Fundamentals of the Theory of Evolution

Lecturer:prof. Jacek Radwan

Recommended reading and course materials:

evobio.home.amu.edu.pl

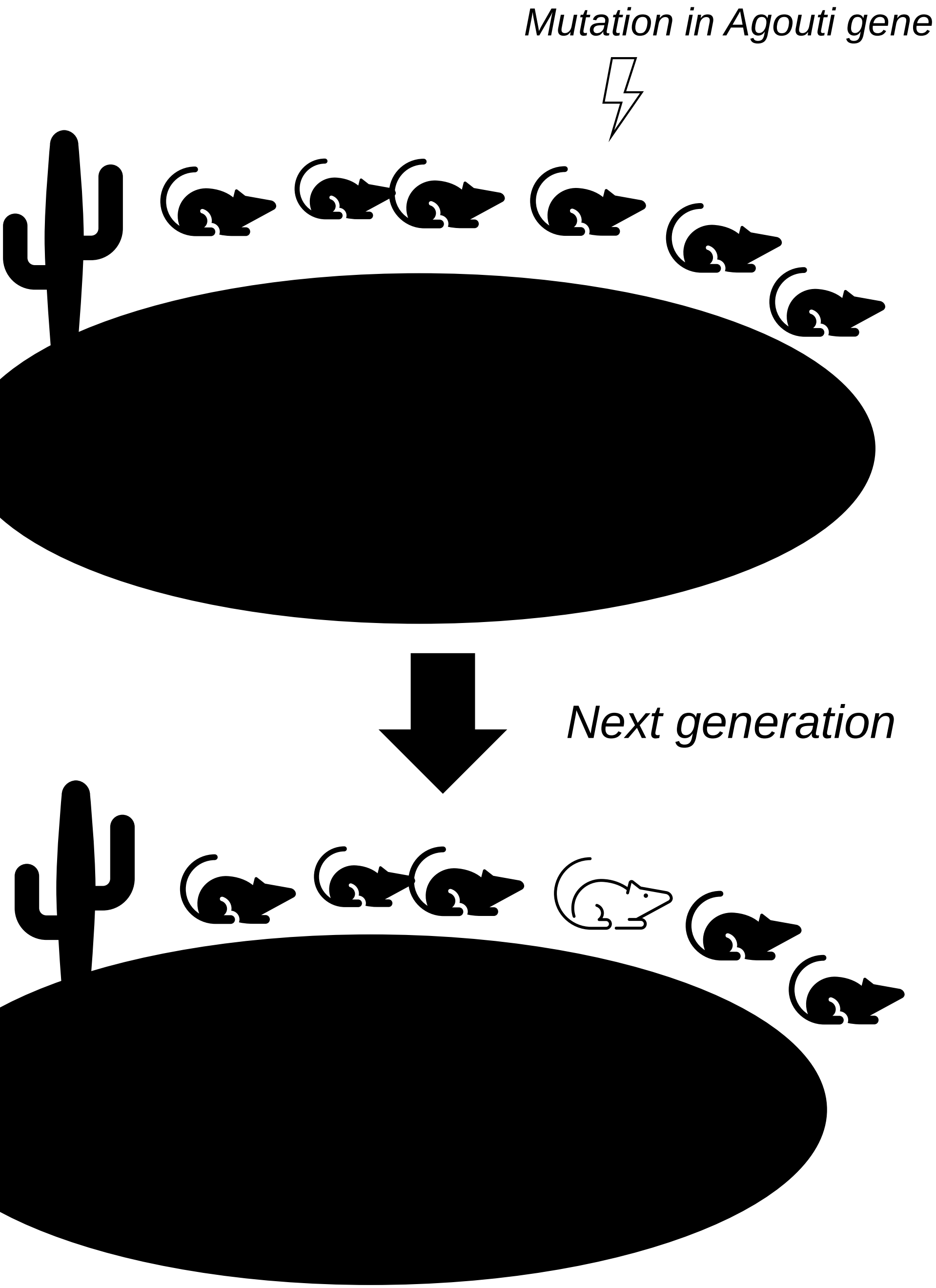
Douglas Futuyma „Evolution”

Additional reading:
J. A. Coyne „Why evolution is true”
R, Dawkins: „Blind Watchmaker”

Exam: written test, >50% correct answers

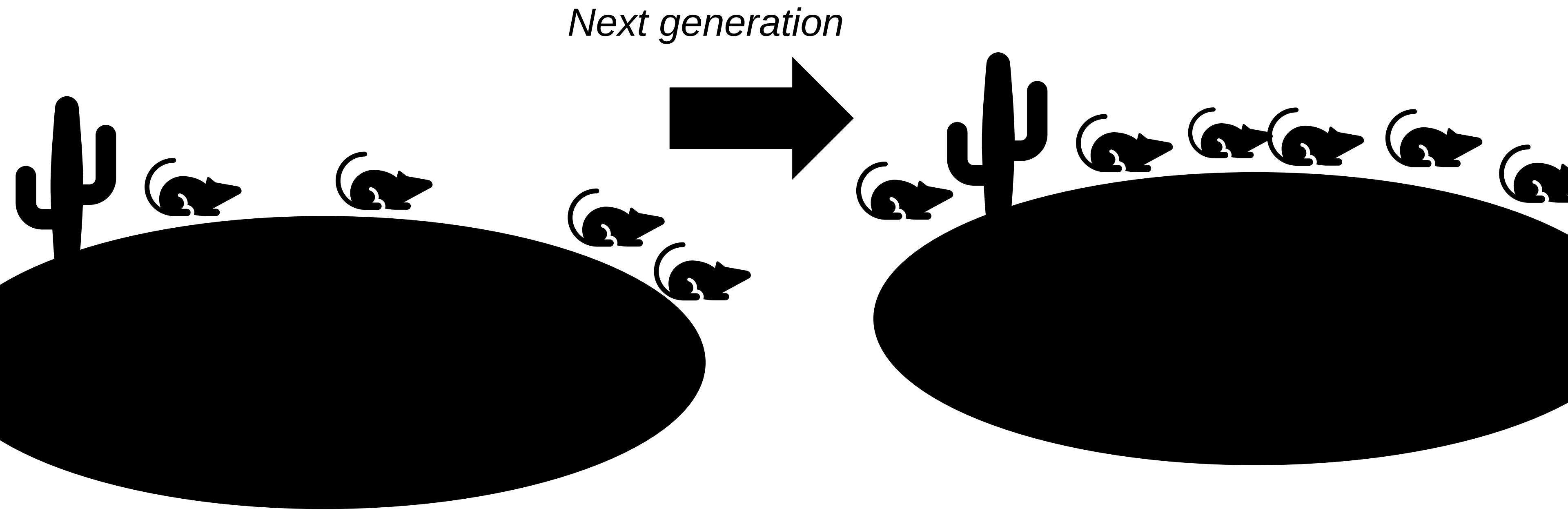
One of the conditions of evolution by natural selection is:

( ) inheritance of traits determining lifetime reproductive success
( ) non-overlapping generations
( ) inheritance of acquired traits
( ) …

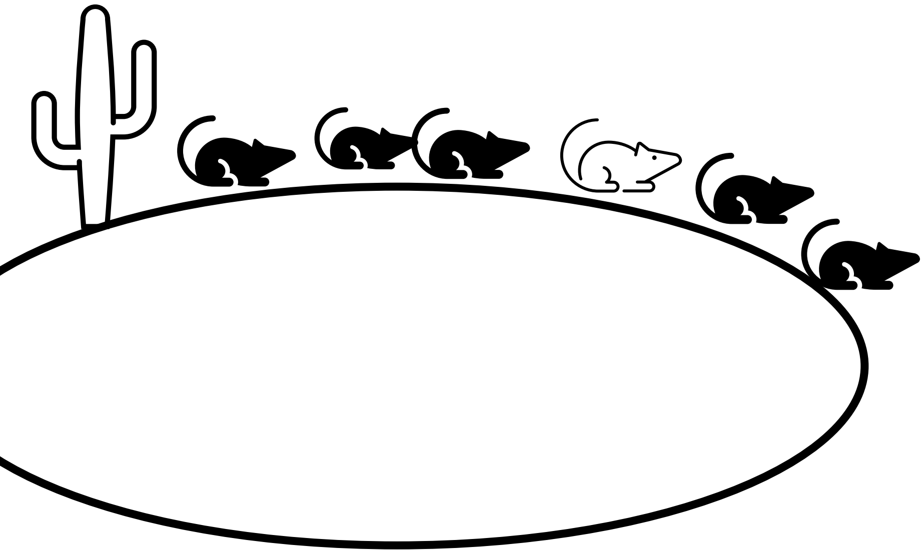

Mutation in Agouti gene
Next generation

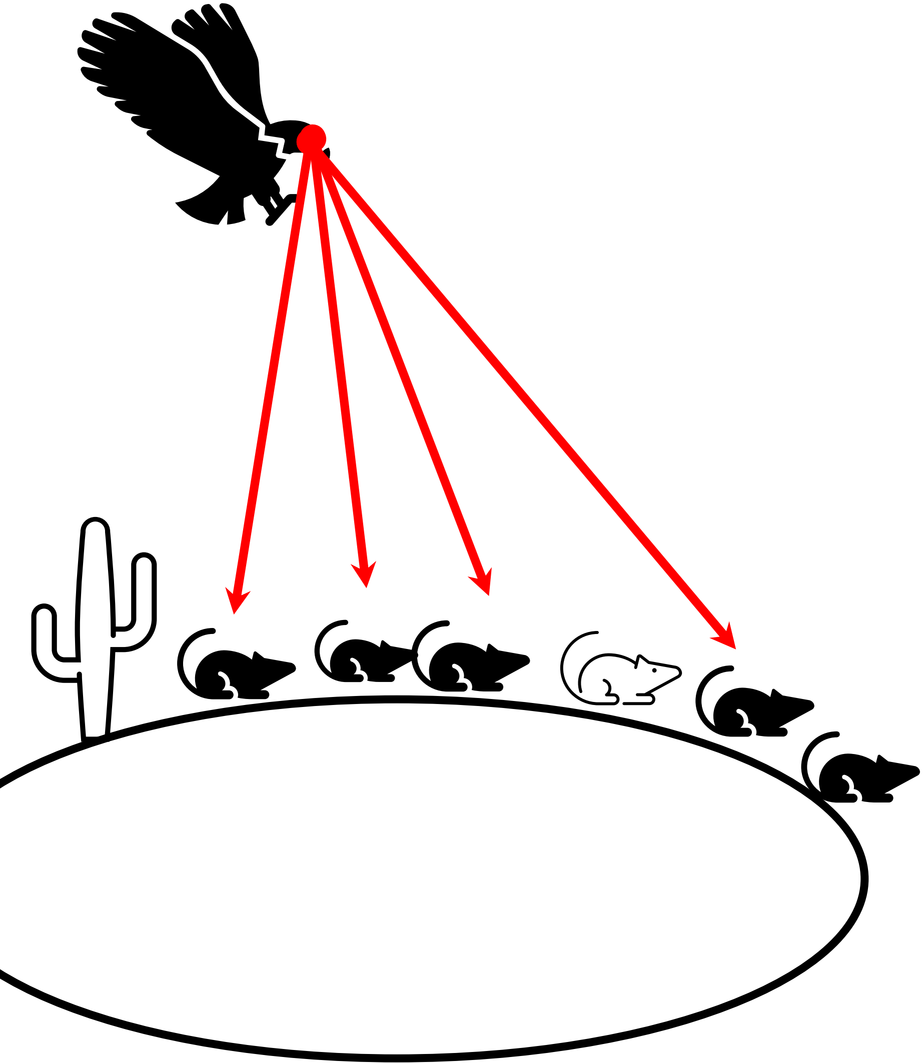
Mutations are random, and therefore mostly detrimental

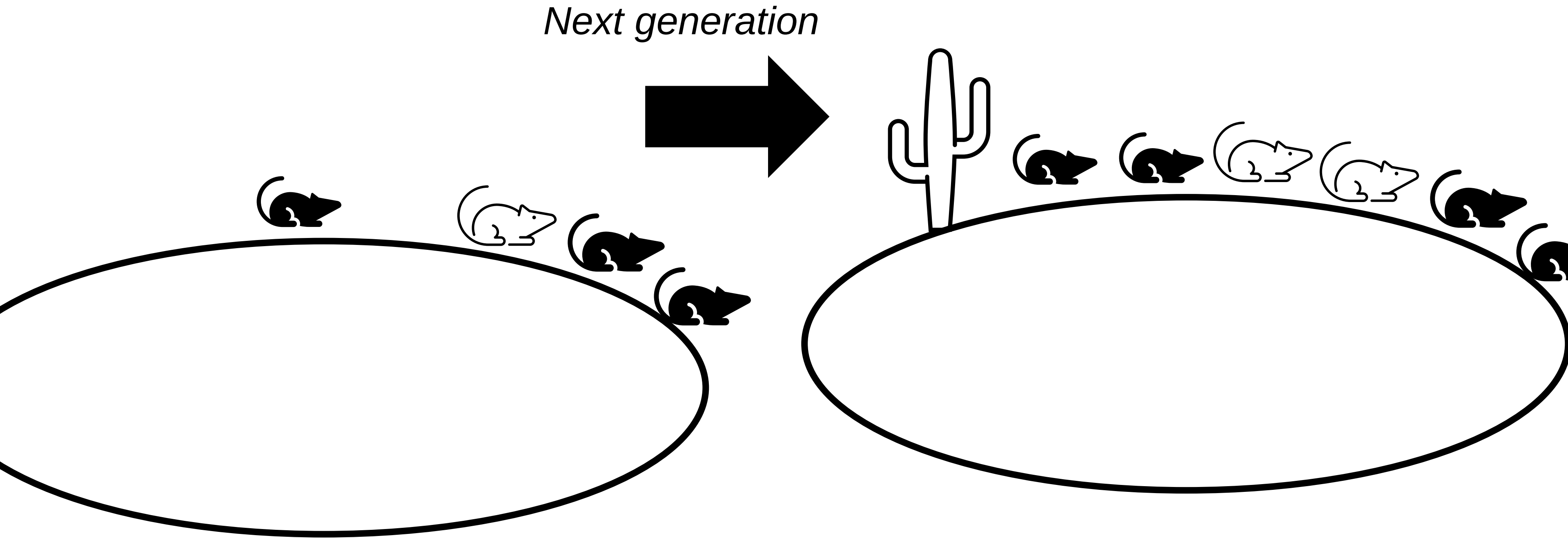
Mutation in Agouti gene decreses fitness of its beares
= has low chance to be passed to next generation



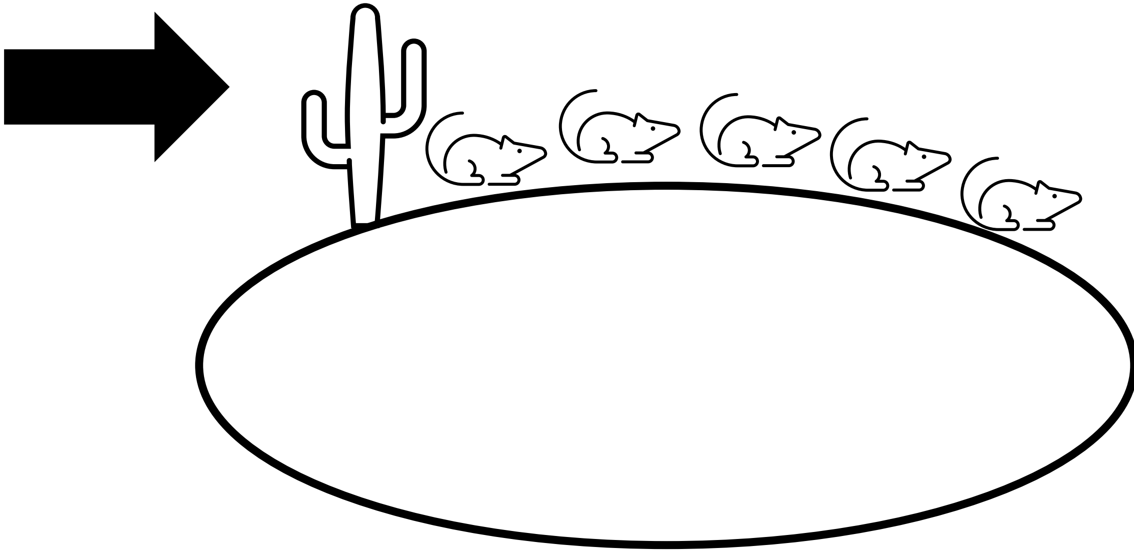
Colonisation of new area/environmental change







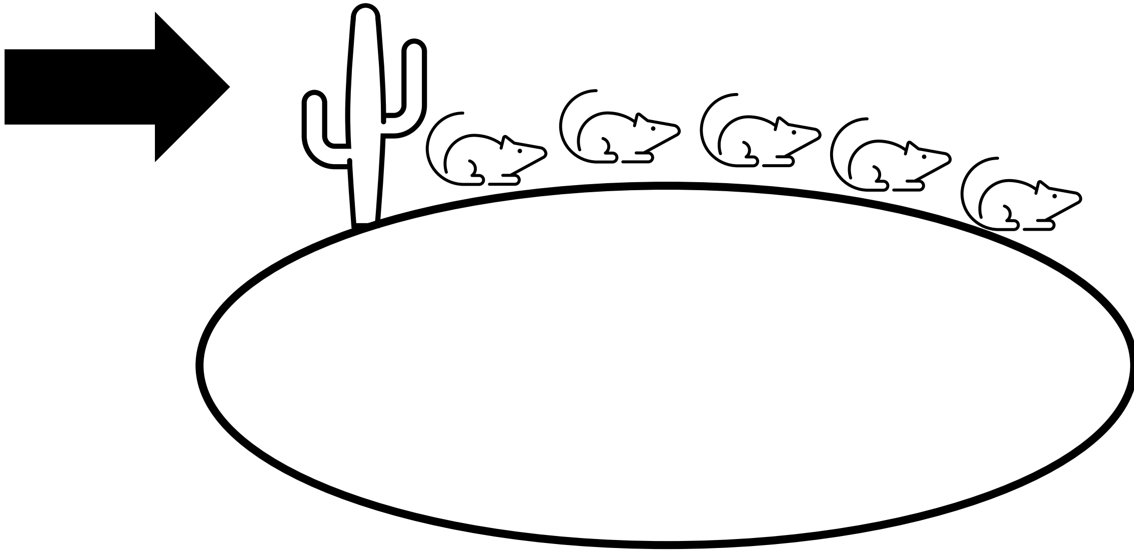
Next generation



Several genetations

Sometime mutations are adaptive!

More generations



Evolution of antibiotic resitance

- In pre-antibiotic era, **30%** deaths in USA caused by bacteria
- *Since discovery of penicillin (1928) over a dozen of new antibiotic classes were introduced*
- *With time, bacteria acquire resistence to each of them!*

Davies J, Davies D, Microbiol Mol Biol Rev. 2010 74: 417–433.

A number of enzymatic variants decomposing β-laktams (anti gram-negative bacteria, eg. Salmonella enterica, Klebsiella pneumoniae)

Evolution of antibiotic resistance in real time

Evolution by natural selection

- ***Heritable variation****: random mutations*
- ***Selection****: strains capable of faster growth replace competitors*

www.npr.org/sections/health-shots/2016/09/08/492965889/watch-bacteria-invade-antibiotics-and-transform-into-superbugs

Selection on human personality traits

Personalities are heritable (Vervij et al. 2012)

- Standard psychological survey of 30 000 USA inhabitants
- More extravert, less conscientious and less open persons had more descendants

Evolution in the city

Gray cross (bridge) spiders *Larinioides sclopetarius* in cities built nets near artificial light sources (Heiling, A. 1999 BES)

In contrast to their forest conspecifics, spindle ermines *Yponomeuta cagnagella* living in cities avoid light

Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution

Florian Altermatt[1,2,3] and Dieter Ebert[3]

Example questions addressed by evolutionary biology

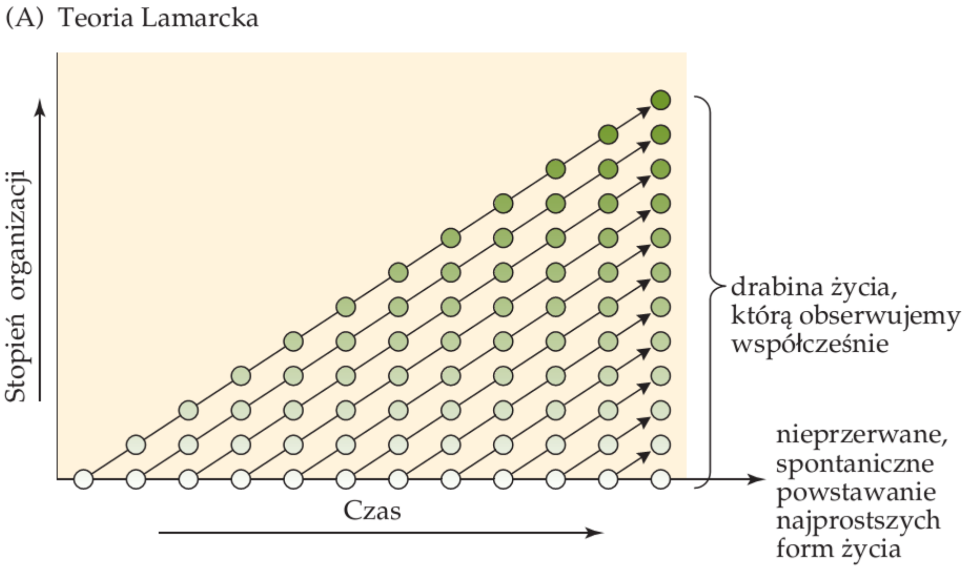
- Do we still evolve and in which direction?
- Why do we age?
- Why organism evolve sexually despite availability of simpler options?
- Why some species change sex during their lifetime?
- Why are males often more colourful than females?
- Why incest can be harmful?
- Why microroganisms sometimes kill their hosts?

„Nothing in biology makes sense except in the light of evolution”

Theodosius Dobzhansky

Before Darwin

- 1735: Linneus developed hierarhical taxonomy reflecting in his view creators' fondness of order
- Georges Cuvier (1769-1832), documented with detailed anatomical studies that many forms known from fossils went extinct
- 1809 Lamarck's in his philosophy of zoology argued, that:
  - organisms arise spontaneously from inorganic matter
  - evolve via inheritance of changes acquired by using organs
  - the ladder of life reflects the time since origin



Charles Darwin

- Beagle journey (1832-35):
  - observed phenotypic variation in mockingbirs on different island of Galapagos
  - noted similarities between fossil and extant south-American species
- An Essay on the Principle of Population btThomasa Malthusa: food production limits population growth

za zgodą: The American Philosophical Library

CHARLES ROBERT DARWIN

“the most defective in ...necessary qualities would be the most subject to perish, and that those who employed them in greatest perfection would be best preserved” (James Hutton **1794**).

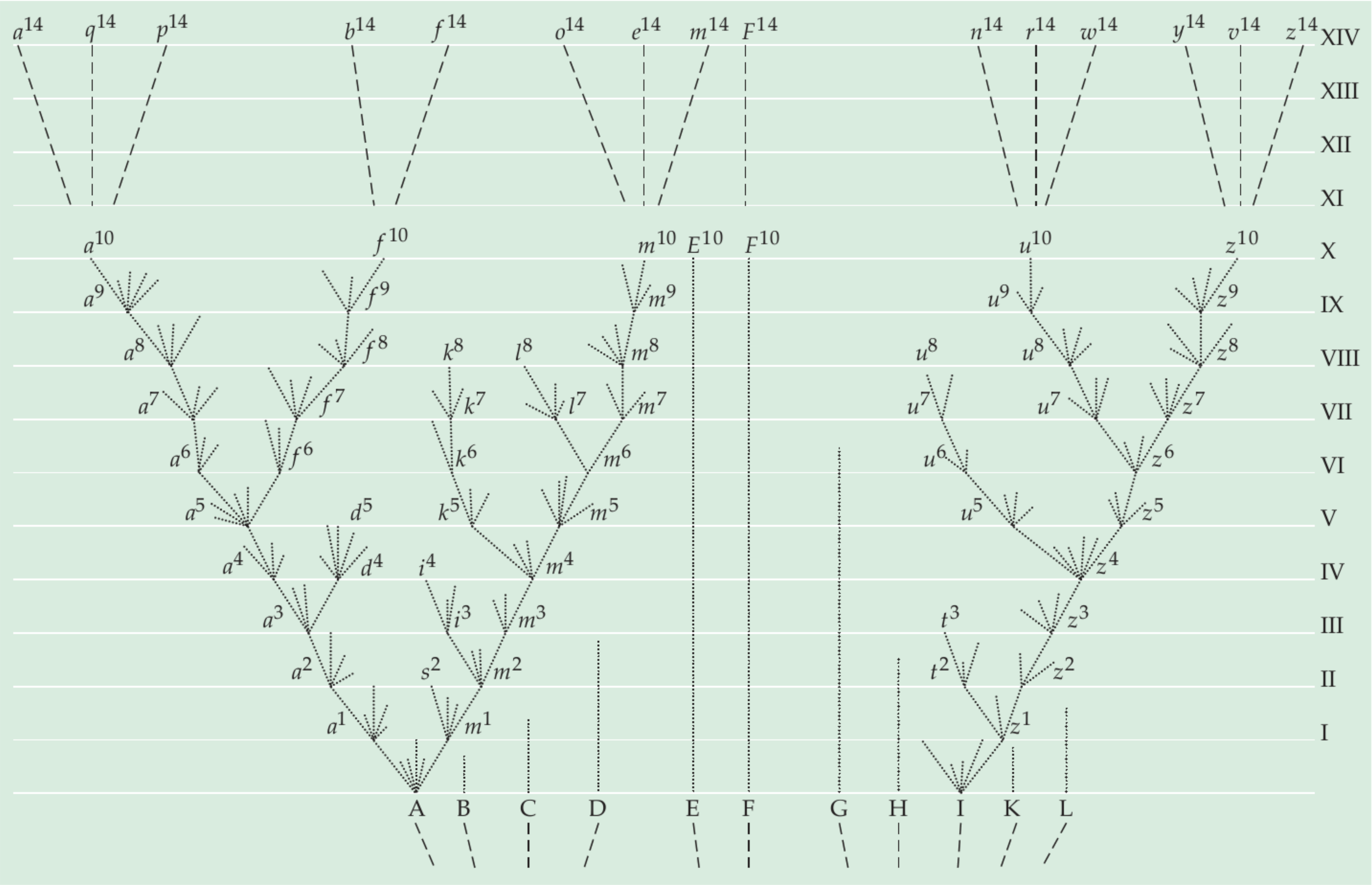
„The use of the infinite seedling varieties in the families of plants…procure room for full extension, and thus affording, at the same time, a continual selection of the strongest, best circumstance-suited, for reproduction….. and even in man himself… is referrible to nearly similar selecting law—the weaker individual sinking under the ill treatment of the stronger, or under the common hardship”.

Patrick Matthew 1831 *On Naval Timber and Arboriculture*.

- 1858 - Darwin receives manuscript of Alfred Wallace, who independently developed the theory of natural selection
- 1859 - publication of *The origin of species by Means of Natural Selection, or the Preservation of Favoured Races in the Struggle for Life*
- 1930te – Fisher, Haldane, Wright develop genetic theory of natural selection (population genetics)

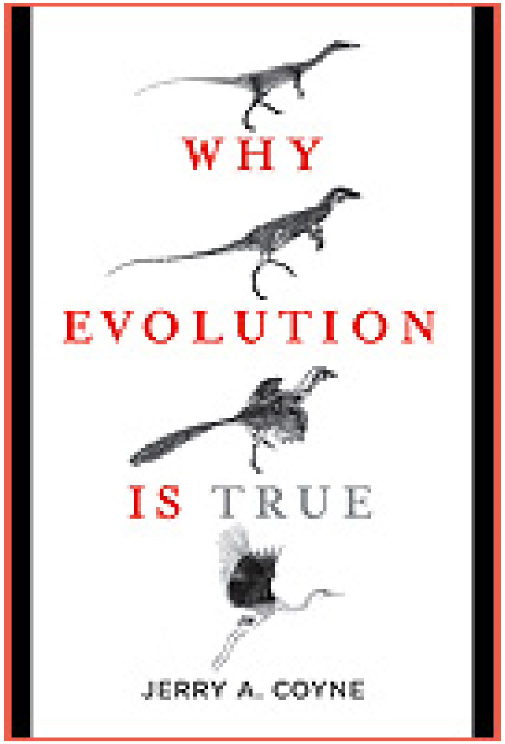
- All organisms evolved from a common ancestor by means of **natural selection**

- Natural selection is a consequence of differential survival and/or reproduction caused by variation in heritable traits



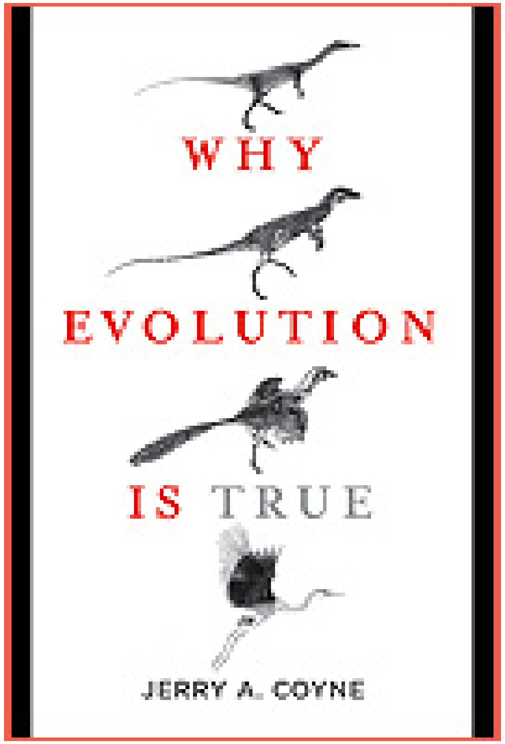
Darwin's diagram showing his view of evolution

Evolution: theory or fact?


WHY EVOLUTION IS TRUE

JERRY A. COYNE

Evolution is a fact explained by the theory of natural selection



Scientific theory: a coherent group of propositions formulated to explain a group of facts or phenomena in the natural world and repeatedly confirmed through experiment or observation (Oksford dictionary*)*

Facts supporting evolution:

-Documented changes in fossil record

-Homologies reflecting common origin

-Observations of evolution in real time

-Agreement between predictions of natural selection and facts

- Fossil forms are different from extant species
- Dating rocks enables re-construction of evolutionary history

Radiometic dating

- ,

Isotop		decay product	t1/2 (yeas)
Ur238	->	Pb-206	4.50 x 10^9
Ur235	->	Pb207	7.04 x 10^7
K-40	->	Ar-40	1.25 x 10^9

Fossils are found in sedimentary which can be dated based on layered volcanic rocks.

Molecular clock: divergence of protein and nucleotide sequences allow estimation of time from common ancestor

- In 1960ties: observation that protein sequences are more dissimilar with time since the split between taxa inferred based on fossil record
- Presently DNA sequences are used
- Molecular clock needs to be calibrated with radioactive dating

Some changes in the history of life were drastic: geological eras are defined by specific fossils

Fossils are preserved only in particular conditions – most past life perished

Mass extinctions were followed by recovery of biodivierstiy (but new species)

Sixths mass extinction of Anthropocene era

- Extinction rate comparable to five mass extinctions (100 faster than in other periods) *S. L. Pimm et al., Science, 344, 1246752 (2014); G. Ceballos et al., Sci. Adv. 1, e1400253 (2015).*

- To recover biodiversity, millions of years of evolution is needed, and space!

Hoffmann i in. 2010 Science

- Expansion of agriculture
- Forest cutting
- Overexploitation (eg. fisheries)
- Purposeful eradication and trophy hunting
- Invasive species

History of life in fossil record

- Earh formed ca. 4.5 bya
- First half bya conditions adverse to life
- Fist traces of life 3.6-3.8 bya: „chemical fossils”:
  - Kerogen („immature oil”)
  - stromatolites - sedimentary formations of due to activity mainly of photosynthetic microorganisms such as cyanobacteria

First life forms left little traces

Self-replication is a universal property of life

How life originated = how entities characterised by heritable variation formed in chemical environment of early Earth w jaki sposób w chemicznym środowisku pierwotnej (Maynard-Smith i Szathmary)

Prebiotic synthesis: Stanley Miller experiment and alternatives

In highly reducing atmosphere with H_2, CH_4, NH_3 aminoacids, nucleotides and sugars can form

… but early atmosphere contained CO_2 i N_2 limiting organic synthesis

Such synthesis could occur in hydrothermal springs in oceans or on rock surphaces

De Duve: tioesthers (R'-COOH) involved in many basic biological processes could easily arise in primordial soup

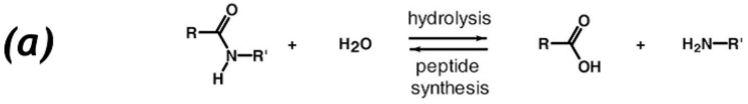
Chicken and egg problem: you need long DNA to produce protein enzymes, but you cannot replicate DNA accurately without proteins

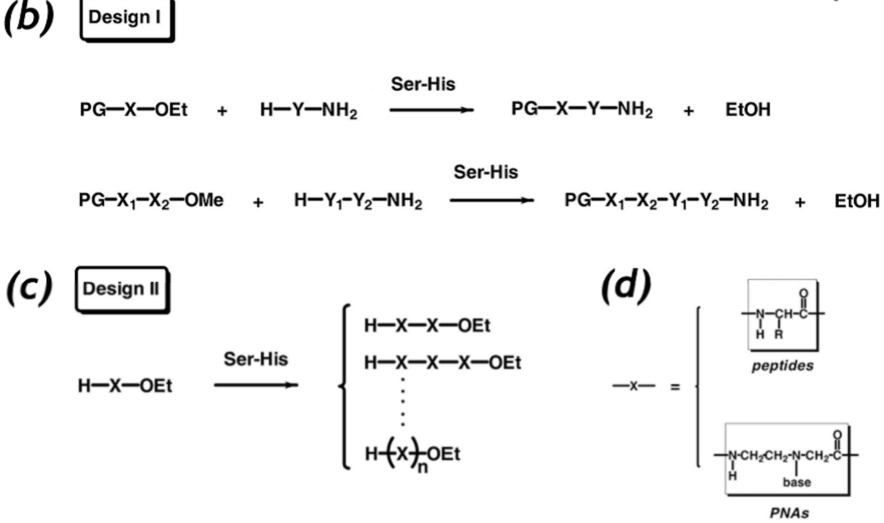
RNA world: RNA can be both replicator and an enzyme

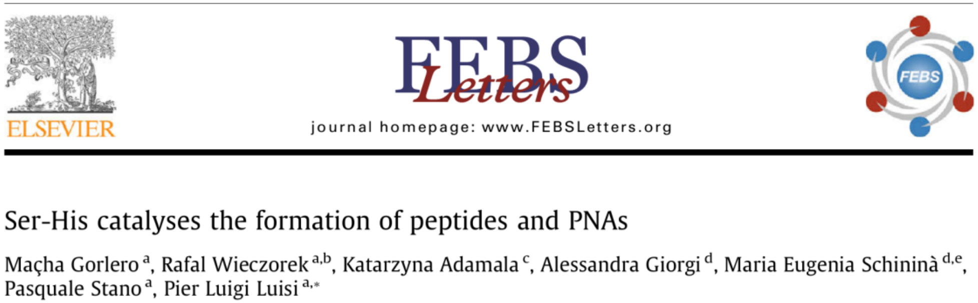
RNA can form complex 3D structures that have enzymatic functions (Cech & Altman)

Alternative: proteins first!
Some oligopeptides, e.g. Ser-His, Gly-Gly, Gly-Gly-Gly
san catalyse peptides and polynucleotides

Ser-His catalyses the formation of peptides and PNAs
Gorlero et al.







journal homepage: www.FEBSLetters.org

Ser-His catalyses the formation of peptides and PNAs

Maçha Gorlero[a], Rafal Wieczorek[a,b], Katarzyna Adamala[c], Alessandra Giorgi[d], Maria Eugenia Schininà[d,e], Pasquale Stano[a], Pier Luigi Luisi[a,*] *For interested:*

Prof. Jack Szostak – lectures on the „origin of life” available on YouTube

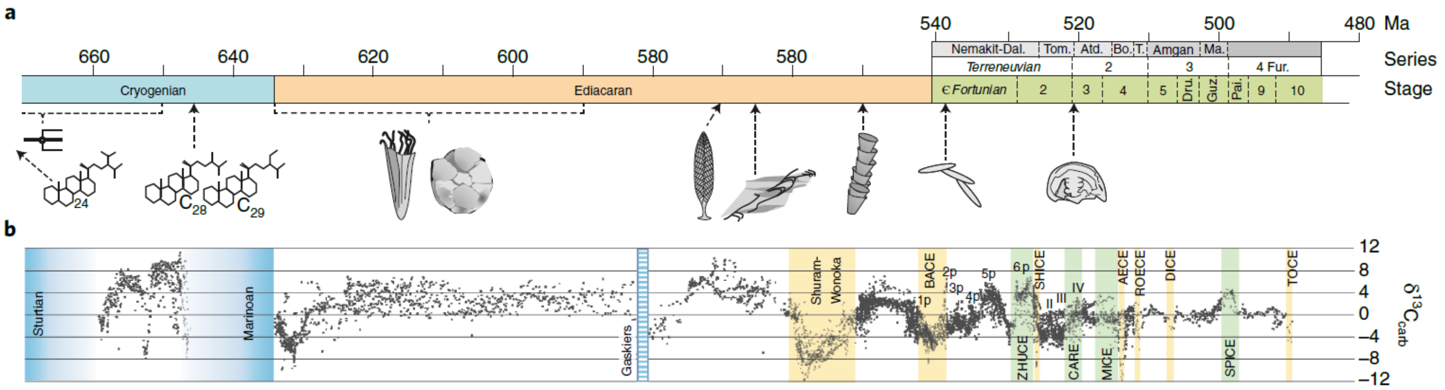
Appearance of multicellular orgnisms

- Doushantuo fauna (China) 635-551 mln lat
- Ediacara fauna (Australia) 575-542 mln lat

- unclear relation to currently living organisms
- disappear before „cambrian explosion”

Cambrian explosion?

