The replicator dynamics for age structured populations

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Abstract

In this paper is presented the new modelling framework combining the replicator dynamics (which is the standard model of the frequency dependent selection) with the Leslie Matrix model of the age-structured population. Firstly the continuous version of the discrete Leslie Matrix model is derived. It is shown that Euler–Lotka equation is satisfied when new model reaches the steady state (ie. stable related frequencies between the age classes). Due to the long expected lifespan of an individual in comparison with the ecological timescale, the real life model should contain a large number of equations. This problem is solved by the introduction of the large age classes concept. The underlying assumption is that within a single large age class the individuals do not differ in the demographic parameters (fertility and mortality). Then according to this result, a more complex model containing different individual strategies is presented. The methodology of the multipopulation games is used for derivation of two, mutually equivalent systems of equations. First contains equations describing the evolution of the strategy frequencies in the whole population completed by subsystems of equations describing the evolution of the age structure for each strategy. Second system contains equations describing the changes of general populations age structure, completed with subsystems of equations describing the selection of the strategies within each age class.

Introduction

Among the most important approaches to modeling of evolutionary processes are life history optimization and evolutionary game theory. The classical approach to life history theory (Stearns 1992, Roff 1992) relies on optimization models. In effect, there are no interactions among individuals or density dependence:

"Life history evolution usually ignores density and frequency dependence. The justification is convenience, not logic, or realism" (Stearns 1992)"

On the other hand, in classical game theoretic models there is no age or stage structure. Payoffs describes the averaged lifetime activity of an individual, which can be found for example in Cressman 1992:

"...an individual’s strategy is fixed over lifetime or, alternatively, the life history of an individual is its strategy."

The classical approach to evolutionary game theory that can be found in the textbooks (Maynard Smith 1982, Cressman 1992, Hofbauer and Sigmund 1988 and 1998, Weibull 1995, Nowak 2006) mostly relies on the mathematical structure of a two-person matrix game. However, during recent years there has been a huge development in a field, which extends the matrix game paradigm describing population outcomes of local two-player interactions. There are papers related to modeling of hierarchy formation (Broom (2002), Broom & Cannings
where more than two individuals are involved in a single interaction event and density dependent selection (Krivan et al. 2008, Argasinski and Kozlowski 2008). In addition, there are generalizations of basic evolutionary game approaches to cases where individuals are characterized by a continuous trait or a set of continuous traits. Therefore, there is progress in game theoretic methods to using similar methodology to that of life history theory. The closest approaches are state based games (Houston and McNamara , 1988, 1991, 1992, 1999, Webb et al, 1999, McNamara et al., 1994, McNamara et al, 2004, McNamara et al., 2009). Another important approach in theoretical evolutionary ecology is individual based modeling (multiagent computer simulation techniques). This is a methodology based on the assumption that the individual is the basic subject of selection and that a model should explicitly consider unique traits of individuals. The creators of this approach (Lomnicki 1988, Grimm, Wyszomirski, Aikman, Uchmanski 2003, Grimm and Railsback, 2005) criticize classical mathematical models as oversimplified.

Methods used in life history optimization are closely related to classical demographic methods and are expressed in demographic terms. However, how to construct a general description of the relationships between demographic structure and population dynamics is still unsolved problem (Caswell 2011). Game theoretic models operate in abstract terms of costs and benefits measured in units of fitness mostly without deeper insight in their meaning or interpretation. This problem was analyzed in Argasinski and Broom (2012) where relationships between classical demography and evolutionary games are described in detail. The main conclusion there is that instead of the excess from average fitness, models should be described explicitly by mortality and fertility, which are basic opposite forces shaping population dynamics. Those results are significant progress in ecological realism; they emphasize the role of background mortality and fertility or turnover of individuals (this was originated by Argasinski and Kozlowski, 2008). However, that approach is still very primitive. Background mortality is described by a single constant, which describes an exponential decay of the population, which implies that the length of an individuals lifetime is potentially unbounded, and there is no aging and no age specific payoffs. The goal of this paper is to fill this gap and develop a mathematical structure combining selection of individual strategies with an age structured population.

0.1 Classical theory

The classical approach to the modelling of age structured populations is related to Leslie matrices, following the following matrix equation:

\[
\begin{pmatrix}
  n_0 \\
  n_1 \\
  \vdots \\
  n_m
\end{pmatrix}_{t+1} =
\begin{pmatrix}
  f_0 & f_1 & \cdots & f_m \\
  s_0 & 0 & \cdots & 0 \\
  0 & \cdots & 0 & 0 \\
  0 & 0 & s_{m-1} & 0 \\
  \vdots & \vdots & \vdots & \vdots \\
  0 & 0 & 0 & s_m
\end{pmatrix}
\begin{pmatrix}
  n_0 \\
  n_1 \\
  \vdots \\
  n_m
\end{pmatrix}_t.
\]
This age-structured growth model suggests a steady-state, or stable, age-structure and growth rate. The growth rate can be calculated from characteristic polynomial of the Leslie Matrix called the Euler-Lotka equation:

\[ f_0 + \sum_{i=1}^{m} e^{-ir} f_i \prod_{j=0}^{i-1} s_j = 1, \]

where \( r \) is the intrinsic growth rate of the population. Now let us focus on populations diversified by individual strategies.

When a population with a finite number of individual strategies is considered, then a system of differential equations called the replicator dynamics can be defined. It describes changes of the population state in time and can be derived in the following way. Assume that we have a finite number \( I \) of arbitrarily chosen strategies. For each strategy some payoff function \( r_i \) is assigned (for example in matrix form, as in the classical Hawk-Dove Game, however the form of payoff function depends on the modelled problem and can be more complicated). Then the growth of the population of \( i \)-strategists can be described by the Malthusian equation

\[ \dot{n}_i = n_i r_i. \] (1)

Then by following a change of coordinates,

\[ q_i = \frac{n_i}{n} \] (2)

where \( n = \sum_{i=1}^{I} n_i \) is the population size, we can derive a system of ordinary differential equations (see e.g. Cressman (1992)),

\[ \dot{q}_i = q_i (r_i - \bar{r}) \] (3)

where \( \bar{r} = \sum_{i=1}^{I} q_i r_i \) is the average payoff in the population. However, instead of the Malthusian parameter describing payoff we can explicitly consider individual fertility \( f_i \) and individual mortality \( d_i \) of an \( i \)-strategist. In effect we obtain the following variant of the replicator equations that can be called the sex and violence equations,

\[ \dot{q}_i = q_i (f_i - \bar{f} - d_i + \bar{d}) = q_i ((f_i - \bar{f}) - (d_i - \bar{d})), \] (4)

for details see Argasinski and Broom (2012). It was shown (Argasinski, 2006) that every single population system described by the replicator equations (3) can be divided into the product of subsystems describing the dynamics in arbitrary chosen subpopulations (described by a vector of frequencies \( q^i \) for the \( i \)-th subpopulation) and an additional system describing dynamics of proportions between those subpopulations \( p \) (see appendix A for details). The dynamics in each subpopulation will have the form (3) and will depend on the excess of the strategy payoff from the average payoff in this subpopulation. Therefore, the
same operation can be carried out for equations (4). In effect we obtain the following system:

\[ \dot{q}_j^i = q_j^i \left( (f_j^i - \bar{f}) - (d_j^i - \bar{d}) \right), \]  

(5)

\[ \dot{p}_s = p_s \left( (\bar{f} - \bar{d}) - (\bar{d} - \bar{d}) \right), \]  

(6)

where \( W_j^i \) and \( d_j^i \) are the fertility and mortality, respectively, of the \( j \)-th strategy in the \( i \)-th subpopulation and \( \bar{f} \) and \( \bar{d} \) are the mean fertility and mortality, respectively, in the \( i \)-th subpopulation and \( \bar{f} \) and \( \bar{d} \) are the respective values in the global population. When fertility and mortality are density dependent, the system should be completed by an equation on the population size (scaling parameter):

\[ \dot{n} = n(\bar{f} - \bar{d}). \]  

(7)

0.2 A continuous version of the Leslie Matrix

A major technical difference between Leslie matrices and replicator dynamics is the fact that the first describes discrete system and the second is a system of continuous differential equations. The Leslie matrix can be presented as a system of algebraic equations, describing changes of age structure with \( m \) age classes:

\[ n_0(t + 1) = f_0n_0(t) + f_1n_1(t) + \ldots + f_mn_m(t), \]

\[ \ldots \]

\[ n_i(t + 1) = s_{i-1}n_{i-1}(t), \]

\[ \ldots \]

\[ n_m(t + 1) = s_{m-1}n_{m-1}(t). \]

We can imagine a continuous version of this system:

\[ \dot{n}_0 = \sum n_i f_i - n_0, \]

\[ \dot{n}_1 = s_0n_0 - n_1, \]

\[ \ldots \]

\[ \dot{n}_m = s_{m-1}n_{m-1} - n_m. \]

(8)

