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Hamilton's Rule in Reciprocal Altruism and Symbiosis

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Hamilton's Rule in Reciprocal Altruism and Symbiosis

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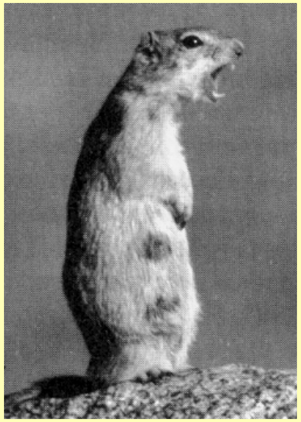


The Plan

- Do Inclusive Fitness and Reciprocal Altruism Models embody *different* or *similar* mechanisms?
- Background
  - The Prisoner’s Dilemma (PD), Hamilton’s Rule (Queller’s version)
- Apply Hamilton’s Rule to Reciprocal Altruism:
  - Iterated Prisoner’s Dilemma model
  - A model of symbiosis
- Towards a Unified Theory

Additive Prisoner’s Dilemma (PD)

Actor's Fitness (Utility)

opponent’s behavior

actor’s behavior	**C**	**D**
C	4	0
D	5	1

Additive Prisoner's Dilemma (PD)

Actor's Fitness (Utility)

		opponent's behavior C contributes b	*opponent's behavior* D contributes 0
actor's behavior	C sacrifices c	$w_0 + b - c$ 4	$w_0 - c$ 0
actor's behavior	D sacrifices 0	$w_0 + b$ 5	w_0 1

- $w_0 = 1$; $b = 4$; $c = 1$

Non-Additive PD

Actor's Fitness (Utility)

		opponent's behavior	
		C contributes b	**D** contributes 0
actor's behavior	**C** sacrifices c	$w_0 + b - c$ (+d) 3	$w_0 - c$ 0
	D sacrifices 0	$w_0 + b$ 5	w_0 1

- $w_0 = 1$; $b = 4$; $c = 1$; $d = -1$

An Iterated PD Model of Reciprocal Altruism

- Players paired randomly from a large population, then play *i* iterated games
- Each player has an overall heritable strategy (genotype), here only:
  - Always Defect (ALLD)
  - Tit-For-Tat (TFT)
- Number of offspring in next generation proportional to cumulative fitness payoffs
- Model parameters: *i and b/c*

What Does Hamilton's Rule (HR) Say?

- If $rb > c$, then the altruistic trait will increase in the next generation

$$r = \frac{\text{cov}(G_A, G_O)}{\text{var}_t(G_A)}$$

- Two Problems
  - Random pairing of types, $r = 0$
  - PD used is non-additive
- Axelrod and Hamilton (1981) offered Reciprocal Altruism and Inclusive Fitness as two ***different*** mechanisms by which cooperation (altruism) could evolve

