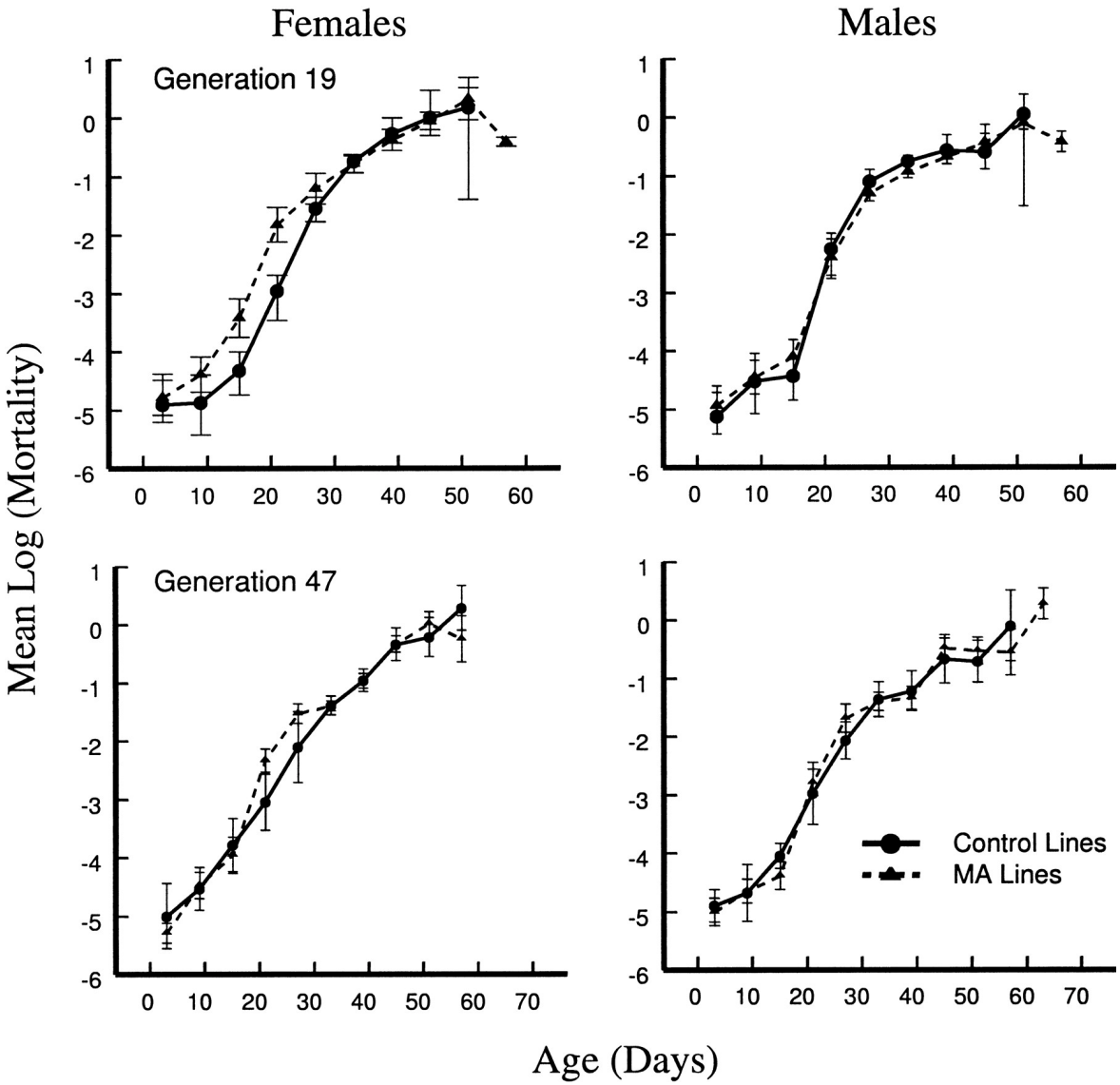
Evolution of functional traits
(Joel Kingsolver, Biology)

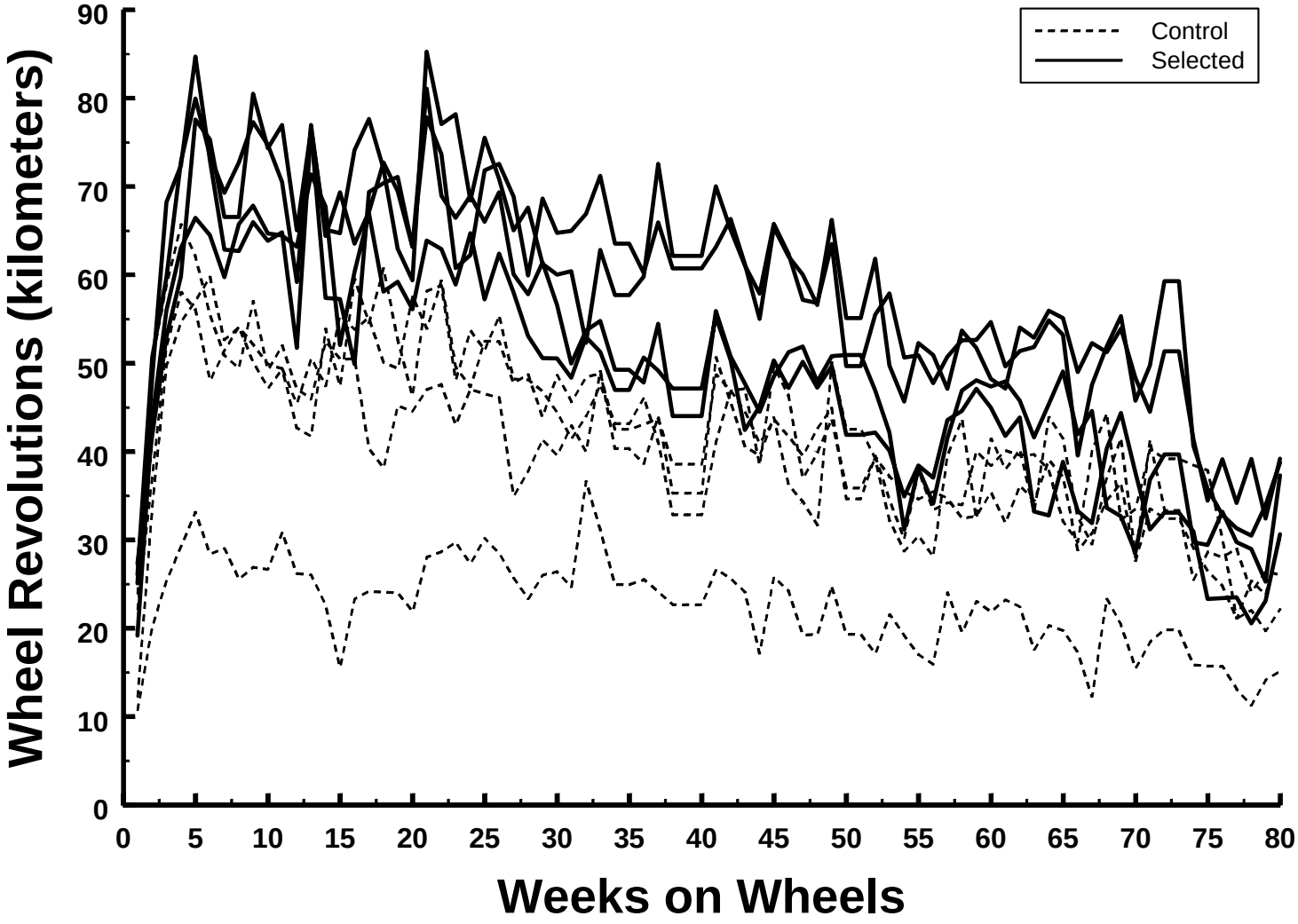
- Traits as functions: functional, function-valued, infinite-dimensional
- A primer in evolutionary models:
  - Variation, inheritance, selection, evolution
- Approaches to analysing functional traits:
  - understanding genetic variation
  - Estimating selection
  - Predicting evolutionary responses & constraints

Examples of functional traits

- Functions of age:
  - growth trajectories; life history; aging
- Functions of environmental state:
  - Physiological ‘reaction norms’
- Descriptions of 2-D or 3-D shape, etc

Age-specific mortality rates (*Drosophila*)
Pletcher et al, Genetics (1999)





