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

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

for $k = 0, 1, 2, \ldots$, 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 $\mathrm{d}W(N)/\mathrm{d}N < 0$ 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

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = n_i(f_i + W(N)) \tag{1}$$

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

$$\frac{\mathrm{d}x}{\mathrm{d}t} = x(1 - x)(f_1 - f_2) \tag{4}$$

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 $k = 1, 2, \ldots$, i.e., the impulsive effect takes place after equal time intervals.

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

$$\frac{\mathrm{d}n_i}{\mathrm{d}t} = n_i(f_i + W(N)), \quad t \neq k\tau,$$

$$\Delta n_i = \gamma_i n_i, \quad t = k\tau, \quad k = 0, 1, 2, \ldots \tag{5}$$

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 $\mathrm{d}U(x)/\mathrm{d}x = -U(x)^2$. Thus, similarly to Eq. (5), the impulsive differential equation for the frequency

dynamics can be given by

$$\frac{\mathrm{d}x}{\mathrm{d}t} = Q(x), \quad t \neq k\tau,$$

$$\Delta x = U(x)x(1-x), \quad t = k\tau, \ k = 0, 1, 2, \ldots, \tag{8}$$

where $Q(x) = x(1-x)(f_1 - f_2)$.

3. Stability analysis

In order to show the dynamical properties of Eq. (8), we first introduce two definitions:

Definition 1. $x(t,\tilde{x})$ is a τ-periodic solution of Eq. (8) if there exists a $\tau > 0$ such that, for any $t \geqslant 0$, $x((t+\tau)^{\pm}, \tilde{x}) = x(t^{\pm}, \tilde{x})$. Here, $x(0, \tilde{x}) = \tilde{x}$.

Definition 2. A τ-periodic solution of Eq. (8), $x(t, \tilde{x})$, is stable if there exists a deleted neighborhood of $\tilde{x}$, denoted by $\cup^{\mathrm{o}}(\tilde{x})$ with $\tilde{x} \notin \cup^{\mathrm{o}}(\tilde{x})$, such that for any $x_0 \in \cup^{\mathrm{o}}(\tilde{x})$ the limit points of the solution $x(t, x_0)$ are on the periodic orbit $x(t, \tilde{x})$.

From the existence and uniqueness of the solution of impulsive differential equation (see Bainov and Simeonov, 1993), for Eq. (8) there must exist a unique $F(x) \in (0,1)$ such that for all $x \in (0,1)$

$$\int_{h(x)}^{F(x)} \frac{\mathrm{d}s}{Q(s)} = \tau, \tag{9}$$

where $h(x) = x + \Delta x$ with $h(x) \in (0,1)$ and $\mathrm{d}h(x)/\mathrm{d}x = (1 - xU(x))(1 + (1-x)U(x)) > 0$.

Lemma 1. *Eq. (8) has a τ-periodic solution if and only if $F(x)$ has a fixed point.*

Proof. Let $\tilde{x} = F(\tilde{x})$ with $\tilde{x} \in (0,1)$. Then, from Eq. (9), we have

$$\int_{h(\tilde{x})}^{\tilde{x}} \frac{\mathrm{d}s}{Q(s)} = \tau.$$

Notice that $x(t, \tilde{x})$ is the solution of Eq. (8), i.e.,

$$\int_{h(\tilde{x})}^{x(\tau)} \frac{\mathrm{d}s}{Q(s)} = \tau.$$

Thus, $x(\tau) = F(\tilde{x}) = \tilde{x}$. Clearly, for all $k = 0, 1, 2, \ldots$ we have $x(k\tau) = \tilde{x}$, i.e., $\tilde{x}$ is a fixed point of $F(x)$. $\square$

Lemma 2. *$F(x)$ is an increasing function of x, i.e., $F(x_1) \geqslant F(x_2)$ for all $x_1 \geqslant x_2$ with $x_1, x_2 \in (0,1)$.*

Proof. Notice that $h(x)$ is an increasing function in the interval $0 < x < 1$. From Eq. (9), we have

$$\int_{h(x_1)}^{F(x_1)} \frac{\mathrm{d}s}{Q(s)} = \int_{h(x_2)}^{F(x_2)} \frac{\mathrm{d}s}{Q(s)} = \tau.$$

This implies also that

$$\int_{h(x_2)}^{h(x_1)} \frac{\mathrm{d}s}{Q(s)} = \int_{F(x_2)}^{F(x_1)} \frac{\mathrm{d}s}{Q(s)}.$$

Thus, $F(x)$ is an increasing function of x in the interval $0 < x < 1$. $\square$

Theorem 1. *Assume $F(x)$ has a fixed point $\tilde{x}$. Then $x(t,\tilde{x})$ is a stable τ-periodic solution of Eq. (8) if and only if*

$$\lim_{x \to \tilde{x}} \mathrm{sgn}((F(x) - x)(x - \tilde{x})) = -1, \tag{10}$$

where $\mathrm{sgn}(x)$ is the sign function, which is defined as $\mathrm{sgn}(x) = 1$ if $x > 0$, $\mathrm{sgn}(x) = -1$ if $x < 0$, and $\mathrm{sgn}(x) = 0$ if $x = 0$.