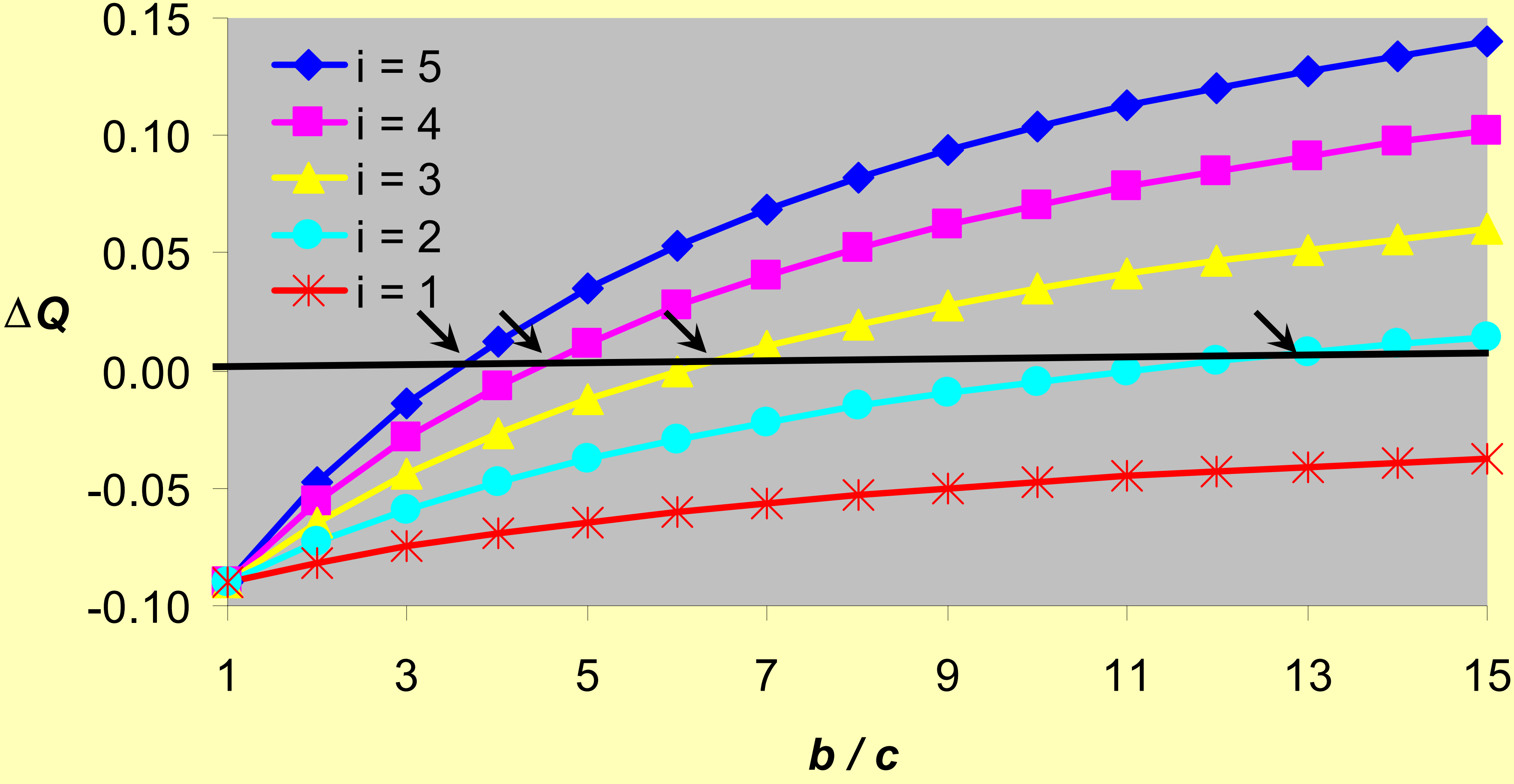
Queller's Generalization

- Queller (1985) showed that it is the *phenotypes* (behaviors) of others that should count in HR, not their *genotypes*
- Hamilton Queller

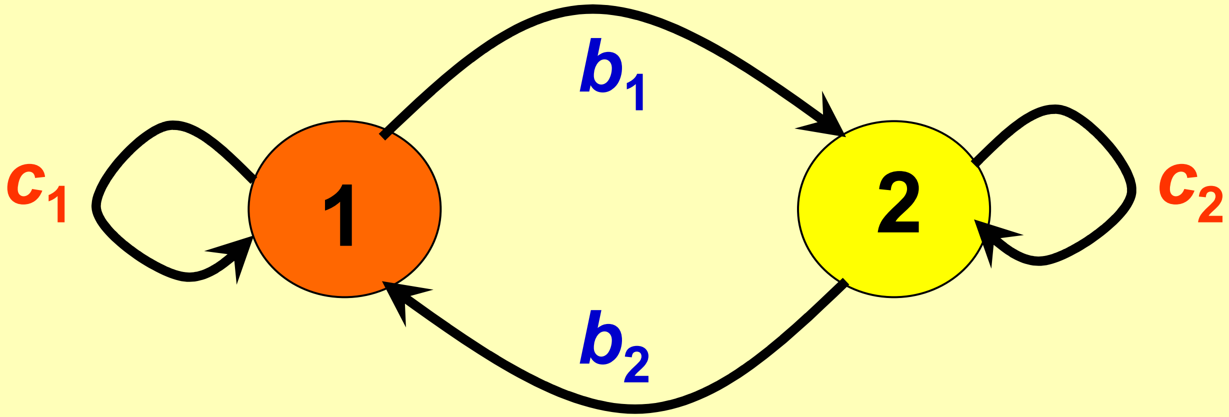
$$r = \frac{\mathrm{cov}(G_A, G_O)}{\mathrm{var}_t(G_A)} \qquad\qquad r = \frac{\mathrm{cov}(G_A, P_O)}{\mathrm{cov}(G_A, P_A)}$$

- Notice, no G_O term in Queller's version
- Queller also solved the non-additive problem
- Surprisingly, Queller's version not used to analyze reciprocal altruism

