feedbacks

i.e., a positive response coefficient $\rho$

Makes deviations from ESS actions not profitable

# Complementarity promotes other-regard

Complementarity:

Apples and carrots are both needed for growth, so if I have more apples, carrots become worth more.

Example for complementary actions:

Mobbing of predators by two individuals

Example for non-complementary (substitute) actions:

Providing food to the offspring

# Complementarity promotes other-regard

Complementarity:

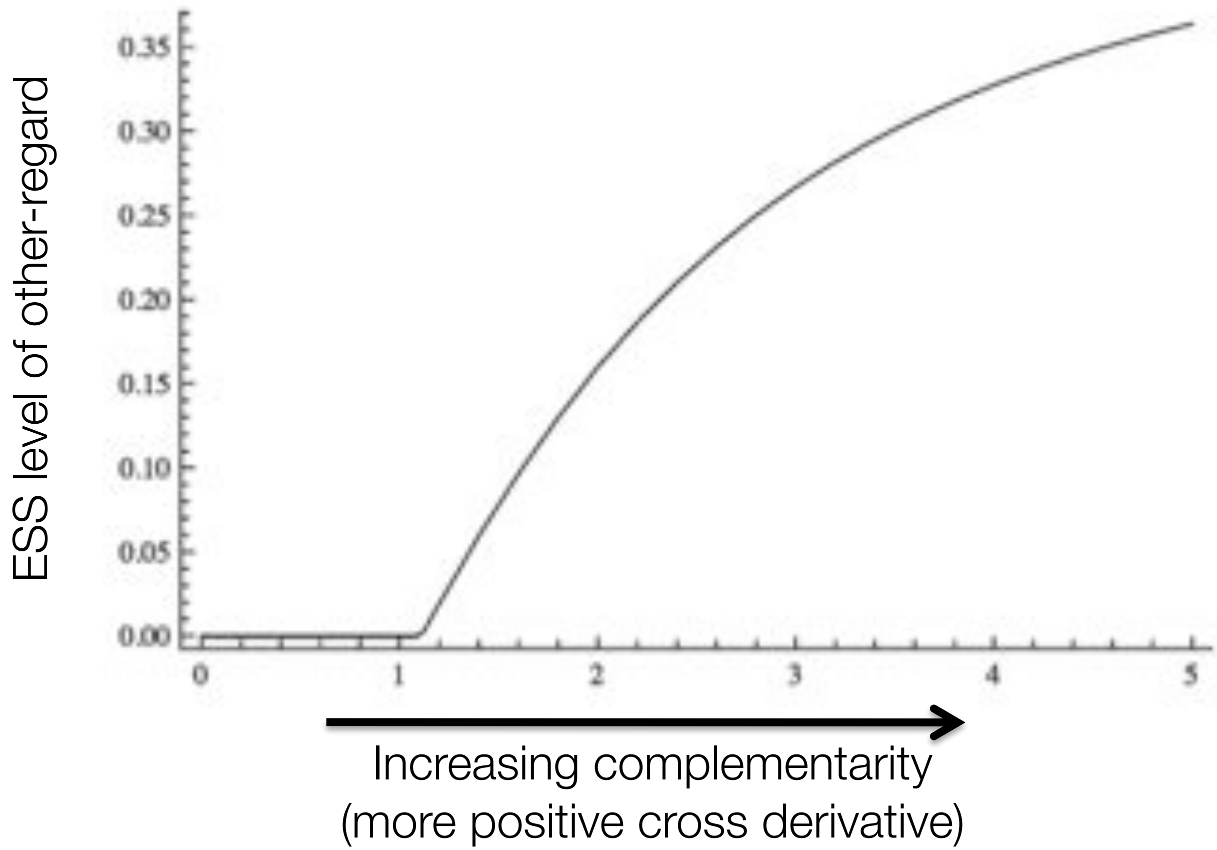
Apples and carrots are both needed for growth, so if I have more apples, carrots become worth more.