To solve this system we can apply the theory of delayed differential equations because equation (8) leads to \( n_i(t) = n_0(t - i\tau)s_0s_1s_2\ldots s_{i-1} \) where \( \tau \) is the respective time interval. This will lead to Euler-Lotka equation for continuous system. However we will use alternative way to do it by application of the replicator dynamics. What happens when we describe the system in related
frequencies \( a_i = \frac{n_i}{\sum_j n_j} \) and a scaling parameter (see Appendix b)? We obtain the following system:

\[
\dot{a}_i = a_{i-1}s_{i-1} - a_i \left( \sum_{i=1}^{m} a_i (f_i + s_i) \right) \quad \text{for} \quad i = 1, \ldots, m, \quad (9)
\]

\[
\dot{n} = n \left( \sum_{i=0}^{m} a_i (f_i + s_i) - 1 \right), \quad (10)
\]

where \( a_0 = 1 - \sum_{i=1}^{m} a_i \) and the malthusian parameter is \( r = \sum_{i=1}^{m} a_i (f_i + s_i) - 1 \). For a detailed derivation see Appendix B. For the system (9) the following steady state can be calculated:

\[
a_1 = \frac{a_0 s_0}{\sum_{i=0}^{m} a_i (f_i + s_i)},
\]

\[
a_2 = \frac{a_0^2 s_0 s_1 \left( \sum_{i=0}^{m} a_i (f_i + s_i) \right)^2 \ldots}{\left( \sum_{i=0}^{m} a_i (f_i + s_i) \right)^2},
\]

\[
\ldots
\]

\[
a_i = \frac{a_0 \prod_{j=0}^{i-1} s_j}{\left( \sum_{i=0}^{m} a_i (f_i + s_i) \right)^i},
\]

\[
\ldots
\]

In addition in state (11) Euler-Lotka equation is satisfied (for a derivation and proof, see Appendix C). The above model is the continuous equivalent of the basic approach related to the Leslie matrices used in life history modelling. According to this theory natural selection promote strategies which maximize \( r \) (which is the root of the Euler-Lotka equation). However, in the above model there is no explicit density dependence. It is hard to imagine the unlimited growth of the population indicated by this model. In addition, the problem of a universal fitness measure is more complicated when density dependence is explicitly considered. Thus our model should be develop further.

### 0.3 The impact of density dependence

To explicitly model density dependence we can apply a selectively neutral mechanistic approach from evolutionary games (Argasinski and Kozłowski, 2008; Argasinski and Broom, 2012) which is related to a modification of the classical logistic growth (Kozłowski 1980, Kuno 1991, Ginzburg 1992, Gabriel 2005, Hui 2006, Argasinski and Kozłowski 2008). This constitutes the eco-evolutionary feedback affecting the fitness (Argasinski and Kozłowski, 2008; Zhang and Hui,
This approach is closer to current developments in the evolutionary theory focused on the relationship of selection processes with ecological factors (Schoener 2011, Morris 2011, Pelletier et al. 2009). In this approach each fecundity should be multiplied by the logistic suppression coefficient \( \left( 1 - \frac{n}{K} \right) \) describing the survival of newborns introduced to the environment (where the carrying capacity \( K \) is interpreted as the maximal environmental load, Hui 2006). As was shown in Argasinski and Broom (2013), at population size equilibrium density dependent growth equation can be expressed in terms of the turnover coefficient (i.e. the number of newborns per single dead individual during \( \Delta t \)). If there are other strategies in the population, this induces a frequency dependent selection mechanism called the nest site lottery in Argasinski and Broom (2013).

The same reasoning can be applied to the age structured model. The above model describes a homogenous population divided only by age classes. Thus according to frequency dependent selection, a corresponding model of this type should be presented for each strategy present in the population, since frequency dependence needs information about the state of the whole population. However, in the case of the nest site lottery mechanism, the value of the turnover coefficient for the general population is sufficient. Thus our model will be extended to the density dependent case by the assumption that there are other strategies in the population (but not explicitly considered in the model) and their presence affects the dynamics of our model via a phenomenological parameter describing average turnover coefficient in the general population.

Now, let us calculate the turnover coefficient describing the number of newborns introduced into the population per single dead individual removed from the population during \( \Delta t \). Then \( F = \sum_{i=0}^{m} a_i f_i \) is the total number of newborns with the focal strategy introduced to the population and \( T = \sum_{i=0}^{m} a_i (1 - s_i) \) is the number of dead individuals of the focal strategy removed from the population (Argasinski and Broom, 2013). Assume that the subpopulation of the carriers of the focal strategy is the part of some general population described phenomenologically by total population is of size \( n_{pop} \) and the average turnover coefficient is \( L_{pop} = \frac{F_{pop}}{T_{pop}} \) (where \( F_{pop} \) is the total number of newborns and \( T_{pop} \) is the total number of dead individuals in the whole population during \( \Delta t \)). Thus the turnover coefficient for some individual strategy \( s \) will be:

\[
L \left( f(t), s(t) \right) = \frac{F}{T} = \frac{\sum_{i=0}^{m} a_i f_i}{\sum_{i=0}^{m} a_i (1 - s_i)},
\]

and the equation on the scaling parameter for equation (10) describing the growth of the population of carriers of this strategy can be presented as
\[
\dot{n} = n\left(1 - \frac{n_{\text{pop}}}{K}\right)\sum_{i=0}^{m} a_i f_i - \sum_{i=0}^{m} a_i (1 - s_i) \right)
\]

\[
= n \sum_{i=0}^{m} a_i (1 - s_i) \left(\frac{1 - \frac{n_{\text{pop}}}{K}}{\sum_{i=0}^{m} a_i (1 - s_i)} - 1\right)
\]

\[
= n \left(L(f(t), s(t))\left(1 - \frac{n_{\text{pop}}}{K}\right) - 1\right) \sum_{i=0}^{m} a_i (1 - s_i)
\]

(13)

(14)

(15)

However, here we have an age structured population. When we assume that the population is at the stable age structure, then the turnover coefficient has the form:

\[
L(f(t), s(t)) = \frac{\sum_{i=0}^{m} \prod_{j=0}^{i-1} s_j f_i (1 + r)^{m-i}}{\sum_{i=0}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (1 - s_i)}
\]

(16)

and the growth equation can be presented as follows (see Appendix D for a detailed derivation):

\[
\dot{n} = n_0 \left(L(f(t), s(t))\left(1 - \frac{n_{\text{pop}}}{K}\right) - 1\right) \sum_{i=1}^{m} \prod_{j=0}^{i-1} \frac{s_i}{(1 + r)^j} (1 - s_i).
\]

(17)

It was shown in (Argasinski and Broom 2013) that when the population reaches a stable size then frequency dependent selection emerges on individual strategies. This is the nest site lottery mechanism (Argasinski and Broom 2013) related to the turnover of individuals. Each newborn introduced to the environment should find a nesting place. At the population equilibrium size all newborns produced by all strategies compete for free places released by dead adult individuals. In effect each newborn can be drawn from the pool of candidates with probability \(F/F_{\text{pop}}\) to replace a dead adult and during time \(\Delta t\) there will be \(T\) trials. Thus survival probability of a single newborn equals the number of all dead individuals during time \(\Delta t\) (in the number of free places) divided by number of newborns introduced (number of candidates) i.e. which becomes the reciprocal of the turnover coefficient of the whole population \(\frac{1}{L_{\text{pop}}}\). Thus we have:

\[
\dot{n} = n_0 \left(L(f_i(t), s_i(t))_{L_{\text{pop}}(t)} - 1\right) \sum_{i=1}^{m} \prod_{j=0}^{i-1} \frac{s_i}{(1 + r)^j} (1 - s_i).
\]

(18)

Thus for an \(L\)-maximizing strategy it is profitable to maximize \(T = \sum_{i=1}^{m} \prod_{j=0}^{i-1} \frac{s_i}{(1 + r)^j} (1 - s_i)\).
Note that for $r = 0$ $L$ reduces to the lifetime reproduction $\sum_{i=0}^{m} \prod_{j=0}^{i-1} s_{j} f_{i}$, because $\sum_{i=0}^{m} \prod_{j=0}^{i} s_{j} = 1$. The structure from (Argasinski and Broom 2013) works and juvenile mortality will be $1/L \left( \tilde{f}(t), \tilde{s}(t) \right)$. However, at (Argasinski and Broom 2013) strategies are constant two-dimensional vectors, while here we have age depended fecundity and survival. Thus the turnover coefficient depends on the age structure of the carrier population of the respective strategy. Arguments of $L \left( f(t), s(t) \right)$ are sums or integrals $\sum_{i=0}^{m} a_{i} f_{i}$ and $\sum_{i=0}^{m} a_{i} s_{i}$ but the nest site lottery works in the same way. Thus at first stage the turnover coefficient

$$L \left( f(t), s(t) \right) = \frac{\sum_{i=0}^{m} \prod_{j=0}^{i-1} s_{j} f_{i} (1 + r)^{m-i}}{\sum_{i=0}^{m} \prod_{j=0}^{i-1} s_{j} (1 + r)^{m-i} (1 - s_{i})}$$

should be maximized. Subsequently, among $L$-maximizers

$$T = \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_{i} (1 + r)^{-i} (1 - s_{i})$$

should be maximized. Note that younger age classes gave greater weight $(1 + r)^{m-i}$ for $L$ and $(1 + r)^{-i}$ for $T$. The average lifetime is

$$\sum_{i=1}^{m} \prod_{j=0}^{i-1} s_{j} (1 - s_{i}) i,$$

and so increase in $T$ will lead to decrease in the average lifetime.

To use the nest site lottery mechanism, we need information about the turnover coefficient of the whole population $L_{\text{pop}}$, in this section assumed phenomenologically. To provide this information we need the model of the age structure of each strategy in the population. In effect the model will be extremely complicated. However, even the age structured model of the homogeneous population is too complicated to be practical. Every time moment $\Delta t$ in the lifetime of the individual should be described by a separate equation. A realistic model would contain hundreds or thousands of equations. This should be simplified before diversity among strategies is introduced into our framework. This is the task for the next section.

