

## Tinbergen: eggshell removal diminishes predation

15 cm                      42%

100 cm                    32%

200 cm                    21%

How far would you carry the eggshell?

2 m or 200m?

Eggshells carried far from nest

Take it very far away: no predation risk?

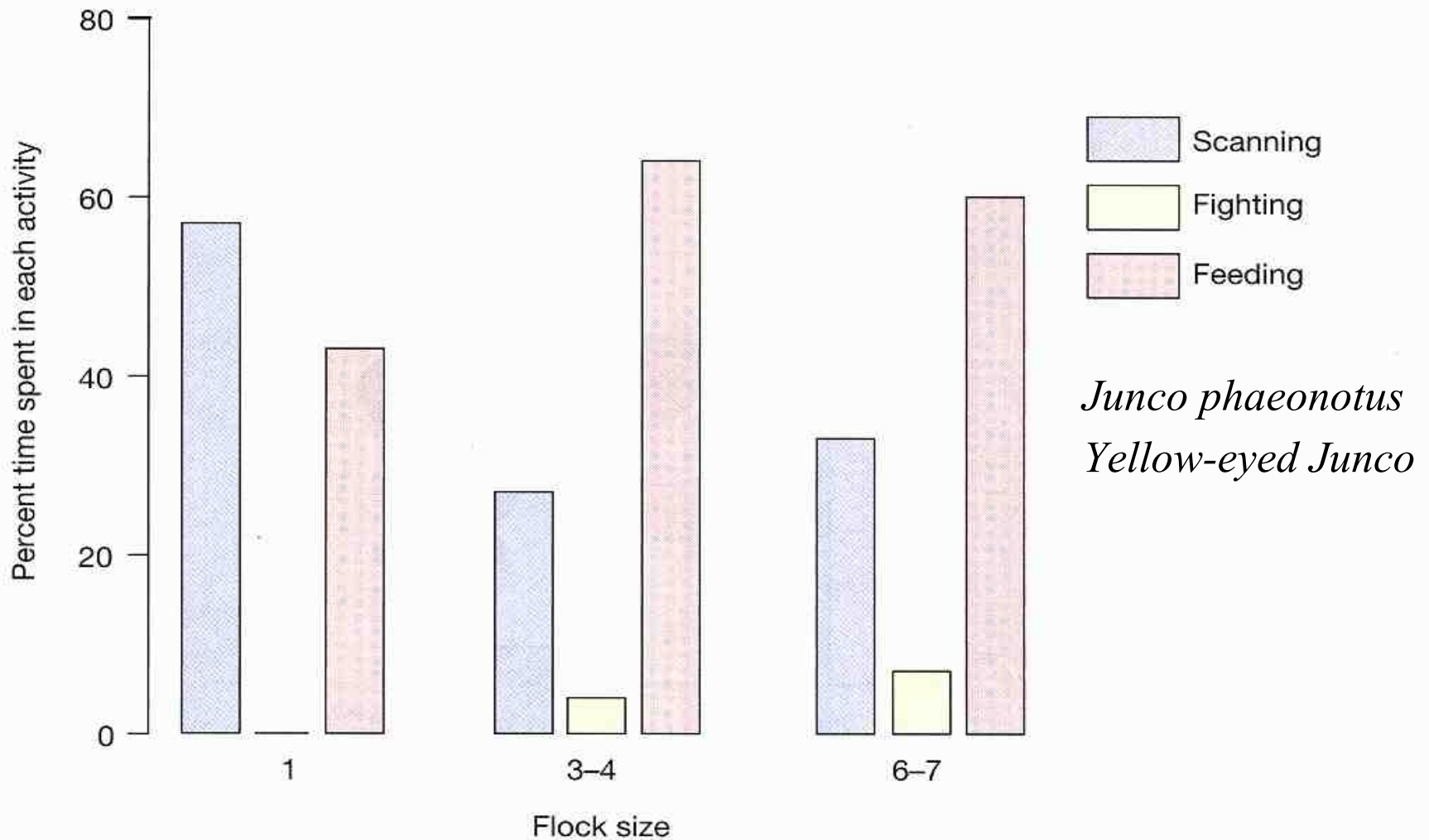
- When parent away, nest can be predated
- Time
- Energy

Every action has costs

Single action: time, energy, risk of predation, injury, infection etc.

Between actions: when you do A, you can't do B

# Trade-offs



**Figure 4.13** The increase in fighting and decrease in scanning of yellow-eyed juncos with increasing flock size yields the highest rate of feeding at intermediate flock size. (From data in Caraco et al., 1980.)

## Adaptationist approach

Behaviour is shaped by selection.

