



Centrum voor Wiskunde en Informatica

REPORTRAPPORT

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AM-R9520 1995

Report AM-R9520
ISSN 0924-2953

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SMC is sponsored by the Netherlands Organization for Scientific Research (NWO). CWI is a member of ERCIM, the European Research Consortium for Informatics and Mathematics.

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The Many Facets of Evolutionary Dynamics

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Abstract

In this note we present an outsider's view on the mathematical description of long term biological evolution as driven by natural selection. It is an outlook to the future, more than an account of what has been achieved so far.

AMS Subject Classification (1991): 92D15

Keywords & Phrases: ESS (Evolutionarily Stable Strategy), natural selection, trait substitution sequence, invader, resident.

Note: this report will be submitted to the Proceedings of the 4th International Conference on Mathematical Population Dynamics, Houston, May 23-27, 1995.

1. INTRODUCTION

Let me begin by listing the sources of inspiration for the present account on evolutionary dynamics:

- many conversations during the last five years with Hans Metz
- two workshops on Evolutionary Dynamics (in Trento and Amsterdam) which were activities of the European Science Foundation Network "Dynamics of Complex Systems in Bio-Sciences" (coordinated by Jean-Pierre Aubin) and the special issue of the Journal of Mathematical Biology (to appear in 1995) which resulted from these workshops. In this connection I like to mention Ilan Eshel, Peter Hammerstein, Carlo Matessi, Peter Taylor, Paul Marrow, Ulf Dieckmann, Richard Law, Josef Hofbauer, Franjo Weissing, Karl Sigmund, David Rand which all, one way or another, taught me aspects of the subject
- a paper by V. Kaitala and W.M. Getz (1995) on the timing of reproduction of Pacific salmon. When handling this paper as an editor of the Journal of Mathematical Biology, I noted that it was concerned with a rich and illuminating special example that serves very well to stimulate thinking about general theory. So together with a student, Janneke ten Donkelaar, I started to investigate other aspects of the model
- collaboration with Sido Mylius and Hans Metz on the (often neglected) importance of the precise form of density dependence for evolutionary considerations

For me it has been a pleasure to gradually begin to understand the aims, ideas, concepts, conjectures and results. At the same time I noticed that, as in many other fields, the literature is often hardly accessible for outsiders. Perhaps an enthusiastic newcomer could explain the basic ideas, assumptions and open problems in a naïve but accessible way, since he is not hindered by too much knowledge about subtle aspects? That at least is the hope that triggered the writing of this note. The key point, however, is that I think that the subject is interesting, largely open and very challenging, both from a biological and from a mathematical point of view, and that it therefore deserves a lot of attention.

2. WHEN AND WHERE TO REPRODUCE?

For a full account of the motivation underlying the following model for Pacific salmon we refer to KAITALA & GETZ [1995]. Let $y(t)$ denote the number of larvae produced in year t and let $x(t)$ denote the number of larvae that survive the competition in the nursery area and enter the sea in year t . We assume that

$$y(t) = \alpha c_3 x(t-3) + (1-\alpha)c_4 x(t-4) \quad (2.1)$$

which expresses that a fraction α reproduces after three years and a fraction $(1-\alpha)$ after four years. The coefficients c_3 and c_4 combine information about survival at sea and survival during the trip upstream to the spawning pool. Secondly we assume that

$$x(t) = f(y(t)) = y(t)g(y(t)) \quad (2.2)$$

where g describes the adverse effects of crowded conditions on survival in the nursery. We ask the following question: what value of α is favoured by natural selection? And how does the answer depend on c_3 , c_4 and g ? And if, alternatively, density dependence would act far stronger during the stay at sea than in the nursery, would the same value of α be favoured?

So far we assumed that the larvae are growing up in one well-mixed pool. Suppose, instead, that there are two pools (for instance, the second one is higher upstream). Then we replace (2.2) by

$$x(t) = f(y_1(t)) + f(y_2(t)) \quad (2.3)$$

and (2.1) by

$$\begin{aligned} y_1(t) &= \alpha \phi_2 c_3 x(t-3) + (1-\alpha)\phi_4 c_4 x(t-4) \\ y_2(t) &= \alpha(1-\phi_3)\tilde{c}_3 x(t-3) + (1-\alpha)(1-\phi_4)\tilde{c}_4 x(t-4) \end{aligned} \quad (2.4)$$

where ϕ_i is the fraction of i -year old that choose pool 1 to reproduce and the difference between c_i and \tilde{c}_i accounts for the fact that those swimming on to pool 2 may incur an extra risk of a fatal event (such as encountering a hungry bear). One may likewise argue that f_1 and f_2 are needed, but we have chosen to ignore their difference. We now ask the question: what combination of α , ϕ_3 and ϕ_4 does natural selection favour?

