CONFLICT AND COOPERATION II.

natural theology: nature precisely tuned for some function,
traits perfectly adapted by the Creator („argument from design“)
× traits often suboptimal (cf. inverse eye, laryngeal nerve)

if fitness depends on abundance of other species, interactions between individuals or frequences of other genotypes, selection may not necessarily result in fitness increase (see frequency-dependent sel.)

ie. there may be no „best“ solution

selection can result in the decrease of fitness of all organisms – contradiction to Fisher´s fundamental theorem of natural selection

→ in this situation we cannot use simple arguments of optimization

→ GAME THEORY

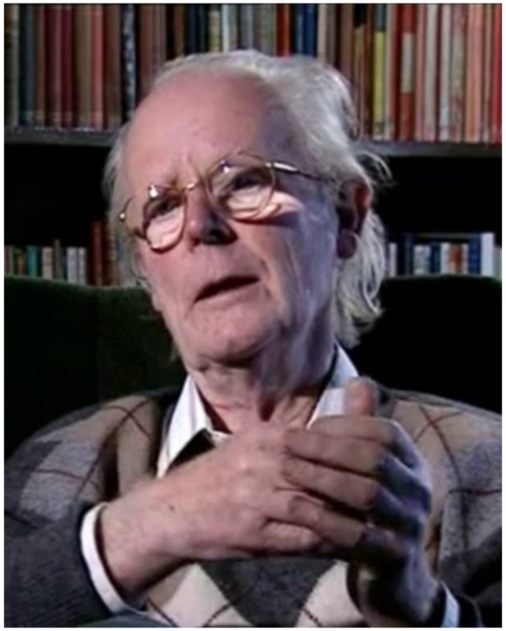
Game theory

1944 (John von Neumann a Oskar Morgenstern), 1950s

in biology William Hamilton (1967), John Maynard Smith

economy, applied mathematics, politology, philosophy, informatics,...

8 game theory experts were Nobel Prize winners
biology: J. Maynard Smith (Crafoord Prize)



J. Maynard Smith

Evolutionary game theory:

phenotype, not corresponding genes

assumption: asexual population, ignoring species biology

contrary to other branches (eg. economy) obvious advantage in that benefit can be expressed as the number of genome copies in next generations, ie. a strategy increasing player´s fitness will spread in the population by natural selection

strategy = phenotype

eg. body size, growth rate, behaviour, growth in varied environments etc.

payoff matrix: benefit = more offspring = higher fitness

John Maynard Smith, George Price (1973):

evolutionarily stable strategy (ESS) = strategy which, if fixed in a population, does not allow any alternative strategy to invade it (due to natural selection)

evolution to a particular ESS depends on initial conditions

strategy:

pure → only 1 type of behaviour
mixed → more types of behaviour

games:

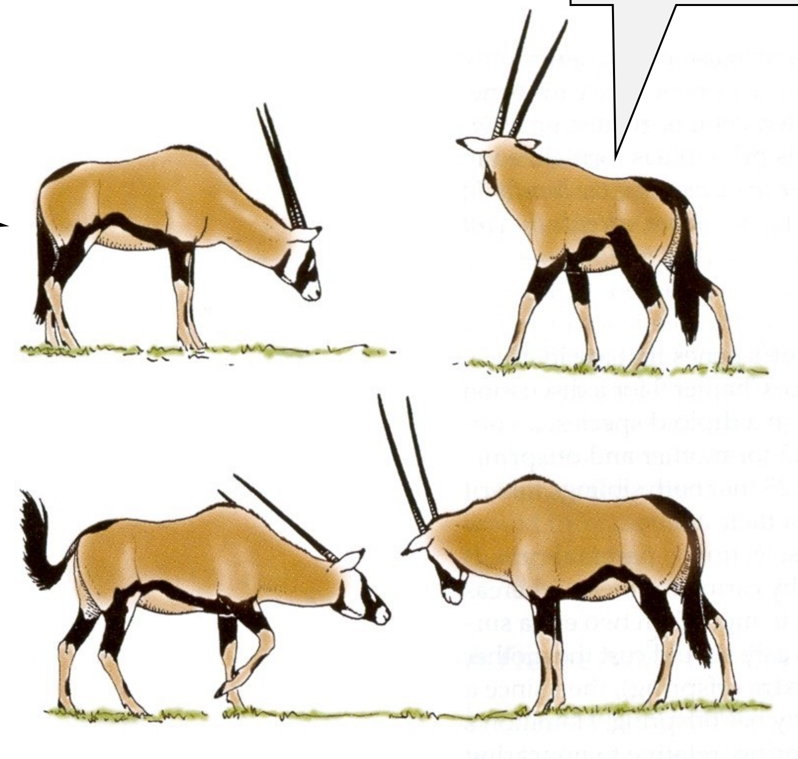
symmetric → all players same
asymmetric → different players

AGGRESSION AND ALTRUISM

Ritualization:

traditional explanation of ritualization as species´ advantage

individual advantage?



Why don´t males try to kill other males?

Symmetric models – Hawk and Dove

Hawk: always attacking

Dove: never attacking

payoff matrix:

	H	D
H	(V-C)/2	V
D	0	V/2

- (V-C)/2: both attacking, one loses (zero benefit), both losing due to risk of injury
- V: Hawk is attacking (gain)
- 0: Dove is escaping (no gain)
- V/2: both Doves are waiting, then one escapes (no gain) and the other wins (V)

Is Hawk or Dove ESS?

Eg.: V = 1, C = 2

payoff matrix:

	H	D
H	-1/2	1
D	0	1/2

average gain of H: (1 – 1/2)/2 = 1/4

average gain of D: (1/2 – 0)/2 = 1/4

Conclusion: neither Hawk nor Dove are evolutionarily stable

⇒ mixed strategy (in this case D : H = 1 : 1)

if we add a delay penalty of -1/4 to both Doves, the average Dove payoff will be (1/2 – 0 – 1/4)/2 = 1/8

⇒ the Hawk strategy will be more favourable and its frequency will increase → in this case equilibrium of a mixed strategy or D : H polymorfism would be 1 : 2

group selection (Dove population): works only in the case of conscious behaviour (conspiracy) – mostly only in humans and only theoretically (in practice usually betraying)

⇒Doves is never ESS ...

... but what about Hawk?

→ only if $V > C$
eg. $V = 2$, $C = 1$

payoff matrix:

	H	**D**
H	1/2	2
D	0	1

average gain of H:
(2 – 1/2)2 = 3/4

average gain of D:
(1 – 0)/2 = 1/2

Eg.: pinnipeds:

though frequent injuries but payoff high (harem system ⇒ the winner takes all)

therefore aggressiveness pays off males

but sometimes alternative strategies

Conditional symmetric strategies:

For example we can imagine the following alternative strategies:

Retaliator: starts as Dove, if attacked → retaliation

if you meet Dove behave as Dove, if you meet Hawk play Hawk

Bully: starts as Hawk, when retaliated – escape

play Hawk but if you meet Hawk, play Dove

Prober-retaliator: retaliator which sometimes tries conflict

closest to ESS is a mixed strategy of Retaliator, Prober-retaliator, and Dove

Conclusion: don´t behave as Bully, repay good with good but repay aggression with aggression!

Assymetric models

one opponent weaker or smaller

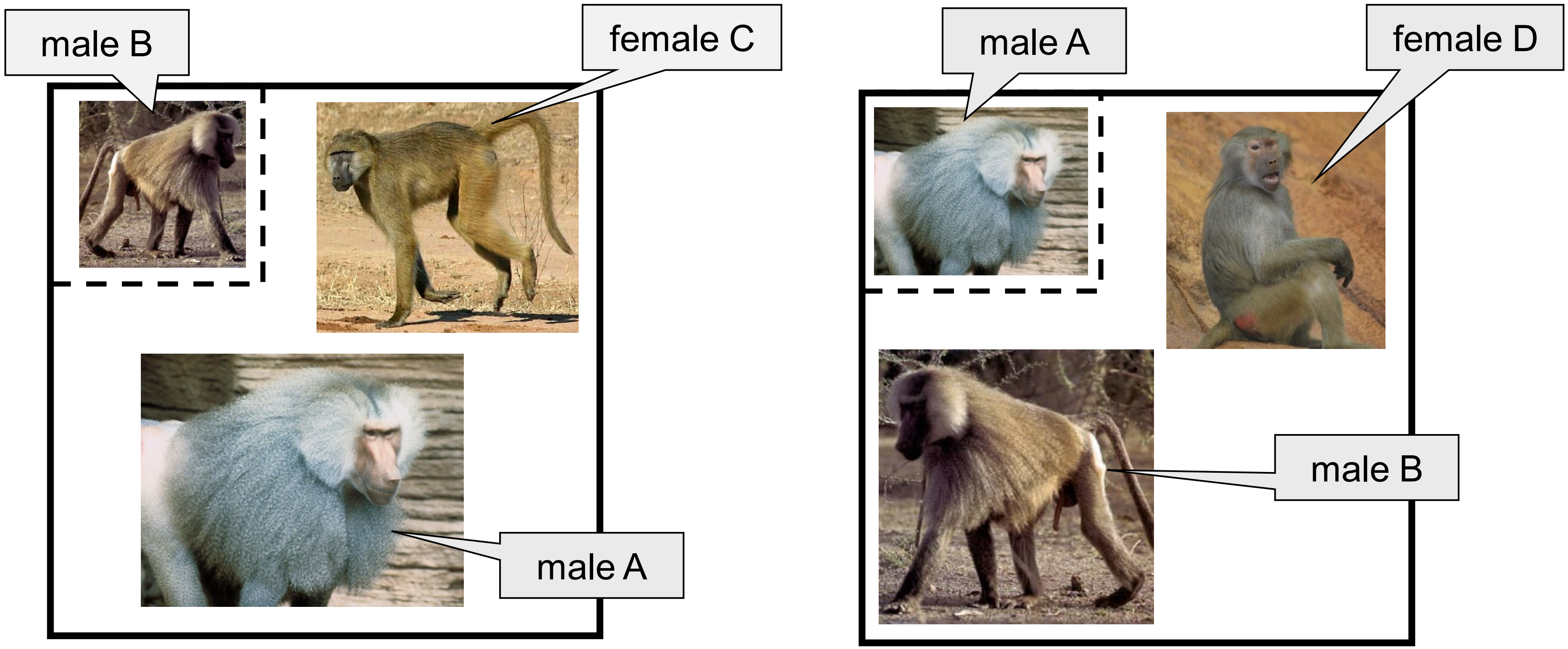
one opponent has less to lose

one opponent sooner at the locality = Lord of the Mountain principle

burgeois strategy:

if you are the resident, attack (play Hawk); if you are the intruder, retreat (play Dove)

... eg. territory defence (passerines, sticklebacks)


male B
female C
male A
male A
female D
male B

Three strategies in the population:

there may be no equilibrium $\rightarrow$ cycles

eg. „rock-paper-scissors“ game:
rock beats scissors, scissors beats paper, paper beats rock

payoff matrix:

