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Evolution of mixed reproductive strategies in simple life-history models

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Contents

Abstract

Frequency-dependent selection may favour the evolution of mixed reproductive strategies, resulting in polymorphic life-histories within a population. Here I explore the theoretical and ecological possibilities for evolution of mixed reproductive strategies in two minimal age-structured life-history models. The first model addresses evolution of delayed maturity (i.e., competition between annuals and biennials), and the second one deals with evolution of semelparity versus iteroparity. A necessary condition for evolution of stable polymorphism is that the description of environmental feedback in the model is two-dimensional. A two-dimensional description is necessary if different age-classes experience the influence from the environment differently and have a different influence on the environment. This might be caused by resource utilization or predation risk being different between age-classes.

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Evolution of mixed reproductive strategies in simple life-history models

Mikko Heino

1 Introduction

The diversity of life-histories between species, or between different populations of a single species, can be attributed to differences in the environments they live in. The theory of life-history evolution has been successful in giving understanding to why certain environmental conditions favour, for example, delayed maturation, while in others it might be better to reproduce at the earliest possible age (Roff 1992, Stearns 1992). Most simple life-history models predict that in a certain environment (represented as a set of parameters in the model) a single life-history is evolutionarily 'optimal'. This result implies that populations should evolve towards monomorphic composition, because individuals of a single population share the same environment. Therefore, the observation that life-history strategies may be diverse even within populations has been theoretically perplexing. Here I explore the theoretical and ecological possibilities for evolution of mixed reproductive strategies, resulting in polymorphic life-histories, in two simple life-history models. The first model addresses the evolution of delayed maturity (i.e., competition between annuals and biennials), and the second one the evolution of semelparity versus iteroparity.

Two explanations are commonly offered to close the gap between the theory predicting monomorphic populations and observations showing polymorphisms. First, the observed variation is not adaptive and merely reflects mutation-selection balance, or that evolution has had not enough time to bring a population to the optimal monomorphic composition. Therefore, the variation is seen as a mere 'noise' around the optimal condition. The second explanation is that environmental variability or non-equilibrium dynamics may select for strategies that help 'spreading the risk'. Such bet-hedging strategies usually involve producing offspring of two or more phenotypes, one doing better under certain environmental conditions, the other under some other environmental conditions. In constant environments, polymorphic strategies should then not occur.

The third explanation, largely overlooked in life-history theory, is that polymorphic life-history strategies can be maintained by frequency-dependent selection (more precisely, strong frequency-dependence, see Heino, Metz and Kaitala 1998). This mechanism allows evolution of phenotypic polymorphisms even under constant environmental conditions (for life-history examples, see Bulmer 1994, Kaitala and Getz 1995, Heino, Metz and Kaitala 1997, Kaitala, Mappes and Ylönen 1997). Under selection with strong frequency-dependence, coexisting phenotypes get selective advantage when rare, such that at some intermediate frequency all coexisting phenotypes are equally fit. In other words, it is necessary that environmental feedback levels down the fitnesses of the common phenotypes, and the rare phenotypes get a relative advantage. The ecological processes that can cause frequency-dependence are diverse. For example, predators specializing on the most frequent prey types give advantage to the rare ones. Another example is a scenario in which different phenotypes have only partially over-lapping resource usage, resulting in a sort of resource refugium which helps to maintain rare phenotypes in a population. Theoretically, both of these examples have one thing in common: they require that the description of the environmental feedback is at least two-dimensional. In general, strong frequency-dependency, which makes stable coexistence of different phenotypes possible, is only possible if the dimension of the feedback environment is at least two (Heino, Metz and Kaitala 1997, 1998, Meszéna and Metz, this volume).

Traditionally, life history theoreticians have sought optimal life-histories that maximize some density independent fitness 'measure', such as the expected lifetime fecundity (or basic reproductive number) R_0, or intrinsic rate of increase r (Roff 1992; Stearns 1992). This approach is valid only if the dimension of the feedback environment is one (Mylius and Diekmann 1995, Metz, Mylius and Diekmann 1996, Metz and Mylius, this volume). The other way round: determining optimal life-histories by assuming that they maximize a certain optimization criterion is a valid approach, but its implicit assumptions generically preclude the possibility that selection will maintain polymorphic phenotypic composition of a population. The adaptive dynamics approach does not share this severe shortcoming. In this paper I address two classical problems in life-history theory with the adaptive dynamics approach: timing of first reproduction, and competition between semelparous (reproducing only once during the lifetime) and iteroparous (reproducing more than once) life-histories. Specifically, I seek for the conditions under which polymorphic life-history strategies are expected to evolve. For this purpose, I use two minimal population dynamical models with only two age-classes and two possible life-histories (phenotypes). The first model has been already analyzed in Heino, Metz and Kaitala (1997).