Example for complementary actions:

Mobbing of predators by two individuals

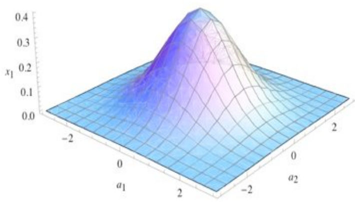
$$\frac{\partial^2 u}{\partial a_1 \partial a_2} > 0$$

# Complementarity promotes other-regard

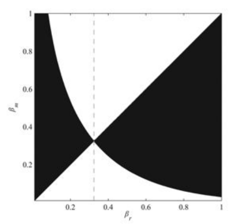



Akçay et al. 2009 PNAS

# Summary of Part I



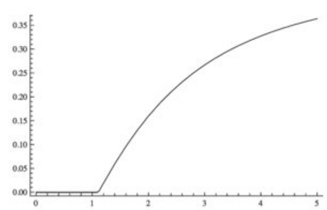

A simple, tractable model that integrates the proximate and ultimate causation of behavior




Other-regarding objectives become evolutionarily stable through the behavioral feedbacks they generate

no need for kin selection

(not altruism in the evolutionary sense)




Synergism in the payoffs promotes other-regarding objectives

# Some observations

- A “toy model”, but analytically tractable and extendable.

- The evolution of other-regard drives cooperative behavior.

- There is by design conflict at the level of the payoffs But the evolutionary conflict over other-regard trait ($\beta$) is much reduced, so no “puzzle” here.

- Specifying the proximate mechanism is important for the definition of the “ultimate question”.

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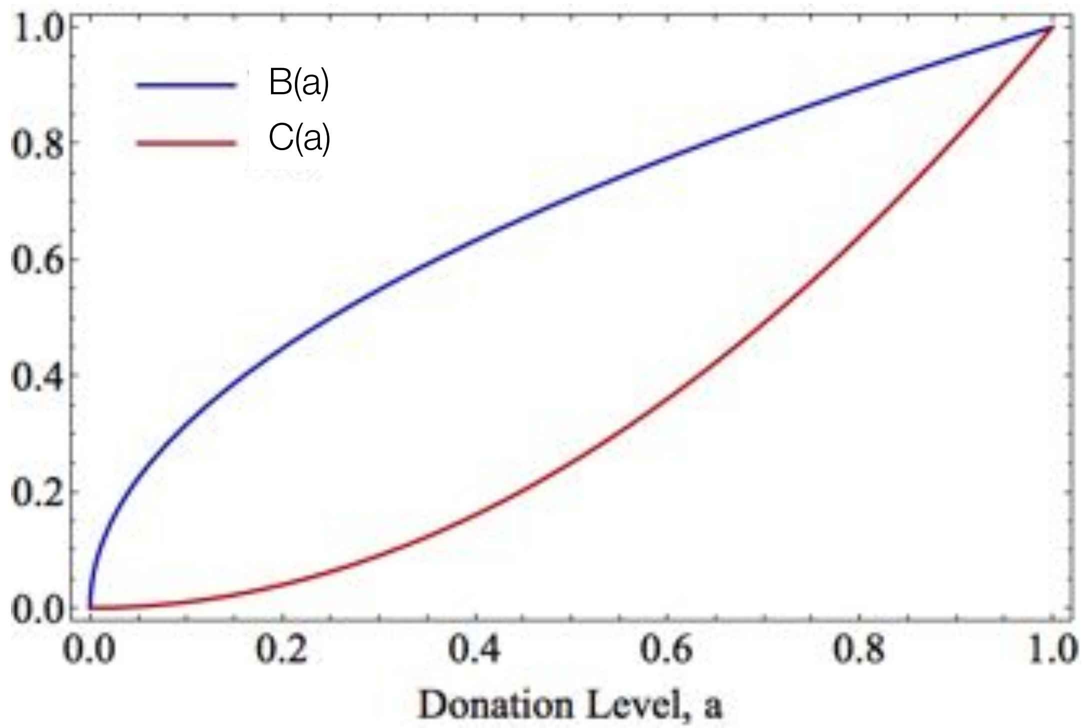
# The group selection controversy

- A persistent debate, with several “resolutions” and flare-ups since the 60’s
- Some issues are purely or mainly semantic, but some substantive questions, too.
- One of the most important questions:

What does it take for evolution to result in group adaptation?

