Session 4:

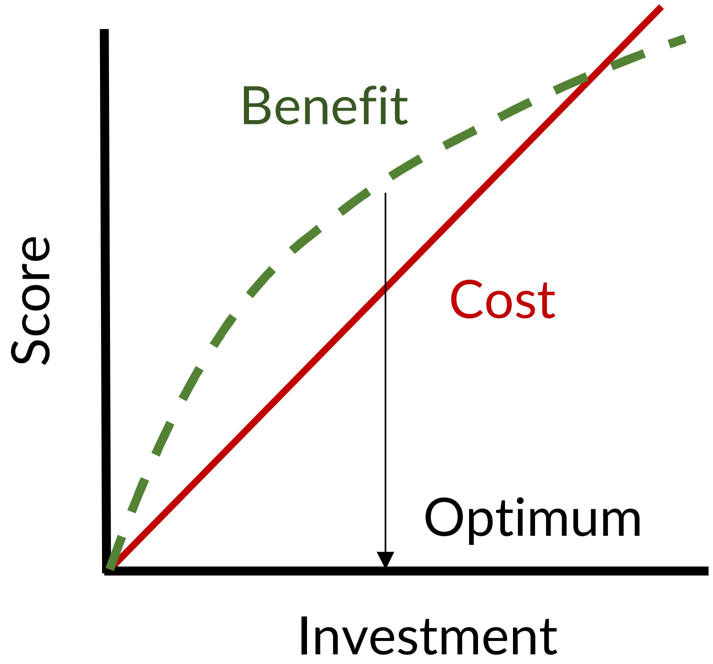
Evolutionary Stable Strategies (ESS) and Game Theory

Optimization theory

Prof. John Maynard Smith

✓ Identifies the selective factors which determine the strategies living beings use to organize their lives

$$Optimum = \max(Benefits - Costs)$$



Example: Reproduction VS growth (I)

