Working Paper

Delayed maturation in temporally structured populations with non-equilibrium dynamics

T.J.M. Van Dooren and J.A.J. Metz

WP-96-70
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Delayed maturation in temporally structured populations with non-equilibrium dynamics

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Summary

In this paper we study the evolutionary dynamics of delayed maturation in semelparous individuals. We model this in a two-stage clonally reproducing population subject to density-dependent fertility. The population dynamical model allows multiple - cyclic and/or chaotic - attractors, thus allowing us to illustrate how (i) evolutionary stability is primarily a property of a population dynamical system as a whole, and (ii) that the evolutionary stability of a demographic strategy by necessity derives from the evolutionary stability of the stationary population dynamical systems it can engender, i.e., its associated population dynamical attractors.

Our approach is based on numerically estimating invasion exponents or “mutant fitnesses”. The invasion exponent is defined as the theoretical long-term average relative growth rate of a population of mutants in the stationary environment defined by a resident population system. For some combinations of resident and mutant trait values, we have to consider multi-valued invasion exponents, which makes the evolutionary argument more complicated (and more interesting) than is usually envisaged. Multi-valuedness occurs (i) when more than one attractor is associated with the values of the residents' demographic parameters, or (ii) when the setting of the mutant parameters makes the descendants of a single mutant reproduce exclusively either in even or in odd years, so that a mutant population is affected by either subsequence of the fluctuating resident densities only.

Non-equilibrium population dynamics or random environmental noise selects for strategists with a non-zero probability to delay maturation. When there is an evolutionary attracting pair of such a strategy and a population dynamical attractor engendered by it, this delaying probability is a Continuously Stable Strategy, that is an Evolutionary Unbeatable Strategy which is also Stable in a long term evolutionary sense. Population dynamical coexistence of delaying and non-delaying strategists is possible with non-equilibrium dynamics, but adding random environmental noise to the model destroys this coexistence. Adding random noise also shifts the CSS towards a higher probability of delaying maturation.

1. Introduction

Populations can be temporally structured, i.e., subdivided into a number of temporally separate subpopulations with little or no exchange between them. Below we refer to such subpopulations as temporal populations. Consider, for instance, a biennial semelparous organism. Such an organism can have two temporal populations. One population breeds in even years, the other one in odd years. Individuals from both temporal populations never breed together. The temporal separation is incomplete when some, but not all individuals delay maturation for one further year. Individuals then delay with a probability different from zero or one, and this delaying probability can be considered a mixed strategy of an individual’s genotype. A number of field studies provide examples of temporally structured populations (e.g., Aspinwall 1974, Hori 1982); in some cases not all possible temporal populations were present (Heliövaara 1994).

Mixed delaying strategies are commonly seen as adaptations to temporally variable environments and referred to as 'risk aversion' or 'bet hedging’ strategies. Evolutionary arguments underpinning this idea should be based on a fitness measure which naturally incorporates environmental variability. This fitness measure is found in the long term growth rate of a population of organisms with the envisaged properties, where we assume these organisms to reproduce asexually, and to live in the environment under consideration without affecting it (e.g., Lacey et al. 1983, Philippi & Seger 1989, Metz et al. 1992). Examples of delaying strategies that can be advantageous in temporally varying environments are seed dormancy, delayed reproduction in annuals or biennials, and insect diapause. Delayed germination in plant populations has been thoroughly studied theoretically (e.g., Bulmer 1984, Ellner 1985 a&b), and considerable attention has been devoted to models of biennial life histories and delayed reproduction (De Jong et al. 1987, Roerdink 1988, Tuljapurkar 1990).

Environmental variability can be the consequence of stochastic environmental inputs, of fluctuating population densities resulting from non-equilibrium population dynamics, or both. Ferrière and Clobert (1992) and Gatto (1993) have shown that evolution may drive a population towards non-equilibrium dynamics. For evolutionary models dealing with delaying strategies, the non-equilibrium dynamics itself is the driving force of the evolutionary process. Bulmer (1984), studying the effect of non-equilibrium dynamics on delaying germination, for a model without further age structure, found that non-equilibrium dynamics favoured non-zero delaying probabilities. The probability of delaying in turn affects the population dynamics. Increasing this probability usually makes the fluctuations in the population densities less severe and in many models can even lead to their disappearance. This suggests the potential existence of scenarios in which evolution of a delaying probability drags a population onto the stability boundary of its point equilibrium.

In this paper we study delayed maturation in a stage structured model with non-equilibrium dynamics, assuming clonal inheritance. We analyse the evolutionary dynamics of this model family by means of an example with, hopefully, sufficient generality. The dynamical behaviour of the model urges a definition of Evolutionary Stability conditional on the population dynamical attractors engendered by a strategy. We show that the evolutionary dynamics simplifies considerably when we extend the model by adding on to it some stochastic variation in the environment. First we consider the adaptive dynamics in the fully deterministic case, then we show what happens if stochastic environmental variation is added.

Our analysis may be compared to that in a recent paper by Kaitala and Getz (1995) who studied a comparable, though more complicated, model of a structured semelparous population harbouring a temporal population structure, but limited the ESS analysis to a deterministic population dynamics leading to a global point attractor. It is precisely for models with nonlinearities and non-equilibrium behaviour, that the consequences of temporal population structure really matter in our evolutionary reasoning, as we will show and explain below.

2. The Population Dynamical Model

We chose to model a family of discrete two-phase models with reproduction in the second phase. Deterministic models like these are justified as approximations to individual based models, if population sizes are sufficiently large to neglect demographic stochasticity. The numbers in different developmental phases are then better interpreted as densities, i.e., number of individuals per unit of area.

Instars of clonal type *i* with density $I_{i,t}$ survive between reproductive seasons with a probability *s*. This survival probability is independent of clonal type. A fraction p_i of these instars postpones maturation and remains instar, a fraction (1-p_i) maturates. Adults with density $A_{i,t}$ reproduce during a short period before they die. Adult fertility *M* (which is independent of clonal type) is multiplied by a factor exp(-E_t) that stands for the influence of the environment E_t on fertility. The summed densities of all adults types *i* in the population system constitute the environment in which a population lives: $E_t = \sum_i A_{i,t}$.

With a single type present in the population system, E_t equals the adult density $A_{i,t}$ of that type. Stages don't interact, so when no individual delays maturation (p = 0) each temporal population has independent dynamics. We can omit the index *i* when there is only one clonal type in the population system and represent the population dynamics at successive steps (e.g. years) by the following matrix projection equation:

$$\begin{pmatrix} I_{t+1} \\ A_{t+1} \end{pmatrix} = \begin{pmatrix} sp & M\exp(-A_t) \\ s(1-p) & 0 \end{pmatrix} \begin{pmatrix} I_t \\ A_t \end{pmatrix} \tag{1}$$

This model is the density dependent deterministic analogue of a model family studied by Tuljapurkar (1990). The cell *M*exp(-A_t) replaces the random variable with mean *M* in that family. The model family of our study has only intra-class density dependence in the fertility parameter. Density dependence is incorporated in the model through the Ricker reproduction curve (Ricker 1954). This negative exponential curve describes a situation with overcompensating competition. For simple population dynamical models based on it, the attractor of the population dynamics can be a stable equilibrium or not, depending on a single parameter (May and Oster 1976).

We chose to model delaying maturation in terms of a fixed probability *p* of delaying (postponing) maturation. The decision to delay maturation is taken anew at each timestep, which is different from the way decisions are taken in the salmon model studied by Kaitala and Getz (1995) and ten Donkelaar (pers. comm.). In that model individuals can delay maturation only once.

