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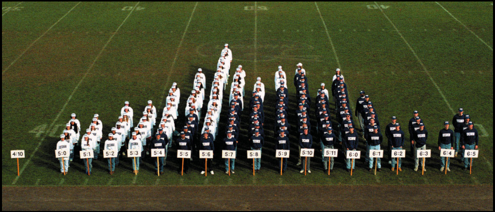
- Eelke Jongejans
- Pirmin Nietlisbach
- Philipp Becker
- Judith Bachmann

Phenotypic variation within population

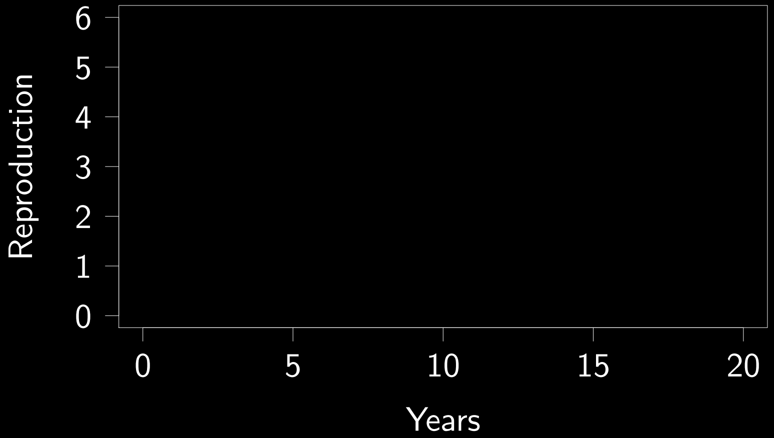


Phenotypic variation within population

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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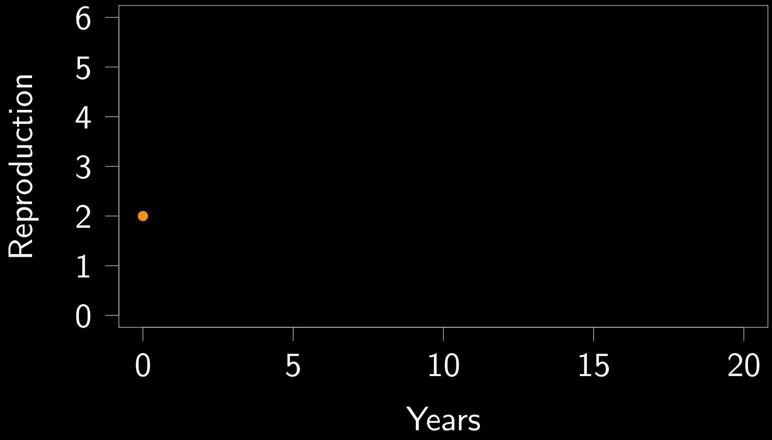
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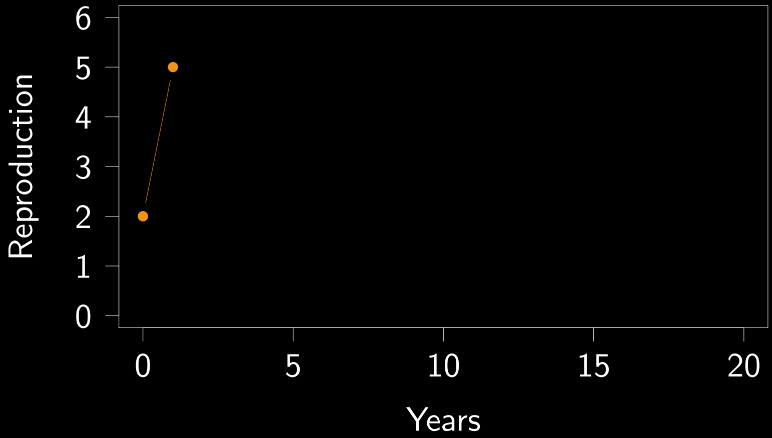

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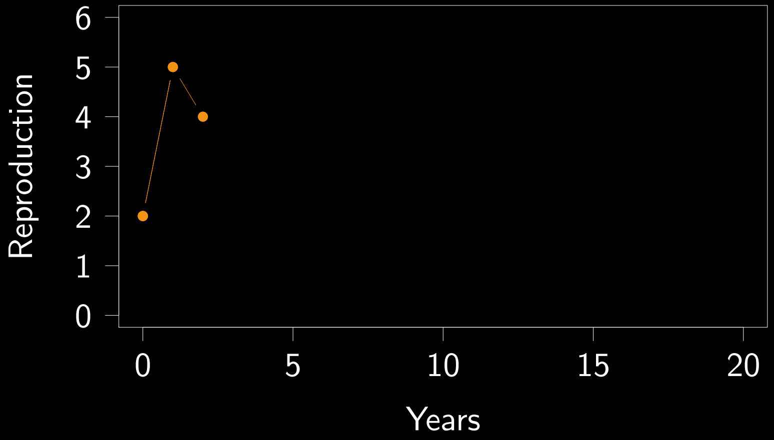
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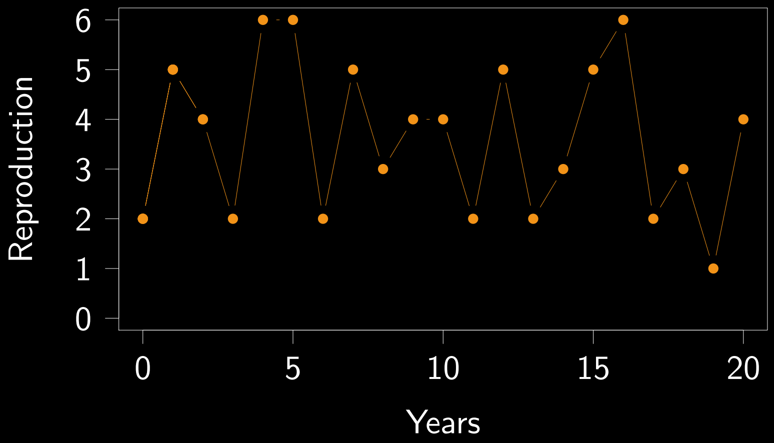

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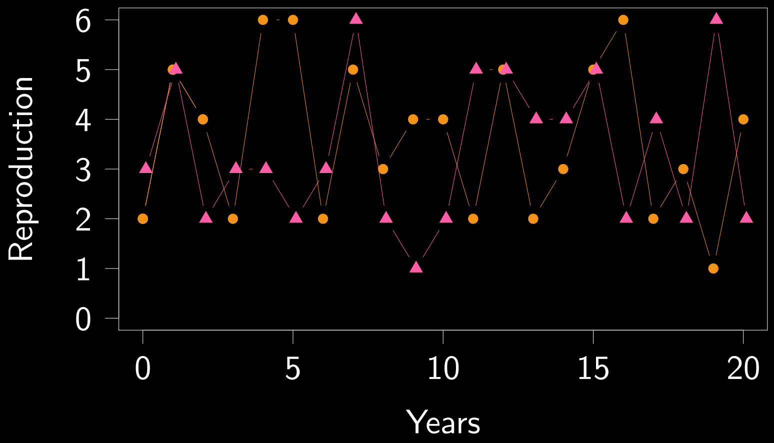

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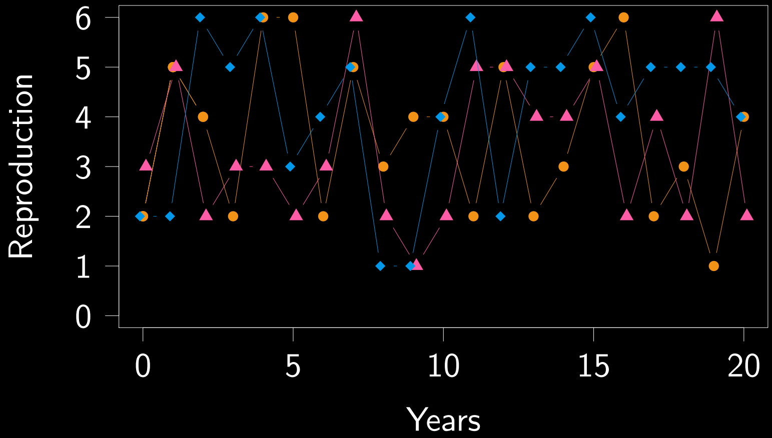

