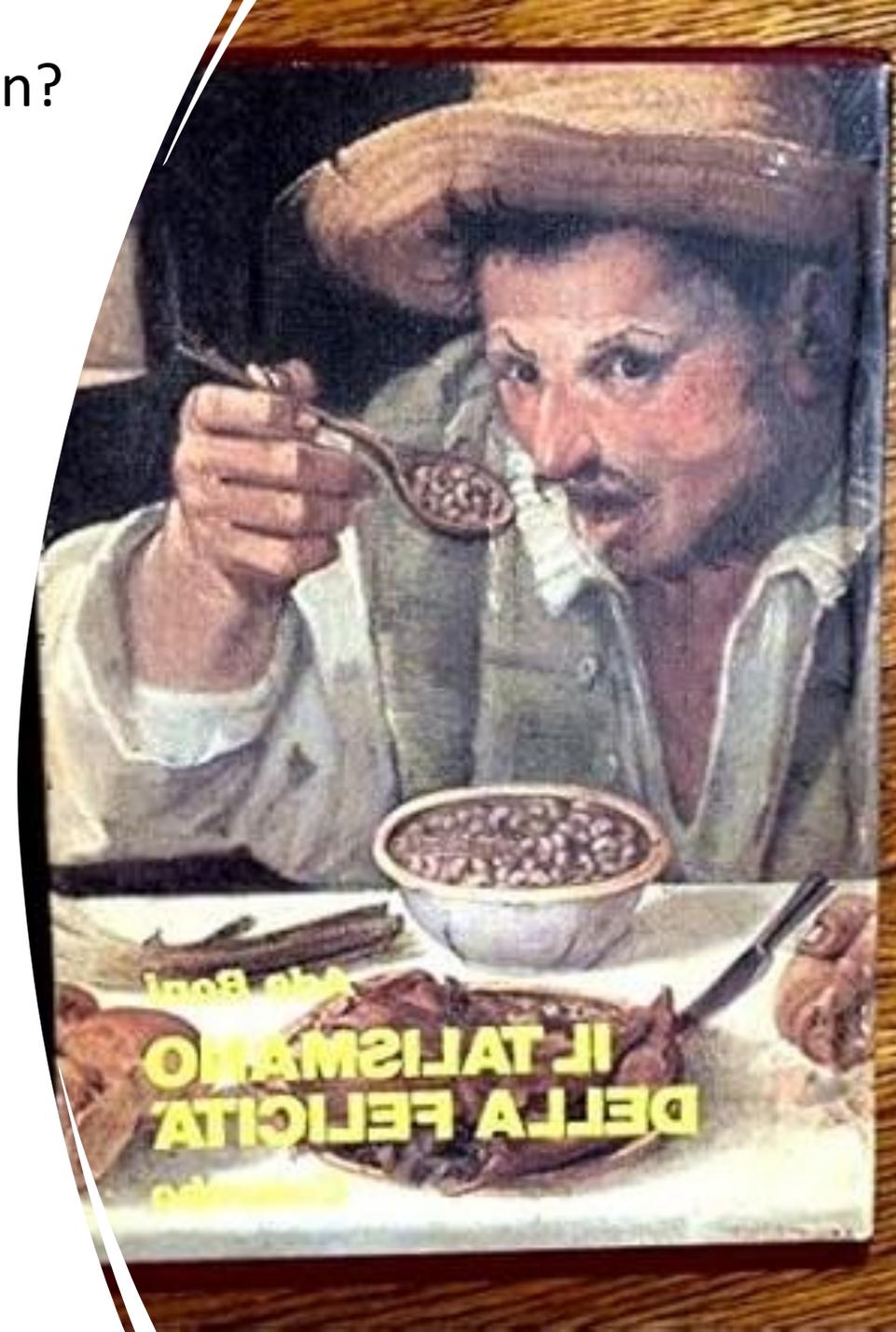


What are the basic ingredients of natural selection?

Your suggestions

- Natural selection/filter
- Environmental change
- Resources
- Competition
- DNA
- Inheritance
- Mutations
- Variability



What are the basic ingredients of natural selection?
Your suggestions

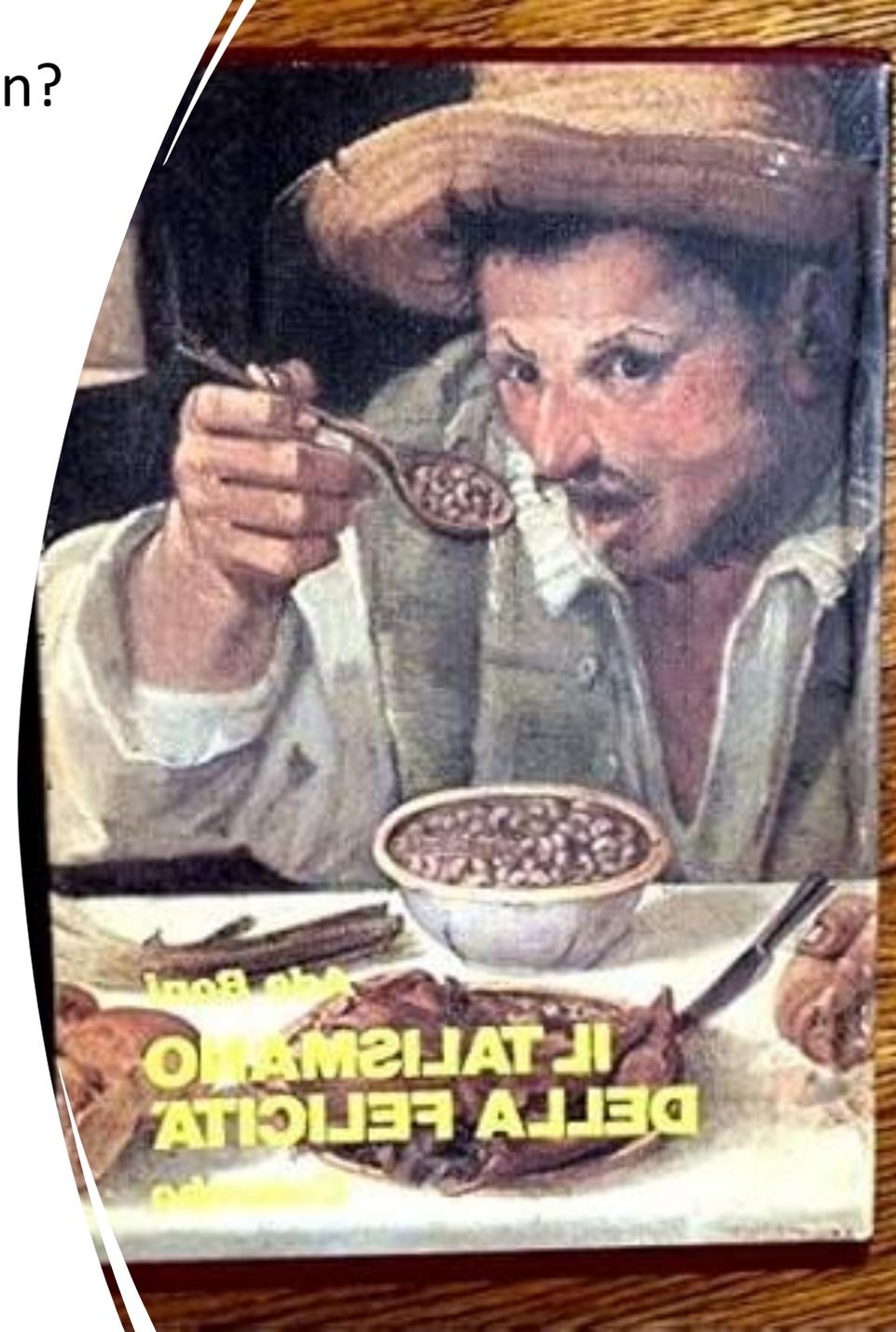
- **Natural selection/filter**
- Environmental change
- Resources
- Competition
- DNA
- Inheritance
- Mutations
- Variability



What are the basic ingredients of natural selection?

Your suggestions

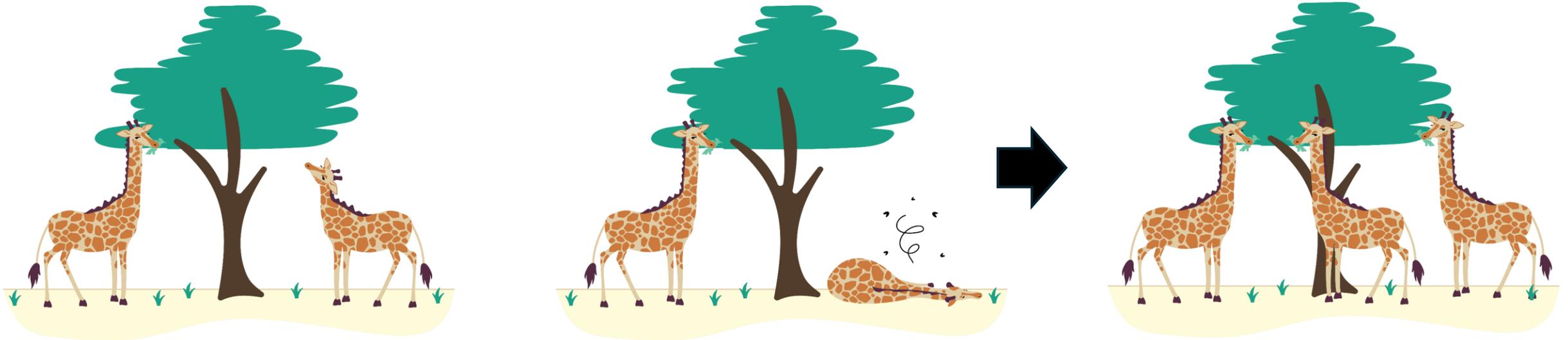
- **Natural selection/filter**
- Environmental change
- Resources
- Competition
- DNA (not only)
- **Inheritance**
- Mutations
- **Variability**



What are the basic ingredients of natural selection?

In other words, what do we need to make it work?

- **Variability** among individuals
- Differential contribution to successive generations (**Natural selection**)
- Mechanism of **inheritance**



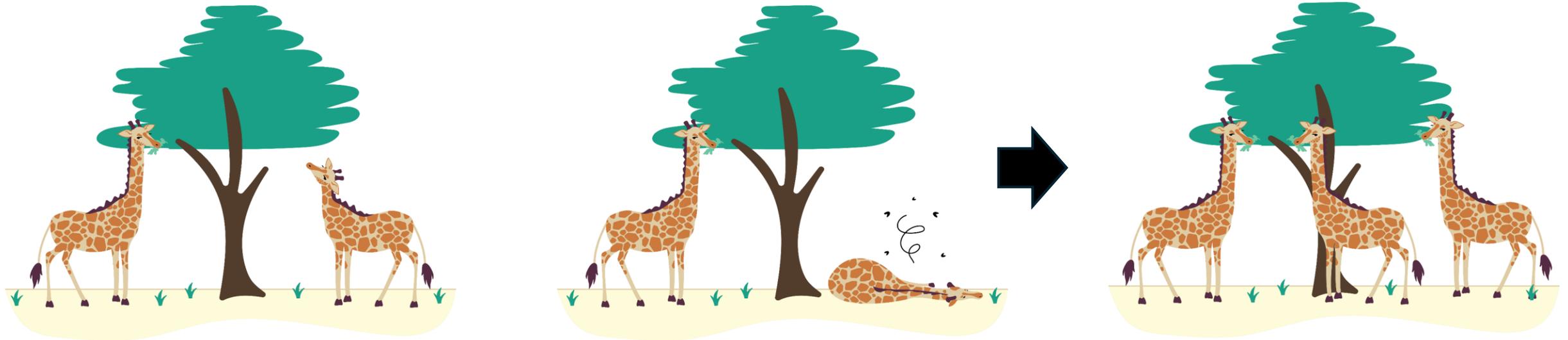
We would like to ask:

*Are **variability**, **genetic inheritance** and **differential contribution** all the ingredients for evolution?*

Are they sufficient?

Are they strictly necessary?

What are their implications?



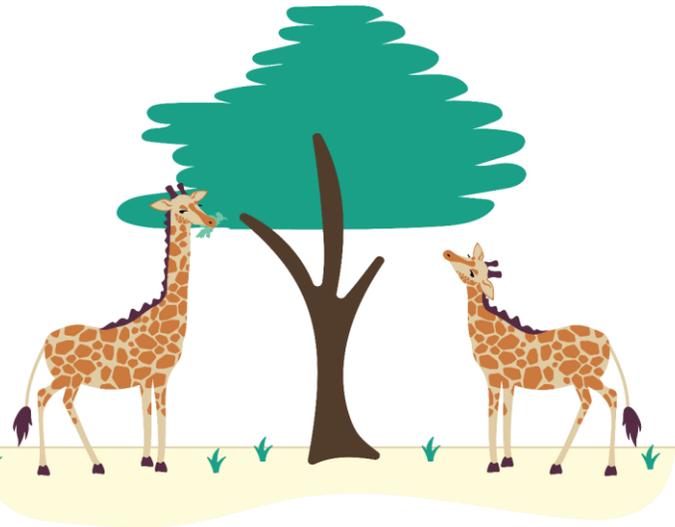
Was Darwin's theory correct?

What are its predictions?

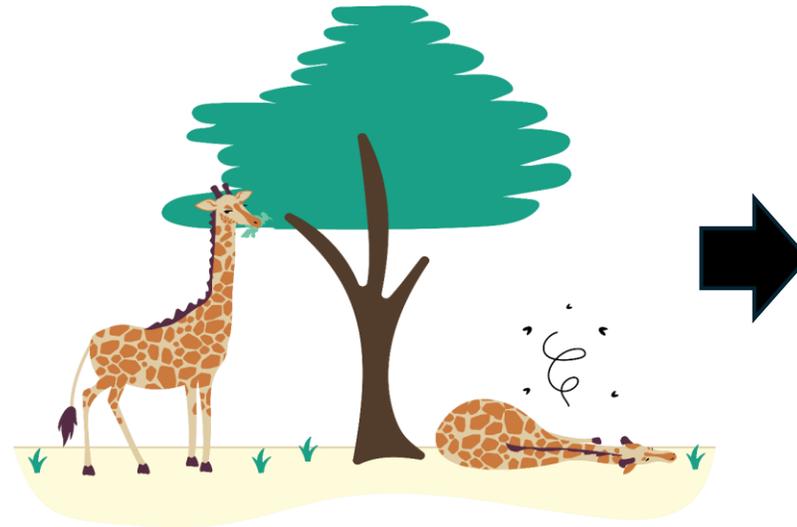
When does it work and when not?

How to explore the predictions and implications of a theory?

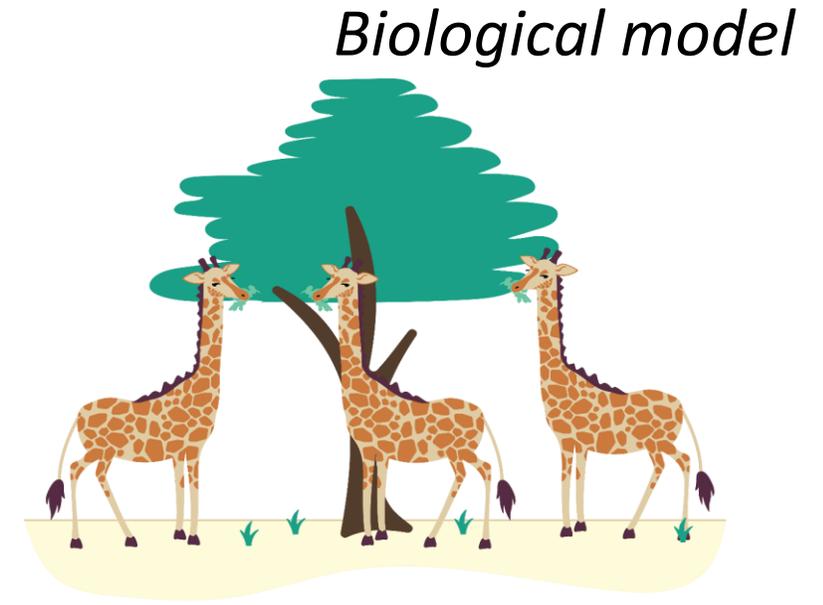
Variability among individuals



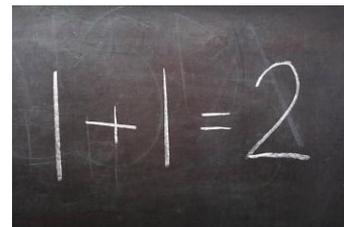
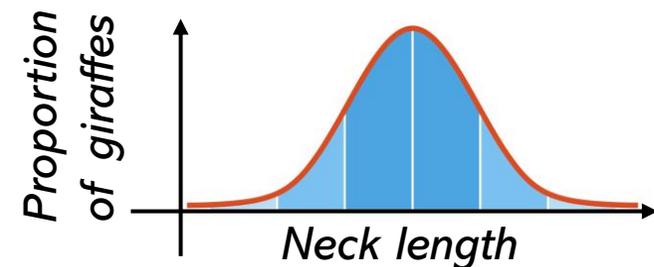
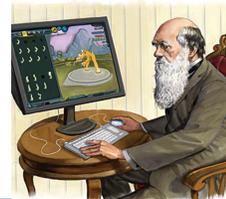
Selection on individuals



Inheritance

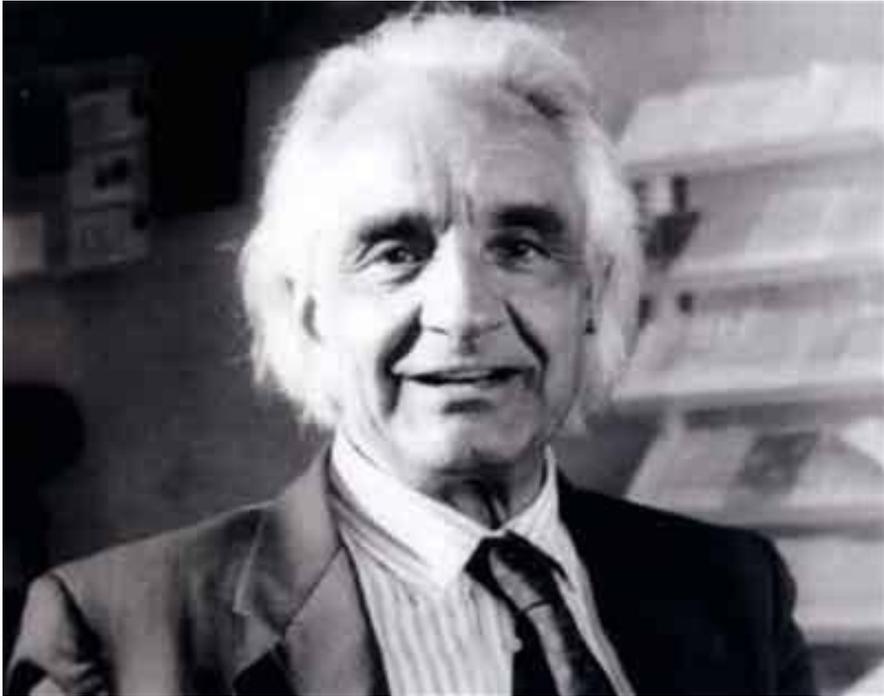


Computational model/simulations

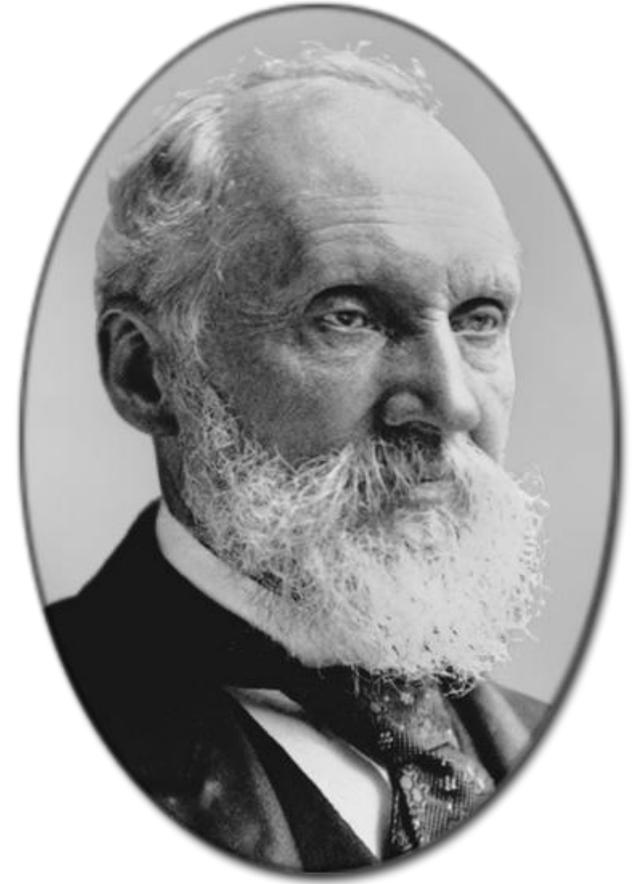


Mathematical/graphical model

Evolutionary theory has no mathematical foundation and makes wrong predictions



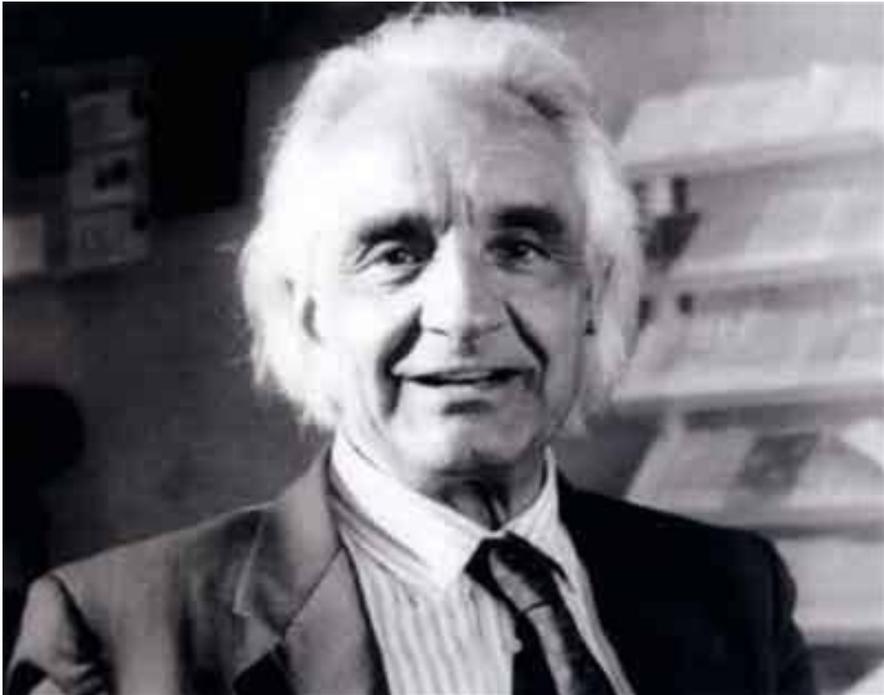
Antonio Zichichi 1929-2026



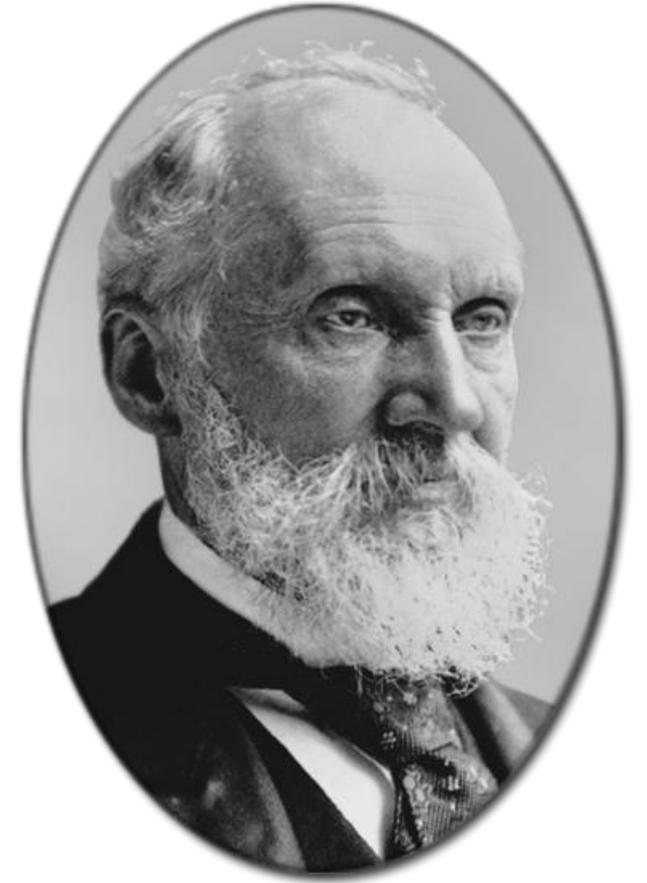
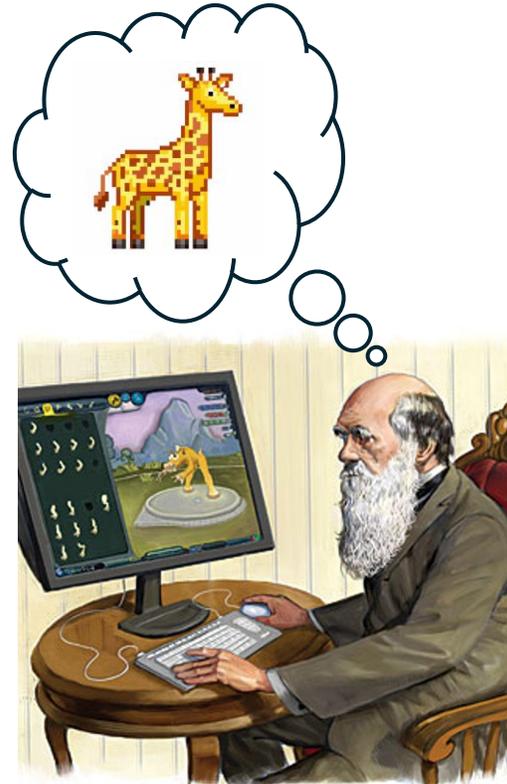
Lord Kelvin (1824-1907)

[L'evoluzionismo non è una scienza - di Antonino Zichichi | Corrispondenza romana](#)

Evolutionary theory has no mathematical foundation and makes wrong predictions



Antonio Zichichi 1929-2026



Lord Kelvin (1824-1907)

A Primer in

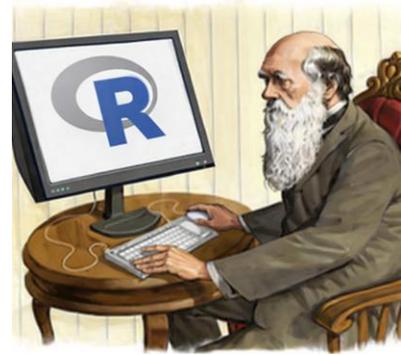
```
x=1  
print(x)
```

Assign a value to a *variable* and print

```
1
```

```
x
```

```
1
```



A Primer in

```
x=1  
print(x)
```

Assign a *value* to a *variable* and print

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

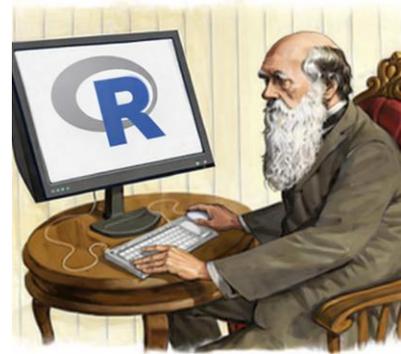
Operations with variables

```
3
```

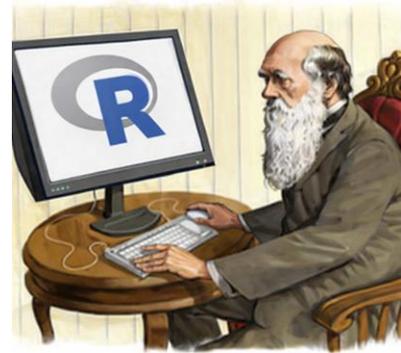
```
y=x
```

```
y
```

```
1
```



A Primer in



```
x=1  
print(x)
```

Assign a *value* to a *variable* and print

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

Operations with variables

```
3
```

```
y=x
```

```
y
```

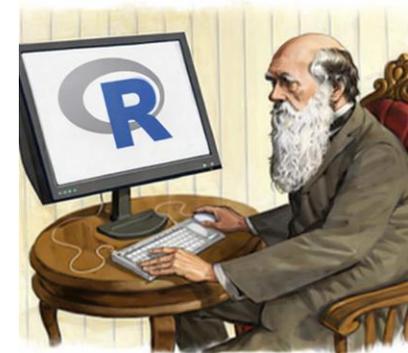
```
1
```

```
y=rep(1,4)
```

Variables can take the values of *vectors*

```
1 1 1 1
```

A Primer in



```
x=1  
print(x)
```

 Assign a *value* to a *variable* and print

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

 Operations with variables

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

 Variables can take the values of *vectors*

```
1 1 1 1
```

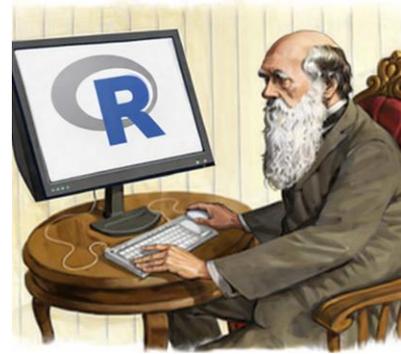
```
x=c(1,2,3,4)
```

c(..) concatenate values in a vector

```
x
```

```
1 2 3 4
```

A Primer in



```
x=1  
print(x)
```

Assign a *value* to a *variable* and print

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

Operations with variables

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

Variables can take the values of *vectors*

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

c(..) concatenate values in a vector

```
x
```

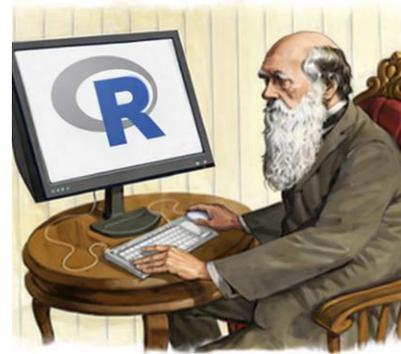
```
1 2 3 4
```

```
x[x>2]
```

Square brackets select specific values from a vector

```
3 4
```

A Primer in



```
x=1  
print(x)
```

Assign a *value* to a *variable* and print

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

Operations with variables

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

Variables can take the values of *vectors*

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

c(..) concatenate values in a vector

```
x
```

```
1 2 3 4
```

```
x[x>2]
```

Square brackets select specific values from a vector

```
3 4
```

```
1:4
```

```
1 2 3 4
```

A Primer in

```
x=1  
print(x)
```

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

```
x
```

```
1 2 3 4
```

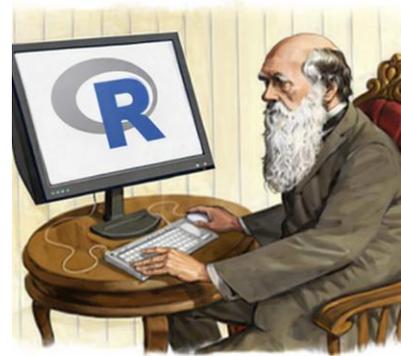
```
x[x>2]
```

```
3 4
```

```
1:4
```

```
1 2 3 4
```

```
for ( x in 1:4 )  
{  
  print(x)  
}
```



For-loops iterate for all values of x in $1:4$, repeating the operations within $\{ .. \}$ for each value

A Primer in

```
x=1  
print(x)
```

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

```
x
```

```
1 2 3 4
```

```
x[x>2]
```

```
3 4
```

```
1:4
```

```
1 2 3 4
```

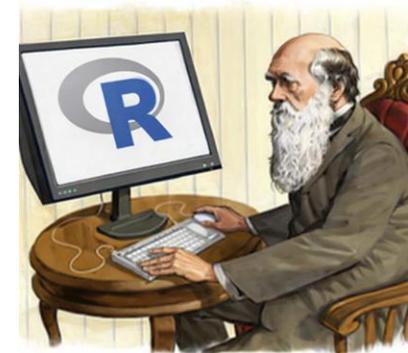
```
for ( x in 1:4 )  
{  
  print(x)  
}
```

```
1
```

```
2
```

```
3
```

```
4
```



For-loops iterate for all values of x in 1:4, repeating the operations within { .. } for each value

A Primer in

```
x=1  
print(x)
```

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

```
x
```

```
1 2 3 4
```

```
x[x>2]
```

```
3 4
```

```
1:4
```

```
1 2 3 4
```

```
for ( x in 1:4 )  
{  
  print(x)  
}
```

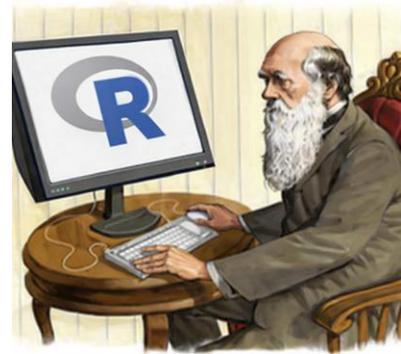
```
1
```

```
2
```

```
3
```

```
4
```

```
x=0  
for (y in 1:4)  
{  
  x=x+1  
}  
x
```



For-loops iterate for all values of x in 1:4, repeating the operations within { .. } for each value

A Primer in

```
x=1  
print(x)
```

```
1
```

```
x
```

```
1
```

```
y=2
```

```
y
```

```
2
```

```
x+y
```

```
3
```

```
y=x
```

```
y
```

```
1
```

```
y=rep(1,4)
```

```
1 1 1 1
```

```
x=c(1,2,3,4)
```

```
x
```

```
1 2 3 4
```

```
x[x>2]
```

```
3 4
```

```
1:4
```

```
1 2 3 4
```

```
for ( x in 1:4 )  
{  
  print(x)  
}
```

```
1
```

```
2
```

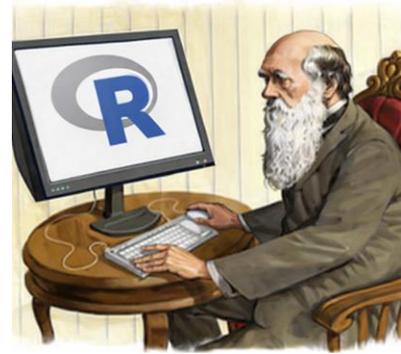
```
3
```

```
4
```

```
x=0  
for (y in 1:4)  
{  
  x=x+1  
}
```

```
x
```

```
4
```



For-loops iterate for all values of x in 1:4, repeating the operations within { .. } for each value

Probability in R

```
mean(0:10)
```

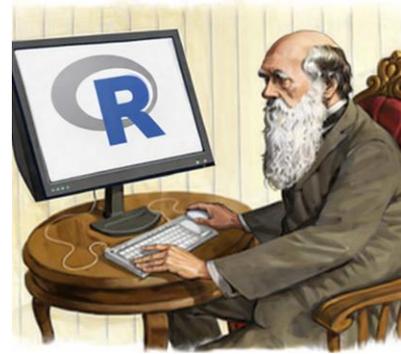
```
5
```

```
median(0:10)
```

```
5
```

```
1:10
```

```
1 2 3 4 5 6 7 8 9 10
```



Probability in R

```
mean(0:10)
```

```
5
```

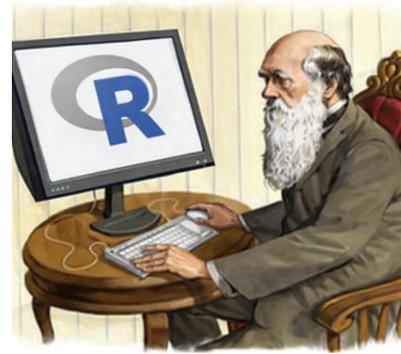
```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

Generate 100 values sampled from a
Gaussian/Normal distribution



Probability in R

```
mean(0:10)
```

```
5
```

```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

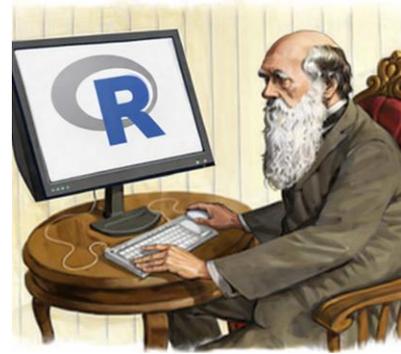
```
x=rnorm(100)
```

```
sd(x)
```

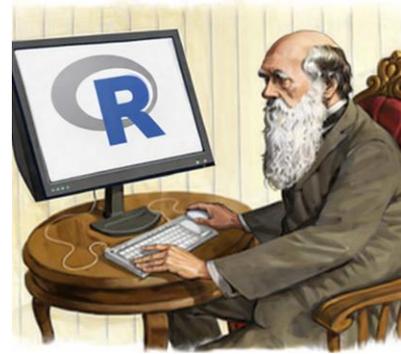
```
1.011
```

Generate 100 values sampled from a Gaussian/Normal distribution

If one does not specify mean and sd, rnorm assumes a standard normal distribution (mean=0, sd=1)



Probability in R



```
mean(0:10)
```

```
5
```

```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

```
x=rnorm(100)
```

```
sd(x)
```

```
1.011
```

```
rbinom(n=5, size=10, prob=0.1)
```

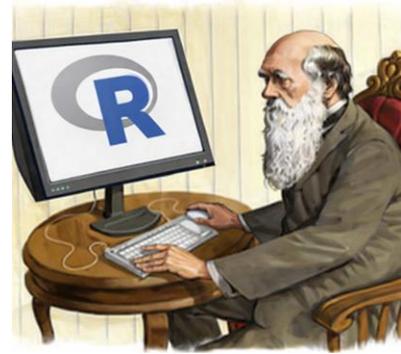
```
1 1 2 0 1
```

Generate 100 values sampled from a Gaussian/Normal distribution

If one does not specify mean and sd, rnorm assumes a standard normal distribution (mean=0, sd=1)

The same can be done for any distribution (e.g. Binomial distribution with `rbinom`, `rexp` for exponential, etc.)

Probability in R



```
mean(0:10)
```

```
5
```

```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

```
x=rnorm(100)
```

```
sd(x)
```

```
1.011
```

```
rbinom(n=5, size=10, prob=0.1)
```

```
1 1 2 0 1
```

```
1:10
```

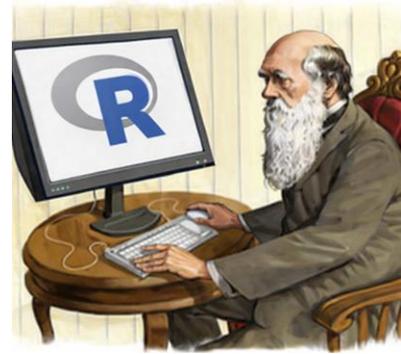
```
1 2 3 4 5 6 7 8 9 10
```

```
sample(1:10)
```

```
1 4 3 7 5 10 9 8 6 2
```

Shuffle/sample without replacement the vector 1:10

Probability in R



```
mean(0:10)
```

```
5
```

```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

```
x=rnorm(100)
```

```
sd(x)
```

```
1.011
```

```
rbinom(n=5, size=10, prob=0.1)
```

```
1 1 2 0 1
```

```
1:10
```

```
1 2 3 4 5 6 7 8 9 10
```

```
sample(1:10)
```

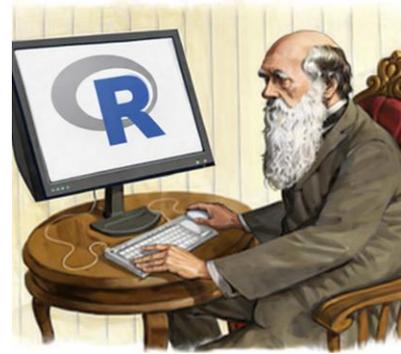
```
1 4 3 7 5 10 9 8 6 2
```

```
sample(1:10, replace=TRUE)
```

```
1 4 8 5 4 1 5 9 1 4
```

Sample WITH replacement

Probability in R



```
mean(0:10)
```

```
5
```

```
median(0:10)
```

```
5
```

```
rnorm(n=100, mean=0, sd=1)
```

```
0.59162486 0.54468991 0.93817635 ...
```

```
x=rnorm(100)
```

```
sd(x)
```

```
1.011
```

```
rbinom(n=5, size=10, prob=0.1)
```

```
1 1 2 0 1
```

```
1:10
```

```
1 2 3 4 5 6 7 8 9 10
```

```
sample(1:10)
```

```
1 4 3 7 5 10 9 8 6 2
```

```
sample(1:10, replace=TRUE)
```

```
1 4 8 5 4 1 5 9 1 4
```

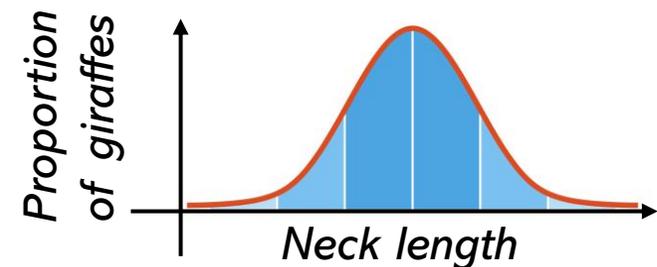
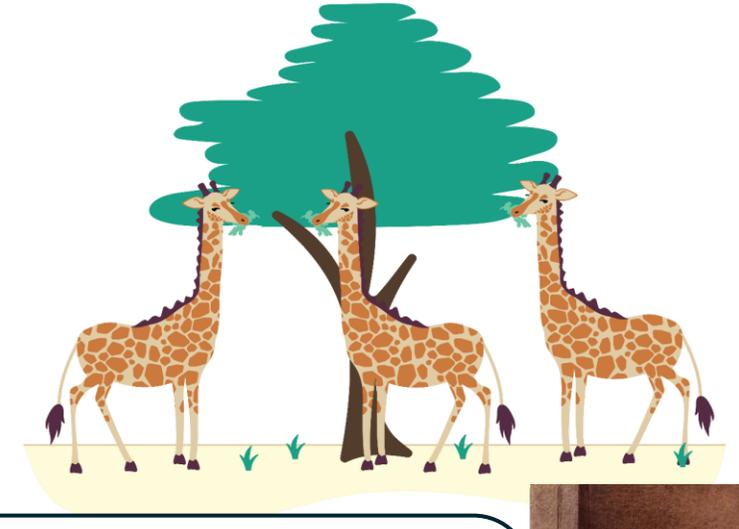
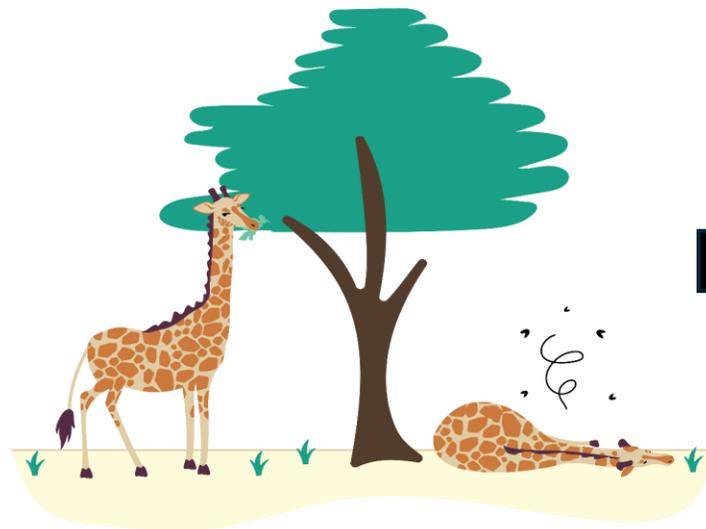
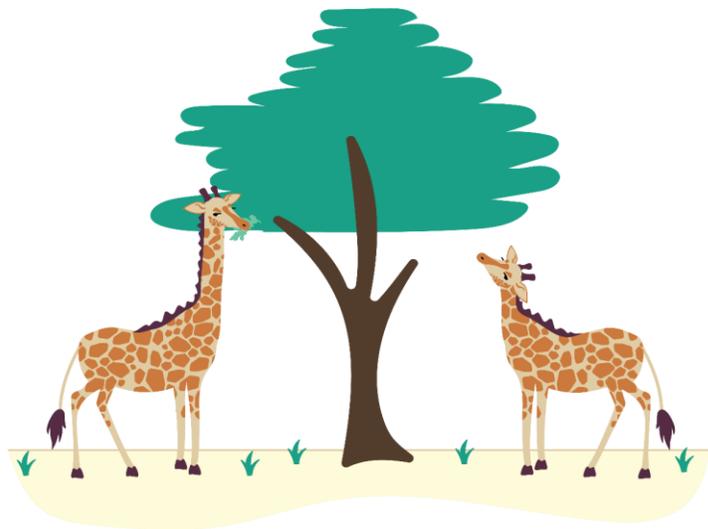
```
sort(sample(1:10, replace=TRUE))
```