1 The behavioural and demographic timescales

In game theoretic models there is a distinction between behavioural and evolutionary timescales (Vincent and Brown 2005, Krivan and Cressman 2009). There is the possible situation when the behavioural process operates on a different timescale to life history (demographic) dynamics. Generally, we can assume that demographic dynamics is shaped by aggregated outcomes of interaction.
events that occur on the behavioural timescale. For example during a few days individual interactions may cause the population to significantly change, while differences between different age classes may be measured in years. During the time period referred to as an age class, an individual can perform several mating events and other activities with a mortality risk. For technical reasons we shall define “age class” as a long time period divided into small age sub-classes operating in the behavioural time-scale when an interaction may occur. Assume that probabilities of death and reproduction are constant during long age class, which are sub-divided into small age sub-classes where individuals do not differ in payoffs. Under this assumption we can significantly reduce the number of equations by considering only the large age classes, with \( N_v = n_g + ... + n_k \), where small age class \( g \) is the first, and small age class \( k \) is the last, of the sub-classes of larger age class \( v \). We can assume that all small age classes inside long age class are in equilibrium (11). In effect system (8) has the form (for a detailed derivation see Appendix E):

\[
\dot{N}_0 = N_0 \left( \sum_i \frac{N_i}{N_0} f_i - (1 - s_0) - D(s_0) \right), \quad (20)
\]

\[
\dot{N}_v = N_v \left( \frac{N_{v-1}}{N_v} D(s_{v-1}) - (1 - s_v) - D(s_v) \right), \quad (21)
\]

where

\[
D(s_v) = \frac{s_v^{k-g}}{\sum_{i=1}^{k-g} s_v^{i-1} (\sum_{i=0}^{m} a_i (f_i + s_i))^{k-g-i}}
\]

describes the fraction of individuals passing to the next large age class (\( h_v \) is the number of small age classes within the \( v \)-th long age class, i.e. its “length”).

1.1 Frequency dynamics for large age classes

Now we can transform system (21) to the related frequencies \( A_i = \frac{N_i}{N} \). Obtained system will be analogous to (9,10), but described in coordinates \( A_i \) instead of \( a_i \). All parameters of the system, such growth \( r \) should be described in the new coordinates. Thus, when we average malthusian coefficients from equations (20,21) we obtain \( r = \sum_{i=1}^{m} A_i (f_i + s_i) - D(s_m) - 1 \), which is equivalent to the \( r \) from the previous section (\( D(s_m) \) describes dying survivors of the last \( m \)-th age class). In effect we obtain:
\[
\dot{A}_i = A_i \left( \frac{A_{i-1}}{A_i} D(s_{i-1}) - (1 - s_i) - D(s_i) - \sum_{i=1}^{m} A_i (f_i + s_i) + D(s_m) + 1 \right) 
\]

\[
= A_{i-1} D(s_{i-1}) + A_i \left[ s_i - D(s_i) - \sum_{i=1}^{m} A_i (f_i + s_i) + D(s_m) \right].
\]  

Analogously to equations (9) we have \( A_0 = \sum_{i=1}^{m} A_i \) and equation on scaling parameter:

\[
\dot{N} = N \left( \sum_{i=1}^{m} A_i (f_i + s_i) - D(s_m) - 1 \right).
\]

Equilibrium of this system should satisfy the following condition:

\[
A_i = A_{i-1} D(s_{i-1}) + d_i + r = \frac{A_{i-1} D(s_{i-1})}{D(s_i) - s_i + \sum_{i=1}^{m} A_i (f_i + s_i) - D(s_m)}
\]

which can be presented in the form:

\[
A_i = \frac{A_0 \prod_{z=0}^{i-1} D(s_z)}{\prod_{z=1}^{i} [D(s_z) - s_z + \sum_{z=1}^{m} A_z (f_z + s_z) + D(s_m)]}.
\]

Since the sum of the \( A_i \) terms equals 1, we have:

\[
A_0 = \frac{1}{\prod_{z=0}^{i-1} D(s_z)}.
\]  

1.2 Extension to multipopulation replicator dynamics

Now we can incorporate the above model into a multipopulation evolutionary game (see Appendix A for details of the applied methods). Assume that we have \( w \) strategies and \( m + 1 \) age classes indexed from 0 to \( m \). Assume that the upper index describes the number of age class and the lower index describes the number of the strategy, \( p \) describes the strategy (phenotype) fraction and \( a \)
describes the related size of the age class. Thus, \( f_j^i \) and \( s_j^i \) describe, respectively, the fertility and survival of the \( j \)-strategist in age class \( i \). Two perspectives are possible (see fig 1):

a) First problem is the impact of the age structure in subpopulations strategically homogenous on selection of the strategies. It can be described by coordinates:

\[
A_x^0, ..., A_x^m \quad \text{for } x = 1, ..., m \quad \text{the age structure of the } x\text{-strategists subpopulation},
\]

\[
p_1, ..., p_w \quad \text{the strategy frequencies in the whole population}
\]

b) The second approach is focused on how strategic selection within each age class affects the age structure of the overall population. It can be described by coordinates:

\[
p^x_1, ..., p^x_w \quad \text{for } x = 1, ..., m \quad \text{strategy frequencies in age class } x,
\]

\[
A^1, ..., A^m \quad \text{the age structure of the population}
\]

Now we describe the transition of coordinates between both formulations. First we should define the auxiliary canonical metasimplex coordinates (see appendix A which is a single simplex without division into subclasses):

\[
q^x_i = A_x p^x_i = p_i A^x_i.
\]

Now according to the Appendix A we can define transitions between the two systems:

a to b:

\[
p^x = [p^x_1, ..., p^x_w] = \left[ \frac{A^x_1 p_1}{\sum_{z=1}^w A^x_z p_z}, ..., \frac{A^x_w p_w}{\sum_{z=1}^w A^x_z p_z} \right] \quad (28)
\]

\[
A = \left[ \sum_{z=1}^m A^z_1 p_z, ..., \sum_{z=1}^m A^z_w p_z \right], \quad (29)
\]

and b to a:

\[
A_x = [A_x^1, ..., A_x^m] = \left[ \frac{A^0_1 p^0_1}{\sum_{z=0}^m A^z_1 p^z_1}, ..., \frac{A^m_1 p^m_1}{\sum_{z=0}^m A^z_1 p^z_1} \right] \quad (30)
\]

\[
p = \left[ \sum_{z=0}^m A^z p^z_1, ..., \sum_{z=0}^m A^z p^z_w \right]. \quad (31)
\]

Now let us derive systems of equations operating in both coordinates.
For system a (see Appendix F for detailed derivation):

\[
A^i_j = A^{i-1}_j D(s^{i-1}_j) + A^i_j \left[ s^i_j - D(s^i_j) - \left( \tilde{f}_j \left(1 - \frac{N}{K}\right) + \bar{s}_j - D(s^m_j) \right) \right] \tag{32} \\
\dot{p}_j = p_j \left( (\tilde{f}_j - \bar{f}) \left(1 - \frac{N}{K}\right) + (\bar{s}_j - \bar{s}) - (A^m_j D(s^m_j) - \bar{D}_global^m) \right), \text{ or } \tag{33} \\
\dot{p}_j = p_j \left( (\tilde{f}_j - \bar{f}) \left(1 - \frac{N}{K}\right) - (\bar{d}_j - \bar{d}) - (A^m_j D(s^m_j) - \bar{D}_global^m) \right), \tag{34}
\]

and the equation on the scaling parameter

\[
\dot{N} = N \left( \bar{f} \left(1 - \frac{N}{K}\right) + \bar{s} - \bar{D}_global^m - 1 \right), \tag{35}
\]

where \( \bar{f}_j = \sum_{i=1}^{m} A^i_j f^i_j \), \( \bar{f} = \sum_{j=1}^{w} p_j \bar{f}_j \), \( \bar{s}_j = \sum_{i=1}^{m} A^i_j s^i_j \), \( \bar{s} = \sum_{i=1}^{w} p_i \bar{s}_i \), \( \bar{D}_global^m = \sum_{j=1}^{w} p_j A^m_j D(s^m_j) \).

