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Incorporating Phenotype Plasticity into the Indirect Evolutionary Approach

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I. Introduction

The indirect evolutionary approach (IEA), initiated by Güth and Yaari (1992), has become an established rationale for preferences which are deviating from the standard payoff-maximizing preference. For a formal description of the IEA, see Königstein and Müller (2000). The IEA is used primarily within the fields of social preferences and fairness preferences. See for example: Güth (1995); Bester and Güth (1998); Kockesen, Ok and Sethi (1998); Güth and Ockenfels (2000); Possajennikov (2000); Ok and Vega-Redondo (2001); Sethi (2001); Fehr and Henrich (2004); Güth et al. (2007).

The IEA differentiates from the standard evolutionary approach, in that it is based on preference parameters, in lieu of evolutionary strategies. Hence the object of heredity is not the strategy, but the preference parameter. This preference parameter specifies a utility function which represents a preference order. An assumption is made that agents behave rationally in the sense of selecting a strategy which maximizes their utility function. A preference is evolutionary stable if it induces a strategy, which is an evolutionary stable strategy. (Güth and Yaari, 1992). Hence, preferences influence behavior and in turn behavior influences the preference distribution within the population.

It is important to note that in this approach, a phenotype is represented by a given, unchangeable preference parameter and by a time - invariant utility function. The related preference parameter is inherited by an agent's descendants. As the preferences of any agent cannot change over time, the phenotype is unchangeable, too.

So far, the IEA excludes the phenomenon of phenotype plasticity. In its current manifestation, it is the population composition which changes and not

individual preferences. The paradigm of stable preferences, which was introduced by Becker and Stigler (1977), rules the IEA.

Some authors, who use the IEA, stress explicitly that, in their model, the individual preferences are not subject to change. Some examples are; Güth and Yaari (1992), Ockenfels (1993), Bester and Güth (1998), Güth and Kliemt (2007). Other authors use the assumption of stable preferences, without any reasoning. Altogether, the IEA literature does not provide any suitable argument why to preclude ex ante phenotype plasticity (that is time - variant individual preferences) from the analysis of the indirect evolutionary approach. In the face of the vast amount of literature which indicates that phenotype plasticity can be advantageous in an unstable environment (West - Eberhard, 2003), and also in a stable environment, due to social interactions (Fagen, 1987), the following question arises: Can time - variant preferences be a stable phenomenon in a stable environment? “Stable environment” means that selection mechanism does not change with time.

In our paper, we provide evidence that there are conditions where mutants with unstable preferences have greater fitness than mutants with stable preferences. We provide a population model with random and pairwise matching in which agents live for more than one period. They choose their strategies in accordance with their preference. Individual fitness depends on the amount of material resources gained through pairwise social interaction. Agents of the non - plastic phenotype cannot change their preference, whereas agents of the plastic phenotype can do so.

For 2x2 symmetric evolutionary games, we identify conditions under which a population of non - plastic phenotypes can be invaded by mutants of a plastic phenotype, but not by mutants of a non - plastic phenotype.

The rest of the paper is organized as follows: In section two, we develop the model. In section three, we analyze this model and isolate conditions under

which mutants with a plastic phenotype can invade a population, but mutants with a stable phenotype cannot. In section four, we discuss our findings and give some hints for further research.

II. The Model

First, we arrange the population structure, to ensure a population dynamic with limited growth (see section A). In section B, using a game, we describe the environment, in which the agents struggle for material resources. Next, we provide an appropriate definition of fitness (section C), and define and operationalize phenotype plasticity (section D). This leads to the final model specification (section E).

A. Population Structure

Consider a large population which is of size N_t , at time t . The population consists of two classes of agents. These are plastic agents and non - plastic agents.

In this context ‘plasticity’ means that an agent’s phenotype can change over time, and ‘non-plasticity’ means that it is unchangeable over time. A plastic agent’s phenotype at time t is denoted with $b_t \in B = \{\beta_i, \beta_j\}$, where $\beta_i \neq \beta_j$ and $\beta_i, \beta_j \in \mathbb{R}$. A non - plastic agent’s phenotype is time invariant, so that we can write $b_t = b$. We assume $b \in B$. Thus, at time t in the population, there are four different types of agents available: non - plastic agents of phenotype β_i (non – plastic - β_i), non - plastic agents of phenotype β_j (non – plastic - β_j), plastic agents of phenotype β_i (plastic - β_i) and plastic agents of phenotype β_j (plastic - β_j). Thus, the total population consists of four different subpopulations.

The number of plastic - β_i agents at time t is denoted by W_t , the number of non-plastic - β_i agents by X_t , the number of plastic - β_j agents by Y_t and the number of non - plastic - β_j agents by Z_t . At any time t it holds: $W_t + X_t + Y_t + Z_t = N_t$. We denote the corresponding fractions of each agent type with small letters w_t, x_t, y_t, z_t .

In the following, we assume limited population growth. We define the dynamics on numbers of agents and restrict the population size to $N_t \leq K$ for all $t = 1, \dots, T$. $K > 0$ denotes the population's carrying capacity. In the following, we are assuming the population size (and thus the carrying capacity) to be large enough for the approximation $\frac{1}{N_t} \approx 0$ to hold.

Let R_{W_t} denote the net adds of individuals in subpopulation of plastic - β_i agents, R_{X_t} the net adds of individuals in the subpopulation of non-plastic - β_i agents, R_{Y_t} the net adds of plastic - β_j - agents and R_{Z_t} the net adds of non-plastic - β_j - agents from time t to time $t+1$.

The population dynamics with limited growth is of the following form.

$$(1) \quad W_{t+1} = W_t + R_{W_t} \cdot (K - N_t)/K$$

$$(2) \quad X_{t+1} = X_t + R_{X_t} \cdot (K - N_t)/K$$

$$(3) \quad Y_{t+1} = Y_t + R_{Y_t} \cdot (K - N_t)/K$$

$$(4) \quad Z_{t+1} = Z + R_{Z_t} \cdot (K - N_t)/K$$

B. The Environment

The agents are matched randomly and pairwise to play a symmetric two - person normal form game $G = (I; S_m; S_{m'}; v_m; v_{m'})$ with complete information. $I = \{m, m'\}$ denotes the set of players, v_m the payoff of player m and $v_{m'}$ the payoff of player m' . $m, m' \in M = \{i, j\}$. $S = S_m \times S_{m'}$ denotes the set of all nonempty pure strategy vectors and $s_m \in S_m$ a pure strategy of player m and $s_{m'} \in S_{m'}$ a pure strategy of player m' . As G is a symmetric game, it holds $S_m = S_{m'}$ and $v_m(s_m, s_{m'}) = v_{m'}(s_{m'}, s_m)$. Here, we assume S_m to contain two elements and thus G to be a symmetric 2x2 game.

The agents are programmed to maximize their individual utility function $u_m: S \rightarrow \mathbb{R}$ over strategy $s_m \in S_m$ for all $m \in M = \{i, j\}$. S_m denotes the nonempty set of phenotype β_m 's pure strategies. Thus $S = S_i \times S_j$. The individual utility function depends on the phenotype specific parameter $b_t \in B$.

Thus, for a given $\beta_i \in \mathbb{R}$ and $\beta_j \in \mathbb{R}$, the optimal choice of phenotype β_i in a game with an agent of phenotype β_j is $s_i^*(\beta_i, \beta_j) = \arg \max_{s_i \in S_i} u_i(\beta_i, \beta_j)$ and in a game with phenotype β_i it is $s_i^*(\beta_i, \beta_i) = \arg \max_{s_i \in S_i} u_i(\beta_i, \beta_i)$.

Similarly, we define $s_j^*(\beta_j, \beta_j) = \arg \max_{s_j \in S_j} u_j(\beta_j, \beta_j)$ and $s_j^*(\beta_j, \beta_i) = \arg \max_{s_j \in S_j} u_j(\beta_j, \beta_i)$. The payoff of an agent of phenotype β_i , who is playing the game with an agent of phenotype β_j , is given by $v_i^*(\beta_i, \beta_j) \equiv v_i(s_i^*(\beta_i, \beta_j), s_j^*(\beta_j, \beta_i))$. Playing the game with an agent of phenotype β_i leads to $v_i^*(\beta_i, \beta_i) \equiv v_i(s_i^*(\beta_i, \beta_i), s_i^*(\beta_i, \beta_i))$.

