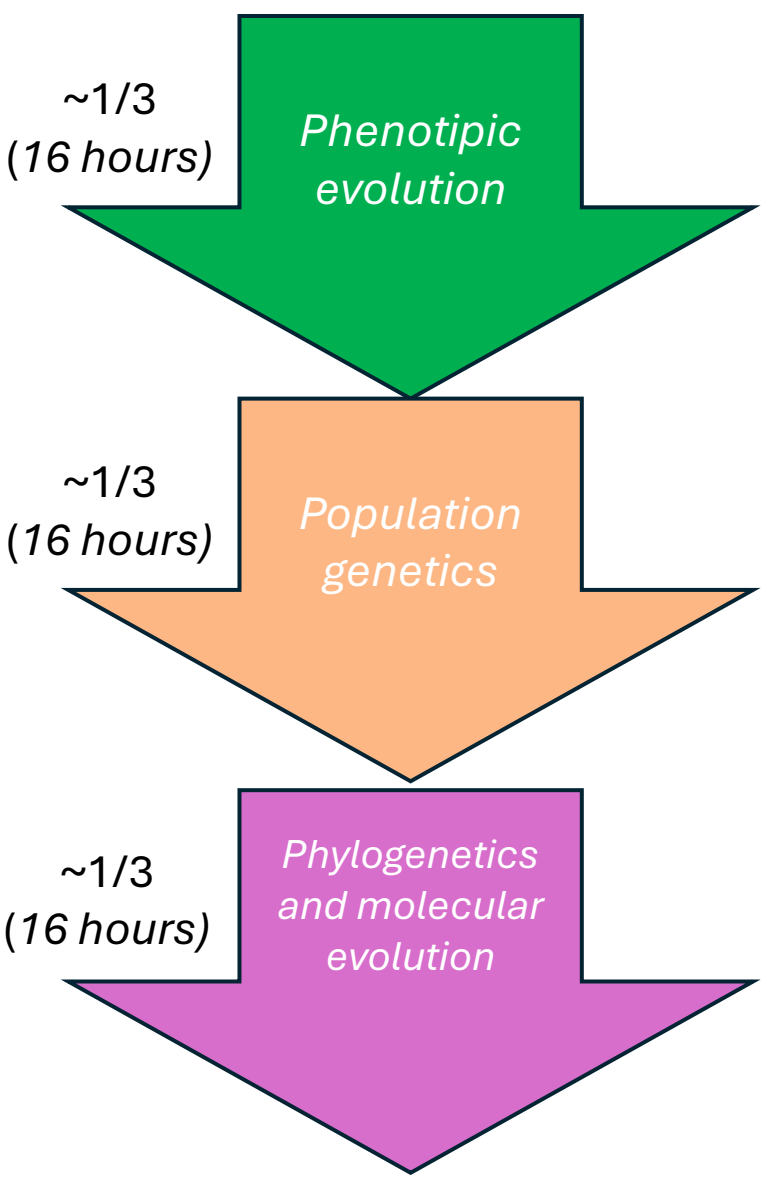
Evolutionary trade-offs and fitness landscapes

Fabrizio Mafessoni, Universita’ di Trieste, 2025/2026, Corso di Laurea in Scienze e Tecnologie Biologiche

Structure of the course



- *Darwin and inheritance*
- *Quantitative genetics*
- *Fitness landscapes*
- *Evolutionary game theory*

Phenotipic evolution

- *Genetic drift*
- *Molecular clock*
- *Coalescent theory*
- *Hardy-Weinberg*
- *Population substructure*
- *Selection scans*
- *Human evolution*

Population genetics

- *Phylogenetic trees*
- *Genome evolution*
- *Viral evolution*
- *Cancer evolution*

Phylogenetics and molecular evolution

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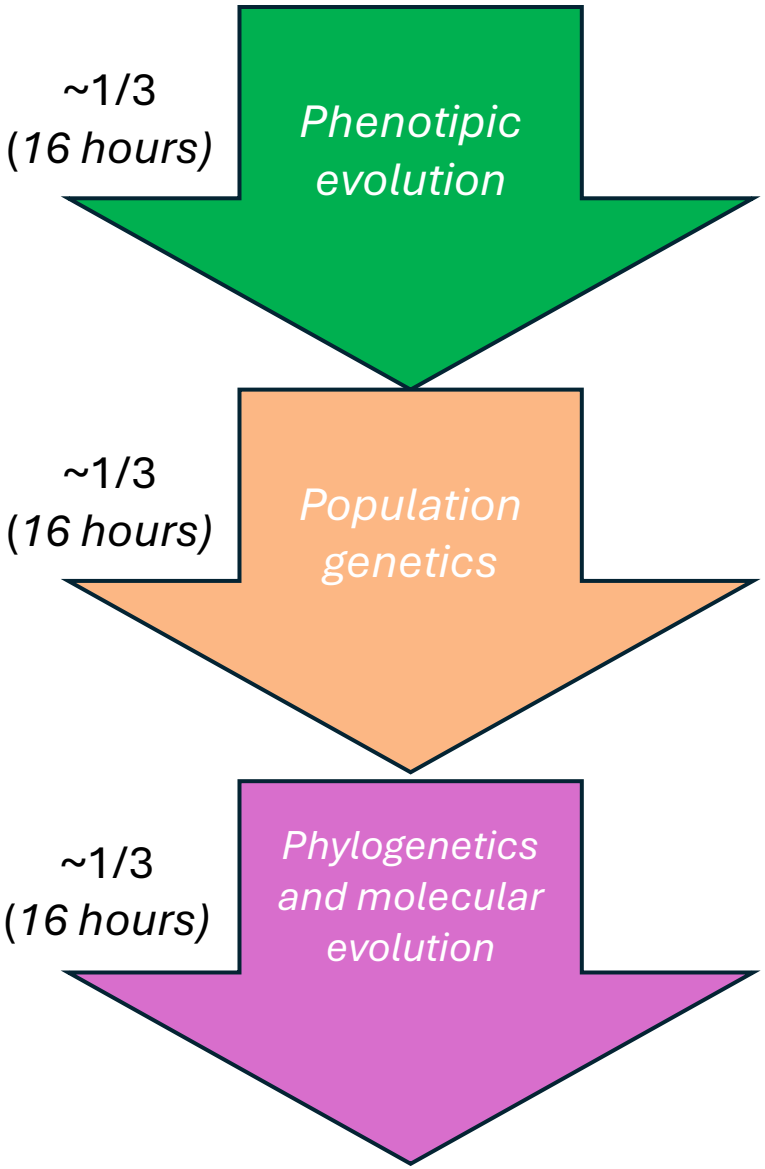

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- *Quantitative genetics*
- *Fitness landscapes*
- *Evolutionary game theory*

Next time. Please come!

- *Genetic drift*
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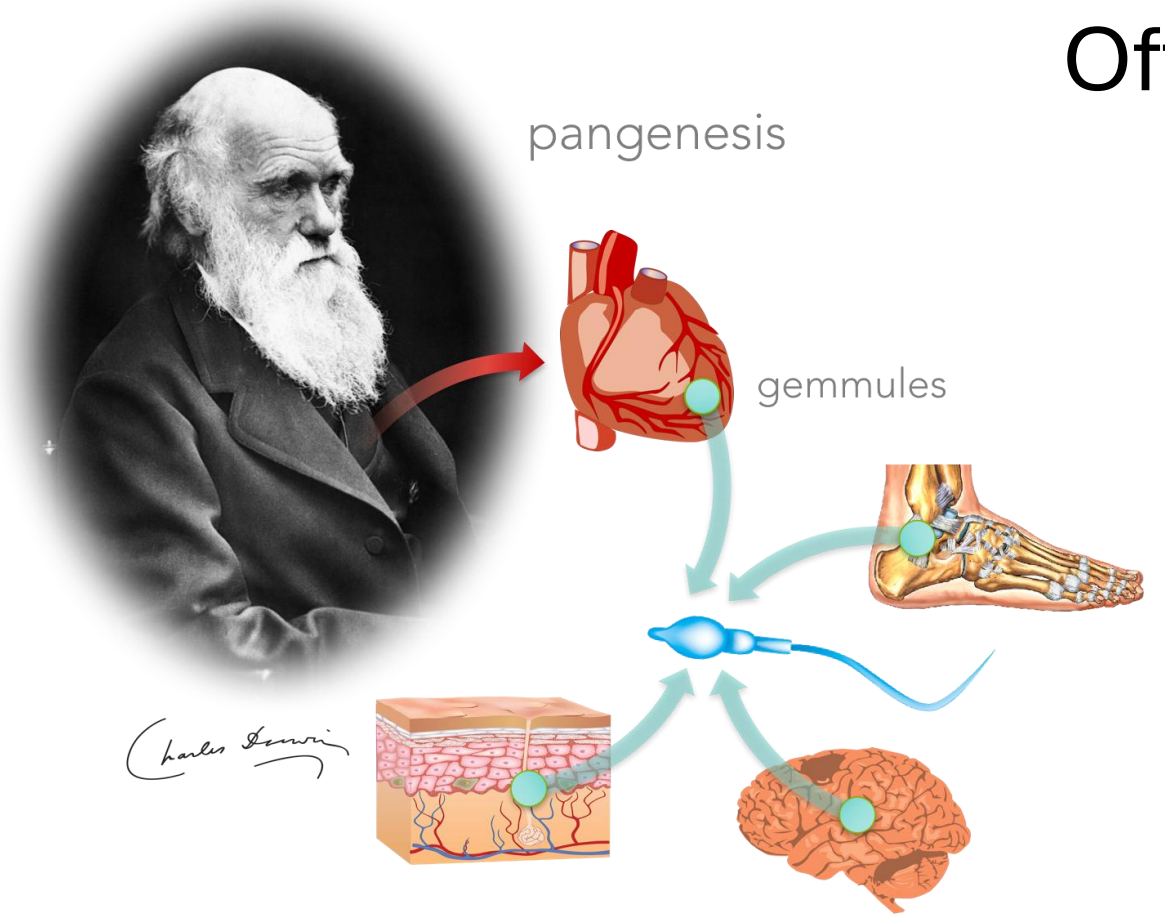
Phenotipic evolution

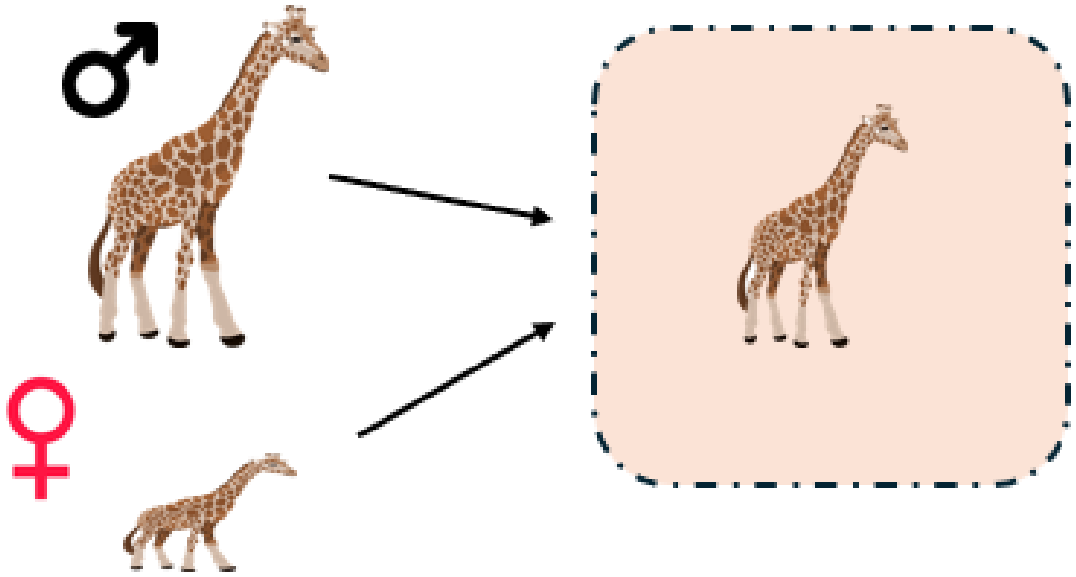
Population genetics

Phylogenetics and molecular evolution

Darwin’s pangenesis implies leads to the problem of blending inheritance



Offspring average neck length



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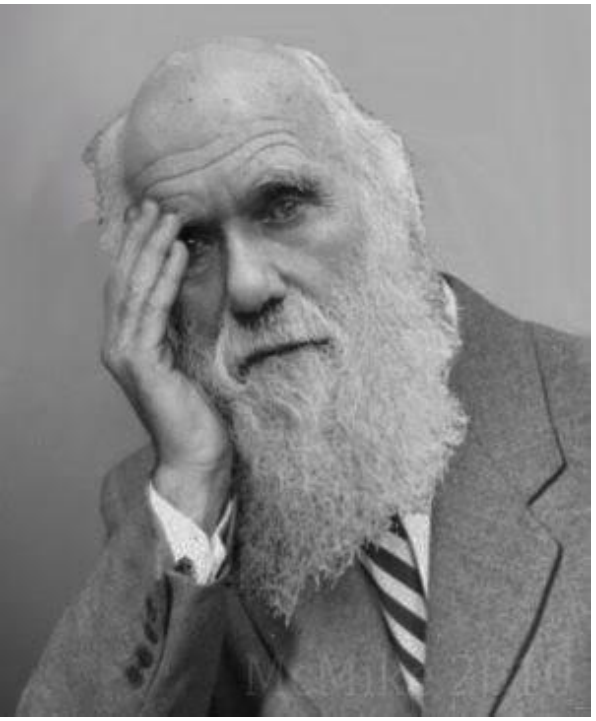
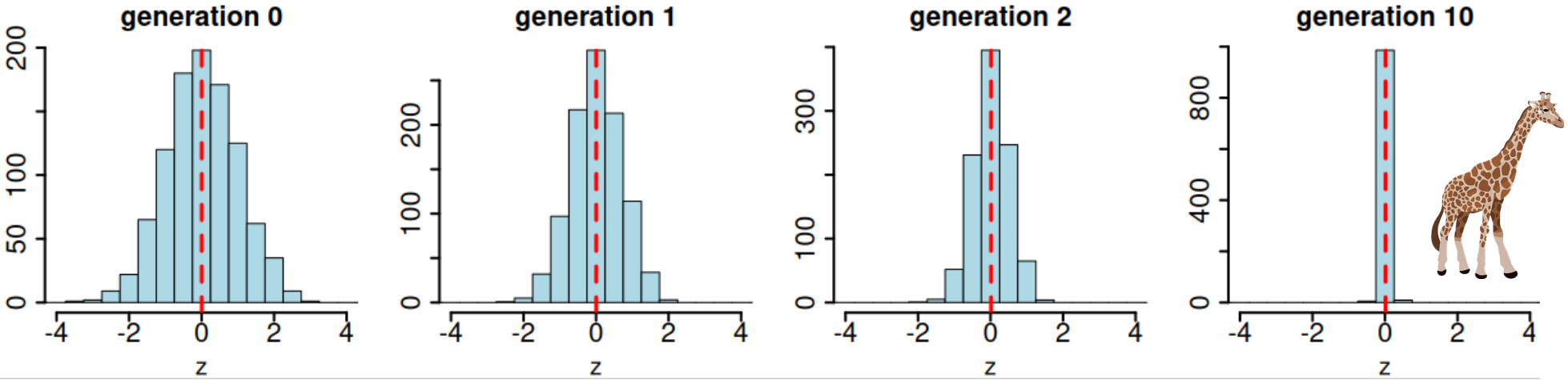
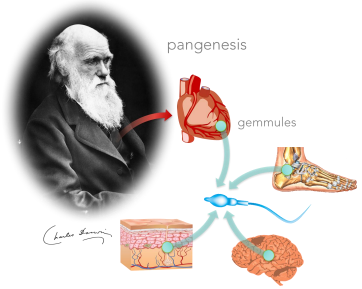


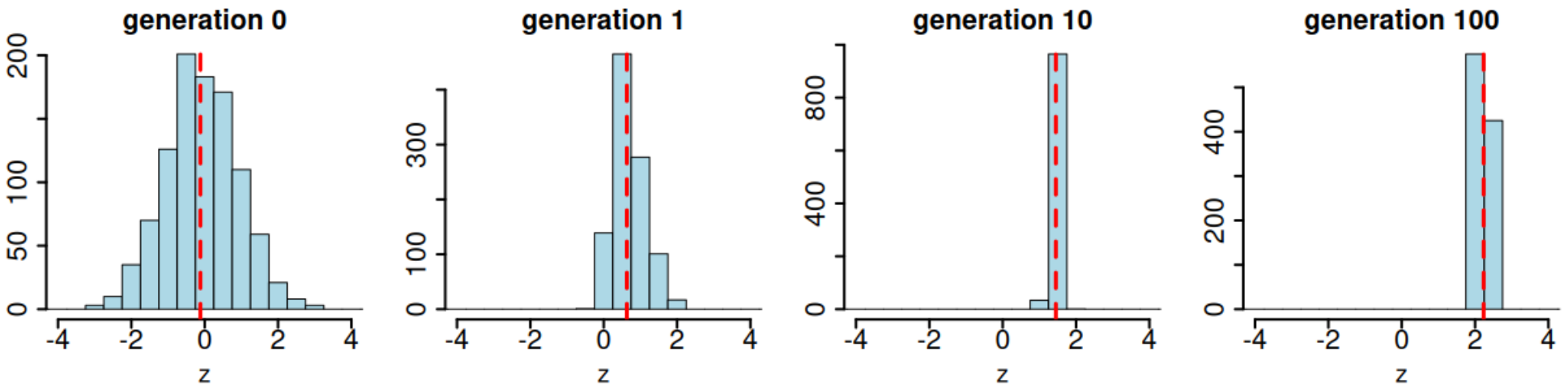
No variability → No evolution!

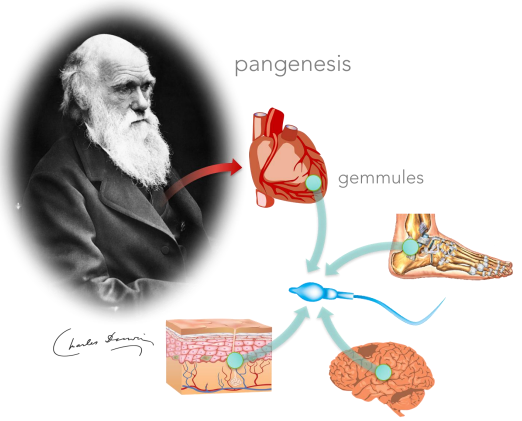
Even without selection populations completely lose their variability over time

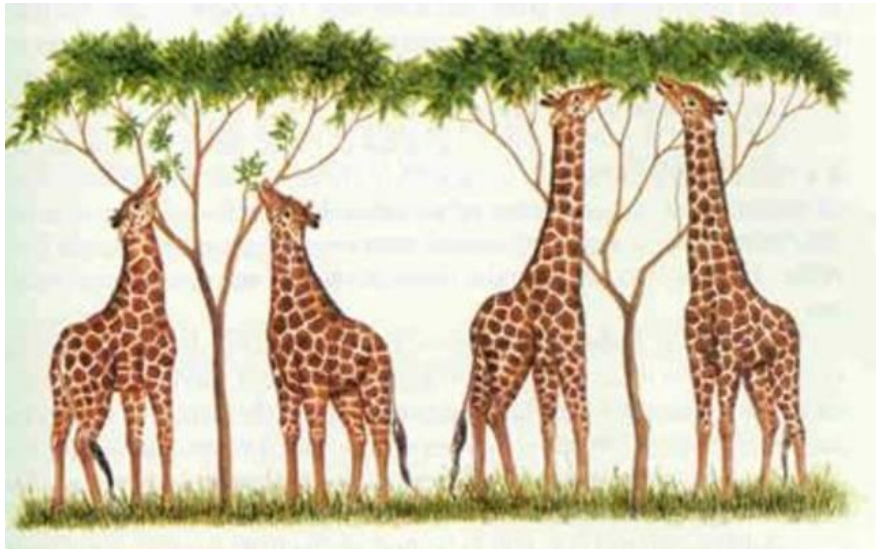




Darwin's solution: acquired characters



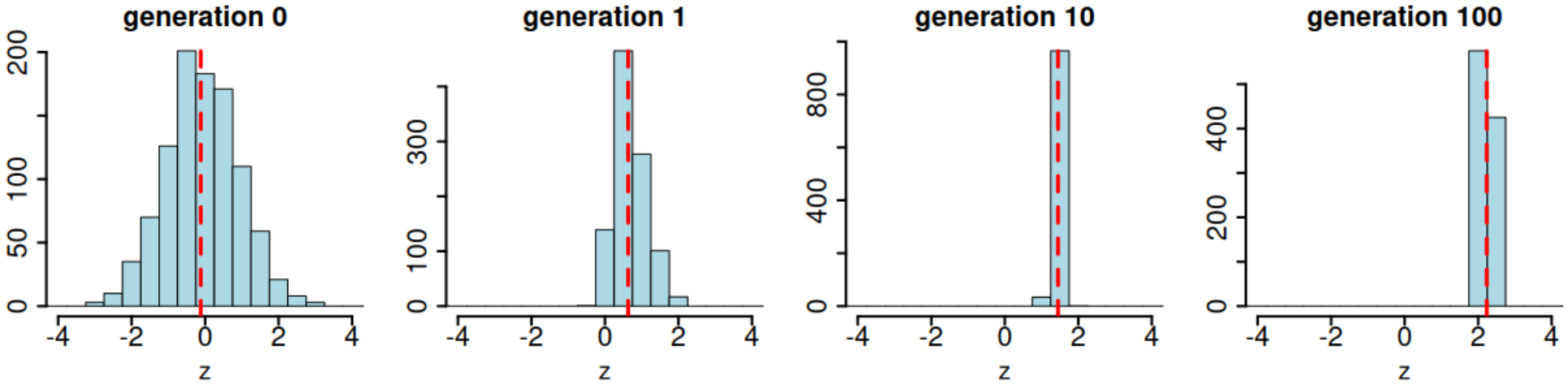


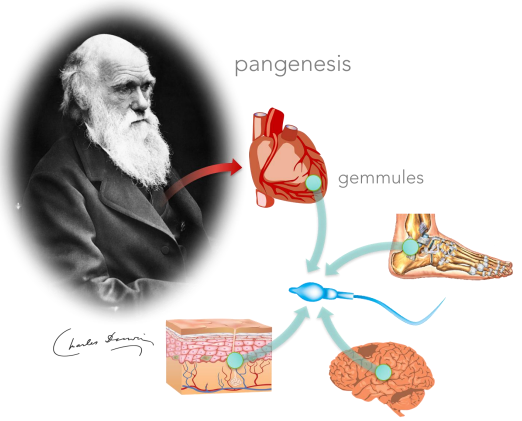


Note that for Lamarck there can also be no variation!

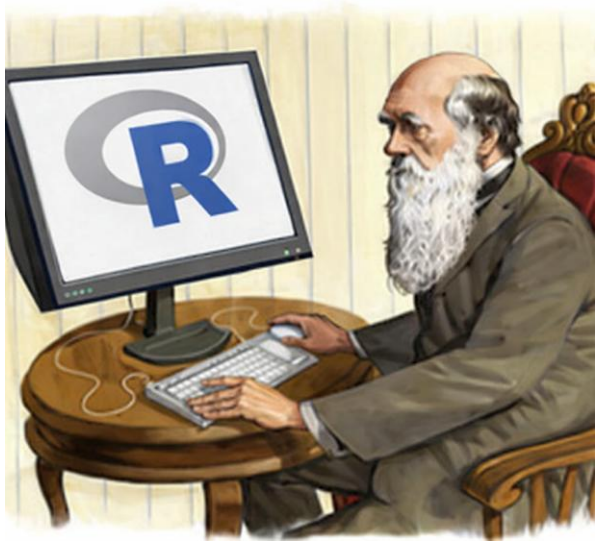
«Information from the enviroment»: **similar to Lamarckian inheritance**, but acquired characters mostly have the function of **generating variation** (akin to mutations) rather than «directional evolution» like Lamarck

Darwin's solution: acquired characters






```
fitness_values=fitness_f(z)
fitness_values[fitness_values<0]=0
survivors=sample(gametes,size=1,prob=fitness_values)
gametes=survivors+rnorm(N,sd=mutsd)
z=gametes + rnorm(N,sd=envsd)
```



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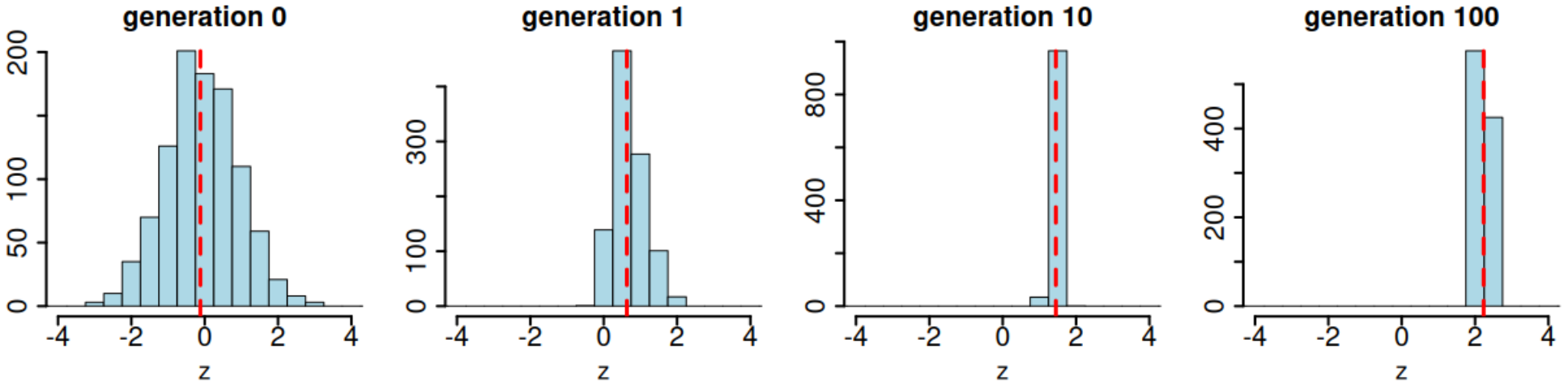
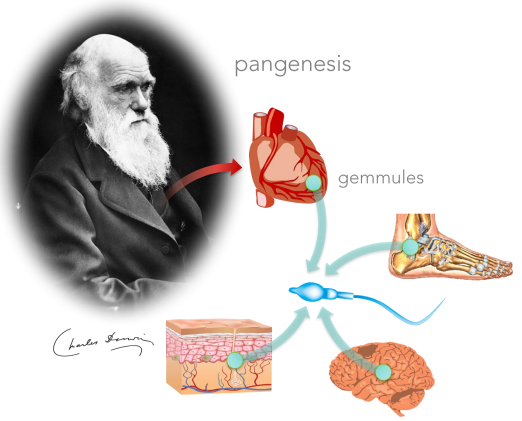
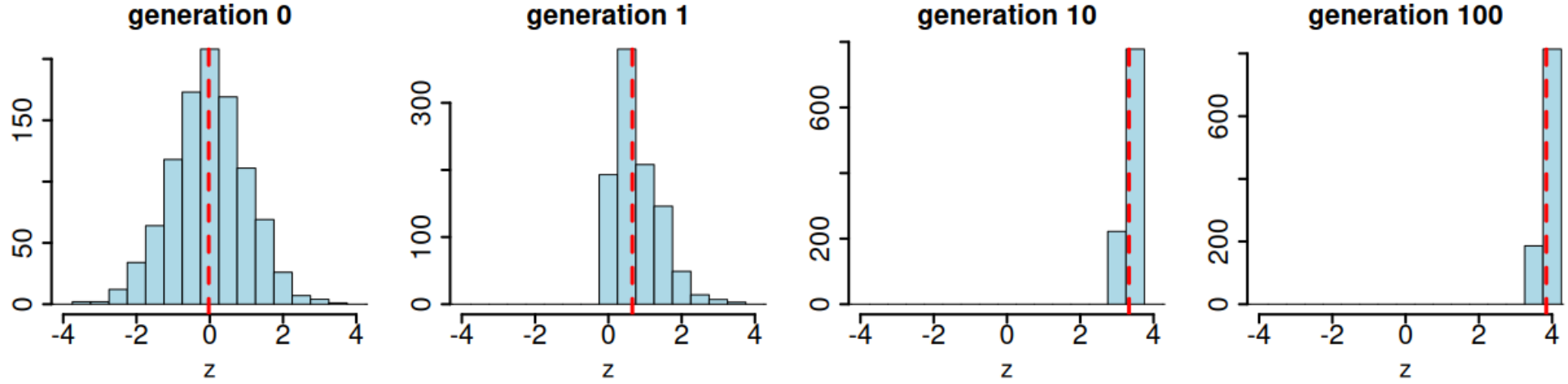
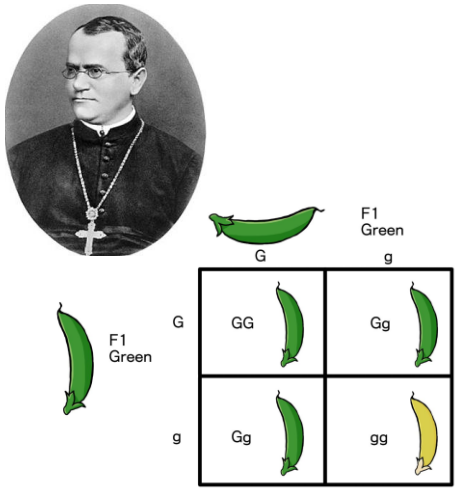




Mendel's solution (DNA is discrete, no blending)

..and real diploids' organisms





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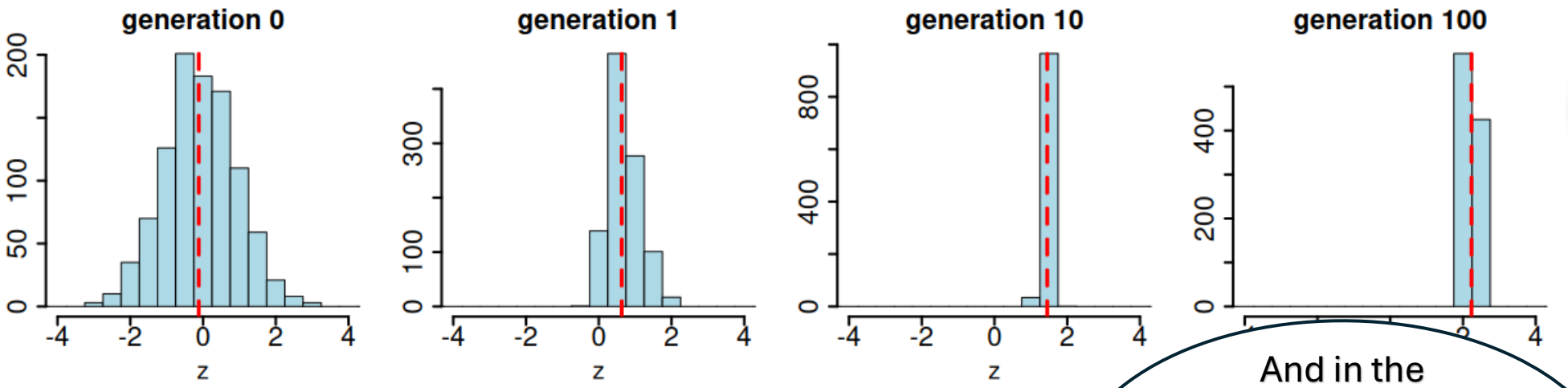

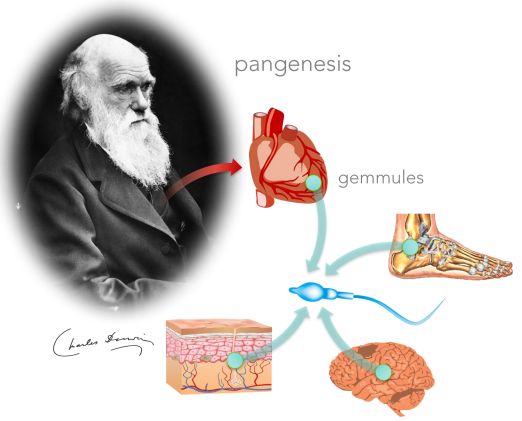

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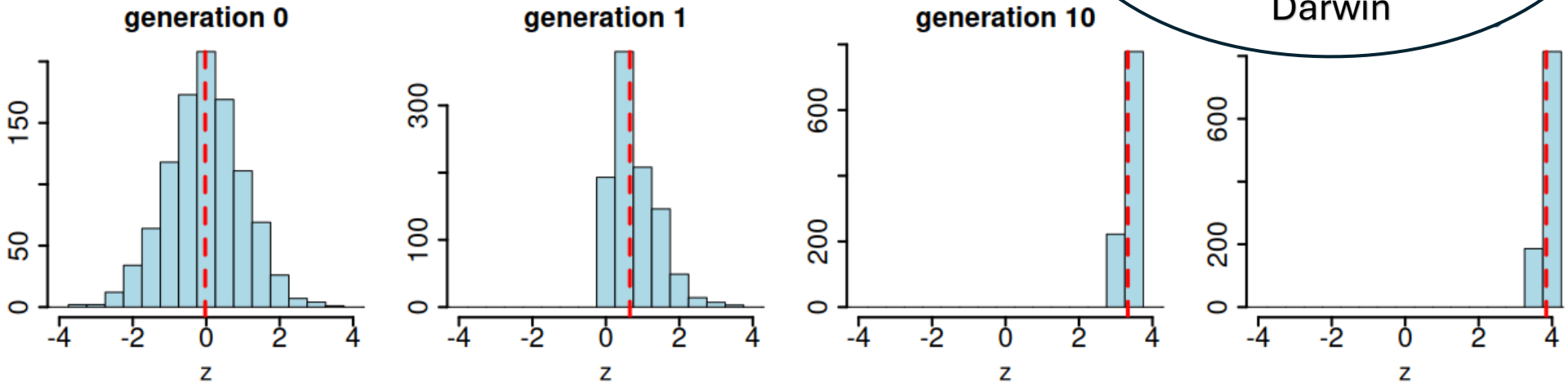
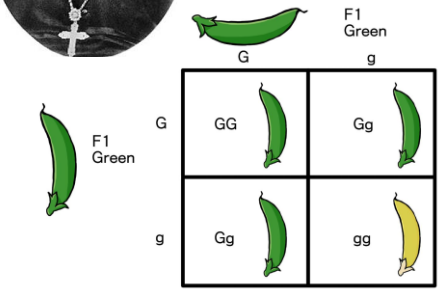
And in the simulations below mutations introduced much less variation than for Darwin





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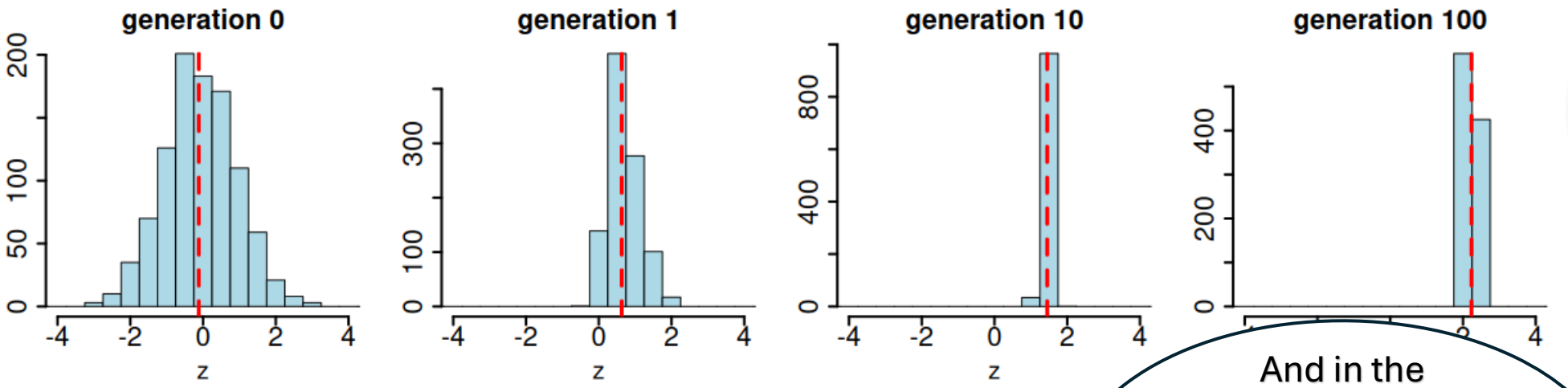

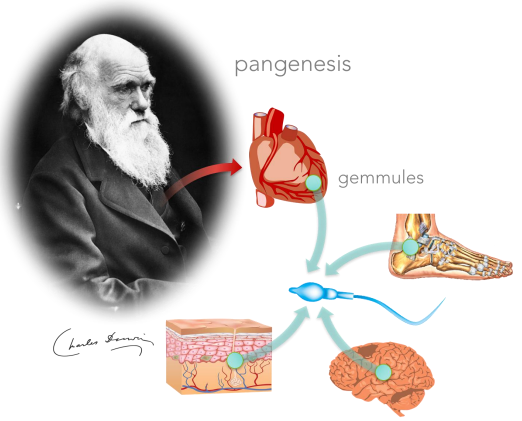

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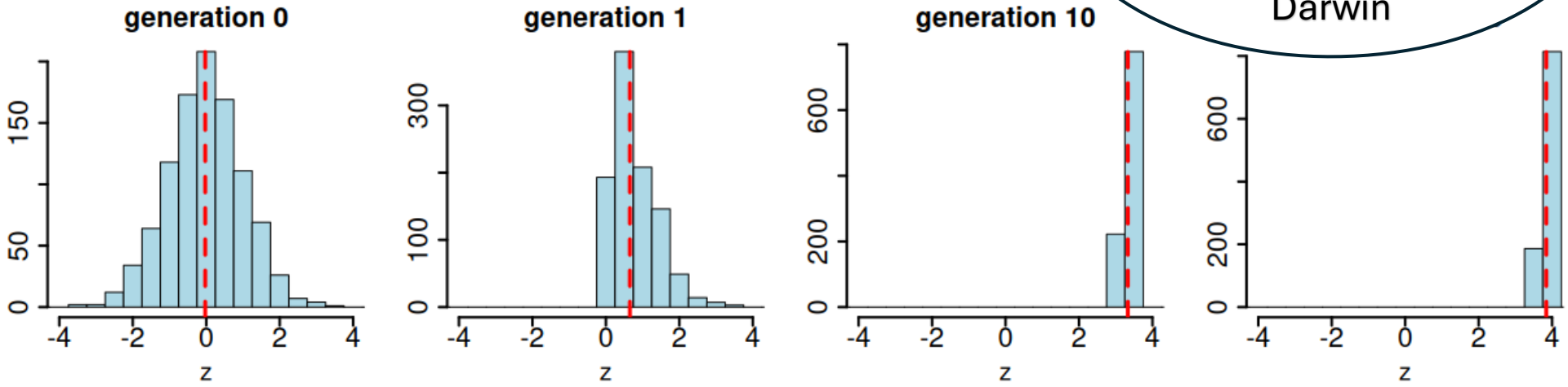

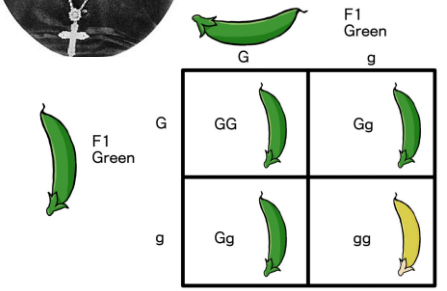

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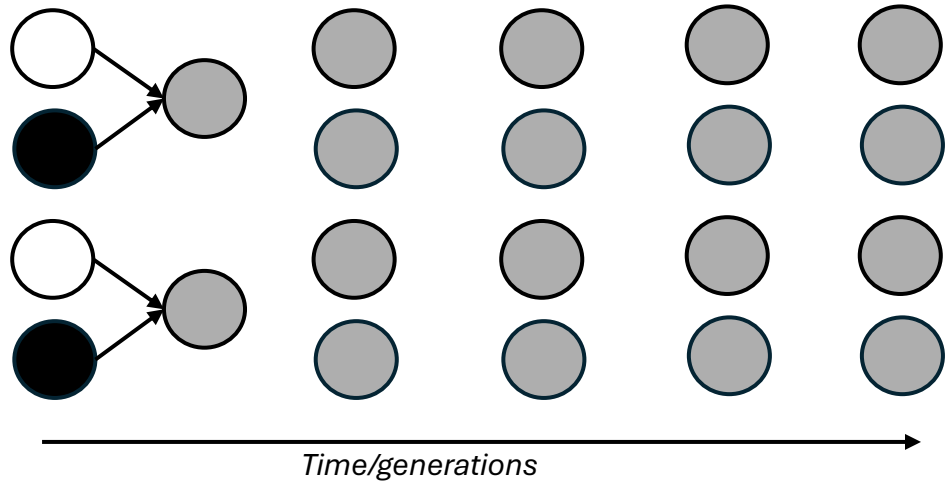

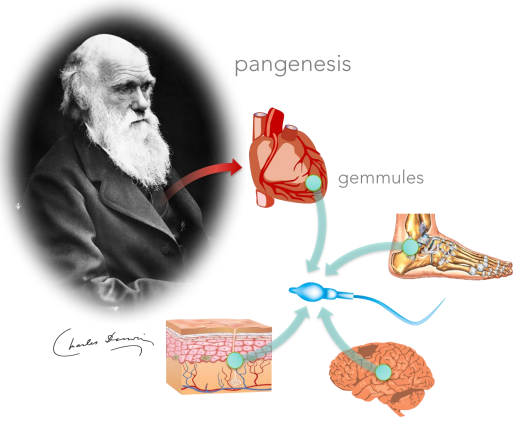

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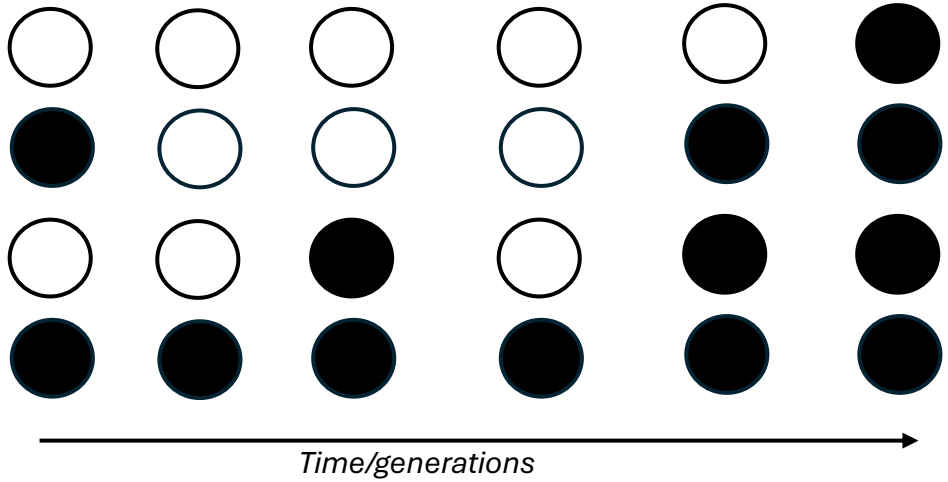
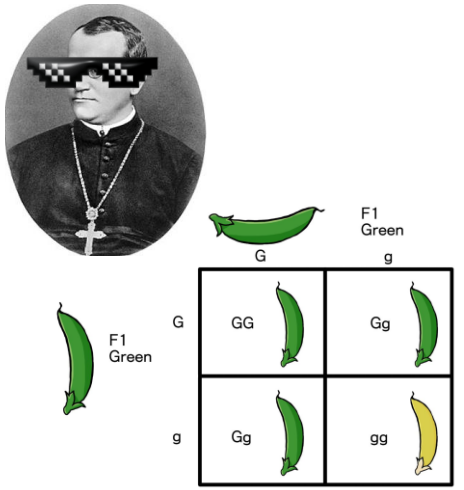
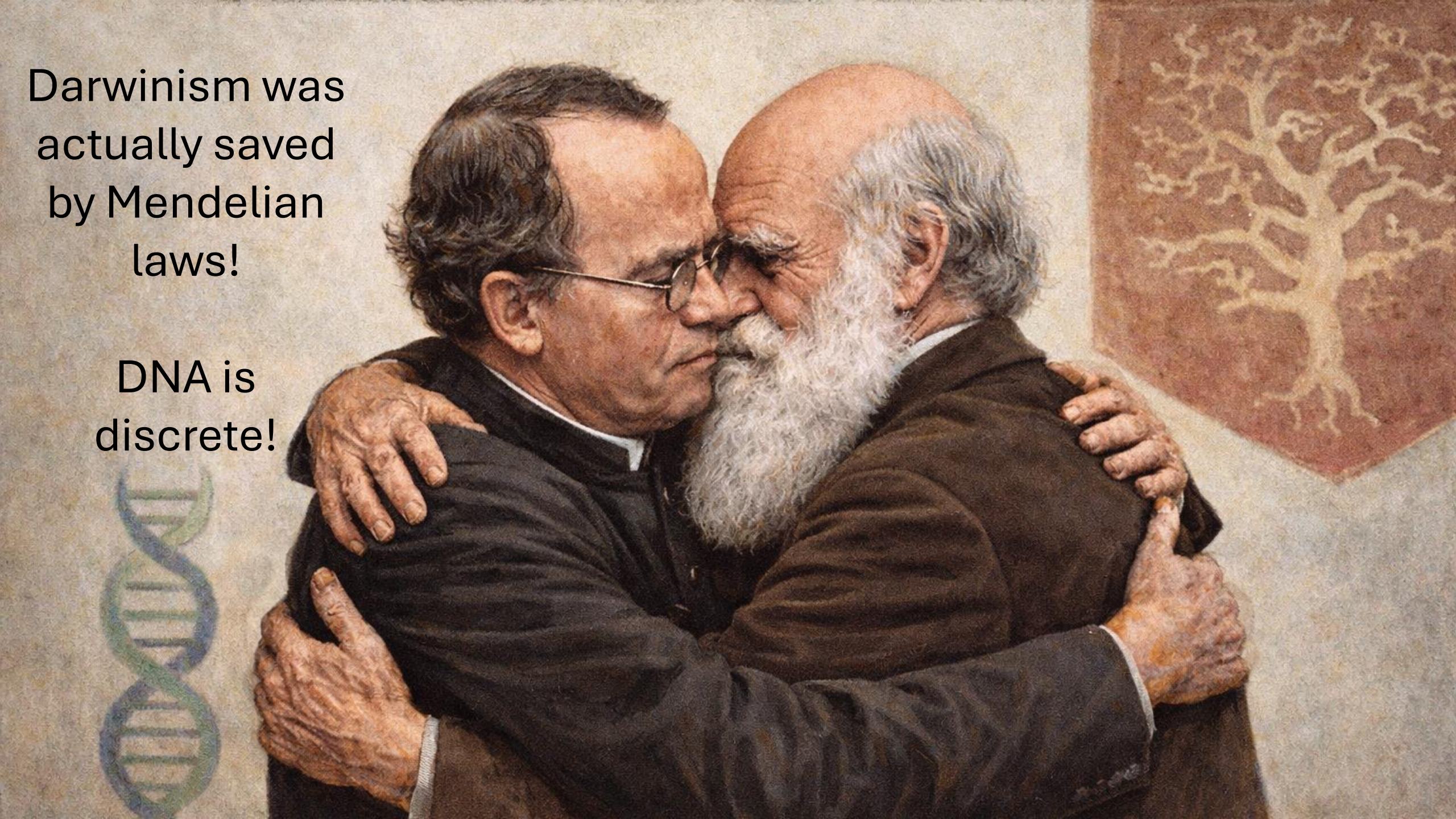
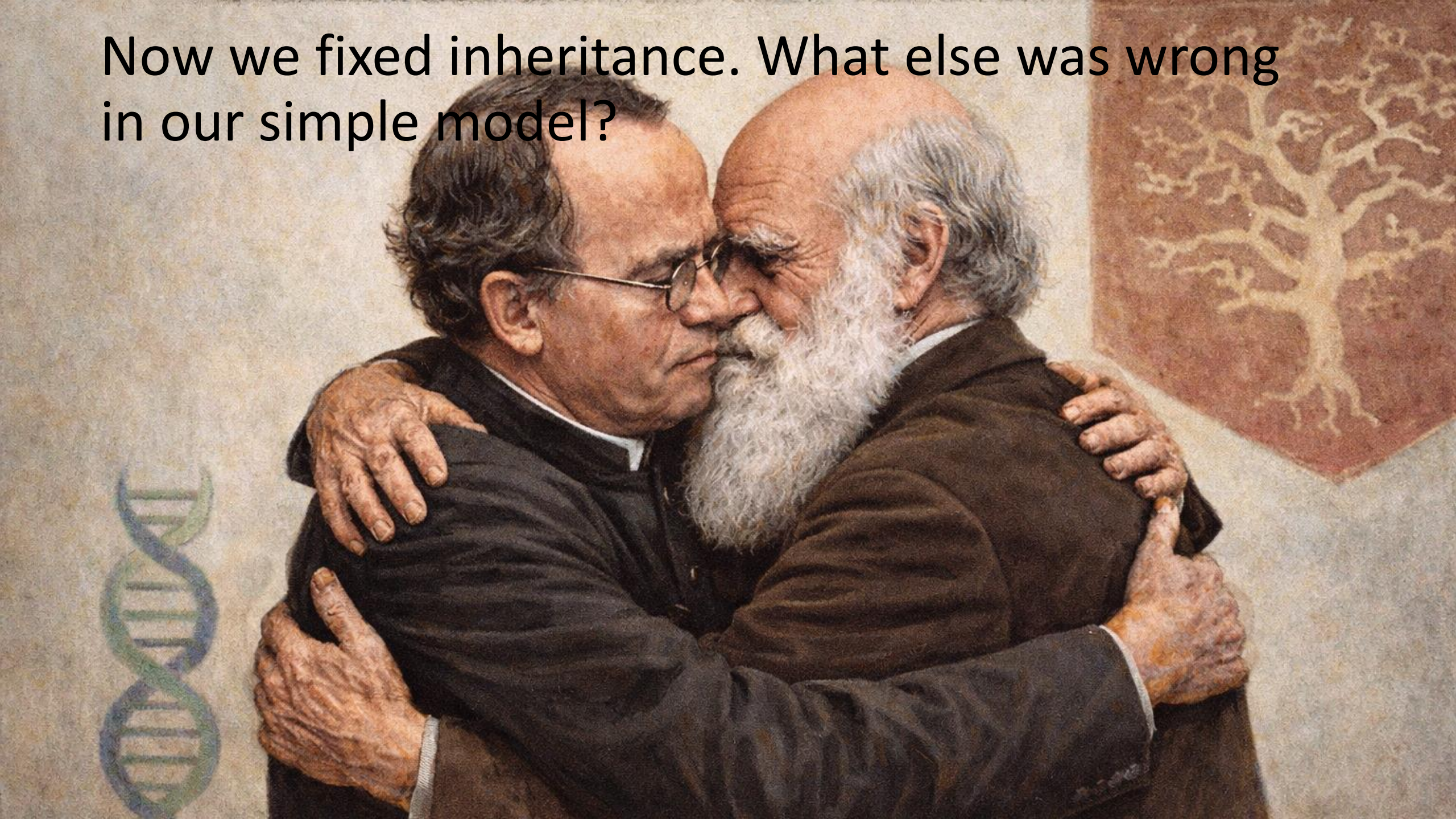




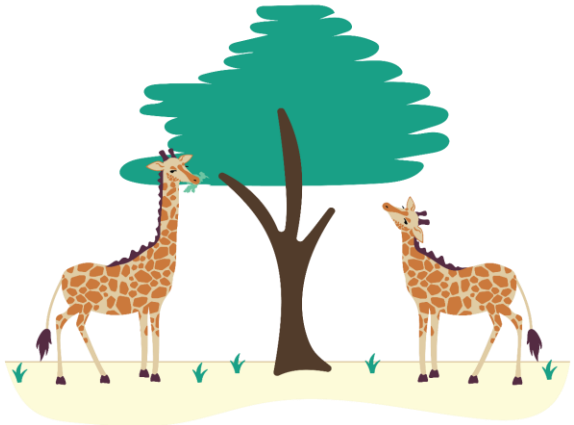

Darwinism was actually saved by Mendelian laws!
DNA is discrete!

