Game theory and adaptive dynamics

LSM 4255 Methods in Mathematical Biology

Week 12

Outline

- Brief history of game theory
- 2-strategy games, evolutionary analysis
- Adaptive dynamics
- Tragedy of the Commons

Natural selection

- In previous lectures, you looked at population genetic models like this

$$p_{n+1} = u\,(p_n + q_n)^2\,\frac{1}{d_n} \quad \text{freq. AA} \tag{1}$$

$$q_{n+1} = v\,(p_n + q_n)\,(q_n + r_n)\,\frac{1}{d_n} \quad \text{half freq. Aa} \tag{2}$$

$$r_{n+1} = w\,(q_n + r_n)^2\,\frac{1}{d_n} \quad \text{freq aa} \tag{3}$$

$$d_n = u(p_n + q_n)^2\; 2v(p_n + q_n)(q_n + r_n)\; w(q_n + r_n)^2 \tag{4}$$

  where u, v, w are fitness.
- Where does fitness come from?
  - Previously assumed a constant, reflecting something about a static or averaged environment,
  - But might be more complicated than that

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photo BBC

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photo BBC

Need some mathematical framework to deal with this

- Game theory
- Came to biology from economics / military

A brief history of game theory - 1. cooperative game theory

- John von Neumann and Oskar Morgenstern in 1944
  - Book – *Theory of Games and Economic Behavior*
    - "we wish to find the mathematically complete principles which define 'rational behaviour' for the participants in a social economy, and to derive from them the general characteristics of that behaviour"
  - cooperative game theory
    - About humans forming coalitions, making agreements, splitting costs/profits
    - e.g. Several nearby towns want a water supply
  - Not yet so interesting to biologists ...

Morgenstern (left) and von Neumann (right)

A brief history of game theory - 2. non-cooperative games

- John Nash - non-cooperative games
  - A more general theory
  - No enforcement mechanisms (e.g. contracts to split costs) outside the game itself
  - Not about coalitions, agreements and side-payments possible between players, but rather individual strategies and payoffs
- Individualistic
  - 'Darwinian' view of the world: each works for themselves and maximises own payoff

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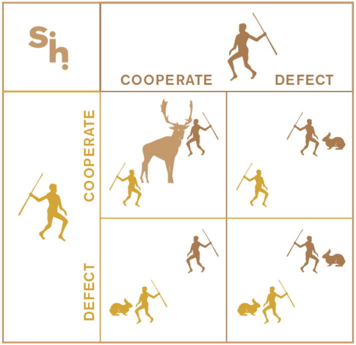
- 'Games'
  - All players are rational and have full information about game
  - Players cannot coordinate with each other
  - Single-shot
  - Only objective is to maximise own payoff

Example: The stag hunt

Two people go on a hunt. Each can either hunt stag or hunt hare. A stag is worth more but takes two people. A hare is easily caught alone.

- What should an individualistic rational player do?



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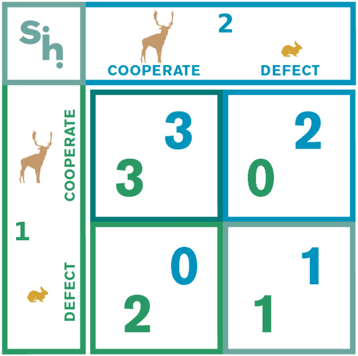

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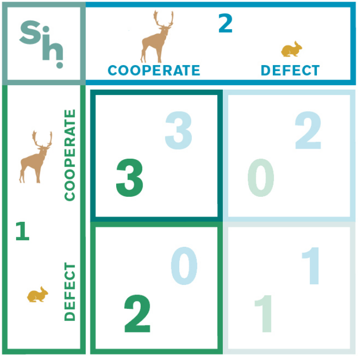

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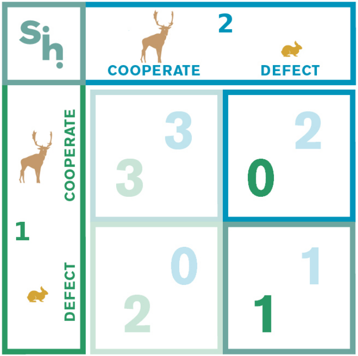

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- What should an individualistic rational player do?
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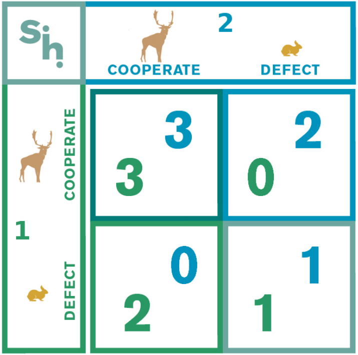
  - If other player hunting stag?
  - If other player hunting hare?
- My best strategy depends on others' strategy



Example: The stag hunt

- Nash equilibrium:
  - A strategy is a Nash equilibrium (x^*) if no player can do better by unilaterally changing their strategy.

$$f(x^*, x^*) \geq f(x, x^*) \tag{5}$$

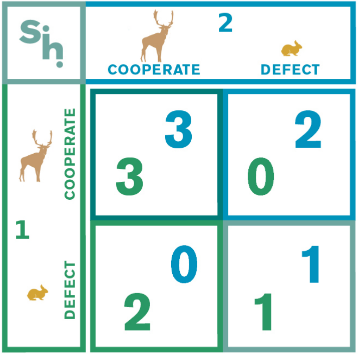
for all other strategies x

  - The stag hunt has two Nash equilbria:

$$f(\text{stag}, \text{stag}) > f(\text{hare}, \text{stag}) \tag{6}$$

$$f(\text{hare}, \text{hare}) > f(\text{stag}, \text{hare}) \tag{7}$$

Notation: payoff to a focal individual is f(focal individ's strategy, others' strategy)



