Experimental evolution of biocontrol agents: does it meet its promises?

Sara Magalhães

CE3C: Centre for Ecology, Evolution and Environmental Changes

Faculdade de Ciências, Universidade de Lisboa

What is experimental evolution?

Review

Feature Review

Experimental evolution

Tadeusz J. Kawecki[1], Richard E. Lenski[2], Dieter Ebert[3], Brian Hollis
Isabelle Olivieri[4], and Michael C. Whitlock[5]

PROCEEDINGS OF THE ROYAL SOCIETY B BIOLOGICAL SCIENCES

How does adaptation sweep through the genome? Insights from long-term selection experiments

Molly K. Burke

Proc. R. Soc. B published online 25 July 2012
doi:10.1098/rspb.2012.0799

Letters

Cell PRESS

Strengths and weaknesses of experimental evolution

Sara Magalhães and Margarida Matos

Centro de Biologia Ambiental, Faculdade de Ciências da Universidade de Li
Lisbon, Portugal

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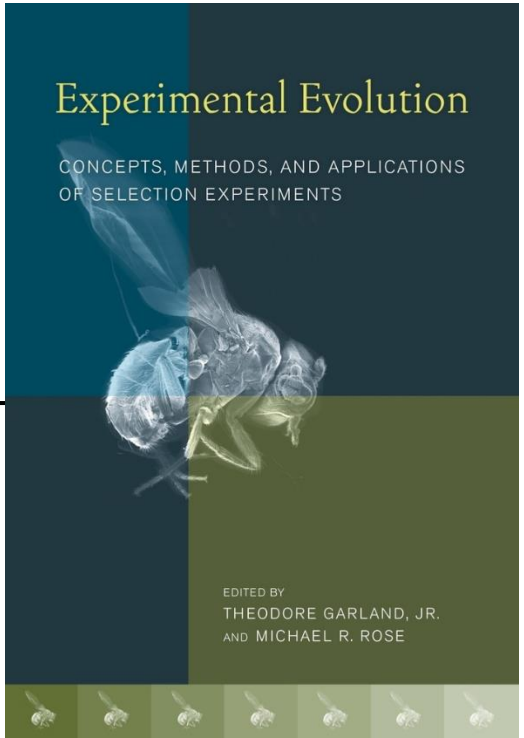
Experimental Evolution

ADAM K. CHIPPINDALE



What is experimental evolution?

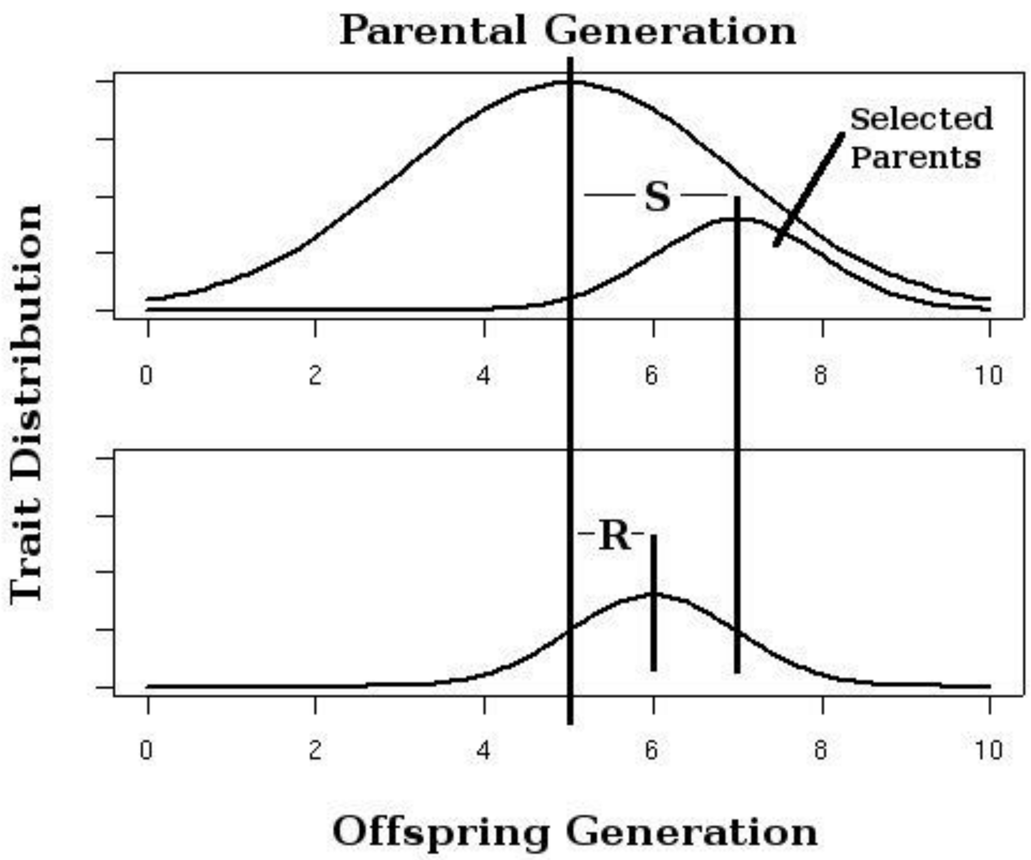
- **Artificial selection:**

  The experimenter selects parents with particular traits.

- **(Quasi-natural) experimental evolution:**

  Organisms are placed in different environments and their evolution is followed across generations.

Artificial selection



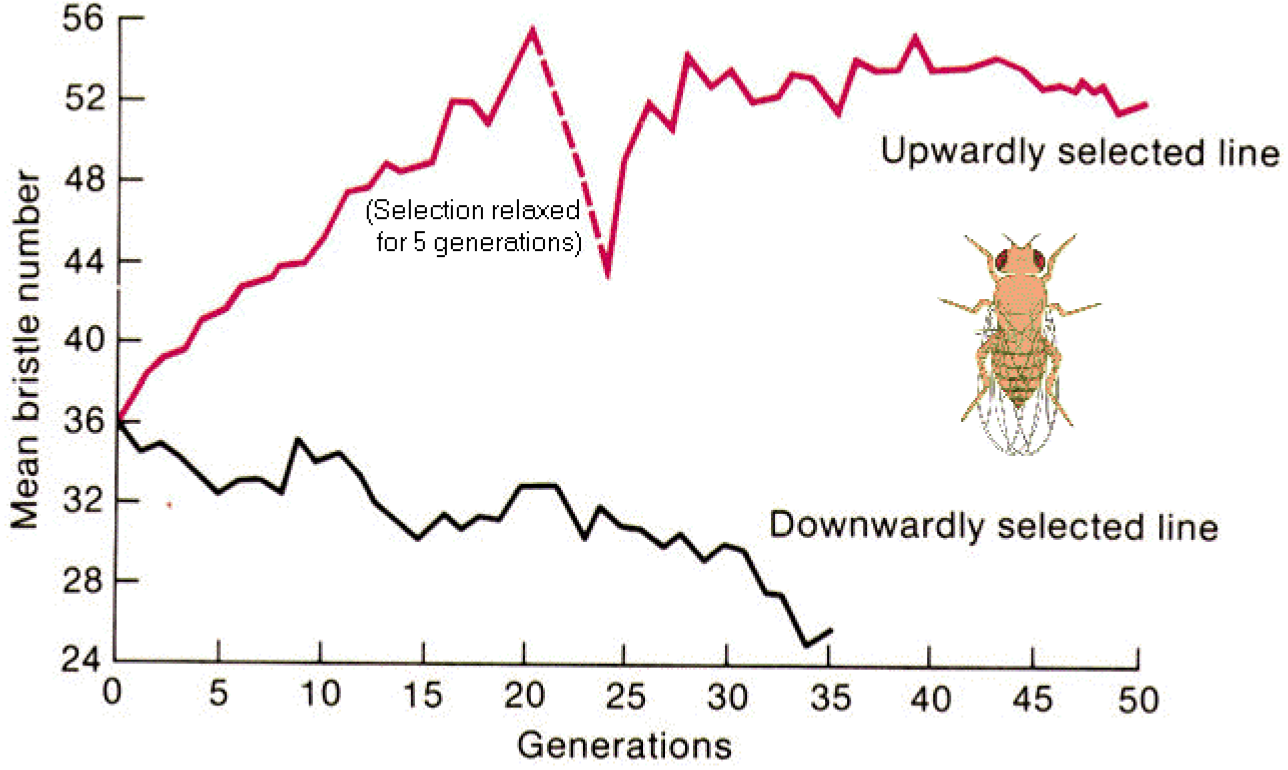
S = Difference between the mean trait value of the selected parents and that of the whole population.

R = Difference between the mean trait value of the offspring and that of the whole parent population.

$$R = S \times h^2$$

The breeders' equation

Artificial selection: A classical example



Payne 1918 PNAS

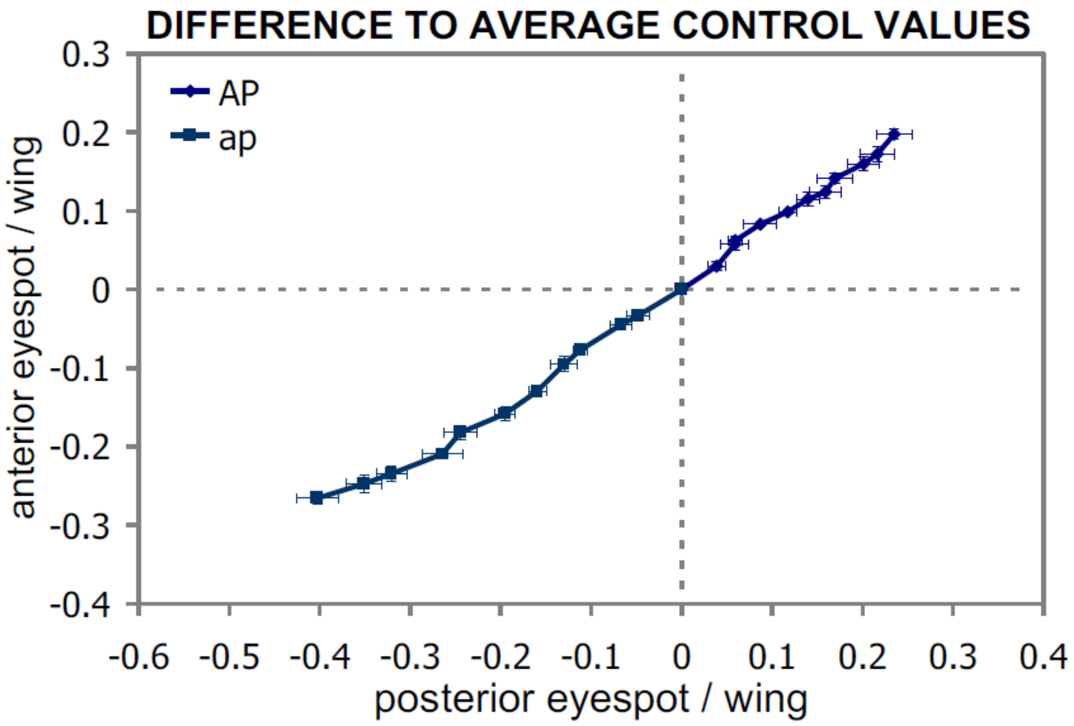
Artificial selection: Another example

Selection for eyespot size in butterflies

B. anynana

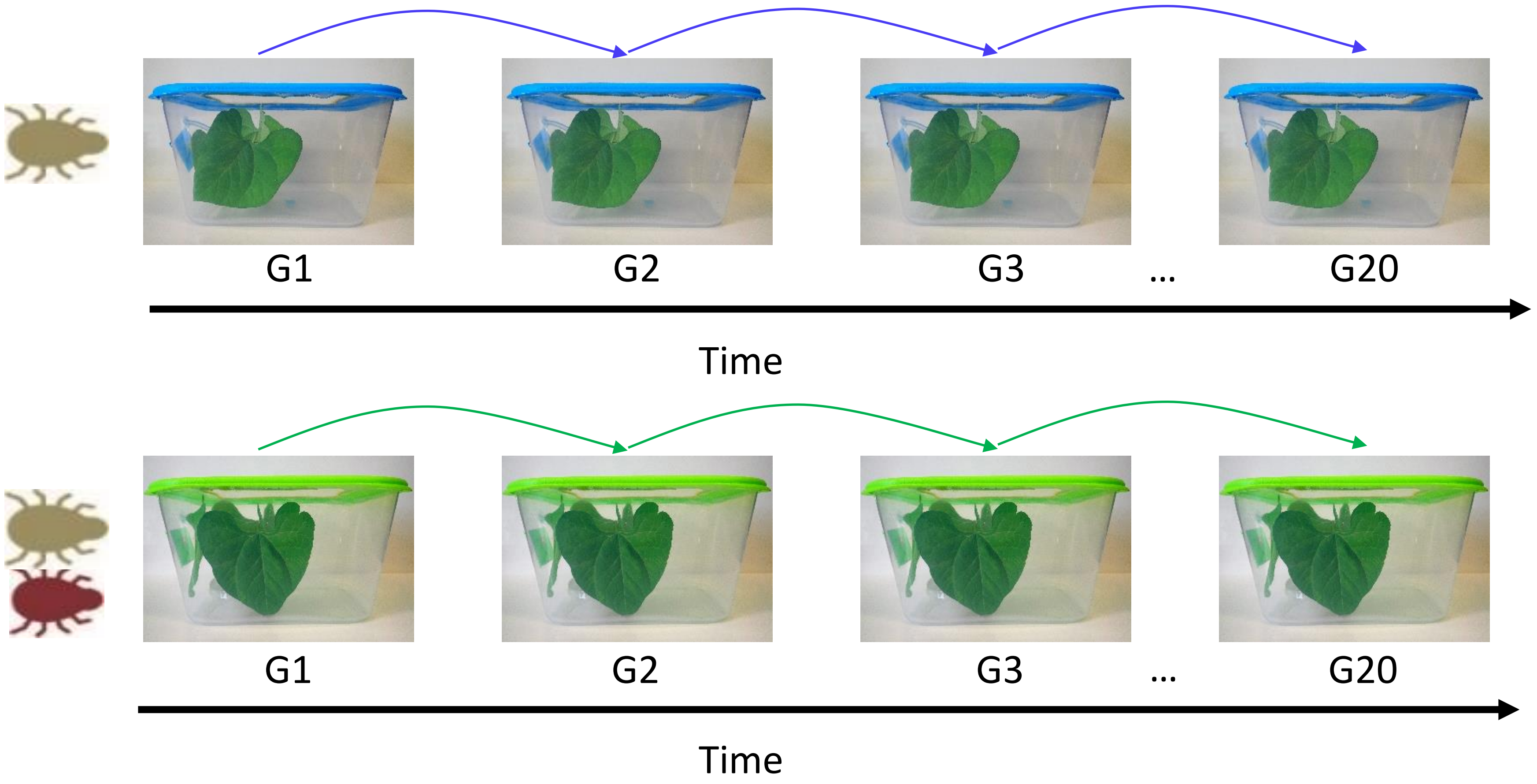
Patricia Beldade

Changes in both eyespots simultaneously

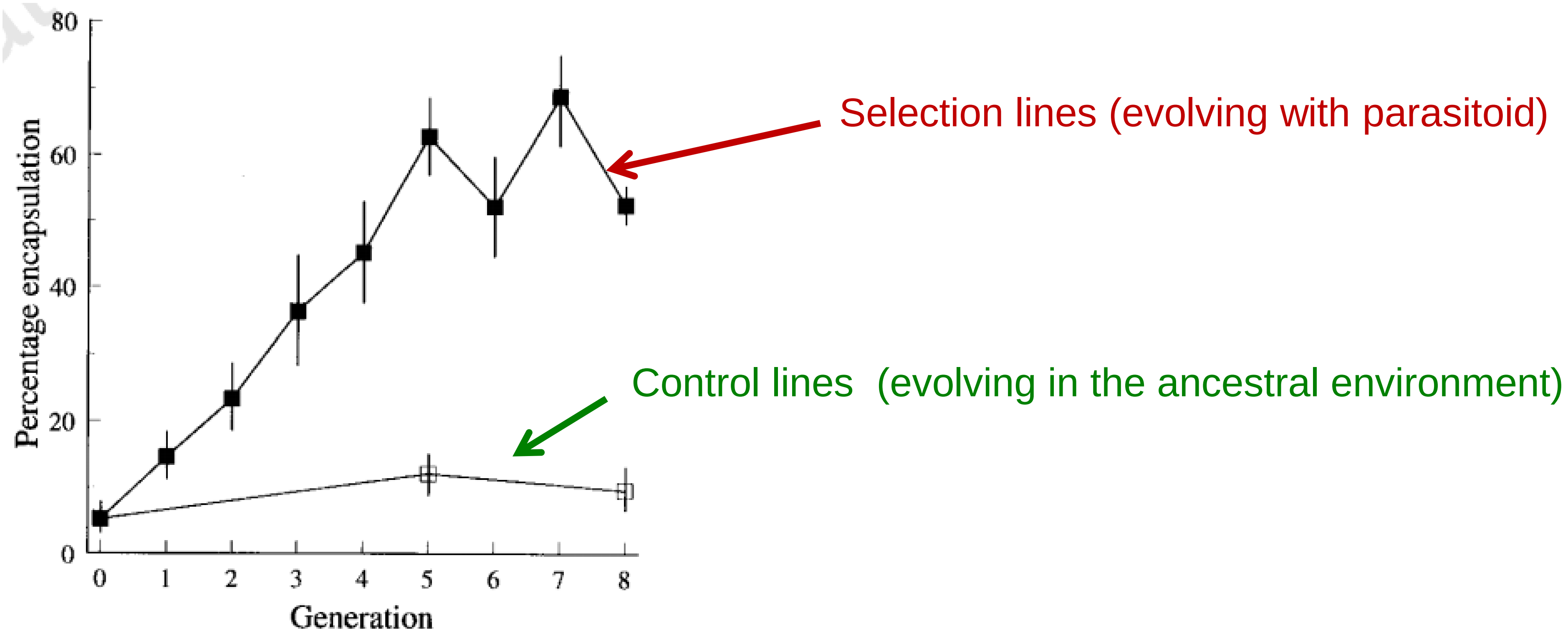


Beldade et al. Nature 2002

Experimental evolution



Experimental evolution: A classical example



Encapsulating ability of *Drosophila* exposed to a parasitoid increases across generations in lines evolving in presence of the parasitoid, as compared to control lines.