3. THE GENERAL PERSPECTIVE

Assume that a population dynamics model is specified. In particular we think of a physiologically structured population model based on the notions of individual state and interaction via environmental variables, usually denoted by E (the defining characteristic of the environmental variables is that for given E , as a function of time, the population dynamic model is linear and so density dependence results from feedback to E ; in the salmon example $E(t) = g(y(t))$ or, for the alternative, the yearly survival at sea as it depends on the (weighted) sum of the year class densities.) The population dynamics model may involve several species.

The parameters in such a population dynamics model describe properties of the individuals and how these depend on the individual state and the environmental variables. We single out a (possibly multi-dimensional) parameter called *trait* or *strategy* or *phenotype* and which we presume is under natural selection (often the choice of which parameters we consider as fixed and which as changeable in the course of evolution is rather arbitrary and mainly a reflection of our interests; for instance, KAITALA & GETZ [1995] consider ϕ_3 and ϕ_4 as fixed given parameters in the two pool version of the salmon model). If we are honest, we realise that the heritable aspects of the trait are genetically determined and that, in addition to phenotype, we should consider genotype. We then should make the genotype part of the individual state and define mating rules to derive the genotypes of the offspring from these and Mendel's laws. (See MATESSI & DI PASQUALE, to appear, and WEISSING, to appear.) Often

we choose to be less honest, that is we pretend that reproduction is clonal, i.e. the offspring simply inherits the trait from the mother.

In the case of several species, like predator and prey or host and parasite, different components of the trait may refer to different species. That's how co-evolution is incorporated.

When animal behaviour is studied, the interaction is often modelled in more detail, while the rest of population dynamics is reduced to a caricature. More precisely, the strategies refer to a *game* and the population dynamical consequences are in terms of pay-offs called (inclusive) fitness. But essentially this is just the same setting.

The crucial assumption in most descriptions of evolutionary dynamics is *time scale separation* (but see [VAN DER LAAN & HOGEWEG, preprint]): we imagine that the population dynamics settles down on an attractor which then is “challenged” by the introduction, through mutation, of some individuals with a trait value that was not present in the current population. So we assume that the time scale at which mutations occur is much longer than the time scale of convergence to the attractor and motion on the attractor. As a consequence, we restrict attention to the fate of a single mutant and neglect the possibility of two or more mutants trying their luck simultaneously (but see [VAN DER LAAN & HOGEWEG, preprint]).

Conceptually then, the evolutionary *state* is the population dynamical attractor (see RAND, WILSON & MCGLADE, 1994; as explained in more detail when we discuss mutation below, it is a state in the true Markovian sense only when the individual state includes genotype). But what information about the attractor is really required? Can we consider such attractors as elements of a (linear) space?

To decide about the relative likeliness of the various mutations possible, we need to know $b(t, \xi)$, the time course of the number of individuals born per unit of time, distinguished according to individual state-at-birth ξ (e.g., mutation in the predator is more likely during periods in which many predators are born). To decide about the chances of a mutant to really “make it” in the world, we need to know $E(t)$, the time course of the environmental variables. Since they describe an attractor, both $t \mapsto b(t, \xi)$ and $t \mapsto E(t)$ should be stationary, i.e. they should exhibit some recurrence properties. Often one simply *assumes* that the attractor is a steady state and then the functions of time reduce to constants.

Another assumption that is frequently made is that the current population is *monomorphic*, i.e. the individuals composing the population all have the same trait. At the background of this is the so-called competitive exclusion principle. But in general one can only be sure that, in steady state, the number of types is bounded by the dimension of E . And in fluctuating environments one can, as far as I know, say nothing at all in general.

If one knows or assumes that there is a *unique* steady state for a monomorphic population, one can use the current trait value as the evolutionary state since it determines, perhaps somewhat implicitly, all relevant information. HANS METZ [see METZ E.A., preprint] has extended this idea to the polymorphic and non-steady world by taking as his starting point that a (feasible) list of trait values *uniquely* fixes a population dynamical attractor describing a population composed of individuals with one of the listed traits. So the evolutionary state now is a list of trait values (the set of all such lists has a complicated topological structure; some of the subtlety is hidden in the word “feasible” above; see [METZ E.A., preprint]).