Now we fixed inheritance. What else was wrong in our simple model?

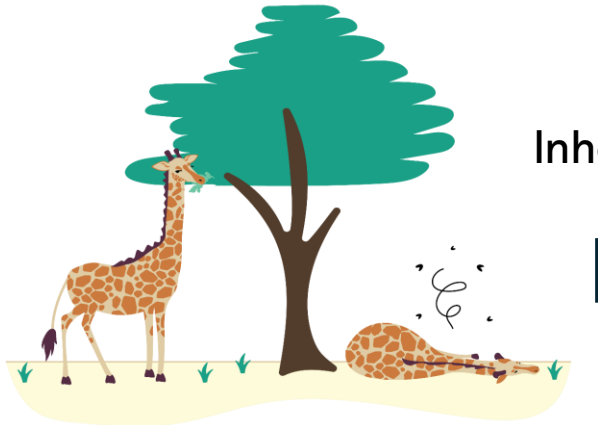


Now we fixed inheritance.

Is there anything wrong in our model?

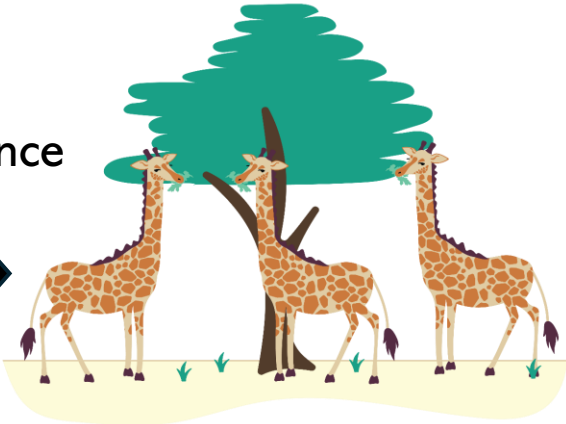


A population of giraffes with variable (heritable) neck lenghts



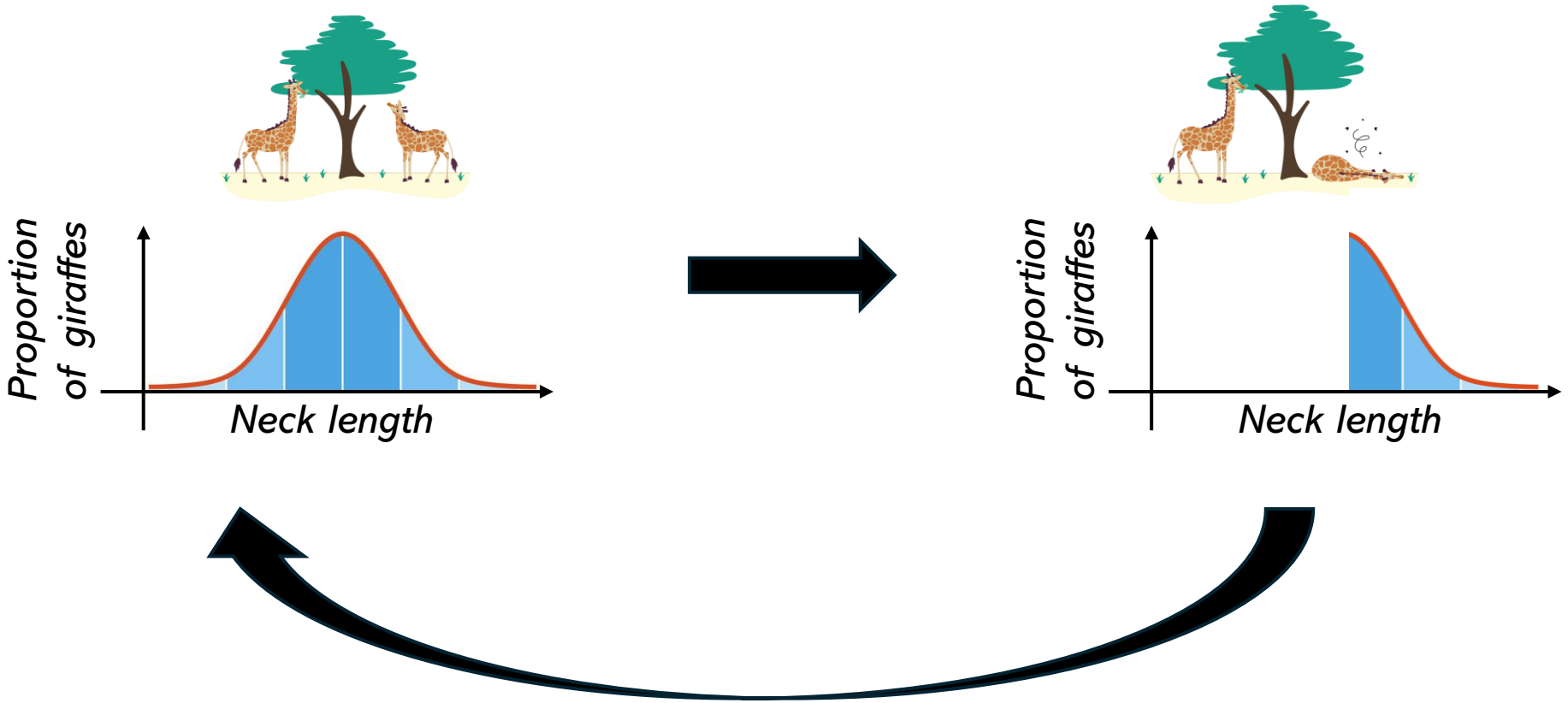
Giraffes with longer necks survive/reproduce more

Inheritance



Over many generations

What will happen over a long time?



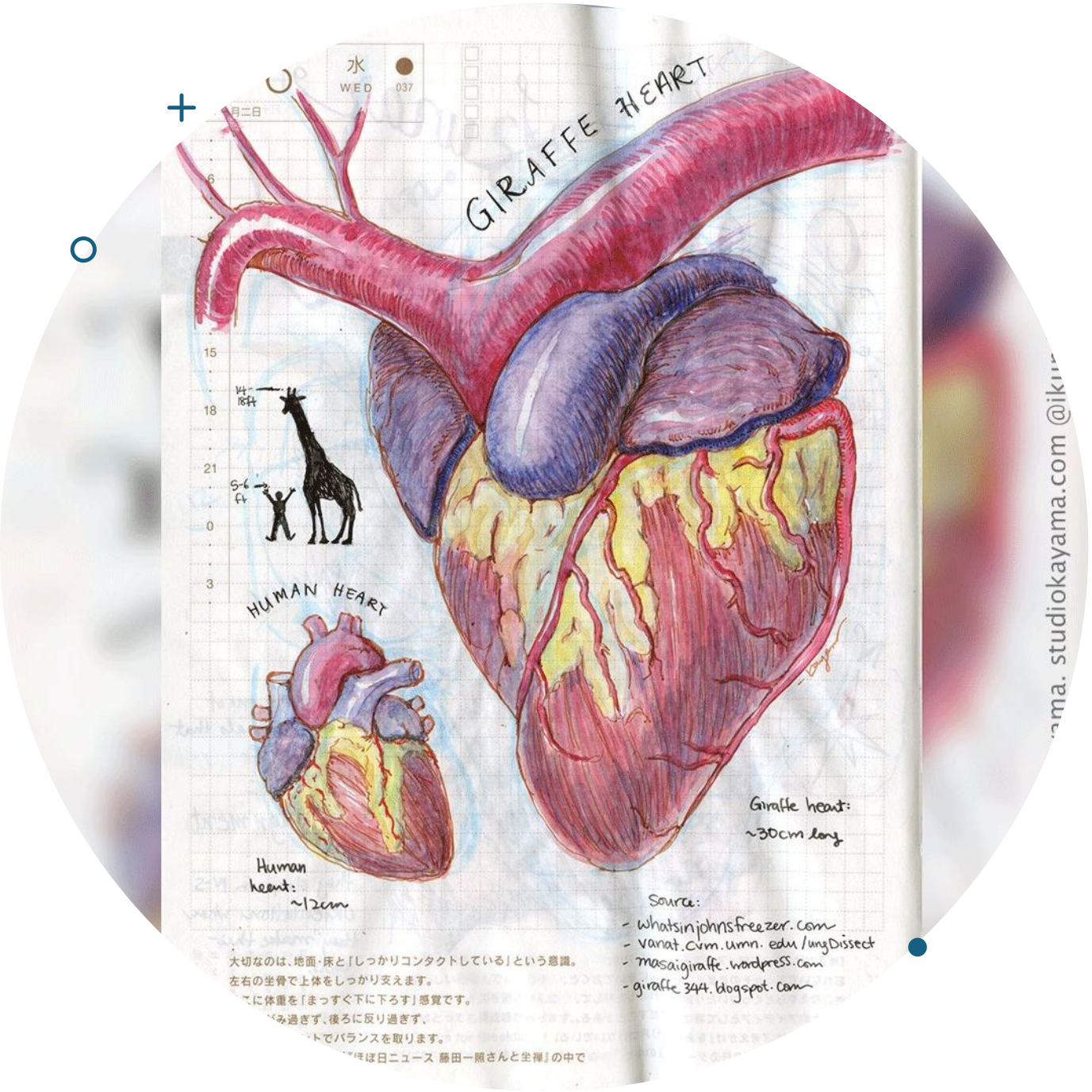
Reproduction with «correct inheritance» (heritability>0, no «blending of inheritance», new variation via mutations)

This..

..eventually
becomes this!

Why doesn’t the neck grow taller and taller till the moon?

OK, sure..but then?



A giraffe's heart

11 kg!! (ours is 250-350g)

GRAPHIC WARNING

News > World News

‘I’M OVER THE MOON’ Trophy hunter slammed for posing with bloody HEART from giraffe hubby paid £1.5k for her to shoot as ‘Valentine’s gift’

Alice Fuller

Published: 15:01, 22 Feb 2021

WARNING

CONTAINS SCENES SOME VIEWERS MAY FIND UPSETTING

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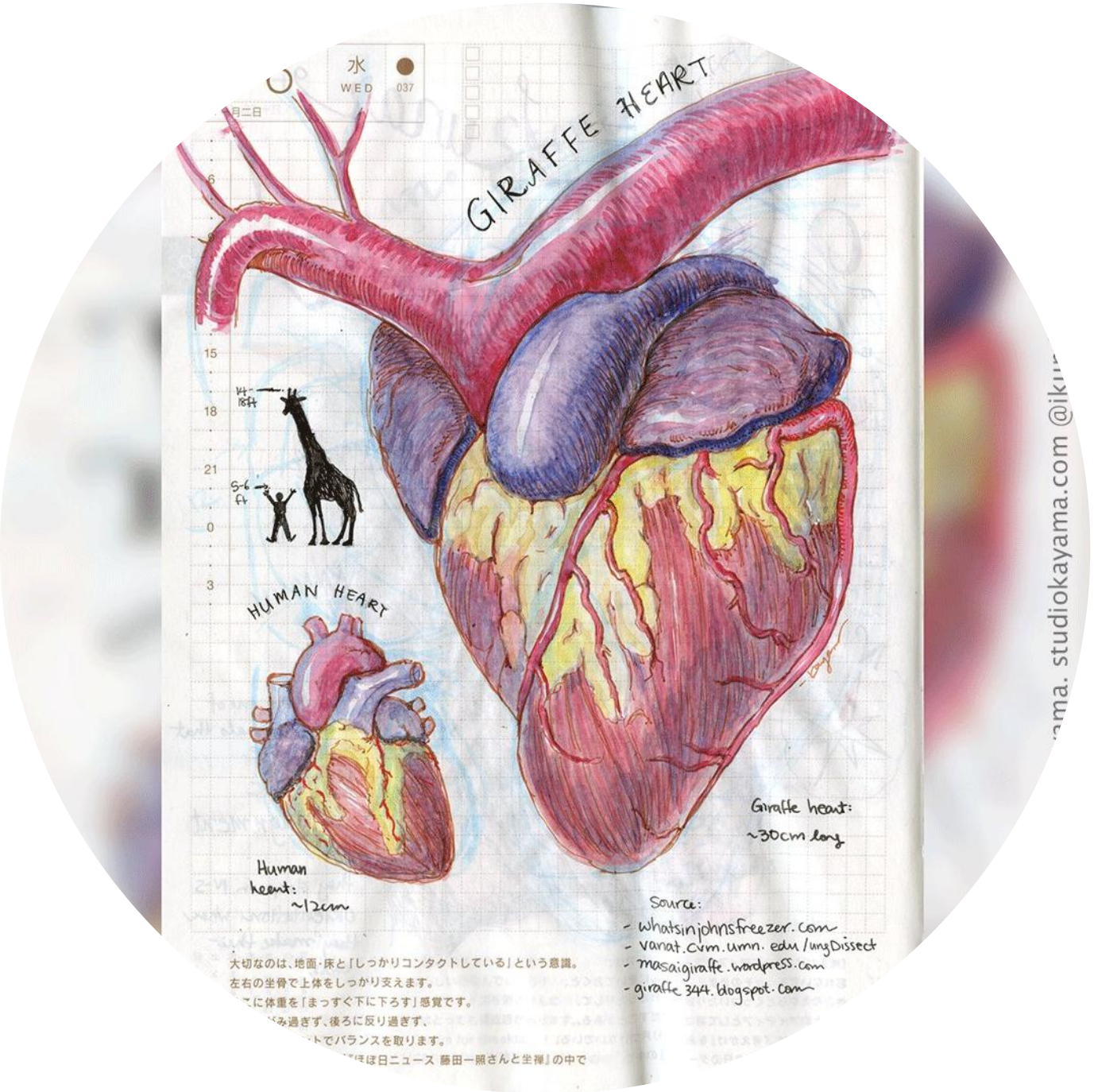
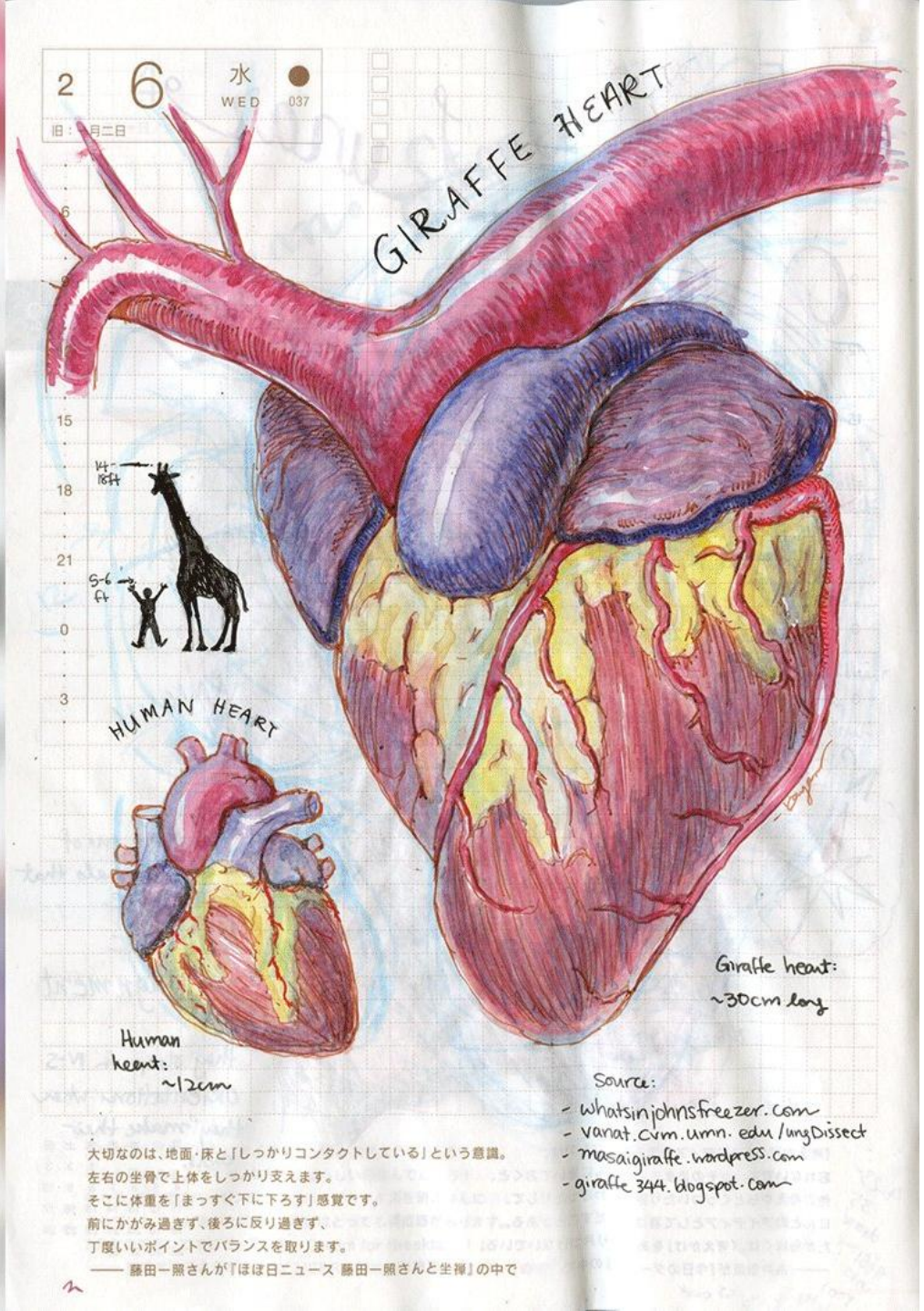


A giraffe's heart

- 11 kg
- Very muscular and thick-walled
- Systolic pressure double as humans
- Specialized arterial valves and one-way jugular vein prevent sudden surges in brain blood pressure when bending



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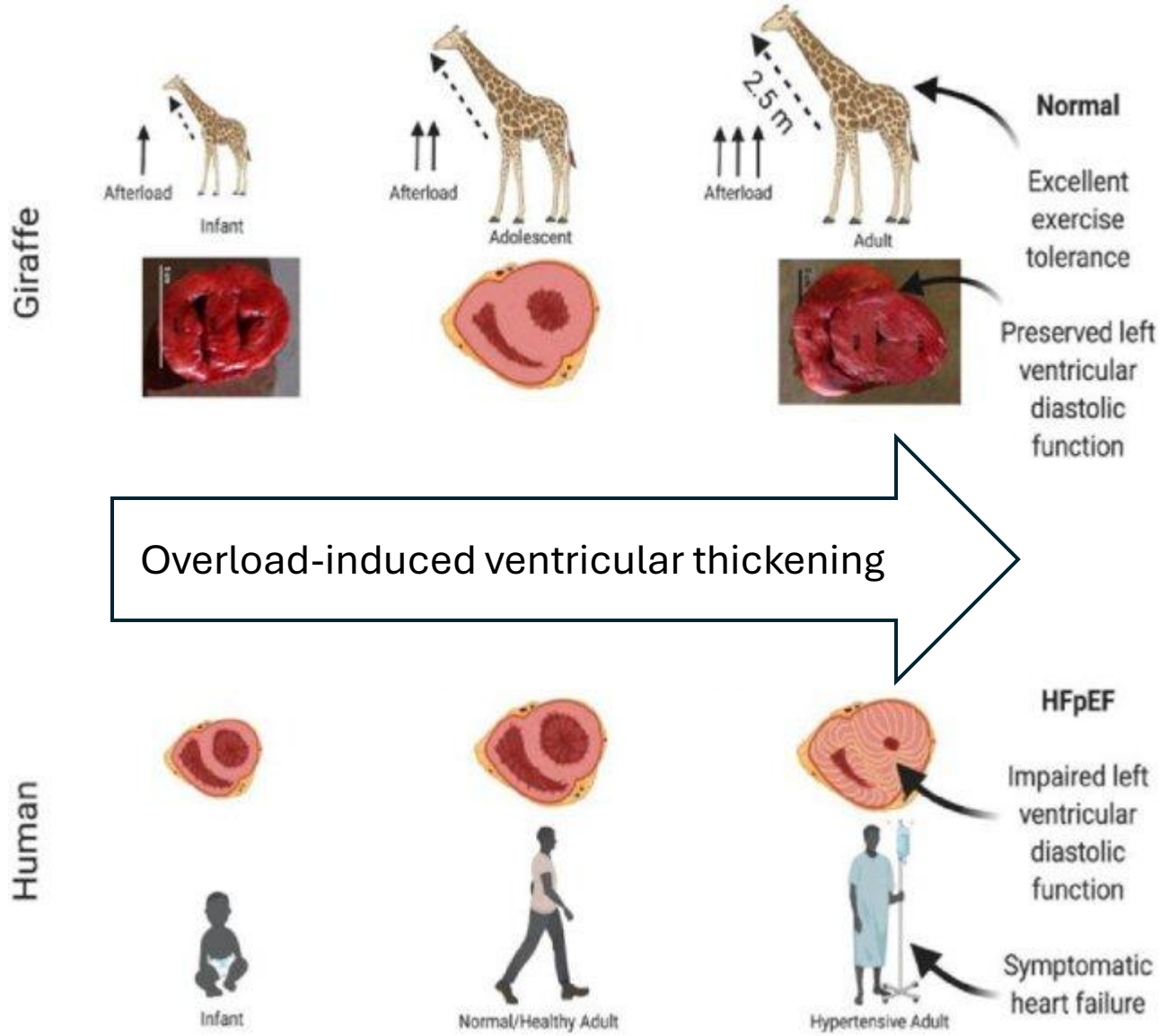

Natterson-Horowitz et al.,2021, Evolution Medicine and Publich Health

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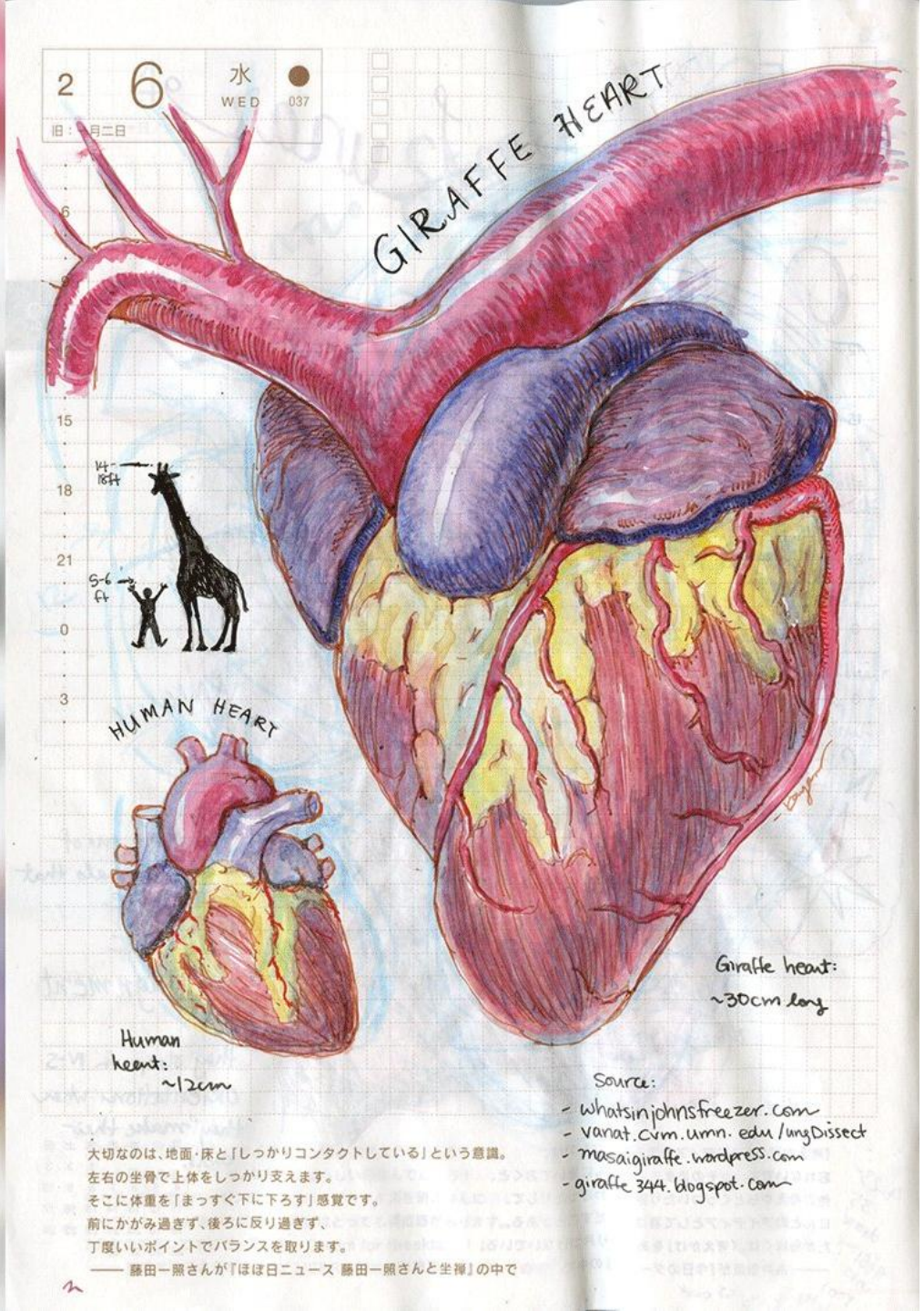

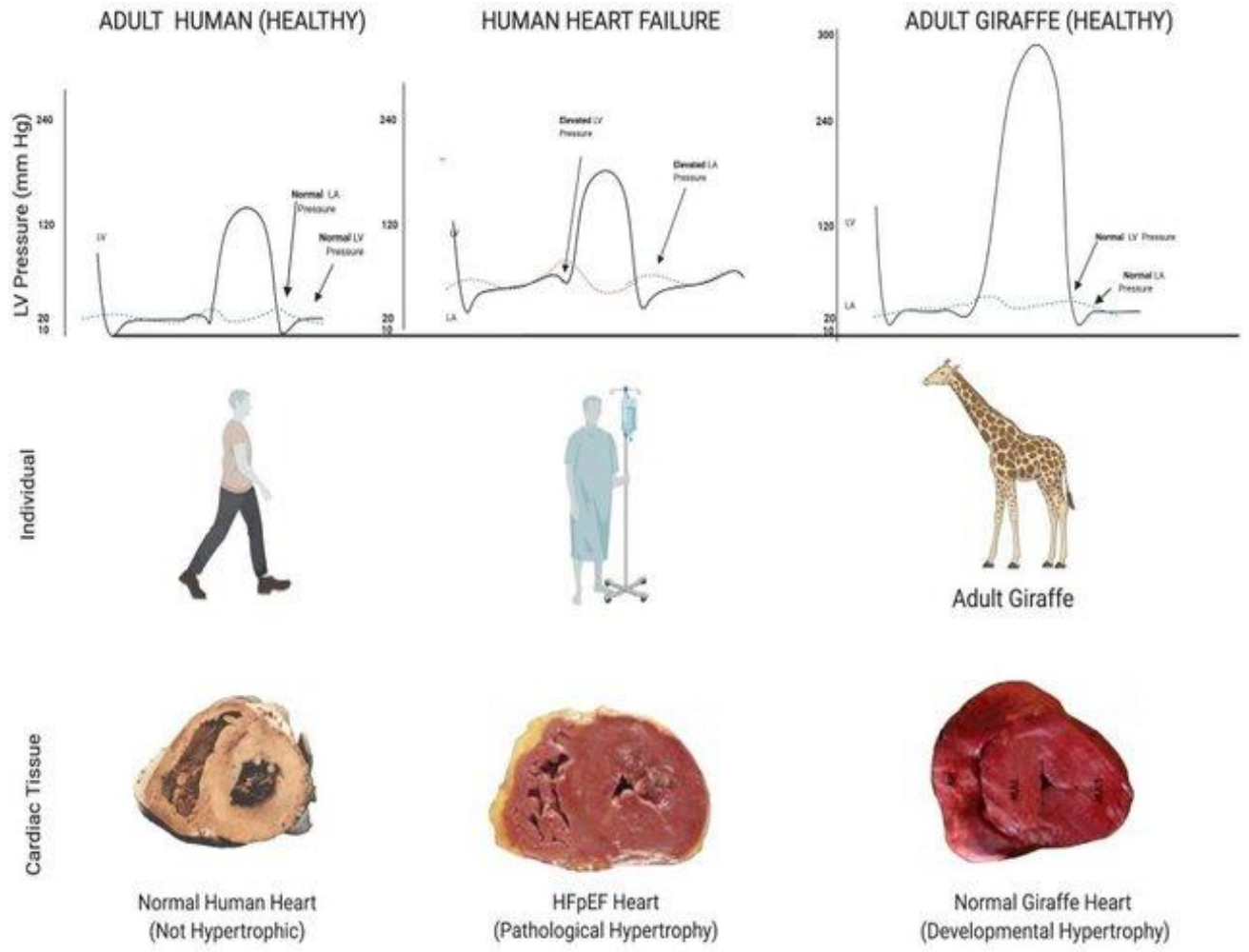

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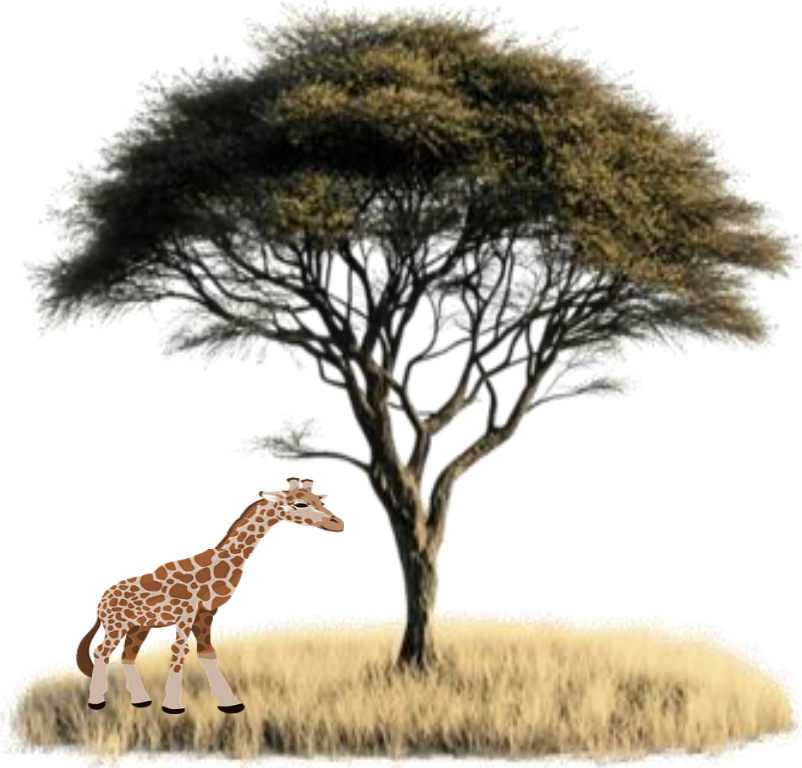
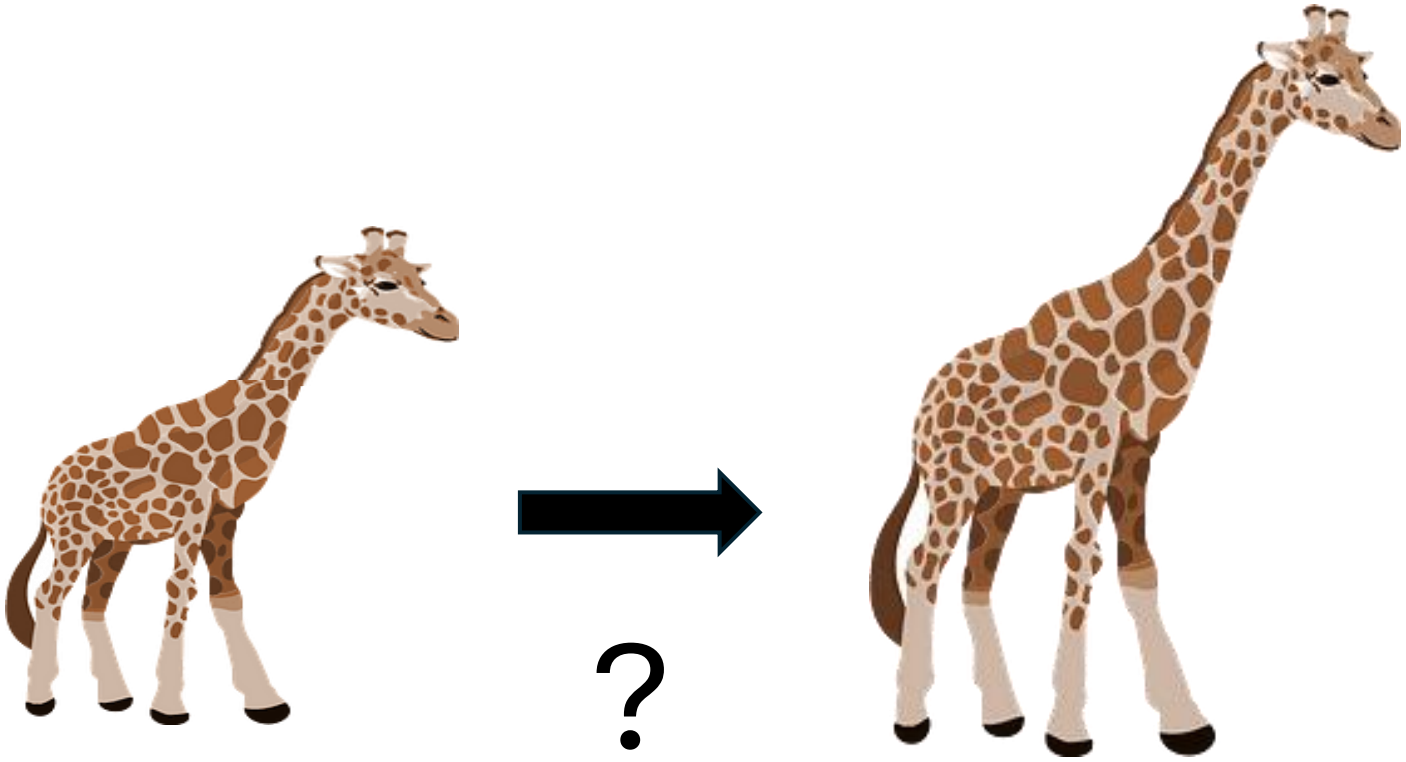
Evolutionary trade-offs limit unilmited directional selection



What are the dis/advantages of being taller?



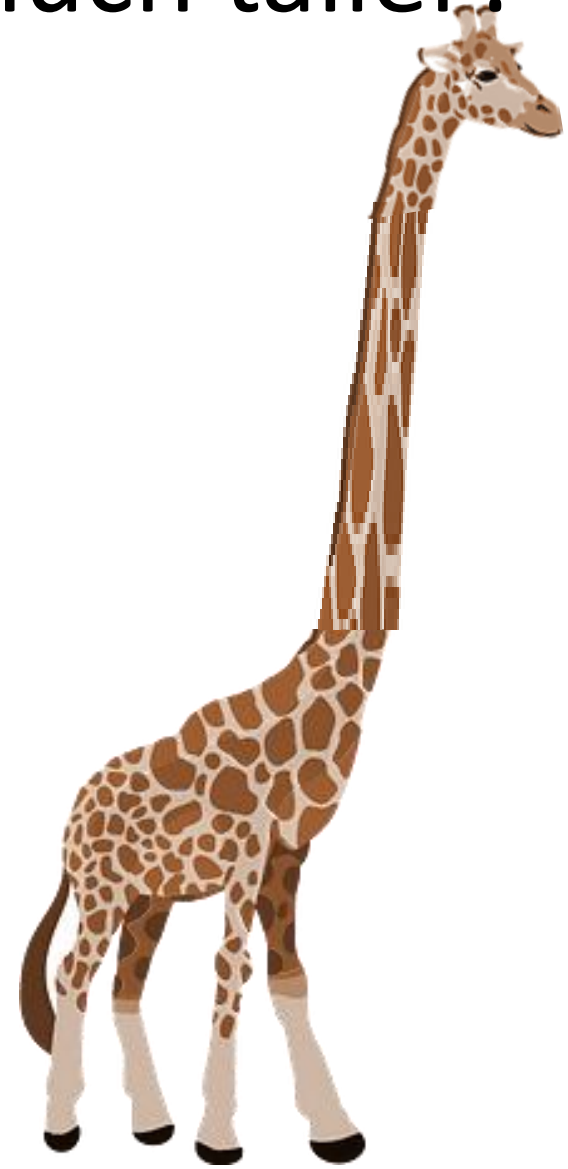
«Optimal» giraffe

What are the dis/advantages of being much taller?

+ food
-energy

«Optimal» giraffe

?



What are the dis/advantages of being much taller?

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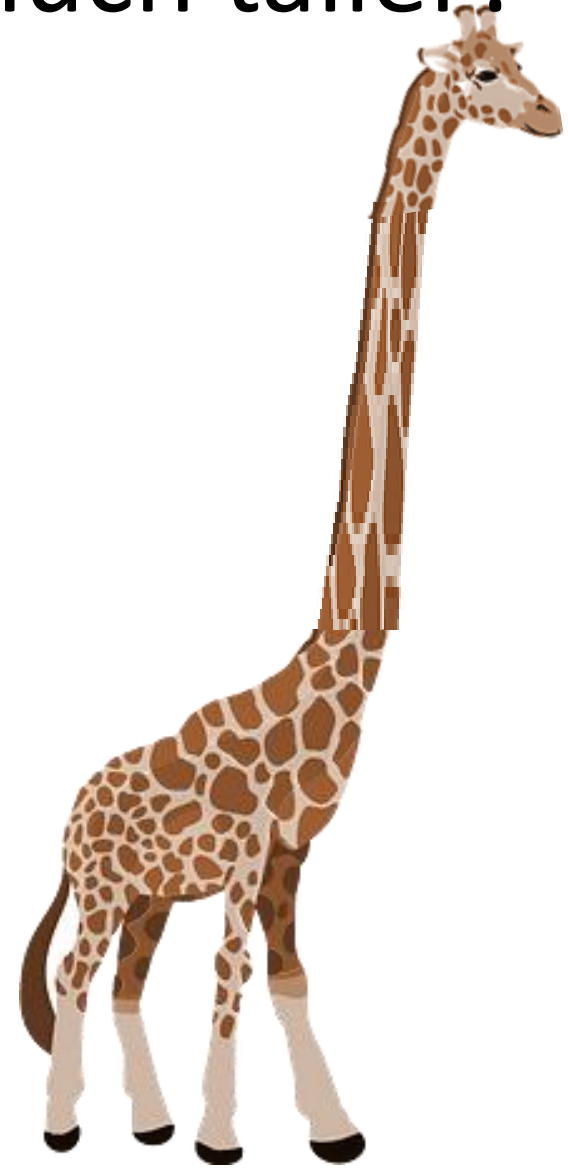
«Optimal» giraffe

≃ food
--energy
-longevity



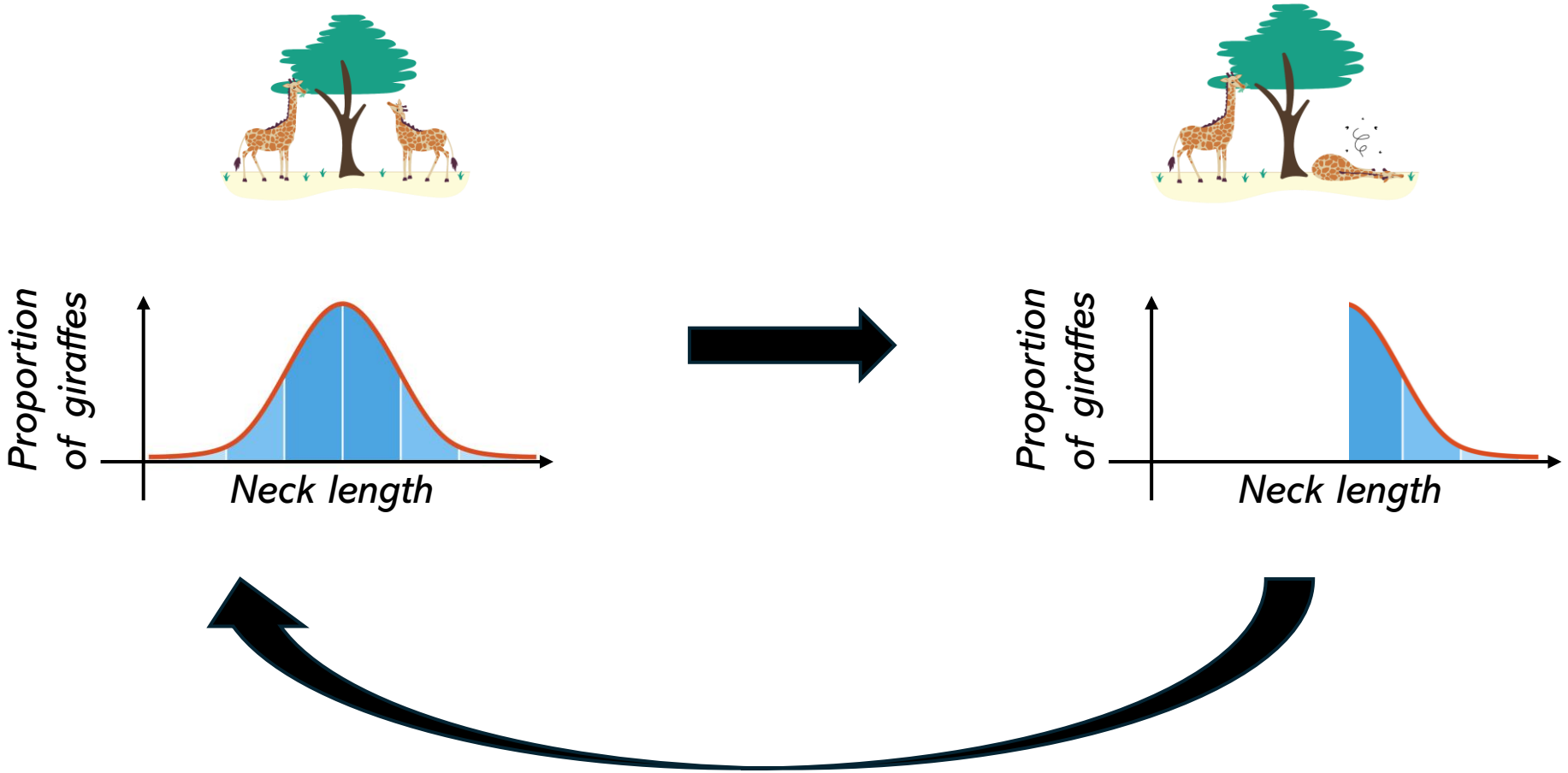
How do we model this?

+ food
-energy

«Optimal» giraffe

≃ food
--energy
-longevity

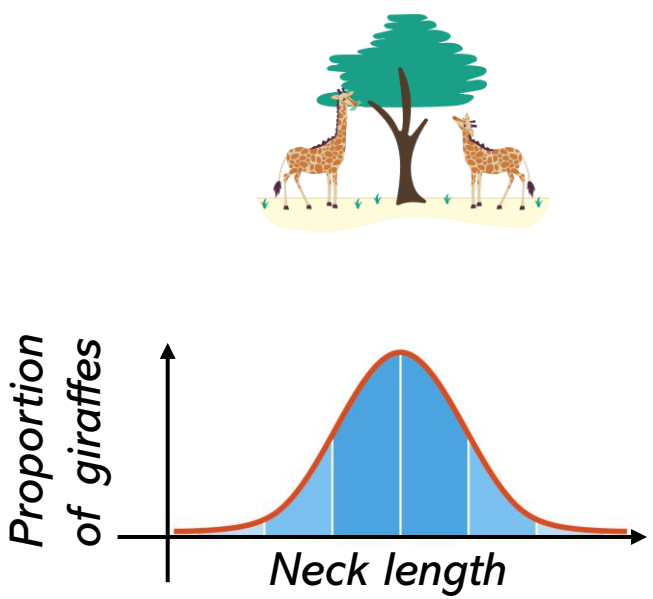
What would you change that in the model?

