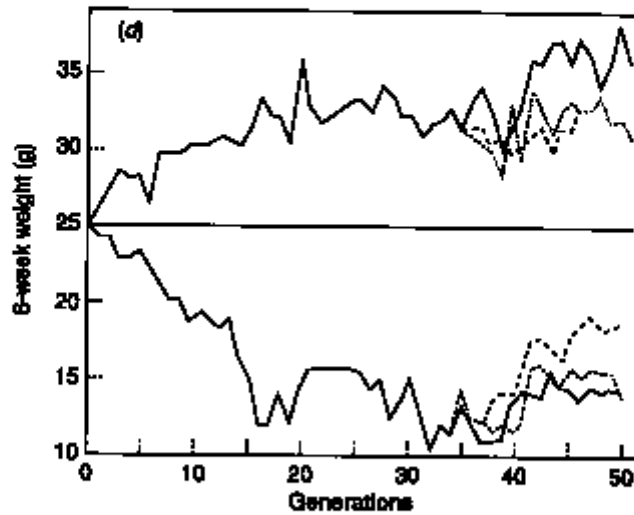
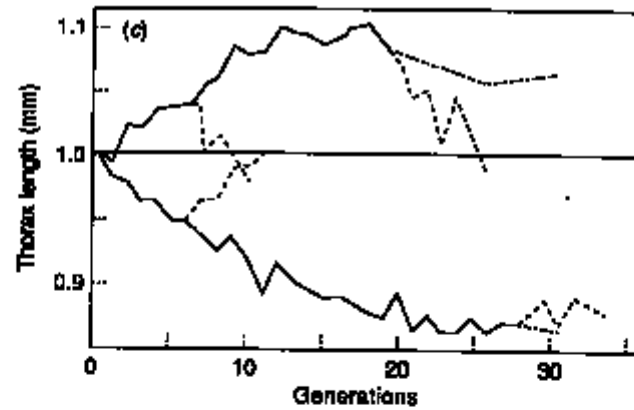


THE BREEDER'S EQUATION



Tom Van Dooren 11/2012
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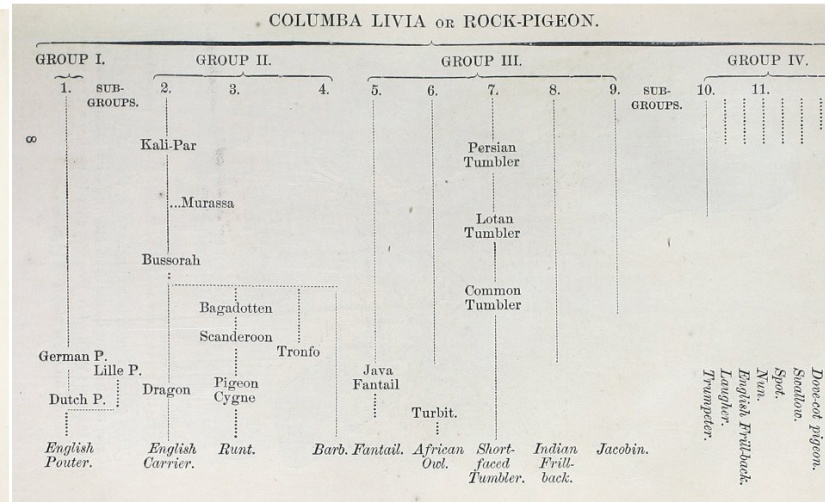
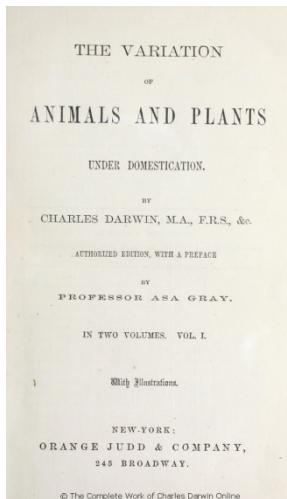


(c) *Drosophila melanogaster*, thorax length. (After F. W. Robertson, 1955.)

(d) Mouse, six-week body weight. (Adapted from Roberts, 1966b.)

Dashed lines are responses to selection in the reverse direction; dotted lines are responses to natural selection, with artificial selection suspended.

(All figures redrawn from the above sources with permission of the authors and publishers.)



1. Background
2. Response to selection
3. Fitness gradient
4. Stabilizing and disruptive selection

PS. Selection on reaction norms

1. BACKGROUND

x_1, x_2, \dots, x_n are random variables with

means $\mu_1, \mu_2, \dots, \mu_n$

variances $\sigma_1^2, \sigma_2^2, \dots$ (or $\sigma_{11}, \sigma_{22}, \dots, \sigma_{nn}$) and covariances $\sigma_{12}, \sigma_{13}, \dots, \sigma_{n-1,n}$

means as a vector $\boldsymbol{\mu}$

variance-covariance matrix $\boldsymbol{\Sigma}_x$ of \mathbf{x}

$$\text{var}(\mathbf{x}) = \boldsymbol{\Sigma}_x = \begin{pmatrix} \sigma_{11} & \sigma_{12} & \dots & \sigma_{1n} \\ \sigma_{21} & \sigma_{22} & \dots & \sigma_{2n} \\ \vdots & & & \vdots \\ \sigma_{n1} & \dots & \dots & \sigma_{nn} \end{pmatrix}$$

THE MULTIVARIATE NORMAL DISTRIBUTION $MVN(\boldsymbol{\mu}, \boldsymbol{\Sigma}_x)$