If $p \neq 0$, the model in this study has a unique equilibrium with non-zero densities, n^*:

$$n^* = \begin{pmatrix} I^* \\ A^* \end{pmatrix} = \begin{pmatrix} \frac{1}{s(1-p)} \ln \frac{s(1-p)M}{1-sp} \\ \ln \frac{s(1-p)M}{1-sp} \end{pmatrix} \tag{2}$$

If p equals zero, there can be one or two temporal populations present. The situation with only one temporal population present is always unstable to perturbations: a second temporal population can establish from any initial density because both populations do not influence one anothers dynamics. Squaring the projection matrix (1) brings all entries on the diagonal, i.e., we get dynamically identical one-dimensional models for each phase if we use new timesteps that are twice the original ones. In this case these models are both dynamically equivalent to the one-dimensional Ricker model (May and Oster 1976). If we write the dynamics in terms of a single temporal population we get the following equation for adult densities:

$$A_{t+2} = sI_{t+1} = [sM \exp(-A_t)]A_t \tag{3}$$

This expression (3) has an equilibrium for instars ($s^{-1}\ln(sM)$) and adults ($\ln(sM)$). Instars and adults of one temporal population appear at equilibrium densities in alternating years, and each temporal population experiences the effect of adult densities every second year.

When the delaying probability is zero, the projection matrix from (1) is cyclic. Temporally separate populations imply cyclic projection matrices, and vice versa. In the life cycle graph corresponding to a cyclic matrix, the greatest common divisor of the loop lenghts (a loop is a sequence of arcs from a node to itself) is greater than 1 (Caswell 1989). Little attention has been given to life history evolution in populations that are temporally structured, and in some cases complications in the analysis resulting from this cyclicity have been overlooked (this was already pointed out by Charlesworth, 1994, p.204). For a discussion of these complications concerning the asymptotic behavior of such models we refer to Caswell (1989).

3. Bifurcation Analysis

The attractor of the population dynamics from equation (1), can be a stable equilibrium or not, depending on the values of the demographic parameters. From a bifurcation analysis one can find the boundaries in parameter space that separate regions with qualitatively different dynamics. Details of the bifurcation analysis for this model family can be found in Appendix A. Aronson et al. (1982) published a detailed study of the non-equilibrium behavior of two-dimensional maps. Here we limit ourselves to a global discussion.

Regions of parameter combinations with equilibrium and non-equilibrium attractors are separated by a plane, which is in this case a so-called Neimark-Sacker bifurcation plane (Kuznetsov 1995):

On the non-equilibrium side of such a boundary, attractors can be periodic, quasiperiodic or chaotic, but parameter combinations close to the bifurcation boundary always have periodic or quasiperiodic attractors. Figure 1 shows a section of parameter space with the Neimark-Sacker boundary indicated.

On the face of parameter space where $p = 0$, the population dynamics is equivalent to the dynamics of the one-dimensional Ricker model as explained in section 2. On this face, the point equilibrium bifurcates into a four-cycle (which is the start of a period-doubling cascade that ends in a chaotic region). These four cycles also exist in the interior of parameter space (figure 1).

Typical for structured models with temporal populations is that the attractors of both independent temporal populations can combine into different mixed attractors. The number of different possible mixed attractors can be calculated as follows. When the attractor of a single temporal population is a cycle of period n, then it consists of $n/2$ different adult densities and $n/2$ different instar densities. When both temporal populations are present, individuals from different populations are always in different stages. As a consequence, the different possible densities for adults and instars in a cycle can combine in $n^2/4$ different combinations of adults and instars present at one instant. Because a cyclic attractor of the combined populations runs along n of these combinations as well, $n/4$ mixed cyclic attractors that each run through different density combinations are possible. This also means that for deterministic chaotic attractors there is an infinite number of possible mixed orbits.

We give an example of how varying the delaying parameter can affect the dynamical regime:with $s = 0.8$ and $M = 18$ as fixed parameter values and varying p, we get at $p = 0$ sixteen-cycles and four different possible mixed attractors as explained. For $p \neq 0$, there are different attractors if p is smaller than 0.025. At $p = 0.015$, for instance, the attractor can be an eight or a sixteen cycle, at $p = 0.025$ there is a single eight-cycle. If we increase p further above 0.025, we see four-cycles, then quasiperiodic behavior with narrow periodic windows and finally a stable equilibrium point.

4. Evolutionary Considerations: the Basic Concepts

In this section we describe the invasion criterion that we use as a master fitness concept in evolutionary considerations. This invasion criterion is a function of mutant trait(s) and the population dynamical attractor of the resident population. The approach of Rand et al. (1994) explicitly acknowledges this dependence on the resident attractor in its terminology, but no examples are given of resident populations that have multiple attractors for the same value of the trait parameters. Ferrière and Gatto (1995), mention the possible existence of multiple attractors, but then concentrate on one of them. Complications in studying evolutionary stability arising from cyclicity of projection matrices or multiple attractors have not been considered yet. We define evolutionary stability in a manner wich allows for the existence of cyclic matrices and multiple attractors.

invasion criteria

Every strategy or coalition of strategies, defines at least one population dynamical attractor. We call these attractors the environment, because these attractors are the stationary environments set by a resident population that mutant clonal types (at low densities) experience. When the mutant population size has grown that large that demographic stochasticity and its associated possibility of random extinction can be neglected, the further fate of the mutants can be read from the sign of the long-term relative growth rate of the total mutant population density in the stationary - but not necessarily time-invariant - environment set by the residents (Metz et al. 1992, 1996). The sign of this long-term growth rate tells us whether a mutant will be able to invade a certain resident coalition of types or not, and we use this sign as an invasion criterion. A positive sign also means a positive probability of invasion. The sign is necessarily zero for any mutant which is indistinguishable from one of the resident types.

The hypothetical average long term growth rate is given by the dominant Lyapunov exponent (4) of the matrix process describing the growth of the total mutant population density N_t in a stationary resident environment (Metz et al., 1992). σ is also called the invasion exponent (Rand et al. 1994). Metz et al. (1992) just call σ fitness.

$$\sigma = \lim_{t\to\infty} \frac{1}{t} \ln \frac{N_t}{N_0} \tag{4}$$

Estimates of long-term growth rates from simulations of invasions with different random starting densities in the same stationary resident environment, will converge to a fixed value, namely σ, if we simulate invasions over an infinite timespan (Rand et al. 1994, Ferrière & Gatto 1995). Such simulation spans are obviously irrelevant for practical purposes, but this convergence guarantees that our simulations estimate a well-defined quantity. When mutants can experience a single stationary resident environment only, then σ will be unique. It is of course possible that the mutants can experience different possible resident environments. That is the case when the dynamics of the resident type has multiple attractors, or when the mutant type can occur in different temporal populations (see Appendix B). In these cases convergence to a fixed value σ only is guaranteed for every different stationary resident environment which the mutants can experience separately. For a given combination of resident and mutant types we therefore need to estimate invasion exponents for all these possible environments separately.

evolutionary stability

Evolutionarily stable attractors are the final stops of evolutionary substitution processes. Population dynamical attractors are evolutionarily unbeatable, to be abbreviated EU, if no mutant genotype at low frequency can invade. Then all mutants have a negative fitness except for mutants identical to a resident type. If the mutant dynamics is cyclic, the fitnesses of all temporal populations should be negative. A strategy (a point in trait space) that has a unique EU population dynamical attractor, or multiple attractors that are all EU, is an evolutionarily unbeatable strategy, or EUS. If we assume that all possible points in trait space can be realised by homozygote as well as heterozygote genotypes, then monomorphic EUS's that we find from a clonal model, certainly are monomorphic EUS's when realised by a homozygote genotype in models with sexual reproduction.

[We follow Eshel's (1996) definition of evolutionary unbeatability. The concept was originally formulated by Hamilton (1967), but he apparently meant being unbeatable by 'mutants' appearing in any possible initial frequency (Hamilton 1996).]

