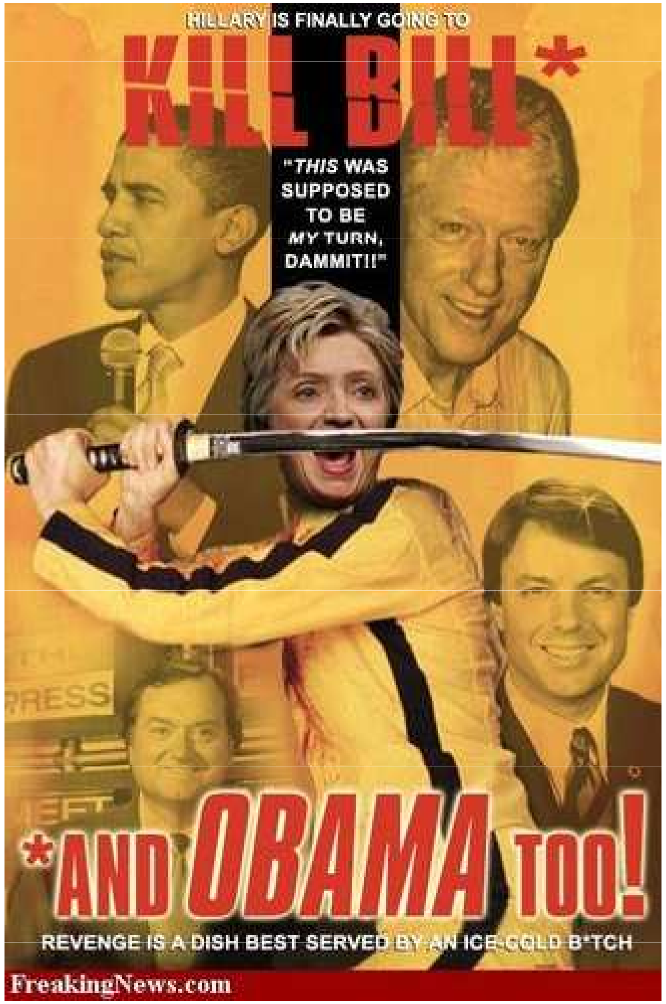
CONFLICT AND COOPERATION I.



natural selection essentially a competitive process ⇒

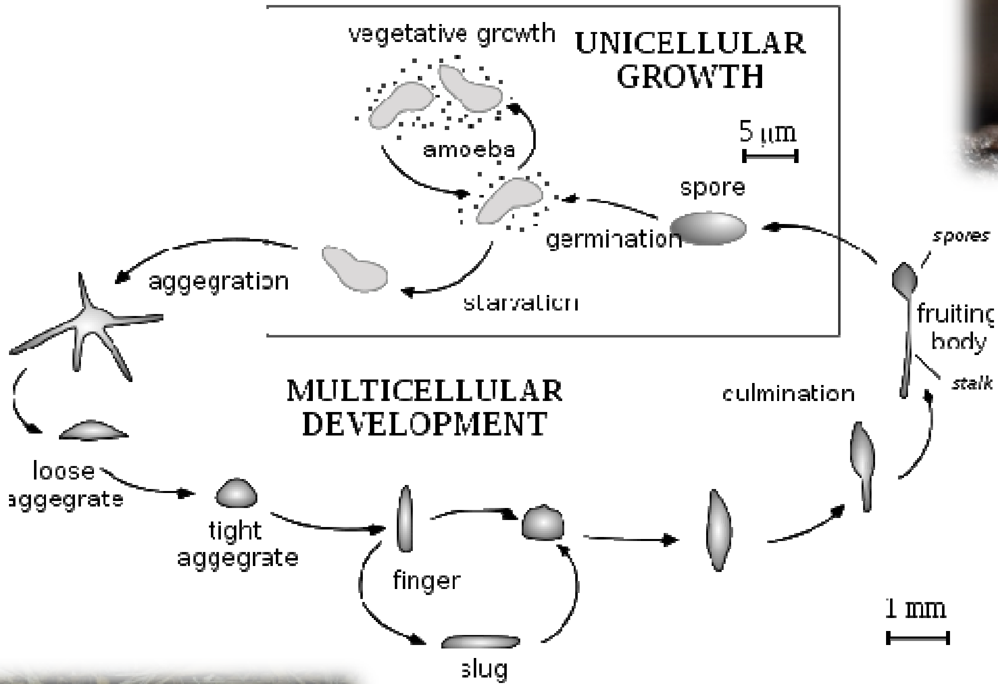
cooperation between organisms is one of nature´s most peculiar features

- social insects, humans
- mutualism






Eg.: slime molds



How can, in spite of conflict between organisms, cooperation evolve?

Charles Darwin: struggle for life

but also cooperation between a cow and her calf (cooperation between relatives))

Neodarwinism: evolution in populations, selection affects individuals

× till the 1960s, this assumption rather implicit (cf. Wright´s „interdemic selection“)

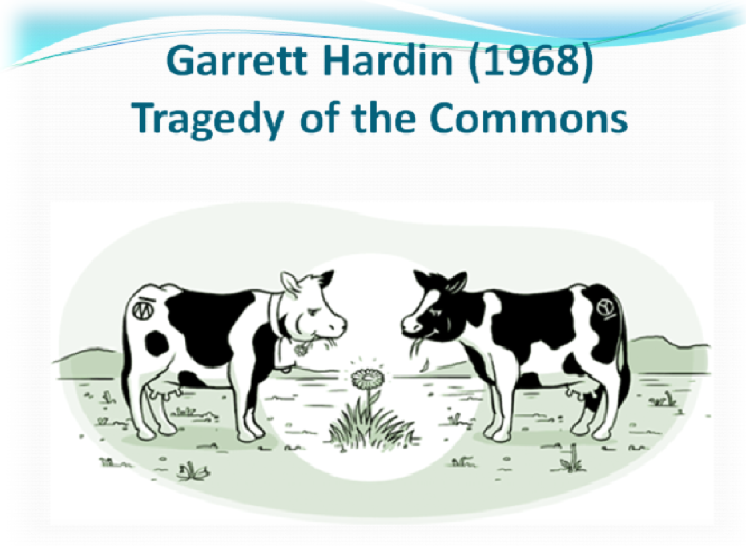
Darwin, Wallace, Konrad Lorenz etc.: „benefit of species“, „survival of species“....

William Forster Lloyd (1833) → Garrett Hardin (1968):

Tragedy of the commons

adding 1 sheep to the herd ⇒ direct benefit for the owner
× costs (drop of pasture) shared by the whole group

⇒ if people behave with respect to their benefit independently and rationally, eventually the sources are necessarilly depleted



Solution = voluntary restriction by herders →

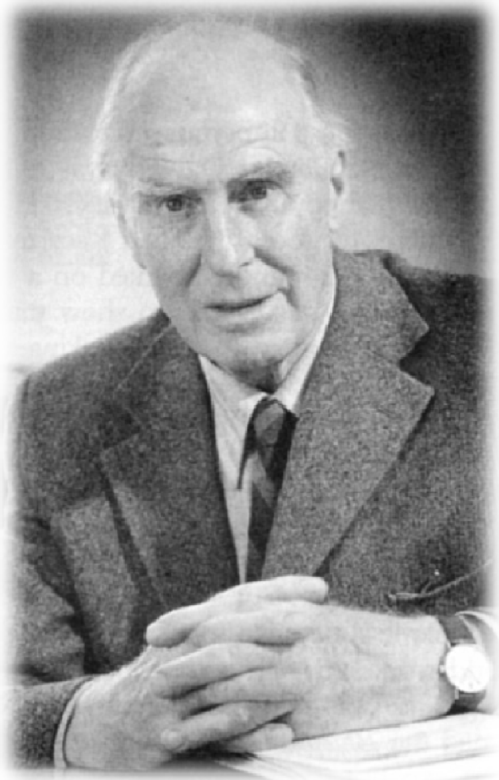
Why should such behaviour be favoured by selection?

1962 – Vero Copner Wynne-Edwards:

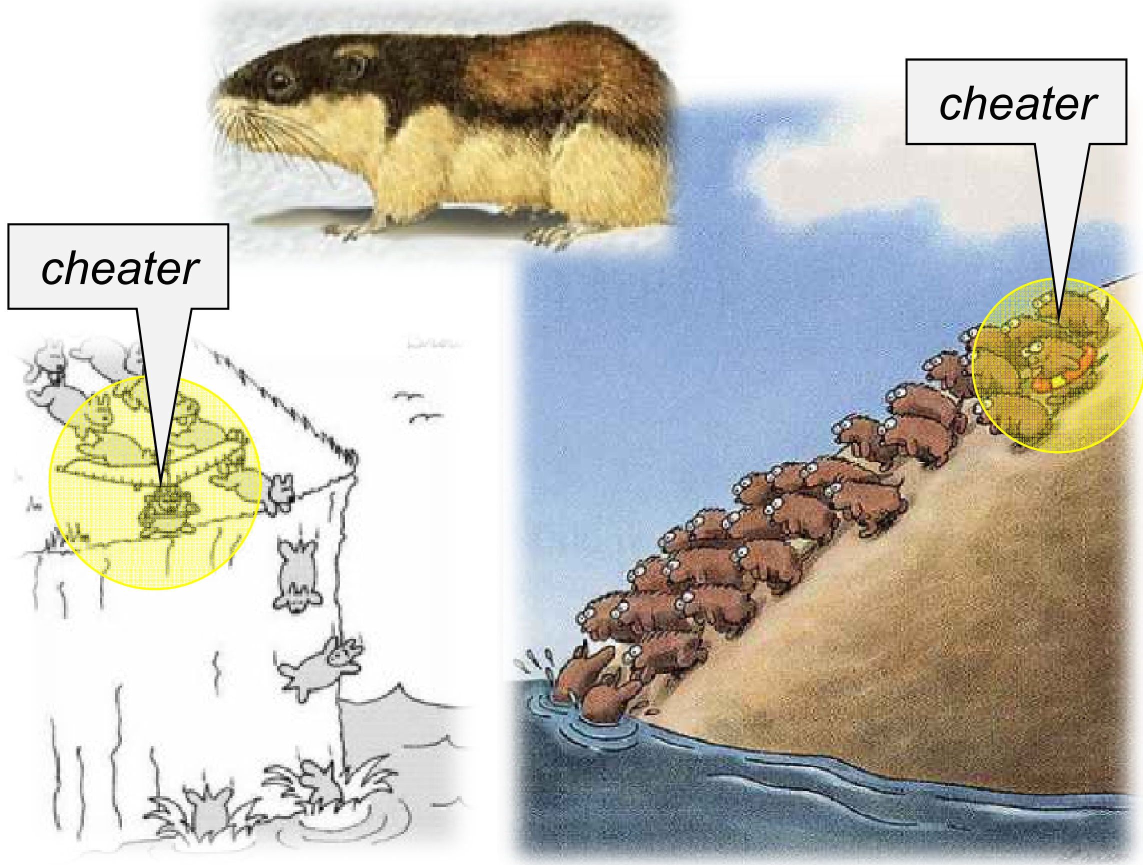
Animal Dispersion in Relation to Social Behaviour

flocking, dispersion, restriction of reproduction, altruism

cooperation explained as the selection of whole groups rather than individual selection (in extreme form „adaptation for species´ survival“)



V. C. Wynne-Edwards

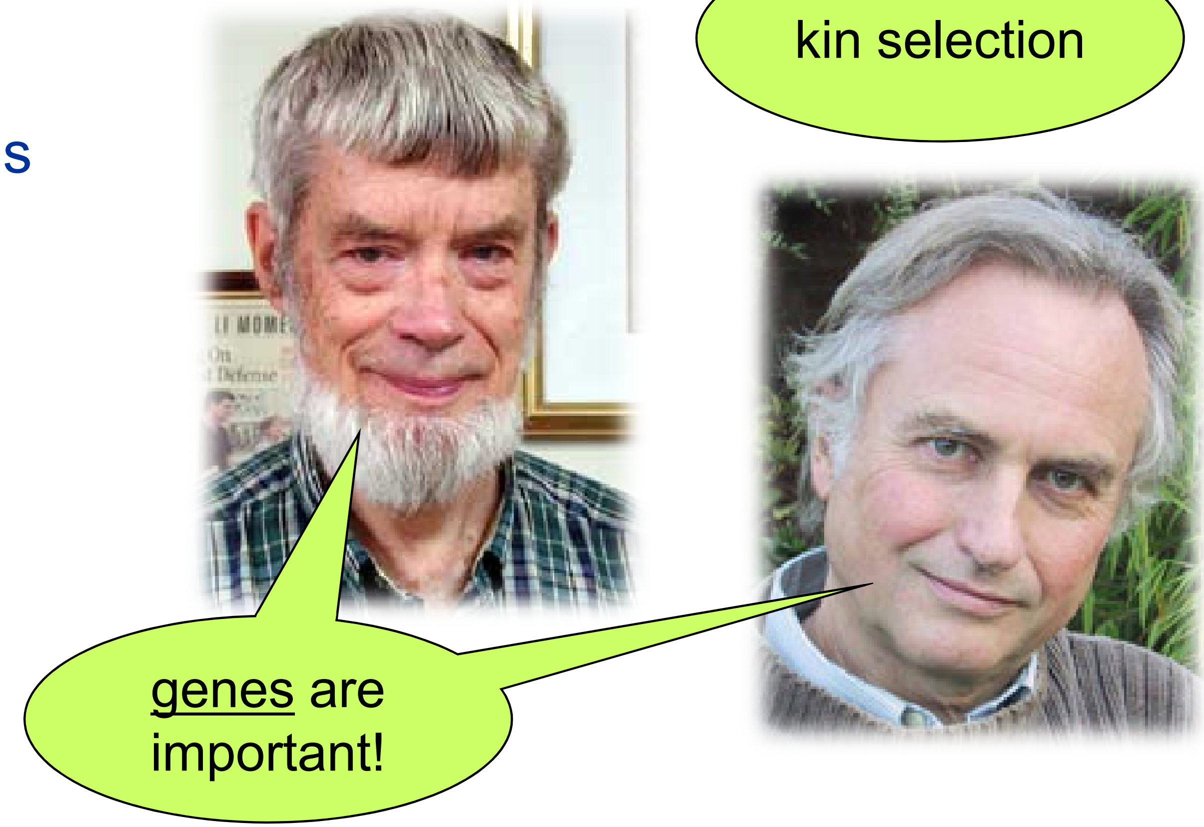


reaction:

1964: William D. Hamilton,
John Maynard Smith

1966: George C. Williams

1976: Richard Dawkins



GROUP SELECTION

V.C. Wynne-Edwards:

dispersion in order to avoid depletion of sources

production of fewer offspring than potentially possible

alarm calls, fish shoals

„stotting“

Thomson´s gazelle, springbok, mule deer, pronghorn etc.

