

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}**

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



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- Philipp Becker
- Judith Bachmann





Phenotypic variation within population



Phenotypic variation within population



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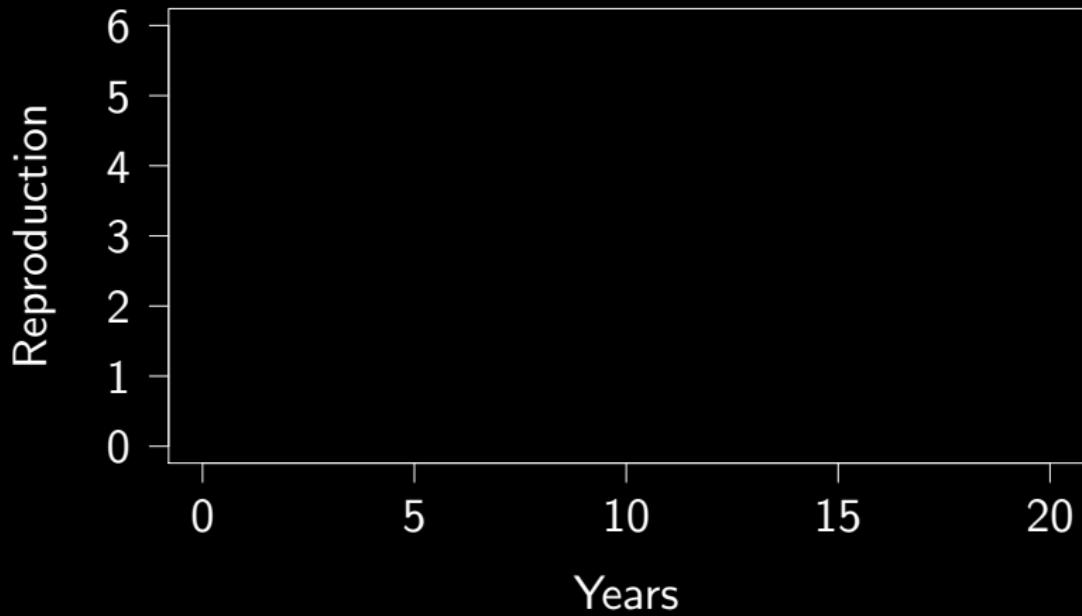
Fitness variation

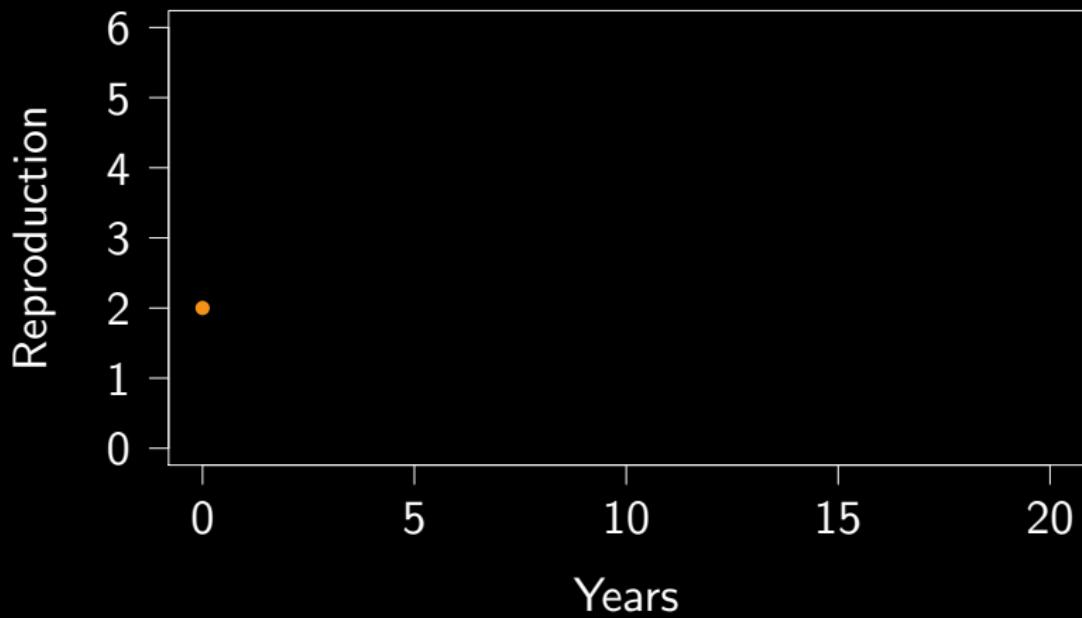


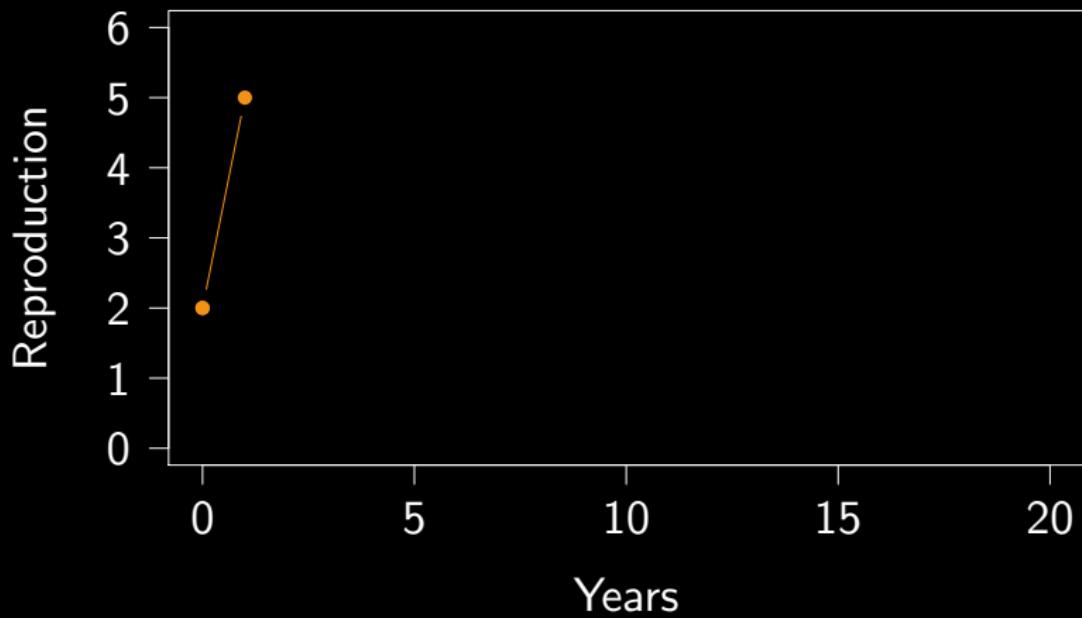
What is fitness?

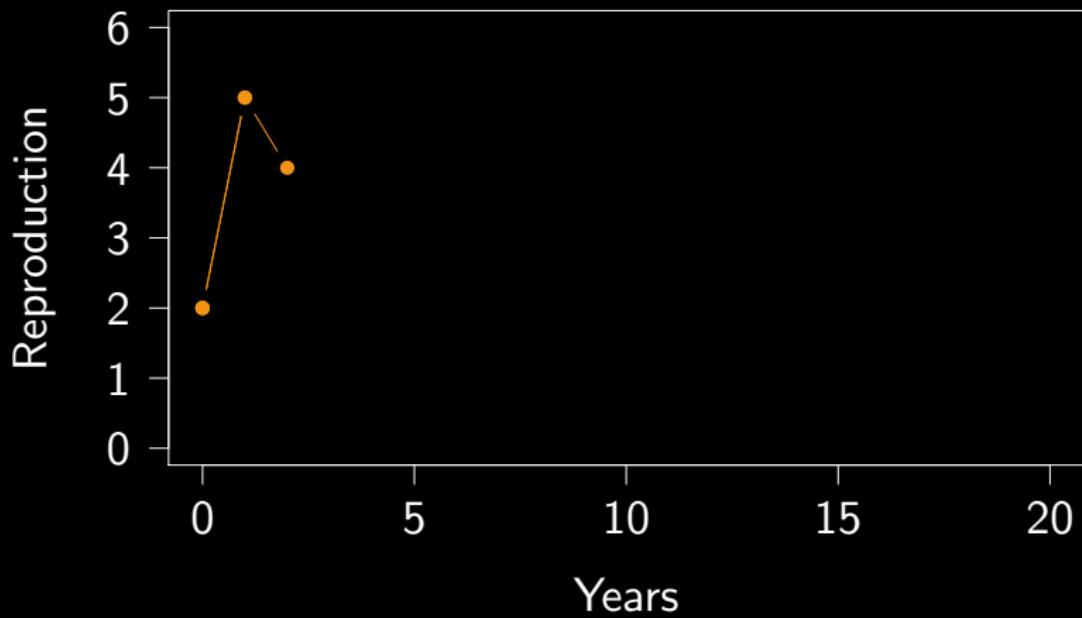
The expected relative contribution of an individual to the next generation

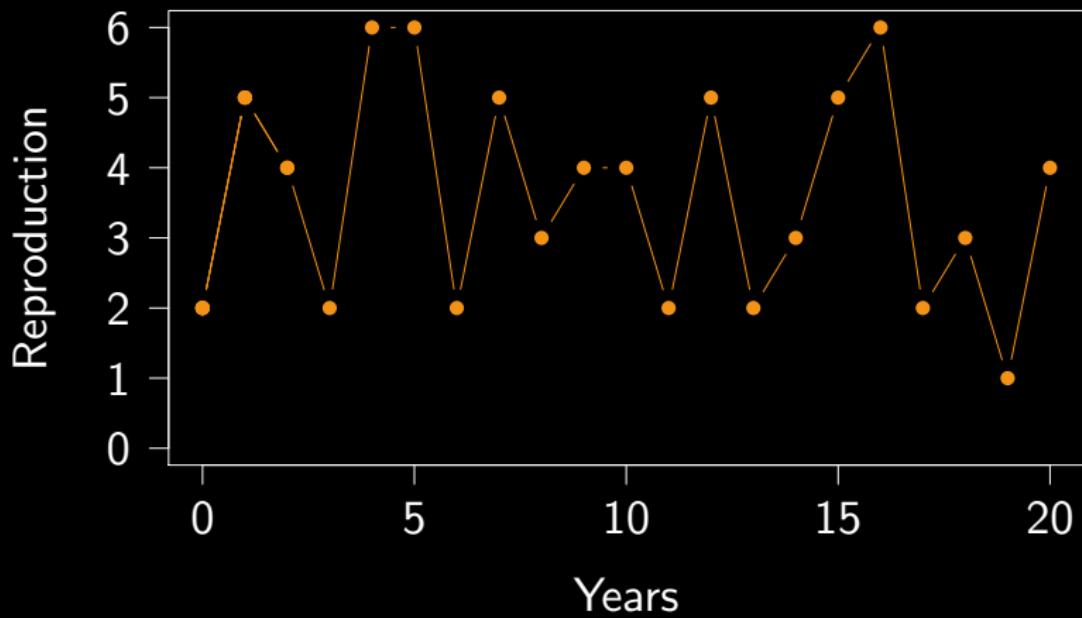
**Chance or fate? Why do survival
and fertility vary?**