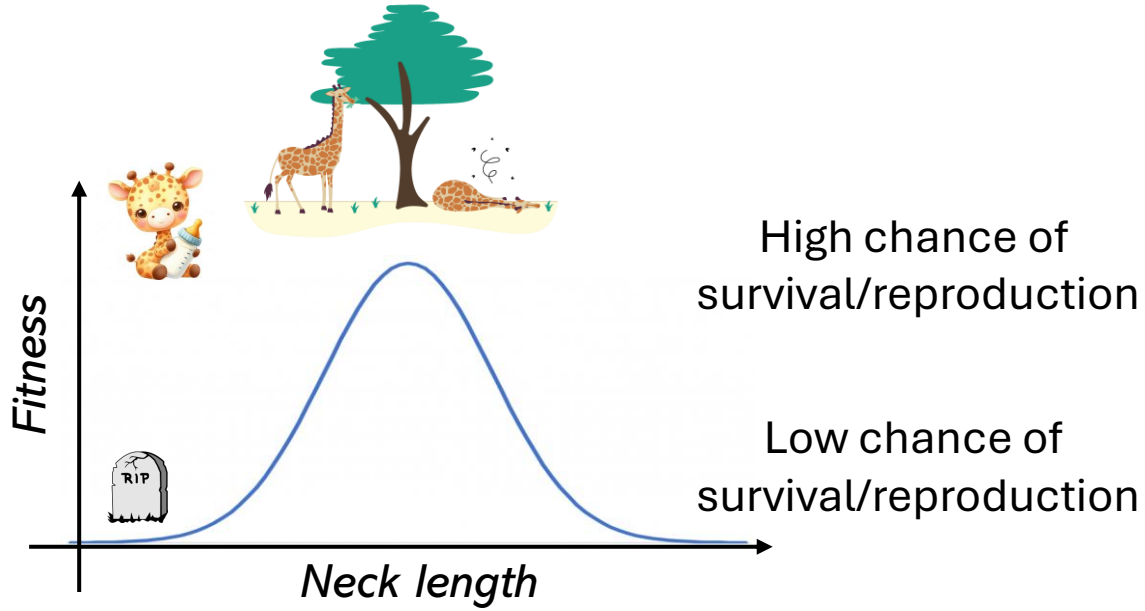


Reproduction with «correct inheritance» (heritability>0, no «blending of inheritance», new variation via mutations)

Evolutionary fitness

Fitness represents an organism's ability to survive, reproduce, and pass its genes to the next generation relative to others in its population





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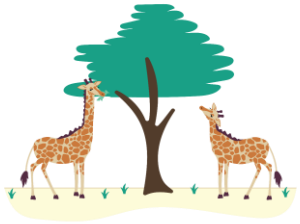
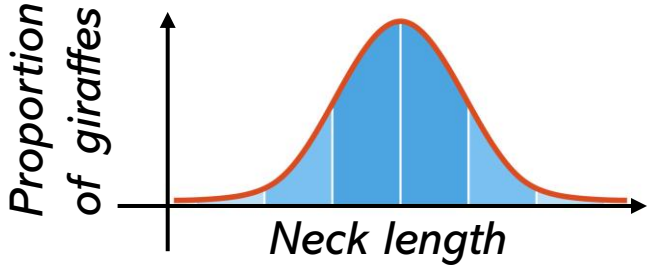
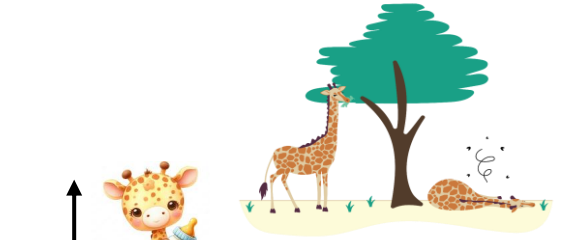
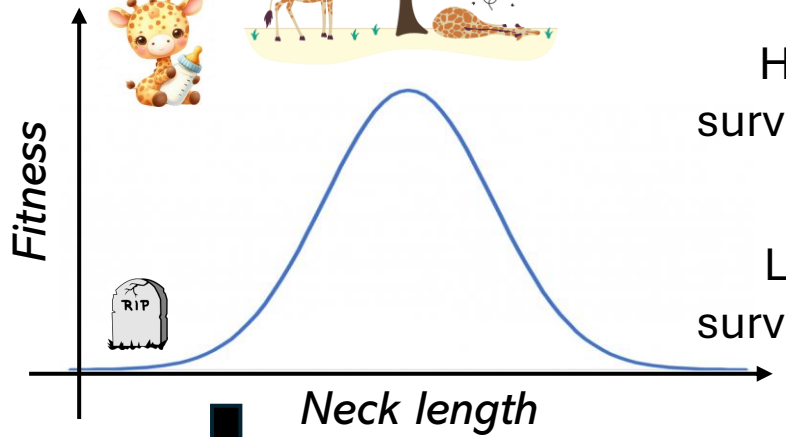


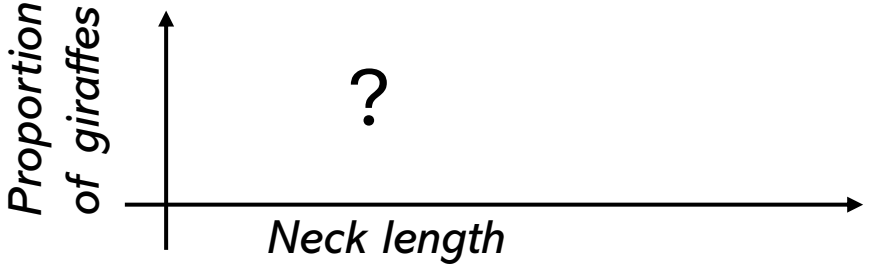


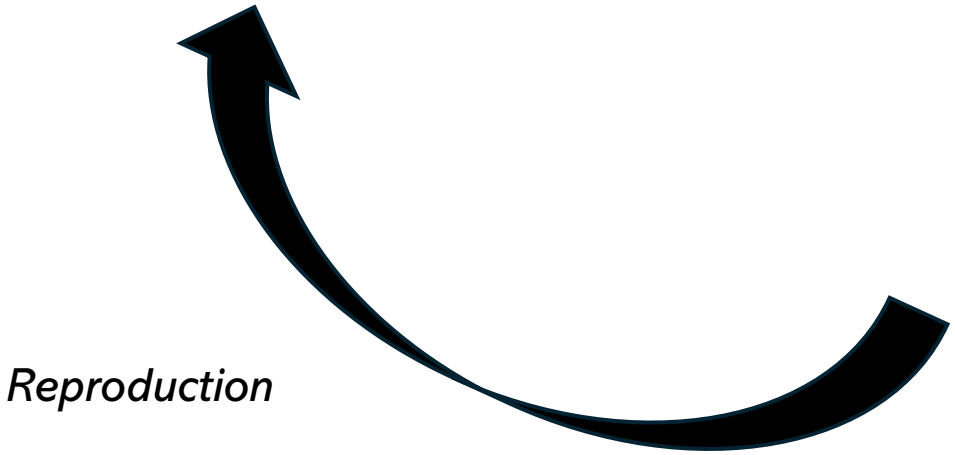




High chance of survival/reproduction

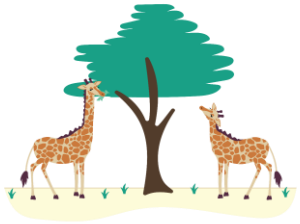
Low chance of survival/reproduction

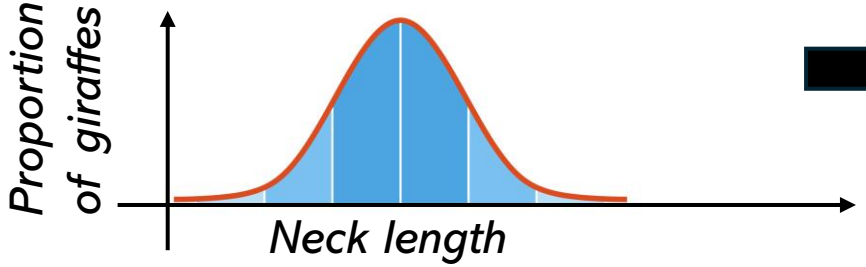


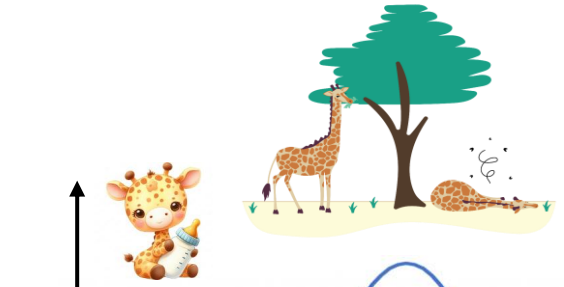


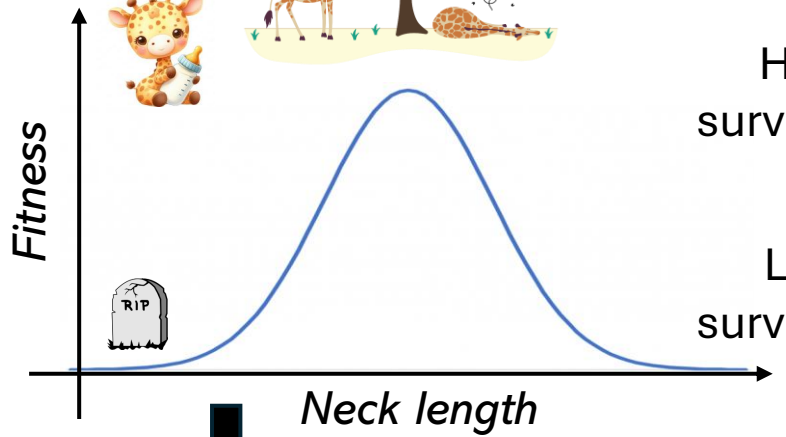
Evolutionary fitness

Fitness represents an organism's ability to survive, reproduce, and pass its genes to the next generation relative to others in its population









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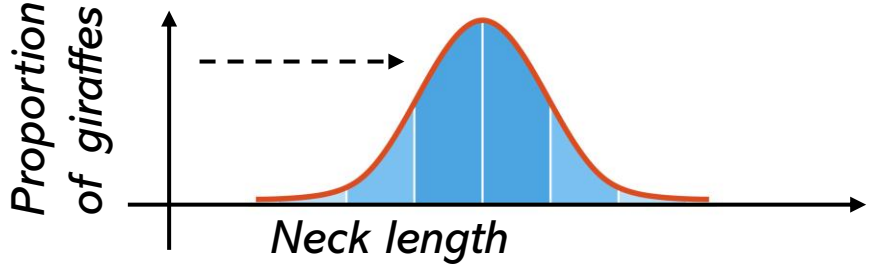

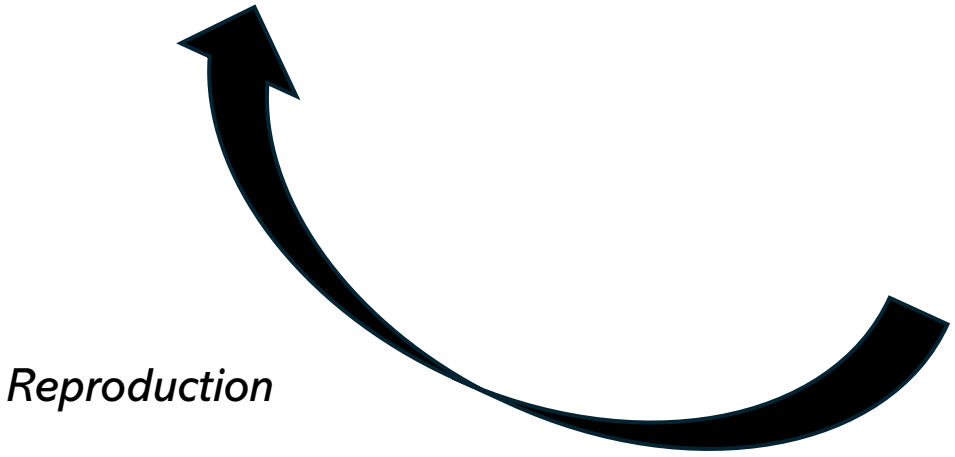

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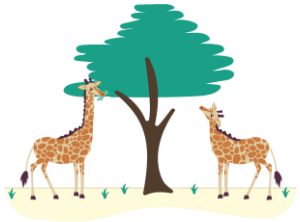

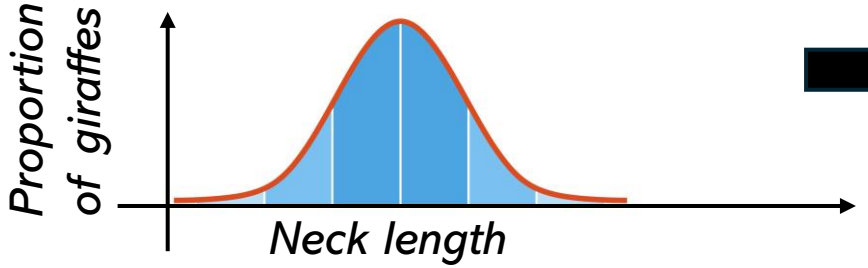

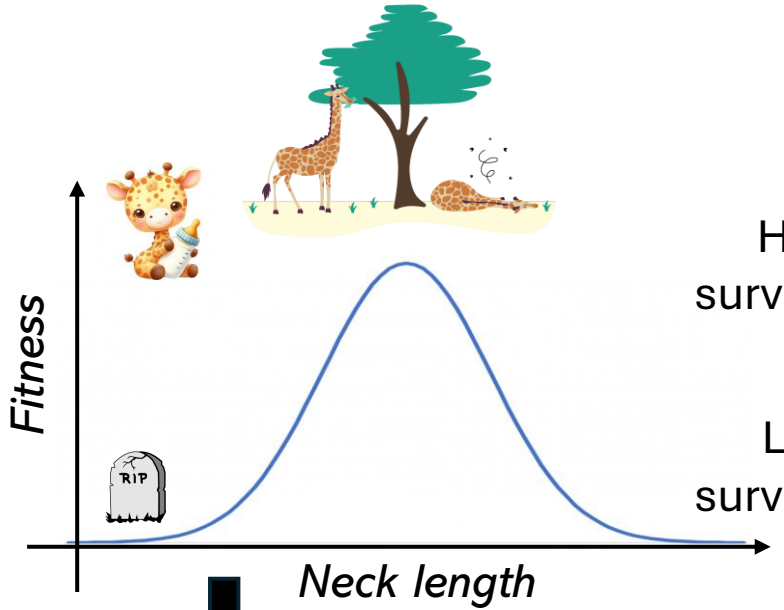

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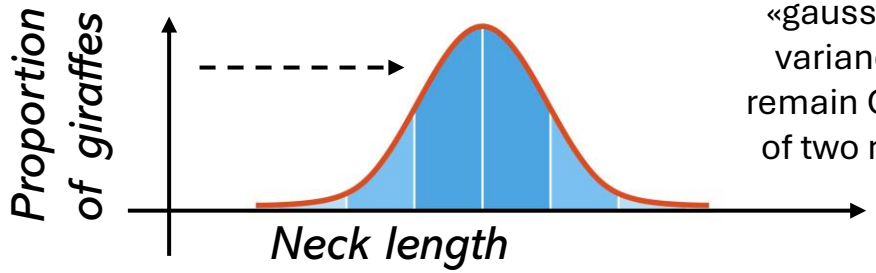
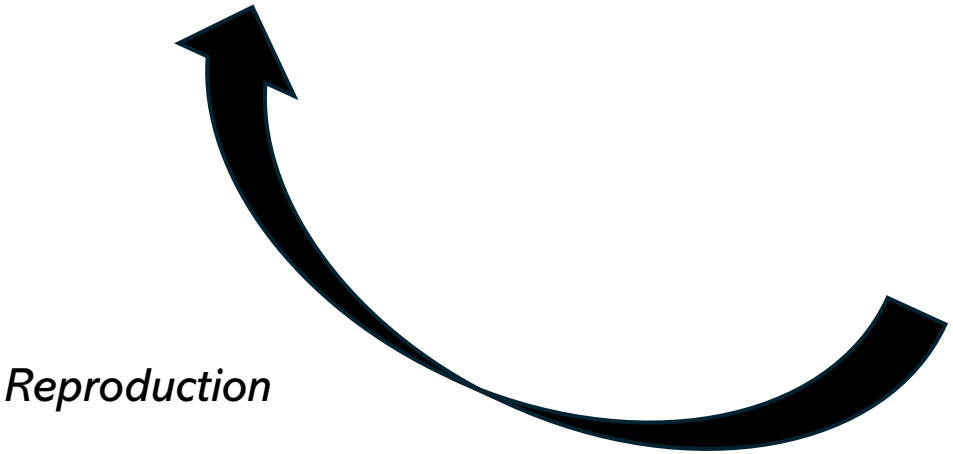
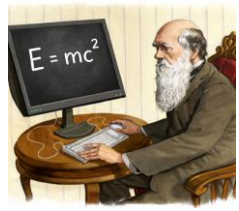
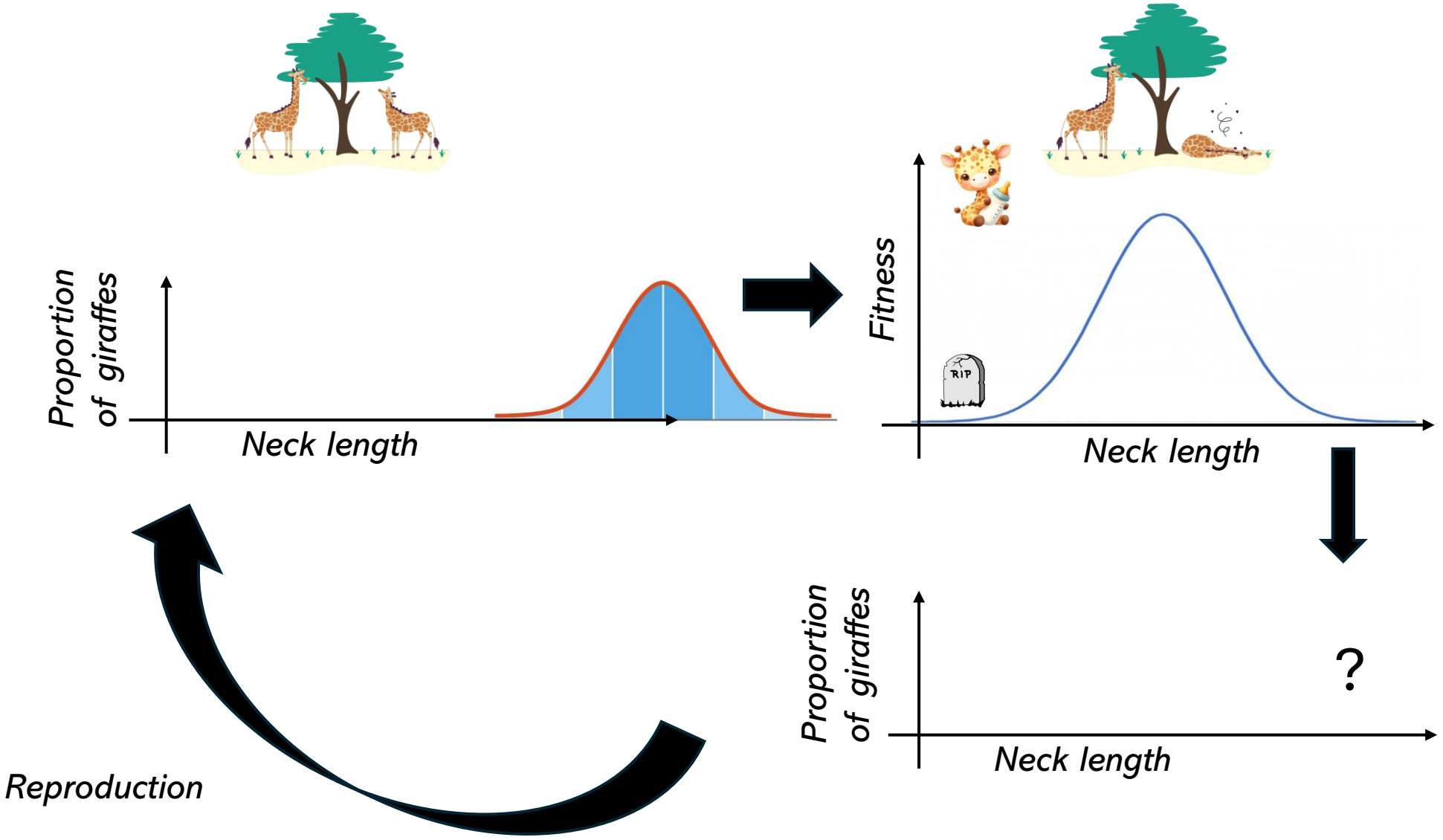


Near a more-or-less «gaussian» fitness peak the variance of the population remain Gaussian: the product of two normal distribution is still normal!

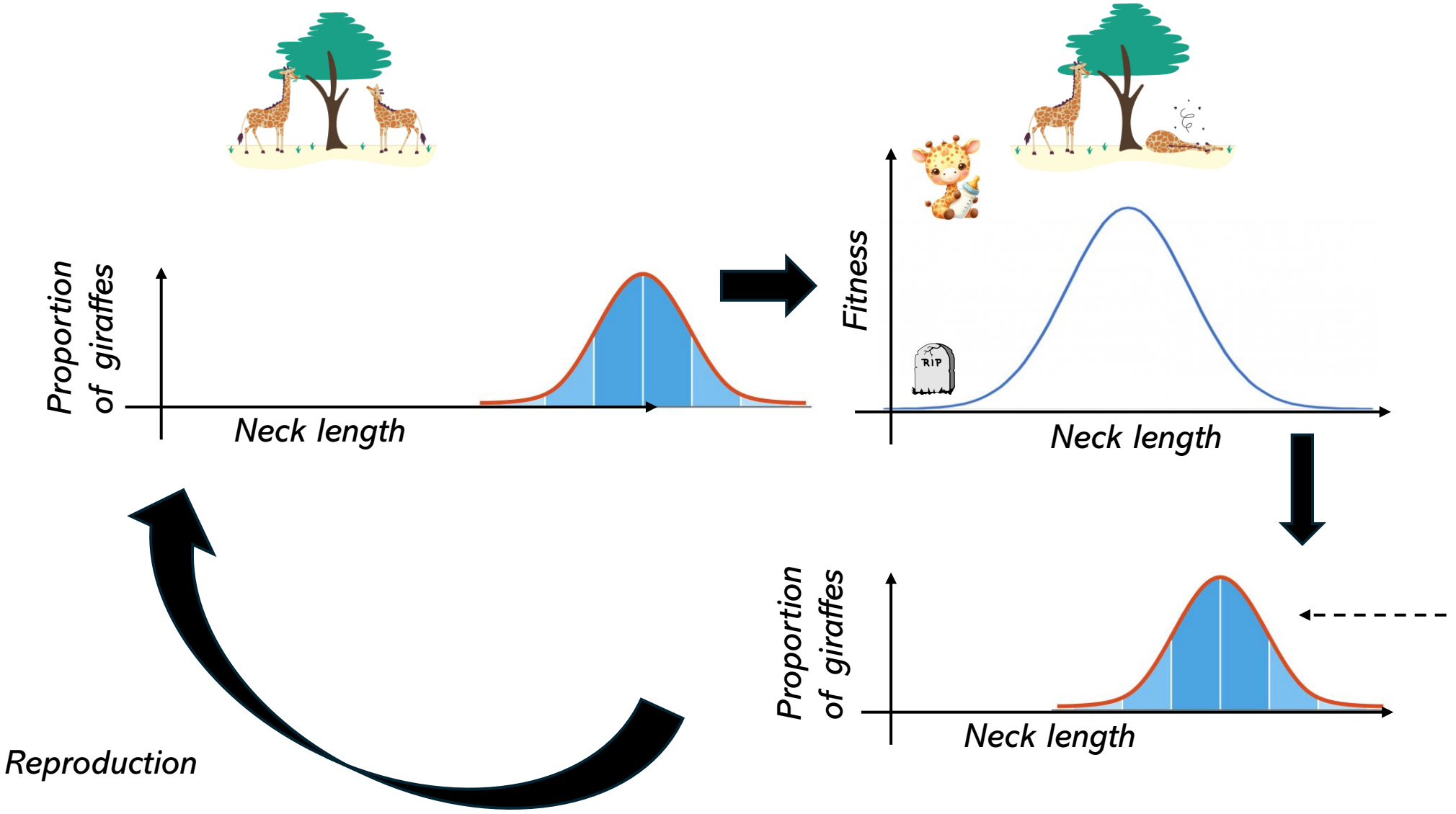




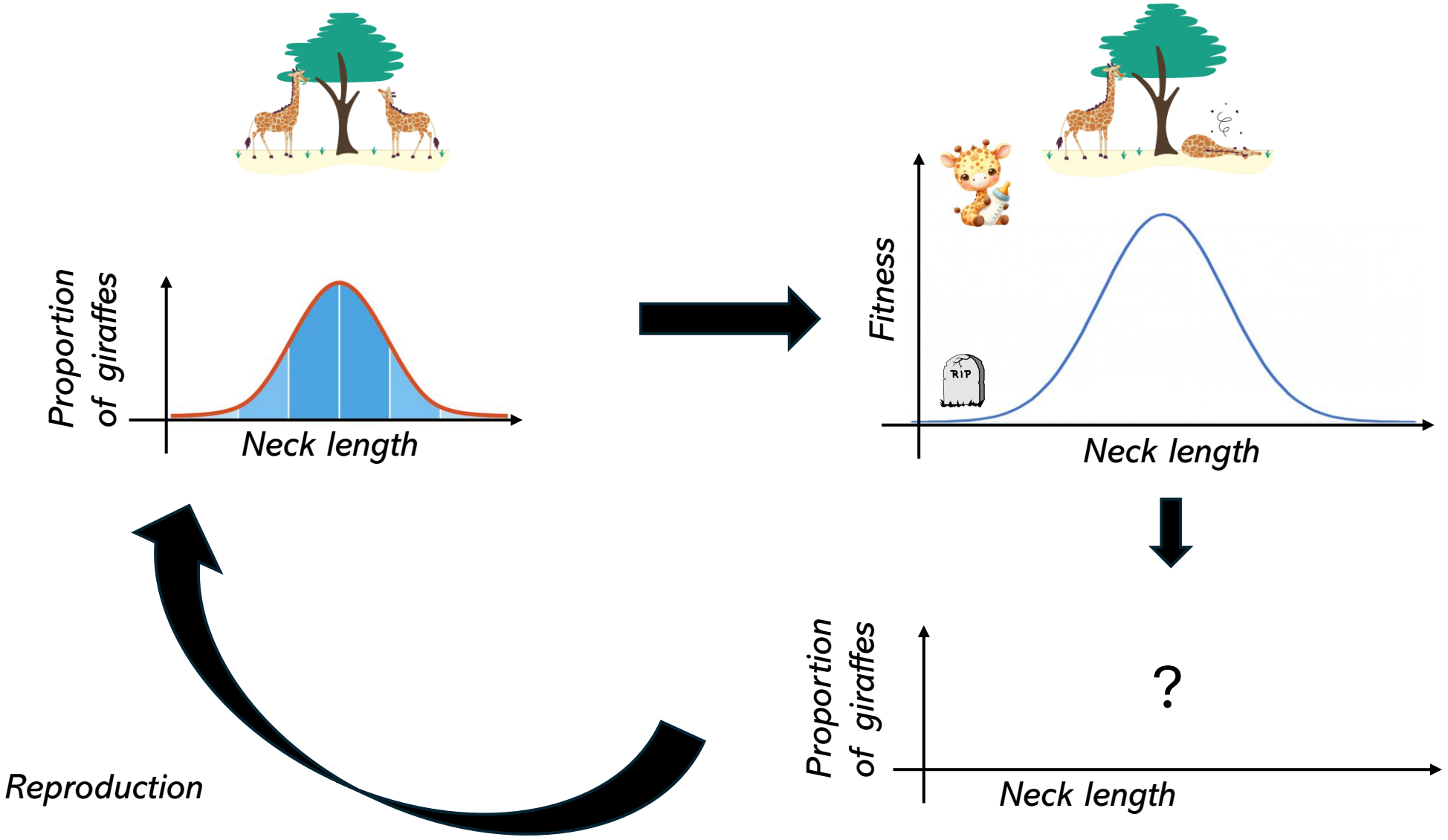
What will happen now?



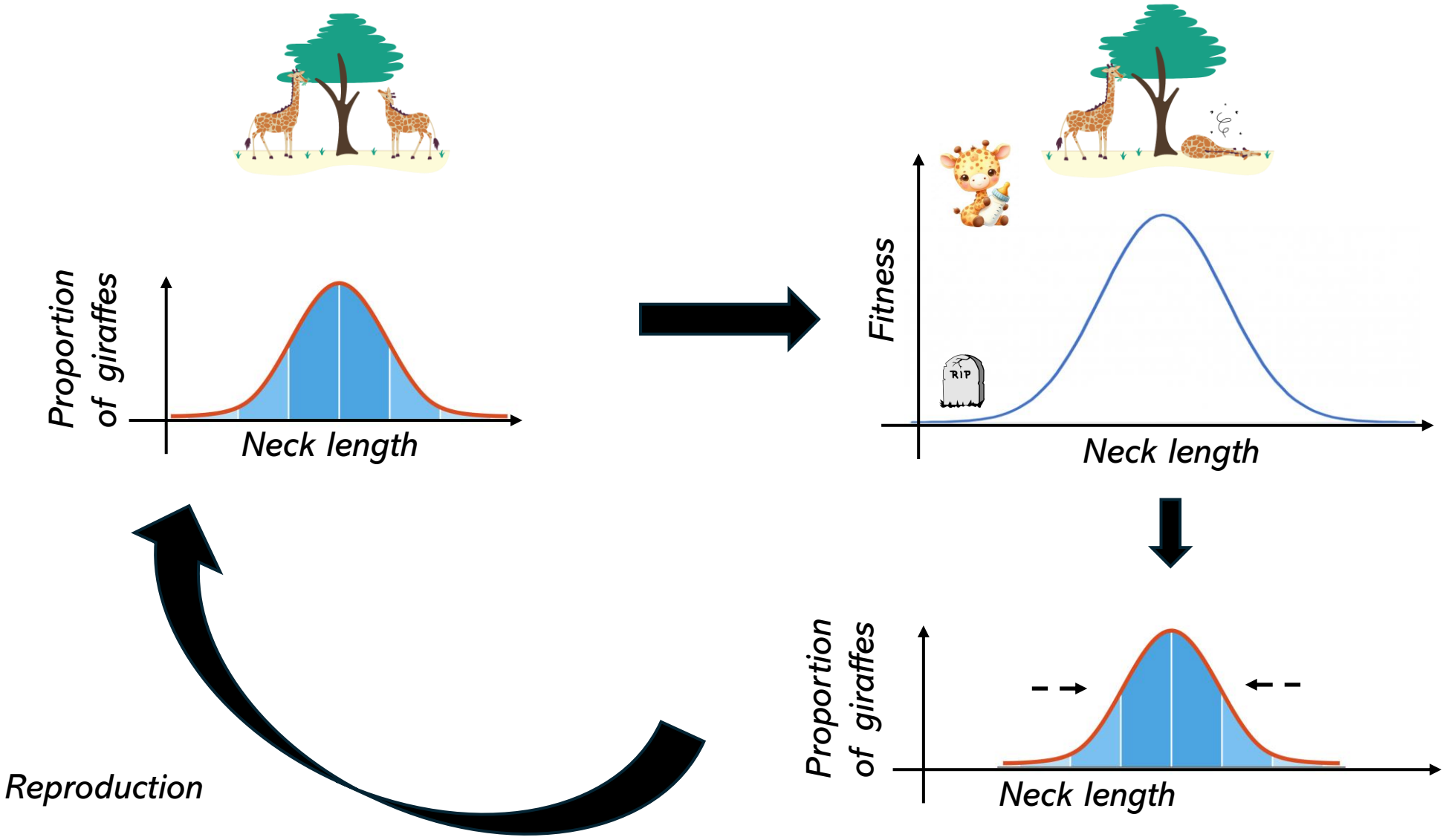
What will happen now?



What will happen now?



Stabilizing selection



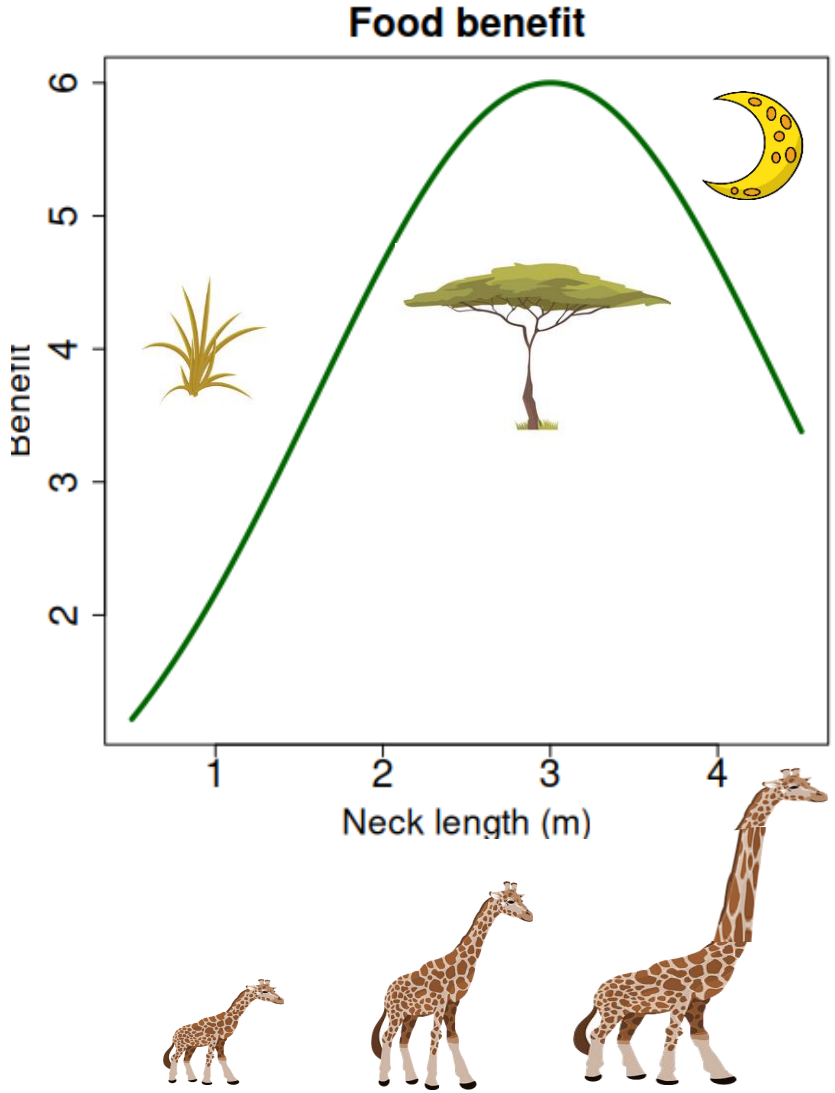
How do we model this?

+ food
-energy

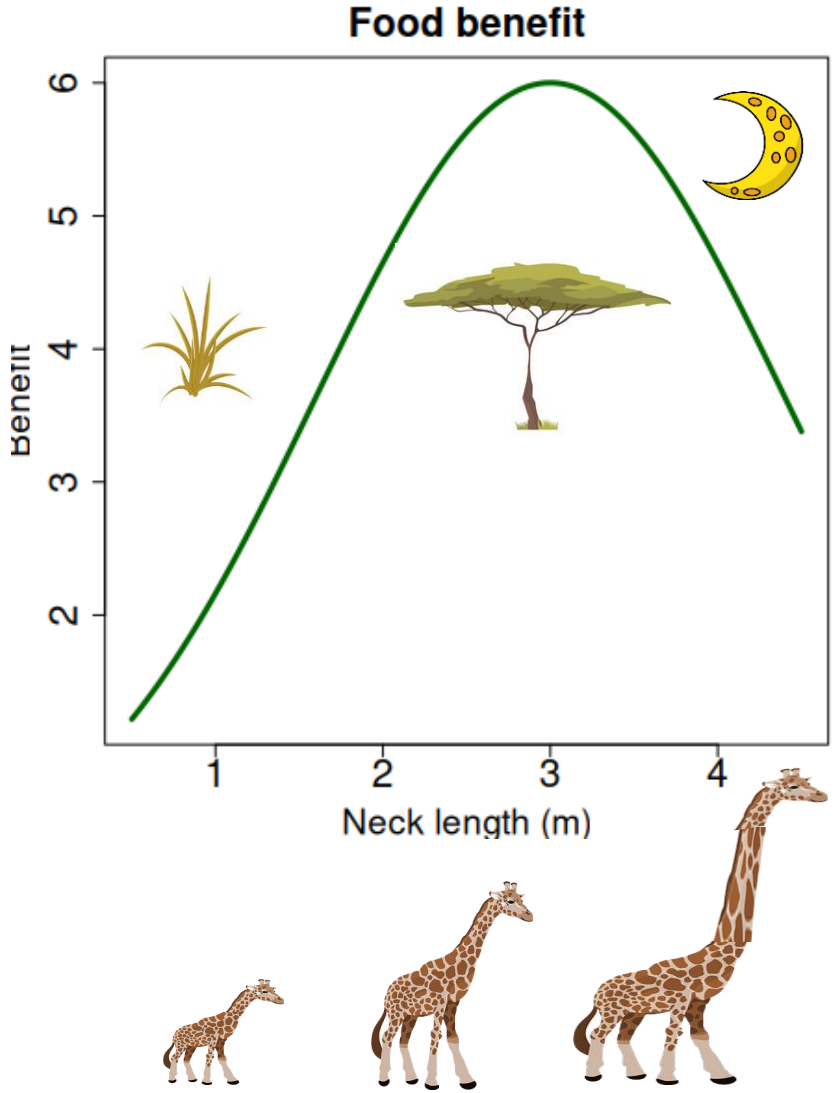
«Fittest» giraffe

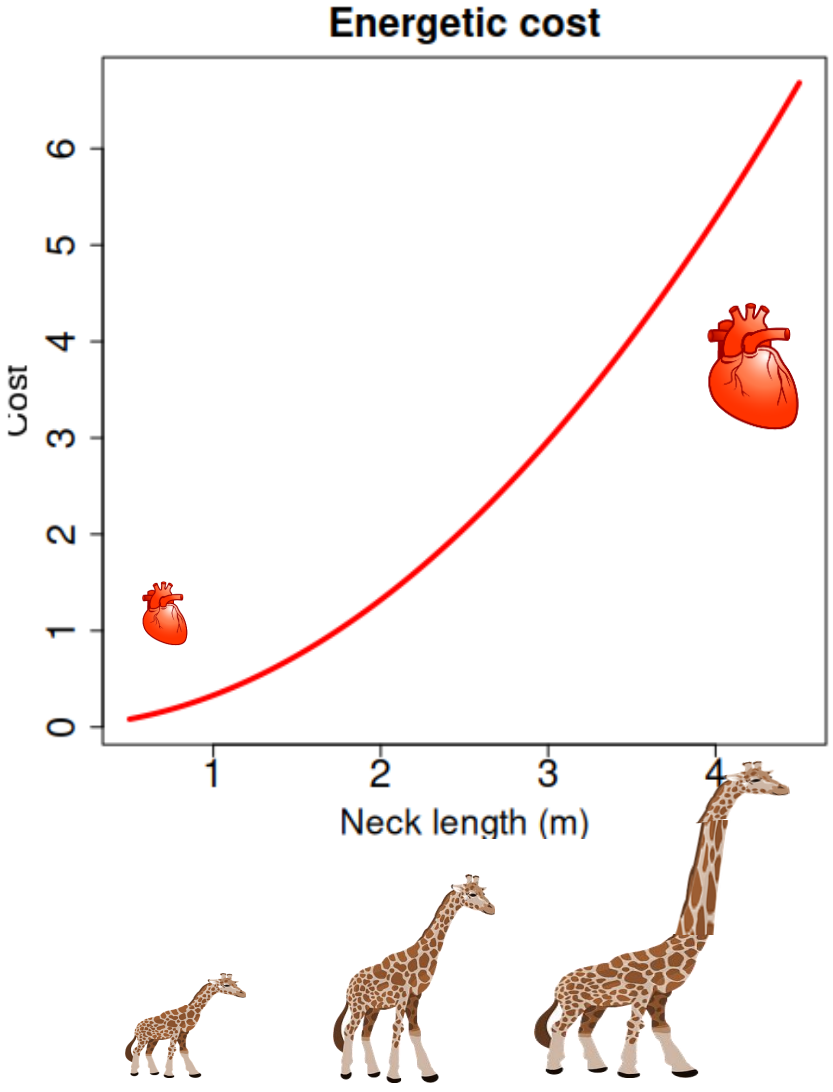
≃ food
+energy
+longevity

Building our evolutionary-trade-off

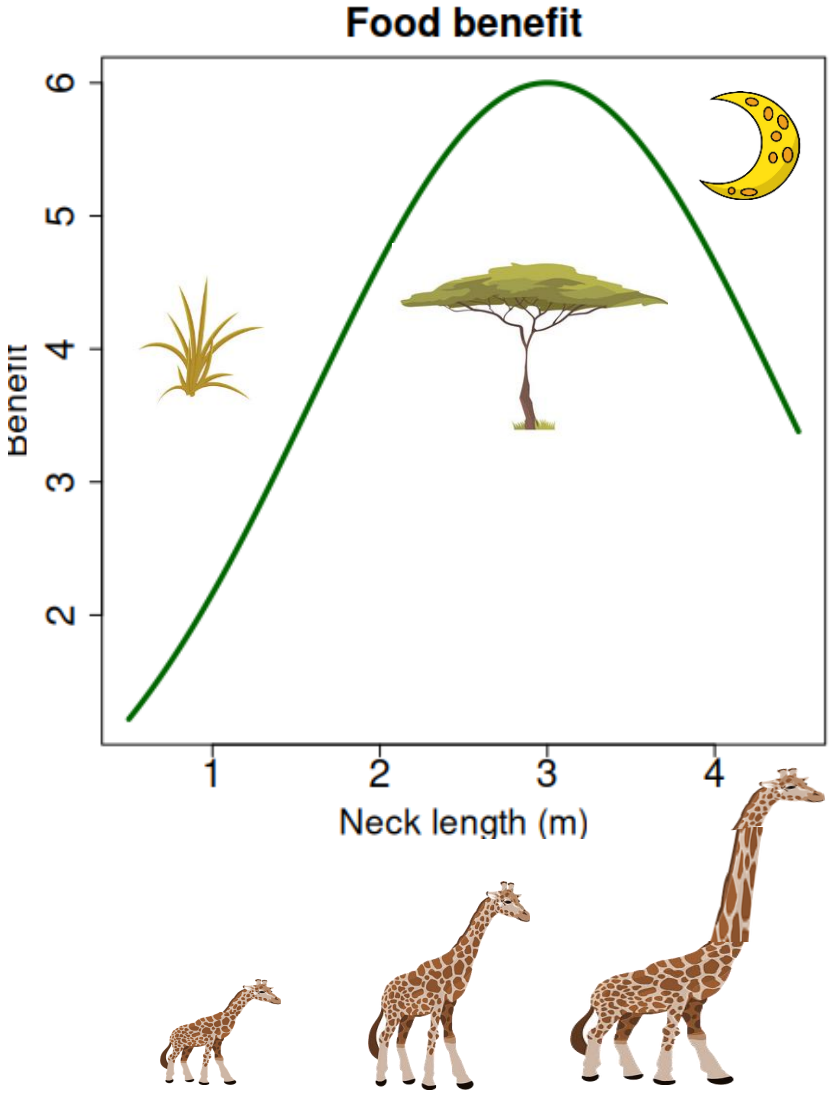


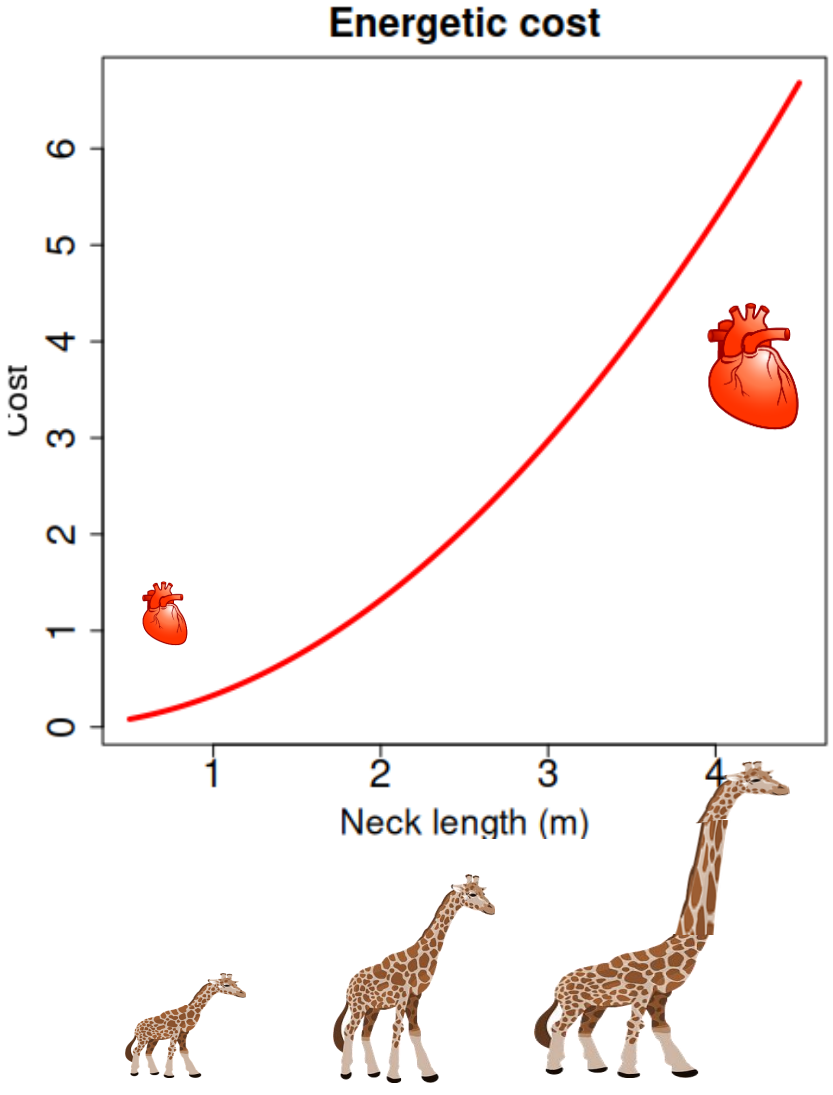
Building our evolutionary-trade-off

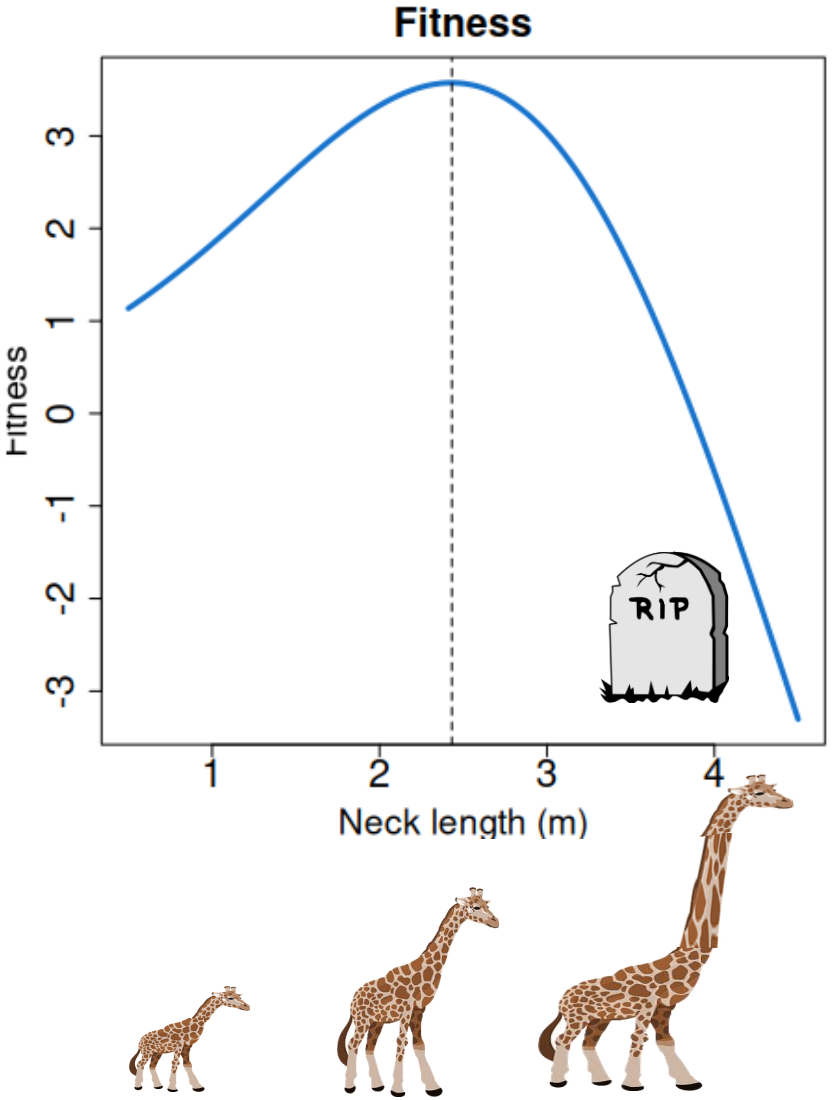




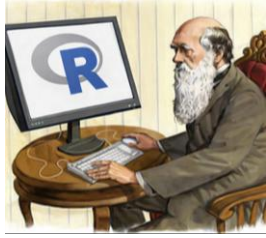
Fitness = benefits - costs







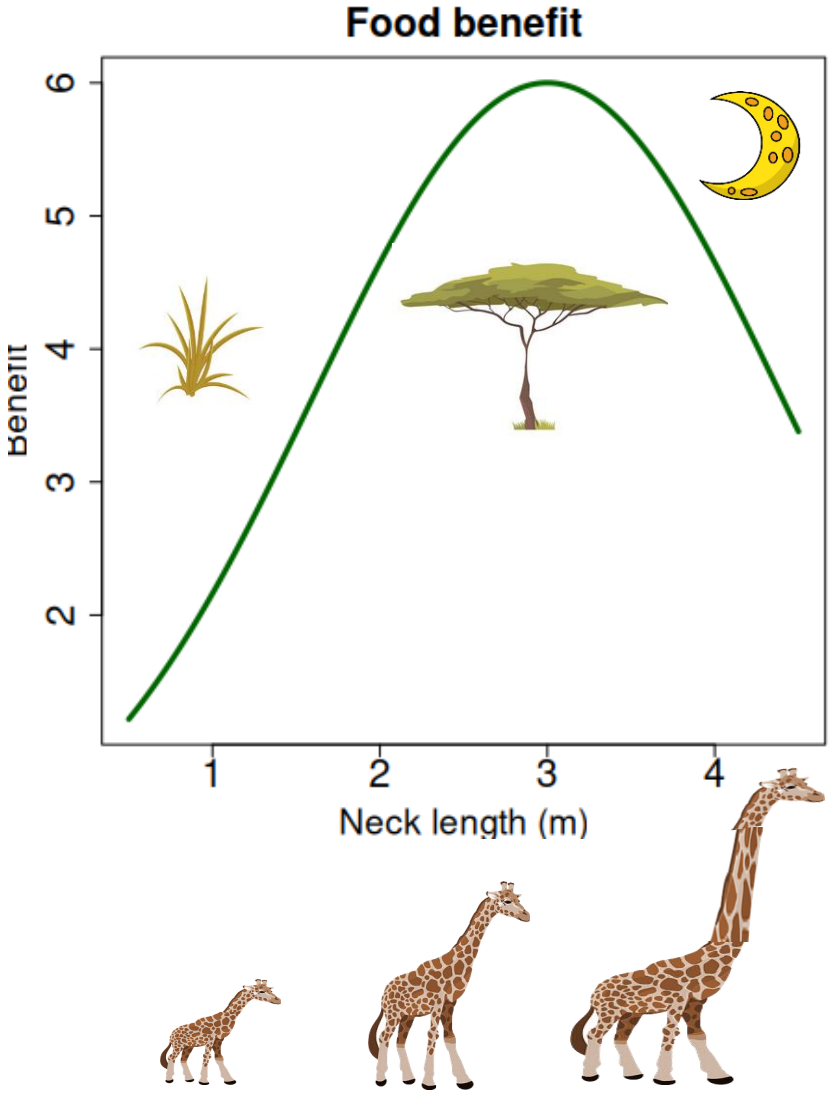
Fitness = benefits - costs

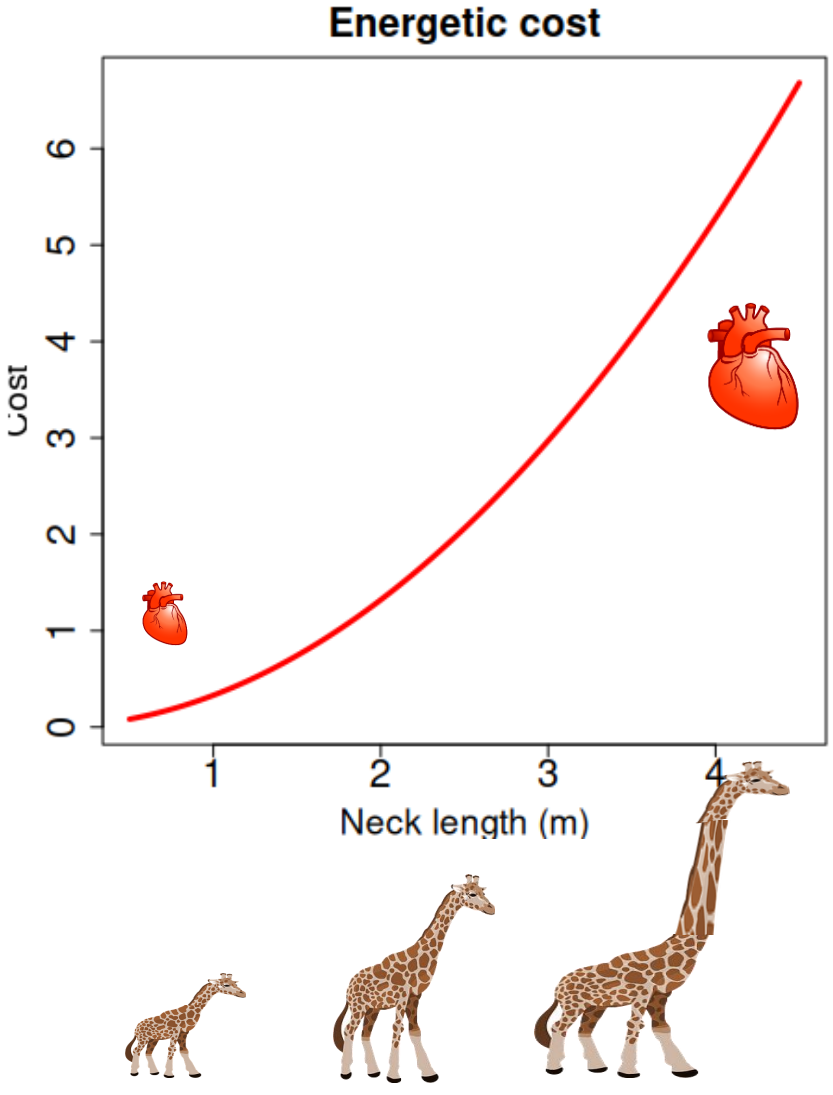


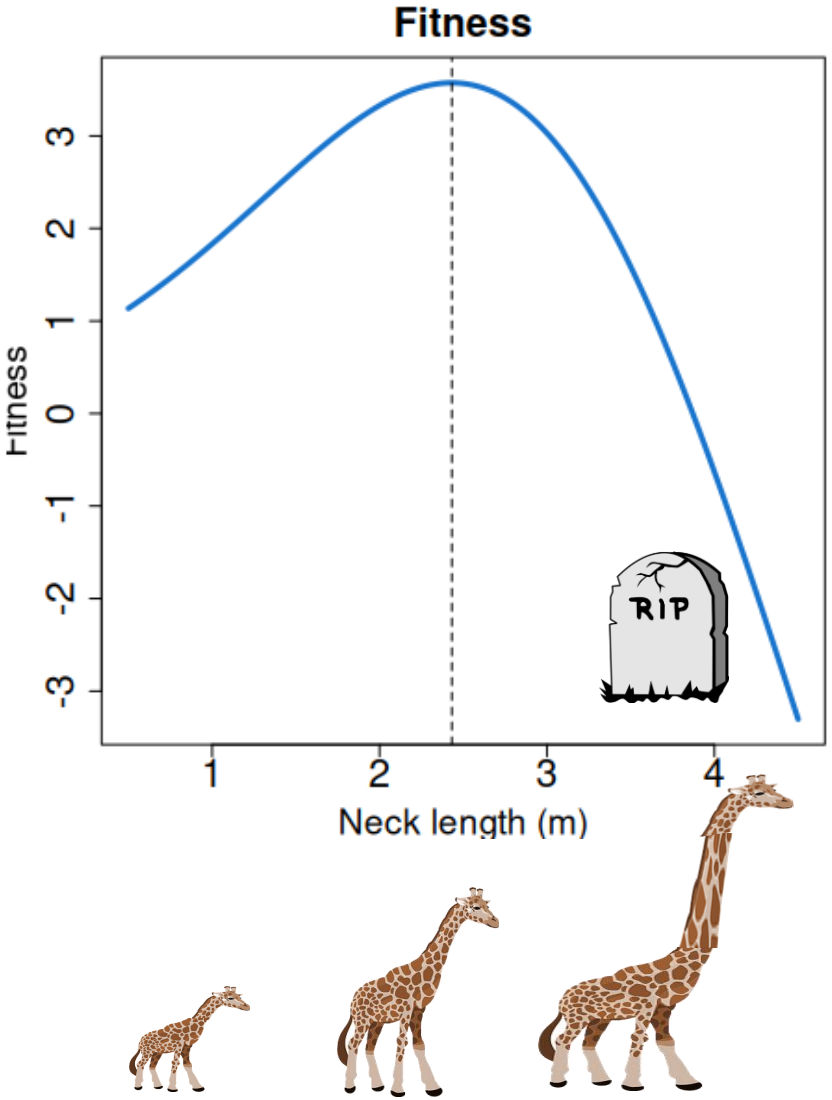

```
benefit=A*exp(-(L-mu)^2/(2*sigma^2))
```

```
cost=c*L^2
```

