Survival Phenotype, Selfish Individual versus Darwinian Phenotype

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Abstract

Consider and infinitely large asexual population without mutations and direct interactions. The activities of an individual determine the fecundity and the survival probability of individuals, moreover each activity takes time. We view this population model as a simple combination of life history and optimal foraging models. The phenotypes are given by probability distributions on these activities. We concentrate on the following phenotypes defined by optimization of different objective functions: selfish individual (maximizes the average offspring number during life span), survival phenotype (maximizes the probability of non-extinction of descendants) and Darwinian phenotype (maximizes the phenotypic growth rate).

We find that the objective functions above can achieve their maximum at different activity distributions, in general. We find that the objective functions above can achieve their maximum at different activity distributions, in general. The novelty of our work is that we let natural selection act on the different objective functions. Using the classical Darwinian reasoning, we show that in our selection model the Darwinian phenotype outperforms all other phenotypes.

1. Introduction

Here we consider an asexual, sufficiently large and non-ageing population (i.e., the survival rate and fecundity of individuals do not depend on their age) and the generations are overlapping (i.e., parents and their offspring can reproduce at the same time). We suppose that the individuals are engaged in different activities, which determine the fecundity, and the survival rate. All activities have certain time durations. We emphasize that there are no interactions between individuals. Our basic assumption is that individuals may only differ in their activity distributions, but they are alike in all other respects. Consequently, in the present model, the phenotypes are fully defined by their activity distributions. Finally, we assume that mutation is absent.

We note that from the mathematical point of view, this selection situation is possibly the first step towards a combination of life history theory (Stearns 1992, Charnov 1993), and optimal foraging theory (Stephens & Krebs 1986), for it contains the essential elements of both these theories. Namely, we work with overlapping generations like life history theory does, but for simplicity we assume there is no aging. Furthermore, each action takes time as in optimal foraging theory. To keep things simple, in our model the activity distribution depends exclusively on the phenotype, whereas in optimal foraging theory the energy intake depends on both the foraging strategy (activity) of the forager and the actual density of food. In optimal foraging theory it was found that the time constraints have essential effect on the optimal foraging strategy (e.g., Stephens & Krebs 1986, Garay & Móri 2010).

Our basic assumption is that the individuals may only differ in their activity distributions, but they are alike in all other respects. Consequently, in the present model, the phenotypes are fully defined by their activity distributions. We seek phenotypes which maximize interesting objective functions (cf. Garay et al. 2016, Garay & Varga 2005).

The challenge is to find the optimal phenotype, i.e., the optimal distribution on the activities. However, this question is ambiguous, since there are trade-offs (i.e., negative correlations) between either fecundity and survival rate, or fecundity and time duration, or both. In general no phenotype maximizes fecundity and survival rate simultaneously. The problem can be made precise mathematically, if we define an objective function, and find the phenotype that maximizes it, thus we seek the optimal phenotype with respect to a prescribed objective function. Now we are facing the problem of choosing the "right" objective function. We mention two biological examples of this trade-off phenomenon, together with an (incomplete) list of some previously proposed objective functions, to demonstrate the ambiguity.

Firstly, in the theory of survival cost of reproduction (e.g., Harshman & Zera 2007, see also life history theory), it is usually assumed that there is a trade-off between fecundity and survival rate. Four widespread objective functions of this theory are as follows. Fisher (1930) proposed *reproductive value*, and later Schaffer (1974) suggested *optimal reproductive effort*. The selfish individual maximizes her *life reproductive success* (e.g., Yearsley et al. 2002), which is the average number of offspring during the individual life span. Finally, the fourth objective function is the *growth rate of a phenotype* (e.g., Caswell 2001, Garay et al. 2016).

Secondly, in the theory of optimal foraging under predation risk (e.g., Stephens & Krebs 1986, Brown & Kotler 2004), it is usually assumed that there is a trade-off between fecundity and survival rate. A multitude of objective functions have been proposed, as follows. Gilliam (1982) introduced the *mortality per fecundity* rule. Houston et al. (1993) consider two objectives: (a) the animal must collect a fixed amount of food to reproduce;

(b) the animal must survive for a fixed time. Finally, Brown & Kotler (2004) study (a) and (b) above, and two further ones: the sum and the product of fecundity and survival rate (see also Bednekoff & Lima 2011). Observe that all cited objective functions refer to either an individual or a phenotype.

