Survival of Replicators with Parabolic Growth Tendency and Exponential Decay*

ISTVÁN SCHEURING† AND EÖRS SZATHMÁRY‡

- Research Group for Ecology and Theoretical Biology and Department of Plant Taxonomy and Ecology, Eötvös Únivrsity, Ludovika tér 2, H-1083 Budapest, and §Collegium Budapest (Institute for Advanced Study), and Szentháromság u. 2, H-1014 Budapest, Hungary

(Received on 19 July 2000, Accepted in revised form on 24 May 2001)

The claim that the competition of parabolically growing self-replicators leads to dynamically stable coexistence was challenged by Lifson & Lifson [(1999). J. theor. Biol. 199, 425–433]. They have shown that, if single- and double-strands are treated separately, and only single-strands undergo spontaneous decay, then there is natural selection rather than survival of everybody. We use their models to show that if double-strand decay is not neglected, then dynamical coexistence is still possible under a wide range of parameter values, in agreement with the chromatographized replicator model of von Kiedrowski & Szathmáry [(2000). Selection 1–3, 173–179]. Coexistence is always ensured above a critical resource (monomer) inflow rate. Recycling of decayed replicators into monomers further favours dynamical coexistence. The claim that parabolic growth invariably results in coexistence remains valid for the model for which it was meant to apply, namely for parabolic growth without template decay. Exponential decay acting on single- and double-strands, combined with parabolic growth, may or may not result in a dynamical coexistence of self-replicators.

© 2001 Academic Press

1. Introduction

Von Kiedrowski (1986) realized that his artificial self-replicator (a modified hexadeoxynucleotide) underwent parabolic, rather than exponential growth:

\[ \dot{x}_i = k_i x_i^p, \]

where \( x_i \) is the concentration of replicator type \( i \), \( k_i \) is the analogue to (Malthusian) growth rate and \( 0 < p < 1. \) More specifically, for almost all experimentally investigated artificial replicators \( p \approx 1/2. \) This is due to the fact that these replicators self-associate to form a replicationally inert duplex, making only the dissociated single-strands available as templates for replication [see von Kiedrowski (1993) for a detailed dynamical analysis and von Kiedrowski (1999) for a review of artificial self-replicators]. Szathmáry & Gladkikh (1989) realized that parabolic growth as expressed in eqn (1) results in coexistence whenever the replicators are in a competitive situation. The system they used was

\[ \dot{x}_i = k_i x_i^p - x_i \sum_j k_j x_j^p; \]
which implies a constraint of constant total population size (cf. Eigen, 1971). The unusual result of the analysis of this system was “survival of everybody” (Szathmáry, 1991), in contrast to the classical (Darwinian) case of exponential growth \((p = 1)\), where survival of the fittest prevails. This result was mathematically confirmed by Varga & Szathmáry (1997) who, by finding an appropriate Liapunov function, demonstrated that there was a single internal, globally stable rest point of system (2). Lifson & Lifson (1999) recently challenged these findings, demonstrating that if single-strands do decompose by spontaneous (exponential) decay, coexistence is not possible any more, and “selection of the unfittest” sets in again. Independently, von Kiedrowski (1998) announced that in a simulated chromatographic system of competing self-replicators natural selection could occur, despite the fact that this would not be possible in the spatially homogeneous case, modelled by eqn (2). We shall return to this system in the Discussion.

Let us first point out that it is not system (2) that the Lifsons modified. If one introduces decay rates into the model, one obtains:

\[
\dot{x}_i = k_i x_i^p - d_i x_i - x_i \sum_j (k_j x_j^p - d_j x_j),
\]

for which survival of everybody is still guaranteed, despite the specific decay rates \(d_i\). Using essentially the original rationale of Szathmáry & Gladkih (1989) one finds that

\[
\dot{x}_i = x_i^p \left[ k_i - x_i^{1-p} \left( d_i + \sum_j (k_j x_j^p - d_j x_j) \right) \right]
\]

\[
> x_i^p (k_i - x_i^{1-p} k_{\text{max}}),
\]