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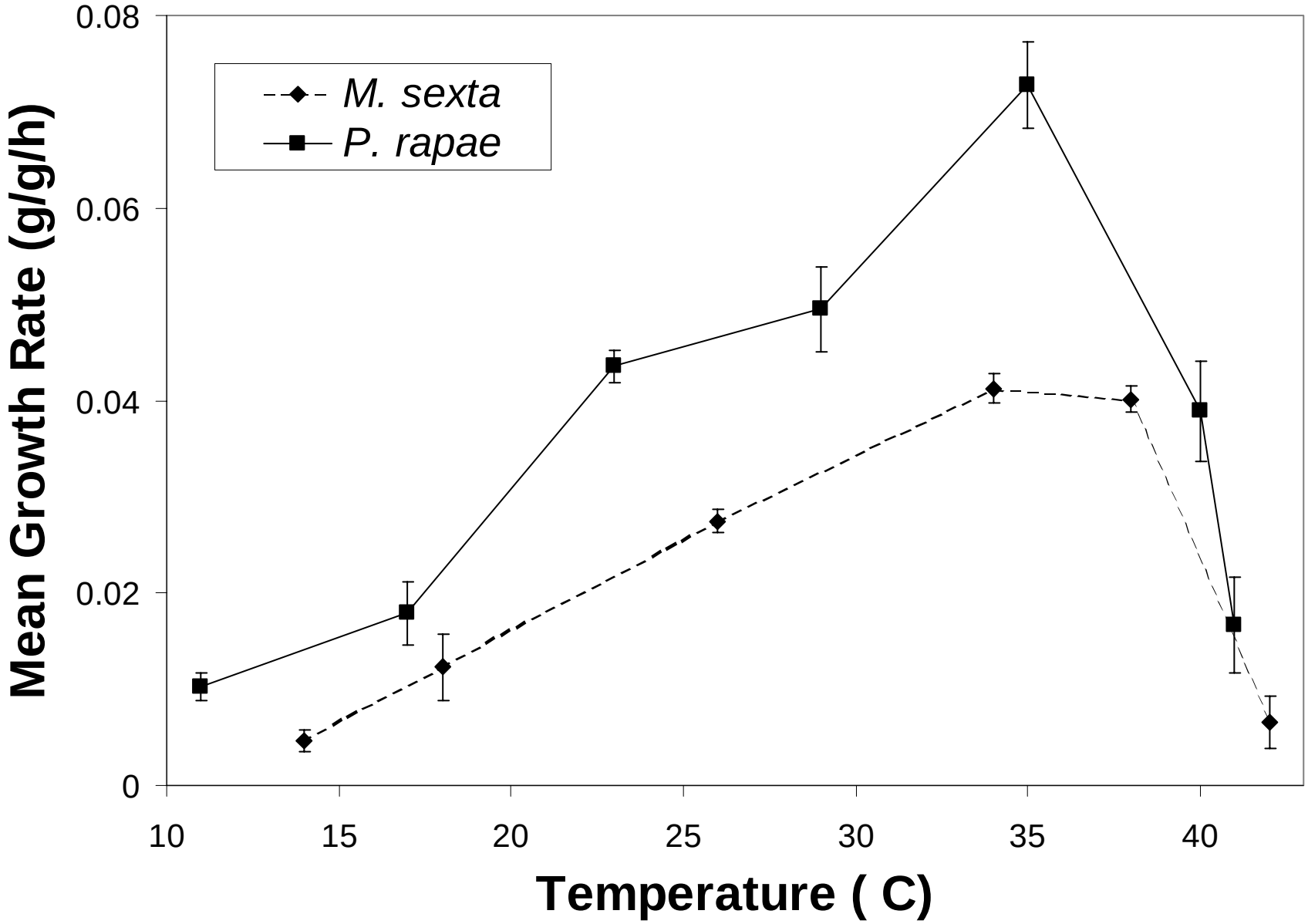
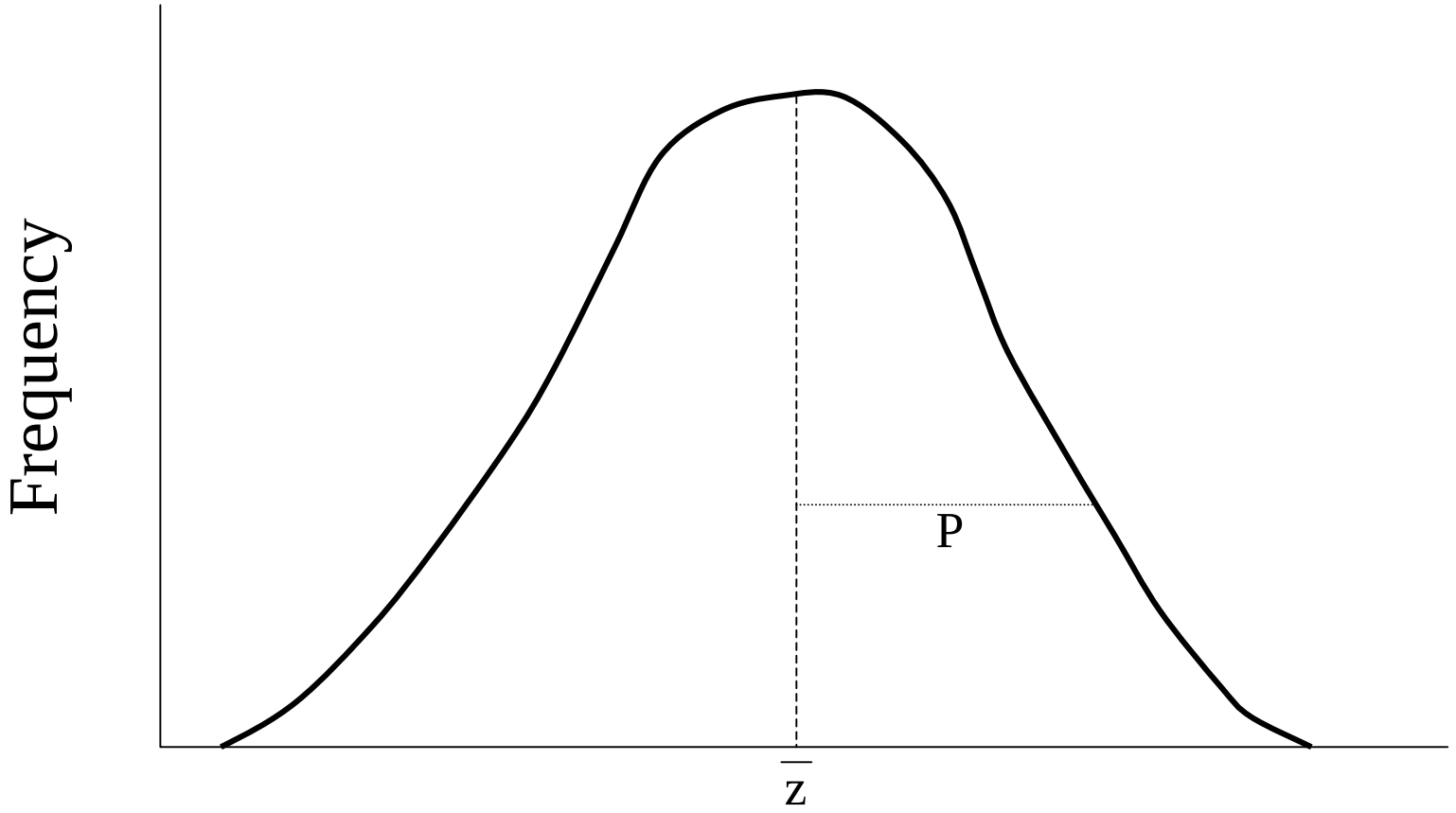

0.08
0.06
0.04
0.02
0
Mean Growth Rate (g/g/h)
M. sexta
P. rapae
10
15
20
25
30
35
40
Temperature (C)

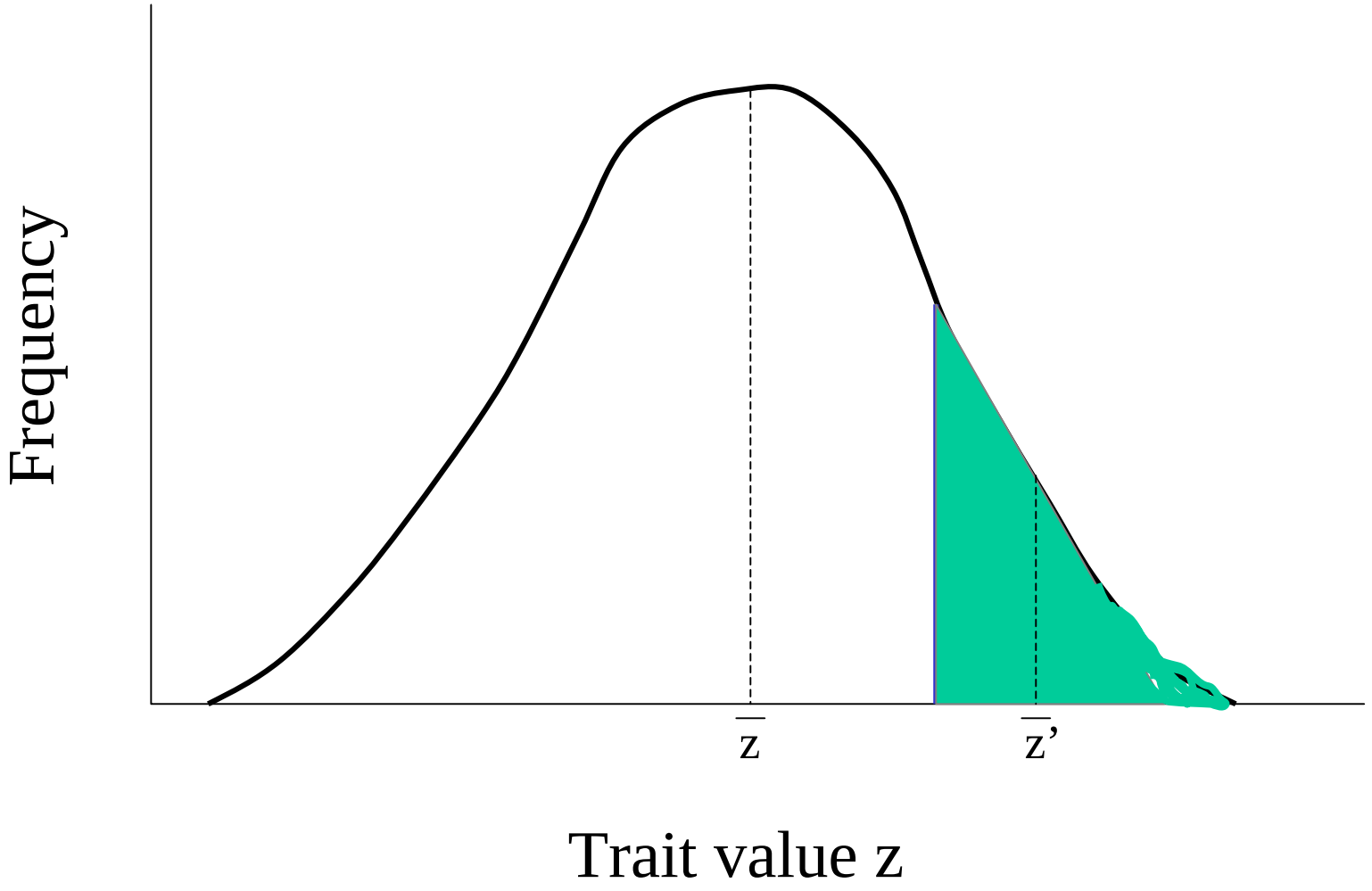
Evolution of quantitative traits: some basics

