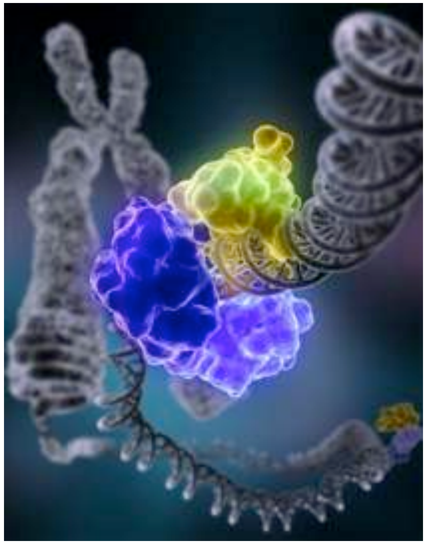
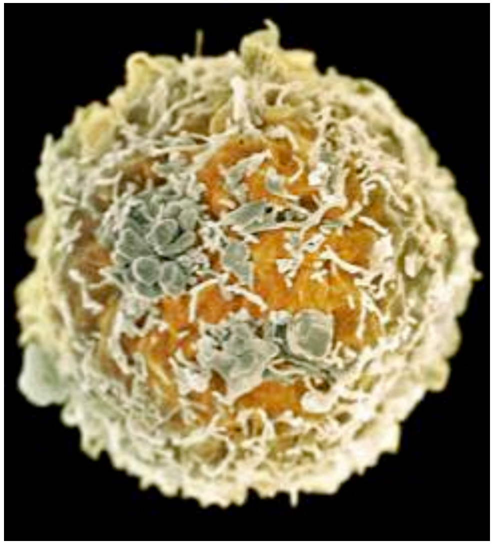
Levels of Selection:
"Multilevel Selection Theory"





Natural Selection

higher levels

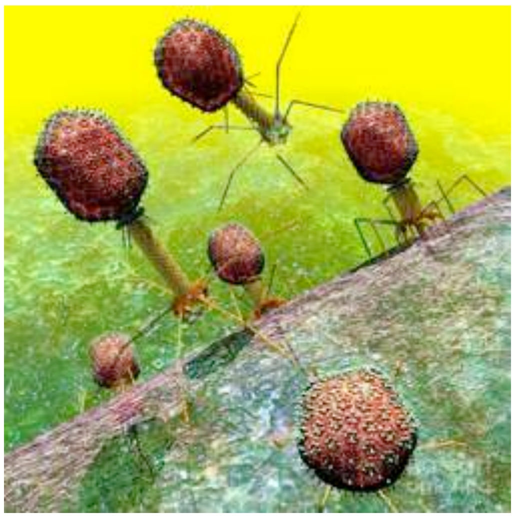
lower levels

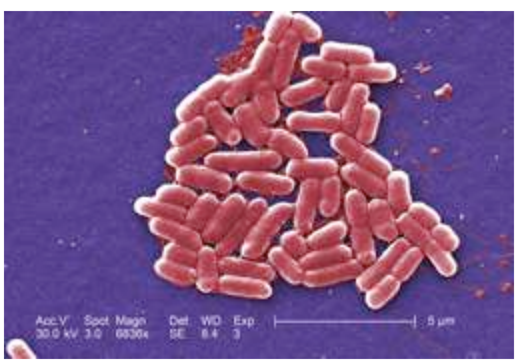
Lineage
Species
Trait Group
Kin Group
Individual
Cell
Organelle
Gene

Natural Selection Basics

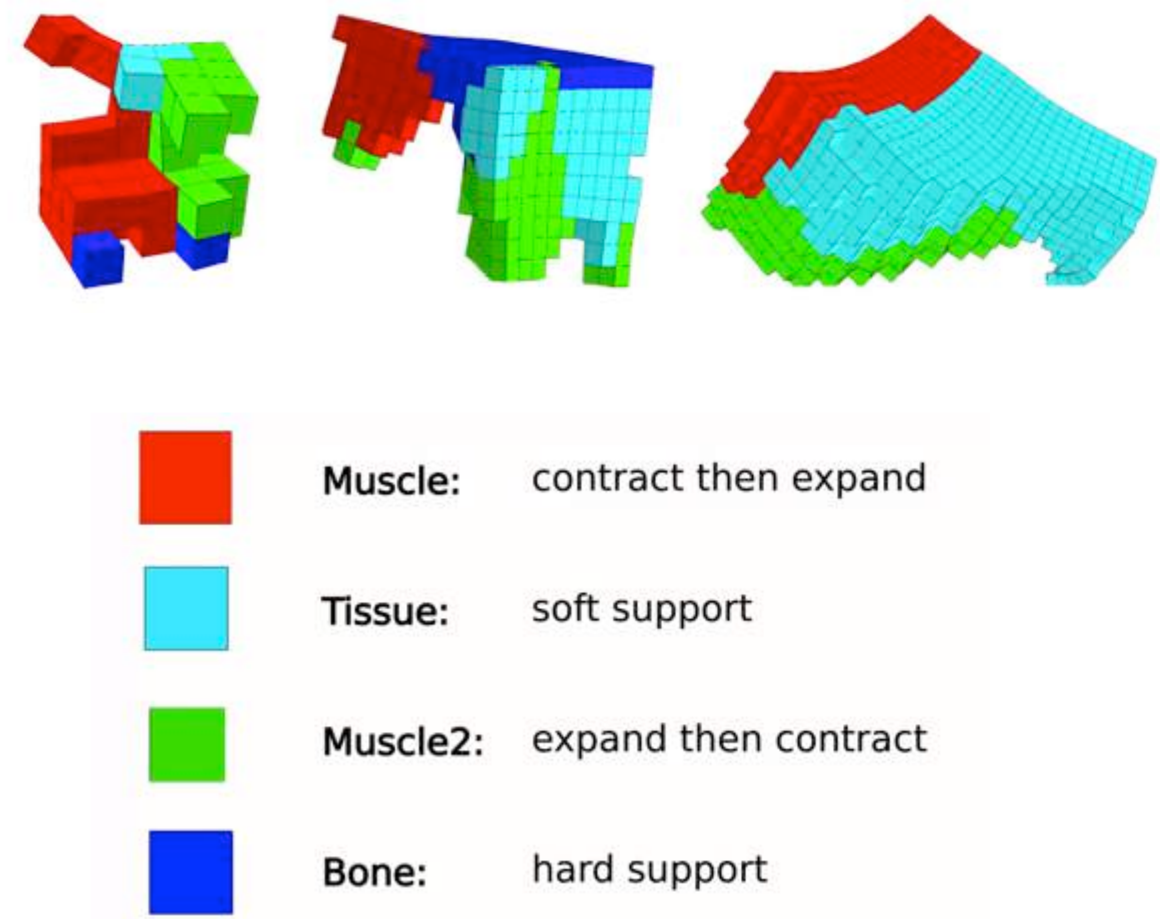
- Entities (individuals) produce more copies (offspring) each generation than can possibly survive
- Entities vary in their traits.
- Some of this variation is heritable, and can therefore be passed on to the next generation
- Certain variants are better able to survive and reproduce than others
- The more fit variants produce (on average) more of the next generation – and these offspring will also tend to possess the special “fit” trait
- Over time, that trait will increase in frequency