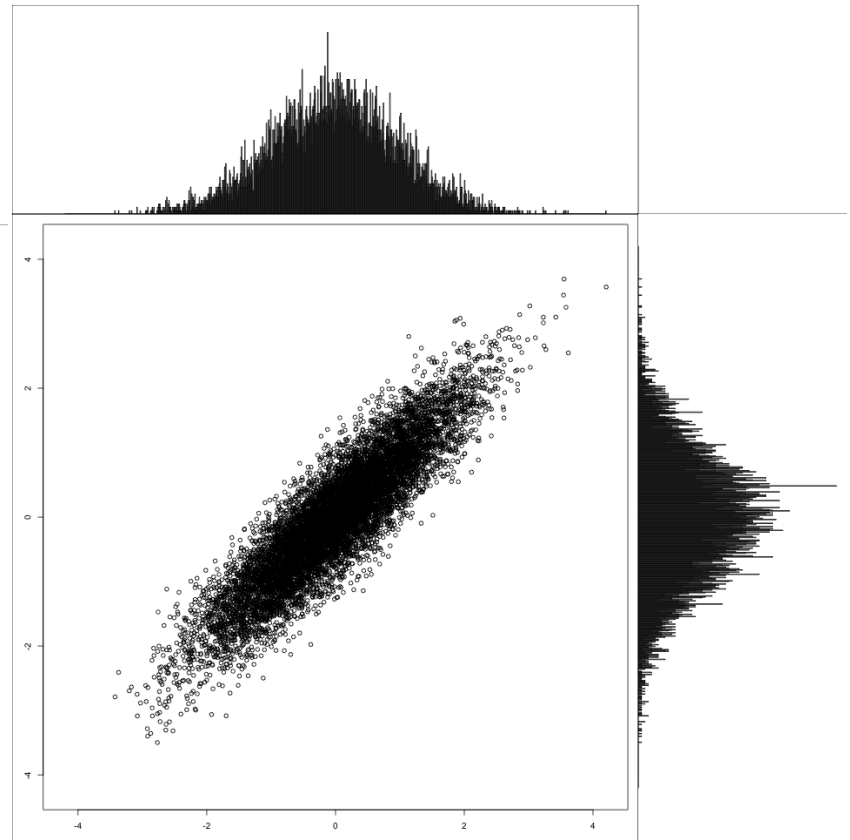
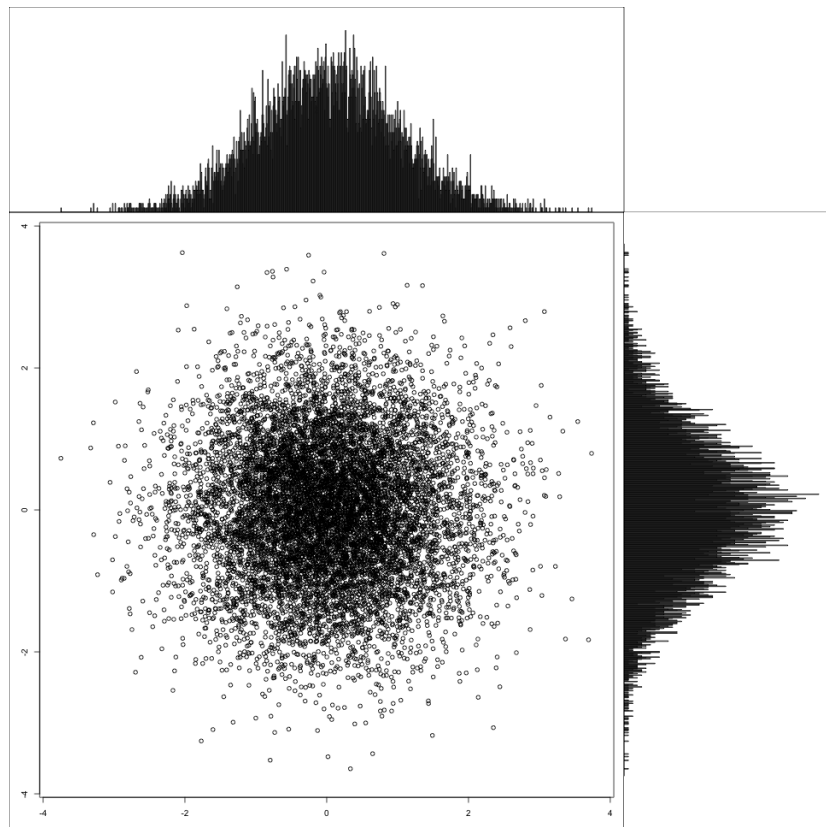
The probability density function $f(\mathbf{x})$ of a multivariate normal distribution with vector of means $\boldsymbol{\mu}$ and covariance matrix $\boldsymbol{\Sigma}_x$ equals

$$f(\mathbf{x}) = (2\pi)^{-n/2} |\boldsymbol{\Sigma}_x|^{-1/2} \exp\left(-\frac{1}{2}(\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\right)$$

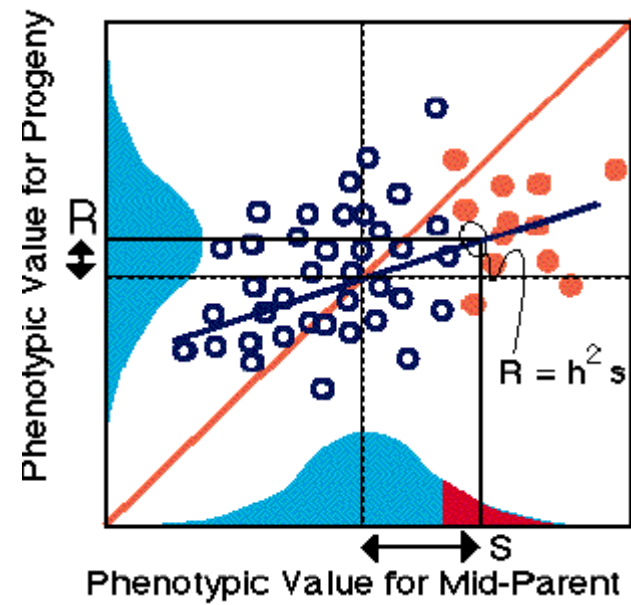
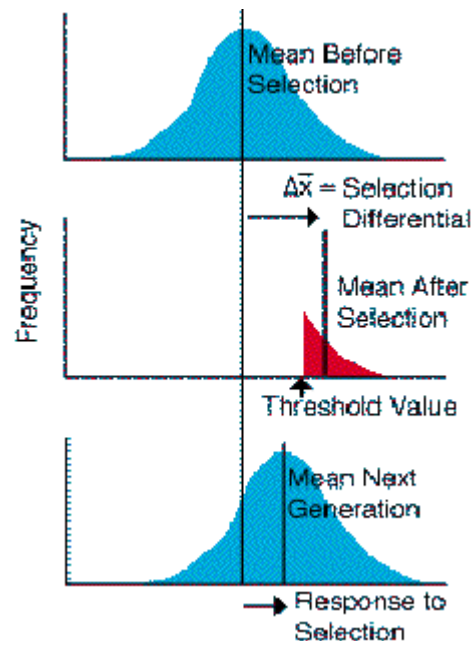
$$\mathbf{x} = \begin{pmatrix} \mathbf{x}_1 \\ \mathbf{x}_2 \end{pmatrix}, \boldsymbol{\mu} = \begin{pmatrix} \boldsymbol{\mu}_1 \\ \boldsymbol{\mu}_2 \end{pmatrix}, \text{ and } \boldsymbol{\Sigma}_x = \begin{pmatrix} \boldsymbol{\Sigma}_{x_1} & \boldsymbol{\Sigma}_{x_1, x_2} \\ \boldsymbol{\Sigma}_{x_1, x_2}^T & \boldsymbol{\Sigma}_{x_2} \end{pmatrix}$$

$$\boldsymbol{\mu}_{x_1|x_2} = \boldsymbol{\mu}_1 + \boldsymbol{\Sigma}_{x_1, x_2} \boldsymbol{\Sigma}_{x_2}^{-1}(\mathbf{x}_2 - \boldsymbol{\mu}_2) \text{ and } \boldsymbol{\Sigma}_{x_1|x_2} = \boldsymbol{\Sigma}_{x_1} - \boldsymbol{\Sigma}_{x_1, x_2} \boldsymbol{\Sigma}_{x_2}^{-1} \boldsymbol{\Sigma}_{x_1, x_2}^T$$

$$\mathbf{x}_1 = \boldsymbol{\mu}_1 + \boldsymbol{\Sigma}_{x_1, x_2} \boldsymbol{\Sigma}_{x_2}^{-1}(\mathbf{x}_2 - \boldsymbol{\mu}_2) + \boldsymbol{\varepsilon} \text{ with } \boldsymbol{\varepsilon} \sim MVN(\mathbf{0}, \boldsymbol{\Sigma}_{x_1|x_2})$$