For an agent of phenotype β_j , we have $v_j^*(\beta_j, \beta_i) \equiv v_j(s_j^*(\beta_j, \beta_i), s_i^*(\beta_i, \beta_j))$ and $v_j^*(\beta_j, \beta_j) \equiv v_j(s_j^*(\beta_j, \beta_j), s_j^*(\beta_j, \beta_j))$. Here, the payoff of the game G is assumed to be a materialistic item which is, among others, used for survival and for raising an agent's descendants.

C. Defining and Measuring Fitness

Concerning the definition of fitness, which “has plagued evolutionary biologists for many years, partly because the term has been applied differently and with different definitions” (Barker, 2009, 4), we rely on the propensity interpretation of fitness introduced by Mills and Beatty (1979, reprint 2006). For an overview of the vast amount of concepts which operate under the name of “fitness,” see Barker (2009).

Definition 1: Fitness

The individual fitness of a specific organism in a specific environment is defined as the expected number of descendants which this organism will leave in this environment and the fitness of a type (genotype or phenotype) is defined as the average individual fitness.

Thus the fitness of a type reflects the contribution of a particular trait to the expected descendant contribution i.e., the individual fitness of those descendants possessing the trait. (Mills and Beatty, 2006, 12). This notion of fitness can be measured by the amount of viable offspring born in the next generation. Hence, we treat fitness on par with the average number of viable offspring of a specific phenotype. Thus, comparative growth rates of specific phenotypes can serve as a measure of fitness too. In line with this notion of fitness, we characterize an agent by the distribution of its viable offspring.

As here, agents of the same phenotype are assumed to be identical, we define the distribution of viable offspring in period t for each phenotype and take into account that the game payoff influences the amount of viable offspring. In contrast to the literature on evolution of preferences, we relate this distribution to a single period t , and not to the entire lifespan of an agent. This is because the

capability of having viable offspring depends on the game payoff, and thus on the preference parameter which is assumed for plastic agents to be changeable from period to period. For simplicity, we assume every agent to have only one descendant per period who can either survive or not. This leads us to define the distribution of viable offspring:

Definition 2: Distribution of viable offspring

Let $\theta: \mathbb{R} \times \mathbb{R} \rightarrow [0,1]$, $\theta(v_m^*(\beta_m; \beta_{m'})) \equiv \theta_{mm'}$ with $m, m' \in \{i, j\}$. Then, the distribution of viable offspring of an agent of type $m \in \{i, j\}$, who encountered an agent of type $m' \in \{i, j\}$ at time t is represented by the density function $f_{mm'}(x) = \theta_{mm'}^x \cdot (1 - \theta_{mm'})^{1-x}$, where: $x \in \{0,1\}$.

In the following, we assume (weak) payoff-monotonicity, i.e. $\frac{\partial \theta_{mm'}}{\partial v_m^*} \geq 0$. That is, the more resources a parental agent manages to acquire, the greater the probability its offspring will survive.

As a matter of fact, the *average number of viable offspring of a specific phenotype* depends on the design of the matching mechanism, as it is the matching mechanism that puts in motion a stochastic process. Thus, analyzing stochastic processes as deterministic systems, is a widespread and accepted approach in economics and evolutionary biology. For some discussions of this approximation, see Boylan (1992), and Duffie and Sun (2012). In line with the vast amount of literature using this approximation, we assume that in a large population with two types i and j , by the law of large numbers and the central limit theorem, the probability with which a single agent of any type i meets an agent of type j equals the proportion of agents with type j .

Note that the fraction of agents who are of phenotype β_i at time t equals $\frac{W_t+X_t}{N_t}$ and the fraction of agents who are of phenotype β_j at time t equals $\frac{Y_t+Z_t}{N_t}$. Thus, the death rates among the offspring of any phenotype $m = \{i, j\}$ are given by $\frac{W_t+X_t}{N_t} \cdot (1 - \theta_{mi}) + \frac{Y_t+Z_t}{N_t} \cdot (1 - \theta_{mj})$. The average amount of viable offspring of any specific type of agents is determined by the number of births at time t minus the number of deaths among those born at time t . Thus, for the average amount of viable offspring of the four different types of agents lemma 1 holds:

Lemma 1: Average amounts of viable offspring

If $\frac{1}{N_t} \approx 0$, the average amount of viable offspring of non - plastic - β_i - agents at time $t+1$ is given by $X_t \cdot \left(\frac{W_t+X_t}{N_t} \cdot \theta_{ii} + \frac{Y_t+Z_t}{N_t} \cdot \theta_{ij} \right)$, of plastic - β_i - agents by $W_t \cdot \left(\frac{W_t+X_t}{N_t} \cdot \theta_{ii} + \frac{Y_t+Z_t}{N_t} \cdot \theta_{ij} \right)$, of plastic - β_j - agents by $Y_t \cdot \left(\frac{W_t+X_t}{N_t} \cdot \theta_{ji} + \frac{Y_t+Z_t}{N_t} \cdot \theta_{jj} \right)$ and of non - plastic - β_j - agents by $Z_t \cdot \left(\frac{W_t+X_t}{N_t} \cdot \theta_{ji} + \frac{Y_t+Z_t}{N_t} \cdot \theta_{jj} \right)$.

For proof of Lemma 1 see appendix A.

Note that here we have defined fitness slightly differently than in standard evolutionary game theory. There, fitness is *equalized* with the game payoff. Agents are either programmed to play a certain strategy (direct evolutionary approach), or choose their strategy by maximizing their utility (indirect evolutionary approach). The preference is defined on the game payoff and thus on fitness. But we think defining a preference on fitness (that is on the average amount of offspring) is not appropriate. Here, the payoff of the underlying game

represents an amount of tangibles, i.e. resources which are used among others for surviving and raising descendants. Thus, the game payoff represents fitness only indirectly via the function θ . The function θ induces an evolutionary game in which the phenotypes β_m , represent the strategies, and $\theta_{mm'}$ with $m' \in \{i, j\}$ represents the current fitness of an agent of type m , who encountered an agent of type m' . If the agent were to live for one period only, then the fitness values would be the same as those used in standard evolutionary game theory. But, as an agent's strategies can change over time, the life span of an agent influences fitness as well. So, besides the mechanism of phenotype change, the lifespan will play a crucial role in our analysis. In the next step we clarify this process of phenotype change.

D. Defining and Operationalizing Phenotype Plasticity

“Plasticity is the ability of an organism to react to an internal or external environmental input with a change in form, state, movement or rate of activity. It may or may not be adaptive.” (West-Eberhard, 2003). That is, plasticity is composed of two distinct components; the plastic trait and the switching rule. It specifies the environmental input or event which causes a change of the trait, and it specifies the new manifestation of the plastic trait which will occur. We refer to reversible plasticity only. That is, an agent can alter the plastic trait several times and can alter it back to its original form.

Here, phenotype plasticity is defined within the framework of the indirect evolutionary approach by Güth and Yaari (1992), so its components are defined within the paradigm of utility theory. Hence, we define the plastic trait as a preference parameter, which represents a class of attitudes, such as; attitudes concerning the received game payoff, the division of game payoffs among

players, the intentions of players, etc. . By this definition a specific parameter value represents a certain attitude. Examples for preferences which deal with attitudes can be found in the literature on fairness preferences or social preferences. For examples, see: Levine (1997); Fehr and Schmidt (1999), Cox, Friedman and Gjerstad (2007).

With this specification, an agent's phenotype is represented by a time variant preference parameter of its utility function. Hence, this utility function is time - variant. The utility function $u_t(b_t) : S \times T \rightarrow \mathbb{R}$ represents an agent's preference at time t whose phenotype $b_t \in B = \{\beta_i, \beta_j\}$ can alter from time to time. $u_t(b_t)$ is continuous, and twice differentiable, concerning the game payoffs.

