

Modelling Phenotypic Plasticity

It's Plasphentastic

The relation between the vector of character states in n environments, $\mathbf{z}^T = (z_1 \dots z_n)$, and the coefficients of a polynomial function of order m (intercept, slope, etc.), $\mathbf{g}^T = (g_0 \dots g_m)$, for a genotype can be written in matrix form as:

$$\mathbf{z} = \mathbf{X}\mathbf{g} \quad (1)$$

TJM Van Dooren
tvdooren@gmail.com

Institute of Ecology and Environmental Sciences iEES Paris

Dept. Evolutionary Ecology
team Phenotypic Variability and Adaptation (VPA)

Overview of different ways individual states can be specified

Quantitative genetics: selection response with plasticity

Adaptive Dynamics: phenotypic plasticity as an adaptation

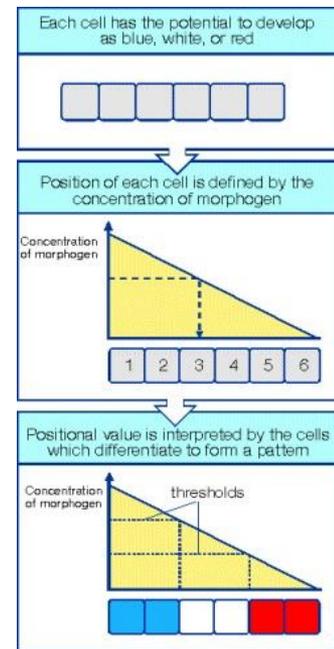
An overview of different ways to represent the dependence of phenotypes on the environment

& how they relate

The relation between the vector of character states in n environments, $\mathbf{z}^T = (z_1 \dots z_n)$, and the coefficients of a polynomial function of order m (intercept, slope, etc.), $\mathbf{g}^T = (g_0 \dots g_m)$, for a genotype can be written in matrix form as:

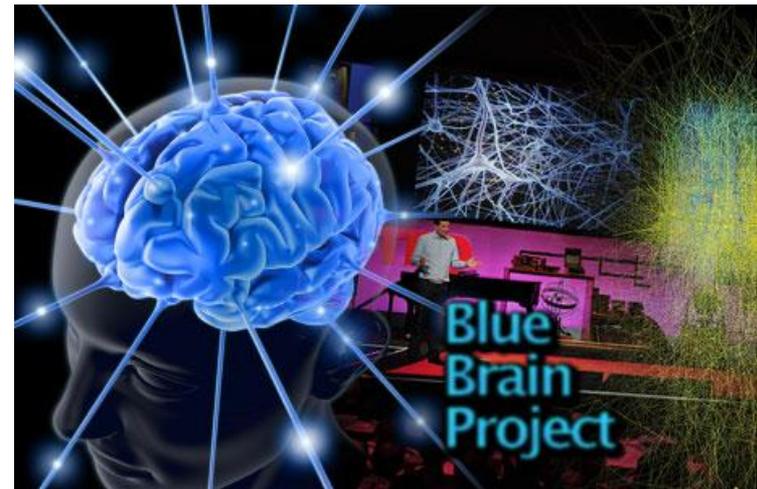
$$\mathbf{z} = \mathbf{X}\mathbf{g} \quad (1)$$

https://en.wikipedia.org/wiki/French_flag_model



A Model?

- Strategic: to obtain insight, to improve ideas and qualitative predictions: "toy" model
- "naïve brute force approach, faithful one-to-one reflection of biological complexity" (Levins 1966)



Purpose, usage?

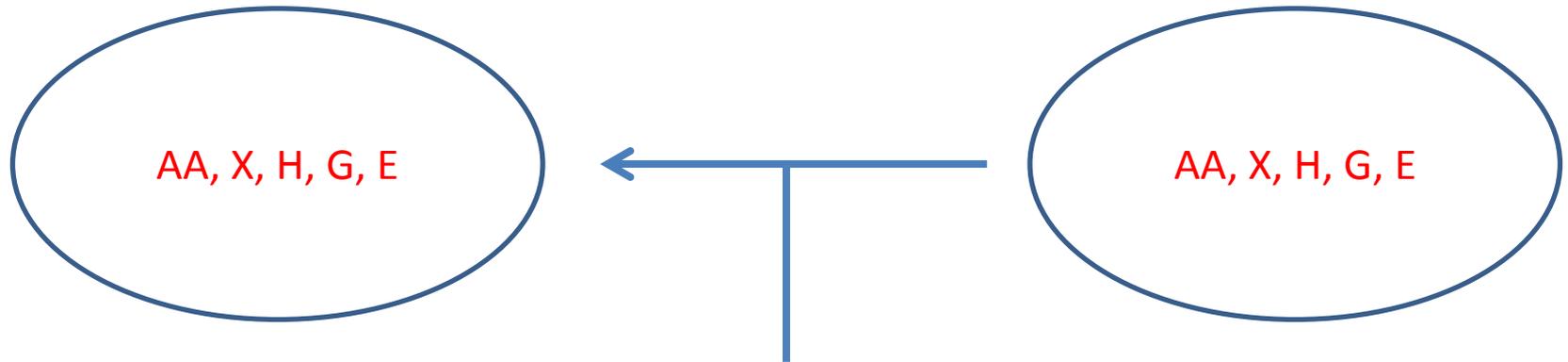
Predict outcomes of eco-evolutionary dynamics

Predict relative magnitudes of components of phenotypic variation

Predict dynamics of phenotype distributions in populations

Distributions – components

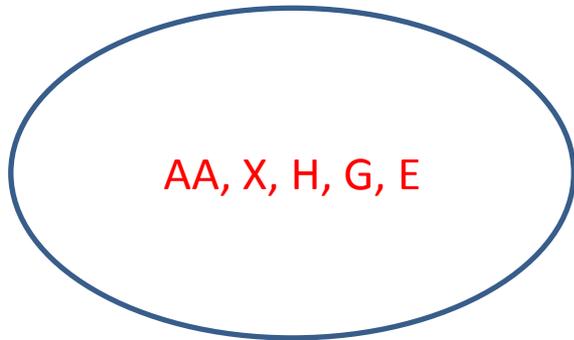
of INDIVIDUAL STATE



Reproduction, development, growth,
heredity, environmental change

Distributions – components

of INDIVIDUAL STATE



We want to simplify where possible and not track state variation and dynamics when it's not necessary

- Random environmental variation
- lots of loci of small effects
- Choose properties that are not variable

Replace stochastic variables by means and variances of their distributions

$$z = g + e$$

$$e \sim N(0, \sigma)$$

Distributions – components

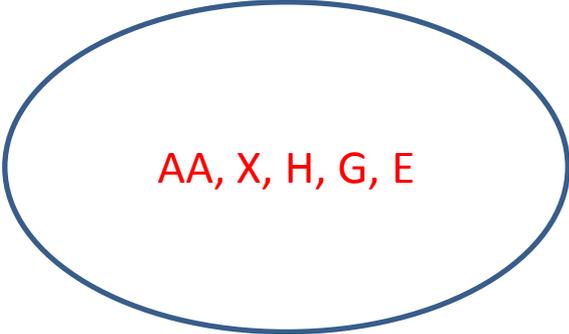
of INDIVIDUAL STATE

It can still become relatively complicated

Often we are prepared to sacrifice some generality

And simplify when that allows us to use more “reliable”

mathematical tools



AA, X, H, G, E

Quantitative genetics

Adaptive Dynamics

(a)