Genetic selection

Mental selection (trial and error, cognition)

Every action has costs and benefits.

Lowest possible cost with highest benefit: optimal

Individuals performing optimal behaviour leave more offspring

Behavioural ecology: studying and modelling optimal behaviour

Within individual: optimisation models

Between individuals: game theory models

## Adaptationist approach

behaviour is assumed optimal within constraints

Constrain: cannot be modified (anatomy, cognitive capacity etc.)

Applied to human behaviour: evolutionary psychology

A few people with ADHD in a group can be advantageous  
(Attention deficit hyperactivity disorder)

Gene linked to ADHD was positively selected

Applied to in medical science: Darwinian medicine

Morning sickness in first trimester.

Benefit: avoiding toxins

Costs: weight loss (embryo weighs few grams)

## Adaptationist approach - *caveats*

### Evolutionary lags

Sudden change in the environment

(global climate change)

Coevolutionary arm races

(hosts and parasites)

### Rules of thumb

Approximations

(eat green bugs, avoid red ones)

### Local versus global optima

Two populations in different environment with gene flow

# optimisation

Assumption:  
behaviour is optimal within constraints

Aim of studies:

What are the constraints?

What is the benefit, cost and profit

- Optimisation models

What are the alternative strategies?

- Game theory models

# Optimal territory size

Roebuck:  
territory in spring  
(fighting, chasing, marking)

Mating in summer (july-august)  
with females on territory  
2-3 females on average

Larger, better quality territory

- More offspring → fitness
- More costly to defend

Where is the optimum?



Optimal territory size:

Cost increases by

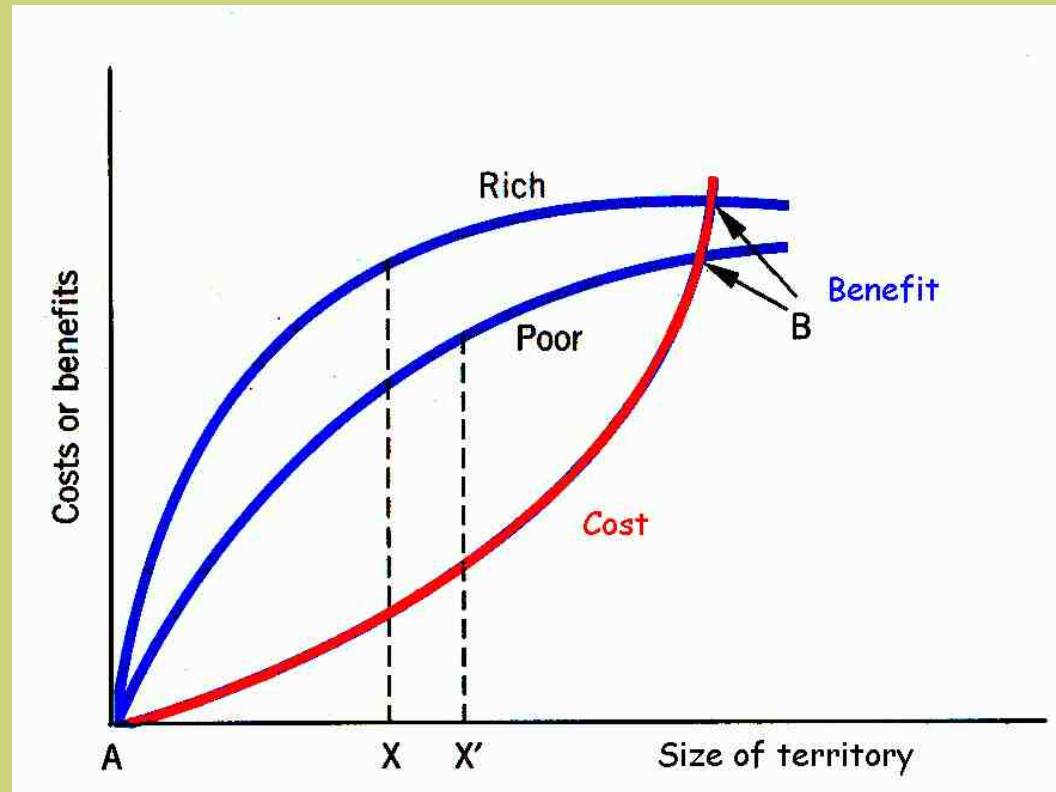
size of territory

density of males

Benefit increases by

size of territory

quality of territory



# Amerikai varjú (*Corvus caurinus*)

- Crows picked up only large whelks about 3.5 – 4.4 cm long
- They flew up about 5 meters to drop their chosen whelk
- They kept trying until the whelk broke, even if many flights were required