After having discussed the notion of state, we now turn to dynamics. We distinguish three aspects: i) initiation by mutation; ii) testing based on linearization (the invasion exponent and demographic stochasticity); iii) the switching to a new attractor as the result of (nonlinear) competition.

The theory of long term evolution centers around rare but extremely influential mutations. When elaborating such a statement in more technical detail, many complications call for attention (see ESHEL, to appear):

- mutation affects the alleles, hence the possible genotypes, but not directly the trait itself
- the map from genotype to phenotype (= trait) is many to one; so if we work with traits only and forget about genes, the probability that certain mutations occur depends on hidden information

(the system is non Markovian in the sense that it exhibits history dependence)

- a full neighbourhood (in whatever reasonable sense) of the set of alleles present may not cover a full neighbourhood of the set of traits present (e.g. due to pleiotropy)
- connected to the “reasonable” above, what mutations are feasible? How big is the world of alternatives that we want to test?
- the frequency distribution for the mutant that will appear on the scene is determined both by the frequency distribution per reproduction event and the frequency of the various reproduction events; so even if the support of the probability distribution for mutants can be specified, it may be hard (or, rather, impossible) to give complete information
- the price we have to pay for allowing all conceivable (whatever that may mean) alleles to arise by mutation is that *genotypic* evolutionary dynamics will never stop: one can always introduce “new” alleles which are phenotypically indistinguishable and hence neutral with respect to natural selection; it is for this reason that we will concentrate below on phenotypic stability (in the sense of attractivity); and it is also for this reason that one often chooses to be dishonest and work with phenotypes all the time
- since mutation is inherently stochastic, there are many realisations to be considered when studying evolutionary dynamics; should we be able to say something about (almost) all possible realisations? (Perhaps we should here restrict our attention to SMALL mutations? Below we will find that, in addition, the dimension of the trait space matters a lot.)

Individuals carrying the mutated trait are collectively denoted as the “invader”, while those with the conventional traits are called “residents”. In the *test phase* we ignore the feedback of the invader on the environment; that is, we consider the environment as set by the resident; mathematically, this amounts to linearization.

We then ask the following questions:

- is the invader *in principle* able to grow exponentially in that environmental regime?
- if yes, does it *actually* start to grow exponentially?

The answer to the first question involves only the sign of $\rho_E(T)$, the so-called *invasion exponent* or *dominant Lyapunov exponent* of the trait T in the environment E (see [METZ, GERITZ & NISBET, 1992], where it is argued that this exponent is what one should think of when talking about the *fitness* associated with T in the environment E ; note that E is, in general, a function of time; see [RAND, WILSON & MCGLADE, 1994] for the subtleties associated with the precise definition of $\rho_E(T)$ when dealing with a complicated attractor). More precisely, the answer is yes if $\rho_E(T) > 0$ and no if $\rho_E(t) < 0$. When dealing with steady states, we can alternatively discuss growth on a generation basis and work with the basic reproduction ratio R_0 . The test whether or not $R_0 > 1$ leads to equivalent results as $\text{sign}(R_0 - 1) = \text{sign}\rho$.

Even if the exponent is positive, the invader may still go extinct due to demographic stochasticity (as the invader by definition starts off with one individual, this possibility can certainly not be ignored). To calculate the probability that it will do so, one has to elaborate the branching process description of population growth in the given environment E . All of this effectively amounts to an algorithm (not so easily implemented though) for computing the probability distribution of *successful* mutants.

If the trait space is one-dimensional and we restrict to small mutations and (although this is less essential) to monomorphic populations, the probability distribution of successful mutants is necessarily concentrated on one side of the current trait, which allows us to deduce the direction in which natural selection will “push” the trait. In higher dimensions, we get an invasibility set which is locally like a *cone* and the probability distribution of successful mutants puts weight to the various directions

within this cone. In other words, the left-right distinction of the one-dimensional case implies that crude information suffices to classify the possibilities, but in higher dimensional trait spaces there are plenty of directions which carry weights according to submodels for mutation and population dynamics; in practice such weights are usually not easy to determine.

The success-test for the invader cares only about the one way influence, via the environment, of the resident on the invader. If the invader passes the test, we next have to consider the *interaction* between the resident and the invader. If we work with genotypes, we have to consider the short term selection as it is described in population genetics models. Otherwise we have to deal with some ecological model for competition. Our task is to find out what the new population dynamical attractor will be, now that a mutation has created a successful invader. (The new population dynamical attractor may not be *uniquely* determined by the old attractor and the mutant as, possibly, the moment of mutation matters as well.) For a class of Lotka-Volterra systems competitive exclusion guarantees that a successful mutant necessarily takes over. The repeated replacement of a current trait by a new trait then leads to what is called a *trait substitution sequence*. Often it is assumed, without justification, that this scenario holds for other models as well. But below we shall see that it may easily happen that a (*protected*, as it is called) *polymorphism* arises since the former resident is actually a superior competitor when it becomes rare, i.e. if the environment is set by the former invader. Anyhow, this last part of the description of evolutionary dynamics requires that we obtain global information about complicated nonlinear equations, from ecology or population genetics which is, clearly, a daunting task.