(4)

which means that the time derivative is positive if the concentration \(x_i\) is sufficiently low. Furthermore, Lifson & Lifson (1999) in their eqns (13) and (14) write the general phenomenological system for resource competition as:

\[
\dot{A}_i = \alpha_i R A_i^{p(i)} - \beta_i A_i, \quad (i = 1, \ldots, n),
\]

\[
\dot{R} = \rho - R \sum_j \alpha_j A_j^{p(j)},
\]

where now, \(A_i\) is the concentration of replicator \(i\), \(R\) is the common resource for growth, \(\alpha_i\) and \(\beta_i\) are the growth and decay rate constants, respectively, and again \(0 < p(i) < 1\). It is again easy to see (we leave it as an exercise to the reader), that although we now have a different selection constraint from that in system (3), survival of everybody still holds. Lifson & Lifson (1999) do not mention this fact.

Instead of the previously mentioned systems, the Lifsons use yet another one in order to demonstrate natural selection, where they explicitly assume that double-strands do not decompose [“double-strands do not replicate and are resistant to decomposition”; cf. their eqns (11) and (28)]. This fact turns out to be the crucial assumption, since by putting a single decay rate for species \(i\) in systems (3) and (5) above, one is tacitly assuming that the decay rates for double- and single-strands are equal. This is an unrealistic assumption, no doubt. The assumption by Lifson & Lifson (1999) that double-strands do not decompose at all is equally unrealistic. A real scientific problem is lurking between these two extreme assumptions. In the following we demonstrate, essentially in agreement with von Kiedrowski & Szathmáry (2000), that competitive coexistence is still possible under a range of parameter values for self-replicators with a parabolic growth tendency. Extremist claims to the contrary should be abandoned.

### 2. Dynamics of Self-replicators when Double-strands Also Decay

The assumption in Lifson & Lifson (1999) that double-strands do not replicate and are resistant to decomposition is crucial for the dynamics of replicators. We show in the following that coexistence is not impossible for parabolic growth if double-strands decompose at some rate, even if it must be much smaller than the decomposition rate of the single-strands. Interestingly, if the resource influx rate is high, then coexistence is typical; while Darwinian selection occurs at low resource inflow.

Let \(C\) denote the concentration of all strands, and \(A\) that of the single, while \(B\) that of the double-strands (for easier comparison from now
on we use Lifsons’ notation). Then the balance rate equation for \( C \) is

\[
\dot{C} = \alpha R A - \beta A - \delta B,
\]  

(6)

where \( R \) is the concentration of resource and \( \delta \) is the decomposition rate of double-strands. The rate equation for \( R \) is

\[
\dot{R} = \rho - \alpha R A.
\]  

(7)

Here \( \rho \) is the resource inflow rate and \( \alpha \) describes the depletion rate of the resource by the replicating molecules. If single- and double-strands are in association–dissociation quasi-equilibrium (this is a common approximation), then

\[
A^2 = KB,
\]  

(8)

where \( K \) is the equilibrium dissociation constant. It follows from the conservation of mass that \( A + 2B = C \). Combining these two equations one arrives at

\[
A = f(C) = \frac{K}{4} (1 + 8C/K)^{1/2} - 1,
\]  

(9)

(Lifson & Lifson, 1999). Substituting eqns (8) and (9) into eqns (6) and (7) one obtains

\[
\dot{C} = \alpha R f(C) - \beta f(C) - \frac{\delta}{K} f^2(C),
\]  

(10a)

\[
\dot{R} = \rho - \alpha R f(C).
\]  

(10b)

Let us first analyse this system if \( K \ll 1 \), i.e. when the equilibrium is shifted strongly to the double-stranded molecules. Then \( f(C) \rightarrow (K/2) \sqrt{2C/K} \). The second term in eqn (10a) can be neglected in this limit case if \( \beta \ll (\delta/K) f(C) \). Since \( \delta \) is smaller than \( \beta \) by orders of magnitude, this is legitimate if the association–dissociation equilibrium is shifted to double-strands (\( K \ll 1 \)), and if the total concentration is high (\( f(C) \gg 1 \)). Thus eqn (10) simplifies to

\[
\dot{C} = \alpha \left( \frac{K}{2} \right)^{1/2} RC^{1/2} - \frac{\delta}{2} C,
\]  

(11a)

\[
\dot{R} = \rho - \alpha \left( \frac{K}{2} \right)^{1/2} RC^{1/2}.
\]  

(11b)

These equations are structurally identical to the phenomenological equations (5) of parabolic replication studied above, where competitors remain in coexistence.