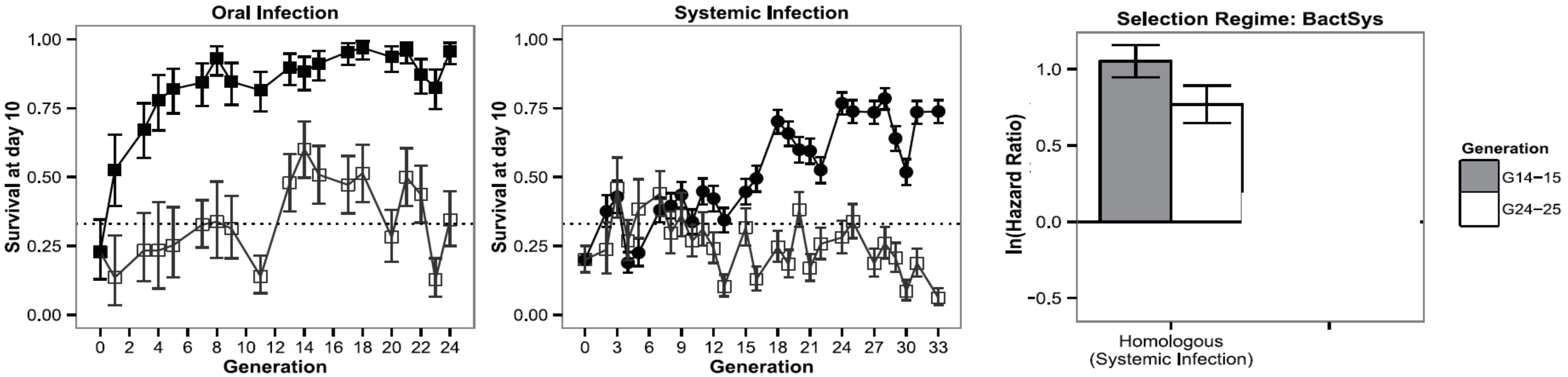
Kraaijeveld & Godfray Nature 1997

Élio Sucena

Experimental evolution: Another example

Vitor Faria

Nelson Martins



Drosophila evolving with bacterial infection have higher survival wnen exposed to those bacteria than control lines.

Martins et al. 2013 PloS Pathogens

Why is experimental evolution useful for evolutionary biologists?

- Knowledge of the initial, ancestral state. ALLOWS MEASURING THE RATE OF ADAPTATION.
- Precise control of the selection pressures that populations are exposed to. ALLOWS INFERRING CAUSALITY.
- Having replicates at the population level. ALLOWS FOLLOWING THE HISTORY OF POPULATIONS.

- Importantly, we can:
  - control for environmental effects (by placing individuals from all selection regimes in the same environment during few generations), thereby singling out genetic adaptation.
  - Measure the consequences of such adaptation for the performance in other environments, i.e., the correlated responses to selection.

- **In this way, we can follow the adaptation process, instead of inferring it from the pattern observed.**

Experimental evolution studies in biocontrol

Experimental & Applied Acarology, 21 (1997) 507–518 507

Improved control capacity of the mite predator *Phytoseiulus persimilis* (Acari: Phytoseiidae) on tomato

Bas Drukker[a]*, Arne Janssen[a], Willem Ravensberg[b] and Maurice W. Sabelis[a]
[a]*University of Amsterdam, Institute for Systematics and Population Biology, Kruislaan 320, 1098 SM Amsterdam, The Netherlands* [b]*Koppert Biological Systems, Research and Development Department, P.O. Box 155, 2650 AD Berkel en Rodenrijs, The Netherlands*

The Canadian Entomologist.
LXXIX MARCH, 1947 No. 3

IMPROVEMENT OF THE SEX-RATIO OF A PARASITE BY SELECTION

BY F. J. SIMMONDS,
Imperial Parasite Service, Belleville, Ontario.

日本応用動物昆虫学会誌（応動昆）
第 57 巻　第 4 号：219–234（2013）
http://odokon.org/

総　説

天敵の育種：飛翔能力を欠くテントウムシ系統の育成と品質管

世古　智一*・三浦　一芸
農業・食品産業技術総合研究機構近畿中国四国農業研究センター

Genetic Improvement of Invertebrate Natural Enemies—Breeding and Quality Control of a Flightless Beetle—. Tomokazu Seko* and Kazuki Miura National Agriculture and Food Research Organization We Region Agricultural Research Center; 6–12–1, Nishifukatsu, Fukuyama, Hiroshima 721–8514, Japan. *Jp Appl. Entomol. Zool.* 57: 219–234 (2013)

JOURNAL OF Evolutionary Biology
doi: 10.1111/j.1420-9101.2010.02207.x

Rapid evolution of parasitoids when faced with the symbiont-mediated resistance of their hosts

E. DION*, F. ZÉLÉ*†, J.-C. SIMON* & Y. OUTREMAN*
**UMR 1099 INRA-Agrocampus Ouest-Université Rennes 1 'Biologie des Organismes et des Populations appliquée à la Protection des Plantes', Rennes Cedex, Le Rheu Cedex, France*
†CNRS UMR 2724 'Génétique et Evolution des Maladies Infectieuses', IRD, Montpellier, France

HILGARDIA
JOURNAL OF AGRICULTURAL SCIENCE PUBLISHED BY THE CALIFORNIA AGRICULTURAL EXPERIMENT STATION
Volume 40, Number 6, · May, 1970

Artificial Selection for Genetic Adaptation to Temperature Extremes in *Aphytis lingnanensis* Compere (Hymenoptera: Aphelinidae)

Ernest B. White, Paul DeBach, and Morris J. Garber

Genetic Improvement of *Metaseiulus occidentalis*[1]: Selection with Methomyl, Dimethoate, and Carbaryl and Genetic Analysis of Carbaryl Resistance[2]

RICHARD T. ROUSH[3] AND MARJORIE A. HOY[4]
Department of Entomological Sciences, University of California, Berkeley, California 94720

ABSTRACT

J. Econ. Entomol. 74: 138–141 (1981)

The effects of selective breeding on the laboratory propagation of insect parasites*

By A. Wilkes, *Dominion Parasite Laboratory, Belleville, Ontario*

(*Communicated by W. R. Thompson, F.R.S.—Received 23 April 1946*)

Brief conclusions over this brief literature search

- I found few studies (< 30). Maybe a more thorough search would yield better results, but it is clearly not a flourishing research area…
- Actually, most studies are rather old…
- Most studies do not meet the quality criteria of the field.

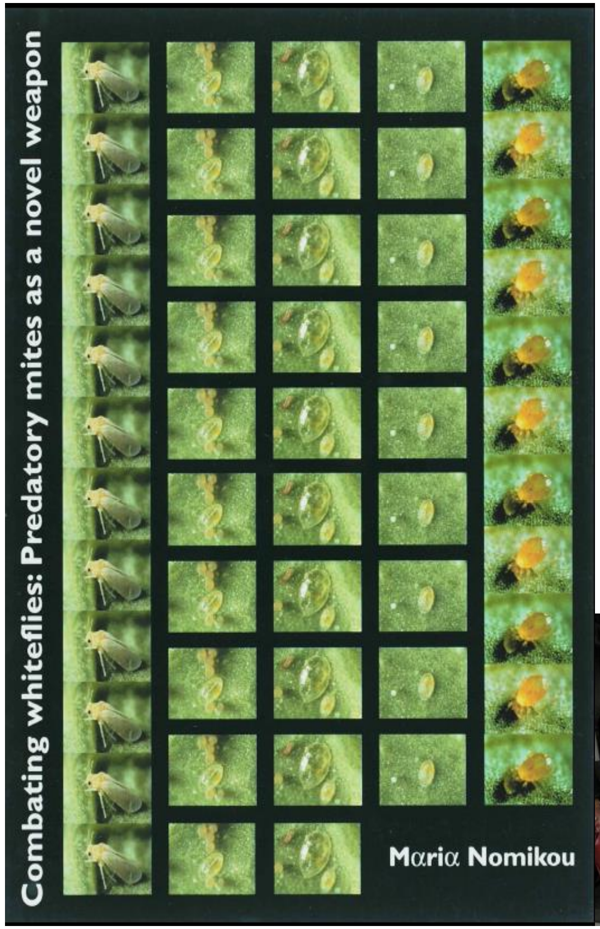
How was experimental evolution in biocontrol done?

- Knowledge of the initial, ancestral state. OFTEN, NOT ALWAYS
- Precise control of the selection pressures that populations are exposed to. OFTEN, NOT ALWAYS
- Having replicates at the population level. VERY RARELY!!!

- Importantly, we can:
  - **control for environmental effects** (by placing individuals from all selection regimes in the same environment during few generations), thereby singling out **genetic** adaptation. VERY RARELY!!!
  - Measure the **consequences** of such adaptation for the performance in other environments, i.e., the **correlated responses to selection**. VERY RARELY!!!

- **In this way, we canNOT follow the adaptation process, instead of inferring it from the pattern observed.** BUT… DO BIOCONTROL STUDIES NEED THIS?

How can experimental evolution be useful for biocontrol?



How can experimental evolution be useful for biocontrol?

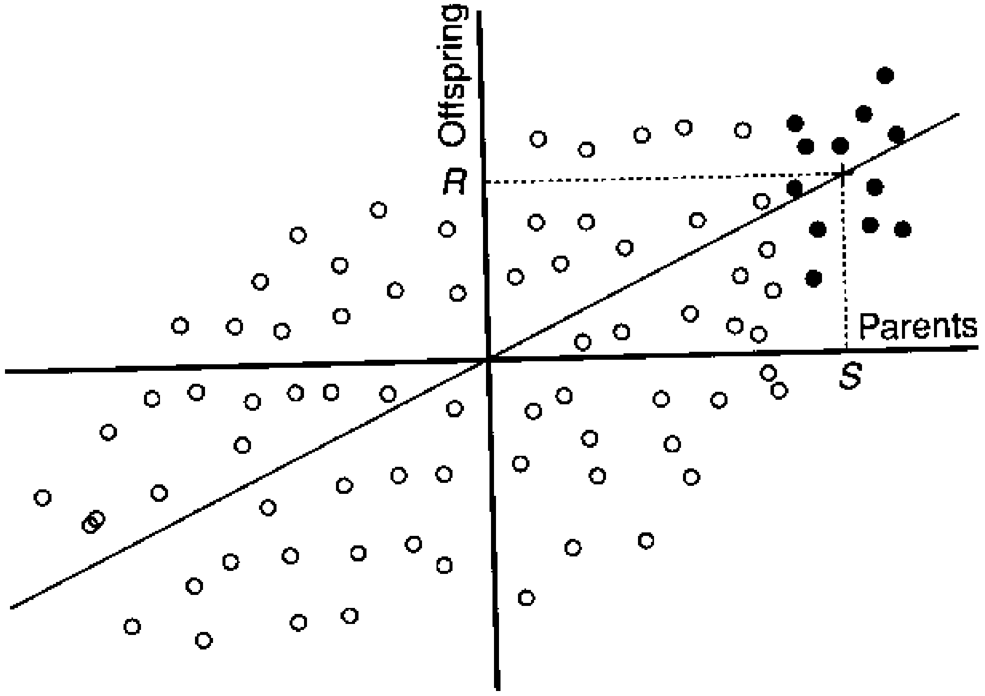
How can we guarantee that experimental evolution will produce super-bugs?

- For a trait to evolve by natural selection, there has to be genetic variation for that trait in the population.

$R = S \times h^2$

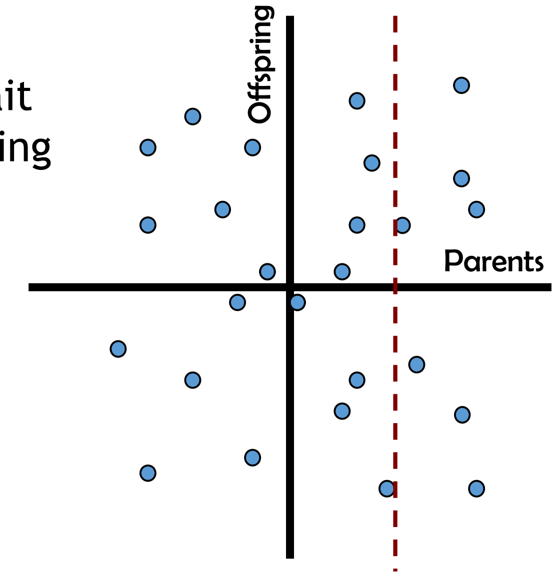
R depends on S and h^2, but the latter also depends on the variability present in the population:

$h^2 = Va/Vp$

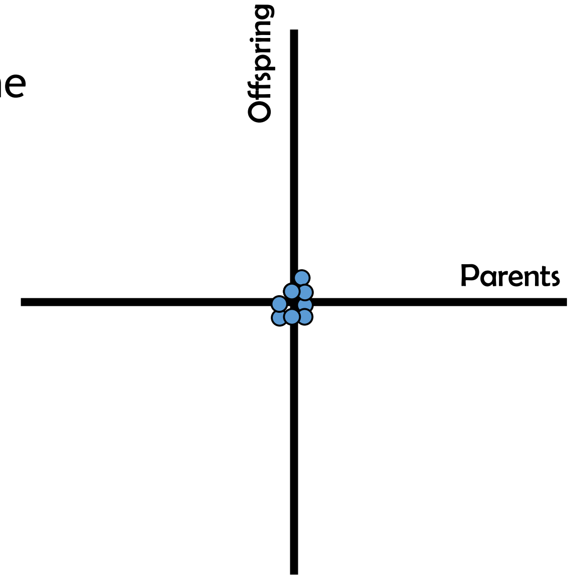


$h^2 = 0$

No correlation between trait values in parents and offspring



No genetic variation for the trait in the population



Which traits are targeted by exp evol biocontrol studies?

- Experimental evolution is used in biological control to improve useful traits of natural enemies:

    - Predation rate
    - Fecundity
    - Resistance to pesticides
    - Tolerance to temperature extremes
    - …

- In general, studies aim to improve fitness-related traits of biological control agents.