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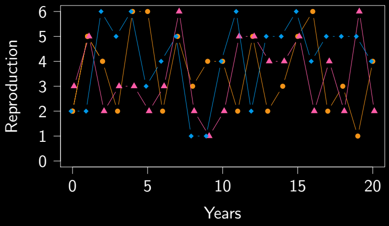
One dice theory



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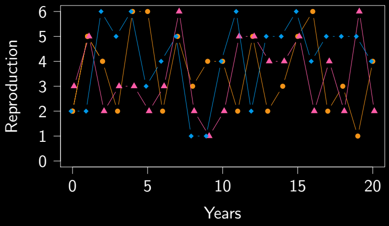
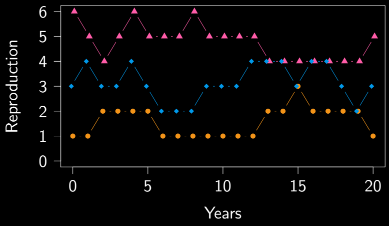


Real pattern



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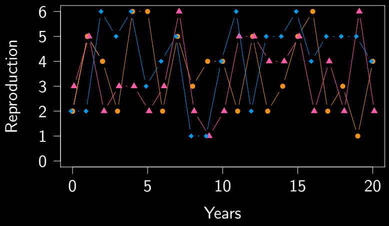

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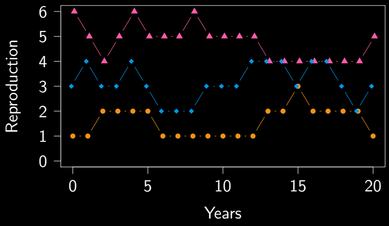
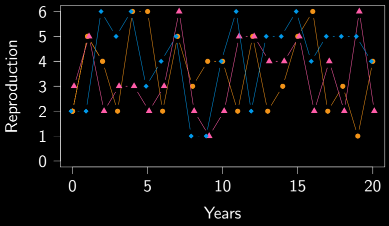


?

Individuals
are different

One dice theory



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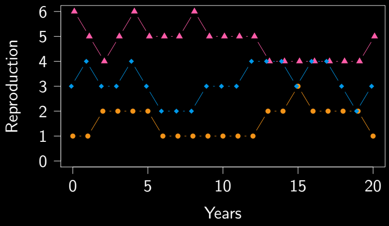
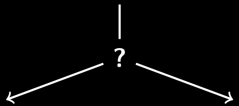
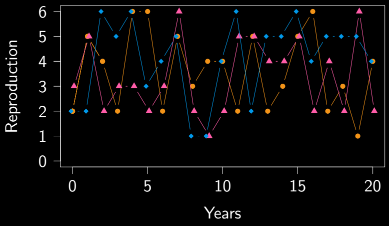




Individuals are different

Stages are different

One dice theory



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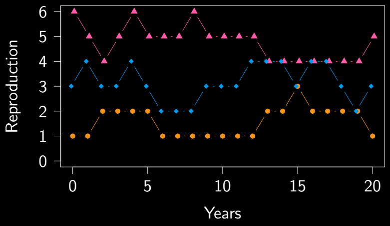

?

Individuals are different → Selection/Evolution

Stages are different → Neutrality

The neutral theory

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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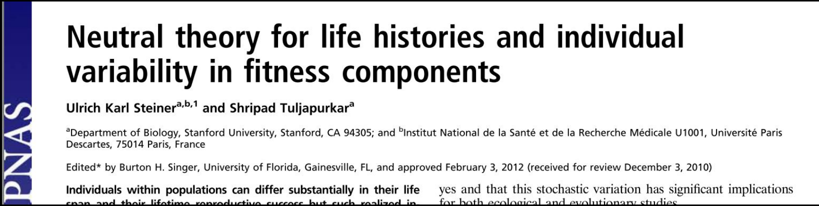

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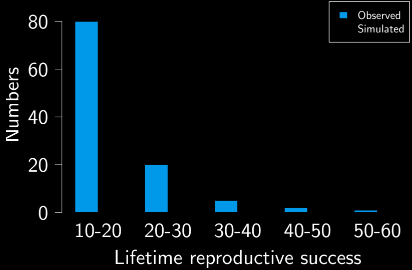

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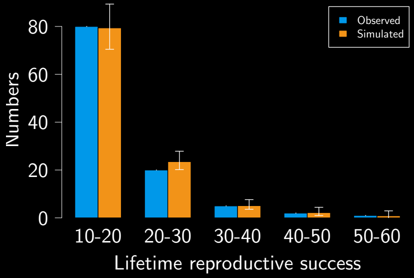


No variation in fitness among individuals

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 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

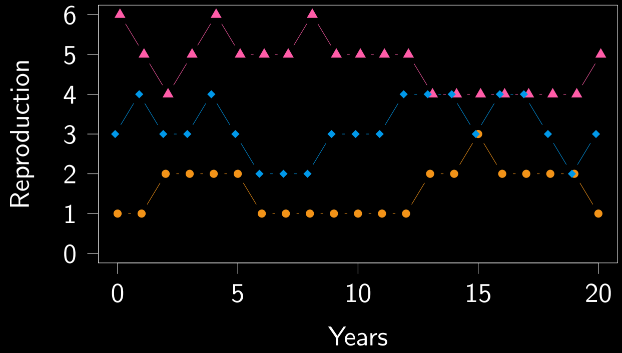
Conflicting results

Neutral matrix method

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

Mixed model method & Quantitative genetics

- Individual performances are repeatable



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Mixed model method & Quantitative genetics

- Individual performances are repeatable
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Conflicting results

Neutral matrix method

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- . . . very little and due to chance only

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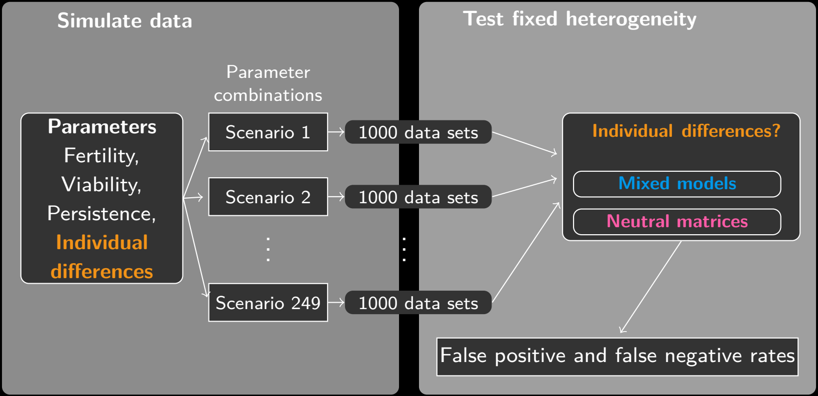
Why?

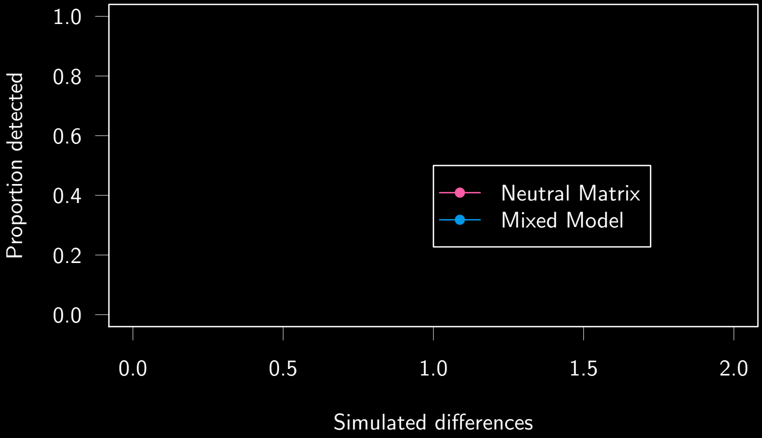
- **Neutral matrix method** =**false negative**?
- **Mixed model method** =**false positive**?

