Chaos, Solitons and Fractals 108 (2018) 32–38

Contents lists available at ScienceDirect

Chaos, Solitons and Fractals

Nonlinear Science, and Nonequilibrium and Complex Phenomena

journal homepage: www.elsevier.com/locate/chaos

Allee effect induced diversity in evolutionary dynamics

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A R T I C L E I N F O

Article history:
Received 1 November 2017
Revised 18 January 2018
Accepted 18 January 2018

Keywords:
Allee effect
Cyclic dominance
Replicator dynamics

A B S T R A C T

Cyclic dominance is observed in predator-prey interactions, the mating strategy of side-blotched lizards, the overgrowth of marine sessile organisms and competition in microbial populations and many other natural systems. Rock-Paper-Scissor(RPS) is a popular game which demonstrates cyclic dominance. In this paper, we investigate replicator dynamics of RPS-game under logistic growth functions with Allee effect. The results obtained are compared with the case of no Allee effect. Due to Allee effect the number of stable attractors increases in a certain parameter region. The obtained result can be interpreted biologically that diversity of an ecological system increases due to Allee effect.

1. Introduction

Evolutionary game theory is essential for explaining all aspects of evolution from individual behaviors up to the history of life [1]. Game theory not only applies to social games [2], it also applies to ecology [3],and even in infectious diseases control [4]. Motivated by the applications of evolutionary game theory in almost all areas of natural science stimulate many researchers to concentrate on this field [5–9].

Games of cyclic dominance [10] play an eminent role in explaining the biodiversity in nature [11,12], structural complexity [13], prebiotic evolution [14] and Darwinian's selection [15] . Cyclic interactions have been observed in different ecological systems e.g. microbial populations [11,16], plant systems [17,18] and marine benthic systems [19]. Cyclic dominance is also useful in explaining the mating strategy of side-blotched lizards [20,21], the overgrowth of marine sessile organisms [22], the genetic regulation in the repressilator [23], and in explaining the oscillating frequency of lemmings [24] and of the Pacific salmon [25]. Biodiversity in models of cyclic dominance was observed even in presence of site-specific heterogeneous invasion rates [26]. Cyclic dominance may even lead to collapse of biodiversity due to accidental extinction of one of the participating species [26]. Cyclic interactions were also reported by Perc et al. [27] to address fundamental problems of stability for the competition of two defensive alliances. It should be noted that the importance of cyclic dominance extends far beyond biodiversity, with applications in human cooperation [28], in human bargaining [29], and public goods provisioning and punishment [30,31]. Szolnoki et al.[32] demonstrated that protection spillovers may fundamentally change the dynamics of cyclic dominance in structured populations and they outlined the possibility of programming pattern formation in microbial populations.

In the Rock-Paper-Scissors(RPS) game, there is cyclic domination among three strategies. In this game-rock is wrapped by paper, paper is cut by and scissors are crushed by rock. So we see a case of cyclic dominance where rock wins over scissors loses to paper, scissor wins over paper and loses to rock and paper wins over rock while losing to scissor.

RPS is observed in the mating habit of the side-blotched lizard (uta-stansburiana) [20]. The male side-blotched lizard has a coloured throat that is either orange, blue, or has a yellow stripe. The orange throated male is tough, and tries to mate with as many females as possible, defending a large area of territory to do so. The blue-throats are the next most tough, but have taken the evolutionary strategy of (effective) monogamy, defending only the territory enough for one female. Finally, there are the weakest, the yellow stripes, who sneak up on the orange throats while they aren't looking and mate with the females in the orange throat's territory. In effect, orange beats blue because they are tougher, blue beats yellow because they are more alert, and yellow beats orange because they are sneaky. The standard zero sum pay-off matrix for a RPS game is given as [33]

$$A = \begin{bmatrix} 0,0 & 1,-1 & -1,1 \\ -1,1 & 0,0 & 1,-1 \\ 1,-1 & -1,1 & 0,0 \end{bmatrix}$$

which is suitable for modeling cyclic dominance of natural systems. Here a payoff of 1 means win while a payoff of -1 signifies loss. It is a familiar fact that replicator dynamics for RPS game orbits around the equilibrium (1/3, 1/3, 1/3) but it does not reach an ESS for an exponential growth [33].

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https://doi.org/10.1016/j.chaos.2018.01.026

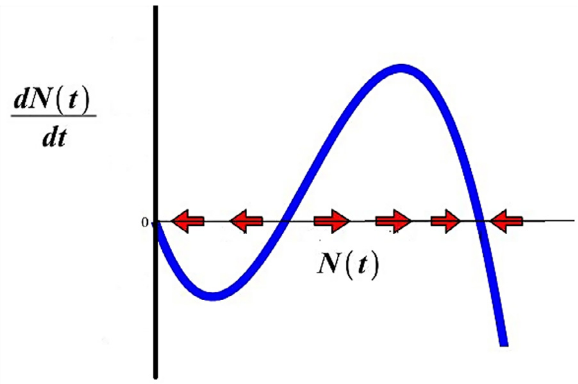

Fig. 1. Phase diagram of the Allee flow field $\dot{N} = rN\left(\frac{N}{m} - 1\right)\left(1 - \frac{N}{k}\right)$.