Pairwise Invasibility Plots

If the strategies under consideration are characterised by a scalar, we can check whether candidate EUS's are really EUS's on a Pairwise Invasibility Plot. Criteria connected with evolutionary stability are easily read from such Pairwise Invasibility Plots (Van Tienderen and De Jong 1986, Kisdi & Meszena 1992 and Metz et al. 1992, 1996). In such a plot we have the trait value of the resident population on the horizontal axis, and the trait value for the mutant on the vertical axis. On the plot regions are delineated that have positive invasion exponents. Invasion exponents are necessarily zero on the diagonal (Metz et al. 1992,1996; Rand et al. 1994). These plots can be drawn for the whole range of the strategy parameter (globally), or just around candidate EUS's (locally).

5. Delayed Maturation: a Structured Example

In our case we describe the evolution of one scalar trait, the strategy parameter *p* - the probability to delay maturation. The purpose of this analysis is to find out which value or set of values of parameter *p* is evolutionarily stable, and this for a fixed combination of *s* and *M*.

$$\begin{pmatrix} I_{m,t+1} \\ A_{m,t+1} \end{pmatrix} = \begin{pmatrix} sp_m & M(\exp - A_{r,t}) \\ s(1-p_m) & 0 \end{pmatrix} \begin{pmatrix} I_{m,t} \\ A_{m,t} \end{pmatrix} \qquad (5)$$

We start by studying the fate of a mutant population (I_m, A_m) with a deviant phenotype for the parameter *p* in the attractors of a *p*-monomorphic resident population as described by (5). The mutant is characterised by its delaying probability p_m. The mutant dynamics is affected by densities of all adult types *i* in the population system, $E_t = \sum_i A_{i,t}$. The densities of mutant adults initially are negligible compared to densities of resident adults. It is therefore obvious that we approximate the influence of the environment as the density of adults of the resident type, $A_{r,t}$. The mutant population grows at first in the environment set by the resident.

For some parameter combinations σ can be calculated explicitly, when this was not the case we just estimated the long term growth rates from simulations.

simulations

Simulation programs were written in Mathematica 2.2 (Wolfram Research Inc. 1993). All simulations were performed only for a value $s = 0.8$ of the yearly survival, and for a selected set of values of M. We only calculated exponents for values of p on a grid with resolution 0.01. The mutant dynamics can experience multiple stationary environments from the residents, when there are multiple attractors of the resident dynamics, or when the mutants occur in different temporal populations (see Appendix B). Invasion exponents were calculated for up to 10 possible orbits on the resident attractors. Orbits of different stationary environments on the same attractor were obtained by varying the initial density of mutants in such a way that each simulation was with mutants in a single temporal population. We simulated for a range of parameter values the population dynamics of initial conditions with two different clonal types present. These simulations suggest that no pair of types can coexist unless each of them increases in frequency when rare relative to the other type. Under that condition the evolutionary substitution process is fully determined by the invasion criteria, and we therefore decided to base our conclusions on invasion criteria only.

First, we look for trait values that are possibly EUS’s. An easy way to do this is to calculate for all parameter values p whether a mutant with a slightly bigger p can invade or not. If mutual coexistence of types is impossible, then a mutant that can invade a resident population with a smaller delaying probability, but cannot be invaded by a mutant population with a bigger delaying probability, might be an EUS. The candidate EUS’s which we find in this way clearly are reachable from nearby trait values and we call them EA Evolutionarily Attracting. If we find a trait value that is not reachable from nearby trait values, then we call it Evolutionarily Repelling (Rand et al. 1994, Geritz et al. in press, compare

Eshel 1996). Candidate EUS's can likewise be found from looking at invasions of mutants with a slightly smaller delaying probability than that of the resident population.

Figures 2a and b give examples of invasion exponents calculated for mutants with a delaying probability slightly different from the resident delaying probability. This was done for $M = 15$. Figure 2a gives invasion exponents for mutants with a delaying probability that is p+0.01 compared to the resident delaying probability p. Figure 2b gives invasion exponents for mutants whose delaying probability is p-0.01 compared to the resident delaying probability p. The dynamical regime of resident attractors is indicated. For each delaying probability we simulated 10 invasions over 5000 timesteps.

For the values $s = 0.8$ and $M = 15$, there is a unique population dynamical attractor for all values of p. The scatter for some delaying probabilities is solely a consequence of the finite simulation length.

Close to $p = 0.2$, there is an EA delaying probability that is a candidate EUS.

If we now look at a Pairwise Invasibility plot around the candidate EUS (fig. 3a), we see that no mutant in the range]0.16,0.24[can invade that delaying probability. When $M = 15$, there is a single attractor for all p-parameter values, therefore from this plot we can safely conclude that the candidate EUS is locally an Evolutionary Unbeatable Strategy. An EU strategy that is locally EA is also called a Continouously Stable Strategy (Eshel & Motro 1981, Eshel 1983). The sign of the exponents in this plot was determined from simulations over 20.000 timesteps. Close to the CSS, invasion exponents are nearly zero. Therefore, if we decrease the simulation length (see fig. 3b, for 5000 timesteps), scatter around the asymptotic value can change the sign of the invasion exponent. Since the absolute value of an invasion exponent can be understood as a selection differential (Rand et al. 1994), different clonal types here are nearly selectively neutral. However, they are not completely neutral. Close to the CSS, the estimated invasion exponents for a given resident trait value are parabolic functions of the mutant delaying probabilities (fig. 4). From figure 4 one can also see that the CSS is globally evolutionarily unbeatable.

Fig 2b shows that the invasion exponents for $p = 0$ mutants in a $p = 0.01$ resident population can have two very different values with different sign. That is because mutants that do not delay, exist in two temporal populations, and individuals from one temporal population are all in the adult phase every two timesteps. It is only in the adult phase that they experience density dependence and thus the resident environment. Because a p = 0.01 resident population lives on a four cycle, the p = 0 mutant dynamics can depend on two different combinations of resident densities: each temporal population will experience a different combination. If the evolutionary trait substitution proces starts away from a zero delaying probability, it will end up at the CSS. But when a p = 0.01 mutant invades a resident pair of temporal populations, then it will drive one of them to extinction but will coexist - in a polymorphic attractor - with the temporal population having a positive invasion exponent in figure 2b. Figure 5b shows mean adult densities of the delaying and non-delaying type in a polymorphic attractor. Coexistence is possible over two ranges of delaying probabilities. Figure 5a shows invasion exponents on these attractors for mutants with a delaying probability slightly bigger than the delaying probability of the type in the polymorphic attractor. We now see that a proces starting from p = 0 will branch into a coexistence of delaying and non-delaying types, where delaying types can be replaced by clonal types with a bigger delaying probability. As the CSS is approached, the non-delaying type appears at lower densities in the attractor, until a mutant taking over from the resident coalition drives both resident types to extinction. Here we cascade back to a monomorphic attractor and the proces then continues towards the CSS. The polymorphic attractors of delaying and non-delaying types for delaying probabilities larger than the CSS value, are not reachable from a monomorphic start.

Other combinations of parameter values for s and M we studied, give similar results. The EU delaying probabilities always have unique quasiperiodic attractors and are CSS's. Such a CSS is in all cases reachable starting from any initial monomorphic attractor. We followed the same procedure we described for M = 11.5, 18 and 21. For M = 11.5, fluctuations in densities are small. As these density fluctuations make up the environmental variability needed for the delaying to be advantageous, the selection differential towards a non-zero delaying probability is small. Simulations of invasions in the same stationary environment need to be done over extended periods to get the same sign of the invasion exponent from all simulations. For M = 18, branching towards a dimorphism occurs for only one mixed attractor of the p = 0 strategists. For M = 21, coexistence of delaying and not delaying types is impossible.