```
1 3 3 5 6 7 8 9 9 9
```

We now sorted the resampled values in ascending order

Our first basic “evolutionary model”

- **Variability among individuals**
- Differential contribution to successive generations
- Mechanism of inheritance



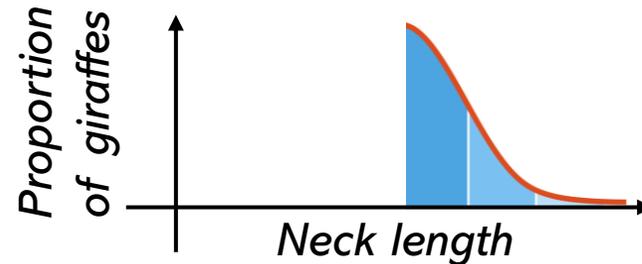
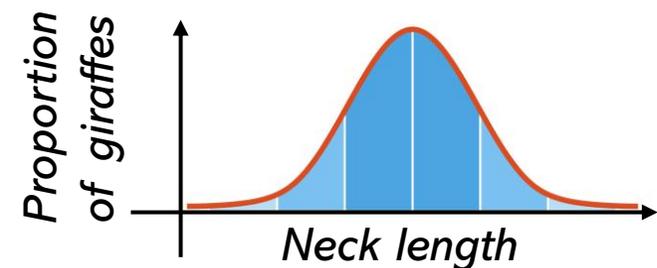
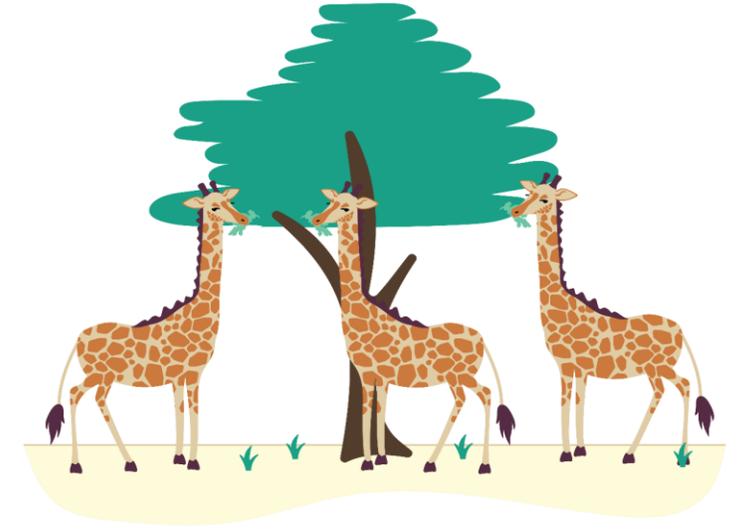
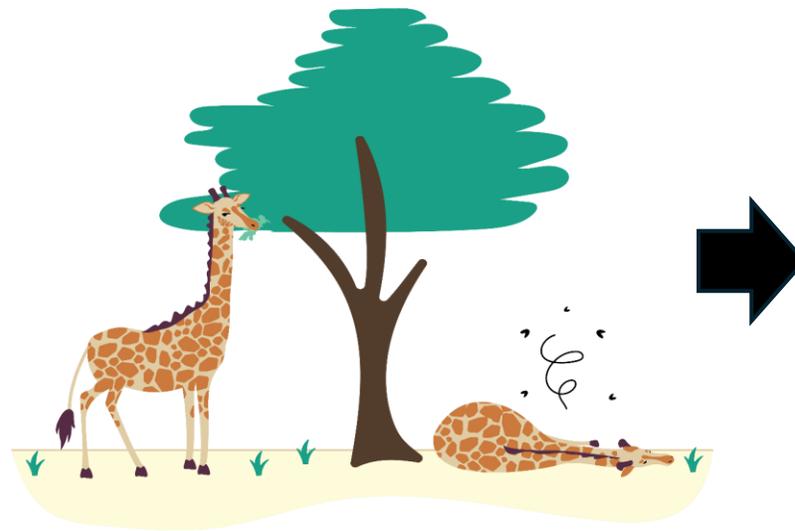
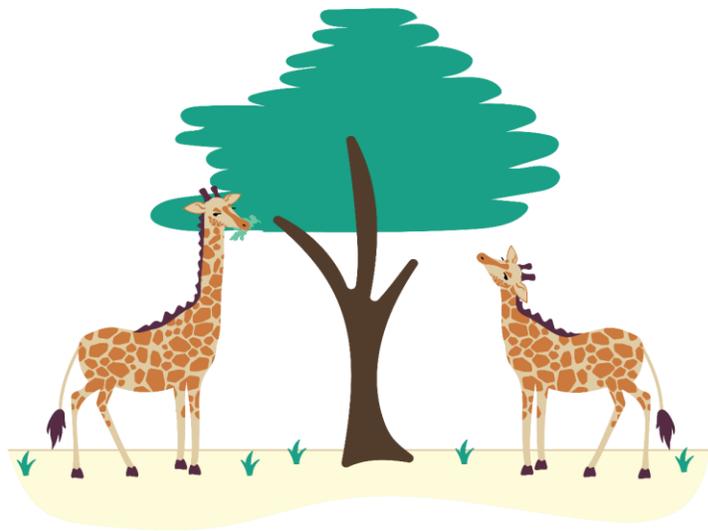
Normal distribution

You could have chosen any other distribution. But it is not just because I am his cousin!
Francis Galton, 1822-1911



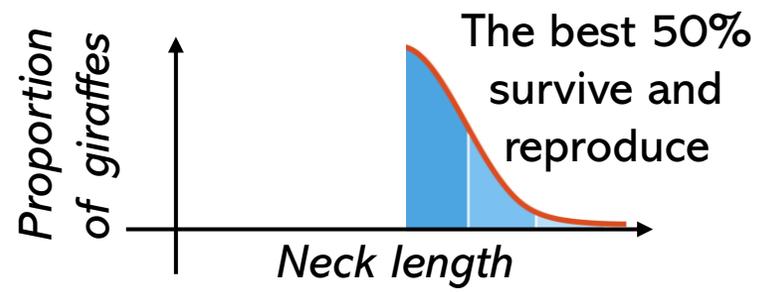
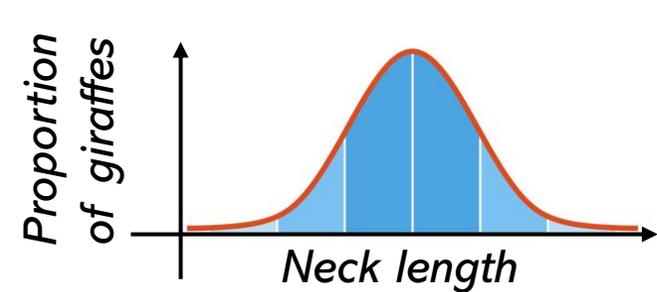
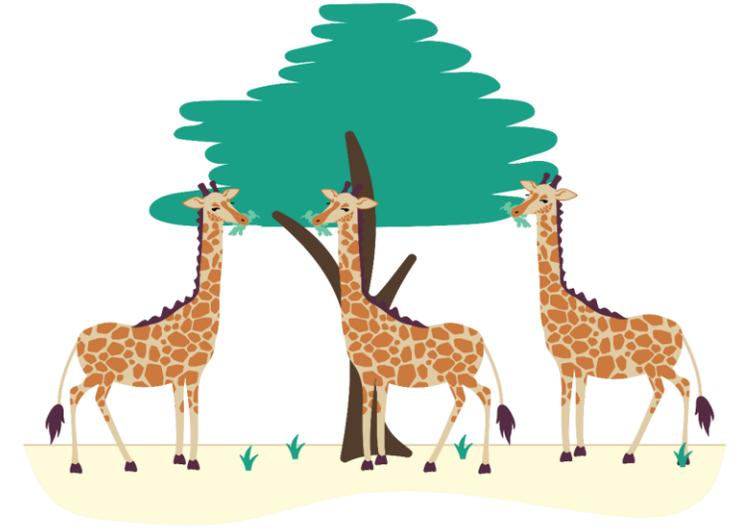
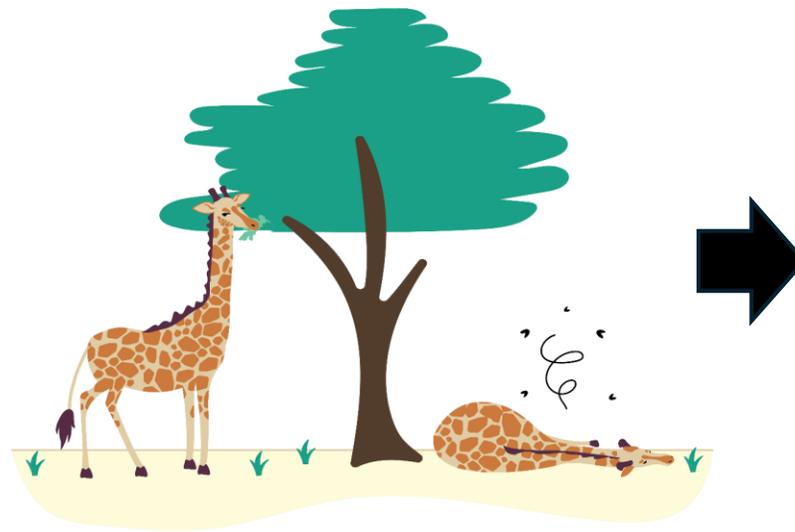
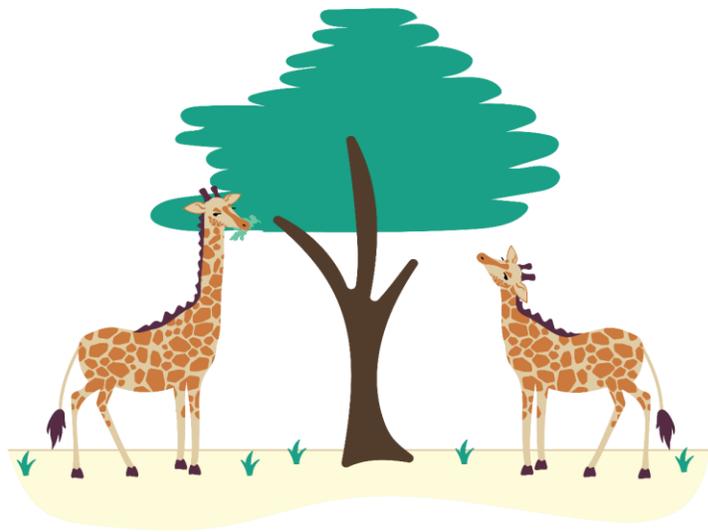
Our first basic “evolutionary model”

- Variability among individuals
- **Differential contribution to successive generations**
- Mechanism of inheritance



Our first basic “evolutionary model”

- Variability among individuals
- **Differential contribution to successive generations**
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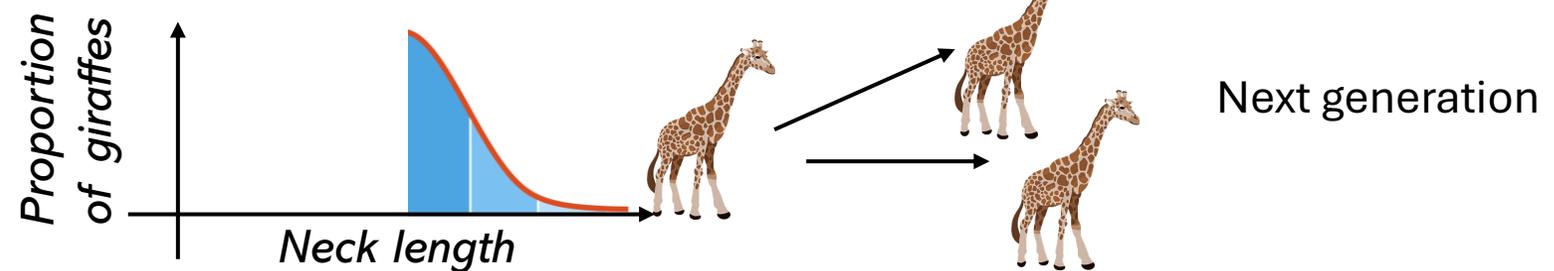
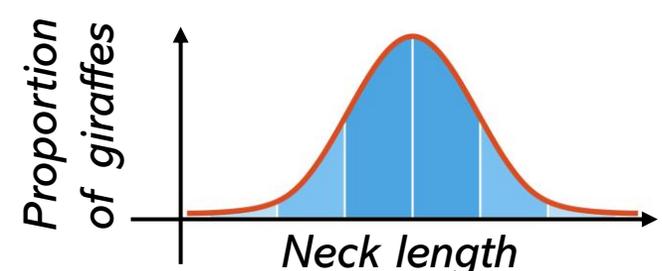
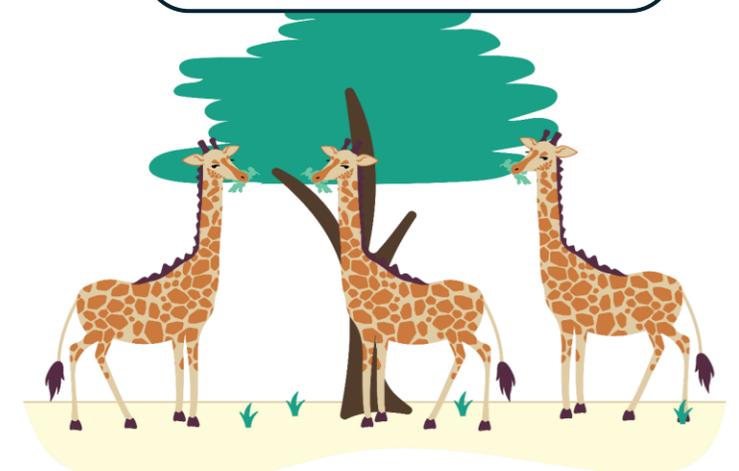
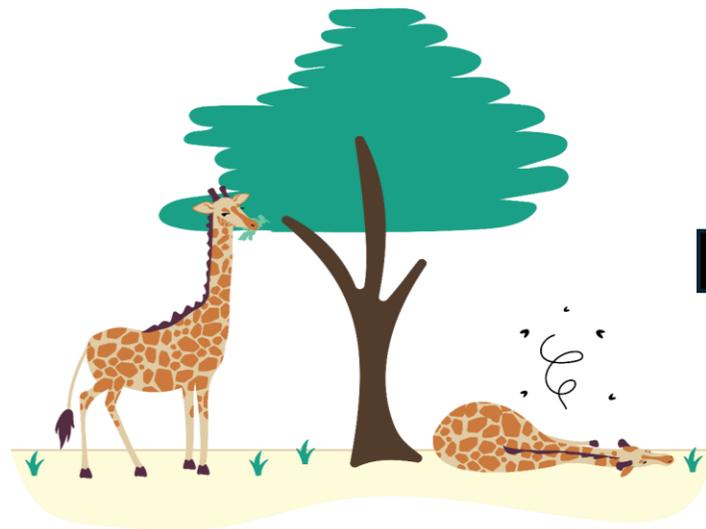
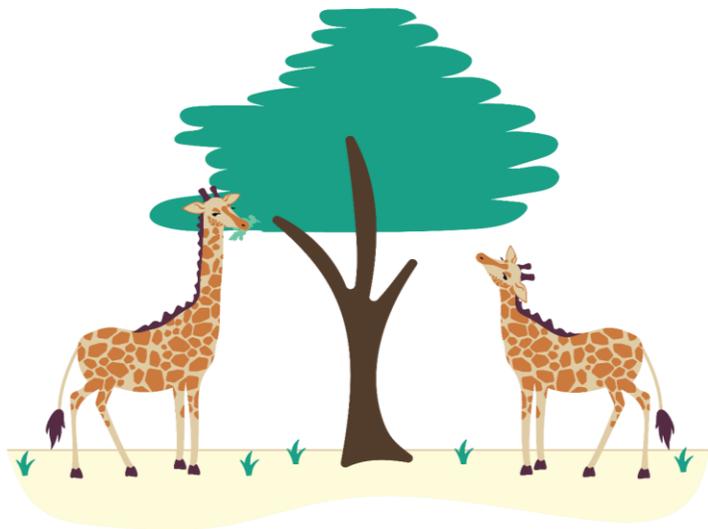


Our first basic “evolutionary model”

- Variability among individuals
- Differential contribution to successive generations
- **Mechanism of inheritance**



We want giraffes giving birth to «resembling» baby-giraffes



Our first basic “evolutionary model”

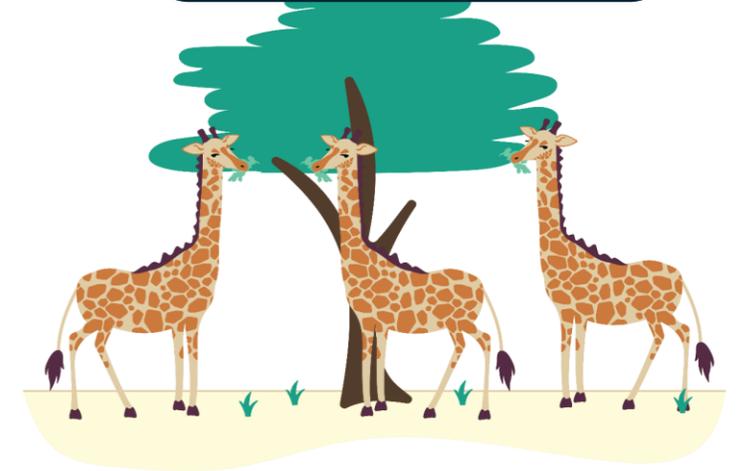
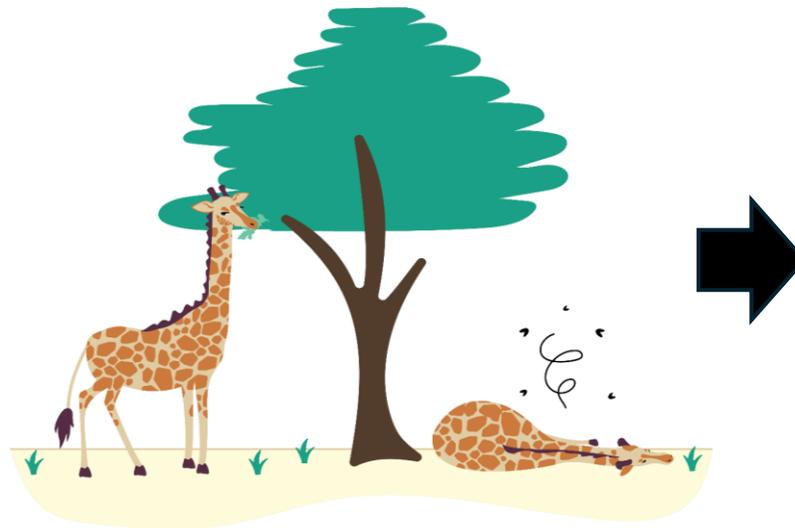
- Variability among individuals
- Differential contribution to successive generations
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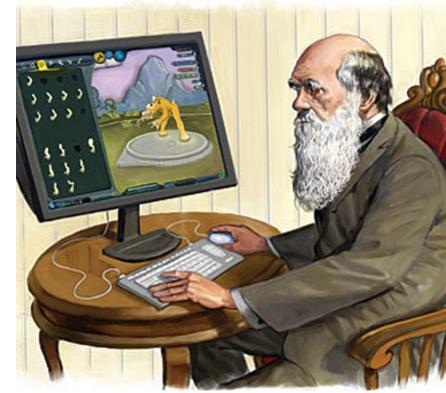
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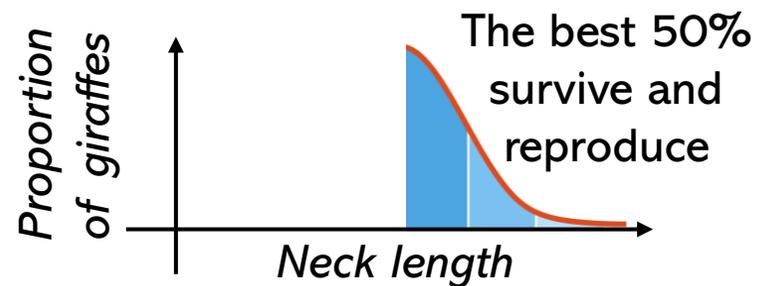
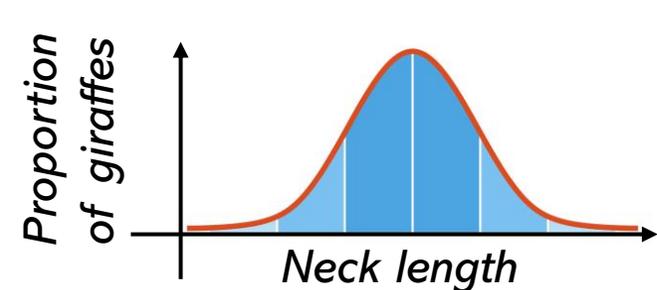
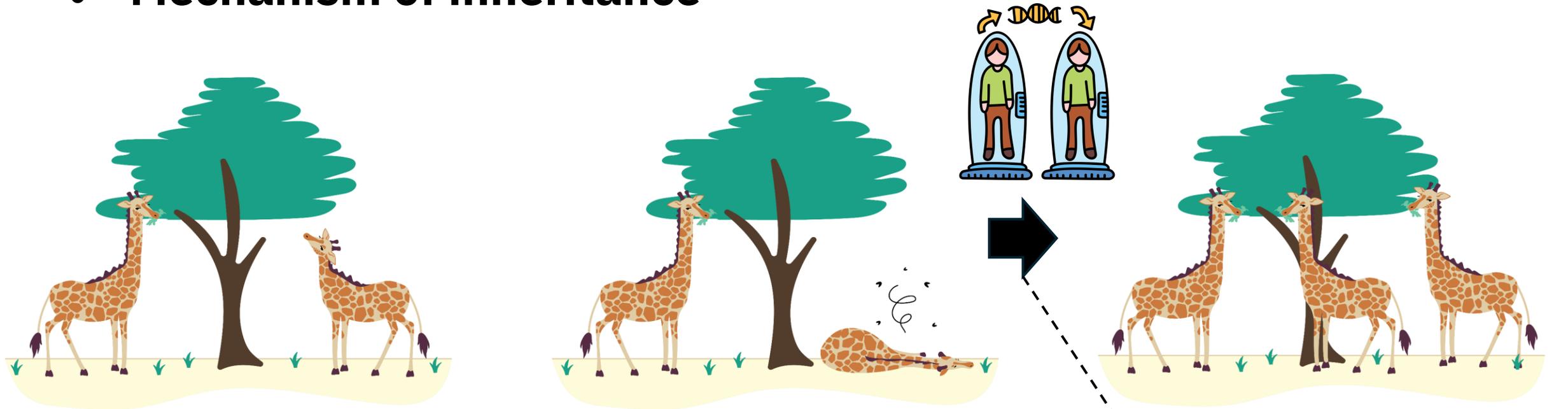
Precocial or altricial babies?



Our first basic “evolutionary model”



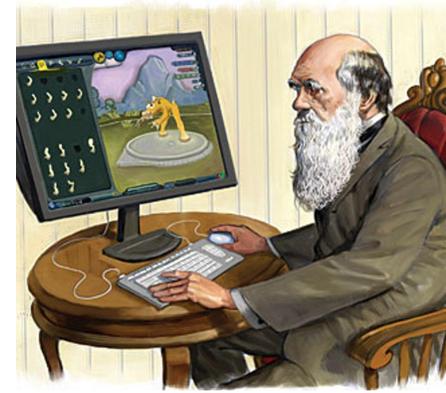
- Variability among individuals
- Differential contribution to successive generations
- **Mechanism of inheritance**



Perfect cloning of parents
(same neck length as parents)

Our first ~~basic~~ "evolutionary model"

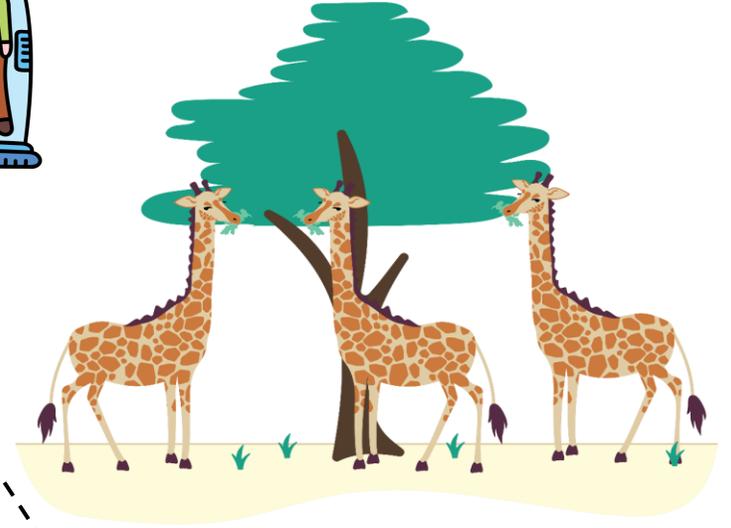
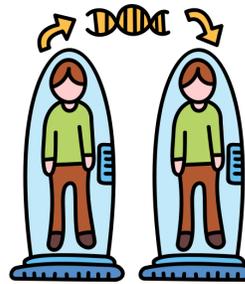
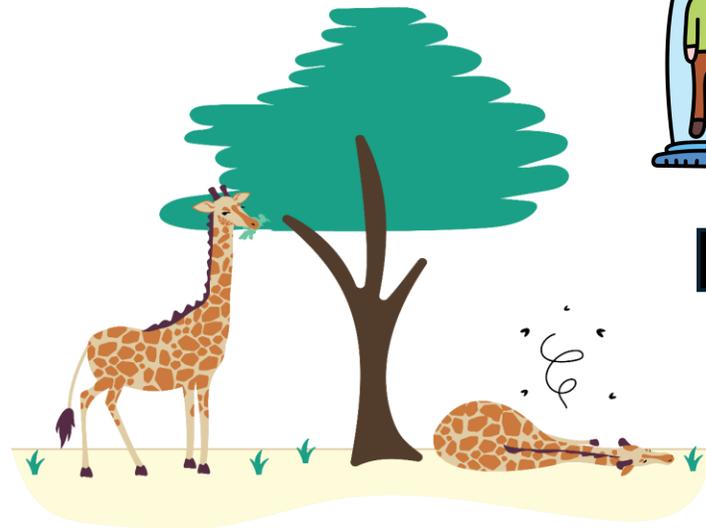
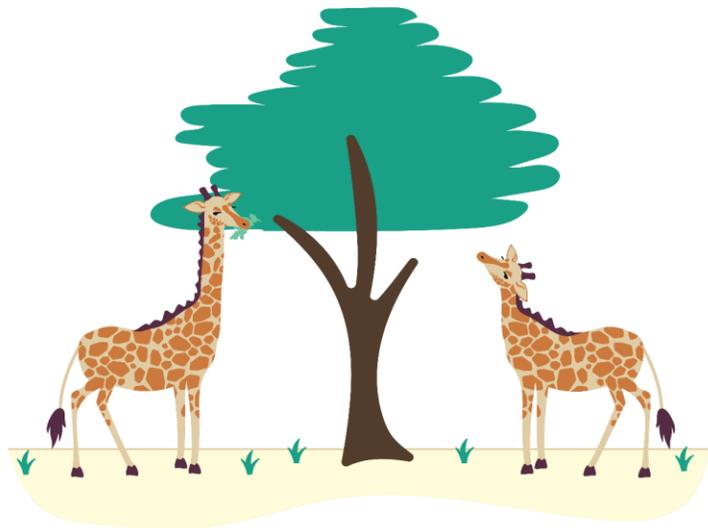
very basic



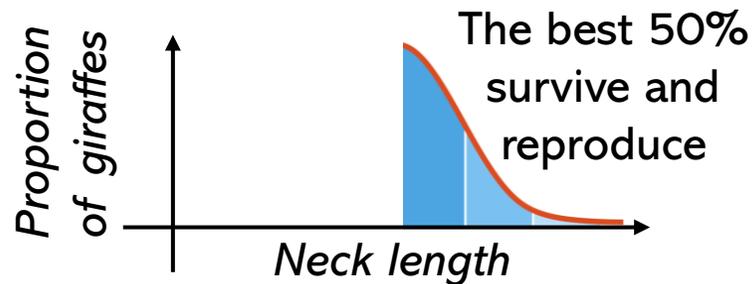
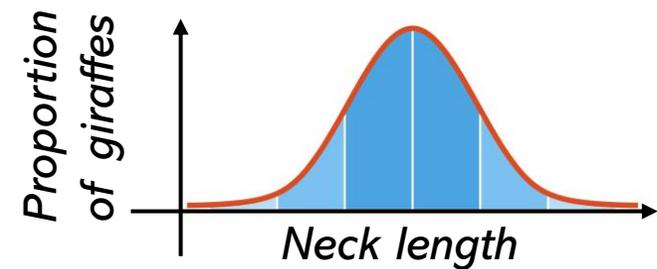
Simplifying assumption



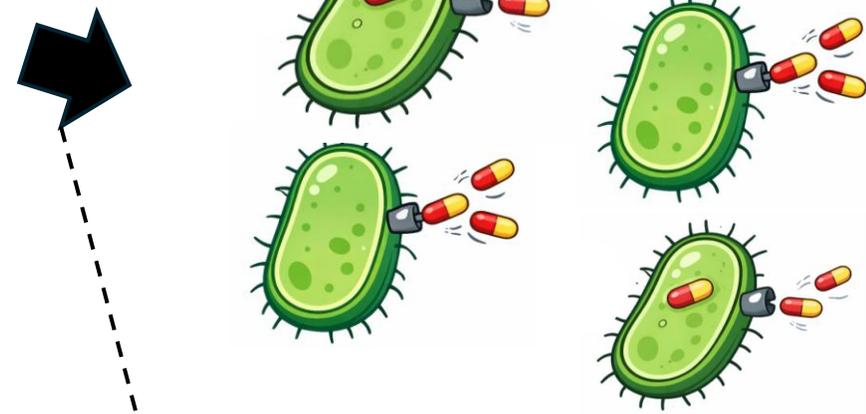
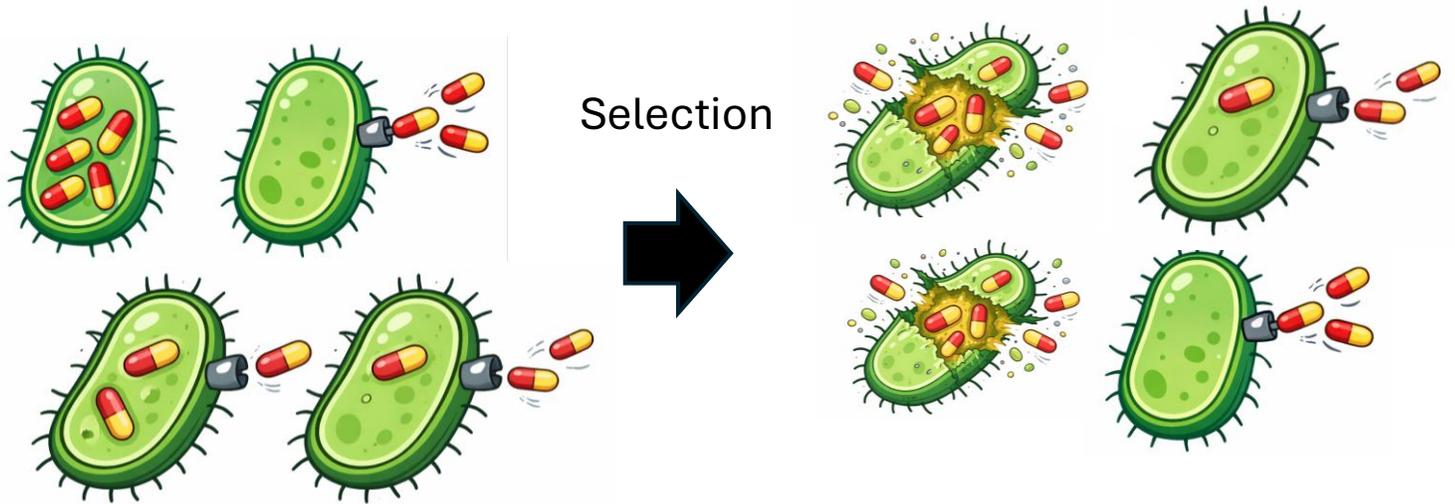
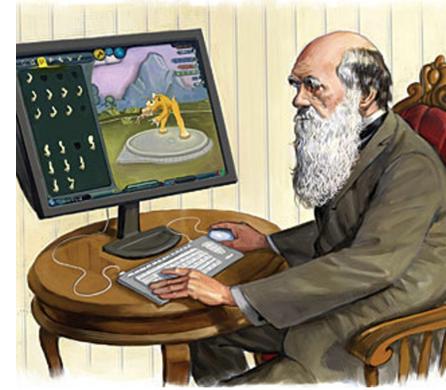
Dolly the sheep



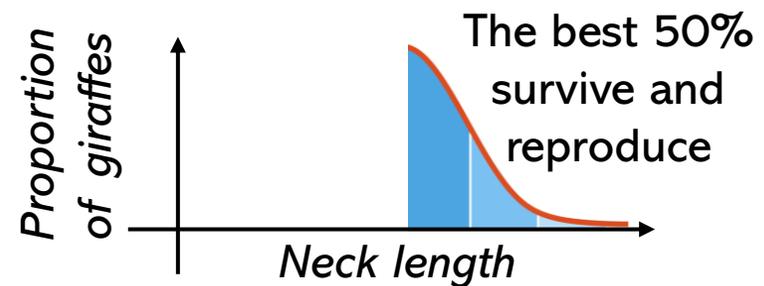
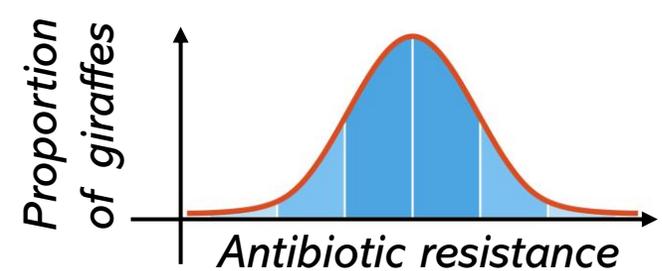
Perfect cloning of parents
(same neck length as parents)



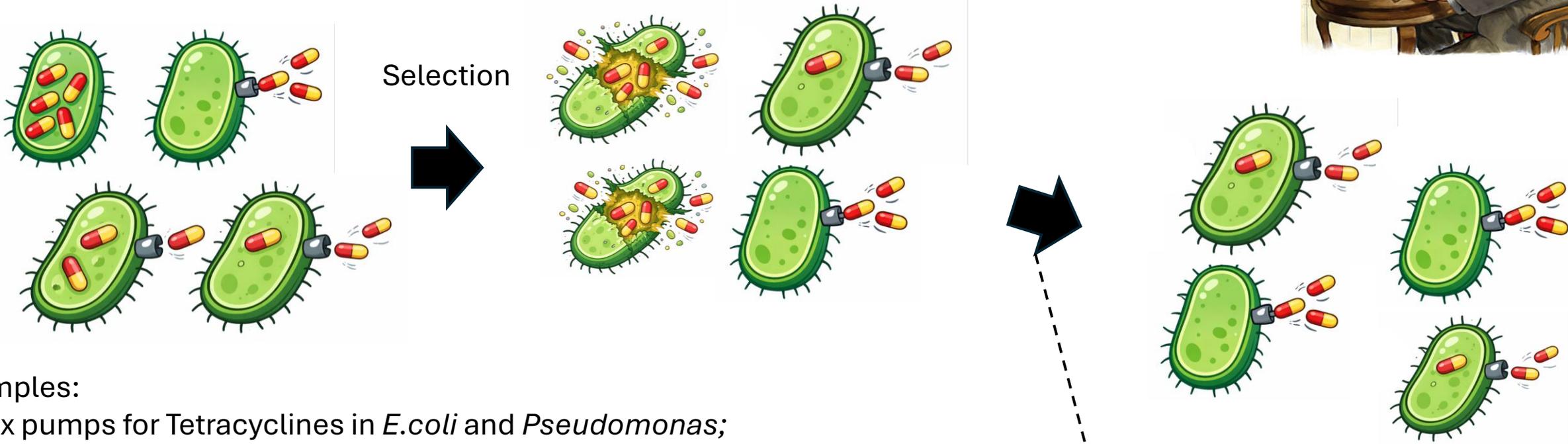
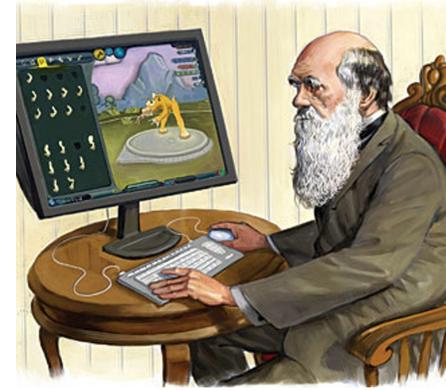
Haploid giraffes (or bacteria)



Perfect cloning of parents
(same neck length as parents)



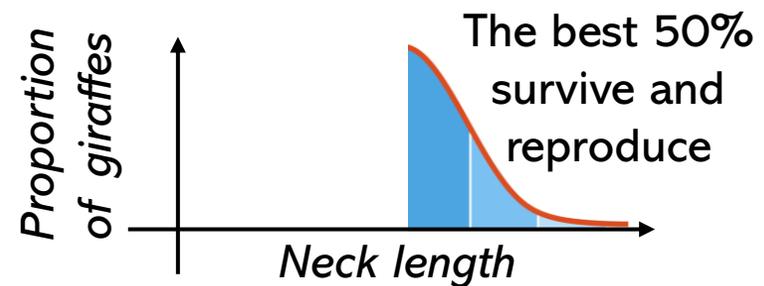
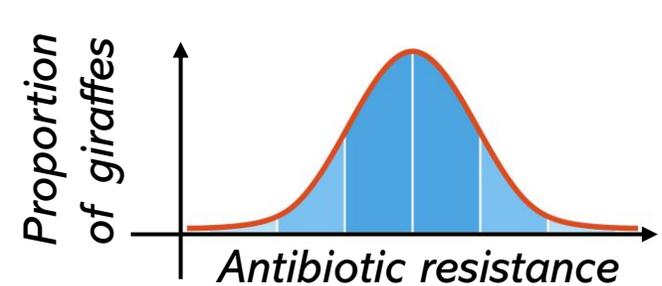
Haploid giraffes (or bacteria)



Examples:

Efflux pumps for Tetracyclines in *E.coli* and *Pseudomonas*;

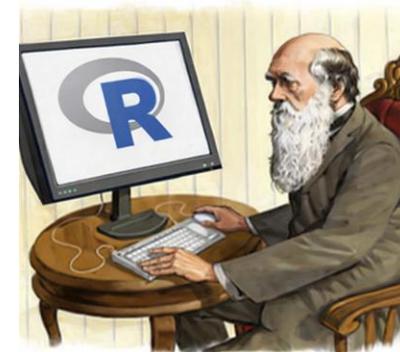
For fluoroquinolones like ciprofloxacin in *S.aureus* and *Pseudomonas*



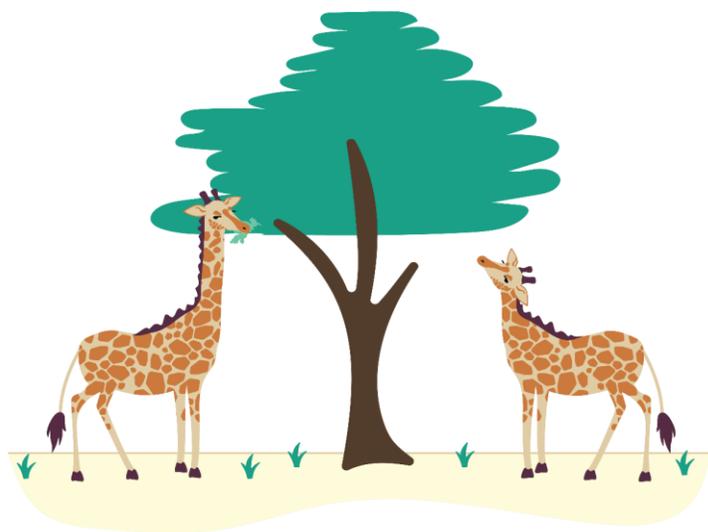
Perfect cloning of parents
(same neck length as parents)



Our first basic “evolutionary model”



- **Variability among individuals**
- Differential contribution to successive generations
- Mechanism of inheritance



Sample 100 individuals from a Normal/Gaussian distribution

```
rnorm(100)
```



-1.9



0.2

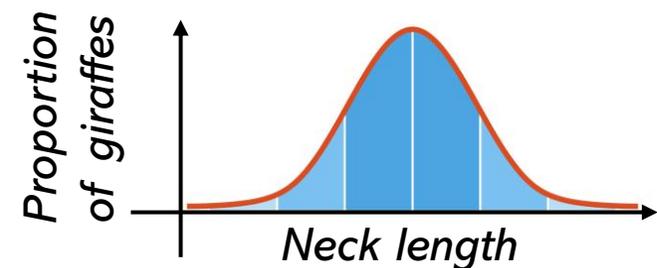


-0.1



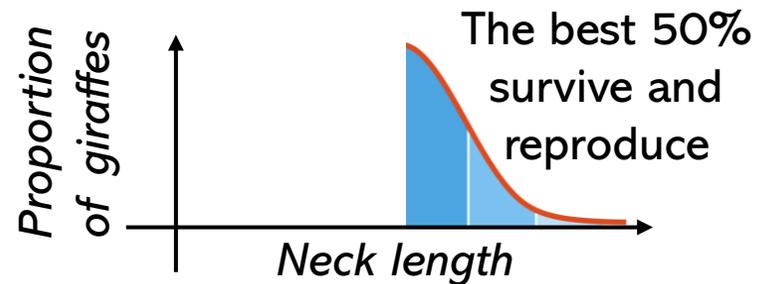
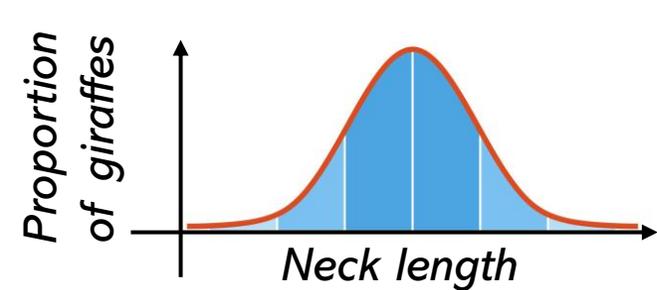
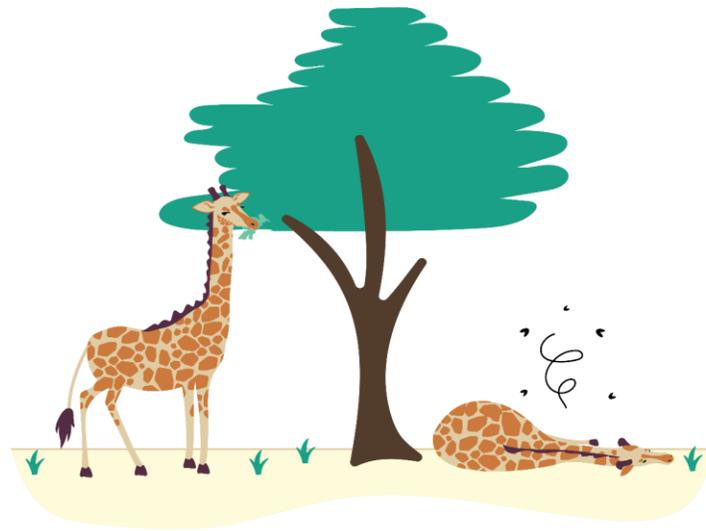
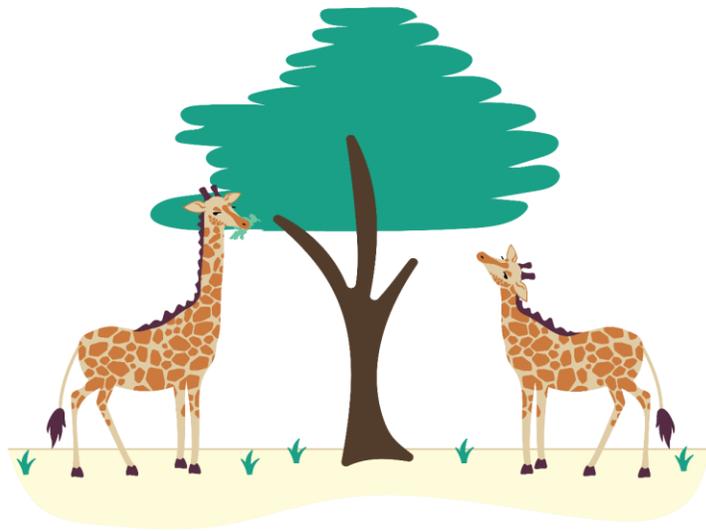
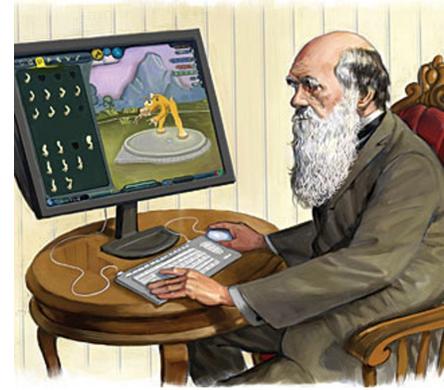
0.7

.....



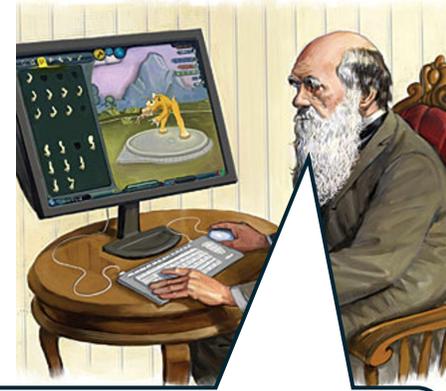
Our first basic “evolutionary model”

- Variability among individuals
- **Differential contribution to successive generations**
- Mechanism of inheritance

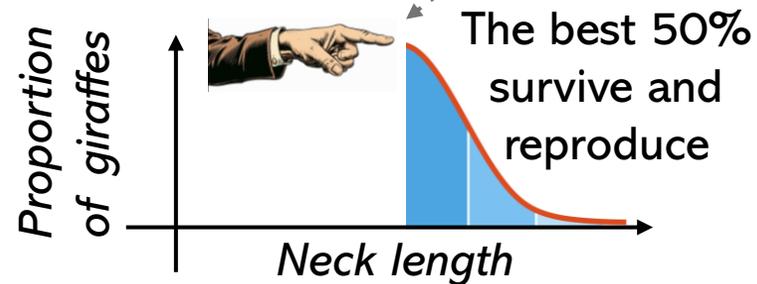
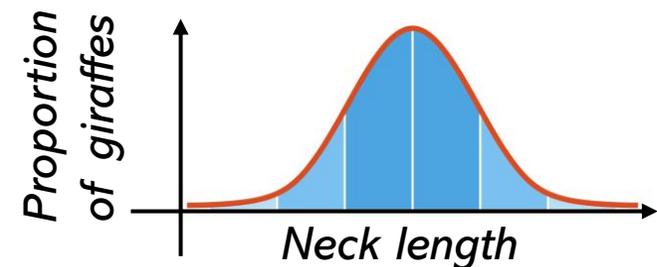
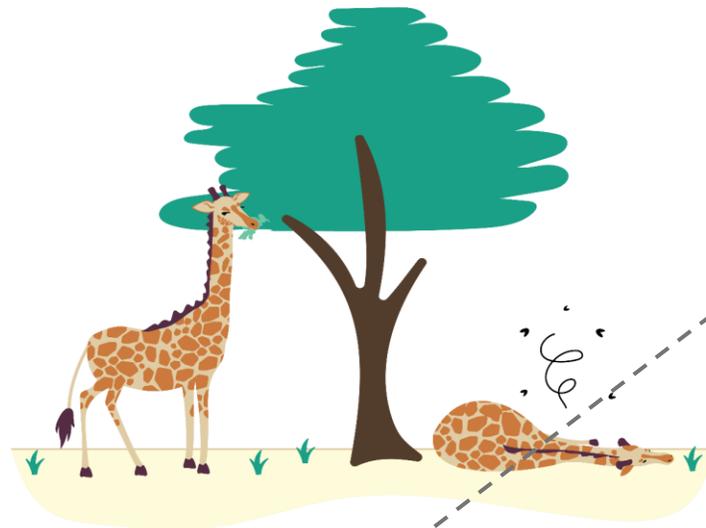
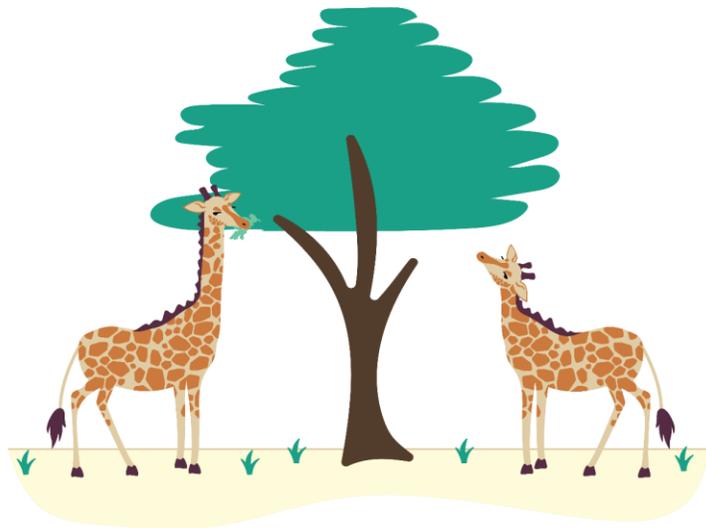


Our first basic “evolutionary model”

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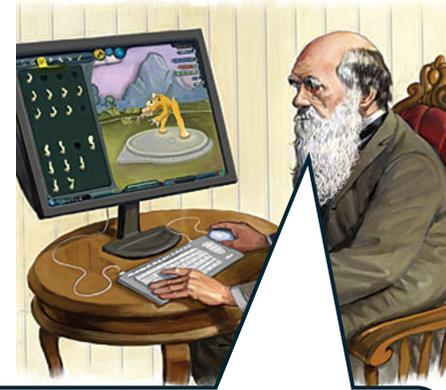


How do you call this?

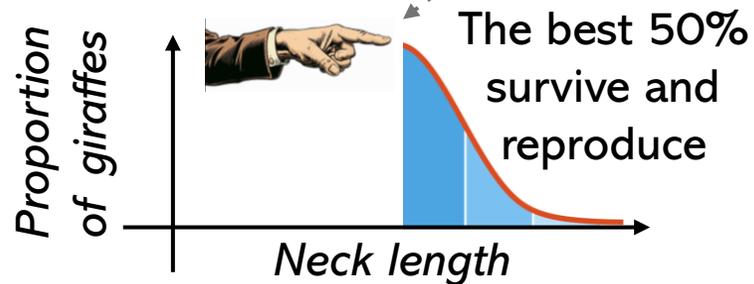
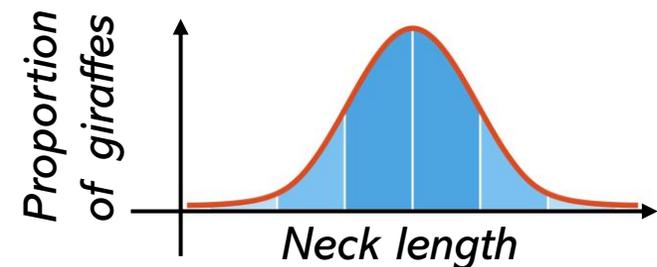
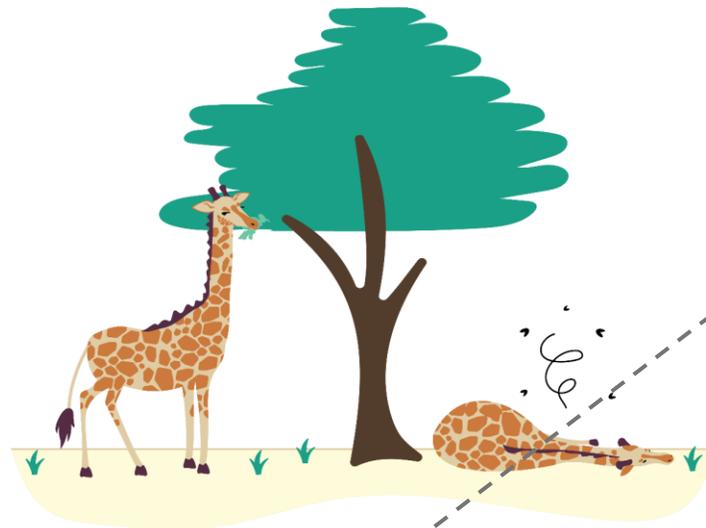
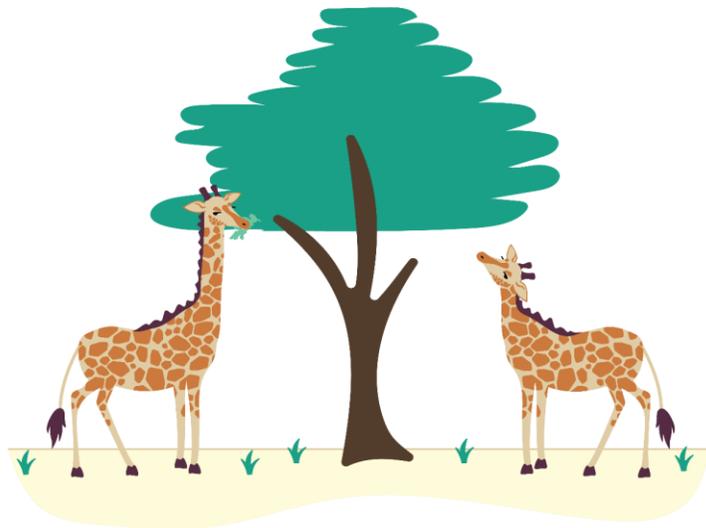


Our first basic “evolutionary model”

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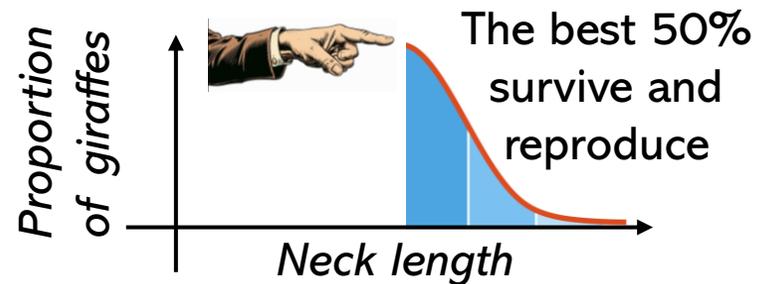
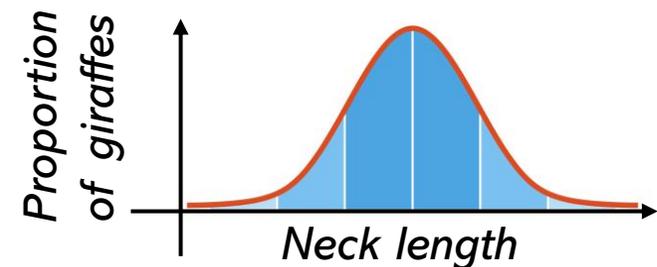
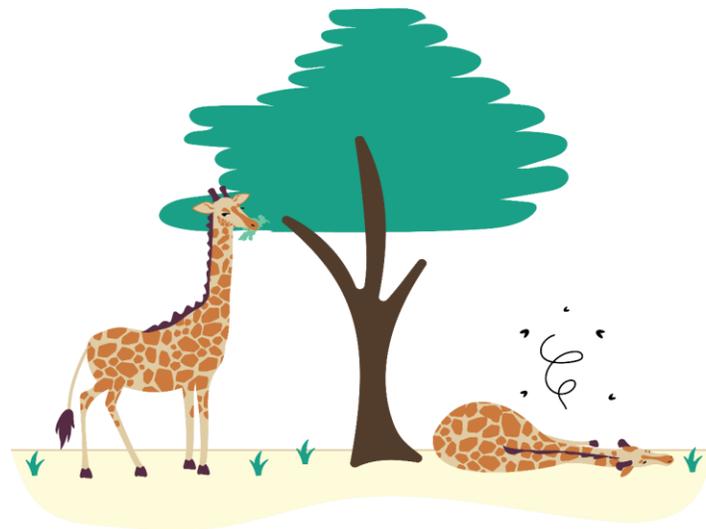
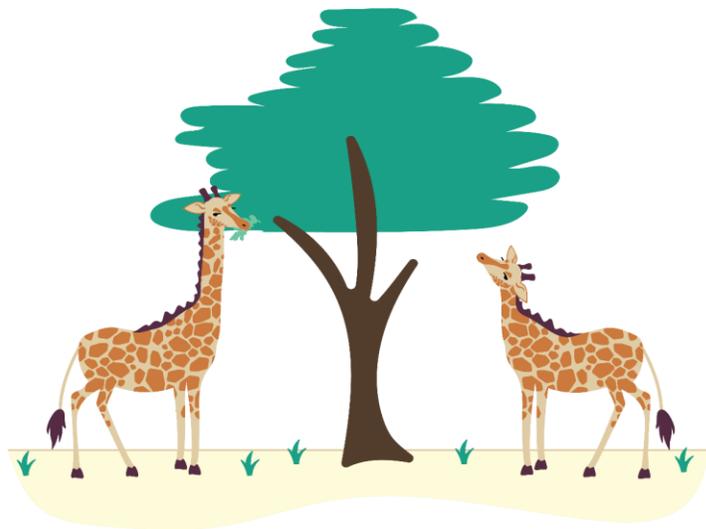


How do you call this?
median (z)



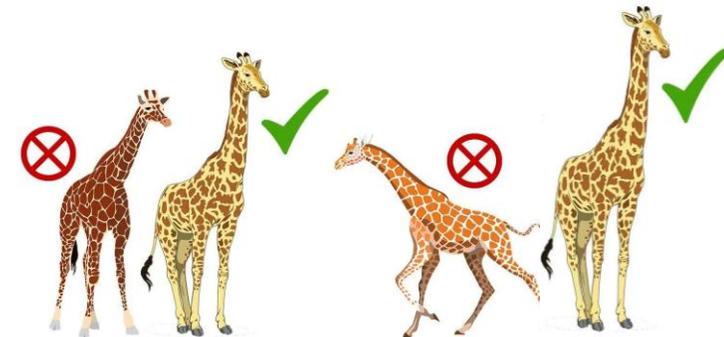
Our first basic “evolutionary model”

- Variability among individuals
- **Differential contribution to successive generations**
- Mechanism of inheritance



Let's now «select» only the giraffes with neck longer than the median.