(b)



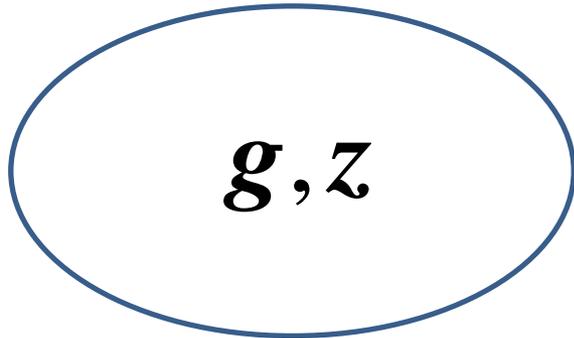
(c)



The role of developmental plasticity in evolutionary innovation. Moczek et al. 2011.
10.1098/rspb.2011.0971

Character state approach

Multivariate phenotype: list all traits in different environments
Genetic variation for a plastic trait is managed in the same way as for a multivariate phenotype



$$\mathbf{z} = (z_1, \dots, z_n)$$

each "trait"

$$z_i = g_i + e_i$$

$$\mathbf{z} = \mathbf{g} + \mathbf{e} \quad \text{and} \quad \mathbf{e} \sim MVN(\mathbf{0}, \Sigma)$$



0 s



90 s



150 s



180 s



270 s

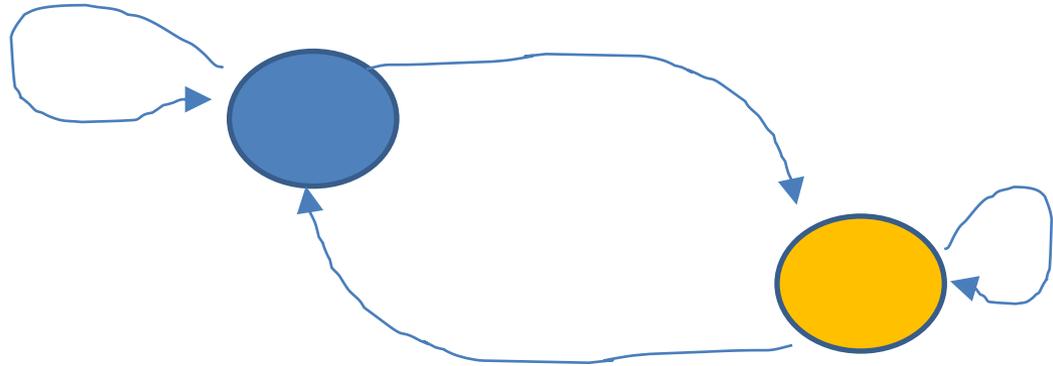


330 s



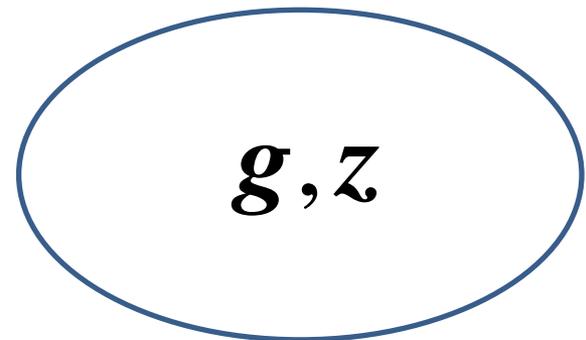
Pristimantis mutabilis skin texture transformation

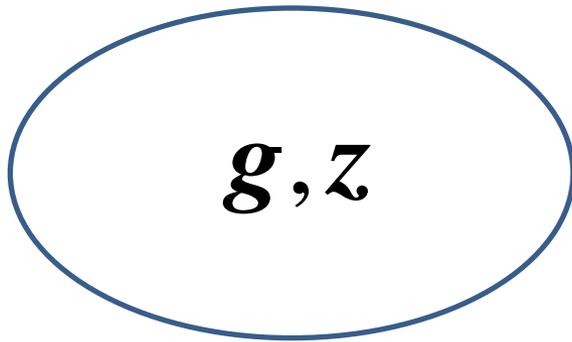
Over the course of 330 seconds, the skin of the mutable rain frog (*Pristimantis mutabilis*) changed from highly textured and rough to smooth.



Simplify: Markov chain with two states,
ergodic, unique stationary distribution

~ fixed fraction of time in each state



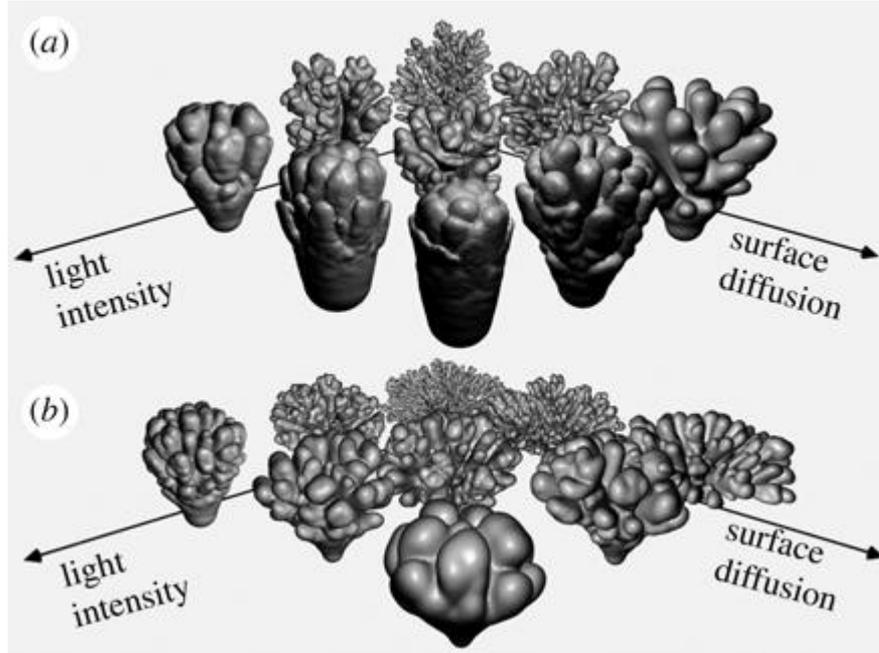


Genetic variation for phenotypes in alternative states
Phenotypes in alternative states

Genetic variation for parameters of the Markov chain
Genetic variation for stationary distributions

Plasticity?

A comparison between coral colonies of the genus *Madracis* and simulated forms



Morphospace of simulated coral colonies in two different environments: (a) nutrient source is above the object (i.e. mimicking the presence of competing colonies near the simulated colony); (b) side planes act also as the nutrient source (i.e. mimicking the absence of competing colonies near the simulated colony). The axes represent parameters that can be gradually changed in order to change colony morphology. Light intensity is the α parameter from equation (2.1). Surface diffusion is the diffusion constant D in equation (2.2).