For system b (see Appendix G for a detailed derivation):

\[
\dot{p}^0_j = \frac{1}{A^0} \left( \sum_i A^i p^i_j f^i_j - p^0_j \sum_i A^i \sum_v p^i_v f^i_v \right) \left(1 - \frac{N}{K}\right) + p^0_j \left[ (s^0_j - \bar{s}^0) - (D(s^0_j) - \bar{D}^0) \right], \tag{36} \\
\dot{p}_j^i = \frac{A^{i-1}}{A^i} \left( p_j^{i-1} D(s^{i-1}_j) - p_j^i \bar{D}^{i-1} \right) + p_j^i \left[ (s^i_j - \bar{s}^i) - (D(s^i_j) - \bar{D}^i) \right], \tag{37} \\
\dot{A}^i = A^{i-1} \bar{D}^{i-1} + A^i \left[ \bar{s}^i - \bar{D}^i - \left( \bar{s} + \bar{f} \left(1 - \frac{N}{K}\right) - \bar{D}_global^m \right) \right], \tag{38}
\]

and the equation on the scaling parameter

\[
\dot{N} = N \left( \bar{f} \left(1 - \frac{N}{K}\right) + \bar{s} - \bar{D}_global^m - 1 \right) \tag{39} 
\]

where \( \bar{D}^{i-1} = \sum_{j=1}^{w} p_j^i D(s^{i-1}_j) \), \( \bar{D}^i = \sum_{v=1}^{w} p^i_v D(s^i_v) \), \( \bar{D}_global^m = A^m \bar{D}^m \)

\[
\bar{s}^i = \sum_{v=1}^{w} p^i_v s^i_v \quad \bar{s} = \sum_{v=1}^{m} A^v \bar{s}^v \\
\bar{f}^i = \sum_{v=1}^{w} p^i_v f^i_v \quad \bar{f} = \sum_{v=1}^{m} A^v \bar{f}^v.
\]

Note that \( \bar{D}^i \) is the average number of survivors of the \( i \)-th age class per single \( i \) aged individual, while \( \bar{D}_global^m \) is the average number of individuals that survived the last, \( m \)-th age class (and will die afterwards) per single individual in
the whole population. Both systems have the same equation on scaling parameter which is equivalent to (24). In effect in both cases equilibrium population size is:

\[
1 - \frac{N}{K} = \frac{1 + \bar{D}_m^{global} - \bar{s}}{f}
\]

\[
N = K \left( 1 - \frac{1 + \bar{D}_m^{global} - \bar{s}}{f} \right)
\]

1.3 Background fitness and neutral density dependence

In this section let us consider the selective neutral (i.e. the same for all strategies) factors and their impact on the dynamics. One of such factors is the neutral density dependence (Argasinski Kozlowski 2008, Argasinski Broom 2012, Argasinski Broom 2013a, Argasinski Broom 2013b). According to this approach we can assume that each newborn should find a nest site to live and reproduce. The probability of finding a nest site (in effect newborn survival probability) is proportional to the fraction of free places and can be described by logistic suppression coefficient \(\left(1 - \frac{N}{K}\right)\), where \(K\) is the carrying capacity (number of nest places). Thus each newborn can survive with probability \(\left(1 - \frac{N}{K}\right)\). Therefore every fecundity should be multiplied by \(\left(1 - \frac{N}{K}\right)\). The case of background fertility and mortality is more complicated. In (Argasinski Broom 2013b) a more realistic approach to the background fitness (fertility and mortality caused by other events than the game interactions). It relies on the assumption that some number of newborns can be produced and some number of adults can be killed during other activities (i.e. background events). We can assume that there is a background fertility and mortality acting at the same rate for all individuals, in this case those factors will appear only in the equation on scaling parameter. Assumption that there are factors acting in the same way on the individual in the every age is biologically unrealistic. It is more realistic to assume that outcomes of the background events should be the same for all strategies, but they should be different for different age classes. Thus we can assume that within each age class there is background fertility \(\Phi^i\) \(\left(1 - \frac{N}{K}\right)\) and background mortality \(\Psi^i\). According to the equations (4,5,6) each additive factor included to the growth equation (1), in replicator equations (2) will appear as the bracketed term describing the excess of the value of this factor from the averaged value of that factor in the population. Respectively, after division of the population into subpopulations, the intraspecific dynamics will contain the bracketed term describing the the excess of the factor value \(r\) from the averaged factor valuer
in that subpopulation (see 5), while dynamics of the subpopulation relative size will contain term describing the excess of the average factor value in the respective subpopulation from the average factor value in whole population (6). Thus according to these relations we can derive the terms describing the impact of the factor $\Phi^i - \Psi^i$, i.e. age specific background fertility and mortality on the dynamics.

Let us begin from the system a:

$$\dot{N}_0 = N_0 \left( \sum_i \frac{N_i}{N_0} f_i - (1 - s_0) - D(s_0) \right)$$

$$\dot{N}_v = N_v \left( \frac{N_{v-1}}{N_v} D(s_{v-1}) - (1 - s_v) - D(s_v) \right)$$

In subsystem (32) there are no equation on the age class $A_{0j}$ which is influenced by aggregated fertility $\sum_{i=1}^m A_{ij} \Phi^i$, thus additional term will be

$$-\Psi_i - \sum_{i=1}^m A_{ij} \left( \Phi^i - \Psi^i \right) = -\Psi_i - \left( \sum_{i=1}^m A_{ij} \Phi^i - \sum_{i=1}^m A_{ij} \Psi^i \right)$$

(40)

In subsystem (33)

$$\sum_{i=1}^m A_{ij} \Phi^i - \sum_{i=1}^m A_{ij} \Psi^i - \sum p_j \left( \sum_{i=1}^m A_{ij} \Phi^i - \sum_{i=1}^m A_{ij} \Psi^i \right)$$

(41)

$$= \left( \sum_{i=1}^m A_{ij} \Phi^i - \sum p_j \sum_{i=1}^m A_{ij} \Phi^i \right) - \left( \sum_{i=1}^m A_{ij} \Psi^i - \sum p_j \sum_{i=1}^m A_{ij} \Psi^i \right)$$

(42)

and in equation on scaling parameter (43)

$$\sum p_j \left( \sum_{i=1}^m A_{ij} \Phi^i - \sum_{i=1}^m A_{ij} \Psi^i \right)$$

In the case of system b.

For equations (36) individual background fitness can be described as average per capita number of introduced newborns $\frac{N_j}{N_0} \sum_{i=1}^m A_{ij} \Phi^i$ per single newborn present in the age class 0, and specific newborn background mortality $\Psi^0$. Since according to (30) $\frac{N_j}{N_0} = \frac{1}{A_{j0}} = \frac{1}{A_{j0}} \sum_{j=0}^m A_{j0} p_j^0$ and per capita number of newborns will be:
\[
\frac{N_j}{N_0} \sum_{i=1}^{m} A_i^j \Phi^i = \sum_{i=1}^{m} \frac{A_i^j p_j^0}{A^0 p_j^0} \Phi^i
\]  
(44)

the bracketed term for equations (36) will be

\[
\sum_{i=1}^{m} \frac{A_i^j p_j^0}{A^0 p_j^0} \Phi^i - \Psi^0 - \sum_{k=1}^{w} p_k^0 \left( \sum_{i=1}^{m} \frac{A_i^j p_k^0}{A^0 p_k^0} \Phi^i - \Psi^0 \right)
\]  
(46)

\[
= \sum_{i=1}^{m} \frac{A_i^j p_j^0}{A^0 p_j^0} \Phi^i - \sum_{k=1}^{w} \sum_{i=1}^{m} \frac{A_i^j p_k^0}{A^0} \Phi^i
\]  
(47)

Respectively for equations (37) there are no direct impact of fertility and we have specific age dependent mortality \(\Psi^i\) the same for all strategies, thus it is selectively neutral (the bracketed term is 0). For equations (38) we have impact of aggregated fertility only in newborns age class 0 and in the next age classes acts only specific age dependent mortality \(\Psi^i\). Since class 0 is not explicitly described in the subsystem (38), the bracketed term will be:

\[
\Psi^i - \left( A_i^0 \sum_{k=1}^{w} p_k^0 \left( \sum_{i=1}^{m} \frac{A_i^j p_k^0}{A^0 p_k^0} \Phi^i - \Psi^0 \right) - \sum_{i=1}^{m} A_i^i \Psi^i \right)
\]  
(48)

\[
= \Psi^i - \left( \sum_{k=1}^{w} \sum_{i=1}^{m} A_i^j p_k^0 \Phi^i - \sum_{i=0}^{m} A_i^i \Psi^i \right)
\]  
(49)

\[
= \Psi^i - \left( \sum_{i=1}^{m} A_i^i \Phi^i - \sum_{i=0}^{m} A_i^i \Psi^i \right)
\]  
(50)

In equation on scaling parameter (39) should be added:

\[
\sum_{i=1}^{m} A_i^i \Phi^i - \sum_{i=0}^{m} A_i^i \Psi^i
\]  
(51)

To consider the neutral density dependence fertility factors \(\Phi^i\) should be multiplied by logistic coefficient \(1 - \frac{N}{K}\).

But in the equations we have also operator \(D\). Another decay channel driven by background mortality pressure should be represented in the argument of \(D\). Thus we should calculate the per capita fraction of survivors introduced
to the next short age class. The problem is that in this case we have two types of mortality operating at different rates, thus we cannot reduce this to the simple subtraction from 1. Let us consider a simplified equation containing only mortality components \( \dot{n} = n \left[ \tau_1 (1 - s) + \tau_1 (1 - b) \right] \).

Thus we can use first order Taylor expansion to derive approximation of the fraction of survivors passing to the next age class:

\[
n(t_0 + \Delta t) = n(t_0) + \dot{n}(t_0) \Delta t = n(t_0) - n(t_0) \left[ \tau_1 (1 - s) + \tau_1 (1 - b) \right] \Delta t
\]

\[
= n(t_0) \left( 1 - \left( 1 - s_i \right) + \frac{\tau_2}{\tau_1} (1 - b) \right) \tau_1 \Delta t.
\]

When \( \tau_1 \Delta t \) is set to 1 by change of the timescale \( \tilde{t} = t / \tau_1 t \), then we obtain:

\[
n(t_0 + \Delta t) = n(t_0) \left( 1 - \left[ \left( 1 - s_i \right) + \frac{\tau_2}{\tau_1} (1 - b_2) \right] \right)
\]

And fraction of survivors can be approximated by \( s_i - \Psi \) where \( \Psi = \frac{\tau_2}{\tau_1} (1 - b_2) \).