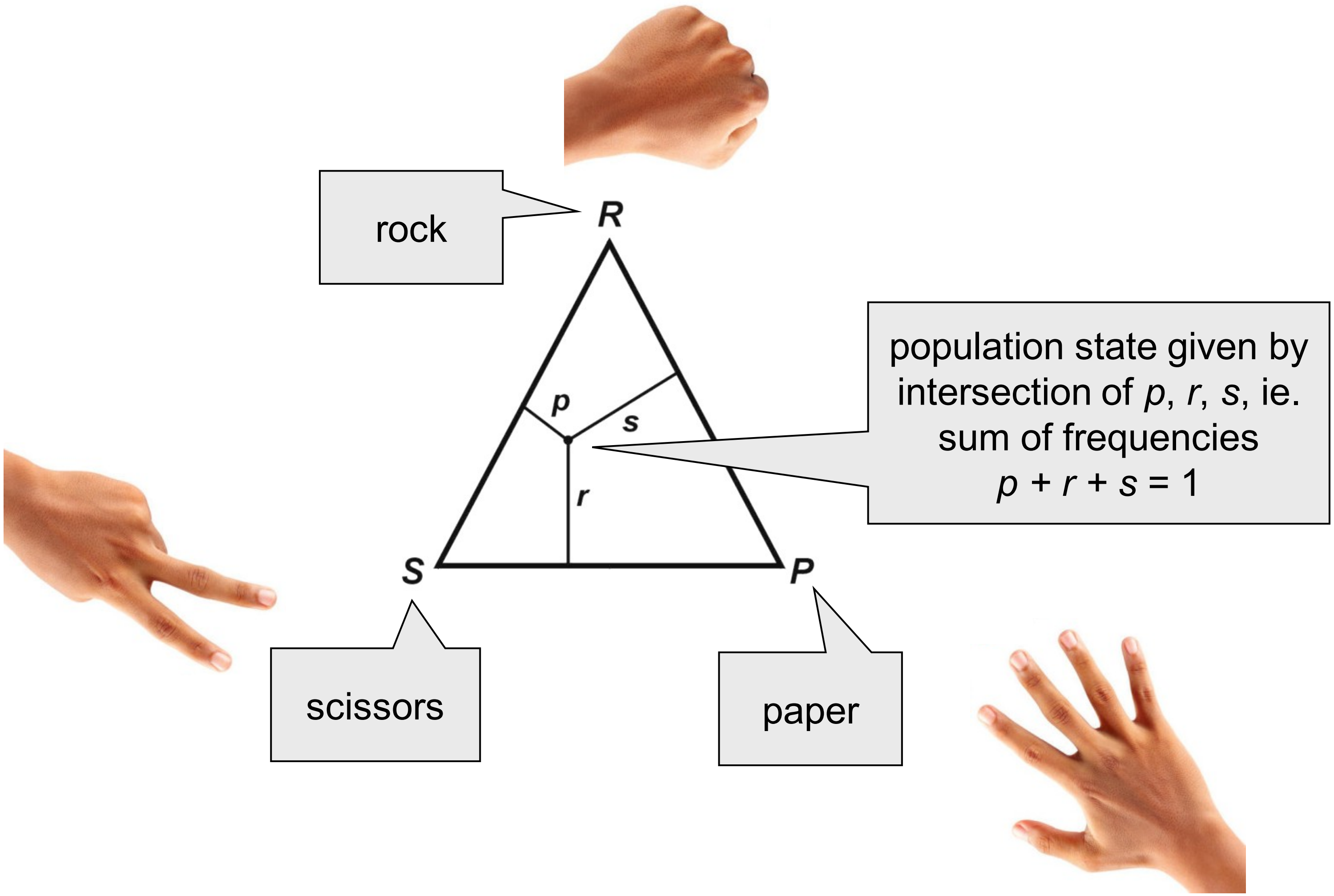
	rock	scissors	paper
rock	ε	1	-1
scissors	-1	ε	1
paper	1	-1	ε

depends on ε value:

If *game cost* is low ($\varepsilon < 0$)

→ stable polymorphism
or mixed strategy

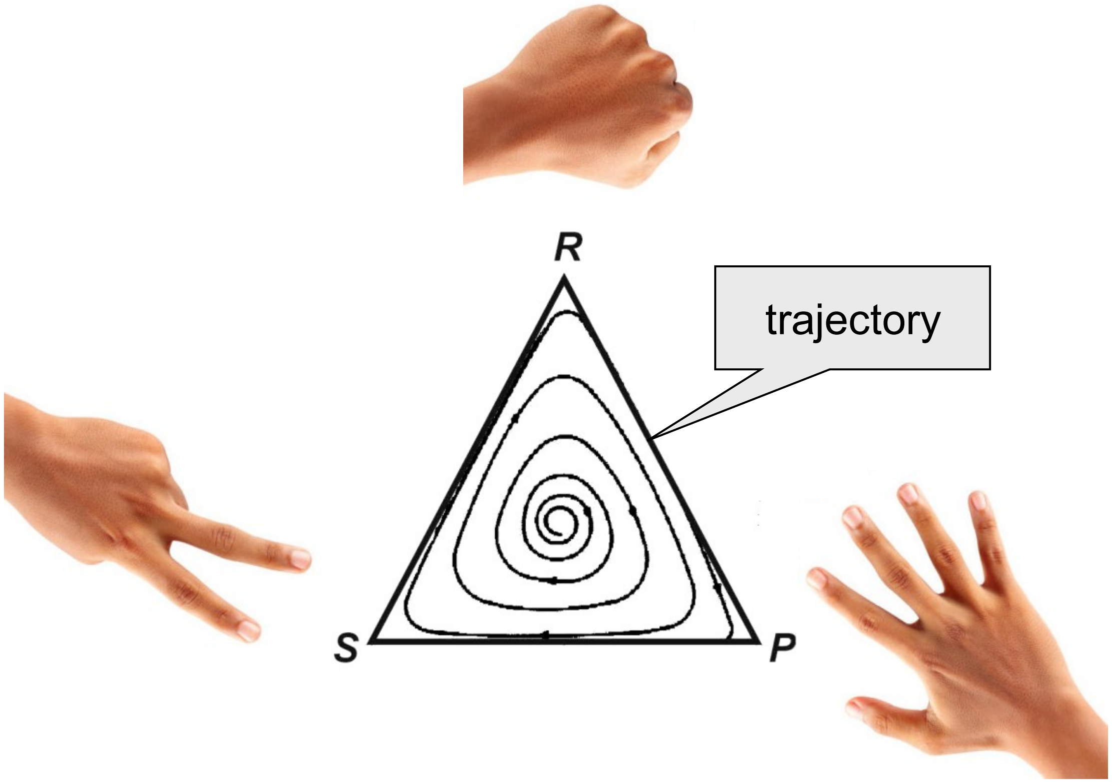
	rock	scissors	paper
rock	ε	1	-1
scissors	-1	ε	1
paper	1	-1	ε



If *game payoff* is low ($\varepsilon > 0$)

$\rightarrow$ strategies are cycling, no ESS genetically unstable polymorphism

	rock	scissors	paper
rock	ε	1	-1
scissors	-1	ε	1
paper	1	-1	ε

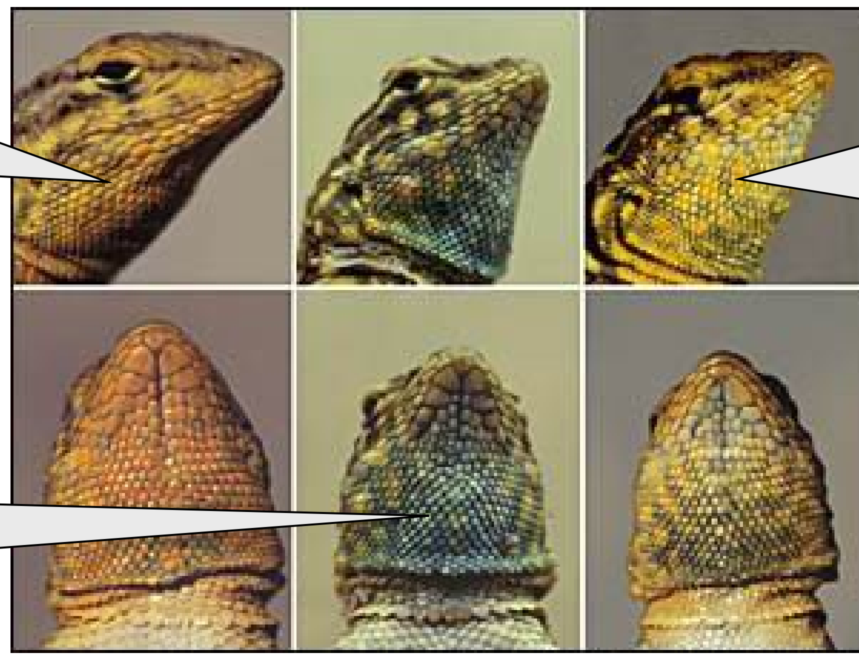


Eg.: *Uta stansburiana*:

orange throat: large territory, several females

blue throat: small territory, one female → but easier defence against sneakers

yellow throat: no territory, „stealing“ of copulations

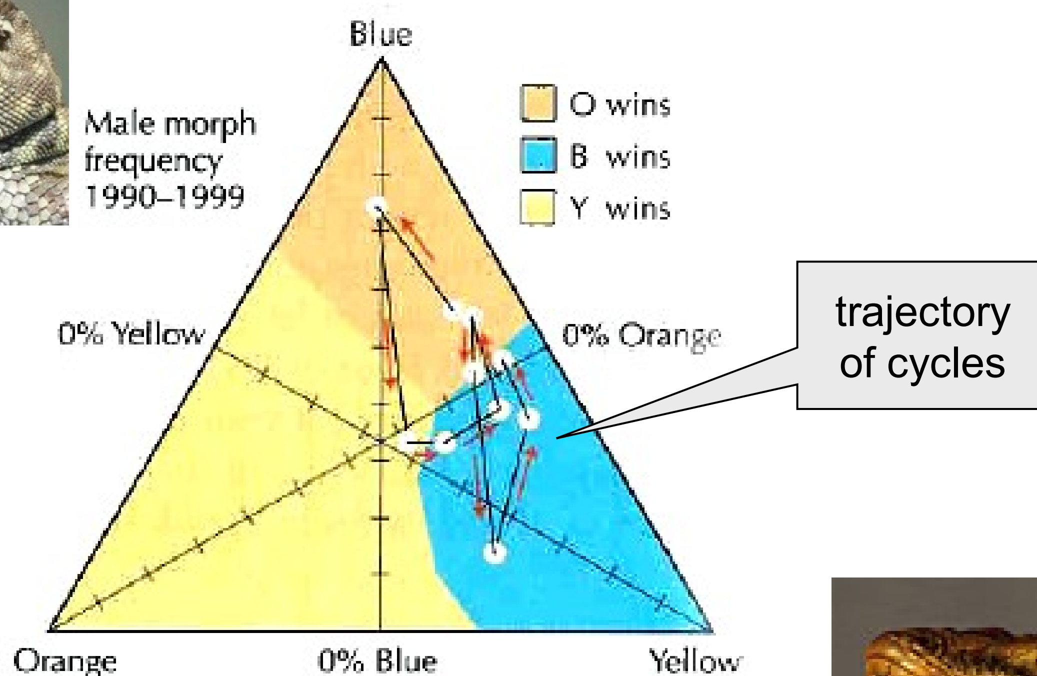


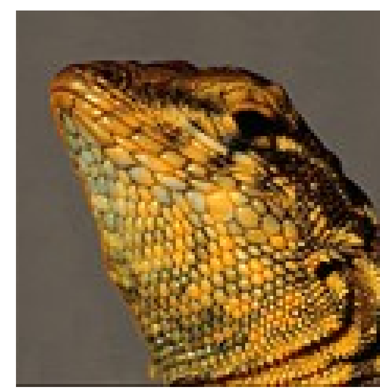
orange throat: big, territorial, several females

yellow throat: non-territorial, mimics females – stealing copulations

blue throat: smaller, territorial, single female

each strategy prevails for 4-5 years → cycles





RECIPROCAL ALTRUISM

kin altruism (kin selection)

altruism between non-relatives

sometimes altruism only imaginary (benefit for „altruists“, manipulation etc.)