- Individual organism:
  - Phenotype: observable trait with value *z*
  - Genotype: genetic 'type' (usually inferred)
- Population:
  - Phenotypic variance, $P = G + E$
  - Genetic variance, G
- Evolution = change in mean trait value per generation, $\Delta\bar{z}$

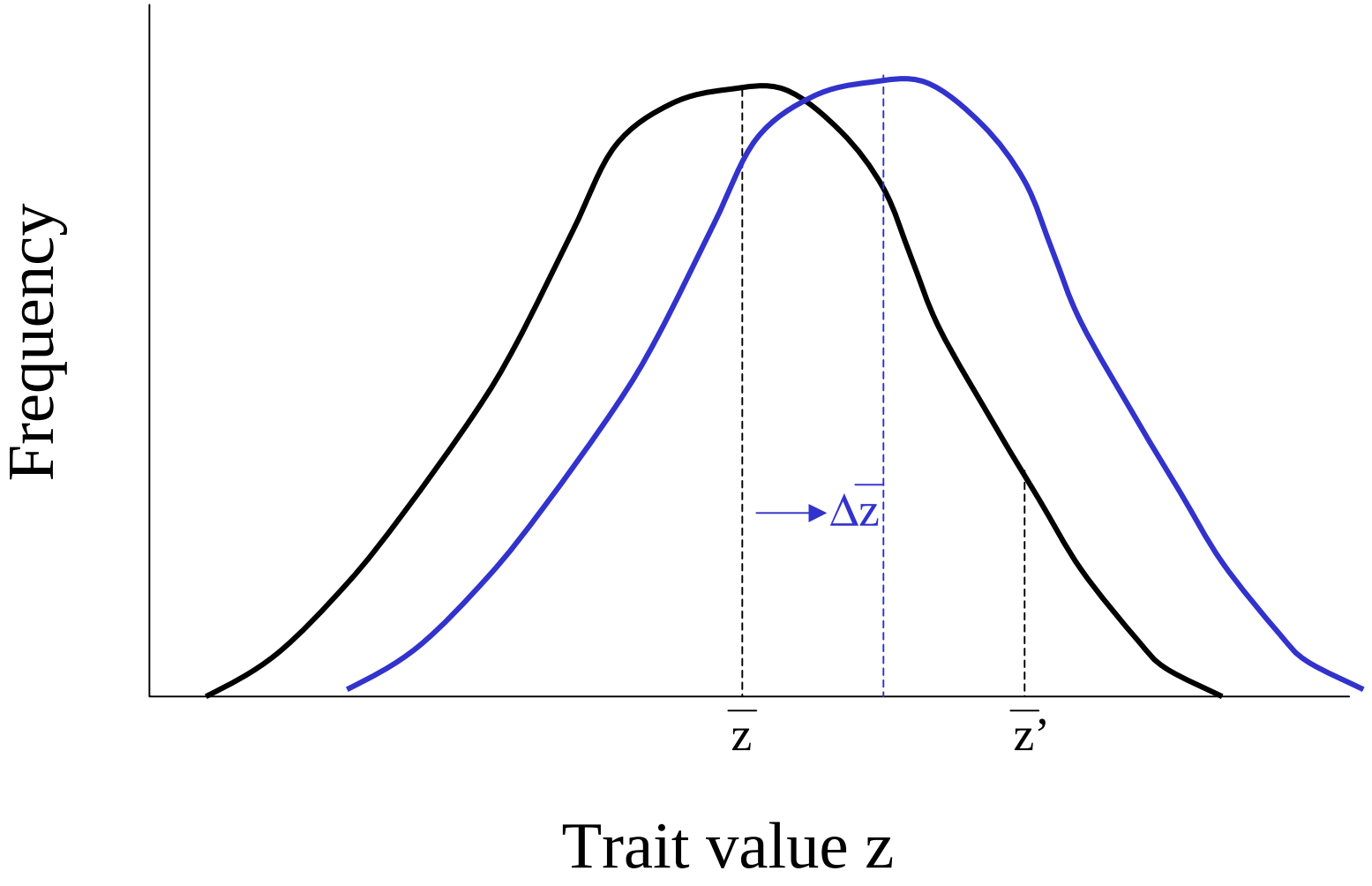
Evolution, in 3 easy steps



Evolution, in 3 easy steps (2)



Evolution, in 3 easy steps (3)

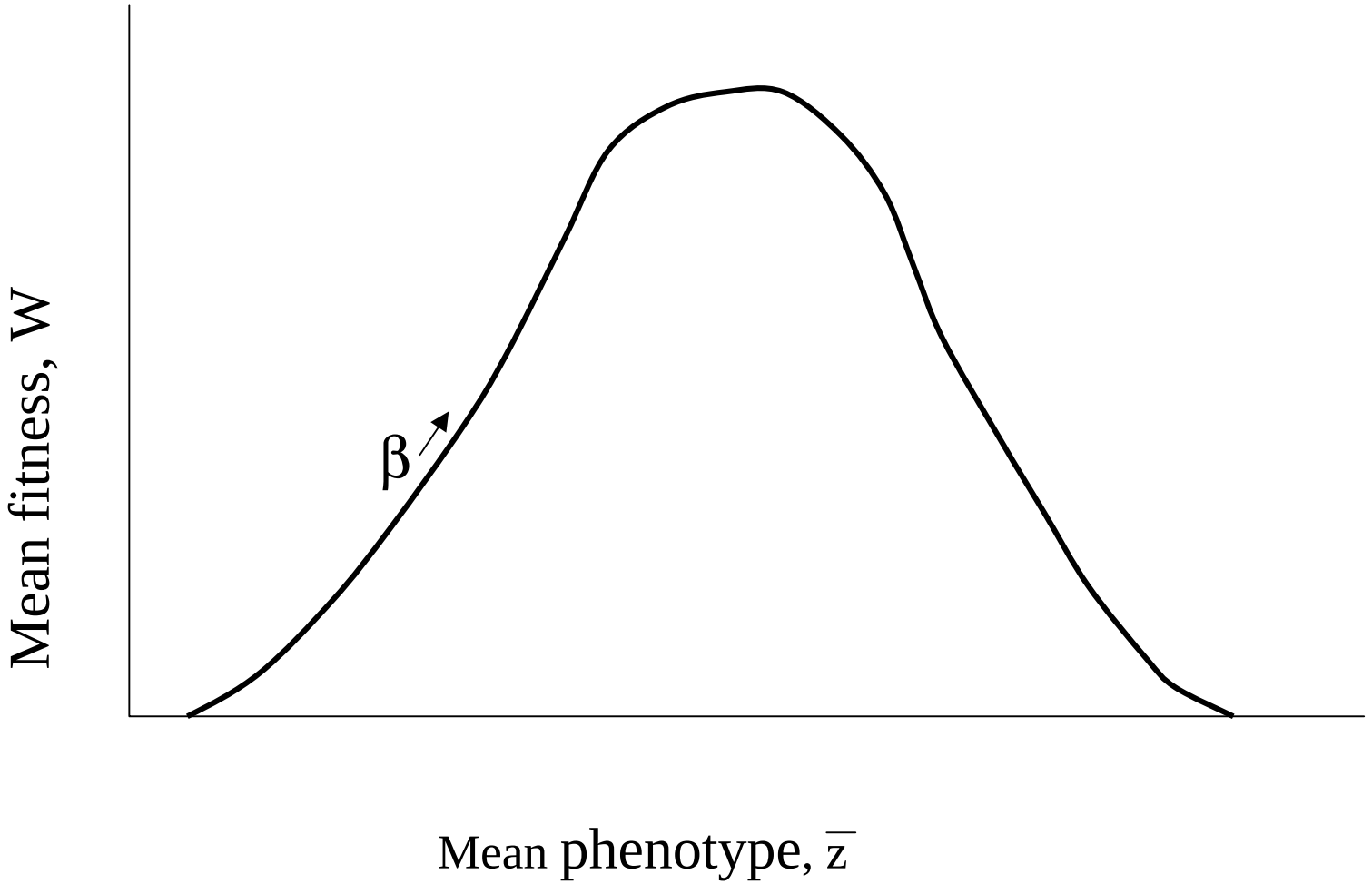


A simple evolutionary model

- Variation and inheritance
  - Variance: $P = G + E$
- Selection
  - Selection gradient: $\beta = P^{-1}(\bar{z}' - \bar{z})$
  - Also: $\beta = d[\ln(\bar{W})]/dz$, where $\bar{W}$ = mean population fitness
- Evolutionary response

  $\Delta\bar{z} = G \beta$

Evolution on an adaptive landscape



$$\Delta\bar{z} = G\,\beta$$

z may be:

