

Kin Selection

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July 2023

Sources and further reading

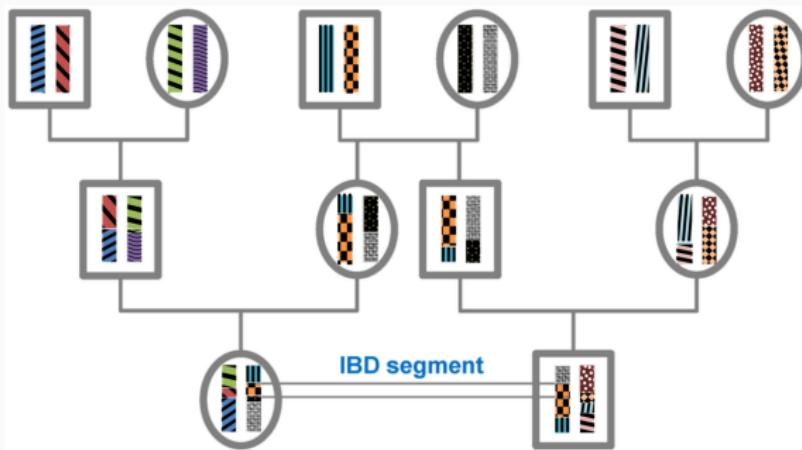
- Lehmann, L., & Rousset, F. (2010). How life history and demography promote or inhibit the evolution of helping behaviours. *Philosophical Transactions of the Royal Society B*, 365(1553), 2599–2617.
- Frank, S. A. (1998). Foundations of social evolution. Princeton University Press.
- Birch, J. (2014). Hamilton's rule and its discontents. *The British Journal for the Philosophy of Science*, 65(2), 381–411.

Motivation

Natural selection can favour a trait due to its positive effects on individual's relatives even at a cost to the individual's own survival and reproduction. Kin selection can lead to the evolution of altruistic behaviour.

Identical by descent

Identical alleles in two or more individuals that are identical because they have been inherited from a common ancestor without recombination or mutation



cf., identical by state: alleles that are identical because of coincidental mutational processes

Hamilton's rule

Consider two types:

1. Cooperators: pay cost C to provide benefit B to partner
2. Defectors: do nothing

Hamilton's Rule: Cooperation is favoured by natural selection when

$$rB > C$$

where r is (dyadic) **relatedness**: the probability that, for two individuals, a gene picked randomly from the same locus is identical by descent.

Let's derive Hamilton's rule from the replicator dynamics

Goal: $rB > C$

Replicator dynamics:

$$\dot{p}_C = p_C(1 - p_c)(f_C - f_D)$$

Let r be the probability that two (clonal) individuals randomly matched for the game are IBD

Find the conditions under which cooperators are favoured.

Maladaptation hypothesis ('big mistake')

Some human behaviors are the result of past selective forces that are no longer operative.

Classic example: preference for salty / sweet / fatty food.

Three ingredients:

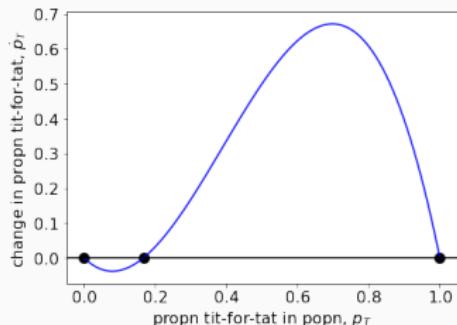
1. General proximate mechanism
2. Adaptively relevant environment
3. Rapid change

Notes:

- Mistake \neq misunderstanding
- We're not eusocial...
- Why not the other primates?

Tit-for-tat / reciprocity

- Both tit-for-tat and always defect are evolutionarily stable
- Raises the question of how cooperation got started in the first place
- But remember, when we considered mutation before, the mutants were few and almost always interact at random



Axelrod & Hamilton (1981): “kinship theory suggests a plausible escape”

Invasion fitness

A type s can invade a population if its invasion fitness is positive

$$\frac{\dot{p}_s}{p_s} \Big|_{p_s=0} > 0$$

For example, for the replicator dynamics with $\mathbf{p} = (p_C, p_D)$

$$\frac{\dot{p}_C}{p_C} \Big|_{\mathbf{p}=(0,1)} = f_C - f_D \text{ evaluated at } \mathbf{p} = (0, 1)$$

Exercise: Tit-for-tat

Exercise:

		tit-for-tat	defect
tit-for-tat	16, 16	1, 11	
defect	11, 1	2, 2	

We know that, under random matching, tit-for-tat cannot invade an all-defect population. But perhaps it can if $r > 0$.

