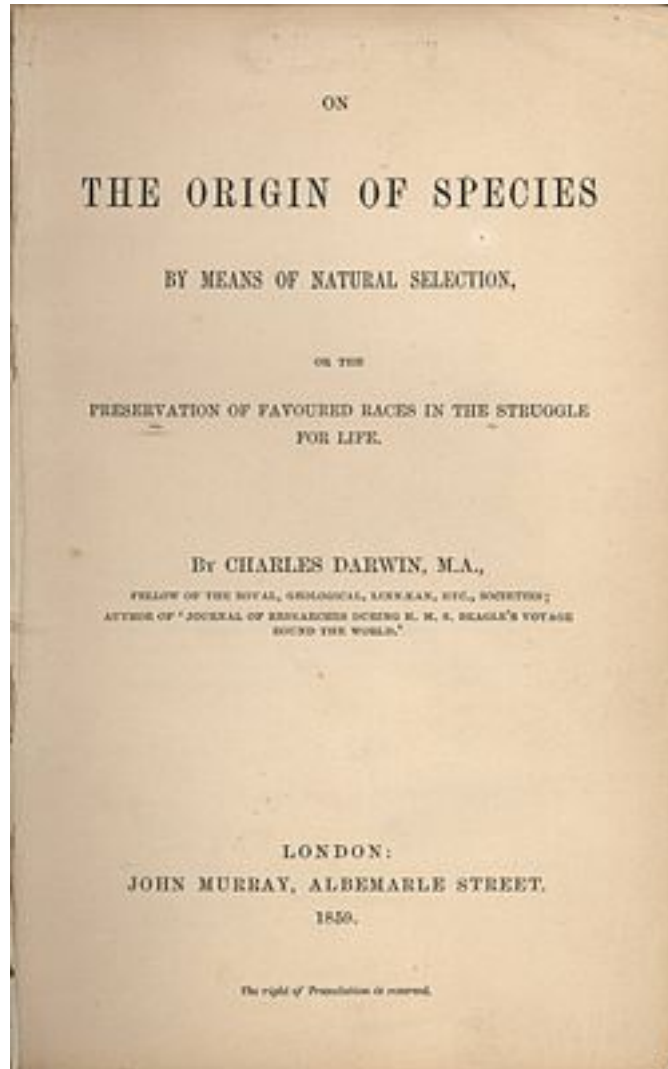


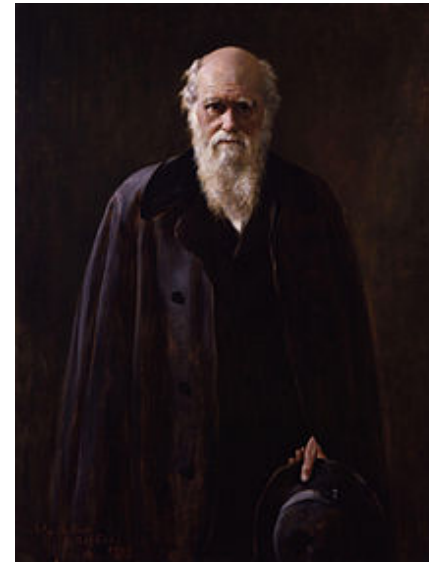
# Sympatric Speciation

# Summary

- Speciation mechanisms: allopatry x sympatry
- The model of Dieckmann & Doebeli
- Sex