As noted earlier, the question arises: is there a method for selecting the "correct" objective function, if any? As we will see, the answer is positive. Based on our earlier results we propose the following method (Garay et al. 2016, Garay & Varga 2005). Consider a selection situation with different phenotypes and (at least) two different objective functions. For any pair of different objective functions, there are two possibilities: they attain their maximum either at the same phenotype or at different phenotypes. In the former case there is no difference between them in the given selection situation, while in the latter case we have an evolutionary selection problem, namely, a selection situation with different phenotypes, and we can see which phenotype wins the struggle of coexistence. Thus, we can say that the winner phenotype's objective function is maximized by selection. For instance, in the recently introduced kin demographic selection model (Garay et al. 2016), the Darwinian phenotype (which maximizes the phenotype's long term growth rate) is shown to outperform all other possible phenotypes (maximizing other objective functions). That model is based on the classical Leslie model, which assumes age dependent survival rate and fecundity. In the present paper, we investigate whether this recent result remains valid in the different selection situation considered here.

In Darwinian evolution theory, natural selection maximizes the fitness of a phenotype. In asexual models, fitness is defined as the average growth rate of the phenotype per capita, i.e., the average number of descendants of an individual with the given phenotype born in a unit of time.

Since phenomena in ecology are the results of evolution (Hutchinson 1965), it is reasonable to the fitness (i.e., the average growth rate) is the object of maximization in ecology as well.

In the present paper, we consider three objective functions: *the average offspring number during life span*, *the probability of non-extinction of descendants*, and *the phenotypic growth rate*. By finding the optimal phenotypes with respect to these objective functions, we demonstrate that in the selection situation under study, different objective functions are maximized by different phenotypes, in general. We emphasize that from the mathematical point of view all objective functions are possible. Subsequently, we investigate which phenotype wins the struggle of coexistence. Given that in our selection situation there are no interactions between individuals, one may ask: what kind of competition mechanism can arise, if any? Our selection mechanism is based on the classical Darwinian reasoning (Darwin 1859), namely, though individuals produce more offspring than the carrying capacity, natural selection keeps the population size bounded. In our case, every possible phenotype must have an exponential growth rate in order to exist at all. Since we assumed that phenotypes only differ in their activity distributions, they are equivalent (interchangeable) in this process of survival according to the carrying capacity. Thus in our case natural selection is realized by a random and uniform selection mechanism, where, as we will see, the highest Malthusian parameter will win the struggle of existence (cf. Garay et al. 2016).

2. Phenotypes, objective functions, and optimal strategies

Suppose an individual member of a population can choose from r activities (choice does not necessarily presume deliberation, since in biology a lot of species have a genetically fixed behavior). Her choice is random: activity s is chosen with probability p_s, $s = 1,\ldots,r$. Clearly, $p_1 + \cdots + p_r = 1$. We define a phenotype by this activity distribution $\mathbf{p} = (p_1,\ldots,p_r)$. Activity s takes time τ_s. At the end of the activity the individual either perishes without descendants, this happens with probability q_s, or the individual gives birth to c_s offspring, and the whole process starts over: independently of its past, the survivor makes a new choice, and so on. The progeny size c_s can be random, but finite expectation (and sometimes more, cf (5) in subsection 2.2) is required. We assume $0 < q_s < 1$ to exclude trivialities. This ensures that the lifetime of the individual is finite with probability 1.

Let us extend this model by allowing a more general set of activities. Suppose activities are parametrized from a general measurable space $(\mathcal{S},\mathfrak{I})$, where the parameter set $\mathcal{S}$ is called the activity space, its elements represent different activities, and $\mathfrak{I}$ is the σ-field of measurable subsets of $\mathcal{S}$. Every individual chooses an activity at random, according to an activity distribution (probability measure) $\mathbf{p} : \mathfrak{I} \to [0,1]$, called strategy (phenotype). We suppose that the joint distribution of the triplet (τ_s, q_s, c_s) is a measurable function of s (this condition holds automatically if the activity space is countable, since in that case every subset of $\mathcal{S}$ is traditionally supposed measurable). By the law of total probability, the joint distribution of (τ, q, c) is a mixture of the distributions of (τ_s, q_s, c_s), $s \in \mathcal{S}$, with mixing measure **p**.

Each child follows her parent's strategy, and the characteristic triplets of activity times, terminal probabilities, and offspring numbers of different individuals are independent and identically distributed.