Robert Trivers (1971): reciprocal altruism

especially in stable groups

reciprocal altruism between species = mutualism

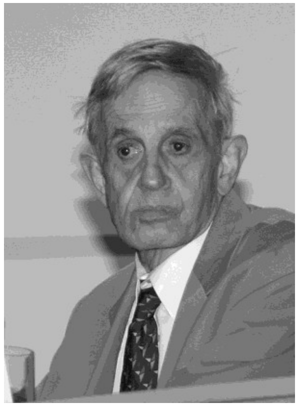

Eg. removing parasites → possible strategies:

- Sucker: always helps
- Cheat: never helps, abuses others
- Grudger: helps only in some situations

Prisoner s dilemma

a type of so called Nash equilibrium = situation when none of the players can unilaterally improve his/her position (it depends on action of other players)

John Forbes Nash



basic scheme of the game:

coope-rate ♥ ? defect ♣

JÁ:

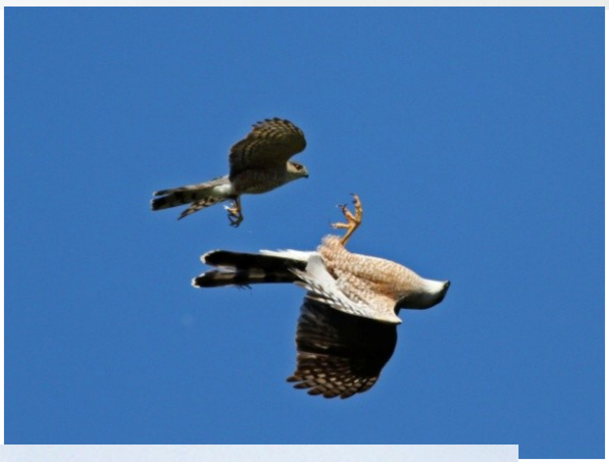
	C	B
C	300	-100
B	500	-10

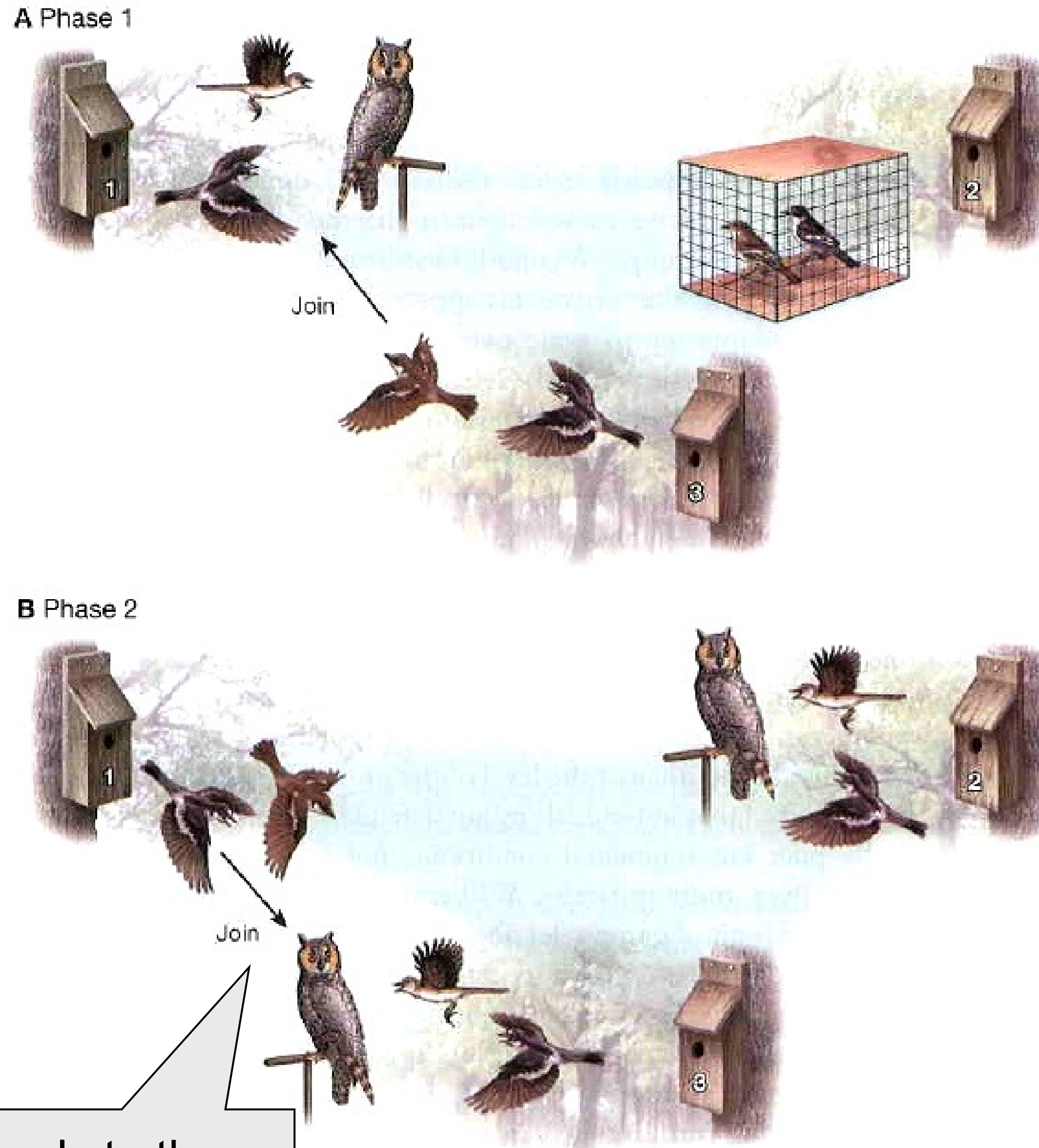
problem: we don´t know other player´s step

Conclusion: when we don´t know what other player does it is better to defect

In other words, in the Prisoner´s dilemma defect is the only Nash equilibrium

Eg.: bird mobbing





help only to those which helped previously

Robert Axelrod: in the 1970s and 1980s computer tournament

Robert Axelrod

14 programs = 13 strategies + 1 random (7 „bad“ strategies)

each game: 200 random encounters with other strategies including own strategy

225 independent games

points based on Prisoner´s dilemma: 5, 3, 1, 0 $\Rightarrow$ min. 0, max. 15 000 points

winner = Tit for Tat (TfT):
during first encounter cooperation, then repeating the step of a previous opponent

subsequently Tit for Two Tats (J. Maynard Smith): first two steps cooperation, then normal TfT $\rightarrow$ if it would be included in the original tournament it would win

R. Axelrod – 2nd tournament:

62 + 1 strategies, only 15 „good“
winner = again Tit for Tat
Why Tit for Two Tats did not win?

3rd tournament:
same strategies as in 2nd tournament
instead of points increasing/decreasing of the number of program copies (simulation of evolution)
always victory of „good“ strategies, in 5 of 6 games TfT

Caution! Tit for Tat is not ESS! (possible coexistence with other strategies, eg. Tit for Two Tats)

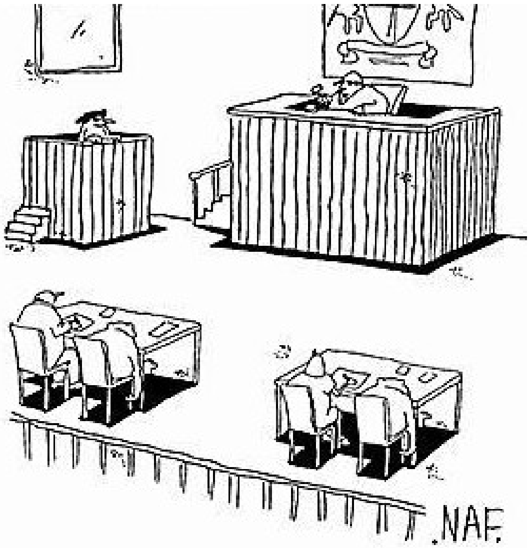
„Good“ strategies must be at a certain critical frequency:

random drift

relativeness

viscosity

Computer simulations and existence of altruism in nature itself seem to be in contradiction both to results of Prisoner´s dilemma and psychological practice



"I've considered all the evidence and I'm awarding custody of Tarzan to the female ape."

Non-zero-sum games

zero-sum game:

eg. football matches (but not always – see R. Dawkins: Premier League 1977)

non-zero-sum game:

divorce

common vampire bat (*Desmodus rotundus*)

Desmodus rotundus

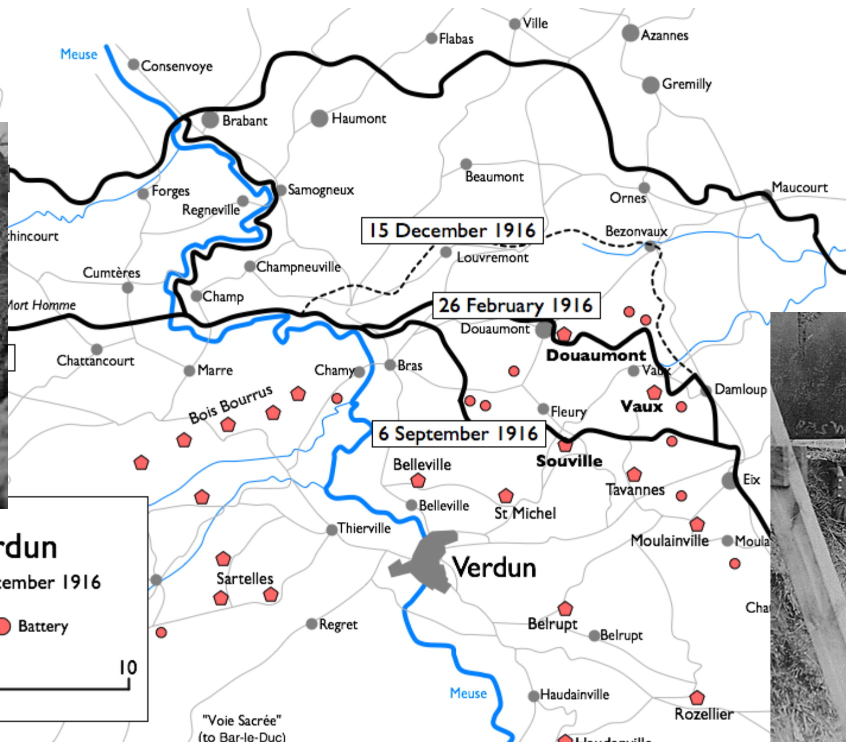
Time perspective

Axelrod´s tournament: repeating games = repeated Prisoner´s Dilemma

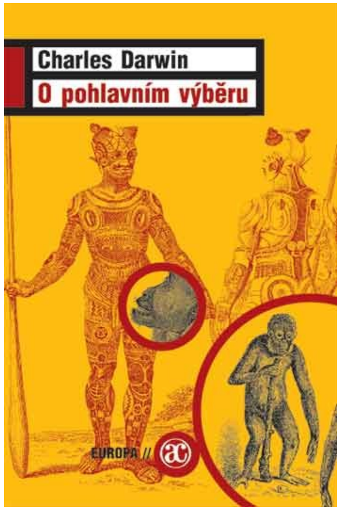
we don´t know end of the game ⇒ cooperation