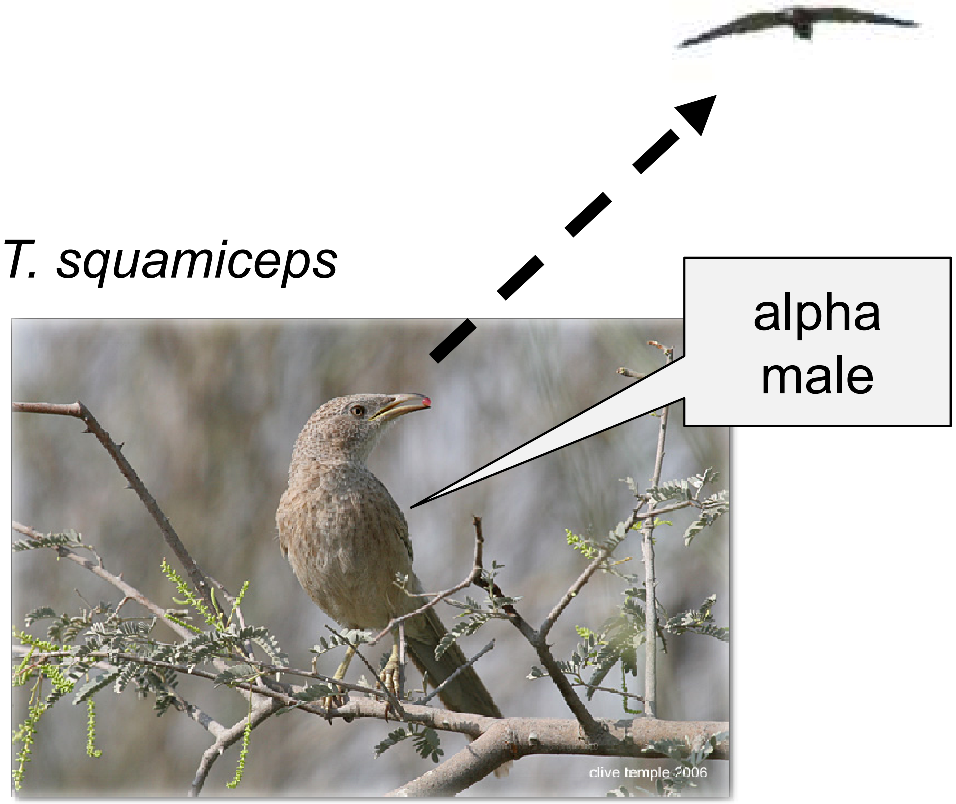
Individual advantage!

https://www.youtube.com/watch?v=jMIiB9DnRXg

guards of the Arabian babbler (*Turdoides squamiceps*)

and meerkats (*Suricata suricatta*)

T. squamiceps

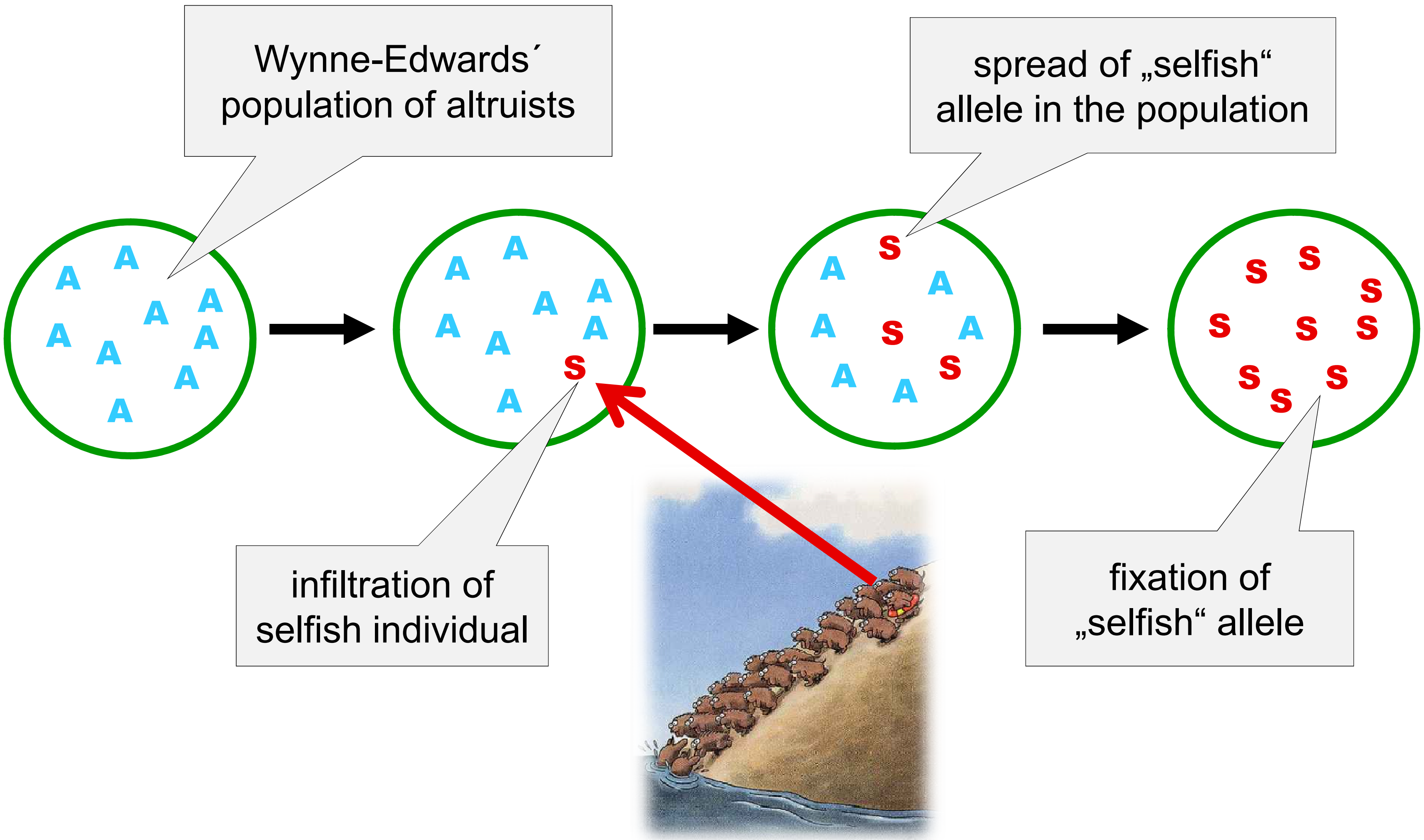


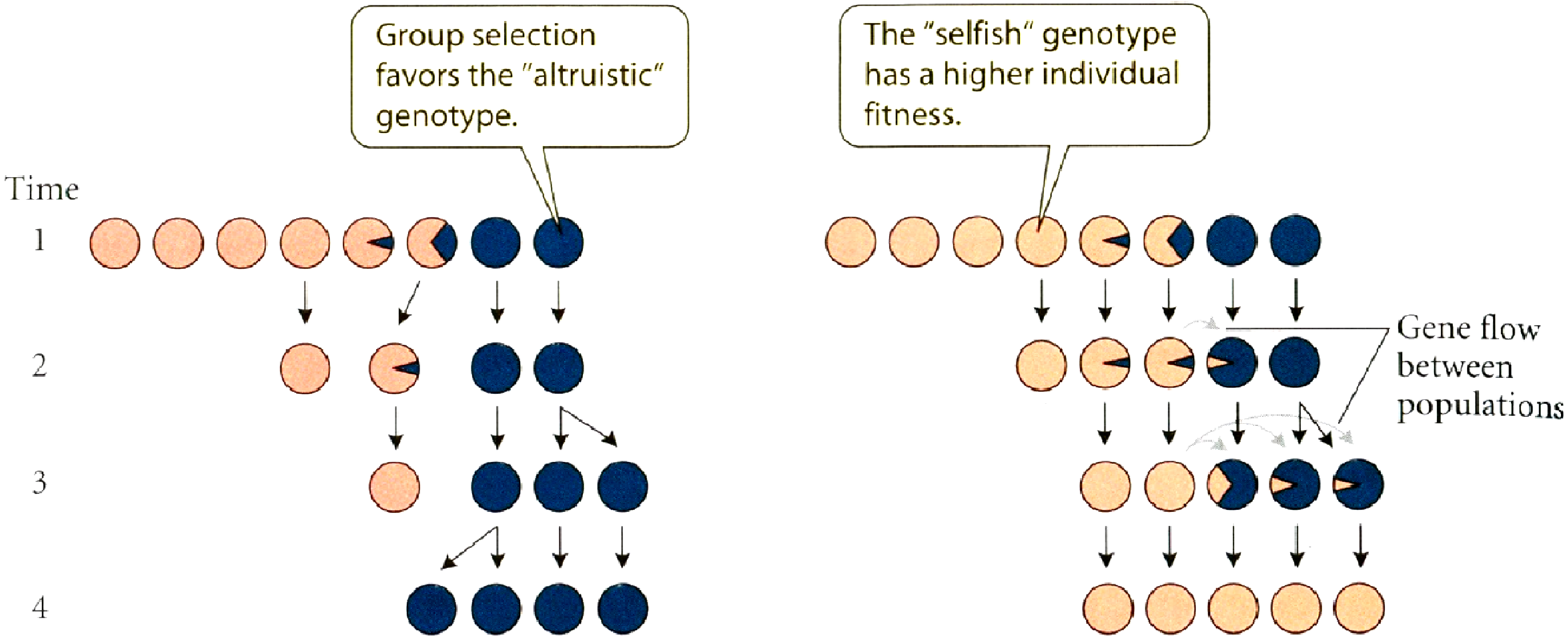
Suricata suricatta

Individual advantage!

Theoretical arguments against group selection:

altruism = behaviour increasing recipient´s fitness and, at the same time, decreasing donor´s fitness





Wynne-Edwards: Altruistic behavior will evolve because group selection favors it (i.e., more "selfish" populations go extinct.)

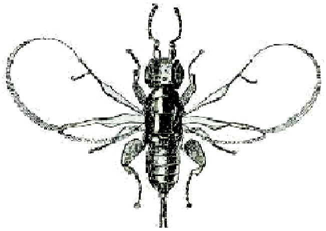
Williams: Within-population selection favors the "selfish" allele and increases it more rapidly than whole-population events, so the "selfish" allele will become fixed.

