Working Paper

Evolution of mixed maturation strategies in semelparous life histories: the crucial role of dimensionality of feedback environment

Mikko Heino, J.A.J. Metz & Veijo Kaitala

WP-96-126
November 1996

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Evolution of mixed maturation strategies in semelparous life histories: the crucial role of dimensionality of feedback environment

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We study the evolution of the age-at-maturity in a semelparous life history with two age-classes. An individual may either breed in the first year of its life and die, or delay breeding to the second year. In this setting a mixed strategy means that a fraction of the individual's offspring breed in the first possible breeding event, while the remaining fraction delay breeding. Current theory seems to imply that mixed strategies are not evolutionarily stable strategies (ESS) under a steady state population dynamical regime. We show that a two-dimensional feedback environment may allow the evolution of mixed age-at-maturity. Furthermore, different phenotypes need to perceive the environment differently. The biological reasoning behind these conditions is different resource usage or predation pressure between two age-classes. Thus, the conventional explanations for the occurrence of mixed strategies in natural populations, environmental stochasticity or complex dynamics, are not needed.

1 Introduction

Life-history theory is concerned with finding life histories that are favoured by natural selection. The assumed end-points of selection are considered to be "optimal" in an evolutionary sense. Until recently, the standard procedure in determining optimal life histories was to assume that evolution maximizes some density independent fitness "measure" (Roff 1992; Stearns 1992). The most common measures used are expected lifetime fecundity (or basic reproductive number) R_0, and intrinsic rate of increase (or population growth rate) r, defined by the Euler-Lotka equation. Other paradigms also exists, including evolutionarily stable strategies (ESS, Maynard Smith & Price 1973) based on an invasion criterion (e.g. Metz *et al.* 1992). It has been puzzling when maximizing a density-independent fitness measure is consistent with the theoretically sounder ESS concept. This problem was attacked by Mylius & Diekmann (1995), and later elaborated by Metz *et al.* (1996), who showed that the fitness maximization approach is restricted to one-dimensional environments, the specific optimization criterion depending on further details of the environmental feedback. The "environment" here refers to the feedback environment, i.e. the environment as it occurs in the equations for the population state. Usually the feedback loop is assumed to be direct, i.e. this environment can be considered as a function of population state. The dimension of the environment refers here to the number of scalars needed to describe the environmental condition, as it appears in the environmental feedback loop. This dimensionality is essentially a mathematical property: it does not refer directly to reality, but rather to the way reality is described in the particular model.

The adherence to simple maximization tools — and to one-dimensional environments in particular — has restrained the development of life-history theory. The ESS concept is not restricted to one-dimensional environments, although the great majority of ESS life history studies are restricted to this special case! Sticking to one-dimensional environments rules out the possibility of frequency-dependent selection, if density-dependence is accounted for. Consequently, in one-dimensional, constant environments, we can expect to find only a single phenotype value to be optimal. However, under frequency-dependent selection, which requires the environment to be at least two-dimensional, mixed strategies become feasible.

By frequency-dependent selection we refer to a type of selection in which the fitness of a phenotype depends on its frequency in the population in a

such way that a phenotype gains advantage when its frequency decreases (i.e. negative frequency-dependence, see Gromko 1977). This usage is common in life-history theory and behavioural ecology, but broader usages are used in some other branches of evolutionary biology.

We adopt the terminology promoted by Eshel (1996, cf. also Geritz *et al.* 1998): An *evolutionarily stable strategy,* when common, is unbeatable, or immune, against invasion of any alternative strategy (Maynard Smith & Price 1973; for a rigid definition, see e.g. Eshel 1996). If a strategy is also evolutionarily attractive, i.e. convergent-stable, it is referred to as a *continuously stable strategy* (CSS). Finally, we refer to a strategy that is an ESS but not convergent stable as an *evolutionarily stable repeller* (ESR).

In this paper we study the evolution of a polymorphic or mixed age-at-maturity within the simplest possible scenario of a semelparous life-cycle with two age-classes. A polymorphic age-at-maturity may indicate that the underlying population strategy is mixed, that is, the strategy is to mature at a certain age i with probability γ_i. A wide range of organisms possess a life-cycle which qualitatively fits the pattern studied here, including opossum shrimps (Hakala 1979; Morgan 1980), Pacific salmon (Kaitala & Getz 1995), and several monocarpic plants (De Jong *et al.* 1987). Often environmental stochasticity or fluctuations are invoked to explain the evolution of mixed life history strategies (Kisdi & Meszéna 1993; Bulmer 1994). Another possibility is that fluctuations are inherent in the population dynamics: non-equilibrium dynamics, for example, may favour mixed strategies (Getz & Kaitala 1993; Van Dooren & Metz 1998). In both cases, a mixed maturation strategy can be seen to represent a bet-hedging strategy. In this paper we show that mixed maturation strategies may evolve under a steady state population dynamical regime if selection is frequency-dependent. Thus, our theory clearly demonstrates the crucial importance of considering multi-dimensional feedback environments in the population dynamics.

The paper is composed as follows. In § 2 the population dynamical model is introduced. Adaptive dynamics in a one-dimensional environment is briefly treated in § 3. Our main results for multi-dimensional environments are presented in § 4. The paper concludes with a discussion (§ 5).

