COOPERATION: *Non-relatives*

Mutualism, Conditional Cooperation, Reciprocal Altruism

Evolution, Maintenance by Natural Selection

Plausible Basis for Ethics, Justice

Mutualism: Each Individual Benefits Simultaneously

Easily Explained by Selfishness

Conditional Cooperation

Both Benefit **if** Both Cooperate

Individual Tempted to "Cheat"

Requires Repeated Interaction

Reciprocal Altruism

Alternating Roles, Altruist and Recipient

Temptation to Cheat

Requires Repeated Interaction

Conditional Cooperation as Paradigm

Game Theory: *Prisoner's Dilemma*

Repeated Play = Non-random Interaction

2-Person, n-Person discrete game

Single-Play Strategies: **C** cooperate, **D** defect

Nash Equilibrium Solution, Pareto Optimality

Numerical Example

Generalize

Recall 2-Player Symmetric Game

Nash Equilibrium: Each player has a Nash Strategy

Neither player tempted to change strategy
as long as opponent continues with its strategy

"Not tempted" by change in behavior: Lower payoff

Nash Equilibrium with Equal Payoffs: ***ESS***

Behaviors: A, B & C

2-Player, Symmetric Game: Payoff matrix

	A	B	C
A	3	**4**	1
B	**6**	1	2
C	3	0	**8**

2 **Nash Equilibria** with Pure Strategies

Pair (A, B) and Pair (C, C)

Pure C: ESS

Pareto Optimal Solution

Neither player can improve it payoff without causing a decrease in other player's payoff

Pareto optimality: advantage of "cooperation"

Can players coordinate & reach optimality?

Game Theory: *Prisoner's Dilemma*

Behaviors: A & B

2-Player, Symmetric Game: Payoff matrix, Example

	A	B
A	5	2
B	6	3

ESS: Pure B, diagonal dominance

B better response to A, and to B

E(B, B) = 3 at ESS

But, if both play pure A (**Pareto solution**)

E(A, A) = 5

Prisoner's Dilemma

2-player, symmetric, discrete game

Single Play

C: Cooperate **D**: Defect

	C	D
C	R	S
D	T	P

Reward, **S**ucker's payoff, **T**emptation, **P**enalty

$T > R > P > S$; $R > (T + S)/2$

Single Play: Pure D Only ESS

Probabilistically Repeated Play: Pure D An ESS

Conditional Cooperation (TFT) ESS,

If Duration of Play Sufficient

Tit-for-Tat (**TFT**)

1. Cooperate on First Play

2. Thereafter, Do What Opponent Did Last Play

2 TFT Players Never Defect

TFT Switches to D Against Defector
(Non-Cooperator)

If **Know** Last Play, Should Defect

Probabilistically Repeated Play:

Don’t Know When Interaction Ends

Shadow of the Future

w: Pr[Next interaction occurs]

Independent of Number Interactions

(1 - w): Pr[Current interaction is last]

If $w \geq \max\left\{ (T-R)/(R-S),\ (T-R)/(T-P) \right\}$

Then: Pure TFT Nash Equilibrium

Recall:

	A	B
A	5	2
B	6	3

Consider TFT, All D as Strategies:

After 10 Iterations, Cumulative "Scores"

D vs D (All B): 30

D vs TFT (B vs A, 9 B vs B): 6 + 27 = 33

TFT vs TFT (All A): 50

TFT vs D (A vs B, 9 B vs B): 2 + 27 = 29

	TFT	All D
TFT	50	29
All D	33	30

(As if) 2 ESS: Pure TFT, Pure D

Evolution Non-relatives' Cooperative Behavior

Cooperation: Both (All) Players Benefit Simultaneously

Unstable Without *Probabilistically Repeated Play*

Altruism: One Benefits; Other Altruist

Prisoner's Dilemma

Single Play:

C: Cooperate **D**: Defect

	C	D
C	R	S
D	T	P

Reward, **S**ucker's payoff, **T**emptation, **P**enalty

$T > R > P > S$; $R > (T + S)/2$

Single Play: Pure D Only ESS

Probabilistically Repeated Play: Pure D An ESS

Conditional Cooperation (TFT) ESS,

If Duration of Play Sufficient

1. Communally Breeding Birds:

    Parents Feed Own *and* Non-relatives' Nestlings

    Individual Nests: (Female) Parentage Certain

Mutualism

Feed Loudest Begging Nestling(s)

Avoid Attracting Predators (To Own Offspring)

Cooperation

Feed Hungriest Nestling, All Parents Benefit

Desert Seed-harvester Ant (*Messor pergandei)*

Initial Colony Foundation

- Multiple Co-foundresses, Non-relatives

Colonies Fiercely Territorial

- Brood-raiding
  - Capture and raise brood from another nest
  - Increases number soldiers/workers

More foundresses, More workers initially,

- Increases Defense Own Brood, Capturing Other Brood

Foundresses: Mutual Benefit of Mixing Own Broods

- *Mutualism, Cooperation*?

