



Evolutionary game dynamics with impulsive effects

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ABSTRACT

The jumps in population size due to the occurrence of an unfavorable physical environment (e.g. the effects of periodic climate disaster on the population size), or due to the intrinsic physiological and reproductive mechanisms of the population (e.g. the seasonal reproduction of most animal populations), can be called impulsive perturbations. A two-phenotype evolutionary game dynamics with impulsive effects is investigated. The main goal is to show how the evolutionary game dynamics is affected by the impulsive perturbations. The results show that the impulsive perturbations not only result in periodic behavior, but also it is possible that an ESS strategy based on the traditional concept of evolutionary stability can be replaced successfully by a non-ESS strategy.

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1. Introduction

The jumps in population size due to the occurrence of an unfavorable physical environment (e.g. the effects of periodic climate disaster on the population size), or due to the intrinsic physiological and reproductive mechanisms of the population (e.g. the seasonal reproduction of most wild animal populations), are called impulsive perturbations. Theoretically, the Lotka–Volterra systems with impulsive perturbations have been analyzed by some authors using the theory of impulsive differential equation (Laksmikantham et al., 1989; Bainov and Simeonov, 1993; Ballinger and Liu, 1997; Liu and Rohlf, 1998; Liu and Chen, 2003, 2004; Tang and Chen, 2003; Jin et al., 2004; Pei et al., 2005; Zhang et al., 2005; Song and Xiang, 2006; Liu et al., 2007). For example, consider the classic Logistic model

$$\frac{dN}{dt} = rN \left(1 - \frac{N}{K} \right),$$

where N represents the population size, r the intrinsic growth rate, and K the carrying capacity of environment. For the population dynamics with impulsive effects, the key assumption is that the impulsive perturbations (external effects) can cause jumps in the population size (Bainov and Simeonov, 1993). As a result of an impulsive perturbation at the moment $t = \tau_k$ let the

population size suffer an increment δ_k , that is

$$\Delta N(\tau_k) = N(\tau_k^+) - N(\tau_k^-) = \delta_k,$$

where $N(\tau_k^-)$ and $N(\tau_k^+)$, are respectively, the population sizes before and after the impulsive effect. For the case with $\Delta N = C$ and $N(\tau_k^-) = \tilde{N}$ ($\tau_k = kT$), the Logistic model with impulsive effect has a T -periodic solution

$$N(t) = \begin{cases} \frac{K(\tilde{N} + C)}{\tilde{N} + C + (K - \tilde{N} - C)e^{-rt}} = N_0(t) & \text{for } 0 < t \leq T, \\ N_0(t - kT) & \text{for } kT < t \leq kT + T \end{cases}$$

for $k = 0, 1, 2, \dots$, where

$$T = \frac{1}{r} \ln \frac{(K - \tilde{N} - C)\tilde{N}}{(\tilde{N} + C)(K - \tilde{N})}$$

(see Bainov and Simeonov, 1993). Although the theory of population dynamics with impulsive perturbations has been used to explain the impulsive stabilization and optimal control of population dynamics (Liu, 1995; Fan and Wang, 1998; Angelova and Dishliev, 2000; Tang and Chen, 2002; Xiao et al., 2006), the species coexistence (Chesson et al., 2004; Wang et al., 2007; Pei et al., 2005), the biological control and management of pesticide (Grasman et al., 2001; Tang and Cheke, 2005), and the mechanisms of epidemiology (Donofrio, 1997; Shulgi et al., 1998; Roberts and Kao, 1998), the effects of impulsive perturbations on the population evolutionary dynamics are still not clear.

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In order to explain the evolution of animal behavior, **Maynard Smith (1982)** developed the concept of an evolutionarily stable strategy (ESS) (see also **Maynard Smith and Price, 1973**). According to **Maynard Smith's (1982)** definition, an ESS is a strategy which, if adopted by a population of players, cannot be invaded by any alternative strategy. For the standard evolutionary game dynamics based on the payoff matrix, it has been shown that if an interior equilibrium is an ESS equilibrium, then it must be asymptotically stable (**Taylor and Jonker, 1978; Maynard Smith, 1982; Hofbauer and Sigmund, 1988, 1998; Cressman, 1992**). Recently, **Nowak et al. (2004)** studied the emergence of cooperation and evolutionary stability in finite populations using the Moran process. Cooperators help others at a cost to themselves, while defectors receive the benefits of altruism without providing any help in return. In general, defectors are stable against invasion by cooperators. This is based on the traditional concept of evolutionary stability and dynamics in infinite populations. However, for evolutionary game dynamics in finite populations, **Nowak et al. (2004)** showed that a single cooperator can invade a population of defectors with a probability that corresponds to a net selective advantage.

It is well known that the seasonal reproduction is one of the most important characteristics of most wild animal populations. **Tang and Chen (2002)** developed a single-species model with stage structure for the dynamics in a wild animal population for which births occur in a single pulse once per time period. Their main result shows that the dynamical behavior of the single species model with birth pulse can be very complex. From an evolutionary game perspective, a natural question is how the evolutionary stability of phenotypes is affected by the seasonal reproduction (or the impulsive perturbations due to the other reasons). For example, for the classical hawk–dove model developed by **Maynard Smith (1982)**, if the characteristic of seasonal reproduction (or the mechanism of impulsive perturbations) is introduced into this model, we have to answer whether the traditional concept of evolutionary stability is still valid. In this paper, a simple two-phenotype evolutionary game model with impulsive perturbations is investigated. Our main goal is to show how the evolutionary game dynamics is influenced by the impulsive perturbations, and to reveal the relationship between the dynamical properties of the system and the traditional concept of evolutionary stability.