The Fundamental Theorem of Natural Selection

Ronald Fisher

$$R_W=V_{AW}$$

The rate of increase in fitness of any organism at any time is equal to its additive genetic variance in fitness at that time.

So, genetic variability is the **motor** that drives fitness increases in populations.

The Fundamental Theorem of Natural Selection

Ronald Fisher

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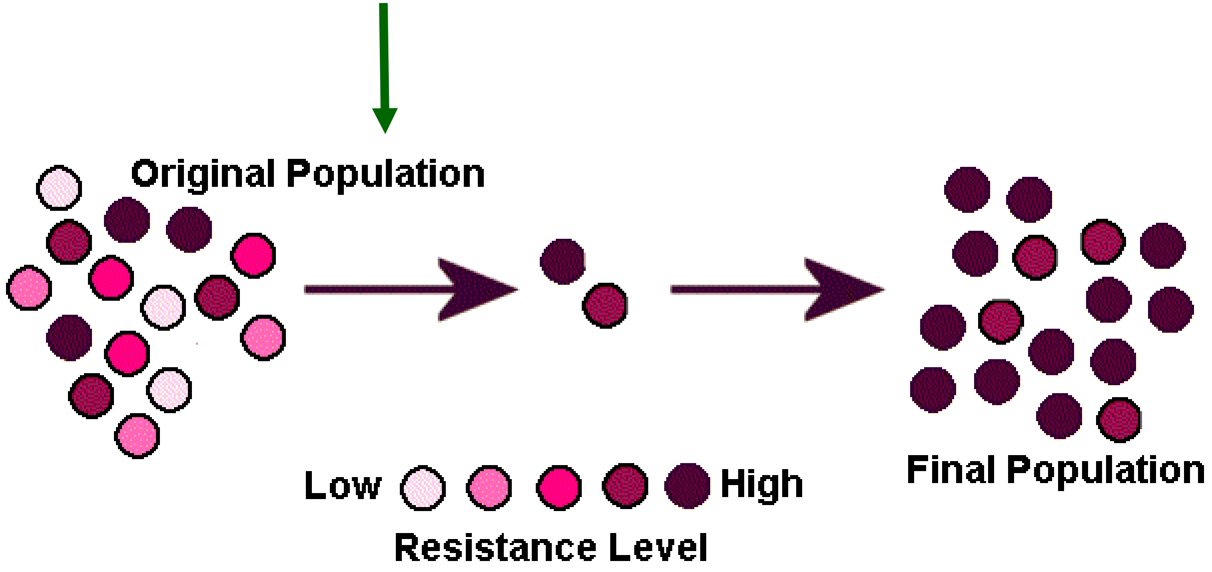
The rate of increase in fitness of any organism at any time is equal to its additive genetic variance in fitness at that time.

So, genetic variability is the **motor** that drives fitness increases in populations.
Problem: as fitness increases, it eliminates genetic variability…

How natural selection operates

Selection pressure (e.g., pesticide)



Natural selection eliminates the variants with the lowest fitness.
This means that only some variants (the fitter) remain, hence genetic variance decreases as fitness increases, **particularly for fitness-related traits!**

Heritability of fitness-related traits

Heritabilty of fitness-related traits is generally lower than that of other traits.

Trait	Heritability (%)
Back fat thickness	30-70 (high)
Growth rate	20-50 (medium)
Feed conversion ratio	20-50 (medium)
Litter size at birth	0-20 (low)
Litter size at weaning	0-20 (low)

Heritability and evolutionary responses in spider mites

Isabelle Olivieri

Julien Fayard

Aurelie Cailleau & Elodie Blanchet

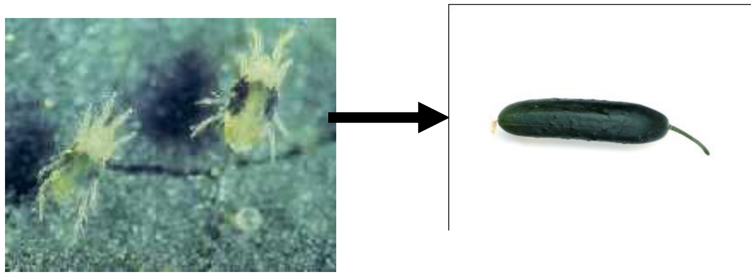
Cassandra Marinosci

Ophélie Ronce

Arne Janssen

Martijn Egas

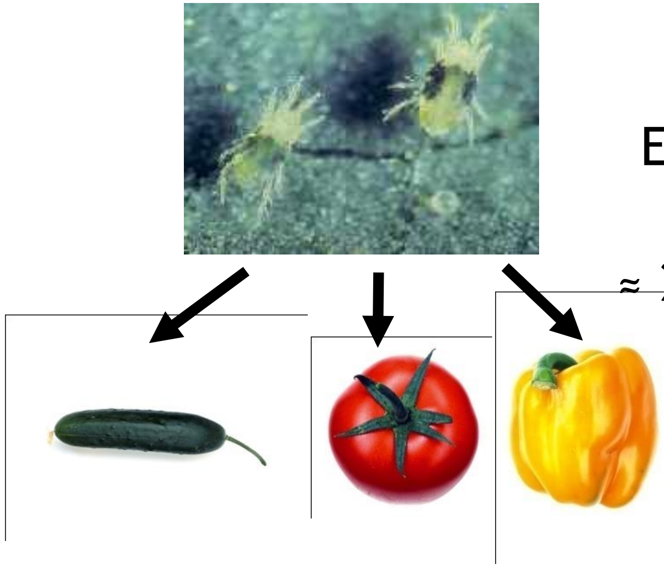
Heritability and evolutionary responses in spider mites



Tetranychus urticae

BASE POPULATION:

Mite strain on cucumber for ≈ 400 generations.

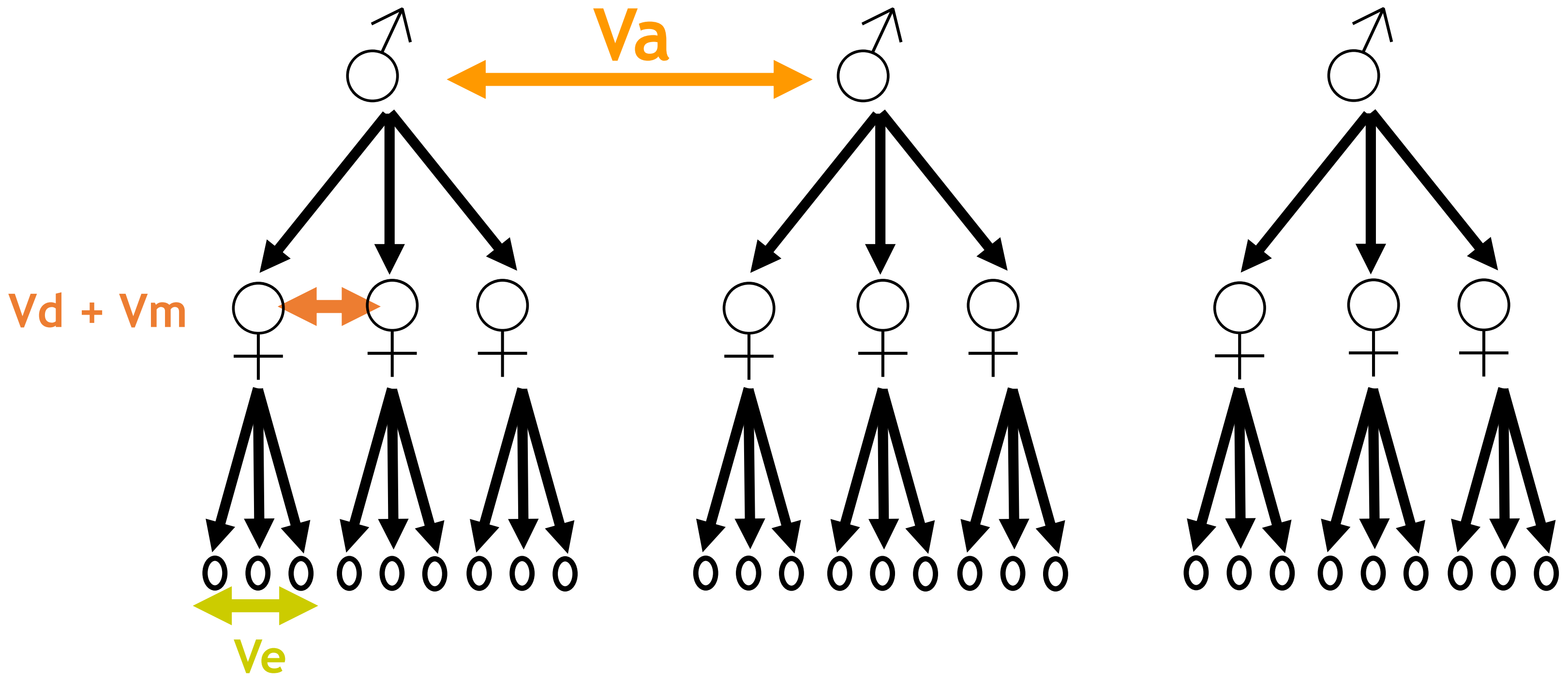


EXPERIMENTAL EVOLUTION

≈ 25 generations

5 lines per selection regime

Is there additive genetic variance for traits potentially underlying adaptation to novel hosts?



Half-sib design

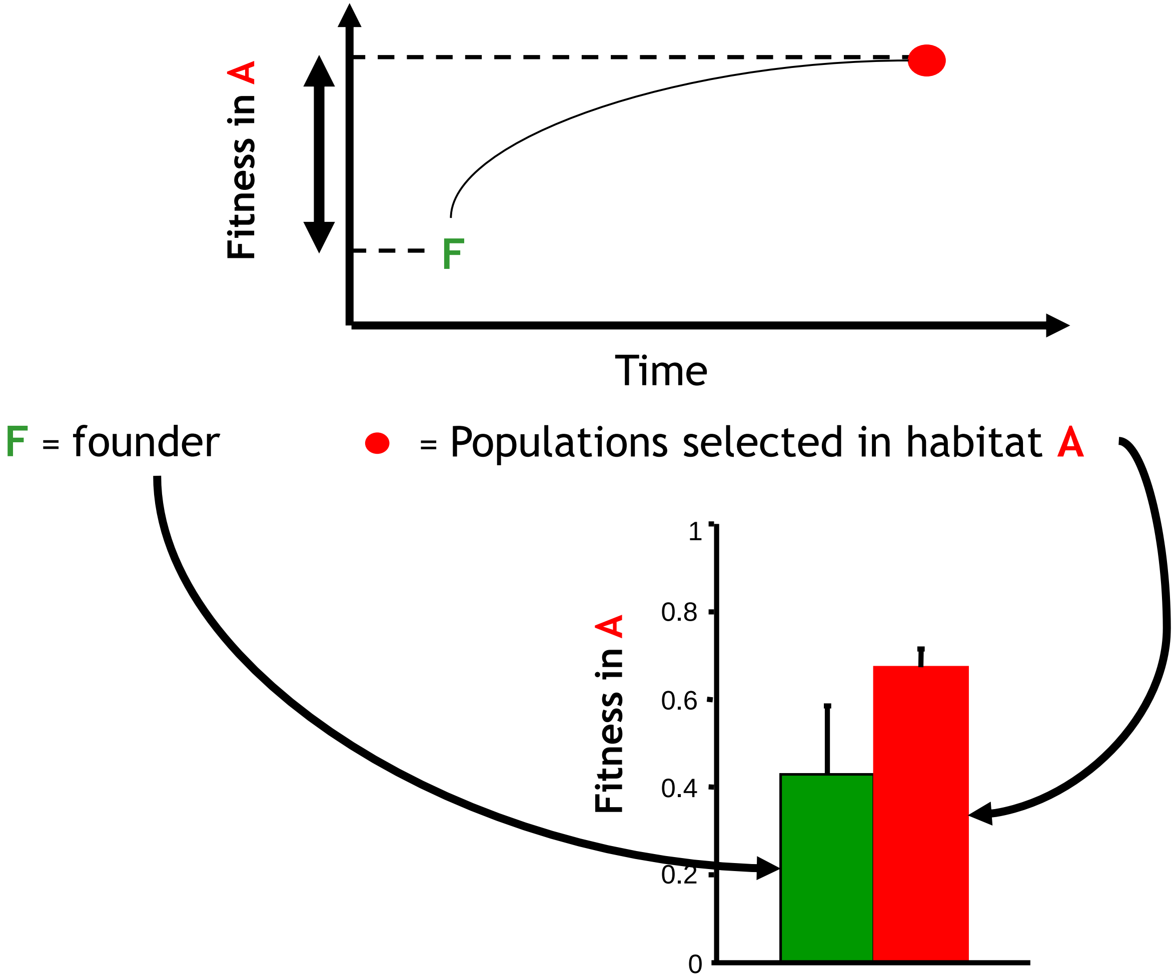
Genetic variance (Va)

<table>
<tr><th></th><th></th><th></th></tr>
<tr><td>Development time</td><td>0</td><td>0</td></tr>
<tr><td>Juvenile survival</td><td>√</td><td>√</td></tr>
<tr><td>Fecundity</td><td>√</td><td>√</td></tr>
<tr><td>Longevity</td><td>√</td><td>√</td></tr>
<tr><td>Host choice</td><td colspan="2">0</td></tr>
</table>

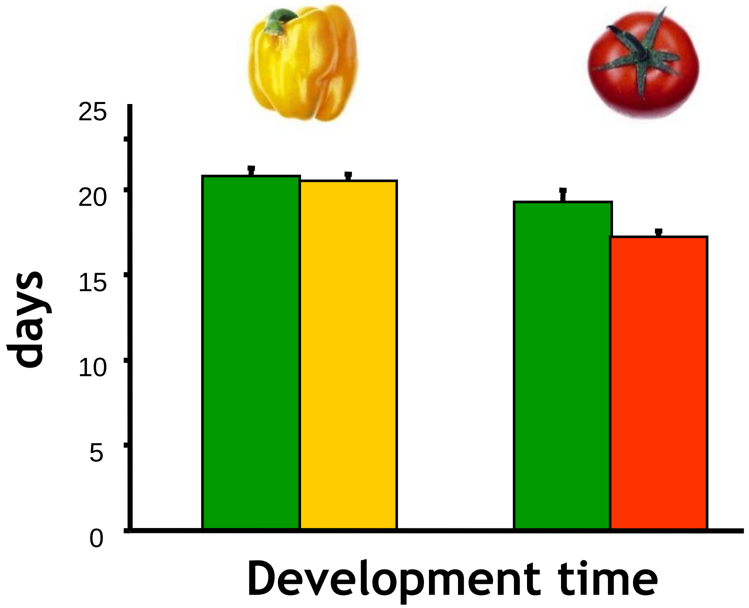
Magalhães et al. J. Evol. Biol. 2007

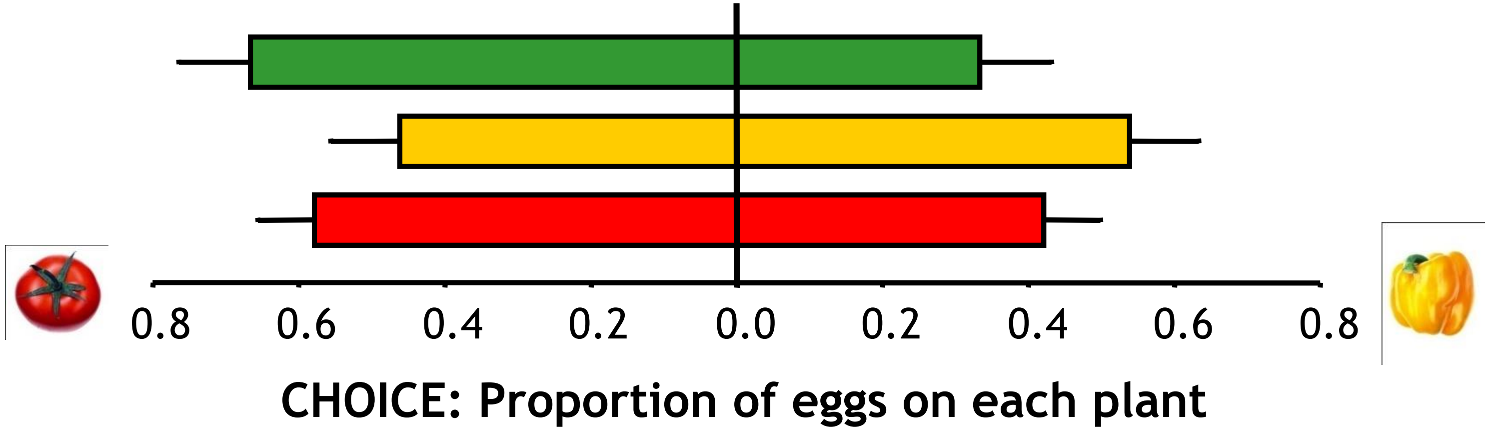
Do these traits evolve when populations are placed in those novel environments?