After insertion of the terms \( 40, 42, 43 \) system a will have form:

system a:

\[
\dot{A}_j = A_j^{-1} D (s_j^{-1} - \Psi) + A_j^i [s_j^i - \Psi^i - D (s_j^i - \Psi^i)]
\]

\[
- \left( \sum_{i=1}^{m} A_j^i \left( f_j^i \left( 1 - \frac{N}{K} \right) + s_j^i \right) - D(s_j^m - \Psi^i) \right) - \left( 1 - \frac{N}{K} \right) \sum_{i=1}^{m} A_j^i \Psi^i - \sum_{i=1}^{m} A_j^i \Psi^i \right) \right]
\]

\[
\hat{p}_j = p_j \left[ \left( \overline{f}_j - f \right) + \left( \sum_{i=1}^{m} A_j^i \Phi^i - \sum_{i=1}^{m} p_j \sum_{i=1}^{m} A_j^i \Phi^i \right) \right] \left( 1 - \frac{N}{K} \right)
\]

\[
+ (s_j - s) - (A_j^m D(s_j^m - \Psi^m) - \overline{D}_{global}^m) - \left( \sum_{i=1}^{m} A_j^i \Psi^i - \sum_{j=1}^{w} p_j \sum_{i=1}^{m} A_j^i \Psi^i \right) \right)
\]

and equation on scaling parameter

\[
\hat{N} = N \sum_{j=1}^{w} p_j \left( \sum_{i=1}^{m} A_j^i \left( f_j^i \left( 1 - \frac{N}{K} \right) + s_j^i \right) - A_j^m D(s_j^m - \Psi^m) - 1 \right)
\]

\[
+ \sum_{j} p_j \left( \left( 1 - \frac{N}{K} \right) \sum_{i=1}^{m} A_j^i \Phi^i - \sum_{i=1}^{m} A_j^i \Psi^i \right) \right) =
\]

\[
N \left( \overline{f} \left( 1 - \frac{N}{K} \right) + \bar{s} - \bar{D}_{global}^m - 1 + \sum_{j} p_j \left( \left( 1 - \frac{N}{K} \right) \sum_{i=1}^{m} A_j^i \Phi^i - \sum_{i=1}^{m} A_j^i \Psi^i \right) \right)
\]
For system b (see appendix F for detailed derivation):

\begin{align}
\dot{p}_j^0 &= \frac{1}{A^0} \left[ \left( \sum_i A^i p_j^i f_j^i - p_j^0 \sum_i A^i \sum v p_i^i f_v^i \right) + \left( \sum_{i=1}^m A^i \Phi_i^i - p_j^0 \sum_{i=1}^m A^i \sum_k p_k^i \Phi^i \right) \right] \\
&\quad \left( 1 - \frac{N}{K} \right) + p_j^0 \left( s_j^0 - \bar{s}^0 \right) + \left( D(s_j^0) - \bar{D}^0 \right) \\
&\quad \left( 1 - \frac{N}{K} \right) + p_j^0 \left( s_j^0 - \bar{s}^0 \right) + \left( D(s_j^0) - \bar{D}^0 \right) \\
&= \frac{A_i^{i-1}}{A_i} \left( p_j^{i-1} D(s_j^{i-1} - \Psi^{i-1}) - p_j^i \bar{D}^{i-1} \right) + p_j^i \left[ (s_j^i - \bar{s}^i) + \left( D(s_j^i - \Psi^{i-1}) - \bar{D}^i \right) \right] \\
&= A_i^{i-1} \bar{D}^{i-1} + \\
&\quad A_i^i \left[ \bar{s}^i - \bar{D}^i - \left( \bar{s} + \bar{f} \left( 1 - \frac{N}{K} \right) - A^m \bar{D}^m \right) \right] - \left( \bar{\Psi}^i - \left( \sum_{i=1}^m A^i \Phi^i \left( 1 - \frac{N}{K} \right) - \sum_{i=0}^m A^i \Phi^i \right) \right) \\
&= \bar{N} \left( \bar{f} + \bar{s} - \bar{D}^m_{global} - 1 + \sum_{i=1}^m A^i \Phi^i \left( 1 - \frac{N}{K} \right) - \sum_{i=0}^m A^i \Phi^i \right)
\end{align}

bo indeksowane od 1 to nie ma zerowej klasy i fertility per capita and equation on scaling parameter

1.3.1 Discussion

In this work was presented a new modelling framework combining evolutionary dynamics with demographic structure. This approach can be useful tool in the development of the synthesis between evolutionary game theory and life history theory. The obtained results clearly show that life cycle perspective plays crucial role in the evolutionary processes. In the classical approaches to the evolutionary game theory individuals cannot change the properties during the lifetime. Thus their life history is the memoryless process, survival of the single interaction does not change the state of the individual. This is caused by the fact that the classical approaches to the evolutionary games are focused on the strategies interpreted as the patterns of behaviour, not on individuals itself. The exception from this rule is the state based approach (Houston McNamara 1999). The new approach presented in this paper is the natural background for the dynamic extension of the state based approach.
Appendix A Change of coordinates in the space of population states.

Assume that we want to decompose an entire population into \( z \) subgroups. Define

\[
d^i = [d^i_1, ..., d^i_{u_i}]
\]

as a vector of indexes of strategies exhibited by individuals from \( i \)-th subgroup \((d^i_j \in \{1, ..., u_i\}, u_i \text{ number of strategies in the } i \text{-th subgroup})\). For example notation \( d^2 = [1, 3, 5] \) means, that in second subgroup there are individuals with strategies 1, 3 and 5. Every strategy should belong to a single unique subgroup (and cannot belong to two). Then according to Argasinski (2006), by the following change of coordinates:

\[
l^{i} = \left[ \frac{q^{d_{1}^{i}}}{\sum_{j=1}^{u_{i}} q^{d_{j}^{i}}}, ..., \frac{q^{d_{u_{i}}^{i}}}{\sum_{j=1}^{u_{i}} q^{d_{j}^{i}}} \right] \quad \text{for } i = 1, ..., z
\]

we obtain distribution of relative frequencies of strategies in the \( i \)-th subpopulation. Distribution of proportions between subpopulations has the form:

\[
p = [p_1, ..., p_z] = \left[ \sum_{i=1}^{u_1} q_{d_1}^i, ..., \sum_{i=1}^{u_z} q_{d_z}^i \right]
\]

where \( p_i \) is the proportion of the \( i \)-th subpopulation. Every decomposition into subpopulations can be reduced again to a single population model by the opposite change of coordinates \( q(p, q_1^1, ..., q_z^z) \) where:

\[
q_{d_j}^i = p_i q_j^i
\]

Note that we can decompose an entire population to \( z \) subpopulations. When we apply the above transformations to replicator equations, we obtain a set of equations that describes dynamics inside subpopulations (intraspecific dynamics). Because the argument of a fitness function is a set of relative frequencies of all individuals \( q \) (without division to subpopulations), the opposite change of coordinates \( q(p, q_1^1, ..., q_z^z) \) should be applied (Argasinski 2006). When the set of strategies in each subpopulation is characterized by vector of indexes \( d^i \), then the system of replicator equations will be:

\[
\begin{align*}
\dot{q}^i_j &= q^i_j \left[ W^i_j(q(p, q^1, ..., q^z)) - \bar{W}^i(q(p, q^1, ..., q^z)) \right] \\
\text{for } j &= 1, ..., u_i - 1 \text{ and } i = 1, ..., z \\
\dot{p}_s &= p_s \left[ \bar{W}^s(q(p, q^1, ..., q^z)) - \bar{W}(q(p, q^1, ..., q^z)) \right] \\
\text{for } s &= 1, ..., z - 1
\end{align*}
\]

where \( \bar{W}^s(q) = \sum_{i=1}^{u_s} q_i W^s(q(p, q^1, ..., q^z)) \) is mean fitness in the \( s \)-th subpopulation. In simplified notation this system has form (57) In practical applications of this method to modeling of biological problems, replicator equations
can be defined on decomposed population. This will simplify the formulation of the model, because when strategies are initially assigned to subpopulations, then there is no need to change their indexes. Choice of subpopulations is arbitrary and depends on the biological assumptions underlying the analyzed problem. The entire population may be divided into two competing subpopulations of hosts and parasites or preys and predators. On the other hand, it may be divided into two subpopulations of males and females, then interspecific dynamics will describe the evolution of secondary sex ratio, and intraspecific dynamics will describe changes of frequencies of strategies inside male and female subpopulation. The entire population can be divided into more subpopulations than two. The subpopulations can be divided into subsubpopulations, and the entire population may be transformed into a complex multilevel cluster structure. However, all these structures are equivalent to a single population replicator dynamics model.