0
1mm



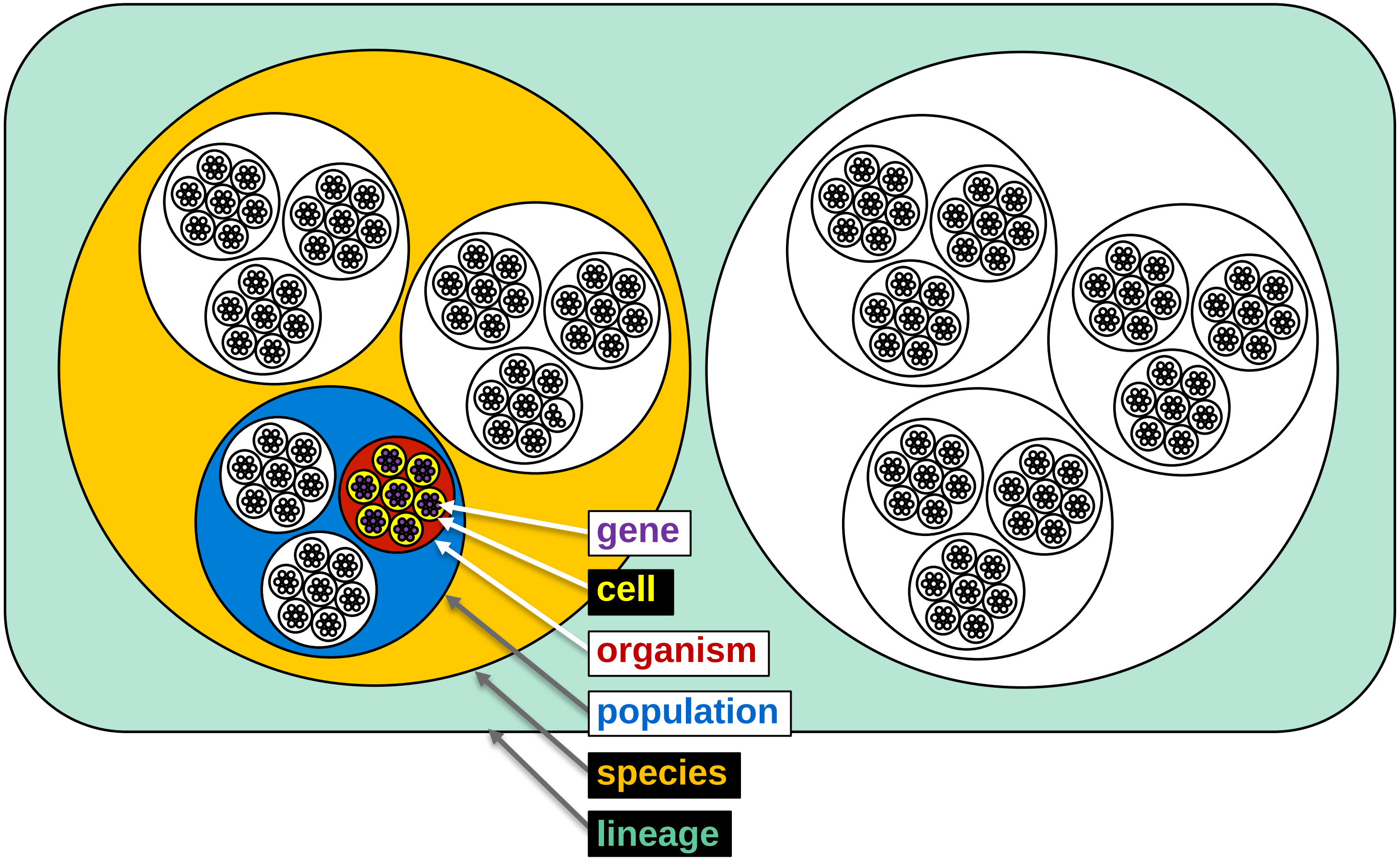

5 µm

Selection Simulations



Levels of Selection:

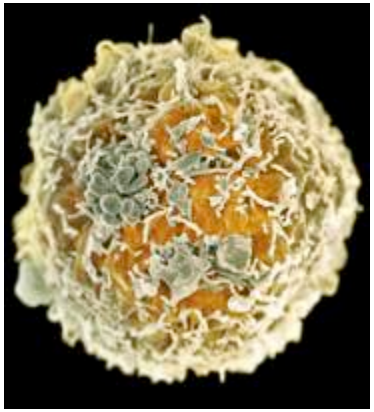
"Multilevel Selection Theory"



Conflicts Between Levels of Selection

There *is* selection at higher and lower levels, but what is the relative *strength* of selection, i.e., will selection at other levels be swamped out by individual selection because…

What's good for the gene, cell, population, etc. is <u>not</u> necessarily good for the organism



Examples of conflict: uneven sex-ratios, cancers, cannibalism, lower virulence, altruism, etc.

higher levels

- Lineage
- Species
- Trait group
- Kin group

Individual organism

lower levels

- Cell line
- Organelle
- Gene

Selection at the Gene Level

Some (Richard Dawkins, John Maynard Smith, Robert Trivers) have argued that genes are the unit of selection because…

Individuals are short-lived. They die and (in sexual species) only ½ of their genes are passed on to their direct offspring.

- Grandchildren only share 1/4 of their genes with their grandparents
- Great-grandchildren only 1/8 their genes
- After 4 generations, only 1/16 of the original ancestor's genes remain

Gene, however, persist relatively unchanged much longer than individuals. C01 gene (present in all animals) has changed very little over the last 700 million years.

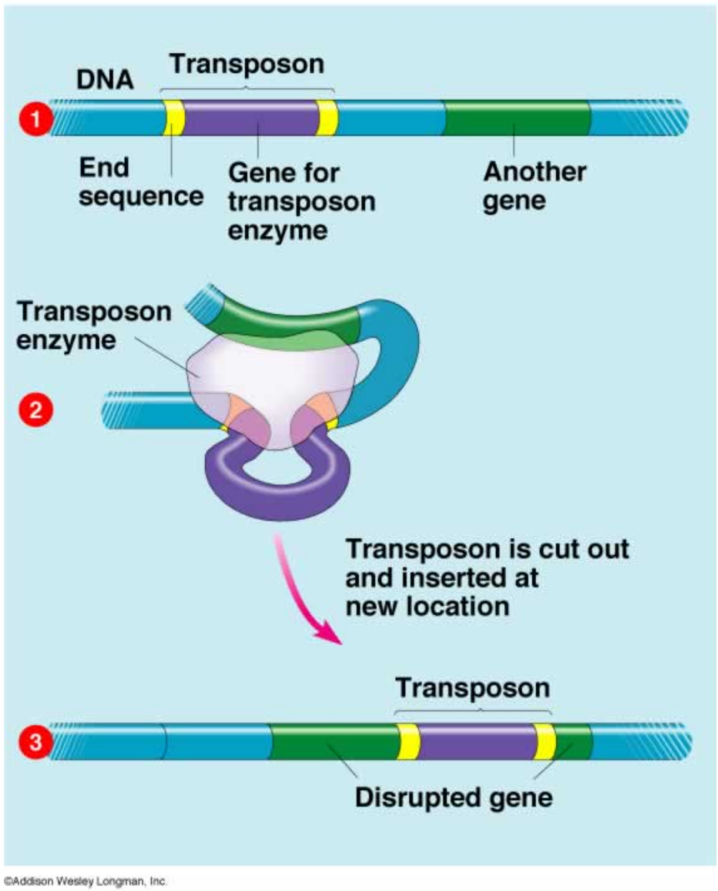
Conflict between Genes and the Individual Organism

- What is best for the gene is often best for the whole organism
- "Good genes" make the organism better able to survive and reproduce, thus passing on more copies of its genes

- But sometimes, a gene can increase in frequency without being good for the individuals. If the gene can increase its own frequency in the gene pool, it will spread, despite helping or harming the individual it is in → "selfish gene"

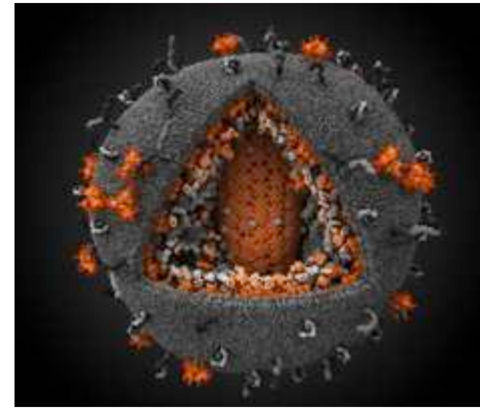
Conflict at the Gene level

Transposon – (jumping gene) DNA sequence that can change its position in the genome. Discovered by Barbara McClintock → Nobel Prize



Gene level conflict continued

Retrotransposon– type of transposon (= jumping gene). Transcribed from DNA to RNA, then from RNA back to DNA which is inserted back into the genome. Increase in frequency in genome. “Selfish gene”

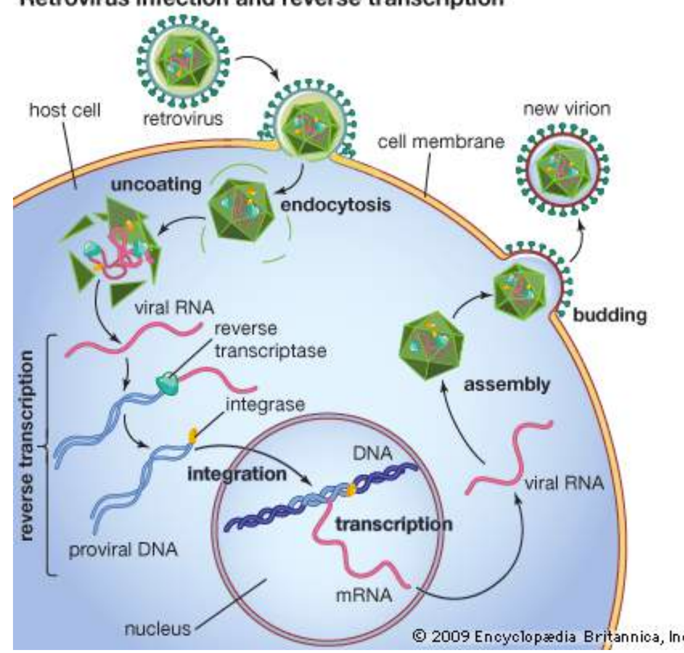


Endogenous retroviruses – type of retrotransposon, similar to retrovirus sequences. 8% of human DNA is made up of endogenous retroviruses!

Research suggests some retroviruses may have evolved from retrotransposons.

That makes retroviruses jumping genes that are able to jump from one *cell to another*!