Proof. For simplicity, we here give only the proof for sufficiency. If Eq. (10) holds, there must exist a deleted neighborhood of $\tilde{x}$,

denoted by $\cup^{\mathrm{o}}(\tilde{x})$ with $\tilde{x} \notin \cup^{\mathrm{o}}(\tilde{x})$, such that $(F(x) - x)(x - \tilde{x}) < 0$ for $x \in \cup^{\mathrm{o}}(\tilde{x})$ with $F(\tilde{x}) - \tilde{x} = 0$. Denote $x_k = x(k\tau)$ for $k = 0, 1, 2, \ldots$, i.e., $x(k\tau^+) = h(x_k)$ and $x_{k+1} = F(x_k)$. For $x_0 > \tilde{x}$ with $x_0 \in \cup^{\mathrm{o}}(\tilde{x})$, we have $x_1 - x_0 = F(x_0) - x_0$, i.e., $\tilde{x} < x_1 < x_0$. By similar arguments, we have $\tilde{x} < x_{k+1} < x_k$ for $k = 0, 1, 2, \ldots$. Similarly, for $x_0 < \tilde{x}$ with $x_0 \in \cup^{\mathrm{o}}(\tilde{x})$, we have $\tilde{x} > x_{k+1} > x_k$ for $k = 0, 1, 2, \ldots$. $\square$

Corollary 1. *$x(t,\tilde{x})$ is a globally asymptotically stable τ-periodic solution of Eq. (8) if and only if $(F(x) - x)(x - \tilde{x}) < 0$ for all $x \in (0,1)$ with $x \neq \tilde{x}$.*

Proof. The proof is similar to Theorem 1. $\square$

Corollary 2. *$x(t,\tilde{x})$ is a semi-stable τ-periodic solution of Eq. (8) if and only if the following one-sided limits exist and satisfy*

$$\lim_{x \to \tilde{x}^+} \mathrm{sgn}((F(x) - x)(x - \tilde{x})) = -\lim_{x \to \tilde{x}^-} \mathrm{sgn}((F(x) - x)(x - \tilde{x})). \tag{11}$$

Proof. The proof is similar to Theorem 1. $\square$

Corollary 3. *For Eq. (8), if no periodic solution exists in the interval $0 < x < 1$, then the trajectory will either converge to the boundary $x = 1$ or 0.*

Proof. The straightforward proof is omitted. $\square$

According to Eq. (9), let

$$\Phi(x) = \int_{h(x)}^{x} \left(\frac{\lambda_1}{s} + \frac{\lambda_2}{1-s} + \frac{\lambda_3}{\alpha s + \beta(1-s)} \right) \mathrm{d}s$$

$$= \ln \left[\left(\frac{x}{h(x)} \right)^{\lambda_1} \left(\frac{1-x}{1-h(x)} \right)^{-\lambda_2} \left(\frac{(\alpha-\beta)x + \beta}{(\alpha-\beta)h(x) + \beta} \right)^{(\lambda_3/\alpha - \beta)} \right], \tag{12}$$

where $\alpha = a_{11} - a_{21}$, $\beta = a_{12} - a_{22}$, $\lambda_1 = 1/\alpha$, $\lambda_2 = 1/\beta$ and $\lambda_3 = -(\alpha - \beta)^2/(\alpha\beta)$. From Lemma 1, if Eq. (8) has a τ-periodic solution $x(t,\tilde{x})$, then we must have $\Phi(\tilde{x}) = \tau$.

Corollary 4. *(i) If $x(t,\tilde{x})$ is a τ-periodic solution of Eq. (8), then $x(t,\tilde{x})$ is locally stable if and only if*

$$\frac{\mathrm{d}\Phi(x)}{\mathrm{d}x} Q(x) > 0 \tag{13}$$

for all x in some deleted neighborhood $\cup^{\mathrm{o}}(\tilde{x})$. (ii) If $x(t,\tilde{x})$ is a τ-periodic solution of Eq. (8), then $x(t,\tilde{x})$ is locally semi-stable if and only if

$$\frac{\mathrm{d}\Phi(x)}{\mathrm{d}x} Q(x)(x - \tilde{x}) \tag{14}$$

has the same sign for all $x \in \cup^{\mathrm{o}}(\tilde{x})$. (iii) The boundary $x = 0$ is locally stable if and only if

$$\lim_{x \to 0^+} (\Phi(x) - \tau)Q(x) > 0, \tag{15}$$

and, similarly, the boundary $x = 1$ is locally stable if and only if

$$\lim_{x \to 1^-} (\Phi(x) - \tau)Q(x) < 0. \tag{16}$$

Obviously, the boundary $x = 0$, or $x = 1$, is globally stable if and only if $(\Phi(x) - \tau)Q(x) > 0$, or $(\Phi(x) - \tau)Q(x) < 0$, in the interval $0 < x < 1$.