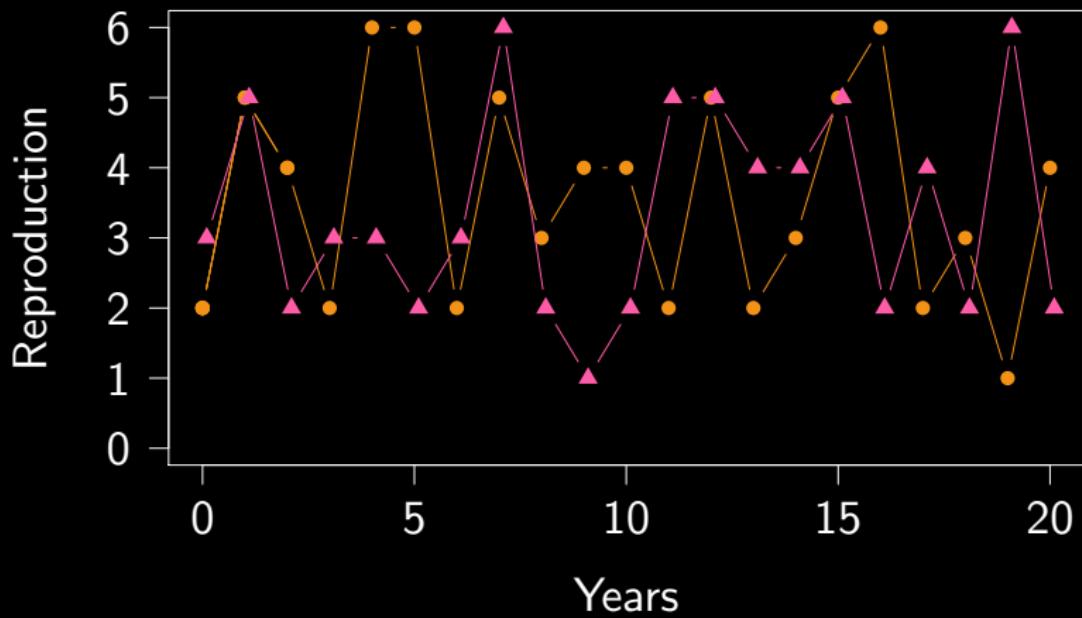


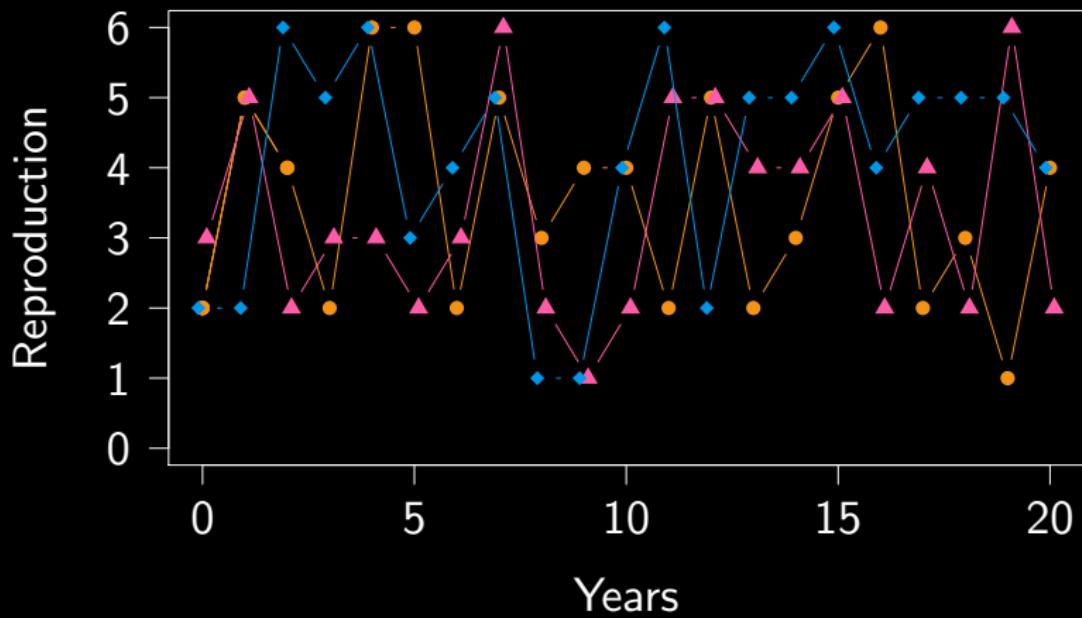




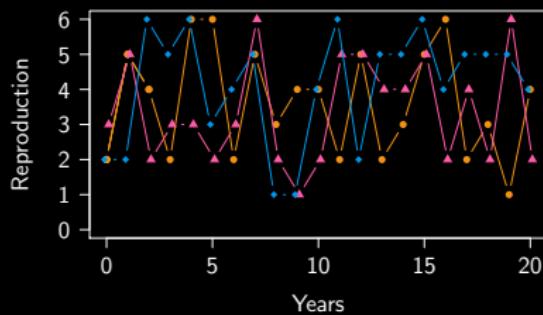




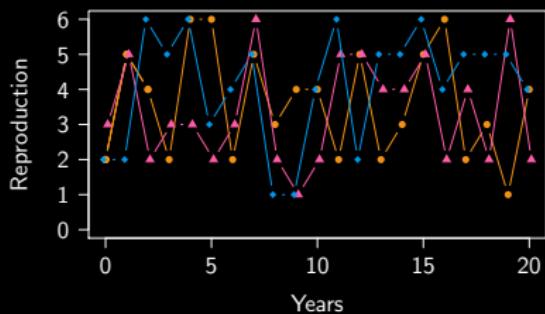




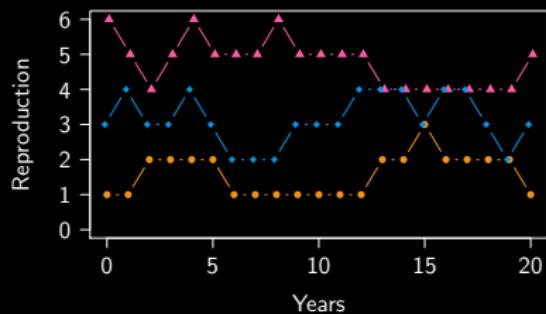
One dice theory



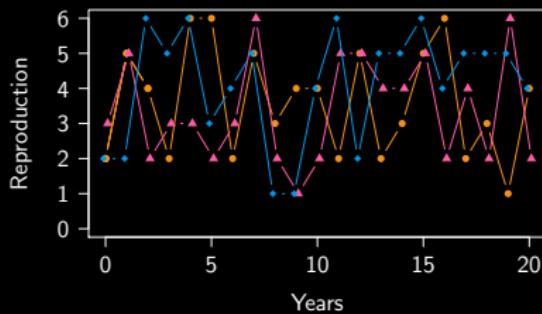
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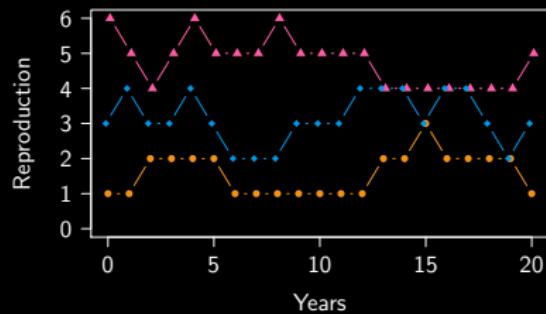
Real pattern



One dice theory



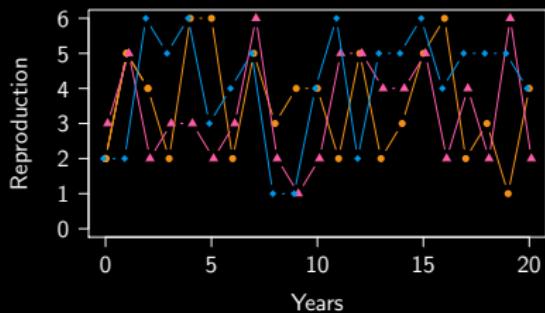
Real pattern



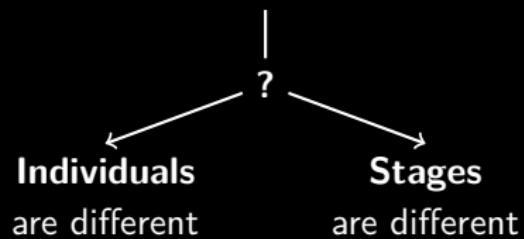
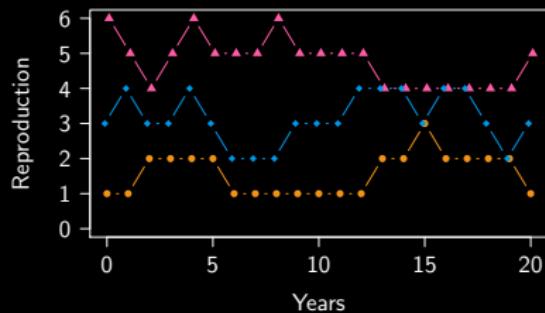
Individuals
are different

?

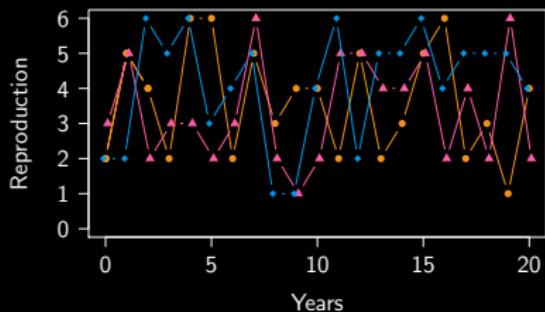
One dice theory



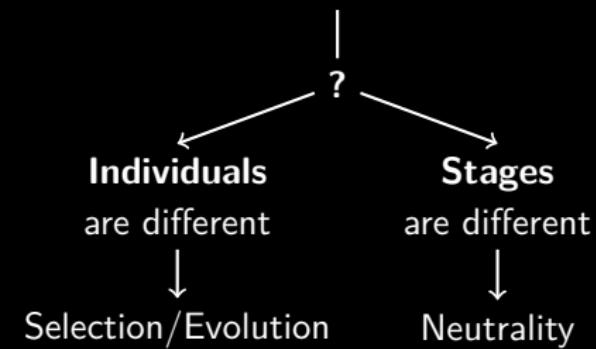
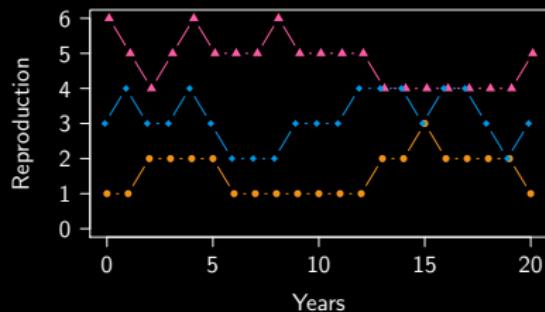
Real pattern



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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Neutral theory for life histories and individual variability in fitness components

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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. We show here that this is not true, and that this stochastic variation has significant implications for both ecological and evolutionary studies.

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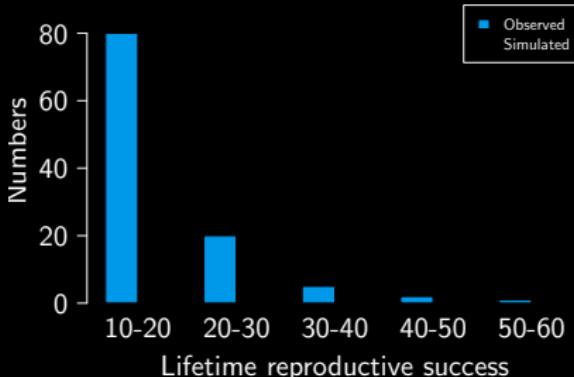
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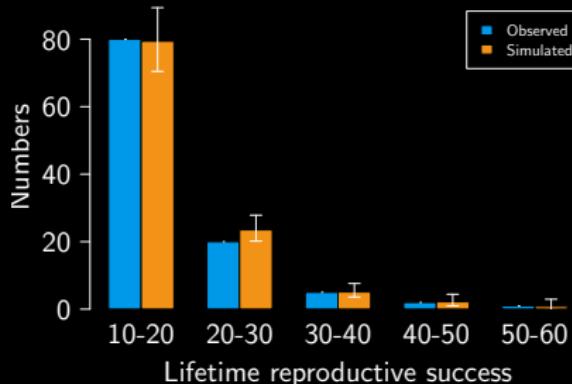
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Individuals within populations can differ substantially in their life spans and their lifetime reproductive success, but such realized fitness components are often highly correlated. This correlation is often interpreted as evidence for selection, but it may also arise from stochastic variation in individual life spans and reproductive success. We show here that the observed correlation between life spans and reproductive success is consistent with a neutral model in which individuals have equal fitness components and experience stochastic variation in both life spans and reproductive success. This finding suggests that stochastic variation in individual life spans and reproductive success may be more important than selection in determining population dynamics and evolution.

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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

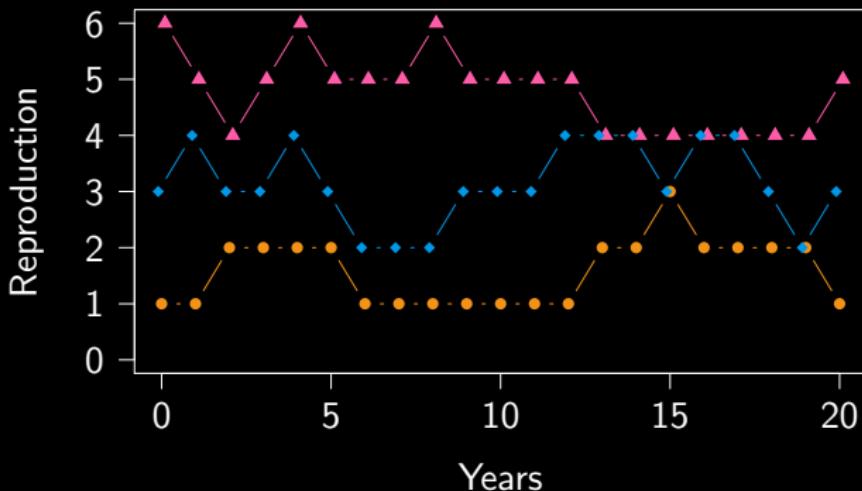
Conflicting results

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
- ... because of stage structure

Mixed model method & Quantitative genetics

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

Conflicting results

Neutral matrix method

- No significant differences between individuals
- ... because of stage structure
- ... very little and due to chance only

Mixed model method & Quantitative genetics

- Individual performances are repeatable
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Conflicting results

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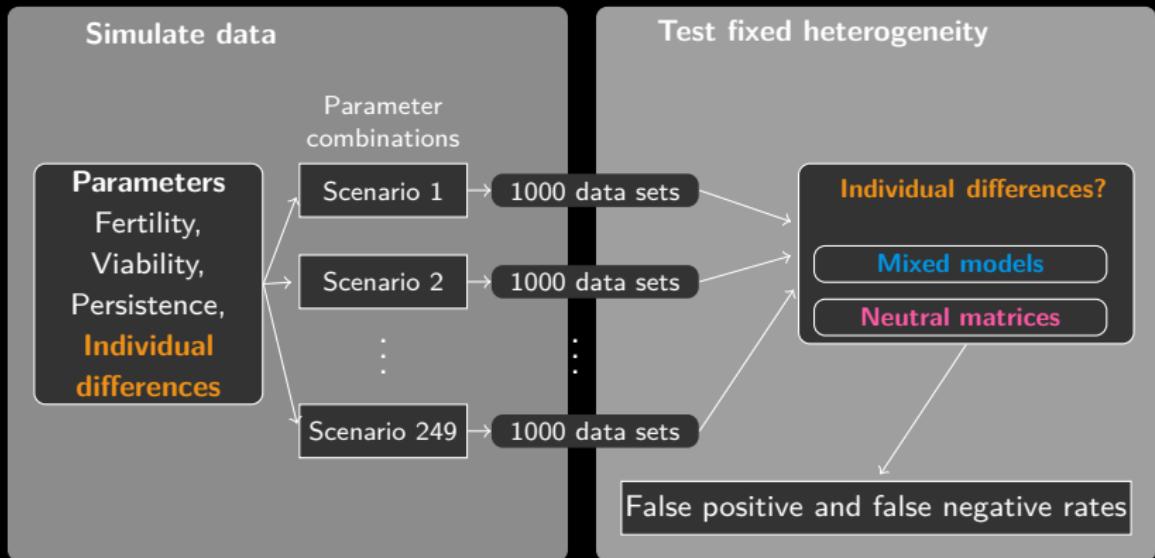
Mixed model method & Quantitative genetics

- Individual performances are repeatable
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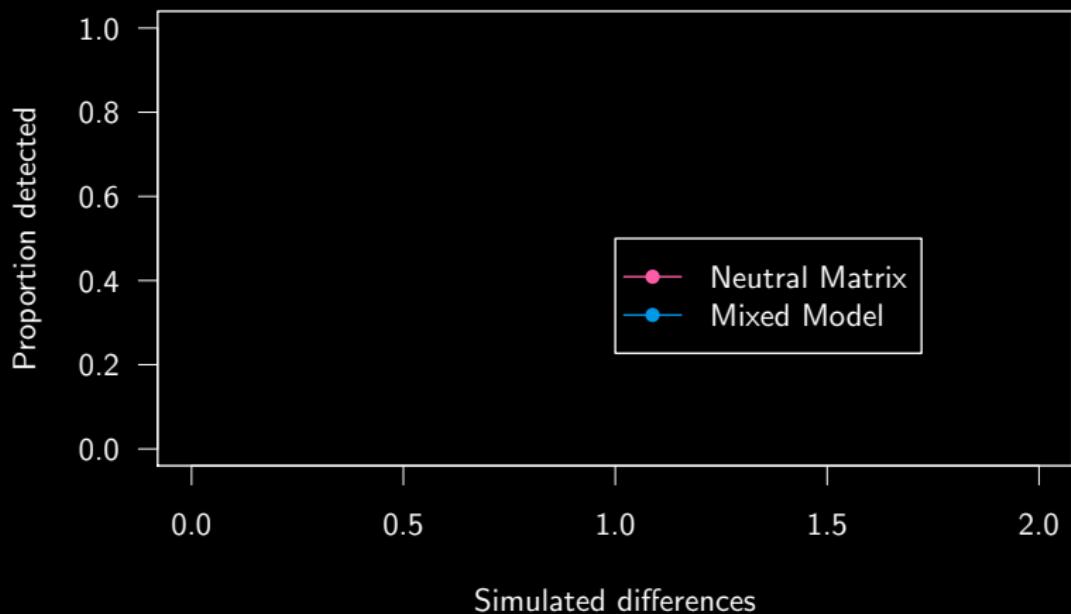
Why?

