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Saumon à la Kaitala et Getz, sauce hollandaise

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ABSTRACT

We investigate the interplay of population dynamics and adaptive dynamics via the timing of reproduction, in the context of a caricatural discrete-time model. We find that semelparity can cause co-existence of different population-dynamical attractors and that resonance of life-span relative to population-dynamical fluctuations can have a profound effect on invasibility and the resulting evolutionarily stable life-history. Different local attractors of the resident population dynamics can have different invasion properties. Successful invasion in one attractor can be followed by extinction of the former invader, ultimately leading the resident to the same attractor, but phase-shifted, or to another attractor. So a strategy can be 'invasible, yet invincible'. In addition, our analysis emphasizes that, for a fluctuating population, one must carefully distinguish between polymorphisms and mixed strategies.

Keywords: adaptive dynamics, age at reproduction, complex population dynamics, evolutionarily stable strategy, evolutionary dynamics, extinction, invasion, life history, multiple attractors, resonance.

INTRODUCTION

The aim of this paper is to call attention to certain often neglected aspects of adaptive dynamics, and to do so by means of a simple model involving a specific life-history characteristic – the timing of reproduction of semelparous individuals. Our key question is: What influence does the often-made restriction to population-dynamical steady state have on evolutionary predictions? To answer this question, we study invasibility and evolutionary stability of low-period population-dynamical attractors. Our work is in the same spirit as that of Van Dooren and Metz (1998), but is more analytical and less numerical.

Triggered by the stimulating paper by Kaitala and Getz (1995), we take Pacific salmon (*Oncorhynchus* spp.) as the motivating example. Pacific salmon reproduce in upstream rivers. The fry migrate soon after birth to the ocean and, after a variable number of years, the mature fish return to their natal river to spawn and die.

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To set the scene, consider a population of salmon and assume that individuals have precisely two options for the period in between birth and reproduction: 3 and 4 years. We combine survival and reproductive potential in a number c_k, with $k \in \{3, 4\}$, and simply ignore that reproduction involves gametes produced by two individuals of opposite sex. That is, we neglect pair formation, sexual reproduction and genetic inheritance and pretend that reproduction is clonal.

When all surviving individuals reproduce after k years, we describe the population dynamics with the delayed difference equation:

$$x(t) = c_k x(t-k)E(t) \tag{1}$$

where $E(t)$ summarizes the effect of intraspecific competition in the breeding spots up the river. Here $x(t)$ measures the number of young entering the sea in year t, and we take the relation

$$E(t) = g(c_k x(t-k)) \tag{2}$$

(with g a decreasing function and $0 < g \leq 1$) to describe density-dependent survival in the nursery.

What if some individuals reproduce after 3 years and others after 4 years? Even if we assume that the offspring is identical to the parent in this respect, there are at least two ways to describe such a situation, depending on our interpretation of the difference between 'some' and 'others'.

Suppose, first, there are really two different types of individuals, each strictly adhering to a fixed life-span. That is, the population is *dimorphic.* Then we can postulate that

$$\begin{aligned} x(t) &= c_3 x(t-3)\, E(t) \\ y(t) &= c_4 y(t-4)\, E(t) \end{aligned} \tag{3}$$

with

$$E(t) = g(c_3 x(t-3) + c_4 y(t-4))$$

where x and y measure the number of young entering the sea of the types with a life-span of 3 and 4 years, respectively.

Suppose, next, that the population is *monomorphic*, but that individuals experience (spatial) environmental stochasticity in the sea, resulting in a certain distribution of life-spans summarized in one parameter a, which gives, conditional on being still alive, the probability to return to the breeding water after 3 years. We call this a 'mixed strategy' when $0 < a < 1$, and a 'pure strategy' when $a = 0$ or $a = 1$. (So, incidentally, note that the dimorphic population is composed of two pure-strategy subpopulations.) Then we might take

$$z(t) = [ac_3 z(t-3) + (1-a)c_4 z(t-4)]\, E(t) \tag{4}$$

with

$$E(t) = g(ac_3 z(t-3) + (1-a)c_4 z(t-4))$$

where $z(t)$ measures the number of young entering the sea in year t.

Whenever population dynamics leads to a steady state, the two situations are indistinguishable. Indeed, if we define $a := x/(x+y)$, $z := x+y$, the second formulation follows from the first. Conversely, when a and z are time independent and we define $x := az$, $y := (1 - a)\, z$, then the first formulation is consistent with the second. However, when the population fluctuates, no such identification is possible! (This is also stressed by Rand *et al.*, 1994.)

In the first formulation, the reduced state spaces $x \equiv 0$ and $y \equiv 0$ are invariant and we may (and will) study the stability of the boundary attractors living there. This is an example of an invasibility question: Given a resident type, will a different type, called an 'invader', grow when rare? The underlying assumption is that the invader originated from the resident by mutation. Note that, in the first formulation above, it is natural to restrict attention to a finite number of types (in this case, two).