Successfulness of a strategy can be measured in several ways. Concentrating on the individual, the measure of success is the average number of offspring produced during the whole lifetime. On the other hand, if, following Darwin, we concentrate on the phenotype, then we have to deal with the growth rate of the number of living descendants. However, the average size of progeny can also be large in such a way that with a considerable probability there are no living descendants at all, but otherwise a reproduction boom takes place. Thus it is meaningful to use the probability of non-extinction of the phenotype as an alternative index.

Let us compute these quantities. We will also investigate which strategies optimize them.

2.1. Selfish individual $\mathbf{p}_I$ maximizes the average offspring number of an individual.

Let X denote the number of descendants produced by an individual during her whole lifetime (several activity cycles). If the individual does not perish without reproduction at the end of the first activity period, the remainder of her life has the same distribution as if it were born at the very moment. Thus, if she chooses activity s, the average number of her offspring equals zero with probability q_s, and $\mathsf{E}c_s + \mathsf{E}X$ with probability $1 - q_s$. Hence, by the theorem of total expectation we can write

$$\mathsf{E}X = \int_{\mathcal{S}} (1-q_s)(\mathsf{E}c_s + \mathsf{E}X)\,\mathbf{p}(\mathrm{d}s), \tag{1}$$

from which

$$\mathsf{E}X = \frac{\int_{\mathcal{S}} (1-q_s)\mathsf{E}c_s\,\mathbf{p}(\mathrm{d}s)}{1-\int_{\mathcal{S}} (1-q_s)\mathbf{p}(\mathrm{d}s)} = \frac{\int_{\mathcal{S}} (1-q_s)\mathsf{E}c_s\,\mathbf{p}(\mathrm{d}s)}{\int_{\mathcal{S}} q_s\,\mathbf{p}(\mathrm{d}s)} \tag{2}$$

follows, provided the average number of offspring in one cycle is finite, that is, $\int_{\mathcal{S}} (1-q_s)\mathsf{E}c_s\,\mathbf{p}(\mathrm{d}s) < \infty$. In fact, equation (1) is also satisfied by $\mathsf{E}X = \infty$, but it cannot occur, since the number of activity cycles before death can be majorized by geometric distribution, which is of finite expectation.

Note that in the calculation above the activity lengths τ_s did not appear directly. They are only present in the effect they have on the number of offspring.

Let us find the strategy $\mathbf{p}_I$ that maximizes $\mathsf{E}X$.

Since $\mathsf{E}X = \frac{\int_{\mathcal{S}} q_s a_s\,\mathbf{p}(\mathrm{d}s)}{\int_{\mathcal{S}} q_s\,\mathbf{p}(\mathrm{d}s)}$, where $a_s = \frac{(1-q_s)\mathsf{E}c_s}{q_s}$, it can easily be seen that

$$\mathsf{E}X \le \sup_{\mathcal{S}} a_s = \sup_{\mathcal{S}} \frac{(1-q_s)\mathsf{E}c_s}{q_s},$$

and equality holds if and only if $\mathbf{p}_I$ is concentrated on activities s for which a_s is equal to its supremum (if it is attained at all).

Remark 1. We note that the same objective function is used in the problem of optimal foraging under predation danger (e.g. Clark & Dukas1994, Higginson & Houston 2015).

2.2. Darwinian phenotype $\mathbf{p}_D$ maximizes the average growth rate of the phenotype, i.e., the growth rate of the expected number of living descendants, as time tends to infinity. For the computation we need to change our viewpoint. Instead of letting an individual repeat her activity/reproduction cycles until death, we consider the end of the first activity period as the end of life, and, in the case where the individual would survive the period, we consider her as one of her siblings. Thus, we now think of τ_s as life span, and the offspring number ξ_s is defined to be 0 with probability q_s, and $1+c_s$ with probability $1-q_s$. One can express q_s and c_s in terms of ξ_s, for $q_s = \mathsf{P}(\xi_s = 0)$, and the distribution of c_s is equal to the conditional distribution of $\xi_s - 1$, provided $\xi_s > 0$. Let τ and ξ denote the life span and offspring size of the individual, resp., when it chooses strategy **p** (that is, their distribution is a mixture of (τ_s, ξ_s) with mixing measure **p**). Let Z_t denote the population size at time *t*. This way we obtain an age dependent branching process, or in other words, a so called Crump–Mode–Jagers (CMJ) process (Haccou et al. 2005), with reproduction process $\eta(t) = \mathbb{1}_{\{\tau \le t\}} \xi = \int_{\mathcal{S}} \mathbb{1}_{\{\tau_s \le t\}} \xi_s \, \mathbf{p}(\mathrm{d}s)$, where $\mathbb{1}_{\{\cdot\}}$ stands for the indicator of the event in brackets. ($\eta(t)$ is the number of offspring up to time *t*: it is either 0 or $1+c_s$ if the activity period, now lifetime, is already over by *t*, and 0 otherwise.) Since reproduction is only allowed at the end of the lifetime, we have a well known and widely studied particular case of CMJ processes: a Sevast'yanov process. An informal introduction to CMJ processes is provided in Appendix A. We may and will suppose that our process is supercritical, that is,