2. THE RESPONSE TO SELECTION



Phenotypic trait vector $\mathbf{z} = \mathbf{g} + \mathbf{e}$,

Base population: $\mathbf{g} \sim \text{MVN}(\boldsymbol{\mu}_g, \mathbf{G})$ en $\mathbf{e} \sim \text{MVN}(\mathbf{0}, \mathbf{E})$

$\mathbf{z} \sim \text{MVN}(\boldsymbol{\mu}_z, \mathbf{P})$ with $\mathbf{P} = \mathbf{G} + \mathbf{E}$ and $\boldsymbol{\mu}_z = \boldsymbol{\mu}_g$.

Regress genotype on phenotype

$$\mathbf{x} = \begin{pmatrix} \mathbf{g} \\ \mathbf{z} \end{pmatrix} = \text{MVN} \left(\begin{pmatrix} \boldsymbol{\mu}_g \\ \boldsymbol{\mu}_z \end{pmatrix}, \begin{pmatrix} \mathbf{G} & \mathbf{G} \\ \mathbf{G} & \mathbf{P} \end{pmatrix} \right)$$

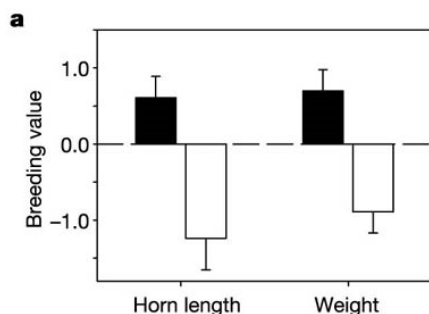
$$\sigma(\mathbf{g}, \mathbf{z}) = \sigma(\mathbf{g}, \mathbf{g} + \mathbf{e}) = \sigma(\mathbf{g}, \mathbf{g}) + \sigma(\mathbf{g}, \mathbf{e}) = \sigma(\mathbf{g}, \mathbf{g}) = \mathbf{G}$$

$$\sigma(\mathbf{g}, \mathbf{g}) = \mathbf{G}$$

$$\sigma(\mathbf{z}, \mathbf{z}) = \mathbf{P} = \mathbf{G} + \mathbf{E}$$

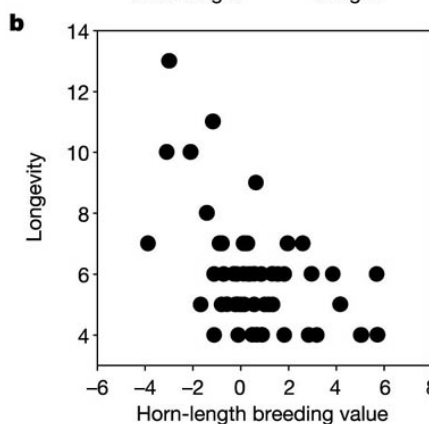
Conditional Genotypic Average Trait Vector:

$$\mu_{g|z} = \mu_g + GP^{-1}(z - \mu_z)$$



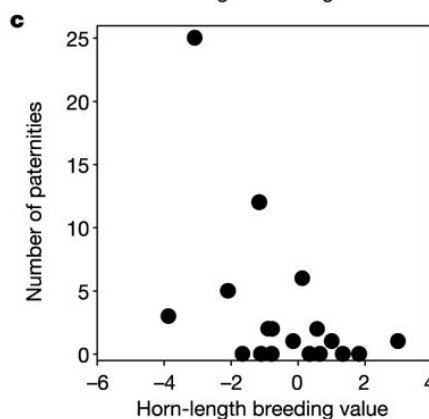
$$V_{\varepsilon} = V_{g|z} = G - GP^{-1}G$$

The linear regression of g on z becomes



$$g = \mu_{g|z} + \varepsilon = \mu_g + GP^{-1}(z - \mu_z) + \varepsilon$$

$$g - \mu_g = GP^{-1}(z - \mu_z) + \varepsilon, \quad \text{and} \quad \varepsilon \sim \text{MVN}(\mathbf{0}, V_{\varepsilon})$$



$g - \mu_g$ is often called the *breeding value* of phenotype z .

Intermezzo: "Undesirable evolutionary consequences of trophy hunting". Coltman et al. 2003 (Nature)



For a univariate phenotype we find, with

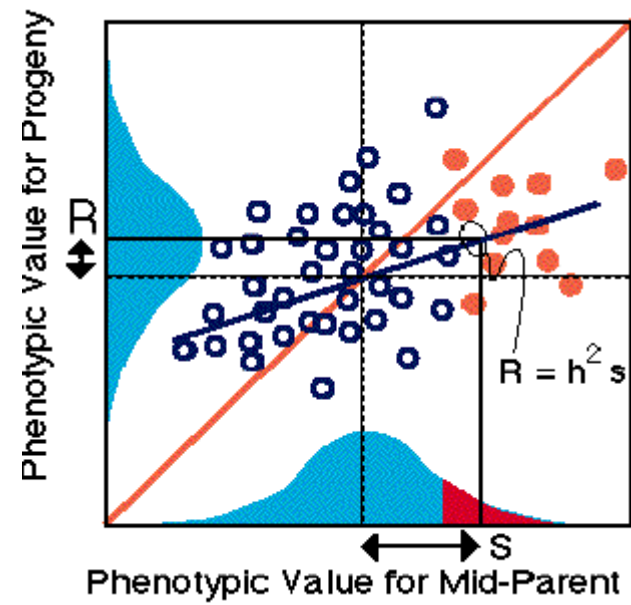
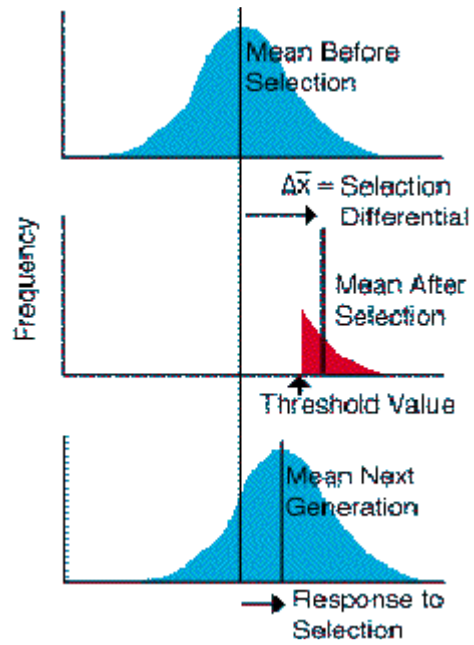
$$\mathbf{g} = g$$

$$\mu_g = \mu_z = \mu$$

$$\mathbf{G} = \sigma_g^2 \text{ and } \mathbf{P} = \sigma_z^2$$

$$g - \mu = \sigma_g^2 \sigma_z^{-2} (z - \mu) + \varepsilon = h^2(z - \mu) + \varepsilon$$

$$\text{and } \sigma_\varepsilon^2 = \sigma_{g|z}^2 = \sigma_g^2 - \sigma_g^2 \sigma_z^{-2} \sigma_g^2 = \sigma_g^2(1 - h^2)$$



