

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

Timothée Bonnet

Department of evolutionary biology and environmental studies (IEU)



**University of
Zurich^{UZH}**

- Erik Postma



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- Lukas Keller
- Barbara Tschirren
- Arpat Ozgul
- Marc Kéry
- Jarrod Hadfield



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- Eelke Jongejans
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- Philipp Becker
- Judith Bachmann





Phenotypic variation within population



Phenotypic variation within population



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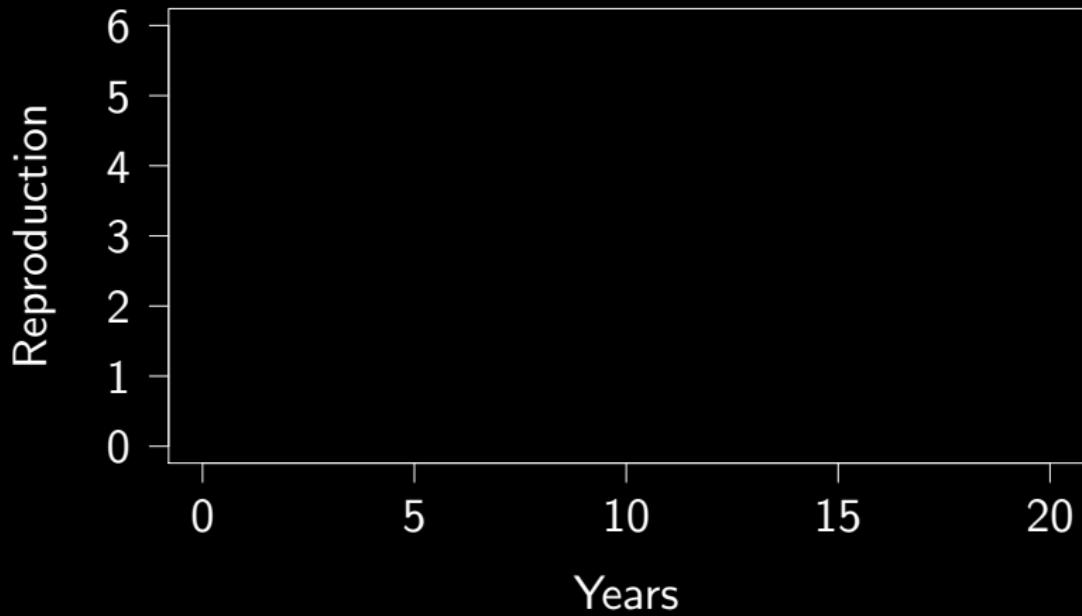
Fitness variation

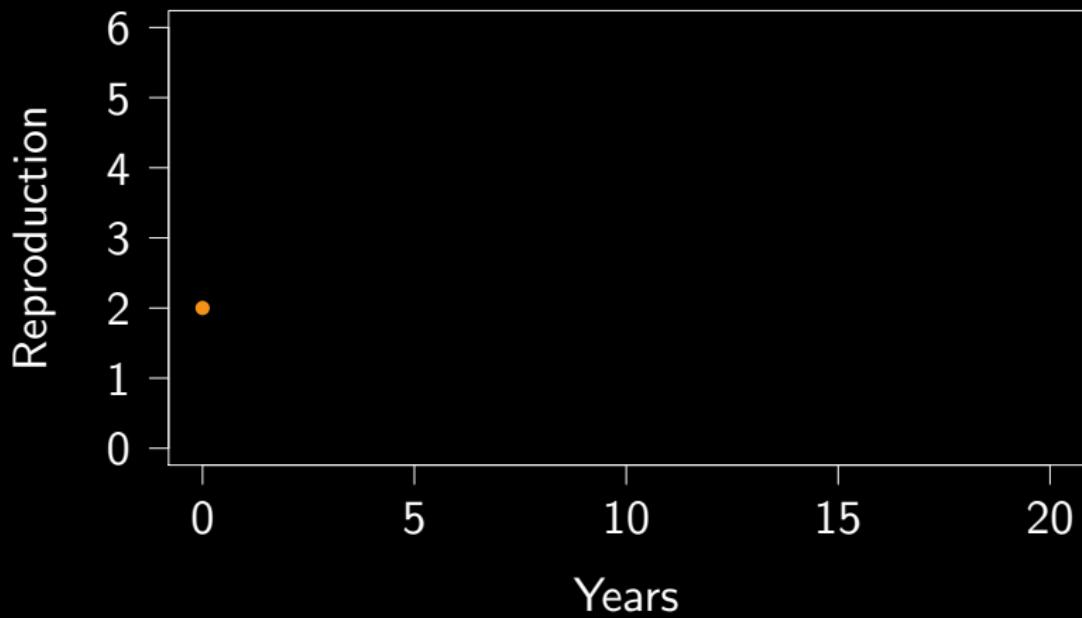


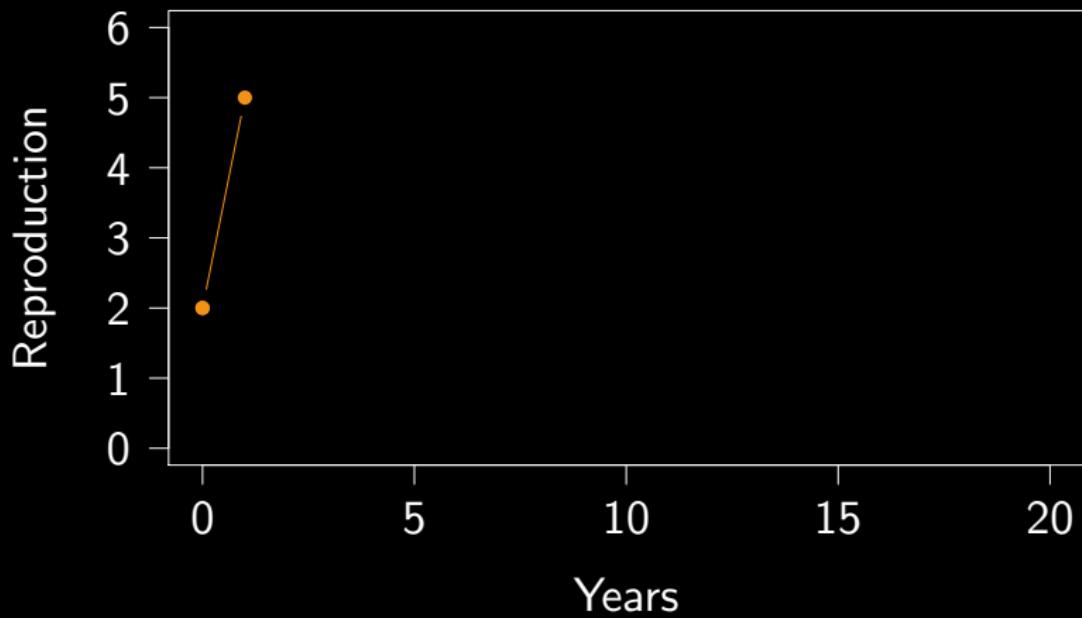
What is fitness?

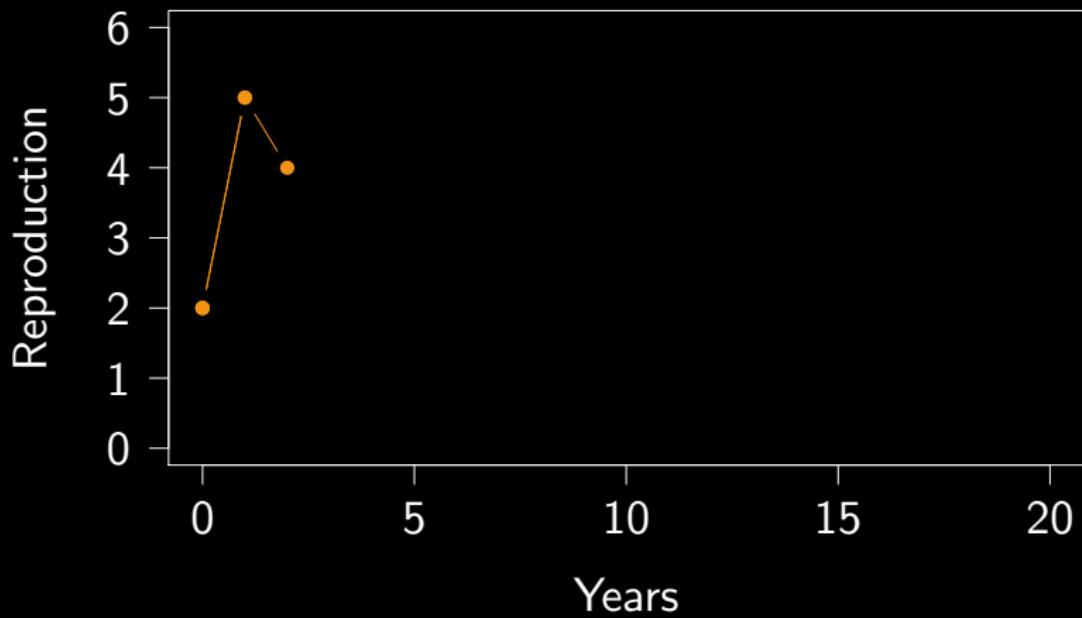
The expected relative contribution of an individual to the next generation

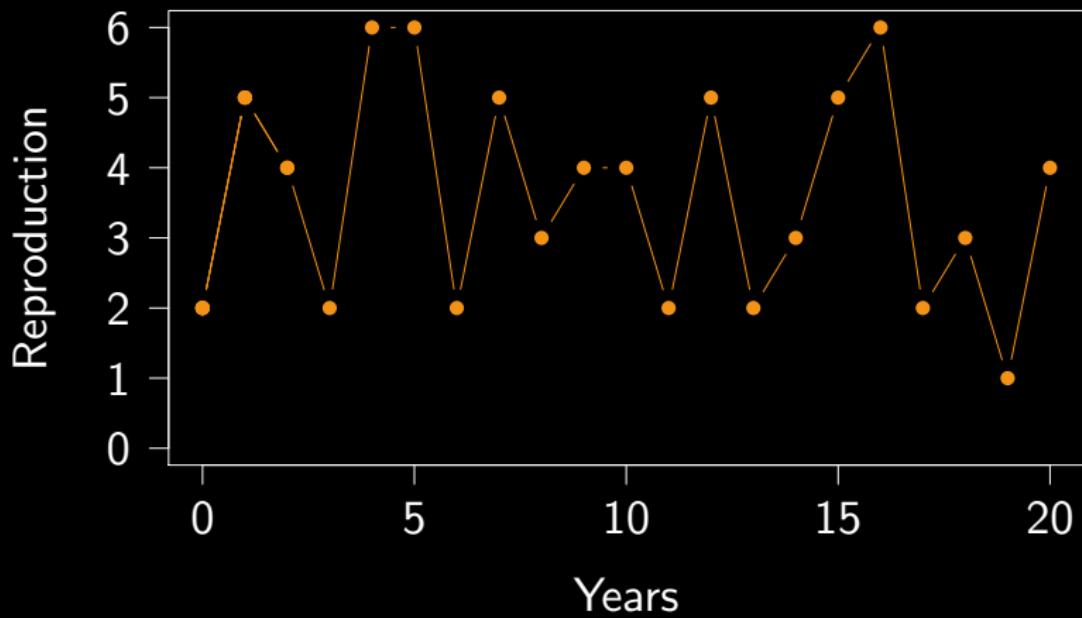
**Chance or fate? Why do survival
and fertility vary?**

