Game theory and adaptive dynamics

LSM 4255 Methods in Mathematical Biology

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Outline

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

Note-takers: slides will be online some time tomorrow

Natural selection

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

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

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

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

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

  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

Fitness depends on genotypes and frequencies of others

Fitness is determined not just by an individual's own genotype but by the types and frequencies of other genes in the population

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

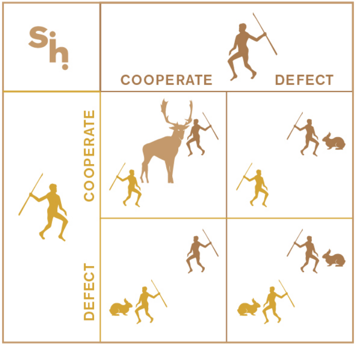
- John Nash - non-cooperative games
  - A more general theory
  - No enforcement mechanisms (e.g. contracts to split costs) outside the game itself
  - Not about coalitions, agreements and side-payments possible between players, but rather individual strategies and payoffs

- Individualistic
  - 'Darwinian' view of the world: each works for themselves and maximises own payoff
- '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

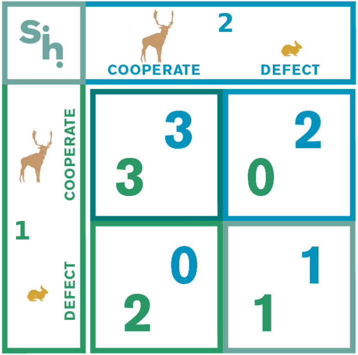
Two people go on a hunt. Each can either hunt stag or hunt hare. A stag is worth more but takes two people. A hare is easily caught alone.

- What should an individualistic rational player do?
- This is the simplest example of a 'game'
  - 2 players, 2 strategies, a single symmetric situation



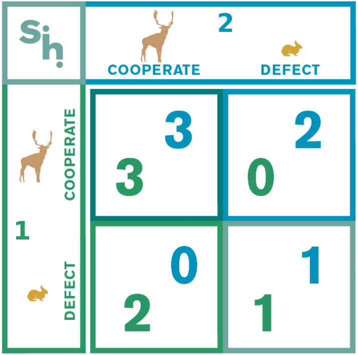
Example: The stag hunt

- Payoff matrix
  - Cells represent each possible situation
    - 'Cooperate': hunt stag together; or
    - 'Defect': hunt hare alone.
  - Values represent payoffs to each player in each situation
    - Player 1 (rows) gets green payoffs and player 2 (columns) gets blue payoffs
  - Payoffs represent the situation:
    - Stag is worth most
    - But it takes 2 people to hunt stag, so if one hunts stag by themselves then they get nothing
    - If both hunt hare then they get half the hares each



Example: The stag hunt

- Analyse the payoff matrix:
  - Imagine yourself as player 1
  - If other player hunting stag?
    - Best to hunt stag
  - If other player hunting hare?
    - Best to hunt hare
  - Symmetric game so the same is true for player 2
- Notice:
  - Making the best choice for myself only
  - My best strategy depends on others' strategy
- Best strategy is to do whatever the other player is doing



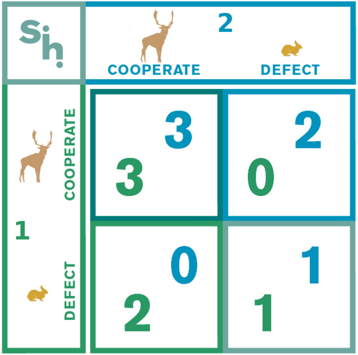
Example: The stag hunt

- Notation:
  - x is a strategy: 'stag' or 'hare'
  - f payoff to focal individual
  - f is a function of focal individual's strategy, also others' strategies, i.e. $f(x_i, x_j)$ is payoff to player i
- Nash equilibrium:
  - A strategy is a Nash equilibrium if no player can do better by unilaterally changing their strategy.
  - Call Nash equilibrium x^*

$$f(x^*, x^*) \geq f(x, x^*) \qquad (5)$$

for all other strategies x

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



Example: The stag hunt

- Nash equilibrium x^*

$$f(x^*, x^*) \geq f(x, x^*) \qquad (6)$$

for all other strategies x

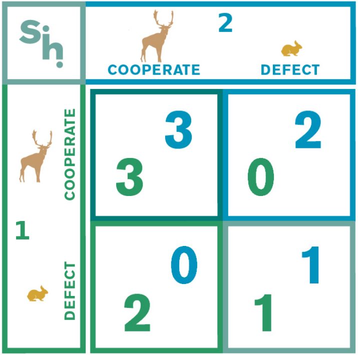
- The stag hunt has two Nash equilbria:
  1. $x^* = \text{stag}$

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

  2. $x^* = \text{hare}$

$$f(\text{hare}, \text{hare}) > f(\text{stag}, \text{hare}) \qquad (8)$$

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
- 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 - For your interest

- Nash equilibrium $f(x^*, x^*) \geq f(x, x^*)$ for all x
- Maynard Smith concept of an *evolutionarily stable strategy* (ESS), two criteria:
    1. $f(x^*, x^*) > f(x, x^*)$ for all x OR
    2.
        1. $f(x^*, x^*) = f(x, x^*)$ AND
        2. $f(x^*, x) > f(x, x)$ for all x
- Meaning of two ESS criteria:
    1. Strong ESS: no alternative strategy can invade
    2. Weak ESS: if an alternative strategy is neutral, x^* cannot be eliminated from population