Retrovirus infection and reverse transcription



higher levels

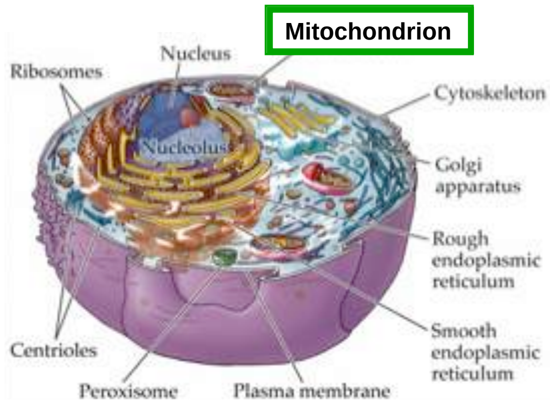
- **Lineage**
- **Species**
- **Trait group**
- **Kin group**

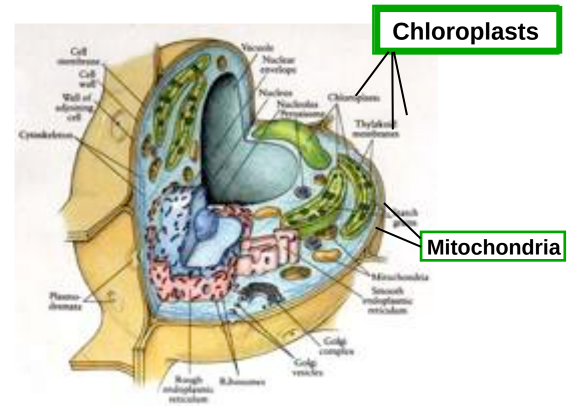
Individual organism

lower levels

- **Cell line**
- **Organelle**
- **Gene**

Selection at the Organelle Level

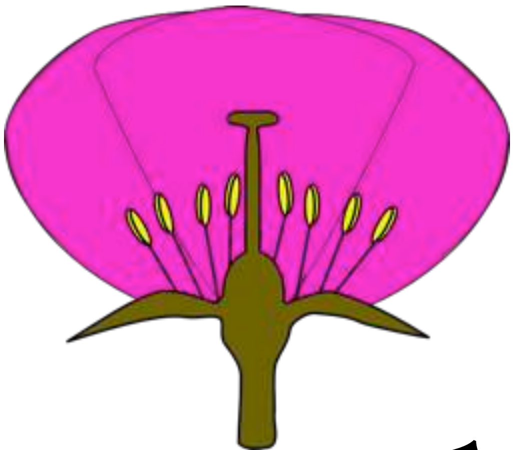


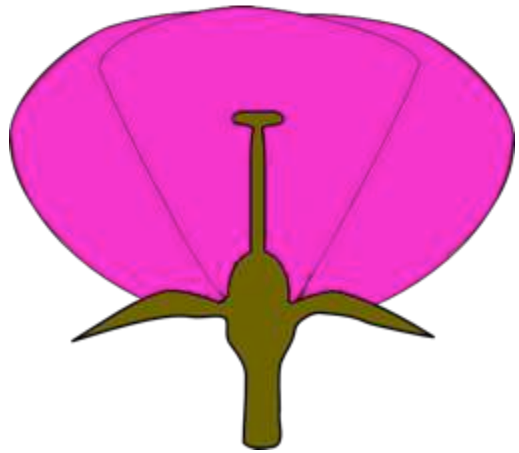


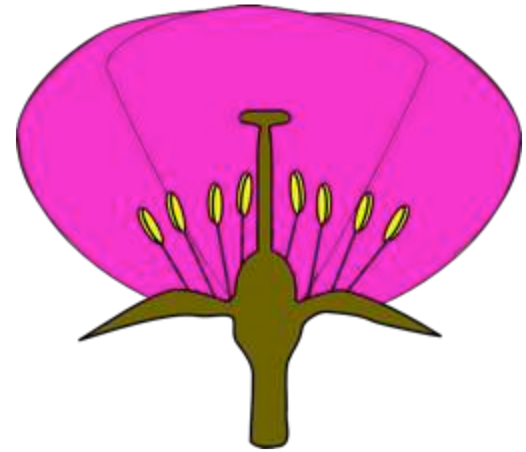
- Mitochondria and chloroplasts – originally bacteria captured by another cell.
- Mitochondria and chloroplasts are usually transmitted in the cytoplasm of the egg, maternally inherited.
- Unlike nuclear DNA, which is divided evenly, no mechanism to divide the mtDNA evenly during reproduction.
- Two sexes, with uniparental transmission of organelles, originated to eliminate this source of genomic conflict. Nuclear genes police the DNA in organelles.

Example of Organelle vs. Organism Conflict

Cytoplasmic male sterility (CMS) in thyme plants



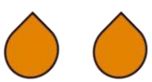


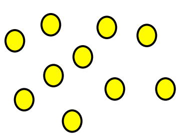


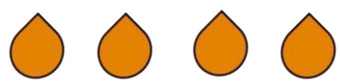
Normal Flower ⚥

Mitochondrial CMS Flower ♀

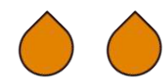
Mitochondrial CMS Flower + nuclear restorer allele ⚥

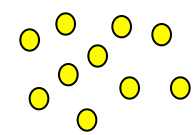
seeds 

pollen 

seeds 

Since MT are maternally inherited, the allele increases. Good for the MT gene, bad for other genes