# What is group adaptation?

- Behavior that maximizes the total group fitness
- Will not in general be individually optimal.
- Remember the game from Part 1

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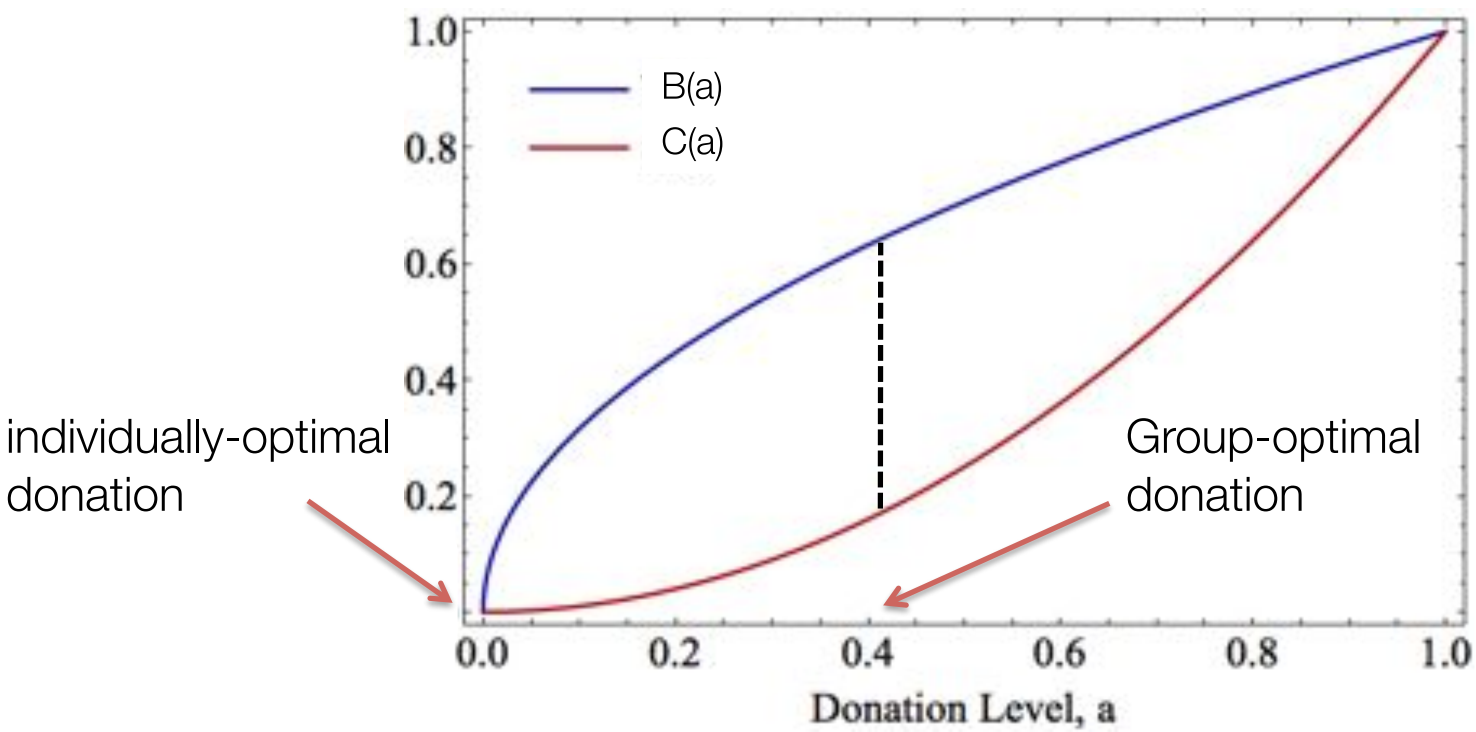



# Current thinking on the “kin-selection side”

- Group adaptations are only possible with clonal groups

- For example, Gardner&Grafen, 2009, JEB conclude
  - “between-group selection can lead to group adaptation, but only in rather special circumstances” (i.e. clonal groups)
  - “mechanisms of conflict resolution such as policing cannot be regarded as group adaptations”

- They use these conclusions to argue that inclusive fitness is a more general theory of social evolution

# But, is it true?

- Gardner&Grafen's framework does not incorporate behavioral responses and proximate mechanisms
- Their main (negative) conclusions stem from this restriction

When behavioral responses are considered:

(i) Group adaptation (or near-adaptation) is possible for a wider range of conditions