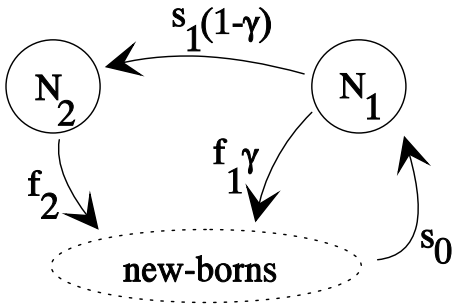

Figure 1: Schematic representation of semelparous life-history with two age-classes studied in this paper. The strategy γ controls the fraction of phenotypes breeding at the end of their first year of life. f_i = age-specific fecundity, s_i = age-specific survival probability.

2 Population Dynamics

Consider a following general life-cycle for a semelparous organism with two age-classes, N_1 and N_2 (figure 1). The population census takes place just before breeding. The two age-classes have age-specific fecundities $\tilde{f}_1$ and $\tilde{f}_2$. Here a tilde denotes the parameters which may be influenced by the environmental condition. However, only a fraction γ, $0 \leq \gamma \leq 1$, of age-class one breed, while the others delay their breeding. Those which delay have a probability $\tilde{s}_1$ to survive to the next breeding season. Thus, the adult population gives birth to $\tilde{f}_1\gamma N_1 + \tilde{f}_2 N_2$ offspring, which survive to age one with probability $\tilde{s}_0$. By definition, all animals die after breeding. The age-class dynamics are given by the following equations:

$$N_1(t+1) = \tilde{s}_0\tilde{f}_1\gamma N_1(t) + \tilde{s}_0\tilde{f}_2 N_2(t) \tag{1}$$

$$N_2(t+1) = \tilde{s}_1(1-\gamma)N_1(t), \tag{2}$$

in which any of the parameters may be affected by density dependence. It is reasonable to assume that both phenotypes are viable if there is no density dependence: $\tilde{s}_0\tilde{f}_1 > 1$ and $\tilde{s}_0\tilde{s}_1\tilde{f}_2 > 1$ in the virgin environment.

The expected lifetime fecundity (or basic reproductive number) R_0 is given by

$$R_0(\gamma, E) = \tilde{s}_0\tilde{f}_1\gamma + \tilde{s}_0\tilde{s}_1\tilde{f}_2(1-\gamma) = \tilde{s}_0\tilde{s}_1\tilde{f}_2 + \gamma\tilde{s}_0(\tilde{f}_1 - \tilde{s}_1\tilde{f}_2), \tag{3}$$

where E denotes the condition of feedback environment. The intrinsic rate of increase r (i.e. the population growth rate which would ensue under constant environmental conditions) can be solved explicitly from the Euler-Lotka equation:

$$r(\gamma, E) = \begin{cases} \ln(\tilde{s}_0 \tilde{f}_1) & \text{if } \gamma = 1, \\ \ln \frac{2\tilde{s}_0 \tilde{s}_1 \tilde{f}_2 (1-\gamma)}{-\tilde{s}_0 \tilde{f}_1 \gamma + \sqrt{(\tilde{s}_0 \tilde{f}_1 \gamma)^2 + 4\tilde{s}_0 \tilde{s}_1 \tilde{f}_2 (1-\gamma)}} & \text{otherwise.} \end{cases}$$

3 Constant, One-Dimensional Environments

3.1 General Theory

We say that the environment is one-dimensional, if all the relevant information on the environment can be characterized by a single scalar E. Let E_γ denote steady state environment created by a monomorphic population playing strategy γ.

Assume now that the population dynamics reaches a point equilibrium state, in which necessarily $R_0 = 1$. According to the pessimization principle of Mylius & Diekmann (1995), the strategy which survives under the worst environmental conditions, is an ESS. The expected life-time fecundities of the pure strategies are $R_0(0, E) = \tilde{s}_0 \tilde{s}_1 \tilde{f}_2$ and $R_0(1, E) = \tilde{s}_0 \tilde{f}_1$. From equation (3) it follows that the expected life-time fecundity of a mixed strategy $\gamma \in]0, 1[$ will never exceed that of the pure strategy having the higher expected life-time fecundity. Only when $R_0(0, E_0) = R_0(1, E_1)$, a mixed strategy will have an equal fitness to both pure strategies. However, then any population strategy is an ESS, but lacks convergence stability. Hence, no population strategy is a CSS.

Result 1 *In constant, one-dimensional environments mixed CSSs are not possible.*

It can be shown that this result is robust, since it still holds true in the great majority of cases if the feedback environment is actually high dimensional, but restricted to a narrow tube around a one-dimensional curve (Appendix 1).

3.2 Fitness Maximization

The case of a one-dimensional environment contains two examples of special interest, as they provide a link to the methodology of the bulk of earlier life history theory. In these cases the maximization of density independent optimization criterion, either the expected lifetime fecundity or the intrinsic rate of increase, is valid in a density-dependent context (Mylius & Diekmann 1995; Metz *et al.* 1996).