Adaptation :



Are evolutionary responses limited by genetic variation?





Cucumber lines   Pepper lines   Tomato lines

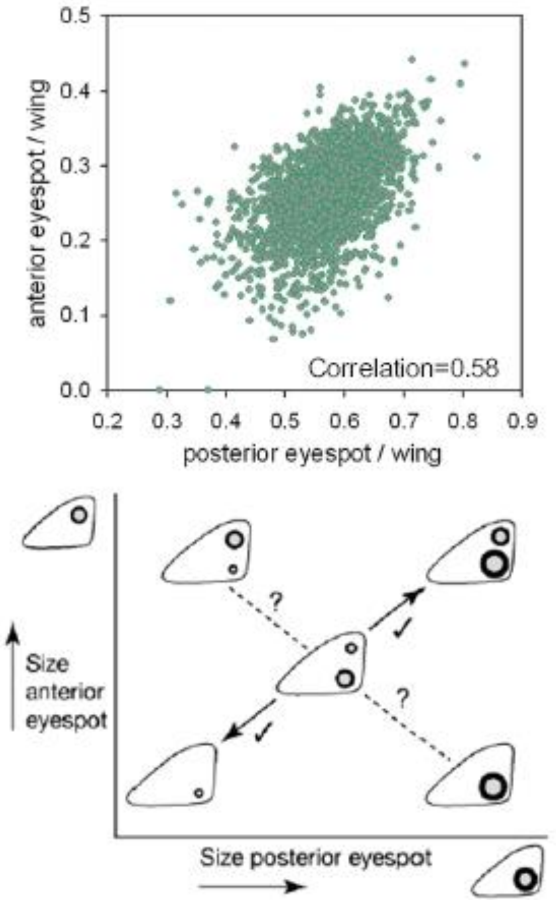
YES

Magalhães et al. J. Evol. Biol. 2007

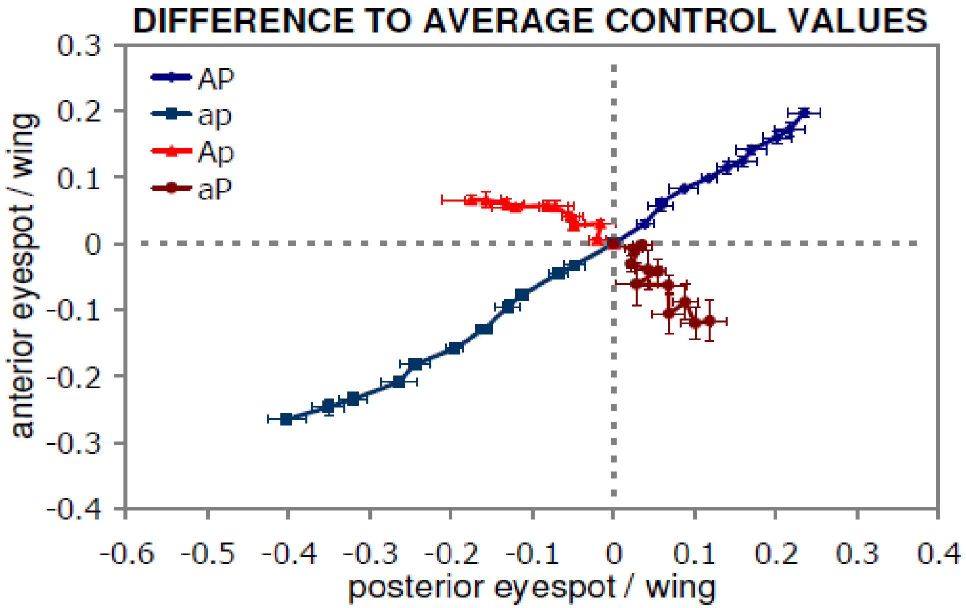
Are evolutionary responses limited by genetic variation?

B. anynana

Patricia Beldade



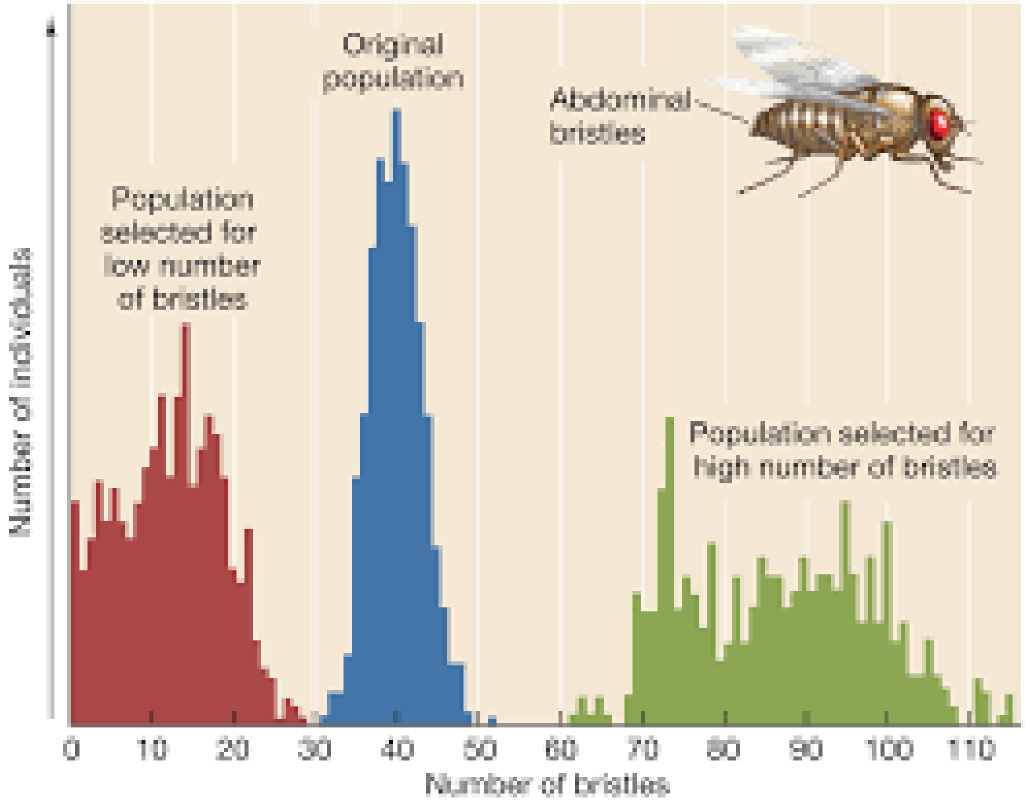
Changes in both eyespots simultaneously



A BIT

Beldade et al. Nature 2002

Are evolutionary responses limited by genetic variation?



APPARENTLY NOT…

Are evolutionary responses limited by genetic variation?

Ecology, 86(6), 2005, pp. 1371–1384

A REASSESSMENT OF GENETIC LIMITS TO EVOLUTIONARY CHANGE

MARK W. BLOWS[1,3] AND ARY A. HOFFMANN[2]

[1]*School of Integrative Biology, University of Queensland, Brisbane 4072, Australia*
[2]*Centre for Environmental Stress and Adaptation Research, La Trobe University, Melbourne 3083, Australia*

IT'S NOT CLEAR

But beware you choose a population with high effective size to begin with

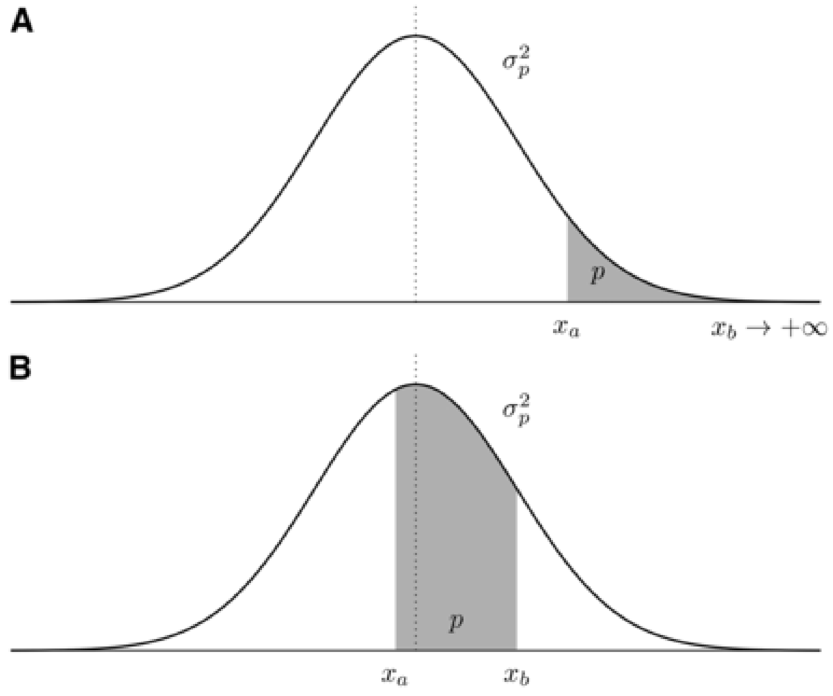
How can we guarantee that experimental evolution will produce super-bugs?

- For a trait to evolve by natural selection, there has to be genetic variation for that trait in the population.

- For a trait to evolve, it has to respond to a given selection pressure.

Selection pressures

- Under artificial selection, the experimenter sets him/herself the selection pressure on a given trait. So he knows which trait will respond.



The higher S, i.e., the further is the average of the selected parents from the average of the population, the fewer the number of parents to be selected will be available.

Selection pressures

- Under artificial selection, the experimenter sets him/herself the selection pressure on a given trait. So he knows which trait will respond.

- Under (quasi-natural) experimental evolution, we don’t know which trait will respond, if any.

Back to the mites…

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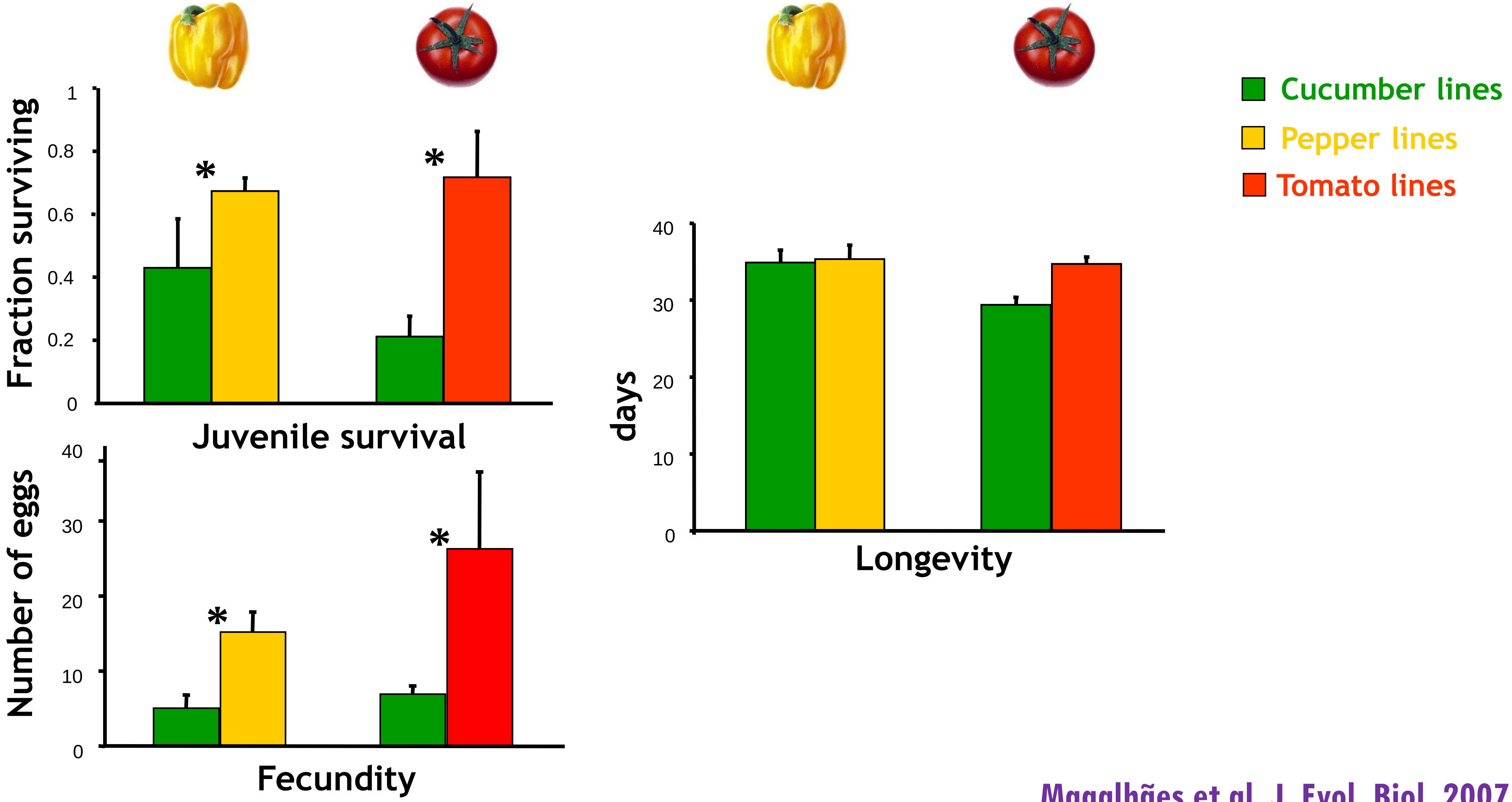
Magalhães et al. J. Evol. Biol. 2007

Adaptation – Life history traits



Magalhães et al. J. Evol. Biol. 2007

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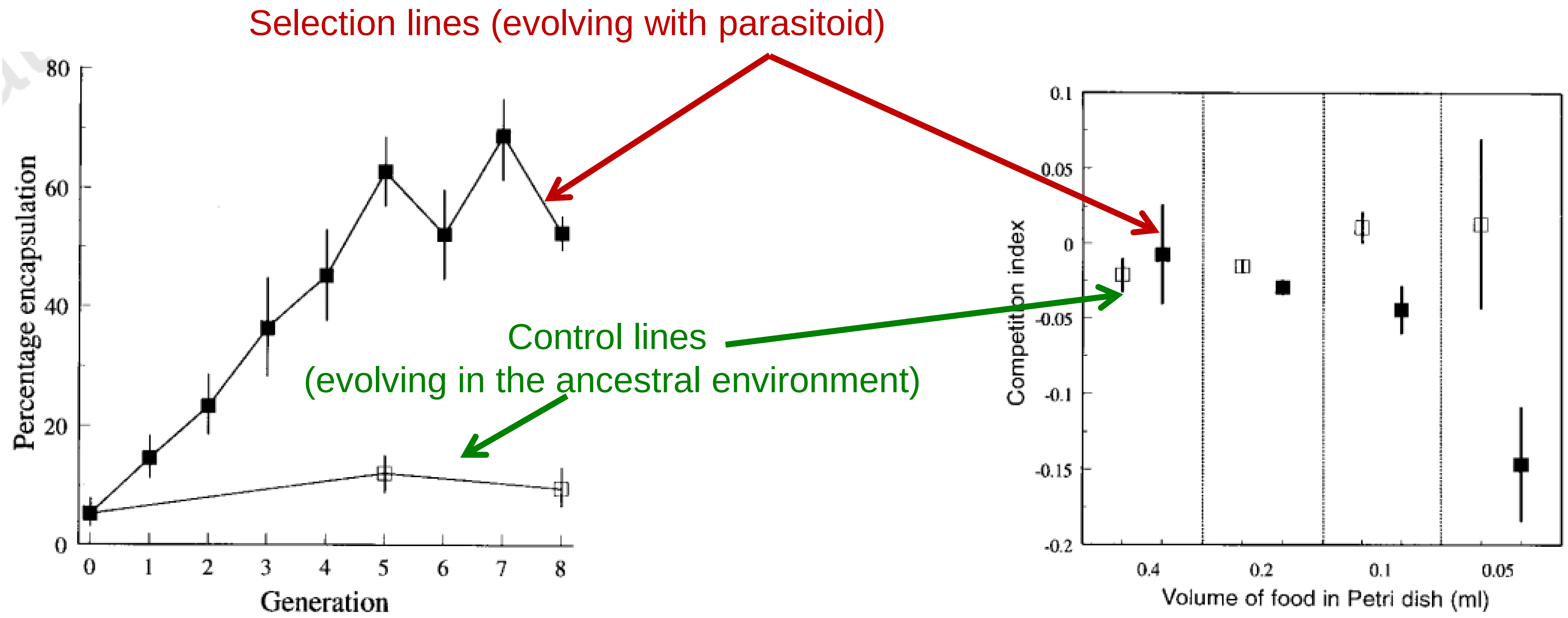
- For a trait to evolve, it has to respond to a selection pressure.
- For an evolutionary change to be beneficial for biological control, no other relevant trait should trade off with the target trait.