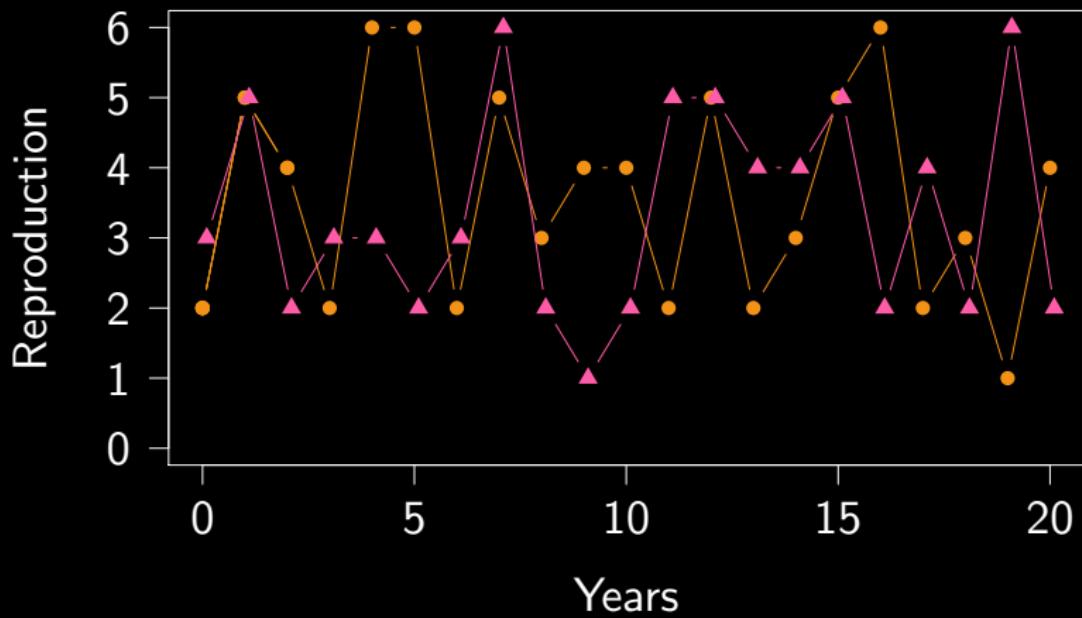


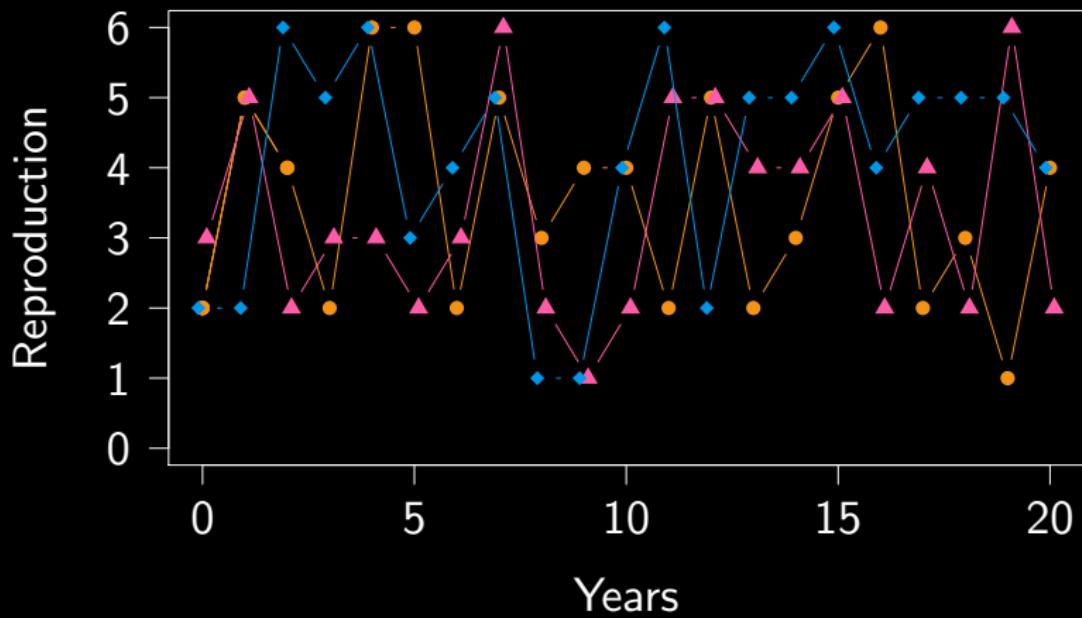




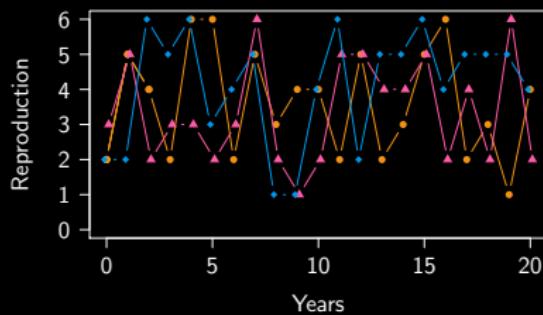




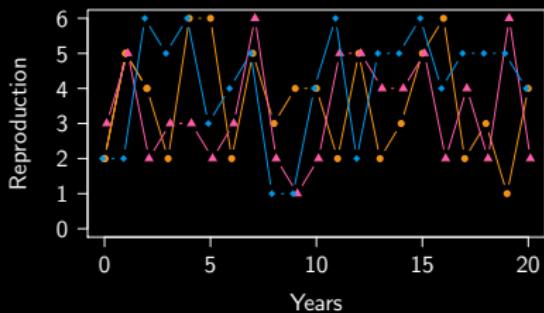




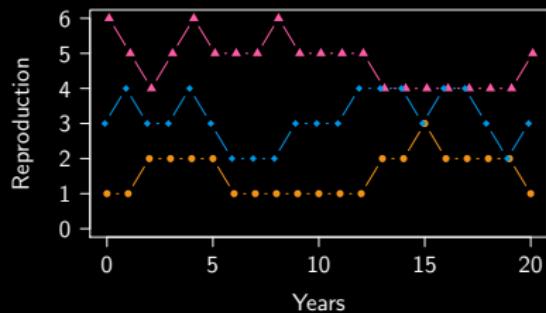
One dice theory



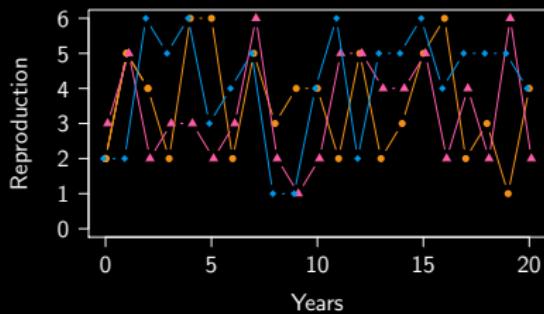
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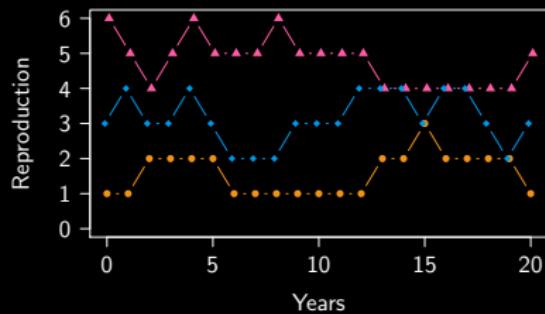
Real pattern



One dice theory



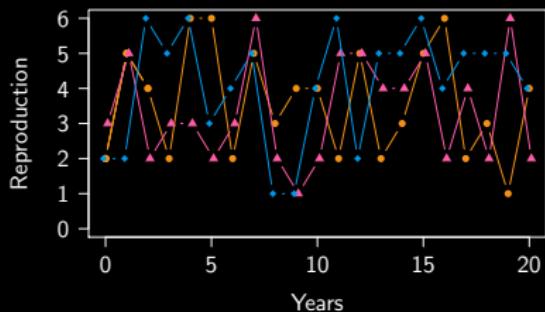
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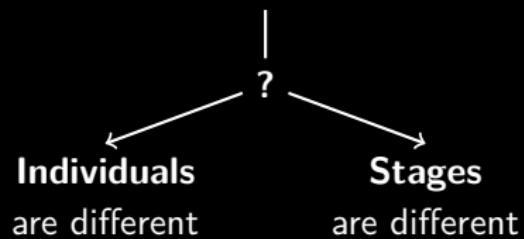
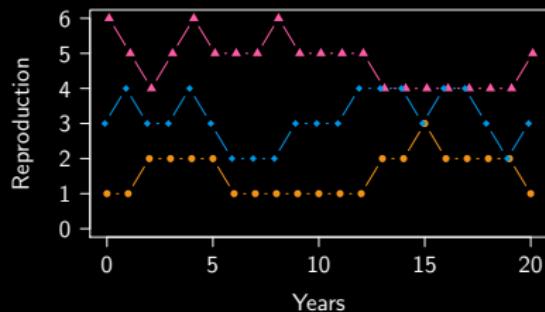
Individuals
are different

?

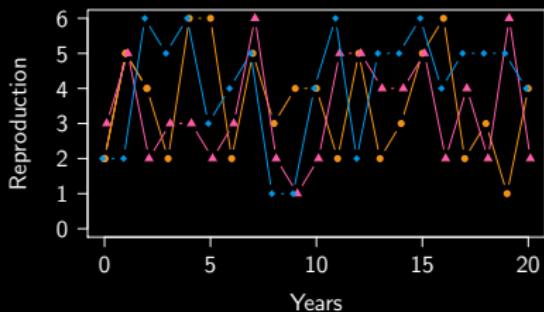
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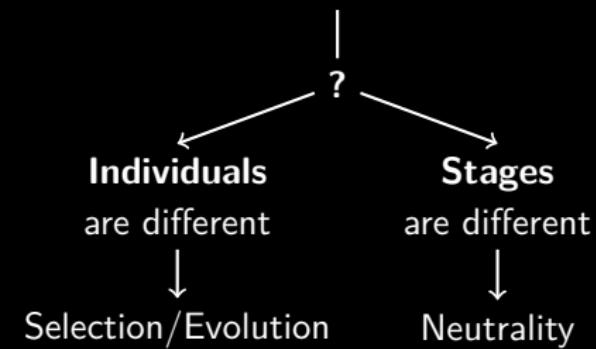
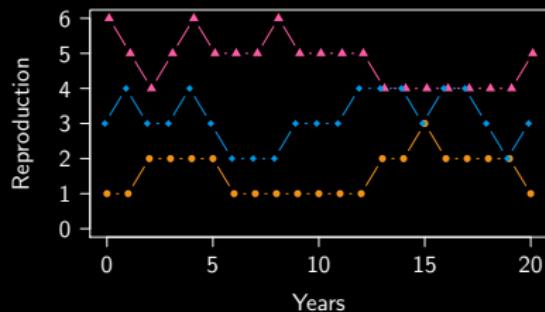
Real pattern



One dice theory



Real pattern



The neutral theory

PNAS

Neutral theory for life histories and individual variability in fitness components

Ulrich Karl Steiner^{a,b,1} and Shripad Tuljapurkar^a

^aDepartment of Biology, Stanford University, Stanford, CA 94305; and ^bInstitut 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 is small enough to be negligible, 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 | 0 | 0.2 | 0.8 | |

No variation in fitness among individuals

The neutral theory

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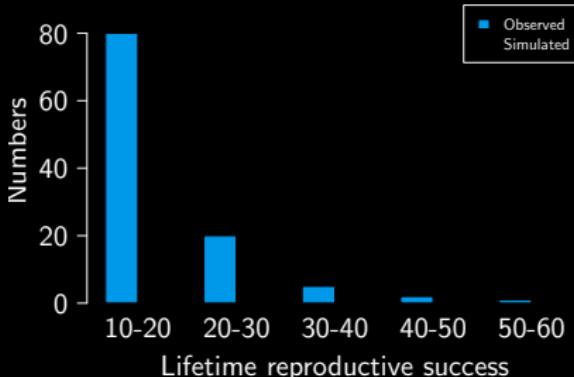
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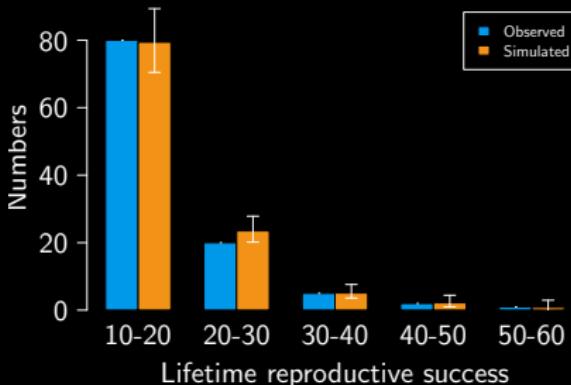
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No variation in fitness among individuals

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^{1*}, Shripad Tuljapurkar¹ and Steven Hecht Orzack²

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

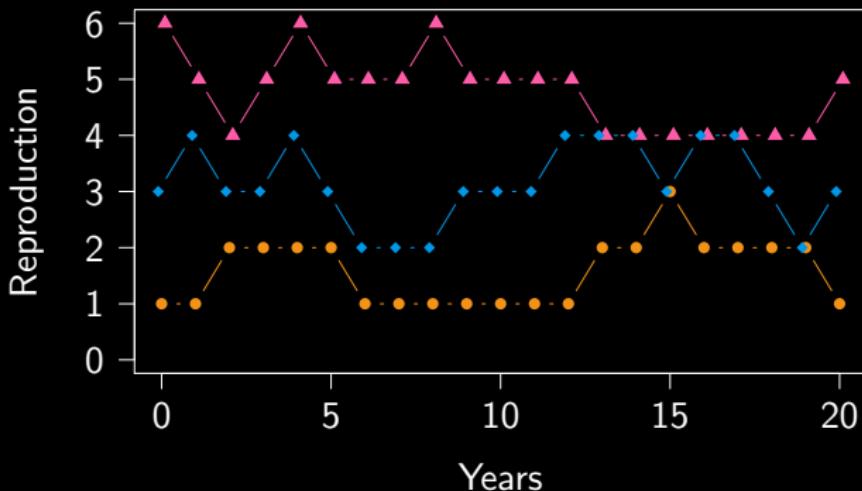
Conflicting results

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

- No significant differences between individuals
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Mixed model method & Quantitative genetics

- Individual performances are repeatable
- ... fitness traits are heritable

Conflicting results

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- ... very little and due to chance only