```
parents=z[z>median(z)]
```

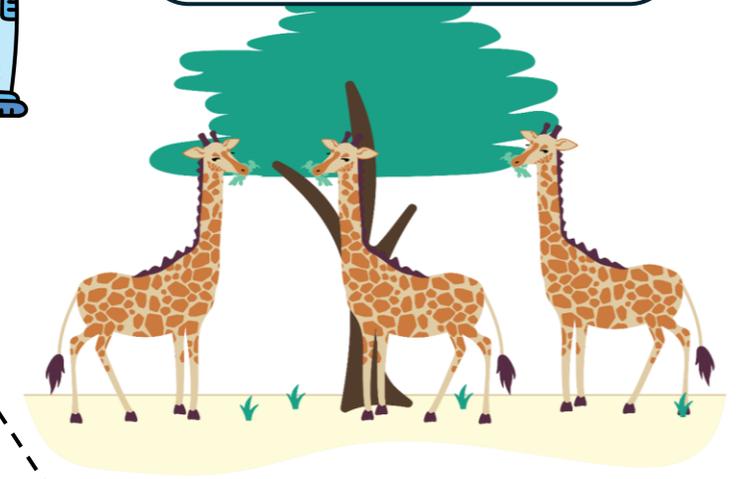
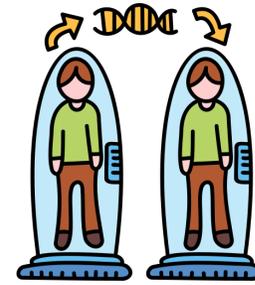
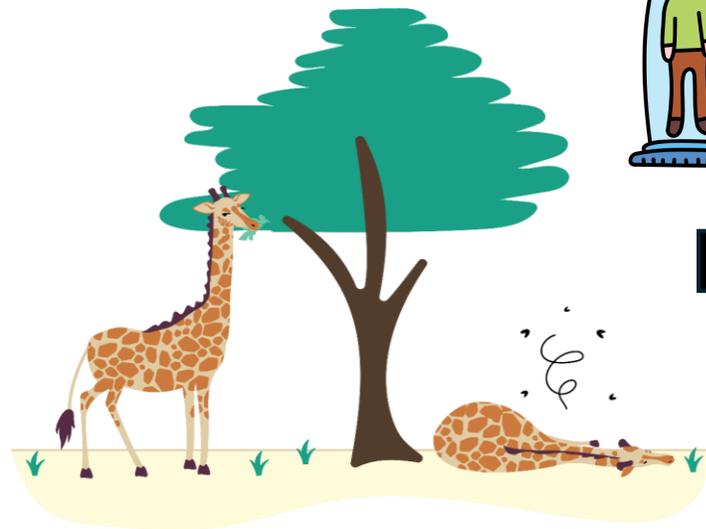
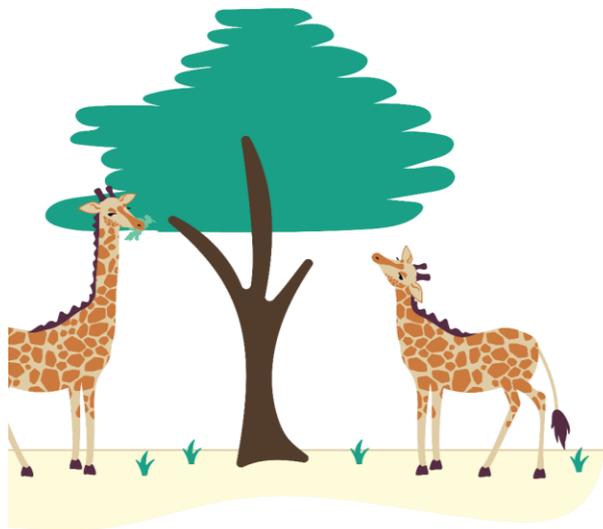


Our first basic “evolutionary model”

- Variability among individuals
- Differential contribution to successive generations
- **Mechanism of inheritance**



We want giraffes giving birth to «resembling» baby-giraffes



Perfect cloning of their parents (same neck length as parents)

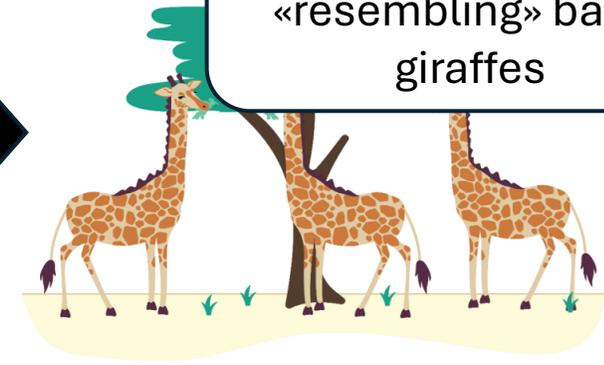
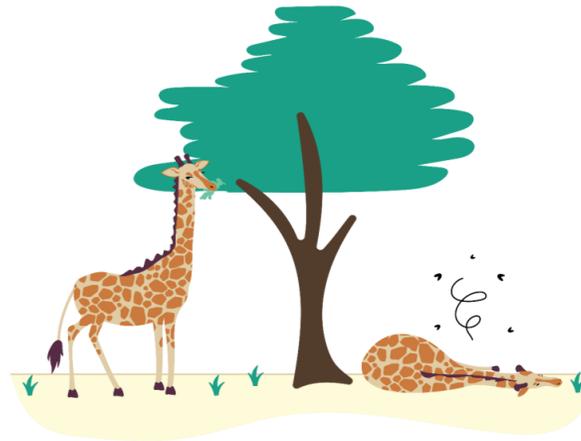
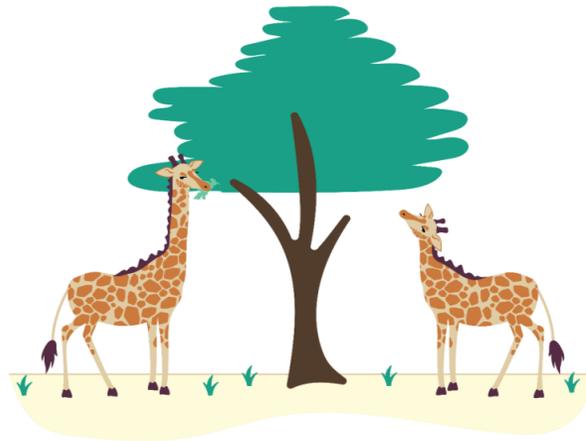
$z = \text{parents}$

Would this be enough for evolution?

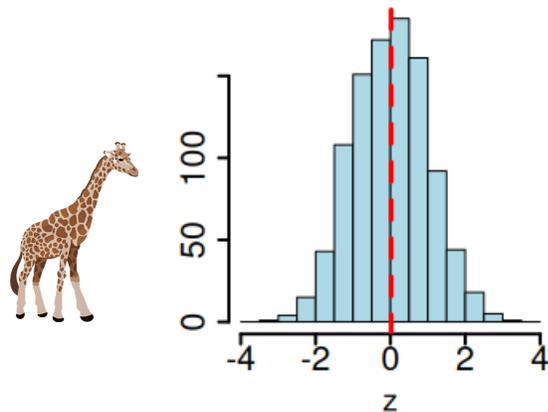
- Variability among individuals
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We want giraffes giving birth to «resembling» baby-giraffes

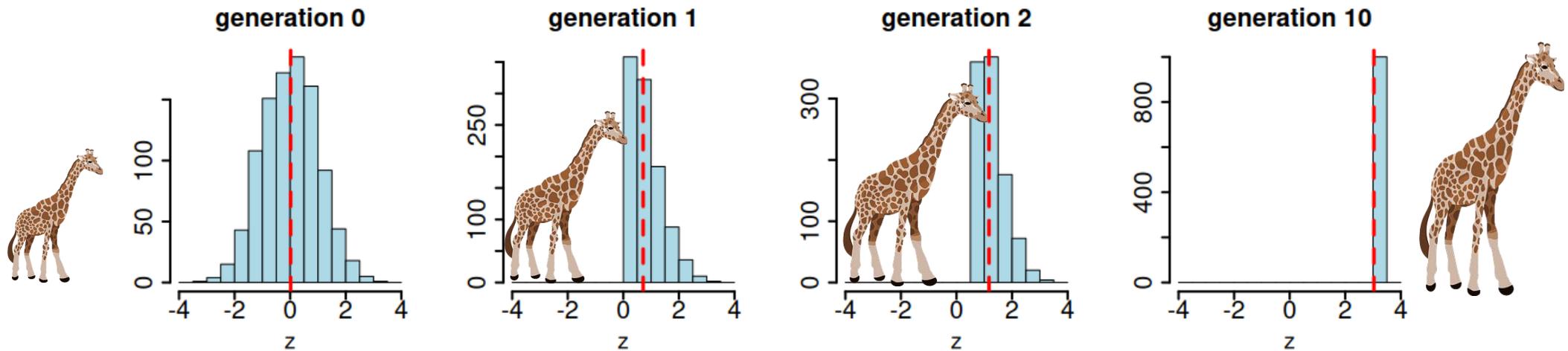
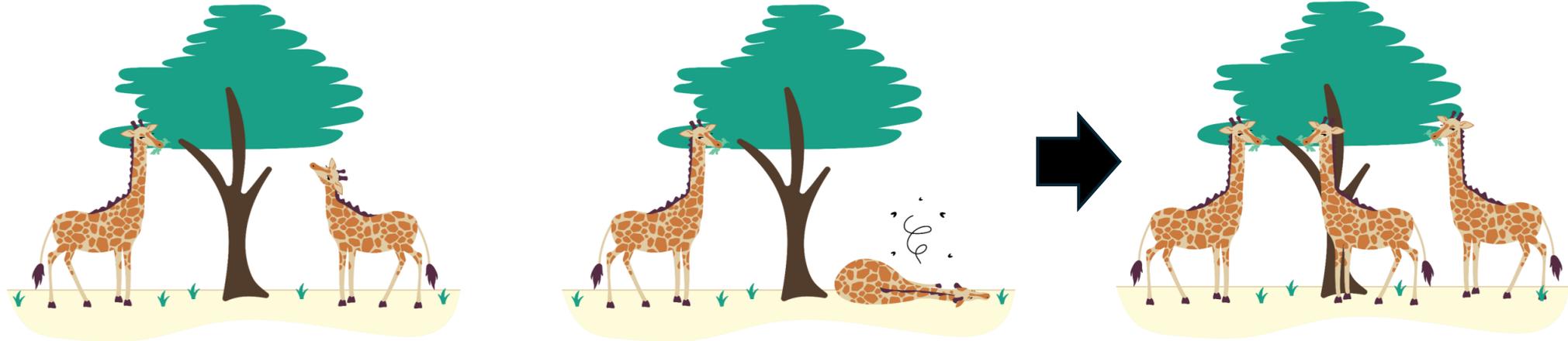
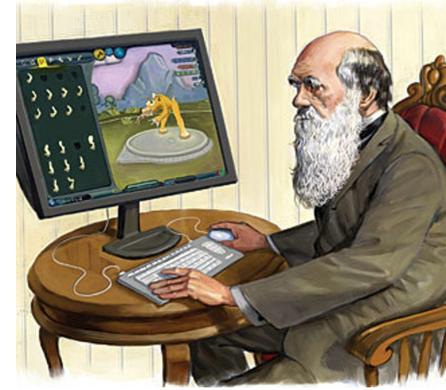


generation 0



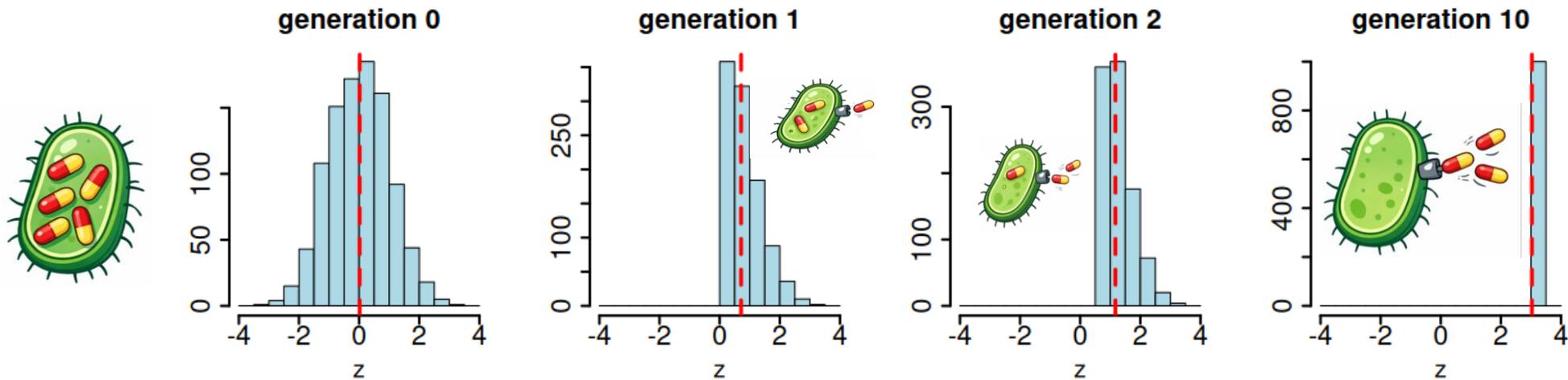
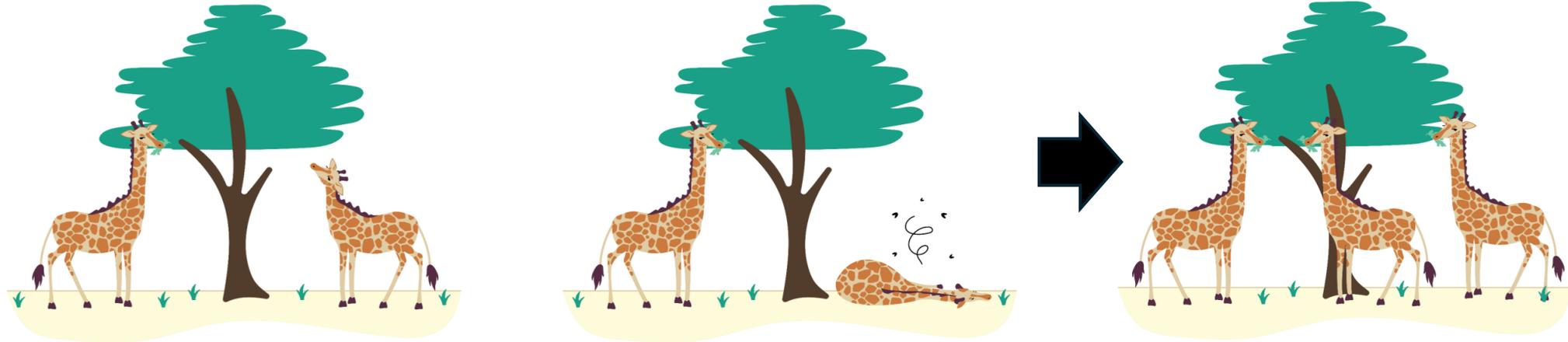
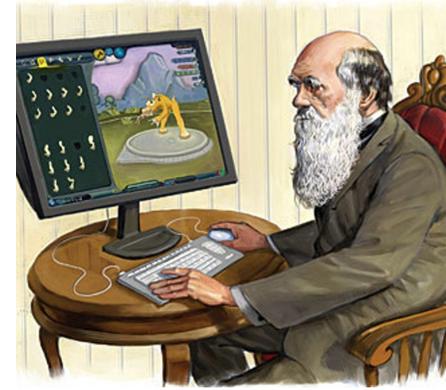
Our giraffes evolved a longer neck!

- Variability among individuals
- Differential contribution to successive generations
- Mechanism of inheritance



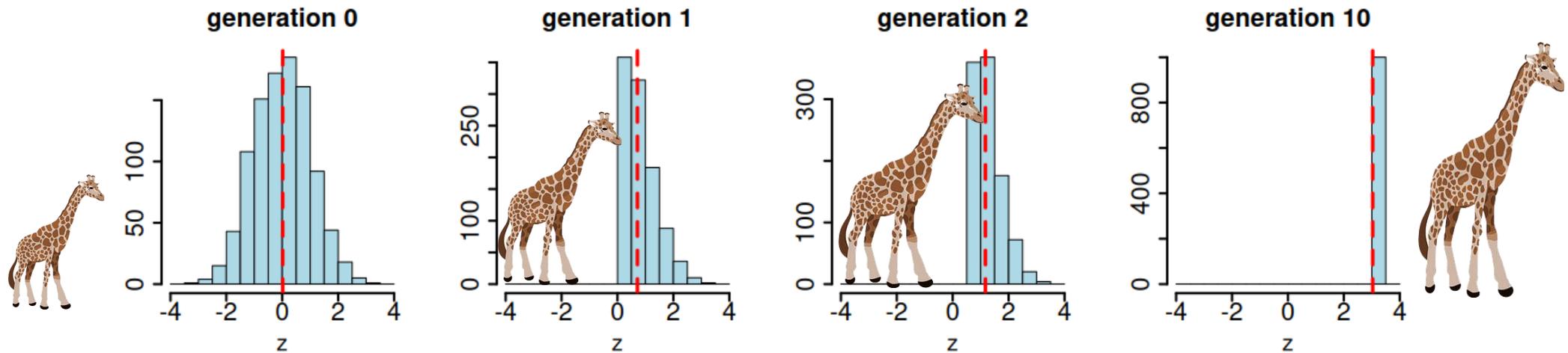
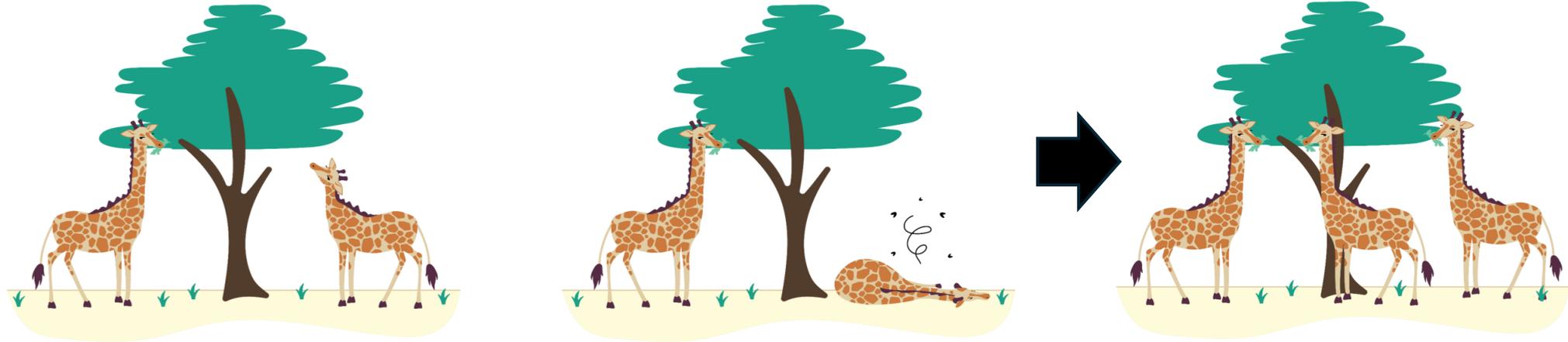
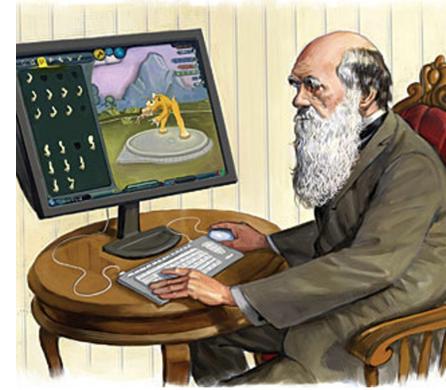
Our bacteria became more antibiotic resistant

- Variability among individuals
- Differential contribution to successive generations
- Mechanism of inheritance



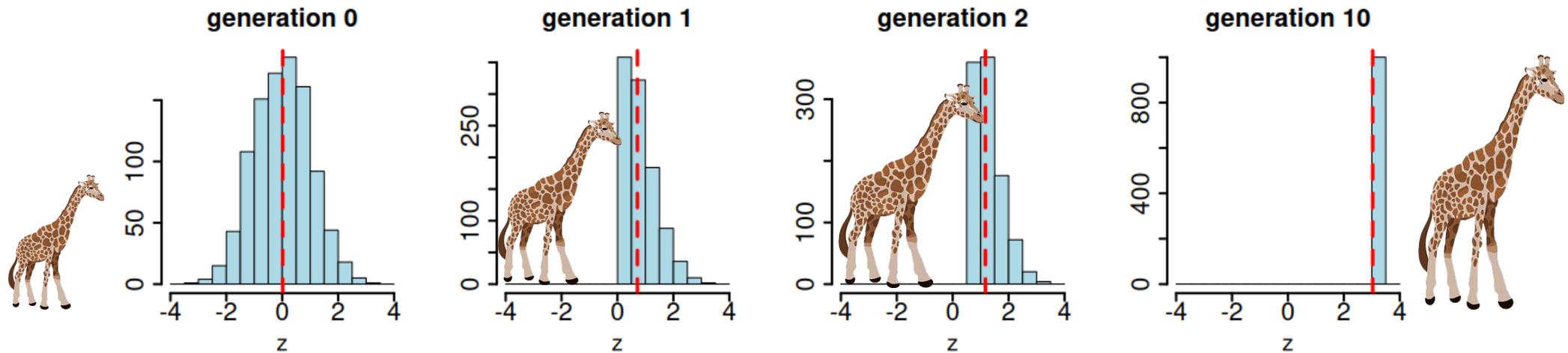
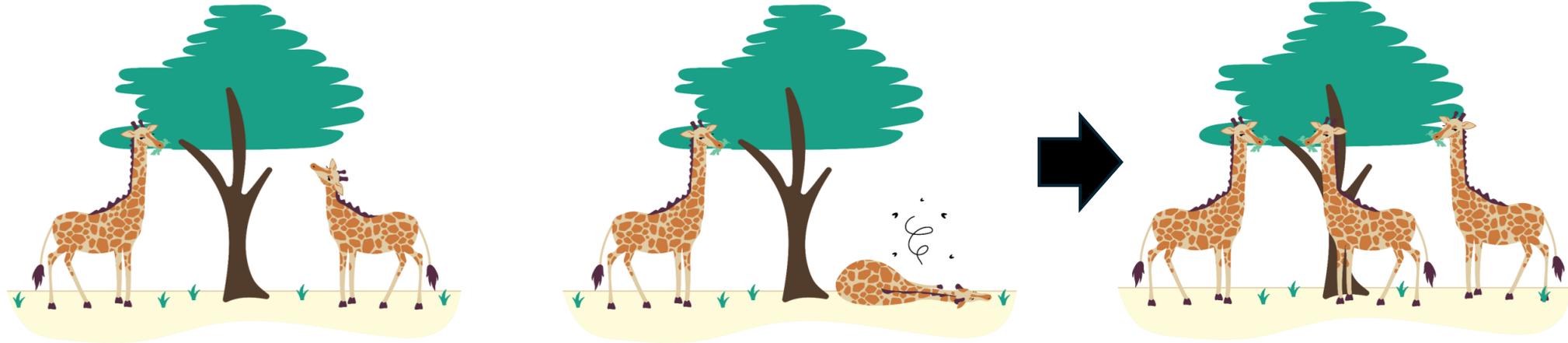
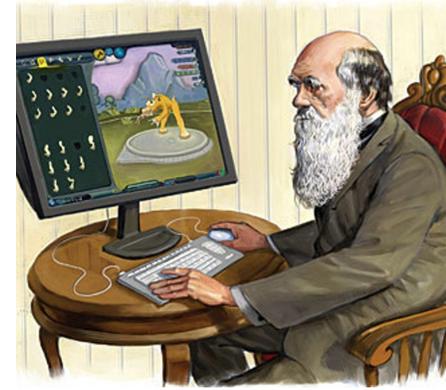
Our three ingredients are sufficient!

- Variability among individuals
- Differential contribution to successive generations
- Mechanism of inheritance

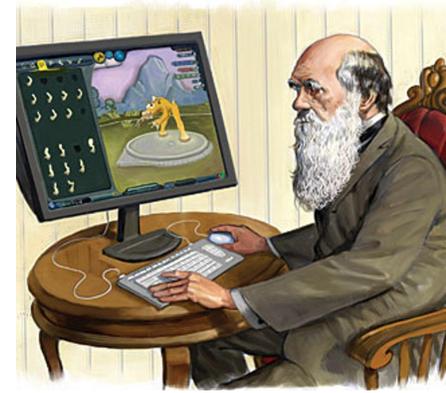


But are they also all necessary?

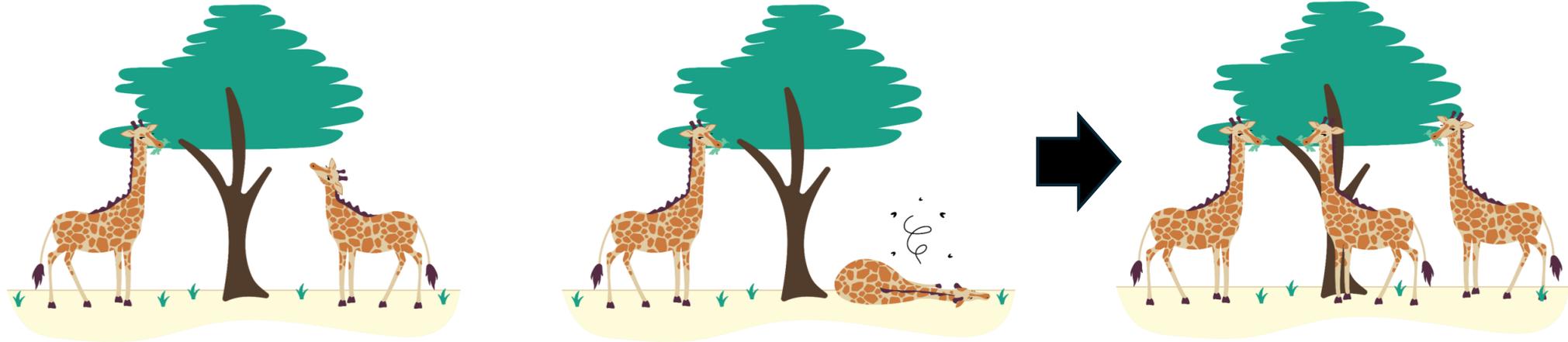
- Variability among individuals
- Differential contribution to successive generations
- Mechanism of inheritance



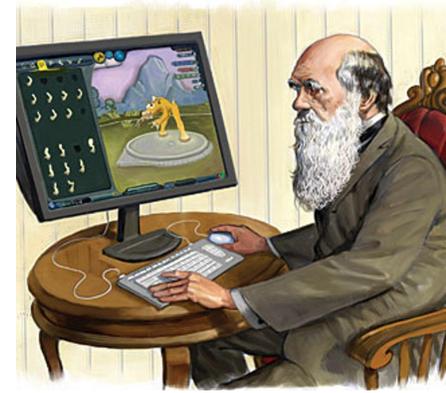
Let's remove them in turn: no variability



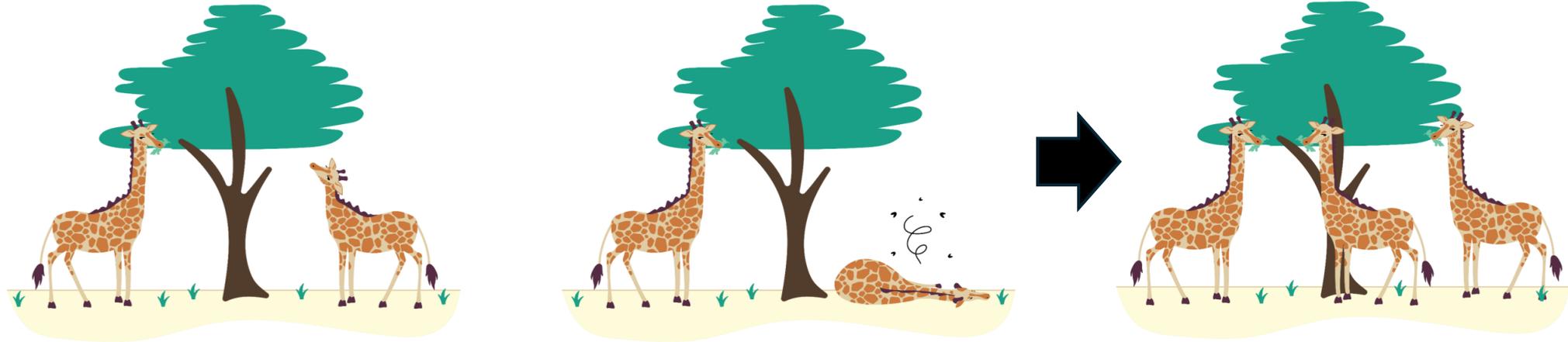
- ~~Variability among individuals~~
- Differential contribution to successive generations
- Mechanism of inheritance



Let's remove them in turn: no variability



- ~~Variability among individuals~~
- Differential contribution to successive generations
- Mechanism of inheritance



`rep(1, 1000)` → 1 1 1 1 1

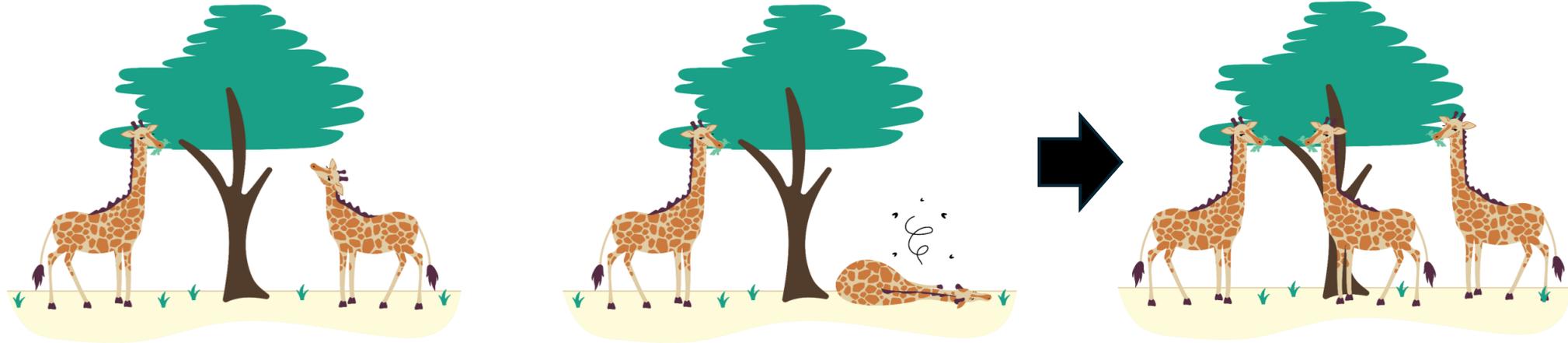
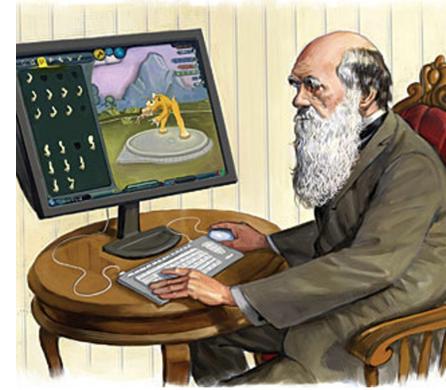
or

`rnorm(1000, sd=0.001)`



No variability \rightarrow No evolution!

- ~~Variability among individuals~~
- Differential contribution to successive generations
- Mechanism of inheritance

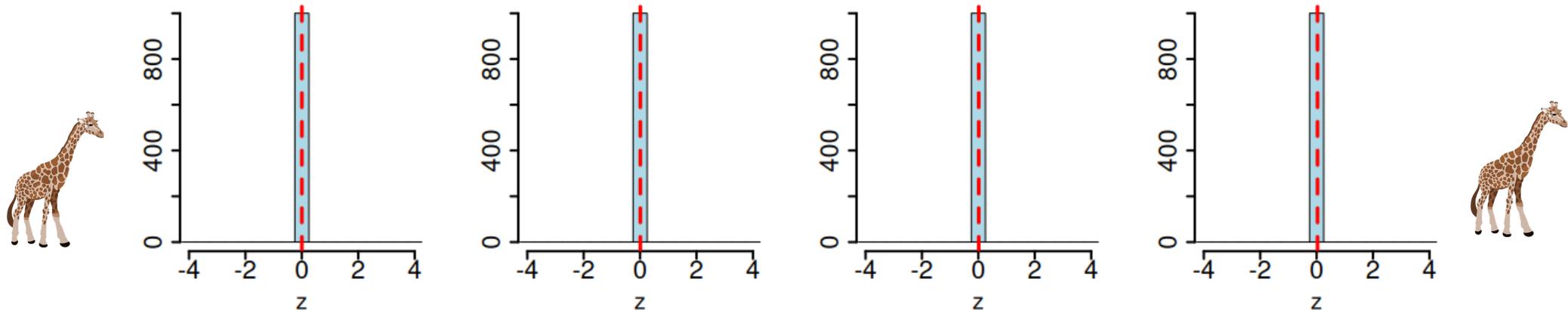


generation 0

generation 1

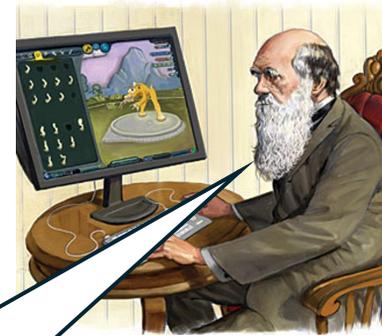
generation 2

generation 10

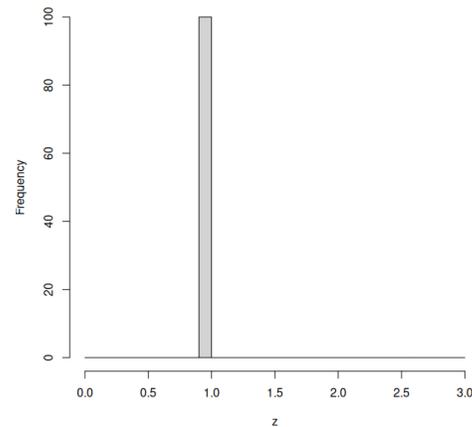
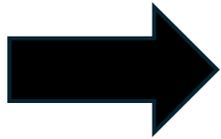
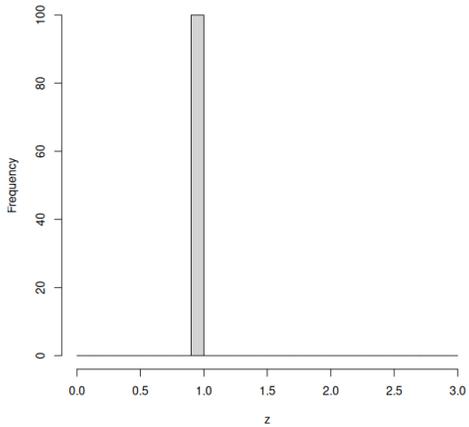


No variability → No evolution!

Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



Phytophthora infestans



What does it remind you in real life?



Crops with low variability

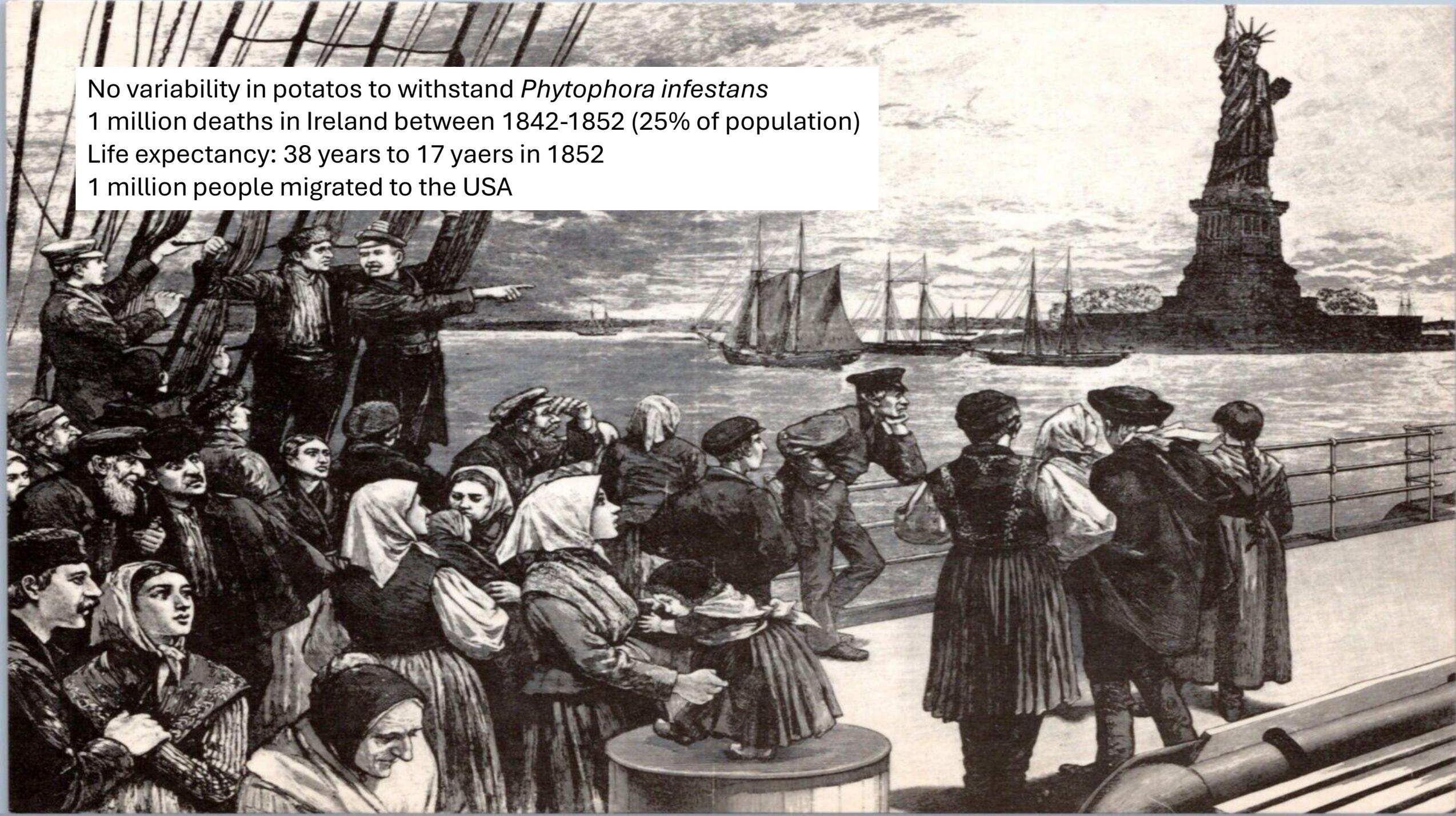
Ireland 1842-1852

No variability in potatoes to withstand *Phytophora infestans*
1 million deaths in Ireland between 1842-1852 (25% of population)
Life expectancy: 38 years to 17 years in 1852



Ireland 1847 - The Great Hunger.

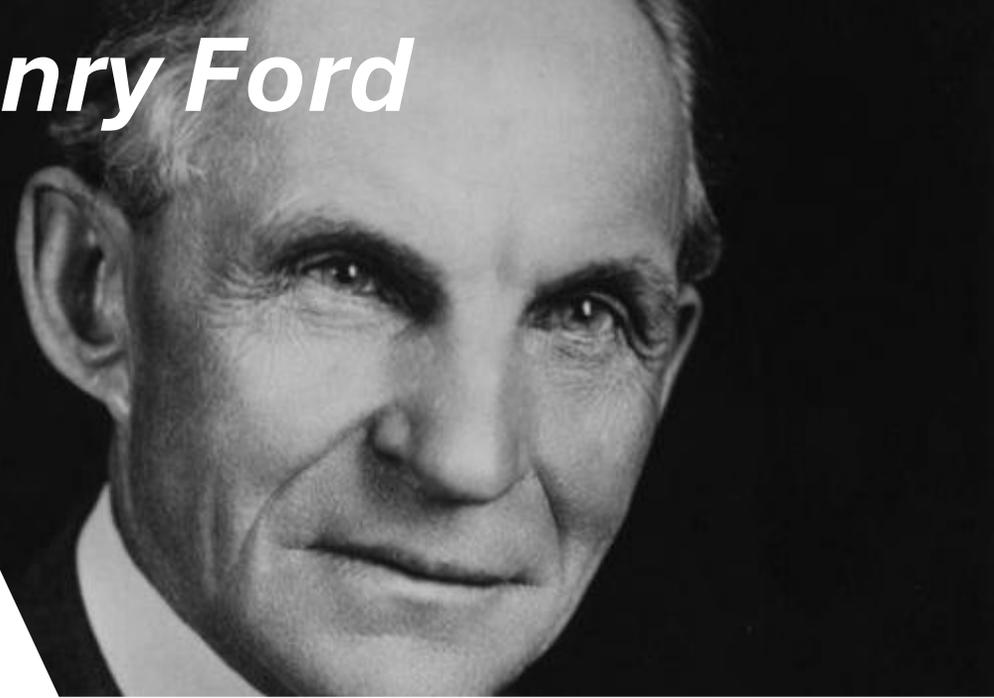
No variability in potatoes to withstand *Phytophora infestans*
1 million deaths in Ireland between 1842-1852 (25% of population)
Life expectancy: 38 years to 17 years in 1852
1 million people migrated to the USA





JFK

Henry Ford



Ronald Reagan

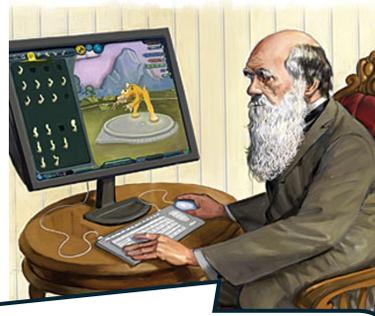


What happens with no “selection”?

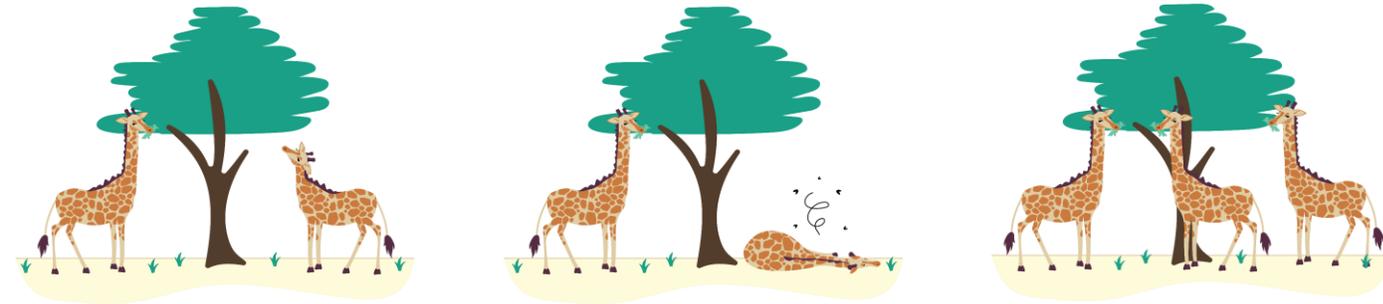
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



How would you model that?

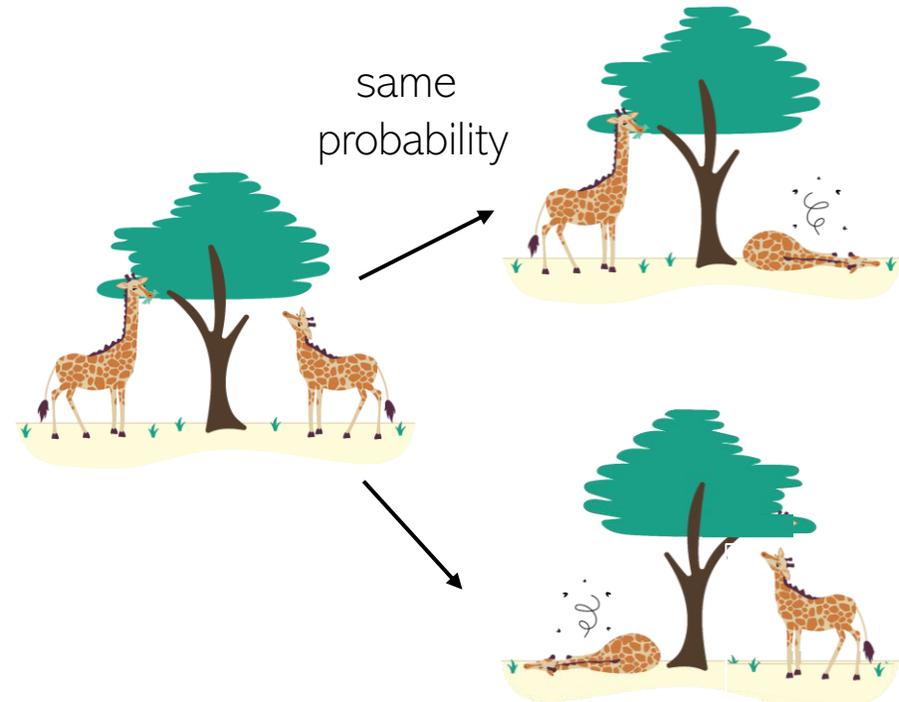
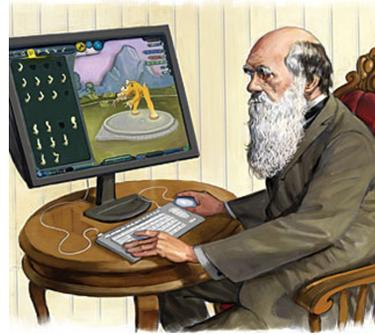


What happens with no “selection”?

Variability among individuals

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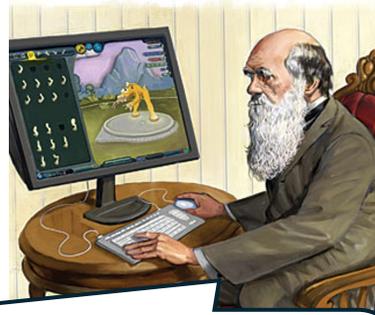


What happens with no “selection”?

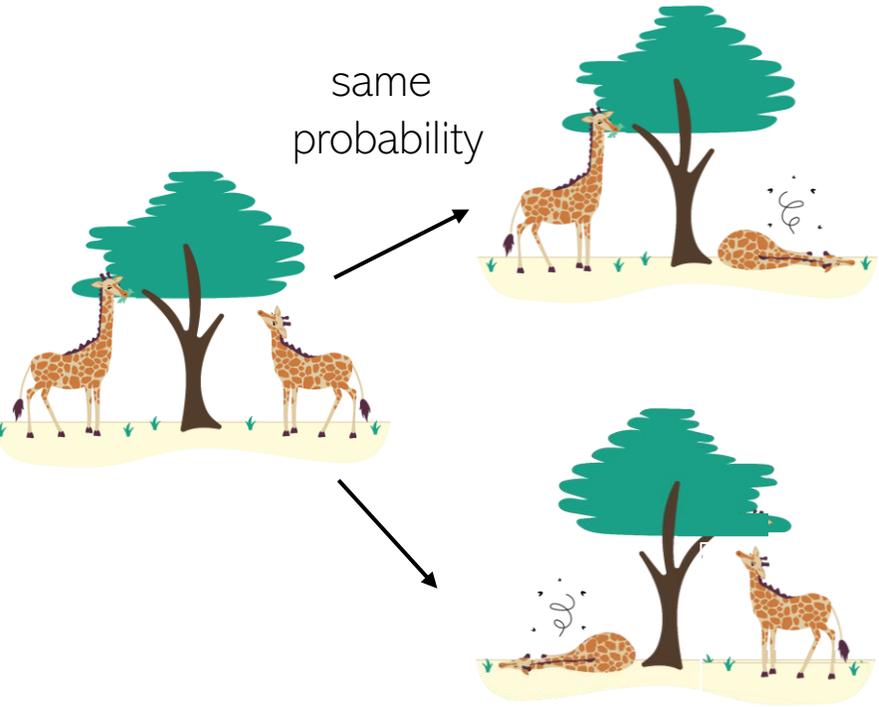
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



What happens?

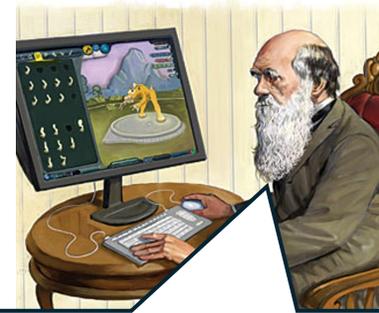


No selection → No evolution?

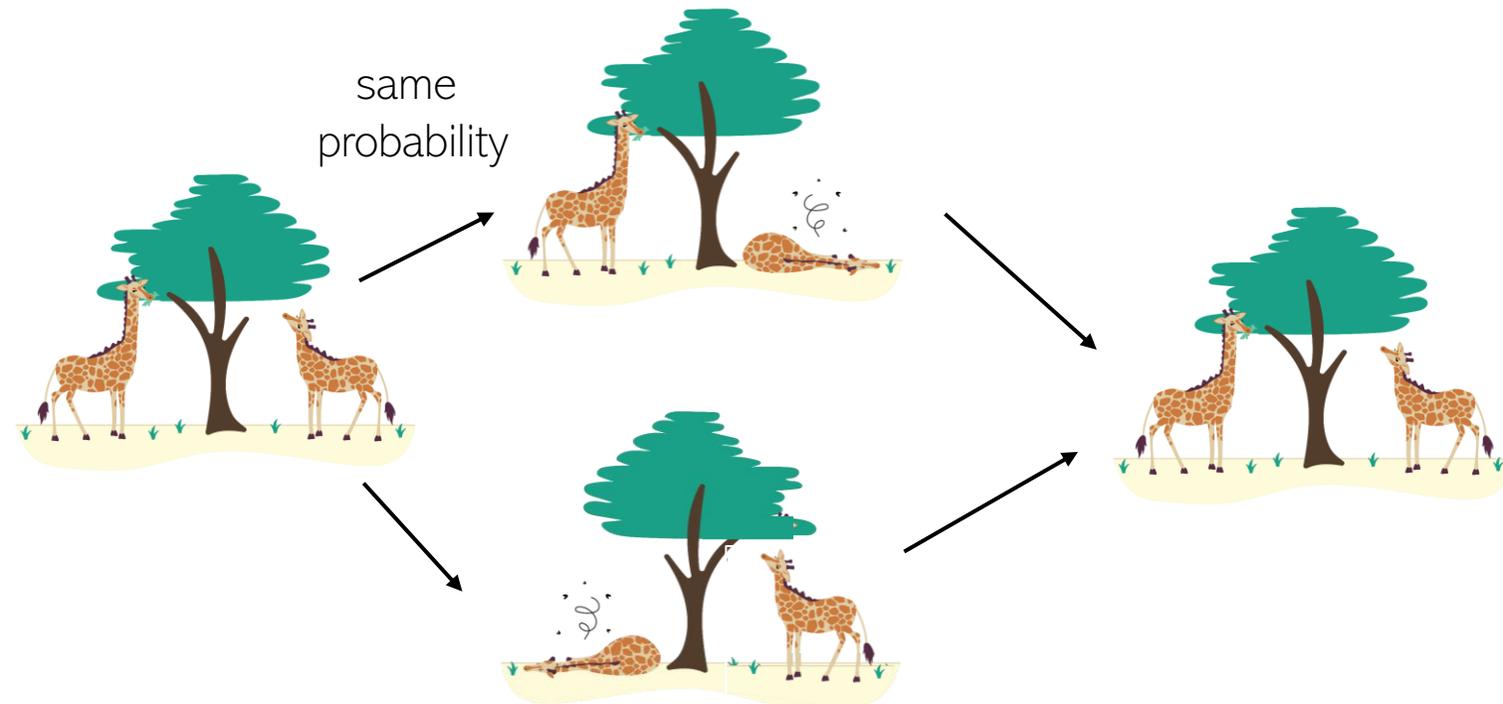
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



Well, no «biased» change..



No selection \rightarrow No evolution?

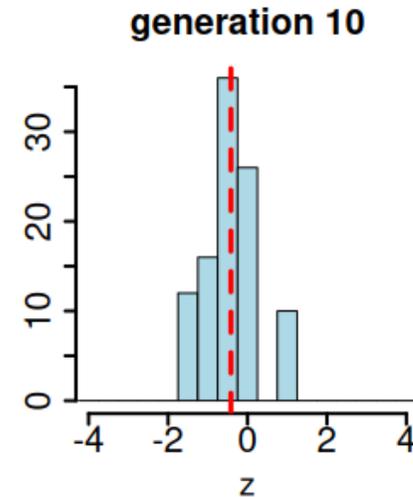
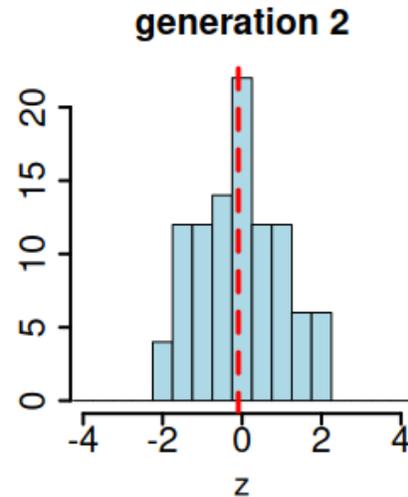
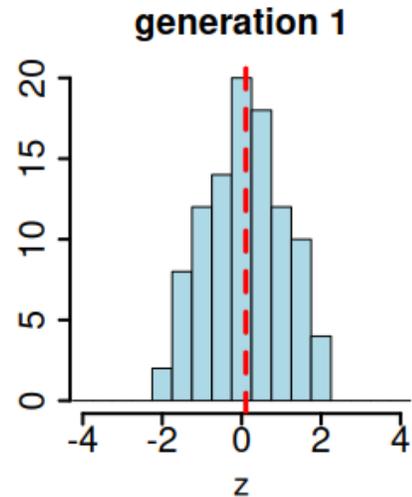
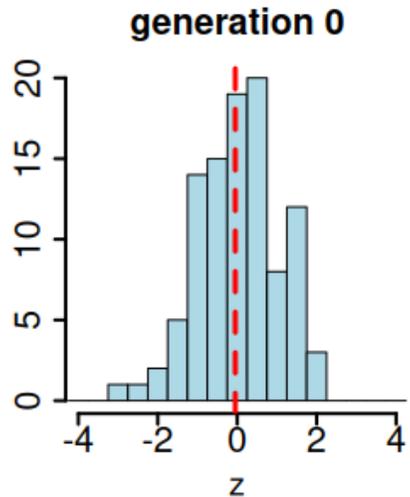
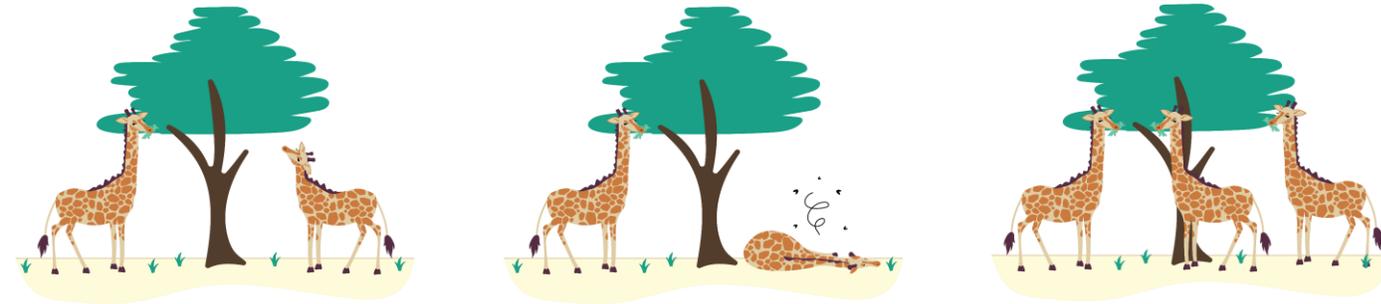
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



There is some small change/evolution!



No selection \rightarrow No evolution?

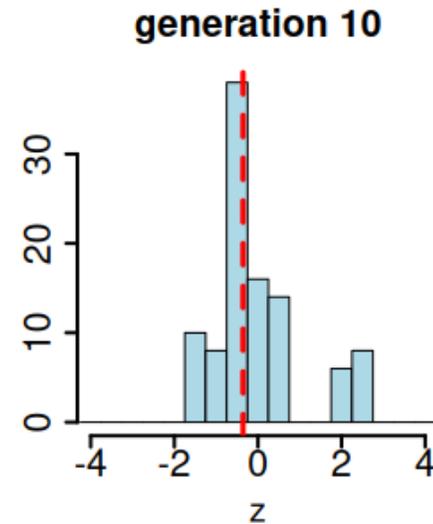
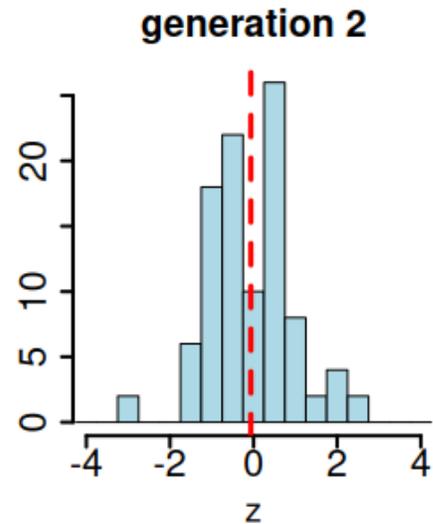
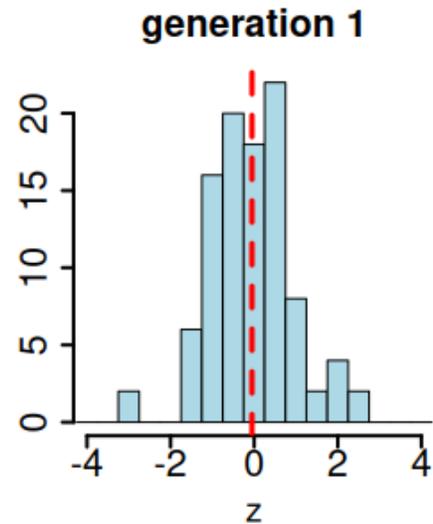
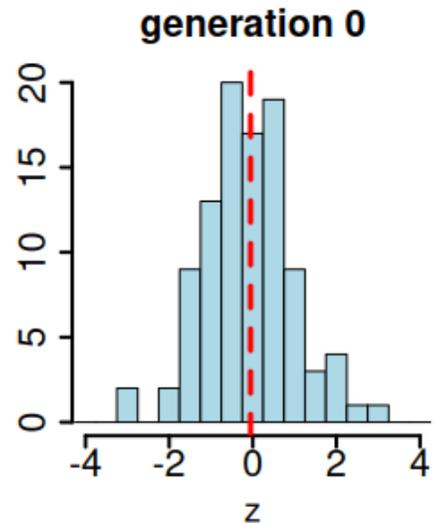
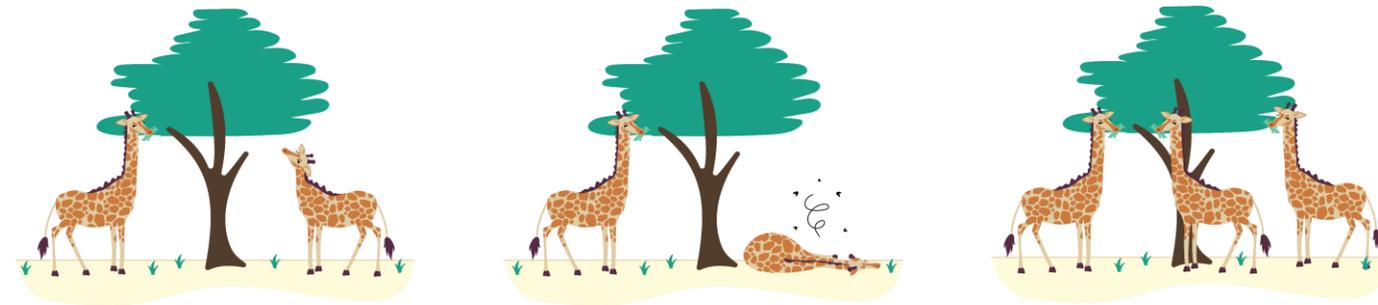
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



There is some small change/evolution!



No selection → No evolution?

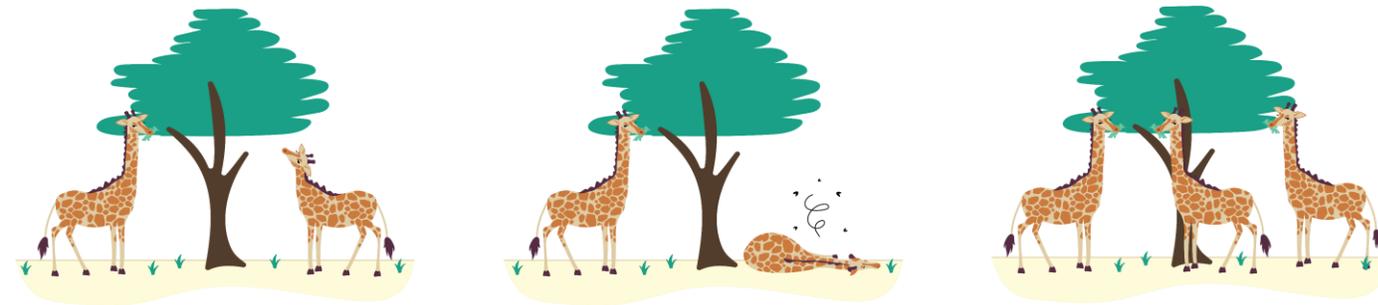
Variability among individuals

Differential contribution to successive generations

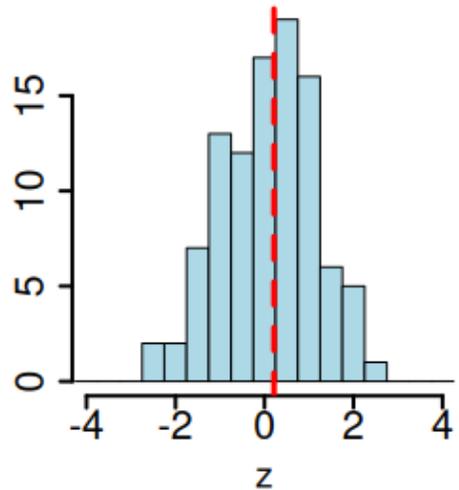
Mechanism of inheritance



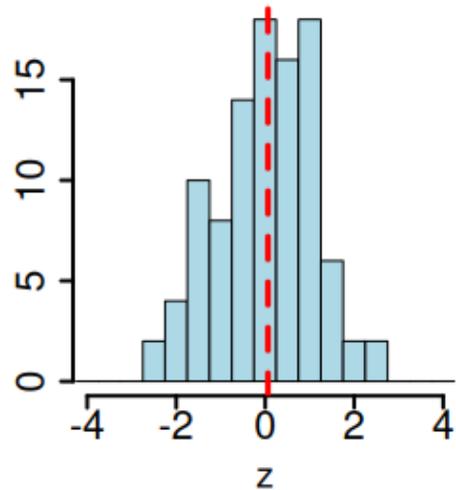
There is some small change/evolution!



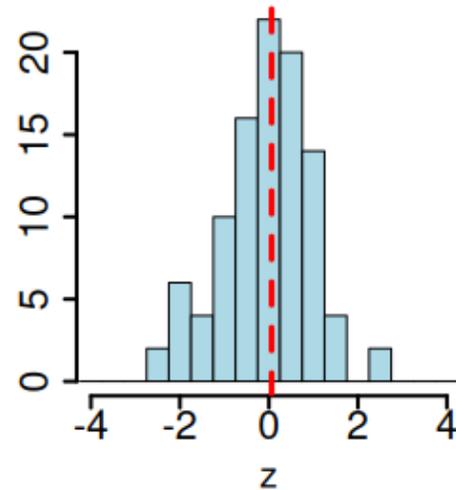
generation 0



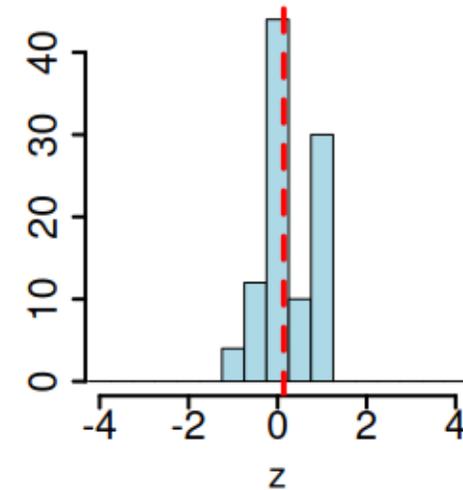
generation 1



generation 2



generation 10

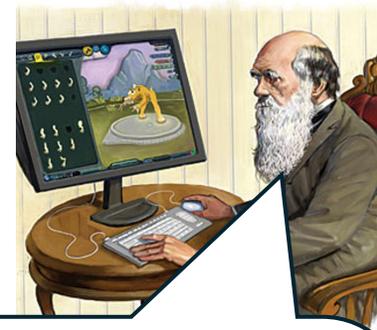


No selection → No directional evolution (on average)

Variability among individuals

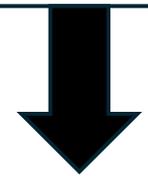
Differential contribution to successive generations

Mechanism of inheritance

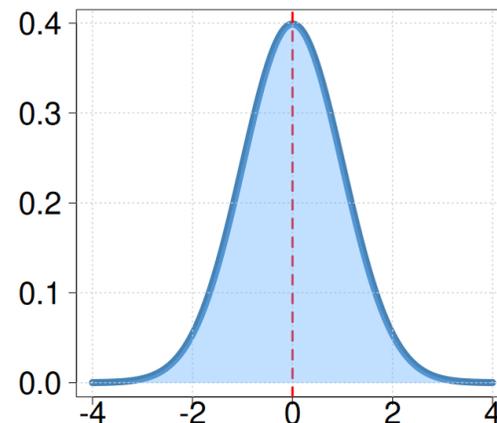
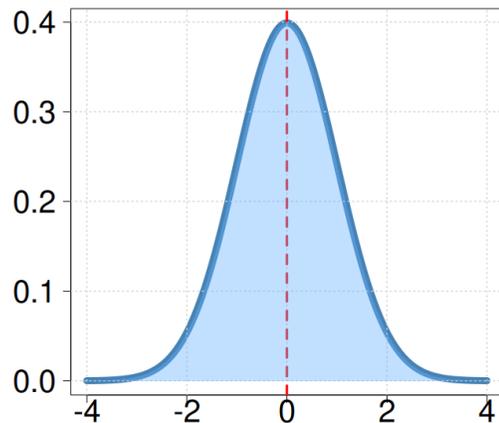
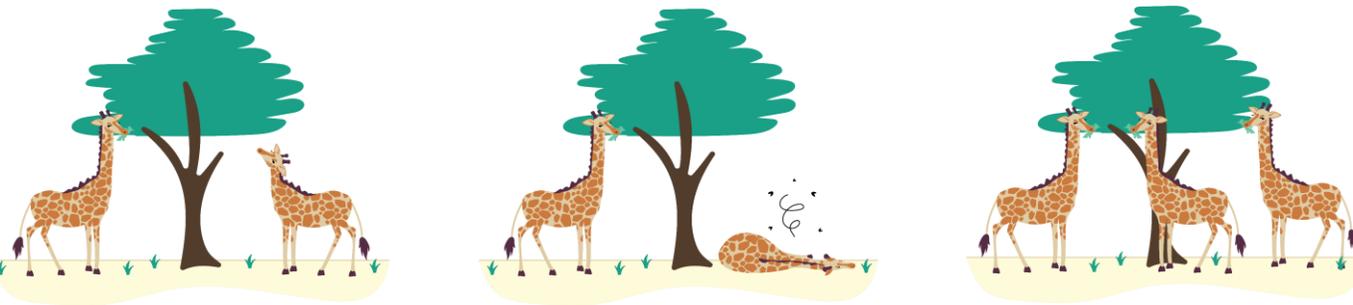


If we do it many times, on average populations keep the same neck length.

But each population still evolves in random directions!



This is **random genetic drift** and we will study it in population genetics



Neck length

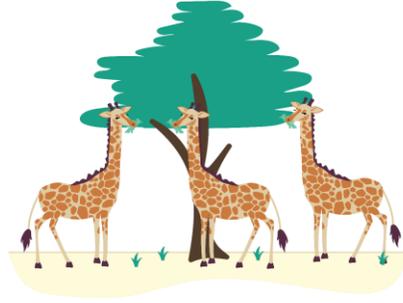
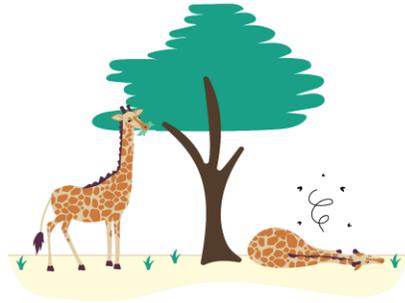
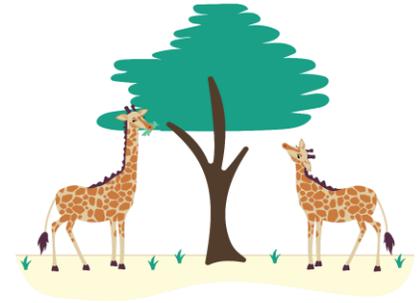
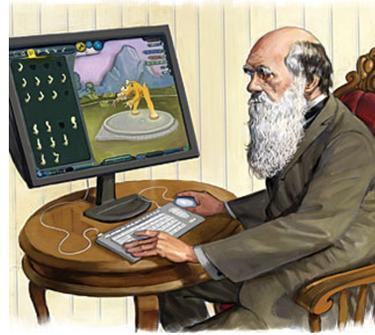
Neck length

What happens with no inheritance?

Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance

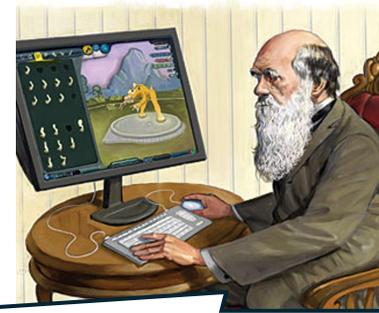


What happens with no inheritance?

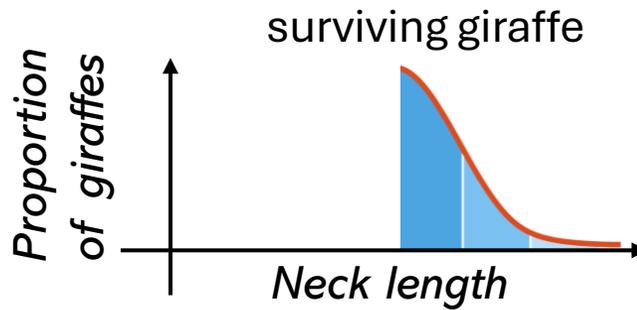
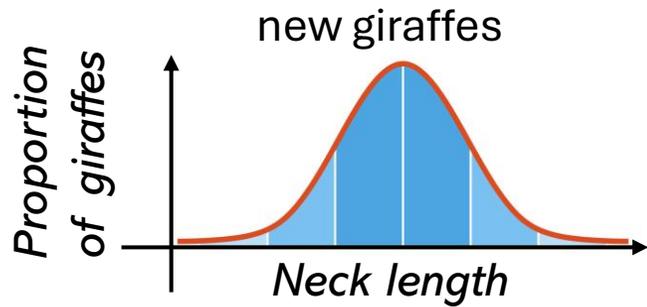
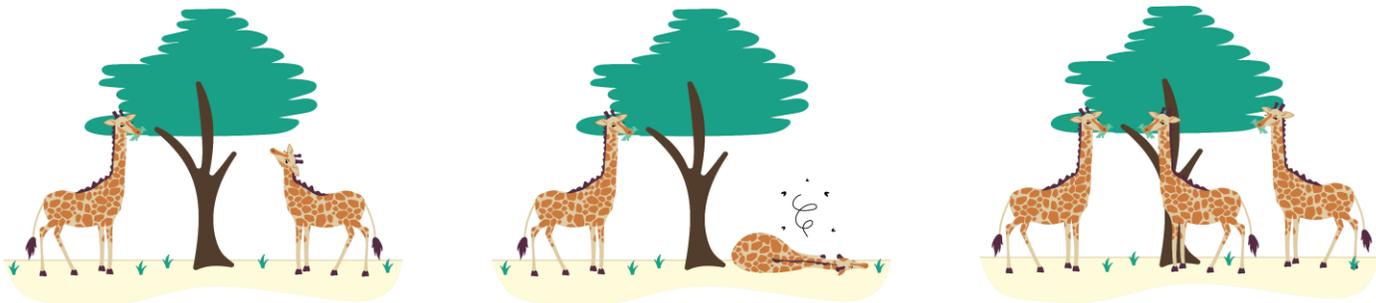
Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



All variability in neck length is just random

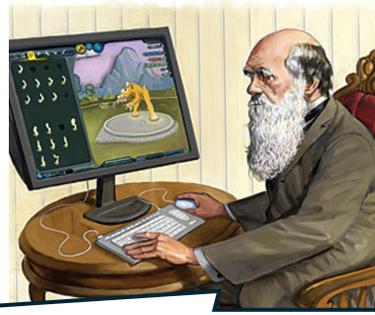


No inheritance → No evolution!

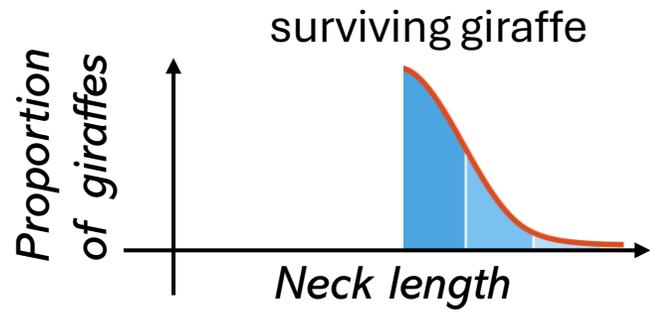
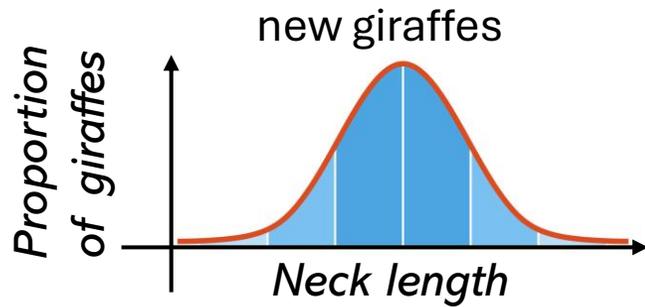
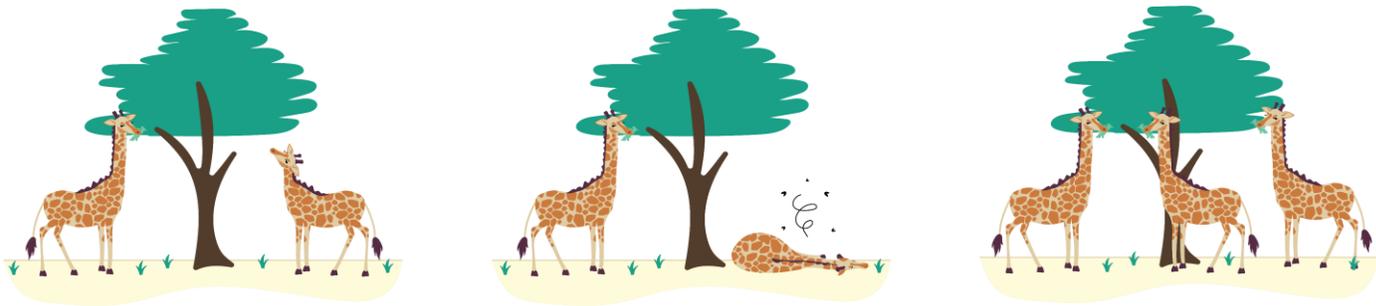
Variability among individuals

Differential contribution to successive generations

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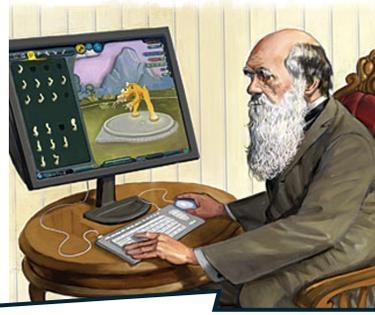


All variability in neck length is just random

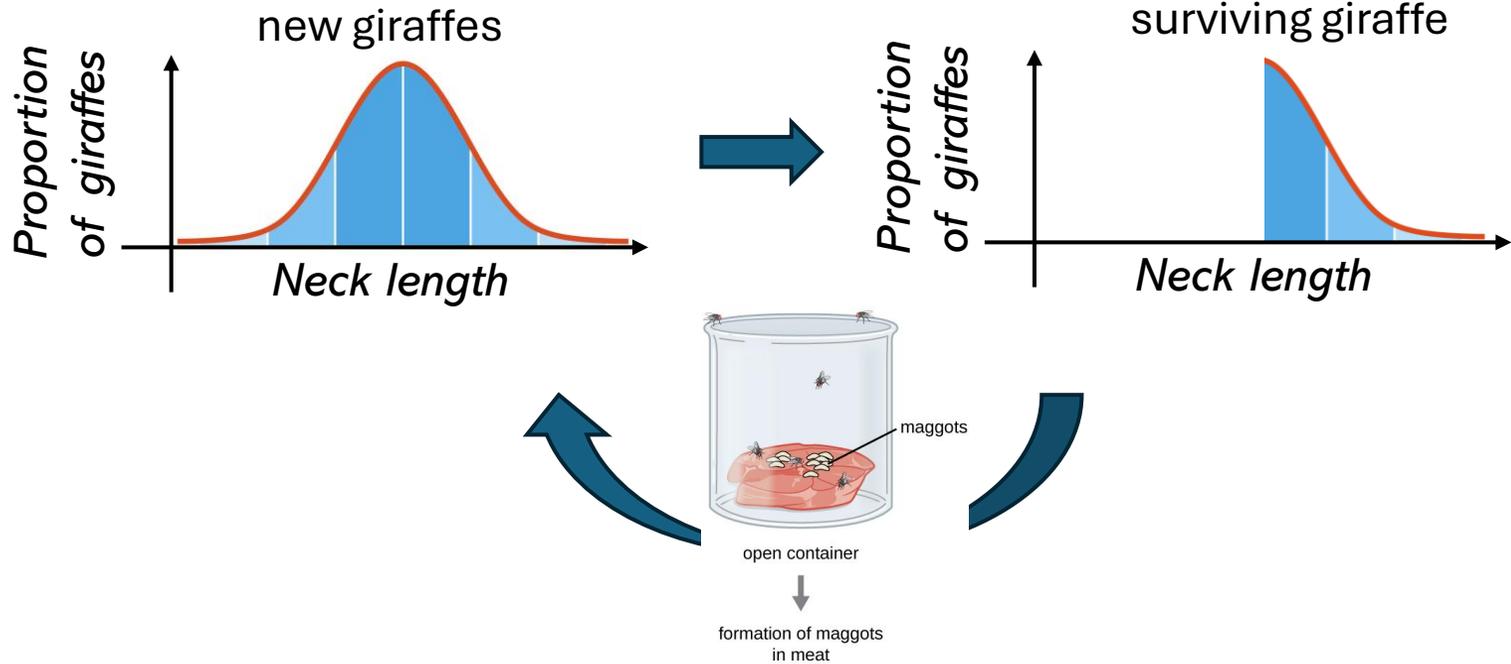
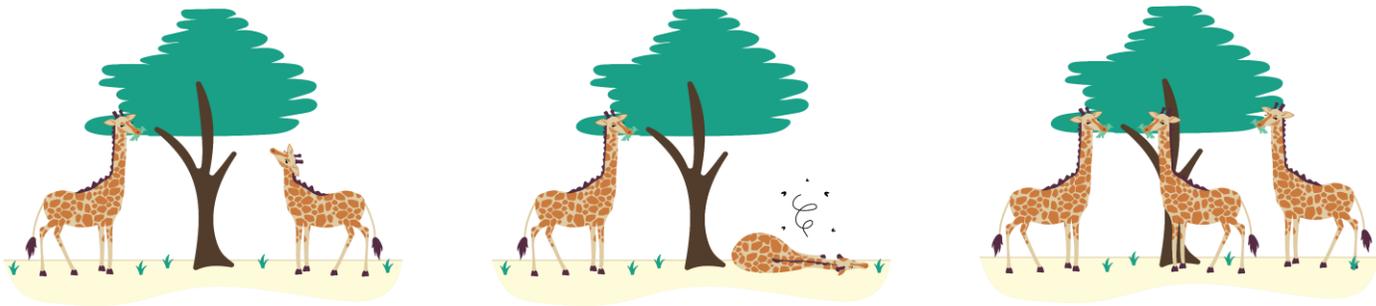


No inheritance → No evolution!

Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



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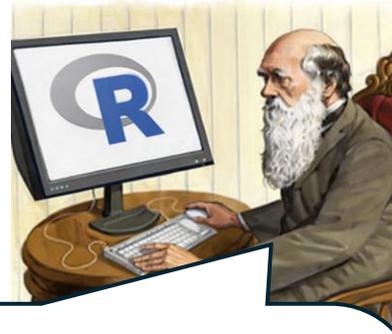


No inheritance → No evolution!

Variability among individuals

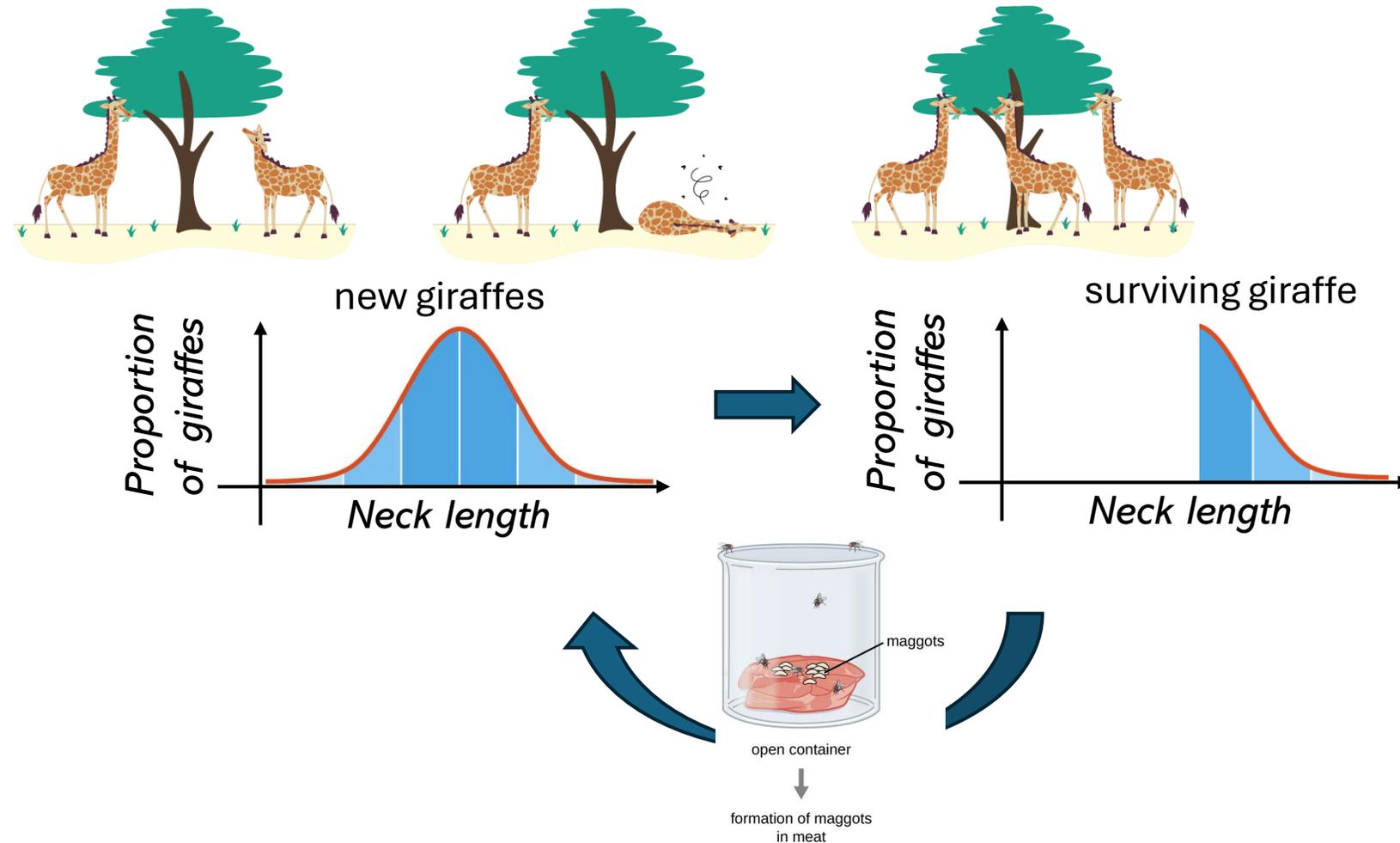
Differential contribution to successive generations

Mechanism of inheritance



No «inheritance»