(ii) Behavioral mechanisms can (sometimes) be understood as group adaptations

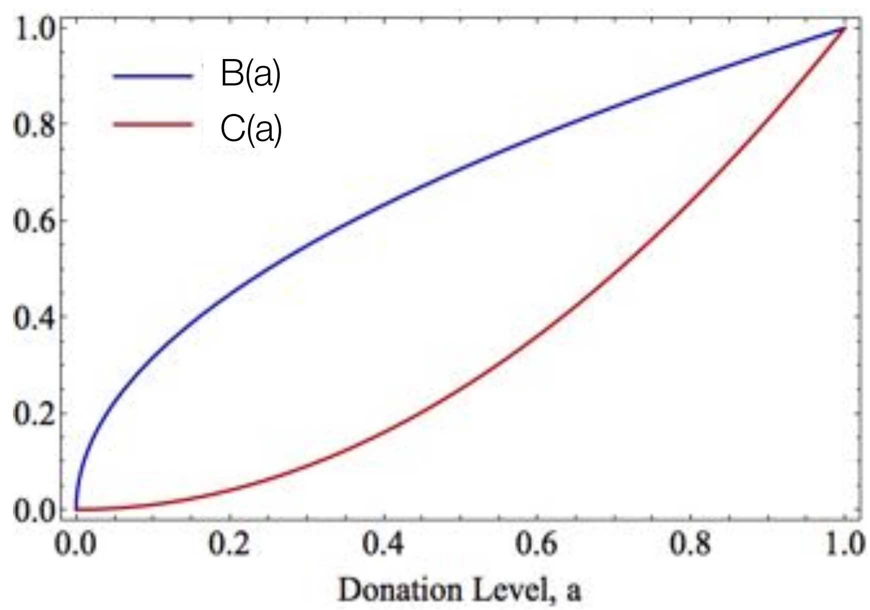
# The response coefficient $\rho$

- Measures how individuals (on average) respond to each other
- If $\rho > 0$, individuals respond in the same direction (e.g. increasing help elicits more help)
- If $\rho < 0$, individuals respond in opposite directions (e.g. increasing help elicits less help)

- If $\rho = 0$, individuals don't respond at all. (the implicit assumption in many models)

# Public goods cooperation in groups

- Consider a public goods game, where individuals carry out an action *a* that provides a benefit *B(a)* to all others in their group, but cost the focal actor *C(a)*
- (*B(a)* and *C(a)* might change nonlinearly with donation)
- Let *b* and *c* denote the first derivatives of *B* and *C.*



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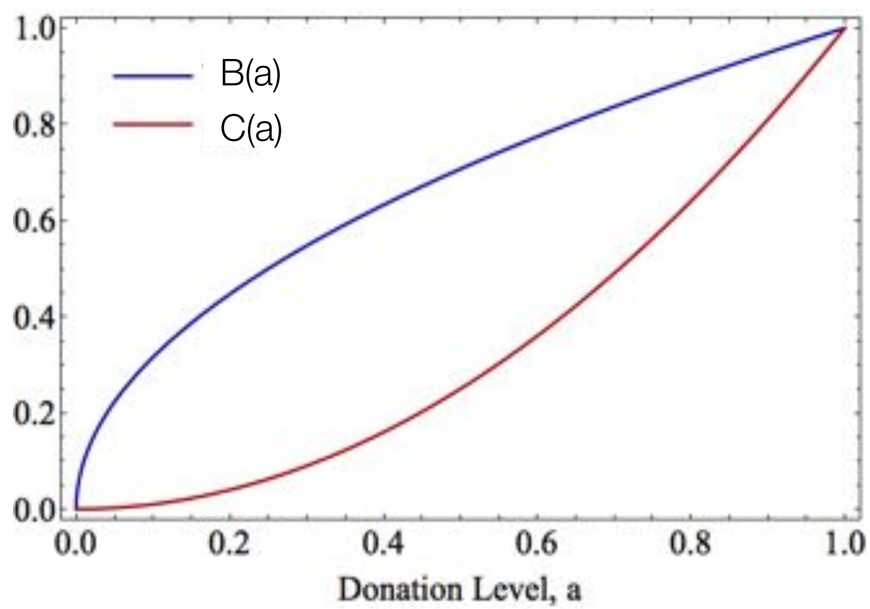
When will selection lead to more contributions to the public good?



# Use the Price equation

$$\Delta G = \text{cov}(G_i, w) = \beta_{w,p_i}\text{cov}(G_i, p_i) + \sum_{j \neq i} \beta_{w,p_j}\text{cov}(G_i, p_j)$$

$p$: the phenotype (e.g. how other-regarding an individual is)

$\beta_{w,pi}$: the regression of individual *i*'s phenotype on *i*'s fitness.
$\beta_{w,pj}$: the regression of individual *j*'s phenotype on *i*'s fitness.

