Collective Behaviour
Lecture 2

Functional explanations

Functional and mechanistic explanations

The examples of modelling given so far describe **mechanisms**. (how?)

The **functional** approach to theoretical biology and economics revolves around the ‘individual as the maximising agent’. (why?)

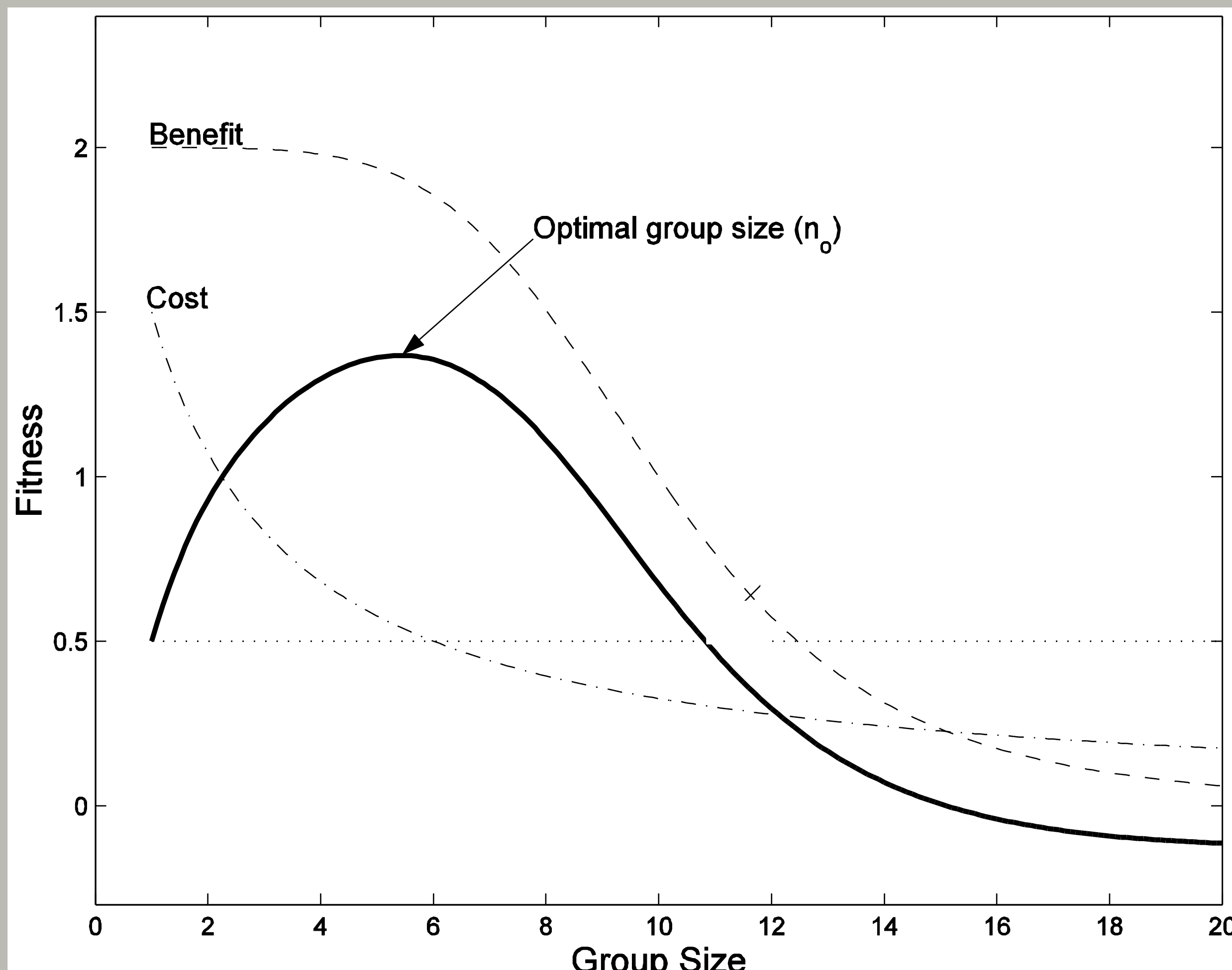
I now give some examples of functional models.

Optimal group size

Why join a group?