Reaction norms

“Explanatory variables”: phenotypic plasticity describes causal effects of environmental variables on phenotype variation

$$z = b_0 + b_1 e_1 + \varepsilon$$

The trait is a polynomial equation of variables characterizing the environmental state

Example
$$z = b_0 + b_1 e_1 + b_{12} e_1^2 + b_2 e_2 + \varepsilon$$

$$z = \mathbf{e}^T \mathbf{b} \qquad \mathbf{e}^T = (1, e_1, \dots, e_n)$$

Reaction norms

We see the "parameters" \mathbf{b} as the traits, not z

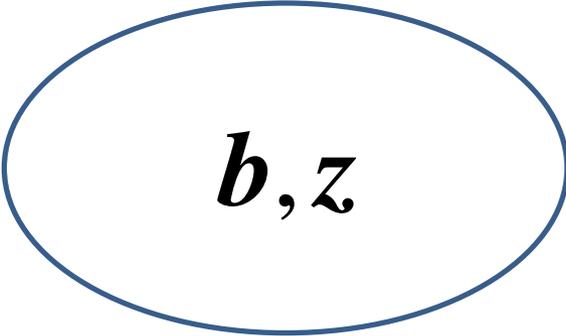
$$z = b_0 + b_1 e_1 + \varepsilon$$

$$z = \mathbf{e}^T \mathbf{b}$$

$$\mathbf{z} = \mathbf{E} \mathbf{b}$$

$$\mathbf{E} = (\mathbf{1}, \mathbf{e}_1, \dots, \mathbf{e}_n)$$

Character states: reaction norms mapped to the different environmental states by matrix \mathbf{E} , with the properties of the environmental states in the columns



b, z

Phenotypes and parameters of a polynomial
that are maybe genetically variable

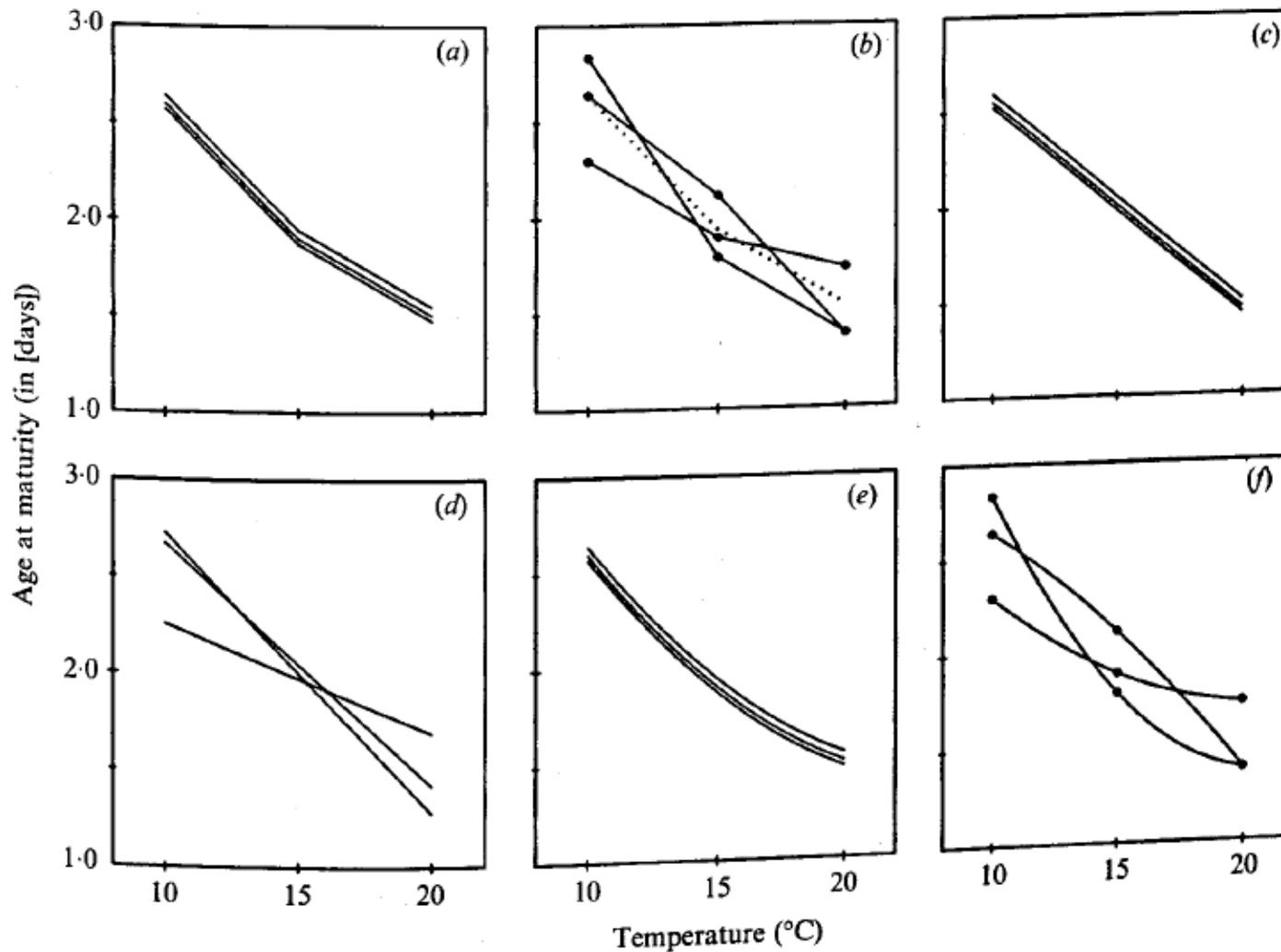


Fig. 1. Reaction norms of three clones in an experiment with *Daphnia galeata* at three temperature levels. (a) Main effects model, (b) full-factorial model (dashed line is mean reaction norm), (c) equidistant linear norms, (d) linear norms, (e) equidistant quadratic norms, (f) quadratic norms.

Van Tienderen, Peter H., and Hans P. Koelewijn. "Selection on reaction norms, genetic correlations and constraints." *Genetics Research* 64.2 (1994): 115-125.