Available resources

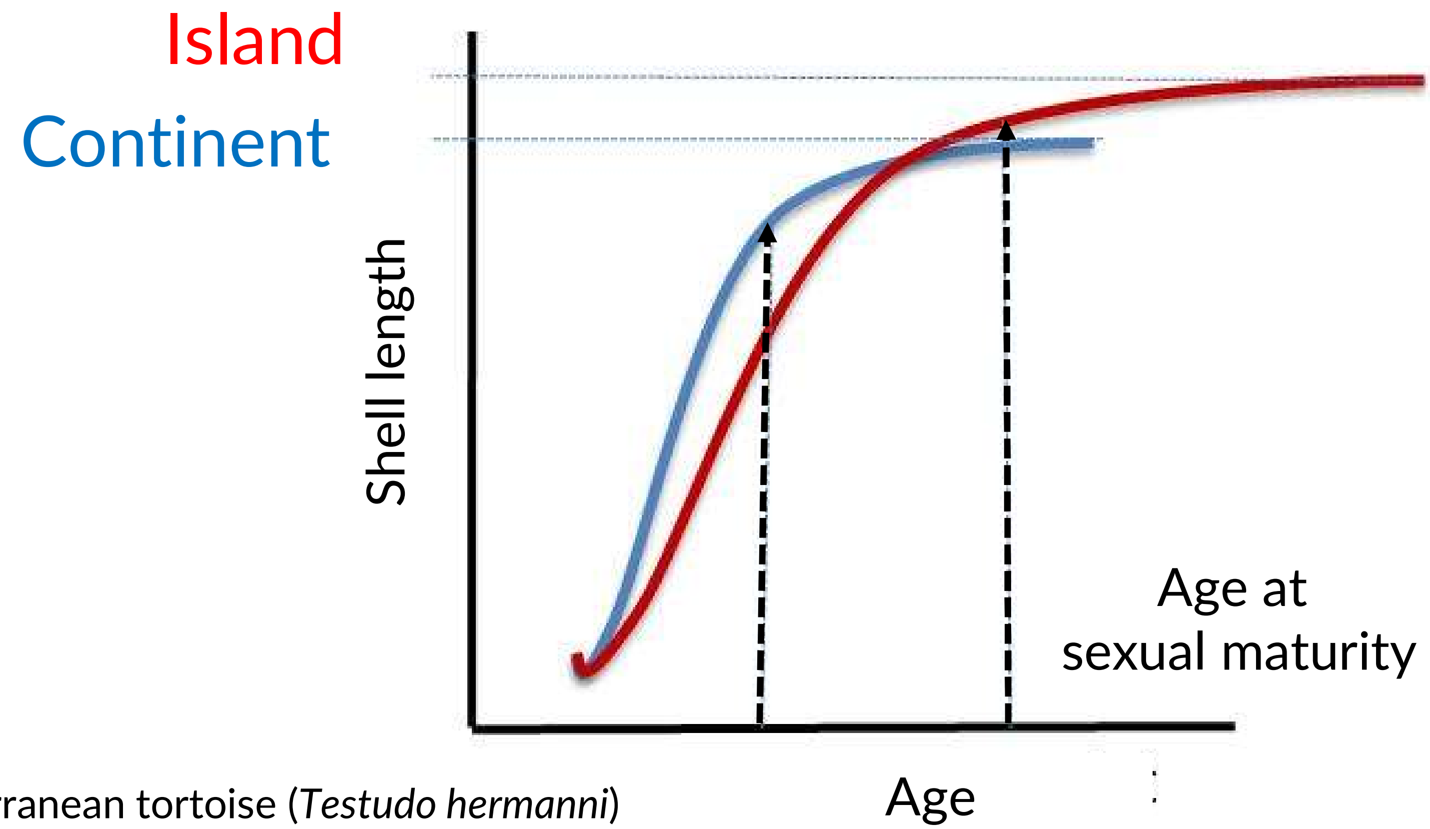
(x)
Growth and survival

(1-x)
Reproduction

Fitness

Optimization problem on "x"

Example: Reproduction VS growth (II)



