

# **Individual-level causes and population-level consequences of variation in fitness in an Alpine rodent**

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**Timothée Bonnet**

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**University of  
Zurich<sup>UZH</sup>**



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- Lukas Keller
- Barbara Tschirren
- Arpat Ozgul
- Marc Kéry
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- Marjolein Bruijning
- Eelke Jongejans
- Pirmin Nietlisbach
- Philipp Becker
- Judith Bachmann





# Phenotypic variation within population



# Phenotypic variation within population



# Fitness variation

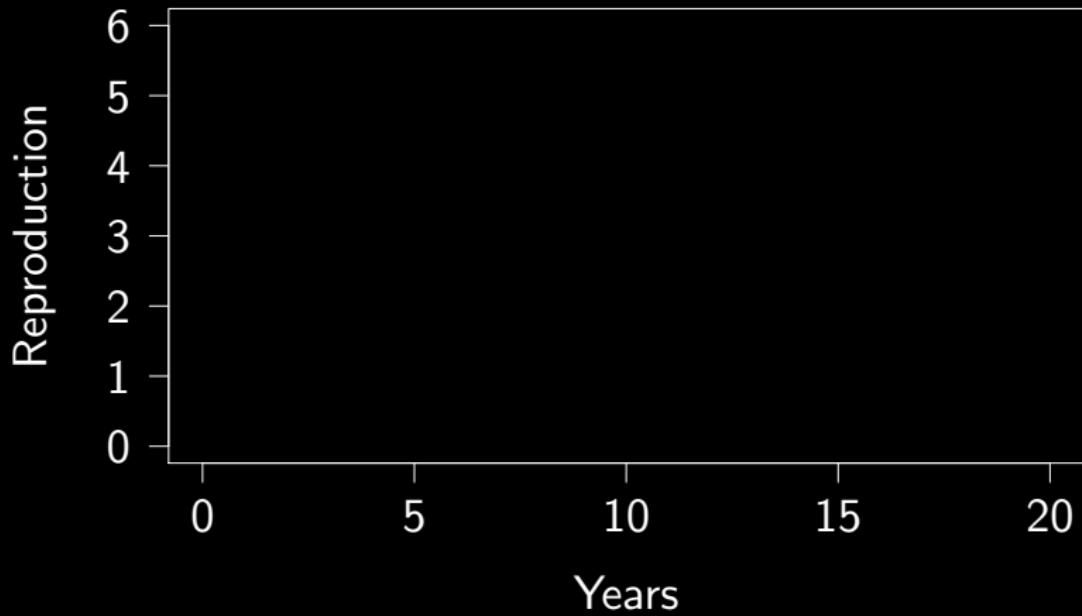


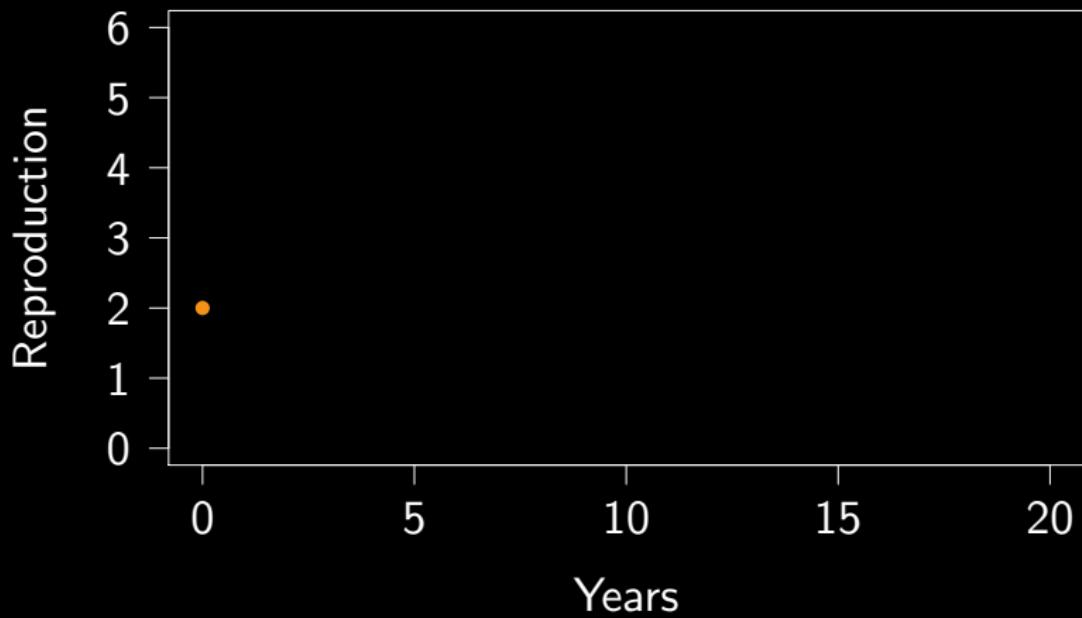
## What is fitness?

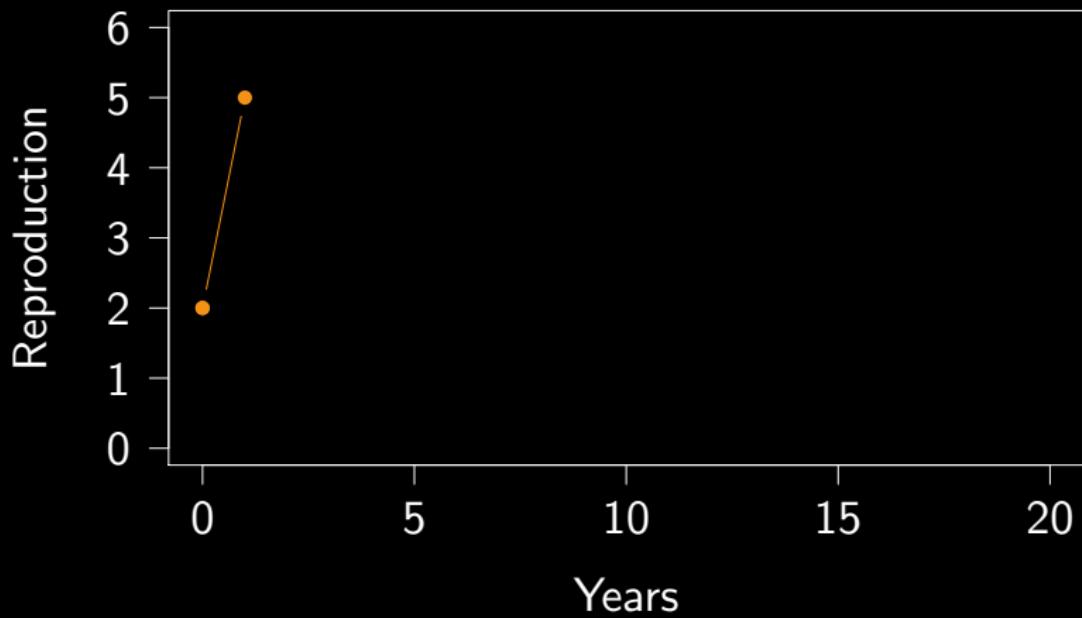
The expected relative contribution of an individual to the next generation

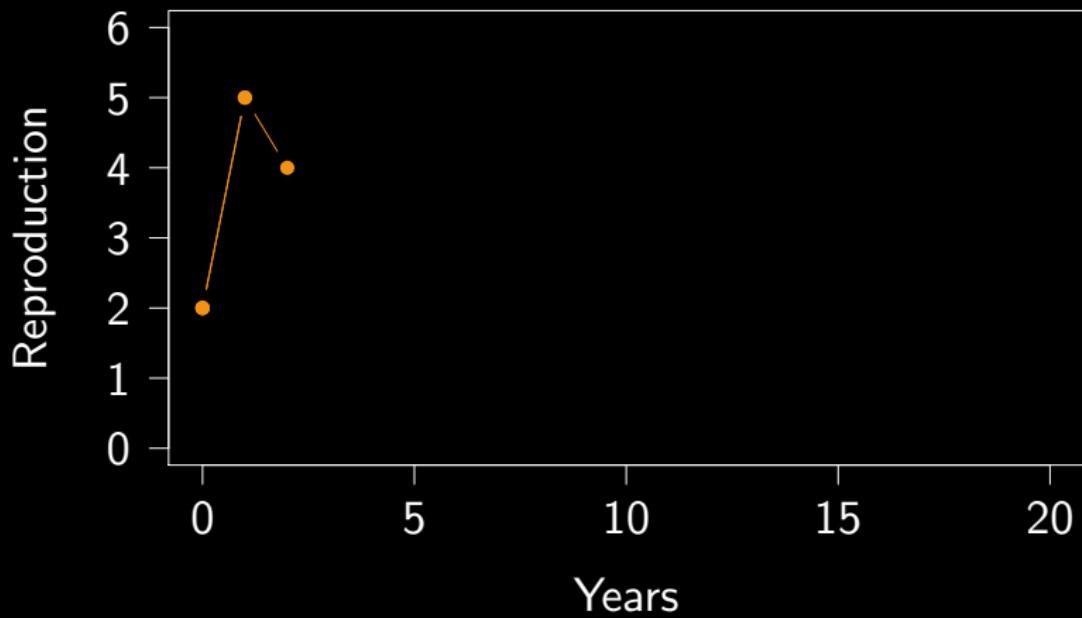
**Chance or fate? Why do survival  
and fertility vary?**

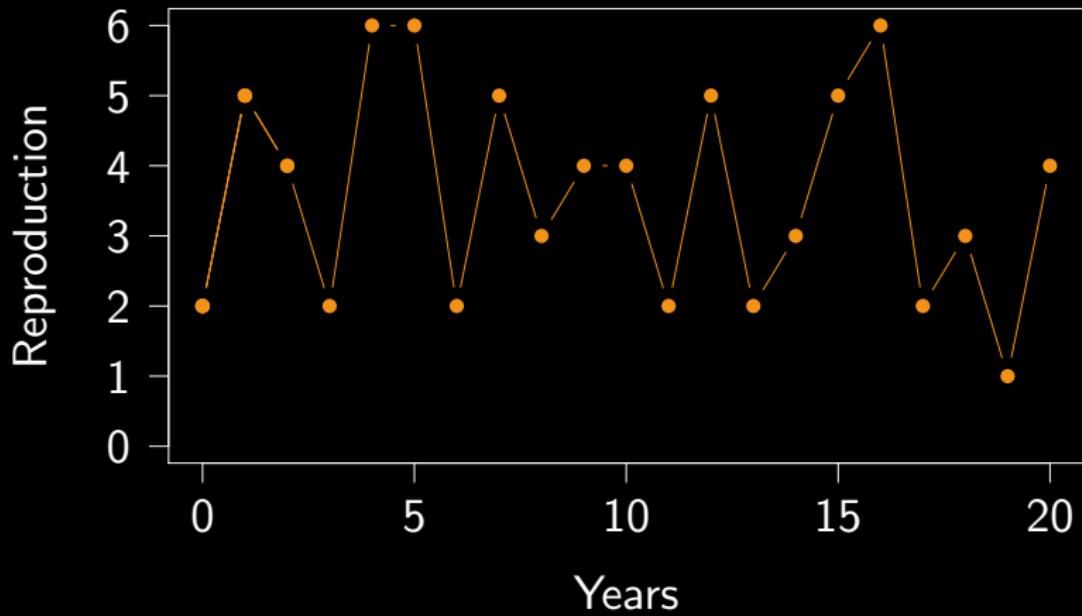
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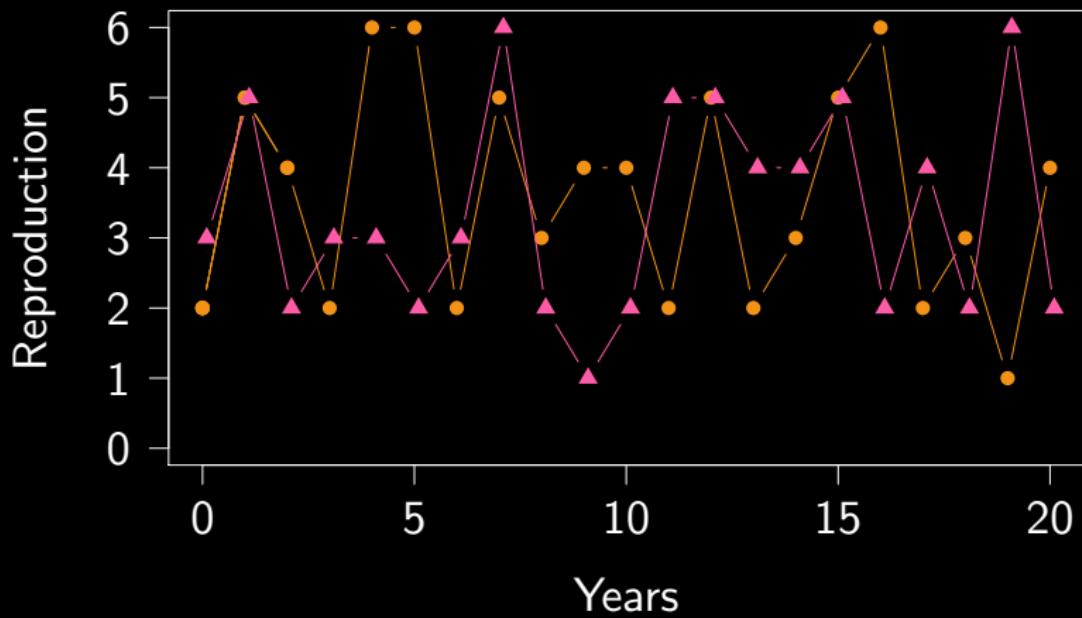


