Social Evolution

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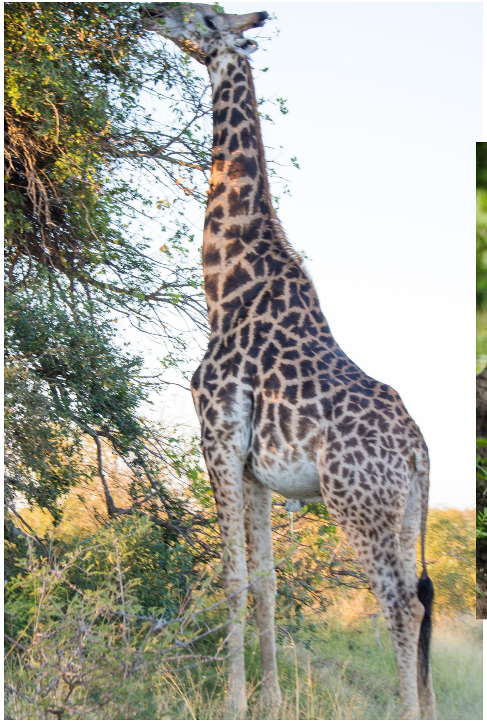
What is social evolution?



What is social evolution?

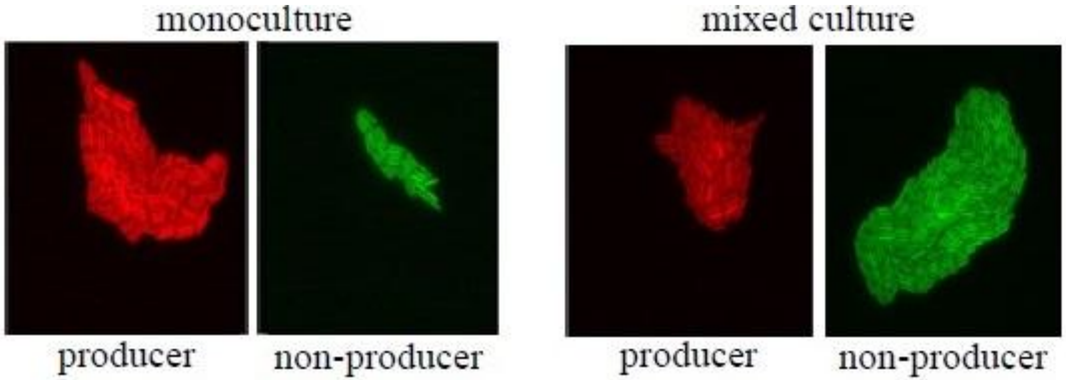
- Evolution without social effects is about how fit are individuals with given traits
- Selection makes sure that number of offspring increases with fitness
- Fitness depends on individual trait

What is social evolution?

- Traits undergo social evolution if they have effects not only on the individual, but also on the individual’s social environment, i.e., other individuals of the same species
- Fitness of an individual then depends not only on its trait but also on its social environment, e.g., the group the individual lives in

What is social evolution?

- Example: Some bacteria produce and excrete siderophores which facilitate iron uptake. Production decreases individual fitness but is beneficial for social environment



Games as formal models of social evolution

- Interaction between two or more individuals
- Each individual has a strategy
- Outcome for each individual depends on strategies of others
- Each individual has own utility (payoff, fitness, etc.)

Examples

- Everyday examples: chess, poker, Monopoly, rock-paper-scissors
- Economics: rival petrol station owners deciding what to charge per litre (strategy A: £1, strategy B: £2)

Payoff matrix:

	vs A	vs B
Payoff for A	£0.50	£1
Payoff for B	£0	£1

Why game theory in evolutionary biology?

- Non-social models assume that trait determines fitness
- But social traits have effects on others
- My fitness depends not only on my strategy but also on the strategy of others around me
- Examples: fighting, cooperation, reciprocal grooming

Why game theory in evolutionary biology?

- Suppose the strategy of an individual is genetically determined
- Suppose population is a mix of types (individuals with different strategies) with different fitnesses depending on composition
- The growth rate of each type is determined by its fitness
- How will the dynamics look like? What about the petrol stations?