Mediterranean tortoise (*Testudo hermanni*)
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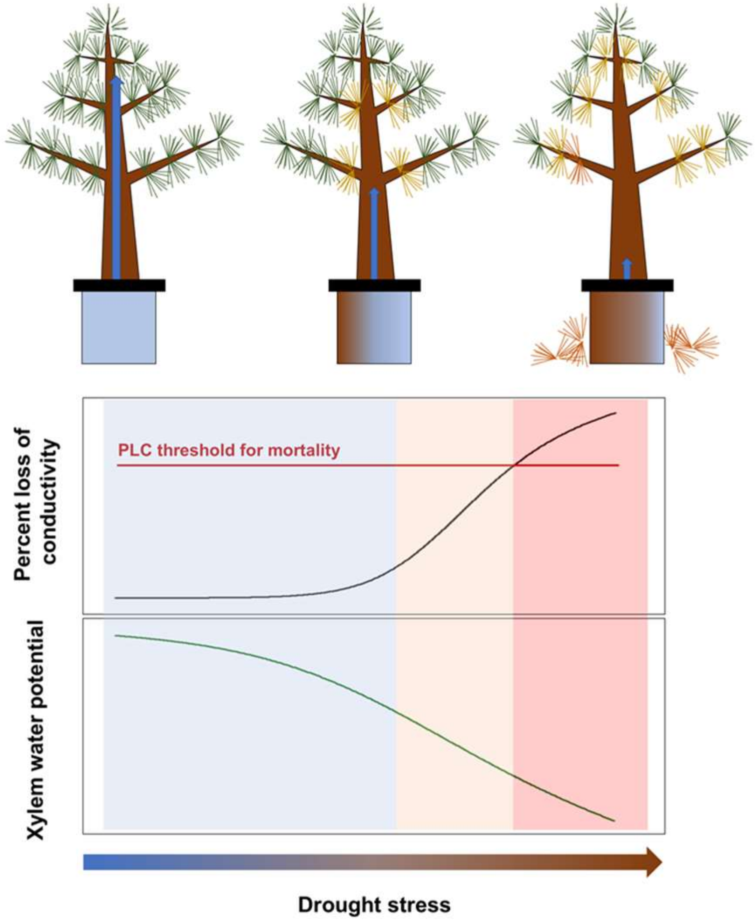
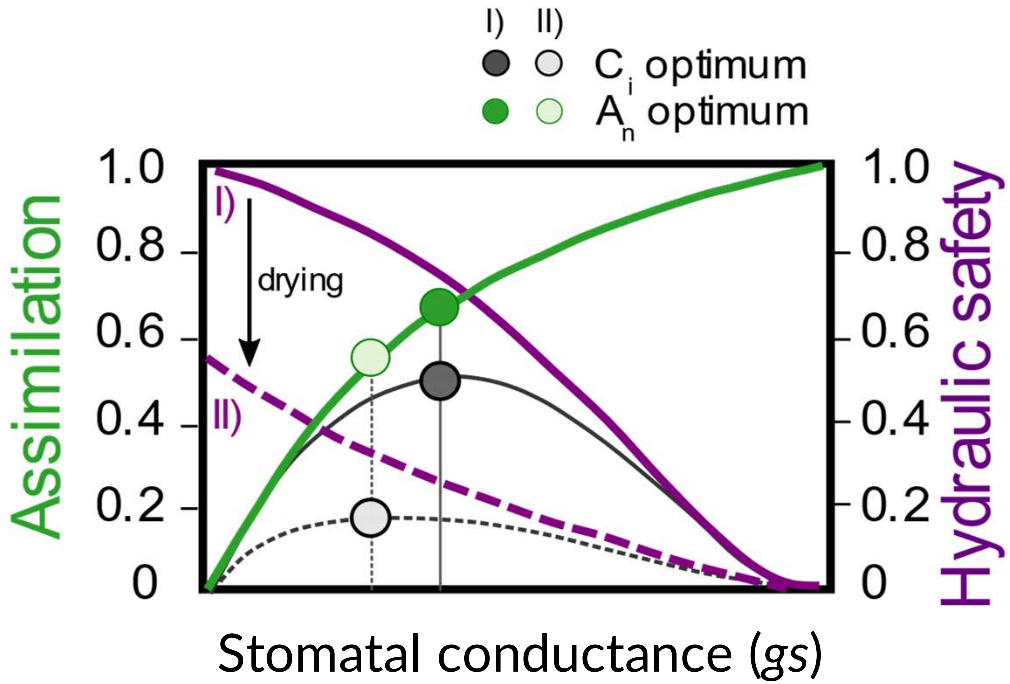
Different selection pressures result in different solutions for the optimization

Example: Plant hydraulics





Optimum g_s = max(A_n * Hydraulic safety)

Nadal-Sala et al., (2021),
Modified from Eller et al., (2020)

Example: War of attrition (I)

Assumptions:

The resource for which both individuals are competing is valuable but non-infinite valuable.

Neither individual has any knowledge about the others investment intentions.

There is no risk of a serious injury for any of the contenders.

No asymmetry that the contenders may use to end the dispute.

Example: War of attrition (II)

Dung fly
Scathophaga stercoraria

For each individual, exist a reward V to be won (e.g. mating).

Each individual invests a time “t” for the display., which reduces the chances of mating again.

$$Optimum = \max[f(V_i) - f(t * (V_{i+1})]$$

Benefit of current interaction | Future opportunities lost

Defecting probability:

$$p(t) = 1 - e^{-\frac{t}{V}}$$

$$if\ [p(t_1) < p(t_2)] \rightarrow Benefit_1 = V_1 - C_1 t_2$$

$$if\ [p(t_1) > p(t_2)] \rightarrow Benefit_1 = 0 - C_1 t_1$$

So, the **blue fly** will likely invest more time if $V_1 > V_2$ or $C_1 < C_2$. Likely, if a contender has lost before, its urgency (V) will be higher the next encounter.