Character state models

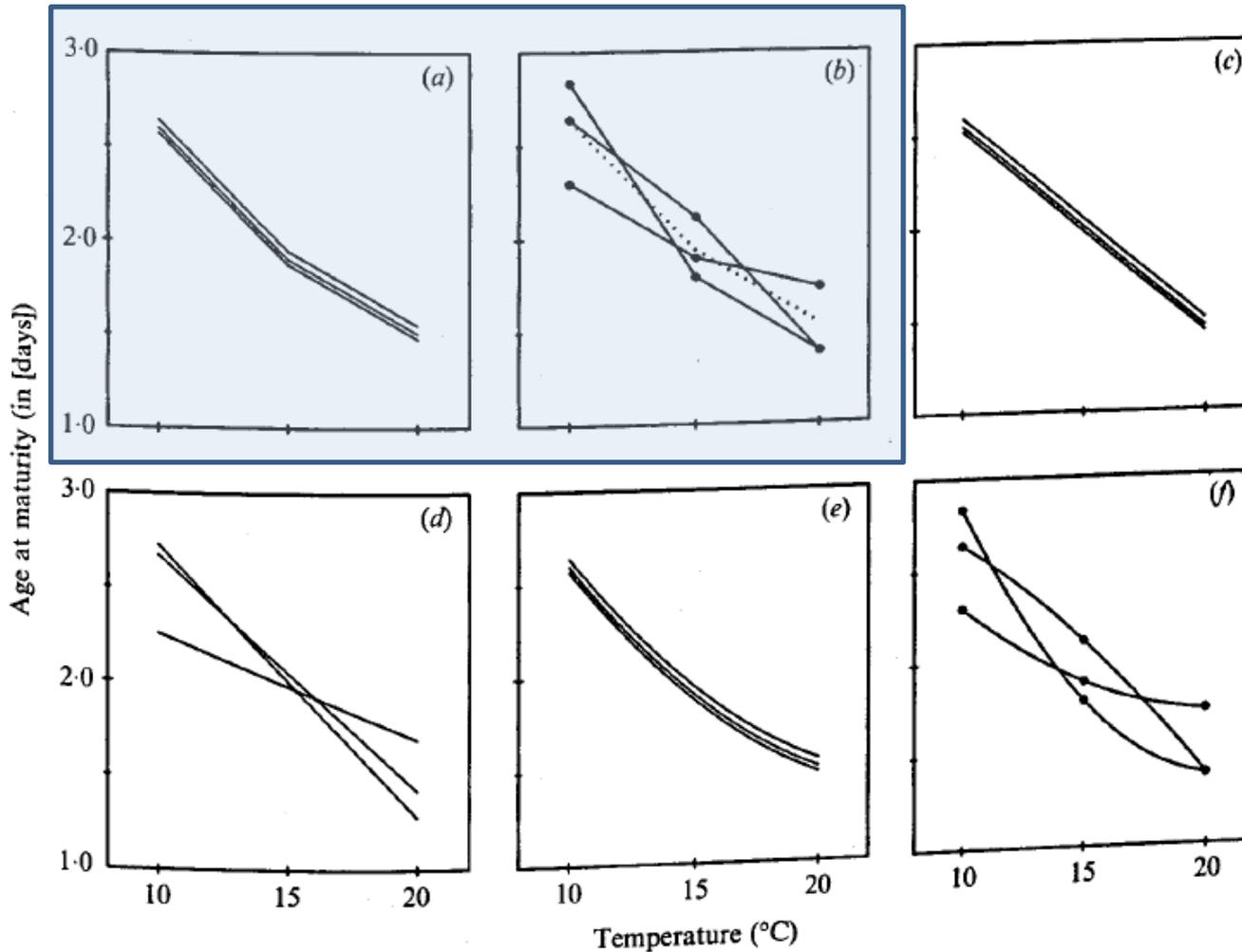


Fig. 1. Reaction norms of three clones in an experiment with *Daphnia galeata* at three temperature levels. (a) Main effects model, (b) full-factorial model (dashed line is mean reaction norm), (c) equidistant linear norms, (d) linear norms, (e) equidistant quadratic norms, (f) quadratic norms.

Van Tienderen, Peter H., and Hans P. Koelewijn. "Selection on reaction norms, genetic correlations and constraints." *Genetics Research* 64.2 (1994): 115-125.

Two formalisms

$$z = \mathbf{g} + \boldsymbol{\varepsilon}$$

$$\mathbf{G}_g$$

$$z = \mathbf{E}b + \boldsymbol{\varepsilon}$$

$$\mathbf{G}_b$$

Map one to the other

$$\mathbf{z} = \mathbf{g} + \boldsymbol{\varepsilon}$$

$$\mathbf{z} = \mathbf{E}\mathbf{b} + \boldsymbol{\varepsilon}$$

$$\mathbf{G}_g$$

$$\mathbf{G}_b$$

$$\mathbf{g} = \mathbf{E}\mathbf{b}$$

$$\mathbf{b} = \mathbf{U}\mathbf{g}$$

$$\mathbf{U} = (\mathbf{E}^T \mathbf{E})^{-1} \mathbf{E}^T$$

\mathbf{U} exists only when the number of environments is larger than the number of parameters in \mathbf{b}

Genetic variation

$$\mathbf{z} = \mathbf{g} + \boldsymbol{\varepsilon}$$

$$\mathbf{z} = \mathbf{E}\mathbf{b} + \boldsymbol{\varepsilon}$$

$$\mathbf{G}_g$$

$$\mathbf{G}_b$$

$$\mathbf{g} = \mathbf{E}\mathbf{b}$$

$$\mathbf{b} = \mathbf{U}\mathbf{g}$$

$$\mathbf{G}_g = \mathbf{E}\mathbf{G}_b\mathbf{E}^T$$

$$\mathbf{G}_b = \mathbf{U}\mathbf{G}_g\mathbf{U}^T$$

Response to selection

$$\mathbf{z} = \mathbf{g} + \boldsymbol{\varepsilon}$$

$$\mathbf{z} = \mathbf{E}\mathbf{b} + \boldsymbol{\varepsilon}$$

$$\Delta\mathbf{z} = \mathbf{G}_g\boldsymbol{\beta}_g$$

$$\Delta\mathbf{b} = \mathbf{G}_b\boldsymbol{\beta}_b$$

$$\boldsymbol{\beta}_g = \frac{\partial\mathbf{b}}{\partial\mathbf{g}}\boldsymbol{\beta}_b$$

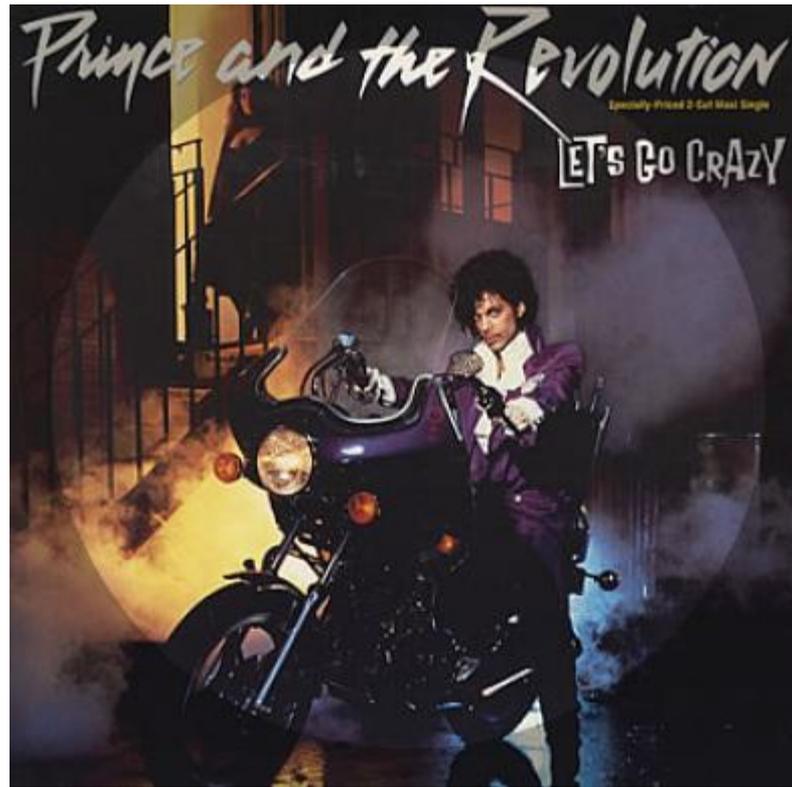
$$\boldsymbol{\beta}_b = \frac{\partial\mathbf{g}}{\partial\mathbf{b}}\boldsymbol{\beta}_g$$