The regressions depend on individuals' behavioral responses to each other.

$$\beta_{w,p_i} \propto \rho\, b(N-1) - c$$

$$\beta_{w,p_j} \propto b(\rho(N-2)+1) - \rho c$$

Finally, relatedness $r$ = cov($G_j$, $G_i$)/var($G_i$)

# After a bit of algebra…

- A higher donation level in a group of size N will evolve when

$$\frac{b}{c} > \frac{1 + r\rho(N-1)}{(N-1)(r + \rho + (N-2)r\rho)}$$

Note: right-hand side is symmetric in *r* and $\rho$
=> Behavioral responses and genetic relatedness fulfill exactly analogous roles

- But *both* appear separately in the condition
=> Cannot ignore either one without loss of generality

# Group optimality

- Group adaptation maximizes the total payoff of the group.

- In a symmetric game with *N* players, this means maximizing *(N-1)B(a)-C(a)*

$$\frac{b}{c} = \frac{1}{N-1}$$

- Evolutionary stability condition for group optimal outcomes:

$$\frac{b}{c} = \frac{1 + r\rho(N-1)}{(N-1)(r + \rho + (N-2)r\rho)}$$

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# Group optimality

- Group adaptation maximizes the total payoff of the group.
- In a symmetric game with $N$ players, this means maximizing $(N-1)B(a)-C(a)$

Either $r$=1 or $\rho$=1 is sufficient for group optimality by themselves.

Group optimality is not only possible for clonal groups but also for groups where individuals perfectly coordinate their responses.

- Evolutionary stability condition for group optimal outcomes:

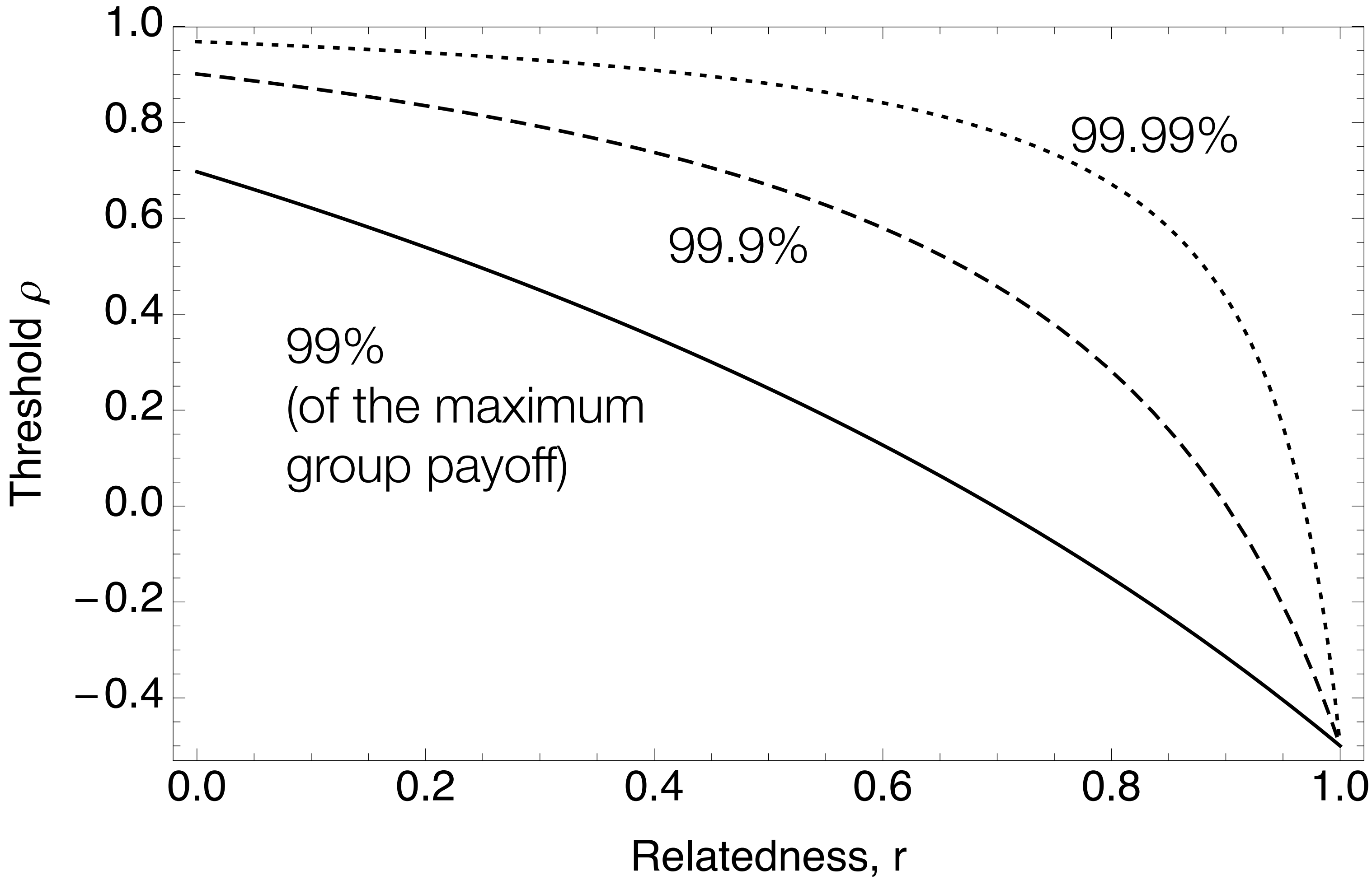
$$\frac{1}{N-1} = \frac{1 + r\rho(N-1)}{(N-1)(r+\rho+(N-2)r\rho)}$$