we know end of the game ⇒ defection

Eg.: World War I – strategy „Live-and-let-live strategy“

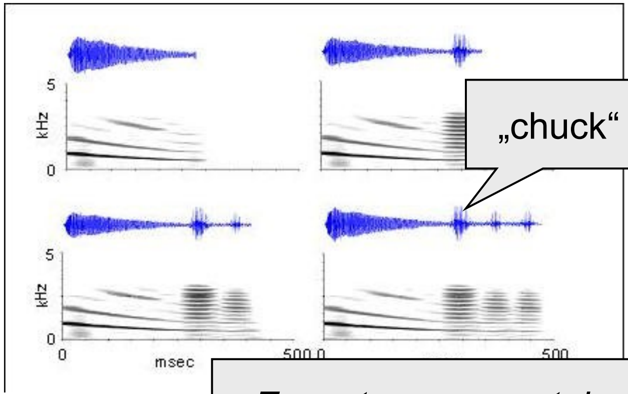


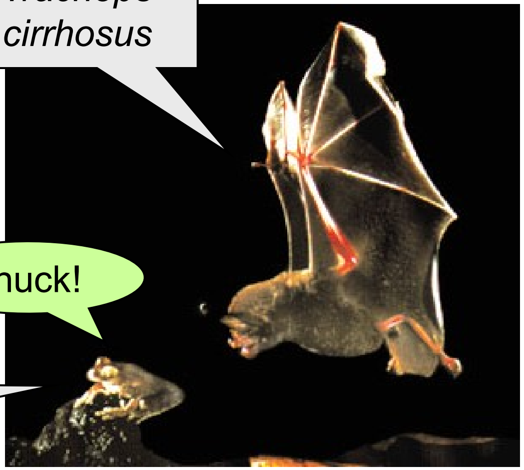
SEXUAL SELECTION



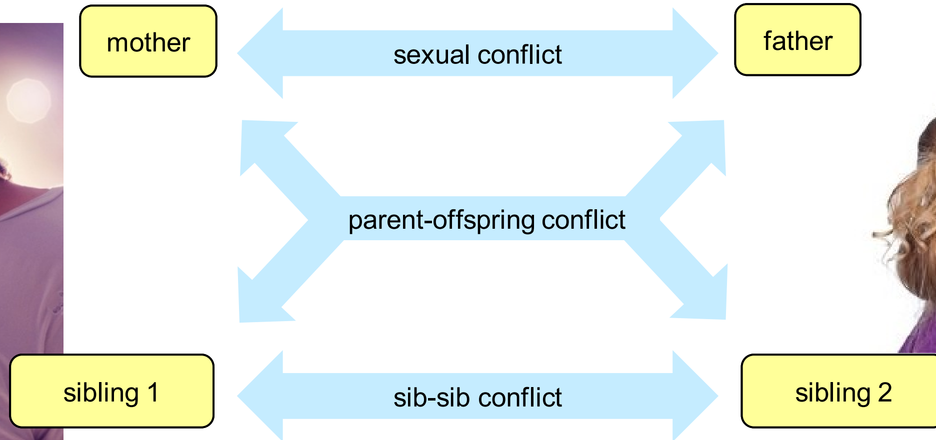
Why are males so conspicuous?

Darwin (1871): sexual selection





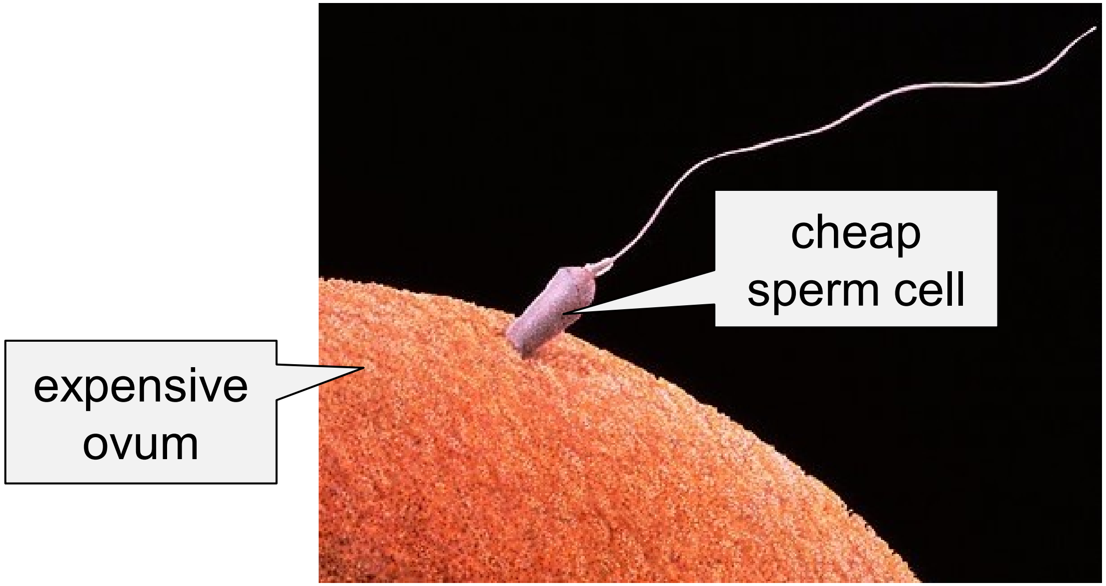
Sexual reproduction → cooperation but also conflict between individuals of the same sex as well as between sexes



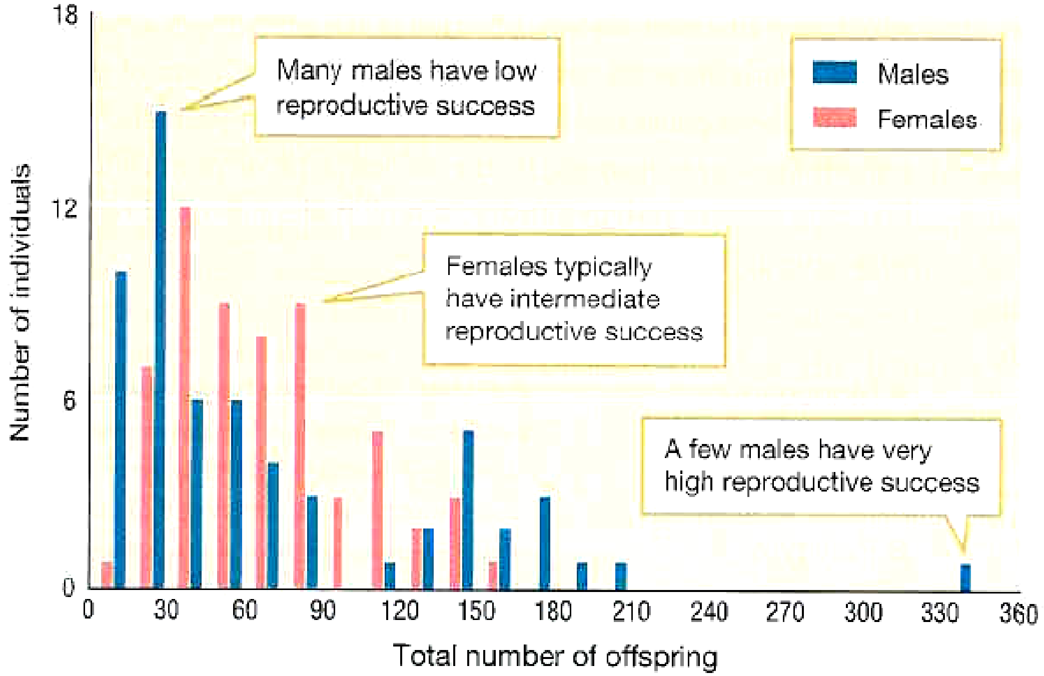
If the partners are not relatives none of them is interested in survival or reproductive success of the other!!

Primary cause of sexual selection = different parental investments

cheap sperm × expensive eggs



operational sex ratio = number of reproducing males and females → male-biased because males copulate more often ⇒ males limited by number of females, females limited by number of eggs or offspring ⇒ conflict of reproductive interests (Trivers 1972) range of reproductive success in males almost always higher than in females



Conclusion: sexes differ in reproductive behaviour:

males are (mostly) competitive
females are (mostly) choosy

Strength of sexual selection is not the same in various species:

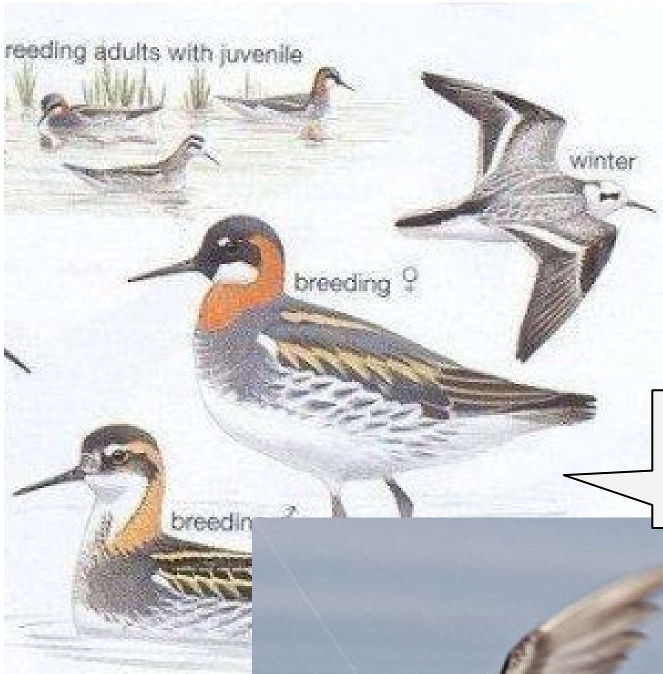
monogamous species: weak selection, no or moderate dimorphism

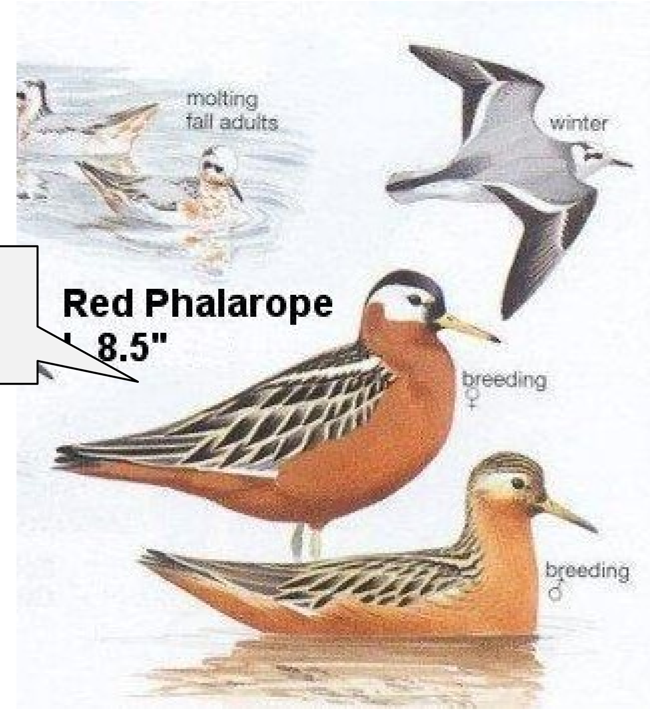
polygamous species: strong selection, <u>strong dimorphism</u>

- polygyny ♀♀♂
- polyandry ♀♂♂
- promiscuity / polygynandry ♀♀♂♂

… what about humans?