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

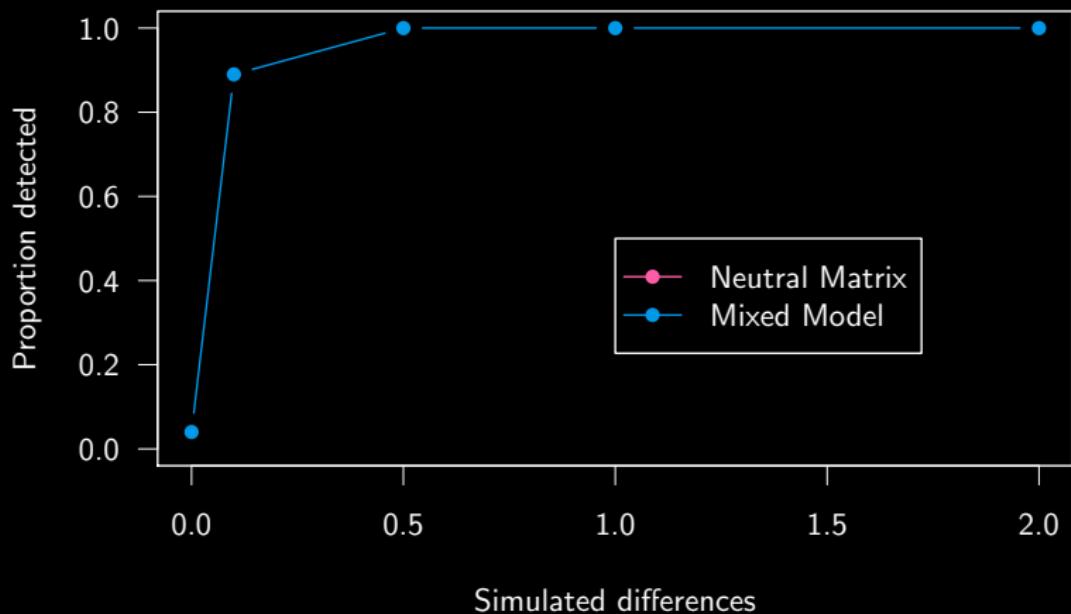
Method



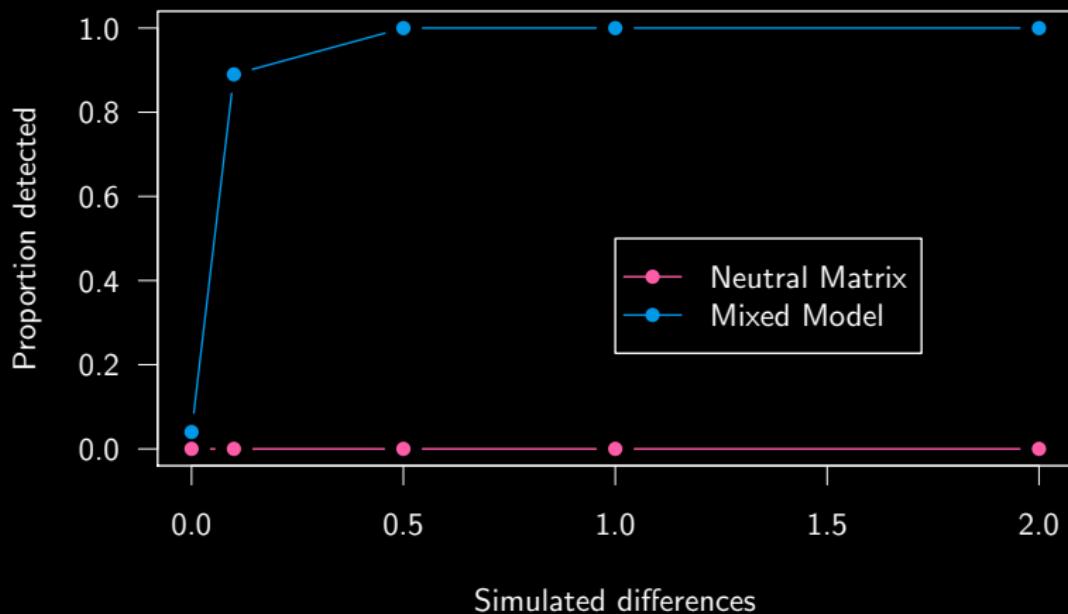
Results



Results



Results



Conclusion

Why conflicting methods?

Conclusion

Why conflicting methods?

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

Conclusion

Why conflicting methods?

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

→ Individual differences in fitness components are common

Conclusion

Why conflicting methods?

- 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**

→ Individual differences in fitness components are common

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



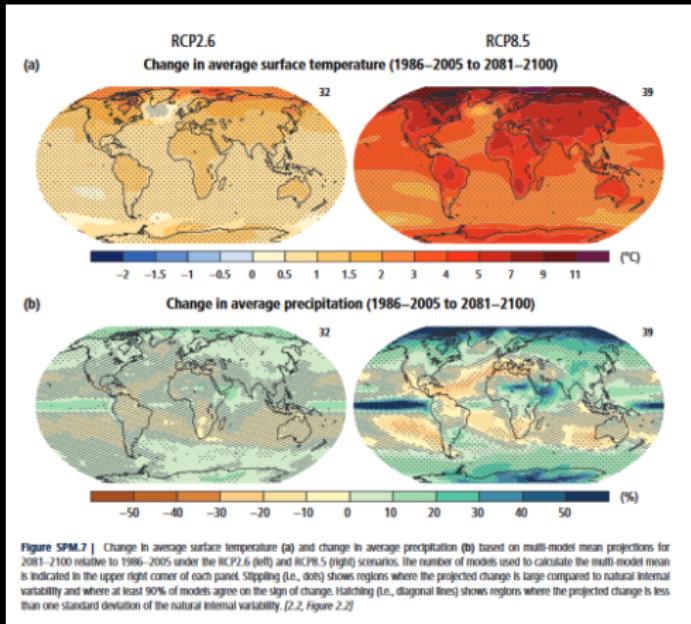
R.A. Fisher G. Price

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

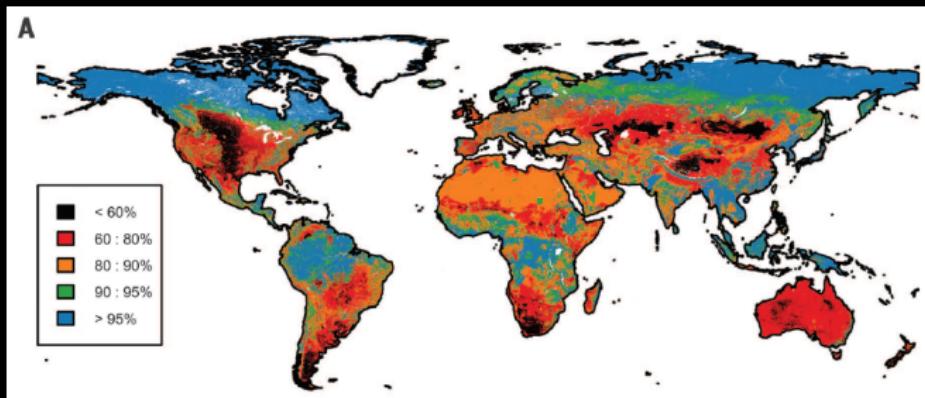
Timothée Bonnet* and Erik Postma

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

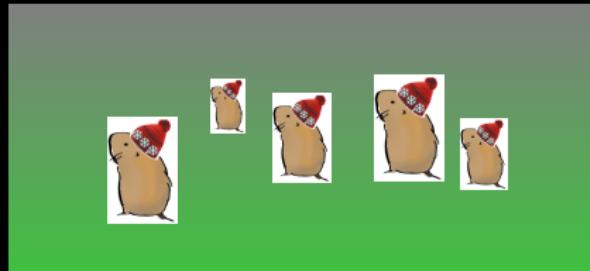
Vol. 37: 637-669 (Volume publication date December 2006)

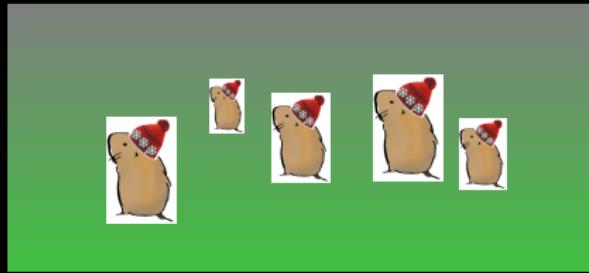
First published online as a Review in Advance on August 24, 2006

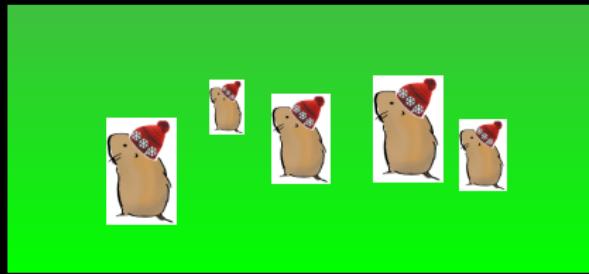
DOI: 10.1146/annurev.ecolsys.37.091305.110100

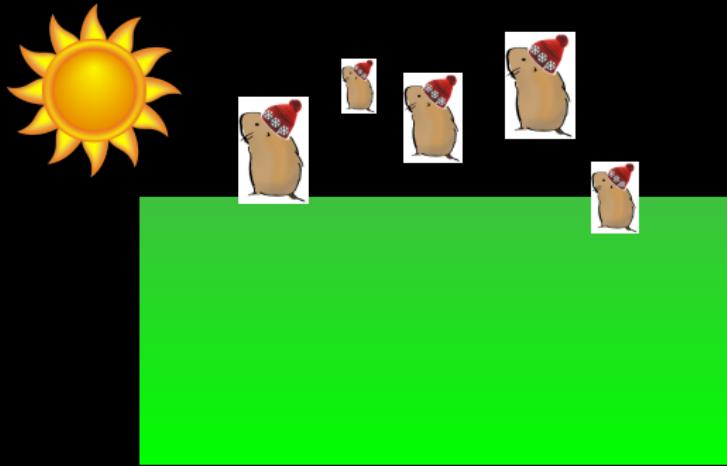
Camille Parmesan

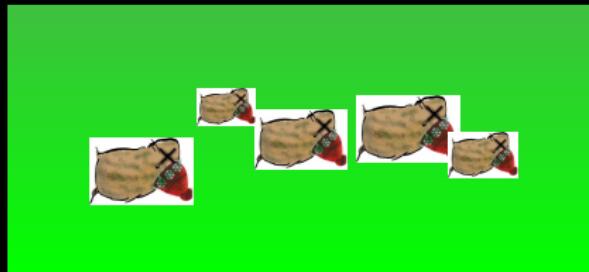
Section of Integrative Biology, University of Texas, Austin, Texas 78712; email:
parmesan@mail.utexas.edu

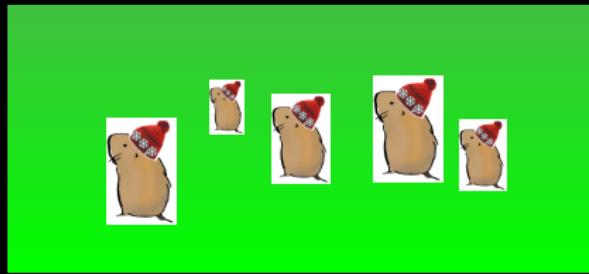
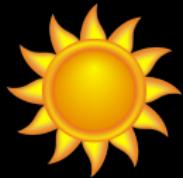


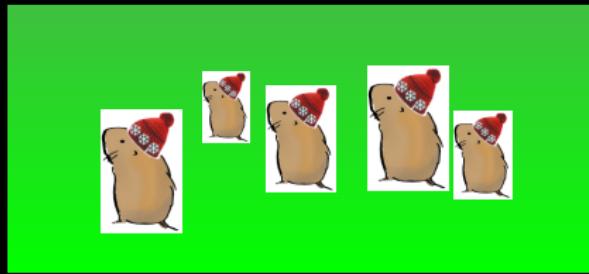


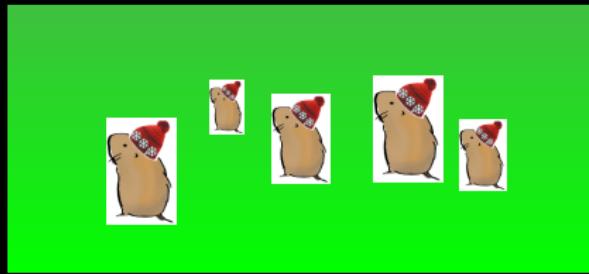


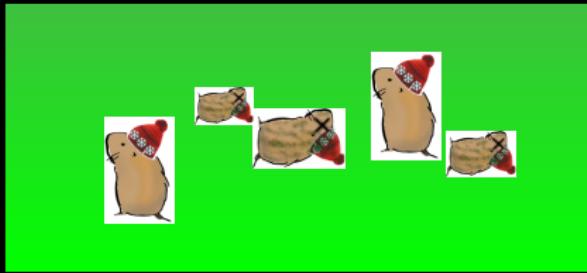


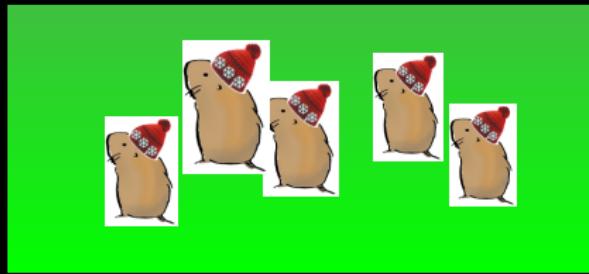












Evolution or plasticity? What drives phenotypic change?

