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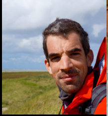
- Lukas Keller
- Barbara Tschirren
- Arpat Ozgul
- Marc Kéry
- Jarrod Hadfield



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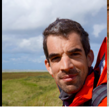





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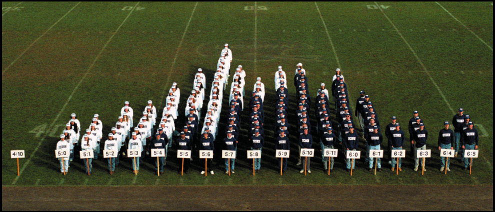
- Eelke Jongejans
- Pirmin Nietlisbach
- Philipp Becker
- Judith Bachmann

Phenotypic variation within population



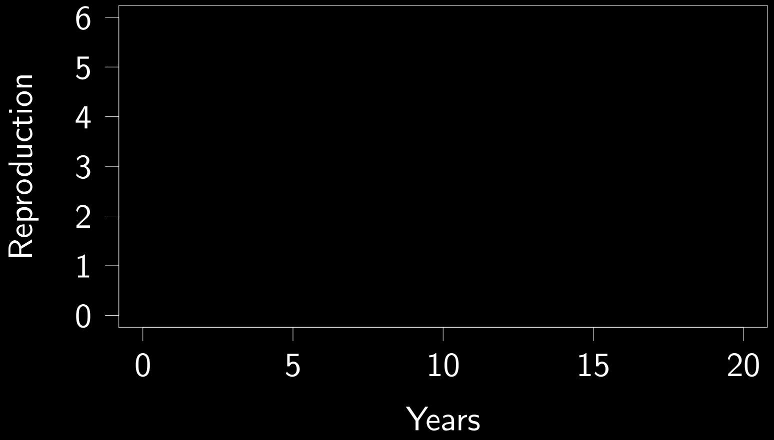
Phenotypic variation within population

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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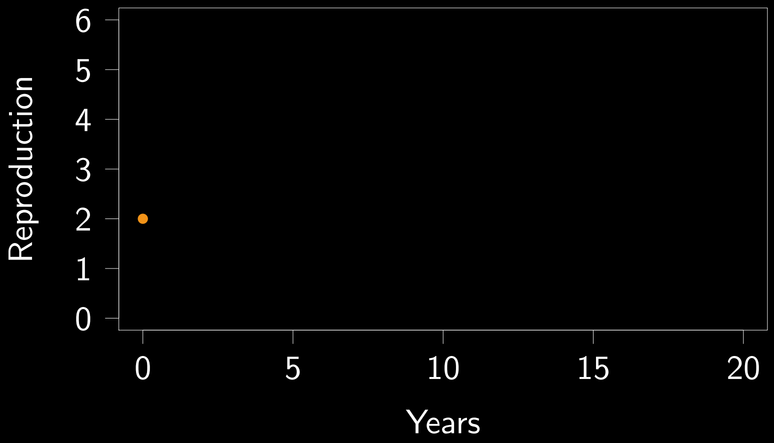

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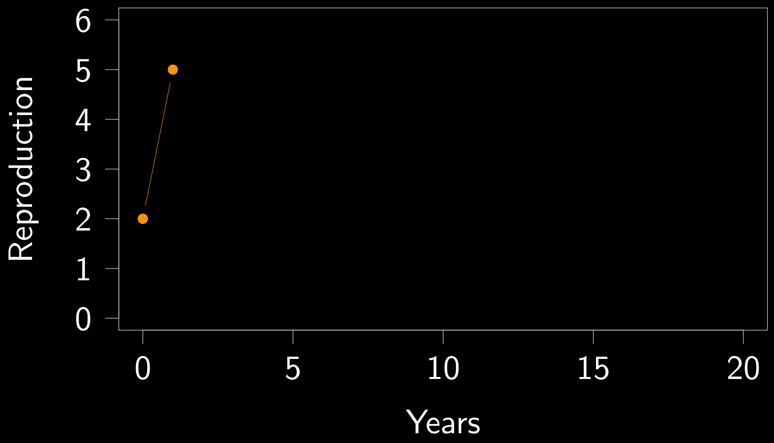
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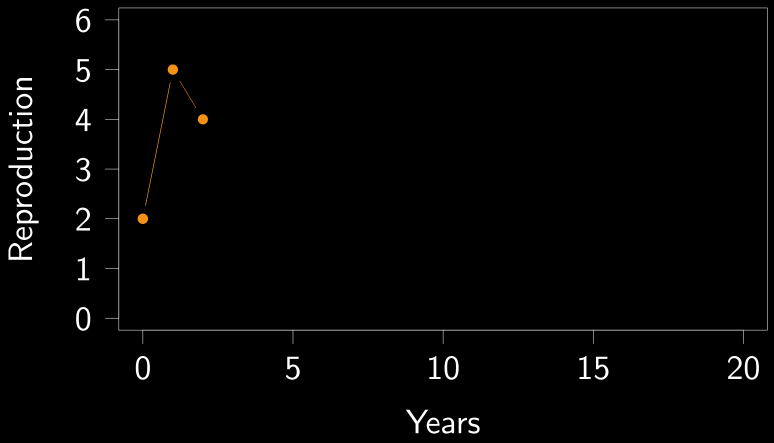
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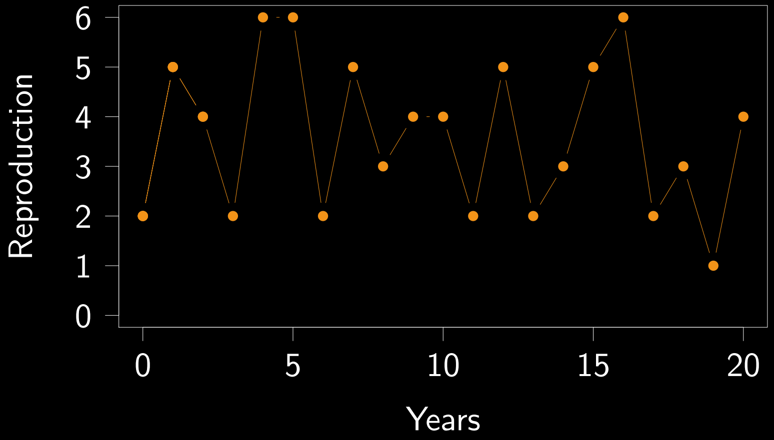
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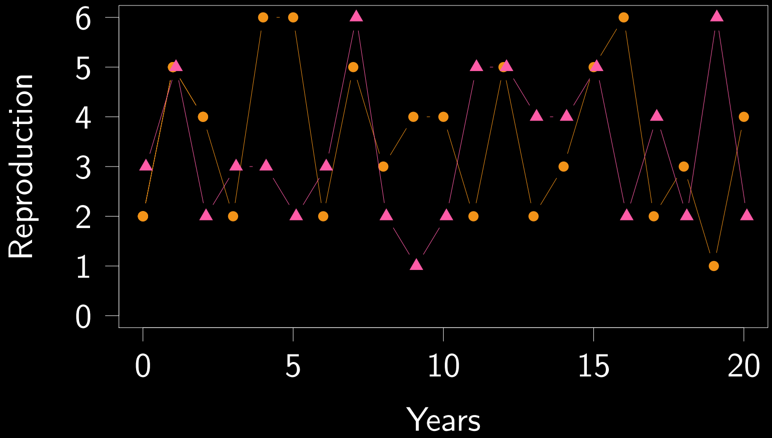

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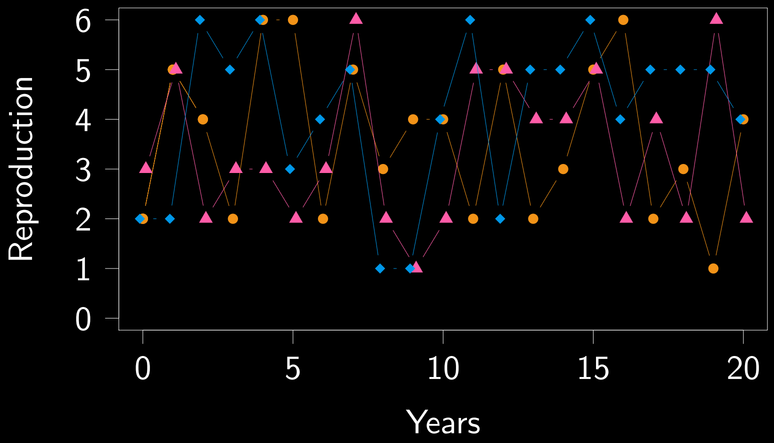

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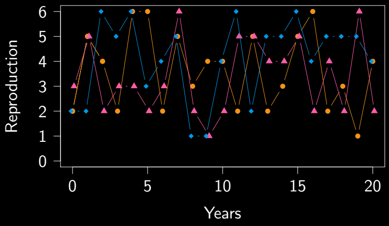
One dice theory



