OIKOS 74: 218–224. Copenhagen 1995

On evolutionarily stable life histories, optimization and the need to be specific about density dependence

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Mylius, S.D. and Diekman, O. 1995. On evolutionarily stable life histories, optimization and the need to be specific about density dependence. — *Oikos* 74: 218-224.[1]

Concentrating on monomorphic populations in demographic steady state, we give three different conditions under which the evolutionarily stable life-history strategy can be characterized as the life-history strategy at which a relatively simple function is maximal. Depending on the way density dependence acts, this function, or fitness measure, can be the life-time production of offspring, the population growth rate, or another quantity from a large range of possible optimization criteria. We illustrate this by examining the optimal age at maturity for a hypothetical example organism. All of this demonstrates that, when studying the evolutionary aspects of life-history characteristics, one cannot escape the task of specifying how density dependence limits population growth.

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Introduction

Optimization arguments in the evolutionary study of life-history strategies often start with the *choice* of a criterion of optimality, referred to as fitness measure. The two most widely used fitness measures are the population growth rate r and the basic reproduction number R_0. r Is also called the intrinsic rate of natural increase or the Malthusian parameter, and is defined as the exponential population growth rate on a continuous time basis (see, *e.g.*, Roughgarden 1979, Yodzis 1989). For a population in demographic steady state, we have $r = 0$. R_0 is also known as the expected life-time production of offspring, and is defined as the multiplicative population growth rate on a discrete, generation basis (Roughgarden 1979, Yodzis 1989, Diekmann *et al.* 1990). In steady state, we have $R_0 = 1$: the population number stays constant from generation to generation, so on average each individual will produce one offspring.

[1] Accepted 27 March 1995

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But when should one work with r and when with R_0 (Roff 1992, Stearns 1992, Charnov 1993, Kozłowski 1993)? Moreover, in steady state $r = 0$ and $R_0 = 1$, so how can one maximize a quantity that assumes a given value (Kozłowski 1993, Maynard Smith 1993)? And how does optimization relate to the idea of an evolutionarily stable strategy (ESS) (Roff 1992, Kozłowski 1993)? These questions have now been a matter of debate for quite some time. Here we present a simple framework to help clarify these issues.

We emphasize three things: (1) Evolutionary considerations should first of all be based on an invasion criterion, not on an assumed, *fixed*, fitness measure. (2) The choice that actually has to be made concerns the way density dependence (or environmental feedback) is supposed to act (Meszéna and Pásztor 1990, also see Michod 1979 and Pásztor 1988). (3) One can make this choice such that the ESS is equivalently characterized as the life history that maximizes R_0 in any constant environment, at least for monomorphic populations in demographic steady state. By making an alternative choice about the assumed environmental feedback, one forces r to be maximized, and by making other choices yet other quantities. Additionally, for more complicated kinds of feedback, no simple optimization criterion may exist. The unpleasant fact that we usually know little about the way density dependence operates in real populations should not seduce us to pursue an ostrich policy.

The setting

We concentrate on the following situation: The individuals of a population are characterized by their type T, a (possibly multi-dimensional) variable specifying all relevant aspects of the life history in which they may differ; and the world in which they live is fully characterized by the *constant* environmental condition E. So R_0 and r are completely determined by T and E. Now specify a population dynamic model that makes the dependence on T and E precise and defines $R_0(T,E)$ and $r(T,E)$. (Often, one has an explicit formula for R_0 as a function of T and E, whereas r is implicitly defined by the Euler–Lotka equation; see, *e.g.*, Roughgarden 1979 or Yodzis 1989.) A first key observation is

$$R_0 \overset{>}{\underset{<}{=}} 1 \qquad \text{if, and only if,} \qquad r \overset{>}{\underset{<}{=}} 0\,. \tag{1}$$