$$\mathbf{b} = \mathbf{U}\mathbf{g}$$

$$\mathbf{g} = \mathbf{E}\mathbf{b}$$

$$\Delta\mathbf{g} = \mathbf{G}_g\mathbf{U}^T\boldsymbol{\beta}_b$$

$$\Delta\mathbf{b} = \mathbf{G}_b\mathbf{E}^T\boldsymbol{\beta}_g$$



Prince and the Revolution

Specialty-Priced 2-CD Maxi Single

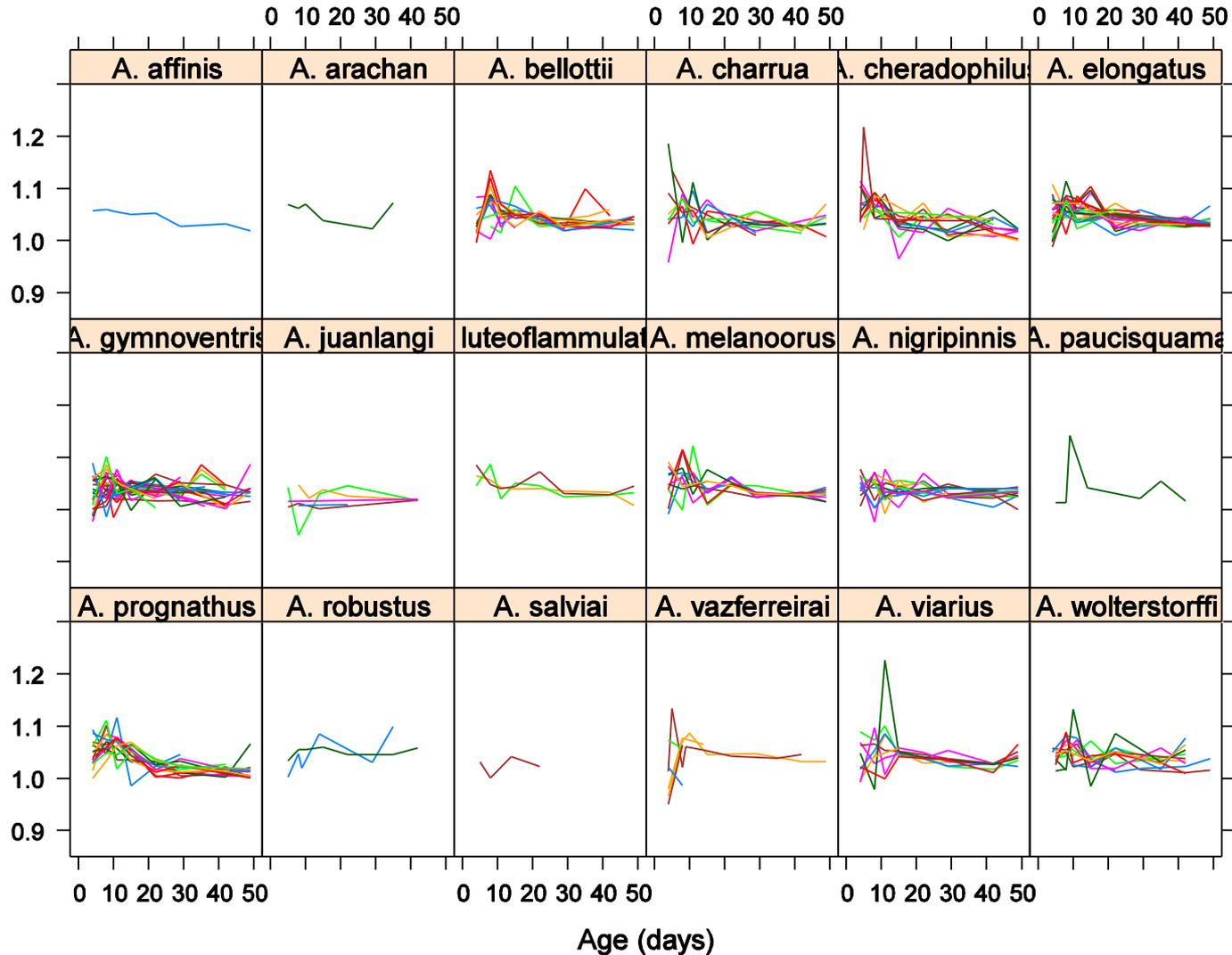
LET'S GO CRAZY

Reaction norms for individual state variation



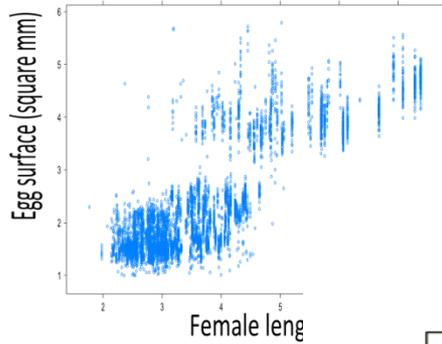
1.2
1.1
1.0
0.9

Relative growth / Day

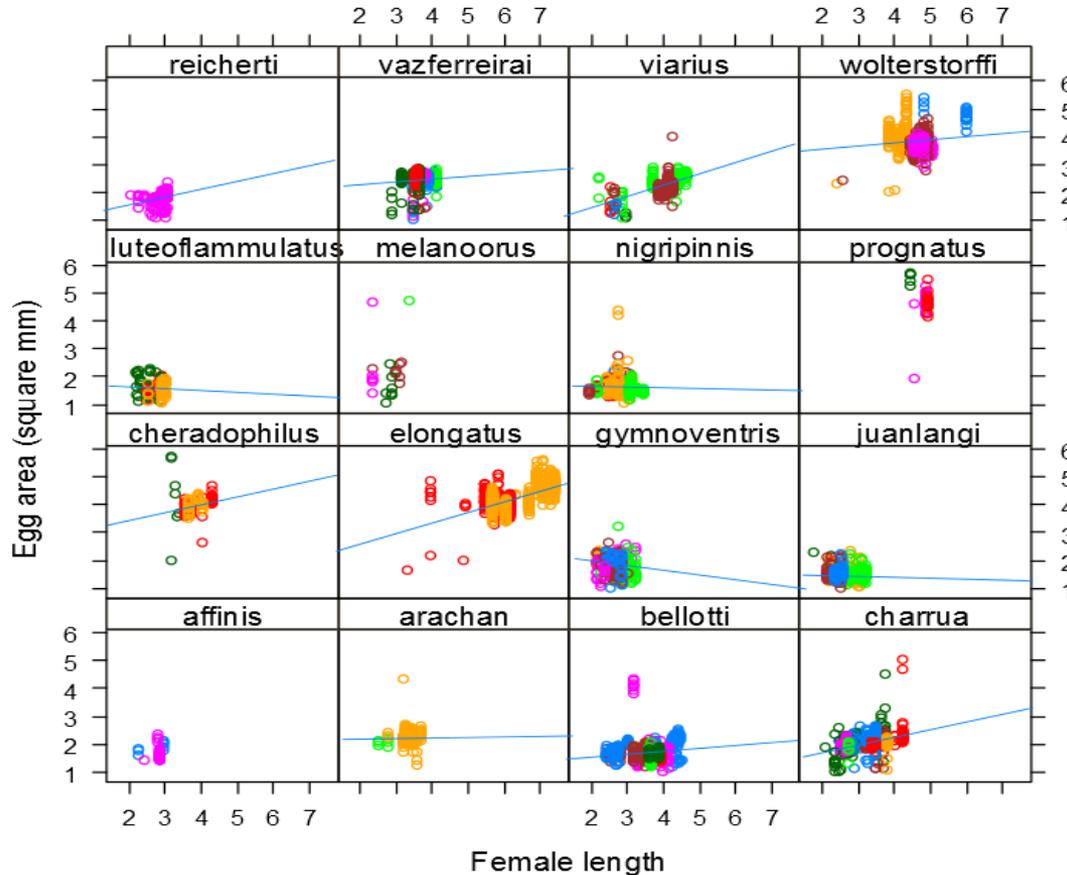


“Fixed” external environment = we didn’t deliberately change it during the experiment

