Evolution des systèmes de reproduction chez les escargots

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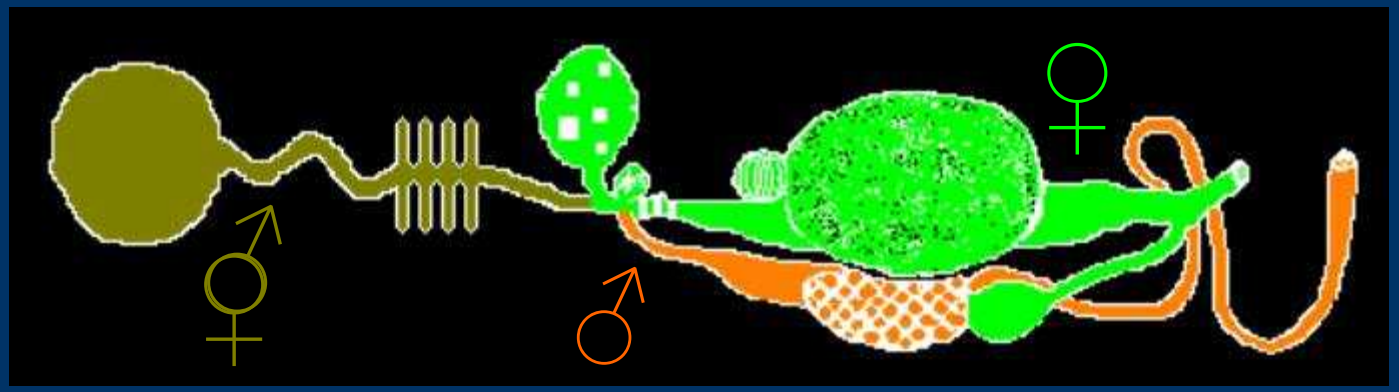
Hermaphroditism

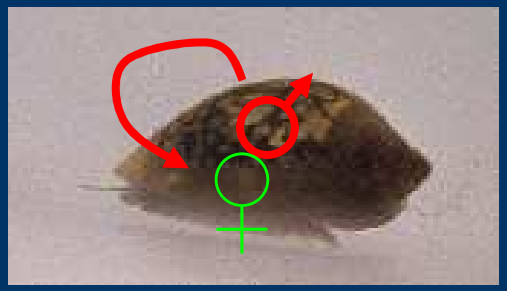


Pulmonate reproductive anatomy

A variety of possible mating systems

Outcrossing

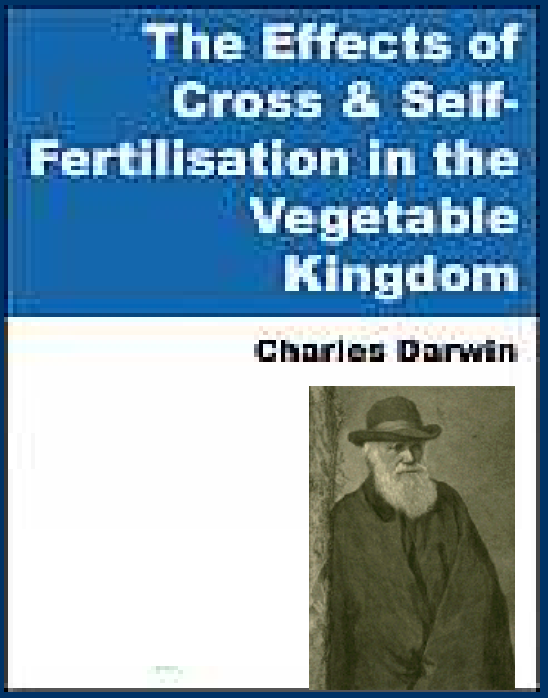
Selfing

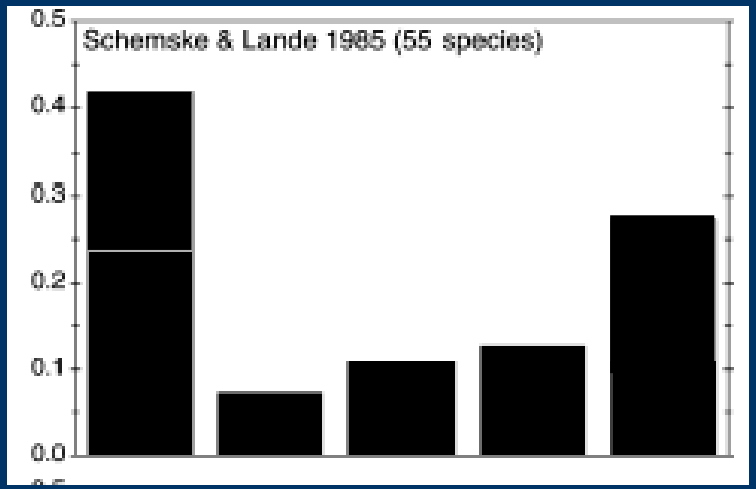


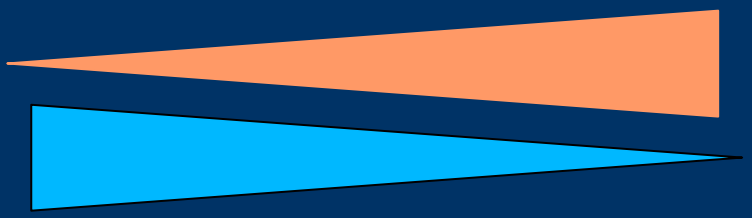
Mating strategies are diverse

- Darwin : Plants evolve specific strategies to control selfing rates : eg self-incompatibility, anther-stigma distance, etc

- Inbreeding depression is a major selective force against selfing







inb. depression δ

selfing rate s

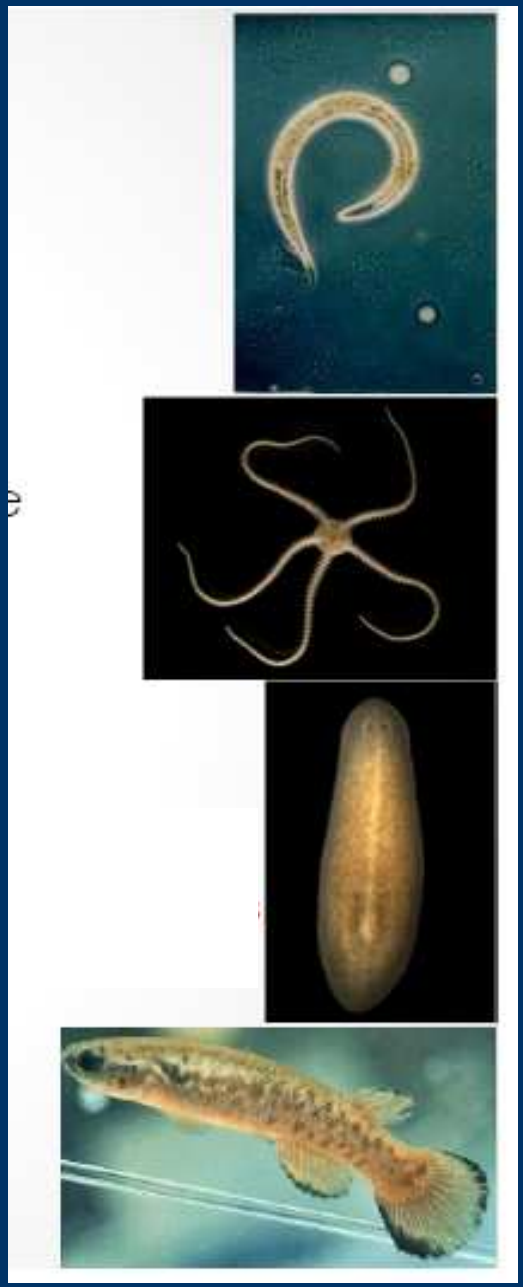
Hermaphroditic animals have been less well studied