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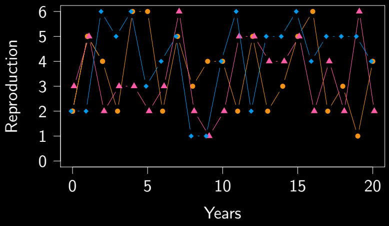
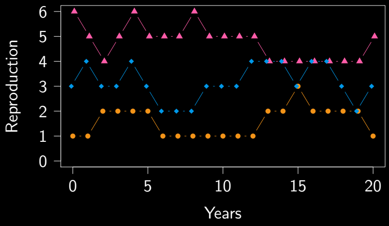


Real pattern



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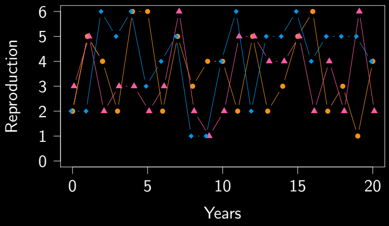

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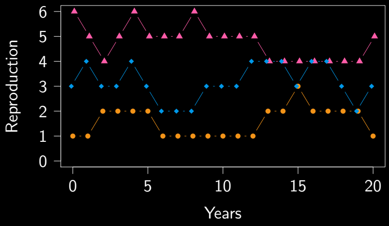

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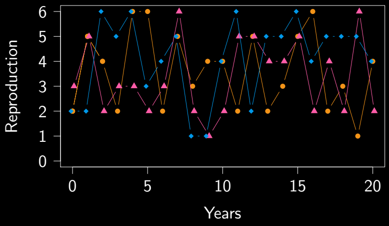
Individuals
are different

One dice theory



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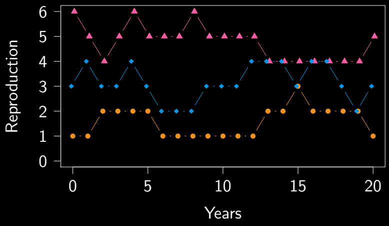
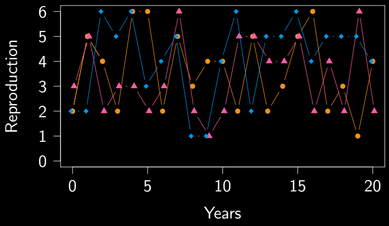


?

Individuals are different

Stages are different

One dice theory



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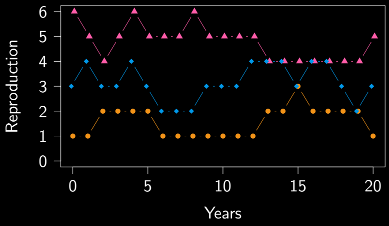

?

Individuals are different → Selection/Evolution

Stages are different → Neutrality

Neutral theory for life histories and individual variability in fitness components

Ulrich Karl Steiner[a,b,1] and Shripad Tuljapurkar[a]

[a]Department of Biology, Stanford University, Stanford, CA 94305; and [b]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

yes and that this stochastic variation has significant implications

Neutral matrix method

	next year		
	1	2	3
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

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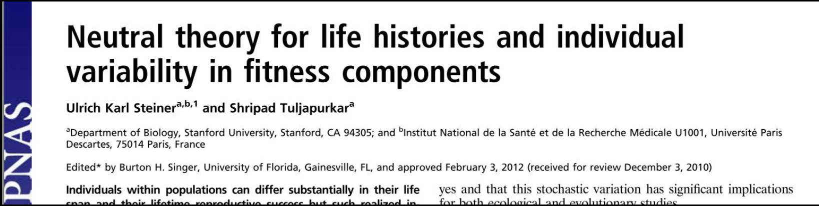

PNAS

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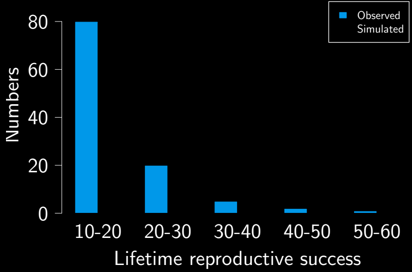

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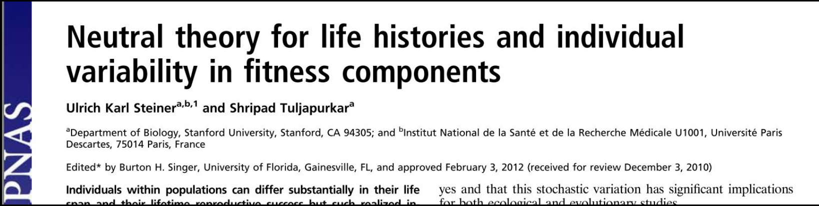
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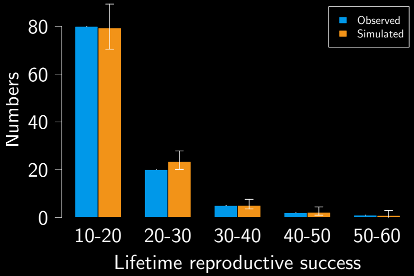


No variation in fitness among individuals

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

British Ecological Society

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 Tuljapurkar[1] and Steven Hecht Orzack[2]

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

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

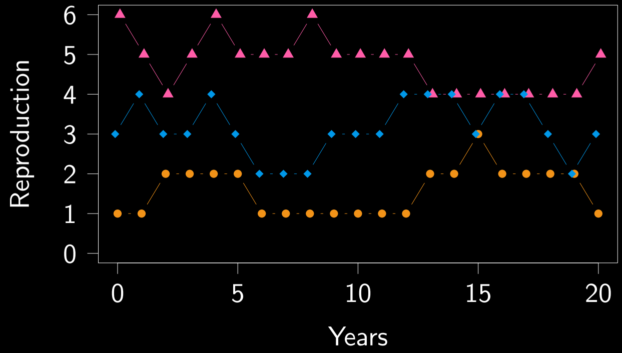
Conflicting results

Neutral matrix method

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

Mixed model method & Quantitative genetics

- Individual performances are repeatable



Conflicting results

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Mixed model method & Quantitative genetics

- Individual performances are repeatable
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Conflicting results

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Mixed model method & Quantitative genetics

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- . . . eh?

Conflicting results

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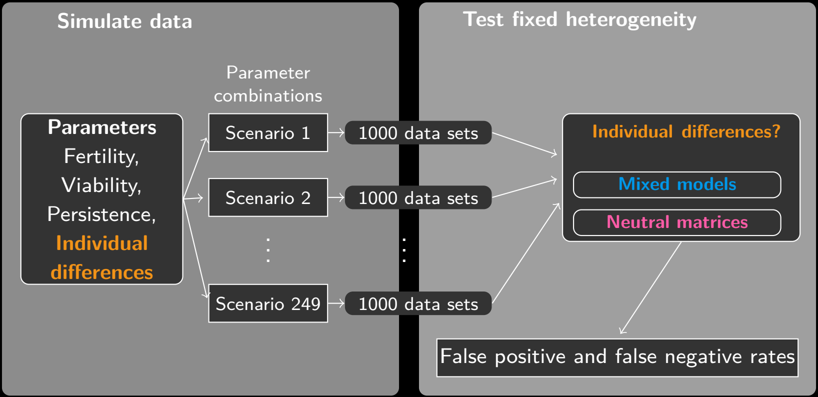
Mixed model method & Quantitative genetics

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

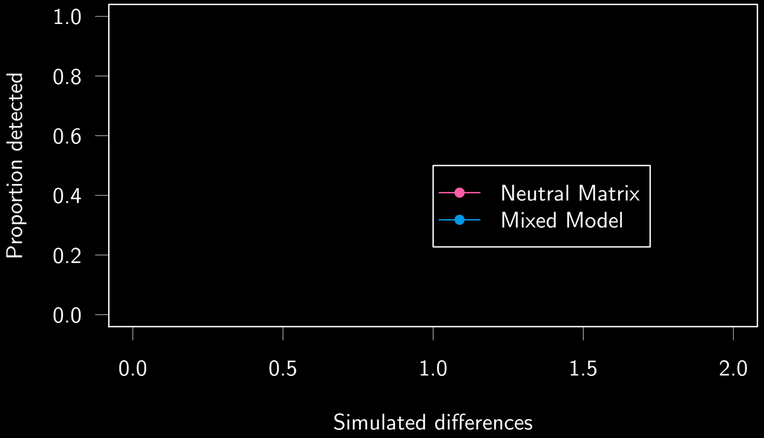
Why?