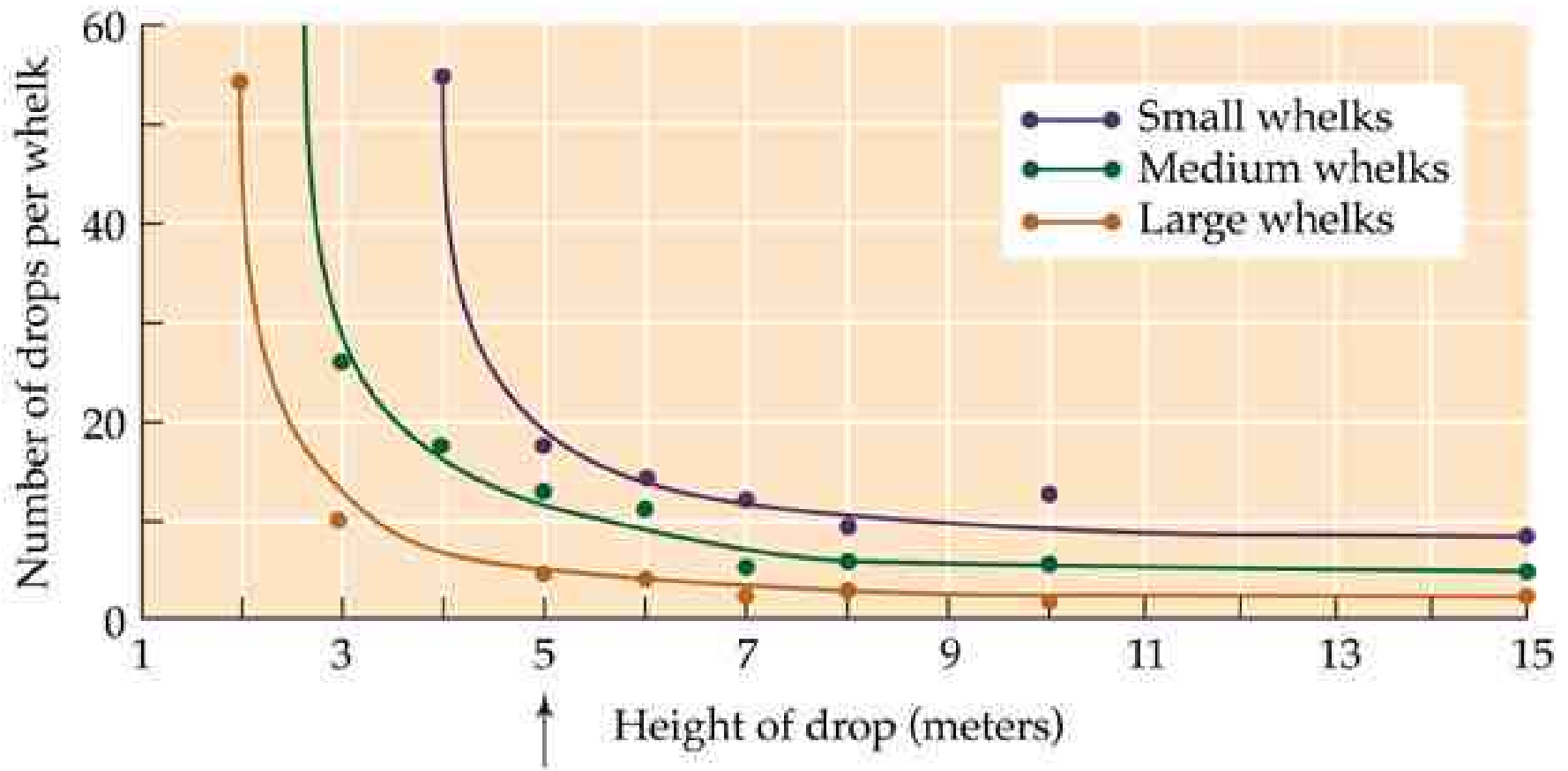
# Optimality Hypothesis Predictions:

Large whelks should be more likely than small ones to shatter after a drop of 5 meters

Drops of less than 5 meters should yield a reduced breakage rate, whereas drops of much more than 5 meters should not greatly improve the chances of opening a whelk