Yet they are in fact very common

Freshwater snails (Pulmonates)
= good model systems

Physa acuta

Bulinus truncatus

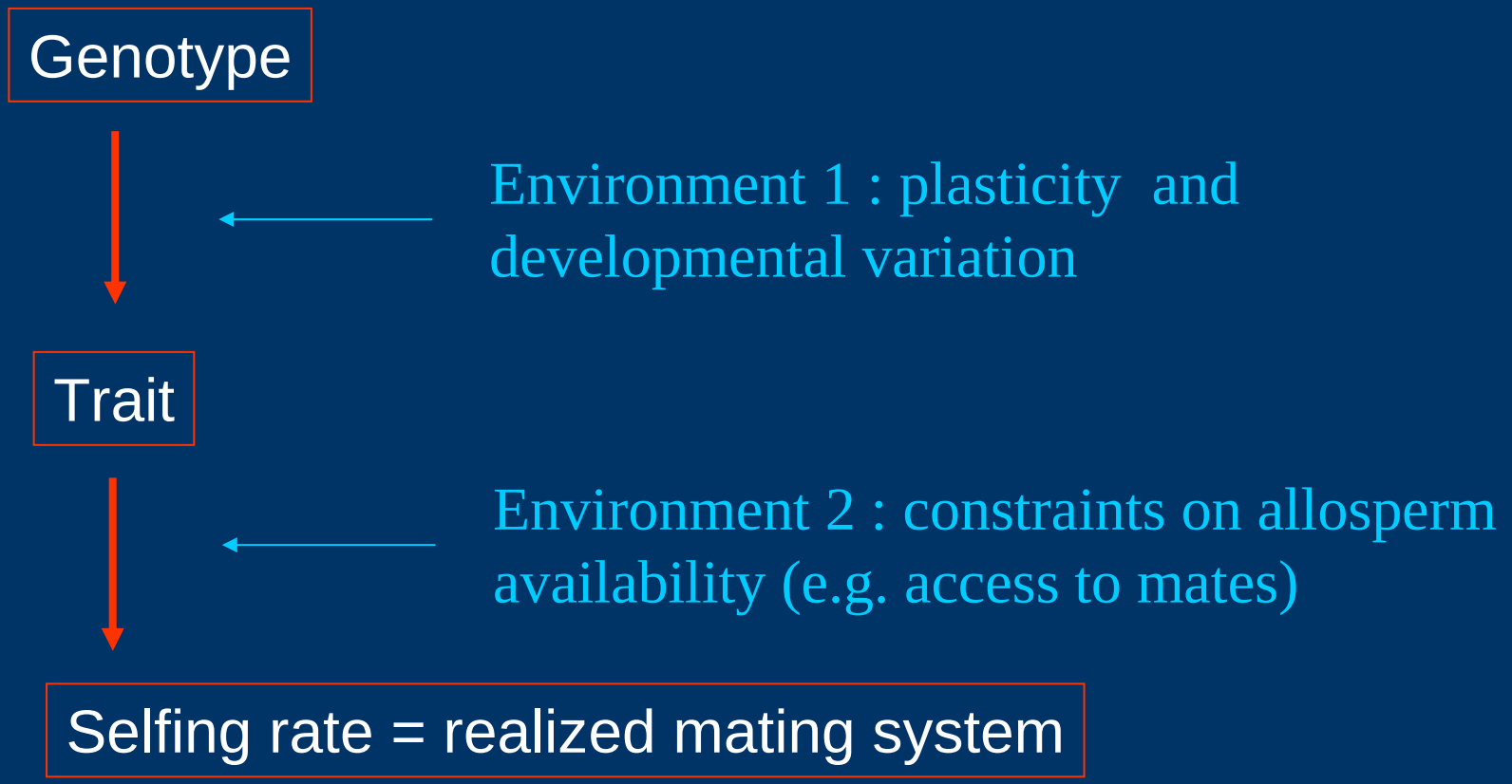


Empirical issues

-Is there variation in reproductive systems in these species ?

- To what extent can animals control their selfing rate and through what traits ? Are these traits genetically variable and can they evolve ?