This ends our, admittedly vague and superficial, description of a mathematical model for long term evolution. We have concentrated on a conceptual description of a general programme and on the underlying ideas, the many open ends and on several debatable assumptions. HAMMERSTEIN [to appear] speaks about the streetcar theory of evolution, with the endpoints of short term selection as temporary stops. As soon as a new passenger (the mutant) gets in, the tram may (or may not) start again. The interplay of the new passenger and the old passengers determines where the tram will go (contrary to the usual situation, the rails are not laid a priori). On the way to the next stop, the new passenger may (or may not) kick out one or more of the old passengers. A key question is: does the tram ultimately come to complete rest? Is there a final stop, an evolutionary trap? And can we predict where the final stop will be, with as little information as possible on the process of mutation?

An ESS is a population dynamical attractor such that any feasible mutant is necessarily unsuccessful (the feasibility condition may include that only small mutations are considered). The symbols stand for Evolutionarily Stable Strategy, but the “Stable” is actually quite misleading (as I will explain below) and I prefer to substitute any of the alternatives “Steady”, “Singular” or “Superior”. The meaning of the words presumes a monomorphic situation but the concept as formulated above does not (the choice of the words is rooted in the game theoretical context, where it is often impossible to distinguish between polymorphism and mixed strategy). An ESS is also called an unbeatable strategy. It is immune to (and in that sense stable against) any mutant strategy. It is a steady state for the evolutionary dynamics.

A pleasant feature is that we do not need to be very specific about the mutation structure when trying to find an ESS (simply because *all* feasible mutations should be unsuccessful; of course we need to specify what is feasible, but we are always safe if we are not too restrictive in this respect). Wishful thinking held that likewise we could characterise an ESS without being specific about the density dependence embodied as nonlinear feedback to the environment. As we shall see in the salmon example below, this is simply not true (also see [MYLIUS & DIEKMANN, to appear, METZ, MYLIUS & DIEKMANN, PREPRINT]). It is, on the other hand, possible to take advantage of the low dimensionality of E when characterising ESS (see below). It seems a relevant research topic to develop algorithms that are able to find ESS, given additional structure, i.e. for specific special classes of models and under specific additional assumptions such as monomorphy.

An ESS, being a steady state for the evolutionary dynamics, may or may not be a (local) attractor for the evolutionary dynamics (the “stable” misleadingly suggests that it always is). When the trait

FIGURE 1

space is one-dimensional, one can graphically analyse the situation by plotting the sign of $\rho_{\bar{E}(T_{resident})}(T_{invader})$ as a function of both $T_{resident}$ and $T_{invader}$. Figure 1 gives an example.

At the 45° line, necessarily $\rho = 0$. Generically, the neutrality set defined by $\rho = 0$ consists of curves. Such curves may cross the 45° line. A trait \hat{T} determined by such a crossing is called a *singular point*. One can completely classify singular points according to the angle that the tangent to the neutrality curve makes with the 45° line and the sign of ρ in a designated sector, say the one containing the 90° line. This classification has been developed by METZ e.a. [preprint; also see GERITZ E.A., in preparation], building on earlier work of ESHEL [1983] and TAYLOR [1989]. Readers are invited to take pencil and paper and to figure it out by themselves, as this actually is the best method for gaining inside. Such an exercise should in particular lead to the following conclusions:

- an ESS may be an attractor or a repellor (in the latter case it was aptly called a “Garden of Eden” by HOFBAUER and SIGMUND [1990]).
- mutual invasibility leading to a protected dimorphism is possible; this dimorphism may either converge (i.e. contract as far as the two traits are concerned) or diverge (i.e. expand, a situation that we may liken to speciation) as further successful mutations happen. [CHRISTIANSEN, 1991, METZ E.A., preprint]
- provided that mutations cover a full neighbourhood in trait space, the classification is independent of the mutation structure.

In higher dimensional trait spaces, the situation is a lot more complicated (METZ [work in progress; personal communication]). A striking and important difference is that the mutation process may have

a decisive influence on the attractivity (see examples in [MARROW, DIECKMANN & LAW, to appear] and [MATESSI & DI PASQUALE, to appear]).