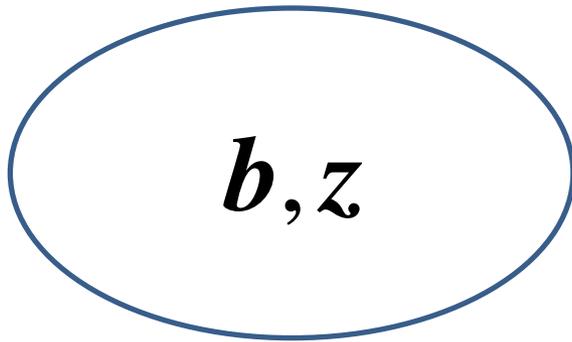




Reaction norms for individual state variation
 Explanatory variable: a state variable



“Fixed” external environment = we recreated it every time



Rates of growth (relative)

Parameters describing phenotype as a function of another phenotypic state variable

\mathbf{b} is a vector of spline coefficients

Arabidopsis Bur-0 Relative Growth Rates deseccation regime

Start getting dry at day 5 intended dryness reached at day 9/10.

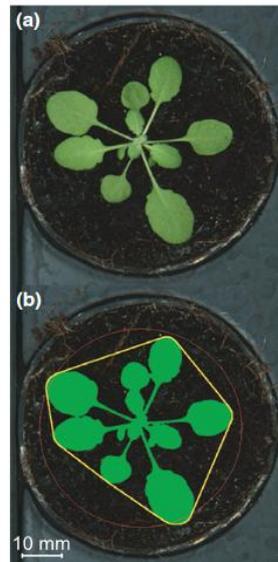
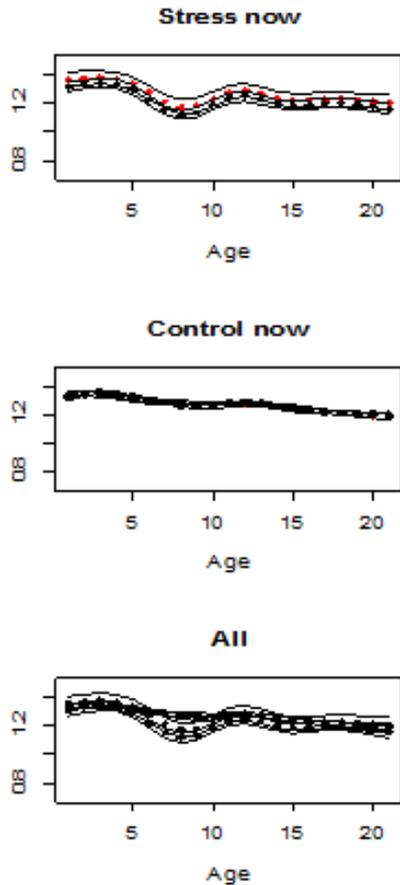
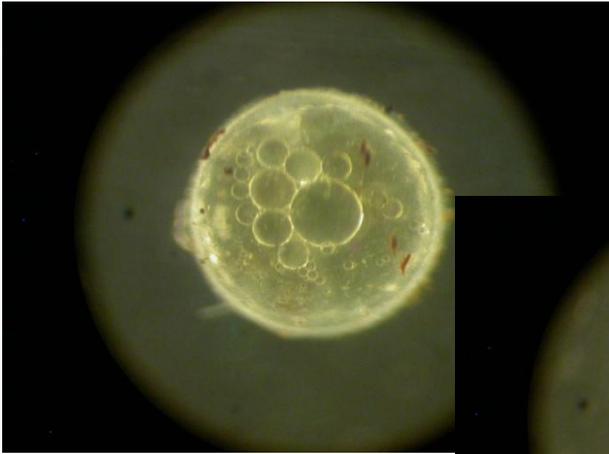


Fig. 2 Example of a plant image before and after processing. Plant image before (a) and after (b) analysis using the LemnaGrid software delivered with the system. In (b) the green area is the detected leaf area and the yellow line outlines the convex hull; the compactness is the total leaf area divided by the convex hull area. The red circle defines the region where the image analysis algorithm expects to find the majority of the plant surface. Outside of this area only green surfaces connected to internal surfaces are included, to avoid inclusion of small patches of moss or algae.

Phenotyping:
Phenoscope robots
INRA Versailles





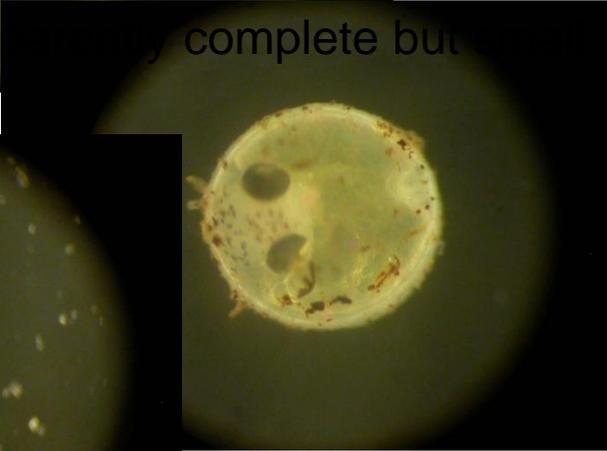
blastula – dispersed cells **Diapause 1**



