REACTION NORMS – FUNCTION-VALUED STRATEGIES

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1. INTRODUCTION

A reaction norm function describes which collection of phenotypes a single genotype will produce over a range of environmental conditions (Woltereck 1909). The term developmental reaction norm (Schlichting & Pigliucci 1998) has been coined to stress the fact that each morphological phenotype is a state of an ontogenetic or developmental dynamical system. For reaction norms with a property that is called *plasticity*, the dynamics (trajectory and attractor) of such a developmental dynamical system is dependent on environmental parameters. Reaction norms for morphological traits that have completed their development will then show the attracting equilibrium states of the developmental dynamics over a range of values of the environmental variable or variables. As such, reaction norms correspond to bifurcation diagrams of the developmental dynamics.

Discontinuous reaction norms can occur and the state of the environment where the discontinuity is situated corresponds to an environmentally controlled bifurcation of the developmental dynamical system. Such bifurcations correspond to qualitative changes in the dynamical behaviour that occur when a control variable is slightly altered. However, the focus is usually on smooth reaction norms, where no bifurcation occurs over the range of environments and where the measured traits are continuous variables.

Another viewpoint on reaction norms is via so-called *age dependent traits* (Kirkpatrick and Heckman 1989). In that case, the environmental variable is the time axis, and reaction norms are simply descriptions of developmental trajectories, such as growth curves.

Now that the focus has come to be on developmental reaction norms, little attention is given to reversible phenotypes. In principle, behaviour can also be seen as a reaction norm, where cues that elicit behaviour are the environmental variables.

2. REACTION NORMS

It is not really easy to characterize developmental reaction norms in full generality. They are function-valued or infinite-dimensional traits or strategies, where function arguments are parameters that derive from genetic effects, from time series of phenotype determining environmental variables, and environmental variables recorded at the moment of observation. Moreover, we should keep in mind that these function-valued traits are trajectories or stationary states of non-linear (infinite-dimensional) dynamical systems.

I will discuss function-valued traits that are in a sense most similar to univariate traits, namely functions that map a single environmental variable to a single scalar phenotype per environment.

Function representations are always simplified by ignoring as many of the arguments as possible, i.e., I will only write one environmental variable e explicitly.
Reaction norm developmental dynamical systems cannot be completely deterministic, noise effects and stochasticity have to kick in at some point. The stochastic part of the developmental reaction norm is usually neglected as much as possible, and treated as sample variance or insignificant noise, while this noise may be adaptive (Haccou and Iwasa 1995, Van Dooren 2001).

We follow the description of functional traits as in Pletcher and Geyer (1999, using stochastic processes. Note that we describe a trait that is a scalar function per environment, not a vector-valued one. That class of reaction norms doesn't seem to have been (openly) tackled yet, although the necessary extension from the material discussed here seems straightforward.

A stochastic process is a family of random variables $z(e)$. Function z can be taken to be the function-valued phenotype observed over a range of environments e, with $e \in [a, b]$ and $[a, b]$ is a subset of the real line (Doob 1953). A specific realization is called a sample path, and in the case of an age-dependent trait that would be an individual developmental trajectory. We assume so-called second-order processes that have finite variance per environment: $E[z(e)^2] < \infty$. The expectation is taken over the distribution of phenotypes conditional on the state of the environment e.
We can define a mean function of such a process as

$$\mu_z(e) = E[z(e)] \tag{2.1}$$

And a covariance function

$$\sigma_z(e_i, e_j) = COV[z(e_i), z(e_j)] \text{ with } e_i, e_j \in [a, b] \tag{2.2}$$

The expectations in (2.1) and (2.2) are taken over the distributions of phenotypes conditional on the states of the environment e or e_i.
Such a covariance function must be non-negative definite in order to have positive variances always, i.e., for any finite set of environments e_i and any set of real numbers b_i both indexed from 1 to n,

$$\sum_{i=1}^{n}\sum_{j=1}^{n} b_i b_j \sigma_z(e_i, e_j) \geq 0 \tag{2.3}$$

Stochastic processes are *Gaussian* if the joint distribution of every finite set $\{z(e)\}$ is multivariate normal. Gaussian processes are completely determined by their mean and covariance function. It must be clear that these processes have special interest in the context of quantitative genetics, where multivariate normal probability distributions play an important role.