In the second formulation, we may, in a similar spirit, ask what happens when, by mutation, a new type arises with a somewhat different value of a. (The idea, of course, is that some internal parameter is changed slightly, such that the environmental stochasticity then leads to a different fraction returning after 3 years.) Thus one is led to consider the system

$$\begin{aligned} z_1(t) &= [a_1 c_3 z_1(t-3) + (1-a_1) c_4 z_1(t-4)]\, E(t) \\ z_2(t) &= [a_2 c_3 z_2(t-3) + (1-a_2) c_4 z_2(t-4)]\, E(t) \end{aligned} \tag{5}$$

with

$$E(t) = g(a_1 c_3 z_1(t-3) + (1-a_1) c_4 z_1(t-4) + a_2 c_3 z_2(t-3) + (1-a_2) c_4 z_2(t-4))$$

Again there are boundary attractors that might be stable (invasion fails) or unstable (invasion is successful). But a difficulty, of course, is that a continuum of a-values is possible. And even if the a of the resident is fixed at some value and only small mutations are allowed, there is still a continuum of possibilities.

Underlying the dynamic description of natural selection known as 'adaptive dynamics' (or 'evolutionary dynamics', when genetics is taken into account) are therefore two further assumptions. The first concerns a time-scale difference between mutation and convergence to a population-dynamical attractor. The idea is to ignore the possibility of a next (potentially) successful mutation arising before the transients triggered by a successful mutation have died out. The second assumption asserts that successful invasion, together with failure of invasion under role reversal of resident and invader, guarantees replacement: the invader becomes the resident. (For special models, one can actually prove that such a competitive exclusion principle holds.)

Thus adaptive dynamics is described, on an (implicit) discrete time basis, as a trait substitution sequence. The states are the attractors of the population dynamics and the jumps are driven by an ill-known stochastic process (i.e. mutation). [See Eshel (1996) and references therein for pioneering work; see Rand *et al.* (1994), Metz *et al.* (1996) and Geritz *et al.* (1997, 1998) for the state-of-the-art in adaptive dynamics. For a combination of game theory and genetics, Hammerstein (1996) has coined the term 'Streetcar Theory of Evolution'. One of the nice things about this metaphor is the question it suggests: Does the streetcar ever reach its final stop? Also, see the other papers in this special issue of the *Journal of Mathematical Biology* on 'Evolutionary Dynamics' edited by Diekmann, Christiansen and Law (1996).]

An evolutionarily stable strategy (ESS; Maynard Smith and Price, 1973; Maynard Smith, 1982) is an unbeatable trait value (or strategy) in the sense that, if the resident has (plays) it, any invasion by individuals with a different trait value or strategy is bound to fail. (A 'local'

ESS restricts competitors to have only slightly different trait values or strategies.) Note that this corresponds to a steady state of the adaptive dynamics, but that it is not built into the definition (Maynard Smith, 1982) that an ESS is an *attractor* of the adaptive dynamics. (So the 'stable' in the ESS acronym is misleading and to interpret the first S as meaning 'steady' is to be preferred. It would be even more appropriate to call a strategy defined in this way a 'non-invasible strategy'.) Therefore, the ESSs need further classification, for which we refer to Metz *et al.* (1996) and Geritz *et al.* (1997, 1998). The possibilities include the so-called 'Garden of Eden', which is an adaptive repellor, and a 'branching point', at which monomorphism is lost by means of an expanding protected dimorphism resulting from mutual invasibility.

Even though the description above does not unambiguously fix a mathematical framework, the program should now be clear: find attracting ESSs (and study how they depend on the model parameters that are considered to be fixed, i.e. not under natural selection).

ASSUMING POPULATION DYNAMICS LEADS TO A STEADY STATE

Following Kaitala and Getz (1995), we carry out the program for the monomorphic setting in this section under one more assumption: that the population dynamical attractor is a steady state. In such a context, the criterion for successful invasion takes the form

$$R_0(a_{\text{inv}}, \bar{E}_{a_{\text{res}}}) > 1 \tag{6}$$

where 'inv' stands for invader and 'res' stands for resident. Or, in words, the expected lifetime production of offspring of an individual with strategy $a = a_{\text{inv}}$, in the steady environmental condition $E = \bar{E}_{a_{\text{res}}}$ as set by the resident with $a = a_{\text{res}}$, should exceed 1. For arbitrary a and E we have

$$R_0(a, E) = (ac_3 + (1 - a)c_4)\, E \tag{7}$$

and steady state amounts to

$$R_0(a_{\text{res}}, \bar{E}_{a_{\text{res}}}) = 1 \tag{8}$$

because, on a generation basis, in a steady state the average resident individual exactly replaces itself. From (7) and (8) it follows (see Appendix 1) that a strategy a^* is an ESS if, and only if, the function

$$a \mapsto \bar{E}_a \tag{9}$$

has a minimum at $a = a^*$ or, equivalently,

$$a \mapsto ac_3 + (1 - a)c_4 \tag{10}$$

has a maximum at $a = a^*$. The first formulation, (9), expresses the other side of the coin of optimal adaptation to the environment: If density dependence acts by feedback to a one-dimensional environmental variable, then only the type that makes – as a resident – life as hard as possible is invulnerable to invasion. The second formulation, (10), tells us the outcome: $a^* = 1$ is an ESS if $c_3 > c_4$ and $a^* = 0$ is an ESS if $c_3 < c_4$.