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)

Evolution or plasticity?

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3. **Geber's Method** - Ellner, Geber & Hairston (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*, 14(6)

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3. **Geber's Method** - Ellner, Geber & Hairston (2011). Does rapid evolution matter? Measuring the rate of contemporary evolution and its impacts on ecological dynamics. *Ecology Letters*, 14(6)
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

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

The animal model

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

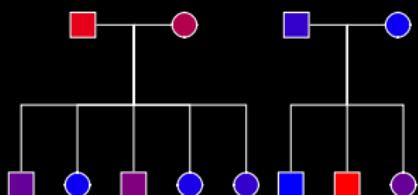
$$\text{heritability} = \frac{\text{additive genetic variance}}{\text{phenotypic variance}}$$

The animal model

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

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

heritability ≈ 0

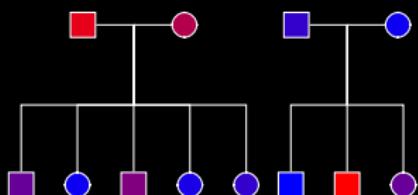


The animal model

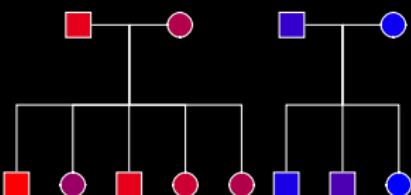
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heritability ≈ 1

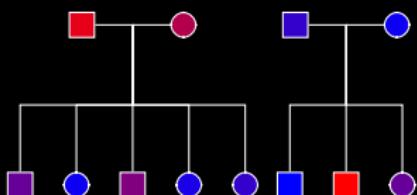


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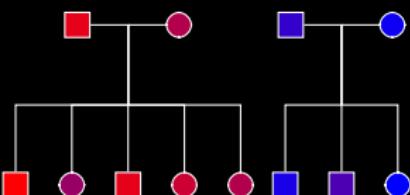
Pedigree → similarity between relatives → **additive genetic variance**

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

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

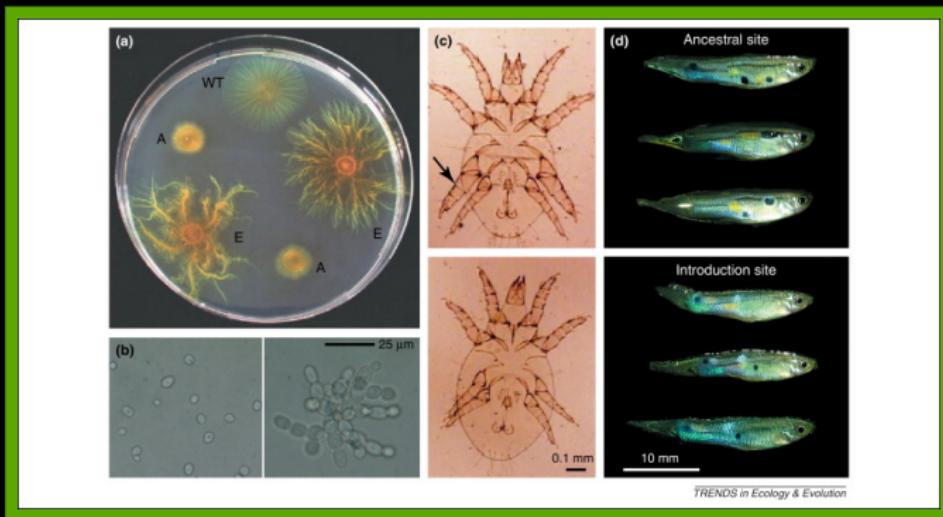
Adaptive evolution in the wild

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Adaptive evolution in the wild

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

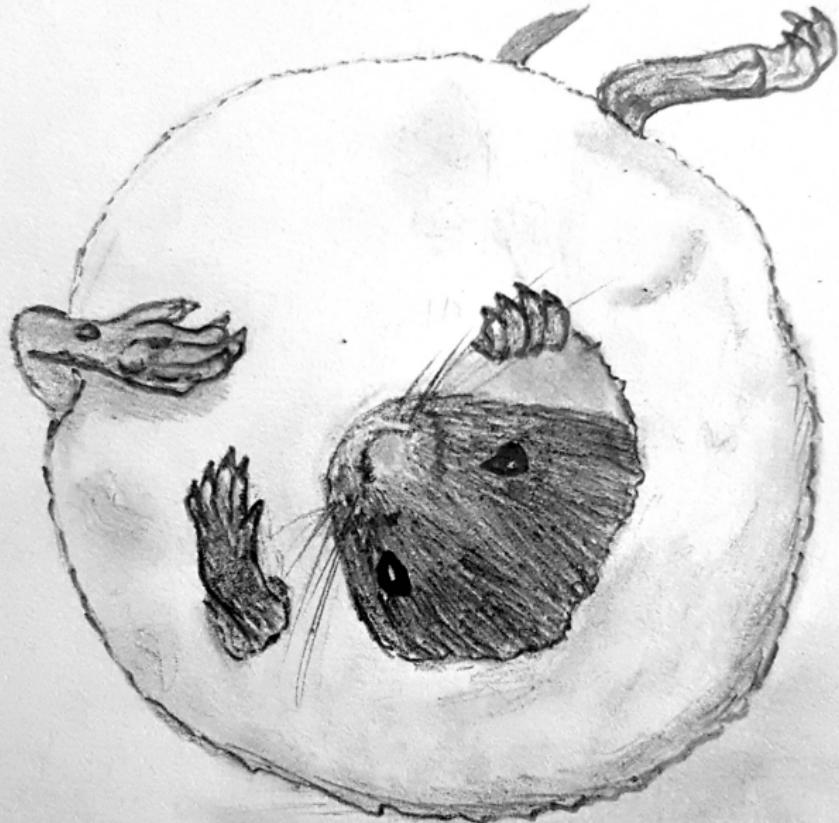
Adaptive evolution in the wild

Adaptive evolution = Selection \times heritability

2016

The screenshot shows a journal article from BioEssays. At the top, there's a banner with the journal logo and the text "Ideas that Push the Boundaries". Below the banner, a link says "Explore this journal >". The main title of the article is "Why are estimates of the strength and direction of natural selection from wild populations not congruent with observed rates of phenotypic change?", written by John F.Y. Brookfield. Below the title, it says "Prospects & Overviews". To the right, there's a thumbnail of the journal cover for Volume 38, Issue 9, dated September 2016, with the title "BioEssays 9/16". Below the thumbnail, there are links to "View issue TOC", "Volume 38, Issue 9", "September 2016", and "Pages 927-934". At the bottom of the screenshot, there are links for "First published: 12 July 2016" and "Full publication history", and "DOI: 10.1002/bies.201600017" and "View/save citation".

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)

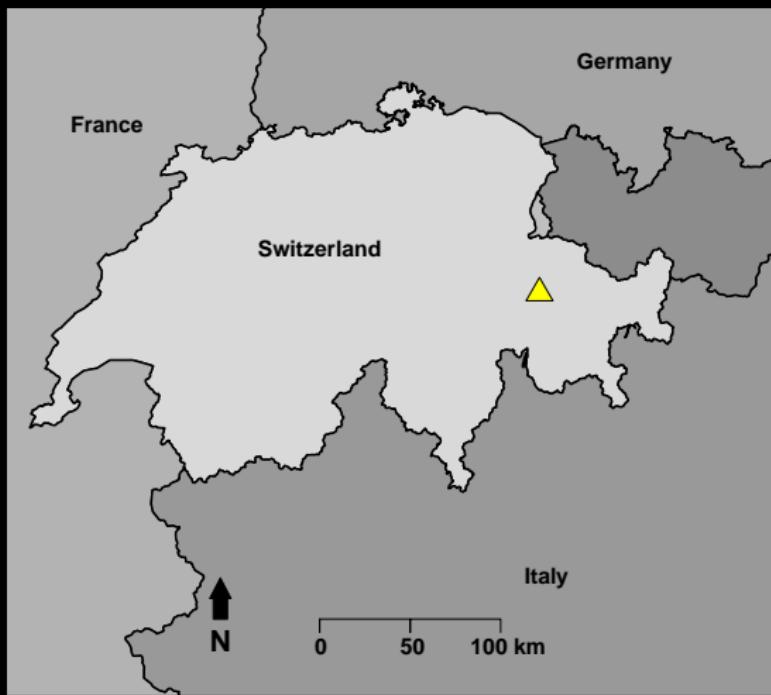
- NOT white
- Rock-dweller
- 30-45g
- 10-14cm long + 5-8cm tail



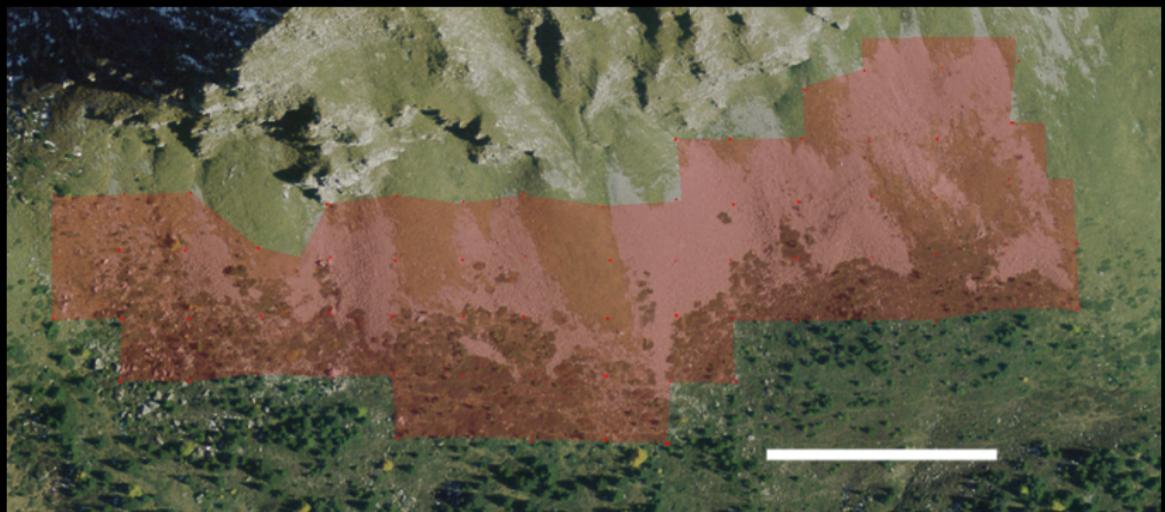
Snow vole (*Chionomys nivalis*, Martins 1842)

- 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



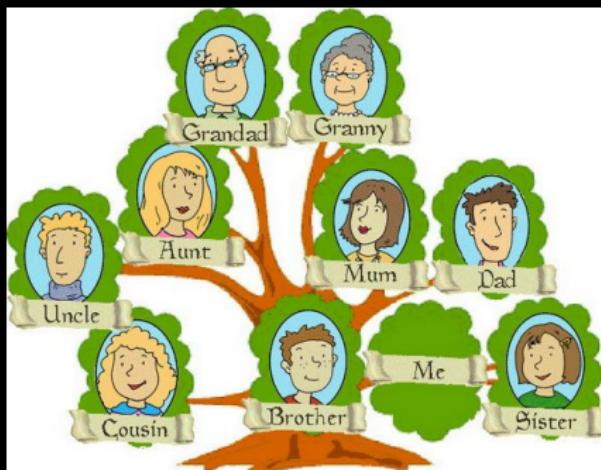
What we measure

- Morphology
 - Body mass
 - Body length
 - Tail length
- Capture/Recaptures
 - Death/emigration
 - Location
- DNA
 - 20 “neutral” markers
 - Sex identification
 - Any genotyping



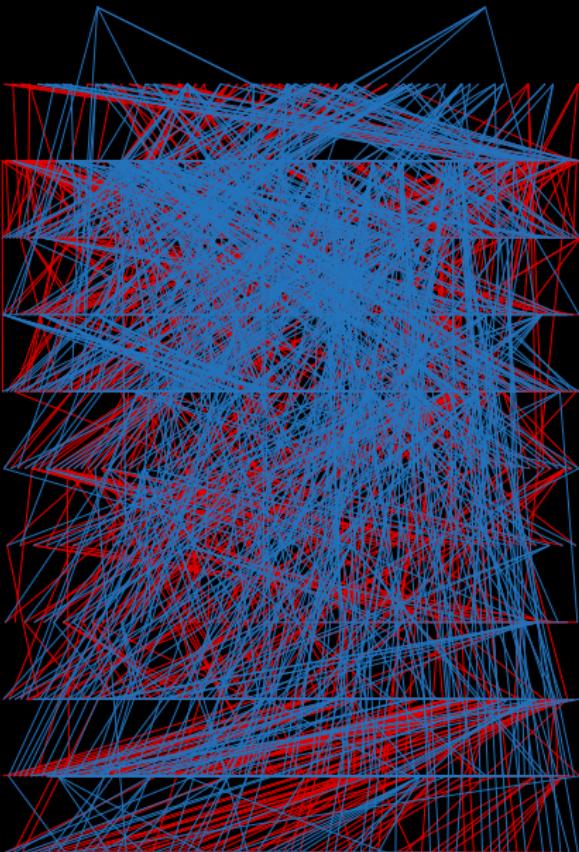
What we measure

- Morphology
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 - **Pedigree**



What we measure

- Morphology
 - Body mass
 - Body length
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- Capture/Recaptures
 - Death/emigration
 - Location
- DNA
 - 20 “neutral” markers
 - Sex identification
 - Any genotyping
 - **Pedigree**

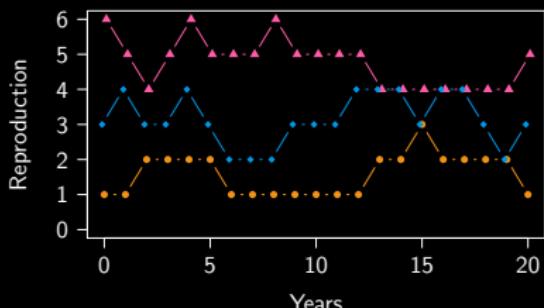


Are snow vole evolving? Why?