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

Method


Simulate data
Test fixed heterogeneity
Parameter combinations
Parameters
Fertility,
Viability,
Persistence,
Individual differences
Scenario 1
Scenario 2
Scenario 249
1000 data sets
1000 data sets
1000 data sets
Individual differences?
Mixed models
Neutral matrices
False positive and false negative rates

Results



1.0
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Proportion detected
Neutral Matrix
Mixed Model
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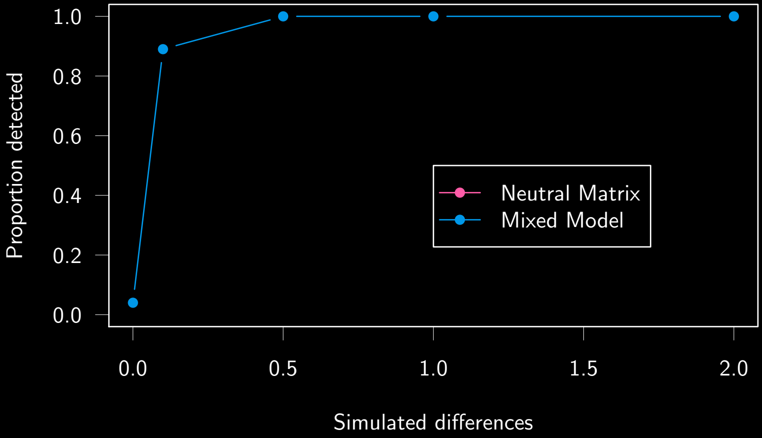
1.0
1.5
2.0
Simulated differences

Results



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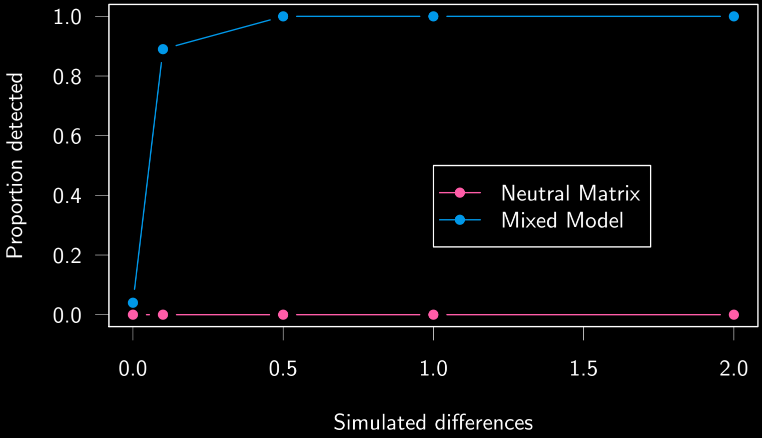
Results



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Simulated differences

Conclusion

Why conflicting methods?

Conclusion

Why conflicting methods?

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

Conclusion

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→ Individual differences in fitness components are common

Conclusion

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$\rightarrow$ Individual differences in fitness components are common

Implications

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Implications

- Phenotypic variation in fitness → opportunity for selection

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Why conflicting methods?

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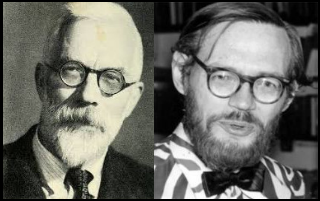
- **Mixed model method** =**false positive**? **NO**

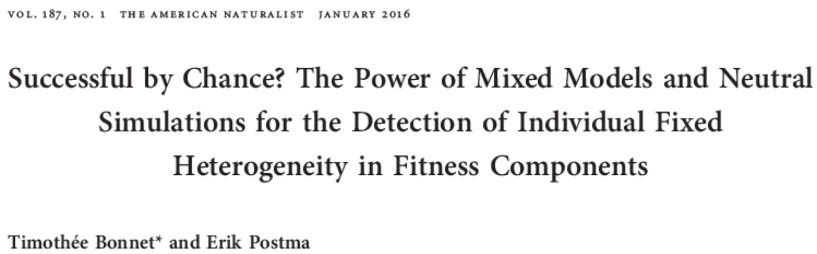
$\rightarrow$ Individual differences in fitness components are common

Implications

- Phenotypic variation in fitness $\rightarrow$ 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

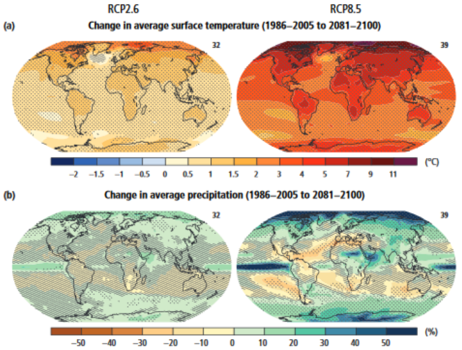
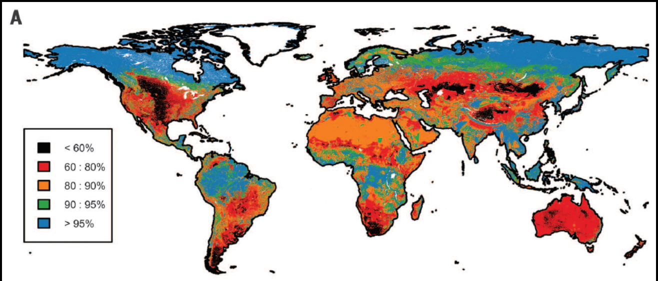


Figure SPM.7 | Change in average surface temperature **(a)** and change in average precipitation **(b)** based on multi-model mean projections for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarios. The number of models used to calculate the multi-model mean is indicated in the upper right corner of each panel. Stippling (i.e., dots) shows regions where the projected change is large compared to natural internal variability and where at least 90% of models agree on the sign of change. Hatching (i.e., diagonal lines) shows regions where the projected change is less than one standard deviation of the natural internal variability. *[2.2, Figure 2.2]*

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

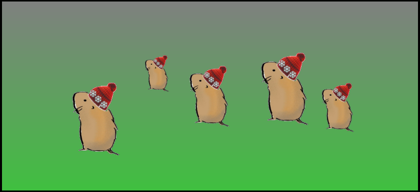
Vol. 37: 637-669 (Volume publication date December 2006)

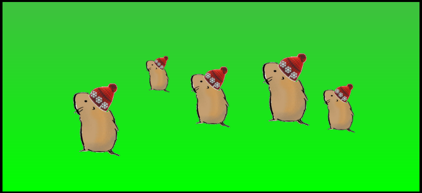
First published online as a Review in Advance on August 24, 2006

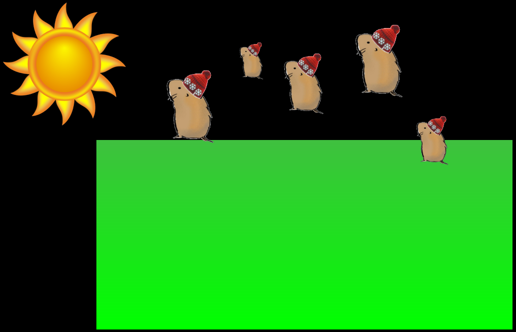
DOI: 10.1146/annurev.ecolsys.37.091305.110100

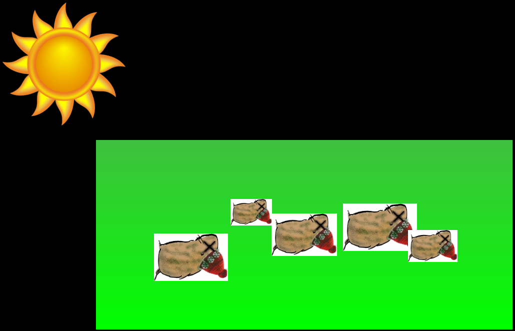
Camille Parmesan

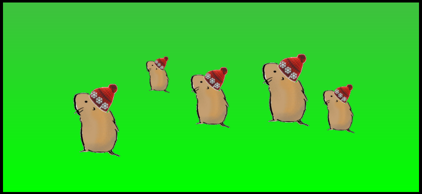
Section of Integrative Biology, University of Texas, Austin, Texas 78712; email: parmesan@mail.utexas.edu

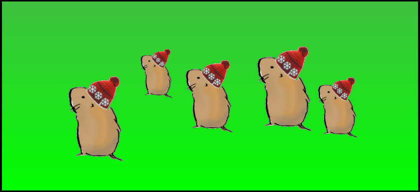


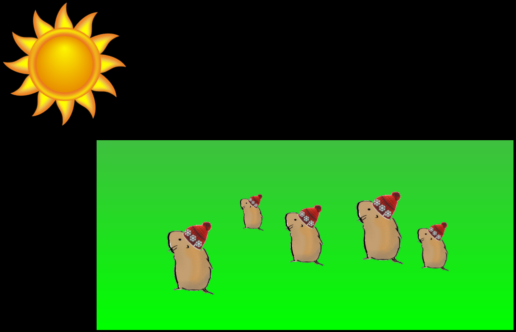


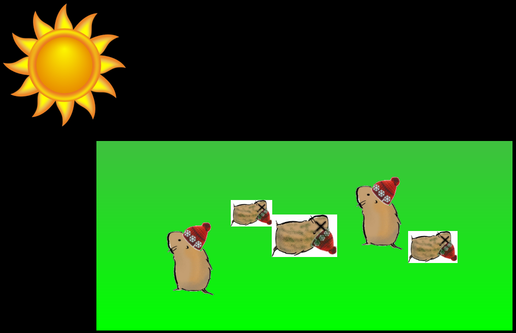


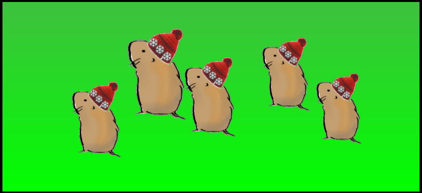












Evolution or plasticity? What drives phenotypic change?