In quantitative genetics, the following linear decomposition of phenotype is used. Phenotype z is the sum of a mean function μ_z, plus a genotypic g and an environmental contribution e, which are assumed to be independent and to have zero mean:

$$z(e) = \mu_z(e) + g(e) + \varepsilon(e) \tag{2.4}$$

We can also omit the environmental argument and write phenotype as the sum of functions $z = \mu_z + g + \varepsilon$.
This is usually done when the function valued trait is not considered at a specific value of the environment e.

The phenotypic covariance function of (2.4) can be decomposed as

$$\sigma_z(e_i, e_j) = \sigma_g(e_i, e_j) + \sigma_\varepsilon(e_i, e_j) \tag{2.5}$$

Further simplification of functional reaction norms is done along the following lines that lead to finite-dimensional representations again (Via et al. 1995):
(*i*) The functional strategy is discretized as an indexed array or vector of function values in different environments. This is called the *character state approach*, where we obtain a trait vector of mean strategies per environment with genetic variances and covariances between them.
(*ii*) The function is specified by a specific function prescription with –next to the environmental variable- a finite number of arguments or parameters. For instance, this can be done by a polynomial function of the environmental variable. In that case, one speaks of the *polynomial approach*. Analysis proceeds with a trait vector of polynomial coefficients and covariances between them.
In fact, to some extent the two approaches can be equivalent, since you can transform polynomial reaction norms to character state vectors easily (De Jong 1995). The reverse operation is a bit more involved.

The descriptions of a reaction norm in the alternative approaches are either as a vector of character states $z^T = (z_1, z_2,\ldots, z_n)^T$ in environments indexed i, $i = 1,\ldots,$ n; or by a vector of coefficients of a polynomial function (of order m) of an environmental variable, $v^T = (v_0, v_1, v_2,\ldots, v_m)^T$.
The character states can be calculated from the polynomial coefficients, using the values of the environmental variables in the different indexed environments, e_i, as follows:

$$z = Ev \tag{2.6}$$

with E a matrix with m = 1 columns that has per row a polynomial series of e_i:

$$E_i = \begin{pmatrix} 1 & e_i & e_i^2 & \ldots e_i^m \end{pmatrix} \tag{2.7}$$

Per entry in the character state vector one then obtains

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$$z_i = v_0 + v_1 e + v_2 e^2 + \ldots + v_m e^m$$

Notice that E defines a linear mapping between two trait spaces. With non-linear dependencies, we can approach by a polynomial Taylor expansion around a reference value of the environmental variable. This works well only with small ranges of an environmental variable and smooth (several times differentiable) reaction norm functions.

In the reverse direction, the transformation is often not straightforward, since E usually will not be a square matrix (and then does not have an inverse). We can use the least-squares assumption, and find the trait vector v that minimizes the squared distance between z and Ev. Trait vector v then can be mapped from z as follows:

$$v = (E^T E)^{-1} E^T z = Uz \tag{2.8}$$

This transformation is possible provided that the matrix $E^T E$ is invertible. That is usually the case when the order of the polynomial m is smaller than the number of different indexed environments (Searle 1982).

The linear mapping (2.6) relates the genetic variance covariance matrix of z to the one of v.

$$G_z = E G_v E^T \tag{2.9}$$

and for the reverse direction, we use (2.8) again,

$$G_v = U G_z U^T \tag{2.10}$$

Such genetic covariances can be estimated from covariances between groups of individuals with different relatedness coefficients (Lynch and Walsh 1998 give a review).

3. SELECTION ON REACTION NORMS

Selection on infinite-dimensional traits is inherently more difficult to handle than a low-dimensional approach. In order to achieve some degree of generality, concepts and techniques are needed from functional analysis, and from integration and measure theory. An in-depth treatment is really beyond the scope of this text. Consult Kirkpatrick and Heckman (1989) next to Beder and Gomulkiewicz (1998) in order to appreciate the level of sophistication that comes with increased mathematical generality. I will present the main results (showing that selection equations can often be written in familiar ways) in a rather naïve way.