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

- For these 2-strategy games they are equivalent

Evolutionary game theory - Hawk-Dove

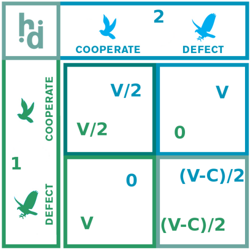
- Apply 'hawk-dove' game to our snakes case-study
- Here 'hawk' and 'dove' don't refer to literal species of birds, they are terms from politics and foreign policy
  - e.g. "John Bolton, a known hawk, has advocated for pre-emptive strikes against North Korea"
- A hawkish strategy for snakes is to use their powerful venom against each other

Evolutionary game theory - Hawk-Dove

- Set up:
  - Two animals contesting a favoured territory or other resource with value V
  - Losing a fight over it has an injury cost C
  - The important thing:

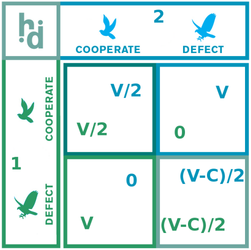
$$V < C \tag{9}$$

  - In other words, the cost of losing is greater than the value of the resource itself
  - Makes sense for our snakes example



Evolutionary game theory - Hawk-Dove

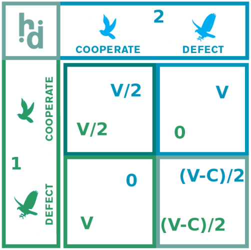
- Fill in matrix:
  - $V/2$: 50% chance of V, 50% chance of nothing
  - V vs 0: a hawk will take the whole resource from a dove, dove gets nothing
  - $(V-C)/2$: if two hawks, still a 50% chance of winning, but also a 50% chance of incurring cost $-C$



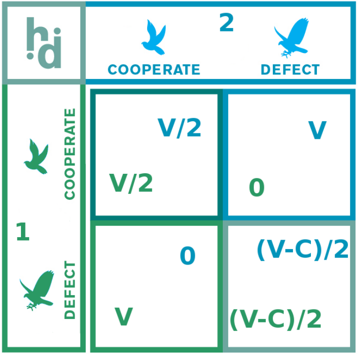
Evolutionary game theory - Hawk-Dove

- Analysis:
  - Recall $f(x^*, x^*) \geq f(x, x^*)$ for all x
  - Hawk-hawk i.e. total war?
    - $f(\text{hawk}, \text{hawk}) < f(\text{dove}, \text{hawk})$
  - Dove-dove, i.e. peace?
    - $f(\text{dove}, \text{dove}) < f(\text{hawk}, \text{dove})$
- A player always does better by unilaterally changing their strategy
- Therefore no pure strategy is a Nash equilibrium

Remember: $V < C$

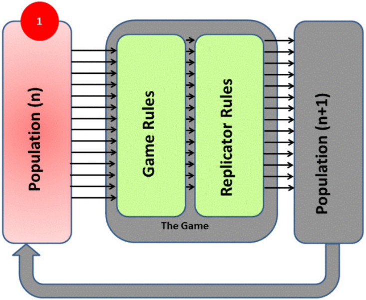


- Neither hawk nor dove are an ESS, intuition suggests that best strategy is something 'in between'
- Your text (Hastings) investigates a *mixed strategy*, where players pursue 'hawk' or 'dove' with some probability
- An alternative is to look at the evolution of the *proportions* of hawk- and dove-strategests in a population
  - Move from two players to many players
  - Provides an example for replicator dynamics



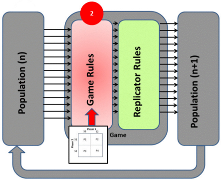
Replicator dynamics

- 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



Replicator dynamics equation

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



- n_i: number of individuals pursuing strategy i
- N: total number of individuals
- β: background reproduction rate
- $p_i = n_i/N$: proportion of individuals pursuing strategy i
- Want dynamics of p_i
- Assume that fitness is a function of *proportions* of strategies in population
  - $f_i(\mathbf{p})$: fitness effect of strategy i

  where $\mathbf{p}$ is a vector i.e. $[p_1, p_2, \ldots, p_n]$ that sums to 1

Replicator dynamics equation

- I want the dynamics of p_i

$$\frac{dp_i}{dt} = \dot{p}_i = \ ?$$

- I know that

$$p_i = \frac{n_i}{N}$$

so rearrange that

$$n_i = p_i N$$

take derivatives (use product rule)

$$\dot{n}_i = \dot{p}_i N + p_i \dot{N}$$

- Rearrange

$$\dot{p}_i N = \dot{n}_i - p_i \dot{N}$$

Replicator dynamics equation

- We are here:

$$\dot{p}_i N = \dot{n}_i - p_i \dot{N}$$

- Total pop size is sum of no. of each strategists

$$N = \sum_i n_i$$

so

$$\dot{N} = \sum_i \dot{n}_i$$

So it looks like we need to say something about the dynamics $\dot{n}_i$ to solve this

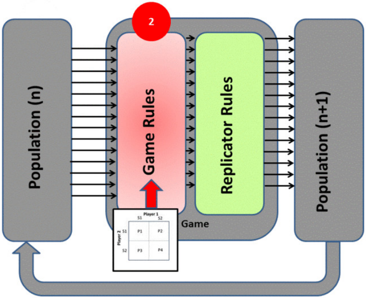
Replicator dynamics equation

- Dynamics of i strategists

$$\frac{dn_i}{dt} = \dot{n}_i = n_i(\beta + f_i) \quad (10)$$

where:

- β is the background reproduction rate
- f_i is the fitness effect of strategy i, resulting from the game rules



Replicator dynamics equation

- Bring together:

$$\dot{p}_i N = \dot{n}_i - p_i \dot{N}$$
$$\dot{N} = \sum_i \dot{n}_i$$
$$\dot{n}_i = n_i(\beta + f_i)$$

- Sort out our $\dot{N}$:

$$\begin{aligned} \dot{N} &= \sum_i \dot{n}_i \\ &= \beta \sum_i n_i + \sum_i f_i n_i \\ &= \beta N + N \sum_i f_i \frac{n_i}{N} \\ &= N(\beta + \bar{f}) \qquad (11) \end{aligned}$$

  where $\bar{f}$ is mean fitness

Replicator dynamics equation

- So now we have

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

- Sub into $\dot{p}_i N$ equation:

$$\begin{aligned}\dot{p}_i N &= \dot{n}_i - p_i \dot{N} \\ &= (\beta + f_i)n_i - p_i N(\beta + \bar{f})\end{aligned}$$

- Move N to the other side

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

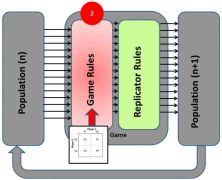
Replicator dynamics equation

- Replicator dynamics

$$\dot{p}_i = p_i(f_i - \bar{f}) \tag{12}$$

- For two strategies
  - Sub in $\bar{f} = f_1 p_1 + f_2 p_2$
  - Sub in $p_2 = 1 - p_1$
  - Gives:

$$\dot{p}_1 = p_1(1 - p_1)(f_1 - f_2) \tag{13}$$



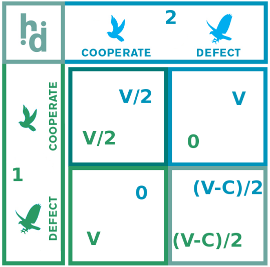
- Replicator dynamics

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

- Fitness effect of hawk strategy? Hint: $f_i(\mathbf{p})$

$$f_H(\mathbf{p}) = p_H \frac{V - C}{2} + p_D V$$

$$f_D(\mathbf{p}) = p_H\, 0 + p_D \frac{V}{2}$$



- 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

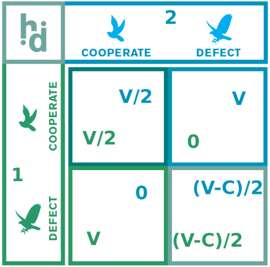
$$\dot{p}_H = \frac{dp_H}{dt} = p_H(1-p_H)\left(p_H\frac{V-C}{2} + (1-p_H)\frac{V}{2}\right)$$

- Equilibrium? Solve $\frac{dp_H}{dt} = 0$

$$p_H^* = 0,\ 1,\ \frac{V}{C}$$

- Asymptotic stability?

$$\left.\frac{d\dot{p}_H}{dp_H}\right|_{p_H=p_H^*} < 0$$

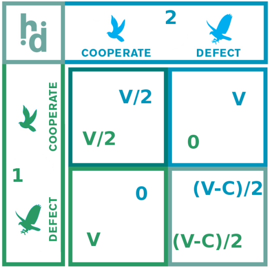


Hawk-Dove replicator analysis

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

$$(uvw)' = u'vw + uv'w + uvw'$$

$$\begin{aligned}\frac{d\dot{p}_H}{dp_H} &= (1-p_H)\left(\frac{V-C}{2}p_H + \frac{V}{2}(1-p_H)\right)\\ &\quad - p_H\left(\frac{V-C}{2}p_H + \frac{V}{2}(1-p_H)\right)\\ &\quad + p_H(1-p_H)\left(\frac{V-C}{2} - \frac{V}{2}\right)\end{aligned}$$



$$\left.\frac{d\dot{p}_H}{dp_H}\right|_{p_H=0} = \frac{V}{2} > 0$$

$$\left.\frac{d\dot{p}_H}{dp_H}\right|_{p_H=1} = -\frac{V-C}{2} > 0$$

$$\left.\frac{d\dot{p}_H}{dp_H}\right|_{p_H=\frac{V}{C}} = -\frac{V}{2}\left(1-\frac{V}{C}\right) < 0$$

$$p_H^* = 0,\ 1,\ \frac{V}{C}$$

$$\left.\frac{d\dot{p}_H}{dp_H}\right|_{p_H=p_H^*} < 0$$

Hawk-Dove summary - what have we learnt?

- We found a stable steady state $p_H = \frac{V}{C}$
- Hastings text book describes in terms of a mixed strategy
- Our question was, why is "limited war" common?
  - Intuitively, male snakes could fight to the death? ($p_H = 1$?)
  - Maybe they don't for the good of the species?