Seleção Natural

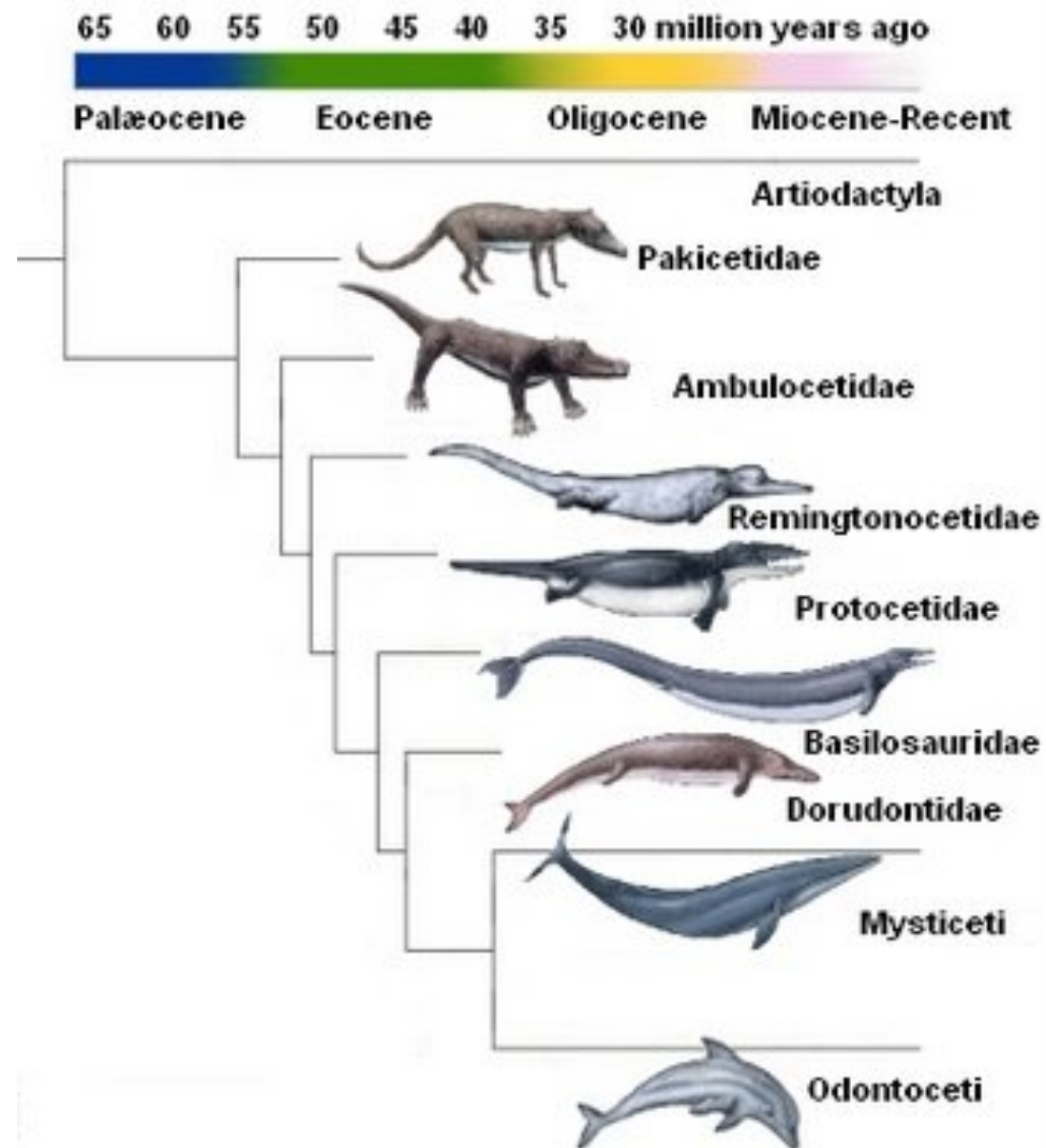


Charles Darwin  
1809-1882

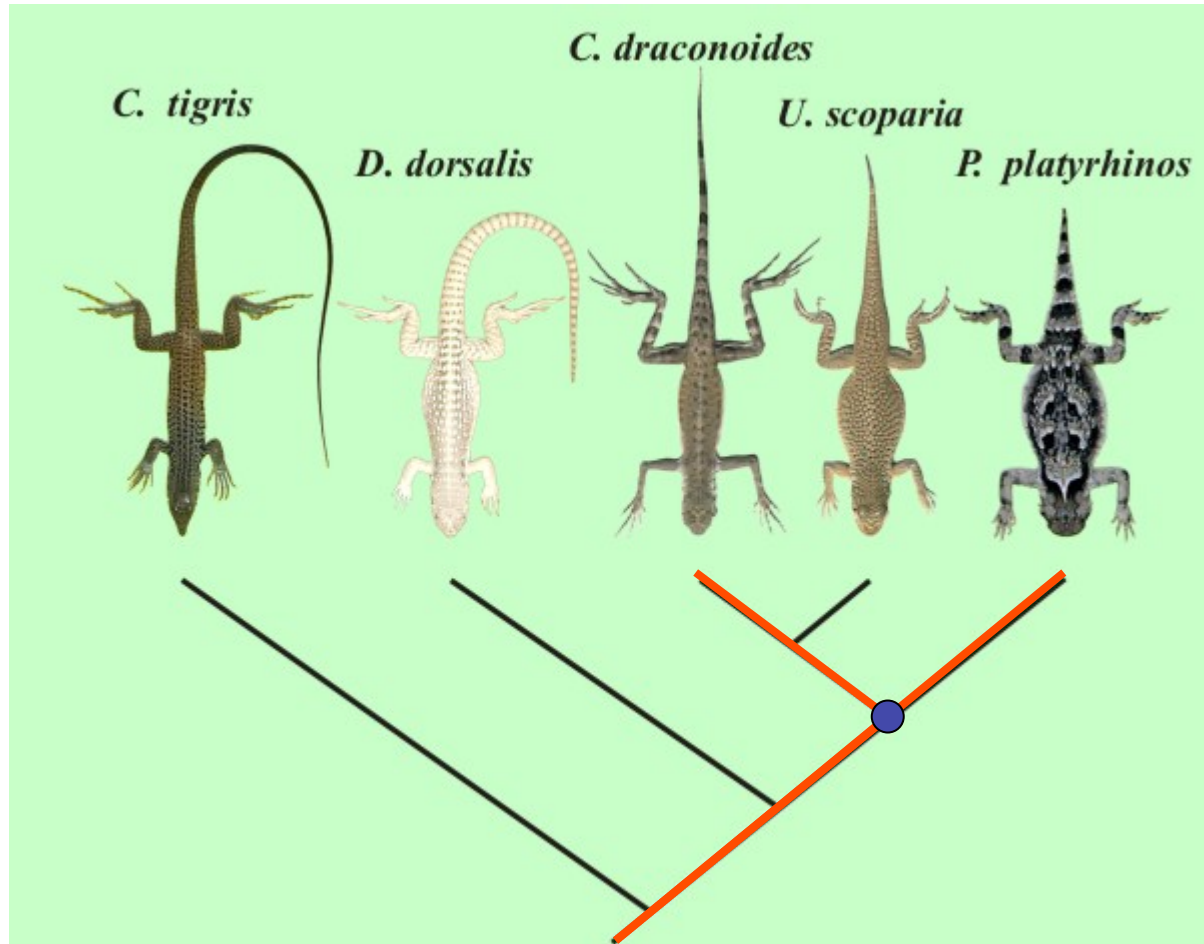