Method



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

Results



Proportion detected
1.0
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0.6
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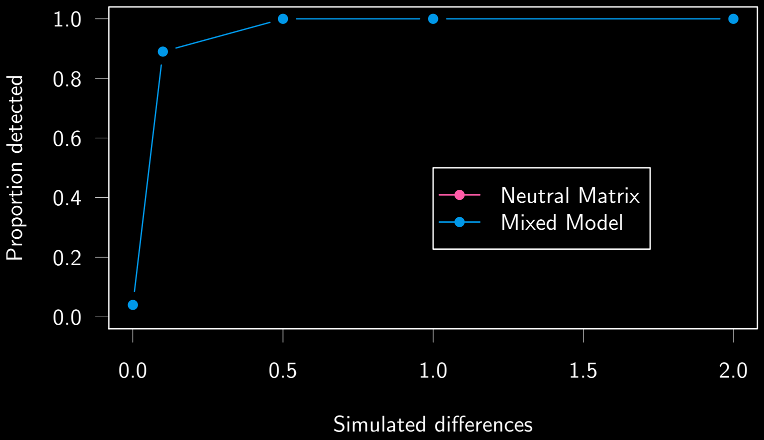
1.0
1.5
2.0
Simulated differences
Neutral Matrix
Mixed Model

Results



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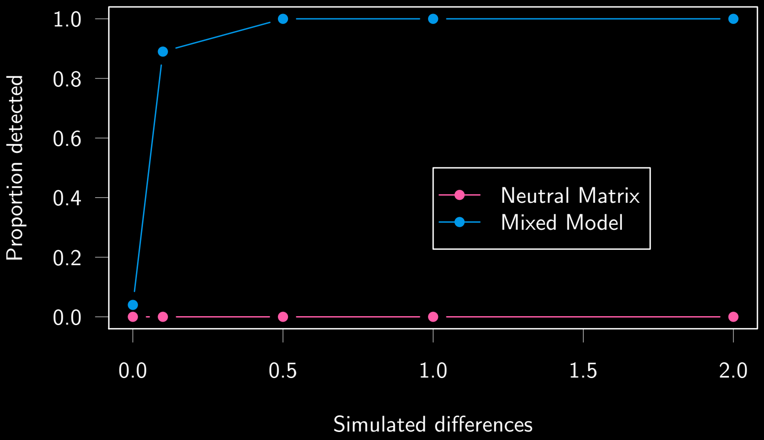
Results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Proportion detected
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0.0
0.5
1.0
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Simulated differences

Conclusion

Why conflicting methods?

Conclusion

Why conflicting methods?

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

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→ Individual differences in fitness components are common

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Implications

- Phenotypic variation in fitness → opportunity for selection

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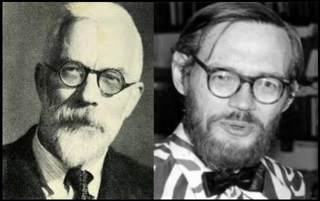
→ Individual differences in fitness components are common

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

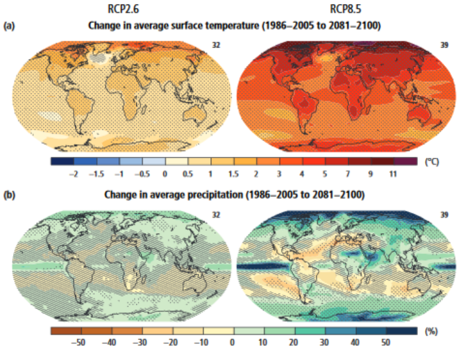
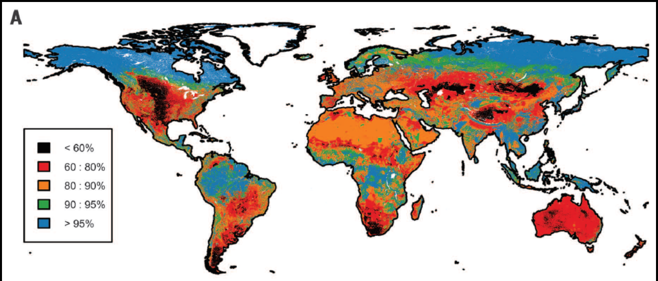


Figure SPM.7 | Change in average surface temperature **(a)** and change in average precipitation **(b)** based on multi-model mean projections for 2081–2100 relative to 1986–2005 under the RCP2.6 (left) and RCP8.5 (right) scenarios. The number of models used to calculate the multi-model mean is indicated 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

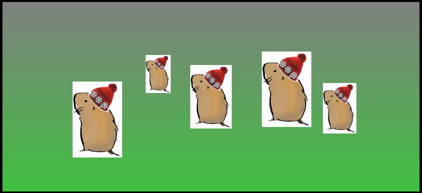


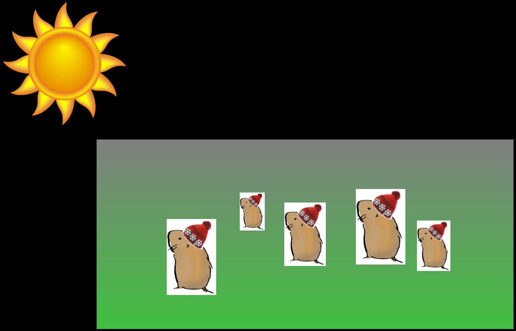
Newbold & al. (2016). Has land use pushed terrestrial biodiversity beyond the planetary boundary? A global assessment. Science, 353

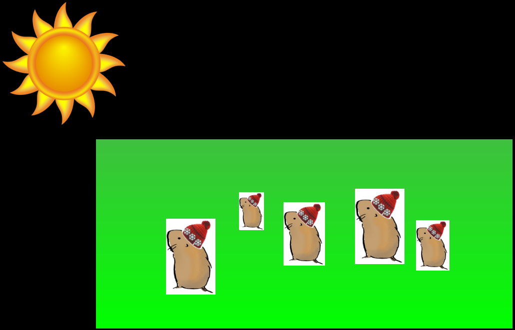
Ecological and Evolutionary Responses to Recent Climate Change

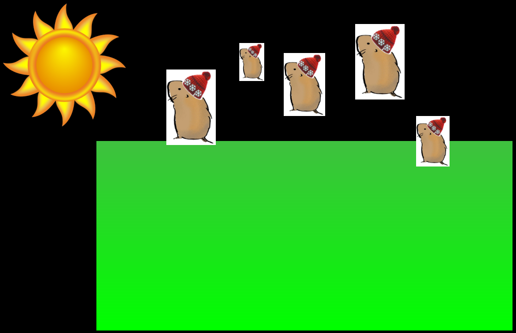
Annual Review of Ecology, Evolution, and Systematics
Vol. 37: 637-669 (Volume publication date December 2006)
First published online as a Review in Advance on August 24, 2006
DOI: 10.1146/annurev.ecolsys.37.091305.110100

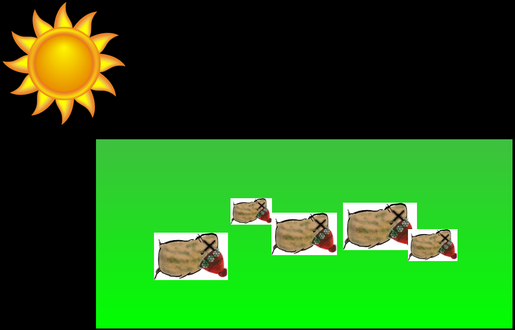
Camille Parmesan
Section of Integrative Biology, University of Texas, Austin, Texas 78712; email: parmesan@mail.utexas.edu