Appendix B Derivation of frequency equations

Initial system can be presented in the form of malthusian equations:

\[ \dot{n}_0 = \sum n_i f_i - n_0 = n_0 \left( \sum_{i=0}^{m} \frac{n_i f_i}{n_0} - 1 \right) \]

\[ \dot{n}_1 = s_0 n_0 - n_1 = n_1 \left( \frac{n_0 s_0}{n_1} - 1 \right) \]

... 

\[ \dot{n}_m = s_{m-1} n_{m-1} - n_m = n_m \left( \frac{n_{m-1} s_{m-1}}{n_m} - 1 \right) \]

therefore Malthusian growth coefficients \( M_i = \frac{n_{m-1} s_{m-1}}{n_m} - 1 \) of those equations can be presented as frequency dependent functions of age structure, where \( a_i = \frac{n_i}{n} \) where \( n = \sum_i n_i \) are frequencies among age classes. In effect we obtain:

\[ \dot{n}_0 = n_0 \left( \sum_{i=0}^{m} \frac{a_i f_i}{a_0} - 1 \right) \]

... 

\[ \dot{n}_i = n_i \left( \frac{a_{i-1} s_{i-1}}{a_i} - 1 \right) \]

... 

\[ \dot{n}_m = n_m \left( \frac{a_{m-1} s_{m-1}}{a_m} - 1 \right) \]

therefore, this system can be presented as system of frequency dependent replicator equations \( \dot{a}_i = a_i (M_i - r) \) and a single equation on scaling parameter \( \dot{n} = nr \). what we need is an average malthusian growth rate:
\[ r = a_0 \left( \sum_{i=0}^{m} \frac{a_i f_i}{a_0} - 1 \right) + \sum_{i=1}^{m} a_i \left( \frac{a_{i-1}s_{i-1}}{a_i} - 1 \right) = \]
\[ = \sum_{i=0}^{m} a_i f_i - a_0 + \sum_{i=1}^{m} (a_{i-1}s_{i-1} - a_i) \]
\[ = \sum_{i=0}^{m} a_i f_i + \sum_{i=1}^{m} a_{i-1}s_{i-1} - 1 = \sum_{i=0}^{m} a_i (f_i + s_i) - 1 \]

therefore we can formulate system of frequency dependent replicator equations by transforming eq. from 1 to m:

\[ \hat{a}_i = a_i \left( \frac{a_{i-1}s_{i-1}}{a_i} - \sum_{i=1}^{m} a_i (f_i + s_i) \right) = a_{i-1}s_{i-1} - a_i (\sum_{i=1}^{m} a_i (f_i + s_i)) \]

where \( a_0 = 1 - \sum_{i=1}^{m} a_i \) and equation on scaling parameter:

\[ \hat{n} = nr = n \left( \sum_{i=1}^{m} a_i (f_i + s_i) - 1 \right) \]

Appendix C Stationary age distribution and Euler-Lotka equation in the continuous case

Stationary points of this system are:

- for age structure:

\[ \frac{a_{i-1}s_{i-1}}{a_i} = \sum_{i=1}^{m} a_i (f_i + s_i) \quad \text{for } i \text{ to } m - 1 \]

therefore

\[ a_i = \frac{a_{i-1}s_{i-1}}{\sum_{i=1}^{m} a_i (f_i + s_i)} \]

which implies:

\[ a_1 = \frac{a_0s_0}{\sum_{i=1}^{m} a_i (f_i + s_i)} \]
\[ a_2 = \frac{a_0s_0s_1}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} \]

\[ \vdots \]
\[ a_i = \frac{a_0 \prod_{j=0}^{i-1} s_j}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} \]

and \( \sum_i a_i = 1 \) implies
1 (this is similar to Euler-Lotka equation)

\[ a_0 \left(1 + \frac{s_0}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 s_1}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \ldots + \frac{\prod_{j=0}^{i-1} s_j}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} + \ldots \right) = \]

\[ 1 \]

thus:

\[ a_0 = \frac{1}{1 + \frac{s_0}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 s_1}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \ldots + \frac{\prod_{j=0}^{i-1} s_j}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} + \ldots} \]

therefore stable age structure is unique vector of frequencies among age classes, conditional on average malthusian growth rate of the population. Now let us proof the equivalence with Euler-Lotka equation. After substitution of stable age frequencies to \( \dot{n}_0 = n_0 \left( \frac{\sum_{i=0}^{m} a_i f_i}{a_0} - 1 \right) \) equation we obtain:

\[ \dot{n}_0 = n_0 \left( \frac{1}{a_0} \left( a_0 f_0 + \frac{s_0 a_0 f_1}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 s_1 a_0 f_2}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \ldots + \frac{\prod_{j=0}^{i-1} s_j a_0 f_i}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} + \ldots \right) - 1 \right) = \]

\[ \dot{n}_0 = n_0 \left( f_0 + \frac{s_0 f_1}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 s_1 f_2}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \ldots + \frac{\prod_{j=0}^{i-1} s_j f_i}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} + \ldots - 1 \right) \]

frequency equilibrium implies that growth rates in all age classes are equal to the average growth rate \( \dot{A} = \sum_{i=1}^{m} a_i (f_i + s_i) - 1 \), which implies:

\[ f_0 + \frac{s_0 f_1}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 s_1 f_2}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \ldots + \frac{\prod_{j=0}^{i-1} s_j f_i}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} + \ldots - 1 = \sum_{i=1}^{m} a_i (f_i + s_i) - 1 \]

then

\[ \frac{f_0}{\sum_{i=1}^{m} a_i (f_i + s_i)} + \frac{s_0 f_1}{(\sum_{i=1}^{m} a_i (f_i + s_i))^2} + \frac{s_0 s_1 f_2}{(\sum_{i=1}^{m} a_i (f_i + s_i))^3} \]

\[ + \ldots + \frac{\prod_{j=0}^{i-1} s_j f_i}{(\sum_{i=1}^{m} a_i (f_i + s_i))^{i+1}} + \ldots = 1 \]
Form: $T$ mortality as coefficient we have (note that $1 + r = \sum_{i=1}^{m} a_i (f_i + s_i)$):

$$L(f(t), s(t)) = \frac{\sum_{i=0}^{m} a_0 \prod_{j=0}^{i-1} s_j f_i}{(\sum_{i=1}^{m} a_i (f_i + s_i))^i} = \frac{\sum_{i=0}^{m} a_0 \prod_{j=0}^{i-1} s_j f_i (1 + r)^{m-i}}{(1 + r)^m}$$

Analogously we can substitute the stable age structure to the growth equation (for simplicity without logistic suppresion coefficient):

$$\dot{n} = n \left( \sum_{i=1}^{m} a_0 \prod_{j=0}^{i-1} s_j (f_i + s_i - 1) \right) = \frac{\sum_{i=1}^{m} a_0 \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (f_i + s_i - 1)}{(1 + r)^m}$$

$$\frac{na_0}{(1 + r)^m} \left( \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j f_i (1 + r)^{m-i} + \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} s_i - \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (1 - s_i) \right) =$$

$$\frac{na_0}{(1 + r)^m} \left( \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j f_i (1 + r)^{m-i} - \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (1 - s_i) \right) =$$

for simplicity denote $F = \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j f_i (1 + r)^{m-i}$ and averaged per capita mortality as $T = \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (1 - s_i)$ in effect above equation have form:

$$\dot{n} = \frac{na_0}{(1 + r)^m} (F - T) = \frac{na_0}{(1 + r)^m} T \left( \frac{F}{T} - 1 \right) = \frac{na_0}{(1 + r)^m} T (L(f(t), s(t)) - 1)$$
because \( L(f(t), s(t)) = \frac{F}{T} \), when we remove the auxiliary notation and add the logistic suppression \( \left( 1 - \frac{n_{\text{pop}}}{K} \right) \) describing density dependent survival of the newborns, we have:

\[
\dot{n} = na_0 \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{m-i} (1 - s_i) \left( L(f(t), s(t)) \left( 1 - \frac{n_{\text{pop}}}{K} \right) - 1 \right)
\]

\[
= na_0 \left( L(f(t), s(t)) \left( 1 - \frac{n_{\text{pop}}}{K} \right) - 1 \right) \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_j (1 + r)^{-i} (1 - s_i)
\]

when we introduce the nest site lottery by assuming that population is in the equilibrium size, we obtain:

\[
\dot{n} = na_0 \left( \frac{L}{L_{\text{pop}}} - 1 \right) \sum_{i=1}^{m} \prod_{j=0}^{i-1} s_i (1 + r)^{i} (1 - s_i)
\]

**Appendix E Long age classes**

Assume that there are some number of small age classes where individuals did not differ in payoffs. Under this assumption we can significantly reduce number of age classes by substituting them by large age classes \( N_v = n_g + ... + n_k \)

\[
\dot{N}_v = (n_g + ... + n_k) = \dot{n}_{g+1} + \dot{n}_{g+2} + \dot{n}_{g+3} + ... + \dot{n}_m =
\]

\[
= \sum_{i=g}^{k} (s_i-1) n_{i-1} - n_i = s_{v-1} n_{g-1} - (1 - s_v) \sum_{i=g}^{k-1} n_i - n_k
\]

\[
= s_{v-1} n_{g-1} - (1 - s_v) \sum_{i=g}^{k} n_i - s_v n_k
\]

Therefore system can be presented in the form:

\[
\dot{N}_0 = \sum_i N_i f_i - (1 - s_0) N_0 - s_0 n_k \quad (59)
\]

\[
\dot{N}_v = s_{v-1} n_{g-1} - (1 - s_v) N_v - s_v n_k \quad (60)
\]

Now we can assume that inside of large age class system is in equilibrium \( \Box \) and simplify. Because \( a_i = \frac{n_i}{n} \) and that survivals \( s_v \) are the same inside each long age class, we have

\[
n_k = \frac{n_g s_v^{k-g-1}}{\left( \sum_{i=0}^{m} a_i (f_i + s_i) \right)^{k-g}} \quad (61)
\]
Now we can substitute small age class notation with long age classes. Because from (61) we have
\[
N_v = n_g + \ldots + n_k = n_g \sum_{i=1}^{k-g} \frac{s_v^{i-1}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^i}
\]
(62)

thus
\[
n_g = \frac{N_v}{\sum_{i=1}^{k-g} \frac{s_v^{i-1}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^i}}
\]
(63)

which substituted to (61) leads to:
\[
s_v n_k = \frac{N_v}{\sum_{i=1}^{k-g} \frac{s_v^{i-1}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^i}} \frac{s_v^{k-g}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^{k-g}} = N_v \frac{s_v^{k-g}}{\sum_{i=1}^{k-g} \frac{s_v^{i-1}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^{k-g}}}
\]
(64)