```
for (i in 1:1000)
  {z= rnorm(N)}
```

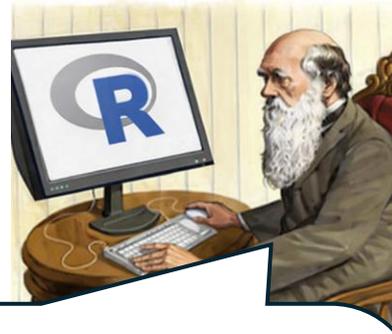


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Variability among individuals

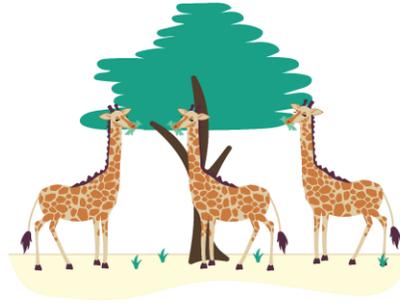
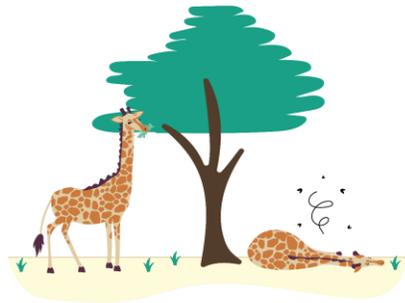
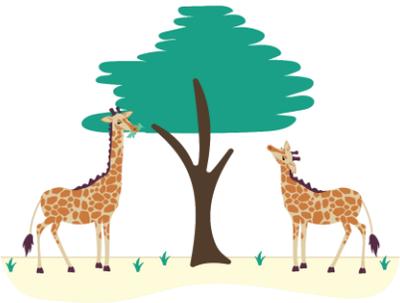
Differential contribution to successive generations

Mechanism of inheritance

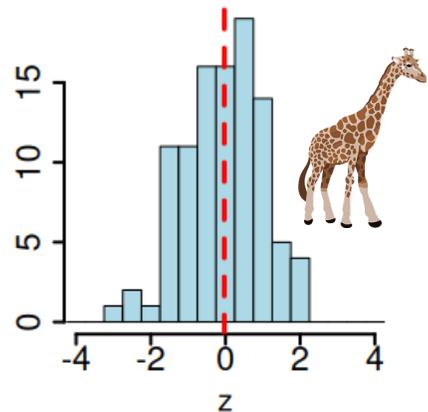


No «inheritance»

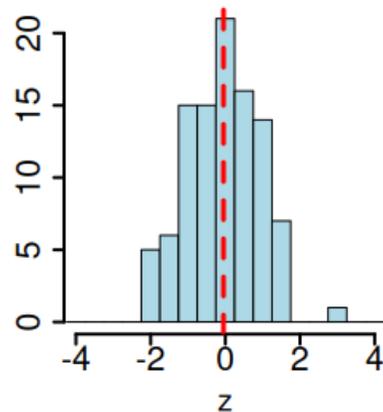
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for (i in 1:1000)  
  {z= rnorm(N)}
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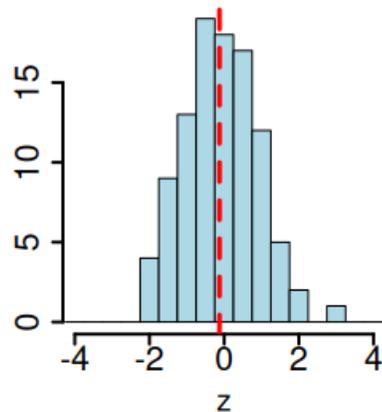
generation 0



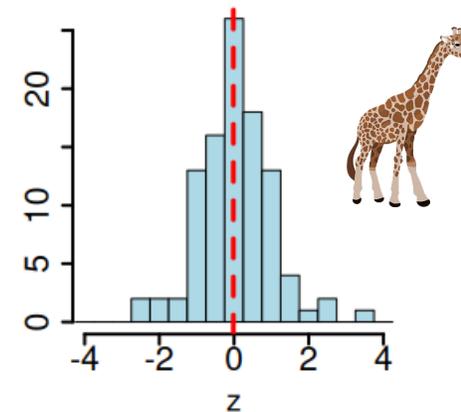
generation 1



generation 2



generation 10

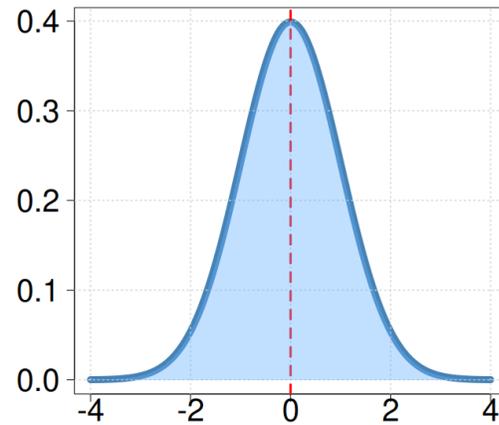
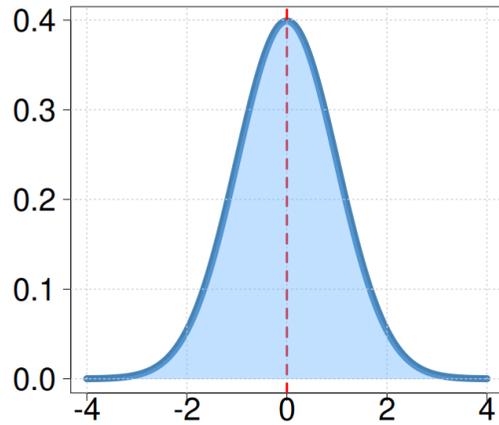
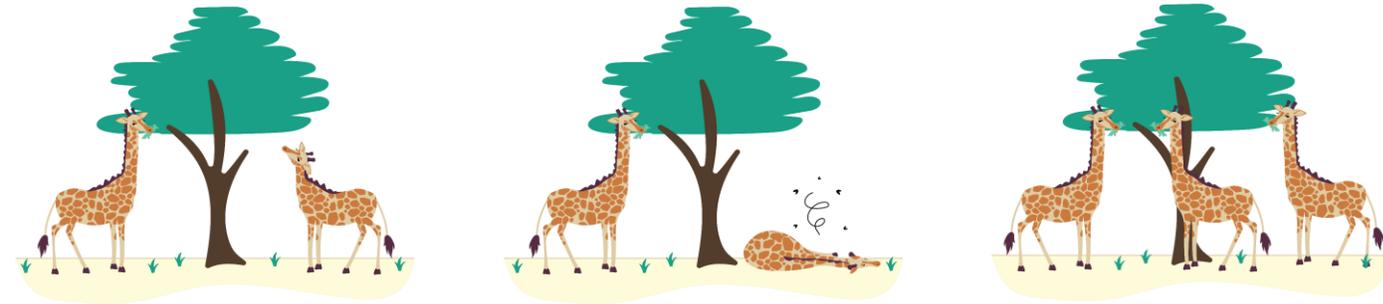
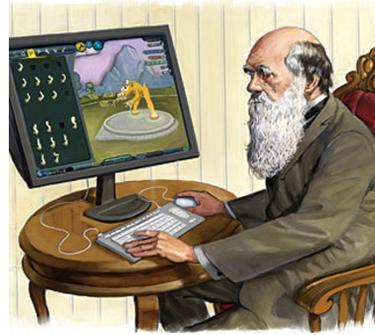


No inheritance \rightarrow No evolution!

Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



Neck length

Neck length

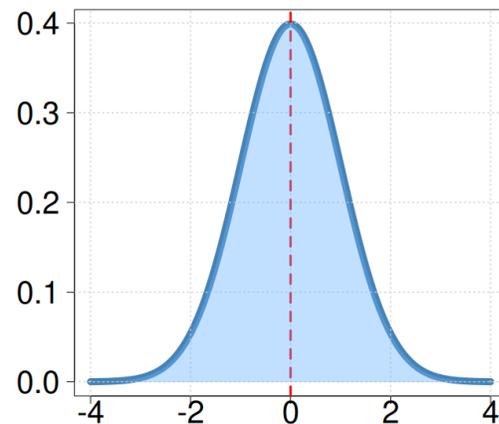
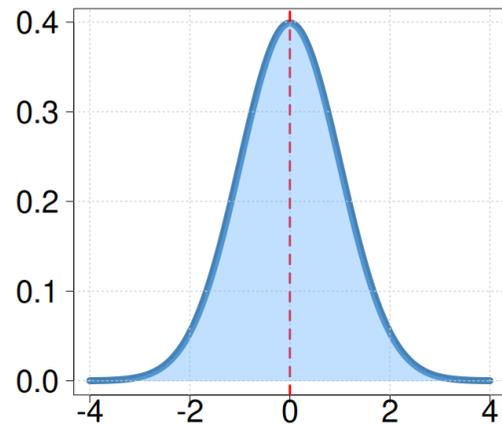
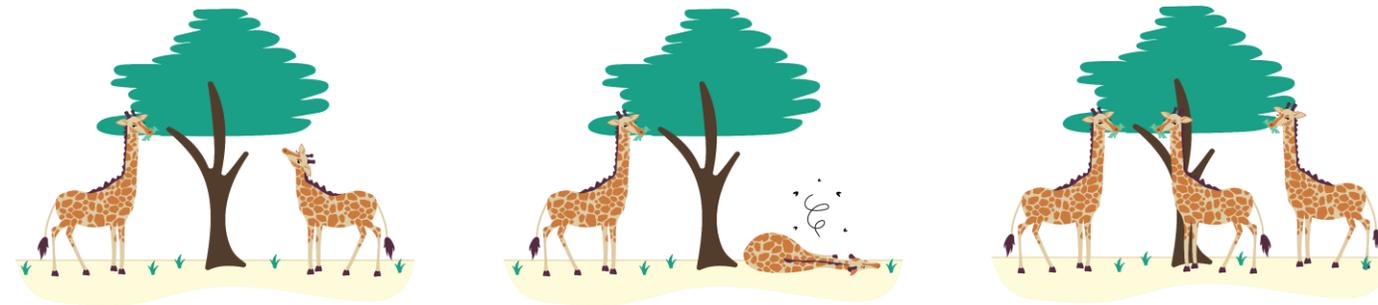
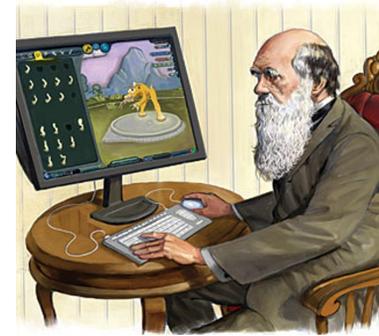
All three ingredients are necessary and sufficient

Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance

in silico



Neck length

Neck length

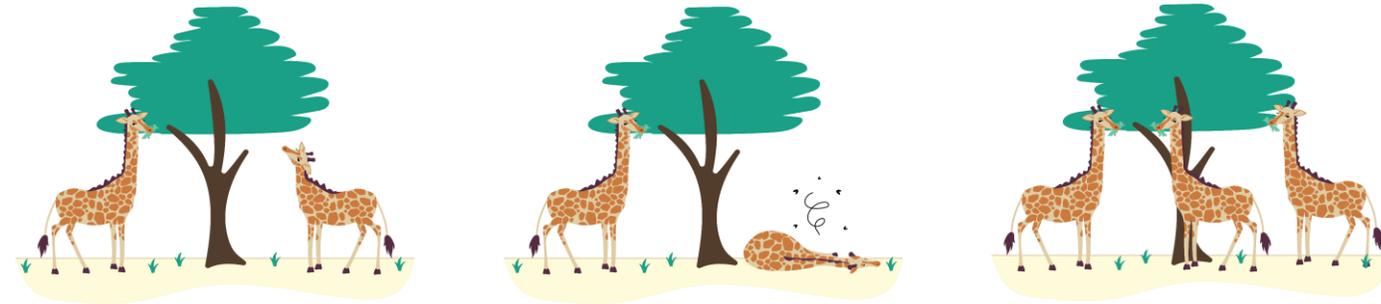
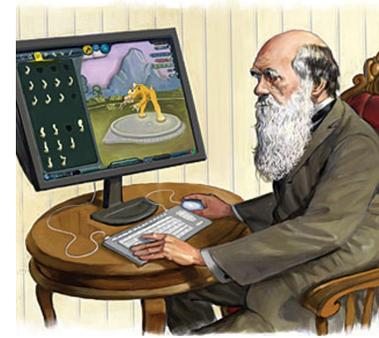
All three ingredients are necessary and sufficient

Variability among individuals

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Mechanism of inheritance

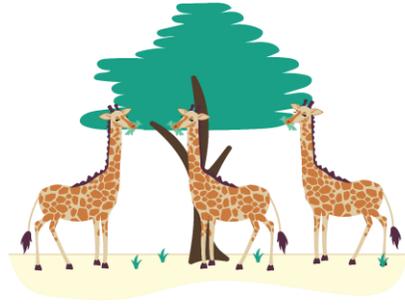
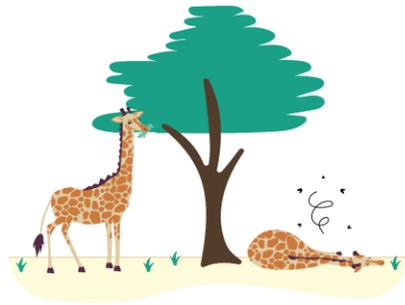
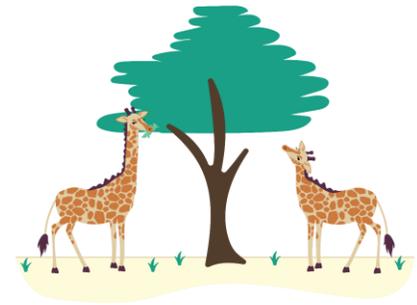
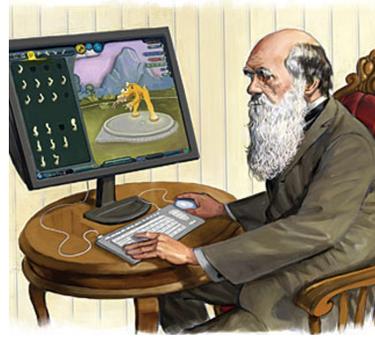
in silico



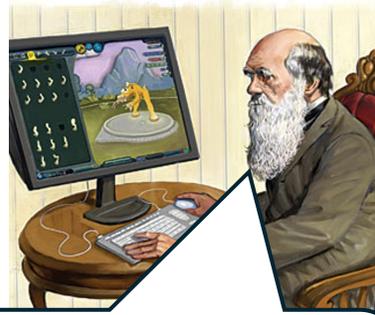
..and in our **toy** model



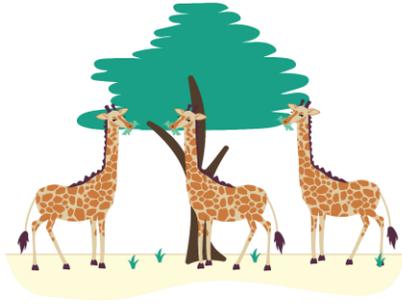
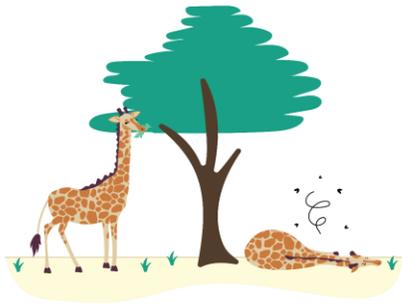
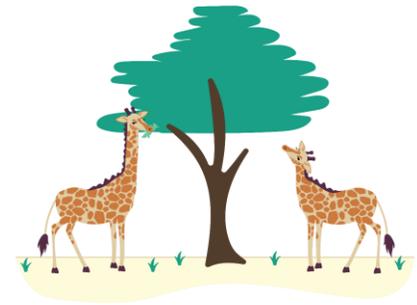
Limitations of our toy model?



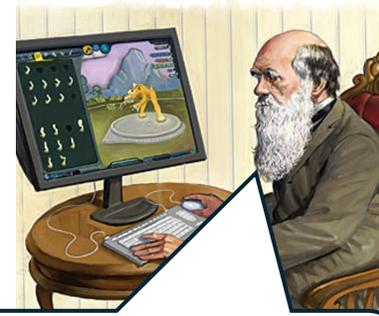
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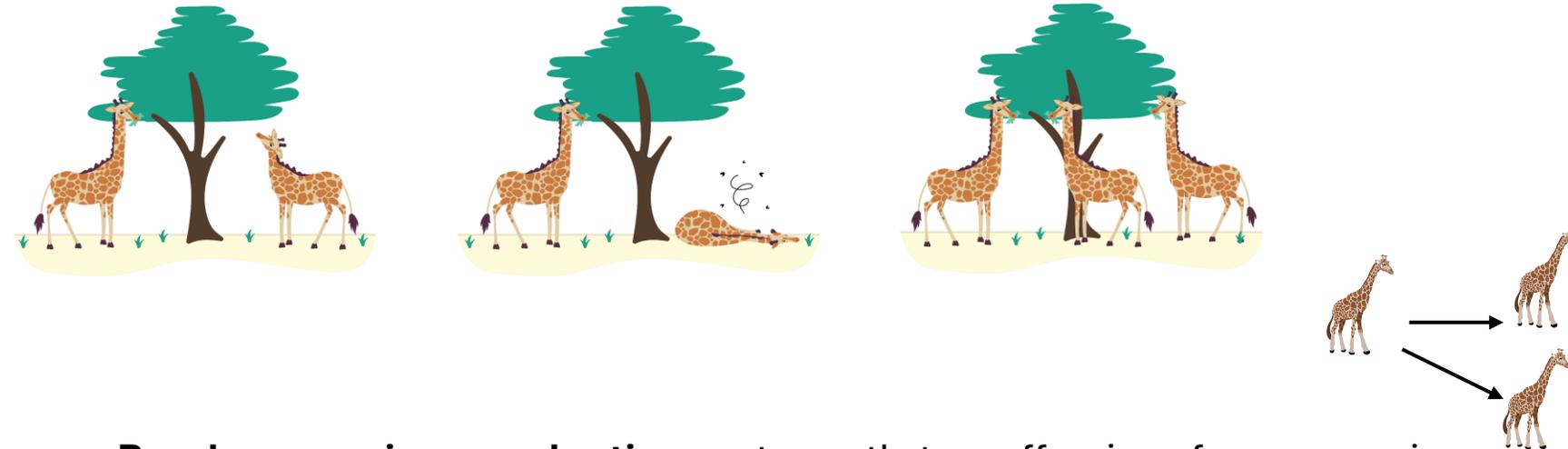
So far we used an extremely simplistic inheritance model.
What is missing?



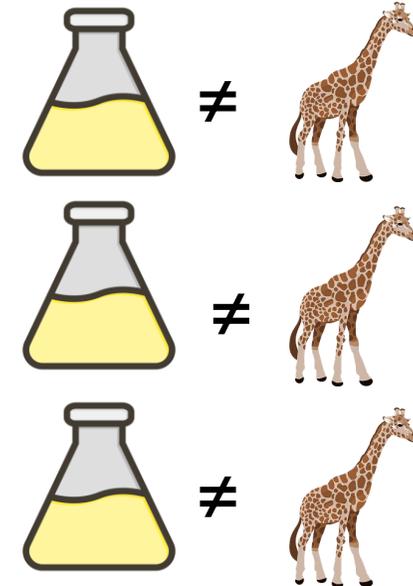
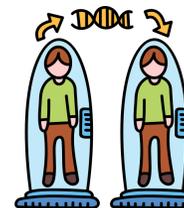
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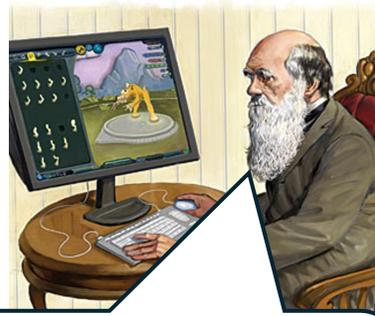
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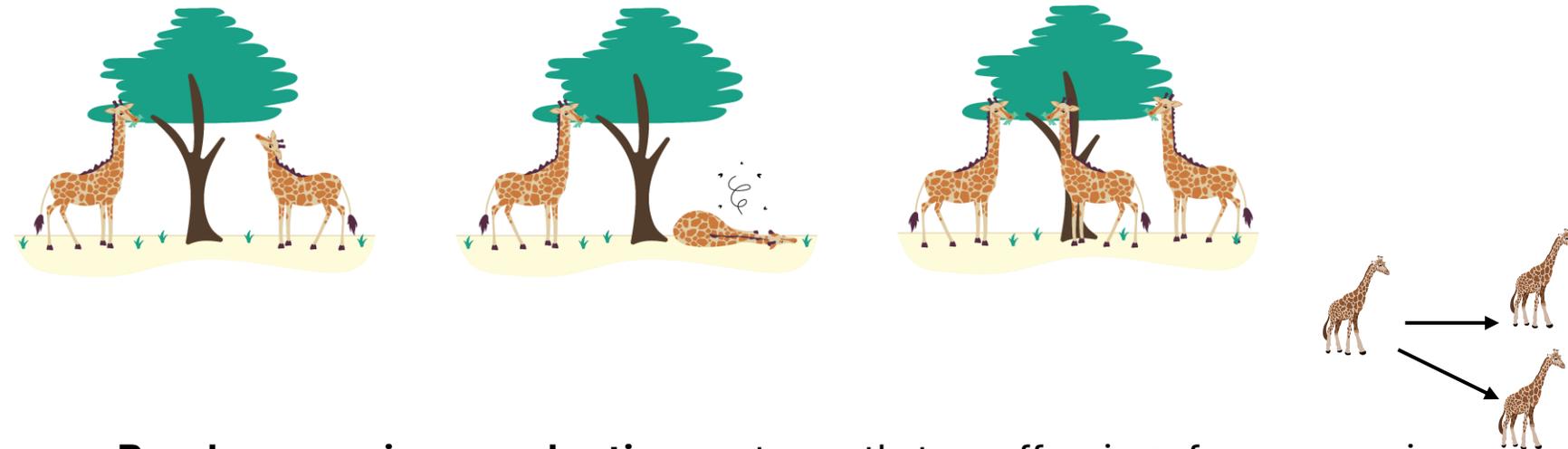
- **Randomness in reproduction:** not exactly two offsprings for one survivors – giraffes are not bacteria!
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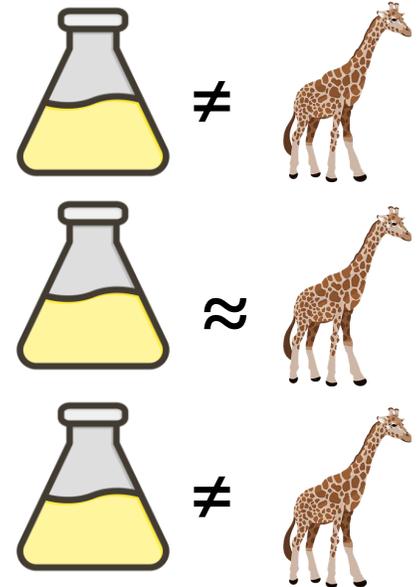
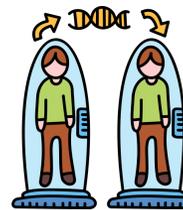
Limitations of our toy model



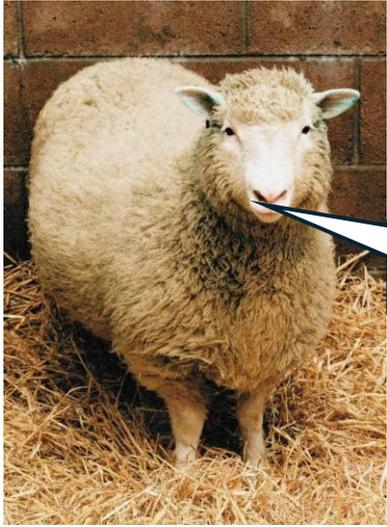
Actually not even bacteria in flask



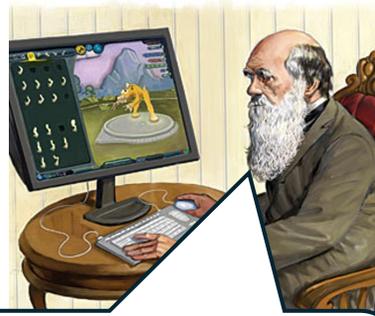
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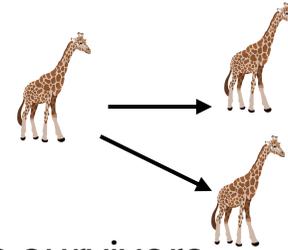
Limitations of our toy model



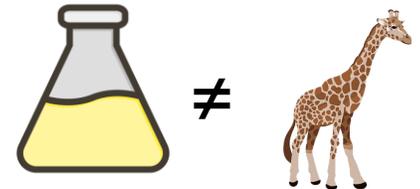
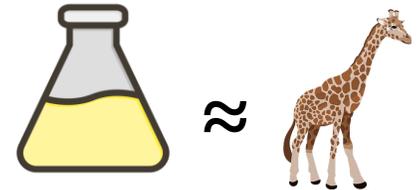
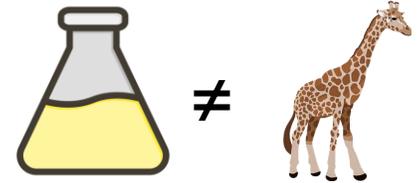
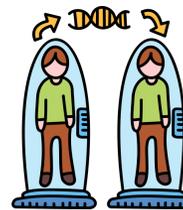
Not even me



Actually not even bacteria in flask



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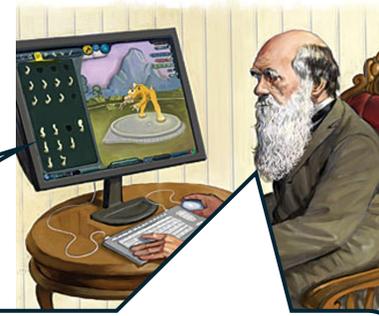


Limitations of our toy model

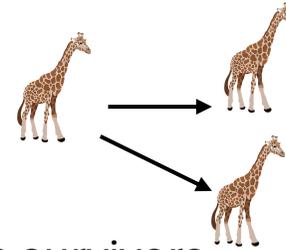


Not even me

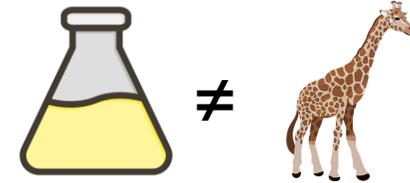
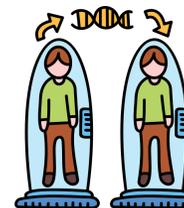
And I know, many other things are missing: mutation, recombination, culture, changes in the environment..but let's start simple



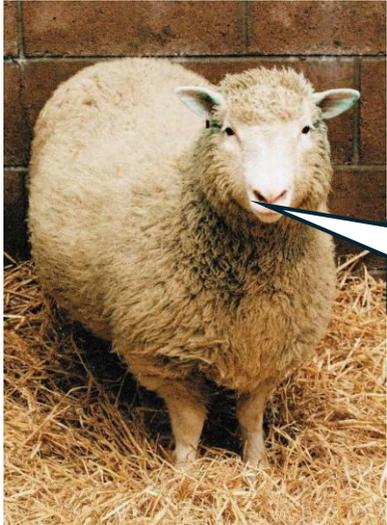
Actually not even bacteria in flask



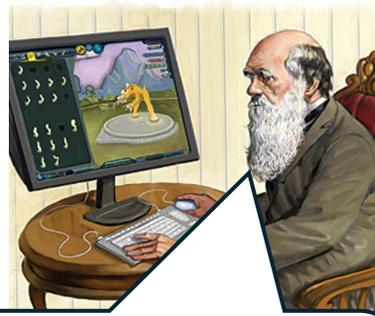
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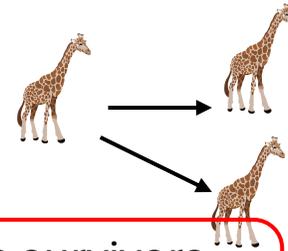
Let's address these limitations



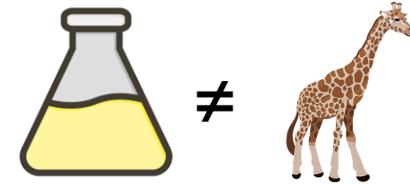
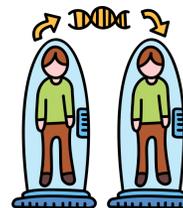
Not even me



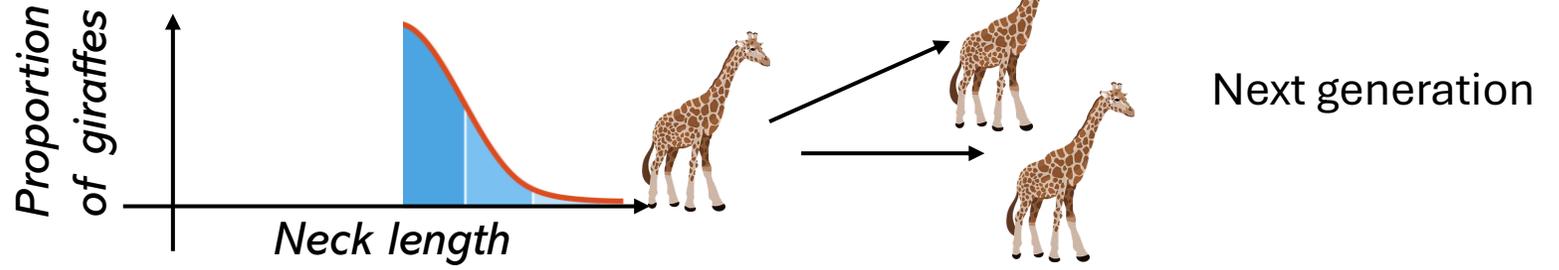
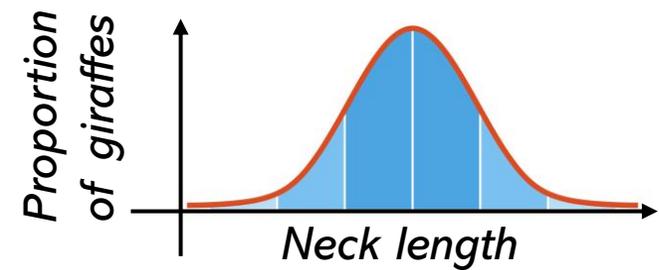
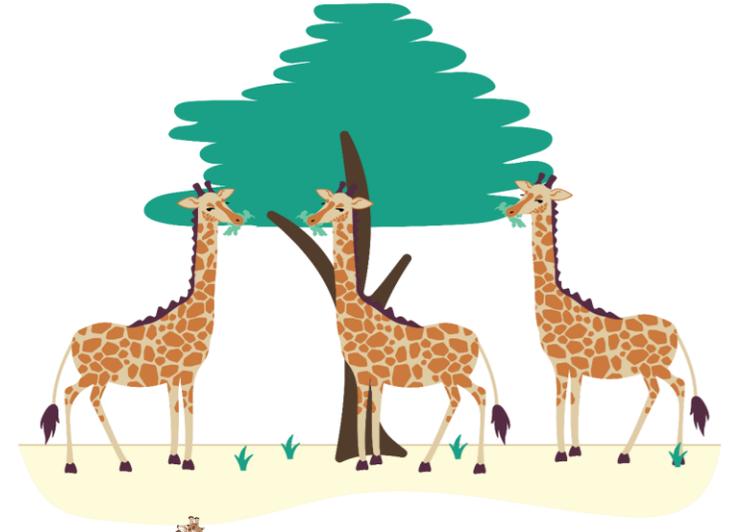
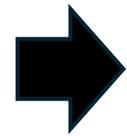
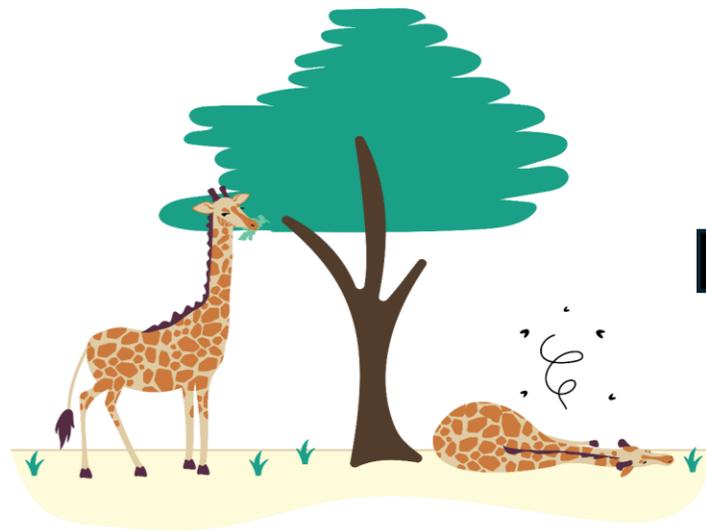
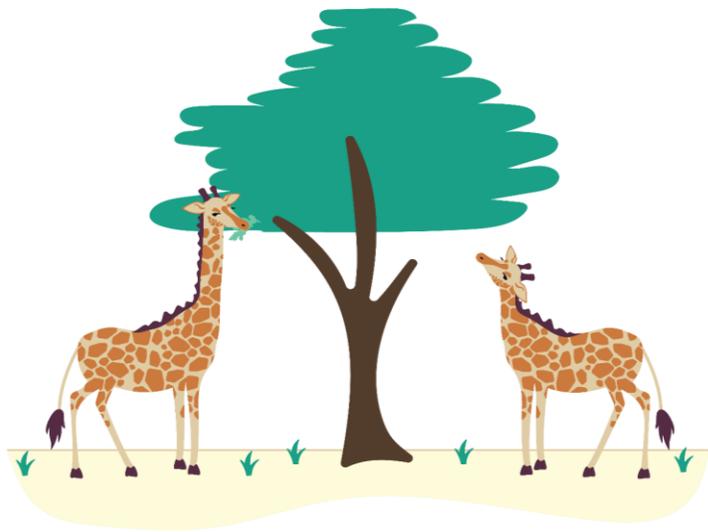
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Randomness in reproduction

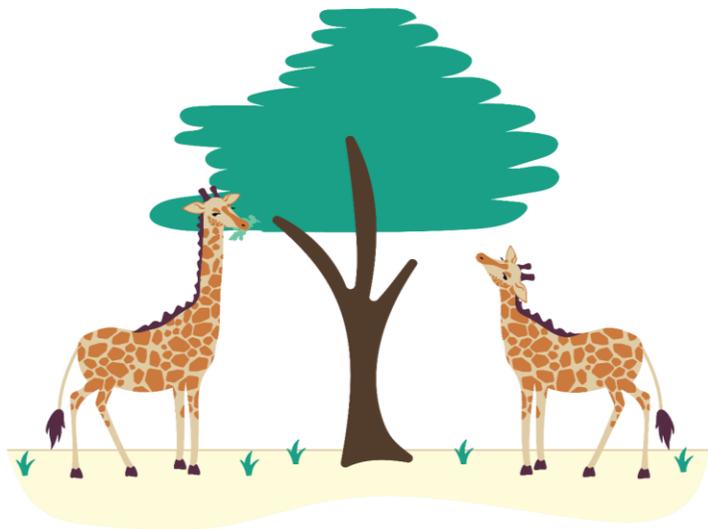


Randomness in reproduction

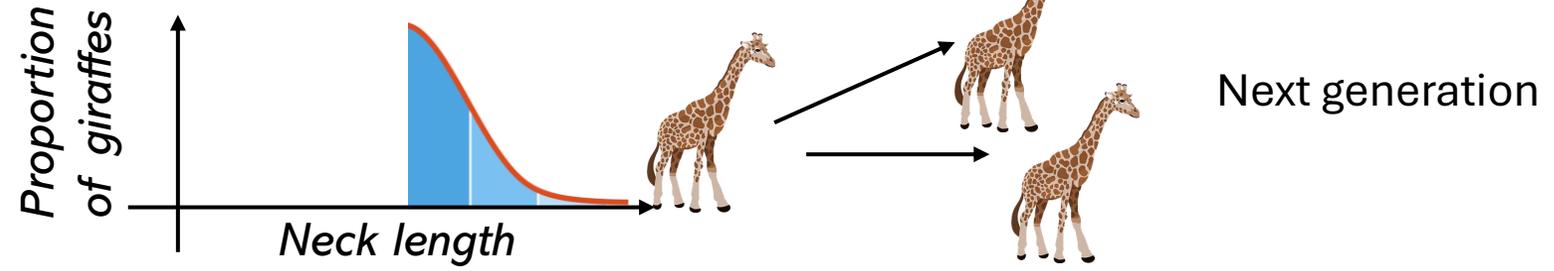
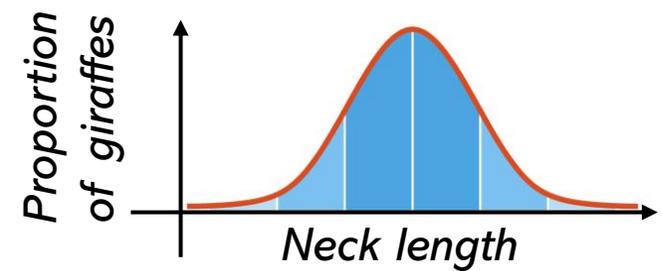
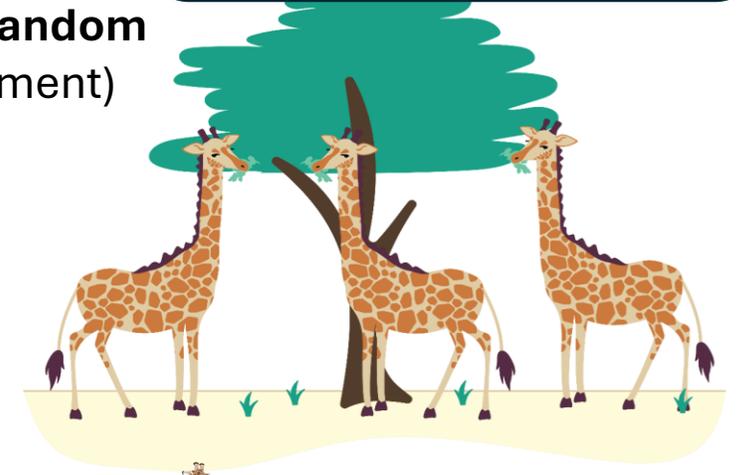
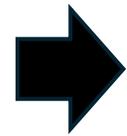
Assume that each surviving individual has the same chance of reproducing



«Same as before», but now we do not force each giraffe to have the same number of babies



sampling **at random**
(with replacement)



Randomness in reproduction

Assume that each surviving individual has the same chance of reproducing

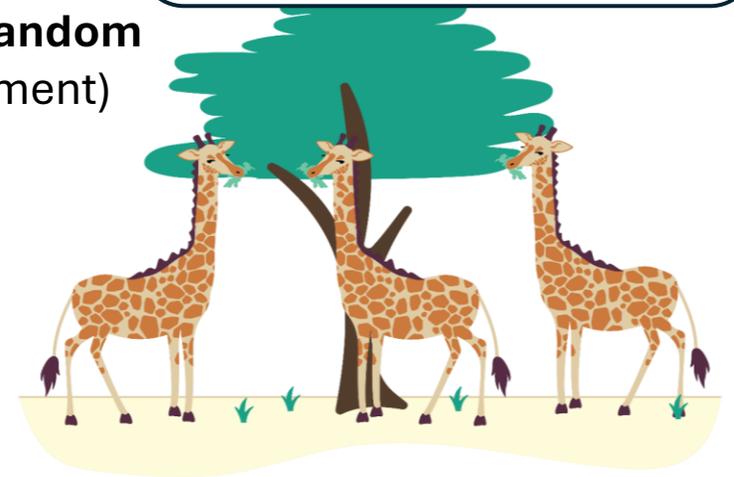


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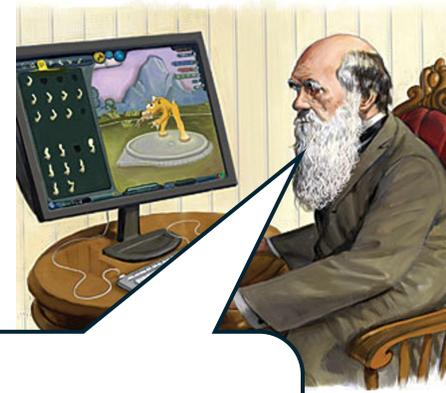
sampling **at random**
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```
sample(survivors, N, replace = TRUE)
```

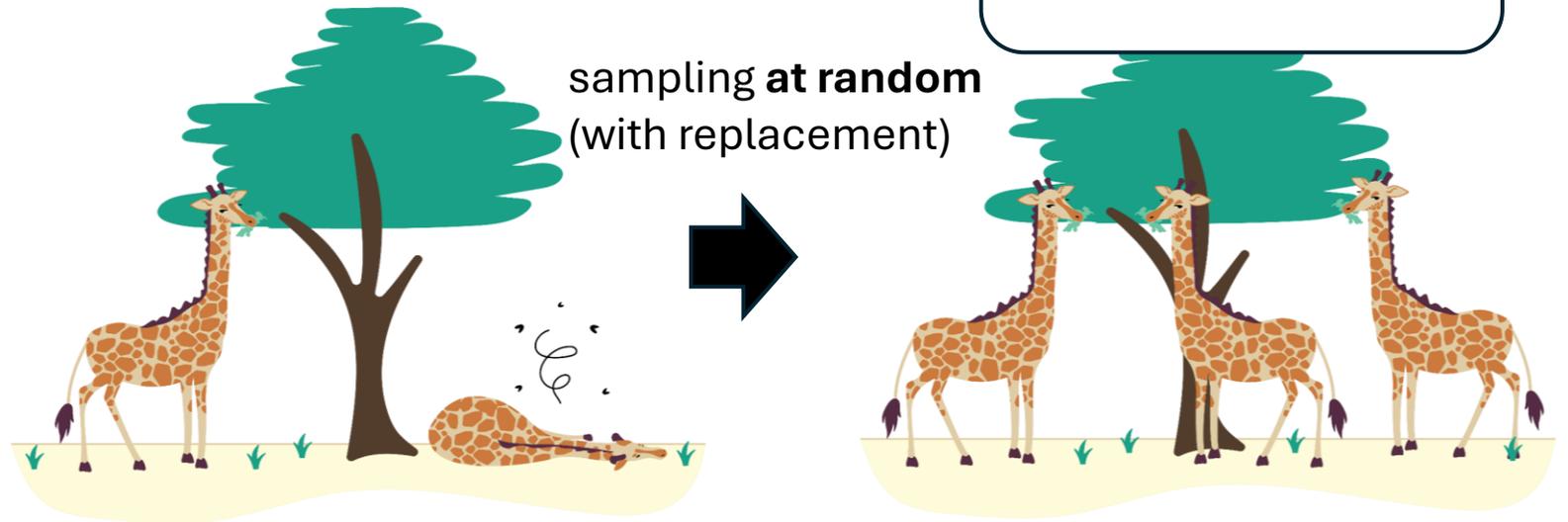
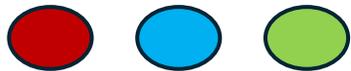
Randomness in reproduction

Assume that each surviving individual has the same chance of reproducing



In our model only half giraffes were surviving

sampling at random
(with replacement)

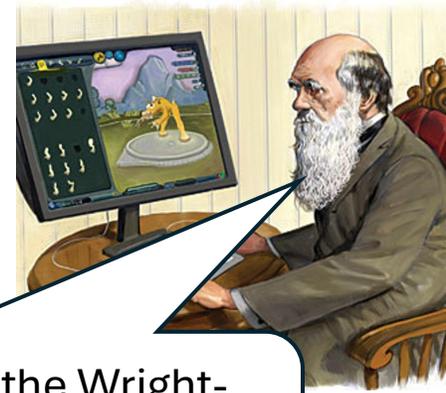


sampling **at random**
(with replacement)

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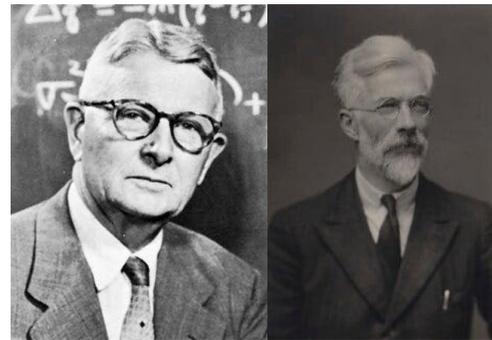
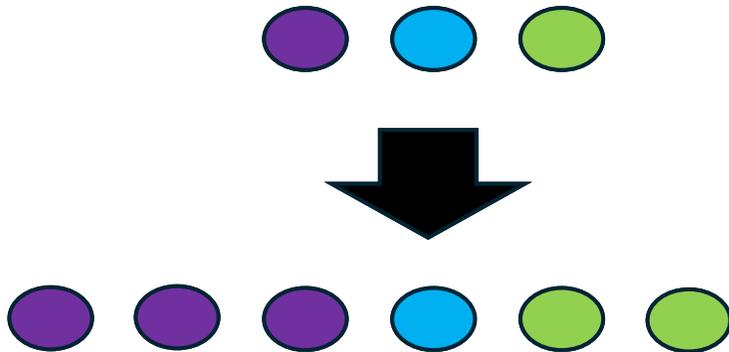
Our first basic “evolutionary model”

- Variability among individuals
- Differential contribution to successive generations
- **Mechanism of inheritance**



This will be the basis for the Wright-Fisher model, which is at the cornerstone of all population genetics!