Low heritability and longer generation time of the group relative to heritability and generation time of individuals ⇒ changes at the individual level much faster

⇒ infiltration of selfish individuals, extinction of the altruistic population

Conditions for group selection:

rapid alternations of extinction and re-creation of demes

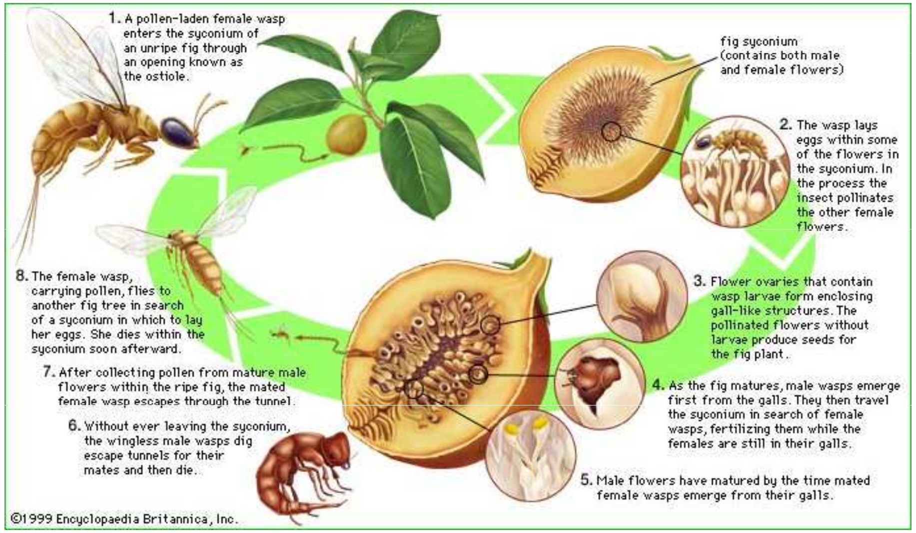


Eg.: fig wasps (Agaonidae)

virtually no migration:

c … cost for an individual

($b - c$) … benefit for the group

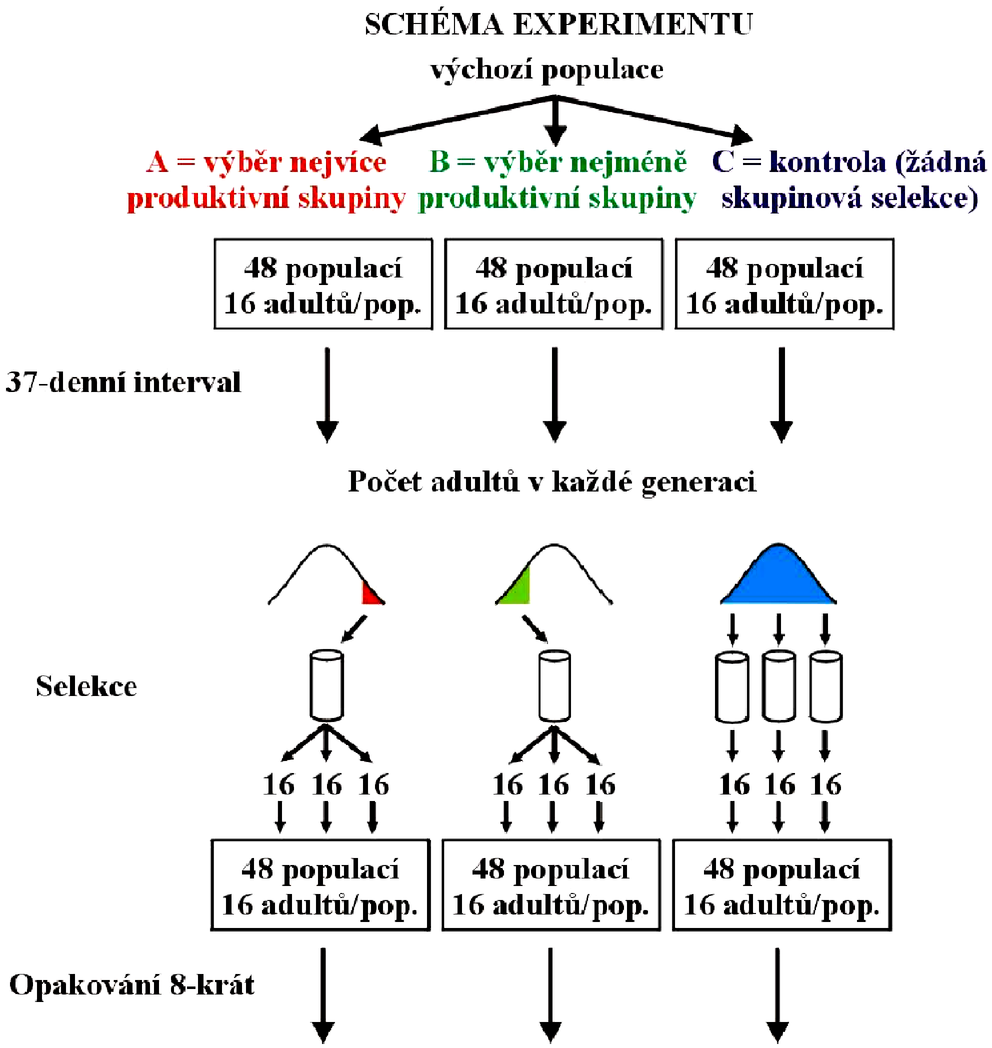


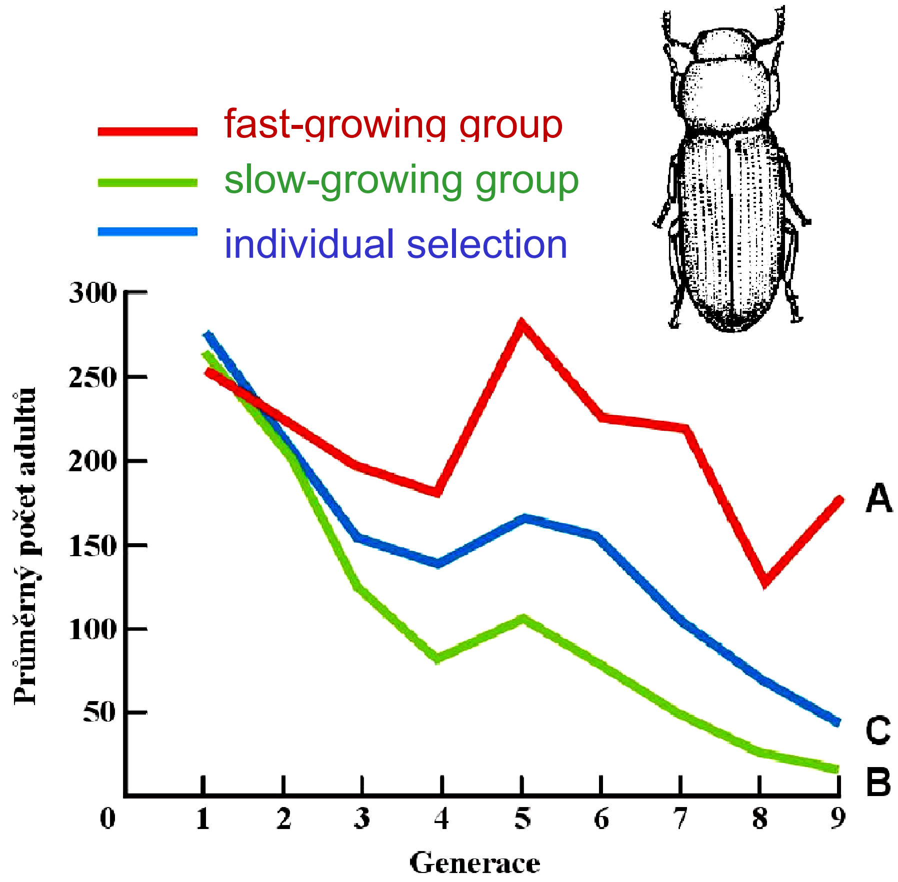
island model:

$$\frac{b - c}{c} > 2\,Nm$$

Conclusion: interdemic (group) selection will be stronger than intrademic (individual) selection only if the group benefit relative to the individual cost is higher than the average number of migrants per generation.

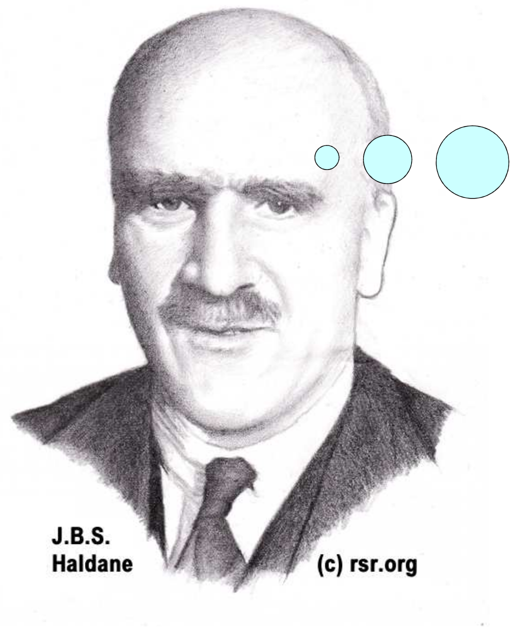
Michael Wade (1977): group selection experiment in the red flour beetle (*Tribolium castaneum*)





But in nature the role of group selection probably minimal

KIN SELECTION



If I rescued my two brothers from drowning in the river, it would be the same as to rescue myself!

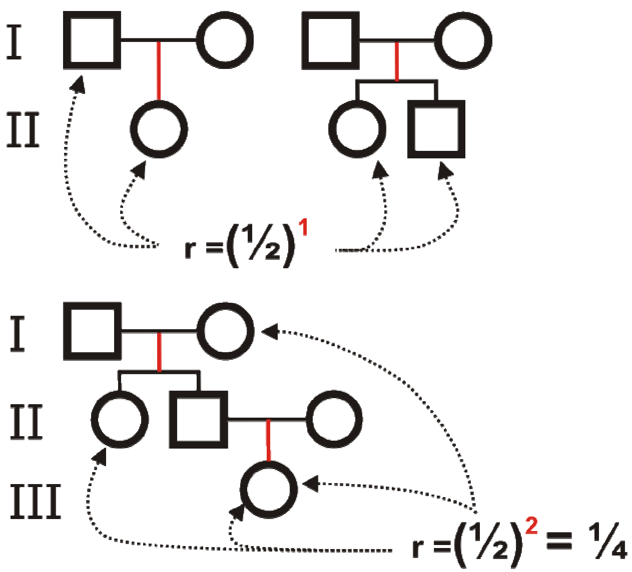
William Hamilton (1964):

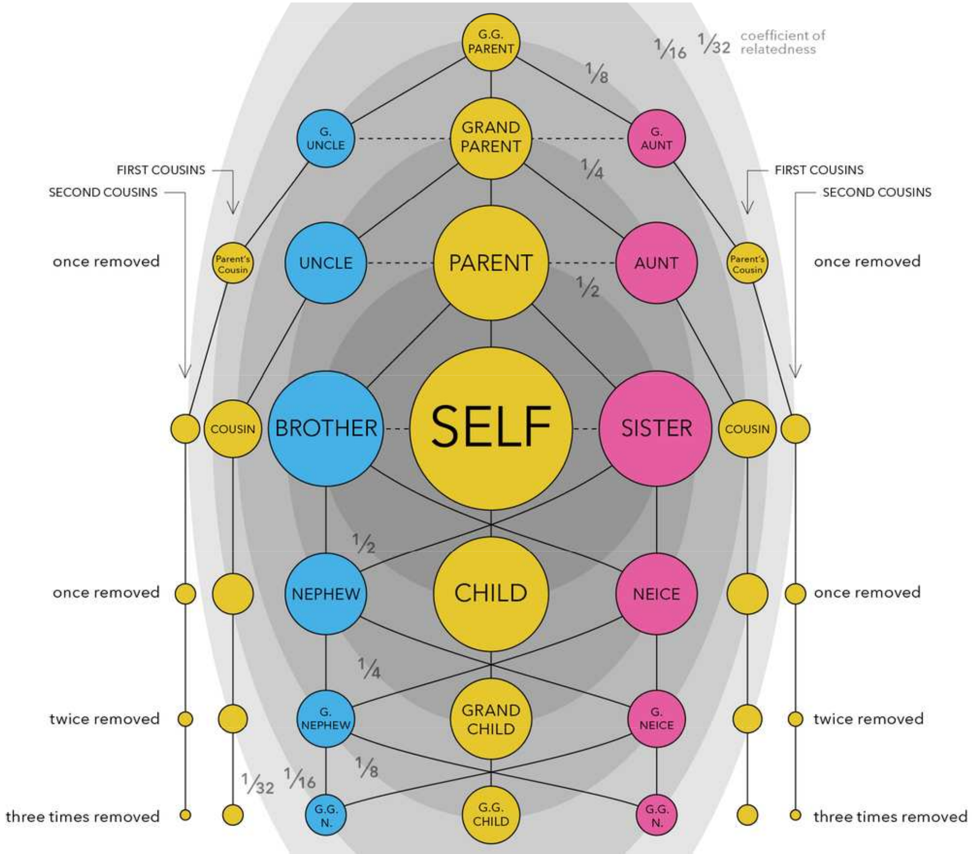
Hymenoptera: haplo-diploid system of sex determination:
females 2N, males N

⇒ relationship:
worker – worker = ¾
queen – descendants = ½
worker – drone = ¼

inclusive fitness = fitness of an individual and his/her relatives

altruism between relatives = kin altruism





coefficient of relationship:

Degree of relationship	Relationship	Coefficient of relationship (r)
0	identical twins; clones	100%[4]
1	parent-offspring[5]	50% (2^{-1})
2	full siblings	50% ($2^{-2}+2^{-2}$)
2	3/4 siblings or sibling-cousins	37.5% ($2^{-2}+2\cdot2^{-4}$)
2	grandparent-grandchild	25% (2^{-2})
2	half siblings	25% (2^{-2})
3	aunt/uncle-nephew/niece	25% ($2\cdot2^{-3}$)
4	double first cousins	25% ($2^{-3}+2^{-3}$)
3	great grandparent-great grandchild	12.5% (2^{-3})
4	first cousins	12.5% ($2\cdot2^{-4}$)
6	quadruple second cousins	12.5% ($8\cdot2^{-6}$)
6	triple second cousins	9.38% ($6\cdot2^{-6}$)
4	half-first cousins	6.25% (2^{-4})
5	first cousins once removed	6.25% ($2\cdot2^{-5}$)
6	double second cousins	6.25% ($4\cdot2^{-6}$)
6	second cousins	3.13% ($2^{-6}+2^{-6}$)
8	third cousins	0.78% ($2\cdot2^{-8}$)
10	fourth cousins	0.20% ($2\cdot2^{-10}$)[6]

dependence on degree of relationship between donor and recipient (= on probability they share genes)

Hamilton´s rule:

$$rb > c$$

r = relationship; *b* = benefit; *c* = cost

relation between relationship and group selection: $$r > \frac{b-c}{c}$$

Eusociality:




Hymenoptera

Isoptera (termites)

H. glaber

mammals: naked mole-rat (*Heterocephalus glaber*),
Fucomys mole-rats (Bathyergidae)

Fukomys sp.