Alfred R. Wallace  
1823-1913

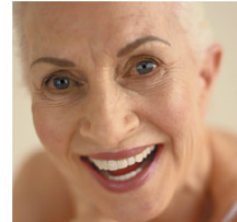
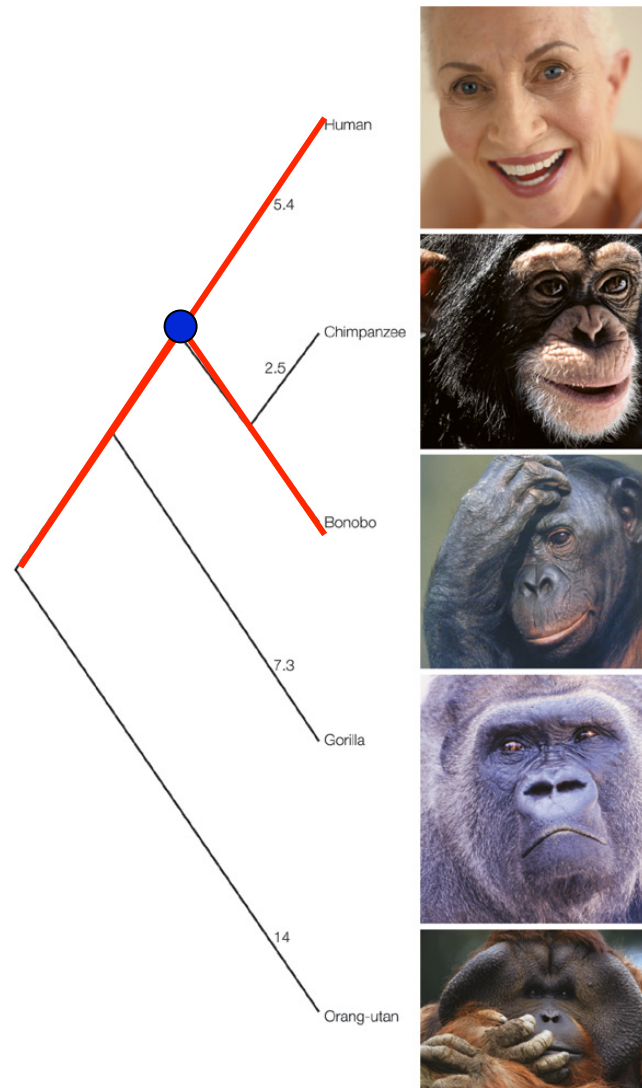
## Evolution by natural selection