2. Basic model

Consider a standard two-phenotype matrix evolutionary game model, where the two pure strategies are denoted by R_1 and R_2 , respectively, and the payoff matrix is given by $\mathbf{A} = (a_{ij})_{2 \times 2}$. In this model, it is assumed that (a) each individual uses one of two possible pure strategies; (b) individuals interact in random pairwise contests; and (c) a_{ij} is the payoff of strategy R_i when interacting with strategy R_j for $i, j = 1, 2$ (**Maynard Smith, 1982**). We assume also that all individuals are pure strategists and that they have the same density-dependent background fitness, denoted by $W(N)$ with $dW(N)/dN < 0$ where N is the population size (**Maynard Smith, 1982**). Let n_i denote the number of individuals using strategy R_i ($i = 1, 2$), i.e., $N = n_1 + n_2$, and x the frequency of strategy R_1 in the population, i.e., $x = n_1/N$. According to **Maynard Smith (1982)**, the dynamics for n_i can be given by

$$\frac{dn_i}{dt} = n_i(f_i + W(N)) \tag{1}$$

for $i = 1, 2$, where f_i represents the expected payoff of strategy R_i , i.e.,

$$f_i = xa_{i1} + (1 - x)a_{i2}, \tag{2}$$

and the mean payoff of the population is

$$\bar{f} = xf_1 + (1 - x)f_2. \tag{3}$$

Clearly, the frequency dynamics can be given by

$$\frac{dx}{dt} = x(1 - x)(f_1 - f_2) \tag{4}$$

and is also density-independent. For this simple evolutionary game dynamics, **Maynard Smith (1982)** showed that (a) Eq. (4) has a unique interior positive equilibrium $x^* = (a_{12} - a_{22}) / (a_{12} - a_{22} + a_{21} - a_{11})$ with $x^* \in (0, 1)$ if and only if both $a_{12} - a_{22}$ and $a_{21} - a_{11}$ are positive, or both are negative; (b) the interior positive equilibrium x^* is asymptotically stable if and only if x^* is an ESS equilibrium, i.e., $a_{12} > a_{22}$ and $a_{21} > a_{11}$; (c) the boundary $x = 1$ (or $x = 0$) is asymptotically stable if and only if the pure strategy R_1 (or R_2) is an ESS, i.e., $a_{11} > a_{21}$ (or $a_{22} > a_{12}$) (see also **Lessard, 1984; Hofbauer and Sigmund, 1988, 1998; Cressman, 1992**).

As pointed out in Section 1, we introduce the mechanism of impulsive perturbations into the above standard evolutionary game model, where the impulsive perturbations can be due to the intrinsic physiological and reproductive mechanisms of animal population (e.g. seasonal reproduction), or due to the occurrence of an unfavorable physical environment. In order to do this, we make some basic assumptions:

- (i) There are effects of impulsive perturbations on the number of individuals that can cause jumps in the number of individuals with phenotype R_i ($i = 1, 2$), $n_i(t)$. As a result of an impulsive perturbation at the moment $t = t_k$, the number of individuals with phenotype R_i ($i = 1, 2$), $n_i(t)$, suffers an increment $\Delta n_i(t_k)$, that is $\Delta n_i(t_k) = n_i(t_k^+) - n_i(t_k^-)$ where $n_i(t_k^+)$ and $n_i(t_k^-)$ are, respectively, the numbers of individuals with phenotype R_i after and before the impulsive effect. A natural constraint is $n_i(t_k^+) = n_i(t_k^-) + \Delta n_i(t_k) > 0$ which means that the number of individuals with phenotype R_i is not destroyed as a result of the impulsive effect (**Bainov and Simeonov, 1993**).
- (ii) For the phenotype R_i ($i = 1, 2$), the increment $\Delta n_i(t_k)$ depends on $n_i(t_k^-)$, that is defined as $\Delta n_i = \gamma_i n_i$ for $t = t_k$ where γ_i is a constant with $\gamma_i > -1$ (i.e., $n_i(t_k^+)$ must be positive) (**Bainov and Simeonov, 1993**). For $\gamma_1 \neq \gamma_2$, it means that the effects of impulsive perturbations on the numbers of individuals with phenotype R_1 and with phenotype R_2 are different.
- (iii) For simplicity, it is assumed that the moments t_k are τ -periodic: $t_k = t_0 + k\tau$ for $k = 1, 2, \dots$, i.e., the impulsive effect takes place after equal time intervals.

According to the above three assumptions, Eq. (1) can be rewritten as

$$\frac{dn_i}{dt} = n_i(f_i + W(N)), \quad t \neq k\tau, \tag{5}$$

$$\Delta n_i = \gamma_i n_i, \quad t = k\tau, \quad k = 0, 1, 2, \dots$$

for $i = 1, 2$. Normally, this equation is called the impulsive differential equation. For our main goal, we are more interested in the effects of impulsive perturbations on the frequency dynamics. Notice that, at the moment $t = k\tau$, the increment in the frequency of phenotype R_1 , x , denoted by Δx , is

$$\Delta x = U(x)x(1 - x), \tag{6}$$

where

$$U(x) = \frac{\gamma_1 - \gamma_2}{1 + x\gamma_1 + (1 - x)\gamma_2} \tag{7}$$

with $-1 < U(x) < 1$ and $dU(x)/dx = -U(x)^2$. Thus, similarly to Eq. (5), the impulsive differential equation for the frequency

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