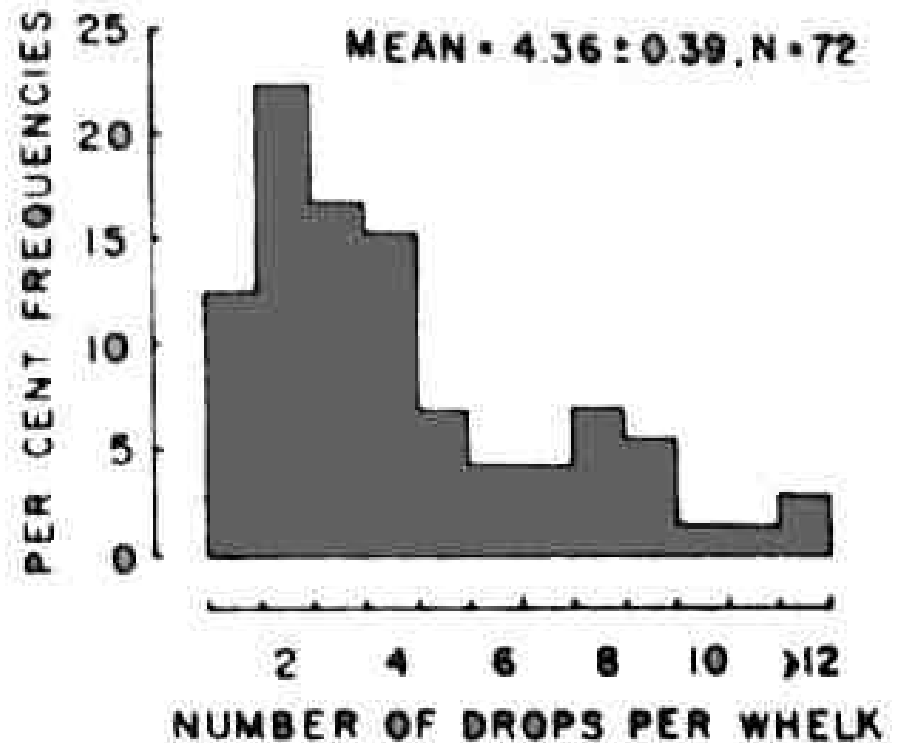
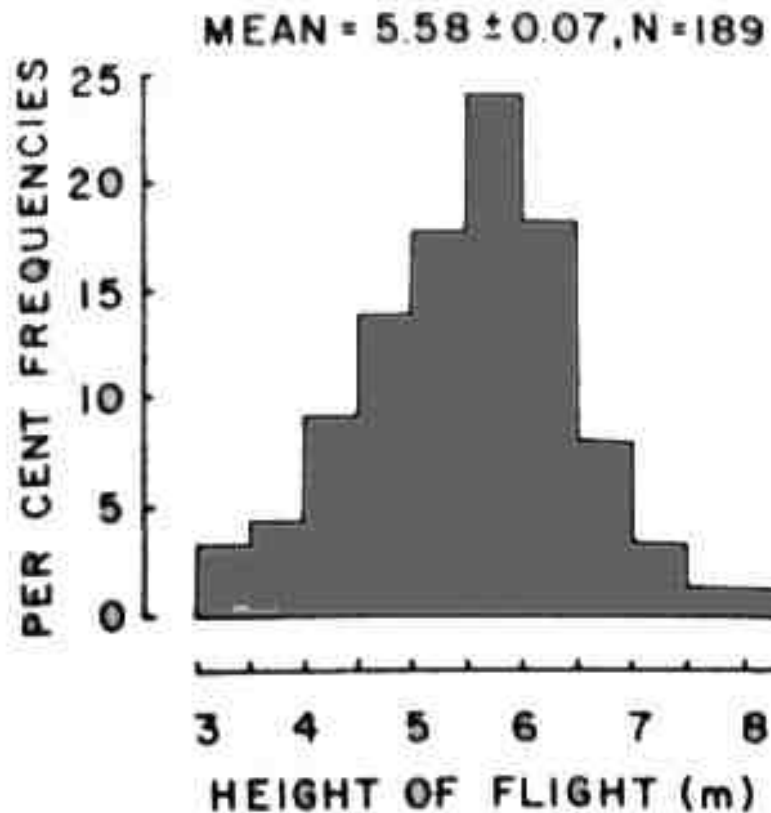
The probability that a whelk will break should be independent of the number of times it has already been dropped.

# First Test: Size of Whelks



## Second Test: Height of Drop

Why do the crows consistently fly to about 5.25 m and use about 4.4 drops to split open a whelk? Is this explained by minimizing the energy spent, thus supporting an optimal foraging strategy?



# Third Test: Chance of breaking a Whelk

Third Prediction: The chance that a large whelk would break was unaffected by the number of previous drops.