In our population model, density dependence acts through feedback to the environment and for any given T the equation for population-dynamical equilibrium, $R_0(T,E) = 1$ (and hence the equation $r(T,E) = 0$), together with the equations for E deriving from the feedback, define a *unique* solution for E. This steady-state environmental condition we denote by $E = \eta(T)$. So by definition

$$R_0(T,\eta(T)) - 1 = 0 = r(T,\eta(T))\,. \tag{2}$$

Now consider a *monomorphic* population consisting of individuals of a certain type T_{res}, where *res* stands for resident. If by mutation (or immigration) an individual of type T_{inv}, where *inv* stands for invader, enters the population, the question is whether or not its clan will initially grow exponentially. Only then

In a stationary monomorphic population, with environmental condition $\eta(T_{\text{res}})$ set by the resident with type T_{res}, the following test determines whether a type T_{inv} can invade:

$$\text{Is } R_0(T_{\text{inv}}, \eta(T_{\text{res}})) > 1 \text{ ?}^{\,a} \quad \begin{cases} \text{Yes} & \Rightarrow \quad \text{invasion successful}^{\,b} \\ \text{No} & \Rightarrow \quad \text{invasion fails}^{\,c} \end{cases}$$

[a] Notice that the test “Is $r(T_{\text{inv}}, \eta(T_{\text{res}})) > 0$?” is completely equivalent.
[b] Notice that we do not take demographic stochasticity into account.
[c] Strictly speaking, the degenerate case $R_0(T_{\text{inv}}, \eta(T_{\text{res}})) = 1$ needs scrutiny and may require more complicated second-order conditions, as in the case of evolutionary games defined by a pay-off matrix.

Table 1: The invasibility test.

the invader can take over and drive the resident to extinction. By assumption, the population dynamics leads to a steady state with constant environmental condition $E = \eta(T_{\text{res}})$. So to answer the invasibility question we only have to test whether $R_0(T_{\text{inv}}, \eta(T_{\text{res}})) > 1$ and $r(T_{\text{inv}}, \eta(T_{\text{res}})) > 0$ (see table 1).

A type $\hat{T}$ is called an ESS if no other type is able to invade when $\hat{T}$ is the resident (Maynard Smith and Price 1973, Maynard Smith 1982). Clearly this is only the case if $R_0(T, \eta(\hat{T}))$ is smaller than 1 for all T unequal to $\hat{T}$. Therefore $\hat{T}$ is an ESS if and only if $T \mapsto R_0(T, \eta(\hat{T}))$ is maximal for $T = \hat{T}$. (Here and below, we use the notation $T \mapsto R_0(T, E)$ to indicate that we consider $R_0(T, E)$ momentarily as a function of the variable T, with fixed E.) Because of (1) and (2) this is equivalent to $T \mapsto r(T, \eta(\hat{T}))$ being maximal at $\hat{T}$. Yodzis (1989, pp. 263–265), Caswell (1989, pp. 256–258), and Charlesworth (1994) contain formulations of this basic observation which are phrased in different words and symbols, but which are actually identical. When applying these observations to particular cases, it can be important to distinguish between local and global maxima. We can define a local ESS by restricting T_{inv} to a neighbourhood of T_{res}, that is by looking for local maxima of $T \mapsto R_0(T, \eta(\hat{T}))$.

It is important to bear in mind that the maxima of $T \mapsto R_0(T, E)$ and $T \mapsto r(T, E)$ occur in general for different values of T; it is only for $E = \eta(\hat{T})$ and $\hat{T}$ an ESS that these two functions are necessarily both maximal at $\hat{T}$.

The environment and density dependence

Often there exists a special environmental condition V, to be called *virgin*, which corresponds to the situation in which individuals experience no negative effect (yet) from the presence of other individuals. In other words, V is the best possible environment. One can then ask the question whether, perhaps, the type which does best in the virgin environment, either in the sense that $T \mapsto R_0(T, V)$ is maximal or in the (different!) sense that $T \mapsto r(T, V)$ is maximal, is an ESS. As we will see, the answer depends on the way density dependence acts. With respect to R_0 and r one can prove (see appendix A) the following two results:

Result 1 (Reduction of life-time offspring production) *If density dependence has the effect that only the expected life-time production of offspring is reduced by an E-dependent multiplication factor then $\hat{T}$ is an ESS if and only if $T \mapsto R_0(T, V)$ is maximal for $T = \hat{T}$.*

Result 2 (Uniform increase of mortality) *If density dependence has the effect that only the probability per unit of time of dying increases uniformly (in particular age-independently) then $\hat{T}$ is an ESS if and only if $T \mapsto r(T, V)$ is maximal for $T = \hat{T}$.*

We conclude that both maximization of $R_0(T, V)$ and maximization of $r(T, V)$ may be meaningful; it all depends on the precise form of the density dependence.