For convenience, we assume that all mutant agents switch their phenotype according to the *same* switching rule. We use a switching rule which is similar to that defined by Schmitt (2010). This consists of two elements; the activator and a specification by which the current preference parameter value is being replaced. The activator is an occurrence which activates switching the parameter. Here, we assume that the death of the current offspring, for reasons of not having gained enough material resource in period t, activates switching the preference parameter from $b_t \in B$ to $b_{t+1} \neq b_t \in B$. This changes both fractions of plastic - β_i - agents and plastic - β_j - agents in accordance with the following lemma 2.

Lemma 2 (switching rule)

In average $\frac{W_t+X_t}{N_t} \cdot (1 - \theta_{ii}) \cdot W_t + \frac{Y_t+Z_t}{N_t} \cdot (1 - \theta_{ij}) \cdot W_t$ plastic - β_i - agents and $\frac{W_t+X_t}{N_t} \cdot (1 - \theta_{ji}) \cdot Y_t + \frac{Y_t+Z_t}{N_t} \cdot (1 - \theta_{jj}) \cdot Y_t$ plastic - β_j - agents suffer death of their descendant in period t for resource scarcity, and thus change their preference from β_i to β_j respectively or vice versa.

Schmitt (2010) embeds this switching rule into a cognitive framework and relies on theories of cognitive dissonance, in particular on Cooper and Fazio (1984), and on Aronson (1992). For the detailed psychological foundation of the switching rule, we point to Schmitt (2010).

Here, we will not focus on any details of the cognitive process which yields switching. Instead we will look at the outcome only, and the effect switching has on the population composition. Thus, we treat the cognitive process as a black box. This behavioristic approach is a reasonable simplification, as we are considering 2x2 games with two (pure) strategies and two preference parameters only. In this setting, changing behavior implies playing the other strategy, and changing the preferences parameter implies switching to the other parameter.

In the next step, we embed the switching rule into the model. Switching the preference parameter is similar to migration and immigration between subpopulations. Thus, the preference switch affects the net gains R_{W_t}, R_{Y_t} .

E. The Final Model Specification

The net gains (growth factors) $R_{W_t}, R_{X_t}, R_{Y_t}, R_{Z_t}$ depend crucially on the life span of the (adult) agents. Adult agents are assumed to live for an indefinite time but will eventually die in the long run. So we allow a fraction of $l \in]0; 1[$ adult agents to die in each period. Death occurs independently of any individual trait, and independently of others agents' deaths. On the individual level, this corresponds to the assumption that for each adult agent, there is the same independent probability to survive. From lemma 1, lemma 2 and the death rate $l \in]0; 1[$ among adult agents, it follows that the net gains $R_{W_t}, R_{X_t}, R_{Y_t}, R_{Z_t}$ are of the following form:

Lemma 3:

$$R_{W_t} = -W_t + \left(a \cdot \frac{W_t + X_t}{N_t} + b \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot W_t \cdot (2 - l) + \left(1 - \frac{W_t + X_t}{N_t} \cdot c - \frac{Y_t + Z_t}{N_t} \cdot d \right) \cdot (1 - l) \cdot Y_t$$

$$R_{X_t} = -l \cdot X_t + \left(\frac{W_t + X_t}{N_t} \cdot a + \frac{Y_t + Z_t}{N_t} \cdot b \right) \cdot X_t$$

$$R_{Y_t} = -Y_t + \left(c \cdot \frac{W_t + X_t}{N_t} + d \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot Y_t \cdot (2 - l) + \left(1 - \frac{W_t + X_t}{N_t} \cdot a - \frac{Y_t + Z_t}{N_t} \cdot b \right) \cdot (1 - l) \cdot W_t$$

$$R_{Z_t} = -l \cdot Z_t + \left(\frac{W_t + X_t}{N_t} \cdot c + \frac{Y_t + Z_t}{N_t} \cdot d \right) \cdot Z_t$$

For proof see appendix B.

Inserting the net gains $R_{W_t}, R_{X_t}, R_{Y_t}, R_{Z_t}$ into the population dynamics and carrying out some mathematical operations leads to the final model specification.

Final model (limited growth):

$$(5) \quad W_{t+1} = W_t + \left(-W_t + \left(\frac{W_t + X_t}{N_t} a + \frac{Y_t + Z_t}{N_t} b \right) W_t (2 - l) + \left(1 - \frac{W_t + X_t}{N_t} c - \frac{Y_t + Z_t}{N_t} d \right) (1 - l) Y_t \right) \frac{K - N_t}{K}$$

$$(6) \quad X_{t+1} = X_t + \left(-l X_t + \left(\frac{W_t + X_t}{N_t} a + \frac{Y_t + Z_t}{N_t} b \right) X_t \right) \frac{K - N_t}{K}$$

$$(7) \quad Y_{t+1} = Y_t + \left(-Y_t + \left(\frac{W_t+X_t}{N_t} c + \frac{Y_t+Z_t}{N_t} d \right) Y_t (2-l) + \left(1 - \frac{W_t+X_t}{N_t} a - \frac{Y_t+Z_t}{N_t} b \right) (1-l) W_t \right) \frac{K-N_t}{K}$$

$$(8) \quad Z_{t+1} = Z_t + \left(-l Z_t + \left(\frac{W_t+X_t}{N_t} c + \frac{Y_t+Z_t}{N_t} d \right) Z_t \right) \frac{K-N_t}{K}$$

$$(9) \quad W_{t+1}W_t + X_t + Y_t + Z_t = N_t$$

The final model is a discrete nonlinear dynamic system. As we are interested in the fitness differences of plastic and non-plastic mutants, in the next section we discuss the differences in growth factors.

III. Discussion: Fitness of Plastic and Non - Plastic Mutants

In this section, we are searching for differences in the abilities of plastic and non - plastic mutants to invade a population of non - plastic agents. For that purpose, we apply the above formulated model to detect those environment - related parameter constellations $(l, \theta_{ii}, \theta_{ij}, \theta_{ji}, \theta_{jj})$ for which a plastic mutant who can switch between phenotype β_j and β_i is able to invade a monomorphic population of non - plastic - β_i - agents, whereas a non - plastic - β_j - mutant is not able to invade. Here, it is important to bear in mind that the number of plastic agents at any time t is given by $W_t + Y_t$. Thus, we will find the parameter values in question by ascertaining those cases for which $R_{Z_t} < 0$ and $R_{W_t} + R_{Y_t} \geq 0$. We can identify certain classes of symmetric 2x2 games, in which plastic mutants can enter a population which cannot be invaded by non - plastic mutants. Whether the non - plastic mutants, whose growth rates are negative,

become extinct or not depends on the number of time steps left from the time of mutation occurrence to the time when the capacity constraint of the population starts to become apparent. That is, the factor $\frac{K-N_t}{K}$ is becoming so small that the products of $\frac{K-N_t}{K}$ and the growth factors are reaching zero before the non - plastic mutants go extinct.