The change in the expected value of \mathbf{g} after selection becomes:

$$\begin{aligned}
 \Delta\boldsymbol{\mu}_g &= \boldsymbol{\mu}_g^* - \boldsymbol{\mu}_g \\
 &= \mathbf{E}[\mathbf{GP}^{-1}(\mathbf{z} - \boldsymbol{\mu}_z) + \boldsymbol{\varepsilon}] \\
 &= \mathbf{GP}^{-1} \mathbf{E}[(\mathbf{z} - \boldsymbol{\mu}_z)] \\
 &= \mathbf{GP}^{-1}\mathbf{s} \\
 &= \mathbf{G}\boldsymbol{\beta}
 \end{aligned}$$

The vector \mathbf{s} is the *selection differential*, and $\boldsymbol{\beta}$ the *selection gradient*.

The genetic variance-covariance matrix after selection is

$$\begin{aligned}
 \mathbf{G}^* &= \mathbf{E}[(\mathbf{g} - \boldsymbol{\mu}_g^*)(\mathbf{g} - \boldsymbol{\mu}_g^*)^T] \\
 &= \mathbf{E}[(\mathbf{g} - \boldsymbol{\mu}_g - \Delta\boldsymbol{\mu}_g)(\mathbf{g} - \boldsymbol{\mu}_g - \Delta\boldsymbol{\mu}_g)^T] \\
 &= \mathbf{E}[(\mathbf{GP}^{-1}(\mathbf{z} - \boldsymbol{\mu}_z) + \boldsymbol{\varepsilon})((\mathbf{z} - \boldsymbol{\mu}_z)^T \mathbf{P}^{-1} \mathbf{G} + \boldsymbol{\varepsilon}^T)] \\
 &= \mathbf{GP}^{-1} \mathbf{P}^* \mathbf{P}^{-1} \mathbf{G} + \mathbf{G} - \mathbf{GP}^{-1} \mathbf{G}
 \end{aligned}$$

$$\Delta\mathbf{G} = \mathbf{G}^* - \mathbf{G} = \mathbf{GP}^{-1}(\mathbf{P}^* - \mathbf{P})\mathbf{P}^{-1} \mathbf{G}$$

TRANSFER OF SELECTION RESPONSE ACROSS GENERATIONS

The joint distribution of parental and offspring phenotypes is

$$\begin{pmatrix} \mathbf{z}_o \\ \mathbf{z}_s \\ \mathbf{z}_d \end{pmatrix} = MVN \left(\begin{pmatrix} \boldsymbol{\mu}_o \\ \boldsymbol{\mu}_s \\ \boldsymbol{\mu}_d \end{pmatrix}, \begin{pmatrix} \mathbf{P}_o & \mathbf{G}_{z_o, z_s} & \mathbf{G}_{z_o, z_d} \\ \mathbf{G}_{z_o, z_s}^T & \mathbf{P}_s & \mathbf{G}_{z_s, z_d} \\ \mathbf{G}_{z_o, z_d}^T & \mathbf{G}_{z_s, z_d}^T & \mathbf{P}_d \end{pmatrix} \right)$$

With random mating among selected parents, the genetic covariance between parental phenotypes becomes zero.

$$\boldsymbol{\mu}_{z_o | (z_s, z_d)} = \boldsymbol{\mu}_o + \begin{pmatrix} \mathbf{G}_{z_o, z_s} & \mathbf{G}_{z_o, z_d} \end{pmatrix} \begin{pmatrix} \mathbf{P}_s & \mathbf{G}_{z_s, z_d} \\ \mathbf{G}_{z_s, z_d}^T & \mathbf{P}_d \end{pmatrix}^{-1} \begin{pmatrix} \mathbf{z}_s - \boldsymbol{\mu}_s \\ \mathbf{z}_d - \boldsymbol{\mu}_d \end{pmatrix} + \boldsymbol{\varepsilon}$$

Averaging gives

$$\mu_o^* - \mu_o = \begin{pmatrix} \mathbf{G}_{z_o, z_s} & \mathbf{G}_{z_o, z_d} \end{pmatrix} \begin{pmatrix} \mathbf{P}_s & \mathbf{G}_{z_s, z_d} \\ \mathbf{G}_{z_s, z_d}^T & \mathbf{P}_d \end{pmatrix}^{-1} \begin{pmatrix} \mathbf{s}_s \\ \mathbf{s}_d \end{pmatrix}$$

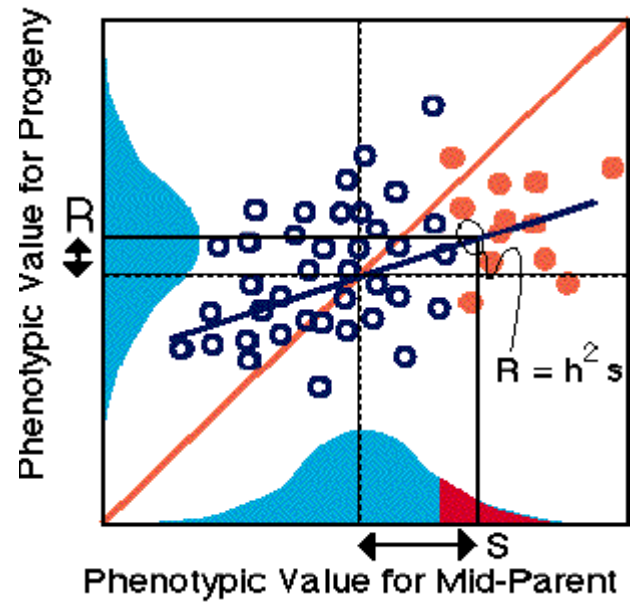
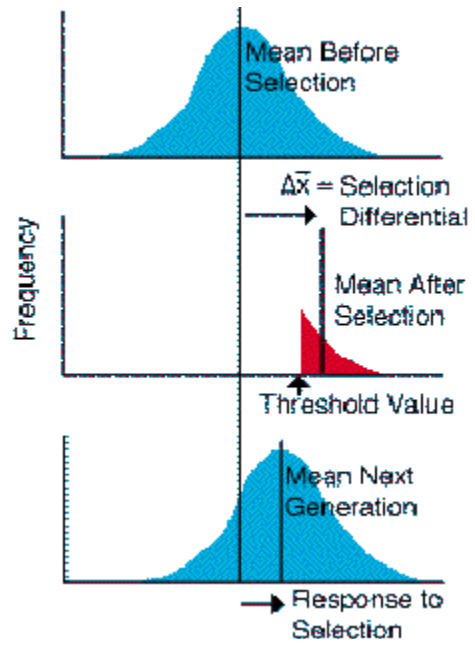
With equal phenotypic and genetic (co)variances in sires and dams, random mating among parents, and without sex differences in selection

$$\mu_o^* - \mu_z = \begin{pmatrix} \frac{1}{2}\mathbf{G} & \frac{1}{2}\mathbf{G} \end{pmatrix} \begin{pmatrix} \mathbf{P} & \mathbf{0} \\ \mathbf{0} & \mathbf{P} \end{pmatrix}^{-1} \begin{pmatrix} \mathbf{s} \\ \mathbf{s} \end{pmatrix} = \mathbf{G}\mathbf{P}^{-1}\mathbf{s} = \mathbf{G}\boldsymbol{\beta}$$