First, density-dependence affects fecundity (f_1 and f_2) and/or new-born survival (s_0), in a such manner that the basic reproductive number can be written as $R_0(\gamma, E) = \nu(E)s_0[f_1\gamma + s_1 f_2(1-\gamma)]$, where $\nu(E)$ is a decreasing function of the environmental condition E and $\nu(E_V) = 1$. E_V is the virgin environment with no detrimental effects from density-dependence. The environmental condition E is assumed to increase with increasing population density, i.e., crowding. Note that the parameters s_0, s_1, f_1 and f_2 reflect the situation in a virgin environment. According to Result 1 of Mylius & Diekmann (1995), a strategy γ which maximizes the $R_0(\gamma, E_V)$ is an ESS. Thus,

$$\gamma^* = \begin{cases} 1 & \text{if } f_1 > s_1 f_2 \\ 0 & \text{if } f_1 < s_1 f_2. \end{cases}$$

When $f_1 = s_1 f_2$, any γ is an ESS in a sense that all mutants will have zero growth rate in an environment set by the resident strategy. However, for the same reason no strategy is a CSS.

The second case is that survival (s_0 and s_1) is density-dependent in such way that $s_i(E) = \nu(E)s_i(E_V)$, $i = 0, 1$, where $\nu(E)$ is some decreasing function of environmental condition. Then a strategy γ which maximizes $r(\gamma, E_V)$ is an ESS (Mylius & Diekmann 1995). We may now write

$$\gamma^* = \begin{cases} 1 & \text{if } (s_0 f_1)^2 > s_0 s_1 f_2 \\ 0 & \text{if } (s_0 f_1)^2 < s_0 s_1 f_2. \end{cases}$$

In the special case that $(s_0 f_1)^2 = s_0 s_1 f_2$, $r(\gamma, E_V)$ is independent of γ, and all strategies are evolutionary unbeatable, but no strategy is a CSS.

4 Constant, Multi-Dimensional Environments

4.1 General Theory

We consider the feedback environment to be n-dimensional if n scalars are needed to provide the relevant information on the environmental time series which, together the population dynamical equations (1)–(2), determines the state of the population one time step further. Moreover, we assume that the feedback environment depends on some, as yet unspecified, way on N_1 and N_2. Moreover we assume that for all γ the population dynamics necessarily converges to a stable point equilibrium. Therefore, we can restrict ourselves to $n = 2$, without loss of generality. We denote the two-dimensional environment as a vector $\mathbf{E} := (E_1, E_2) \in \mathbf{R}^2$. Finally, we restrict to cases in which *(i)*, for every strategy γ the unique globally stable population dynamical equilibrium $(\hat{N}_1, \hat{N}_2)$ has different values for different γ, and *(ii)*, there exists a mapping $(\hat{N}_1, \hat{N}_2) \mapsto (\hat{E}_1, \hat{E}_2)$, with again $(\hat{E}_1, \hat{E}_2)$ different whenever $(\hat{N}_1, \hat{N}_2)$ is different. Conditions *(i)* and *(ii)* imply that there exist an inverse mapping sending any feasible condition $(\hat{E}_1, \hat{E}_2)$ to a value γ.

For our argument it is essential that the two phenotypes experience the environmental feedback, or density-dependence, in different ways. We assume density dependent survival rates (s_0 and s_1), which obviously satisfies the above assumption. We include density-dependence explicitly in the formula of R_0:

$$\begin{aligned} R_0(\gamma, \mathbf{E}) &= \nu(\mathbf{E}) s_0 f_1 \gamma + \nu(\mathbf{E}) s_0 \mu(\mathbf{E}) s_1 f_2 (1-\gamma) \\ &= \nu(\mathbf{E}) s_0 \mu(\mathbf{E}) s_1 f_2 + \gamma \nu(\mathbf{E}) s_0 (f_1 - \mu(\mathbf{E}) s_1 f_2), \end{aligned} \tag{4}$$

where $\nu(\mathbf{E})$ and $\mu(\mathbf{E})$ are functions representing effects of density dependence, which we assume to be smooth, positive and decreasing in both E_1 and E_2, and such that the population dynamics converges to a stable point equilibrium. Necessarily $\nu(\mathbf{E}_V) = \mu(\mathbf{E}_V) = 1$.

If a mixed ESS γ^* exists, any rare mutant arriving into a monomorphic resident population will have zero growth rate. In particular, $R_0(0, \mathbf{E}_{\gamma^*}) = R_0(1, \mathbf{E}_{\gamma^*})$, which can be rewritten as

$$f_1 = \mu(\mathbf{E}_{\gamma^*}) s_1 f_2 \tag{5}$$

Equation (5) can hold true only if $s_1 f_2 > f_1$ — a necessary condition for the existence of a mixed ESS. Note for further reference that any $\mathbf{E}$ in which

the reproductive number of all different phenotypes are equal satisfies equation (5), even if this $\mathbf{E}$ is not an environment corresponding to a population dynamical equilibrium. Sticking to population dynamical equilibria, we necessarily have $R_0(1, \mathbf{E}_{\gamma^*}) = 1$, which expands to

$$\nu(\mathbf{E}_{\gamma^*}) s_0 f_1 = 1. \tag{6}$$

If equations (5)–(6) have a common solution corresponding to a $\gamma \in]0, 1[$, then a mixed strategy is an ESS.

Next we consider the evolutionary attractivity of such mixed ESSs. The problem is to characterize adaptive dynamics in population dynamical equilibrium points $(\hat{E}_1, \hat{E}_2)$ close to $\mathbf{E}_{\gamma^*}$. For that task we should know the fate of rare mutants entering monomorphic equilibrium populations. These monomorphic equilibrium populations define a curve $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$ in $\mathbf{R}^2$. The endpoints of this curve correspond to monomorphic populations playing pure strategies.