A classical example

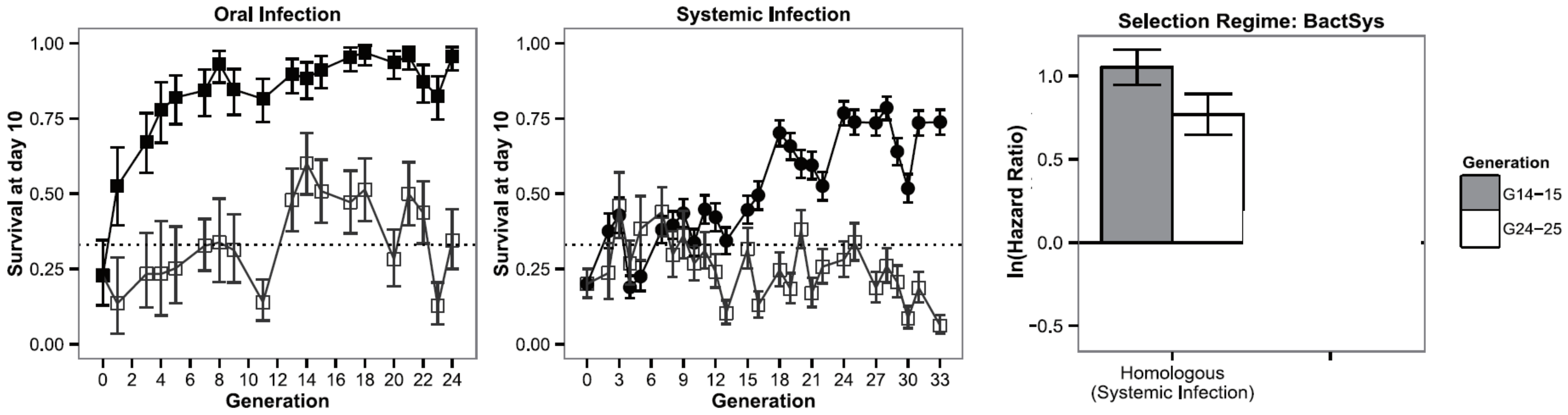


Encapsulating ability of *Drosophila* exposed to a parasitoid increases across generations in lines evolving in presence of the parasitoid, as compared to control lines…

But this trades off with larval competitive ability with little food.

Kraaijeveld & Godfray Nature 1997

Are trade-offs universal?



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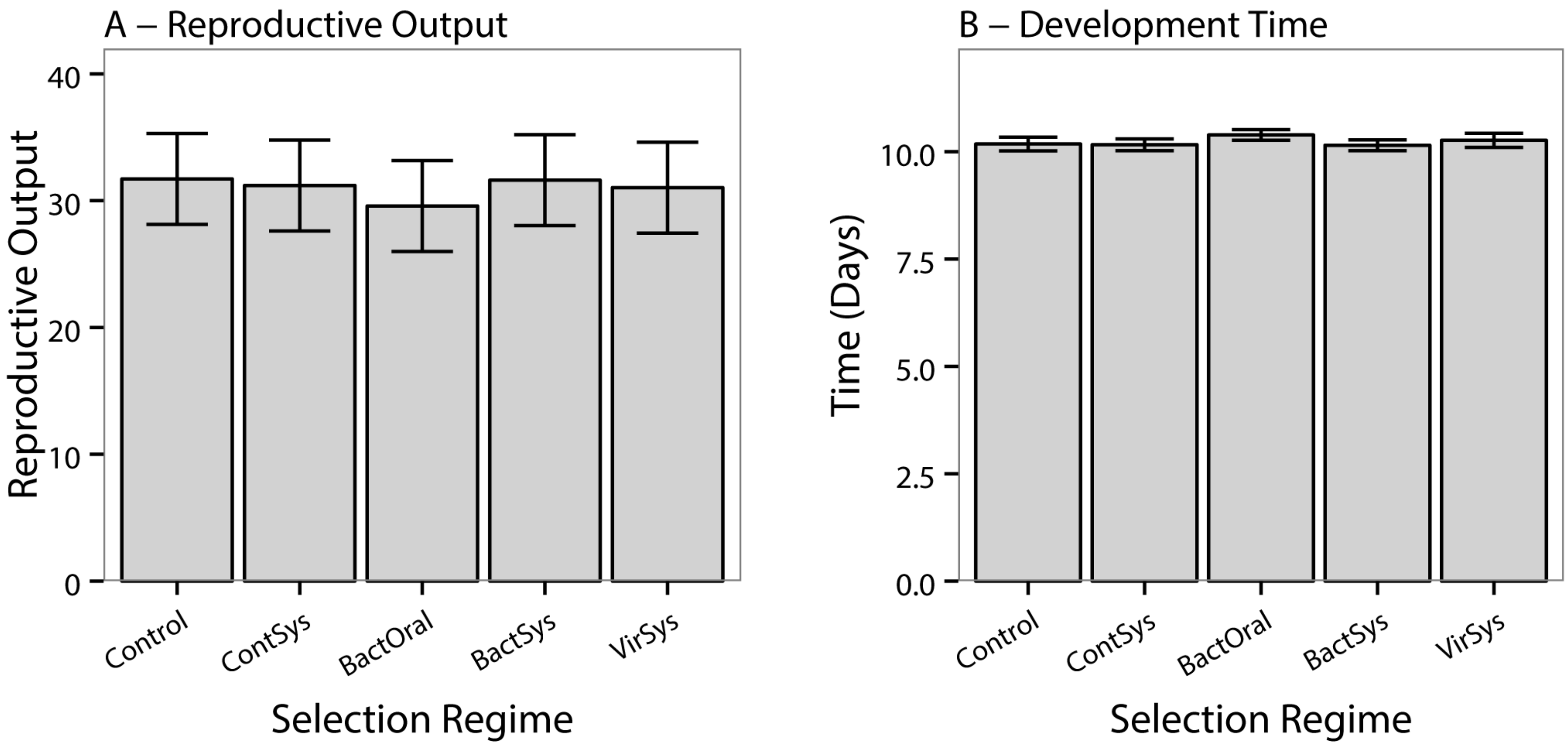
Martins et al. 2013 PloS Pathogens

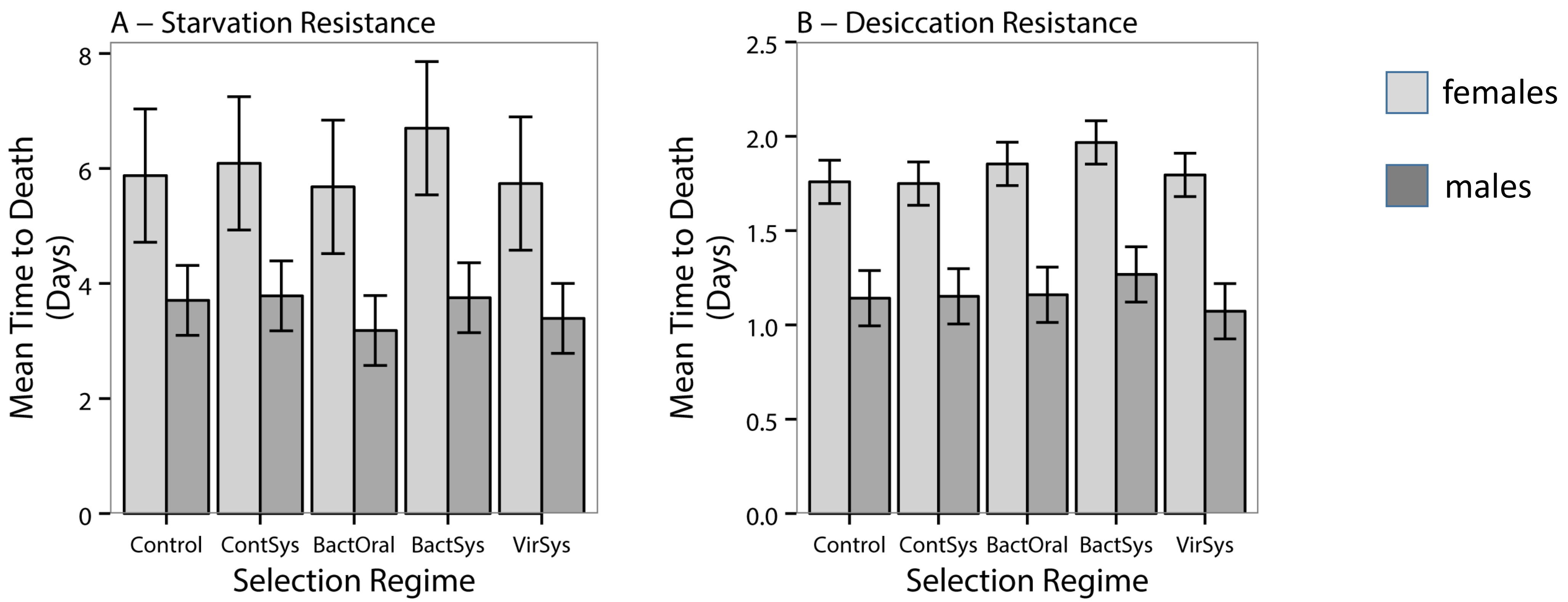
Costs in the ancestral environment?



NO!

Faria et al. 2015 Evolution

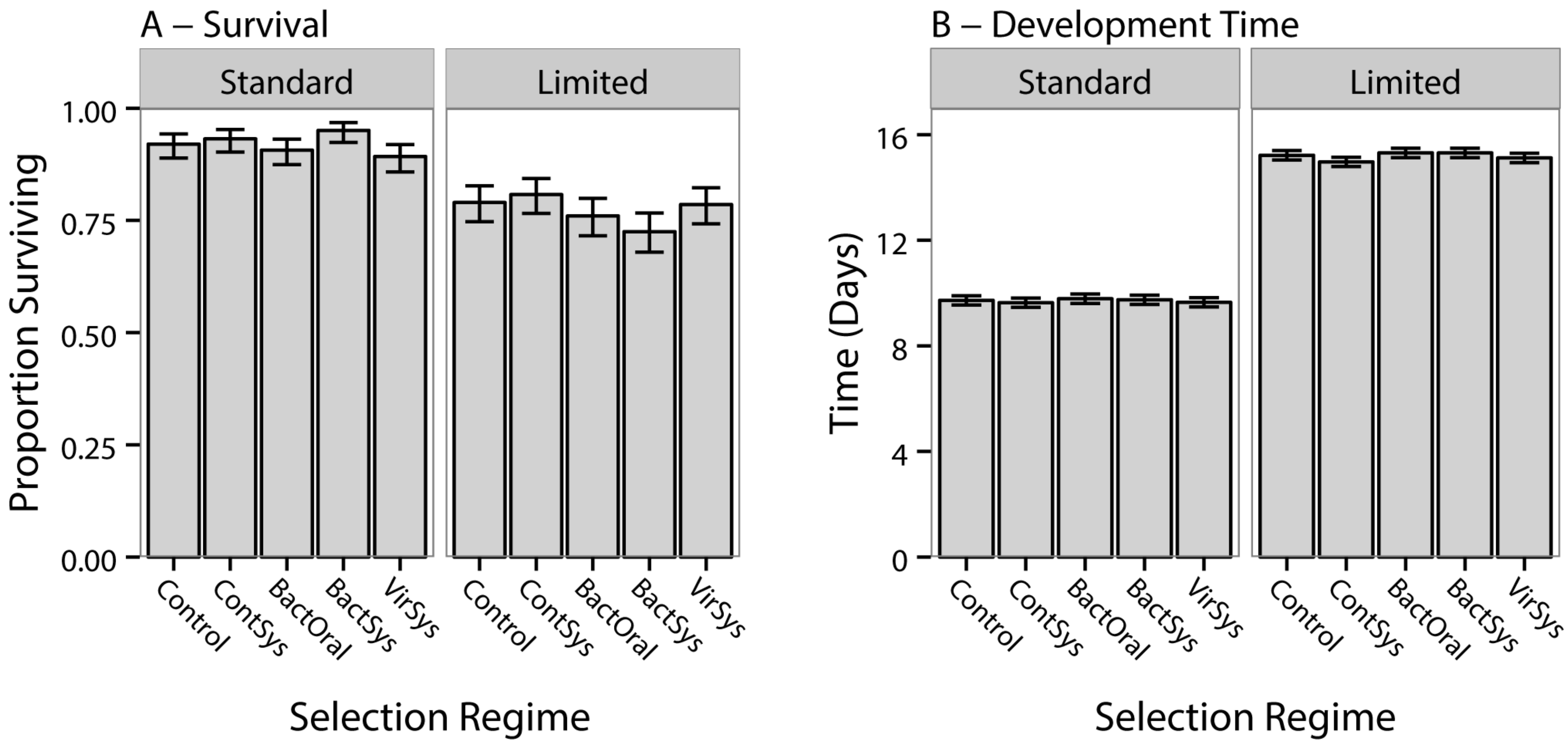
Costs in more extreme environments?



NO!

Faria et al. 2015 Evolution

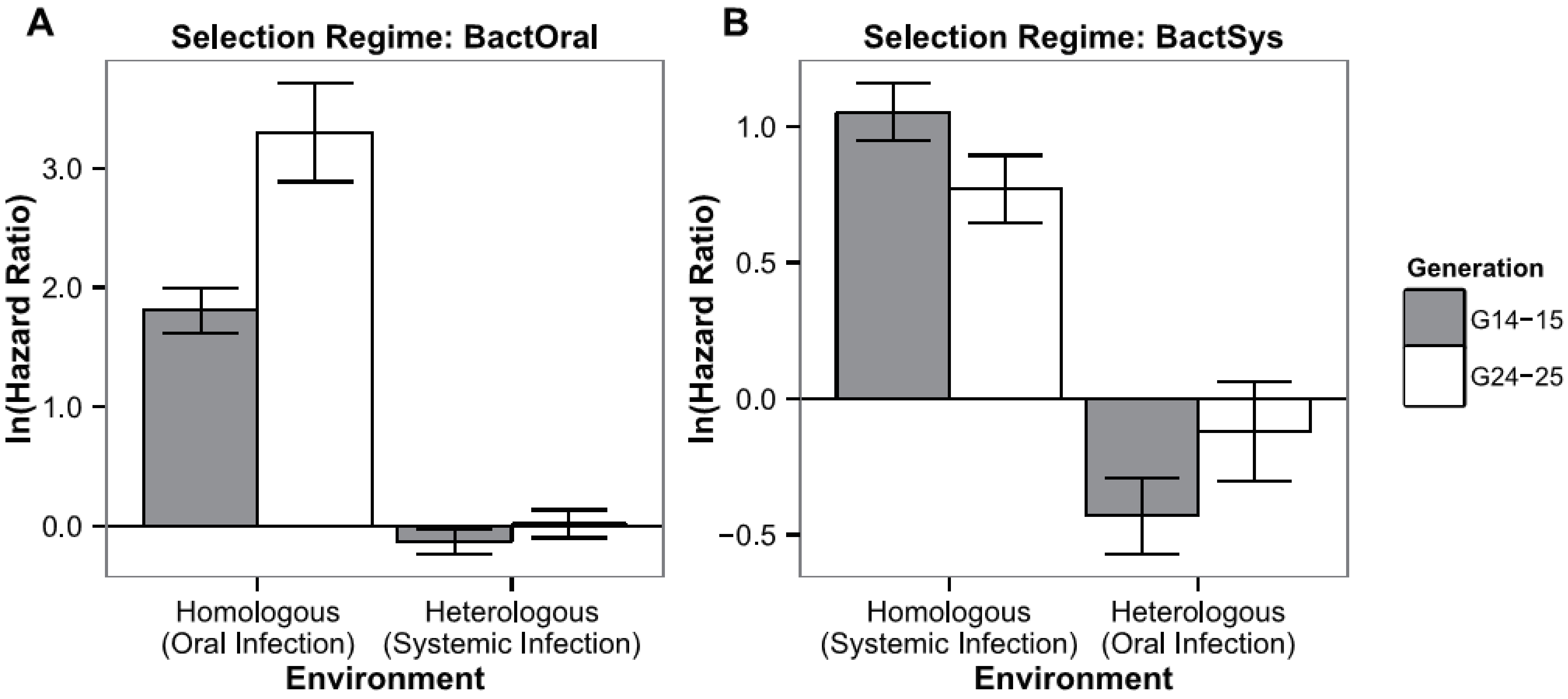
Costs in more extreme environments?