Selfing rates : two layers of environment, one layer of genetics

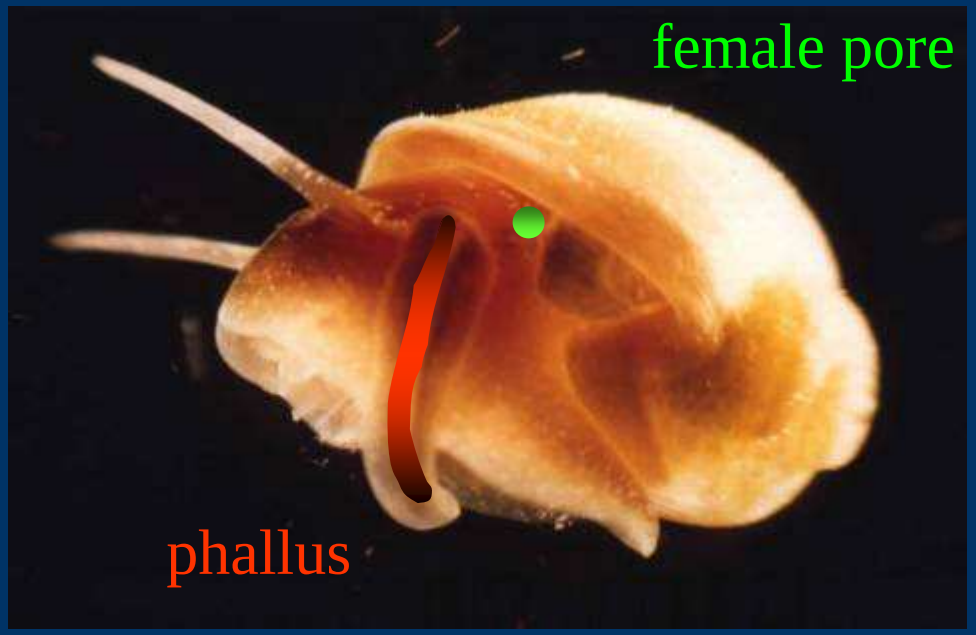


Bulinus truncatus

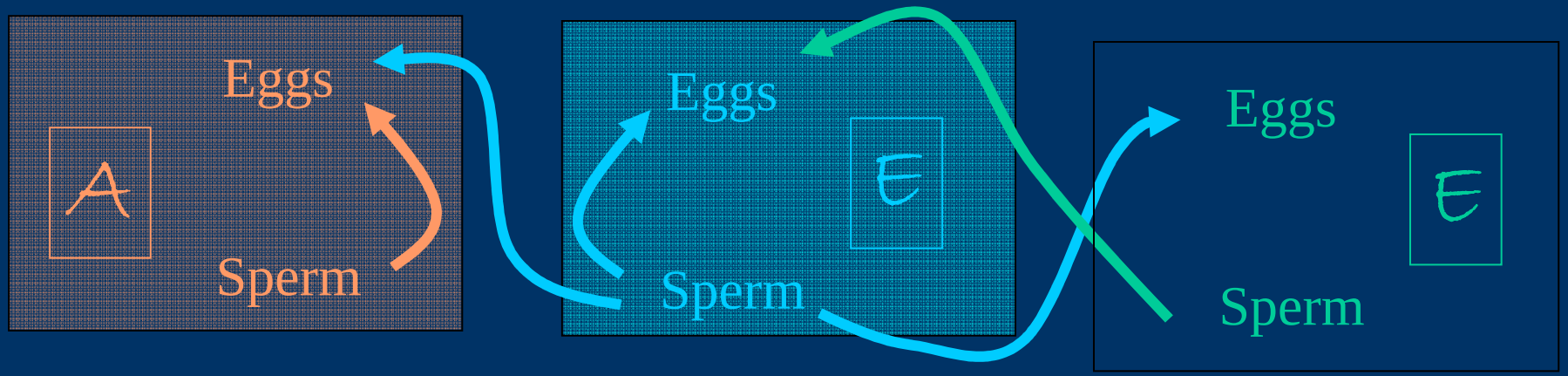
Preferential selfer

Two hermaphroditic morphs

- Euphallics (regular)
- Aphallics (without phallus)



Both morphs can self and cross-fertilize; allosperm comes only from E

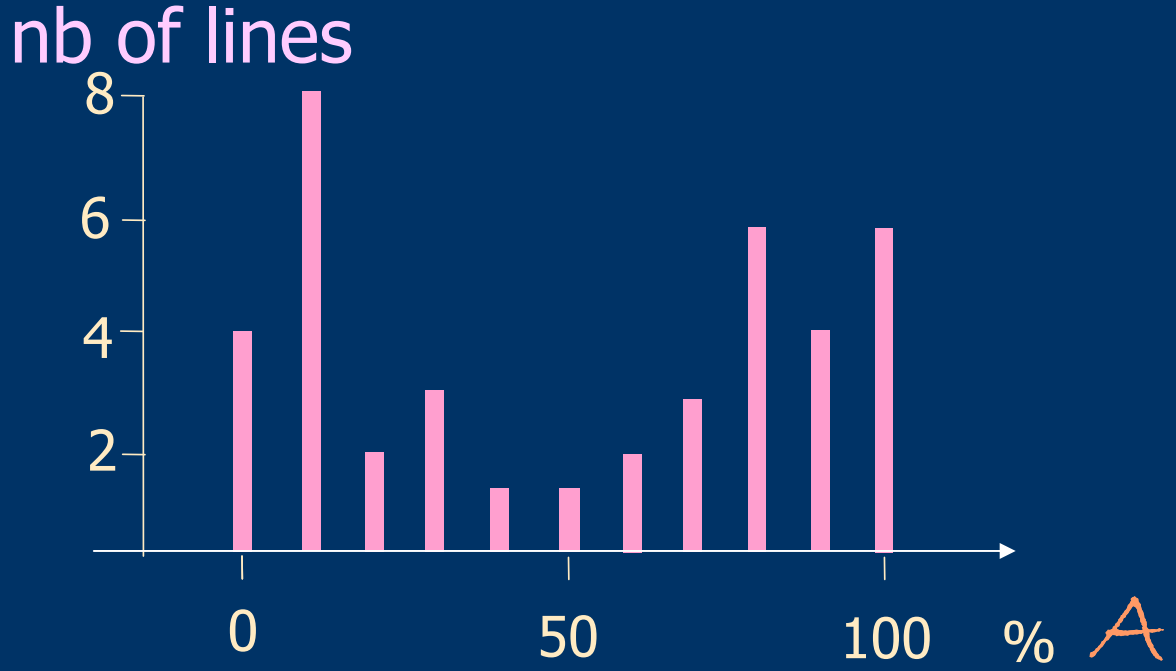


Quantitative genetic variation of aphally

- Is the inheritance of aphally Mendelian ?
- 40 Inbred lines (>14 gen enforced selfing) from 4 pops in Niger

VE : two genetically identical ind can have different morphs

Threshold trait : lines differ in their %A but all values are possible in [0,100]



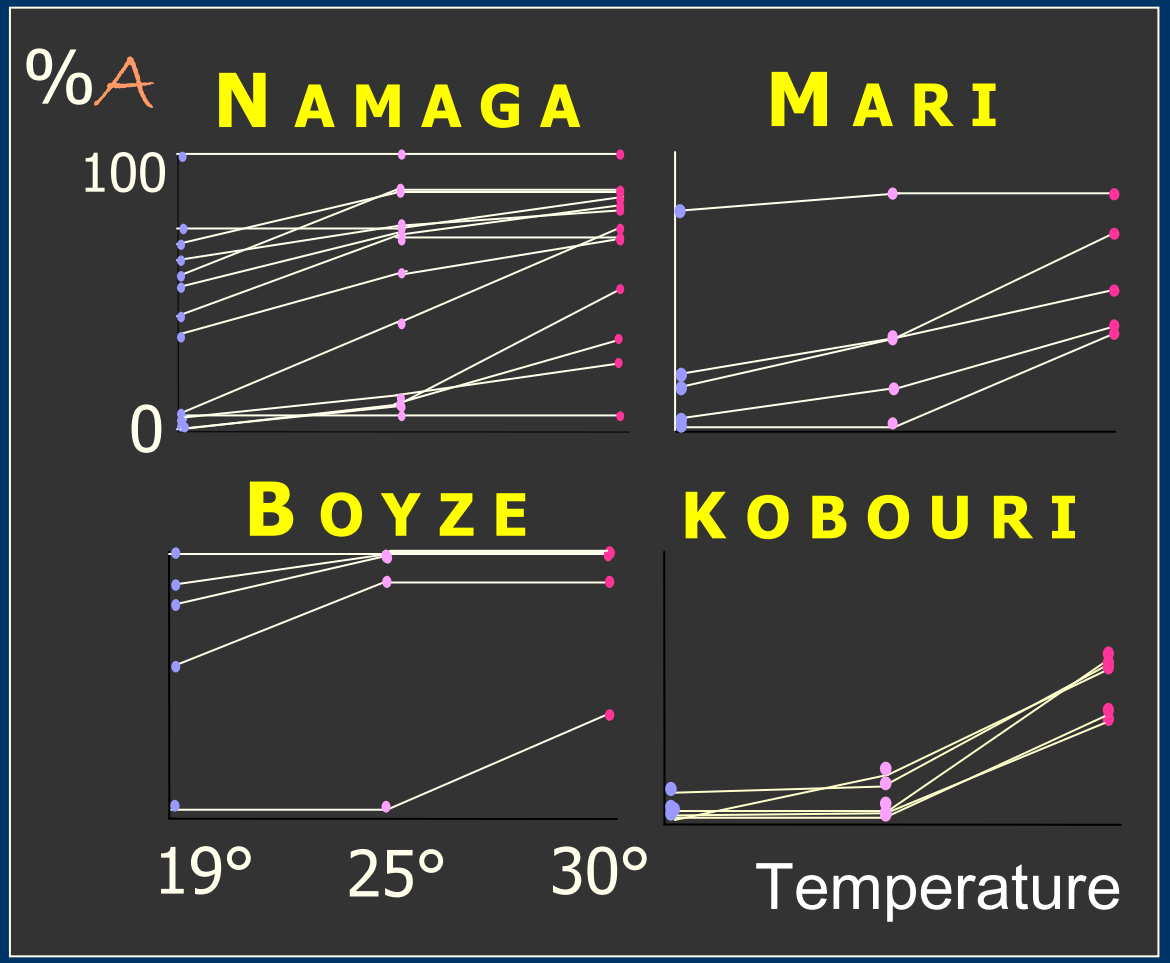
Pop	H^2
Namaga	0,6
Mari	0,8
Boyze	0,5
Kobouri	0