As with selection in the finite multivariate case, we will use linear mappings or operators again on a vector space. We need to multiply objects, and take their inverses or transpose. Multiplication of functional strategies goes as follows:

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

$$\eta^T\xi = \int_a^b \eta(e)\xi(e)de \tag{3.1}$$

Where $[a, b]$ specifies the domain of both functions. This is a definite integral over the range of the environmental variable e. If you feel for a measure theoretical approach, you have to integrate over the measure space of e.

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

$$(\Psi\xi)(e) = \int_a^b \Psi(e, f)\xi(f)df \tag{3.2}$$

The transpose Ψ^{T} of a bivariate function Ψ satisifies

$$\Psi^T(f, e) = \Psi(e, f) \tag{3.3}$$

and an inverse Θ^{-1} of the operation (2.7) pre-multiplies that equation to give

$$\Theta^{-1}\Psi\xi = \xi \tag{3.4}$$

for any univariate function ξ.

After a lot of work, one can show (Kirkpatrick and Heckman 1989) that the evolutionary change of the mean function $\mu_g(e)$ over a round of selection equals

$$\Delta\mu_g(e) = \mu_g(e)^* - \mu_g(e) = \left(\sigma_g\sigma_p^{-1}s\right)(e) \tag{3.5a}$$

or

$$\Delta\mu_g(e) = \mu_g(e)^* - \mu_g(e) = \int_a^b dh \int_a^b df \sigma_g(e, h)\sigma_p^{-1}(h, f)s(f) \tag{3.5b}$$

where s is the phenotypic selection differential $s(f) = \mu_z(f)^* - \mu_z(f)$, σ_p the phenotypic covariance function and σ_g the genetic covariance function. One can also define

$$\beta = \left(\sigma_p^{-1}s\right) \tag{3.6}$$

as the *function-valued selection gradient*.

Reproduction with random mating and without new mutational input will not affect this change, so that it can predict the change in mean phenotype across a generation.

4. FUNCTION-VALUED FITNESS GRADIENT

Often, the phenotypic selection differential or the selection gradient is obtained by taking partial derivatives of fitness. Lande (1979) used such a gradient argument to show that evolution proceeds upwards on a hill where mean fitness in a population determines the height or the level. In the case of function-valued strategies, that requires functional derivatives, which are derivatives of a functional. Such a functional is a scalar calculated from a function object. So in the case of function-valued strategies, fitness W will be a real-valued functional.

Functional differentials and derivatives are explained in many textbooks of mathematical physics. Consult Beder and Gomulkiewicz (1998), and for example Luenberger (1969) for definitions. Let's get a bit more technical here for a moment.

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,

$$d\Lambda(\eta;\rho) = \lim_{c \to 0} \frac{\Lambda(\eta + c\rho) - \Lambda(\eta)}{c} \tag{4.1}$$

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.

Since fitness will be a real-valued functional, our normed vector space $\mathbb{V}$ will be in fact the real line.
The Gateaux differential of fitness $W(z)$ of a function valued strategy z then becomes

$$dW(z) = \frac{d}{d\alpha} W(z + \alpha u)\Big|_{\alpha=0} \tag{4.2}$$

with α a scalar and u a function-valued perturbation of z (sorry for the switch of fonts between functions and scalars here).

There is also the *strong* or *Fréchet differential* at η, which makes use of the norm of ρ, so $\mathbb{U}$ has to be a normed vector space for that.
If for a fixed η and for each increment ρ, $d\Lambda(\eta;\rho)$ in (4.3) exists and is (*i*) continuous in ρ, and (*ii*) linear in ρ such that

$$\lim_{\|\rho\| \to 0} \frac{\|\Lambda(\eta + \rho) - \Lambda(\eta) - d\Lambda(\eta;\rho)\|}{\|\rho\|} = 0 \tag{4.3}$$

then $d\Lambda(\eta;\rho)$ in (4.3) 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,

$$d\Lambda(\eta;\rho) = \Lambda'_s(\eta)\rho . \tag{4.4}$$

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

This all looks at least superficially similar to standard calculus.

