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Modeling evolutionary games in populations with demographic structure

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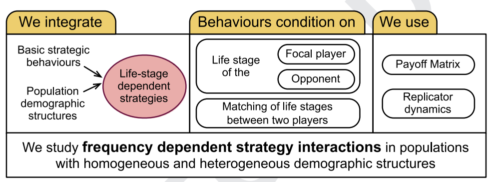
HIGHLIGHTS

- We define a strategy as a set of life stage dependent behaviours in a game.
- Behaviours can be conditioned on the life stage of one of the two players.
- Behaviours can be conditioned on the matching of life stages between the two players.
- We use the replicator dynamics to study the evolution of life stage dependent strategies.
- The equilibrium with life stage dependence can deviate from the game equilibrium.

GRAPHICAL ABSTRACT



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ABSTRACT

Classic life history models are often based on optimization algorithms, focusing on the adaptation of survival and reproduction to the environment, while neglecting frequency dependent interactions in the population. Evolutionary game theory, on the other hand, studies frequency dependent strategy interactions, but usually omits life history and the demographic structure of the population. Here we show how an integration of both aspects can substantially alter the underlying evolutionary dynamics. We study the replicator dynamics of strategy interactions in life stage structured populations. Individuals have two basic strategic behaviours, interacting in pairwise games. A player may condition behaviour on the life stage of its own, or that of the opponent, or the matching of life stages between both players. A strategy is thus defined as the set of rules that determines a player's life stage dependent behaviours. We show that the diversity of life stage structures and life stage dependent strategies can promote each other, and the stable frequency of basic strategic behaviours can deviate from game equilibrium in populations with life stage structures.

1. Introduction

The evolution of life history traits is of central importance in evolutionary theory. Classic life history theory models often use optimization arguments, focusing on how environmental conditions shape survival and reproduction, and how life history traits affect each other (Roff, 1992;

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Stearns, 1992, 2000). But the fitness landscapes of evolving populations are often not static, rather constantly changed by the phenotypic dynamics of the interacting populations (Nowak and Sigmund, 2004). Therefore, it is necessary to also consider the density and frequency dependent aspects in studying the evolution of life history. Effects of density dynamics on life history evolution have been studied thoroughly (Abrams, 1993; Hastings, 1997; Higgins et al., 1997; Williams and Day, 2003), with recent advancements in particular under the framework of adaptive dynamics (Metz et al., 1996; Meszéna et al., 2001; Ernande et al., 2004; Ernande and Dieckmann, 2004; Miethe et al., 2009; Marty et al., 2011).

Evolutionary Game Theory (Hofbauer and Sigmund, 1998; Nowak, 2006; Broom and Rychtář, 2013) provides a natural framework that includes frequency dependent selection for modelling evolution in the phenotypic space. But classic evolutionary game theory models often study populations in which an individual's strategic behaviour keeps fixed over the entire life time (Cressman, 1992). This is largely due to the fact that demographic structure of the population is typically not taken into consideration (for rare exceptions, see Day and Taylor, 1996; Cressman, 2003; Argasinski and Broom, 2013). By integrating evolutionary game dynamics and life history theory, here we study the interplay of the two fundamental aspects of evolutionary processes. We show that a more intricate dynamics is produced when both aspects are taken into consideration (McNamara, 2013).

In a population where individuals differ in life stages, it is natural that the strategic behaviour can vary accordingly. Since behavioural changes may not necessarily depend on age (Groenendael et al., 1988), here we adopt the idea of a life stage based model (Caswell, 2001). For simplicity, we assume that individuals only have two life stages, young and senescent. In addition, we assume that compared to the dynamics of strategic interactions (which is determined by biological reproduction in evolutionary game theory), the update of demographic structure (which reflects chronological ageing) is fast and thus typically in equilibrium. Therefore, the proportions of young and senescent individuals are constant for each strategic group. These proportions correspond to the elements of the appropriately normalized right eigenvector, corresponding to the leading eigenvalue, of the population projection matrix that contains the vital rates of the relevant group. This vector is proportional to the stable stage distribution of the population (Caswell, 2001). It should be noted that we have adopted the terminology "young" and "senescent" to suggest that the two stages through which individual's transition can often be interpreted as ages. However, one should keep in mind that our models can be interpreted as composed of two age classes only in cases where the proportion of young individuals is greater than one-half. This is a prerequisite for sustaining population size in the long term.