Also if V1 = V2, the benefit will go to the highest t.

For the same “t” and V, the benefit of both contenders will be V / 2.

Example: War of attrition (III)

The stable solution for the equation will be:

$$p(t) = {}^{1}\!/_{v}\, e^{-t/v}$$

However, this result in a ESS in which the payoff is always 0 on average (all resources gained must be invested in the fight)

In the nature, we will most likely find within a population a distribution of individuals presenting different “t” strategies around a local minimum K (time), such as $t = K+N(0,v^2)$

Smith, 1974

Game Theory (I)

Prof. John von Newman

Prof. John Nash

Game theory is the study of mathematical models of strategic interactions among rational agents (e.g. If them do that, which is the optimal move for me?)

Initially, designed to optimize two-persons zero-sum games (von Newman)

Nash equilibrium integrates non-zero sum games: There is an optimal strategy for a given player at the population equilibrium, which makes gainless for this player to shift the strategy. -> Not always the case!

Visually addressed via a payoff matrix

Payoff matrix

Rock, Paper, Scissors	Rock	Paper	Scissors
Rock	0, 0	-1, 1	1, -1
Paper	1, -1	0, 0	-1, 1
Scissors	-1, 1	1, -1	0, 0

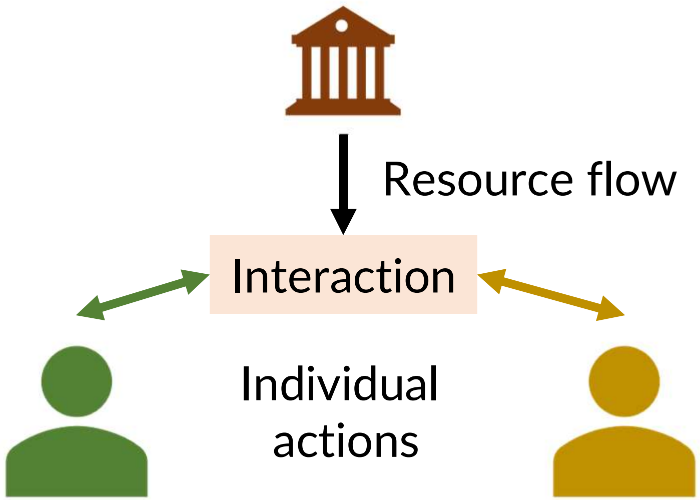
No Nash equilibrium (always shifting is the best strategy)

Zero sum and non-zero sum games

Prisoners dilemma
(To be continued...)

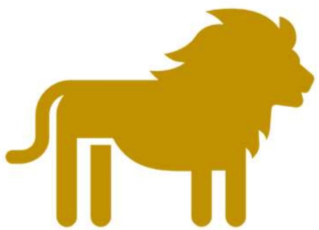
Zero-sum game
(One winner, all other losers)

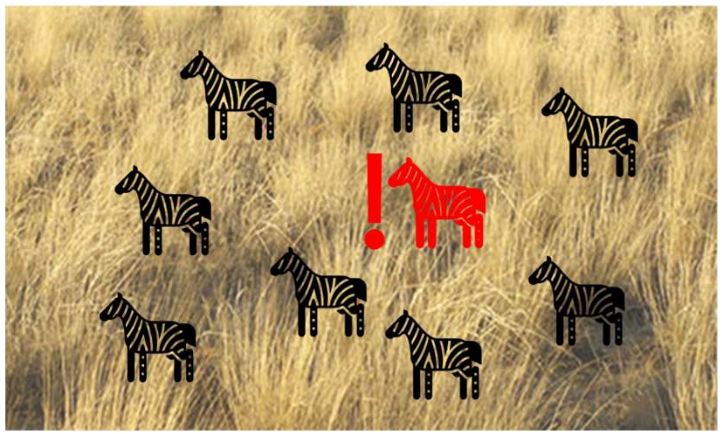
Non-zero sum game
(Allow for more than one winner)



Evolutionarily stable strategy

- An evolutionarily stable strategy (ESS) is a strategy or set of strategies that, when adopted by a population, it cannot be displaced by an alternative strategy.
- Following the Nash equilibrium, an individual of a population can't gain more adopting another strategy.
- It can be addressed globally (i.e. the whole population) or locally (i.e. if parts of the population would shift their behavior together).