- 542 to 505 mya 11/20 basic body plans found in fossil record (Burgess Shale, Canada; Yunnan, Chiny)
- Wray et al. (1996): molecular divergence suggested that it started earlier (some 1bya)
- geochemical analyses point to continuum between Ediacaran and Cambrian faunas (Woods et al. 2019; Nature Ecology and Evolution)



Land Plants (Ordovician, ca. 450 mya)

Land animals

Only thee major taxa well adapted to land (arthropods, molluscs and vertebrates)

Hominids
appeared only
5 mya

Observing evolution in real time: Darwin zwrócił uwagę, że selekcja hodowlana może spowodować różnicującą ewolucję fenotypów

Real-time evolution in nature

Ewolucja ryjka służącego do przebijania strąków u pluskwiaka *Jadera haematoloma*

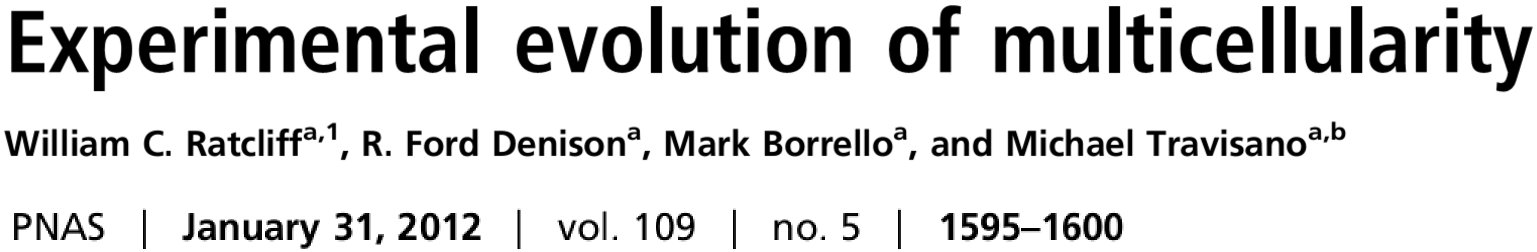
Koelreuteria elegans

(introdukowana)

serconasiennica

(rodzima)

Real-time evolution in the lab:



Experimental evolution of multicellularity

William C. Ratcliff[a,1], R. Ford Denison[a], Mark Borrello[a], and Michael Travisano[a,b]

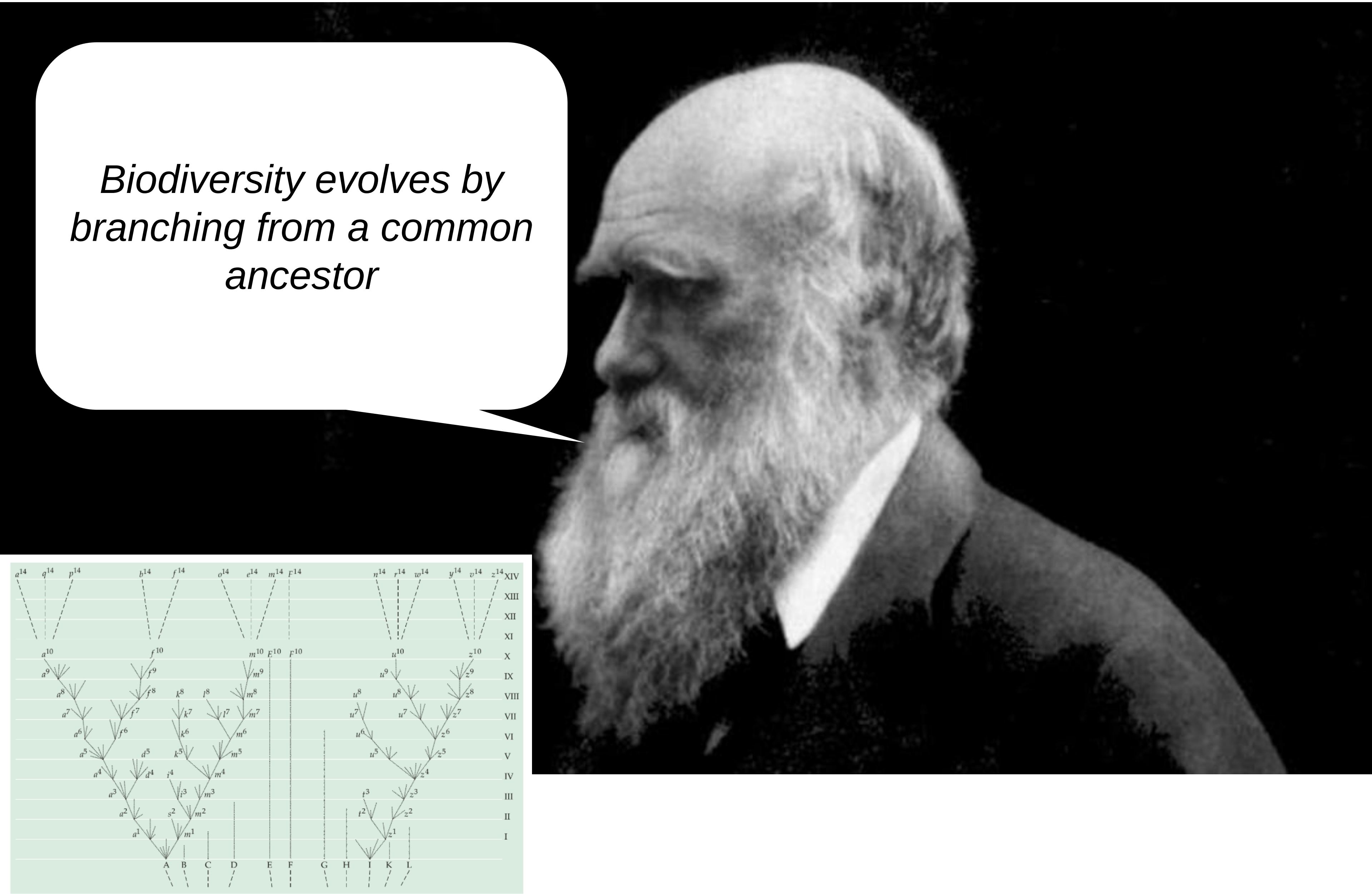
PNAS | **January 31, 2012** | vol. 109 | no. 5 | **1595–1600**

Po 60 transferach drożdży:

- Powtarzalna ewolucja wielokomórkowości na drodze adhezji komórek macierzystych i potomnych
- Ewolucja rozmnażania przez propagule
- Ewolucja cykli życiowych: rozmnażanie po osiągnięciu krytycznego rozmiaru

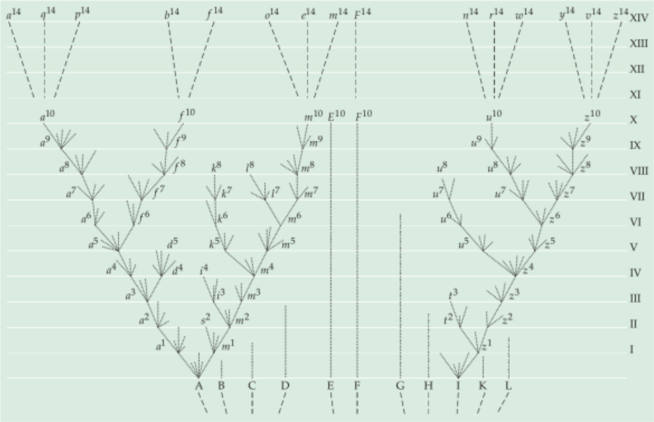
Boraas i in. 1998: w obecności orzęsków ewoluują 8-komórkowe agregaty *Chlorella*

Predictions supported by empirical findings



Phylogenetcially related organism inherit some traits form their ancestors

Evolutionary genealogy (phylogeny) is reconstructed based on shared homologous traits



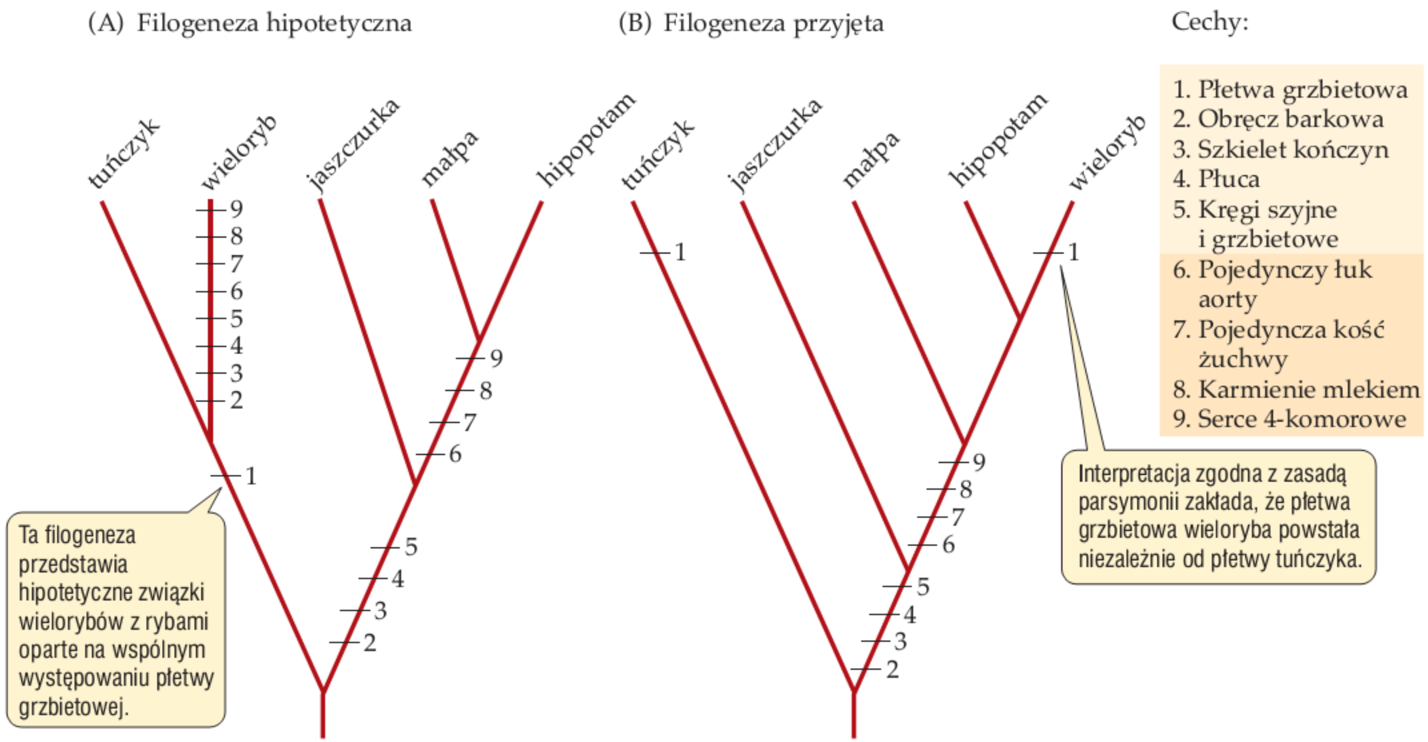
Homology – similarities inherited from common ancestor

Homoplasy – similarities that arose independently (convergently)

Evolution often proceeds by modification of existing structures, rather than creating them de novo

Some structures are homologous despite their modification for different functions

Parsimony principle: phylogeny reconstruction should assume fewest possible number of evolutionary changes



Ta filogeneza przedstawia hipotetyczne związki wielorybów z rybami oparte na wspólnym występowaniu płetwy grzbietowej.

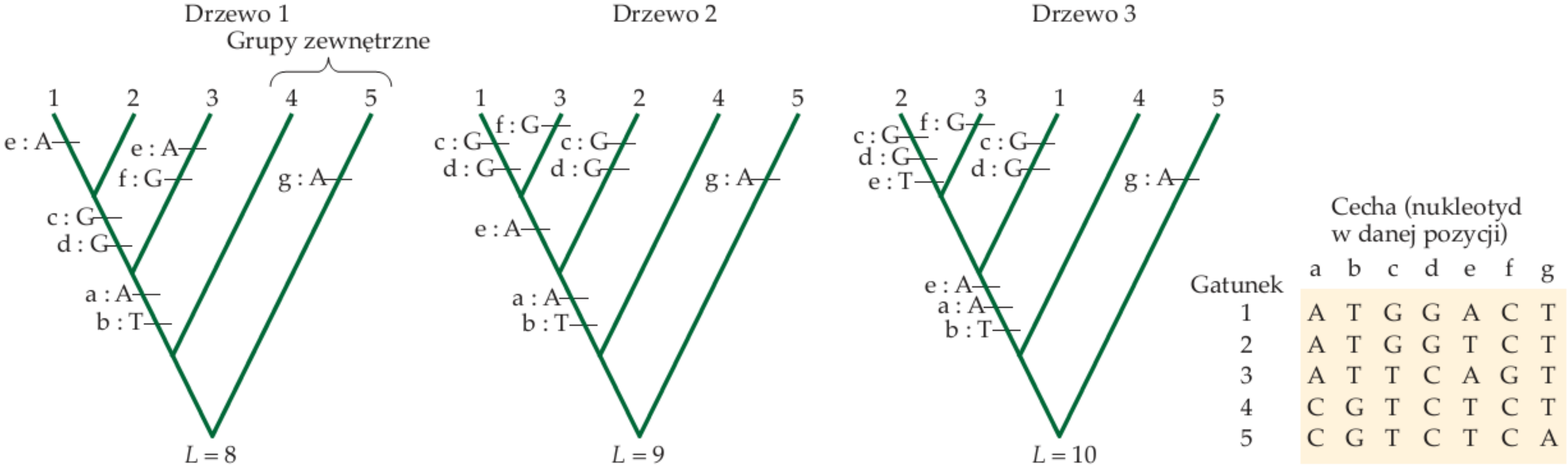
Interpretacja zgodna z zasadą parsymonii zakłada, że płetwa grzbietowa wieloryba powstała niezależnie od płetwy tuńczyka.

Cechy:

1. Płetwa grzbietowa
2. Obręcz barkowa
3. Szkielet kończyn
4. Płuca
5. Kręgi szyjne i grzbietowe
6. Pojedynczy łuk aorty
7. Pojedyncza kość żuchwy
8. Karmienie mlekiem
9. Serce 4-komorowe

Rycina 2.6 Dwie hipotetyczne filogenezy wielorybów. (A) Filogeneza hipotetyczna postulująca bliskie pokrewieństwo wielorybów i ryb (jak tuńczyk), oparta na wspólnym występowaniu płetwy grzbietowej. (B) Przyjęta jest filogeneza postulująca najbliższe pokrewieństwo wielorybów z innymi ssakami. Kreski oznaczają zmiany wybranych cech pojawiające się w danej filogenezie. Cechy 2–5 to jednorazowo powstałe synapomorfie czworonogów, a 6–9 – ssaków. Ta filogeneza wymaga mniejszej ilości zmian niż w przypadku (A) i dlatego jest bardziej zgodna z zasadą parsymonii

DNA sequences are now widely used to reconstruct phylogenies



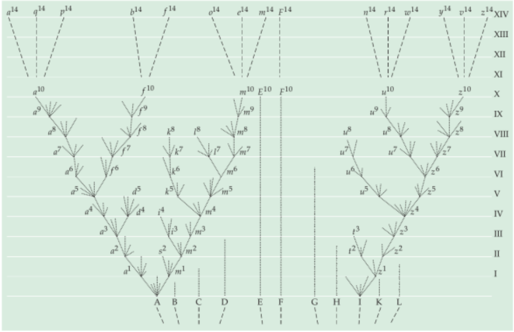
Cecha (nukleotyd w danej pozycji)

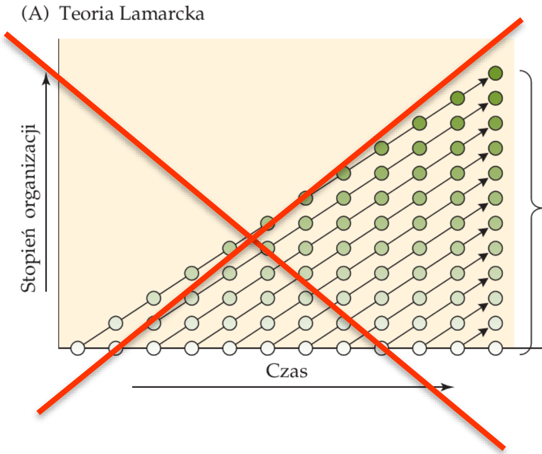
Gatunek	a	b	c	d	e	f	g
1	A	T	G	G	A	C	T
2	A	T	G	G	T	C	T
3	A	T	T	C	A	G	T
4	C	G	T	C	T	C	T
5	C	G	T	C	T	C	A

Rycina 2.7 Konstrukcja drzewa filogenetycznego metodą maksymalnej parsymonii. Tabelka z prawej strony podaje stany cech (nukleotydy) dla siedmiu pozycji (a–g) w sekwencjach DNA. Każde z trzech drzew przedstawia hipotetyczne pokrewieństwa między gatunkami 1, 2 i 3; zaznaczono pozycje powstałych apomorfii. Porównując długości (*L*) tych drzew stwierdzamy, że najkrótsze jest drzewo 1 (*L* = 8), ponieważ wymaga wprowadzenia najmniejszej liczby apomorfii

Problem of discriminating homology and homoplasy avoided if non-functional (neutral) sequences are used

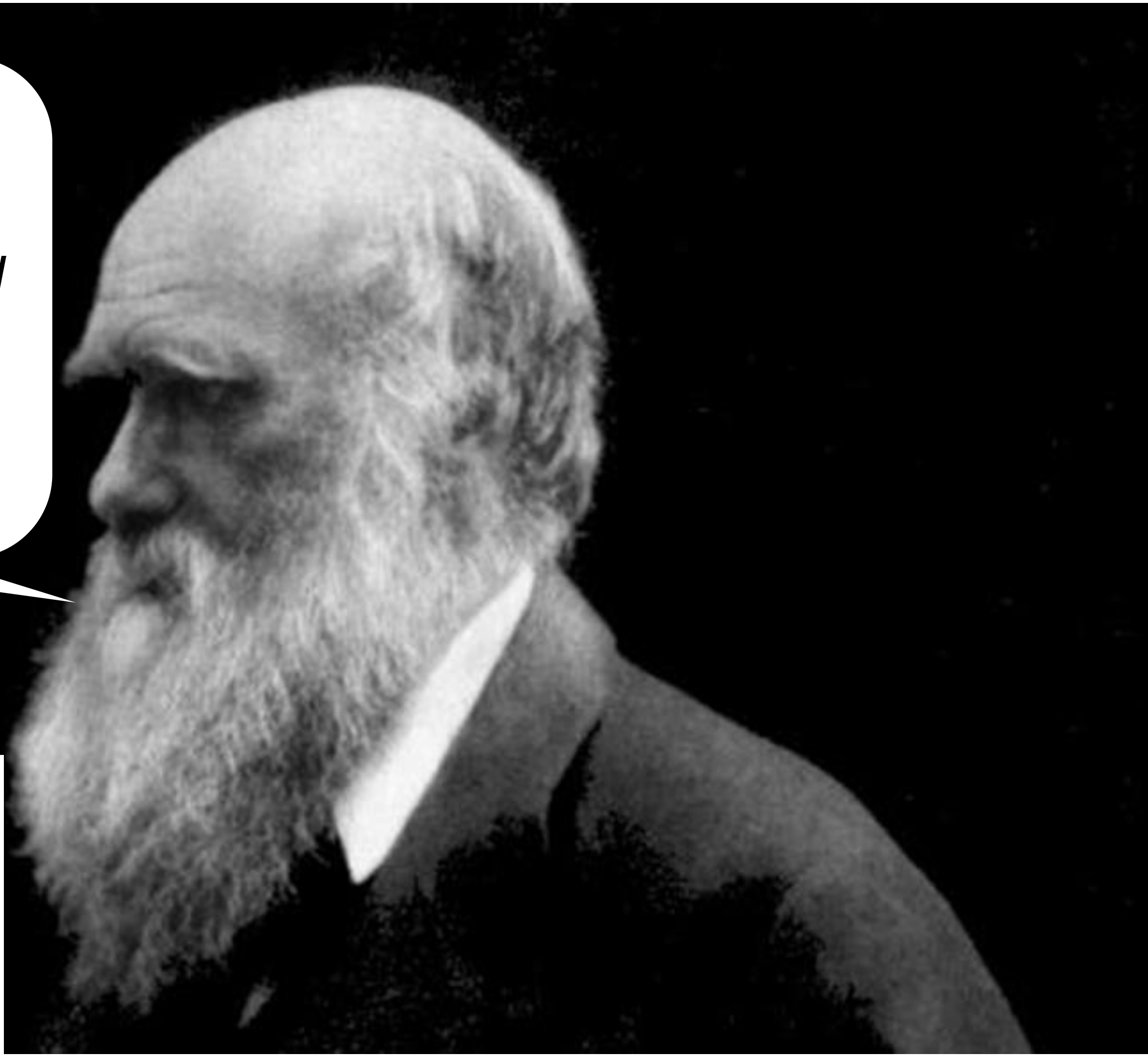
Phylogenies reconstructed from nucleotide sequences and phenotypic traits are consistent with predicted branching pattern

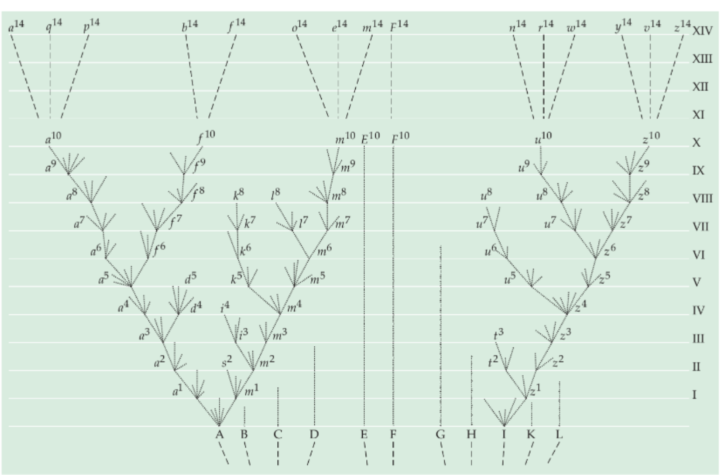




Predictions supported by empirical findings

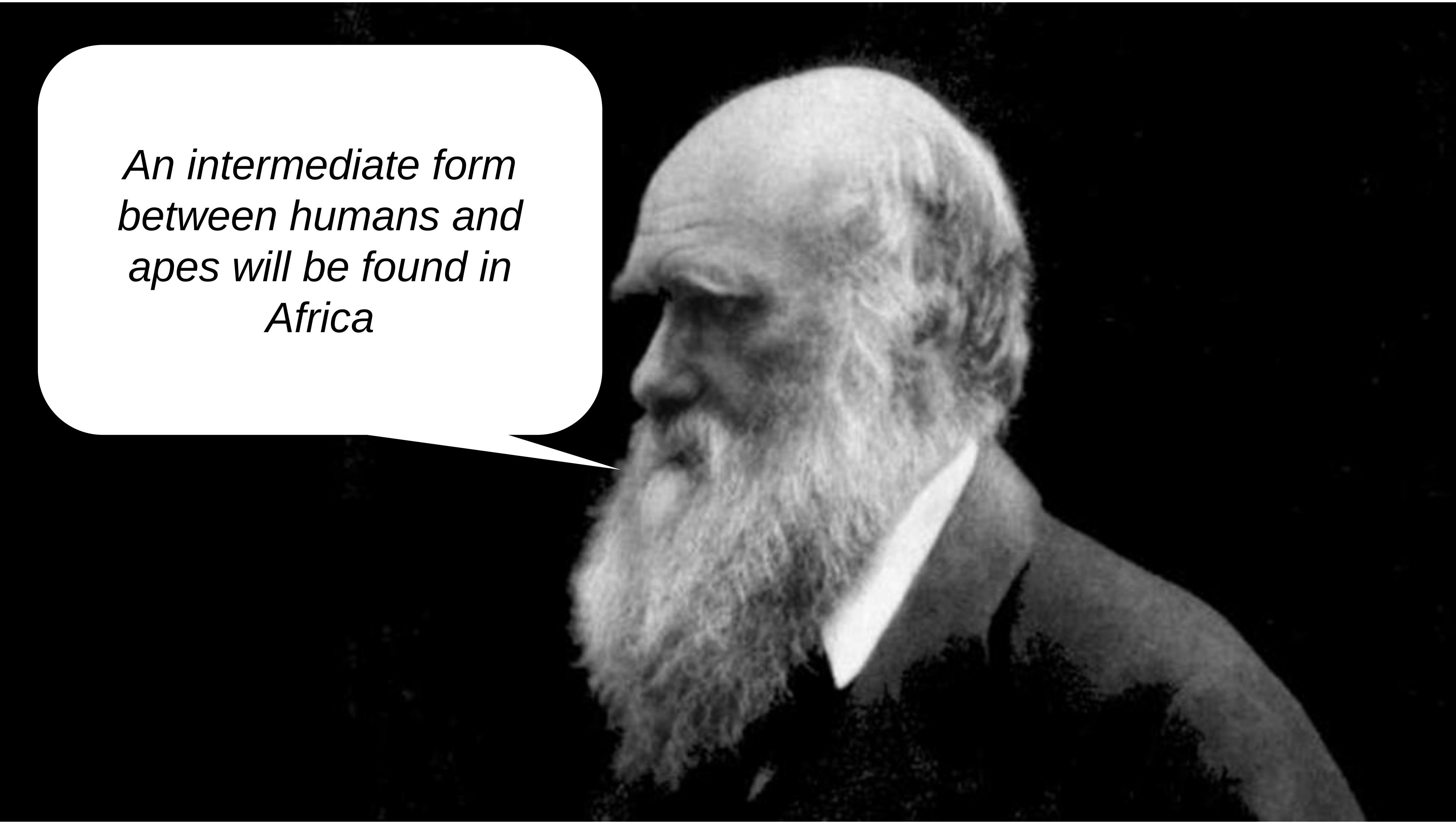
Intermediate forms should be found in fossil record





Intermediate forms were abundantly represented in fossil record (despite its fragmentariness)

Predictions supported by empirical findings



R. Dart 1923 –*A. africaus skull found in South Africa*

A. afarensis (3 mln lat)

Johnson 1974*: Lucy (Ethiopia)*

Human-like traits

- *small fangs*
- *arched feet*
- *non-grasping toe*
- *shoter, wider pelvis*
- *valgus knee joint*

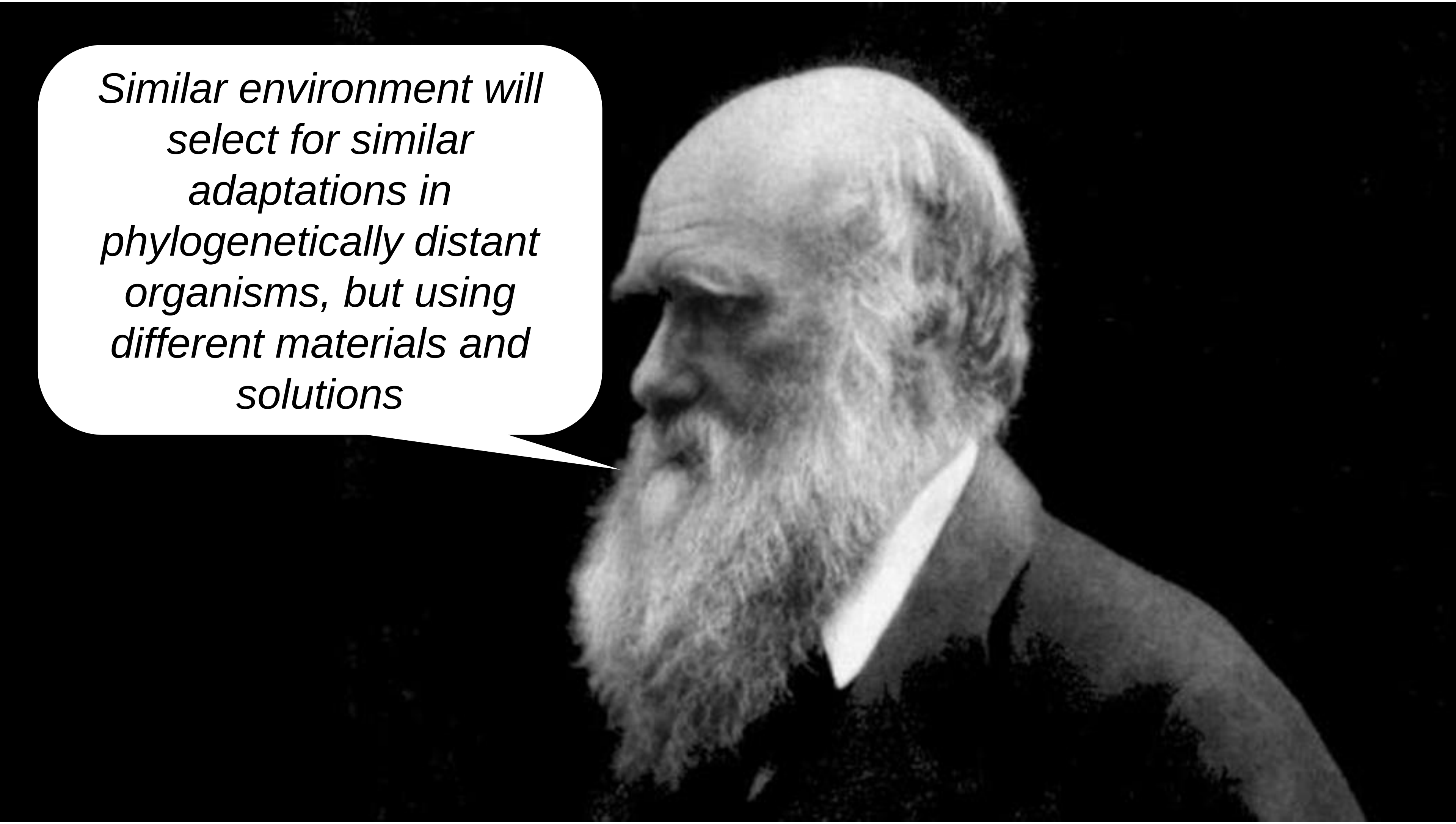
Ape-like traits

- *massive jaw*
- *short legs*

Bipedalism associated with energetic benefits during walking

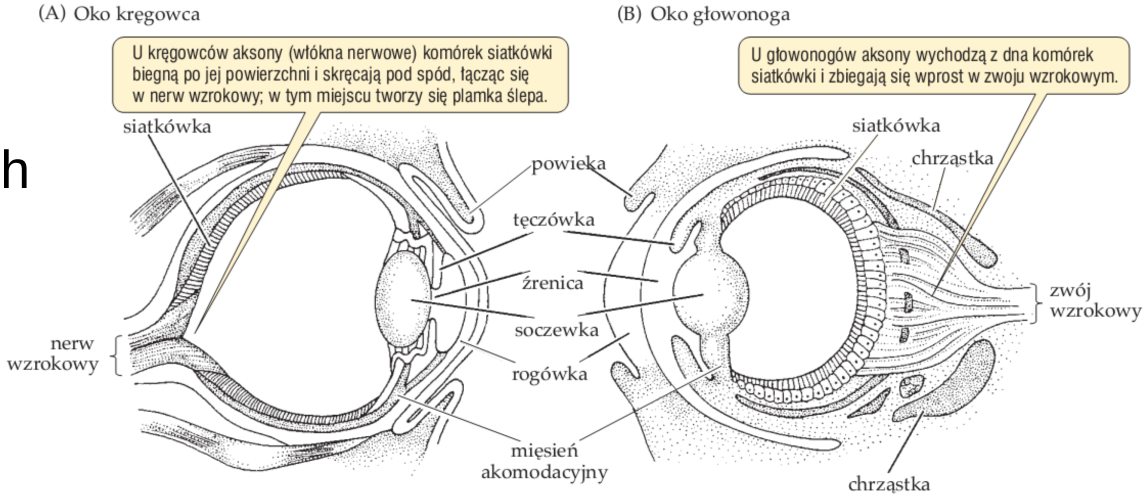
Upright posture decreases exposure to sun beams

Predictions supported by empirical findings



Similar environment will select for similar adaptations in phylogenetically distant organisms, but using different materials and solutions

Examples of **konwergence** agree with this predcitoin

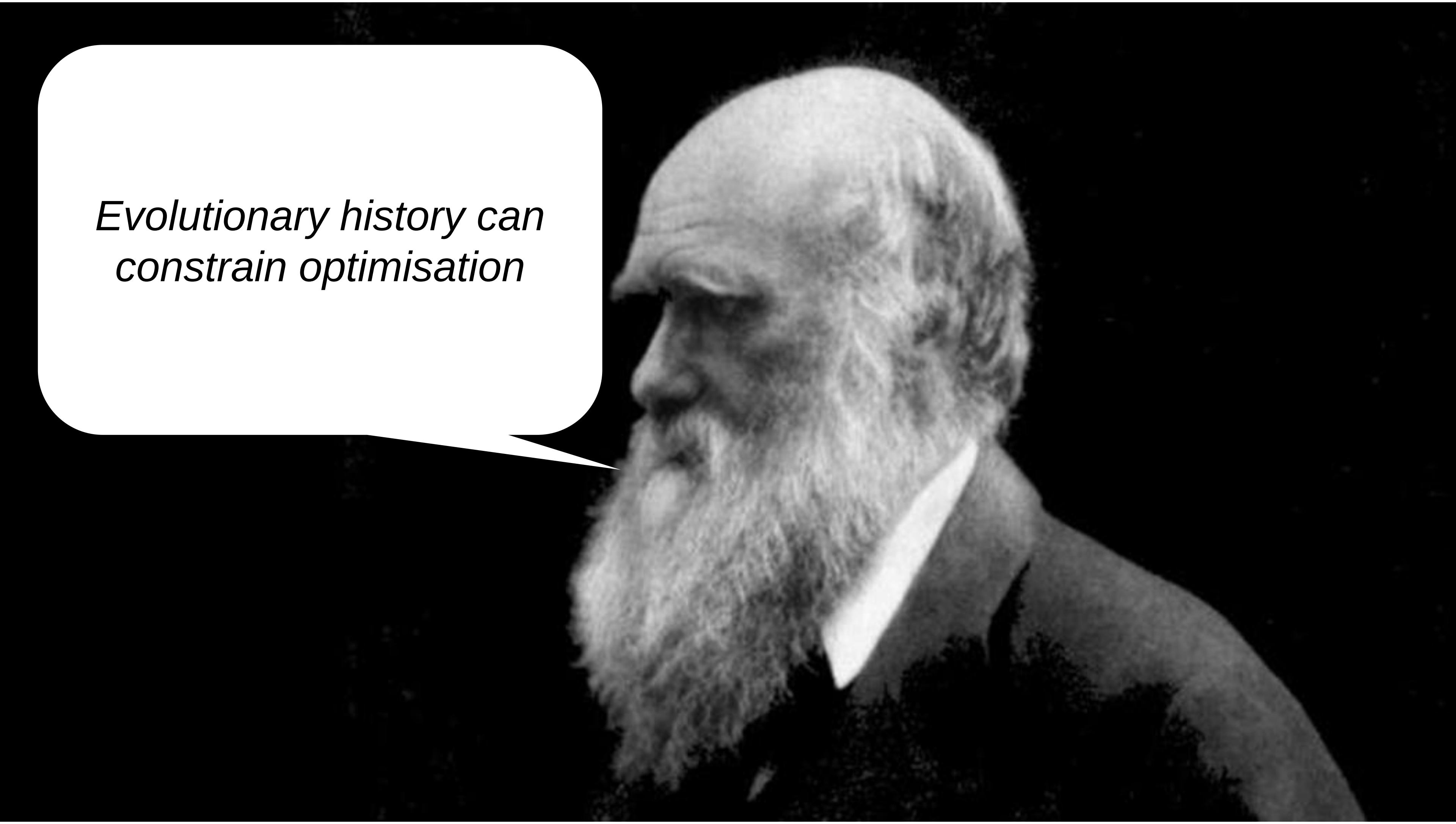

(A) Oko kręgowca

U kręgowców aksony (włókna nerwowe) komórek siatkówki biegną po jej powierzchni i skręcają pod spód, łącząc się w nerw wzrokowy; w tym miejscu tworzy się plamka ślepa.

(B) Oko głowonoga

U głowonogów aksony wychodzą z dna komórek siatkówki i zbiegają się wprost w zwoju wzrokowym.

Predictions supported by empirical findings



Evolutionary recycling may lead to suboptimal solutions

The risk of chocking is a consequence of evolutionary history: lobe-finned *Osteolepiformes* swallowed air, nasal cavities used for chemoreception were later co-opted for breathing

Problems in human births – a conseqauence of mammalian ancestry

Evolution by natural selection requires **heritable variation in traits affecting survival and/or reproduction**

.education.nationalgeographic.org

Jednak rozbić jak poniżej żeby np.
dać deninicję dostosowania

- Differential survival and/or reproduction

T. Malthus: only a fraction of progeny that is born reaches maturity

- Variation

For selection to occur, differential survival/reproduction has to be due to phenotypic differences (at least to some extent)

- Heritability

For natural selection to result in evolutionary change, phenotypic difference need to be inherited by the next generation

- Zróżnicowane przeżywanie i reprodukcja

Thomas Malthusa, Principle of Population (1798): zwierzęta wydają na świat dużo więcej potomstwa niż przeżywa

- Zmienność

- Dziedziczność

„Przeżywanie najstosowniejszego (survival of the fittest)” – myląće, sukces w doborze naturalnym zależy także od tempa reprodukcji

Dostosowanie (fitness)

Przy nie zachodzących na siebie pokoleniach
R=BS (B, rozrodczość; S, prawdopodobieństwo przeżycia)

Przy zachodzących pokoleniach i ograniczonej pojemności środowiska: parametr maltuzjański r
dN/dt = (b - d)N = rN

gdzie
b – liczba urodzin/osobnika
/jednostkę czasu
d – prawdopodobieństwo śmierci

- Zróżnicowane przeżywanie i reprodukcja

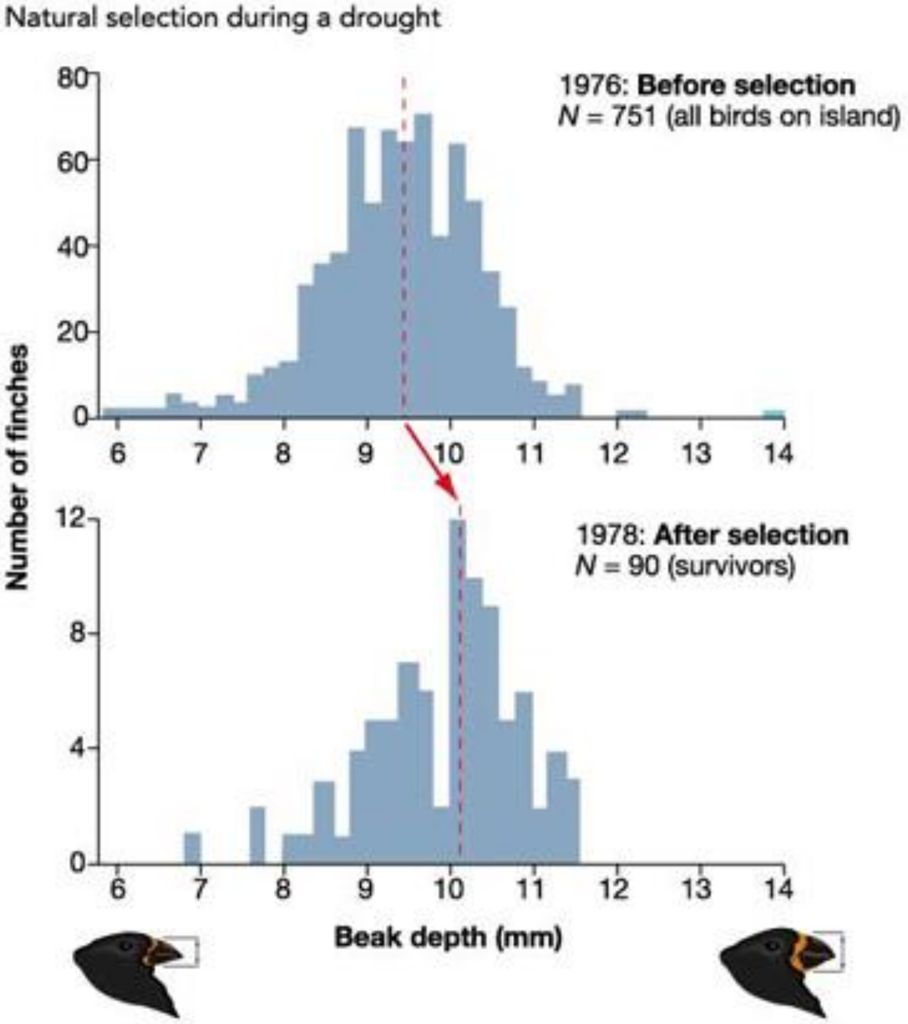
Thomas Malthusa, Principle of Population (1798): zwierzęta wydają na świat dużo więcej potomstwa niż przeżywa

- Zmienność

Aby miał miejsce dobór (selekcja), zróżnicowanie przeżywania i reprodukcji musi być nielosowe w odniesieniu do cech fenotypowych

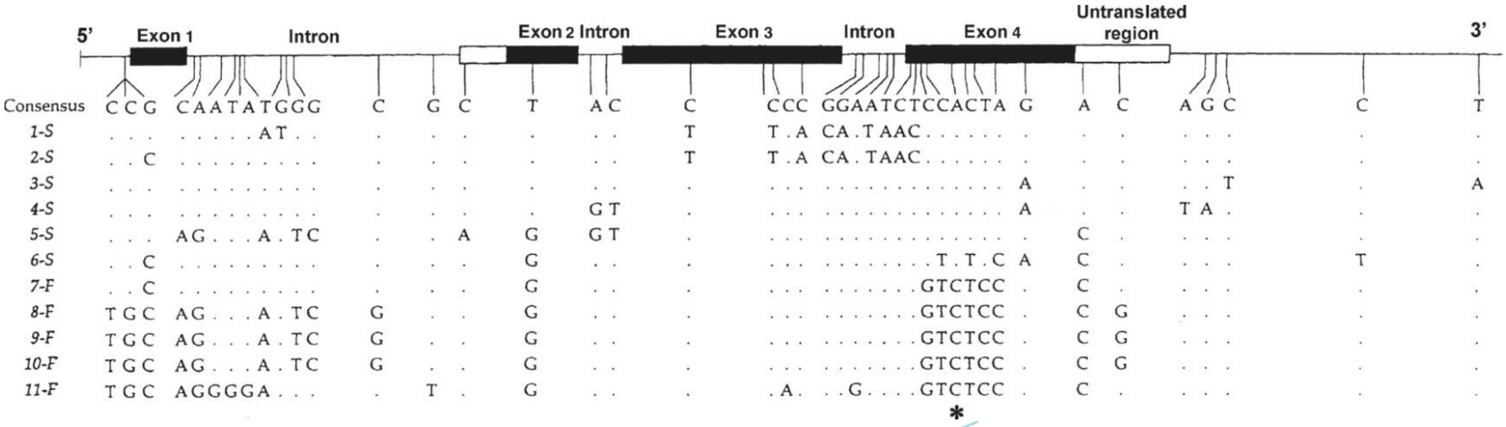
- Dziedziczność

Dobór na wielkość dzioba o darwinki czarnej (*Geospiza fortis*)



Grant 1986

Sources of genetic variation



Drosophila alcohol dehydrogenase sequence alignment

Nuccleotide substitution causing a change in coded protein polarity

Variation in:

- *protein coding sequences*
- *regulatory sequences*
- *geene copy number (CNV)*

Mutations are mostly random:

Despite that some mutations may be more likely the other, the chance of their occurrence does not depend on its adaptive utility

Mutation rate is low, but genomes have many target sites!