Anyhow, insight in the classification of ESS, as evolutionarily steady states or traps, with respect to the *dynamics* of long term evolution is emerging and the extent to which the mutation process matters is under investigation. In addition, results on the bifurcation of singular points are under way. Hopefully this will lead, in the future, to numerical tools à la AUTO [DOEDEL & KERNÉVEZ, 1986] and LOCBIF [KHIBNIK E.A., 1993] for the systematic interactive analysis of simple invariant sets and their stability.

4. FITNESS MEASURES AND OPTIMISATION

In the foregoing we have emphasized invasibility of a resident population dynamics attractor by a rare mutant invader leading, if successful, to a different population dynamics attractor. Thus evolutionary dynamics is described as a substitution sequence, incorporating an element of chance due to mutation. We then paid attention to the steady states of the evolutionary discrete time (the lapse of time in between two steps being only implicitly defined) dynamics and their attractivity.

When opening books [ROFF, 1992, STEARNS, 1992] on life history adaptation often a quite different picture emerges. A frequent procedure is to choose a so-called fitness measure and to search for the life history, i.e. trait in our terminology, that maximises this fitness measure. It is then said that natural selection acts accordingly.

Is there any relationship between these two, seemingly so different, approaches? Following [MYLIUS & DIECKMANN, to appear, METZ, MYLIUS & DIECKMANN, preprint] we shall show that indeed there is. The key feature in determining which fitness measure is appropriate turns out to be the way density dependence acts!

To set the scene, we brutally assume that the population dynamics attractor is always a monomorphic steady state. As is customary in the case of constant environments, we denote the invasion exponent by $r_E(T)$. We assume that the equation $r_E(T) = 0$, together with the feedback conditions, yields a unique constant environment, denoted by $\bar{E}(T)$. So note that $r_{\bar{E}(T)}(T) = 0 = 1 - R_0^{\bar{E}(T)}(T)$.

We next assume that, as far as the sign of r is concerned, only a one-dimensional characteristic of E matters or, more precisely, that

$$\text{sign } r_E(T) = \text{sign } F(T, \phi(E))$$

where ϕ and E both take values in \mathbb{R} . Finally we assume that F is a monotone function of its second argument. To be specific, we take it increasing. The assumptions are chosen such that the following result from [METZ, MYLIUS & DIECKMANN, preprint] becomes a triviality. Yet, as we shall see below, the assumptions are not as contrived as they may seem at first sight.

LEMMA. *Under the assumptions listed above, \hat{T} is ESS if and only if the function $T \mapsto \phi(\bar{E}(T))$ is minimal at \hat{T} .*

PROOF. If $T \mapsto \phi(\bar{E}(T))$ is minimal at \hat{T} then

$$F(T, \phi(\bar{E}(\hat{T}))) < F(T, \phi(\bar{E}(T))) = 0$$

for all $T \neq \hat{T}$ whereas if this function is not minimal there exists a $T \neq \hat{T}$ for which the reverse inequality holds. By carrying this information over to the sign of r it follows that \hat{T} is an ESS in the first case, whereas it cannot be an ESS in the second case. \square

So the optimisation of T actually amounts to the pessimisation of the most relevant environmental characteristic, a true example of a Verelendungs principle.

COROLLARY 1. *Suppose the density dependence affects the basic reproduction ratio R_0 (i.e. the expected life time offspring production) in a multiplicative way, i.e.*

$$R_0^E(T) = \phi(E)R_0^V(T)$$

(where V refers to the “virgin” environment) then \hat{T} is ESS if and only if R_0^V (and hence R_0^E for any E) is maximal in \hat{T} .

COROLLARY 2. Suppose the density dependence affects the Malthusian parameter r in an additive way, i.e.

$$r_E(T) = r_V(T) + \phi(E)$$

(where once more V means “virgin”) then \hat{T} is ESS if and only if r_V (and hence r_E for any E) is maximal in \hat{T} .

COROLLARY 3. Suppose E is one-dimensional and $E \mapsto R_0^E(T)$ is increasing for any T , then \hat{T} is ESS if and only if \hat{E} is minimal in \hat{T} .

These cases respectively apply to uniform reduction of fecundity, uniform increase of death rate and, e.g., competition for food. They show that it depends on the mechanism for population regulation which fitness measure, R_0 , r or steady state environmental condition, is appropriate (the latter is in simple models inversely proportional to population density; in the literature one finds accordingly often the equilibrium population density taken as a fitness measure; we prefer the formulation in terms of a one-dimensional environmental characteristic, because it avoids that ambiguity arises in complicated models).