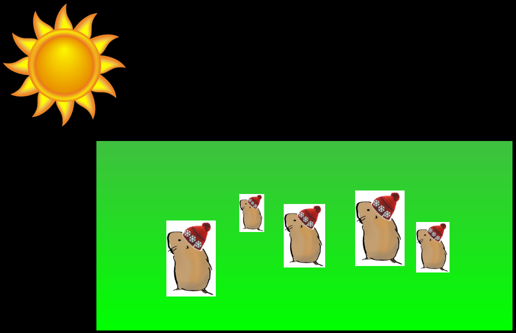


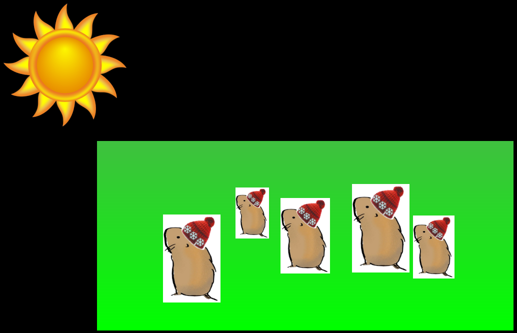


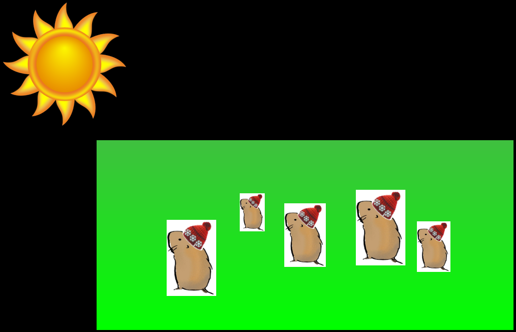


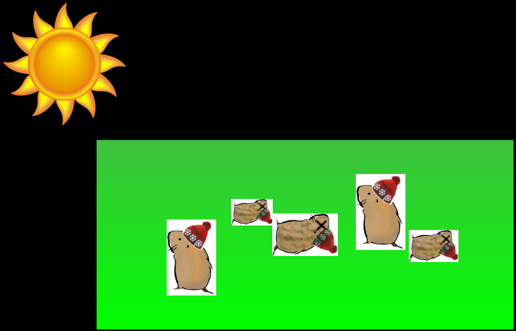


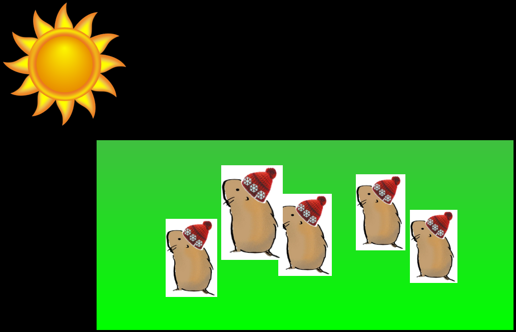












Evolution or plasticity? What drives phenotypic change?

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)

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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)

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)
2. **Integral Projection Models** - Easterling, Ellner & Dixon (2000). Size-specific sensitivity: applying a new structured population model. Ecology, 81(3)
   Coulson, Tuljapurkar & Childs (2010). Using evolutionary demography to link life history theory, quantitative genetics and population ecology. The Journal of Animal Ecology, 79(6)
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

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

Pedigree $\rightarrow$ similarity between relatives $\rightarrow$ **additive genetic variance**

The animal model

Pedigree $\rightarrow$ similarity between relatives $\rightarrow$ **additive genetic variance**

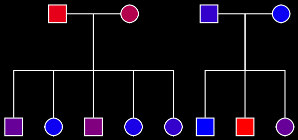
$$\textbf{heritability} = \frac{\text{additive genetic variance}}{\text{phenotypic variance}}$$

The animal model

Pedigree $\rightarrow$ similarity between relatives $\rightarrow$ **additive genetic variance**

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

heritability$\approx$0

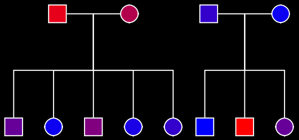


The animal model

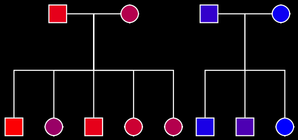
Pedigree $\rightarrow$ similarity between relatives $\rightarrow$ **additive genetic variance**

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

heritability≈0



heritability≈1



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Pedigree $\rightarrow$ similarity between relatives $\rightarrow$ **additive genetic variance**

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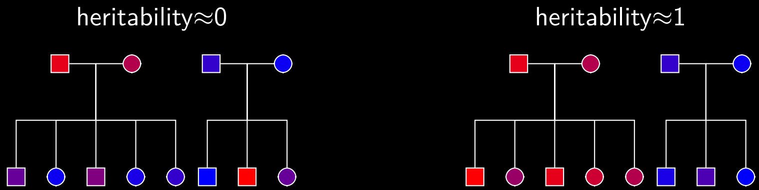


Breeding value

= Individual additive genetic value

Change with time = evolution

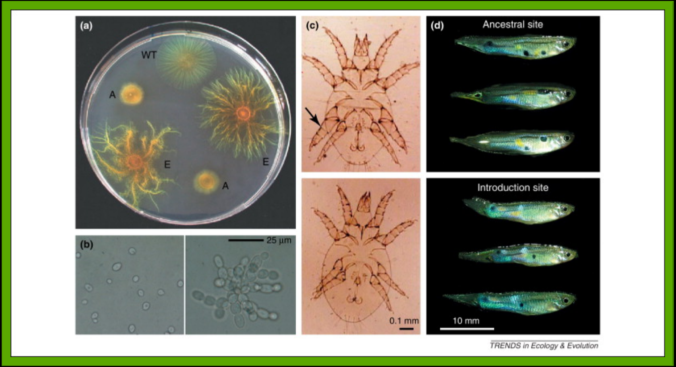
Adaptive evolution in the wild

Adaptive evolution in the wild

Adaptive evolution $=$ Selection $\times$ heritability

Adaptive evolution in the wild

Adaptive evolution $=$ Selection $\times$ heritability



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

Adaptive evolution in the wild

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

Adaptive evolution in the wild

Adaptive evolution $=$ Selection $\times$ 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 × heritability

2014

Evolutionary Applications

Open Access

Evolutionary Applications ISSN 1752-4571

PERSPECTIVE

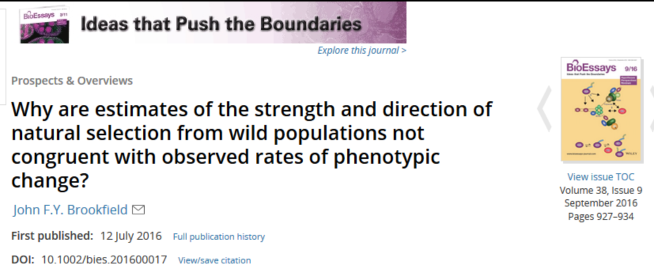
Climate change, adaptation, and phenotypic plasticity: the problem and the evidence

Juha Merilä[1,*] and Andrew P. Hendry[2,*]