# Evolution versus Speciation

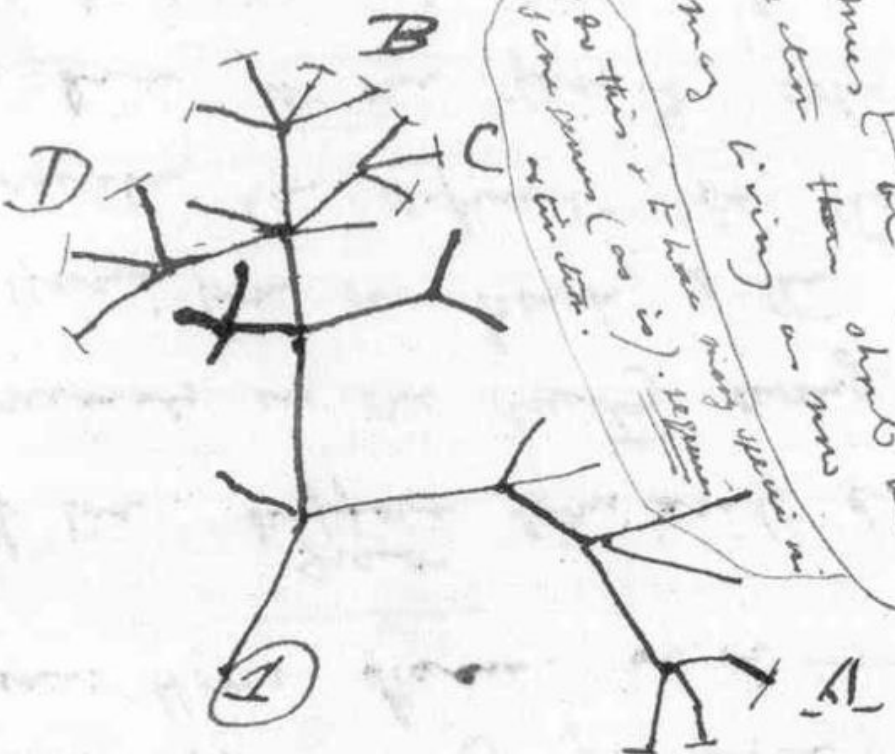


# Speciation

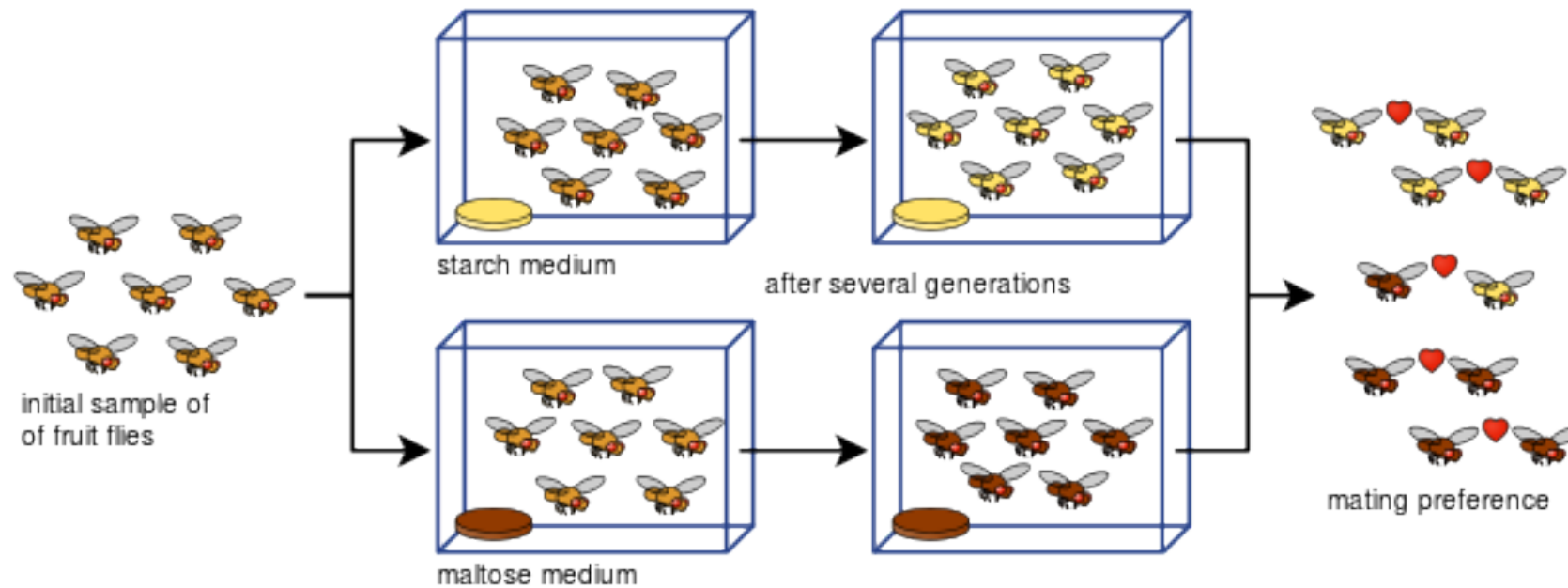


36

I think



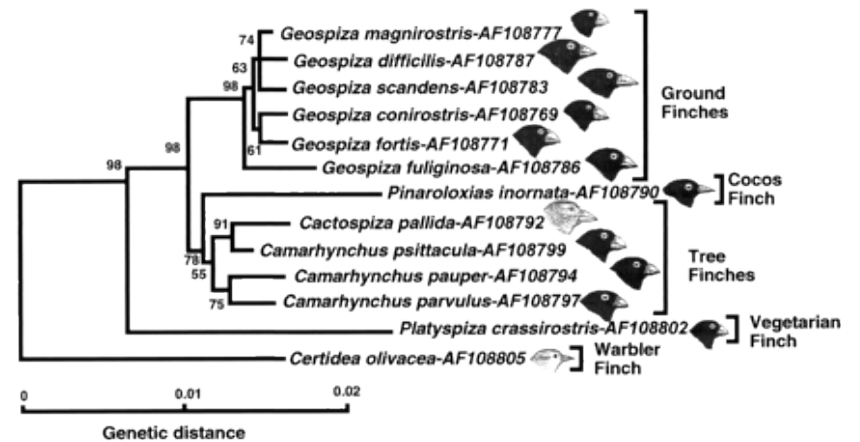
# Allopatry: the basic mechanism of speciation