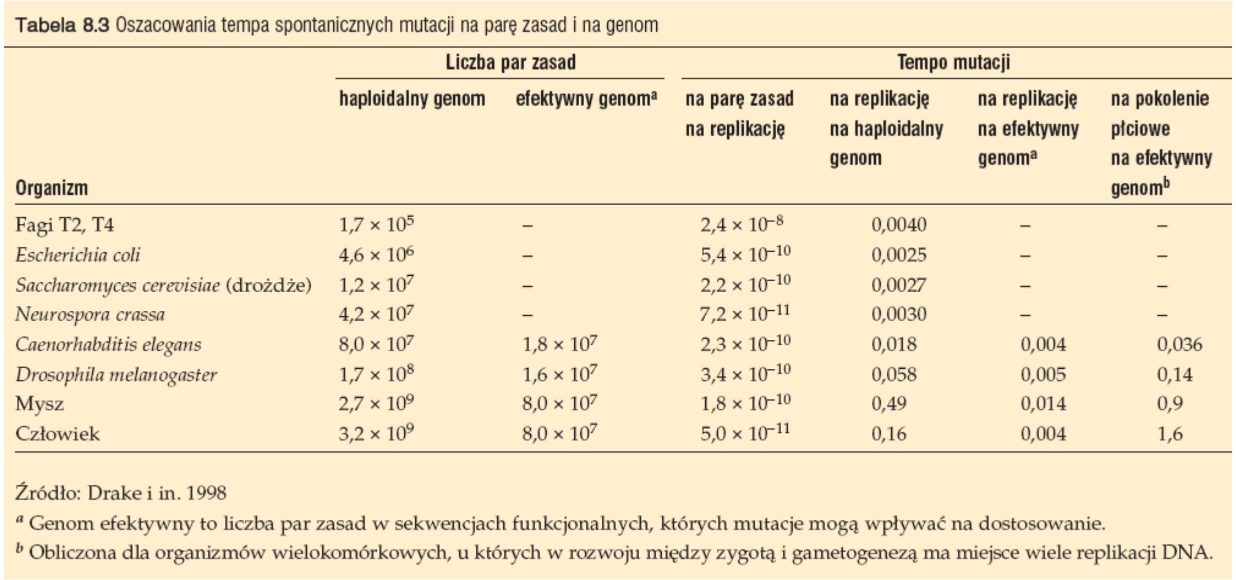


Tabela 8.3 Oszacowania tempa spontanicznych mutacji na parę zasad i na genom

	Liczba par zasad		Tempo mutacji			
Organizm	haploidalny genom	efektywny genom[a]	na parę zasad na replikację	na replikację na haploidalny genom	na replikację na efektywny genom[a]	na pokolenie płciowe na efektywny genom[b]
Fagi T2, T4	$1{,}7 \times 10^{5}$	–	$2{,}4 \times 10^{-8}$	0,0040	–	–
Escherichia coli	$4{,}6 \times 10^{6}$	–	$5{,}4 \times 10^{-10}$	0,0025	–	–
Saccharomyces cerevisiae (drożdże)	$1{,}2 \times 10^{7}$	–	$2{,}2 \times 10^{-10}$	0,0027	–	–
Neurospora crassa	$4{,}2 \times 10^{7}$	–	$7{,}2 \times 10^{-11}$	0,0030	–	–
Caenorhabditis elegans	$8{,}0 \times 10^{7}$	$1{,}8 \times 10^{7}$	$2{,}3 \times 10^{-10}$	0,018	0,004	0,036
Drosophila melanogaster	$1{,}7 \times 10^{8}$	$1{,}6 \times 10^{7}$	$3{,}4 \times 10^{-10}$	0,058	0,005	0,14
Mysz	$2{,}7 \times 10^{9}$	$8{,}0 \times 10^{7}$	$1{,}8 \times 10^{-10}$	0,49	0,014	0,9
Człowiek	$3{,}2 \times 10^{9}$	$8{,}0 \times 10^{7}$	$5{,}0 \times 10^{-11}$	0,16	0,004	1,6

Źródło: Drake i in. 1998

[a] Genom efektywny to liczba par zasad w sekwencjach funkcjonalnych, których mutacje mogą wpływać na dostosowanie.

[b] Obliczona dla organizmów wielokomórkowych, u których w rozwoju między zygotą i gametogenezą ma miejsce wiele replikacji DNA.

Inheritance causes similarity within families

Heritability (h^2) measures on the scale 0 to 1 a proportion of phenotypic variation that is due to genetic variation

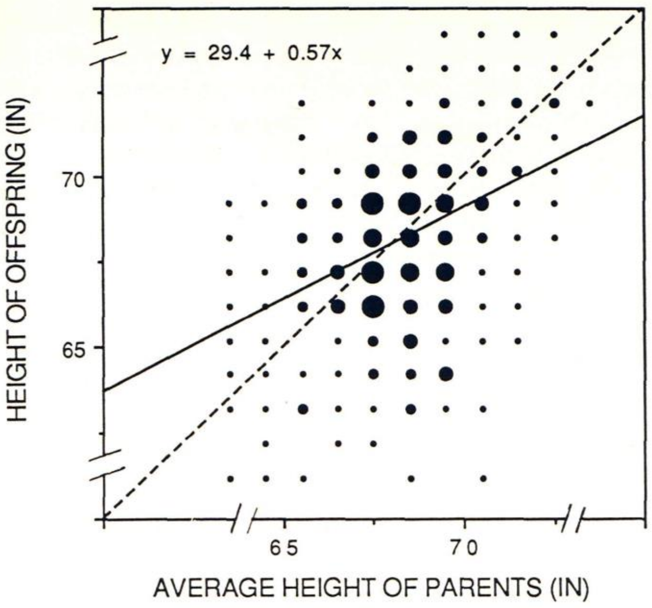
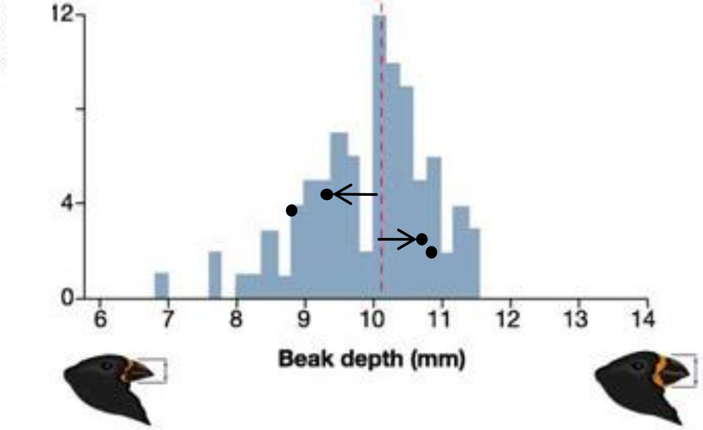


Fig. 2.1 Galton's (1889) data showing the height of adult human offspring (*N* = 928) as a function of the average height of their parents (*N* = 205 sets) in a British population. The dashed line describes perfect inheritance. The calculation of the regression slope (solid line) excluded 36 offspring for which the exact heights of offspring and/or parents were not reported. These 36 extreme points are for parents with average heights less than 63.5 inches or greater than 73.5 inches and for offspring less than 61.2 or greater than 74.2 inches in height.



$$V_P = V_G + V_E$$

$$V_p = \sum(\mathit{trait\ value - mean})^2$$

V_P- phenotypic variance

V_G- genetic variance (variance in genetic effects)

Heritability: $h^2 = V_G/V_P$

Estimating heritability:

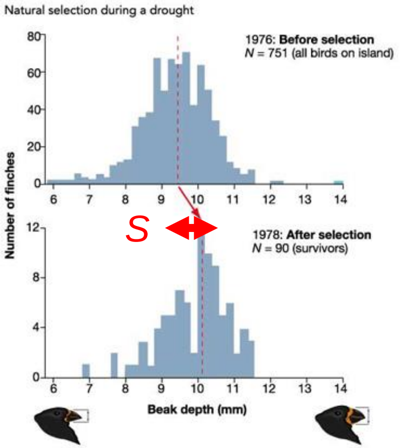
Similarity between relatives, eg. from the slope of regression of offspring mean value on mean values of parents (assumption: no common environment effect)

In small ground finch beak height heritability estimate (= slope) = 0.51 (Keller et al. 2001)

Heritability determines evotionary response to selection

$$R = Sh^2$$

R –response, a change in phenotype between generations
S – selection differential (difference between selected individuals and population mean*)*



Response to selection of beak height in small ground finch Geospiza fortis agreed with prediction (za Roff 1997 i Grant i Grant 1989)

Evolution of complex traits

To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree…

Charles Darwin

- Creationists: complex traits „designed” by the creator
- Saltactionists: complex traits may arise due to „macromutations” (hopeful monsters, R. Goldschmidt)

- Gradualists: complex traits may evolve by small steps, each increasing fitness

Learn genetics Utah

Homeobox genes regulate developmental processes of multicellular organisms

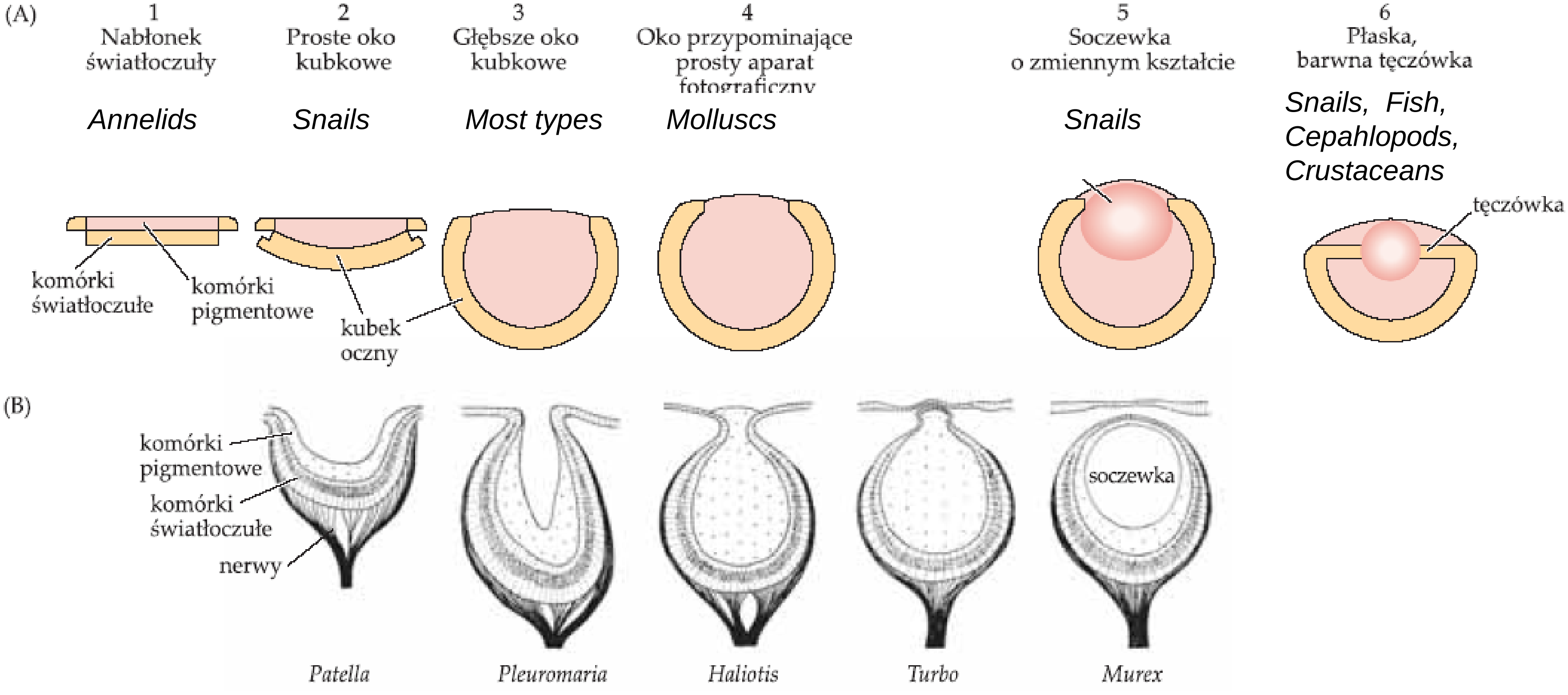
Mutations may lead to large effects, e.g. change in the type of body segment
(e.g *Ultrabithorax, antennapedia)*

Evolution of quadruped limbs associated with changes in expression of Hox genes 9-13

To suppose that the eye with all its inimitable contrivances for adjusting the focus to different distances, for admitting different amounts of light, and for the correction of spherical and chromatic aberration, could have been formed by natural selection, seems, I freely confess, absurd in the highest degree… **Reason tells me, that if numerous gradations from a simple and imperfect eye to one complex and perfect can be shown to exist, each grade being useful to its possessor, as is certainly the case; if further, the eye ever varies and the variations be inherited, as is likewise certainly the case and if such variations should be useful to any animal under changing conditions of life, then the difficulty of believing that a perfect and complex eye could be formed by natural selection, though insuperable by our imagination, should not be considered as subversive of the theory.**

Charles Darwin

Gradation of eye complexity, which each type serving its function in different taxa



Genetic theory of natural selection (population genetics)

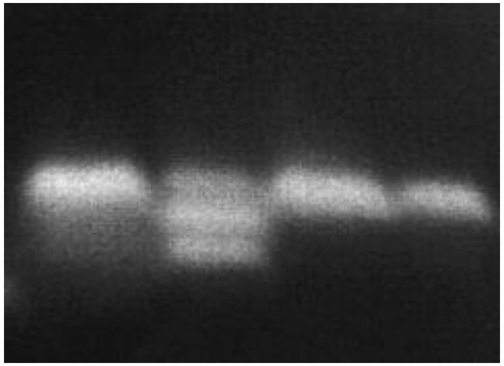
Genotypes at ovoalbumine of common eider

	Genotyp			
Genotype	FF	FS	SS	total
number	37	24	6	67
frequency	37/67=0,552	24/67=0,358	6/67=0,090	1

P, frequency of an F allele; q = 1-p, S allele

$p = (2*FF + FS)/(2*\text{number of individuals})$
$p = (2*37 + 24)/(2*67) = 0,73$

$q = 1 – p = 0.27$



Hardy and Weinberga low: under random mating, in the absence of selection, mutation and migration, genotypes will occur in the same proportions across generations, defined by allele frequencies

p,q, frequency of A, a alleles, respectively

Frequencies of genotypes AA, Aa, aa will be p^2, 2pq, q^2, respectively

For example: A=0.8 (p); a=0.2 (q)

	A	A	A	A	a
A	AA	AA	AA	AA	Aa
A	AA	AA	AA	AA	Aa
A	AA	AA	AA	AA	Aa
A	AA	AA	AA	AA	Aa
a	Aa	Aa	Aa	Aa	aa

AA genotype frequency =16/25 = p^2 = 0.64
Aa genotype frequency = 8/25 = 2pq = 0.32
Aa genotype frequency = 1/25 = q^2 = 0.04

Population genetic model example: selection against recessive a allele

s-selection coefficient

	AA	Aa	aa	total
Frequency at birth	p^2	2pq	q^2	1
fitness (w)	1	1	1-s	
Frequency after selection	p^2	2pq	$q^2(1-s)$	$1-sq^2$

$$p' = \frac{2p^2 + 2pq}{2(p^2 + 2pq + q^2(1-s)} = = \frac{p(p+q)}{1-sq^2} = \frac{p}{1-sq^2}$$

Denominator = $\mathbf{p^2} + \mathbf{2pq} - \mathbf{q^2} - sq^2 = \mathbf{1} - sq^2$

Larger portion of mutations deleterious

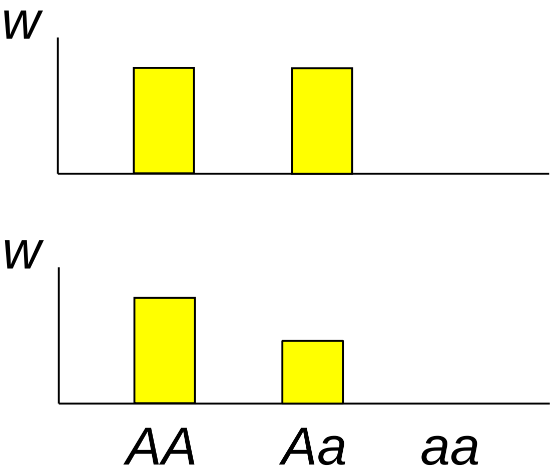
e.g. in *Caenorabditis* ca. 90% non-synonymous mutations delteriou (Stein i in. 2003)

Each human individual carries ~30–60 de novo mutations that arose in the germ line of his or her parents (Shendure & Akey 2015)

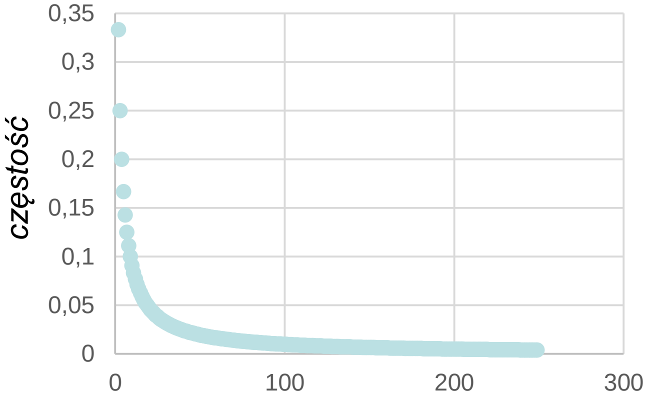
Can deleterious mutations stay in populations?

Selection against lethal mutation (s=1)

$$\Delta p = \frac{spq^2}{1-sq^2} = \frac{pq^2}{1-q^2}$$

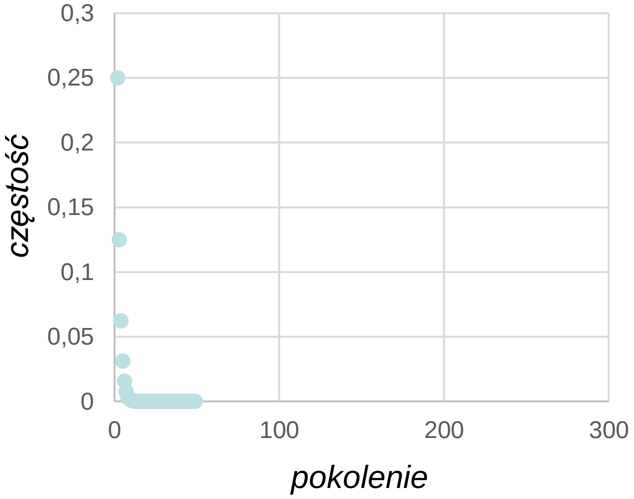


Mutation a recessive



No dominance: heterozygote intermediate

$$\Delta p = \frac{pq}{2(1-q)}$$



Selection against recessive mutations will be less effective: when such mutations are rare, they occur mostly in heterozygotes (q^2 low), hence invisible to selection!

Fragment of human genome sequence:

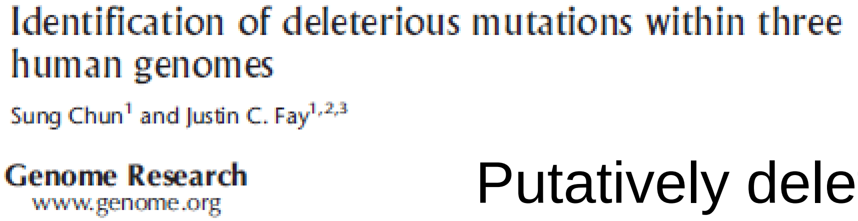
```
GTGATCTCAGCTCACTGCAACCTCTGCCTCCCGGGTTCAAGTGATTCTCCCGCCTCAGCTTCCTGAGTAA
GCTGGGACTACAAGTGCACGCCACCACGCCTGGCTAATTTTTGTATTTTTAGTAGAGACGGGGTTTCACC
ATATTGCCCAAGCTGGTCTCGAACTCCTGAACTCAAGTGATCCTCCCACCTCGACTTCCCAAAGTGCTGG
GATTACAGGTGTGAGCCACCGCGCCAGGCCAAGTTTTTTTTTTTCTTATTGGAAAAGTGAAATATGCTTA
TTACAGAAACCTCAGAAAATATAAAGTAGAAAAATACCAAAATTTCTTTCATAATTCTCTCTACCCAAAG
GCATCGGTCAGTCCCTCTCCAGACCAGAAGCAGTTAGTTCTGACACCAACAAGTGGTGATAAGAGGTTGA
TAGCCTAGCAAGGGGGAAGAAGCCACCACCAAACCAAACACAAAAAATGACACTGCACAGCAGTCTGGGG
ACATGTCCTTGAAGGACACAGCCCCAAAGATACTGGCAGGTGAGGTAGTGTCCCTAAGATCAACAGGCAT
CATCATGAATCCTATTTCAGAATGCCACAAAGAATACGTTTTAGAGAAGATTCTAAGAGAAAAAGCTAAG
GTGATTTTTTTTTTCAGTCGTTTTTTGTTCTCAGACAGTGTCTCACTCTGTCGCCCAGGCCAGAGTGCAG
TGGTGCGATCACAGCTCACTGCAGCCTCAACCTCCAGGGCTCAAACGATCCTCCCACCTCAGCCACCTGA
GTAGCTGAGACTACAGGCGTGTGCCACCACACCCGGCTAATTTTTTTTTTTTTTTTTTTGTAGAAATGGG
ATCTCACTATGTTGCCAGGGCTTGTCTCAAACTCCTGGGCTCAAGCGATCTACCTGCCTTGGCCTCCCAA
AGCATTGGGCAGGCCCATTACGCCATGAGCCACCACACCTGCTGGTTTTTGTTTTTTAAATGGAATTGAA
AGGAACTAGCCTTGGCTAGTTGCAGAATTCACACATATGGGGCTATGGCAACAGCAGATTCTGGAGTCTC
AGGGTCTTTTCTTTCTAGATAAGTTACAGGGCAATTGCTTTTCAGAGTACTTTTACATTTCTATTCCATT
CTTGTCAGTAAAGACAAGGATCCCATAAGCTGATGGAGAAACTGAGGCCTCTAGAAACTAAACGCTGGGA
ATGGCACCCAGGGTGCTGAATTCCAGGGTCTCCTCTTTTCTGCCACAGGCACACATGCCCCAGCAGCCCC
TTTGGAGAGCCCCCTCTCTATAGGGTACTAGCCGGGGGCTCAGACTCTGGAGTCAGACGGCTTCCGAGGG
ATGAGGCCTCAGACAAGTAACTCAGCTTTGAAATGTTTTCAGTGGGGAGAGAAATAGCCCCCTCCCAGGG
CTGTGCTCCGGGAACTGACTGAGGGCTAACTATTATGGGCCCACCCCATTGTTGGAATGTCTTCAGCCAC
ATGGGGGAATGGGTGGAAGAGGCCGGGATGTGTCCTGCCAGCTAGAGCAGCGAAGAAATCCCAGCGGGGC
CCCAGGAAGTCCAAGCCCATGGGGTTCAGGTGCTCCTCTCTGGCTATTCCTTCAGACCCGCAGCTGCTGG
ACACAGGCCACAGAGCTGGTGCCTCCCGCGCCATCACTGCAGTGCAGCCTGGGTGGACGGAGGAAGCCAA
GGGGAACGGCCTGGGCTCAGAGTAAGGAGACCTTGCCCCGGGGGACAAACGGTGTCTGAAGTGCAGGGGT
GAAGCGGTCTCCAGTCCTCAGGGGCCTGGAAATCAGCTCCTTGGGACACGGTCTTATGTGTATTGACCAT
```

Pracownicy Uniwersytetu w Leicester z wydrukowanym ludzkim genomem

3 bln nucleotides

Printout: 130 volumes

Reading aloud over 90 years



Identification of deleterious mutations within three human genomes

Sung Chun[1] and Justin C. Fay[1,2,3]

Genome Research
www.genome.org

Putatively deleterious mutations in human genomes (predicted based on substitutions in conserved codons)

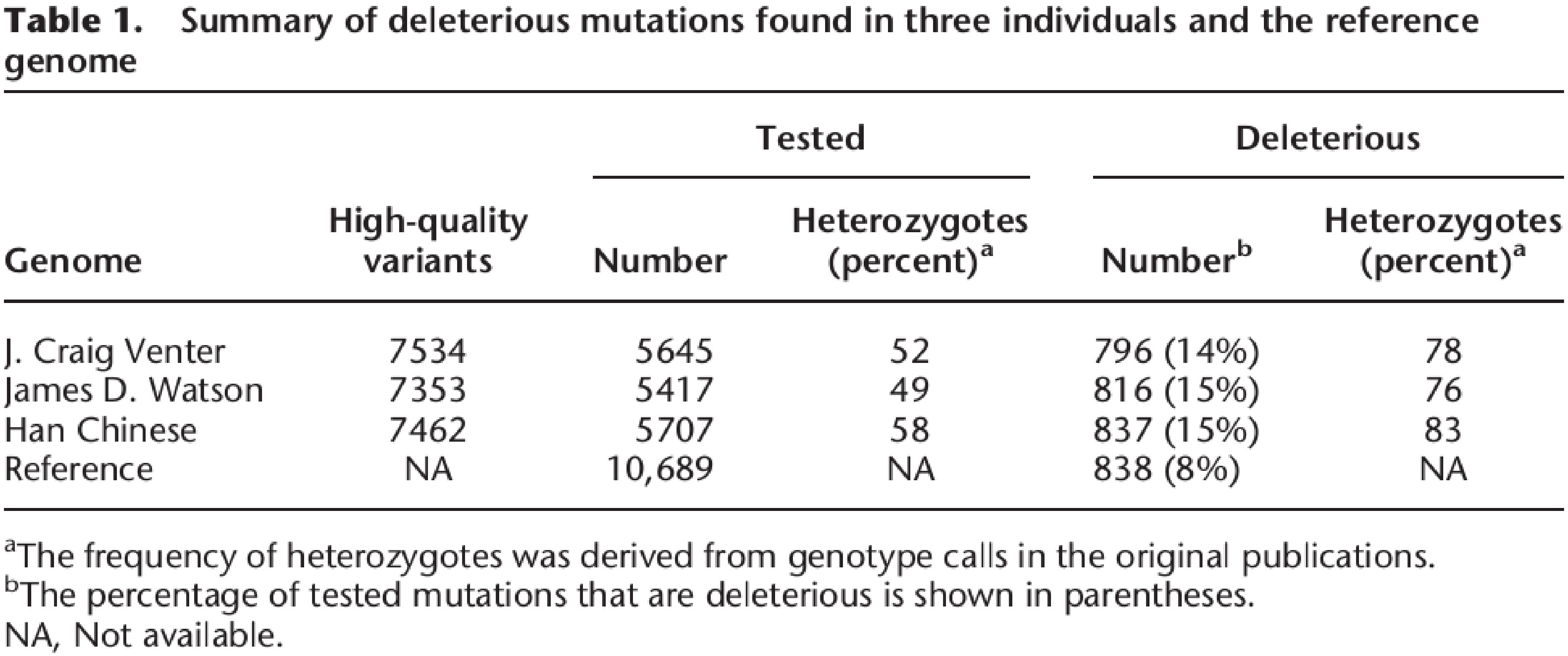
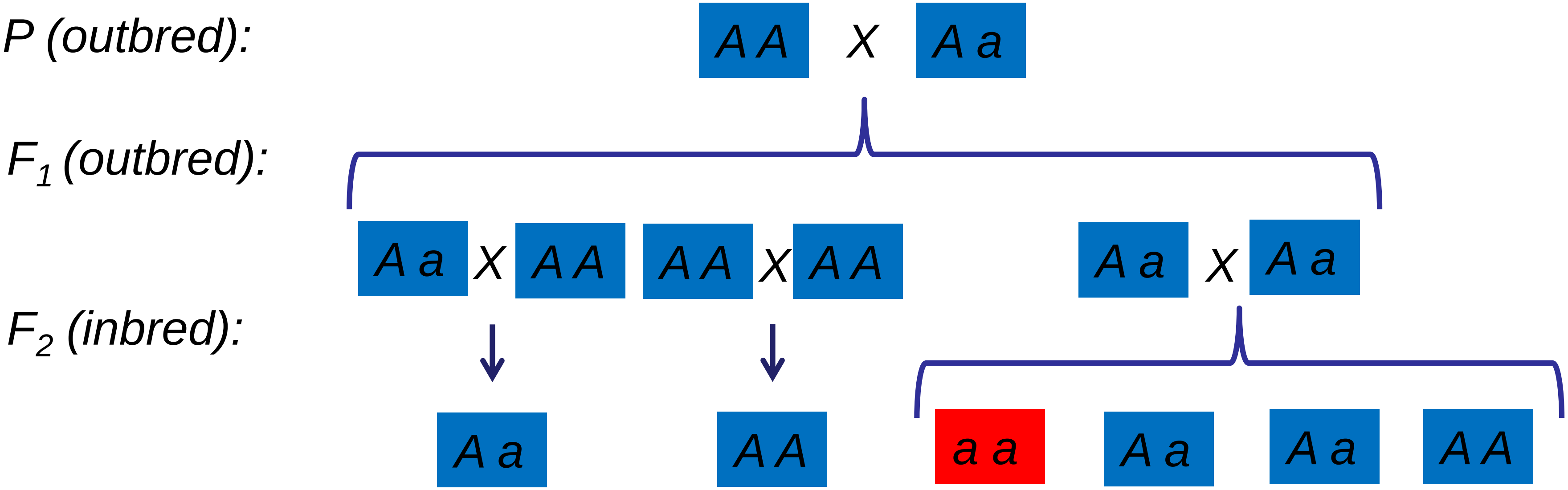


Table 1. Summary of deleterious mutations found in three individuals and the reference genome

Genome	High-quality variants	Tested		Deleterious	
		Number	Heterozygotes (percent)[a]	Number[b]	Heterozygotes (percent)[a]
J. Craig Venter	7534	5645	52	796 (14%)	78
James D. Watson	7353	5417	49	816 (15%)	76
Han Chinese	7462	5707	58	837 (15%)	83
Reference	NA	10,689	NA	838 (8%)	NA

[a] The frequency of heterozygotes was derived from genotype calls in the original publications.
[b] The percentage of tested mutations that are deleterious is shown in parentheses.
NA, Not available.

Maintenance of **recessive (or partially recessive)** deleterious mutations underlies genetic disorders as a consequence of inbreeding (e.g. due to incest)



P (outbred): A A X A a

F_1 (outbred): A a X A A   A A X A A   A a X A a

F_2 (inbred): A a   A A   a a   A a   A a   A A

Do our genomes crumble in consequence of relaxed selection?

$$\Delta q = (1-q)\mu - \cancel{sq^2(1-q)/(1-sq^2)}$$

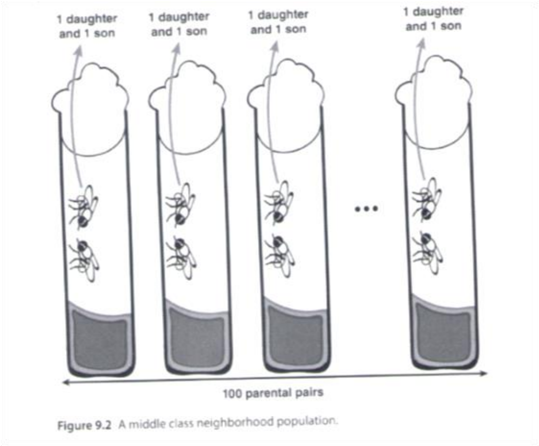
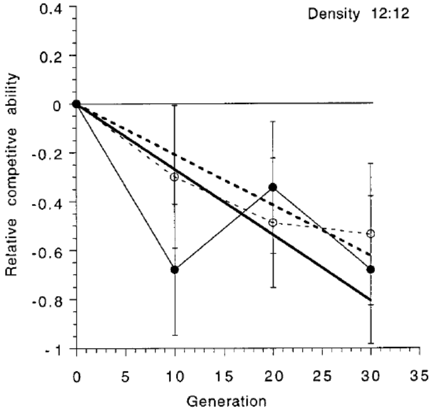


Figure 9.2 A middle class neighborhood population.

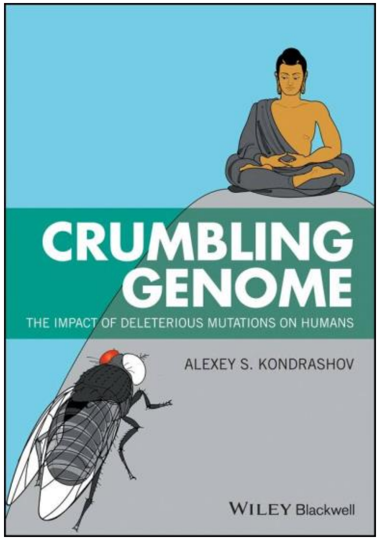


Fot. P. Kozioł; www.poznan.wyborcza.pl

Shabalina et al. 199

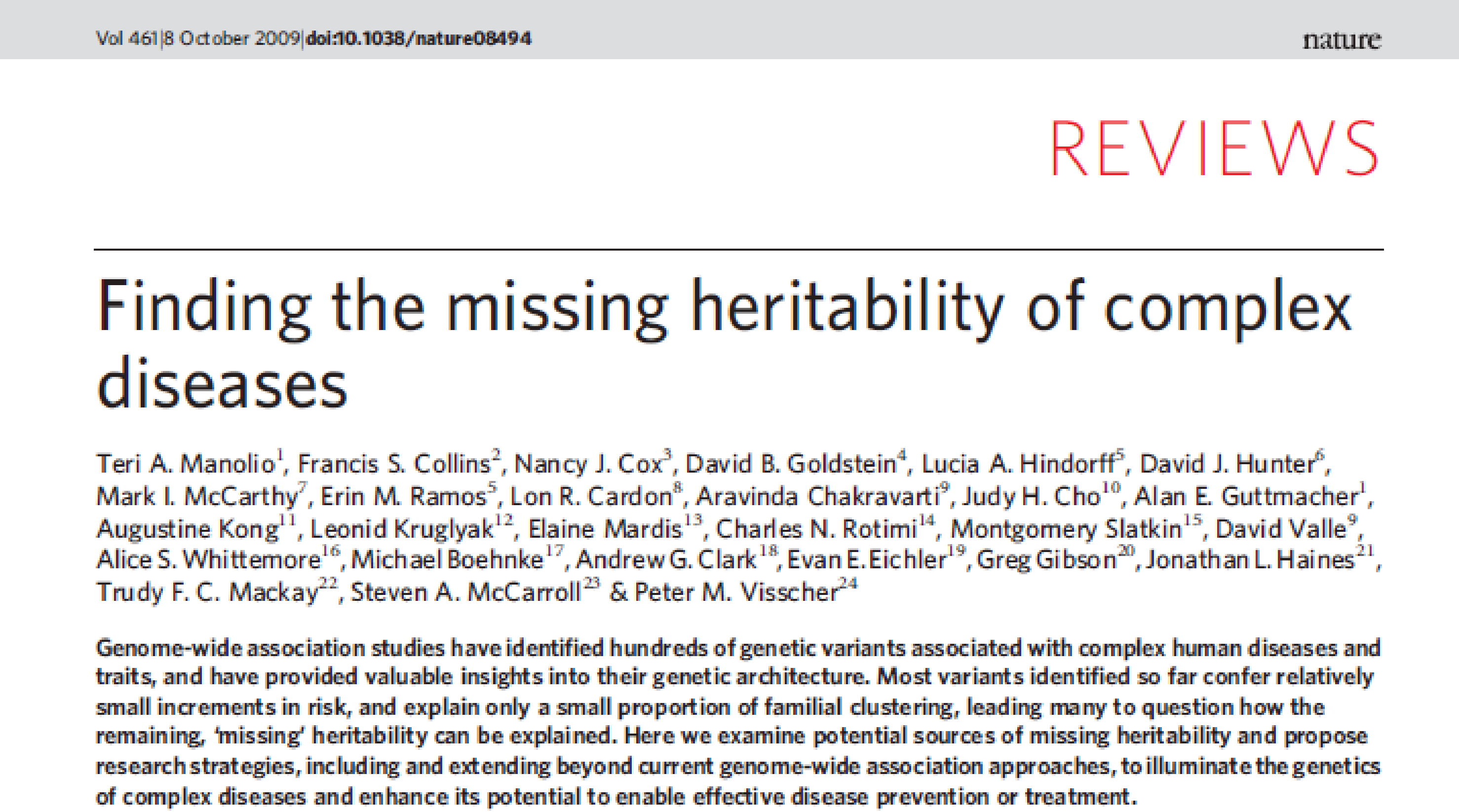
Crumbling human genome?

In pessimistic scenario, when selection eliminates only most deleterious mutations, we can expect ~30-40% decline in viability within next 10 generations some traits, like proportion of people with IQ > 140, will decline even more



A. Kondrashov 2016

Can we bioingeneer mutations ?



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nature

REVIEWS

Finding the missing heritability of complex diseases

Teri A. Manolio[1], Francis S. Collins[2], Nancy J. Cox[3], David B. Goldstein[4], Lucia A. Hindorff[5], David J. Hunter[6], Mark I. McCarthy[7], Erin M. Ramos[5], Lon R. Cardon[8], Aravinda Chakravarti[9], Judy H. Cho[10], Alan E. Guttmacher[1], Augustine Kong[11], Leonid Kruglyak[12], Elaine Mardis[13], Charles N. Rotimi[14], Montgomery Slatkin[15], David Valle[9], Alice S. Whittemore[16], Michael Boehnke[17], Andrew G. Clark[18], Evan E. Eichler[19], Greg Gibson[20], Jonathan L. Haines[21], Trudy F. C. Mackay[22], Steven A. McCarroll[23] & Peter M. Visscher[24]

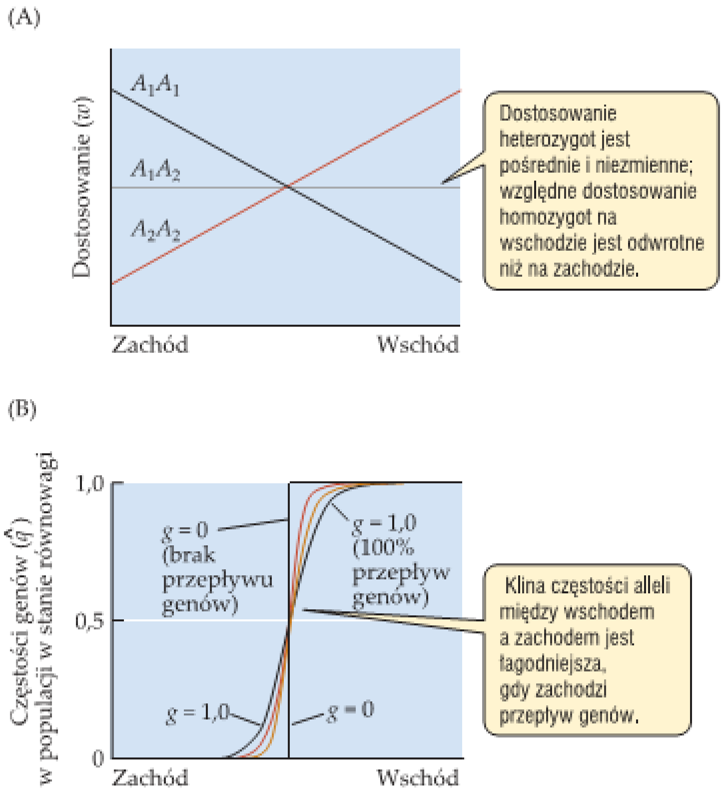
Genome-wide association studies have identified hundreds of genetic variants associated with complex human diseases and traits, and have provided valuable insights into their genetic architecture. Most variants identified so far confer relatively small increments in risk, and explain only a small proportion of familial clustering, leading many to question how the remaining, 'missing' heritability can be explained. Here we examine potential sources of missing heritability and propose research strategies, including and extending beyond current genome-wide association approaches, to illuminate the genetics of complex diseases and enhance its potential to enable effective disease prevention or treatment.

Many impornant traits (and medical conditions) polygenic, know mutation explain only small portion of variation

Maintenance of genetic variation

- Mutation-selection balance
- Fluctuations in space and time
  - Migration-selection balance
  - Fluctuating selection
- Balancing selection
  - Heterozygote advantage
  - Negatively frequency-dependent selection
  - Negative pleiotropy/sexual antagonism

Utrzymywanie zmienności genetycznej: równowaga miedzy doborem a migracjami



Dostosowanie heterozygot jest pośrednie i niezmienne; względne dostosowanie homozygot na wschodzie jest odwrotne niż na zachodzie.

Klina częstości alleli między wschodem a zachodem jest łagodniejsza, gdy zachodzi przepływ genów.