Thus coefficient \(D(s_v) = \frac{s_v^{k-g}}{\sum_{i=1}^{k-g} \frac{s_v^{i-1}}{(\sum_{i=0}^{m} a_i (f_i + s_i))^{k-g-i}}} \) describes fraction of individuals passing to next large age class. In effect equation (61) can be presented the form:
\[
\dot{N}_v = N_{v-1} D(s_{v-1}) - N_v (1 - s_v) - N_v D(s_v) = N_{v-1} D(s_{v-1}) - N_v (1 - s_v + D(s_v))
\]
(65)

where \(N_{v-1} D(s_{v-1})\) is entering from previous age class, \(N_v D(s_v)\) are surviving to the next age class and \(N_v (1 - s_v)\) die. \(k - g\) is the length of large age class and can be substituted by something. Assume that \(h_v = k - g\) is the length of \(v\)-th long age class, i.e. the number of small age classes. After simplification and transition into Malthusian form we obtain
\[
\dot{N}_0 = N_0 \left( \sum_i \frac{N_i}{N_0} f_i - (1 - s_0) - D(s_0) \right)
\]
\[
\dot{N}_v = N_v \left( \frac{N_{v-1}}{N_v} D(s_{v-1}) - (1 - s_v) - D(s_v) \right)
\]

**Appendix F Derivation of system a**

We start from the Malthusian system describing exponential in subpopulation of carriers of the \(j\)-th strategy:
\[ \dot{N}^0_j = N_j^0 \left( \sum_i \frac{N_i^j}{N_j^0} f_i^j - (1 - s_j^0) - D \left( s_j^0 \right) \right) \]

\[ \dot{N}^v_j = N_j^v \left( \frac{N_j^{v-1}}{N_j^v} D \left( s_j^{v-1} \right) - (1 - s_j^v) - D \left( s_j^v \right) \right) \]

According to (23) above system can be transformed into frequency replicator dynamics of age classes:

\[ \dot{A}_j^i = A_j^{i-1} D \left( s_j^{i-1} \right) + A_j^i \left[ s_j^i - D \left( s_j^i \right) - \sum_{i=1}^m A_j^i \left( f_j^i + s_j^i \right) + D(s_j^m) \right] \]

Malthusian equation describing growth of subpopulation of \( j \)-th strategists is \( N_j = \sum_i N_j^i \)

\[ \dot{N}_j = N_j^0 \left( \sum_i \frac{N_i^j}{N_j^0} f_j^i - (1 - s_j^0) - D \left( s_j^0 \right) \right) + \sum_{v=1}^m N_j^v \left( \frac{N_j^{v-1}}{N_j^v} D \left( s_j^{v-1} \right) - (1 - s_j^v) - D \left( s_j^v \right) \right) = \]

\[ = \sum_i N_j^i f_j^i - N_j^0 \left[ (1 - s_j^0) - D \left( s_j^0 \right) \right] + \sum_{v=1}^m N_j^{v-1} D \left( s_j^{v-1} \right) - \sum_{v=1}^m N_j^v \left( 1 - s_j^v \right) - \sum_{v=1}^m N_j^v D \left( s_j^v \right) = \]

\[ = \sum_i N_j^i f_j^i - \sum_{v=0}^m N_j^v \left( 1 - s_j^v \right) + \sum_{v=1}^m N_j^{v-1} D \left( s_j^{v-1} \right) - \sum_{v=0}^m N_j^v D \left( s_j^v \right) = \]

\[ = \sum_i N_j^i f_j^i - \sum_{v=0}^m N_j^v \left( 1 - s_j^v \right) \]

\[ = N_j \left( \sum_i A_j^i f_j^i - \sum_{v=0}^m A_j^v s_j^v \right) - A_j^m D \left( s_j^m \right) \]

and now we can formulate replicator dynamics describing evolution of the gene pool:

\[ \dot{p}_j = p_j \left( \sum_i A_j^i f_j^i + \sum_{v=0}^m A_j^v s_j^v - A_j^m D \left( s_j^m \right) - \sum_z p_z \left( \sum_i A_z^i f_z^i + \sum_{v=0}^m A_z^v s_z^v - A_z^m D \left( s_z^m \right) \right) \right) = \]

\[ = p_j \left( \left( \sum_i A_j^i f_j^i - \sum_z p_z \sum_i A_z^i f_z^i \right) + \left( \sum_{v=0}^m A_j^v s_j^v - \sum_z p_z \sum_{v=0}^m A_z^v s_z^v \right) - \left( A_j^m D \left( s_j^m \right) - \sum_z p_z A_z^m D \left( s_z^m \right) \right) \right) \]

therefore for system a it will have form

\[ \dot{A}_j^i = A_j^{i-1} D \left( s_j^{i-1} \right) + A_j^i \left[ s_j^i - D \left( s_j^i \right) - \left( \sum_{i=1}^m A_j^i \left( f_j^i + s_j^i \right) - D(s_j^m) \right) \right] \]
\[ \dot{p}_j = p_j \left( \bar{f}_j - \bar{f} \right) + (\bar{s}_j - \bar{s}) - (A^m_j D(s^m_j) - \sum_z p_z A_z^m D(s^m_z)) \]

and equation on scaling parameter

\[ \hat{N} = N \sum_{j=1}^{w} p_j \left( \sum_{i=1}^{m} A^i_j \left( f^i_j + s^i_j \right) - A^m_j D(s^m_j) - 1 \right) = N \left( \bar{f} + \bar{s} - \bar{D}_\text{global} - 1 \right) \]

where \( \bar{f}_j = \sum_{i=1}^{m} A^i_j f^i_j \quad \bar{f} = \sum_{j=1}^{w} p_j \bar{f}_j \quad \bar{s}_j = \sum_{i=1}^{m} A^i_j s^i_j \)

\[ \bar{s} = \sum_{i=1}^{w} p_i \bar{s}_i \quad \bar{D}_\text{global} = \sum_{j=1}^{w} p_j A^m_j D(s^m_j) \]

Then to add the neutral density dependence the fertilities should be multiplied by logistic suppression coefficient \( \left( 1 - \frac{N}{K} \right) \).

### Appendix G Derivation of system b

System b produces more complicated form of equations. Again let us start from malthusian equations:

\[
\begin{align*}
\dot{N}^0_j &= N^0_j \left( \sum_i \frac{N_i}{N_j} f^i_j - (1 - s^0_j) - D(s^0_j) \right) \quad \text{(66)} \\
\dot{N}^v_j &= N^v_j \left( \frac{N_j}{N_j} D(s^{v-1}_j) - (1 - s^v_j) - D(s^v_j) \right) \quad \text{(67)}
\end{align*}
\]

Let us derive malthusian equations describing growth of age classes in global population. Then \( N^i = \sum_j N^i_j \) and \( p^i_j = \frac{N^i_j}{N^i} \) since \( \dot{N}^i = \sum_j \dot{N}^i_j \)

\[
\begin{align*}
\dot{N}^0_j &= \sum_j N^0_j \left( \sum_i \frac{N_i}{N_j} f^i_j - (1 - s^0_j) - D(s^0_j) \right) = \sum_j \left( \sum_i N^0_i f^i_j - N^0_j (1 - s^0_j) - N^0_j D(s^0_j) \right) \\
&= \sum_j N^0_j f^i_j - \sum_j N^0_j (1 - s^0_j) - \sum_j N^0_j D(s^0_j)
\end{align*}
\]

because \( \sum_j N^0_j f^i_j = \sum_i N^i_j \sum_j p^0_j f^i_j = N^0 \sum_i \frac{N^i_j}{N^0} \sum_j p^0_j f^i_j = N^0 \sum_i \frac{A^i_j}{A^0} \sum_j p^0_j f^i_j \) above equation has form:

\[ \dot{N}^0 = N^0 \left( \sum_i \frac{A^i_j}{A^0} \sum_j p^0_j f^i_j - \sum_j p^0_j (1 - s^0_j) - \sum_j p^0_j D(s^0_j) \right) \]

analogously:
\[ N^v = \sum_j N_j^v \left( \frac{N_i^{v-1}}{N_i^v} D(s_j^{v-1}) - (1 - s_j^v) - D(s_j^v) \right) = \sum_j N_j^{v-1} D(s_j^{v-1}) - \sum_j N_j^v (1 - s_j^v) - \sum_j N_j^v D(s_j^v) \]

because \( \sum_j N_j^{v-1} D(s_j^{v-1}) = N^{v-1} \sum_j p_j^{v-1} D(s_j^{v-1}) = N^v \frac{N^{v-1}}{N^v} \sum_j p_j^{v-1} D(s_j^{v-1}) \)

above equation has form:

\[ N^v = N^v \left( \frac{A^{v-1}}{A^v} \sum_j p_j^{v-1} D(s_j^{v-1}) - \sum_j p_j^v (1 - s_j^v) - \sum_j p_j^v D(s_j^v) \right) \]

therefore we obtain system:

\[
\begin{align*}
\dot{N}^0 &= N^0 \left( \sum_i A_i^1 \sum_j p_j^i f_j^i + \sum_j p_j^0 s_j^0 - \sum_j p_j^0 D(s_j^0) - 1 \right) \\
\dot{N}^v &= N^v \left( \frac{A^{v-1}}{A^v} \sum_j p_j^{v-1} D(s_j^{v-1}) + \sum_j p_j^v s_j^v - \sum_j p_j^v D(s_j^v) - 1 \right)
\end{align*}
\]