Let’s play a game

- You can choose to cooperate or to defect
- If everyone cooperates, everyone gets an (imagined) **chocolate**
- If one of you defects and all others cooperate, the defector gets a **whole box of chocolates**
- If more than one of you defects, **no one gets any chocolate**
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Social dilemmas/Evolution of cooperation

- Cooperators produce public good that is shared with everyone, regardless of their strategy
- Production of public good comes at a cost
- Average fitness highest if all cooperate

b, c > 0

	Cooperate	Defect
Cooperate	b-c	-c
Defect	b	0

Social dilemmas/Evolution of cooperation

- But evolutionary stable strategy is Defect: defectors are always fitter than cooperators
- In a population with frequency of cooperators x:

$$w_C = x(b-c) + (1-x)(-c) = xb - c$$
$$w_D = xb$$

- Consequently, defectors will increase until x=0
- But average fitness (‘public interest’) is highest when all cooperate

Social dilemmas/Evolution of cooperation

- Dilemma lies in the problem that if everyone does what’s best for them, then all are worse off in the end
- We have shown that cooperation cannot evolve if cooperators and defectors mix freely
- How can we explain bacterial altruism, guarding meerkats, insect societies?

Tragedy of the commons

See NetLogo

Assortment as solution to social dilemmas

- What if individuals were assorted according to their strategy?
- If strategies are genetically determined then this would be the case if individuals stay around their families
- High relatedness can lead to assortment

Hamilton's rule

- If individuals interact with others with the same strategy with probability r and a random individual in the population with probability 1-r

$$\begin{aligned} w_C &= r(b-c) + (1-r)(x(b-c) + (1-x)(-c)) \\ &= rb - c + (1-r)xb \\ w_D &= r0 + (1-r)(xb + (1-x)0) = \\ &= (1-r)xb \end{aligned}$$

- If $r > \frac{c}{b}$ then $w_C > w_D$ and cooperators take over!

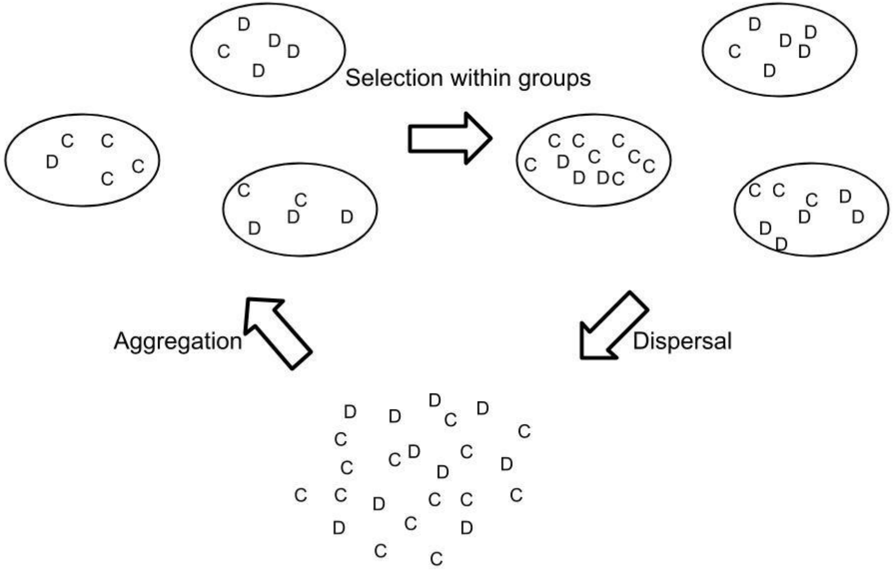
Group selection

- Suppose that our population of cooperators and defectors is organised in groups and that interactions take place only within groups
- Positive effects of trait benefit all members of a group
- Meerkats: guarding decreases probability that group will be eaten by predator, i.e. increases group fitness, but decreases fitness of guardian

Group selection

- But reproduction is individual, so how can altruistic trait evolve?

Trait-group model of social evolution



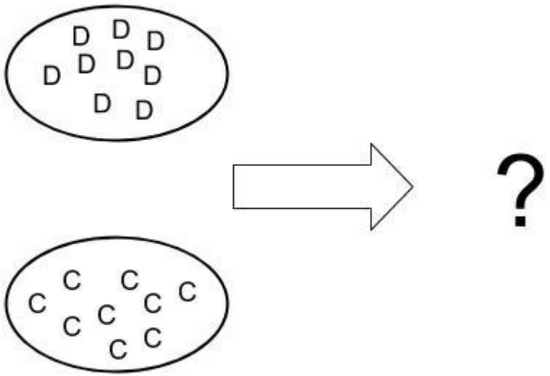
Group selection

- What is required for cooperators to take over in trait-group model?
- If all groups have same proportion of cooperators x, it cannot work, since cooperators are less fit than defectors