seeds 

pollen 

A new allele that restores anther function will spread through population

higher levels

- Lineage
- Species
- Trait group
- Kin group

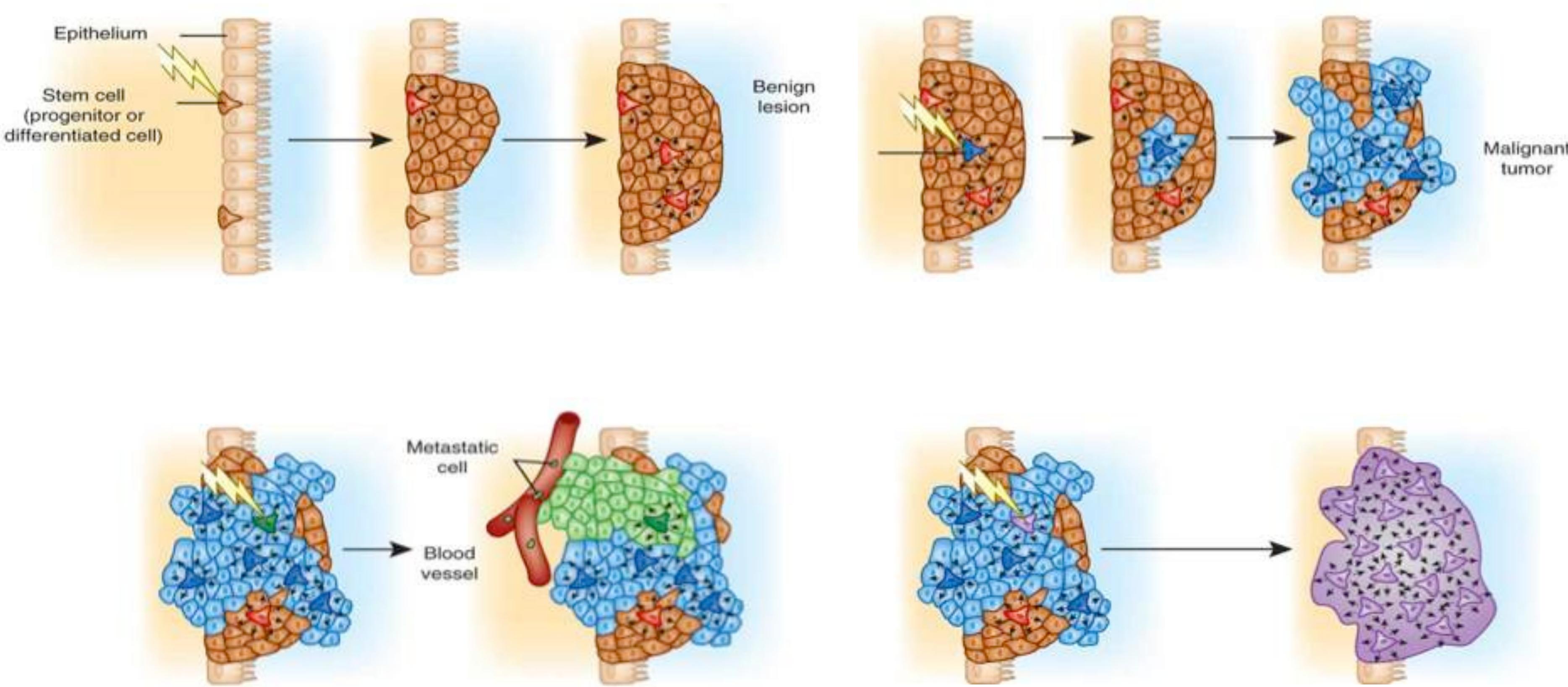
Individual organism

lower levels

- Cell line
- Organelle
- Gene

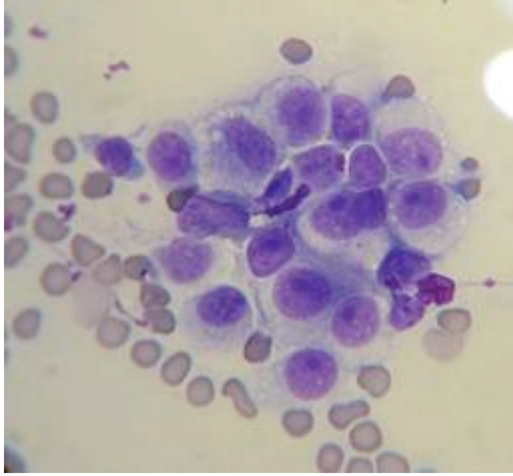
Cell level: Cancer

~6+ mutations required for cancer

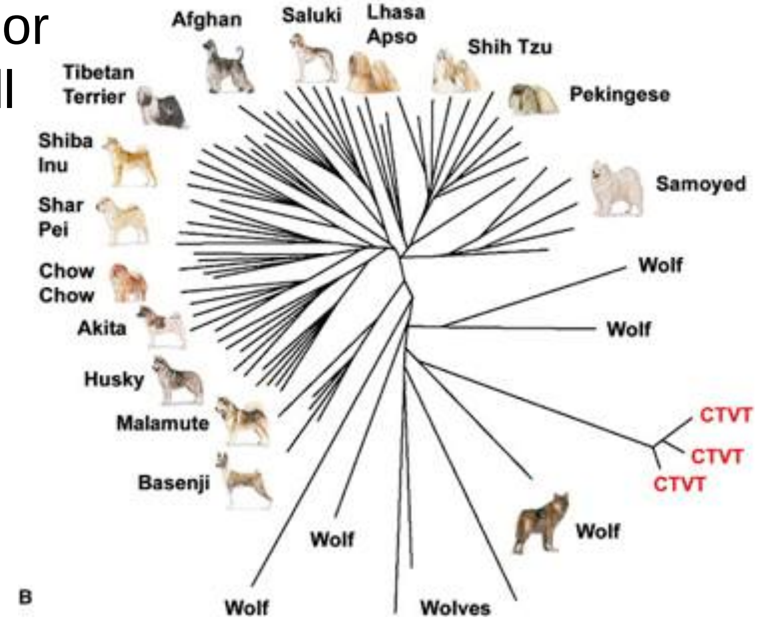


Modified from Clevers (2011) *Nature Science*

Canine Transmissible Venereal Tumor



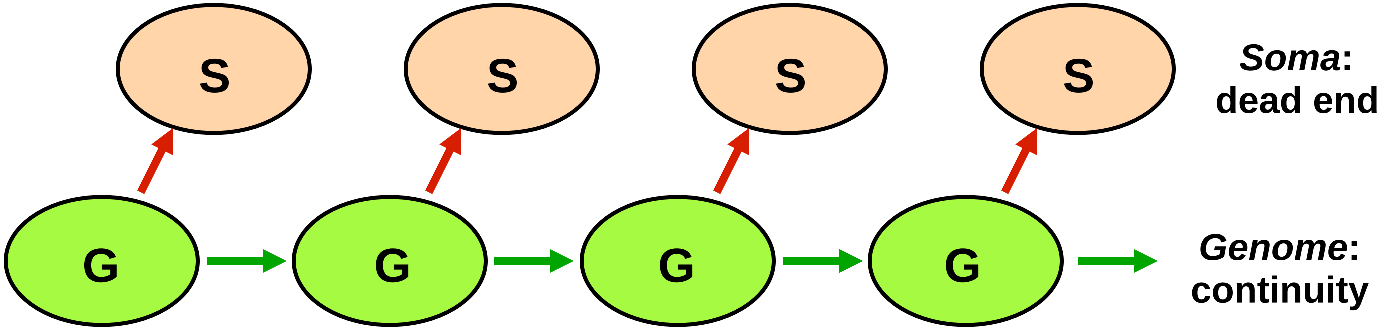
- Tumor on canid (dogs, fox, coyotes) genitalia
- One of 2 or 3 identified horizontally transmitted tumors (e.g. tasmanian devil facial tumors)
- Transmitted during intercourse or sniffing (open wound)
- Most recent common ancestor of extant tumor cells over 2000 years ago. 2000 year old cell line – oldest continuous animal cell line on Earth!



- Accumulated over 1.9 million mutations, lost ~25 chromosomes
- 1 runaway canid cell! A parasitic cell line?

Non-Clonal Organisms

(like us; not clonal plants or animals)



- **Non-clonal organisms: Somatic cell line is independent of the germ cell line (actually, true of *less than 50%* of organisms)**
- **Somatic cell lines die when the organism dies.**
- **This separation limits the possibilities for selection at the level of individual cell lines.**
  - **A cell may mutate to a super reproducer – a "cancer" – but this "adaptation" will not be passed on**

Levels of Selection

"Multilevel selection theory"

higher levels

- Lineage
- Species
- Population
- Trait Group
- Kin Group
- Individual
- Cell
- Organelle
- Chromosome
- Gene

lower levels

Selection at the Group Level

higher levels

Levels (of organization) *above* that of the individual organism:

- **Lineage – multiple species from a common ancestor (clade)**
- **Species**
- **Trait group – packs, schools, other cooperative social units**
- **Kin group – immediate and extended families**

lower levels

Levels *below* that of the individual organism:

- **Cell line – cancers**
- **Organelle – mitochondria, chloroplasts, endosymbionts**
- **Gene – segregation distorters, outlaw alleles**

~~For the "good of the species…"~~

- If traits evolve by individual selection (differential survival/ reproduction of individuals) the possibility of future extinction CANNOT affect the course of evolution

Frank Cotham

"All I'm saying is <u>now</u> is the time to develop the technology to deflect an asteroid."

~~For the “good of the species…”~~

- Under *individual* selection altruistic behaviors (a cost to the individual doing the behavior, a benefit to the recipient) would *have* to decline over time, since altruists would leave fewer offspring

Group Selection

- Traits that benefit the population at the cost of the individual could evolve by:

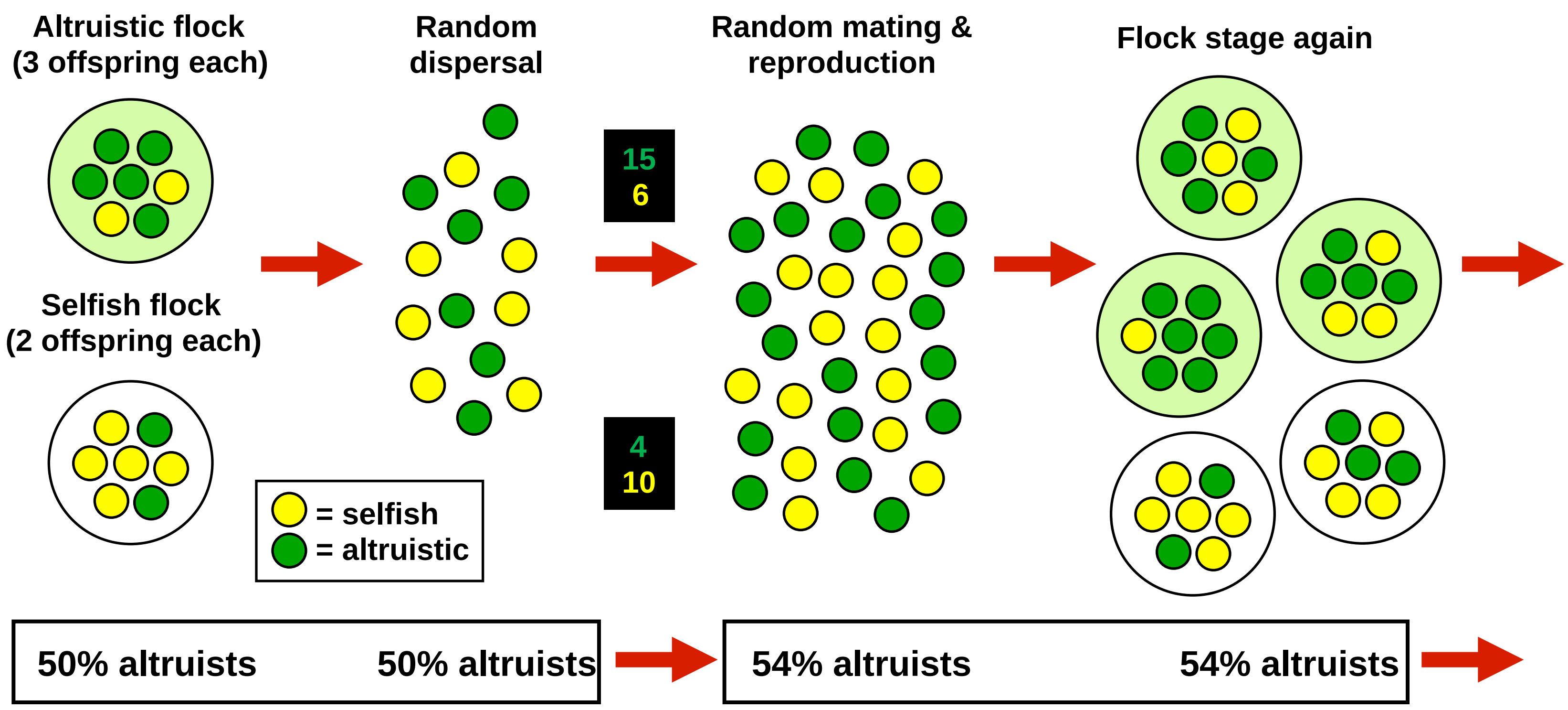
  Group Selection – differential survival of groups that differ in their genetic composition

- These adaptations benefit the group but <u>NOT</u> the individual organism.
- Example: Populations of selfish individuals with high reproductive rates may over eat their food supply and go extinct more often then populations that have lower reproductive rates and eat less (even though individual selection prefers maximum reproduction).