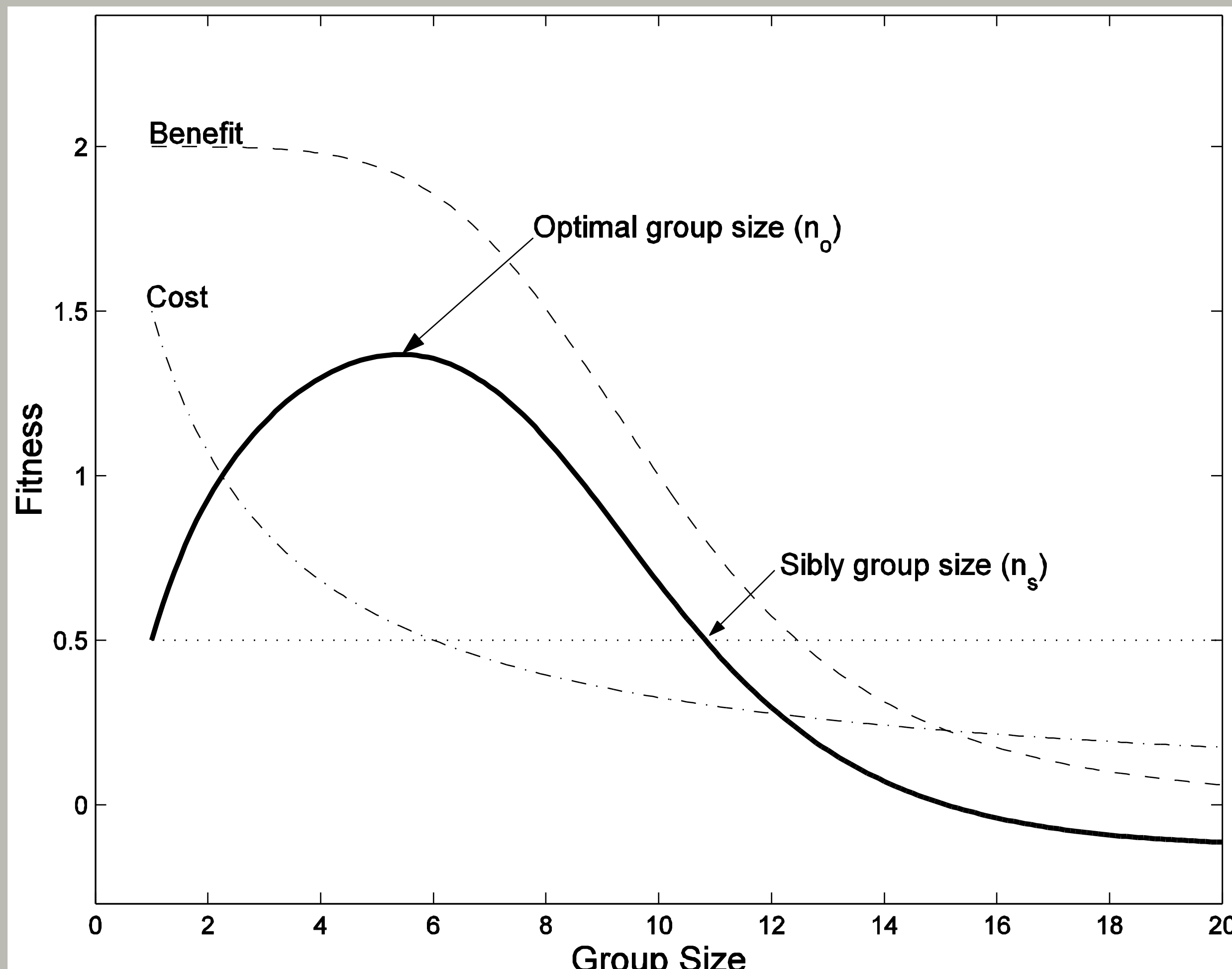
- Can conserve energy by being near others.
- Someone else will get eaten if a predator attacks.
- Can eat the food that others find.
- Can build structures together which can't be built alone.

Optimal group size



Sumpter (2010) *Chapter 2*

Optimal ≠ Stable group size



Sumpter (2010) *Chapter 2*

Simulating stable group size

Consider $f(n) = n \exp(n/10)$ and an environment with s=2000 available sites. Assume initially that at half the sites, i=1 to 1000, the number of individuals at the site, $n_i(0)$, is drawn from a uniform distribution with minimum 10-r and maximum 10+r. The other half of the sites, i=1001 to 2000, are unoccupied, i.e. $n_i(0)=0$.