Example of stag hunt in nature - carousel hunting

Evolutionary game theory

Maynard Smith & Price (1973):

- Males often compete for territory, etc. $\rightarrow$ transmission of genes
- Might expect natural selection to favour maximally effective weapons and fighting styles for a "total war" strategy, battles to the death
- Instead, a "limited war" type is common
- 'Group selection' type explanation was accepted explanation

Evolutionary game theory

- Maynard Smith & Price recast the game theory into biological context:
  - 'Game' $\rightarrow$ interaction that determines fitness (e.g. snakes fighting for territory)
  - 'Strategy' $\rightarrow$ genetically encoded behaviour or trait
  - 'Player' $\rightarrow$ individual animal, though better to think of as gene
  - 'Payoff' $\rightarrow$ fitness

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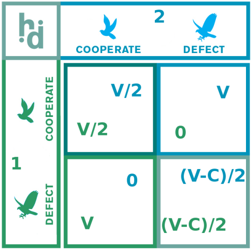
- Recall the four processes of population genetics:
  1. Selection
  2. Mutation
  3. Genetic drift
  4. Gene flow

  Basic evolutionary game theory only includes the first (replicator dynamics), and second (ESS, adaptive dynamics), though can be extended to include others

Evolutionary game theory - Hawk-Dove

- ‘Hawk-Dove’ game (see Hastings text)
  - two animals contesting favoured territory with value V
  - fighting over it has injury cost $C > V$
- So ... total war?



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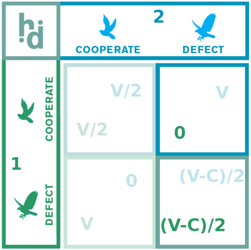

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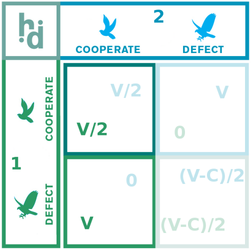

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- Recall Nash equilibrium

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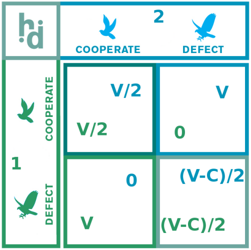

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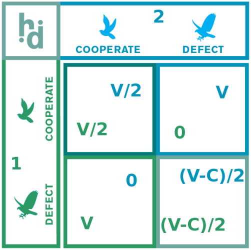
- Neither pure strategy is a Nash equilibrium



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Evolutionary game theory - A technical point

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- Nash equilibrium $f(x^*, x^*) \geq f(x, x^*)\,\forall x$
- Maynard Smith concept of an *evolutionarily stable strategy* (ESS), two criteria:
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     1. $f(x^*, x^*) = f(x, x^*)$ AND
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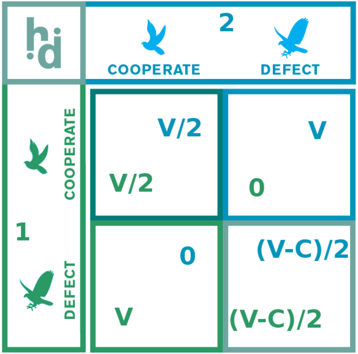
ESS $\rightarrow$ Nash equilibrium

- For these 2-strategy games they are equivalent

Evolutionary game theory - Hawk-Dove

- Neither hawk nor dove are an ESS, intuition suggests that best strategy is something ‘in between’
- Your text (Hastings) investigates a *mixed strategy*, where players pursue ‘hawk’ or ‘dove’ with some probability
- An alternative is to look at the evolution of the *proportions* of hawk- and dove-strategests in a population



Replicator dynamics

- Agents do not have to be conscious or rational: all they need is a strategy that they pass on
- No change in strategy, no mutation to new strategy
- Interested in change in distribution of strategies in population
- 'Goal' of the game is to produce as many replicates of oneself as possible

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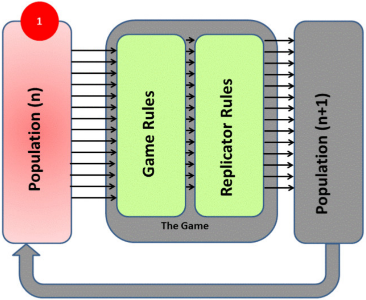

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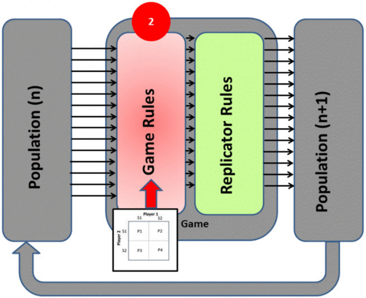

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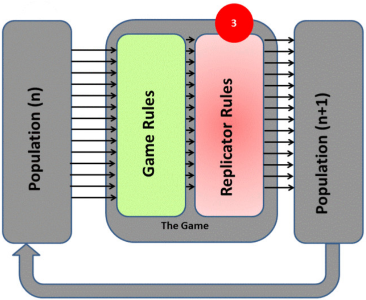

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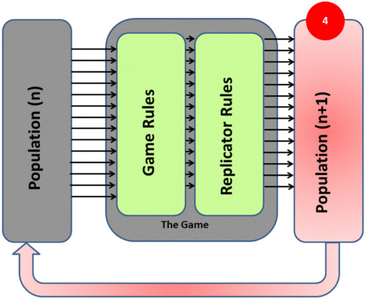

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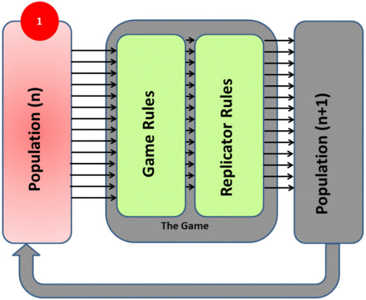