Proof. (i) Similar to the proof of Theorem 1, we here give only the proof of the sufficiency. For $x \in \cup^{\mathrm{o}}(\tilde{x})$, if $Q(x) > 0$, then $(\mathrm{d}\Phi(x)/\mathrm{d}x)Q(x) > 0$ implies that $\Phi(x) < \Phi(\tilde{x})$ if $x < \tilde{x}$, and $\Phi(x) > \Phi(\tilde{x})$ if $x > \tilde{x}$. Notice that

$$\int_{h(x)}^{x} \frac{\mathrm{d}s}{Q(s)} < \int_{h(x)}^{F(x)} \frac{\mathrm{d}s}{Q(s)} = \int_{h(\tilde{x})}^{\tilde{x}} \frac{\mathrm{d}s}{Q(s)} = \tau \tag{17}$$

if $x < \tilde{x}$, and

$$\int_{h(x)}^{x} \frac{\mathrm{d}s}{Q(s)} > \int_{h(x)}^{F(x)} \frac{\mathrm{d}s}{Q(s)} = \int_{h(\tilde{x})}^{\tilde{x}} \frac{\mathrm{d}s}{Q(s)} = \tau \tag{18}$$

if $x > \tilde{x}$. Thus, we have $(F(x) - x)(x - \tilde{x}) < 0$. Similarly, for the situation $Q(x) < 0$ with $x \in \cup^o(\tilde{x})$, we have the same result. (ii) The proof is similar to (i). (iii) From the definition of $F(x)$, the proof is obvious. $\square$

4. Results

In general, it is not easy to obtain the analytic expression of $F(x)$. However, as a special case with $\lambda_1 = \lambda_2 = \lambda$ and $\lambda_3 = 0$, i.e., $\alpha = \beta$, and $\lambda = 1/\alpha = 1/\beta$, the function $F(x)$ can be expressed as

$$F(x) = \frac{x(1 + U(x)(1 - x))}{e^{-\tau/\lambda} + (1 - e^{-\tau/\lambda})x(1 + U(x)(1 - x))}. \tag{19}$$

For the fixed points of $F(x)$, it is easy to see that both $x = 0$ and 1 are trivial solutions of equation $F(x) = x$, and that if

$$\frac{1}{1 - e^{-\tau/\lambda}} + \frac{1 + \gamma_2}{\gamma_1 - \gamma_2} = 0,$$

then $F(x) = x$ holds for all possible $x \in (0, 1)$, and, conversely, if

$$\frac{1}{1 - e^{-\tau/\lambda}} + \frac{1 + \gamma_2}{\gamma_1 - \gamma_2} \neq 0,$$

then no interior positive fixed point can exist. This means that for $\alpha = \beta$ if $1/(1 - e^{-\tau/\lambda}) + (1 + \gamma_2)/(\gamma_1 - \gamma_2) = 0$, i.e., $\tau = -\lambda \ln((1 + \gamma_1)/(1 + \gamma_2))$, then for any initial value $x_0 \in (0, 1)$, $x(t, x_0)$ will be a τ-periodic solution of Eq. (8) (see Fig. 1).

For the situation with $\alpha \neq \beta$, notice that $dh(x)/dx = (1 - U(x)x)(1 + U(x)(1 - x))$, i.e., $dh(x)/dx > 0$. Thus, we have that

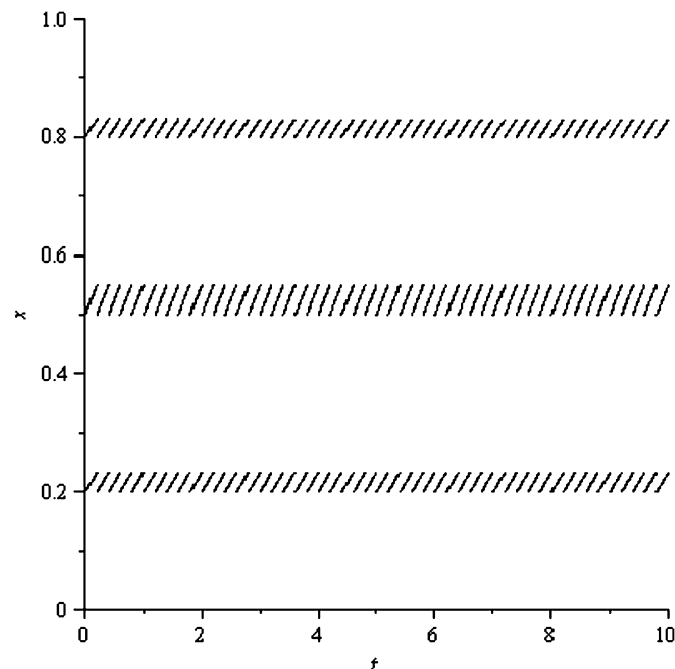$$\frac{d\Phi(x)}{dx} = \frac{(\alpha - \beta)U(x)}{S(x)}, \tag{20}$$