On each time step t a random individual is picked. It then calculates the fitness function for all of the sites were it to move to that site, i.e. $f(n_j(t)+1)$ for all sites apart from the site i that is already at. If

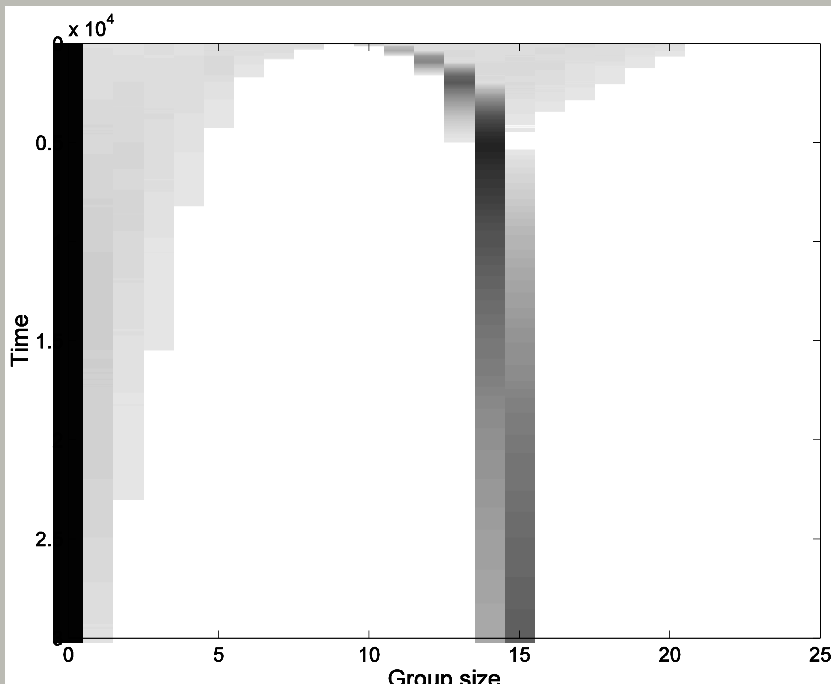
$$f(n_j(t)+1) > f(n_i(t))$$

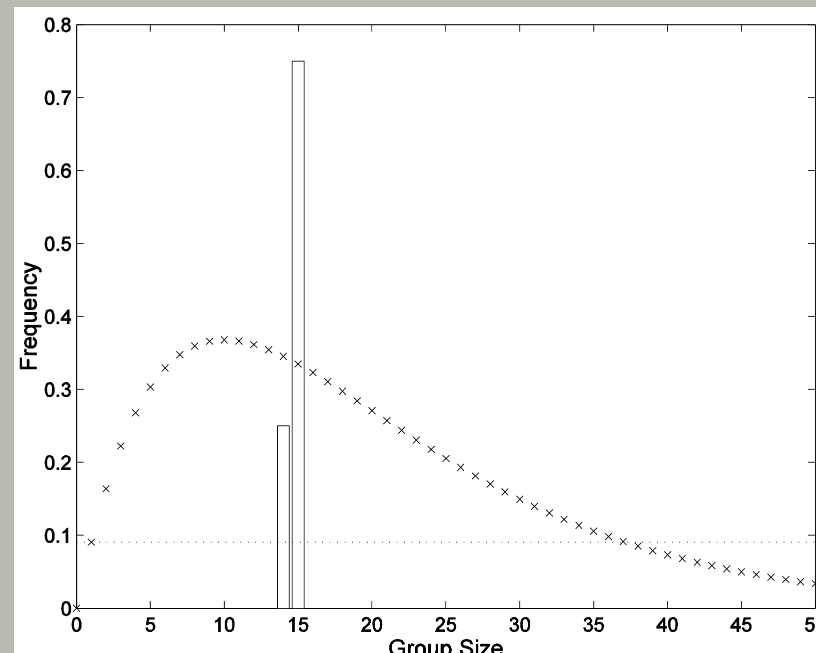
for some j then the individual moves to the site which has the maximum value of $f(n_j(t)+1)$. If more than one site has the same value of $f(nj(t)+1)$ then one of these sites is picked at random.

The above process is continued until no further moves are possible.

