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Unifying Reciprocal Altruism and Inclusive Fitness Theories of Altruism

Jeffrey Fletcher
Portland State University, jeff@pdx.edu

Martin Zwick
Portland State University, zwick@pdx.edu

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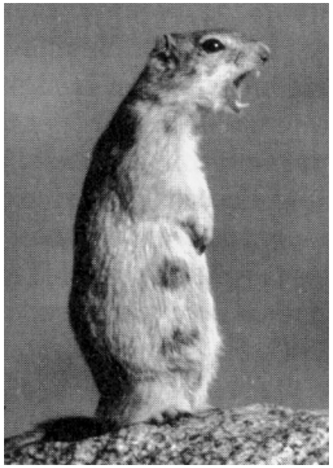
Jeffrey A. Fletcher
Department of Zoology
University of British Columbia
fletcher@zoology.ubc.ca

Martin Zwick
Systems Science Ph.D. Program
Portland State University
zwick@pdx.edu



What special circumstances or mechanisms thus favor cooperation? Currently, evolutionary biology offers a set of disparate explanations, and a general framework for this breadth of models has not emerged.

- Sachs *et al*. 2004, **The Evolution of Cooperation**. *QRB* 79:135-160

Outline

- Background
  - Some History
  - IPD Model of Reciprocal Altruism
  - Problems Applying Hamilton's Rule (HR)
- Unification: Applying HR to Reciprocal Altruism
  - Queller's Generalized HR
  - Conditional Behaviour and Non-Additivity
  - Symbiotic Mutualisms
- Implications of Unification
  - Progressive Generalization of HR
  - What happened to "indirect" fitness?
  - Conceptual Parsimony

Main Theories for the Evolution of Altruism

- Multilevel Selection
  - Cooperative groups do better—emphasizes tension between hierarchical levels
- Inclusive Fitness/Kin Selection
  - Gene self interest, Hamilton's rule ($rb > c$)
  - $w_{incl.} = w_{direct} + w_{indirect}$
- Reciprocal Altruism
  - Conditional behaviour, Iterated Prisoner's Dilemma (IPD)
- Others
  - By-product mutualism, conflict mediators, policing

Unification Program

- Unifying Multilevel Selection and Inclusive Fitness Theories
  - (Price 1970, Wade 1980, Breden 1990, Queller 1992, Frank 1998, Sober and Wilson 1998)
- Unifying Reciprocal Altruism and Inclusive Fitness Theories
  - (Queller 1985, Nee 1989, Frank 1994, 1998, Sober and Wilson 1998)
  - Less successful; less formal; less accepted

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 behaviour	
		C contributes b	**D** contributes 0
actor's behaviour	**C** sacrifices c	$w_0 + b - c$ 4	$w_0 - c$ 0
	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

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

Reciprocal Altruism: Iterated Conditional Behaviours

- In random single-generation pairings, D wins
- Axelrod's tournaments (late 1970s on)
  - Evolutionary experiments where offspring proportional to cumulative fitness payoffs
  - Tit-For-Tat (TFT)
- Our Simple Model
  - Random pairing, play *i* iterated games
  - Each player has an overall heritable strategy (genotype), here only: Always Defect (ALLD) or TFT

Can We Apply HR?

- $rb > c$
- Start with the additive PD (no *d* term)

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

- Hamilton's $r = 0$ for random pairing
  - for all initial fractions of TFT (*Q*)
- Hamilton's rule using only genotypic associations gives wrong result
- Conditional behaviour not accounted for

Summary I

- Axelrod and Hamilton (1981) distinguished two mechanisms
  - Inclusive Fitness for relatives
  - Reciprocal Altruism for non-relatives
- Still current thinking
  - Sachs et al 2004 QRB
  - Now Reciprocal Altruism more questioned
- Two Problems
  1. Phenotype/Genotype differences
  2. PD used has non-additive fitness functions

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Queller's Generalization

- To solve problem 1
  - Use *phenotypes* (behaviours) of others (not their *genotypes*) in HR
  - Hamilton (1975) Queller (1985)