By replacing $\mathbf{E}_{\gamma^*}$ with any $\mathbf{E}$, equation (5) defines a curve

$$m := \{(x, y) \mid \mu(x, y) s_1 f_2 - f_1 = 0, x \in E_1, y \in E_2\},$$

which is an isovalue contour on which all rare mutants arriving into population have equal reproductive numbers. In a similar manner, equation (6) defines a unity reproductive number contour for the non-delaying strategy $(\gamma = 1)$,

$$n := \{(x, y) \mid \nu(x, y) s_0 f_1 = 1, x \in E_1, y \in E_2\}.$$

We assume that m and n can be regarded as the graphs of two functions, which we shall also denote as $m : E_1 \mapsto E_2,\ n : E_1 \mapsto E_2$.

The equilibrium points $(\hat{E}_1, \hat{E}_2)$ must lie between the curves m and n. The argument is as follows (see figure 2): If $E_2 < m(E_1),\ \mu(x, y) s_1 f_2 > f_1$, which means (remember equation (4)) that the delaying phenotype $(\gamma = 0)$ has higher reproductive number than the non-delayer $(\gamma = 1)$. If $E_2 < n(E_1),\ \nu(x, y) s_0 f_1 > 1$ and non-delayers have a reproductive number greater than one. Thus, below m and n the population size will grow, whatever the strategy is. In a similar manner, above both m and n, the non-delayers have smaller reproductive number than the delayers, which have negative growth rate. So we are confident that the isovalue contour for $R_0(0, \mathbf{E}) = 1$ of delayers $(\gamma = 0)$, lies between the curves m and n. Furthermore, the equilibrium points $(\hat{E}_1, \hat{E}_2)$ in which $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$, must lie between n and the isovalue contour $R_0(0, \mathbf{E}) = 1$.

Consider a monomorphic population with strategy γ, with associated equilibrium point $\hat{\mathbf{E}}_\gamma$. If the unity reproductive number contour n lies above $\hat{\mathbf{E}}_\gamma$ (in that case necessarily the curve m and unity reproductive number contour for $\gamma = 0$ lie below $\hat{\mathbf{E}}_\gamma$), a mutant with $\gamma' > \gamma$ can increase in numbers, while a mutant with $\gamma' < \gamma$ will vanish. Thus, the population strategy will increase until either the curves m and n cross each other, or $\gamma = 1$ is reached. These end results correspond to a mixed and a pure ESS, respectively. These ESSs are moreover CSSs. The opposite dynamics occurs, if $\hat{\mathbf{E}}_\gamma$ lies above n and below m. Thus, the number and the attractivity of ESSs depends on the pattern of crossings of m and n. However, we cannot simply say that, for example, an intersection in which n crosses m from above to below corresponds to a mixed CSS, or to an ERS, as the graphical concepts "above" and "below" depend on the numbering of $\mathbf{E}$-components, which we still have left arbitrary.

To simplify the presentation, we from now on shall adhere to the following convention: the components of $\mathbf{E}$ are numbered in such a way that γ increases with increasing E_1. The right endpoint of the curve $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$ corresponds then to a population strategy $\gamma = 1$, and the left endpoint to a population strategy $\gamma = 0$. Combined with our earlier assumption about the uniqueness of the population dynamical equilibrium conditions, this convention implies that the equilibrium curve can be represented as a monotone decreasing function from E_1 to E_2.

We can now draw together the results on existence and attractivity of mixed ESSs:

Result 2

(i) *All mixed ESSs correspond to points of intersection of the isovalue contours m and n.*

(ii) *Following the numbering convention that the components of $\mathbf{E}$ are numbered in such a way that γ increases with increasing E_1 along the curve $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$,*

   (a) any mixed ESS such that n crosses m from above, corresponds to a (local) mixed CSS, and

   (b) any mixed ESS such that n crosses m from below, corresponds to a mixed ESR.

If the components of **E** are numbered in the opposite way, the m and n just switch the roles.

In many concrete examples the isovalue contours m and n are simply linear. In that case we have the following classification of the possible outcomes of the adaptive dynamics:

Result 3 *For linear isovalue contours m and n, either of the following three statements applies:*

(i) *there exists a unique mixed global CSS (i.e. a globally attractive mixed ESS), or*

(ii) *there exists a unique mixed ESR (i.e. a repelling ESS), and both pure strategies are local CSSs, or*

(iii) *no mixed ESS exists, and either one or the other pure strategy is a global CSS.*

Figure 3 illustrates these scenarios.

We have now demonstrated that a two- or higher dimensional environment allows mixed CSSs. Below we consider a more concrete example to get some insight into the ecological situations in which we may expect mixed strategies to occur.