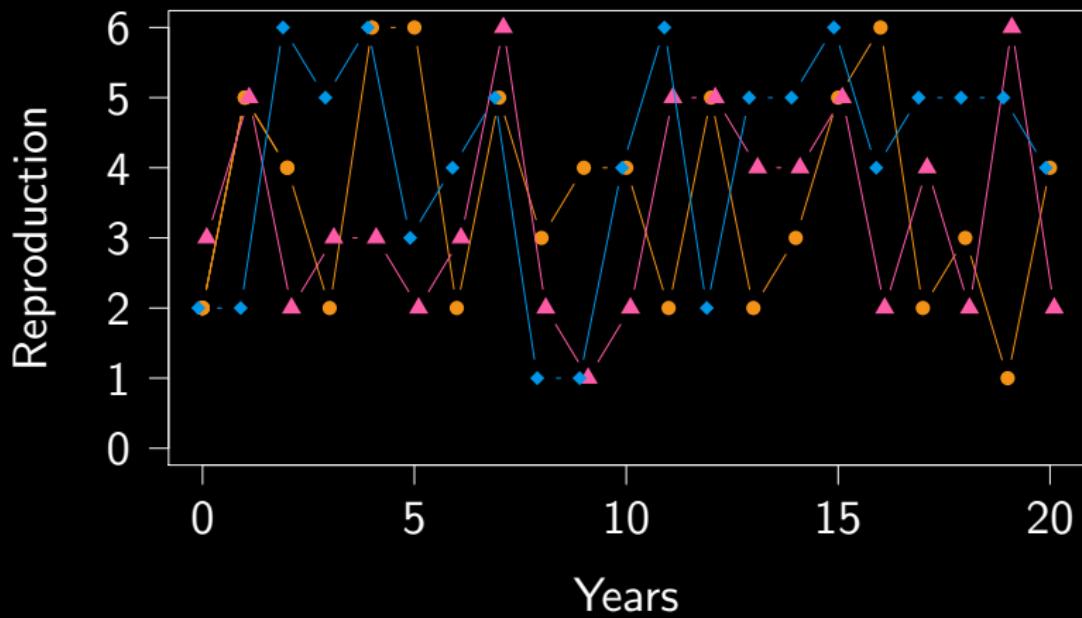




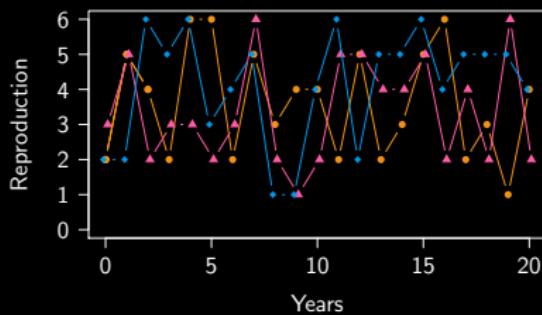




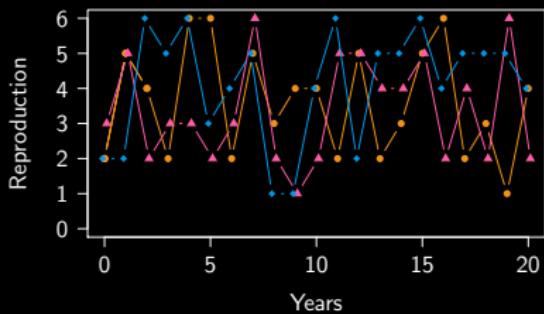




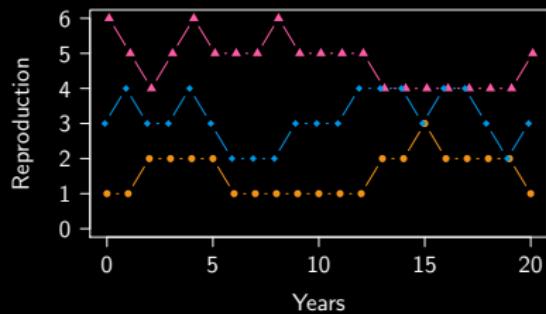
## One dice theory



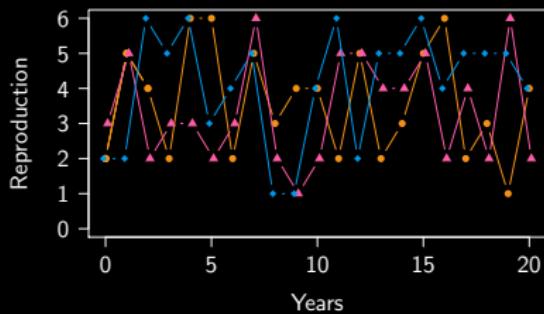
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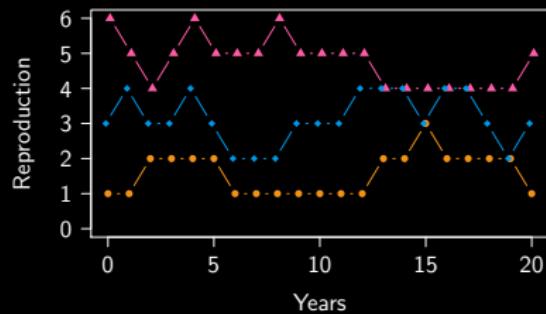
## Real pattern



## One dice theory



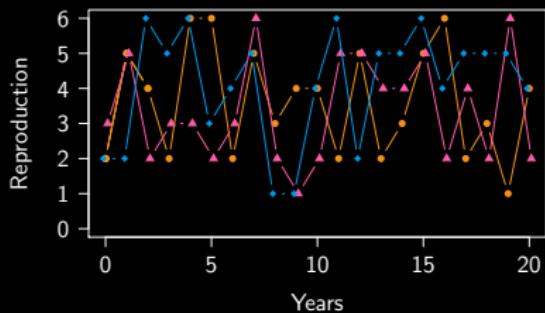
## Real pattern



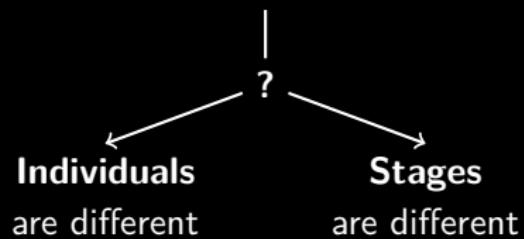
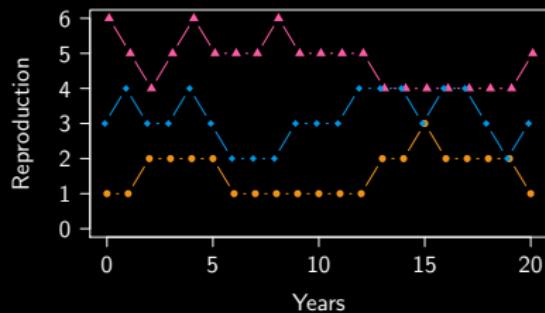
Individuals  
are different

?

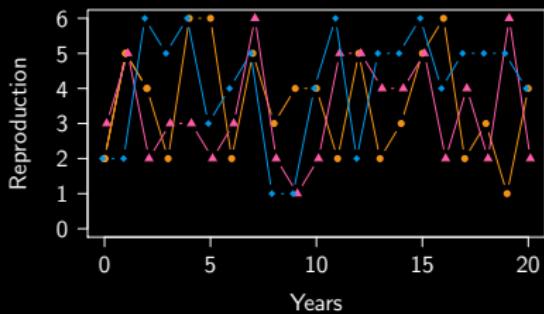
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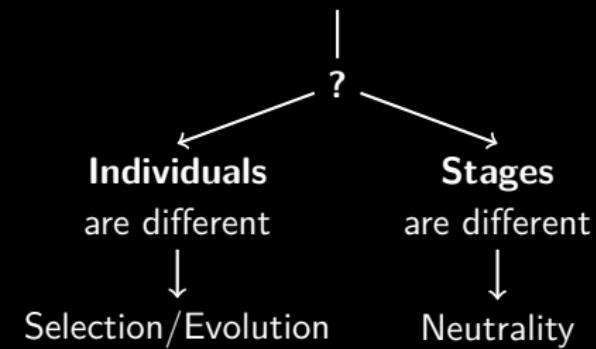
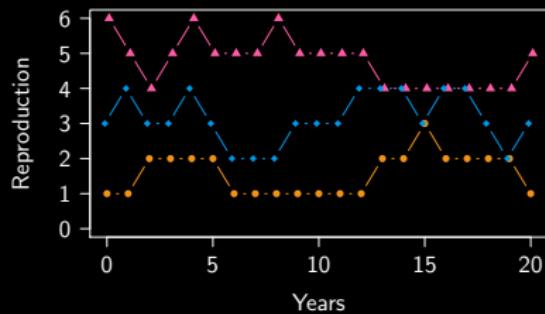
## Real pattern



## One dice theory



## Real pattern



# The neutral theory

PNAS

## Neutral theory for life histories and individual variability in fitness components

Ulrich Karl Steiner<sup>a,b,1</sup> and Shripad Tuljapurkar<sup>a</sup>

<sup>a</sup>Department of Biology, Stanford University, Stanford, CA 94305; and <sup>b</sup>Institut National de la Santé et de la Recherche Médicale U1001, Université Paris Descartes, 75014 Paris, France

Edited\* by Burton H. Singer, University of Florida, Gainesville, FL, and approved February 3, 2012 (received for review December 3, 2010)

Individuals within populations can differ substantially in their life spans and their lifetime reproductive success, but such realized fitness components are often highly correlated. This suggests that stochastic variation in fitness components may be small enough to be negligible. We show here that this is not the case, and that this stochastic variation has significant implications for both ecological and evolutionary studies.

### Neutral matrix method

		next year		
		1	2	3
1	1	0.9	0.08	0.02
	2	0	0.7	0.3
3	3	0	0.2	0.8

No variation in fitness among individuals

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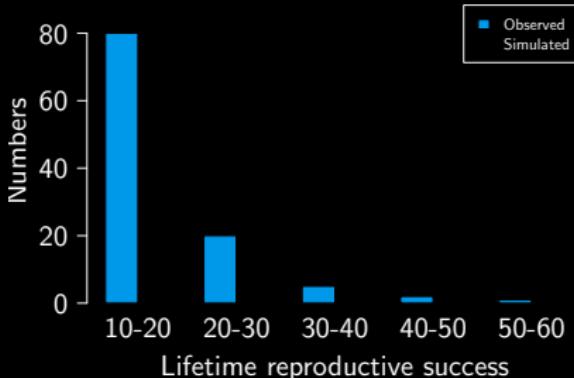
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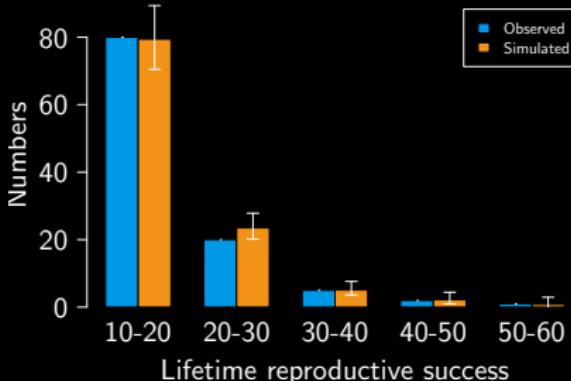
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No variation in fitness among individuals

# Conflicting results

Neutral matrix method

Mixed model method &  
Quantitative genetics



# Conflicting results

## Neutral matrix method

- No significant differences between individuals

## Mixed model method & Quantitative genetics

### Journal of Animal Ecology

*Journal of Animal Ecology* 2010, **79**, 436–444



doi: 10.1111/j.1365-2656.2009.01653.x

### Dynamic heterogeneity and life history variability in the kittiwake

Ulrich K. Steiner<sup>1\*</sup>, Shripad Tuljapurkar<sup>1</sup> and Steven Hecht Orzack<sup>2</sup>

# Conflicting results

## Neutral matrix method

- No significant differences between individuals

## Mixed model method & Quantitative genetics

- Individual performances are

Oikos 122: 739–753, 2013

doi: 10.1111/j.1600-0706.2012.20532.x

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Subject Editor: Matthew Symonds. Accepted 7 June 2012

## Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population

Emmanuelle Cam, Olivier Gimenez, Russell Alpizar-Jara, Lise M. Aubry, Matthieu Authier, Evan G. Cooch, David N. Koons, William A. Link, Jean-Yves Monnat, James D. Nichols, Jay J. Rotella, Jeffrey A. Royle and Roger Pradel

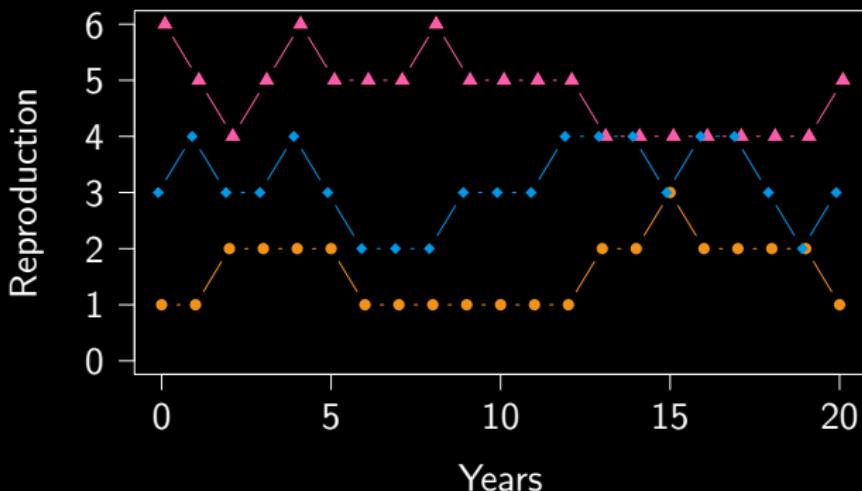
# Conflicting results

## Neutral matrix method

- No significant differences between individuals
- ... because of stage structure

## Mixed model method & Quantitative genetics

- Individual performances are repeatable



# Conflicting results

## Neutral matrix method

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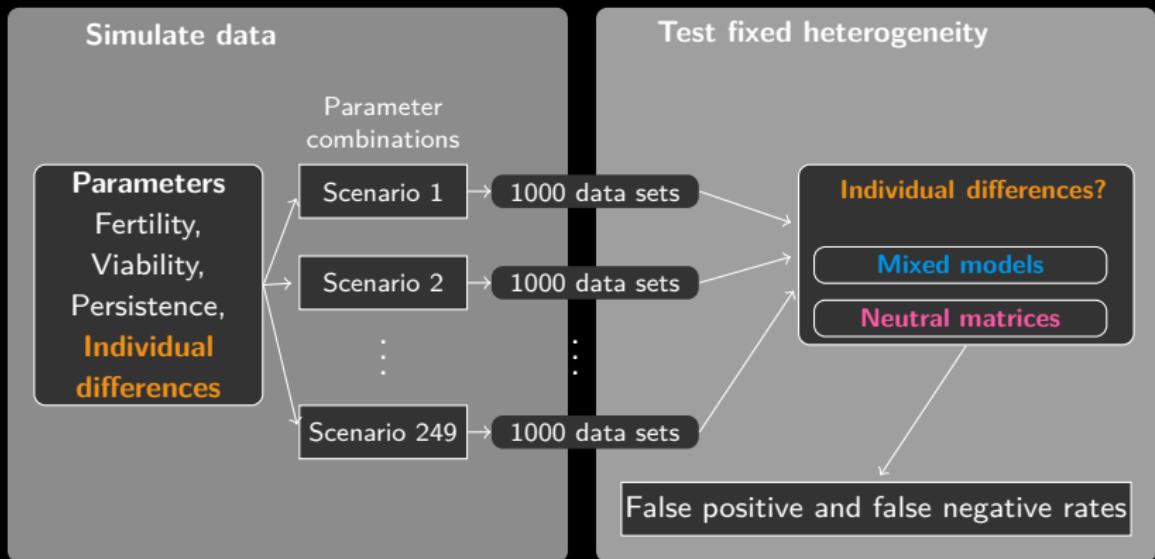
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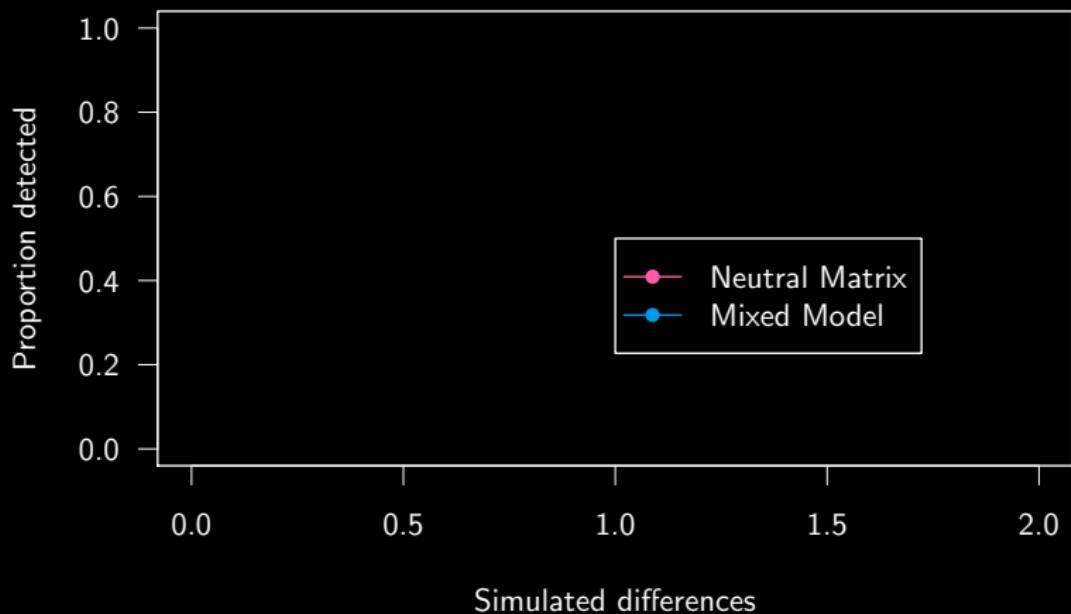
## Why?

- Neutral matrix method =false negative?
- Mixed model method =false positive?