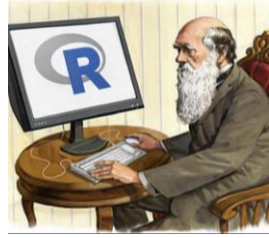
```
Fitness = benefit - cost
```

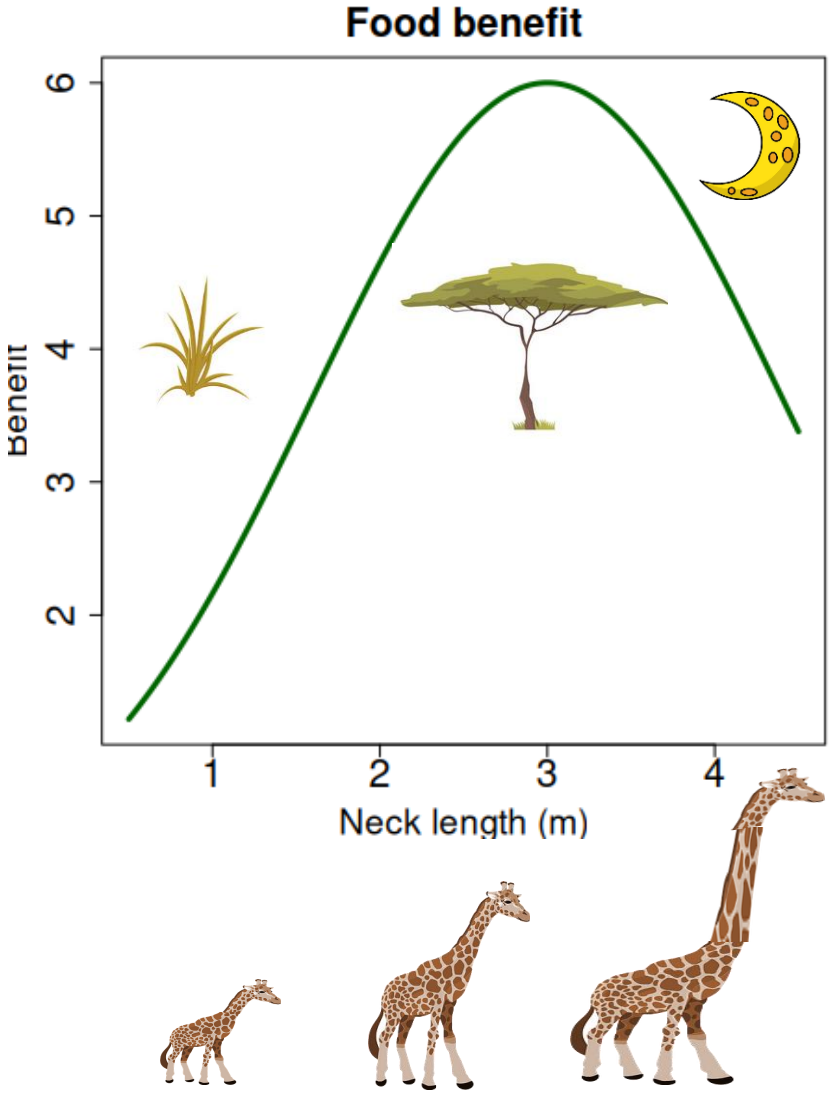






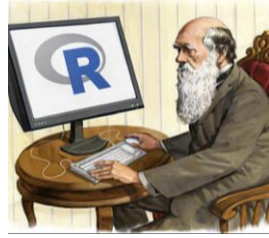
Fitness = benefits - costs

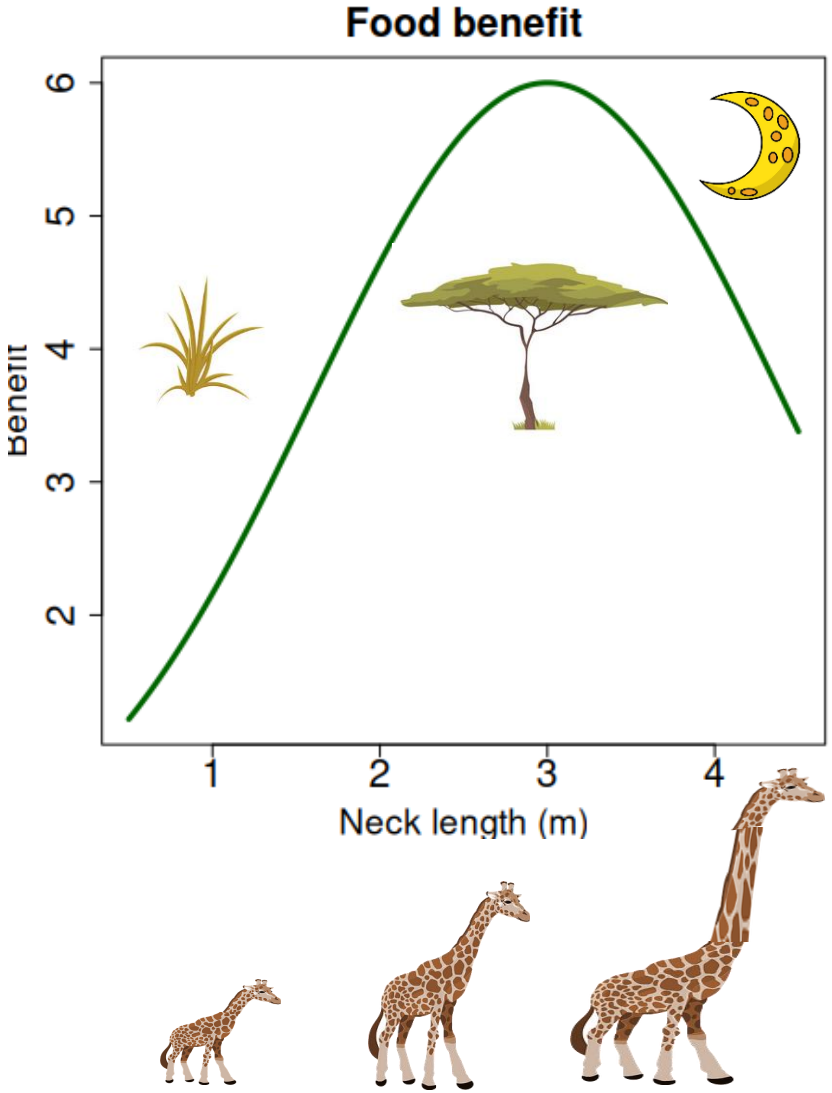


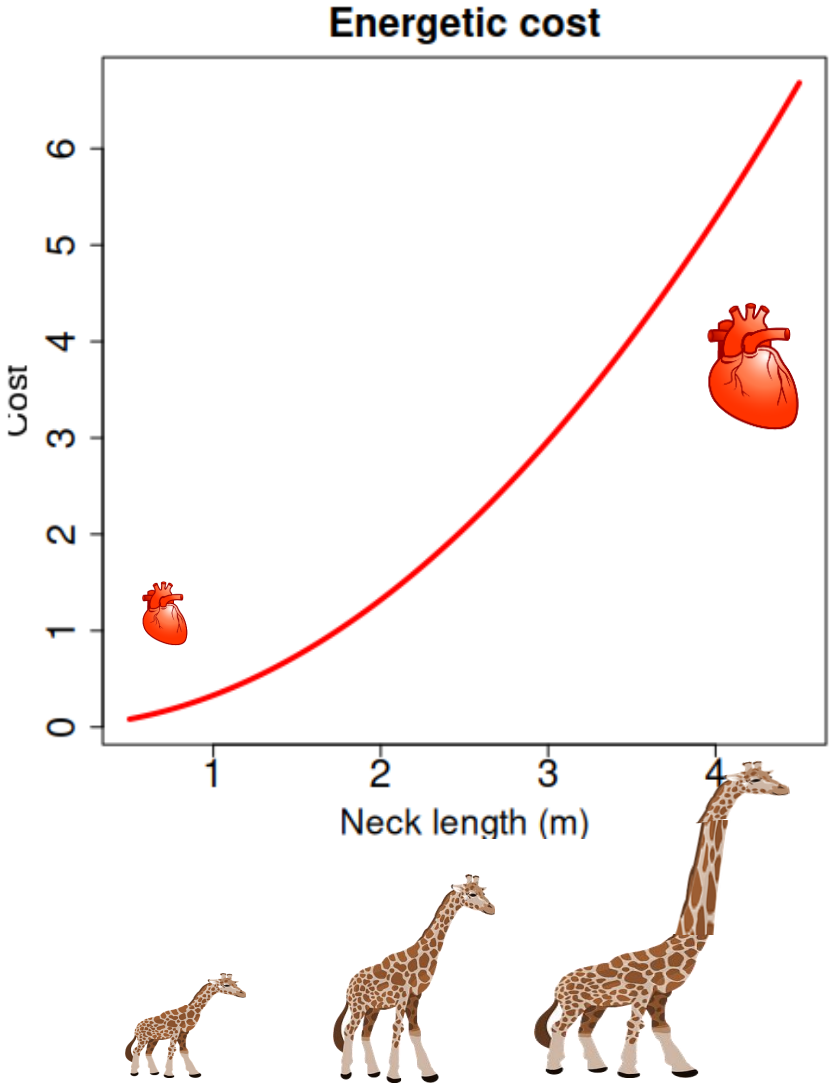



```r
A <- 6 #size of the benefit
mu <- 3.0 # ~ average tree height
sigma <- 1.4 # ~ variance of the trees that giraffes can eat

# ---- functions ----
benefit <- A * exp(-(L - mu)^2 / (2 * sigma^2))
```

Fitness = benefits - costs

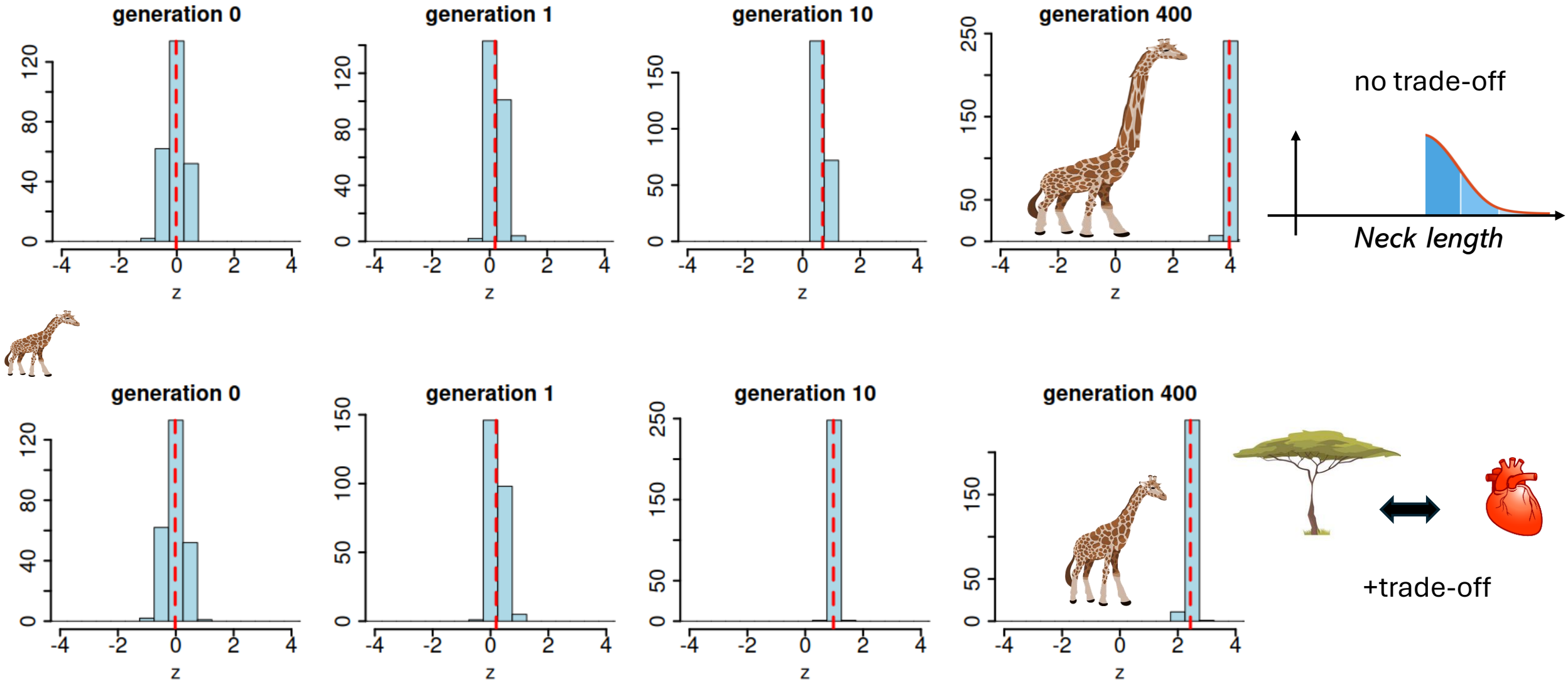




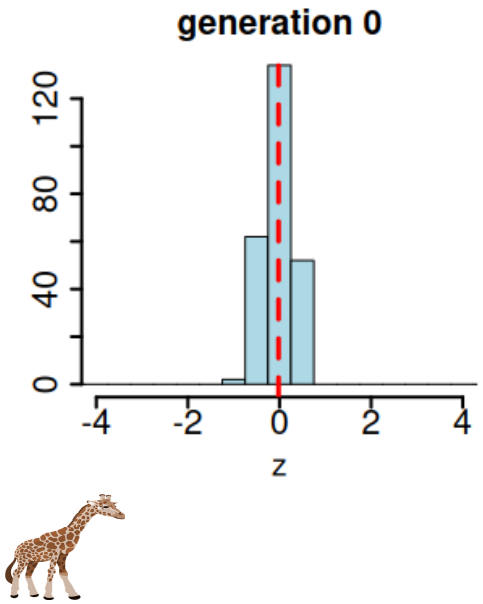


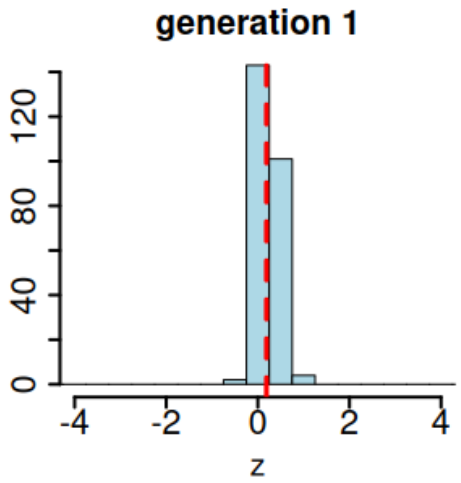

```r
A <- 6 #size of the benefit
mu <- 3.0 # ~ average tree height
sigma <- 1.4 # ~ variance of the trees that giraffes can eat
c <- 0.33
# ---- functions ----
benefit <- A * exp(-(L - mu)^2 / (2 * sigma^2))

cost <- c * L^2

fitness <- benefit - cost
```

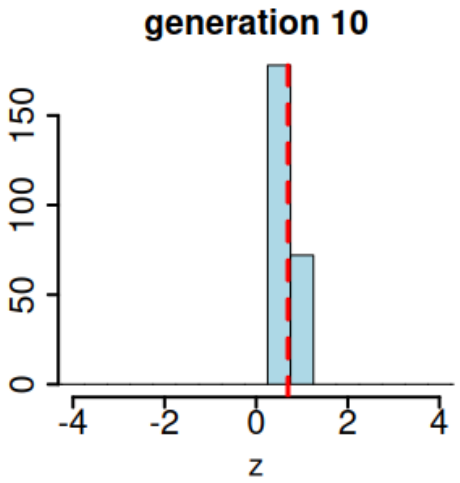
Evolutionary trade-offs constrain phenotypes

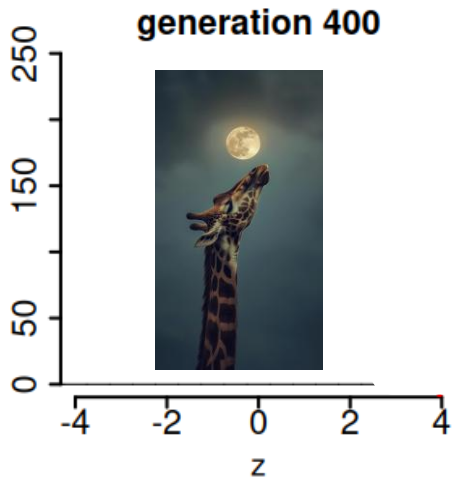


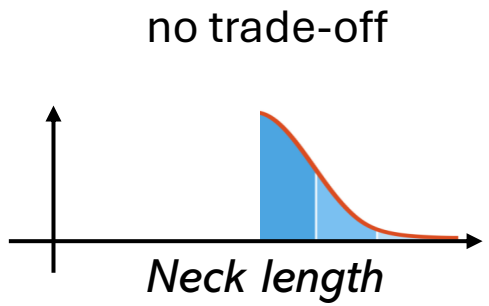
Directional evolution does not proceed forever

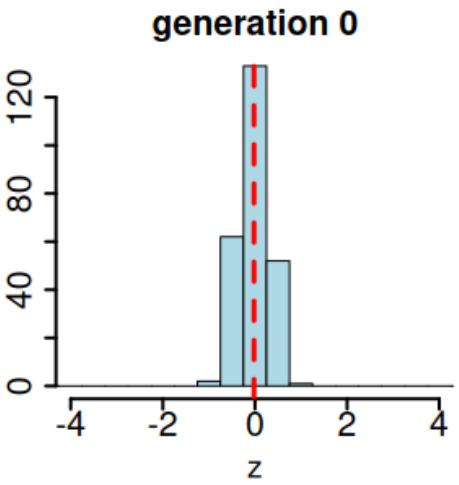


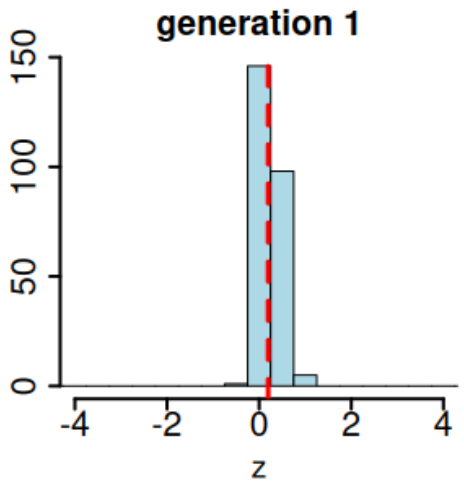


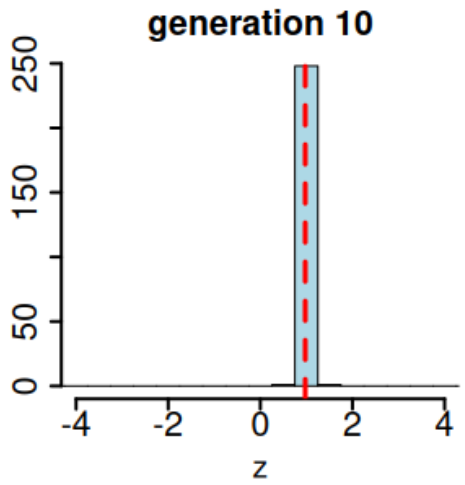


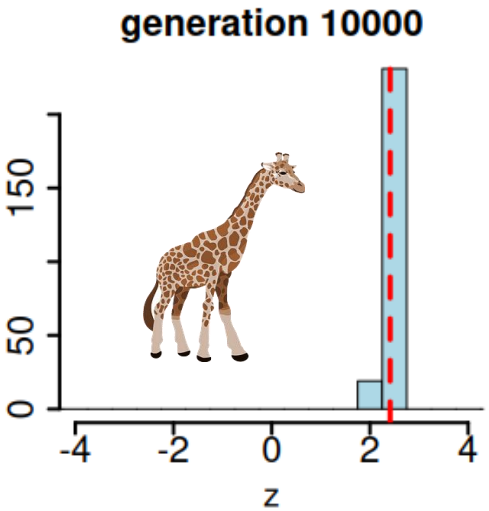


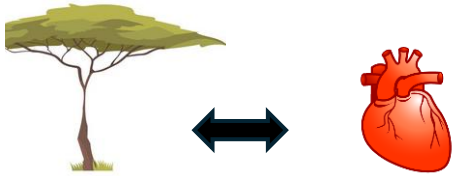










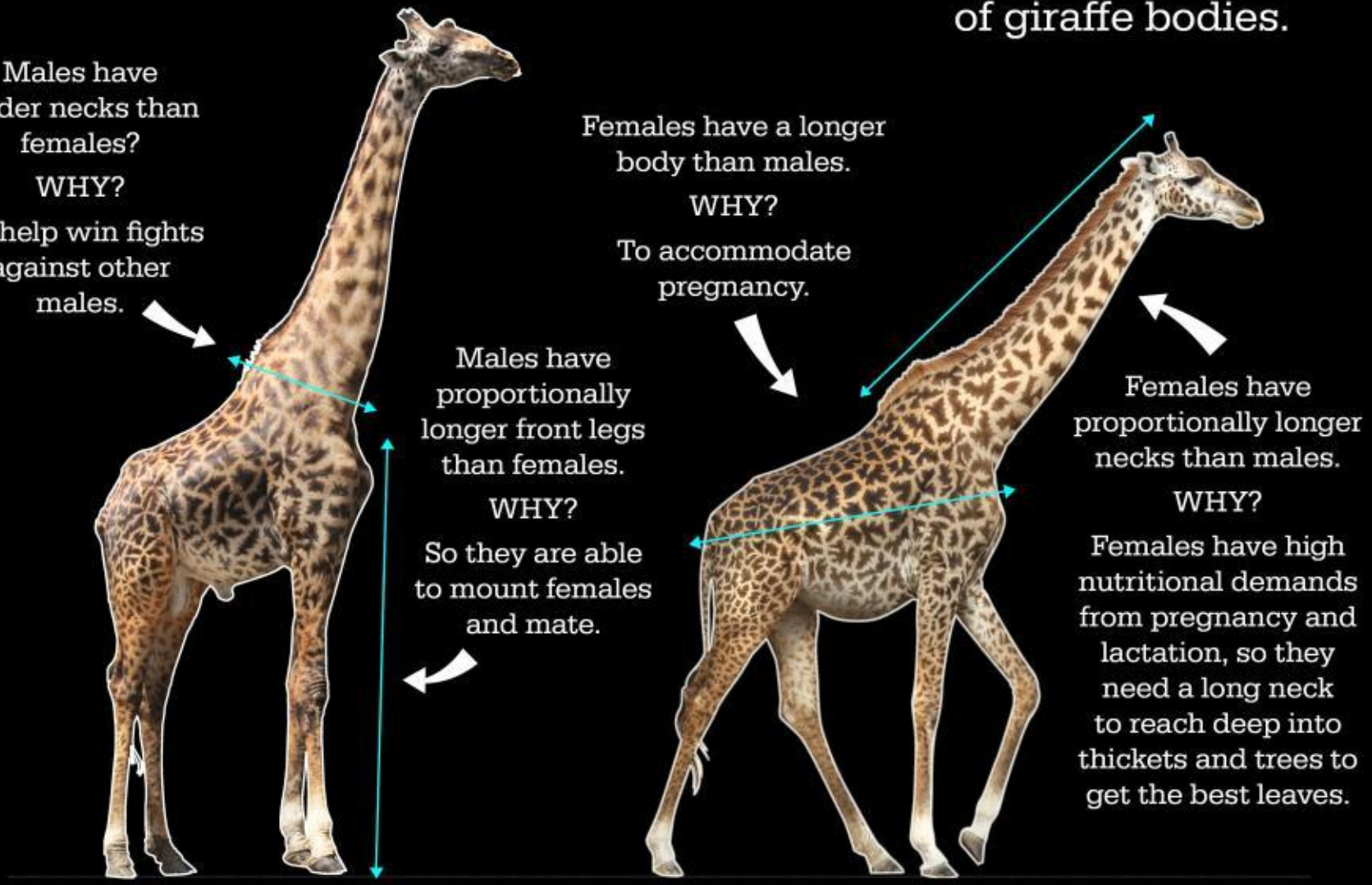


+trade-off

The Giraffe's Body

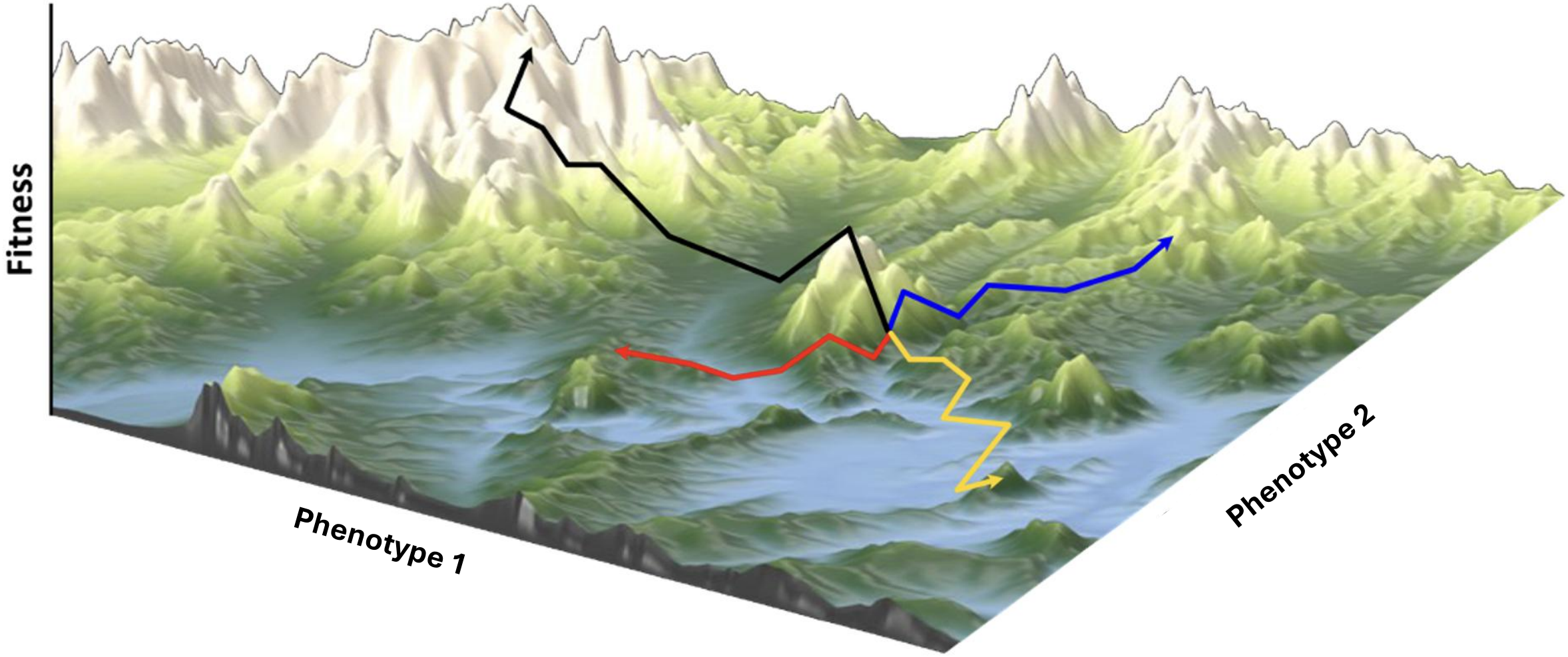
IT'S A LOOOOOOOOOONG STORY

Both food and sex shaped the evolution of giraffe bodies.



Evolutionary trade-offs can be multidimensional

*Fitness functions are often represented as «**fitness lanscapes**»*



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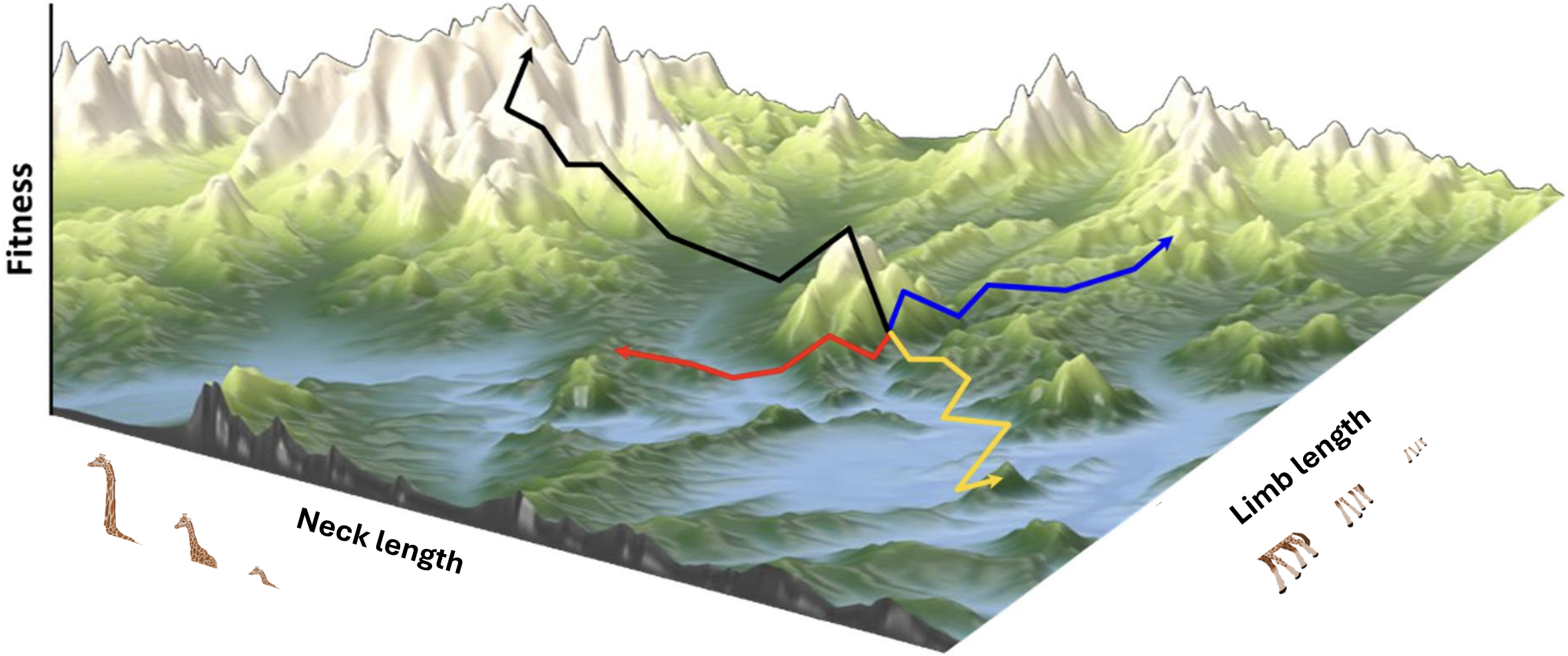

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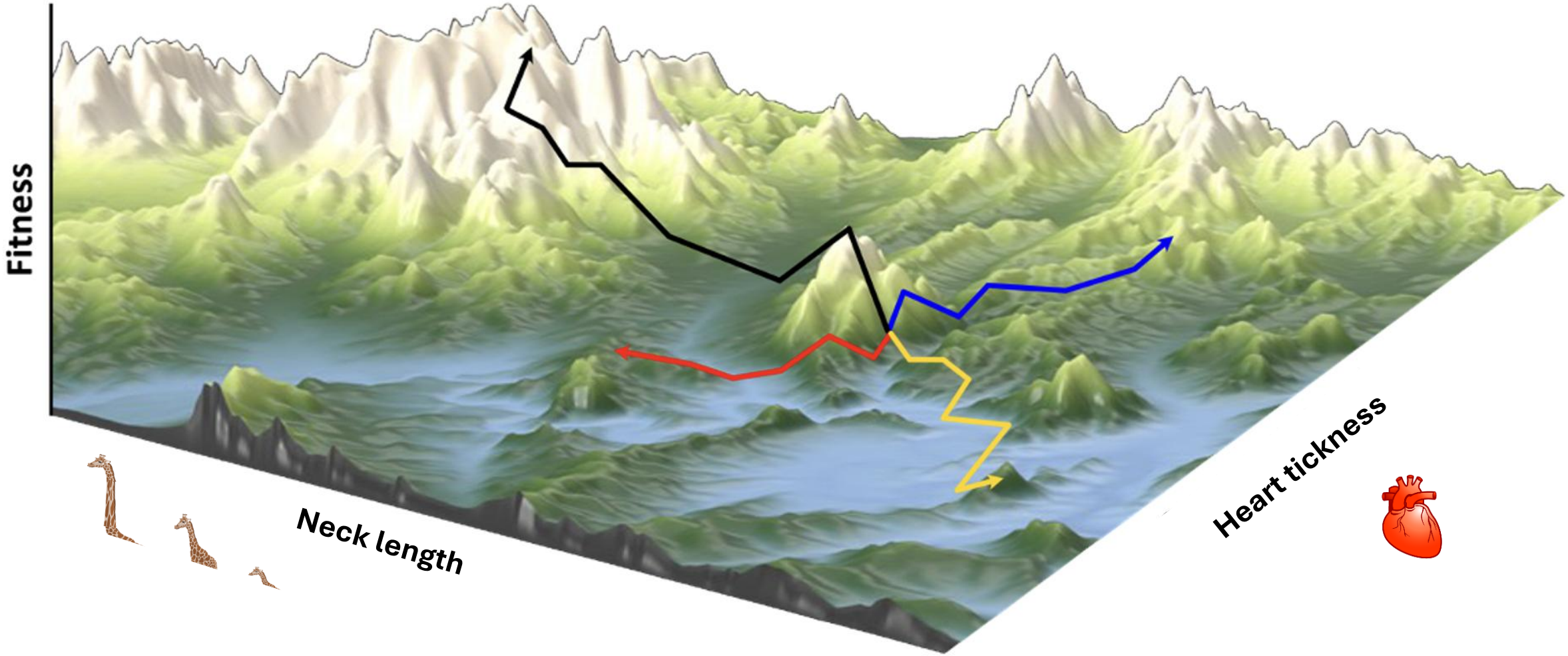
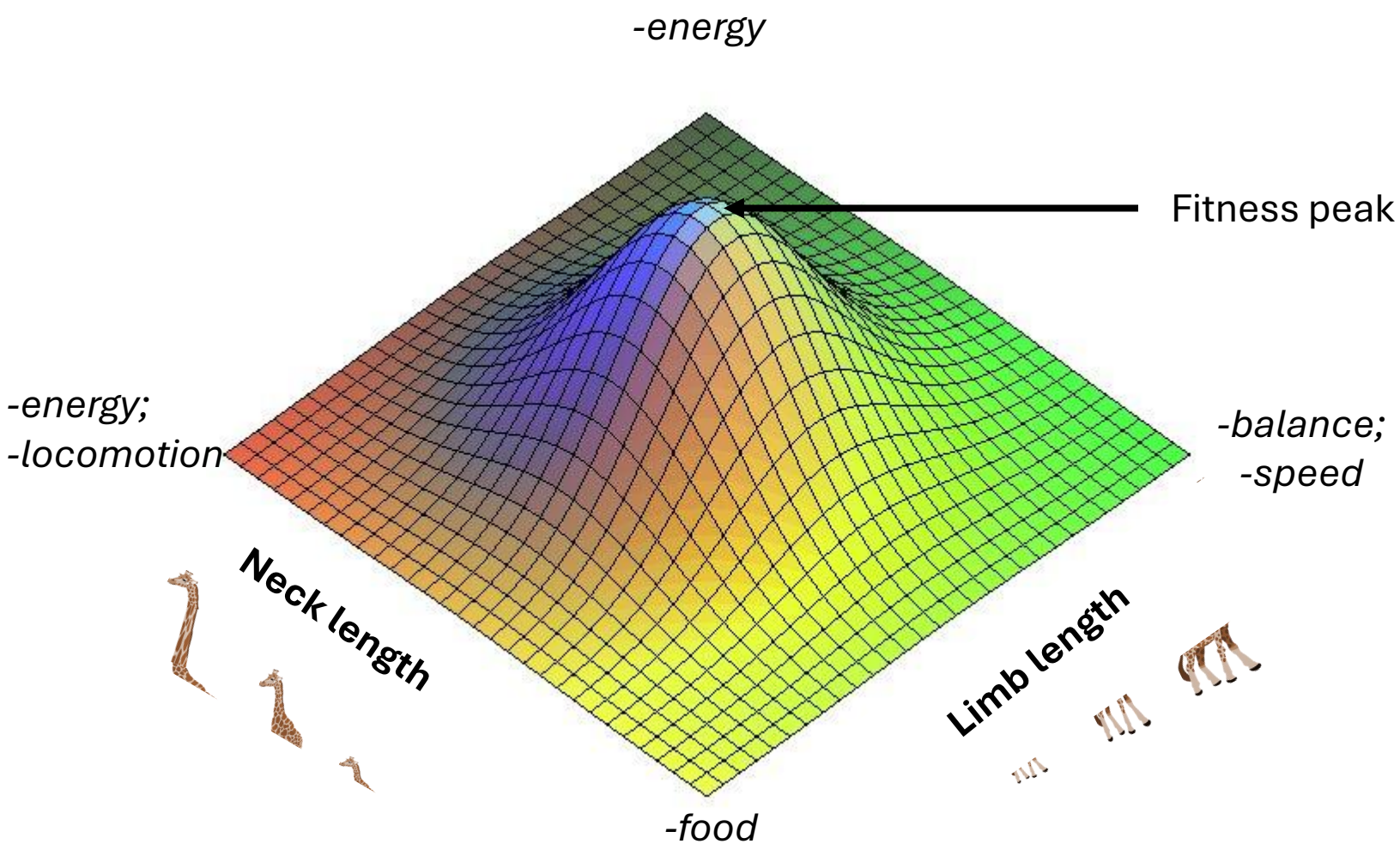


Evolutionary trade-offs can be multidimensional




TRADE-OFF-OPOLY
• SPEND YOUR FITNESS WISELY! •
GROWTH
REPRODUCTION
MATING
IMMUNITY
OFFSPRING
LONGEVITY
ENVIRONMENT
RISK!
ENERGY
PAY THE COST!
GO
Choose your strategy:
Grow Fast
Reproduce More
Survive Longer..
TRADE-OFF-OPOLY

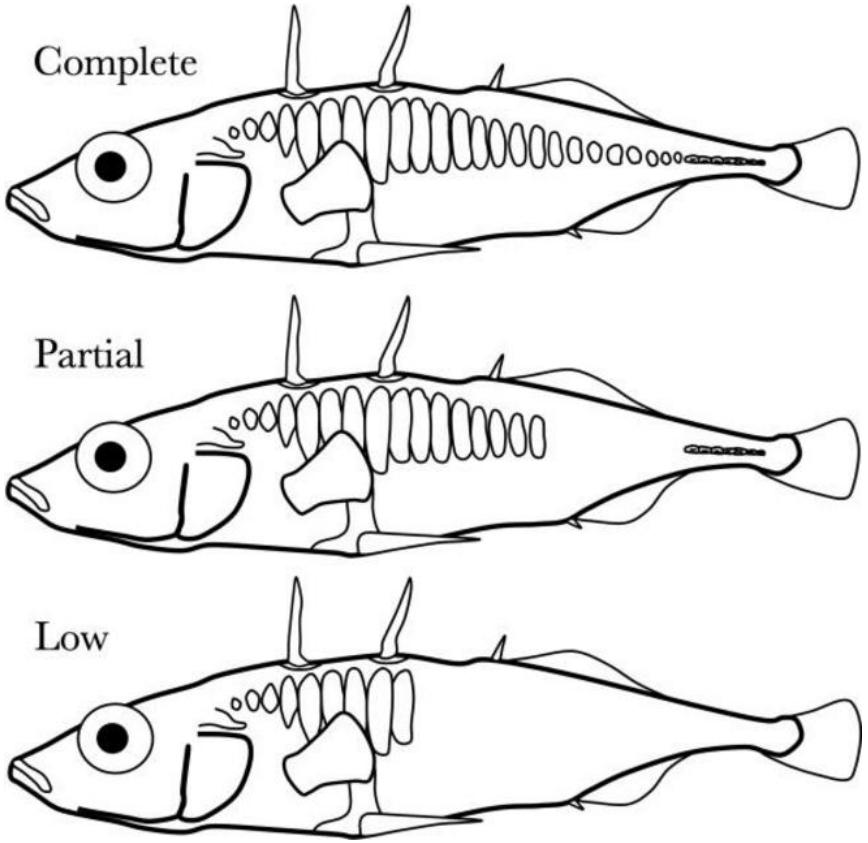
What potential evolutionary trade-offs can you imagine?

What potential evolutionary trade-offs can you imagine?

- Anatomy?
- Physiology?
- Clinic?
- Microbiology?
- Ecology?
- Animal behavior?

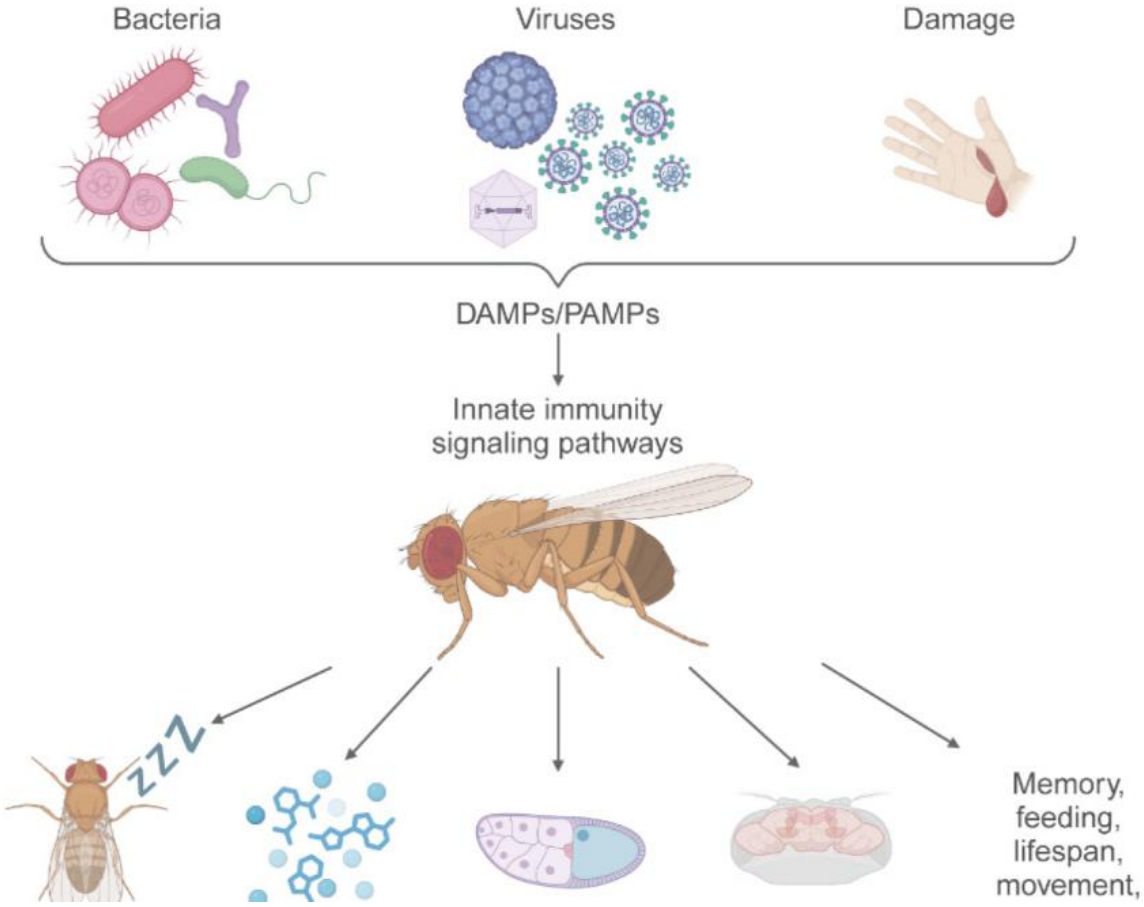
Speed vs Armor (Morphological trade-off)

- **Example: Three-spined stickleback** *(Gasterosteus aculeatus)*
- **Trade-off:**
  Body armor ↔ sw g efficiency
- **Observation**
  - Marine sticklebacks have **heavy armor plates**.
  - Freshwater populations often evolve **reduced armor**.
- **Why?**
- Armor:
  - protects from predators
  - but increases **drag and energy cost**
  - Freshwater environments often have fewer large predators → selection favors **faster, lighter fish**.
- **Genetic basis: EDA locus**



Immune Defense vs Reproduction (Insects)

- **Example: *Drosophila melanogaster***
- **Trade-off:**
  Immune defense ↔ reproduction
- **Evidence**
  Experimental evolution studies show:
  - Flies selected for **strong immune response**
  - produce **fewer eggs**
- Mechanism:
  - immune activation consumes energy
  - antimicrobial peptide production is metabolically costly
- **Key papers**
- Zuk & Stoehr 2002
- Schmid-Hempel 2003



Guppy reproduction vs predation (Trinidad guppies)

- *Poecilia reticulata* in Trinidad streams (Reznick et al.)
- **Trade-off**
- **Early reproduction vs survival/growth**
- **Observation**
- Populations exposed to predators evolve:
  - earlier reproduction
  - more but smaller offspring
  - shorter lifespan
- Low-predation populations evolve:
  - delayed reproduction
  - fewer larger offspring
  - longer lifespan.

