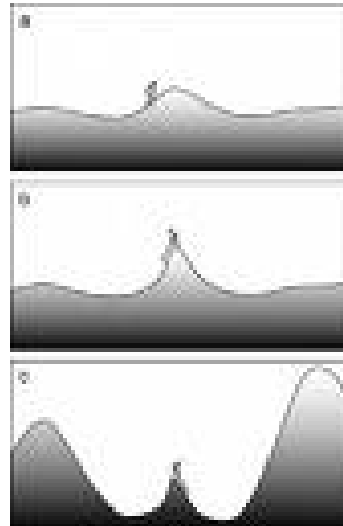


# SHIFTING FITNESS LANDSCAPES – GENERAL SELECTION SCHEMES

## Towards more Ecology



Tom Van Dooren  
11/2012  
vandoore@biologie.ens.fr

**1. Frequency-dependent selection**

**2. Approximation – adaptive dynamics**

**3. Selection response in structured populations**



Tom JM Van Dooren, H van Goor and M van Putten 2010 Handedness and asymmetry in scale-eating cichlids: antisymmetries of different strength. *Evolution* 64: 2159-2165.

## RECAP FIXED FITNESS LANDSCAPES

Breeder's equation

$$\Delta\boldsymbol{\mu}_z = \mathbf{G}\mathbf{P}^{-1}(\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) = \mathbf{G}\boldsymbol{\beta}$$

Fitness gradient if the phenotype distribution of  $\mathbf{z}$  is MVN

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

Another way of writing the selection gradient

$$\begin{aligned}\beta &= \mathbf{P}^{-1} \left( \int dz f(\mathbf{z}) w(\mathbf{z}) \mathbf{z} - \mu_{\mathbf{z}} \int dz f(\mathbf{z}) w(\mathbf{z}) \right) \\ &= \mathbf{P}^{-1} \text{Cov}(\mathbf{z}, w(\mathbf{z}))\end{aligned}$$

## 1. FREQUENCY DEPENDENT SELECTION

Fitness  $W(z, \mu_z)$  depends on population average

Mean fitness  $\overline{W}(z, \mu_z) = \int dz f(z, \mu_z) W(z, \mu_z)$

With MVN phenotype distribution

$$\begin{aligned}
\nabla_{\mu_z} \ln(\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)) &= \overline{W}^{-1} \nabla_{\mu_z} \overline{W}(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \nabla_{\mu_z} \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \int d\mathbf{z} w(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} f(\mathbf{z}, \boldsymbol{\mu}_z) + \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \mathbf{P}^{-1} \int d\mathbf{z} f(\mathbf{z}) \mathbf{z} w(\mathbf{z}, \boldsymbol{\mu}_z) - \mathbf{P}^{-1} \boldsymbol{\mu}_z + \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} w(\mathbf{z}, \boldsymbol{\mu}_z) \\
&= \mathbf{P}^{-1} (\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) + \overline{W}^{-1} \int d\mathbf{z} f(\mathbf{z}, \boldsymbol{\mu}_z) \nabla_{\mu_z} [W(\mathbf{z}, \boldsymbol{\mu}_z)]
\end{aligned}$$

The frequency-dependent breeder's equation becomes

$$\begin{aligned}\Delta\boldsymbol{\mu}_z &= \mathbf{G}\mathbf{P}^{-1}(\boldsymbol{\mu}_z^* - \boldsymbol{\mu}_z) \\ &= \mathbf{G}\left(\nabla_{\boldsymbol{\mu}_z} \ln(\bar{W}(z, \boldsymbol{\mu}_z)) - \bar{W}^{-1} \int dz f(z, \boldsymbol{\mu}_z) \nabla_{\boldsymbol{\mu}_z} [W(z, \boldsymbol{\mu}_z)]\right)\end{aligned}$$

→ Evolution does not climb to a top of the mean fitness landscape  
(Day and Taylor 1996)



## 2. ESS APPROXIMATIONS adaptive dynamics

goal: get an equation for the selection gradient that depends on the phenotypic mean  $\mu_z$  only.

$$\begin{aligned}\Delta\mu_z &= \mathbf{GP}^{-1}(\mu_z^* - \mu_z) \\ &= \mathbf{GP}^{-1} \overline{W}(\mathbf{z}, \mu_z)^{-1} \int d\mathbf{z} f(\mathbf{z}, \mu_z)(\mathbf{z} - \mu_z) W(\mathbf{z}, \mu_z)\end{aligned}$$