Replicator dynamics equation

Following Chapter 9 of Webb *Game Theory: Decisions, Interaction and Evolution*

- n_i: number of individuals pursuing strategy i
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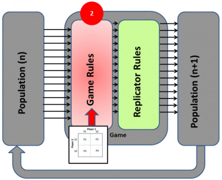

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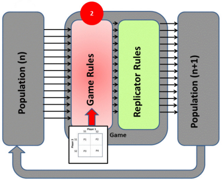

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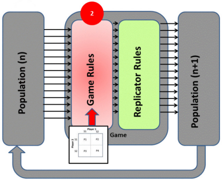
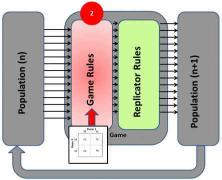
- $p_i = n_i/N$: proportion of individuals pursuing strategy i
- Want dynamics of p_i



Replicator dynamics equation

- Dynamics of i strategists

$$\frac{dn_i}{dt} = \dot{n}_i = n_i(\beta + f_i) \tag{8}$$



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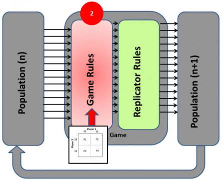
- Dynamics of whole population

$$\begin{aligned} \dot{N} &= \sum_i \dot{n}_i \\ &= \beta \sum_i n_i + \sum_i f_i n_i \\ &= \beta N + N \sum_i f_i \frac{n_i}{N} \\ &= N(\beta + \bar{f}) \end{aligned} \tag{9}$$

where $\bar{f}$ is mean fitness



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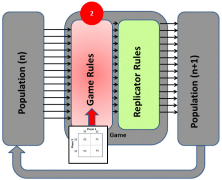

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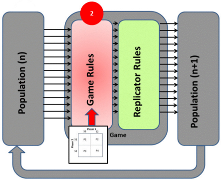

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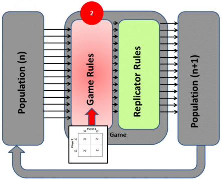

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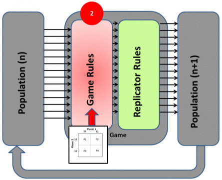

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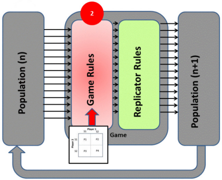

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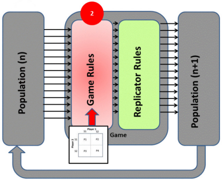

$$\dot{p}_i = (\beta + f_i)\frac{n_i}{N} - p_i(\beta + \bar{f})$$
$$= (\beta + f_i) p_i - p_i(\beta + \bar{f})$$
$$\dot{p}_i = p_i(f_i - \bar{f})$$

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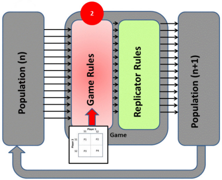
$$\dot{p}_i = p_i(f_i - \bar{f}) \qquad (10)$$



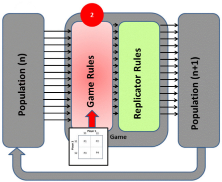
Replicator dynamics equation

- Replicator dynamics

$$\dot{p}_i = p_i(f_i - \bar{f}) \tag{10}$$

- For two strategies

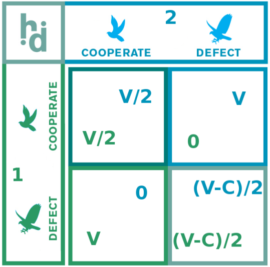
$$\dot{p}_1 = p_1(1 - p_1)(f_1 - f_2) \tag{11}$$



Hawk-Dove replicator dynamics

- Replicator dynamics

$$\dot{p}_H = p_H(1 - p_H)(f_H - f_D)$$



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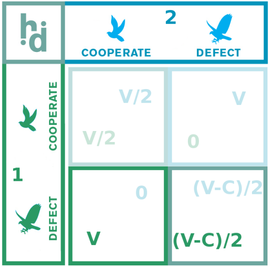

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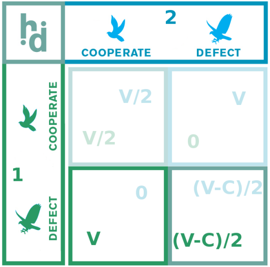

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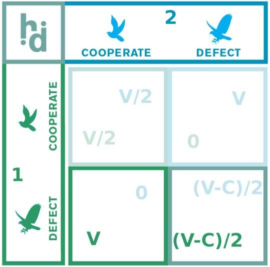

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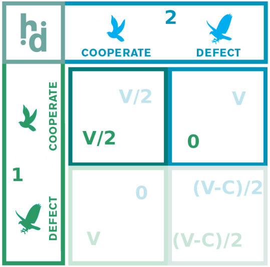

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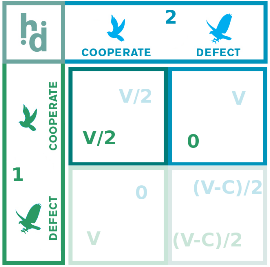

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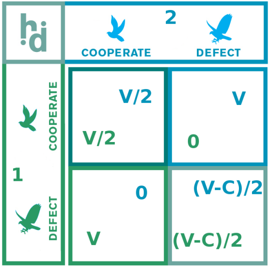

- Sub $(1 - p_H) = p_D$, rearrange

$$\dot{p}_H = p_H(1 - p_H)\left(p_H \frac{V - C}{2} + (1 - p_H)\frac{V}{2}\right)$$