4.2 An Example

We make an explicit assumption about the form of density dependence in the population dynamics: The population regulation is assumed to take place by a reduction of age-specific survival probabilities or fecundities. To assure that the population dynamics has a point attractor in a largish range of parameter space, we use a Beverton-Holt –type density dependence. For the environmental condition **E** we take a linear combination of the densities of individuals entering age-classes one and two, before mortality takes place:

$$(E_1, E_2) := (f_1\gamma N_1 + f_2 N_2, (1-\gamma)N_1).$$

The ecological interpretation is that the two age-classes differ in resource usage or predators. The dynamics that we have in mind can be written as:

$$N_1(t+1) = \frac{s_0[f_1\gamma N_1(t) + f_2 N_2(t)]}{1 + \alpha_{11}E_1(t) + \alpha_{12}E_2(t)} \tag{7}$$

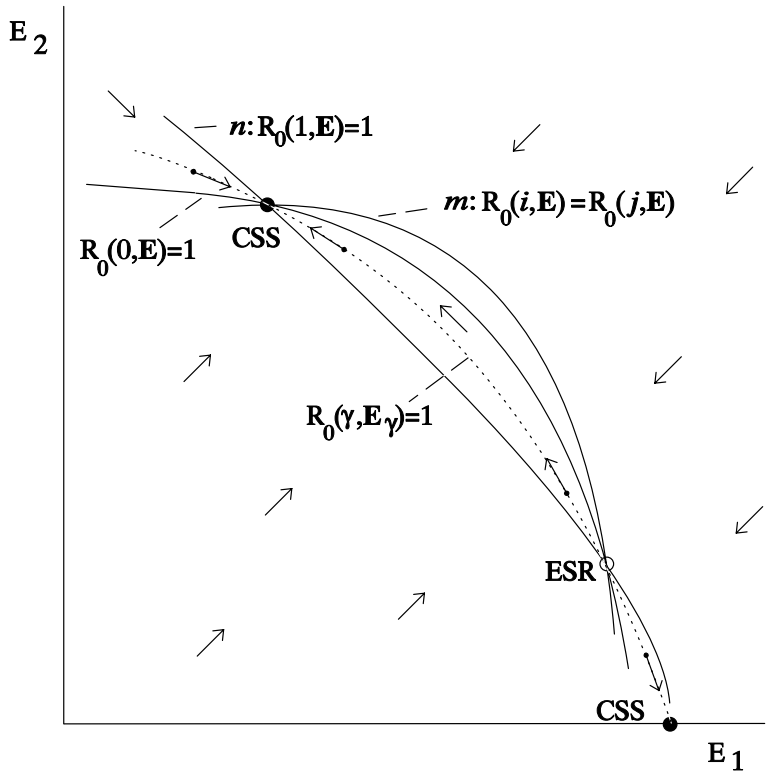

Figure 2: The adaptive dynamics depends on how the isovalue contours m and n are situated relative to each other. The delaying phenotype ($\gamma = 1$) has a unity reproductive number on curve n. On curve m all phenotypes have equal reproductive numbers. The monomorphic equilibrium populations are on the dotted curve; the narrow arrows symbolically represent the movement of $\mathbf{E}$ towards its equilibrium value. Following the numbering convention, the right endpoint of the curve corresponds to population strategy $\gamma = 1$. This curve is known to lie between isovalue contours m and n. The arrows on the dotted equilibrium curve depict the direction of steps of the adaptive dynamics. A point in environmental state space (E_1, E_2) where the curves intersect corresponds to an ESS. If n crosses m from above, it is a continuously stable strategy (CSS), otherwise it is an ESS lacking convergence stability, i.e. an evolutionarily stable repeller (ESR).