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

- To solve problem 2
  - Use an additional term to account for deviations from additivity

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

Mathematical Details

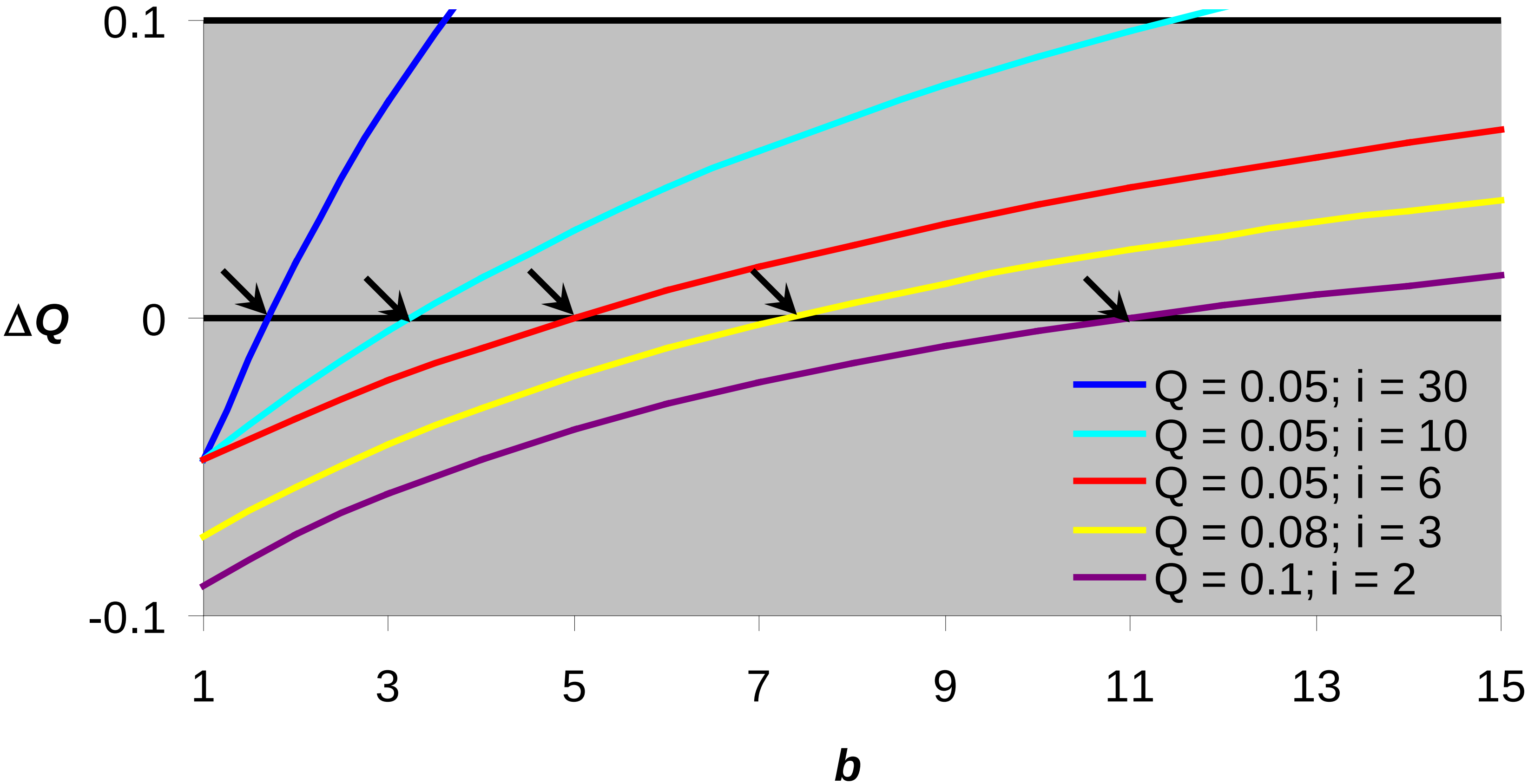
Actor (A)	Opponent (O)	G_A	P_A	P_O
TFT	TFT	1	1	1
TFT	ALLD	1	1 / *i*	0
ALLD	TFT	0	0	1 / *i*
ALLD	ALLD	0	0	0