- a scalar
- a vector
- a function

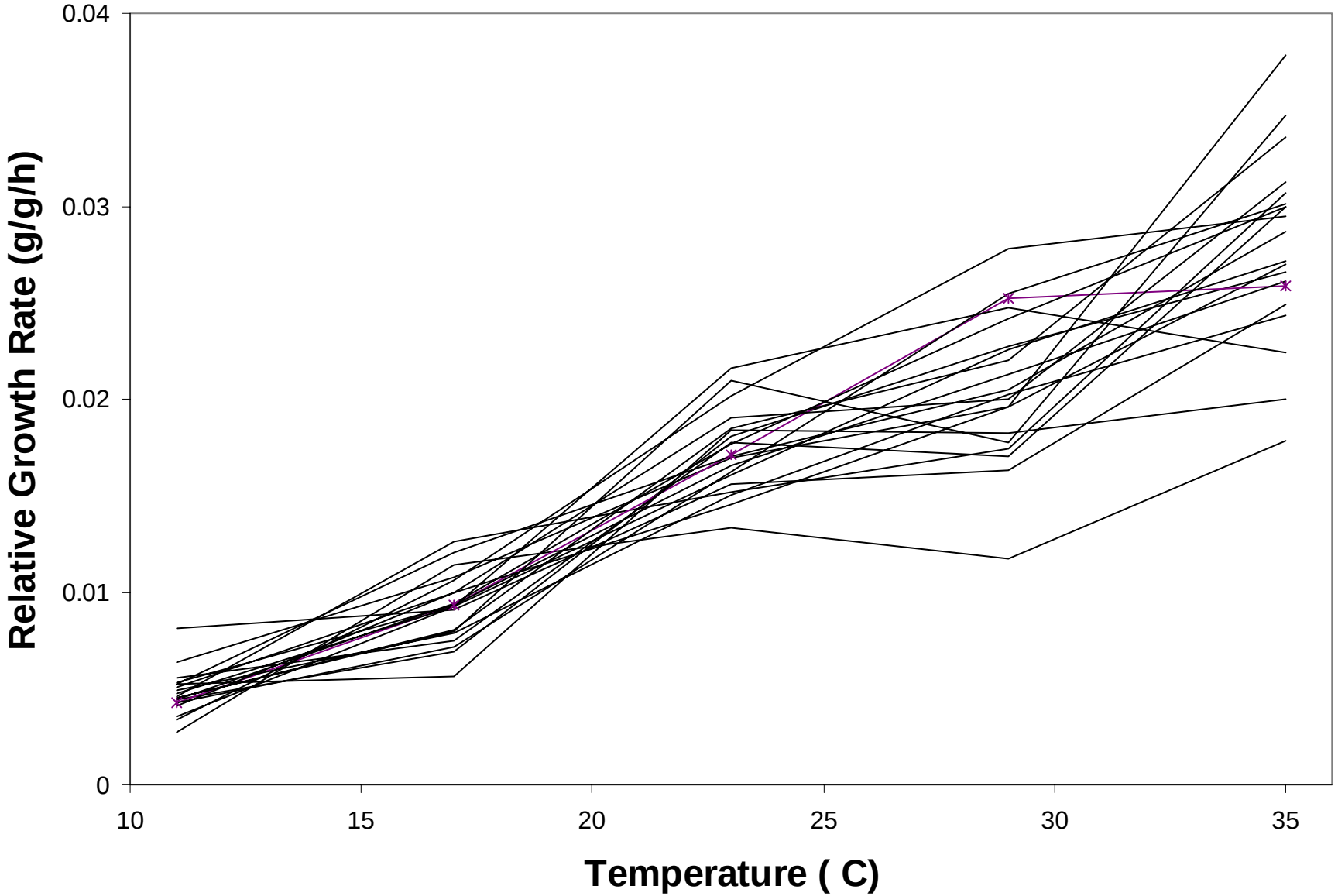
$$\Delta\bar{z}(t) = \int G(t,s)\,\beta(s)ds$$

Analysing genetics of functional traits

- Estimating G: an example
- Biological hypotheses about G: eigenfunction analysis
- G and the response to selection

Temperature & caterpillar growth rates: Thermal performance curves (TPCs)

z(t), where t = temperature

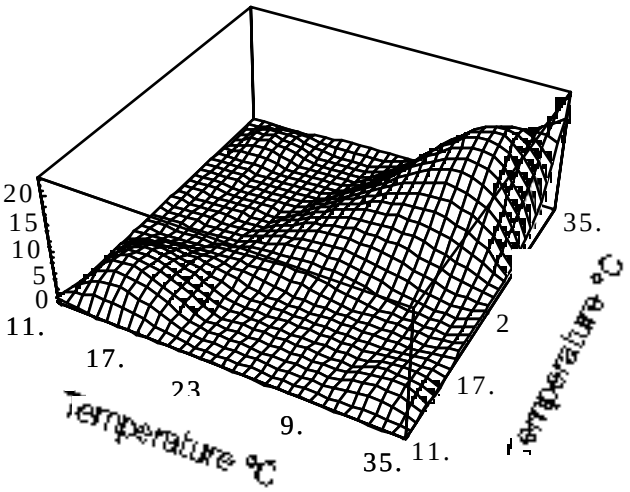

0.04
0.03
0.02
0.01
0
Relative Growth Rate (g/g/h)
10
15
20
25
30
35
Temperature (C)

GeneticVar-Cov for RGR

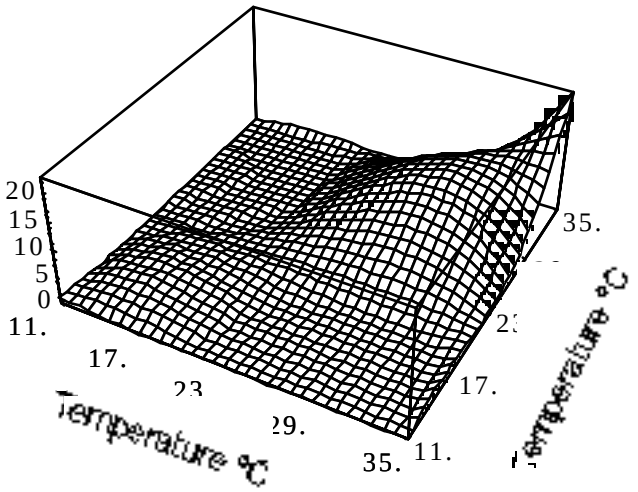
35	-0.214	0.735	1.613	3.947	**23.094**
29	-1.027	-1.026	3.725	**14.393**	3.947
23	0.043	-1.099	**4.505**	3.725	1.613
17	-0.229	**3.156**	-1.099	-1.026	0.735
11	**1.255**	-0.229	0.043	-1.027	-0.214
Temp	**11**	**17**	**23**	**29**	**35**