The concept of evolutionarily stable strategies (ESS) play an important role in understanding evolution of life-history strategies because ESSs represent potential resting points of long-term evolutionary change. An ESS, when common, is unbeatable, or immune, against invasion of any alternative strategy (Maynard Smith and Price 1973; for a rigid definition, see e.g. Eshel 1996). However, the ESS property does not guarantee that a population playing some other strategy will evolve towards an ESS. Convergence towards an ESS requires that mutants with a trait value closer to an ESS than the resident trait value can invade. Such an ESS is then evolutionarily attractive, i.e. convergent-stable, and it is referred to as a *continuously stable strategy* (CSS, Eshel and Motro 1981). Alternatively, a strategy that is an ESS but not convergent stable is an *evolutionarily stable repeller* (ESR).

Two main assumptions restricting the applicability of the theory outlined in this paper should be mentioned: First, population dynamics converges to a stable point equilibrium. This assumption is commonly made in order to keep models analytically tractable. The second assumption is more specific: invasion fitness of a rare

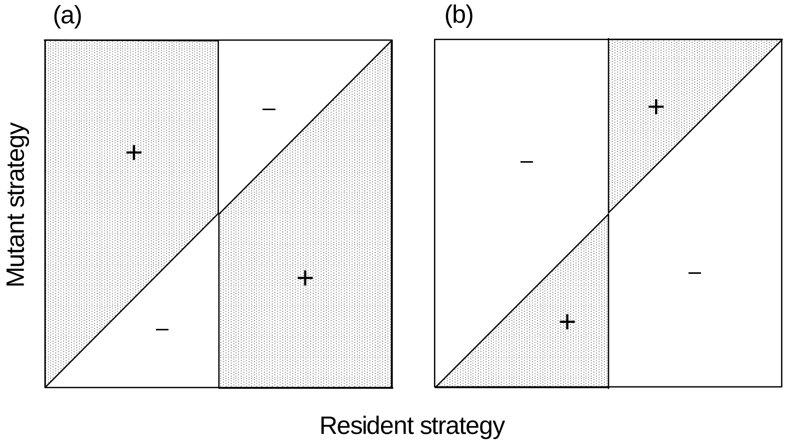

Figure 1 The pairwise invasibility plots in vicinity of an evolutionarily stable strategy (ESS) when mutant fitness is linear in its strategy. Only two non–generic configurations are possible: in (a), the ESS is evolutionarily attractive and called as a continuously stable strategy. In (b), the ESS is an evolutionary stable repeller.

mutant can be given as a linear function of its strategy. While making the analytical description of adaptive dynamics particularly easy, this latter assumption also restricts the possible kinds of adaptive dynamics that can be observed. Adaptive dynamics can be conveniently studied by means of "pairwise invasibility plots" (PIPs) (Metz *et al.* 1996, Geritz *et al.* 1997a, 1997b, Geritz, this volume). In a PIP, sign of the mutant fitness for different mutant strategies is plotted against different resident strategies. A positive sign indicates invasibility of resident population by a mutant type. If mutant fitness is linear in its strategy, then the PIP has a non-generic configuration in which the curve with zero mutant fitness intersects the diagonal vertically (Figure 1, see also Dieckmann and Metz, this volume). This configuration precludes the existence of evolutionary branching points. Therefore, the model always has at least one ESS, which, nevertheless, may be either a CSS or an ESR.

In the next section I will present the two life-history models. Section 3 outlines the way to analyze adaptive dynamics of life-history strategies in models with linear mutant fitness. This first requires introduction of some theoretical concepts which are not yet in common use in life-history theory. In section 4 the theory is applied to the analysis of adaptive dynamics of reproductive strategies in two simple age-structured models. The details of the analysis are given in the appendix.

2 Life-history models

Consider an organism with potentially two reproductive age-classes (N_1 and N_2) and with age-specific fecundities (f_i) and survival probabilities (s_i). Three types of life-histories which differ qualitatively in their age schedules of reproduction and survival are now possible:

1. *Annual (semelparous) life-history*: reproduction at age one and dying thereafter

2. *Biennial (semelparous) life-history*: reproduction is delayed until age two
3. *Iteroparous life-history*: reproduction occurs at both ages

These basic types of life-histories are common in both animals and plants. However, in botanical phrasing, the third life-history is called as perennial, and the term monocarpic is used as a synonym for semelparous.

The different life-histories can be viewed as different phenotypes of a single species. By studying competition between these phenotypes, two basic questions of life-history theory can be addressed: When is delayed reproduction favoured (life-history 1 vs. 2)? When does selection favour iteroparity over semelparity (life-history 3 vs. 1 or 2)? The reproductive strategy, denoted as γ, can now be defined as the proportion of a given phenotype among the offspring. An equivalent interpretation is that the reproductive strategy is the probability of expressing certain phenotype. Reproductive strategies $\gamma = 0$ and $\gamma = 1$ are then pure strategies: parents and their offspring are phenotypically alike. A reproductive strategy between zero and one is a mixed strategy. An individual playing a mixed strategy will produce a phenotypically polymorphic progeny. A reproductive strategy is called as a population strategy if it is adopted by all the individuals in a population.