Tit-for-tat can invade when its invasion fitness is greater than zero, i.e.,

$$\left. \frac{\dot{p}_T}{p_T} \right|_{p_T=0} > 0.$$

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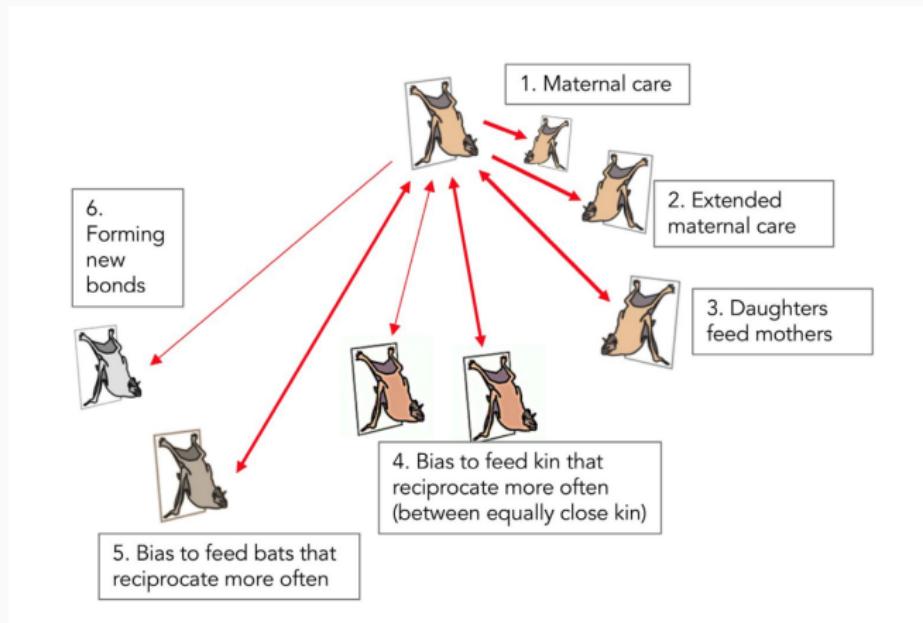
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Find that tit-for-tat can invade when $r > 1/15$.

Co-optation hypotheses

Carter, G. G. (2021). Co-option and the evolution of food sharing in vampire bats. *Ethology*, 127(10), 837-849.



The Price Equation

A population is split into groups i . Each group has: size n_i , genetic value g_i , and fitness w_i . How does the average genetic value change over 1 generation?

$$\Delta g = g' - g = ?$$

Answer is the Price equation:

$$w\Delta g = \underbrace{\text{Cov}[w_i, g_i]}_{\text{selection}} + \underbrace{\mathbb{E}[w_i \Delta g_i]}_{\text{transmission}}$$

where w is average fitness in population ($w = 1$ if size constant).

When the characteristic values g_i do not change from the parent to the child generation (no mutation):

$$w\Delta g = \text{Cov}[w_i, g_i]$$

Direct fitness approach (Taylor & Frank 1996, J Theor Biol)

Consider a population with a constant genetic value x , take one allele and mutate it and all of its IBD copies, ask how that influences the fitness of its bearer.

The fitness of an individual $W(y, z)$ depends on their own phenotype y and their neighbours' average phenotype z . Ask how W changes with x . Using the chain rule

$$\frac{dW}{dx} = \frac{\partial W}{\partial y} \underbrace{\frac{dy}{dx}}_{\beta_{yx}} + \frac{\partial W}{\partial z} \underbrace{\frac{dz}{dx}}_{\beta_{zx}}$$

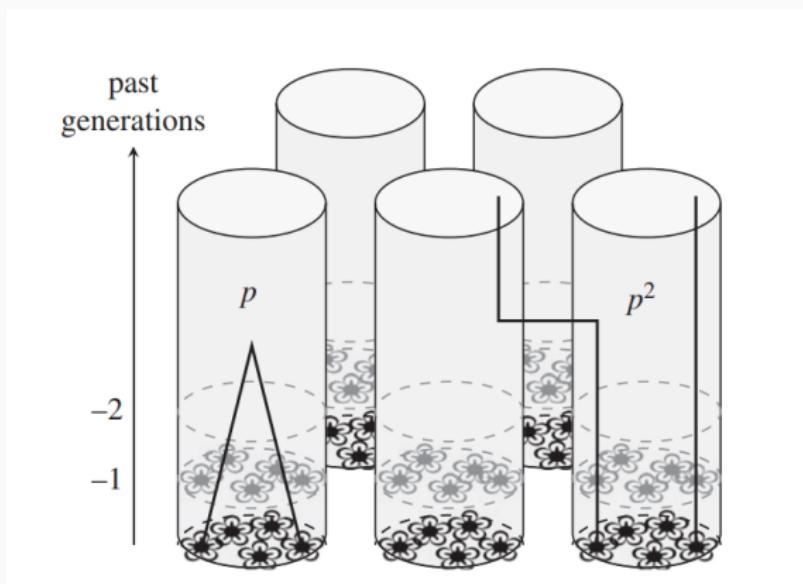
where β are regression coefficients. Have relatedness $R = \frac{\text{Cov}[z, x]}{\text{Cov}[y, x]}$.