Sumpter (2010) *Chapter 2*

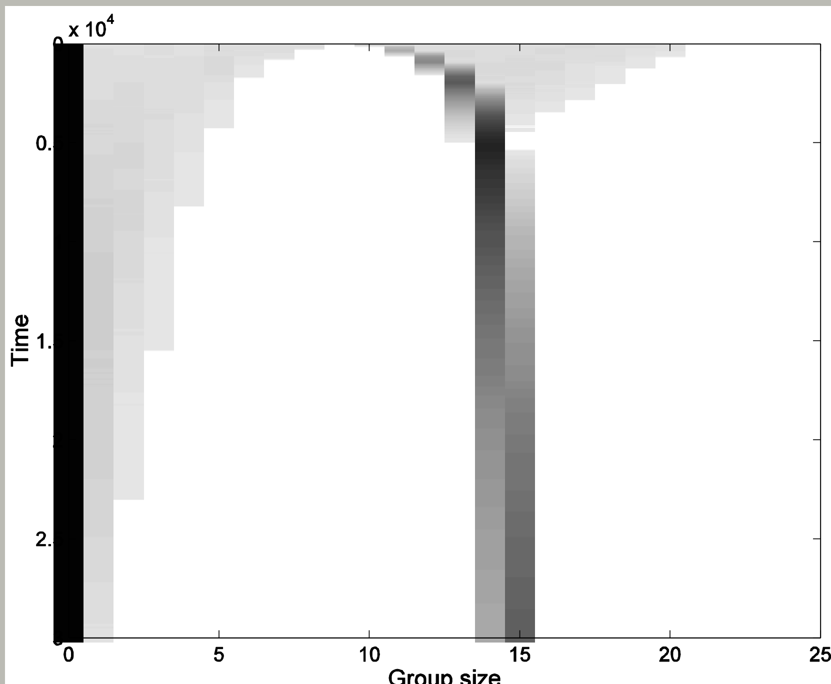
Simulating stable group size

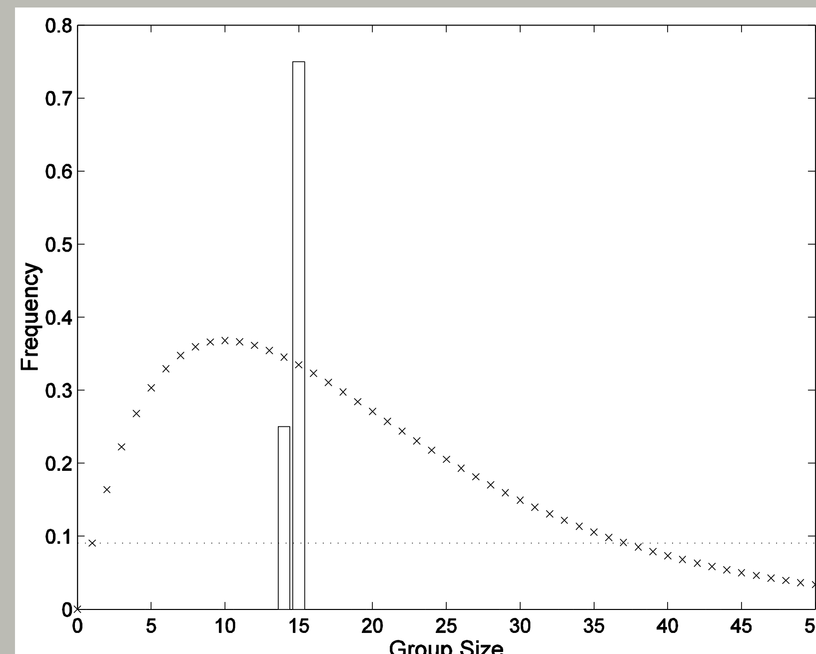




Sumpter (2010) *Chapter 2*

Optimal ≠ Stable group size





Stable groups are larger than optimal size, but smaller than Sibly size.

Very narrow group size distribution.

Sumpter (2010) *Chapter 2*

Group Optimal ≠ Evolutionary Stable

What is best for the individual is not generally what is good for the group.

An individual's fitness is affected by the behaviour of others.

We typically expect individuals to maximize their own chance of survival and not that of their group or species.

Co-operation needs to be explained, both in humans and in animals.

Nowak (2006), Five Rules for the Evolution of Cooperation, *Science*
Lehmann & Keller (2006), *Journal of Evolutionary Biology*

Evolutionary Stability

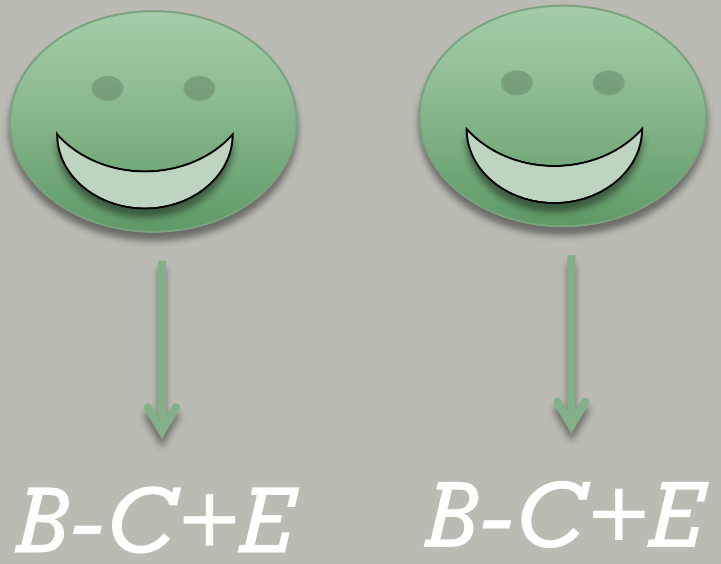
All two player games can be expressed as follows:

Focal/Partner	Co-operate	Defect
Co-operate	$B - C + E$	$D - C$
Defect	B	0

Assume an infinite population which form random pairs on each generation, play the game and get a payoff determined by the table.