Hawk-Dove replicator analysis

$$\dot{p}_H = \frac{dp_H}{dt} = p_H(1-p_H)\left(p_H\frac{V-C}{2} + (1-p_H)\frac{V}{2}\right)$$

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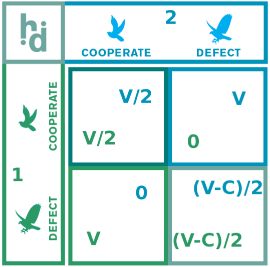

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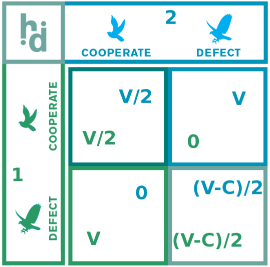

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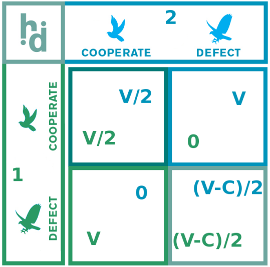

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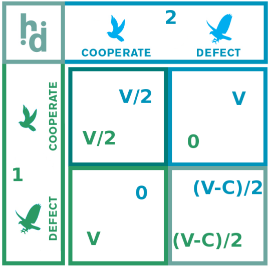

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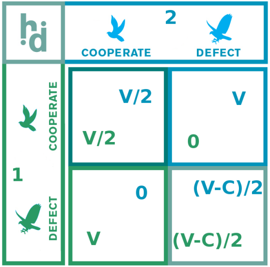

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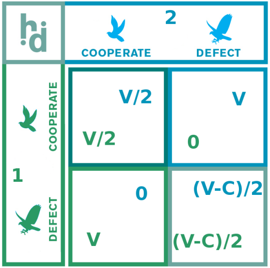

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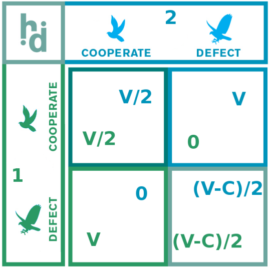

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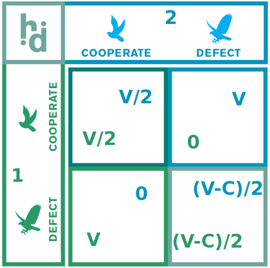

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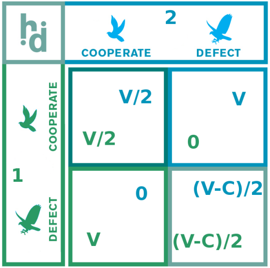

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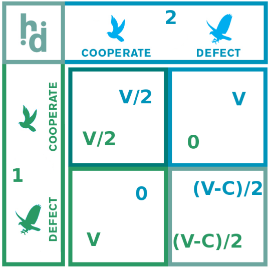

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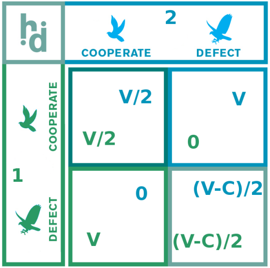

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Replicator dynamics - A technical point

$$\text{ESS} \rightarrow \text{asymptotically stable} \rightarrow \text{Nash equilibrium}$$

- e.g. variants on rock-scissors-paper have stable replicator dynamics but are not ESS

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- For 2-player 2-strategy games they are all equivalent

Adaptive dynamics

- Adaptive dynamics (1990s onwards)
  - About evolution of some continuous ‘trait’ in a ‘resident population’ by successive invasions of a mutant traits
  - ‘Ecoevolutionary’: feedbacks between ecological dynamics and evolutionary dynamics
    - In replicator dynamics, fitness a function of *proportions*
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- Clarifies meaning of evolutionary trajectory and end-points

Adaptive dynamics example - migratory birds

Reference - Johansson & Jonzén (2012)

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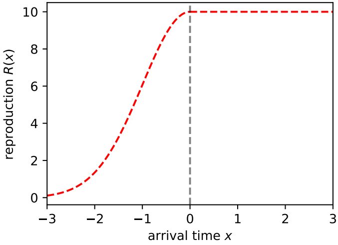

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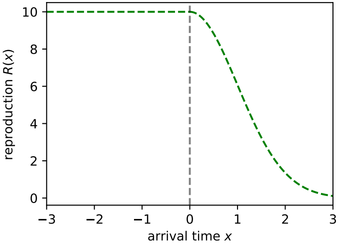

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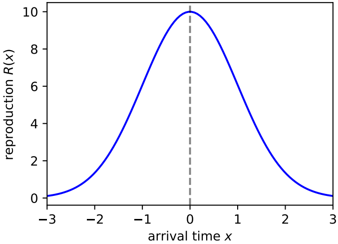

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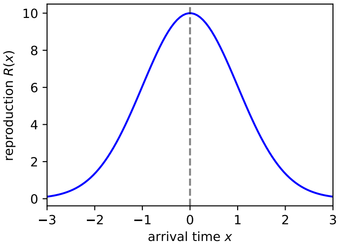
- Timing of arrival back from migration
  - Arrive too early - cold, low food
  - Arrive too late - not enough time to nest, lay eggs, raise chicks before winter
  - So obviously best arrival time is at peak?
- But there is competition for limited nesting territories
  - Those who arrive earlier have a better chance at obtaining and defending a territory
  - If everyone else arrives at peak, may be better overall for an individual to arrive a bit earlier?