$$1 < \mathsf{E}\xi = \int_{\mathcal{S}} (1-q_s)(1+\mathsf{E}c_s)\mathbf{p}(\mathrm{d}s) < \infty . \qquad (3)$$

From the general theory it follows that Z_t grows exponentially with exponent $\alpha > 0$ called the *Malthusian parameter*. It can be obtained as follows. Let $\mu(t)$ denote the expected number of children born up to time *t*, that is, $\mu(t) = \mathsf{E}\left(1_{\{\tau \le t\}}\xi\right)$. Then $\mu(t)$ is bounded, for $\mu(\infty) = \mathsf{E}\xi < \infty$. The Malthusian parameter α is the only positive solution of the equation

$$\int_0^\infty e^{-\alpha t}\mu(\mathrm{d}t) = \mathsf{E}(e^{-\alpha\tau}\xi) = \int_{\mathcal{S}} \mathsf{E}(e^{-\alpha\tau_s}\xi_s)\mathbf{p}(\mathrm{d}s) = 1, \qquad (4)$$

see Appendix A. The left hand side, as function of α, is continuous, and strictly decreases from $\mu(\infty) = \mathsf{E}\xi > 1$ to 0 by the monotone convergence theorem.

In order to apply the Theorem and Remark of Appendix A we have to check the moment condition. Clearly, $M = \int_0^\infty e^{-\alpha t}\,\eta(dt) = e^{-\alpha\tau}\xi \le \xi$, thus it suffices to require that

$$\mathsf{E}(\xi\log\xi) = \int_{\mathcal{S}} (1-q_s)\mathsf{E}[(1+c_s)\log(1+c_s)]\mathbf{p}(\mathrm{d}s) < \infty. \qquad (5)$$

Now, using formulae (8) and (9), we can characterize the growth of Z_t.

If the distribution of τ is non-lattice, that is, not concentrated on any lattice $\{0, h, 2h, 3h, \ldots\}$, $h > 0$, then

$$\lim_{t\to\infty} e^{-\alpha t}\mathsf{E}Z_t = K := \frac{\int_0^\infty e^{-\alpha t}\mathsf{E}\phi(t)\mathrm{d}t}{\int_0^\infty t e^{-\alpha t}\mu(\mathrm{d}t)} = \frac{\mathsf{E}(1-e^{-\alpha\tau})}{\alpha\mathsf{E}(\tau e^{-\alpha\tau}\xi)} = \frac{\int_{\mathcal{S}} \mathsf{E}(1-e^{-\alpha\tau_s})\mathbf{p}(\mathrm{d}s)}{\alpha\int_{\mathcal{S}} \mathsf{E}(\tau_s e^{-\alpha\tau_s}\xi_s)\mathbf{p}(\mathrm{d}s)}. \qquad (6)$$

Moreover, $e^{-\alpha t}Z_t$ converges to a random variable *W* almost surely, $\mathsf{E}W = K$, and *W* is positive almost everywhere outside the set of extinction.

If the distribution of τ is lattice, say τ is integer valued (the case of discrete time), then for integer *t* we have $Z_t \sim W e^{\alpha t}$ as $t \to \infty$, where now

$$\mathsf{E}W = K = \lim_{\substack{t\to\infty \\ t \text{ integer}}} e^{-\alpha t}\mathsf{E}Z_t = \frac{\int_{\mathcal{S}} \mathsf{E}(1-e^{-\alpha\tau_s})\,\mathbf{p}(\mathrm{d}s)}{(1-e^{-\alpha})\int_{\mathcal{S}} \mathsf{E}(\tau_s e^{-\alpha\tau_s}\xi_s)\,\mathbf{p}(\mathrm{d}s)}. \tag{7}$$

Consequently, the Malthusian parameter α appears to be an adequate measure of successfulness in the Darwinian sense, both in the lattice and non-lattice cases.