In any ecologically realistic model, it is important to recognize that individuals influence the environment they live in – by depleting resources, or by being a resource (a prey or a host) for other individuals of the same or another species. At the same time, the combined effect of other conspecifics on the environment influences the well-being of individuals of the focal population. This is the feedback from the environment. The part of the environment which is both influenced by the population, and which will have influence on the population, is called the feedback environment. Assume that the condition of the feedback environment can be described with a two-dimensional vector $\mathbf{E} = (E_1, E_2)$ depending on some, as yet unspecified way on the densities N_1 and N_2. The increase of population size must eventually be manifested as changes in mortality risk and/or reproductive rate. Here I specifically assume that the age-specific survival probabilities are decreasing functions in both components of the feedback environment. The density-dependence of the survival parameters is denoted with a tilde.

Figure 2 shows two life-history models which are used to study competition between annual and biennial phenotypes (Figure 2a), and competition between annual (semelparous) and iteroparous phenotypes (Figure 2b). The population dynamical equations can be directly read from these life-cycle graphs. Note that in the graphs, the newborns occur as a “pseudo-stage”: newborns are not present at the time of population census (which is assumed to take place just before reproduction), and therefore they do not occur at the population dynamical equations. Nevertheless, their inclusion to life-cycle graphs makes them more readable.

In *evolution of delayed reproduction* model, the age-class dynamics are given by the following equations (Figure 2a):

$$N_1(t+1) = \tilde{s}_0 f_1 \gamma N_1(t) + \tilde{s}_0 f_2 N_2(t) \tag{1}$$

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

where f_i is the fecundity at age i.

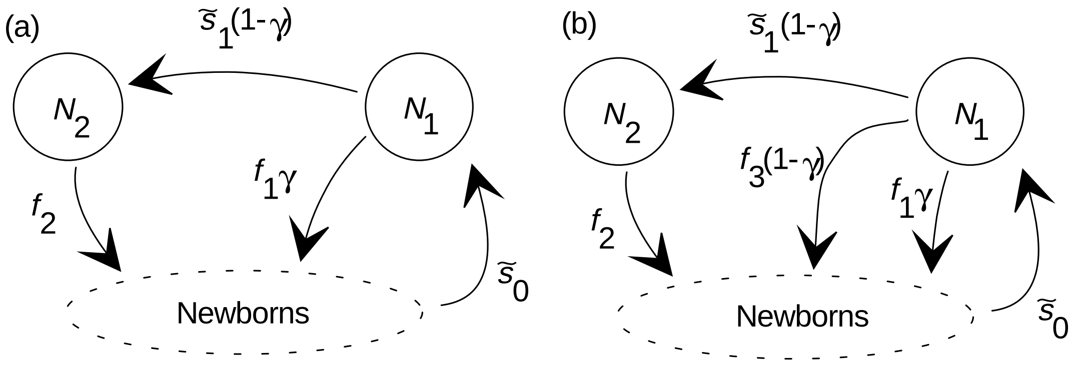

Figure 2 The life-history models. Model (a) is the "evolution of delayed maturity" model in which two possible phenotypes, annual and biennial. Model (b) is the "evolution of semelparity versus iteroparity" model with an annual semelparous and an iteroparous phenotype. In both model, reproductive strategy γ is the fraction annual phenotype among the offspring. Survival probabilities $\tilde{s}_i$ are assumed to be influenced by environmental feedback. f_i denote the age- and phenotype-specific fecundities.

The reproductive strategy γ can be interpreted as the fraction of annuals among the offspring, i.e. individuals maturing in their first year of life. This model has been analysed by Heino, Metz and Kaitala (1997). The basic reproductive number is (Figure 2a):

$$R_0(\gamma, \mathbf{E}) = \tilde{s}_0[f_1\gamma + \tilde{s}_1 f_2(1-\gamma)]. \tag{3}$$

The second model the *evolution of semelparity versus iteroparity* model. The dynamics for this model can be written as (see Figure 2b):

$$N_1(t+1) = \tilde{s}_0[(f_1\gamma + f_3(1-\gamma))N_1(t) + f_2 N_2(t)] \tag{4}$$

$$N_2(t+1) = \tilde{s}_1(1-\gamma)N_1(t). \tag{5}$$

Here f_1 is the fecundity of the annuals, and f_2 and f_3 are the fecundities of the perennials at ages two and one, respectively. In this model, the reproductive strategy γ is the fraction of individuals reproducing only once, at their first year of life. Note that setting $f_3 = 0$ would yield the first model.