What we can expand, is the fitness of an individual:

$$W(\mathbf{z}, \mu_z) = W(\mu_z, \mu_z) + (\mathbf{z} - \mu_z)^T D_1 W(\mu_z, \mu_z) + \frac{1}{2} (\mathbf{z} - \mu_z)^T D_{11} W(\mu_z, \mu_z) (\mathbf{z} - \mu_z) + h.o.t$$

ESS APPROXIMATIONS  
adaptive dynamics

Inserting this expansion yields

$$\Delta\boldsymbol{\mu}_z = \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \boldsymbol{\mu}_z)^{-1} \left( \begin{array}{l} \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) \\ + \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)^T D_1 W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z) \\ + \frac{1}{2} \int dz f(\mathbf{z}, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z)^T D_{11} W(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)(\mathbf{z} - \boldsymbol{\mu}_z) \\ + h.o.t. \end{array} \right)$$

With symmetric probability distributions  $f$  (of phenotypes), the integrals over odd powers of  $\mathbf{z} - \boldsymbol{\mu}_z$  will vanish.

We retain the following approximate expression:

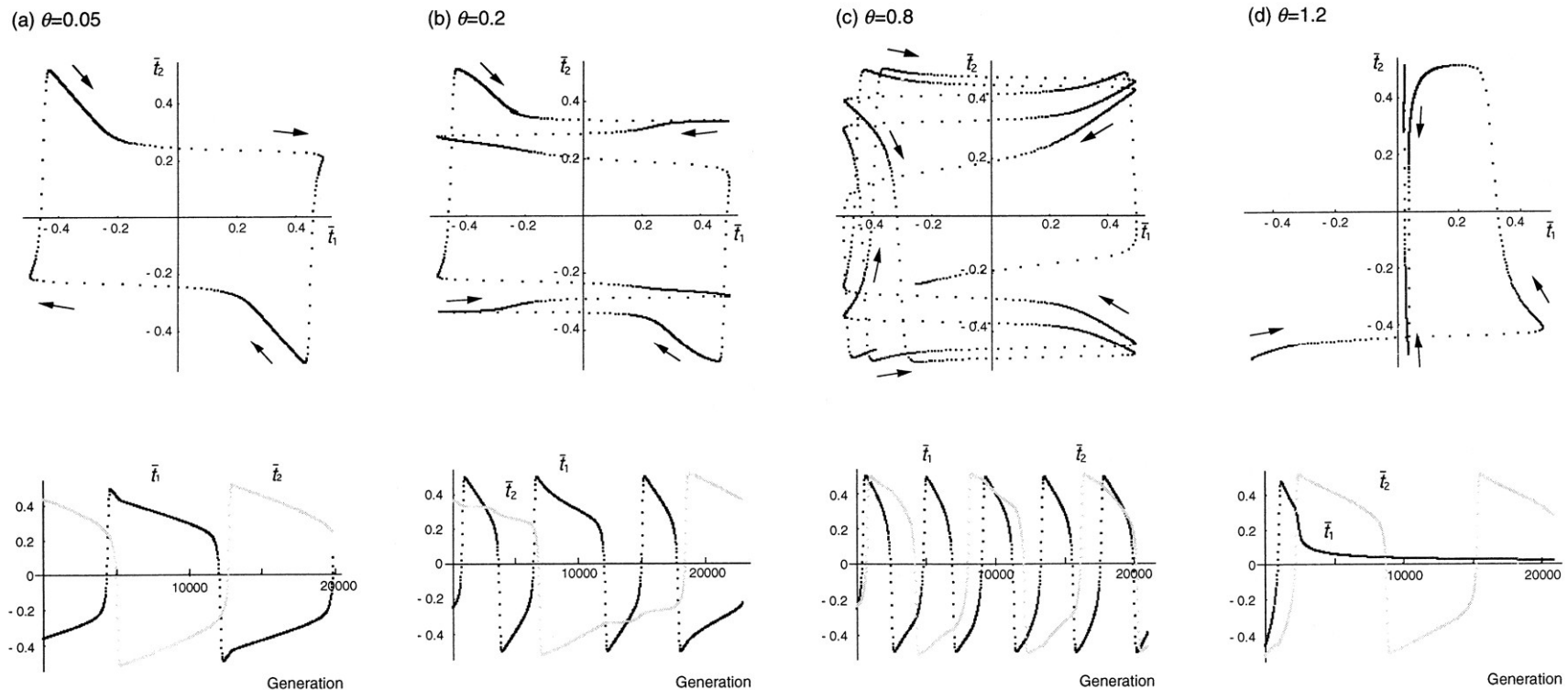
$$\begin{aligned}
 \Delta\mu_z &= \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \mu_z)^{-1} \left( \int dz f(\mathbf{z}, \mu_z) (\mathbf{z} - \mu_z)(\mathbf{z} - \mu_z)^T D_1 W(\mu_z, \mu_z) + h.o.t. \right) \\
 &= \mathbf{GP}^{-1}\overline{W}(\mathbf{z}, \mu_z)^{-1} \left( \mathbf{PD}_1 W(\mu_z, \mu_z) + h.o.t. \right) \\
 &\cong \mathbf{G}\overline{W}(\mathbf{z}, \mu_z)^{-1} D_1 W(\mu_z, \mu_z)
 \end{aligned}$$