Toupo and Strogatz [34] have reported that for a class of mutation patterns, the replicator-mutator equations for the RPS game was seen to have stable limit cycle solution. For those classes of mutation patterns, a tiny rate of mutation and a tiny departure from a zero-sum game was enough to destabilize the coexistence state of a RPS game and to set it into self-sustained oscillations. Wesson and Rand [35] have generalized the results obtained by Hofbauer and Sigmund [33] and formulated the replicator equations for a general type of growth functions. This formulation is very useful in modeling natural or social systems that are not adequately described by the usual replicator dynamics. They had used growth function $g(x) = x - ax^2$, for all the three species and it was shown that with appropriate choice of parameter values there are multiple fixed points of the system that do not exist in the usual model $g(x) = x$. In particular they had chosen logistic growth function for all three species and shown the existence of center character in the neighborhood of the critical point (1/3, 1/3, 1/3).

It is well recognized that individuals of many species can benefit from the presence of conspecifics, a concept broadly referred to as the Allee effect [36]. The Allee effect occurs when population growth rate is reduced at low population size [37–39]. Allee effect may arise due to difficulties in finding mates when population density is low, social dysfunction at small population sizes and inbreeding depression [40]. Recently, the mathematical models with Allee effect have received considerable attention from theoreticians [41–43] as well as experimentalists [44]. Allee effect is characterized by a correlation between population size or density and the mean individual fitness (often measured as per capita population growth rate) of a population. The growth model in presence of Allee effect [45] can be written as

$$\dot{N} = rN\left(\frac{N}{m} - 1\right)\left(1 - \frac{N}{k}\right).$$

Here m, k represents Allee threshold population and carrying capacity respectively. If a population tries to evolve according to the above evolution it runs to extinction when it is less than m while if it is more than m it grows until reaching the carrying capacity k. However, if it ever crosses k it falls back to the carrying capacity as the resources are limited. This can be noticed by flow field in Fig. 1. The importance of Allee effect in natural environment motivated us to inspect its influence in replicator dynamics.

The presence of Allee effect in many real world biological systems [36] motivated us to modify the replicator equations of Wesson and Rand [35] by using Allee effect induced growth function. The objective of this study is to analyze the effects in the proposed dynamics when logistic growth with Allee effect is used instead of the usual exponential growth [34] or logistic growth [35]. Here the fitness is assumed to be governed by the payoff attained in the RPS game. The replicator equations are formulated and analysed.

This paper is organized as follows: in Section 2, we introduce our model where species deviate from regular growth and formulate the replicator equations in case of general logistic growth and under Allee effect. In Section 3, we examine the models presented in the previous section analytically, presenting the necessary observations. Last section summarizes the findings and discusses their potential implications.

2. Model

Evolutionary game theory helps to model the evolution of competing strategies within a population by combining the classical tools of game theory with differential equations. The most common approach [33] focuses on the relative frequencies of different strategies in a population using replicator equation,

$$\dot{x}_i = x_i(f_i - \phi), i = 1, 2, \ldots, n$$

where x_i is the frequency of strategy i, $f_i(x_1, x_2, \ldots, x_n)$ is the fitness of strategy i, and $\phi = \sum f_i x_i$ is the average fitness across the population.

The above form for replicator equations is achieved using an exponential model of population growth

$$\dot{\xi}_i = \xi_i g_i \quad i = 1, 2, \ldots, n$$

where ξ_i is a real valued function that approximates the population of strategy i and $g_i(\xi_1, \xi_2, .., \xi_n)$ is the fitness of that strategy. Let us define relative abundance of strategy i as $x_i \equiv \frac{\xi_i}{p}$ where p is the total population. We have,

$$p(t) = \sum_i \xi_i(t).$$

We see that

$$\dot{p} = \sum_i \dot{\xi}_i(t) = \sum_i \xi_i g_i = p \sum_i \frac{\xi_i}{p} g_i = p \sum_i x_i g_i$$

$$\dot{p} = p\phi \tag{1}$$

where $\phi = \sum_i x_i g_i$ is the average fitness of the whole population.

By product rule we get

$$\dot{x} = \frac{\dot{\xi}_i}{p} - \frac{\xi_i}{p^2}\dot{p} = \frac{\xi_i}{p} g_i - \frac{\xi_i}{p}\frac{\dot{p}}{p} = \frac{\xi_i}{p}\left(g_i - \frac{\dot{p}}{p}\right) = x_i(g_i - \phi). \tag{2}$$

The fitness of a strategy is assumed to depend only on the relative abundance of each strategy in the overall population, since the model seeks to capture the effect of competition between strategies, not any environmental or other factors.

Therefore, we assume that

$$g_i(\xi_1, \xi_2, \ldots, \xi_n) = f_i\left(\frac{\xi_1}{p}, \frac{\xi_2}{p}, \ldots, \frac{\xi_n}{p}\right) = f_i(x_1, x_2, \ldots, x_n). \tag{3}$$

Here f_i only tells about the fitness of strategy i and finally the replicator equation takes the following form

$$\dot{x} = x_i(f_i - \phi).$$

Mathematically, ϕ is the coupling term that introduces dependence on the abundance and fitness of other strategies.

The replicator equation was generalized by Wesson and Rand [35] for an arbitrary growth function. They proposed the replicator equation for the growth function $g(x)$ as

$$\dot{x}_i = g(x_i)(f_i - \phi)$$

where ϕ is now a modified average fitness defined by

$$\phi = \frac{\sum_i g(x_i) f_i}{\sum_i g(x_i)}.$$