Variance in fitness?

Adaptive evolution in the snow vole?

Variance in fitness?

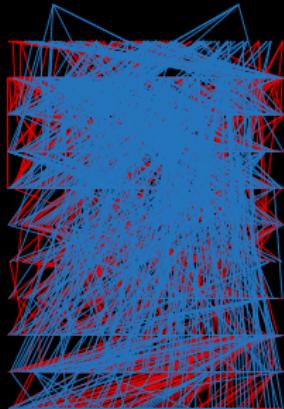


	Estimate	95% CI	p-value
Latent variance in survival	0	[0;0.248]	0.50
Latent variance in reproduction	0.37	[0.25, 0.49]	$< 10^{-16}$

Adaptive evolution in the snow vole?

- Non random variation fitness components

Variance in fitness?

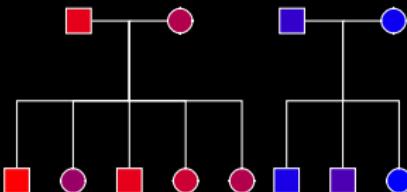


Relative lifetime reproductive success
variance ≈ 1.7

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

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

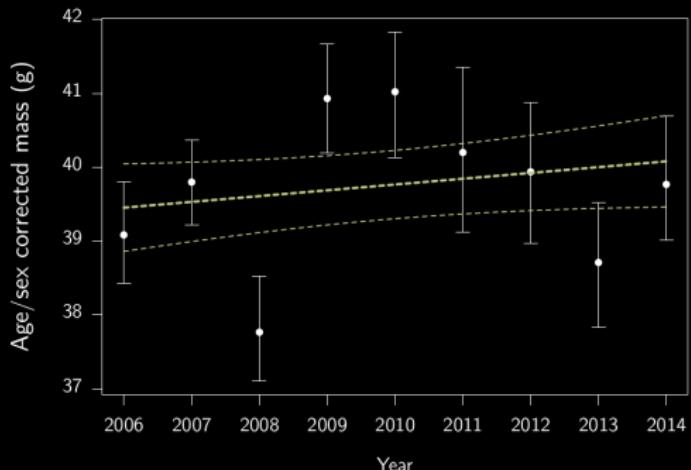
- Selection = $+0.86\text{g}$ ($p < 10^{-3}$)
- Heritability = 20% ($p < 10^{-3}$)
- Response = Selection \times heritability = $+ 0.22\text{g/year}$

Evolution of body mass

Prediction

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

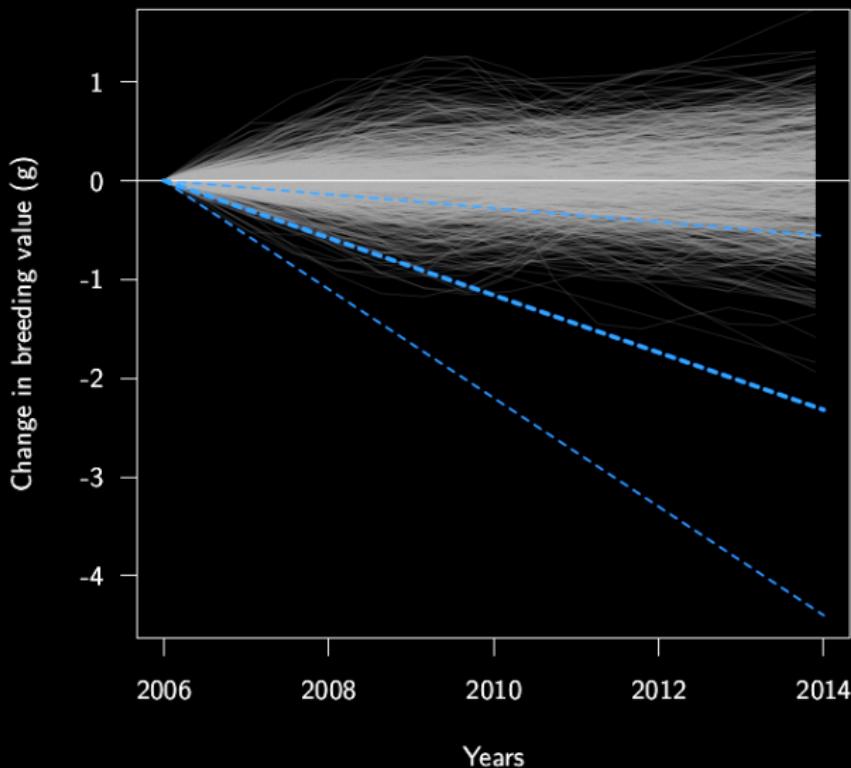
Phenotypic observation



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

Evolution of body mass

Estimation of genetic change



Evolution of body mass

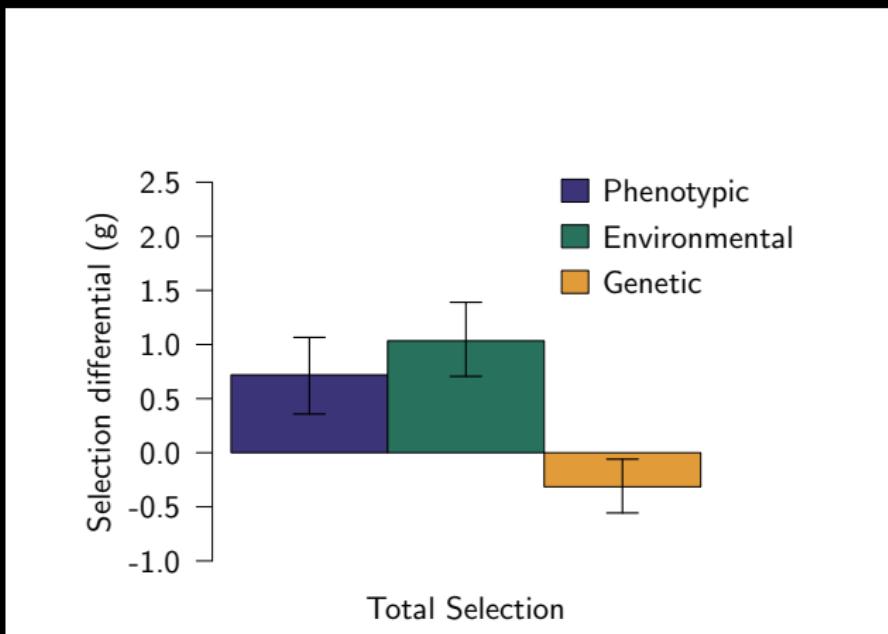
Evolution Paradox

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

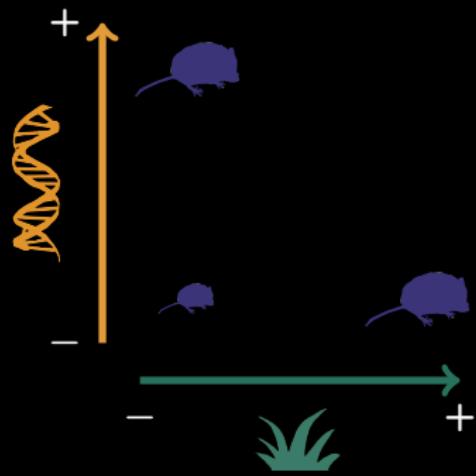
Evolution of body mass

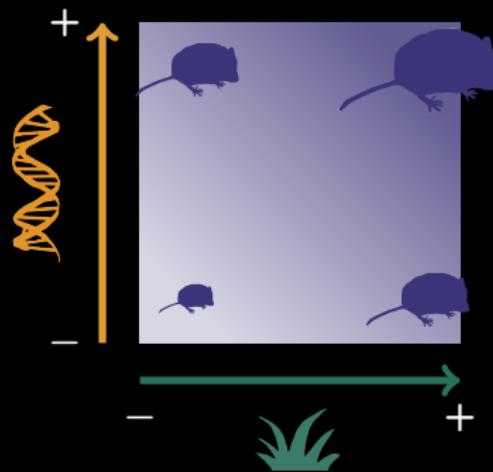
Evolution Paradox

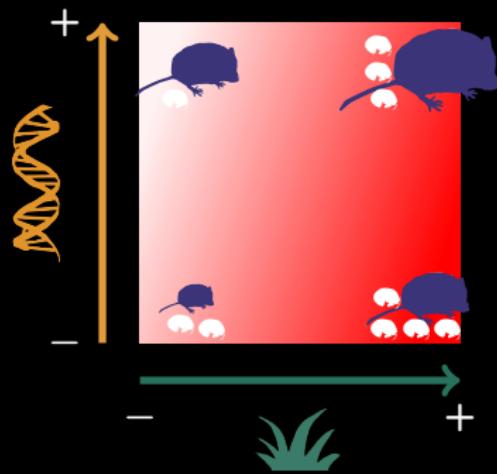
- Apparent selection for higher mass
- Adaptive evolution for lower mass