Figure 6a shows invasion exponents for $p = 0.01$ mutants in couples of resident temporal populations for a range of fertilities M. Non-equilibrium dynamics selects for an advantage to delay reproduction, but close to the bifurcation boundary fluctuations in densities are not big enough to do so. The scatter between $M = 10$ and $M = 14$ is a consequence of the dependence on the starting point on the orbit. It disappears for longer simulation lengths (e.g. 10.000 steps). If the resident populations live on an eight-cyle, then two mixed attractors are possible and we see a branching in the invasion exponent for the corresponding M. A branching of this kind is independent of the simulation length. Figure 6b shows invasion exponents for $p = 0$ mutants in $p = 0.01$ resident populations, again over a range of values of M. This figure nicely summarises possibilities of getting multiple valued long term growth rates for the same combination of mutant and resident trait values (see Appendix B).

equilibrium dynamics

When the dynamics of the residents converges to a stable equilibrium, then the environment in which the mutant spreads can be considered constant, and is given by the equilibrium adult density of the resident population system. In that case the dynamics of the mutants (I_m, A_m) can be written as:

$$\begin{pmatrix} I_{m,t+1} \\ A_{m,t+1} \end{pmatrix} = \begin{pmatrix} sp_m & \dfrac{1-sp_r}{s(1-p_r)} \\ s(1-p_m) & 0 \end{pmatrix} \begin{pmatrix} I_{m,t} \\ A_{m,t} \end{pmatrix} \tag{6}$$

When resident attractors are stable equilibria, the largest Lyapunov exponent of the mutant dynamics corresponds to the largest eigenvalue of this projection matrix, but R_o (the basic reproduction number) is a lot easier to handle and in this case equivalent to that eigenvalue in determining the fate of an invader. For the invader, R_o is

$$R_o = \sum_c l_c m_c = \sum_{n=0}^{\infty} s(1-p_m)(sp_m)^n \left(\frac{1-sp_r}{s(1-p_r)} \right) = \left(\frac{s(1-p_m)}{1-sp_m} \right) \left(\frac{1-sp_r}{s(1-p_r)} \right) \tag{7}$$

R_o is one for ‘invasion of a resident population in itself’ (when $p_m = p_r$). Populations with R_o larger (smaller) than one can (cannot) invade the resident under consideration. R_o decreases with p_m, as delaying maturation increases the chance to die. No population at stable equilibrium can be invaded by a mutant with a larger probability to delay maturation. Conclusions based on R_o only apply if resident populations are at a stable equilibrium. So the evolutionary walk will approach the Neimark-Sacker bifurcation plane at least from the side of larger p, which is the side where the dynamics goes to a stable point equilibrium. Mutants having non-equilibrium dynamics as residents, can invade any residents with stable equilibria. This means that $p = 0$ is evolutionary stable only if the population dynamics has stable equilibria for $p = 0$.

6. Environmental Noise

Some of the results from the simulations for $p = 0$ invaders in periodic environments, can also be obtained halfway analytically. For $p = 0$ invaders, the projection matrix in (1) is cyclic and we can recast our dynamical system into a one-dimensional equation. Equation (8) gives the recurrence relation of the adult mutant densities. The mutant dynamics only depends on adult densities of the resident population in alternating years.

$$A_{m,t+2} = sI_{m,t+1} = [sM \exp - A_{r,t}]A_{m,t} \tag{8}$$

We now rescale time units to t', typical for the dynamical system (3) and (12), $t' \to t'+1$ corresponds to $t \to t+2$ or $t+1 \to t+3$, depending on which temporal population one is looking at. The Lyapunov exponent σ_0 is given by (9).

$$\sigma_0 = \lim_{t' \to \infty} \frac{1}{t'} \ln \frac{A_{m,t'}}{A_{m,0}} = \lim_{t' \to \infty} \frac{1}{t'} \ln \prod_{t=0}^{\infty} sM \exp(-A_{r,t'}) \tag{9}$$

After a bit of rearrangement this leads to the following expression:

$$\sigma_0 = \ln(sM) - \quad (p_r), \qquad \text{with} \quad \mathsf{A}(p_r) := \mathrm{E}(A_{r,t'}) \tag{10}$$

where $\mathrm{E}(A_{r,t'})$ is the mean resident adult population density experienced by the mutant population. $\mathsf{A}(p_r)$ can depend on whether we calculate the mean for even or odd t-timesteps. We know that the Lyapunov exponent is zero for a population invading in itself, and therefore $\mathsf{A}(0)$ has to be equal to $\ln(sM)$ for whatever attractor or initial condition.

From expression (10) it is clear that noise in the parameters s or M will decrease the first term and therefore noise will decrease the mean density $\mathrm{E}(A_{r,t'})$ of $p = 0$ residents. We ran some simulations to get an idea of how noise affects mean adult densities - the second term in (10) - for populations with delayed maturation. We multiplied M in (1) at each step of the map with a lognormally distributed random variable with mean 1, and simulated population trajectories on the resulting stochastic attractor. All parameter combinations show the same pattern if we increase the coefficient of variation of the distribution used.

Figure 7 illustrates this for $s = 0.8$ and $M = 15$. From (10), $p = 0$ mutants will be able to invade a deterministic orbit that has an $\mathsf{A}(p_r)$ smaller than $\ln(sM)$. On the lower branch of the 'bubble' we see in figure 7a, there clearly are points that fulfill this condition. In those cases, populations with a probability to delay maturation slightly different from $p = 0$ can be invaded by $p = 0$ mutants, and evolutionary walks starting at $p = 0$ will branch to a polymorphism. We see from figure 7 that noise ruins the advantage that $p = 0$ mutants had from differing initial conditions on an attractor. The bubble more or less 'collapses' onto a single value for $\mathrm{E}(A_{r,t'})$ and the difference between values close to $p = 0$ increases. If at each step of the map we multiply the parameter M with a lognormally distributed random variable, the evolutionary attractor moves to larger p values and stays a CSS. The effect is small for a distribution with a coefficient of variation of 0.1. If distributions with a coefficient of variation around 1 are used, the non-equilibrium dynamics is completely dominated by the stochasticity, and the CSS lies close to $p = 0.5$. Figure 8 shows that adding some noise detroys the history dependent structure of the invasion function. This figure repeats figures 6a and 6b, but here the models have added random noise. Noise restores smoothness of the invasion function. Different attractors no longer exist, but for small coefficients of variation and the simulation length we used, the dependence on initial conditions remains for M between 12 and 14 (figure 8b). However, this does not affect the sign of the invasion function anymore. Random environmental noise ruins any possibility for coexistence of $p = 0$ and $p = 0.01$ clonal types. If the variance of the distribution is small, the pattern of delaying advantage does not change with respect to the deterministic model (compare figures 6a, 6b and 8), but for large coefficients of variance, $p = 0$ can be invaded by $p = 0.01$ for any M (figure 8).

7. Discussion

The combination of non-equilibrium population dynamics and evolutionary dynamics proves fruitful in refining contemporary evolutionary thinking. Other studies (Ferrière and Clobert 1992, Gatto 1993) have shown that evolution can favour non-equilibrium dynamics. We showed here why the definition of evolutionary stability of strategies is conditional on the attractors of their population dynamics. Invasibility and evolutionary stability are in the first place properties of these population dynamical attractors. When an invasion exponent, which is a function of resident and mutant traits, is multi-valued and its signs differ between these values, the distinction between being able to invade or imminence for extinction is not uniquely determined by the trait values. When there are multiple values with different sign for the same resident attractor, this will translate itself into a temporal structuring of the effective occurrence of types: we assume that mutants just keep on appearing, and that eventually all possibilities are tried out. With multiple attractors, we might find differences between them with respect to the set of mutants that can invade. Furthermore, these differences can be such that multiple attractors differ in evolutionary stability: one attractor might be an EU attractor, the other ones not. When we would indeed find a dependence of invasion exponents on the attractor, then that can be understood as a dependence on historical aspects of the system. Whether such a historical constraint is effective or not, depends on whether attractor switches are made or not. If only mutants slightly different from the residents appear, we expect that the deterministic system stays on the same attractor during their invasion attempts. However, a rigorous underpinning of this belief is as yet lacking.