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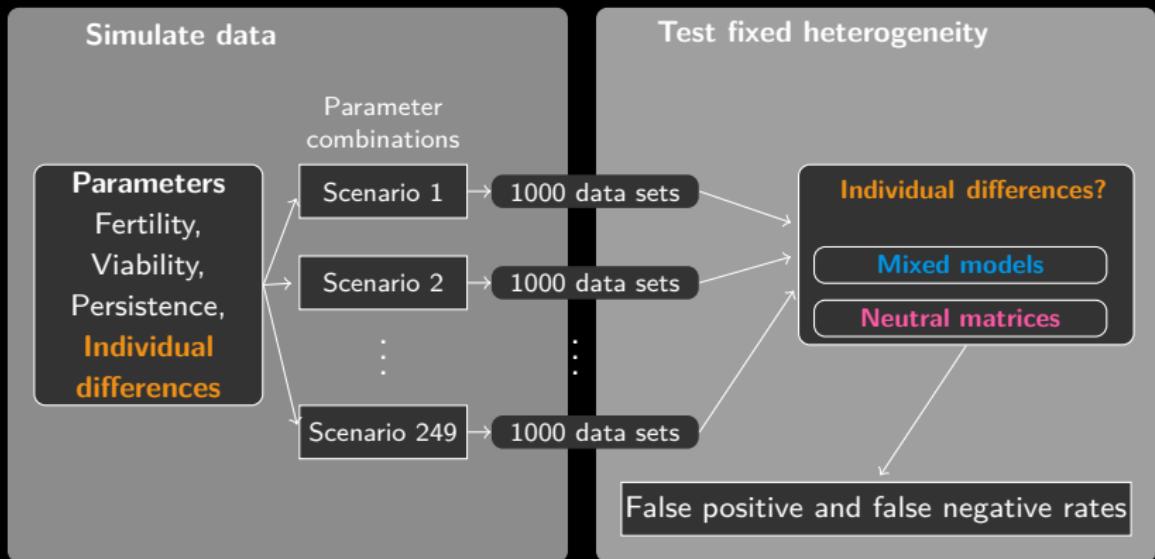
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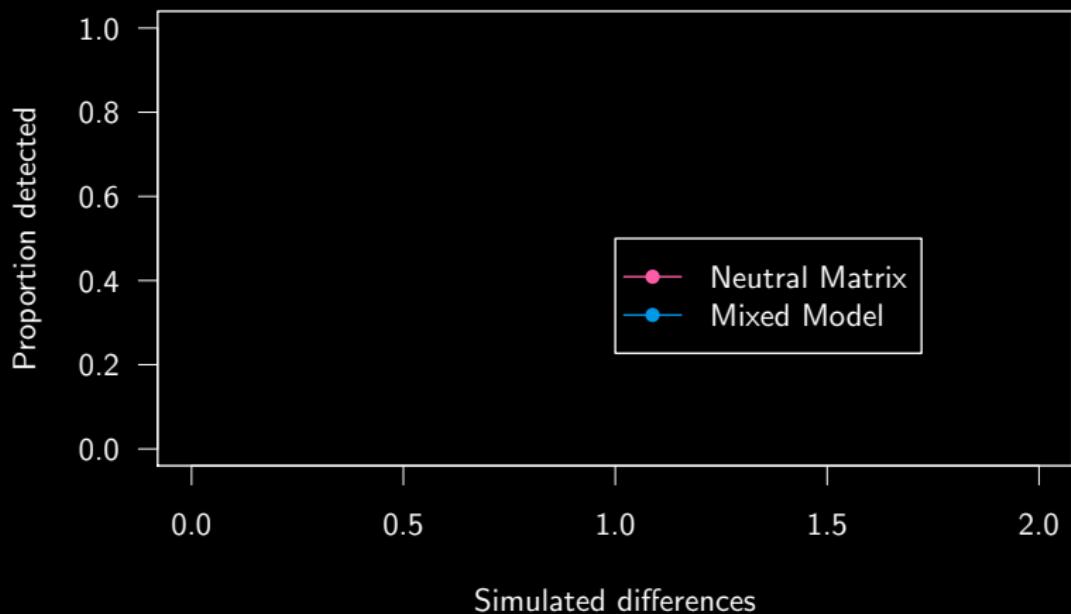
Why?

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

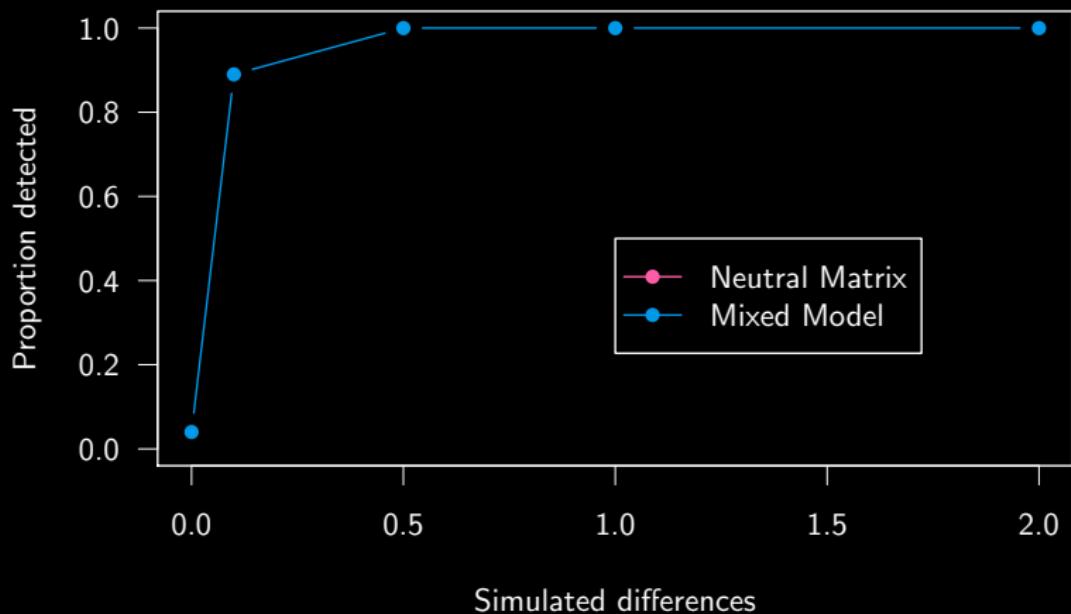
Method



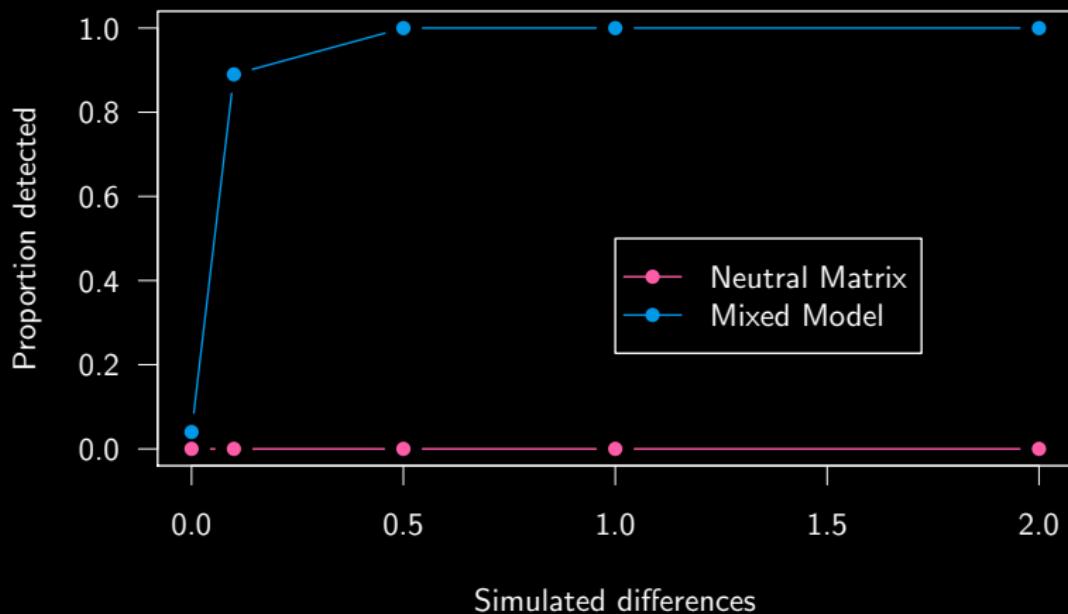
Results



Results



Results



Conclusion

Why conflicting methods?

Conclusion

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

Conclusion

Why conflicting methods?

- **Neutral matrix method** =false negative? YES
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→ Individual differences in fitness components are common

Conclusion

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Implications

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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



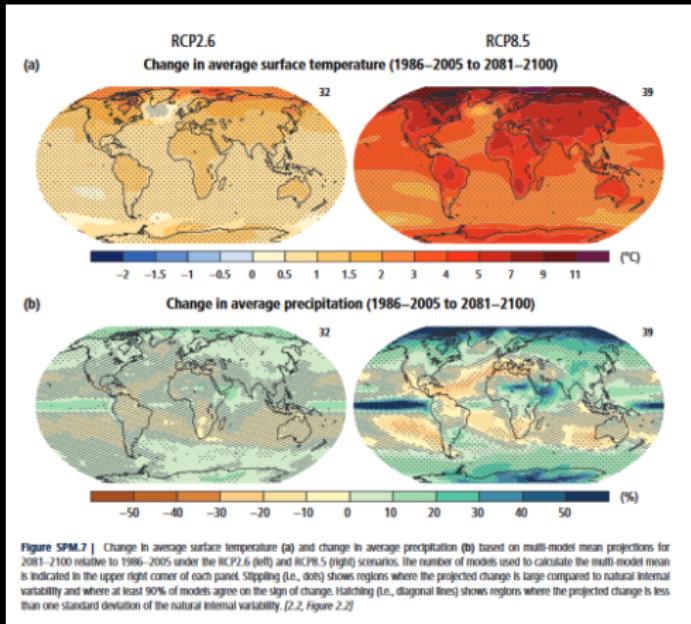
R.A. Fisher G. Price

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

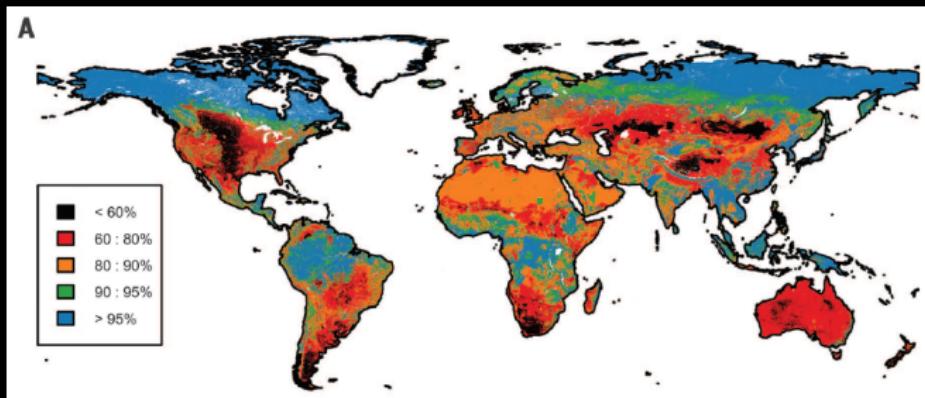
Timothée Bonnet* and Erik Postma

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

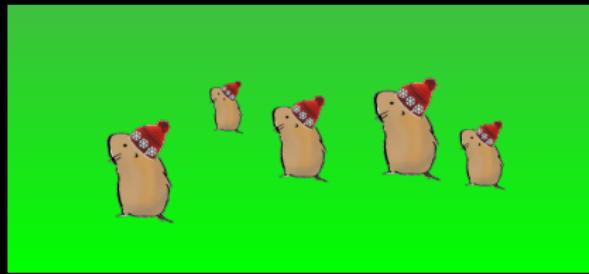
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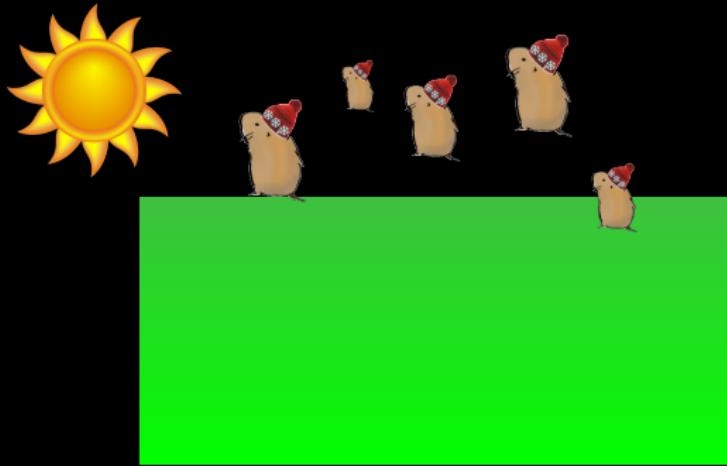
Camille Parmesan

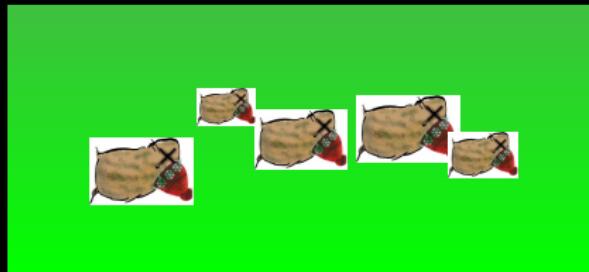
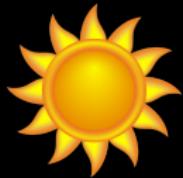
Section of Integrative Biology, University of Texas, Austin, Texas 78712; email:
parmesan@mail.utexas.edu

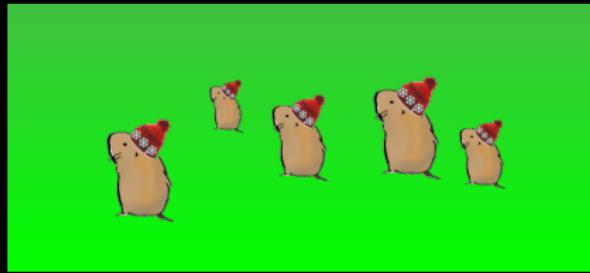
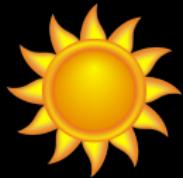




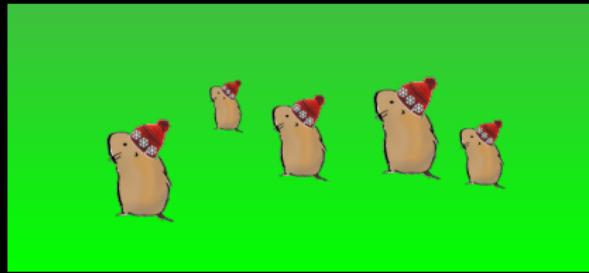


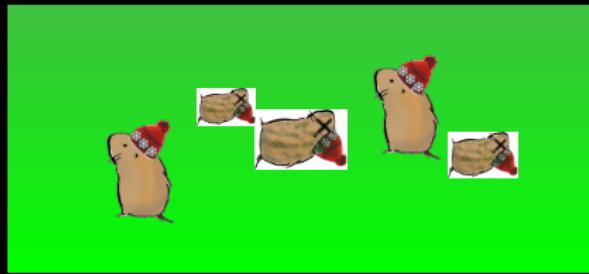


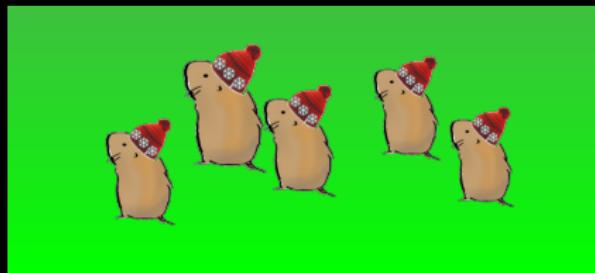












Evolution or plasticity? What drives phenotypic change?