NO!

Faria et al. 2015 Evolution

Trade-off between resistance to different infection modes?

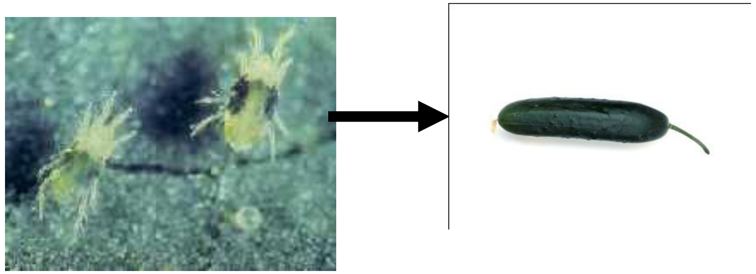


NO!

Martins et al. 2013 PloS Pathogens

Are there trade-offs during adaptation to novel environments?

Isabelle Olivieri



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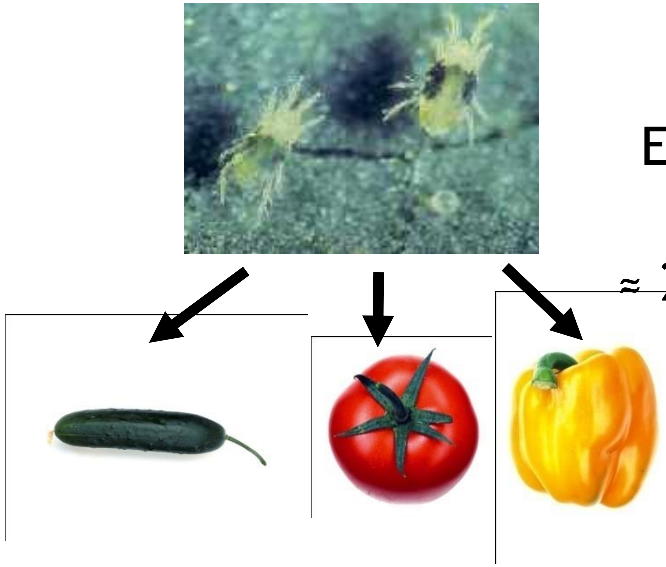
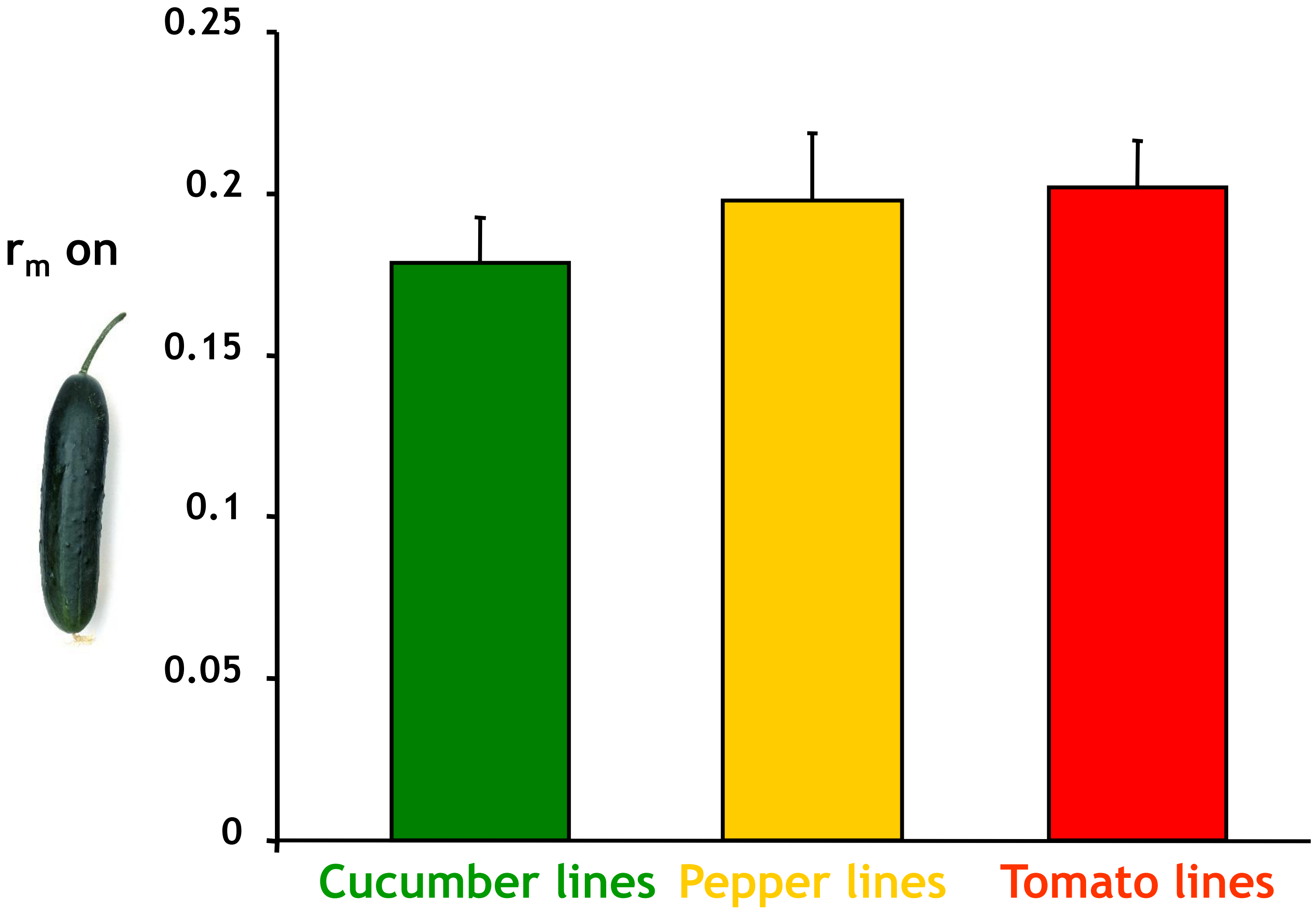


