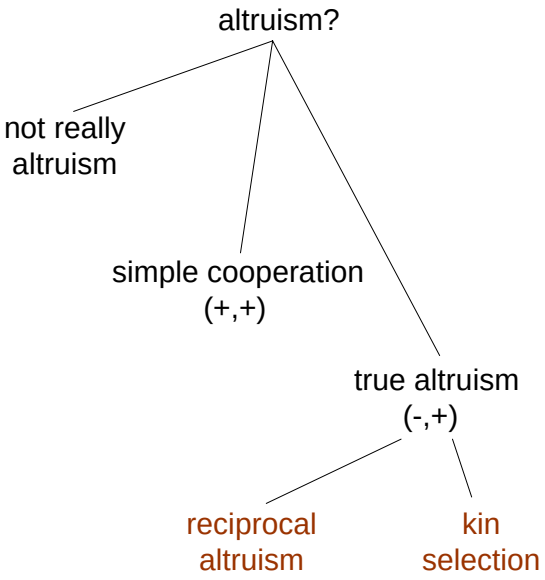
ALTRUISM

Altruism: behavior that benefits another individual at a cost to the altruist's personal fitness (ability to produce offspring).

- C + B

Altruist → Recipient

How could altruism evolve?



ALTRUISM & KIN SELECTION

Kin Selection: selection of a trait through helping relatives, either

1. descendant kin (offspring):
   direct selection

- OR -

2. non-descendant (collateral) kin:
   indirect selection

inclusive fitness = direct + indirect fitness

ALTRUISM & KIN SELECTION

Three factors are important in the spread and maintenance of an altruism gene by kin selection:

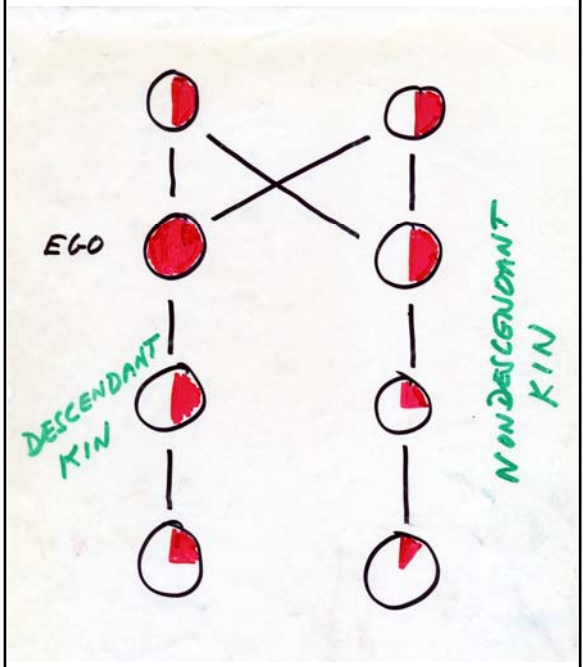
1. benefit to recipient, B
2. cost to altruist, C
3. degree of relatedness between altruist and recipient, r

Coefficient of Relatedness, r =

1. probability that a rare gene is shared by two individuals,

OR

2. the proportion of genes Identical By Descent (IBD) shared by two individuals.



ALTRUISM & KIN SELECTION

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Hamilton's Rule states the conditions under which altruism will spread. In its simplest form it is:

$$rB > C$$

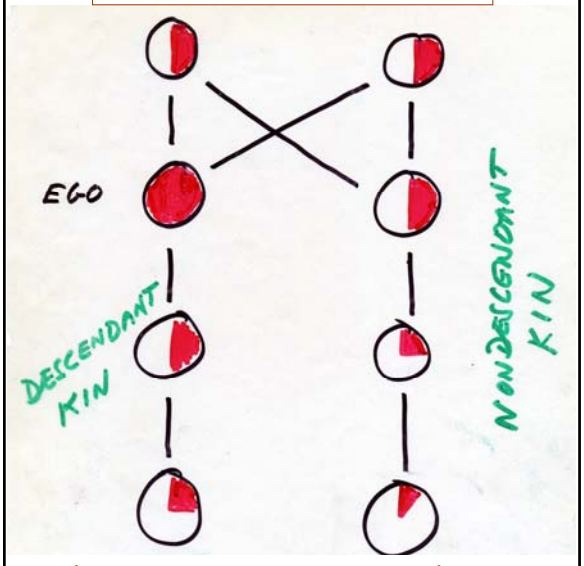
When should you be altruistic?