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^{1*}†, Marjolein Bruijning²†, Timothée Bonnet¹†, Eelke Jongejans²‡,
Erik Postma¹‡ and Arpat Ozgul¹‡

¹Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; and ²Department 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

Pedigree → similarity between relatives → **additive genetic variance**

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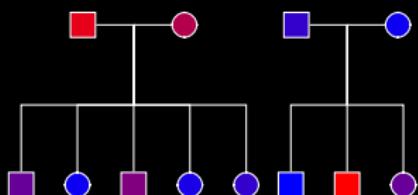
$$\text{heritability} = \frac{\text{additive genetic variance}}{\text{phenotypic variance}}$$

The animal model

Pedigree → similarity between relatives → **additive genetic variance**

$$\text{heritability} = \frac{\text{additive genetic variance}}{\text{phenotypic variance}}$$

heritability ≈ 0

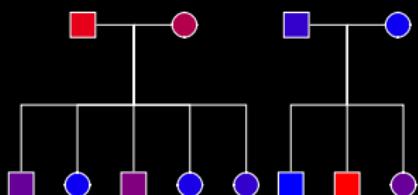


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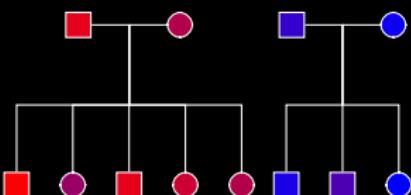
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heritability ≈ 1

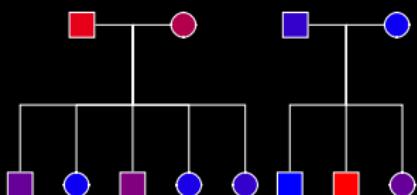


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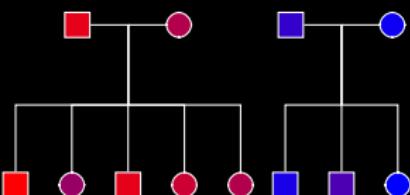
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$$\text{heritability} = \frac{\text{additive genetic variance}}{\text{phenotypic variance}}$$

heritability ≈ 0



heritability ≈ 1



Breeding value

= Individual additive genetic value
Change with time = evolution

Adaptive evolution in the wild

Adaptive evolution in the wild

Adaptive evolution = Selection \times heritability

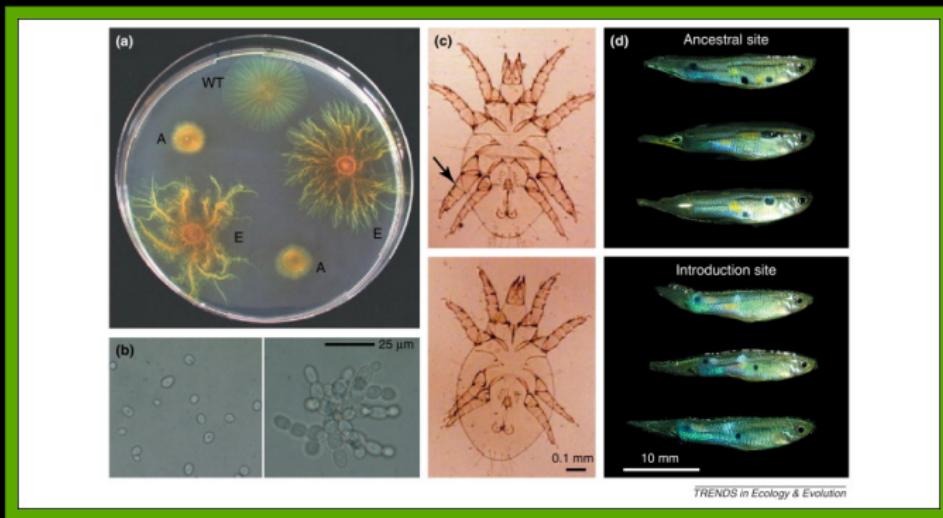
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Experimental evolution. Kawecki & al. (2012) Trends in Ecology & Evolution 27(10)

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^{1*}, B.C. Sheldon² & L.E.B. Kruuk³

Adaptive evolution in the wild

Adaptive evolution = Selection × heritability

2014

The image shows a screenshot of a journal article from the 'Evolutionary Applications' journal. The article is a 'PERSPECTIVE' piece titled 'Climate change, adaptation, and phenotypic plasticity: the problem and the evidence'. It is authored by Juha Merilä^{1,*} and Andrew P. Hendry^{2,*}. The journal logo 'Open Access' is visible, along with the ISSN number 1752-4571.

Evolutionary Applications

Open Access

Evolutionary Applications ISSN 1752-4571

PERSPECTIVE

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

Juha Merilä^{1,*} and Andrew P. Hendry^{2,*}

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?

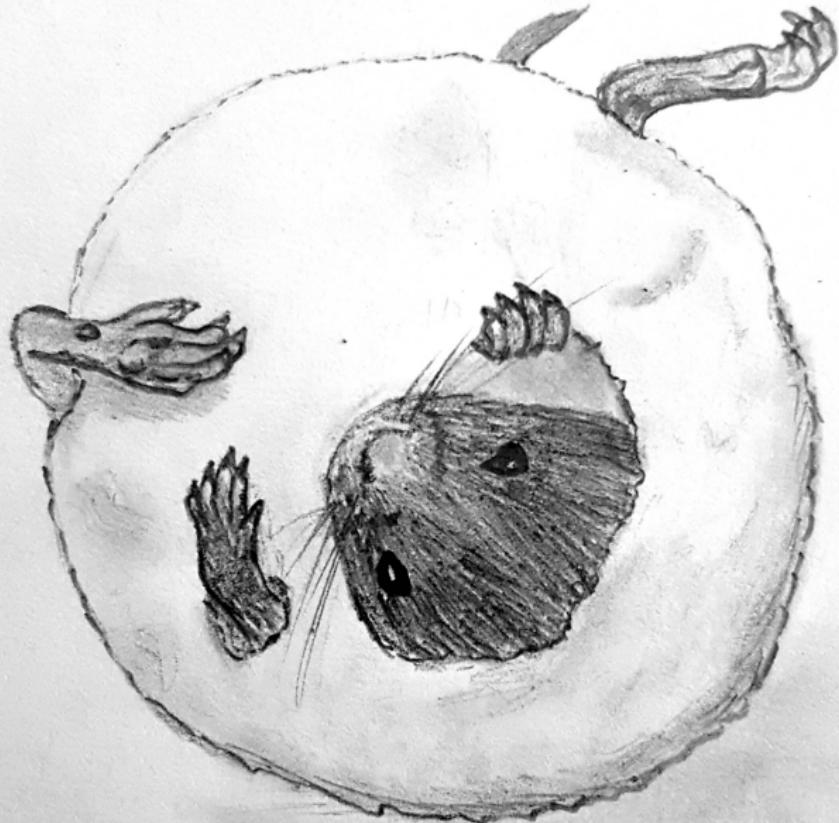
John F.Y. Brookfield

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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)

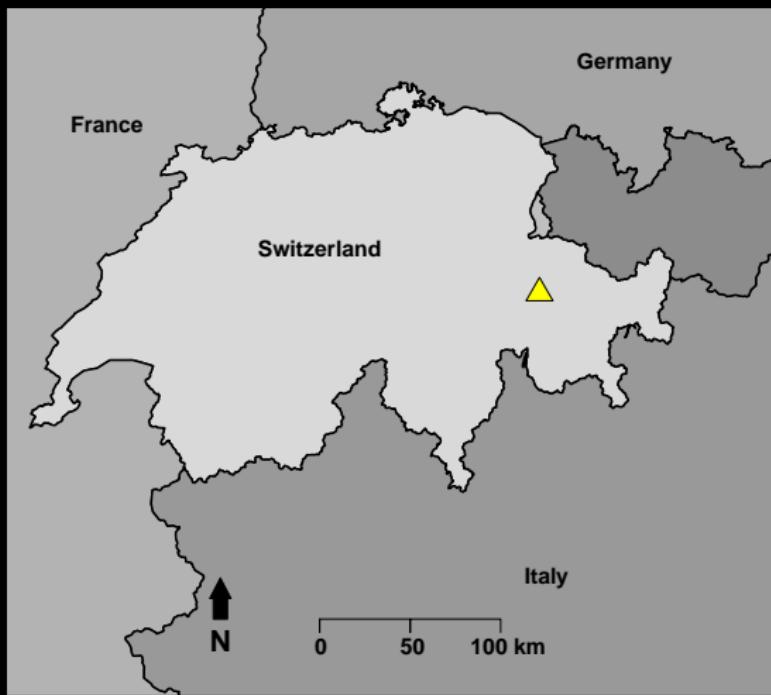
- NOT white
- Rock-dweller
- 30-45g
- 10-14cm long + 5-8cm tail



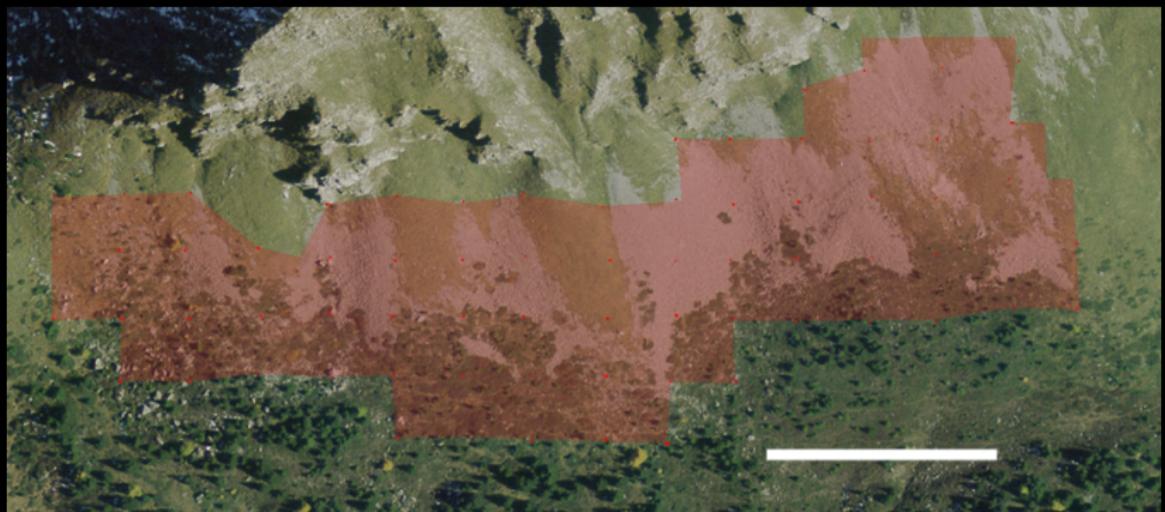
Snow vole (*Chionomys nivalis*, Martins 1842)

- 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



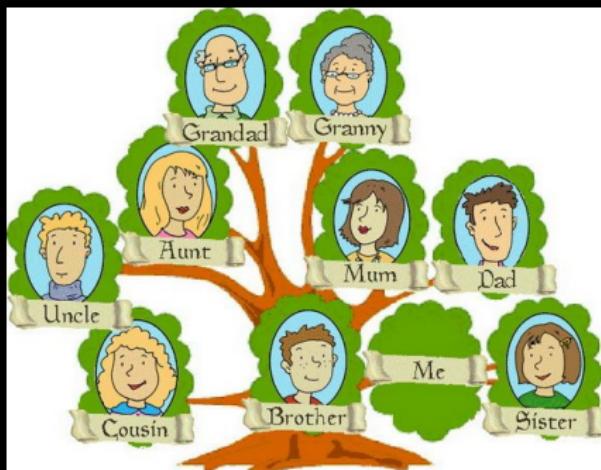
What we measure

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 - Location
- DNA
 - 20 “neutral” markers
 - Sex identification
 - Any genotyping



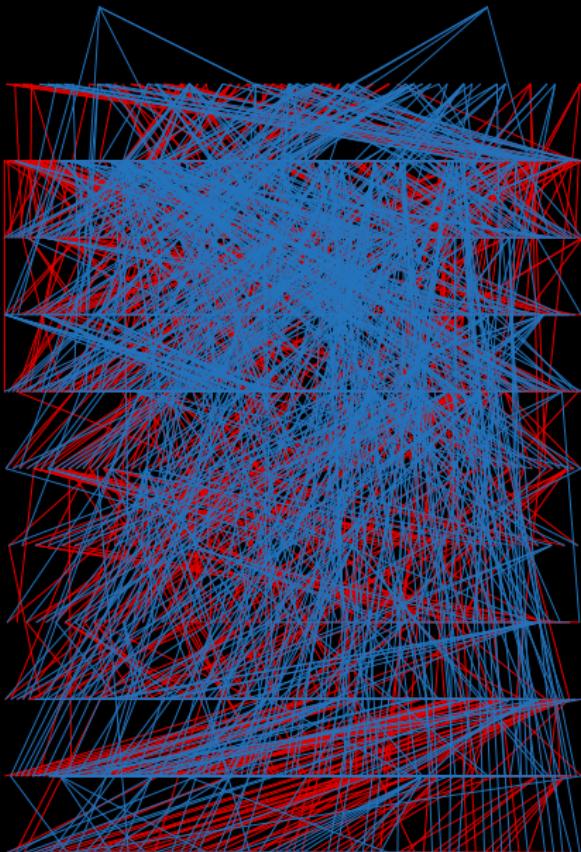
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 - **Pedigree**



What we measure

- Morphology
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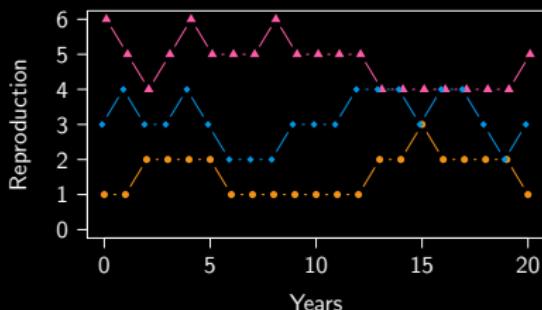


Are snow vole evolving? Why?