Concerning fitness, assuming that the Fréchet differential exists, it is equal to the Gateaux differential (4.2), that is

$$dW(z) = \frac{d}{d\alpha}W(z+\alpha u)\Big|_{\alpha=0} = W'_s(z)u = \int_a^b W'_s(z)(e)u(e)de \tag{4.5}$$

In order to extract values of the functional fitness Fréchet derivative at specific values of e, say at a value $e^{\#}$, we can use the dirac delta function $\delta_{e^{\#}}(e)$ as an increment, which, when integrated, returns the following:

$$W'_s(z)(e^{\#}) = \int_a^b W'_s(z)(e)\delta_{e^{\#}}(e)de = \frac{d}{d\alpha}W(z+\alpha\delta_{e^{\#}})\Big|_{\alpha=0} \tag{4.6}$$

The function-valued fitness gradient $\beta(e^{\#})$, is equal to $W'_s(z)(e^{\#})$. It is the function-valued counterpart of the standard fitness gradient in finite-dimensional trait spaces.

5. ADAPTIVE DYNAMICS OF REACTION NORMS

In adaptive dynamics approximations (Metz et al. 1996), the invasion fitness of a mutant depends on its own strategy, but also on the population state, which is usually represented as a list of all the resident strategies. Invasion fitness can also be specified for function-valued strategies, and thus is a multivariate functional which I abbreviate s^{ad} in this section. For the purpose of classifying evolutionary singular strategies, function-valued traits where the fitness gradient (4.6) vanishes for all e, we need to use Fréchet derivatives.

In the case of a single resident strategy, similar to the univariate expression in Dieckmann and Law (1996), the canonical equation for the dynamics on the trait space becomes

$$\frac{d}{dt}z(e) = c(z)\int_a^b \sigma_g^{mut}(z)(e,f)\frac{d}{d\alpha}s^{ad}(z+\alpha\delta_f,z)\Big|_{\alpha=0}df \qquad (5.1)$$

Here $z+\alpha\delta_f$ is a mutant strategy that corresponds to a perturbation of the resident strategy in one environment f, with z the resident strategy. The mutational variance-covariance function $\sigma_g^{mut}(z)(e,f)$ depends on the resident strategy as well.

Evolutionary dynamics will halt when (5.1) becomes equal to the zero function. This can happen in two ways, either (*i*) the function-valued invasion fitness gradient vanishes, or (*ii*) the function-valued fitness gradient lies in the null space of the covariance function $\sigma_{g,\mu}(z)(e,f)$.

How to define non-invasibility for a function-valued resident strategy is relatively straightforward. One can apply the fundamental lemma of the variational calculus (see Arnol'd 1978, p. 57) to show that at a singular strategy z^*,

$$\frac{d}{d\alpha}s^{ad}(z^*+\alpha\delta_f,z^*)\Big|_{\alpha=0} = 0 \text{ for all } f \qquad (5.2)$$

and one should have

$$\frac{d}{d\alpha}s^{ad}(z^*+\alpha(z_m-z^*),z^*)\Big|_{\alpha=0} \leq 0 \text{ for all perturbations of the strategy } (z_m-z^*) \qquad (5.3)$$

in order for invasion for invasion fitness to be a local maximum (Luenberger 1969) and for invasion stability to hold with respect to any perturbation of the resident strategy. Concerning convergence stability, a lot will depend on the pattern of covariances assumed. Similar results to the ones in Leimar (2001) might be within reach, but they require mathematical sophistication. For getting acquainted with the analysis of infinite-dimensional dynamical systems and the stability of their stationary points (which corresponds to the notion of convergence stability), Hale (2002) might be a useful starting point.

4. PARAMETRIC REACTION NORMS

For practical reasons, it is always tempting to replace an infinite-dimensional trait specification by a finite-dimensional one.
Next to that, this is the preferred approach to model specific assumptions concerning the genetic machinery behind a function-valued trait, in other words: genetic/developmental constraints. Any genetic system has a finite number of loci, therefore, in the end, development might be far from an infinite-dimensional system. Also when reaction norms are considered that are attractors of infinite-dimensional dynamical systems, then one has to keep in mind that such attractors often live in a reduced number of dimensions.

That should keep no one from trying to model the evolution of function-valued traits. In any specific case, it is useful to understand what selection would do when unhindered by developmental constraints, and it is also necessary in order to avoid bad choices of specific parametrized reaction norms. For instance, as a very simple example, consider that when evolution favours a reaction norm that increases with the value of e, there is no reason to assume that the slope should be negative always. Extremely bad choices of parametrized function-valued traits, probably lead to very misleading evolutionary scenarios.

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