where

$$S(x) = ((\alpha - \beta)x + \beta)((\alpha - \beta)(x + U(x)x(1 - x)) + \beta). \tag{21}$$

For convenience, assume $\gamma_1 < \gamma_2$, i.e.,

$$\frac{\gamma_1 - \gamma_2}{1 + \gamma_1} < U(x) < \frac{\gamma_1 - \gamma_2}{1 + \gamma_2} < 0.$$

The analysis for the case with $\gamma_1 > \gamma_2$ will be similar. For the existence and stability of periodic solution of Eq. (8), we have that:

(i) If both α and β are positive, i.e., the pure strategy R_1 is an ESS, then $Q(x) > 0$, $S(x) > 0$, and $d\Phi(x)/dx < 0$ (or > 0) if $\alpha - \beta > 0$
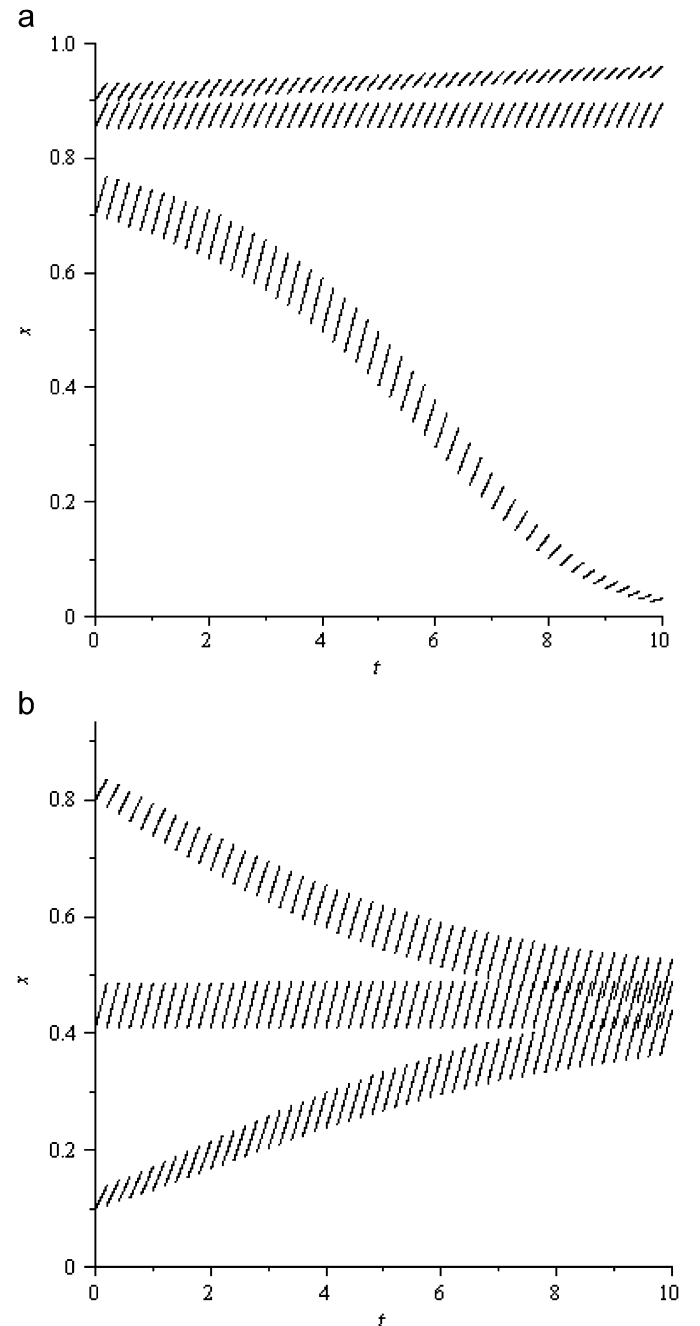
Fig. 2. $\alpha > 0$ and $\beta > 0$, i.e., the pure strategy R_1 is an ESS. (a) Payoff matrix is $\begin{pmatrix} 6 & 4 \\ 4 & 3 \end{pmatrix}$ with $\alpha = 2$ and $\beta = 1$. The parameters γ_1 and γ_2 are taken as $\gamma_1 = 0.1$ and $\gamma_2 = 0.6$. Since $\Phi(1) = 0.155$ and $\Phi(0) = 0.310$, there is a unstable τ-periodic solution with $\tau = 0.2$. (b) Payoff matrix is $\begin{pmatrix} 5 & 5 \\ 4 & 3 \end{pmatrix}$ with $\alpha = 1$ and $\beta = 2$. The parameters γ_1 and γ_2 are taken as $\gamma_1 = 0.1$ and $\gamma_2 = 0.5$. Since $\Phi(0) = 0.155$ and $\Phi(1) = 0.310$, a stable τ-periodic solution exists with $\tau = 0.2$.