The invasibility criterion also shows that the trait substitution sequence exhibits a monotone increase to $a^* = 1$ in the first case and a monotone decrease to $a^* = 0$ in the second case. That is, the ESS is an attractor of the adaptive dynamics. If we consider the dimorphic (rather than the monomorphic) setting and *assume* that population dynamics inevitably results ultimately in a steady state, we obtain likewise that the pure strategy $a = 1$ outcompetes the pure strategy $a = 0$ if $c_3 > c_4$, whereas the opposite happens if $c_3 < c_4$.

So, under the restrictive assumption of convergence to a steady state (and taking for granted that takeover is guaranteed when invasibility is not mutual), the situation is crystal clear. What if we assume that population dynamics leads to sustained oscillations?

PERIODIC SOLUTIONS WITH LOW PERIOD

Motivated by the outcome of our steady-state analysis, we first investigate what are the periodic attractors for the pure-strategy situation described by

$$x(t) = f(cx(t-k)) \tag{11}$$

with $f(x) = xg(x)$ and $k = 3$ or $k = 4$. Essentially, this delayed difference equation consists of k independent copies of the equation

$$x(\tilde{t}) = f(cx(\tilde{t}-1)) \tag{12}$$

derived by putting

$$\tilde{t} = kt + j, \qquad j \in \{1, \ldots, k\} \tag{13}$$

(In other words, the delayed difference equation is a non-linear analogue of a Leslie matrix describing k uncoupled populations, each reproducing after exactly k years; or, in more technical terms, an irreducible but *non*-primitive positive Leslie matrix.) For the 'one-humped' functions f that we consider, an increase in c will lead to a sequence of period-doubling bifurcations for the 'ordinary' difference equation with $k = 1$ (see Fig. 1 for a numerical example). At the first of these, the steady state loses stability and a stable period-two solution hl originates. Here h means 'high' and l means 'low' and both refer to, here and in the rest of this paper, the E-values of the period-two solution, which is an endless repetition of the block hl.

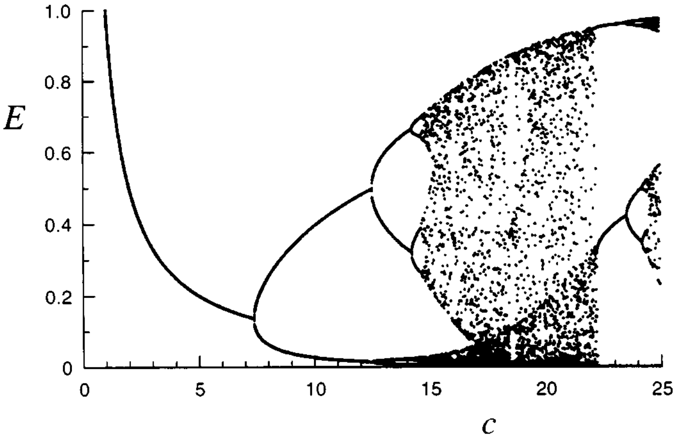

Fig. 1. Bifurcation diagram of the delayed difference equation (1), $x(t) = cx(t-1)E(t)$, with $E(t) = \exp(-cx(t-1))$, (take $g(x) = \exp(-x)$ in (2)), and c ranging from 1 to 25.

The delayed version shows a k-fold copy of this bifurcation, in the sense that the bifurcation concerns the behaviour of (12); however, to cover the full set of integer time values, we need all $j \in \{1, \dots, k\}$ in (13). What pattern in time results? It will always be $2k$-periodic, but the minimal period may in fact be a divisor of $2k$. To find out about this more precisely, one has to perform an elementary combinatorial exercise, in particular since we want to identify patterns that are translates of each other. It turns out that the k subpopulations, co-existing independently in time, show, for small k, only a relatively small number of periodic patterns. We invite the reader to verify that for $k = 2$ there exists, modulo translation, only a period-four solution *hhll*, that for $k = 3$ the complete catalogue of possibilities consists of a period-two solution *hl* and a period-six solution *hhhlll*, while for $k = 4$ it consists of the two period-eight solutions *hhlhllhl* and *hhhhllll* (see Table 1). We refer to Diekmann and Van Gils (in press) for a systematic analysis for general k and general periodic solutions of the 'ordinary' difference equation.

As the decoupling argument guarantees that these periodic solutions are stable, we conclude that semelparity promotes the co-existence of local attractors, when the life-span exceeds 1 year. The different attractors correspond to different combinations of phase of the uncoupled subpopulations.

Invasibility of the attractors

Next, we have to check invasibility for each of the attractors. Without going into quantitative detail (but see Appendix 2), we present a qualitative argument which clearly exemplifies its essence (i.e. resonance). To facilitate the description, we simply call individuals with a life-span of k years k-individuals.