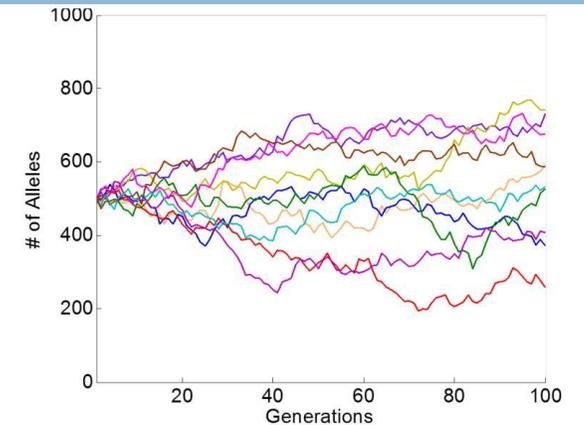
sampling at random
(with replacement)



Sir Ronald-Fisher
(1889-1988)

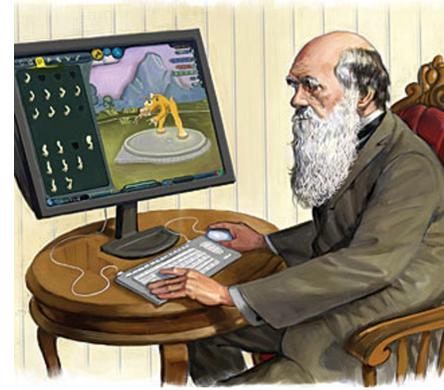
Sir Ronald-Fisher
(1890-1962)

The Basic Wright-Fisher Model
10 Simulations, $2N=1000$



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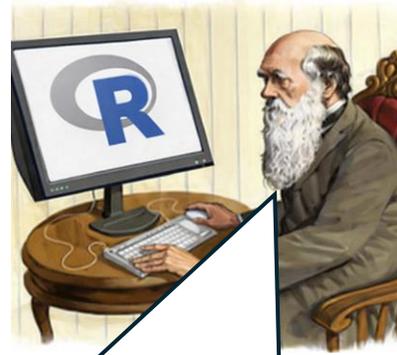


Our **toy** model

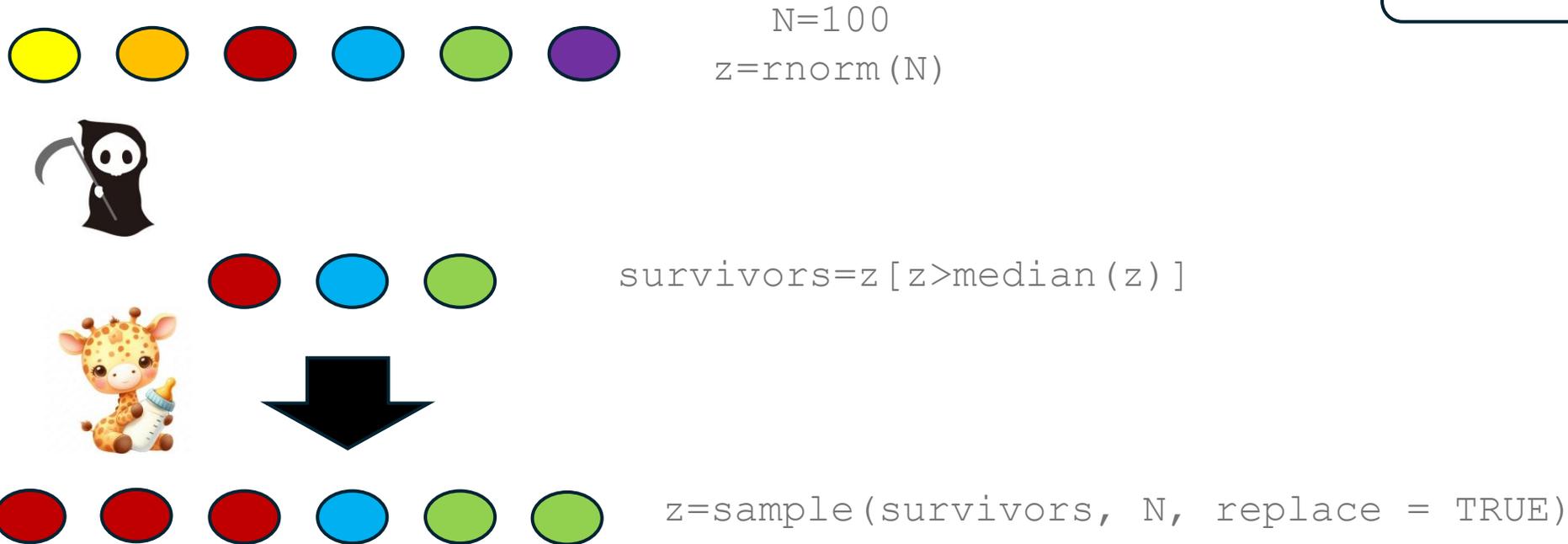


Our first basic “evolutionary model”

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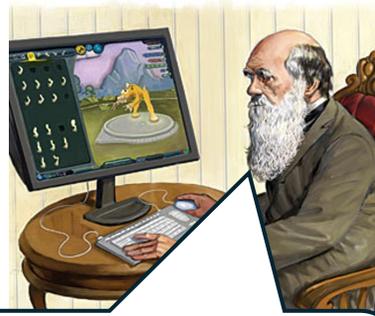
Let's put together our toy model



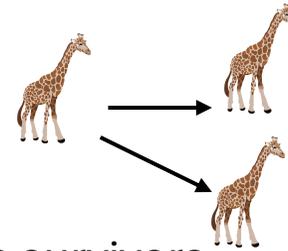
Let's address these limitations



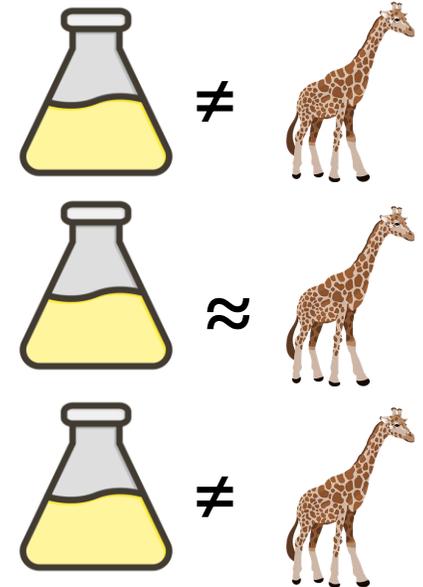
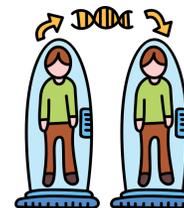
Not even me



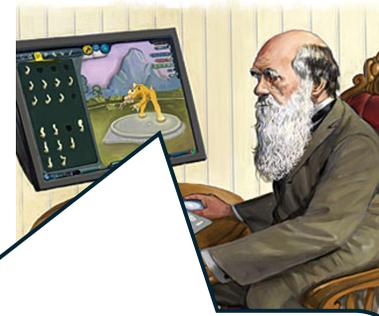
Actually not even bacteria in flask



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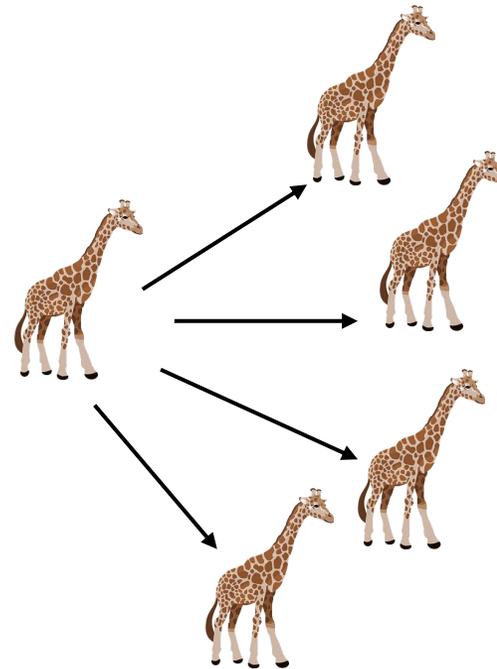
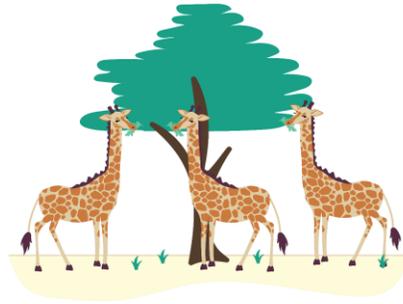
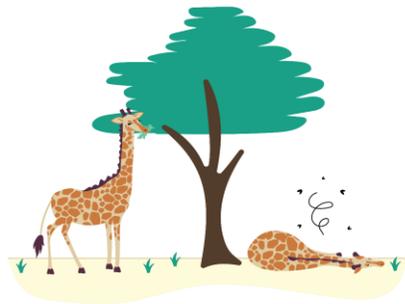
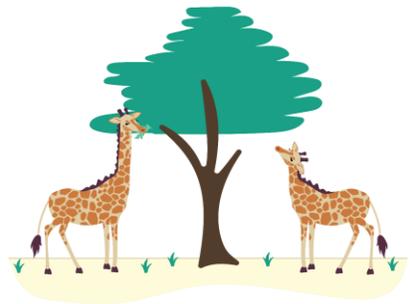
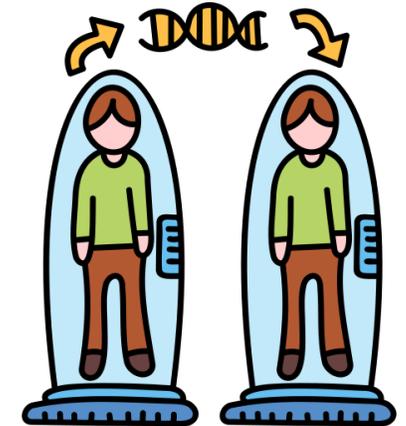
A more realistic inheritance model



Perfect
cloning/asexual
reproduction

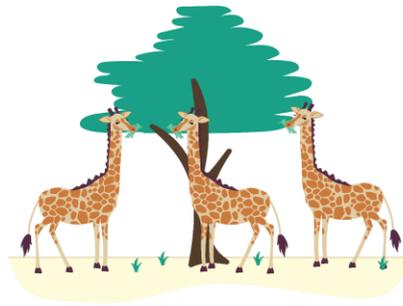
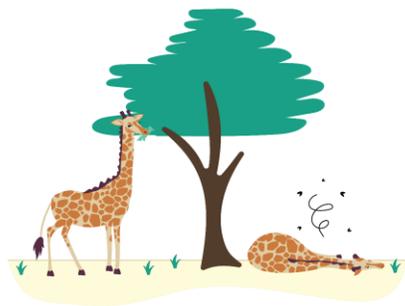
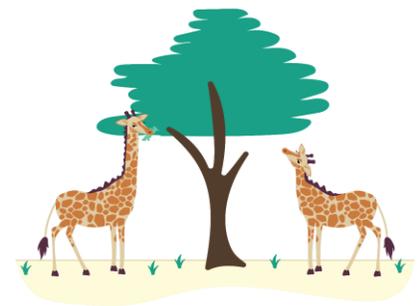
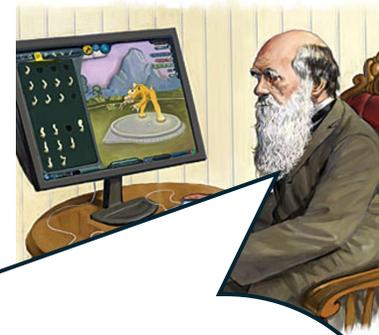
+

Environmental
variability

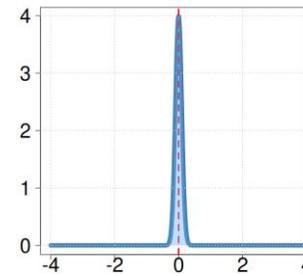


Dolly the sheep

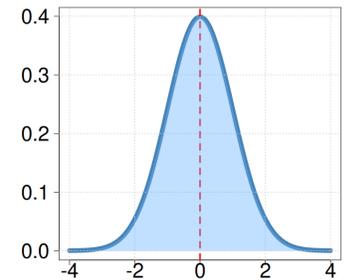
A more realistic inheritance model



A trait with low environmental variability?



Low

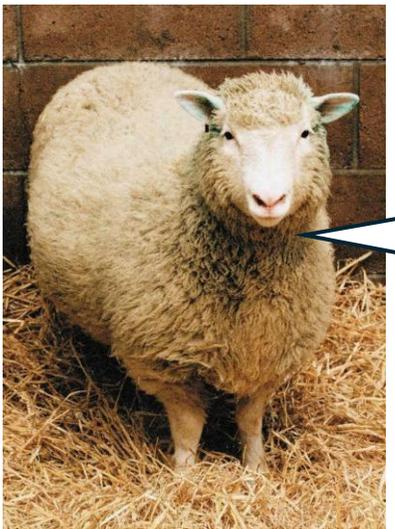
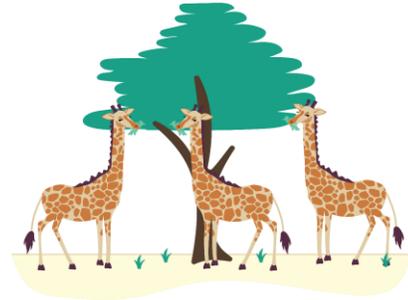
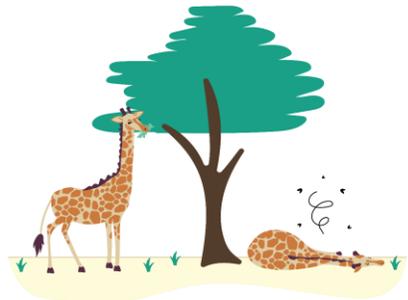
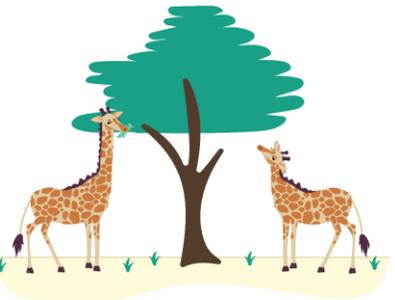
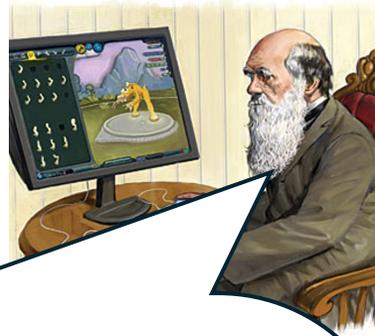


High

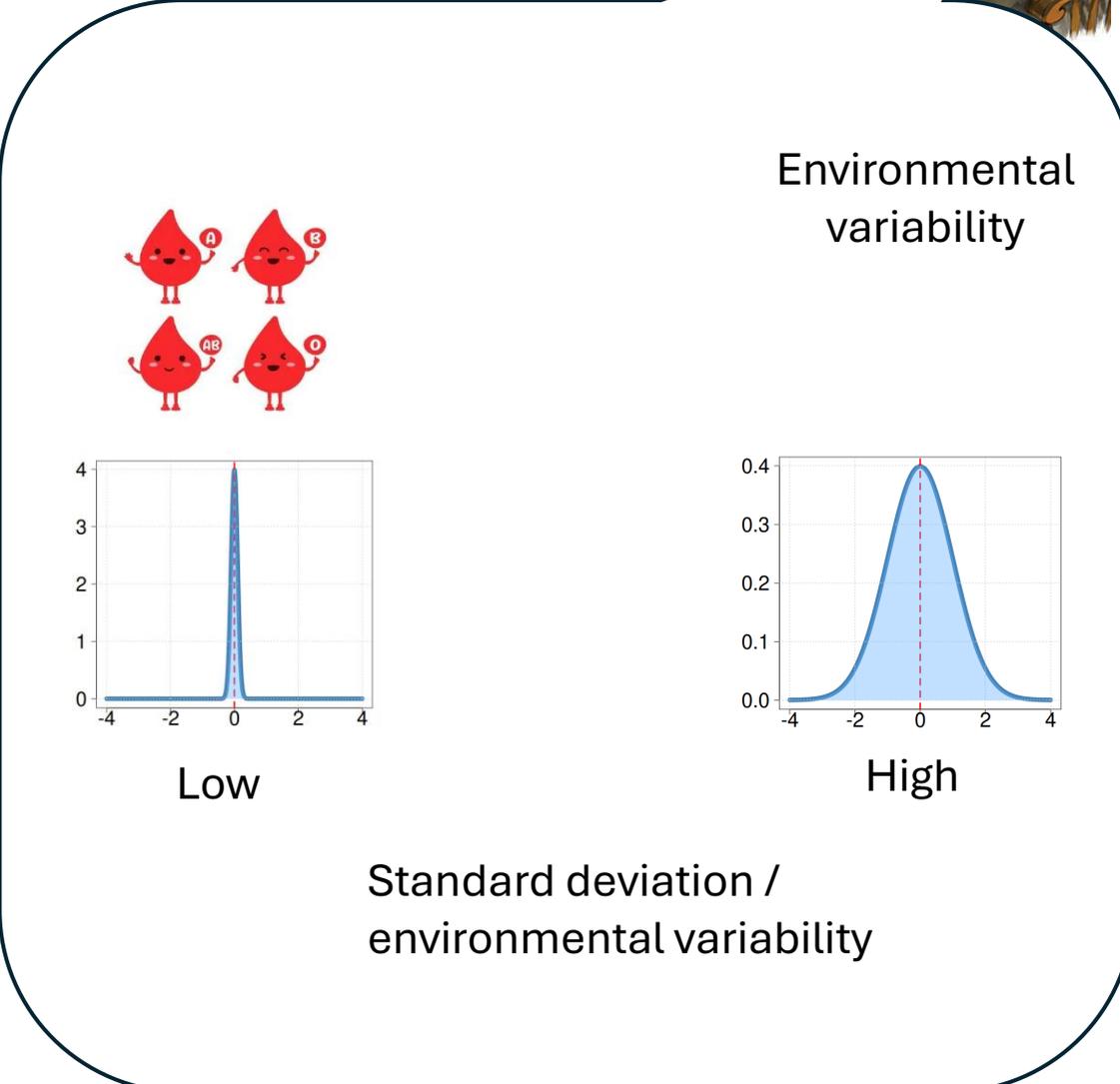
Environmental variability

Standard deviation / environmental variability

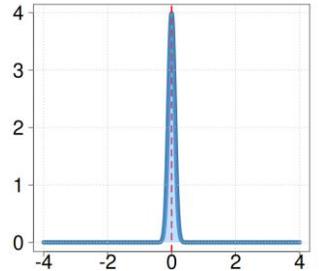
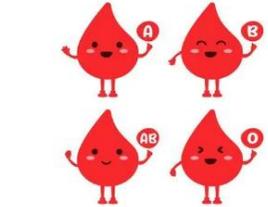
A more realistic inheritance model



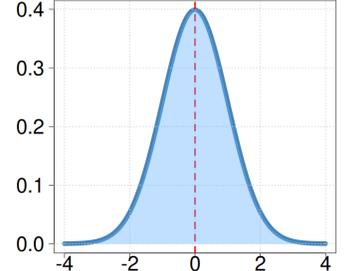
In the cloning model it was as if we had standard deviation $sd=0$



Environmental variability



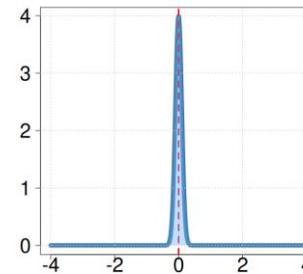
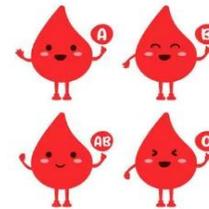
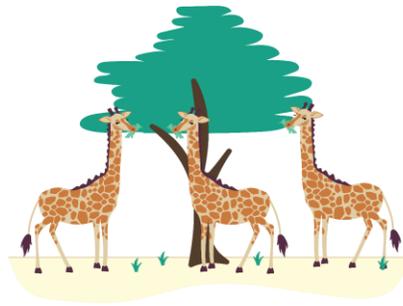
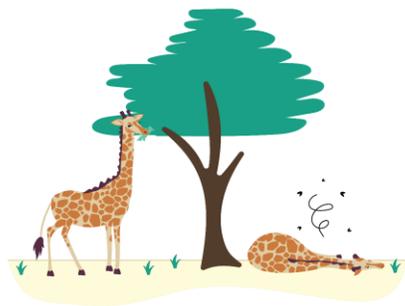
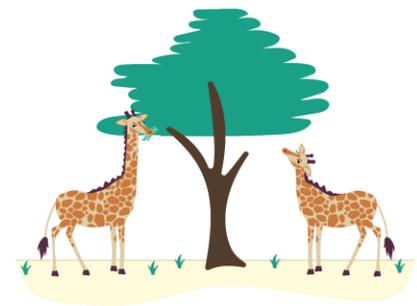
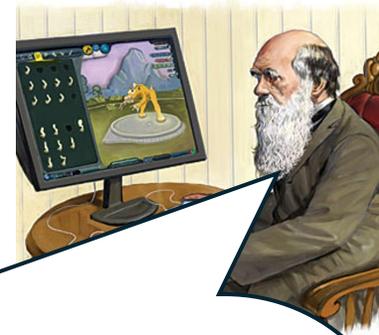
Low



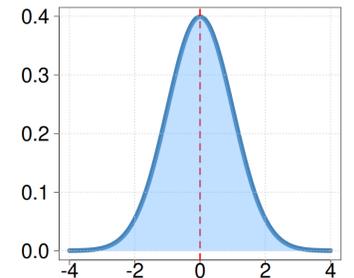
High

Standard deviation / environmental variability

A more realistic inheritance model



Low



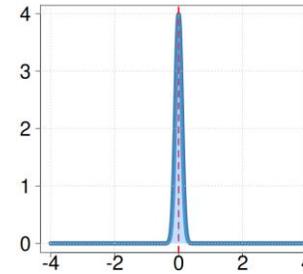
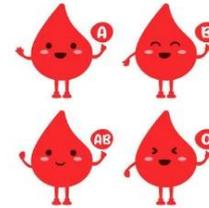
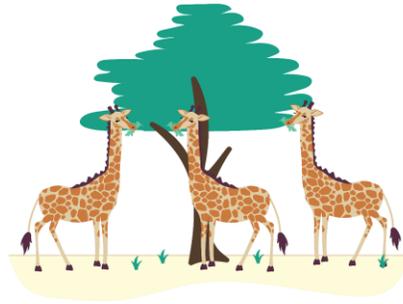
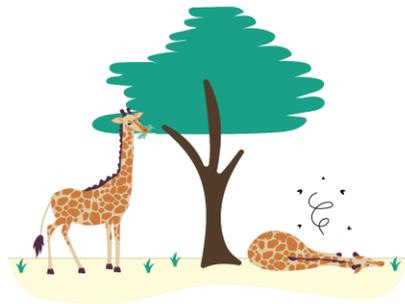
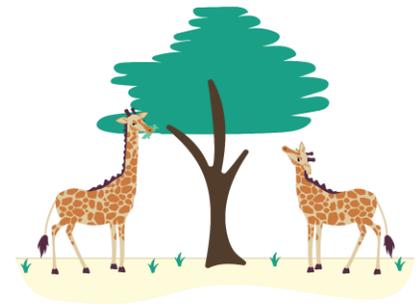
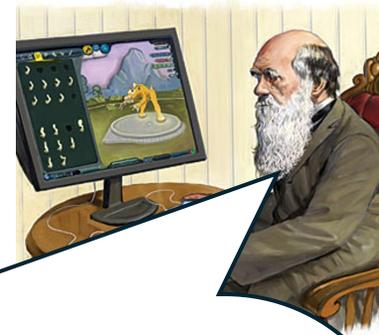
High

Environmental variability

?

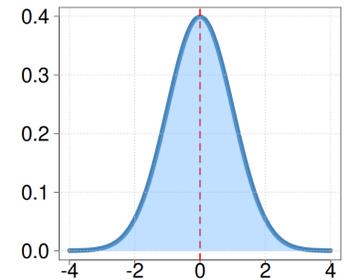
Standard deviation /
environmental variability

A more realistic inheritance model



Low

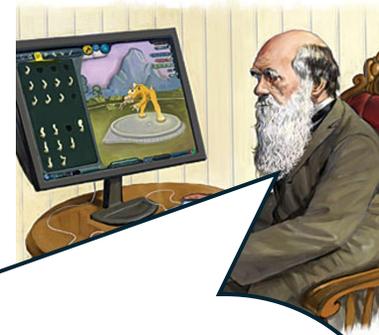
Environmental variability



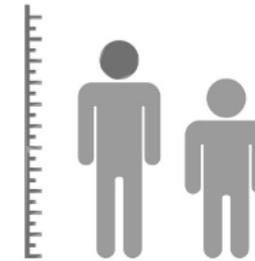
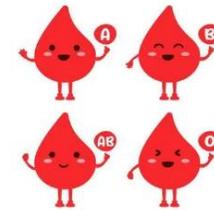
High

Standard deviation /
environmental variability

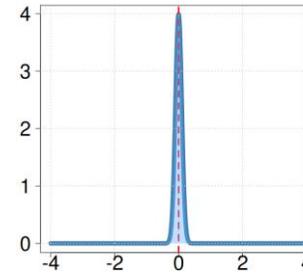
A more realistic inheritance model



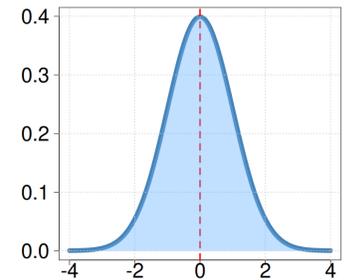
Height is 70-80% heritable



Environmental variability

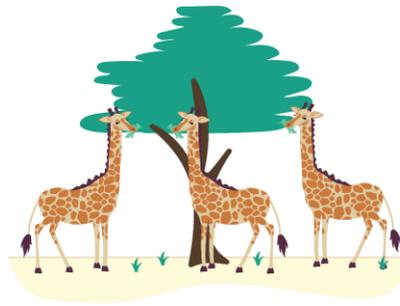
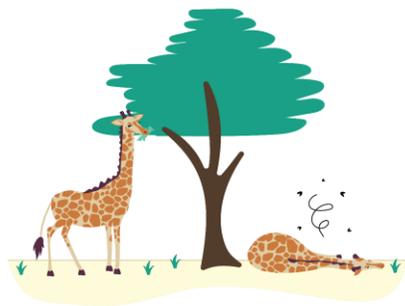
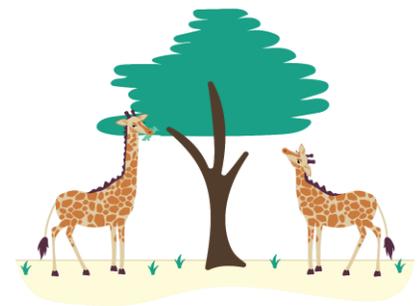


Low

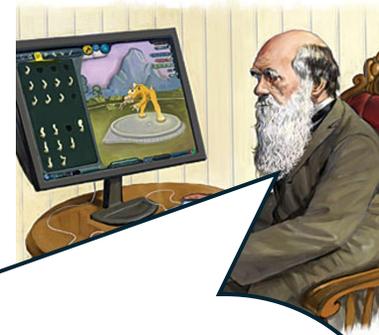


High

Standard deviation /
environmental variability



A more realistic inheritance model

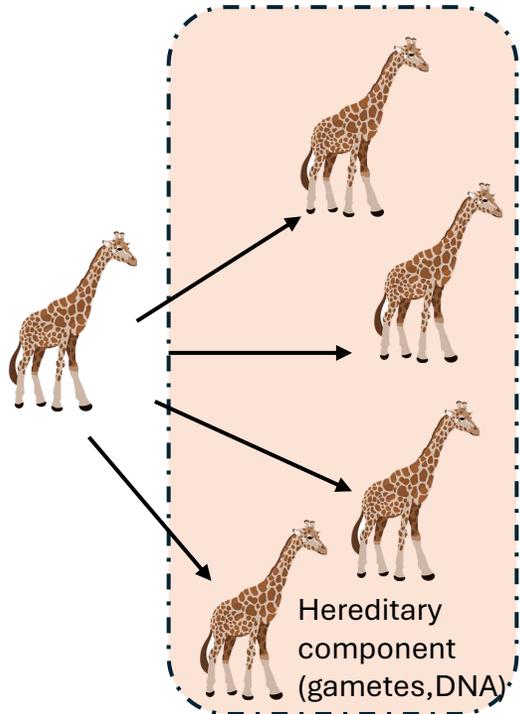
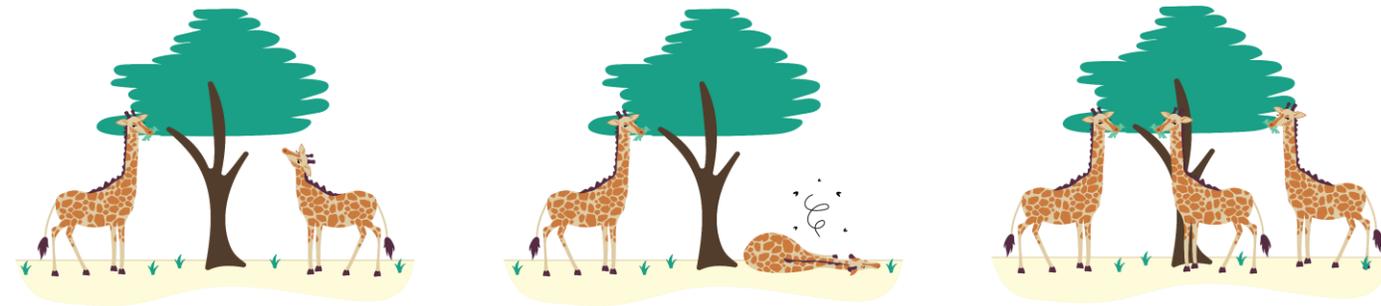


More realistic model

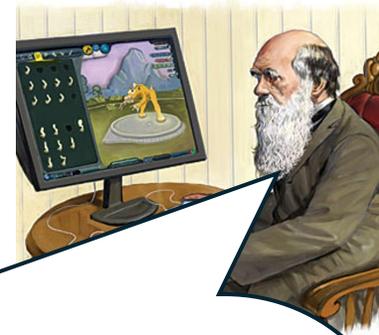
Perfect
cloning/asexual
reproduction

+

Environmental
variability



A more realistic inheritance model

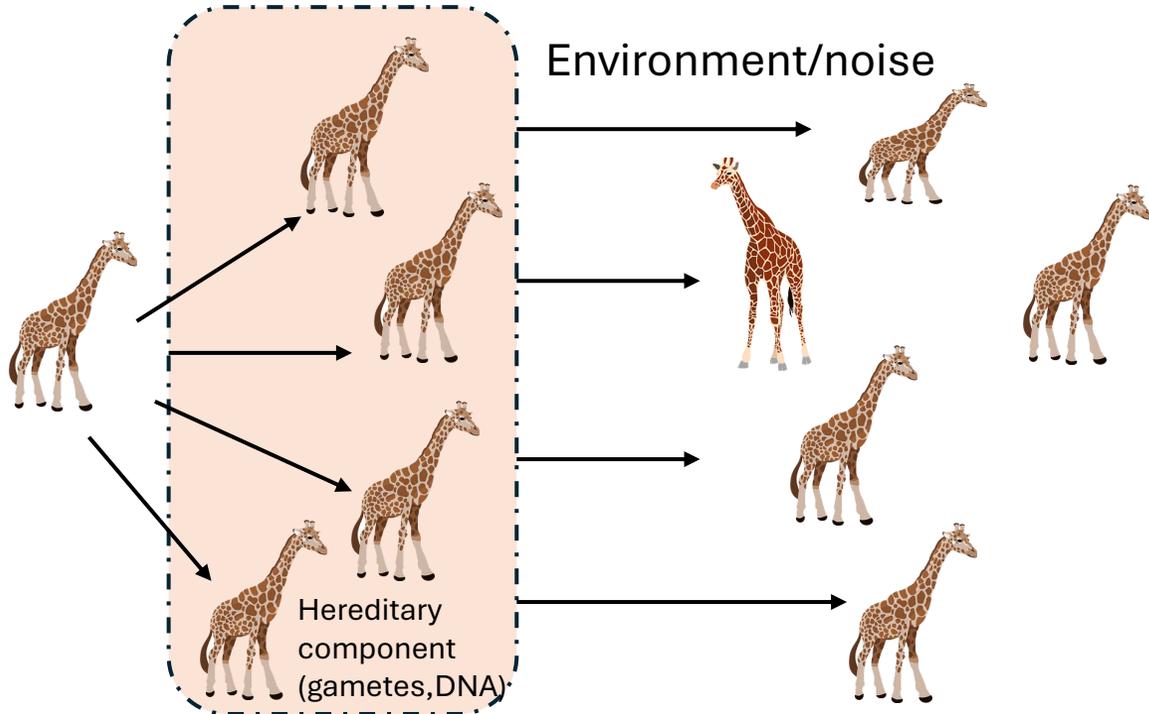
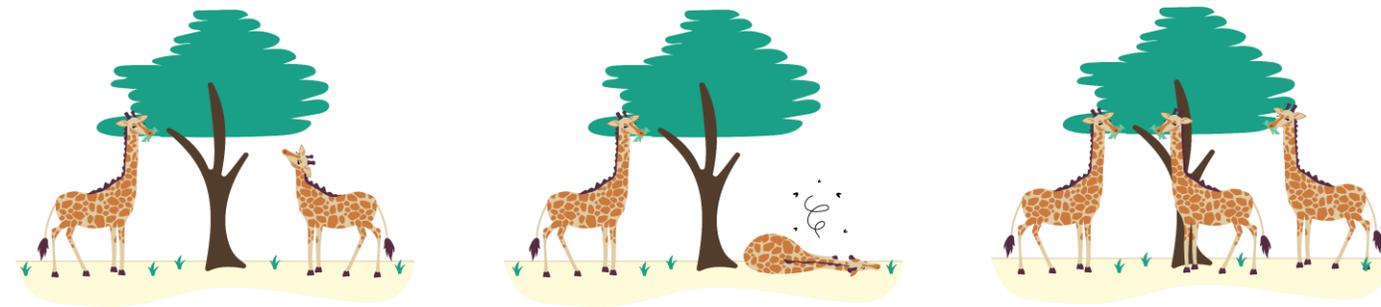


More realistic model

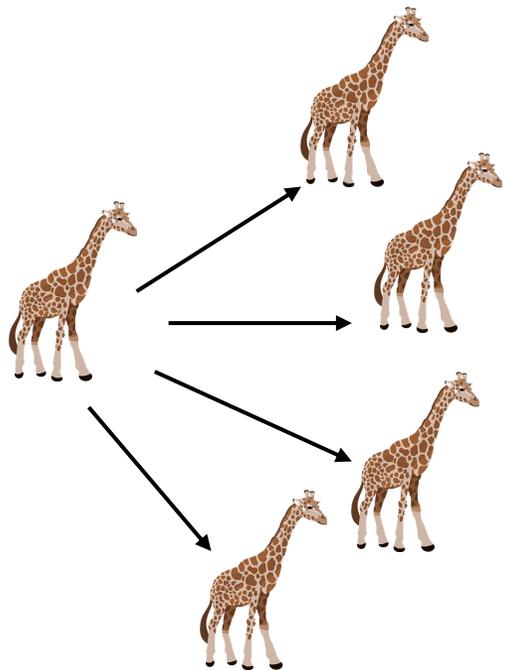
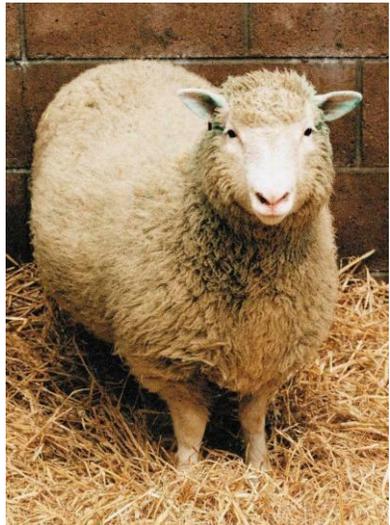
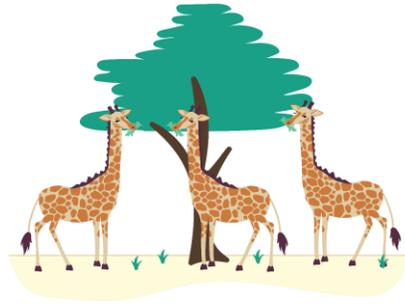
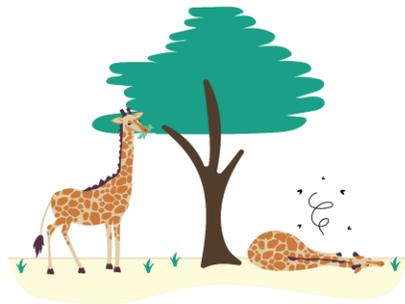
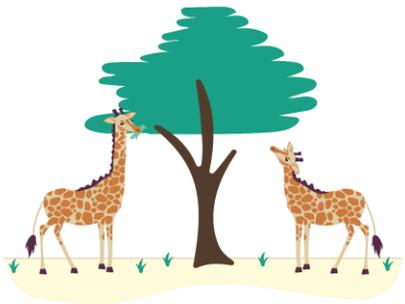
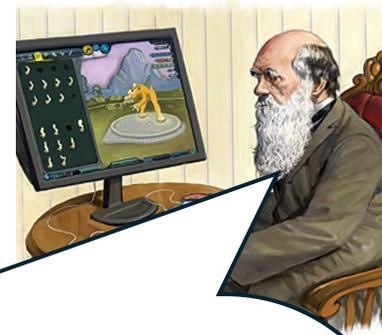
Perfect
cloning/asexual
reproduction

+

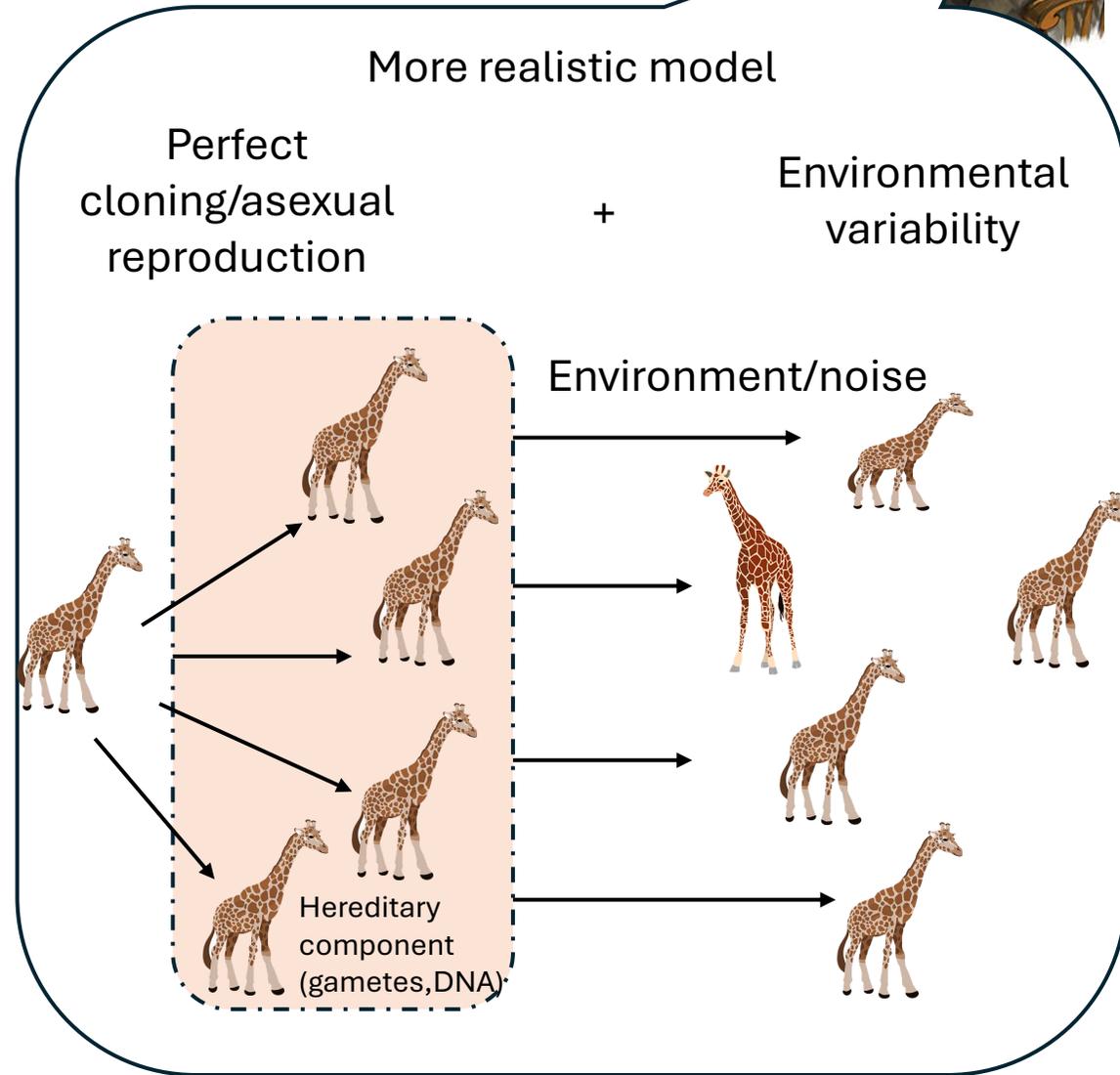
Environmental
variability



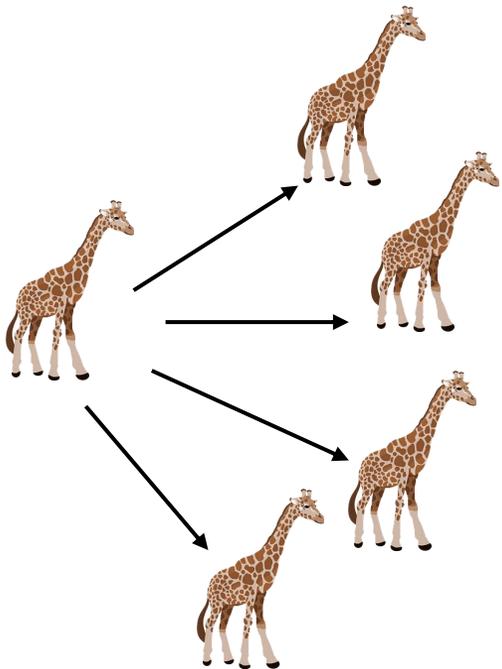
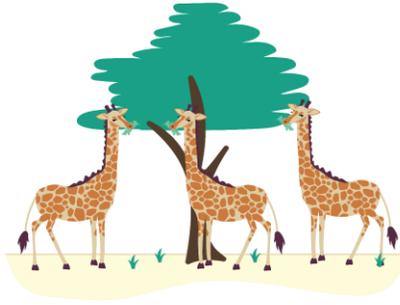
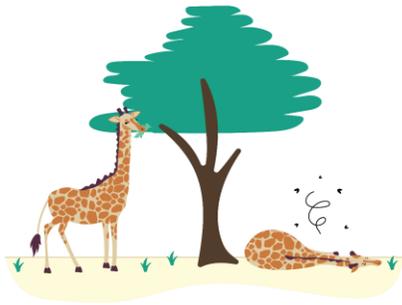
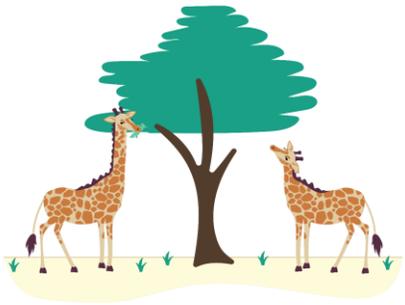
Cloning vs realistic model



VS

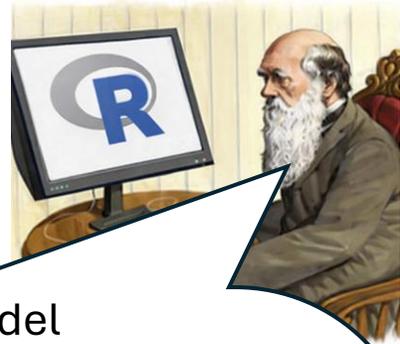


A more realistic inheritance model (code)



```
First basic model with cloning
z=rnorm(N)
survivors=z[z>median(z)]
parents=survivors
z=sample(parents,N,replace=TRUE)
```

A more realistic inheritance model (code)



More realistic model

Perfect
cloning/asexual
reproduction

+

Environmental
variability

```
parents=survivors
```

```
gametes=sample(parents,N,replace=TRUE)
```

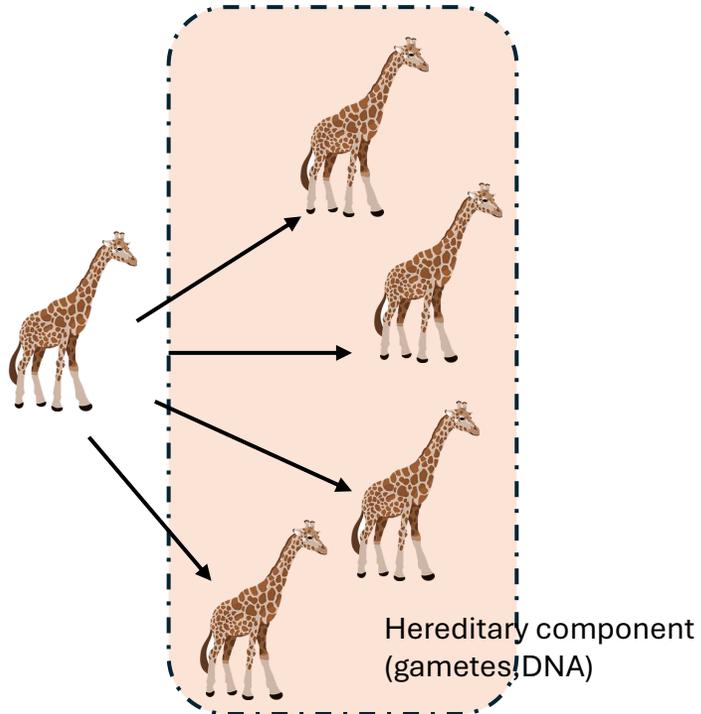
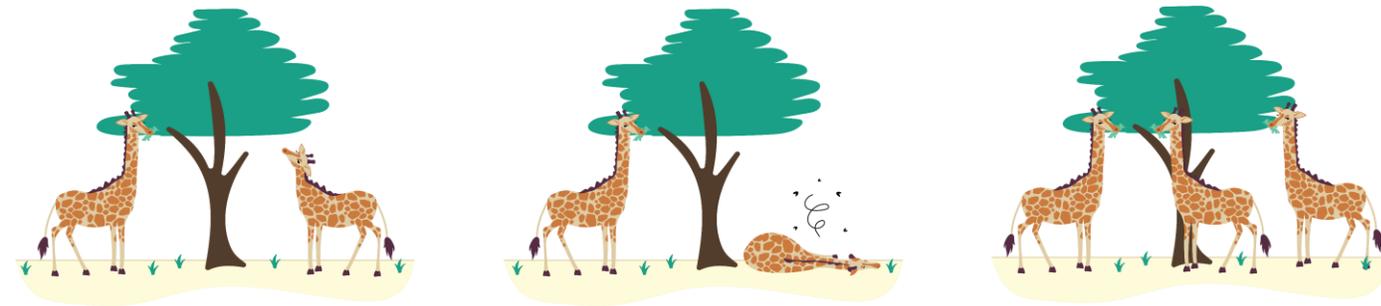
First basic model with cloning

```
z=rnorm(N)
```

```
survivors=z[z>median(z)]
```

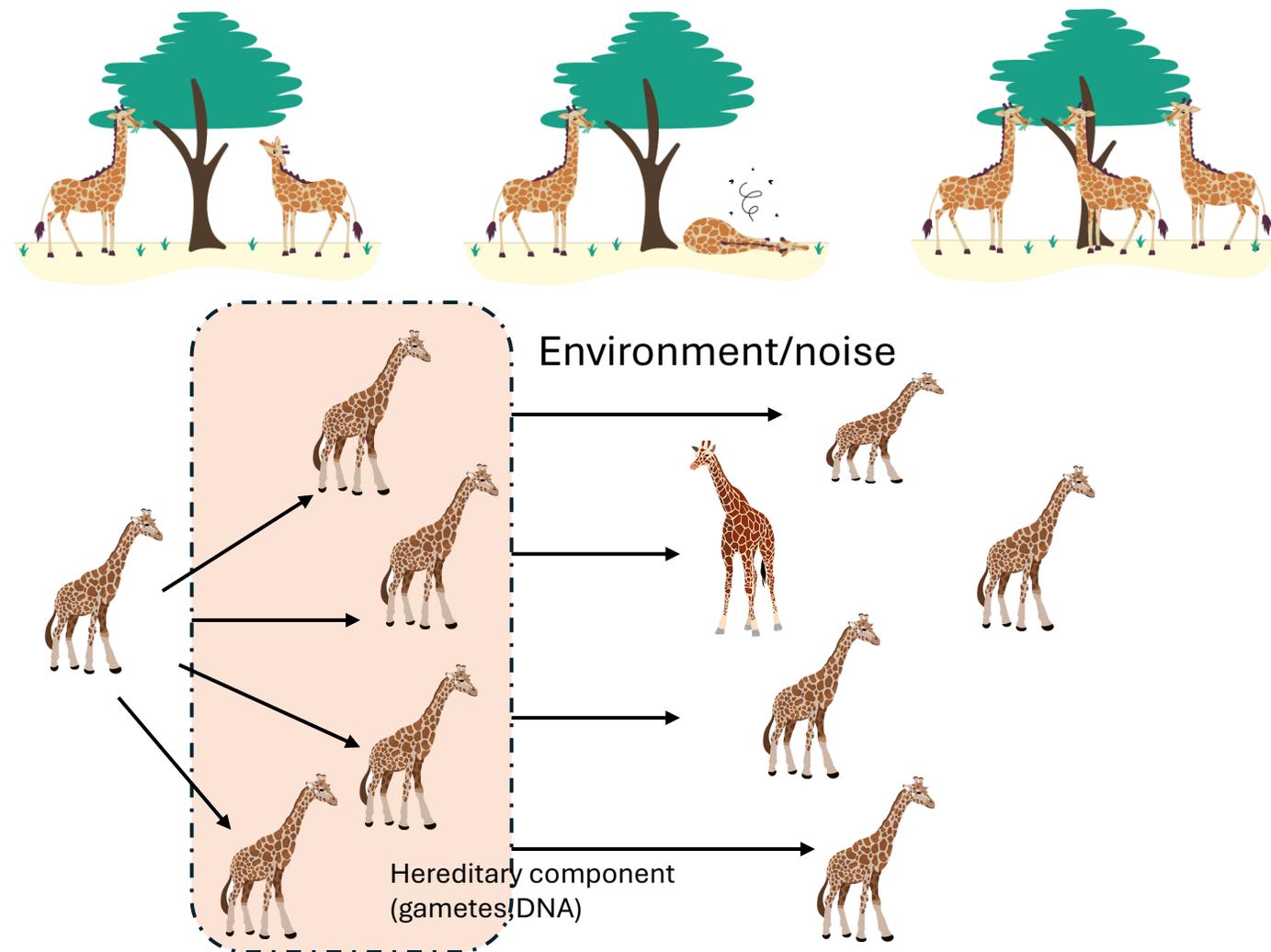
```
parents=survivors
```

```
z=sample(parents,N,replace=TRUE)
```



Hereditary component
(gametes!DNA)

A more realistic inheritance model (code)



Perfect
cloning/asexual
reproduction

+

Environmental
variability

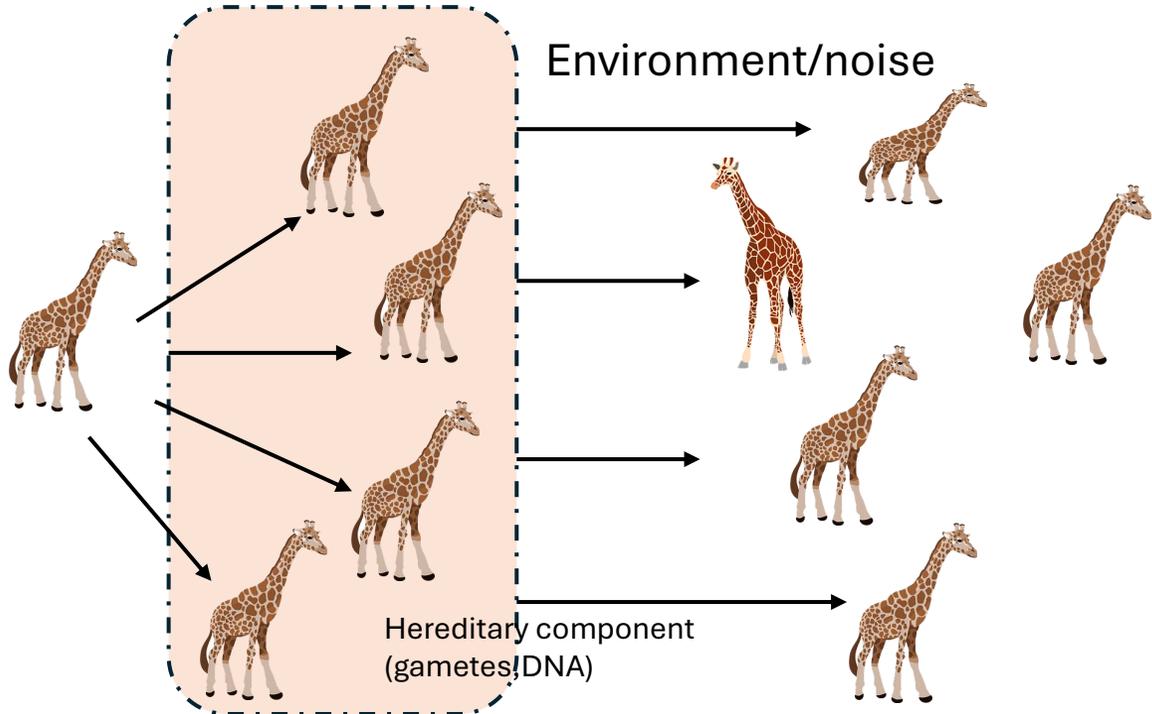
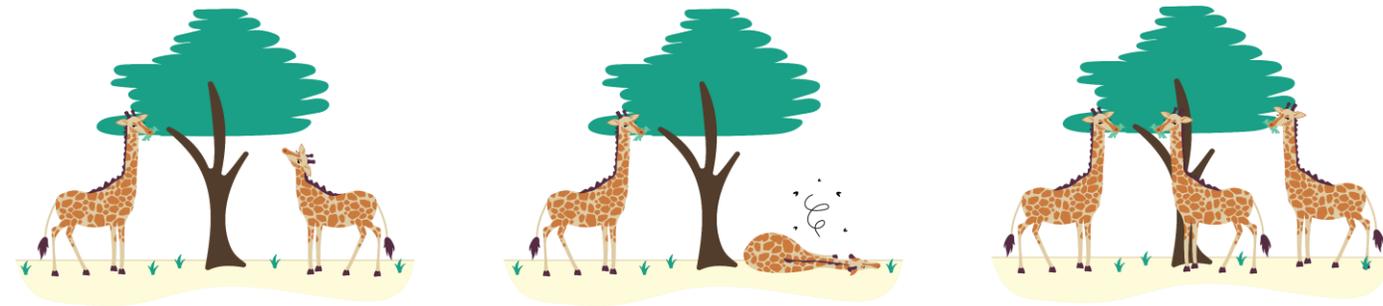
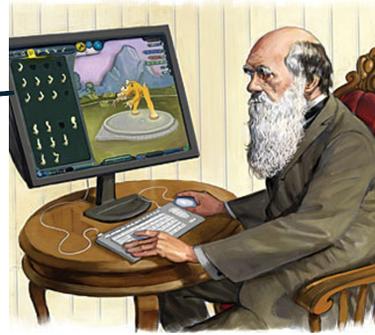
```
parents=survivors  
gametes=sample(parents,N,replace=TRUE)  
z=gametes + rnorm(sd=0.1)
```

First basic model with cloning

```
z=rnorm(N)  
survivors=z[z>median(z)]  
parents=survivors  
z=sample(parents,N,replace=TRUE)
```

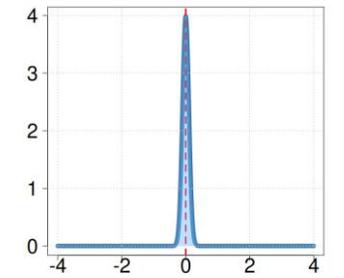
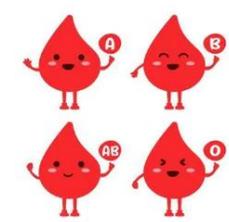
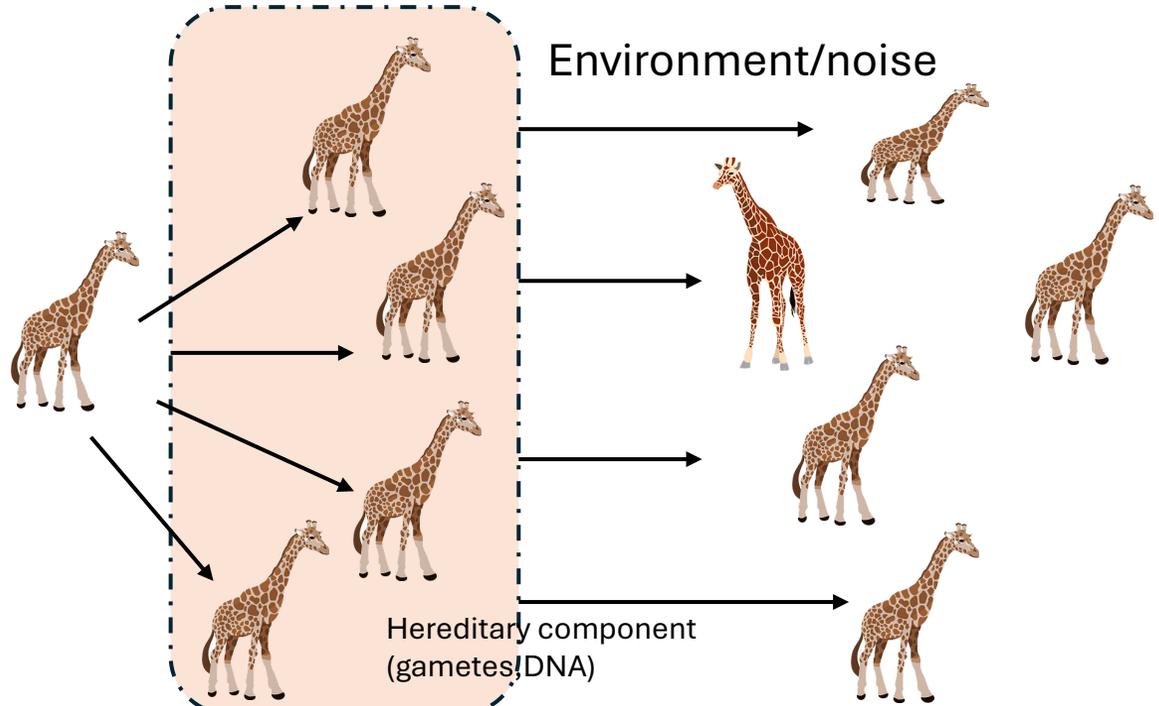
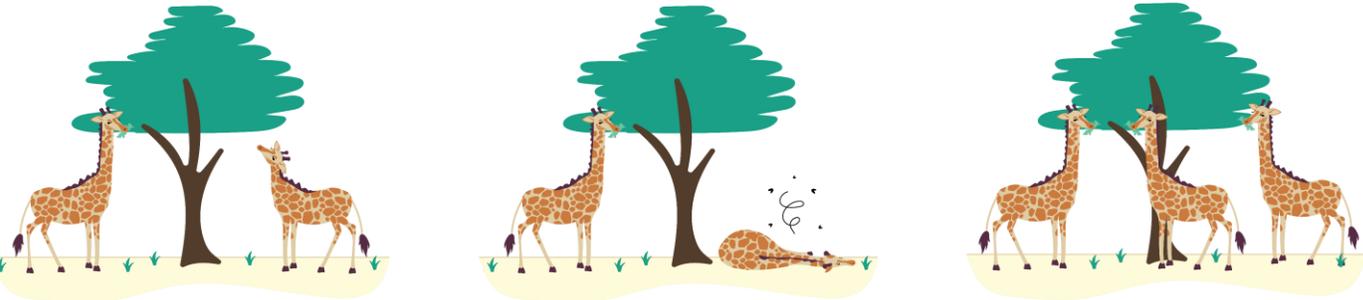
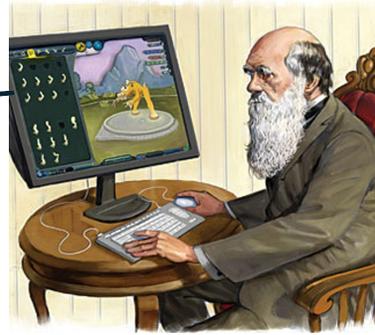
A more realistic inheritance model

Does my theory work even with environmental variability and a more realistic inheritance model?
What happens?