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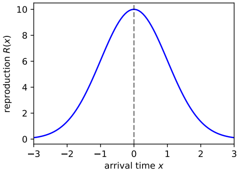

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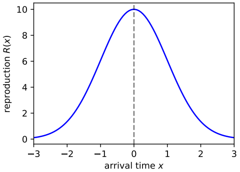

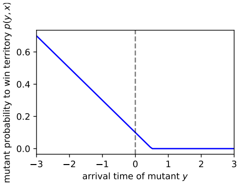

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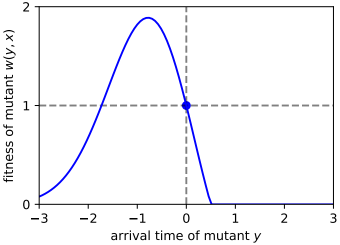

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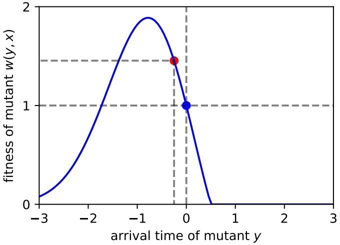

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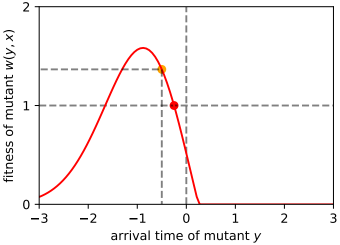

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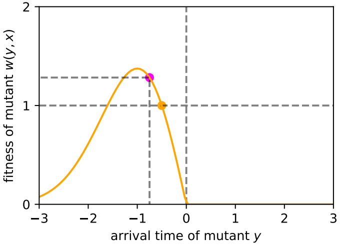

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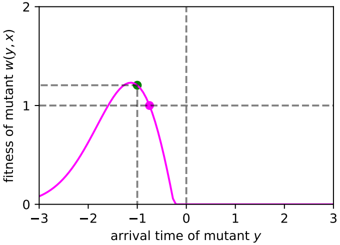

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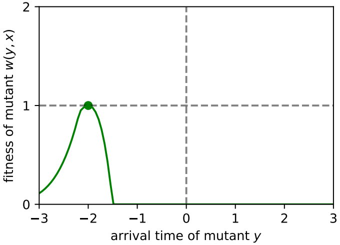
- End-point where no further invasions possible

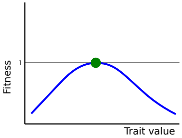


Adaptive dynamics clarifies concepts

- AD is interested in the two concepts from example above:
  1. Which strategy will evolutionary trajectory head towards?
     Convergence stability
  2. Can population pursuing strategy be invaded by alternative strategy?
     Evolutionary stability
- Not every ESS is an evolutionary attractor
  - e.g. gregarious behaviour (Eshel 1983)
- *Continuously stable strategy*: An evolutionarily singular strategy that is both evolutionarily stable and convergence stable

Adaptive dynamics approach

- Call fitness $w(y, x)$, where y is mutant trait and x is resident trait
- Adaptive dynamics approach works 'backwards' from end-point



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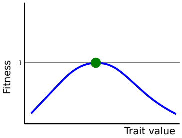

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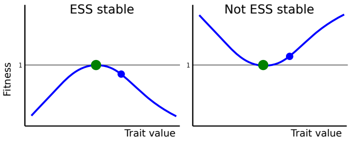

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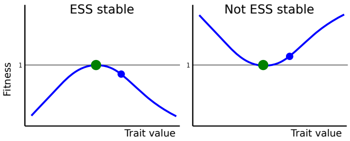

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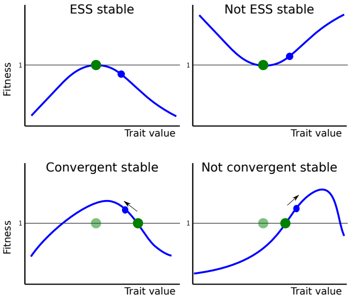

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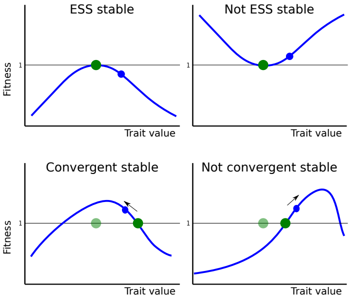

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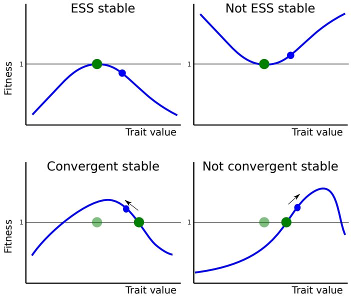
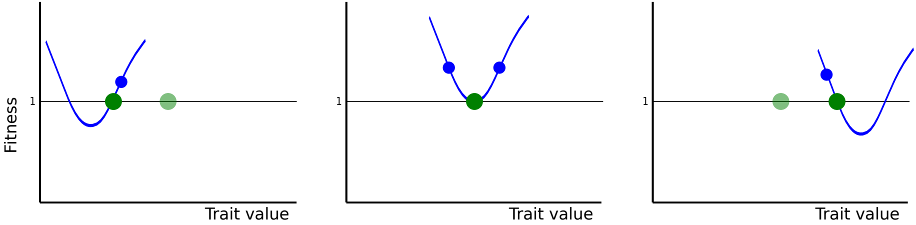


All combinations possible

Aside: Adaptive dynamics and speciation

- How could an evolutionarily singular strategy be convergence stable but not evolutionarily stable?