If Result 1 applies, then $T \mapsto R_0(T, E)$ is maximal at $\hat{T}$ for *any* environmental condition E, not just for $E = V$. An analogous observation can be made concerning Result 2. So after all the "virgin" condition can be replaced by just any environmental condition.

Another relatively simple situation results when E is one-dimensional and $E \mapsto R_0(T, E)$ is monotonic. Note that now the function η, which assigns to a type the environmental condition at which a population will be steady, is completely determined by the equation $R_0(T, E) = 1$ (or equivalently $r(T, E) = 0$) and that the feedback map does not matter at all. In this case one can prove (see appendix A):

Result 3 (One-dimensional environment) *If E is one-dimensional and $E \mapsto R_0(T, E)$ is increasing (decreasing) then $\hat{T}$ is an ESS if and only if the function η is minimal (maximal) for $T = \hat{T}$.*

The interpretation is obvious: The type that can keep its position under the worst environmental conditions cannot be invaded by any other type. In the special case where E corresponds to the concentration of food, this principle is well known. In general one could call it a "negative optimization" or "pessimization" principle.

When E is food density and, for a simple unstructured population model, equilibrium population size $\bar{N}$ is inversely proportional to food density in steady state, minimization of E amounts to maximization of $\bar{N}$. This is the formulation one frequently finds in the literature (*e.g.* Charlesworth 1994,pp. 184–186). But the minimization of (one-dimensional!) food easily generalizes to population models involving physiological structure whereas population size can be measured in many ways (biomass, dry weight, numbers) and it is not necessarily the case that each of these is maximized. Therefore we advocate the formulation of Result 3 as it is given here.

Finally, we emphasize that there are many situations in which both Result 1 and Result 3 or both Result 2 and Result 3 apply (see the Cases 1, 3 and 5 of the example below).

An example: optimal age at maturity

Consider a hypothetical organism. First we describe its life history in the virgin environment. We distinguish juveniles and adults. The type of an individual

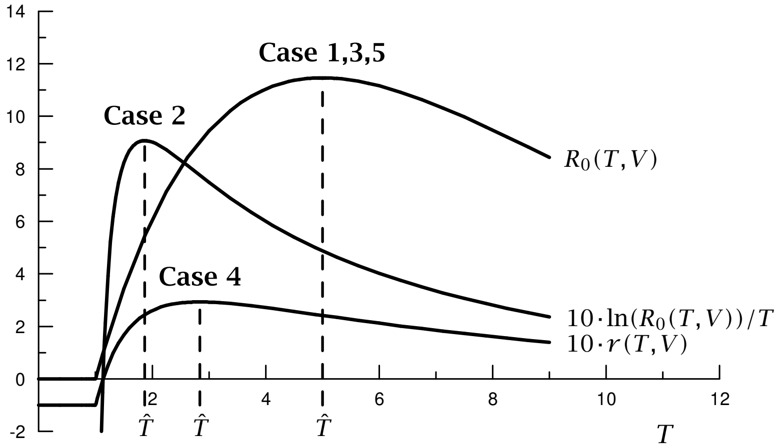

Fig. 1: Plots of the functions $R_0(T,V)$, $10{\cdot}\ln(R_0(T,V))/T$ and $10{\cdot}r(T,V)$ for the special case where the adult reproduction rate $b(T) = 0$ for $T \le 1$, and $b(T) = T - 1$ for $T > 1$, the juvenile mortality rate $\mu_1 = 0.25$ and the adult mortality rate $\mu_2 = 0.1$. (The results are qualitatively the same for other smooth non-decreasing functions $b(T)$ with $0 = b(0) < b(\infty)$.) The ESS's $\hat{T}$ corresponding to the different Cases are indicated with dashed lines.

is given by the length T of its juvenile period. After becoming an adult, every individual produces offspring at a constant rate, which depends on T. The *per capita* death rates can be different for the two stages. To illustrate the importance of the precise form of the density dependence we shall introduce and compare several variants of (the effect of) the environmental variable E. For details and explanations we refer to appendix B.