Variance in fitness?

Adaptive evolution in the snow vole?

Variance in fitness?

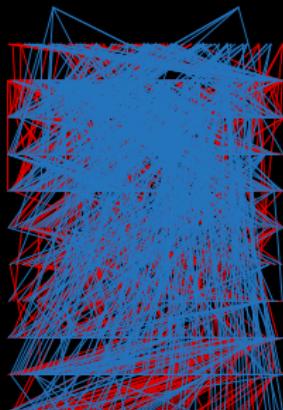


| | Estimate | 95% CI | p-value |
|---------------------------------|----------|--------------|--------------|
| Latent variance in survival | 0 | [0;0.248] | 0.50 |
| Latent variance in reproduction | 0.37 | [0.25, 0.49] | $< 10^{-16}$ |

Adaptive evolution in the snow vole?

- Non random variation fitness components

Variance in fitness?

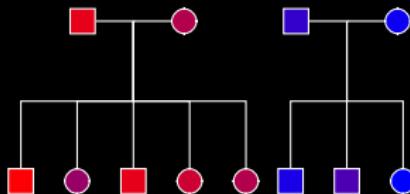


Relative lifetime reproductive success
variance ≈ 1.7

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

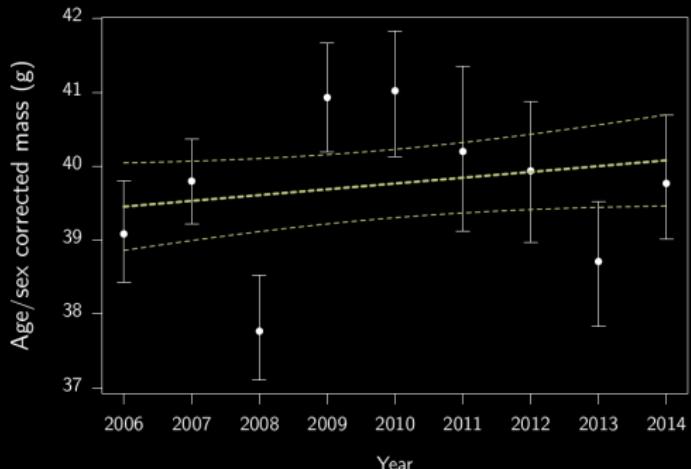
- Selection = $+0.86\text{g}$ ($p < 10^{-3}$)
- Heritability = 20% ($p < 10^{-3}$)
- Response = Selection \times heritability = $+ 0.22\text{g/year}$

Evolution of body mass

Prediction

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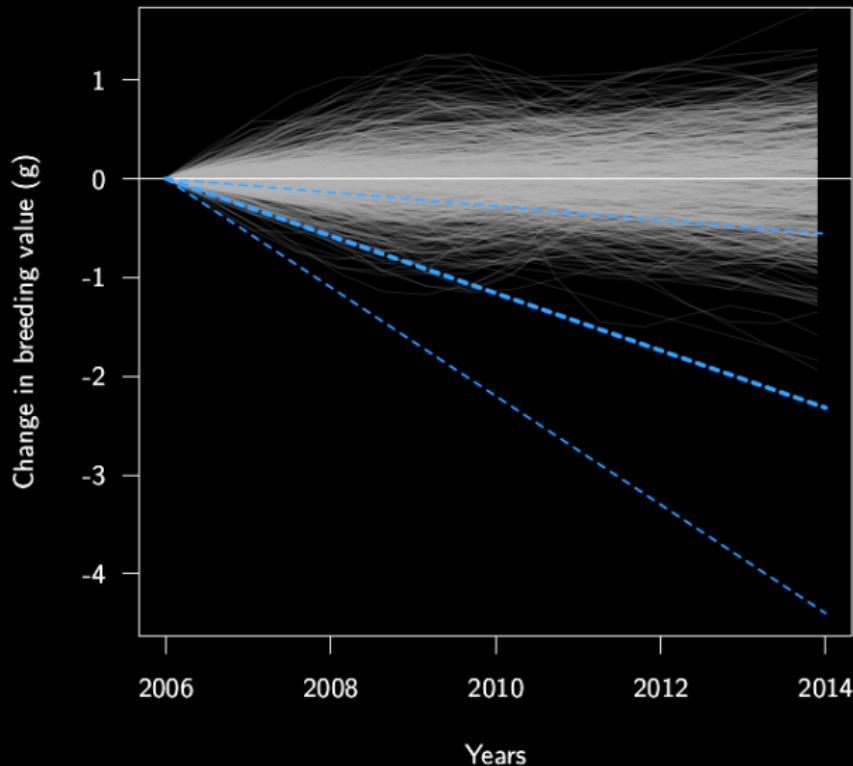
Phenotypic observation



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

Evolution of body mass

Estimation of genetic change



Evolution of body mass

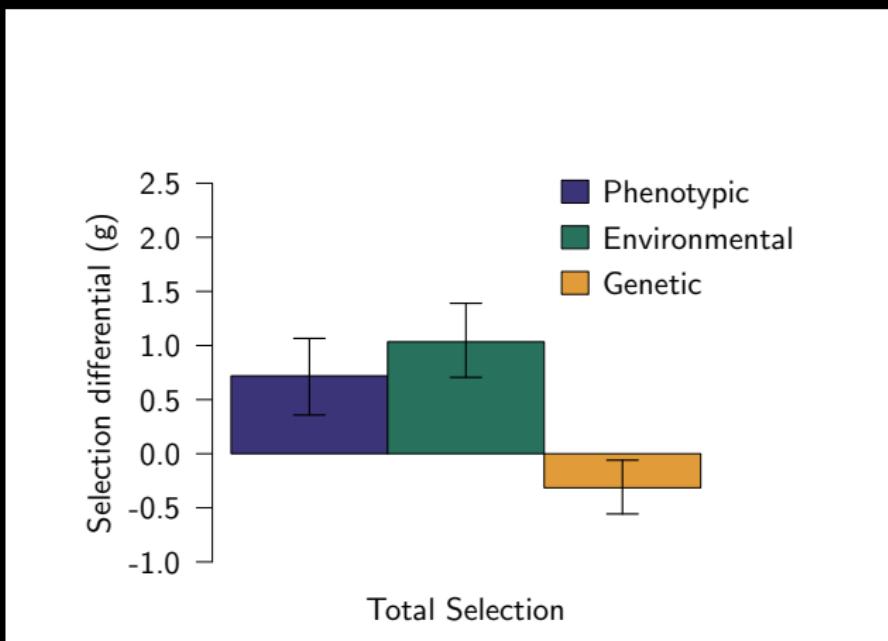
Evolution Paradox

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

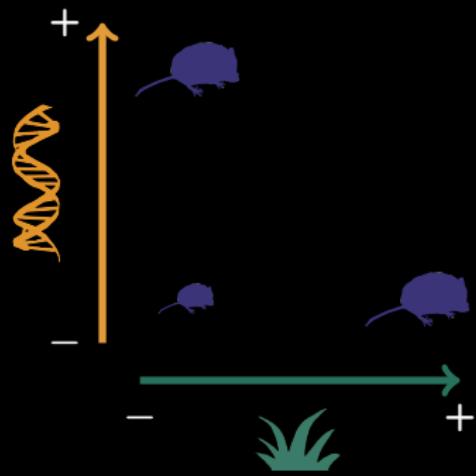
Evolution of body mass

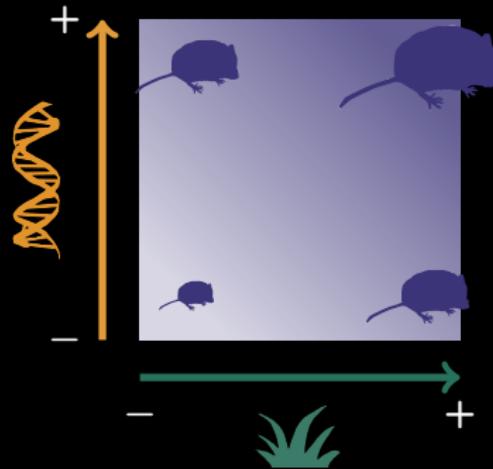
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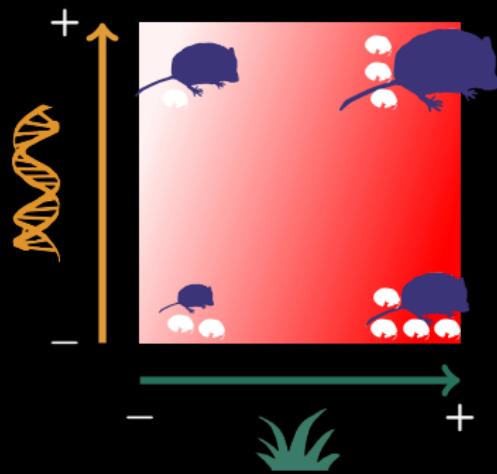
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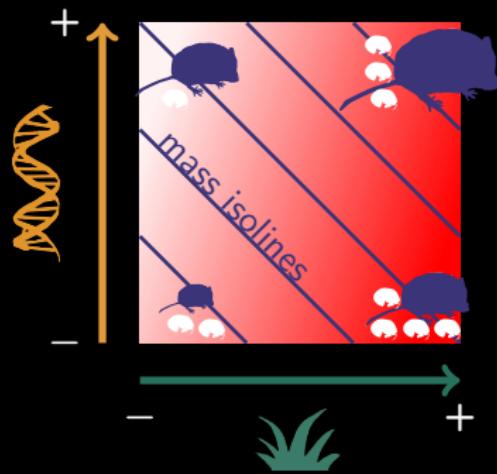