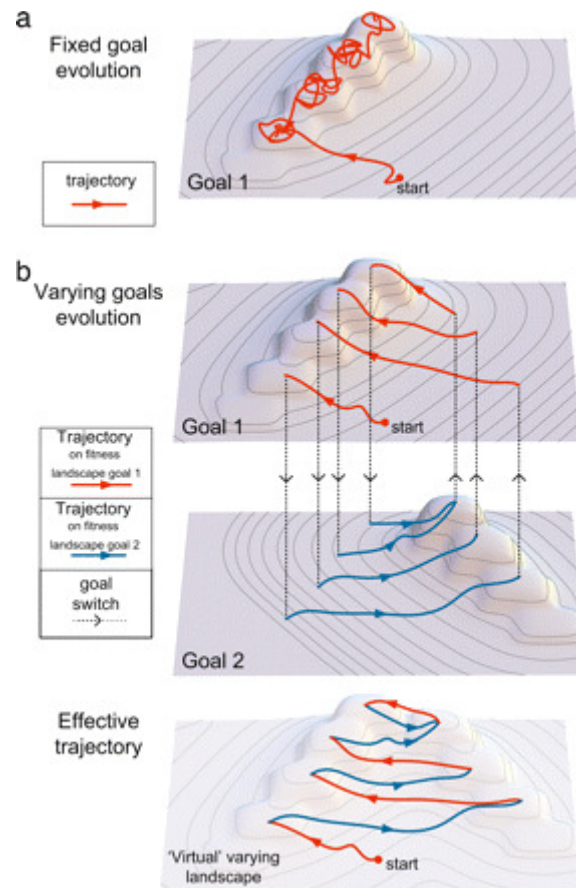
that reduces to the well-known

breeder's equation

$$\Delta\mu_z = \mathbf{G}\boldsymbol{\beta}$$



3. FITNESS GRADIENTS



(NIFTY TRICKS TO CLIMB FASTER)

3. FITNESS GRADIENTS

The gradient of a function f with respect to a vector \mathbf{x} is written as

$$\nabla_{\mathbf{x}} f = \frac{\partial f}{\partial \mathbf{x}} = \begin{pmatrix} \frac{\partial f}{\partial x_1} \\ \vdots \\ \frac{\partial f}{\partial x_n} \end{pmatrix}$$

With \mathbf{A} a symmetric matrix, derivatives of quadratic forms become

$$\nabla_{\mathbf{x}} (\mathbf{x}^T \mathbf{A} \mathbf{x}) = 2\mathbf{A} \mathbf{x}$$

$$\nabla_{\mathbf{x}} ((\mathbf{x} - \mathbf{y})^T \mathbf{A} (\mathbf{x} - \mathbf{y})) = 2\mathbf{A} (\mathbf{x} - \mathbf{y})$$

When $f(\mathbf{x})$ is a MVN probability distribution with

$$f(\mathbf{x}) = (2\pi)^{-n/2} |\boldsymbol{\Sigma}_x|^{-1/2} \exp\left(-\frac{1}{2}(\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\right)$$

then $\nabla_x f(\mathbf{x})$ becomes

$$\begin{aligned}\nabla_x f(\mathbf{x}) &= f(\mathbf{x}) \cdot \nabla_x \left(-\frac{1}{2}(\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\right) \\ &= -f(\mathbf{x}) \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\end{aligned}$$

If we consider $f(\mathbf{x})$ as a function of the mean $\boldsymbol{\mu}$, we get instead the partial derivative

$$\begin{aligned}\nabla_\mu f(\mathbf{x}, \boldsymbol{\mu}) &= f(\mathbf{x}, \boldsymbol{\mu}) \cdot \nabla_\mu \left(-\frac{1}{2}(\mathbf{x} - \boldsymbol{\mu})^T \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\right) \\ &= f(\mathbf{x}, \boldsymbol{\mu}) \boldsymbol{\Sigma}_x^{-1}(\mathbf{x} - \boldsymbol{\mu})\end{aligned}$$

For the special case where \mathbf{z} is MVN

3. THE FITNESS GRADIENT EQUALS A DERIVATIVE OF MEAN FITNESS

$$\nabla_{\mu_z} \ln(\bar{W}(\mathbf{z})) = \beta$$

$$\begin{aligned}\nabla_{\mu_z} \ln(\bar{W}(\mathbf{z})) &= \bar{W}^{-1} \nabla_{\mu_z} \bar{W}(\mathbf{z}) \\ &= \nabla_{\mu_z} \int d\mathbf{z} f(\mathbf{z}, \mu_z) \frac{W(\mathbf{z})}{\bar{W}} \\ &= \nabla_{\mu_z} \int d\mathbf{z} f(\mathbf{z}, \mu_z) w(\mathbf{z}) \\ &= \int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \mathbf{P}^{-1}(\mathbf{z} - \mu_z) \\ &= \mathbf{P}^{-1} \left(\int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \mathbf{z} - \mu_z \int d\mathbf{z} w(\mathbf{z}) f(\mathbf{z}) \right) \\ &= \mathbf{P}^{-1}(\mu_z^* - \mu_z) = \mathbf{P}^{-1} \mathbf{s} = \beta\end{aligned}$$

For the special case where z is MVN

3. THE FITNESS GRADIENT EQUALS A DERIVATIVE OF MEAN FITNESS

$$\nabla_{\mu_z} \ln(\bar{W}(z)) = \beta$$

and this is extremely useful, because we didn't specify any particular W !