Case 1 The effect of the environmental condition (that is, density dependence) is to tune the rate of offspring production, by multiplying it with an E-dependent factor. Because the expected life-time production of offspring (R_0) is proportional to the rate of offspring production, this is a case in which Result 1 applies. Consequently, an ESS coincides with a point at which $T \mapsto R_0(T,V)$ is maximal. In Fig. 1 the graph of $R_0(T,V)$ is presented and the ESS is indicated. To illustrate how Result 1 derives from the general situation we have added Fig. 2. In general, an ESS is found by intersecting a curve where

$$R_0(T,E) - 1 \quad = \quad 0 \quad = \quad r(T,E) \tag{3}$$

with a curve defined by one of the following two conditions: (i) $T \mapsto R_0(T,E)$ is maximal, (ii) $T \mapsto r(T,E)$ is maximal. Such curves are shown in the B panes of Fig. 2, while the A panes serve to indicate how they derive from three-dimensional information. The key point is that in B1 we actually don't need to compute the curve where $R_0(T,E) = 1$, since the other curve is a vertical line. This is the computational simplification of Result 1 caught in a picture.

In the above, we have decomposed $R_0(T,E)$ in $R_0(T,V)$ and an E-dependent multiplication factor. So alternatively, Result 3 may be invoked, with the multiplication factor in the role of E. (Clearly, the larger this factor, the larger R_0 will be, so $E \mapsto R_0(T,E)$ is increasing.) At population-dynamical equilibrium, this

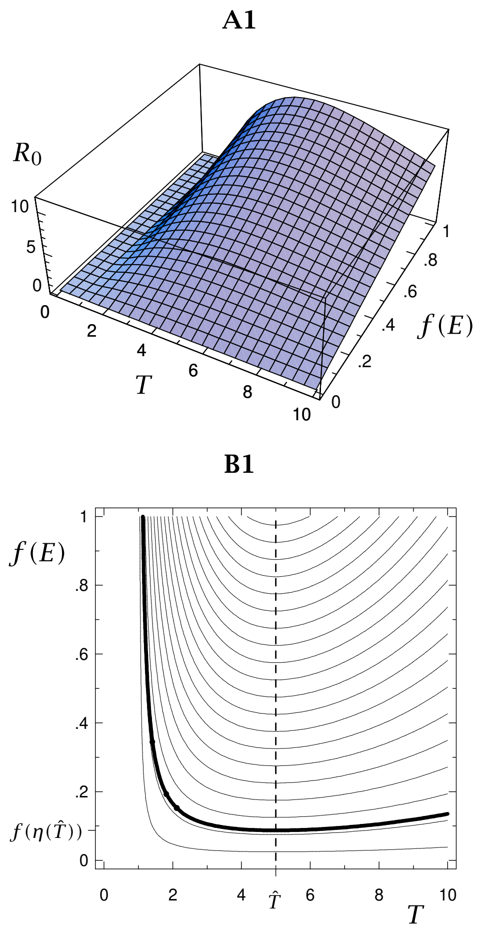

Fig. 2: Plots of the functions $R_0(T, E)$ and $r(T, E)$ for Case 1 of the example in the text. The environment is parameterized by the multiplication factor for the offspring production, $f(E)$. Upper panes: R_0 (**A1**) and r (**A2**) as functions of T and $f(E)$. Lower panes: Contour plots of the corresponding upper panes. The contour lines of $R_0(T, f(E)) = 1$ (**B1**) and $r(T, f(E)) = 0$ (**B2**) are indicated with bold curves, and the maxima of $T \mapsto R_0(T, f(E))$ and $T \mapsto r(T, f(E))$ with dashed curves. Parameter values are the same as in Fig. 1.