Sumpter (2010) *Chapter 10*

Evolutionary Stability



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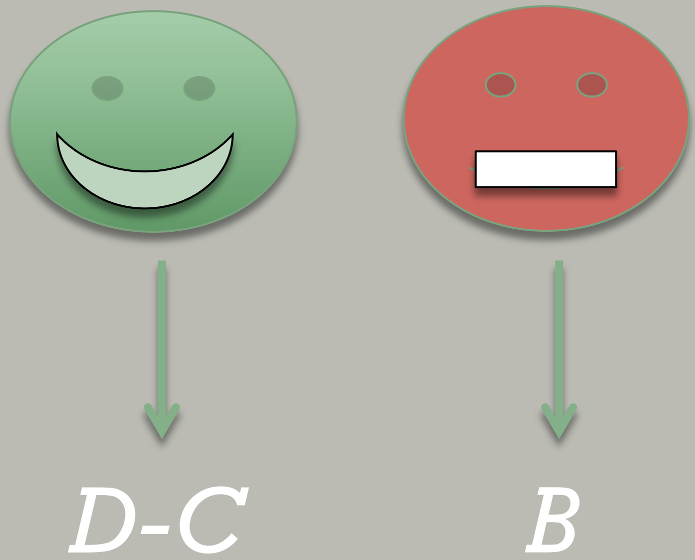
Co-operate	$B - C + E$	$D - C$
Defect	B	0

Sumpter (2010) *Chapter 10*

Evolutionary Stability



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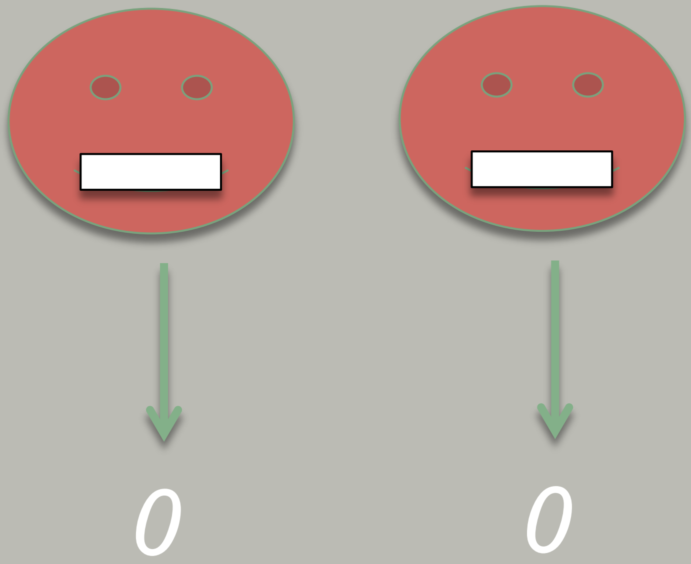
Sumpter (2010) *Chapter 10*

Evolutionary Stability



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Sumpter (2010) *Chapter 10*

Evolutionary Stability

All two player games can be expressed as follows:

Focal/Partner	Co-operate	Defect
Co-operate	$B - C + E$	$D - C$
Defect	B	0

B is benefit to partner.

C is cost to self.

D is direct benefit, if partner defects.