Genetic Covariance Function

Full Fit



Smooth Fit



Basis = orthogonal polynomials

Analysing genetics of functional traits

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- Biological hypotheses about G: eigenfunction analysis
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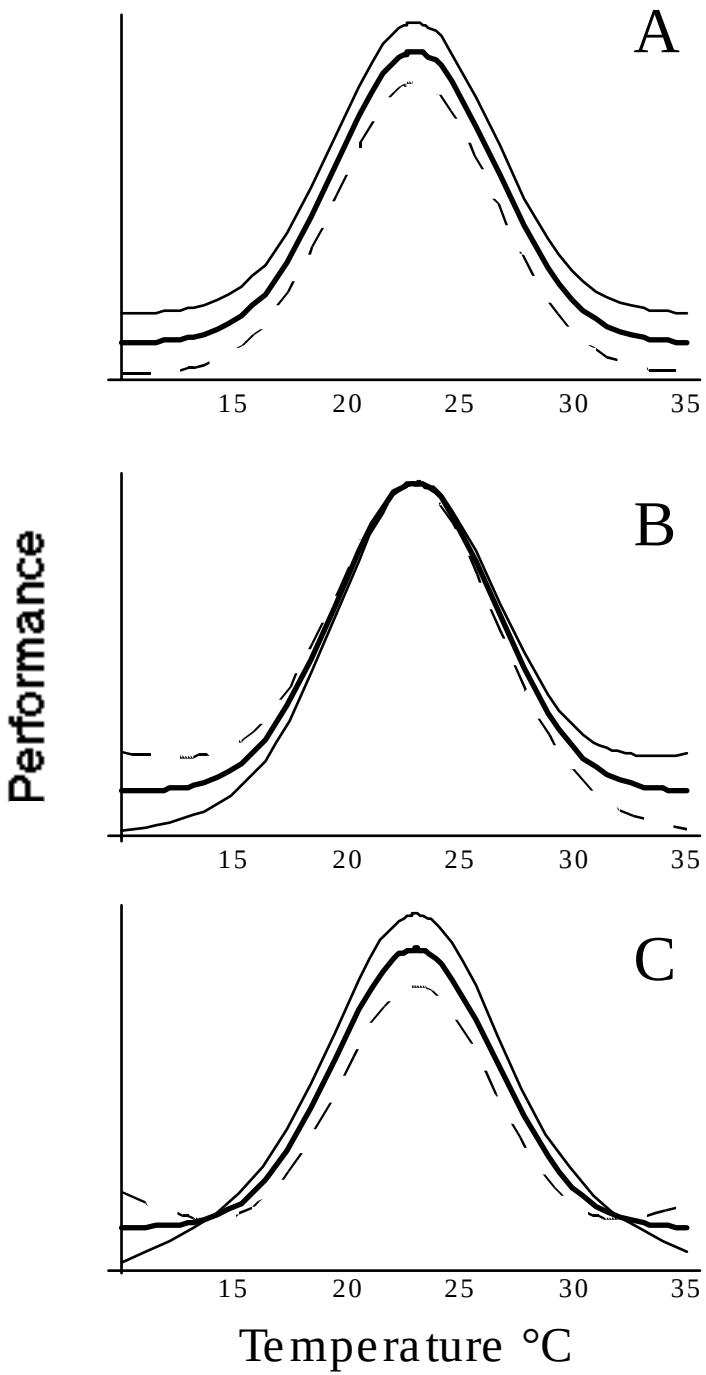
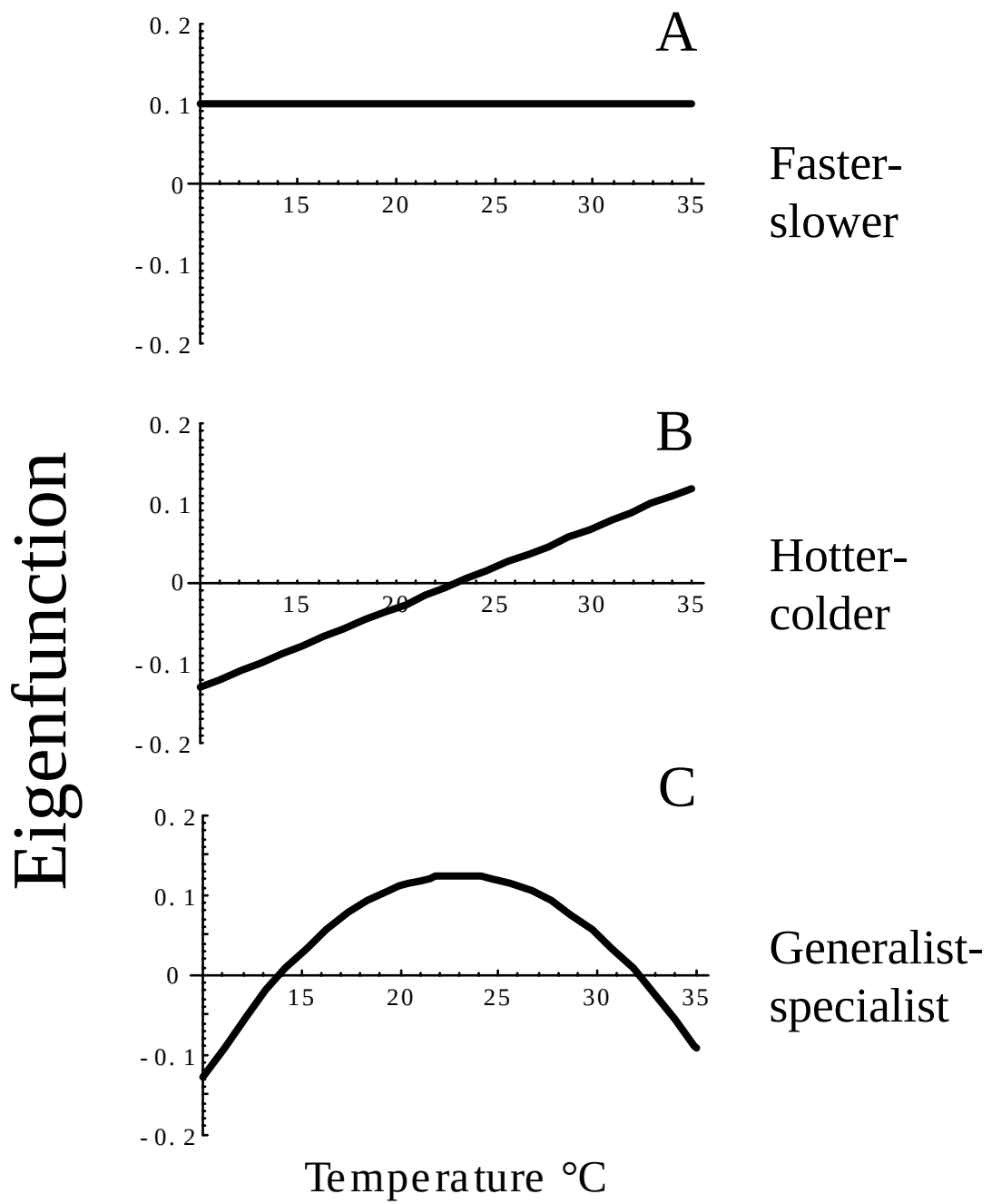


Faster-slower

Hotter-colder

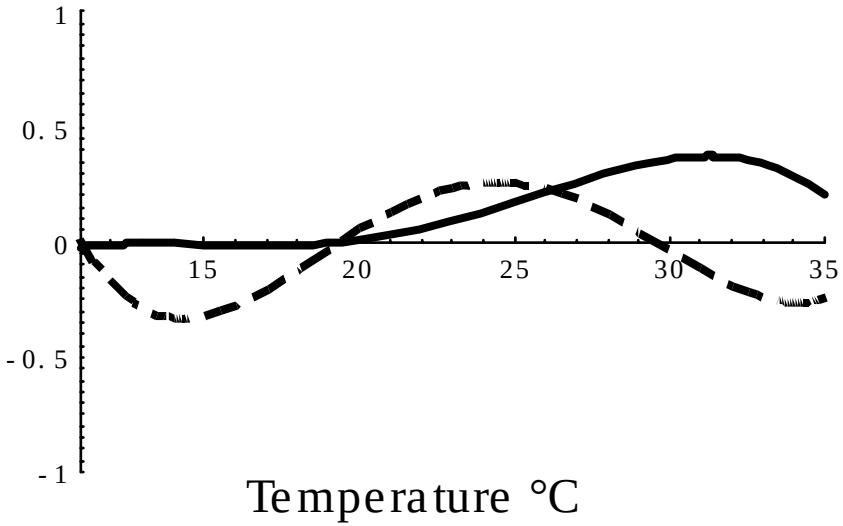
Generalist-specialist


A
B
C
0.2
0.1
0
-0.1
-0.2
15
20
25
30
35
Eigenfunction
Temperature °C
Faster-slower
Hotter-colder
Generalist-specialist