factor equals $1/R_0(T,V)$. So pessimizing E is equivalent to optimizing $R_0(T,V)$. □

Case 2 The effect of the environmental condition is to tune the juvenile death rate, by adding an E-dependent term. Result 3 allows us to deduce that an ESS coincides with a point at which $T \mapsto \ln(R_0(T,V))/T$ is maximal. (It is hard to explain verbally why it should be exactly this function: those readers wishing the mathematical argument should consult appendix B.)

This result is in the spirit of Results 1 and 2, in that we can restrict our attention to what happens in the virgin environment, but we have to study a function which is different from both R_0 and r. In Fig. 1 the graph of this function is presented and the ESS is indicated. □

Case 3 The effect of the environmental condition is to tune the adult death rate, by adding an E-dependent term. Because adult death rate is inversely proportional to adult life time, and expected life-time offspring production is proportional to adult life time, we can again think of this case as of $R_0(T,E)$ being composed of $R_0(T,V)$ and a multiplication factor, depending on the density-dependent additional adult death rate. A twice as high (total) adult death rate halves the expected life-time offspring production. So just as in Case 1, Result 1 and Result 3 apply. Even though the biological mechanism of density dependence is completely different from that in Case 1, the result is exactly the same. □

Case 4 The effect of the environmental condition is to tune both, and in the same degree, the juvenile and the adult death rate, by adding an E-dependent term. This is just what is covered by Result 2. Consequently, an ESS coincides with a point at which $T \mapsto r(T,V)$ is maximal. In Fig. 1 the outcome of a numerical calculation of $r(T,V)$ is presented graphically and the ESS is indicated. □

Case 5 The effect of the environmental condition is to tune the length of the juvenile period T, by adding an E-dependent term. (Note that the rate of offspring production should not be affected by the increase in the juvenile period as we imagine that the environmental conditions are changed in such a way that it takes more time to complete the same physiological development.) During this extra period before maturation, individuals experience the constant juvenile mortality rate, so $R_0(T,E)$ can be decomposed in $R_0(T,V)$ multiplied with the E-dependent probability of surviving the extra juvenile period. Consequently, Result 1 and Result 3 apply. This is yet another mechanism of density dependence which nevertheless leads to the same evolutionary outcome as we found in the Cases 1 and 3. □

Comparing the five cases in Fig. 1, we note once more that it depends on the precise way in which density dependence limits population growth, which length of the juvenile period is an ESS. We also conclude that, even in a stationary population, it is not just a matter of taste whether to use r or R_0 *in other than steady-state environmental conditions* as a fitness measure, as seems to be suggested in, for example, Kozłowski (1993).

Concluding remarks

We have seen that *in steady state* the use of two indicators, the basic reproduction number R_0 and the intrinsic growth rate r, for population growth is not at all a problem since the ordering relative to 1 and 0, respectively, is always the same. Moreover, one can consider R_0 as well as r to be maximal, even though their values are constrained to 1 and 0. This is because they are functions of *two* variables, one referring to the environment, which is determined by the resident, and the other to the (type of the) invader. The maximization is with respect to the (type of the) invader. It is important to bring this out explicitly in the notation.

In the literature one finds that several fitness criteria are being used and it seems a matter of taste which one one should choose (but see also Pásztor *et al.* 1995). However, the question which traits are maintained by evolution should be answered by an ESS argument. There is only one master fitness concept, deriving from the invasion criterion, which can be formulated as the average exponential growth rate of the invader, growing in the environment set by the resident (Metz *et al.* 1992). In this environment, R_0 and r are necessarily both maximal at the ESS. Depending on the way density dependence acts, the invasion criterion *may* have an alternative equivalent formulation in terms of a maximization criterion for a specific fixed fitness measure, such as R_0 or r under "virgin", or other standard, environmental conditions. From a general viewpoint, however, R_0 and r under standard environmental conditions are but a special selection of a much larger range of possible optimization criteria. We have presented three results that enable the characterization and calculation of life history ESS in a relatively simple manner, given reasonable assumptions on the way density dependence delimits population growth.