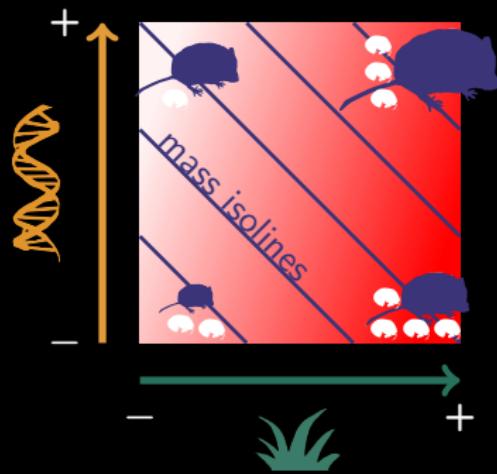


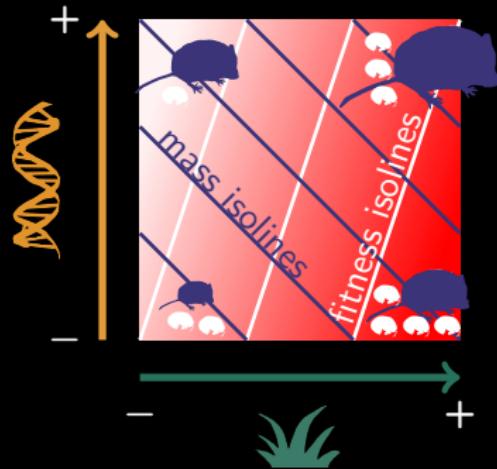


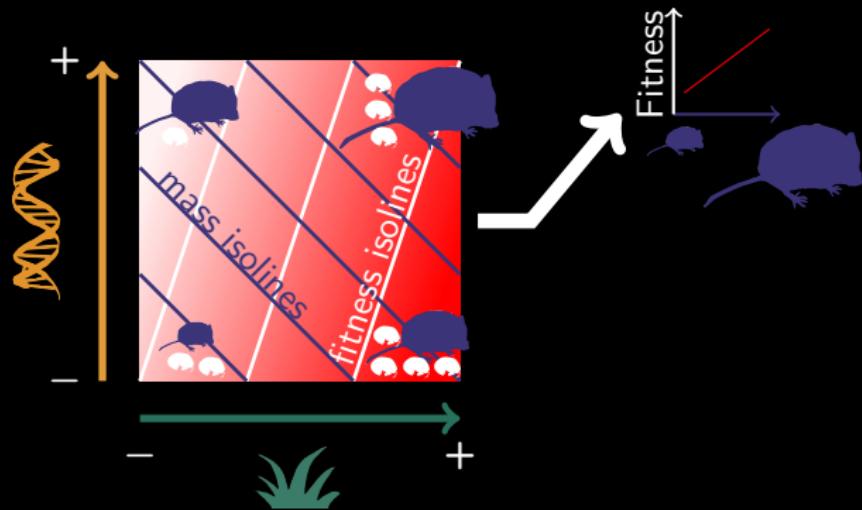


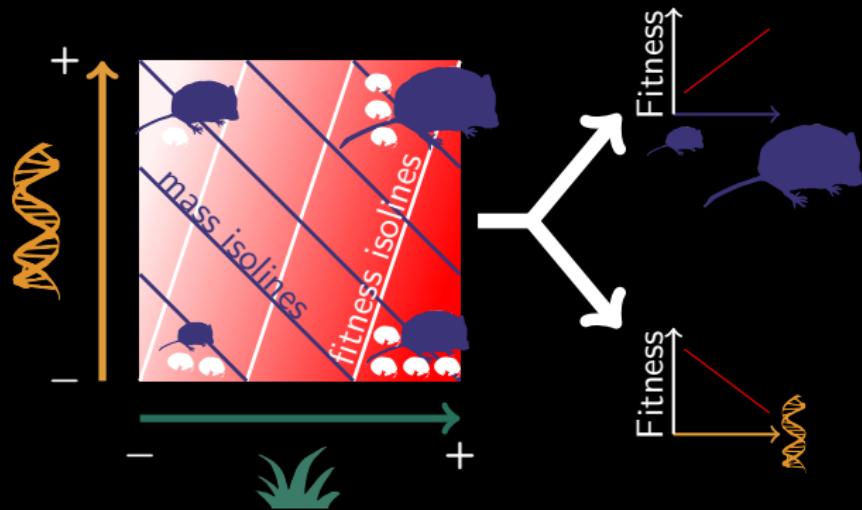


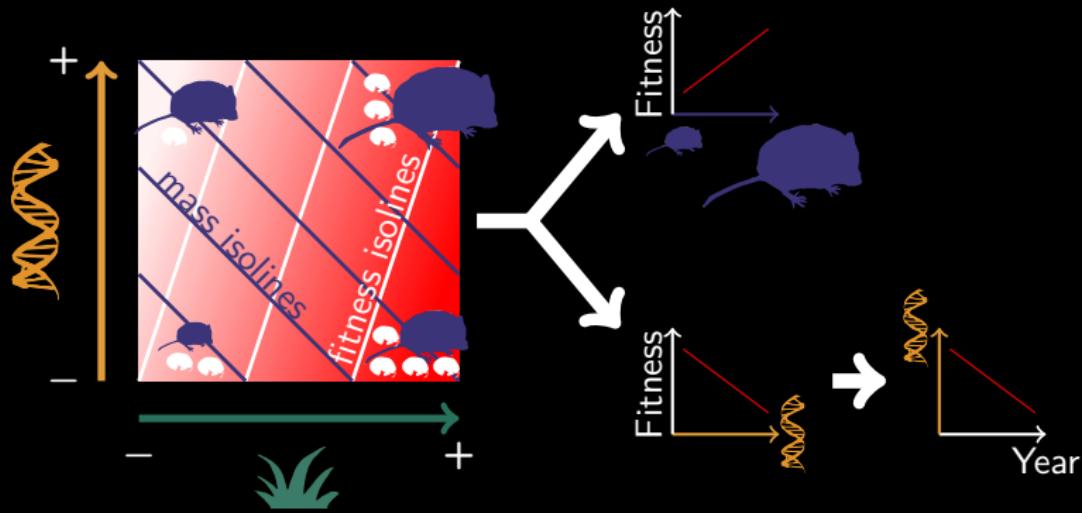


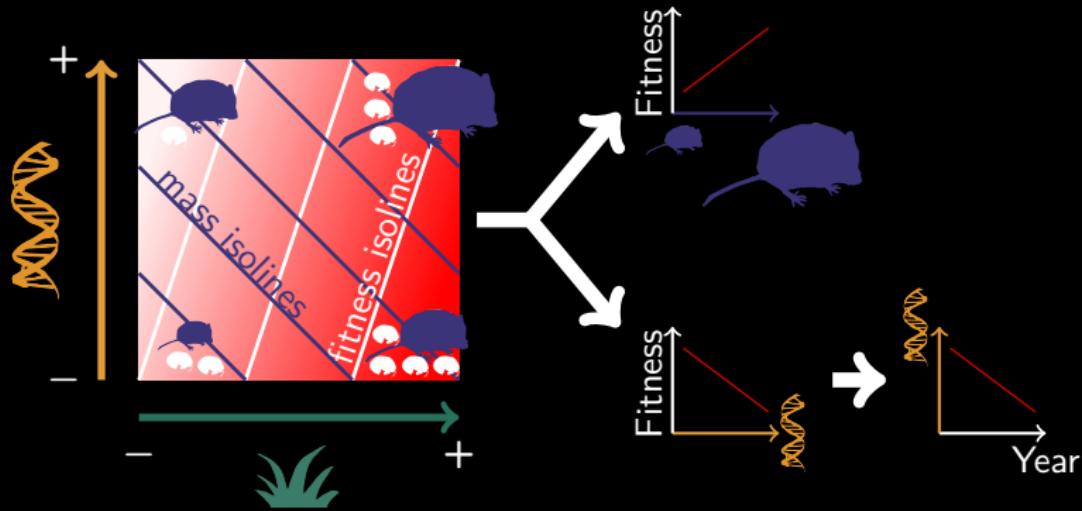






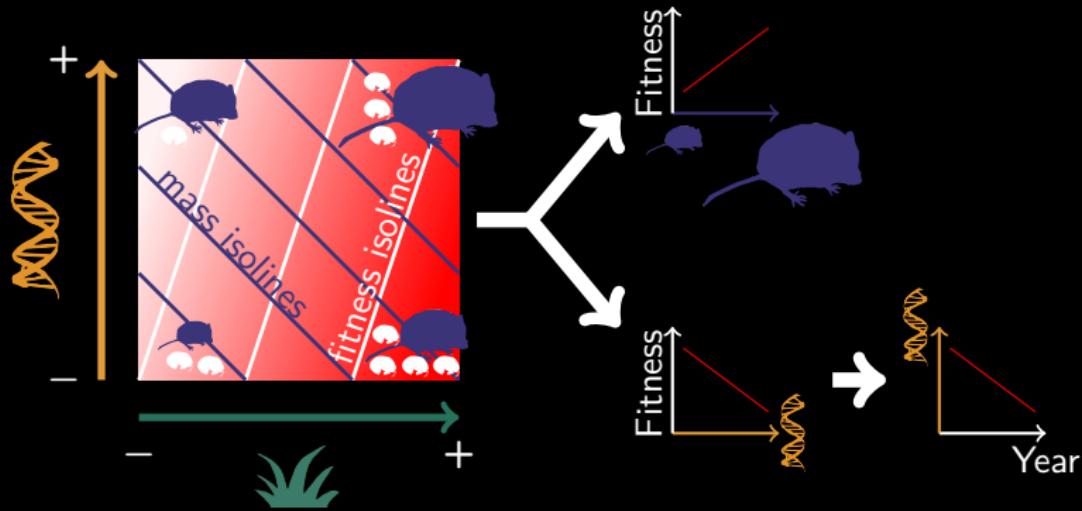






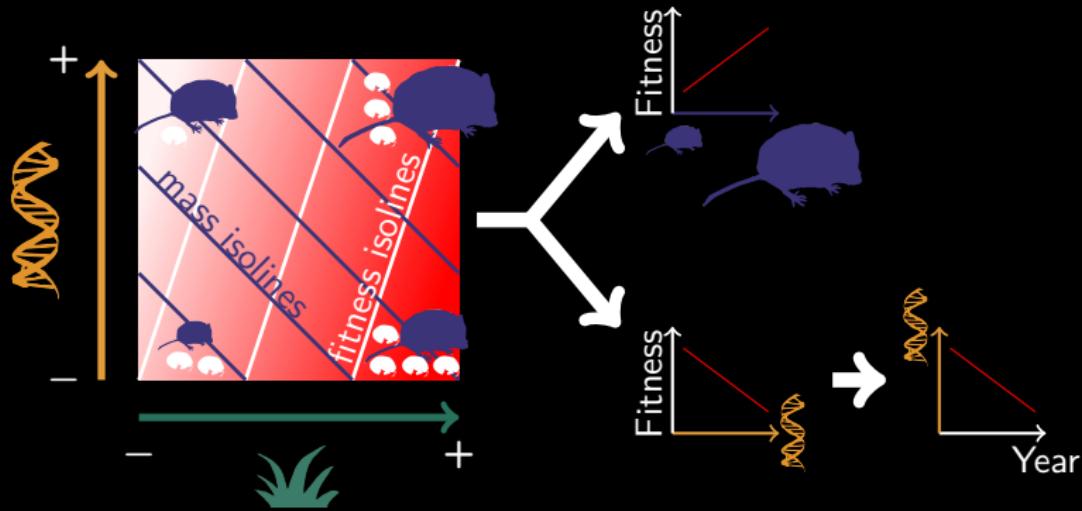
Summary

1. Apparent stasis...



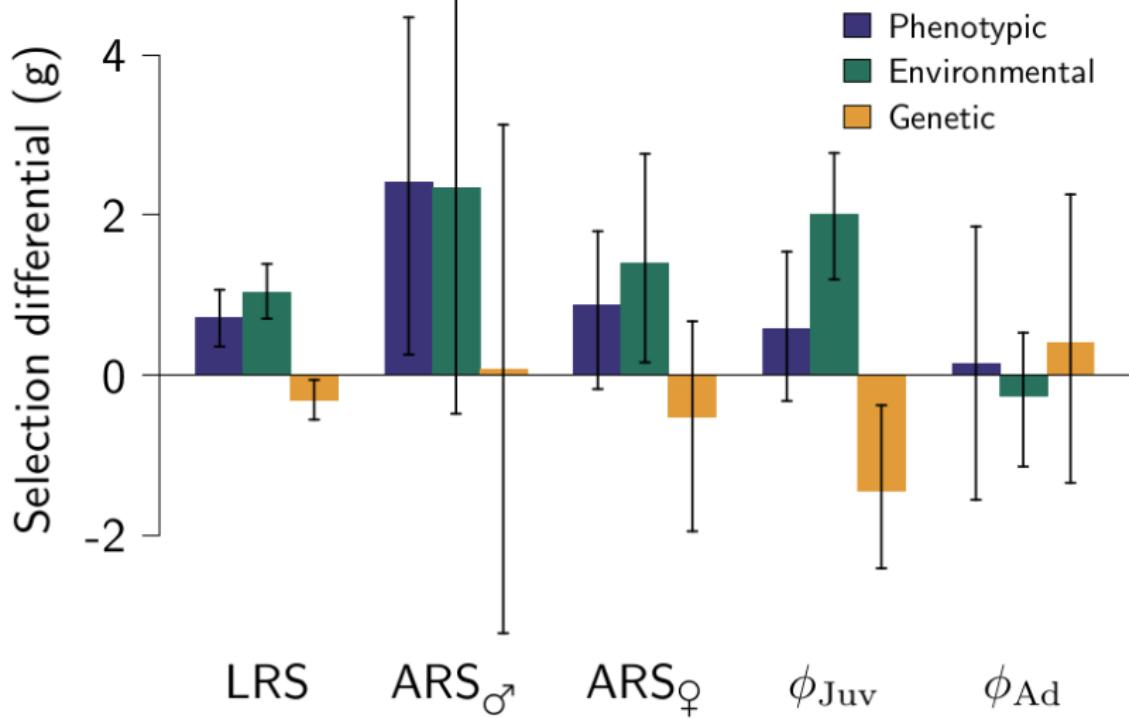
Summary

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

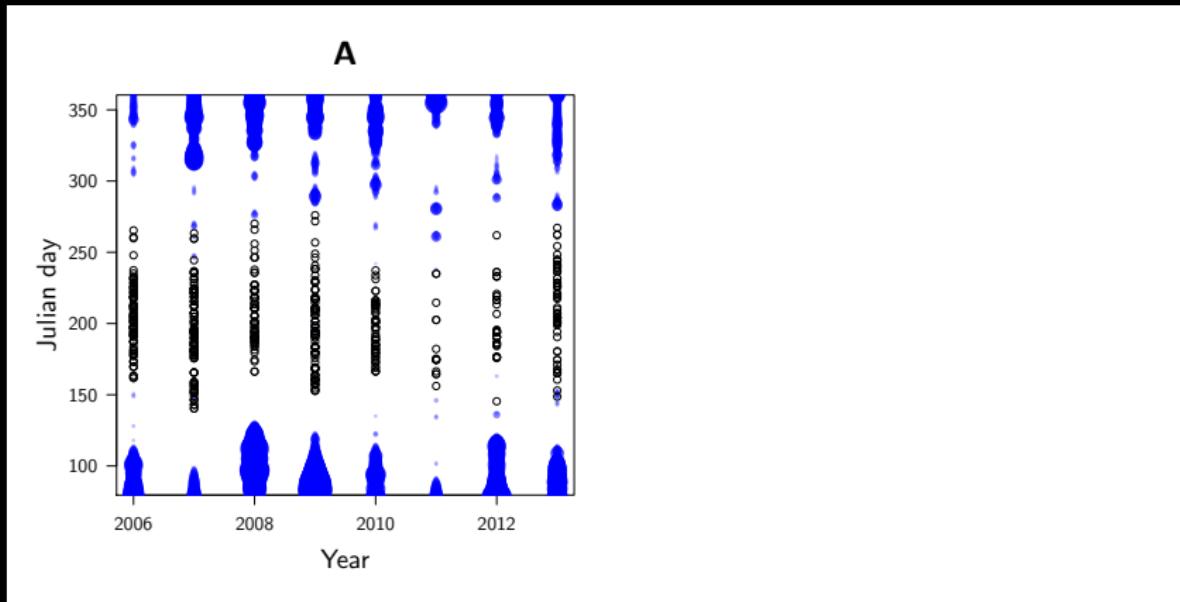


Summary

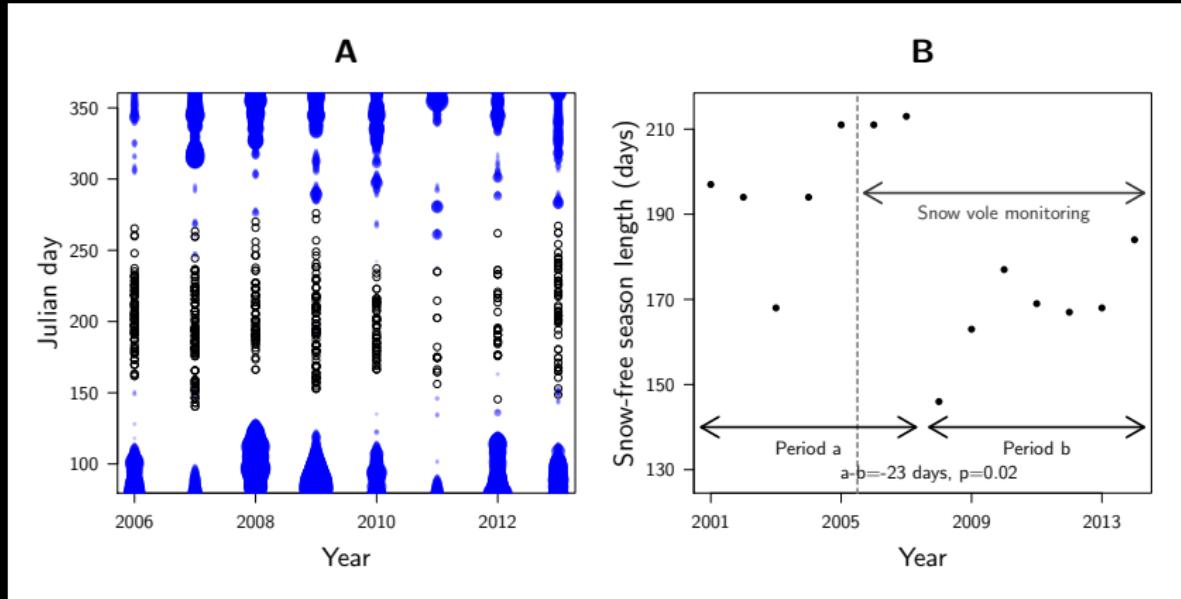
1. Apparent stasis . . .
2. . . . but evolution towards lower mass
3. *Selective pressure?*