Sometimes females brighter, eg. phalaropes:





red phalarope

red-necked phalarope

Intrasexual selection

Males compete – directly ...

direct combat

Males compete – directly ...

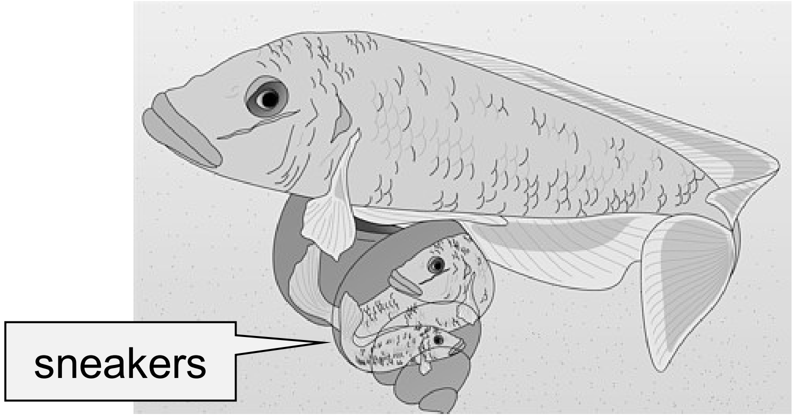
displaying

eg. mating calls, leks
manakin dances
bowers of bowerbirds etc.

Alternative strategies:

marine iguana: fast transmission of sperm during short copulation of subordinate males

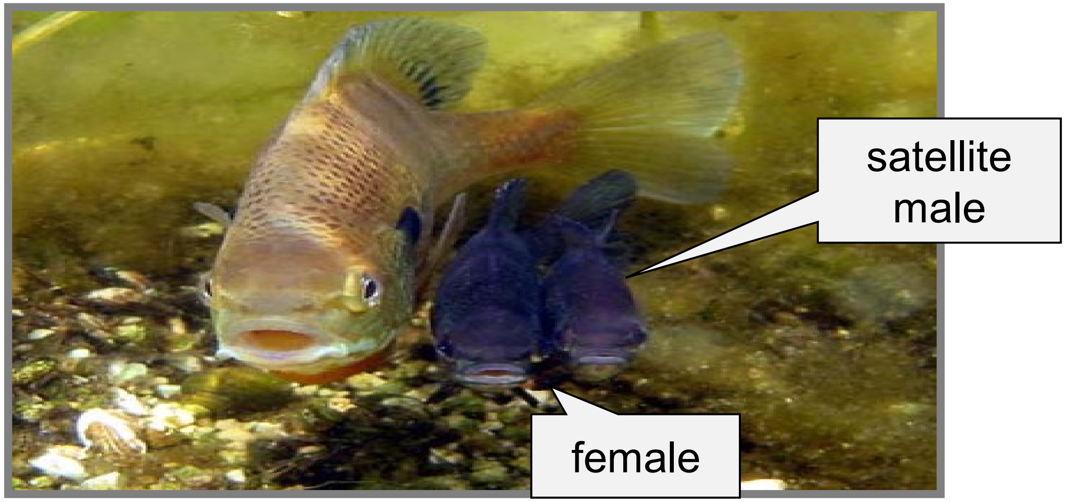
non-territorial males – „stealing“ of copulations („sneakers“): *Uta stansburiana*, salmons, sunfish, cichlids, bitterling



Lamprologus callipterus (Lake Tanganyika)

bitterling

often mimicking females (smaller size, colouration): cichlids, salmons



bluegill *Lepomis macrochirus*
(North America)

consequences of existence of non-territorial males:

for territorial (dominant) males negative

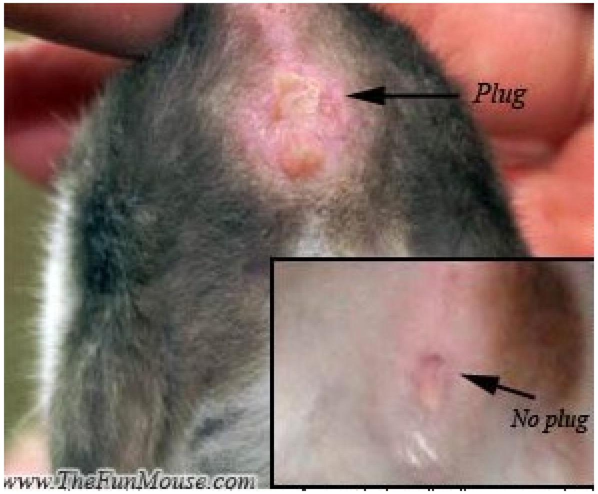
for females negative (reduction of offspring fitness), ambivalent but also positive (increased number of fertilized eggs, variation of offspring, and genetic compatibility)

… and indirectly

prevention of fertilisation by other males

guarding of female

copulatory plugs (rodents, insects, scorpions)



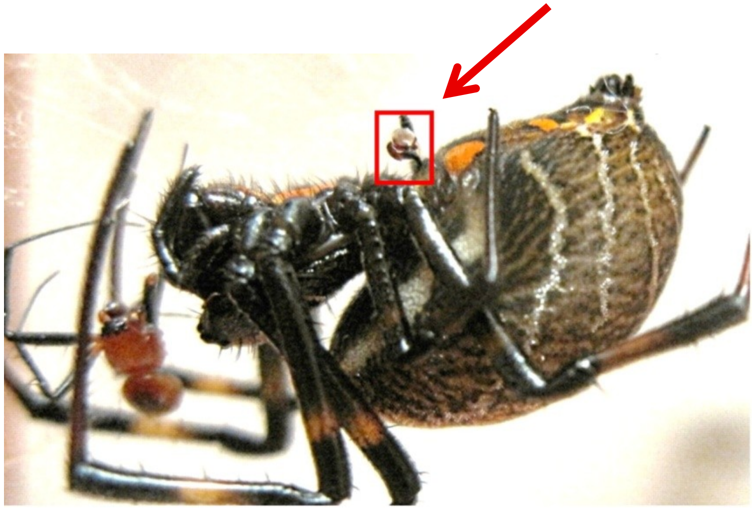
Vaejovis punctatus

… and indirectly

prevention of fertilisation by other males

breaking of copulatory organ in female´s duct (spiders):

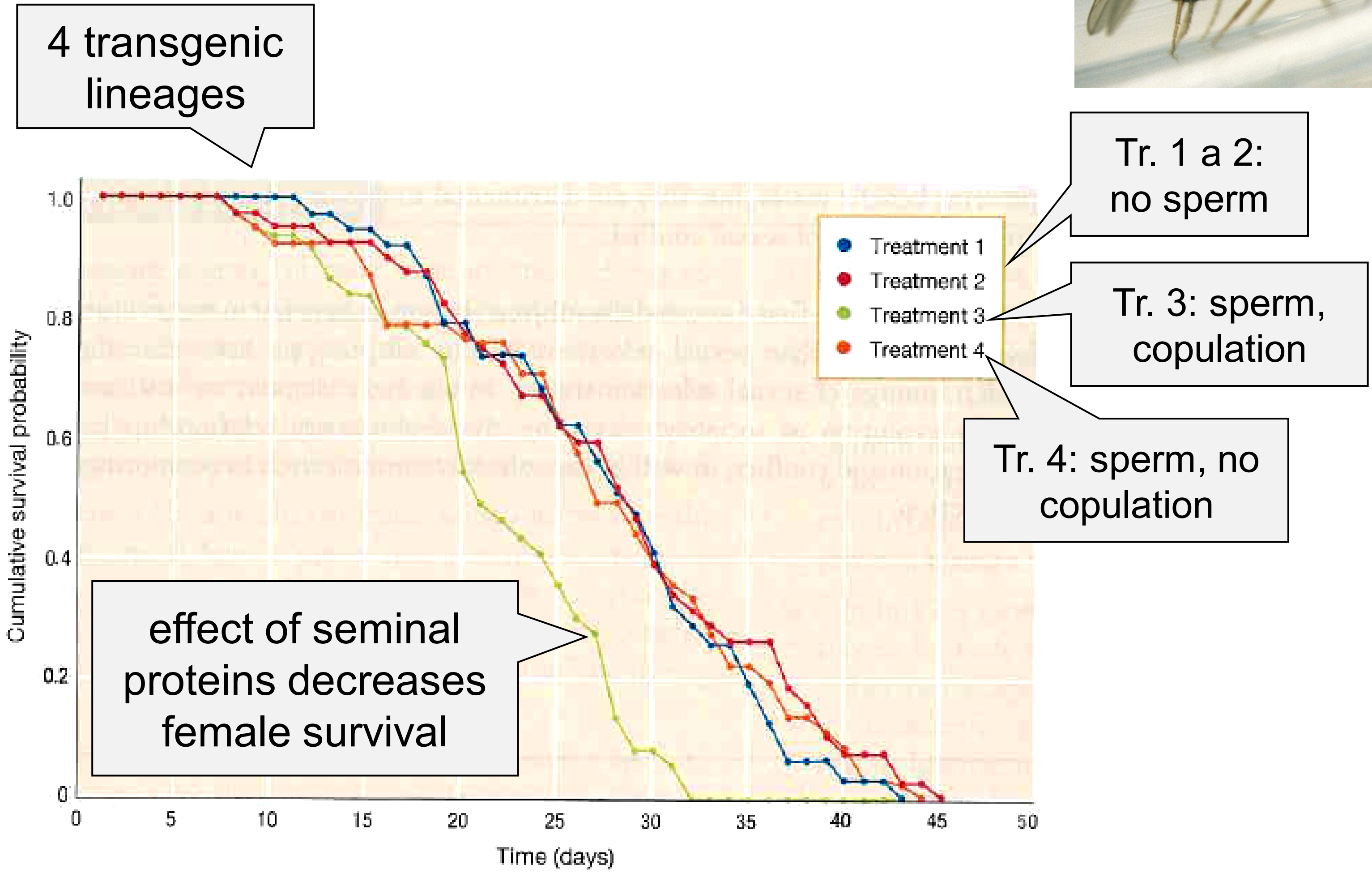
eg. spider *Tidarren argo* breaks off one of his pedipalps, adhers to female´s epigyne ~ 4 h



Nephilengys malabarensis

chemical repelents in sperm (*Drosophila*, snakes)

Drosophila: proteins of accessory glands in sperm → increase of egg production, plug, repellent effects



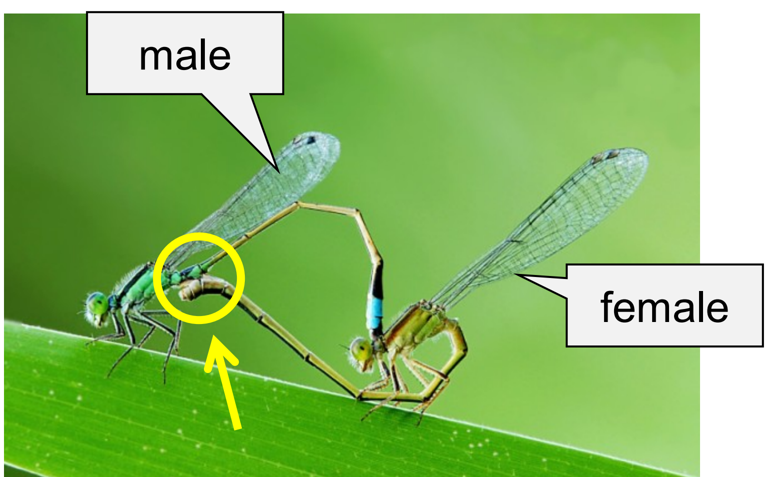
conflict between reproductive interests of males and females!!