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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2. **Integral Projection Models** - Easterling, Ellner & Dixon (2000). Size-specific sensitivity: applying a new structured population model. Ecology, 81(3)
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4. **Animal model** - Henderson (1950) Estimation of genetic parameters. Annals of Mathematical Statistics, 21

Methods in Ecology and Evolution 2016 doi: 10.1111/2041-210X.12627

REVIEW

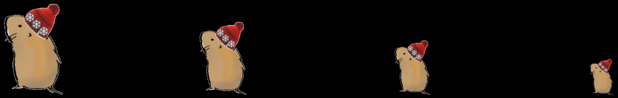
Disentangling evolutionary, plastic and demographic processes underlying trait dynamics: a review of four frameworks

Koen J. van **Benthem**[1]*†, Marjolein **Bruijning**[2]†, Timothée **Bonnet**[1]†, Eelke **Jongejans**[2]‡, Erik **Postma**[1]‡ **and** Arpat **Ozgul**[1]‡

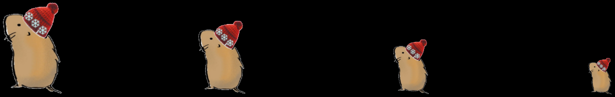
[1]*Department of Evolutionary Biology and Environmental Studies, University of Zurich, Winterthurerstrasse 190, 8057 Zurich, Switzerland; and* [2]*Department of Animal Ecology and Physiology, Radboud University, 6500 GL Nijmegen, The Netherlands*

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

The animal model



The animal model



The animal model

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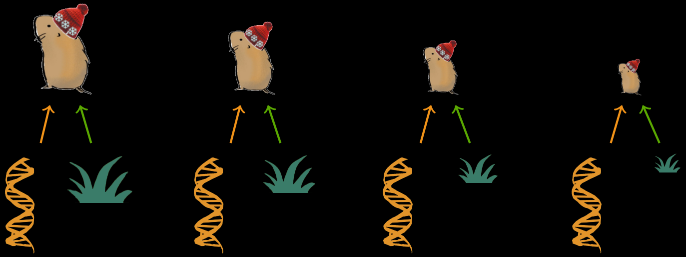
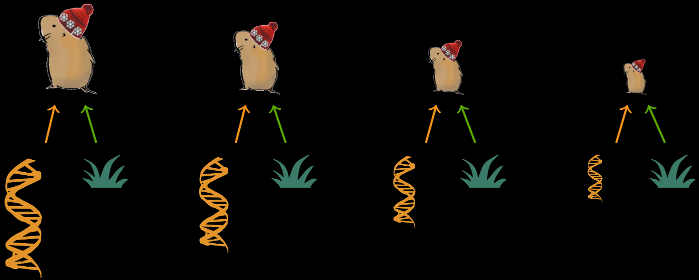
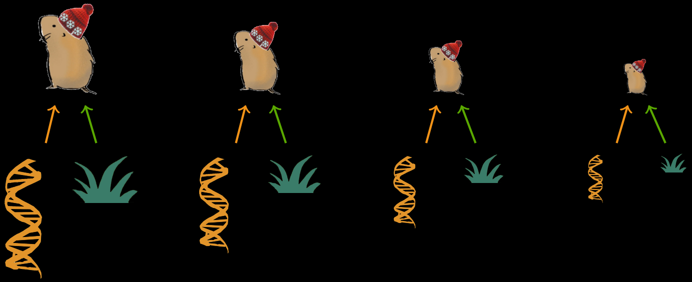


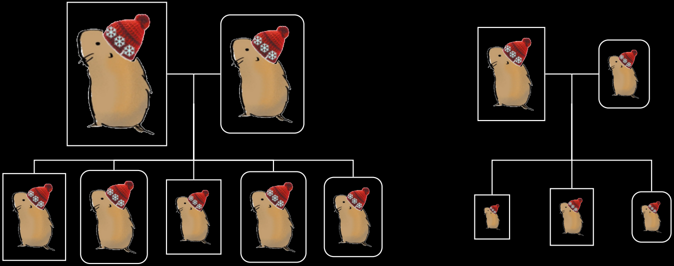
The animal model



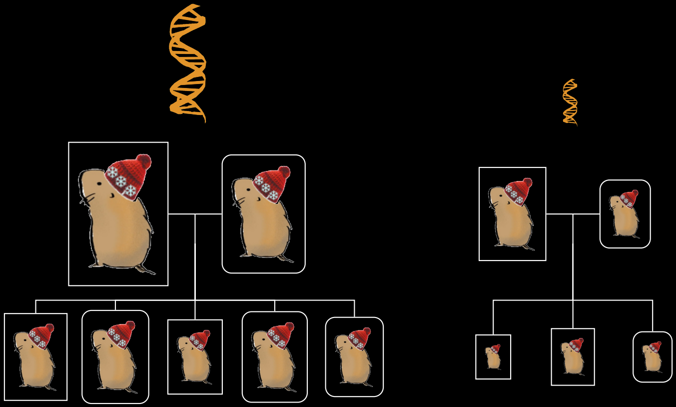
The animal model



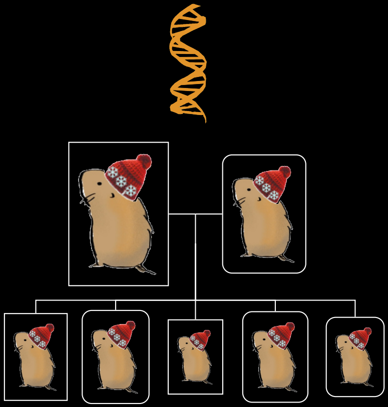
The animal model

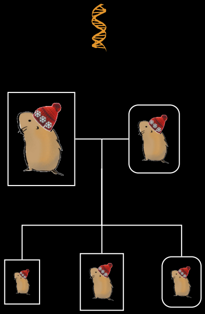


The animal model

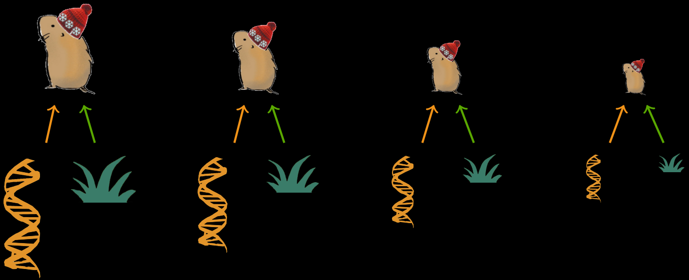


The animal model





The animal model



Additive Genetic Variance $= V_A$ $=$ variance ()

Additive Genetic Variance $= V_A$ = variance ()

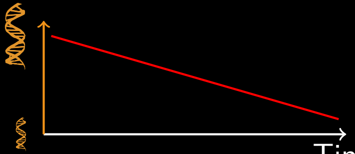
Heritability $= h^2 = \frac{V_A}{V_P}$ = variance () / variance ()

The animal model

Additive Genetic Variance $= V_A$ = variance ()

Heritability $= h^2 = \frac{V_A}{V_P}$ = variance () / variance ()

Evolution



Adaptive evolution in the wild

Adaptive evolution in the wild

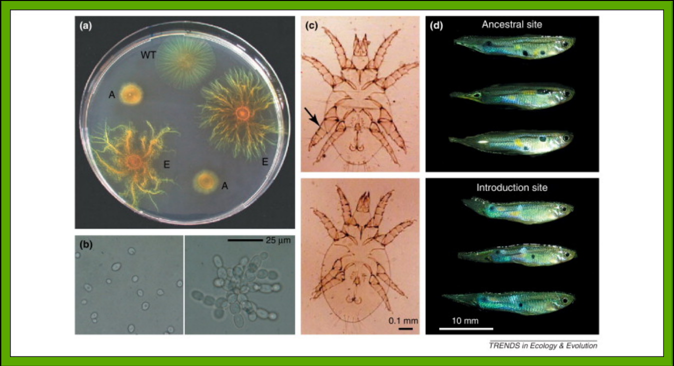
$$\text{Adaptive evolution} = \text{Selection} \times \text{heritability}$$

Adaptive evolution in the wild

Adaptive evolution = Selection $\times$ heritability

Adaptive evolution in the wild

$$\text{Adaptive evolution} = \text{Selection} \times \text{heritability}$$



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.