All Small Nests Raid Until Only One Nest Remains

Then Queens Fight Until Only One Survives, Large Nest

- Cooperative Behavior Disappear With Its Benefits

Conditional Cooperation / TFT

Humans

Caporeal, L. *et al*. 1989. Selfishness examined: cooperation in the absence of egoistic motives. *Behavioral and Brain Sciences* 12:683.

Dawes, R. 1980. Social dilemmas. *Annual Review of Psychology* 31:169.

Non-human animals

- Difficult to verify PD/IPD in nature
- Temporal discounting, Impulsiveness
  - Value immediate over future payoffs
  - Relatively strong in animals
  - Impulsiveness promotes defection?

Stephens, D.W. *et al.* 2002. Discounting and reciprocity in an iterated prisoner's dilemma. *Science* 298:2216.

Blue jays in laboratory apparatus: Foraging pairs

Payoffs (food) Prisoner's dilemma

Keypeck C or D

Subject Bird:

Treatment Bird (All D or TFT)

Food Un-accumulated, Accumulated (4 iterations)

Tested effect of temporal discounting

Subjects "cooperators": Does cooperation wane?

Accumulated payoffs (low discounting) and TFT opponent:
Cooperation stable

Un-accumulated payoffs and All-D opponent:
Fastest decay of cooperation

Conditional Cooperation – Non-relatives

Reciprocal Altruism: Donor & Recipient

Motivate: Modify Prisoner's Dilemma

2-player, Symmetric, Discrete game, 2 pure strategies

C: Cooperate **D**: Defect

	C	D
C	R	S
D	T	P

$T > R > P > S$;

Suppose $T + S > 2R$

Alternating Between T and S

Greater Average Payoff than Mutual Cooperation

Reciprocal Altruism: Same Individuals

Alternating Roles: Donor ("Altruist") and Recipient

Play C against D: Donor

Play D against C: Recipient

Repeated Play, Same Individuals

Exchange Roles Frequently

3 Conditions: Selection for Reciprocal Altruism

1. Repeated Interaction (Viscous population)

   Permits Exchange of Roles

2. Benefit to Recipient > Cost to Donor

3. Donor Must Avoid Individuals Fail to Reciprocate

Wilkinson, G.S. 1984. Reciprocal food sharing in the vampire bat. *Nature* 308:181.

Vampire bats (*Desmodus rotundus*): Feed on cattle at night

Females roost in groups during day

Primary social unit:
8 –12 Adult females & dependent offspring

Average coefficient of relatedness among adults, r = 0.11,

Reciprocity not strictly between kin

Some subadult females disperse between groups

Regurgitate blood: food sharing

App. 75%: Between Mother & Nursing offspring

25%: More Distant Relative or a *Non-Relative* Associate Fed

Non-related associate: Roost together commonly

Females live up to 18 years, groups stable

Adult females: successful 90% foraging bouts

Foraging females < 2 yrs old: successful 60% bouts

Risk starvation

Successful foragers often regurgitate blood (feed)
for unsuccessful foragers

Conditions for Reciprocal Altruism (Non-Relative):

1) Repeated Interaction, Permit Role exchange

2) Benefit to recipient > **Cost** to Donor

3) Donors Recognize Non-reciprocators;