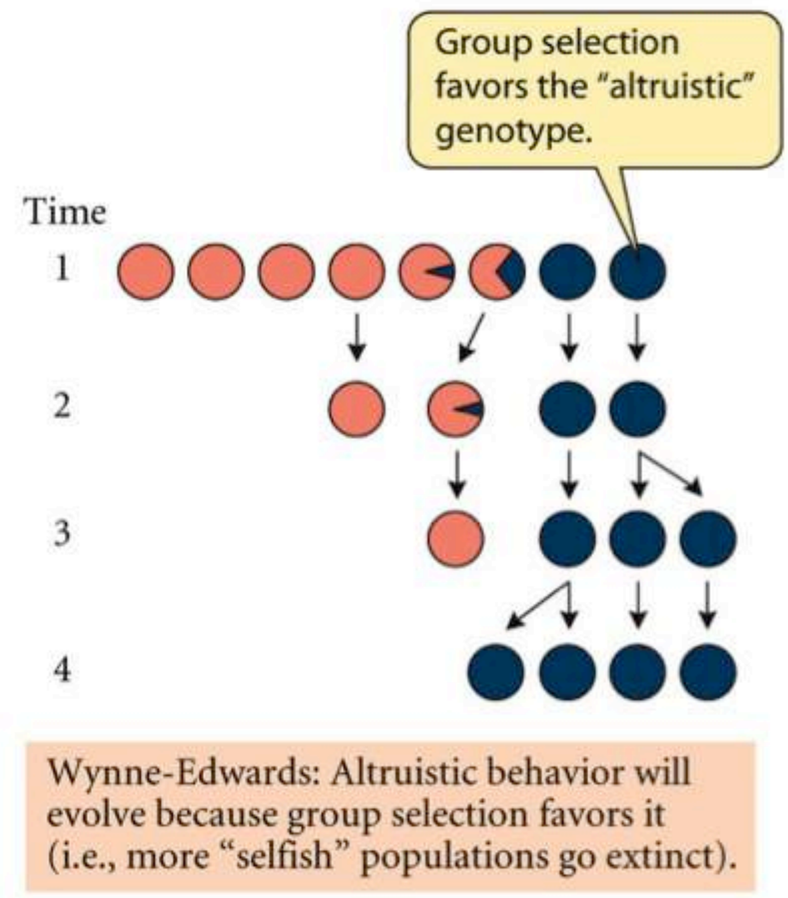
How trait-group selection increases a trait for altruism

(there's more of G. C. Williams than D. S. Wilson in this model)

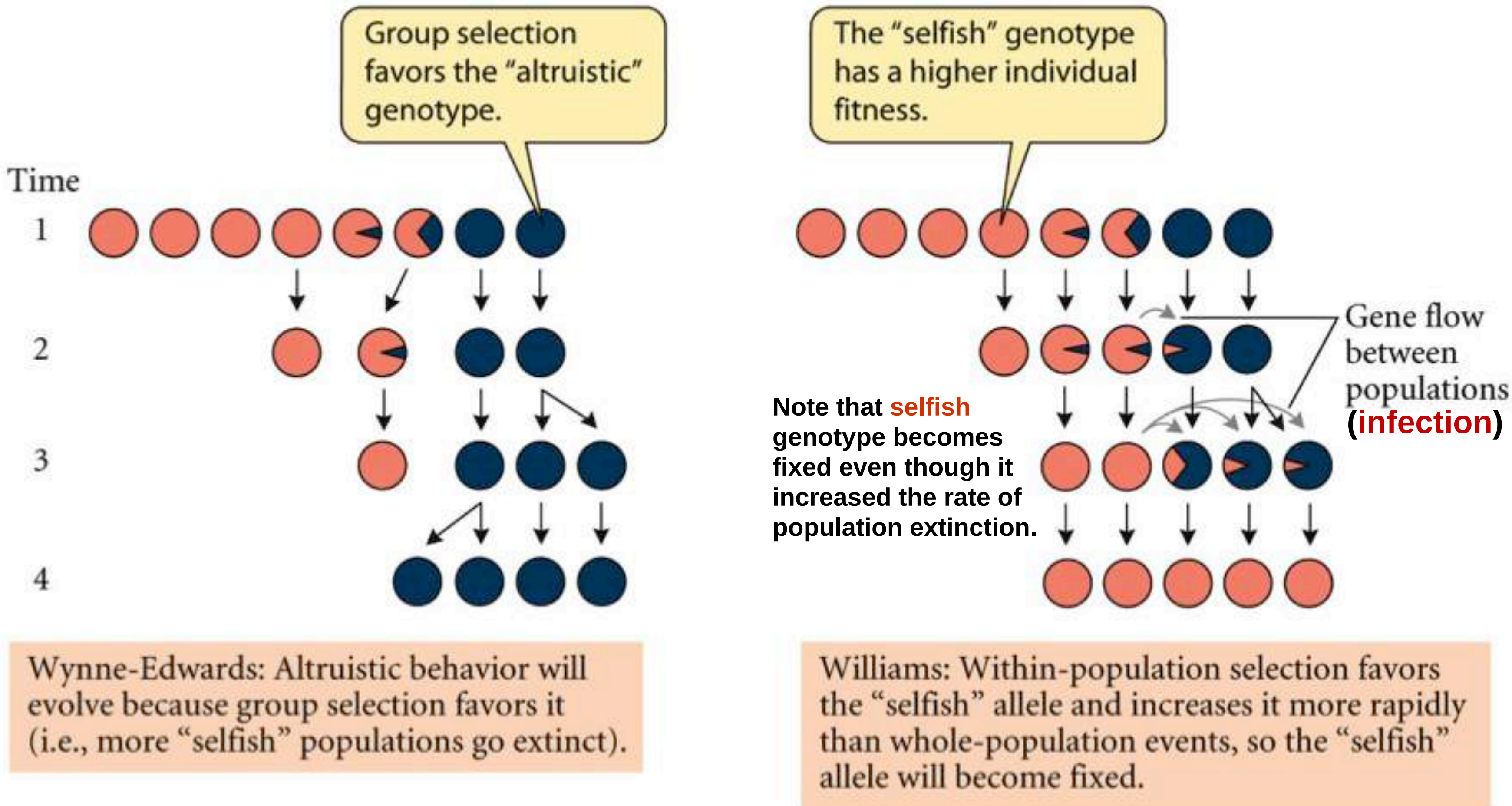
Each individual derived from an *altruistic* flock can fledge 3 offspring, each individual derived from a *selfish* flock can fledge 2 offspring



V. C. Wynne-Edwards:
Group Selection



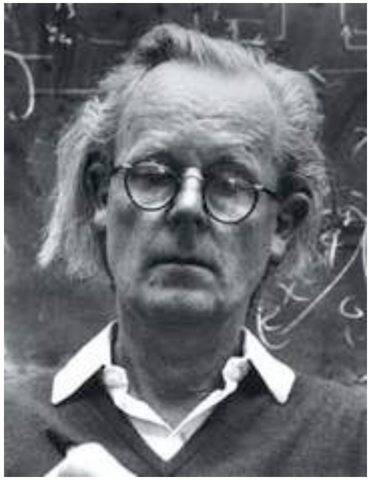
G. C. Williams:
Individual Selection



G. C. Williams argues: Greater abundance and more rapid turnover of individuals: selection will be stronger at the individual level than it will be at the group level.

V. C. Wynne-Edwards vs. John Maynard Smith

- **Maynard Smith proposed an infection model:**
  - **Given selfish (*S*) vs. altruist (*A*) alleles, groups with mainly altruists will go extinct at a lower rate.**
  - **But individual selection favors selfish individuals within groups.**
  - **So altruistic groups infected by selfish individuals will be taken over by the latter.**
  - **Even if the "migration" of selfish individuals is only *one successful immigrant during the lifetime of the group, the selfish allele (S) will go to fixation.***