We consider a population of 3-individuals, assume $c_3 > c_4$, and ask whether or not 4-individuals can invade (i.e. increase in numbers when rare). If the population of 3-individuals settles to a steady state, then, as we saw above, the answer is 'no'. Now suppose

Table 1. Possible periodic patterns of population numbers after the first period-doubling bifurcation of equation (11), for populations of individuals with a life-span (k) of 2, 3 and 4 years respectively. The elementary block that is repeated is indicated by filled dots

life-span 2	period 4	*h*	●	●			○	○			○	○			○	○			○	○			○	○				
		l			●	●			○	○			○	○			○	○			○	○			○	○		
life-span 3	period 2	*h*	●		○		○		○		○		○		○		○		○		○		○		○		○	
		l		●		○		○		○		○		○		○		○		○		○		○		○		○
	period 6	*h*	●	●	●				○	○	○				○	○	○				○	○	○					
		l				●	●	●				○	○	○				○	○	○				○	○	○		
life-span 4	period 8 (a)	*h*	●	●		●			●		○	○		○			○		○	○		○			○			
		l			●		●	●		●			○		○	○		○			○		○	○		○		
	period 8 (b)	*h*	●	●	●	●					○	○	○	○					○	○	○	○						
		l					●	●	●	●					○	○	○	○					○	○	○	○		

c_3 is such that the steady state is unstable and the 3-population will evolve either to the period-two attractor or to the period-six attractor. These are both characterized by two E-values, the high E_+ of good years and the low E_- of bad years. [Please note our terminology: the 'good' refers to a high environmental value (i.e. high survival); that is, we take the point of view of a newborn individual. This is exactly opposite to the 'good' that human observers may use to characterize a year in which many salmons migrate up river and in which many larvae are produced.] These E-values are such that $c_3^2E_+E_- = 1$, since for successive generations of 3-individuals, good and bad years of reproduction alternate and on (geometric) average the number of offspring must be 1.

Now imagine the 3-population has settled into the period-two attractor and a 4-individual happens to be born in a good year. Then its offspring will also be born in a good year. And so on. So the average number of offspring is simply c_4E_+ and we want to know whether or not this number exceeds 1. To make the comparison with 3-individuals easier, we look two generations ahead and, using $c_3^2E_+E_- = 1$, write

$$(c_4E_+)^2 = \frac{c_4^2E_+^2}{c_3^2E_+E_-} = \left(\frac{c_4}{c_3}\right)^2 \frac{E_+}{E_-} \tag{14}$$

which clearly demonstrates that the inherent disadvantage $c_4/c_3 < 1$ can, in principle, be overcome by systematic tuning to good years as reflected in the factor $E_+/E_- > 1$. For a given ratio of c_3 and c_4 (i.e. a fixed value of c_4/c_3), the effect will not be strong enough close to the period-doubling bifurcation, where E_+ and E_- do not differ very much (see Fig. 1). But once E_+/E_- exceeds $(c_3/c_4)^2$, 4-individuals tuned to the good years do increase in numbers when rare.

In the same way, it follows that when a 4-individual is born in the first or the third good year, or in the middle bad year, of the period-six solution, its descendants will experience two good years and one bad year out of every three reproduction events. Hence the invasibility condition becomes $c_4^3E_+^2E_- > 1$, which, by looking six generations ahead and using $c_3^2E_+E_- = 1$, we can rewrite in the form:

$$\frac{E_+}{E_-} > \left(\frac{c_3}{c_4}\right)^6 \tag{15}$$

We observe that the period-six attractor is more difficult to invade for the 4-individuals than the period-two attractor, since the synchronization with the good years is less perfect (see also the next section, especially Fig. 2).

Two conclusions derive from these observations. First, the steady-state analysis does *not* yield reliable evolutionary predictions when extended to parameter regions in which the population actually fluctuates. This is well known in the context of fluctuating environments, where 'bet-hedging' is probably the key issue. In the present context, it is more a matter of resonance, with the invader taking advantage of its better synchronization with the good years. Secondly, the invasion criterion is different for different attractors and, as a consequence, we cannot simply state that a population with $a = 1$ is (or is not) invadable by individuals with $a = 0$. The co-existence of attractors undermines the idea of representing the adaptive dynamics as a trait substitution sequence.

So far, we have concentrated on the invasion properties of the pure strategy $a = 0$. As one might guess from the synchronization argument, for given c_3/c_4, invaders with a mixed strategy $a \in (0, 1)$ need a bigger E_+/E_- for success than those with $a = 0$. In fact, the E_+/E_- that is required for success is a monotone increasing function of a, with a finite limit for $a \uparrow 1$. So $a = 1$ also loses its *local* (in a-space) uninvasibility once E_+/E_- is sufficiently large.

In Appendix 2 we present the calculations that underlie the above assertions, for the technically somewhat simpler case of competition between annuals and biennials.

Finally, what if $c_4 > c_3$? Then the steady-, period-two and period-six attractors of a 3-resident are all invadable by 4-individuals. Conversely, a steady- or any of the two period-eight attractors of a 4-resident is uninvadable by 3-individuals, the point being that 3 and 8 do not have a common factor, which makes tuning to good years impossible. (See Appendix 2 for the technical elaboration in the context of competing annuals and biennials.)

Successful invasion leading to co-existence

Motivated by our finding above that the pure strategy $a = 0$ is the 'best' invader in the low-period attractors of the $a = 1$ resident, from now on we restrict our attention to the competition between the two pure strategies. In this and the following subsection, we describe some numerical experiments that are based on equation (3) with the choice $g(x) = \exp(-x)$ and the parameterization $c_3 = c$, $c_4 = \gamma c$, with fixed $\gamma \in (0, 1)$. That is, we now use c as a bifurcation parameter.