- $\overline{G} = Q$
- $\overline{P} = f_{TT} 2i + f_{AT}$

$$r = \frac{\mathrm{cov}(G_A, P_O)}{\mathrm{cov}(G_A, P_A)} = \frac{\sum_{j=1}^{N} (G_j - Q)(P_{O_j} - \overline{P})}{\sum_{j=1}^{N} (G_j - Q)(P_j - \overline{P})}$$

- Can group by frequency of pairings

Numerical Simulations of Iterated PD varying *Q*, *i*, and *b* (*c* = 1)



G/P Differences vs. Non-additivity

$i = 10$

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

		opponent's behavior	
		TFT	**ALLD**
actor's behavior	**TFT**	40	9
	ALLD	14	10

G/P Differences vs. Non-additivity

$i = 10$

opponent's behaviour

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

opponent's behavior

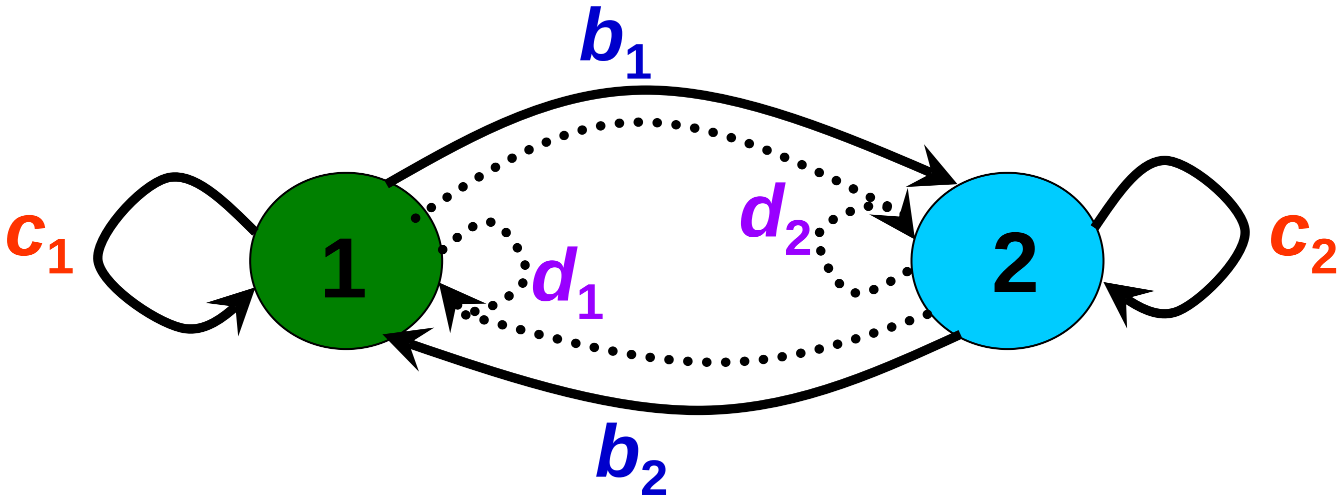
		TFT contributes b	ALLD contributes 0
actor's behavior	TFT sacrifices c	$w_0 + b - c$ (+d) 40	$w_0 - c$ 9
	ALLD sacrifices 0	$w_0 + b$ 14	w_0 10