About hawks and doves

We will not talk about actual species, but instead about strategies at the individual level during intra-specific competition

About hawks and doves

A given population of the **same species** has two strategies when competing for the resources, called Doves and Hawks

Will never actually fight for a resource

Staring competition until one abandons

Will physically fight for a resource

Fight until one is severely wounded

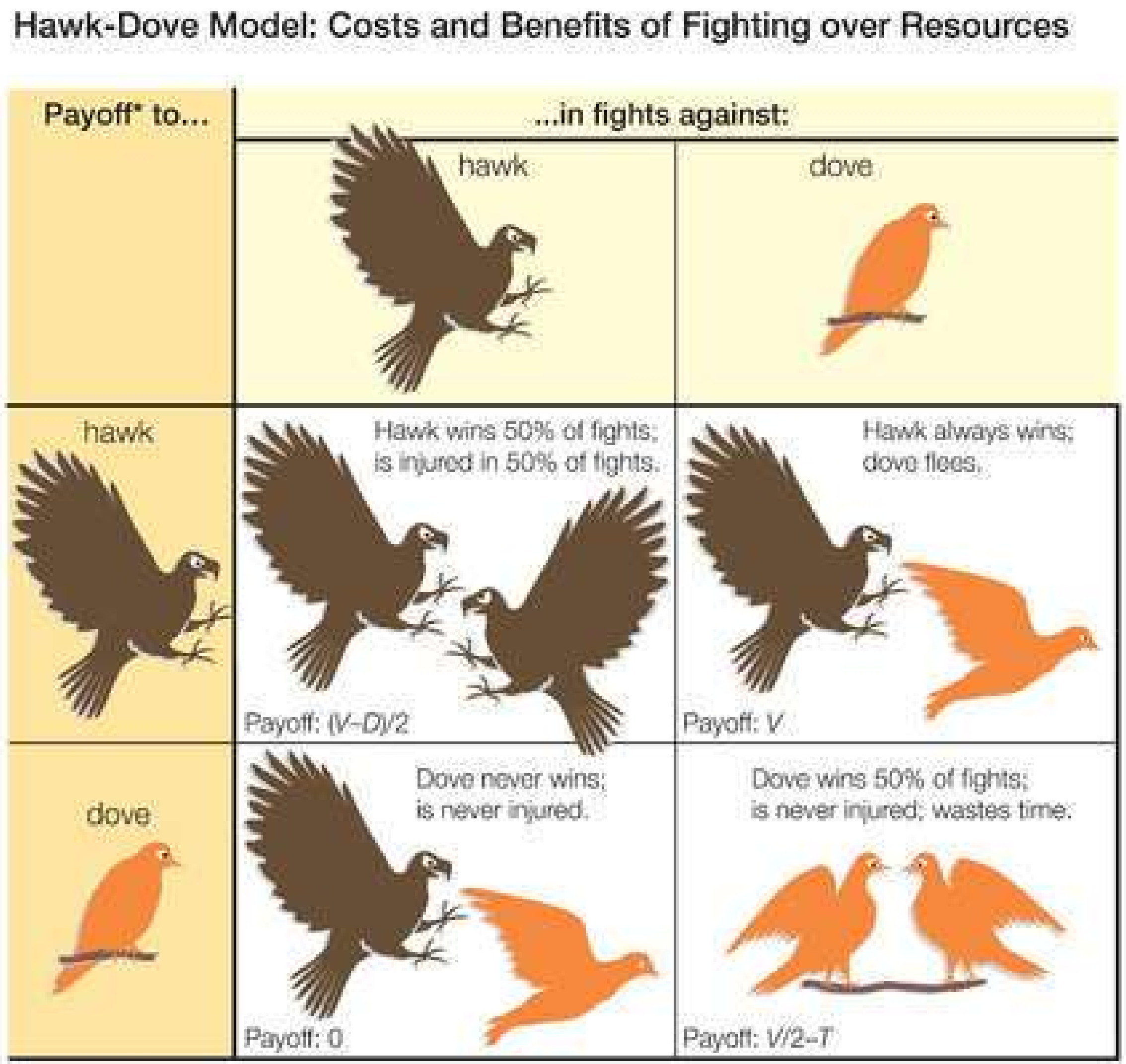
Model assumptions

Victory (V): 10 fitness units

Severe injury (C): -20 fitness units

Loss of time in staring contest (T): -3 fitness units

Interaction payoff matrix



*V = fitness value of winning resources in fight
D = fitness costs of injury
T = fitness costs of wasting time

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Calculate the payoff matrix

Half of the time it will win

Example: E(Dove, Dove) = E(D,D) = $\frac{1}{2}V - T = \frac{1}{2}5 - 3 = 2$ fitness points

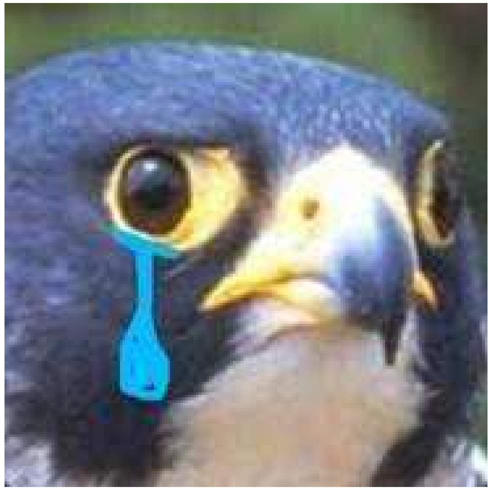