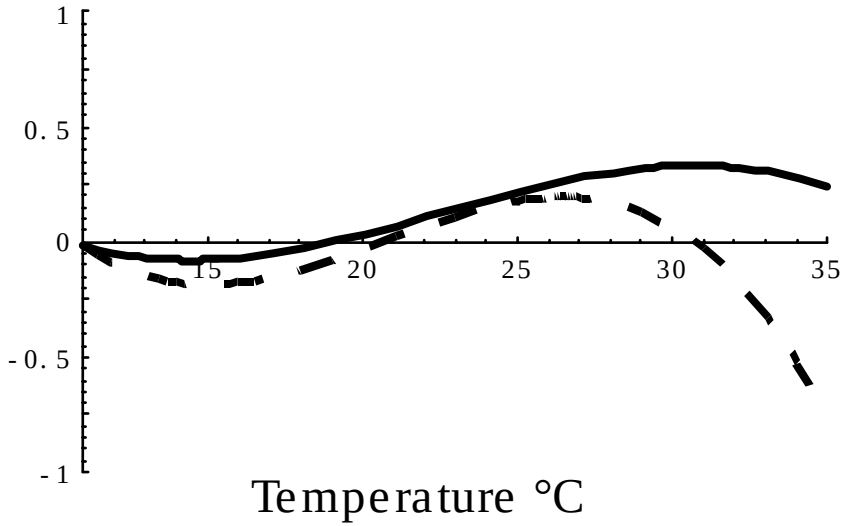
Caterpillar growth rates

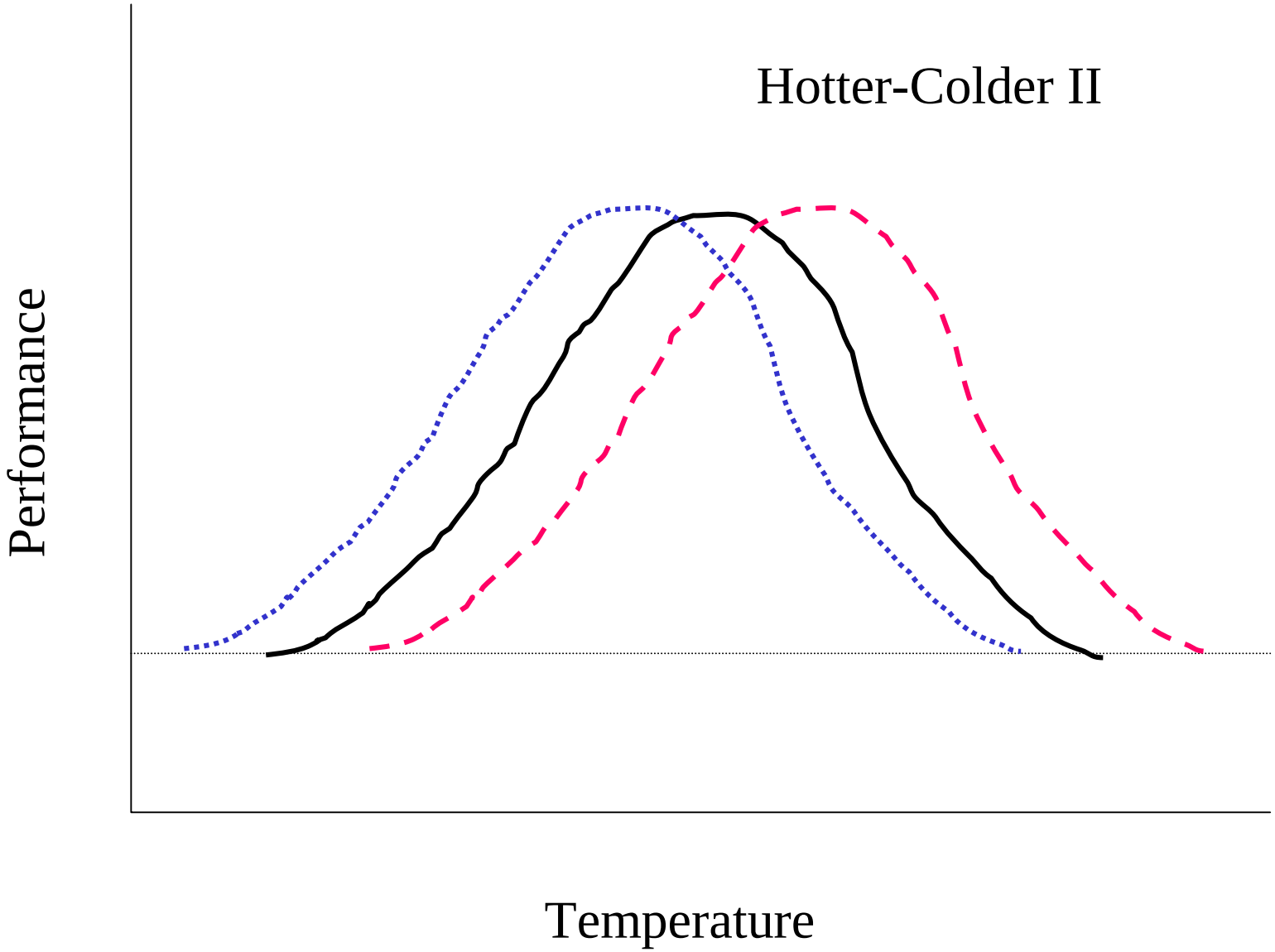
Leading and Second Eigenfunctions

Full Fit

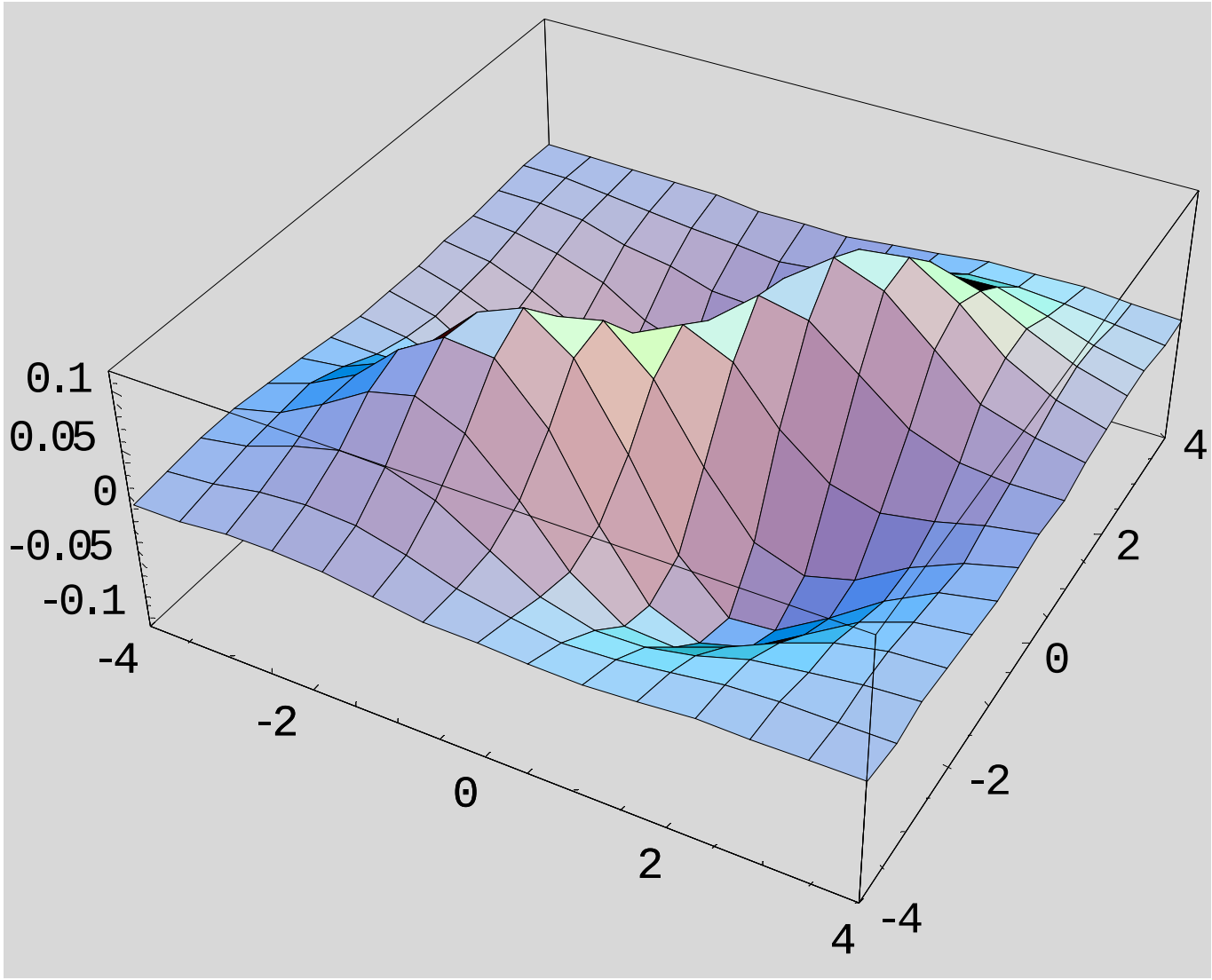


Smooth Fit

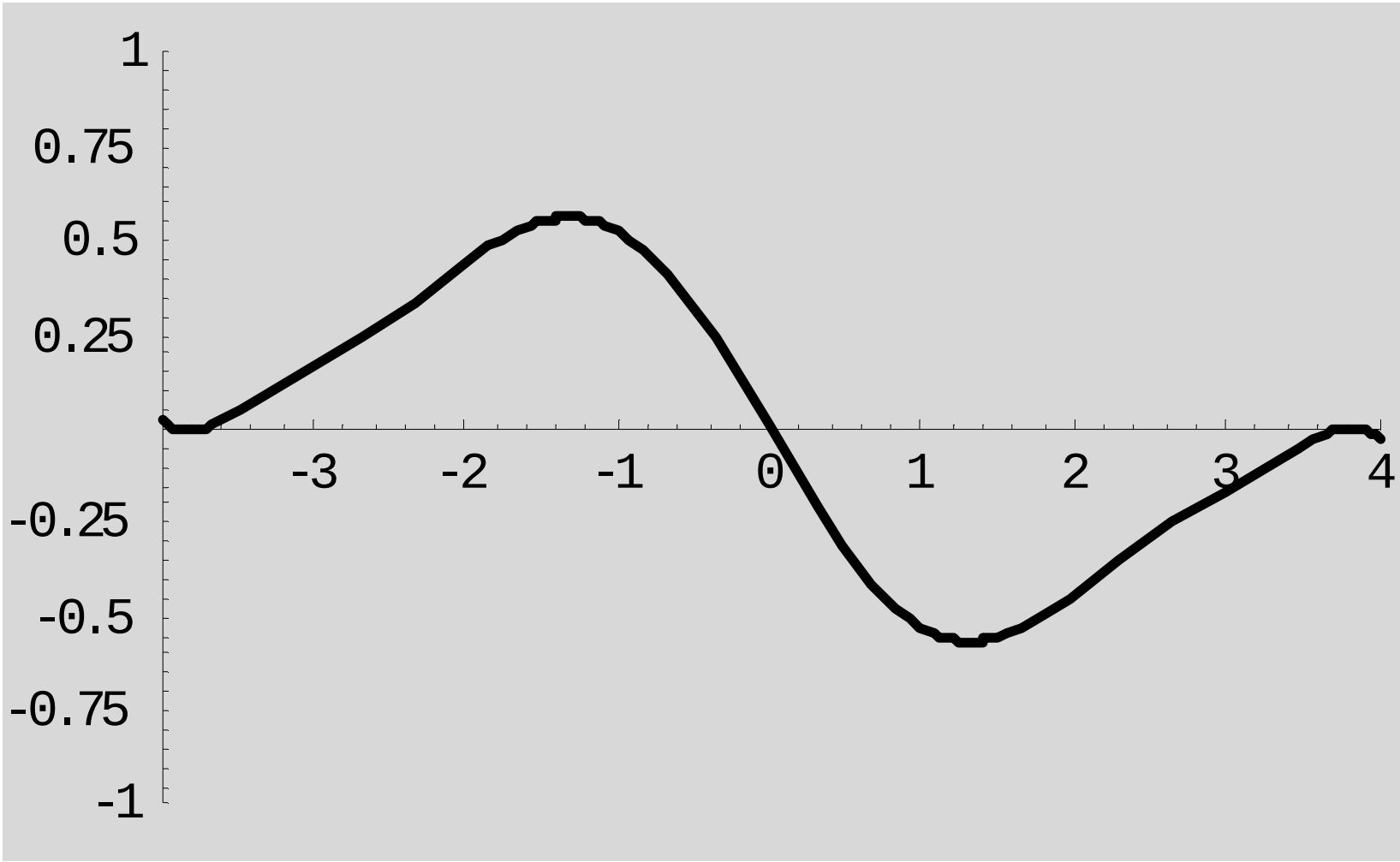



Hotter-Colder II
Performance
Temperature

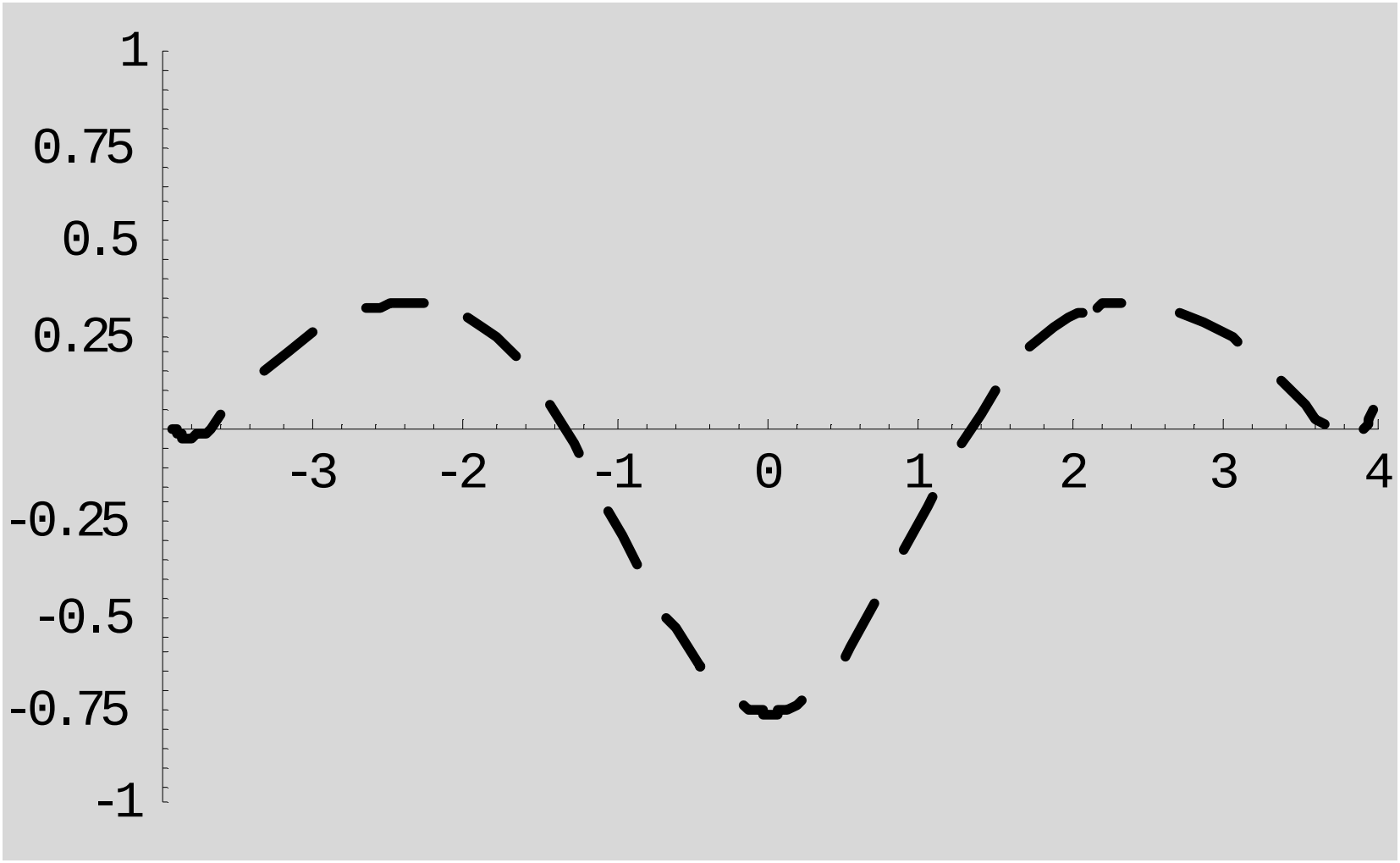
G-covariance function: Variation in TPC position



First eigenfunction (65%)

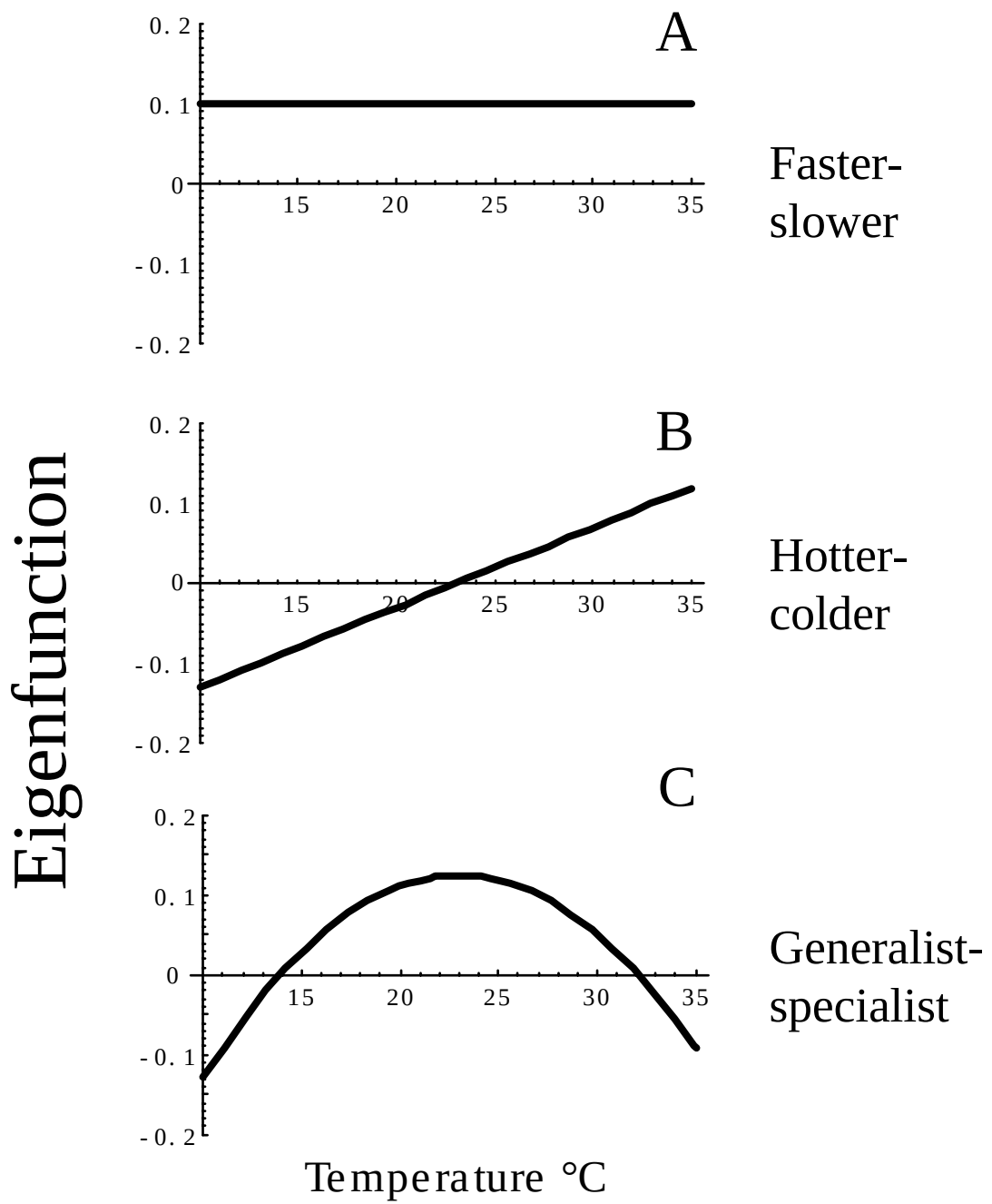