Adding some random environmental noise destroys the intricate pattern of history dependence we found in the fully deterministic case. The randomness creates so to speak transitions between the different stationary environments found in the deterministic case. That results in a single stationary environment. The simulations suggest that noise also restores smoothness across bifurcation boundaries. Although adding some noise can simplify our evolutionary considerations considerably, it can complicate time scale arguments used to justify this approach to evolutionary dynamics, when the noise creates only rarely transitions between environments with different evolutionary possibilities. We also showed that the separation of timescales of invasion and mutation breaks down when trait values approach an EU situation: there invasions can take a long time to be decided because long-term growth rates are nearly zero. With finite population sizes, demographic stochasticity will exert its influence and it can even come to dominate selection. We therefore expect that there will always be genetic variation present in a population close to an EU situation. We do believe that results on evolutionary unbeatability and reachability are robust with respect to the timescale assumption, and that the comparison of invasion criteria remains relevant.

Doebeli and Koella (1995) have shown that scenarios are possible where evolution drags a population onto a bifurcation boundary in parameter space. We believe it is rather unlikely to happen when the evolving strategic parameter is a delaying probability. We did not find any dependence of our conclusions about the final stop of the evolutionary process on the attractor and therefore the conclusions do not substantially differ between the deterministic and the stochastic cases with non-equilibrium dynamics. The effect of environmental variation on the evolutionary stability of delaying strategies are clear: a mixed strategy is advantageous in a variable environment. The source of this variation seems to matter little for the eventual outcome of natural selection. Density dependent processes or purely random fluctuations in the environment all lead to a mixed strategy CSS. We can therefore expect that also in finite populations the trait substitution process will evolve away from the $p = 0$ boundary if the environment is variable. As the process comes closer to the CSS value, the effects of demographic stochasticity and mutation mechanics on the presence and abundance of differently delaying types will become ever more prominent. The end result will be a mixture of genotypes all closely resembling one another, straddling the ESS, kept into existence by a mutation-selection balance with stabilising selection. It should be noted though that this pattern of stabilising selection does not result from fixed phenotypic fitnesses, but from an intricate population dynamical process.

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Appendix A

We did a local stability analysis of equilibria to determine how the asymptotic dynamics depend on parameters s, p and M. We used the LOCBIF bifurcation analyzer (Khibnik et al. 1990-1992) for numerical explorations. The parameter space is limited as follows: M is strictly greater than 1, $p \in [0,1]$, en $s \in]0,1[$.

It is possible to write out the equations for a set of bifurcation planes that separate regions in parameter space where nontrivial (i.e. with non-zero densities) equilibria differ in stability. The equations of these planes can be calculated using standard methods (May 1974, Caswell 1989, Nisbet & Onyiah 1994), from the characteristic equation (A1) of the linear recurrence relation that approximates the perturbation dynamics around equilibria from equation (2):

$$\lambda^2 - sp\lambda - (1 - sp)(1 - \ln\frac{Ms(1-p)}{1-sp}) \qquad \text{(A1)}$$

One bifurcation plane - called the Neimark-Sacker bifurcation plane - is relevant for our further considerations. Across this bifurcation boundary, described by (A2) below, a limit cycle bifurcates from an equilibrium point. On the non-equilibrium side of this boundary, attractors can be periodic, quasiperiodic or chaotic.

$$-(1-sp)\left(1-\ln\frac{Ms(1-p)}{1-sp}\right)=1 \Leftrightarrow M=\frac{1-sp}{s(1-p)}e^{\frac{2-sp}{1-sp}} \qquad \text{(A2)}$$

On the non-equilibrium side of the Neimark-Sacker plane wedgelike regions originate in which frequency locking occurs. The periodic attractors of parameter combinations in these regions are strong and weak resonances. Solutions with period four are what is called strong resonances (Arnol'd 1977). The width of the corresponding resonance horn does not decrease according a power law when approaching the Neimark-Sacker plane (figure 1). It can easily be seen that at p = 0 such a 4-cycle resonance horn starts for any value of s. Orbits with other periods approach the bifurcation plane in a narrow horn: these are Arnold-tongues (e.g., Arnol'd 1977, Kuznetsov 1995, see Lauwerier and Metz 1986, for a biological example). It can be shown (following Lauwerier and Metz 1986) that close to the bifurcation boundary, winding numbers within these resonance horns need to be rationals in the interval]1/6,1/4].

For completeness, we also give the following equation of an other bifurcation plane:

$$1-sp-(1-sp)\left(1-\ln\frac{s(1-p)M}{1-sp}\right)=0 \Leftrightarrow M=\frac{1-sp}{s(1-p)} \qquad \text{(A3)}$$

When crossing this plane in the direction of decreasing *M* the stable nontrivial equilibrium becomes unstable, and the unstable trivial one stable.

For *p* = 0 the local stability analysis for the two-year interval based on equation (3) is identical to the stability analysis for the standard one-dimensional Ricker recurrence relation (May and Oster 1976). *sM* needs to be at least one in order to get a stable nontrivial equilibrium. This equilibrium becomes unstable, and a period-doubling cascade (that ends in a chaotic region) starts as *sM* gets bigger than e^2.

Appendix B

Because resident trait values determine the resident attractor and mutant traits the mutant dynamics, the long-term growth rate σ is a function of resident x and mutant y traits σ(x,y), but not necessarily a single valued function. There are some complications.

1. σ(x,y) can be, first of all, not smooth in its parameters at bifurcations of the resident attractor. In particular at a hard (i.e. subcritical) bifurcation σ will in general be discontinuous in x.

2. When there are multiple attractors of the resident dynamics, then σ(x,y) is multi-valued. In principle σ*(x,y)* can be multi-valued for any chaotic attractor, because every chaotic attractor has an infinite number of periodic orbits embedded in it, and each of these corresponds to a possible resident environment (Rand et al. 1994). We see this possibility for multi-valued σ*(x,y)* as of minor importance. A perturbation caused by the appearance of any mutant drives the resident dynamics away from such an unstable orbit, and the least amount of environmental noise makes these orbits disappear.

3.a. Let the size of the matrix that describes the mutant dynamics be L. If the mutant matrix is cyclic with period m, then this m is necessarily a divisor of L. We then have m temporally separated populations of mutants. If the 'period' of a resident attractor n is relatively prime to m, then there are m equal dominant Lyapunov exponents. Each one gives the hypothetical average long term growth rate of one of the temporally separated populations of mutants.

3.b. When m and n are not relatively prime, let k be their largest common divisor. Then there are generically k different values for the dominant Lyapunov exponents of the temporal populations. The number of possible values k for the dominant Lyapunov exponents is determined by the number of stationary resident environments mutants can experience. The total number of dominant Lyapunov exponents, m, is then partitioned over k classes with each m/k equal exponents.

3.c. For a nonperiodic resident attractor but the matrix of the mutant dynamics m-cyclic, there are up to m different dominant Lyapunov exponents. The number of possible values for the dominant Lyapunov exponent depends on the divided structure of the attractor. For example, for a chaotic attractor i) consisting of n separate regions, such that the trajectory visits all n regions in n steps, and ii) the dynamical systems that sample each n timesteps on this attractor are all mixing (consult Gray 1988, for a definition of mixing), there are k different dominant Lyapunov exponents, with k the largest common divisor of n and m.

Figure 6b gives examples of different possibilities resulting in multivalued invasion exponents. In the region where the resident dynamics is a four-cycle, mutants can experience two different resident environments on the same attractor (Appendix B, case 3.b). For some parameter values there are multiple attractors, e.g. for $M = 18$, and the value of the invasion exponent depends on the attractor (Appendix B, case 2, and, because the resident dynamics is cyclic, case 3.b). Even in the region with chaotic dynamics the σ-function is multi-valued. For values of M where the chaotic attractor is divided in regions that are successively visited and each densely filled with points of the resident trajectory, we find different exponents (Appendix B, case 3.c). For M below 21.4, the chaotic attractor consists of four such separate regions.

Figure Legends

Figure 1. Bifurcation diagram for the model family defined by equation (1) with the parameter s fixed at 0.8. The area - within the region of non-equilibrium dynamics - indicated by R is the region with strong resonances, i.e., cycles of period four.