- Game theory gives us a reason why 'limited war' is common, from a purely individualistic perspective
- Gives us the mathematical machinery we need to take into account the unintuitive situation where fitness depends on strategies of others

Replicator dynamics - For your interest

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

- e.g. variants on rock-scissors-paper have stable replicator dynamics but are not ESS
- For 2-player 2-strategy games they are all equivalent

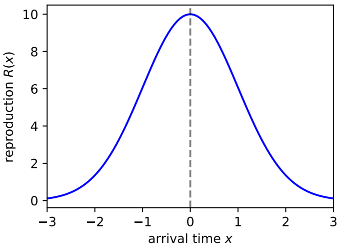
Adaptive dynamics

- 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*
    - In AD, fitness a function of absolute population size
  - Good introduction 'Hitchhiker's guide to Adaptive Dynamics' (Brännström et al. 2013)
- Key assumptions of Adaptive Dynamics
  1. Clonal reproduction
  2. Small mutational steps and few mutants
     - Mutant does not affect fitness of residents but residents' strategy affects fitness of mutant
  3. Separation of timescales
     - Resident population in ecological equilibrium when new mutant appears
- Clarifies meaning of evolutionary trajectory and end-points

Adaptive dynamics example - migratory birds

Reference - Johansson & Jonzén (2012)

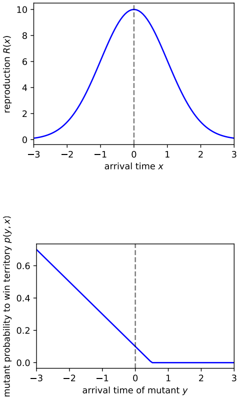
- Timing of arrival back from migration
  - Arrive too early - cold, low food
  - Arrive too late - not enough time to nest, lay eggs, raise chicks before winter
  - So obviously best arrival time is at peak?
- But there is competition for limited nesting territories
  - Those who arrive earlier have 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?



Adaptive dynamics example - visual

Reference - Johansson & Jonzén (2012)

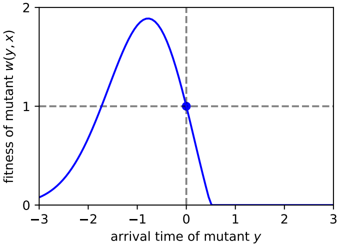
- Combine
  - Overall reproduction is hump-shaped with arrival time
  - Greater chance to obtain breeding territory with earlier arrival



Adaptive dynamics example - visual

Reference - Johansson & Jonzén (2012)

- Combine
  - Overall reproduction is hump-shaped with arrival time
  - Greater chance to obtain breeding territory with earlier arrival
  - Fitness function of mutants when all others at reproduction peak



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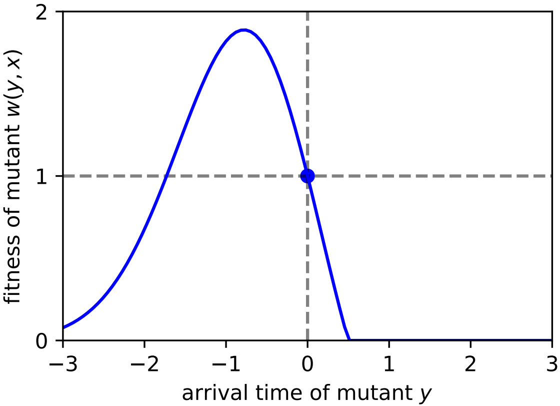

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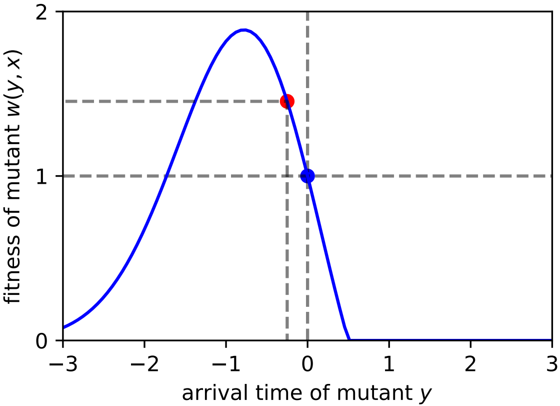

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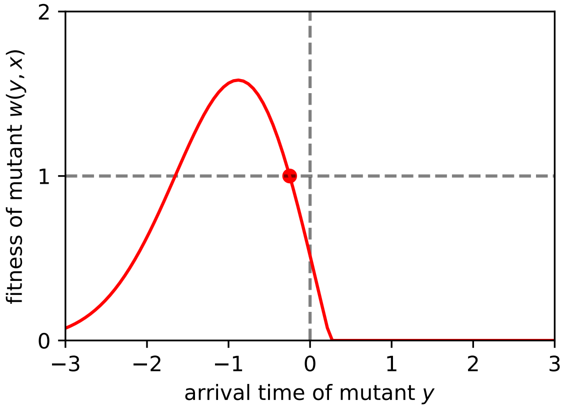

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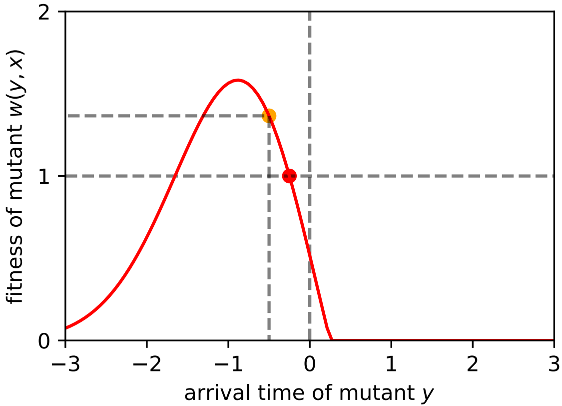

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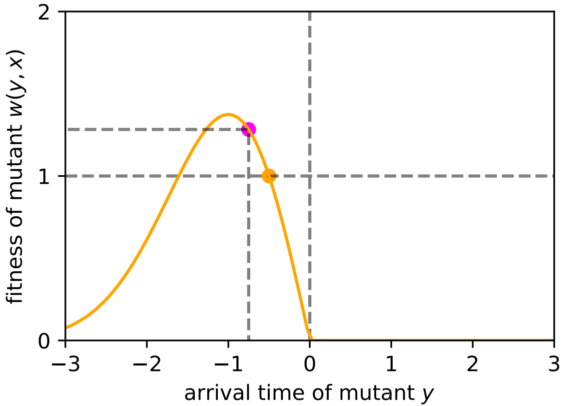