The replicator equations describe deterministic strategy dynamics in infinitely large, well-mixed populations, serving as the starting point and most standard approach for studying evolutionary game interactions (Taylor and Jonker, 1978; Zeeman, 1980; Hofbauer and Sigmund, 1998). As a first step of integrating life history structures into evolutionary game dynamics, we start from the very basic and choose the replicator dynamics as the underlying mechanism of strategy updates.

In populations with no demographic structure, a two-player evolutionary game with two strategic behaviours A and B can be written in the form of a payoff matrix as

$$\begin{array}{cc} & \begin{array}{cc} A & B \end{array} \\ \begin{array}{c} A \\ B \end{array} & \begin{pmatrix} a & b \\ c & d \end{pmatrix} \end{array} \tag{1}$$

Individuals meet randomly and interact in pairs. If both players play the A strategy, each of them receives a payoff of a. If one player plays the A strategy and the other plays the B strategy, the A strategy player receives a payoff of b and the B strategy player receives a payoff of c. If both players play the B strategy, they both receive a payoff of d.

If individuals have distinct young and senescent life stages in the population, their behaviours can be conditioned on the focal player's life stage, the opponent's life stage, or the matching of life stages between the two players. In the following, we study these cases separately.

2. Behaviour conditioned on the player's own life stage

2.1. Payoff matrix

In a population where individuals have young and senescent life stages and two strategic behaviour options, there can be four different life-stage dependent strategies: always play A (AA), play A when young but play B when senescent (AB), play B when young but play A when senescent (BA), and always play B (BB), if an individual's behaviour is determined by its current life stage. In the following we denote the proportions of young individuals in the four strategic subpopulations as p_A^A, p_A^B, p_B^A, and p_B^B.

If population demography is fixed, p_A^A, p_A^B, p_B^A and p_B^B are constant. Since individuals condition behaviours on their own life stages, the demographic substructures of AA and BB individuals do not matter, because these individuals behave in the same way all the time. Therefore the values of p_A^A and p_B^B do not appear in the payoff matrix here. Only p_A^B and p_B^A affect an individual's payoff.

Now the average payoff for each pair of strategy interactions can be calculated. For example, the average payoff of an AB individual playing against a BA individual is $p_A^B p_B^A b + p_A^B q_B^A a + q_A^B p_B^A d + q_A^B q_B^A c$, where $q_A^B = 1 - p_A^B$ and $q_B^A = 1 - p_B^A$ are frequencies of senescent individuals in the AB and BA subpopulations. In this way, the payoff matrix M of all pairwise interactions can be written as

$$\begin{array}{cc} & \begin{array}{cccc} AA & AB & BA & BB \end{array} \\ \begin{array}{c} AA \\ AB \\ BA \\ BB \end{array} & \begin{pmatrix} a & p_A^B a + q_A^B b & p_B^A b + q_B^A a & b \\ p_A^B a + q_A^B c & (p_A^B)^2 a + p_A^B q_A^B (b+c) + (q_A^B)^2 d & p_A^B p_B^A b + p_A^B q_B^A a + q_A^B p_B^A d + q_A^B q_B^A c & p_A^B b + q_A^B d \\ p_B^A c + q_B^A a & p_B^A p_A^B c + p_B^A q_A^B d + q_B^A p_A^B a + q_B^A q_A^B b & (p_B^A)^2 d + p_B^A q_B^A (b+c) + (q_B^A)^2 a & p_B^A d + q_B^A b \\ c & p_A^B c + q_A^B d & p_B^A d + q_B^A c & d \end{pmatrix} \end{array} \tag{2}$$

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