- $w_0 = 10$; $b = 4$; $c = 1$; $d = 27$
- Iterations = Non-Additivity

A Simple Symbiosis Model

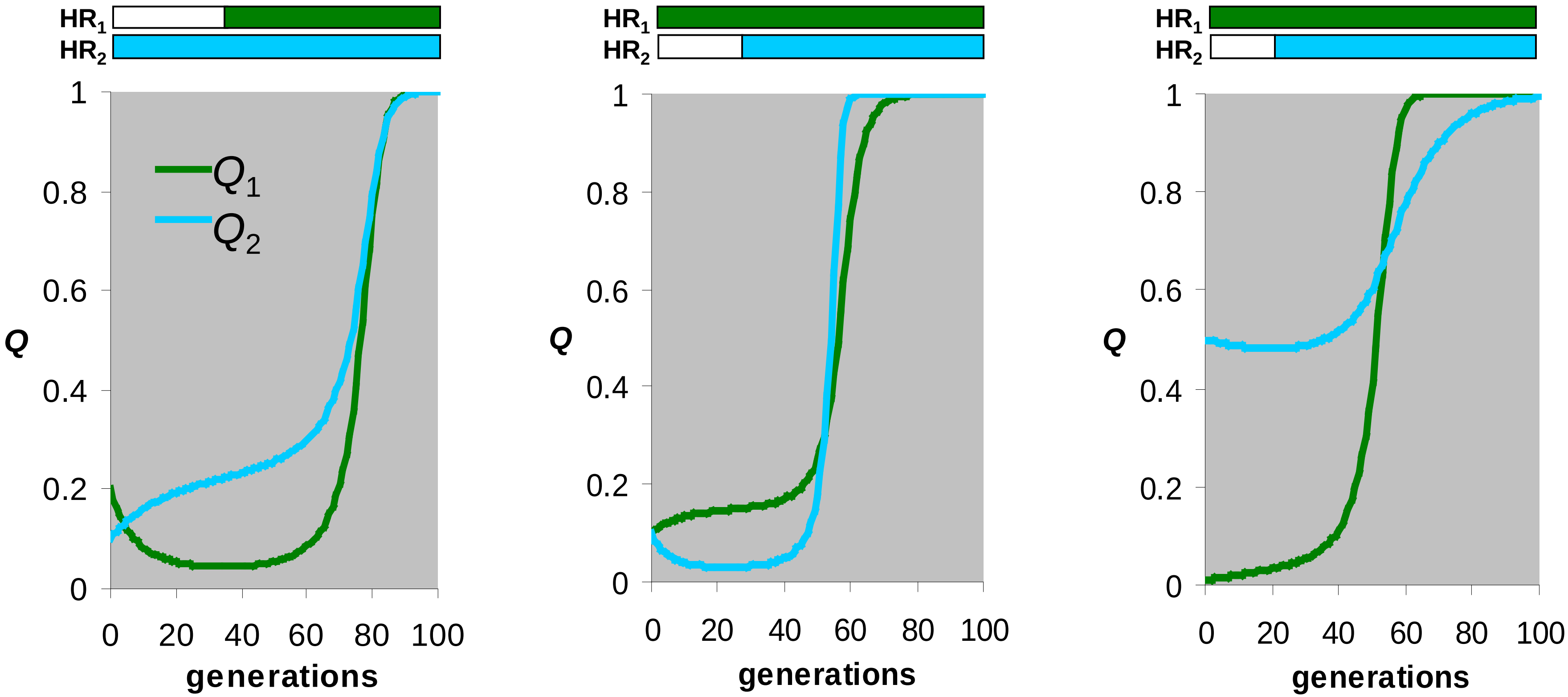
- Interactions are heterospecific and pair-wise
- Each species has two types
  - ALLD type
  - a cooperative type (e.g. TFT)
- *b, c, d,* and cooperative strategy can all vary between species

A Simple Symbiosis Model



$$r_1 = \frac{\mathrm{cov}(G_1, P_2)}{\mathrm{cov}(G_1, P_1)} \qquad r_2 = \frac{\mathrm{cov}(G_2, P_1)}{\mathrm{cov}(G_2, P_2)}$$