The basic reproductive number in the evolution of semelparity versus iteroparity model is

$$R_0(\gamma, \mathbf{E}) = \tilde{s}_0[f_1\gamma + f_3(1-\gamma) + \tilde{s}_1 f_2(1-\gamma)]. \tag{6}$$

3 Theoretical background

I assume that population dynamics converges to a stable point equilibrium. Further, assume that the condition of the feedback environment depends on these densities in such a way that each reproductive strategy uniquely determines the steady state condition of the feedback environment, and vice versa. Therefore, on the long run, the time-dependence of the condition of the feedback environment can be neglected: after possible transient dynamics, the condition of the feedback environment stays constant. The dimension of the feedback environment can then be conveniently defined as the dimension of the vector $\mathbf{E}$ (for non-point-equilibrium dynamics the situation is more complex, see Meszéna and Metz, this volume). In the present context, the dimension of the feedback environment is then two. The dimension of the feedback environment plays a crucial role in adaptive dynamics of reproductive strategies: two is the lowest dimension which allows evolution of mixed reproductive strategies which result in phenotypic polymorphisms.

Under steady state population dynamical regime, fitness can be most conveniently measured as the basic reproductive number (also known as the expected reproductive success). Fitness depends on both strategy of an individual (γ), and the feedback environment ($\mathbf{E}$) it lives in, which is made explicit in the notation: $R_0(\gamma, \mathbf{E})$ (cf. Mylius and Diekmann 1995). Only mutants with the basic reproductive number greater than one can spread, while those with the basic reproductive number less than one are doomed to go extinct. Necessarily, for a population strategy, the basic reproductive number $R_0(\gamma, \mathbf{E}_\gamma) = 1$ – the population size will stay constant and every individual will, an average, just replace itself. Further, I assume that the basic reproductive number is monotonically decreasing in both of the components of the feedback environment, E_1 and E_2, and that mutant fitness is linear in the reproductive strategy γ. This latter assumption makes the analysis of adaptive dynamics particularly easy, and is crucial for the line of analysis presented here.

If a population strategy is an evolutionary stable strategy (ESS), then all mutant strategies have zero or negative fitness in the resident feedback environment. In models with linear fitness in the mutant strategy, ESSs that make the mutant fitness exactly zero play a key role in understanding the adaptive dynamics. In particular, this is true for pure strategies, which implies equalities

$$R_0(0, \mathbf{E}_{\gamma^*}) = R_0(1, \mathbf{E}_{\gamma^*}) = 1. \tag{7}$$

Generically, these ESSs are mixed strategies ($\gamma \in]0, 1[$), although a pure strategy can also have this special property. The analysis can be outlined as follows (skipping the non-generic case):

1. Determine if there exist an ESS which makes fitness of all possible mutant types equal by finding out if there exists a reproductive strategy γ which satisfies the equation (7). This involves first solving $\mathbf{E}$ from the equation (7) and then checking if it is an equilibrium feedback environment for some feasible reproductive strategy (i.e. $0 < \gamma < 1$). If such a solution exists, then it is a mixed ESS γ^*. Otherwise, a pure strategy is the only ESS (and CSS).

2. If a mixed ESS exists, determine its attractivity. This can be deduced from the configuration of isovalue contours $R_0(0, \mathbf{E}) = 1$ and $R_0(1, \mathbf{E}) = 1$ relative to the steady state feedback environments determined by equation $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$ (Figure 3). Assuming that the components of the feedback environment have been numbered in such a way that γ increases from left to right on the curve $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$, then a crossing of isovalue contour $R_0(0, \mathbf{E}) = 1$ by $R_0(1, \mathbf{E}) = 1$ from above implies that the ESS is also evolutionarily attractive (Figure 3a): if equilibrium point $\mathbf{E}_\gamma$ is on the right hand side of $\mathbf{E}_{\gamma^*}$ (necessarily $\gamma > \gamma^*$), then mutants γ' with $\gamma^* < \gamma' < \gamma$ can invade. The opposite dynamics occur on the left hand side of $\mathbf{E}_{\gamma^*}$. The reproductive strategy γ^* is therefore a convergent

stable ESS, i.e. a CSS. The opposite pattern of crossing between the isovalue contours would imply that the mixed ESS lacks attractivity (Figure 3b). The mixed ESS would then be called as an evolutionarily stable repeller (ESR, Heino, Metz and Kaitala 1997).

If a model structurally allows at most one mixed ESS (which occurs if isovalue contours are linear), adaptive dynamics can have only three different, mutually exclusive outcomes (Heino, Metz and Kaitala 1997):

1. There is a single, unique, globally attractive pure ESS.
2. There is a single, unique, globally attractive mixed ESS.
3. There are two locally attractive pure ESSs, separated by a repelling mixed ESS.