It was always about 1 in 4 on any given drop

So a crow who abandoned an unbroken whelk would not have a better chance of breaking a replacement whelk of the same size on its next attempt

Plus it will lose energy in the new search

# Mobbing behavior of colonial, ground-nesting gulls



**ANIMAL BEHAVIOR 9e, Figure 6.1**

# Alternative strategies

Approach a Herring Gull colony, the birds will fly at you

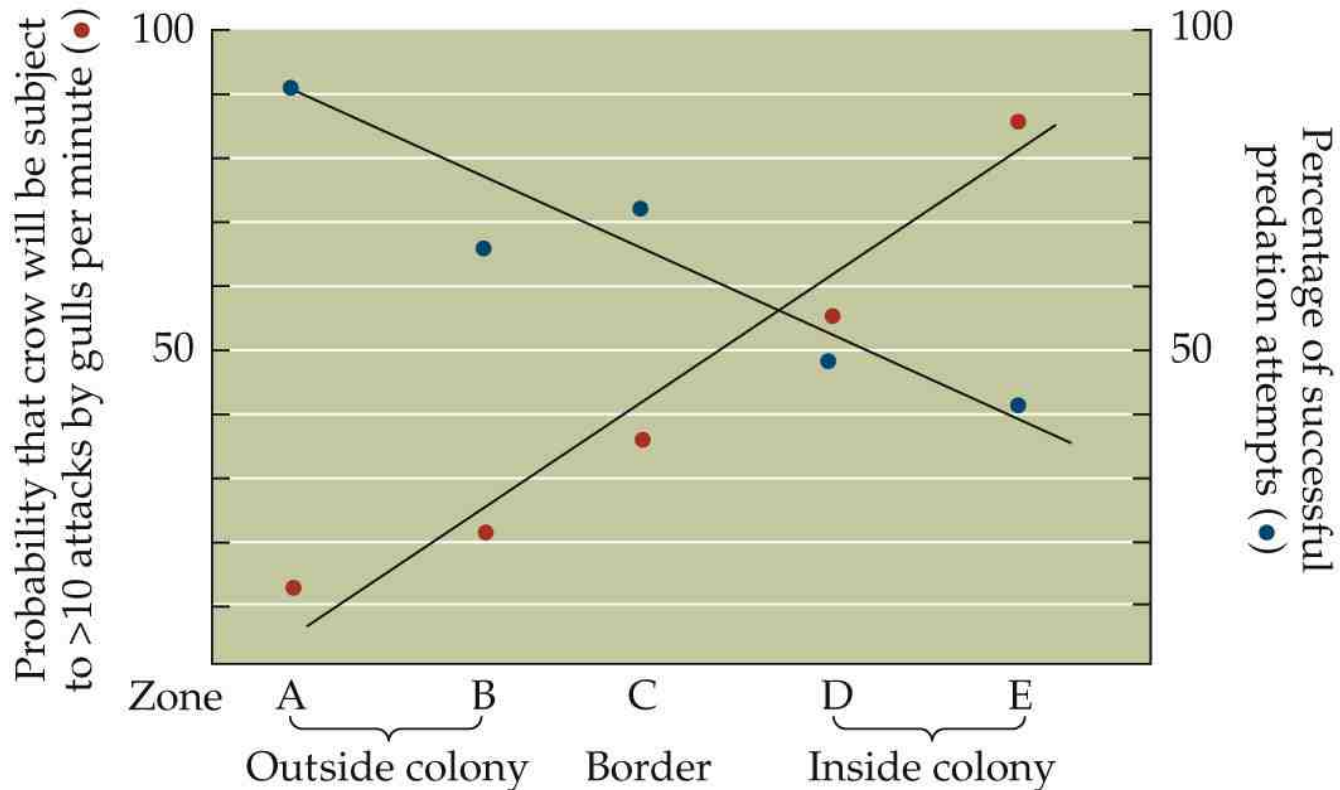
Cost: risk of predation

Benefit: predator distracted from nest

# Does mobbing protect eggs?

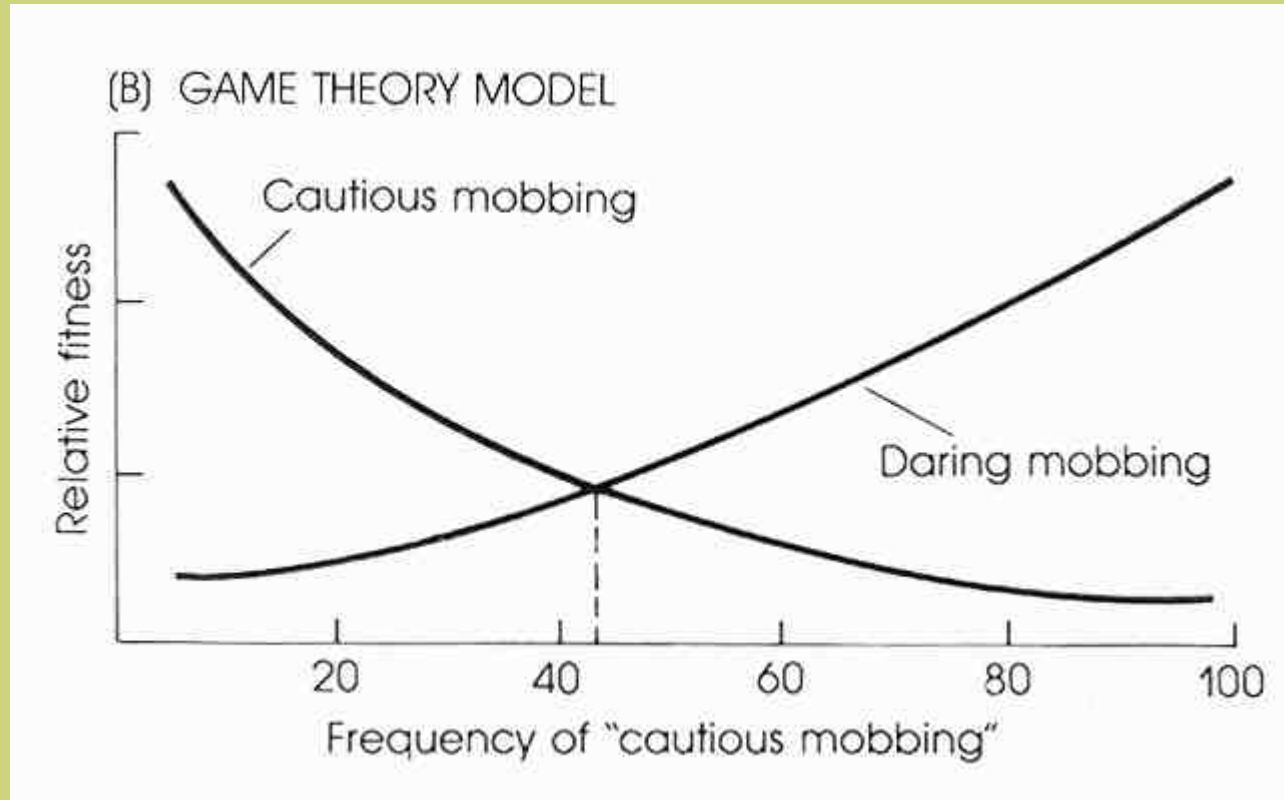


Black-headed gull



# Evolutionary Stable Strategy (ESS)

Benefit depends  
on others



If most gulls are daring, cautious strategy wins

If most gulls are cautious, daring strategy wins

ESS: stable ratio

# Interaction among individuals

	donor	receiver
Mutualism:	+	+
Reciprocity:	+ (delayed)	+
Altruism :	-	+
Selfishness	+	-
Spite:	-	-

which of these can work?

Game theory developed by János Neumann  
Neumann (1928)