HR$_1$: $r_1 b_2 > c_1$ HR$_2$: $r_2 b_1 > c_2$



	1	2
b	1.5	5
c	2.0	0.1
***w*0**	2	2
d	0	0
Str	TFT	TFT
i	4	

	1	2
b	4	4
c	1	4
***w*0**	1	1
d	0	0
Str	TF2T	Pavlov
i	80	

	1	2
b	2	2.2
c	1	0.1
***w*0**	1	1
d	0	1.3
Str	ALLC	TFT
i	100	

Summary II

- Queller's version of HR accurately predicts the direction of selection:
  - In a classic model of Reciprocal Altruism (IPD)
  - In a model of symbiosis where altruists and recipients are clearly unrelated
- Queller's version works generally for plastic behaviours
  - Different games definable by *b*, *c*, and *d*
  - N-player versions (group size > 2)
  - Other population structures (not just binomial)
  - Degrees of cooperation (not just C and D)
  - Other forms of conditionality

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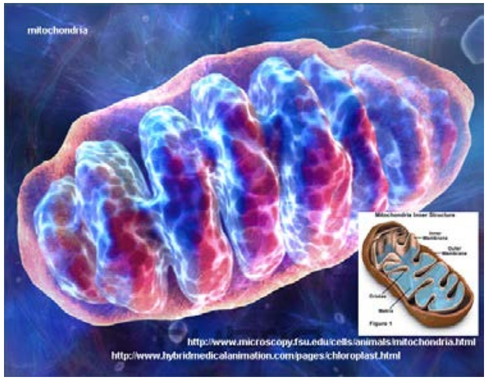


Past Contributions to Unification

- Applying HR to Reciprocal Altruism (IPD)
  - (Queller 1985, but not Queller 1992a, 1992b)
  - (Nee 1989)
- A similar model of symbiosis with two instances of HR
  - (Frank 1994, 1997)
- Show some similarities between Hamilton's models and IPD models
  - (Sober and Wilson 1998)

Is Queller's Version More General?

- Queller's version often seen as special case (for *G*/*P* differences or non-additivity)
  - "Hamilton's rule OK" (Grafen 1985)
- *"Thus, for genes of small effect, additivity is restored and the correctness of Hamilton's rule is restored with it."*

Generalizations of Hamilton's Rule

- Hamilton's original version:

$$rb > c \tag{1}$$

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

$$\frac{\mathrm{cov}(G_A, G_O)}{\mathrm{var}(G_A)} b > c \tag{2}$$

- Queller's version with phenotype/genotype differences:

$$\frac{\mathrm{cov}(G_A, P_O)}{\mathrm{cov}(G_A, P_A)} b > c \tag{3}$$

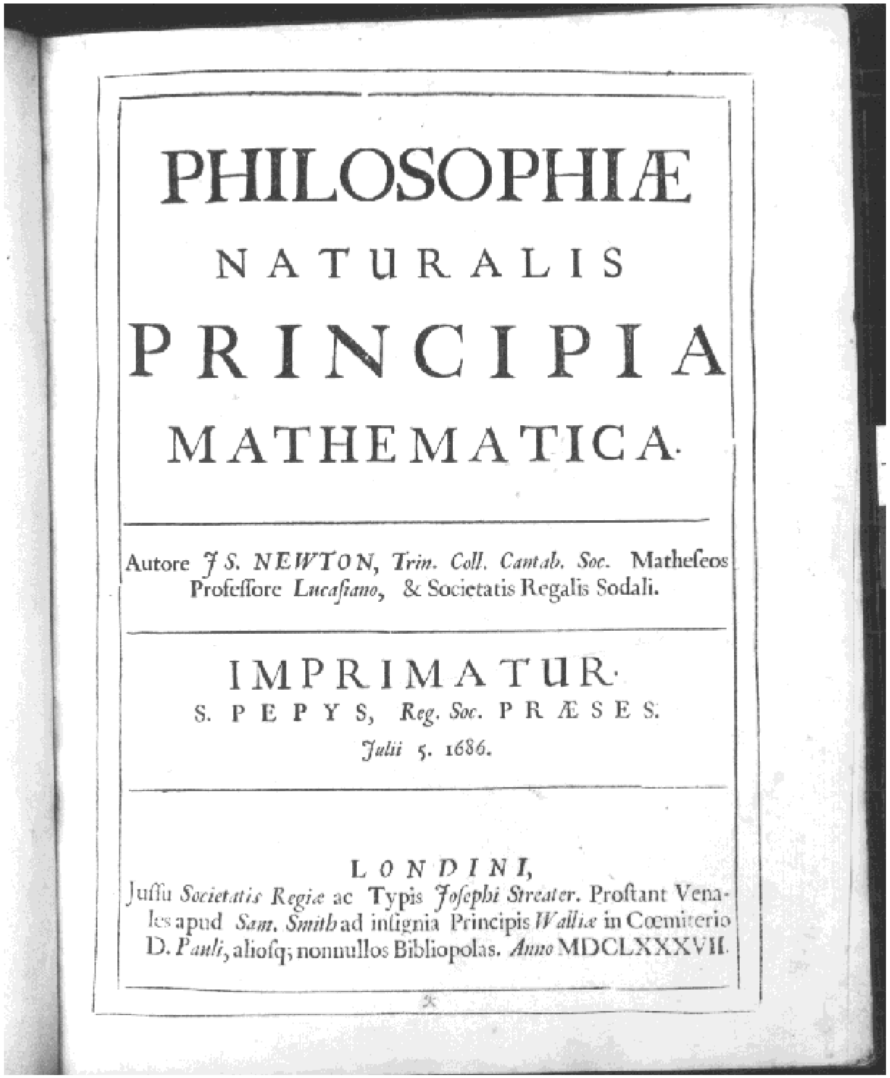
- Queller's most general version with non-additivity:

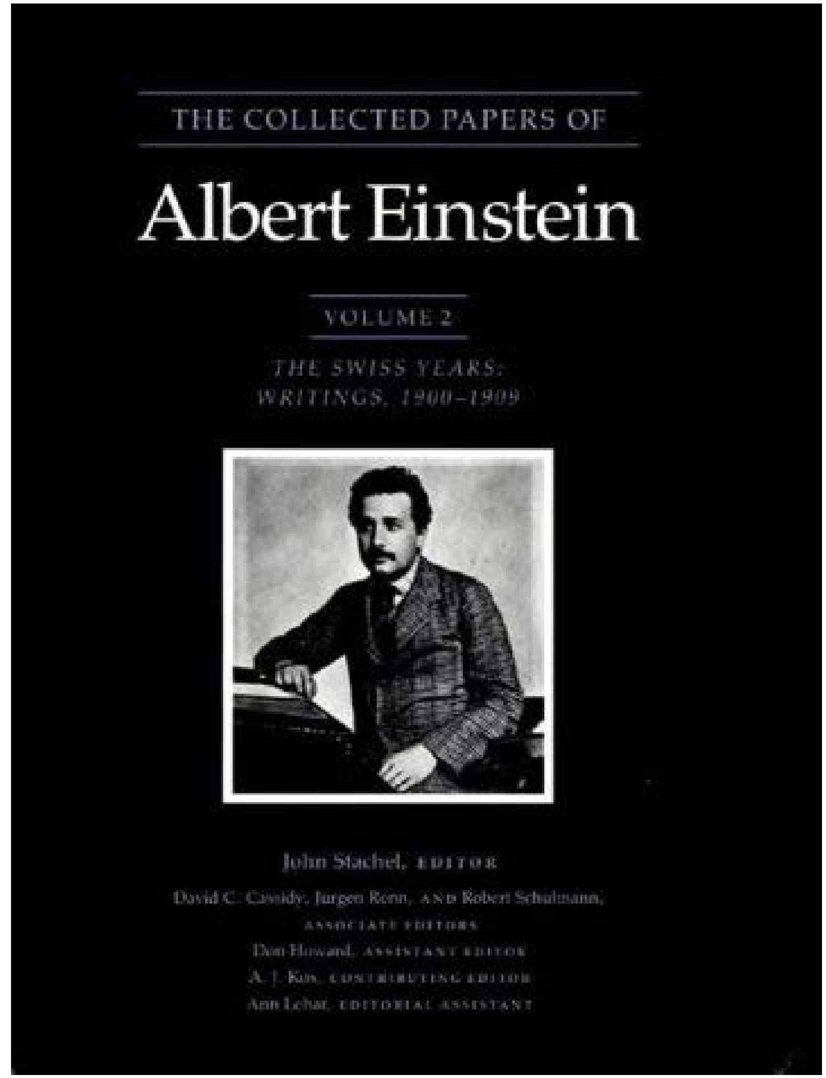
$$\frac{\mathrm{cov}(G_A, P_O)}{\mathrm{cov}(G_A, P_A)} b + \frac{\mathrm{cov}(G_A, P_A P_O)}{\mathrm{cov}(G_A, P_A)} d > c \tag{4}$$