This approximation holds good as long as selection is not too weak (Abrams 1993).

If we expand mean fitness as well (Iwasa et al. 1991):

$$\Delta\mu_z \cong \mathbf{G}\nabla_z \ln W(\mu_z, \mu_z)$$

....Hey ! That looks simple!

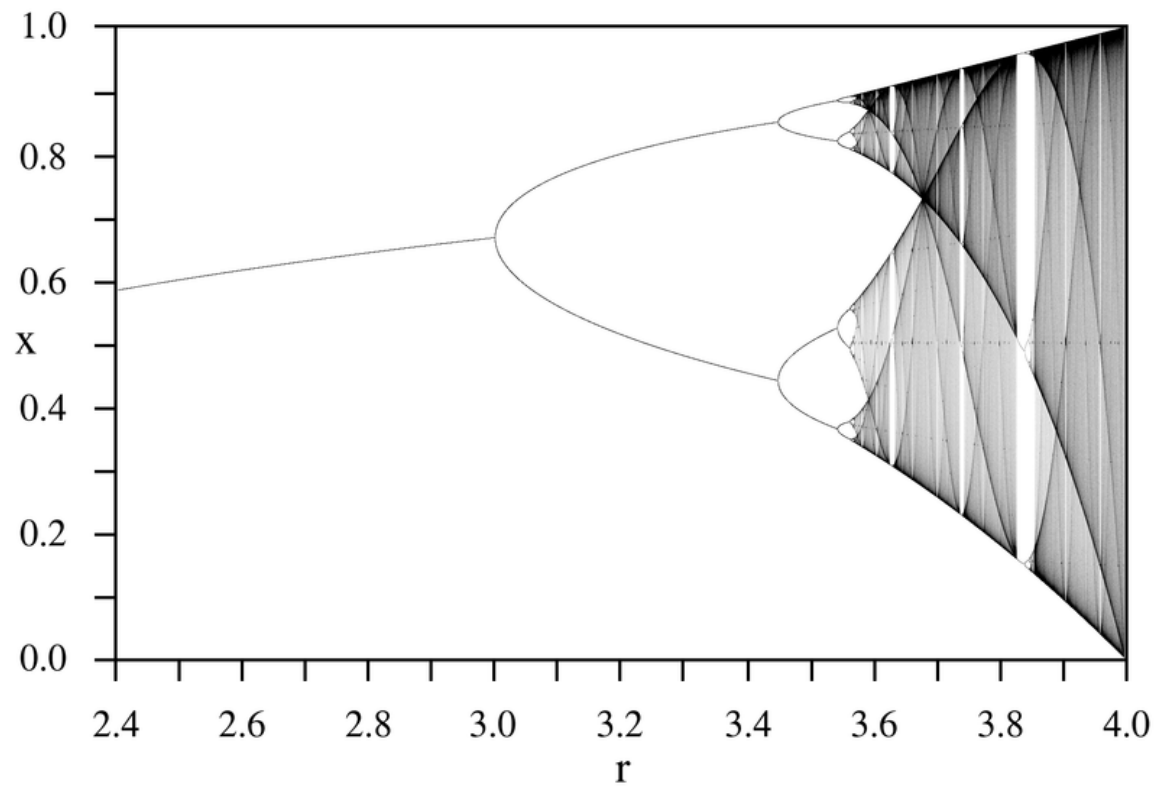


Coevolution of two preferences for separate male ornaments as a function of epistasis in the joint cost of choice  $\theta$ . Phase-space of the mean male ornaments ( $\bar{t}_1$  and  $\bar{t}_2$ ) every 20 generations; second as  $\bar{t}_1$  (black) and  $\bar{t}_2$  (gray) values through time.

Iwasa, Y. and A. Pomiankowski, 1995. Continual change in mate preferences. Nature 377:420-422.