In conclusion of this section we emphasize the importance of notation. Only by writing r and R_0 explicitly as functions of T and E becomes it clear in what sense maximisation of r or R_0 is meaningful, despite the fact that in steady state always $r = 0 = 1 - R_0$.

5. BACK TO SALMON

If density dependence acts in the nursery we set

$$R_0^E(\alpha) = (\alpha c_3 + (1 - \alpha)c_4)E$$

and conclude that we should maximise $\alpha c_3 + (1 - \alpha)c_4$. So if $c_3 < c_4$ then $\hat{\alpha} = 1$ is an ESS while for the reverse inequality $\hat{\alpha} = 0$ is an ESS. Exploiting the one-dimensionality of α we easily deduce that the ESS is a global attractor for the evolutionary dynamics.

If density dependence acts by uniformly reducing the survival probability at sea, we first of all note that $r_E(\alpha)$ is the real root of the Euler-Lotka equation

$$\alpha c_3 E^{-3} \lambda^{-3} + (1 - \alpha)c_4 E^{-4} \lambda^{-4} = 1.$$

It follows that $r_E(\alpha) = E r_1(\alpha)$ and that we should maximise $r_1(\alpha)$. A simple argument then establishes that $\hat{\alpha} = 1$ is ESS when $c_3^{1/3} > c_4^{1/4}$ while $\hat{\alpha} = 0$ is ESS if the reverse inequality holds. As to be expected, the condition for delayed reproduction, i.e. $\hat{\alpha} = 0$ hence $c_3^{1/3} > c_4^{1/4}$, is more severe than before. Again it can be shown that the ESS is a global attractor (but note that we did not prove the competitive exclusion principle that should justify the monomorphy assumption; more importantly, the assumption of a steady state population dynamical attractor may be unwarranted; see below).

We reiterate that c_3 and c_4 may be such that $\hat{\alpha} = 0$ is ESS in the first case while $\hat{\alpha} = 1$ is ESS in the second. Thus this example illustrates that the form of density dependence (i.e. which environmental components are affected by population density) matters for the outcome of natural selection.

Let us return to competition in the nursery. The results so far seem to indicate that the function g has no great influence on the results. However, one should realise that the form of the function g determines, together with α , whether or not the unique steady state is stable with respect to the population dynamics. In work in progress Janneke ten Donkelaar, Sido Mylius and myself investigate whether, for instance, $\hat{\alpha} = 1$ is still an ESS when the evolutionary state is a periodic population

dynamical attractor. The preliminary conclusion is that this is not necessarily so. An interesting but complicating aspect is that two stable periodic solutions (respectively with period 2 and 6) can coexist for $\alpha = 1$. Remarkably, the invasibility depends on the attractor considered (a similar conclusion has been reached by TOM VAN DOOREN [personal communication]). Anyhow, the key point is that optimality considerations for (arbitrary!) constant environments lose their significance in fluctuating environments, even when the fluctuations are endogeneous in the sense that they result from delayed negative feedback. It is tempting to conjecture that the evolutionary dynamics has a tendency to damp the population dynamical fluctuations (also see GATTO [1993], FERRIÈRE & GATTO [1993, 1995], HANSSON [1991], METZ, GERITZ, & NISBET [1992]).

Let us now turn to spatial heterogeneity. The two pool situation leads to

$$R_0^E(\alpha, \phi_3, \phi_4) = (\phi_3 \alpha c_3 + \phi_4 (1 - \alpha) c_4) (E_1 + ((1 - \phi_3) \alpha \tilde{c}_3 + (1 - \phi_4) (1 - \alpha) \tilde{c}_4) E_2)$$

where

$$E_1 = g((\phi_3 \alpha c_3 + \phi_4 (1 - \alpha) c_4) \bar{x})$$

$$E_2 = g(((1 - \phi_3) \alpha \tilde{c}_3 + (1 - \phi_4) (1 - \alpha) \tilde{c}_4) \bar{x})$$

and \bar{x} then is determined by the requirement that $R_0 = 1$. In addition to the pessimisation principle we now need an equilibration principle for the two environmental components (or, in other words, we should look for an ideal free distribution; in still other words Geza Meszèna (personal communication) speaks about a run-away effect when we do not obey the ideal free distribution). The technical elaboration is given in the appendix. Restricting attention to the generic case $c_3 \neq c_4$ and $\tilde{c}_3 \neq \tilde{c}_4$ we find that there are basically four cases:

CASE I: $c_3 > c_4$ & $\tilde{c}_3 > \tilde{c}_4$.