Therefore

$$\Delta W_{IF} = \frac{\partial W}{\partial y} + R \frac{\partial W}{\partial z}$$

Infinite islands model

Lehmann & Rousset (2014, Phil Trans Roy Soc B)

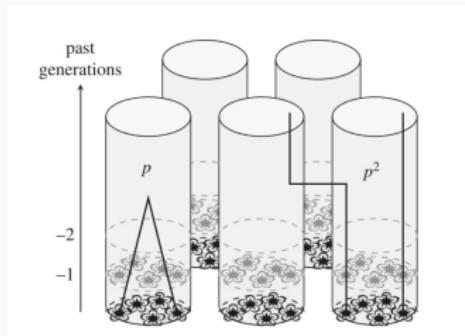


Mutate an individual's genetic value and all values in its lineage. What effect does that have?

Infinite islands model

Infinite islands:

- Infinite population
- Infinite number of islands
- Fixed pop size on each island N
- Each individual produces a large number of offspring
- A small proportion of offspring m disperse to other islands



Lehmann & Rousset (2014, Phil Trans Roy Soc B)

Key assumptions:

- Additive interactions, e.g., random pairwise interacts
- Weak selection (helps us estimate R)

Does limited dispersal promote cooperation?

Consider the invasion of a small number of altruistic mutants who increase the fecundities of their neighbours by B at a cost to own fecundity C .

z_\bullet : phenotype of the focal individual

z_0 : average phenotype of adults on the focal island

z_0^R : average phenotype of juveniles on the focal island before dispersing

z : average phenotype in the population

Steps:

1. Write $w(z_\bullet, z_0, z_0^R)$

2. Evaluate derivs in $W_{IF} = \frac{\partial w}{\partial z_\bullet} + \frac{\partial w}{\partial z_0} R + \frac{\partial w}{\partial z_0^R} R^R$ at zero helping ($z_\bullet = 0$ etc).

3. Obtain R, R^R etc.

4. Check when $W_{IF} > 0$

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Does limited dispersal promote cooperation?

Invasion fitness of helping mutant:

$$W_{IF} = -C(1 - R) < 0.$$

What happened? Limited dispersal has two effects:

1. increase interactions between relatives (positive)
2. increase competition between relatives (negative)

Cancelling-out effect first shown by Taylor (1992).

How to avoid: increase relatedness at the temporal point when altruism occurs, or export competition.

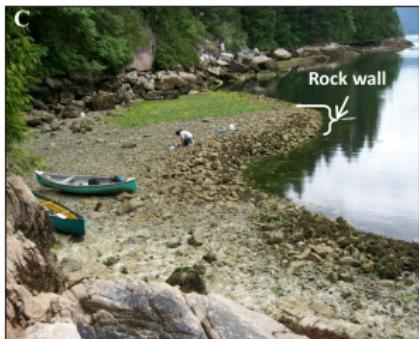
Traditional management semi-wild resources

Examples from British Columbia (Turner et al. 2013, BC Studies)



Traditional management semi-wild resources

Groesbeck et al. (2014, PLOS One)



Model: traditional management

Helping act provides benefit B for the current generation but also provides benefits for future generations.

Assume the benefit decays at a rate λ so that the benefit t generations later is

$$B_t = \lambda^t B.$$

For a long-lasting behaviour, the relative fecundity of the focal individual is

$$f_\bullet = 1 + Bz_0 - Cz_\bullet + \sum_{t=1}^{\infty} B_t z_t,$$

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Model result: traditional management

Invasion criterion:

$$\frac{C}{B} < \frac{\lambda(1-m)}{N(1-\lambda(1-m))}$$

Interpretation:

- No ecological inheritance $\lambda = 0$ recovers $W_{IF} = -C(1-R)$ and the Taylor cancelling-out effect
- Intergenerational helping evolves when:
 - costs are low
 - benefits are high
 - population size small

Exercise: overfishing

Let B be the benefit to the focal individual of overexploiting the pool, and C_t be the cost from exploiters t generations ago.

If over-harvesting reduces the availability of resources in the pool by some proportion γ , then the costs to future generations of repeated over-harvesting will be cumulative

$$C = \gamma^t C_t \rightarrow C_t \rightarrow \left(\frac{1}{\gamma}\right)^t C$$

The relative fecundity of the focal individual

$$f_{\bullet} = 1 + Bz_{\bullet} - \sum_{t=1}^{\infty} C_t z_t.$$

Result: overfishing

Overfishing invades when

$$0 < B - \frac{C}{N} \sum_{t=1}^{\infty} \left(\frac{1-m}{\gamma} \right)^t$$

1. If offspring always disperse ($m = 1$), then over-fishing will always invade.
2. If $\frac{1-m}{\gamma} > 1$, then overfishing will never invade.
 - If γ is small, i.e., there is a strong effect of overfishing.
 - If most stay, even weak overfishing effect

If $\frac{1-m}{\gamma} < 1$, then we can solve the sum

$$\frac{B}{C} > \frac{1}{N} \frac{\gamma(1-m)}{\gamma - (1-m)}$$

Overfishing promoted by: high benefit of overfishing B , low impact on the pool C , large group size N .