In Fig. 2 we introduce, for c-values above the first period-doubling bifurcation, mutants with a life-span of 4 years at low frequencies in a 'good year' of a fluctuating resident population with a life-span of 3 years and plot the resulting population-dynamical attractor. (That is, we wait until the transients have disappeared. Also note that, because $c = c_3$, period-doubling bifurcations of the 3-resident population dynamics occur for the same values of c as in Fig. 1.) We see that the period-two attractor (Fig. 2A) 'inherits' the uninvasibility from the steady state at lower c-values, but can be invaded if c is greater than approximately 8.0, whereas the period-six attractor (Fig. 2B) remains evolutionarily stable for c-values substantially greater than 8.0. The dimorphic system which results after successful invasion has a period-four attractor, still characterized by yearly alternations of 'good' and 'bad', but with two levels of each.

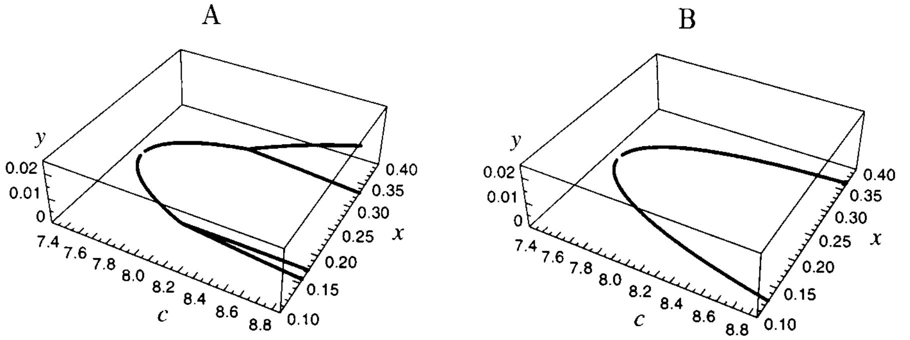

Fig. 2. The attractor of population numbers $x(t)$ and $y(t)$, of individuals with a life-span of 3 and 4 years respectively, of the dimorphic system (3) with $g(x) = \exp(-x)$, $c_3 = c$ and $c_4 = 0.5c$, for c-values just above the first period-doubling bifurcation. The resident population with life-span 3 was fluctuating either on the period-two attractor (A) or on the period-six attractor (B) when life-span 4 mutants were introduced in small numbers.

From Fig. 3 we conclude that, in this case, evolution tends to diminish the environmental fluctuations caused by population dynamics. (One could call this another instance of evolution making the world closer to 'ideal free'. However, one should not apply this conclusion to other situations without critical examination, as it may depend crucially on the way the trait under investigation is constrained in its steering effect on population dynamics.)

The resident strikes back: Resilience despite invasibility

More numerical experiments (S.D. Mylius and O. Diekmann, in prep.) have revealed that a striking phenomenon occurs when c is increased further beyond the value at which the period-two attractor becomes invasible.

Let us begin with a population of 3-individuals that oscillates with period two, the *good* years being the *even* years. Next, introduce a small population of 4-individuals in an *even* year. After a while, the 4-population will constitute an appreciable part of the total population, and a subtle interaction between the 3- and 4-subpopulations sets in. As a result of this interaction, the quality of even years deteriorates, while the quality of the odd years increases. In fact, after a certain period, the even years are worse than the odd years. At this point, the competitive advantage of 4-individuals turns into a competitive disadvantage, as now the reproduction events take place in bad years. Therefore, the 4-subpopulation is doomed to become extinct. In the end, we have a population of 3-individuals that oscillates with the period two, the *good* years being the *odd* years.

Similarly, depending on the value of c, the invasion of the period-two attractor may lead, after a temporary phase of turmoil, to the period-six attractor in a phase at which the 4-individuals are at a disadvantage.

The following question about terminology presents itself: Should we call the trait or strategy of a resident an ESS (or, for that matter, an unbeatable trait or strategy) when the resident ultimately outcompetes every invader, yet the invader population may first reach a non-negligible size? We coin the term 'invasible yet invincible' for such strategies and emphasize that the phenomenon is possible only when the invasion exponent is multi-valued as a reflection of co-existing attractors, which should be expected in particular whenever the population consists of subpopulations that interact only weakly or not at all.

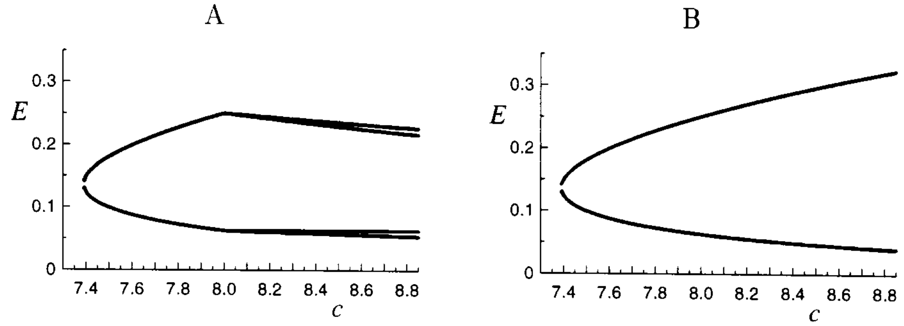

Fig. 3. Values of the environmental variable $E(t)$ for the attractors of the dimorphic system (3) shown in Fig. 2. (A) and (B) correspond to panels (A) and (B) of Fig. 2.