Figure 2. Estimates of invasion exponents (M = 15, s = 0.8). The qualitative dynamics of resident populations are indicated. Q stands for quasiperiodic dynamics of the resident, E for a stable point equilibrium. For periodic orbits, their period is given, which is four in this case. (a) invasion exponents for a mutant with a delaying probability p_m,, 0.01 larger than the one of the resident population, p_r (b) for a mutant with a delaying probability 0.01 smaller than the one of the resident population, p_r..

Figure 3. Pairwise Invasibility Plot around the candidate EUS for M = 15 and s = 0.8. Only positive estimates of σ are shown. There are no repeats of simulations for each pairwise combination or resident and mutant delaying probabilities. Simulations were done over (a) 20.000, (b) 5000 timesteps on the resident orbit.

Figure 4. Estimates of invasion exponents as a function of the mutant delaying probability p_m (M = 15, s = 0.8). This estimated invasion function is shown for resident delaying probabilities p_r = 0.195 (dotted), 0.2025 (line) and 0.210 (dotted). In all cases it is a parabolic function. The delaying probability p_r = 0.2025 is a globally Evolutionarily Unbeatable Strategy.

Figure 5. (a) Estimates of invasion exponents for a mutant with a delaying probability 0.01 bigger than the probability p_r of the delaying type in the polymorphic attractor (M = 15, s = 0.8). (b) Mean adult densities for delaying and non-delaying residents. Near the EUS, no polymorphic attractor is possible.

Figure 6. Estimates of invasion exponents for a range of values of M with s fixed at 0.8. C stands for chaotic behavior of the map. Between the region of periodic dynamics with period 16 and the chaotic region, cycles of higher periods are found. (a) for mutants with a delaying probability p_m = 0.01 in resident populations with p_r = 0 (b) for mutants with delaying probability p_m = 0 in a resident population with p_r = 0.01. For values of M above 20, 100 estimates over

different orbits were calculated. In between the E region and the region with a cycle of period four, the resident attractor has quasiperiodic behavior.

Figure 7. Estimates of mean adult densities when parameter M in equation (1) was multiplied every step by a lognormal random variable with mean 1 ($M = 15$ and $s = 0.8$). The horizontal line corresponds to the value of $\ln(sM)$, which is approximately 2.48 in this case. Plot (a) gives the means of the deterministic models; the coefficients of variation are for (b) 0.1, (c) 0.31, and (d) 0.53.

Figure 8. (a) and (c): Estimates of invasion exponents for mutants with a delaying probability $p_m = 0.01$ in resident populations with $p_r = 0$ for a range of values for M and s fixed at 0.8. The parameter M in equation (1) was multiplied every step by a lognormally distributed random variable with mean 1. The coefficients of variation are for (a) 0.1, and (c) 0.53.

(b) and (d): Estimates of invasion exponents for mutants with a zero delaying probability in a resident population with $p_r = 0.01$ for a range of values for M and s fixed at 0.8. The parameter M in equation (1) was multiplied every step by a lognormally distributed random variable with mean 1. Coefficients of variation are for (b) 0.1, and (d) 0.53. Notice the tenfold increase in values of σ in (c) and (d).