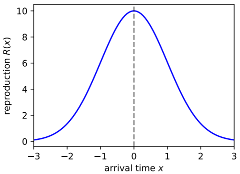
- Because AD assumes clonal reproduction, leads to polymorphism or 'speciation'
- In reality however, gene flow prevents trait divergence
- See Dieckmann & Doebeli (1999) versus Gavrilets (2005)

Adaptive dynamics worked example - preliminaries

First consider population all following same strategy – *resident strategy*

- No. offspring fnc arrival time

$$R(x) = R_0 e^{-\frac{x^2}{2}} \tag{12}$$



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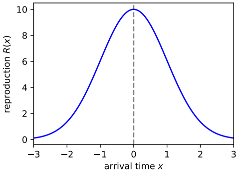

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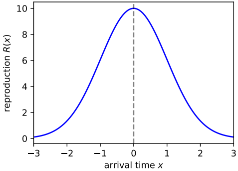

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$$n_{t+1} = pR(x)\, n_t \qquad (14)$$

Adaptive dynamics worked example - separation of timescales

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- Population dynamics
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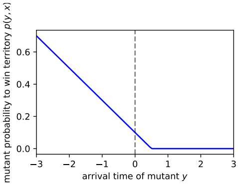
- *Assume* that evolutionary dynamics happening on a slower timescale than population dynamics
- Therefore assume population at steady state

$$n_{t+1} = n_t = n^* \tag{16}$$

$$p_r = \frac{1}{R(x)} = \frac{K}{n^*(x)} \tag{17}$$

Adaptive dynamics worked example - very few mutants

- Residents' probability of obtaining a territory $p_r = \frac{1}{R(x)}$
- *Assume* only one mutation at a time
- What happens if a mutant with a different arrival time y arises?



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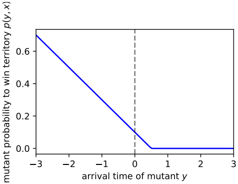

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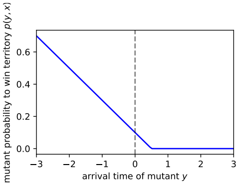
- But mutant definitely affected by residents
  - For purpose of example, assume a linear relationship truncated between 0 and 1

$$p(y, x) = p_r \left(1 + a \left(x - y\right)\right) \tag{19}$$



Adaptive dynamics worked example - invasion fitness

- Now have two components: $R(y)$ and $p(y, x)$
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- Notice the assumptions
  1. Separation of timescales - resident population at ecological equilibrium, one mutant at a time
  2. Resident fitness not affected by mutant, but mutant fitness affected by resident strategy

Adaptive dynamics worked example - find singular strategy

Find evolutionarily singular strategy x^*

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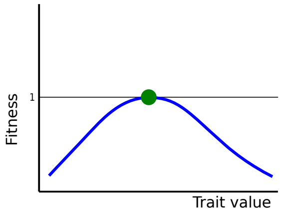

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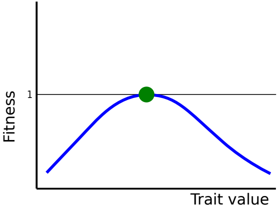
$$\frac{\partial w(y,x)}{\partial y} = -R(y)\left(ap_r + yp(y,x)\right) \tag{22}$$



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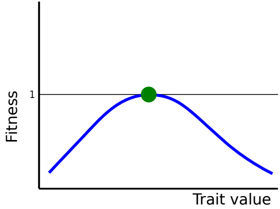

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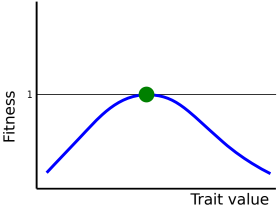

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  - x^* is when $g_x = 0$

$$\rightarrow x^* = -a \tag{24}$$

Adaptive dynamics worked example - is singular strategy evolutionarily stable?

Is x^* an *evolutionarily stable strategy*?

- $\left.\frac{\partial^2 w(y,x)}{\partial y^2}\right|_{\substack{y=x \\ x=x^*}} < 0$
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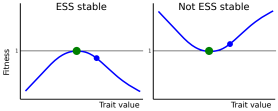

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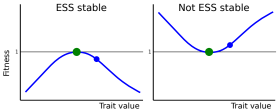

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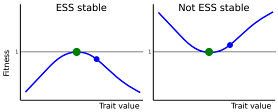

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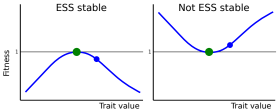

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Adaptive dynamics worked example - is singular strategy convergence stable?

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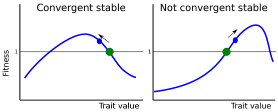

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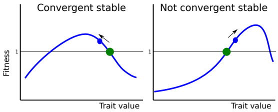

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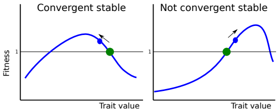

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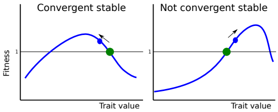

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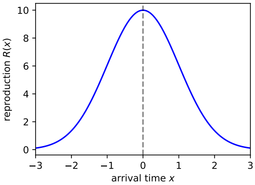
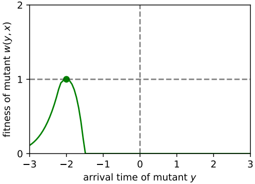
$$\left.\frac{dg_x}{dx}\right|_{x=x^*} = -p_r R(-a) < 0 \tag{30}$$

Adaptive dynamics worked example - meaning

- One singular strategy $x^* = -a$
  - In example right, I've set $a = 2$
- Continuously stable strategy
- What does it mean biologically?