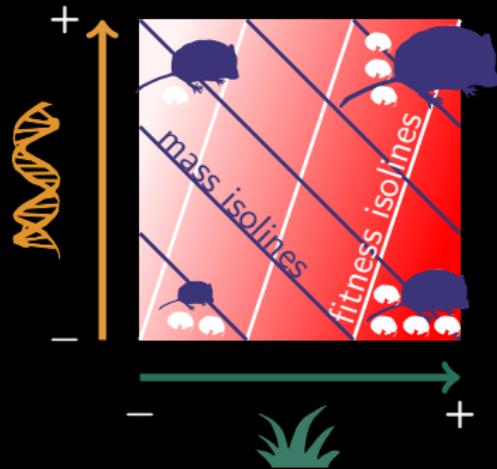


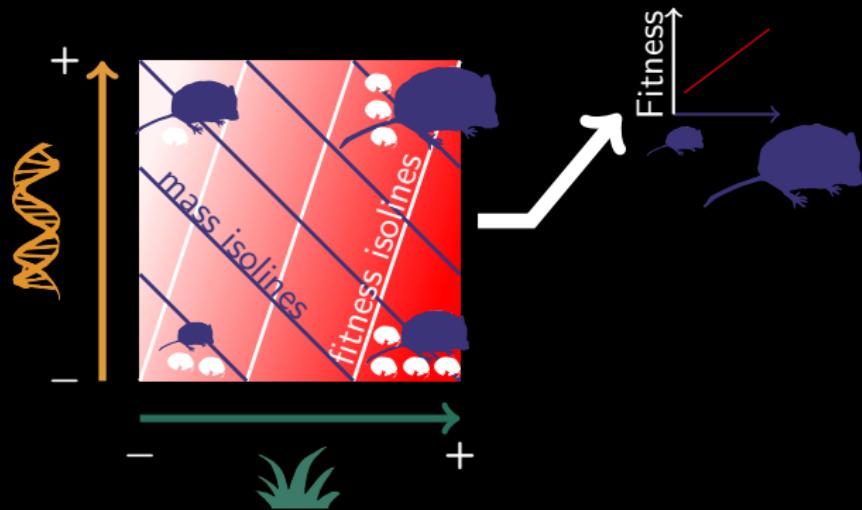


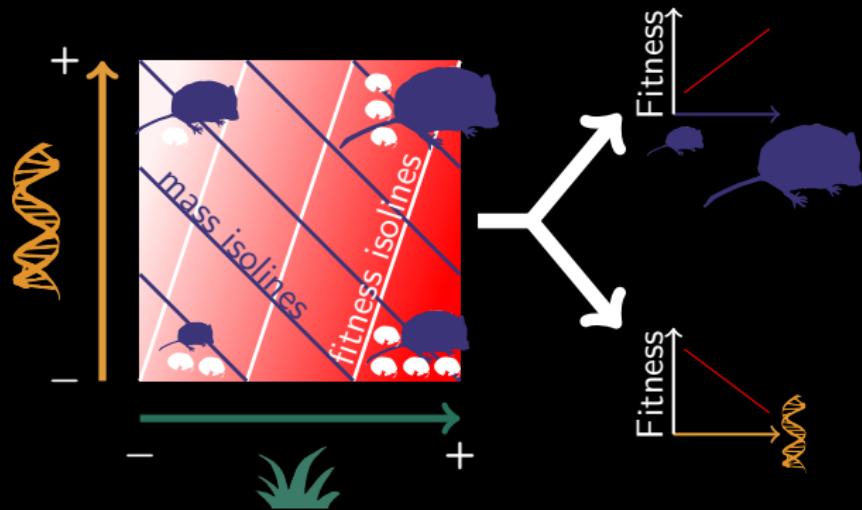


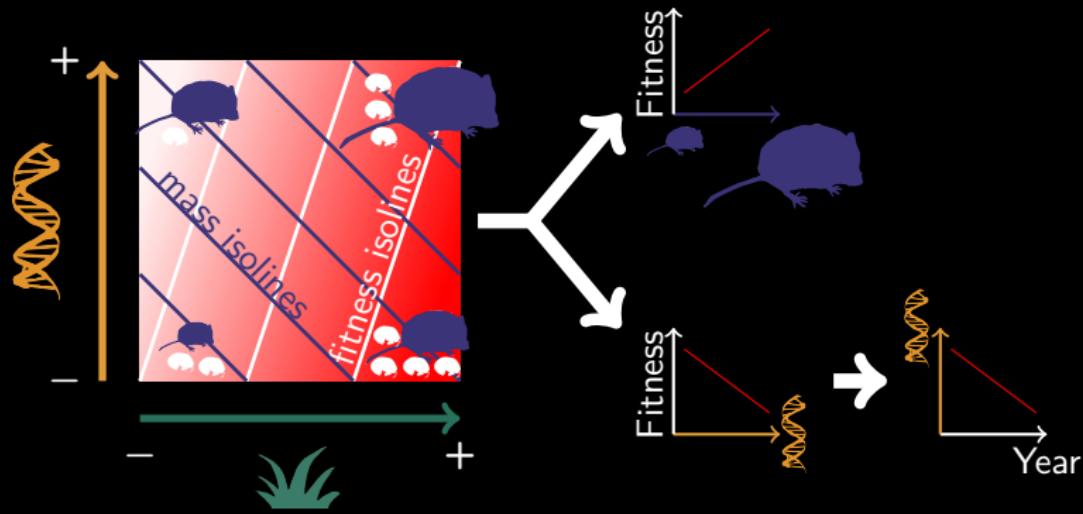


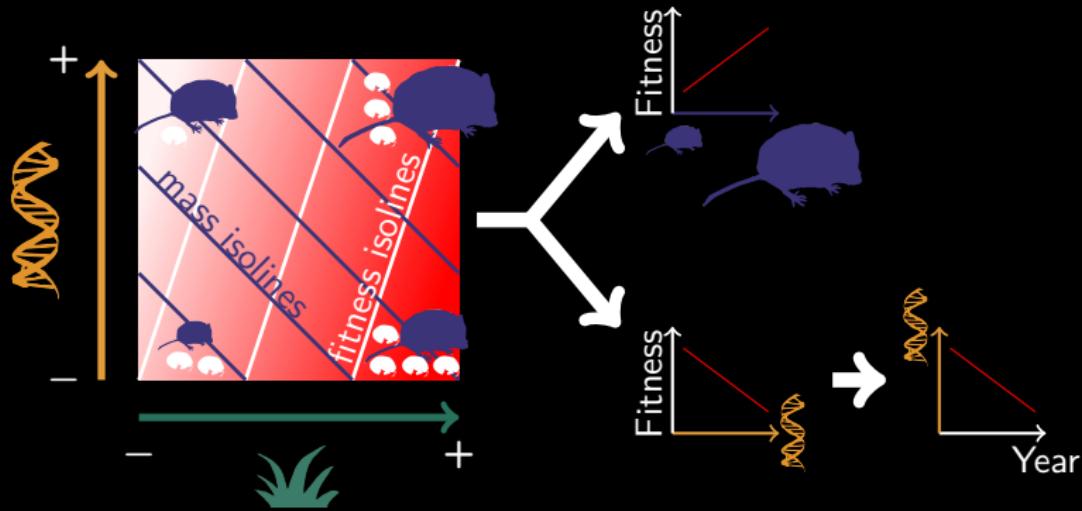






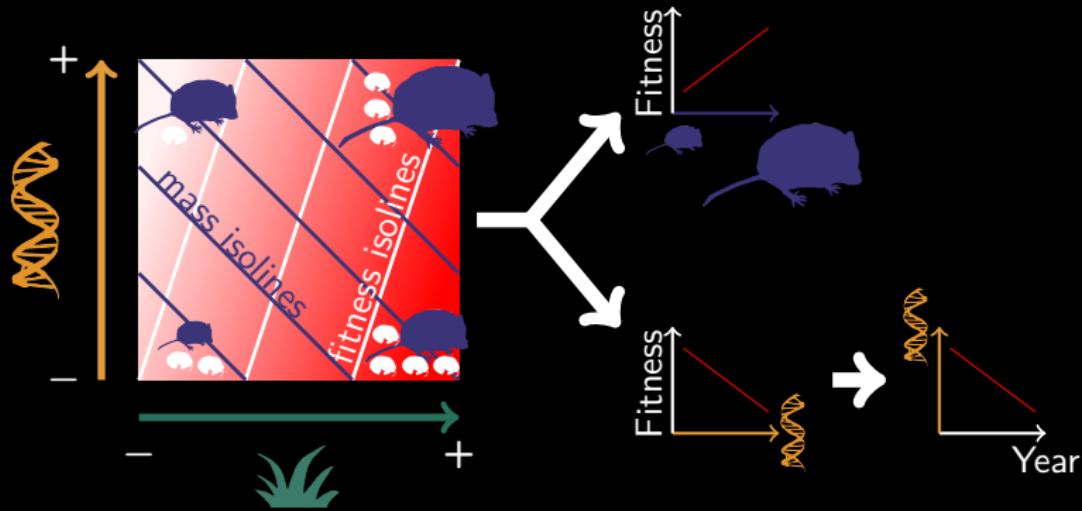






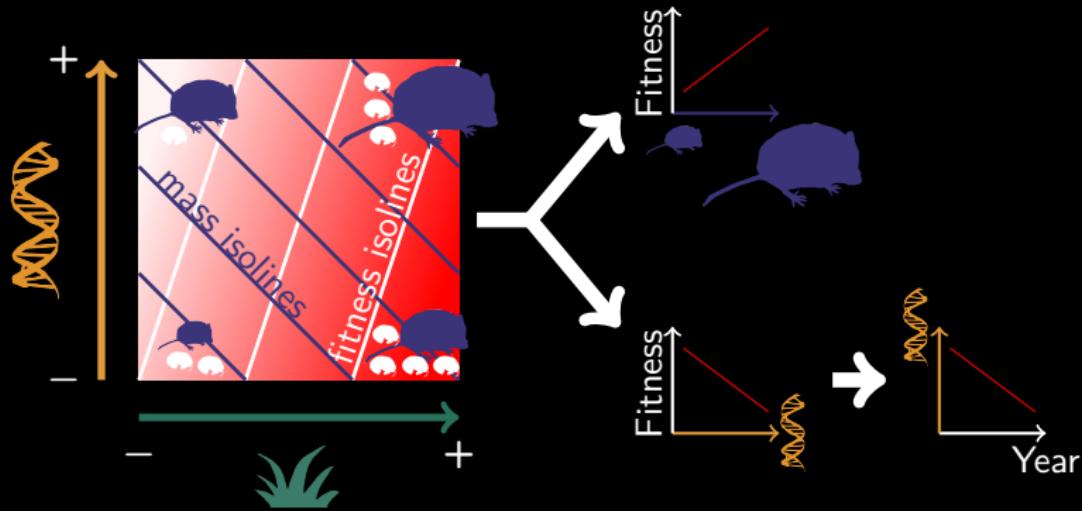
Summary

1. Apparent stasis...



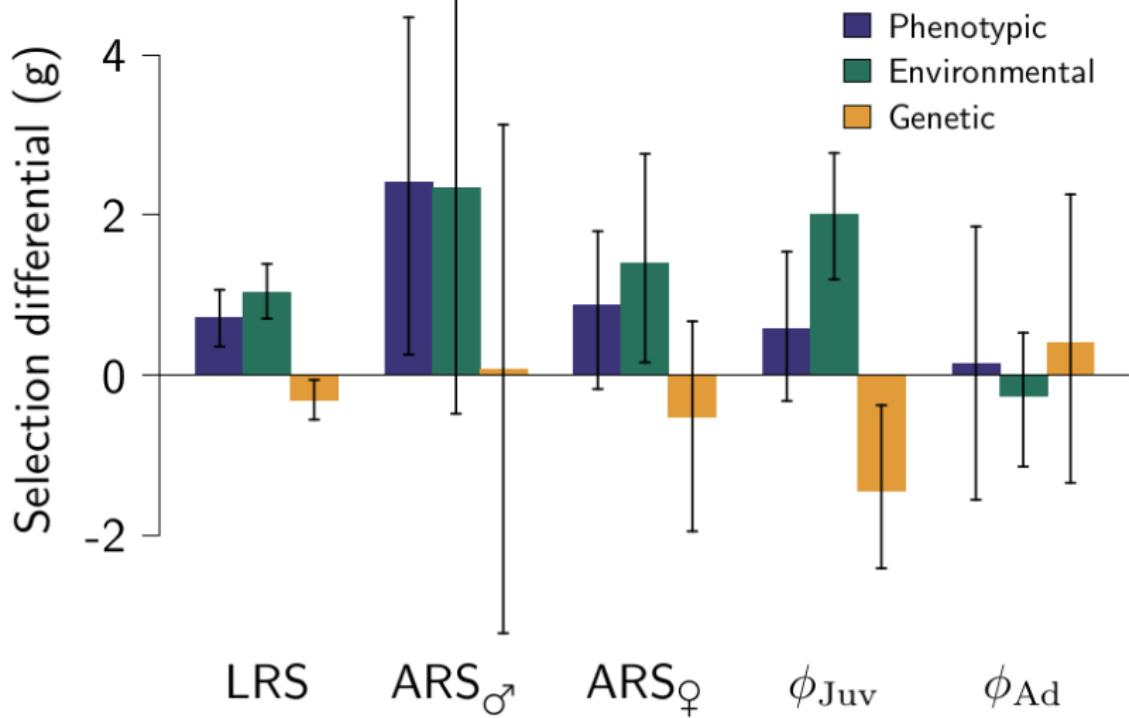
Summary

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

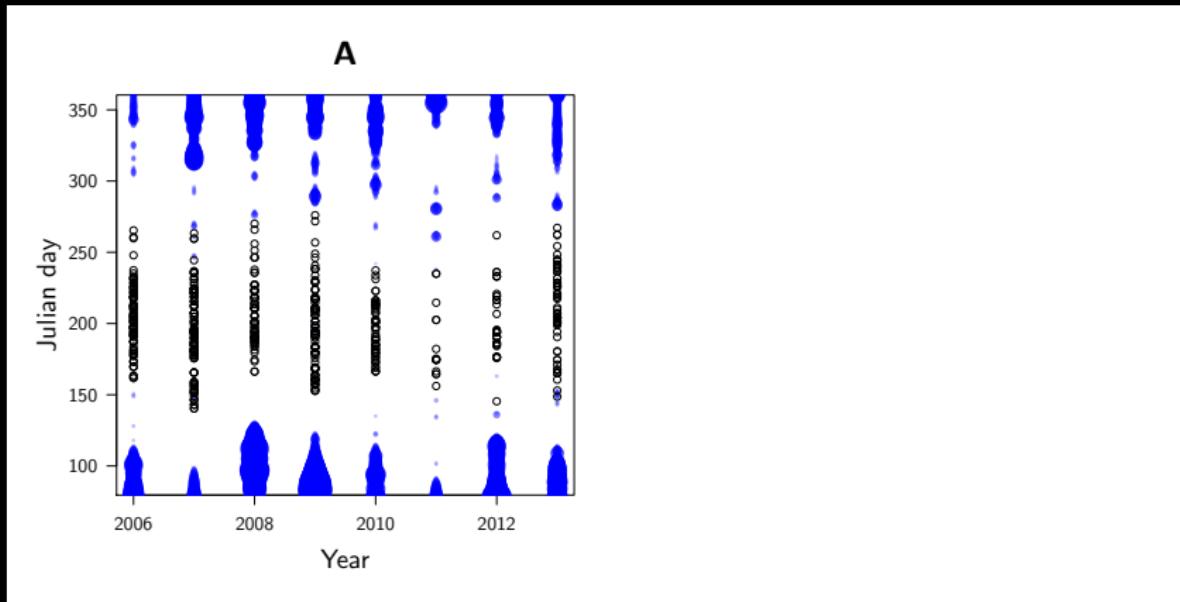


Summary

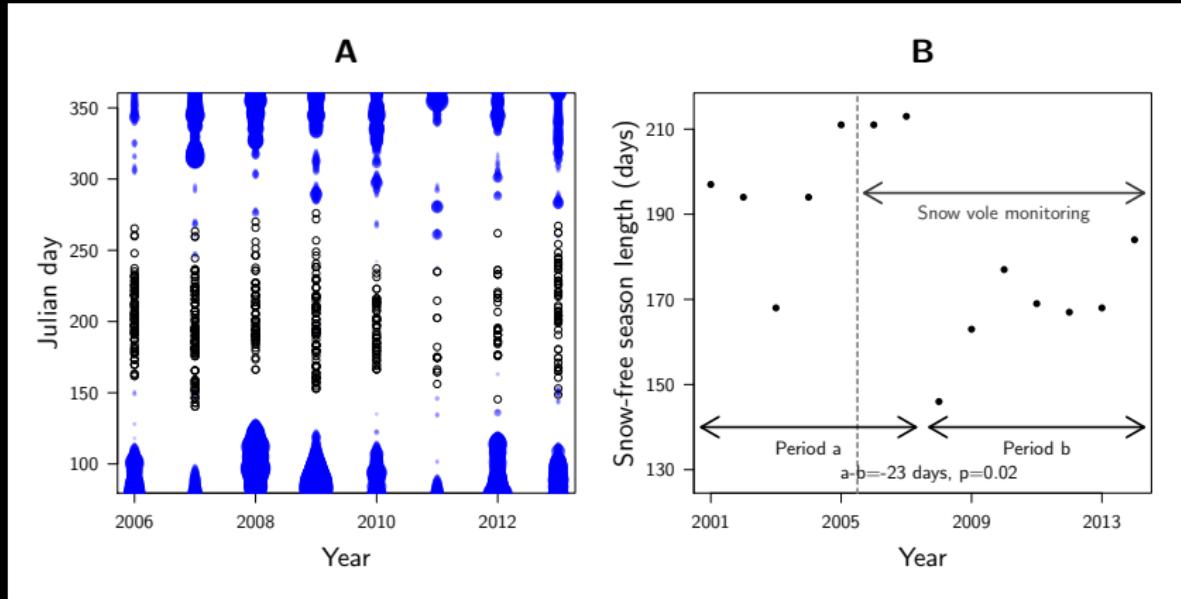
1. Apparent stasis . . .
2. . . . but evolution towards lower mass
3. *Selective pressure?*