CONCLUSIONS AND DISCUSSION

In an earlier publication (Mylius and Diekmann, 1995), two of the present authors emphasized that evolutionary predictions depend on the precise form of density dependence. In a similar spirit, we have tried to unravel in the present paper the potential influence of some other, often implicit and therefore rather hidden, assumptions that are frequently made when analysing the influence of natural selection on life-history characteristics.

The difficulty of analytically calculating any attractor more complicated than a steady state, is a strong stimulus to simply pretend that population dynamics leads to a steady state and then start evolutionary considerations from there (however, see Metz *et al.*, 1992; Gatto, 1993; Rand *et al.*, 1994; Ferrière and Gatto, 1995). That the conclusions may be misleading is in the main demonstrated by models that show how risk aversion or 'bet-hedging' in a not entirely predictable world provides an advantage to strategies that would be inferior in a steady world (Tuljapurkar, 1990, 1994). Here we found a different reason why conclusions based on the assumption of a steady world may be misleading: When the trait is related to the timing of life-history events, an invader may sample the fluctuating environment in a rhythm that differs from that of the resident and thus, by partly synchronizing to favourable conditions, take advantage.

In a steady world there is no need to distinguish between a polymorphism and a mixed strategy. When time is heterogeneous, either by externally driven environmental fluctuations or by endogenous fluctuations resulting from feedback, the distinction between polymorphisms and mixed strategies cannot be ignored, as it leads to differences in both population and adaptive dynamics.

In our opinion, this is a strong motivation to work with traits that allow for a mechanistic, rather than a phenomenological, interpretation. For instance, it seems reasonable to assume that salmon base the irreversible transition to prepare for the return to freshwater on some indicator of their physi(ologi)cal condition, such as size. In combination with a stochastic food supply, this then may easily lead to some returning after 3 years and others after 4 years. Thus it seems reasonable to replace the phenomenological parameter a by the critical size, together with some probabilistic description of growth. [We intend to study such a model in the near future. We would also like to study the similarity with delayed flowering in biennial plants (see also de Jong *et al.*, 1987; Wesselingh, 1995).]

Another, related, point is that the need to consider genetics may be greater when the trait relates to timing while population dynamics creates fluctuations, since the resonance phenomenon has assortative mating as a side-effect. [To these suggestions we like to add one more (i.e. the addition of spatial structure), to remedy the rather weak points of the model discussed here, as a description of real-world salmon. The point is that the physical strength resulting from an extended stay at sea may allow more favourable breeding waters higher upstream to be reached. As noted by Kaitala and Getz (1995), spatial heterogeneity may easily lead to assortative mating. For some preliminary results concerning the interplay of timing and positioning of offspring, see Diekmann (1997). Our longer-term objectives include the study of a model – discrete or continuous – which combines size considerations with spatial structure.]

Conceptually, the state of the adaptive dynamics process is given by the attractor of the population dynamics process (Rand *et al.*, 1994). Unfortunately, these attractors are, in general, not easily parameterized. Or, in other words, it is not easy to define a state space for the adaptive dynamics. In Metz *et al.* (1996), the approach was to assume that a list of the traits which are represented in the population-dynamical attractor *uniquely* fixes the attractor. Despite the topological complexity of the space of all such lists, the authors managed to give a complete classification of ESSs for the case of a one-dimensional trait. [For higher dimensional traits, aspects of the mutation process may crucially come into play; see, for instance, Dieckmann and Law (1996) and Matessi and Di Pasquale (1996).]

The example presented here quite naturally leads to co-existing attractors. Thus, like the example presented by Van Dooren and Metz (1998), it provides the newly shaped theory of adaptive dynamics with a stimulating challenge.

For certain parameter values, we found (a form of, as one boundary attractor was not invasible) mutual invasibility, yet no protected polymorphism (i.e. no internal attractor). The resident was able to outcompete the invader, but only by achieving a phase-shift during the interaction that took place after the invader population had grown to an appreciable size. When building a general theory of adaptive dynamics, this phenomenon of resilience, or 'invincibility despite invasibility', as we like to call it, cannot be ignored. [After this work was completed, M. Doebeli (1998) informed us that he constructed an example of this phenomenon in the context of a metapopulation model.]

As we intend to demonstrate in detail in future work (S.D. Mylius and O. Diekmann, in prep.), the co-existence of attractors with different invasion properties is a robust phenomenon (that is, it will survive small perturbations of the model). The phenomenon that successful invasion of one boundary attractor leads in the end to another attractor in the same boundary is also robust. In the rather degenerate situation considered here, we also found that successful invasion could ultimately result in the same (but phase-shifted) attractor. When perturbing the model, such a (non-generic homoclinic) connection will inevitably be broken and an internal attractor will be formed. Yet one should realize that many points on this internal attractor will lie close to the boundary attractor, which means that the successful invader is likely to experience long periods of low density, with the associated risk of going extinct (due to demographic stochastic effects that are not incorporated in the model). So even this phenomenon, despite its non-generic character, may be of some importance.