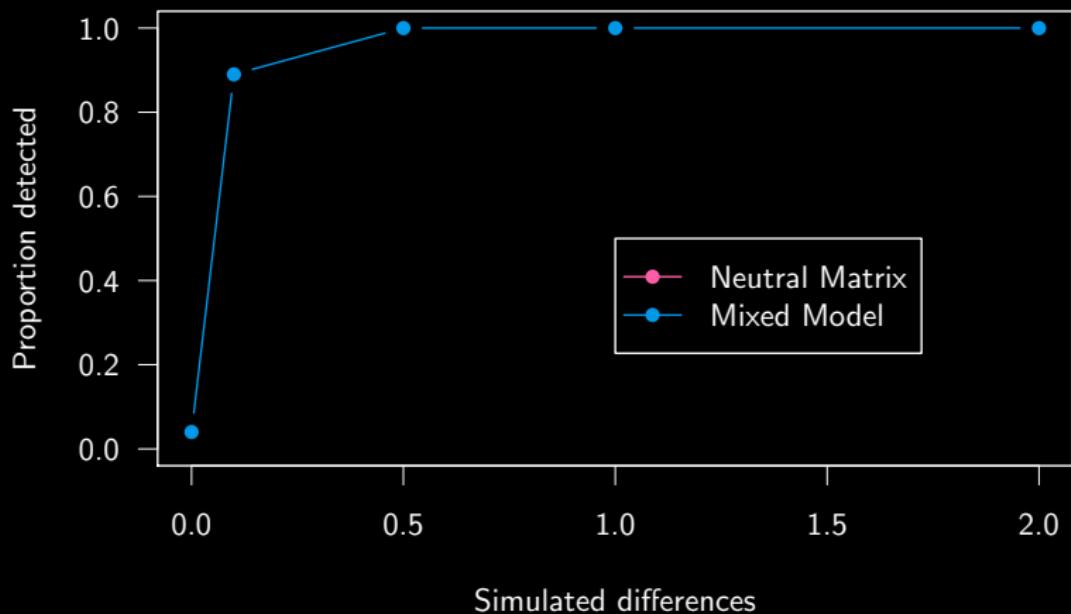
# Method



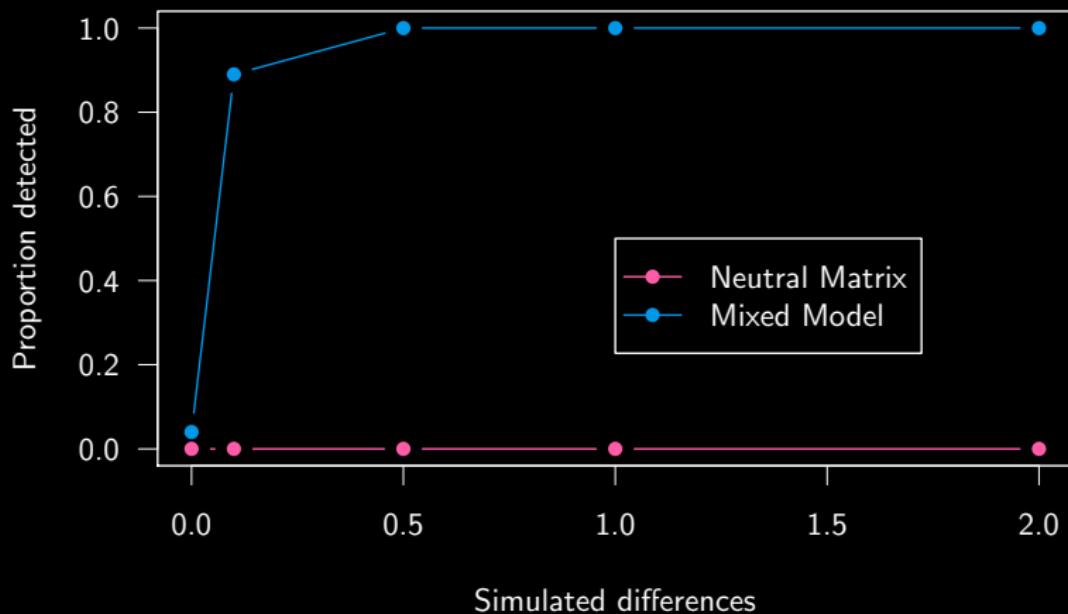
# Results



# Results



# Results



# Conclusion

Why conflicting methods?

# Conclusion

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- Neutral matrix method =false negative? YES
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# Conclusion

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→ Individual differences in fitness components are common

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- Neutral matrix method =false negative? YES
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## Implications

# Conclusion

## Why conflicting methods?

- **Neutral matrix method** =false negative? **YES**
- **Mixed model method** =false positive? **NO**

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## Implications

- Phenotypic variation in fitness → opportunity for selection

# Conclusion

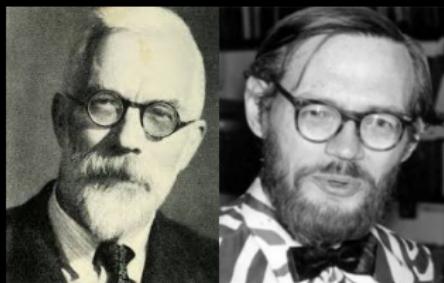
## Why conflicting methods?

- Neutral matrix method = false negative? YES
- Mixed model method = false positive? NO

→ Individual differences in fitness components are common

## Implications

- Phenotypic variation in fitness → opportunity for selection
- Heritability of fitness = evolution



R.A. Fisher    G. Price

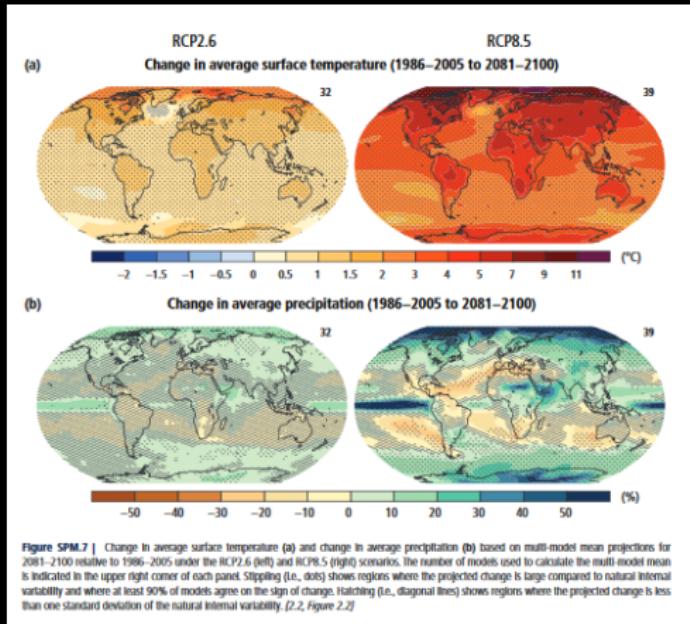
VOL. 187, NO. 1 THE AMERICAN NATURALIST JANUARY 2016

# Successful by Chance? The Power of Mixed Models and Neutral Simulations for the Detection of Individual Fixed Heterogeneity in Fitness Components

Timothée Bonnet\* and Erik Postma

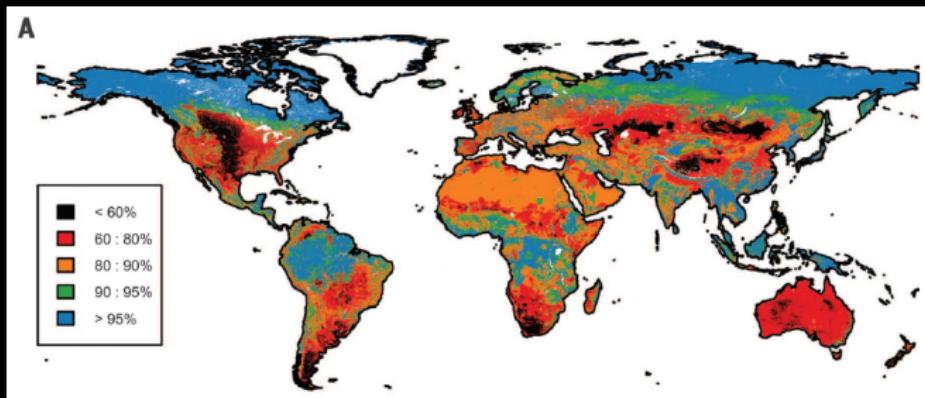


# Evolution in a changing world



Intergovernmental panel on climate change 5th Report (2014)

# Evolution in a changing world



Newbold & al. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science, 353

# Evolution in a changing world

## **Ecological and Evolutionary Responses to Recent Climate Change**

Annual Review of Ecology, Evolution, and Systematics

Vol. 37: 637-669 (Volume publication date December 2006)

First published online as a Review in Advance on August 24, 2006

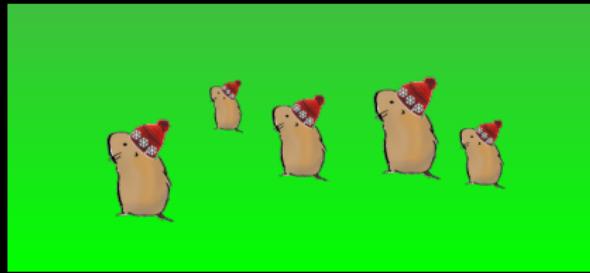
DOI: 10.1146/annurev.ecolsys.37.091305.110100

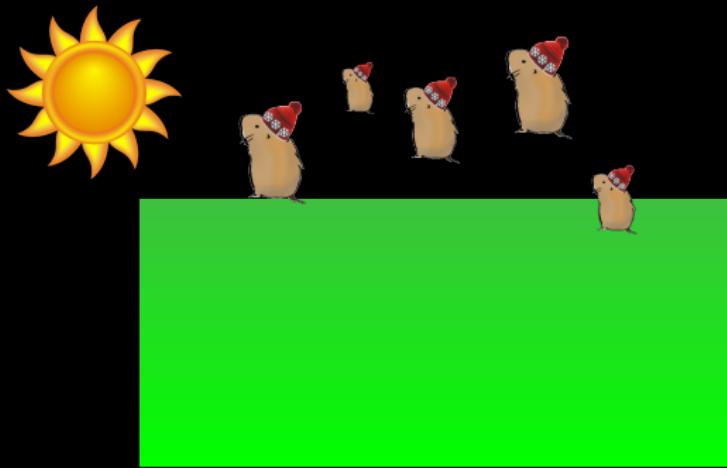
**Camille Parmesan**

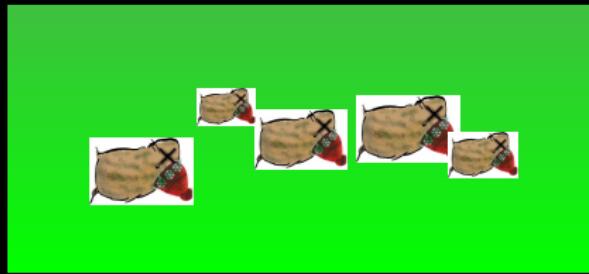
Section of Integrative Biology, University of Texas, Austin, Texas 78712; email:  
[parmesan@mail.utexas.edu](mailto:parmesan@mail.utexas.edu)

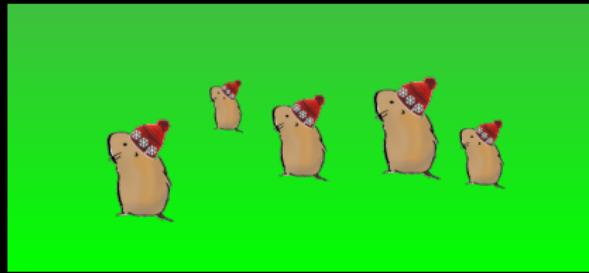




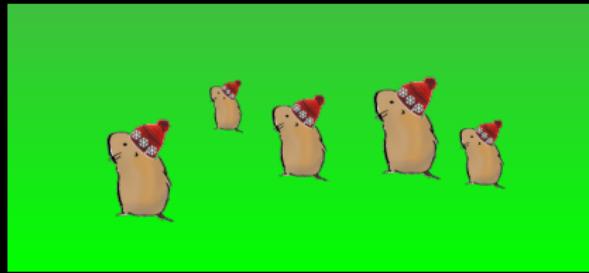


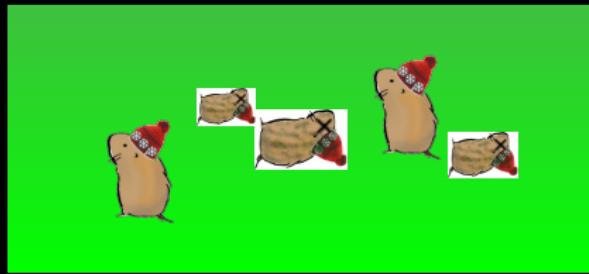


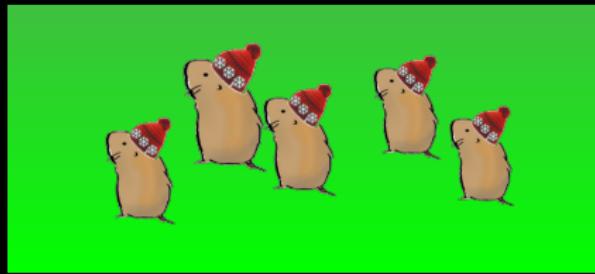












# **Evolution or plasticity? What drives phenotypic change?**

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# Evolution or plasticity?

1. **Age-structured Price's equation** - Coulson & Tuljapurkar (2008). The dynamics of a quantitative trait in an age-structured population living in a variable environment. *The American Naturalist*, 172(5)

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4. **Animal model** - Henderson (1950) Estimation of genetic parameters. *Annals of Mathematical Statistics*, 21

REVIEW

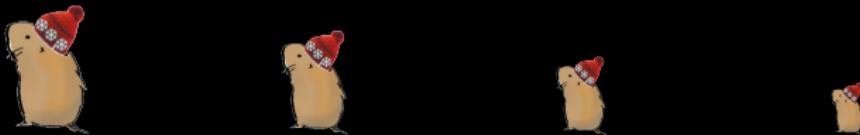
## Disentangling evolutionary, plastic and demographic processes underlying trait dynamics: a review of four frameworks

Koen J. van Benthem<sup>1\*</sup>†, Marjolein Bruijning<sup>2</sup>†, Timothée Bonnet<sup>1</sup>†, Eelke Jongejans<sup>2</sup>‡,  
Erik Postma<sup>1</sup>‡ and Arpat Ozgul<sup>1</sup>‡

<sup>1</sup>Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; and <sup>2</sup>Department of Animal Ecology and Physiology, Radboud University, 6500 GL Nijmegen, The Netherlands

Question	Animal model	Geber's method	Age-structured Price's equation	Integral projection models
Evolution?	++	+	--	--
Selection?	+	+	++	++
Heritability?	++	±	-	-
Changing age structure?	+	±	++	++