Lots of variation within most pops

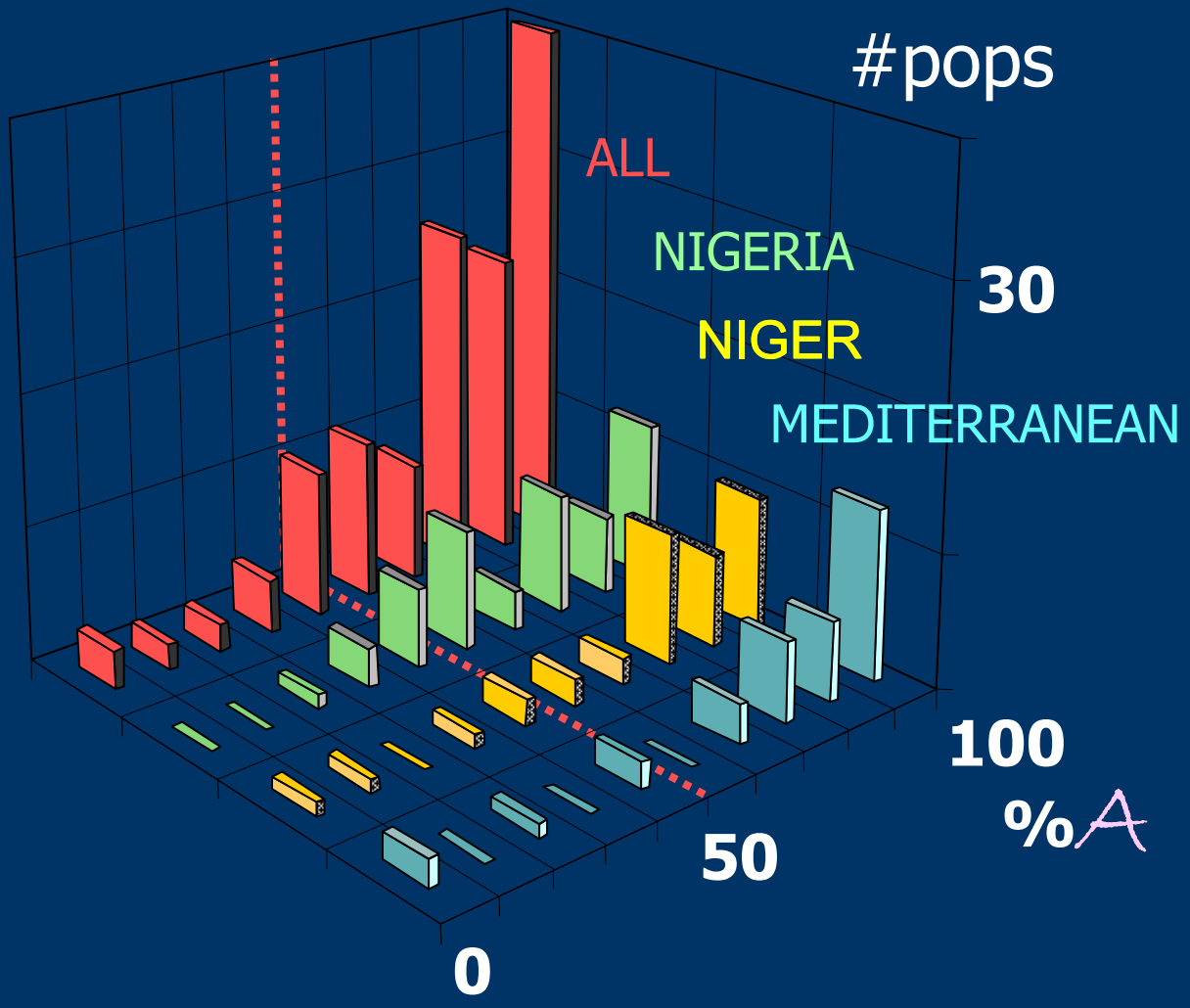
Thermal responses of aphally

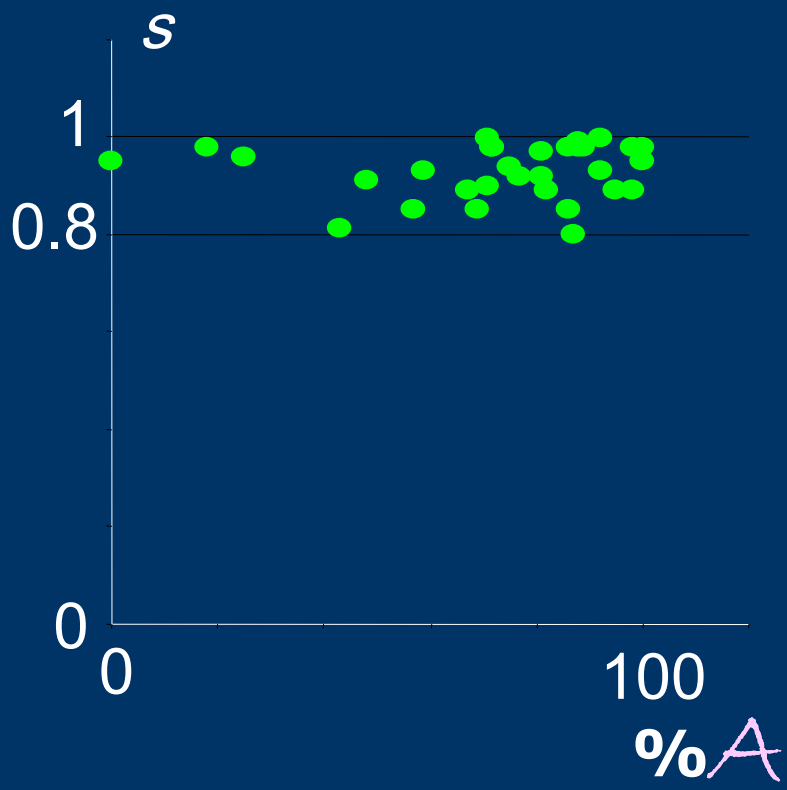
Plasticity : The % A increases with temperature

Variation in reaction norms among lines :



How is aphally related to the selfing rate ?