Second eigenfunction (25%)



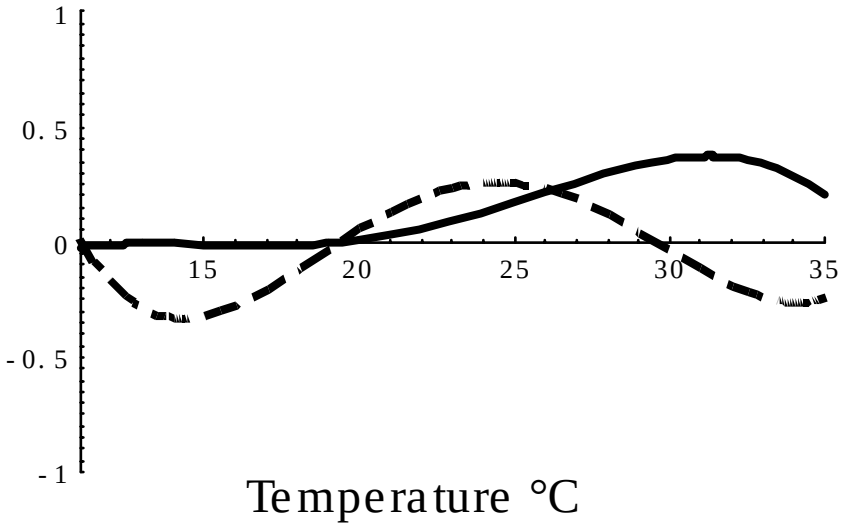
Analysing genetics of functional traits

- Estimating G: an example
- Biological hypotheses about G: eigenfunction analysis
- G and the response to selection
  - $\Delta\bar{z}(t) = \int G(t,s)\beta(s)ds$

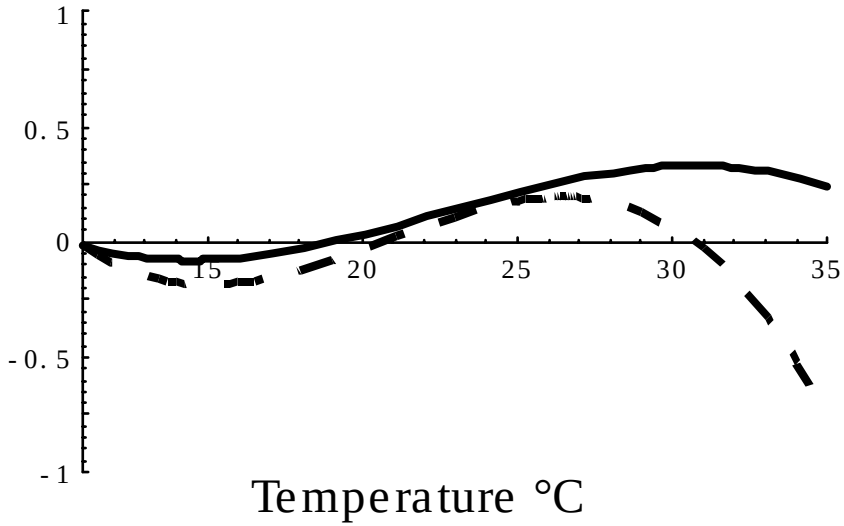

A
B
C
0.2
0.1
0
-0.1
-0.2
15
20
25
30
35
Eigenfunction
Temperature °C
Faster-slower
Hotter-colder
Generalist-specialist