Maximal average growth of phenotype. Let us find the strategy $\mathbf{p}_D$ that maximizes α. Suppose $\mathsf{E}\xi_s = (1-q_s)(1+\mathsf{E}c_s) > 1$ for some $s \in \mathcal{S}$. Let α_s denote the Malthusian parameter associated with the pair (τ_s, ξ_s), that is, the only positive solution of the equation $\mathsf{E}(e^{-\alpha\tau_s}\xi_s) = 1$. We will show that the optimal rate is

$$\alpha_D = \sup\{\alpha_s : \mathsf{E}\xi_s > 1\},$$

and it can be attained if and only if $\mathbf{p}_D$ is concentrated on activities *s* for which a_s is maximal. Indeed, for every $s \in \mathcal{S}$ we have $\mathsf{E}(e^{-\alpha_D\tau_s}\xi_s) \le 1$, hence $\int_{\mathcal{S}} \mathsf{E}(e^{-\alpha_D\tau_s}\xi_s)\mathbf{p}(\mathrm{d}s) \le 1$, implying $\alpha \le \alpha_D$. The condition of equality is obvious.

In the particular case of constant activity times, the Malthusian equation reads

$$\sum_{s=1}^{r} p_s(1-q_s)(1+\mathsf{E}c_s)e^{-\alpha\tau_s} = 1,$$

and the maximum of the Malthusian parameter is equal to

$$\alpha_D = \max_{1\le s\le r} \frac{\log[(1-q_s)(1+\mathsf{E}c_s)]}{\tau_s}.$$

Remark 2. When all survival rates are the same (i.e., $q_s = q$), the maximal possible growth rate of the phenotype is similar to the objective function of optimal foraging theory, namely, to the maximum of the intake energy rate in the case when one type of prey is more profitable than the other ones (e.g., Stephens & Krebs 1986).

2.3. Survival phenotype $\mathbf{p}_e$ minimizes the extinction probability of phenotype, or, in other words, maximizes the probability of phenotype survival. Though in the supercritical case the mean population size tends to infinity at an exponential rate, the phenotype can still become extinct with positive – occasionally high – probability. An alternative criterion of optimality can be the probability of the survival of the phenotype, that is, one can aim at minimizing the probability π of extinction.

In the age-dependent branching model this probability can easily be found by considering the discrete time Galton–Watson process embedded in the general Sevast'yanov process. Starting from a single ancestor, let us call her offspring the first generation, the offspring of the first generation the second generation, and so on. Then the successive generations form a Galton–Watson process with offspring size ξ. The extinction probability π is the smallest positive solution of the equation $\pi = g(\pi)$, where $g(x) = \mathsf{E}(x^{\xi})$, the probability generating function of ξ (see Theorem 2.3.1. of Jagers 1975). Particularly, let $g_s(x) = q_s + (1 - q_s)x\mathsf{E}(x^{C_s})$, then $g(x) = \int_{\mathcal{S}} g_s(x)\mathbf{p}(ds)$.

Minimal extinction probability. Let us find the strategy $\mathbf{p}_e$ that minimizes π. First we show that the infimum of the extinction probability as **p** runs over all possible strategies is equal to $\pi_e = \inf_{\mathcal{S}} \pi_s$, where π_s is the extinction probability under the pure strategy s, that is, the smallest positive solution of the equation $g_s(x) = x$. Thus, π_e is the infimum of π over all pure strategies.

Indeed, since $g_s(x)$, being a probability generating function itself, downcrosses the identity function at π_s, we have $g_s(x) \geq x$ for $x \leq \pi_s$. Therefore,

$$g(\pi_e) = \int_{\mathcal{S}} g_s(\pi_e)\mathbf{p}(ds) \geq \int_{\mathcal{S}} \pi_e \mathbf{p}(ds) = \pi_e,$$

implying that π_e is less than or equal to the extinction probability under an arbitrary strategy **p**. On the other hand, we can get arbitrarily close to π_e by using pure strategies only.