## BIFURCATION ANALYSIS

Parameter changes provoke changes between qualitative regimes



LOGISTIC MAP [http://en.wikipedia.org/wiki/Bifurcation\\_diagram](http://en.wikipedia.org/wiki/Bifurcation_diagram)

## STABILITY ANALYSIS

Use this approximation to define a dynamics system with discrete time steps

$$\mu_{z,t+1} = \mu_{z,t} + \Delta\mu_{z,t}$$

We can investigate the (convergence) stability of an equilibrium  $\mu_z^{\text{CS}}$

$$\begin{aligned}(\mu_{z,t+1} - \mu_z^{\text{CS}}) &= \frac{\partial}{\partial \mu_{z,t}} (\mu_{z,t} + \Delta\mu_{z,t}) \Big|_{\mu_{z,t} = \mu_z^{\text{CS}}} (\mu_{z,t} - \mu_z^{\text{CS}}) \\ &= 1 + \frac{\partial}{\partial \mu_{z,t}} \Delta\mu_{z,t} \Big|_{\mu_{z,t} = \mu_z^{\text{CS}}} (\mu_{z,t} - \mu_z^{\text{CS}}) \\ &= \left( 1 + \frac{\partial}{\partial \mu_{z,t}} \Delta\mu_z^{\text{CS}} \right) (\mu_{z,t} - \mu_z^{\text{CS}})\end{aligned}$$

## HESSIAN- INVASIBILITY

What about invasibility of  $\mu^{\text{CS}}_z$  by new mutants?

$$\mathbf{H}_{ij}(\mu^{\text{CS}}_z) = \left( D_{11} W(\mu^{\text{CS}}_z, \mu^{\text{CS}}_z) \right)_{ij} = \frac{\partial^2}{\partial z_i \partial z_j} W(z, \mu^{\text{CS}}_z) \Bigg|_{z=\mu^{\text{CS}}_z}$$

When the Hessian  $\mathbf{H}$ , evaluated at a point  $\mu^{\text{CS}}_z$ , is positive definite, then  $\mu^{\text{CS}}_z$  is a local minimum

with  $\mathbf{H}$  negative definite,  $\mu^{\text{CS}}_z$  is a local maximum

When some eigenvalues of  $\mathbf{H}$  are negative and some positive, the hessian  $\mathbf{H}$  corresponds to a saddle at  $\mu^{\text{CS}}_z$

## DIRECTIONAL EVOLUTIONARY DYNAMICS

'Continuous' time (e.g. Day and Taylor 2003)

$$\frac{d\boldsymbol{\mu}_z}{dt} = \text{cov}(\mathbf{z}, w(\mathbf{z}, \boldsymbol{\mu}_z))$$

If the derivative of  $w$  does not change much over the distribution of  $\mathbf{z}$

$$\frac{d\boldsymbol{\mu}_z}{dt} = \mathbf{G}(\boldsymbol{\mu}_z) \nabla_{\mathbf{z}} w(\boldsymbol{\mu}_z, \boldsymbol{\mu}_z)$$

The points in trait space which are equilibria of this dynamic are often written as

$$\boldsymbol{\mu}^*$$

Where the  $\mathbf{z}$  is now omitted too...



## CONVERGENCE STABILITY OF CANDIDATE ESS'S

Expand the selection gradient  $D_1 w$  around the singular point.  
That gives, eventually,

$$D_1 w(\boldsymbol{\mu}^*, \boldsymbol{\mu}^*) \cong (\mathbf{H}(\boldsymbol{\mu}^*) + \mathbf{Q}(\boldsymbol{\mu}^*))(\boldsymbol{\mu} - \boldsymbol{\mu}^*) \cong \mathbf{J}(\boldsymbol{\mu}^*)(\boldsymbol{\mu} - \boldsymbol{\mu}^*)$$

$$\frac{d(\boldsymbol{\mu} - \boldsymbol{\mu}^*)}{dt} = \mathbf{G}(\boldsymbol{\mu}^*)\mathbf{J}(\boldsymbol{\mu}^*)(\boldsymbol{\mu} - \boldsymbol{\mu}^*)$$

Summarizing: the eigenvalues of  $\mathbf{H}$  determine INVASIBILITY,  
the eigenvalues of  $\mathbf{J}$  will determine CONVERGENCE STABILITY.