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APPENDICES: DERIVATION OF THE INVASIBILITY CONDITIONS

We analyse the invasibility conditions for the case where the population dynamics leads to a steady state (Appendix 1), and for the case where the population dynamics has a low-periodic solution (Appendix 2). The first case is explained for the competition between 3-individuals and 4-individuals (as covered in the text). The second case is treated in the setting of the competition between annuals and biennials: this yields smaller matrices and is consequently easier to analyse, but analogous to the case where 4-individuals compete with 3-individuals.

1. Equilibrium populations

Combining (7) and (8) we deduce

$$\bar{E}_{a_{\text{res}}} = \frac{1}{a_{\text{res}}c_3 + (1 - a_{\text{res}})c_4} \tag{16}$$

Substituting this in (7) we find that

$$R_0(a_{\text{inv}}, \bar{E}_{a_{\text{res}}}) = (a_{\text{inv}}c_3 + (1 - a_{\text{inv}})c_4)\,\frac{1}{a_{\text{res}}c_3 + (1 - a_{\text{res}})c_4} \tag{17}$$

A strategy a^* is an ESS if it cannot be invaded by any alternative strategy; in other words, if $R_0(a, \bar{E}_{a^*}) < 1$ for every $a \neq a^*$. From (17) it is clear that this is the case if, and only if, the function $a \mapsto \bar{E}_a$ has a minimum at $a = a^*$ or, equivalently, $a \mapsto ac_3 + (1 - a)c_4$ has a maximum at $a = a^*$.

2. Periodically fluctuating populations

Here, we present the invasibility analysis of periodic solutions of low period in the setting of the competition between annuals and biennials, as described by

$$\begin{aligned} z_i(t) &= [a_ic_1z_i(t-1) + (1-a_i)c_2z_i(t-2)]\,E(t), \qquad i \in \{1, 2\} \\ E(t) &= g\left(\sum\nolimits_{i=1}^{2} [a_ic_1z_i(t-1) + (1-a_i)c_2z_i(t-2)]\right) \end{aligned} \tag{18}$$

(cf. equation (5)) when considering mixed strategies and by

$$\begin{aligned} z_1(t) &= c_1z_1(t-1)\,E(t) \\ z_2(t) &= c_2z_2(t-2)\,E(t) \\ E(t) &= g(c_1z_1(t-1) + c_2z_2(t-2)) \end{aligned} \tag{19}$$

(take $a_1 = 1$ and $a_2 = 0$ in (18)) when considering pure strategies and the possibilities of dimorphism.

We shall contrast the situation $c_1 > c_2$, where the annual outcompetes the biennial under steady-state conditions, with the situation $c_2 > c_1$, where the opposite is the case.

Assume $c_1 > c_2$ and assume that c_1 and g are such that $z_1(t) = c_1z_1(t-1)g(c_1z_1(t-1))$ has a stable period-two solution, which we characterize by the two values E_+ and E_- that $g(c_1z_1(t))$ takes, with the convention that $E_+ > E_-$. Note that, necessarily

$$1 = c_1^2\,E_+E_- \tag{20}$$

since in two steps z_1 should return to its original value.

Imagine the annual cycles in this manner and, by mutation, a variant originates that has a different value of a. Will it start to increase in numbers? To decide this, we form a matrix with entries m_{ij} giving the expected number of offspring produced in year i by an individual that was itself born in year j, with years counted modulo two and, to fix the phase of the resident cycle, $E = E_+$ in odd years and $E = E_-$ in even years. This definition in words immediately implies that the matrix is given by

$$\begin{pmatrix} (1-a)c_2E_+ & ac_1E_+ \\ ac_1E_- & (1-a)c_2E_- \end{pmatrix} \tag{21}$$

Consequently, the characteristic equation is

$$\lambda^2 - (1-a)c_2(E_+ + E_-)\lambda + (1-a)^2\, c_2^2\, E_+E_- - a^2 = 0 \tag{22}$$

and all we have to do is to check whether or not the positive real solution λ_d exceeds 1. To emphasize the dependence on the invader's a, we shall write $\lambda_d(a)$. We claim that:

- $\lambda_d(0) > 1$ if, and only if, $c_2E_+ > 1$ (note that, by (20), this is equivalent to $E_+/E_- > (c_1/c_2)^2$);
- when $c_2E_+ > 1$ but $c_2(E_+ + E_-) < 2$, there is an interval $[0,\bar{a})$ on which $\lambda_d(a)$ exceeds 1, whereas on the complementary interval $(\bar{a},1)$, $\lambda_d(a)$ is less than 1;
- $\bar{a}$ is, for fixed c_1/c_2, an increasing function of E_+/E_-;
- when $c_2(E_+/E_-) > 2$, $\lambda_d(a)$ exceeds 1 on $[0,1)$.