Florida scrub jay (*Aphelocoma coerulescens*)
(Florida): c = 7%, b = 14%

INTRAGENOMIC CONFLICT

conflict between individuals within populations

conflict between relatives (siblings, mother – descendant)

conflict between males and females (sexual selection)

cooperation and conflict at the genomic level:

George Williams:

body mortal × genes (almost) immortal

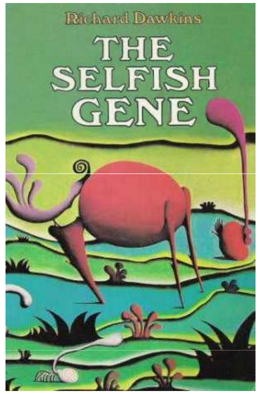
„gene view“

Richard Dawkins:

the term selfish gene (book *The Selfish Gene*, 1976):

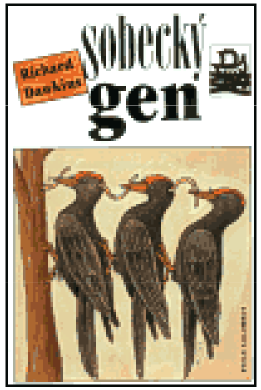
body only as a vehicle for spreading replicators (genes)
which cannot spread on their own

therefore selection affects genes rather than the whole organism

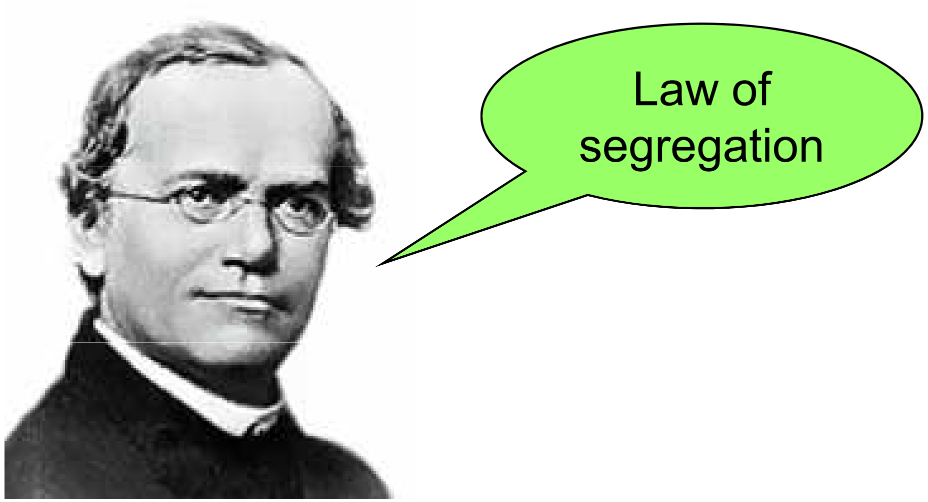


genes must cooperate (the eight analogy)

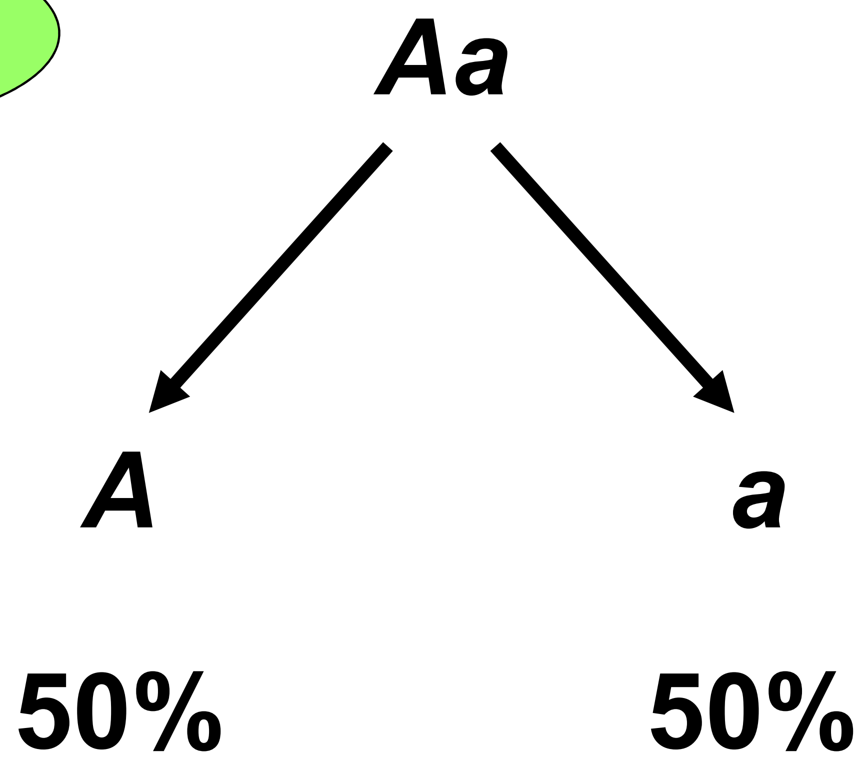
BUT! the term „selfish“ must be understood as a metaphor!



sometimes some genetic element behaves „unfair“
$\rightarrow$ ultraselfish DNA

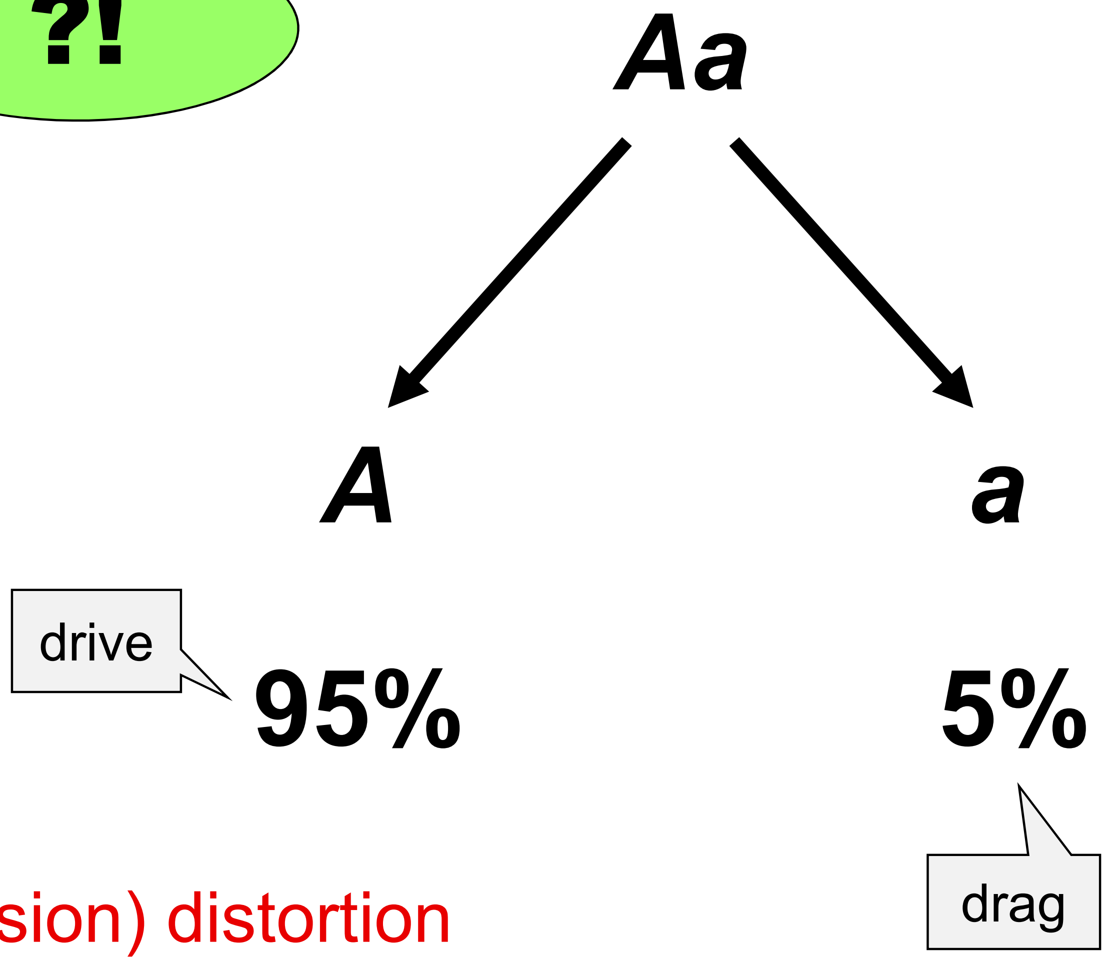


Gregor Mendel



Intragenomic conflict results in higher frequency of some genomic elements in the next generation

Gregor Mendel



segregation (transmission) distortion

Intragenomic conflict may have many forms, eg.:

Interference
= prevention of transmission of an alternative allele

Gonotaxis
= preferential transmission to germinal lineage

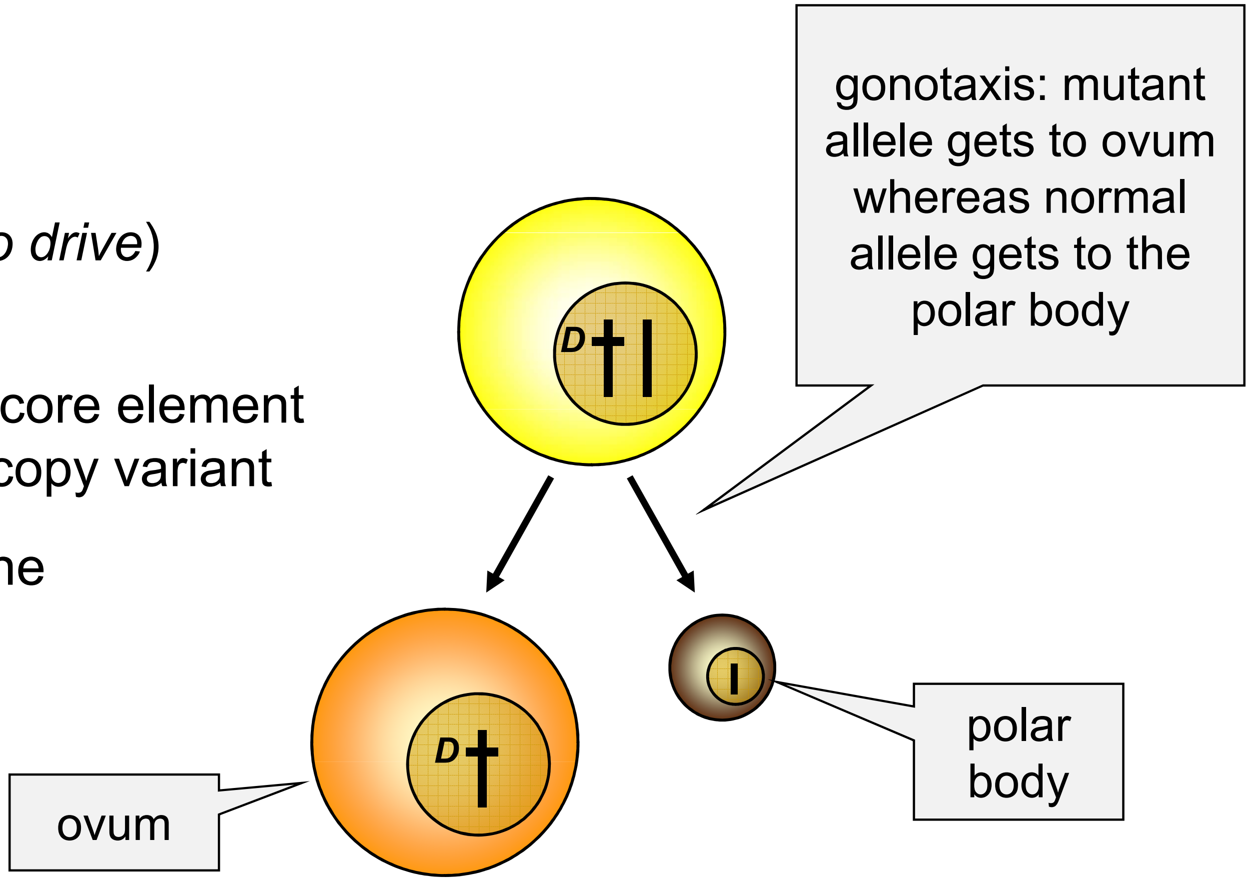
MEIOTIC DRIVE

Overreplication
eg. transposons

Ex.: *R2d2* locus (*responder to drive*)
mouse chromosome 2

increased number of 127 kb core element
→ gonotaxis against low-copy variant

R2d2 includes the *Cwc22* gene
(spliceosomal protein)