A. Invasion of Mutants

In order to find those parameters which allow for an invasion of non - plastic - β_j - mutants into a monomorphic population of non - plastic - β_i - agents, we need to set $W_t = 0$ and $Y_t = 0$ for all times t . If we are seeking parameters which allow an invasion of plastic - mutants able to switch between phenotype β_j and β_i in the same monomorphic population of non-plastic - β_i - agents, we set $Z_t = 0$ for all times t . For analysis of an invasion of non - plastic - β_j - mutants in the case of limited growth, this leads to the following model specification: $X_{t+1} = Y_t + R_{X_t} \cdot (K - N_t)/K$ and $Z_{t+1} = Z_t + R_{Z_t} \cdot (K - N_t)/K$ with $R_{X_t} = -l \cdot X_t + \left(\frac{X_t}{N_t} \cdot a + \frac{Z_t}{N_t} \cdot b\right) \cdot X_t$ and $R_{Z_t} = -l \cdot Z_t + \left(\frac{X_t}{N_t} \cdot c + \frac{Z_t}{N_t} \cdot d\right) \cdot Z_t$. If the number of mutants at time $t = 0$ is denoted with M , then $Z_0 = M$ and $N_0 = M + X_0$. The following net gains result:

$$(10) \quad R_{X_0} = -l \cdot X_0 + \left(\frac{X_0}{M+X_0} \cdot a + \frac{M}{M+X_0} \cdot b\right) \cdot X_0$$

$$(11) \quad R_{Z_0} = -l \cdot M + \left(\frac{X_0}{M+X_0} \cdot c + \frac{M}{M+X_0} \cdot d\right) \cdot M$$

The specifications for analyzing the invasion of plastic - β_j - mutants in the same population are: $W_{t+1} = W_t + R_{W_t} \cdot (K - N_t)/K$ and $X_{t+1} = X_t + R_{X_t} \cdot$

$(K - N_t)/K$ and $Y_{t+1} = Y_t + R_{Y_t} \cdot (K - N_t)/K$. As here, $Z_t = 0$, the net gains change to $R_{W_t} = -W_t + \left(a \cdot \frac{W_t + X_t}{N_t} + b \cdot \frac{Y_t}{N_t}\right) \cdot W_t \cdot (2 - l) + \left(1 - \frac{W_t + X_t}{N_t} \cdot c - \frac{Y_t}{N_t} \cdot d\right) \cdot (1 - l) \cdot Y_t$ and $R_{X_t} = -l \cdot X_t + \left(\frac{W_t + X_t}{N_t} \cdot a + \frac{Y_t}{N_t} \cdot b\right) \cdot X_t$ and $R_{Y_t} = -Y_t + \left(c \cdot \frac{W_t + X_t}{N_t} + d \cdot \frac{Y_t}{N_t}\right) \cdot Y_t \cdot (2 - l) + \left(1 - \frac{W_t + X_t}{N_t} \cdot a - \frac{Y_t}{N_t} \cdot b\right) \cdot (1 - l) \cdot W_t$. Note that $R_{W_t} + R_{Y_t} = -l \cdot (Y_t + W_t) + \left(a \cdot \frac{W_t + X_t}{N_t} + b \cdot \frac{Y_t}{N_t}\right) \cdot W_t + \left(c \cdot \frac{W_t + X_t}{N_t} + d \cdot \frac{Y_t}{N_t}\right) \cdot Y_t$ (See appendix C.) and that $W_0 + Y_0 = M$ and $N_0 = M + X_0$, if we denote the number of mutants at time $t = 0$ with M . Thus, the net gains for $t = 0$ can be written as:

$$(12) \quad R_{X_0} = -l \cdot X_0 + \left(\frac{W_0 + X_0}{M + X_0} \cdot a + \frac{M - W_0}{M + X_0} \cdot b\right) \cdot X_0$$

$$(13) \quad R_{W_0} + R_{Y_0} = -l \cdot M + \left(a \cdot \frac{W_0 + X_0}{M + X_0} + b \cdot \frac{M - W_0}{M + X_0}\right) \cdot W_0 + \left(c \cdot \frac{W_0 + X_0}{M + X_0} + d \cdot \frac{M - W_0}{M + X_0}\right) \cdot (M - W_0).$$

If we don't want the original monomorphic population of non - plastic - β_i - agents to become extinct in the long run, we need to ensure that $R_{X_t} \geq 0$ for $W_t = 0, Y_t = 0, Z_t = 0$. This is the case if $a \geq l$.

Now, we check for parameters for which $R_{Z_0} < 0$ and $R_{W_0} + R_{Y_0} > 0$. This leads to theorem 1.

Theorem 1:

Let X_0 be the number of non - plastic agents of type β_i , Z_0 the number of non-plastic mutants of type β_j and $W_0 + Y_0 = M$ the number of plastic - mutants who can switch between type β_j and β_i at time $t = 0$. W_0 is the

number of plastic agents with type β_i at time $t = 0$. Y_0 is the number of plastic agents with type β_j at time $t = 0$.

Then, for any initial state (X_0, M) and for all parameters $a \in]0,1[$ and all $b \in]0,1[$ there exists a death rate $l^* \in \left] \frac{X_0}{X_0+M} \cdot c + \frac{M}{X_0+M} \cdot d ; a \cdot \frac{(W_0+X_0) \cdot W_0}{(M+X_0) \cdot M} + b \cdot \frac{(M-W_0) \cdot W_0}{(M+X_0) \cdot M} + c \cdot \frac{(M-W_0) \cdot (W_0+X_0)}{(M+X_0) \cdot M} + d \cdot \frac{(M-W_0)^2}{(M+X_0) \cdot M} \right[$ and a capacity $K \gg N_0$ for which M plastic mutants can invade a population of non-plastic agents of type β_i which is uninvadable by M non-plastic mutants of type β_j providing for parameters c and d the following holds:

$$(I) \quad c < -d \cdot \frac{2M-W_0}{W_0+X_0-M} + a \cdot \frac{W_0+X_0}{W_0+X_0-M} + b \cdot \frac{M-W_0}{W_0+X_0-M}$$

and

$$(II) \quad d < a \cdot \frac{W_0+X_0}{2M-W_0} + b \cdot \frac{M-W_0}{2M-W_0}$$

For proof see appendix D

Note that the definition set of the death rate l in theorem 1 is the whole range from zero to 1. But we have required the parameter a to exceed (weakly) the death rate l , so that a monomorphic population of non - plastic agents of type β_i will not become extinct. Thus, we need to modify theorem 1 for death rates l^* below a . That is $a \cdot \frac{(W_0+X_0) \cdot W_0}{(M+X_0) \cdot M} + b \cdot \frac{(M-W_0) \cdot W_0}{(M+X_0) \cdot M} + c \cdot \frac{(M-W_0) \cdot (W_0+X_0)}{(M+X_0) \cdot M} + d \cdot \frac{(M-W_0)^2}{(M+X_0) \cdot M} \leq a$. We find some additional restrictions for parameter c and d , and a new restriction for parameter b (see appendix E). We sum up these findings in proposition 1.

Proposition 1

If the conditions for theorem 1 to hold are given and in addition for parameter c , d and b , the following three conditions hold, then $l^* \leq a$ exists.

$$(I') \quad c \leq a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot (W_0+X_0)} - b \cdot \frac{W_0}{(W_0+X_0)} - d \cdot \frac{(M-W_0)}{(W_0+X_0)}$$

$$(II') \quad d < a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot (M-W_0)} - b \cdot \frac{W_0}{(M-W_0)}$$

$$(III') \quad b < a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot W_0}$$

For large populations and a small mutation rate, the definition set of l^* does not depend on the magnitudes of b and d , as $\lim_{X_0 \rightarrow \infty} \frac{M}{X_0+M} = 0$, $\lim_{X_0 \rightarrow \infty} \frac{(M-W_0)^2}{(M+X_0) \cdot M} = 0$, and $\lim_{X_0 \rightarrow \infty} \frac{(M-W_0) \cdot W_0}{(M+X_0) \cdot M} = 0$. As $\lim_{X_0 \rightarrow \infty} \frac{X_0}{X_0+M} = 1$ the lower bound of l^* is about the

same size as c . The upper bound of l^* is about $c + \frac{W_0}{M} (a + c)$, because the

$$\lim_{X_0 \rightarrow \infty} a \cdot \frac{(W_0+X_0) \cdot W_0}{(M+X_0) \cdot M} + c \cdot \frac{(M-W_0) \cdot (W_0+X_0)}{(M+X_0) \cdot M} = a \cdot \frac{W_0}{M} + c \cdot \frac{W_0+M}{M} = c + \frac{W_0}{M} (a + c).$$

Moreover, for large populations with few mutants, theorem 1 can hold only if $c < a$, which follows from the boundary value analysis of condition (I). As we will discuss in the next section, $c < a$ implies that theorem 1, holds for the Prisoners Dilemma.