Now let us consider the competition of two replicators in the general situation:

\[
\dot{C}_1 = \alpha_1 R f_1(C_1) - \beta_1 f_1(C_1) - \frac{\delta_1}{K_1} f_1^2(C_1),
\]  

(12a)

\[
\dot{C}_2 = \alpha_2 R f_2(C_2) - \beta_2 f_2(C_2) - \frac{\delta_2}{K_2} f_2^2(C_2),
\]  

(12b)

\[
\dot{R} = \rho - R (\alpha_1 f_1(C_1) + \alpha_2 f_2(C_2)).
\]  

(12c)

If both the replicators grow when rare, then they can mutually invade each other; hence competitors can coexist. Following this way of thinking, after calculations (see Appendix) we obtain the condition for competitive coexistence

\[
\frac{\alpha_1}{2\alpha_2} \left( 1 + \sqrt{1 + \frac{4\delta_1\rho}{\beta_1^2 K_1}} \right) \beta_2 > \beta_1,
\]  

(13)

\[
\frac{\alpha_2}{2\alpha_1} \left( 1 + \sqrt{1 + \frac{4\delta_1\rho}{\beta_2^2 K_2}} \right) \beta_1 > \beta_2.
\]  

These relations hold only at high \( \rho \) or low \( K \)-s: both of them can be satisfied, mainly if \( \alpha_1 \) and \( \alpha_2 \) are of the same order of magnitude, and the same applies to \( \beta_1 \) and \( \beta_2 \). In the limit of \( \delta_1 = \delta_2 = 0 \), i.e. when double-strands do not decompose at all, then both the inequalities cannot be satisfied simultaneously, thus coexistence is impossible. This is the case dealt with by the Lifsons.

We plot the numerical solutions to system (12) for various values of \( \rho \) in Fig. 1. One can see that the replicators are in coexistence at high resource inflow, while one of them dies out below a critical level.

### 3. Condition for Competitive Coexistence with Nutrient Recycling

We now analyse a case, also treated by Schuster & Sigmund (1982) for conventional
replicators, in which decaying replicators become nutrients by some energy rich reactions (Lifson, 1997). For analytic simplicity, we assume that this recycling occurs instantaneously, i.e. without time delay. The validity of this simplification has been checked by numerical solutions. We assume that monomers for replication result from template decay, and that they are the limiting resource.

Consider the following system:

\[ \dot{C}_1 = \alpha_1 R f_1(C_1) - \beta_1 f_1(C_1) - \frac{\delta_1}{K_1} f_1^2(C_1), \quad (14a) \]

\[ \dot{C}_2 = \alpha_2 R f_2(C_2) - \beta_2 f_2(C_2) - \frac{\delta_2}{K_2} f_2^2(C_2), \quad (14b) \]

\[ \dot{R} = \rho + \varepsilon \left( \beta_1 f_1(C_1) + \frac{\delta_1}{K_1} f_1^2(C_1) + \beta_2 f_2(C_2) + \frac{\delta_2}{K_2} f_2^2(C_2) \right) - R (\alpha_1 f_1(C_1) + \alpha_2 f_2(C_2)). \quad (14c) \]

Notations are as before. There is one new parameter \( \varepsilon \), determining the fraction of decaying replicators that transform into resource (\( 0 \leq \varepsilon \leq 1 \)). This parameter is the same for all replicator species. The analysis follows the same rationale as for the system without recycling. What is the condition for the increase in \( C_2 \) if \( C_1 \) and \( R \) assume equilibrium values and \( C_2 \) is small? The single-species equilibrium can be obtained through somewhat more inconvenient calculations than before

\[ f_1(\hat{C}_1) = \frac{\beta_1 K_1}{\delta_1} + \frac{\beta_1^2 K_1^2}{\delta_1^2} + \frac{4\rho K_1}{\delta_1(1-\varepsilon)}, \]

\[ \hat{R} = \frac{\beta_1 + \sqrt{\beta_1^2 + \frac{4\beta_1 \rho}{K_1(1-\varepsilon)}}}{2\alpha_1}. \quad (15) \]