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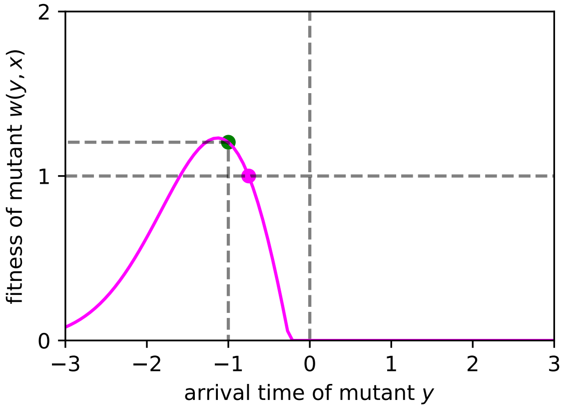
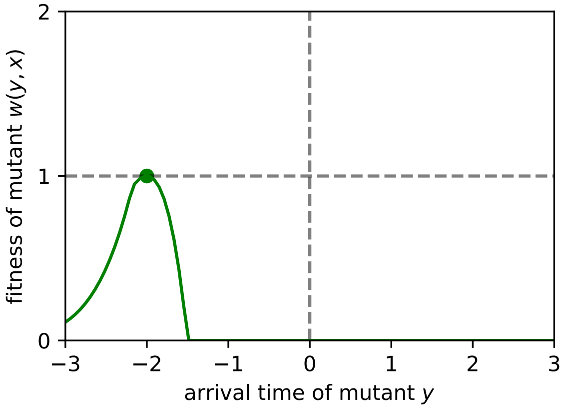
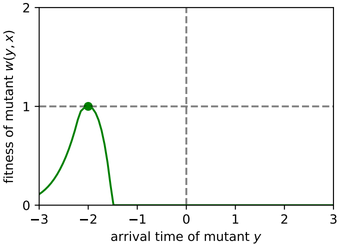


Adaptive dynamics example - visual

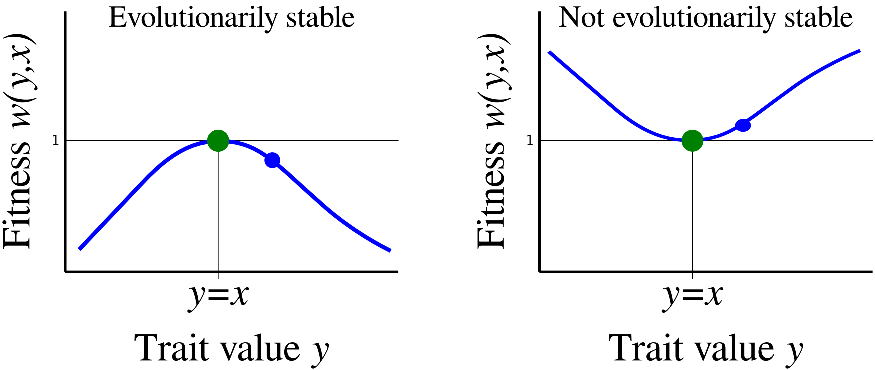


Adaptive dynamics example - visual summary

- Successive invasions move the trait value in the population to some evolutionary end-point
- AD is about finding where this end-point is
- End-point strategy has two qualities:
  1. Evolutionary trajectory will go towards it: *Convergence stability*
  2. Once there, population cannot be invaded by alternative strategy: *Evolutionary stability*
- *Continuously stable strategy*: Both evolutionarily stable and convergence stable



- *Evolutionarily stable strategy*: population cannot be invaded by an alternative strategy
- An ESS is a fitness *maximum* with respect to the mutant trait value



Adaptive dynamics - check evolutionary stability

- Call fitness $w(y, x)$, where y is mutant trait and x is resident trait

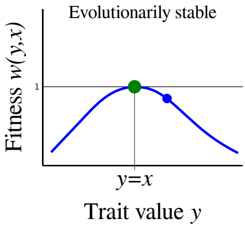
1. Find evolutionarily singular strategy x^* where mutant fitness gradient is zero

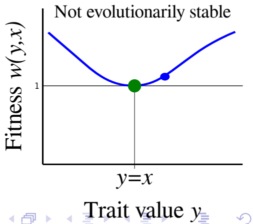
$$g_x = \left.\frac{\partial w(y,x)}{\partial y}\right|_{y=x} = 0$$

2. Is x^* an *evolutionarily stable strategy*?

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

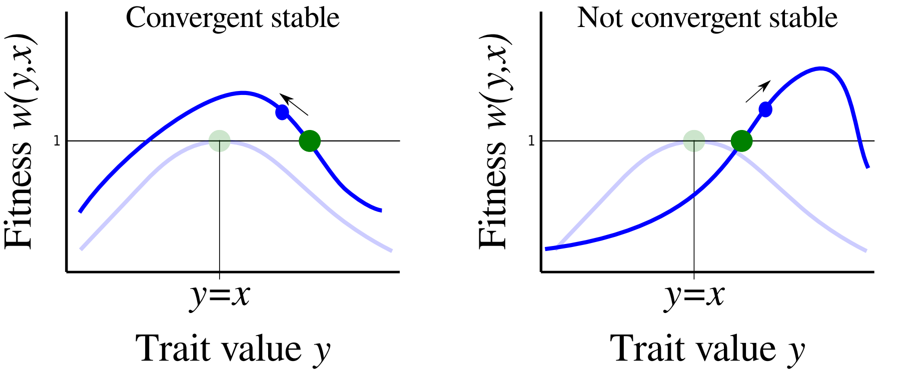
   - Fitness gradient at x^* a maximum wrt change in mutant trait