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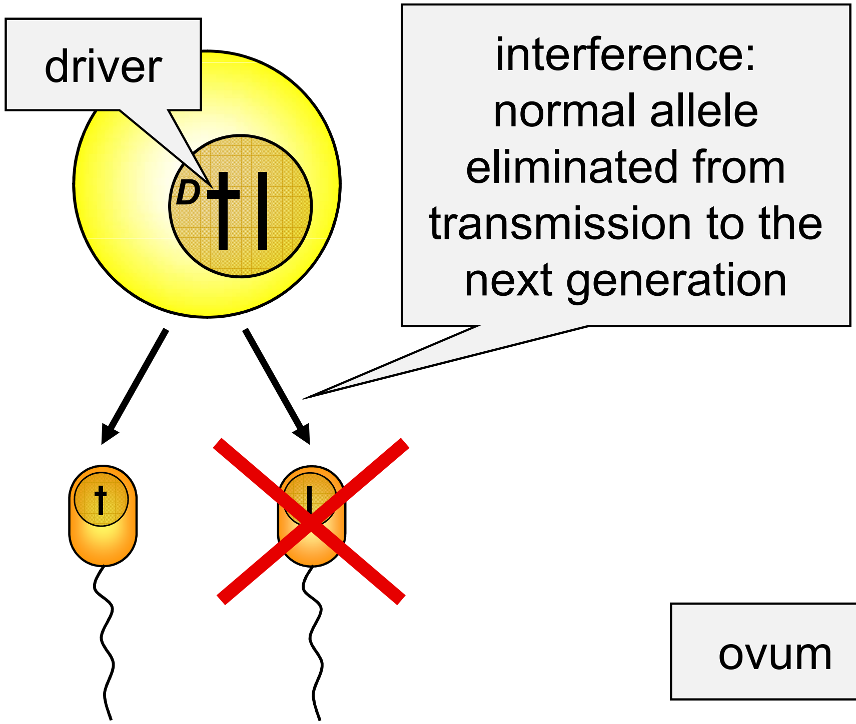
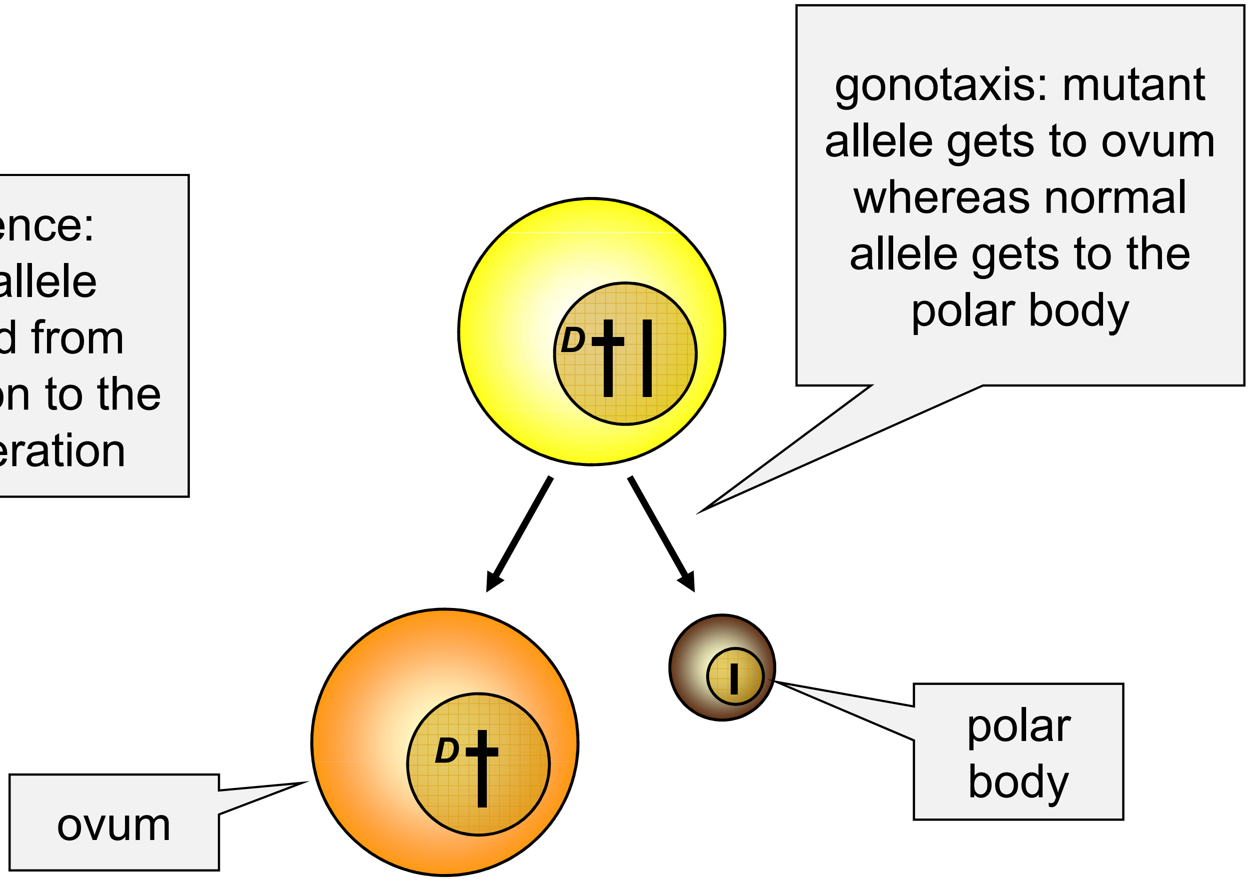




Interference

1. Autosomal

SD (segregation distorters) genes:

males *Drosophila melanogaster*

preferential transmission 95–99%

distorter and *responder*

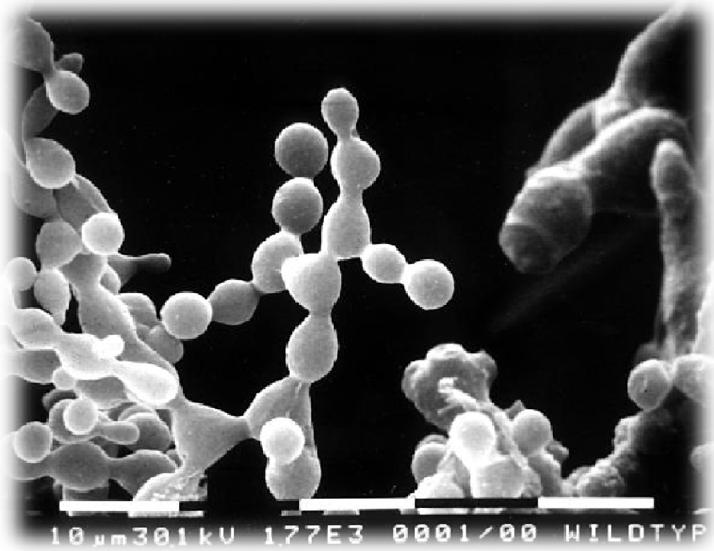
spermatogenetic block in cells with disabled allele

often emergence of modifiers

SD genes = „outlaw genes“

„Spore killers“ (*sk* genes):

Neurospora crassa



t haplotype:

male house mouse

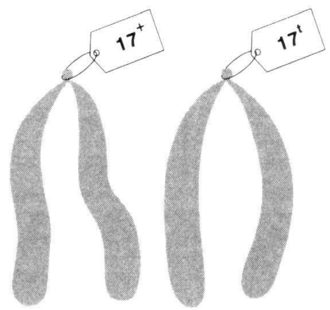
~ proximal third of Chromosome 17

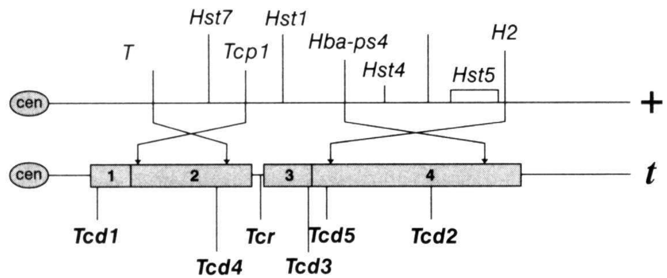
preferential transmission 95–99%

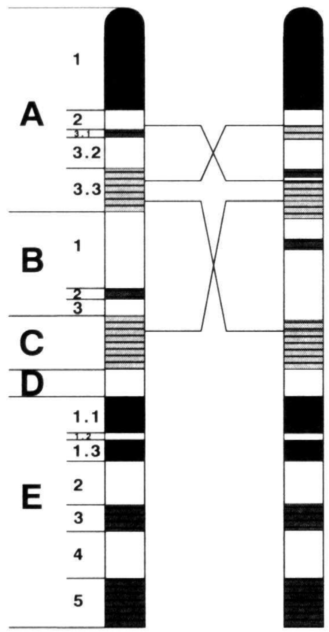
4 paracentric inversions ⇒ recombination only 2%

responder + several distorters

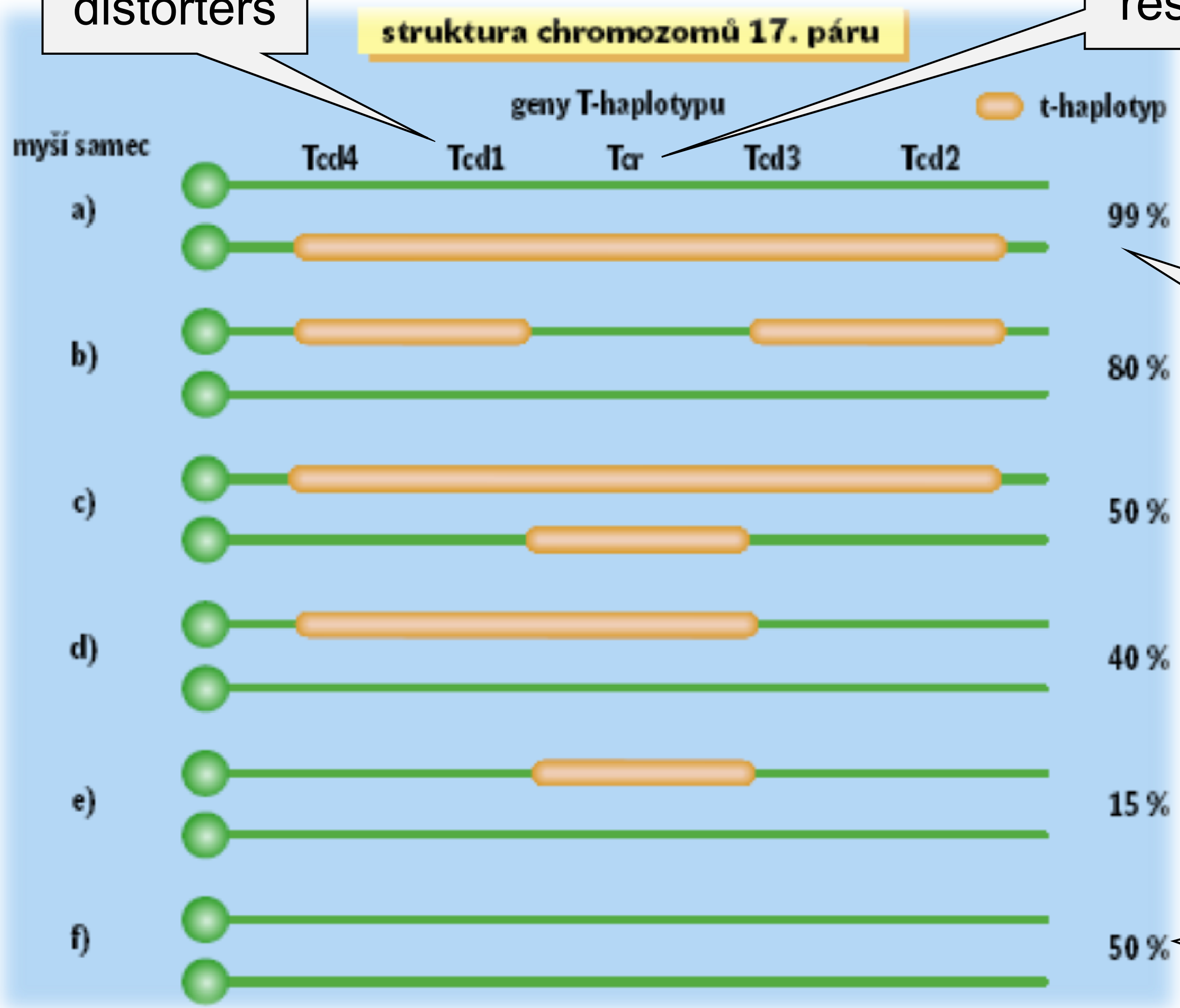
t/t males sterile ⇒ more than 15 lethal genes







diverse genetic structure leads to different drive results:



distorters

respoder

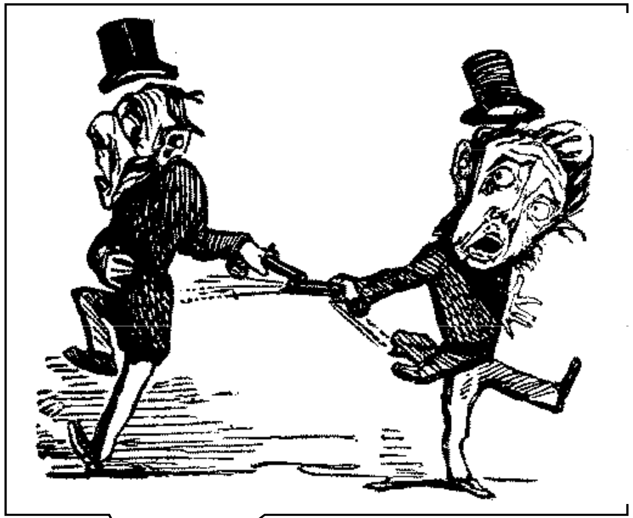
highest transmission distortion when complete *t* haplotype and normal chromosome combination