EXPERIMENTAL EVOLUTION

≈ 25 generations

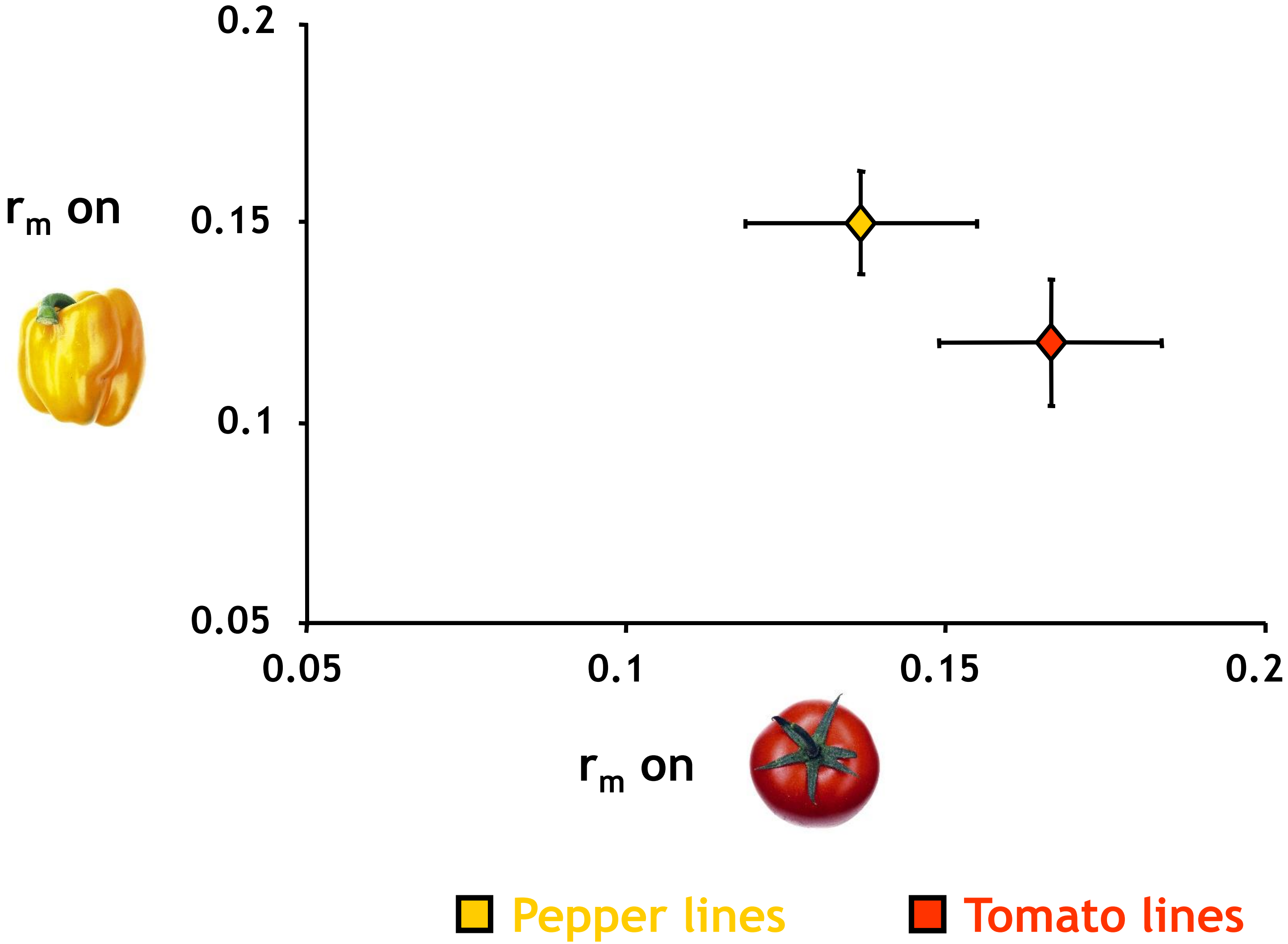
5 lines per selection regime

Performance on the ancestral host



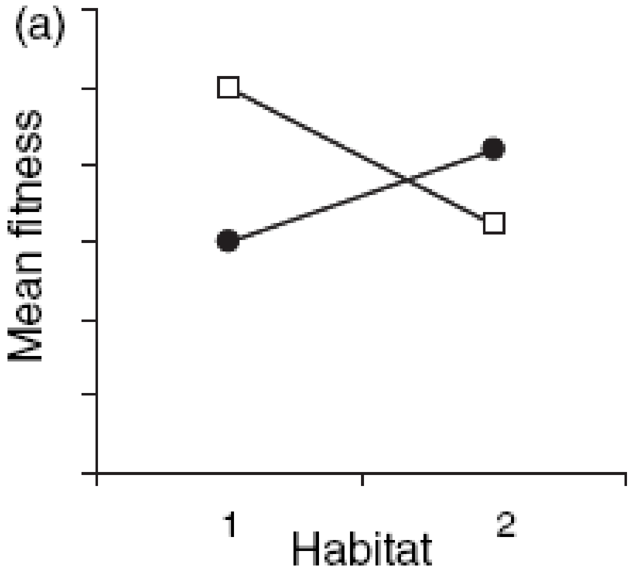
Magalhães et al. BMC Evol. Biol. 2009

Performance on the other novel host

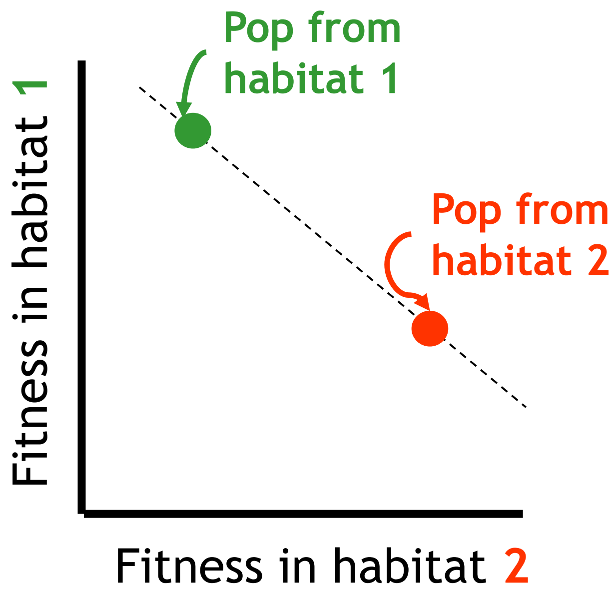


Magalhães et al. BMC Evol. Biol. 2009

Local adaptation

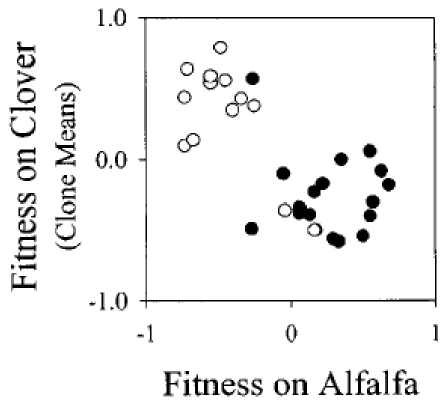


That is,



□ Population from habitat 1

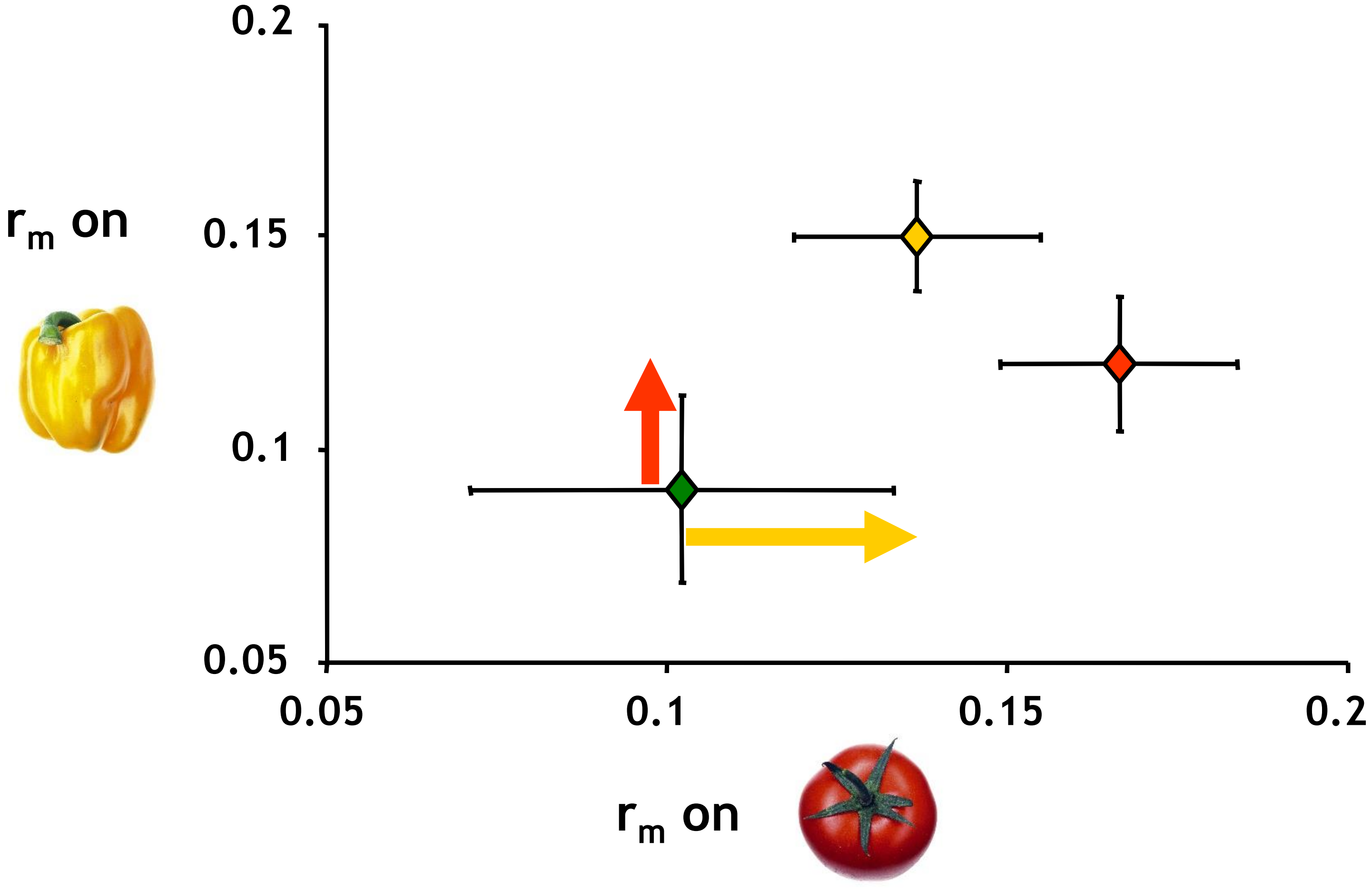
● Population from habitat 2



Kawecki & Ebert Ecol Lett 2004

Via and Hawthorne Am Nat 2002

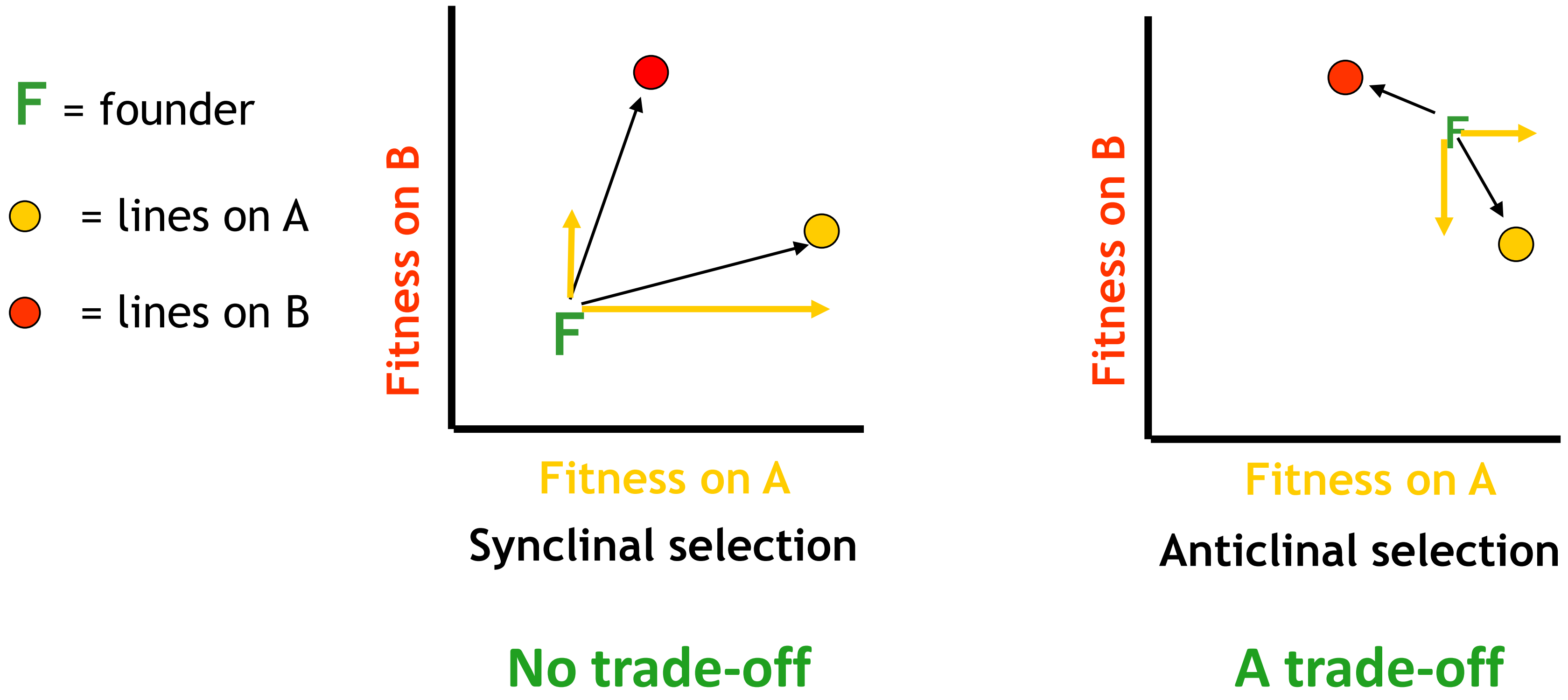
Performance on the other novel host



Cucumber lines   Pepper lines   Tomato lines

Magalhães et al. BMC Evol. Biol. 2009

Don't confuse pattern and process!



Bell and Reboud, Heredity 1997

How can we guarantee that experimental evolution will produce super-bugs?

- For a trait to evolve by natural selection, there has to be genetic variation for that trait in the population.

THIS IS OFTEN THE CASE, but may depend on the population and trait.

- For a trait to evolve, it has to respond to a selection pressure.

THIS IS OFTEN THE CASE, but we should be explicit about which traits are under selection.

- For an evolutionary change to be beneficial for biological control, no other relevant trait should trade off with the target trait.

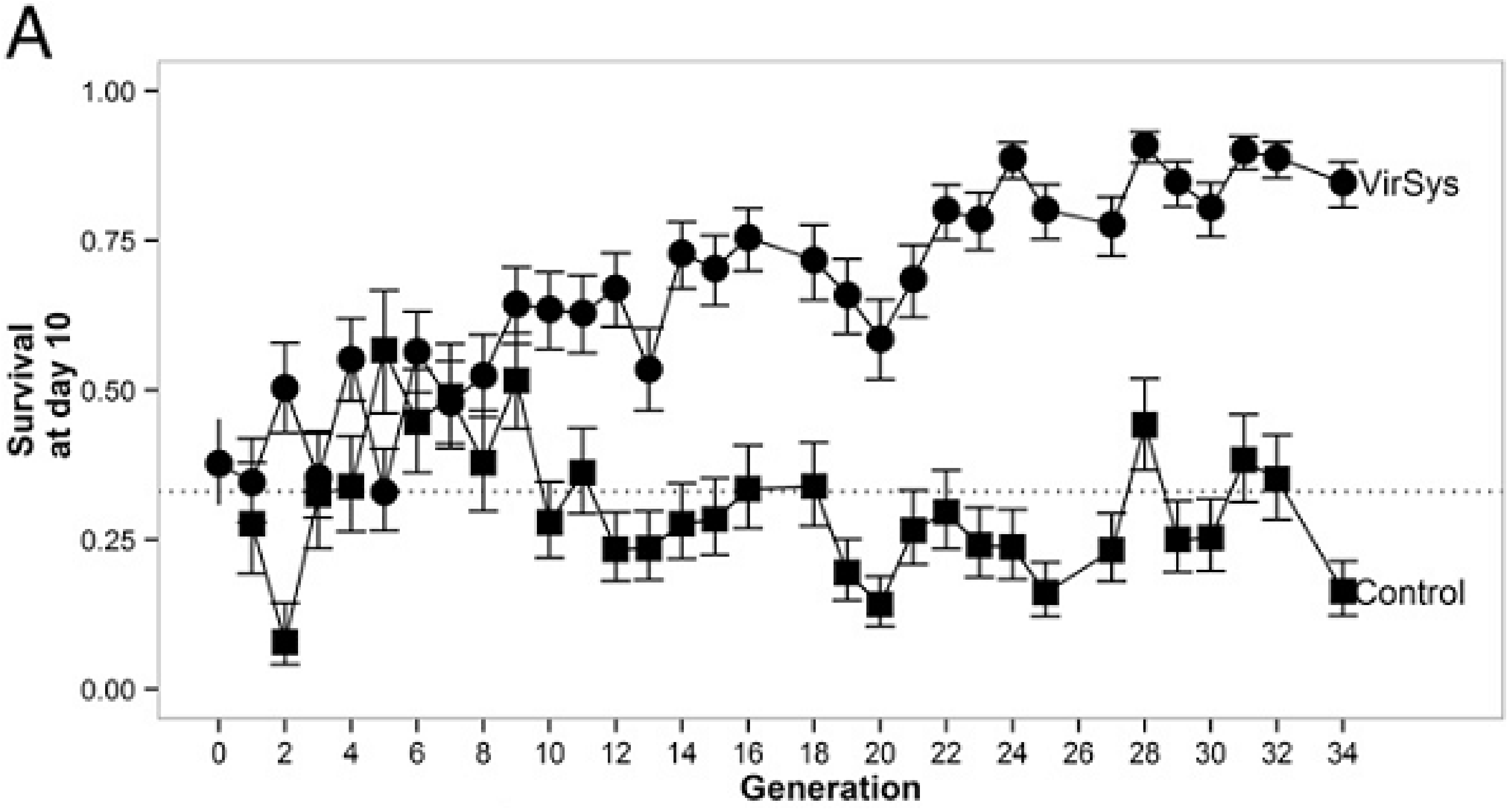
THIS MAY OFTEN BE THE CASE…

How can genomics contribute to improving natural enemies?

- If genetic changes underlying trait evolution have a simple genetic basis, then (in the near future) it may be possible to genetically manipulate biocontrol agents (e.g., CRISPR-CAS9) and introduce the alleles of choice in any population.

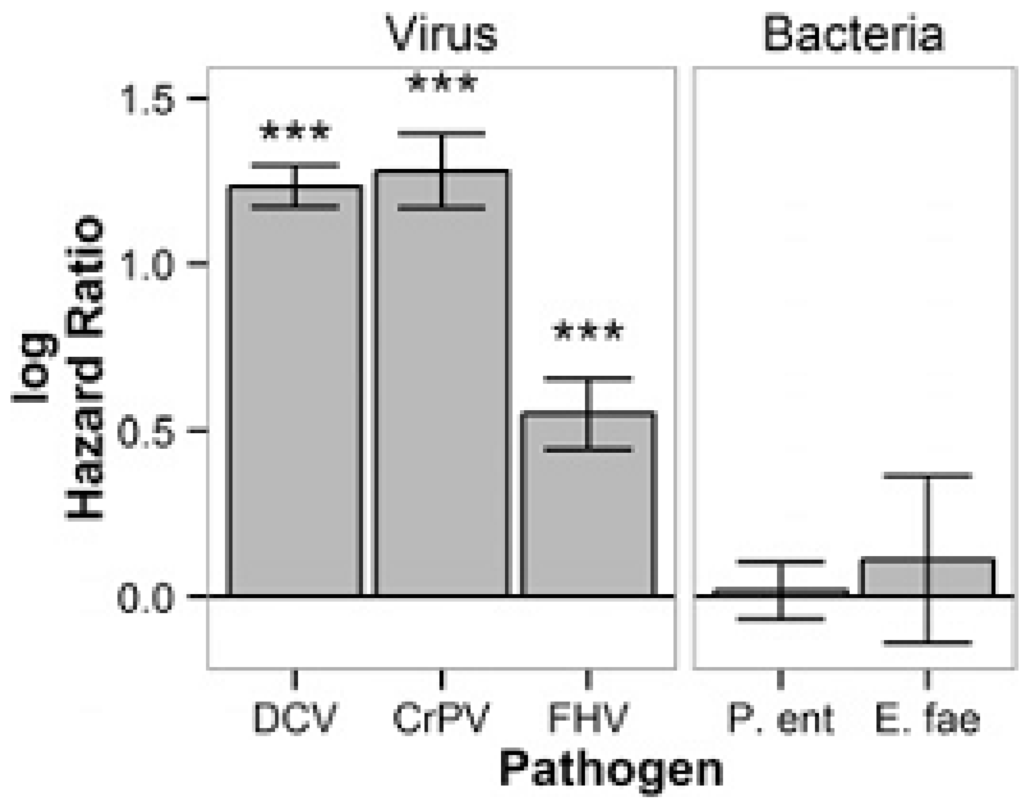
- Identifying the basis of trade-offs, or any correlated response to selection, may allow manipulating the environment in which biocontrol agents are placed in order to maximize their efficiency.

Adaptation to viral infection



Martins et al. PNAS 2014

Does adaptation entail a cost in other environments?



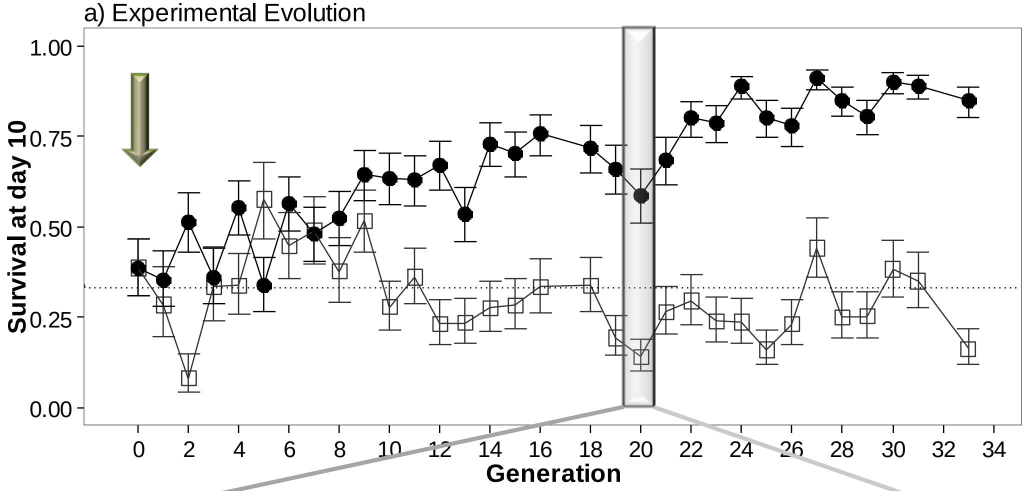
Flies evolving with DCV were more resistant to other viruses than control lines.
This adaptation did not affect performance when flies were exposed to bacteria.

Martins et al. PNAS 2014

What is the genetic basis of adaptation to viruses?