Adaptive evolution in the wild

Adaptive evolution = Selection × heritability

2016


Ideas that Push the Boundaries

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Prospects & Overviews

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

John F.Y. Brookfield

First published: 12 July 2016 Full publication history

DOI: 10.1002/bies.201600017 View/save citation

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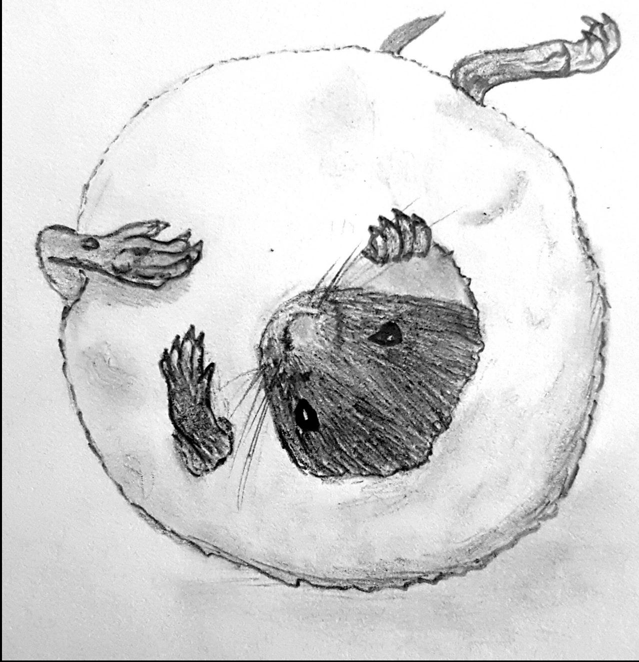
Volume 38, Issue 9
September 2016
Pages 927–934



Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white

Snow vole (*Chionomys nivalis*, Martins 1842)

- NOT white
- Rock-dweller

Snow vole (*Chionomys nivalis*, Martins 1842)

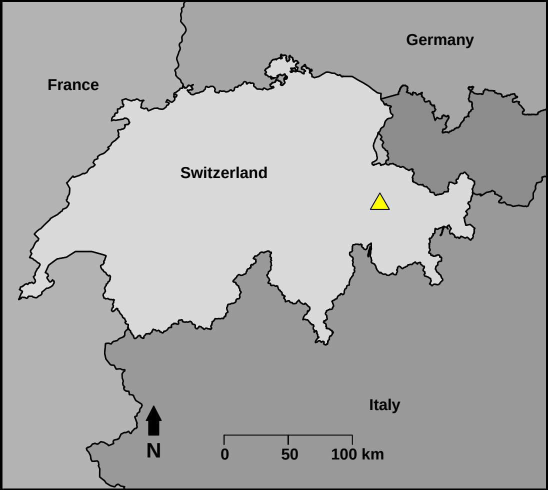
- NOT white
- Rock-dweller
- 30-45g

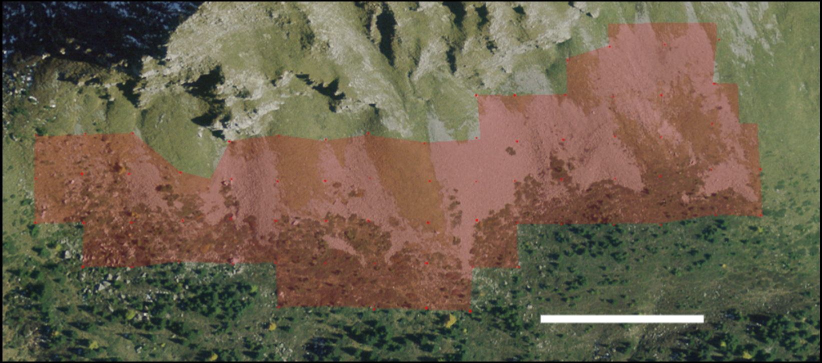
Snow vole (*Chionomys nivalis*, Martins 1842)

- 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
N
0
50
100 km



What we measure

What we measure

- Morphology
  - Body mass
  - Body length
  - Tail length

What we measure

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

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  - Sex identification
  - Any genotyping

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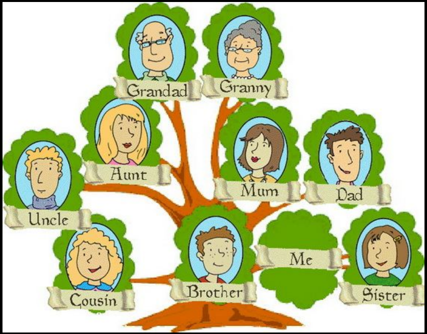
  - **Pedigree**



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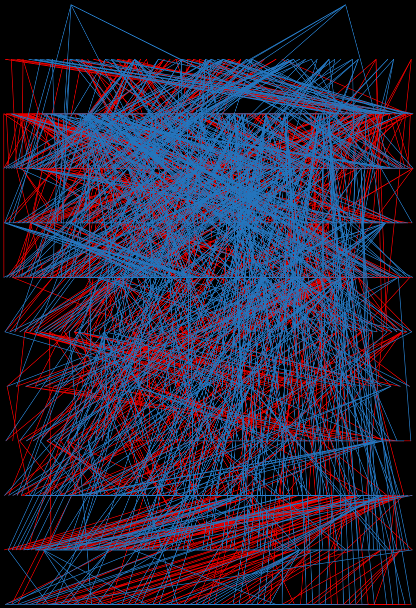
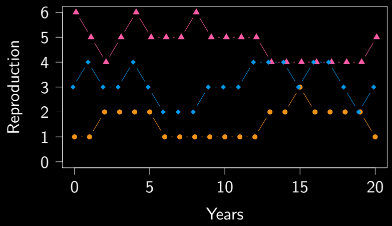


Are snow vole evolving? Why?

Variance in fitness?

Adaptive evolution in the snow vole?

Variance in fitness?

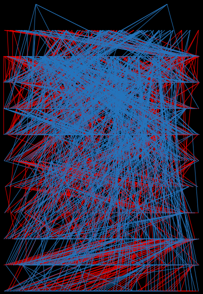


	Estimate	95% CI	p-value
Latent variance in survival	0	[0;0.248]	0.50
Latent variance in reproduction	0.37	[0.25, 0.49]	$< 10^{-16}$

Adaptive evolution in the snow vole?

- Non random variation fitness components

Variance in fitness?



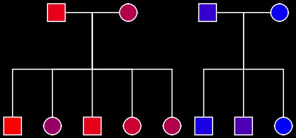
Relative lifetime reproductive success

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

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

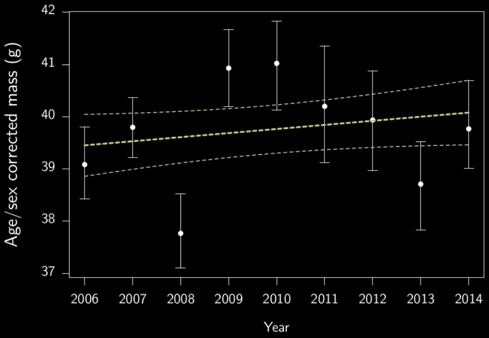
- Selection $= +0.86$g (p$< 10^{-3}$)
- Heritability $= 20\%$ (p$< 10^{-3}$)
- Response $=$ Selection $\times$ heritability $= +\ 0.22$g/year

Evolution of body mass

Prediction

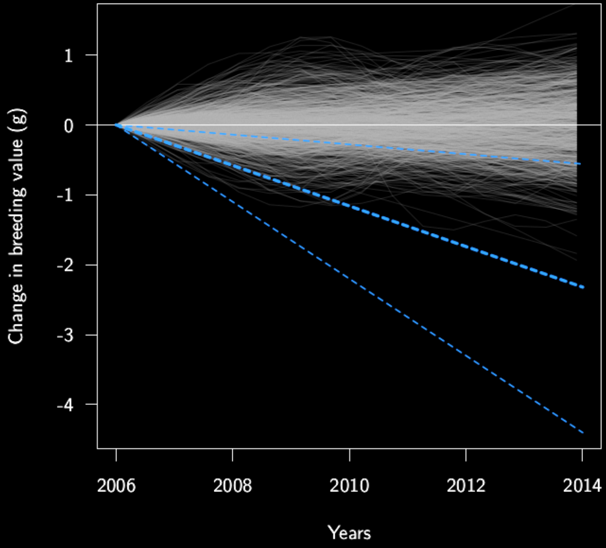
- Selection $= +0.86$g (p$< 10^{-3}$)
- Heritability $= 20\%$ (p$< 10^{-3}$)
- Response $=$ Selection $\times$ heritability $= +\ 0.22$g/year