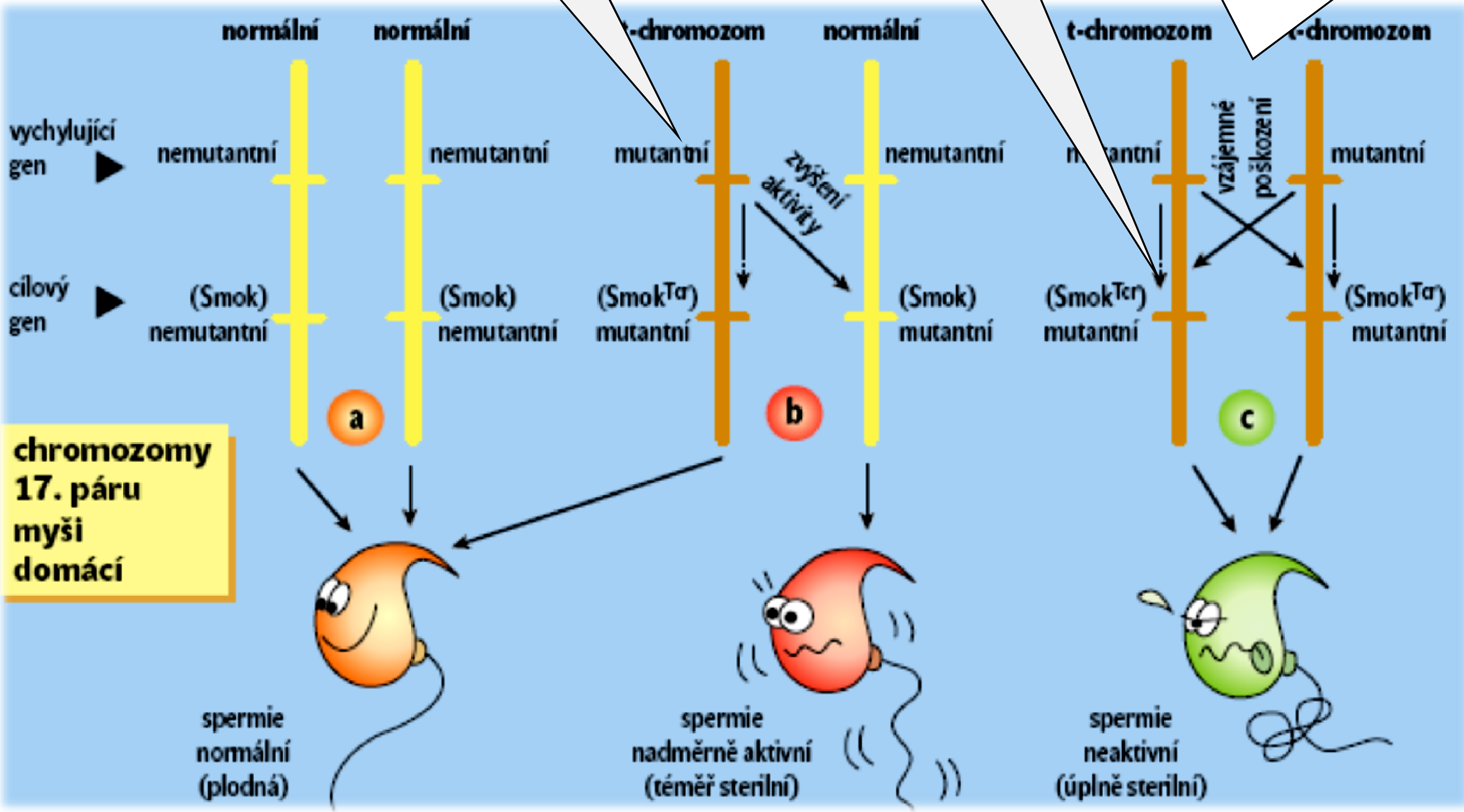
both chromosomes normal ⇒ 1:1 segregation

TRD mechanism different from drosophila:

responder = *Smok* (fused gene)

regulation of gene cascade involved
in flagellum formation





2. Maternal-effect killers

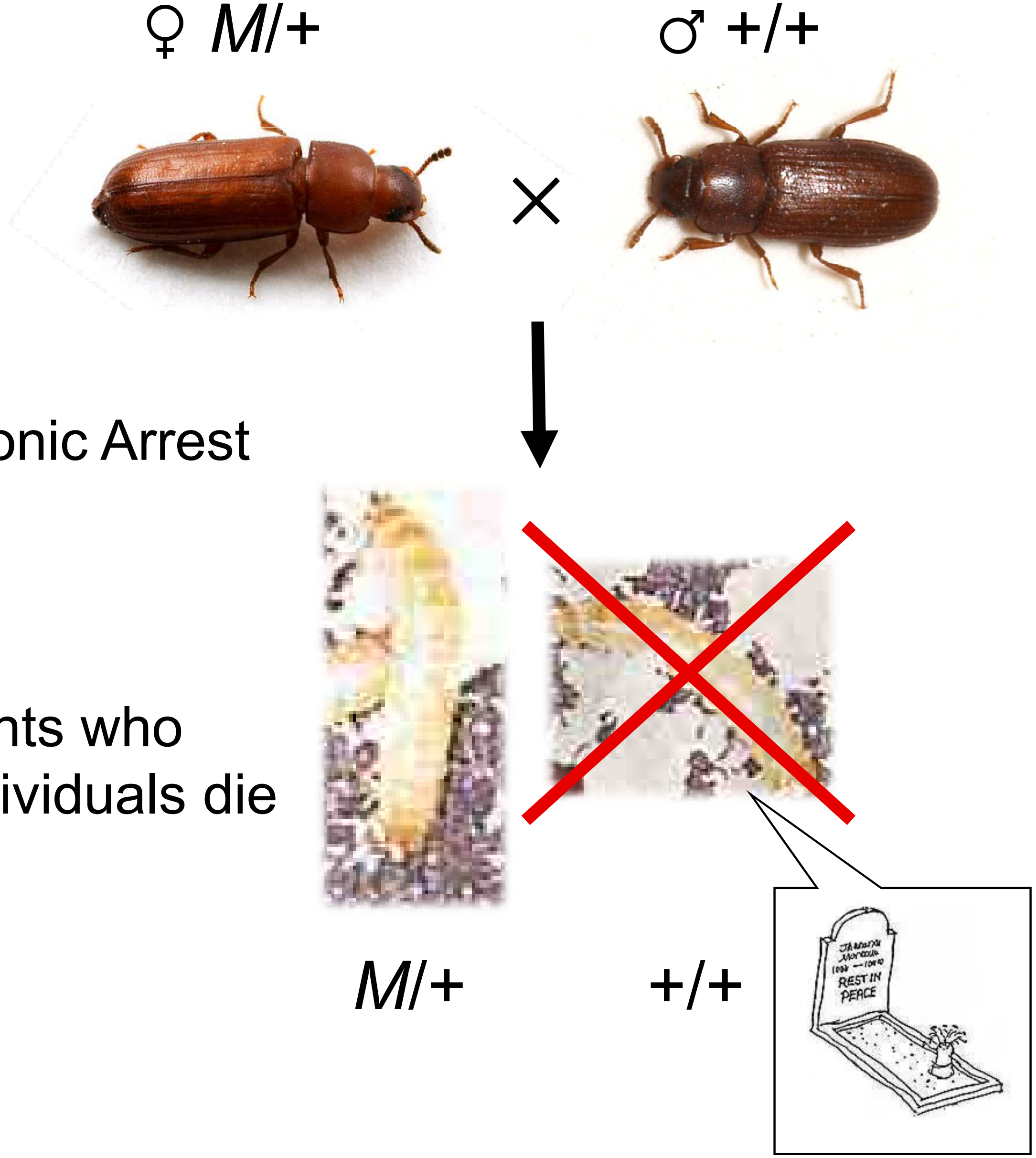
Medea gene:

Maternal-Effect Dominant Embryonic Arrest

Tribolium castaneum

mother *M*/+

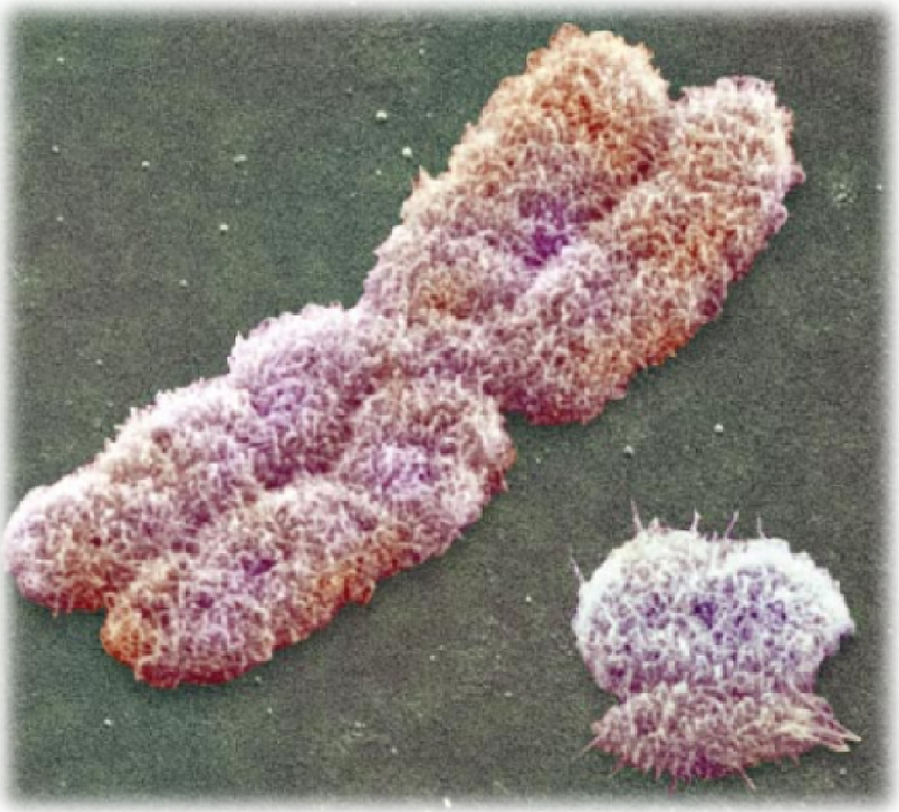
the gene eliminates all descendants who do not possess it – the +/+ individuals die in the second larval instar



3. Sex-biased inheritance

uniparentally inherited genes are interested just in reproduction of the particular sex ⇒ sex ratio distortion

X chromosome drive ⇒ female-biased sex ratio ⇒ selection will favour return to the original state



Model of the conflict between X-linked gene (*Slx*) and Y-linked gene (*Sly*)