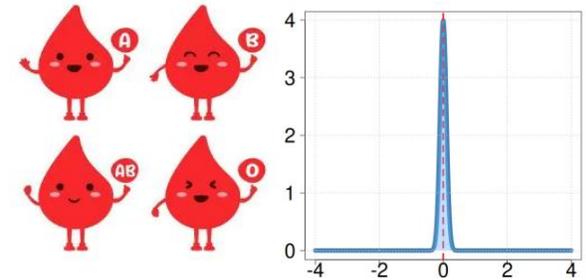
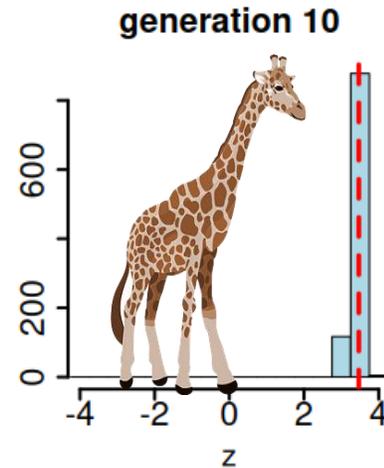
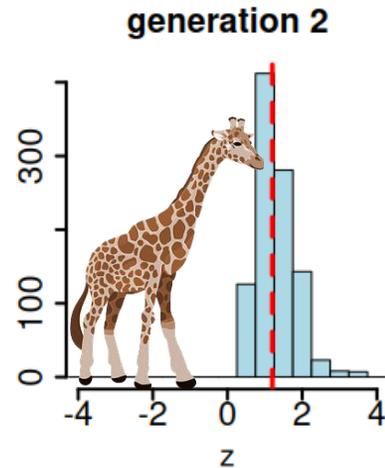
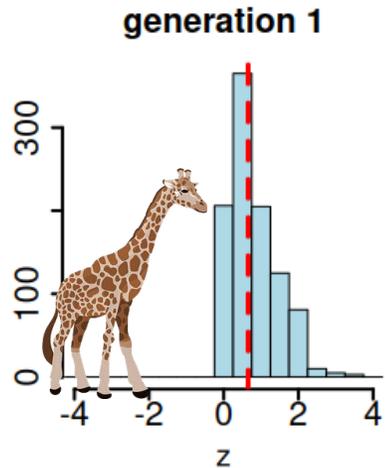
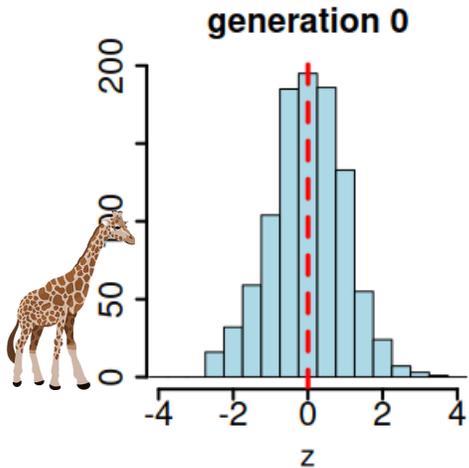
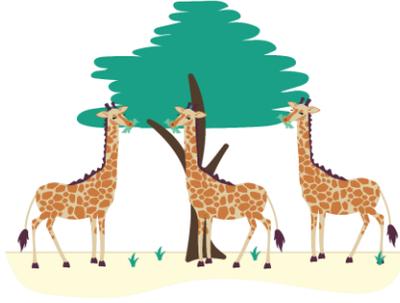
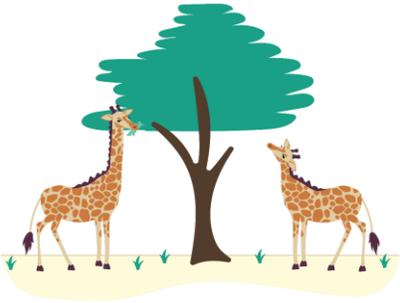
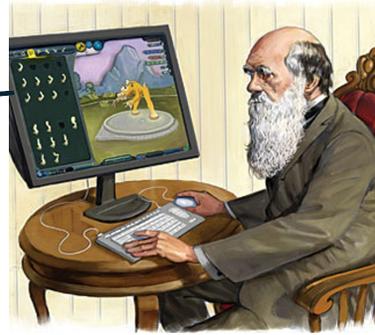
A more realistic inheritance model

Does my theory work even with environmental variability and a more realistic inheritance model?
What happens?



A more realistic inheritance model

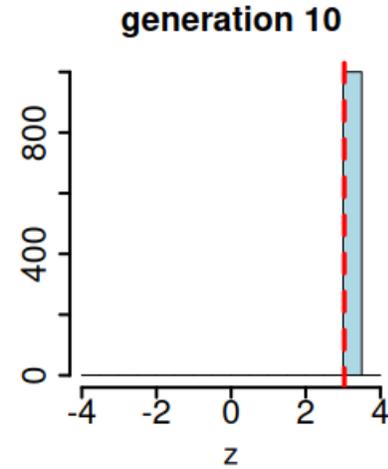
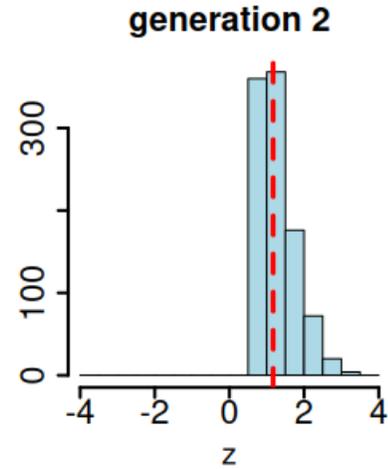
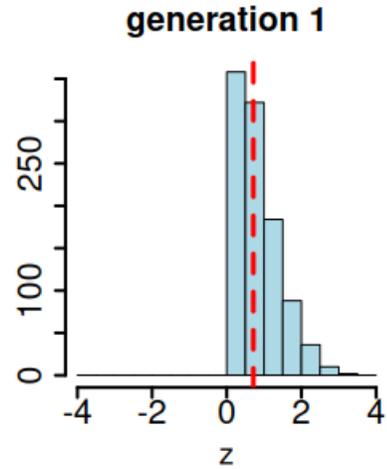
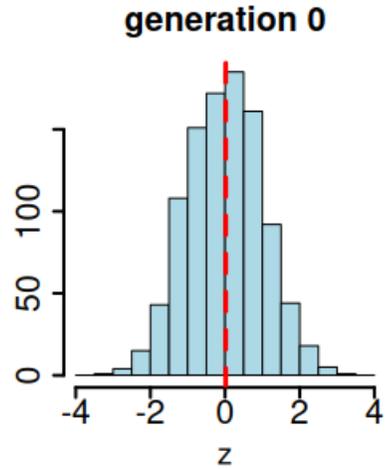
Does my theory work even with environmental variability and a more realistic inheritance model?
What happens?



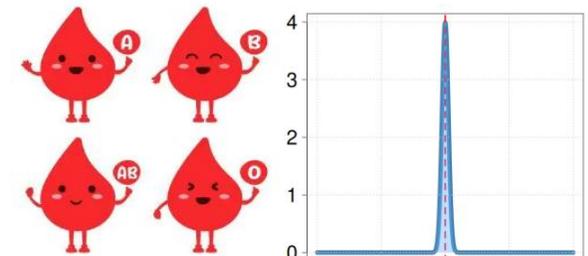
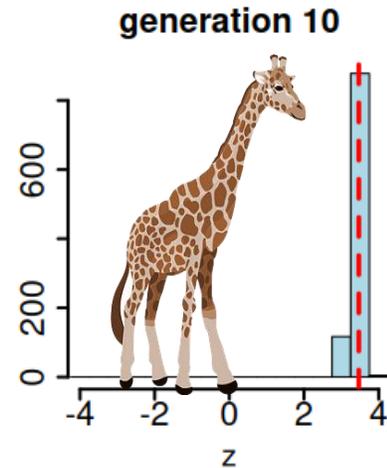
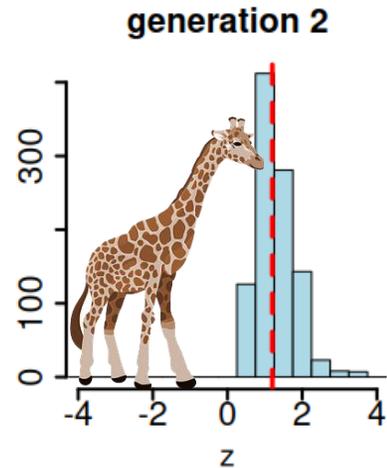
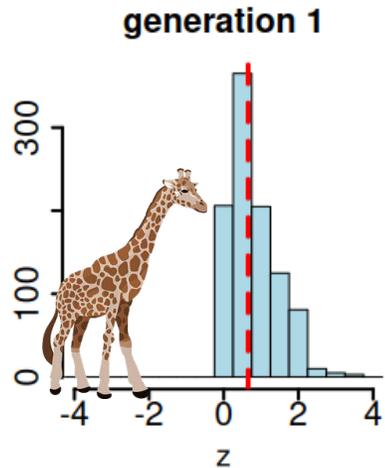
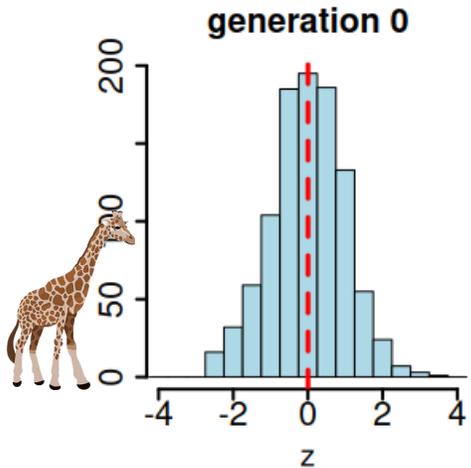
A more realistic inheritance model



Similar to what happened with no randomness or environment: fast evolution



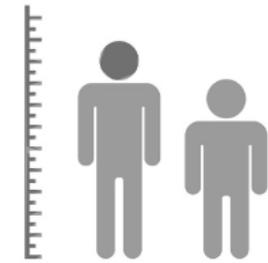
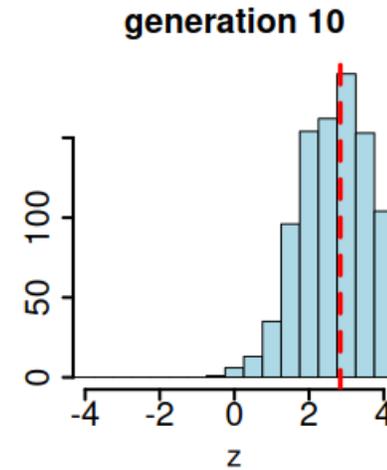
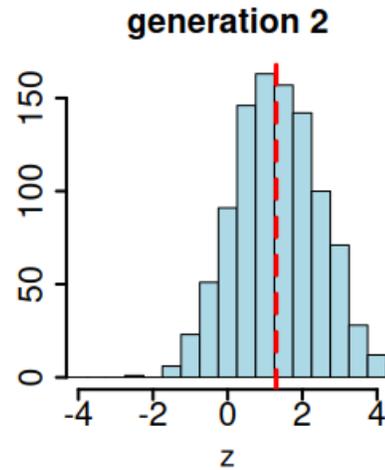
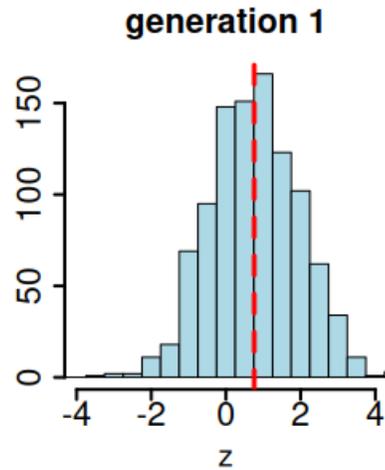
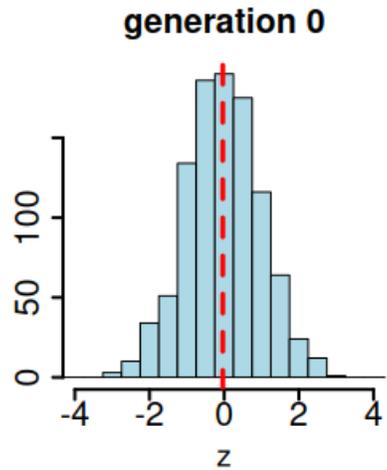
Very basic model
(cloning, no environment)



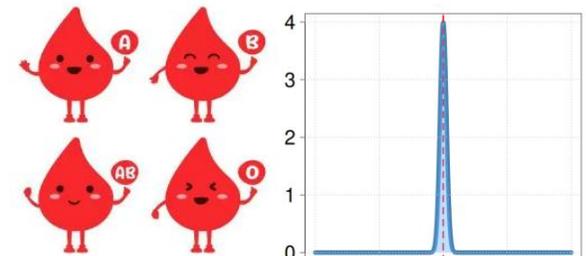
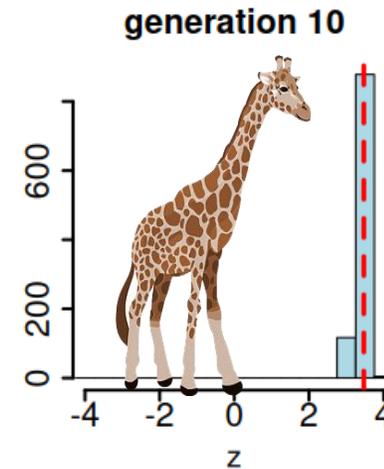
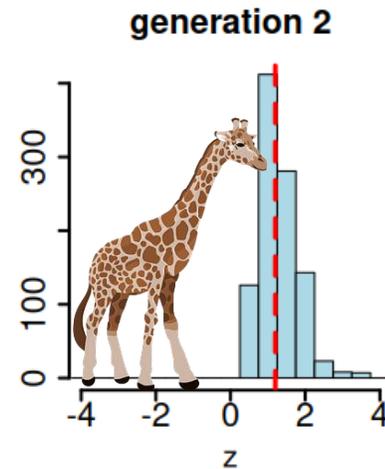
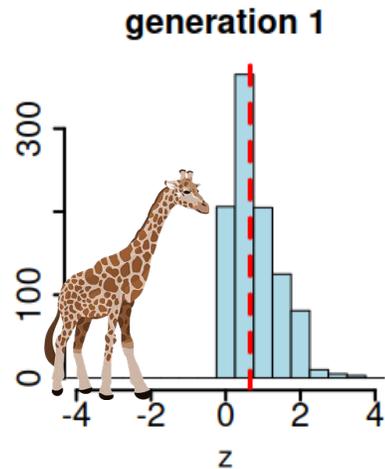
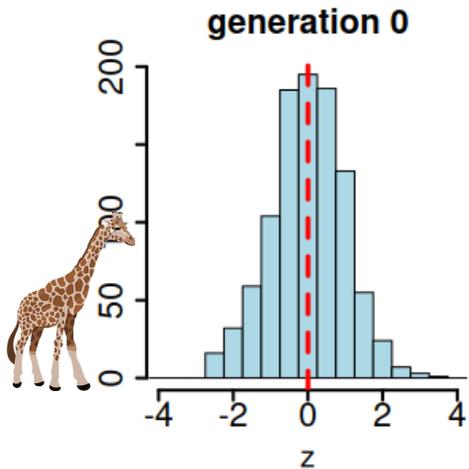
Low environmental variability

A more realistic inheritance model

Environmental variance slows down a bit (but does not impede) evolution!



High environmental variability
($sd=0.9$)



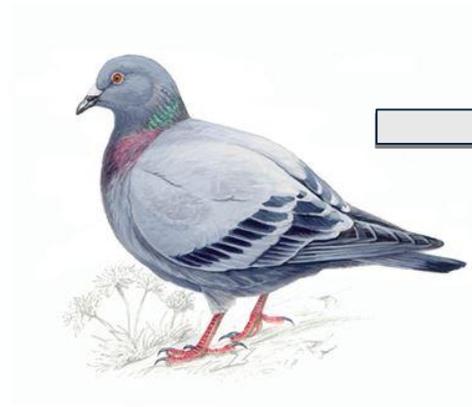
Low environmental variability
($sd=0.1$)

In future lectures we will see that..

$$R = h^2S$$

Breeder's equation (Lush, 1937)

- **R**= the response to natural selection
- **h²**= heritability (the proportion of “genetic variation” – variation that can be inherited)
- **S**=Selection strength



More people thinking of natural selection *before Darwin...*



(..and acknowledged by Darwin himself)

Patrick Matthew (Scottish agronomist)

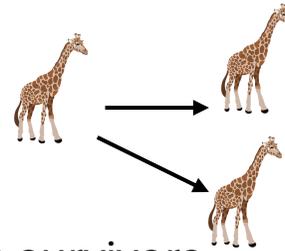
On Naval Timber and Arboriculture (1831)

There is a law universal in nature, tending to render every reproductive being the best possibly suited to its condition that its kind [...]

... those individuals who possess not the requisite strength, swiftness, hardihood, or cunning, fall prematurely without reproducing [...], their place being occupied by the more perfect of their own kind, who are pressing on the means of subsistence.

The law of entail, necessary to hereditary nobility, is an outrage on this law of nature which she will not pass unavenged ..

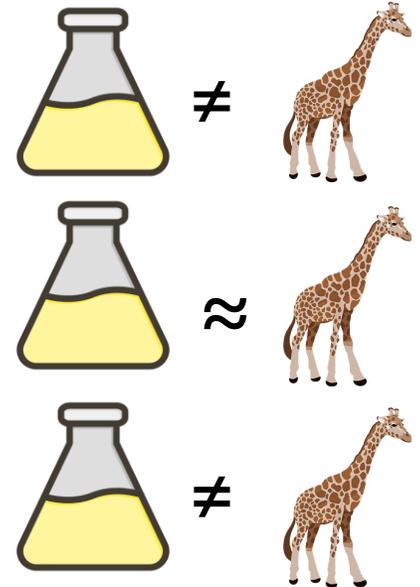
Finally, let's make our giraffe stop cloning and have....be diploid



- **Randomness in reproduction:** not exactly two offsprings for one survivors – giraffes are not bacteria!

- There is **variation in the environment** – giraffes are not bacteria in a flask!

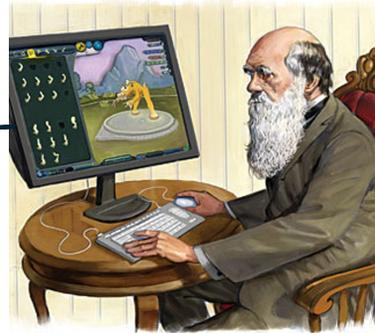
- **Diploidy** and sexual reproduction – giraffes are not bacteria!



Finally, let's make our giraffe stop cloning and have....be diploid

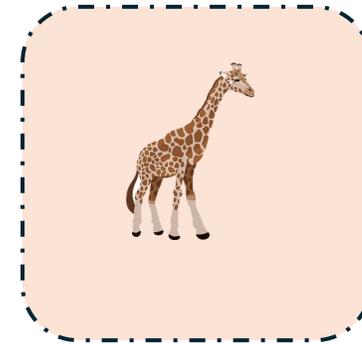
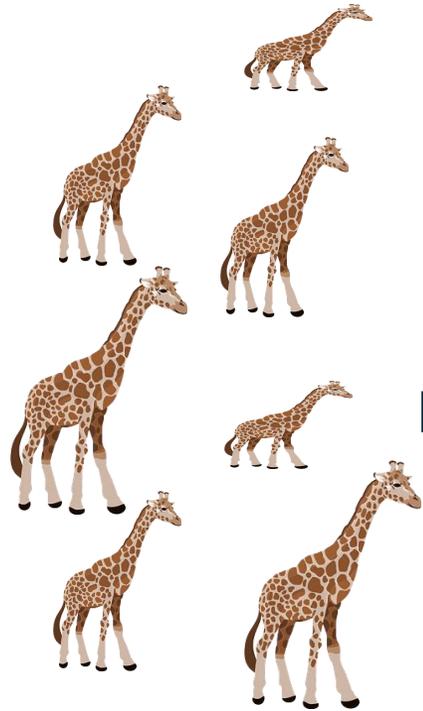


How would you model that?



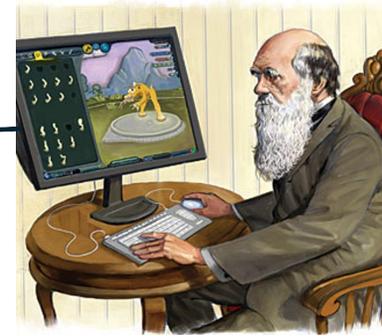
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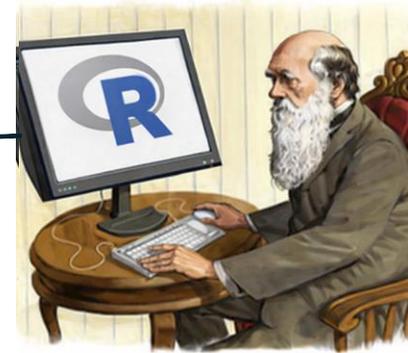


Offspring has neck that is average of mom and dad

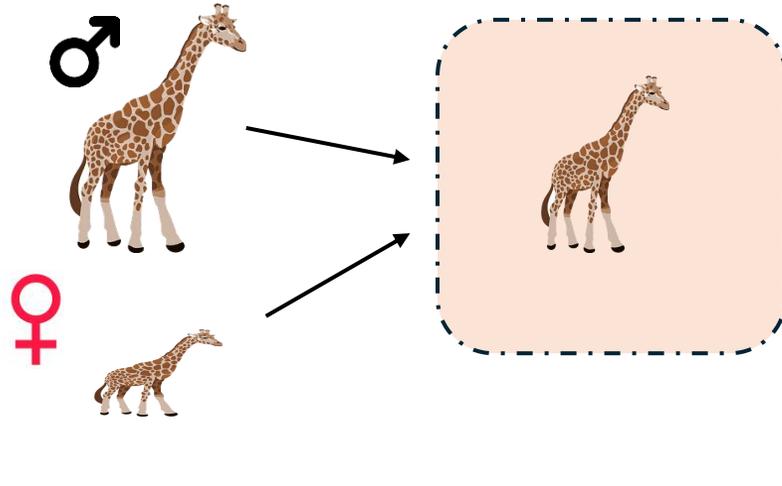
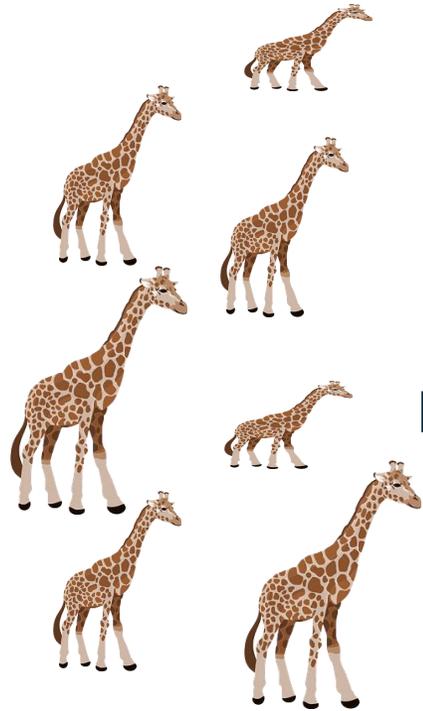
How would you model that?



Finally, let's make our giraffe stop cloning and have....be diploid



How would you model that?

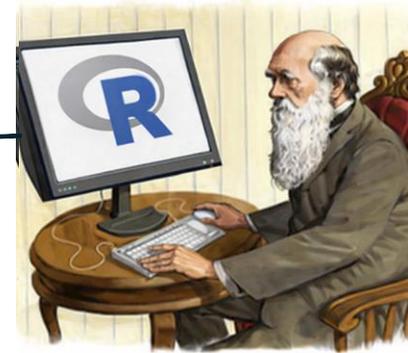


Offspring has neck that is average of mom and dad

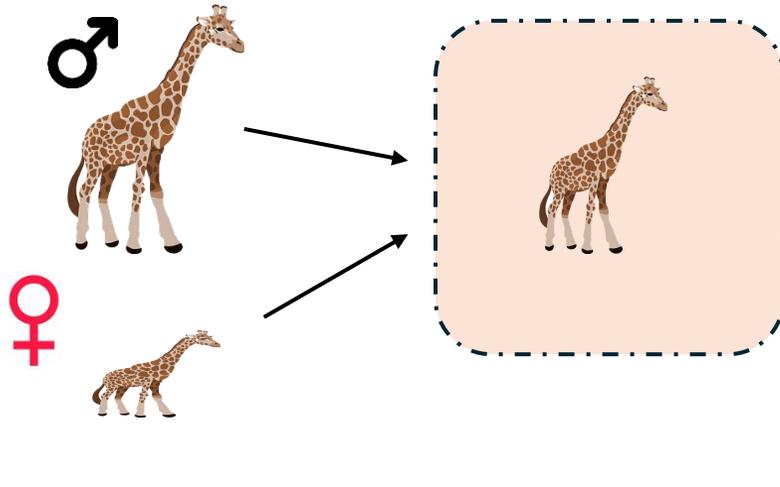
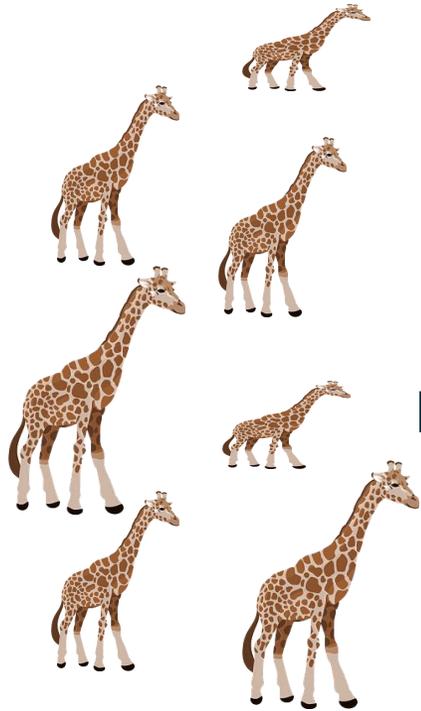
fathers=survivors
mothers=sample(survivors)

gametes=(fathers+mothers)/2

Finally, let's make our giraffe stop cloning and have....be diploid



How would you model that?

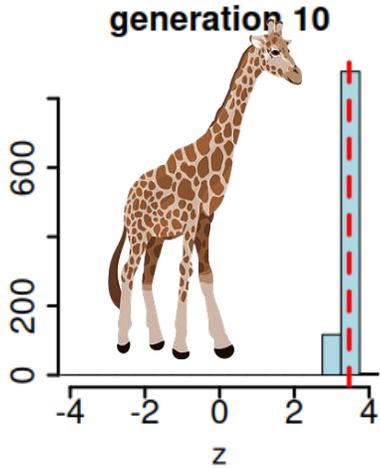


Offspring has neck that is average of mom and dad

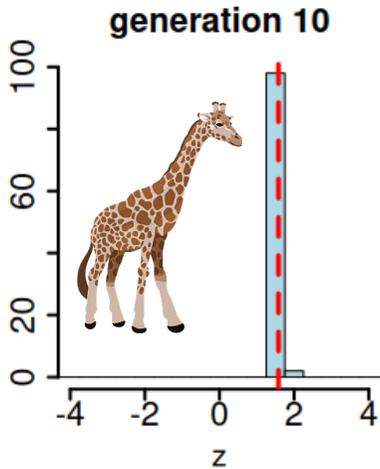
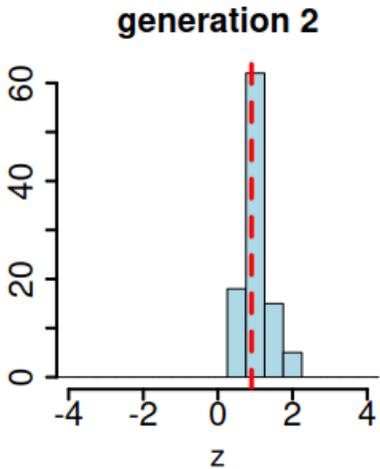
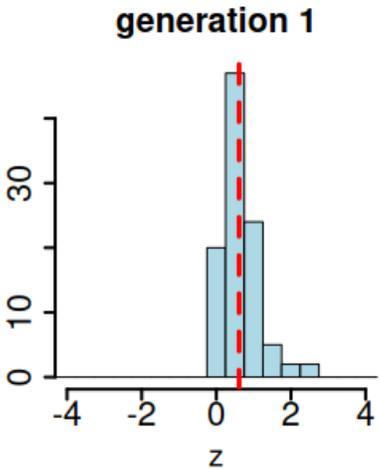
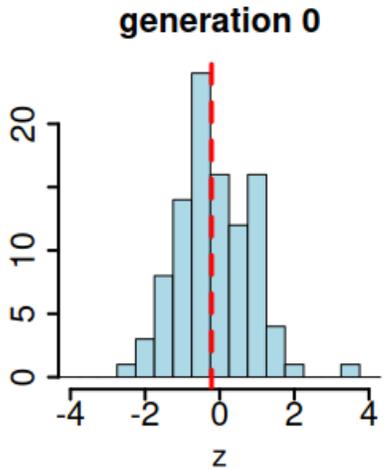
$$\text{gametes} = (\text{fathers} + \text{mothers}) / 2$$

```
N=100; i=0
z=rnorm(N); gametes=z
for (i in 1:10){
survivors=sort(gametes)[((N/2)+1):N]
survivors=c(survivors,survivors)
fathers=survivors
mothers=sample(survivors)
gametes=(fathers+mothers)/2
z=gametes + rnorm(N,sd=0.1)}
```

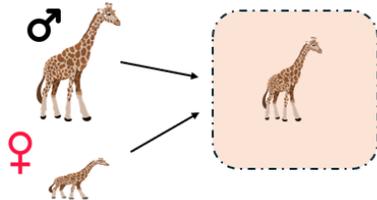
Evolution still happens, but apparently less than in haploids



Haploid model

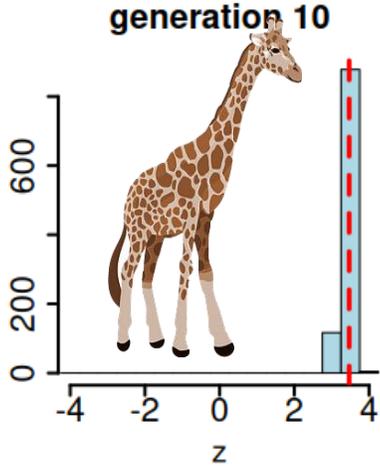


Diploid model.
Offspring average neck length

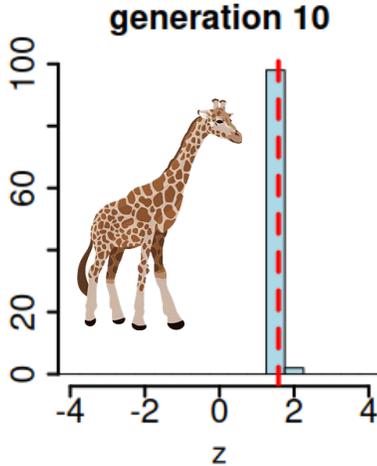
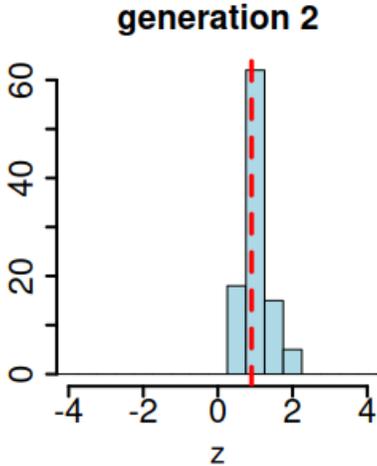
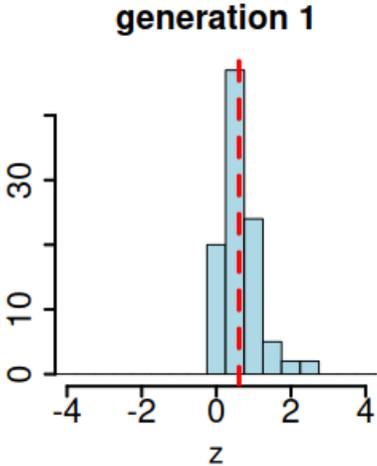
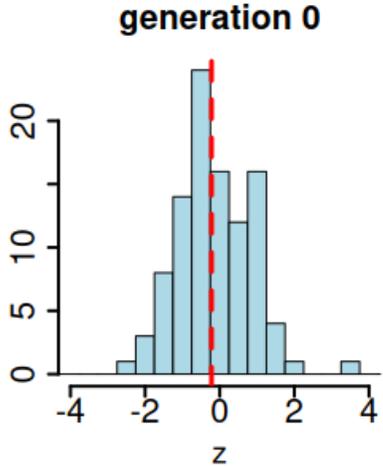


Evolution still happens, but apparently less than in haploids

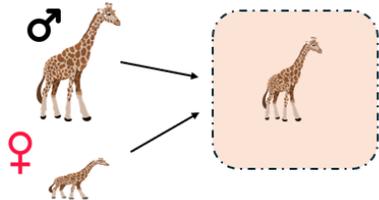
Why? Is this correct?



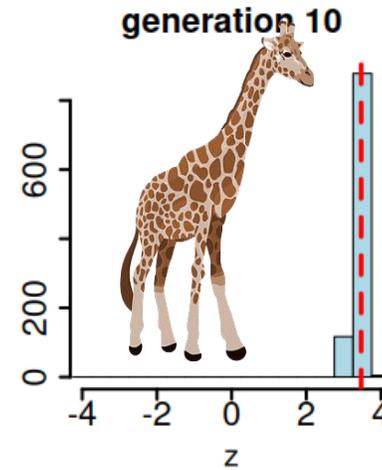
Haploid model



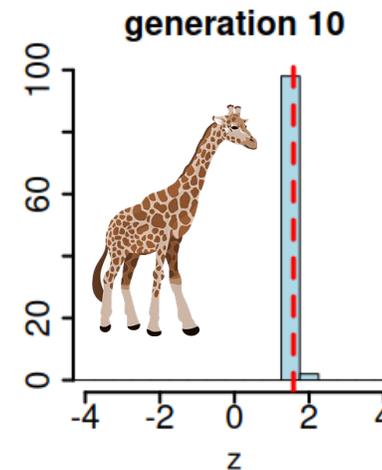
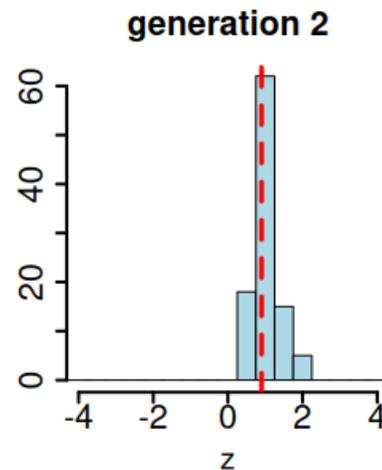
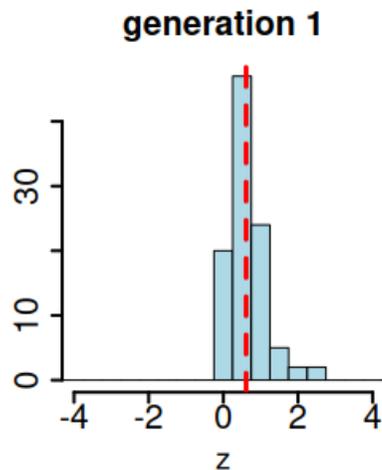
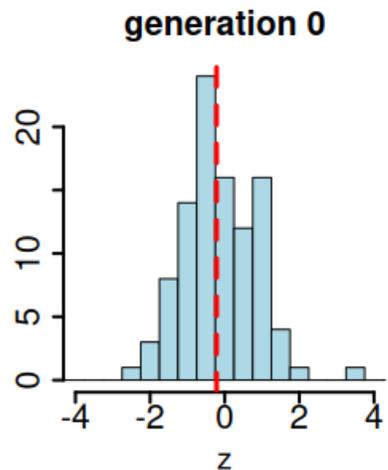
Diploid model.
Offspring average neck length



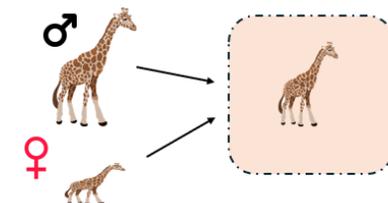
The «blending inheritance» problem



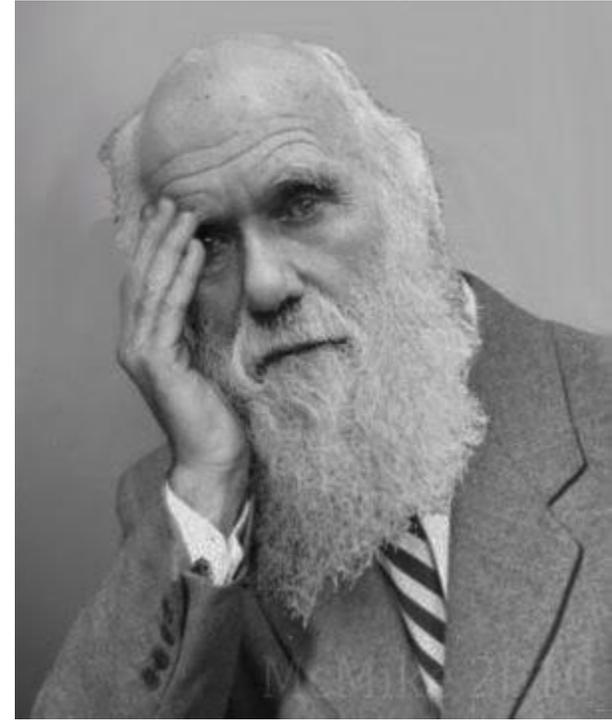
Haploid model



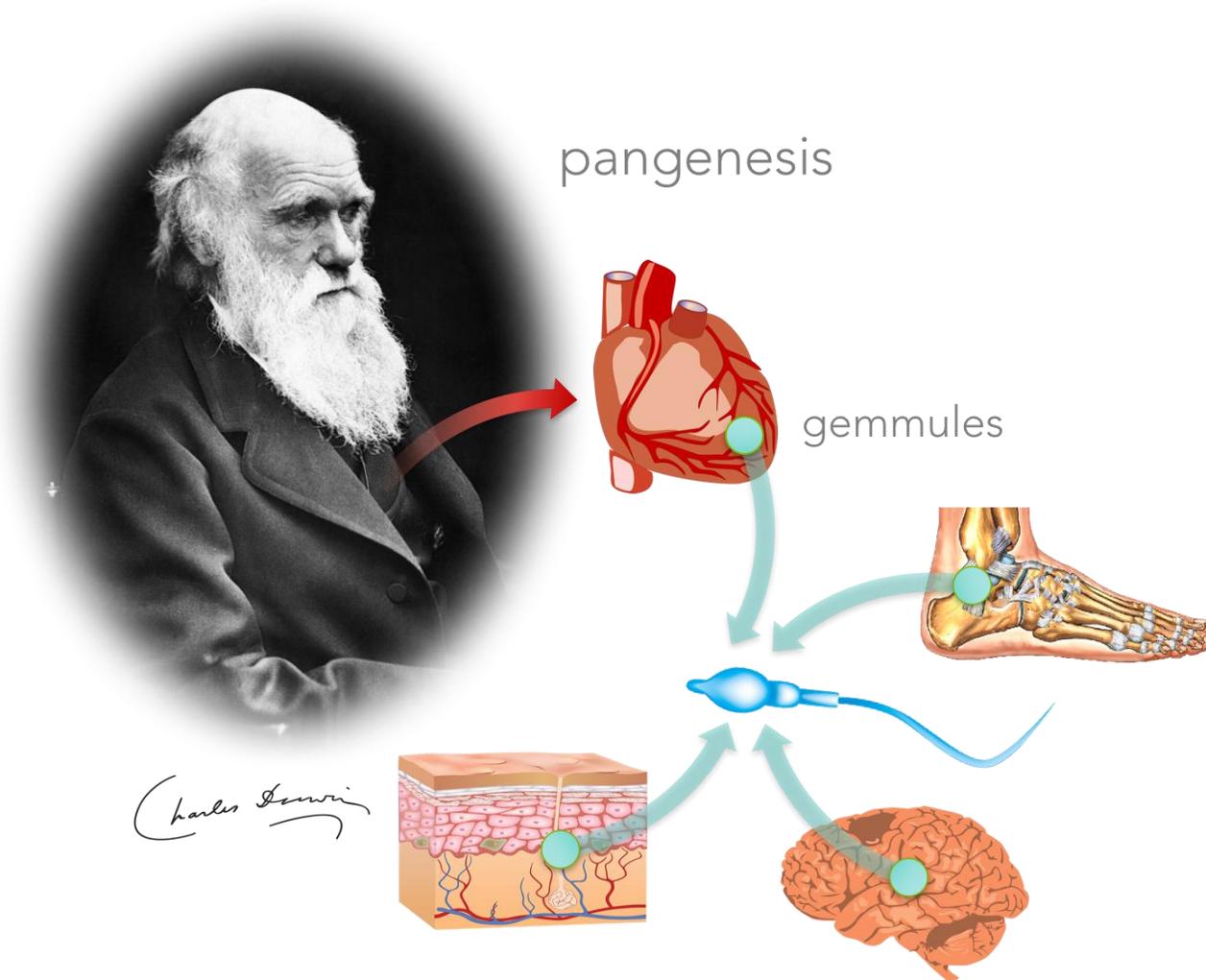
Diploid model.
Offspring average
neck length



What did Darwin think about inheritance?

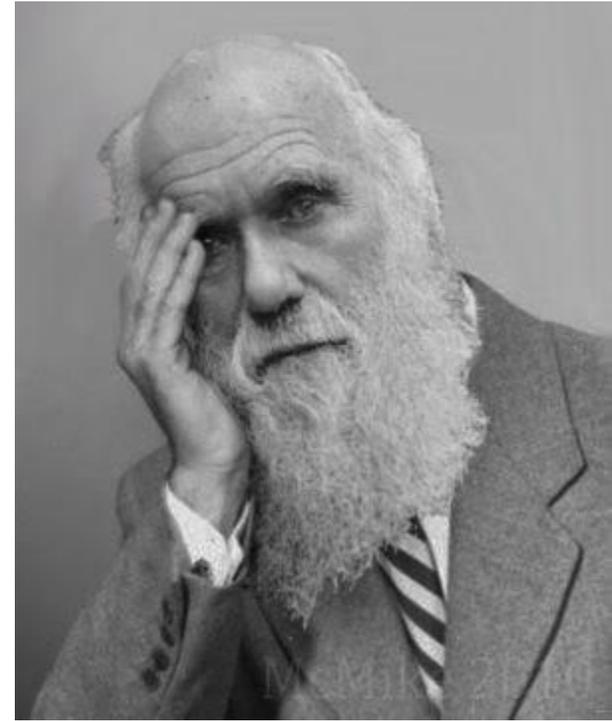
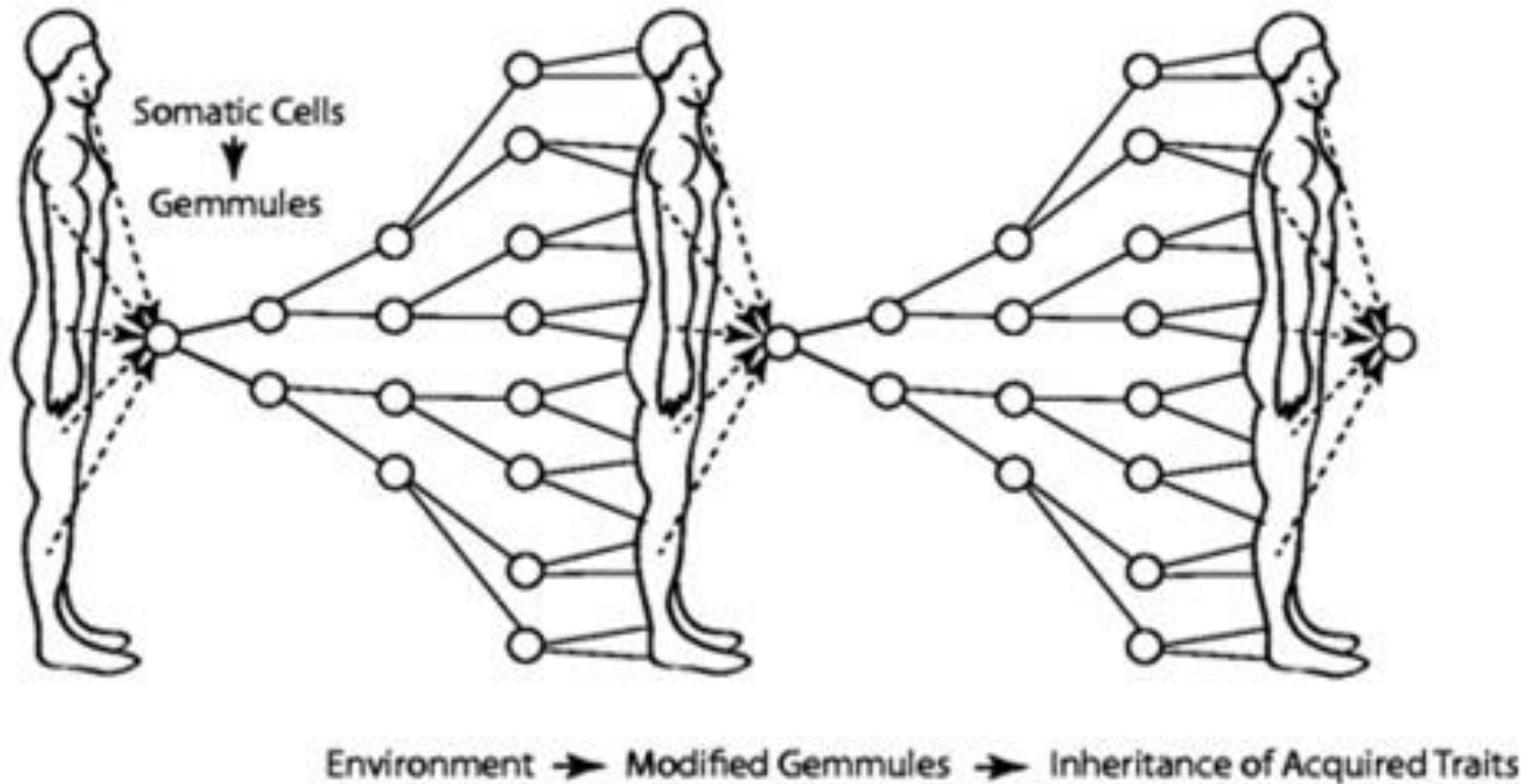


Darwin believed
in ***pangenes***!



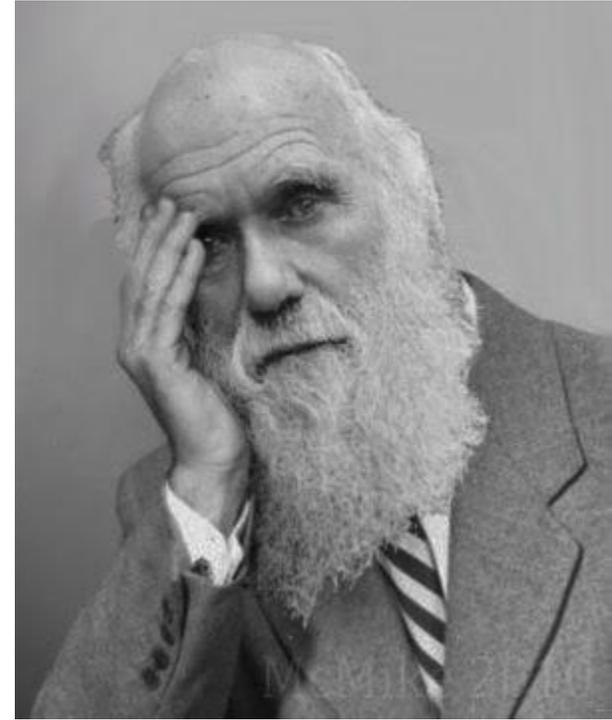
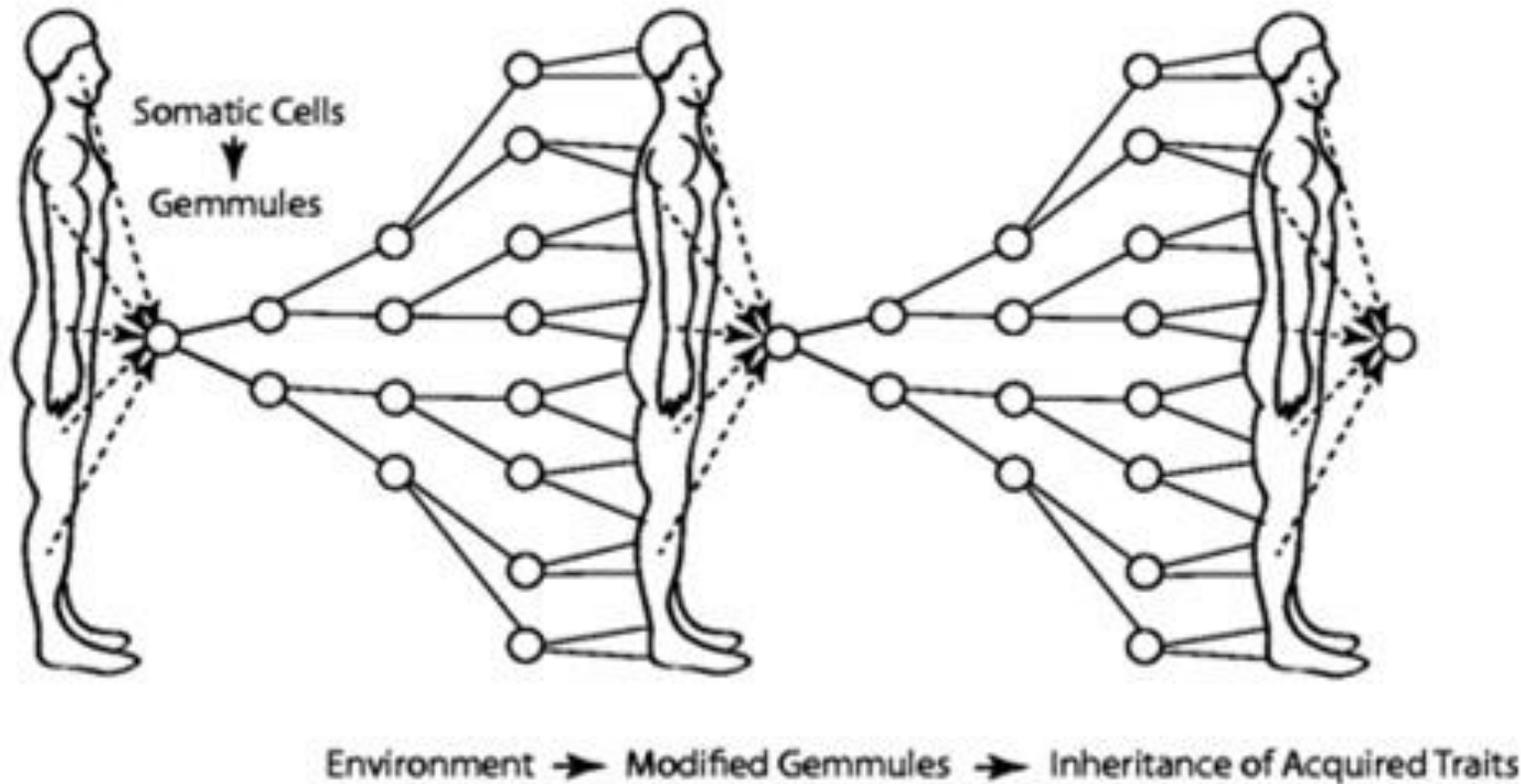
What did Darwin think about inheritance?