# The animal model



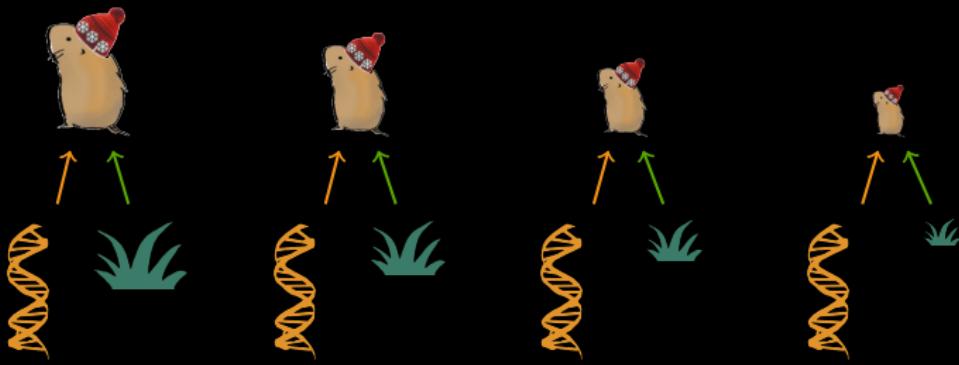
# The animal model



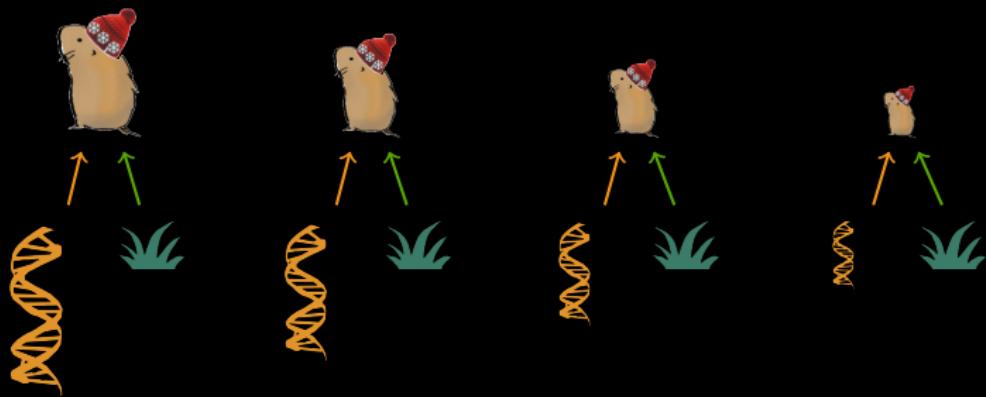
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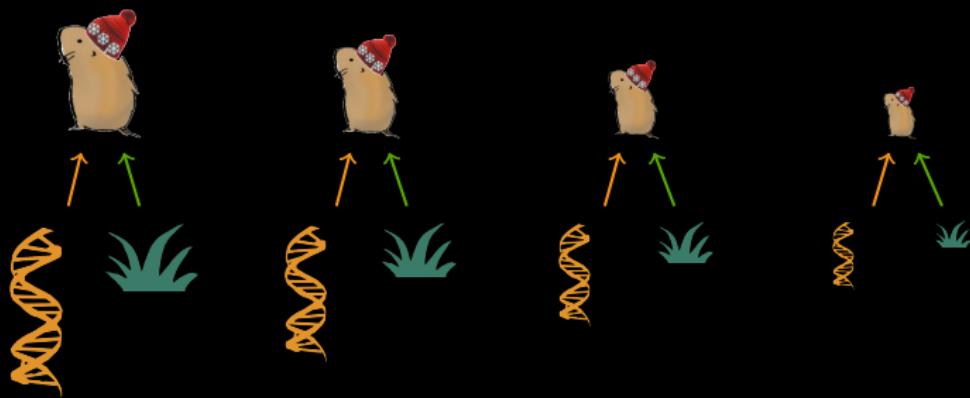
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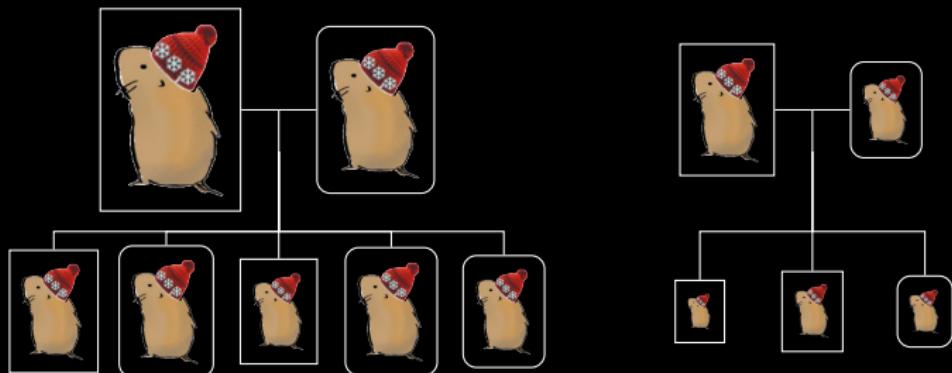
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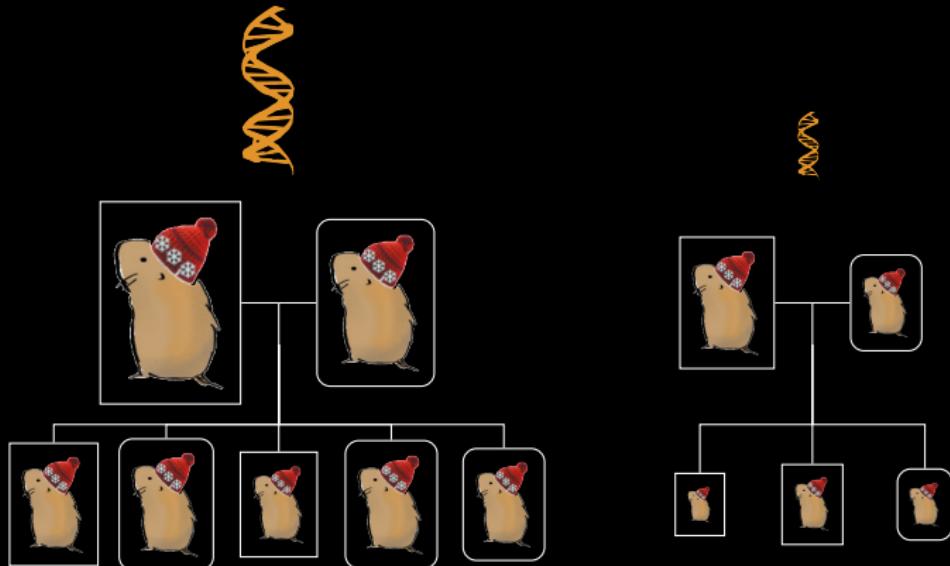
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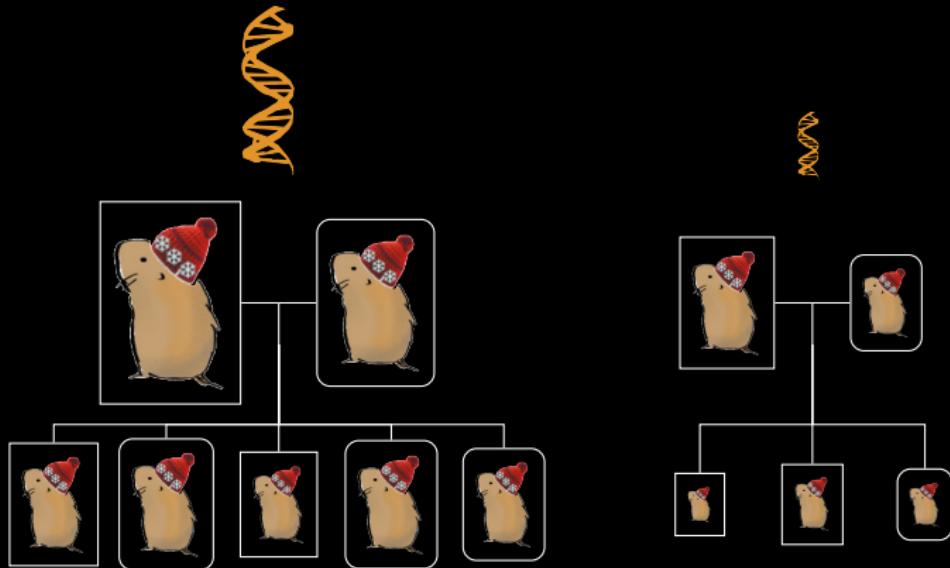
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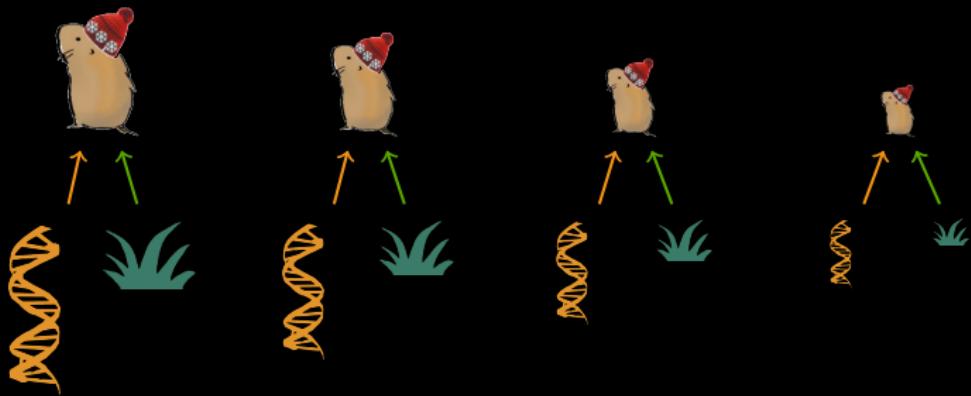
# The animal model



$$\text{Trait} = \text{Environment} - \text{Genotype}$$

The equation at the bottom decomposes a trait into its environmental and genetic components. On the left is a green plant icon. An equals sign follows, then a mouse icon wearing a red and white hat, and finally a minus sign followed by a yellow DNA double helix icon. This represents the additive effect of genes on a trait, adjusted for environmental influences.

# The animal model



# The animal model

Additive

Genetic

Variance

= variance



variance



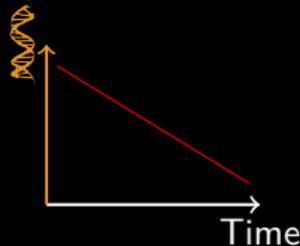
Heritability

$$= \frac{\text{variance}}{\text{variance}}$$

variance



Evolution





# Adaptive evolution in the wild

## Adaptive evolution in the wild

Adaptive evolution = Selection  $\times$  heritability

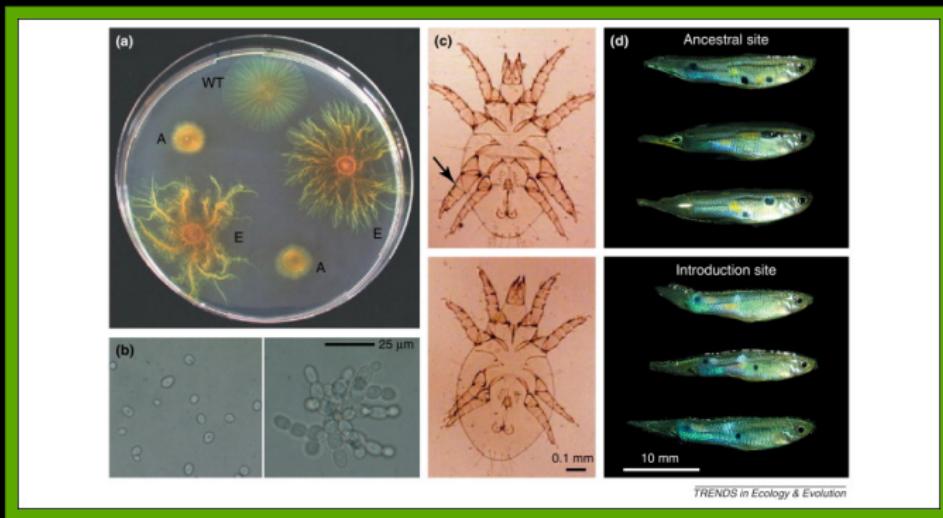
# Adaptive evolution in the wild

Adaptive evolution = Selection  $\times$  heritability



# Adaptive evolution in the wild

Adaptive evolution = Selection  $\times$  heritability



Experimental evolution. Kawecki & al. (2012) Trends in Ecology & Evolution 27(10)

# Adaptive evolution in the wild

Adaptive evolution = Selection  $\times$  heritability



# Adaptive evolution in the wild

Adaptive evolution = Selection × heritability

2001



*Genetica* 112-113: 199–222, 2001.  
© 2001 Kluwer Academic Publishers. Printed in the Netherlands.

## Explaining stasis: microevolutionary studies in natural populations

J. Merilä<sup>1\*</sup>, B.C. Sheldon<sup>2</sup> & L.E.B. Kruuk<sup>3</sup>

# Adaptive evolution in the wild

Adaptive evolution = Selection × heritability

2014

The image shows a screenshot of a scientific article from the journal "Evolutionary Applications". The article is a "PERSPECTIVE" piece titled "Climate change, adaptation, and phenotypic plasticity: the problem and the evidence". It is authored by Juha Merilä<sup>1,\*</sup> and Andrew P. Hendry<sup>2,\*</sup>. The journal is Open Access and has an ISSN of 1752-4571. The background of the slide is black.

Evolutionary Applications

Open Access

Evolutionary Applications ISSN 1752-4571

PERSPECTIVE

**Climate change, adaptation, and phenotypic plasticity:  
the problem and the evidence**

Juha Merilä<sup>1,\*</sup> and Andrew P. Hendry<sup>2,\*</sup>

# Adaptive evolution in the wild

Adaptive evolution = Selection  $\times$  heritability

2016

**Ideas that Push the Boundaries**

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Prospects & Overviews

**Why are estimates of the strength and direction of natural selection from wild populations not congruent with observed rates of phenotypic change?**

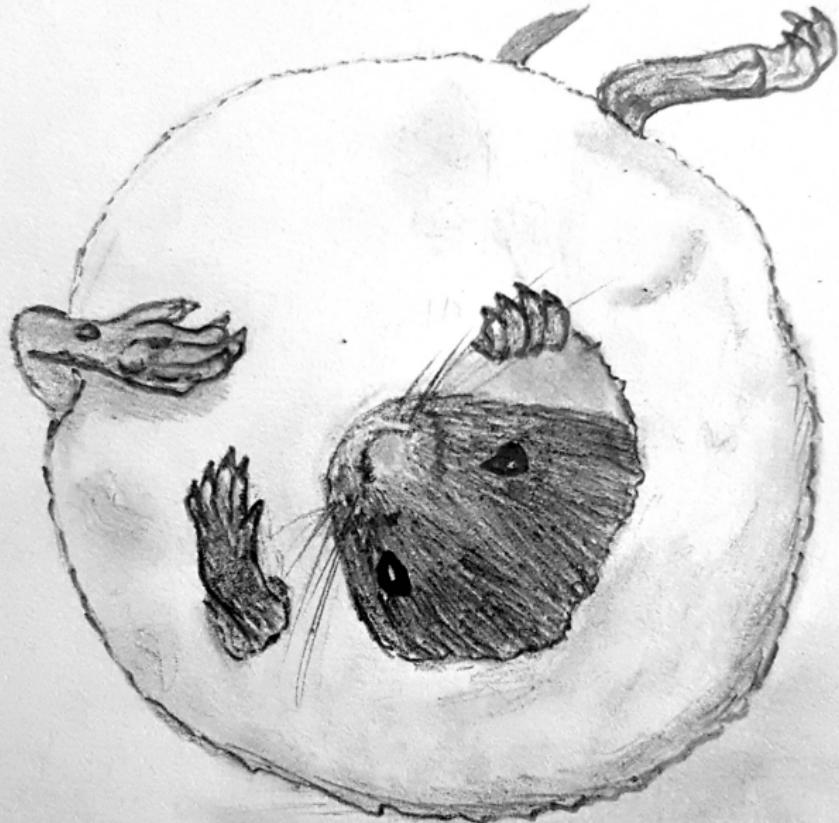
John F.Y. Brookfield

First published: 12 July 2016 [Full publication history](#)

DOI: 10.1002/bies.201600017 [View/save citation](#)

**View issue TOC**  
Volume 38, Issue 9  
September 2016  
Pages 927–934

Long-term individual-based monitoring



## Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white



## Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white
- Rock-dweller



## Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white
- Rock-dweller
- 30-45g