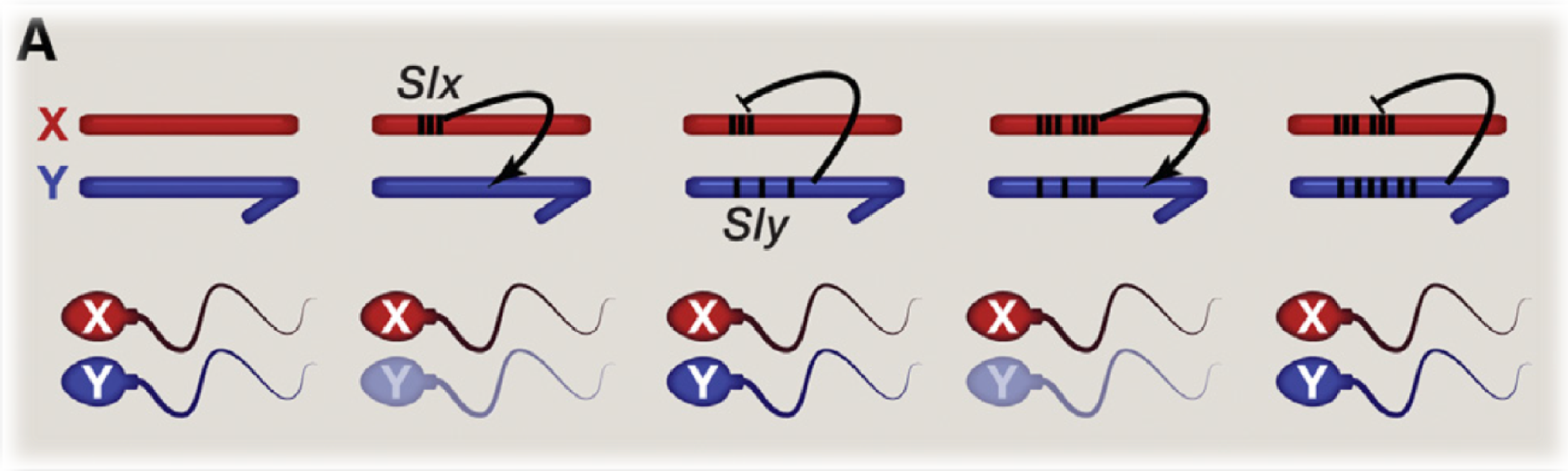
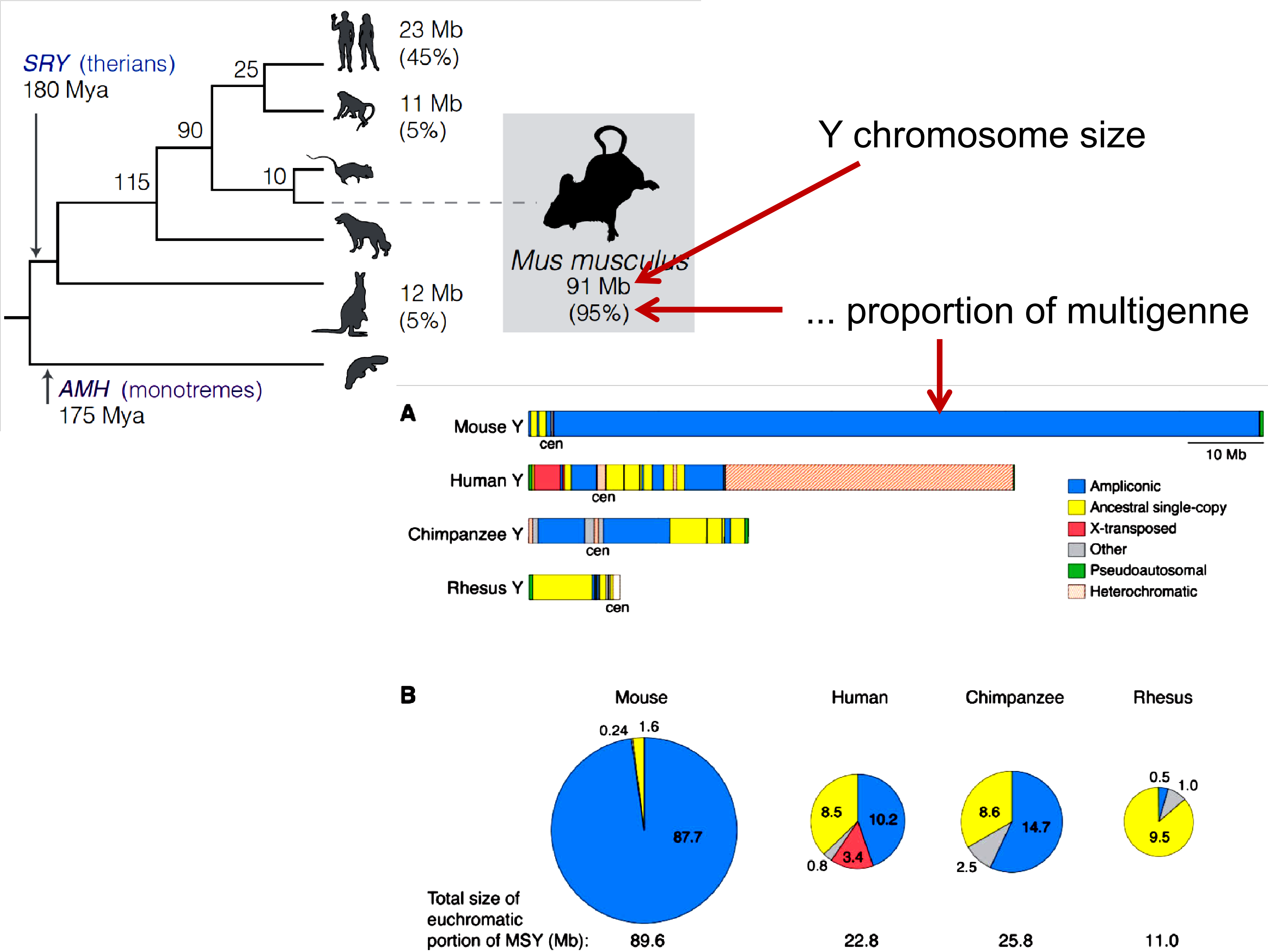


Figure 1. Why Convergent Acquisition and Amplification of Genes on Mouse X and Y Chromosomes May Occur, Yielding a Gene-Rich Euchromatic Mammalian Y Chromosome

(A) Model of recurrent bouts of coevolution between sex ratio distorters and suppressors. A sex ratio distorter on the X chromosome (*Slx*) that incapacitates Y-bearing sperm (indicated by arrow and transparent sperm) invades the population, skewing the population sex ratio. This creates a selective advantage to evolve a Y-linked suppressor (*Sly*) that is resistant to the distorter (indicated by repression line). Increased copy number of *Slx* can increase its ability to drive against the Y chromosome, and the Y will respond by increasing the copy number of *Sly* to neutralize the effects of increased *Slx*-dose.



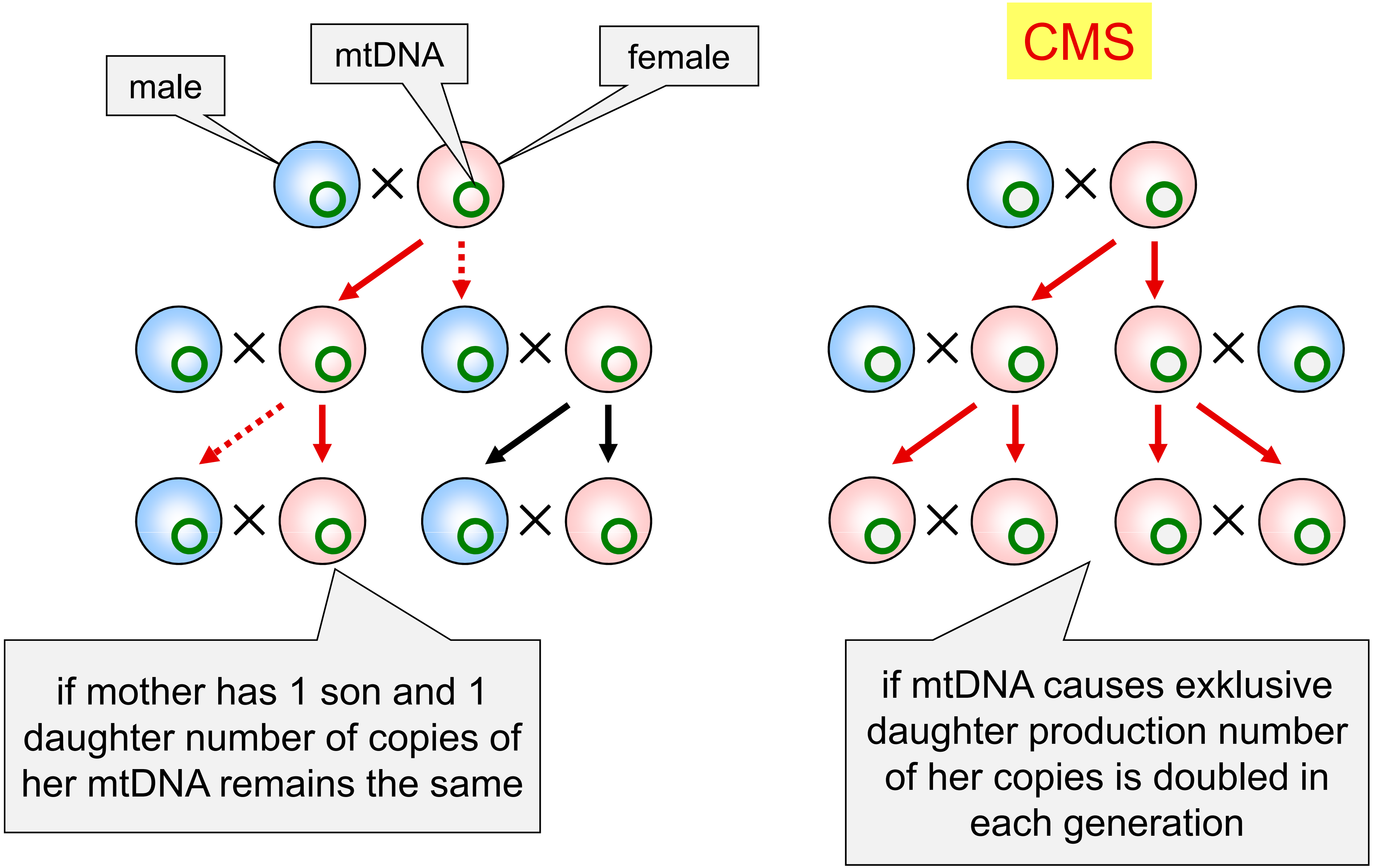
SRY (therians)
180 Mya
25
90
115
10
23 Mb
(45%)
11 Mb
(5%)
12 Mb
(5%)
AMH (monotremes)
175 Mya
Mus musculus
91 Mb
(95%)
Y chromosome size
... proportion of multigenne
A
Mouse Y
cen
10 Mb
Human Y
cen
Chimpanzee Y
cen
Rhesus Y
cen
Ampliconic
Ancestral single-copy
X-transposed
Other
Pseudoautosomal
Heterochromatic
B
Mouse
Human
Chimpanzee
Rhesus
0.24
1.6
87.7
8.5
10.2
3.4
0.8
8.6
14.7
2.5
0.5
1.0
9.5
Total size of euchromatic portion of MSY (Mb):
89.6
22.8
25.8
11.0

Cytoplasmic male sterility (CMS)

in 5-10% populations of monoecious plants
    mixed populations with sterile male plants

this sterility caused by mutant mitochondrial
    genome

advantage when the plants with sterile male sex invest more to pollen
    than to seeds $\Rightarrow$ transmission of more mitochondria



male
mtDNA
female
CMS
if mother has 1 son and 1 daughter number of copies of her mtDNA remains the same
if mtDNA causes exklusive daughter production number of her copies is doubled in each generation

similar effect is caused by *Wolbachia*

intracellular parasite of arthropods

killes males who do not possess *Wolbachia*

reduction of competition for sources – kin selection

besides killing males *Wolbachia* can have other phenotypic effects:

feminisation: infected males are developing as females or infertile pseudofemales

parthenogenesis: eg. in *Trichogramma* wasps males rare (likely due to wolbachias) → wolbachias help females to reproduce parthenogenetically, ie. without males

cytoplasmic incompatibility: inability of males with wolbachias to reproduce with females which does not possess them or which have wolbachias of other strain → reproductive barier, speciation

Overreplication

Transposable elements (transposons)

incorporating of copies to other genome site
(Barbara McClintock: „jumping genes" in maize)

usually not removed from genome
$\rightarrow$ molecular fossils

usually huge numbers
human: > half of genome

horizontal transfer, also between species

in some cases effect on gene regulation

1. DNA elements

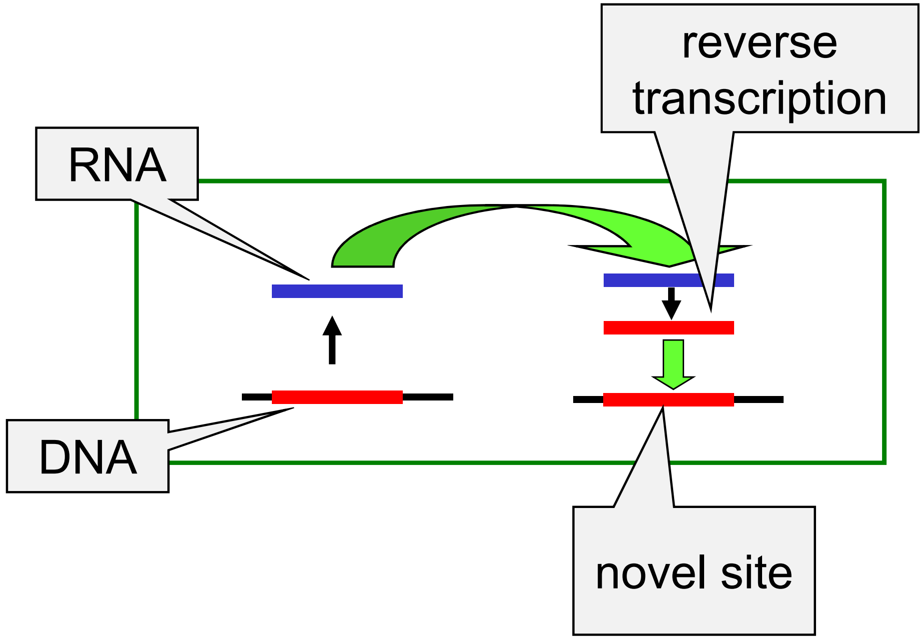
„cut-and-paste“

enzyme transposase

Ac a *Ds* elements in maize (B. McClintock), *mariner* in animals, *P* elements in *Drosophila*