somites **Diapause 2**



head formation

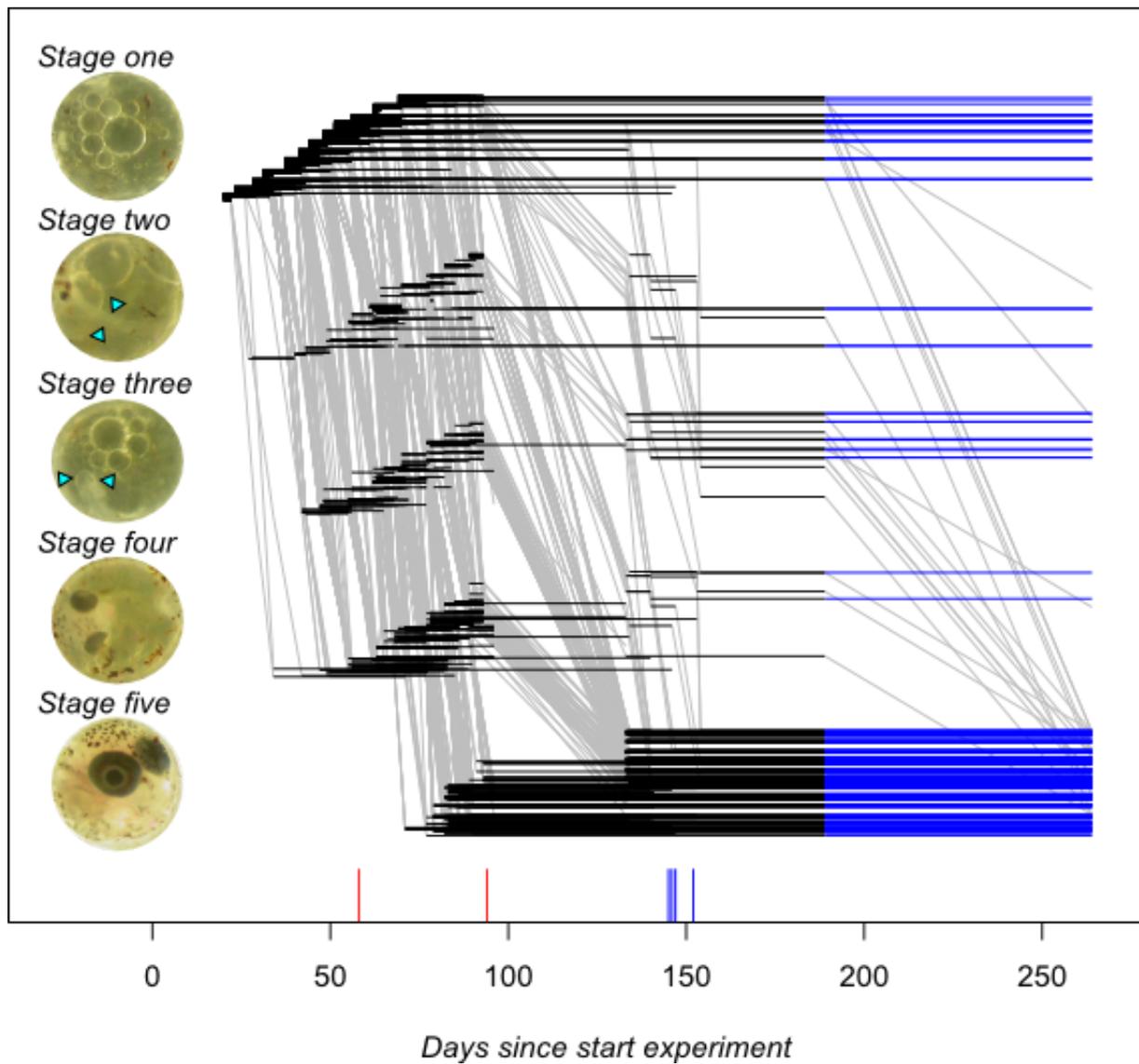


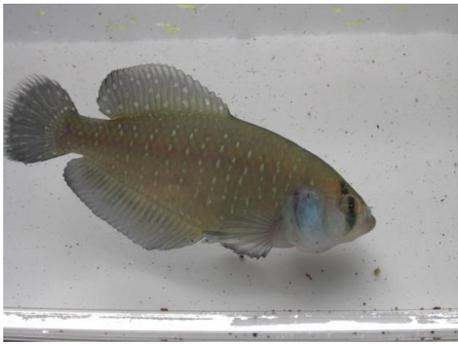
ap... complete but



seemingly ready to hatch **Diapause 3**

Strategy determination is relatively accessible, observable





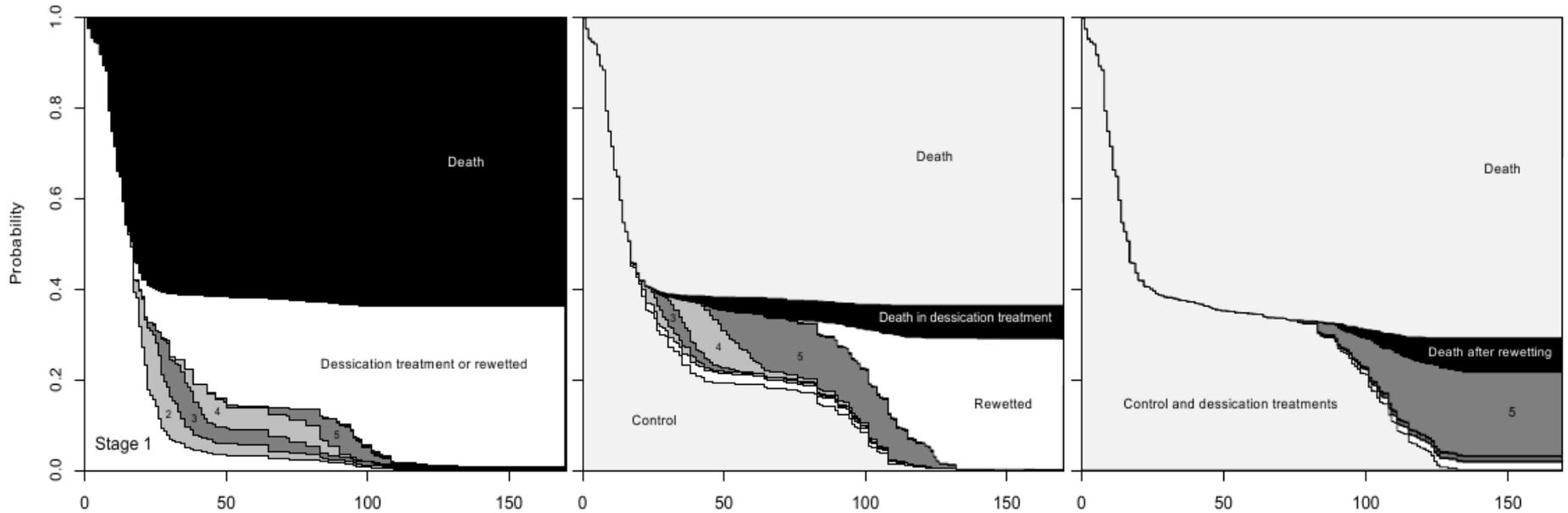
Argentinian pearl killifish
A. bellottii



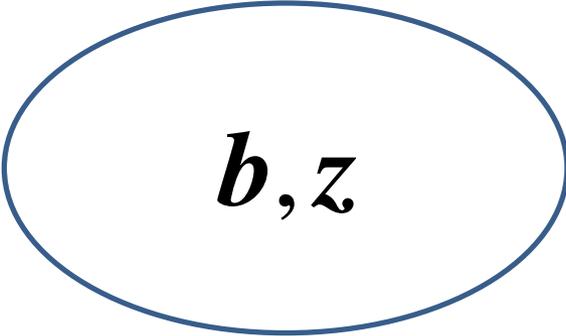
Control

Dessication treatments

Rewetted



Only faster development in air in stage two, early embryos survive better



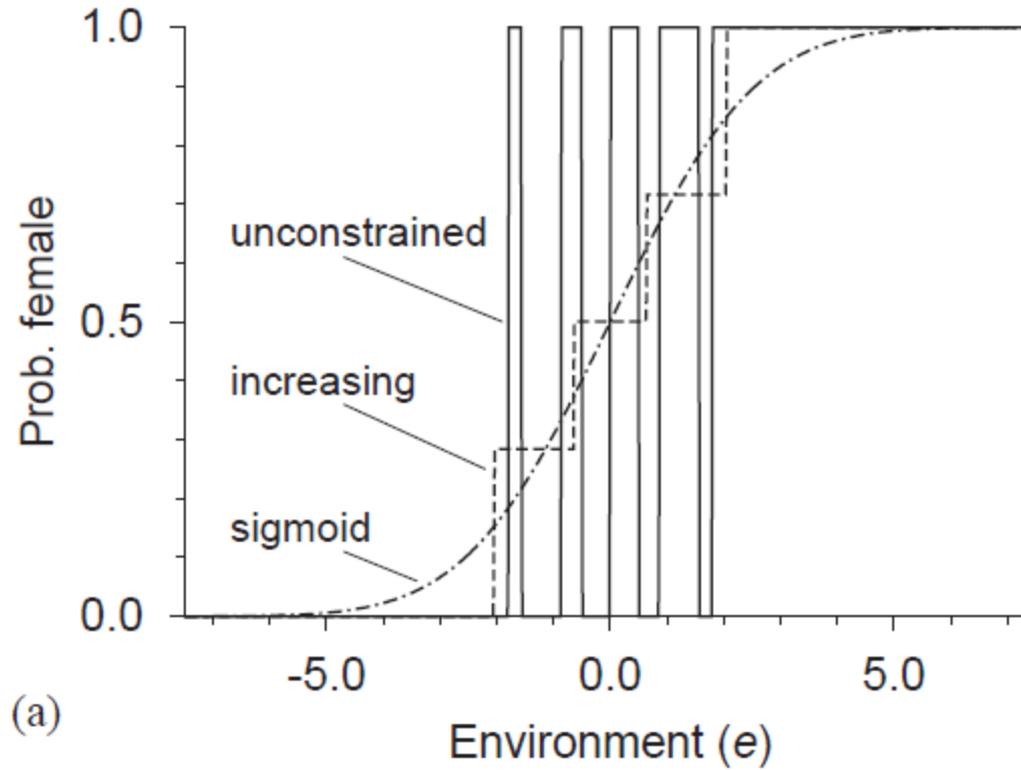
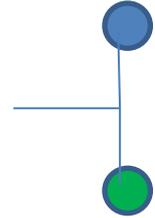
b, z