Phenotypic observation



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

Estimation of genetic change



Evolution of body mass

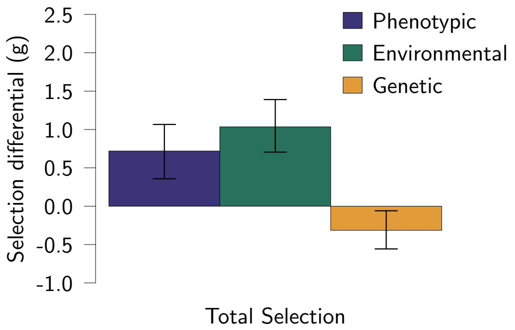
Evolution Paradox

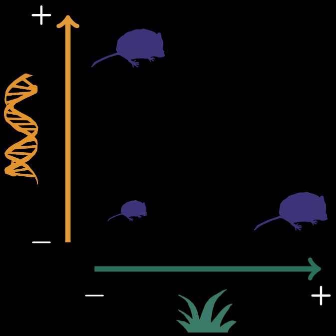
- Apparent selection for higher mass
- Adaptive evolution for lower mass

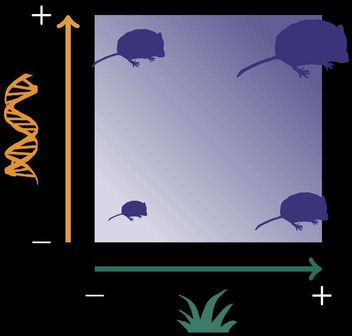
Evolution of body mass

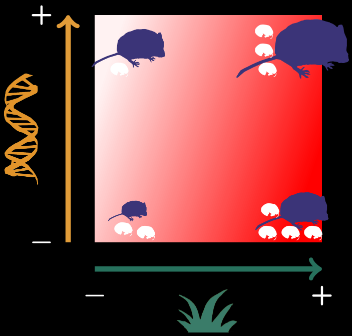
Evolution Paradox

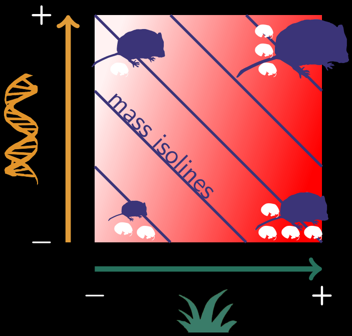
- Apparent selection for higher mass
- Adaptive evolution for lower mass