Fig. 1. Payoff matrix is $\begin{pmatrix} 5 & 4 \\ 4 & 3 \end{pmatrix}$, i.e., $\lambda = 1/\alpha = 1/\beta = 1$, where R_1 is an ESS. Here, the parameters γ_1, γ_2, and τ are taken as $\gamma_1 = 0.228$, $\gamma_2 = 0.5$, and $\tau = 0.2$. Notice that $1/(1 - e^{-\tau/\lambda}) + (1 + \gamma_2)/(1 + \gamma_1) = 0$. Thus, $F(x) = x$ holds for all possible $x \in (0, 1)$.

(or $\alpha - \beta < 0$). (a) For $\alpha - \beta > 0$, if a τ-periodic solution $x(t, \tilde{x})$ exists, then it must satisfy $\Phi(1) < \tau < \Phi(0)$, i.e.,

$$\frac{1}{\alpha} \ln \frac{1 + \gamma_2}{1 + \gamma_1} < \tau < \frac{1}{\beta} \ln \frac{1 + \gamma_2}{1 + \gamma_1},$$

and it must be also unstable since $(d\Phi(x)/dx)Q(x) < 0$ (see Fig. 2a). (b) For $\alpha - \beta < 0$, if a τ-periodic solution $x(t, \tilde{x})$ exists, then it must satisfy $\Phi(0) < \tau < \Phi(1)$, i.e.,

$$\frac{1}{\beta} \ln \frac{1 + \gamma_2}{1 + \gamma_1} < \tau < \frac{1}{\alpha} \ln \frac{1 + \gamma_2}{1 + \gamma_1},$$

and it is stable since $(d\Phi(x)/dx)Q(x) > 0$ (see Fig. 2b). Result (a) implies that if an unstable τ-periodic solution exists, then the non-ESS boundary ($x = 0$) must be locally stable, i.e., it is possible that an ESS strategy can be replaced successfully by a non-ESS strategy under the impulsive perturbations (see Fig. 2a). On the other hand, result (b) shows that if a stable τ-periodic solution exists, then the ESS boundary ($x = 1$) must be unstable (see Fig. 2b).

(ii) If both α and β are negative, i.e., the pure strategy R_2 is an ESS, then we must have $Q(x) < 0$ for all possible $x \in (0, 1)$. Notice also that $\Delta x = U(x)x(1 - x) < 0$. Thus, no periodic solution can exist, and the system state will be attracted by the ESS boundary $x = 0$ (see Fig. 3).

(iii) If $\alpha > 0$ and $\beta < 0$, then both the phenotypes R_1 and R_2 are ESS strategies, and the phenotypic equilibrium exists, i.e., $x^* = -\beta/(\alpha - \beta)$. For convenience, the function $Q(x)$ and $S(x)$ can be rewritten as

$$Q(x) = (\alpha - \beta)x(1 - x)(x - x^*),$$
$$S(x) = (\alpha - \beta)^2(x - x^*)(h(x) - x^*). \qquad (22)$$