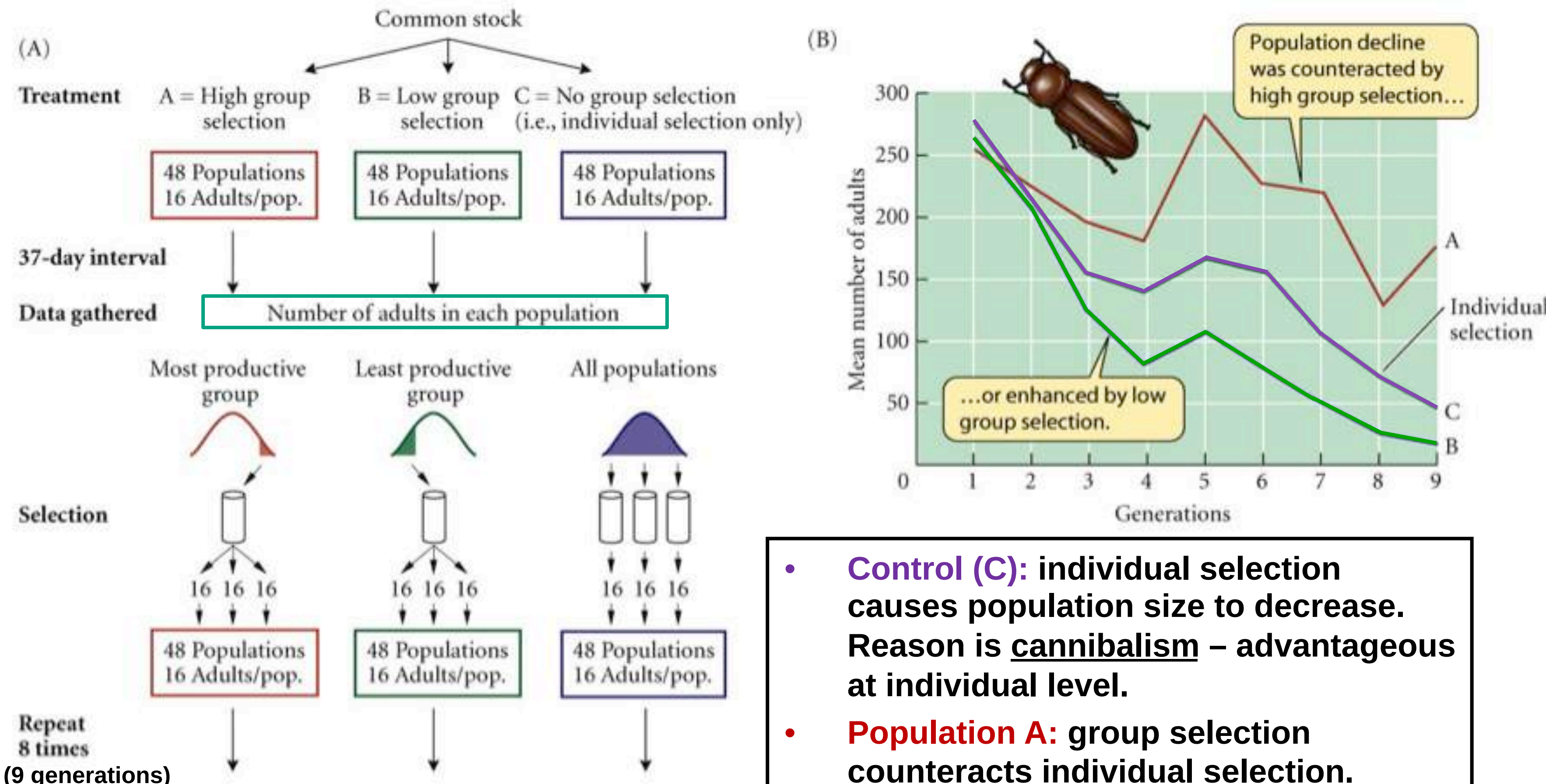


John Maynard Smith

Can Group Selection Occur?

Experimental group selection

Tribolium castaneum **flour beetles (Wade 1977, 1979)**

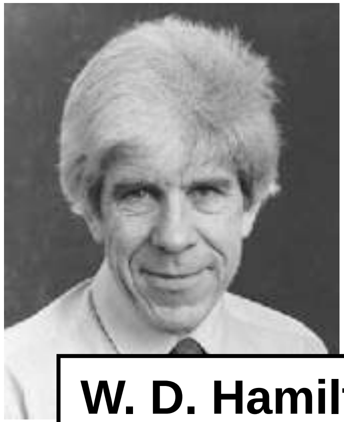


- **Control (C):** individual selection causes population size to decrease. Reason is <u>cannibalism</u> – advantageous at individual level.
- **Population A:** group selection counteracts individual selection.
- **Population B:** group selection reinforces individual selection.

Does Group Selection occur in Nature?

Kin Selection

1. Kin selection (William D. Hamilton, 1964): Altruistic behavior toward *very close relatives.* Reconciles group selection with individual selection



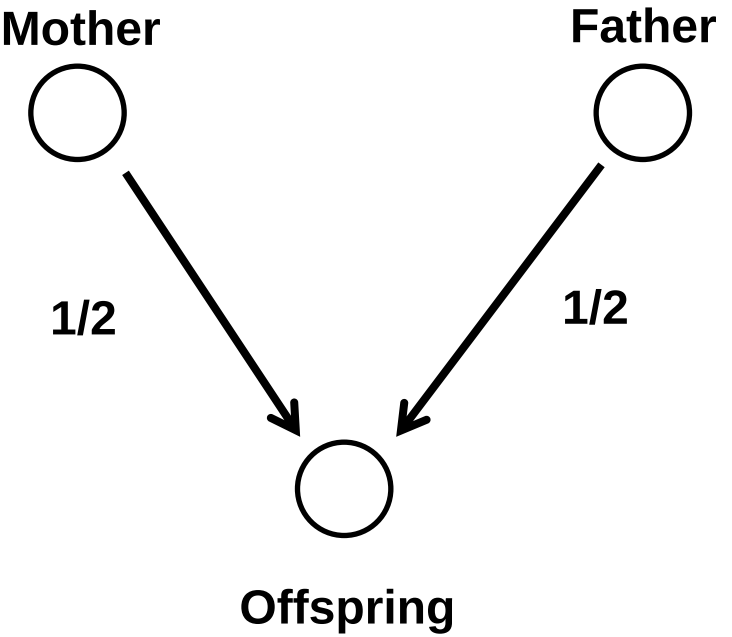
W. D. Hamilton

- When you help kin, then you are helping (at least to some extent) your own genes, and therefore yourself
- So: Your fitness = direct fitness + proportion of the fitness you confer on genes that you share with your relatives = Inclusive fitness

Kin Selection

- **Kinship is based on degree of relatedness of individuals.**
- **Darwin first recognized greater cooperation among relatives (1859).**
- **Degree of relatedness (r) measures the percentage of genes shared between individuals**
- **In diploid sexual organisms, each gets half its genes from each parent:**

  $r = 0.50$ This is a symmetrical relationship.



Mother
Father
1/2
1/2
Offspring

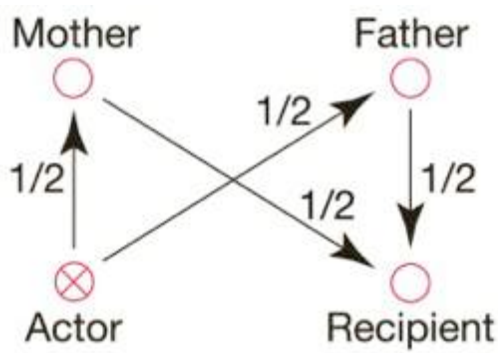
Degree of Relatedness (r)

Relationship	Relatedness (r)
Yourself	1
Identical Twins	1
Parent-Child	0.5
Siblings	0.5
Grandparent-Grandchild	0.25
Half Siblings	0.25
Aunts/Uncles	0.25
Cousins	0.125

Relatedness Calculations

- **Multiply to find the probability of success events. (e.g. probability rolling a 1 twice)**
- **Add to find the probability of mutually exclusive (independent) events. (e.g. probability of rolling a 1 or 2)**
- **So: multiply *r*'s that connect the various individuals; if 2 individuals are related through more than one connection, add the values for each connection.**

Full-siblings



Actor to recipient via mother:

$$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$$

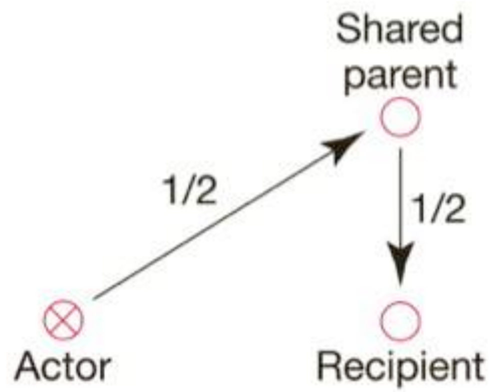
Actor to recipient via father:

$$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$$

Actor to recipient, sum:

$$r = \frac{1}{4} + \frac{1}{4} = \frac{1}{2}$$

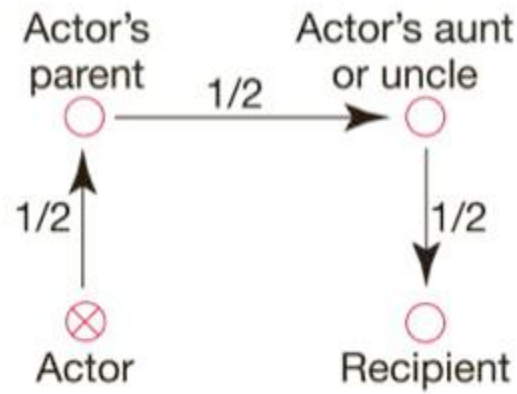
Half-siblings



Actor to recipient via shared parent:

$$r = \frac{1}{2} \times \frac{1}{2} = \frac{1}{4}$$

Cousins



$$r = \frac{1}{2} \times \frac{1}{2} \times \frac{1}{2} = \frac{1}{8}$$

Hamilton's Rule (1964)

Altruism will be favored when:

$$Br > C$$

The benefit to the recipient (B) weighted by the degree of relationship (r) is greater than the cost to the altruist (C):

Before you will consider helping your sibling (*r* = 0.5), the benefit to him/her must be twice the cost to you

$$(B/2) > C \text{ or } B > 2C$$

J. B. S. Haldane

So, should you give up 1 offspring, if you can help your sibling have 3 more?

$3*0.5 > 1$ **Yes**

When once asked if he would risk his life to save a drowning man, Haldane replied, "No. But I would to save two brothers or eight cousins." (B > 8C)

Example: Lions. Prides usually consist of closely related females and 1 male.

Non-mated females help raise cubs: if you didn’t have any offspring, it pays to raise your sisters offspring, since you share ½ your genes with her, and thus 1/4 your genes with her cubs.

Many similar examples in mammals and birds.

Examples of Kin Selection: Social Insects

Eusocial – defined by a multigenerational colony with non-reproductive castes and a minority reproductive caste

Often, only a single queen reproduces; 1,000's of sterile workers maintain colony.

Why would workers totally give up reproduction?