- Researchers **transplanted guppies between streams**, and the life-history traits evolved within a few generations.
- ➞ One of the **cleanest demonstrations of natural selection shaping trade-offs**.

Guppy reproduction vs predation (Trinidad guppies)

- *Poecilia reticulata* in Trinidad streams (Reznick et al.)
- **Trade-off**
- **Early reproduction vs survival/growth**
- **Observation**
- Populations exposed to predators evolve:
  - earlier reproduction
  - more but smaller offspring
  - shorter lifespan

  } **r-strategies** *«quantity not quality»*
- Low-predation populations evolve:
  - delayed reproduction
  - fewer larger offspring
  - longer lifespan.

  } **K-strategies** *«quality not quantity»*

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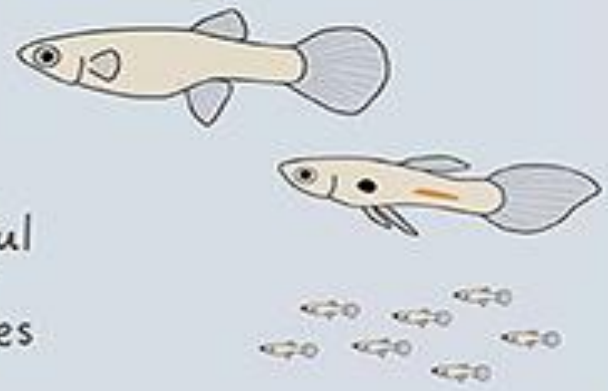
LOW-PREDATION HABITAT

- larger
- more colorful
- less babies

HIGH-PREDATION HABITAT



- smaller
- less colorful
- more babies

DANGER!!

Long gestations, generally **precocial** (born fully ferred, eyes open, able to walk).

Atriciality

Short gestations, generally **altricial** (hairless, blind, helpless newborns).

Dispersal of seeds vs Local Adaptation

- **Example: plant seed strategies**
- **Trade-off:**
  Dispersal ability ↔ competitive success
- **Wind-dispersed seeds:**
  - small
  - travel far
  - lower establishment probability
  - (e.g. Dandelions makes about 200 lightweight seeds in one flower head with tiny resources)
- **Large seeds:**
  - heavy
  - stay near parent
  - better seedling survival.

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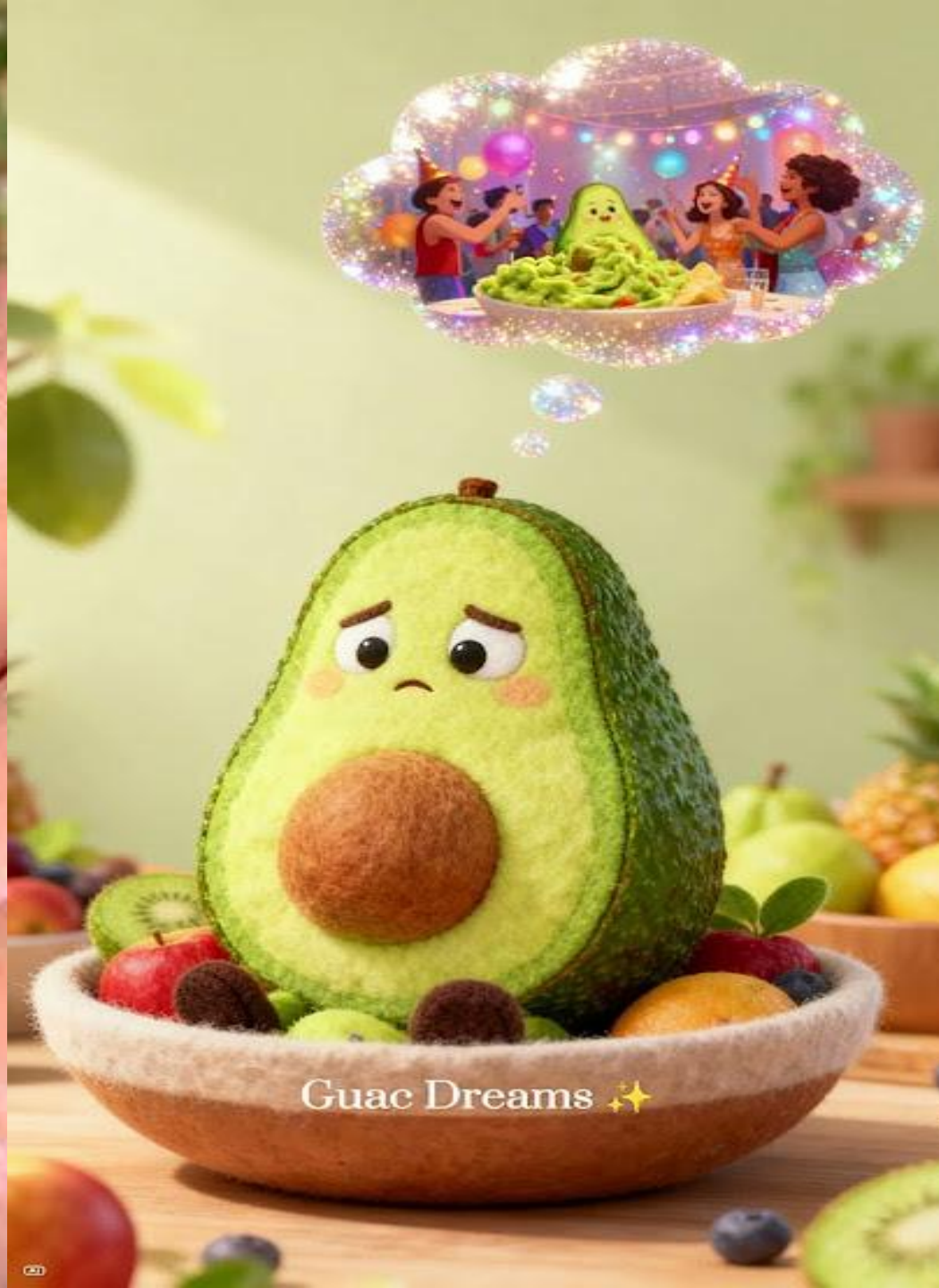
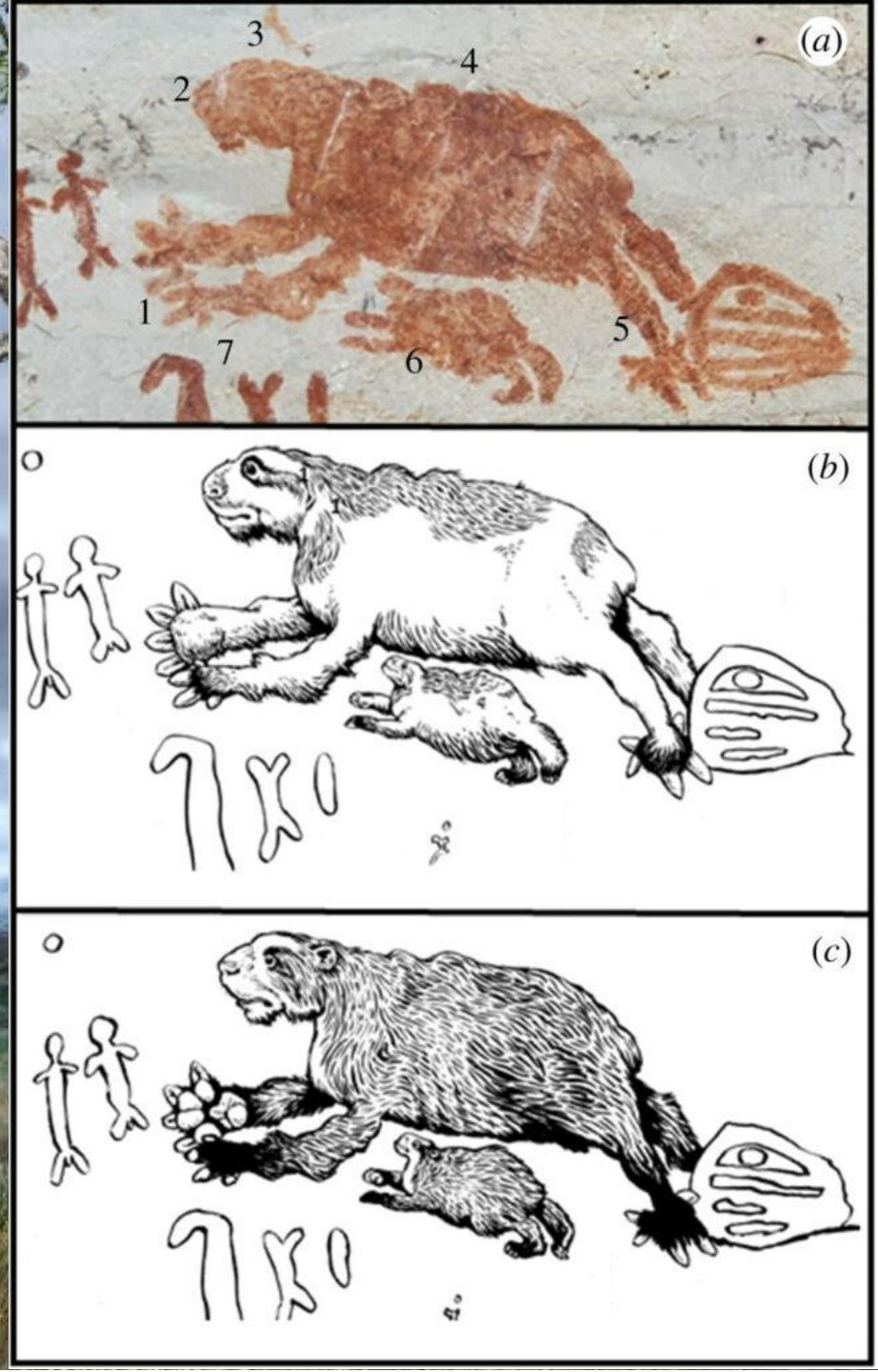
  - Oak acorns.


Guac Dreams ✨

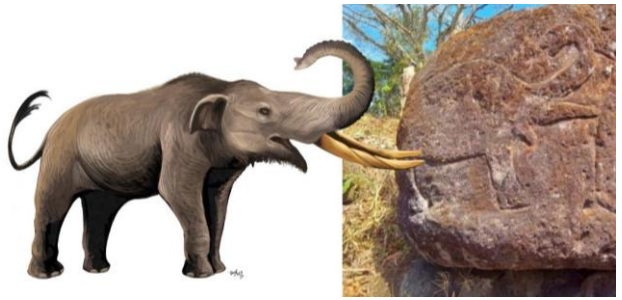

I am alone, nobody wants to eat me!
Guac Dreams ✨

Megatherium

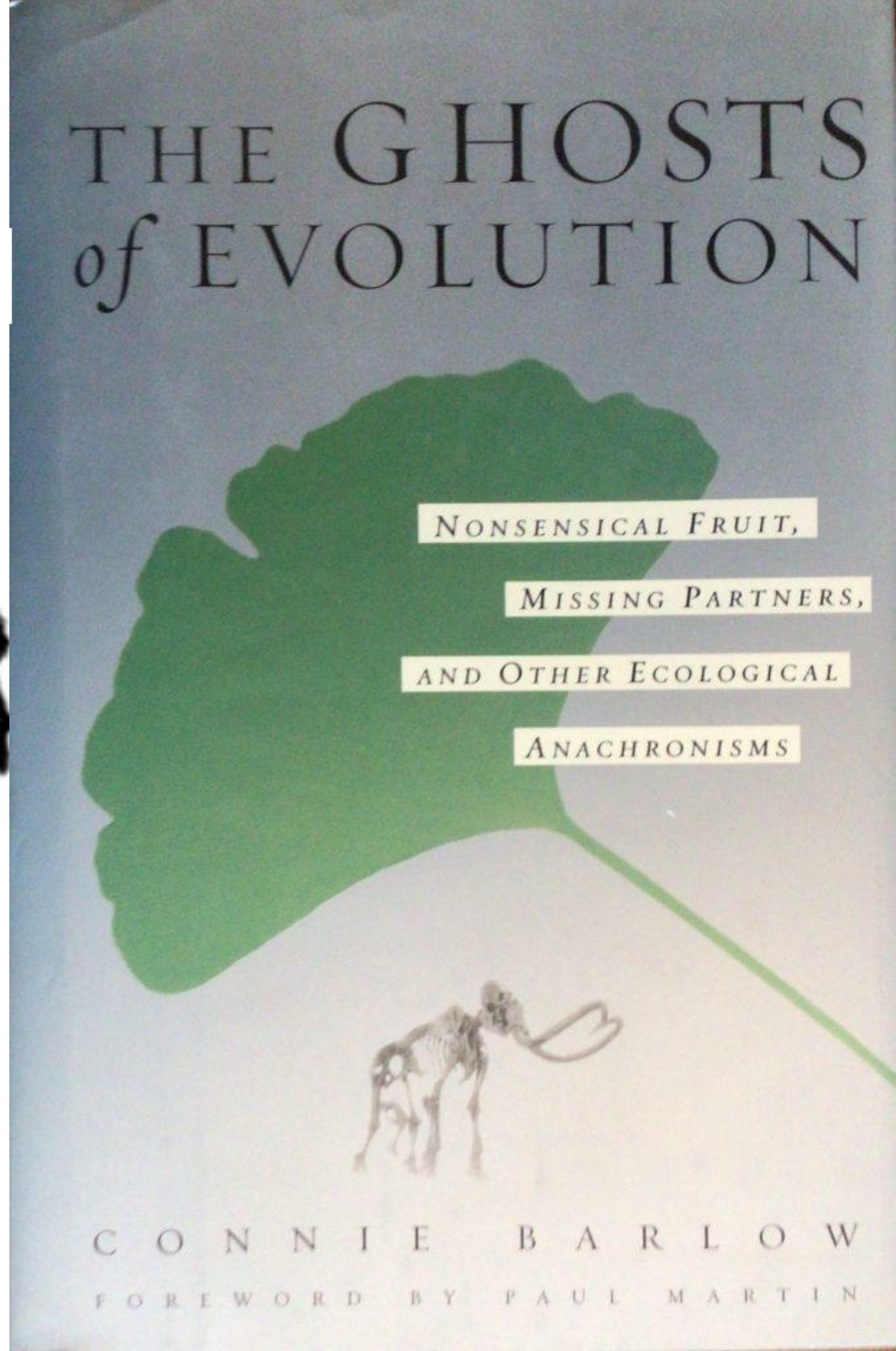



Extinct mammal

Gomphoteres like *Covieronus* roamed the Americas (and probably ate avocados)



There are is some rock art of Coveronius as wel (from Nicaragua)l!



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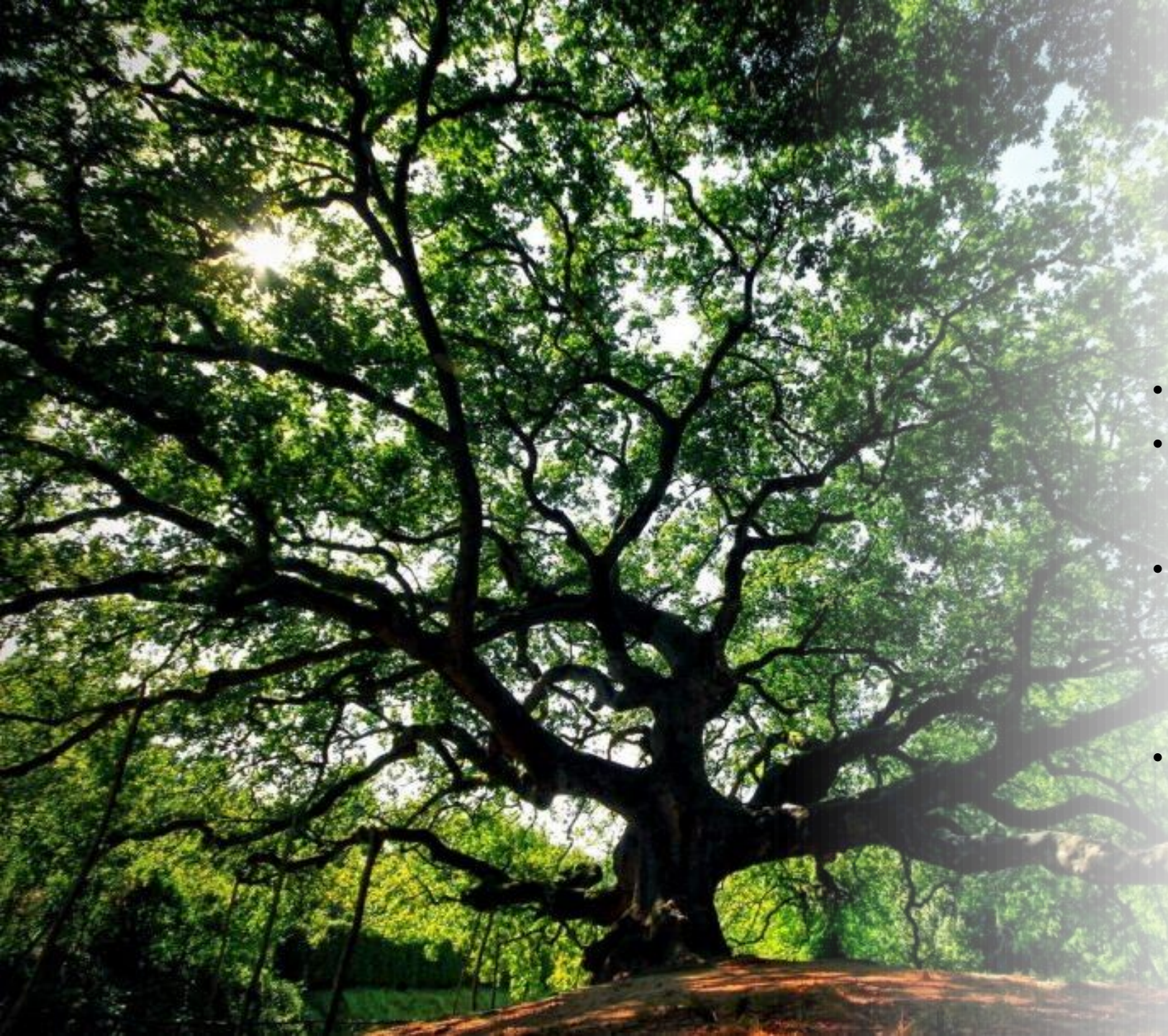

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  - heavy
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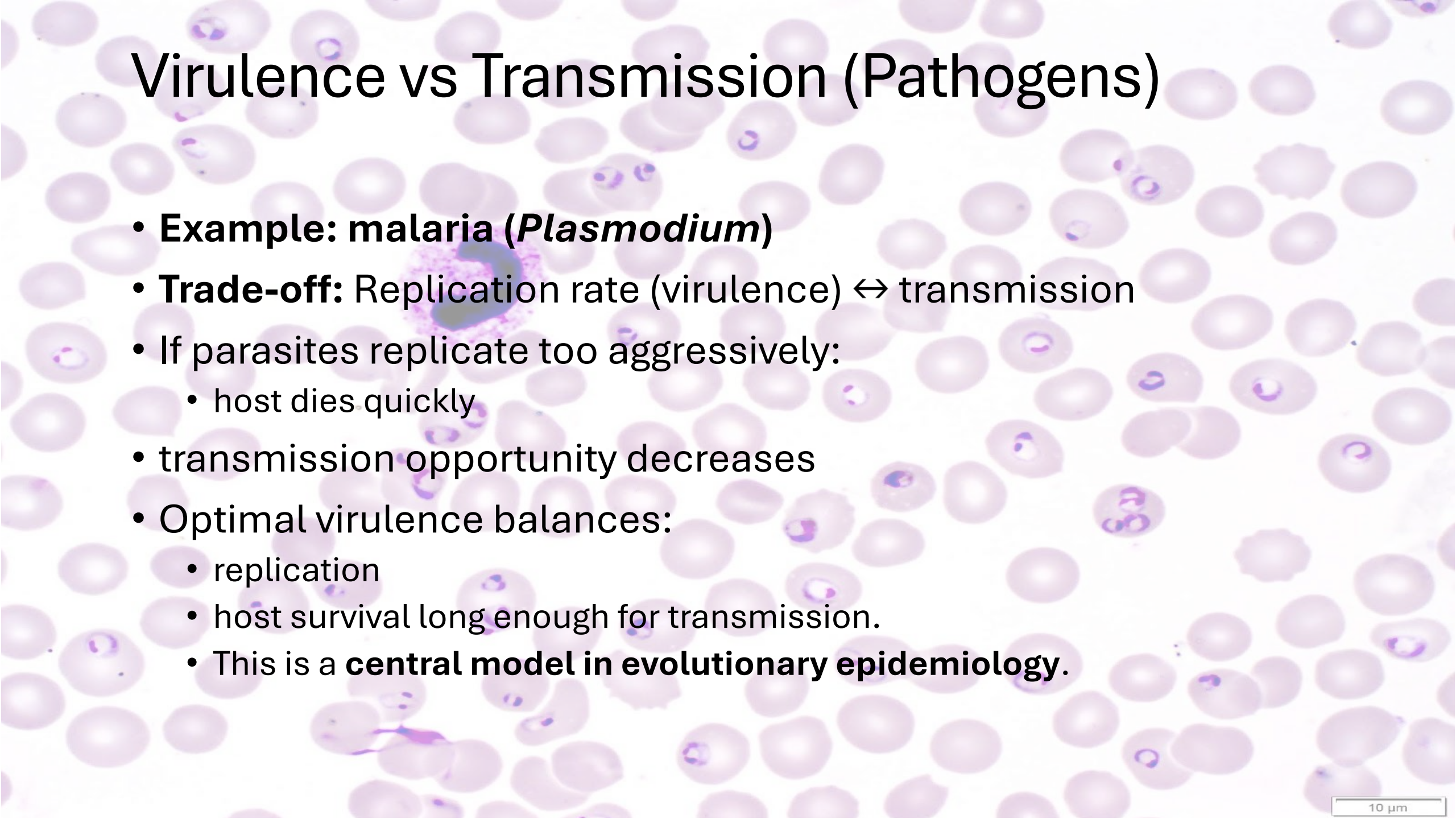
Growth vs Reproduction (Plants)

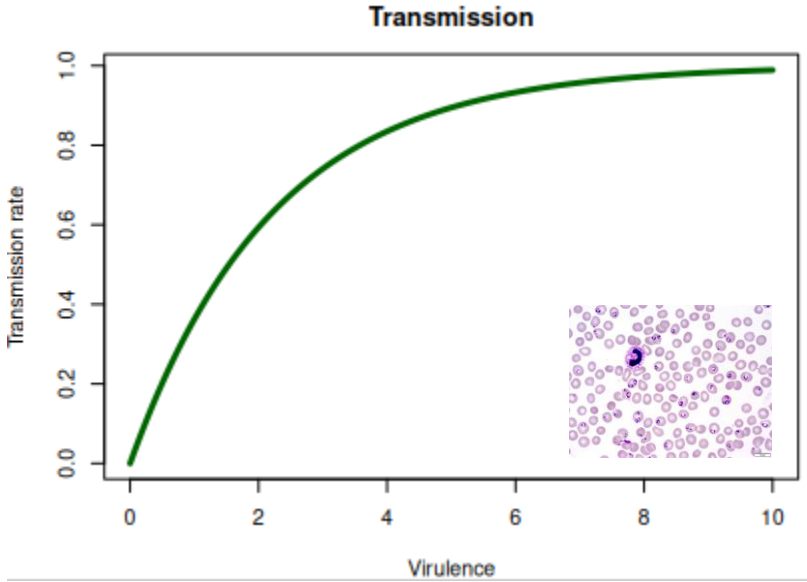
- **Example: *Arabidopsis thaliana***
- **Trade-off:**
  Vegetative growth ↔ early reproduction
- **Observation**
  Genotypes that flower early:
- produce seeds sooner
- but are **smaller plants with fewer seeds**
- Genotypes that delay flowering:
- grow larger
- produce more seeds later
- **Genes involved**
- **FLC**
- **FRI**
- These genes regulate flowering timing and illustrate the genetic basis of life-history trade-offs.

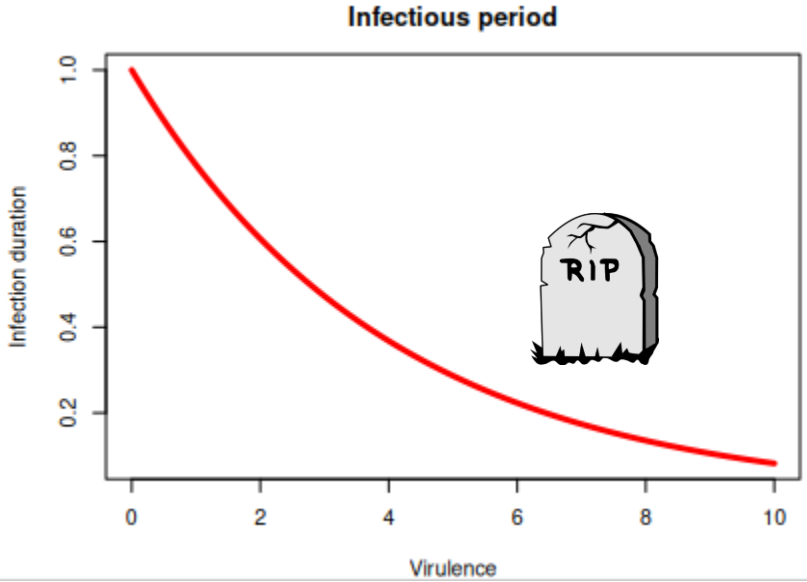
Virulence vs Transmission (Pathogens)

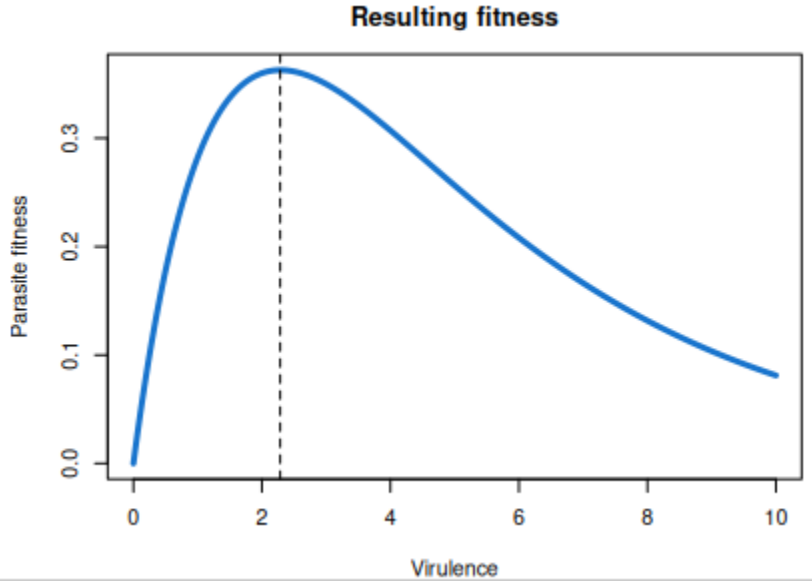
- **Example: malaria (*Plasmodium*)**
- **Trade-off:** Replication rate (virulence) ↔ transmission
- If parasites replicate too aggressively:
  - host dies quickly
- transmission opportunity decreases
- Optimal virulence balances:
  - replication
  - host survival long enough for transmission.
  - This is a **central model in evolutionary epidemiology**.



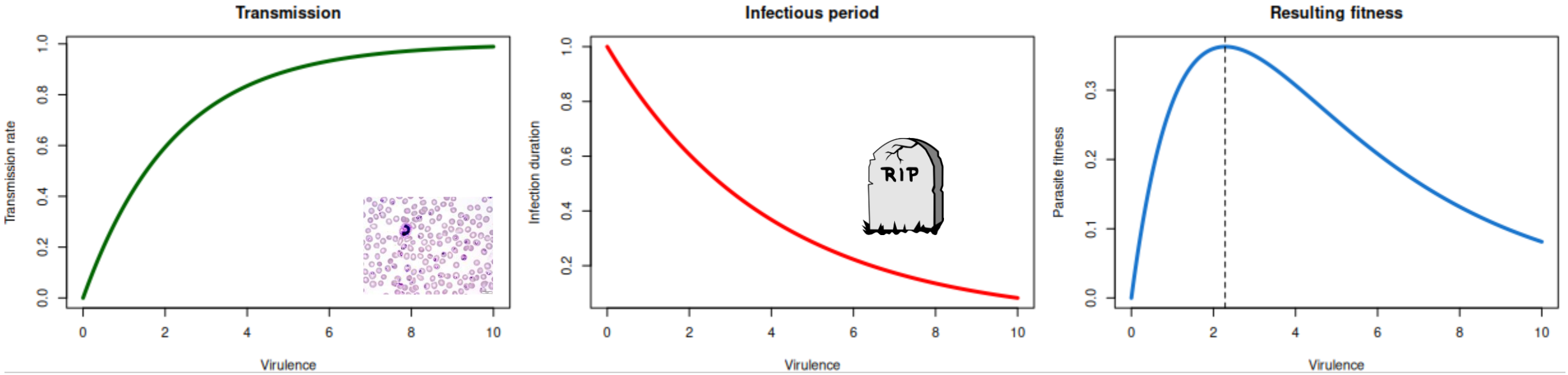
Virulence vs Transmission (Pathogens)



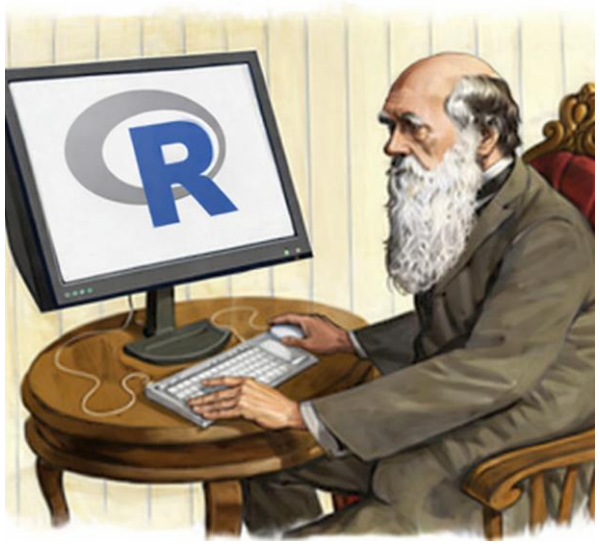




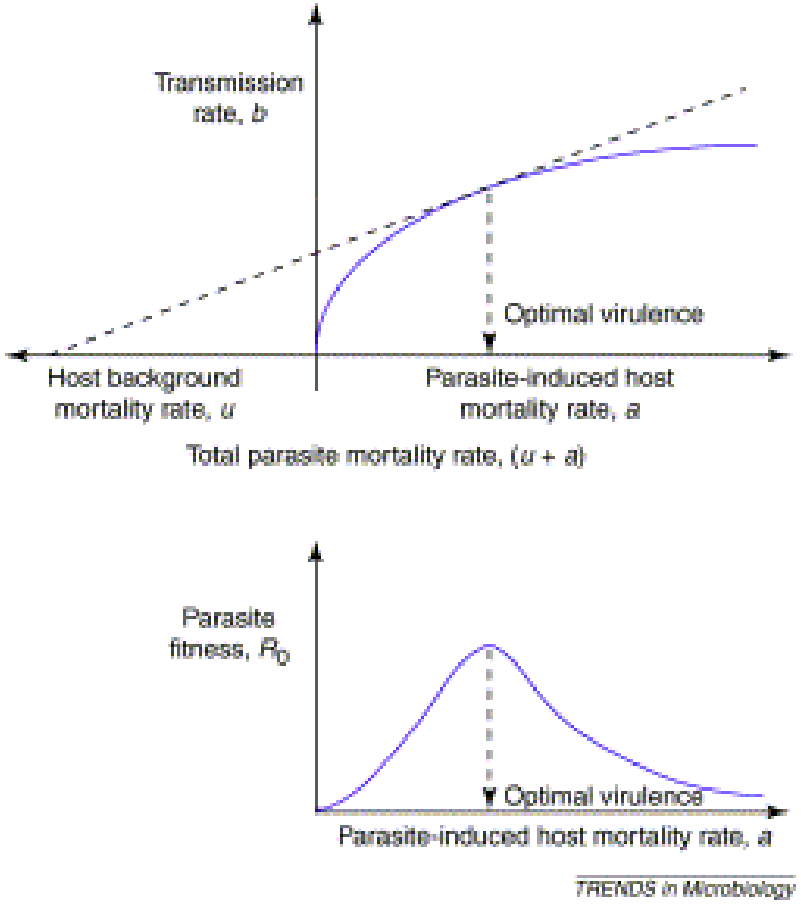
Virulence vs Transmission (Pathogens)

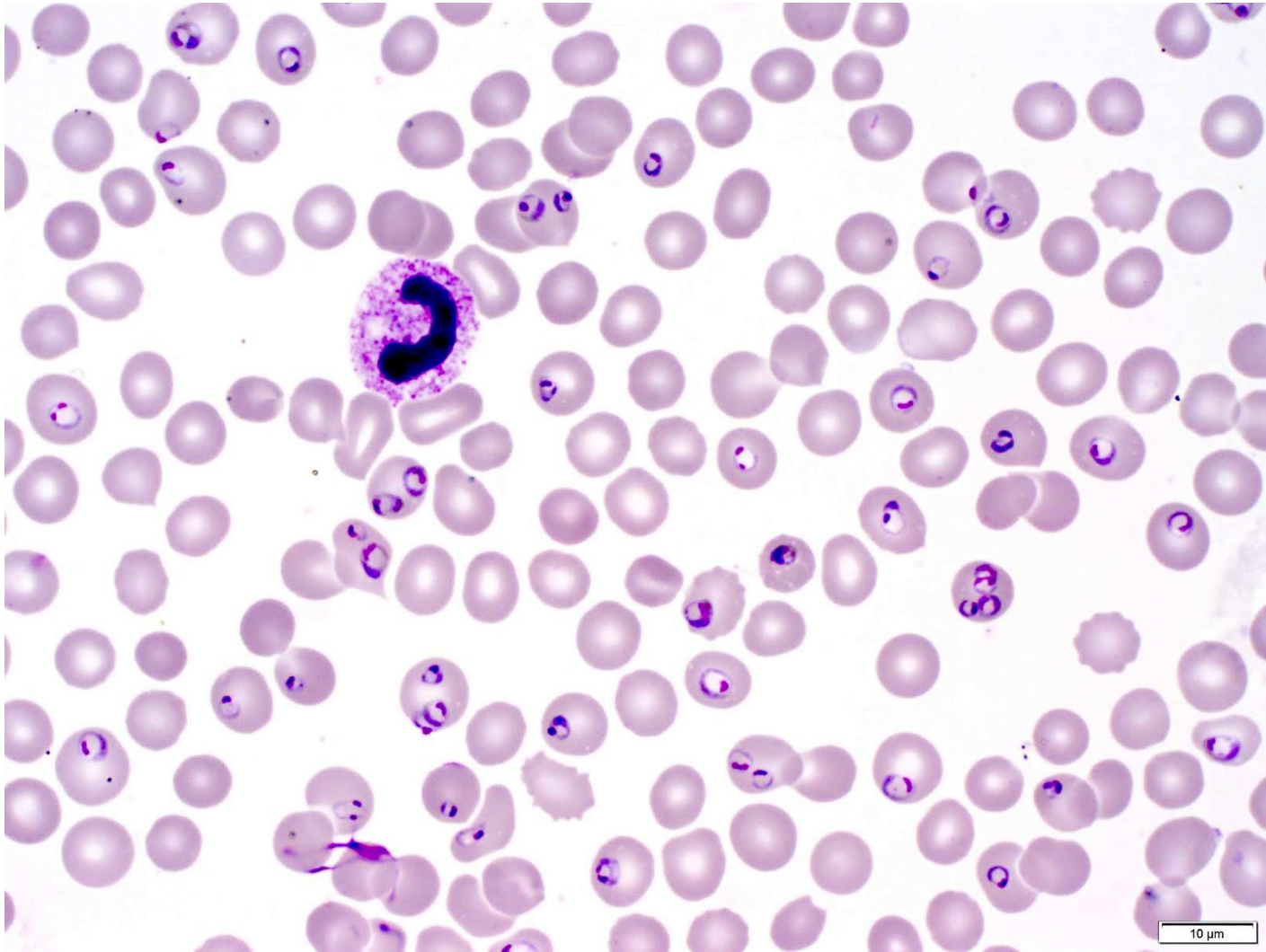



```
transmission <- 1 - exp(-0.45 * v)

# infection duration decreases with virulence
duration <- exp(-0.25 * v)

# parasite fitness (approx R0)
fitness <- transmission * duration
```



Benefit of increasing transmission grows linearly while «mortality» reaches a plateau

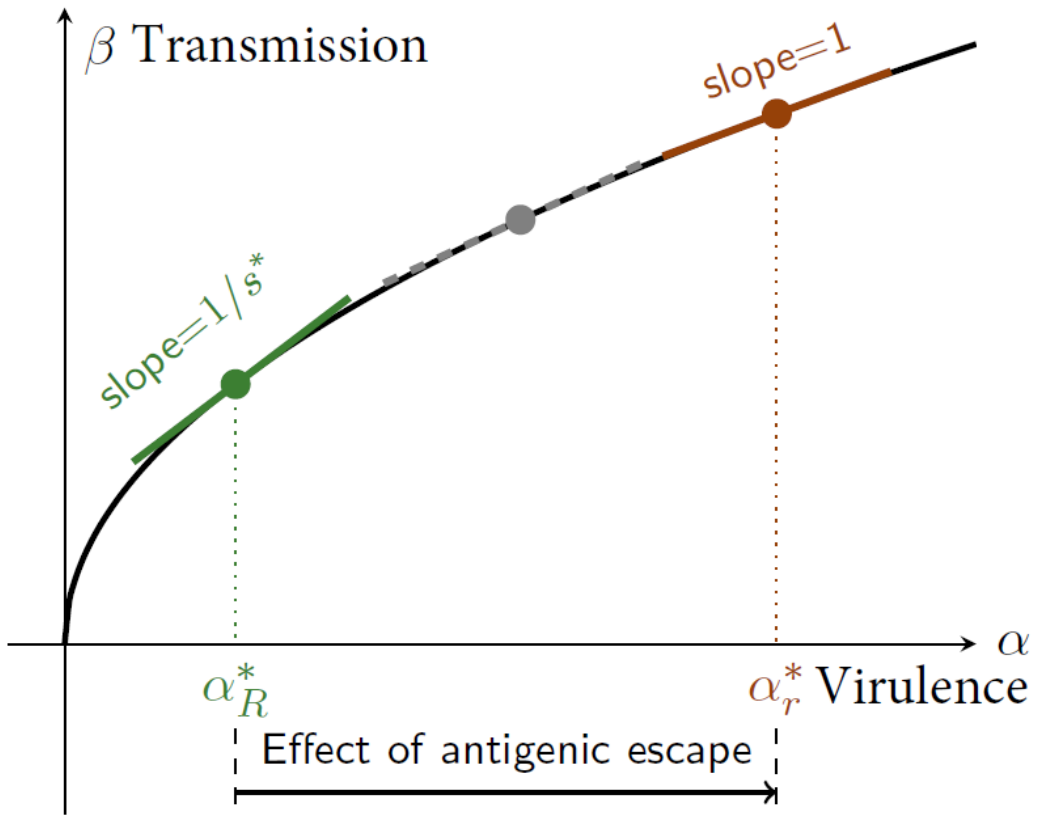




Benefit of increasing transmission grows linearly while «mortality» reaches a plateau

Antigenic escape and cross immunity determines a higher need of virions to transmit and die

Pathogen evolve higher virulence



Bacterial growth vs stress resistance

- **Trade-off**
- **Fast growth vs stress resistance**
- **Observation**
- Mutations that increase growth rate often reduce:
- stress tolerance
- survival during starvation
- resistance to oxidative damage.
- **Mechanism**
- Resource allocation in cellular metabolism.
- This trade-off appears in **adaptive laboratory evolution experiments**.

Bacterial growth vs stress resistance

Rpos gene

- Encodes **σS**, the major **general stress response sigma factor**.
- It activates genes for:
  - oxidative stress resistance
  - starvation survival
  - osmotic stress
  - acid resistance
  - DNA protection
- High **rpoS activity**:
  - ✓ better survival under stress
    ✗ slower growth rate
- Low **rpoS activity**:
  - ✓ faster growth
    ✗ poor stress tolerance.

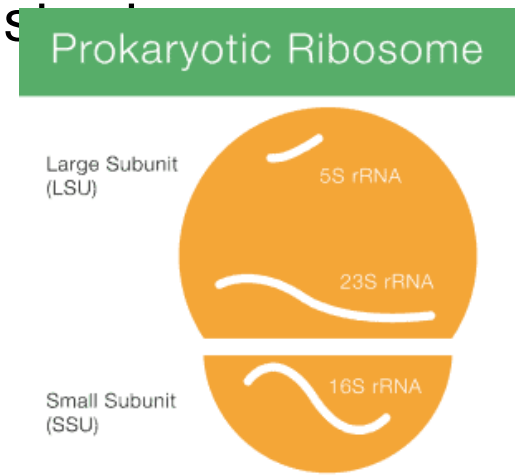
Handler & Kirkpatrick, 2024

Bacterial growth vs stress resistance

- **Ribosomal genes in E.coli**
- **Trade-off**
  - More ribosomes → faster protein synthesis → faster growth.