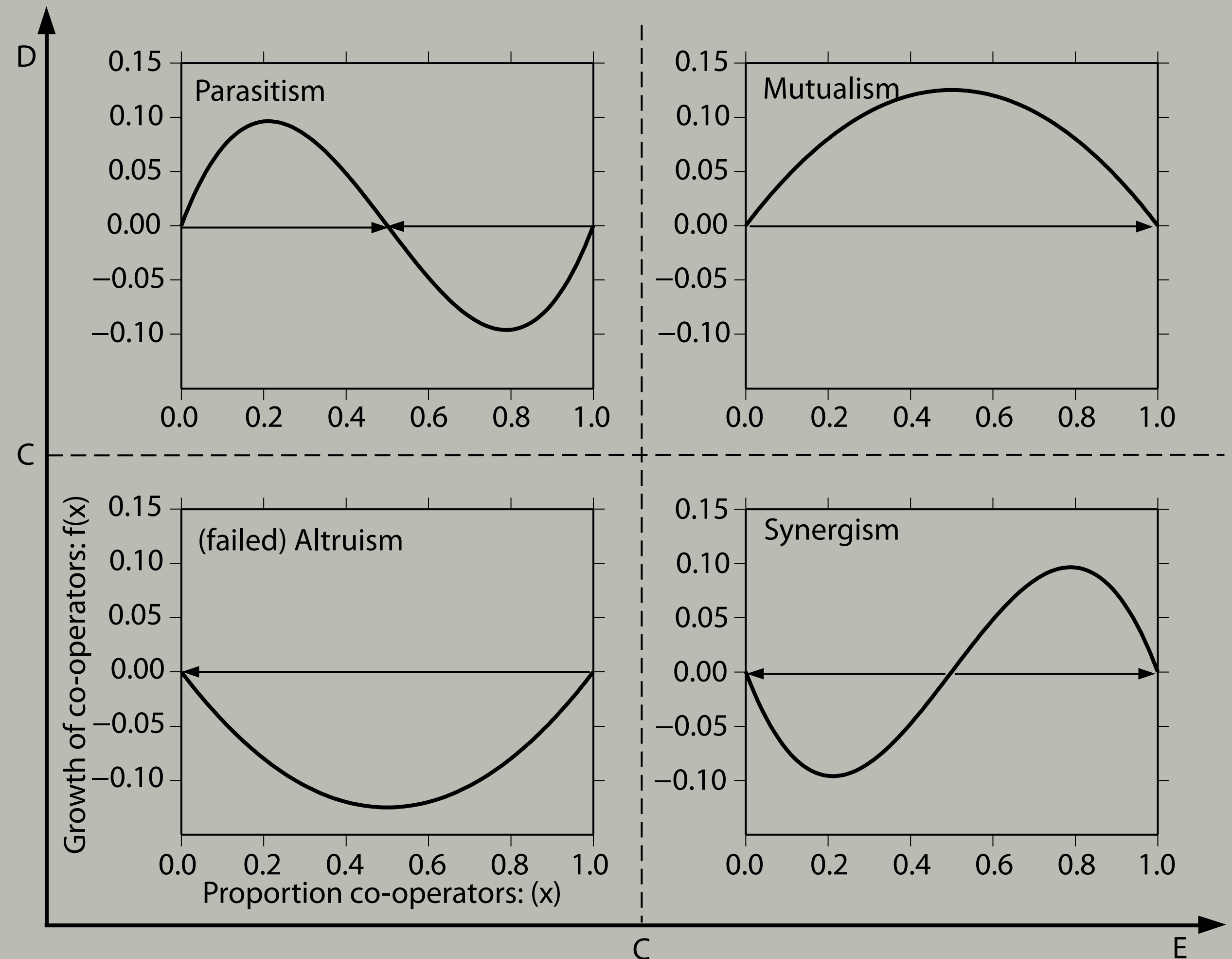
E is extra benefit, if both co-operate.

Sumpter (2010) *Chapter 10*

Evolutionary Stability

Sumpter (2010) *Chapter 10*

Evolutionary Stability



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Evolutionary Stability

All (simple) forms of co-operation can be labelled as mutualism ($D>C$ & $E>C$), parasitism ($D>C$), synergism ($E>C$) or altruism ($rB>C$).

Much of the study of collective behaviour is about finding unexpected synergisms and hidden parasitisms.