Rates of transition between developmental stages
Mortality rates

that are age/time/age-within-stage dependent

that depend on the state of the environment

Sex determination evolution



Function – valued traits

g: trait values per environmental state
infinite-dimensional

b: spline coefficients

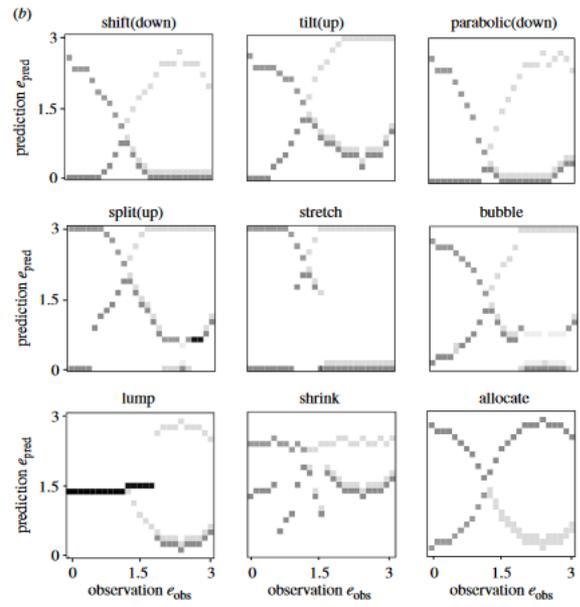
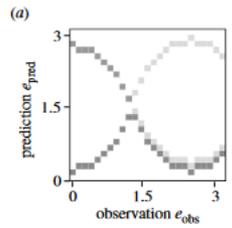
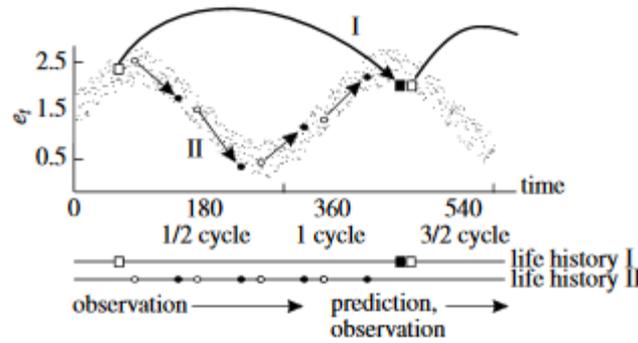
To explain the approach, we will again use the example of flowering strategy for a monocarpic perennial. The ‘strategy’ is a function $p_b(z)$ giving the relationship between size z and flowering probability. Up to now, we have described it by logistic regression. But any analytic formula limits variation to a few ‘degrees of freedom’, which creates the risk that the optimum within those limits may be highly suboptimal (Dieckmann, Heino & Parvinen 2006).

We would ideally not put any restrictions at all on the shape, and for some deterministic models that can be done using optimal control theory or the calculus of variations (Parvinen, Dieckmann & Heino 2006; [Parvinen, Heino & Dieckmann 2013](#)). For stochastic IPMs with density or frequency dependence, and many other models, we do not know of any analytical solution method, so we take a computational approach using methods from functional data analysis ([Ramsay & Silverman 2005](#); [Ramsay, Hooker & Graves 2009](#)). The simplification that leads to a practical solution is to allow a finite but arbitrarily large number of degrees of freedom. B-splines are a convenient and popular way to do this. We want to let flowering probability be any smooth function of size with values between 0 and 1. We do that by setting

$$\text{logit } p_b(z, t) = \sum_{j=1}^d c_j \varphi_j(z) \quad \text{eqn 35}$$



© Antonia Monteiro



(a) probability of bet-hedging at intermediate e_{obs} 0 10

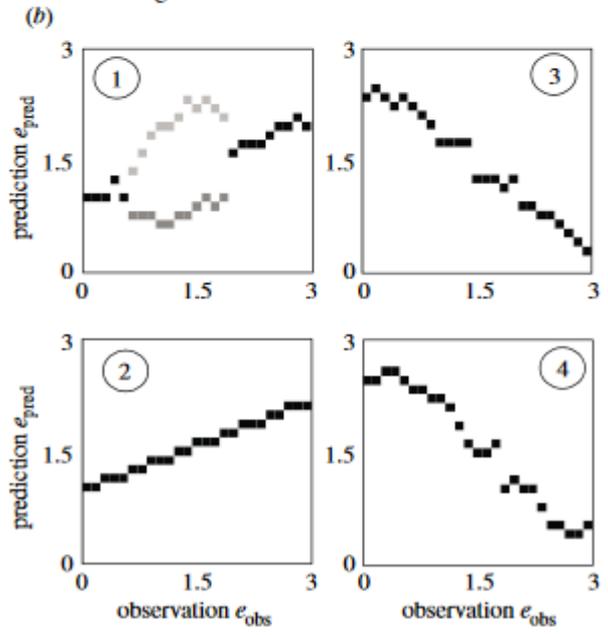
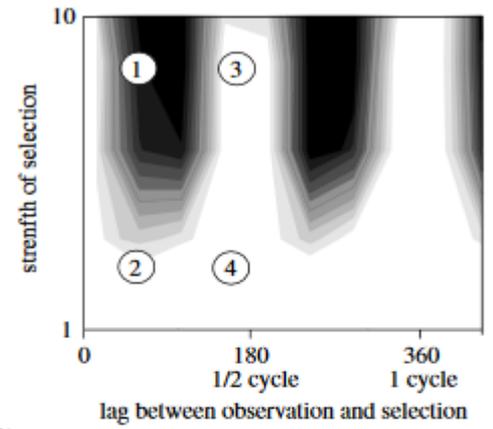


Figure 2. Mutational mappings picture gallery. In the first model version, strategies are specified by matrices with probability weights of observation-prediction combinations of environmental states. Such matrices can be drawn as a grid of combinations with the intensity of filling directly proportional to the probability weight in that matrix cell. Mutations are modelled as random 'deformations' of probability weights in the matrix. Each mutation mapping is given a name that describes the way a probability weight is moved across cells. (a) A progenitor reaction norm and (b) a number of one-step mutants are drawn. The progenitor was obtained from a flat reaction norm by applying two successive and well-aimed bubble mappings.