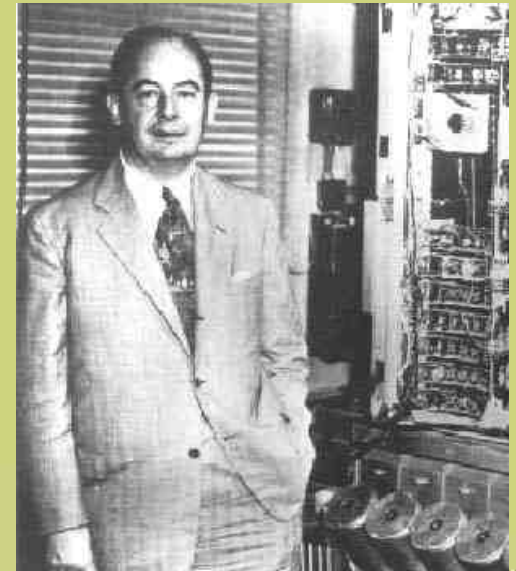
On the Theory of Parlor Games

Neumann és Morgenstern (1944):

Theory of Games and Economic Behavior

In economics: e.g. John Nash (A beautiful mind)

In ethology: John Maynard-Smith



# Evolutionary game theory

## Dove – hawk game

### Rules

two animals compete for a resource valued „B”, the winner has a an increase in fitness by „B”

individuals have any of two strategies depending on genotype

- Dove: no war, cuing, if other attacks, withdraws immediately
- Hawk: always attacks until wins or loses, inflicts or receives injury costing „C” drop in fitness

# Evolutionary game theory

## Payoff matrix

	H	D
H	$(B-C)/2$	B
D	0	$B/2$

D: dove H: hawk
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- **H vs H:** 50% chance to get resource and 50% chance of injury
- **H vs. D:** hawk gets the reward, dove retreats, none of them hurt
- **D vs. D:** one receives (or they share) the resource by 50-50% chance (or ratio)

Let  $B > C$ . what happens?