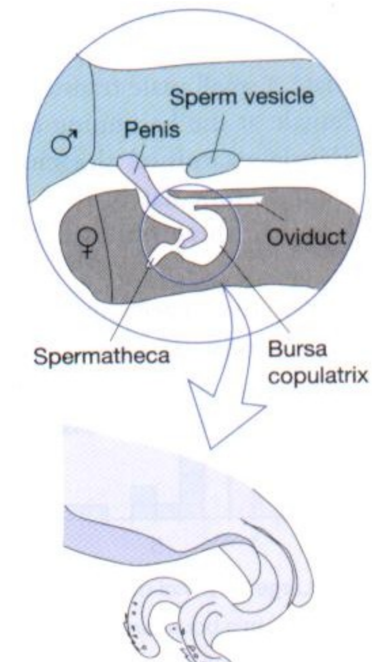
… and indirectly

prevention of fertilisation by other males

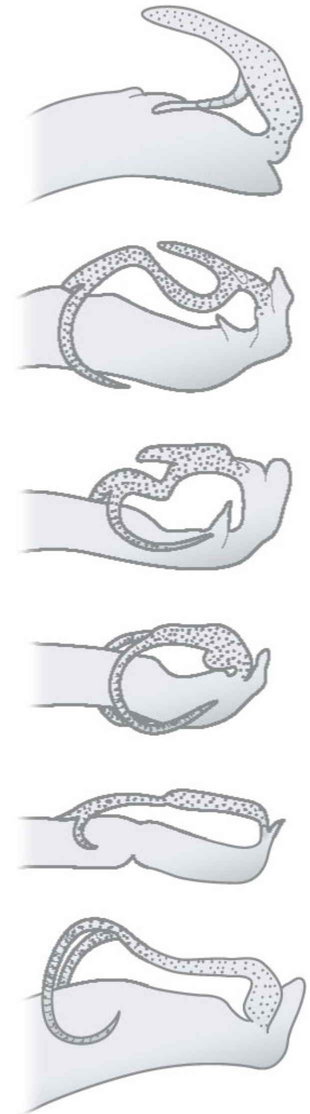
prolonged coupling after copulation (canids)

removing sperm of preceding male(s)





copulatorz organ of *Argia* damseflies:



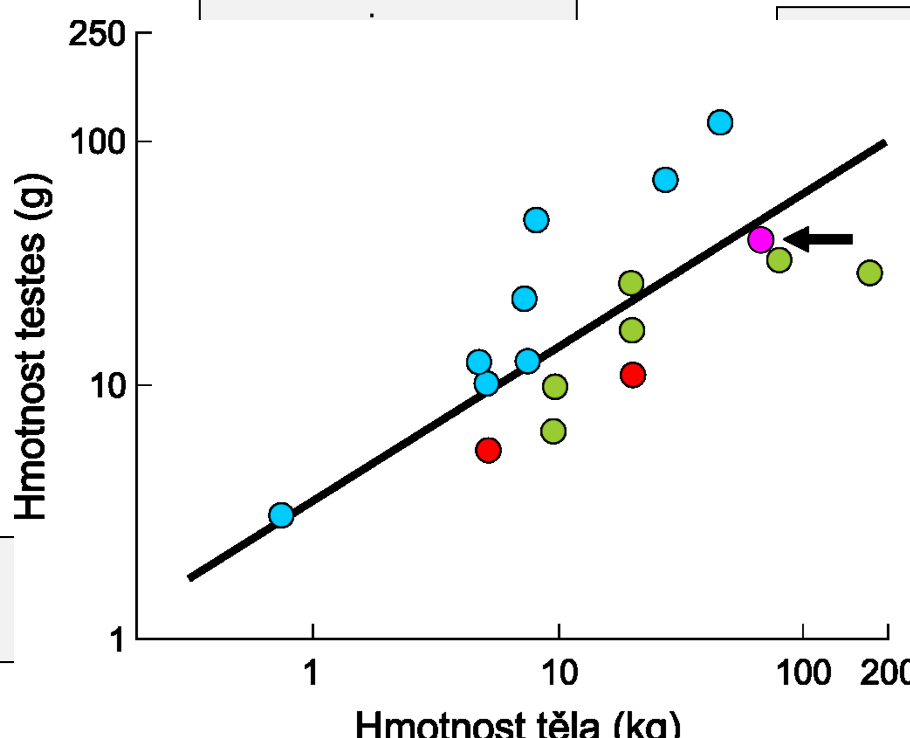
… and indirectly

sperm competition

prolonged intercourse

larger ejaculate → larger testes:

chimp > human > gorilla > gibbon



polygynous primates (green)

monogamous primates (red)

… and indirectly

infanticide

killing youngsters: felids (lion, domestic cat)

rodents (mouse, brown rat, lemmings, hamsters, meadow vole):

Bruce effect = abortion triggered by odour of unfamiliar male

although male benefit is clear it is <u>female</u> strategy – prevention of probable future infanticide (thwarted investment)

Intersexual selection

Females choose...

… but based on what?

1. direct benefit

male care for offspring:

larger territory ($\Rightarrow$ more sources)

bringing food

nest building

How to secure male care?

→ delaying copulation – „the Concord fallacy“

hiding eggs

3 possible male strategies:

„Daddy“ – remains with the female

„If not you, then other“ – escapes before copulation, looks for more permissive females

„Lad“ – escapes after copulation

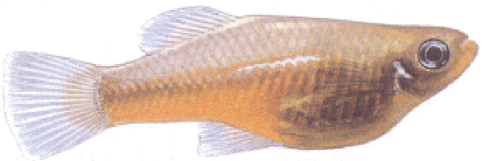
2. sensory bias

= preference occurs before emergence of the male trait
eg. stronger response to superstimuli

Eg.: swordtails of the genus *Xiphophorus*:
females of „non-sworded“ species prefer males with the „sword“

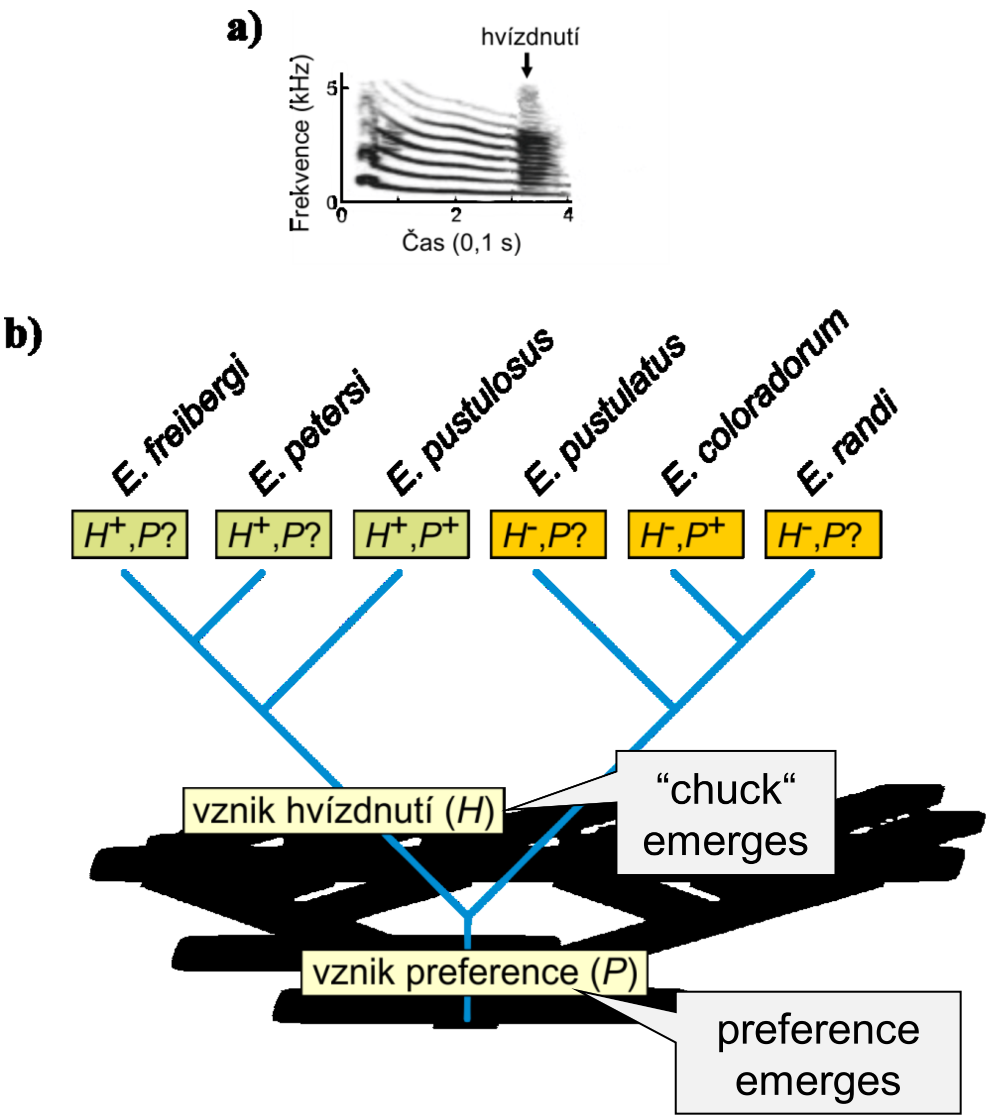
preference of females of the genus *Priapella* stronger than preference of own species´ females

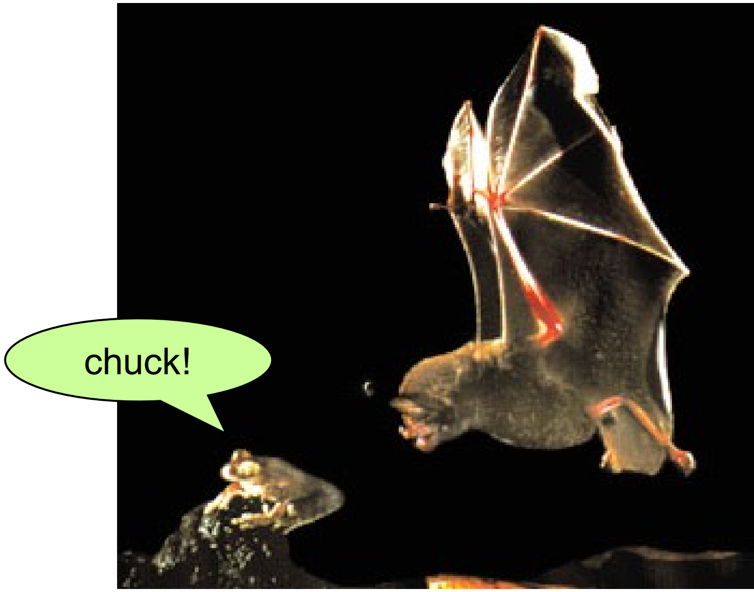
Xiphophorus helleri



Priapella intermedia

Eg. túngara frogs of the genus *Engystomops*:





3. indirect benefit

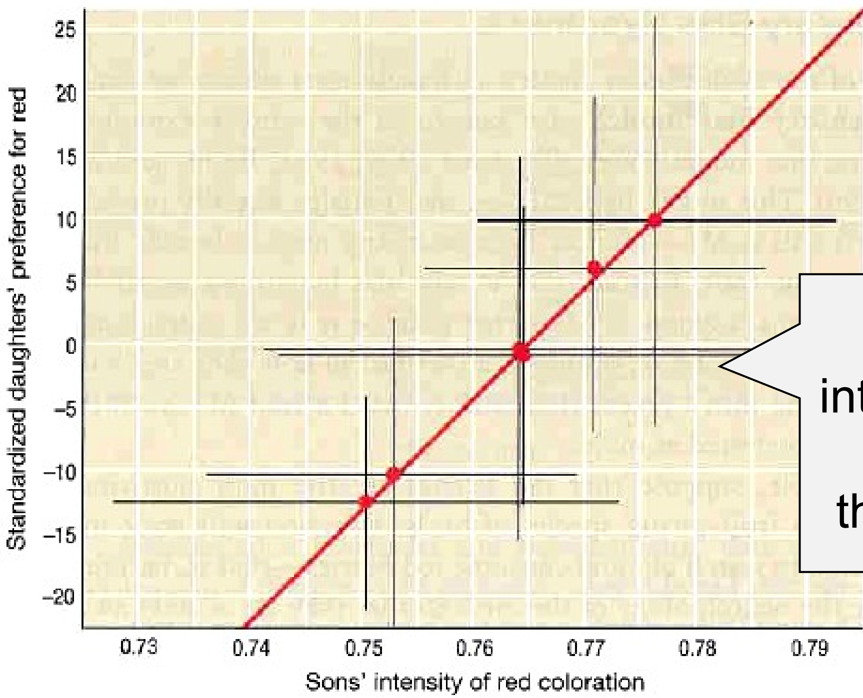
male investment = only genes contributed

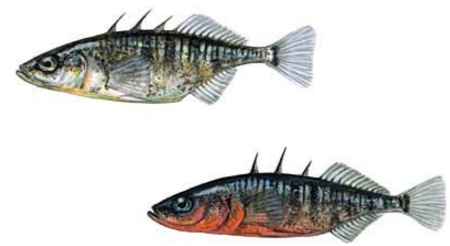
„sexy sons“ hypothesis: R. A. Fisher (1915, 1930):

runaway sexual selection

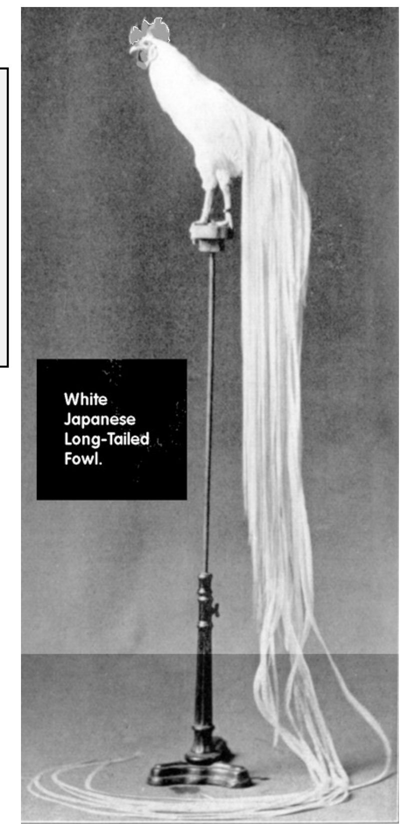
a male trait may not render a benefit to an individual but for some reason it is preferred by females ⇒ it is advantageous to produce offspring with such males (sons will be attractive for other females)

prerequisite = strong linkage between the gene for female preference and that for male trait (both genes in both sexes but different expression)





correlation between intensity of red colour and preference for red in three-spined stickleback



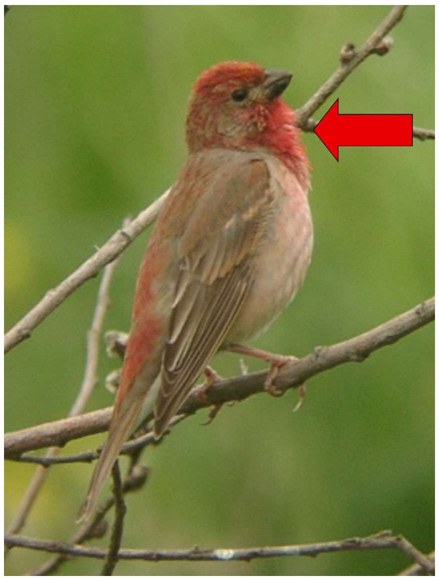
„snowball effect“ – runaway process ⇒ origin of extraggerated or eccentric structures

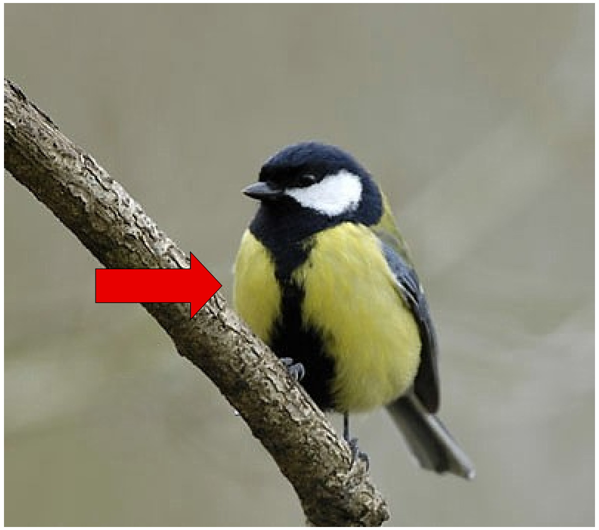
this process ends when ekvilibrium between female selection and normal (environmental) selection

„good genes“ hypothesis:

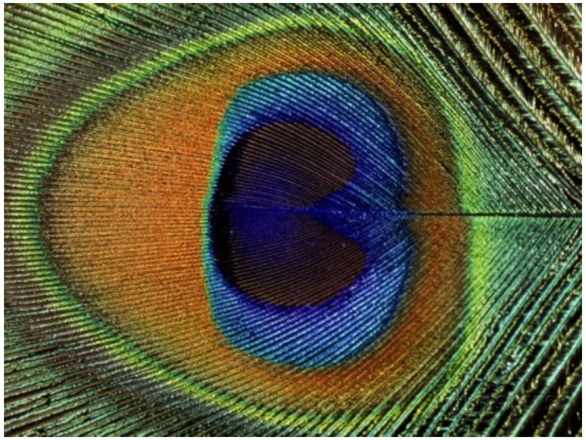
preferred trait indicates high genetic quality of the offspring

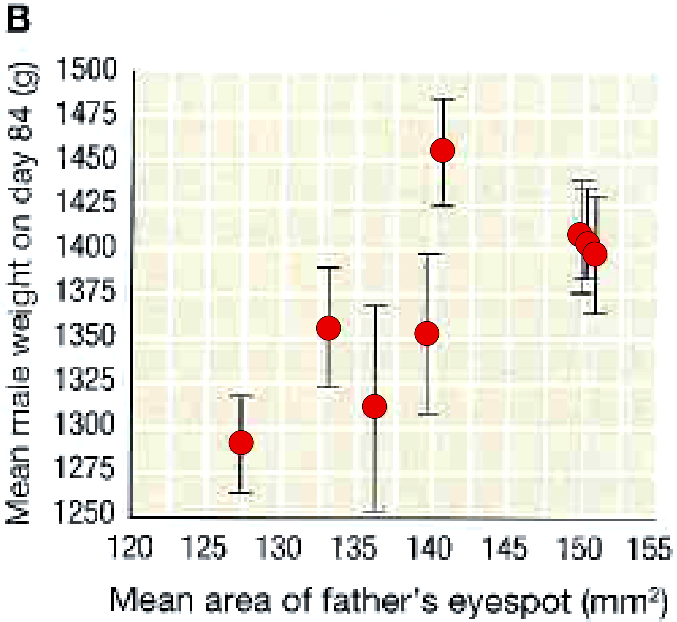
Eg.: three-spined stickleback, great tit, scarlet rosefinch, barn swallow

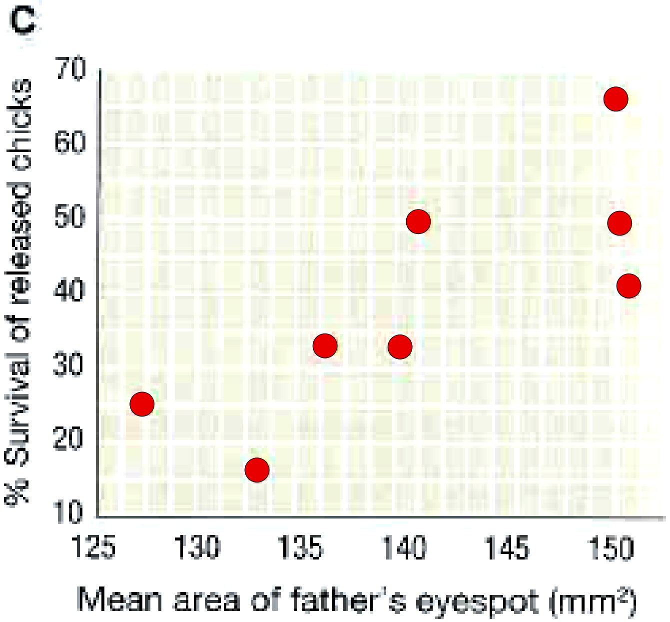




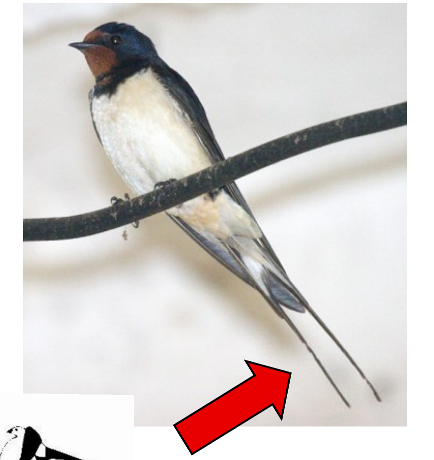
peacock (*Pavo cristatus*): correlation between size and number of „eyes“ and fitness of descendants