  But:
  - high ribosome production consumes energy
  - reduces stress tolerance

  But:
  - higher fidelity of translation, so in experiment actually more resis
    when upregulating the 16S operon *rrnH*



Handler & Kirkpatrick, 2024

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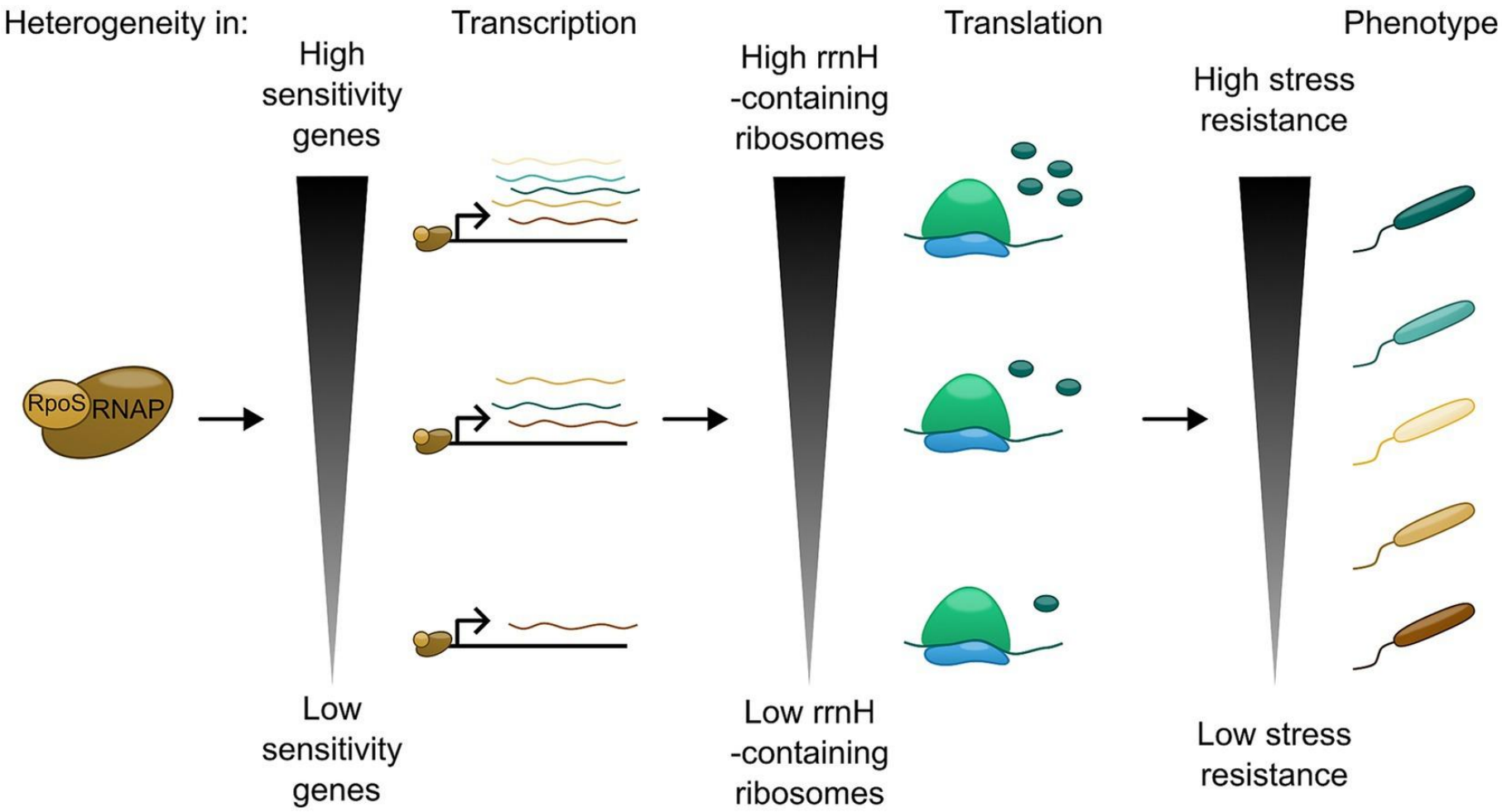
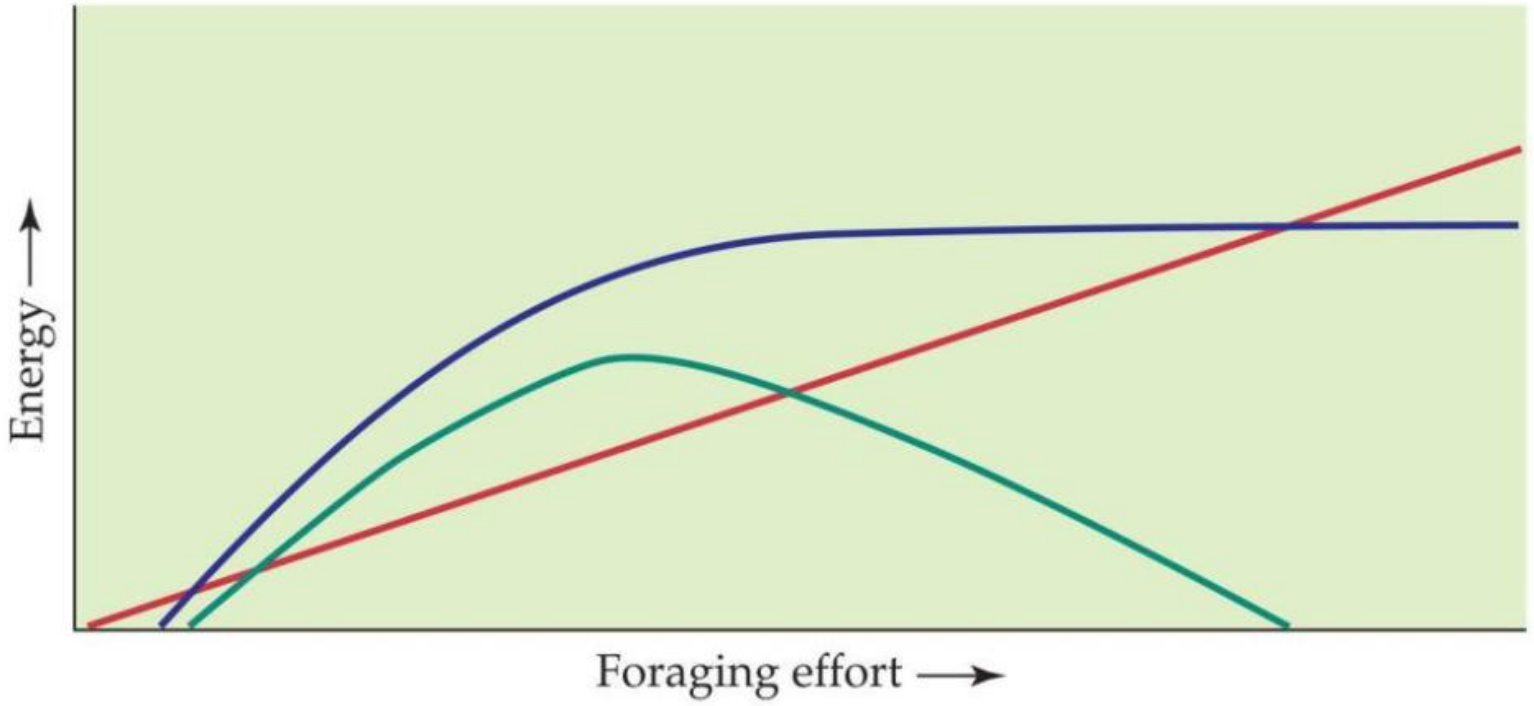


Handler & Kirkpatrick, 2024

«Optimal foraging theory» predicts when an animal will move to eat somewhere else



ECOLOGY 3e, Figure 8.6

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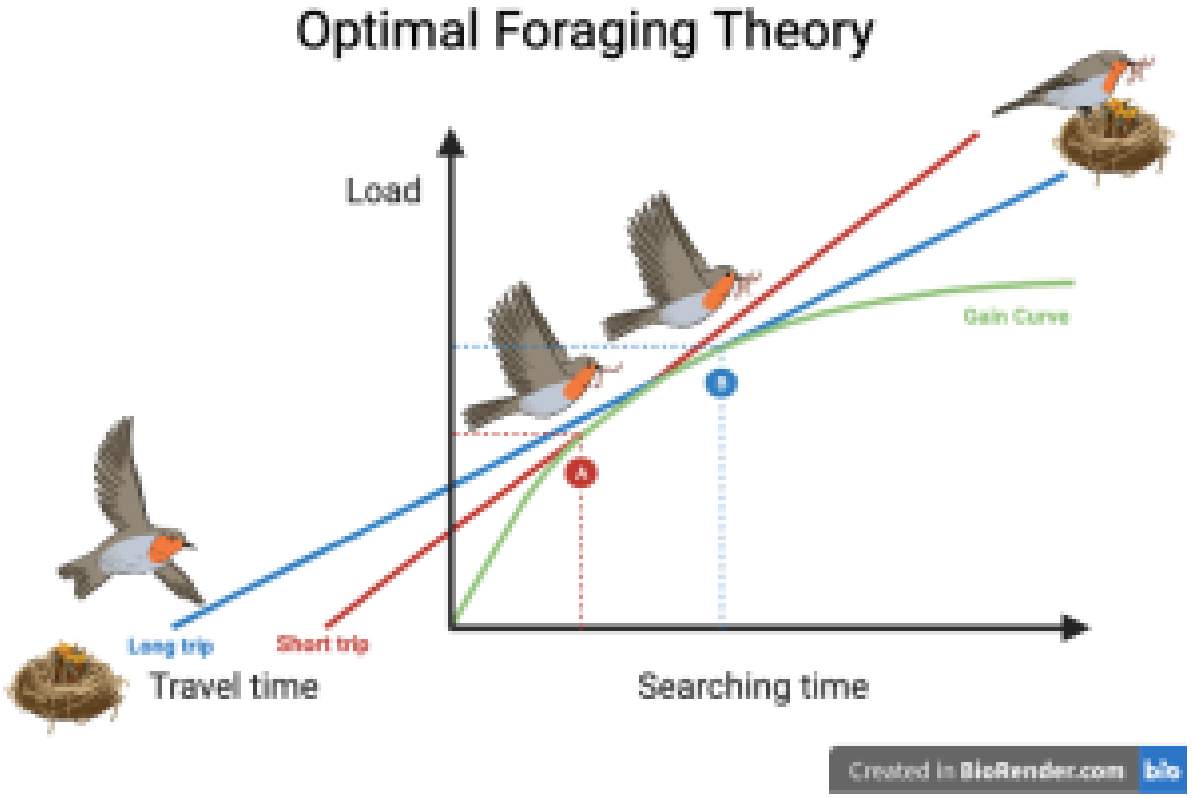


3. Optimal foraging theory

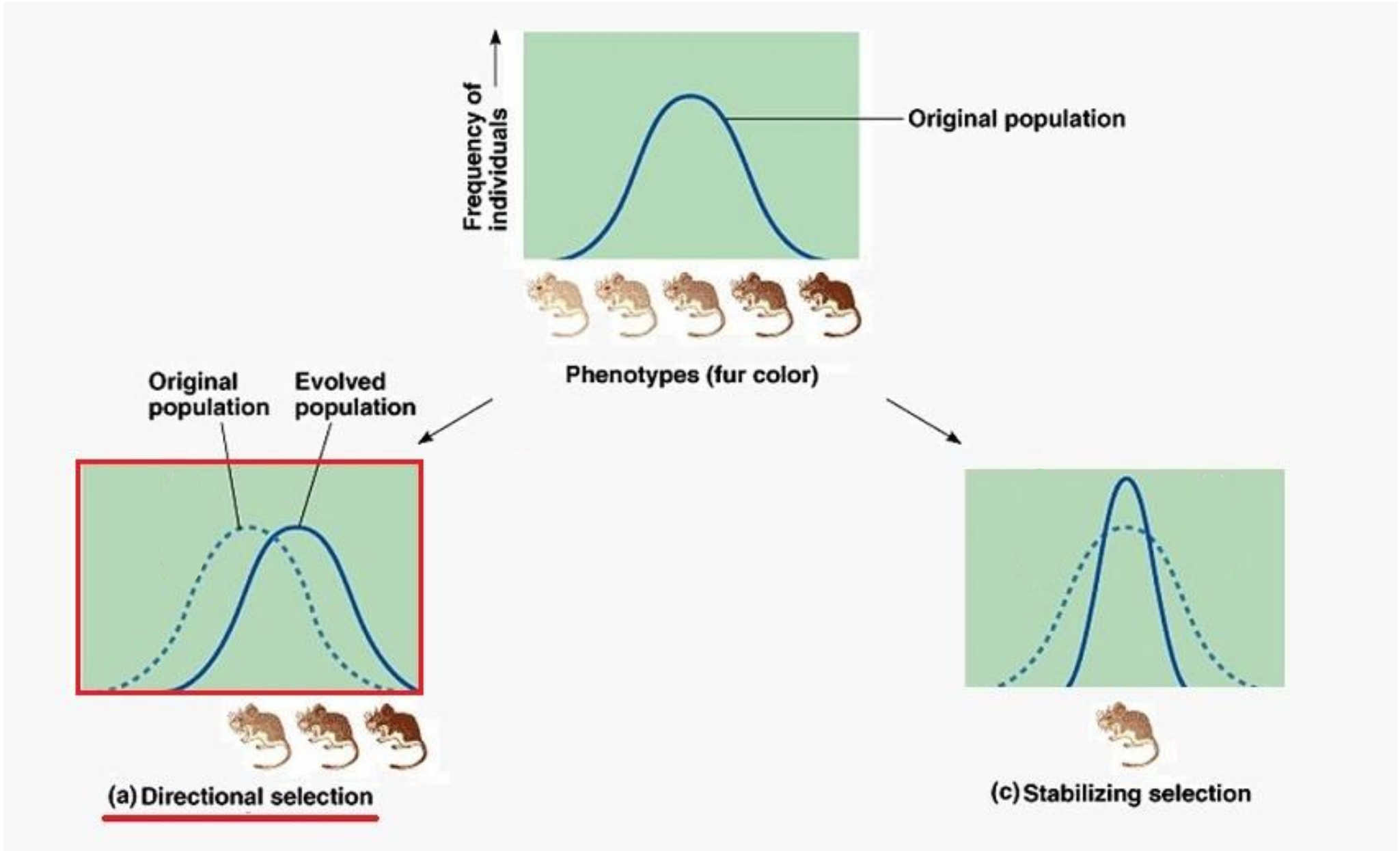
Aa Aa

There has been a great deal of research into something called optimal foraging theory, which looks at the costs and benefits of foraging for different types of prey. The idea behind this theory is that animals will behave in a way that maximizes the amount of energy obtained from prey in a given unit of time. In general, you can think of the profitability of a particular food source as $\frac{E}{h}$, where E is the amount of energy contained in the prey and h is the handling time for that prey. Handling time refers to the amount of time (after the prey has been spotted) required to capture, kill, eat, and digest the prey.

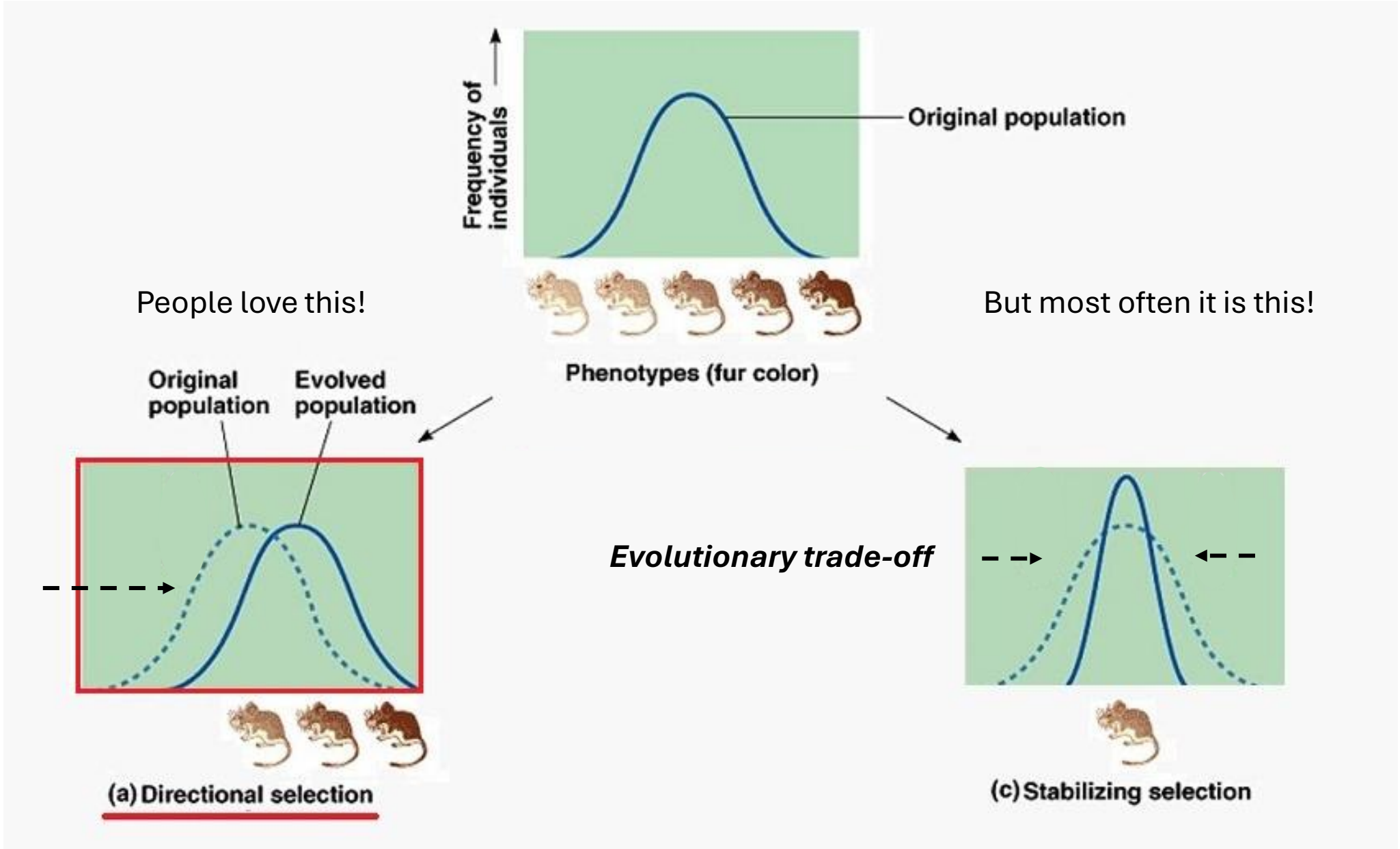
Consider this example of foraging by the great tit (*Parus major*). Imagine these birds have the choice between two types of mealworms: Type 1 is larger and contains 9 kcal/worm, and Type 2 is smaller and contains 6 kcal/worm. Given these values of E_1 and E_2, what values of h_1 and h_2 would make the profitability of these two worms equal?

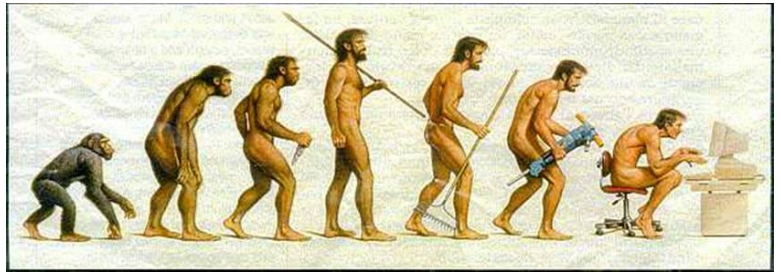
- $h_1 = 12$; $h_2 = 18$
- $h_1 = 6$; $h_2 = 9$
- $h_1 = 18$; $h_2 = 12$

Modes of phenotypic evolution

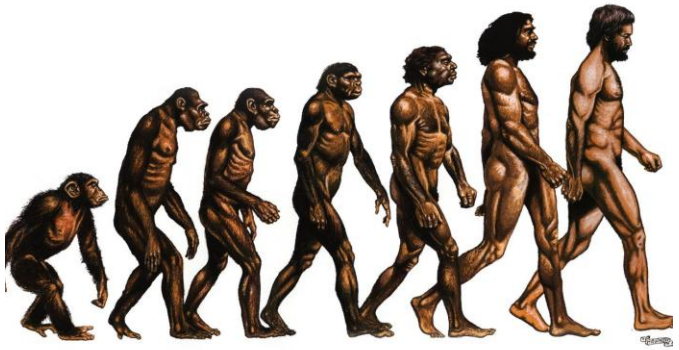


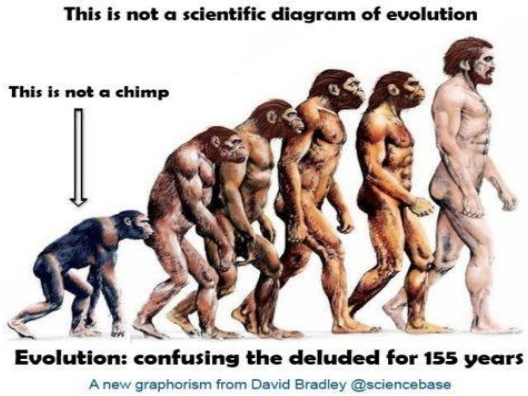
Modes of phenotypic evolution

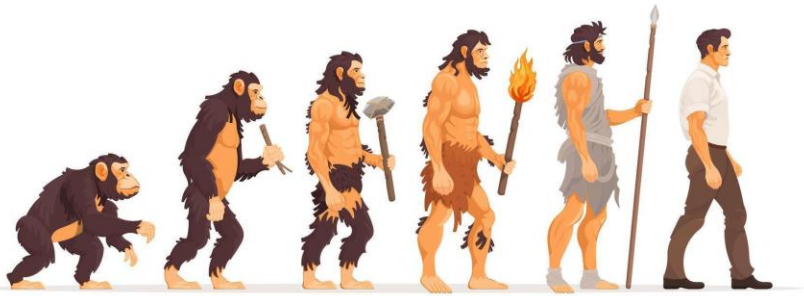


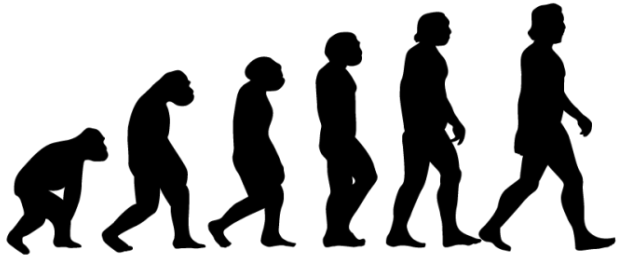


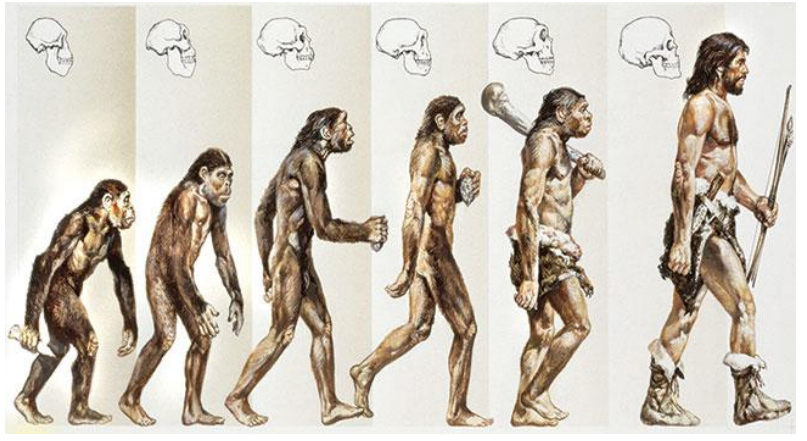
Long-term «directional selection»











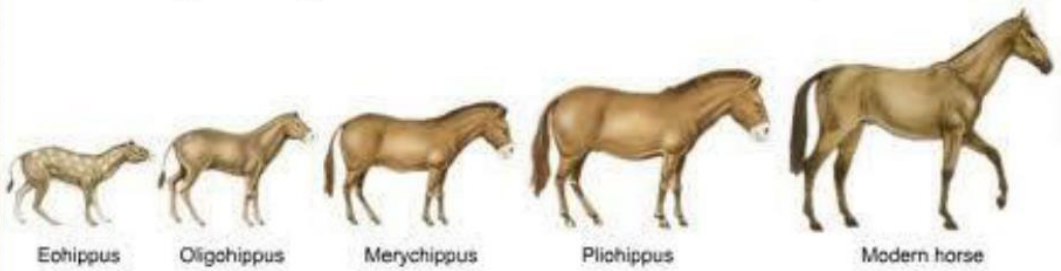
Long-term «directional selection»

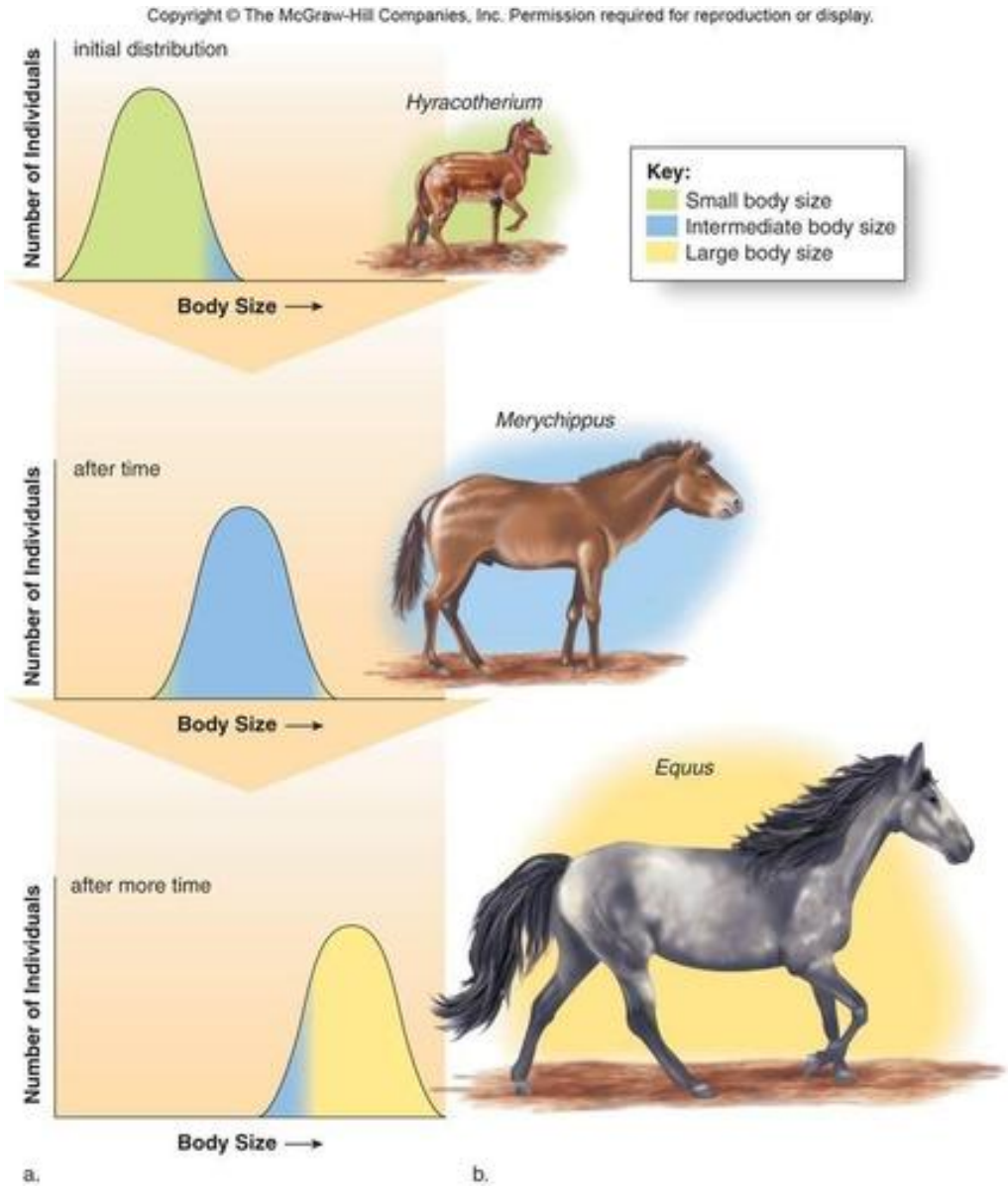
Directional Selection

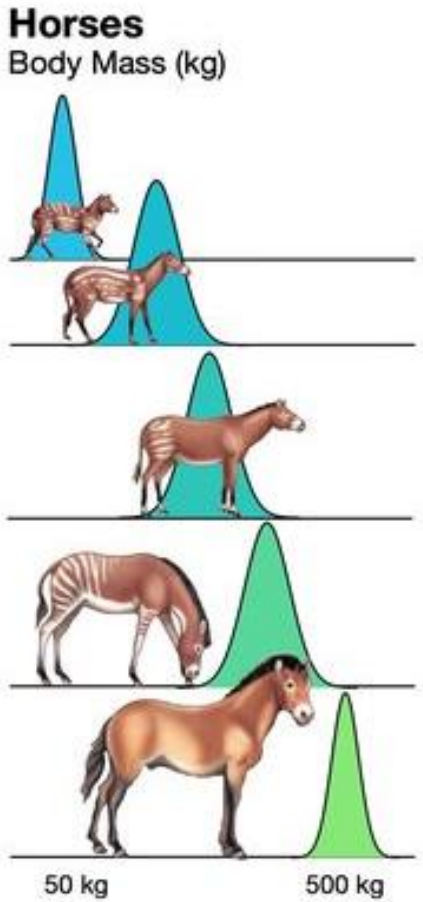
One of the extremes is selected for, the other against

Example: Horse leg length

- Longer legs are better to outrun predators







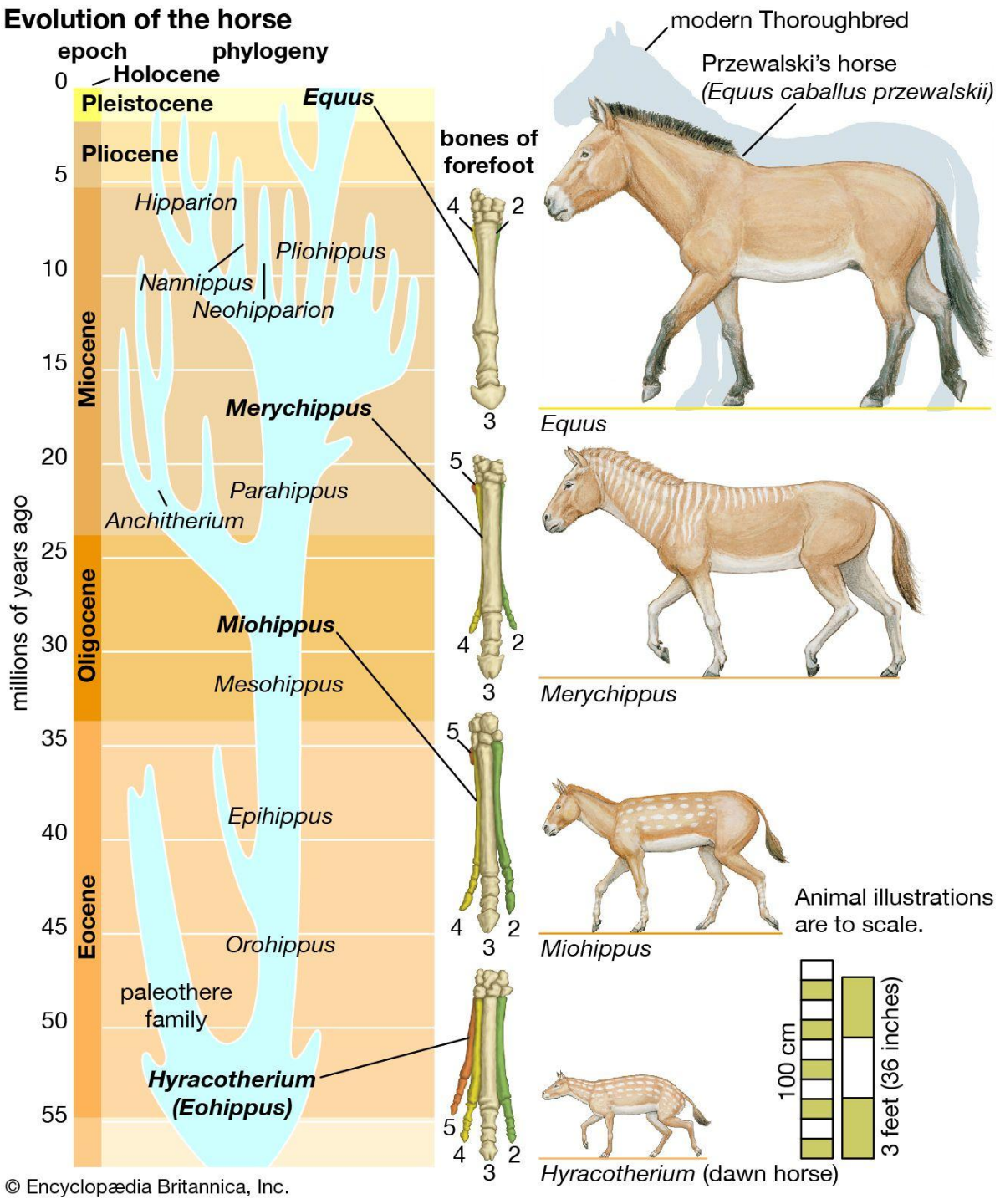
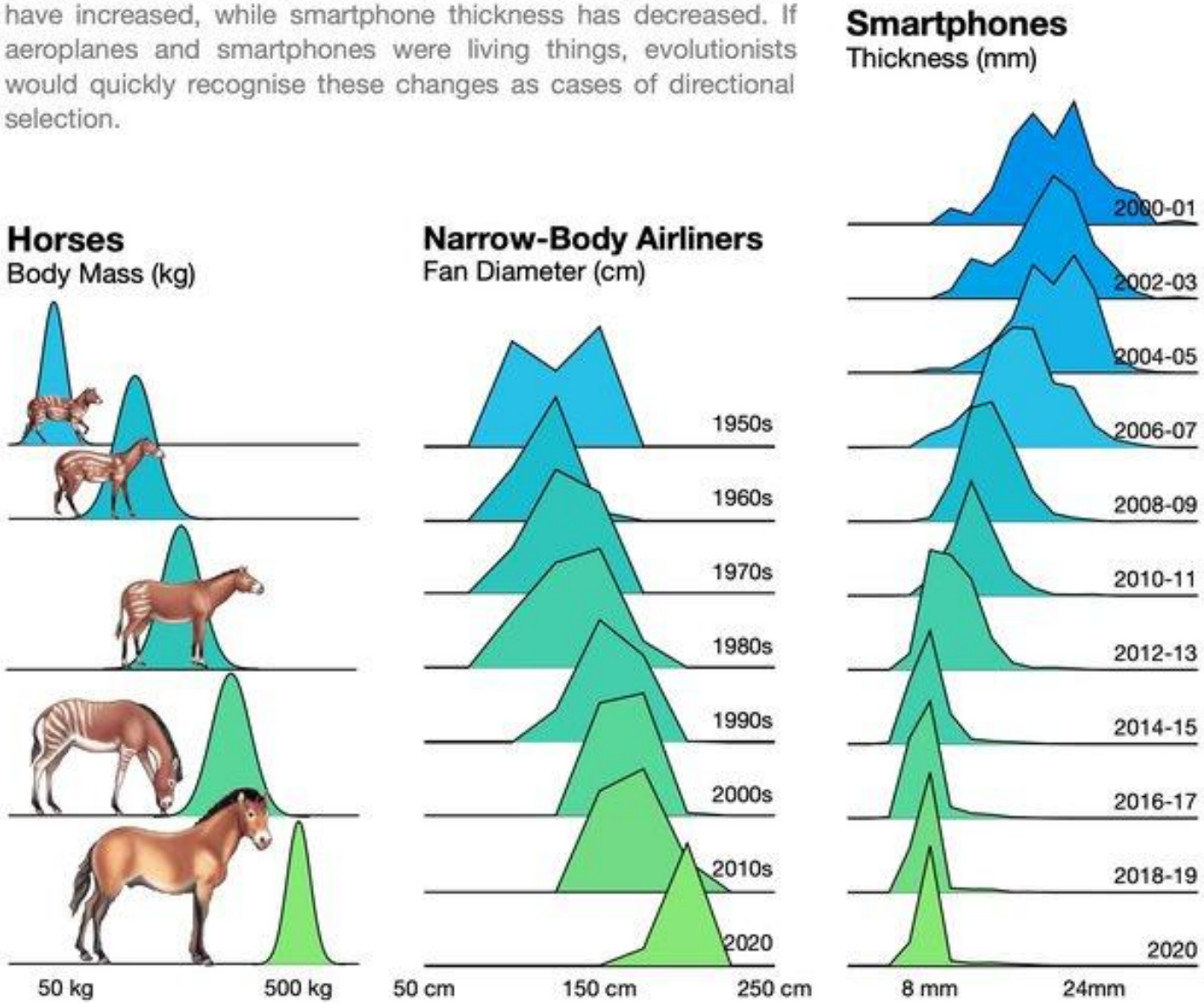
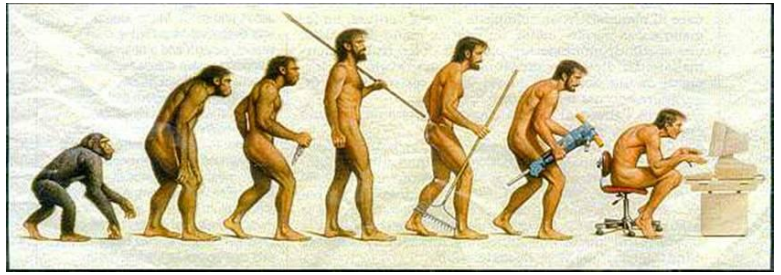


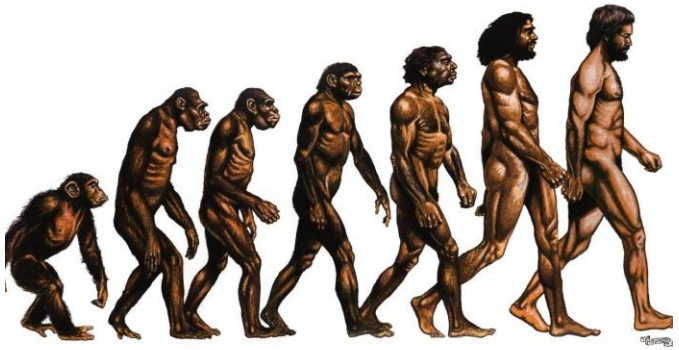
Figure 1.2.2 Directional Selection & Directional Innovation.

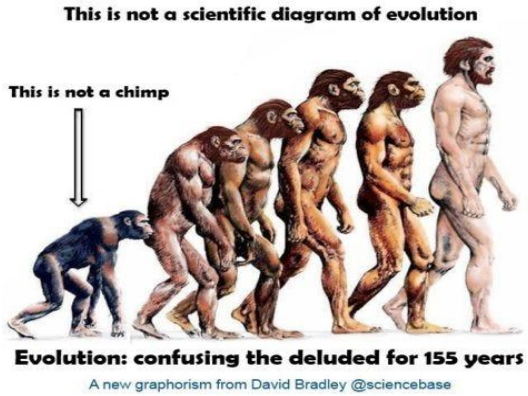
In the examples below, horse body mass and engine diameters have increased, while smartphone thickness has decreased. If aeroplanes and smartphones were living things, evolutionists would quickly recognise these changes as cases of directional selection.

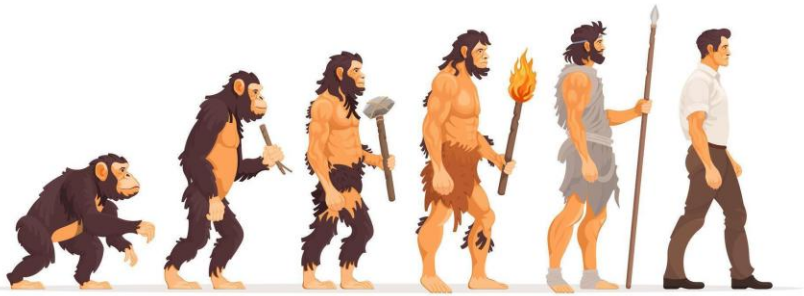


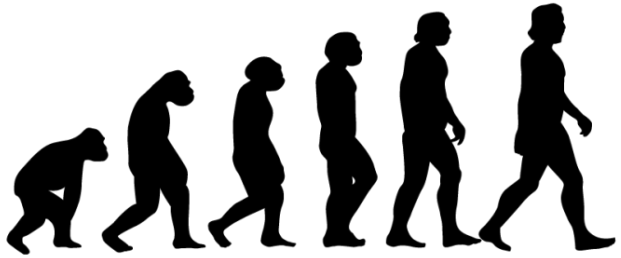


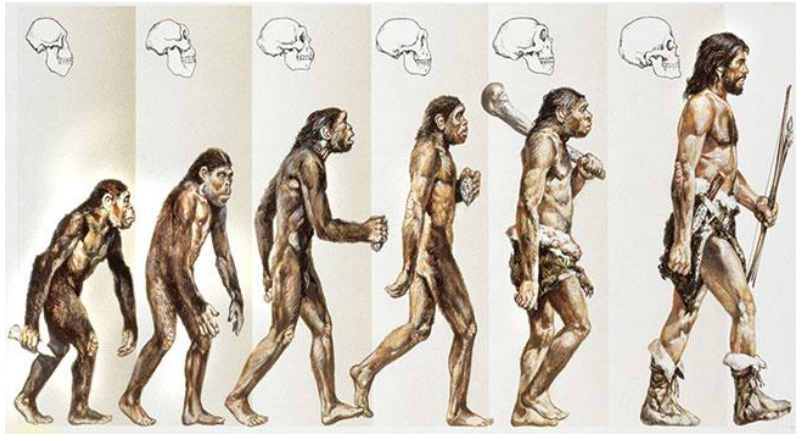
Long-term «directional selection» is **not** the rule



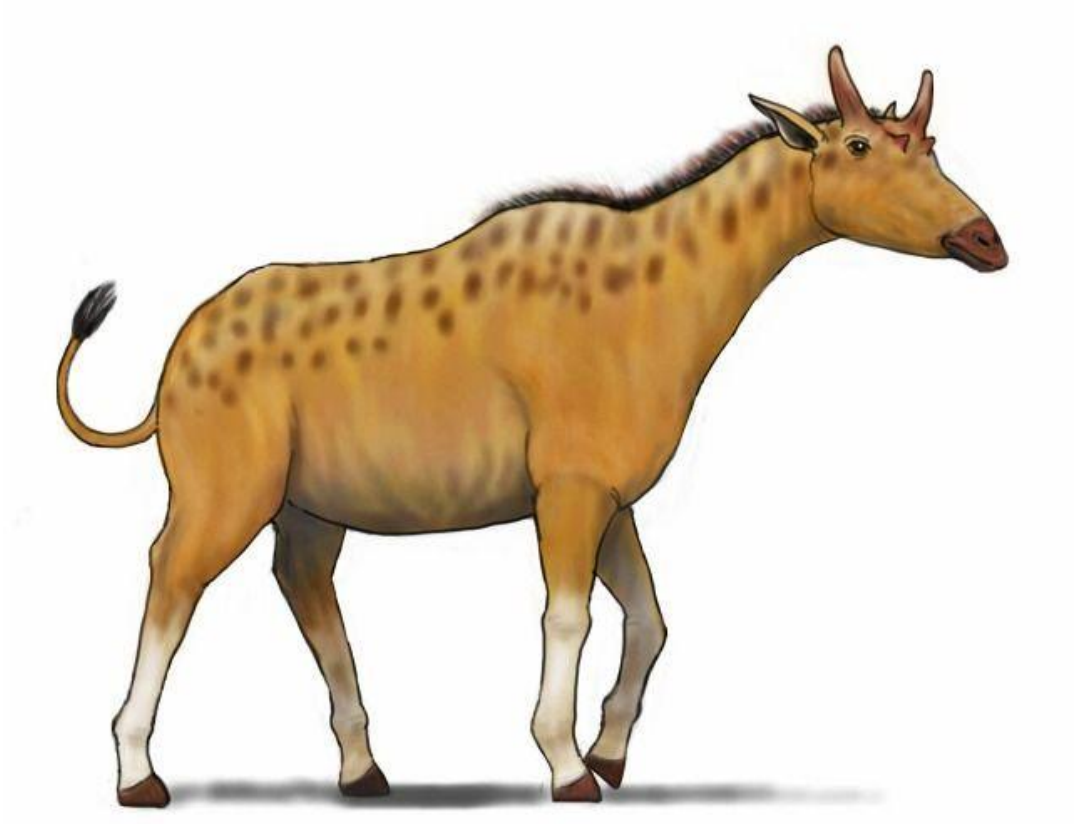






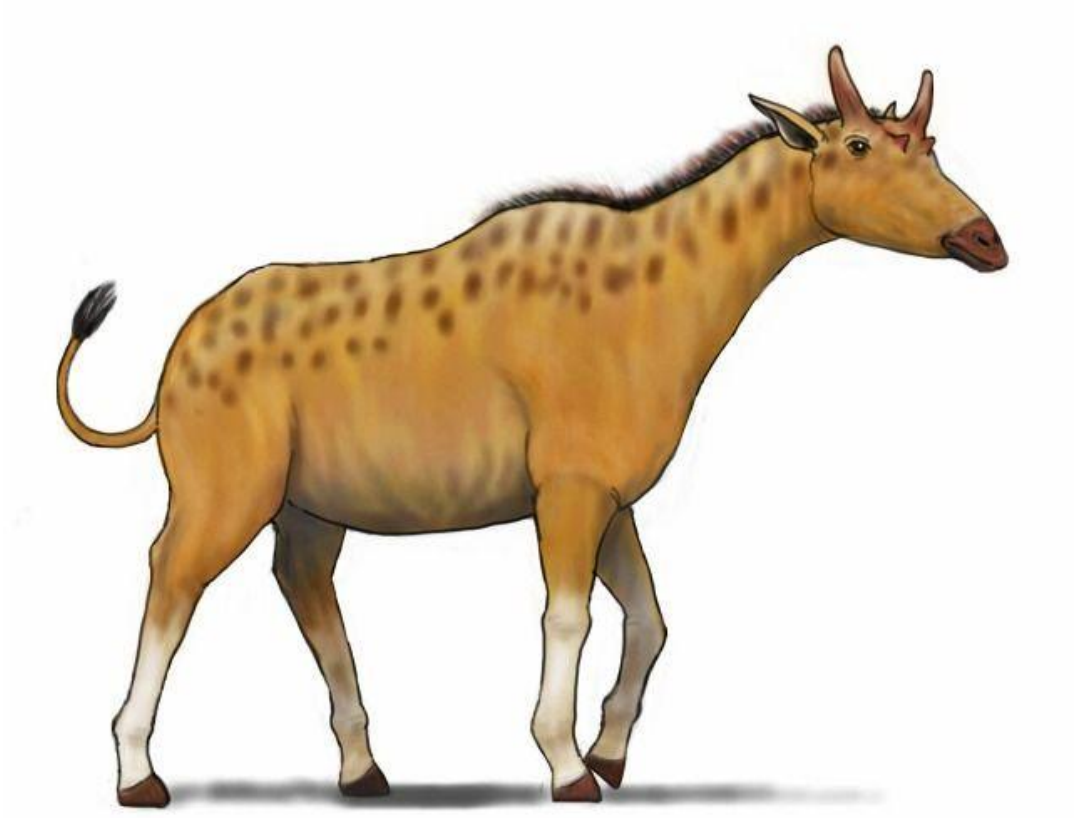


«Directional selection» is often an oversimplification



Samoitherium boissieri
9-7 million years ago

Selectively neglected taxa

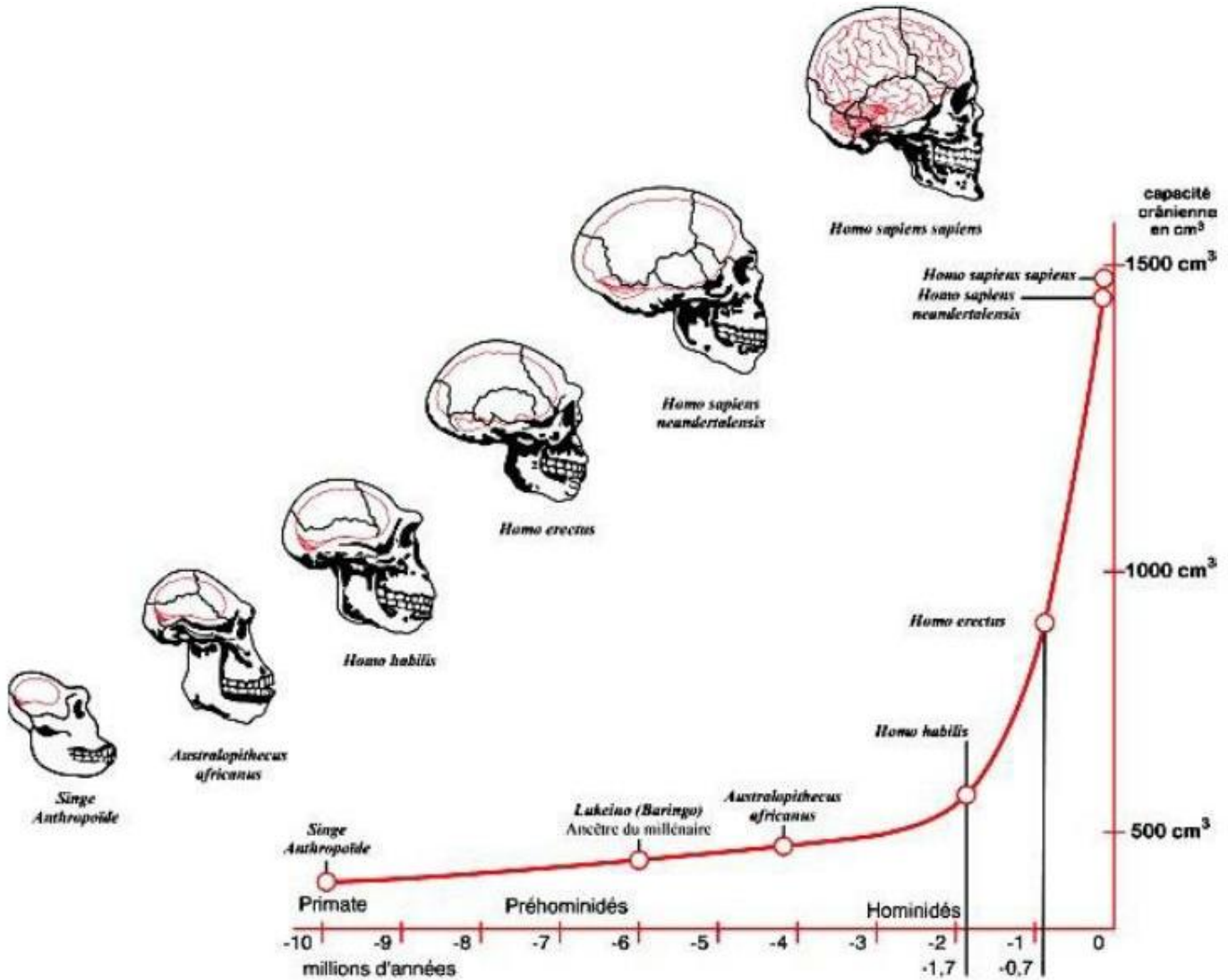


Samoitherium boissieri
9-7 million years ago

Okapia johnstoni (today)


Cacajao calvus
Homo sapiens
Cebus capucinus
Cheirogaleus major
Australopithecus afarensis
Aegyptopithecus zeuxis
Hylobates lar
Pan troglodytes

Encephalization among hominins



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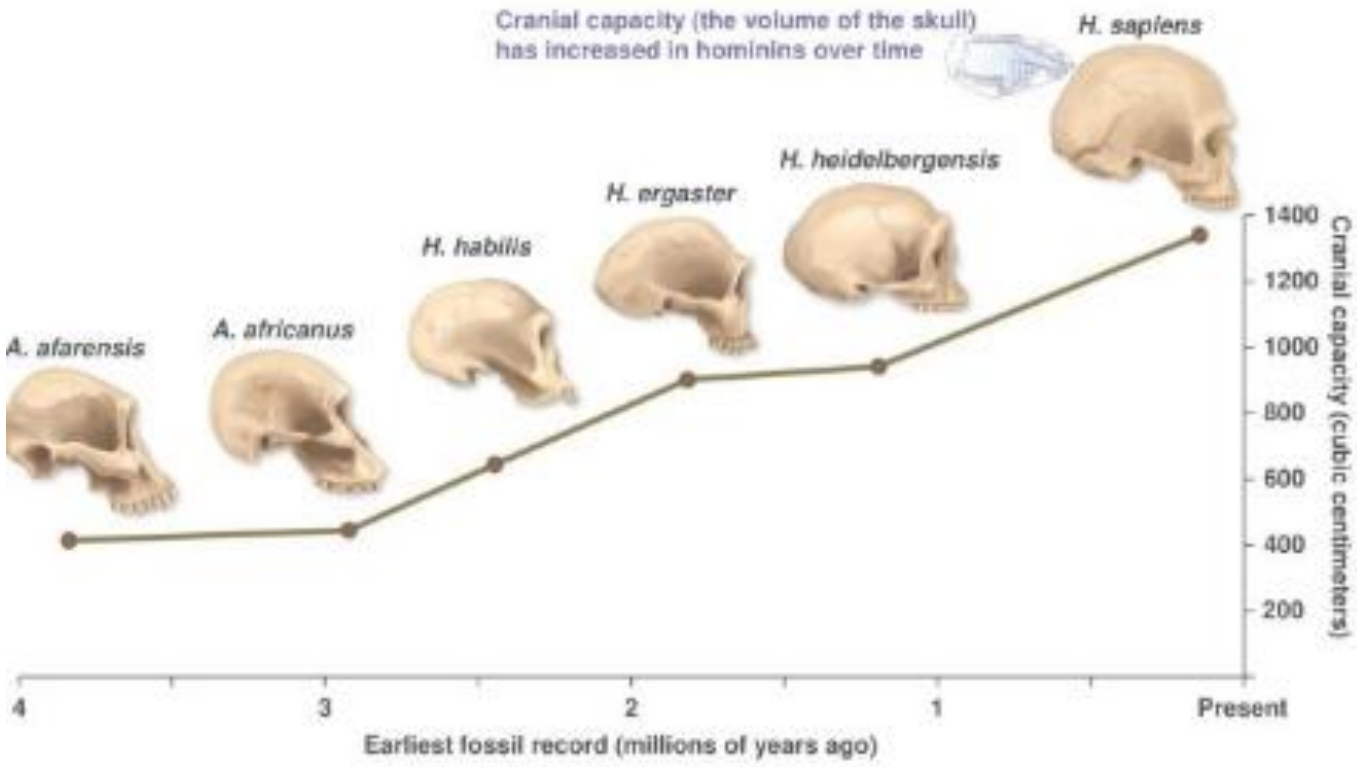

Actually Neanderthal brains were larger

(about 1450 cc vs 1350 cc)