Genetic variance can be maintained if different sites connected by gene flow favour different alleles (Lenormand 2002)

But with complete mixing selection can fix an allele associated with higher average fitness across environments (Dempster 1955)

Aminopeptidase alleles in blue mussel Mytilus edulis for a cline in salinity gradient in Long Island bay

Aminopeptidase removes end-amino-acids form proteins, increasing their concentration and helping to maintain cell osmotic equilibrium,

Environmental fluctuations can help maintain genetic polymorphism

Fluctuations of ~ 1750 SNPs related to seasonal enviromnent changes in D. melanogaster

OPEN ACCESS Freely available online

PLOS | GENETICS

Genomic Evidence of Rapid and Stable Adaptive Oscillations over Seasonal Time Scales in Drosophila

Alan O. Bergland[1]*, Emily L. Behrman[2], Katherine R. O'Brien[2], Paul S. Schmidt[2], Dmitri A. Petrov[1]

1 Department of Biology, Stanford University, Stanford, California, United States of America, 2 Department of Biology, University of Pennsylvania, Philadelphia, Pennsylvania, United States of America

Balancing selection maintains polymorphism by itself

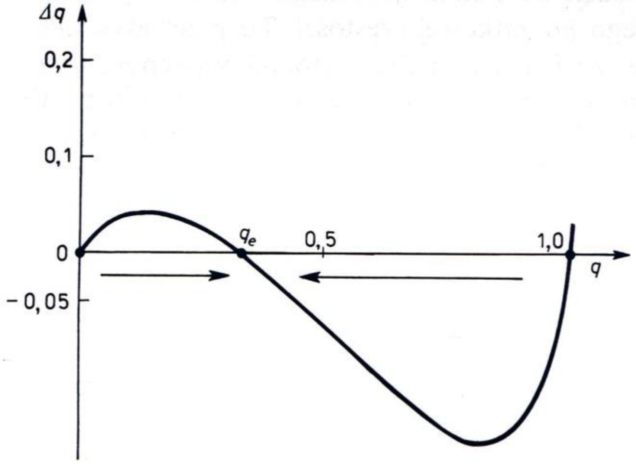
Most important mechanisms

- Heterozygote advantage
- Negatively frequency-dependent selection
- Negative pleiotropy/sexual antagonism

Example of selection favouring heterozygotes:

Genotype:	AA	Aa	aa
Fitness:	0.6	1	0.2

Leads to balanced polymorphism: A i a reach equilibrium proportions



Ryc. 4.3. Zmiana częstości Δq, allelu recesywnego a jako funkcja częstości q tego allelu przy doborze przeciw obu homozygotom. Pozostałe objaśnienia jak przy ryc. 4.2. Dla ryciny tej założono dostosowania genotypów: $W_{AA} = 0{,}6$, $W_{Aa} = 1$ i $W_{aa} = 0{,}2$. Zauważ jeden punkt równowagi stabilnej przy $q_e = 0{,}33$ i dwa punkty równowagi niestabilnej przy $q = 0$ i $q = 1$

e.g. p=0.9

	AA	Aa	aa
frequency	0,810	0,180	0,010
fitness	0,600	1,000	0,200
post selection	0,486	0,180	0,002

p'=(0.486+0,18/2)/(0.486+0,18+0,002) = 0.86

MHC proteins bind pathogen antigens with high specificity, inciting adaptive immune response

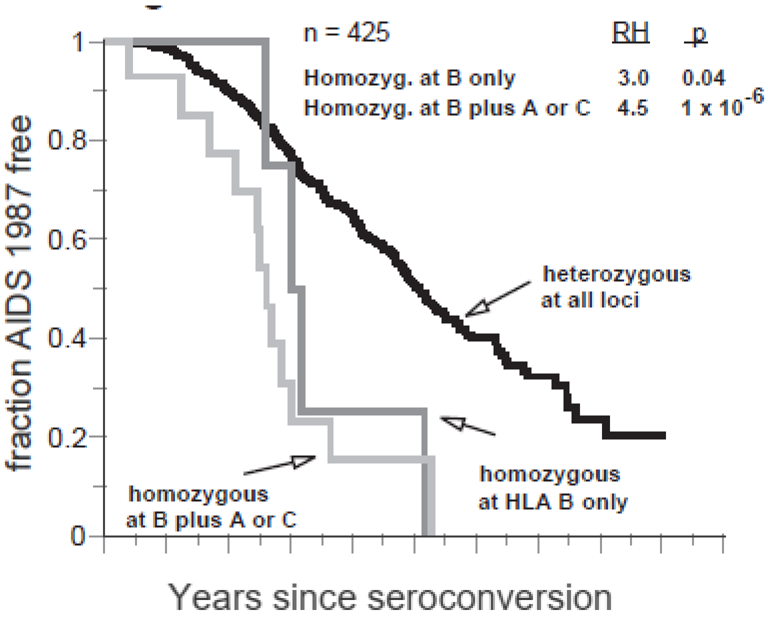
Most variable genes in vertebrates, e.g. MHC I (=HLA-I) over1000 alleles in humans

Related to susceptibility to disease (e.g. HLA-B27 protects form HIV (szczep B) in Caucasian population

MHC heterozygote advantage: producing more MHC variants can help recognise more pathogens

HLA and HIV-1: Heterozygote Advantage and _B*35-Cw*04_ Disadvantage

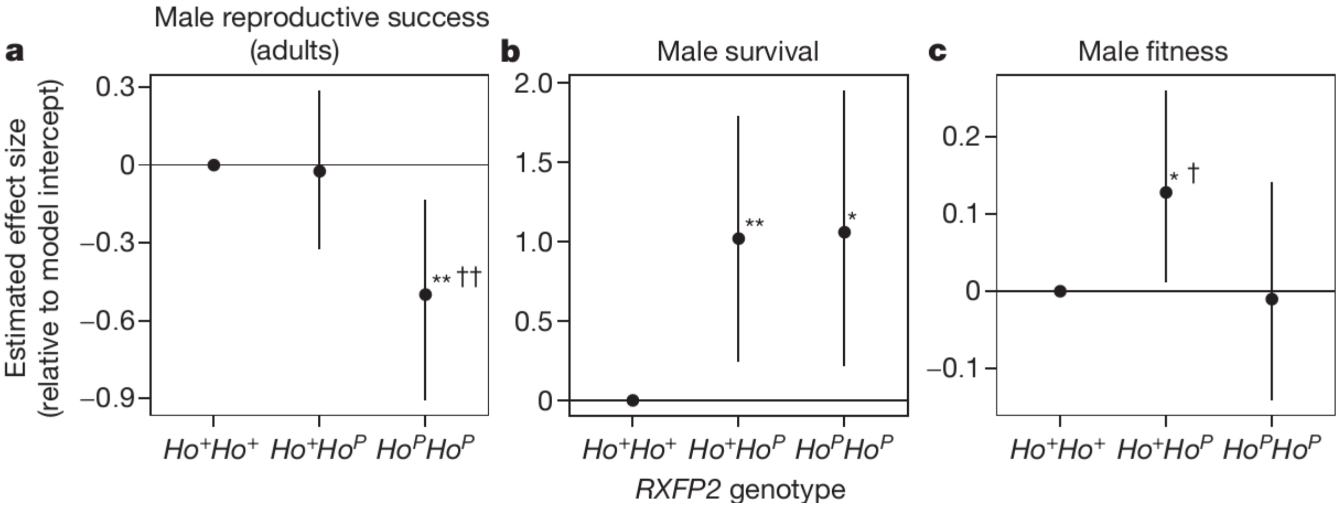
Mary Carrington,[1] George W. Nelson,[1] Maureen P. Martin,[1]
Teri Kissner,[1] David Vlahov,[2] James J. Goedert,[3]
Richard Kaslow,[4] Susan Buchbinder,[5] Keith Hoots,[6]
Stephen J. O'Brien[7]*



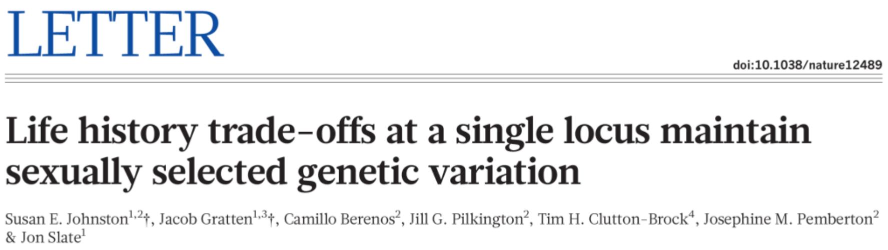
12 MARCH 1999 VOL 283 SCIENCE www.sciencemag.org

HLA-I heterozygosity associated with improved resistance to AIDS

Heterozygote advantage resulting from negative pleiotropy (trade-off)



- RXFP2 gene affects horn size in Kilda island sheep
- Horns give reproductive advantage, but horned homozygotes survive less well
- Beneficial dominance reversal makes heterozygotes the fittest!



LETTER

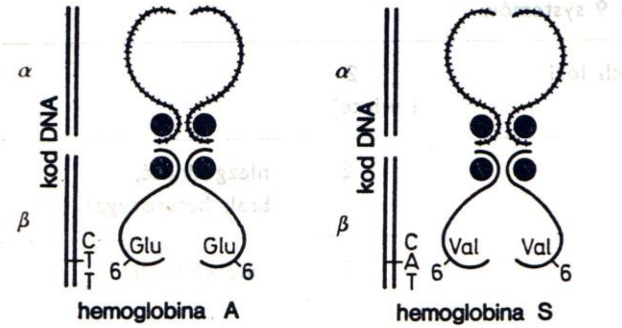
doi:10.1038/nature12489

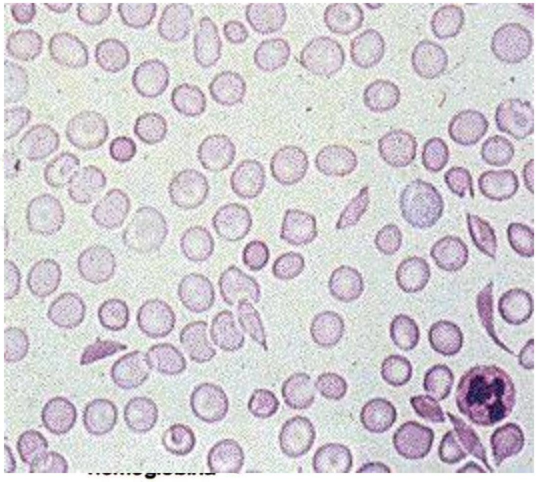
Life history trade-offs at a single locus maintain sexually selected genetic variation

Susan E. Johnston[1,2]†, Jacob Gratten[1,3]†, Camillo Berenos[2], Jill G. Pilkington[2], Tim H. Clutton-Brock[4], Josephine M. Pemberton[2] & Jon Slate[1]

Heterozygote advantage resulting from negative pleiotropy (trade-off)

Sickle-cel aneamia

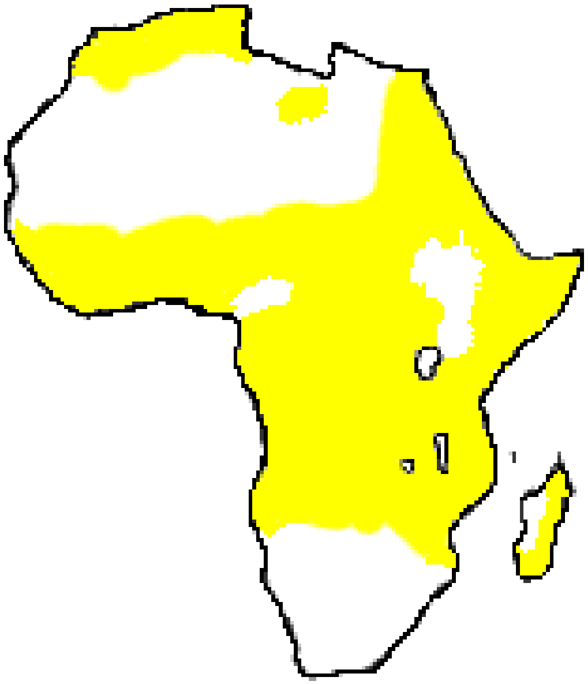




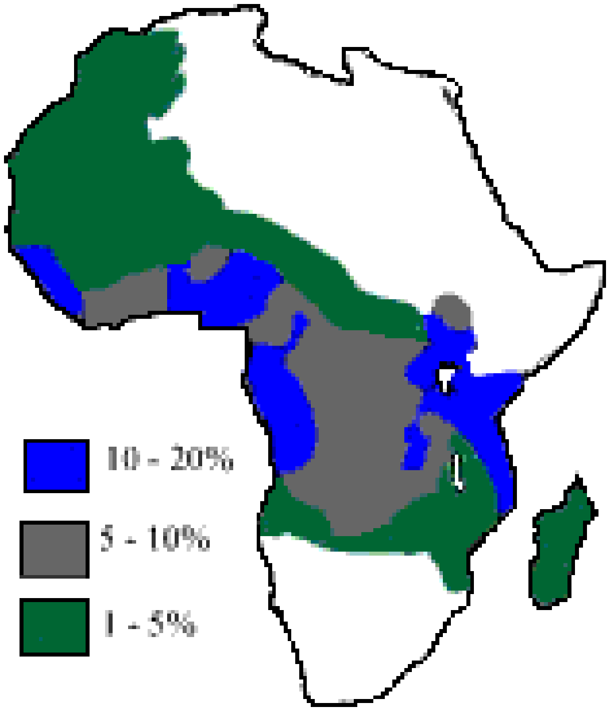
Ryc. 68 Hemoglobina składa się z czterech grup hemowych ●, 2 identycznych łańcuchów α i 2 identycznych łańcuchów β. W hemoglobinie *A* aminokwasem w pozycji 6 jest kwas glutaminowy, w hemoglobinie anemii sierpowatej *HbS* jest tam walina, w hemoglobinie *C* — lizyna. Znaczy to, że zmienione zostały tylko pojedyncze zasady kodu DNA

Sickle-cell genotypes fitness:
Europe AA>SA>SS
Africa AA<SA>SS

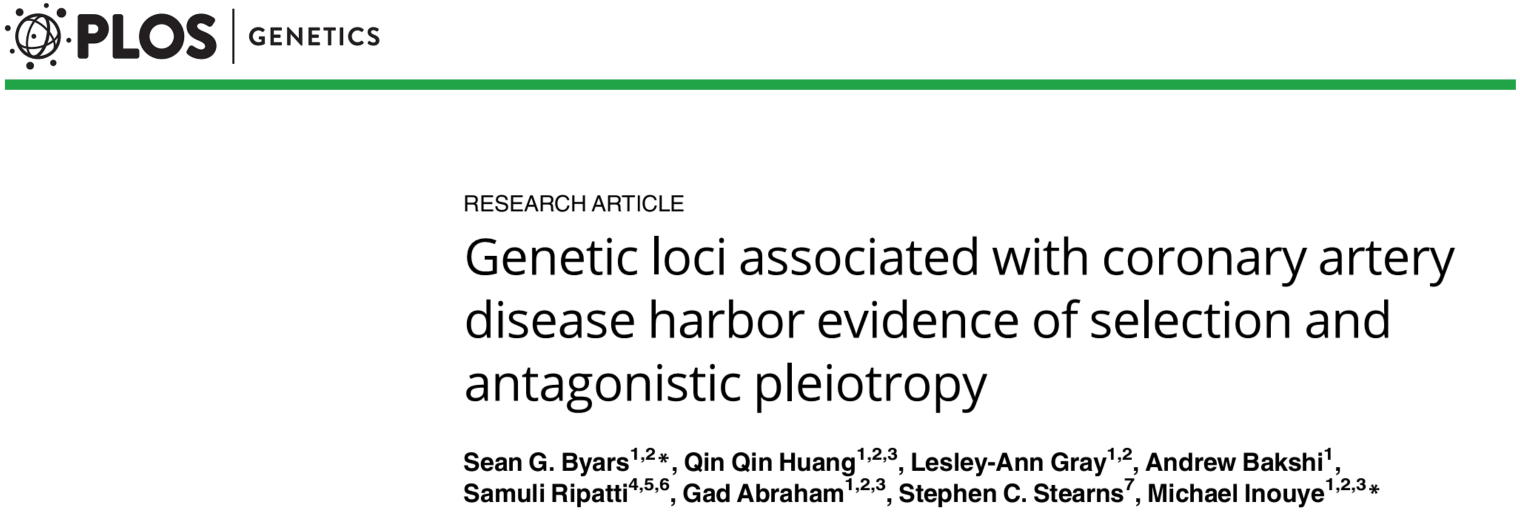
Trade-off between anaemia and malaria resistance favours heterozygotes in Africa



Malaria



%Hb^{s}



PLOS | GENETICS

RESEARCH ARTICLE

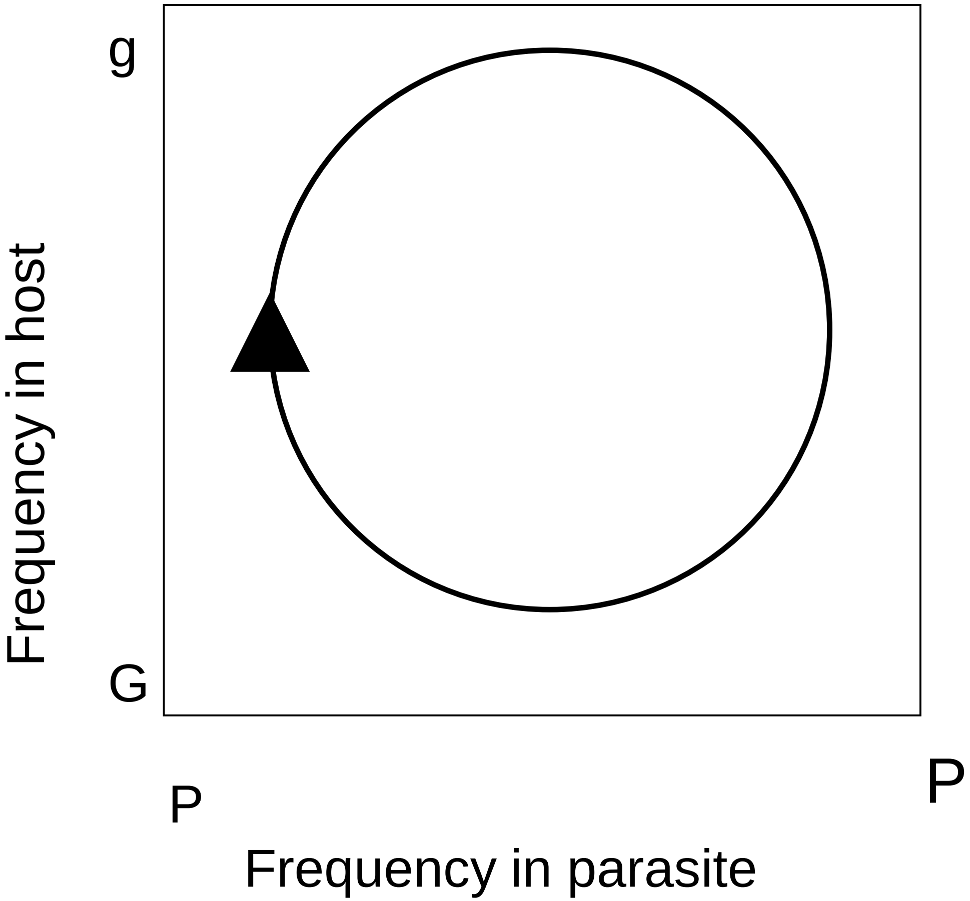
Genetic loci associated with coronary artery disease harbor evidence of selection and antagonistic pleiotropy

Sean G. Byars[1,2]*, Qin Qin Huang[1,2,3], Lesley-Ann Gray[1,2], Andrew Bakshi[1],
Samuli Ripatti[4,5,6], Gad Abraham[1,2,3], Stephen C. Stearns[7], Michael Inouye[1,2,3]*

Example of sexual antagonism:

Variants increasing coronary disease in males are associated with increased female fecundity

Host-parasite coevolution may favour rare alleles, leading to **negatively frequency-dependent selection** (NFDS)



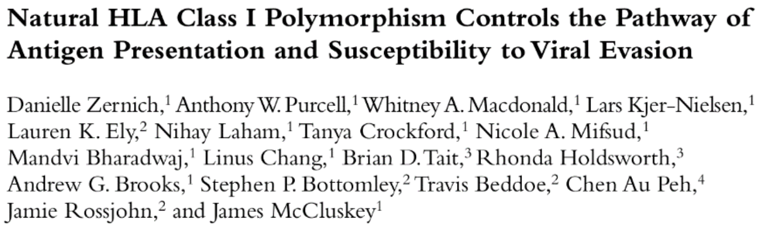
G resistant to P
g resistant to p

Pathogens evolve to avoid host immunity

E.g. viruses may avoid MHC binding by blocking peptide loading complex (PLC)

Host are under selection to counter-adapt

MHC mutation (substitution of Asp to Tyr in F-pocket) allows binding viral antigens without PLC



Natural HLA Class I Polymorphism Controls the Pathway of Antigen Presentation and Susceptibility to Viral Evasion

Danielle Zernich,[1] Anthony W. Purcell,[1] Whitney A. Macdonald,[1] Lars Kjer-Nielsen,[1]
Lauren K. Ely,[2] Nihay Laham,[1] Tanya Crockford,[1] Nicole A. Mifsud,[1]
Mandvi Bharadwaj,[1] Linus Chang,[1] Brian D. Tait,[3] Rhonda Holdsworth,[3]
Andrew G. Brooks,[1] Stephen P. Bottomley,[2] Travis Beddoe,[2] Chen Au Peh,[4]
Jamie Rossjohn,[2] and James McCluskey[1]

The Journal of Experimental Medicine

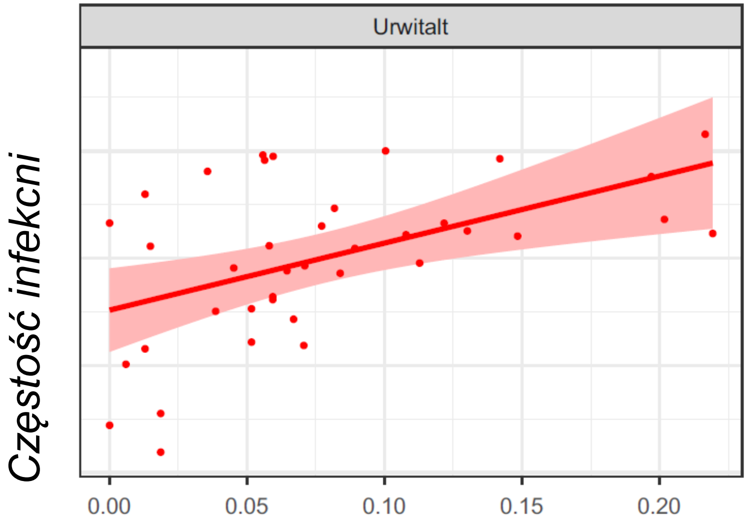
ORIGINAL ARTICLE

MOLECULAR ECOLOGY WILEY

Long term patterns of association between MHC and helminth burdens in the bank vole support Red Queen dynamics

Magdalena Migalska[1] | Karolina Przesmycka[2] | Mohammed Alsarraf[3] | Anna Bajer[3] | Jolanta Behnke-Borowczyk[4] | Maciej Grzybek[5] | Jerzy M. Behnke[6] | Jacek Radwan[2]

Prevalence of Aonchotheca annulosa worm infection is the highest among voles with most common MHC types



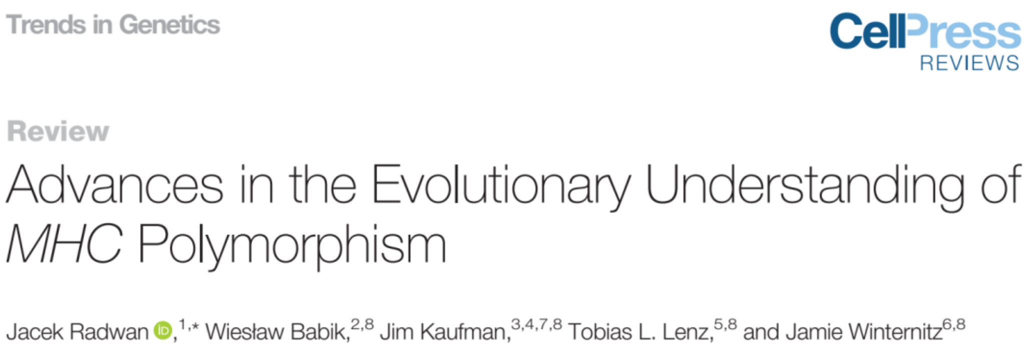
Częstość w poprzedzającym roku

Cell

Artic

Emergence of immune escape at dominant SARS-CoV-2 killer T cell epitope

*Mutation in ARS-Cov2 spike protein escapes immune memory in bearers of the most HLA I (HLA A*02)*



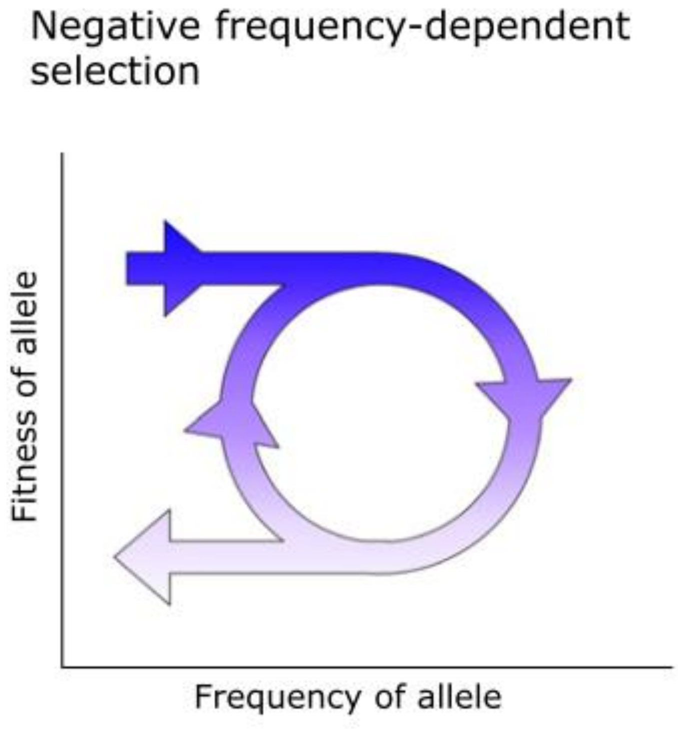
Trends in Genetics

CellPress REVIEWS

Review

Advances in the Evolutionary Understanding of *MHC* Polymorphism

Jacek Radwan,[1,*] Wiesław Babik,[2,8] Jim Kaufman,[3,4,7,8] Tobias L. Lenz,[5,8] and Jamie Winternitz[6,8]



Negative frequency-dependent selection

NFDS can maintain polymorphism and ***favour novel MHC alleles*** *(Bodmer 1972)*

NFDS favour MHC introgression?

MOLECULAR ECOLOGY

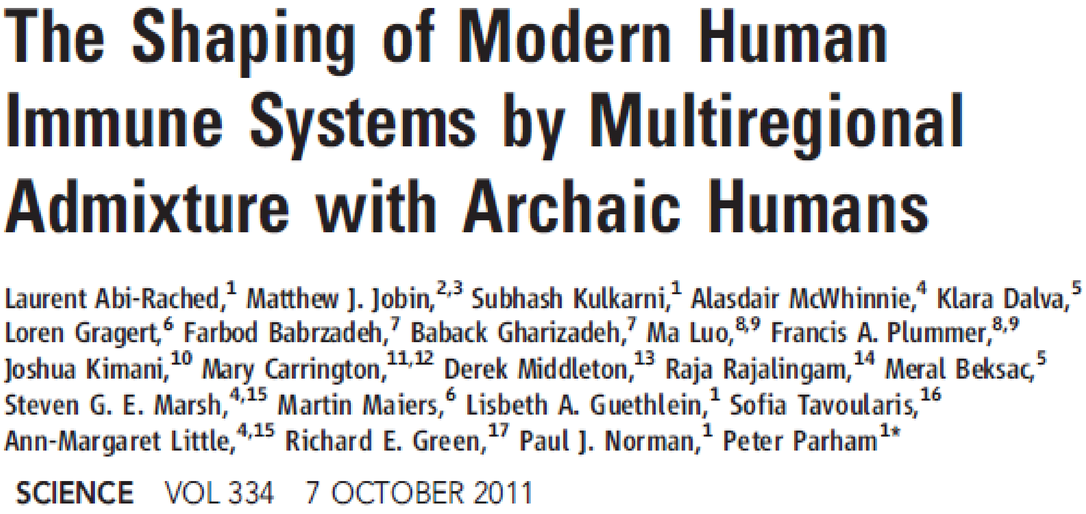
Molecular Ecology (2011) doi: 10.1111/j.1365-294X.2011.05347.x

Interspecific hybridization increases MHC class II diversity in two sister species of newts

KRYSTYNA NADACHOWSKA-BRZYSKA,*,‡ PIOTR ZIELIŃSKI,* JACEK RADWAN* and WIESŁAW BABIK†

**Institute of Environmental Sciences, Jagiellonian University, Gronostajowa 7, 30-387 Kraków, Poland,*

†Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland



The Shaping of Modern Human Immune Systems by Multiregional Admixture with Archaic Humans

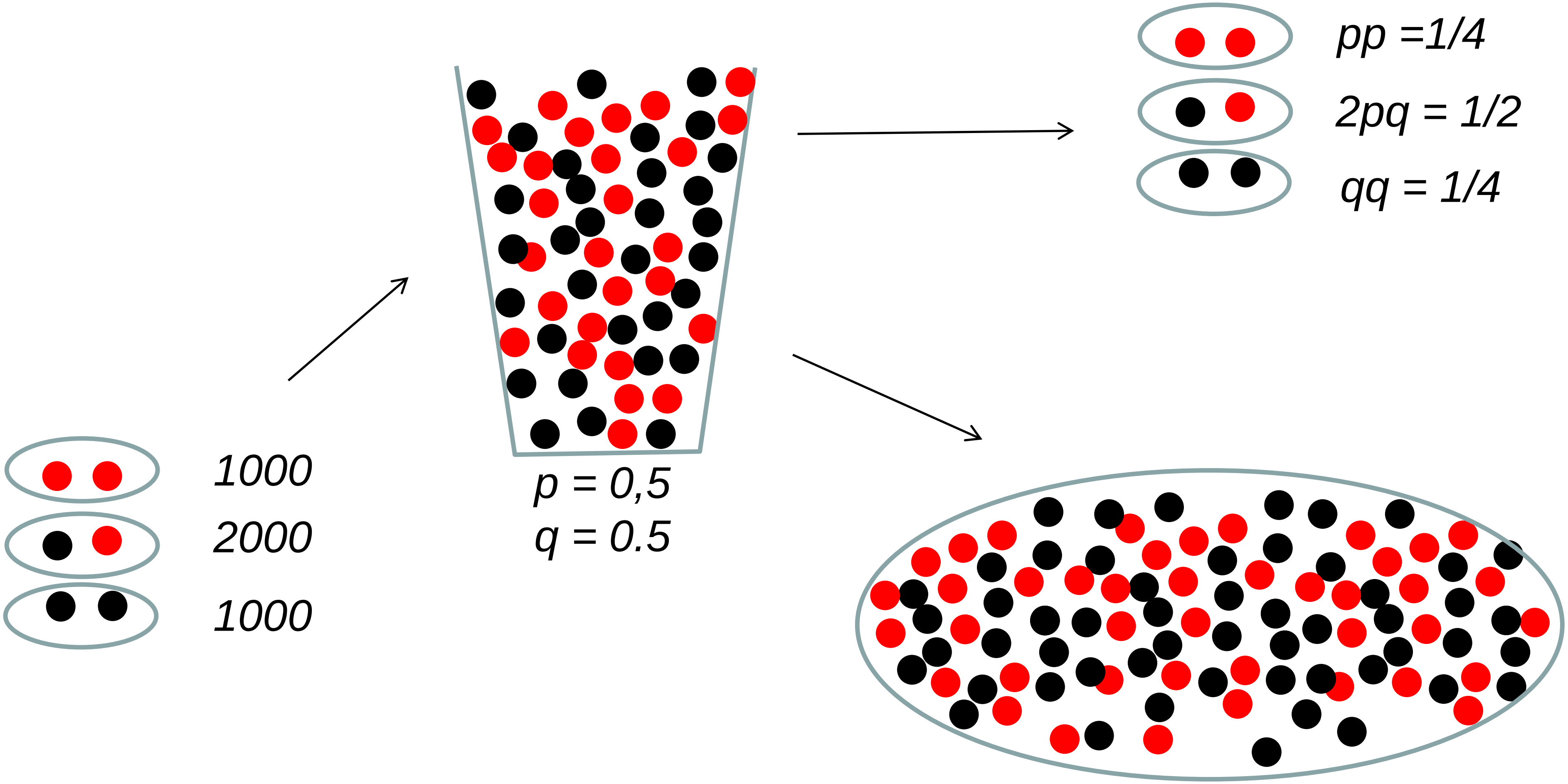
Laurent Abi-Rached,[1] Matthew J. Jobin,[2,3] Subhash Kulkarni,[1] Alasdair McWhinnie,[4] Klara Dalva,[5] Loren Gragert,[6] Farbod Babrzadeh,[7] Baback Gharizadeh,[7] Ma Luo,[8,9] Francis A. Plummer,[8,9] Joshua Kimani,[10] Mary Carrington,[11,12] Derek Middleton,[13] Raja Rajalingam,[14] Meral Beksac,[5] Steven G. E. Marsh,[4,15] Martin Maiers,[6] Lisbeth A. Guethlein,[1] Sofia Tavoularis,[16] Ann-Margaret Little,[4,15] Richard E. Green,[17] Paul J. Norman,[1] Peter Parham[1*]

SCIENCE VOL 334 7 OCTOBER 2011

Chance in evolution

Genetic drift: random changes in gene frequencies

Dryf genetyczny: losowe zmiany częstości alleli



1000

2000

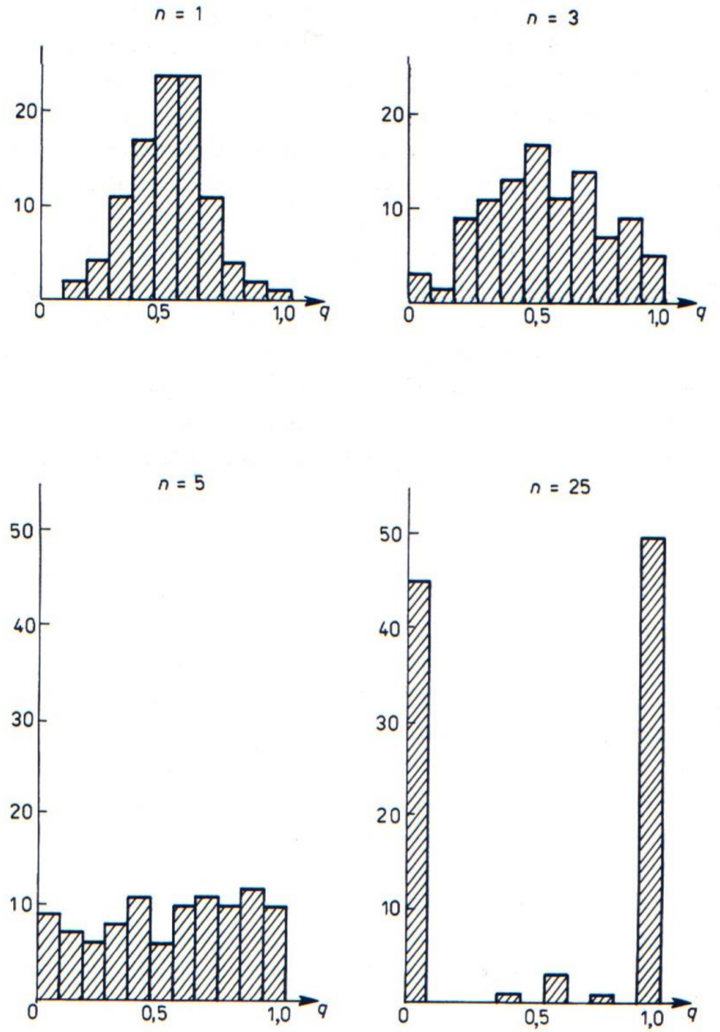
1000

p = 0,5
q = 0.5

pp =1/4

2pq = 1/2

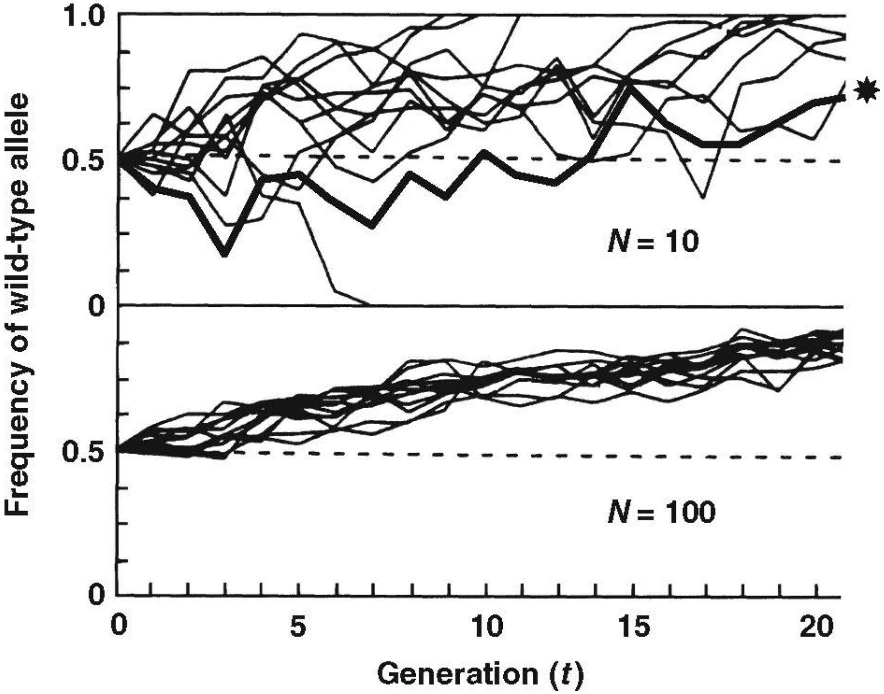
qq = 1/4



Ryc. 4.9. Histogramy przedstawiające naśladowanie dryfu po $n = 1$, 3, 5 i 25 pokoleniach, w 100 populacjach po 5 osobników każda, z tym że na początku rozpatrywany allel a miał częstość $q = 0{,}5$. Po 25 pokoleniach prawie wszystkie populacje mają albo tylko allel a $(q = 1)$, albo tylko allel alternatywny $(q = 0)$. Zauważmy, że histogramy też nie są zupełnie symetryczne, tak jak przewiduje teoria dla $q_0 = 0{,}5$, bo naśladowaliśmy dryf tylko w 100 populacjach, inne naśladowanie przy tych samych założeniach może dać histogramy bardziej symetryczne lub skośne w przeciwnym kierunku. Histogramy te obrazują przejściowe rozkłady frekwencji genów przy kumulatywnym działaniu dryfu. Przy przeciwdziałaniu doboru, migracji i mutacji może nie dojść do utrwalenia alleli we wszystkich lokalnych populacjach.

Simulation of drift acting on neutral alleles:

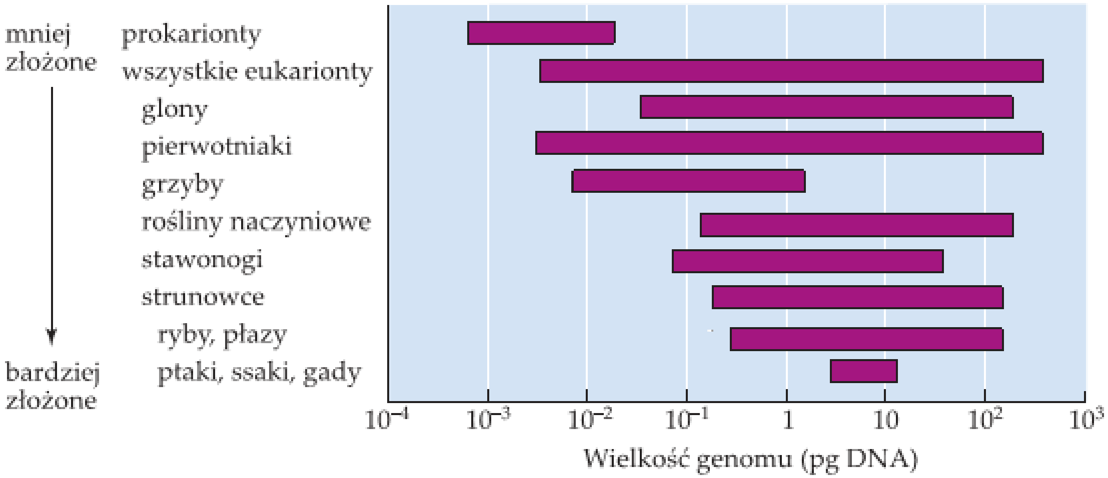
- Loss of genetic polymorphism within populations
- Probability of fixation = initial frequency
- Increases differentiation between populations



Kimura: non-neutral alleles become effectively neutral when ***s<1/(2N)***

Genetic drift in four beetle Tribolium castaneum; in one of small population deleterious allele was fixed (Falconer and Mackay 1996)

Michael Lynch: genetic drift may explain genome size evolution



- C-value paradox: genome size very weakly correlates with complexity

Genome size variation explained mostly by non-coding DNA

Non-coding DNA mostly consist of ‘junk DNA’: repetitive DNA, transposable elements, pseudogenes

Junk DNA accumulates faster in smaller populations – a role of drift

Junk DNA can be a source of evolutionary innovation!

Niebieskie symbole: Prokaryota;
Żródło: Lynch i Connery 2003

OPEN ACCESS Freely available online

PLoS GENETICS

De Novo Origin of Human Protein-Coding Genes

Dong-Dong Wu[1], David M. Irwin[1,2,3], Ya-Ping Zhang[1,4]*

Emergence of new genes from non-coding DNA.