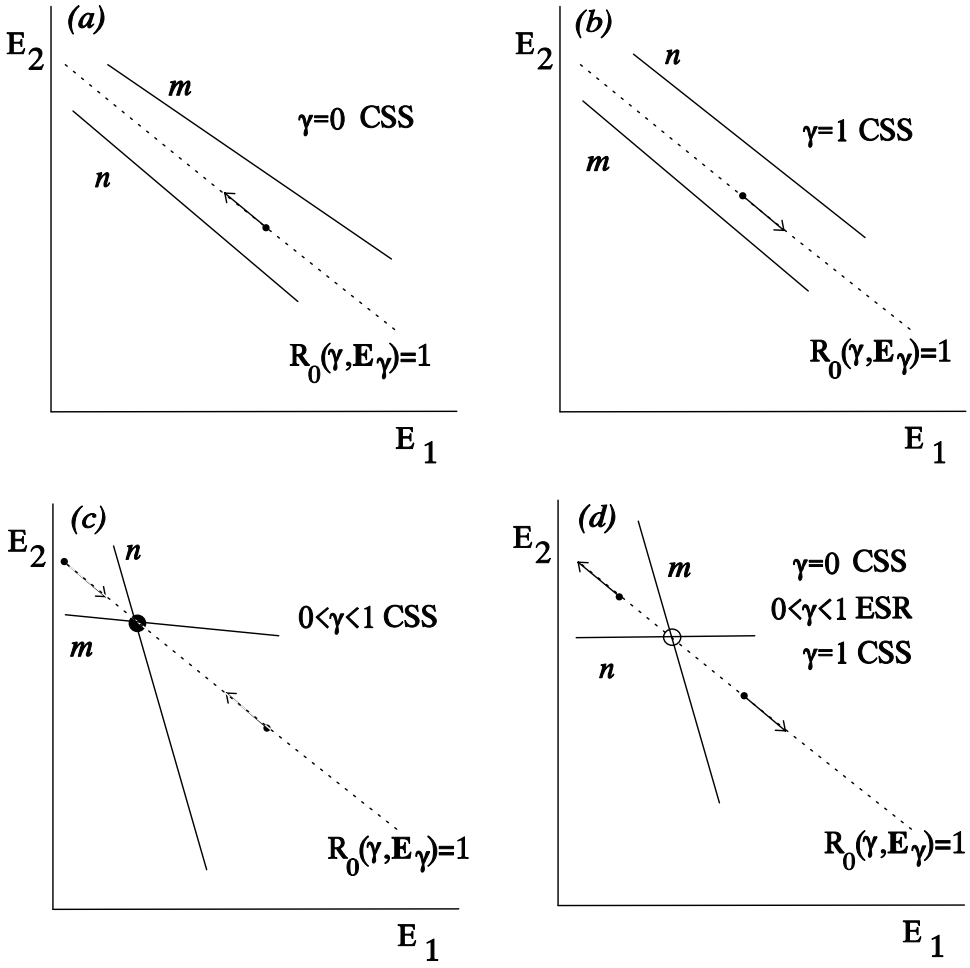

Figure 3: Four possible types of adaptive dynamics when the isovalue contours m and n are linear, and the components of $\mathbf{E}$ are numbered following our numbering convention (see text or caption for figure 2 for explanations). A CSS may be a pure strategy (a, b, d), or a mixed strategy (c). In (d) the CSS to which the adaptive dynamics is attracted will depend on the initial conditions; the boundary case is an ESR.

$$N_2(t+1) = \frac{s_1(1-\gamma)N_1(t)}{1+\alpha_{21}E_1(t)+\alpha_{22}E_2(t)} \tag{8}$$

where α_{ij} (≥ 0) denotes the relative competitive effect of age j individuals to age-class i; high relative values mean high impact. For simplicity we call the $\alpha's$ competitive effects even though they may represent only apparent competition. We assume that at least $\alpha_{11} > 0$ so that the dynamics will have a non-trivial attractor for all γ. We introduce some notational conventions to simplify the presentation of the results:

$$\Delta := s_1 f_2 - f_1,$$

which is a measure for the difference in the reproductive ratio in the virgin environment of those maturing at age two and one, and

$$\phi := s_0 f_1 - 1 > 0,$$

which is just a rescaled measure for the basic reproductive ratio in the virgin environment of those maturing at age one.

The derivation of CSS maturation strategies goes now in a similar way as in the previous section, and we skip the details here (see Appendix 2 for full derivation). Note that the results apply only for population dynamics with stable point attractors. For $\gamma \approx 0$ this assumptions is not fulfilled with all parameter combinations – see Appendix 2 for a discussion. Here we confine ourselves to the parameter combinations for which our stability assumption is fulfilled. Result 2 implies that mixed CSSs are possible only if $\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$. The CSS age-at-maturity is then given by

$$\gamma^* = \begin{cases} 1 & \text{if } \Delta \leq \frac{\alpha_{21}}{\alpha_{11}} f_1 \phi, \\ 1 + f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta}{f_1\alpha_{22}\phi - \alpha_{12}\Delta} & \text{if } -1 < f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta}{f_1\alpha_{22}\phi - \alpha_{12}\Delta} < 0, \\ 0 & \text{otherwise.} \end{cases} \tag{9}$$

If $\alpha_{11}\alpha_{22} < \alpha_{12}\alpha_{21}$, only mixed ESRs are possible. Now we get

$$\gamma^* = \begin{cases} 1 \text{ only} & \text{if } \Delta \leq \frac{\alpha_{21}}{\alpha_{11}} f_1 \phi, \\ 0 \text{ or } 1 & \text{if } -1 < f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta}{f_1\alpha_{22}\phi - \alpha_{12}\Delta} < 0, \\ 0 \text{ only} & \text{otherwise.} \end{cases} \tag{10}$$

***(i)* No competition between age-classes**

In this case $\alpha_{21} = \alpha_{12} = 0$. If $\gamma = 0$, we have two temporal populations which do not interact. The situation in which only one temporal population is present is necessarily unstable. Therefore we assume that both temporal populations exist, in which case all mutants face a constant environment. Then we get

$$\gamma^* = \begin{cases} 1 & \text{if } \Delta \leq 0, \\ 0 & \text{if } \Delta \geq \frac{\alpha_{22}}{\alpha_{11}}\phi, \\ 0 < 1 - \frac{\alpha_{11}\Delta}{\alpha_{22}\phi} < 1 & \text{otherwise} \end{cases}$$

Thus, mixed strategies are evolutionarily optimal if delaying increases the reproductive success in the virgin environment over that of non-delayers, but density dependence acts to equalize the realized reproductive success of the strategies. An example illustrating the dependence of CSS maturation strategy on the relative reproductive successes and the strengths of the density-dependence is given in figure 4.

5 Discussion

In this paper we have demonstrated that polymorphic age-at-maturity may evolve because different age-classes experience the environment in different ways, so that the feedback environment has at least two dimensions. Thus, neither environmental stochasticity nor complicated population dynamics are necessary for the evolution of mixed maturation strategies. Our results do not void, however, the significance of the aforementioned factors. Indeed, we have also carried out numerical simulations with the model in § 4*b* which clearly show that both environmental stochasticity and chaotic dynamics (if the Beverton-Holt –type density dependence is replaced with the Ricker one) may greatly promote the evolution of mixed maturation strategies: a mixed strategy is an ESS for a large part of the parameter space in which the deterministic analysis predicts pure strategies.