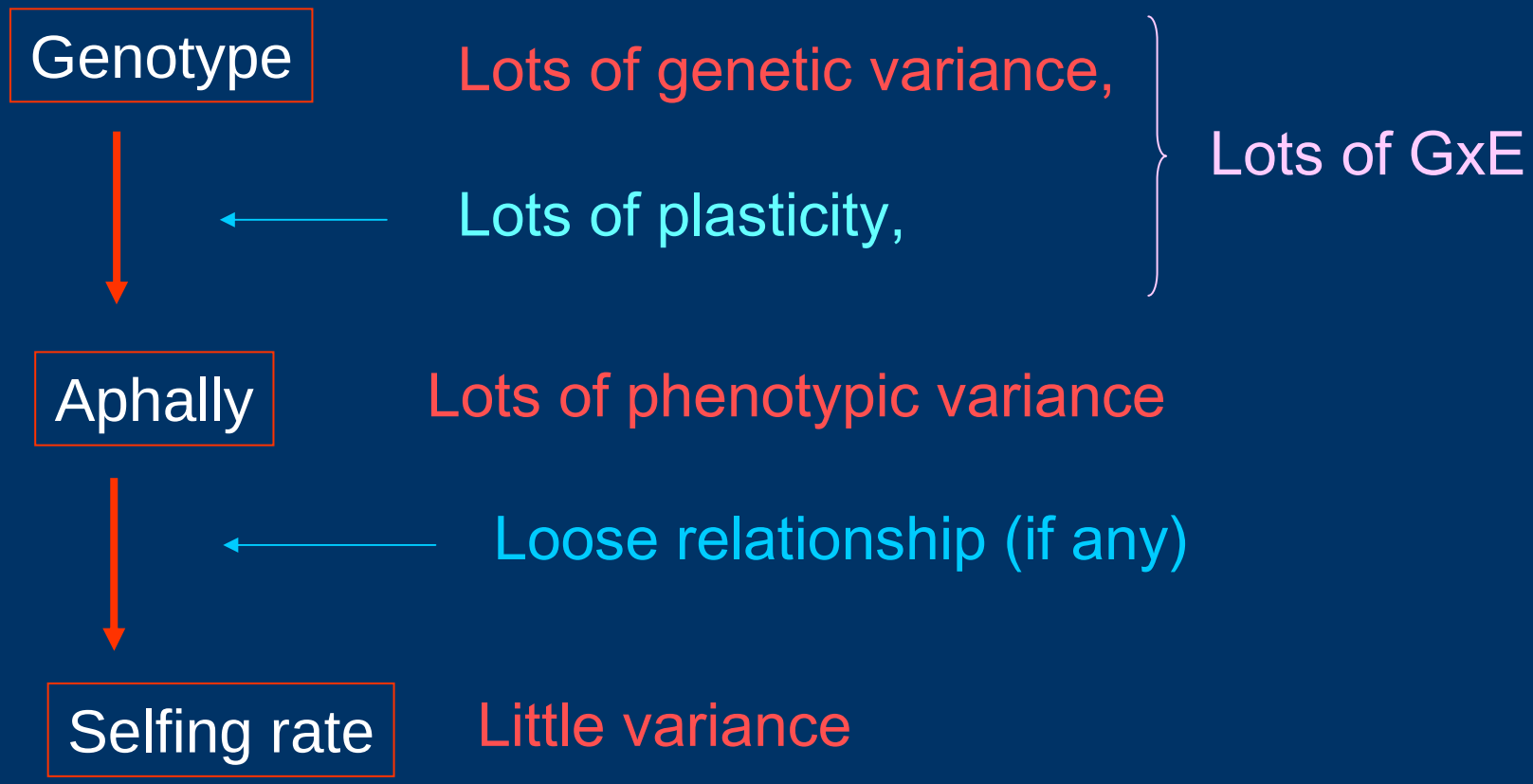


Many populations are obligate selfers (100% A implies s=1)

All pops 0.8 < s < 1

No correlation with % A

Aphally in Bulinus truncatus



Selfing may have evolved first (e.g. through behavioral acceptance of allosperm) then driven the evolution of aphally rather than the reverse !

Physa acuta

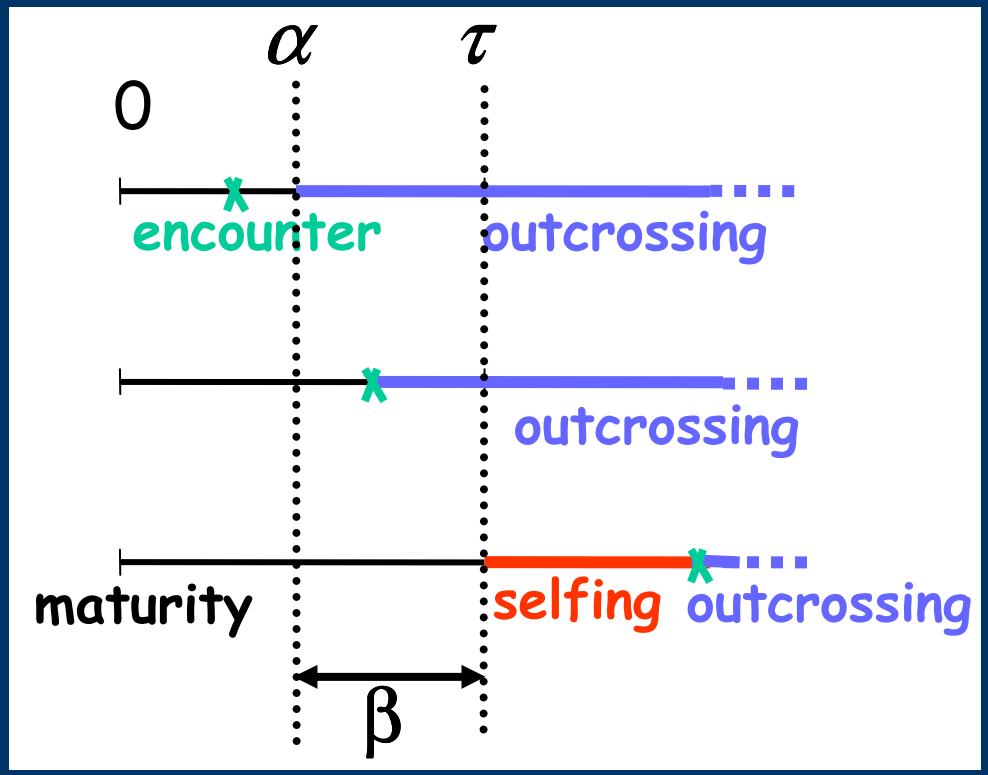
- Preferential outcrosser
  s=0.1

- Large depression
  δ = 0.9

- No sexual dimorphism

- Hypothesis : uses selfing only as a last chance of reproducing when there are no mates… = reproductive assurance