Evolution, 33(1), 1979, pp 402–416

QUANTITATIVE GENETIC ANALYSIS OF MULTIVARIATE EVOLUTION, APPLIED TO BRAIN:BODY SIZE ALLOMETRY

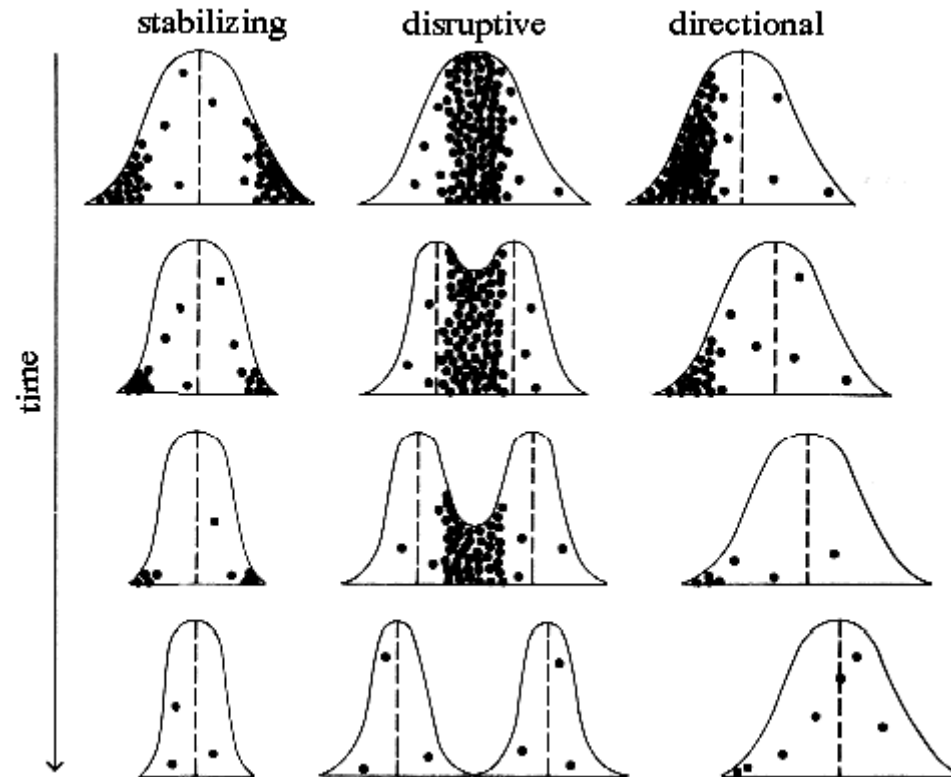
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Received November 28, 1977. Revised August 4, 1978

Darwin (1859, pp. 11–14, 143–150) where k and α are constants. In large stressed the evolutionary importance of taxonomic groups, such as an order of

4. STABILIZING AND DISRUPTIVE SELECTION



MULTIVARIATE SELECTION WITH GAUSSIAN SELECTION/FITNESS FUNCTIONS

The *Gaussian* fitness function $W(\mathbf{z})$ is often used in selection models. It is a special case with properties that allow extensive analytical work.

$$W(\mathbf{z}) = \exp(\boldsymbol{\alpha}^T \mathbf{z} - \frac{1}{2}(\mathbf{z} - \boldsymbol{\theta})^T \mathbf{W}(\mathbf{z} - \boldsymbol{\theta})) = \sum_i \alpha_i z_i - \frac{1}{2} \sum_i \sum_j (z_i - \theta_i)(z_j - \theta_j) W_{ij}$$

- (1) Directional selection occurs when $\boldsymbol{\alpha} \neq 0$ and/or $\boldsymbol{\mu}_z \neq \boldsymbol{\theta}$
- (2) Stabilising selection occurs, for example, when \mathbf{W} is a diagonal matrix and $W_{ii} > 0$
- (3) Disruptive selection occurs when \mathbf{W} is a diagonal matrix and $W_{ii} < 0$

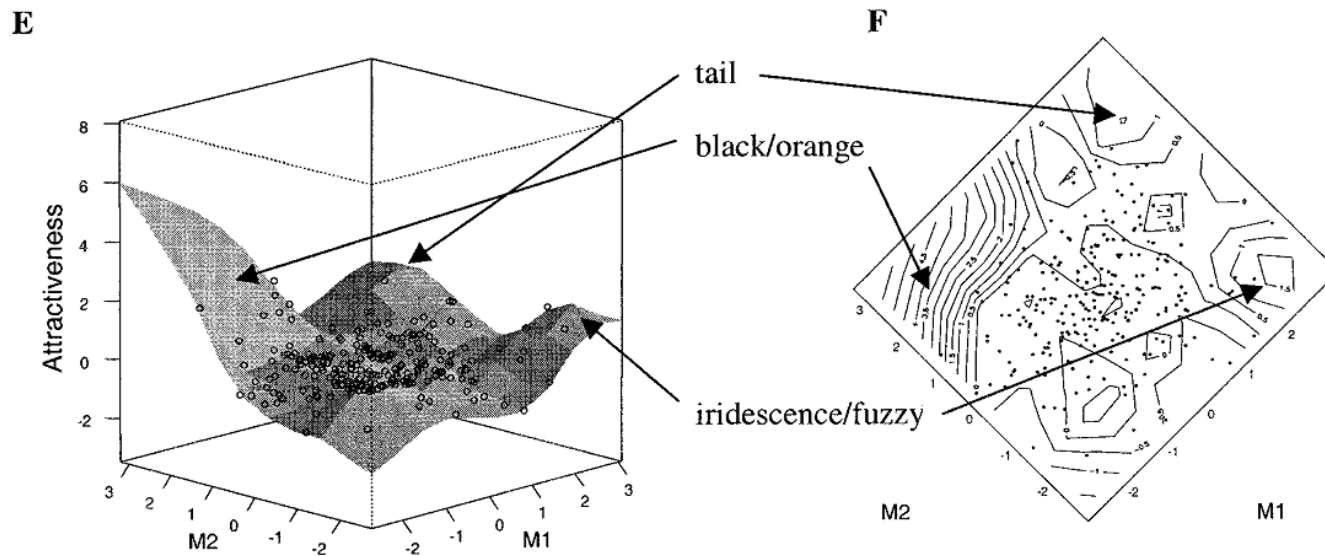


FIG. 1. Fitness surfaces of the pairwise combinations of the three significant canonical axes \mathbf{m}_1 , \mathbf{m}_2 , and \mathbf{m}_6 . The three-dimensional surfaces on the left (A, C, E) have been fitted using a thin-plate spline. The contour diagrams on the right (B, D, F) are the same surfaces from above. Plotted points in each diagram are the predicted values for each individual from the thin-plate splines. Peaks on the surfaces are labeled with the original traits that contribute most strongly to these regions when the coefficients of both eigenvectors (Table 2) are interpreted simultaneously (see text).

FROM BLOWS, BROOKS & KRAFT. EVOLUTION 57: 622-630 (2003).



4 .STABILIZING AND DISRUPTIVE SELECTION

Hessian $\mathbf{H}(f(\mathbf{x}))$

$$\mathbf{H}_x f(\mathbf{x}) = \nabla_x (\nabla_x f(\mathbf{x}))^T = \frac{\partial^2 f}{\partial \mathbf{x} \partial \mathbf{x}^T} = \begin{pmatrix} \frac{\partial^2 f}{\partial x_1^2} & \cdots & \frac{\partial^2 f}{\partial x_1 x_n} \\ \vdots & \ddots & \vdots \\ \frac{\partial^2 f}{\partial x_1 x_n} & \cdots & \frac{\partial^2 f}{\partial x_n^2} \end{pmatrix}$$

Under regular conditions, this matrix is symmetric.