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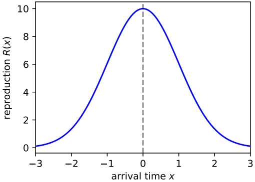
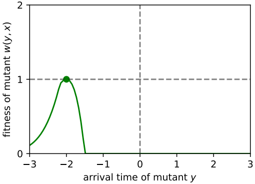




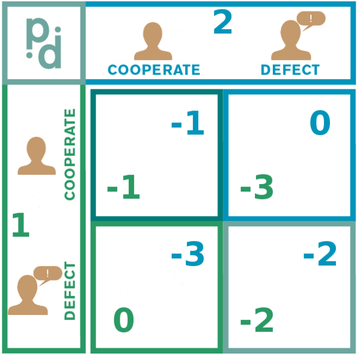
Species	Date	Location	Conditions	Numbers	Source
(a) Mortality during spring migration					
Various species (> 23 species)	April 1881	Off Louisiana coast*	Gale	'Many thousands'	Frazar (1881)
Lapland Longspurs *Calcarius lapponicus*	March 1904	Minnesota–Iowa	Snowstorm	1.5 million	Roberts (1907a, 1907b)
Mainly Lapland Longspurs *Calcarius lapponicus*	February 1922	Nebraska	Snowstorm	'Thousands'	Reed (1922), Swenk (1922)
Magnolia Warblers *Dendroica magnolia* and others (39 species)	May 1951	Off Texas coast*	Rainstorm	> 10 000	James (1956)
Ducks, geese and swans	April 1954	Wisconsin	Hailstorm	'Many'	Hochbaum (1955)
Various (> 14 species)	May 1954	Minnesota	Snowstorm	> 175	Frenzell and Marshall (1954)

"In each documented example, the migrants could have avoided the cold spell if they had arrived in breeding areas some days later than they did" Newton (2007, *Ibis*)

Prisoner's dilemma

Two criminals interrogated separately by police. If both stay silent, get a lesser charge and 1 year jail. But police make an offer - testify against the other, and if the other doesn't testify, you go free and they 3 years jail. But if both testify against each other, both get 2 years jail.

Should the criminals cooperate with each other and stay silent?



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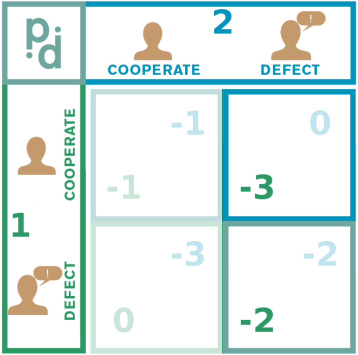

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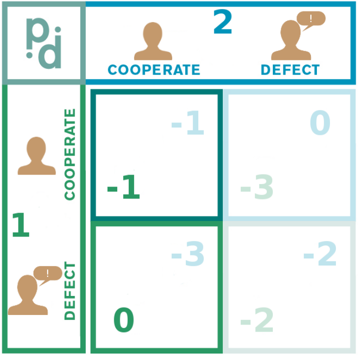

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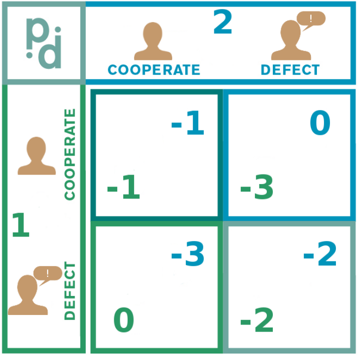
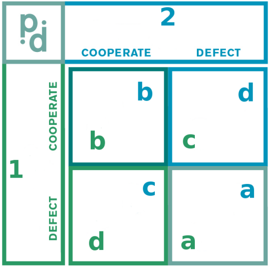


Generalised Prisoner's Dilemma and replicator dynamics



$$d > b > a > c$$

Generalised Prisoner's Dilemma and replicator dynamics

- Fitness effects:

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f_C &= p_C b + p_D c \\
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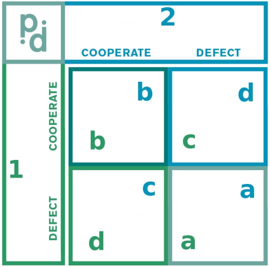

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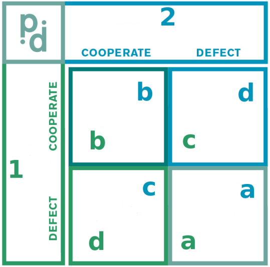

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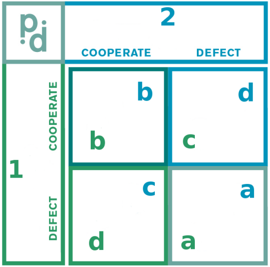
$$p_C^* = 0,\ 1,\ \frac{a-c}{a-c\ +\ b-d}$$



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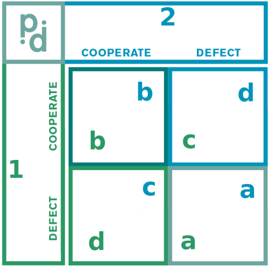

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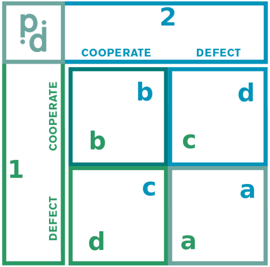

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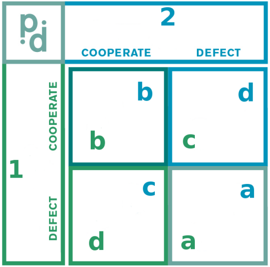
$$

$$
\left.\frac{d\dot{p}_C}{dp_C}\right|_{p_C=1} = -(b-d) > 0; \text{ and } \left.\frac{d\dot{p}_C}{dp_C}\right|_{p_C=0} = (c-a) < 0
$$



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Prisoner's dilemma and the environment

- Two countries.
- A fossil-fuel economy is worth 20 units.
- A switch to renewables reduces economic benefit to 10 units.
- But cost of CO_2 emissions paid by both countries via climate change.
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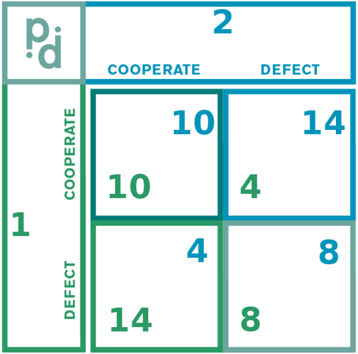

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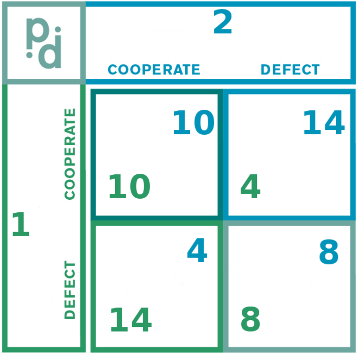


It is in the interests of each country, *regardless of what the other is doing*, to keep on polluting.