Queller's Version is More General!

	Applies to …			
Eq.	Kin interactions	Non-kin genetic similarity	Genotype-phenotype differences	Non-additive fitness functions
(1)	**YES**	—	—	—
(2)	**YES**	**YES**	—	—
(3)	**YES**	**YES**	**YES**	—
(4)	**YES**	**YES**	**YES**	**YES**

Analogy with Physics





What about “indirect” fitness?

- *“Shared genes cooperation differs from all other models considered here in that the cooperative individual need not benefit from its act.”*
    - Sachs, *et al*. 2004. **The Evolution of Cooperation**. *QRB* 79:135-160.
- What does this mean?
    - Some individuals don’t get anything back
    - Confusing whole-group/other-only distinction
    - Cooperators don’t need anything back themselves because their relatives benefit

A More Intuitive Form

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

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

- Direct reciprocity is a perfectly good alternative interpretation of HR

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

A Unified View

- The frequency of an altruistic genotype (allele) increases if individuals carrying that allele receive more fitness benefits from others than their costs (relative to alternate genotypes)
- This positive assortment between cooperators and cooperation from others is necessary
  - whether “others” are relatives or heterospecifics
  - whether thinking in terms of inclusive fitness or reciprocity

Causes of Positive Assortment

- **spatially structured populations among kin** (Hamilton 1964)
- **or across species** (Doebeli and Knowlton 1998)
- **iterated and conditional behavior based on past behaviors** (Axelrod 1984; Axelrod and Hamilton 1981; Dugatkin 1997; Trivers 1971)
- **or the reputations** (Nowak and Sigmund 1998; Panchanathan and Boyd 2003)
- **policing** (Frank 1995; Frank 2003)
- **punishment** (Boyd et al. 2003; Boyd and Richerson 1992; Fehr and Gächter 2002)
- **constraint of social norms** (Bowles et al. 2003)
- **foraging in heterogeneous resource distributions** (Pepper and Smuts 2002)
- **periodic environmental disturbances** (Mitteldorf and Wilson 2000)
- **presence of fixed or conditional non-participants** ((Aktipis 2004, Hauert et al. 2002)
- **coevolution of group joining and cooperative behaviors** (Avilés et al. 2004)
- **multigenerational groups** (Fletcher and Zwick 2004)
- **recognition of arbitrary tags** (Axelrod et al. 2004; Riolo et al. 2001)

Final Summary

- Queller's version of Hamilton's "inclusive fitness" rule applies to models of reciprocal altruism including mutualistic symbiosis
- Queller's version is more general than Hamilton's and has a quite different interpretation
- Implications of this generalization have yet to be fully appreciated

Final Quote

There is no general theory of mutualism that approaches the explanatory power that ‘Hamilton’s Rule’ appears to hold for the understanding of within-species interactions.

– Herre et al. 1999, **The evolution of mutualisms: Exploring the paths between conflict and cooperation**. *TREE* 14:49-53

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