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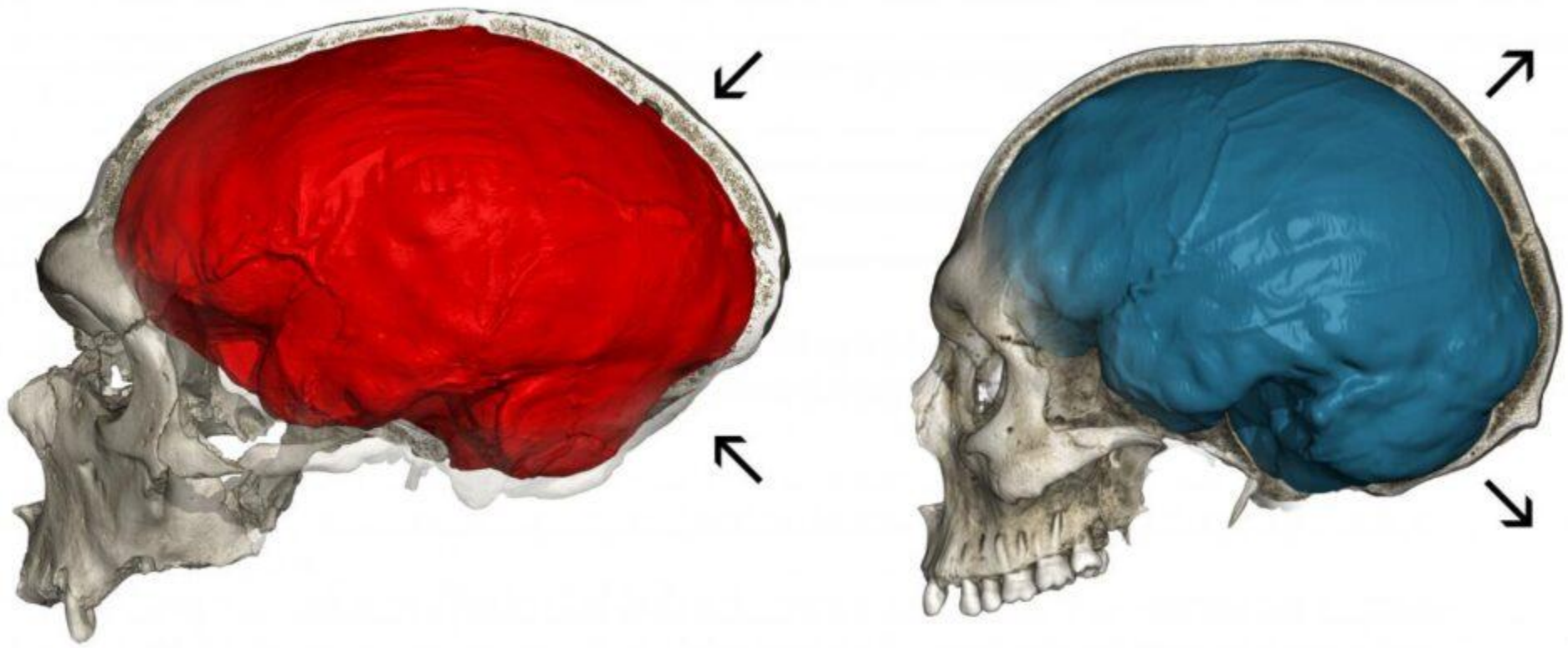

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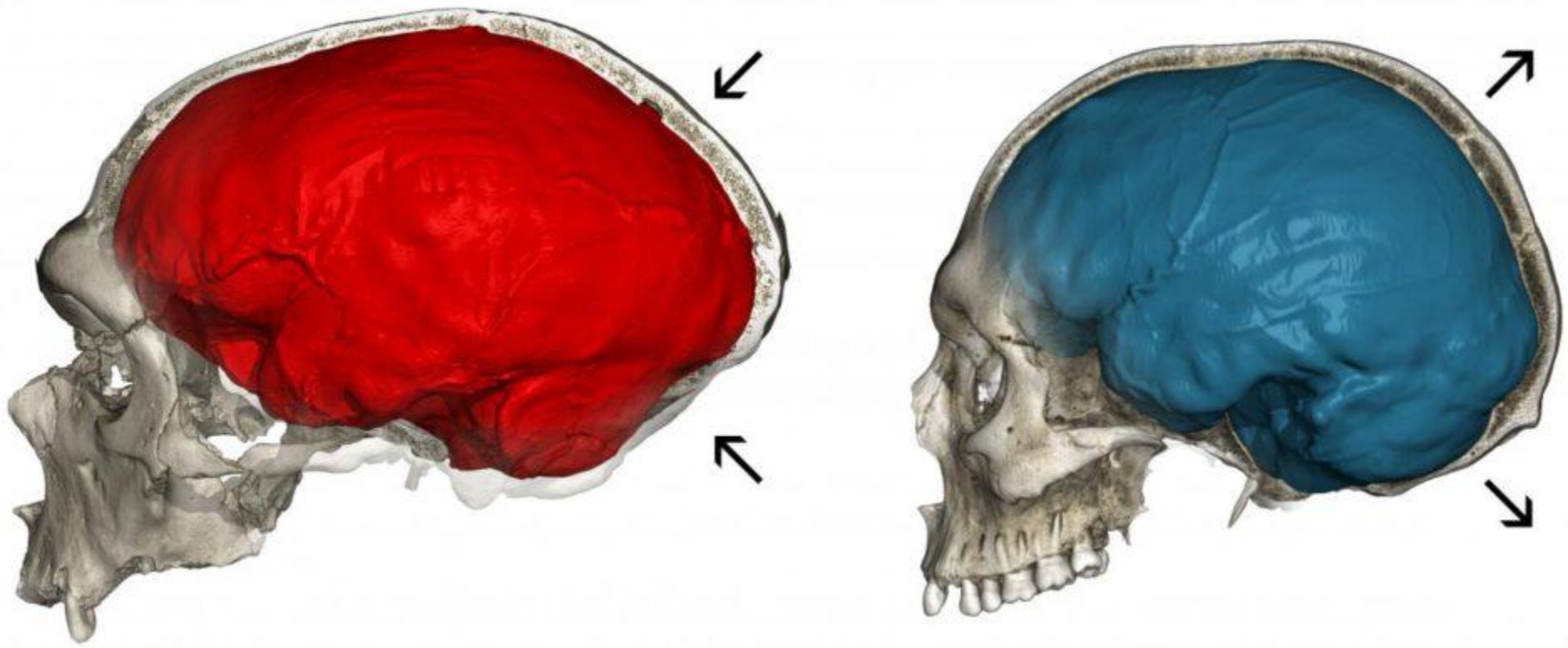
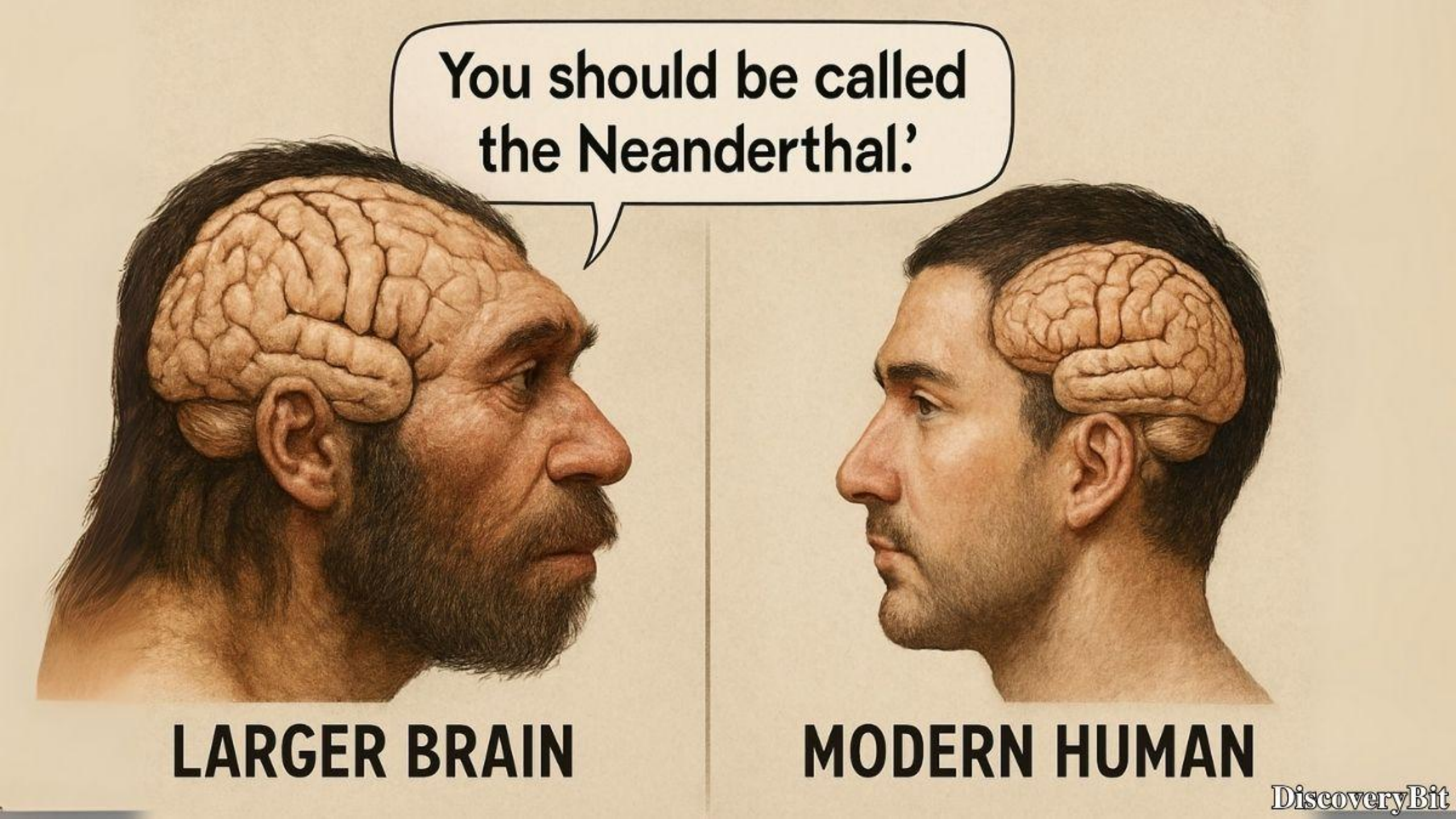
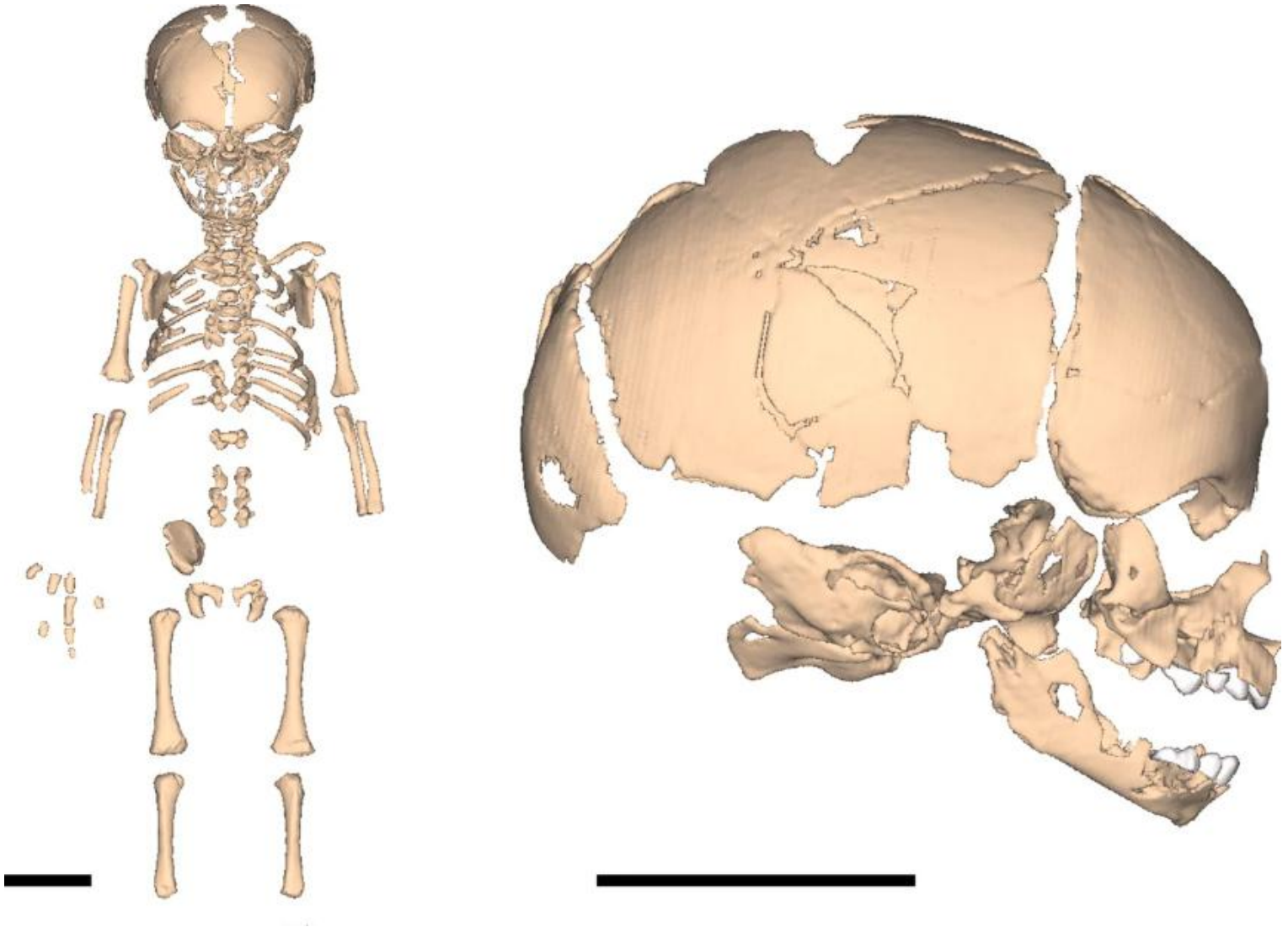
(about 1450 cc vs 1350 cc)





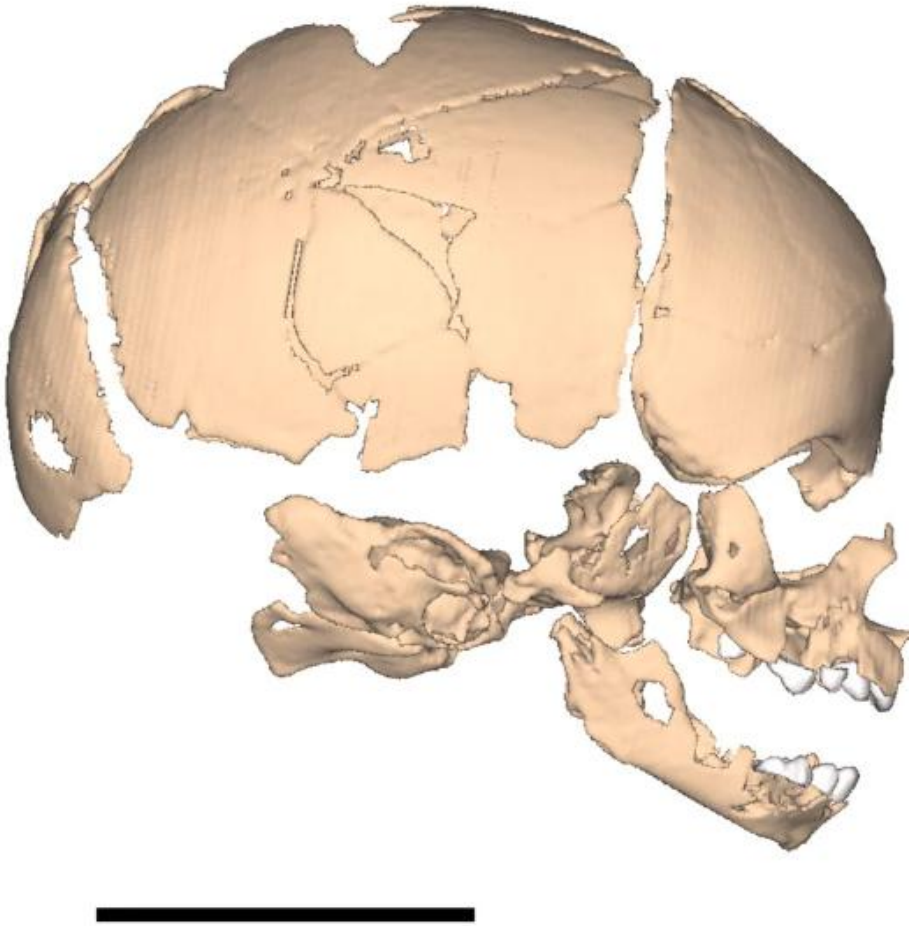
But they were growing faster..



Ponce de León et al.,2008, PNAS

But they were growing faster..

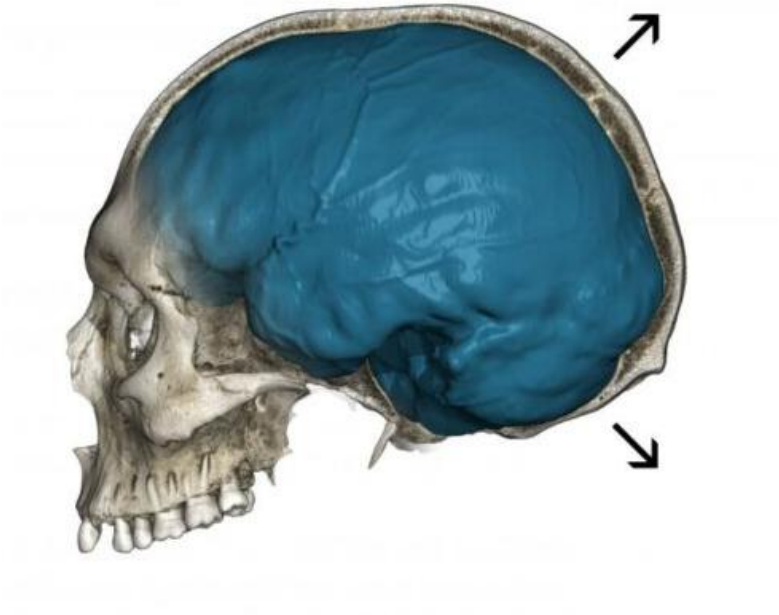
..so probably they were not «more intelligent»



Ponce de León et al.,2008, PNAS

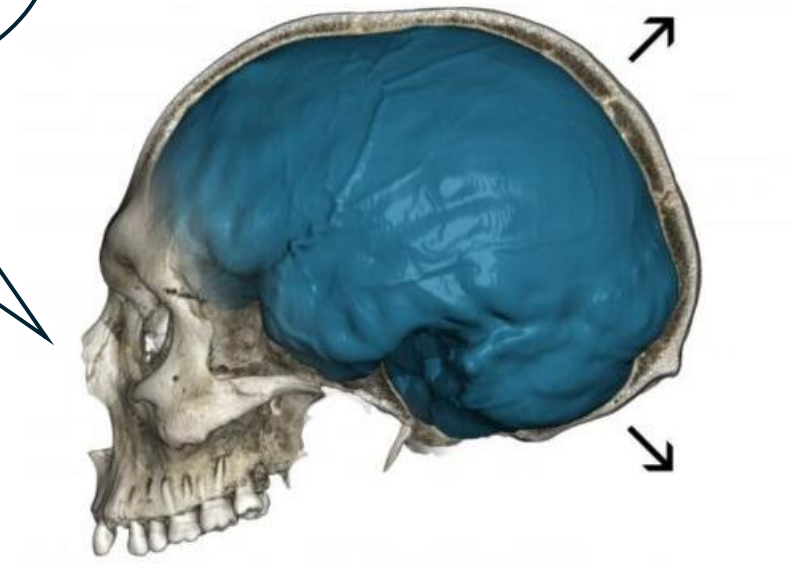
Brain Size vs Energetic Cost (Vertebrates)

- **Example: vertebrate brain evolution**
- **Trade-off:**
  Cognitive ability ↔ energetic cost
- Brains are extremely expensive organs.
- Humans:
  - brain ≈ **2% body mass**
  - consumes ≈ **20% of energy**
- The **expensive tissue hypothesis** proposes a trade-off between:
  - brain size
  - gut size
  - metabolic energy allocation.



Brain Size vs Ene… …rtebrates)

Even traits under apparent directional selection are subjected to **trade-offs** and **constrains**!



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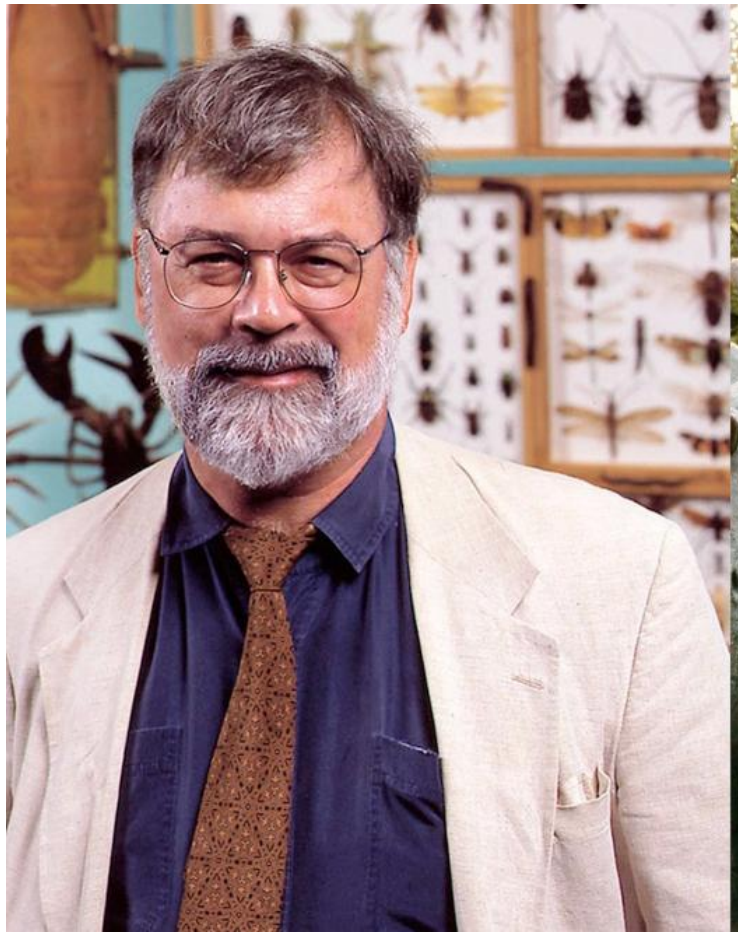
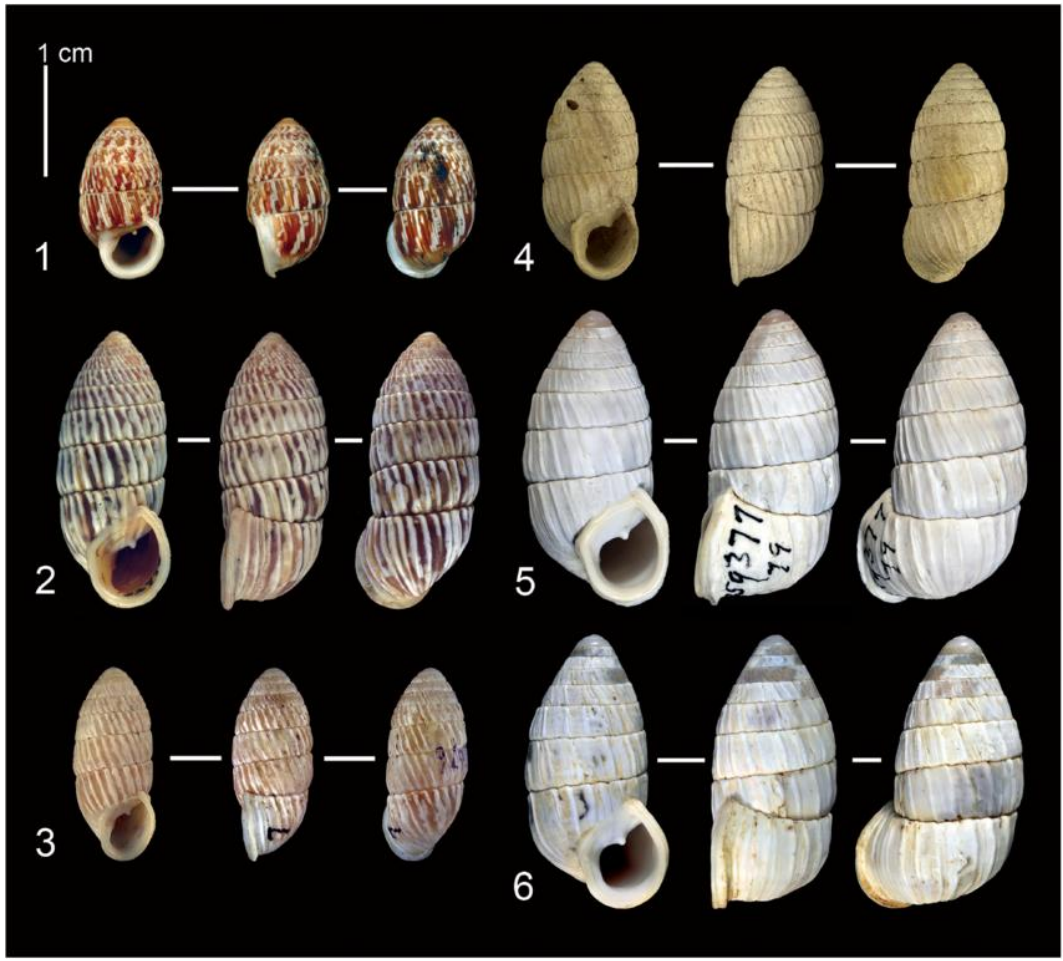
Fossil evidences on the pace of evolution



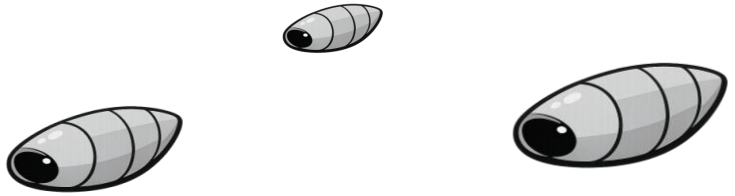
Niles Eldredge
(1943)

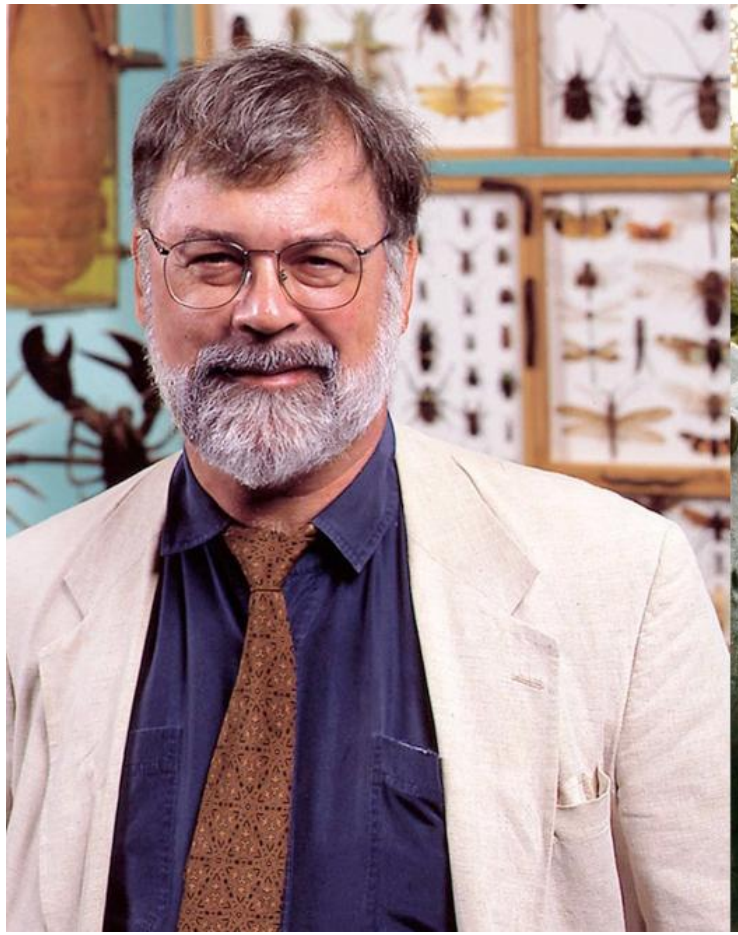
Stephen Jay Gould
(1941-2002)



Cerion (above) and *Poecilozonites* land snails

What do you think that they found?





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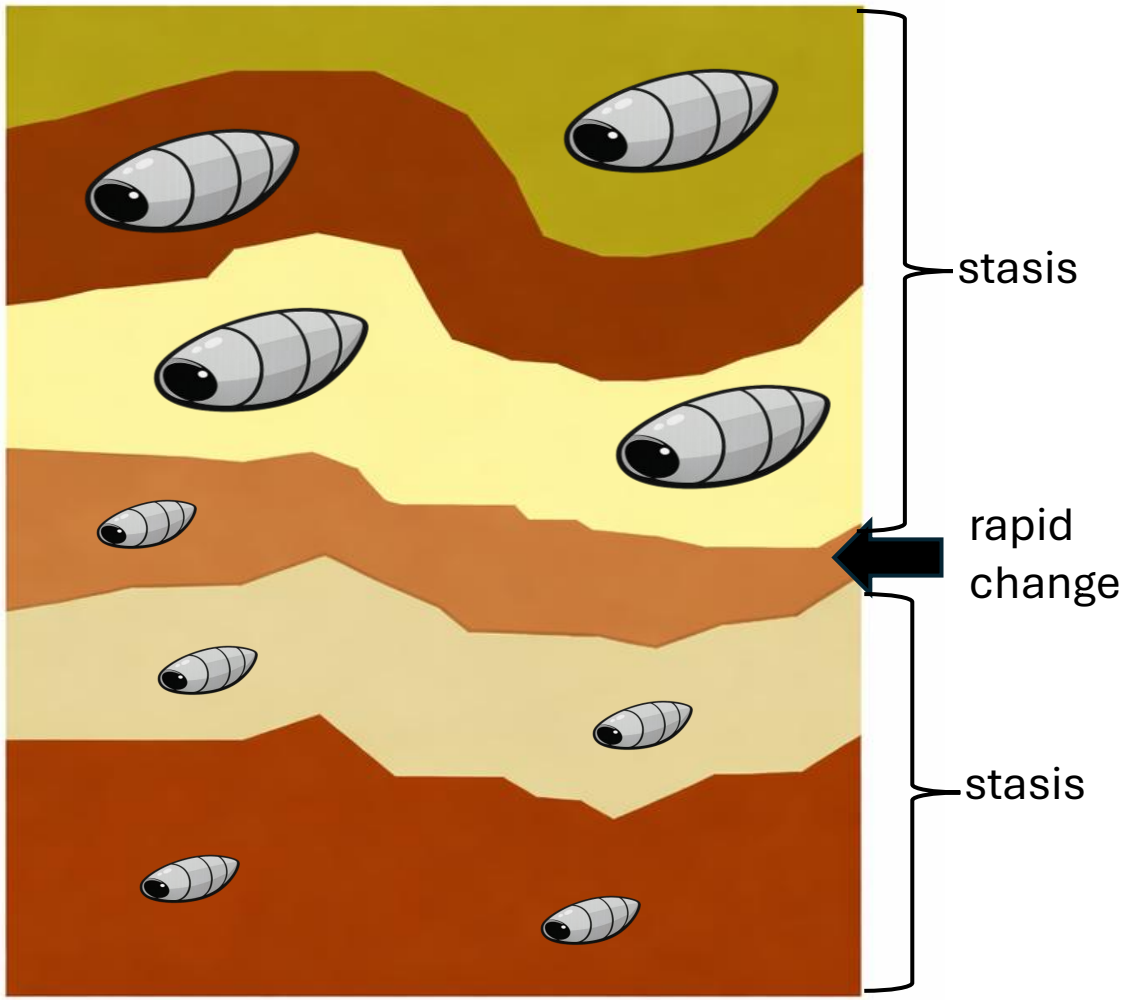
Punctuated equilibria

Evolution is generally not gradual and behave in «bursts» - long periods of stasis alternated with rapid events of change and diversification (Eldredge, N., & Gould, S. J. (1972), *Punctuated equilibria: an alternative to phyletic gradualism)*.

Punctuated equilibria



Gradual evolution

Punctuated equilibria

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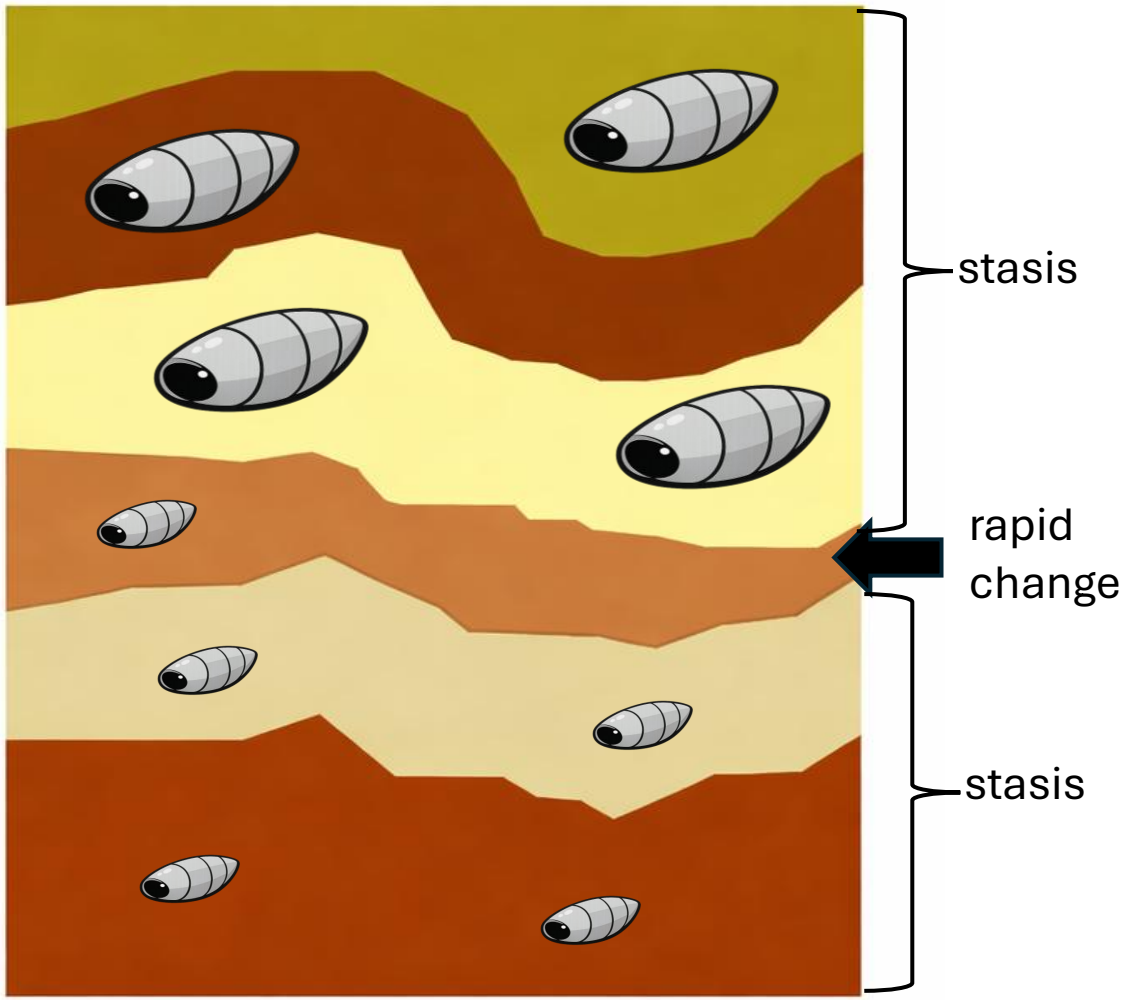
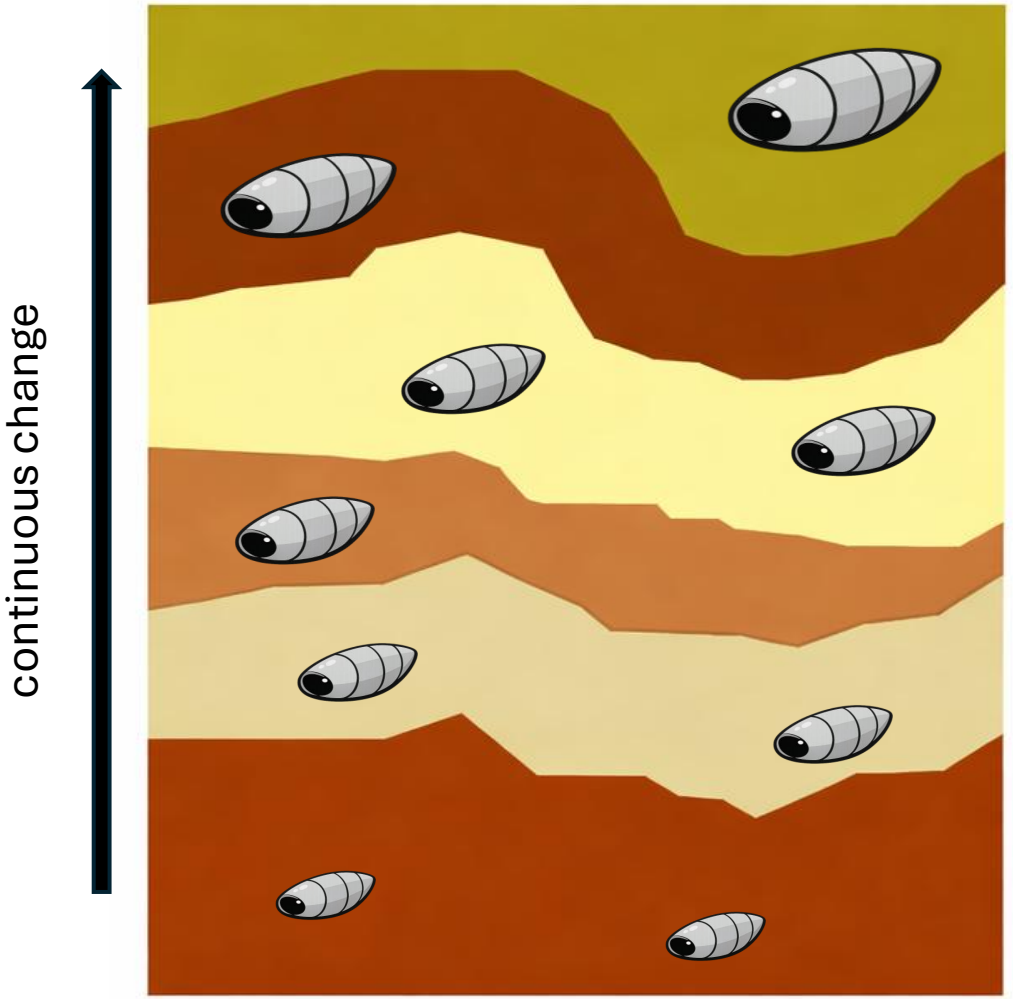


Gradual evolution



Punctuated equilibria

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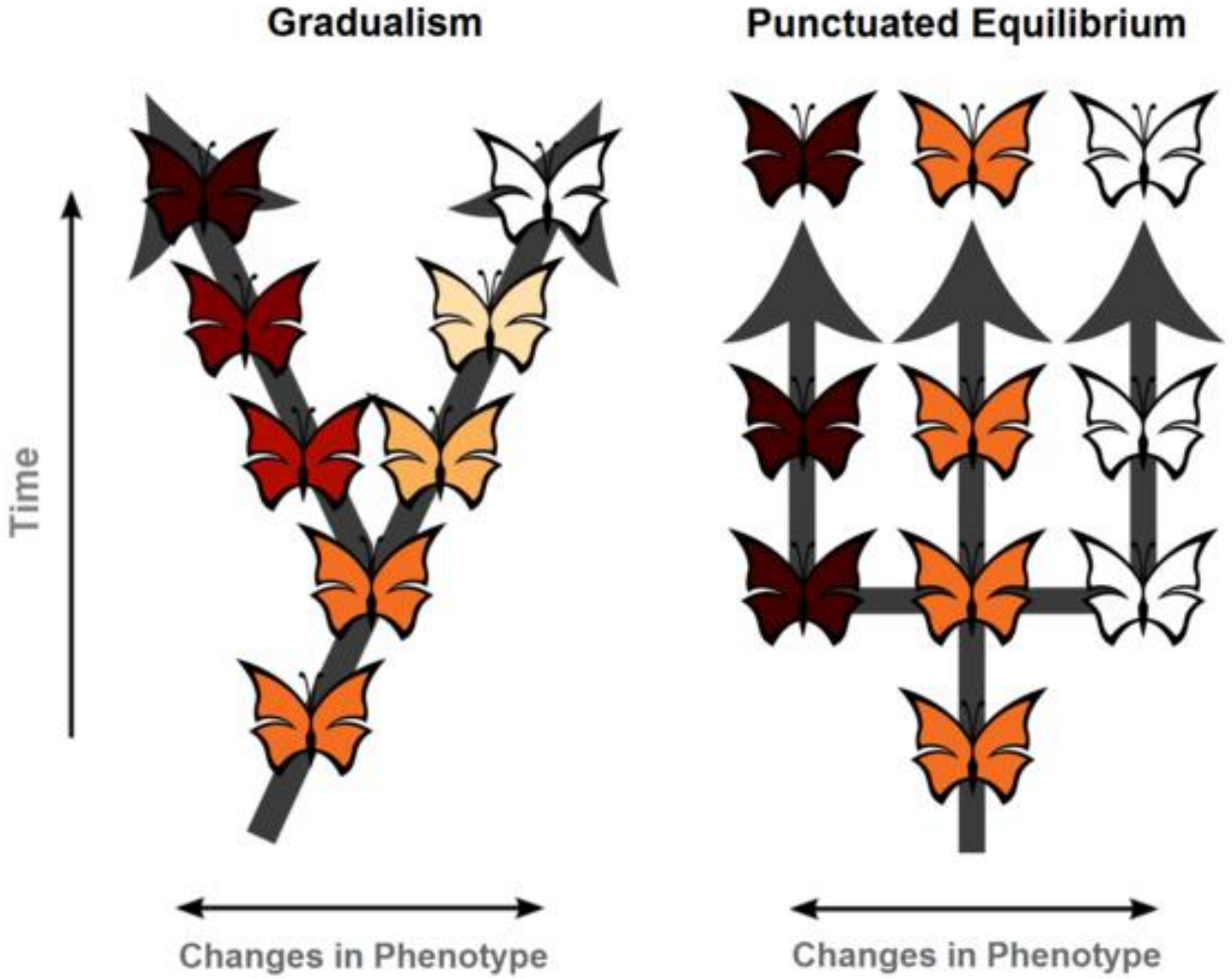
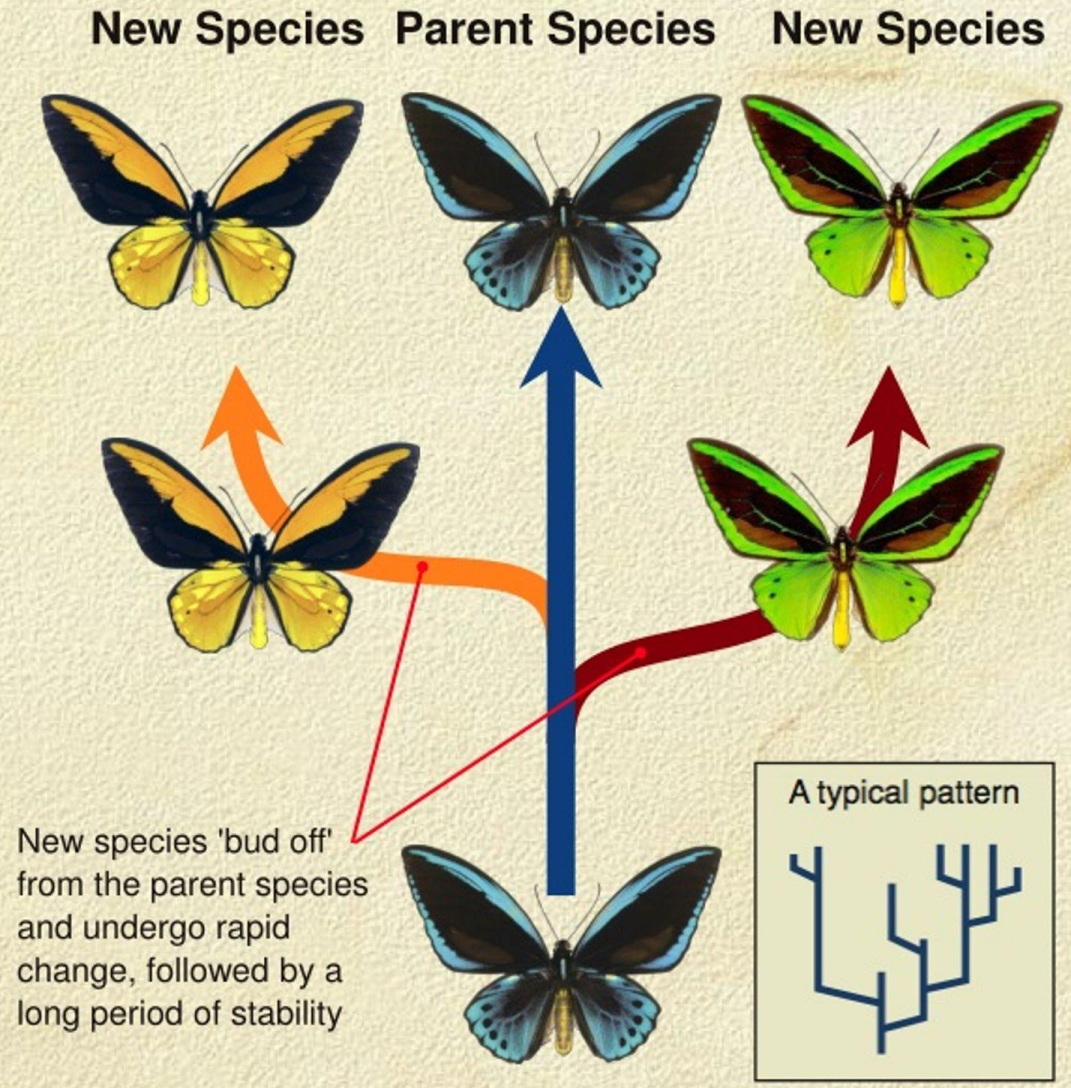


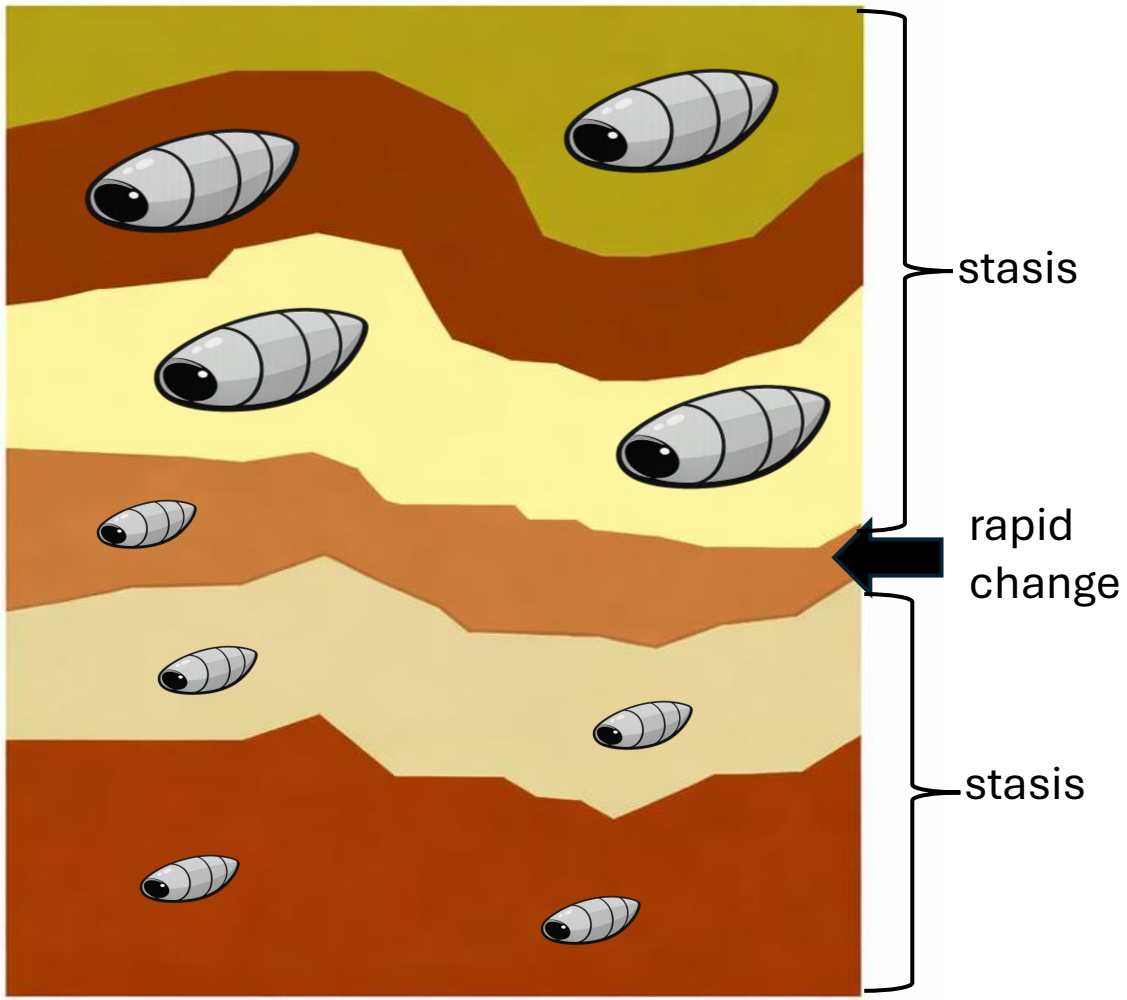
Punctuated Equilibrium

- There is abundant evidence in the fossil record that, instead of gradual change, species stay much the same for long periods (**stasis**) and then have short bursts of evolution that produce new species quite rapidly.
- According to this **punctuated equilibrium theory,** most of a species existence is spent in stasis and little time is spent in active evolutionary change.