The waiting time model



abundant mates:
optimal age at first reproduction α

no (or rare) mates
waiting time β before selfing

$$\tau = \alpha + \beta$$

baseline time

additional delay to limit selfing

Theoretical Results : optimal waiting times

α baseline time

β additional delay when mates are absent

$(1/m) - (1/k)$

$$\frac{e}{m\,(m+e)}\;\frac{(2\,\delta - 1)}{2(1-\delta)}$$

↘ with mortality m

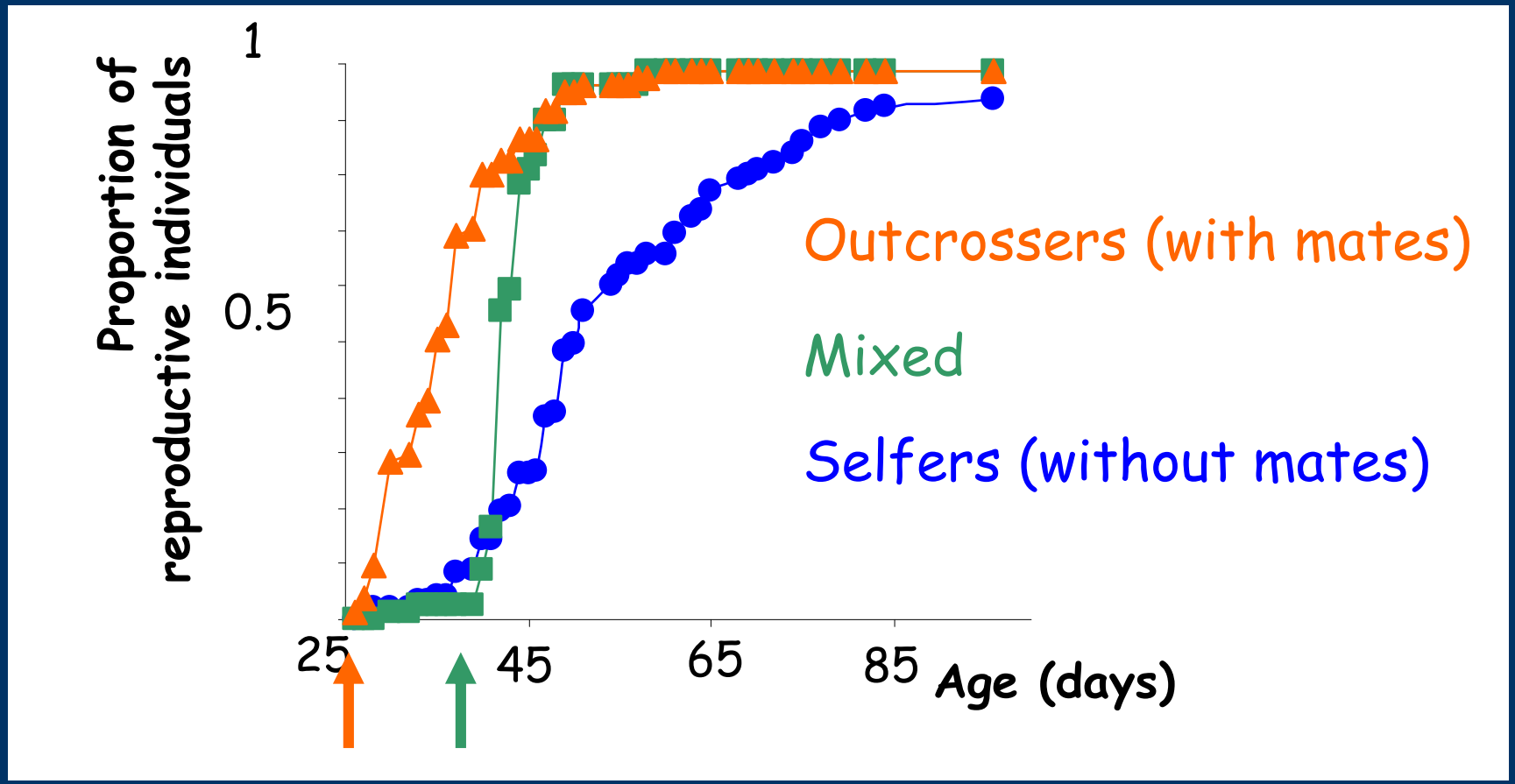
↗ with reallocation efficiency k
(reallocation from early to late reproduction)

↘ with mortality m

↗ with encounter rate e

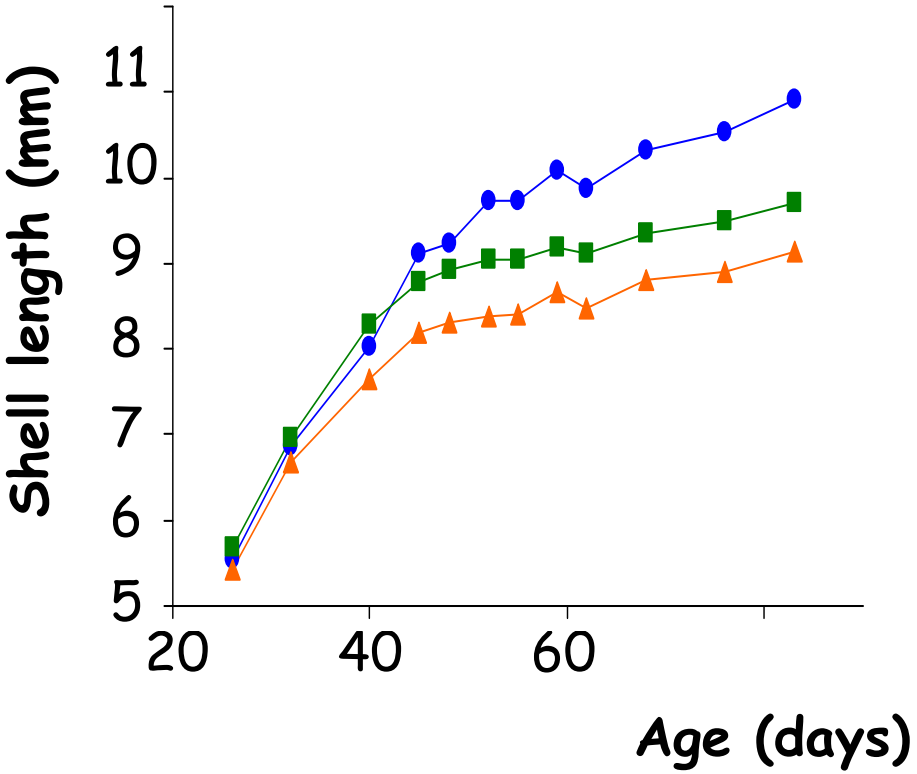
↗ with inbreeding depression δ

Data



β =2 weeks

Delayed benefits of waiting behavior in selfers



Selfers reproduce later but grow bigger and survive longer

Comparison between model and data, heritability

Survival CMR 0.009 d^{-1}
Senescence γ =4.15
Sexual maturity a=21 d
Reallocation (fec): k=0.07 d^{-1}
Inbreeding depression : 0.9
Encounter rate : ? 0.1-0.9 d^{-1}

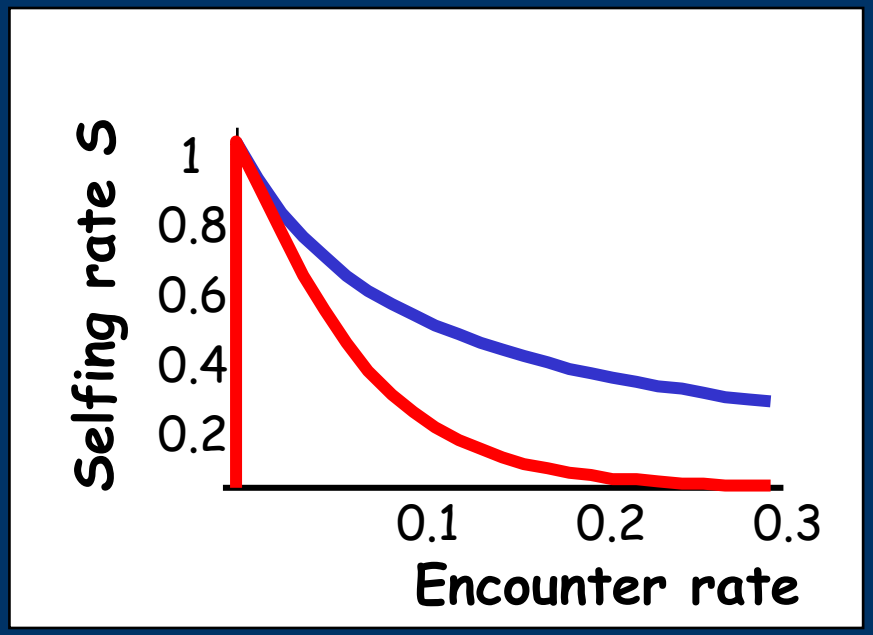
Treatment	family	h^2
self	p <0.001	0.41+
outcr	NS	(0)