Since $h(x) = x + U(x)x(1 - x)$, there must exist an $\check{x}$ with $\check{x} \in (0, 1)$ such that $h(x) > x^*$, or $h(x) < x^*$, if $x > \check{x}$, or $x < \check{x}$. It is easy to see that (a) no periodic solution can exist in the interval $0 < x < x^*$ since $Q(x) < 0$; (b) since $h(x) < x^*$ for $x \in (x^*, \check{x})$, when the system state is in the interval $x^* < x < \check{x}$, it will be moved to the interval $0 < x < x^*$ after one impulse, i.e., no periodic
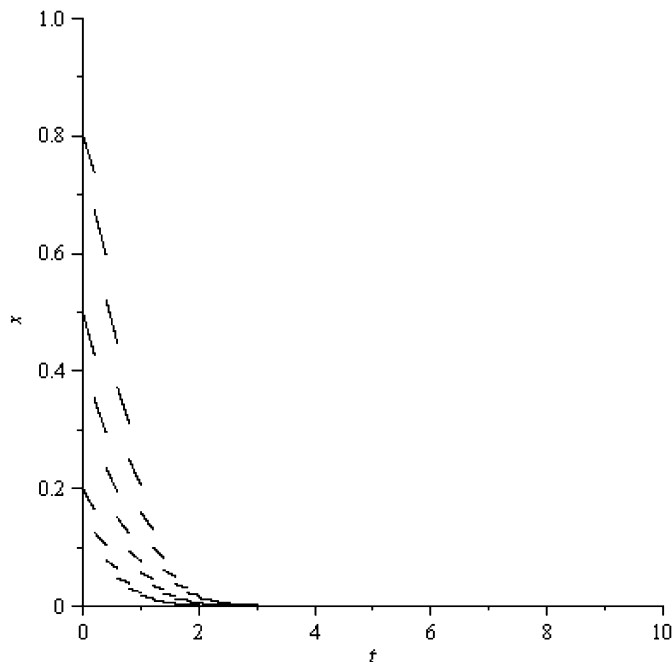
Fig. 3. $\alpha < 0$ and $\beta < 0$, i.e., the pure strategy R_2 is an ESS. Payoff matrix is $\left(\begin{smallmatrix} 4 & 3 \\ 6 & 4 \end{smallmatrix}\right)$ with $\alpha = -2$ and $\beta = -1$. The parameters γ_1 and γ_2 are taken as $\gamma_1 = 0.1$ and $\gamma_2 = 0.5$. Since $Q(x) < 0$ for all $x \in (0, 1)$, no periodic solution can exist, and the system state will be attracted by the boundary $x = 0$, where τ is taken as $\tau = 0.2$.
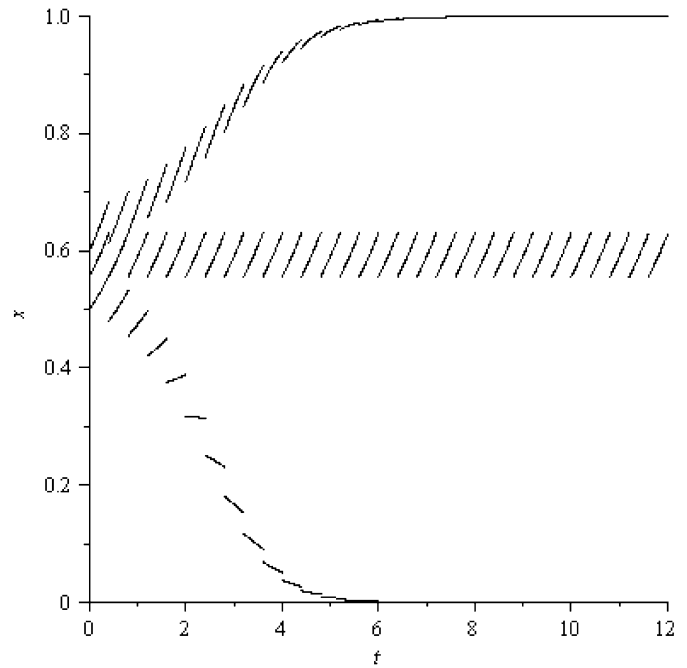
Fig. 4. $\alpha > 0$ and $\beta < 0$, i.e., both pure strategies R_1 and R_2 are ESS strategies, but the phenotypic equilibrium $x^* = -\beta/(\alpha - \beta) \in (0, 1)$ is not an ESS equilibrium. Payoff matrix $\left(\begin{smallmatrix} 6 & 2 \\ 4 & 3 \end{smallmatrix}\right)$ with $\alpha = 2$ and $\beta = -1$. The parameters γ_1 and γ_2 are taken as $\gamma_1 = 0.1$ and $\gamma_2 = 0.5$. There exists an $\check{x}$ such that $h(x) - x > 0$ if $x > \check{x}$ and $h(x) - x < 0$ if $x < \check{x}$, where $x^* = \frac{1}{3}$ and $\check{x} = 0.276$. In the interval $\check{x} < x < 1$ there is an unstable τ-periodic solution with $\tau = 0.4$.
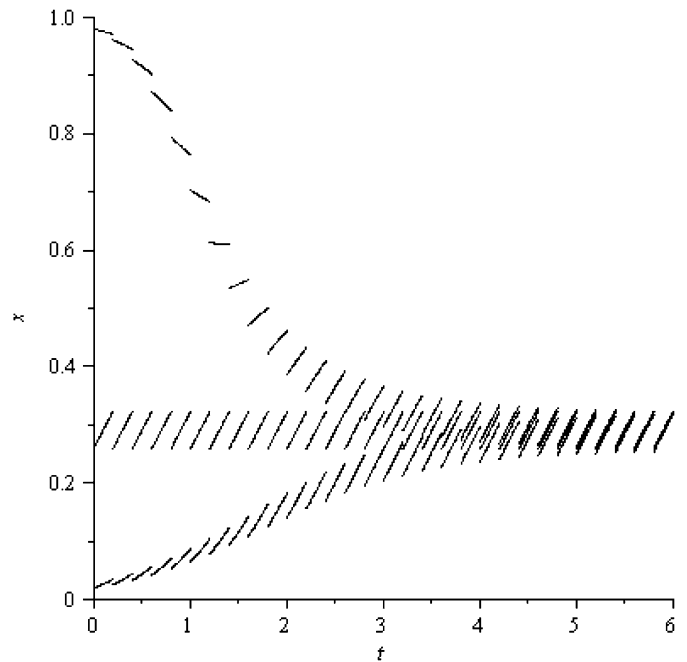
Fig. 5. $\alpha < 0$ and $\beta > 0$, i.e., both pure strategies R_1 and R_2 are not ESS strategies, but the phenotypic equilibrium $x^* = -\beta/(\alpha - \beta) \in (0, 1)$ is an ESS equilibrium. Payoff matrix is $\left(\begin{smallmatrix} 4 & 5 \\ 6 & 2 \end{smallmatrix}\right)$ with $\alpha = -2$ and $\beta = 3$. The parameters γ_1 and γ_2 are taken as $\gamma_1 = 0.1$ and $\gamma_2 = 0.5$. In the interval $0 < x < x^*$, there is a stable τ-periodic solution with $\tau = 0.2$, where $x^* = \frac{3}{5}$.