An equivalent characterization of π_e is the following. Introduce the function

$$f(x) = \inf_{\mathcal{S}} \, g_s(x), \; 0 \leq x \leq 1.$$

Then π_e is the largest solution of the equation $x = f(x)$ in the interval [0, 1). Indeed, for every positive ε there exists an $s \in \mathcal{S}$ such that $\pi_s \leq \pi_e + \varepsilon$, hence

$$f(\pi_e) \leq f(\pi_s) \leq g_s(\pi_s) = \pi_s \leq \pi_e + \varepsilon.$$

Thus $f(\pi_e) \leq \pi_e$. On the other hand, for every positive ε there exists an $s \in \mathcal{S}$ such that $g_s(\pi_e) \leq f(\pi_e) + \varepsilon$. Since $\pi_e \leq \pi_s$, we have $\pi_e \leq g_s(\pi_e)$, and by that, $\pi_e \leq f(\pi_e)$. Finally, if $\pi_e < x < 1$, then there exists an $s \in \mathcal{S}$ such that $\pi_s < x$, thus $f(x) \leq g_s(x) < x$.

Clearly, strategy **p** attains π_e if and only if it is concentrated on activities s for which $\pi_s = \pi_e$.

Observe that the above objective functions can generally take their maximums at different strategies **p**. On the other hand, if the same activity has the largest survival probability, the highest fecundity, and the shortest time duration, then it maximizes all considered objective functions simultaneously.

Example 1. Consider the following parameters. For the sake of simplicity, both the offspring size and the time duration are non-random.

	Activity 1	Activity 2	Activity 3
Probability of death, q	$q_1 = 0.4$	$q_2 = 0.4$	$q_3 = 0.2$
Offspring size, c	$c_1 = 11$	$c_2 = 8$	$c_3 = 3$
Time duration τ	$\tau_1 = 5$	$\tau_2 = 1$	$\tau_3 = 5$

Table 1. *A simple model with three activities.*

For the pair of activities 1 and 2, there is a trade-off between fecundity and time duration. Moreover, for the pair of activities 2 and 3, there is a trade-off between fecundity and survival rate. Simple calculations show that the selfish individual must choose activity 1, the Darwinian phenotype activity 2, while the survival phenotype uses activity 3.

	Activity 1	Activity 2	Activity 3
Mean offspring size	$\mathsf{E}X = 16.5$	$\mathsf{E}X = 12$	$\mathsf{E}X = 12$
Growth rate (Malthusian parameter)	$\alpha_1 = 0.394$	$\alpha_2 = 1.686$	$\alpha_3 = 0.232$
Probability of extinction	$\pi_1 = 0.400$	$\pi_2 = 0.400$	$\pi_3 = 0.201$

Table 2. *Values of objective functions for the activities in Table 1.*

Intuitively, the selfish individual concentrates on the number of her own offspring. The Darwinian phenotype also takes account of the number of its children, grandchildren, great-grandchildren, and so on, and how fast its reproduction can be. The survival phenotype concentrates on the long time survival of its posterity.

For deeper biological insight, we describe a theoretical selection situation during reproductive season, where the above example is reasonable. Firstly, assume that if a parent dies before her offspring grow up, then so do all her offspring. Consider three types of non-exhausted patches, i.e. $r = 3$. Parents have to stay in the same patch during one reproduction cycle. In patch s the parent's survival rate is $1 - q_s$, her fecundity is c_s, and the development time of her offspring (from birth to the first reproduction, while parental care is needed for the survival of the juveniles) is τ_s. Observe that here the patch type determines the survival rate and fecundity of parents and the development time of her offspring. Furthermore, the different objective functions determine different patch preference.

3. A simple selection model

We consider a monomorphic model where in a resident population a mutant phenotype appears, and natural selection has sufficient time to select out the less fit phenotype.

In Section 2 we determined the optimal phenotypes corresponding to different objective functions. Clearly, if two phenotypes have different activity distributions, they generally have different growth rates (Malthusian parameters) α. Let us consider the Darwinian phenotype with Malthusian parameter α_D and a mutant phenotype with a smaller $\alpha_M < \alpha_D$. Let f_D resp. f_M denote the frequencies of Darwinian resp. mutant phenotypes.