In biological terms, this means that when the strict biennial cannot invade, no strategy can, so the annual strategy is a global ESS. There is a range of parameter values for which the annual strategy is a 'local' ESS, in the sense that it cannot be invaded by the 'a-is-slightly-smaller-than-1' strategy, yet not a global ESS, since it can be invaded by 'a-is-small' strategies. For the choice $g(x) = 1 - x$, one can check analytically that, by increasing c_1 and c_2, while keeping their ratio constant, the annual strategy ceases to be a local ESS. And for the choice $g(x) = \exp(-x)$, this is easily checked numerically.

To prove the claims, we denote the left-hand side of (22) by $F(\lambda,a)$ and note that it is a quadratic polynomial in λ (for fixed a) and in a (for fixed λ) which satisfies

$$F(1,1) = 0 \tag{23}$$

So, $F(1,a)$ can have at most one other zero. Next note that

$$\frac{\partial F}{\partial a}(1,1) = c_2(E_+ + E_-) - 2 \tag{24}$$

and

$$\frac{\partial F}{\partial \lambda}(1,a) = 2 - (1-a)c_2(E_+ + E_-) \tag{25}$$

and

$$F(1,0) = (1 - c_2E_+)(1 - c_2E_-) \tag{26}$$

Now, suppose that $c_2(E_+ + E_-) < 2$: then, $(\partial F/\partial a)(1,1) < 0$ and so $F(1,a) = 0$ has a root in $(0,1)$ if, and only if, $F(1,0) < 0$ (since there is either no root or exactly one root, but never two, three or more roots). Since $c_2E_- < c_1E_- < 1$, the sign of $F(1,0)$ equals the sign of $1 - c_2E_+$. Under the condition $c_2(E_+ + E_-) < 2$, we deduce from (25) that $(\partial F/\partial\lambda)(1,a) > 0$. For fixed a, $F(\lambda,a)$ is a parabola with a minimum. So

$$F(1,a) > 0 \quad \text{and} \quad \frac{\partial F}{\partial \lambda}(1,a) > 0 \quad \Rightarrow \quad \lambda_d(a) < 1 \tag{27}$$

$$F(1,a) > 0 \quad \Rightarrow \quad \lambda_d(a) > 1$$

Hence the first two claims are justified.

With the help of (20) we can rewrite (22) as

$$\lambda^2 - (1-a)\frac{c_2}{c_1}\left(\theta + \frac{1}{\theta}\right)\lambda + (1-a)^2\left(\frac{c_2}{c_1}\right)^2 - a^2 = 0 \tag{28}$$

where $\theta = c_1E_+ = \sqrt{E_+/E_-} > 1$ and $1/\theta = c_1E_- < 1$. Then $\bar{a}$ as a function of θ is determined by the equation $\lambda_d(\bar{a}, \theta) = 1$, where λ_d is the positive real root. We know already (see the second claim) that $\partial\lambda_d/\partial a < 0$, so if we can check that $\partial\lambda_{\mathrm{d}}/\partial\theta > 0$, the result $\partial\bar{a}/\partial\theta > 0$ follows directly from the implicit function theorem. Let us call the left-hand side of (28) $G(\lambda,\theta)$. Then $\partial G/\partial\theta = -(1 - a)(c_2/c_1)(1 - 1/\theta^2) < 0$. At the root λ_{d} we have $\partial G/\partial\lambda > 0$ (see above). So by the implicit function theorem, we conclude that $\partial\lambda_{\mathrm{d}}/\partial\theta > 0$. That shows that the third claim is warranted.

When $c_2(E_+ + E_-) > 2$, $(\partial F/\partial a)(1,1) > 0$ and $F(1,0) < 0$, so $F(1,a)$ cannot have a zero on [0,1), and consequently $\lambda_{\mathrm{d}}(a) > 1$. We have verified the fourth claim as well.

In terms of system (19), describing the competition between pure strategies, the conclusion is that the period-two solution with $z_2 \equiv 0$ loses its stability when c_2E_+ exceeds 1 and a period-two solution in which annuals co-exist with biennials that are present only in odd years takes over. The synchronization to good years overcomes the disadvantage $c_2 < c_1$.

Now let us look at the reverse situation, $c_2 > c_1$. Assume the biennials cycle with period four, characterized by two values E_+ and E_- that satisfy $c_2^2E_+E_- = 1$ and occur in repeated $E_+E_+E_-E_-$ blocks (see Table 1). Let us fix the phase by requiring that, in year 1, we have the first E_+ of such a block and let us count years modulo four. The next generation matrix then takes the form

$$\begin{pmatrix} 0 & 0 & (1-a)c_2E_+ & ac_1E_+ \\ ac_1E_+ & 0 & 0 & (1-a)c_2E_+ \\ (1-a)c_2E_- & ac_1E_- & 0 & 0 \\ 0 & (1-a)c_2E_- & ac_1E_- & 0 \end{pmatrix} \tag{29}$$

We restrict our attention to $a = 1$ and then find the characteristic equation

$$\lambda^4 - c_1^4E_+^2E_-^2 = 0 \tag{30}$$

But since $c_2^2E_+E_- = 1$ and $c_1 < c_2$, necessarily $c_1^4E_+^2E_-^2 < 1$ and therefore $|\lambda| < 1$. The annuals cannot profit from the time-inhomogeneity and their disadvantage in the periodic situation is as strong as in the steady situation.