$$w_C = xb - c$$
$$w_D = xb$$

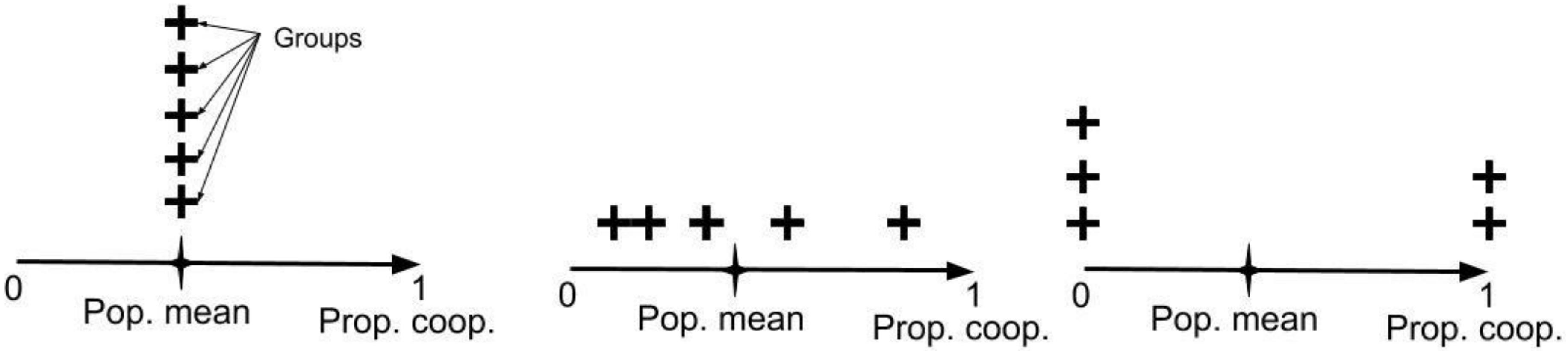
Group selection

- Conversely, if groups are monomorphic, i.e. only cooperator or only defectors, cooperation wins
- Why?