When the rare mutants appear, there are two possibilities: they either die out within a short time due to random fluctuation (we will not investigate this case), or the mutant phenotype survives for such a long time that it reaches its asymptotic growth rate. Since evolution is a long process, we are interested in the second possibility. Let T_R denote the time duration of the long reproductive season, when different phenotypes reproduce according to their activity distributions. When the reproductive season is over, the size of the population decreases in accordance with the carrying capacity. One may think of the reproductive season as taking place during spring and summer time, when the activity determines the survival rate and the fecundity of individuals; moreover, the average number of generations during the reproductive season is determined by the time durations. Assume that the reproductive season is long enough to allow a high number of generations, i.e. $T_R >> \max \tau_i$. The carrying capacity is determined by the winter time, when the whole population size is reduced to the carrying capacity by a uniform survival process, which equally affects all phenotypes, i.e., the survival rates are all equal (by our basic assumption, phenotypes differ only in their activity distribution).

Let us denote the carrying capacity by C, supposed sufficiently large. Clearly, $C = f_D + f_M$. Since C is large, we can describe selection as a "mass process", i.e., random fluctuations have no effect on the number of individuals (at least in the order of magnitude). If there are many individuals of a given phenotype, the probability of eventual extinction, being a negative exponential function of the phenotype size, is negligible. Hence, at the end of the reproductive season (before the selection according to carrying capacity) the approximate sizes of the Darwinian, resp. mutant phenotypes are $f_D K_D e^{\alpha_D T_R}$ and $f_M K_M e^{\alpha_M T_R}$, where K_D and K_M denote the current values of the constant K appearing in formulae (6) and (7). Since the considered phenotypes are equivalent with respect to the carrying capacity, each individual will survive with probability $\rho \approx \dfrac{C}{f_D K_D e^{\alpha_D T_R} + f_M K_M e^{\alpha_M T_R}}$, so after selection, at the beginning of the next reproductive season, the phenotype sizes are $f'_D \approx \rho f_D K_D e^{\alpha_D T_R}$ and $f'_M \approx \rho f_M K_M e^{\alpha_M T_R}$, resp. Therefore, the ratio of mutant and Darwinian phenotype frequencies will decrease very fast, namely, at a rate exponential in the number of reproductive seasons:

$$\frac{f'_M}{f'_D} \approx \frac{f_M}{f_D} \cdot Q \text{, where } Q = \frac{K_M}{K_D} e^{-(\alpha_D - \alpha_M) T_R} << 1.$$

We emphasize that Darwinian phenotype does not only win against selfish and survival phenotypes, but it outperforms all other phenotypes based on different objective functions mentioned in Introduction (unless an objective function happens to take its maximum just at the Darwinian phenotype).

5. Conclusion

We considered an asexual, sufficiently large and non-ageing population, where the generations are overlapping, and there is no mutation and no interaction between individuals. The individuals engage in activities, which determine their fecundity and survival probability, moreover these activities take time. A phenotype is identified with a probability distribution on the activities. Our aim was to find the phenotype with optimal evolutionary behavior. The natural candidates are phenotypes which maximize one or another objective function, a multitude of which have already been proposed in the literature. Generally, different objective functions are maximized by different phenotypes. However, without introducing a selection mechanism we cannot find out which phenotype outperforms all other ones. To this end, we proposed a selection method: since in our case the individuals do not interact, and all phenotypes contend under the same conditions, therefore the competition of phenotypes must be uniform. We pointed out that actually the different objective functions (e.g., different definitions of fitness) are the objects of natural selection. We showed that the Darwinian phenotype, which maximizes the average growth rate of the phenotype, outperforms all other phenotypes under consideration (those maximizing the individual's average offspring number during life span or minimizing the extinction probability of descendants, and so on). From the aspect of theoretical biology, this means that the fitness of a phenotype is best defined by the average growth rate of the phenotype in the selection situation where each activity may have different survival rate, fecundity, and time duration.

We have already mentioned that, from the mathematical point of view, our selection situation is possibly the simplest mathematical combination of life history theory and optimal foraging theory. Our objective functions correspond to some objective functions already introduced in optimal foraging theory (Remarks 1 and 2). We conjecture that the Darwinian phenotype wins the struggle of existence more generally, namely, if one lets the time durations of activities be influenced by prey densities in an unbounded and aging population, As an outlook, we mention a few selection situations, where the Darwinian phenotype outperforms other ones. Firstly, in kin selection theory (Hamilton 1964), the altruistic phenotype (at a cost to the own survival and reproduction) helps the reproductive success of one of its own relatives. Secondly, in the kin demography model, it can be pointed out that sib cannibalism between closest relatives can be considered as an extreme mutualism (Garay et al. 2016).