# Almost group-optimal outcomes

- What if we relaxed our requirement?
- Demand that the outcome is almost group optimal.
- Formally, for $\varepsilon > 0$,
  Find the threshold $\rho$ that comes within $\varepsilon$ of the group-optimal b/c ratio.

$$\frac{b}{c} = \frac{1}{N-1} + \epsilon$$

# Almost group-optimal outcomes



# Group adaptation: convergence

- According to Gardner&Grafen, adaptation needs more than group optimal outcome being ES.
- Also, natural selection has to be able to lead there, if not at the equilibrium
- Convergent stable strategy
  Selection positive when contributions are lower then the group-optimal level, and negative when contributions are higher

When is a group optimal outcome convergent stable?

# Con. st. at group optimality

- Again, need to specify the proximate mechanism that generates the behavioral responses.
  - Use the goal-oriented decision making model from section 1, adapted to public goods games
  - Find the objective functions that result in $\rho$=1
  - Determine whether these objective functions are convergent stable.

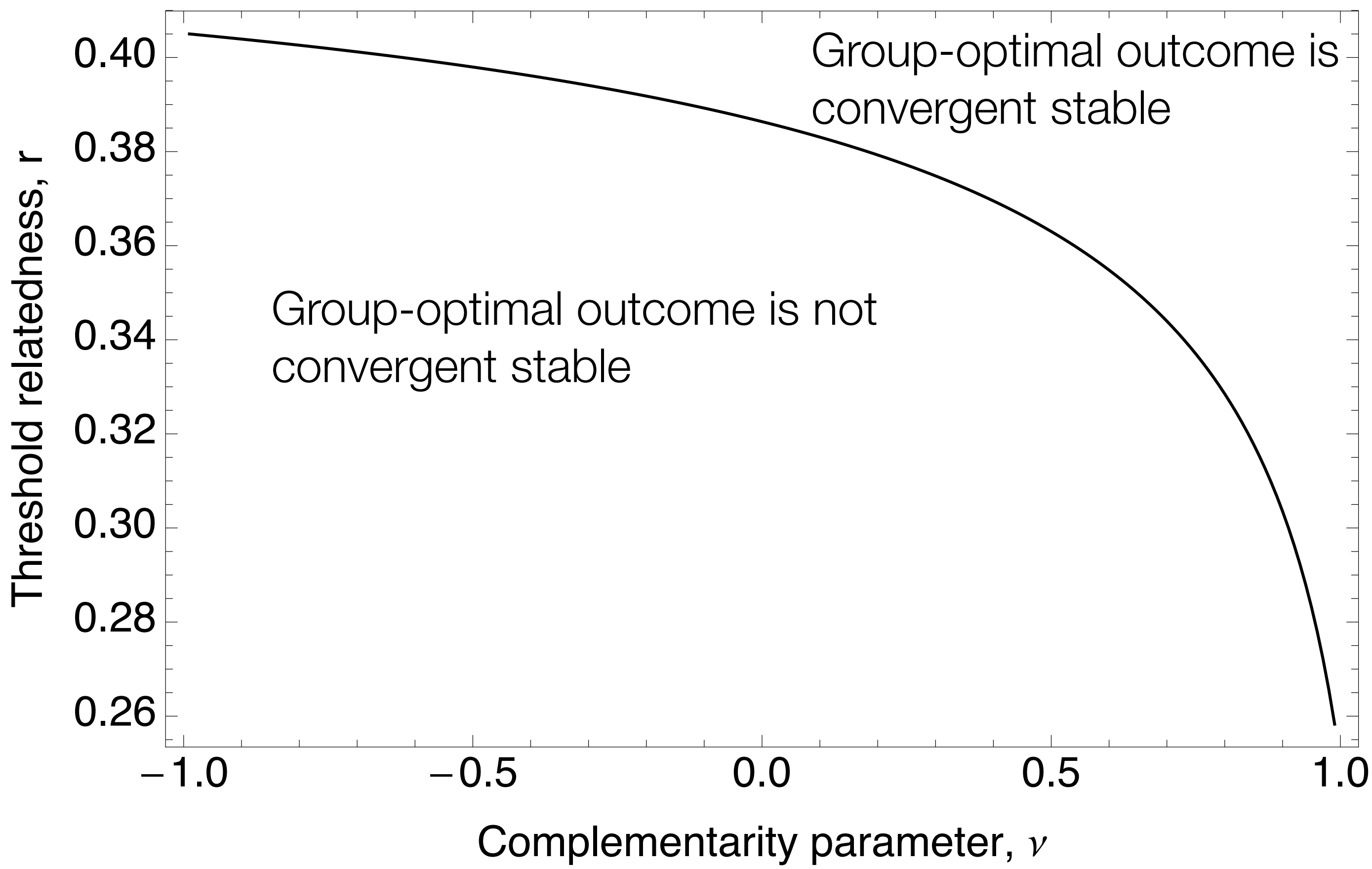
Whether the group optimal objective functions are convergent stable or not depends on the relatedness.