Figure 1, Tom Van Dooren and Hans Metz

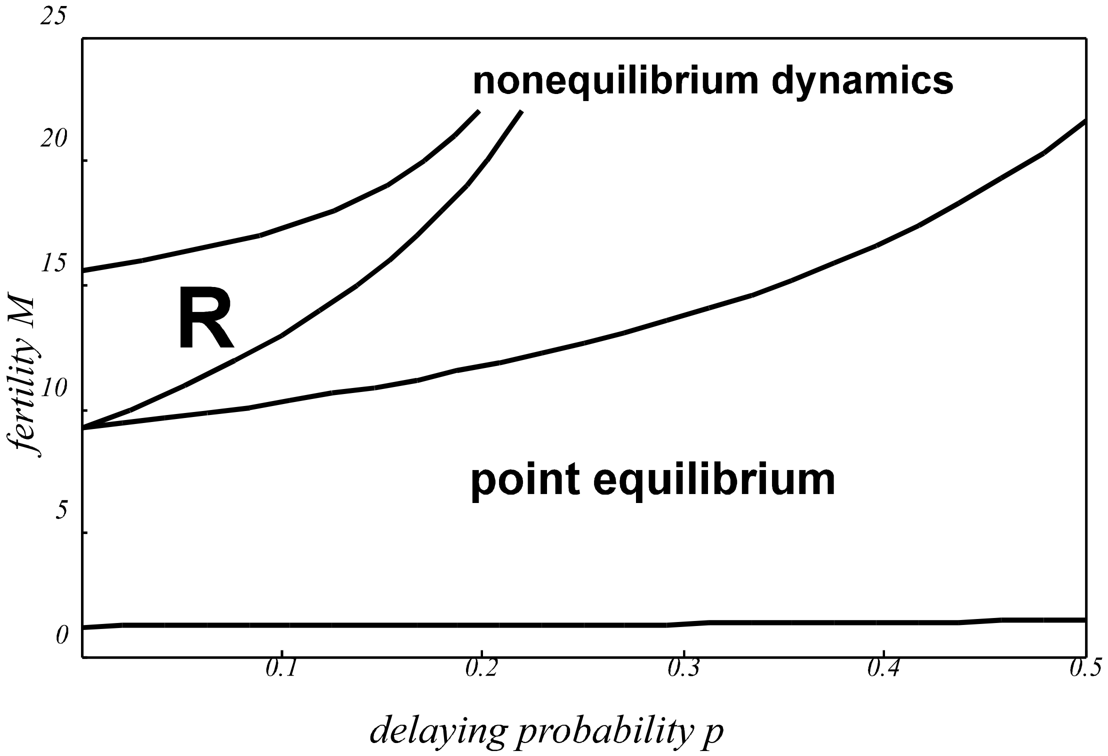

Figure 2, Tom Van Dooren and Hans Metz

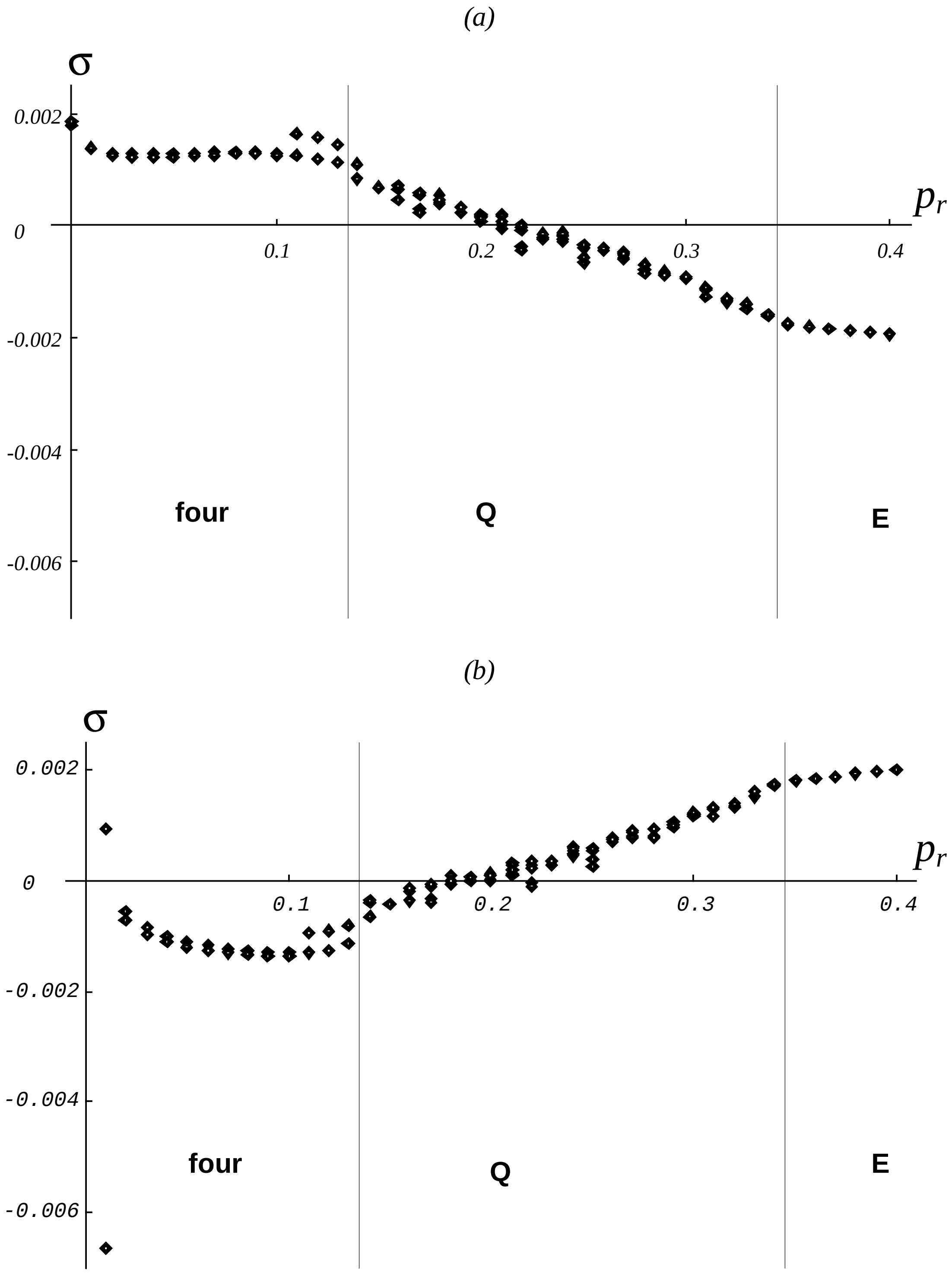

Figure 3, Tom Van Dooren and Hans Metz

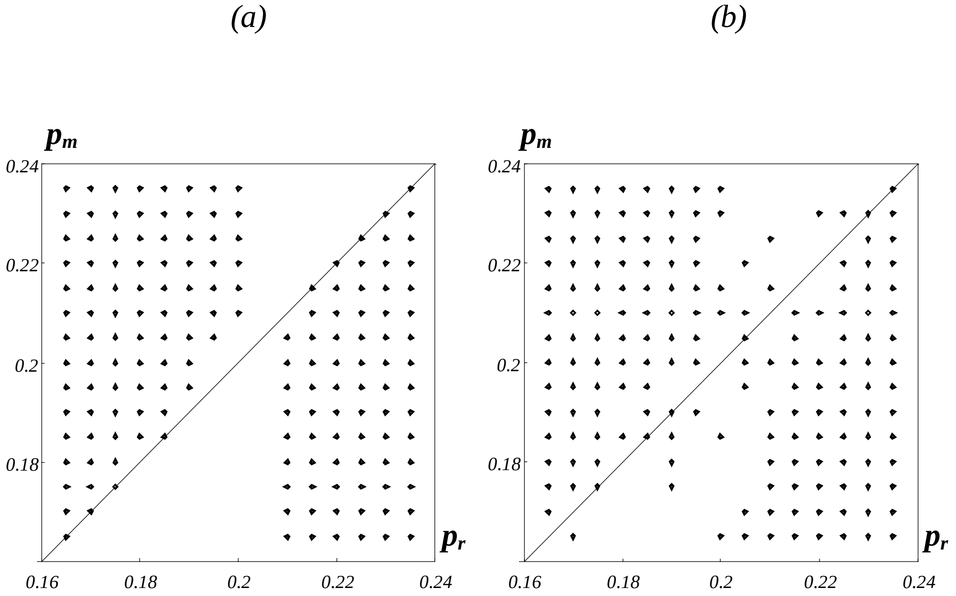

Figure 4, Tom Van Dooren and Hans Metz