- *60 new genes in humans since split from chimpanzees*
- *Most of them expressed in brain!*

Mobile genetic elements:

DNA transposons

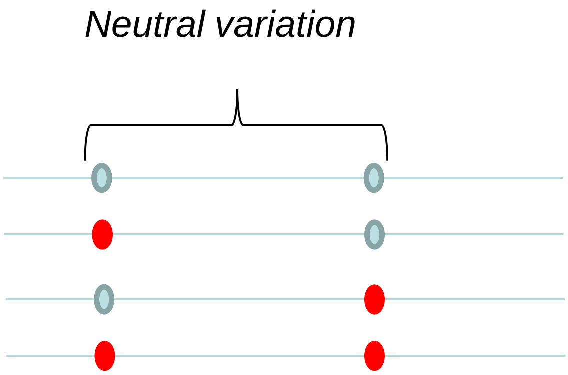
Retrotransposons (450000 in human genome)

Retroposons (LINE – 850000, SINE>100000)

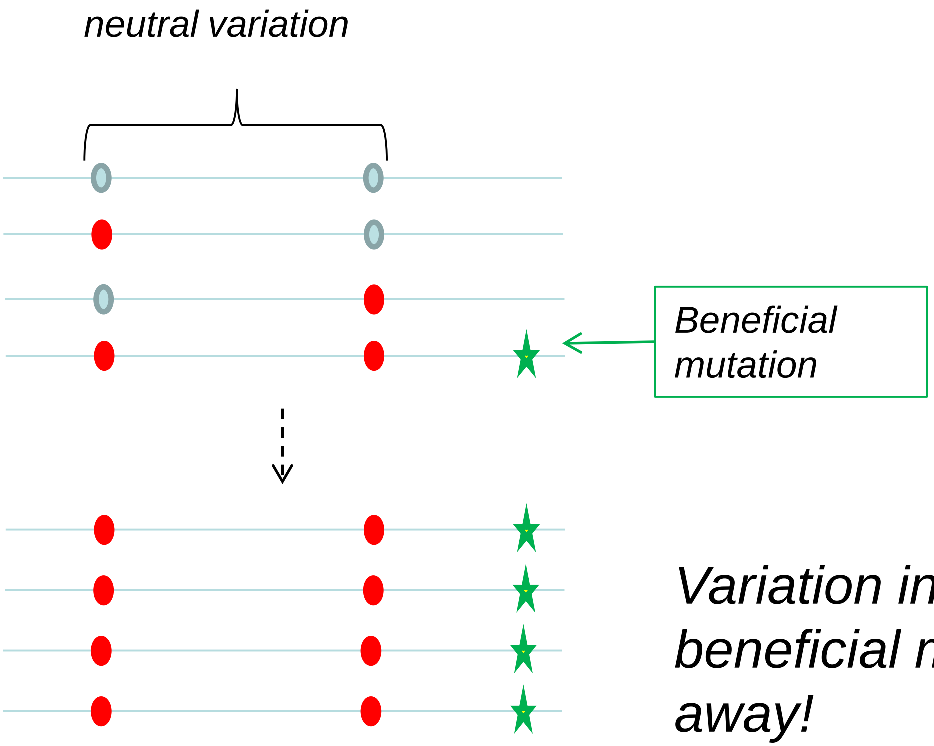
Arc gene, expressed in neurons and necessary in memory formation originates from retrotransposon Gag gene

Molecular inference of selection vs. drift

Selective sweep



Selective sweep



neutral variation

Beneficial mutation

Variation in proximity of beneficial mutation swept away!

Aminoacid			mRNA codon
Ala	A	Alanine	GCA, GCC, GCG, GCU
Arg	R	Arginine	AGA, AGG, CGA, CGC, CGG, CGU
Asn	N	Asparagine	AAC, AAU
Asp	D	Aspartic acid	GAC, GAU
Cys	C	Cysteine	UGC, UGU
Glu	E	Glutamic acid	GAA, GAG
Gln	Q	Glutamine	CAA, CAG
Gly	G	Glycine	GGA, GGC, GGG, GGU
His	H	Histidine	CAC, CAU
Ile	I	Isoleucine	AUA, AUC, AUU
Leu	L	Leucine	UUA, UUG, CUA, CUC, CUG, CUU
Lys	K	Lysine	AAA, AAG
Met	M	Methiodine	AUG
Phe	F	Phenylalanine	UUC, UUU
Pro	P	Proline	CCA, CCC, CCG, CCU
Ser	S	Serine	AGC, AGU, UCA, UCC, UCG, UCU
Thr	T	Threonine	ACA, ACC, ACG, ACU
Trp	W	Tryptophan	UGG
Tyr	Y	Tyrosine	UAC, UAU
Val	V	Valine	GUA, GUC, GUG, GUU
STOP		UAA, UAG, UGA	

Nonsynonymous to synonymous substitution rate (d_n/d_s)	Selection
<1	Purifying (non-synonymous removed)
=1	No (non-synonymous neutral)
>1	Positive (non-synonymous fixed)

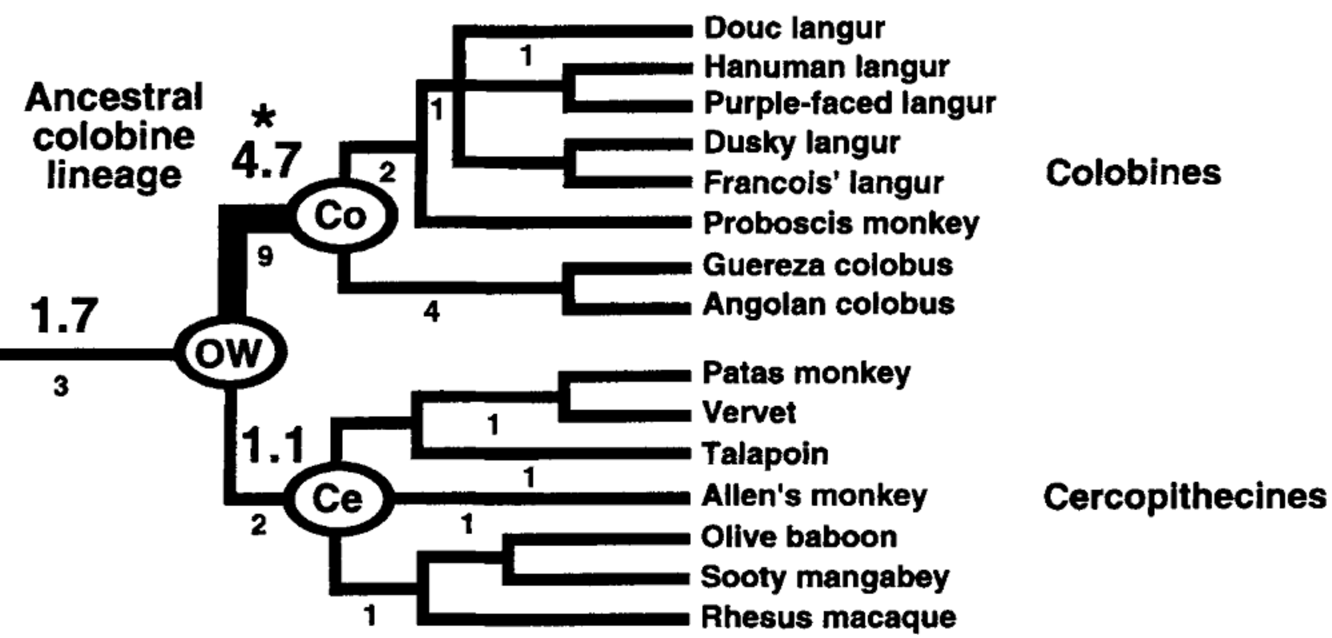
Example of positive selection: evolution of lysozymes helping herbivorous primates to digest bacteria

Episodic adaptive evolution of primate lysozymes

Walter Messier & Caro-Beth Stewart

NATURE · VOL 385 · 9 JANUARY 1997

numbers = d_n / d_s



Levels of selection

Levels characterised by differential survival/reproduction due to heritable traits:

Gene

Individual

Group of individuals

Species (and higher taxa)

Gene level

An example of selfish gene: *t* in mouse

t+ - short tail

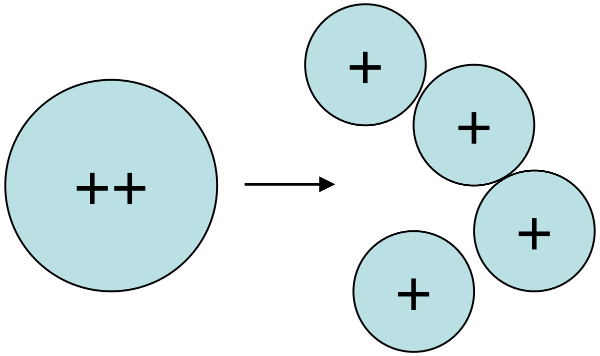
tt - lethal

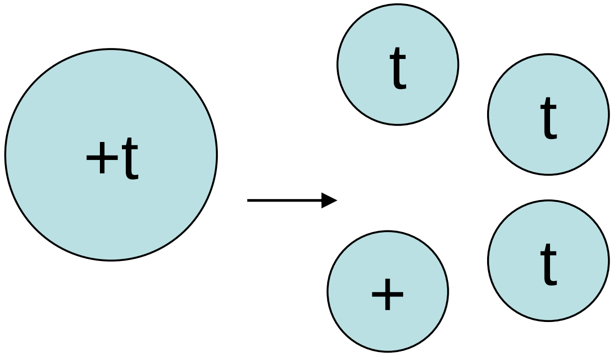
Meiotic drive:

t+ males produce 90-100% t gametes (instead of 50% expected)

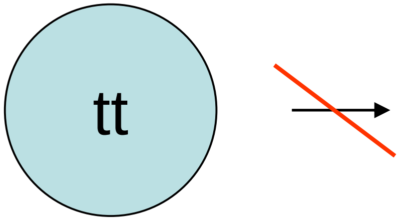
t frequency – up do 18% despite lethal effect in homozygotes!

Conflict between levels of selection:



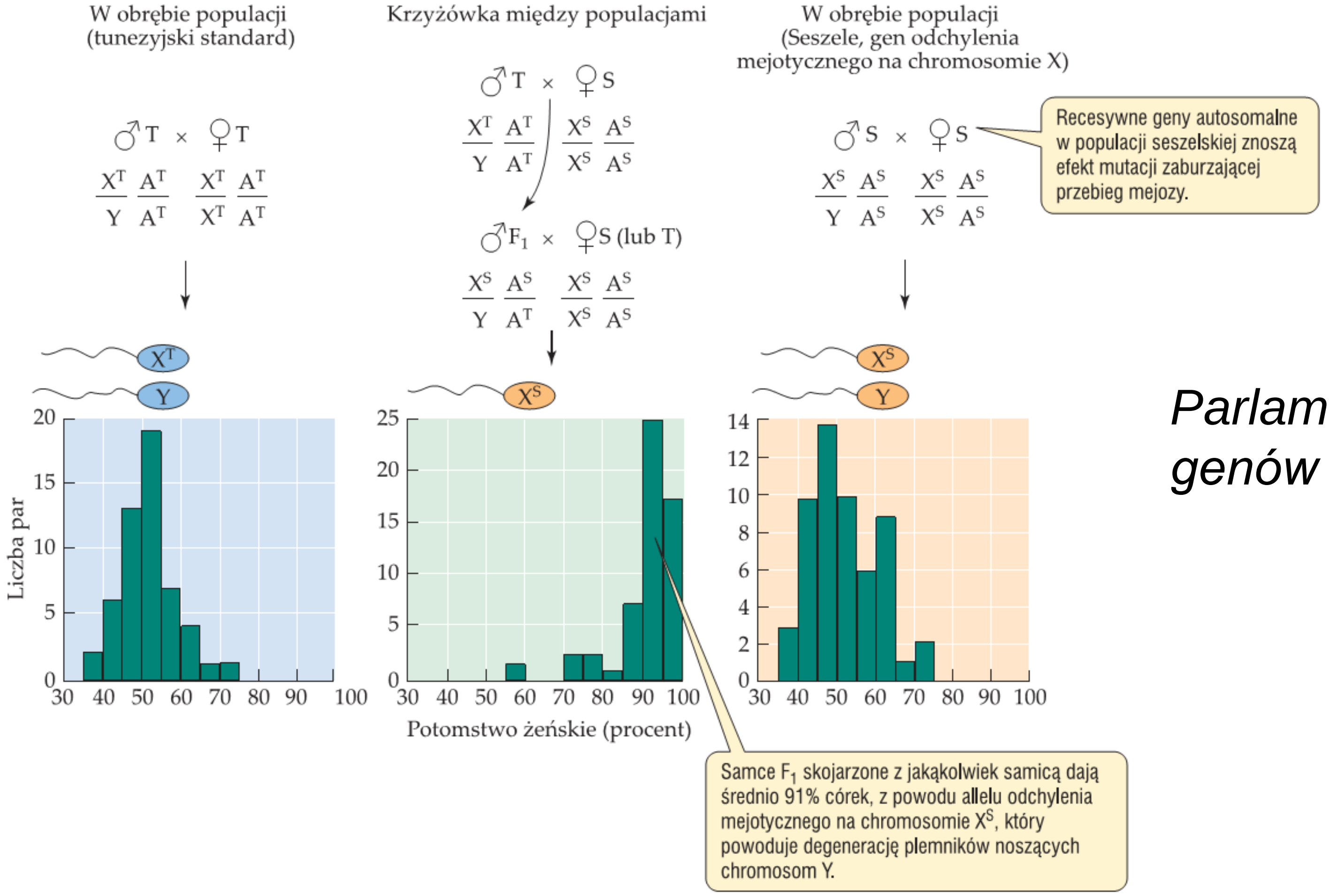


t positively selected at genes level



negatively selected at individual level

Allel X^s powoduje zaburzenie mejozy – degenerację plemników z Y, lecz w populacji seszelskiej nie ujawnia się z powodu recesywnego supresora A^s



Recesywne geny autosomalne w populacji seszelskiej znoszą efekt mutacji zaburzającej przebieg mejozy.

Samce F_1 skojarzone z jakąkolwiek samicą dają średnio 91% córek, z powodu allelu odchylenia mejotycznego na chromosomie X^S, który powoduje degenerację plemników noszących chromosom Y.

Parlament genów

Rycina 14.23 Wpływ konfliktu genetycznego na proporcje płci u *Drosophila simulans*. Na każdym z wykresów pokazano liczby par, które dały potomstwo o określonym procencie samic. Na wykresie, po lewej stronie, pokazano wyniki dla krzyżówek w obrębie „standardowej" populacji tunezyjskiej (T), po prawej, w obrębie populacji seszelskiej (S). Środkowy wykres ilustruje proporcje płci w potomstwie samców F_1, uzyskanych z krzyżówek między tymi dwiema populacjami (środek). Symbole X i Y w genotypach rodziców oznaczają chromosomy płciowe, symbol A – autosomy (za: Atlan i in. 1997)

Selfish ogranelles?

Mmitochondrial circular genome contains 37 genes coding for enzymes producing energy (oxidative phosphorylation)

Chloroplast genome: ca. 100 genów photosynthesis genes (90% na DNA jądrowym)

Endosymbiotic origin of organelles: sequence similarity indicates mitochondria are related to purple bacteria, and chloroplasts to blue algae

Consequence of mitochondrial „domestication” – two genomes in one individual!

Mitochondrial genes transmitted only by females**: cytoplasmic sterility** mutations causing resources to be directed to eggs favoured, causing conflict with nuclear genes

Group selection is a very weak evolutionary force:

Selection much more effective on individuals/genes:

- birth/death on much shorter timescale in individuals than in populations
- Individuals much more numerous than populations (higher probability of beneficial mutation, selection more effective)

Genes beneficial to individual/genes will spread at the cost of genes beneficial to groups!

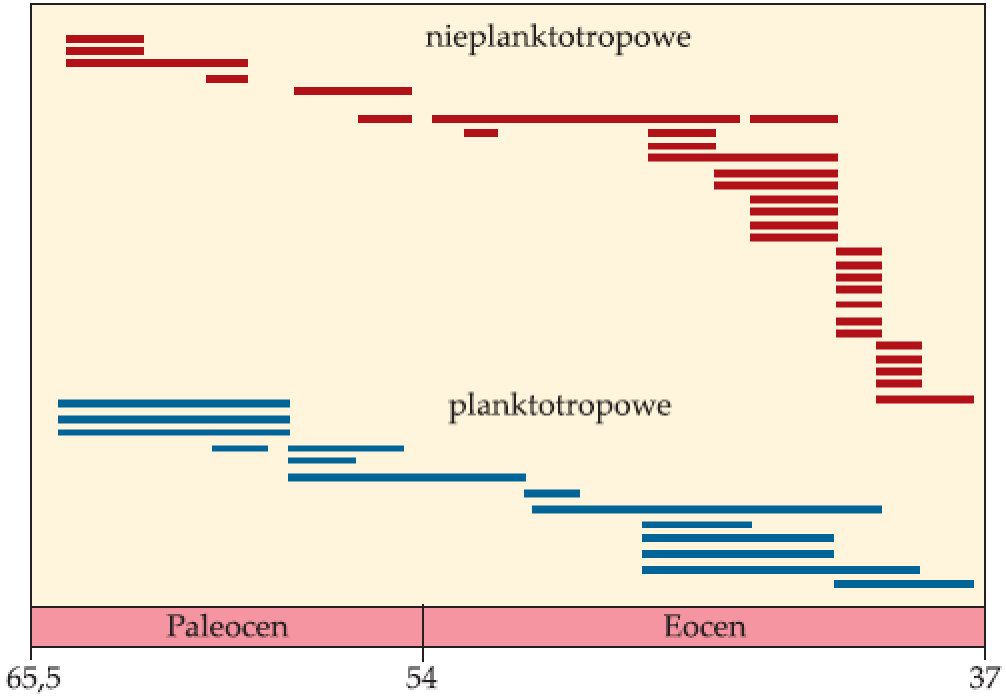
Species level:

- *No gene flow, but selection much more effective on individuals/genes (for same reasons as for groups), hence* ***traits good for species but costly to individual will not spread***
- *Traits which evolved by individual/gene level selection can effect species birth (speciation) and death (extinction)*

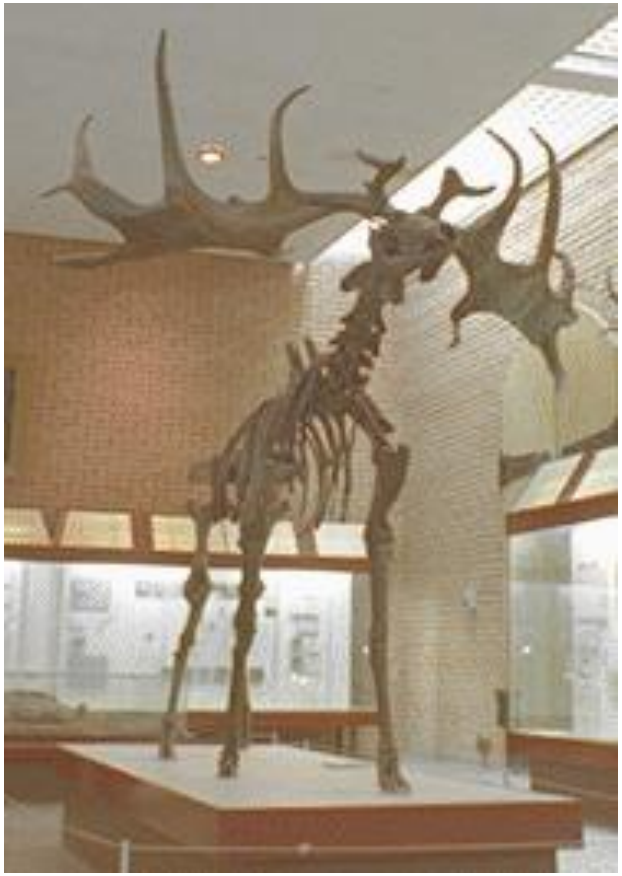
Specialised flowers attract specific pollinator species.

More specialised orchids (19 500 species) higher than in their more generalist Iridaceae relatives (1750 species)

Cecha może wpływać na tempo specjacji bądź wymierania, prowadząc do zmiany średniej wartości cechy w obrębie kladu



Macroevolutionary trend on species level. Lines represent stratigraphic distribution of Volutidae snails. Species with dispersive larval stage (blue) lasted longer, but has lower rate of speciation (Hansen 1980).



Traits beneficial for individual can evolve even if they increase the risk of species extinction

Giant elk *Megaloceros* (1.7m), went extinct during ice age, perhaps because of costly antlers

High male sexual investment as a driver of extinction in fossil ostracods

Maria João Fernandes Martins[1,5], T. Markham Puckett[2], Rowan Lockwood[3], John P. Swaddle[4] & Gene Hunt[1,5]*

366 | NATURE | VOL 556 | 19 APRIL 2018

Among fossil ostracods Cytheromatidae tempo wymierania extinction rate was higher in lineages with larger copulatory apparatus, which helps in reproductive competition.

https://doi.org/10.1371/journal.pone.0177791.g002

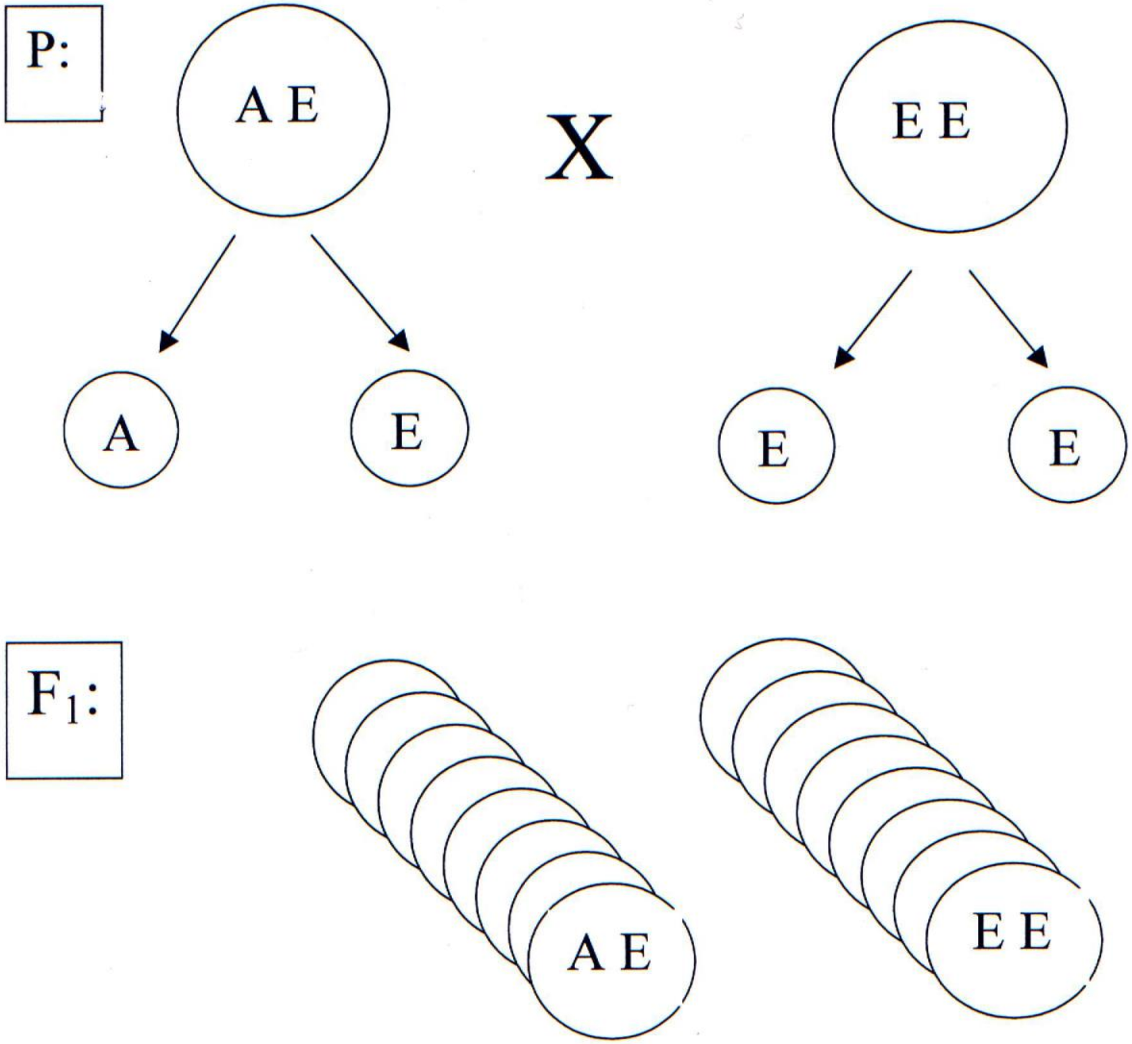
If not group selection, how to explain biological altruism?

Back to gene level: selfish genes for altruism can spread if they help their copies in other individuals

***Biological altruism:** a behaviour/trait decreasing and individual fitness, but increase fitness of a social partner.*

William D. Hamilton

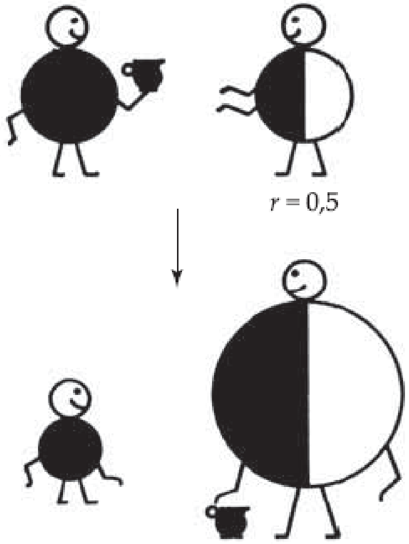
Sibs share genes!



Kin selection theory of W.D. Hamilton explains biological altruism with selfish genes!

(A) **Altruizm**

Altruista dostarcza korzyści bratu, który dzieli z nim ½ genów.



Mimo spadku dostosowania indywidualnego altruisty, następne pokolenie dziedziczy więcej kopii jego genów.

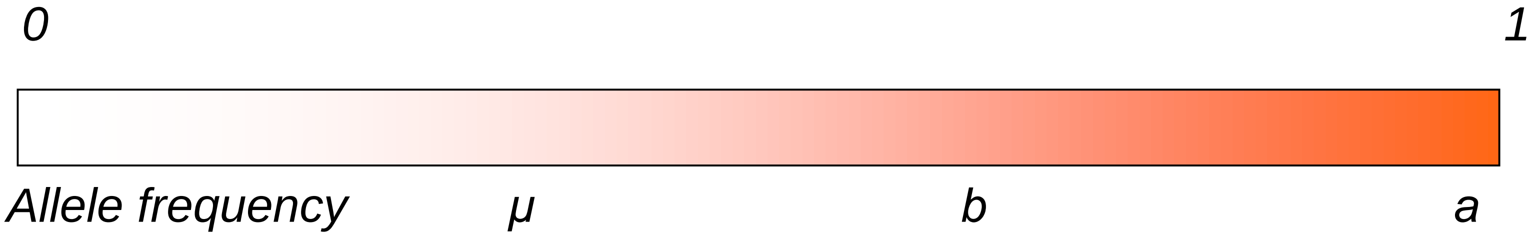
Hamilton’s rule: altruism will spread if

$$rb-c>0$$

where **b**, benefit of help recipient, **c**, cost to altruist, **r**, relatedness coefficient (a measure of probability of finding a the same allele in the recipient relative to population mean)

e.g. sibs, parents-offspring: $r=0.5$, half-sibs: $r=0.25$, cousins: $r=0.125$

Geometric interpretation of the coefficient of relatedness r



0 *1*

Allele frequency *μ* *b* *a*

$$r=(b-\mu)/(a-\mu)$$

where

r – coefficient of relatedness

μ – mean population frequency

a – expected frequency in the altruist

b – expected frequency in the beneficiary

Young long-tailed tit (Aegithalos caudatus) who fail to breed independently help others in the care of offspring, but (almost) only if they are their kin (Russell and Hatchwell 2001)

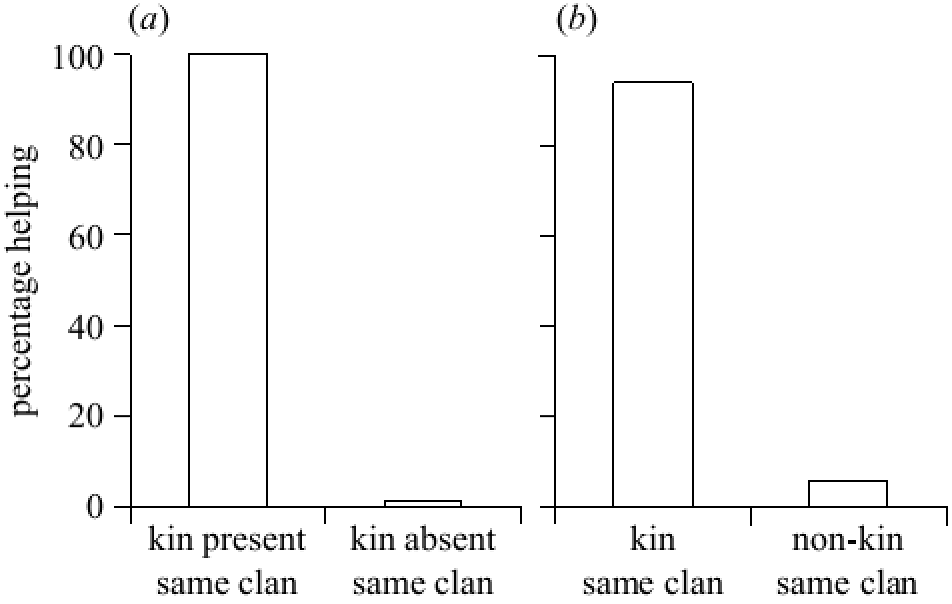


Figure 4. The kin preferences of and helping decisions taken by failed breeders. (*a*) The proportion of potential helpers that helped when kin were present within the same clan ($n = 17$) and absent from the same clan ($n = 9$) (one-tailed binomial test, $p < 0.005$). (*b*) The proportion of potential helpers that helped at the nests of kin and non-kin when both were available in the same clan ($n = 17$) (one-tailed binomial test, $p < 0.001$).

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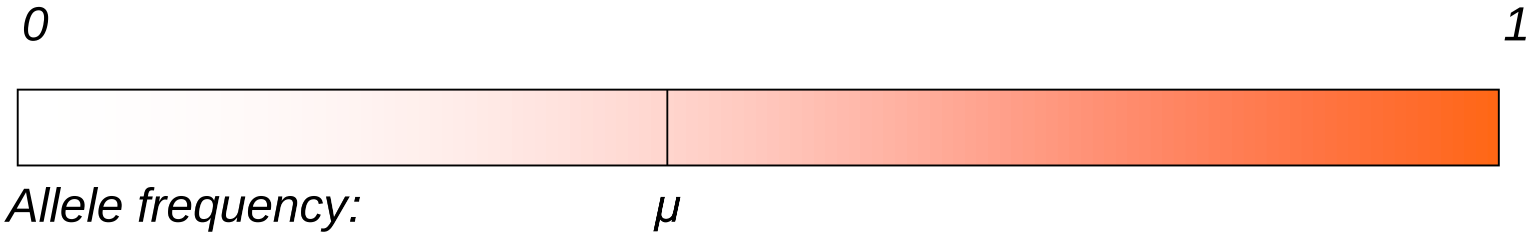
(socio) biological spite: behaviour costly to actor and recipient

Can Hamilton rule :

$$-c_r r^* - c_a > 0$$

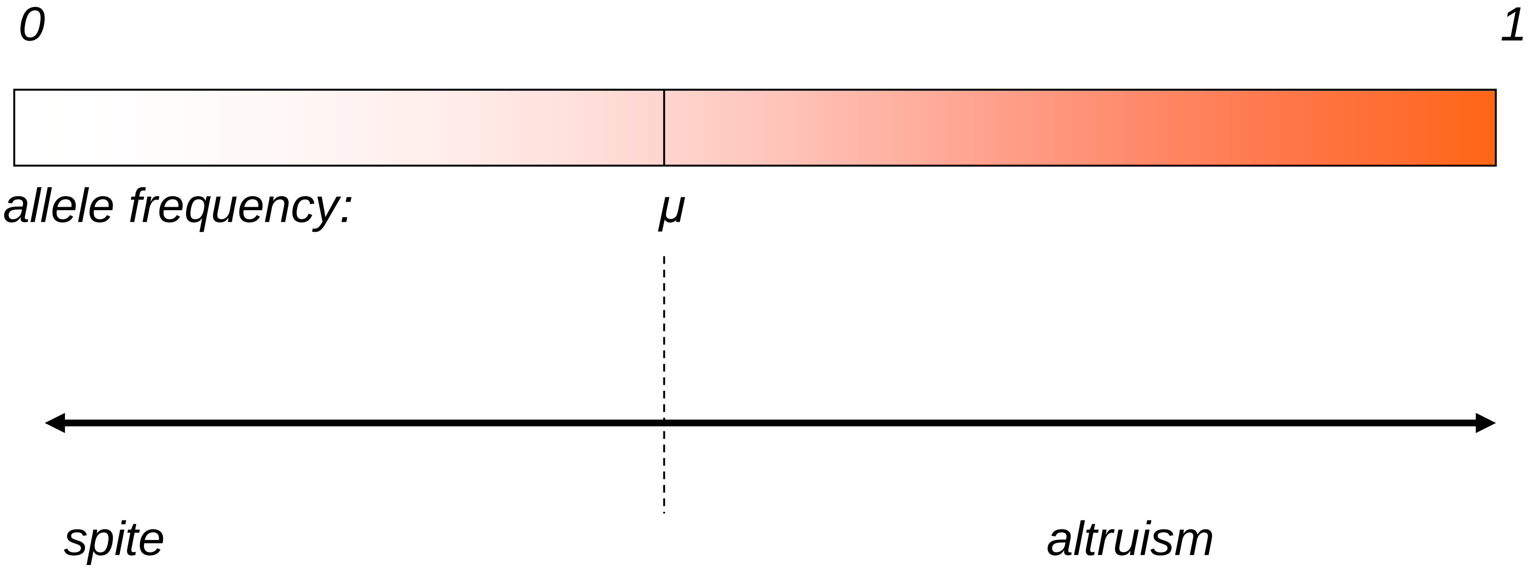
C_a – cost in actor, C_r – cost in recepient

be fulfilled?



$$-r*c_r - c_a > 0$$

true if $r < 0$!



0

1

allele frequency:

μ

spite

altruism

Infanticide in langurs is not spiteful – it benefits actors by bringing females to oestrus

How animals recongize their kin?

Spermophilus beldingi

„Recognition” by context

Recognition by learning

Recongintion using genetic markers

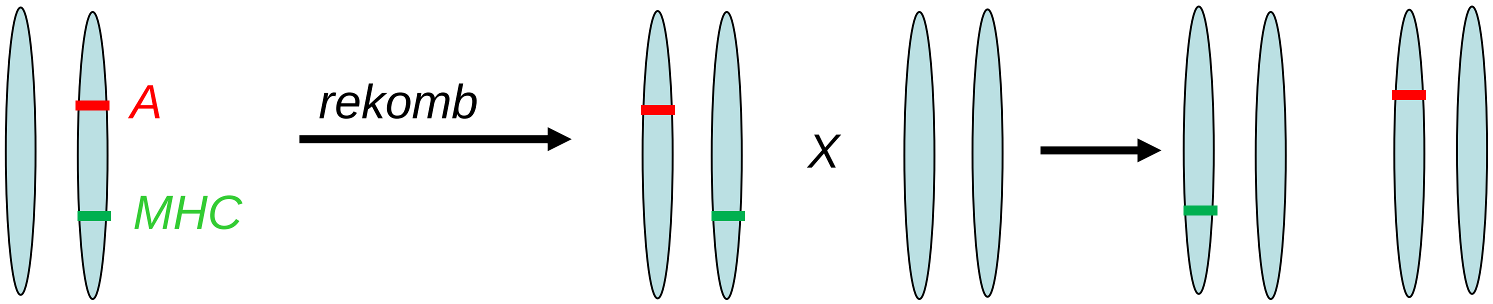
Genetic markers used for kin recognition should be highly polymorphic – otherwise an allele will likely be found in unrelated individuals

This condition is fulfilled eg. for MHC loci

- *Female mice prefer communal nesting with relatives and mate with males of different MHC*
- *V2R receptors bind MHC I ligands*
- *MHC affects microbiome composition*

Wedekind et al. 1995: preferences for MHC type in humans

Polymorphic genes (np. MHC) useful for kin identification, but not for detecting altruist alleles per se: recombination breaks down linkage between altruism allele and MHC



„Greed beard gene" should have pleiotropic effect, or be tightly linked

Solenopsis invicta (fire ants)

Locus Gp-9

Queen:

~~BB~~ – killed by Bb workers (BB non-aggressive)

Bb

~~bb~~ - lethal

Reciprocal altruism and evolution of cooperation

Trivers’ necessary conditions for reciprocal altruism

- cost of altruism < recipient's benefit
- individual recognition of the interactors
- high probability of repeated interactions

Game theory application: Prisoners’ dilemma

Score for		the other convict:	
		„silent”	**„betrays”**
	„silent”	**3**	**-2**
	„betrays”	**5**	**-1**

Game theory application: Prisoners' dillema

Score for		the other convict:	
		„cooperates"	**„deceives"**
	„cooparation"	**3**	**-2**
	„deceit"	**5**	**-1**

Tit for tat strategy outperforms others

C/C: 3/3; 3/3; 3/3; 3/3......

D/D: -1/-1; -1/-1/; -1/-1.......

C/D: -2/5; -2/5; -2/5; -2/5

TfT/TfT: 3/3; 3/3; 3/3; 3/3.....

TfT/D: -2/5; -1/-1; -1/-1; -1/-1.....

Public goods exchange: unrelated vervet monkeys *Chlorocebus aethiops* respond more often to alarm calls of those individuals, who groomed them in the past (Seyfarth and Cheney 1984)

Public goods exchange in mongooses:

- Sentinels groomed more often
- Grooming frequency increased after playbacks of alarm calls

manipulated

control

Julie M. Kern[a] and Andrew N. Radford[a,1]

PNAS | June 12, 2018 | vol. 115 | no. 24 | 6255–6260

Biological market theory: increased supply should devaluate gains (Noe i Hammerstein 1994)

Supply and demand determine the market value of food providers in wild vervet monkeys

Cécile Fruteau[a,b], Bernhard Voelkl[b], Eric van Damme[a,c], and Ronald Noë[b,d,1]

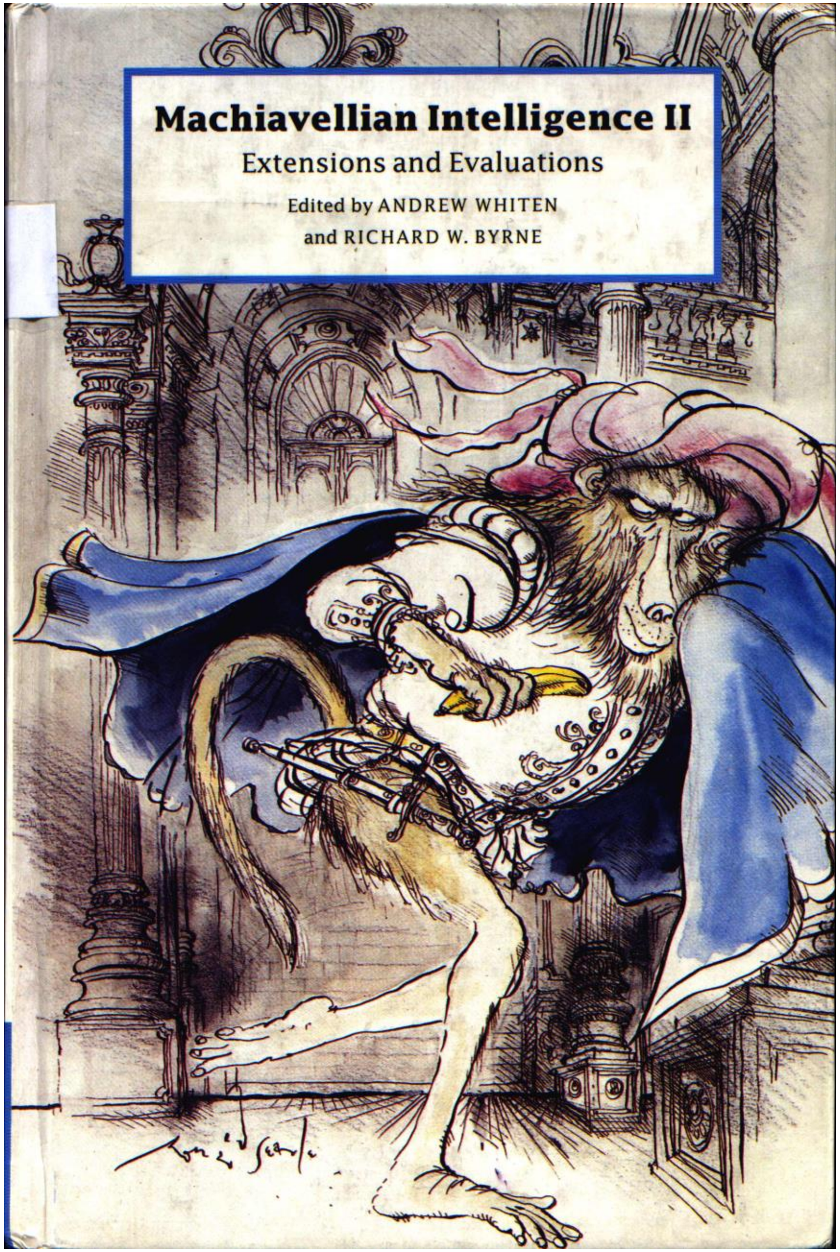
PNAS

Vervet monkeys adjust grooming intensity to oranges supply

Machiavellian Intelligence II

Extensions and Evaluations

Edited by ANDREW WHITEN
and RICHARD W. BYRNE



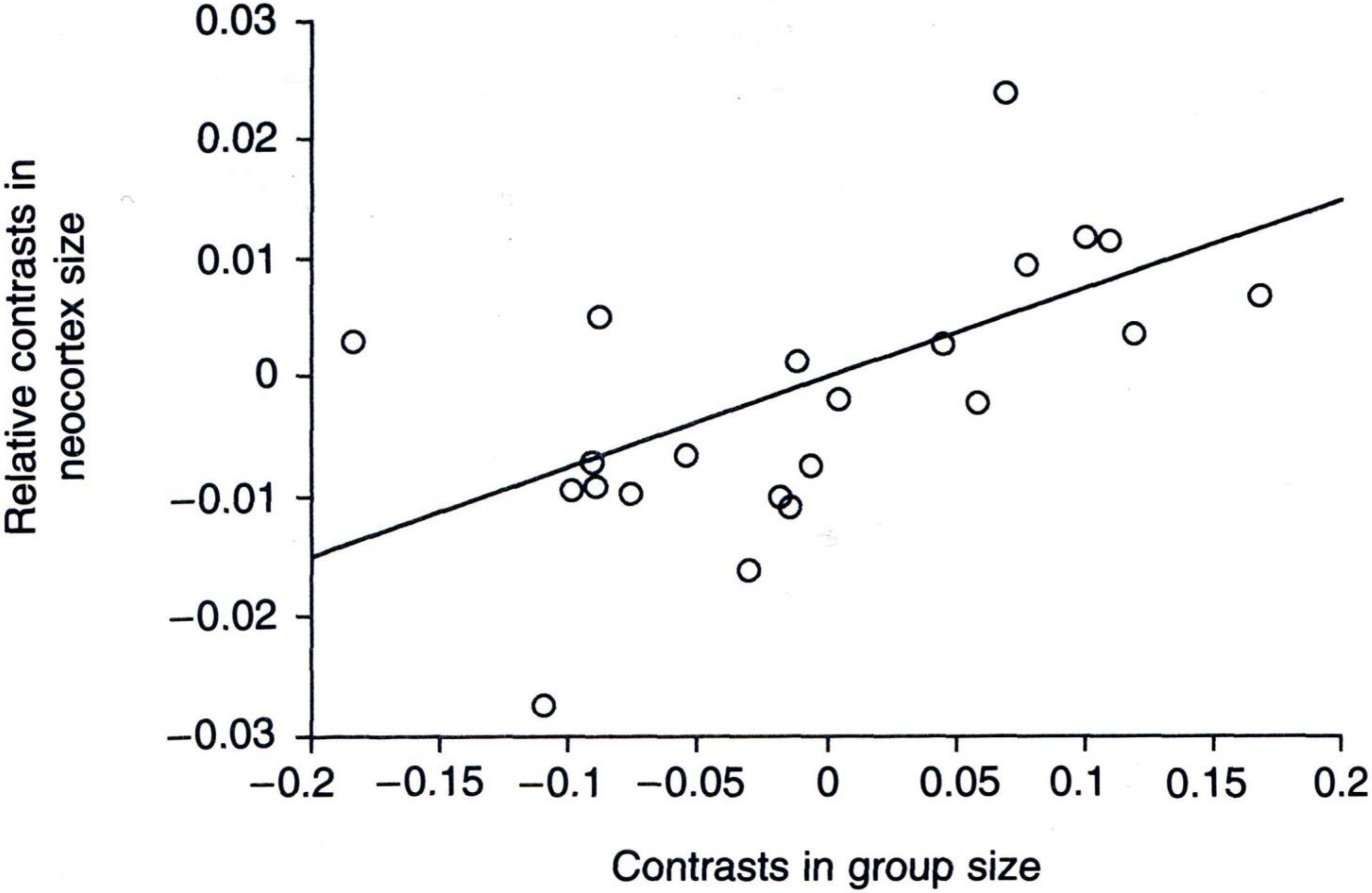


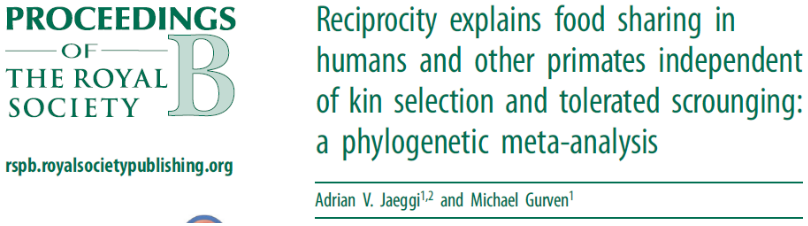
FIGURE 9.1 Correlation between relative neocortex size and group size among diurnal haplorhine primates, based on independent contrasts generated using the C.A.I.C. package (Purvis & Rambaut, 1995). $r^2 = 0.35$, $p < 0.01$.