Explaining stasis: microevolutionary studies in natural populations

J. Merilä[1*], B.C. Sheldon[2] & L.E.B. Kruuk[3]

Adaptive evolution in the wild

Adaptive evolution $=$ Selection $\times$ heritability

2014

Evolutionary Applications

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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 × heritability

2016

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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

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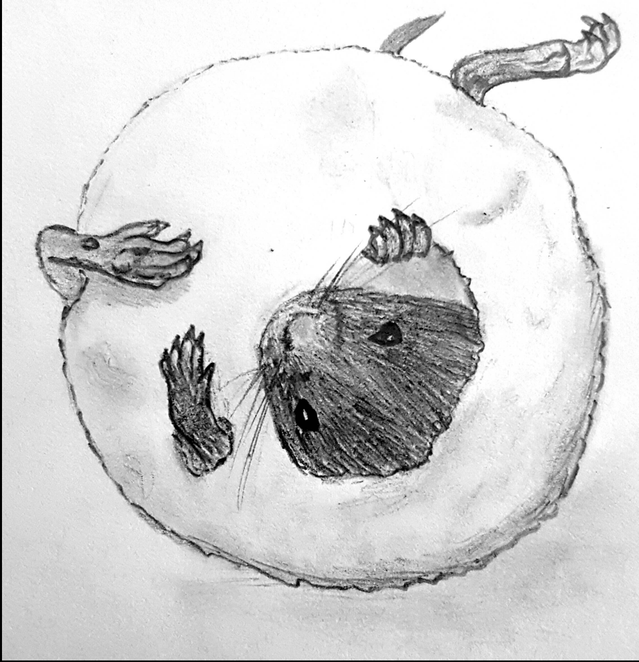
Volume 38, Issue 9
September 2016
Pages 927–934

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)

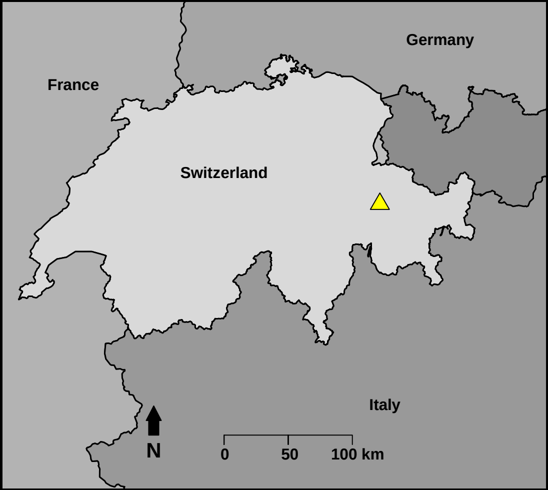
- NOT white
- Rock-dweller
- 30-45g

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


Germany
France
Switzerland
Italy
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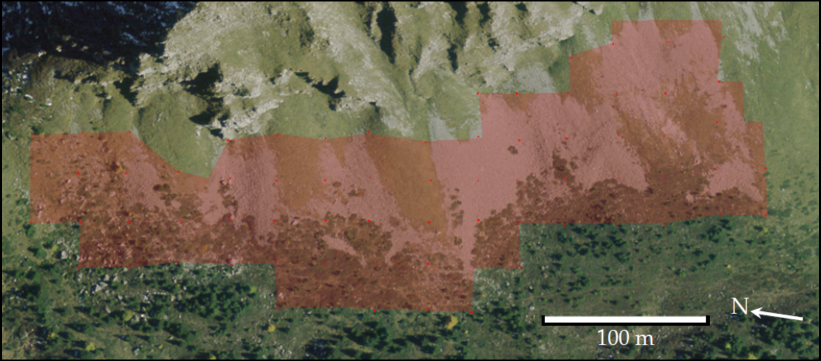
100 km


N
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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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  - 20 “neutral” markers
  - Sex identification
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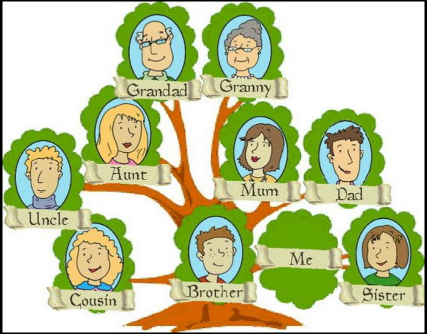
  - Any genotyping
  - **Pedigree**



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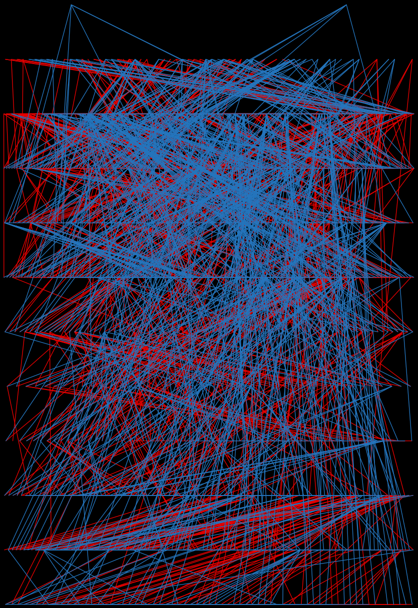
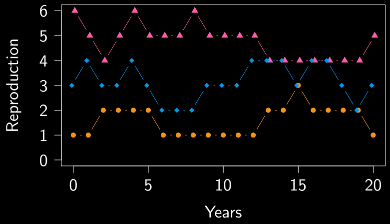


Are snow vole evolving? Why?

Variance in fitness?

Adaptive evolution in the snow vole?

Variance in fitness?

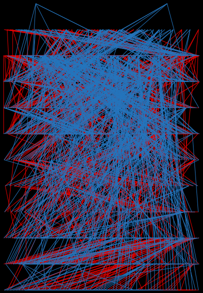


	Estimate	95% CI	p-value
Latent variance in survival	0	[0;0.248]	0.50
Latent variance in reproduction	0.37	[0.25, 0.49]	$< 10^{-16}$

Adaptive evolution in the snow vole?

- Non random variation fitness components

Variance in fitness?



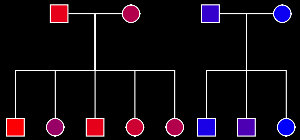
Relative lifetime reproductive success

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

Evolution of body mass

Prediction

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

Evolution of body mass

Prediction

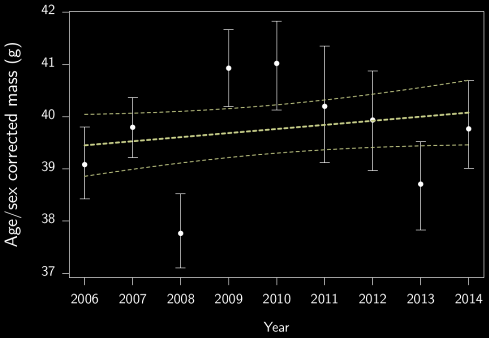
- Selection $= +0.86$g (p$< 10^{-3}$)
- Heritability $= 20\%$ (p$< 10^{-3}$)
- Response $=$ Selection $\times$ heritability $= +\ 0.22$g/year

Evolution of body mass

Prediction

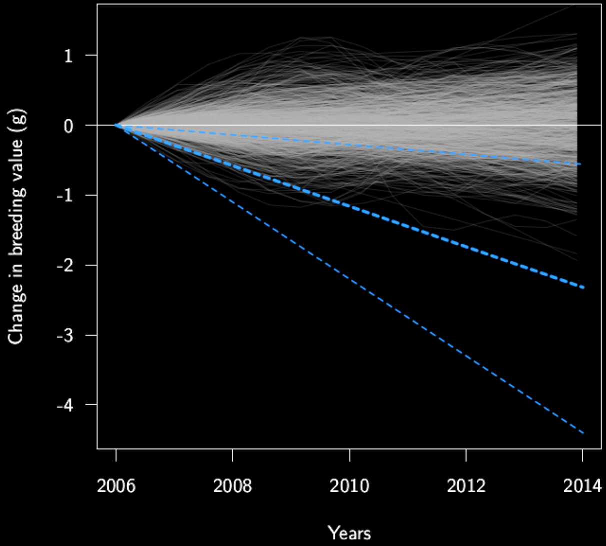
- Selection = +0.86g (p$< 10^{-3}$)
- Heritability = 20% (p$< 10^{-3}$)
- Response = Selection $\times$ heritability = + 0.22g/year

Phenotypic observation



- Observed = +0.07g/year (p=0.14)