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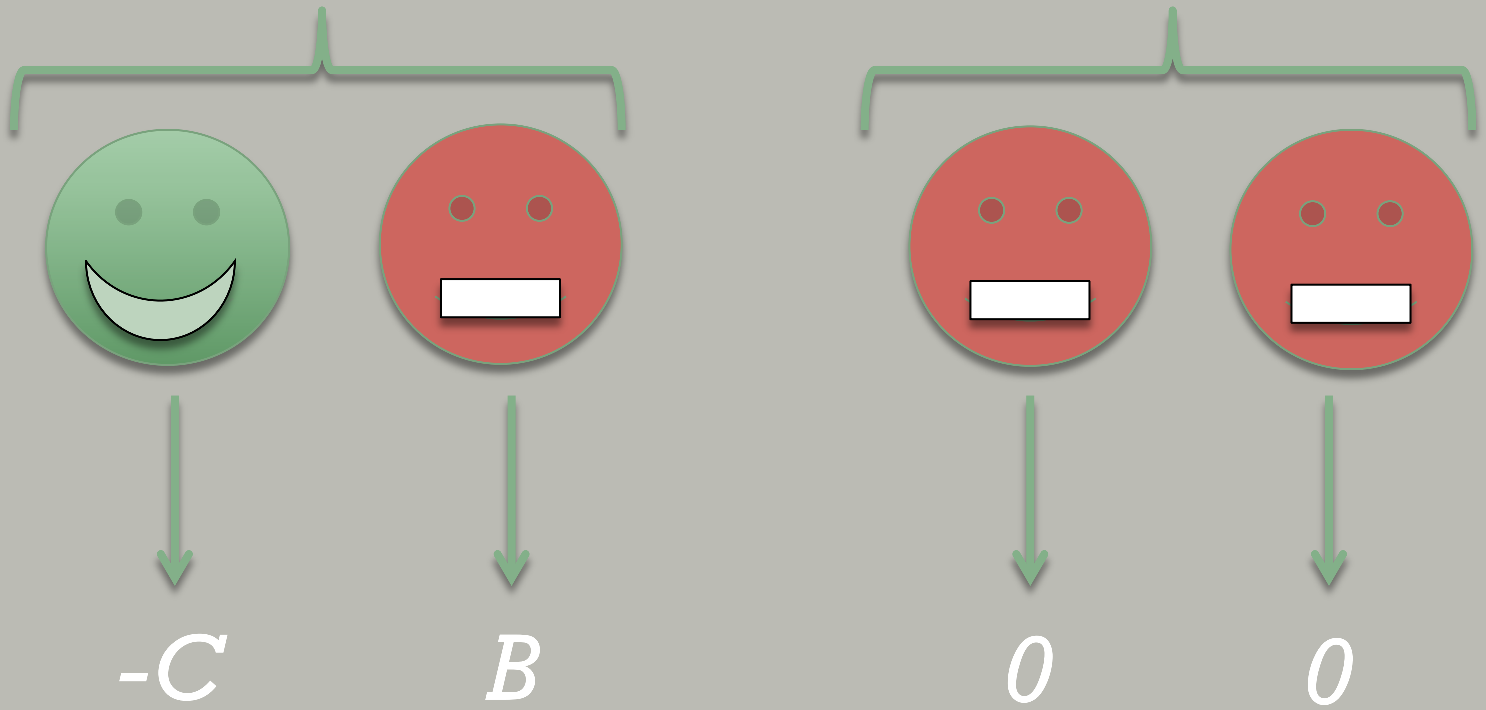
The Subtlety of Synergy



No incentive for defector to change

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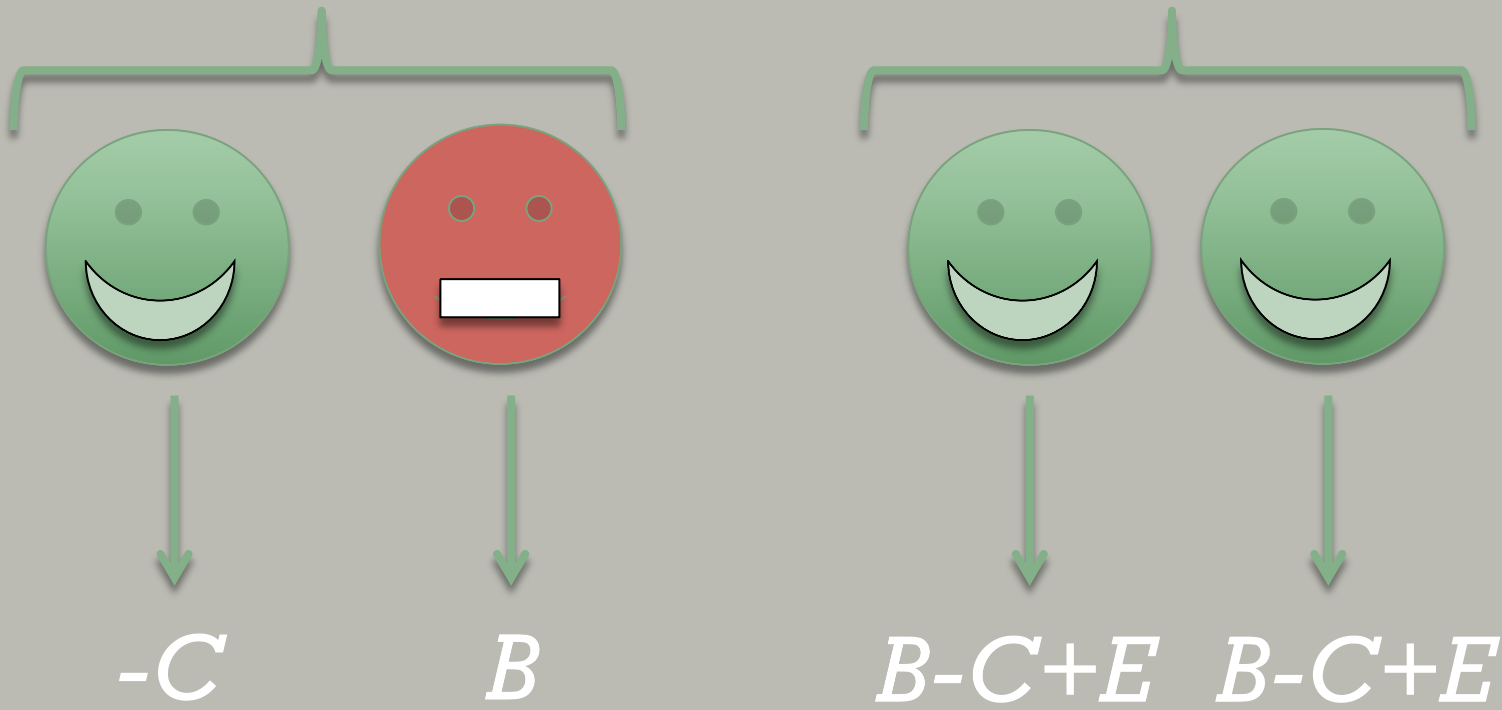
The Subtlety of Synergy