Luis Teixeira

Christian Schlötterer

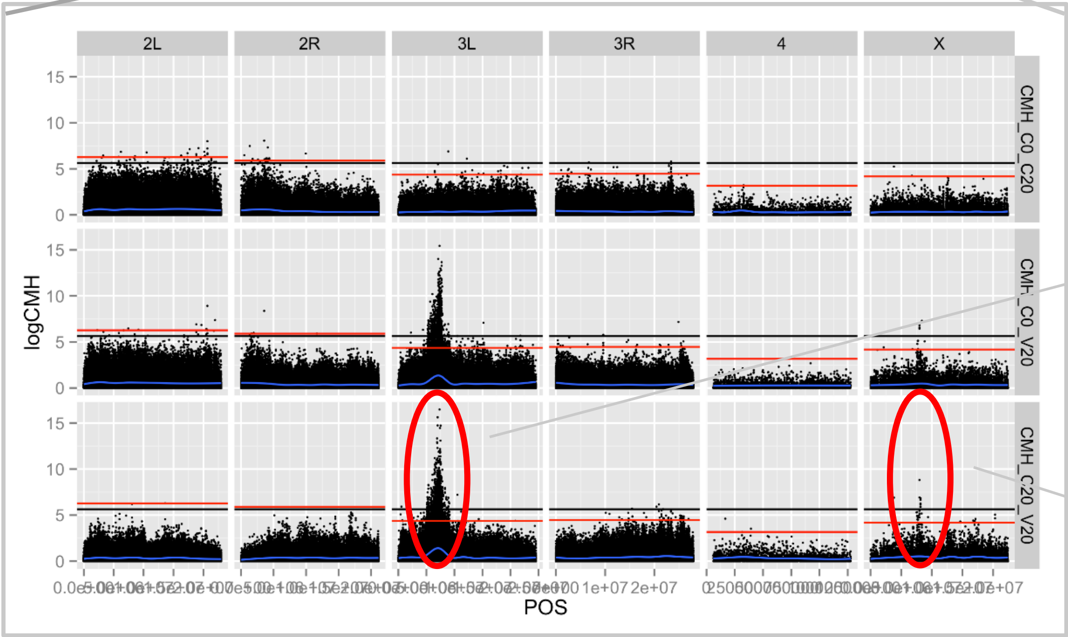


PoolSeq

Base pop vs Control at G20

Base pop vs Vir-sel at G20

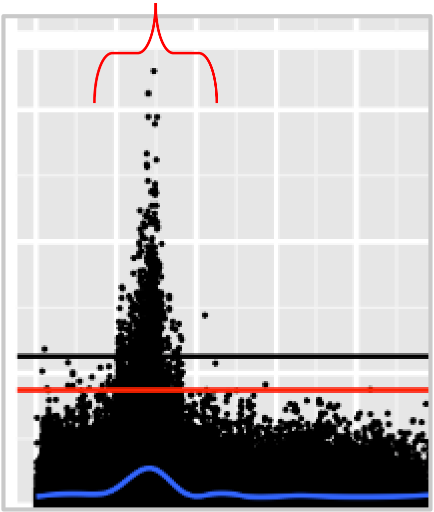
Control at G20 vs Vir-sel at G20



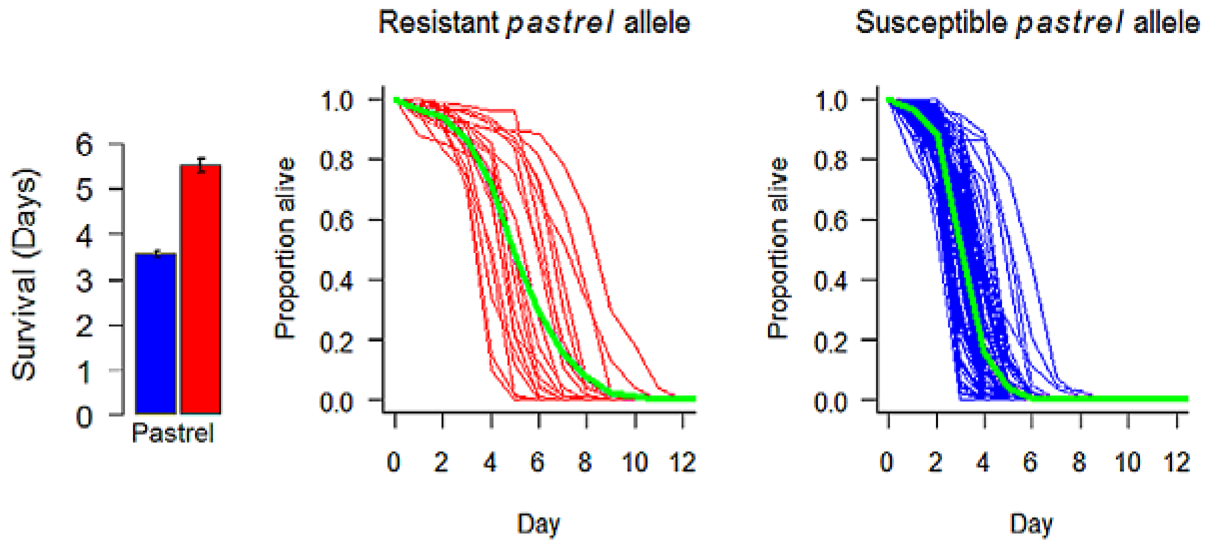
Region with ~ 300 genes

UbcE2H

Genes in the 3L-selected region

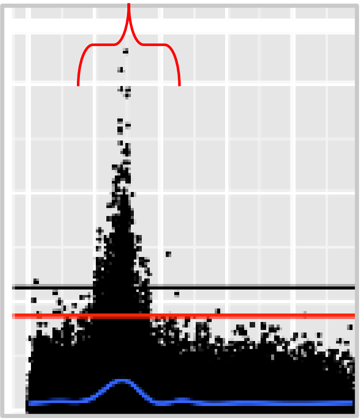


The region peaks at Pastrel (pst), a gene that has been implied in DCV resistance using *Drosophila* inbred lines



Magwire et al. Plos Genet 2012

Candidate genes



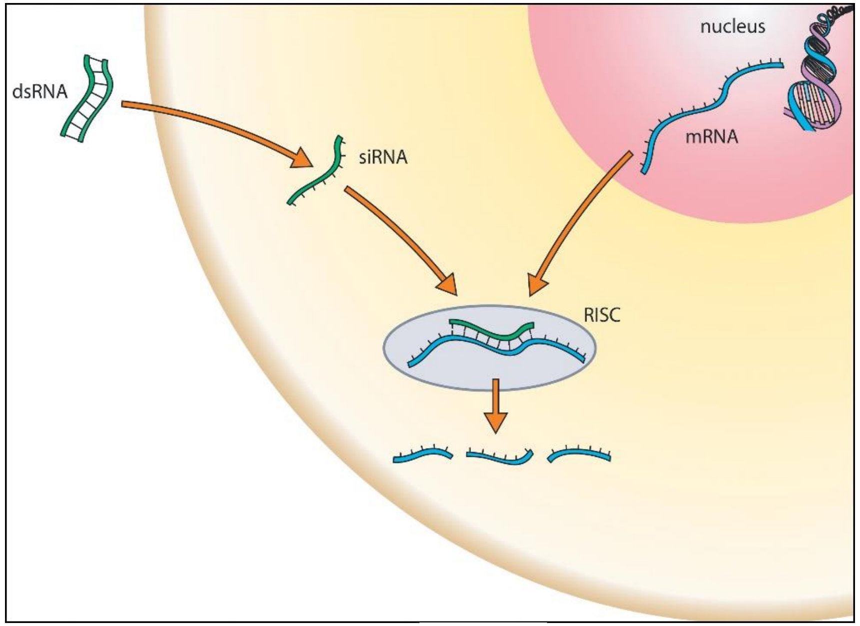
12 non-synonymous coding SNPs in 9 genes

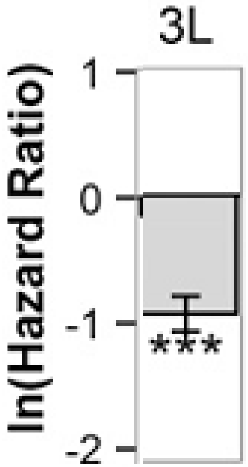
DEFICIENCIES			CANDIDATES	SNPs	Int	syn	n sy	up	dwn	utr	Prot	> 1al	Adul	M&F	Expression	
	1	2	Or65b	3		2	1									olfactory receptor activity/ **sensory** perception of smell
	1		ndl	2			2							ov		**serine-type** peptidase activity
	4	5	CG9953	2		1	1								**high**	**serine-type** carboxypeptidase activity
		7	mus312	5	1		1		1	3				ov		**protein binding**/meiotic chromosome segregation
	8	9	pst	2			2								**high**	olfactory learning; **learning or memory**; **protein secretion**
		9	Cyp316a1	2		1	1									electron carrier activity/ **oxidation-reduction** process
10	8	11	Ank2	10	6	1	1			2						cytoskeletal protein binding/ **sensory** perception of sound
10	8	11	CG7457	1			1									NK (Protein features are: **Ankyrin repeat**)
10	14	11	CG8492	4		2	2								**high/mod**	**lysozyme** activity/ **antimicrobial humoral response**

What is the effect of these genes on resistance to DCV?

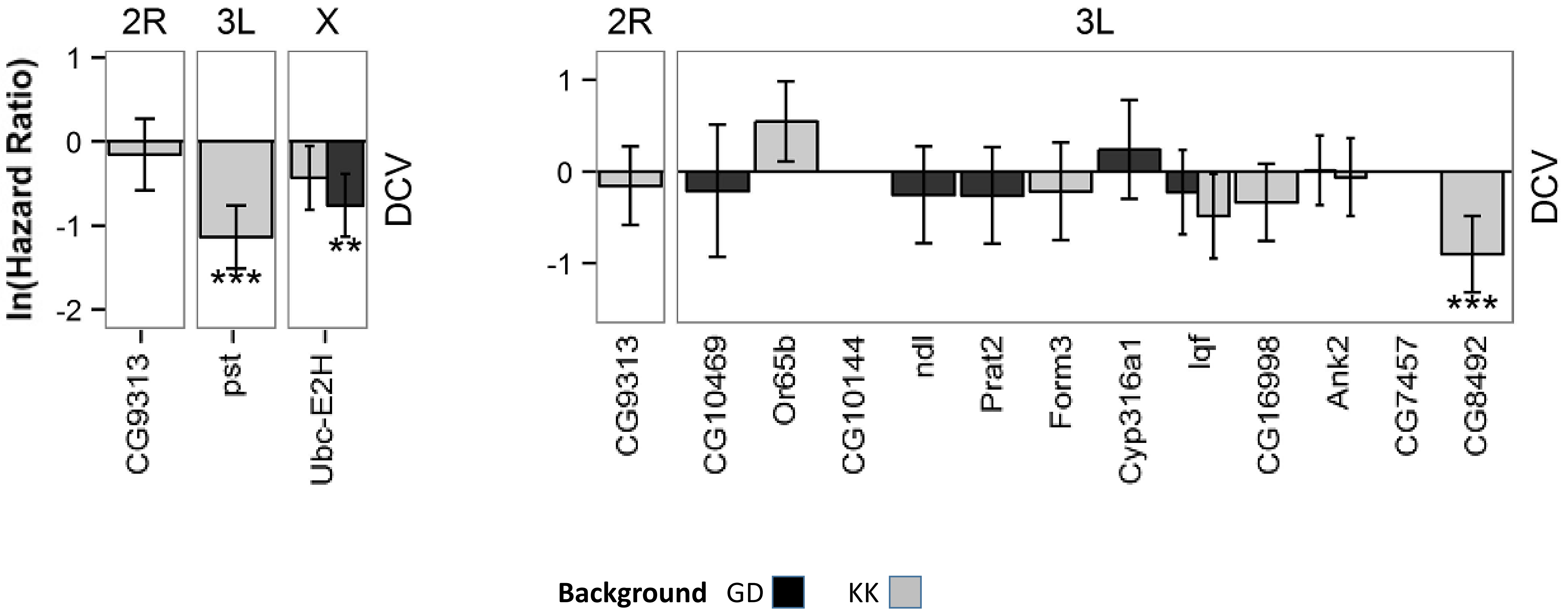
The wonders of Drosophila genetics: RNAi lines

- RNA interference (RNAi) is a process by which an RNA links to an mRNA and blocks gene expression.
- The Drosophila community has created isogenic lines that express RNAi against particular genes.
- We have ordered RNAi lines against the candidate genes that we have identified in the 3L region.
- We then exposed these lines to DCV.
- If the gene targeted by the RNAi would have an effect on DCV resistance, then their survival when exposed to DCV would be reduced relative to control lines.





Functional validation using RNAi lines



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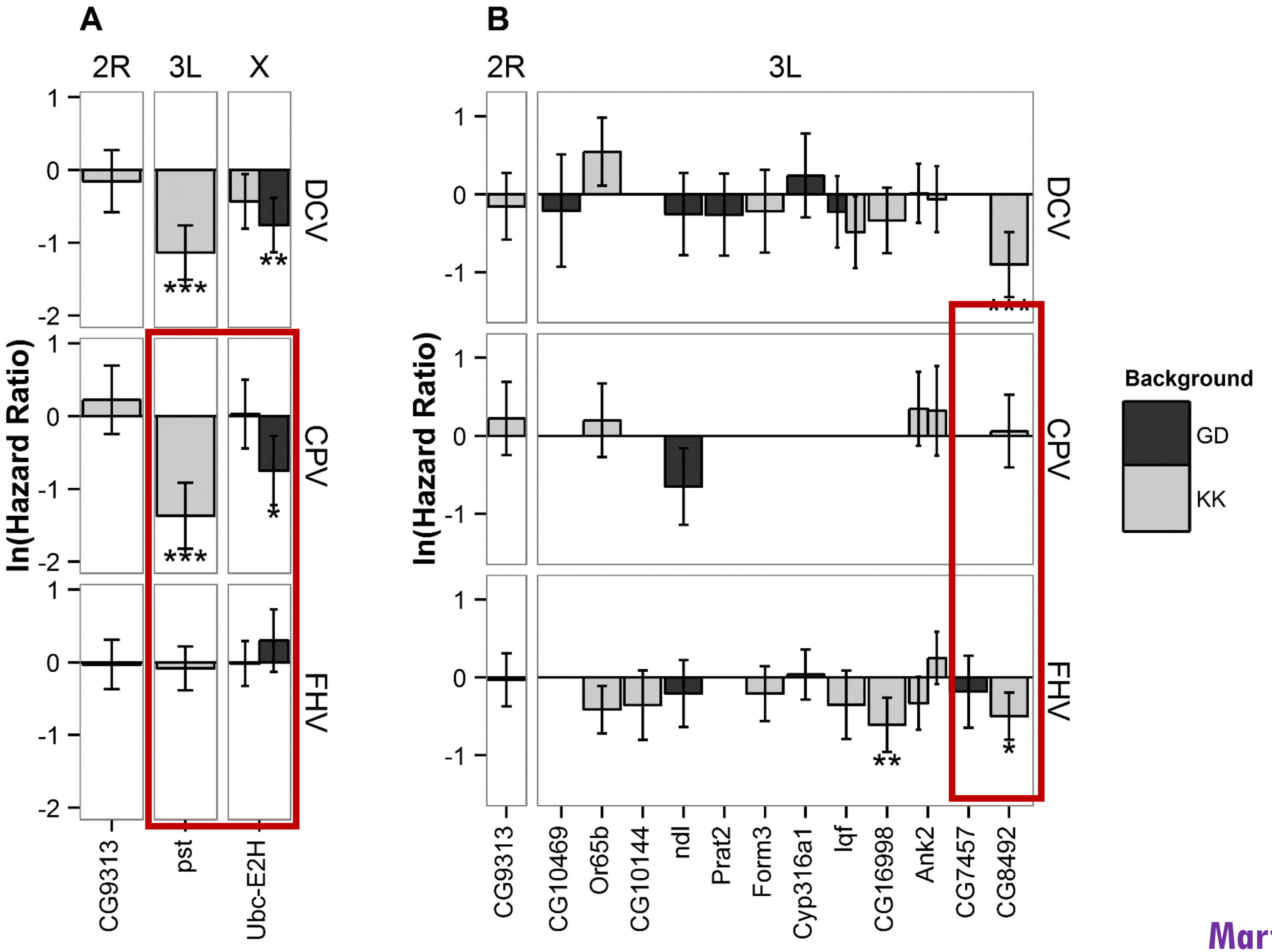
Genes with different cross-resistance properties



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Conclusions

- The field is incipient: few studies have used experimental evolution on biocontrol agents, and most studies are poorly replicated and do not use common environments to test for evolutionary changes.
- Adapting to one environment / trait changes may occur at a rapid pace -> hope for improvement of current biocontrol agents.
- Adaption often entails no trade-offs.
- Knowledge of the genetic basis of adaptation of both predators to prey and prey to predators may help us design future control strategies.

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And especially…