Always will lose time

Me \ Them		
	-5,-5	10,0
	0,10	2,2

Are the pure strategies ESS?

E(D,D) = 2 < E(H,D) = 10 **NO ESS**

E(H,H) = −5 < E(D,H) = 0 **NO ESS**



An intermediate strategy

An intermediated strategy (I) will satisfy (being p the probability to interact as a Hawk, and (1-p) the probability to interact as a dove [p+(1-p) = 1]):

p*E(H) = 10(1-p) – 5(p) -> The payoff for interacting as a Hawk

(1-p)*E(D) = 0(p) + 2(1-p) -> The payoff for interacting as a Dove

<u>Total population</u>: 0 = 10(1-p) – 5(p) + 0(p) - 2(1-p) -> 0 = 10 -10p -5p -2 + 2p

-8 = -13p -> **p = 8/13** to interact as a Hawk (and **5/13** to interact as a Dove)

Payoff matrix for "I" strategy

E(I,D) = $\frac{8}{12} * E(H,D) + \frac{5}{13} E(D,D) = \frac{80}{13} + \frac{10}{13} = \frac{90}{13}$

Me \ Them			
	-5,-5	10,0	$\frac{10}{13}, \frac{-40}{13}$
	0,10	2,2	$\frac{10}{13}, \frac{90}{13}$
	$\frac{-40}{13}, \frac{10}{13}$	$\frac{90}{13}, \frac{10}{13}$	$\frac{10}{13}, \frac{10}{13}$