The waiting time (β) is genetically variable

IT CAN EVOLVE

prediction	observation
Delay 13.1-18.2 d	17.2 d
Size 9.3-9.6mm	9.55 mm

The waiting behavior keeps selfing rates low



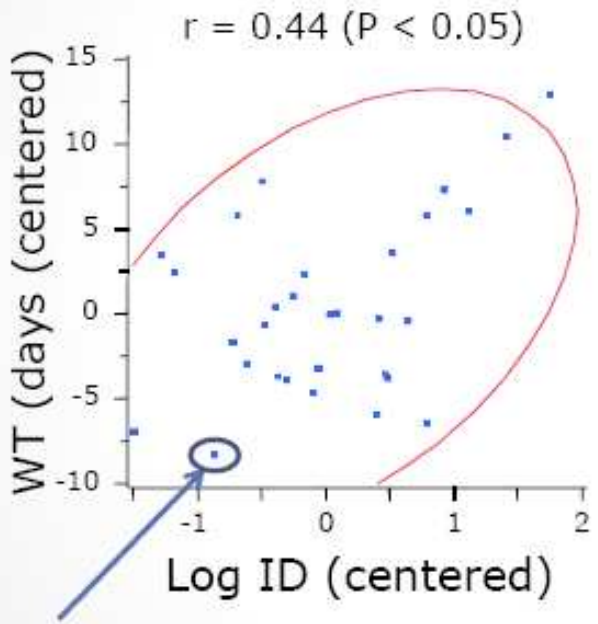
snails with $\beta=0$

snails with optimal β

The waiting behaviour reduces the realized selfing rate except at very low population densities.
Empirically, we usually find $s < 0.2$ (4 populations)

Longer waiting times evolve in populations were selfing is more costly

Variation in WT and ID among populations in *Physa acuta*



1 population (40 isolated+ 40 nonisolated individuals)

- different evolutionary optima of WT depending on ID

Escobar et al. 2009, *Evolution*

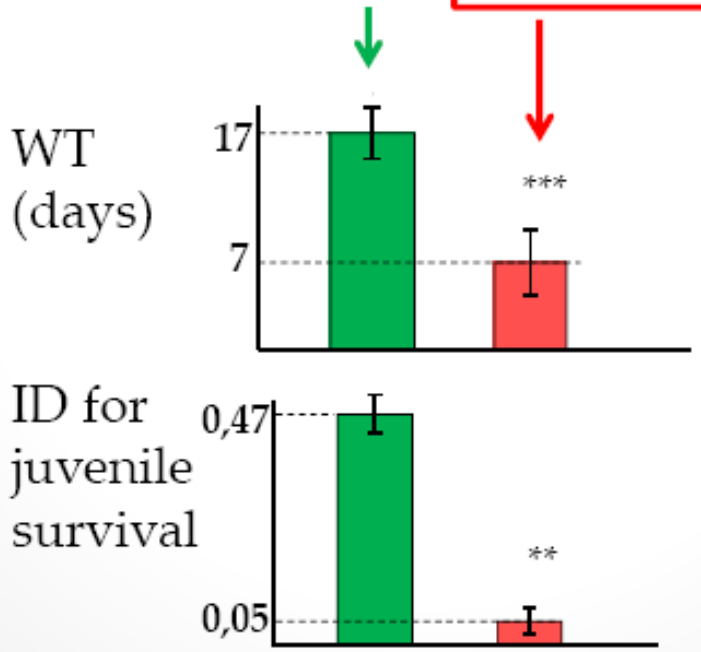
Waiting times rapidly evolve when mates become less available

Coevolution of ID and WT under reduced mating opportunity

- Experimental evolution lines (ca. 20 generations)

C = control lines, many mates available at all times

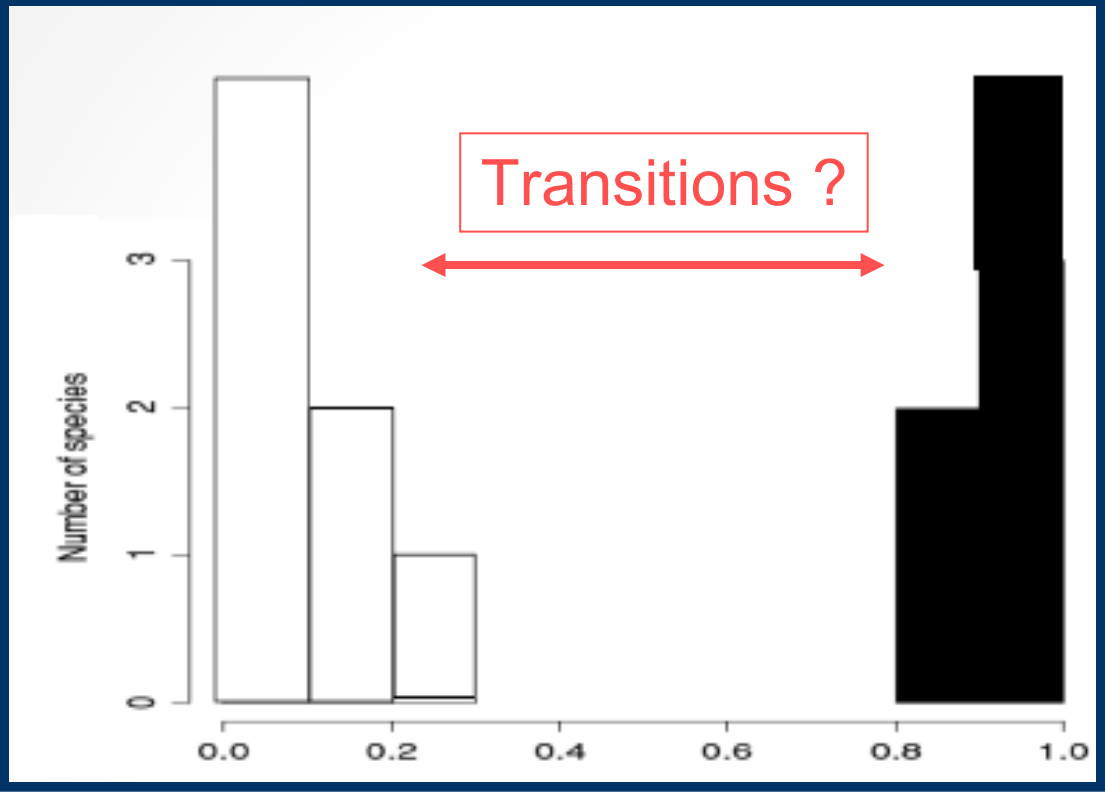
S = constrained lines, 0 or 1 mate, in alternation every other generation



The beginning of a transition towards a highly selfing strategy ?

Evolution of mating system between two stable states ?