Estimation of genetic change



Evolution of body mass

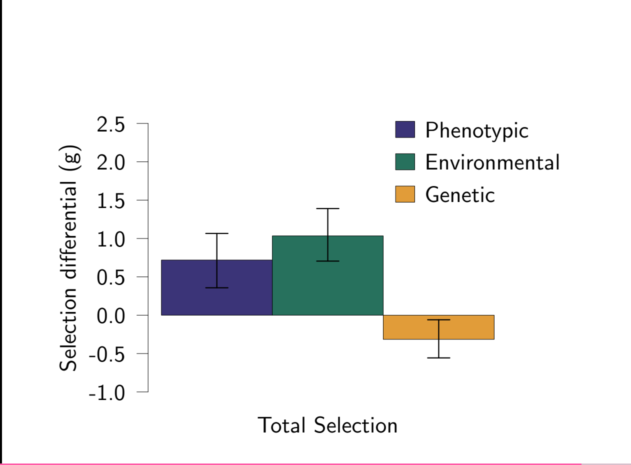
Evolution Paradox

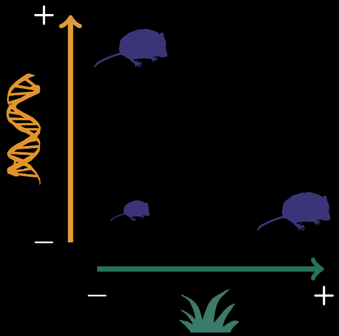
- Apparent selection for higher mass
- Adaptive evolution for lower mass

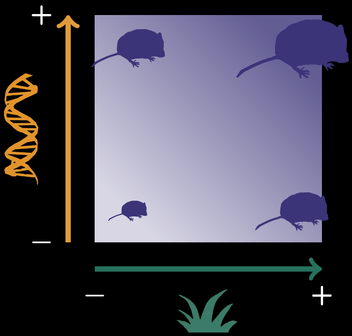
Evolution of body mass

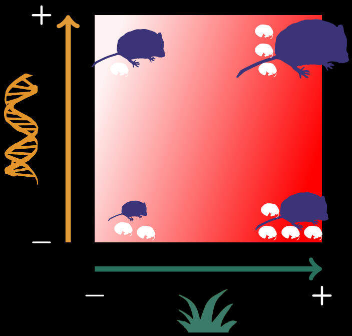
Evolution Paradox

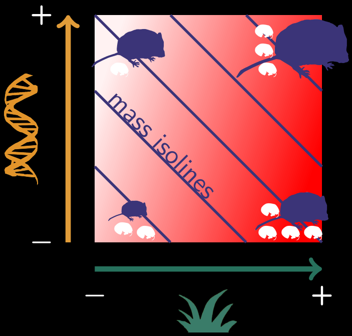
- Apparent selection for higher mass
- Adaptive evolution for lower mass

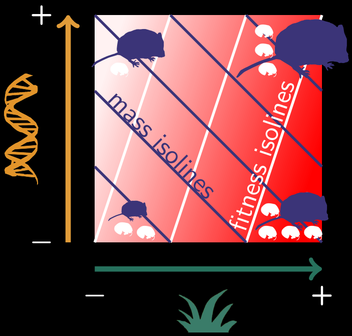


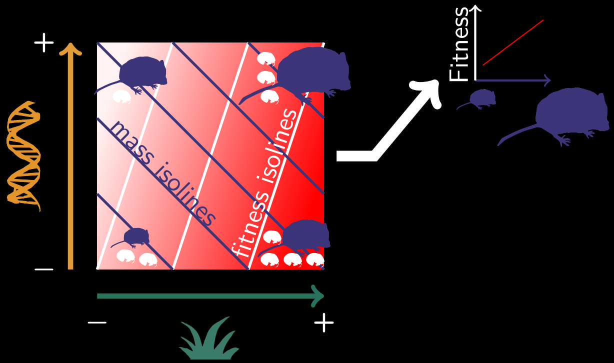


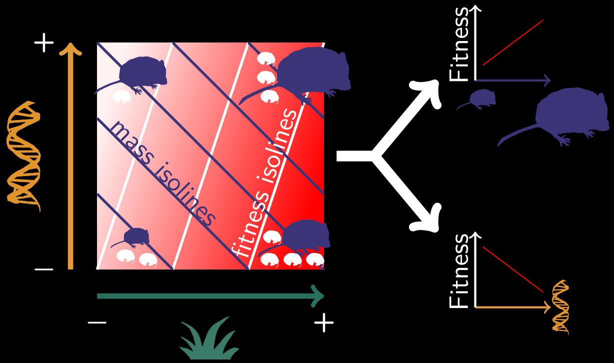


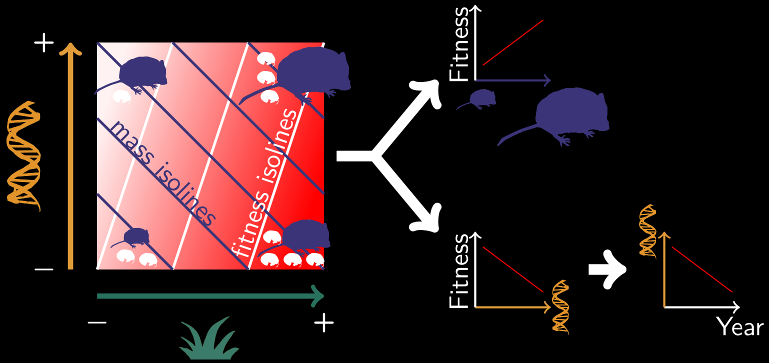



+
−
mass isolines
−
+


+
−
mass isolines
fitness isolines
−
+


Fitness
+
–
mass isolines
fitness isolines
–
+


+
–
mass isolines
fitness isolines
–
+
Fitness
Fitness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+
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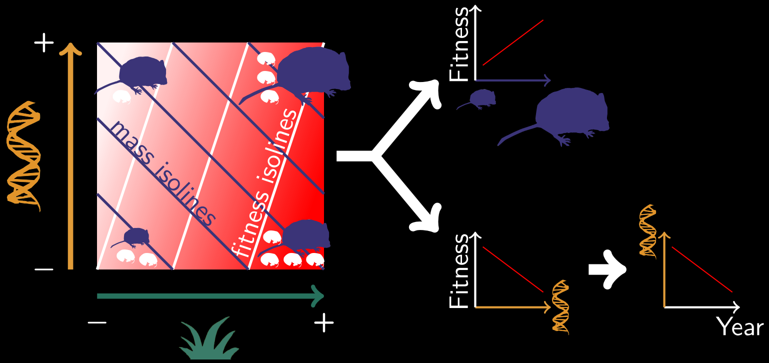
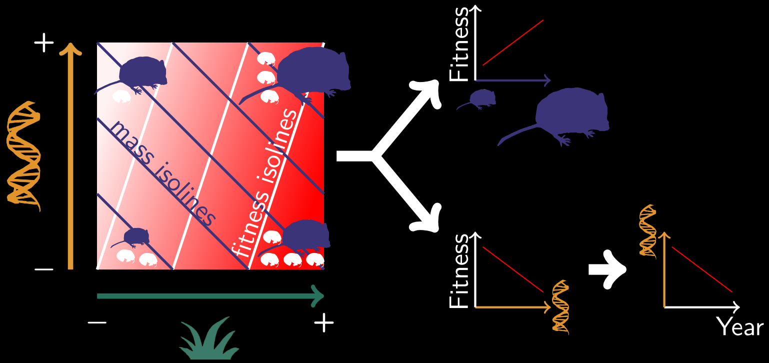
Year