We have already stated that extinction of non-plastic mutants depends on the number of time steps left from the time the mutation occurs to the time when the capacity constraint of the population starts to take effect. That is, extinction of non-plastic mutants does not happen if the factor $\frac{K-N_t}{K}$ becomes so small that the product of $\frac{K-N_t}{K}$ and the growth factors approach zero before Z_t becomes nearly

zero. But, as the growth factor Z_t of the non-plastic mutants is negative and that of the plastic - mutants is positive, the number of plastic - mutants exceeds the number of non-plastic mutants. This means that overall the plastic mutants are more successful. At the beginning of the operation of the dynamic system, the product of the growth factor and $\frac{K-N_t}{K}$ of the established agents is considerably larger than the growth factors of the mutant agents. Hence, that the product of $\frac{K-N_t}{K}$ and the growth factor of the few mutants reaches the limit a number of time periods earlier than does the product of $\frac{K-N_t}{K}$ and the growth factor of the established agents.

B. Validity of the findings for symmetric 2x2 games

In section 2 we have stated that our notion of fitness induces an evolutionary 2x2 game with pure strategies only. Such a game can be represented by the following payoff matrix:

PAYOFF MATRIX OF EVOLUTIONARY GAME

	β_j	β_i
β_j	$\theta_{jj};\theta_{jj}$	$\theta_{ji};\theta_{ij}$
β_i	$\theta_{ij};\theta_{ji}$	$\theta_{ii};\theta_{ii}$

Symmetric 2x2 games can be classified into 4 categories (Weibull, 1997, 30). In games of category I $\theta_{ii} > \theta_{ji}$ and $\theta_{jj} < \theta_{ij}$, so that these games are strictly dominance solvable. A well-known example is the Prisoner's Dilemma Game. In games of category II, which have two symmetric Nash equilibria, it holds $\theta_{jj} > \theta_{ij}$ and $\theta_{ii} > \theta_{ji}$. The Coordination Game is an example of this category of

game. In category III, $\theta_{jj} < \theta_{ij}$ and $\theta_{ii} < \theta_{ji}$. Here there are two asymmetric strict Nash equilibria. The Hawk - Dove Game belongs to this category. Games of category IV, in which $\theta_{jj} > \theta_{ij}$ and $\theta_{ii} < \theta_{ji}$ are also dominance solvable, and structurally identical to games of category I. Thus, the Prisoner's Dilemma is an example of this category.

The boundary value analysis showed that our findings are valid for games of category I and category II, as there it holds $\theta_{ii} > \theta_{ji}$.

In the following, we give an example for each of these categories, and simulate the development of the population from time $t = 0$ to time $t = T$, at which point a stable pattern has established. We assume for all examples that at time $t = 0$, the following population condition is: $X_0 = 10^6$, $M = 5$, $W_0 = 1$, $Y_0 = 4$. The population carrying capacity is $K = 10^9$. For this carrying capacity, the stable pattern is reached after less than 100 time steps. The simulations were carried out in the software environment R.

3.2.1 Example Category (I): The Prisoner's Dilemma $\theta_{ii} > \theta_{ji}$ and $\theta_{jj} < \theta_{ij}$

Let $\theta_{ii} = 0.4$, $\theta_{ij} = 0.7$, $\theta_{ji} = 0.3$ and $\theta_{jj} = 0.5$. We receive the following evolutionary game payoff matrix:

THE PRISONER'S DILEMMA

	β_j	β_i
β_j	0.5;0.5	0.3;0.7
β_i	0.7;0.3	0.4;0.4

Then $l^* \in]0.3 ; 0.32[$. For $l^* = 0.31$ the development of non - plastic mutants of type β_j , which enter a population of non-plastic established agents of type β_i

is pictured in figure 1 for 100 time steps and the development of plastic mutants in figure 2. After 100 time steps, the population composition does not change, as the carrying capacity was reached. In both cases $M_0 = 10$.

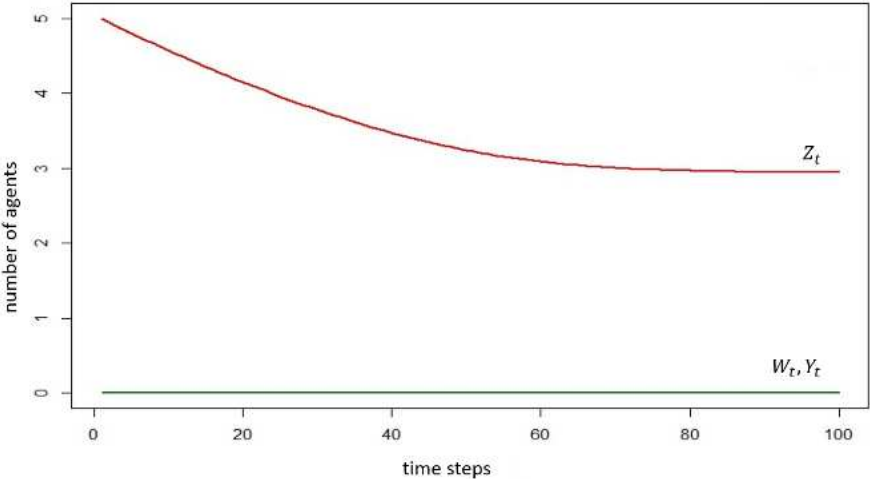


FIGURE 1: DEVELOPMENT OF NON-PLASTIC MUTANTS IN THE PRISONER'S DILEMMA GAME

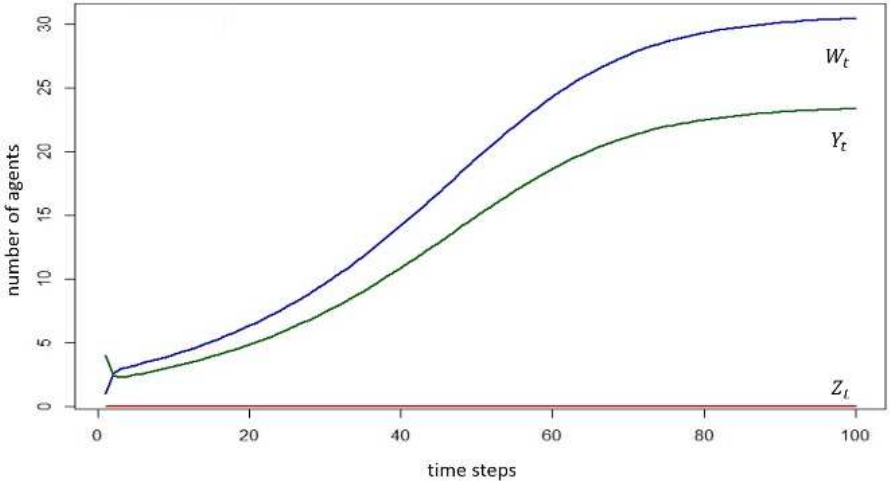


FIGURE 2: DEVELOPMENT OF PLASTIC MUTANTS IN THE PRISONER'S DILEMMA GAME

The development of plastic and non-plastic mutants which occurred simultaneously in a population of non-plastic agents of type β_i is depicted in figure 3 for 100 time steps. Here, $W_0 = 1$, $Y_0 = 4$ and $Z_0 = 5$.