(A) Charles Darwin's Pangenesis Theory



What did Darwin think about inheritance?

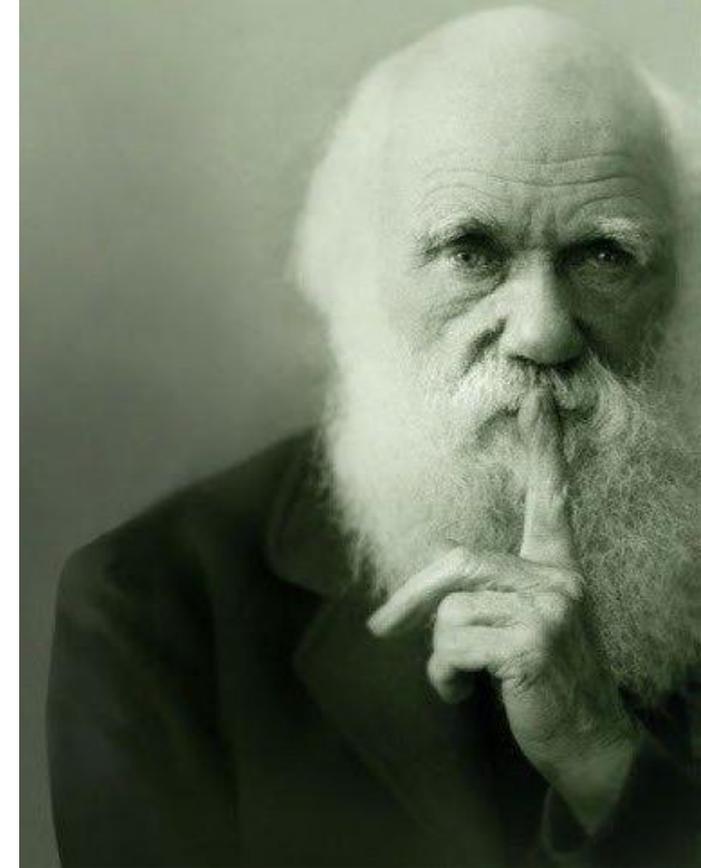
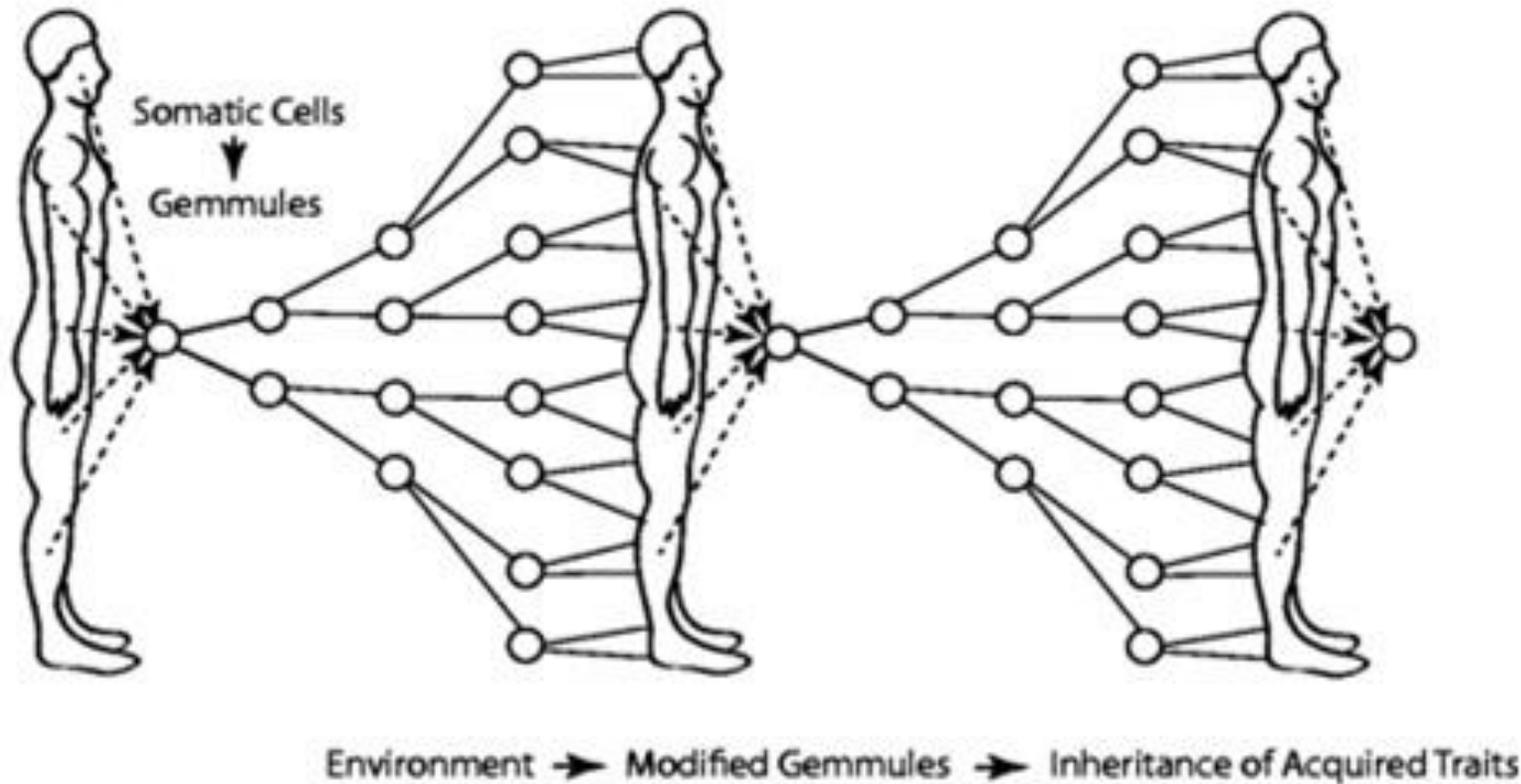
(A) Charles Darwin's Pangenesis Theory



With pangenesis even
Lamarckism would be
plausible!

What did Darwin think about inheritance?

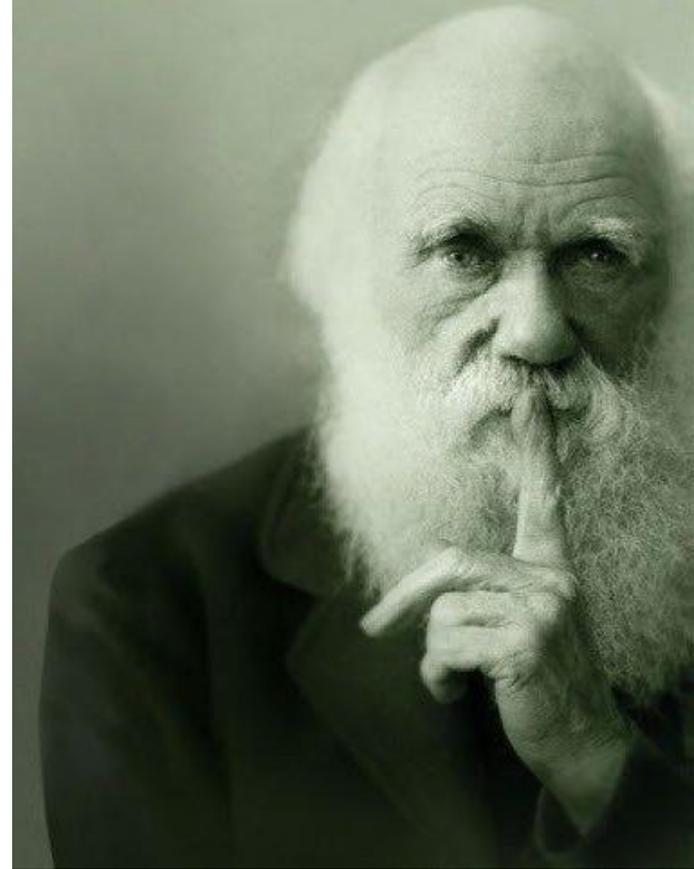
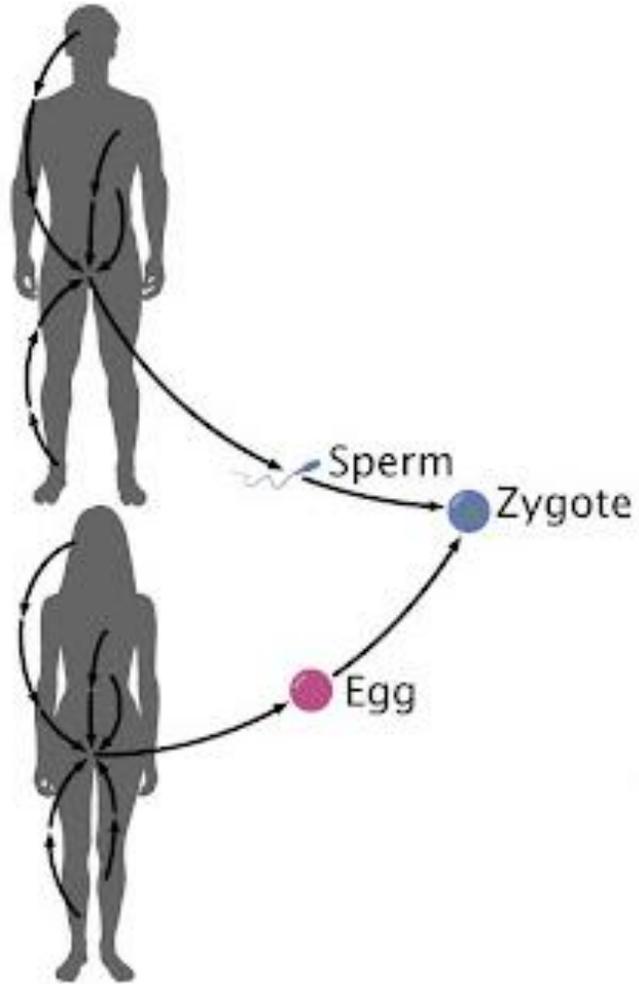
(A) Charles Darwin's Pangenesis Theory



Do you see other problems?

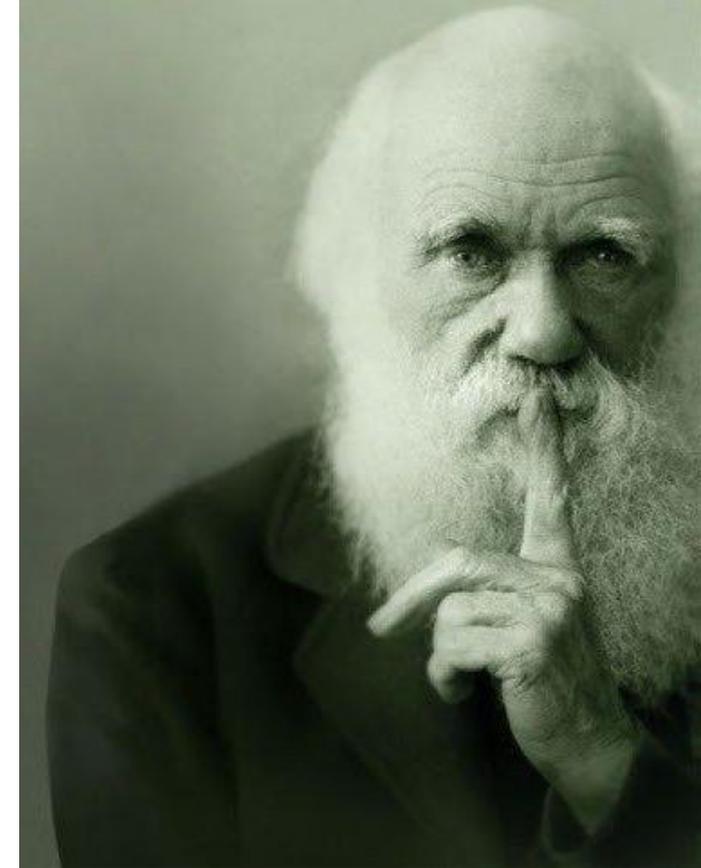
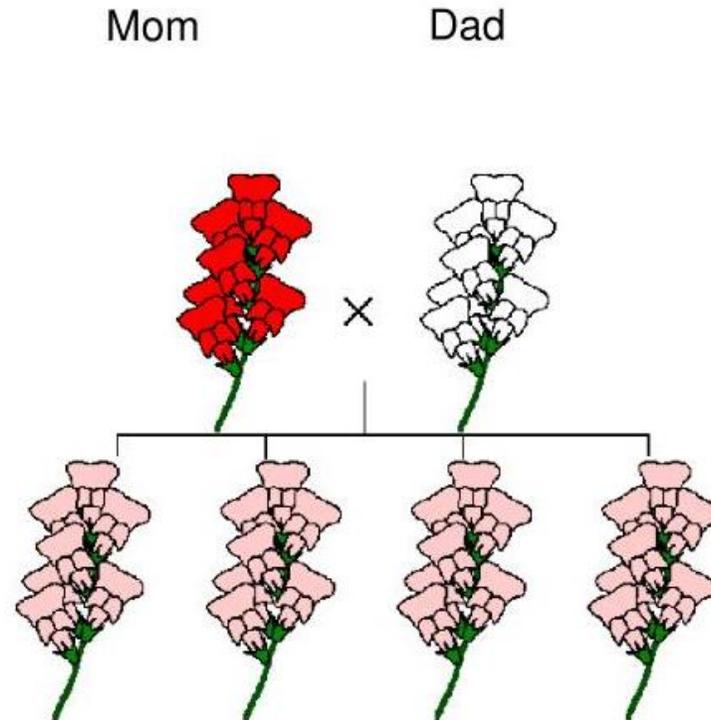
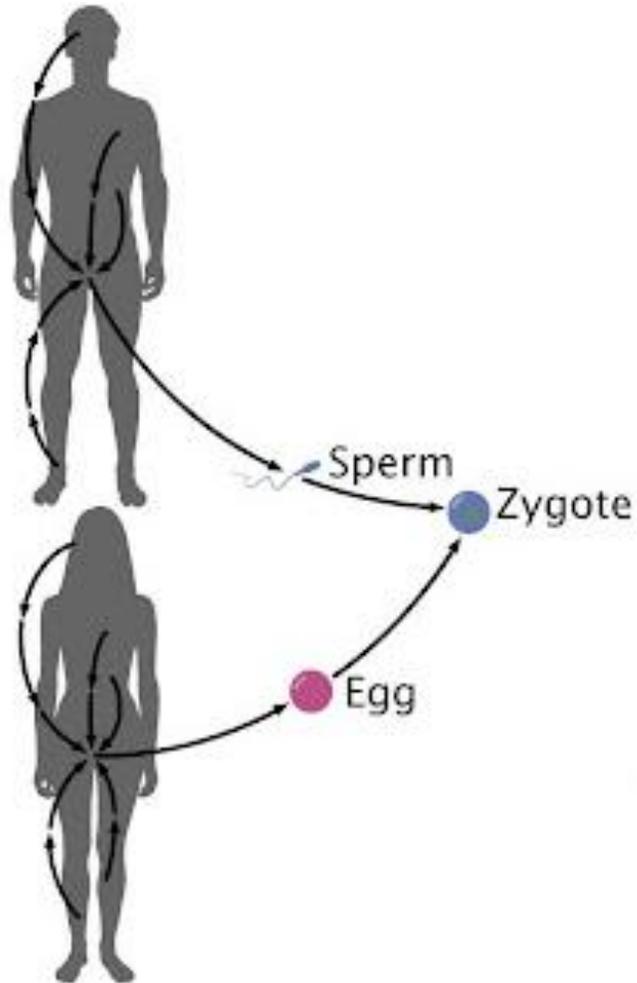
If so, which one?

Another (even bigger!) problem



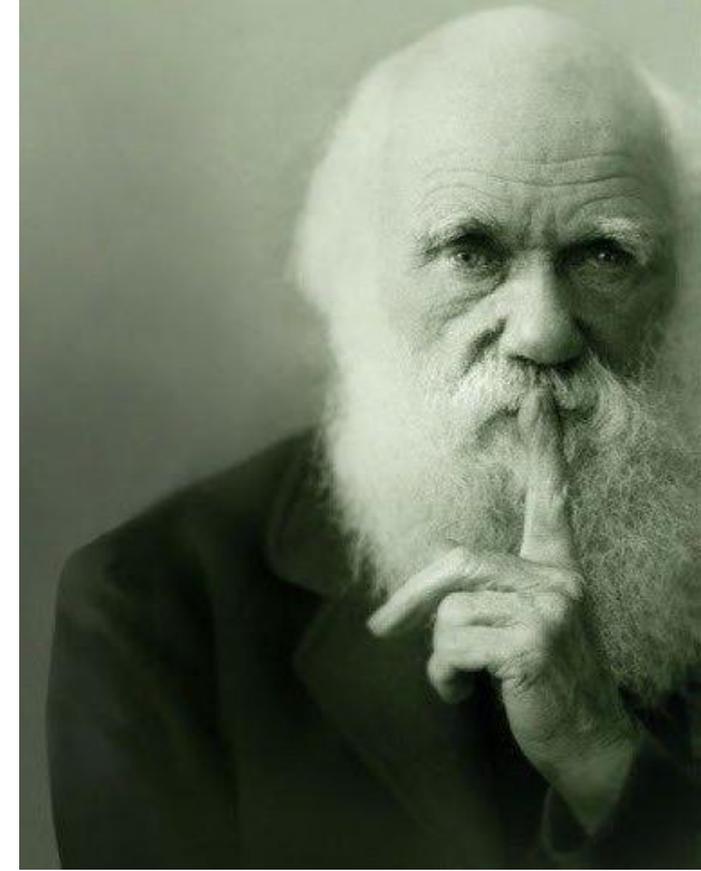
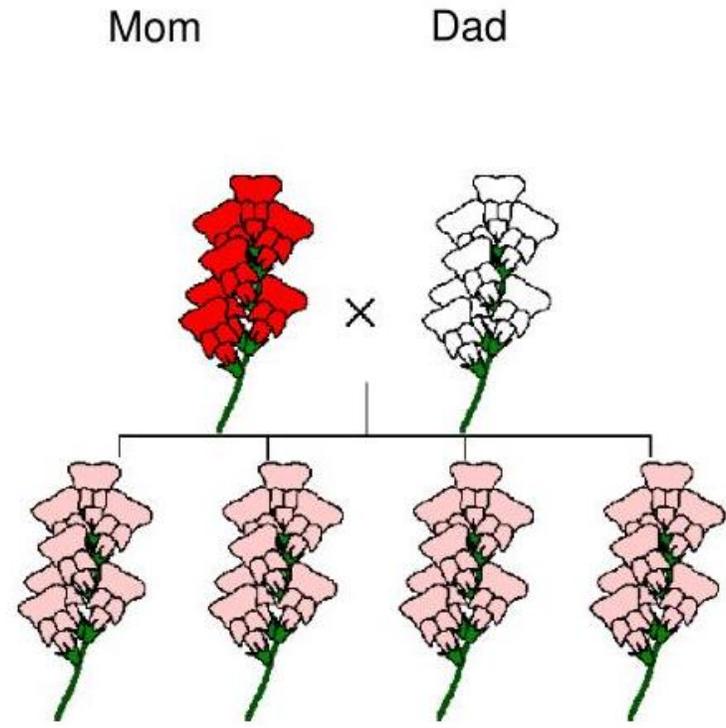
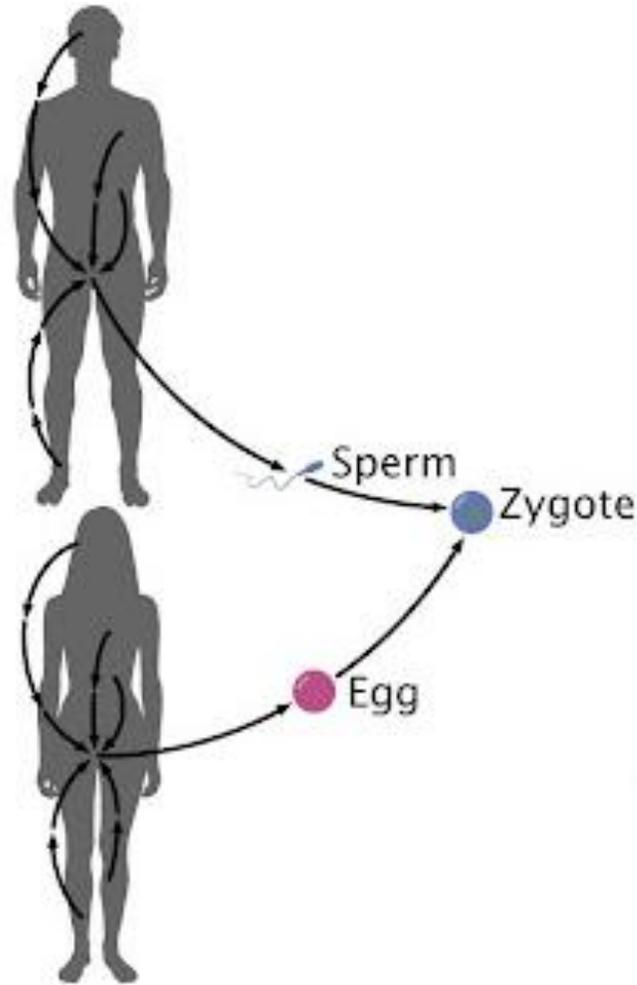
What does this
imply?

Another (even bigger!) problem



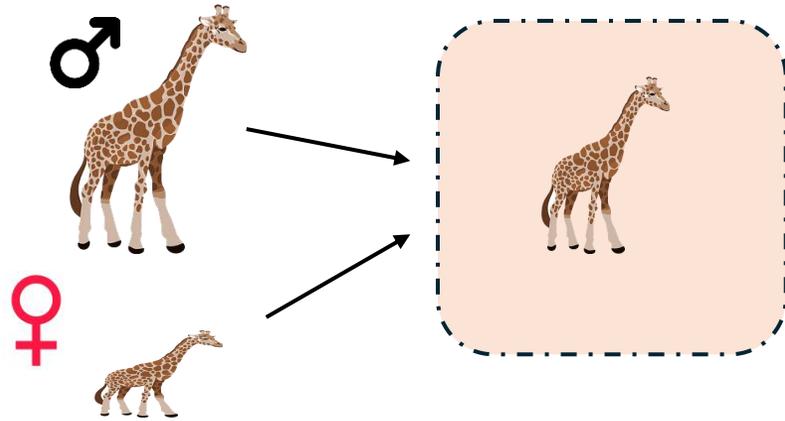
What does this
imply?
**Blending of
inheritance!**

What is the problem with «blending of inheritance»?

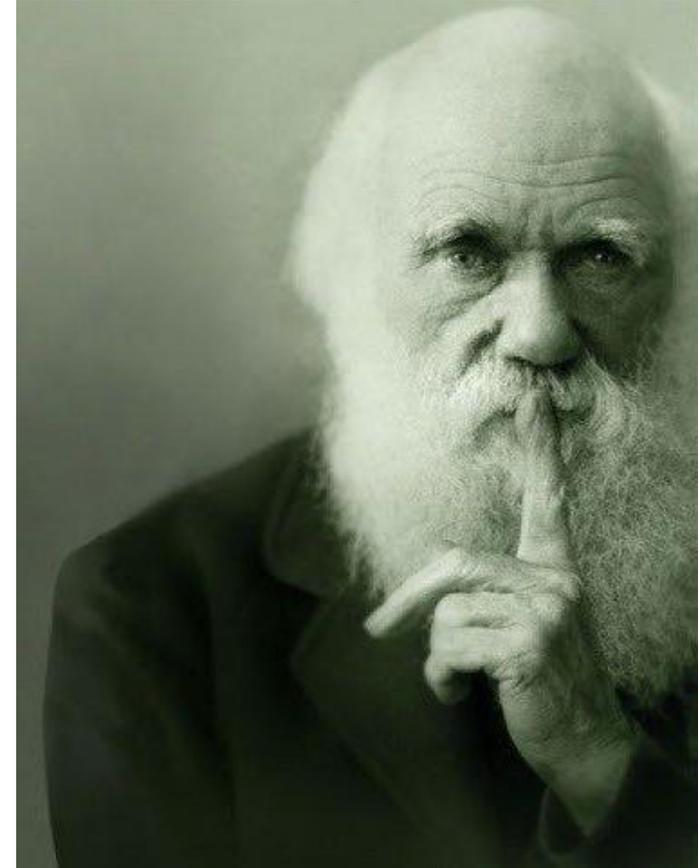


What does this imply?
Blending of inheritance!

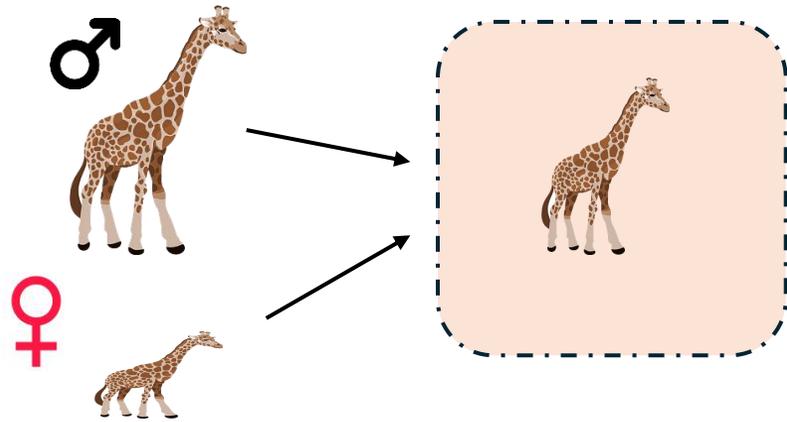
Let's use our toy mode (using Darwin's inheritance)!



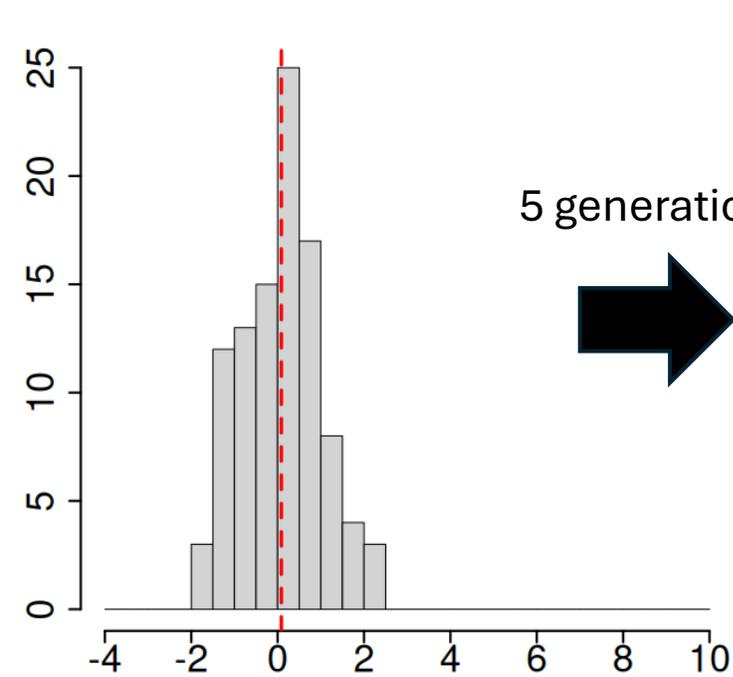
Offspring has neck
that is average of
mom and dad



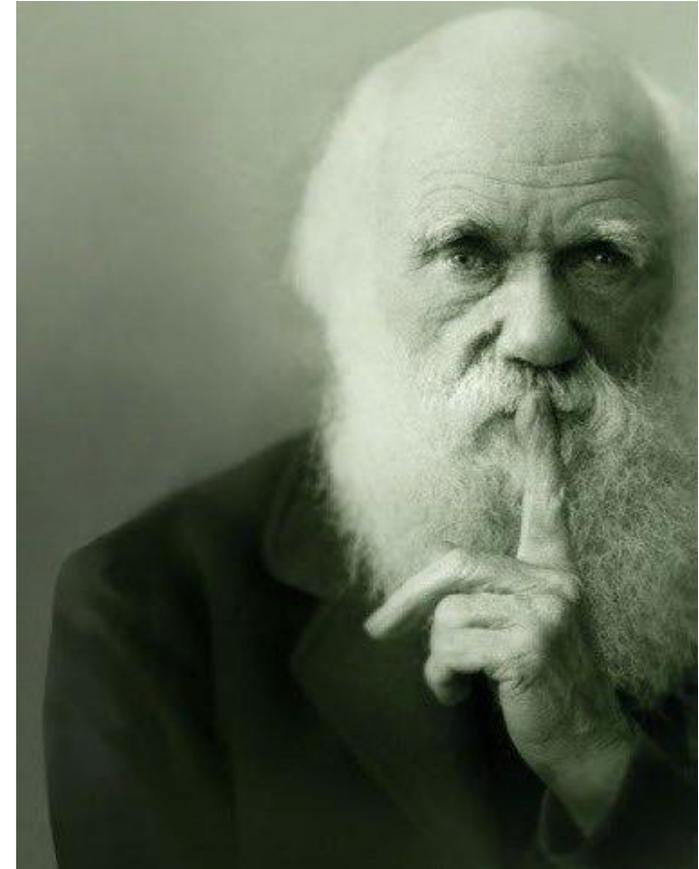
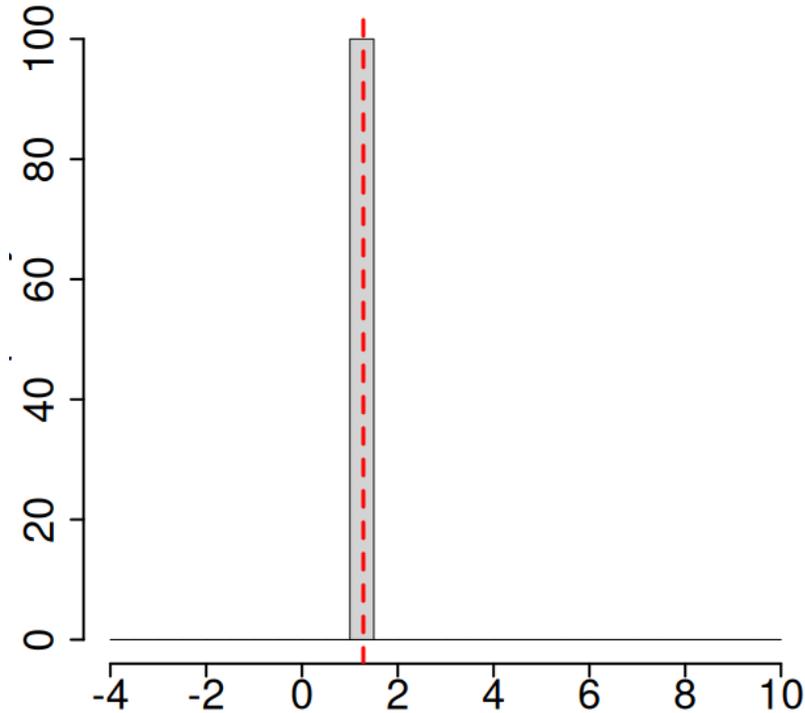
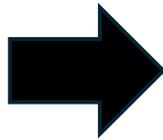
Let's use our toy mode (using Darwin's inheritance)!



Offspring has neck that is average of mom and dad



5 generations



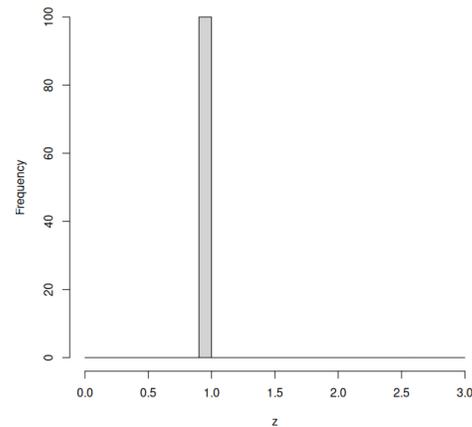
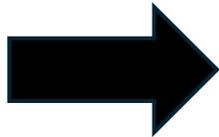
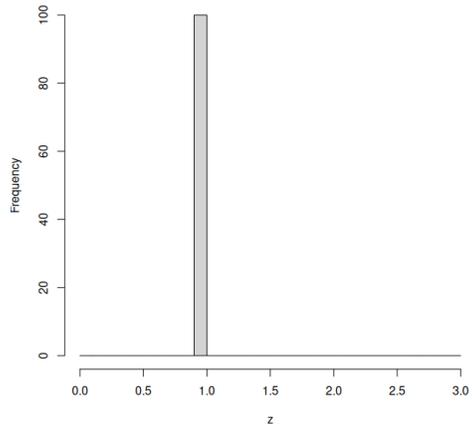
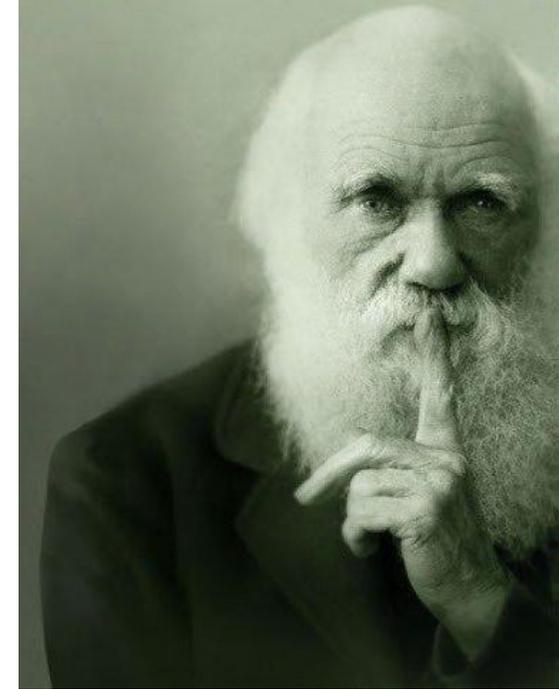
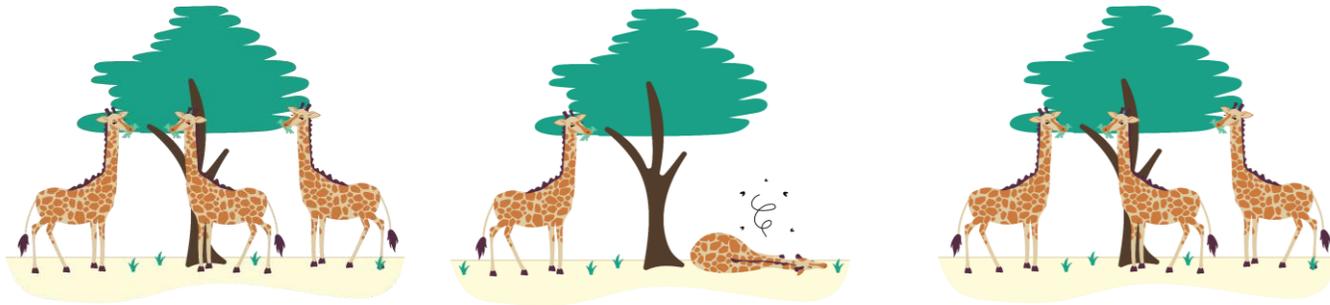
What do you notice?

No variability \rightarrow No evolution!

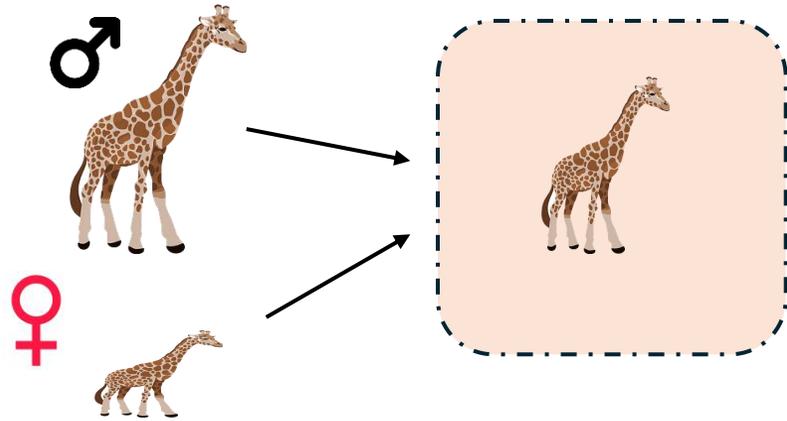
Variability among individuals

Differential contribution to successive generations

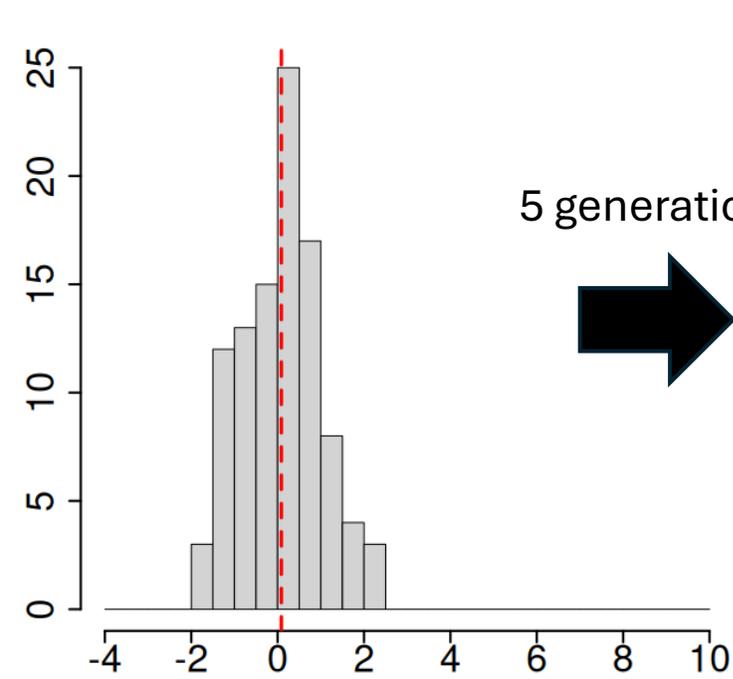
Mechanism of inheritance



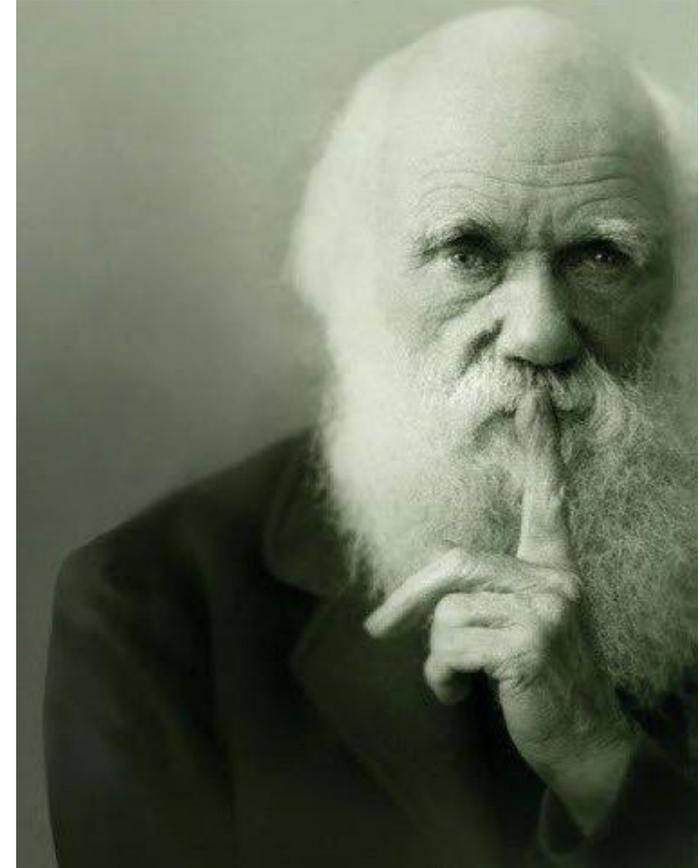
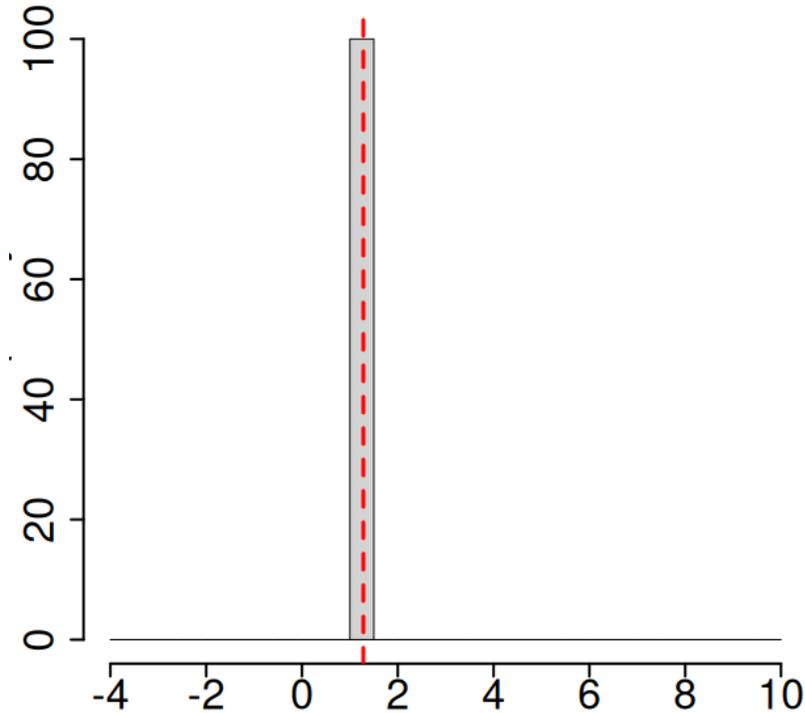
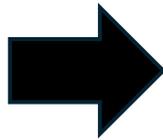
If inheritance «blends», all variability disappears very quickly in a population !



Offspring has neck that is average of mom and dad



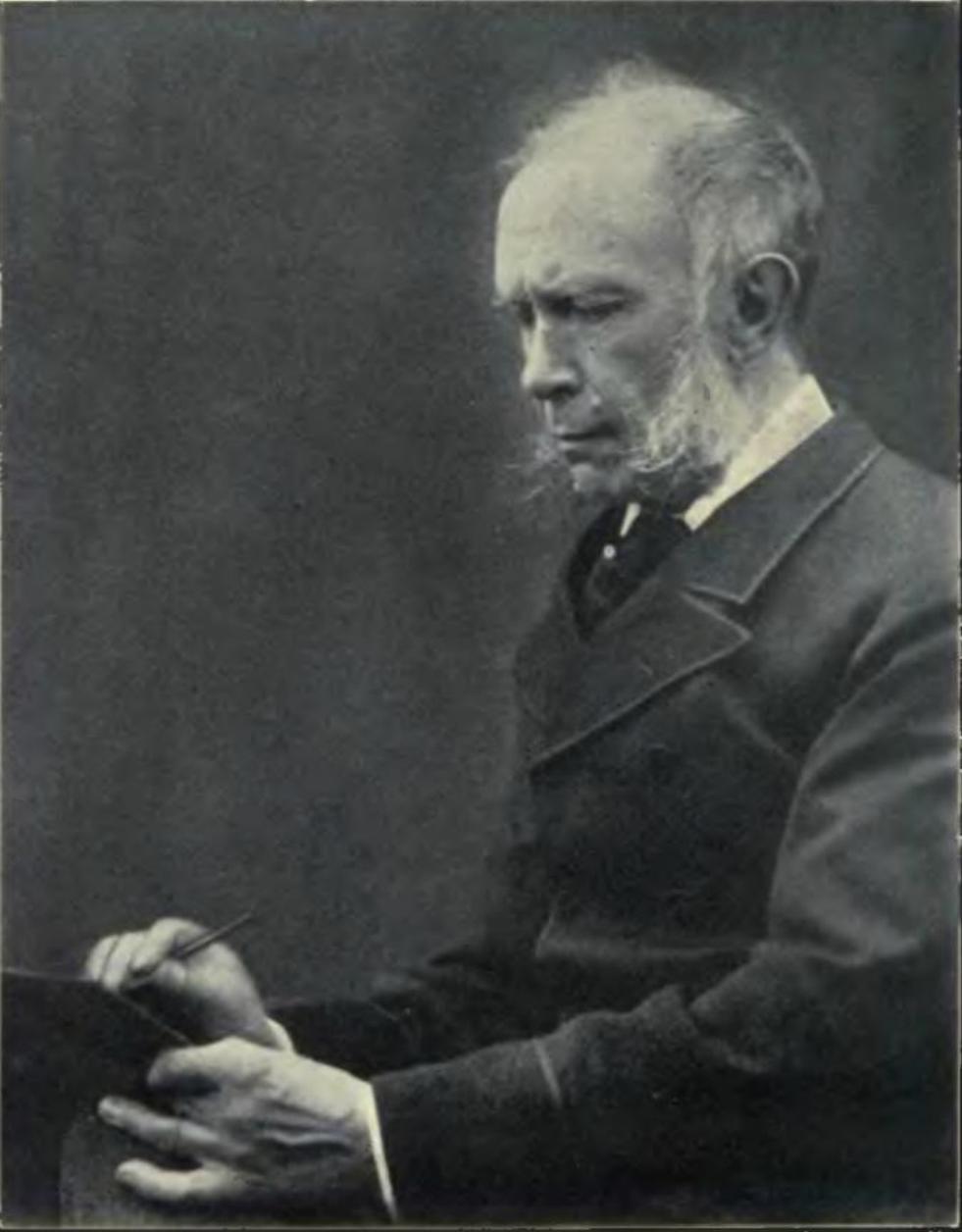
5 generations



“Swaming Argument” of Fleeming Jenkin, 1867

“Darwin's theory of the origin of species is not only without sufficient support from evidence, but is proved false by a cumulative proof.”

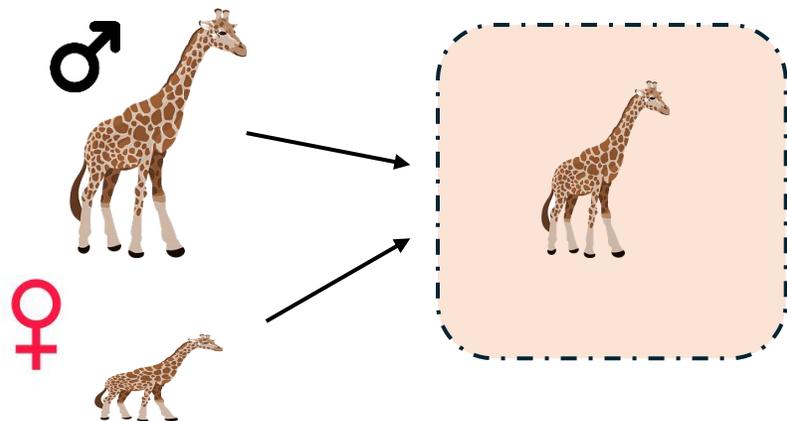
[Jenkin, Fleeming]. 1867. [Review of] The origin of species. The North British Review 46 (June): 277-318.



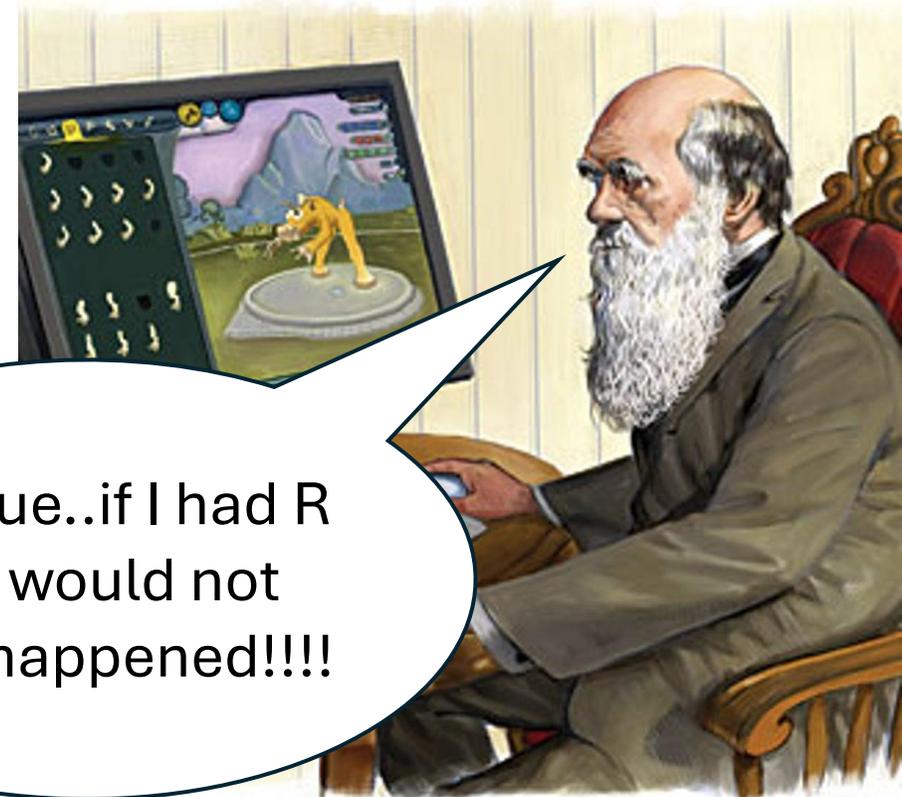
FLEEMING JENKIN, F.R.S., LL.D.

From a photograph kindly lent by Mrs. Dew Smith.

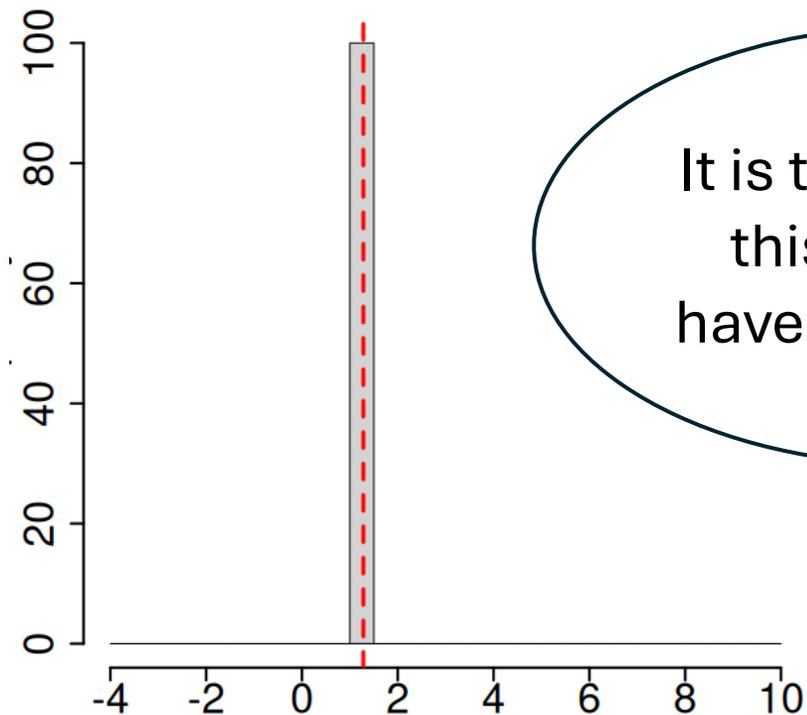
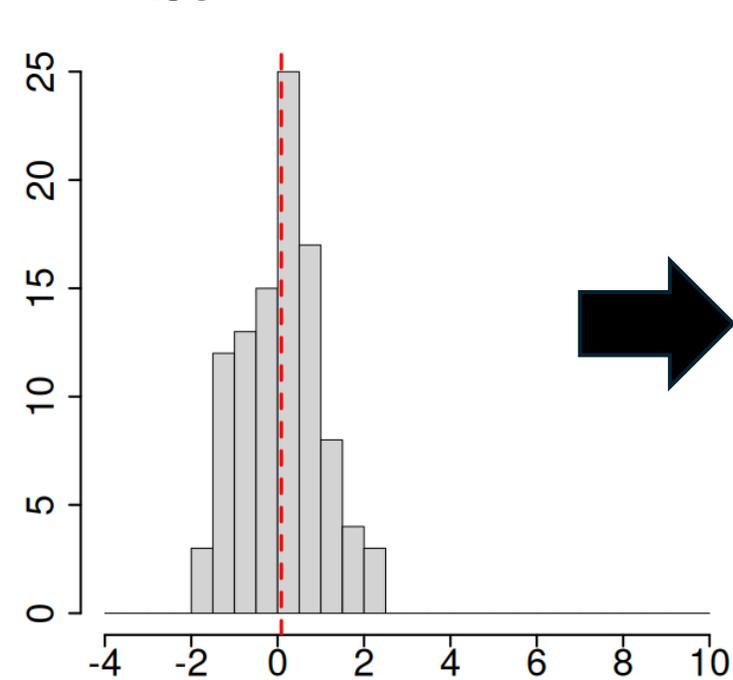
No variability → No evolution!



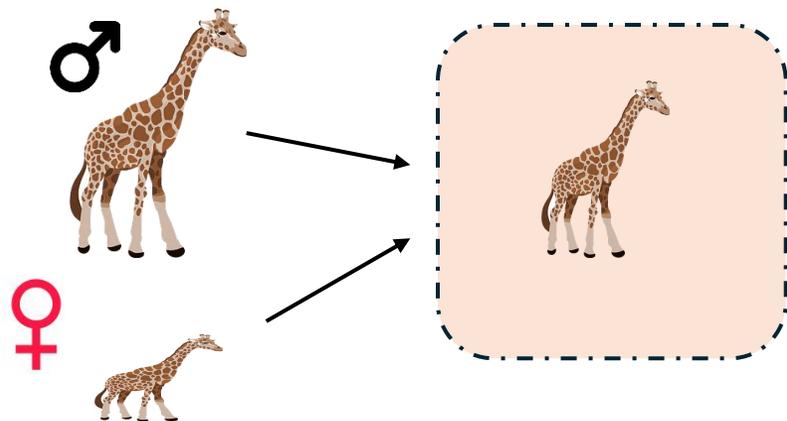
Offspring has neck that is average of mom and dad



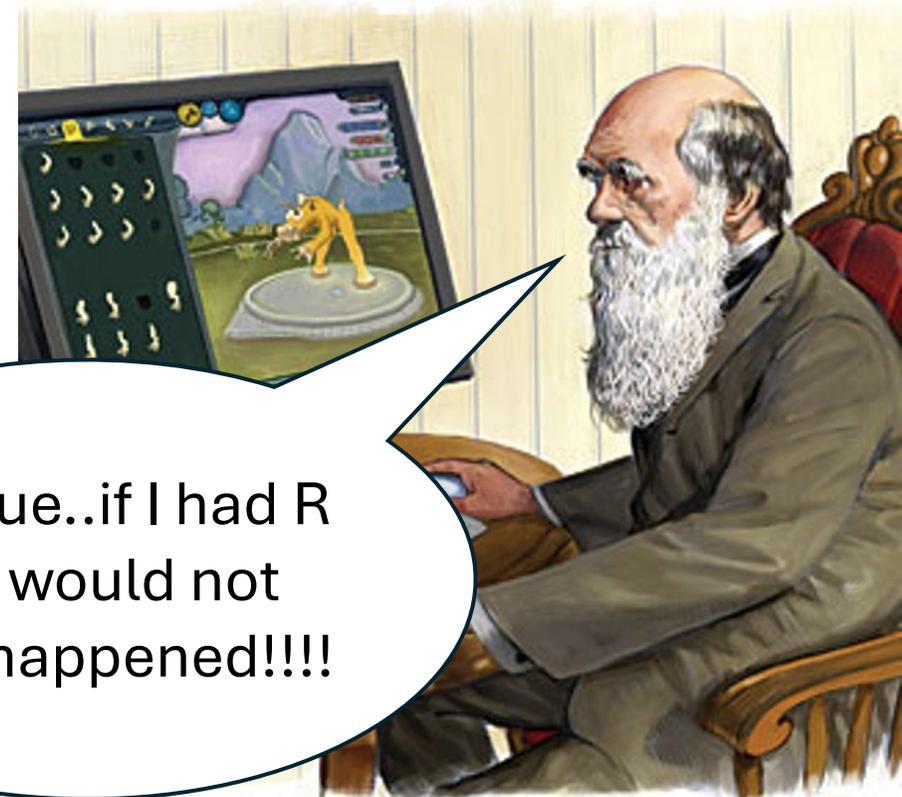
It is true..if I had R this would not have happened!!!!