2. Retroelements

„copy-and-paste“



through RNA stage, reverse transcription (reverse transcriptase)

template stays at the original place ⇒ increase of copy numbers

Retroelements

LTR-retrotransposons: *copia* in *D. melanogaster*

retroposons: LINE – L1 in human: 17% of genome
SINE: short, do not code for own reverse transcriptase
Alu sequence in human – 12% of genome; B1, B2 in mouse

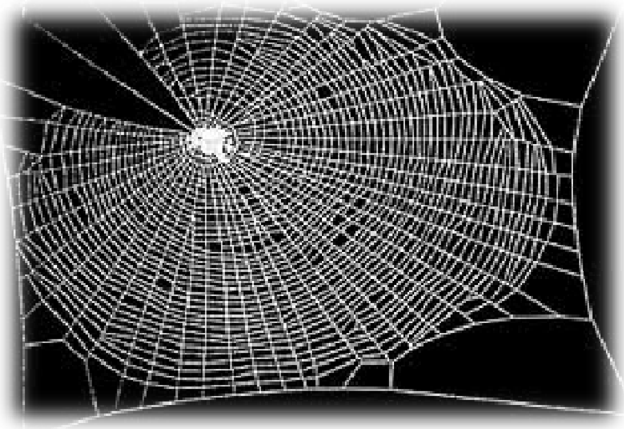
3. MITE (miniature inverted-repeat transposable elements)

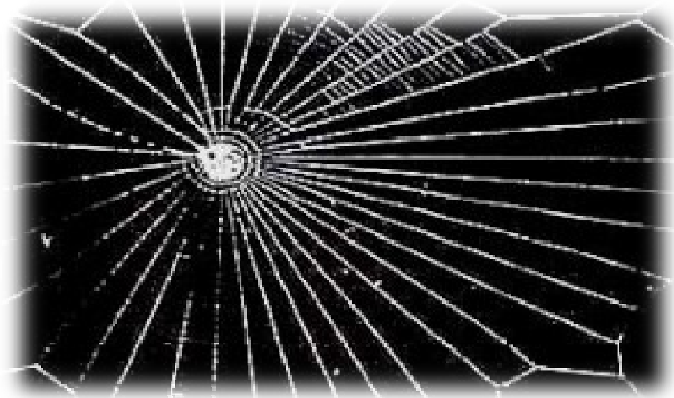
Stowaway, *Tourist*

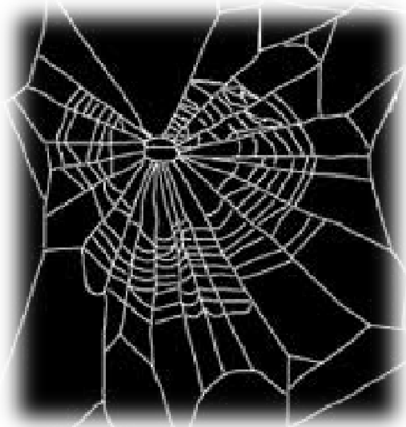
gene effects can extend outside organisms –
R. Dawkins: *The Extended Phenotype*

Eg.: cases of caddisfly larvae, spider webs


chloral hydrate


normal


LSD


amphetamine

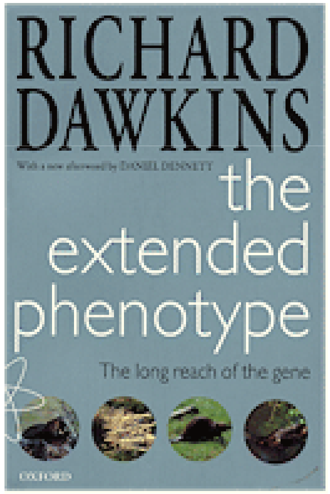

mescaline

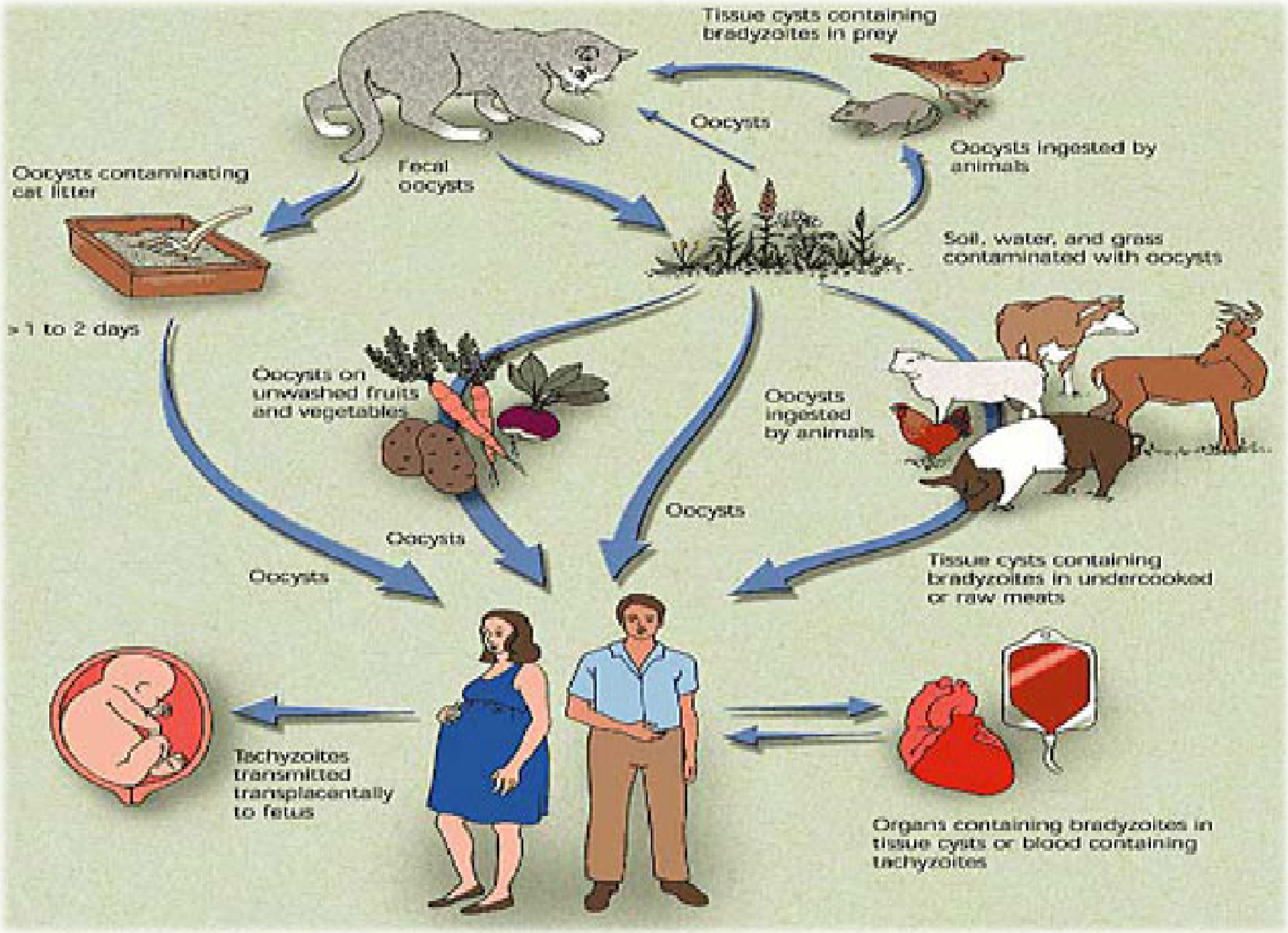

caffeine

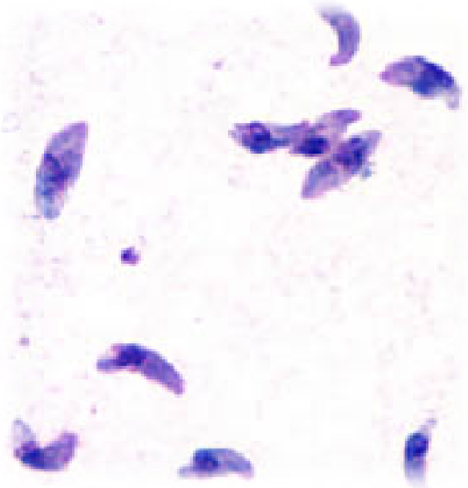

marihuana (THC)

flukes: parasited individuals bulid thicker shells

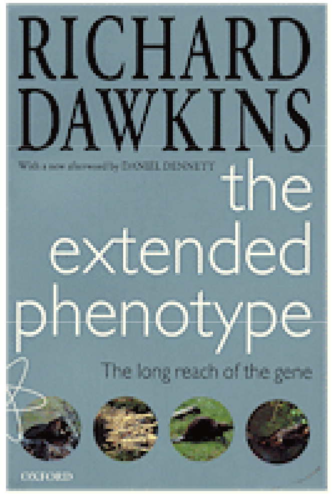
Toxoplasma gondii: decrease of host´s reaction time





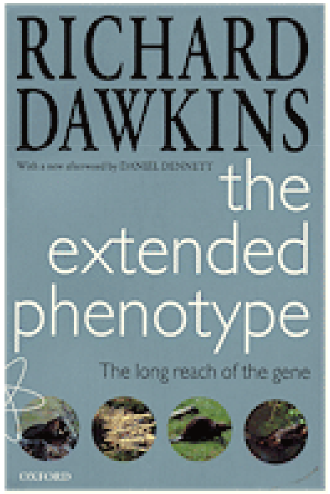


similarly parasitic flukes:



eg. abdomen of parasited ant *Cephalotes atratus* turns red so that resembles edible berry (other species change ants´ behaviour → they climb up a grass blade where they are eaten by cattle or sheeps)

ant *Monomorium santschii*: absence of workers
→ invasion of foreign ant nests, „command“ to kill own queen and to adopt the invader queen



turquoise killifish (*Nothobranchius furzeri*) infected by metacercaria of the fluke *Apatemon* sp.

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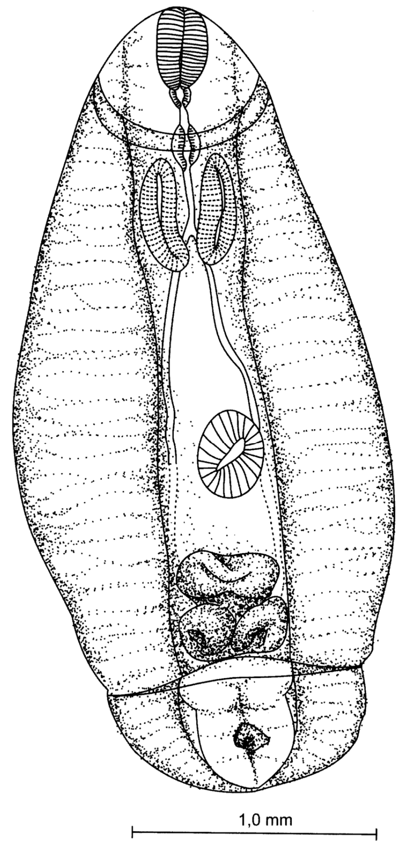
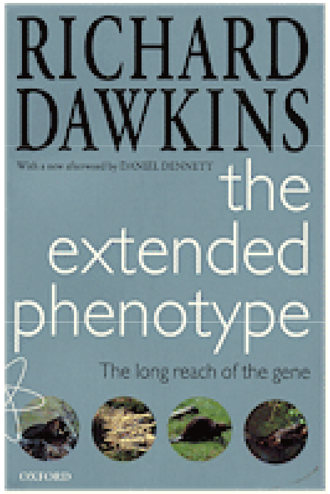


infected fish stays near the surface or even breaks the water → increase of the risk of predation

Duke of Burgundy (*Hamearis lucina*) caterpillars:



on head an organ producing a narcotic nectar; another pair of glands causing increased aggressiveness against all organisms except the caterpillar itself → protection ('bodyguard'), several days of ants' drug addiction, ants do not leave the caterpillar