## Snow vole (*Chionomys nivalis*, Martins 1842)

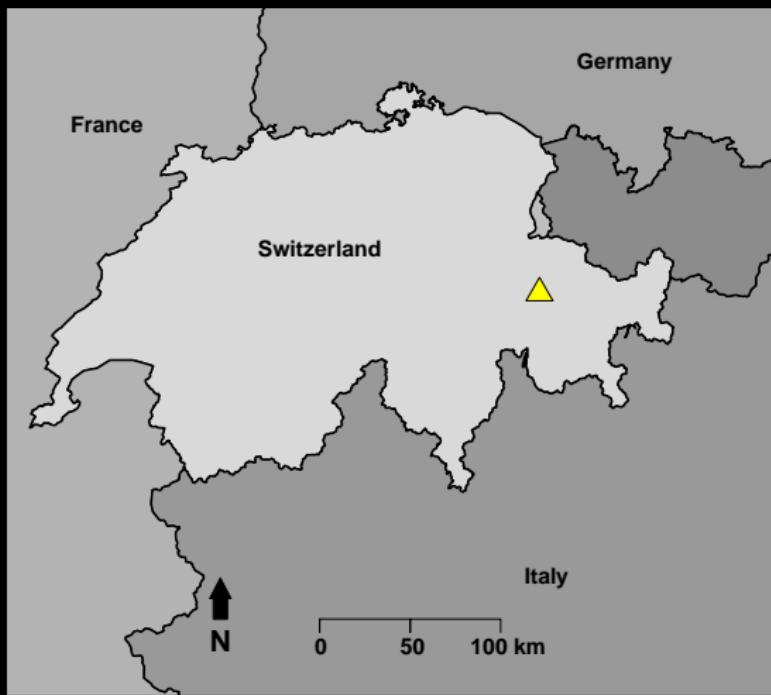
- NOT white
- Rock-dweller
- 30-45g
- 10-14cm long + 5-8cm tail



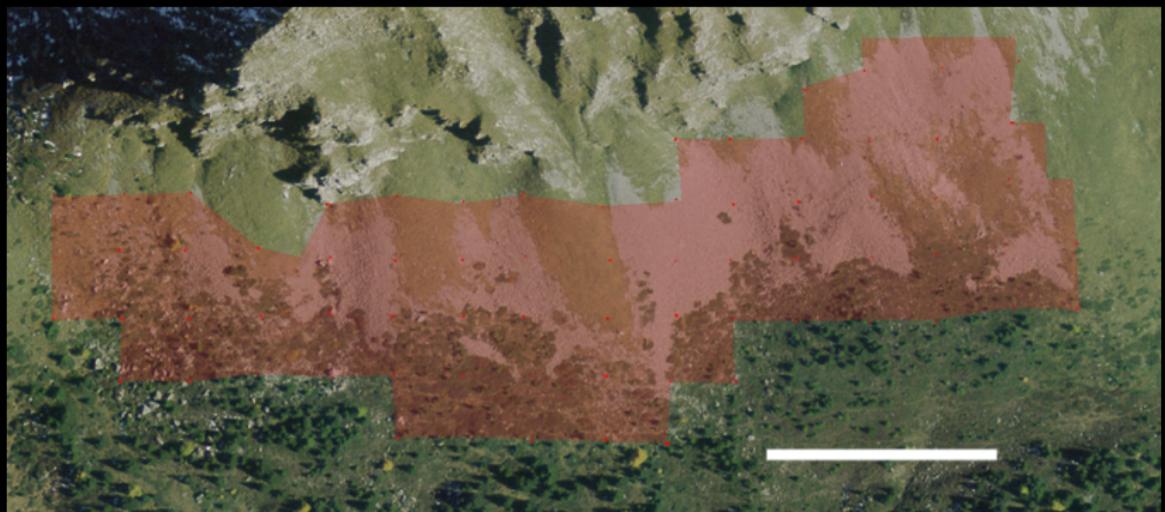
## Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white
- Rock-dweller
- 30-45g
- 10-14cm long + 5-8cm tail
- Slow life pace













## What we measure

# What we measure

- Morphology
  - Body mass
  - Body length
  - Tail length



# What we measure

- Morphology
  - Body mass
  - Body length
  - Tail length
- Capture/Recaptures
  - Death/emigration
  - Location



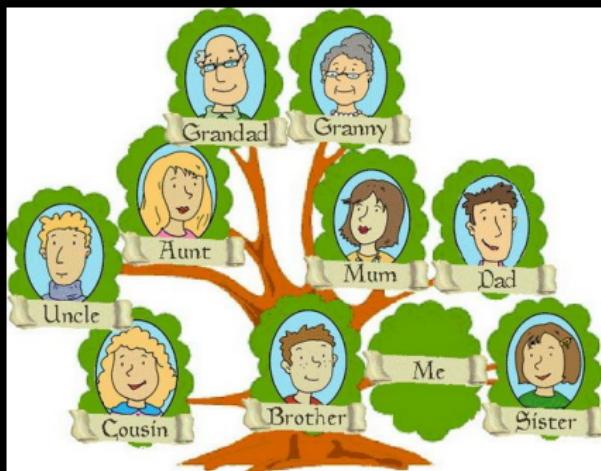
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- Morphology
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  - 20 “neutral” markers
  - Sex identification
  - Any genotyping



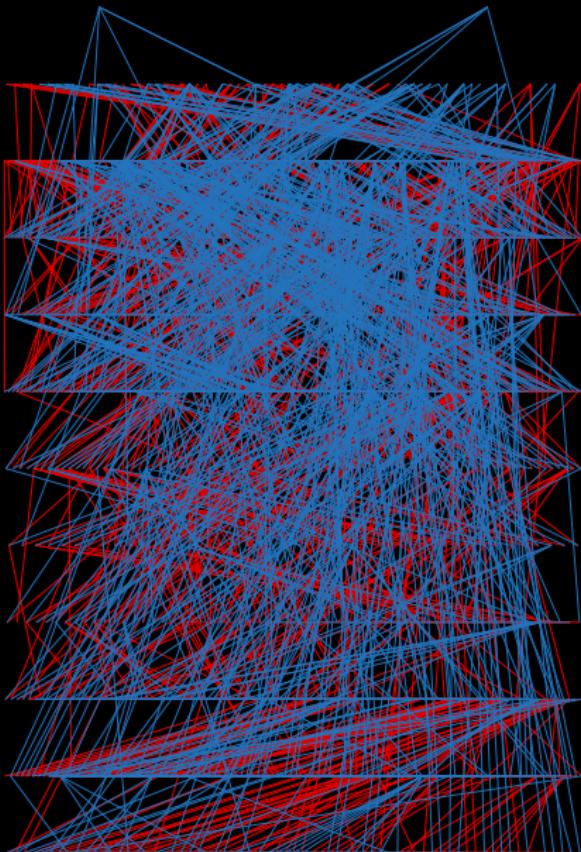
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# What we measure

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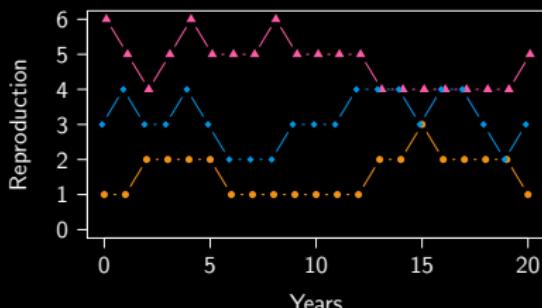
**Are snow vole evolving? Why?**

---

**Variance in fitness?**

**Adaptive evolution in the snow vole?**

# Variance in fitness?

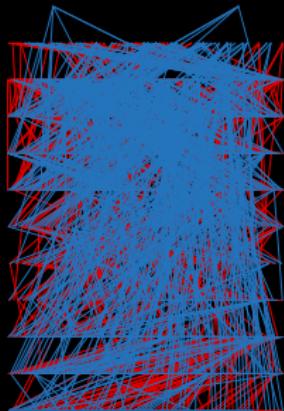


	Estimate	95% CI	p-value
Latent variance in survival	0	[0;0.248]	0.50
Latent variance in reproduction	0.37	[0.25, 0.49]	$< 10^{-16}$

## Adaptive evolution in the snow vole?

- Non random variation fitness components

# Variance in fitness?

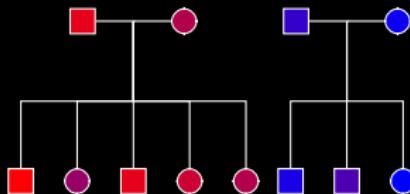


Relative lifetime reproductive success  
variance  $\approx 1.7$

## Adaptive evolution in the snow vole?

- Non random variation fitness components
- Variation in fitness

## Variance in fitness?



	Estimate	95% CI
Additive genetic variation	0.10	[0.06;0.19]
Heritability	0.06	[0.04;0.12]

## Adaptive evolution in the snow vole?

- Non random variation fitness components
- Variation in fitness
- Additive genetic variation in fitness

## Variance in fitness?

### Adaptive evolution in the snow vole?

- Non random variation fitness components
- Variation in fitness
- Additive genetic variation in fitness

**On going evolution and opportunity for selection**

## Body mass

# Body mass



# Evolution of body mass

## Prediction

- Selection =  $+0.86\text{g}$  ( $p < 10^{-3}$ )

# Evolution of body mass

## Prediction

- Selection =  $+0.86\text{g}$  ( $p < 10^{-3}$ )
- Heritability = 20% ( $p < 10^{-3}$ )

# Evolution of body mass

## Prediction

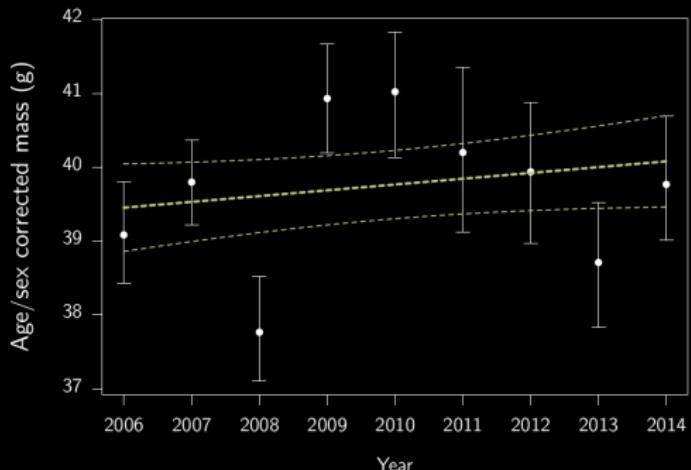
- Selection =  $+0.86\text{g}$  ( $p < 10^{-3}$ )
- Heritability =  $20\%$  ( $p < 10^{-3}$ )
- Response = Selection  $\times$  heritability =  $+ 0.22\text{g/year}$

# Evolution of body mass

## Prediction

- Selection =  $+0.86\text{g}$  ( $p < 10^{-3}$ )
- Heritability = 20% ( $p < 10^{-3}$ )
- Response = Selection  $\times$  heritability =  $+0.22\text{g/year}$

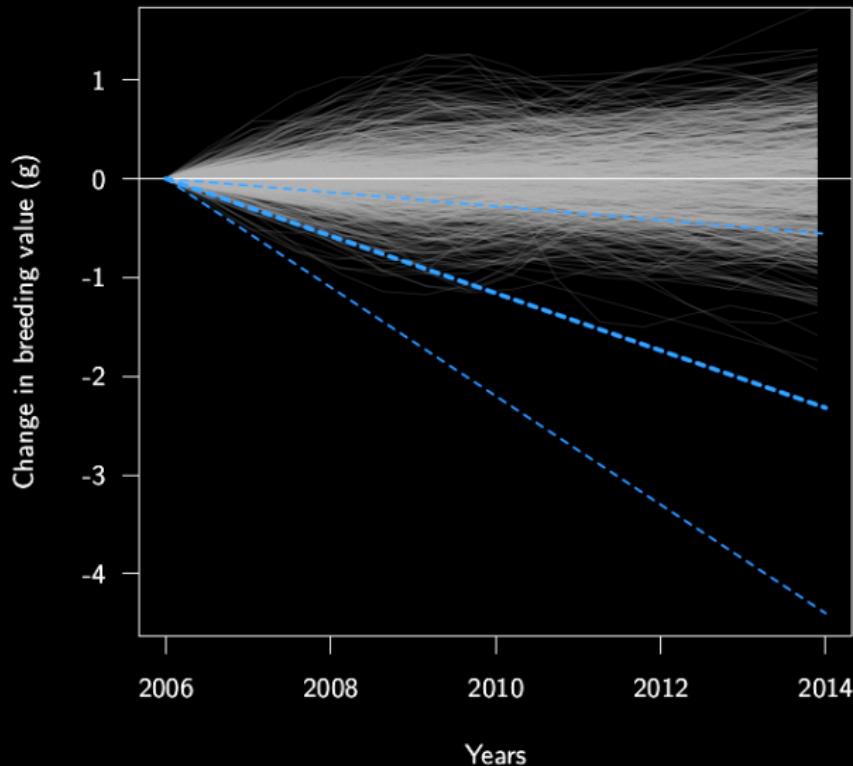
## Phenotypic observation



- Observed =  
 $+0.07\text{g/year}$  ( $p=0.14$ )

# Evolution of body mass

## Estimation of genetic change



# **Evolution of body mass**

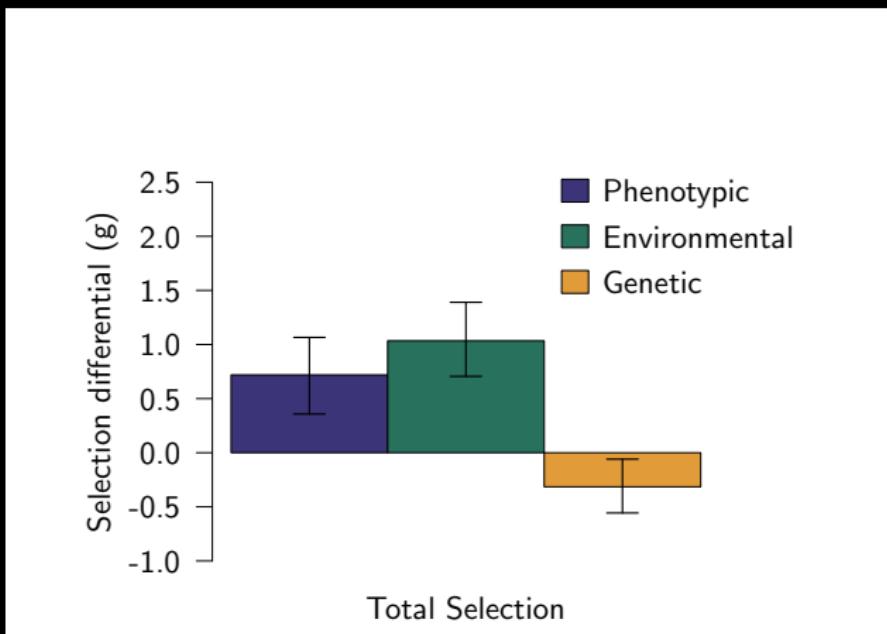
## **Evolution Paradox**

- Apparent selection for higher mass
- Adaptive evolution for lower mass

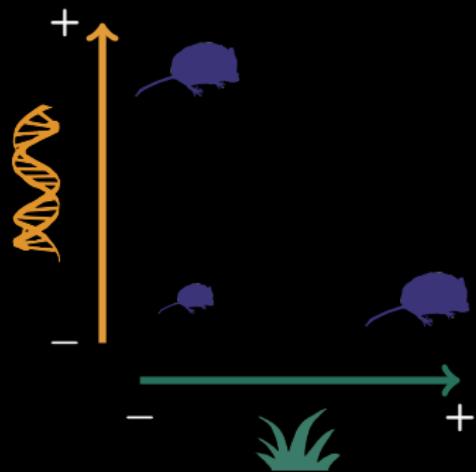
# Evolution of body mass

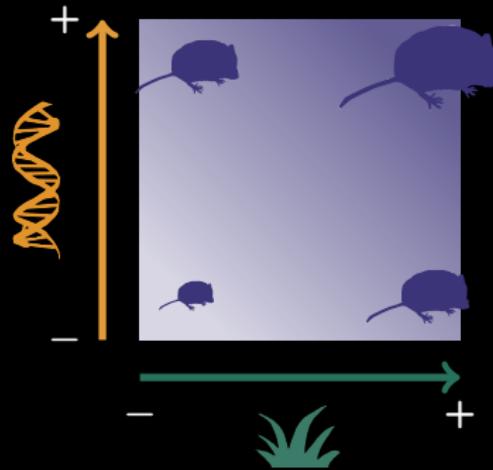
## Evolution Paradox

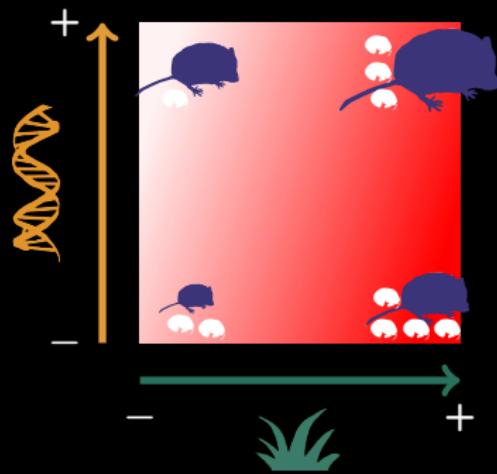
- Apparent selection for higher mass
- Adaptive evolution for lower mass