### 3. POPULATION STRUCTURE



Southern Right Whale



*Protea pudens*

No density nor frequency-dependence

Lande (1982)

Weak selection and overlapping generations

Age structure

Approximation

Replace  $w$  by little  $r$  the intrinsic rate of growth

$$\frac{dz}{dt} = \mathbf{G} \nabla r$$

$$\int_0^{\infty} da e^{-ra} E[l_a(\mathbf{z}) m_a(\mathbf{z})] = 1$$

Day and Taylor (1996)

Approximation + Frequency dependence

Lifetime reproductive output discounted for population growth

$$w(r, z, \mu) = \int_0^{\infty} da e^{-E[r]a} l_a(z, \mu) m_a(z, \mu)$$

$$\frac{dz}{dt} = \frac{dE[r]}{d\mu} - \bar{T}^{-1} \nabla E \left[ \frac{dw}{d\mu} \right]$$

$$\bar{T} = \int_0^{\infty} da e^{-E[r]a} E[l_a(z, \mu) m_a(z, \mu)] a$$

These are still not 'general' population models  
Selection has to be weak.

## TRAIT VECTORS PER INDIVIDUAL STATE

Law (1991)

Different stages/ages where individuals can be in  
 $m$  traits,  $n$  stages

$$\mathbf{M}_t = \begin{pmatrix} \boldsymbol{\mu}_{1,t} \\ \vdots \\ \boldsymbol{\mu}_{n,t} \end{pmatrix}$$

and  $\mathbf{G}$  and  $\mathbf{P}_i$  which are  $m \times m$  matrices

at birth the mean phenotypic values are equal to the mean genotypic values.  
Selection during life makes mean phenotypic and genotypic values different in  
different stages.

Directional selection

update rules for mean trait vectors

$G$  assumed constant and identical for all individual states  
- a first assumption to relax

$$\mathbf{S}_t = \begin{pmatrix} \mu_{1,t}^* - \mu_{1,t} \\ \vdots \\ \mu_{n,t}^* - \mu_{n,t} \end{pmatrix}$$

only non-zero elements for ages where traits are expressed.

Changes in genotypic values

$$\widehat{\mathbf{G}}_t \widehat{\mathbf{P}}_t^{-1} \mathbf{S}_t = \text{diag}(\mathbf{G}_t) \text{diag}(\mathbf{P}_{1,t}^{-1} \cdots \mathbf{P}_{n,t}^{-1}) \begin{pmatrix} \mu_{1,t}^* - \mu_{1,t} \\ \vdots \\ \mu_{n,t}^* - \mu_{n,t} \end{pmatrix}$$

Population dynamics

Transition matrix  $\mathbf{T}$

$T_{ij}$  probability that an individual in state  $i$  receives a gene from an individual in state  $j$

$$\mathbf{M}_{t+1} = (\mathbf{T}_t \otimes \mathbf{I})(\mathbf{M}_t + \widehat{\mathbf{G}}_t \widehat{\mathbf{P}}_t^{-1} \mathbf{S}_t)$$

This framework is still being developed further

For traits that are shared by different ages

For population structures that are modelled with integral projection models:  
continuous state variable - discrete time steps



# The Dynamics of a Quantitative Trait in an Age-Structured Population Living in a Variable Environment

Tim Coulson<sup>1,\*</sup> and Shripad Tuljapurkar<sup>2,†</sup>

---

## Modeling Effects of Environmental Change on Wolf Population Dynamics, Trait Evolution, and Life History

Tim Coulson,<sup>1\*</sup> Daniel R. MacNulty,<sup>2,†</sup> Daniel R. Stahler,<sup>3</sup> Bridgett vonHoldt,<sup>4</sup> Robert K. Wayne,<sup>5</sup> Douglas W. Smith<sup>3</sup>

mental change can have cascading effects across trophic levels (9). Given that environmental change can lead to potentially complex genetic, phenotypic, life history, and demographic responses, how can its likely consequences be explored? We show how integral projection models (IPMs) (10) provide a powerful framework to simultaneously investigate the ecological and evolutionary consequences of environmental change. We developed, applied, and analyzed one to ex-

## References

- Day, T and PD Taylor. 1996. Evolutionarily stable versus fitness maximizing life histories under frequency dependent selection. *Proc. Roy. Soc. Lond. B* 333-338
- Day, T. and P. Taylor. 2003. Evolutionary dynamics and stability in discrete and continuous games. *Evolutionary Ecology Research* 5:605-615
- Iwasa, Y Pomiankowski, A and S Nee. 1991. The evolution of costly mate preference II. The 'handicap' principle. *Evolution* 45: 1431–1442
- Law, R. 1991. On the quantitative genetics of correlated characters under directional selection in age-structured populations. *Phil. trans. Roy. Soc. Lond. B, Biol.* 331:12601260, 213-220
- Lande, R. 1982. 1982. A quantitative genetic theory of life history evolution. *Ecology* 63:607-615