(68) for each \( v \)

Now we can calculate Malthusian parameter:

\[
M = A^0 \left( \sum_i A_i^1 \sum_j p_j^i f_j^i + \sum_j p_j^0 s_j^0 - 1 - \sum_j p_j^0 D(s_j^0) \right) + \sum_{i=1}^n A^i \left( \sum_j p_j^{i-1} D(s_j^{i-1}) + \sum_j p_j^i s_j^i - 1 - \sum_j p_j^i D(s_j^i) \right) = \sum_i A^i \sum_j p_j^i f_j^i + A^0 \sum_j p_j^0 s_j^0 - A^0 - A^0 \sum_j p_j^0 D(s_j^0) + \sum_{i=1}^n A^i \sum_j p_j^{i-1} D(s_j^{i-1}) + \sum_{i=1}^n A^i \sum_j p_j^i s_j^i - \sum_{i=1}^n A^i \sum_j p_j^i D(s_j^i) = \sum_i A^i \sum_j p_j^i f_j^i - \sum_{i=0}^m A^i \sum_j p_j^i (1 - s_j^i) + \sum_{i=1}^m A^{i-1} \sum_j p_j^{i-1} D(s_j^{i-1}) - \sum_{i=0}^m A^i \sum_j p_j^i D(s_j^i) = \sum_i A^i \sum_j p_j^i (f_j^i + s_j^i) - A^m \sum_j p_j^m D(s_j^m) - 1
\]

Then we can derive replicator dynamics of global population age structure:

\[
A^v = A^v \left( \frac{A^{v-1}}{A^v} \sum_j p_j^{v-1} D(s_j^{v-1}) - \sum_j p_j^v (1 - s_j^v) - \sum_j p_j^v D(s_j^v) \right)
\]

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\(- \left( \sum_i A^i \sum_j p^i_j \left( f^i_j + s^i_j \right) - A^m \sum_j p^m_j D \left( s^m_j \right) - 1 \right) \) =
\[= A^{v-1} \sum_j p_j^{v-1} D \left( s_j^{v-1} \right) +
+ A^v \left( \sum_j p_j^v s_j^v - \sum_j p_j^v D \left( s_j^v \right) - \sum_i A^i \sum_j p_j^i \left( f_j^i + s_j^i \right) + A^m \sum_j p_j^m D \left( s_j^m \right) \right) =
\[= A^{v-1} \sum_j p_j^{v-1} D \left( s_j^{v-1} \right) +
+ A^v \left( \sum_j p_j^v \left( s_j^v - D \left( s_j^v \right) \right) - \left( \sum_i A^i \sum_j p_j^i \left( f_j^i + s_j^i \right) - A^m \sum_j p_j^m D \left( s_j^m \right) \right) \right) \]
then from malthusian parameters from equations (67) and (69) we can derive
dynamics of proportions of strategies inside age classes:

\[p_j^i = p_j^i \left( \left( \frac{N_{i-1}^i}{N_j^i} D \left( s_{j-1}^i \right) - \left( 1 - s_j^i \right) - D \left( s_j^i \right) \right) - \sum_j p_j^i \left( \frac{N_{i-1}^i}{N_j^i} D \left( s_{j-1}^i \right) - \left( 1 - s_j^i \right) - D \left( s_j^i \right) \right) \right) =
\]
because \(A^i p_j^i = N_j^i / N \) (see appendix A)
\[= p_j^i \left( \frac{A^{i-1} p_j^{i-1}}{A^i} D \left( s_{j-1}^i \right) - \left( 1 - s_j^i \right) - D \left( s_j^i \right) \right).
- \sum_j p_j^i \left( 1 - s_j^i \right) + \sum_j p_j^i D \left( s_j^i \right) \right) =
\[= \frac{A^{i-1} p_j^{i-1}}{A^i} \left[ p_j^{i-1} D \left( s_{j-1}^i \right) - p_j^i \sum_j A^{i-1} p_j^{i-1} D \left( s_{j-1}^i \right) +
\right. p_j^i \left. \left[ \left( s_j^i - \sum_j p_j^i s_j^i \right) - \left( D \left( s_j^i \right) - \sum_j p_j^i D \left( s_j^i \right) \right) \right] \right)
\]
and
\[p_j^0 = p_j^0 \left( \sum_i N_j^i f_j^i - \left( 1 - s_j^0 \right) - D \left( s_j^0 \right) - \sum_v p_v^0 \left( \sum_i N_v^i f_v^i - \left( 1 - s_v^0 \right) - D \left( s_v^0 \right) \right) \right)
\[p_j^0 = p_j^0 \left( \sum_i A^i p_j^i f_j^i - \left( 1 - s_j^0 \right) - D \left( s_j^0 \right) - \sum_v p_v^0 \left( \sum_i A^i p_v^i f_v^i - \left( 1 - s_v^0 \right) - D \left( s_v^0 \right) \right) \right)
\[p_j^0 = p_j^0 \left( \sum_i A^i p_j^i f_j^i - \left( 1 - s_j^0 \right) - D \left( s_j^0 \right) - \sum_v \sum_i A^i p_v^i f_v^i + \sum_v p_v^0 \left( 1 - s_v^0 \right) + \sum_v p_v^0 D \left( s_v^0 \right) \right)
\[p_j^0 = \left( \sum_i A^i p_j^i f_j^i - p_j^0 \sum_v \sum_i A^i p_v^i f_v^i \right) + p_j^0 \left[ \left( s_j^0 - \sum_j p_j^0 s_j^0 \right) - \left( D \left( s_j^0 \right) - \sum_j p_j^0 D \left( s_j^0 \right) \right) \right]
\]
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therefore for system b:

\[
\dot{p}_j^0 = \frac{1}{A^0} \left( \sum_i A^i p_j^i f_j^i - p_j^0 \sum_i A^i \sum_v p_v^i f_v^i \right) + 
\]

\[
+ p_j^0 \left( \left( s_j^0 - \sum_i p_i^0 s_i^0 \right) - \left( D(s_j^0) - \sum_i p_i^0 D(s_i^0) \right) \right)
\]

\[
\dot{p}_j = \frac{A^{i-1}}{A^i} \left( p_j^{i-1} D(s_j^{i-1}) - p_j^i \sum_v p_v^{i-1} D(s_v^{i-1}) \right) + 
\]

\[
+ p_j^i \left( \left( s_j^i - \sum_w p_j^w s_j^w \right) - \left( D(s_j^i) - \sum_v p_v^i D(s_v^i) \right) \right)
\]  

for all \( j \)

\[
\dot{A}^i = A^{i-1} \sum_w p_j^i D(s_j^{i-1}) + 
\]

\[
+ A^i \left[ \sum_w p_j^i (s_j^i - D(s_j^i)) - \left( \sum_v A^v \sum_j p_j^v (f_j^v + s_j^v) - A^m \sum_j p_j^m D(s_j^m) \right) \right]
\]

and equation on scaling parameter

\[
\dot{N} = N \left( \sum_i A^i \sum_j p_j^i (f_j^i + s_j^i) - A^m \sum_j p_j^m D(s_j^m) - 1 \right)
\]

in simplified form:

\[
\dot{p}_j^0 = \frac{1}{A^0} \left( \sum_i A^i p_j^i f_j^i - p_j^0 \sum_i A^i \sum_v p_v^i f_v^i \right) + 
\]

\[
+ p_j^0 \left( \left( s_j^0 - \sum_i p_i^0 s_i^0 \right) - \left( D(s_j^0) - \bar{D}^0 \right) \right)
\]

\[
\dot{p}_j = \frac{A^{i-1}}{A^i} \left( p_j^{i-1} D(s_j^{i-1}) - p_j^i \bar{D}^{i-1} \right) + 
\]

\[
+ p_j^i \left( \left( s_j^i - \bar{s}^i \right) - \left( D(s_j^i) - \bar{D}^i \right) \right)
\]

\[
\dot{A}^i = A^{i-1} \bar{D}^{i-1} + A^i \left[ \bar{s}^i - \bar{D}^i - (\bar{s} + \bar{f} - A^m \bar{D}^m) \right]
\]

and equation on scaling parameter

\[
\dot{N} = N \left( \bar{s} + \bar{f} - A^m \bar{D}^m - 1 \right)
\]

where \( \bar{D}^{i-1} = \sum_j p_j^i D(s_j^{i-1}) \quad \bar{D}^i = \sum_v p_v^i D(s_v^i) \quad \bar{s}^i = \sum_v p_v^i s_v^i \)

\[
\bar{s} = \sum_v A^v \bar{s}^v \quad \bar{f}^i = \sum_v p_v^i f_v^i \quad \bar{f} = \sum_v A^v \bar{f}^v
\]

As in the previous appendix, to add the neutral density dependence the fertilities should be multiplied by logistic suppression coefficient \( \left( 1 - \frac{N}{K} \right) \).
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Fig.1 The difference between two alternative formulations of the problem: system a describes the evolution of the gene pool according to age structures of carrier subpopulations, system b describes evolution of the global age structure driven by strategy selection in age classes.