In this case it is ESS to reproduce in the third year and to distribute over the two pools such that the reproductive success is the same in both:

$$\hat{\alpha} = 1, \phi_4 \text{ arbitrary, } \hat{\phi}_3 = \text{formula involving } g^{-1}$$

CASE II: $c_3 > c_4$ & $\tilde{c}_3 < \tilde{c}_4$.

In this case it is ESS that all those reproducing in their third year do so in pool 1 while all those reproducing in their fourth year do so in pool 2, while the fraction that reproduces in the third year is such that the reproductive success is insensitive to the decision of going to reproduce in the third or fourth year:

$$\hat{\phi}_3 = 1, \hat{\phi}_4 = 0, \hat{\alpha} = \text{formula involving } g^{-1}$$

The other two cases are defined by reversing all inequalities while the results are obtained by interchanging the indices 3 and 4 and replacing, for α , 1 by 0.

We have not yet investigated the attractivity of these ESS. An interesting aspect, discussed by KAITALA & GETZ [1995], arises when we take the underlying genetics into account: the two pools naturally lead to assortative mating.

It seems relevant to extend this nice example in various ways: a continuous spatial variable, size rather than age, artificial selection due to fishing.

6. SUMMARY

The framework of evolutionary dynamics is conceptually almost clear. But technically many aspects are not clear at all. Often debatable assumptions are made in order to arrive at conclusions. These include in particular steady population dynamics state, monomorphic population composition, unique population dynamics attractor, irrelevance of mutation frequency, irrelevance of the precise form of density dependence. Largely this is unwarranted wishful thinking.

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8. APPENDIX

Let g be defined, positive and decreasing on \mathbb{R}_+ . Let there be given four numbers k_1, k_2, k_3, k_4 such that $k_i g(0) > 1$ for all $i = 1, 2, 3, 4$. For given $\bar{\theta}_1, \bar{\theta}_2, \bar{\theta}_3, \bar{\theta}_4 \in [0, 1]$ such that $\sum_{i=1}^4 \bar{\theta}_i = 1$ define $\bar{x} > 0$ to be the unique solution of the equation

$$(\bar{\theta}_1 k_1 + \bar{\theta}_2 k_2)g((\bar{\theta}_1 k_1 + \bar{\theta}_2 k_2)\bar{x}) + (\bar{\theta}_3 k_3 + \bar{\theta}_4 k_4)g((\bar{\theta}_3 k_3 + \bar{\theta}_4 k_4)\bar{x}) = 1$$

We want to find $\bar{\theta}_i$ such that for all θ_i with $\sum_{i=1}^4 \theta_i = 1$

$$(\theta_1 k_1 + \theta_2 k_2)g((\theta_1 k_1 + \theta_2 k_2)\bar{x}) + (\theta_3 k_3 + \theta_4 k_4)g((\theta_3 k_3 + \theta_4 k_4)\bar{x}) \leq 1$$

and, whenever there is equality in this relation and $\theta_i \neq \bar{\theta}_i$ for at least one i , then

$$(\bar{\theta}_1 k_1 + \bar{\theta}_2 k_2)g((\theta_1 k_1 + \theta_2 k_2)\bar{x}) + (\bar{\theta}_3 k_3 + \bar{\theta}_4 k_4)g((\theta_3 k_3 + \theta_4 k_4)\bar{x}) > 1$$

where now \bar{x} is the solution corresponding to $\theta_1, \theta_2, \theta_3, \theta_4$. Without loss of generality we shall assume that $k_1 > k_2$ and $k_3 > k_4$.

CLAIM. The solution is given by $\bar{\theta}_2 = \bar{\theta}_4 = 0$, $\bar{x} = k_1^{-1}g^{-1}(k_1^{-1}) + k_3^{-1}g^{-1}(k_3^{-1})$, $\bar{\theta}_1 = \bar{x}^{-1}k_1^{-1}g^{-1}(k_1^{-1})$.

PROOF. Suppose $\bar{\theta}_2 \neq 0$. Take $\theta_1 = \bar{\theta}_1 + \varepsilon\bar{\theta}_2$, $\theta_2 = (1 - \varepsilon)\bar{\theta}_2$. Differentiating with respect to ε we find $\bar{\theta}_2(k_1 - k_2)g(\dots) > 0$, which shows that we can violate the inequality. Similarly it follows that necessarily $\bar{\theta}_4 = 0$.