4 Adaptive dynamics of reproductive strategies

The theory outlined above is now used to analyze the life-history models given in section 2. Only the results are given here, while the details of the analysis are to be found in the appendix.

First, however, it is necessary to make the models complete by specifying the form of density-dependence and the relation of the feedback environment to the densities of the age-classes. To assure that the population dynamics has a point attractor in a largish range of parameter space, I use a Beverton-Holt –type density dependence. For the environmental condition **E** I take the densities of newborns and adults which try to survive till the second year of their life, before the density-dependent mortality occurs (compare to Figure 2):

$$(E_1, E_2) := \Big((f_1\gamma + f_3(1-\gamma))N_1 + f_2N_2 \ , \ (1-\gamma)N_1\Big). \tag{8}$$

Note that in Model 1 $f_3 = 0$ and E_1 simplifies accordingly. The survival probabilities can be now given as

$$\tilde{s}_0(t) = \frac{s_0}{1 + \alpha_{11}E_1(t) + \alpha_{12}E_2(t)} \tag{9}$$

$$\tilde{s}_1(t) = \frac{s_1}{1 + \alpha_{21}E_1(t) + \alpha_{22}E_2(t)}, \tag{10}$$

where s_0 and s_1 are survival probabilities in environment with no adverse effects from density-dependence – the virgin environment of Mylius and Diekmann (1995). These equations allow a wide range of ecological interpretations, depending on the non-negative coefficients α. At least α_{11} must be positive so that the population size stays bounded, no matter which reproductive strategy prevails. The terms $\alpha_{11}E_1$ and $\alpha_{22}E_2$ represent the effect of increasing density of an age group to its own survival. This might be due to competition of resources such as food, space or light, or due to predation or parasitism. The coefficients α_{12} and α_{21} represent competition or interference between the age groups, or in case of shared predators or parasites, apparent competition.