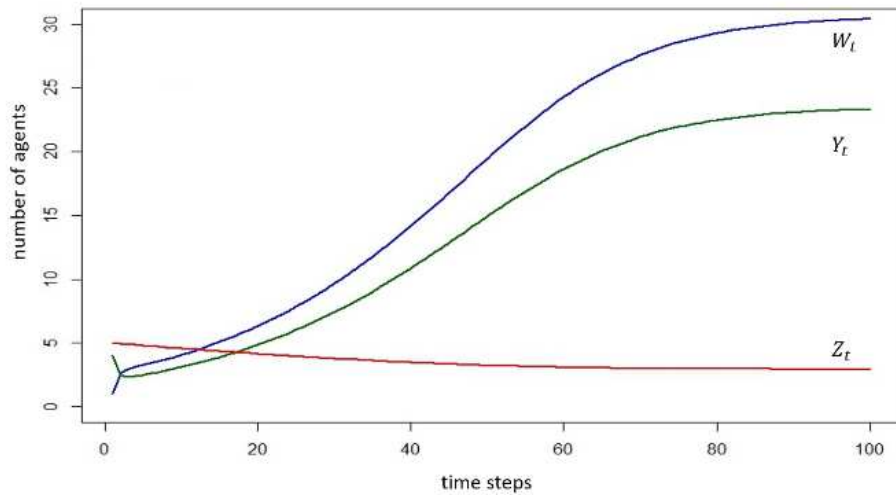


FIGURE 3: DEVELOPMENT OF SIMULTANEOUSLY OCCURRED PLASTIC AND NON-PLASTIC MUTANTS IN THE PRISONER'S DILEMMA GAME

3.2.2 Example Category (II): The Coordination Game $\theta_{jj} > \theta_{ij}$ and $\theta_{ii} > \theta_{ji}$

The Coordination Game for which $\theta_{ii} = 0.4$, $\theta_{ij} = 0.2$, $\theta_{ji} = 0.2$ and $\theta_{jj} = 0.3$ yields the following evolutionary game payoff matrix:

THE COORDINATION GAME

	β_j	β_i
β_j	0.3;0.3	0.2;0.2
β_i	0.2;0.2	0.4;0.4

Then $l^* \in]0.2 ; 0.24[$. For $l^* = 0.22$ the development of non-plastic mutants of type β_j , which occurred in a population of non-plastic agents of type β_i , is depicted in figure 4, and the development of plastic mutants in figure 5:

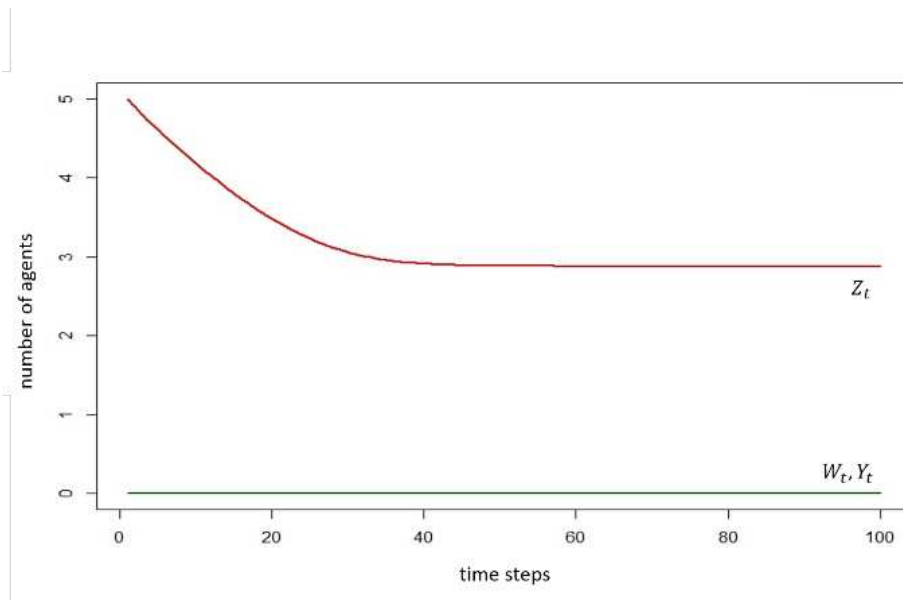


FIGURE 4: DEVELOPMENT OF NON-PLASTIC MUTANTS IN THE COORDINATION GAME

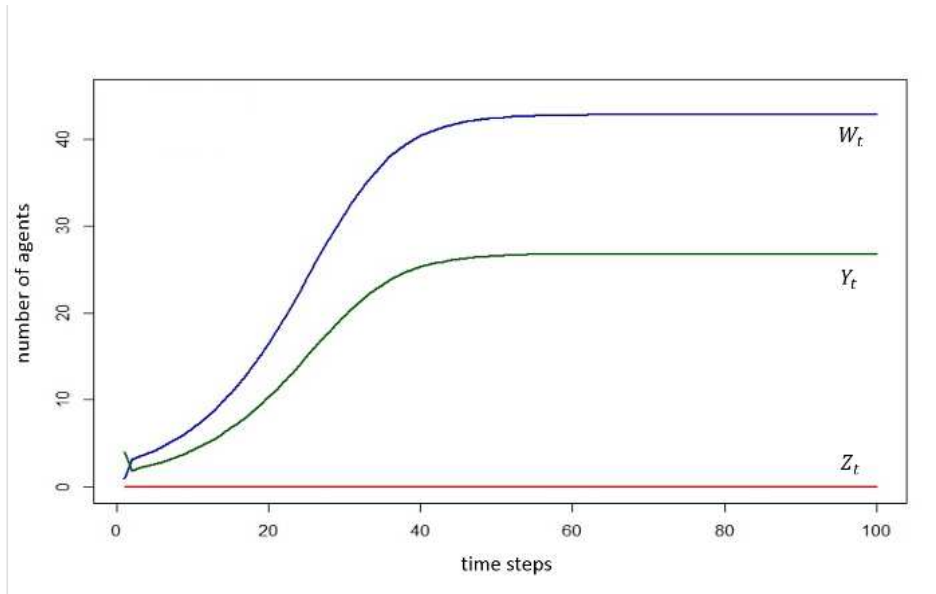


FIGURE 5: DEVELOPMENT OF PLASTIC MUTANTS IN THE COORDINATION GAME

The development of plastic and non - plastic mutants which occurred simultaneously in a population of non-plastic agents is depicted in figure 6.

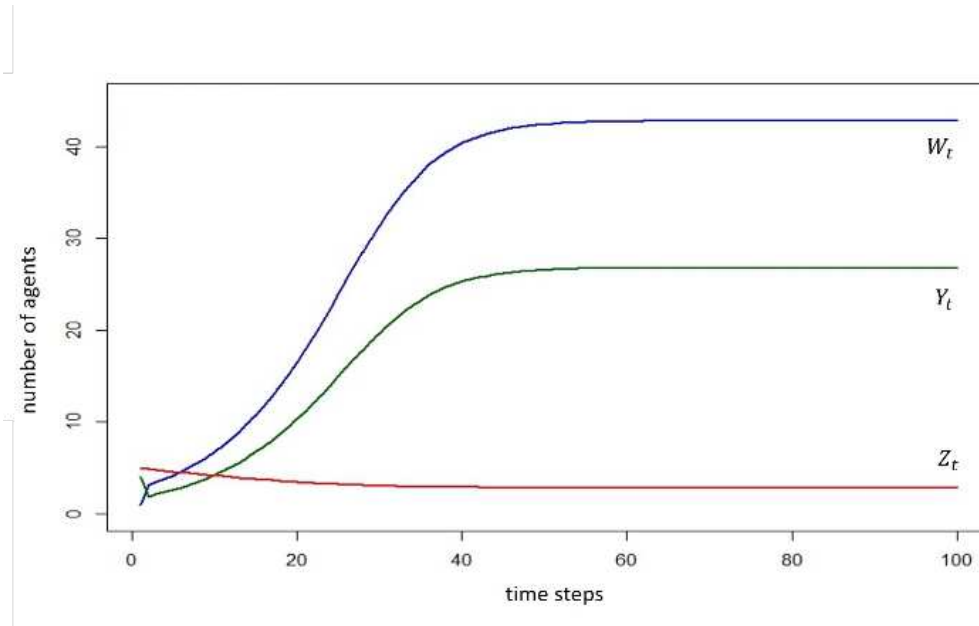


FIGURE 6: DEVELOPMENT OF SIMULTANEOUSLY OCCURRED PLASTIC AND NON-PLASTIC MUTANTS IN THE COORDINATION GAME

In the coordination game, the population reaches its stable pattern faster than in the prisoner's dilemma.

Mutant agents which can change their phenotype become a stable phenomenon in both examples. The number of plastic mutants increases about twelve - fold in the coordination game, and about ten - fold in the prisoner's dilemma game. The number of non-plastic agents stabilizes at a lower value than the initial one. Here, it is about by one half.