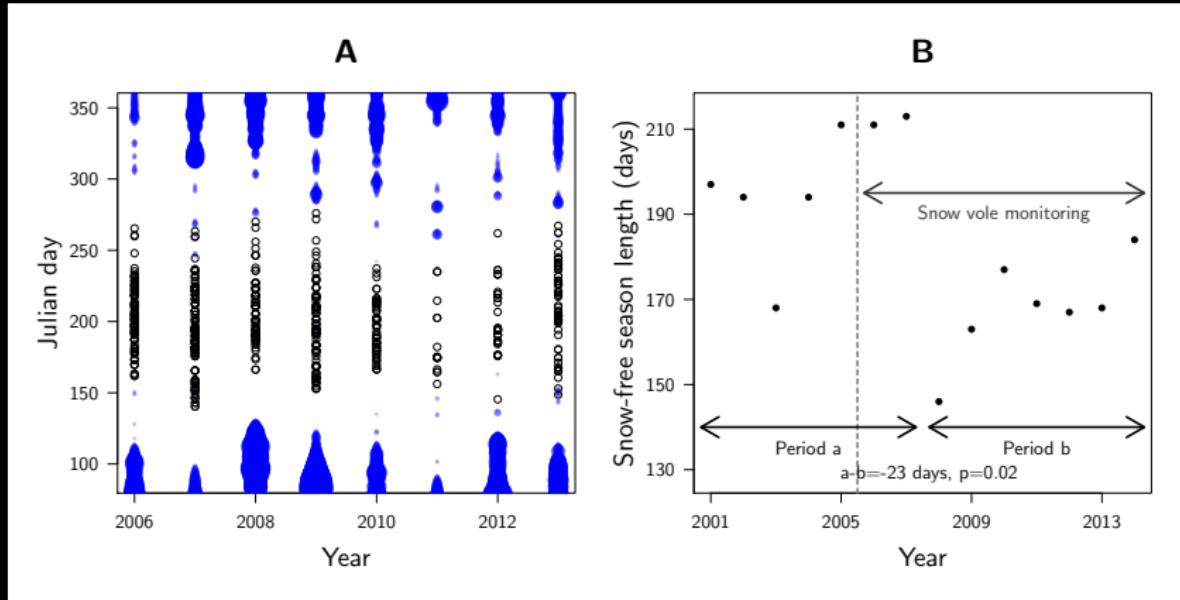
Snow falls and ontogeny



Snow falls and ontogeny



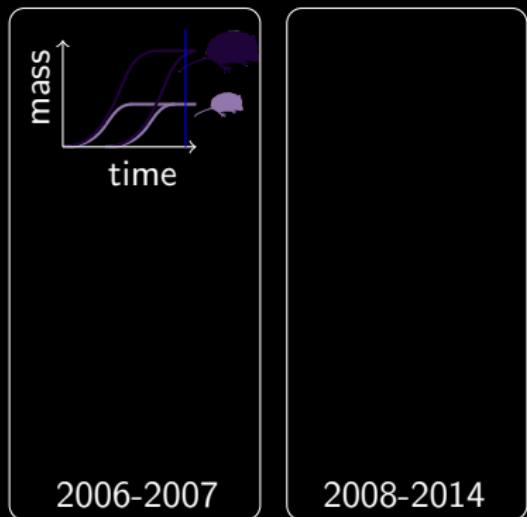
Snow falls and ontogeny



Less time to grow → Selection for smaller voles?

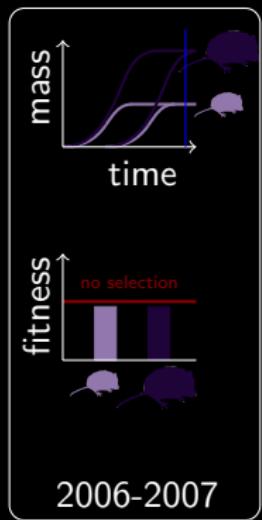
Selection during ontogeny?

D



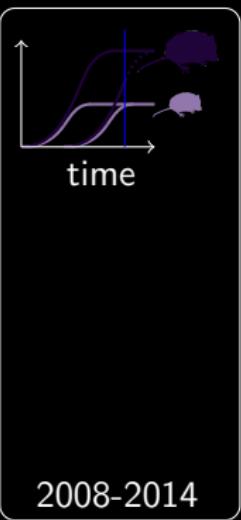
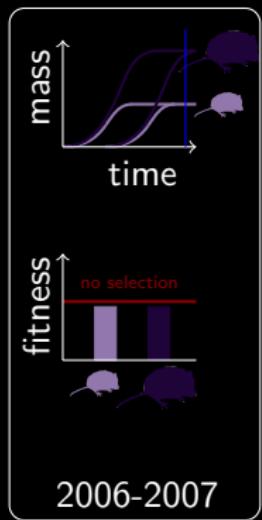
Selection during ontogeny?

D



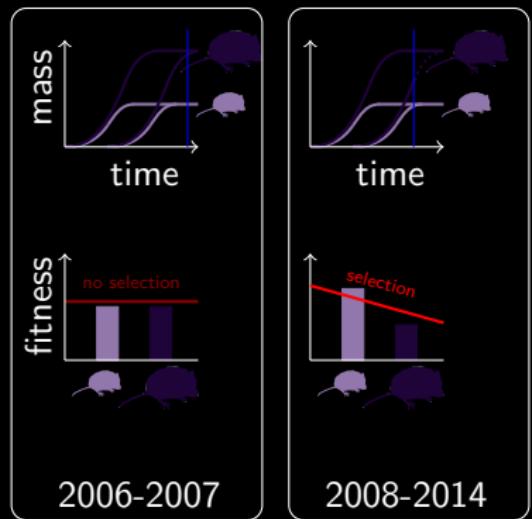
Selection during ontogeny?

D



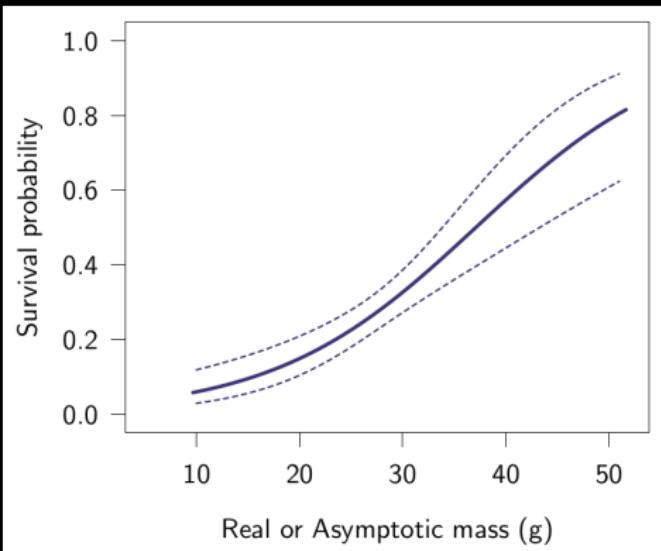
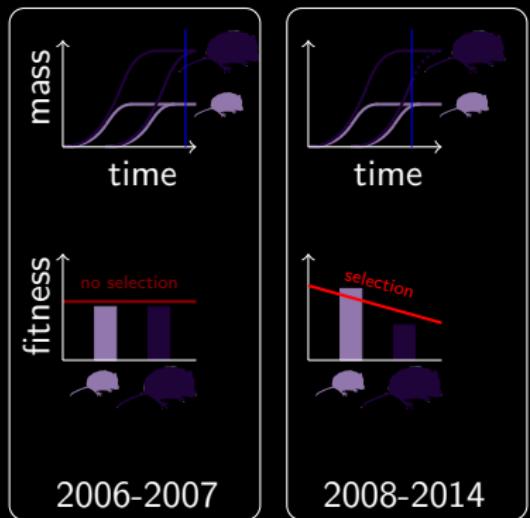
Selection during ontogeny?

D



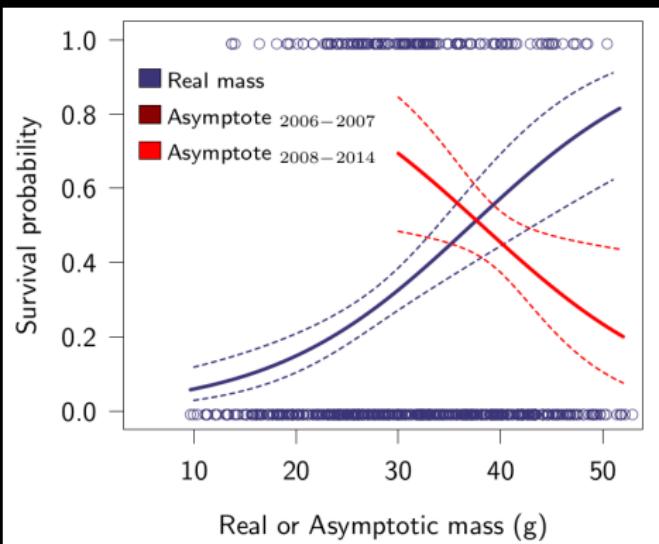
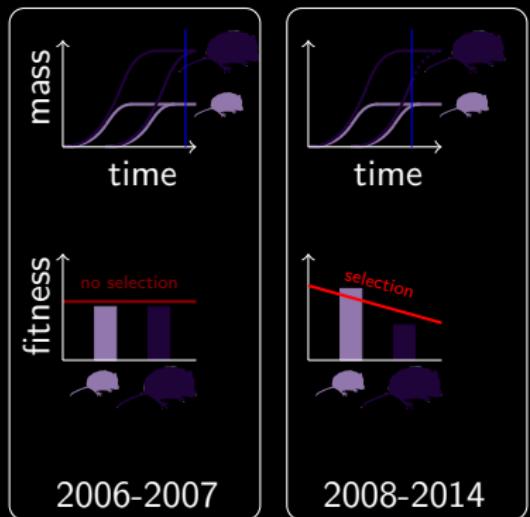
Selection during ontogeny?

D



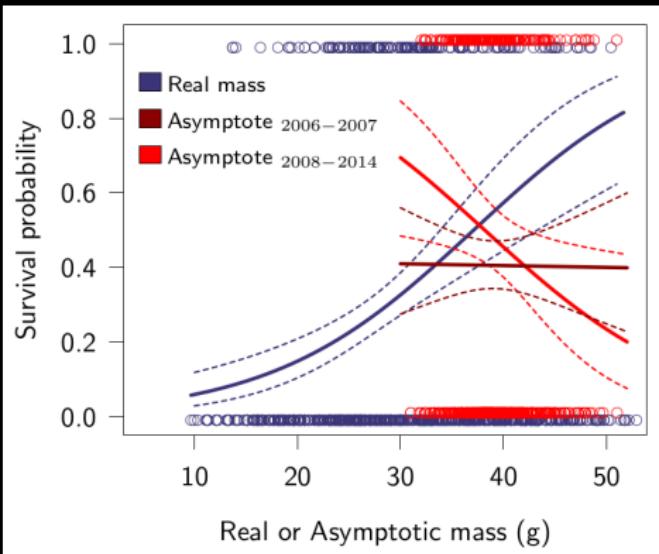
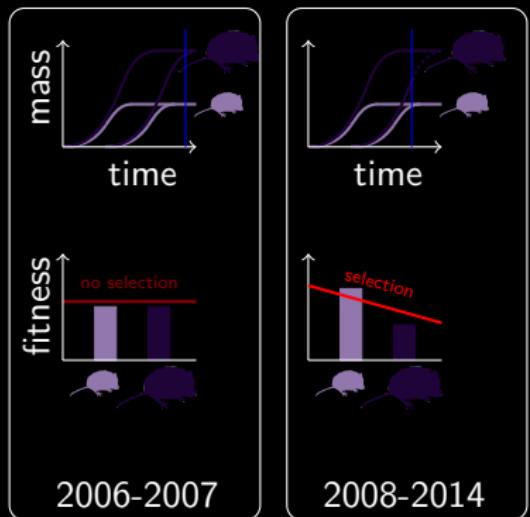
Selection during ontogeny?

D



Selection during ontogeny?

D



Evo**l**eution!

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 screenshot shows the bioRxiv preprint server interface. At the top left is the CSHL logo and the text "Cold Spring Harbor Laboratory". The center features the bioRxiv logo with "beta" underneath and "THE PREPRINT SERVER FOR BIOLOGY" below it. On the right side are links for "HOME" and "A", and a search bar. Below the header, there are two buttons: "New Results" on the left and a red button on the right that says "View current version of this article". The main content area displays a study titled "The stasis that wasn't: Adaptive evolution goes against phenotypic selection in a wild rodent population". It lists four authors: Timothée Bonnet, Peter Wandeler, Glauco Camenisch, and Erik Postma. The DOI provided is <http://dx.doi.org/10.1101/038604>. A note at the bottom states, "This article is a preprint and has not been peer-reviewed [what does this mean?]."