Adaptive dynamics - convergence stable

- *Convergence stable strategy*: evolutionary trajectory will approach it
- The fitness gradient has a negative slope with respect to changes in the resident strategy



- Call fitness $w(y, x)$, where y is mutant trait and x is resident trait

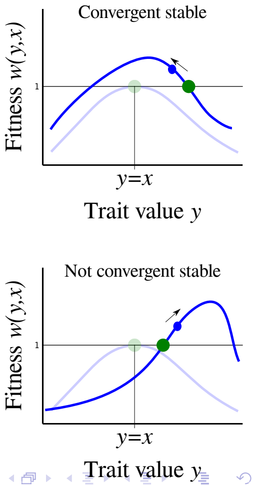
1. From before you have the mutant fitness gradient:

$$g_x = \left. \frac{\partial w(y, x)}{\partial y} \right|_{y=x}$$

2. Is x^* a *convergence stable strategy*?

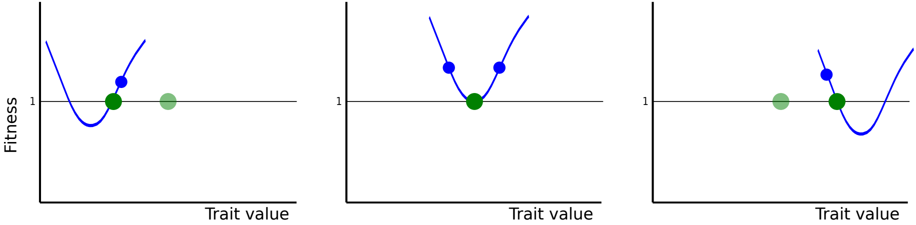
$$\left. \frac{dg_x}{dx} \right|_{x=x^*} < 0 \qquad (14)$$

   - Fitness gradient at x^* a maximum wrt change in resident trait



Aside: Adaptive dynamics and speciation

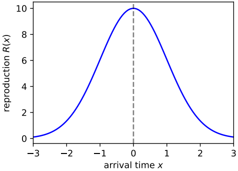
- How could an evolutionarily singular strategy be convergence stable but not evolutionarily stable?



- The singular strategy can be invaded on both sides in the trait-value space
- Linked to speciation, see Dieckmann & Doebeli (1999, Nature)

Adaptive dynamics worked example - preliminaries

First consider population all following same strategy: *resident strategy* x



- No. of offspring is a Gaussian-shaped function of arrival time x

$$R(x) = R_0 e^{-\frac{x^2}{2}} \tag{15}$$

- Probability of obtaining a territory: p
- Population dynamics

$$n_{t+1} = pR(x)\, n_t \tag{16}$$

  - The no. of individuals at $t+1$: the no. at time t, multiplied by the no. of offspring they have each $R(x)$, multiplied by each offspring's probability to obtain a territory for breeding p.

Adaptive dynamics worked example - separation of timescales

- Population dynamics

$$n_{t+1} = pR(x)\, n_t \tag{17}$$

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

$$n_{t+1} = n_t = n^* \tag{18}$$

- Then probability to obtain a territory

$$p_r(x) = \frac{1}{R(x)} \tag{19}$$

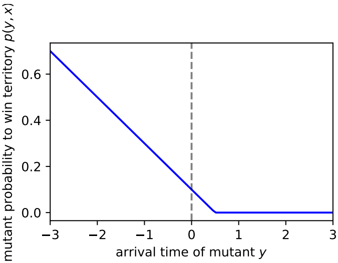
Adaptive dynamics worked example - very few mutants don't affect residents' fitness

- Residents' probability of obtaining a territory $p_r(x) = \frac{1}{R(x)}$
- What happens if a mutant with a different arrival time y arises?
- *Assume* one mutant, large enough population, mutant doesn't affect residents' fitness
- So the probability that a resident strategist obtains a territory remains unchanged

$$\text{keep } p_r(x) = \frac{1}{R(x)} \tag{20}$$

Adaptive dynamics worked example - mutants affected by residents' strategy

- Residents' probability of obtaining a territory stays $p_r(x) = \frac{1}{R(x)}$
- But a mutant's probability to obtain a territory is definitely affected by the strategy of the many residents



- Assume a linear relationship truncated between 0 and 1

$$p(y, x) = p_r(x)\,(1 + a\,(x - y)) \tag{21}$$

- Check it makes sense; if $y = x$

$$p(x, x) = p_r(x)\,(1 + a\,(x - x)) = p_r(x) \tag{22}$$

Adaptive dynamics worked example - invasion fitness

- Fitness is the growth rate
- Recall the population dynamics

$$n_{t+1} = pR(x)\, n_t \tag{23}$$

so at $n_t = n^*$ growth rate of resident $p_r(x)R(x) = 1$

- Fitness of mutant with arrival time y in resident population with x

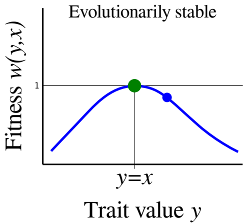
$$w(y,x) = p(y,x)R(y) = p_r(x)(1 + a\,(x - y))\, R(y) \tag{24}$$