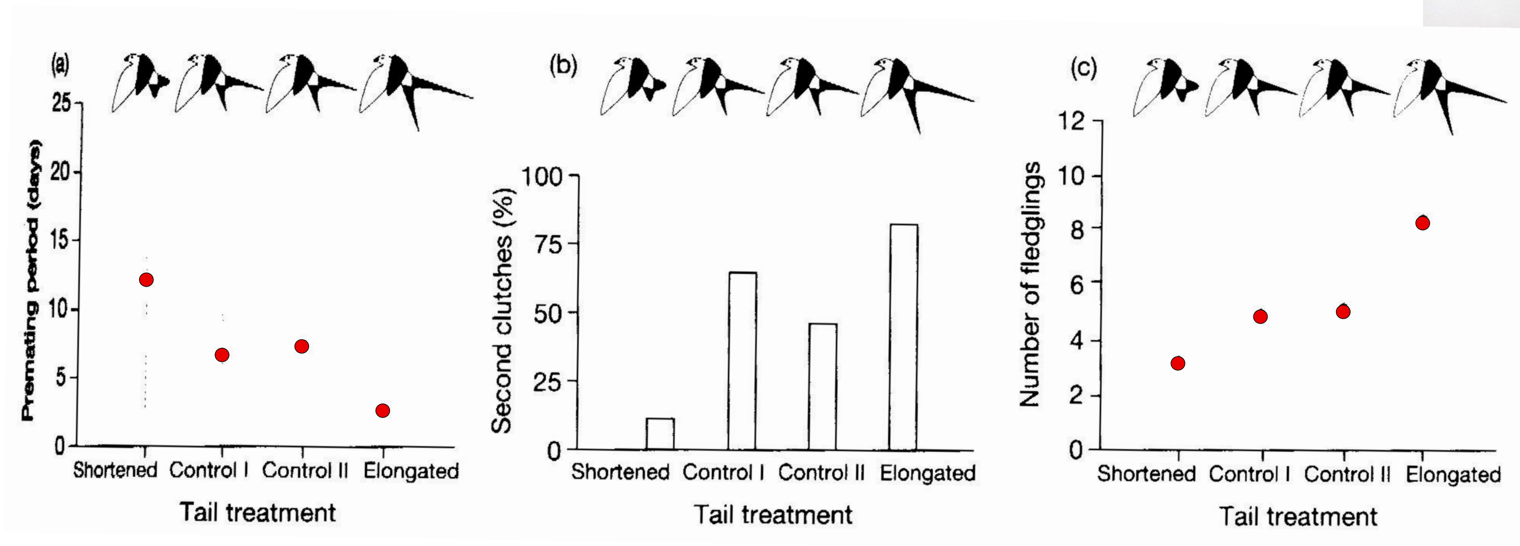






Anders Pape Møller: barn swallow (*Hirundo rustica*)





shorter pre-copulatory phase

more second egg-laying

more offspring

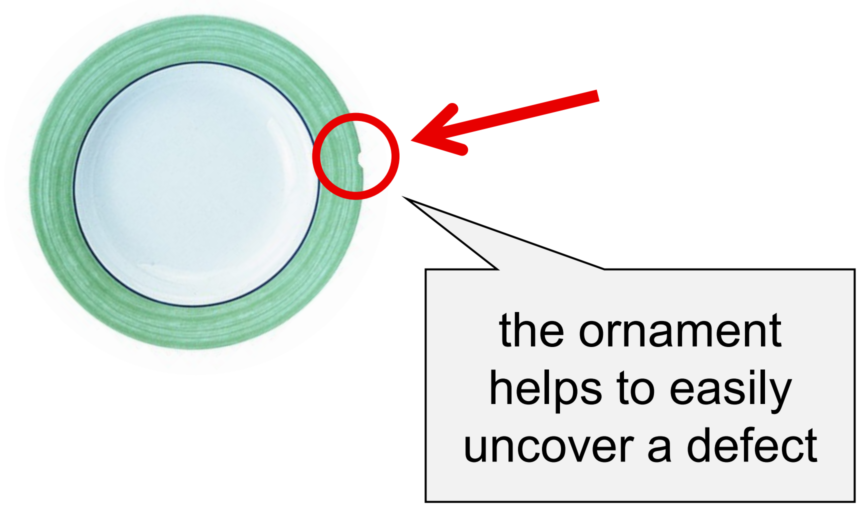
handicap principle:

Amotz Zahavi (1975)

indication of high viability („good genes“) despite the handicap

handicap necessary for the information to be reliable, ie. to prevent the male from “lying“

Amotz Zahavi



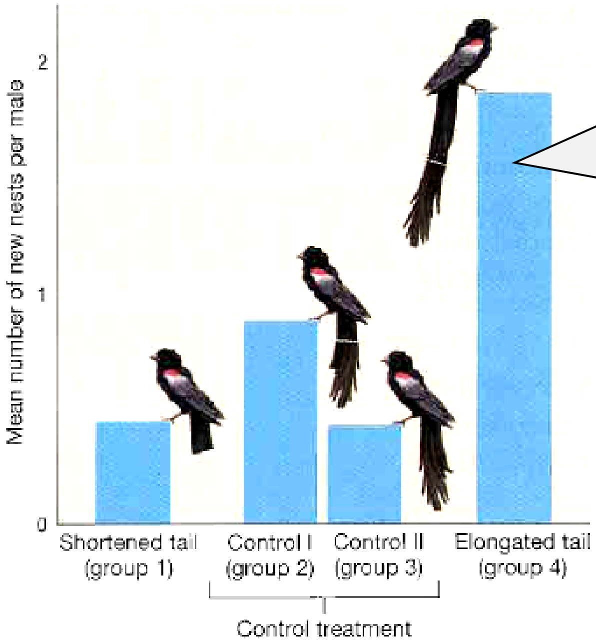
Arabian babbler (*Turdoides squamiceps*)

handicap model:

bright coloration, complex ornaments, structures filled with blood, toxic nature of chemical signals etc.

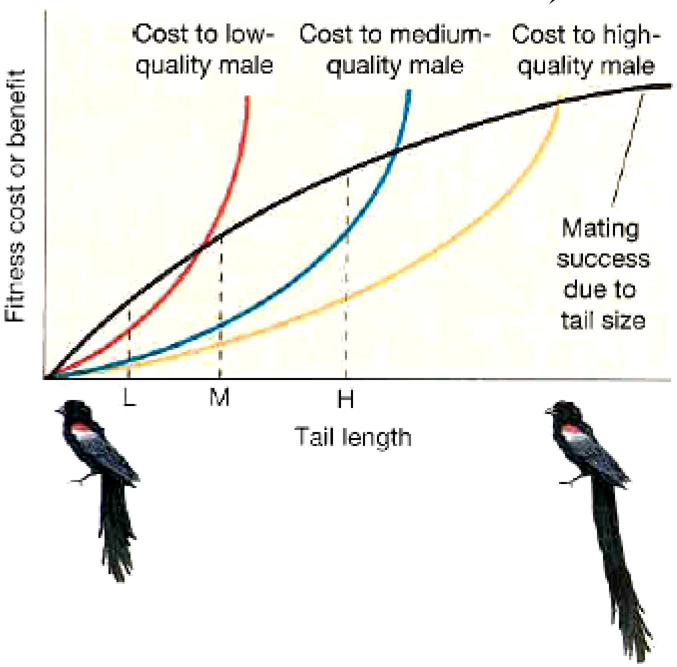
waterbuck
(*Kobus ellipsiprymnus*)

Malte Andersson: long-tailed widowbird (*Euplectes progne*)



highest reproductive success in males with elongated tail feathers

relatively lower costs for genetically high-quality males



increasing fitness

handicap model – bright males hypothesis

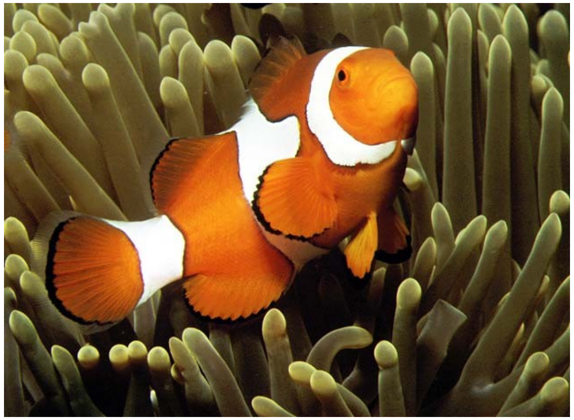
William Hamilton and Marlene Zuk (1982):

problem of repeated preference of certain trait → depletion of variation
= the “lek paradox“

a solution can be variation of a selective optimum – eg. pathogens

sexual selection favours “fairly“ signalizing traits
state of health, ie. the ability to cope with parasites and pathogens

animals with “bad genes“ cannot effectively struggle with infection

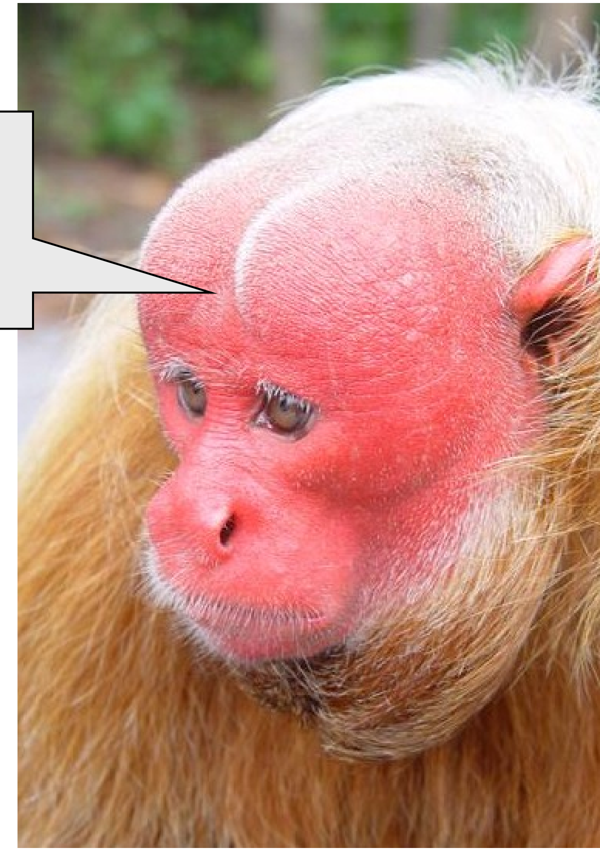


hypothesis: males of more parasitized species are, in general, brighter

→ some passerine species

Eg.: bald uakari (*Cacajao calvus*)

in healthy individuals red colour



in individuals with malaria pale colour

in species from non-malarial areas dark coloration

Extra-pair copulations, EPC
(extra-pair paternity, EPP; extra-pair fertilization, EPF)

males: increase number of fertilized eggs

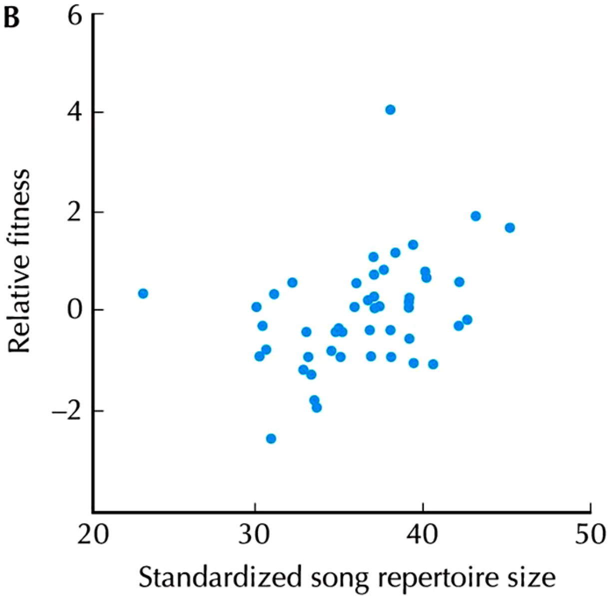
females: increase quality of offspring by mating with males possessing better genes than their partners $\Rightarrow$ increase of offspring fitness

Eg.: great reed warbler: span of song repertoire correlated with fitness

→ in all observed EPPs biological fathers had broader song repertoire than partners

⇒ indirect benefit of females through higher fitness of descendants

great reed warbler
(*Acrocephalus arundinaceus*)



acquiring good or complementary genes?

EPC in humans:

Univ. of Western Australia: 28% males, 22% females – extramarital sex

France, Great Britain, USA: 5–52%

EPP: difficult estimate, overal ~2 %, Yanomami ~10 %, Himba (Namibia) ~17 %

ethnic differences: eg. Michigan: 1,4% in Caucasians, 10,1% in Afro-Americans

South-American Indians (eg. Mehinaku, Kaingang, Araweté, Curripaco, Tapirapé, Yanomami, Bari, Matis, Aché): partible paternity

Canelo (central Brazil): generally more than 12 potential fathers
60% males transiently in polyandric bonds

copulation with multiple males is often part of public ritual

intersexual differences in jealousy:

males: physical cuckoldry (risk of EPP)
females: spiritual affinity (risk of mate´s leaving)