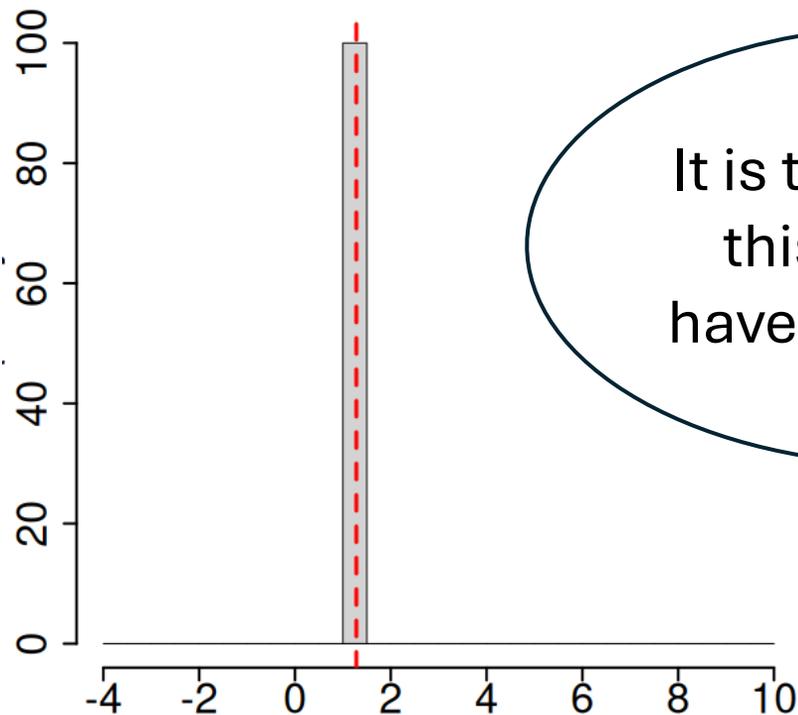
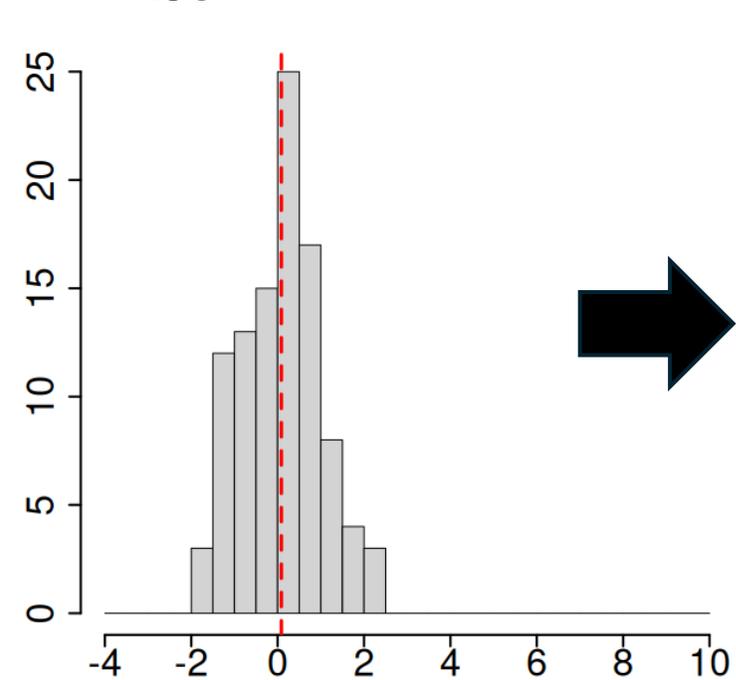
No variability \rightarrow No evolution!



Offspring has neck that is average of mom and dad

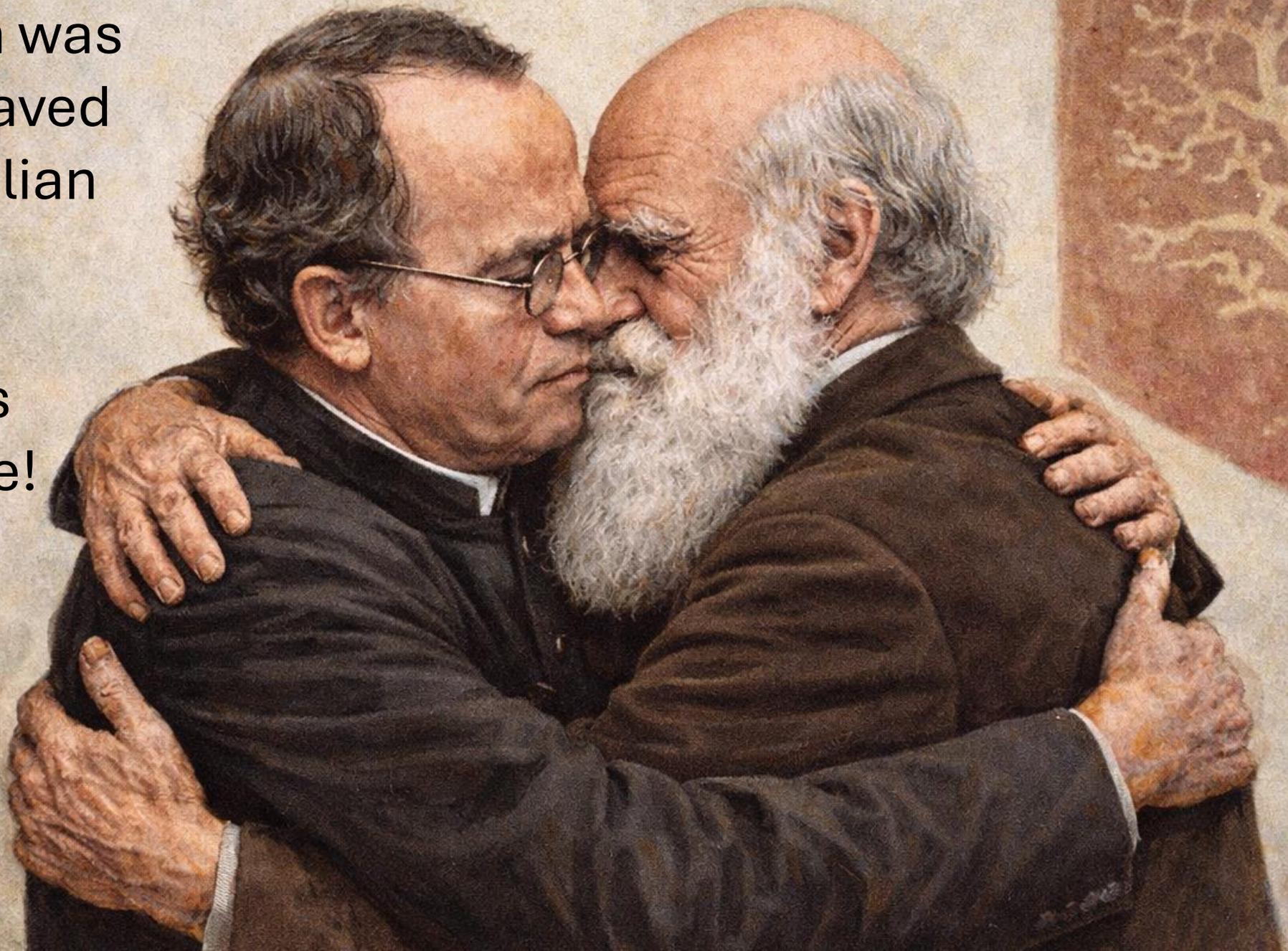
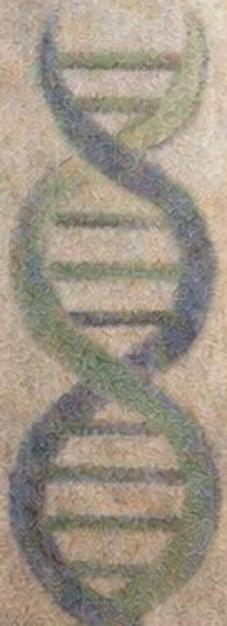


It is true..if I had R this would not have happened!!!!



Darwinism was
actually saved
by Mendelian
laws!

DNA is
discrete!

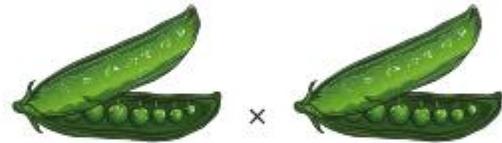


Even continuous traits are transmitted as discrete alleles

P Generation



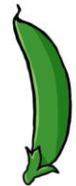
F₁ Generation



F₂ Generation



F1
Green

	G	g
G	GG 	Gg 
g	Gg 	gg 

The Punnett square shows the genetic cross between two heterozygous F1 green pea pods (Gg). The top row represents the male parent (Gg) and the left column represents the female parent (Gg). The four possible genotypes in the offspring are GG (homozygous dominant, green), Gg (heterozygous, green), Gg (heterozygous, green), and gg (homozygous recessive, yellow). Each genotype is accompanied by a small illustration of the corresponding pea pod.

Darwin's "mistakes"

- **Environmental change** is necessary to generate variation

One argument was that **variation is (apparently) more common in artificial conditions**

- **Reproductive organs fail** due to changes from the "natural" conditions
- **Development fails**

(Apparently, Darwin went **deeper and deeper** into this "mistake" with time!)



[Kalds et al., 2022](#)

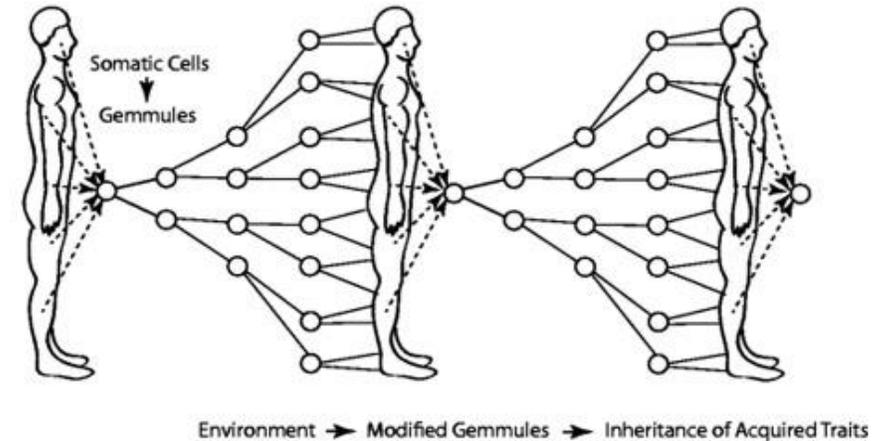
Darwin's "mistakes"

- Environmental change is necessary to generate variation
- ... **Inheritance of acquired characters** (*Pangenesis*)

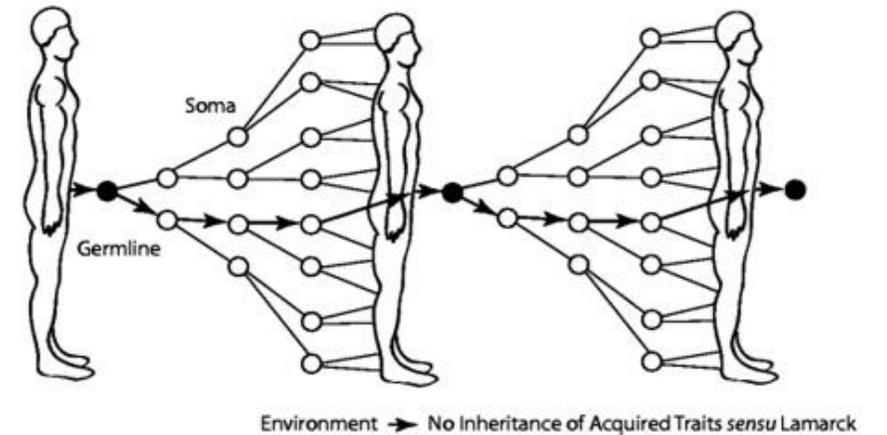
Cells in an organism are capable of shedding minute particles he called gemmules, which are able to circulate throughout the body and finally congregate in the gonads

I fully believe that each cell does actually throw off an atom or gemmule of its content

(A) Charles Darwin's Pangenesis Theory

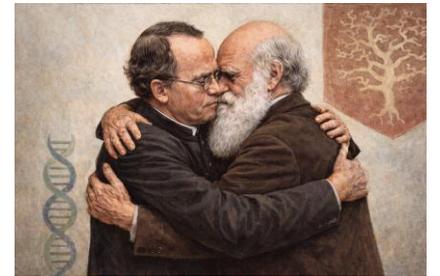
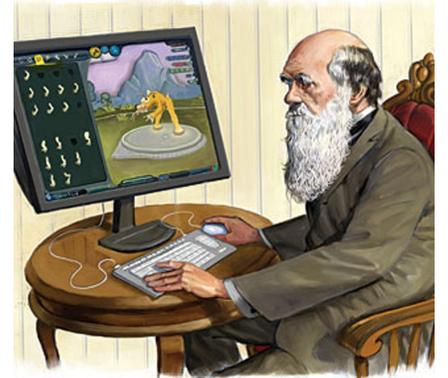


(B) August Weismann's Germplasm Theory



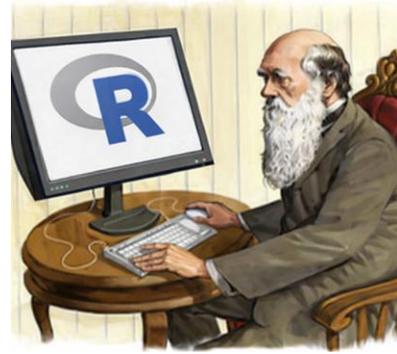
Conclusions

- Formal models can save your life
- Simulations are «less general», but they help a lot too
- We implemented our first evolutionary model
- We tested where Darwin was wrong
- But also why he was right: fundamental principles of «natural selection»:
 - Variability
 - Differential contribution
 - Inheritance



Appendix: some explanations on the code

- This is optional and just for students interested in the code

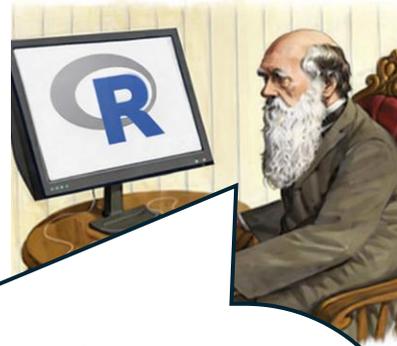


We can now test *in silico* “evolutionary theory”

Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance

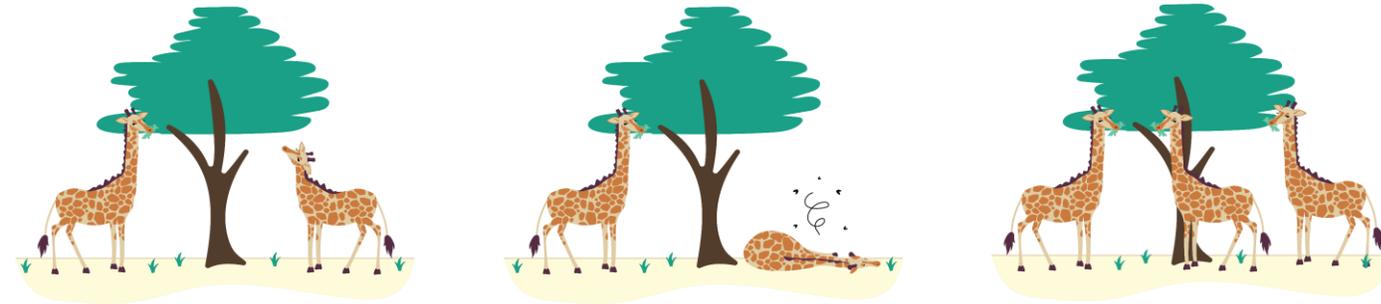


Our first basic model of evolution

```
N=100  
z=rnorm(N) Initialize  
population
```

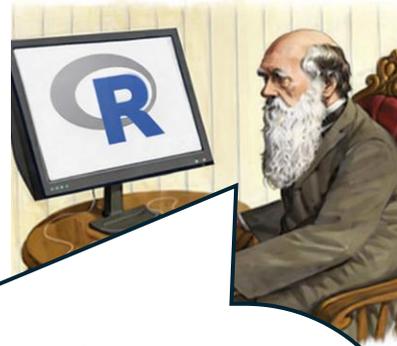
Life cycle

```
survivors=z[z>median(z)]  
z=sample(survivors,N,replace=TRUE)
```



We can now test *in silico* “evolutionary theory”

Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



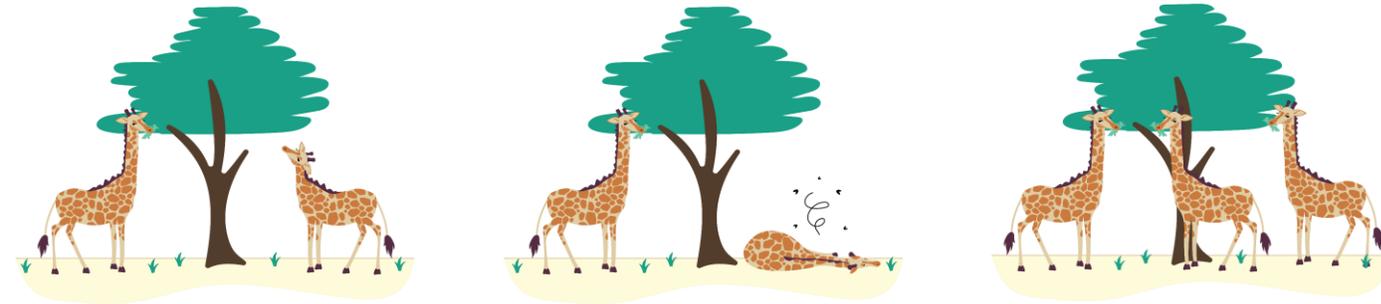
Our first basic model of evolution

```
N=100  
z=rnorm(N) Initialize  
population
```

Life cycle

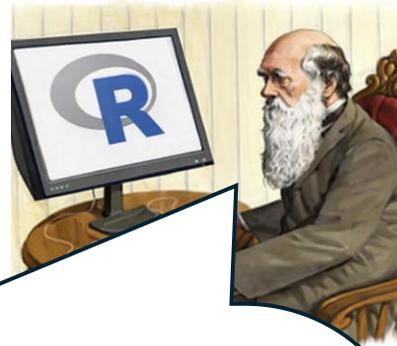
```
survivors=z[z>median(z)]  
z=sample(survivors,N,replace=TRUE)
```

For many times
(generations)



We can now test *in silico* “evolutionary theory”

Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



Our first basic model of evolution

```
N=100      Initialize  
z=rnorm(N) population
```

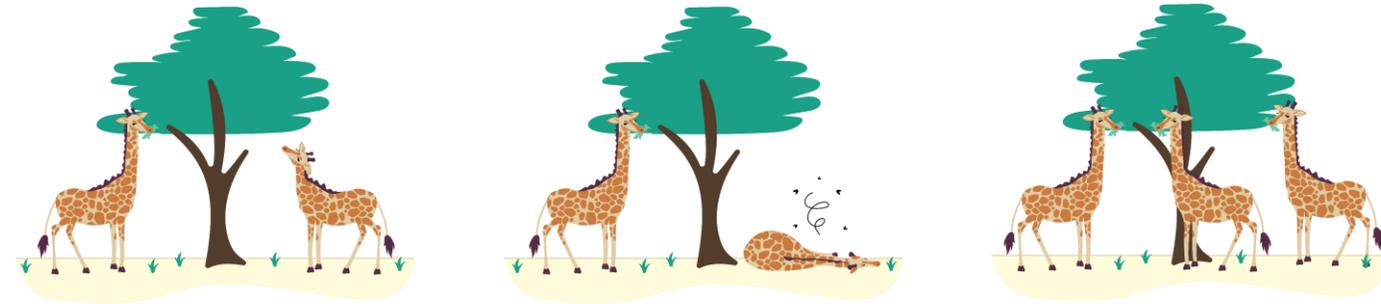
Life cycle

```
survivors=z[z>median(z)]  
z=sample(survivors,N,replace=TRUE)
```

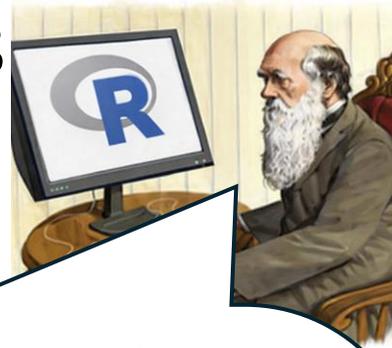
To examine results

```
hist(z)      Histogram of neck lengths  
median(z)    Median of neck lengths
```

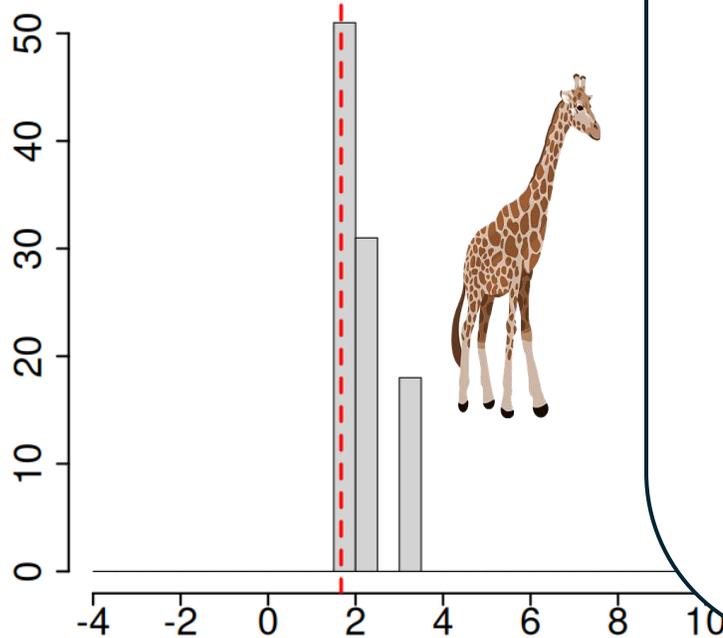
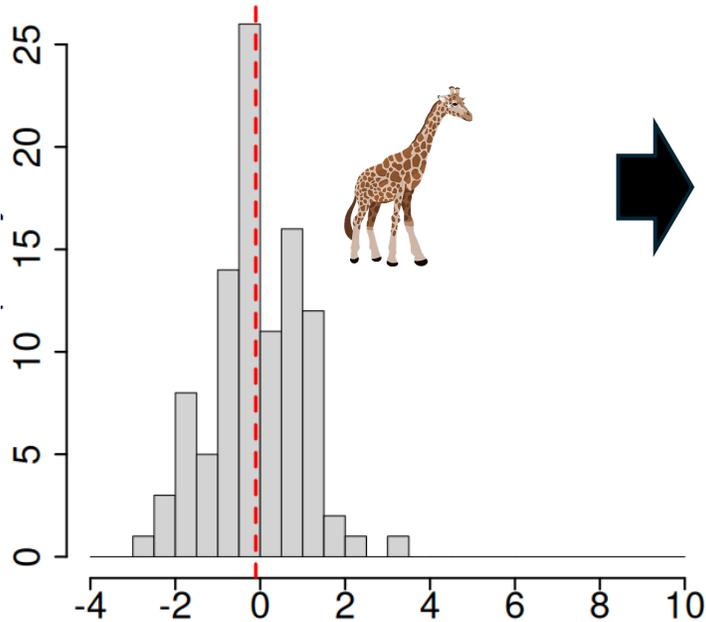
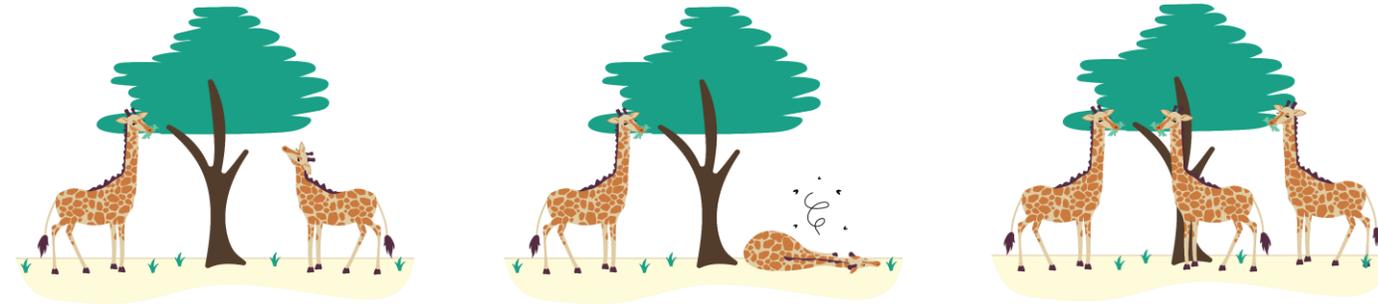
For many times
(generations)



They are sufficient to elongate the necks of our giraffes



- Variability among individuals
- Differential contribution to successive generations
- Mechanism of inheritance



Our first basic model of evolution

```
N=100  
z=rnorm(N)  
hist(z)
```

```
survivors=z[z>median(z)]  
z=sample(survivors,N,replace=TRUE)  
hist(z)
```

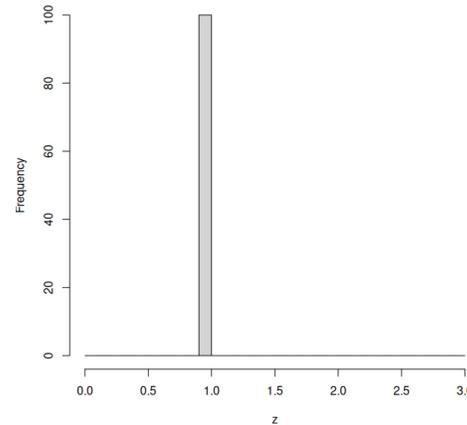
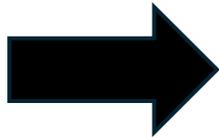
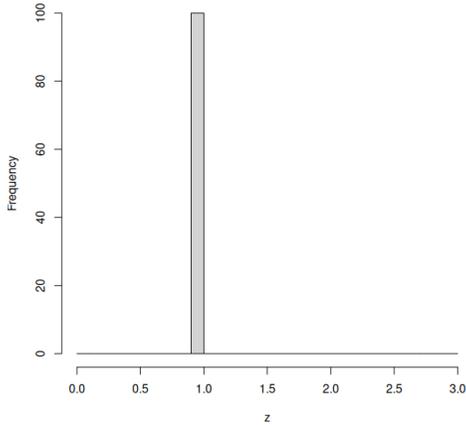
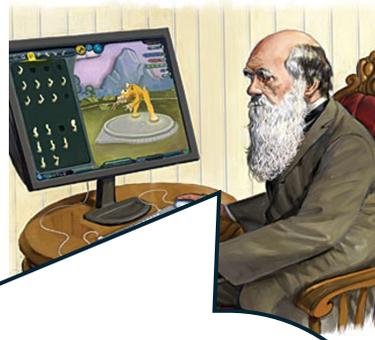
Our new giraffe population has a longer neck!

No variability → No evolution!

Variability among individuals

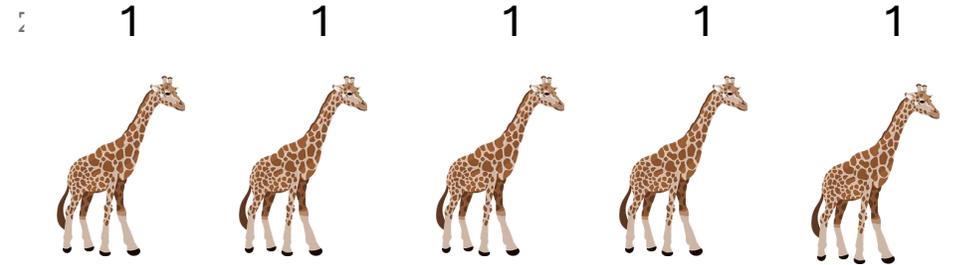
Differential contribution to successive generations

Mechanism of inheritance



Let's give to all giraffes an initial neck long 1

$N=100$
 $z=\text{rep}(1, N)$



These mechanisms are sufficient to elongate the necks of our giraffes

Variability among individuals

Differential contribution to successive generations

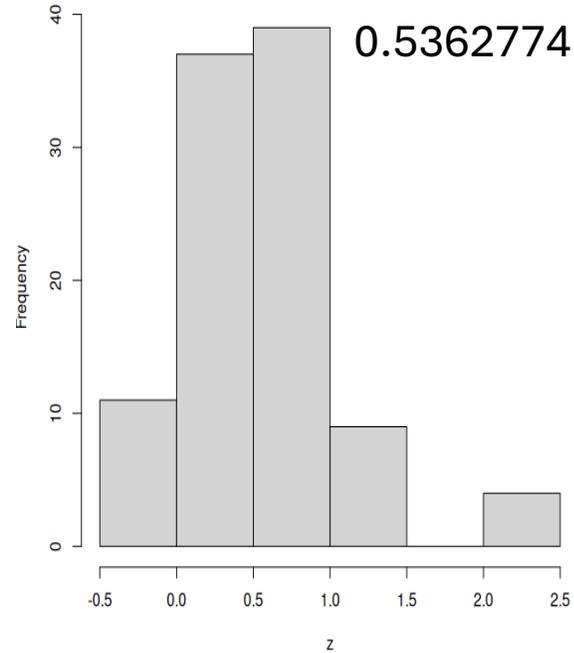
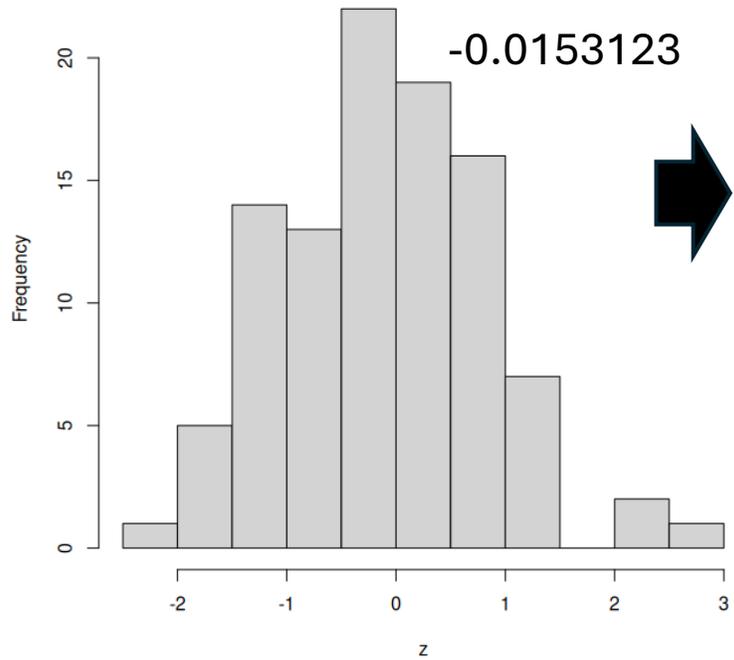
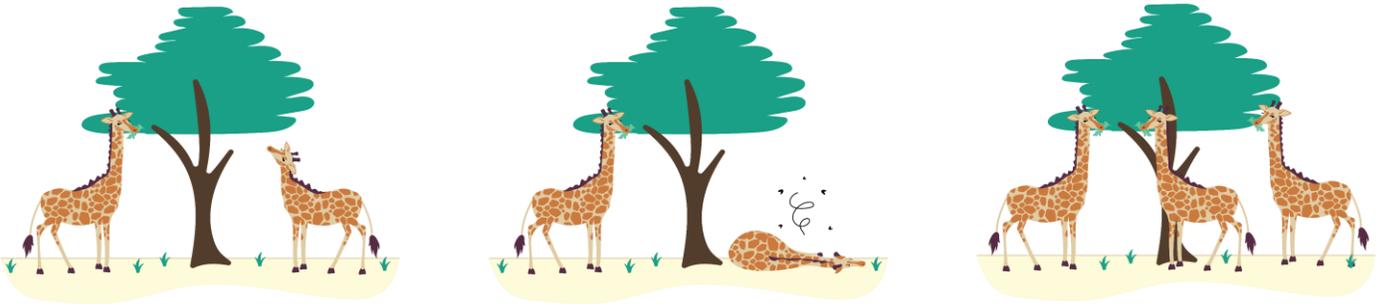
Mechanism of inheritance



Our first basic model of evolution

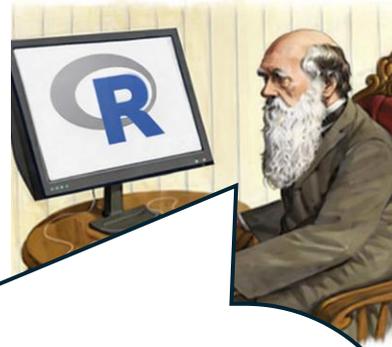
```
N=100
z=rnorm(N)
hist(z)
median(z) → -0.0153123
survivors=z[z>median(z)]
z=sample(survivors,N,replace=TRUE)
hist(z)
median(z) → 0.5362774
```

Our new giraffe population has a longer neck!



.. over generations

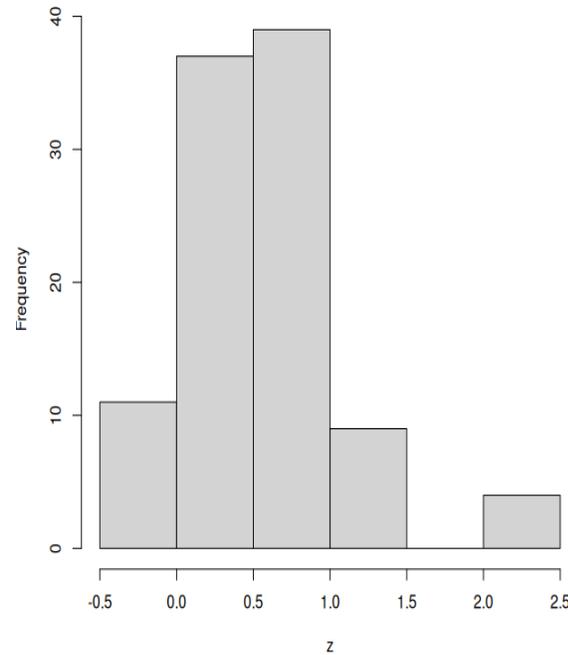
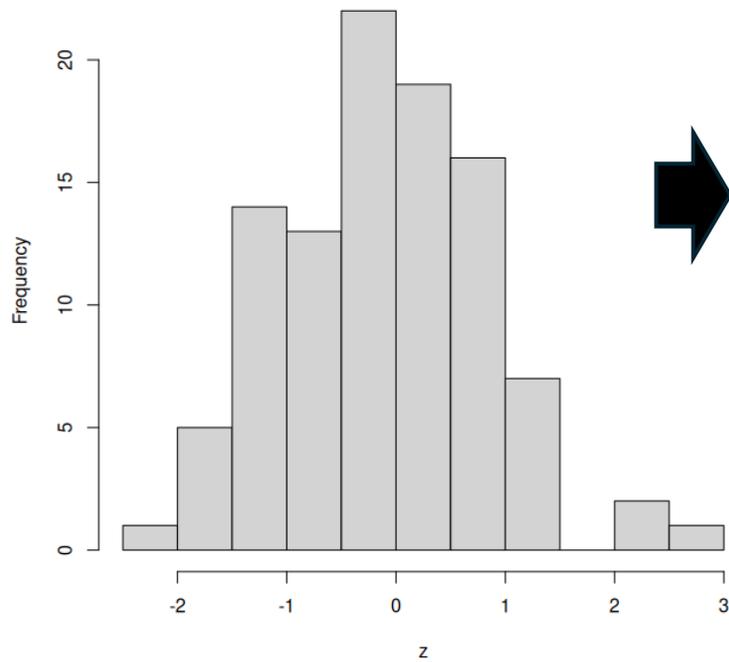
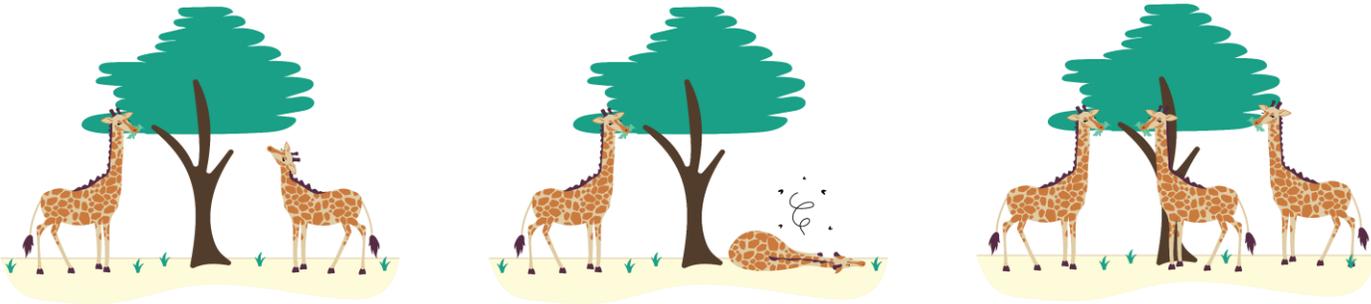
Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



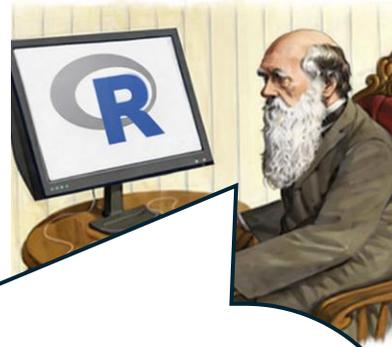
We can iterate this over generations

```
median(z) → 0.5362774
for (i in 1:5)
{
  survivors=z[z>=median(z)][1:50]
  z=sample(survivors,N,replace=TRUE)
}
median(z) → 1.513446
```

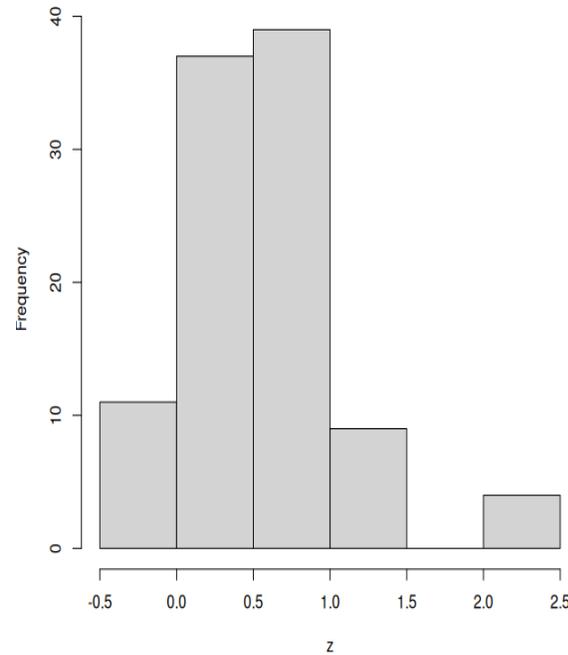
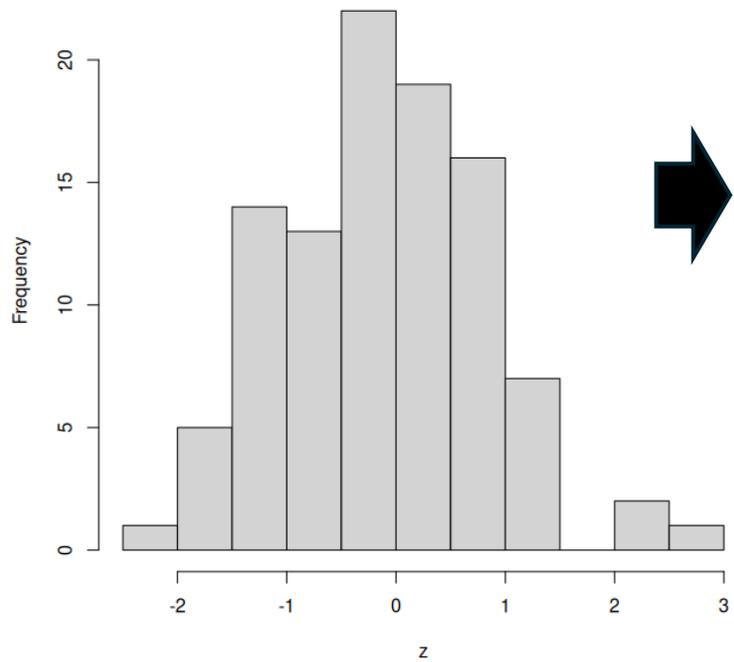
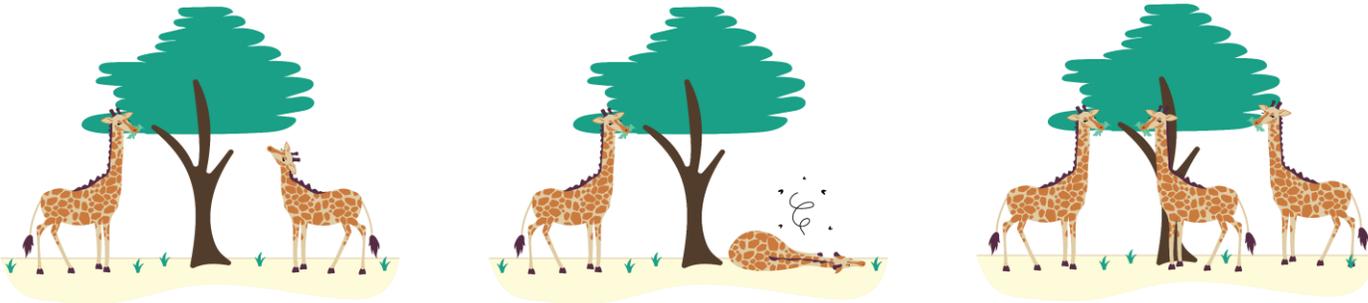
Our new giraffe population has an even longer neck!



Some details of the “code”



Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance



We can iterate this over generations

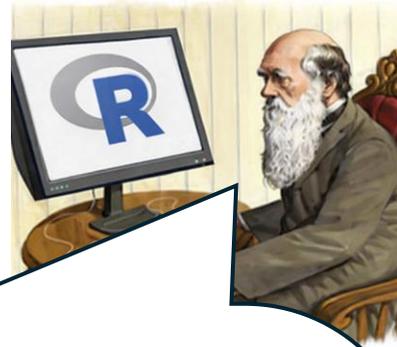
```
median(z) → 0.5362774
for (i in 1:5)
{
survivors=z[z>=median(z)][1:50]
z=sample(survivors,N,replace=TRUE)
}
median(z) → 1.513446
```

This is a «for loop». It only means that we repeat all the code within the curly brackets { } for five times.



Some details of the “code”

Variability among individuals
Differential contribution to successive generations
Mechanism of inheritance

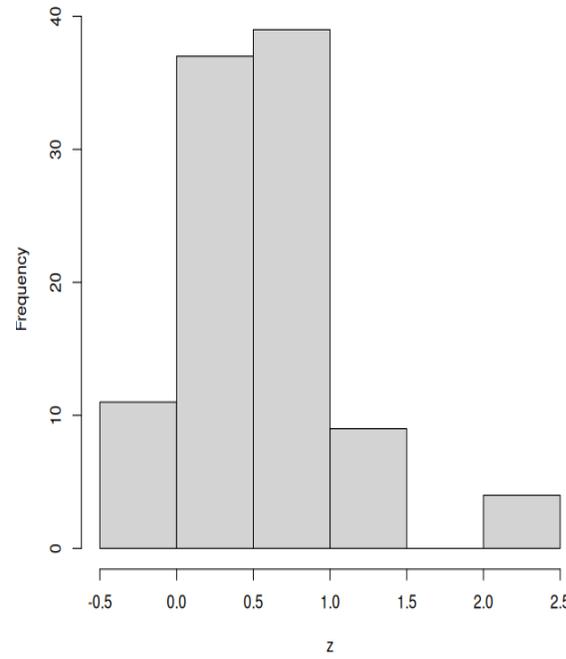
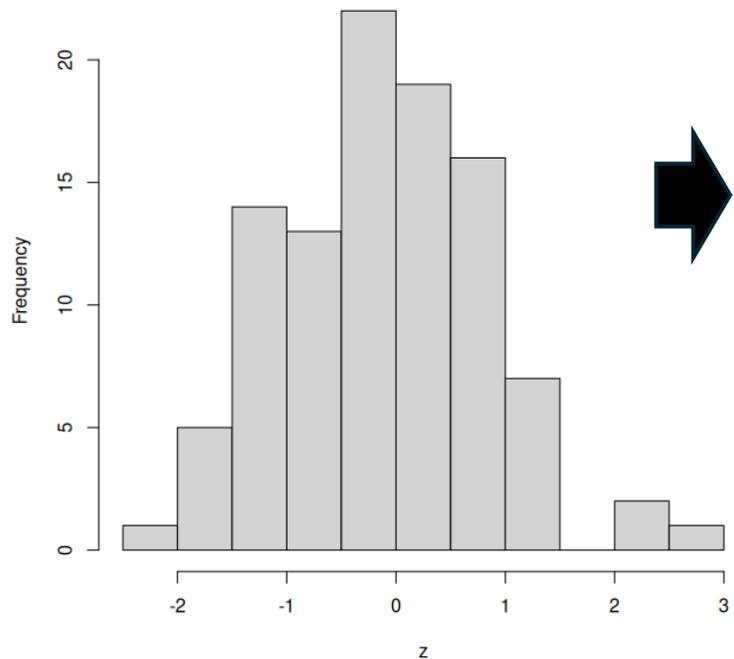
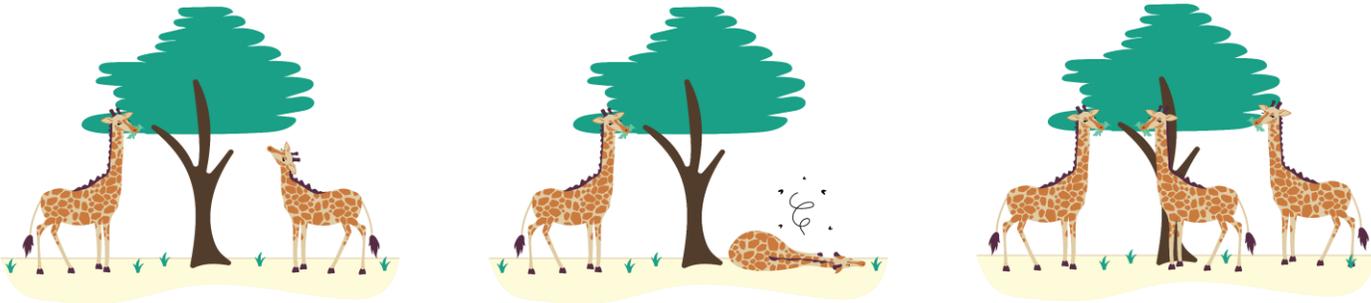


We can iterate this over generations

```
median(z) → 0.5362774  
for (i in 1:5)  
{  
  survivors=z[z>=median(z)][1:50]  
  z=sample(survivors,N,replace=TRUE)  
}  
median(z) → 1.513446
```



This is just to make sure that I sample half the individuals as at some point it might happen that individuals will have the same neck length

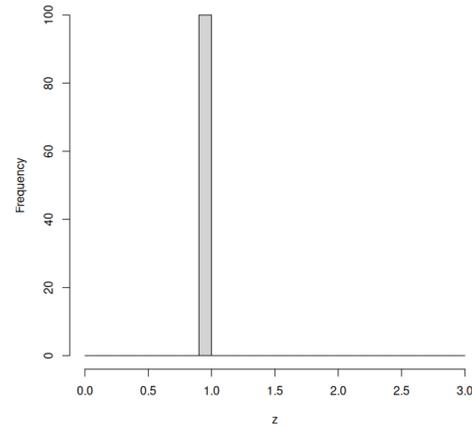
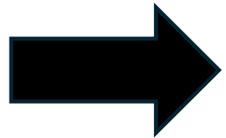
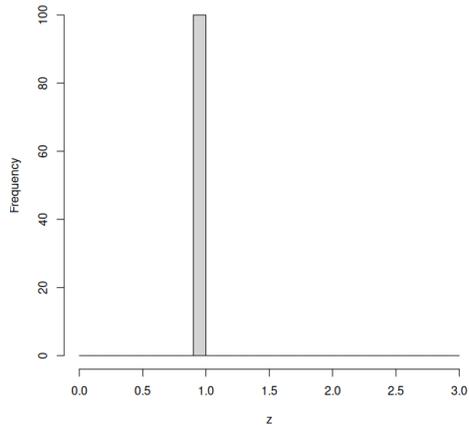
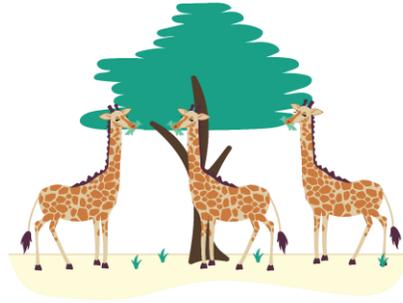
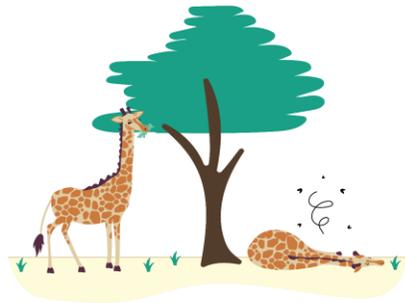
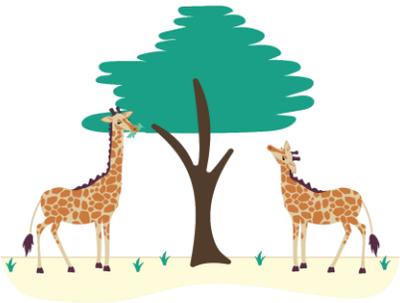


What happens with no variability among individuals?

Variability among individuals

Differential contribution to successive generations

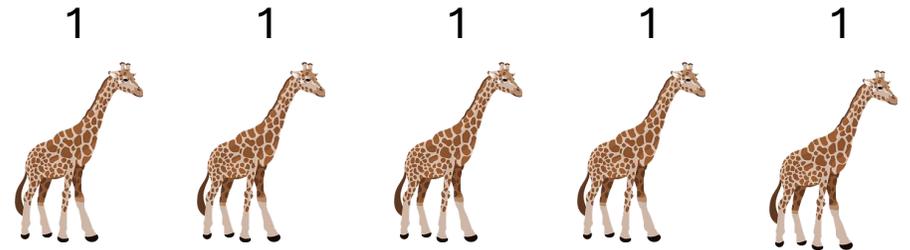
Mechanism of inheritance



Let's give to all giraffes an initial neck long 1

```
N=100  
z=rep(1,N)
```

```
survivors=z[z>=median(z)][1:50]  
z=sample(survivors,N,replace=TRUE)
```

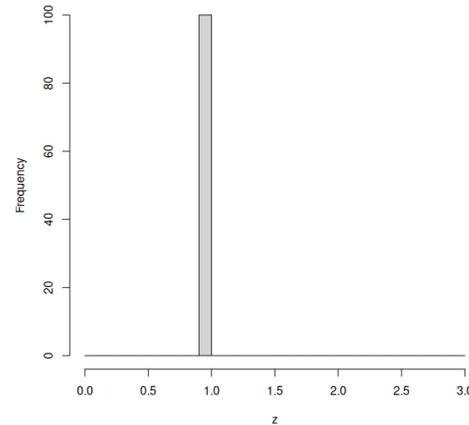
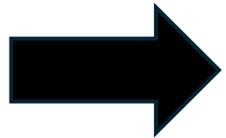
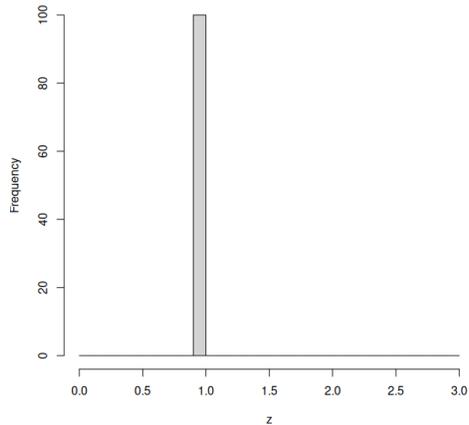
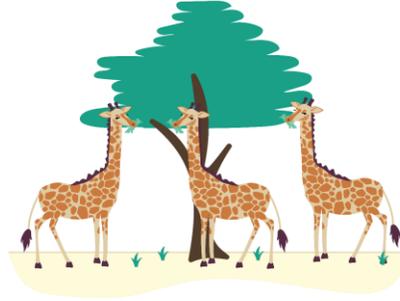
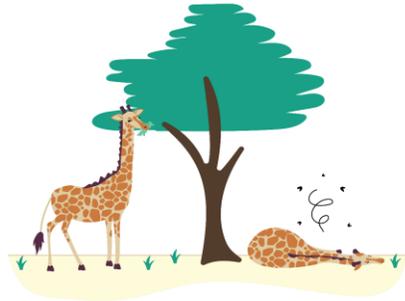
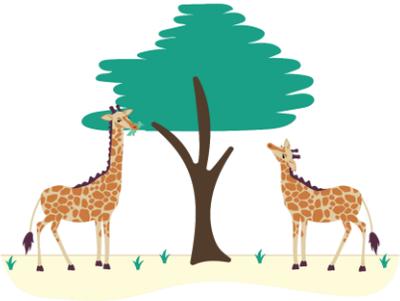
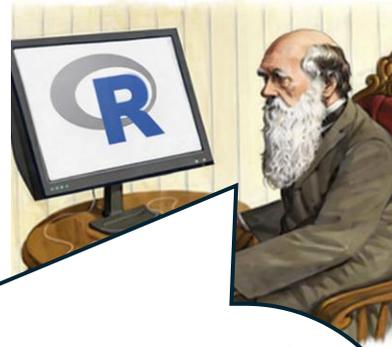


No variability → No evolution!

Variability among individuals

Differential contribution to successive generations

Mechanism of inheritance



Let's give to all giraffes an initial neck long 1

```
N=100  
z=rep(1,N)
```

```
median(z) → 1
```

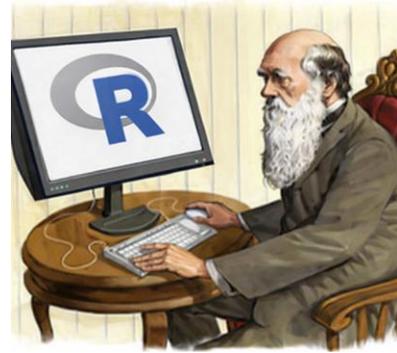
```
survivors=z[z>=median(z)][1:50]  
z=sample(survivors,N,replace=TRUE)
```

```
median(z) → 1
```

Realistic inheritance model

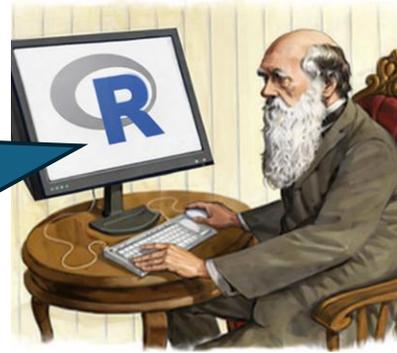
```
N=100  
z=rnorm(N)
```

```
for (i in 1:5){  
  survivors=gametes[z>=median(z)][1:50]  
  parents=survivors  
  gametes=sample(parents,N,replace=TRUE)  
  z=gametes + rnorm(N,sd=0.9)  
}
```



Realistic inheritance model

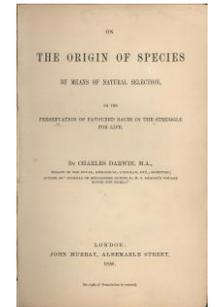
These are just graphical parameters to make nice histograms



```
N=100
z=rnorm(N)
hist(z,breaks=seq(-4,10,0.5),xlim=c(-4,10),lwd = 2,cex.lab =
2,cex.axis = 2)
abline(v = median(z), col = "red", lwd = 3, lty = 2)
median(z)
for (i in 1:3){
survivors=gametes[z>=median(z)][1:50]
parents=survivors
gametes=sample(parents,N,replace=TRUE)
z=gametes + rnorm(N,sd=0.9)
}
hist(z,breaks=seq(-4,10,0.5),xlim=c(-4,10),lwd = 2,cex.lab =
2,cex.axis = 2)
abline(v = median(z), col = "red", lwd = 3, lty = 2)
```

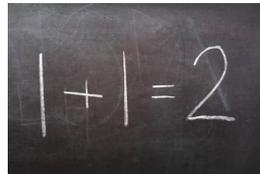
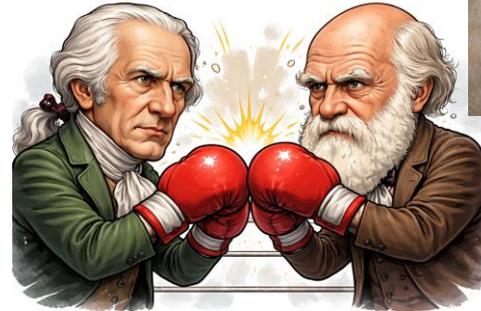
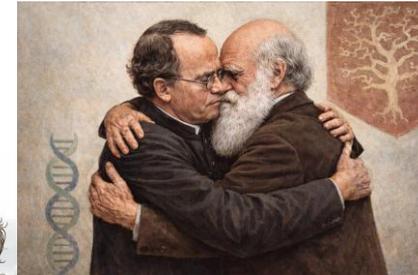
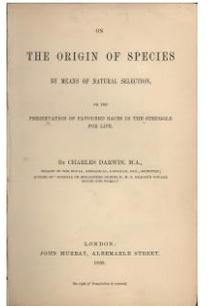

Conclusions

- Modern historical origin of evolutionary thought
- Lamarck
- Darwin and the Origin of Species
- Fundamental principles: variability, differential survival, inheritance
- What Darwin got wrong about inheritance
- Weismann barrier
- Lamarck vs Darwin
 - Empirical evidence
 - From first principles
- Learning vs Evolution
 - Similarities
 - Interactions:
 - When learning helps evolution: Waddington and Baldwin's effect
 - When learning prevents evolution



Next time

- Modern historical origin of evolutionary thought
- Lamarck
- Darwin and the Origin of Species
- Fundamental principles
- What Darwin got wrong about inheritance
- Weismann barrier
- Lamarck vs Darwin
- Empirical evidence
- From first principles
- Learning vs Evolution
- Similarities
- Interactions:
 - When learning helps evolution: Waddington and Baldwin's effect
 - When learning prevents evolution



Geoffrey Hinton,
Nobel in
Physics 2024