Numerical Simulations of Iterated PD varying *i* and *b / c*



A Symbiosis Model

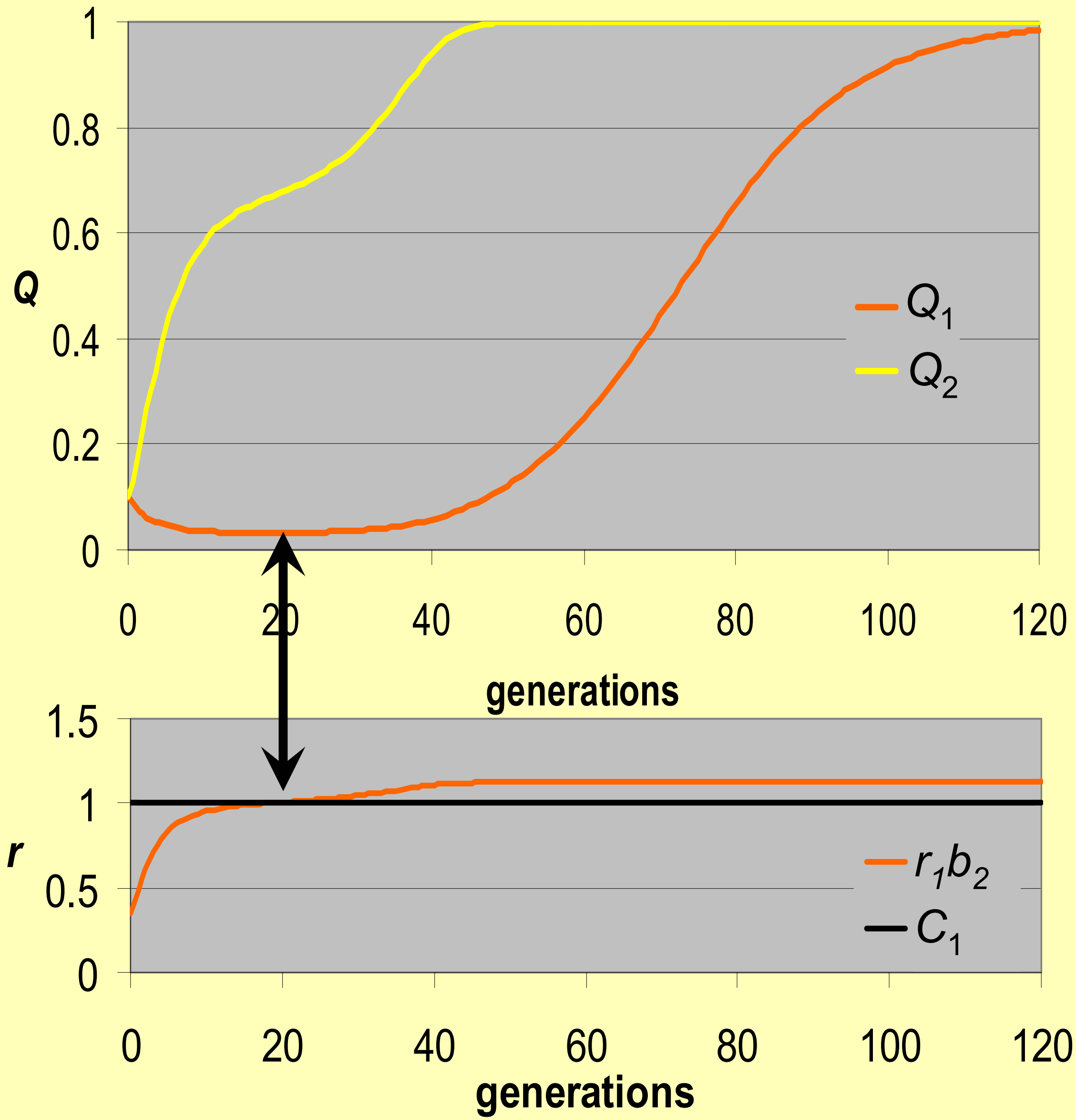


$$r_1 = \frac{\mathrm{cov}(G_1, P_2)}{\mathrm{cov}(G_1, P_1)}$$

$$r_2 = \frac{\mathrm{cov}(G_2, P_1)}{\mathrm{cov}(G_2, P_2)}$$

$$r_1 \, b_2 > c_1$$

$$r_2 \, b_1 > c_2$$



	1	**2**
b	24	1.5
c	1	2.0
w_0	1	1
d	0	0
Str	TFT	TFT
i	4	

Generalizations of Hamilton's Rule

- Hamilton's original version:

$$rb > c$$

- Hamilton's version (based on Price's covariance equation):

$$\frac{\text{cov}(G_A, G_O)}{\text{var}(G_A)} b > c$$

- Queller's version with phenotype/genotype differences:

$$\frac{\text{cov}(G_A, P_O)}{\text{cov}(G_A, P_A)} b > c$$

- Queller's most general version with non-additivity:

$$\frac{\text{cov}(G_A, P_O)}{\text{cov}(G_A, P_A)} b + \frac{\text{cov}(G_A, P_A P_O)}{\text{cov}(G_A, P_A)} d > c$$

Is Inclusive Fitness a Different Mechanism than Reciprocal Altruism?

- Axelrod and Hamilton (1981) said yes
- *"Shared genes cooperation differs from all other models considered here in that the cooperative individual need not benefit from its act."*
  - Sachs, J. L., U. G. Mueller, T. P. Wilcox, and J. J. Bull. 2004. **The Evolution of Cooperation**. *Quarterly Review of Biology* 79:135-160.
- Is the *b* In Hamilton's Rule the benefit given or the benefit received by altruists?