Altruism and cooperation in human societies – unique features

- *Occurs in large groups of unrelated individuals (Hill 2011, Science)*
- *Enforced by social norms (e.g. punishment of desertion)*
- *Enhanced by social preferences for altruism, care, equality*

Hypotheses on human cooperation:

- *Inherited from primate ancestors, in which evolved by kin selection and reciprocity*
- *Result of culture*



PROCEEDINGS OF THE ROYAL SOCIETY B

rspb.royalsocietypublishing.org

Reciprocity explains food sharing in humans and other primates independent of kin selection and tolerated scrounging: a phylogenetic meta-analysis

Adrian V. Jaeggi[1,2] and Michael Gurven[1]

In humans and apes sharing associated with kinship and reciprocity

Large scale cooperation: kin group selection?

Genetic differentiation between groups must exceed the ratio of costs of altruism to average group member benefits

$$F_{ST}/(1 - F_{ST}) > c_i/b_G$$

F_{ST} *– a measure of genetic differentiation between groups*

c_i *- cost of altruism to an individual*

b_G *– average benefit of collaboration (competitive advantage over other groups) (Bowles 2009, Science 324: 1293-7)*

but: subject to invasion by free riders!

Genetic differentiation between human populations similar to that among primates

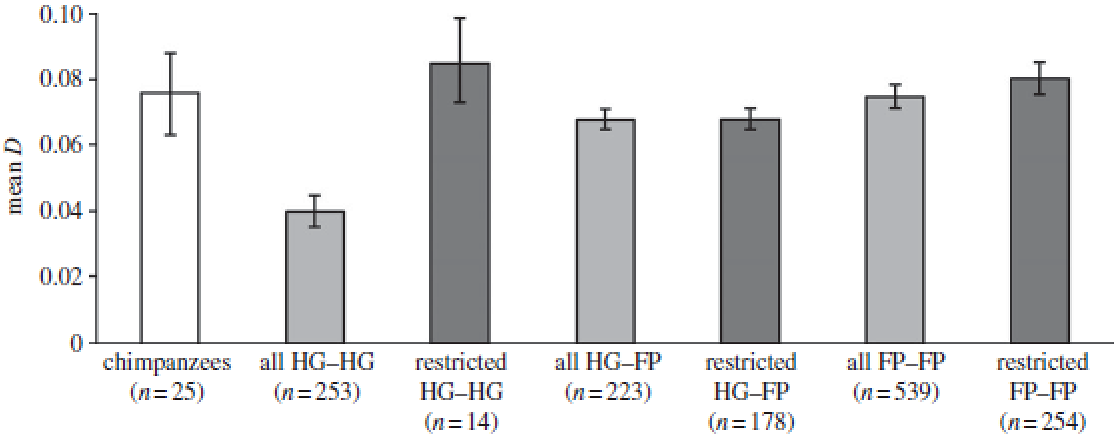


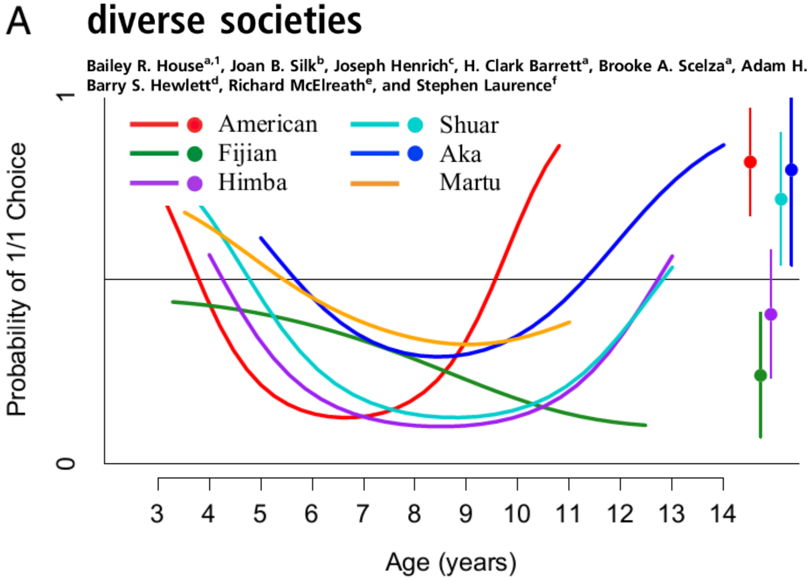
Figure 2. Average pairwise *D*-values (and 95% CIs) of chimpanzee (empty bar) and human groups (grey bars) with different combinations of subsistence systems. Sample sizes (number of pairs of groups) are shown in brackets. For humans, light grey bars represent values for all pairs of groups, and dark grey bars represent values for the restricted sample consisting only of pairs of groups belonging to different ethnolinguistic groups and speaking languages belonging to different language families. HG, hunter–gatherer; FP, food producer.

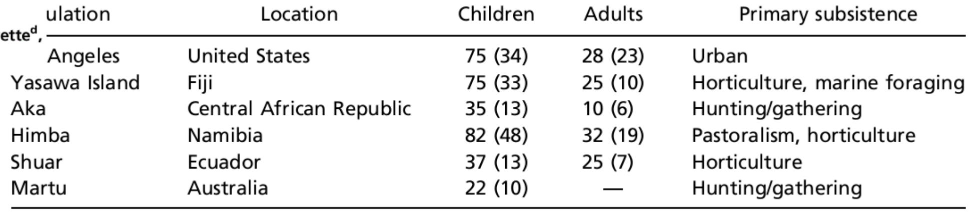
Cultural hypothesis:

- *Social learning and conformism homogenise behaviours within groups, but may increase differences between groups*
- *Inter-group competition favours cooperative behaviours (Boyd i Richerson 2002)*
- *Cultural norms can be enhanced by genetic evolution of pro-social emotions (gene-culture coevolution, Lumsden i Wilson 1980)*

Ontogeny of prosocial behavior across diverse societies

Bailey R. House[a,1], Joan B. Silk[b], Joseph Henrich[c], H. Clark Barrett[a], Brooke A. Scelza[a], Adam H. Boyette[d], Barry S. Hewlett[d], Richard McElreath[e], and Stephen Laurence[f]





ulation	Location	Children	Adults	Primary subsistence
Angeles	United States	75 (34)	28 (23)	Urban
Yasawa Island	Fiji	75 (33)	25 (10)	Horticulture, marine foraging
Aka	Central African Republic	35 (13)	10 (6)	Hunting/gathering
Himba	Namibia	82 (48)	32 (19)	Pastoralism, horticulture
Shuar	Ecuador	37 (13)	25 (7)	Horticulture
Martu	Australia	22 (10)	—	Hunting/gathering

Small children in most culture choose prosocial option in a choice test; older children conform their societies (House i in. 2013)

Cultural differences (gray) among coutries more pronounced than genetic differences

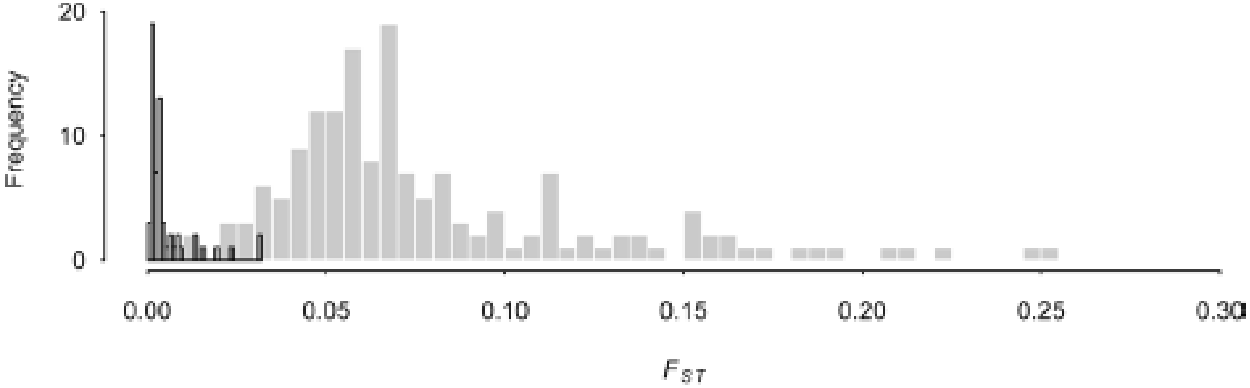


Fig. 1. Comparison of genetic and cultural differentiation. Above: Histogram of 150 cultural F_{ST} (gray fill) and 59 genetic F_{ST} (black border) for neighboring countries calculated from the World Values Survey and in (24), respectively. Bottom: Plot of the cultural against genetic F_{ST} for 59 pairs of neighboring countries.

Bell et al. 2009. PNAS 106, 17671-17674

PROCEEDINGS OF THE ROYAL SOCIETY B

Proc. R. Soc. B (2009) **276,** 355–360
doi:10.1098/rspb.2008.1060
Published online 30 September 2008

Between-group competition and human cooperation

Mikael Puurtinen* and Tapio Mappes

(GC)

- *Four students, each given 20 Euro*

- *Each Euro paid to group account group –gives 0.5 Euro bonus; account shared among group members equally (individual paying 1 Euro loses 0.5 Euro, but if everybody paid, everybody would benefit)*
- *Variant with inter-group competition (GC): group with higher value on the account earns the difference x 2*

GC:

- *higher tendency to pay for group*

- *Higher self-reported **social emotions level***

Alternative evolutionary explanations of warfare, an extreme form of large-scale cooperation

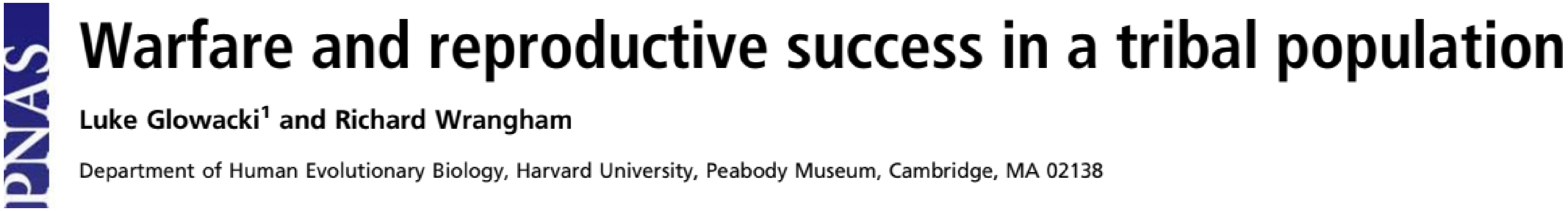
1) Heroic model (reproductive benefits to heroes)

2) Manifestation of psychological mechanisms which evolved is small groups via kin selection or reciprocity (currently maladaptive)

3) Cultural evolution as a result of competition between large ethno-linguistic groups

a greater number of courageous, sympathetic and faithful members, who were always ready to warn each other of danger, to aid and defend each other…would spread and be victorious over other tribes” [Darwin 1871, The descent of man, p. 156

4) Manipulation by group leaders



Warfare and reproductive success in a tribal population

Luke Glowacki[1] and Richard Wrangham

Department of Human Evolutionary Biology, Harvard University, Peabody Museum, Cambridge, MA 02138

In pastoral groups of Nyangatom (East Africa) participation in stealth rides correlates with more wives in older man

Critique:

- *No signficant association with violent rides*
- ***Data only on older males who survived!***

Solving the puzzle of human warfare requires an explanation of battle raids and cultural institutions

Matthew Ryan Zefferman, Ryan Baldini, and Sarah Mathew

Inter-group aggression in chimpanzees

Mahale Mountains (Uganda) chimpanzee group killed 18 strangers during ‘border patrols’

During this time 22% territorial gain

Fergusson 2018: this kind of events rare in other groups: During 426 observation years in 18 sites only 9 cases recorded

Costs and benefits of participation in war among Turkana (Matthew iBoyd 2011, PNAS 108, 11375–11380)

Cooperation in force raids enforced culturally: cowardice and desertion punished

Cooperation thus possible in large ethnolinguistic groups (not only in small kin groups)

SCIENTIFIC AMERICAN

EVOLUTION

War Is *Not* Part of Human Nature

War may not be in our nature after all

By R. Brian Ferguson on September 1, 2018

- Groups of skeletons bearing traits of violent deaths not found until 10-12000 year ago
- Wars associated with appearance of hierarchical, agricultural societies?

Exploitative leaders incite intergroup warfare in a social mammal

Rufus A. Johnstone[a,1,2], Michael A. Cant[b,c,d,1,2], Dominic Cram[a,e], and Faye J. Thompson[b,c,1]

Theoretical model:

Assumption: conformism (e.g. rebels punished)

Costs and benefits differ between leaders and soldiers

Group aggression evolves when $\mathbf{b}_{leader} > \mathbf{b}_{sodkier}$ *and/or* $\mathbf{c}_{leader} < \mathbf{c}_{soldier}$
Even if average fitness decreased

PNAS | **November 24, 2020** | vol. 117 | no. 47 | **29759–29766**

Exploitative leaders incite intergroup warfare in a social mammal

Rufus A. Johnstone[a,1,2], Michael A. Cant[b,c,d,1,2], Dominic Cram[a,e], and Faye J. Thompson[b,c,1]

*Banded mongooses (**Mungos mungo**) violent territorial disputes*

- *High male mortality (20%of all deaths)*
- *Female reproductive success increases with the number of inter-group-interactions!*

- *In accordance with the model, IGIs initiated by females!*

https://www.youtube.com/watch?v=KAxmAk7woyA

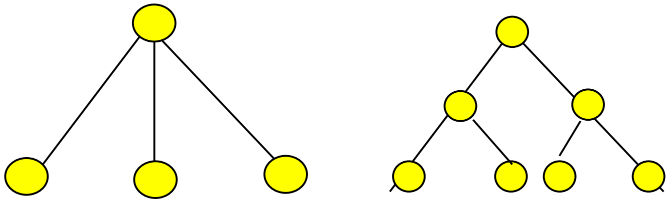
Life history trade-offs

Life-history theory explains diversity of traits like maturation time, body size and lifespan

What is optimal time to start reporduction?

Benefits of early maturation:

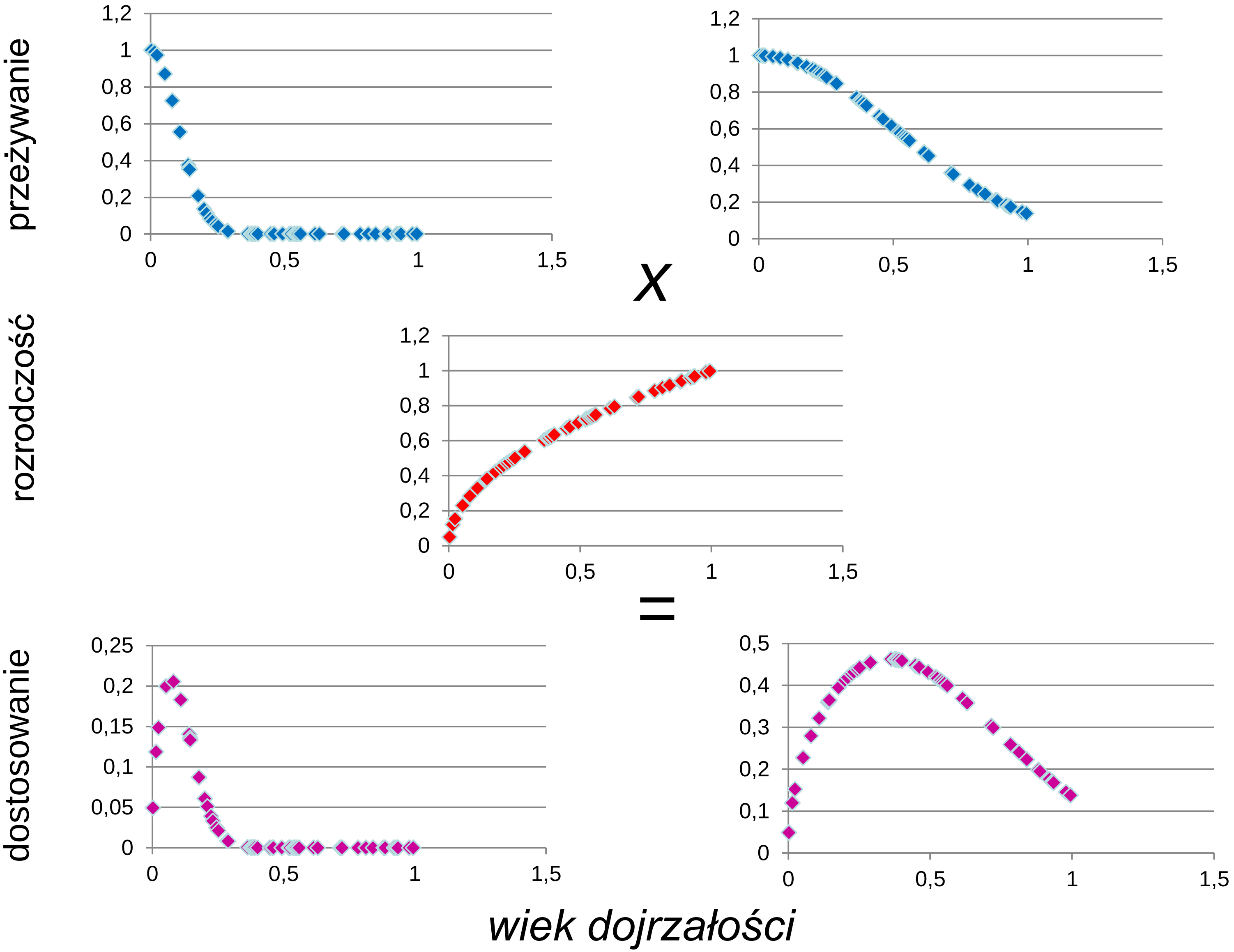
- lower mortality prior to reproduction
- shorter generation time



Costs of early maturation:

- lower body mass
- lower reproductive potential or worse progeny quality

Optimal maturation time for species reproducing once per life



Egg size vs number optimisation in *Uta stansburgiana* lizard

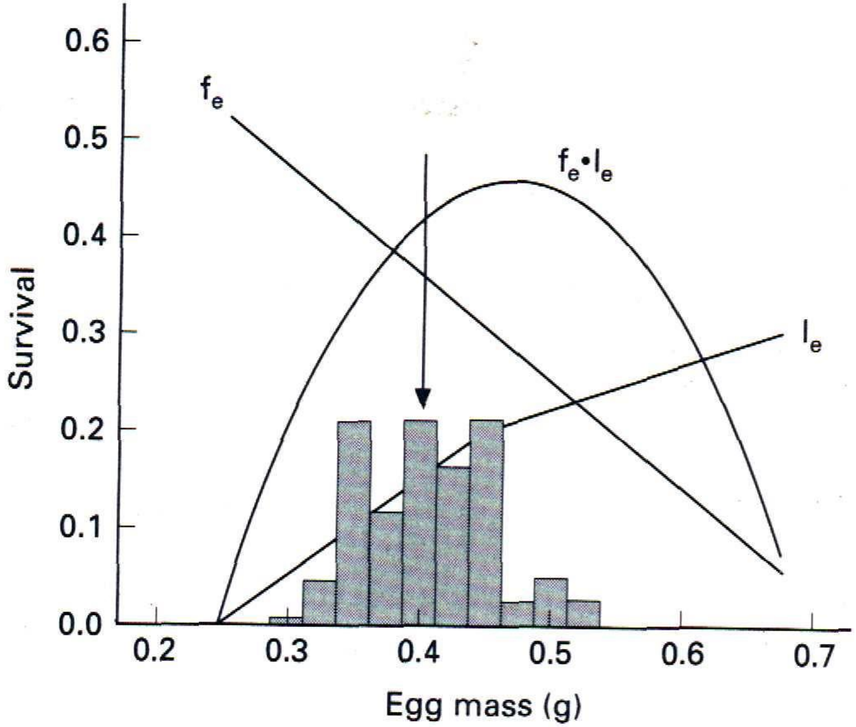


Fig. 13.13 Number of eggs per clutch (f_e), survival of hatchlings (l_e) and the fitted function through their product $f_e l_e$ as an estimator of fitness, in a population of eggs of manipulated size of the lizard *U. stansburiana*. Bars show the natural variation in egg mass. (From Sinervo *et al.*, 1992.)

Trade-off between reproduction and mortality

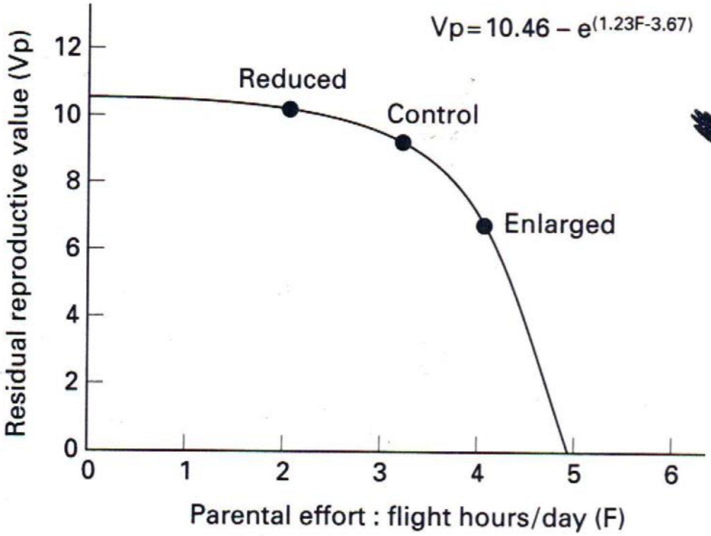
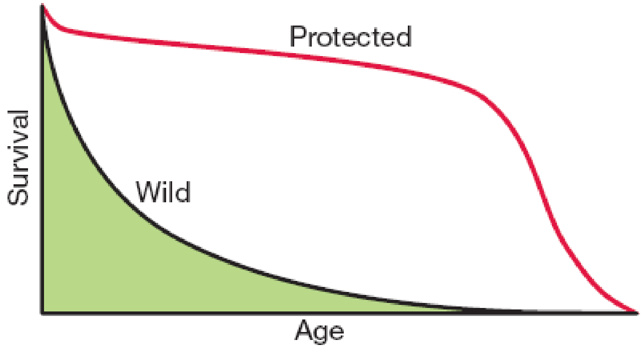


Fig. 13.8 Kestrel residual reproductive value plotted as a function of their parental effort (hours of flight per day). (From Daan *et al.*, 1990a.)

Why do we see ageing?

Mortality:

- Internal, determined by senescence rate
- Zewnętrzne, determined by parasites, predators, food availability etc.



Theories of ageing

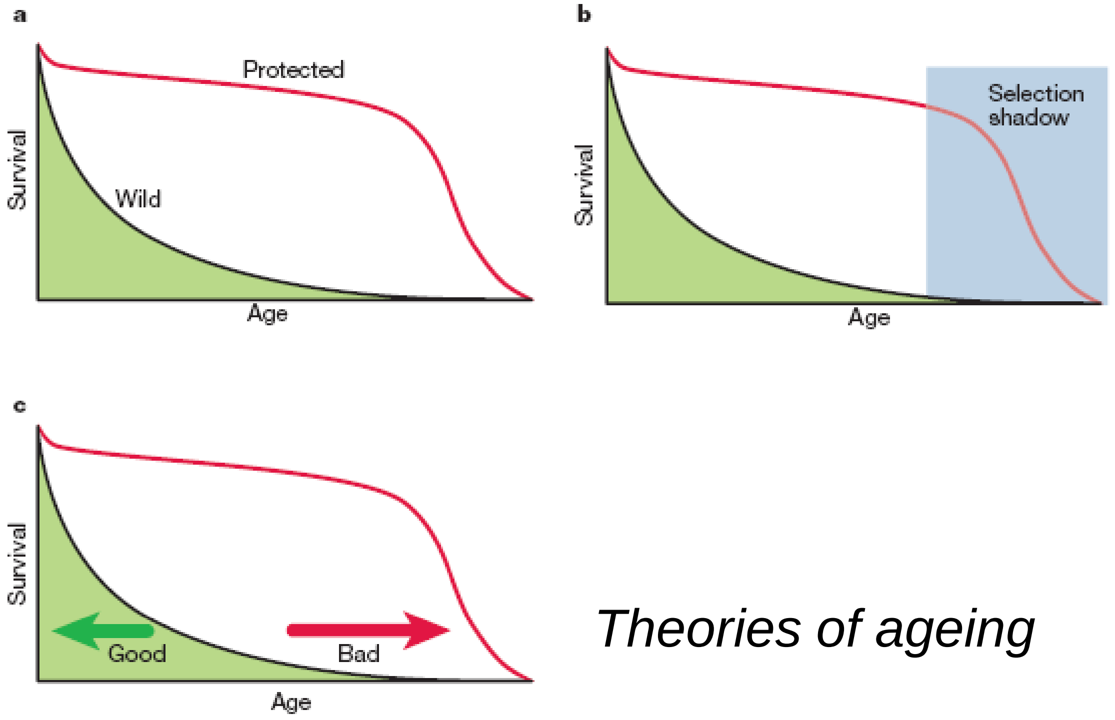
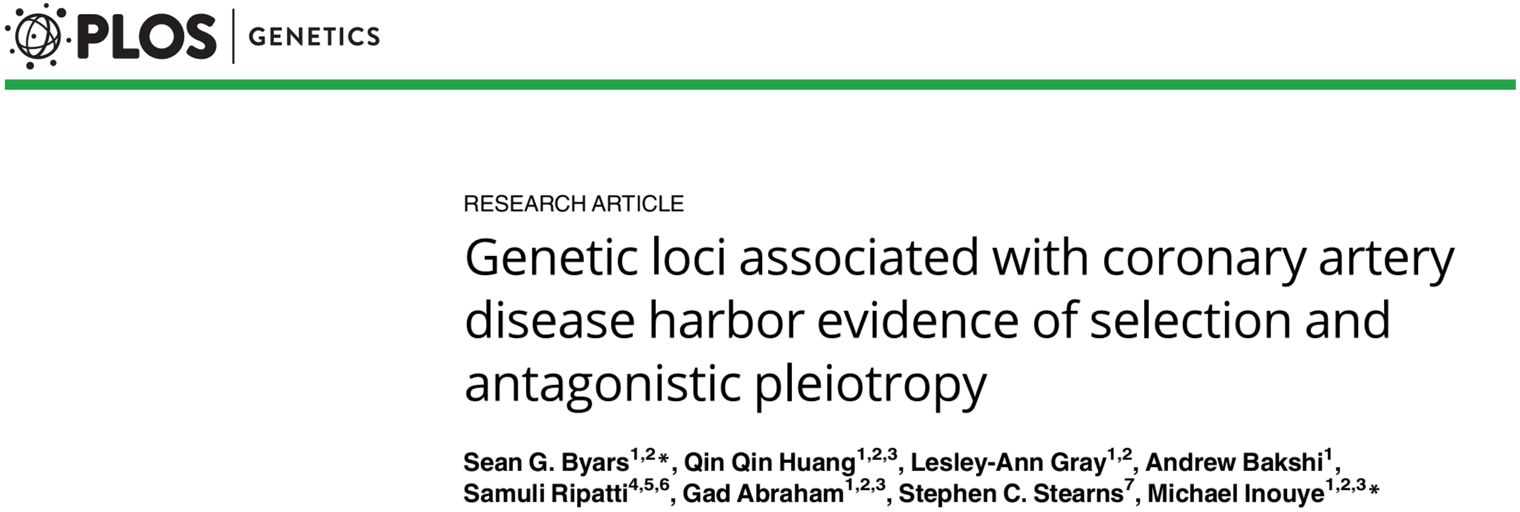


Figure 1 Evolutionary theories of ageing. **a**, Extrinsic mortality in wild environments occurs to an extent that senescence-associated mortality is rare, undermining any idea that genes specifically for ageing have evolved. **b**, The 'selection shadow' at older ages may permit an accumulation of late-acting deleterious mutations (mutation-accumulation theory). **c**, Pleiotropic genes that benefit organisms early in life will be favoured by selection even if they have bad effects at later ages (pleiotropy theory). **d**, Selection pressure to invest metabolic resources in somatic maintenance and repair is limited; all that is required is to keep the organism in sound condition for as long as it might survive in the wild (disposable-soma theory).

a. In the wild, reproductive value of old individuals is low
b. Selection shadow hypothesis: selection against deleterious mutations weak in old individuals
c. Pleiotropy theory: mutations beneficial in young age favoured even though detrimental in old age



PLOS | GENETICS

RESEARCH ARTICLE

Genetic loci associated with coronary artery disease harbor evidence of selection and antagonistic pleiotropy

Sean G. Byars[1,2]*, Qin Qin Huang[1,2,3], Lesley-Ann Gray[1,2], Andrew Bakshi[1], Samuli Ripatti[4,5,6], Gad Abraham[1,2,3], Stephen C. Stearns[7], Michael Inouye[1,2,3]*

Genes associated with fecundity of young women cause CAD in older man

Paradoxes of sexual reproduction

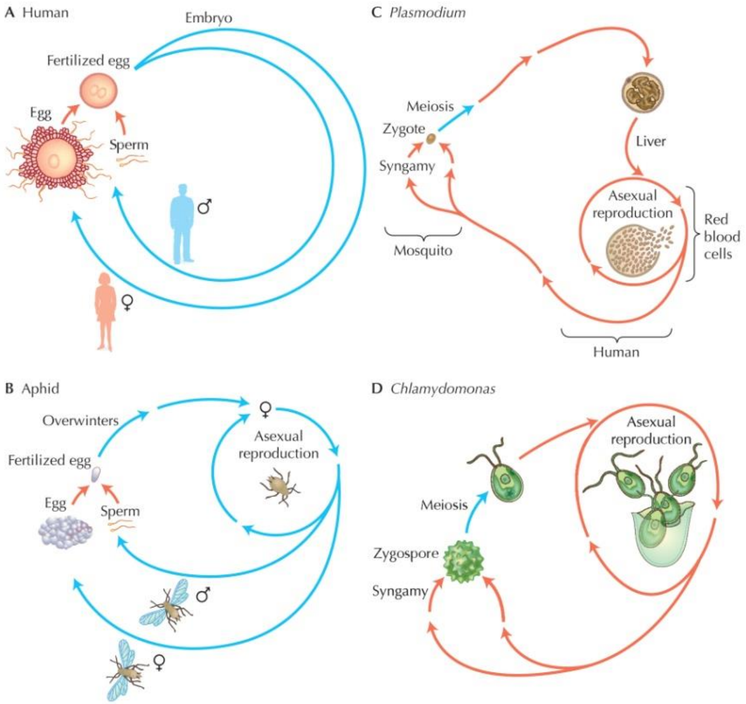
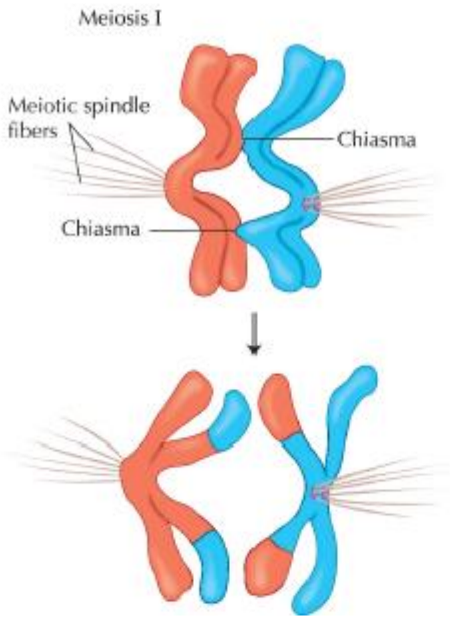


FIGURE 23.6. Examples of eukaryote life cycles. (*A*) Human males and females produce eggs and sperm by meiosis, which unite to give a diploid zygote that develops into a new male or female adult. Sex is required for reproduction, and the haploid stage (*red*) does not divide. (*B*) In aphids, the life cycle is similar, except that sex is facultative. Females reproduce parthenogenetically during the spring and summer, bearing genetically identical daughters. At the end of the season, diploid sexual males and females are produced. These produce haploid sperm and eggs by meiosis, which fuse to give a fertilized egg that overwinters. The egg hatches to give parthenogenetic females in the next season. (*C*) The sporozoan parasite responsible for malaria, *Plasmodium*, spends most of its life cycle as a haploid. It goes through several asexual stages in the host, where it reproduces asexually in the liver and then in the red blood cells. Some haploid asexuals differentiate into gametocytes, which are taken up by mosquitoes. These fuse in the mosquito gut to give a zygote, which immediately goes through meiosis to begin the life cycle anew. (*D*) The green alga *Chlamydomonas* has a similar life cycle to *Plasmodium*, again spending most of it life as a haploid. However, sexual reproduction is now triggered by nutritional conditions, which produce a highly resistant zygospore. When conditions improve, this zygospore goes through meiosis and hatches to produce new haploid cells. Haploid portions of each cycle are shown in *red*; diploid portions are shown in *blue*.

Evolution © 2007 Cold Spring Harbor Laboratory Press



Sexual reproduction is linked to recombination (independent chromosome segregation plus crossing over)

Main costs of sex:

- Need to find a partner
- Spread of selfish genetic elements (in parthenogenesis, fitness of organism = fitness of a gene)
- Cost of males (= cost of anisogamy)

Sexual reproduction enables favours transmission of SEG

Plasmid 2μm:

- Contains 4 genes needed for its transmission
- Each copy decreases host fitness by 0.2%

Selfish mitochondria:

- Increased transmission rate at the cost of metabolic efficiency


JOURNAL OF Evolutionary Biology

doi: 10.1111/jeb.12408

SHORT COMMUNICATION

Sex drives intracellular conflict in yeast

E. HARRISON*[1], R. C. MACLEAN†, V. KOUFOPANOU‡ & A. BURT‡

*NERC Center for Population Biology, Imperial College London, Ascot, UK
†Department of Zoology, University of Oxford, Oxford, UK
‡Division of Ecology and Evolution, Imperial College London, Ascot, UK

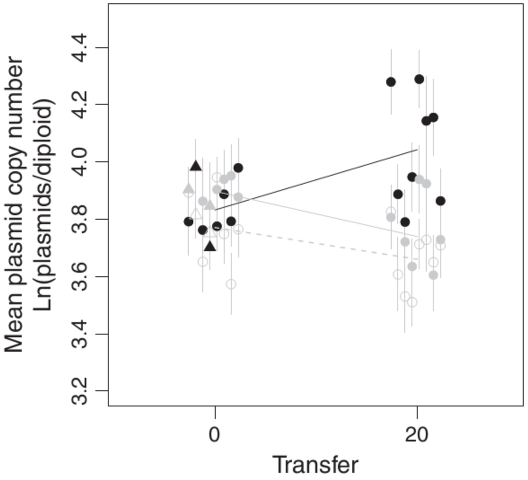


Fig. 1 Two-micrometre plasmid copy number in ancestral and evolved populations. Points show mean copy numbers, averaged from copy number estimates in 15* randomly picked clones, for each of the eight populations per treatment with standard error bars. Symbols denote sexual (black), pseudosexual (closed grey) and budding (open grey) treatments. *NB. estimates taken from <15 clones shown as triangles.

Sexula reproduction (black dots) increases SEG frequency

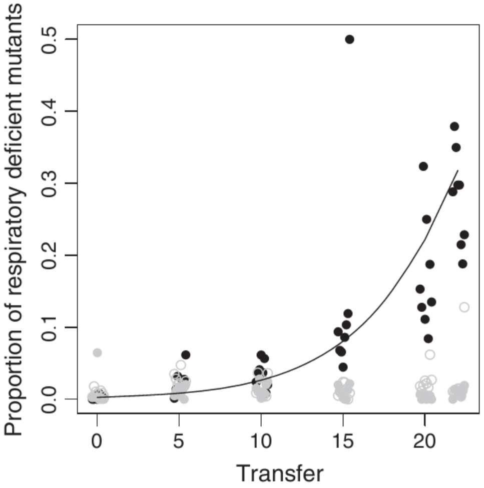
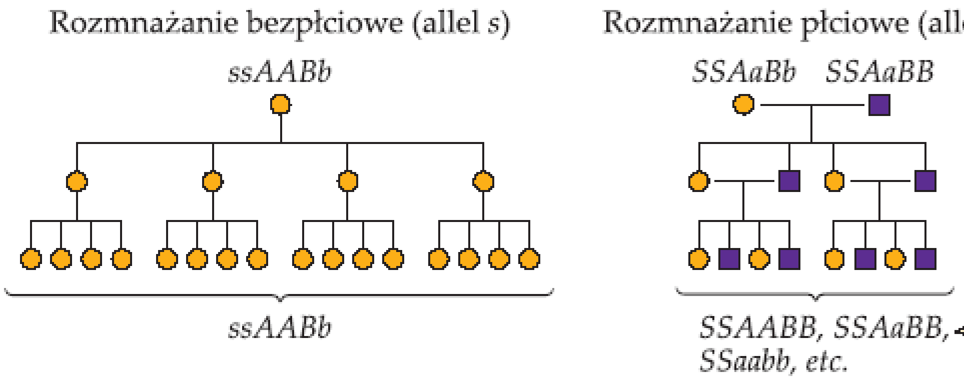


Fig. 2 The frequency of respiratory-deficient mutants over time. Proportions of respiratory mutants in each replicate population based on screening of between 200 and 500 colonies for growth on nonfermentable media. Analysis showed a significant increase in respiratory mutants over time in the sexual population only. Symbols denote sexual (black), pseudosexual (closed grey) and budding (open grey) treatments. The plotted line represents the estimate of drive (*d*) for sexual populations, calculated as 0.63.

Cost of males (= cost of anisogamy)- assuming no male investment in progeny, parthenogenetic females have 2x more descendants



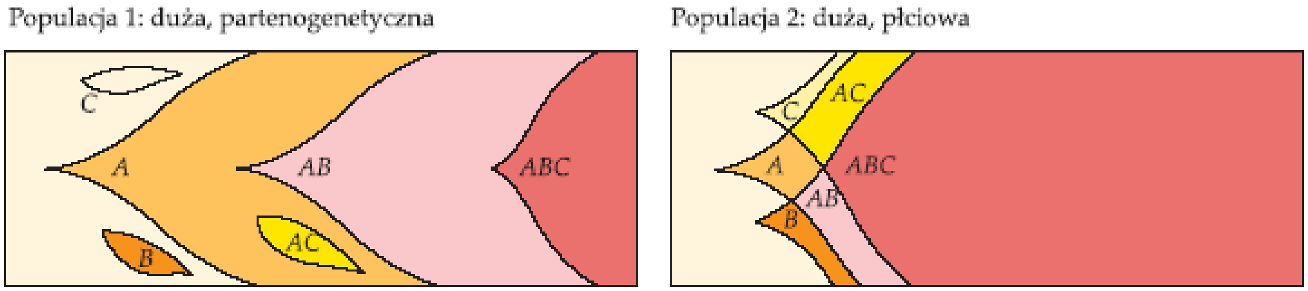
Po dwóch pokoleniach liczba potomków samicy rozmnażającej się płciowo jest równa zaledwie połowie liczby potomków samicy partenogenetycznej.