When $B > C/r$

Recipient	r	$B > C/r$
identical twin	1	$B > C$
1 parent	1/2	$B > 2C$
full sib	1/2	$B > 2C$
half sib	1/4	$B > 4C$
niece/nephew*	1/4	$B > 4C$
uncle/aunt **	1/4	$B > 4C$
1st cousin **	1/8	$B > 8C$

* assumes your sib was full sib
** assumes your parent's sib was full

Be altruistic if $rB > C$



What variables are missing from this equation?

More general form of Hamilton's Rule:

$r_B B > r_C C$

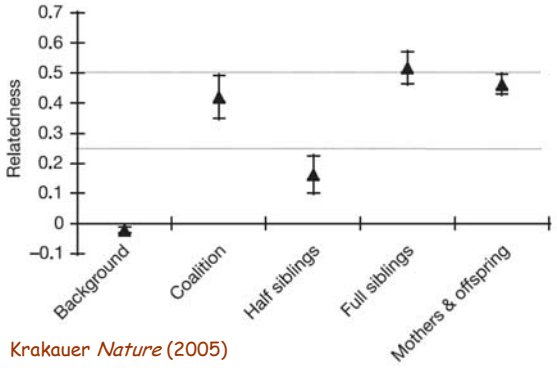
r_B = r of actor to recipient

r_C = r of actor to individual suffering cost

If actor takes cost directly, then $r_C = 1$ and Hamilton's Rule is

$rB > C$

Relatedness values calculated from microsatellite genotypes



Krakauer *Nature* (2005)

Does helping pay in American Turkeys?

Table 1 **Calculation of Hamilton's rule, $rB - C < 0$**

Variable	Description	Calculation	Value*
r	Coefficient of relatedness	Mean pairwise relatedness of subordinates to their dominant display partner	0.42
B†	Benefit to dominant	(No. of offspring per dominant male) – (no. of offspring per solo male)	6.1 (9.0)
C†	Cost to subordinate	(No. of offspring per solo male)– (no. of offspring per subordinate male)	0.9 (2.3)
	Net benefit†	$rB - C$	+1.7 (1.5)

Dominant, solo and subordinate refer to dominant coalition males, solitary non-cooperating males and subordinate male helpers, respectively.
*Values in parentheses exclude non-reproducing males from mean fitness calculations.
† In units of offspring per male.

Krakauer *Nature* (2005)

rB > C?
0.42(6.1) > 0.9?
2.6 > 0.9
yes, helping pays

RECIPROCAL ALTRUISM

baboon alliances
an example of reciprocal altruism

RECIPROCAL ALTRUISM

Reciprocity: altruist repaid at a later date by the recipient

	You	Other
Time 1	-C	+B
Time 2	+B	-C
Time 3	-C	+B
	.	.
	.	.
	.	.
	-----	-----
Average	B-C	B-C

Reciprocity pays if:
(1) B > C
(2) favors reliably returned (no cheating)

Prisoners' Dilemma

"Partner"

payoff to:	coop.	defect
coop.	B - C	- C
defect	B	0

coop.	3	-1
defect	4	0

Let B = 4, C = 1

ESS = Defect! In *one-shot game,* best strategy is to defect, no matter what your 'partner' does. The dilemma (or irony) is that both would do better if they both cooperated than if they both defected!

Prisoners' Dilemma

Situation is changed if we change any of the implied assumptions:

1. Repeated interactions with individuals
2. Recognition/memory: remember who cheats and who reciprocates
3. Flexible behavior: can modify behavior (give or not give) depending on past interactions.