# Con. st. at group optimality

$$
\begin{aligned}
&\left[\frac{\partial^2 a_i}{\partial p_i^2} + (N-1)\frac{\partial^2 a_i}{\partial p_i \partial p_j}\right]\left[b\rho(N-1) - c + r(N-1)\Big(b(\rho(N-2)+1) - \rho c\Big)\right] \\
&+\frac{\partial a_i}{\partial p_i}\left[\left[\frac{\partial a_i}{\partial p_i}[(N-1)\rho+1][(N-2)\rho_3' + \rho_2' + \rho_1'] + (N-2)\rho_{p_3}' + \rho_{p_2}' + \rho_{p_1}'\right]\right. \\
&\qquad \times (N-1)\Big[b + r[(N-2)b - c]\Big] \\
&+\frac{\partial a_i}{\partial p_i}\Big[(N-1)\rho+1\Big]\Big[(N-1)[(N-2)b_3' + b_2' + b_1'][\rho + r((N-2)\rho+1)] \\
&\qquad \left.+[(N-1)b_1' - c'][1+(N-1)r\rho]\Big]\right] < 0
\end{aligned}
$$

Whether the group optimal objective functions are convergent stable or not depends on the relatedness.

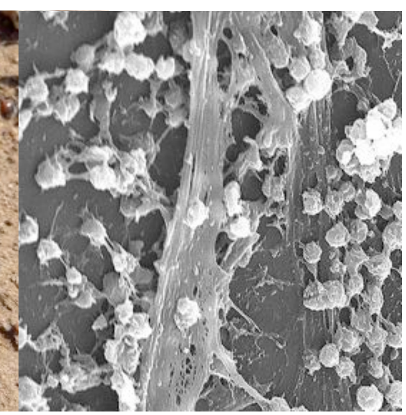
# Con. st. at group optimality




Increasing complementarity
(more positive cross derivative)

# Conclusions from part II

- Behavioral responses offer another route to group-optimality and adaptation
- Possible to reach almost group-optimality with moderate relatedness combined with moderate behavioral responses
- Behavioral responses *can* sometimes be understood as group adaptations, without requiring clonal groups.



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# Final remarks

- My main point is that proximate mechanisms and behavioral dynamics need to be better integrated in our thinking about social evolution

- Not a call for more complex models, necessarily

- Neither an argument saying
“we should do it if possible”;

- We incorporate a proximate mechanism whether we acknowledge or not, but it pays to be explicit about it.

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