Rycina 17.18 Koszt rozmnażania płciowego. Niższe dostosowanie allelu *S*, wywołującego rozmnażanie płciowe, w porównaniu do *s*, kodującego rozmnażanie bezpłciowe. Kółka przedstawiają samice, kwadraty – samce. Oba typy samic w polimorficznej populacji wytwarzają czworo potomków równie dobrze przystosowanych do środowiska, ale z powodu wytwarzania samców częstość *S* gwałtownie zmniejsza się, od 2/3 w pierwszym pokoleniu do 1/3 w trzecim pokoleniu. Jednak częstość allelu *S* mogłaby wzrosnąć na skutek zmian środowiskowych, dających przewagę selekcyjną zrekombinowanym genotypom, takim jak *aabb*

Yet obligate parthenogenesis rare:

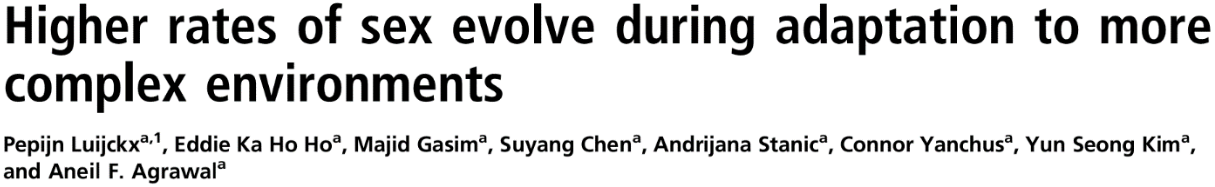
~0.1% animals (Vrijenhoek 1998) i <1% flowering plants (Asker and Jerling 1992; Whitton et al. 2008)

Recombination may help to adapt to a new evironment


Populacja 1: duża, partenogenetyczna

Populacja 2: duża, płciowa

Rotifers *Brachionus calyciflorus* can reproduce parthenogenetically or sexually

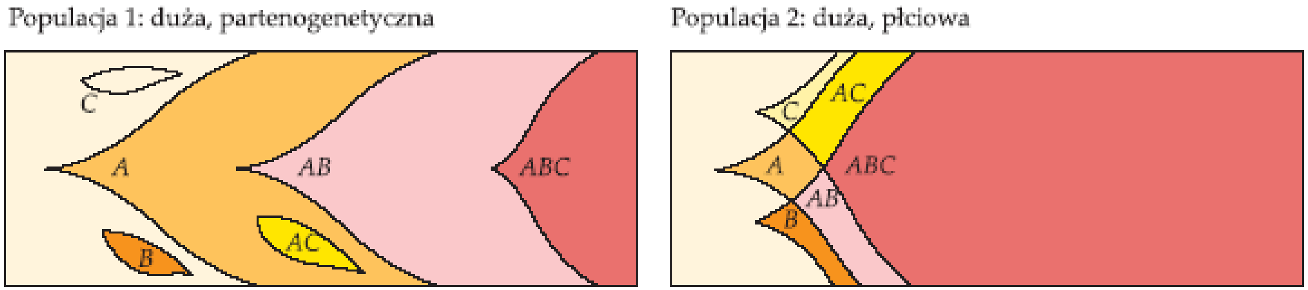


Higher rates of sex evolve during adaptation to more complex environments

Pepijn Luijckx[a,1], Eddie Ka Ho Ho[a], Majid Gasim[a], Suyang Chen[a], Andrijana Stanic[a], Connor Yanchus[a], Yun Seong Kim[a], and Aneil F. Agrawal[a]

Frequency of sex increases during adaptation to novel environment

Recombination may help to adapt to a new evironment



Populacja 1: duża, partenogenetyczna

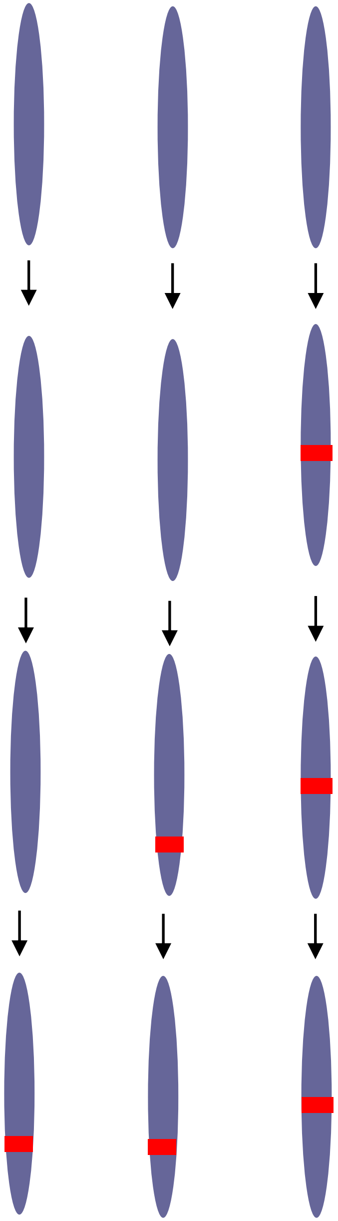
Populacja 2: duża, płciowa

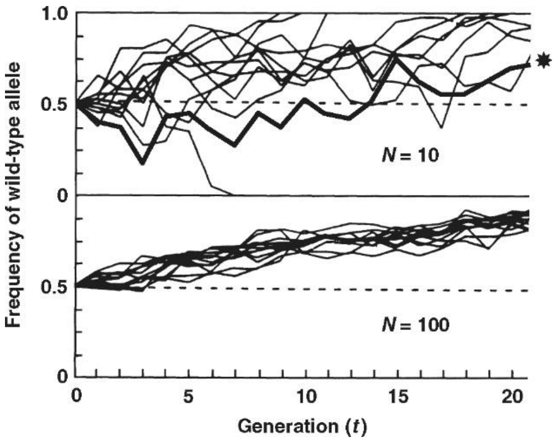
But does environment change often enough?

Yes, in case of the need to adapt to biotic environment which also evolves, eg. parasites (Red Queen hypothesis)

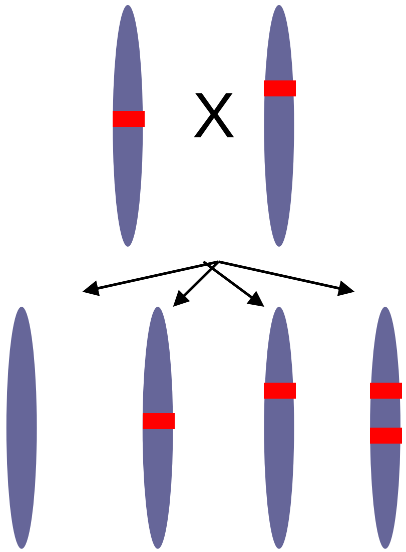
Parthenogenetic females of a snail *Potamopyrgus antipodarum* less frequent when parasites are common

„Mueller’s ratchet” parthenogenetic population accumulate mutations by **genetic drift**



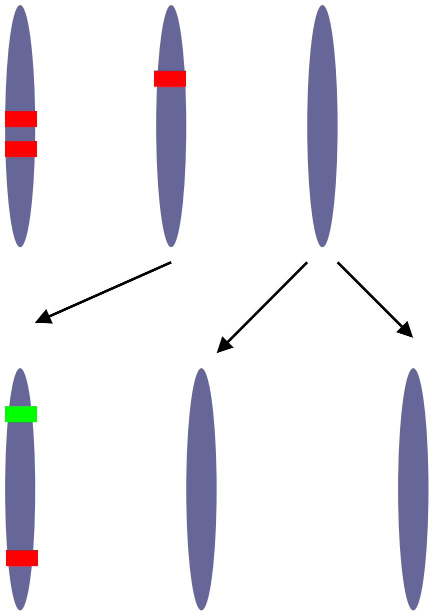


gdy $s<1/(2N)$ dryf>dobór

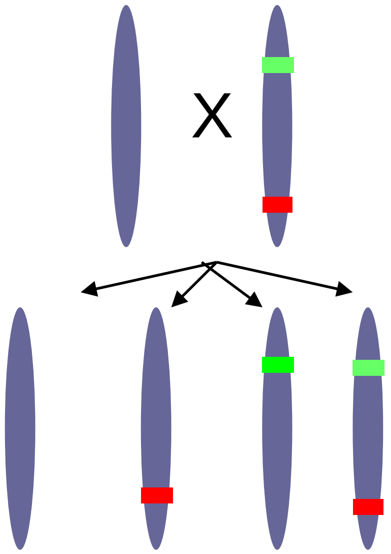


In sexual selection unburdened genomes can be recovered by recombination – ratchet does not work!

Escape from unfavourable „genetic background”



W populacji partenogenetycznej korzystne mutacje mogą być uwięzione w genomie zawierającym niekorzystne szkodliwe mutacje



Rekombinacja uwalnia korzystne mutacje z niekorzystnego tła, ułatwiając ich utrwalenie się w populacji

Sexually reproducing yeast:

- *Adapted to novel environment faster*
- *Accumulated fewer deleterious mutations on the way!*

McDonalds i in. 2016,
Nature 10;531(7593):233-6

Costs and benefits of recombination (and sex)

- Need to find a partner
- Spread of selfish genetic elements (in parthenogenesis, fitness of organism = fitness of a gene)
- Cost of males (= cost of anisogamy)

- Fast adaptation (e.g. to pressure from parasites) by creation of novel gene combinations
- Preventing accumulation of mutations via Mueller's rathet
- Escape from unfavourable genetic backgroud

Why sex ratio 1:1?

Assume: proportion of males =0.25 (1:3)

each female 4 offspring

*Then: average male has 3*4=12 offspring*

*avereage female has 3*4 + 1*12 = 24 grand-offspring*

*Mutant female, producing 0.5 males: 2*4 + 2*12 = 32 grand-offspring*

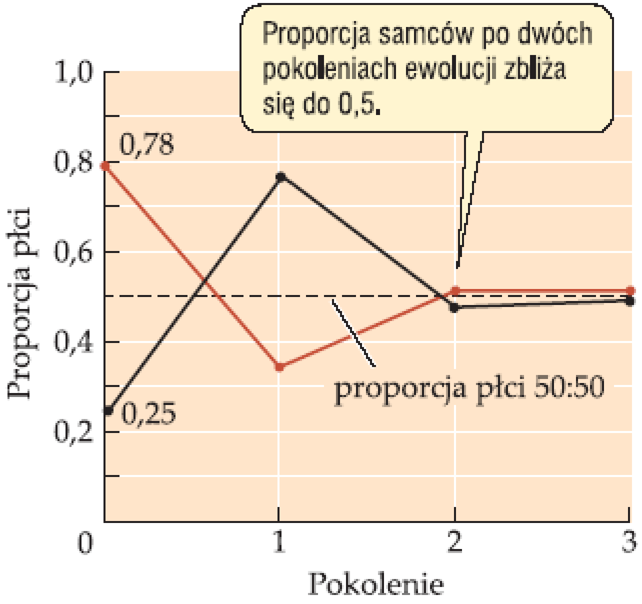
Fisher (1930) explained 1:1 sex ratio by frequency-dependence of male vs female reproductive success

U Xiphophorus maculatus występują trzy rodzaje chromosomów płci: W, X i Y.

XX, WX i WY – samice; XY i YY - samce.

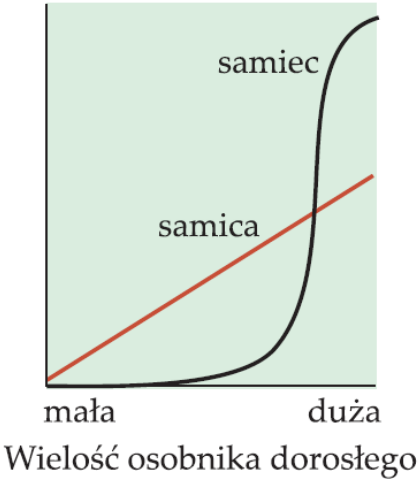
4/6 możliwych krzyżówek daje proporcję płci równą 0,5.
samica XX x samiec YY - wyłącznie samce

samica WX x samiec XY - 25% synów.



Rycina 12.18 Zmiany proporcji samców w dwóch doświadczalnych populacjach zmienniaka plamistego, u którego początkowe proporcje wynosiły 0,25 i 0,78. W obu populacjach proporcja samców ewoluowała, osiągając wartość bliską 0,5 w ciągu zaledwie dwóch generacji (za: Basolo 1994)

Evolution of sex change



Paradox of traits decreasing survival

Fot. Rafał Kowalczyk

Sexual selection arises due to competition for mate and its gamets

Intra-sexual selection favours traits useful in combats for mating partners and their gametes

Inter-sexual selection favours epigamic traits attractive to the opposite sex

Intrasexual selection underlies evolution of weapons

Jelonek rogacz *Lucanus cervus*

Analysis of evolutionary stability of aggression *(Maynard-Smith i Price, 1977)*

Evolutionarily stable stragegy (ESS): strategy resistant to invasion of a mutant/immigrant assuming a specified alternative strategy

		In interaction with	
		Hawk	Dove
Effect on fitness of:	Hawk	**1/2(B-C)**	**B**
	Dove	**0**	**1/2B**

B-benefit of winning the contest, C- cost of losing a fight

<u>Case 1</u>. B>C – which strategy is ESS?

		In interaction with	
		Hawk	Dove
Effect on fitness of:	Hawk	**1/2(B-C)**	**B**
	Dove	**0**	**1/2B**

Case 1: $B>C$

$B-C/2 > 0$ – *Hawk ESS*
$B/2 < B$ – *Dove not ESS*

CAse2: $B<C$

		In interaction with	
		Hawk	Dove
Effect on fitness of:	Hawk	**1/2(B-C)**	**B**
	Dove	**0**	**1/2B**

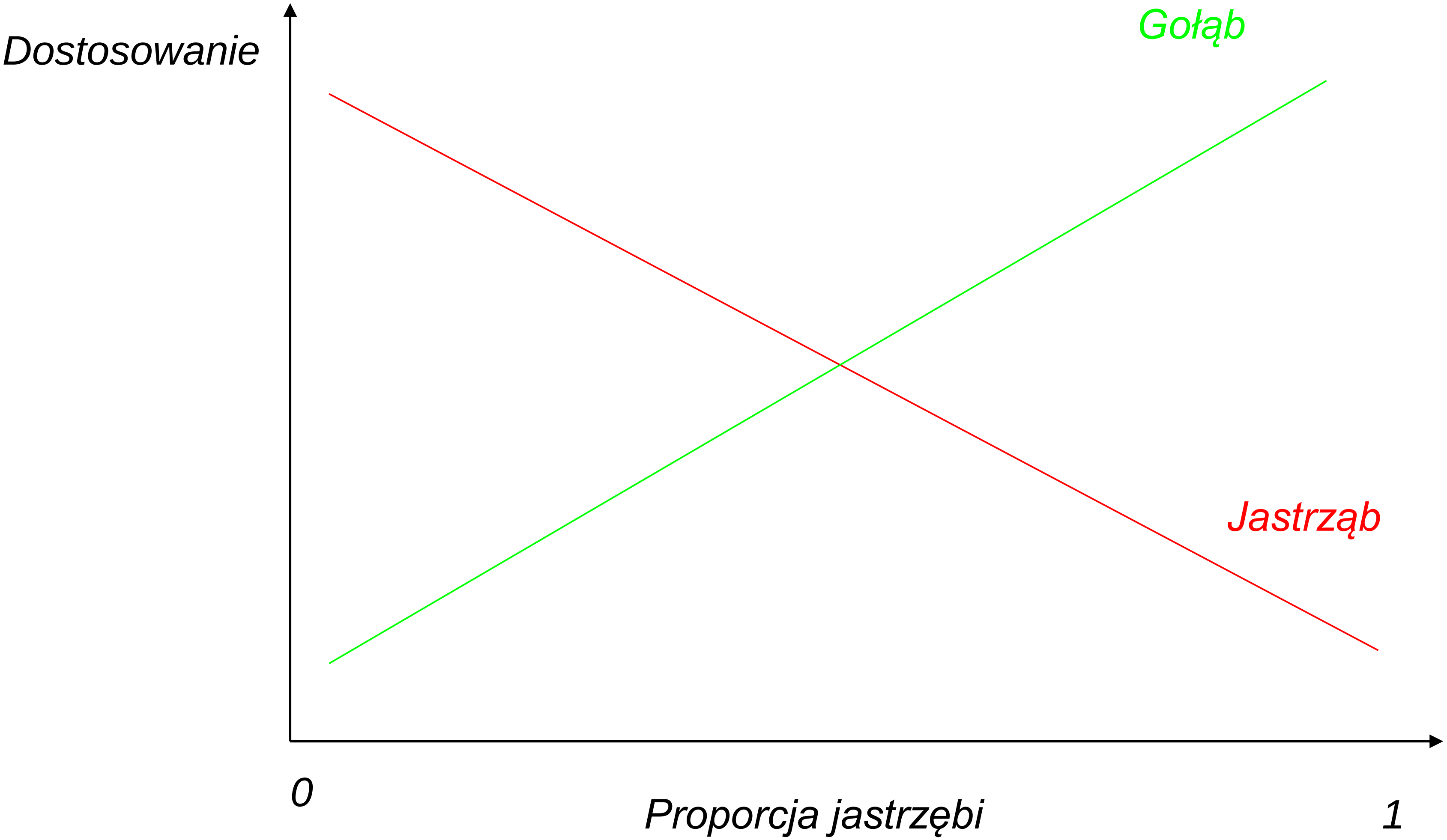
Case 1: B>C

B-C/2 > 0 – Hawk ESS
B/2 < B – Dove not ESS

CAse2: B<C

B-C/2 < 0 – Hawk not ESS
B/2 < B – Dove not ESS

If B<C, neither Hawk nor Dove ESS, but a mix of stragegies stable due to negative frequency-dependence

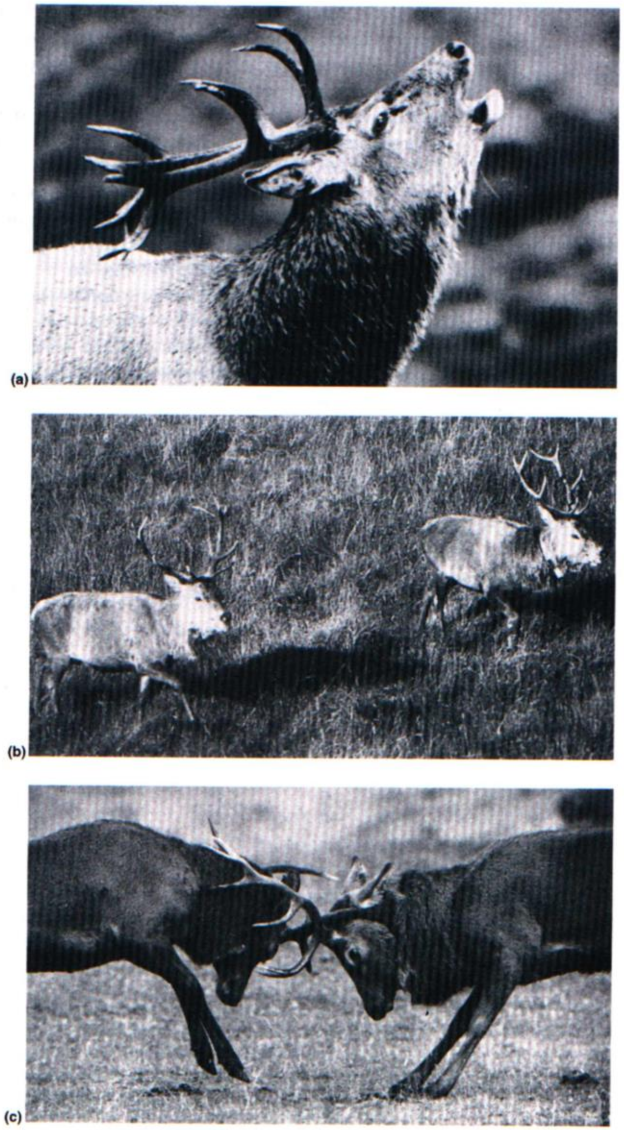


Assessor: a conditional strategy that takes into account relative power

Behaves as Hawk when stronger, but as Dove if weaker than the opponent

		In interaction with		
		Hawk	Dove	Assessor
Effect on fitness of:	Hawk	**1/2(B-C)**	**B**	**1/2(B-C)**
	Dove	**0**	**1/2B**	**¼ B**
	Assessor	**½B**	**¾B**	**½B**

½ cases Asessor stronger than Dove = 1/2B
*½ cases Asessor weaker than Dove = ½*1/2B=1/4B*



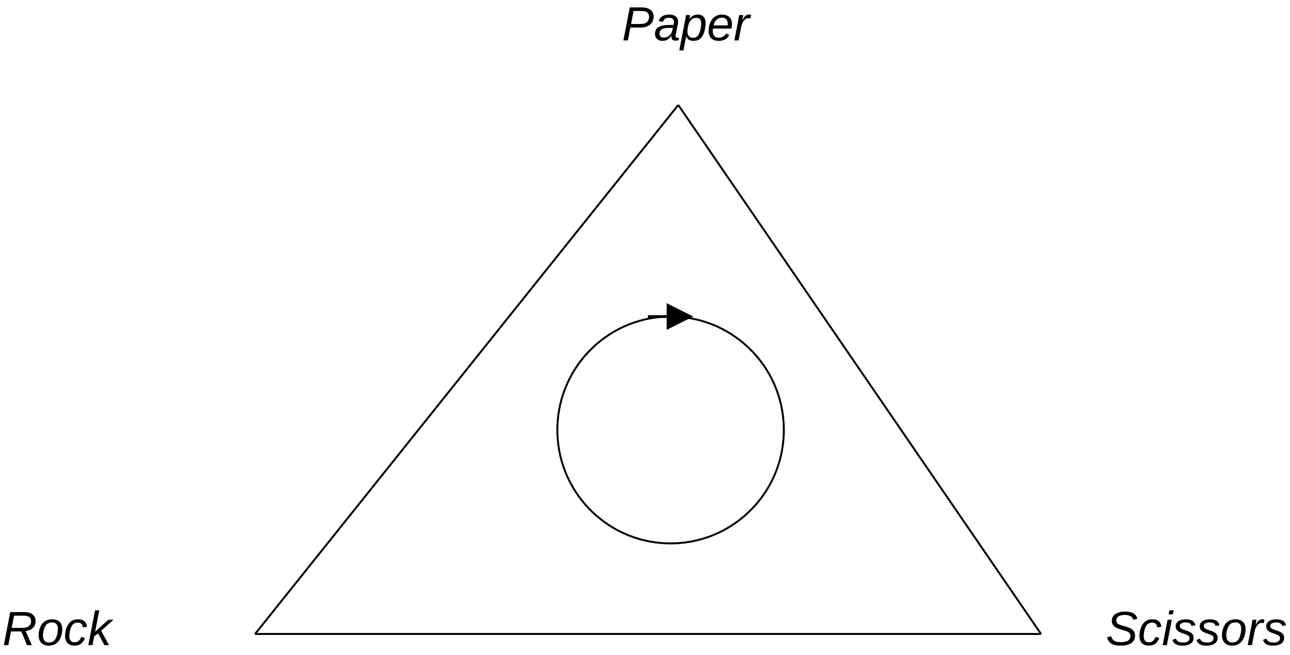
Ryc. 7.5 Stadia pojedynku między dwoma bykami jelenia. Właściciel haremu ryczy w kierunku pretendenta (a). Obaj spacerują równolegle do siebie (b). Wreszcie sczepiają się porożami i zaczynają się przepychać (c). Fot.: Tim Clutton-Brock

1. Roarring involves neck muscles used in figths

2. Parallel walk allows judging size

3. Fights occur mostly when opponents of similar size

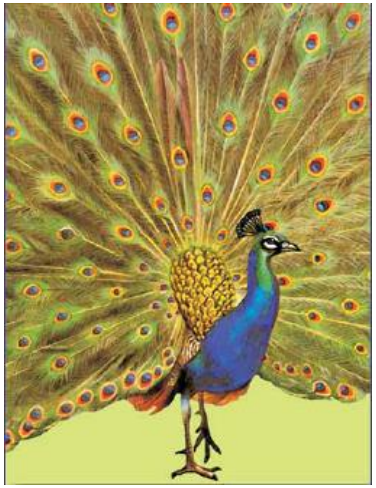
Maynard Smith, J. 1984



A **conundrum of ornamental traits**

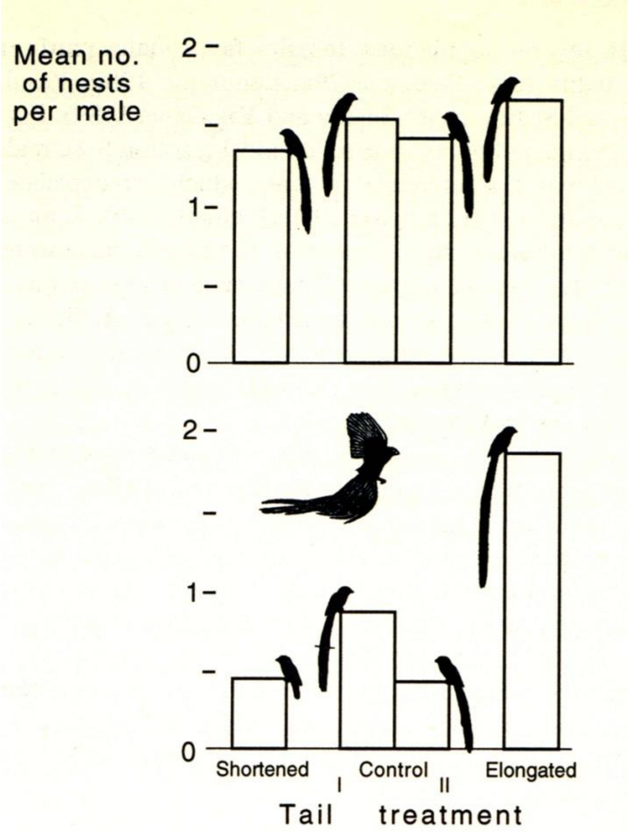
*„I remember well time when the thought of the eye made me cold all over, but I have got over this stage …….**T**he sight of a feather in a peacock's tail, whenever I gaze at it, makes me sick!"*

Charles Darwin, letter to Asa Gray, 3 April 1860



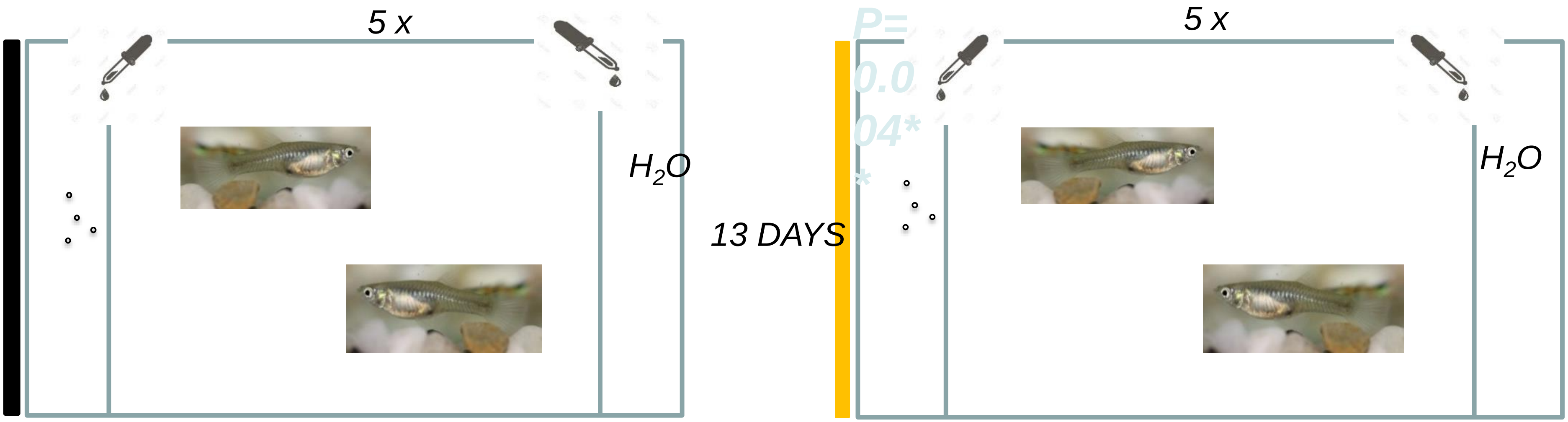
by R. Dzwonkowski

Intrasexual selection in long-tailed widowbird *Euplectes progne*

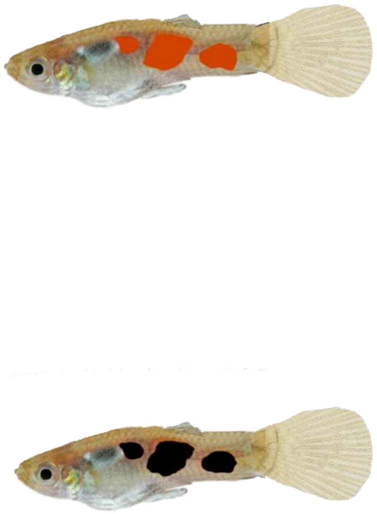


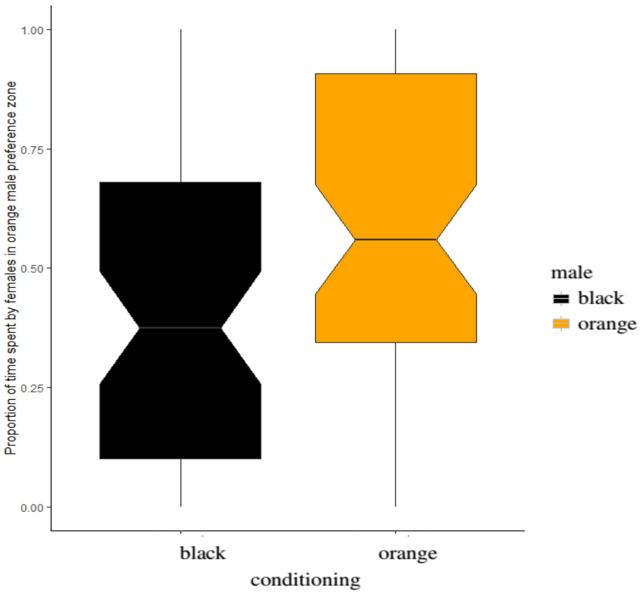
Sexual selection will favour elaboration of epigamic traits until their benefits are dampened by survival (and other) costs

But why females show preferences?



Preferencje samic gupików mogą być kształtowane przez warunkowanie pokarmem (Herdegen-Radwan 2022)





PROCEEDINGS B

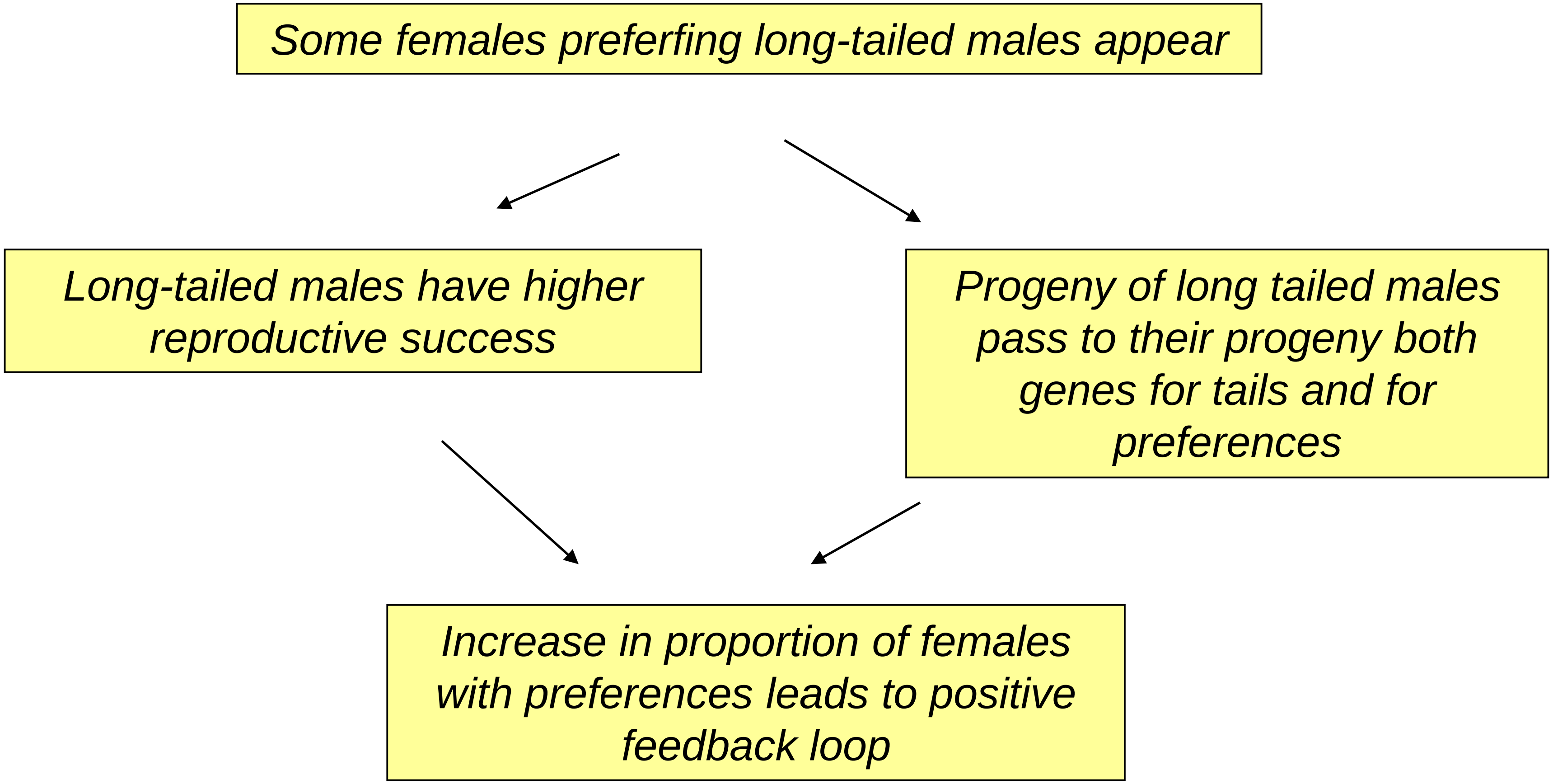
royalsocietypublishing.org/journal/rspb

Samice ryb z rodziny Goodeinae są przyciągane przez żółte paski na ogona samców, przypominające pokarm (pierścienicie); pasek wyewoluował wiele razy niezależnie

Why aren’t useless preferences counter-selected?

Fisher (1930): females mating with ornamented males will have attractive sons, who will pass their tenes to next generations!

Run-away process of sexual selection according to Fisher



Some females preferfing long-tailed males appear

Long-tailed males have higher reproductive success

Progeny of long tailed males pass to their progeny both genes for tails and for preferences

Increase in proportion of females with preferences leads to positive feedback loop

Fisher (1930): females choosing ornamented males will have more attractive sons and thus more grandoffspring

Zahavi (1975): costly ornaments indicate that males have good genes or resources.

Zahavi’s ‘***handicap principle***’ traits need to be costly to be honest indicators of quality

Petrie (1994): progeny of males with more spots in train survived better in semi-natural environment

Meta-analysis of data for 54 species by Prokop et al. (2012; Evolution): epigamic traits do not predict progeny quality, except for attractiveness of sons

META-ANALYSIS SUGGESTS CHOOSY FEMALES GET SEXY SONS MORE THAN “GOOD GENES”

Zofia M. Prokop,[1,2] Łukasz Michalczyk,[3] Szymon M. Drobniak,[1] Magdalena Herdegen,[1] and Jacek Radwan[1]

But some very costly traits can reveal genetic quality!

- *Chemical induction of mutations in male germline*
- *No effect on F_1 males brightness, but males burdened with mutations performed fewer energetically costly displays*

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

ELSEVIER

Effect of induced mutations on sexually selected traits in the guppy, *Poecilia reticulata*

Magdalena Herdegen [a, *], Jacek Radwan [a, b]

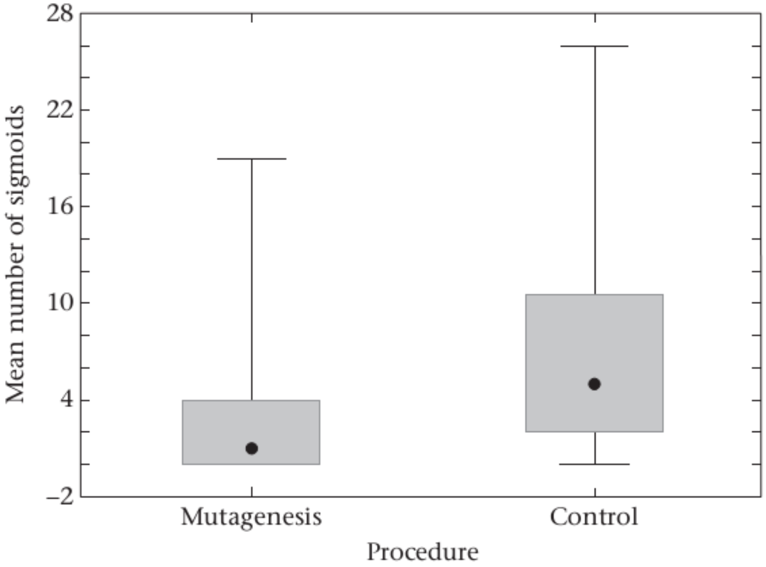
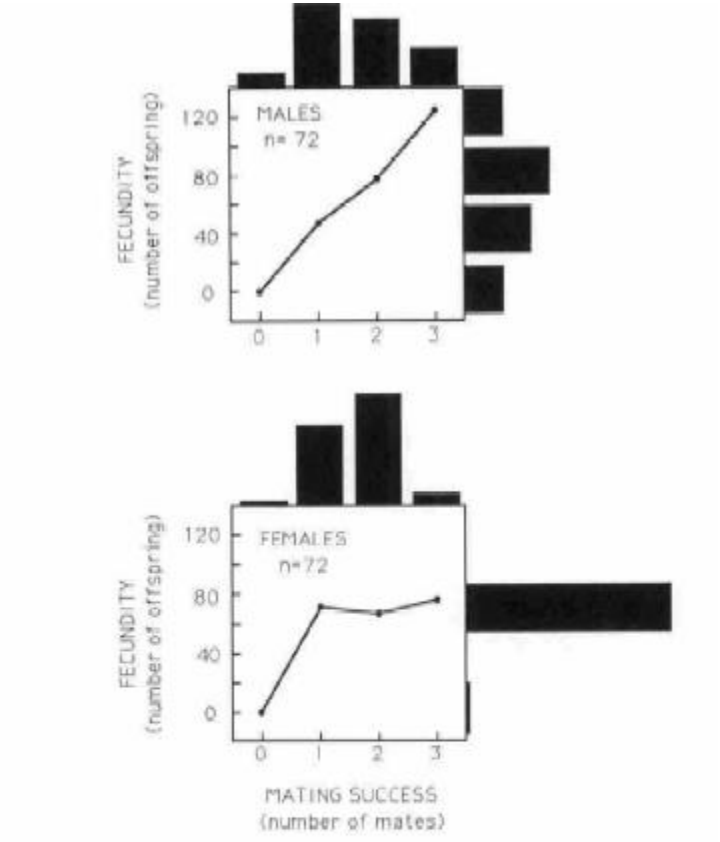


Figure 2. Per male mean number of sigmoid displays performed by F1 males in the presence of a female, in mutagenesis and control treatments. The box plots cover first to third quartiles (with median indicated by a dot); whiskers denote minimum and maximum values.

Why is it males who compete? Are sex roles fixed?



Males produce @excessive@ number of gametes

In *D. melanogaster,* male, but not females reproductive success increases with the number of mates (Bateman 1948)

Bateman’s principle: sexual selection stronger in sex showing steeper relatonship between the number of mates females and reproductive success

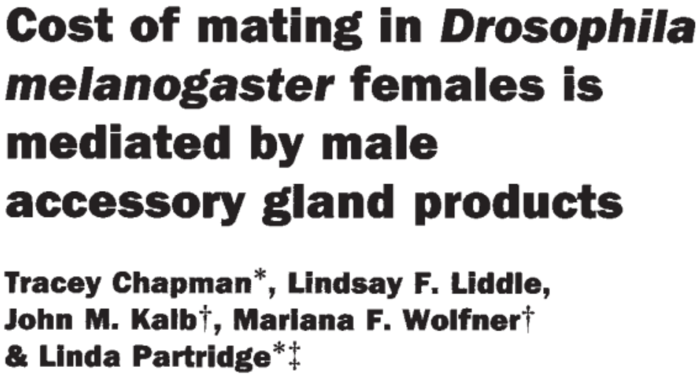
Pipefish Syngnathus typhle: males are pregnant for longer that it takes females to produce a batch of eggs

In consequence, females must compete for non-prengnant males

On average across taxa, sexual selection stronger in males, but with exceptions!