It is apparent that these formulae deviate from the previous ones [see eqns (A.5) and (A.6) in the Appendix] only by the factor \((1-\varepsilon)\). Thus replicator 2 can invade, provided

\[ \frac{\alpha_2}{2\alpha_1} \left( 1 + \frac{4\rho}{\beta_1 K_1(1-\varepsilon)} \right) \beta_1 > \beta_2. \quad (16) \]

Symmetrically, replicator 1 invades the single-species equilibrium of species 2 if

\[ \frac{\alpha_1}{2\alpha_2} \left( 1 + \frac{4\rho}{\beta_2 K_2(1-\varepsilon)} \right) \beta_2 > \beta_1. \quad (17) \]

It is apparent that coexistence is more readily achieved, because the appearance of \((1-\varepsilon)\) relaxes the conditions on mutual invadability. The higher the level of recycling, the easier it is to achieve coexistence. One could say that instead of a nutrient inflow rate \( \rho \), the replicators enjoy...
FIG. 2. The dynamic behaviour of competing replicators when nutrient is recycled. The nutrient influx rate is fixed ($\rho = 5$), while $\varepsilon$, the recycling rate differs in the different plots. Other parameters are the same as in Fig. 1.

a richer medium: $\rho/(1 - \varepsilon)$. It is also noteworthy that if $\varepsilon \to 1$ then $\rho/(1 - \varepsilon) \to \infty$, provided $\rho > 0$. This is obvious, since complete instantaneous recycling obliterates the adverse effects of decay.

Finally, let us consider a numerical example (Fig. 2). With the parameters of the previous case (Fig. 1) and $\rho = 5$, there is no coexistence without recycling. Coexistence becomes possible above $\rho_{\text{crit}} = 6$. For the case with recycling, this condition translates into $\rho/(1 - \varepsilon) > 6$. Fig. 2 shows that coexistence is indeed possible if $\varepsilon > 1/6$.

4. Discussion and Conclusions

Our results essentially agree with those obtained by von Kiedrowski & Szathmáry (2000) for a chromatographized replication model. Originally recognized by von Kiedrowski (1998), natural selection is possible in this case. But, as von Kiedrowski & Szathmáry (2000) show, coexistence is also a possible outcome, depending on the parameter values. In the chromatographic model, it was assumed that double-strands bind to the chromatographic column more strongly than single-strands, which in terms of decay rates corresponds to the assumption that single-strands decay more readily. von Kiedrowski & Szathmáry (2000) show that the rate of inflow of building blocks into the chromatographic column is a critical parameter: we find the same for the “ecological” model introduced by Lifson & Lifson (1999), provided that the decay of double-strands is not neglected (why should it be?). Thus, both “survival of everybody” and “survival of the fittest” are possible outcomes.

Some more general comments are also in order. Note, first, that the statement that

“parabolic growth invariably results in coexistence” (18)

remains valid for the model (Szathmáry & Gladkih, 1989) from which it was originally concluded (cf. Varga & Szathmáry, 1997). There are conditions, of course, under which this is no longer true, but these conditions require different models. Already Szathmáry & Gladkih (1989) noted that, if one abandons the simple kinetics (1) for replicator growth, and single-strands and double-strands are treated separately, coexistence is guaranteed above a critical total concentration only. This is because at low population density, the single-strands do not frequently associate to yield double-strands (this being a second-order process), and self-inhibition becomes weaker then cross-inhibition. But this also means that under such conditions, parabolic growth is replaced by exponential, and statement (18) is not violated.

Introducing death rates into these dynamical models (Lifson & Lifson, 1999) is an important advance in the field. Nevertheless, the finding by the Lifsons, by von Kiedrowski & Szathmáry (2000) and by ourselves, again do not violate, contrary to the interpretation of Lifson & Lifson
(1999), statement (18), because the correct conclusion from the extended models is

Parabolic growth combined with exponential decay may or may not result in coexistence,

\[ \text{(19)} \]

where parabolic growth results from the self-inhibition of strands due to self-association. Note that exponential decay is the most conservative assumption for atoms, molecules and also replicators. Self-association is represented, naturally, by a negative quadratic term, and this quadratic term can lead to coexistence, similar to the results yielding coexistence in the well-known Lotka–Volterra competitive systems (cf. Szathmáry, 1991).