***Geographic isolation leads to Reproductive isolation.***



# Classic example: Darwin finches on the Galápagos islands



Sato et al, PNAS 1998

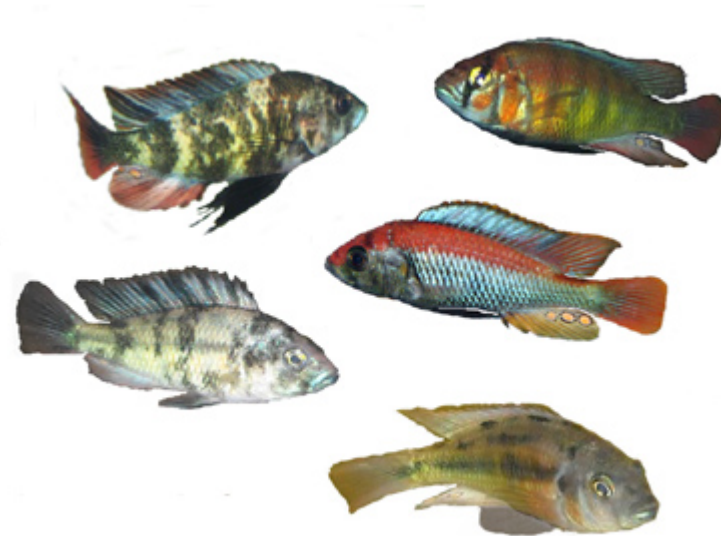


T=ground, A=tree, V=vegetarian, C=singer

## Example: cichlid fishes in lake Victoria (Tanzania, Africa)



There are approximately 400 species of cichlids with a common ancestor that lived about 14 thousand years ago.



No evident geographic separation.

**Is speciation possible without geographic isolation?**

# **On the origin of species by sympatric speciation**

**Ulf Dieckmann & Michael Doebeli**

*Adaptive Dynamics Network, International Institute for Applied Systems Analysis,  
A-2361 Laxenburg, Austria*

*Zoology Institute, University of Basel, Rheinsprung 9, CH-4051 Basel, Switzerland*

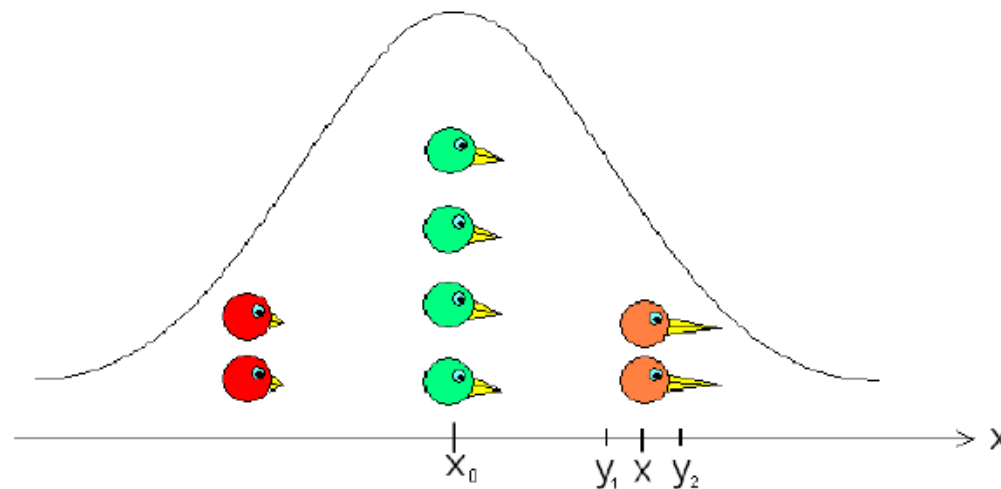
NATURE | VOL 400 | 22 JULY 1999 | [www.nature.com](http://www.nature.com)

# Competition and Disruptive Selection

$z$  = trait associated with resources  $\rightarrow$  beak size

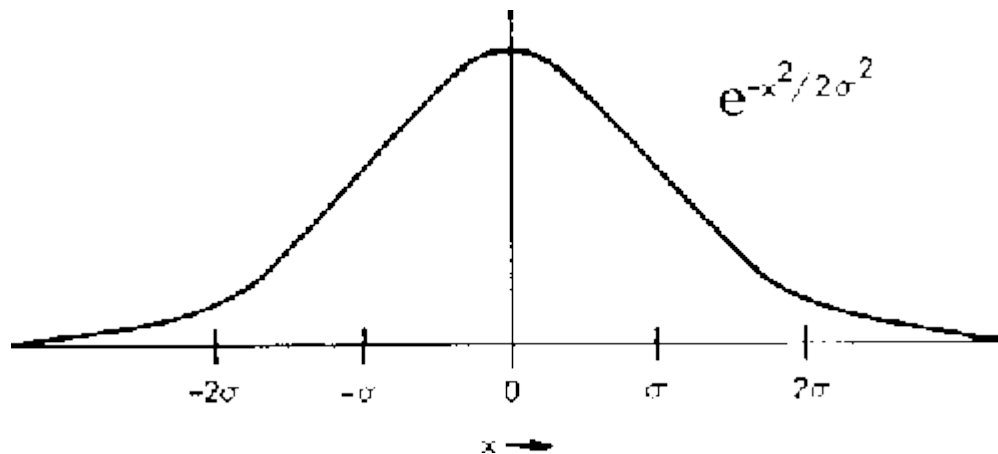
resources are seeds, whose quantity depends on seed size