solution is possible in the interval $x^* < x < \check{x}$; and (c) since $d\Phi(x)/dx < 0$ for $x \in (\check{x}, 1)$, if a τ-periodic solution exists with $\tau > \Phi(1)$ in the interval $\check{x} < x < 1$, then it must be unstable since $(d\Phi(x)/dx)Q(x) < 0$ (see Fig. 4).

(iv) If $\alpha < 0$ and $\beta > 0$, then the phenotypic equilibrium $x^* = -\beta/(\alpha - \beta)$ is an ESS equilibrium. It is also easy to see that (a) no periodic solution is possible in the interval $x^* < x < 1$ since $Q(x) < 0$; (b) similar to the analysis in (iii), if a τ-periodic solution $x(t, \tilde{x})$ exists in the interval $0 < x < x^*$, then it must be stable since $(d\Phi(x)/dx)Q(x) > 0$ (see Fig. 5).

The above results for $\alpha \neq \beta$ can be summarized as follows. (a) The boundary $x = 1$ is stable if and only if

$$\lim_{x \to 1^-}(\Phi(x) - \tau)Q(x) < 0 \Rightarrow (\Phi(1) - \tau)\lim_{x \to 1^-}Q(x) < 0,$$

and, similarly, the boundary $x = 0$ is stable if and only if

$$\lim_{x \to 0^+}(\Phi(x) - \tau)Q(x) > 0 \Rightarrow (\Phi(0) - \tau)\lim_{x \to 0^+}Q(x) > 0.$$

(b) If both boundaries are stable (or unstable), then there must exist a unique unstable (or stable) τ-periodic solution. If one boundary is stable but the other unstable, then no periodic solution can exist, and the stable boundary must be globally attractive.

5. Summary

In this paper, a two-phenotype evolutionary game dynamics with impulsive effects is investigated. As pointed out in Section 1, if the mechanism of impulsive perturbations (e.g. the effects of periodic climate disaster on the population size, or the seasonal reproduction of wild animal population) is introduced into the classical evolutionary game model, we have to answer whether the traditional concept of evolutionary stability is still valid, or how the evolutionary game dynamics is affected by the impulsive perturbations. For our main goal, we mainly focus our attention on the relationship between the traditional concept of ESS in evolutionary game with no impulsive perturbations and the properties of evolutionary game dynamics with impulsive effects. Our main results show that the impulsive perturbations not only result in the periodic behavior of the system, 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. Our results for evolutionary game dynamics with impulsive perturbations provides another theoretical mechanism, besides such mechanisms as the effect of finite populations on evolutionary game dynamics (e.g. Nowak et al., 2004), for the successful invasion of a mutant strategy.

Acknowledgments

References

Angelova, J., Dishliev, A., 2000. Optimization problems for one-impulsive models from population dynamics. Nonlinear Anal. 39, 483–497.

Bainov, D., Simeonov, P., 1993. Impulsive Differential Equations: Periodic Solutions and Applications. Longman Scientific and Technical, New York.