Next consider

$$\theta k_1 g_1 + (1 - \theta)k_3 g_3.$$

When $k_1 g_1 > k_3 g_3$ the derivative with respect to θ is positive and when $k_1 g_1 < k_3 g_3$ it is negative. If we try $\bar{\theta} = 1$ we find $k_1 g_1 = 1$ and $k_3 g_3 = k_3 g(0) > 1$, so the derivative is negative. If we try $\bar{\theta} = 0$ we find similarly that it is positive. We claim that there is a unique value of $\bar{\theta}$, viz. $\bar{\theta}_1$ as given above, for which the derivative is zero. Indeed, if $k_1 g_1 = k_3 g_3$ the condition $\bar{\theta}k_1 g_1 + (1 - \bar{\theta})k_3 g_3 = 1$ implies that the common value equals 1. So (with $\bar{\theta}_3 = 1 - \bar{\theta}_1$)

$$k_1 g(\bar{\theta}_1 k_1 \bar{x}) = 1 \implies \bar{\theta}_1 \bar{x} = k_1^{-1}g^{-1}(k_1^{-1}) \implies \bar{\theta}_1 = \bar{x}^{-1}k_1^{-1}g^{-1}(k_1^{-1})$$

$$k_3 g(\bar{\theta}_3 k_3 \bar{x}) = 1 \implies \bar{\theta}_3 \bar{x} = k_3^{-1}g^{-1}(k_3^{-1})$$

$$\begin{array}{c} \text{-----} + \\ \bar{x} = k_1^{-1}g^{-1}(k_1^{-1}) + k_3^{-1}g^{-1}(k_3^{-1}) \end{array}$$

\implies the claim is justified.

We emphasize that the derivative with respect to θ is positive for $\bar{\theta} < \bar{\theta}_1$ and negative for $\bar{\theta} > \bar{\theta}_1$ and that, therefore, for all $\bar{\theta} \neq \bar{\theta}_1$

$$\bar{\theta}_1 k_1 g(\bar{\theta} k_1 \bar{x}) + (1 - \bar{\theta}_1)k_3 g((1 - \bar{\theta})k_3 \bar{x}) > 1.$$

So along the line $\theta_2 = \theta_4 = 0$, $\theta_1 + \theta_3 = 1$ there is neutrality to first order, but the second order inequality holds. Exactly as in the beginning of the proof it follows that away from this line we have the right first order inequality. \square

APPLICATION TO SALMON

The equation now reads

$$1 = (\alpha\phi_3c_3 + (1-\alpha)\phi_4c_4)g((\alpha\phi_3c_3 + (1-\alpha)\phi_4c_4)\bar{x}) \\ + (\alpha(1-\phi_3)\bar{c}_3 + (1-\alpha)(1-\phi_4)\bar{c}_4)g((\alpha(1-\phi_3)\bar{c}_3 + (1-\alpha)(1-\phi_4)\bar{c}_4)\bar{x})$$

We have to distinguish two cases (other cases follow by interchanging the indices 3 and 4; we restrict to generic cases, i.e. $c_3 \neq c_4$ and $\bar{c}_3 \neq \bar{c}_4$).

CASE I. $c_3 > c_4$ and $\bar{c}_3 > \bar{c}_4$

Choose $k_1 = c_3$, $k_3 = \bar{c}_3$, $\theta_1 = \alpha\phi_3$, $\theta_2 = (1-\alpha)\phi_4$, $\theta_3 = \alpha(1-\phi_3)$ and $\theta_4 = (1-\alpha)(1-\phi_4)$. The condition $\bar{\theta}_2 = \bar{\theta}_4 = 0$ leads to $\bar{\alpha} = 1$ arbitrary. Etc.

CASE II. $c_3 > c_4$ and $\bar{c}_4 > \bar{c}_3$

Choose $k_1 = c_3$, $k_3 = \bar{c}_4$, $\theta_1 = \alpha\phi_3$, $\theta_2 = (1-\alpha)\phi_4$, $\theta_3 = (1-\alpha)(1-\phi_4)$ and $\theta_4 = \alpha(1-\phi_3)$. The condition $\bar{\theta}_2 = \bar{\theta}_4 = 0$ leads to $\bar{\phi}_4 = 0$, $\bar{\phi}_3 = 1$ (since $\bar{\alpha} = 0$ or $\bar{\alpha} = 1$ would fix either θ_1 or θ_3). Etc.

FINAL REMARK. Note that both the result and the proof generalize easily to more than two mating pools and more than two years at which reproduction can take place. Moreover, the function g may be different for different mating pools.