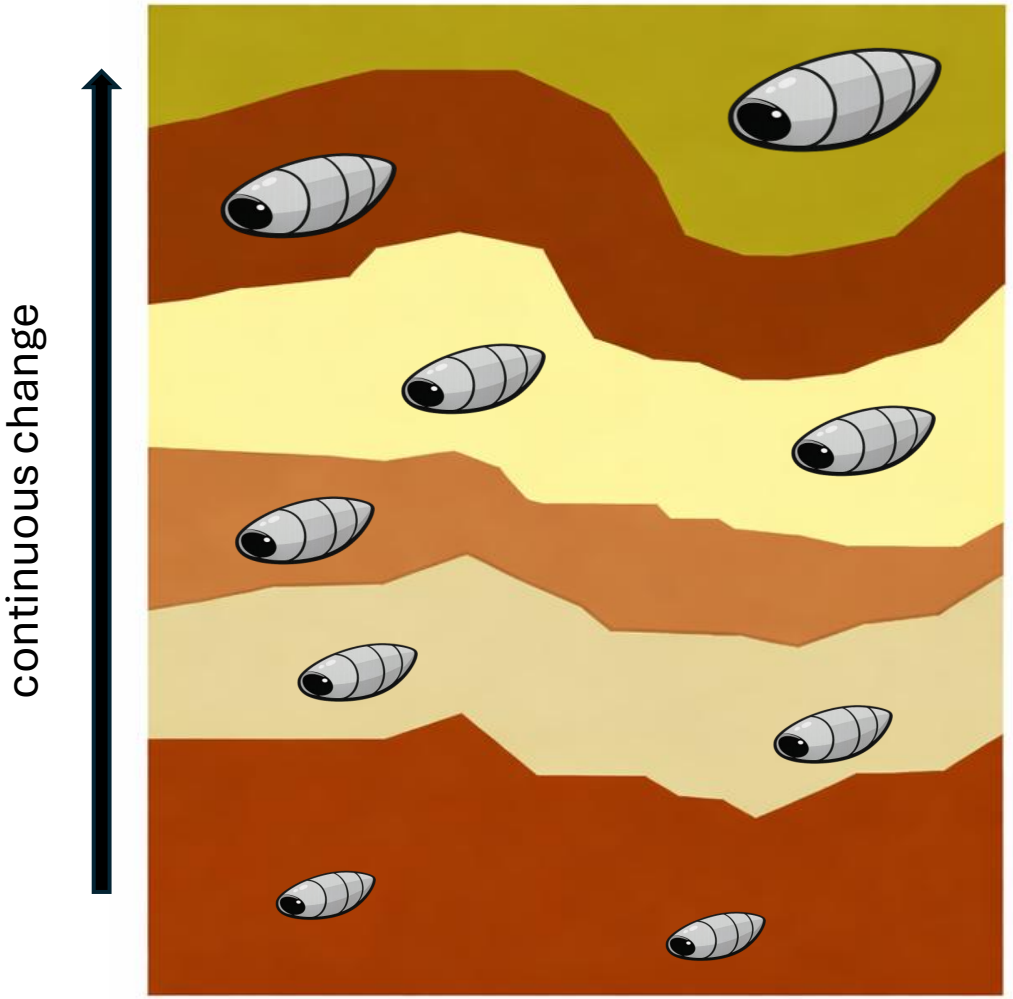


Why do we observed punctuated equilibria?

Punctuated equilibria

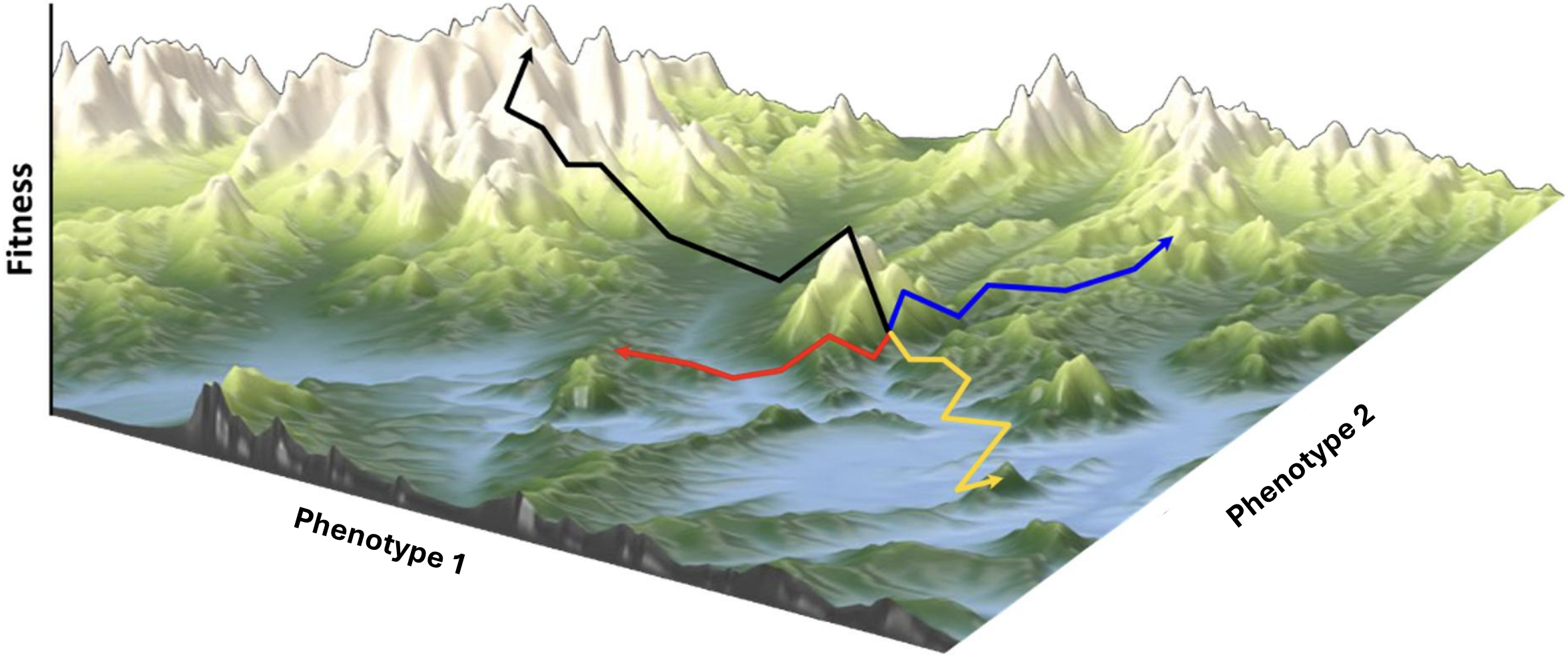


Gradual evolution

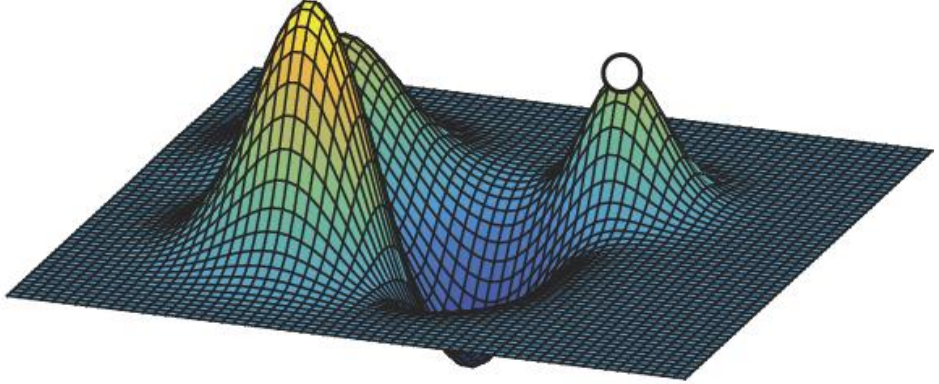


The environment can change

Even landscapes can change because of earthquakes!

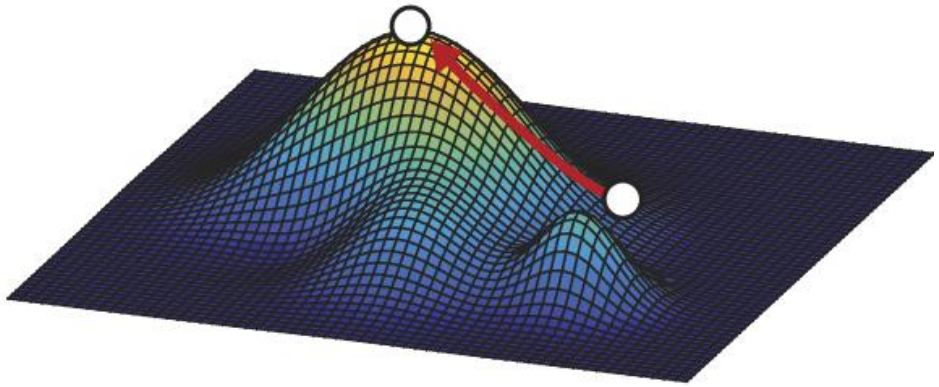


Sitting on a fitness peak → Stabilizing selection

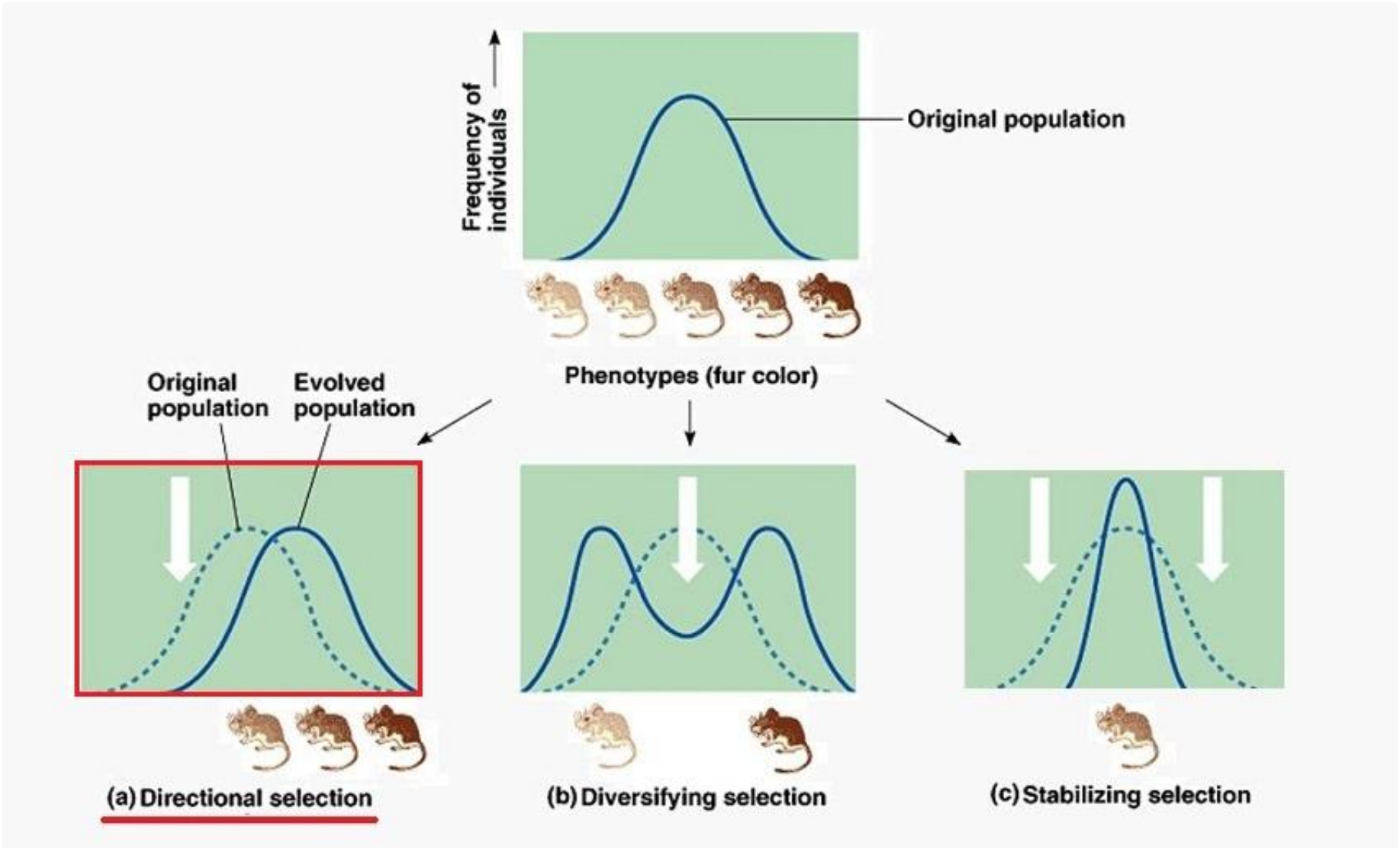


Environmental change

Climbing mount fitness → Directional selection

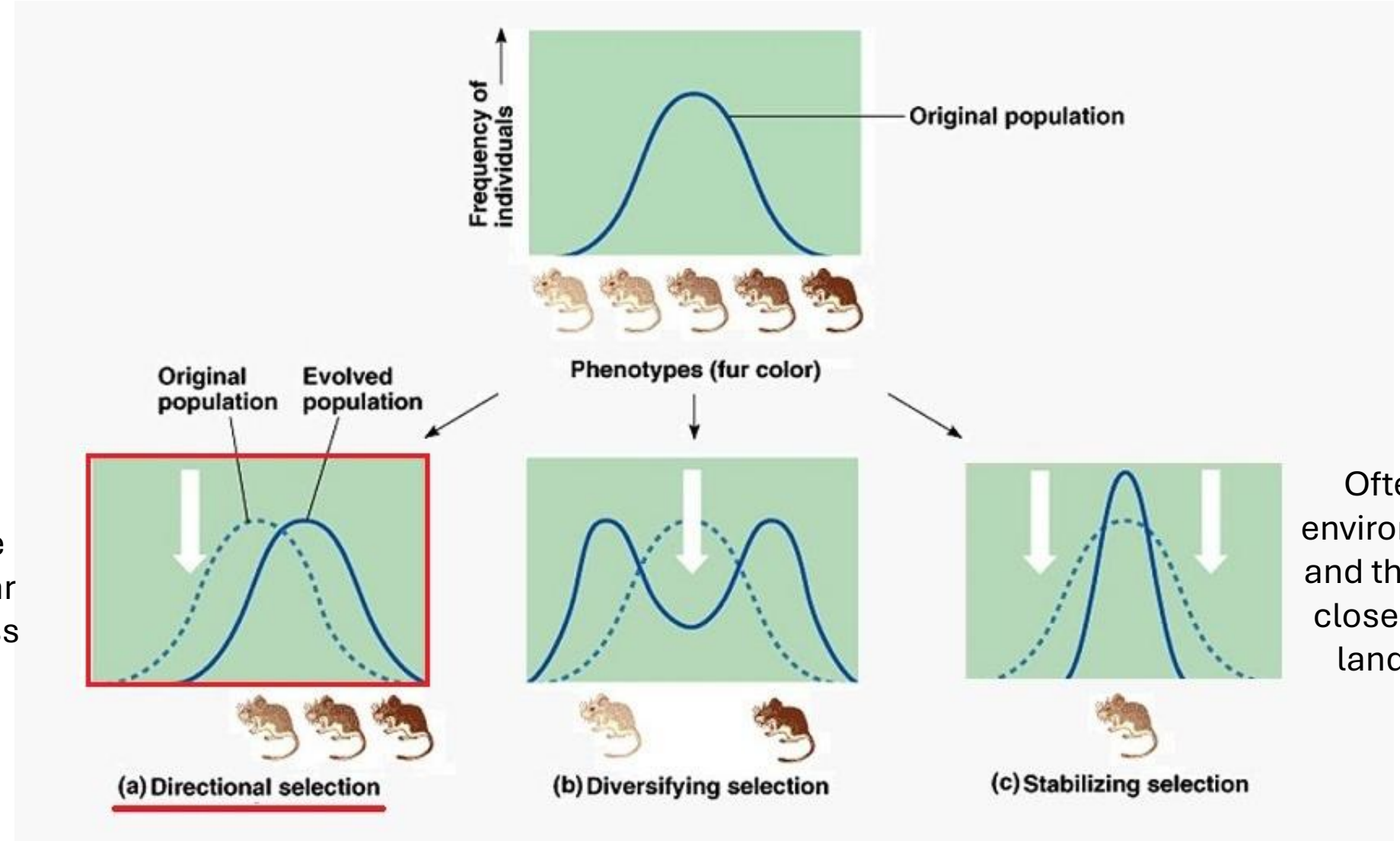


Modes of phenotypic evolution



Modes of phenotypic evolution

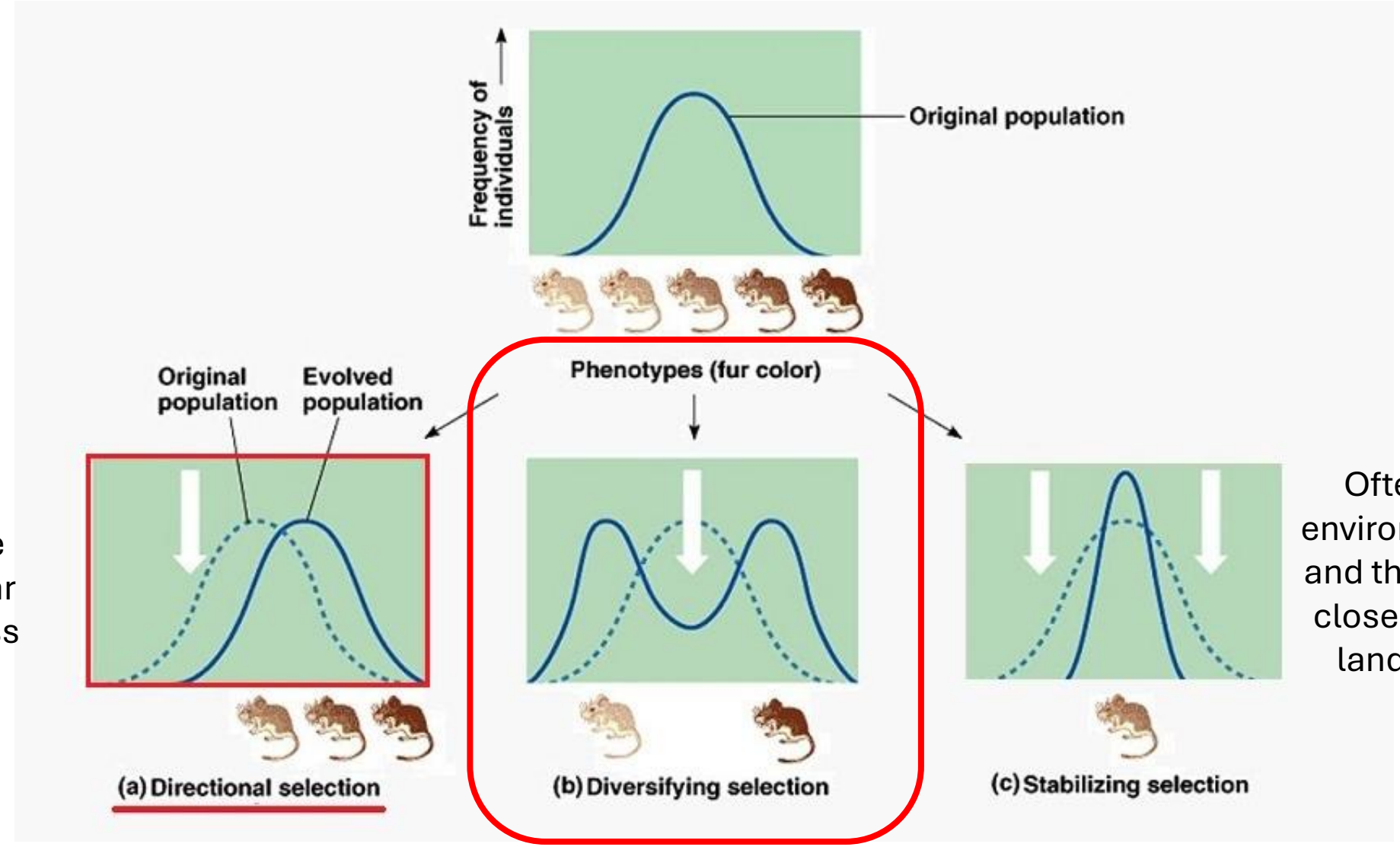
When the environment changes or the population is far from the «fitness peak»



Often, when the environment is stable and the population is close to the «fitness landscape peak»

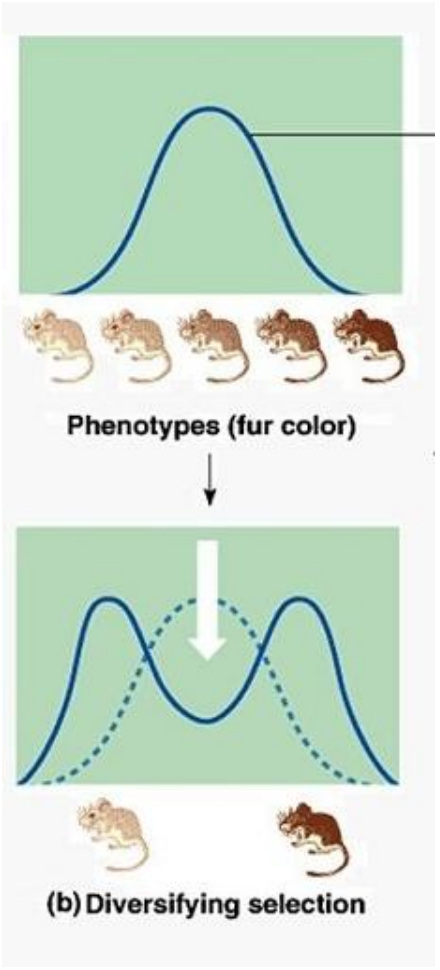
How would you see this in fitness landscapes?

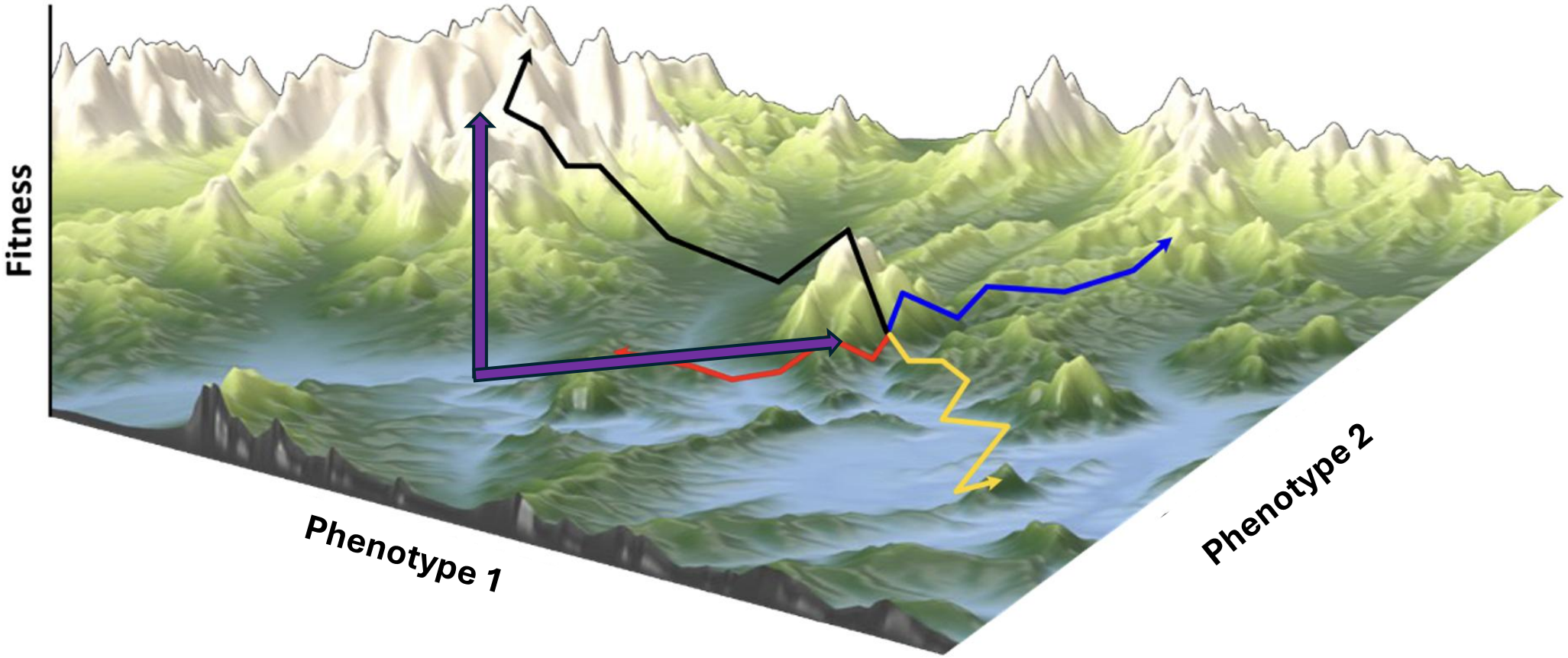
When the environment changes or the population is far from the «fitness peak»



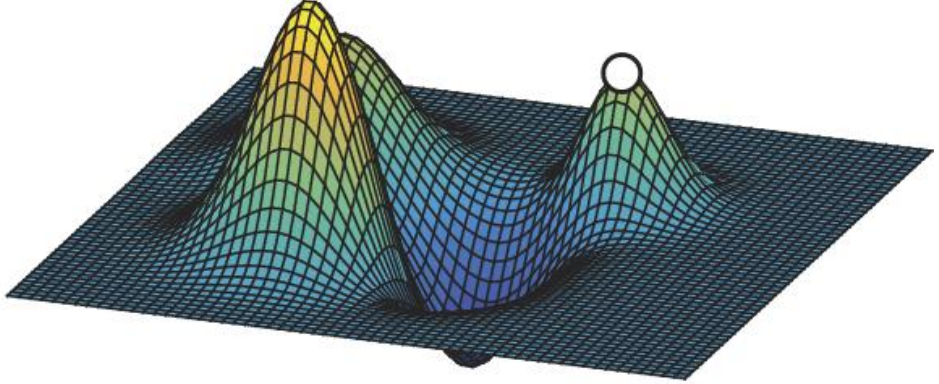
Often, when the environment is stable and the population is close to the «fitness landscape peak»

Divergence in fitness landscape

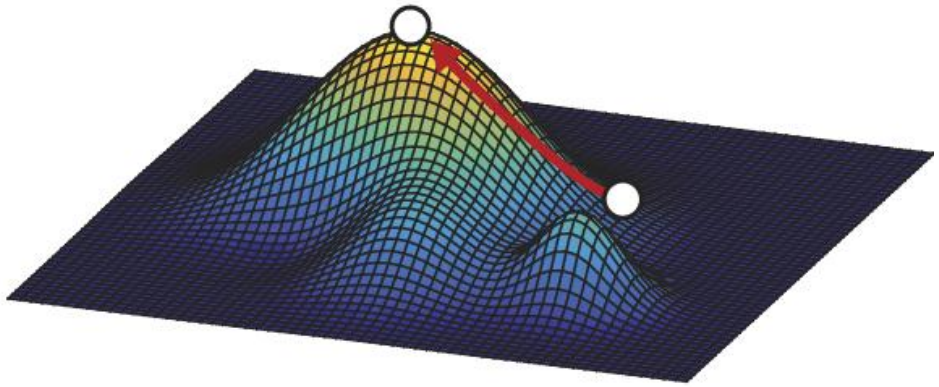




Sitting on a fitness peak → Stabilizing selection



Climbing mount fitness → Directional selection



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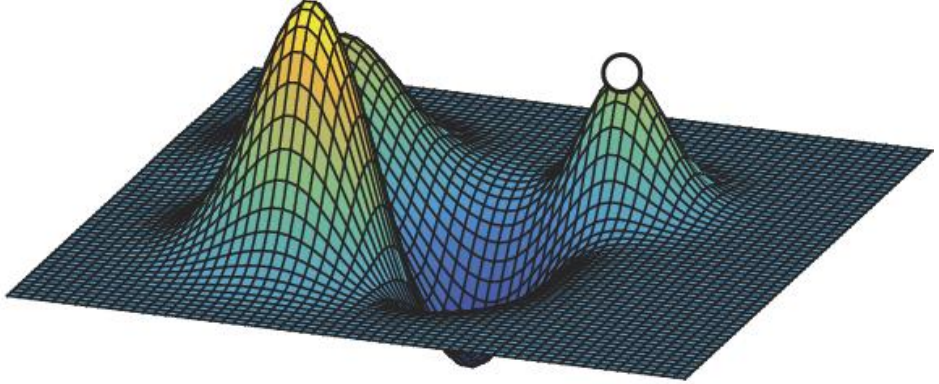

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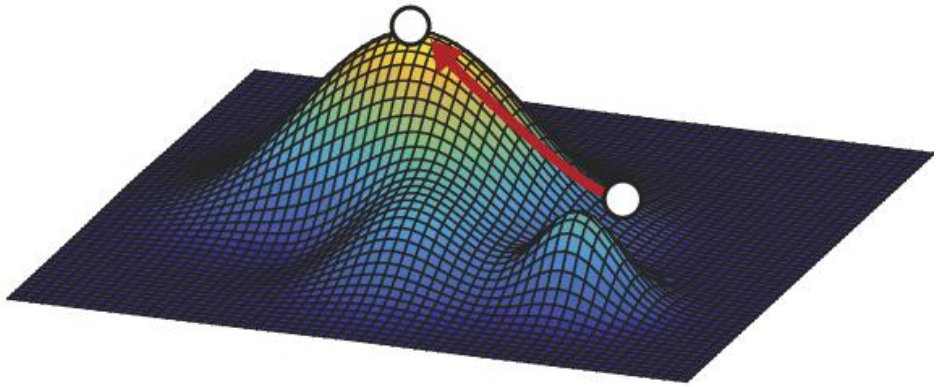
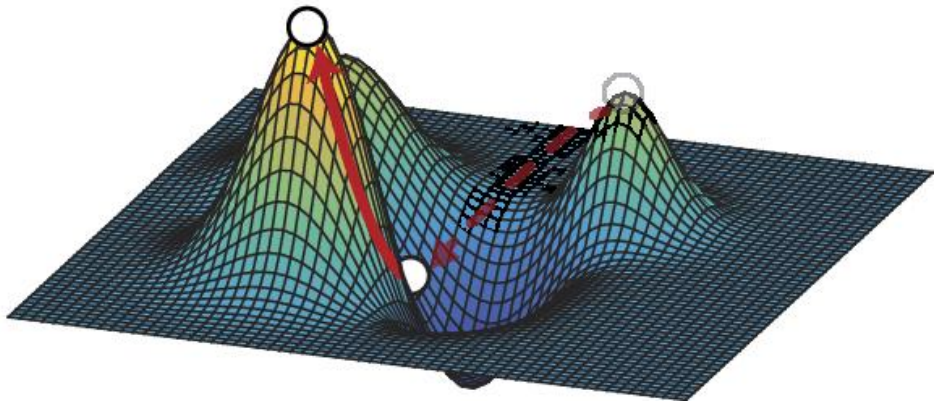
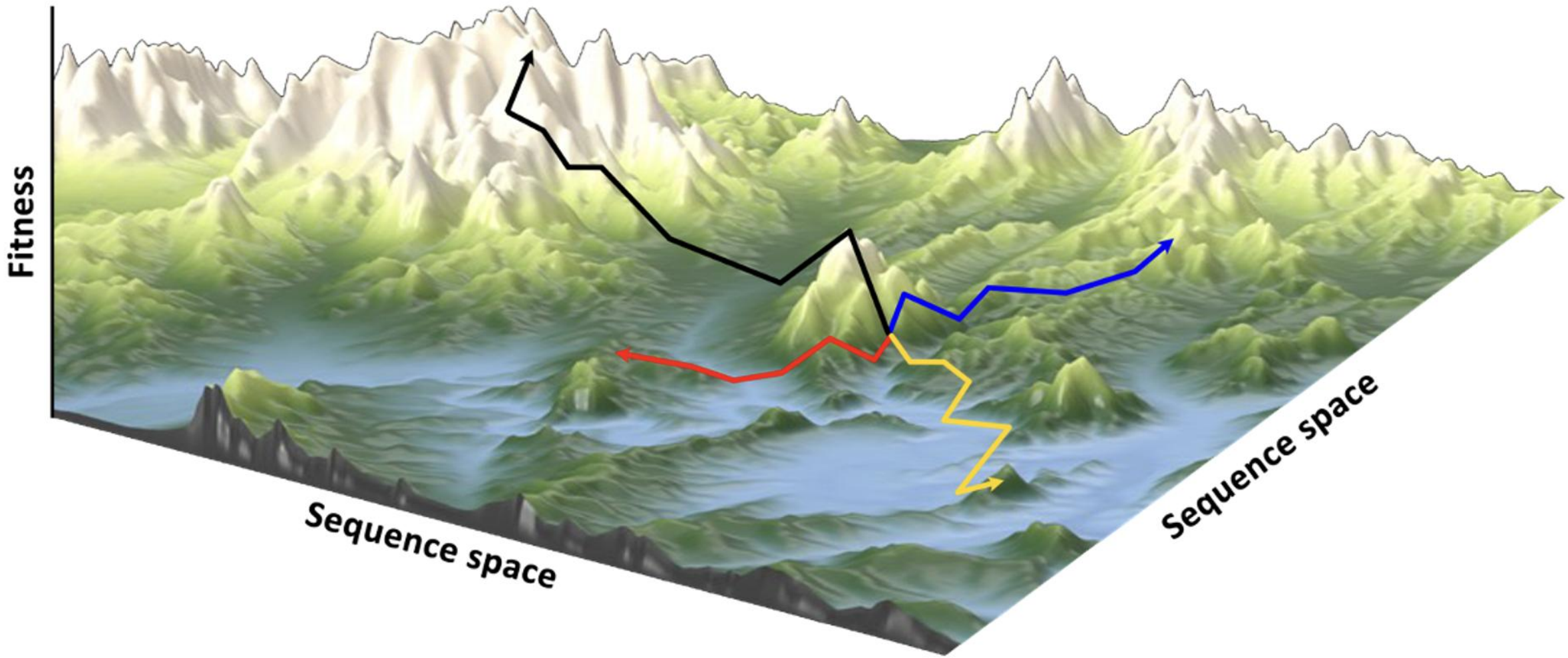


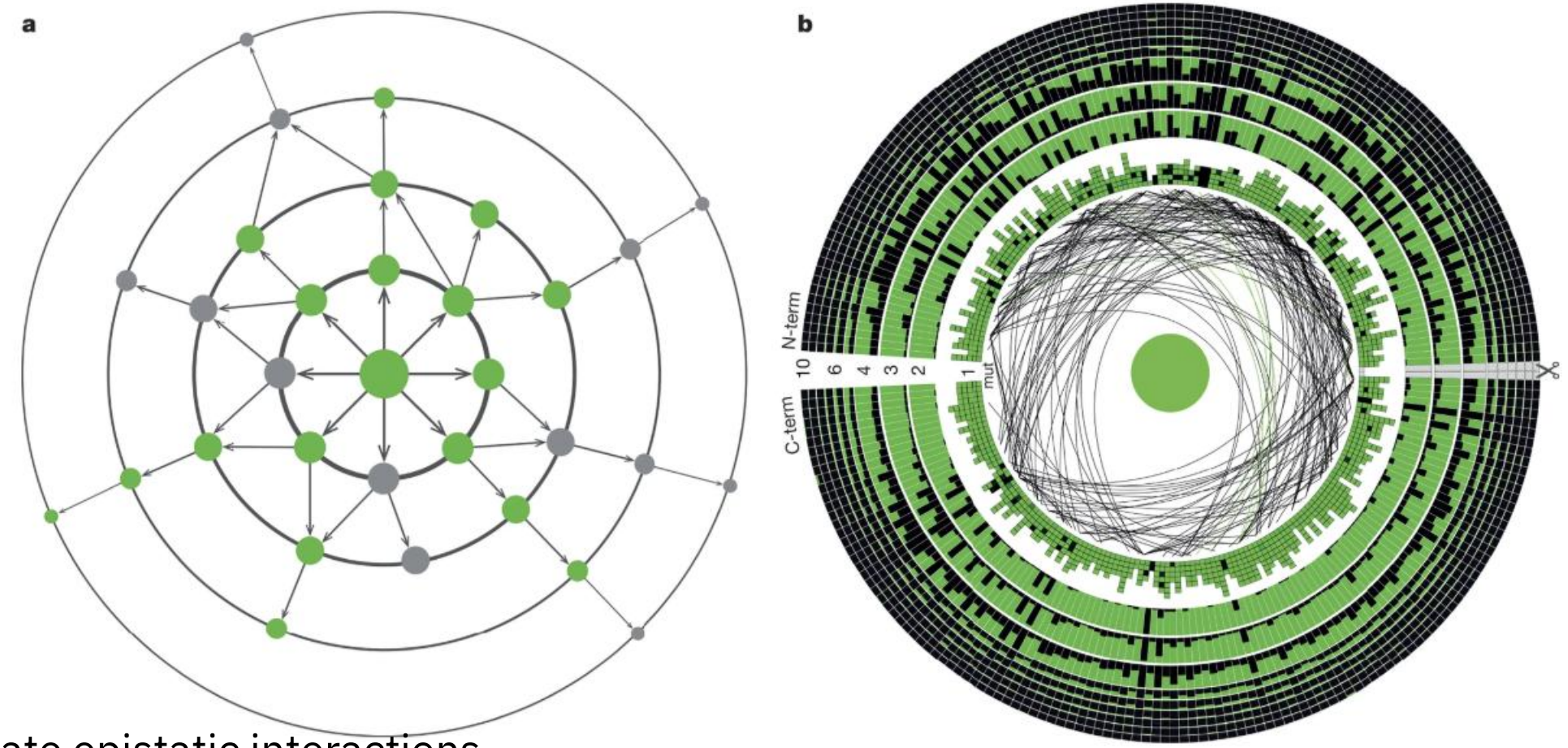
Overcoming fitness valleys How?



Fitness landscape can describe the evolution of molecules, genomes and proteins



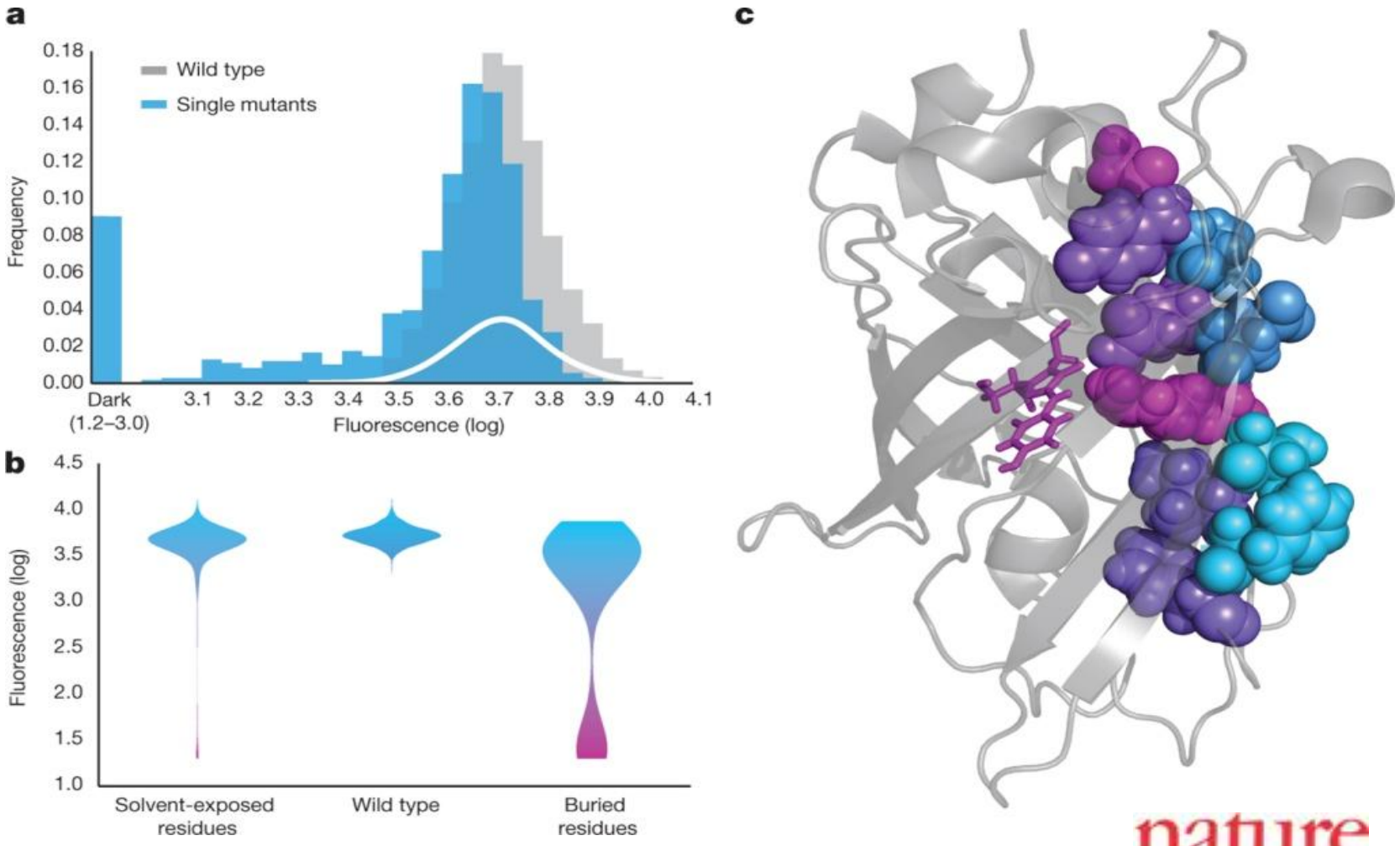
Local fitness landscape of the green fluorescent protein | Nature



- Lines indicate epistatic interactions
- More external circles indicate more mutations from the wild-type (so the squares indicate individual mutations)
- Green indicates the level of fluorescence

Local fitness landscape of the green fluorescent protein | Nature

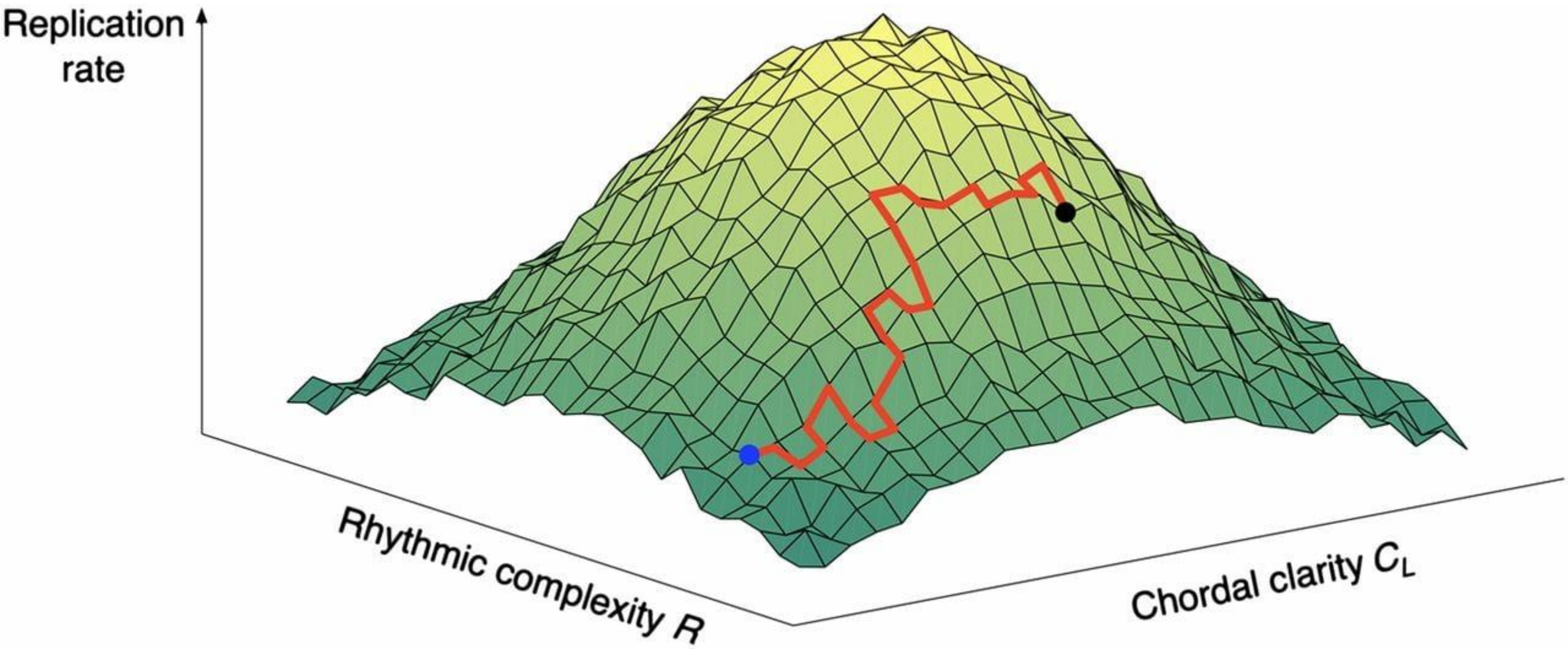
The effect of single mutations on avGFP



K S Sarkisyan *et al. Nature* 1–5 (2015) doi:10.1038/nature17995

Adaptive walks on the fitness landscape of music

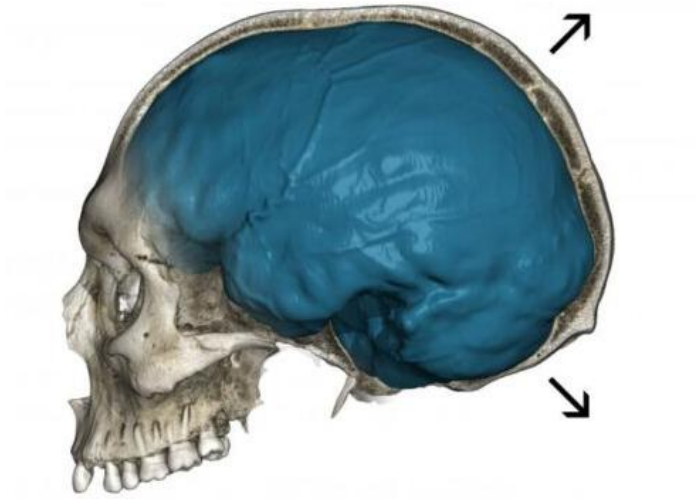
Christoph Adami[1]
Department of Microbiology and Molecular Genetics and BEACON Center for the Study of Evolution in Action, Michigan State University, East Lansing, MI 48824



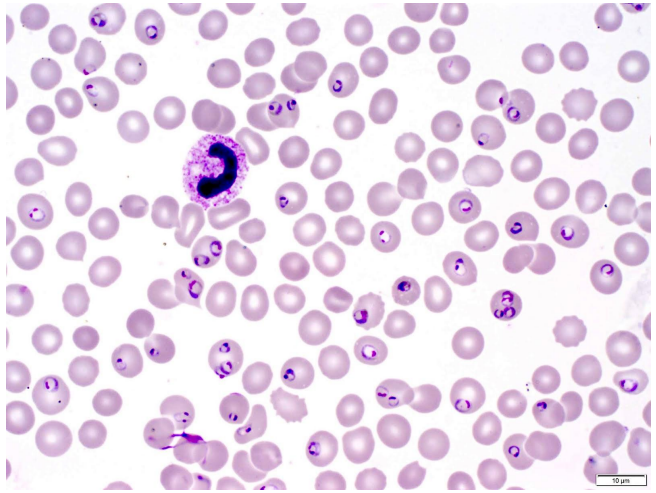
Conclusions

- Phenotypes are usually shaped by evolutionary **trade-offs**

Ecology



Anatomy



Epidemiology

Behavior

Conclusions

- Phenotypes are usually shaped by evolutionary **trade-offs**
- Evolutionary trade-offs generate **stabilizing selection**
- Evolutionary trade-offs can be described by «fitness functions», which can model physiological, ecological, behavioral, anatomical and developmental contrains
- Fitness can be represented by a «**fitness landscape**» and evolution as a walk on such landscapes
- Of course **directional selection** (climbing peaks in the fitness landscape) occurs but it not necessarily the norm
- «**Fitness valleys**» can separate «peaks» in the landscape and help predict evolutionary paths (even in the molecular context)

Conclusions

Also please choose better Valentine’s day gifts