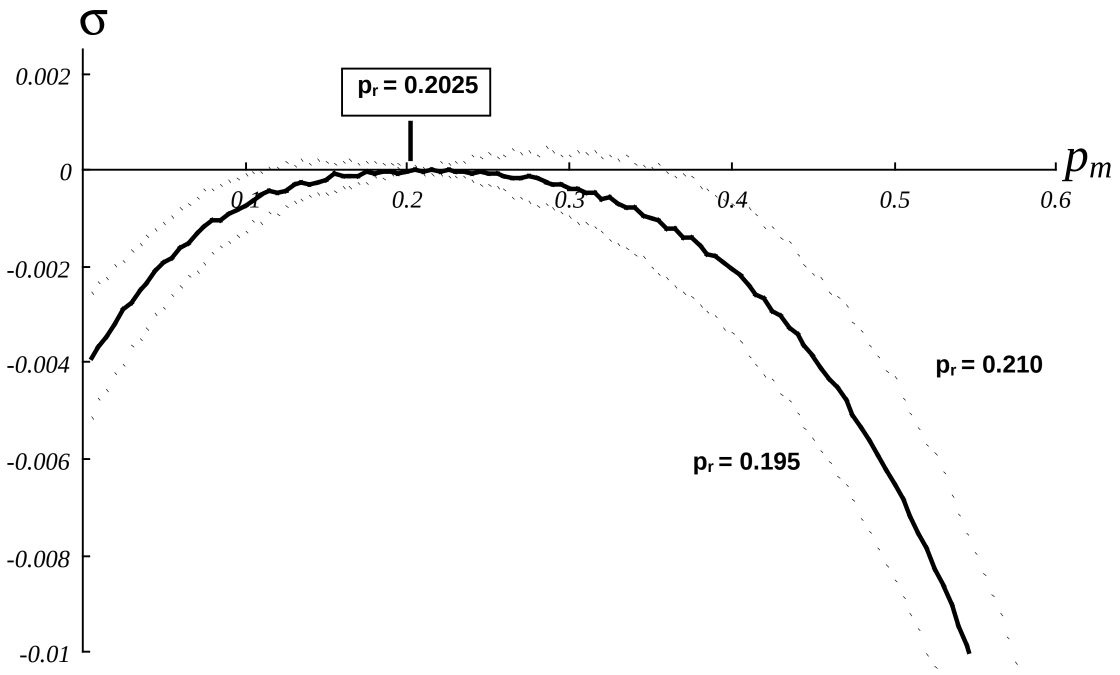

Figure 5, Tom Van Dooren and Hans Metz

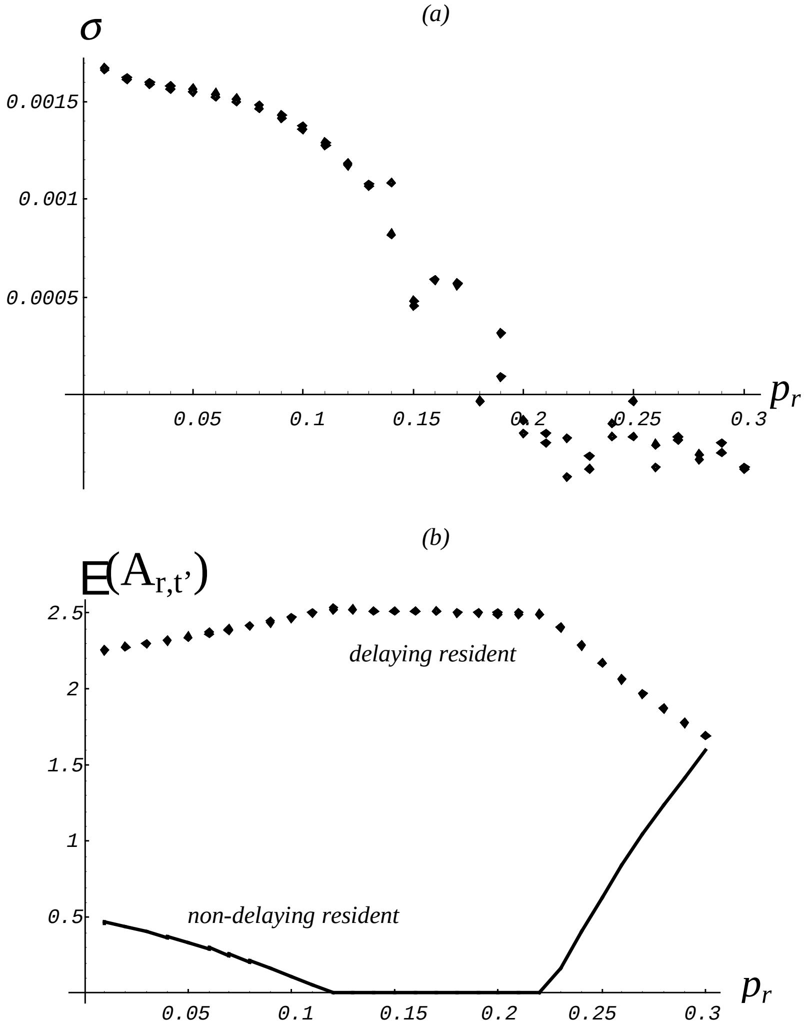

Figure 6, Tom Van Dooren and Hans Metz

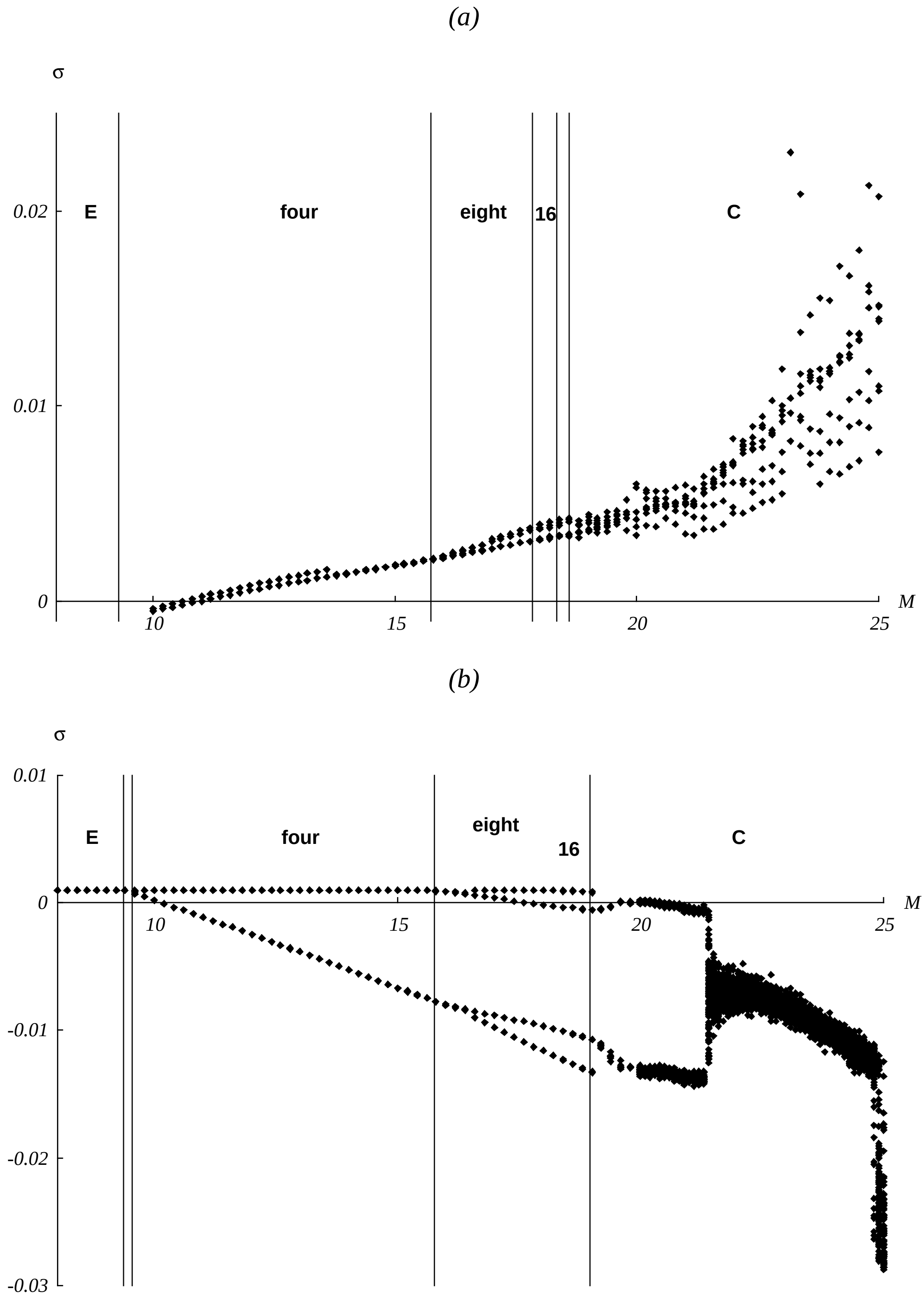

Figure 7, Tom Van Dooren and Hans Metz

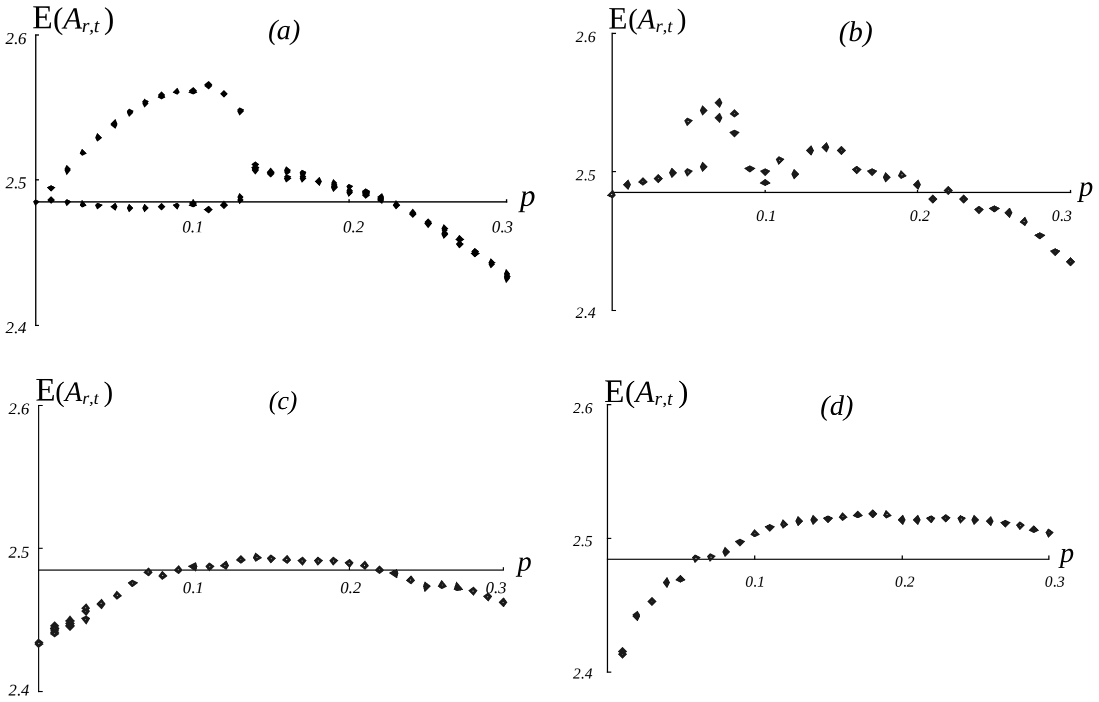

Figure 8, Tom Van Dooren and Hans Metz