To make life simple, there are many important things that we have ignored here: (1) Evolutionary dynamics (Does a successful invader take over? What "type substitution sequence" do we get? Do we obtain convergence to an ESS? See, *e.g.*, Taylor 1989). (2) Non-equilibrium attractors for population dynamics (Tuljapurkar 1989, Metz *et al.* 1992). (3) Demographic stochasticity. (4) Polymorphic population compositions. (5) The case where the effective dimension of E is greater than one. Our aim has been to demonstrate that life is indeed extremely simple within this limited set-up. Yet there are many papers in the literature from which a different picture emerges, despite the fact that the same restrictions are made.

When studying the evolutionary aspects of life-history characteristics in terms of R_0, r or any other fitness measure under standard environmental conditions, one implicitly makes an assumption about the way density dependence limits population growth. Therefore, it seems worthwhile to disentangle the component influences of density dependence on natural populations.

Acknowledgements — This paper was written during a workshop in Les Houches, France, which was an activity of the ESF network *Dynamics of Complex Systems in Biosciences*. We thank Guillemette Duchateau-Nguyen and Gérard Weisbuch for organizing a workshop during which one could really work. Our thinking was greatly influenced by many inspiring conversations with Hans Metz. Ian C.W. Hardy, Patsy Haccou and Ron Otten helped improve the readability of the manuscript. The work of Sido Mylius was supported by the Life Sciences Foundation (SLW), which is subsidized by the Netherlands Organization for Scientific Research (NWO).

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Appendices

A. The rationale behind the optimization principles

The virgin environment

Result 1 If environmental deterioration reduces the expected life-time production of offspring by a certain factor then we can write, for some function f with $0 \le f(E) \le 1$,

$$R_0(T,E) \;=\; f(E)\,R_0(T,V)\;.$$

Since $1 = R_0(T,\eta(T)) = f(\eta(T))\,R_0(T,V)$ we find that $f(\eta(T)) = 1\,/\,R_0(T,V)$ and consequently that

$$R_0(T_{\mathrm{inv}},\eta(T_{\mathrm{res}})) \;=\; \frac{R_0(T_{\mathrm{inv}},V)}{R_0(T_{\mathrm{res}},V)}\;,$$

which directly implies Result 1. The same conclusion holds when $R_0(T,E) = f_1(E)\,R_0(T,V) - f_2(E)$. □

Result 2 In the virgin environment, $r(T,V)$ is the unique real root of the Euler–Lotka equation

$$\int_0^\infty e^{-rx}\,l(x)m(x)\,dx \;=\; 1\;,$$

where $l(x)$ represents the probability of surviving to age x and $m(x)$ the birth rate at age x. If environmental deterioration uniformly increases the mortality rate, say with a term $g(E)$, for some function g with $g(E) \ge 0$, then $r(T,E)$ is the unique real root of the equation

$$\int_0^\infty e^{-rx}\,e^{-g(E)\,x}\,l(x)m(x)\,dx \;=\; 1\;.$$

We now see immediately that

$$r(T,E) \;=\; r(T,V) - g(E)\;.$$

Since $0 = r(T,\eta(T)) = r(T,V) - g(\eta(T))$ we find that $g(\eta(T)) = r(T,V)$ and consequently that

$$r(T_{\mathrm{inv}},\eta(T_{\mathrm{res}})) \;=\; r(T_{\mathrm{inv}},V) - r(T_{\mathrm{res}},V)\;,$$

which directly implies Result 2. The same conclusion holds when $r(T,E) = g_1(E)\,r(T,V) - g_2(E)$. □

A closer look at the algebra above reveals that Results 1 and 2 hold for *any* environmental condition E, not just for $E = V$.