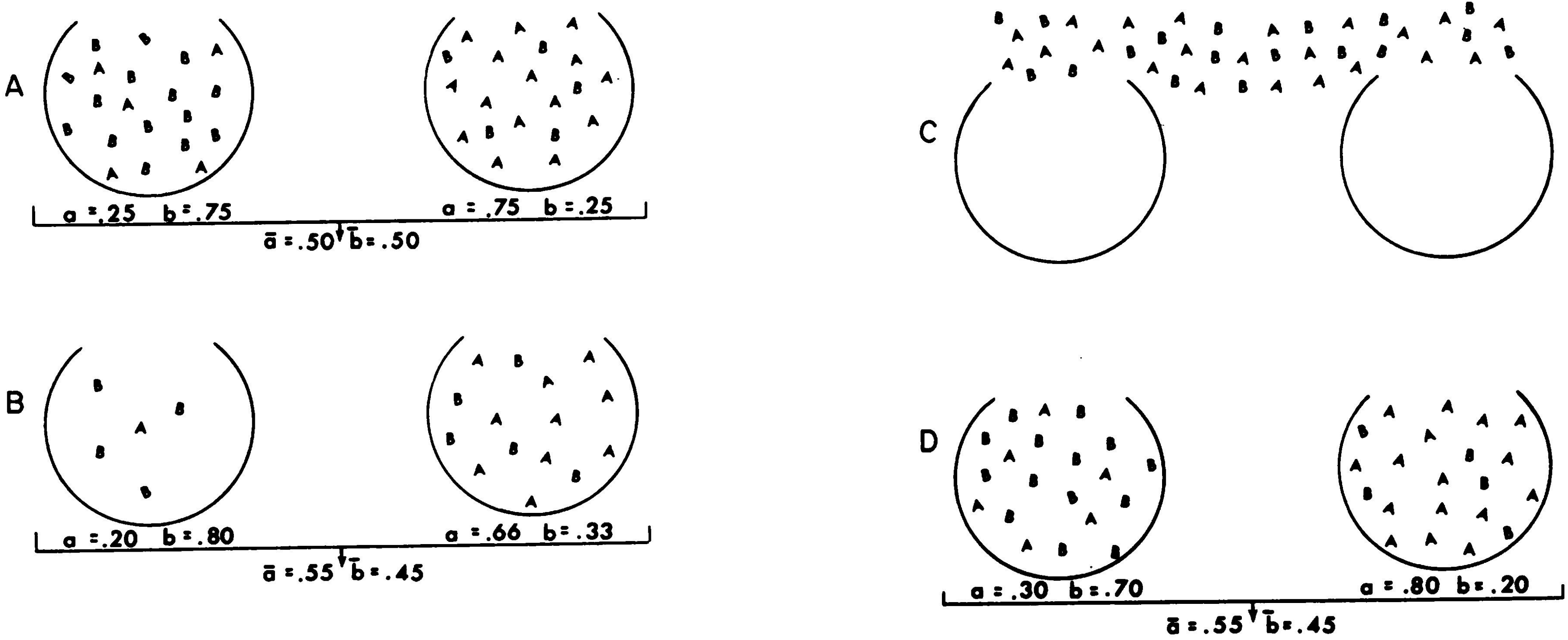


Group selection

- No variance between groups, no cooperation
- All variance between groups, cooperation
- What about in between?

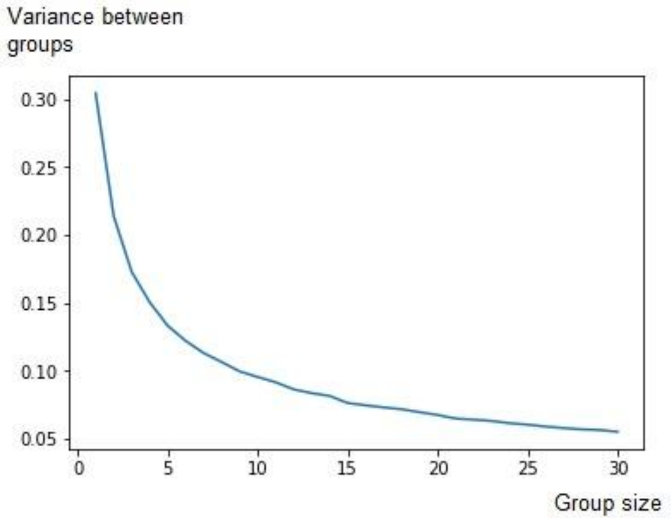


Group selection



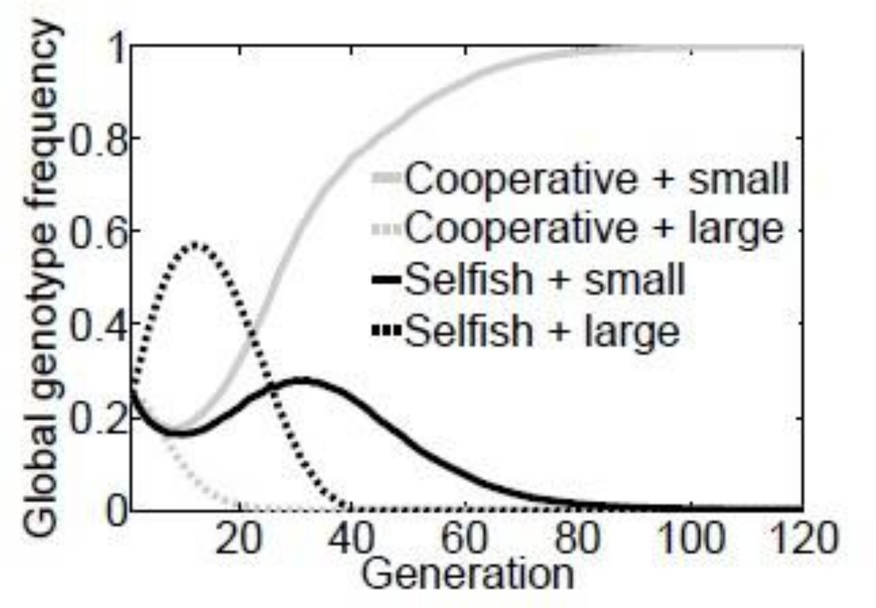
Group selection/Niche construction

- How can variance between groups be created?
- When small groups aggregate randomly, sampling error leads to variance between groups



Group selection/Niche construction

- Individuals have two traits: cooperate/defect and small/large group preference
- Trait-group model (aggregation and dispersal)
- Group-size preference is niche-construction trait



Powers, S. T., Penn, A. S., & Watson, R. A. (2007). Individual selection for cooperative group formation. In *European Conference on Artificial Life* (pp. 585-594). Springer, Berlin, Heidelberg.

Another game as food for thought

- Choose a number between 0 and 40
- Everyone who chooses half the average of all numbers chosen wins!
- E.g., if three people play the game and pick 3, 7, and 8, then half the average is $\frac{1}{2}(\frac{3+7+8}{3}) = \frac{1}{2}(\frac{18}{3}) = \mathbf{3}$, so 3 wins.
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