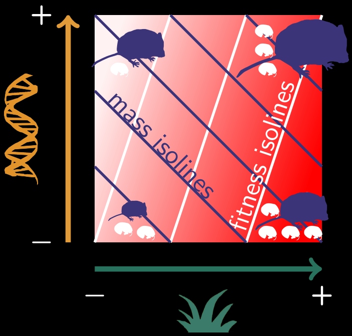


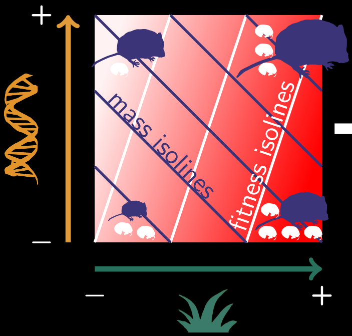


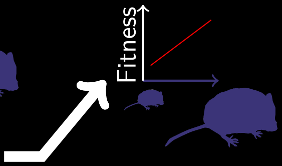


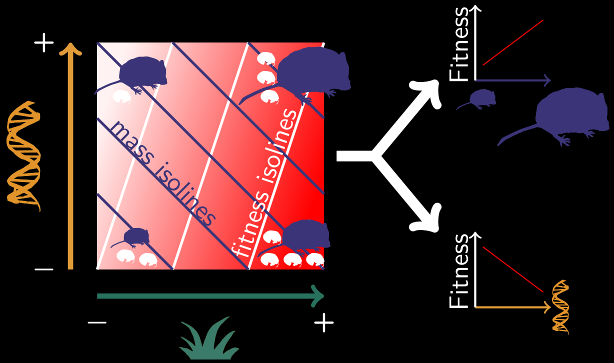


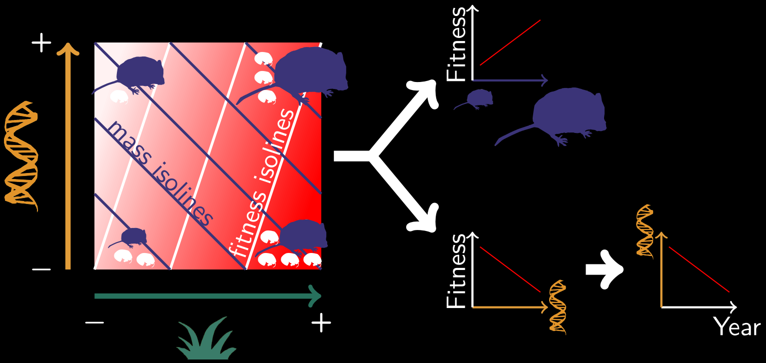
+
−
mass isolines
−
+


+
mass isolines
fitness isolines
−
−
+

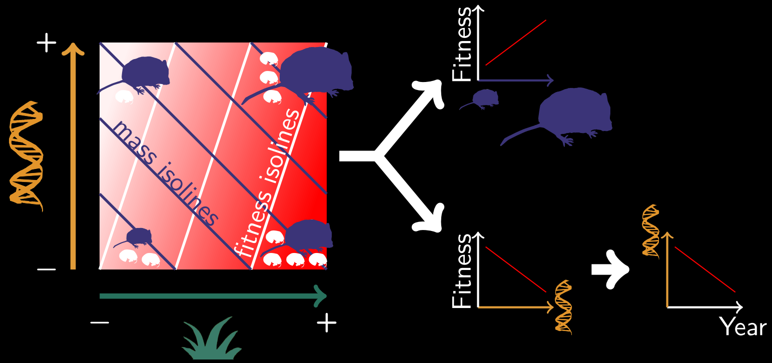

+
–
mass isolines
fitness isolines
–
+


Fitness


+
−
mass isolines
fitness isolines
−
+
Fitness
Fitness

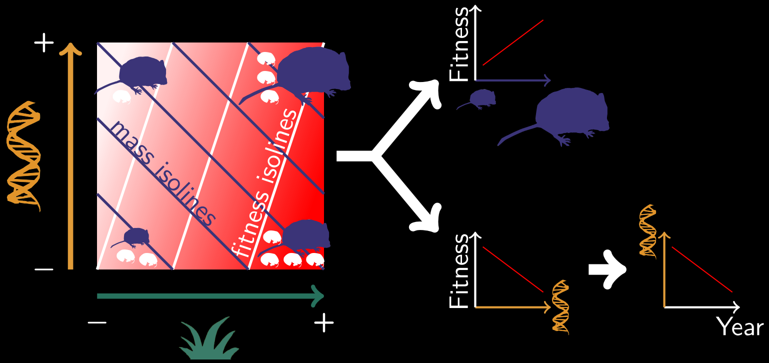


+
–
mass isolines
fitness isolines
–
+
Fitness
Fitness
Year



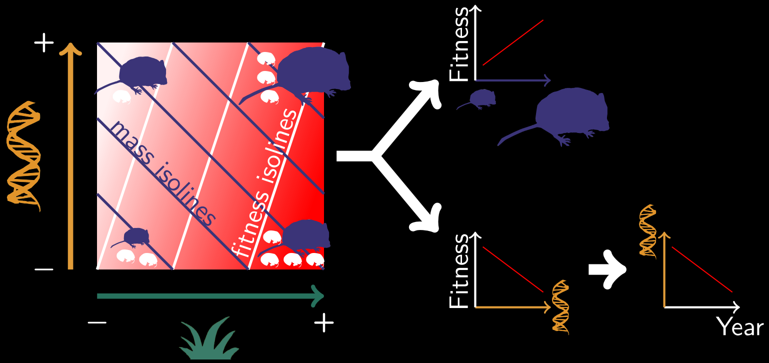
Summary

1. Apparent stasis. . .



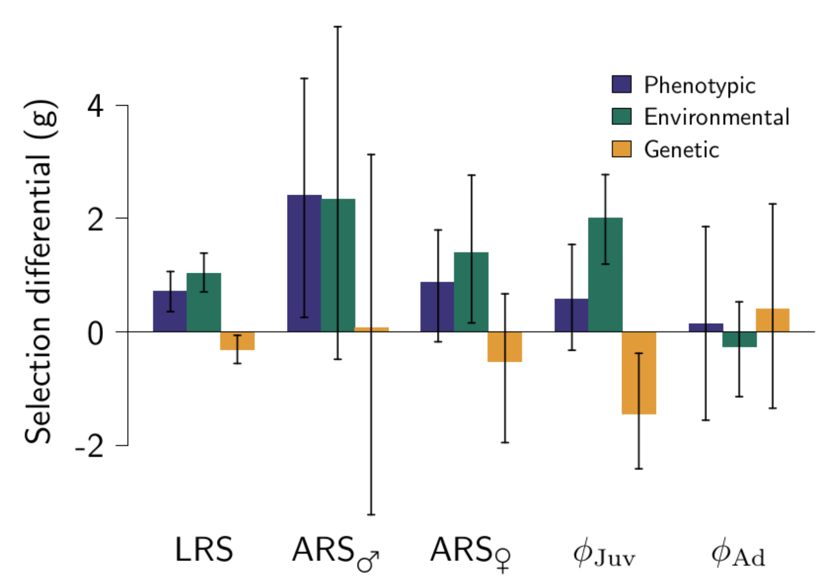
Summary

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



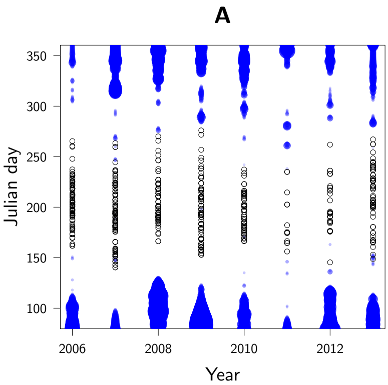
Summary

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

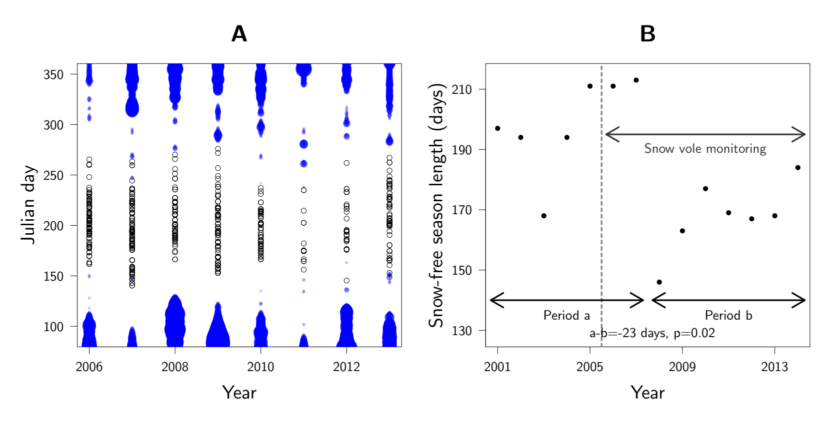


Phenotypic
Environmental
Genetic
Selection differential (g)
4
2
0
-2
LRS
ARS♂
ARS♀
ϕ_{Juv}
ϕ_{Ad}

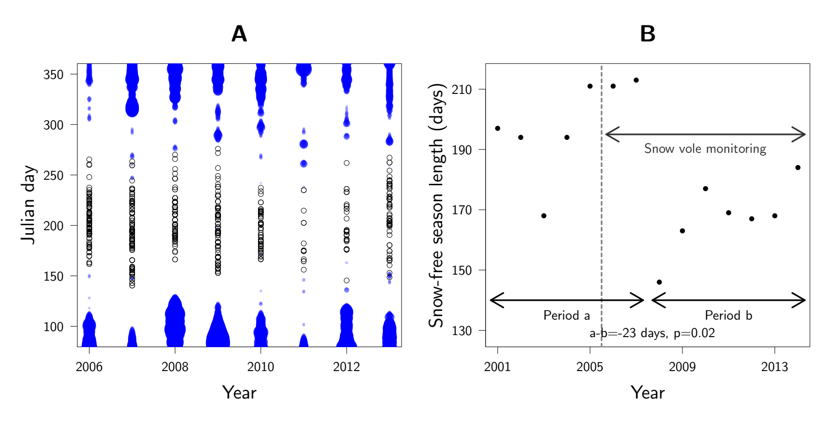
Snow falls and ontogeny



Snow falls and ontogeny



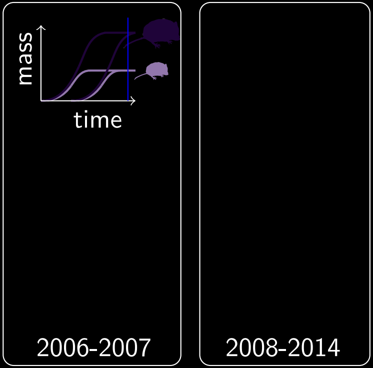
Snow falls and ontogeny



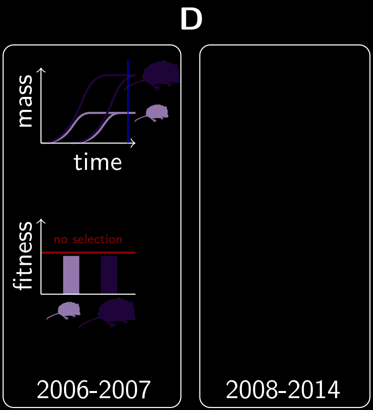
Less time to grow → Selection for smaller voles?

Selection during ontogeny?

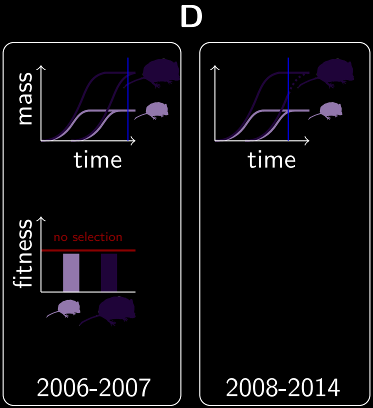
D



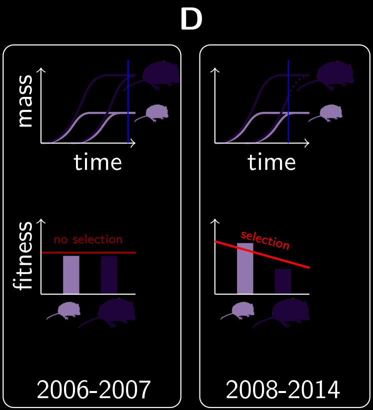
Selection during ontogeny?



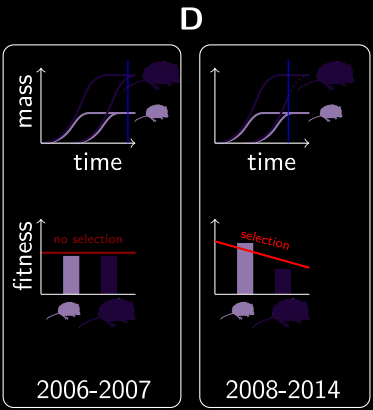
Selection during ontogeny?