Tim Janicke et al. Sci Adv 2016;2:e1500983

Sexual conflict: traits giving males an advantage in reproductive competition may be detrimental to females



Cost of mating in *Drosophila melanogaster* females is mediated by male accessory gland products

Tracey Chapman[*], Lindsay F. Liddle, John M. Kalb[†], Mariana F. Wolfner[†] & Linda Partridge[*‡]

Examples:

- Male seminal fluids, increasing male sperm competitiveness, are harmful to females
- Increased predation risk during copulation in water striders

When should selection favour harming mating partner?

E.g. male trait decreases female partner fitness by 20%, but doubles his number of mates

Assume female lays 10 eggs

Harmless male: 1 female x 10 eggs = 10 offspring
Harmful male: 2 females x 8 eggs = 16 eggs

Sexual conflict in waterstiders

- Copulation every 10 days enough for females to achieve full fecundity (Arnqvist 1992)
- Increased predation on females mounted by males (Rowe 1994)
- Females try to avoid the risk by shaking males off
- In some species males evolve clutching aparatus

nature COMMUNICATIONS

Male water striders attract predators to intimidate females into copulation (Han i Jabłoński 2010)

- Females *G. gracilicornis* evolved a shield covering genital opening to discourage forced copulations
- Females open the shield if males „court” by hitting water surface
- This ‘signal’ attracts predators, and females are more likely to open the shield if predator's are around

Speciation

Ernsta Mayr’s biological species: a reproductively isolated gene pool

Gene pool: a sum of all genes of a population

Speciation: a process of gene pool differentiation leading to reproductive isolation

Reproductive isolation enables independent evolution of species

Pre-zygotic reproductive barrier prevents mating between species

Post-zygotic barriers: lethality or sterility of hynbrids

Allopatric speciation: differentiation of geographically isolated genetic pools

Sympatric speciation: differentiation of genetic pools within the same area

Examples higthlighting the importance of allopatric speciation:

- 1/3 of ca. 20 000 fish species inhabits freswaters, which are ca. 0.5% of waters on earth
- Cricket species number per area 1 000 times higher on Hawaii Islands compared to continental North America

But sympatric speciation occurs when

- **area contains very different habitats**
- **Mating occurs mostly within these habitats**

E.g. two ecotypes of sticklebacks:

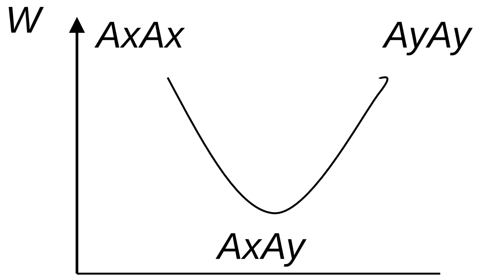
Limnetic, foraging on plankton

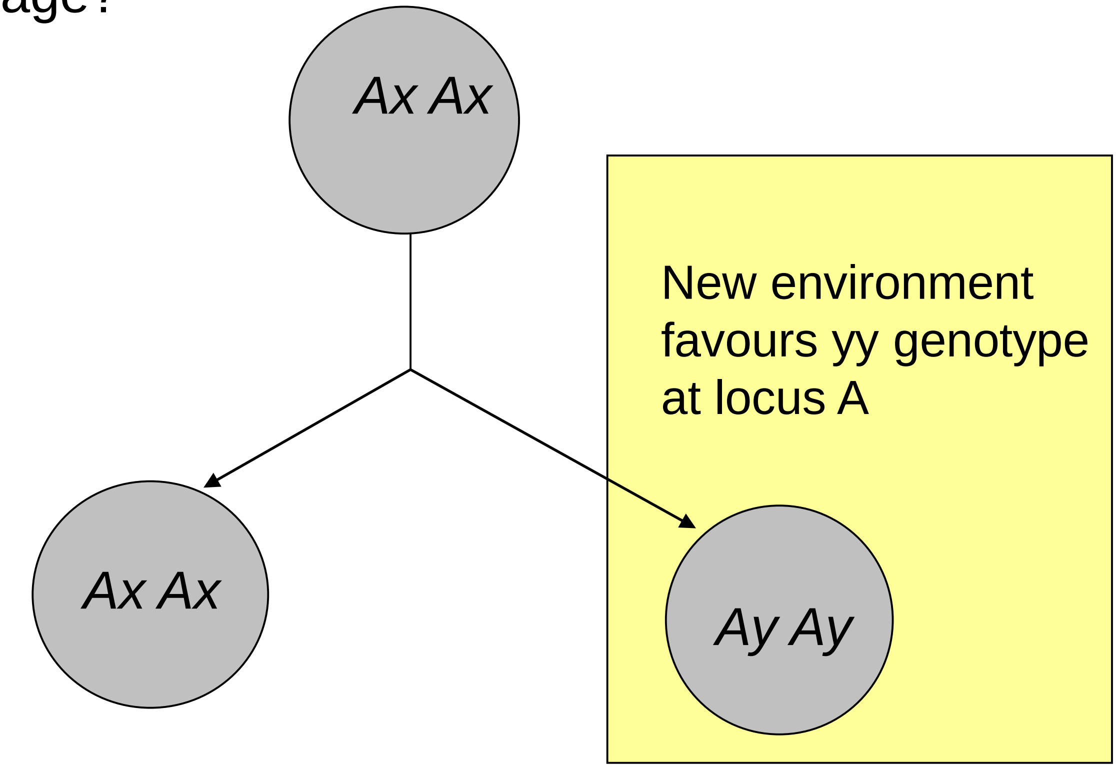
Benthic, eating larger invertebrates

- several lakes in North America colonised independently after last glaciation: ecotypes within lake more similar genetically than the same ecotype in different lakes
- Sexual preferences for the same ecotype (even from different lake)

Evolution of reproductive barriers

Can genetic barriers between species X and Y evolve due to heterozygote disadvantage?





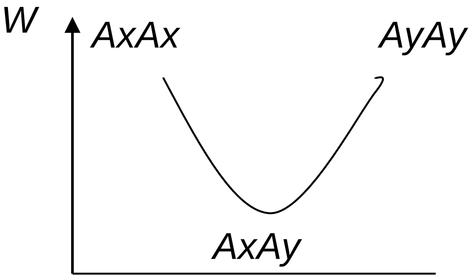
Ax Ax

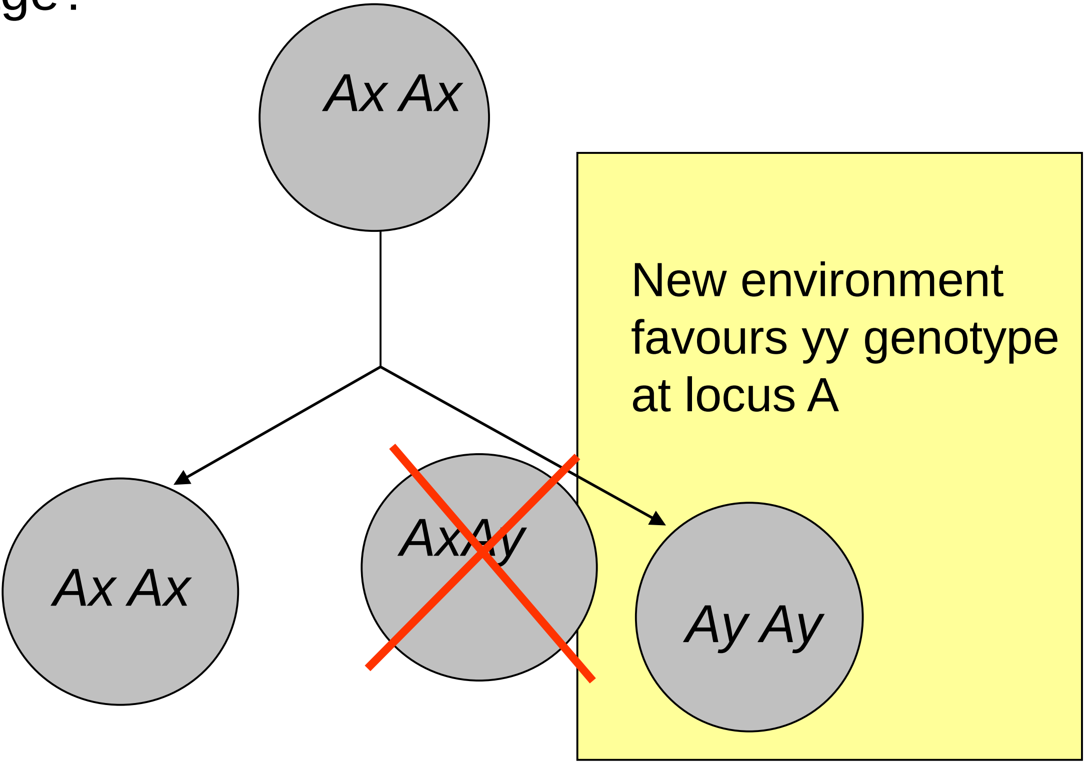
Ax Ax

Ay Ay

New environment favours yy genotype at locus A

Can genetic barriers between species X and Y evolve due to heterozygote disadvantage?

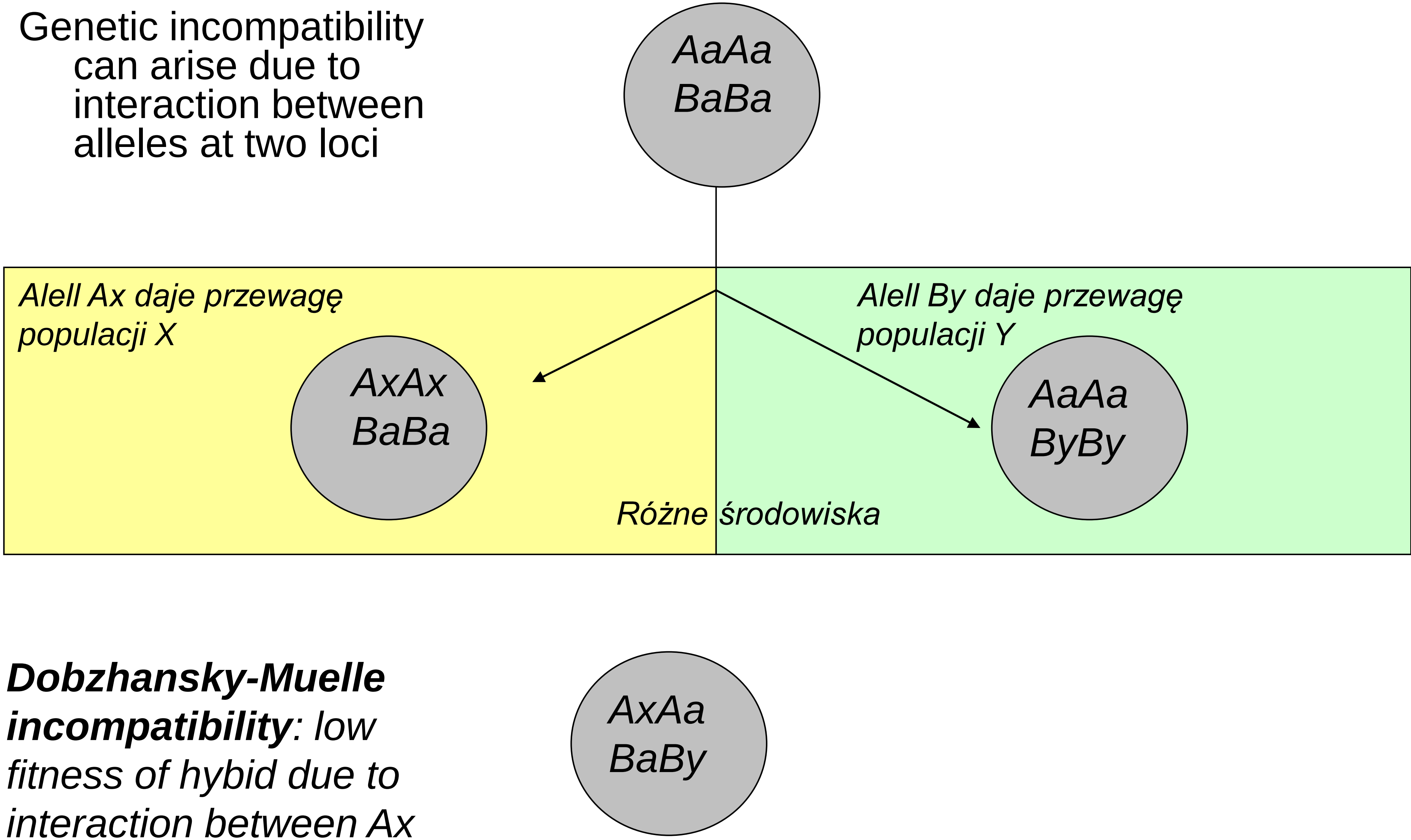




New environment favours yy genotype at locus A

No, mutation Ay initially rare, hence in low fitness heterozygotes!

Genetic incompatibility can arise due to interaction between alleles at two loci



AaAa
BaBa

Alell Ax daje przewagę populacji X

AxAx
BaBa

Alell By daje przewagę populacji Y

AaAa
ByBy

Różne środowiska

AxAa
BaBy

***Dobzhansky-Muelle incompatibility**: low fitness of hybid due to interaction between Ax and By*

Science **368**, 731–736 (2020)

RESEARCH ARTICLE

HYBRID GENOMICS

Natural hybridization reveals incompatible alleles that cause melanoma in swordtail fish

Daniel L. Powell[1,2,3]*, Mateo García-Olazábal[2,3], Mackenzie Keegan[4], Patrick Reilly[5], Kang Du[6], Alejandra P. Díaz-Loyo[7], Shreya Banerjee[1], Danielle Blakkan[1], David Reich[8,9], Peter Andolfatto[10], Gil G. Rosenthal[2,3], Manfred Schartl[2,3,6,11,12], Molly Schumer[1,2]*

Hubrids of *Xiphophorus birchmanni* a *X. malinche* malingnant melanoma due to interaction of two genes:

- Xmark coding for black tail spopt in *X. birchmanni*
- cd97 in *X. malinche* (associates with metastasis in humans)

Sexual selection can lead to fast evolution of preferences for epigamic traits, leading to prezygotic isolation.

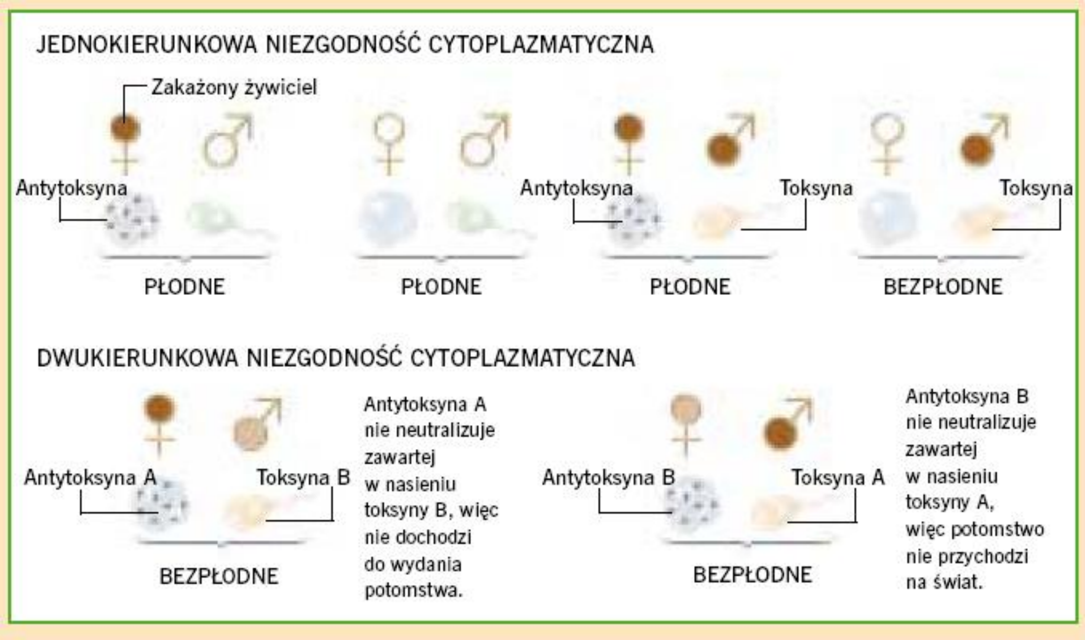
Speciation rate in Estrilidae is associated with evolution of epigamic traits (Gomes i in. 2016, Evolution)

Speciation by selfish microorganisms

Female-transmitted *Wolbachia* evolved adaptations to increase its transmission via cytoplasm :

- ,male killing (np. *Acrea encedon*)
- Feminisaton (e.g. *Armadillum vulgare*)
- Killing of uninfected eggs by sperm from infected males (eg, *Drosophila, Nasonia)*

Unidirectional and bidirectional incompatibilities cause by Wolbachia



Antytoksyna A nie neutralizuje zawartej w nasieniu toksyny B, więc nie dochodzi do wydania potomstwa.

Antytoksyna B nie neutralizuje zawartej w nasieniu toksyny A, więc potomstwo nie przychodzi na świat.

Normally genetically isolaged *Nasonia giraulti i Nasonia longicornis* produce fertile progeny after *Wolbachia* removed with antibiotic! (Werren i wsp. 2001, Nature 409:707-9)

Reinforcement: *reproductive barrier can be enhanced by selection after species meet*

Hyla cinerea females from sympatric populations show stronger discrimination against males of H. gratiosa, compared to allopatric populations

Coevolution

Evolution due to mutual selective pressures imposed by different species (or genes)

Examples of coevolution discussed earlier:

- Host-parasite coevolution
- Antagonistic coevolution between sexes (sexual conlflict)
- Coevolution between plants and pollinators

Host-parasite coevolution: why parasites kill their (host) environment?

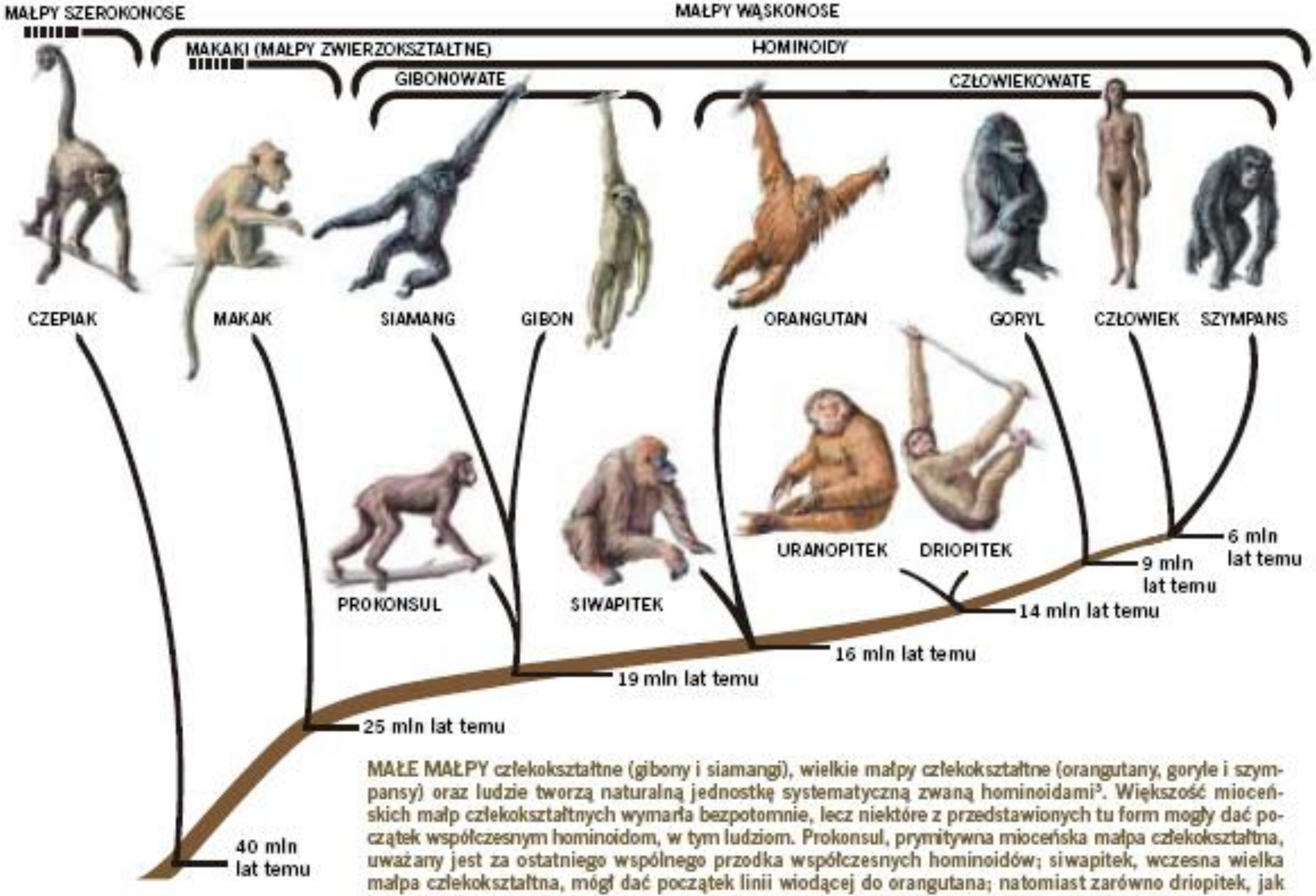
- Natural selection favours infection of new hosts, which may require fast reproduction within host
- Virulence as a by-product of fast reproduction
- Trade-off: transmission limied if a host dies too early!

Virulence evoloution – and example of AIDS

- *The lower HIV infection level, the milder the symptoms*
- *Asymptomatic infectees are less infections…*
- *…but infect for longer*
- *HIV level in infectees from Zambia and Netherlands near optimum set by this trade-off*

PNAS 2007;104:44:17441-17446

The origin of humans



MAŁE MAŁPY człekokształtne (gibony i siamangi), wielkie małpy człekokształtne (orangutany, goryle i szympansy) oraz ludzie tworzą naturalną jednostkę systematyczną zwaną hominoidami[3]. Większość mioceńskich małp człekokształtnych wymarła bezpotomnie, lecz niektóre z przedstawionych tu form mogły dać początek współczesnym hominoidom, w tym ludziom. Prokonsul, prymitywna mioceńska małpa człekokształtna, uważany jest za ostatniego wspólnego przodka współczesnych hominoidów; siwapitek, wczesna wielka małpa człekokształtna, mógł dać początek linii wiodącej do orangutana; natomiast zarówno driopitek, jak i uranopitek wymieniani są jako kandydaci na przodków afrykańskich wielkich małp i człowieka.

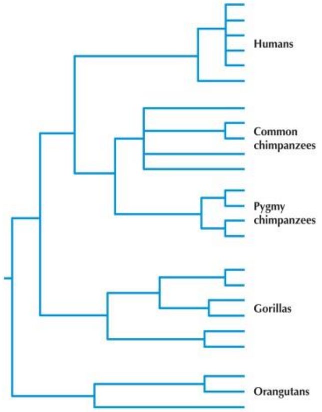


FIGURE 25.5. The phylogeny of Hominidae based on sequences of mitochondrial COII genes.

25.5, adapted from Ruvolo M. et al., *Proc. Natl. Acad. Sci.* **91:** 8900–8904, © 1994 National Academy of S
ences, U.S.A.

Evolution © 2007 Cold Spring Harbor Laboratory Press

Dart 1923 – *A. africaus scull*

A. afarensis (3 mln y.a.)

Johnson 1974*: Lucy*

Human-like traits

- *small canine teeth*
- *arched feet*
- *non-graping toe*
- *knee and pelvis built in a way supporting bipedalism*

Ape-like features

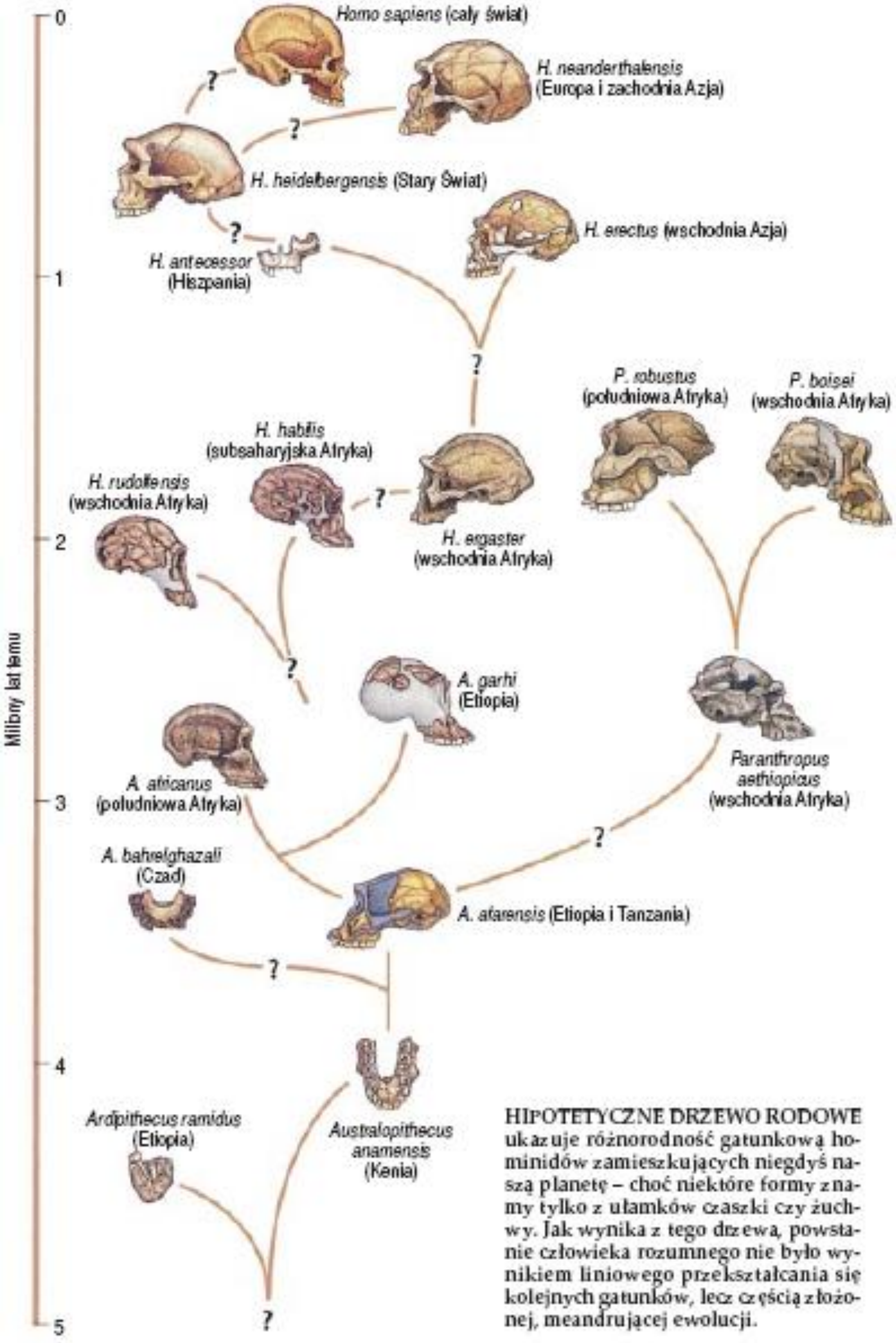
- *massive jaw*
- *proportionally longer arms*

Selective advantages pf bipedality:

- *saves energy during walking*
- *Upright posture decreases exposure to sun*

Unlike apes, humans have two species of lice– head lice and pubic lice (releted to those of gorillas), which split ca. 3ml y.a.

Loss of here facilitates sweating – enables long running – a likely hunting tactics of early humans



HIPOTETYCZNE DRZEWO RODOWE ukazuje różnorodność gatunkową hominidów zamieszkujących niegdyś naszą planetę – choć niektóre formy znamy tylko z ułamków czaszki czy żuchwy. Jak wynika z tego drzewa, powstanie człowieka rozumnego nie było wynikiem liniowego przekształcania się kolejnych gatunków, lecz częścią złożonej, meandrującej ewolucji.

Homo florensis („hobbit”) of Indonesia (18 000 y.a.) – probably a close relative of H. erectus (Kaifu i in. 2015, PlosOne)

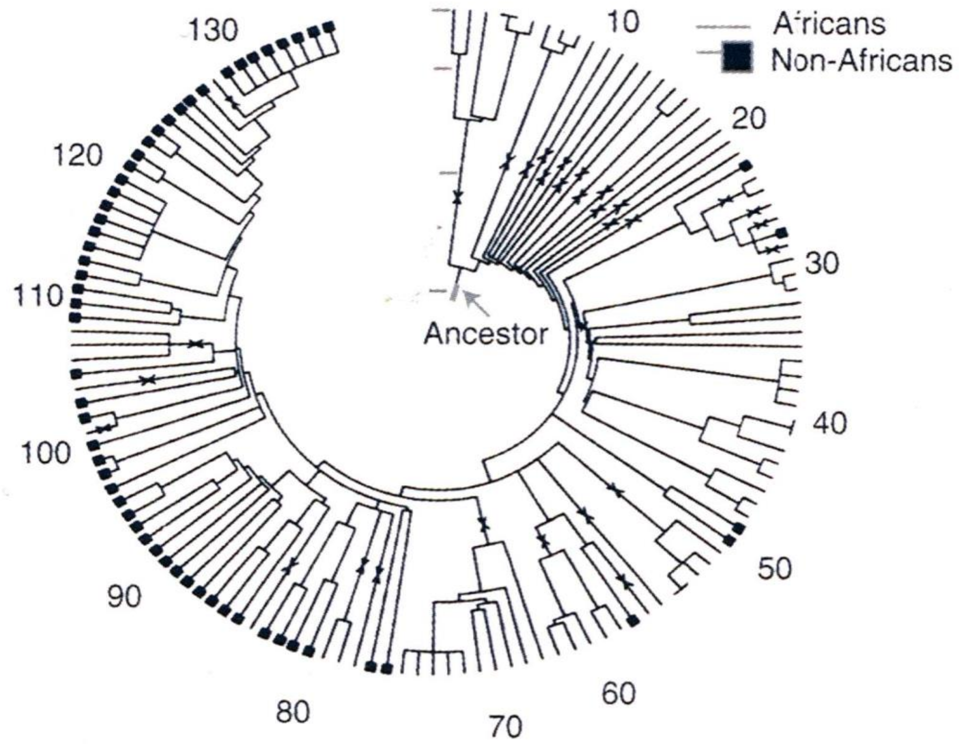
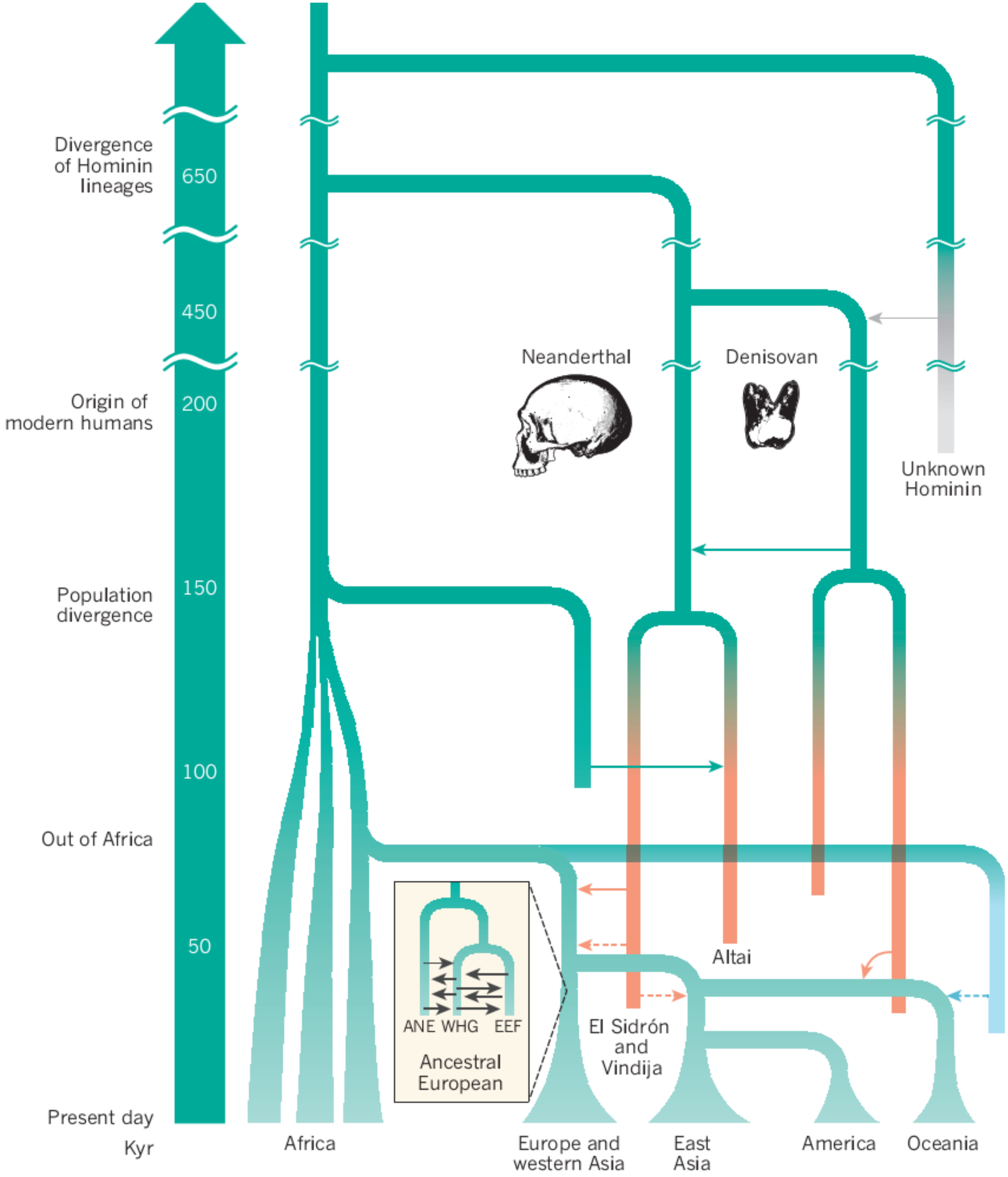


Fig. 15.7 Coalesence analysis of human mitochondria suggests that the common ancestor of all extant mitochondria existed in a woman who lived about 200 000 years ago. (From Vigilant *et al*. 1991.)

Expansion to the north associated with the loss of skin pigmentation to allow vitamin D. synthesis

Clothes devised aourd the time of expaniosn (body lice split from head lice ca 100 000 y.a. (Toups et al. 2010)



Tracing the peopling of the world through genomics

Rasmus Nielsen[1,2,3], Joshua M. Akey[4], Mattias Jakobsson[5], Jonathan K. Pritchard[6,7,8], Sarah Tishkoff[9,10] & Eske Willerslev[3,11,12].

Adaptive introgression form archaic humans

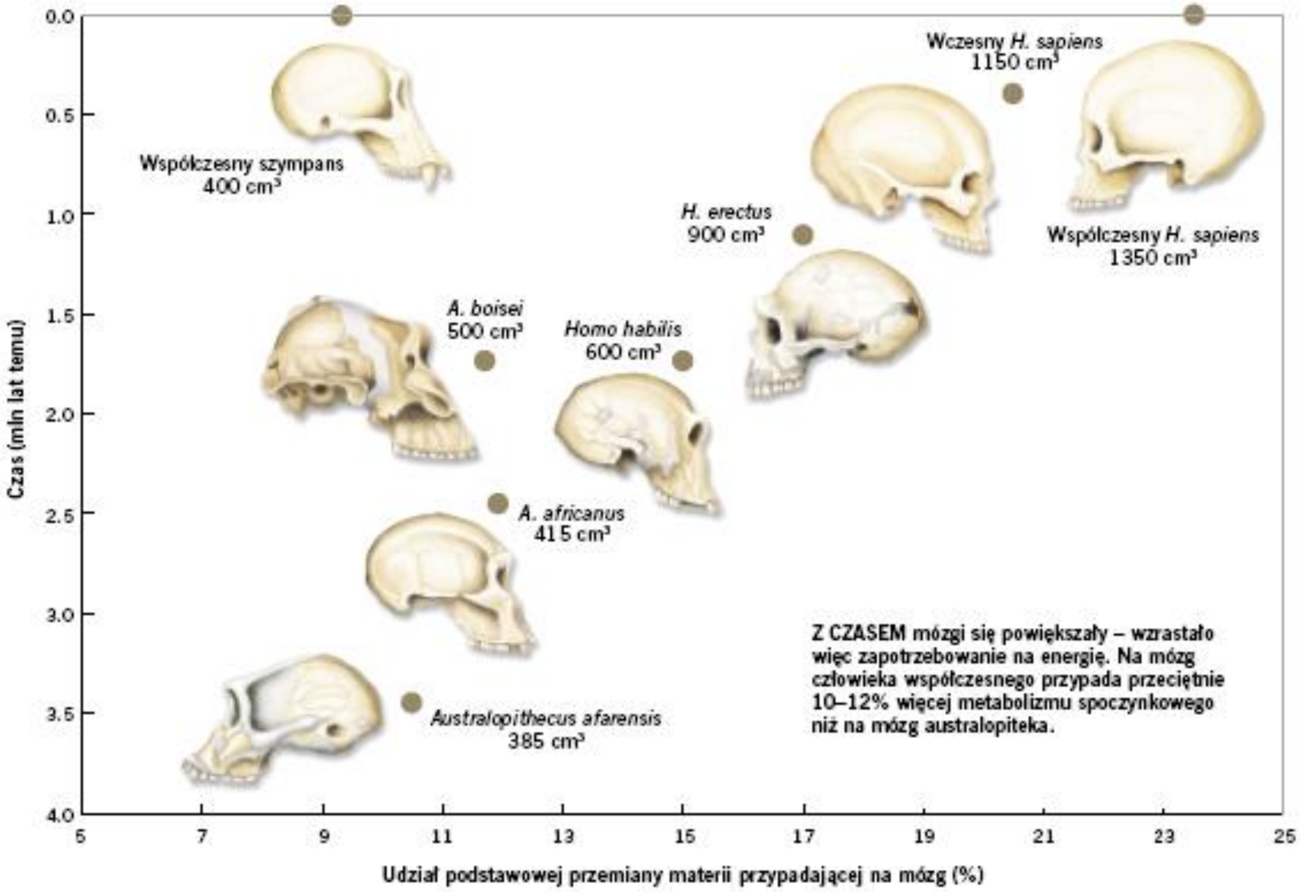
Except for Africa, human genomes contain ca 2-4% admixture from archaic humans (Neanderthals and Denisovans) (Sankararaman i in. 2014)

Their genes underlying adaptation to :

- high altitude (variant of EPAS1 gene)
- Low temperature endurance in Inuits (TBX15)
- Immune response (variants of MHC, TLR)
- Susceptibiliy to COVID-19 (ch. 12 (OAS) -; ch2 (haplotyp DPP4 +, Ch3+)

Bipedality enabled large brain evolution

- *No need for strong neck muscles, less stress on aorta providing blood to the brain*
- *Energetic gains (brain uses ca. 25% of energy budget in humans, compared to 5% in mice)*



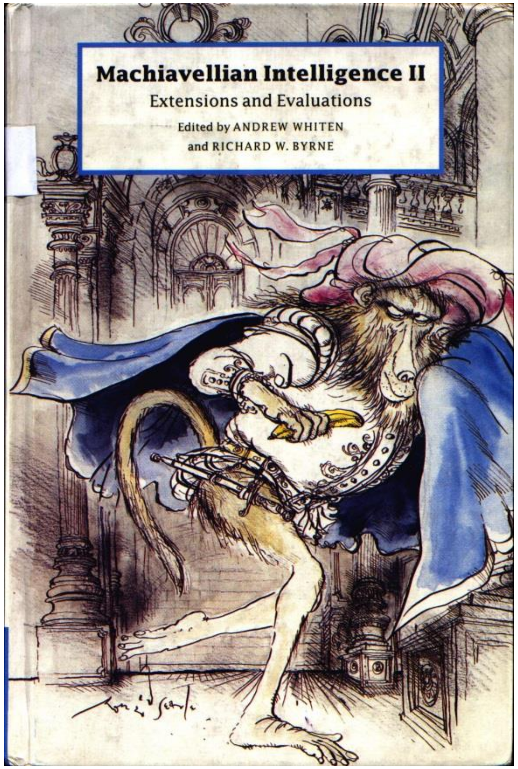
Z CZASEM mózgi się powiększały – wzrastało więc zapotrzebowanie na energię. Na mózg człowieka współczesnego przypada przeciętnie 10–12% więcej metabolizmu spoczynkowego niż na mózg australopiteka.

Diet shift: energetic gains of meet eating, release from stress caused by jaw muscles

Machiavellian Intelligence II

Extensions and Evaluations

Edited by ANDREW WHITEN
and RICHARD W. BYRNE



Techno-cultural hypothesis:

- Brain regions associated with language also responsible for the ability to manipulate objects and predicting sequencs of events
- MSH – mirror system hypothesis (Arbin i in. 2005): observation and understanding activate homologous regions in apes – pre-adaptation to gesture communication?

Brain regions activated during stone tool construction activate IPL i vPM

Stone tools, language and the brain in human evolution

Dietrich Stout[1],* and Thierry Chaminade[2]

Phil. Trans. R. Soc. B (2012) **367**, 75–87
doi:10.1098/rstb.2011.0099

Despite large genome similarity (1% coding sequence divergence, 5% genomewide; Watanabe i in. 2004) humans and chimps differ in gene expression patterns, particularly in the brain

Ennard et al.

SCIENCE VOL 296 12 APRIL 2002