Same fitness against I

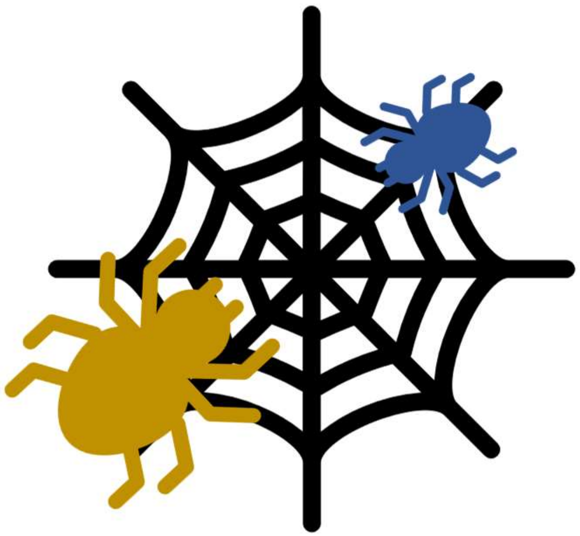
E(I,H) > E(H,H)
E(I,D) > E(D,D)

I is ESS!

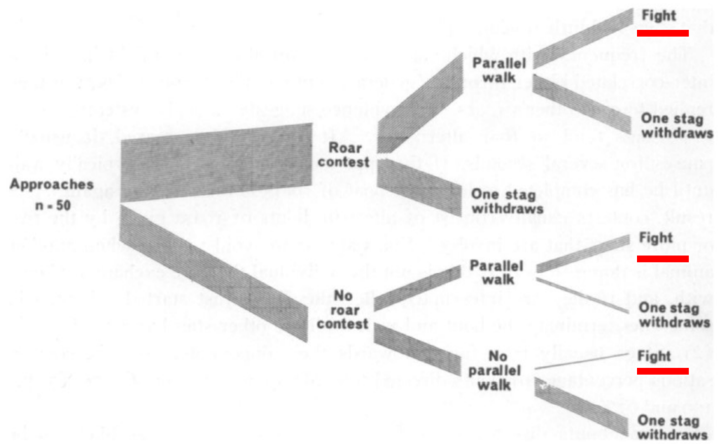
Not all contests are symmetrical

1. Asymmetries in fighting capacity:

- Need for "honest" ways to determine the stronger contender
    - Clear signals
    - Low likelihood to cheat
    - The cheapest way to win is to appear strong



Fight determined by web movements



Only 26% displays (13/50) end up in actual fight

Clutton-Brock et al., (1976)

The bourgeoise strategy

2. Asymmetries in the resource ownership:

- Resource owner will be more willing to defend it than the aspirant.
    - Clear determination of the ownership for a resource (e.g. nests)

Inachis io, after Baker, (1972)

Iguana iguana, after Rand & Rand, (1976)

New competition strategy:

"If I am the owner of the resource, I will take the Hawk strategy, otherwise, I will behave as a Dove"

Smith, J. M. (1979). Game theory and the evolution of behaviour. *Proceedings of the Royal Society of London. Series B. Biological Sciences*, *205*(1161), 475-488.

Bourgeoise payoff matrix

Assumption: Ownership 50% of the time

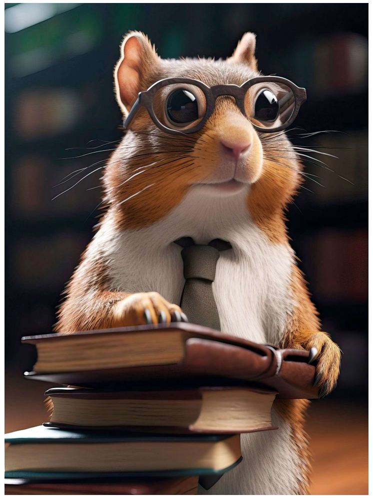
E(B,H) = 0.5E(H,H) + 0.5E(D,H) = 0.5(-5) + 0.5(0) = -2.5
E(B,D) = 0.5E(H,D) + 0.5E(D,D) = 5 + 1 = 6

		Them		
				
Me		-5,-5	10,0	2.5,-2.5
		0,10	2,2	1,6
		-2.5,2.5	6,1	5,5

Greater fitness against B

E(B,H) > E(H,H)
E(B,D) > E(D,D)

B is ESS!



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- *Myerson, Roger B. (1991). Game Theory: Analysis of Conflict. Harvard University Press. ISBN 9780674341166.*

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