birds with similar beak size compete for seeds



Resources are finite and its distribution dictates how many birds of each beak size are possible:

$$K(z) = K_0 \exp\left[-\frac{z^2}{2\sigma_k^2}\right]$$

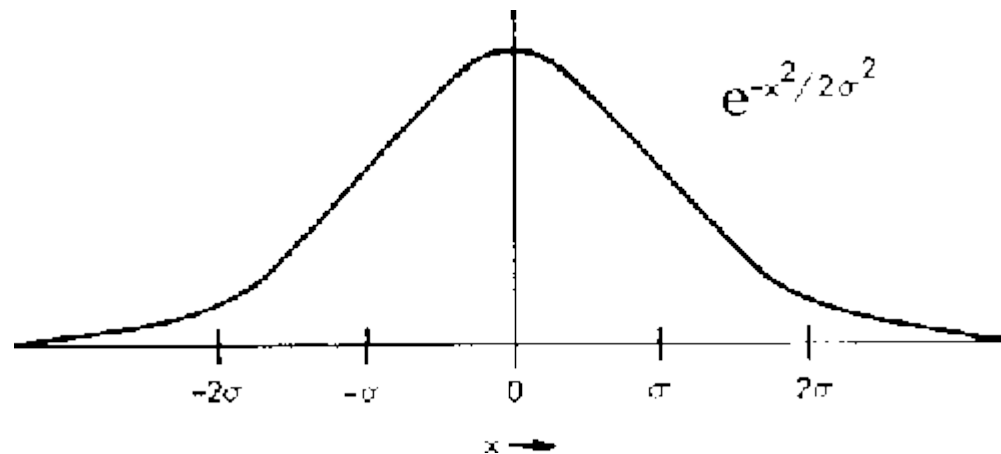


$z=0$  is the beak size corresponding to the most abundant seed



**Competition:** individuals with similar phenotypes compete. The strength of competition is modeled by a Gaussian function:

$$C(z, w) = \exp\left[-\frac{(z - w)^2}{2\sigma_c^2}\right]$$



birds with beak sizes in the interval  $z - \sigma_c$  ---  $z + \sigma_c$  compete significantly with  $z$

**Single population with beak size  $z$ :**

$$\frac{dN(z,t)}{dt} = rN(z,t) \left( 1 - \frac{N(z,t)}{K(z)} \right)$$

$$N(z,t) = \frac{N(z,0) K(z)}{N(z,0) + [K(z) - N(z,0)] e^{-rt}} \rightarrow K(z)$$



What happens if a **mutant** with beak size  **$w = z + \delta z$**  appears?

$$\frac{dN(w,t)}{dt} = rN(w,t) \left( 1 - \frac{C(z,w)K(z)}{K(w)} \right) \equiv R N(w,t)$$

$$C(z,w) = \exp \left[ -\frac{(z-w)^2}{2\sigma_c^2} \right] = \exp \left[ -\frac{\delta z^2}{2\sigma_c^2} \right] = 1 - \frac{\delta z^2}{2\sigma_c^2}$$

$$R \approx r \left( 1 - \frac{K(z)}{K(w)} \right)$$

**As expected, if  $K(w) > K(z)$  the effective growth rate is  $R > 0$  and the mutant grows and invades the population.**

**If  $K(w) < K(z)$  then  $R < 0$  and the population of mutants decreases.**

**The result is that a small mutation rate makes the population evolve towards the maximum carrying capacity  $z=0$ , where more food is available.**

**What happens when the population gets there?**

$$z = 0$$

$$w = 0 + \delta z = \delta z$$

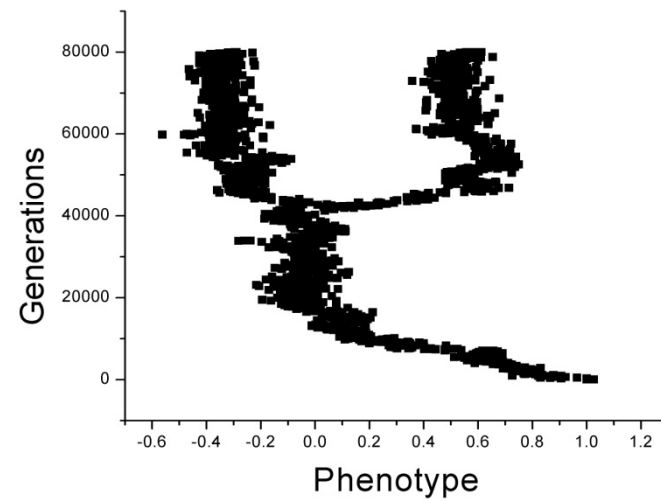
$$R = r \left( 1 - C(0, \delta z) \frac{K(0)}{K(\delta z)} \right) = r \left[ 1 - e^{-\delta z^2 / 2 \sigma_c^2} e^{\delta z^2 / 2 \sigma_k^2} \right]$$

Therefore, if

$$\sigma_k > \sigma_c$$

$R > 0$  and the **mutants**  $\mathbf{w} = \mathbf{0} + \delta \mathbf{z}$  **AND**  $\mathbf{w} = \mathbf{0} - \delta \mathbf{z}$  both grow and invade the  $z = 0$  phenotype!