New Results

View current version of this article

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

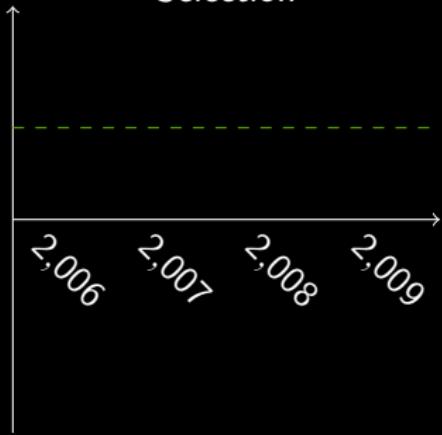
Timothée Bonnet, Peter Wandeler, Glauco Camenisch, Erik Postma
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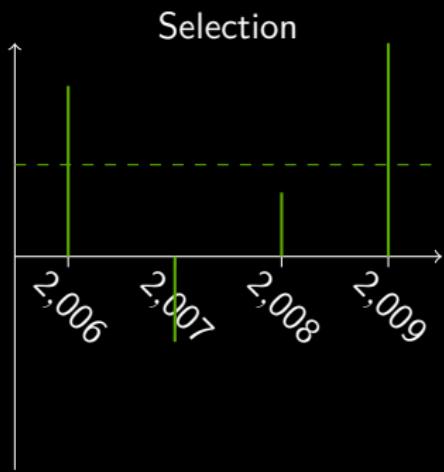
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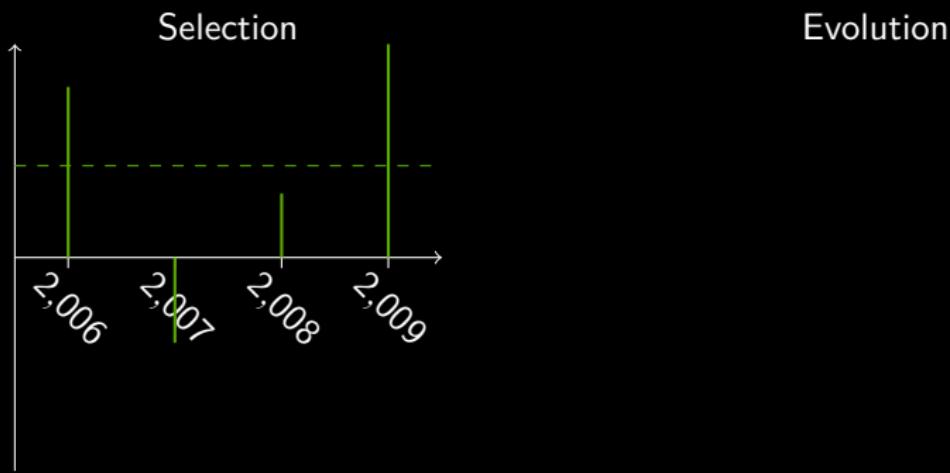
**Do selection and evolution
fluctuate?**

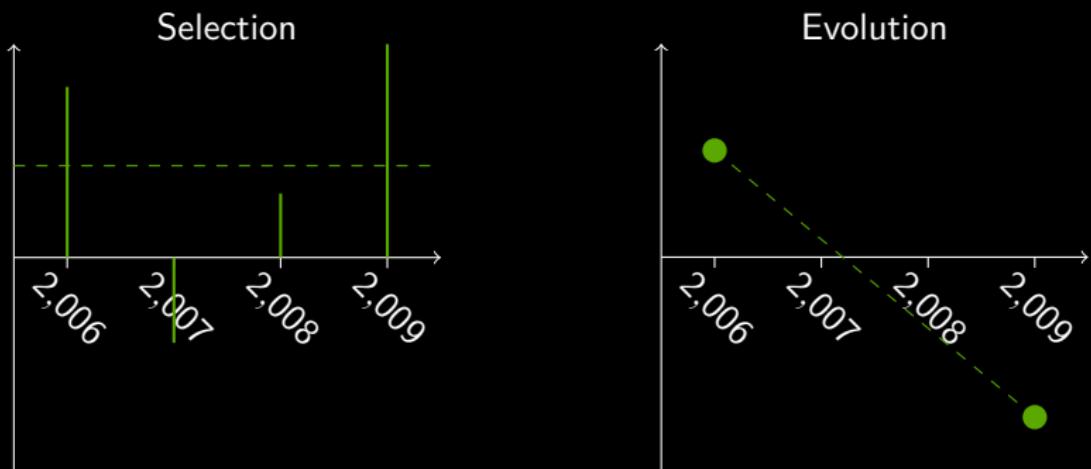
Selection

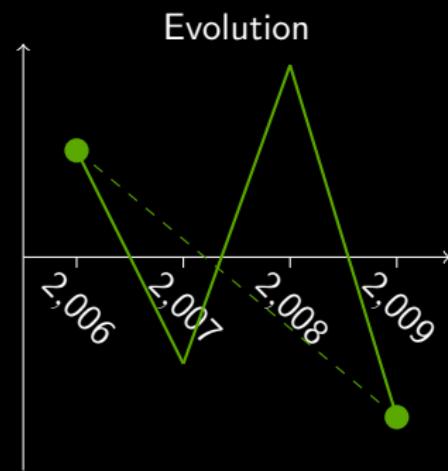
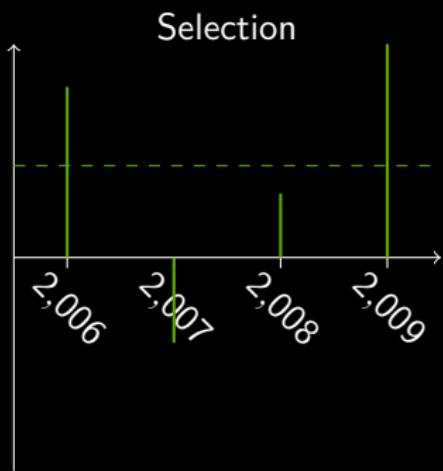
Selection



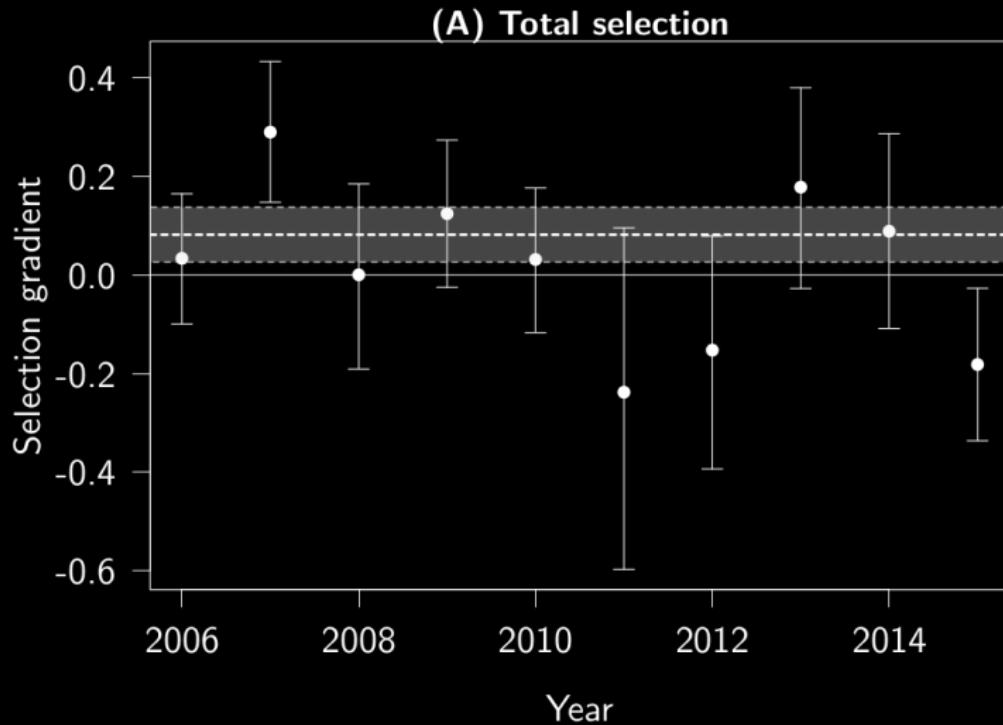






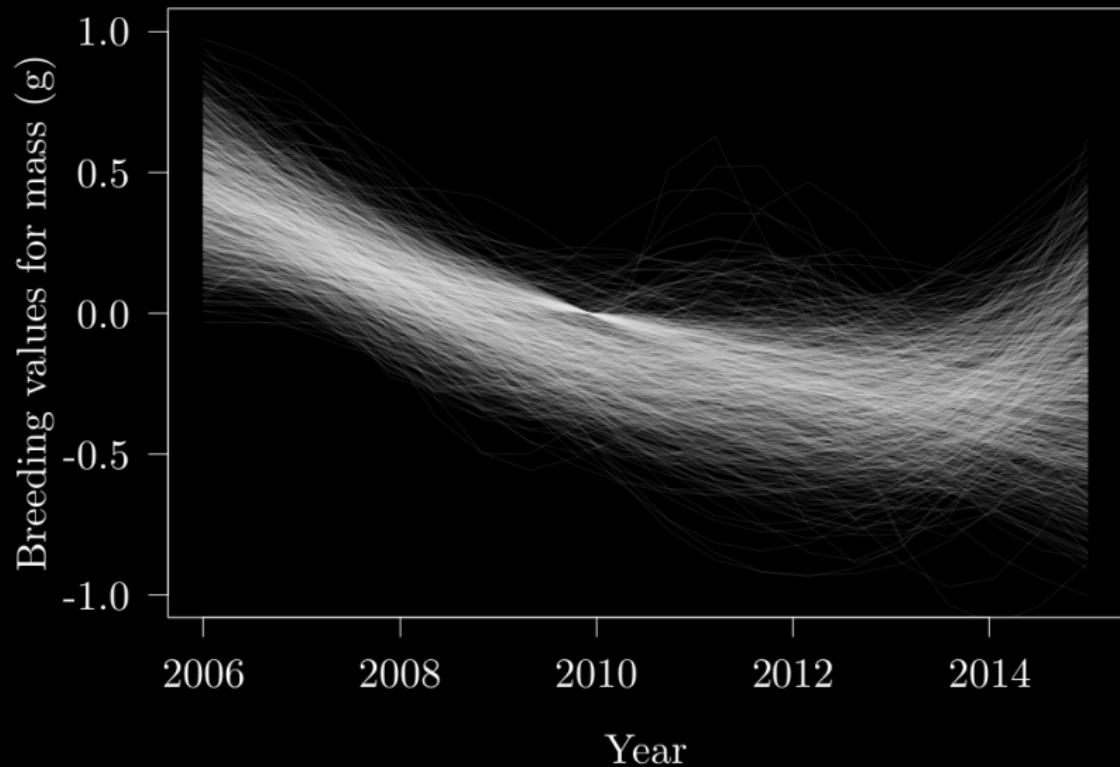


Dynamics of selection

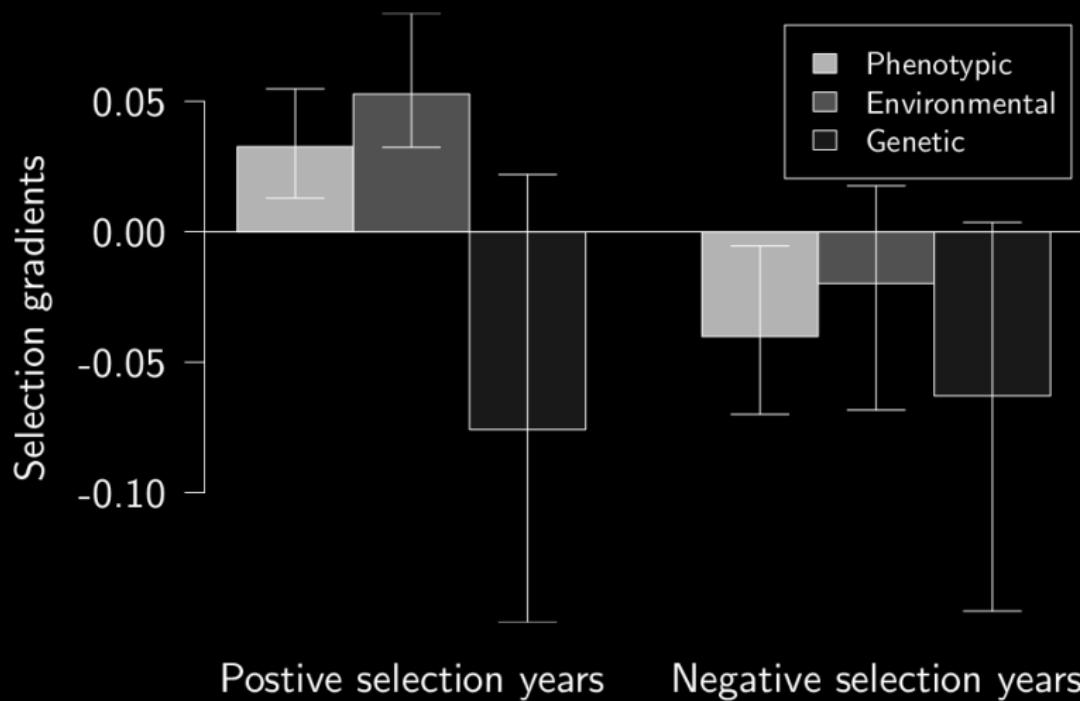


Variance in selection = 0.117 [0.063;0.218], $p=8 \cdot 10^{-6}$

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?