Finally, we note that our result could be applied in both optimal foraging theory and life history theory, where there is a trade-off between any pair of the offspring number, survival rate, and time duration. Our model can deal with these trade-offs, since we do not impose assumptions on the correlation between parameters. An important consequence of our model is that, independently of the “objective functions”, the optimal behavior can always be achieved by pure strategies, i.e., with a single activity. Thus, our results offer the possibility to test, either by experiment or by field observation, which objective function is optimized by natural selection.

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Appendix A.

In this section, we give an informal introduction to general time dependent branching processes, or Crump–Mode–Jagers (CMJ) processes. The interested reader may find more formal descriptions in the monographs (Jagers 1975) or (Haccou et al. 2005).

In a CMJ branching process there are individuals who reproduce and die. This is characterized by a random point process $\eta(t), t \geq 0,$ called the reproduction process, and a nonnegative random variable τ , which is the life span. They are not supposed independent. The random variable $\eta(t)$ is the number of offspring up to time *t*. Most often there is no reproduction after death, i.e., $\eta(t)=\eta(\tau)$ for $t>\tau$ (but this is not necessarily required).

The life history of every individual *e* is described by the pair $(\eta_e(.),\tau_e)$; they are independent and identically distributed copies of $(\eta(.),\tau)$ introduced above. If individual *e* was born at time σ_e, then at time *t* the number of her children (dead or alive) is $\eta_e(t-\sigma_e)$ ($\eta_e(t)$ is defined as zero for negative *t*), and it deceases at time $\sigma_e+\tau_e$. We are interested in the number of individuals alive at time *t*, which we will denote by Z_t.

A CMJ process is called *subcritical*, *critical*, or *supercritical*, according that the expected number of offspring of an individual, $\mathsf{E}[\eta(\infty)]$, is less than, equal to, or greater than 1, respectively. In the sequel we are interested in supercritical processes. For the sake of simplicity we only formulate the basic limit theorem in the form we need it, not in its most general form, because we want to apply it to a model with nice properties. Therefore we suppose that $1<\mathsf{E}[\eta(\infty)]<\infty$. Such processes grow exponentially fast on the event of non-extinction. The rate of growth is described by the so called Malthusian parameter α. It is the only positive solution of the equation $\int_0^\infty e^{-\alpha t}\mu(\mathrm{d}t)=1$, where $\mu(t)=\mathsf{E}[\eta(t)]$, the expected number of offspring of an individual up to time *t* after her birth.

Combining Proposition 2.2, Theorems 3.1 and 5.4 of (Nerman 1981), we get the following limit theorem.

Theorem. *With the definition* $M = \int_0^\infty e^{-\alpha t}\eta(\mathrm{d}t)$, *suppose that* $\mathsf{E}[M\log^+ M] < \infty$ *holds. Furthermore, suppose the Lebesgue–Stieltjes measure generated by* μ *is not lattice, i.e.,* $\mu(t)$ *is not a piecewise constant function with points of increase all belonging to a lattice* $\{0, h, 2h, 3h, \ldots\}$, $h > 0$. *Then*

$$\lim_{t\to\infty} e^{-\alpha t}\mathsf{E}Z_t = K := \frac{\int_0^\infty e^{-\alpha t}\mathsf{P}(\tau > t)\,\mathrm{d}t}{\int_0^\infty t\,e^{-\alpha t}\mu(\mathrm{d}t)}. \tag{8}$$

Moreover, $e^{-\alpha t}Z_t$ *converges to a random variable W almost surely,* $\mathsf{E}W = K$, *and W is positive almost everywhere outside the set of extinction.*

Remark. *If* μ *is lattice, that is, when an individual can reproduce only at times that are multiples of h (the case of discrete time), then formula* (8) *slightly changes. Without loss of generality we can suppose that* $h = 1$. *Then for integer t we have* $Z_t \sim W e^{\alpha t}$ *as* $t \to \infty$, *where*

$$\mathsf{E}W = \frac{\alpha}{1 - e^{-\alpha}} \cdot \frac{\int_0^\infty e^{-\alpha t}\mathsf{P}(\tau > t)\,\mathrm{d}t}{\int_0^\infty t\,e^{-\alpha t}\mu(\mathrm{d}t)}. \tag{9}$$