IV. Conclusion

We have shown that there exist conditions which cause plastic mutants to feature higher fitness than non - plastic mutants.

If the fitness of agents of the original phenotype β_i , who encounter agents of the same phenotype β_i , exceeds the fitness of agents of the mutant phenotype β_j , who encounter agents of the original phenotype β_i , that is $\theta_{ii} > \theta_{ji}$, then there exists a death rate l^* , so that mutant agents who can switch their preference exhibit higher fitness than mutant agent who cannot. In the present model the death rate represents an agent's (expected) life span. The higher the death rate, the shorter an agent's lifetime. Here, we have opted for an exogenously given (expected) life span, because it makes the resulting model more comparable to models which work with the standard assumption that each agent lives 1 period. A life span which lasts longer than one (decision) period of an organism is an important feature that paves the way for the ability to change the phenotype. Thus, further research should tie in with this and endogenize the life span of agents. That is, the death rate of adult agents could depend on the outcome of strategic interactions, and thus could become an object of evolution, too. This would be a model of coevolution of preferences and life-span.

If the carrying capacity of a population is sufficiently large in comparison to the population size at the time the mutation has occurred, then the non-plastic mutants become extinct before the population pattern stabilizes. Conversely the number of plastic - mutants stabilizes at a value above the initial number at the time of mutation occurrence. Thus, there exist conditions under which simultaneously non - plastic mutants are detained from entering, and plastic - mutants are enabled to enter a large population of non-plastic agents.

It appears that preference flexibility provides a greater fitness than preference inflexibility for symmetric 2x2 evolutionary games, which are dominance

solvable or which have two symmetric Nash equilibria. Prominent examples were the Prisoner's Dilemma and the Coordination Game.

This outcome enriches the discussion on instability versus stability of tastes. In the economists' tradition, preferences are viewed as something given with which a decision maker is endowed before making a decision. Preferences are stable. Constructivism views preferences as something that is constructed by the decision maker during the process of decision making on the basis of context factors (Ariely and Hoeffler 1999). Preferences are learned, and are thus unstable. Our model supports the view of unstable preferences, as we are able to show that even within a stable environment (that is, the game payoffs are time independent), an unstable preference can provide greater fitness than stable preferences. We conclude that, time variant preferences should not be excluded from the economic standard logic, but instead should become a part of it.

IV. Appendix

Appendix A: Proof of Lemma 1

The average amount of viable offspring of plastic agents of type β_i at time t is given by:

$$V_W^t = W_t - \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ii}) + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{ij}) \right) \cdot W_t$$
$$\Leftrightarrow V_W^t = W_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ii} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{ij} \right)$$

The average number of viable offspring of non-plastic agents of type β_i at time t is given by:

$$V_X^t = X_t - \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ii}) + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{ij}) \right) \cdot X_t$$
$$\Leftrightarrow V_X^t = X_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ii} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{ij} \right)$$

The average amount of viable offspring of plastic agents of type β_j at time t is given by:

$$V_Y^t = Y_t - \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ji}) + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{jj}) \right) \cdot Y_t$$
$$\Leftrightarrow V_Y^t = Y_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ji} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{jj} \right)$$

The average amount of viable offspring of plastic non-plastic agents of type β_i at time t is given by:

$$V_Z^t = Z_t - \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ji}) + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{jj}) \right) \cdot Z_t$$

$$\Leftrightarrow V_Z^t = Z_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ji} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{jj} \right)$$

Appendix B: Proof of Lemma 3

The net gains can be calculated as the number of viable offspring minus the number of deceased adult agents plus the number of immigrants and emigrants due to phenotype switch. With regard to lemma 1 and lemma 2 and the death rate l , we get the following net gains:

$$R_{W_t} = V_W^t - l \cdot W_t$$

$$+ \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ji}) \cdot Y_t + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{jj}) \cdot Y_t \right) \cdot (1 - l)$$

$$- \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ii}) \cdot W_t + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{ij}) \cdot W_t \right) \cdot (1 - l)$$

$$\Leftrightarrow R_{W_t} = -W_t + \left(\theta_{ii} \cdot \frac{W_t + X_t}{N_t} + \theta_{ij} \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot W_t \cdot (2 - l)$$

$$+ \left(1 - \theta_{ji} \cdot \frac{W_t + X_t}{N_t} - \theta_{jj} \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot (1 - l) \cdot Y_t$$

$$\begin{aligned}
R_{Y_t} &= V_Y^t - l \cdot Y_t \\
&\quad - \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ji}) \cdot Y_t + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{jj}) \cdot Y_t \right) \cdot (1 - l) \\
&\quad + \left(\frac{W_t + X_t}{N_t} \cdot (1 - \theta_{ii}) \cdot W_t + \frac{Y_t + Z_t}{N_t} \cdot (1 - \theta_{ij}) \cdot W_t \right) \cdot (1 - l) \\
\Leftrightarrow R_{Y_t} &= -Y_t + \left(\theta_{ji} \cdot \frac{W_t + X_t}{N_t} + \theta_{jj} \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot Y_t \cdot (2 - l) \\
&\quad + \left(1 - \theta_{ii} \cdot \frac{W_t + X_t}{N_t} - \theta_{ij} \cdot \frac{Y_t + Z_t}{N_t} \right) \cdot (1 - l) \cdot W_t
\end{aligned}$$

The net adds R_{X_t} and R_{Z_t} are not influenced by the switching rule, so the following holds:

$$\begin{aligned}
R_{X_t} &= V_X^t - l \cdot X_t = X_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ii} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{ij} \right) - l \cdot X_t \\
R_{Z_t} &= V_Z^t - l \cdot Z_t = Z_t \cdot \left(\frac{W_t + X_t}{N_t} \cdot \theta_{ji} + \frac{Y_t + Z_t}{N_t} \cdot \theta_{jj} \right) - l \cdot Z_t
\end{aligned}$$

Appendix C: $R_{W_t} + R_{Y_t}$

$$\begin{aligned}
R_{W_t} + R_{Y_t} &= -W_t + (1 - l) \cdot Y_t - Y_t + (1 - l) \cdot W_t \\
&\quad + \left(a \cdot \frac{W_t + X_t}{N_t} + b \cdot \frac{Y_t}{N_t} \right) (W_t \cdot (2 - l) - (1 - l) \cdot W_t) \\
&\quad + \left(c \cdot \frac{W_t + X_t}{N_t} + d \cdot \frac{Y_t}{N_t} \right) (Y_t \cdot (2 - l) - (1 - l) \cdot Y_t)
\end{aligned}$$

$$\begin{aligned} \Leftrightarrow R_{W_t} + R_{Y_t} &= -l \cdot (Y_t + W_t) \\ &+ \left(a \cdot \frac{W_t + X_t}{N_t} + b \cdot \frac{Y_t}{N_t} \right) \cdot W_t + \left(c \cdot \frac{W_t + X_t}{N_t} + d \cdot \frac{Y_t}{N_t} \right) \cdot Y_t \end{aligned}$$

Appendix. D: Proof of Theorem 1

Case 1: $M > W_0$. Hence: $Y_0 > \mathbf{0}$ and $W_0 > \mathbf{0}$.