If competition is too strong, it might be advantageous to have a more extreme phenotype, where there are less resources, but also less competition:



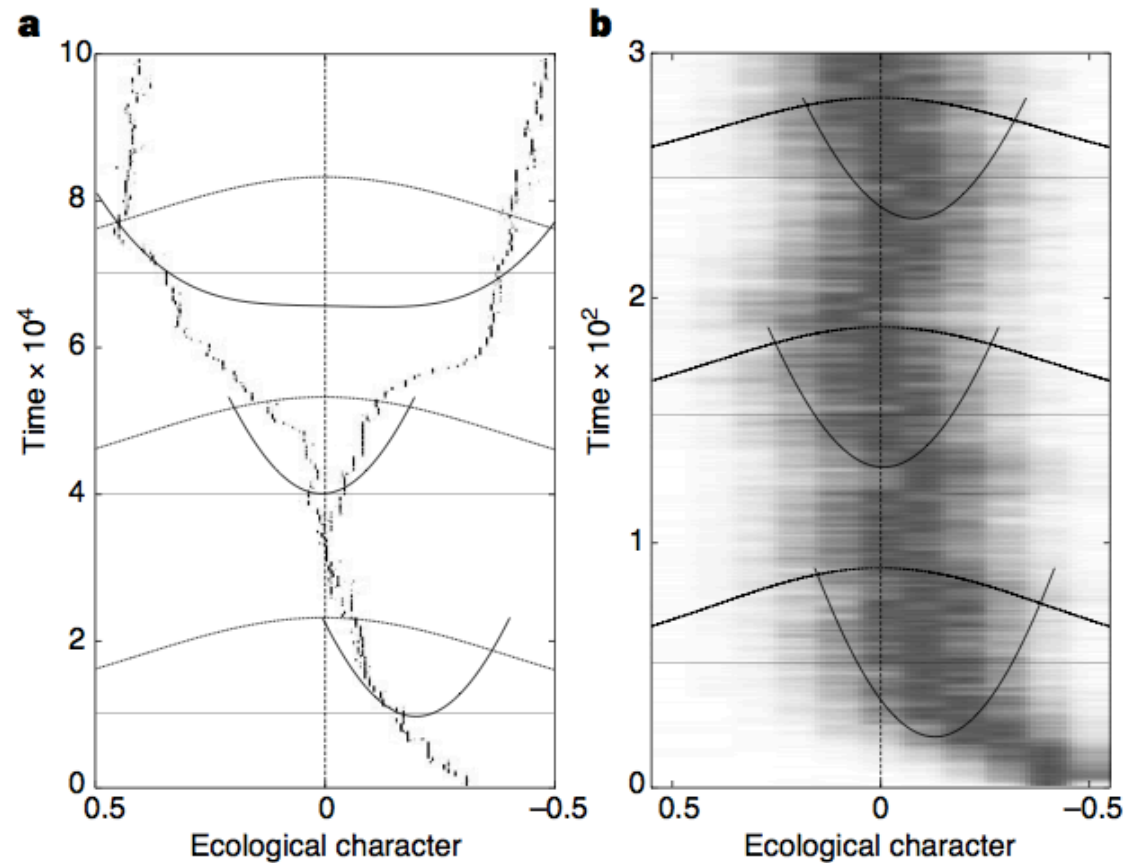
# Asexual Individual Based Model

- each individual has phenotype  $-1 < x < +1$
- reproduction occurs at rate  $r$
- *death rate is*

$$\frac{1}{K(x)} \sum_y N(y, t) C(x, y)$$

- offspring inherit the parent phenotype, but mutations occur with probability  $\mu$ . In that case  $x$  is chosen from a normal distribution with average  $x$  and variance  $\sigma_\mu = 0.05$ .

$$r=1, K_0=500, \sigma_k=1, \mu=0.001$$



**Figure 1** Convergence to disruptive selection **a**, Evolutionary branching in the individual-based asexual model: at the branching point  $x_0 = 0$ , the population splits into two morphs. Three insets show fitness functions (continuous curves) generated by the ecological interactions at different points in time (indicated by horizontal dotted lines). Selection changes from directional to disruptive when evolution reaches  $x_0$ . The resource distribution  $K(x)$  has its maximum at  $x_0$  and is shown for comparison (dashed curve). **b**, As in **a**, but with multilocus genetics for the ecological character and random mating. Shading represents phenotype distributions (5 diploid and diallelic loci result in 11 possible phenotypes). Despite disruptive selection at the branching point (see insets), branching does not occur.