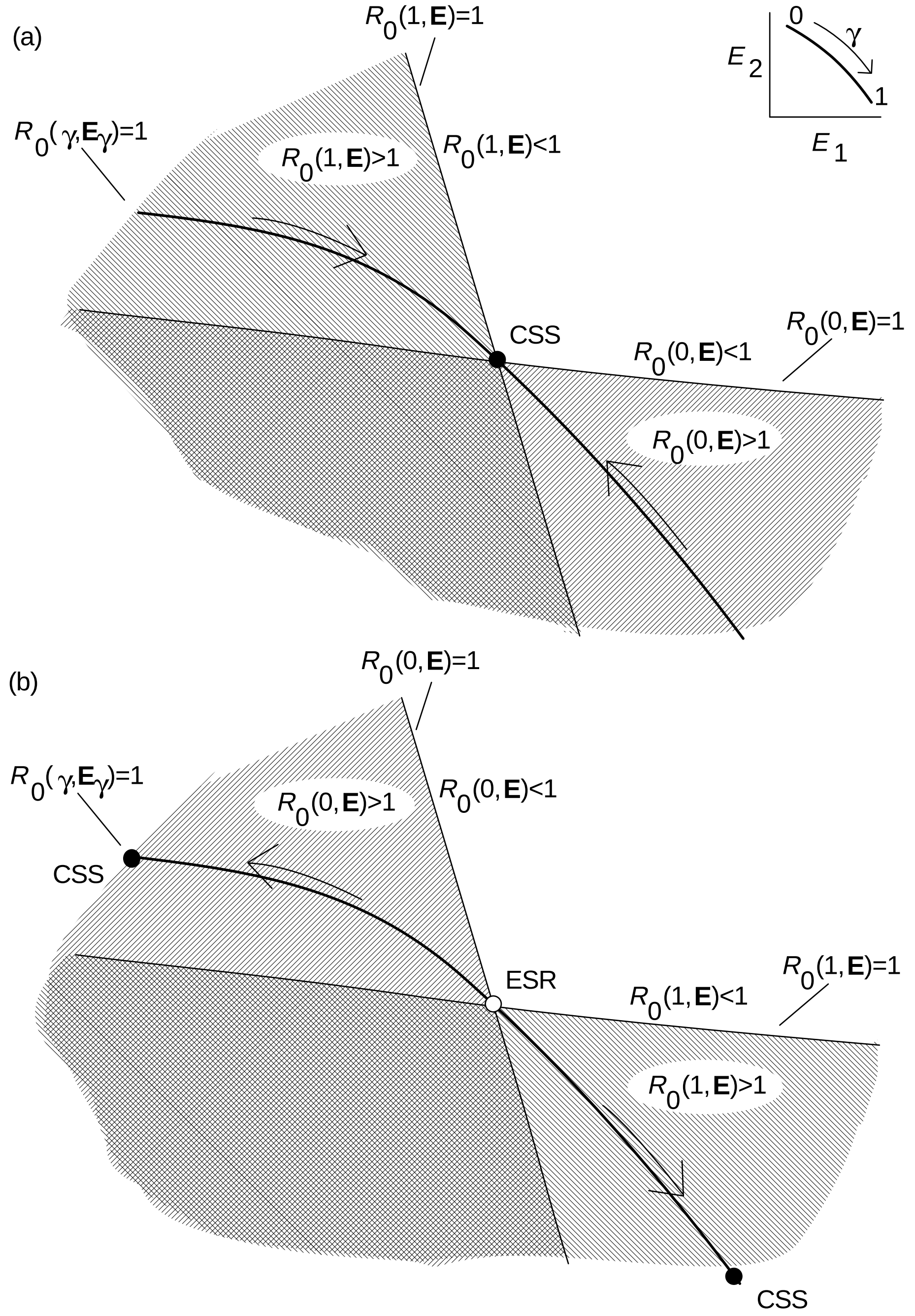

Figure 3 The adaptive dynamics in the vicinity of a mixed evolutionarily stable strategy (ESS). All mixed ESSs are crossing points of unity reproductive number contours for the pure reproductive strategies $\gamma = 0$ and $\gamma = 1$, $R_0(1, \mathbf{E}) = 1$ and $R_0(0, \mathbf{E}) = 1$. Whether an ESS is evolutionarily attractive or not depends on the way these contours cross each other; an ESS is then either a continuously stable strategy (a), or an evolutionary stable repeller (b).

The first main result is that in both models, the attractivity of mixed reproductive strategies depend only on the coefficients α. A necessary condition for existence of a mixed, attractive evolutionarily stable strategy is that

$$\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}. \tag{11}$$

Ecologically, this condition means that phenotypic polymorphisms are only possible if within age-class interactions are more important than interactions between age-classes.

The presentation of the results is greatly simplified by introducing few notational conventions. Let Δ_1 denote the difference in reproductive success between biennials and annuals in the virgin environment: $\Delta_1 := s_1 f_2 - f_1$. Let Δ_2 be a similar measure between iteroparous and semelparous annual phenotypes: $\Delta_2 := s_1 f_2 + f_3 - f_1$. A third shorthand is just a rescaled measure for the basic reproductive ratio of annuals in the virgin environment: $\phi := s_0 f_1 - 1$. The viability of the annual life-history implies that ϕ is positive, the other two measures might be negative as well.

Assuming now that within age-class interactions are more important than interactions between age-classes ($\alpha_{11}\alpha_{22} > \alpha_{12}\alpha_{21}$) and mixed CSSs are therefore possible, an evolutionarily stable and attractive reproductive strategy in the delayed reproduction model is

$$\gamma^* = \begin{cases} 1 & \text{if } \Delta_1 \le \frac{\alpha_{21}}{\alpha_{11}} f_1 \phi, \\ 1 + f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta_1}{f_1\alpha_{22}\phi - \alpha_{12}\Delta_1} & \text{if } -1 < f_1 \frac{f_1\alpha_{21}\phi - \alpha_{11}\Delta_1}{f_1\alpha_{22}\phi - \alpha_{12}\Delta_1} < 0, \\ 0 & \text{otherwise.} \end{cases} \tag{12}$$

If $\alpha_{11}\alpha_{22} < \alpha_{12}\alpha_{21}$, the equations remain virtually intact, but the former mixed reproductive strategy would be an evolutionary repeller. A population would then evolve either towards pure annual life-history ($\gamma = 1$) or towards pure biennial life-history ($\gamma = 0$), depending on the initial population strategy.

Annual life-history can be thought to be the ancestral life-history strategy. A relevant question is then when are biennials able to invade a population of annuals? Because of linearity of the mutant fitness, this happens whenever pure annual strategy is not an ESS. The invasion condition of biennials is therefore (see equation 12)

$$\Delta_1 > \frac{\alpha_{21}}{\alpha_{11}} f_1 \phi. \tag{13}$$

Because the right-hand-side of this equation is always non-negative, a necessary condition for biennial invasion is that biennials have higher reproductive success than annuals in the virgin environment ($\Delta_1 > 0$). The higher effect annuals have on the survival of biennials relative to their on survival (ratio α_{21}/α_{11} is high), the higher must be the advantage of biennials in the virgin environment for biennial life-history to be favoured. Note that the success of biennial invasion does not depend on the effect of biennials on the survival of annuals (coefficient α_{12}), or the severity of density-dependence on the second year (α_{22}). However, whether the eventual outcome of the invasion is either a pure population of biennials or a mixture of both life-histories depends on all the parameters of the model.