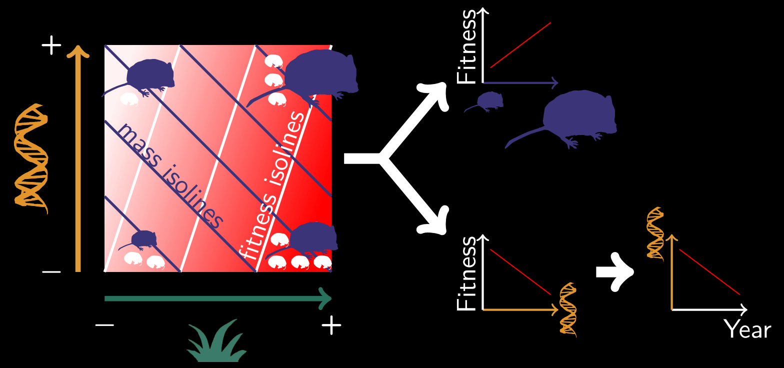
Summary

1. Apparent stasis. . .



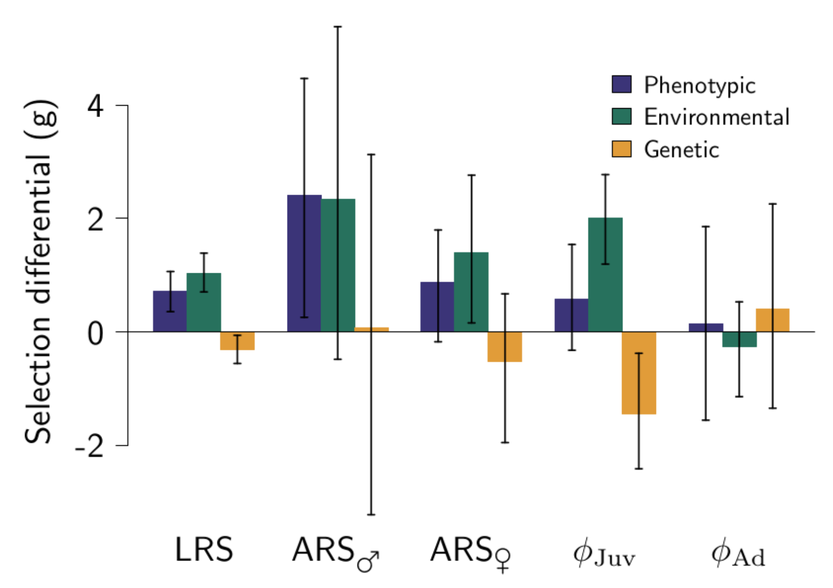
Summary

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

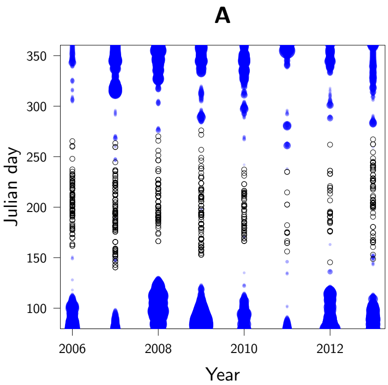


Summary

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


Selection differential (g)
4
2
0
-2
Phenotypic
Environmental
Genetic
LRS
ARS♂
ARS♀
ϕ_{Juv}
ϕ_{Ad}

Snow falls and ontogeny



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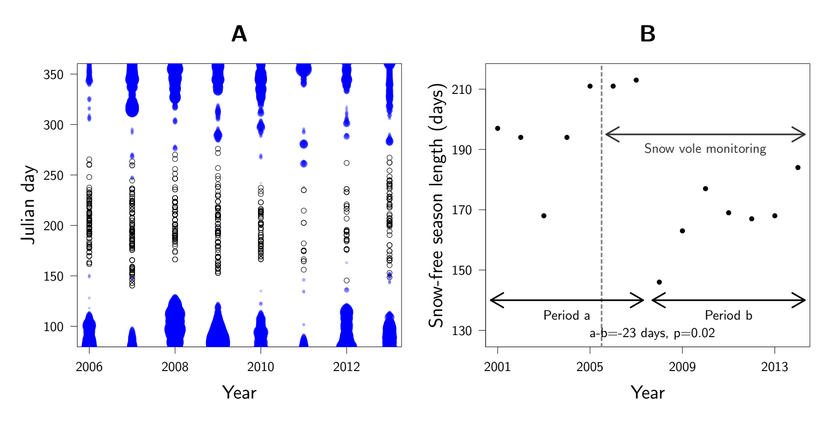
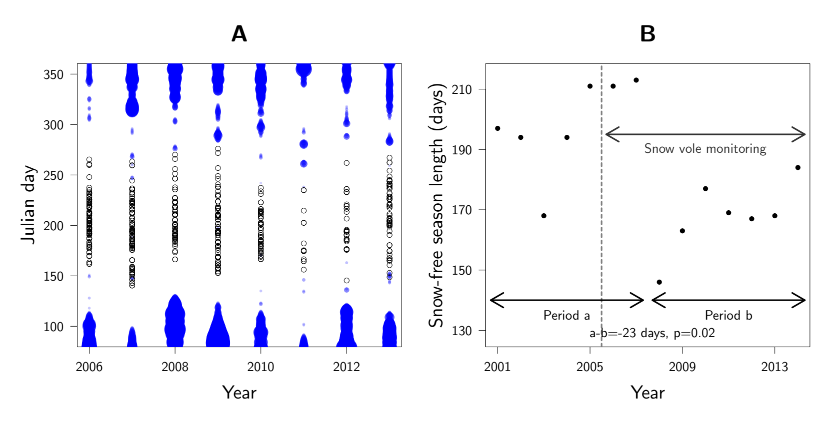


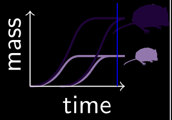
Snow falls and ontogeny



Less time to grow → Selection for smaller voles?

Selection during ontogeny?

D

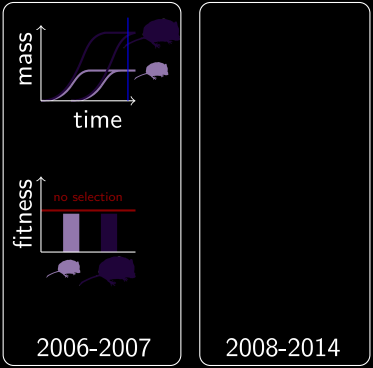


2006-2007

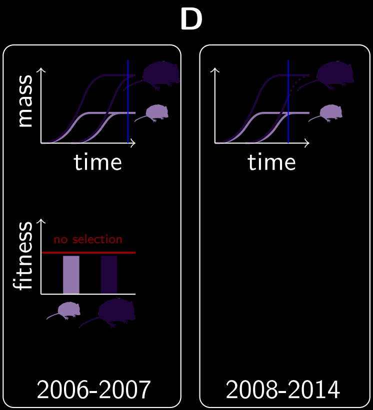
2008-2014

Selection during ontogeny?

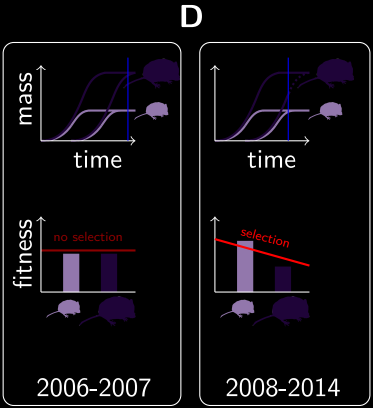
D



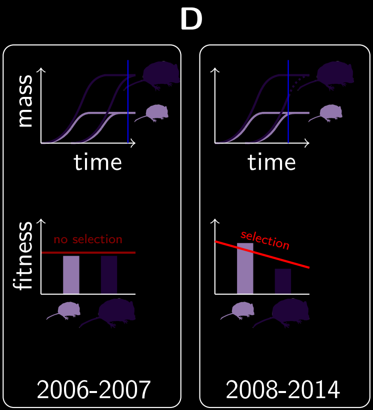
Selection during ontogeny?

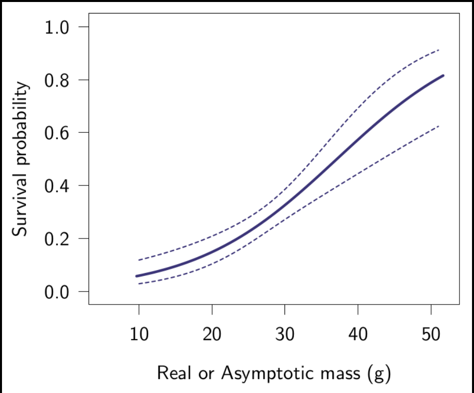


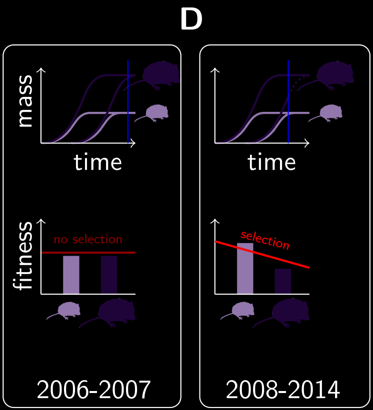
Selection during ontogeny?

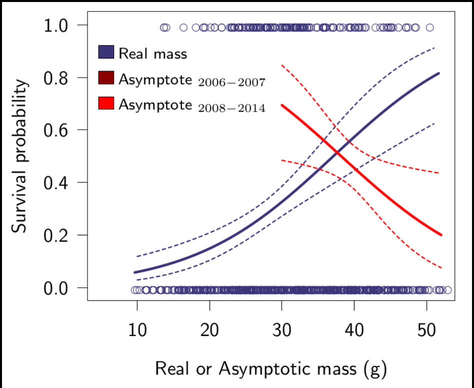


Selection during ontogeny?

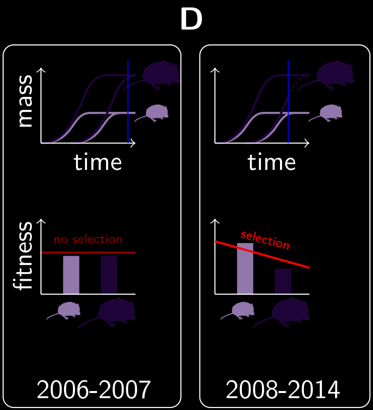


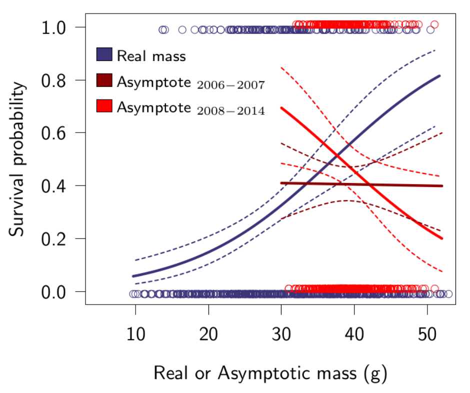



D
mass
time
fitness
no selection
2006-2007
mass
time
fitness
selection
2008-2014


Real mass
Asymptote 2006–2007
Asymptote 2008–2014
Survival probability
1.0
0.8
0.6
0.4
0.2
0.0
10
20
30
40
50
Real or Asymptotic mass (g)

Selection during ontogeny?