Number of species



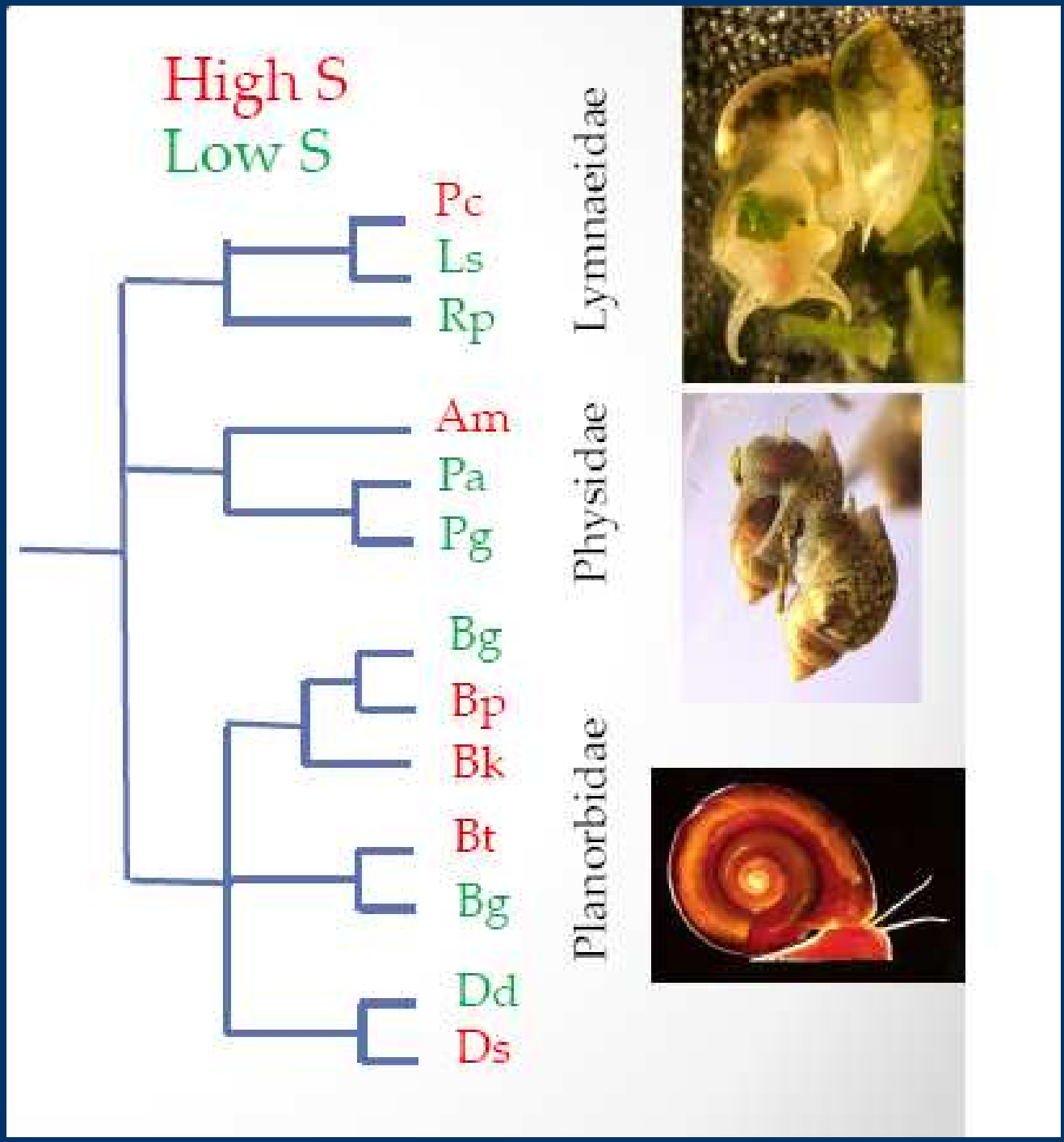
Pulmonate Snails (15 species)

Selfing rate

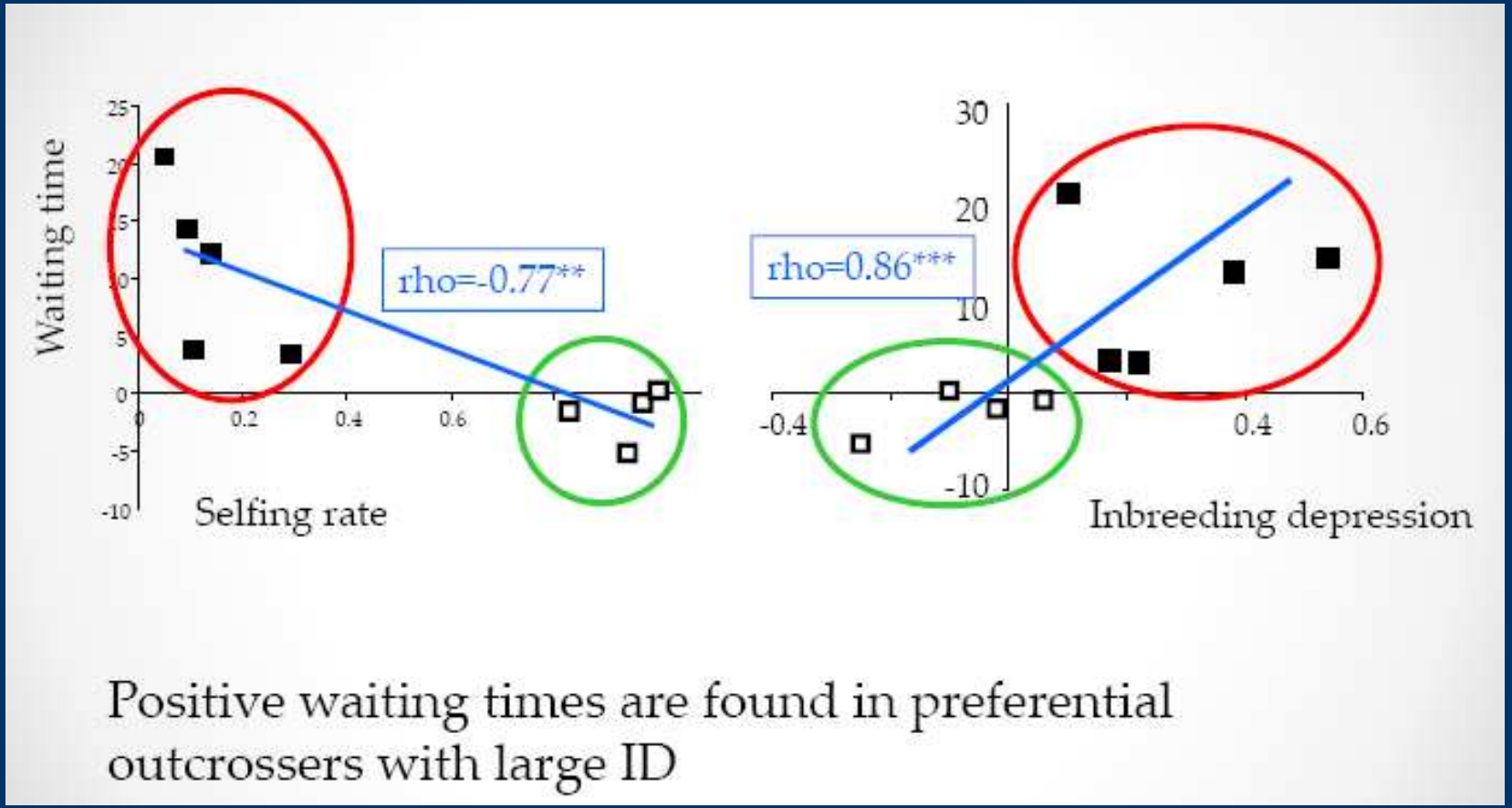
« outcrossers »

« selfers »

Evolutionary transitions have occurred in the pulmonate snails



Inbreeding depression and waiting time coevolve with selfing rates



Positive waiting times are found in preferential outcrossers with large ID

Conclusions

-Hermaphroditism does not mean uniformity : hermaphroditic species contain a diversity of reproductive types, discontinuous (aphallics/euphallics) or continuous (long/short waiting times)

- these types are (partially) genetically determined and influence the opportunity for self-fertilization

-This variation allows EVOLUTION of mating systems ; this evolution provides a spectacular illustration of Darwinian principles and models

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