This study was inspired by the opossum shrimp *Mysis relicta*, which frequently shows polymorphic age-at-maturity (Hakala 1979; Morgan 1980). Our general results offer an explanation for the polymorphic behaviour in the opossum shrimp. A two-dimensional feedback environment may be realized by differences in resource usage or predators between age- or size-classes. Both alternatives are feasible in the species, taking the considerable size

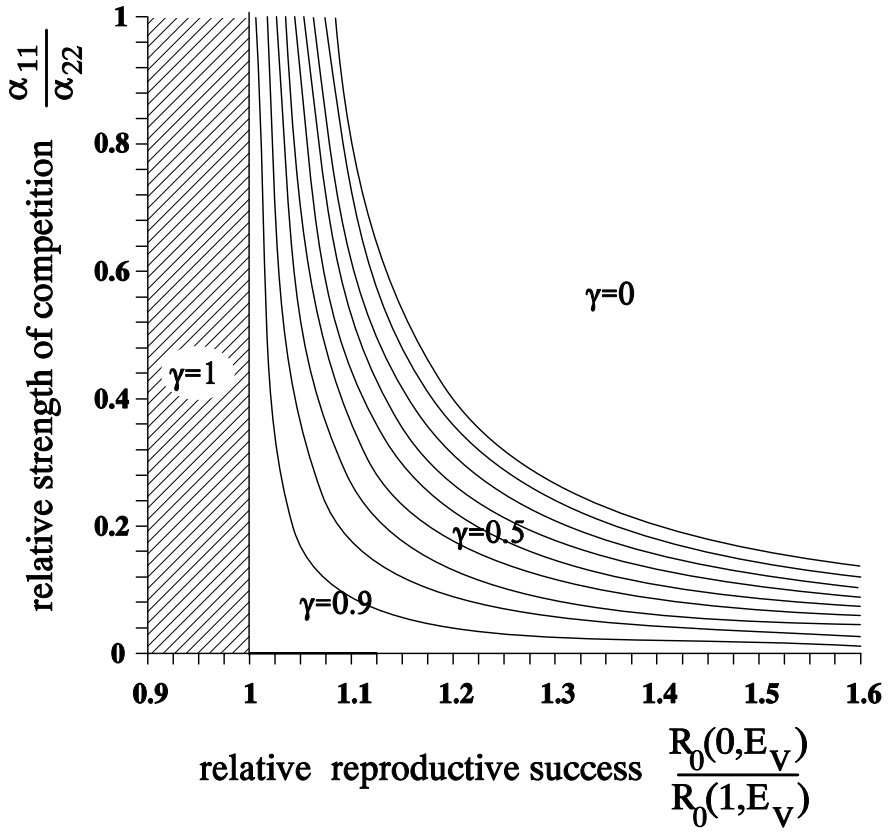

Figure 4: An example of CSS maturation strategies when the age-classes do not compete. On the x-axis lifetime production of offspring of the delaying phenotype increases relative to that of the non-delayers in the virgin environment. On the y-axis the importance of the density-dependence in the new-borns increases relative to the density-dependence in the surviving adults. Other parameter values: $s_0 = 0.1, f_1 = 100$.

differences between differently aged individuals into account (Hakala *et al.* 1993). The possible role of environmental stochasticity in maintaining this polymorphism is not clear, although the species dwells in deep lakes under the thermocline where the environment is rather constant. The low fecundity of the species renders chaotic dynamics unlikely.

The concept of ideal free distributions originally arose in the context of optimal foraging in patchy environment (Fretwell & Lucas 1970). This metaphor is useful also in life-history theory, coined as "reproductive ideal free distribution" by Kaitala & Getz (1995). Life-cycles can be viewed as graphs involving different paths. Different paths may have different expected density-dependent reproductive successes. Individuals following an ideal free choice will choose the path with the greatest expected reproductive success. If the population evolves towards some probabilistic path choice rule corresponding to a mixed strategy, such a rule makes all paths equally bad in terms of the reproductive success of all individuals. In other words, a mixed ESS will balance the reproductive success of all individuals. A pure strategy would correspond to a situation in which one path is better than any other, irrespective of the number of individuals choosing it.

Frequency-dependence has been somewhat neglected issue in life-history theory. Early examples include the analysis by Gross & Charnov (1980) who studied alternative male mating strategies in fish. Later Kaitala & Getz (1995) analyzed maturation strategies in Pacific salmon. In their model with an assortative mating system the environment is two-dimensional, and mixed strategies can occur. Kaitala *et al.* (1997) have studied the evolution of delayed maturity in a model allowing delaying more than once. Because the feedback environment is two-dimensional in their model, only one delaying probability can be fractional at one time.

Examples of frequency-dependence flourish in other fields of evolutionary biology. Indeed, the first application of game theory in biology was concerned with animal contests in which frequency-dependence played an important role (Maynard-Smith & Price 1973). Some modern examples from behavioural ecology bear clear resemblance to the model studied here. For example, Kaitala *et al.* (1993) have demonstrated maintenance of partial migration by frequency-dependent selection: in this example, the evolutionarily stable behavioural decision balances the reproductive success of the migrating and resident phenotypes.

We have shown above that for linear isovalue contours at most one mixed CSS can exist. More than one mixed CSS may occur if isovalue contours have

a sufficiently complex curvature. However, it is unclear whether such complex isovalue contours can arise from biologically plausible assumptions. Examples in which simple, non-linear isovalue contours might occur are interference between age-classes and predators with frequency-dependent prey selection. We are not aware of any published model allowing multiple mixed CSSs.