Leading and Second Eigenfunctions

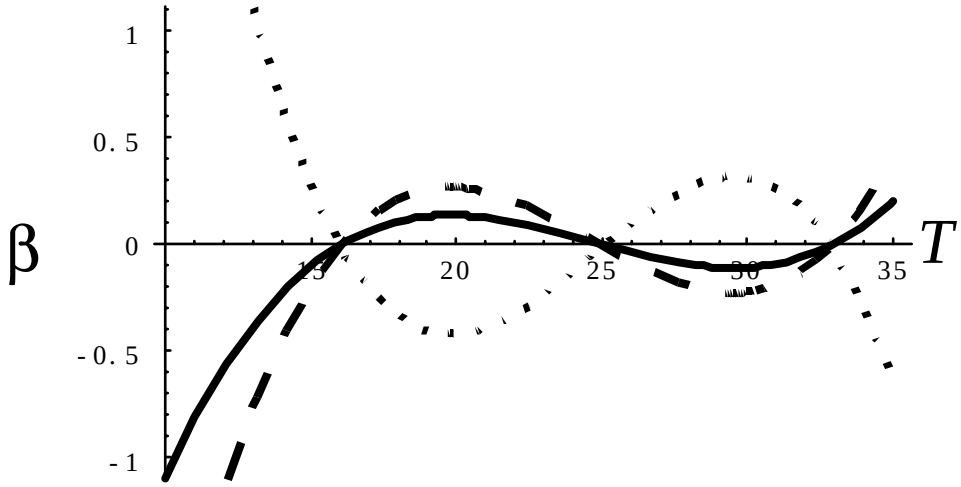
Full Fit



Smooth Fit



Evolutionary Constraints: Identifying zero eigenfunctions



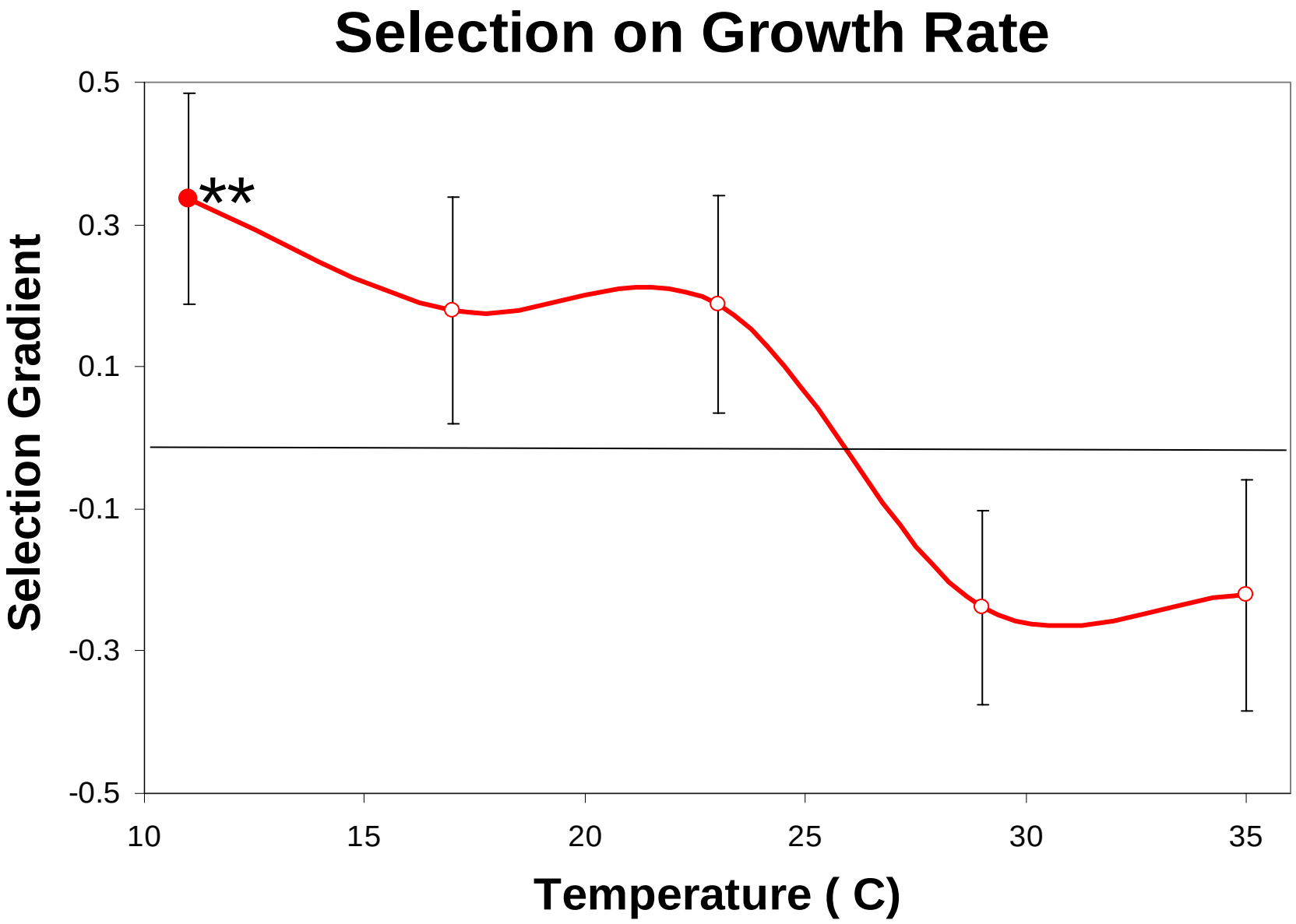
Selection and evolutionary response

- Estimating selection, β(s): an example
- Predicting evolutionary responses

$$\Delta\bar{z}(t) = \int G(t,s)\beta(s)ds$$

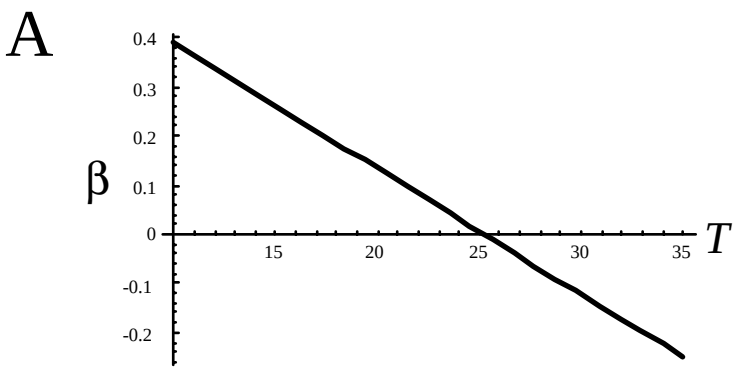
Selection on caterpillar growth rate TPCs

- Measure z(t) for a sample of individuals in the lab --> estimate P(s,t)
- Measure fitness of those individuals in the field
- Estimate $\beta(s)$ (cubic splines)

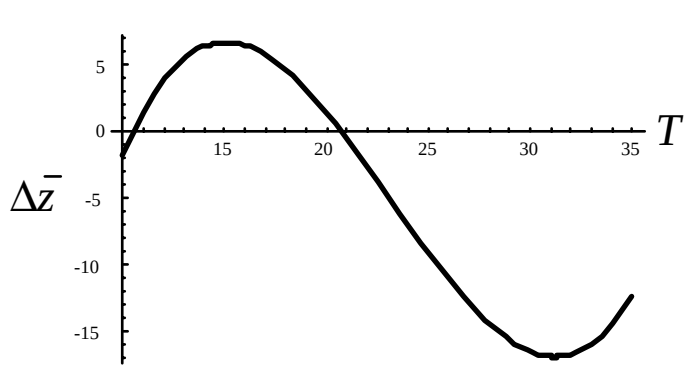

Selection on Growth Rate
Selection Gradient
0.5
0.3
0.1
-0.1
-0.3
-0.5
**
10
15
20
25
30
35
Temperature (C)

Evolutionary Response to Selection

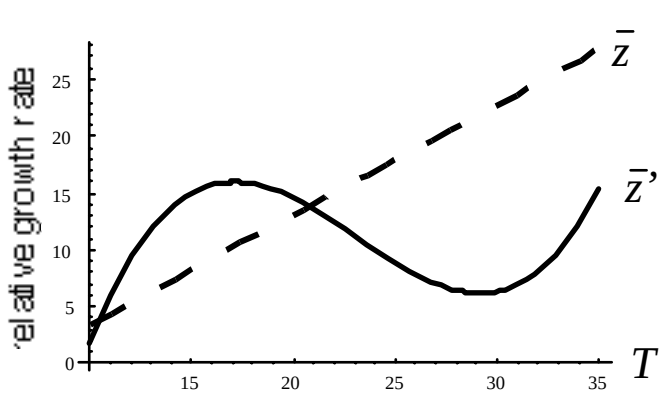
Selection



Evolutionary response



Evolutionary change in one generation



Challenges

- Estimation methods for G
- Hypothesis testing of eigenfunctions
- Estimating zero eigenfunctions
- Estimation methods for β
- Predicting evolutionary responses