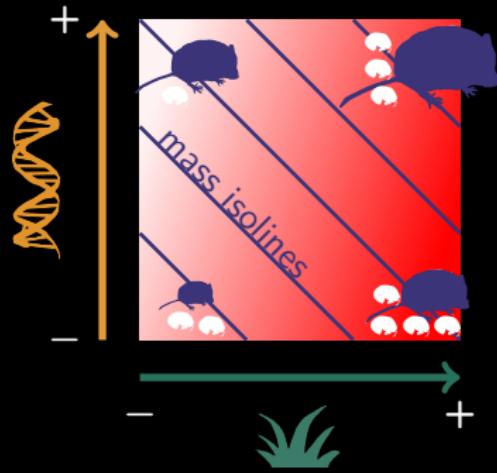


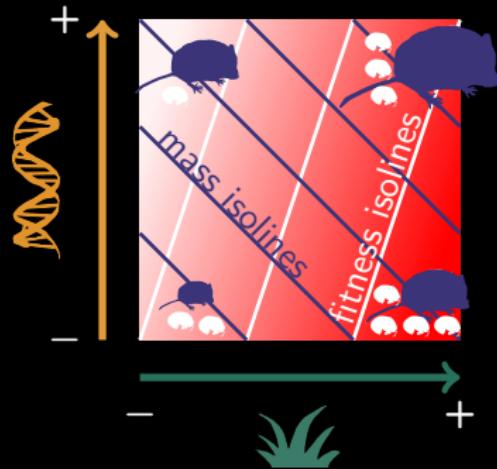


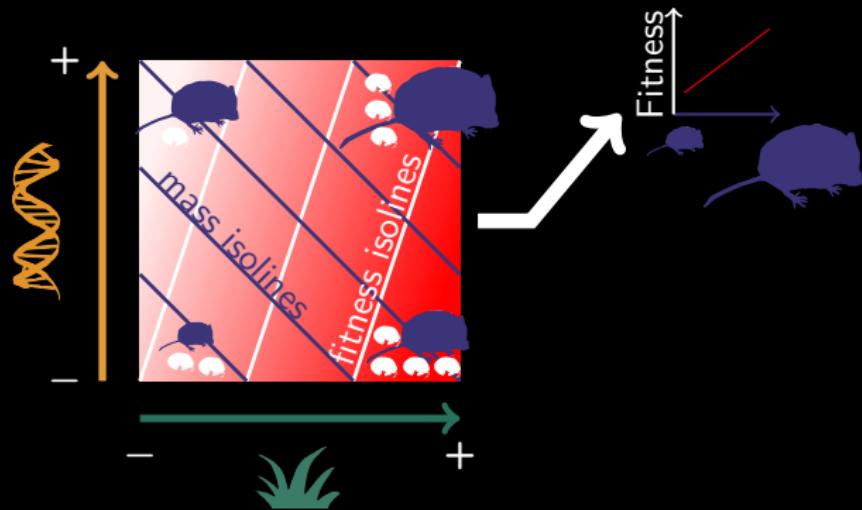


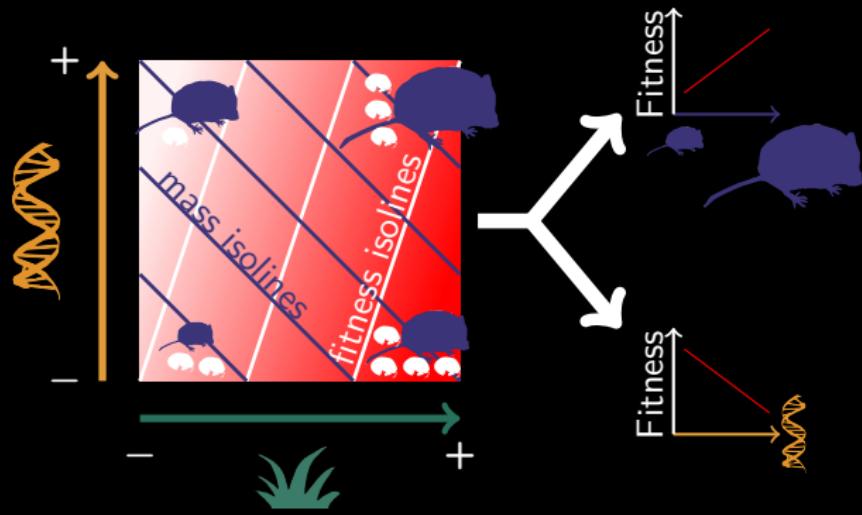


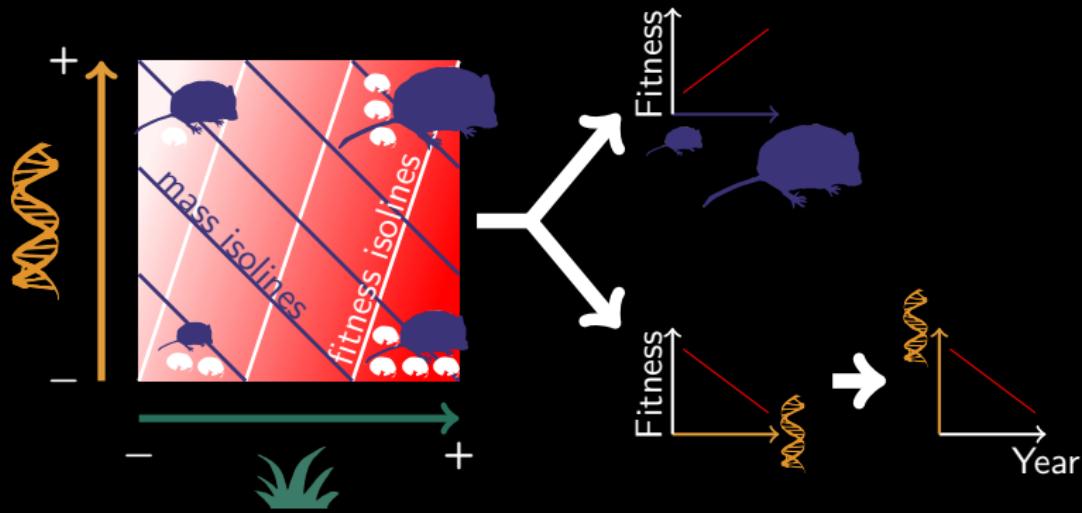


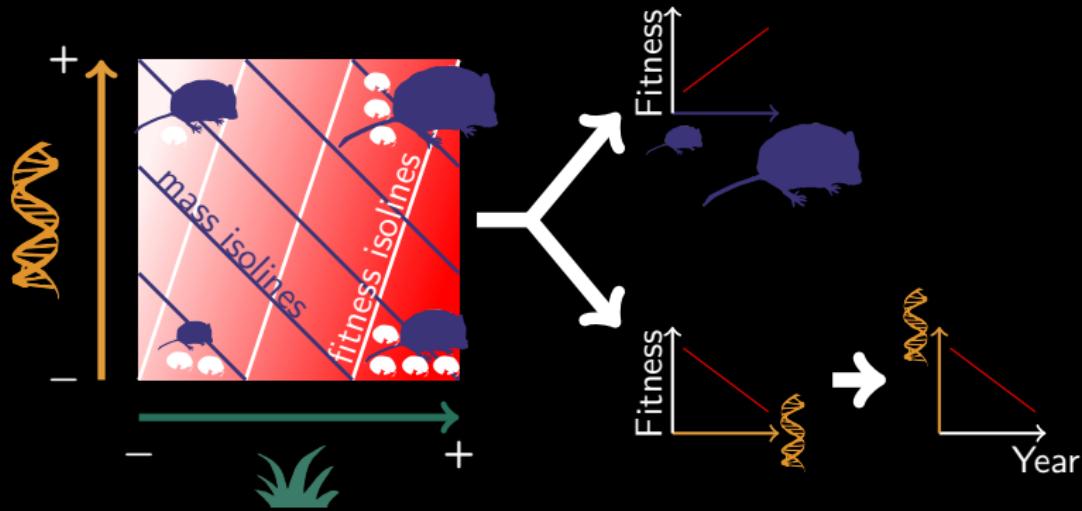






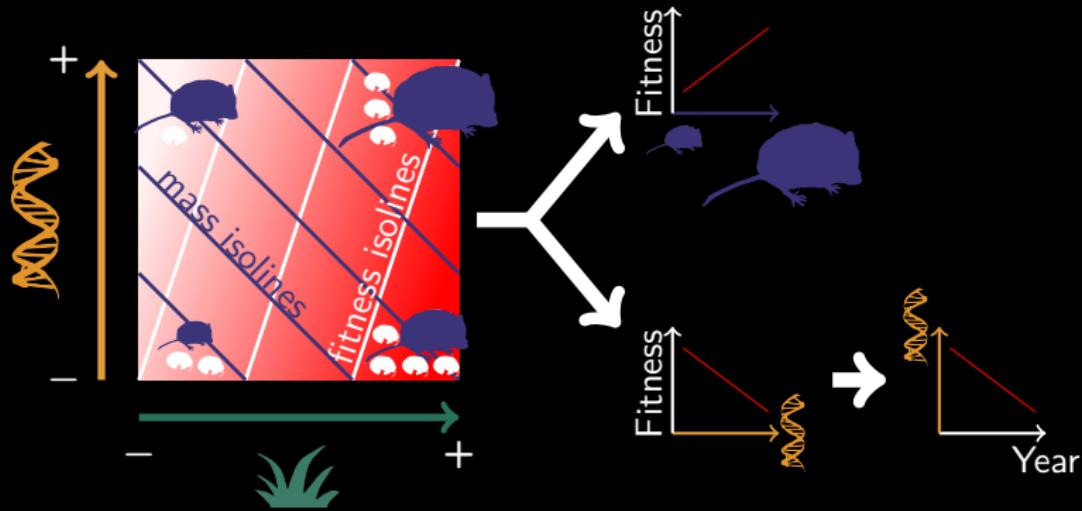






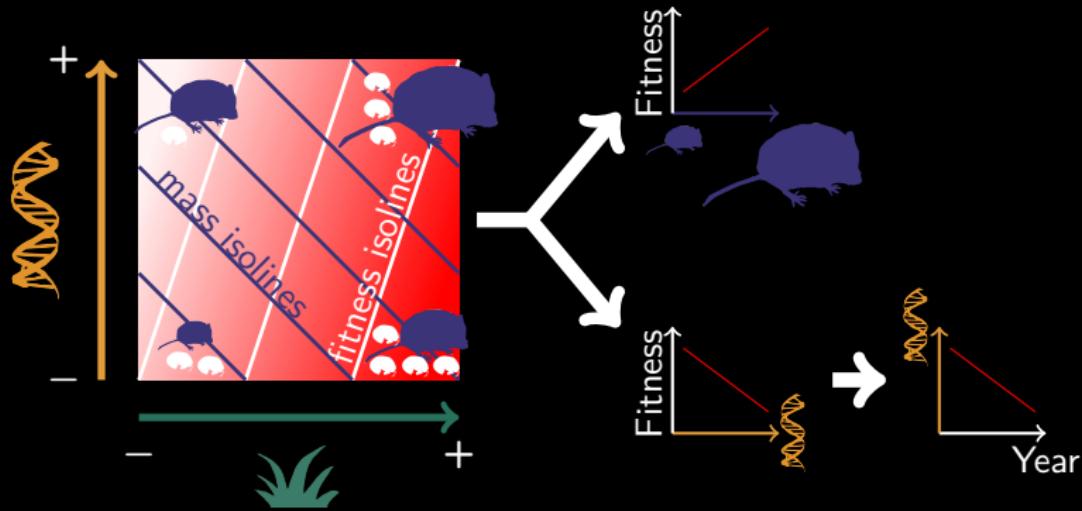
## Summary

1. Apparent stasis...



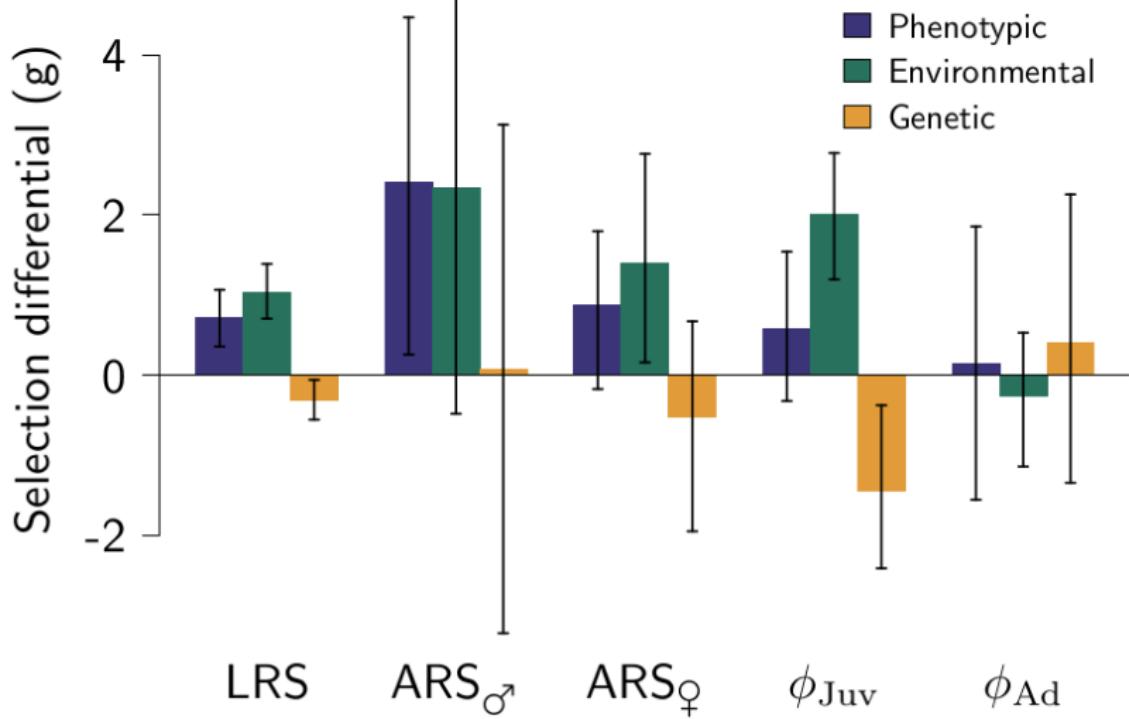
## Summary

1. Apparent stasis . . .
2. . . . but evolution towards lower mass

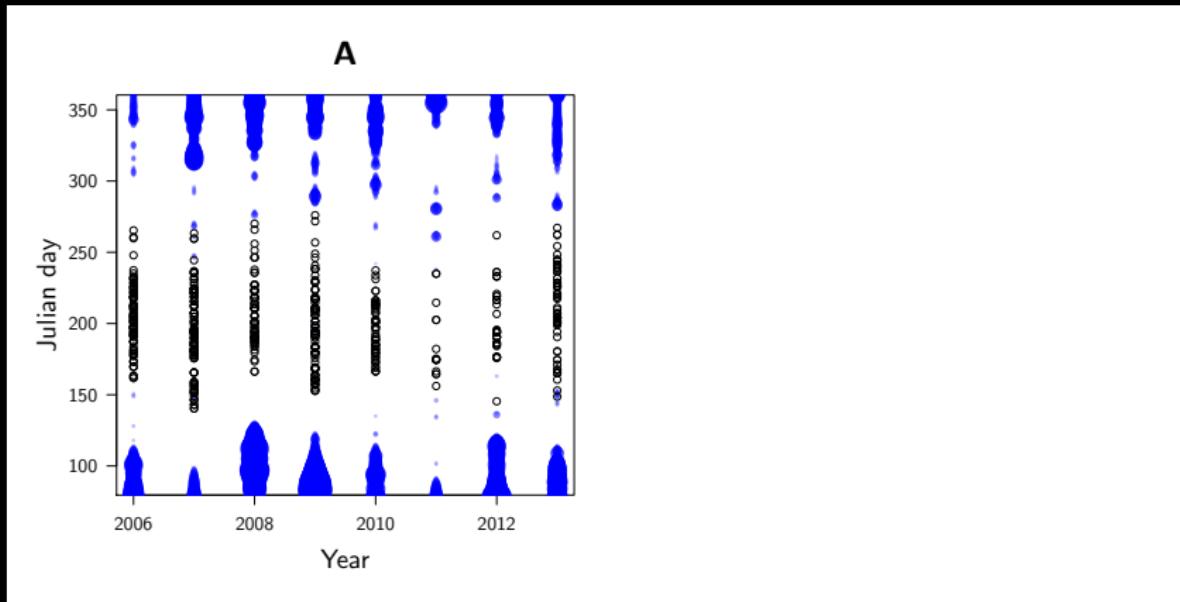


## Summary

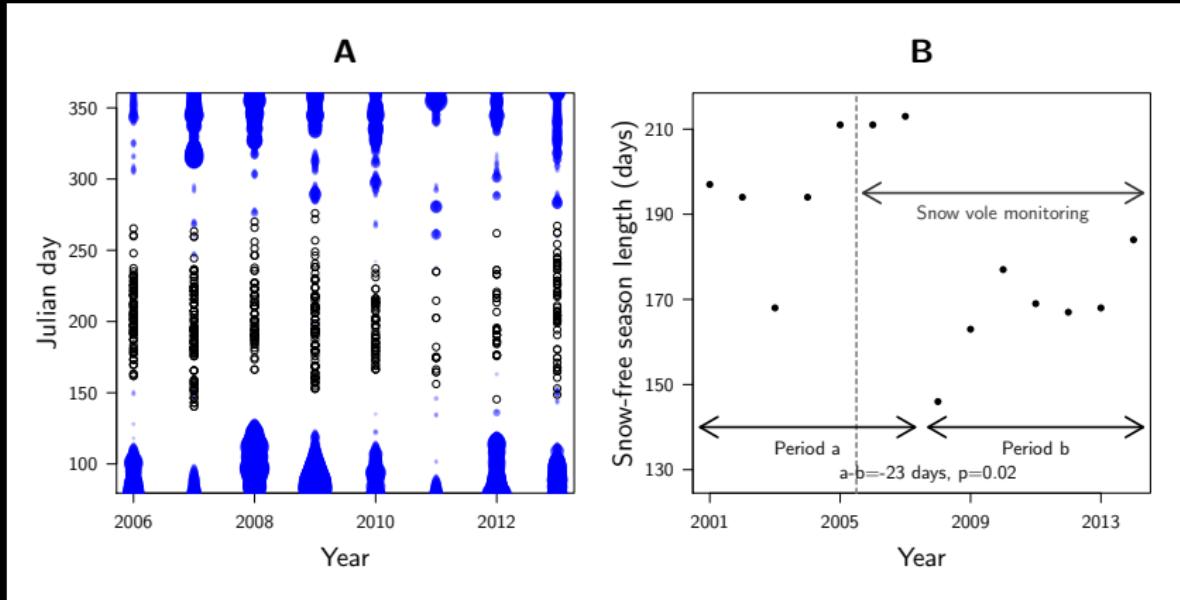
1. Apparent stasis . . .
2. . . . but evolution towards lower mass
3. *Selective pressure?*



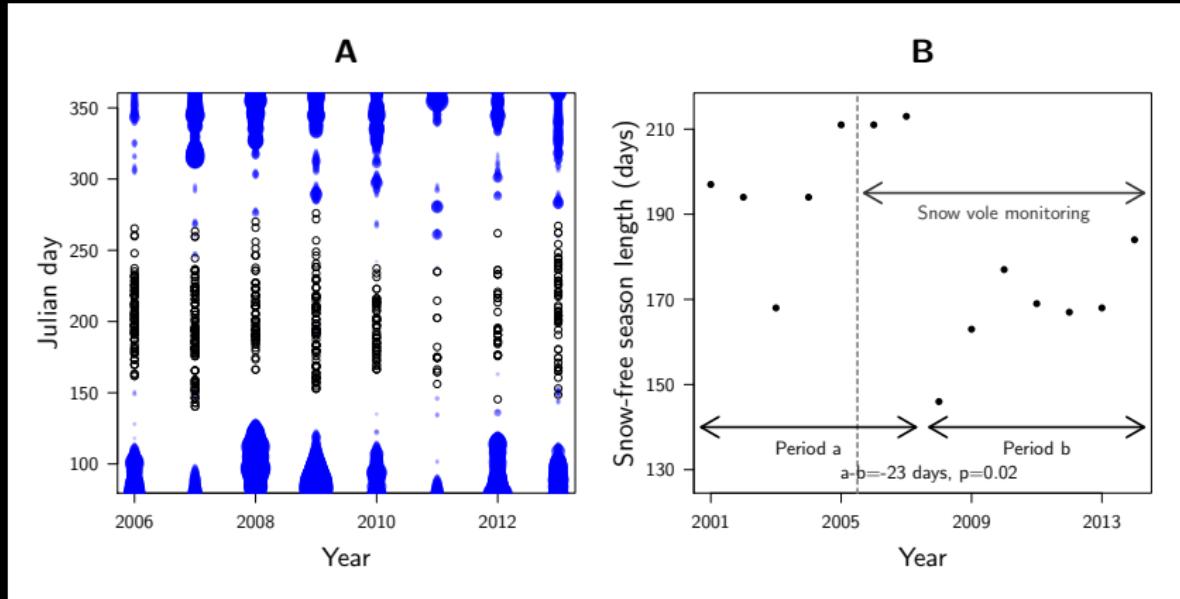