Let  $C > B$ . what happens?

# Evolutionary game theory

## Payoff matrix

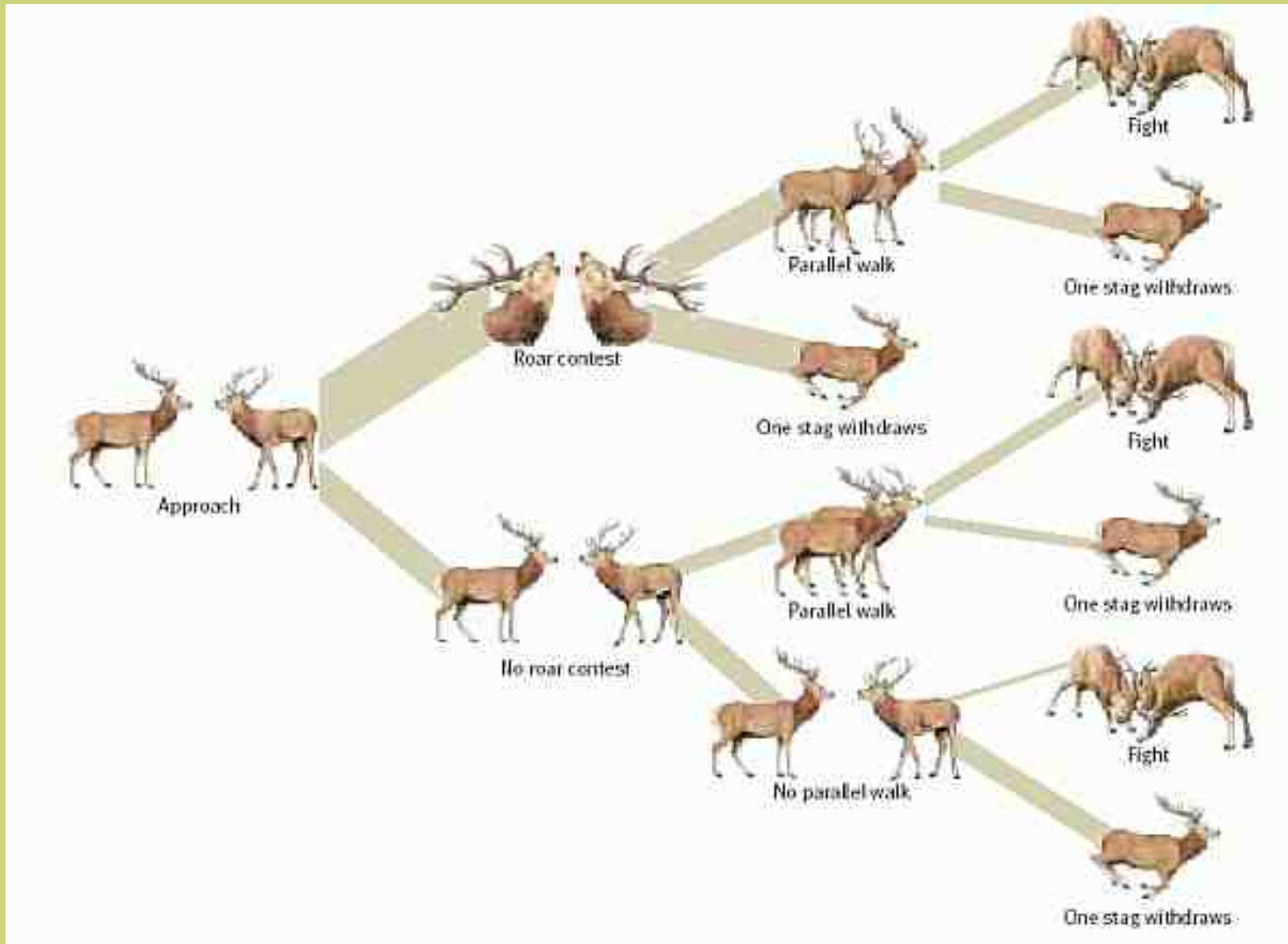
	H	D
H	$(B-C)/2$	B
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D: dove H: hawk
--------------------

