

Kin selection

Emergence in complex systems

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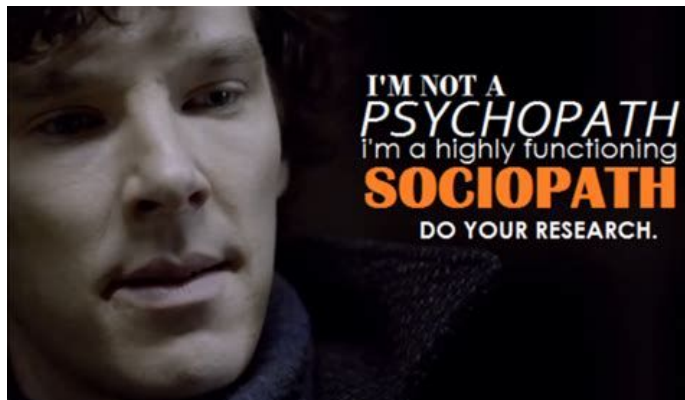
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Why altruism?



Economist: :(
(Game Theory // Nash equilibrium)

Biologist: :) (?)
(Evolutionary Game Theory // ESS,
which resist *mutant* strategies)

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A widespread example: animal altruism towards relatives



Animal altruism towards relatives

Throughout the animal world, altruism abounds in one specific context. Animals appear ready to take on significant costs to help their relatives (kin). This can be explained by the fact that:

- A) Many animals feel unconditional love for their relatives, particularly their children. This motivates them to engage in self-sacrificial behavior in the favour of kin.
- B) Natural selection operates at the level of genes, not individuals. A gene that pushes individuals to behave altruistically towards kin may actually be helping (copies) of itself. When expected benefits exceed costs, representation of that gene in the gene pool should increase.
- C) Family members are often in need of protection, particularly children, who, in most bird and mammal species for instance, go through long developmental periods before being autonomous. Sacrifice on the part of parents is thus required: otherwise the species would quickly go extinct.

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Hamilton's rule

Genes underlying altruistic behavior should spread provided [Hamilton, 1963]:

$$r * B > C$$

Where:

- C is the cost of the behavior to the altruist
- B is its benefits to the recipient
- r is the coefficient of relatedness between both individuals: the probability that a given allele in the altruist is identical by descent to the one in the recipient

Hamilton's rule

Genes underlying altruistic behavior should spread provided [Hamilton, 1963]:

$$r * B > C$$

Rapid proof: one "altruistic" and one "selfish" allele, two individuals with relatedness coefficient r . Altruistic "alleles" are in proportion p in the population:

$$\pi_a = -C + r * B + (1 - r)p * B$$

$$\pi_s = -0 + (1 - r)p * B$$

$$\pi_a > \pi_s \iff r * B > C$$

Note that r is defined *relatively*. Altruism can spread when behavior targets kin more than random individuals.

Kin altruism throughout the natural world

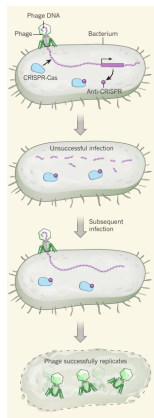


Figure: Virus (phage) cooperation: a first wave succumbs to CRISPR-CAS defences, but enables future invasion [Bernheim and Sorek, 2018]

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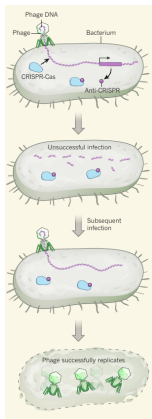


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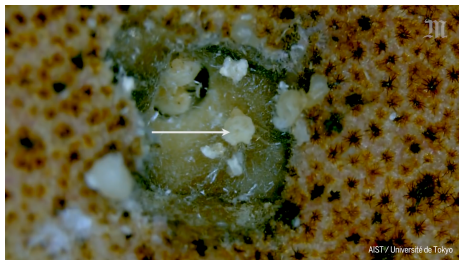


Figure: Social aphids (warrior caste) engage in "self-explosion" to plaster over nest (gall) injuries [Kutsukake et al., 2019]

Public good game episode 2: now with kin

Assumptions:

Collectively shared benefit:

$$B = \sum_{i=1}^n b * x_i$$

Quadratic individual cost:

$$C = \frac{1}{2}c * x^2$$

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Total payoff if I invest x and others x_0 :



$$F(x, x_0^{-1}) = \frac{b*x + (n-1)b*x_0}{n} - \frac{1}{2}c * x^2 + r * \frac{b(n-1)*x}{n}$$

Optimal investment:

$$\forall n \in \mathcal{N}, x^* = r * \frac{b}{c}$$

→ *A population of related individuals can resist the tragedy of the commons*

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