Special case of kin selection: r = 0.75

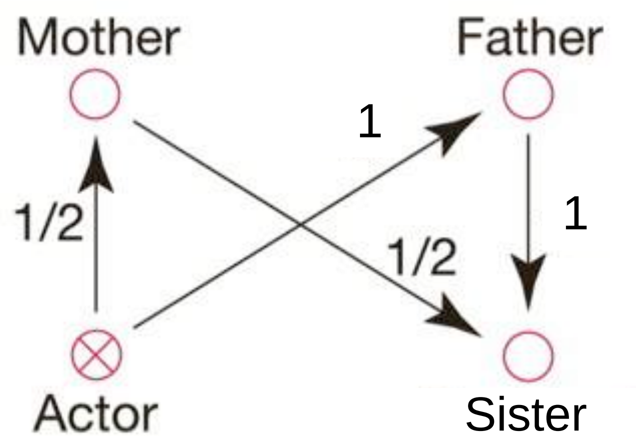
A special case of kin selection: Haplodiploidy

Degrees of relatedness in haplodiploid species under outbreeding

	Daughter	Son	Mother	Father	Sister	Brother	Nephew/ Niece
Female	½	½	½	½	¾	¼	⅜
Male	1	0	1	0	½	½	¼

- **Haplodiploidy: females diploid (2N), males haploid (N). Males develop from unfertilized eggs.**
- **Under monogamy, r is high between sisters (¾) and low between sister-brother (¼).**

Haplodiploid sister relationship



Actor to recipient via mother:

$$r = \tfrac{1}{2} \times \tfrac{1}{2} = \tfrac{1}{4}$$

Actor to recipient via father:

$$r = (1 \times 1) \times (\tfrac{1}{2}) = \tfrac{1}{2}$$

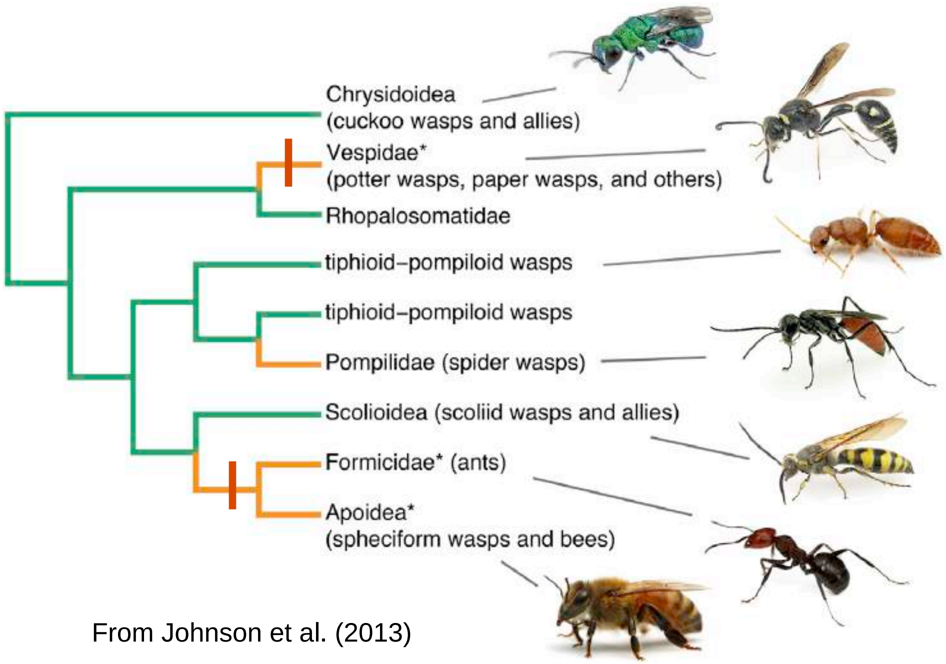
Actor to recipient, sum:

$$r = \tfrac{1}{4} + \tfrac{1}{2} = \tfrac{3}{4}$$

- If females can add more sisters to the world, at the cost of their own offspring, they can trade an $r = \frac{1}{2}$ for an $r = \frac{3}{4}$
- And because they're less related to their brothers, they need to raise more sisters than brothers
- This genetic system is predisposed to evolving eusociality.

Eusociality has evolved multiple times

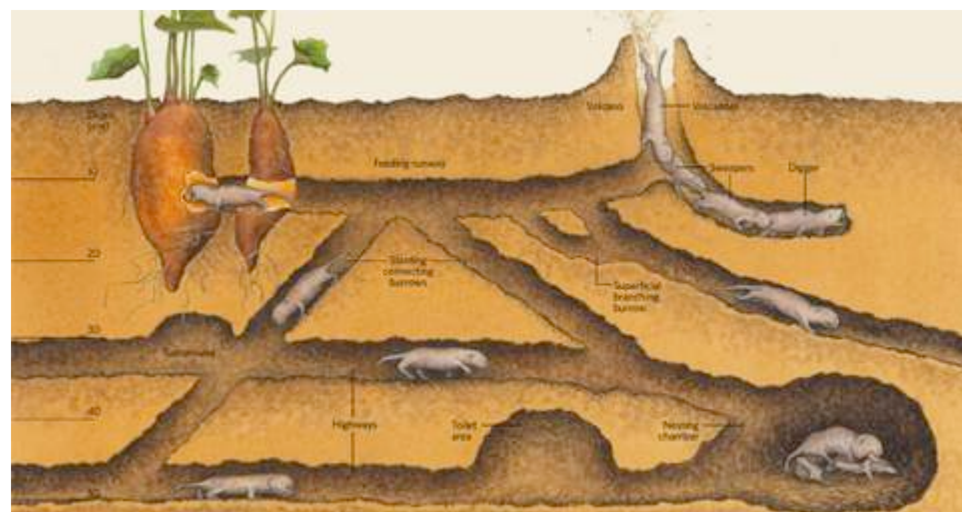
Hymenoptera



From Johnson et al. (2013)

Evolved separately in **termites** (cockroaches)

And once in **mammals**



And once in **shrimp!**

higher levels

- **Lineage**
- **Species**
- **Trait group**
- **Kin group**

Individual organism

lower levels

- **Cell line**
- **Organelle**
- **Gene**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Tit-for-Tat Altruism in Vampire Bats

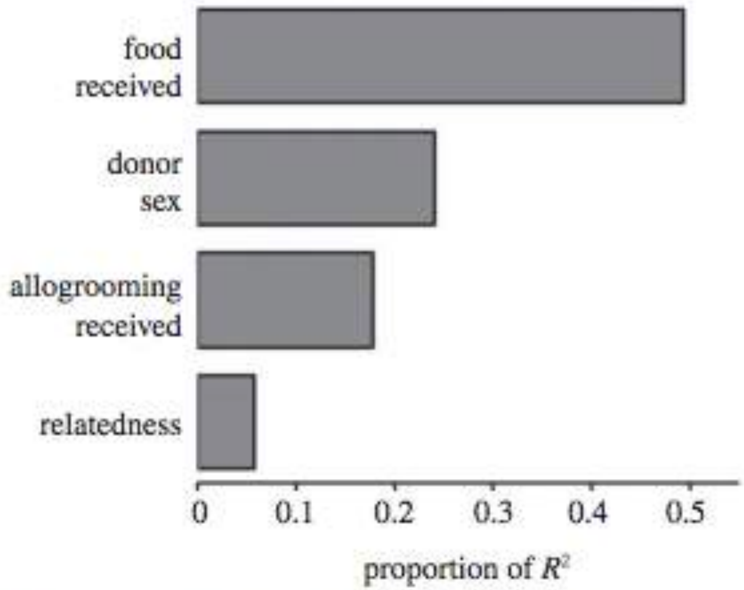


Figure 2. Relative importance on food donated of several predictors. Proportion of R^2 is shown for four predictor variables. An interaction effect (see text) is not shown. The full model explained 38% of the variation in food donated.

From Carter & Wilkinson (2013)

Species and Lineage Level

higher levels

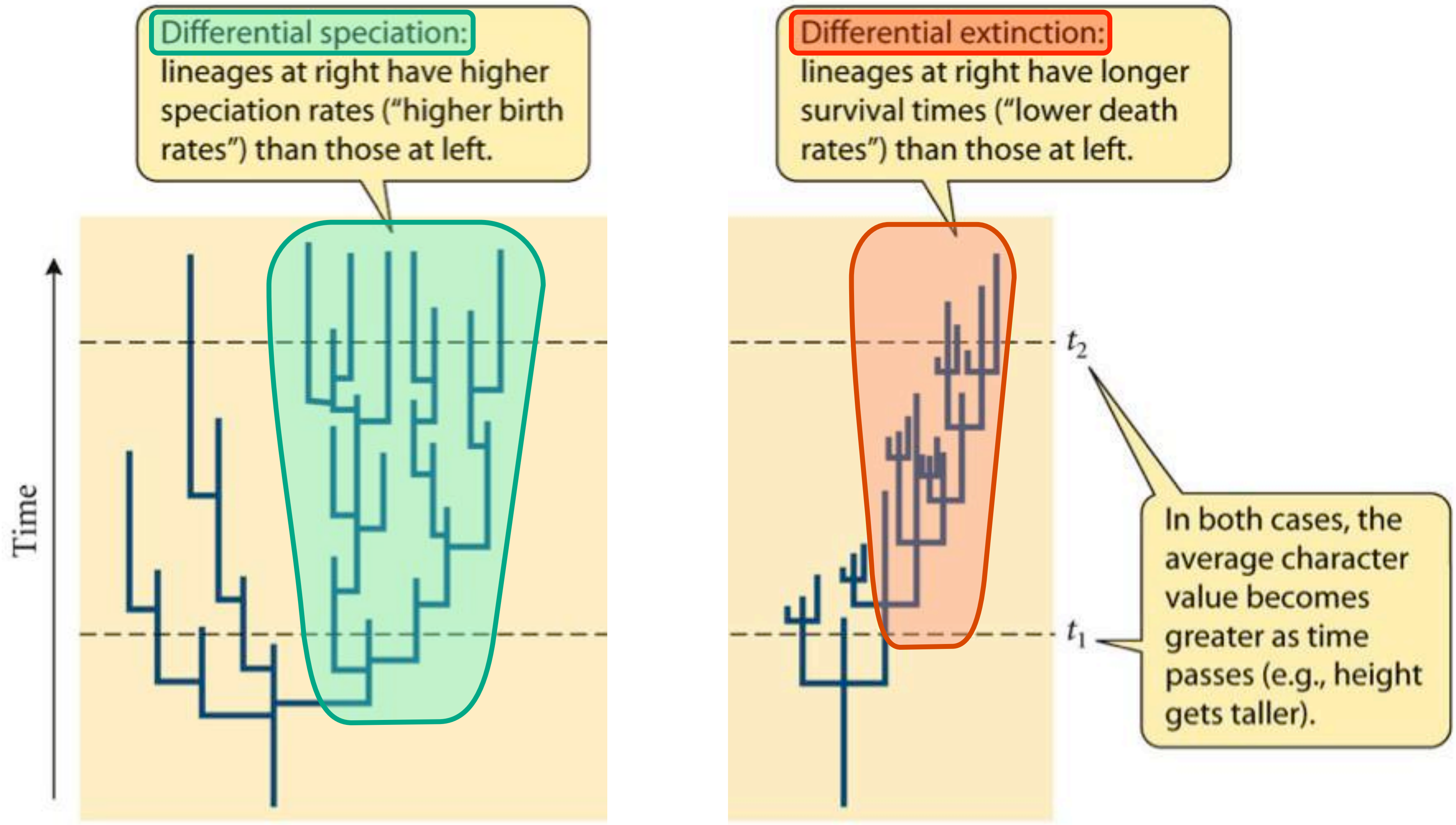
- Lineage
- Species
- Trait group
- Kin group