The adaptive dynamics in our model closely resemble population dynamics of a two-species competition model. Instead of separate species, we essentially study competition between two phenotypes, or two age-classes. The conditions for coexistence are similar (e.g. Renshaw 1991): in one-dimensional environment, coexistence is an exceptional case. In two-dimensional environment, coexistence can occur if intra-specific (intra-phenotypic) competition is more severe than inter-specific (inter-phenotypic) competition.

Finally, we would like to emphasize a few points made in this paper. First, the dimensionality of the environment is important for evolutionary considerations. Modelling efforts confined to one-dimensional, steady state environments or density-independent optimization criteria are deemed to miss the possibility of phenotypic polymorphisms. Models invoking frequency-dependent selection are inherently multi-dimensional. Second, not only is dimensionality important, but also the way population regulation takes place. If all individuals experience the density dependence in a similar manner, regardless of their phenotype, only monomorphisms are expected. And finally, explicit consideration of the dimensionality of the feedback environment provides further insight into any system under study.

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Appendix 1. Robustness of Result 1

A mixed ESS occurs in a one-dimensional environment, if both pure strategies have the expected reproductive success equal to one. This occurs only if the curves $\tilde{s}^{-1}$, $\tilde{f}_1$ and $\tilde{s}_1\tilde{f}_2$ have a common point of intersection. Here $\tilde{s}^{-1}$ is a decreasing function of the environmental condition E, or a constant at most. In a similar manner, $\tilde{f}_1$ and $\tilde{s}_1\tilde{f}_2$ are decreasing functions of the environmental condition E, or constants at most (either $\tilde{s}^{-1}$ or $\tilde{f}_1$ and $\tilde{s}_1\tilde{f}_2$ can be constant at one time).

Now assume that the feedback environment is in reality higher dimensional, but effectively confined to a narrow tube around a one-dimensional curve in a higher dimensional space. In this case the curves $\tilde{s}^{-1}$, $\tilde{f}_1$ and $\tilde{s}_1\tilde{f}_2$ are replaced by narrow bands. As an example we may think of a noisy environment. A mixed ESS is only possible if the three narrow bands intersect. Therefore, for "almost one-dimensional" environments a mixed ESS remains effectively a borderline case.

Appendix 2. Derivation of Equations (9)-(10)

If a mixed strategy γ^* is an ESS, all rare mutants will have equal growth rates in a steady state environment set by the resident strategy, $\mathbf{E}_{\gamma^*}$. In particular, $R_0(0, E_{\gamma^*}) = R_0(1, E_{\gamma^*}) = 1$. Provided that at least $\alpha_{12}\alpha_{21} \neq 0$ or $\alpha_{11}\alpha_{22} \neq 0$, these equations have a solution

$$\gamma^* = 1 + f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta}{f_1\alpha_{22}\phi - \alpha_{12}\Delta} \quad \text{if} \quad -1 < f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta}{f_1\alpha_{22}\phi - \alpha_{12}\Delta} < 0. \tag{A1}$$

The test for evolutionary attractivity (Result 2) is now simple. The isovalue contour functions m and n are $m(E_1) = \frac{s_0 f_1 - \alpha_{11}E_1 - 1}{\alpha_{12}}$ and $n(E_1) = \frac{\frac{s_1 f_2}{f_1} - \alpha_{21}E_1 - 1}{\alpha_{22}}$. These functions yield the test:

$$\text{If} \quad \alpha_{11}\alpha_{22} \quad \begin{cases} > \\ < \end{cases} \quad \alpha_{12}\alpha_{21}, \quad \gamma^* \text{ is } \begin{cases} \text{a CSS} \\ \text{an ESR} \end{cases}. \tag{A2}$$

The interpretation of this test is straightforward: if within-age-class competition is more severe than between-age-class competition, a mixed ESS is also a CSS.

Next we derive conditions under which pure strategies are CSSs. First consider the situation in which all individuals in the population mature at

age one ($\gamma = 1$). The equilibrium population size is

$$\hat{N} = \hat{N}_1 = \frac{\phi}{\alpha_{11} f_1}.$$

The sufficient condition for a successful invasion of mutants maturing at age two ($\gamma = 0$) is that

$$R_0(0, E_{\hat{\gamma}}) > 1 \Leftrightarrow \Delta > \frac{\alpha_{21}}{\alpha_{11}} f_1 \phi. \tag{A3}$$

When all individuals delay maturation ($\gamma = 0$), there are two temporally separated populations, which still interact if $\alpha_{12}\alpha_{21}$ is positive. For certain parameter values the resulting dynamics gives rise to two-year cycles, a situation similar to that studied by Nisbet & Onyiah (1994). This may occur also for small positive γ. Moreover, for other parameter values the amplitude of the cycles may depend on the initial conditions. For yet other parameter values one temporal population excludes the other.

Even if the dynamics are stable for $\gamma = 0$, the population dynamical equilibrium for equations (7)–(8) is a root of third order polynomial, and too complicated to be of any use in invasion considerations. However, using the Result 3, we can still draw the full picture of the adaptive dynamics. We have two different scenarios, depending on whether the attractivity test (A2) fails or not. Combining the information given by equations (A1) and (A3) with Result 3, we get equations (9)-(10).