Evoleution!

Evoleution!

- Contemporary adaptive evolution

Evoleution!

- Contemporary adaptive evolution
- Against apparent selection

Evoleution!

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

Evoleution!

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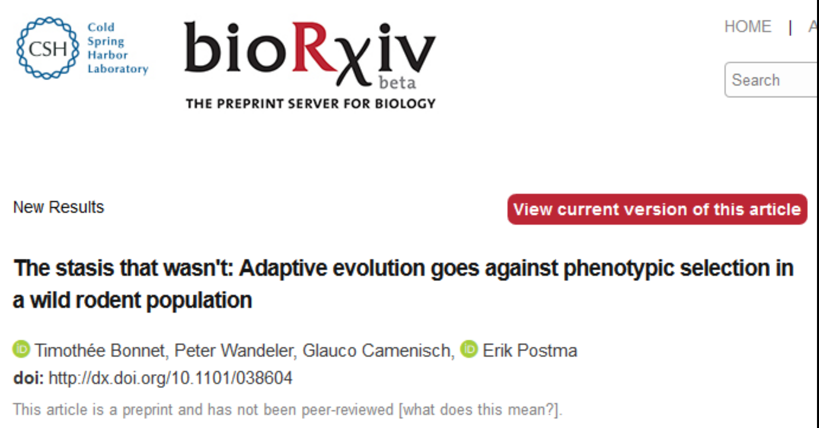
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The stasis that wasn't: Adaptive evolution goes against phenotypic selection in a wild rodent population

Timothée Bonnet, Peter Wandeler, Glauco Camenisch, Erik Postma

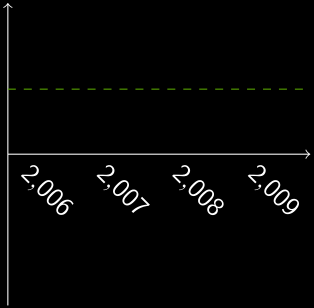
doi: http://dx.doi.org/10.1101/038604

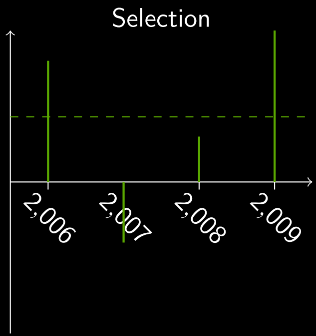
This article is a preprint and has not been peer-reviewed [what does this mean?].

Do selection and evolution fluctuate?

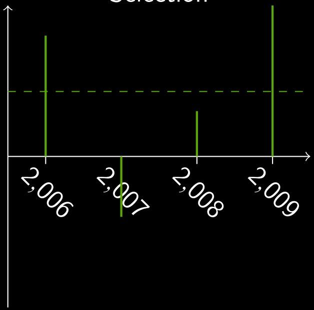
Selection

Selection

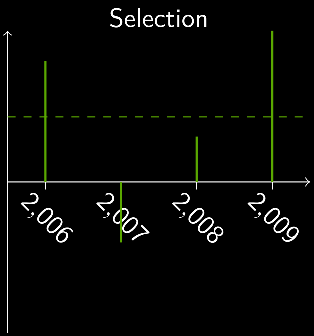



Selection
2,006
2,007
2,008
2,009

Selection



Evolution


Selection
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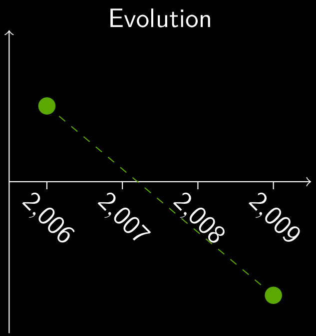
Evolution
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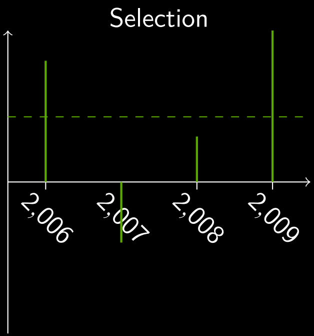
Selection
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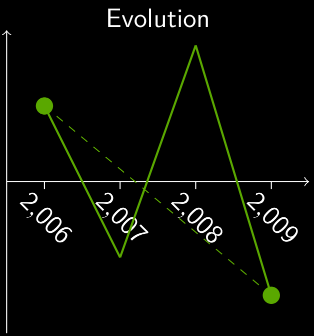
Evolution
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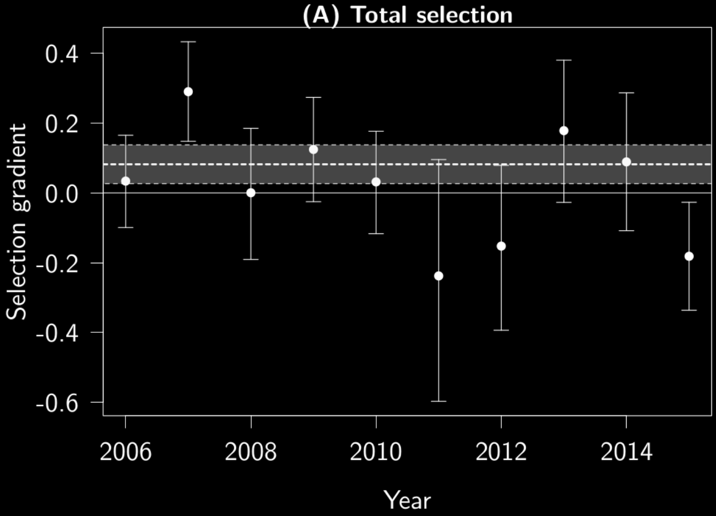
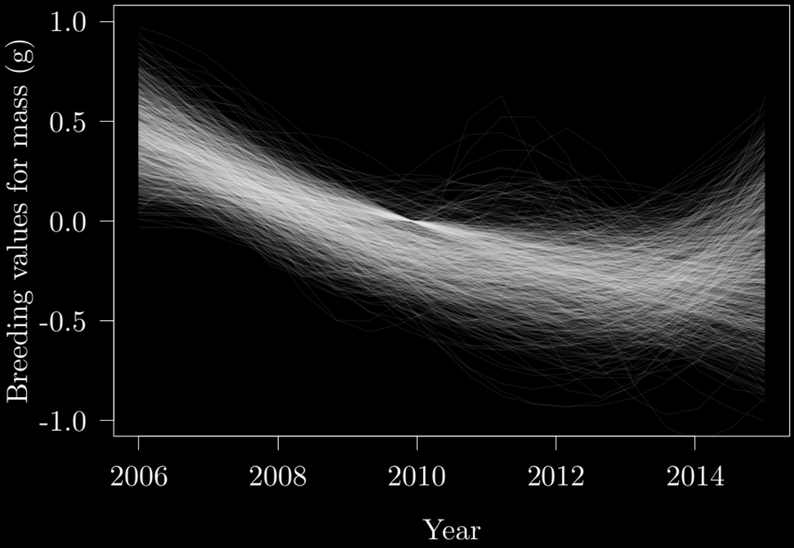
Dynamics of selection

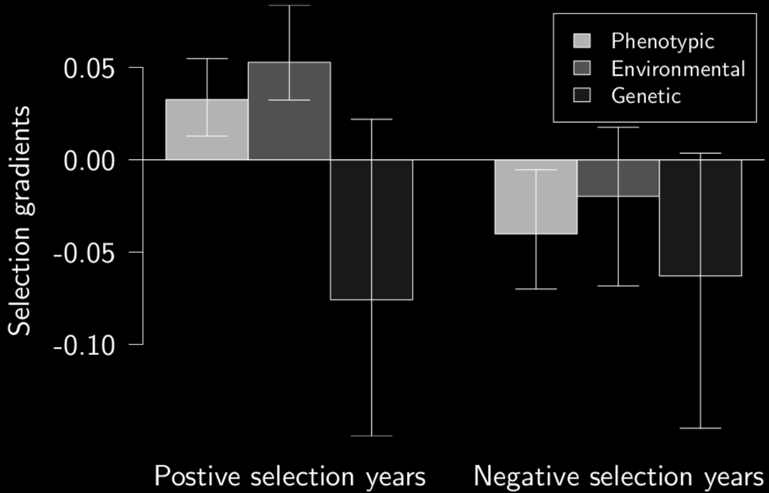


Variance in selection = 0.117 [0.063;0.218], $p=8 \cdot 10^{-6}$

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?