Ballinger, G., Liu, X., 1997. Permanence of population growth models with impulsive effects. Math. Comput. Modelling 26, 59–72.

Chesson, P., Gebauer, R.L.E., et al., 2004. Resource pulses, species interactions and diversity maintenance in arid and semi-arid environments. Oecologia 141, 236–253.

Cressman, R., 1992. The Stability Concept of Evolutionary Game Theory. Springer, Heidelberg, New York.

Donofrio, A., 1997. Stability properties of pulse vaccination strategy in SEIR epidemic model. Math. Comput. Modelling 26, 207–225.

Fan, M., Wang, K., 1998. Optimal harvesting policy for single population with periodic coefficients. Math. Biosci. 152, 165–177.

Grasman, J., van Herwaarden, O.A., et al., 2001. A two-component model of host-parasitoid interactions: determination of the size of inundative releases of parasitoids in biological pest control. Math. Biosci. 169, 207–216.

Hofbauer, J., Sigmund, K., 1988. The Theory of Evolution and Dynamical Systems. Cambridge University Press, Cambridge.

Hofbauer, J., Sigmund, K., 1998. Evolutionary Games and Population Dynamics. Cambridge University Press, Cambridge.

Jin, Z., Zhien, M., Han, 2004. The existence of periodic solutions of the n-species Lotka–Volterra competition system with impulsive. Chaos Solitons Fractals 22, 181–188.

Laksmikantham, V., Bainov, P., Simeonov, S., 1989. Theory of Impulsive Differential Equations. World Scientific, Singapore.

Lessard, S., 1984. Evolutionary dynamics in frequency-dependent two-phenotype models. Theor. Popul. Biol. 25, 210–234.

Liu, B., Chen, L., 2004. The periodic competing Lotka–Volterra model with impulsive effect. Math. Med. Biol. 21, 129–145.

Liu, B., Teng, Z., Liu, W., 2007. Dynamical behaviors of the periodic Lotka–Volterra competing system with impulsive perturbations. Chaos Solitons Fractals 31, 356–370.

Liu, X., 1995. Impulsive stabilization and applications to population growth models. Rocky Mountain J. Math. 25, 381–395.

Liu, X., Chen, L., 2003. Complex dynamic of Holling type II Lotka–Volterra predator–prey system with impulsive perturbations on the predator. Chaos Solitons Fractals 6, 311–320.

Liu, X., Rohlf, K., 1998. Impulsive control of a Lotka–Volterra system. IMA J. Math. Control Inf. 15, 269–284.

Maynard Smith, J., 1982. Evolution and the Theory of Games. Cambridge University Press, Cambridge.

Maynard Smith, J., Price, G.R., 1973. The logic of animal conflict. Nature 246, 15–18.

Nowak, M.A., Sasaki, A., Taylor, C., Fudenberg, D., 2004. Emergence of cooperation and evolutionary stability in finite populations. Nature 428, 646–650.

Pei, Y., Chen, L., Zhang, Q., Li, C., 2005. Extinction and permanence of one-prey multi-predators of Holling type II functions response system with impulsive biological control. J. Theor. Biol. 235, 495–503.

Roberts, M.G., Kao, R.R., 1998. The dynamics of an infectious disease in a population with birth pulses. Math. Biosci. 149, 23–36.

Shulgi, B., Stone, L., Agur, Z., 1998. Pulse vaccination strategy in the SIR epidemic model. Bull. Math. Biol. 60, 1–26.

Song, X., Xiang, Z., 2006. The prey-dependent consumption two-prey one-predator models with stage structure for the predator and impulsive effects. J. Theor. Biol. 242, 683–698.

Tang, S., Cheke, R.A., 2005. State-dependent impulsive models of integrated pest management (IPM) strategies and their dynamic consequences. J. Math. Biol. 50.

Tang, S., Chen, L., 2002. Density-dependent birth rate, birth pulses and their population dynamic consequences. J. Math. Biol. 50, 257–292.

Tang, S., Chen, L., 2003. Multiple attractors in stage-structured population models with birth pulse. Bull. Math. Biol. 65, 479–495.

Taylor, P.D., Jonker, L.B., 1978. Evolutionarily stable strategies and game dynamics. J. Theor. Biol. 40, 145–156.

Wang, W., Wang, L., Li, Z., 2007. The dynamic complexity of a three-species Beddington–type food chain with impulsive control strategy. Chaos Solitons Fractals 32, 1772–1785.

Xiao, Y., Cheng, D., Qin, H., 2006. Optimal impulsive control in periodic ecosystem. System Control Lett. 55, 558–565.

Zhang, Y., Xiu, Z., Chen, L., 2005. Dynamical complexity of a two-prey one-predator system with impulsive effect. Chaos Solitons Fractals 26, 131–139.