Incentive for defector to change ($E>C$).

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The Subtlety of Synergy

- Now some groups are better than others, but selection is still on individuals.
- Observing the co-operating/defector pair is only half the story.
- Allows ‘chains’ of co-operation without repeated interactions or relatedness.

Sumpter & Brännström (2008); Cornforth et al. (2012)

The Real Problem of co-operation is even harder

Payoffs are determined by

F()

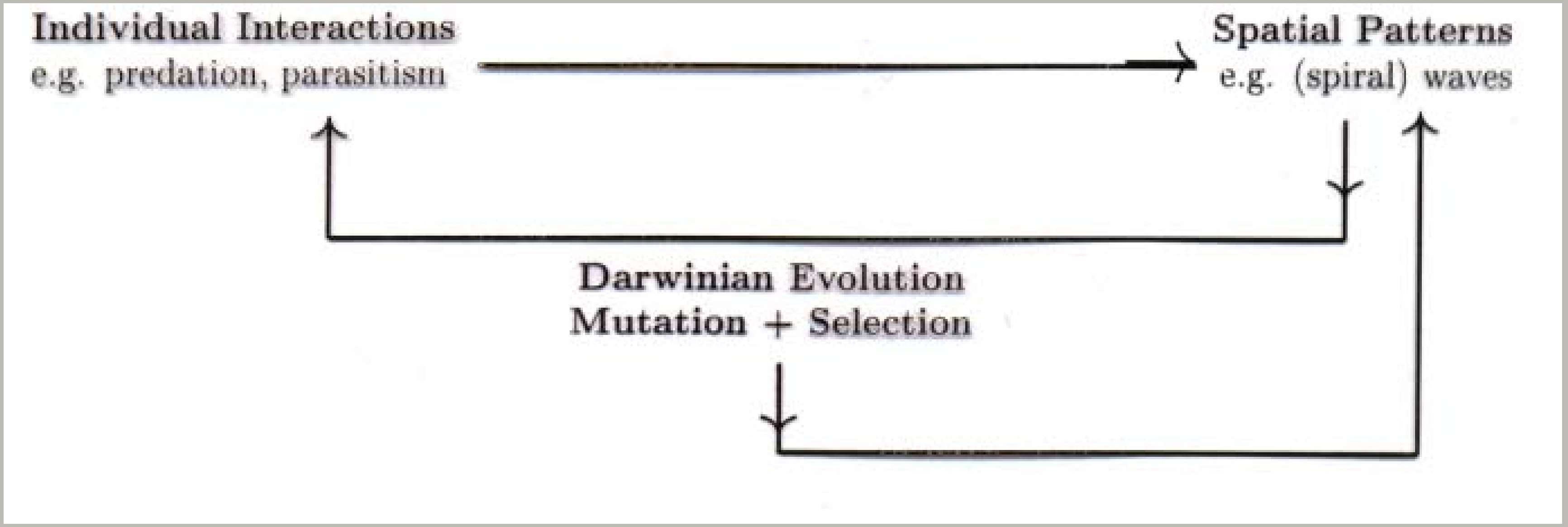
or rather

F(↗ , ↘ , ↗ , ↗ , ↘)

or worse still

F(↗ , ↘ , ↗ , ↗ , ↘)

How to think about evolution?



Hogeweg, P (2012) Toward a theory of multilevel evolution: long-term information integration shapes the mutational landscape and enhances evolvability.

Boerlijst M.A. and Hogeweg P. (1991) P*hysica D*

Summary