Recently, Wills et al. (1998) studied the dynamics of macromolecules replicating by enzyme-free autocatalytic ligation. They concluded that depending on the kinetic parameters, their replicator system could display Darwinian selection (with exponential growth law), coexistence of replicators (with characteristics of parabolic growth), and an intermediate behaviour between these two extreme dynamics.

The authors are grateful to two anonymous reviewers for their comments and criticism. This article is supported by the OTKA (Hungarian Scientific Fund) T 029789 and T 035223.

REFERENCES


APPENDIX

Let us assume first that only replicator 1 is in the field. The corresponding single-species system is

\[ \dot{C}_1 = \alpha_1 R f_1(C_1) - \beta_1 f_1(C_1) - \frac{\delta_1}{K_1} f_1(C_1), \quad (A.1) \]

\[ \dot{R} = \rho - \alpha_1 R f_1(C_1). \quad (A.2) \]

We are interested in the non-trivial equilibrium concentrations, so we have to solve the above equations when \( \dot{C}_1 = 0 \) and \( \dot{R} = 0 \) when \( C_1 > 0 \) and \( R > 0 \). It follows from eqn (A.2) that

\[ \dot{R} = \frac{\rho}{\alpha_1 f_1(C_1)}, \quad (A.3) \]

where \( \dot{R} \) denotes the equilibrium resource concentration. Substituting eqn (A.3) into eqn (A.1) we obtain

\[ 0 = \frac{\rho}{\alpha_1 f_1(C_1)} - \frac{\delta_1}{K_1} f_1(C_1). \quad (A.4) \]

We solve this equation for \( f_1(C_1) \), knowing that \( f_1(C_1) > 0 \)

\[ f_1(C_1) = \frac{-\beta_1 K_1 + \sqrt{\left(\frac{\beta_1 K_1}{\delta_1}\right)^2 + 4\rho K_1}}{2} \]

\[ = \frac{\beta_1 K_1}{2\delta_1} \left( \sqrt{1 + \frac{4\rho}{\beta_1^2 K_1}} - 1 \right). \quad (A.5) \]
Substituting eqn (A.5) into eqn (A.3) and after some rearrangement, we conclude that the resource level at equilibrium is

$$ \hat{R}_1 = \frac{\beta_1 + \sqrt{\beta_1^2 + \frac{4\delta_1 \rho}{K_1}}}{2\alpha_1}. \quad \text{(A.6)} $$

The stability of the fixed point is not studied here. It can be shown that this fixed point is stable except if $\beta$ is so high that replicators decompose faster than they multiply, so the replicator dies out and the resource accumulates continuously.

Now replicator 2 emerges in this system. It invades if its growth rate ($\dot{C}_2$) is greater than zero. Due to the condition of rarity for the invader we have

$$ f_2(C_2) > f_2(C_2). \quad \text{(A.7)} $$

Consequently, replicator 2 invades the equilibrium sustained by replicator 1 if

$$ \dot{C}_2 = (\alpha_2 \hat{R} - \beta_2) f_2(C_2) > 0, \text{ that is if } \alpha_2 \hat{R} - \beta_2 > 0. \quad \text{(A.8)} $$

Expanding and rearranging the above relation, we find that replicator 2 invades if

$$ \frac{\alpha_2}{2\alpha_1} \left( 1 + \sqrt{1 + \frac{4\delta_1 \rho}{\beta_1^2 K_1}} \right) \beta_1 > \beta_2. \quad \text{(A.9)} $$

The analysis is identical if replicator 2 is the resident and replicator 1 is the invader, except that the subscripts must be exchanged. Thus replicator 1 invades if

$$ \frac{\alpha_1}{2\alpha_2} \left( 1 + \sqrt{1 + \frac{4\delta_2 \rho}{\beta_2^2 K_1}} \right) \beta_2 > \beta_1. \quad \text{(A.10)} $$

Replicators are in coexistence if relations (A.9) and (A.10) are simultaneously satisfied.