# Sexual Model

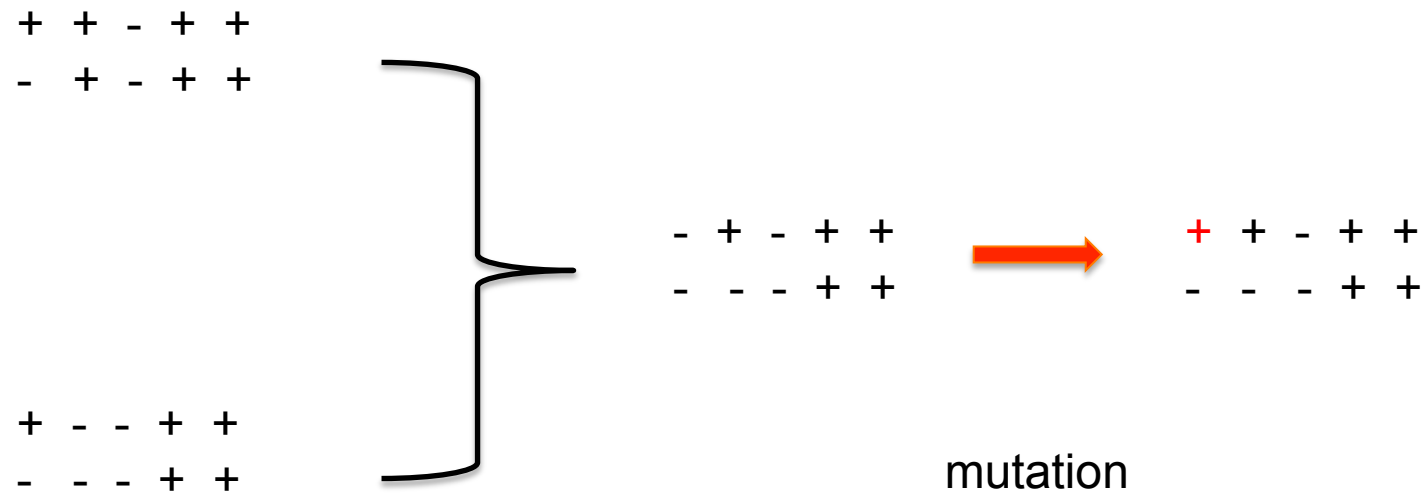
Ecological character (beak size) is attributed according to 5 diploid biallelic loci

$$\begin{array}{ccccc} + & + & - & + & + \\ - & + & - & + & + \end{array} \quad x = (7-3)/10 = 4/10 = 0.4$$

$$\begin{array}{ccccc} + & - & - & + & + \\ - & - & - & + & + \end{array} \quad x = (5-5)/10 = 0$$

$$\begin{array}{ccccc} - & - & - & + & - \\ - & - & - & + & + \end{array} \quad x = (3-7)/10 = -4/10 = -0.4$$

Reproduction:



Result from simulations: population does not branch.

Intermediate phenotypes keep showing up.



# Sexual Model with assortative mating

Besides the ecological character, two other genetic traits are attributed to the individual, each with 5 diploid biallelic loci:

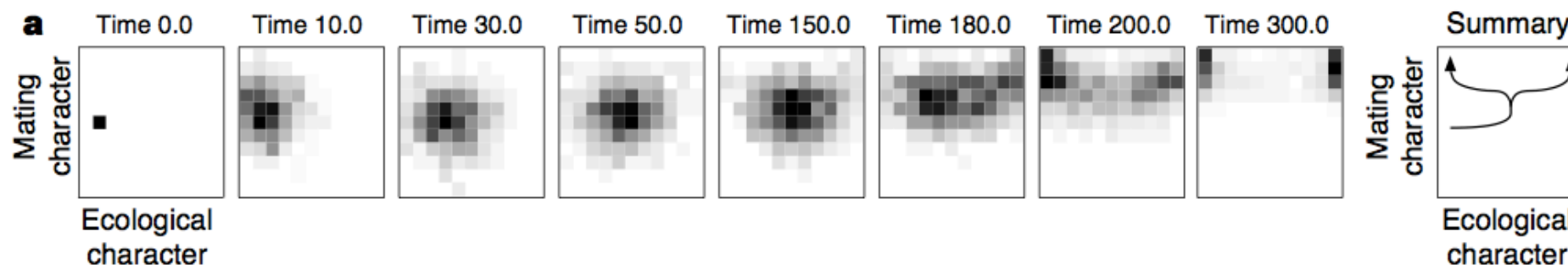
+ + - + +  
- + - + +     x = ecological trait

+ - - + +  
- - - + +     m = mating preference trait:

-1 = mate with opposite  
0 = no preference  
+1 = mate with similar

- - - + -  
- - - + +     n = neutral trait (color of feathers)

If mating preference refers to the ecological trait, the dynamics leads to the fixation of  $m$  close to +1, i.e., to the evolution of positive assortativity for individuals with similar ecological character. This avoids the mixture of extreme phenotypes and results in disruptive selection as in the asexual model.



If preference is with respect to the neutral character (color of feathers), the dynamics still leads to the evolution of positive assortativity, mating with individuals with similar neutral character.

The population splits in two groups according to the neutral character. However, each group also has a different ecological character: blue feathers go with small beak and red feathers with large beak (or vice versa). The time it takes for splitting, however, is almost 10 times larger.