# Snow falls and ontogeny



# Snow falls and ontogeny



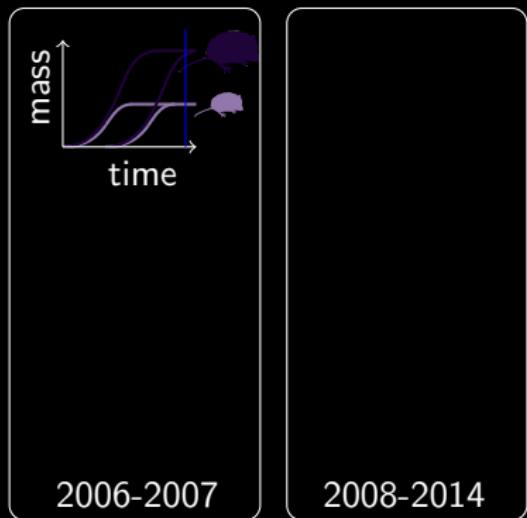
# Snow falls and ontogeny



Less time to grow → Selection for smaller voles?

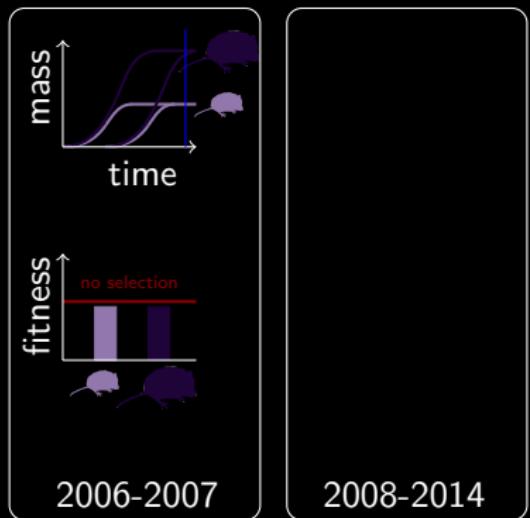
# Selection during ontogeny?

D



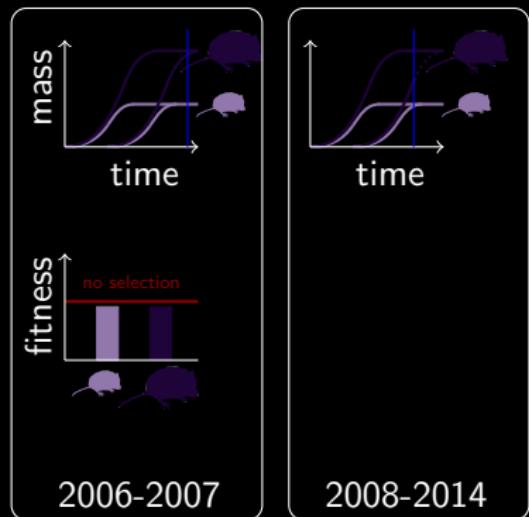
# Selection during ontogeny?

D



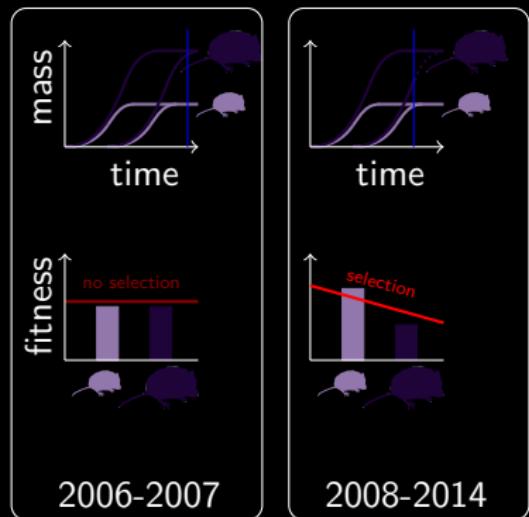
# Selection during ontogeny?

D



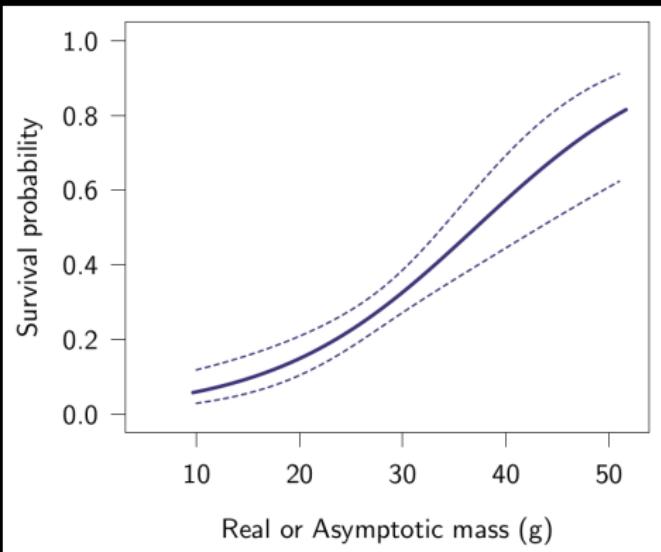
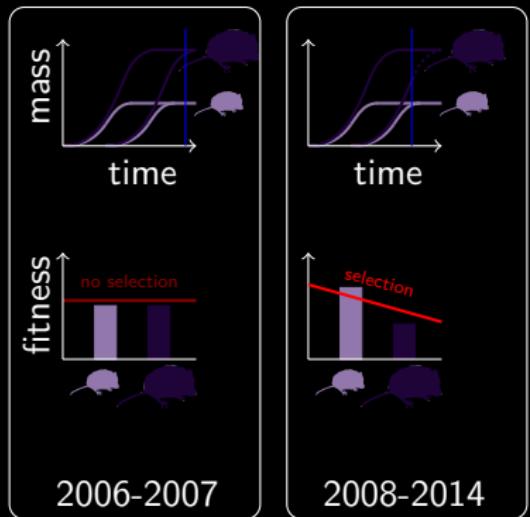
# Selection during ontogeny?

D



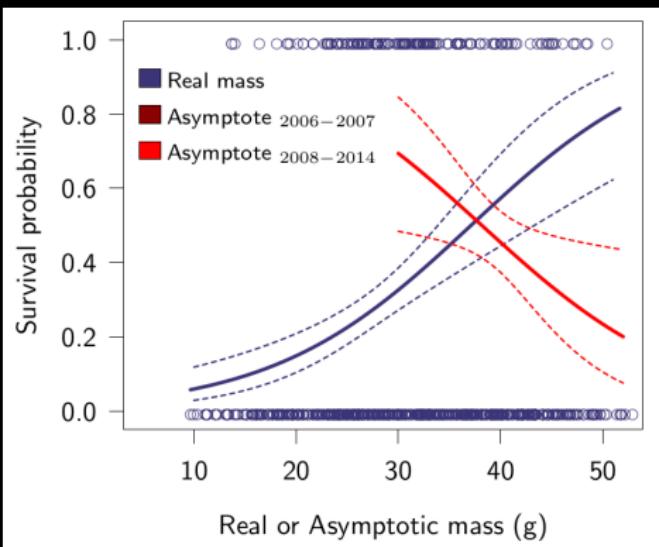
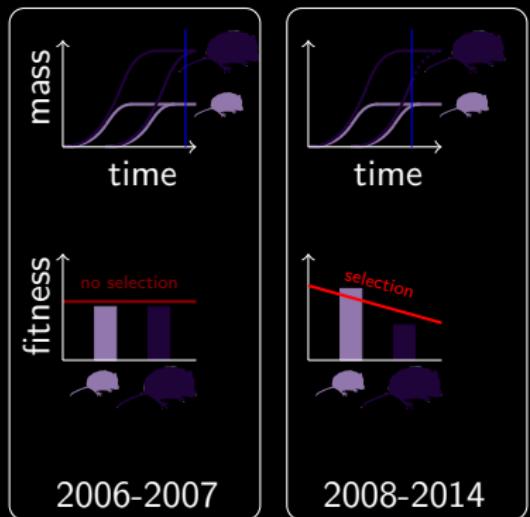
# Selection during ontogeny?

D



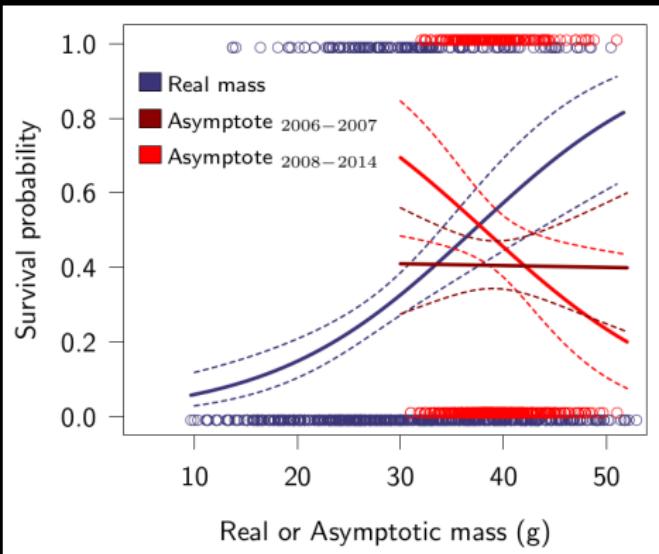
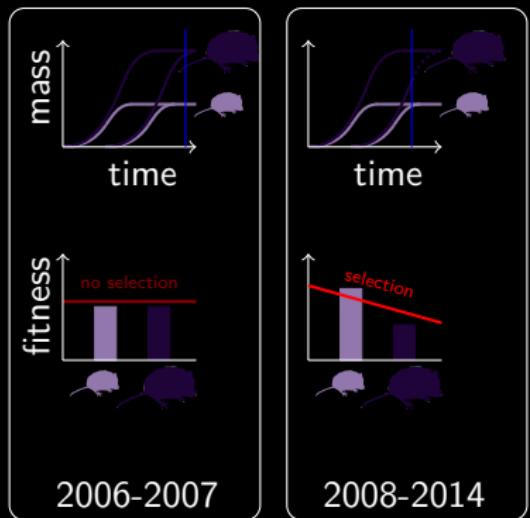
# Selection during ontogeny?