M non-plastic mutants have a negative fitness at the time of their occurrence if:

$$R_{Z_0} < 0$$

$$\Leftrightarrow -l \cdot M + \left(\frac{X_0}{M+X_0} \cdot c + \frac{M}{M+X_0} \cdot d \right) \cdot M < 0$$

$$(D.1) \quad \Leftrightarrow l > \frac{X_0}{M+X_0} \cdot c + \frac{M}{M+X_0} \cdot d$$

The same number of M plastic mutants have a positive fitness at the time of their occurrence if:

$$R_{W_0} + R_{y_0} > 0$$

$$\begin{aligned} \Leftrightarrow -l \cdot M + \left(a \cdot \frac{W_0+X_0}{M+X_0} + b \cdot \frac{M-W_0}{M+X_0} \right) \cdot W_0 + \left(c \cdot \frac{W_0+X_0}{M+X_0} + d \cdot \frac{M-W_0}{M+X_0} \right) \cdot \\ (M - W_0) > 0 \end{aligned}$$

$$(D.2) \quad \Leftrightarrow \left(a \cdot \frac{W_0+X_0}{M+X_0} + b \cdot \frac{M-W_0}{M+X_0} \right) \cdot \frac{W_0}{M} + \left(c \cdot \frac{W_0+X_0}{M+X_0} + d \cdot \frac{M-W_0}{M+X_0} \right) \cdot \frac{M-W_0}{M} > l$$

Let l^* be a death rate which fulfills both inequalities, (D.1) and (D.2). Hence, such a death rate l^* exists, if there exist parameter a, b, c, d for which the following holds:

$$(D.3) \quad \left(a \cdot \frac{W_0 + X_0}{M + X_0} + b \cdot \frac{M - W_0}{M + X_0} \right) \cdot \frac{W_0}{M} + \left(c \cdot \frac{W_0 + X_0}{M + X_0} + d \cdot \frac{M - W_0}{M + X_0} \right) \cdot \frac{M - W_0}{M} > \frac{X_0}{M + X_0} \cdot c + \frac{M}{M + X_0} \cdot d$$

We solve (D.3) for parameter c .

$$(D.4) \quad \Leftrightarrow c < d \cdot \frac{W_0 - 2M}{W_0 + X_0 - M} + a \cdot \frac{W_0 + X_0}{W_0 + X_0 - M} + b \cdot \frac{M - W_0}{W_0 + X_0 - M}$$

Note that (D.4) can hold only if the right side of (D.4) is positive. Thus:

$$(D.5) \quad d \cdot \frac{W_0 - 2M}{W_0 + X_0 - M} + a \cdot \frac{W_0 + X_0}{W_0 + X_0 - M} + b \cdot \frac{M - W_0}{W_0 + X_0 - M} > 0$$

We solve (D.5) for parameter d .

$$(D.6) \quad d < -a \cdot \frac{W_0 + X_0}{W_0 - 2M} - b \cdot \frac{M - W_0}{W_0 - 2M}$$

As in this case, we have assumed that both phenotypes of the plastic mutant exist at time $t = 0$, that is: $M > W_0$, it holds $W_0 - 2M < 0$, the right side of (3.10) is positive for all parameter $a, b \in [0; 1]$.

Case 2: $M = W_0$. Hence $Y_0 = 0$.

We insert $M = W_0$ into equation (13) and get:

$$R_{W_0} + R_{Y_0} = -l \cdot W_0 + a \cdot W_0$$

If $a > l$ then $R_{W_0} + R_{Y_0} > 0$ for all $b, c, d \in [0,1]$ at time $t = 0$. At next time $t = 1$ there it holds $Y_1 > 0$ which is similar to case 1.

Case 3: $M = Y_0$. Hence: $W_0 = 0$:

We insert $M = Y_0$ into (13) and get:

$$R_{W_0} + R_{Y_0} = -l \cdot Y_0 + \left(c \cdot \frac{X_0}{Y_0 + X_0} + d \cdot \frac{Y_0}{Y_0 + X_0} \right) \cdot Y_0$$

$R_{W_0} + R_{Y_0} > 0$ if:

$$(D.7) \quad c \cdot \frac{X_0}{Y_0 + X_0} + d \cdot \frac{Y_0}{Y_0 + X_0} > l$$

We solve (D.7) for c:

$$c > l \cdot \frac{Y_0 + X_0}{X_0} - d \cdot \frac{Y_0}{X_0}$$

Inserting $Y_0 = M$ leads to

$$(D.8) \quad l < c \cdot \frac{X_0}{Y_0 + X_0} + d \cdot \frac{Y_0}{Y_0 + X_0}$$

Note, that equation (D.1) holds.

$$(D.1) \quad l > \frac{X_0}{M + X_0} \cdot c + \frac{M}{M + X_0} \cdot d$$

But (D.1) contradicts (D.8) if, as we assume, the number of mutants is the same in both cases. That is, if $W_0 = 0$ and $Y_0 > 0$, the growth rate at $t=0$ of the plastic mutants cannot be positive if the growth rate of the non-plastic mutants is negative. But, at the next point in time with $t = 1$ and $W_1 > 0$ and as a certain fraction of the plastic mutants change their type, they can invade the population.

The situation at $t = 1$ equals Case 1 and for Case 1 we have already proven that an invasion of plastic mutants is possible provided $R_{Z_0} < 0$.

Thus, the theorem 1 holds for all initial population conditions.

Appendix E: Proof of Proposition 1

$$l^* \leq a$$

$$a \cdot \frac{(W_0 + X_0) \cdot W_0}{(M + X_0) \cdot M} + b \cdot \frac{(M - W_0) \cdot W_0}{(M + X_0) \cdot M} + c \cdot \frac{(M - W_0) \cdot (W_0 + X_0)}{(M + X_0) \cdot M} + d \cdot \frac{(M - W_0)^2}{(M + X_0) \cdot M} \leq a$$

We solve this unequation for c:

$$(E.1) \quad c \leq a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot (W_0+X_0)} - b \cdot \frac{W_0}{(W_0+X_0)} - d \cdot \frac{(M-W_0)}{(W_0+X_0)}$$

$$a \cdot (W_0 + X_0) \cdot W_0 + b \cdot (M - W_0) \cdot W_0 + c \cdot (M - W_0) \cdot (W_0 + X_0) + d \cdot (M - W_0)^2 \leq a \cdot (M + X_0) \cdot M$$

$$c \cdot (M - W_0) \cdot (W_0 + X_0) \leq a \cdot (M + X_0) \cdot M - a \cdot (W_0 + X_0) \cdot W_0 - b \cdot (M - W_0) \cdot W_0 - d \cdot (M - W_0)^2$$

Case 1: $M > W_0$

$c \cdot$

$$\leq a \cdot \frac{(M + X_0) \cdot M}{(M - W_0) \cdot (W_0 + X_0)} - a \cdot \frac{(W_0 + X_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - b$$

$$\cdot \frac{(M - W_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - d \cdot \frac{(M - W_0)^2}{(M - W_0) \cdot (W_0 + X_0)}$$

$c \cdot$

$$\leq a \cdot \frac{(M + X_0) \cdot M - (W_0 + X_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - b \cdot \frac{(M - W_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - d$$

$$\cdot \frac{(M - W_0)^2}{(M - W_0) \cdot (W_0 + X_0)}$$

$$c \cdot \leq a \cdot \frac{(M + X_0) \cdot M - (W_0 + X_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - b \cdot \frac{W_0}{(W_0 + X_0)} - d \cdot \frac{(M - W_0)}{(W_0 + X_0)}$$

(E.1) holds only if the right hand side of (E.1) is positive:

$$a \cdot \frac{(M + X_0) \cdot M - (W_0 + X_0) \cdot W_0}{(M - W_0) \cdot (W_0 + X_0)} - b \cdot \frac{W_0}{(W_0 + X_0)} - d \cdot \frac{(M - W_0)}{(W_0 + X_0)} > 0$$

Solving for d leads to:

$$(E.2) \quad d < a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot (M-W_0)} - b \cdot \frac{W_0}{(M-W_0)}$$

This holds provided the right hand side is positive:

$$a \cdot \frac{(M + X_0) \cdot M - (W_0 + X_0) \cdot W_0}{(M - W_0) \cdot (M - W_0)} - b \cdot \frac{W_0}{(M - W_0)} > 0$$

$$(E.3) \quad b < a \cdot \frac{(M+X_0) \cdot M - (W_0+X_0) \cdot W_0}{(M-W_0) \cdot W_0}$$

(E.3) holds only if:

$$(M + X_0) \cdot M - (W_0 + X_0) \cdot W_0 > 0$$

$$M^2 + X_0 M - W_0^2 - X_0 W_0 > 0$$

$$M^2 - W_0^2 + X_0(M - W_0) > 0$$

As $M, W_0, X_0 \geq 1$ and $M > W_0$, this is fulfilled.

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