A Unified View

- The frequency of an altruistic allele increases if individuals carrying that allele receive more fitness benefits from others than average population members do
- True whether these “others” are relatives or from a different species; whether you are thinking in terms of inclusive fitness or reciprocal altruism
- Many causes, including:
  – Kinship, conditional strategies, policing, reputation, etc.

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Queller's Non-Additive Version of Hamilton's Rule

$$rb + r_{dev}d > c$$

$$r_{dev} = \frac{\mathrm{cov}(G_A, P_A P_O)}{\mathrm{cov}(G_A, P_A)}$$

Iterations = Non-Additivity

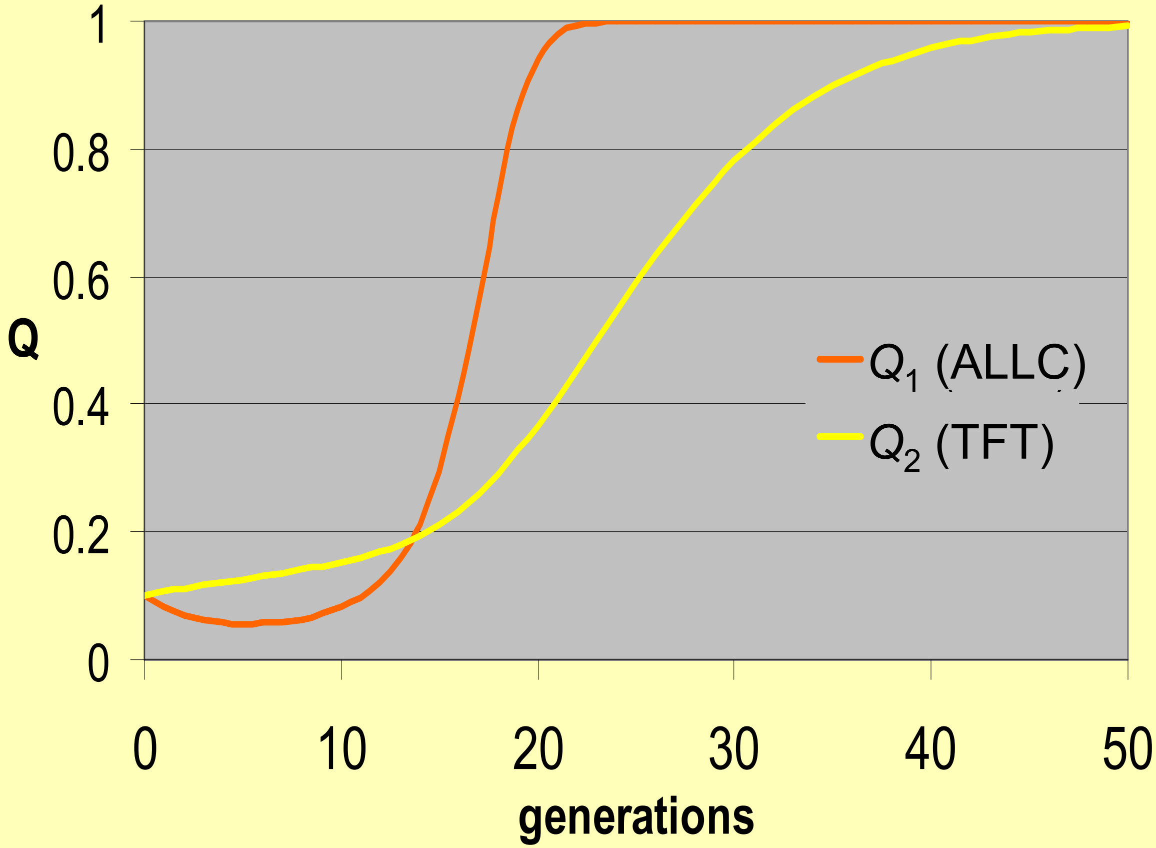
		opponent's behavior TFT contributes b	*opponent's behavior* ALLD contributes 0
actor's behavior	**TFT** sacrifices c	$w_0 + b - c$ (+d) 40	$w_0 - c$ 9
actor's behavior	**ALLD** sacrifices 0	$w_0 + b$ 14	w_0 10

- *iterations = 10*
- **w_0 = 10; b = 4; c = 1; d = 27**

A More Intuitive Form

$$r_1 b_2 > c_1$$

$$\mathrm{cov}(G_1, P_2)\ b_2 > \mathrm{cov}(G_1, P_1)\ c_1$$



	1	2
b	4	4
c	1	1
$\boldsymbol{w_0}$	1	1
d	4	2
Str	ALLC	TFT
i	200	