D



# Selection during ontogeny?

D



**Evo**leution!

# Evo**l**eution!

- Contemporary adaptive evolution

# Evo**l**eution!

- Contemporary adaptive evolution
- Against apparent selection

# Evo**l**eution!

- Contemporary adaptive evolution
- Against apparent selection
- In response to climate

# Evolement!

- Contemporary adaptive evolution
- Against apparent selection
- In response to climate



The bioRxiv logo features the word "bioRxiv" in a large, bold, black font. The "Rx" is stylized with a Greek chi symbol (χ). Below it, the word "beta" is written in a smaller, italicized black font. Underneath the main title, the text "THE PREPRINT SERVER FOR BIOLOGY" is displayed in a smaller, all-caps black font.

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**The stasis that wasn't: Adaptive evolution goes against phenotypic selection in a wild rodent population**

Timothée Bonnet, Peter Wandeler, Glauco Camenisch, Erik Postma

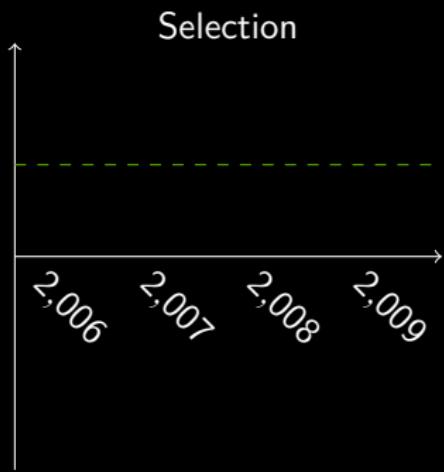
doi: <http://dx.doi.org/10.1101/038604>

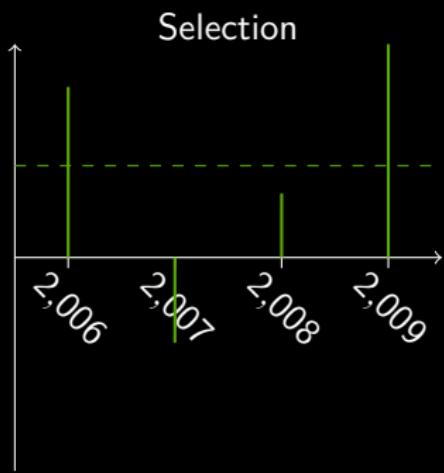
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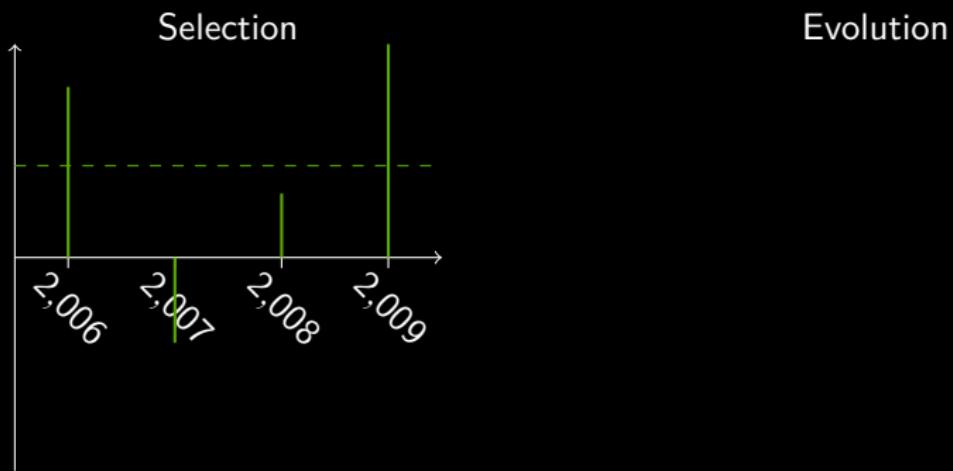
**Do selection and evolution  
fluctuate?**

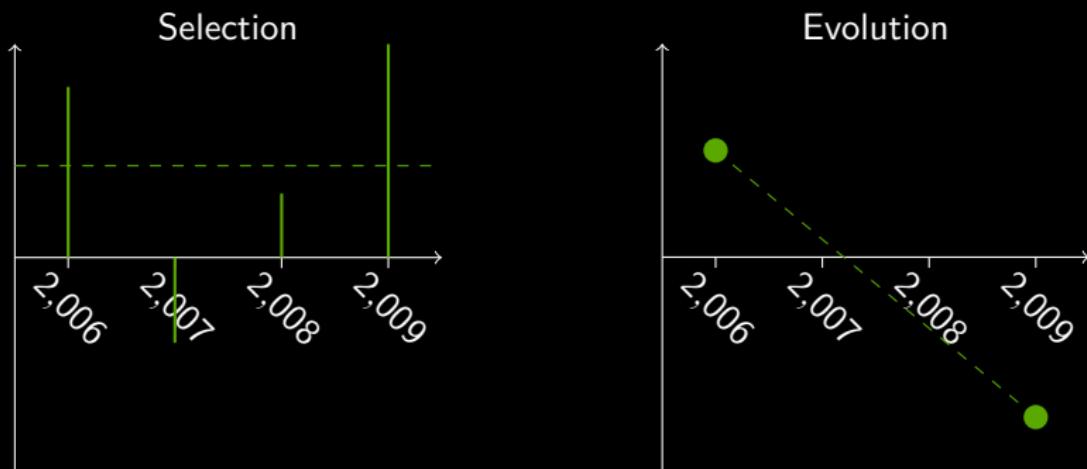
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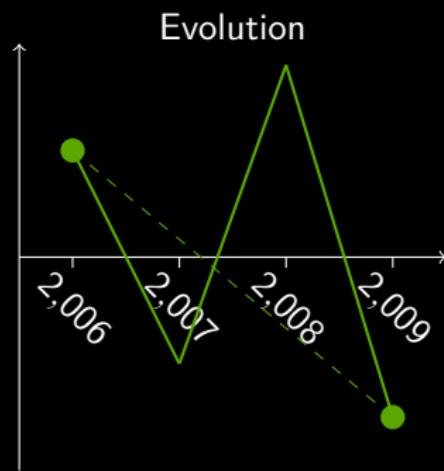
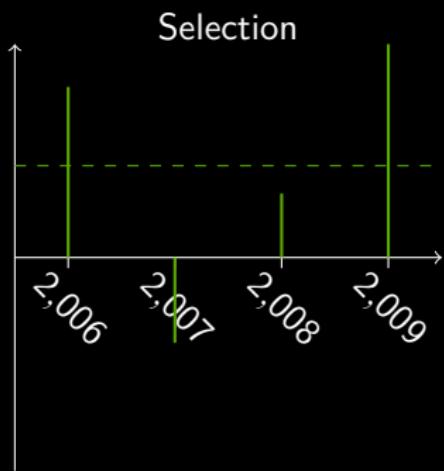
## Selection



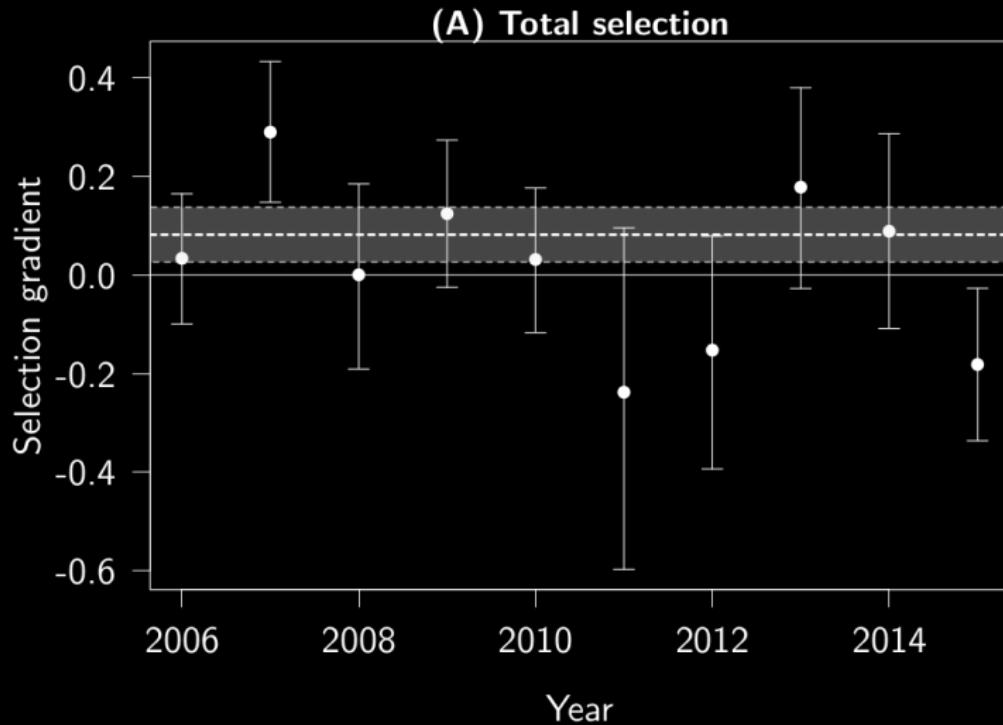






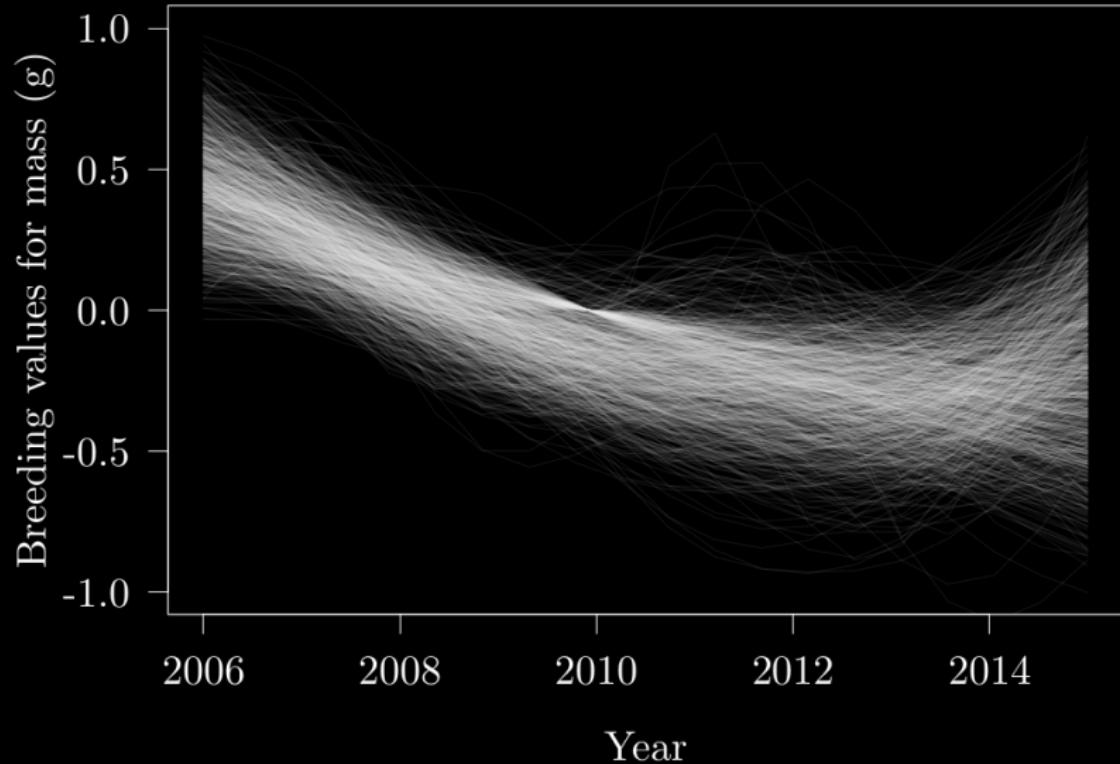


# Dynamics of selection

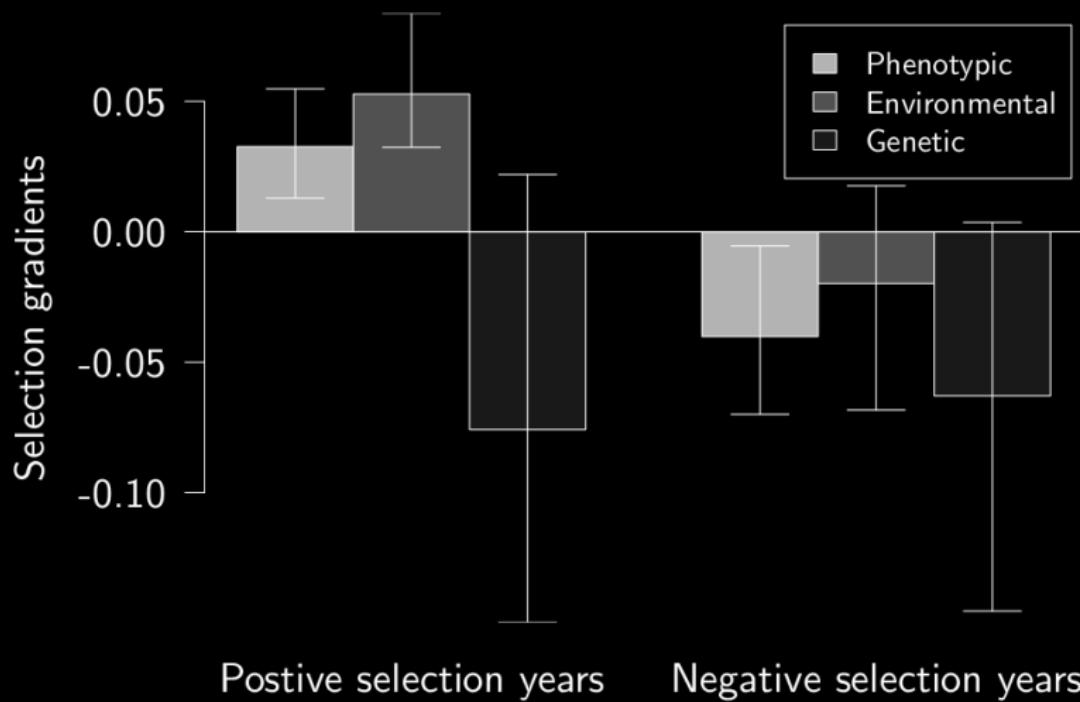


Variance in selection = 0.117 [0.063;0.218],  $p=8 \cdot 10^{-6}$

## Dynamics of evolution



# Dynamics of selection VS. evolution



# Dynamics of selection VS. evolution

- Selection fluctuates

## Dynamics of selection VS. evolution

- Selection fluctuates
- Evolution does not

## Dynamics of selection VS. evolution

- Selection fluctuates
- Evolution does not
- Selection does not predict evolution

# Dynamics of selection VS. evolution

- Selection fluctuates
- Evolution does not
- Selection does not predict evolution

**Fluctuating selection but no fluctuating evolution in a  
wild rodent population**

Timothée Bonnet & Erik Postma

Submitted to Evolution

# Conclusion

---

# Summary

# What is left?

## Causes of variation in fitness

- The genes of others
- Molecular basis

## Predicting responses to environmental change

- Selection & evolution in the wild
- Demographic response

**Questions?**

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