The Tragedy of the Commons

Hardin (1968, *Science*)

- William Forster Lloyd's *Tragedy of the Commons*
  - Herders share a common, limited-size, pasture
  - Utility to an individual herder of adding one more sheep is greater than the cost to themselves, a cost shared by all
  - Rational herders will put as many sheep on the commons as possible

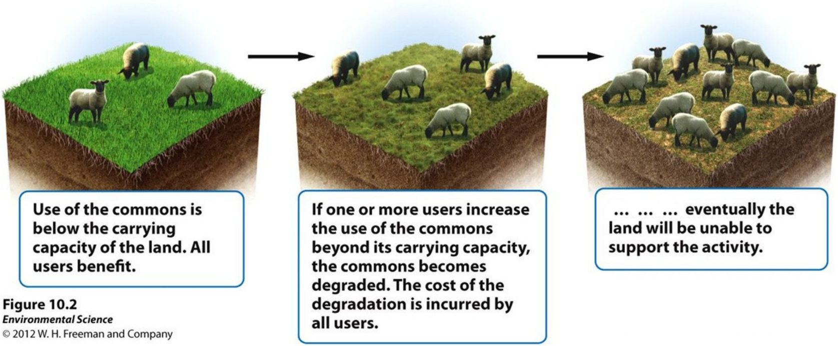
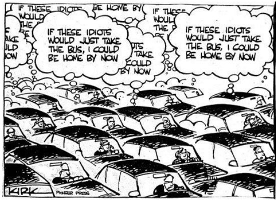


Figure 10.2
Environmental Science

The Tragedy of the Commons

Hardin (1968)

- Overpopulation
  - ‘They think that farming the seas or developing new strains of wheat will solve the problem – technologically’
  - Adam Smith’s ‘invisible hand’
    - Market settles on production and prices beneficial to all
    - ...but not invariably true



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- How to solve? Appeal to people’s conscience?
  - Appealing to conscience will lead to the elimination of conscience
  - Also creates a ‘double-bind’
    - you’re immoral if you don’t cooperate,
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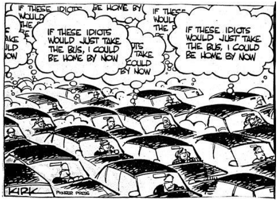

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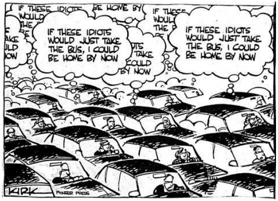

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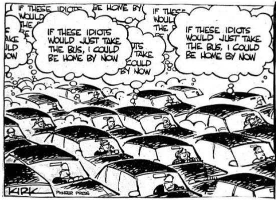

- Key point is that ToC occurs *even if all individuals understand* the consequences of their actions
- Next lab - fishing game

... but wait

- Do you behave like this in daily life?

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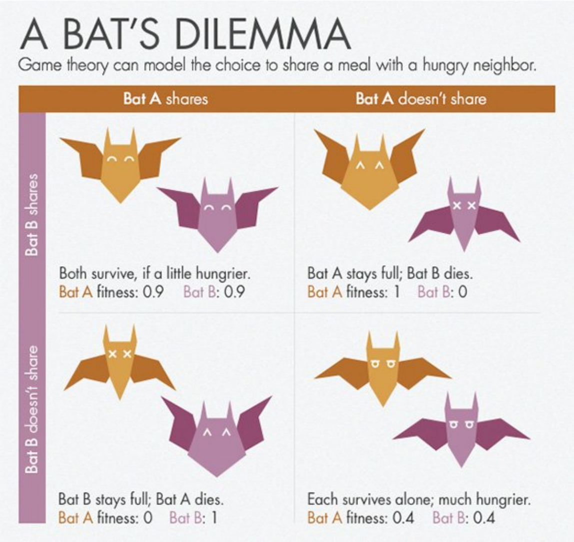
- Consider the cleaner fish - why doesn't the big fish just eat it when it's done?
- Consider the vampire bat
    - Feeds by biting a small hole in some mammal and lapping up blood
    - Two nights without food will die
    - Roost together in colonies in caves
    - Bats who had a feed that night will regurgitate food for those who had none

... but wait



Olena Shmahalo/Quanta Magazine

The Axelrod Tournaments

- 1980s Robert Axelrod held a series of tournaments
  - Scientists could submit their code to play PD
  - Each algorithm would be played against each other for multiple rounds of PD
- Notice: *repeated* plays against same opponent
  - So far looked at *one-shot* PD
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- Small communities actually don't just overgraze and ruin their commons
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- But for large-scale problems, like climate change, conditions above are not met
- Hardin - a necessity that we recognise the problem
  - Privatisation? ('Injustice is preferrable to ruin')
  - 'Mutual coercion'

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  - A way to study Darwinian evolution in a mathematical framework
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    - Explains why cooperation can be difficult to achieve
- Iterated Prisoner's Dilemma
  - One example of how cooperation can evolve