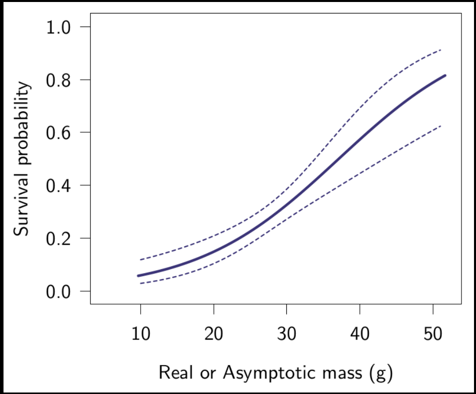


Selection during ontogeny?

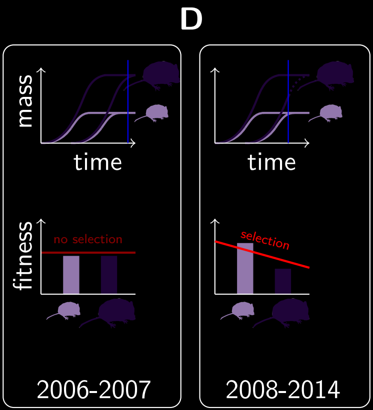


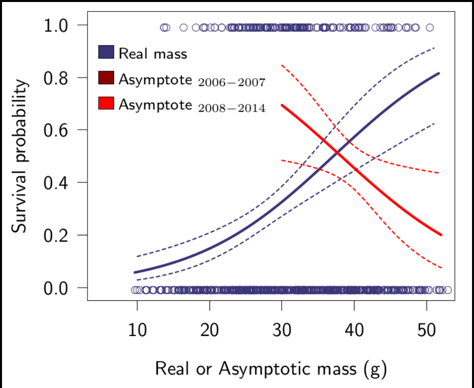
Selection during ontogeny?



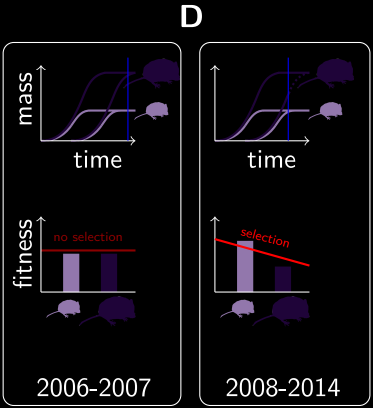


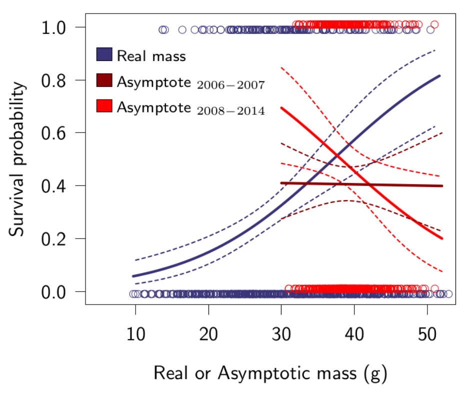
Selection during ontogeny?



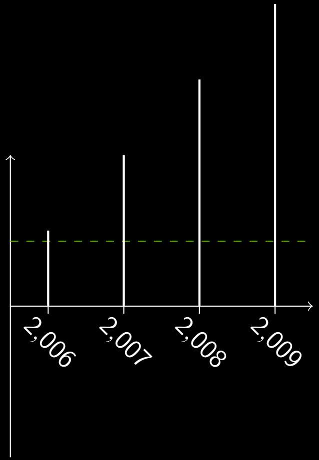


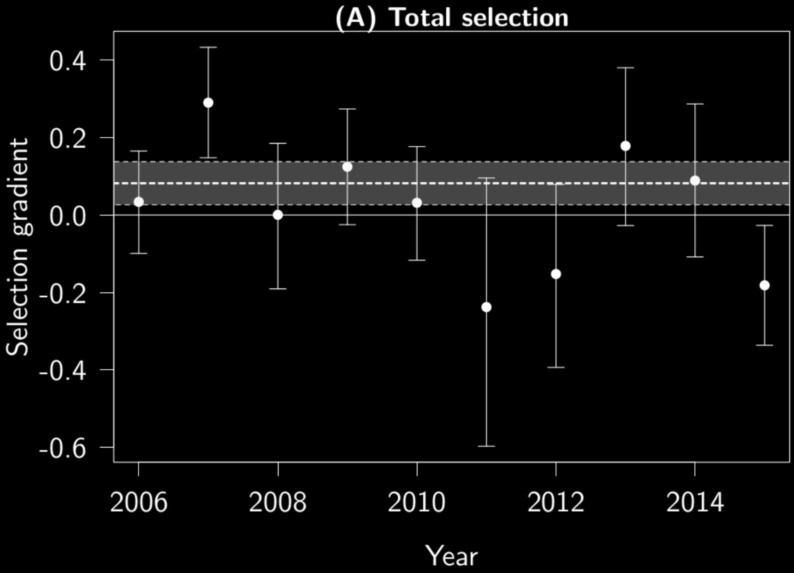
Selection during ontogeny?

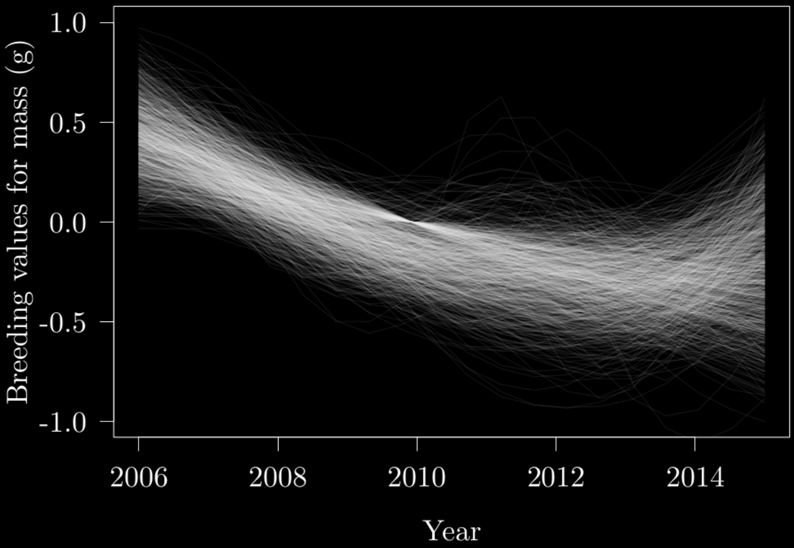




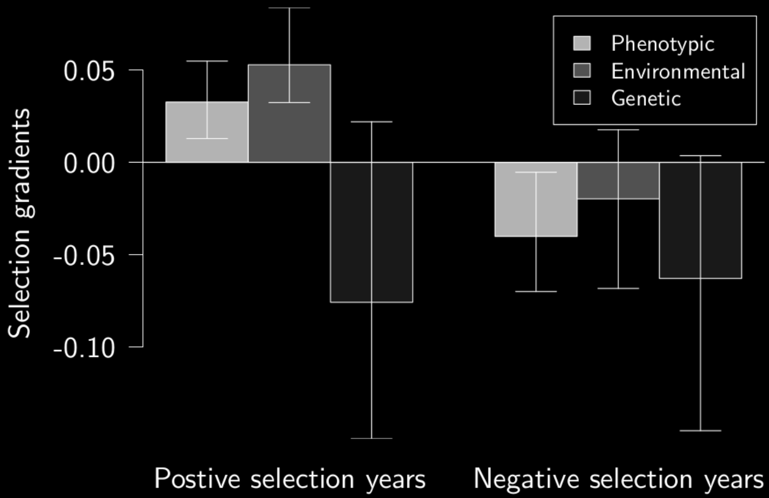
Do selection and evolution fluctuate?


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


(A) Total selection
0.4
0.2
0.0
-0.2
-0.4
-0.6
Selection gradient
2006
2008
2010
2012
2014
Year


Breeding values for mass (g)
1.0
0.5
0.0
-0.5
-1.0
2006
2008
2010
2012
2014
Year

Dynamics of selection VS. evolution



What is left?