When the Hessian \mathbf{H} , evaluated at a point \mathbf{x}_0 , is positive definite, then \mathbf{x}_0 is a local minimum.

with \mathbf{H} negative definite, \mathbf{x}_0 is a local maximum.

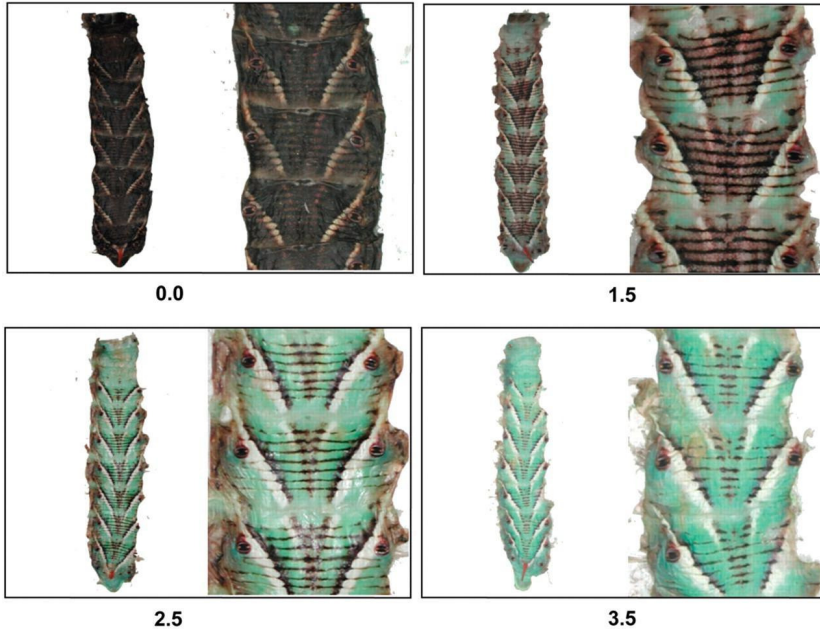
When some eigenvalues of \mathbf{H} are negative and some positive, the hessian \mathbf{H} corresponds to a saddle.

$$\begin{aligned}
\mathbf{H}_\mu \ln(\overline{W}(\hat{\boldsymbol{\mu}}_z)) &= \nabla_\mu \left(\nabla_\mu \ln(\overline{W}(\hat{\boldsymbol{\mu}}_z)) \right)^T \\
&= \nabla_{\boldsymbol{\mu}_z} \left(\mathbf{P}^{-1} (\mathbf{P}^* \mathbf{P}^{-1} - \mathbf{I}) \boldsymbol{\mu}_z + \mathbf{P}^* \mathbf{W} \boldsymbol{\theta} + \mathbf{P}^* \boldsymbol{\alpha} \right) \Big|_{\boldsymbol{\mu}_z = \hat{\boldsymbol{\mu}}_z} \\
&= \mathbf{P}^{-1} (\mathbf{P}^* \mathbf{P}^{-1} - \mathbf{I}) \\
&= \mathbf{P}^{-1} \mathbf{P}^* (\mathbf{P}^{-1} - \mathbf{P}^{*-1}) \\
&= \mathbf{P}^{-1} \mathbf{P}^* (\mathbf{P}^{-1} - \mathbf{W} - \mathbf{P}^{-1}) \\
&= -\mathbf{P}^{-1} \mathbf{P}^* \mathbf{W}
\end{aligned}$$

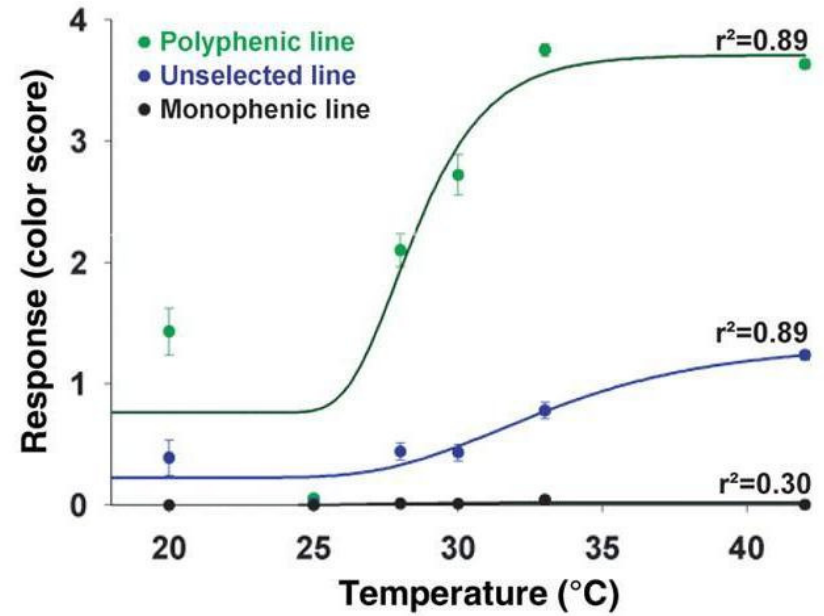
$\mathbf{P}^{-1} \mathbf{P}^*$ will usually be positive definite.

Then \mathbf{W} has as many positive eigenvalues as the \mathbf{H}_μ will have negative ones and vice versa.

Heat-shocked *black* mutant



B



Suzuki, Y. and Nijhout, H.F., Evolution of a polyphenism by genetic accommodation., Science, vol. 311 (2006), pp. 650-652 .

PS. SELECTION ON REACTION NORMS

The inner product of two univariate functions η and ξ is a scalar $\eta^T \xi$:

$$\eta^T \xi = \int_a^b \eta(e) \xi(e) de$$

Multiplying a covariance (bivariate) function Ψ with a univariate one, ψ , gives a univariate function as a result:

$$(\Psi \xi)(e) = \int_a^b \Psi(e, f) \xi(f) df$$

Transpose $\Psi^T(f, e) = \Psi(e, f)$

Inverse $\Theta^{-1} \Psi \xi = \xi$ for any univariate function ξ

$$\Delta\mu_g(e) = \mu_g(e)^* - \mu_g(e) = (\sigma_g \sigma_p^{-1} s)(e) \quad (\text{Kirkpatrick and Heckman 1989})$$

where s is the phenotypic selection differential $s(f) = \mu_z(f)^* - \mu_z(f)$,

σ_p the phenotypic covariance function

σ_g the genetic covariance function.

$\beta = (\sigma_p^{-1} s)$ the *function-valued selection/fitness gradient*.