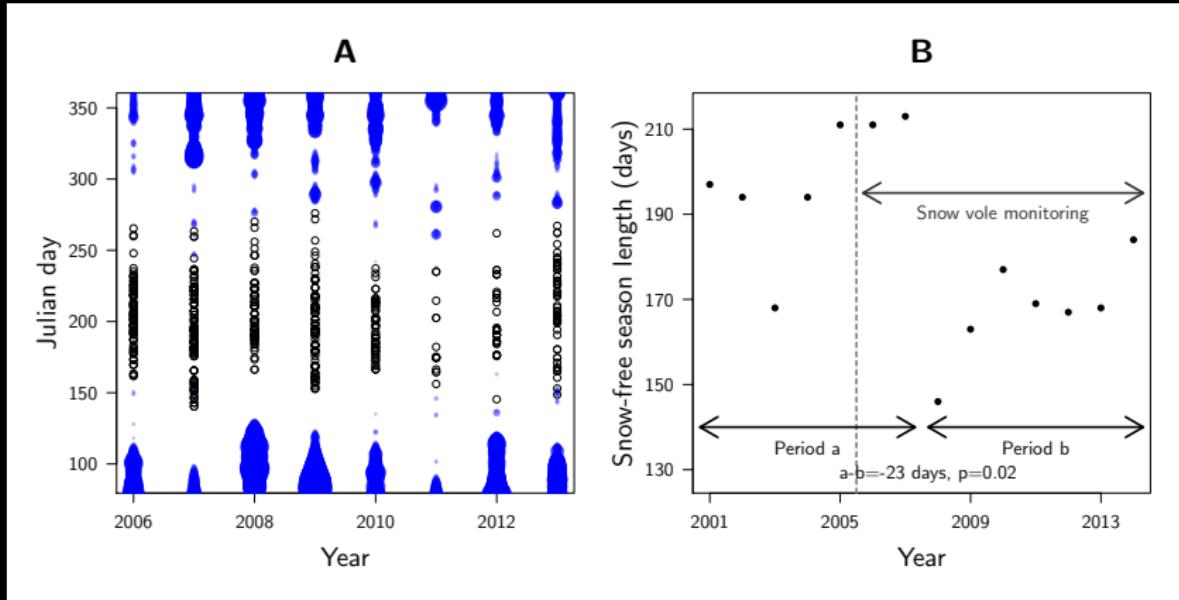
Snow falls and ontogeny



Snow falls and ontogeny



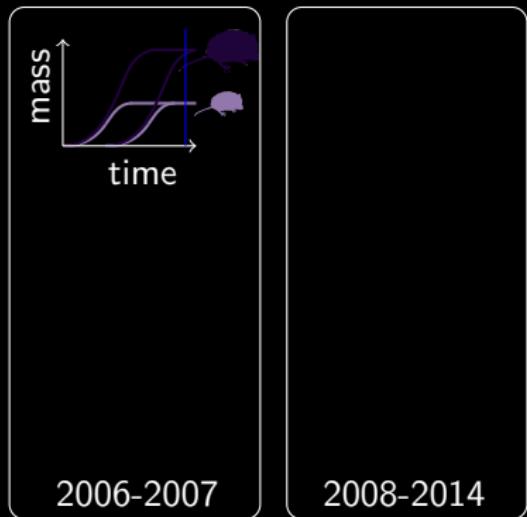
Snow falls and ontogeny



Less time to grow → Selection for smaller voles?

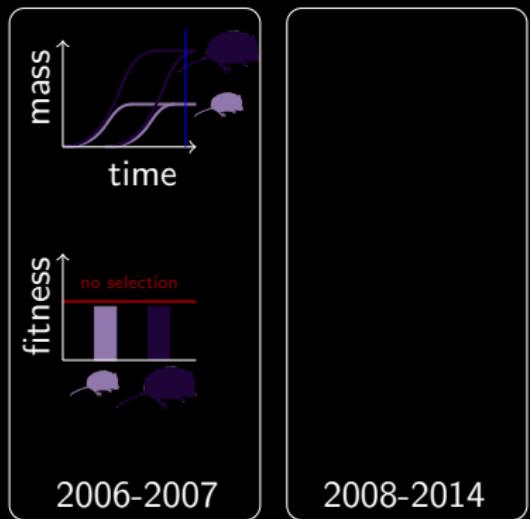
Selection during ontogeny?

D



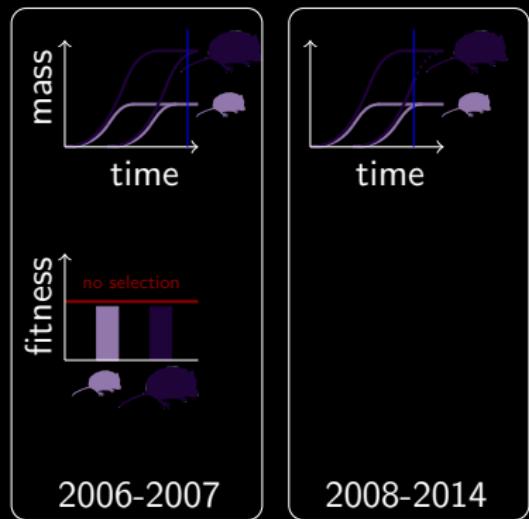
Selection during ontogeny?

D



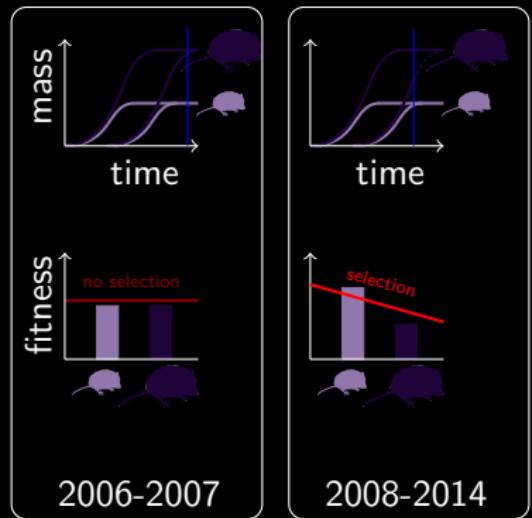
Selection during ontogeny?

D



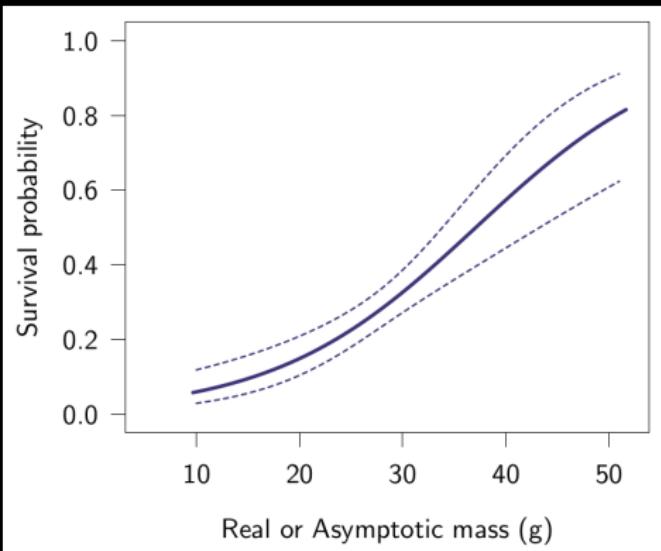
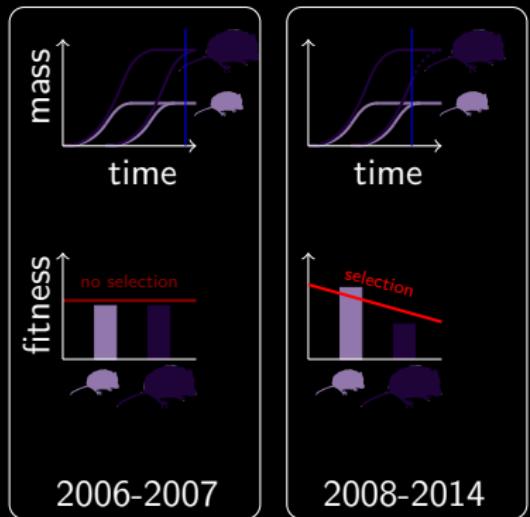
Selection during ontogeny?

D



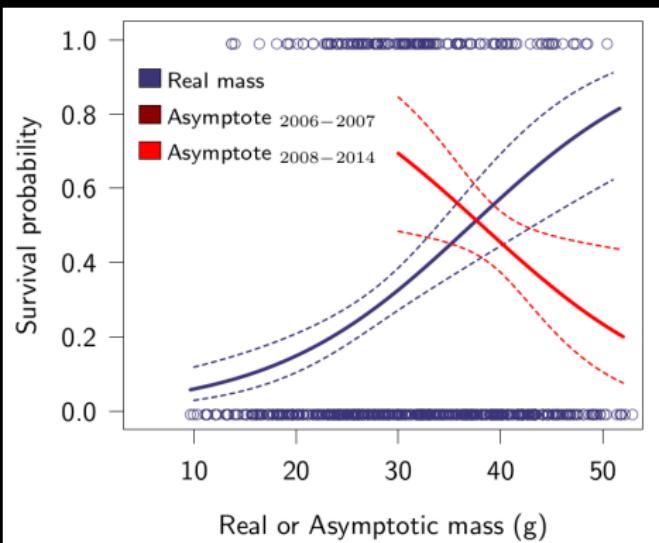
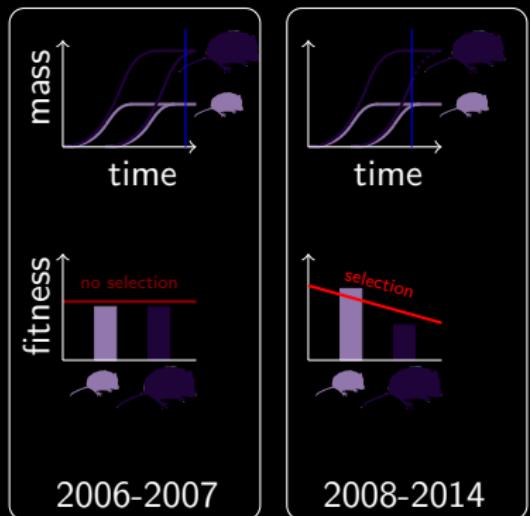
Selection during ontogeny?

D



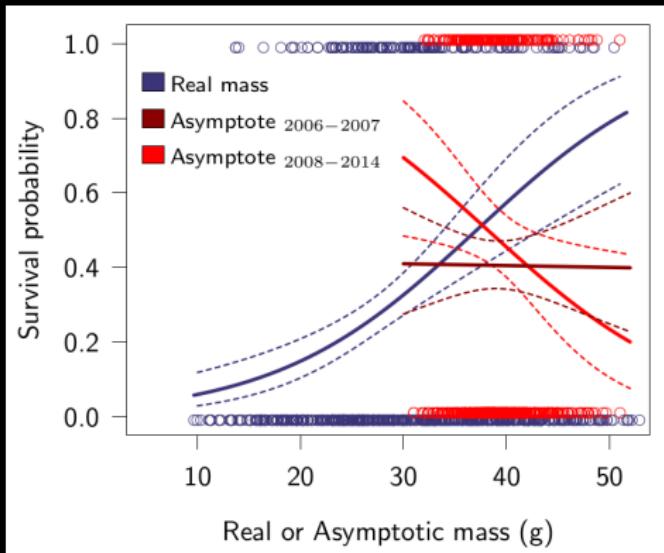
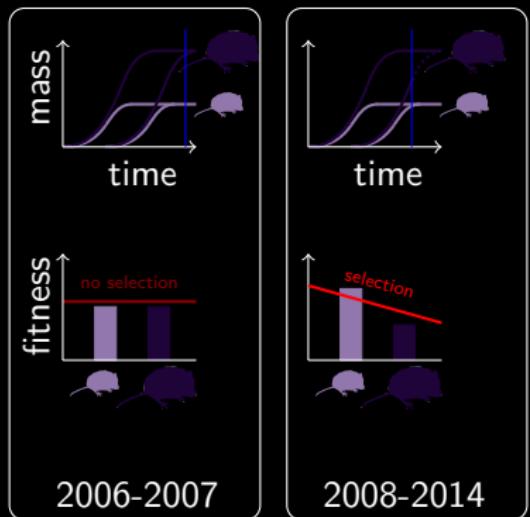
Selection during ontogeny?

D



Selection during ontogeny?

D



Evoleution!

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 letter χ. Below it, the word "beta" is written in a smaller, gray font. Underneath the main title, the text "THE PREPRINT SERVER FOR BIOLOGY" is displayed in a smaller, all-caps font.