Next turn to the evolution of semelparity versus iteroparity. Assuming again that within age-class interactions are more important than interactions between age-classes, an evolutionarily stable and attractive reproductive strategy is

$$\gamma^* = \begin{cases} 1 & \text{if } \Delta_2 \leq \frac{\alpha_{21}}{\alpha_{11}}(f_1 - f_3)\phi, \\ 1 + f_1 \frac{(f_3-f_1)\alpha_{21}\phi - \alpha_{11}\Delta_2}{(f_3-f_1)\alpha_{22}\phi - \alpha_{12}\Delta_2} & \text{if } -1 < f_1 \frac{(f_3-f_1)\alpha_{21}\phi - \alpha_{11}\Delta_2}{(f_3-f_1)\alpha_{22}\phi - \alpha_{12}\Delta_2} < 0, \\ 0 & \text{otherwise.} \end{cases} \tag{14}$$

The first thing to note is the similarity of the results between the semelparity versus iteroparity model and delayed reproduction models. This was, of course, expected on the basis of structural similarity of the models.

The invasion condition of iteroparous reproductive strategy to a population of annuals is (from equation 14):

$$\Delta_2 > \frac{\alpha_{21}}{\alpha_{11}}(f_1 - f_3)\phi. \tag{15}$$

If iteroparous phenotype has higher fecundity in the first year than annuals ($f_3 > f_1$), then it can always invade. However, it is feasible to assume that iteroparous individuals have lower fecundity in their first year of life as a cost for extending their life-span, such that $f_3 < f_1$. This assumption leads to a similar invasion condition to the one in the delayed reproduction model: for a successful invasion to a population of annuals, it is necessary that the iteroparous phenotype have higher expected reproductive success in the virgin environment. How much higher reproductive success is necessary depends on the competitive effects annuals exert on iteroparous phenotype and on annuals themselves.

The results are simplified a lot if the two age-classes do not interact at all ($\alpha_{21} = \alpha_{12} = 0$). All mixed reproductive strategies are then evolutionarily attractive (remember equation 11). A necessary and sufficient condition that a population of annuals can be invaded by either biennial or iteroparous life-history strategies is that they have higher expected reproductive successes in the virgin environment ($\Delta_1 > 0$ or $\Delta_2 > 0$). If environmental feedback is strong enough to reduce the reproductive success of these alternative life-histories to the level of annuals at the population dynamical steady state, then a mixed reproductive strategy is an ESS. In that case only, the population will be phenotypically polymorphic. Otherwise, annuals will be outcompeted to extinction.

5 Discussion

The development of life-history theory shows a tendency towards increased recognition of the importance of environmental feedback in understanding evolutionary change. A parallel change has been observable in the development of fitness concepts. In the early theory, fitness was measured as the intrinsic rate of increase, and the environmental feedback was neglected altogether (e.g., Cole 1954). A major conceptual breakthrough was the introduction of the idea of evolutionarily stable strategies (Maynard Smith and Price 1973), which enabled to study life-history evolution in density-dependent context (e.g., Hastings 1978). In this context, the most powerful fitness concept is based on invasibility of resident populations by mutant strategies (Metz *et al.* 1992, Rand *et al.* 1994, Ferrière & Gatto 1995). However, the choice for the way in which population regulation works in models has often been rather arbitrary – usually just the most 'convenient' way of population regulation has been chosen. In most cases, this means one-dimensional environmental feedback. Unfortunately, this practice restraints the range of potential evolutionary outcomes by precluding existence of polymorphic strategies. Recent models with higher dimensional feedback environments have shown that polymorphic life-history strategies are feasible in variety of models with firm ecological basis (e.g., Bulmer 1994, Kaitala and Getz 1995, Heino, Metz and Kaitala 1997, Kaitala, Mappes and Ylönen 1997).

Cole's paradox – why iteroparity exists at all – fuelled much of the early development of life-history theory. The paradox itself was a result of major oversimplification, and has been resolved by including elementary biology into the model – see Bulmer (1994) for a good account on Cole's paradox. Bulmer (1994) also shows how phenotypic polymorphism (coexistence of annual and perennials) may occur in a two-dimensional feedback environment. The same result was obtained here with a slightly different model. A necessary condition for a successful invasion of iteroparous strategy is that it has higher expected reproductive success than the semelparous strategy in the virgin environment. For exact predictions on when iteroparity is favoured over semelparity and when coexistence of both phenotypes is possible, it is necessary to know the details of the environmental feedback.

Delayed reproduction portrayed a similar kind of dilemma than Cole's paradox until the importance of environmental feedback was recognized (De Jong, Klinkhamer and Metz 1987). Under-density dependence, lengthened generation time need not to be a drawback – all that matters is the expected reproductive success at the steady state. However, the details of population regulation matter again, and two-dimensional feedback environment is probably needed to explain some of the observed phenotypic polymorphisms (Heino, Metz and Kaitala 1997).

The aforementioned analyses have taken the life-history parameters 'as given'. Deeper understanding on the evolution of life-history strategies presumes also knowledge on the trade-offs between the parameters. These trade-offs determine the feasible parameter combinations. For analyses of evolution of basic life-history patterns taking the trade-offs into account, see Yodzis (1989) and Takada (1995).