The one-dimensional environment

Result 3 Suppose that $E \mapsto R_0(T,E)$ is increasing (decreasing). If η is minimal (maximal) at $\hat{T}$ then for all $T \neq \hat{T}$ we have

$$R_0(T,\eta(\hat{T})) \quad < \quad R_0(T,\eta(T)) \quad = \quad 1\ ,$$

from which we conclude that $\hat{T}$ is an ESS. If, on the other hand, there exists a T such that $\eta(T) <(>)\ \eta(\hat{T})$ then

$$R_0(T,\eta(\hat{T})) \quad > \quad R_0(T,\eta(T)) \quad = \quad 1\ ,$$

so T can invade and $\hat{T}$ is not an ESS. □

B. The equations that go with the example

Adult individuals with type T produce offspring at a rate $b(T)$. The *per capita* death rate equals, say, μ_1 during the juvenile period and μ_2 during the adult period. Then the probability of surviving until adulthood is $e^{-\mu_1 T}$ and the expected life time as an adult is $1/\mu_2$. Hence

$$R_0(T,V) \quad = \quad \frac{b(T)\, e^{-\mu_1 T}}{\mu_2}$$

and $r(T,V)$ is the unique real root of the Euler–Lotka equation

$$\frac{b(T)\, e^{-(\mu_1+r)\,T}}{\mu_2 + r} \quad = \quad 1\ .$$

Case 1 If environmental conditions tune the actual rate of offspring production then we have $b(T,E) = f(E)\, b(T)$ for some function f with $0 \leq f(E) \leq 1$, so that

$$R_0(T,E) \quad = \quad f(E)\, R_0(T,V)\ .$$

So we can apply Result 1, to deduce that the ESS coincides with a point at which $T \mapsto R_0(T,V)$ is maximal. According to Result 3, at this point should also $f(\eta(T)) = 1/R_0(T,V)$ be minimal, as it clearly is. □

Case 2 If environmental conditions tune the actual juvenile death rate then we have $\mu_1(E) = \mu_1 + h(E)$ for some function $h(E) \geq 0$, so that

$$R_0(T,E) \quad = \quad \frac{b(T)\, e^{-(\mu_1+h(E))\,T}}{\mu_2} \quad = \quad e^{-h(E)\,T}\, R_0(T,V)\ .$$

According to Result 3, an ESS coincides with a point at which $h(\eta(T))$ is maximal. Solving the equation $R_0(T,E) = 1$, we find $h(\eta(T)) = \ln(R_0(T,V))/T$. □

Case 3 If environmental conditions tune the actual adult death rate then we have $\mu_2(E) = \mu_2 + h(E)$ for some function $h(E) \geq 0$, so that

$$R_0(T,E) \quad = \quad \frac{b(T)\, e^{-\mu_1 T}}{\mu_2 + h(E)} \quad = \quad \frac{\mu_2}{\mu_2 + h(E)}\, R_0(T,V)\ .$$

Either invoke Results 1 and 3 or make a transformation of the environmental variable to conclude that this case leads to the same evolutionary outcome as in Case 1. □

Case 4 If environmental conditions tune the actual juvenile and the actual adult death rate equally then we have $\mu_i(E) = \mu_i + g(E)$ for $i \in \{1, 2\}$ and some function $g(E) \geq 0$, so that $r(T, E)$ is the unique real root of the Euler–Lotka equation

$$\frac{b(T)\, e^{-(\mu_1+g(E)+r)\, T}}{\mu_2 + g(E) + r} = 1 .$$

We now see immediately that

$$r(T, E) = r(T, V) - g(E) .$$

So according to Result 2, an ESS coincides with a point at which $T \mapsto r(T, V)$ is maximal. □

Case 5 If environmental conditions tune the actual length of the juvenile period without affecting the rate of offspring production $b(T)$ then we have

$$R_0(T, E) = \frac{b(T)\, e^{-\mu_1(T+h(E))}}{\mu_2} = e^{-\mu_1 h(E)}\, R_0(T, V)$$

for some function $h(E) \geq 0$. Either invoke Results 1 and 3 or make a transformation of the environmental variable to conclude that this case is equivalent to Cases 1 and 3. □