- Notice the assumptions
  1. Separation of timescales - resident population at ecological equilibrium
  2. One mutant at a time - 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^*

- $g_x = \left.\frac{\partial w(y,x)}{\partial y}\right|_{y=x} = 0$
- Using:
  $w(y,x) = p_r(x)(1 + a\,(x - y))\,R(y)$



- Find the partial derivative wrt y

$$\frac{\partial w(y,x)}{\partial y} = -R(y)\,(ap_r + yp(y,x)) \tag{25}$$

- Evaluate partial derivative at the resident strategy

$$g_x = \left.\frac{\partial w(y,x)}{\partial y}\right|_{y=x} = -R(x)\,(ap_r + xp_r)$$
$$= -\,(a + x) \tag{26}$$

(cancellation because $p_r = \frac{1}{R(x)}$)

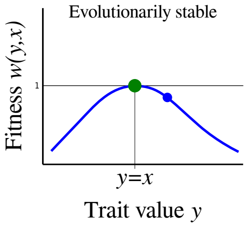
- x^* is when $g_x = 0$

$$\rightarrow x^* = -a \tag{27}$$

Adaptive dynamics worked example - evolutionarily stable?

Is x^* an *evolutionarily stable strategy*?

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



- Find the second partial derivative wrt y

$$\frac{\partial^2 w(y,x)}{\partial y^2} = R(y)\left(p(y,x)(y^2-1) + 2ayp_r\right) \tag{28}$$

- Evaluate second partial derivative at the resident strategy

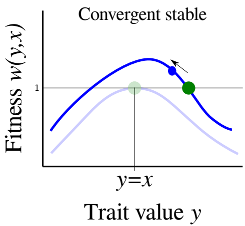
$$\left.\frac{\partial^2 w(y,x)}{\partial y^2}\right|_{y=x} = R(x)p_r\left(x^2-1+2ax\right)$$
$$= x^2 - 1 + 2ax \tag{29}$$

(cancellation because $p_r = \frac{1}{R(x)}$)

- Evaluate at x^*

$$\left.\frac{\partial^2 w(y,x)}{\partial y^2}\right|_{\substack{y=x\\x=x^*}} = -1 - a^2 < 0 \tag{30}$$

Adaptive dynamics worked example - convergence stable?



Is x^* a *convergence stable strategy*?

- $\left.\frac{dg_x}{dx}\right|_{x=x^*} < 0$
- Using: $x^* = -a$

- Recall

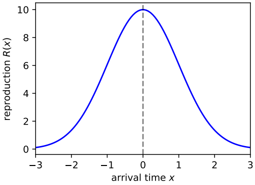
$$g_x = \left.\frac{\partial w(y,x)}{\partial y}\right|_{y=x} = -\left(a + x\right) \quad (31)$$

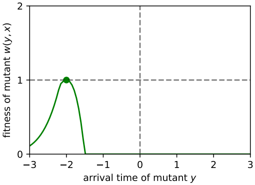
- Find the derivative of $g(x)$ wrt x, evaluate at x^*

$$\left.\frac{dg_x}{dx}\right|_{x=x^*} = -1 < 0 \quad (32)$$

Adaptive dynamics worked example - meaning

- To summarise:
  - Found a singular strategy $x^* = -a$
  - In the example right, I've set $a = 2$
  - Found x^* was continuously stable strategy
- What does it mean biologically?
  - No. of offspring is maximised at $x = 0$
  - However early arrival increases chance to obtain a territory
  - Evolutionary end-point is $x^* = -a$, earlier than the peak
  - The drop-off at the early part of the peak represents decreased survival with early arrival, e.g. because of cold weather





Adaptive dynamics worked example - meaning

- Evolutionary end-point is early arrival in cold weather

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)

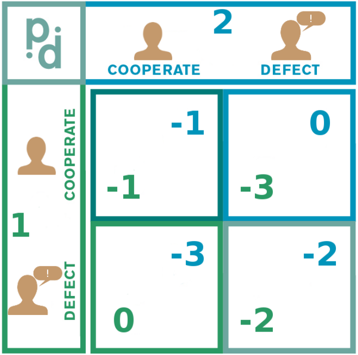
"In each documented example, the migrants could have avoided the cold spell if they had arrived in breeding areas some days later than they did" Newton (2007, *Ibis*)

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?

- If other is cooperating, should still defect
  $f(\mathrm{C},\mathrm{C}) < f(\mathrm{D},\mathrm{C})$
- If other is defecting, should defect
  $f(\mathrm{D},\mathrm{D}) > f(\mathrm{C},\mathrm{D})$
- Defect is only ESS / Nash equilibrium



- Fitness effects:

$$f_C = p_C b + p_D c$$
$$f_D = p_C d + p_D a$$

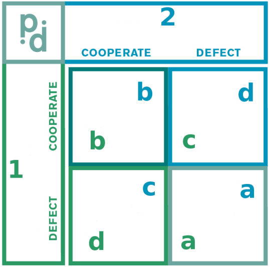
- Replicator dynamics

$$\begin{aligned}\dot{p}_C &= p_C(1-p_C)(f_C - f_D) \\ &= p_C(1-p_C)\{bp_C + c(1-p_C) - dp_C - (1-p_c)a\}\end{aligned}$$

- Steady states:

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

but notice $\frac{a-c}{a-c+b-d} > 1$ so omit that



$$d > b > a > c$$

Generalised Prisoner's Dilemma and replicator dynamics

- Fitness effects:

$$f_C = p_C b + p_D c$$
$$f_D = p_C d + p_D a$$

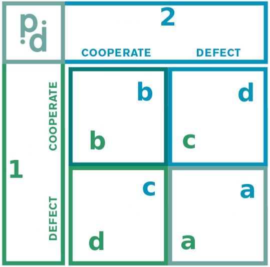
- Replicator dynamics

$$\dot{p}_C = p_C(1-p_C)(f_C - f_D)$$
$$= p_C(1-p_C)\{bp_C + c(1-p_C) - dp_C - (1-p_c)a\}$$

- Steady states: $p_C^* = 0, 1$
- Check asymptotic stability

$$\frac{d\dot{p}_C}{dp_C} = (1-p_C)\{\ \} - p_C\{\ \} + p_C(1-p_C)\frac{d\{\ \}}{dp_C}$$

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



$$d > b > a > c$$

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.
- Cost is 6 units per polluting country.

pd		2: COOPERATE	2: DEFECT
1	COOPERATE	10 (1), 10 (2)	4 (1), 14 (2)
1	DEFECT	14 (1), 4 (2)	8 (1), 8 (2)

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

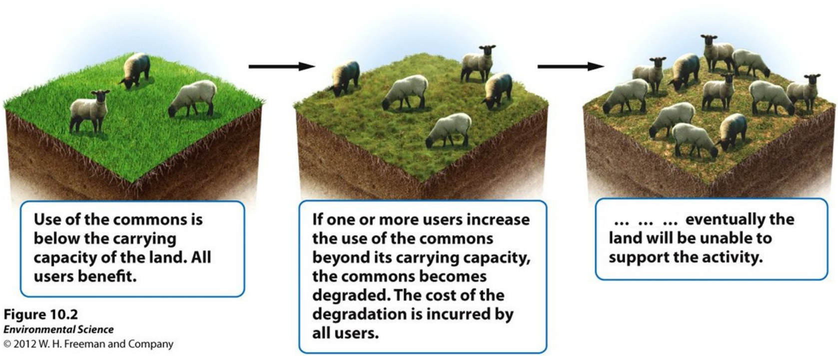
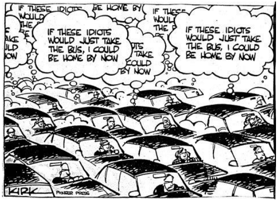


Figure 10.2
Environmental Science

The Tragedy of the Commons

- Hardin (1968) writing in the context of overpopulation
  - 'They think that farming the seas or developing new strains of wheat will solve the problem – technologically'
    - But the world still is finite.
  - Adam Smith's invisible hand: decisions reached individually produce the best result for the group
    - But not invariably true.

- How to solve? Appeal to people's conscience?
  - If we encourage people of conscience have fewer babies, then...
  - Also creates a 'double-bind'
    - you're immoral if you don't cooperate,
    - you're stupid if you do

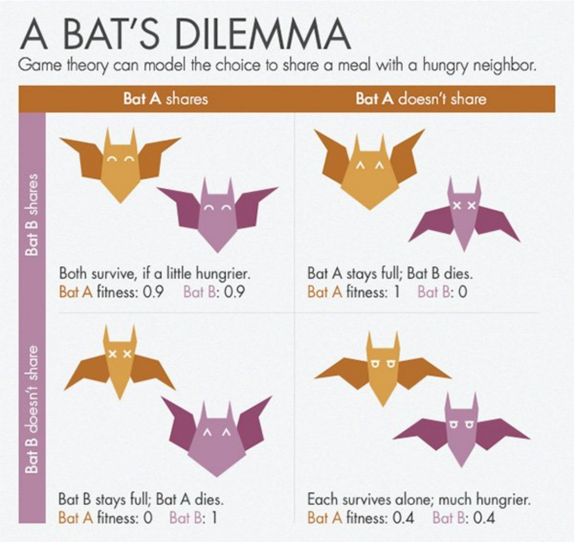


- Key point is that ToC occurs *even if all individuals understand* the consequences of their actions

... but wait

- Do you behave like this in daily life?
- 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
  - This is the *iterated* PD
- Many clever algorithms submitted

R. Axelrod (left)

Winner - Anatol Rapoport - with a very simple program `tit-for-tat`:

1. First play is ‘cooperate’ - be nice
2. Then repeat:
   1. If opponent played ‘defect’, next play is ‘defect’ - be provokable
   2. If opponent played ‘cooperate’, next play is ‘cooperate’ - be forgiving

The usefulness of evolutionary game theory

- Small communities actually don't just overgraze and ruin their commons
- People and other animals do find ways to cooperate in PD-like situations
- Conditions for cooperation in PD incl.:
  1. May play the same player again
  2. Ability to recognise other player
     - Repeated game like Axelrod's Tournament
     - Fixed meeting place, or individual recognition
  3. Unknown number of future games

- 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'

Summary

- Evolutionary game theory
  - Game theory introduced to biology from economics / political science
  - A way to study Darwinian evolution in a mathematical framework
  - Allows fitness to be a function of others' traits or strategies
- Key concepts
  - Nash equilibrium
  - Evolutionarily stable strategy *sensu* Maynard Smith
  - Evolutionary and convergence stability *sensu* adaptive dynamics
- Explanatory power of evolutionary game theory
  - Hawk-Dove – explains limited warfare
  - Prisoner's Dilemma and Tragedy of the Commons
    - Explains why cooperation can be difficult to achieve
- Iterated Prisoner's Dilemma
  - One example of how cooperation can evolve