The ecological processes behind a two-dimensional description of the feedback environment has been mentioned already – differential resource usage, predation or parasitism between age-classes (or between other relevant stages). However, a question why these interactions should depend on age-class in the first place still remains. The most obvious way such differences may arise is size differences between age-classes. In most organisms vulnerability to predation and resource usage are strikingly different between newborns and full-growns. Bigger individuals usually have access to a larger range of food items than small ones. Predators are commonly size-selective in their prey choice, leading to a differential mortality risk between different size groups. In plants, size influences access to resources such as light through shading effects. In models, these various interactions are usually greatly simplified, and they may even take the same functional form. In any case, it is important to recognize that the representation of environmental feedback cannot be arbitrary but has to be rooted to the biological problem under consideration.

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Appendix: Adaptive dynamics in linear fitness models

The technical details of the procedure outlined in section 3, and applied to concrete life-history models in section 4, are given here to a degree that the derivation of the equations 11–15 becomes clear. I follow here a convention that the components of the feedback environment are numbered in such a way that on the curve of equilibrium feedback environments, defined by the equation $R_0(\gamma, \hat{\mathbf{E}}_\gamma) = 1$, reproductive strategy γ increases from left to right. The left and right end points of this curve correspond then to population strategies $\gamma = 0$ and $\gamma = 1$, respectively.

The first step is to check existence of mixed evolutionarily stable strategies. Assume first that a mixed ESS exists, and denote it with γ^*. Mixed reproductive strategies satisty equation $R_0(0, \mathbf{E}_{\gamma^*}) = R_0(1, \mathbf{E}_{\gamma^*}) = 1$. Solving two of the three equalities yields a potential equilibrium feedback environment (E_1, E_2). Correspondence between the environmental variables and the densities N_1 and N_2 (equation 8) allows substitution of (E_1, E_2) with (N_1, N_2), which results in two equations of three unknown variables (N_1, N_2 and γ). Assumption of stable population dynamics provides a third equation ($N_1(t) = N_1(t+1)$), and allows solving γ from these equations. If resulting γ is not feasible ($\gamma \notin [0, 1]$), or there is no solution at all, then the assumption that a mixed ESS exists was false. The borderline case is that the solution is a pure strategy. Note also that there might be more than one feasible solutions.

The next step is to determine attractivity of a mixed ESS $\mathbf{E}_{\gamma^*}$, i.e. will a population strategy which is not an ESS converge towards a mixed ESS or not. This can be evaluated with help of local configuration of isovalue contours $R_0(0, \mathbf{E}) = 1$ and $R_0(1, \mathbf{E}) = 1$, exctracted from equation 7 for arbitrary (E_1, E_2). Also a third isovalue contour, $R_0(0, \mathbf{E}) = R_0(1, \mathbf{E})$, can be extracted from equation 7. Moreover, all these isovalue contours have a common point of intersection. Simple algebra shows that if isovalue contour $R_0(1, \mathbf{E}) = 1$ intersects $R_0(0, \mathbf{E}) = 1$ from above, so will do the isovalue contour $R_0(0, \mathbf{E}) = R_0(1, \mathbf{E})$. Therefore the attractivity of a mixed ESS can be determined from pattern of crossing of any two of the three isovalue contours.

In the life-history models studied here, $R_0(0, \mathbf{E}) = 1$ defines a quadratic expression. However, the other two isovalue contours, $R_0(1, \mathbf{E}) = 1$ and $R_0(0, \mathbf{E}) = R_0(1, \mathbf{E})$, are linear in E_1 with slopes $-\alpha_{11}/\alpha_{12}$ and $-\alpha_{21}/\alpha_{22}$, respectively. Evolutionary attractivity is obtained if $R_0(1, \mathbf{E}) = 1$ crosses $R_0(0, \mathbf{E}) = R_0(1, \mathbf{E})$ from above, i.e. $-\alpha_{11}/\alpha_{12} < -\alpha_{21}/\alpha_{22}$ (equation 11).

The above derivation allows to identify mixed ESSs and their attractivity. For full description of the adaptive dynamics, it still needs to be determined which one of the pure strategies is an ESS if there are no mixed ESSs. In that case, an ESS is known to be unique (Heino, Metz and Kaitala 1997). Therefore it suffices to determine when either one of the pure strategies is an ESS. The other pure strategy is then an ESS if and only if the first pure strategy is not an ESS and there are no mixed ESSs.

In determining whether a pure strategy is an ESS or not, it is necessary to calculate the equilibrium population densities for the pure strategies. In the life-history models analysed here, this task is easily accomplished for the pure annual life-history $\gamma = 1$, while it is formidable for the other pure life-history strategies.

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