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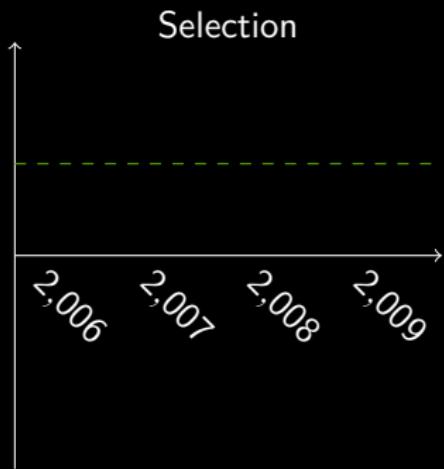
Timothée Bonnet, Peter Wandeler, Glauco Camenisch, Erik Postma

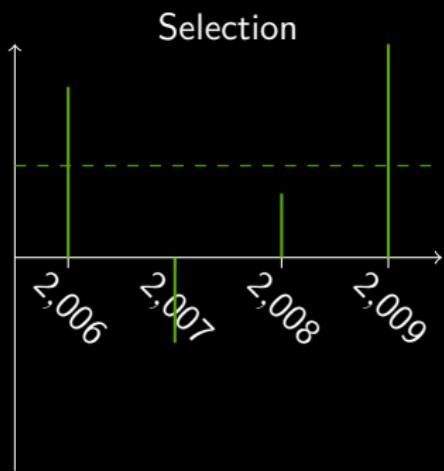
doi: <http://dx.doi.org/10.1101/038604>

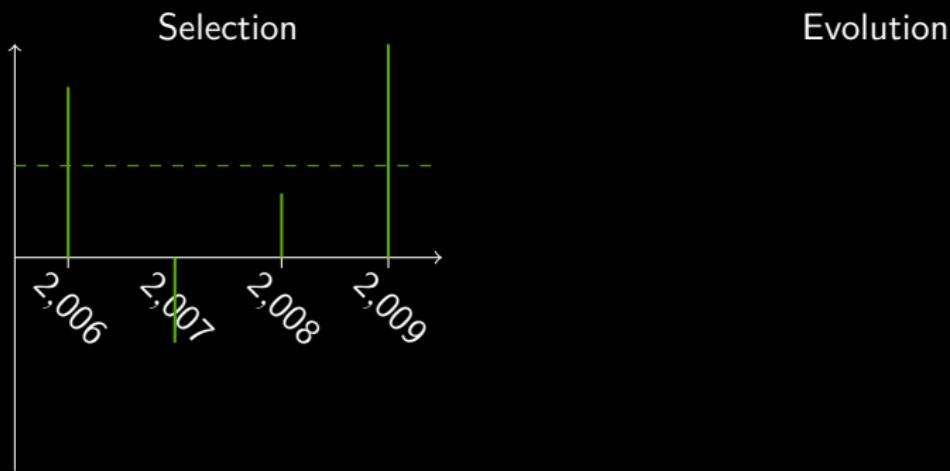
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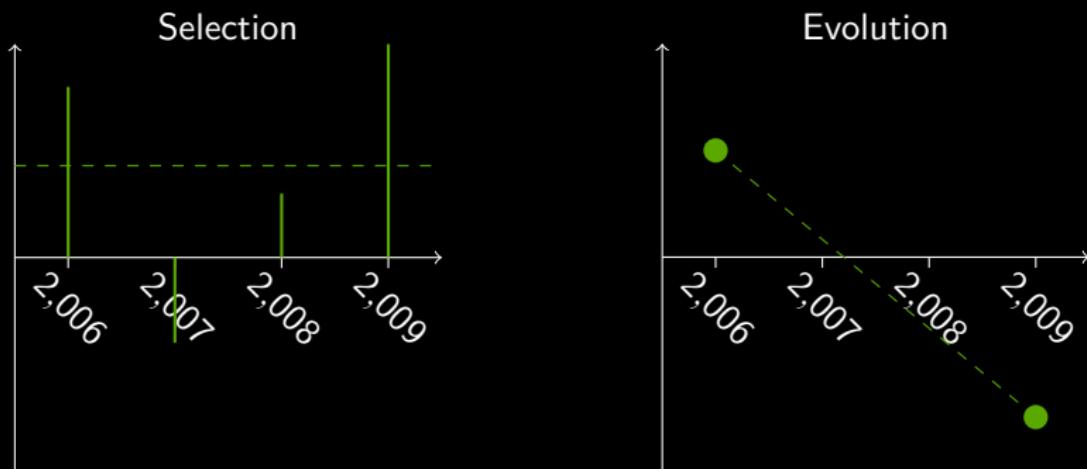
**Do selection and evolution
fluctuate?**

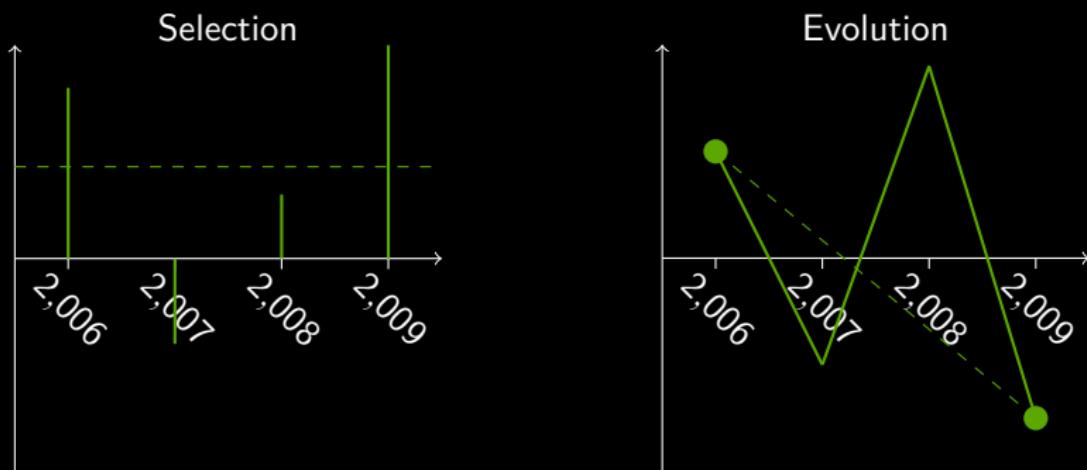
Selection



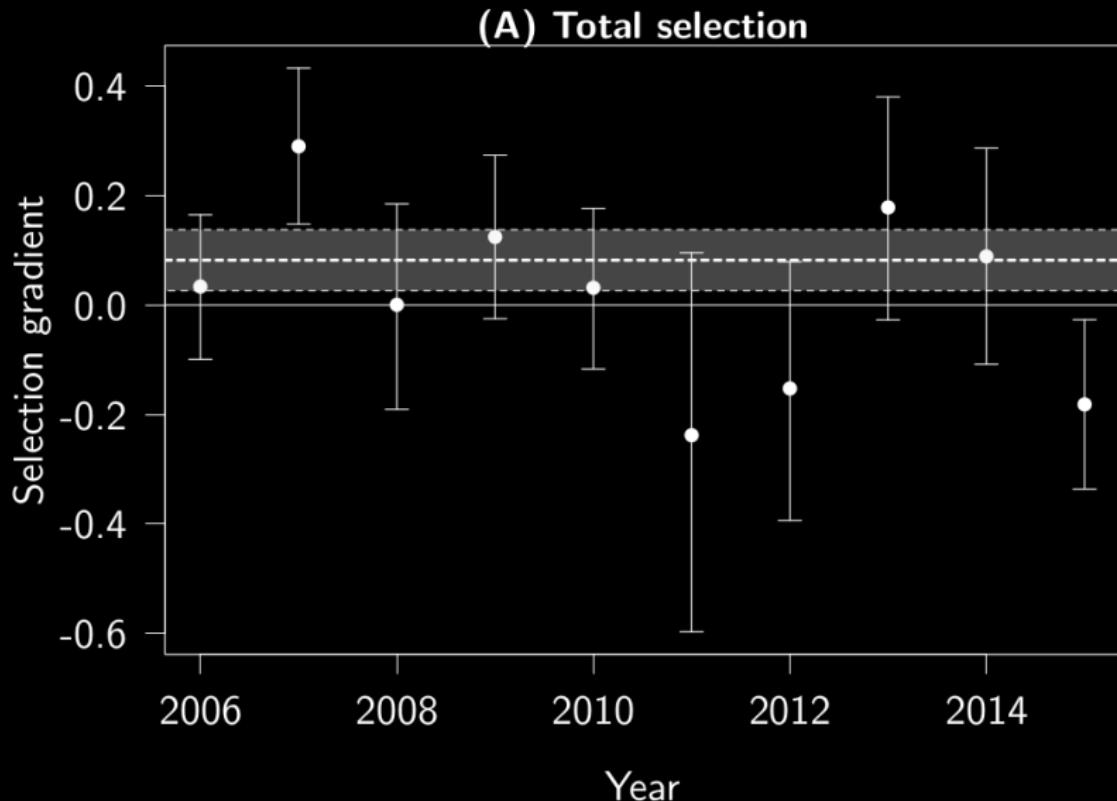






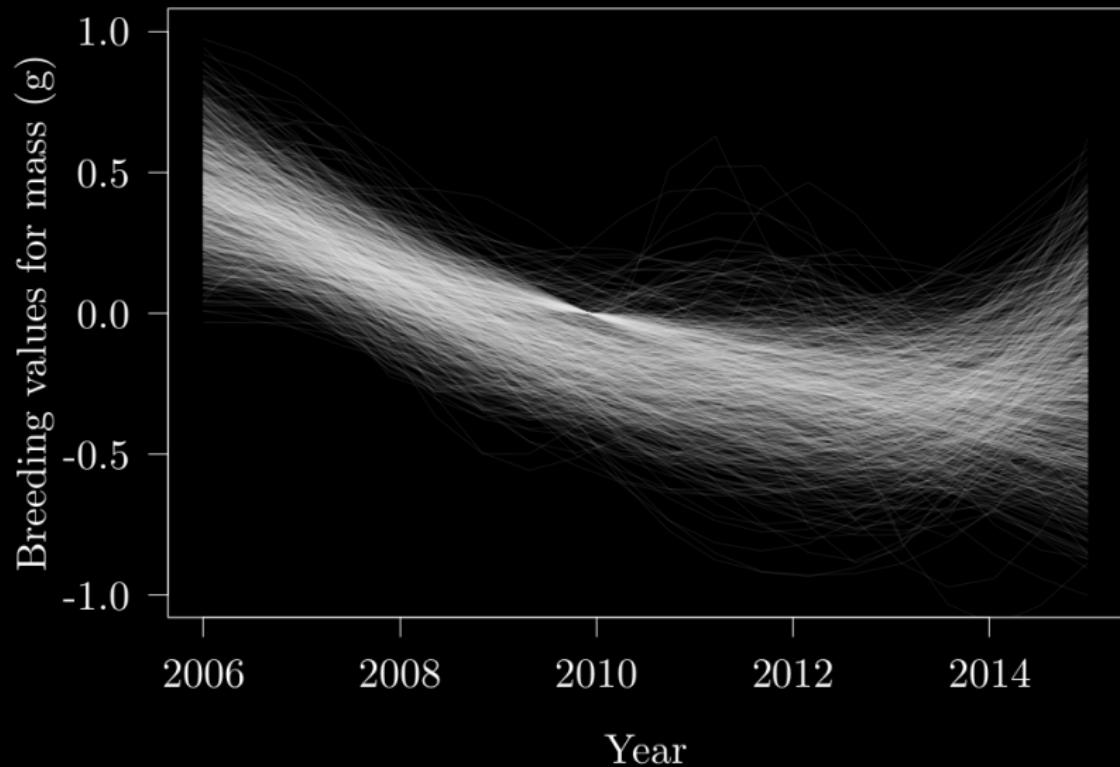


Dynamics of selection

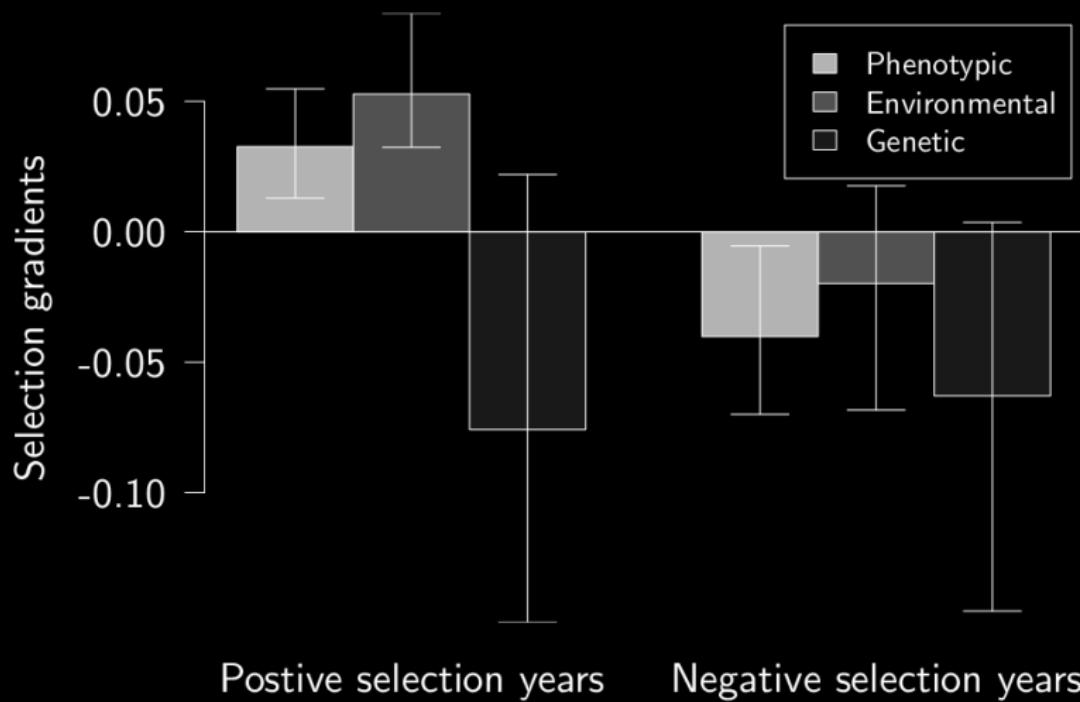


Variance in selection = 0.117 [0.063; 0.218], $p=8 \cdot 10^{-6}$

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

What is left?

Questions?