Don't Feed Individual Fails to Reciprocate

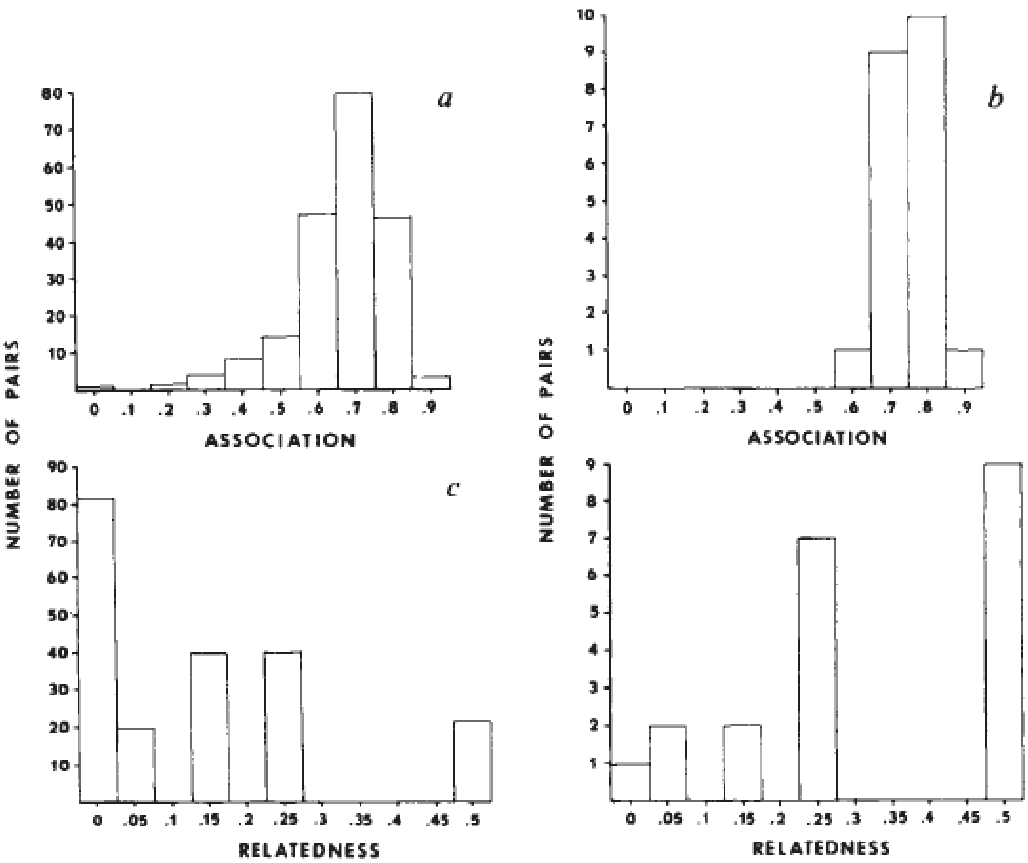
(Conditional Altruism)

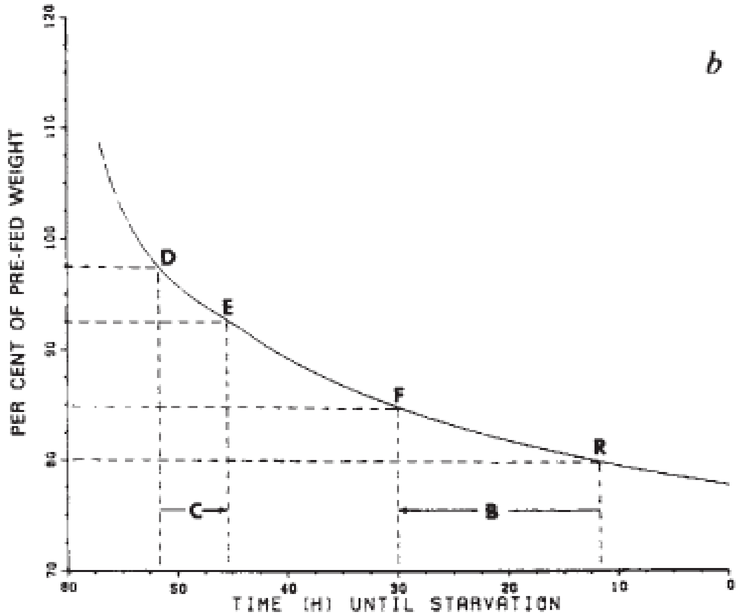
Reciprocal food sharing in the vampire bat

Gerald S. Wilkinson

Time until starvation, function of mass of blood in gut

Lab: Avoid feeding non-regurgitators


a
b
c
d
NUMBER OF PAIRS
NUMBER OF PAIRS
ASSOCIATION
ASSOCIATION
RELATEDNESS
RELATEDNESS


b
PER CENT OF PRE-FED WEIGHT
TIME (H) UNTIL STARVATION
D
E
F
R
C
B