Axelrod (computer simulation):

"Tit-for-Tat" is an ESS

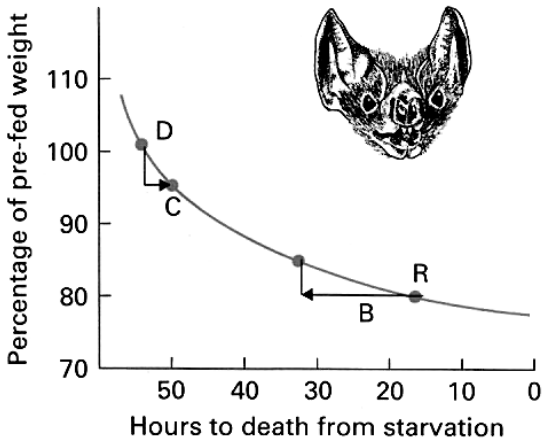
(1) cooperate on 1st play

(2) do what your partner did on the previous play

Reciprocal Altruism in Vampire Bats

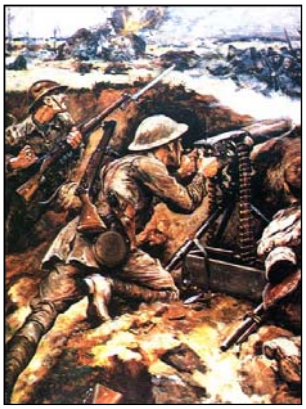
Hungry, unsuccessful bats beg for food from non-related partners.

Desmodus rotundus



D = Donor, R = Recipient
B = Benefit, C = Cost

Trench Warfare



Common form of battle in World War I

Armies in deep trenches on either side of battle line

Machine guns and artillery

Prolonged engagement with same group of enemy troops

Indirect Reciprocity and Image Scoring

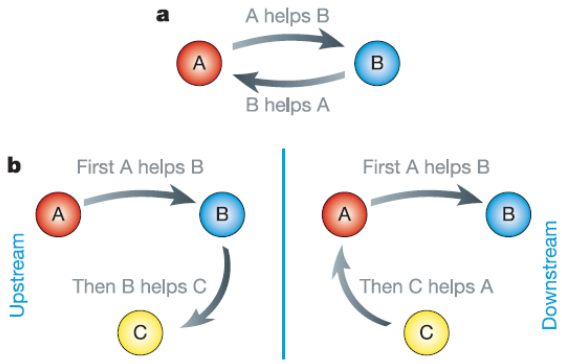


Figure 1 | Direct and indirect reciprocity. **a**, Direct reciprocity means that A helps B and B helps A. **b**, Indirect reciprocity comes in two flavours. 'Upstream reciprocity' (left) is based on a recent positive experience. A person who has been at the receiving end of a donation may feel motivated to donate in turn. Individual B, who has just received help from A, goes on to help C. 'Downstream reciprocity' (right) is built on reputation. Individual A has helped B and therefore receives help from C. Mathematical investigations of indirect reciprocity have shown that natural selection can favour strategies that help others based on their reputation. Upstream reciprocity is harder to understand[2,56,77,78] but is observed in economic experiments. In both cases, the decision to help can be interpreted as a misdirected act of gratitude. In one case recipients are thanked for what another did; in the other case they are thanked by someone who did not profit by what they did.

Indirect Reciprocity and Image Scoring

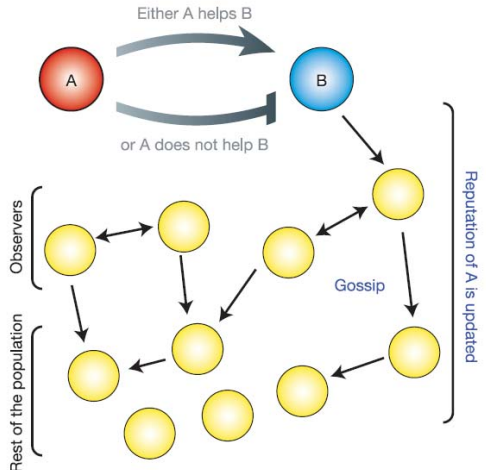


Figure 2 | Building a reputation. In a natural extension of the basic model of indirect reciprocity, an action between donor A and recipient B is observed by a subset of the population[36]. The observers, the donor and the recipient can inform others. People could pass on what has happened (the action) or their assessment of the action. There are many possibilities of error: the action or the intention of the donor can be interpreted differently by different people; some individuals may receive conflicting information from different sources; some individuals may not receive any information at all; people can have different assessment modules. The reputation of a person is therefore not simply a label that is visible to all others, but instead each person has a private list of the reputation of others. Although language could help to synchronize these lists[42], ultimately reputation is in the eyes of the beholder.