



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.

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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 examples of this trade-off phenomenon, together with an (in-

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complete) 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 , $s = 1, \dots, r$. Clearly, $p_1 + \dots + p_r = 1$. We define a phenotype by this activity distribution $\mathbf{p} = (p_1, \dots, p_r)$. 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 Section 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 (S, F) , where the parameter set S is called the activity space, its elements represent different activities, and F is the σ -field of measurable subsets of S . Every individual chooses an activity at random, according to an activity distribution (probability measure) $\mathbf{p}: F \rightarrow [0, 1]$, 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 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) , $s \in S$, with mixing measure \mathbf{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}_1

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

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