Evolutionary Stable Strategy (ESS):

- 1) If one strategy has higher fitness than the other
- 2) If fitness of the two strategies is equal at a given ratio
- 3) Mixed strategy: individuals can shift strategy
  - 1) Randomly by chance of ESS ratio.
    - By assessing their chances

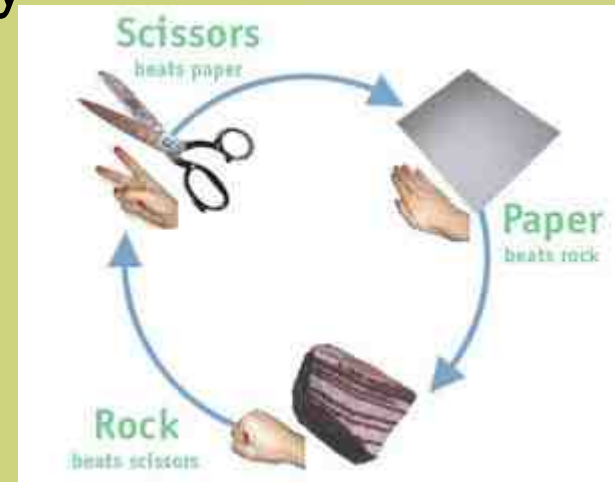
# Signalling quality reduces injuries



# Evolutionary game theory

## Rock – paper – scissors

scissors > paper > rock > scissor > paper...



	R	P	S
R	-ε	-1	1
P	1	-ε	-1
S	-1	1	-ε

If their benefits are equal the three genotypes can coexist

Rare in nature?

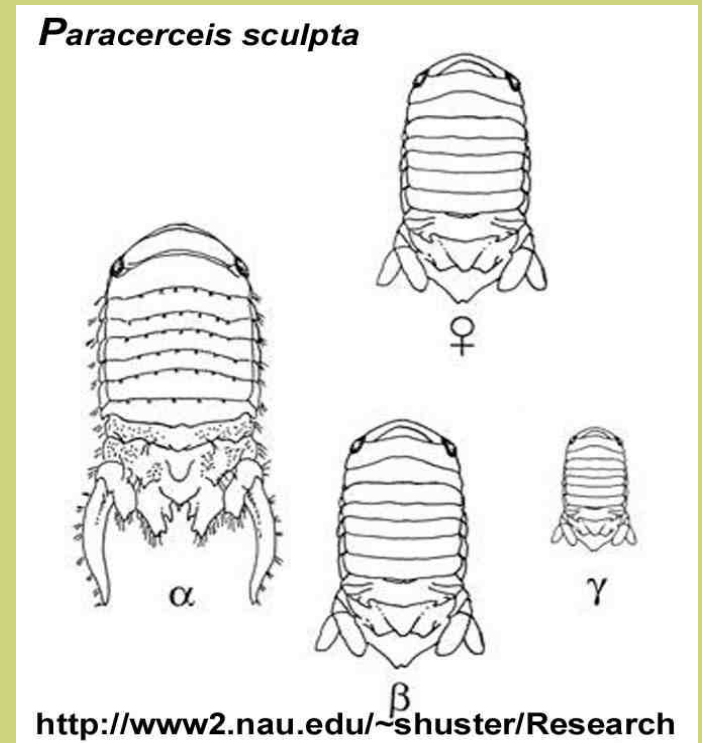
# Marine sponge isopods

- 3 male morphs
  - Territorial, female imitator, sneaker
- Genetically distinct
- One locus, 3 alleles

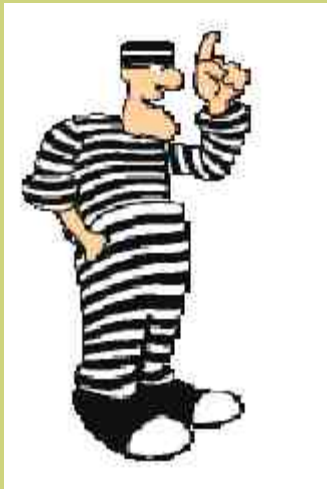
Reproductive success

Alpha: 1,51; Beta: 1,35; Gamma: 1,37  
female / male

ESS!



# Prisoner's Dilemma



		Player B	
		Cooperate	Defect
Player A	Cooperate	Reward for mutual cooperation (only 1 year in prison)	Maximum punishment (10 years in prison)
	Defect	Maximum reward (freedom)	Punishment for mutual defection (5 years in prison)

# Prisoner's dilemma

- Single game without information about the action of partner? Defect is ESS (Trivers, 1971)
- Information is not reliable
- Many games? tit for tat!