FUNCTION-VALUED FITNESS GRADIENT

With Λ an operator from vector space \mathbb{U} to a normed vector space \mathbb{V} , let function η be in the domain of Λ and let ρ be an arbitrary element of \mathbb{U} . If the limit, with c a scalar,

$$d\Lambda(\eta; \rho) = \lim_{c \rightarrow 0} \frac{\Lambda(\eta + c\rho) - \Lambda(\eta)}{c}$$

exists, it is called the *Gateaux* or *weak differential* of Λ at η with increment ρ . If this differential exists for all ρ , we say that Λ is Gateaux differentiable at η .

The Gateaux differential of fitness $W(z)$ of a function valued strategy z then becomes

$$dW(z) = \frac{d}{d\alpha} W(z + \alpha u) \Big|_{\alpha=0}$$

The *strong* or *Fréchet differential* at η , which makes use of the norm of ρ , so \mathbf{U} has to be a normed vector space for that.

If for a fixed η and for each increment ρ , $d\Lambda(\eta; \rho)$ exists and is (i) continuous in ρ , and (ii) linear in ρ such that

$$\lim_{\|\rho\| \rightarrow 0} \frac{\|\Lambda(\eta + \rho) - \Lambda(\eta) - d\Lambda(\eta; \rho)\|}{\|\rho\|} = 0$$

then $d\Lambda(\eta; \rho)$ is the Fréchet differential with increment ρ . When a Fréchet differential exists, it is equal to the Gateaux differential at η .

This differential $d\Lambda(\eta; \rho)$ specifies a continuous linear operator $\Lambda'_s(\eta)$ at η such that for all increments ρ ,

$$d\Lambda(\eta; \rho) = \Lambda'_s(\eta)\rho .$$

$\Lambda'_s(\eta)$ is the *Fréchet derivative* of Λ at η .

Concerning fitness, assuming that the Gateaux/Fréchet differential exists, it is

$$dW(z) = \frac{d}{d\alpha} W(z + \alpha u) \Big|_{\alpha=0} = W'_s(z)u = \int_a^b W'_s(z)(e)u(e)de$$

Fréchet derivative at a specific value of e , say $e^\#$:

$$W'_s(z)(e^\#) = \int_a^b W'_s(z)(e)\delta_{e^\#}(e)de = \frac{d}{d\alpha} W(z + \alpha\delta_{e^\#}) \Big|_{\alpha=0}$$

The *function-valued fitness gradient* $\beta(e^\#)$, is equal to $W'_s(z)(e^\#)$

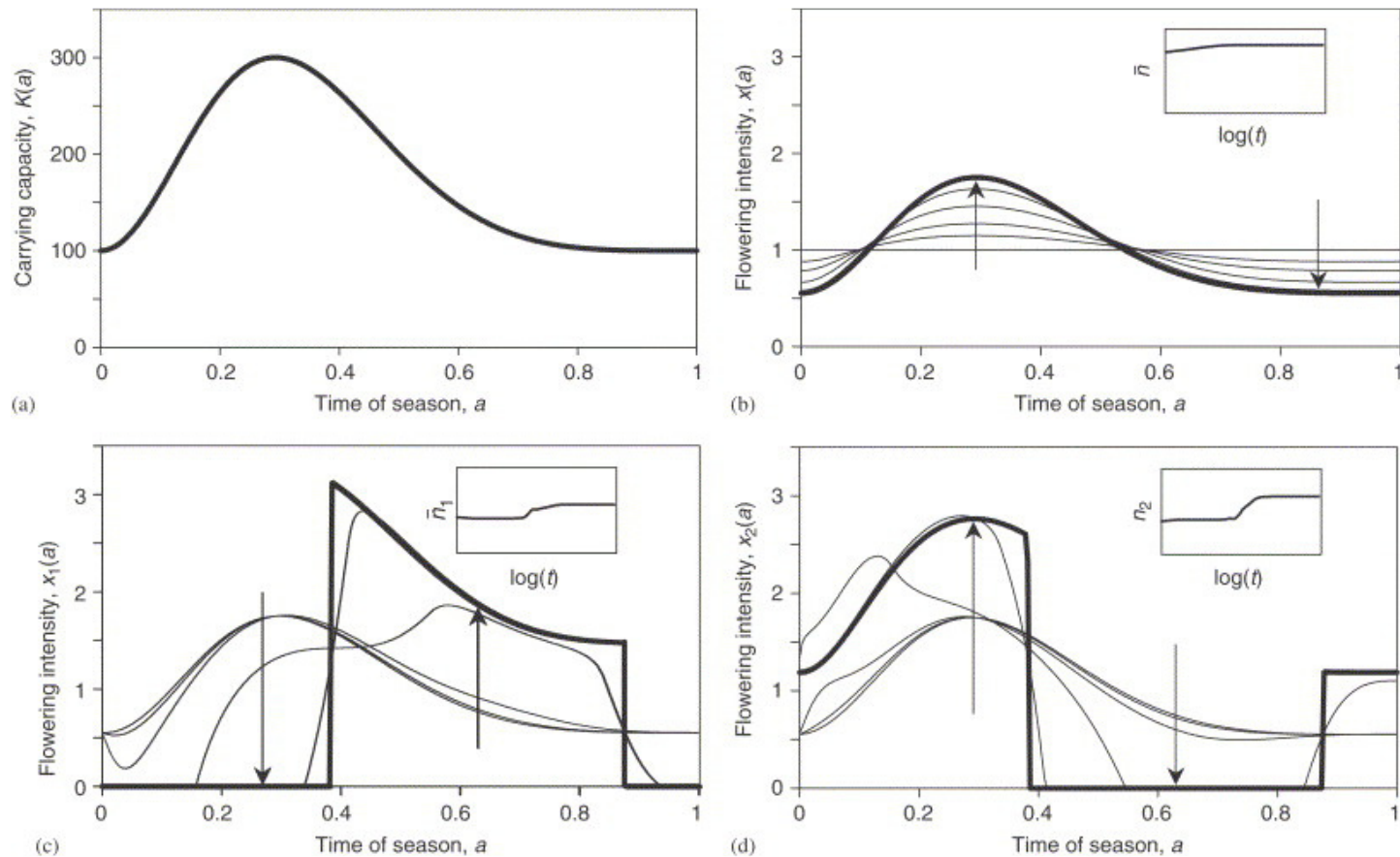


Fig. 3. Evolution of seasonal flowering schedules. (a) Carrying capacity $K(a)$ at different times a during the season. (b) Dynamics and outcome $x^*(a)$ of monomorphic evolution of flowering intensity $x(a)$. (c) and (d) Dynamics and outcome of dimorphic evolution of flowering intensities $x_1(a)$ and $x_2(a)$ started from the neighborhood of the monomorphic evolutionary outcome $x^*(a)$. Initial and intermediate trait values are shown as thin curves, and final values as thick curves. Insets show changes in equilibrium population sizes resulting from the depicted evolutionary change. Dieckmann et al. 2006

References

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http://nitro.biosci.arizona.edu/zbook/volume_2/vol2.html

Dieckmann U, M Heino & K Parvinen. 2006. The adaptive dynamics of function-valued traits. *J. theor. Biol.* 241:370-.