Individual organism

lower levels

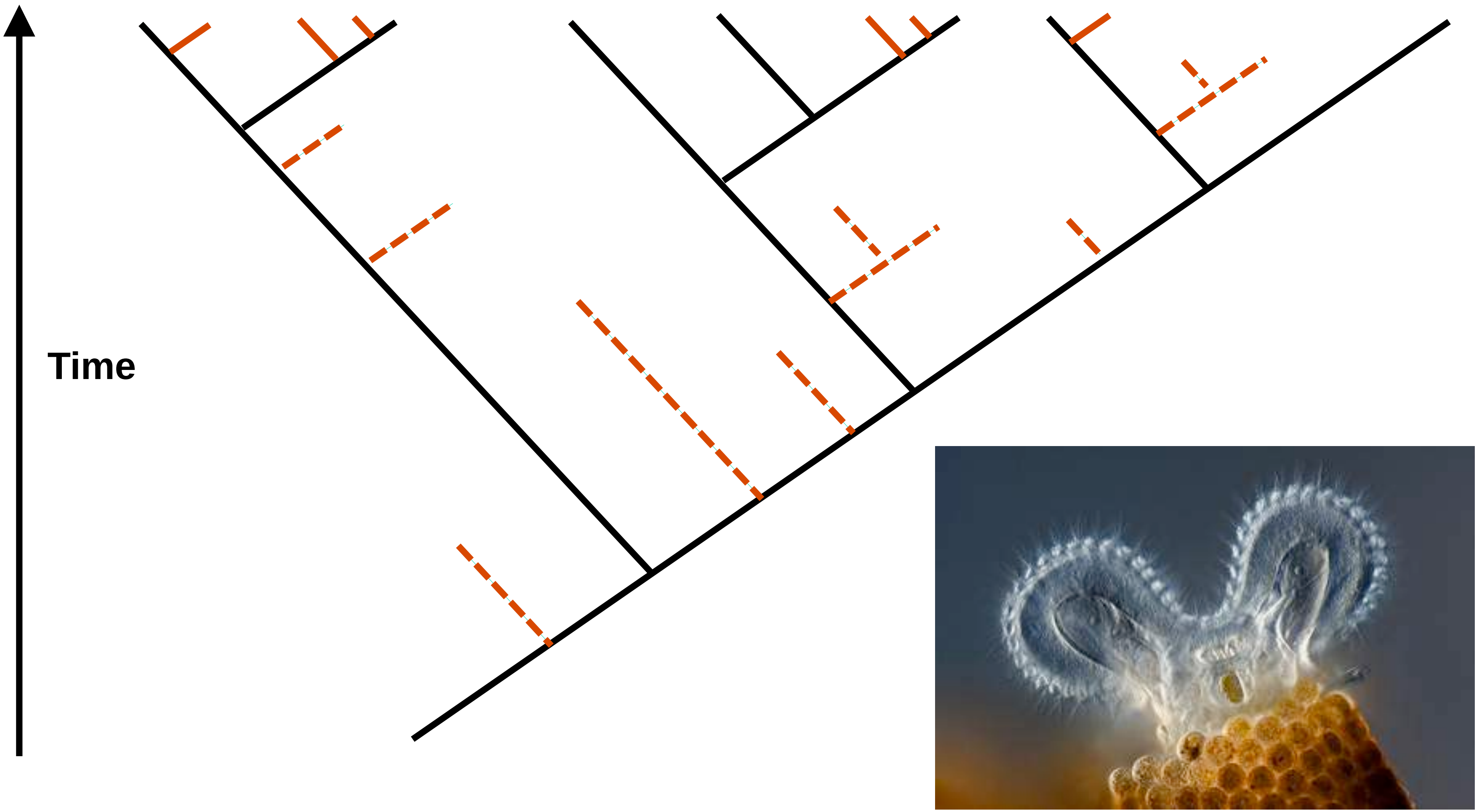
- Cell line
- Organelle
- Gene

Selection at the Species and Lineages Level

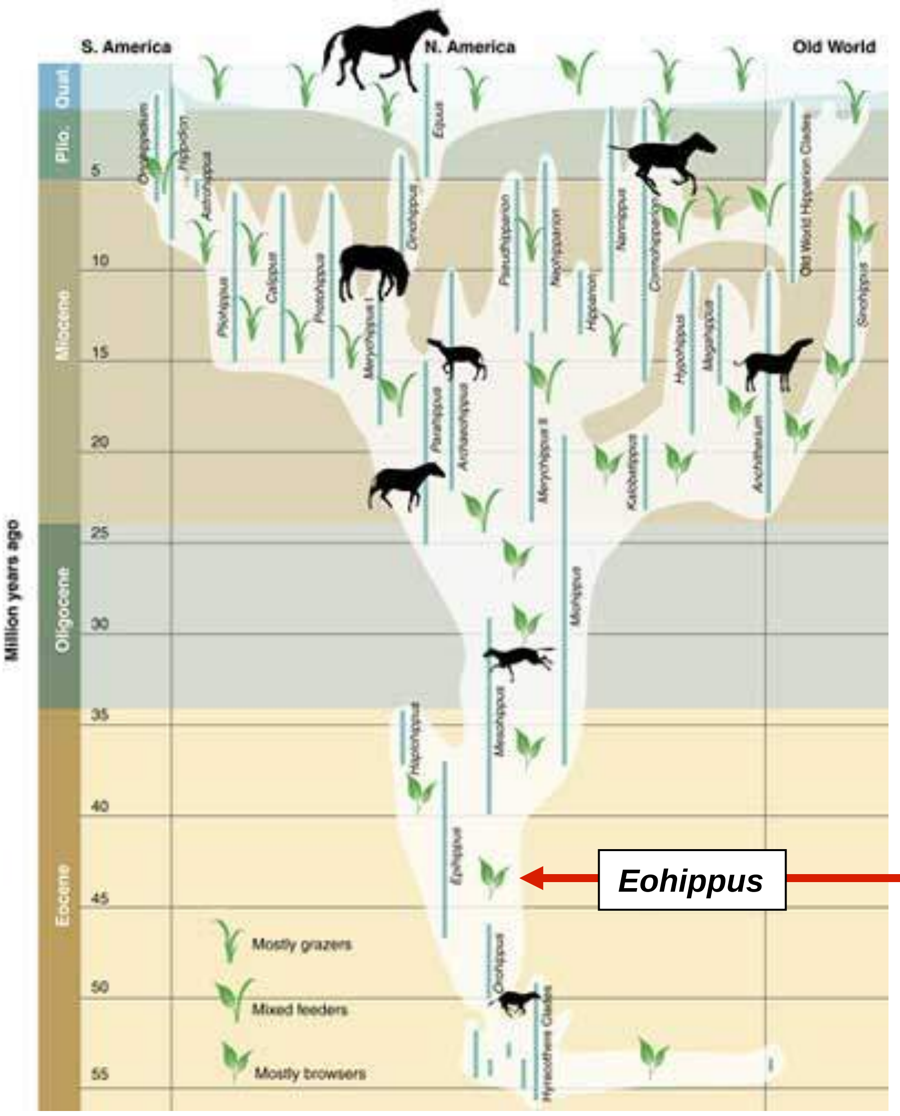


Ultimate result:
Lineages on the right increase in number

Lineage Selection:
Sexual vs. Asexual Taxa



Lineage selection in horse evolution



"Orthogenesis"

- **-- larger body size**
- **-- longer legs**
- **-- longer teeth**
- **-- fewer toes**

Natural Selection

higher
levels

Lineage
Species
Trait Group
Kin Group
Individual
Cell
Organelle
Gene

lower
levels

Levels of Selection:
"Multilevel Selection Theory"